

**THE TAXONOMY OF THREE SYMPATRIC
SPECIES OF CISCOES IN NORTHERN MANITOBA**

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ABSTRACT

664 ciscoes were analyzed from 12 northern Manitoba lakes sampled in 1967 and 1968. In Big Athapap, Coregonus reighardi was distinguished from two sibling species (C. artedii and C. hoyi) by its vertical pre-maxillae, included lower jaw, terete body and 24 to 36 short gillrakers. Discriminant function analysis separated the sibling species. The three species differed in their lateral line scales, pectoral and pelvic rays, gillrakers, gillraker length, lower jaw, head length, eye diameter, pectoral length and pigmentation, dentition, supraethmoid bone, and growth rates. Body depth of all species, and gillraker number of C. artedii were correlated with maximum lake depth.

Correlation and factor analysis confirmed the identifications. Differences between the species from Big Athapap and the Great Lakes and L. Nipigon are probably non-genetic. C. zenithicus and C. reighardi may be ecophenotypes of one species, as may C. artedii and C. nigripinnis; C. hoyi and C. kiyi; and C. johanna and C. alpenae.

In Big Athapap, C. reighardi was the most benthic and C. artedii the most pelagic. C. reighardi ate the greatest per cent volume of benthic and benthic-pelagic organisms, C. hoyi of plankton, and C. artedii of surface organisms. All species are autumn spawners; the atypical spawning time of C. hoyi and C. reighardi (compared with the Great Lakes) is associated with their most northerly known occurrence.

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INTRODUCTION

Morphological and ecological differences between species of coregonids are found most easily when the species occur sympatrically. For this reason the ciscoes of Big Athapap (a basin of L. Athapapuskow), Manitoba were studied to elucidate the taxonomy of the ciscoes in this region and their relationship to the ciscoes of the Great Lakes and L. Nipigon. Specimens were collected in 12 lakes of the Cranberry Portage region between July 1967 and November 1968. Both traditional and numerical taxonomic methods were used to separate two sibling species and to identify all three sympatric species present in Big Athapap.

LITERATURE REVIEW

Taxonomic Characters of Coregonids

The characters used in coregonid taxonomy should be those that supply information as to the genetic similarity of species and their component populations, but because of the plasticity of coregonids, the traditional ichthyological taxonomic characters are of little importance (Koelz, 1929).

Three factors reduce the value of morphometry in coregonid taxonomy. Firstly, growth is rarely isometric, larger fish having relatively smaller body parts (Hile, 1937). Secondly, sexual dimorphism occurs in Coregonus artedii, whose females have smaller heads, eyes, and fins, and wider deeper bodies (Hile, 1937). Thirdly environmental effects cause extensive intraspecific variation.

Deep-water races of C. artedii and C. hoyi have less deep bodies, and longer heads, mandibles, and fins (Koelz, 1929), but the deep-water race of C. clupeaformis from L. Ontario has shorter fins (Hart, 1931). The three deep-water species of ciscoes in the Great Lakes have ovate bodies (Koelz, 1929), but in Sweden Svardson (1949) showed that transplantation can change the contour. C. nigripinnis also has an ovate body in very shallow water. Shallow-water races tend to have longer fins, shorter deeper caudal peduncles and deeper more compressed bodies (Dymond and Hart, 1927). All the coregonids of Ombibika Bay have larger eyes than from elsewhere in L. Nipigon (Dymond, 1926). Eye size changes with the transparency and depth of feeding (Kozikowska, 1961). Salt water races

have larger snouts (Svardson, 1951). The angle of the premaxillae is variable in C. reighardi (Koelz, 1929) and C. autumnalis (Walters, 1955). Maxillae length of C. reighardi differs between the north and south parts of L. Michigan (Koelz, 1929). In L. Erie, half of the C. alpanae have a protruding mandible and half have not (Scott and Smith, 1962). Smaller body parts and greater body width occur in fast-growing fish, and growth rate varies from year to year (Hile, 1937). Size at the four inflections in growth controls the subsequent morphometry (Martin, 1949). Despite this environmental modification, morphometry has been used to differentiate between species (Berg, 1948) and subspecies (Koelz, 1929). Koelz (1929) also used body contour and jaw characteristics to distinguish between species.

Besides affecting morphometry, the rate of early development is capable of modifying meristic characters within certain limits (Mottley, 1937). Factors prolonging development are associated with an increased number of body somites and of most meristic parts (Hubbs, 1926). Autumn spawning fish have more scales than spring spawning fish (Svardson, 1952). Transplantations modified lateral line scale counts by up to eleven units (Svardson, 1952). The exact ^{0.1}rate of temperature in the modification is in question (Tatarko, 1968). Scale counts have been used to distinguish between species (Koelz, 1929) and subspecies (Koelz, 1929; Berg, 1948).

The trophic conditions of a lake affect the growth rate, and morphometry, (Kozikowska, 1961), as was shown by transplantation experiments (Svardson, 1950, 1952). Population density also affects growth

rates (Hile, 1936). Although recognizing this, Wagler (1937) used growth rate as a taxonomic character.

Nusslin (1882) was the first to stress the importance of gillrakers in coregonid taxonomy. The full complement of gillrakers is not reached until a fork length of 100-120 mm. is attained (Svardson, 1952). Gillraker numbers remain constant during transplantation (Freidenfelt, 1934; Wagler, 1937), never changing by more than two units according to Svardson (1952), but aquarium reared C. clupeaformis (Koelz, 1929) and Oncorhynchus nerka (McCart and Andersen, 1967) had gillraker counts modified by up to four units. Kozikowska (1961) found that gillraker counts varied between regions of a lake, and annual variation exceeded two units. Her material was a mixture of native fish and genetically heterogeneous stock introduced each year. The correlation of gillrakers with diets is presumed (Svardson, 1950), and gillrakers are responsive to selection pressure (Svardson, 1949), their number varying with lake productivity (Kozikowska, 1961) and depth (Koelz, 1931). Species with fewer gillrakers usually have better growth (Svardson, 1952). Hybridization experiments suggest that a polygenic complex controls gillrakers numbers (Svardson, 1952).

Although C. wartmanni spawns at the surface (Wagler, 1927), most coregonids spawn on a suitable substrate at a specific depth (Fabricius, 1950). The depth and time of spawning result from the interaction of these factors. Svardson (1957) used gross time of spawning as a taxonomic character; however C. reighardi of L. Michigan was formerly a spring spawner, but is now an autumn spawner (Smith, 1964).

The genetic integrity of a species is best discovered when it is sympatric with other similar species, but Svardson (1949) reported that two "good species" introgressed when a third "species" was introduced into the lake. He used sympatry as a major taxonomic criterion (Svardson, 1957).

Environmental modifications makes most characters unsuitable for the equation of allopatric populations, but any difference in any character may be of use in the separation of sympatric populations. Even if the differences are environmental, they reflect different early development resulting from different parental reproductive behaviour. Such differences may be evidence of sympatric species, but (Frost, 1965) concluded that imprinting, rather than any genetic mechanisms, maintained the differences between two populations of Salvelinus willughbii in L. Windermere, and consequently she called the populations two formæ rather than two species.

North American Ciscoes

North American ciscoes were first classified as Argyrosomus (Agassiz, 1850) and subsequently as Leucichthys (Jordan and Evermann, 1911). They were separated from whitefish, Coregonus, on the basis of having many long gillrakers, antrose premaxillae, and maxillae ending beneath the pupil. L. autumnalis, the type species of Leucichthys, sometimes has retrose premaxillae (Walters, 1955). Some European whitefish have numerous long gillrakers (Berg, 1948) and this condition has also arisen in Prosopium (Norden, 1961). Most American workers, like the Europeans, now consider that both whitefish and ciscoes should be included in the genus Coregonus

(Walters, 1955).

Excluding the Arctic ciscoes, Hubbs and Lagler (1964) recognized eleven species of ciscoes in N. America, distinguished by body contour, jaw characteristics, and gillrakers. Their taxonomy is based on Koelz's (1929) work.

Both C. bartletti and C. hubbsi are restricted to one lake, C. alpenae and C. johannae are endemic to the Great Lakes, and C. kiyi and C. reignardi only occur in the Great Lakes and L. Nipigon. C. artedii, C. nigripinnis and C. zenithicus occur in the Great Lakes Basin, N. Ontario, L. Winnipeg and extend into the North-West Territories. C. nipigon has a similar range except its most north-westerly occurrence is in L. Winnipeg. C. hoyi occurs in the Great Lakes and Bajkov (1932) reported it from L. Winnipeg, but subsequently it has not been recorded. Schweitzer (MS, 1968) recorded a cisco living sympatrically with C. artedii in Cedar Lake, Manitoba.

There are several other nominal species of ciscoes, but at present they are considered to be synonyms of the species mentioned above.

MATERIALS AND METHODS

During 1967 and 1968 the ciscoes were sampled from twelve lakes in the Cranberry Portage region of northern Manitoba ($54^{\circ} 36' N$, $101^{\circ} 22' W$). The three Cranberry lakes drain into the Nelson R. through Grass R., whereas all the other lakes drain into the Nelson R. through the Saskatchewan R. The lakes (Fig. 1.) range in size from 0.3 square miles (Little Twin L.) to 101.5 square miles (L. Athapapuskow), and in maximum recorded depth from 25' (1st Cranberry L.) to 204' (L. Athapapuskow).

Gangs of monofilament gill nets were set simultaneously on the bottom and at the surface. In 1967, the gill nets were usually set overnight and lifted after twelve hours. Both gangs were composed of six nets, each 50' long and 8' deep, arranged randomly. The stretched mesh sizes of the bottom gang were $3\frac{1}{2}'' - 3\frac{1}{4}'' - 3'' - 2'' - 1\frac{1}{2}'' - 3''$, and of the surface gang $1'' - 2'' - 2\frac{1}{2}'' - 3\frac{1}{4}'' - 1\frac{1}{2}'' - 3''$. The fishing procedure was slightly changed in 1968, when nets were usually set in the morning and lifted after 24 hours. Again randomly arranged, 50' X 8' nets were used, but the stretched mesh sizes of the bottom gang were $1'' - 2'' - 3\frac{1}{2}'' - 3\frac{1}{4}'' - 3'' - 1\frac{1}{2}''$, and were $2\frac{1}{2}'' - 1\frac{1}{2}'' - 2'' - 3'' - 3\frac{1}{4}'' - 1''$ for the surface gang. Occasionally other gangs of nets were used, including some 25' deep. The selectivity of gillnets was recognized, but its results ignored.

Table I shows the lakes sampled, dates of sampling, the number of gangs of gillnets set, the approximate number of ciscoes caught, and the

Fig. 1. Map showing the lakes sampled in northern Manitoba.

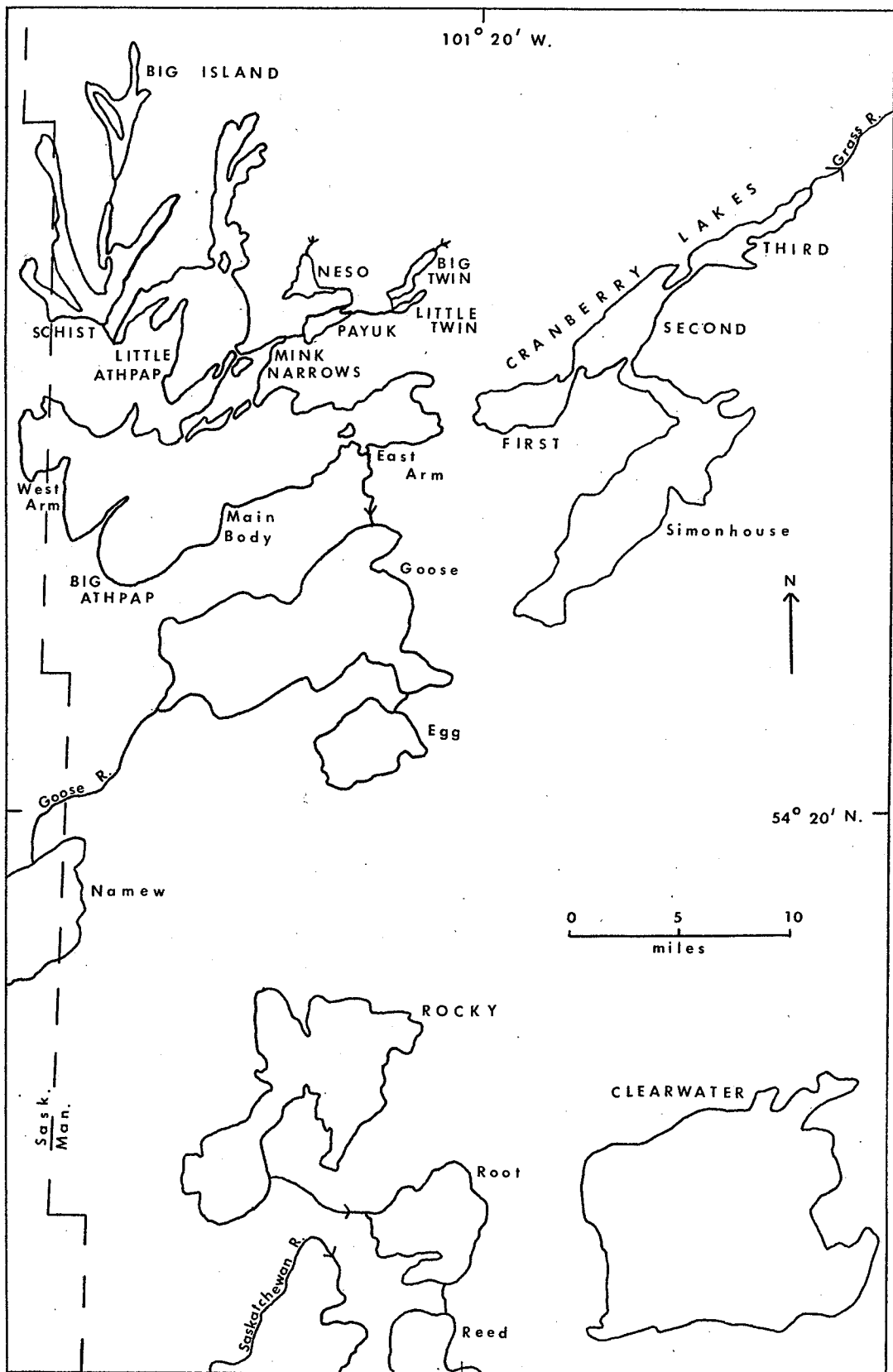


Table I. Sampling and Analysis of Ciscoes Caught in 1967 and 1968.

Lakes Sampled	No. of Gangs Set			Approx. Nos. Total Ciscoe Catch	Nos. Ciscoes Analyzed	Nos. Ciscoes Identified		
	13 July to 31 Aug. 1967	10 May to 27 Aug. 1968	5 Oct. to 4 Nov. 1968			<u>C. artedii</u>	<u>C. hoyi</u>	<u>C. reighardi</u>
Big Island L	5			400	24		24	
Schist L.	3			35	35	35?		?
Big Twin L.	3	18	2	130	13	13		
Little Twin L		15	2	70	17	17		
Neso L.	5	13	4	250	35	35		
Payuk L.	3	10	7	450	52	52		
- Little Athapap	2	8	4	150	34	5	14	15
L. Athapapuskow - Mink Narrows		11	4	200	16	1	14	1
- Big Athapap	9	65	16	1200	352	135	96	23
Rocky L.	4			50	34	?	34?	
Clearwater L.	2			30	30		28	2
1st Cranberry L	3			20	9	9		
2nd Cranberry L.	4			20	13	13		
3rd Cranberry L.	4			20	0			
Total	47	140	39	3025	664	315	210	41

number of ciscoes analyzed and identified.

The 1968 operations concentrated on Big Athapap, the largest (65 square miles), deepest (204') and most southerly basin of L. Athapapuskow, but sampling was more intensive in the sheltered East Arm. Localities of Big Athapap referred to in the text are shown in Fig 1. Spawning ciscoes were caught on the reefs and rocky shores of the East Arm. A more detailed analysis of the Big Athapap catch of ciscoes is given in Table II. Only C. artedii and C. hoyi caught between 18 May and 7 July 1968, and 5 Oct. and 4 Nov. 1968 were included in the multivariate analyses of the Big Athapap ciscoes.

The ciscoes were examined immediately, preserved in 4% formaldehyde, and re-examined after transferring to 40% isopropyl alcohol.

Measurements and Counts

Whenever possible all measurements (Fig. 2) and counts were made in the left side, and followed the procedure of Hubbs and Lagler (1964). All measurements, except Fork Length, were made with dial callipers graduated to 0.05 mm.

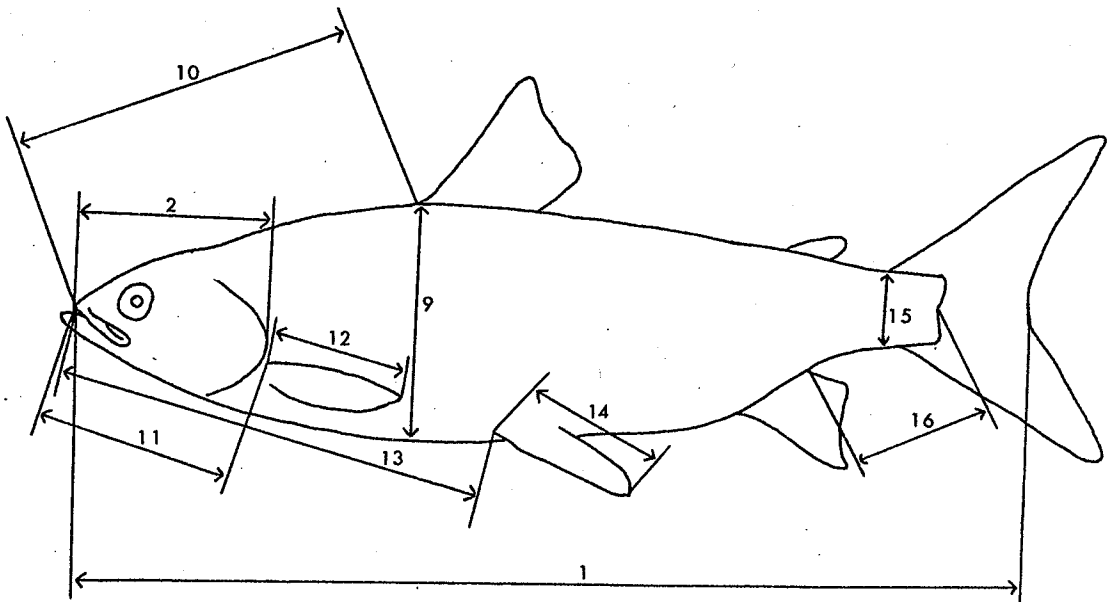
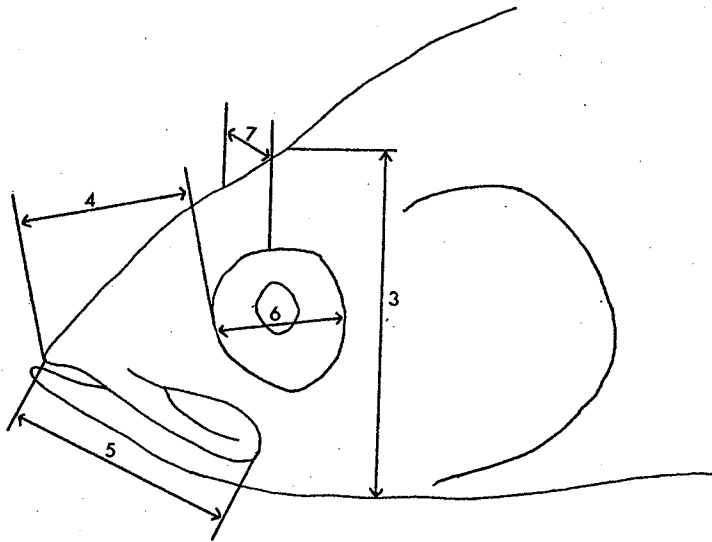
1. Fork Length: the straight line measuring the distance from the tip of the snout to the posterior tip of the central caudal ray. It was measured on a measuring board graduated to 1 mm.
2. Head Length: tip of snout to posterior edge of opercular membrane.
3. Head Depth: vertical distance from occiput midline to ventral side.
4. Snout Length: tip of snout to anterior edge of fleshy margin of orbit.
5. Upper Jaw Length: anterior point of premaxillae to posterior end of maxilla.

Table II. Analysis of the Big Athapap Sample of Ciscoes

	5 Aug. to 8 Aug. 1967	18 May to 27 Aug. 1968	5 Oct. to 4 Nov. 1968
Total Catch: <u>C. reighardi</u>	0	23	0
Total Catch of <u>C. artedii</u> - <u>C. hoyi</u>	44	1100	54
Nos. <u>C. artedii</u> - <u>C. hoyi</u> analyzed	44	308	54
Included in multivariate techniques	0	178	50
Identified as <u>C. artedii</u>		86	45
<u>C. hoyi</u>		91	5
Possible hybrid		1	0

Fig. 2a. Diagram showing Head Measurements. (Key in text.)

Fig. 2b. Diagram showing Body Measurements. (Key in text; body width omitted.)



6. Eye Diameter: greatest horizontal distance between fleshy margins of orbit.
7. Inter-orbital Width: least bony width between bony rims of orbits.
8. Body Width: greatest lateral width.
9. Body Depth: greatest vertical depth.
10. Predorsal Length: tip of snout to structural base of first dorsal ray.
11. Pectoral Origin: tip of snout to pectoral fin origin, measured when fin held at 90° to the body.
12. Pectoral Length: extreme base of outermost ray to farthest tip of fin.
13. Pelvic Origin: tip of snout to pelvic fin origin, measured when fin held at 90° to the body.
14. Pelvic Length: extreme base of outermost ray to farthest tip of fin.
15. Caudal Peduncle Depth: the least vertical depth.
16. Caudal Peduncle Length: posterior end of anal base to base of middle caudal ray.,
17. Gillraker Length: distance from tip to base of the longest raker on the first arch, measured on the ventral side.
18. All counts were made under a binocular microscope.
18. Pectoral Fin Rays: all rays counted.
19. Pelvic Fin Rays: all rays counted.
20. Dorsal Fin Rays: all principal rays counted, but last two bases counted as one. No rudimentary rays included.
21. Anal Fin Rays: all principal rays counted, but last two bases counted as one. No rudimentary rays included.
22. Lateral Line Scales: from scale in contact with pectoral girdle to scale at end of vertebral column. If scales were missing, scale pockets were counted.
23. Caudal Peduncle Scales: horizontal scale rows around the least depth.

24. Gillrakers: the first gill arch was removed and all gillrakers, including small rudimentary rakers, were counted. Some arches were stained in alizarin and KOH and the rakers recounted. There was no discrepancy.

Three other characters were recorded.

25. Premaxillae: lateral profile of premaxillae recorded as vertical or otherwise.

26. Lower Jaw: lateral profile included, recorded as equal to or protruding beyond the upper jaw.

27. Pectoral Fin Pigmentation: present or absent.

Measurements 3, 5, 7, 8, 9, 10, 13, 14, 15, 16, 17 and counts 20, 21 and 23 were not made on all fish as they showed little application for the separation of the species. All characters were recorded from fish transferred to alcohol after preservation in formalin, except for fork length and gillraker numbers, which were recorded from fresh fish.

Factor Analysis

Factor analysis, a branch of multivariate statistics, attempts to describe the complex relations of many variables in terms of the simpler relations of fewer hypothetical variables, the factors, which represent supposed influences underlying the original data. The primary aim of factor analysis is to seek the underlying influences in a set of variables and this is achieved by R-mode analysis, which starts from the correlation matrix of the variables. A subsidiary aim is to classify the samples (the main aim in this study) and this may be achieved either by the factor scores calculated after R-mode analysis, or by the factor loadings from Q-mode analysis, which starts from the correlation matrix of the samples.

Factors were extracted from the appropriate correlation matrix by the principal factor method available on the IBM 360. The resultant principal factor matrix usually does not permit simple explanation (Cattell, 1965a) and has to be rotated to produce an interpretable "simple structure" (Thurstone, 1967). Orthogonal rotation produces uncorrelated factors, oblique rotation produces correlated factors. The varimax rotation performed produces uncorrelated factors loaded chiefly on one variable. It is improbable that the factors underlying the data are uncorrelated, but no oblique solution is available on the IBM 360. In the rotated factor matrix each variable is given a loading on each factor, and these factor loadings show the correlation between the variables and the factors. After R-mode analysis, factor scores were calculated, with a mean of zero and a standard deviation of one, and these measure the extent of influence of each factor upon each sample.

The assumptions underlying the model for factor analysis are that the variables and factors are linearly related, that factors act additively in respect to any variable, and that there is no interaction effect between variables (Cattell, 1965b). If these assumptions are violated, factor analysis gives an approximate solution.

RESULTS

For convenience, the scientific names of the species are used throughout. The justification for the use of these names is given in the section entitled "Taxonomic Identification".

SEPARATION OF THE SPECIES OF CISCOES IN BIG ATHAPAP

The Distinctness of *Coregonus reighardi*

Fish with a fork length greater than 120 mm. were found to have two distinct phenotypes. Nineteen individuals, identified here as *C. reighardi*, had terete bodies, a greenish colouration above the lateral line, and, usually, the premaxillae were vertical and the lower jaw was included. They had noticeably larger eyes and shorter gillrakers than the other fish. In contrast none of the 52 other large fish had an included lower jaw or vertical premaxillae; they had more pigment and were not terete.

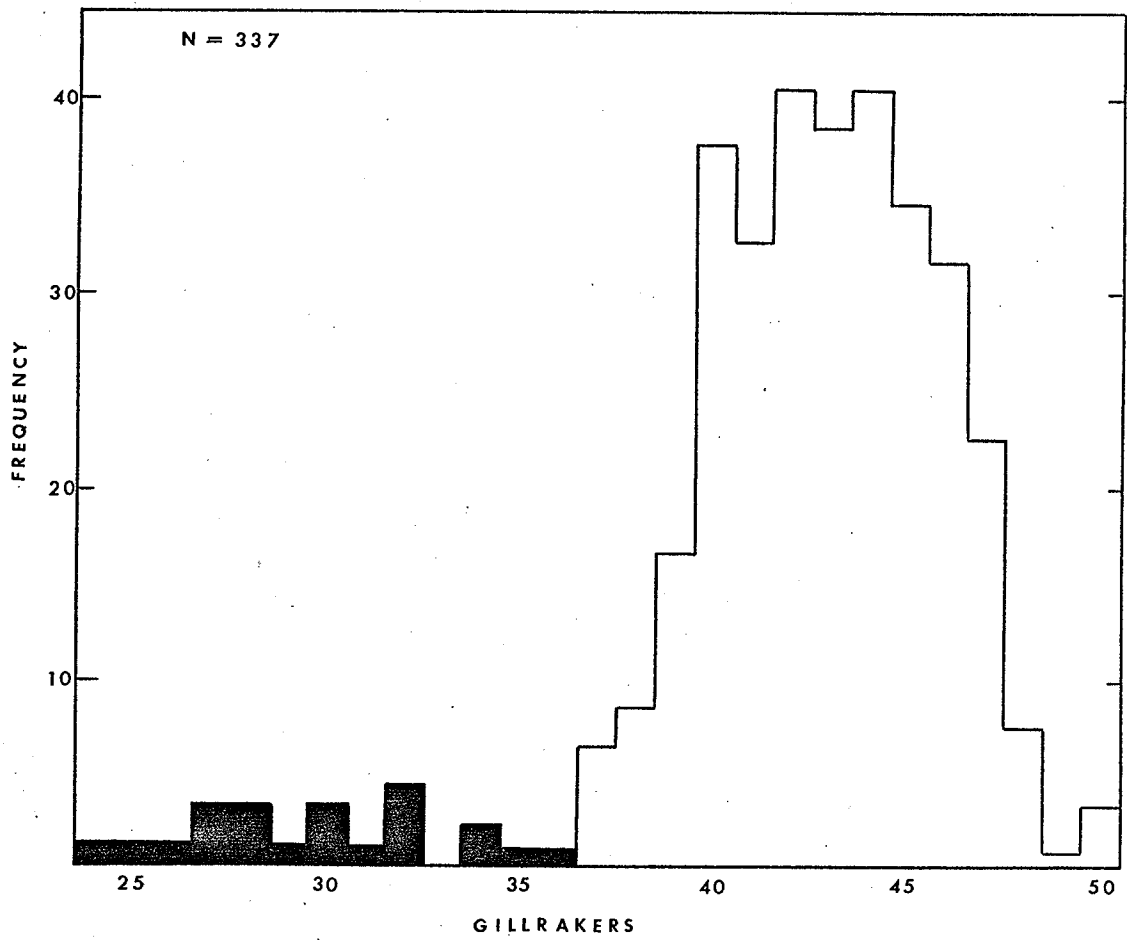
Gillraker counts for all the Big Athapap fish (Fig. 3.) showed that all the *C. reighardi* had gillraker counts of less than 37. Four small fish also had counts of less than 37 and these were subsequently shown to be *C. reighardi*. All other fish had gillraker counts exceeding 36.

Other differences between *C. reighardi* and the remaining fish are treated under the appropriate headings.

Evidence for Two Sibling Species in Big Athapap

After its separation of *C. reighardi*, there was evidence of two sibling species present in Big Athapap.

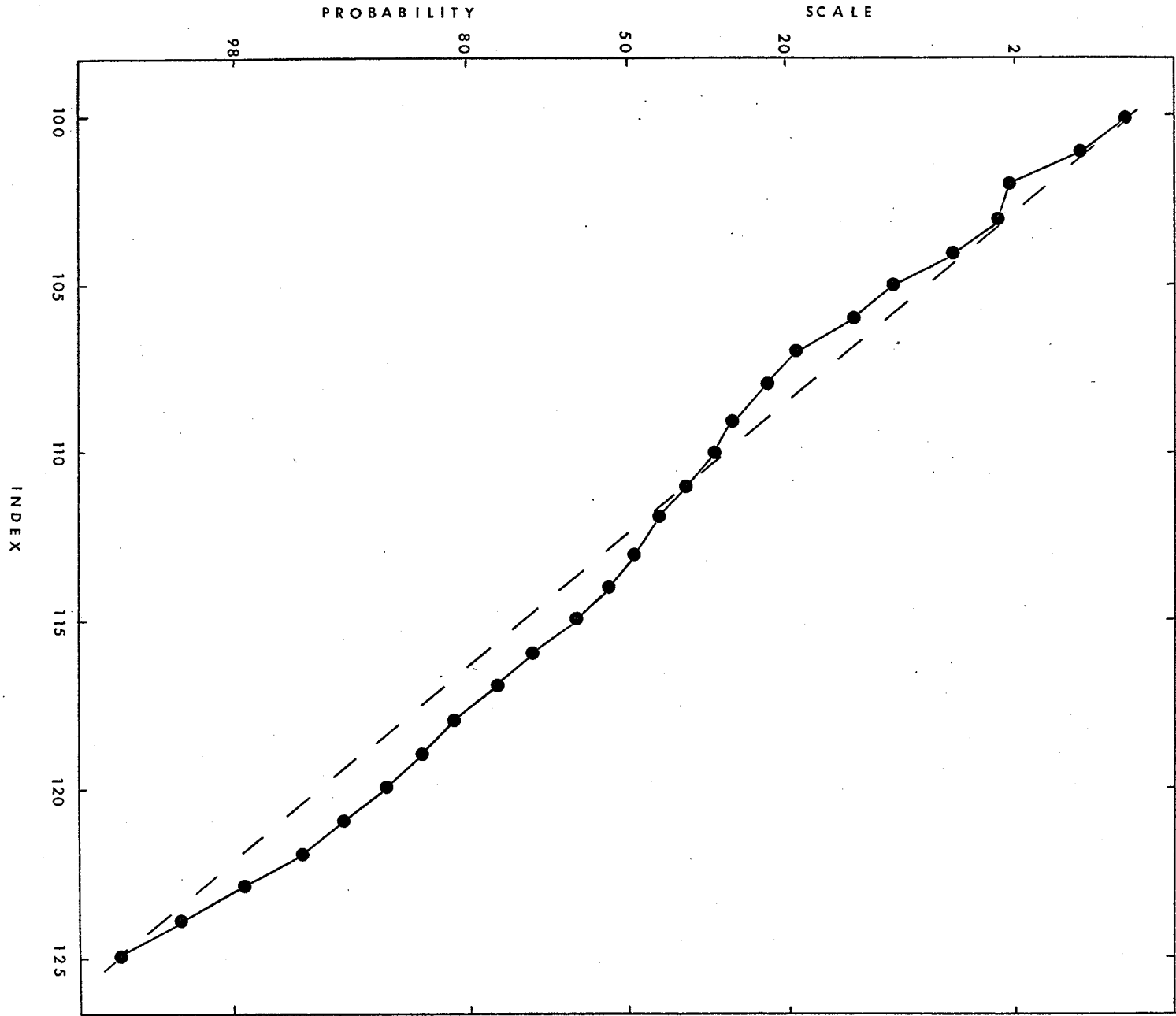
Fig. 3. Distribution of Gillraker Counts in Big Athapap, for 1967 and 1968.
(C. reighardi shaded).



When the gillraker counts of 315 fish were considered, the distributions for both age I and older fish were slightly bimodal, but the lateral line scale counts of 236 fish were more normally distributed. An index was formed by adding together the gillraker and lateral line scale counts for each of the 236 fish. Although the index did not differ statistically from a normal distribution, deviation from the normal distribution was shown by plotting the cumulative frequency per cent on arithmetic probability paper (Fig. 4.). In a normal distribution, the points form a straight line (Harris, 1968).

Besides the gillraker and lateral line scale counts, eye diameter, the lower jaw, pectoral pigmentation, and maturity at age I suggested that the ciscoes were not a homogeneous population. Each character was divided into two character states. The lower jaw was classified as protruding beyond or equal to the upper jaw; pectoral pigmentation was either present or absent; age I fish were either mature or immature. The approximate mid-points of their range were used to divide gillraker counts for age I (40.5) and older fish (44.5) and lateral line scales (70.5) into two character states. Eye diameter was divided into large or small by the regression line $y = 0.94 - 0.05x$, which was the line of best fit for eye diameter on fork length for the 236 fish. χ^2 tests, with Yates' correction (Snedecor and Cochran, 1967) were used to test whether the character states of one character were independent of the character states of another character. This was done for all pairs of characters.

Fig. 4. Probability Plot of Index (Gillrakers plus Lateral Line Scales)
for 236 Ciscoes (C. artedii plus C. hoyi) caught in Big
Athapap in 1968.



The results of 153 age I fish caught between 18 May and 7 July 1968 (Table III) showed that, with the exception of jaw length with gillrakers and eye diameter, the character states of each character were not independent of the character states of other characters. It was then possible to associate the character states into two groups: C. artedii group had high gillraker and lateral line scale counts, small eyes, immaculate pectoral fins, immaturity at age I, and equal jaws; C. hoyi group had low gillraker and lateral line scale counts, large eyes, pigmented pectoral fins, maturity at age I, and protruding lower jaws. With the exception of maturity, a similar association of character states occurred in the 25 other fish caught in the same period.

The morphology of the 54 fish caught on the reefs in October and early November corresponded to that of the C. artedii group, with the exception of the large eyes of age 0 fish and the maturity of age I fish.

Separation of the Two Sibling Species

No entirely objective method was found for separating the two species. All of the 54 fish caught in the autumn were placed into the C. artedii group, as they all resembled this group more closely than the C. hoyi group, but separation of the others was based solely on morphological grounds.

Only 24% of the 153 age I fish had all six character states of one group; 36.4% had five, and 26% had four. The remainder were intermediate. As the X^2 values for independence were lowest for the lower jaw, subsequently this character was ignored, enabling separation of all of the

Table III. Dependence (χ^2 , y.c.) of Character States in Big Athapap
C. artedii and C. hoyi

Character	Gill- rakers	Lateral Line Scales	Matur- ity	Eye Diameter	Pectoral Pigment- ation
Lateral Line Scales	20.2**				
Maturity	21.9**	50.9**			
Eye Diameter	9.0**	29.8**	21.6**		
Pectoral Pigmentation	8.8**	14.4**	19.1**	15.3**	
Lower Jaw	3.1 n.s.	6.9**	14.0**	0.7 n.s.	8.2**

**Significant at 0.01

intermediates. Separation of the 25 older fish was similar. The C. artedii group then contained the 54 autumn fish, 64 age I and 11 older fish; the C. hoyi group 89 age I and 14 older fish.

Remode factor analysis was undertaken on the 178 spring and summer fish analyzed above in the hope of obtaining a single factor that would enable complete objective separation of the two groups. The twelve variables used were fork length, head length, snout length, eye diameter, pectoral origin, pectoral length, pectoral pigmentation (coded: present = 1, absent = 2), condition of the lower jaw (coded: protruding = 1, equal = 2), gillrakers, lateral line scales, pectoral rays and pelvic rays. The raw data was log-transformed before use. The seven resultant factors were identified primarily as size, gillrakers, lateral line scales, pectoral rays, pelvic rays, pectoral pigmentation and lower jaw condition. Two groups of fish coalesced when scores for each factor were plotted against the scores of each other factor. 30% were assigned to a group with difficulty.

Eighty per cent of the fish were placed into the same group by both the character state and factor analytic methods. The remainder were re-examined and placed into the group with which they appeared to be most similar. The C. artedii group then contained the 54 autumn fish, 68 age I and 12 older fish; the C. hoyi group 85 age I and 13 older fish.

The grouping arrived at as described above was refined by a discriminant function analysis available on the IBM 360. The same variables were used as for factor analysis, and the same fish except that only 50

of the autumn fish were included. The programme gave the probabilities of group inclusion for C. artedii on the first function and for C. hoyi on the second. The maximum difference between the two groups occurred after reiteration in which 10% of the fish were reclassified (alone the character state method would have misclassified 19%, and factor analysis 10%). C. artedii then contained 45 autumn fish, 73 age I and 13 older fish; C. hoyi 5 autumn fish, 79 age I and 12 older fish. There was one age I intermediate fish (Fig. 5.).

Placing the intermediate in either group did not alter the analysis, raising the possibility that it may be an hybrid. It resembled C. artedii more closely in three characters (equal jaw, snout and pectoral fin length), C. hoyi in two (pelvic rays and pigmented pectoral fin) and was intermediate in the other seven characters.

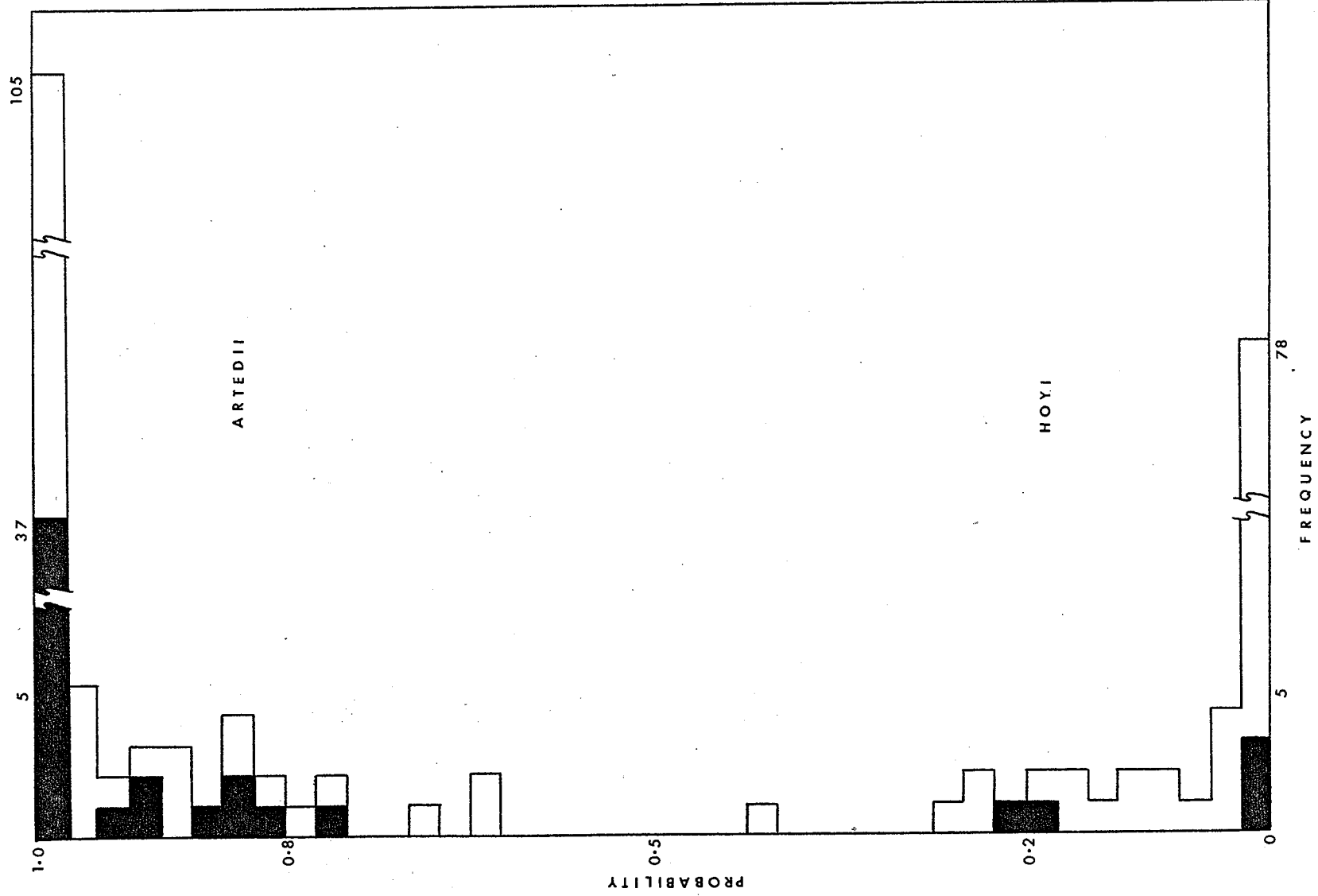
Three members of the C. artedii group were not coalesced with that group. When they were placed into the C. hoyi group, the analysis clearly showed that they belonged in the C. artedii group, although atypical. Examination showed that they resembled C. artedii in four or five characters, C. hoyi in two or three, and were intermediate in four or five characters.

Morphometric Differences Between the Three Species

After the three species had been separated, statistical differences between them were examined. The differences are significant at $p < 0.01$ unless otherwise stated.

Measurements from 96 C. hoyi and 131 C. artedii separated by the discriminant function analysis, and from 13 C. reighardi were used to

Fig. 5. Histogram of Probabilities from the Discriminant Function
Analysis of C. artedii and C. hoyi, Big Athapap 1968.
(Autumn fish shaded).



calculate regression lines by the least squares method. Significant differences between the three species were only found for head length on fork length, eye diameter on head length, and pectoral length on fork length.

C. reighardi had the largest head and C. hoyi the smallest (Fig. 6.). The differences between C. hoyi and the others were significant.

Because of the difference in relative head length, eye diameter was plotted against head length. C. reighardi had significantly larger eyes than the other species (Fig. 7.), and C. hoyi had larger eyes than C. artedii, but this was not significant.

The only other significant difference found was the longer fins of C. artedii in comparison to those of C. hoyi (Fig. 6.). There was no evidence of sexual dimorphism in pectoral fin length, or any other measurement.

Meristic Differences Between the Three Species

Means, 5% confidence limits, and interspecific F and t values for lateral line scales, pectoral and pelvic rays are shown in Table IV. When F values were significant, Cochran's modified t-test was used.

Lateral line scale counts of the three species differed significantly (Fig. 8.). C. artedii differed from the others at $p < 0.01$, whereas C. hoyi and C. reighardi differed only at $p < 0.05$. The number of lateral line scales of age I C. artedii varied significantly between localities of Big Athapap. Those caught at the surface of the East and West Arms had a mean count of 73.4 scales, whereas those caught at the surface of

Fig. 6. Fitted Regression Lines for Head Length and Pectoral Length on Fork Length for the Three Species, Big Athapap, 1968.

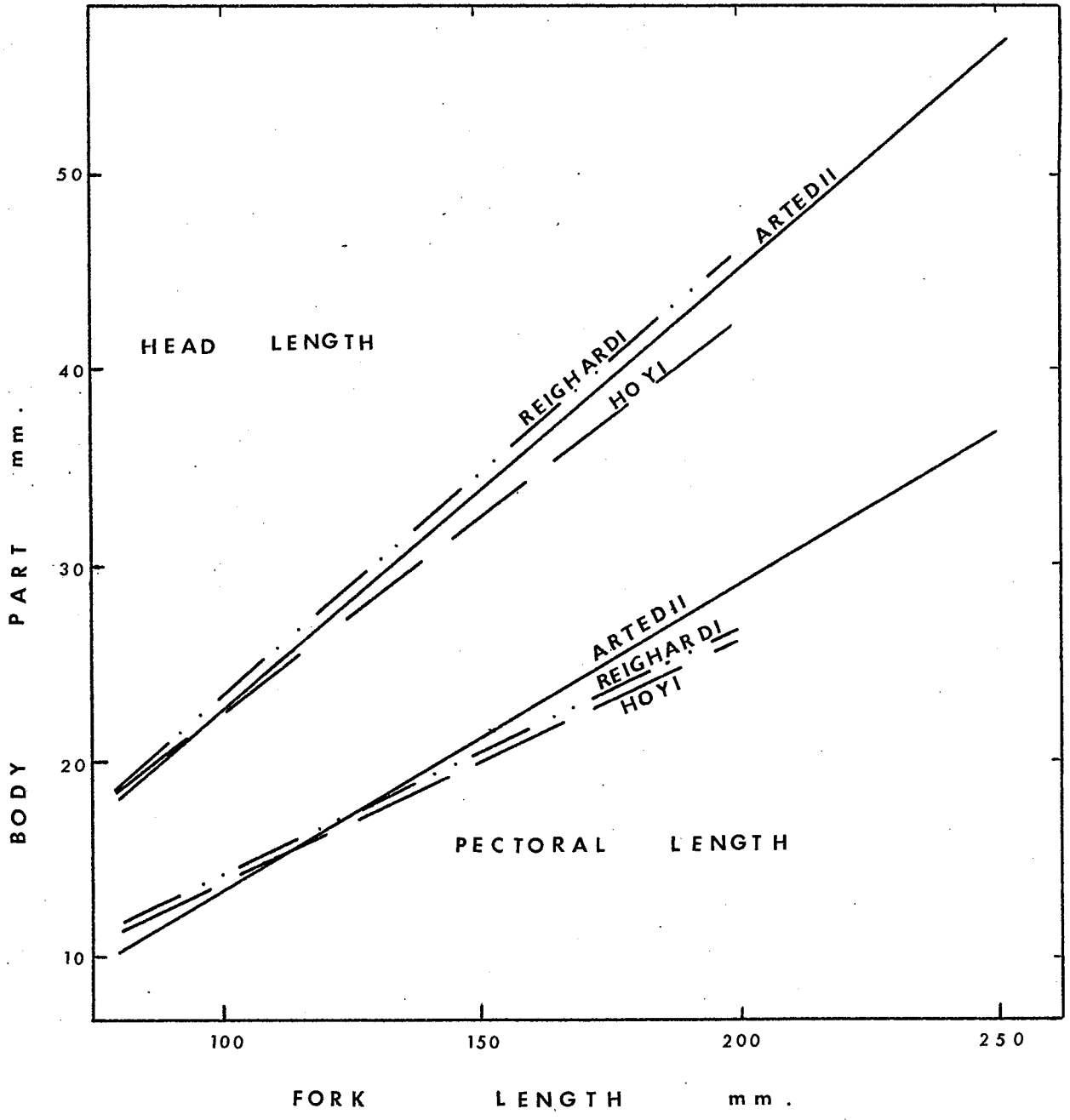


Fig. 7. Fitted Regression Lines for Eye Diameter and Gillraker Length on Head Length for the Three Species, Big Athapap, 1968.

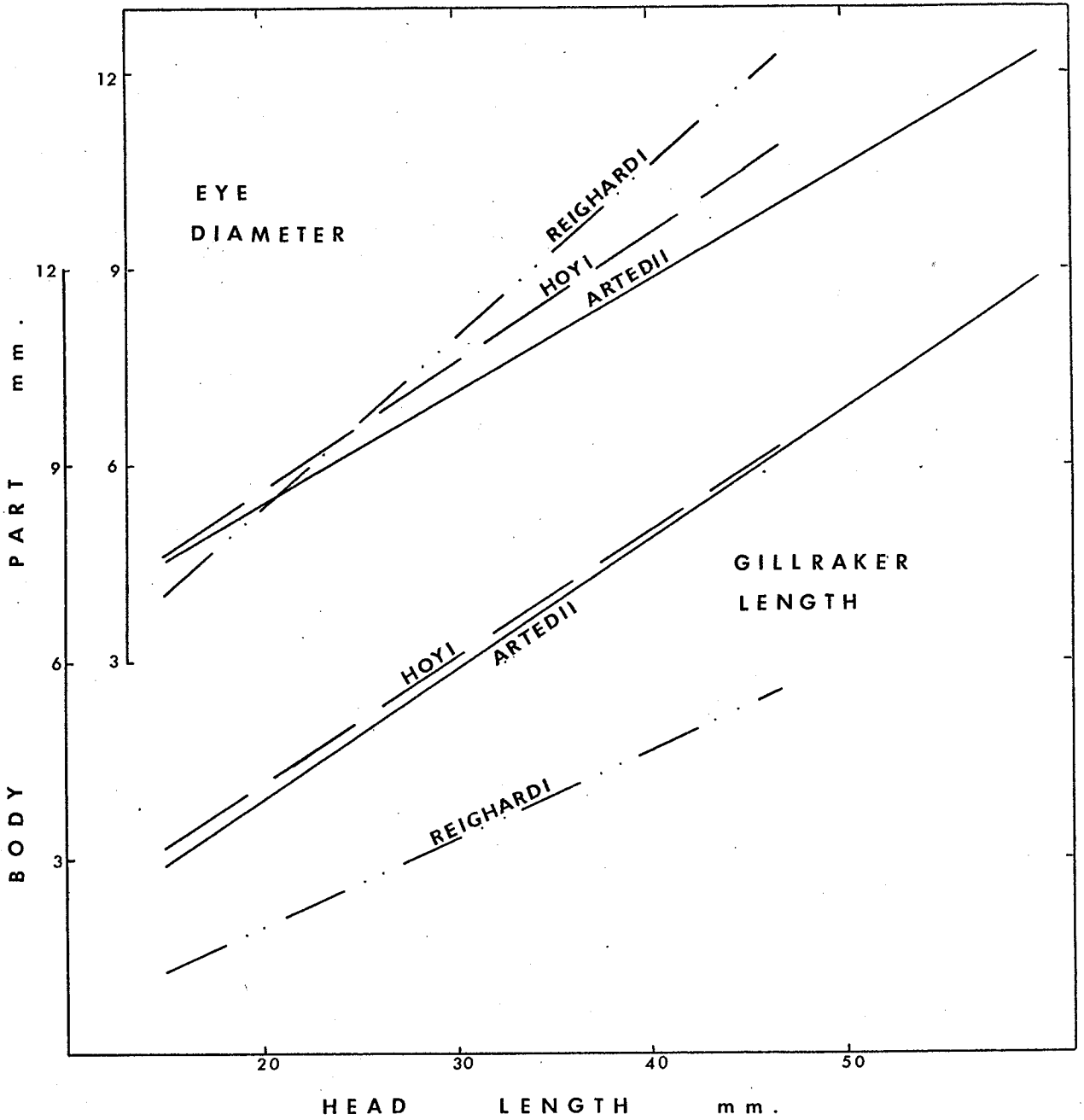


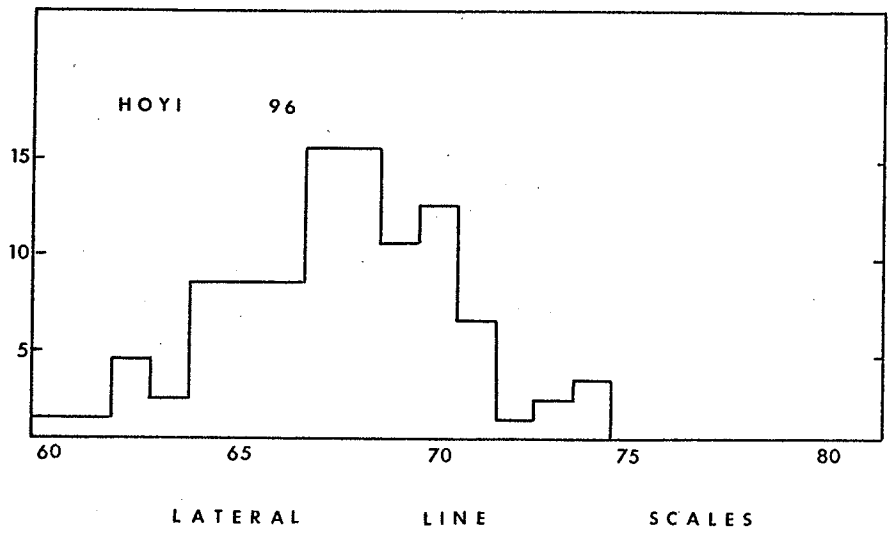
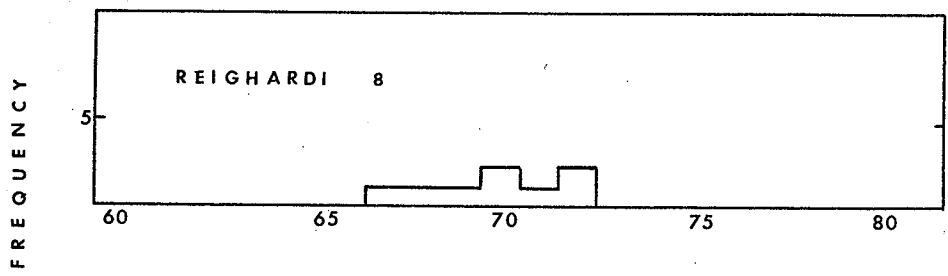
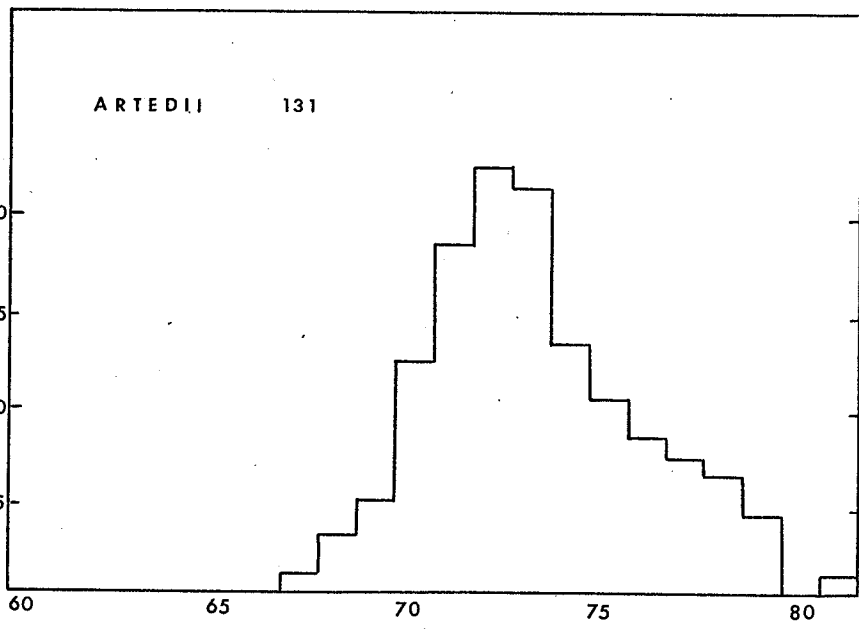
Table IV. Interspecific Differences in Lateral Line Scales, Pectoral and Pelvic Rays, and Gillraker Counts in Big Athapap

	Artedii $\bar{x} \pm 5\% \text{ C.L.}$	Hoyi $\bar{x} \pm 5\% \text{ C.L.}$	Reighardi $\bar{x} \pm 5\% \text{ C.L.}$	Artedii & Hoyi	Artedii & Reighardi	Hoyi & Reighardi
Lateral Line Scales	73.62 \pm 0.48	67.46 \pm 0.59	69.62 \pm 1.84	F = 1.12 n.s. t = 14.93**	F = 1.58 n.s. t = 3.19**	F = 1.77 n.s. t = 1.99*
Pectoral Rays	16.07 \pm 0.13	15.53 \pm 0.14	15.58 \pm 0.42	F = 1.23 n.s. t = 5.44**	F = 1.31 n.s. t = 2.13*	F = 1.07 n.s. t = 0.24 n.s.
Pelvic Rays	11.35 \pm 0.10	11.13 \pm 0.10	11.67 \pm 0.57	F = 1.29 n.s. t = 2.97**	F = 2.55* t = 1.22 n.s.	F = 3.29** t = 2.06 n.s.
Gillraker Counts						
Age I	43.52 \pm 0.45	40.73 \pm 0.44		F = 1.23 n.s. t = 8.69**		
	F = 1.05 n.s. t = 4.02**	F = 1.60 n.s. t = 4.51**				
>Age I	45.32 \pm 0.80	43.29 \pm 0.92		F = 2.08 n.s. t = 3.03**		
Total	43.94 \pm 0.39	41.16 \pm 0.39	29.86 \pm 1.45	F = 1.54 n.s. t = 5.06**	F = 2.13*	F = 2.81**

*Significant at 0.05

**Significant at 0.01

Fig. 8. Histograms of the Lateral Line Scale Counts for the
Three Species, Big Athapap, 1968.



the Main Body had 71.2 scales. Fish caught on the bottom of the East and West Arms had 70.2 scales, but this did not differ significantly from those caught at the surface of the Main Body. For both C. artedii and C. hoyi, older fish had more scales (\bar{x} = 74.09 and 68.90 respectively) than the younger, but this was not significant.

Scale rows around the caudal peduncle were counted, but the counts were inconsistent because of the loss of scales and the small size of the fish. C. hoyi appeared to have fewer scale rows than C. artedii.

C. artedii and C. hoyi also differed significantly in the number of pectoral and pelvic fin rays. C. reighardi differed significantly from C. artedii in the number of pectoral rays ($p < 0.05$).

Some fish of each species were x-rayed and their vertebrae counted. There was no absolute difference between the three species. Four C. reighardi had 58 vertebrae and one had 57. There appeared to be a difference between year classes of C. hoyi in the number of vertebrae. Four age I fish had 56 to 58 vertebrae, and three age II fish had 59 to 61. Four age I C. artedii had 57 to 60 vertebrae as did seven older fish.

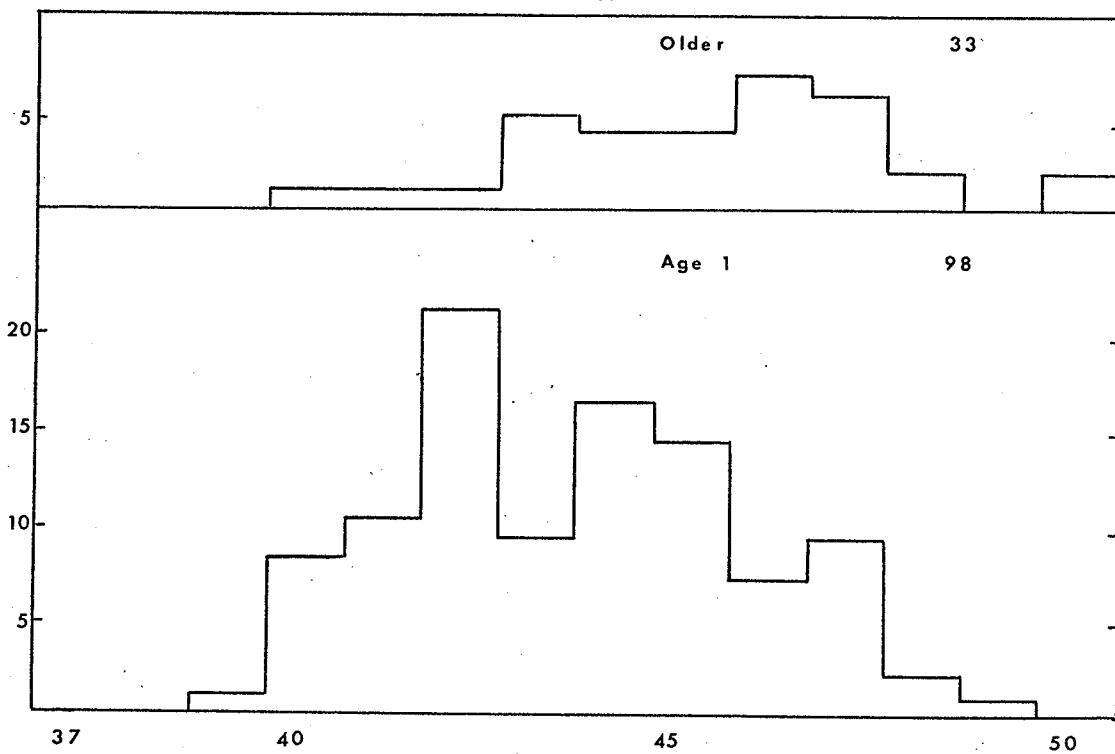
Gillrakers of the Three Species

Means, 5% confidence limits, F and t values are given in Table IV.

The distinctive gillraker counts on the first arch of the 23 C. reighardi were given above (Fig. 3.). There was a significant difference between gillraker counts on the first arch of C. artedii and C. hoyi for both age I and older fish (Fig. 9.). For both species the difference between age I and older fish was also significant. The differences

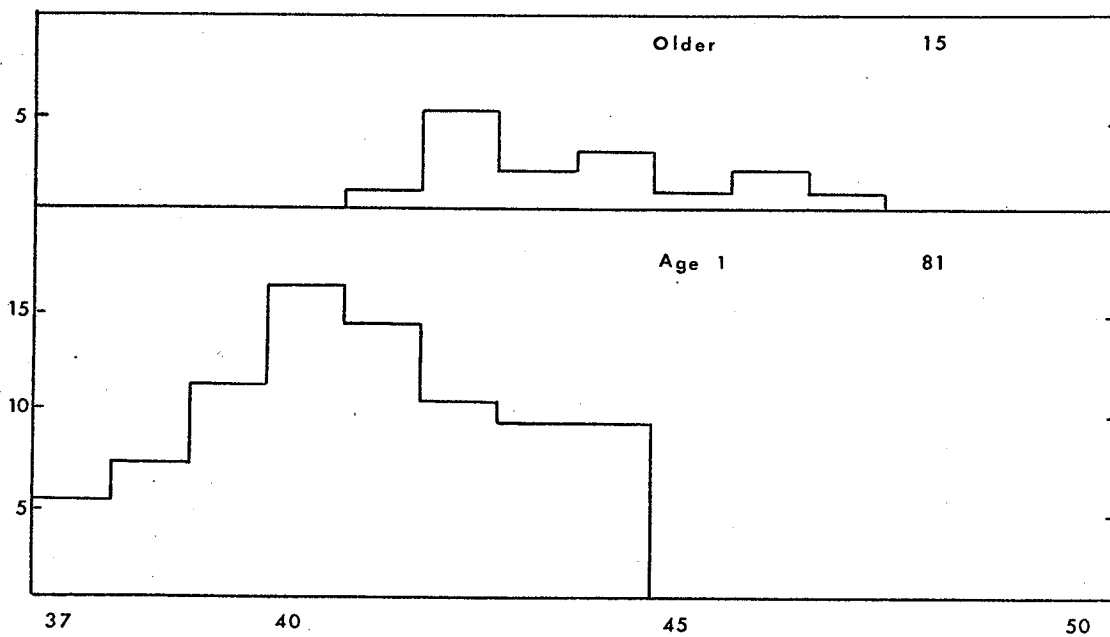
Fig. 9. Histograms of Gillraker Counts for C. artedii and C. hoyi,
Big Athapap, 1968.

ARTEDI



FREQUENCY

HOYI



GILLRAKERS

resulted from an extra gillraker on both upper and lower limbs of the gillarch. There was no significant difference between age I C. artedii and older C. hoyi. There was no evidence of significant intraspecific variation in gillraker counts of fish taken at the surface and bottom, nor from different localities within Big Athapap.

All three species had more gillrakers on the second arch than on the first, and other arches had progressively fewer and shorter gillrakers. Rudimentary gillrakers were present on all arches (except the fifth). Although they were rudimentary on the first arch, they became progressively fewer but longer on the other arches. C. reighardi had fewer primary and rudimentary gillrakers on all arches than did C. artedii and C. hoyi. For the latter two species there was no absolute difference in primary and rudimentary gillraker counts on any arch.

The length of the longest gillrakers on the first arch was plotted against head length, and regression lines were calculated by the least squares method for all three species. Gillrakers were much shorter in C. reighardi and did not overlap in length with C. artedii and C. hoyi. There was no significant difference in gillraker length between C. artedii and C. hoyi (Fig. 7).

Some Osteological Differences Between the Three Species

After staining in alizarin and NaOH, the skulls of two specimens of each species (all < 130 mm. F.L.) were examined for interspecific differences in the occurrence of teeth and the shape of the supraethmoid.

Teeth occurred in all species but were most numerous in C. reighardi. It had four teeth on each premaxilla, two to five palatine teeth, and one specimen had one vomerine tooth. C. hoyi premaxillae were similar, but the vomerine was toothless and only one tooth was found on each palatine. Only one C. artedii had teeth, one premaxillary and one palatine tooth.

The shape of the supraethmoid varied between species and between the specimens of each species (Fig. 10.).

Other Morphological Differences Between the Three Species

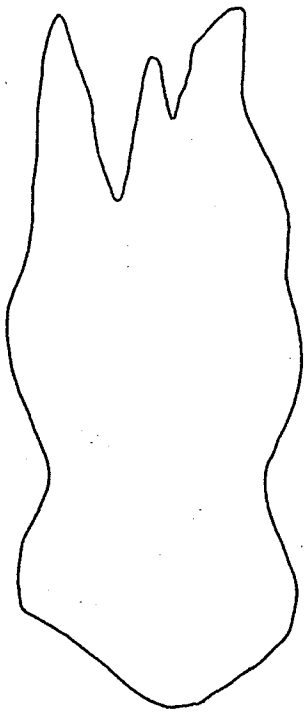
The lower jaw was obviously included in 18 C. reighardi, and equal to the upper jaw in the other five. The jaws were equal in 70% of the 131 C. artedii, but in only 56% of the 96 C. hoyi ($p < 0.05$, $t = 2.22$).

C. reighardi had immaculate pectoral fins. For the other two species the proportion with pigmented pectoral fins was higher in the older fish. For C. artedii 50% of age I and 88% of older fish were pigmented ($p < 0.01$, $t = 3.88$). For C. hoyi the proportions were 84% and 100% respectively, and this was not significant ($t = 0.5$). The differences between the species were significant for age I ($p < 0.01$, $t = 6.3$) but not for older fish ($t = 0.44$).

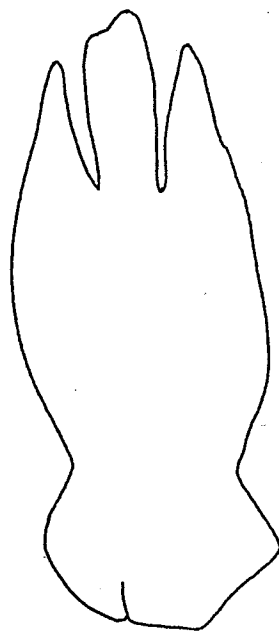
Growth Rates of the Three Species

When possible scales were removed from between the dorsal fin and lateral line, and read under a microprojector. Each annulus (two or more anastomosing circuli) was counted. All fish were aged twice, and discrepant scales were re-read until consistent results were obtained.

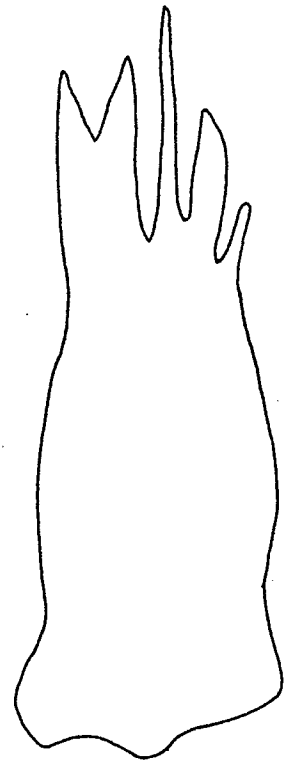
Fig. 10. The Supraethmoid Bones of the Three Species.



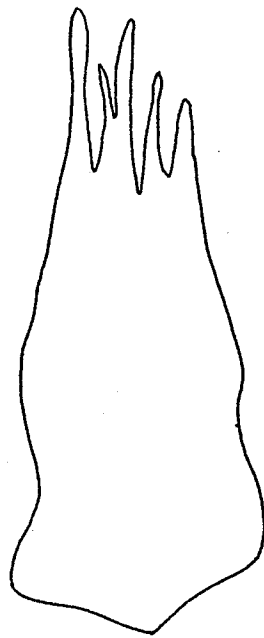
REIGHARDI



x 15



ARTEDII x 20



HOYI x 15

Growth rates of the three species differed, but statistical evaluation was hindered as only 62 fish were older than age I. 25 were age II, and of the remaining 37, 23 were caught in the autumn. The growth rates are shown in Fig. 11.

The three species did not differ in size at age I. The summer catch was divided into four time periods. Again there was no difference between species, but fish caught from 19 to 29 May 1968 were significantly smaller than those caught in later periods.

At age II, C. reighardi was significantly smaller than the other two species, which were similar in size. Subsequent C. reighardi age classes did not overlap those of the other species. The largest C. reighardi was 190 mm. F.L. at age VI.

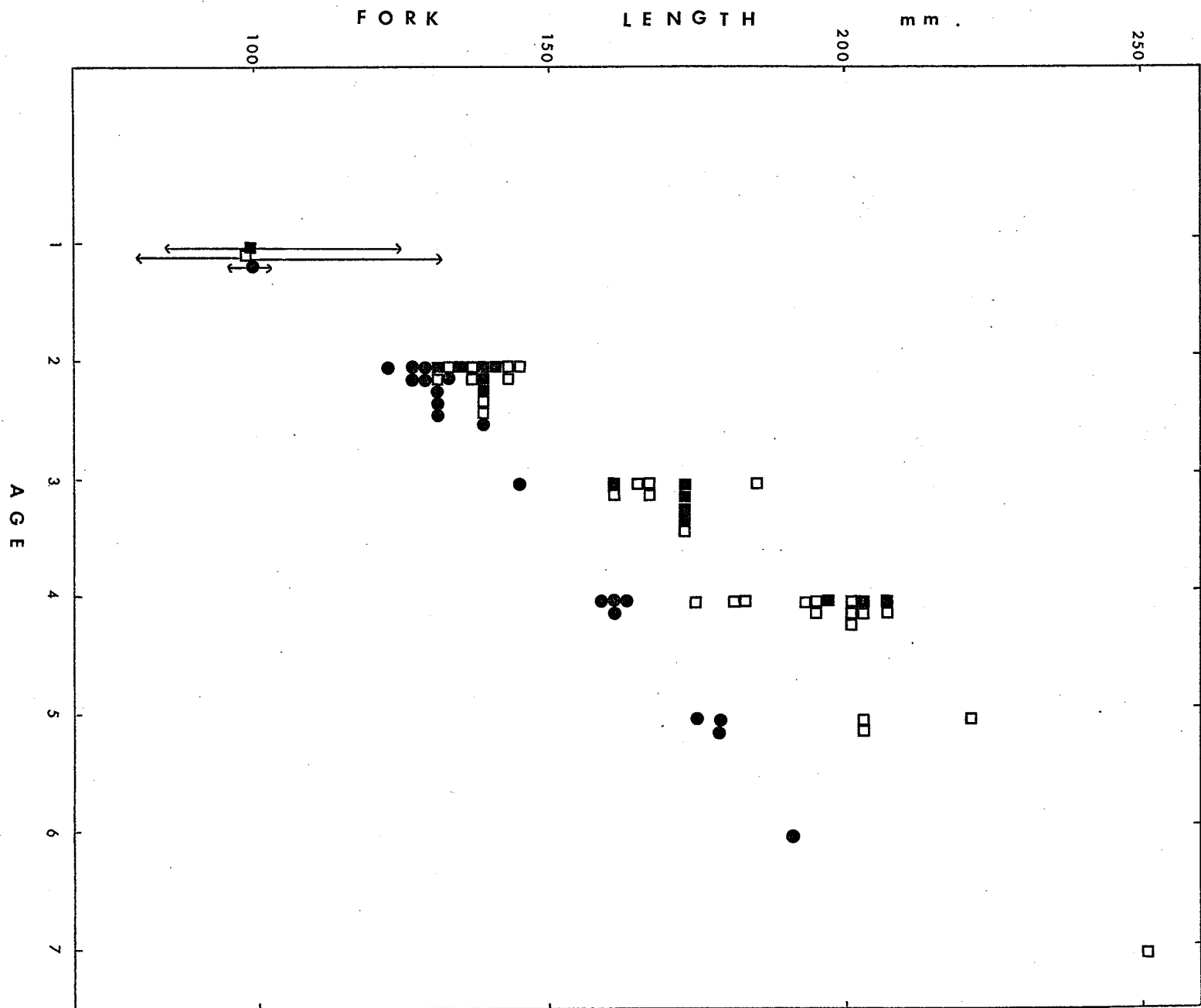
C. artedii and C. hoyi were similar in size at age III, but appeared to differ at age IV. Of the summer age IV fish, the one C. artedii had a F.L. of 180 mm., whereas the two C. hoyi were 196 mm. and 208 mm. F.L. Including both spring and autumn fish the nine C. artedii averaged 191.6 mm. F.L. and the three C. hoyi 202.3 mm. F.L. ($t = 1.73$ n.s.).

No older C. hoyi were caught. A total of five age V C. artedii averaged 206.4 mm. F.L. The largest C. artedii had a 251 mm. F.L. at age VII.

The 1968 year class of C. artedii was caught that autumn averaging 89.4 mm. F.L.

Sexual and spatial differences in growth rate within each species were not significant at age I. They were not tested for older fish.

Fig. 11. 1968 Growth Rates of the Three Species in Big Athapap
(C. artedii □ , C. hoyi ■ , C. reighardi ● ;
only means and range given for age I fish).



Maturity and Reproduction in the Three Species

Following Schweitzer (MS, 1968), fish caught before August were classified as mature if their gonads were thicker than the oviduct or Wolffian Duct. Sex was determined from the appearance of the gonads, though this was not always possible for immature fish. The condition of the gonads suggested that all three species were autumn spawners, and this was confirmed for C. hoyi and C. artedii when ripe specimens of both species were caught on the reefs in late October 1968.

At age I most C. hoyi were mature and most C. artedii were immature (Table V). Within each species there was no significant change in the proportion of mature fish from May to July 1968, but the significance of the difference between the species consistently decreased as time progressed. By July there was no difference, but the sample of C. artedii was small. Except for age 0 C. artedii and one age II C. artedii and C. hoyi, all other fish, including C. reighardi, were mature. The intermediate fish was immature at age I.

During the autumn, fish were sampled in the reefs. Most were ripe C. artedii, though small immature C. artedii were also present. Spent C. artedii were first caught on 29 October 1968. Five C. hoyi were also taken on the reefs at the same time and in the same place. Of these one was immature, one was a spent female, and three were males with milt. Neither species developed spawning tubercles. [Ripe C. reighardi were caught on the bottom in 90' of water in October 1969].

Table V. Maturity of Age I C. artedii and C. hoyi in Big Athapap 1968.

	<u>C. artedii</u>		$\chi^2_{1 \text{ y.c.}}$	<u>C. hoyi</u>	
	Mature	Immature		Mature	Immature
May	3	25	26.7**	18	2
χ^2	2.0 n.s.			0.2 n.s.	
June 1-15	7	16	11.7**	16	2
χ^2	0.0 n.s.			0.6 n.s.	
June 16-30	6	12	6.2*	21	7
χ^2	0.9 n.s.			1.1 n.s.	
July	4	2	0.8 n.s.	14	1
Total	20	55	52.1**	69	11

*Significant at 0.05

**Significant at 0.01

Horizontal Distribution of the Three Species

C. artedii and C. hoyi were found all over Big Athapap, but were more numerous in the shallower water. Fish older than age II were caught only in the Main Body. C. reighardi was restricted to the Main Body.

Vertical Distribution of the Three Species

Figures for the vertical distribution of the three species caught from 18 May to 7 July 1968 are given in Table VIa.

C. reighardi was caught only in bottom sets, and 18 of the 23 fish were caught below 100'.

C. artedii was caught mainly at the surface. The proportion caught in surface and bottom sets did not vary with water depth.

The proportion of C. hoyi in surface and bottom sets did vary with water depth. In water of less than 50', they were caught mainly on the bottom, whereas in water over 100' deep they were caught predominantly at the surface. The difference was significant ($p < 0.01$). At intermediate depths, C. hoyi was evenly distributed between surface and bottom sets, differing ($p < 0.05$) from both shallower and deeper water.

In water deeper than 100', where C. reighardi was caught on the bottom, there was no difference in the vertical distribution of C. artedii and C. hoyi. Between 50' and 100' the difference in distribution between the two species was significant ($p < 0.05$), and in shallower water was also significant ($p < 0.01$).

Whenever possible, the fish were recorded as being in the top, middle or bottom portion of the nets. In both surface and bottom sets

one-quarter of C. artedii and one-half of C. hoyi occurred in the bottom part of the net. When data from surface and bottom sets were pooled, this was significant ($p < 0.05$) (Table VIb).

The intermediate fish was caught in the top portion of a surface set in 30' of water.

In summary, whenever they occurred, C. artedii displayed a propensity for upper waters and C. hoyi for lower.

Feeding in the Three Species

Stomachs were removed from the fish while fresh, and their contents preserved in 70% isopropyl alcohol. The contents were sized by passing through a series of screens of meshes of size 0.84, 0.71, 0.5, 0.35, 0.25, and 0.125 mm. The sized contents were identified to the lowest taxonomic category possible, usually genus, using Pennak (1953) and Ward and Whipple (1966). Imagoes were identified to order. The contents of each stomach were recorded as its approximate per cent volume for each taxon in each size group. The per cent volume was also estimated for some stomachs by volume displacement.

Food organisms were grouped into four categories:

Benthos: Pisidium; Hyallorella, Pontoporeia; Diptera larvae.





Bentho-pelagic: Mysis; Odonata and Plecoptera nymphs, insect pupae.

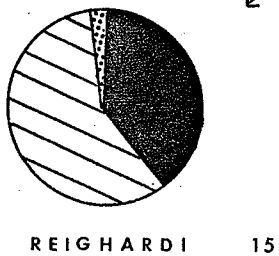
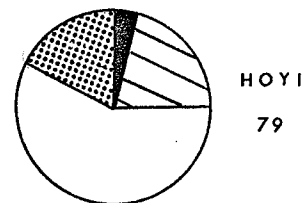
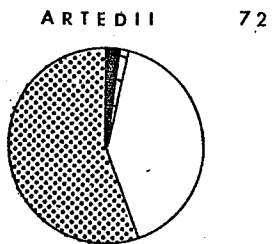
Plankton: Cladocera; Cyclops, Calanoidea.

Surface: adult Insecta, Araneae.

The proportion of food in the four categories differed significantly between the three species (Fig. 12.) for the period from 18 May to 7 July 1968. C. reighardi fed almost exclusively on bentho-pelagic and benthic

Fig. 12. The estimated Per Cent Volume of Food Organisms in the Three Species, Big Athapap 18 May to 7 July 1968.

(Benthos  ; Benthopelagic  ; Plankton  ;
Surface ).



70.5

29.8

34.2

χ^2

$P < 0.01$

organisms, of which Mysis formed one-half. Plankton was the main food of C. hoyi, which also fed on equal proportions of benthopelagic and surface organisms. C. artedii fed predominantly on surface food, with the remainder being mainly plankton.

For C. artedii, there was a significant difference between stomach contents of fish caught at the top and on the bottom, but only five were caught on the bottom with food in their stomachs. One had eaten benthos, one an insect nymph, one plankton, and one a mixture of plankton and adult insects. The contents of one stomach were unidentifiable. Fish caught at the surface fed on plankton and surface food; in May plankton predominated, in June and July adult insects; this difference was significant.

There was also a significant difference in the stomach contents of surface and bottom caught C. hoyi. Fish caught at the surface fed mainly on plankton, but several ate adult insects. For fish caught on the bottom, there was a significant difference in stomach contents between May and June or July caught fish. In May plankton predominated with some benthos; in June and July there was an equal volume of benthopelagic and planktonic organisms with some adult insects and a little benthos.

When spatial and temporal differences were negated in the comparison of the feeding of C. artedii and C. hoyi, the only significant difference occurred in the surface sets of June and July (Fig. 13.). In these C. artedii fed predominantly on surface food, and C. hoyi on plankton. This was the only time and place where both species were caught in relatively

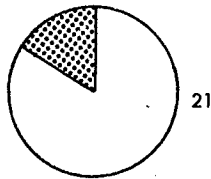
Fig. 13. Temporal and Spatial Differences in the estimated Per Cent Volume of Food Organisms for C. artedii and C. hoyi, Big Athapap, 1968. (Key as in Fig. 12.)

SURFACE SET

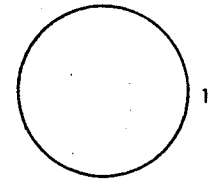
BOTTOM SET

MAY

ARTEDII

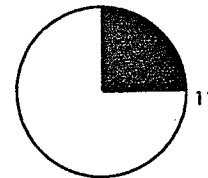
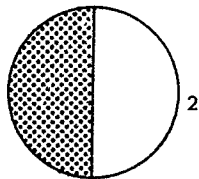


$$\chi^2 = 0.0, \text{ n.s.}$$



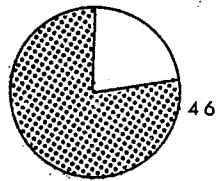
$$\chi^2 = 3.5, \text{ n.s.}$$

HOYI

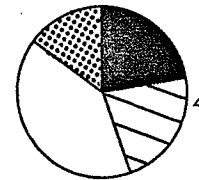


JUNE and JULY

ARTEDII

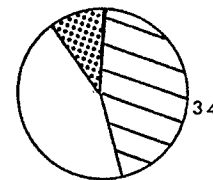
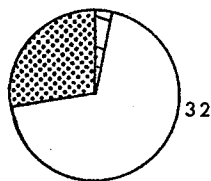


$$\chi^2 = 17.7, P < 0.01$$



$$\chi^2 = 4.4, \text{ n.s.}$$

HOYI



large numbers.

There was no difference between C. artedii and C. hoyi in the composition of the organisms in the four categories, but C. reighardi was the only species that ate molluscs and Mysis. Within each category there was no interspecific difference in the size of food. Nor was there any change in feeding with increased F.L. The proportion of empty stomachs (about 12%) was the same for each species in both top and bottom sets. The intermediate fed on adult insects.

Gillrakers and Feeding in the Three Species

C. reighardi had fewest gillrakers and fed on benthic and benthopelagic organisms, and did not eat plankton. C. hoyi had fewer gillrakers than C. artedii, and differed from the latter in feeding on more plankton.

The gillraker ranges for C. artedii and C. hoyi in Big Athapap were divided into lower and upper halves to see if any differences in feeding were attributable to gillraker number. The differences were not significant, but the two C. artedii that fed on benthos and on insect nymph had gillraker counts of 40 and 42. Also individuals in the lower half of the C. artedii gillraker range fed on less plankton and more surface food than those of the upper half. For C. hoyi individuals with a lower gillraker count ate more benthic and benthopelagic organisms, more plankton and less surface food than those with a higher gillraker count.

TAXONOMIC IDENTIFICATION OF THE CISCOES IN BIG ATHAPAP

Identification of the Species by Taxonomic Keys

Using the keys to N. American coregonids (Koelz, 1929; Hinks, 1957; Hubbs and Lagler, 1964), two Big Athapap species were always identified as C. artedii and C. hoyi, and when C. reighardi was included in the keys, the third species was identified as this. In other keys the third species was closest to either C. johannae or C. zenithicus. It differed from the former in everything except gillraker counts, and from the latter in having fewer gillrakers and scales and slightly different morphometry.

All three species in Big Athapap were atypical in various characters. All had fewer scales; and both C. artedii and C. reighardi had larger eyes than the Great Lakes and L. Nipigon populations of these species. C. reighardi also differed in the fewer gillrakers and autumn spawning, for it resembled the spring spawning C. r. reighardi more closely than the autumn spawning C. r. dymondi. The greenish colouration is typical of C. reighardi. C. hoyi was also atypical in being an autumn spawner, having smaller eyes and shorter fins than the Great Lakes and L. Nipigon C. hoyi. Not all individuals had a protruding mandible and there was little evidence for the presence of a symphyseal knob.

Numerical Taxonomy: Taxonomic Identification by Correlation

Koelz (1929) found eleven characters of most use in separating the species of the Great Lakes and L. Nipigon. The characters were eye diameter, snout length, and maxilla length (all as ratios in head length);

head length and body depth (in standard length); pectoral length (in pectoral-pelvic distance); pelvic length (in pelvic-anal distance); body contour (coded: elliptical = 1, ovate = 2); lower jaw (coded: protruding = 1, equal = 2, included = 3); gillraker and lateral line scale counts. The average values for each of these characters was estimated for the Great Lakes and the L. Nipigon populations, and calculated for the Big Athapap populations. The effect of allometric growth was ignored. A log transformation was applied to the data before use.

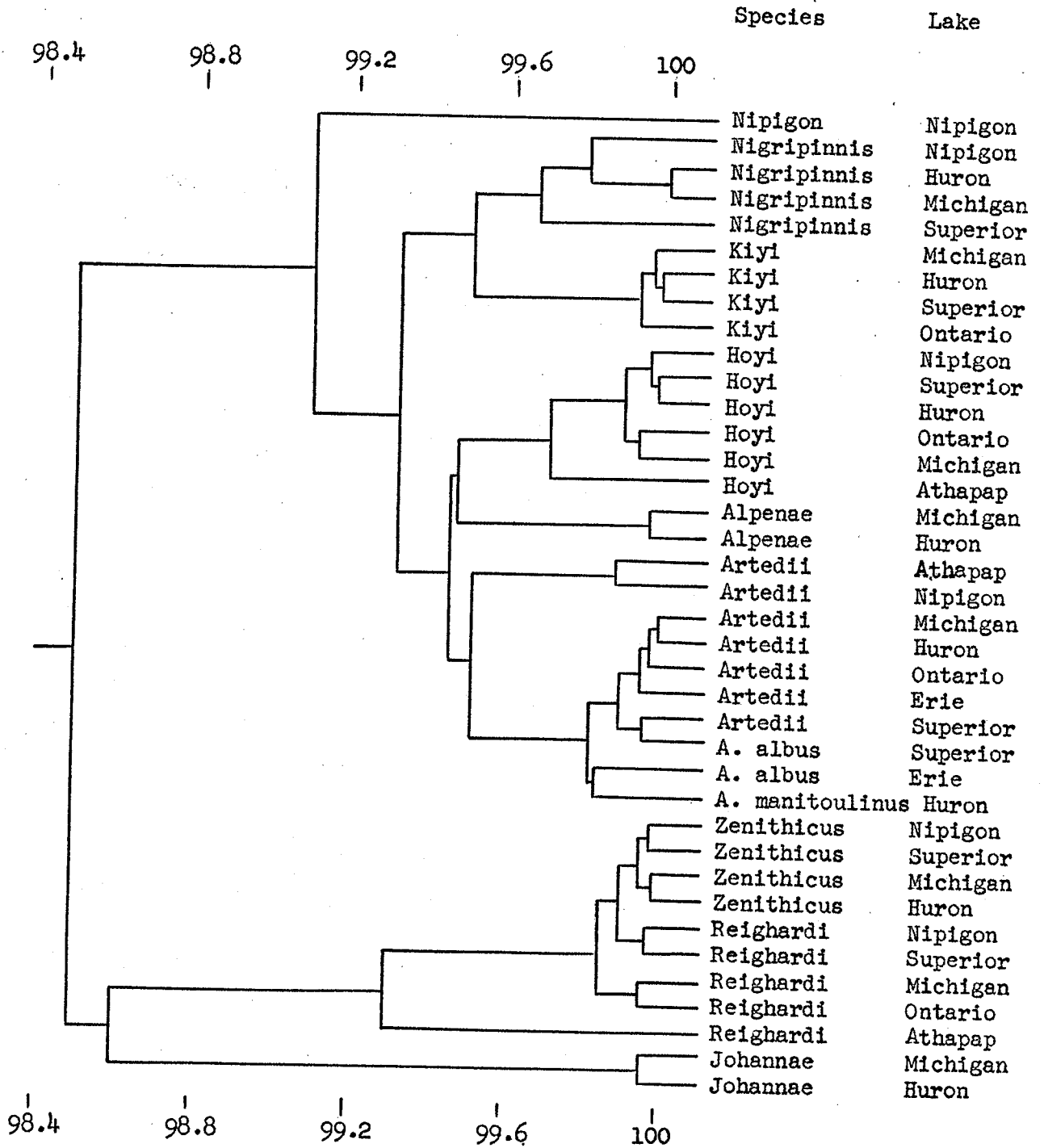
Correlation coefficients were calculated from the data for all pairs of populations. The Big Athapap C. artedii was most similar to the same species in L. Nipigon, and the Big Athapap C. hoyi most closely resembled C. hoyi of L. Huron. The Big Athapap C. reighardi was most similar to the type population in L. Michigan. A phenogram (Fig. 14.), constructed by the average linkage weighted variable group method (Sokal and Sneath, 1963) from the correlation coefficients, showed that the Great Lakes and L. Nipigon populations of C. reighardi and C. zenithicus clustered at a higher level than that at which the Big Athapap population entered the cluster. The Big Athapap C. artedii clustered with the L. Nipigon C. artedii before they both joined the cluster of other C. artedii, and the Big Athapap C. hoyi clustered with the Great Lakes and L. Nipigon C. hoyi.

Numerical Taxonomy: Factor Analysis and Taxonomic Identification

The same data were used in factor analysis as in the correlation of the Big Athapap, Great Lakes and L. Nipigon ciscoes (see above).

Fig. 14. Phenogram of Great Lakes, L. Nipigon and Big Athapap Ciscoes.

Correlation %



Q-mode analysis, starting from the correlation matrix of the samples, gave one factor with five groupings of populations corresponding to an ovate or elliptical body with a protruding, equal or included mandible (there is no ovate body with an included mandible).

R-mode analysis, which starts from the correlation matrix of the variables, was also used. Factor scores calculated from the rotated factor matrix (Table VII) were used to confirm the identification of the three Big Athapap populations. Of the seven factors extracted in the analysis, factors II, III and IV were of little use in identifying any species. Plots of factor scores for factor I against V and factor V against VII are shown (Fig. 15.). These confirmed that the Athapap populations resemble C. artedii, C. hoyi and C. reighardi most closely.

The R-mode analysis gave information as to the interrelationships of the eleven characters. The factor loadings for each factor (Table VII) indicate the correlation of variables and factors.

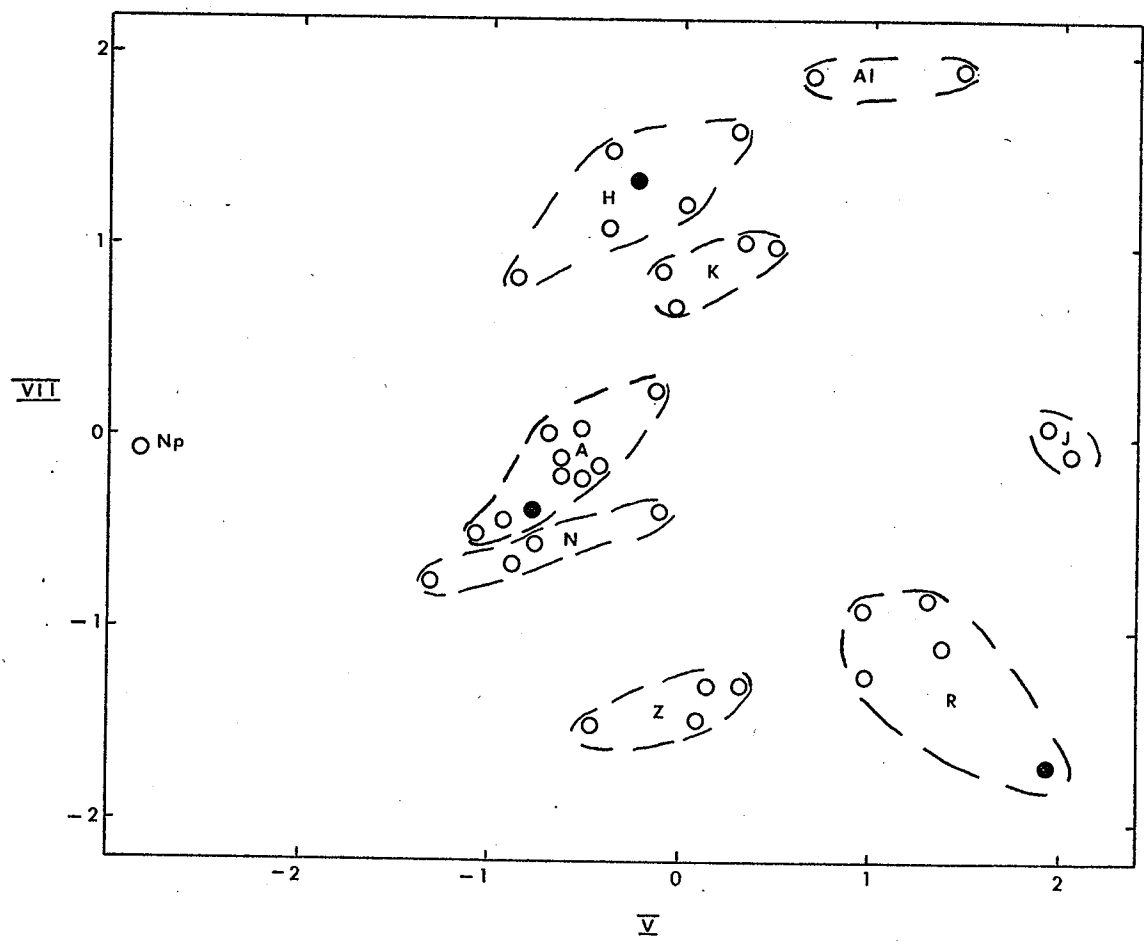
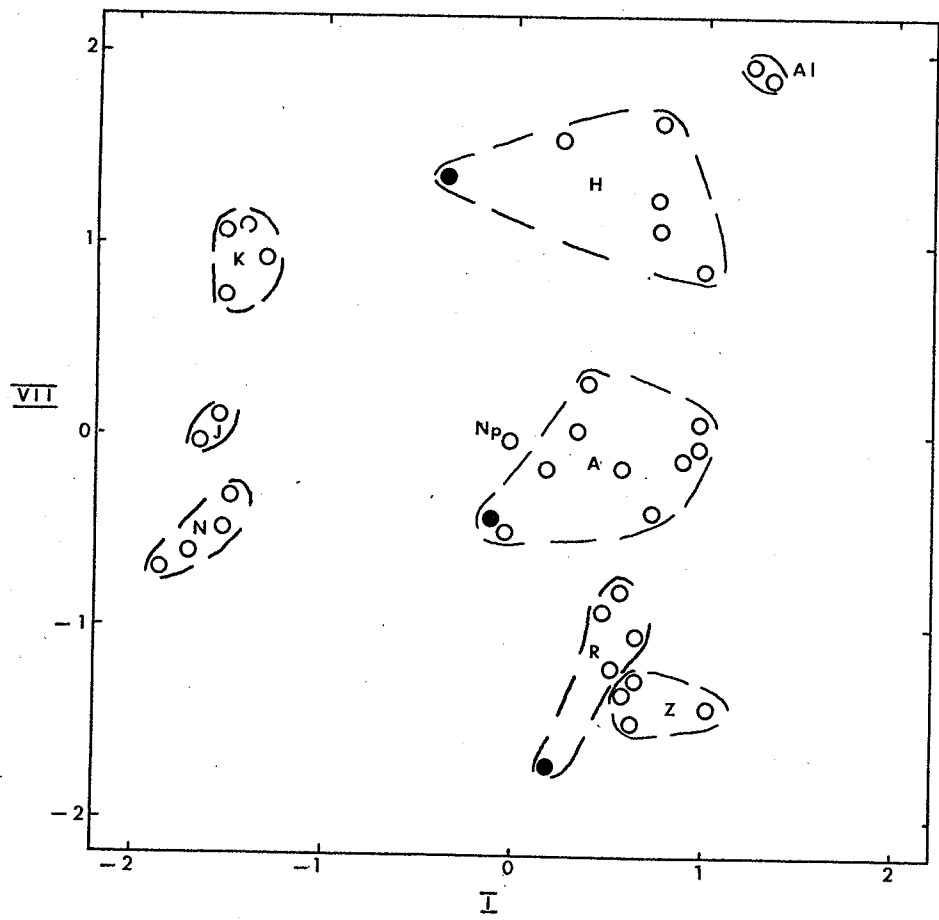
Factor I was a body contour factor, also loaded on fin length and head length. An ovate body was associated with longer fins and head. It showed interspecific differences, but when the species were arranged in order of their factor scores, this arrangement corresponded to the vertical distribution of the species. An ovate body was associated with a greater depth of occurrence.

Factor II was the lateral line scale factor. The next highest loading occurred on body contour, an ovate body having more scales. Scales are known to be environmentally affected. The factor scores for

Table VII. Factor Analysis of Great Lakes, L. Nipigon and Big Athapap
Ciscoes: Rotated Factor Matrix (x100).

Character	Factor						
	I	II	III	IV	V	VI	VII
Lateral Line	-15	95	-13	-16	-0	18	2
Gillrakers	5	1	-29	-4	-94	-4	11
Eye Diameter	11	19	-13	-15	6	92	-18
Snout Length	6	-14	-84	5	-33	-30	-2
Maxilla Length	7	23	-87	-8	-18	18	2
Head Length	26	5	-84	25	7	26	-14
Pectoral Fin Length	61	22	-60	16	26	19	-19
Pelvic Fin Length	58	12	-57	2	-11	36	-36
Body Depth	12	-16	-6	95	5	-13	13
Body Contour	-93	27	11	-11	9	-2	9
Lower Jaw	16	-3	-9	-14	11	17	-95

Fig. 15. Plots of Factor Scores (I and VII; V and VII) showing identification of the Big Athapap ciscoes (Great Lakes & L. Nipigon ○ , Big Athapap ● ; Al-Alpenae, A-Arteidii, H-Hoyi, J-Johannae, K-Kiyi, N-Nigripinnis, Np-Nipigon, R-Reighardi, Z-Zenithicus).



this factor showed significant differences between average scores for each lake.

Factor III had highest loadings on maxilla, snout and head length, and then on fin lengths. The loading on eye diameter was low. Larger maxillae were associated with fewer gillrakers. Besides showing interspecific differences, May spawners had low scores and March spawners high scores. L. Ontario C. kiyi had a lower score than other C. kiyi; and C. r. reighardi a lower score than C. r. dymondi; C. hoyi had the highest score, but autumn spawning C. hoyi of Athapap had a low score. In addition deep water species had higher scores than shallow water species.

Factor IV was its body depth factor. Deeper bodies were associated with longer heads.

Factor V was the gillraker factor. Fewer gillrakers were associated with a longer snout and shorter pectoral fins. It showed interspecific differences.

Factor VI was the eye diameter factor. Large eyes were associated with longer pelvic fins and head, but with a shorter snout.

Factor VII was the lower jaw factor; longer lower jaws were associated with longer pelvic fins. It showed some interspecific differences.

As differences in body contour and body depth are primarily associated with environmental differences, the populations were correlated without these variables. All three Big Athapap species were identified as before, except that C. hoyi was now more similar to the L. Michigan

population, and C. artedii to the L. Ontario population.

In addition it was found that, phenotypically, C. reighardi was most similar to C. zenithicus, and vice versa; C. hoyi to C. kiyi, and vice versa; and C. artedii to C. nigripinnis, and vice versa. C. nipigon was most similar to C. nigripinnis. C. johanna resembled C. alpenae most closely, but C. alpenae was most similar to C. kiyi (Table VIII).

INTER-LAKE VARIATION OF THE THREE SPECIES IN NORTHERN MANITOBA

In the lakes of northern Manitoba that were sampled, both C. artedii and C. hoyi had two intergrading phenotypes. One phenotype was a deep body with a short thick caudal peduncle and much pigmentation. The other phenotype, which was associated with a smaller maximum fork length, was a slim body, a longer thinner caudal peduncle and less pigmentation. It was found that the average body depth, at 250 mm. F.L., of a population was negatively correlated ($p < 0.01$) to the maximum depth of the lake (Fig. 16a.) The same was true at 100 mm. F.L. ($p < 0.05$).

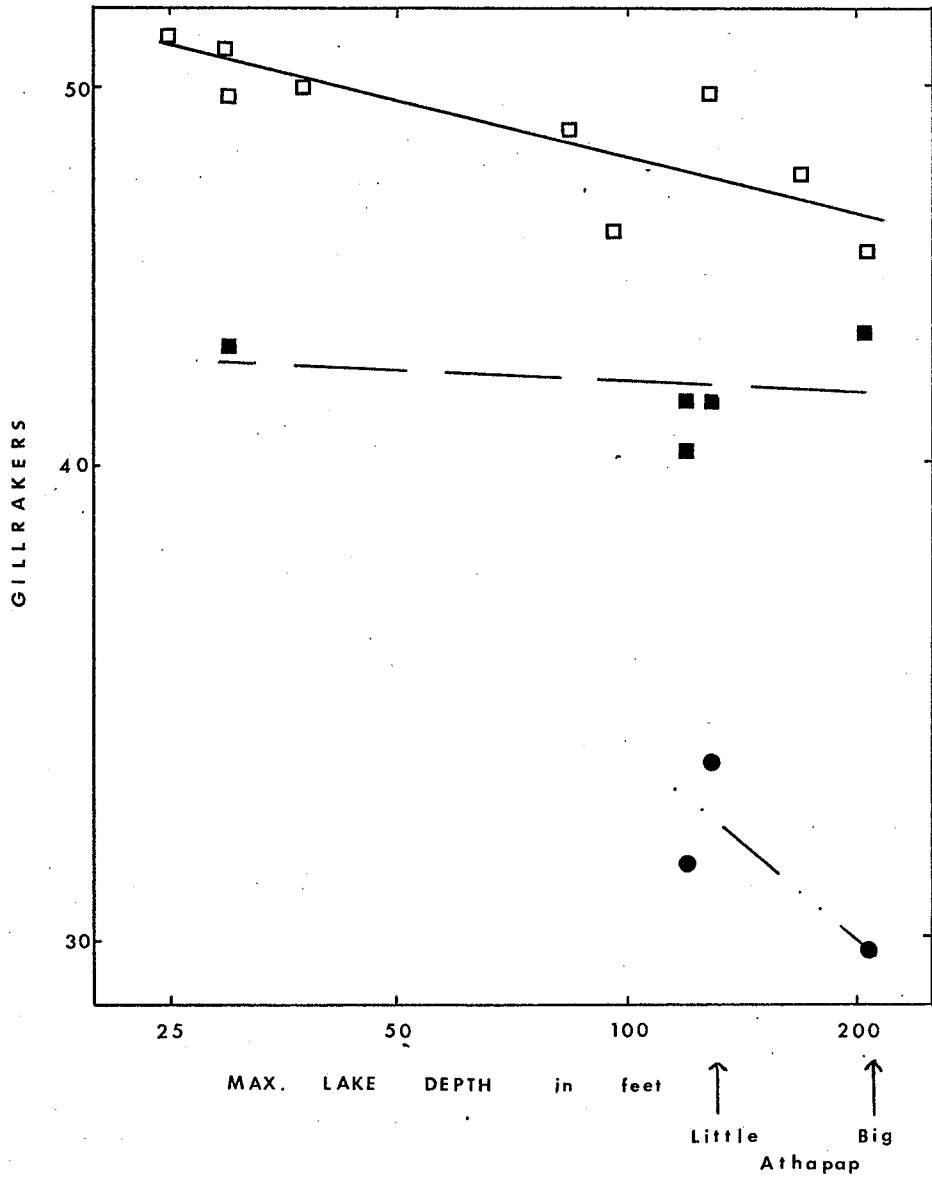
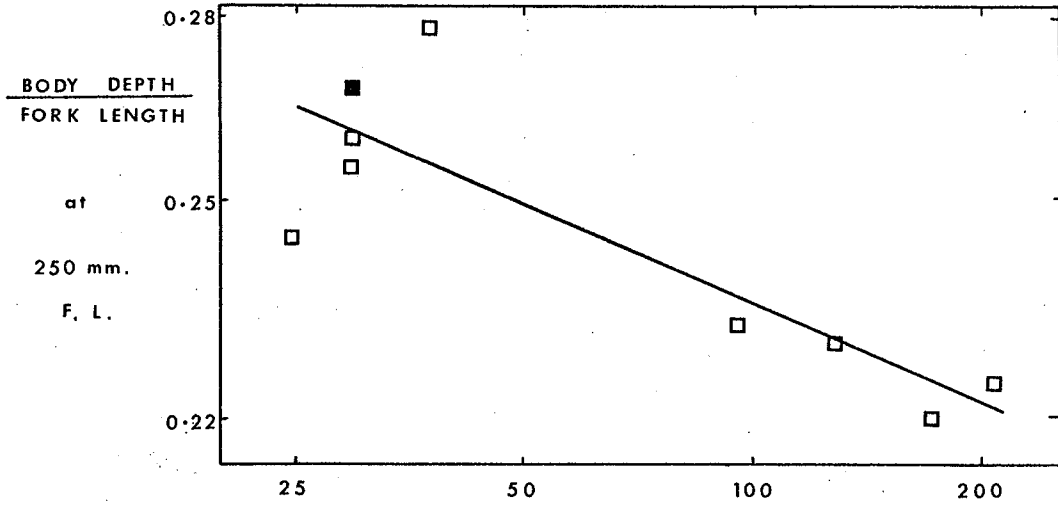
The mean gillraker counts of population of C. artedii sampled in the area ranged from 45.3 (Big Athapap) to 51.7 (1st Cranberry L.). This was also negatively correlated to the maximum lake depth ($p < 0.01$). The mean gillraker counts of populations of C. hoyi and C. reighardi also showed inter-lake variation, but the correlation with maximum lake depth for these species was not significant (Fig. 16b.). The means for C. hoyi ranged from 40.4 (Big Island L.) to 43.3 (Big Athapap); for C. reighardi from 29.9 (Big Athapap) to 33.4 (Little Athapap). The species showed

Table VIII. Correlation (x100) of Ciscoe Species from Central N. America.

	Zenithicus	Reighardi	Johannae	Alpenae	Kiyi	Hoyi	Artedii	Nigripinnis	Nipigon
Zenithicus									
Reighardi	<u>98</u>								
Johannae	91	92							
Alpenae	83	83	93						
Kiyi	85	84	89	97					
Hoyi	83	82	85	96	<u>92</u>				
Artedii	90	88	87	93	97	97			
Nigripinnis	92	90	88	92	96	96	<u>98</u>		
Nipigon	87	83	77	87	90	92	95	96	

Fig. 16a. Inter-Lake Variation: Regression of Body Depth/Fork Length,
at 250 mm. Fork Length, on Maximum Lake Depth (Log axes).
(C. artedii □ C. hoyi ■)

Fig 16b. Inter-Lake Variation: Regression of Mean Gillraker Counts
on Maximum Lake Depth (Log axes). (C. artedii □ , C. hoyi ■ ,
C. reighardi ●)



significant differences in mean gillraker counts between the basins of L. Athapapuskow.

In Big Island L. only C. hoyi was caught, but several lakes contained just C. artedii. Where both these species occurred sympatrically, they could be distinguished easily in phenotypic grounds only in Little Athapap and Mink Narrows. Schist L. and Rocky L. may contain two sympatric species of ciscoes.

C. reighardi was caught only in L. Athapapuskow and Clearwater L., lakes with a maximum depth of over 100'.

DISCUSSION

Morphology of the Three Species

The species concept is based on reproductive isolation (Mayr, 1963), but usually the distinctness of species is inferred from phenotypic differences. However, as coregonids have plastic phenotypes, deductions about the distinctness of coregonid species, based on phenotypic differences, are more difficult to make and more questionable than for most other taxa.

Although responsive to selection pressure, gillrakers are one of the more stable characters used in coregonid taxonomy. Wherever the three species occur sympatrically, C. artedii has more gillrakers than C. hoyi, and both have more than C. reighardi, suggesting that the differences in gillraker counts are probably genetic.

Scale counts are notoriously plastic, as was shown by the variation within Big Athapap C. artedii, but a situation, similar to that found in gillrakers, occurs in lateral line scale counts. C. artedii has most scales and C. hoyi least wherever the three species are sympatric, except in L. Nipigon where C. hoyi has more scales than C. artedii (Koelz, 1929). Autumn spawning fish usually have more scales than spring spawners (Svardson, 1952), but if C. hoyi and C. reighardi are autumn spawners in Big Athapap, this generalization breaks down, as they have fewer scales than the spring spawning C. hoyi and C. r. reighardi of the Great Lakes. The Big Athapap C. reighardi have fewer scales than the autumn spawning C. r. dymondi. Acting through egg size, parent

body size also influences scale numbers (Svardson, 1952), and this could account for the low number of scales in the three species, for they are all mature at 100 mm. F.L. As the differences in scale counts are the same in most cases of sympatry, it suggests a basic genetic difference.

Sympatric species often have different growth rates, but the differences are not consistent when several localities are compared (Pritchard, 1931; Keleher, 1952; Moffett, 1957). In the Great Lakes, C. artedii and C. reighardi had approximately similar growth rates, and C. hoyi the worst. In Big Athapap C. reighardi had the worst growth, and C. hoyi and C. artedii were similar to each other but the latter lived longer.

Growth rate affects the morphometry, with slow growing populations having larger body parts (Hile, 1937). C. reighardi had larger body parts than C. artedii and C. hoyi in both Big Athapap and the Great Lakes, despite different growth rates. C. artedii had a larger head and smaller eyes than C. hoyi, although their growth rates in Big Athapap were similar, whereas in the Great Lakes C. artedii had a smaller head and eye. The difference in head size could result from differences in growth rate, but the difference in eye size is consistent with it being a genetic difference.

The morphological differences between the three Big Athapap species are consistent with mainly genetic, rather than non-genetic effects. The fewer scales of the three species, the larger body parts of C. artedii and C. reighardi, and the smaller body parts of C. hoyi, in comparison to the Great Lakes populations, are all consistent to being

non-genetic. The differences in lateral line scales could result from their small size at maturity; and the morphometric differences from variations in growth rates.

Reproductive Isolation of the Three Species

The accepted criterion for "good species" is reproductive isolation (Mayr, 1963). Hybrids between coregonid species occur in N. America, but little is known of their fertility. Massive introgression between species occurred in Scandinavia (Svardson, 1949) suggesting hybrids can be fertile and viable.

The time and place of spawning is known for C. artedii in Big Athapap, but not for the other two species, though gonadal state suggested that they were also autumn spawners. Among the spawning C. artedii were one spent female and three ripe male C. hoyi, indicating that, perhaps, there is no chronological or spatial barrier to hybridization between these two species in Big Athapap. The presence of one morphologically intermediate fish in the discriminant analysis suggests hybridization does occur.

If hybridization does occur, the gene pools of C. artedii and C. hoyi may be introgressing. The two species are morphologically more similar in Big Athapap than they are in Little Athapap (see Fig. 16b.), Mink Narrows, or the Great Lakes and L. Nipigon. In Little Athapap and Mink Narrows C. artedii had the typical tullibee phenotype and was restricted to shallow water, so the morphological similarity of the species in Big Athapap could be non-genetic, although the more similar distribution

in Big Athapap could also be interpreted as evidence for introgression.

The Big Athapap records of C. hoyi and of C. reighardi are their most north-westerly known occurrence. Their gonad condition suggested autumn spawning. In the Great Lakes and L. Nipigon C. hoyi and C. r. reighardi are spring or early summer spawners, but C. r. dymondi is an autumn spawner. L. Michigan C. r. reighardi is now reported to be an autumn spawner (Smith, 1964). It is known that further north a greater proportion of the fish species are autumn spawners. The difference in spawning time between these two Big Athapap species and their Great Lakes and L. Nipigon relations could have resulted from environmental pressures favoring autumn spawning. If C. hoyi and C. reighardi do spawn at a different time in Big Athapap than in the Great Lakes and L. Nipigon, time of spawning should join the ranks of known plastic characters that have been employed in coregonid taxonomy.

Ecology of the Three Species

The three Big Athapap species have niches differing in vertical distribution. C. artedii was the most pelagic, and C. reighardi the most benthic, occurring mainly below 100'. C. hoyi was found mainly on the bottom in shallow water, but with increasing water depth it became more pelagic. This change in distribution could result from restriction to water shallower than 100', or exclusion from the benthic niche in deeper water by C. reighardi. The three species have a similar vertical distribution in the Great Lakes and L. Nipigon, but C. hoyi is more widespread, occurring down to 600' in L. Huron (Koelz, 1929). C. r. dymondi,

unlike C. r. reighardi, is found in shallow water (Koelz, 1929).

Interspecific differences in feeding appear to be correlated to depth distribution in L. Ontario (Pritchard, 1931). Mysis was the predominant food of all four cisco species in deep water, but where C. artedii occurred in shallow water it ate more adult insects and plankton. With the apparent exception that only C. reighardi ate Mysis in Big Athapap, all other feeding differences between the species can be explained as resulting from their different vertical distributions. When the surface and bottom feeding of C. artedii and C. hoyi were examined separately, the only significant difference occurred in the surface sets where C. hoyi ate more plankton and fewer adult insects than C. artedii. But in surface sets 50% of C. hoyi were caught in the bottom one-third of the net in comparison to 26% of C. artedii.

Feeding, Growth Rate, Gillrakers and Teeth

Coregonids feeding on benthos have faster growth rates (Svardson, 1952). Although whitefish do generally grow faster than ciscoes, this relationship did not apply within the Athapap ciscoes, for C. reighardi is the most benthic cisco and had the slowest growth rate.

N. American ciscoes usually have more gillrakers and feed on more plankton than do whitefish, but plankton feeding apparently is restricted to three species. Of two sympatric species of whitefish in Sweden, the one with fewer gillrakers had eaten plankton, whereas the other had eaten only benthos (Svardson, 1950). In L. Ontario C. artedii had most gillrakers and ate least benthos (Pritchard, 1931). Of the Athapap

ciscoes C. reighardi had fewest gillrakers and ate no plankton. However C. artedii fed on less plankton than C. hoyi, although it had more gillrakers. Gross differences in gillraker numbers do appear to be correlated to dietic differences, but no such correlation exists between species with almost identical gillraker counts.

In Big Athapap the occurrence of teeth in the three species can be correlated to diet. C. reighardi ate the highest proportion of benthic food and had the best developed teeth. C. artedii ate least benthos and had the weakest dentition.

Distribution of the Three Species

Manitoba had five recorded species of ciscoes including C. artedii and C. hoyi. The Big Athapap record of C. hoyi is its most north-westerly known occurrence, but C. artedii is known from further to the north-west. C. reighardi was known previously from the Great Lakes and L. Nipigon, but the Big Athapap population certainly is phenotypically closest to C. r. reighardi. The species most similar to C. reighardi is C. zenithicus, which occurs in L. Winnipeg and the L. Athabasca area, as well as in the Great Lakes and L. Nipigon.

Several hypotheses can explain the distribution of C. reighardi:

- a) the populations in northern Manitoba are relict populations; b) C. reighardi is present but undiscovered between northern Manitoba and the Great Lakes and L. Nipigon; c) C. reighardi and/or C. zenithicus have been misidentified outside of the Great Lakes and L. Nipigon; d) C. reighardi and C. zenithicus are the same species.

Taxonomic Speculation

Although phenotypic similarity is not necessarily correlated to closeness of descent, the phenotypic similarity of C. zenithicus to C. reighardi, C. artedii to C. nigripinnis, and C. hoyi to C. kiyi (see Table VII) does suggest that the members of these pairs may be more closely related to each other than they are to the members of the other pairs. C. alpenae in L. Erie (Scott and Smith, 1962) is intermediate in several characters between C. alpenae and C. johanna from L. Huron and L. Michigan, suggesting that these species may form another pair.

There is additional evidence for two of these pairings. The occurrence of C. zenithicus in L. Winnipeg and from the L. Athabasca area, and the presence of C. reighardi in the intervening area of northern Manitoba can be interpreted as evidence for the common ancestry of the two species. Booke (1968) judged "nearness-of-relationship" of coregonid genera on the percentage of guanine plus cytosine in DNA. If this is extended to species of ciscoes, C. hoyi and C. kiyi are more closely related to each other than to the other ciscoes that he analyzed, but on this basis alone C. reighardi would be more closely related to C. artedii than to C. zenithicus.

The members of each pair occur sympatrically, but neither their distribution within a lake, nor their time and place of spawning are identical (Koelz, 1929). Differences in time and place of spawning can arise allopatrically or sympatrically (Frost, 1965), and if the differences are maintained by imprinting (Frost, 1965) there need not be any genetic differences between the paired species (although such imprinting behaviour

relationships of C. nipigon and C. hubbsi (members of the C. artedii-
C. nigripinnis complex?), of C. bartletti (C. johannae-C. alpense?), and
of C. nigripinnis cyanopterus and C. n. prognathus.

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