THE POSTGLACIAL DISPERSAL OF FRESHWATER FISHES IN NORTHERN NORTH AMERICA

by

J. D. McPhail

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfilment of the requirements for the degree of Doctor of Philosophy.

Department of Zoology,
McGill University,
Montreal.

March 1963

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

ACKNOWLEDGEMENTS

The author is indebted to the Arctic Institute of North America for two Grants-in-aid of research, and to the National Research Council for two studentships. Without this financial support the present study would not have been possible.

The author particularly acknowledges the assistance of Dr. C. C. Lindsey and Mr. D. R. Miller in the field work. The co-operation and hospitality of numerous members of the Fisheries Research Board of Canada, the Alaska Department of Fisheries, the Fisheries Research Institute, and the U.S. Fish and Wildlife Service is also gratefully acknowledged.

The following persons and Institutions generously made available their collections: Dr. R. M. Bailey, University of Michigan; Dr. C. C. Lindsey, University of British Columbia; Mr. D. E. McAllister, National Museum of Canada; Dr. W. B. Scott, Royal Ontario Museum; Dr. L. P. Schultz, U.S. National Museum.

Dr. M. J. Dunbar directed the research, and Mr. J. W. Pollock did the photography.

INTRODUCTION

Glaciated areas offer a unique opportunity to study the dispersal of animals. During glaciation the fauna of glaciated areas was either destroyed or forced into unglaciated refugia. When the icesheets retreated the glaciated regions were open to reinvasion.

Northern North America is particularly well suited to a study of the postglacial dispersal of freshwater fishes. During the last (Wisconsin[1]) glaciation the freshwater fish fauna of northern North America was confined to a few widely separated refugia around the periphery of the icesheets. The following study outlines the present distribution of freshwater fishes in northern North America and attempts to determine the glacial refugia and postglacial dispersal routes used by these species.

Several previous authors discuss postglacial dispersal in parts of northern North America. Wynne-Edwards (1947) derives the freshwater fishes of the Yukon Territory from the Bering Sea region, the Pacific slope, and the Mississippi Valley. Walters (1955) indicates that the fauna of western arctic America is derived from the Yukon Valley, the arctic slope of Alaska, the Pacific slope, and the Mississippi Valley. Lindsey (1956) suggests that fishes in the Mackenzie drainages of British Columbia originated in Alaska, the unglaciated Pacific slope south of the icesheet, and the Mississippi system. Other authors

1 The Wisconsin glaciation here includes the Valders and Cochrane advances.

(Radforth, 1944; Underhill, 1957, and Hubbs and Lagler, 1958) discuss possible glacial refugia for some of the species occurring in northern North America.

The above authors agree that the freshwater fish fauna of glaciated North America is derived from several refugia. They also agree that the main refugia were the Bering region, the unglaciated Pacific slope, the Mississippi Valley, and the Atlantic Coastal Plain (Fig. 1). However, they do not agree on the refugia used by particular species. An example, to illustrate divergence of opinion, is the ninespine stickleback, *Pungitius pungitius*. Several authors discuss possible glacial refugia and postglacial dispersal routes for this species. Radforth (1944) suggests that *Pungitius* survived glaciation in Alaska, and dispersed postglacially from this region. This opinion is based on the absence of *Pungitius* from the upper Mississippi Valley. Walters (1955) postulates two glacial refugia for *Pungitius*: the Bering Refugium, and the upper Mississippi Valley. Walters' hypothesis is based on the presence of *Pungitius* above rapids on the Slave River at Fort Smith. Underhill (1957) postulates the survival of *Pungitius* in some eastern North American refugium, and postglacial dispersal through the eastern outlets of Lake Agassiz. Underhill's suggestion is based on the existence of eastern outlets from Lake Agassiz, and the absence of *Pungitius* from the upper Mississippi Valley.

These conflicting suggestions are all based on

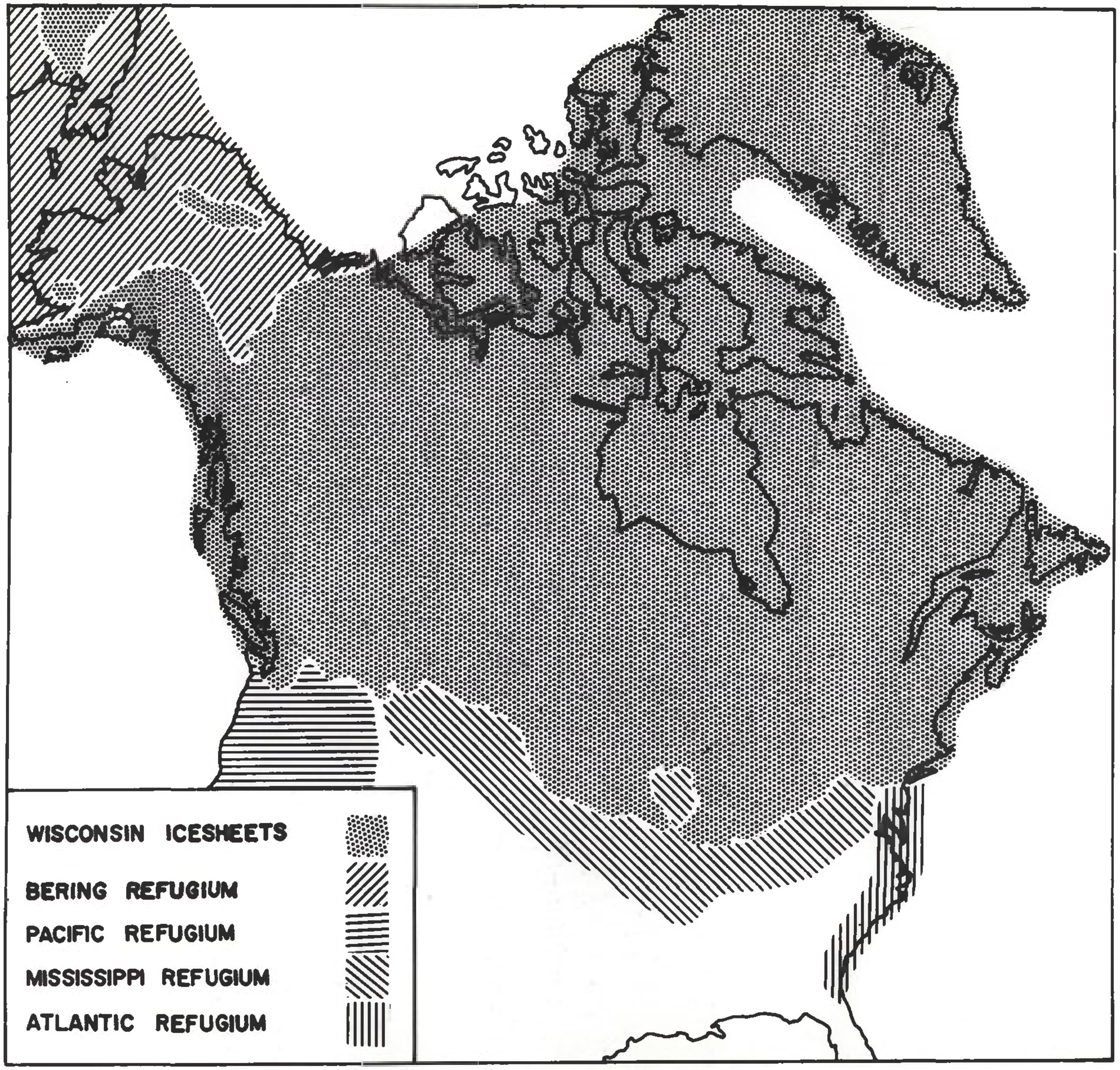


Fig. 1. Unglaciated refugia with the Wisconsin icesheets at their maxima.

details of present distribution. Details of present distribution offer valuable zoogeographic clues, but they must be interpreted with caution. Neither distribution nor topography are static. Absence from a particular unglaciated area does not exclude this area as a refugium (particularly if the species is present in adjacent glaciated areas), and present topographic barriers may not have functioned as barriers in the past. In the case of *Pungitius*, Radforth (1944) and Underhill (1957) object to the upper Mississippi Valley as a refugium for *Pungitius* because this species is now absent from the area. However, *Pungitius* is present in all of the Great Lakes except Lake Erie, and the absence of *Pungitius* from the upper Mississippi Valley may be due to postglacial ecological changes and does not preclude this area as a possible refugium.

Walters (1955) suggests two refugia because *Pungitius* is present above impassable rapids on the Slave River. The supposition is that Alaskan *Pungitius* could not disperse beyond this barrier, and therefore the *Pungitius* above the rapids dispersed downstream from a southern refugium. However, Craig (1960) indicates that the postglacial Slave River flowed south until isostatic readjustment established the present northward drainage. Therefore, the occurrence of *Pungitius* above the present barrier does not necessitate a southern refugium.

In the present study two methods are used to determine refugia: analysis of intraspecific variation, and analysis of distribution patterns. Where possible fossil evidence is included, but accurately dated late Pleistocene fossils are rare.

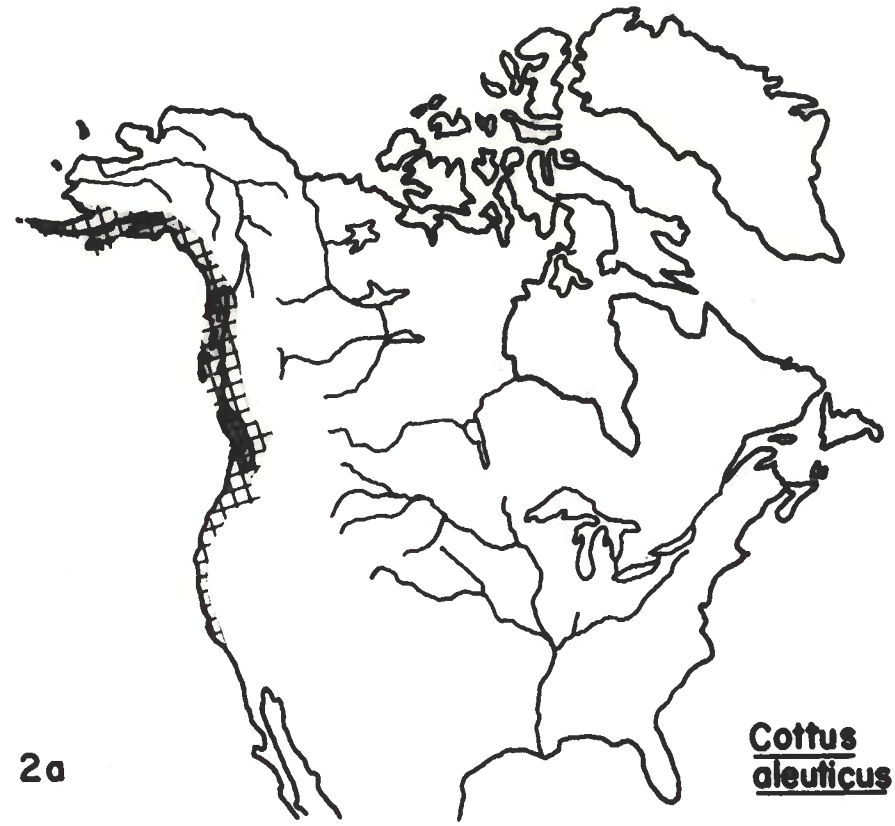
The first method (analysis of intraspecific variation) is used for species whose ranges include a number of possible refugia. This technique is based on the concept that geographic isolation for long periods of time produces morphological differentiation (Mayr, 1942), and therefore, species isolated in multiple refugia during glaciation probably evolved different genotypes in different refugia. Recent studies (McPhail, 1961, 1963; McAllister and Lindsey, 1961) indicate the existence of allopatric, morphologically different forms in several wide ranging species of fish in North America. These forms are interpreted as evidence of isolation in more than one refugium. An objection to this interpretation is that the differences between forms may be phenotypic, and not necessarily a product of isolation as such. Whether different forms are genotypic or phenotypic can only be proven experimentally. In the present discussion allopatric forms of a single species are considered genotypic if they remain relatively constant over wide geographic and climatic areas, and if they intergrade only within a narrow zone of contact.

The second method (analysis of distribution patterns) is most appropriate for endemic North American species with restricted northern distributions. Among such species two distribution patterns in particular are considered significant

(Fig. 2). Figure 2a illustrates the distribution pattern typical of species endemic to western North America. Although species with this pattern often occur in both the Pacific and the Bering Refugia they probably survived glaciation only in the Pacific Refugium. The Bering Refugium included the northeastern tip of Siberia, and it is unlikely that any species now restricted to North America survived glaciation in the Bering Refugium.

Figure 2b illustrates the distribution pattern typical of species endemic to central North America. Species with this pattern probably survived glaciation in the Mississippi Refugium. Some of these species also have restricted distributions within the Atlantic Refugium. Bailey (1945) indicates that the restricted Atlantic distributions of such species are probably due to postglacial dispersal from the Mississippi Refugium.

Throughout this discussion northern North America refers to Alaska, the Yukon Territory, the Northwest Territories, and those parts of British Columbia, Alberta and Saskatchewan draining into these regions (Fig. 3). The Labrador-Ungava Peninsula is omitted from the discussion because that area is poorly collected.



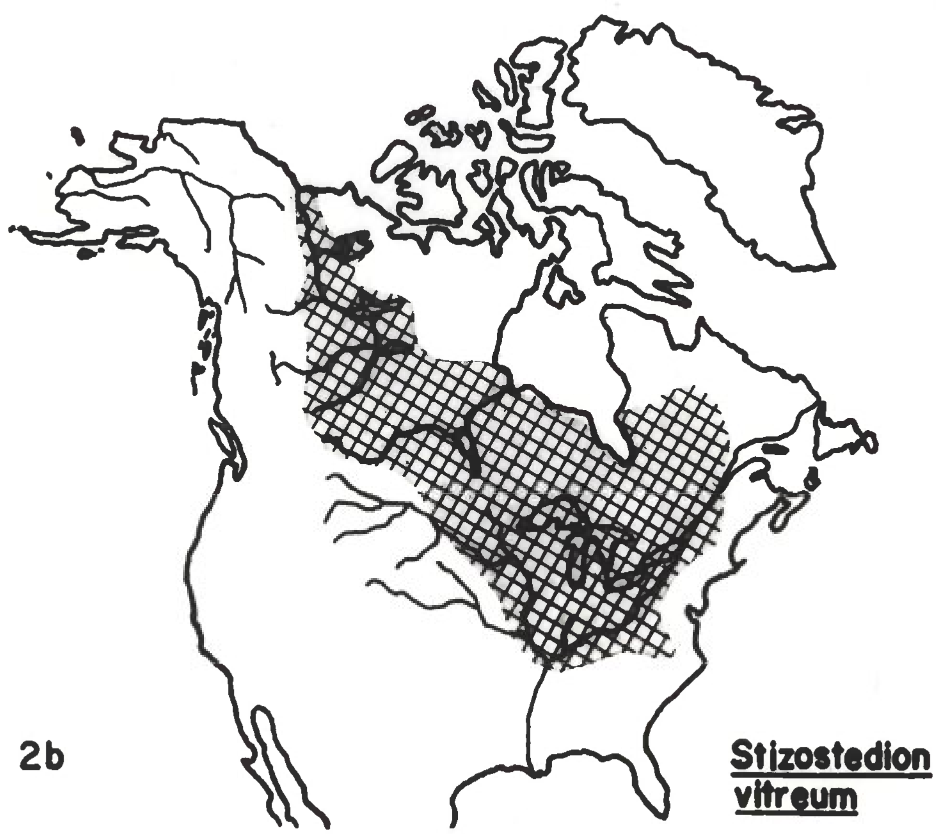


Fig. 2. Distribution patterns that suggest survival in the Pacific Refugium (a), and the Mississippi Refugium (b).

MATERIALS AND METHODS

The following study is based on over 8,000 specimens of 50 species from 542 localities throughout northern North America. Most of this material was collected by the author and Dr. C. C. Lindsey during the summers of 1957 to 1961. These collections were supplemented with material from the following institutions: the National Museum of Canada, the U.S. National Museum, the Royal Ontario Museum, the Museum of Zoology of the University of Michigan, Stanford Museum of Natural History, the Museum of the Institute of Fisheries at the University of British Columbia, and uncatalogued collections in the Arctic Unit of the Fisheries Research Board of Canada. Most of the material collected by the author is now deposited in the Museum of the Institute of Fisheries.

Only species spawning in fresh water and native to northern North America are considered. These species are listed below. Two genera of salmonid fishes are not included. These are Oncorhynchus and Coregonus (including Leucichthys, but not Prosopium). Oncorhynchus is omitted because of lack of adequate samples, and Coregonus because of the confused taxonomic state of the genus. With a few exceptions the scientific nomenclature follows Hubbs and Lagler (1958), and the common names are those recommended in the common names list of the American Fisheries Society (Bailey et al., 1960).

Entosphenus lamottenii (Le Sueur) - Brook lamprey.

Entosphenus tridentatus (Gairdner) - Pacific lamprey.

Lampetra ayresii (Gunther) - River lamprey.

Acipenser medirostris Ayres - Green sturgeon.

Acipenser transmontanus Richardson - White sturgeon.

Hiodon alosoides (Rafinesque) - Goldeye.

Prosopium coulteri (Eigenmann and Eigenmann) - Pygmy whitefish.

Prosopium cylindraceum (Pallas) - Round whitefish.

Prosopium williamsoni (Girard) - Mountain whitefish.

Stenodus leucichthys (Güldenstadt) - Inconnu.

Salmo clarki Richardson - Cutthroat trout.

Salmo gairdnerii Richardson - Rainbow trout.

Salvelinus alpinus (Linnaeus) - Arctic char.

Salvelinus malma (Walbaum) - Dolly Varden.

Salvelinus namaycush (Walbaum) - Lake trout.

Thymallus arcticus (Pallas) - Arctic grayling.

Hypomesus olidus (Pallas) - Pond smelt.

Osmerus eperlanus Linnaeus - Boreal smelt.

Spirinchus thaleichthys (Ayres) - Longfin smelt.

Thaleichthys pacificus (Richardson) - Eulachon.

Catostomus catostomus (Forster) - Longnose sucker.

Catostomus commersonii (Lacépède) - White sucker.

Catostomus macrocheilus Girard - Largescale sucker.

Chrosomus eos Cope - Northern redbelly dace.

Chrosomus neogaeus (Cope) - Finescale dace.

Hybognathus hankonsoni Hubbs - Brassy minnow.

Hybopsis gracilis (Richardson) - Flathead chub.

Hybopsis plumbea (Agassiz) - Lake chub.

Mylocheilus caurinus (Richardson) - Peamouth.

Notropis atherinoides Rafinesque - Emerald shiner.

Notropis hudsonius (Clinton) - Spottail shiner.

Pimephales promelas Rafinesque - Fathead minnow.

Ptychocheilus oregonense (Richardson) - Northern sqawfish.

Rhinichthys cataractae (Valenciennes) - Longnose dace.

Richardsonius balteatus (Richardson) - Redside shiner.

Semotilus margarita (Cope) - Pearl dace.

Dallia pectoralis Bean - Alaska blackfish.

Esox lucius Linnaeus - Northern pike.

Lota lota (Linnaeus) - Burbot.

Culea inconstans (Kirtland) - Brook stickleback.

Gasterosteus aculeatus Linnaeus - Threespine stickleback.

Pungitius pungitius (Linnaeus) - Ninespine stickleback.

Percopsis omiscomaycus (Walbaum) - Trout-perch.

Perca flavescens (Mitchill) - Yellow perch.

Stizostedion vitreum (Mitchill) - Walleye.

Cottus aleuticus Gilbert - Coastrange sculpin.

Cottus asper Richardson - Prickly sculpin.

Cottus cognatus Richardson - Slimy sculpin.

Cottus ricei (Nelson) - Spoonhead sculpin.

Myoxocephalus quadricornis (Linnaeus) - Fourhorn sculpin.

Appendix I lists northern localities from which material was examined. The numbers preceding the localities are referred to in the "results" section of the text. Not all localities are plotted as separate symbols on the distribution maps. Where a number of localities lie close together a single symbol is plotted. The insets in the distribution maps present the distribution patterns of the species discussed. The darkened areas on the inset maps outline total known distribution, but do not necessarily imply that the species are continuously distributed within these areas.

Appendix II lists publications containing literature records for localities in northern North America from which the author has not examined specimens. The numbers preceding each entry are referred to in the "results" section of the text.

Morphological comparisons were made on the following species:

Entosphenus lamottenii

Prosopium coulteri

Prosopium cylindraceum

Salvelinus alpinus[2]

Salvelinus malma[2]

Osmerus eperlanus

Catostomus catostomus

Hybopsis plumbea

Esox lucius

Lota lota

Pungitius pungitius[2]

Myoxocephalus quadricornis

2 Intraspecific morphological comparisons of *S. alpinus*, *S. malma*, and *P. pungitius* have been published previously (McPhail 1961, 1963).

The following counts and measurements were used:

Myotomes - myotomes in lampreys were counted between the last gill opening and the anus.

Scales around the caudal peduncle - the number of scale rows crossing a line around the least depth of the caudal peduncle were counted.

Vertebrae - all vertebral counts were made from radiographs taken by the author. The counts include all elements separated by sutures. In Cyprinids the Weberian apparatus was counted as four vertebrae.

Pyloric caeca - all tips were counted as separate caeca.

Velar tentacles - all tips were counted as separate tentacles. Velar tentacle counts were made under a binocular microscope.

Gill rakers - gill rakers were counted only on the first arch, and all rudimentary rakers were included. Gill raker counts were made under a binocular microscope.

Teeth - all points in lampreys were counted as separate teeth. Tooth nomenclature follows Vladykov (1949).

Total length - used only in lampreys. The length from the tip of the oral fimbriae to the end of the caudal fin.

Standard length - measured from the anterior tip of the snout to the base of the caudal fin (as indicated by the caudal flexure).

Preopercular spine length - measured only on *Myoxocephalus quadricornis*: the distance between the tip of the upper preopercular spine and the apex of the angle formed by the junction of the upper and lower preopercular spines.

Specimens were collected by monofilament and braided-nylon variable-mesh gillnets, nylon seines, or emulsified rotenone. There is considerable variation in length composition and sex ratio between different collections of the same species. Therefore, all of the characters used in comparisons were tested for correlation with length, and for sexual dimorphism. Correlations were tested by the correlation coefficient, and sexual dimorphism by the "t-test". The results of these tests are presented in Appendices III and IV.

The significance of differences in single characters between allopatric forms of species were tested with the "t-test". The discriminant function analysis was used to combine three characters, and to test this combined difference between the two allopatric forms of *Prosopium cylindraceum*. The calculation of the discriminant function and the estimate of percentage error follow Stanley (1962).

The level of significance in all statistical tests is five per cent.

RESULTS

Entosphenus lamottenii (Le Sueur) - Brook lamprey.

Range - Europe, Asia and North America; the North American range is disjunct: Kenai Peninsula, Alaska, to Great Slave Lake, and from the Great Lakes south to Tennessee and Missouri, on the Atlantic coast from New Hampshire to Maryland (Fig. 4).

Northern records - Specimens examined: 55, 70, 72, 74, 84, 86, 92, 110, 112, 126, 146, 149, 159, 184, 189, 192, 210, 332, 334, 335, 374, 377, 420, 436, 442, 488, 524; literature records: 3, 40.

Glacial refugia - Hubbs and Lagler (1958) suggest the Arctic lamprey, E. japonicus, and the American Brook lamprey, E. lamottenii, are conspecific. In the present study adult specimens of E. japonicus, E. lamottenii, and E. tridentatus were compared. Table I indicates E. japonicus and E. lamottenii differ from E. tridentatus in the number and arrangement of teeth and velar tentacles. No morphological characters were found to separate E. japonicus and E. lamottenii. Therefore, E. japonicus is considered a synonym of E. lamottenii. However, the two forms are totally allopatric, and differ biologically. E. lamottenii is mainly non-parasitic, while E. japonicus is both parasitic and non-parasitic. The two forms may warrant sub-specific recognition, but this cannot be decided on the available evidence.

E. lamottenii is not widely distributed in glaciated areas. In North America the northern form is found mainly in unglaciated regions. The southern form is widely distributed

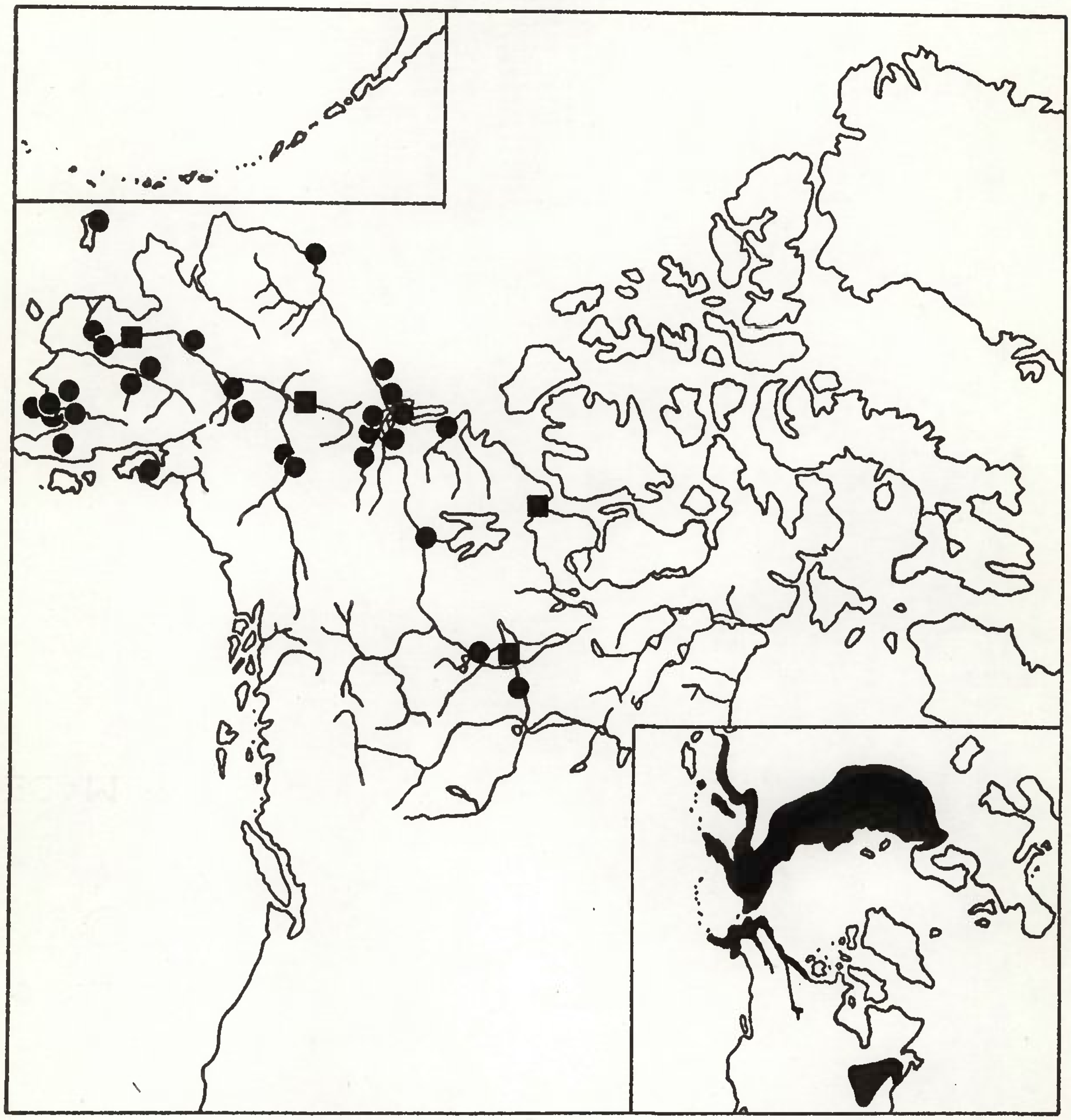


Fig. 4. Northern distribution of E. lamottenii (inset total distribution). Circles indicate specimens examined, and squares literature records.

Table I. Comparison of adult *Entosphenus lamottenii*, *E. japonicus*, and *E. tridentatus*.

	N	Velar tentacles range	Mean	Supraoral cusps	Infraoral cusps range	Mean
E. lamottenii						
Michigan	10	5-6	5.2	2	6-10	8.0
Ontario	30	5	5.0	2	6-10	8.0
E. japonicus						
Alaska	40	5-6	5.1	2	6-10	8.1
Mackenzie System	5	5-6	5.2	2	6-10	8.0
E. tridentatus						
British Columbia	30	13-16	14.2	3 (rarely 2)	5-6	5.3

in the unglaciated portions of the upper Mississippi and Ohio Valleys, but in glaciated areas it is restricted to the Great Lakes Basin and a few localities in the New England states. The distribution of the two forms of E. lamottenii suggest survival in two refugia: the northern form in the Bering Refugium, and the southern form in the Mississippi Refugium. Only the northern form occurs in northern North America.

Entosphenus tridentatus (Gairdner) - Pacific lamprey.

Range - Pacific drainages of Asia and North America. In North America from the Santa Ana River, southern California, to the Aleutian Islands (Fig. 5).

Northern records - Specimens seen: 45, 78, 160, 182, 213, 225; literature records: 11, 14, 29.

Glacial refugia - Creaser and Hubbs (1922) recognize two subspecies of Pacific lamprey in North America: E. t. tridentatus ranging from Unalaska to the Columbia system and characterized by 68 to 74 myotomes, and E. t. ciliatus ranging from the Klamath system to southern California and characterized by 57 to 67 myotomes. Mather (1926) notes that E. tridentatus from near Nanaimo, B.C., have low myotome counts. The number of myotomes in recently metamorphosed Pacific lampreys from the Chilcotin River, B.C., range from 58 to 72. These data show that the present division of E. tridentatus into subspecies on the basis of myotome counts is probably not valid.

The North American range of E. tridentatus includes one unglaciated area, the Pacific Refugium. Within this area

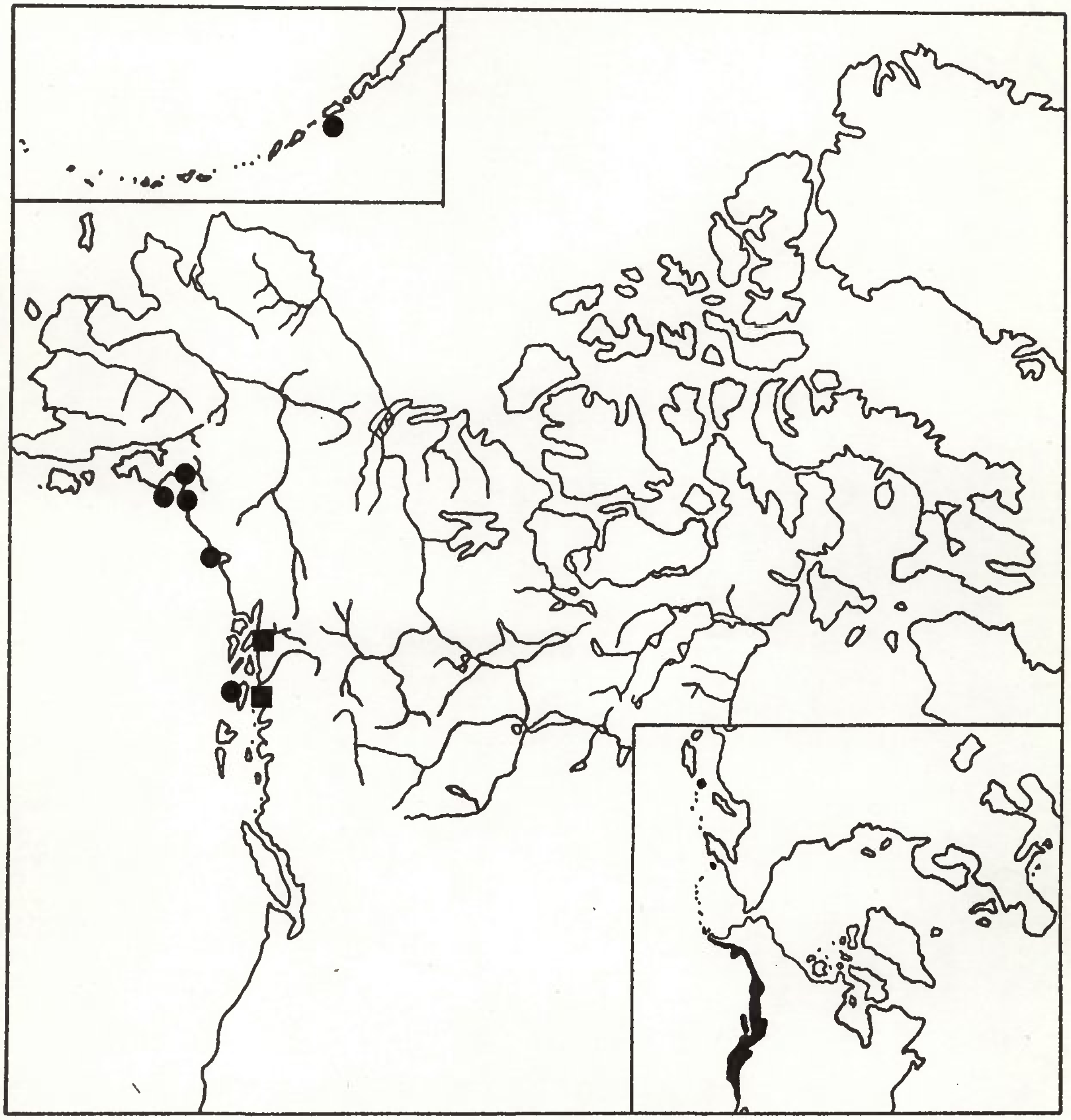


Fig. 5. Northern distribution of E. tridentatus (inset total distribution). Circles indicate specimens examined, and squares literature records.

there are dwarf, non-parasitic Pacific lampreys in Klamath Lake, Oregon, and Goose Lake, California (Hubbs and Miller, 1948). Both lakes are now isolated from the sea. Goose Lake has no outlet, and there is a waterfall on the outlet of Klamath Lake. Entospenus tridentatus must have entered the lakes before the formation of these barriers, and Hubbs and Miller suggest free passage between these lakes and the sea during the Wisconsin. This indicates that E. tridentatus was present in the Pacific Refugium during the Wisconsin.

Lampetra ayresii (Gunther) - River lamprey.

Range - Pacific Coast of North America: Sacramento River, California, to southeastern Alaska (Fig. 6).

Northern records - Specimens examined: 53, 165; no literature records.

Glacial refugia - The distribution pattern of L. ayresii (inset, Fig. 6) indicates survival in the Pacific Refugium.

Acipenser medirostris Ayres - Green sturgeon

Range - Pacific drainages of Asia and North America. In North America from Pt. Vincente, California, to the Copper River, Alaska (Fig. 7).

Northern records - Specimens examined: 190; literature records: 11.

Glacial refugia - The North American range of A. medirostris includes one unglaciated area, the Pacific Refugium. Sinclair (1904) reports Pleistocene fossil remains of A. medirostris from Samwell Cave, California. In North

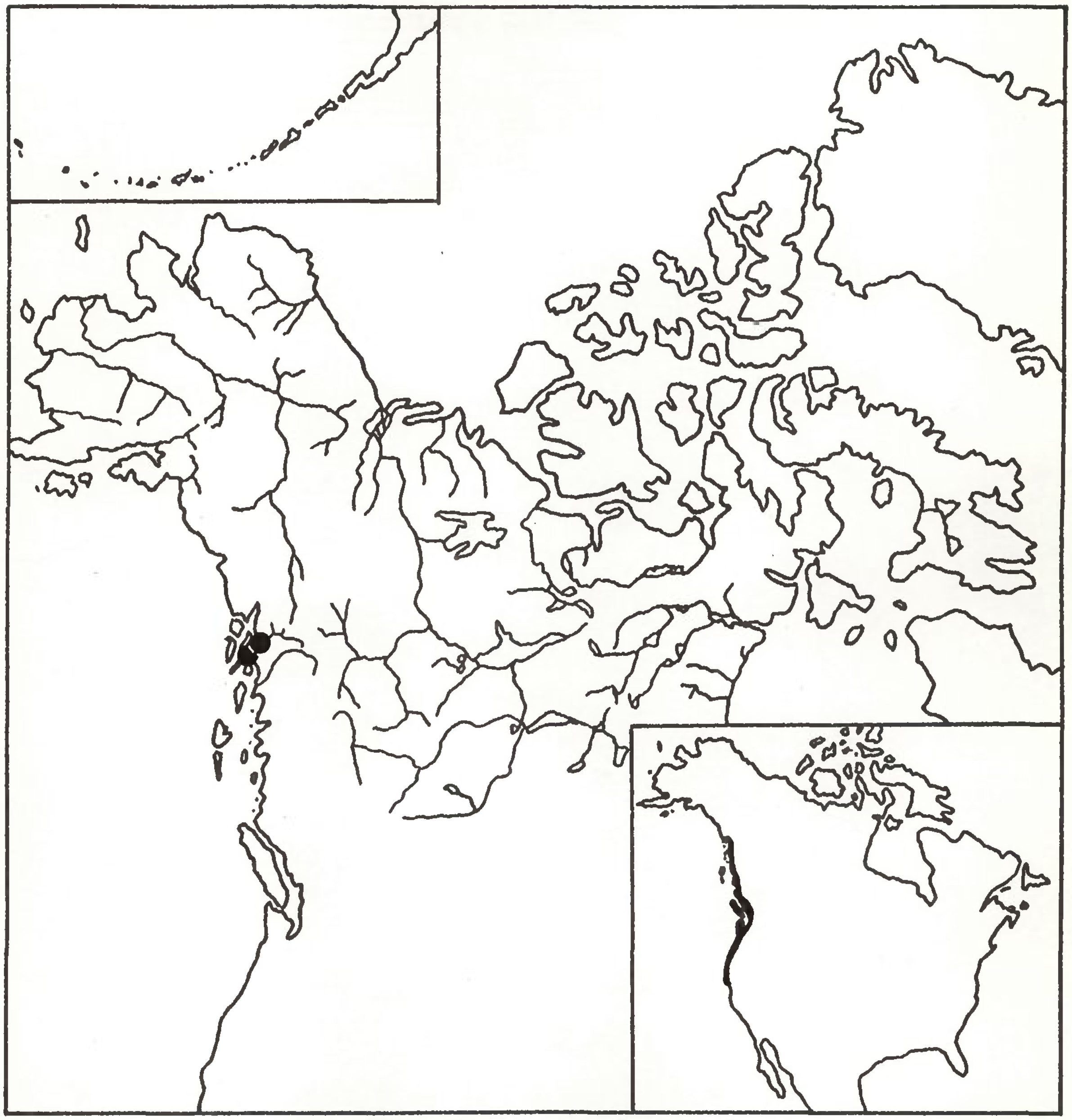


Fig. 6. Northern distribution of L. ayresii (inset total distribution). Circles indicate specimens examined, and squares literature records.

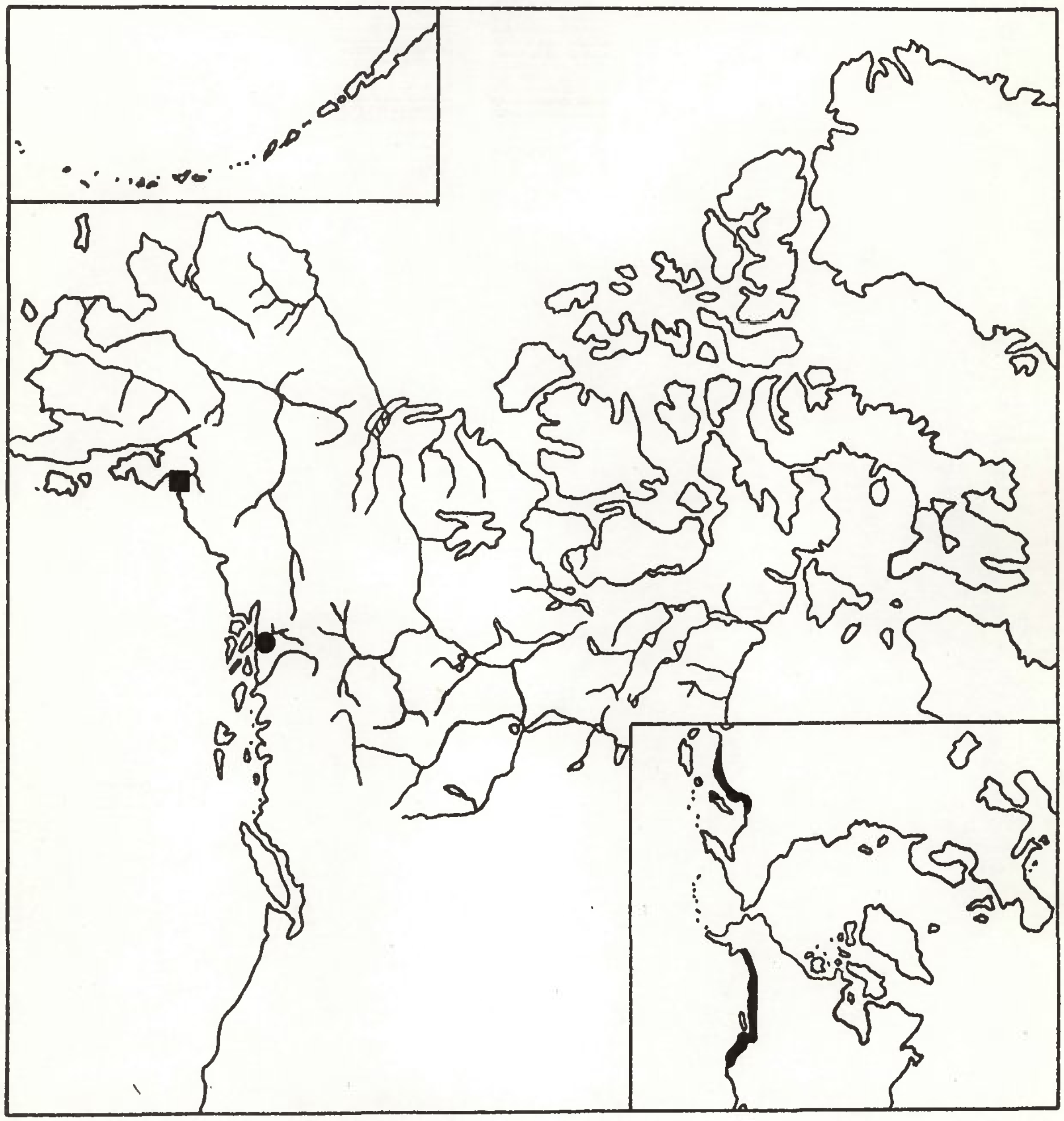


Fig. 7. Northern distribution of A. medirostris (inset total distribution). Circles indicate specimens examined, and squares literature records.

America the Green sturgeon probably survived the Wisconsin in the Pacific Refugium.

Acipenser transmontanus Richardson - White sturgeon.

Range - Pacific Coast of North America: Monterey, northern California, to the Taku River, Alaska (Fig. 8).

Northern records - Specimens examined: none; literature records: 26.

Glacial refugia - The distribution pattern of A. transmontanus (inset, Fig. 8) indicates survival in the Pacific Refugium.

Hiodon alosoides (Rafinesque) - Goldeye.

Range - Central North America; Mississippi River and tributaries from Louisiana north, and across the Great Plains to the Mackenzie system, absent from the Great Lakes (Fig. 9).

Northern records - Specimens examined: 239, 277, 377, 387, 471; literature records: 31, 37.

Glacial refugia - The distribution pattern of H. alosoides (inset, Fig. 9) indicates survival in the Mississippi Refugium.

Prosopium coulteri (Eigenmann and Eigenmann) - Pygmy whitefish.

Range - North America, distribution disjunct: mountain lakes and streams from Washington and Montana north to the Bristol Bay region, Alaska, and Lake Superior (Fig. 10).

Northern records - Specimens examined: 6, 26, 276,

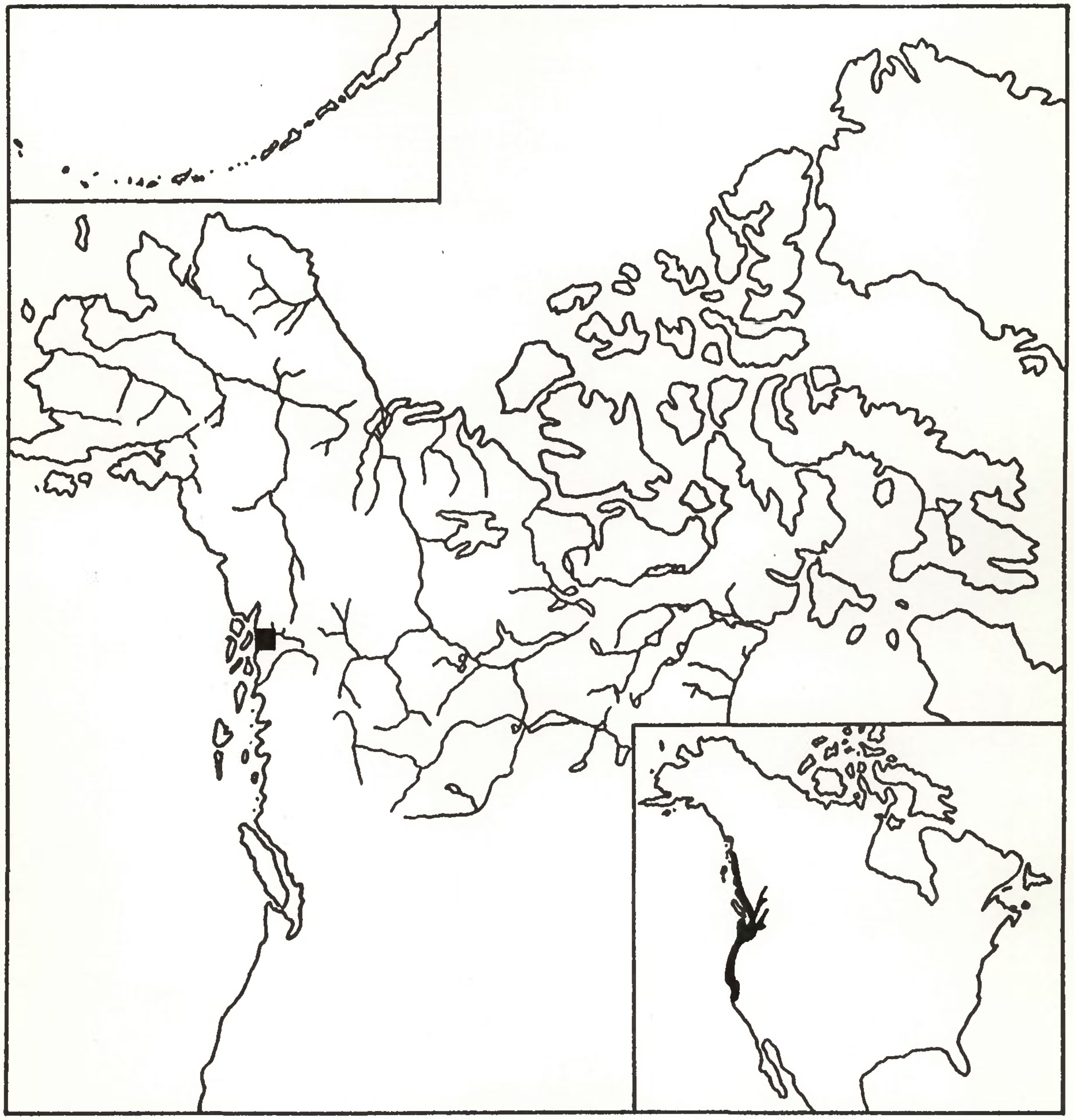


Fig. 8. Northern distribution of A. transmontanus (inset total distribution). Circles indicate specimens examined, and squares literature records.

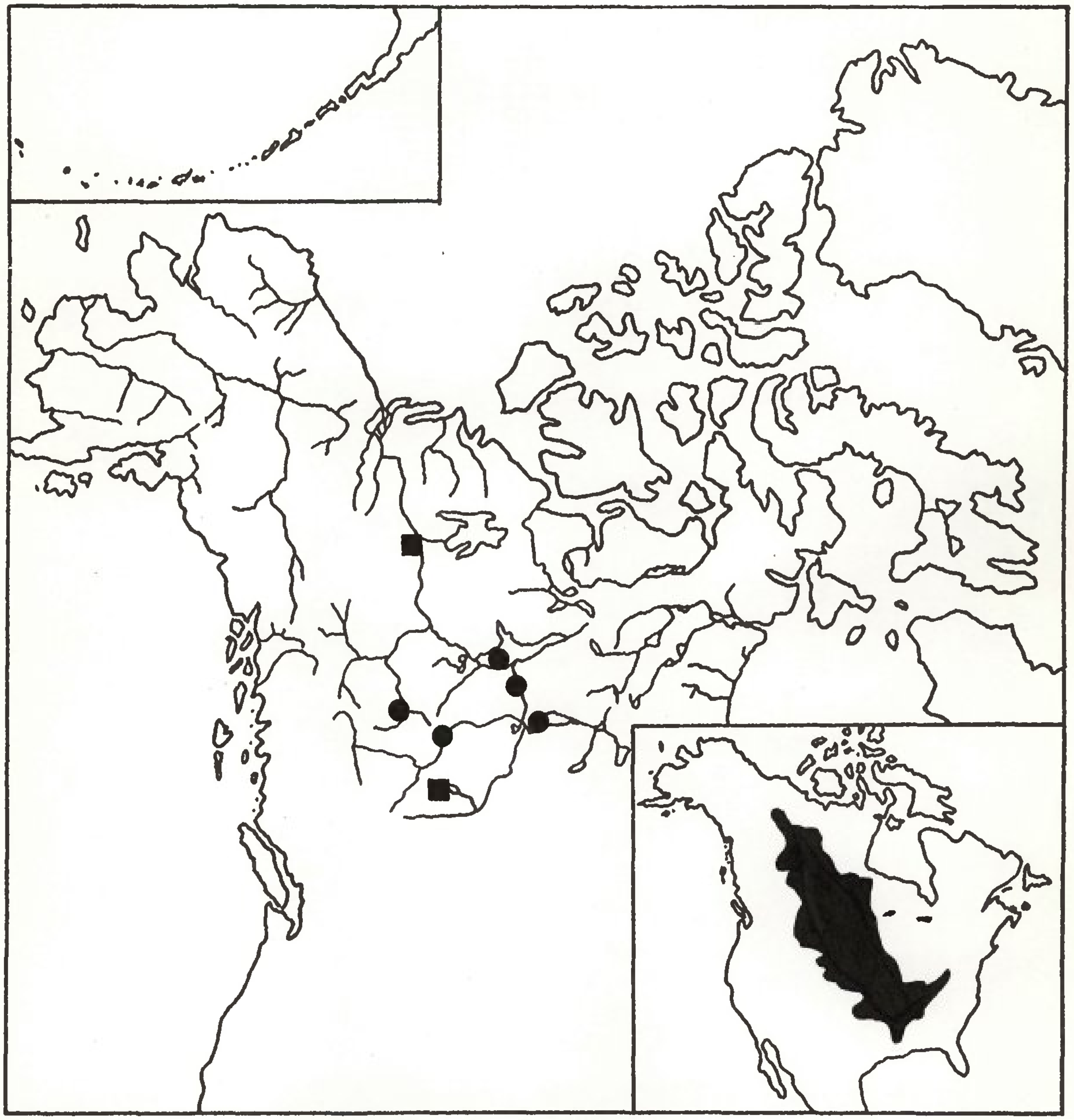


Fig. 9. Northern distribution of H. alosoides (inset total distribution). Circles indicate specimens examined, and squares literature records.

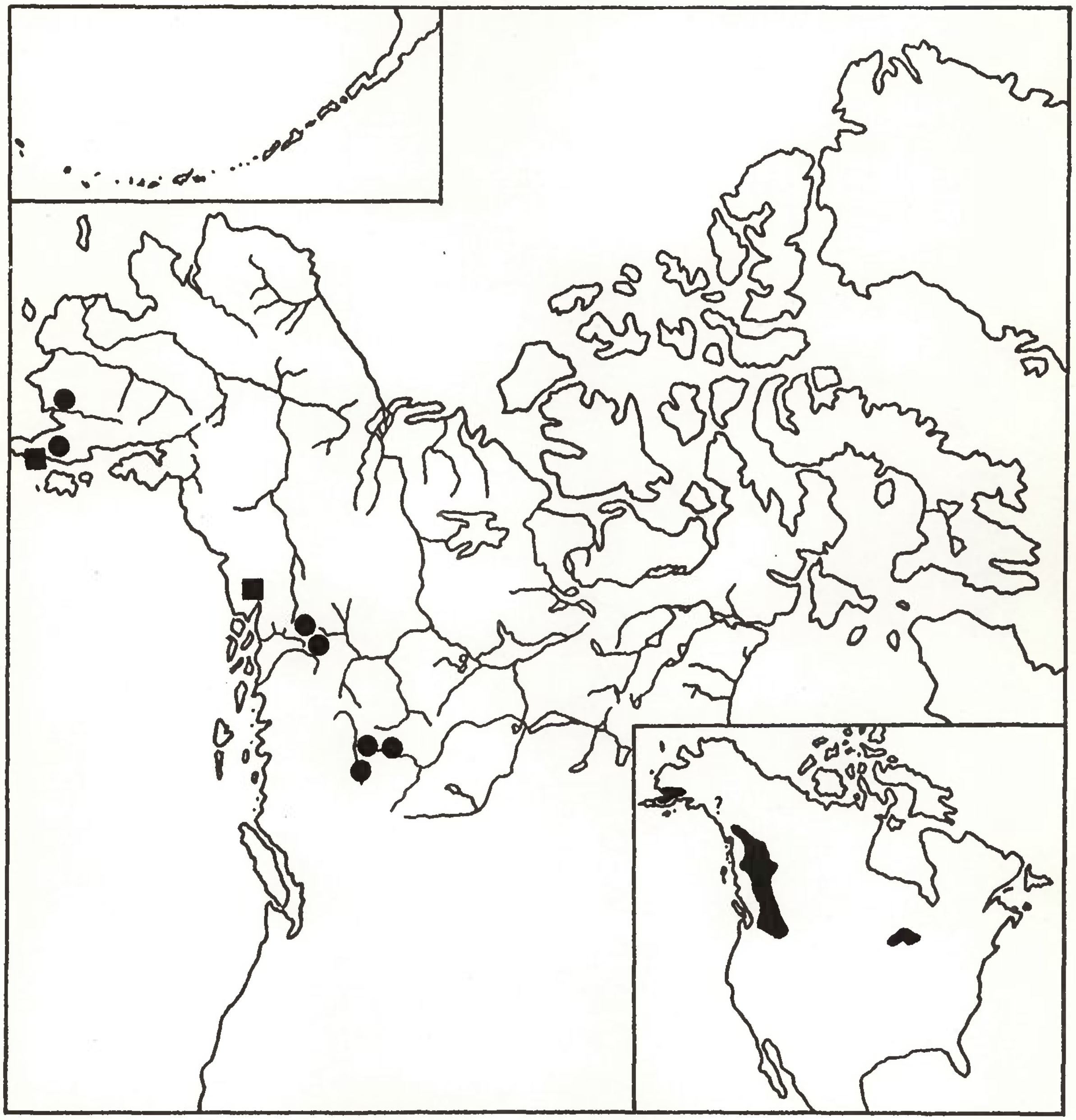


Fig. 10. Northern distribution of P. coulteri (inset total distribution). Circles indicate specimens examined, and squares literature records.

295, 306, 321, 323; literature records: 24, 54.

Glacial refugia - The present distribution of P. coulteri suggests survival in more than one refugium. Eschmeyer and Bailey (1955) compared Lake Superior P. coulteri with northwestern populations, and found that although P. coulteri was not morphologically homogeneous throughout its range the variation showed no consistent geographic pattern.

In the present study the number of gill rakers, pyloric caeca, vertebrae, and scales around the caudal peduncle were compared over the entire range of P. coulteri. In one character, scales around the caudal peduncle (Table II), the Lake Superior population was significantly different ($p < 0.001$) from all northwestern populations.

Within northwestern populations the number of scales around the caudal peduncle remains relatively constant over ten degrees of latitude, which suggests that the difference between the Lake Superior population and the northwestern populations is more than phenotypic. The Lake Superior population is probably the relict of a stock of P. coulteri that survived glaciation in the Mississippi Refugium. The northwestern populations probably survived in the Pacific Refugium, and dispersed north to Alaska postglacially.

Prosopium cylindraceum (Pallas) - Round whitefish.

Range - Asia and North America; in North America from the Taku River, Alaska and British Columbia, to the Great Lakes, and from Labrador to Connecticut (Fig. 11).

Northern records - Specimens examined: 6, 8, 18,

Table II. Geographic variation in the number of scales around the caudal peduncle in Prosopium coulteri.

Locality	Caudal peduncle scales 16	17	18	19	20	N	Mean
Lake Alecknagik	2	3	1		3#	9	17.9
Brooks Lake	1	4	3	2		10	17.6
Dease Lake	1	3	5	1		10	17.6
MacLure Lake	1		8	3	1	13	18.3
Cluculz Lake	1	1	4	1		7	17.7
Moose Lake	1	7	6	1		15	17.5
Liard Creek	1	3	4	2		10	17.7
Blaeberry River	1	3	8	3		15	17.8
Kicking Horse River		2	7	3		12	18.1
Bull Lake#		2	11	5	2	20	18.5
Lake Superior#			3	7	14	24	19.5

Data from Eschmeyer and Bailey (1955).

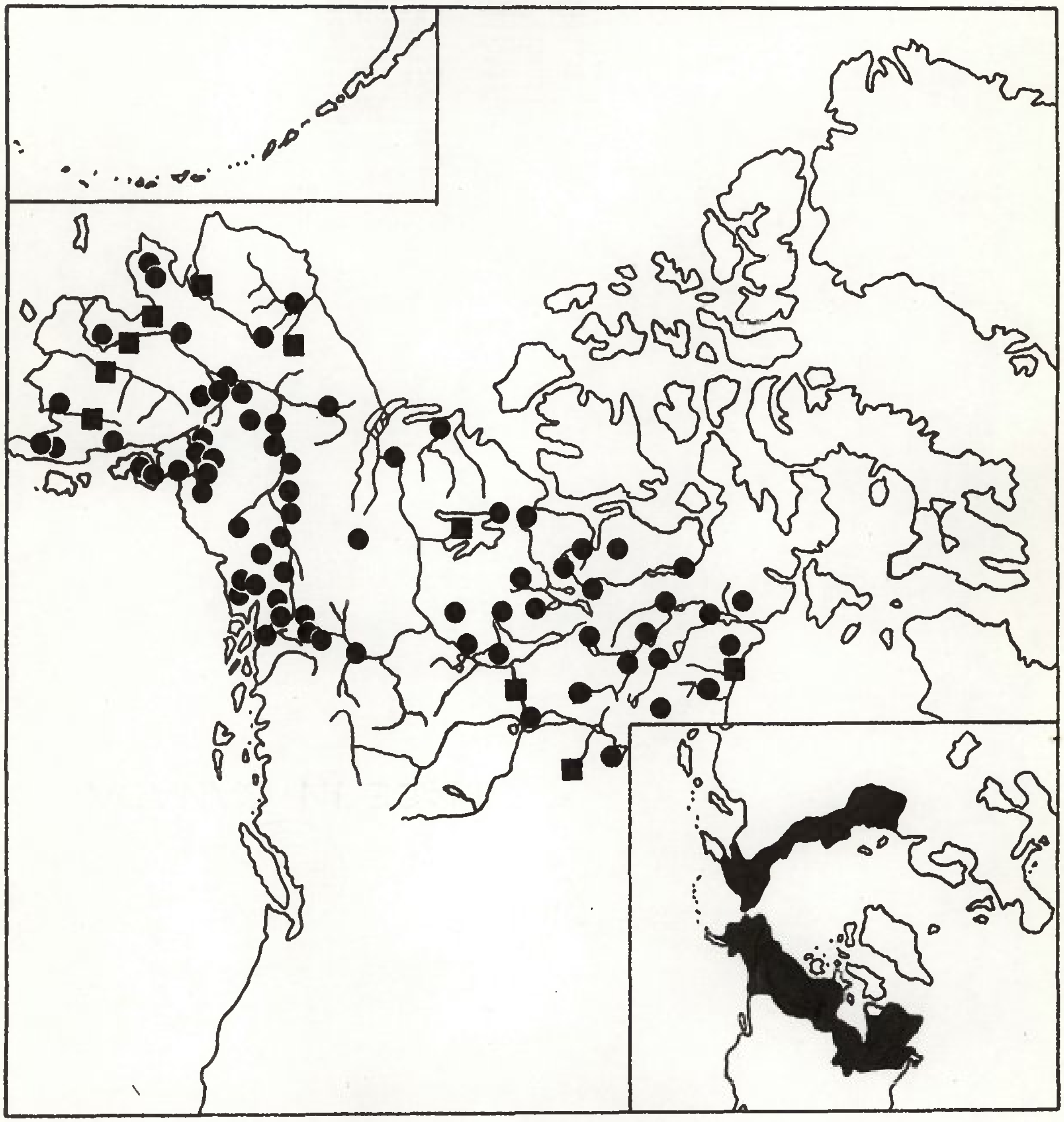


Fig. 11. Northern distribution of P. cylindraceum (inset total distribution). Circles indicate specimens examined, and squares literature records.

26, 30, 31, 35, 38, 41, 42, 44, 54, 67, 69, 79, 79a, 106, 113, 121, 126, 133, 135, 141, 145, 147, 155, 174, 183, 185, 191, 193, 196, 200, 215, 222, 267, 276, 281, 292, 293, 315, 321, 323a, 326, 335, 337, 341, 342, 343, 346, 350, 351, 358, 360, 362, 363, 367, 372, 385, 386, 402, 407, 414, 419, 423, 434, 441, 458, 462, 467, 471, 472, 474, 482, 483a, 490, 493, 494a, 498, 502, 509, 510, 516, 519, 524, 525; literature records: 6, 8, 25, 33, 36, 39, 46, 48, 51.

Glacial refugia - The North American distribution of P. cylindraceum (inset, Fig. 11) is almost disjunct, and suggests postglacial dispersal from two refugia. The number of gill rakers and pyloric caeca were compared over the North American range of the round whitefish (Tables III and IV).

Dymond (1943) suggests a cline in the number of gill rakers in P. cylindraceum across North America. Tables III and IV give no indication of a cline in either gill rakers or pyloric caeca; instead there is an abrupt change in both characters between northern populations and populations from Ontario and further south. The differences in gill rakers and pyloric caeca between these areas are significant ($p < 0.001$), and within each area both characters are relatively constant. Therefore, the differences are probably not phenotypic.

The distribution of the two forms of P. cylindraceum in North America (Fig. 12) suggests that the round whitefish survived glaciation in both the Bering and the Mississippi

Table III. Comparison of gill rakers in North American *Prosopium cylindraceum*.

Locality	14	15	16	17	18	19	20	21	N	Mean
Nome R.				3	3	3	1		10	18.2
Andreafsky R.				1	3	6	3	1	14	19.0
Summit L. (Copper System)				6	6	2	1		15	17.8
Kluane L.				2	6	2			10	18.0
Kathleen L.			2	2	7	3	1		15	17.9
Popcorn L.			3	6	8	6	4		27	18.0
Lac La Martre				1	2	3	2	2	10	19.0
Kathawachage L.				2	4	4	3	2	15	18.9
Beechy L.				3	6	2	2	1	14	18.0
MacDougall L.				1	4	4	3		12	18.7
Whitefish L.			2	4	5	5	2		18	18.1
Beverly L.				1	2	3	2	2	10	19.2
Maguse L.					3	5	3	1	12	19.1
Athabasca L.				2	4	3	2		11	18.1
Wollaston L.							3		3	20.0
Lake Opeongo	2	3	6	1	1				13	16.0
Lake Superior		2	5	4	1				12	16.4
Lake Michigan			2	3	2				7	17.0
Little Two Heart R.		3	5	5	1	1			15	16.4
Connecticut R.		2	4	4	2				12	16.5

Table IV. Comparison of pyloric caeca in North American <u>Prosopium cylindraceum</u>.

Locality	61-65	66-70	71-75	76-80	81-85	86-90	91-95	96-100	101-105	106-110	111-115	116-120	121-125	126-130	N	Mean
Nome R.				1		1	2	2		2		1			9	98.7
Summit L. (Copper System)					1	1	1	2	2		2		1		10	101.5
Kluane L.						3	2	2	1	1		1			10	94.6
Kathleen L.			1		1	3	2		1		2				10	95.8
Lac La Martre						1		1	3	1	1	1	1	1	10	105.8
Kathawachage L.						1		3	1	1	2	1	1	1	10	106.2
Beechy L.						1		3	3		1		2		10	104.1
MacDougall L.			1		1		2	4	1		1				10	97.3
Whitefish L.					1	1	1	3	2	1		1			10	98.5
Beverly L.					1	1		3	3	1			1		10	101.2
Maguse L.		1		1	1	1	2	1	2	1	2				12	94.1
Athabasca L.				1							1		1		3	102.9
Wollaston L.											1				1	
Lake Opeongo	2	3		3	2	2		1							13	78.7
Lake Superior	1	2		2											5	67.0
Lake Michigan				1	3										4	86.3
Little Two Heart R.	2	1	3		1	2									9	74.2
Connecticut R.		1	1		1	2									5	82.8

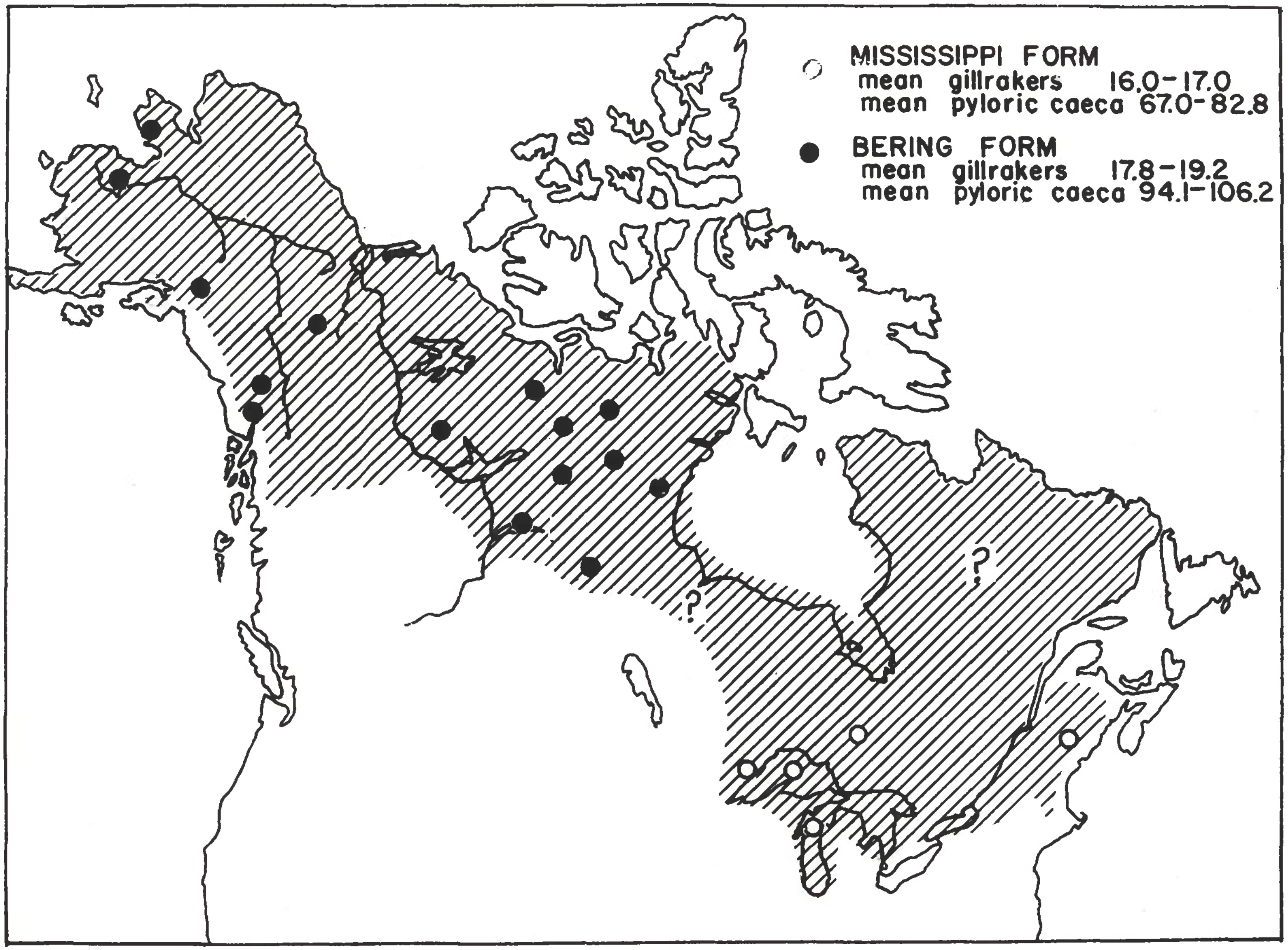


Fig. 12. Geographic variation in the number of gill rakers and pyloric caeca in *Prosopium cylindraceum*.

Refugia. Only the Bering form is present in northern North America.

<u>Prosopium</u> <u>williamsoni</u> (Girard) - Mountain whitefish.

Range - Western North America: Columbia system north to the Stikine River, and the east slope of the Rocky Mountains from the Missouri River north to the Liard River. Isolated populations in the Lahonton, Bonneville, and Colorado systems (Fig. 13).

Northern records - Specimens examined: 228, 247, 262, 266, 274, 277, 278, 284, 292, 293, 295, 302, 307, 308, 310, 316, 320, 327, 330; literature records: 31.

Glacial refugia - The distribution pattern of <u>P</u>. <u>williamsoni</u> (inset, Fig. 13) indicates survival in the Pacific Refugium. However, <u>P</u>. <u>williamsoni</u> also occurs in the Mississippi Refugium, but in this area it is restricted to the upper Missouri system. Holt (1960) compared mountain whitefish from the Columbia and Missouri systems, and found no consistent meristic differences. The restricted distribution of <u>P</u>. <u>williamsoni</u> in the upper Missouri system was probably attained by postglacial dispersal from the Columbia system.

<u>Stenodus</u> <u>leucichthys</u> (Güldenstadt) - Inconnu.

Range - Europe, Asia, and North America; isolated populations in Caspian Sea drainages. In North America from the Kuskokwim River, Alaska, to the Anderson River, N.W.T. (Fig. 14).

Northern records - Specimens examined: 4, 41, 55,

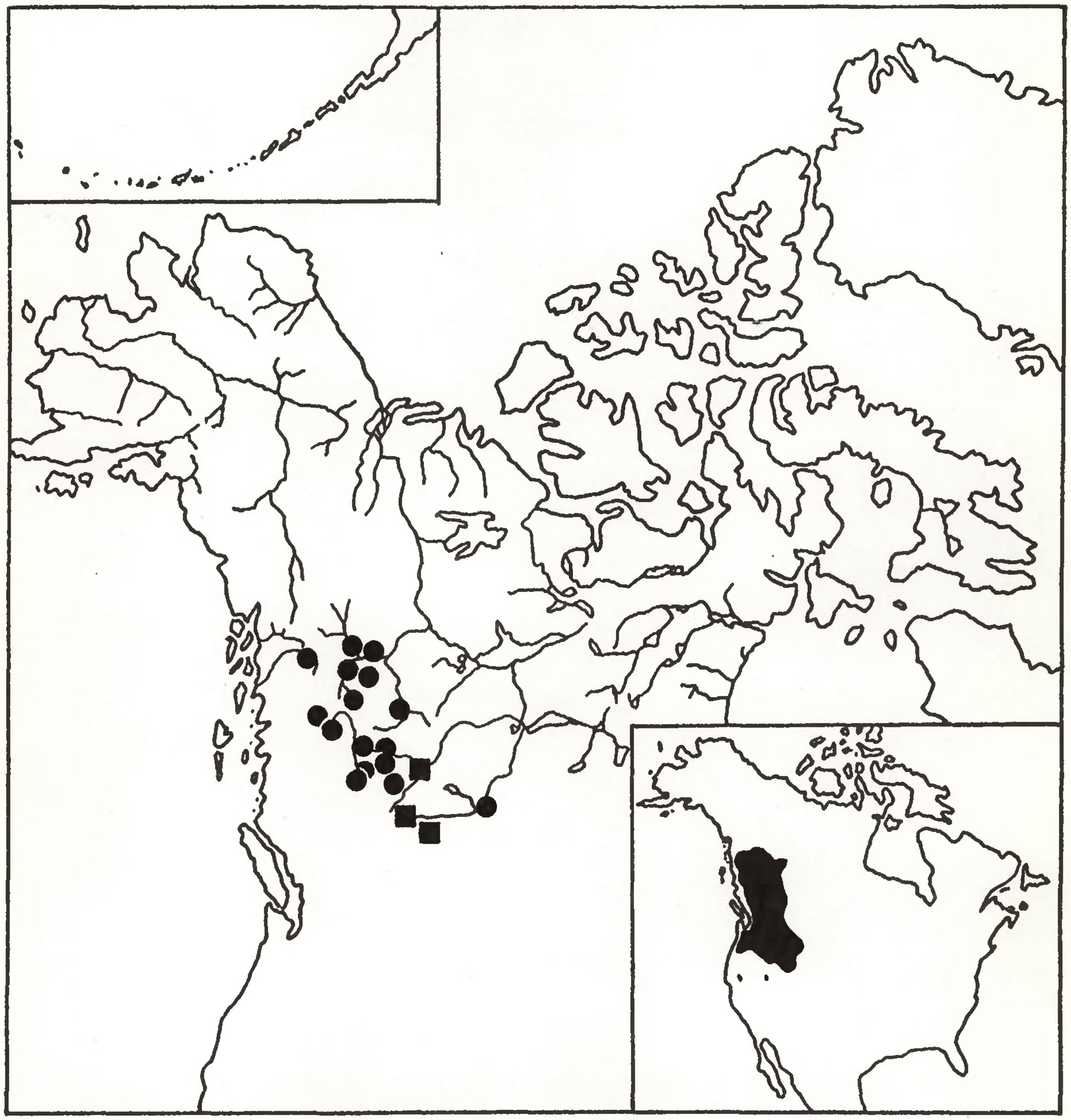


Fig. 13. Northern distribution of P. williamsoni (inset total distribution). Circles indicate specimens examined, and squares literature records.

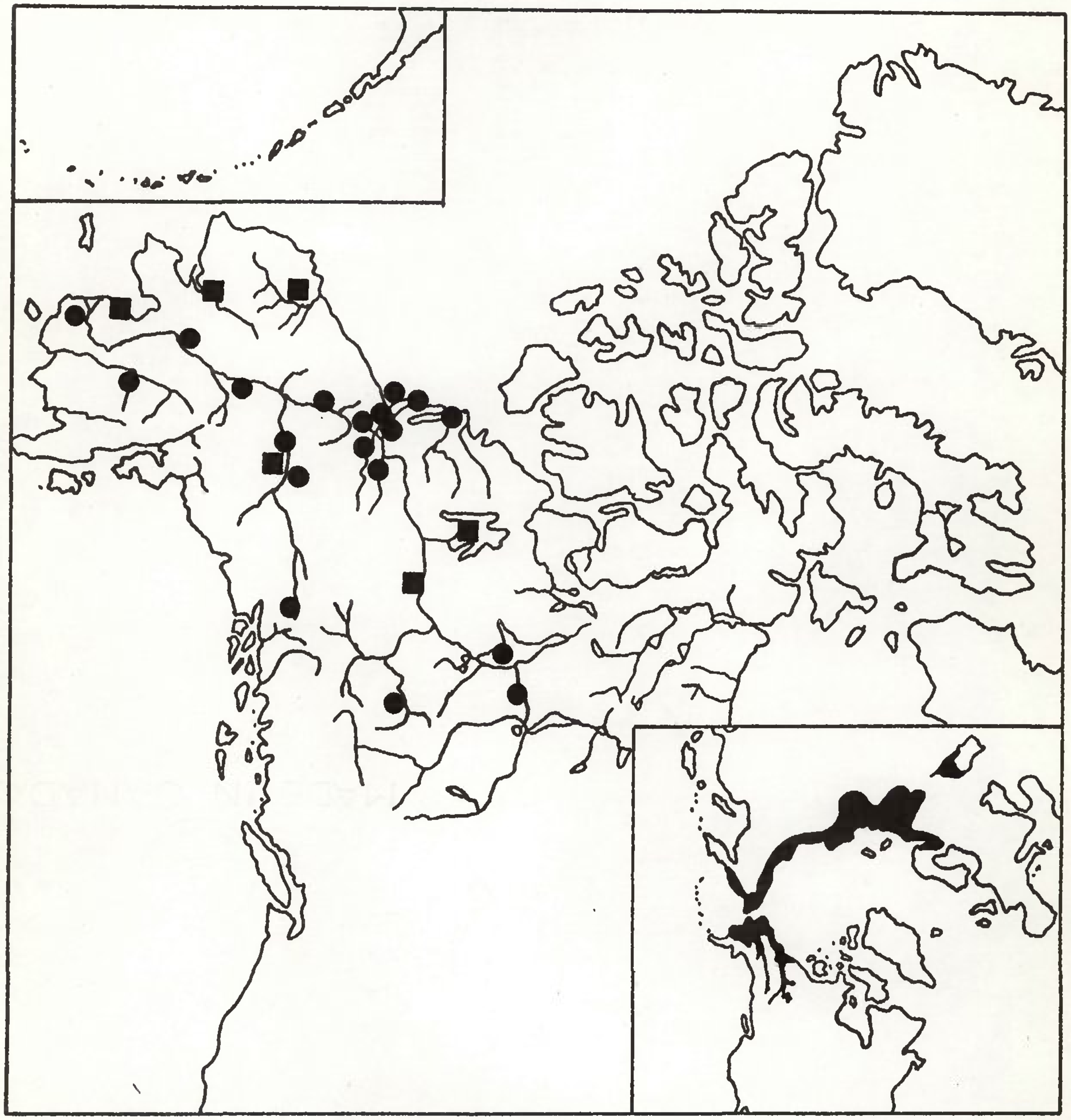


Fig. 14. Northern distribution of S. leucichthys (inset total distribution). Circles indicate specimens examined, and squares literature records.

112, 146, 301, 326, 332, 334, 336, 373, 377, 387, 403, 421, 435, 461, 506, 509; literature records: 11, 37, 47, 53.

Glacial refugia - Zenkevitch (1957) indicates that Stenodus (and other Caspian glacial relicts) entered the Caspian Sea late in the Pleistocene. This suggestion is supported by the slight degree of differentiation between Arctic and Caspian S. leucichthys (Krassikova, 1960). In North America the inconnu probably survived the Wisconsin glaciation in the Bering Refugium.

Salmo clarkii Richardson - Cutthroat trout.

Range - Western North America: Eel River, California, to Prince William Sound, Alaska, and on the east slope of the Rocky Mountains in the Saskatchewan and Missouri Rivers. Isolated populations in the Lahonton, Bonneville, Colorado, and Rio Grande River systems (Fig. 15).

Northern records - Specimens examined, 66, 81, 208, 319; literature records: 11.

Glacial refugia - In British Columbia two allopatric subspecies exist; S. clarkii clarkii the coastal cutthroat, and S. clarkii lewsi the Yellowstone cutthroat (Qadri, 1959). South of British Columbia these forms apparently intergrade (Gilbert and Evermann, 1894). Only S. clarkii clarkii enters northern North America.

The distribution pattern of the coastal cutthroat (inset, Fig. 15), indicates survival in the Pacific Refugium; the presence of S. clarkii in Klamath and Goose Lakes further support this interpretation.

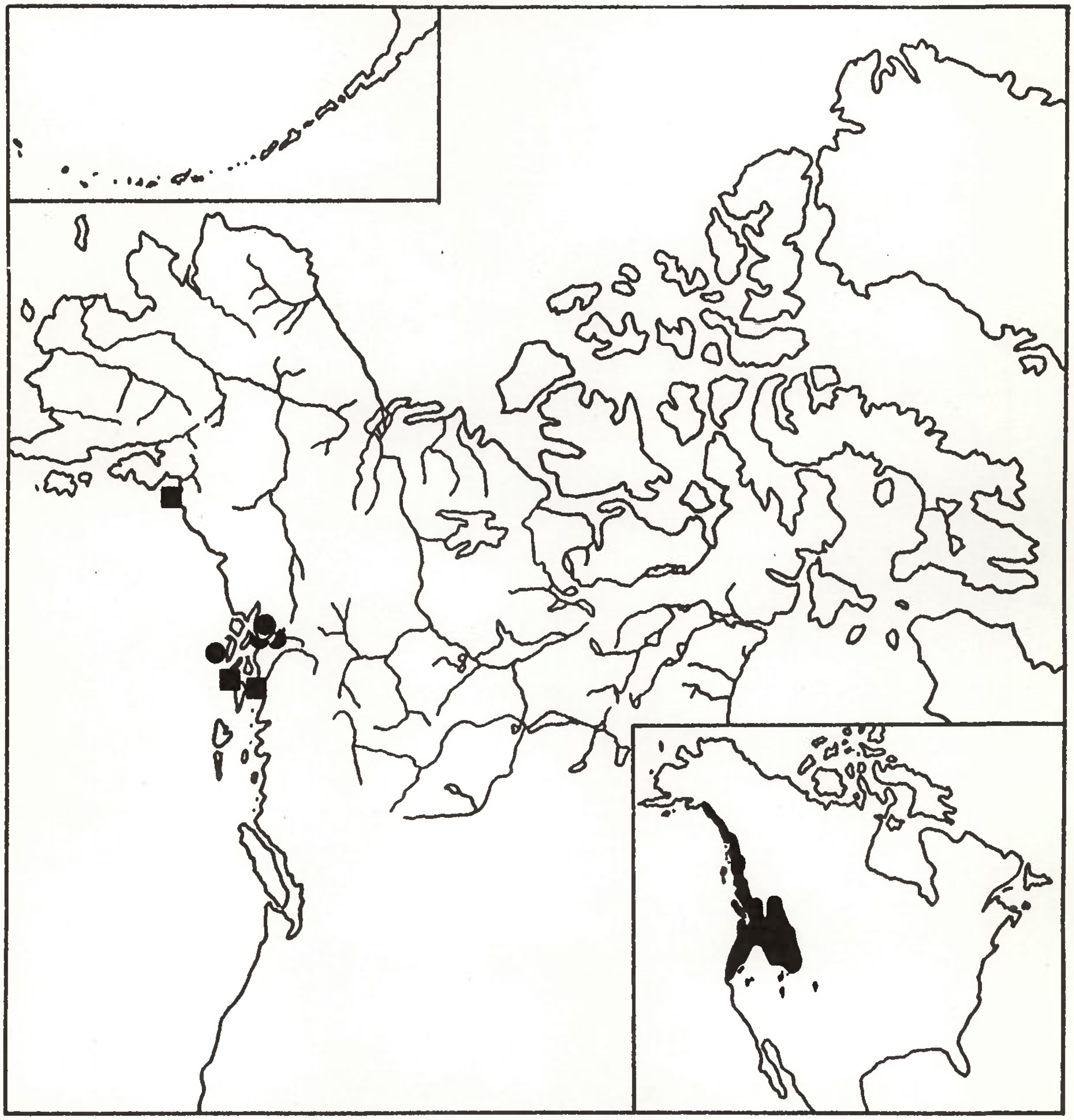


Fig. 15. Northern distribution of S. clarkii (inset total distribution). Circles indicate specimens examined, and squares literature records.

Salmo gairdnerii Richardson - Rainbow trout.

Range - Western North America: Rio Santo Domingo, Mexico, to Aniak River, Alaska, and on the east slope of the Rocky Mountains in the Peace and Athabasca Rivers. Isolated populations in some Mexican Gulf of California drainages (Fig. 16).

Northern records - Specimens examined: 6, 11, 17, 26, 28, 62, 68, 266, 269, 271, 279, 296, 320, 324, 330, 490; literature records: 11, 31.

Glacial refugia - The populations of *S. gairdnerii* north of the Alaska Peninsula and on Kodiak Island suggest that rainbow trout may have survived glaciation in the Bering Refugium. However, there are no apparent morphological differences (gill rakers, pyloric caeca, lateral line scales, and vertebrae were compared) between the rainbow trout from British Columbia and from north of the Alaska Peninsula. This fact, along with the distribution pattern (inset, Fig. 16), indicates *S. gairdnerii* survived glaciation in the Pacific Refugium. Needham and Gard (1959) suggest that the relict Mexican populations of *S. gairdnerii* were derived from anadromous rainbow trout during glaciation.

Salvelinus alpinus (Linnaeus) - Arctic char.

Range - Circumpolar, in North America from the Kenai Peninsula, Alaska, to Newfoundland and the Gulf of St. Lawrence. There are isolated populations on Kodiak Island, and in Quebec, New Brunswick, Maine, and New Hampshire (Fig. 17).

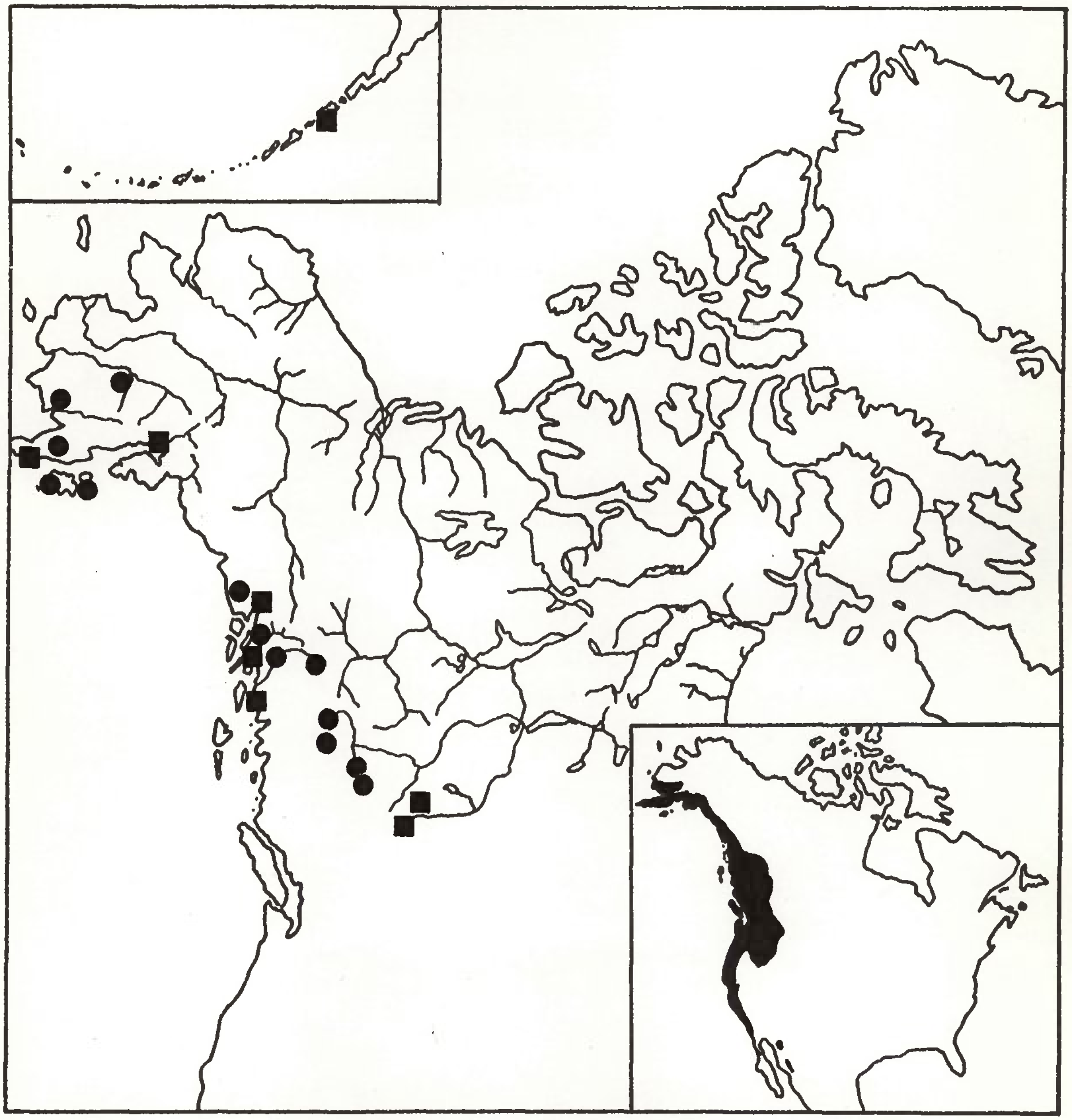


Fig. 16. Northern distribution of S. gairdnerii (inset total distribution). Circles indicate specimens examined, and squares literature records.

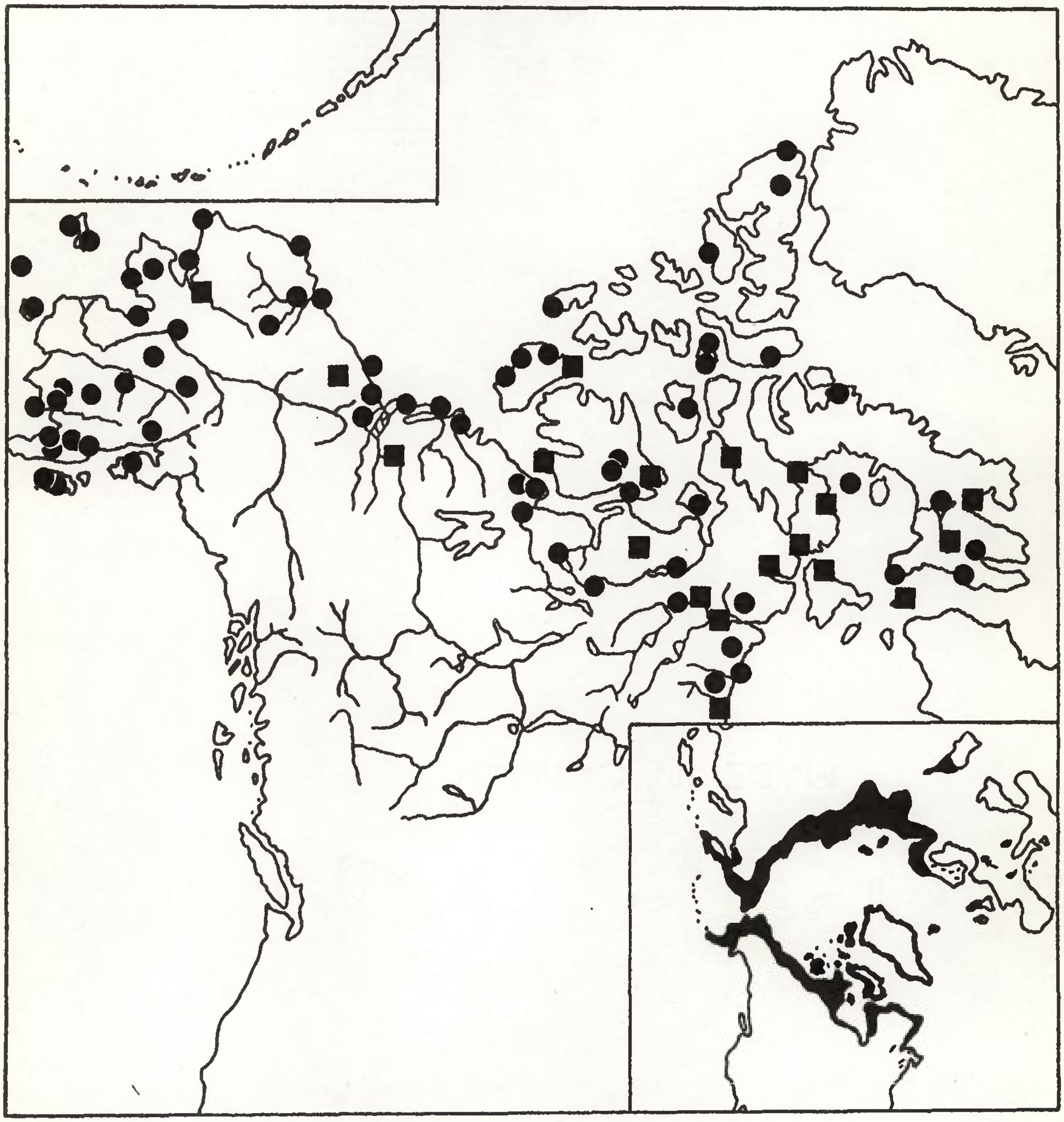


Fig. 17. Northern distribution of S. alpinus (inset total distribution). Circles indicate specimens examined, and squares literature records.

Northern records - Specimens examined: 6, 7, 11, 16, 24, 26, 30, 42, 57, 68, 77, 91, 95, 103, 106, 113, 129, 133, 136, 140, 141, 147, 148, 152, 158, 161, 163, 170, 174, 184, 202, 203, 212, 332, 333, 337, 338, 343, 344, 345, 346, 351, 353, 354, 361, 366, 368, 369, 380, 383, 396, 398, 400, 407, 410, 415, 416, 419, 423, 427, 431, 437, 443, 445, 445a, 447, 457, 460, 461, 481, 485, 488, 491; literature records: 2, 7, 9, 17, 18, 22, 23, 27, 28, 36, 41, 45, 46, 48, 50, 51, 52.

Glacial refugia - McPhail (1961) suggests three allopatric forms of S. alpinus in North America, distinguished by gill raker and pyloric caeca counts. The distributions of these forms are presented in Fig. 18. Each form is relatively uniform throughout its range, but apparently intergrades with the other forms wherever they come in contact.

The presence of three allopatric forms of S. alpinus in North America suggests survival in three refugia. The populations of S. alpinus in Karluk and Fraser lakes on Kodiak Island are morphologically similar to populations in the Bristol Bay area. Karlstrom (1961) indicates much of Kodiak Island was unglaciated during the Wisconsin, and the most likely interpretation is that the Bristol Bay form of S. alpinus probably survived the Wisconsin glaciation on Kodiak Island.

There are relict populations of S. alpinus in southeastern Canada and northern New England. These populations

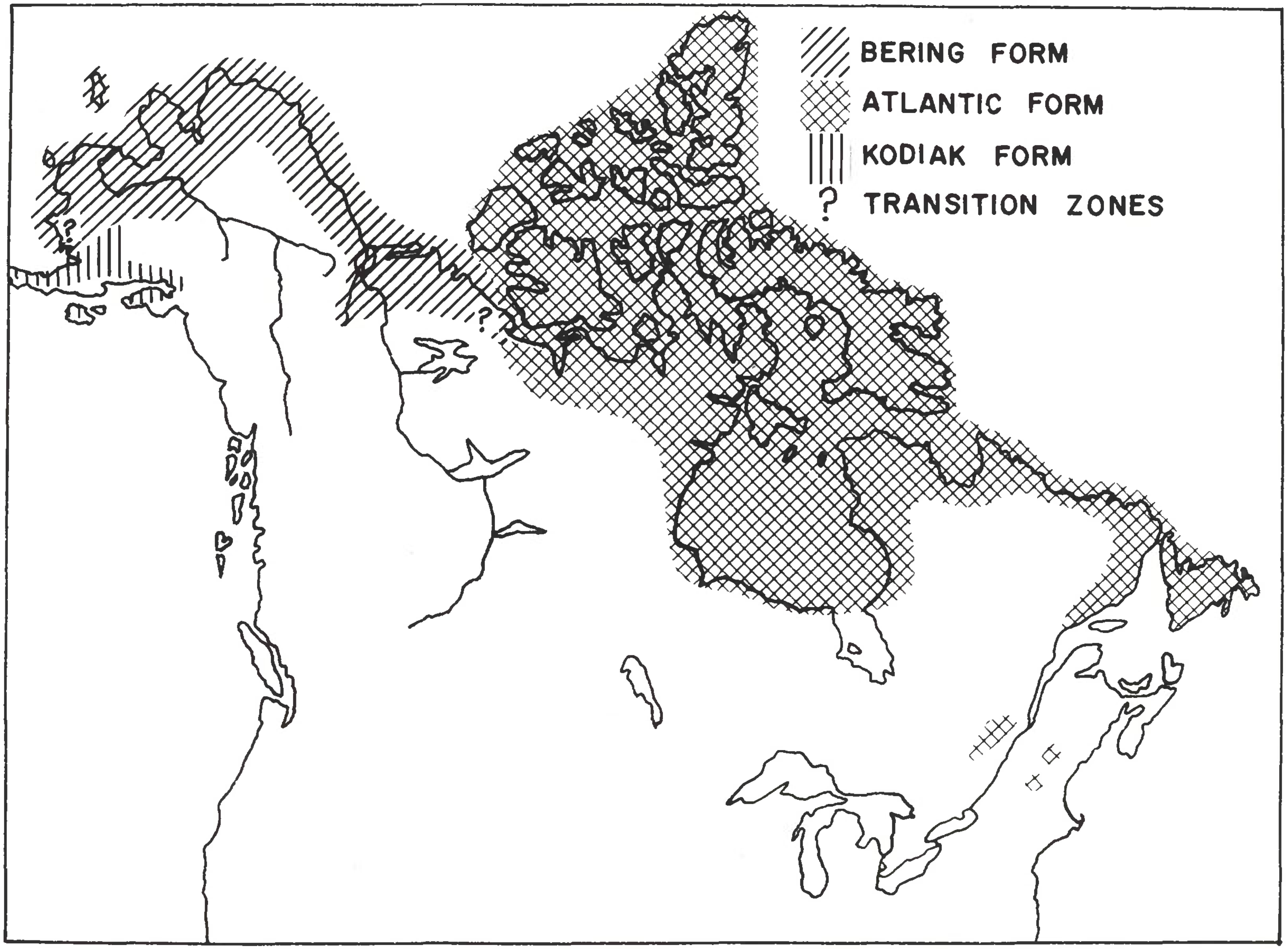


Fig. 18. Distribution of the morphological forms of Salvelinus alpinus in North America (after McPhail, 1961).

are morphologically similar to the eastern arctic form of *S. alpinus*, and suggest this form survived glaciation in the Atlantic Refugium.

The western arctic form of *S. alpinus* is distributed throughout the Bering Refugium, and probably survived glaciation in this area. All three forms of *S. alpinus* occur in northern North America.

Salvelinus malma (Walbaum) - Dolly Varden.

Range - Asia and North America; in North America from the Columbia system to the Seward Peninsula, Alaska. Isolated populations in northern California, Nevada, Alaska and the Yukon Territory (Fig. 19).

Northern records - Specimens examined: 1, 12, 15, 17, 22, 23, 33, 34, 52, 54, 59, 60, 62, 66, 73, 75, 81, 82, 83, 97, 100, 109, 125, 137, 157, 15 , 166, 170, 174, 181, 183, 186, 191, 206, 208, 213, 214, 287, 306, 307, 314, 318, 319, 321, 324, 483a, 490, 494a, 507, 512, 518; literature records: 14, 31.

Glacial refugia - McPhail (1961) suggests two allopatric forms of *S. malma* in North America, distinguished by gill raker and vertebrae counts. The distribution of these forms is presented in Fig. 20. Both forms are relatively uniform within their ranges.

As in *S. alpinus*, the existence of two allopatric forms of *S. malma* in North America points to survival in two refugia. Relict populations in California and Nevada indicate that the southern form survived in the Pacific Refugium. The

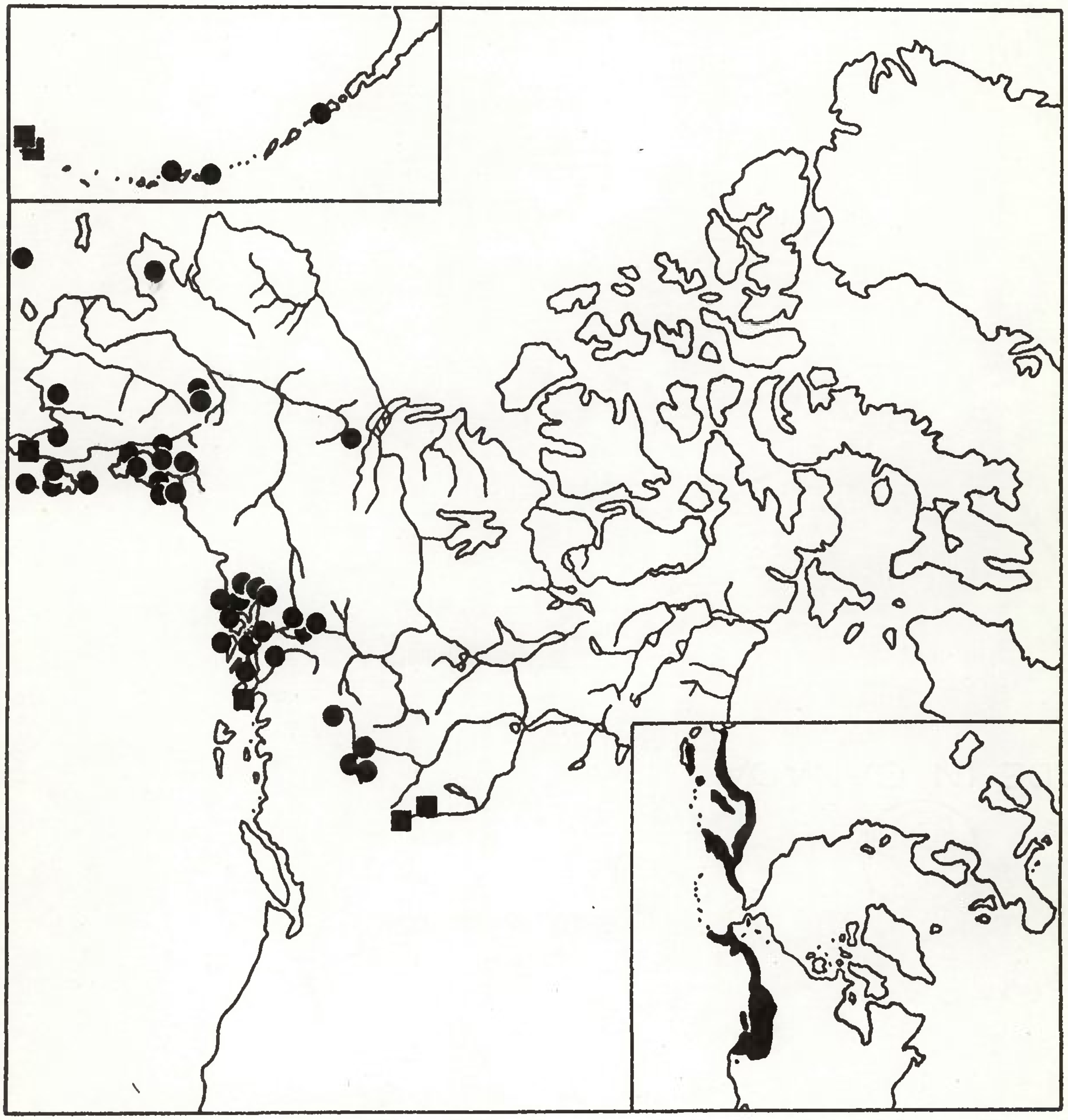


Fig. 19. Northern distribution of S. malma (inset total distribution). Circles indicate specimens examined, and squares literature records.

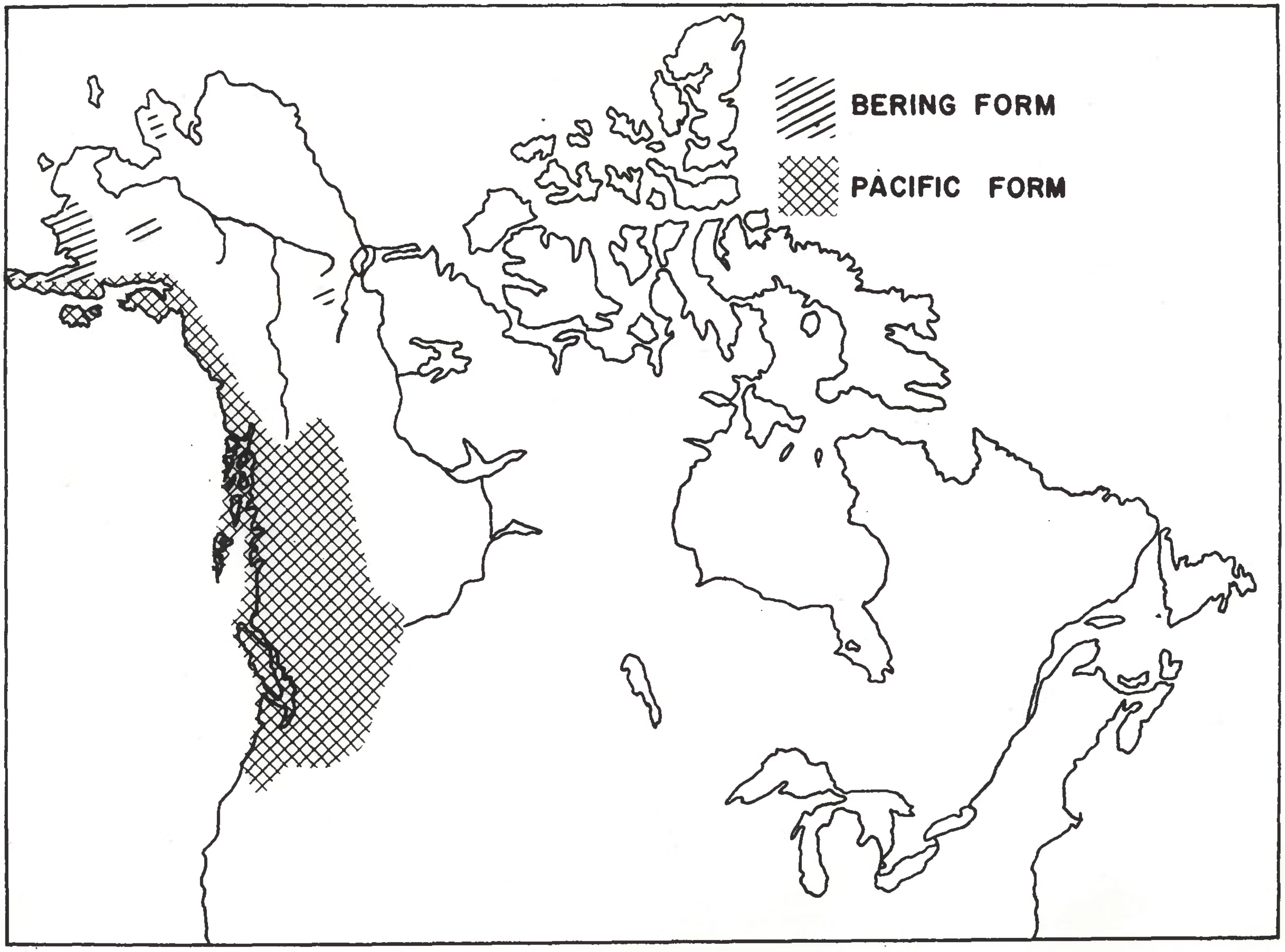


Fig. 20. Distribution of the morphological forms of *Salvelinus malma* in North America (after McPhail, 1961).

northern form of *S. malma* is restricted to the Bering Refugium and probably survived glaciation in this area. Both forms of *S. malma* occur in northern North America.

Salvelinus namaycush (Walbaum) - Lake trout.

Range - North America: from Alaska to the Great Lakes and upper Mississippi system, and from Labrador to New Hampshire; also recorded from Banks, Victoria, King William, Southampton, and possibly Baffin Islands (Fig. 21).

Northern records - Specimens examined: 2, 10, 103, 106, 118, 128, 155, 176, 183, 196, 210, 215, 267, 276, 281, 287, 298, 300, 321, 323, 323a, 326, 331, 332, 335, 342, 343, 346, 347, 353, 358, 362, 367, 370, 371, 384, 385, 387, 402, 407, 409, 413, 414, 419, 422, 425, 438, 441, 448, 460, 462, 465, 468, 469, 471, 484, 487, 490, 493, 497, 521; literature records: 1, 4, 9, 11, 16, 18, 28, 36, 39, 48, 53.

Glacial refugia - The range of *S. namaycush* includes one unglaciated area, the Bering Refugium, a fact that led some authors (Radforth, 1949; Wynne-Edwards, 1947) to suggest that *S. namaycush* survived glaciation in the Bering Refugium. However, Walters (1955) notes that the absence of the lake trout from eastern Siberia makes it unlikely that this species survived in the Bering Refugium, and its absence from apparently suitable habitats on the Seward Peninsula further strengthens this suggestion. Walters indicates that *S. namaycush* probably survived glaciation in the Mississippi Refugium.

A fossil lake trout is known from the Menomonie Beds in Wisconsin. Hussakof (1916) originally correlated

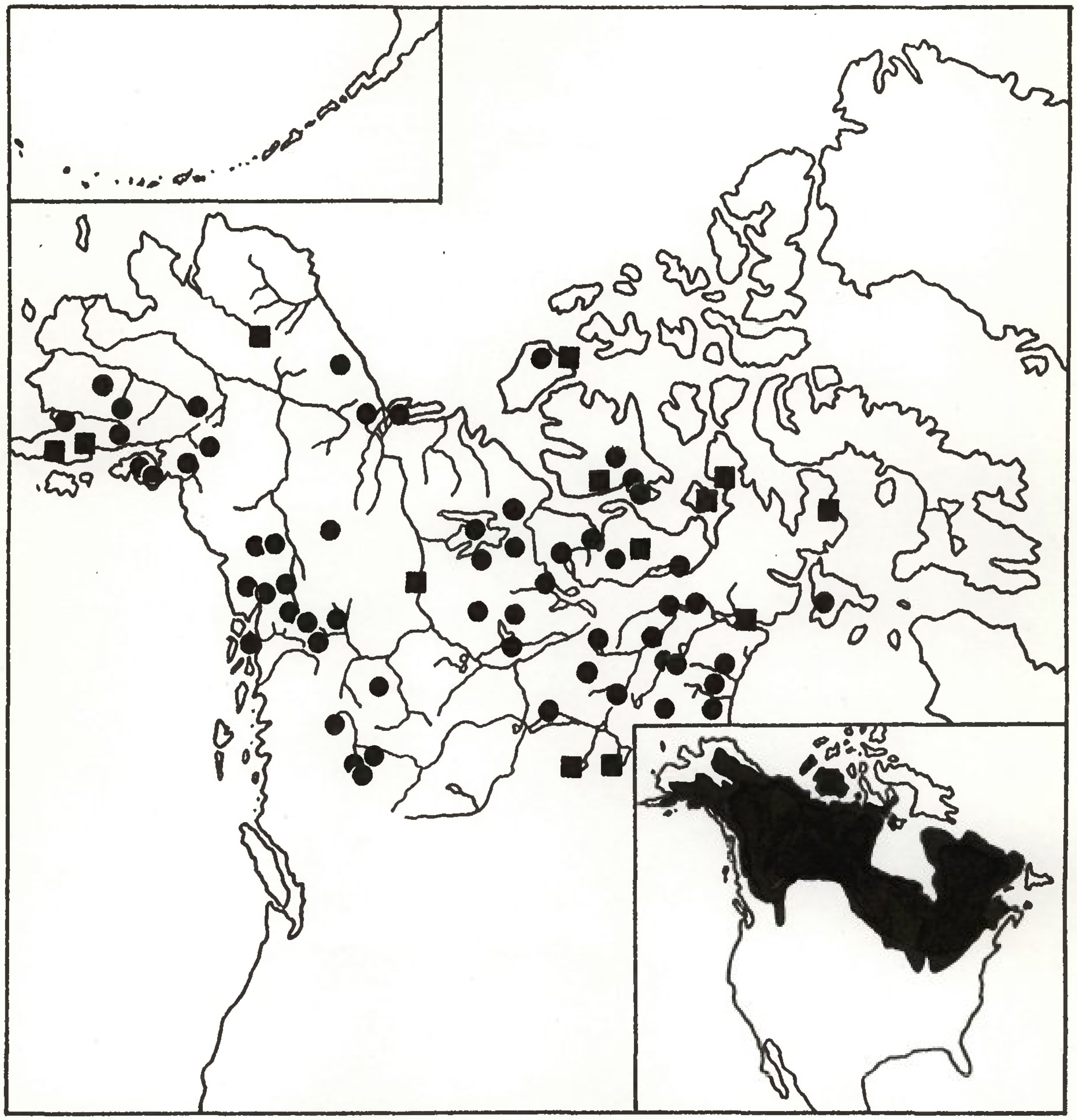


Fig. 21. Northern distribution of S. namaycush (inset total distribution). Circles indicate specimens examined, and squares literature records.

these beds with the Kansan glaciation. However, recent radiocarbon studies (R. F. Black, pers. comm.) indicate they are of late-Wisconsin age (12,500 to 16,000 B.P.). This indicates S. namaycush was present in the Mississippi Refugium during the Wisconsin glaciation. The present restricted distribution of the lake trout in the upper Mississippi system is probably due to postglacial climate changes.

Thymallus arcticus (Pallas) - Arctic grayling.

Range - Asia, and North America; the North American range is disjunct. Three separate populations are known. One population extends from Alaska to Hudson Bay. Another population occurs in the northern headwaters of the Missouri River, and a third population (now extinct) occurred in northern Michigan (Fig. 22).

Northern records - Specimens examined: 3, 4, 8, 10, 11, 18, 27, 31, 33, 35, 39, 42, 44, 50, 54, 61, 64, 67, 69, 79, 88, 101, 106, 108, 113, 118, 129, 135, 139, 145, 147, 155, 157, 158, 188, 198, 198a, 200, 201, 202, 207, 216, 222, 228, 250, 267, 274, 284, 285, 292, 293, 295, 297, 298, 301, 305, 306, 310, 312, 316, 321, 322, 323a, 324, 326, 327, 329, 335, 343, 358, 362, 363, 367, 384, 399, 407, 408, 419, 423, 434, 441, 450, 456, 462, 465, 471, 472, 475, 476, 480, 483a, 487, 490, 492, 493, 497, 500, 503, 505, 506, 509, 511a, 512, 513, 515, 516, 517, 519, 524; literature records: 4, 11, 16, 18, 31, 36, 39, 52, 53.

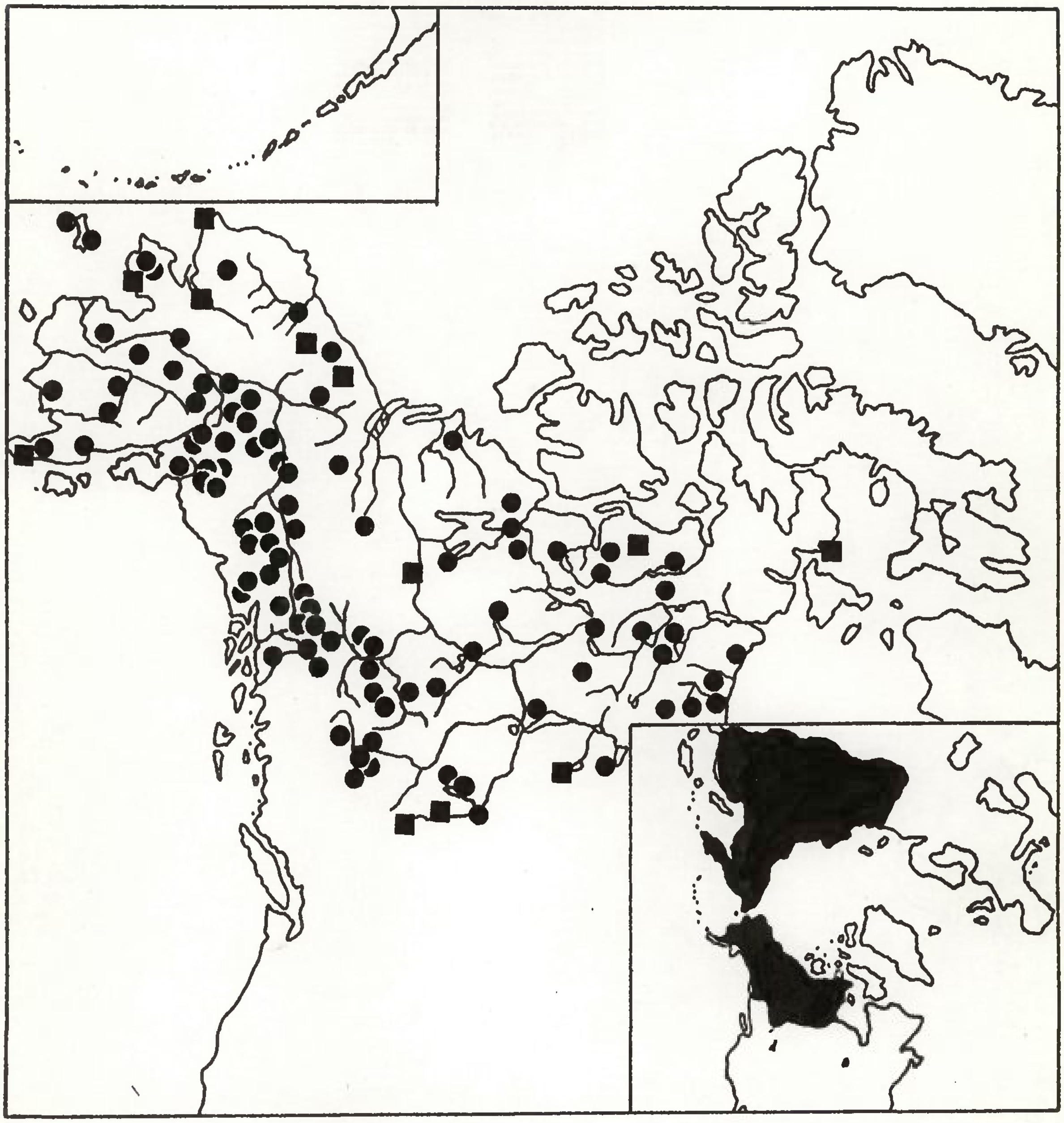


Fig. 22. Northern distribution of T. arcticus (inset total distribution). Circles indicate specimens examined, and squares literature records.

Glacial refugia - The North American range of _T. arcticus_ includes two unglaciated areas: the Bering, and the Mississippi Refugia. The presence of grayling on St. Lawrence Island (a remnant of the Bering Land Bridge) and the relict populations in Montana and Michigan indicate _T. arcticus_ used both refugia during glaciation.

F. M. Atton (Saskatchewan Fisheries Laboratory) is studying the North American populations of _T. arcticus_. Preliminary data (Atton, pers. comm.) indicate that grayling from the Mackenzie system and the area east of the Mackenzie River are indistinguishable from Missouri River grayling, but the grayling west of the Mackenzie system appear to differ from other North American grayling in the number of lateral line scales. This suggests that the northern North American populations of _T. arcticus_ are derived from both the Bering and the Mississippi Refugia.

Hypomesus olidus (Pallas) - Pond smelt.

Range - Asia and North America; in North America from the Copper River, Alaska, to Cape Bathurst, N.W.T. (Fig. 23). A relict population is reported from Lake Krugloe, a Kara Sea drainage in the USSR (Ivanova, 1952).

Northern records - Specimens examined: 25, 45, 87, 101, 105, 110, 149, 171, 184, 386, 403; literature records: 3, 42, 43.

Glacial refugia - The North American range of _H. olidus_ is almost confined to the Bering Refugium. The pond smelt was probably present in that refugium during the Wisconsin glaciation.

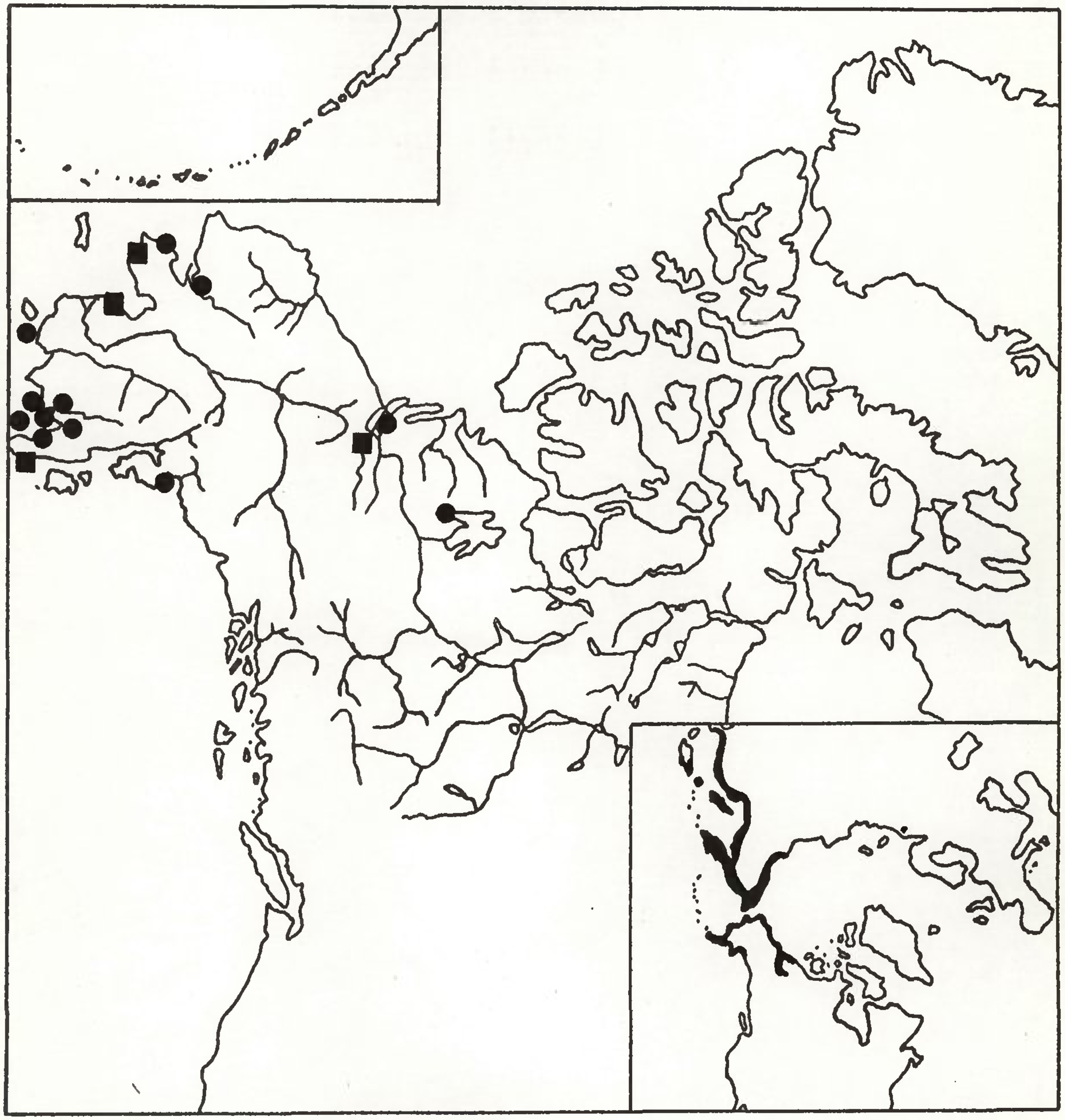


Fig. 23. Northern distribution of H. olidus (inset total distribution). Circles indicate specimens examined, and squares literature records.

Osmerus eperlanus Linnaeus - Boreal smelt.

Range - Europe, Asia, and North America; in North America the range is disjunct: Barclay Sound, Vancouver Island, to Bathurst Inlet, N.W.T., and on the Atlantic coast from Hamilton Inlet, Labrador, to Virginia (Fig. 24).

Northern records - Specimens examined: 25, 40, 107, 108, 109, 110, 133a, 140, 149, 163, 171, 184, 203, 217, 334, 336, 340, 342, 447; literature records: 3, 52.

Glacial refugia - McAllister (1963) synonymizes the western *O. dentex* and the eastern *O. mordax* with the European *O. eperlanus*. He considers the disjunct North American populations a single subspecies, *Osmerus eperlanus mordax*, and suggests either dispersal from a single refugium (the Bering) with recent separation into two populations, or survival in two refugia (the Bering and the Atlantic) followed by almost complete postglacial gene exchange. These suggestions are based on the apparent absence of differentiation between the disjunct North American populations.

In the present study the two North American populations of *O. eperlanus* were compared using gill rakers, pyloric caeca, and vertebrae. There are significant differences ($p < 0.001$) in vertebrae between the two populations. However, vertebral number shows clinal variation within populations and is therefore excluded from the present discussion. The only other character suggesting morphological differentiation is the number of pyloric caeca (Table V). The western population differs significantly ($p < 0.001$) from the eastern population

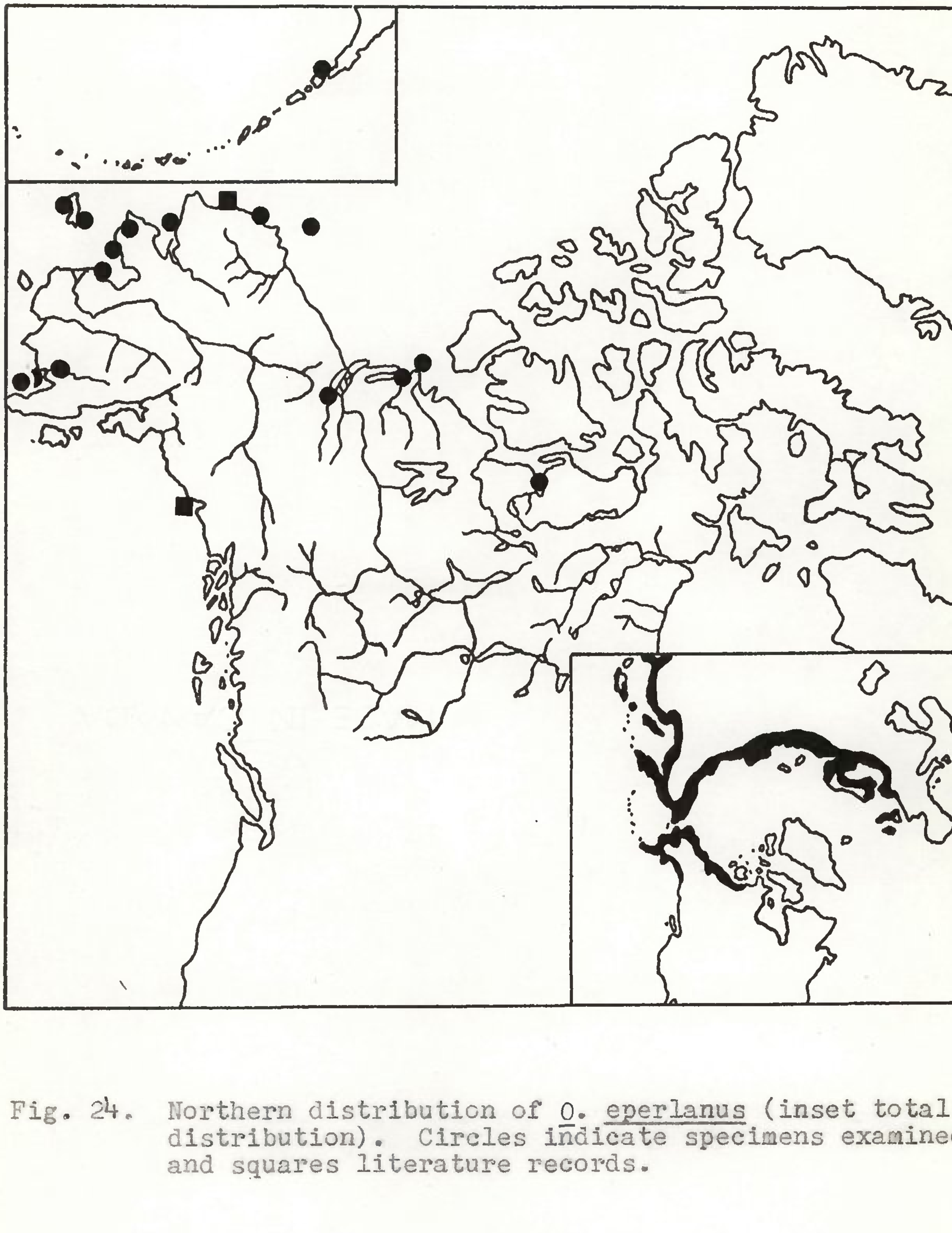


Fig. 24. Northern distribution of O. eperlanus (inset total distribution). Circles indicate specimens examined, and squares literature records.

Table V. Comparison of pyloric caeca in western and eastern North American populations of *Osmerus eperlanus*.

Locality	pyloric caeca 3	4	5	6	7	8	9	N	Mean
Western population									
King Salmon			1	2	6	3	1	13	7.0
St. Lawrence Is.					3	2		5	7.4
Kuk R.			2	3	1	1		7	6.1
Chukchi Sea		1	2	9	13	5		30	6.7
Whitefish Stn.			1	7	3	1		12	6.3
Bathurst Inlet			3	4	5	1		13	6.3
Eastern population									
Cordroy R.	1	7	22	1				31	4.9
Navy Is.		1	5	3	1			10	5.4
Maine		4	12	7				23	5.1

in the number of pyloric caeca. There is no suggestion of a cline in the number of pyloric caeca in either population.

This morphological difference combined with the disjunct range suggests *O. eperlanus* survived glaciation in North America in two areas: the Bering, and the Atlantic Refugia. Only the Bering form of *O. eperlanus* is present in northern North America.

Spirinchus thaleichthys (Ayres) - Longfin smelt.

Range - Pacific Coast of North America: San Francisco Bay to Wide Bay, Alaska (Fig. 25).

Northern records - Specimens examined: 85, 89, 220, 224; literature records: 14.

Glacial refugia - The distribution pattern of *S. thaleichthys* (inset, Fig. 25) indicates survival in the Pacific Refugium.

Thaleichthys pacificus (Richardson) - Eulachon.

Range - Western North America: Klamath River, California, to Bristol Bay and the Pribilof Islands, Alaska (Fig. 26).

Northern records - Specimens examined: 37, 116, 134, 167, 206, 223; literature records: 3, 14.

Glacial refugia - The distribution pattern of *T. pacificus* (inset, Fig. 26) indicates survival in the Pacific Refugium.

Catostomus catostomus (Forster) - Longnose sucker.

Range - North America and northeastern Siberia. In North America from Alaska to Labrador, and from the upper

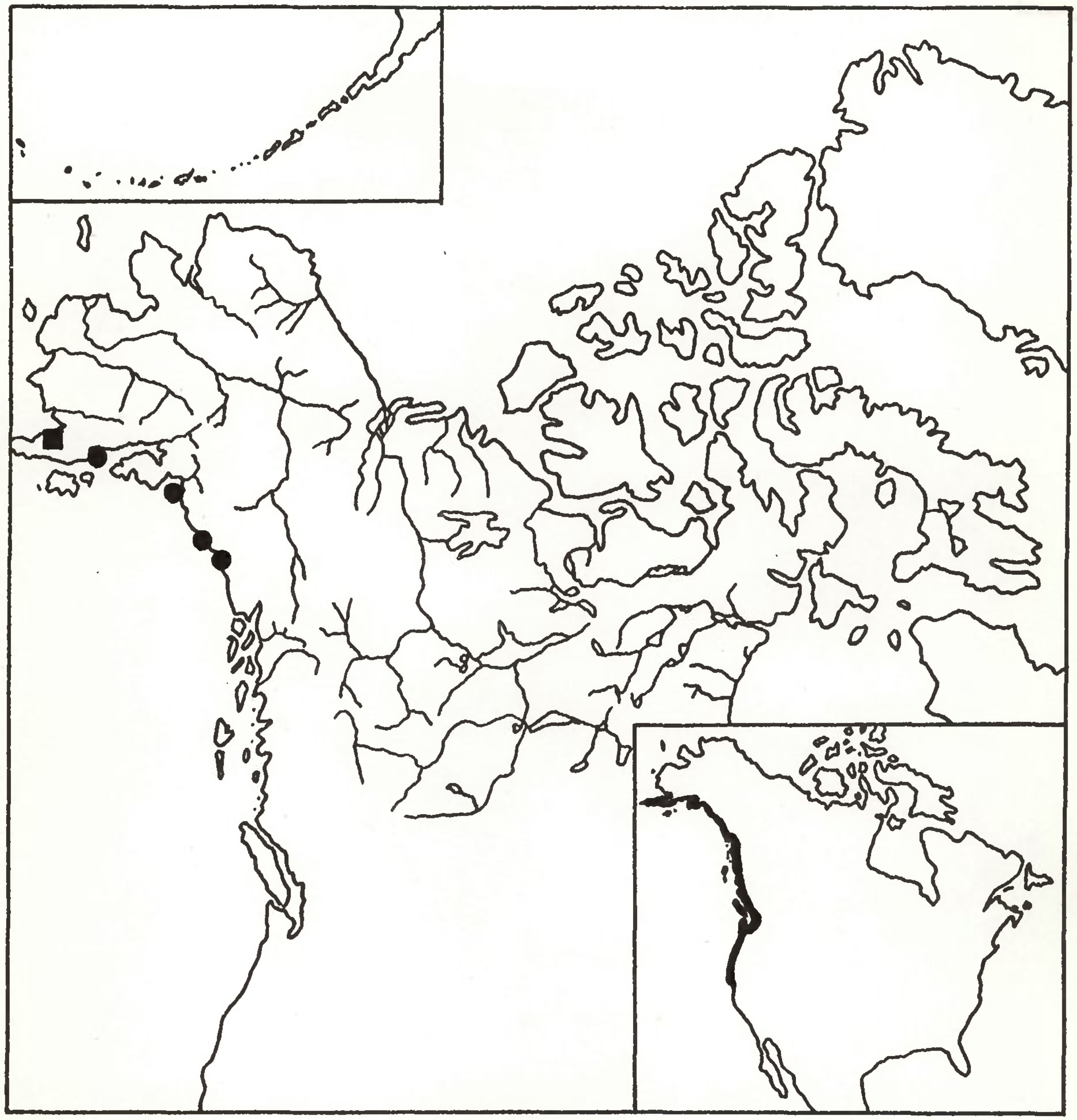


Fig. 25. Northern distribution of S. thaleichthys (inset total distribution). Circles indicate specimens examined, and squares literature records.

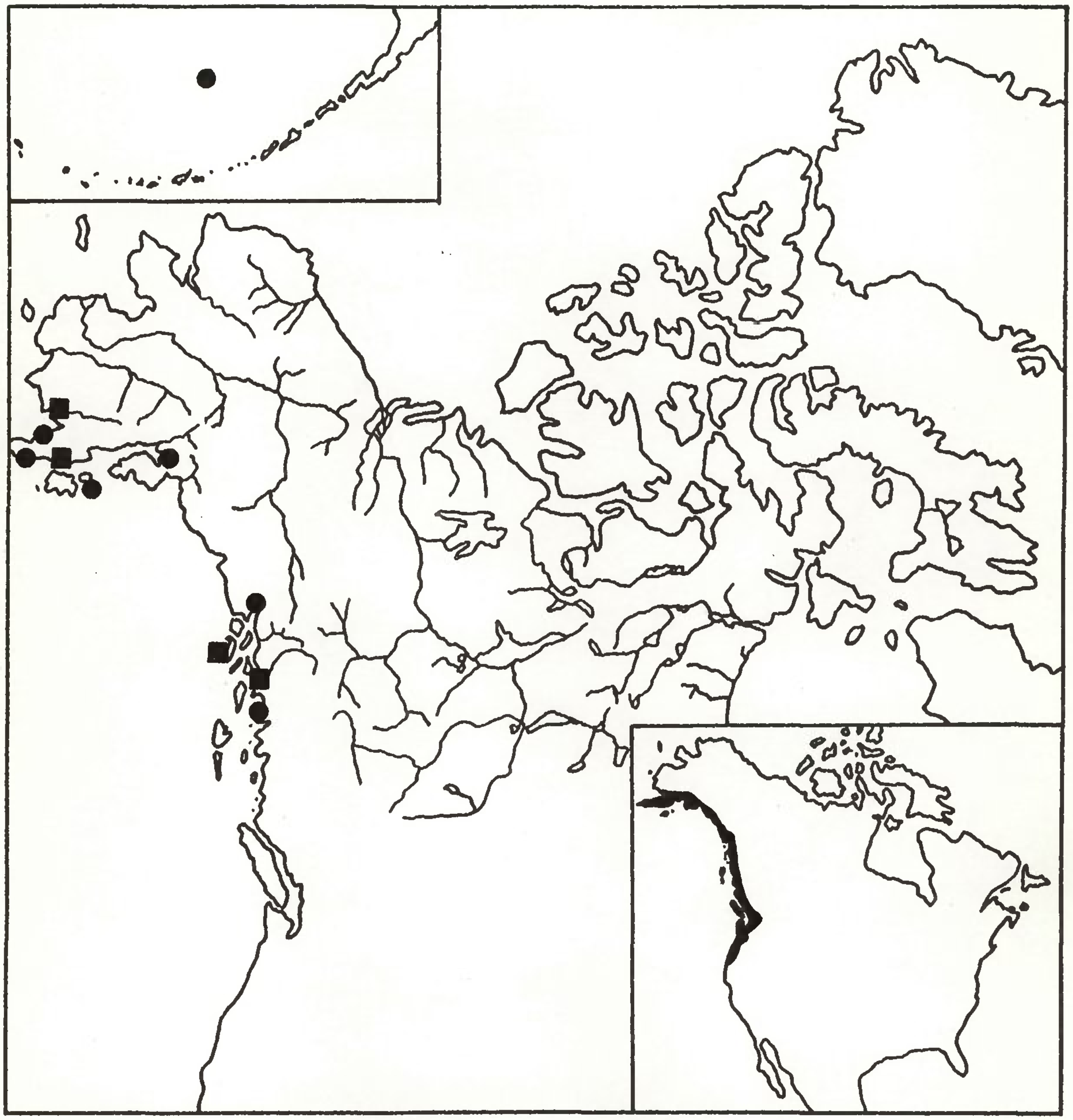


Fig. 26. Northern distribution of T. pacificus (inset total distribution). Circles indicate specimens examined, and squares literature records.

Missouri River and Great Lakes to the Mackenzie Delta; relict populations in South Dakota and Maryland (Fig. 27).

Northern records - Specimens examined: 4, 7, 8, 9, 18, 19, 30, 33, 38, 41, 42, 51, 55, 65, 66, 67, 77, 80, 93, 112, 113, 117, 118, 123, 123, 124, 131, 138, 146, 147, 151, 162, 173, 187, 189, 200a, 208, 209, 211, 226, 228, 230, 232, 239, 244, 247, 248, 250, 251, 252, 254, 257, 260, 262, 265, 267, 269, 281, 285, 289, 290, 293, 296, 297, 298, 300, 301, 307, 309, 311, 312, 320, 321, 323a, 325, 332, 334, 335, 341, 343, 346, 347, 349, 363, 372, 373, 378, 385, 388, 399, 404, 406, 408, 418, 424, 432, 434, 436, 442, 454, 458, 462, 465, 466, 467, 468, 471, 474, 483a, 489, 502, 505, 509, 511a, 519, 522, 523; literature records: 4, 6, 13, 18, 30, 31, 39, 48, 49.

Glacial refugia - The range of C. catostomus includes three unglaciated areas: the Bering, the Pacific, and the Mississippi Refugia. The presence of C. catostomus in northeastern Siberia and on St. Lawrence Island (N. J. Wilimovsky, pers. comm.) indicates the longnose sucker was present in the Bering Refugium during the Wisconsin glaciation. The occurrence of longnose suckers above falls in the Snake River (Columbia system) indicates the Pacific Refugium was also used, while relict populations in South Dakota and Maryland suggest the Mississippi Refugium.

The numbers of caudal peduncle scales, gill rakers, and vertebrae were compared over the North American range of C. catostomus. Only the number of gill rakers showed a

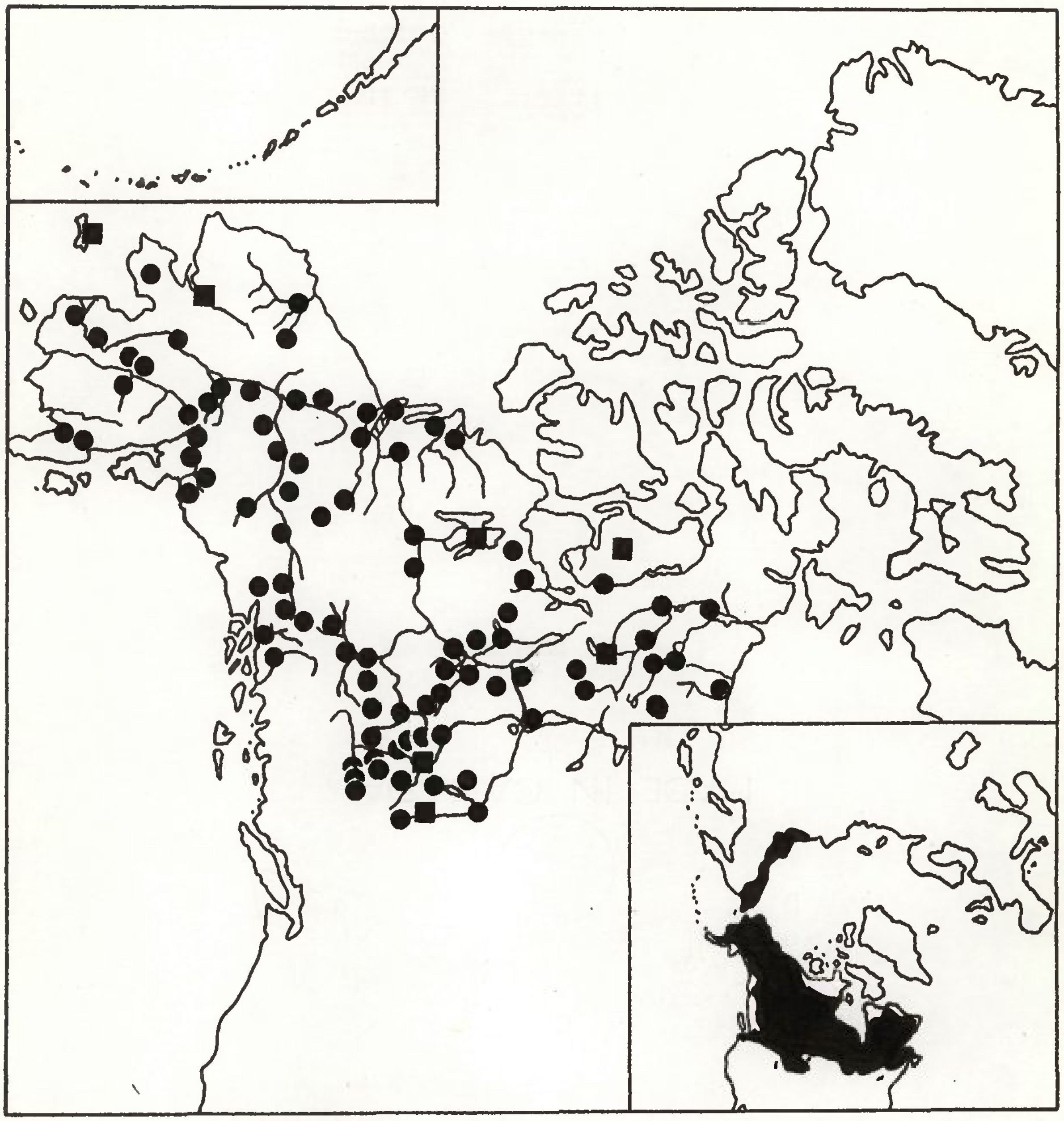


Fig. 27. Northern distribution of C. catostomus (inset total distribution). Circles indicate specimens examined, and squares literature records.

consistent geographic pattern (Table VI). According to gill rakers there are three distinct populations of C. catostomus: a Bering, a Pacific, and a Mississippi population. These populations differ significantly ($p < 0.001$) in gill raker number. Figure 28 presents the distribution of the three forms of longnose sucker in North America. Each form is relatively constant within its range. The Pacific and Bering forms appear to intergrade in the upper Columbia and Fraser systems.

Only the Bering and Mississippi forms of C. catostomus are present in northern North America.

Catostomus commersonii (Lacépède) - White sucker.

Range - North America: Arkansas River north to the Mackenzie Delta, and from the Fraser and Skeena systems east to the Atlantic Coastal Plain (Fig. 29).

Northern records - Specimens examined: 229, 232, 242, 245, 246, 247, 253, 256, 261, 262, 265, 270, 273, 277, 285, 291, 296, 301, 307, 311, 317, 320, 323, 375, 378, 388, 404, 453, 467, 468, 471; literature records: 19, 20, 31, 37, 39.

Glacial refugia - The wide range of C. commersonii suggests survival in multiple refugia. The white sucker is widely distributed in two unglaciated areas: the Mississippi, and the Atlantic Refugia. Catostomus commersonii probably used both refugia during the Wisconsin glaciation.

Because few specimens are available from its wide southern range no attempt was made to analyze geographic

Table VI. Comparison of gill rakers in North American *Catostomus catostomus*.

	Gill rakers												
Locality	20	21	22	23	24	25	26	27	28	29	30	N	Mean
Alakanuk				1		1	5	2	1			10	26.0
Nulato					1		1	2	2	1		7	27.0
Moon L.				2	4	2	2	2	1			13	24.2
Tanana R.				1	2	4	2	1				10	25.0
Pelly R.				1	1	2	1					5	24.8
Atlin L.					1	2	4	2	1			10	26.0
Tazlina R.						2	3	2				9	25.6
Illiamna L.					2	1	2	4	1	2		10	27.1
Chenan L.					1	1	2	1				5	25.6
Stikine R.					2	4	2					8	25.0
Fraser R. (above canyon)				4	2	3	4	4	1			18	25.2
Columbia R. (in B.C.)			1	4	4	2	1					12	24.0
Flint Cr. (Columbia R., Mont.)		1	2	3	3							9	23.6
Salmon R. (lower Fraser)	2	5	3		1							11	21.4
Olympic Pen.		1		1	2							4	22.9
Peel R.								1	2	1	1	5	28.4
Popcorn L.							2	2	3			7	27.1
Lac La Martre							1	2	3	2	1	9	28.2
Great Slave L.							1	4	3	3	1	12	28.1
Athabasca L.							1	2	2	2	1	8	28.0
Whitefish L.									3	1	1	5	28.6
Angikuni L.							1	2	5	1	1	10	27.9
Maguse L.							2	2	3	2	1	10	27.8
Whitemud R.							1	4	3	4	1	13	28.0
Upper Missouri R.					1	4	14	4	3	1		29	26.2
Gods R.						1	1	1	2	1		6	27.2
Attawapiskat R.									2	1		3	28.3
Lake Superior									1	2	1	4	29.0
New England						1	1	5	5	5	3	20	28.0

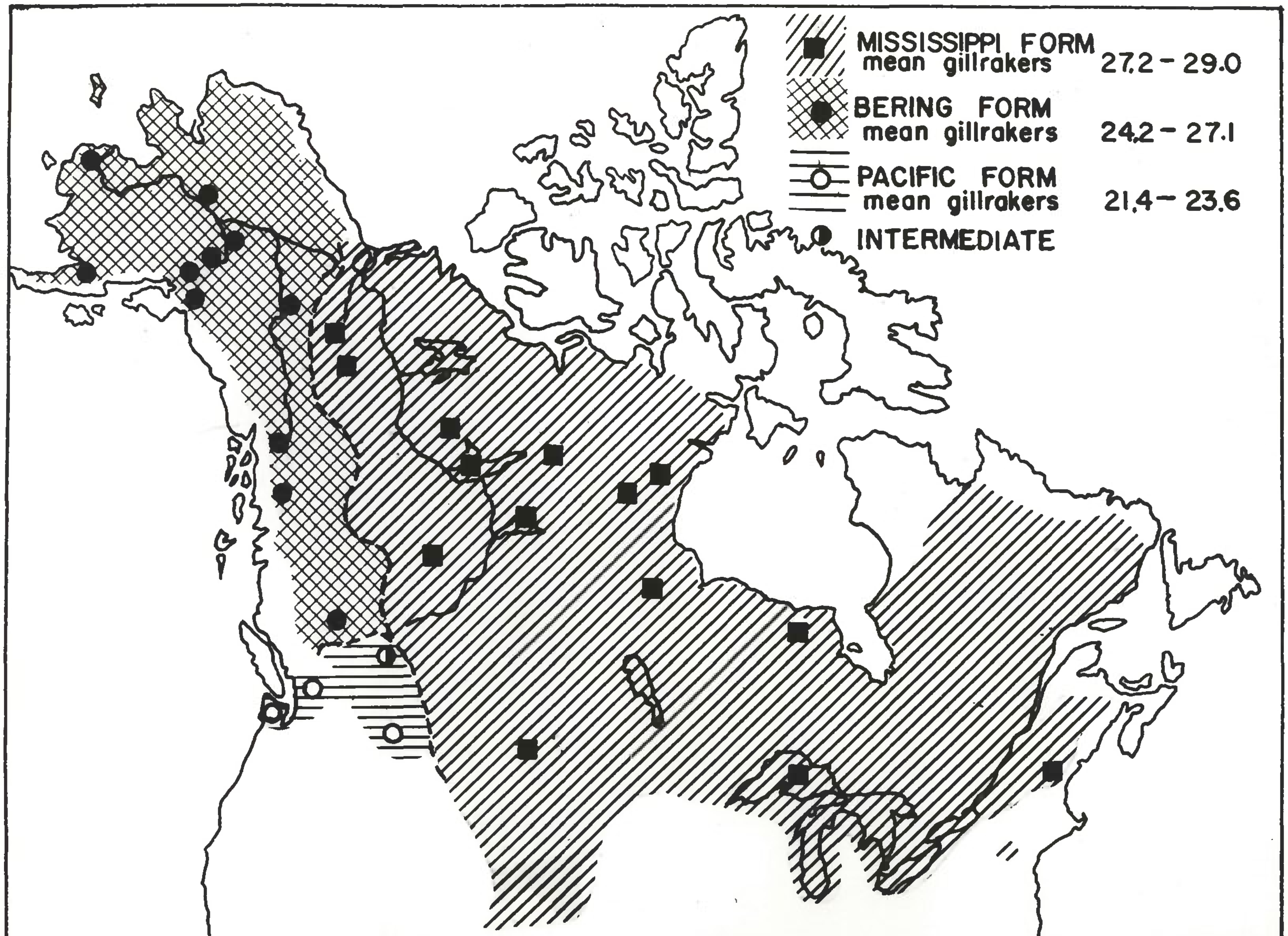


Fig. 28. Geographic variation in the number of gill rakers in *Catostomus catostomus*.

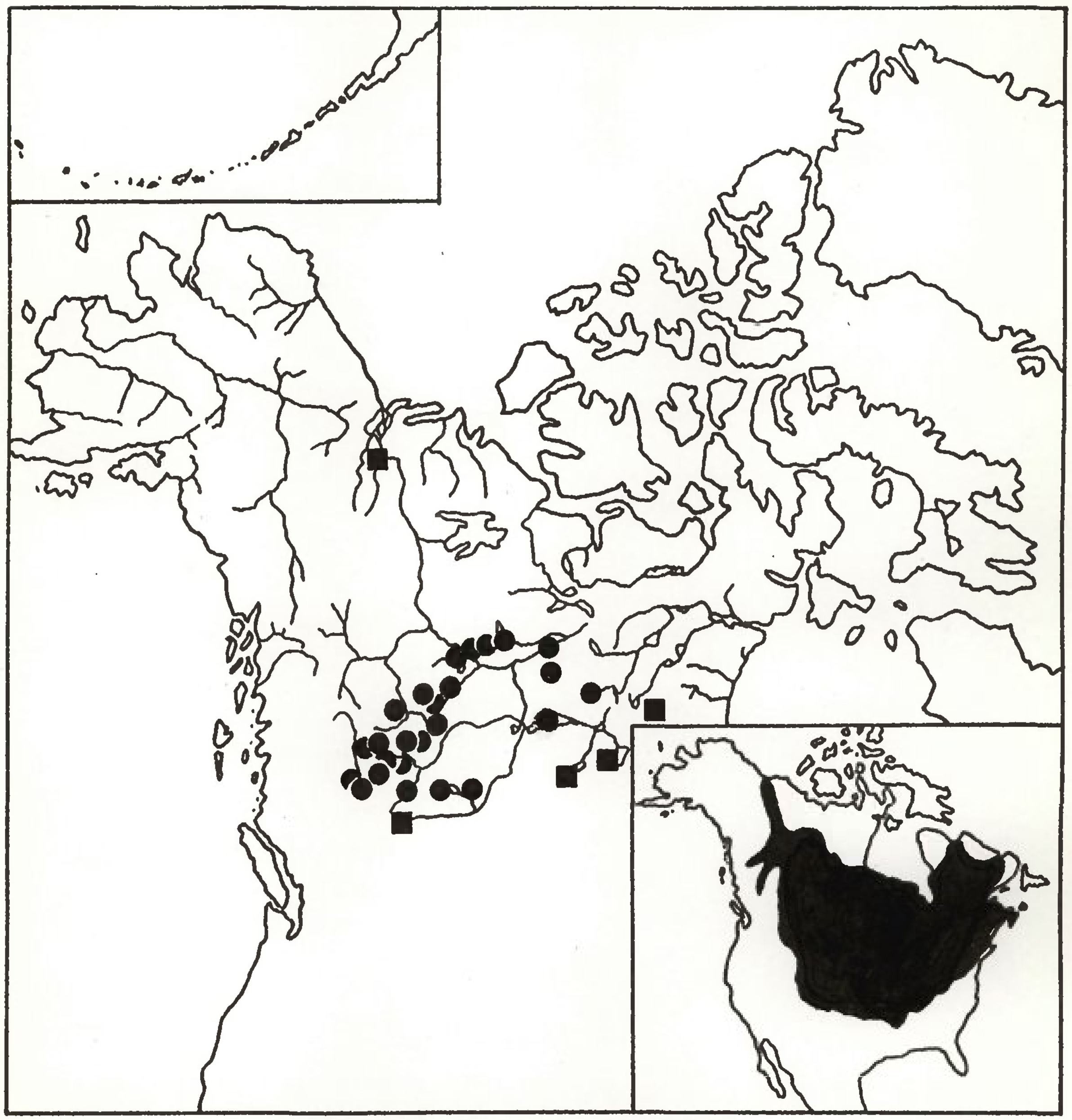


Fig. 29. Northern distribution of C. commersonii (inset total distribution). Circles indicate specimens examined, and squares literature records.

variation in *C. commersonii*. Some authors (Hubbs and Lagler, 1958) indicate that *C. commersonii* is represented on the Great Plains by a weakly differentiated subspecies, *C. c. suckleyi*. If *C. c. suckleyi* is genotypically differentiated it suggests that the Missouri system may have functioned as a separate refugium for *C. commersonii*. However, Bailey and Allum (1962) found no evidence to support the separation of a Great Plains subspecies. The white sucker was probably continuously distributed in the Missouri-Mississippi system during the Wisconsin.

*Catostomus macrocheilus Gi*rard - Largescale sucker.

Range - Western North America: Sixes River, Oregon, to the Nass and upper Peace Rivers, British Columbia (Fig. 30).

Northern records - Specimens examined: 275, 288, 295, 296, 306, 307, 313, 320, 328; literature records: none for which the specimens have not been examined.

Glacial refugia - The distribution pattern of *C. macrocheilus* (inset, Fig. 30) indicates survival in the Pacific Refugium.

Chrosomus eos Cope - Northern redbelly dace.

Range - North America: from the Missouri system north to the lower Sass River, N.W.T., and east through the Great Lakes (except Erie) to the Atlantic Coast; relict populations in South Dakota, Nebraska, and Colorado (Fig. 31).

Northern records - Specimens examined: 273, 418; literature records: none for which the specimens have not been examined.

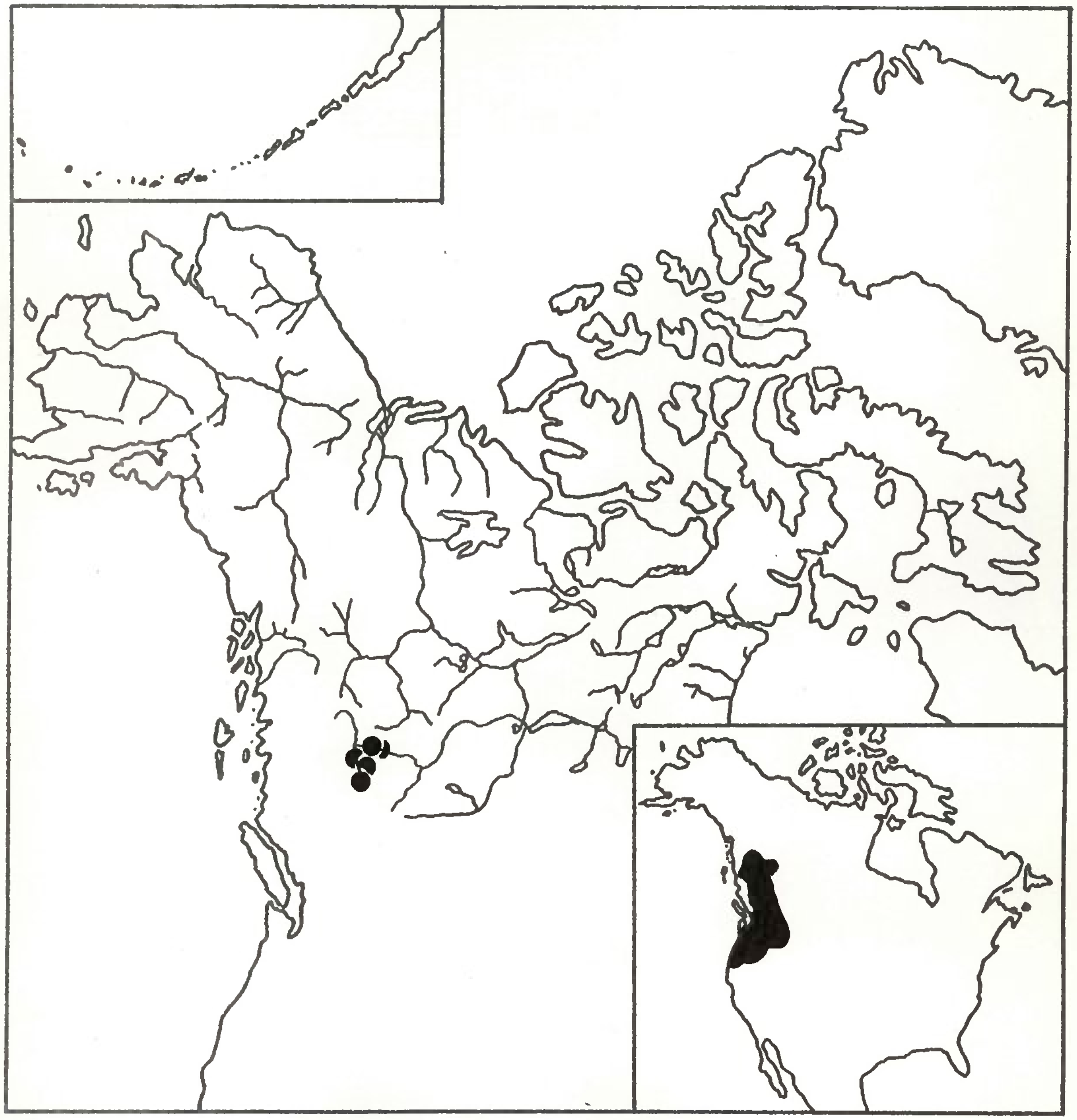


Fig. 30. Northern distribution of C. macrocheilus (inset total distribution). Circles indicate specimens examined, and squares literature records.

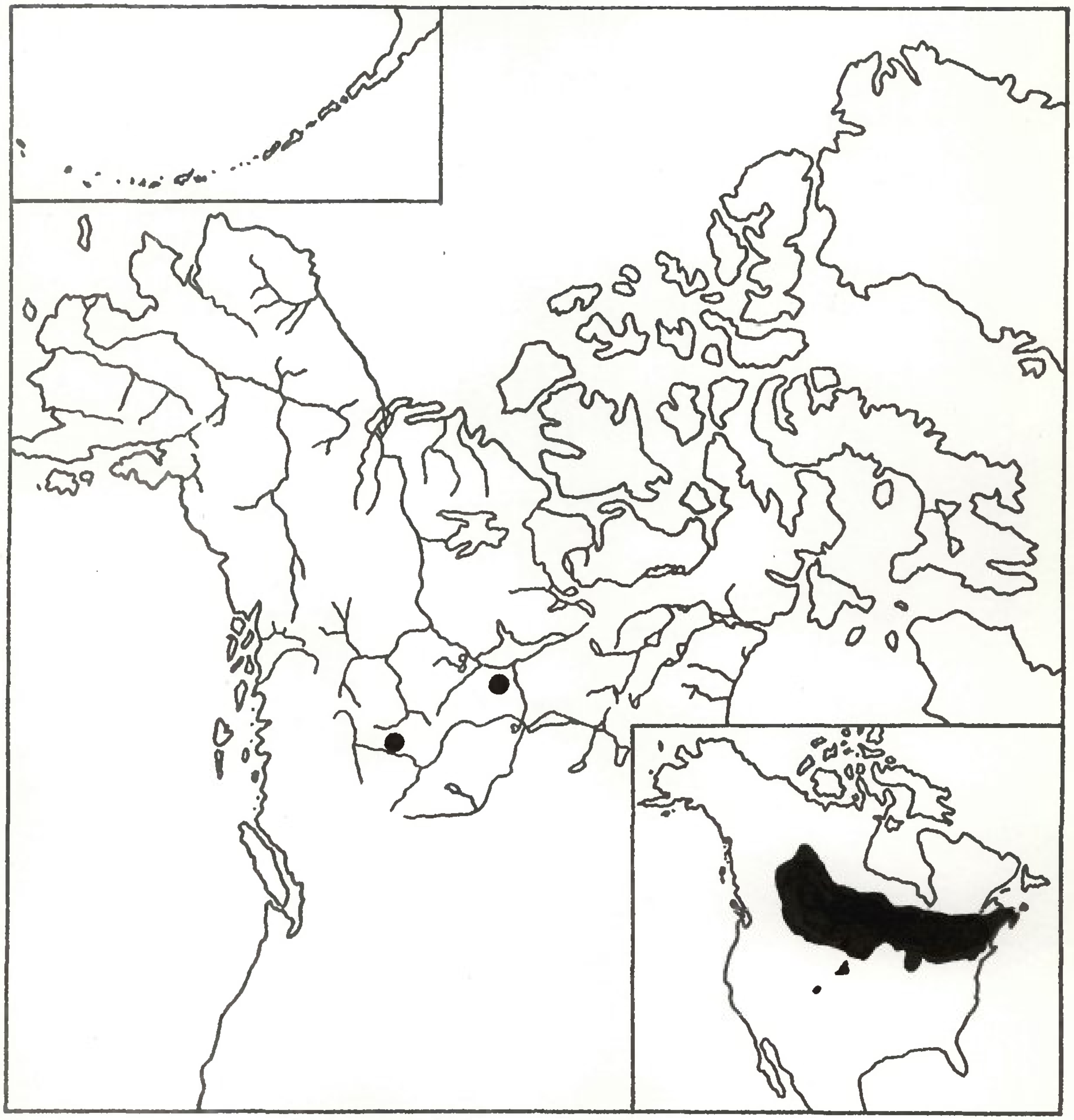


Fig. 31. Northern distribution of C. eos (inset total distribution). Circles indicate specimens examined, and squares literature records.

Glacial refugia - The distribution pattern of *C. eos* (inset Fig. 31) indicates survival in the Mississippi Refugium. The restricted distribution of *C. eos* in the Atlantic Refugium was probably attained postglacially.

Chrosomus neogaeus (Cope) - Finescale dace.

Range - North America: from the upper Mississippi north to Arctic Red River, and east to New Brunswick, Maine, and New Hampshire; relict populations in South Dakota, and Nebraska (Fig. 32).

Northern records - Specimens examined: 235, 277, 303, 336, 397, 418; literature records: 55.

Glacial refugia - The distribution pattern of *C. neogaeus* (inset, Fig. 32) indicates survival in the Mississippi Refugium.

Hybognathus hankonsoni Hubbs - Brassy minnow.

Range - North America: from the Fraser and Peace systems in British Columbia to the Great Lakes (except Lake Erie) and the headwaters of the Hudson River (Fig. 33).

Northern records - Specimens examined: 320; literature records: none for which the specimens have not been examined.

Glacial refugia - The distribution pattern of *H. hankonsoni* (inset, Fig. 33) indicates survival in the Mississippi Refugium. The restricted distribution of the brassy minnow west of the Continental Divide is probably due to postglacial dispersal.

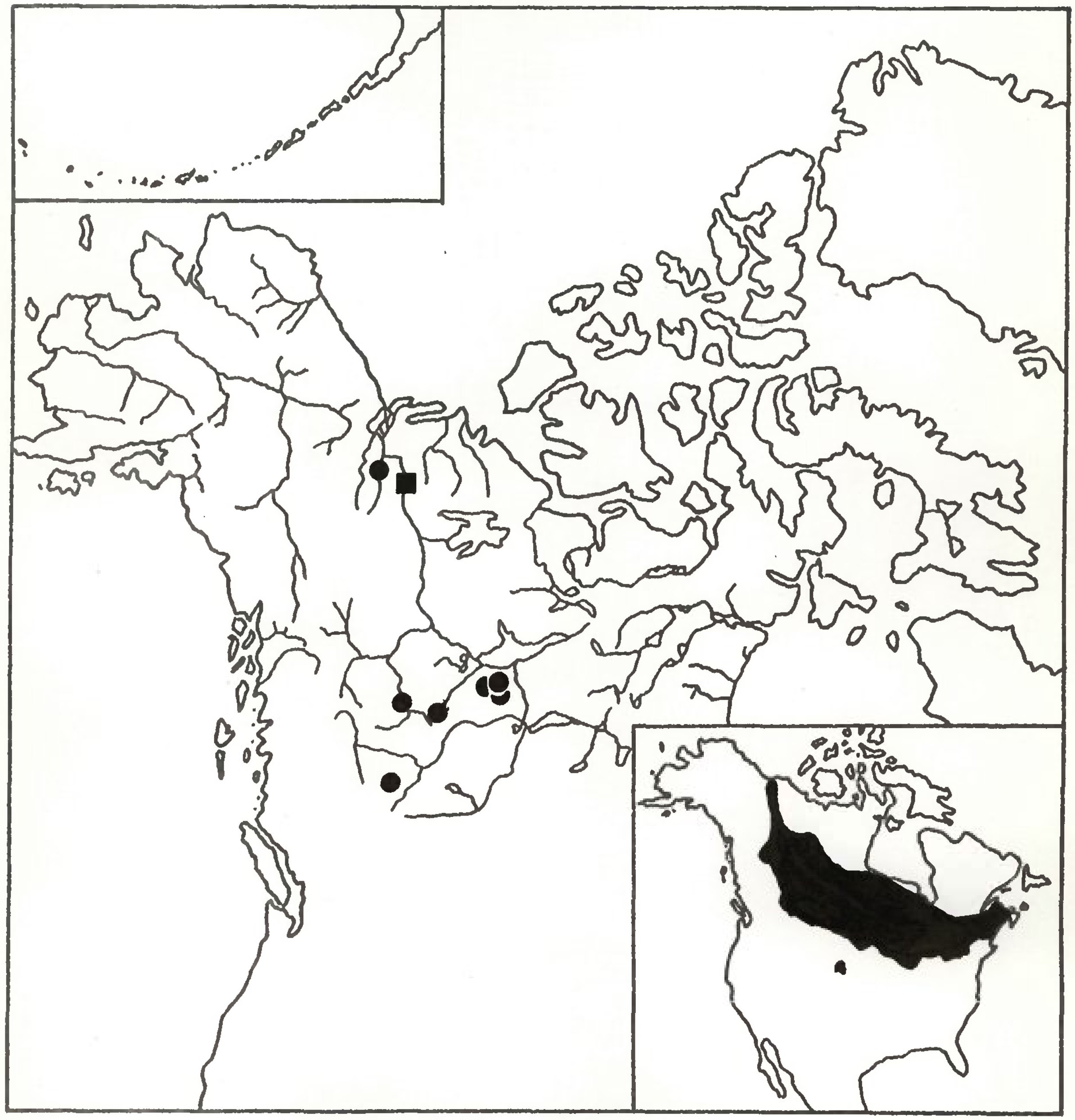


Fig. 32. Northern distribution of C. neogaeus (inset total distribution). Circles indicate specimens examined, and squares literature records.

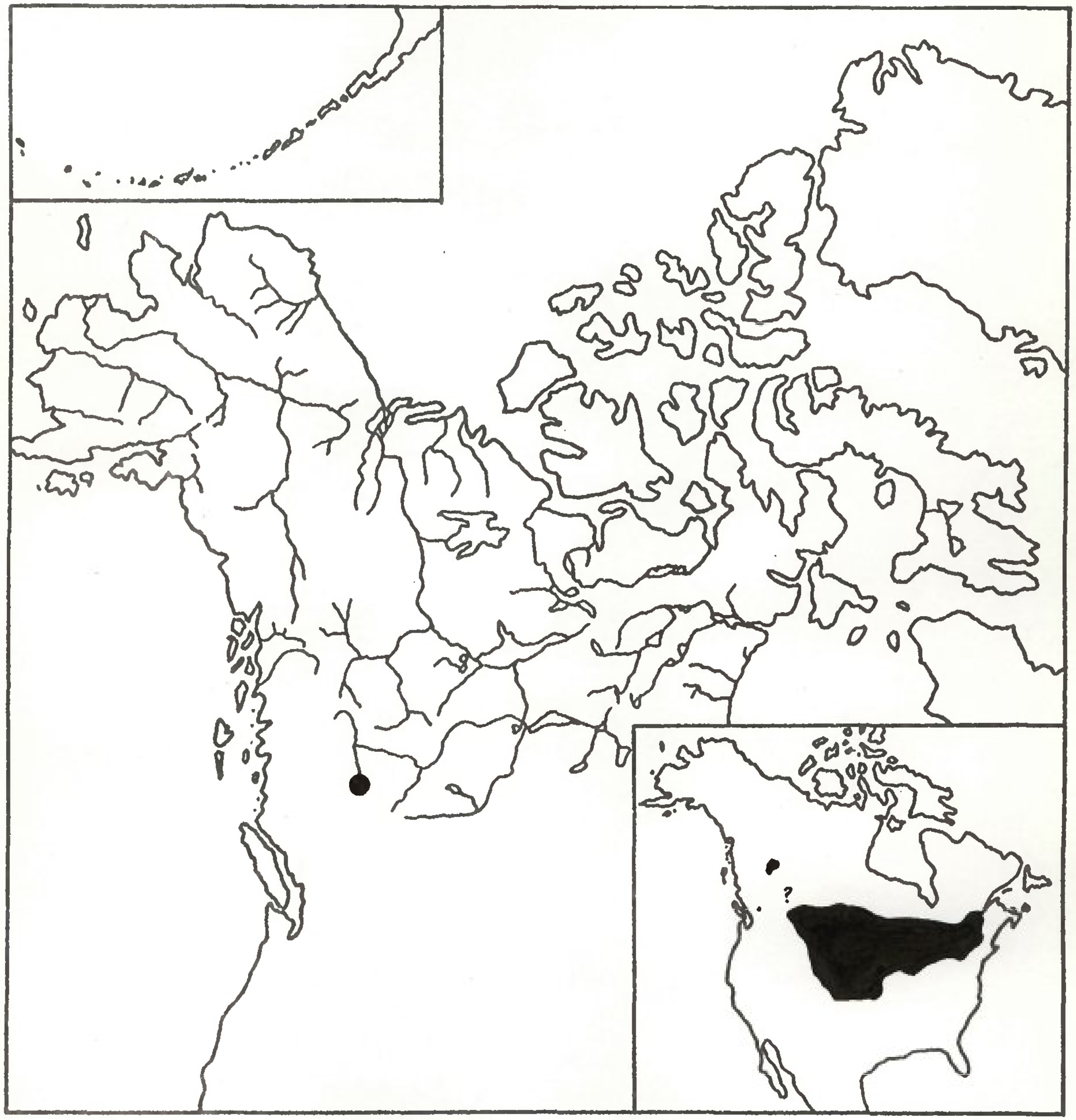


Fig. 33. Northern distribution of H. hankonsoni (inset total distribution). Circles indicate specimens examined, and squares literature records.

Hybopsis gracilis (Richardson) - Flathead chub.

Range - Central North America: from the Rio Grande River north to the Mackenzie Delta (Fig. 34).

Northern records - Specimens examined: 235, 239, 259, 262, 277, 295, 301, 307, 308, 322, 387, 435, 508; literature records: 31, 55.

Glacial refugia - Olund and Cross (1961) recognize two subspecies of flathead chub: H. g. gracilis from Canada, the Missouri and middle Mississippi Rivers, and H. g. gulonella from the Arkansas, Canadian, Pecos, and Rio Grande Rivers. These forms are weakly differentiated, and Bailey and Allum (1962) consider the differences phenotypic.

The distribution pattern of H. gracilis (inset, Fig. 34) indicates survival in the Mississippi Refugium.

Hybopsis plumbea (Agassiz) - Lake chub.

Range - North America: upper Columbia system north to the Yukon River, upper Missouri system east to Nova Scotia and the northern New England states; relict populations in Iowa, South Dakota, Wyoming, and Colorado (Fig. 35).

Northern records - Specimens examined: 15, 19, 38, 41, 55, 131, 146, 173, 193, 194, 228, 239, 246, 248, 251, 254, 262, 265, 268, 281, 289, 292, 294, 296, 298, 301, 308, 311, 320, 325, 330, 334a, 335, 346, 363, 372, 374, 375, 376, 378, 385, 387, 388, 404, 409, 432, 434, 435, 465, 467, 470, 471, 472, 483, 496, 504, 506, 508, 513, 516, 523, 524; literature records: 31, 39.

Glacial refugia - The range of H. plumbea includes

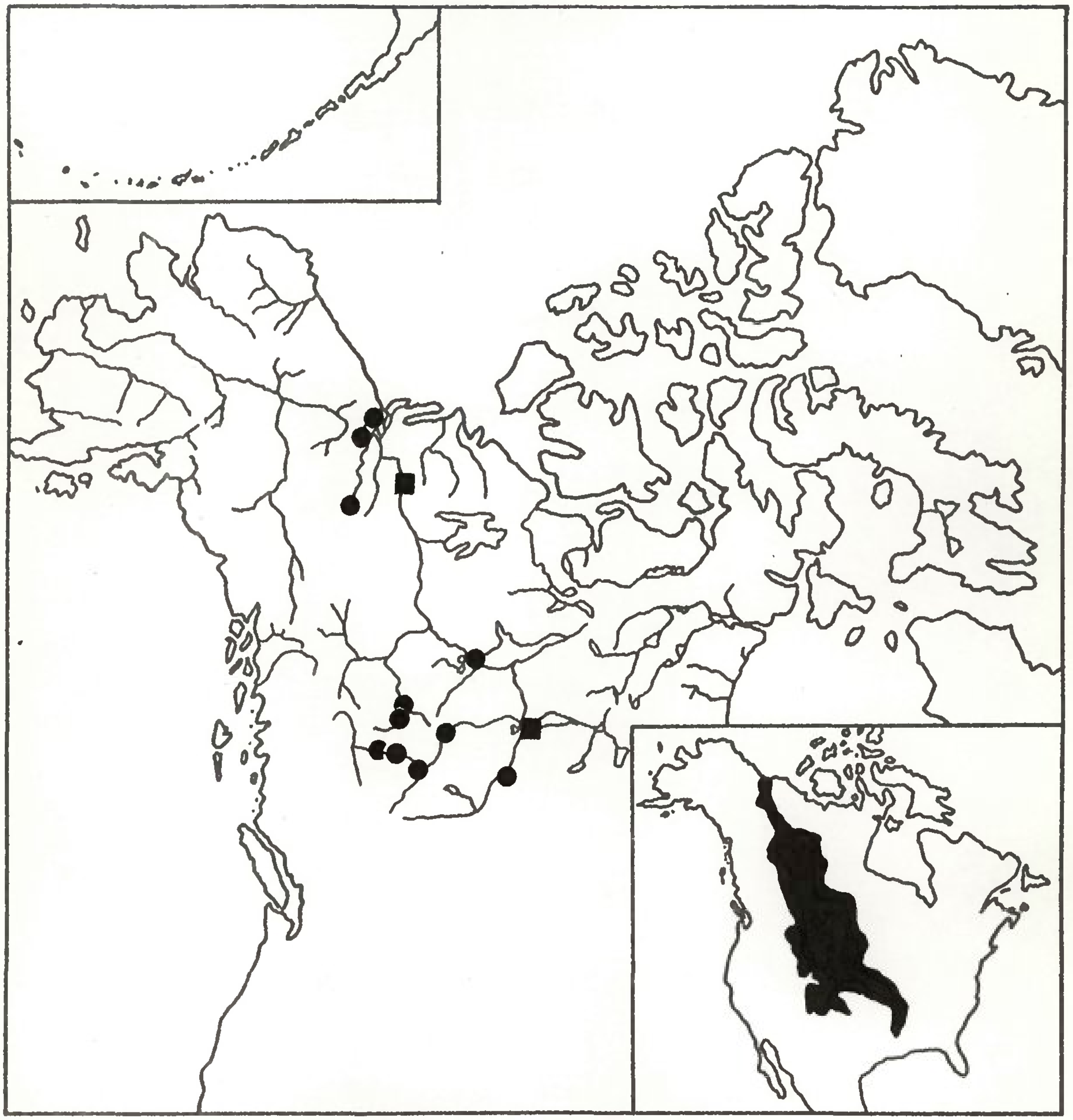


Fig. 34. Northern distribution of H. gracilis (inset total distribution). Circles indicate specimens examined, and squares literature records.

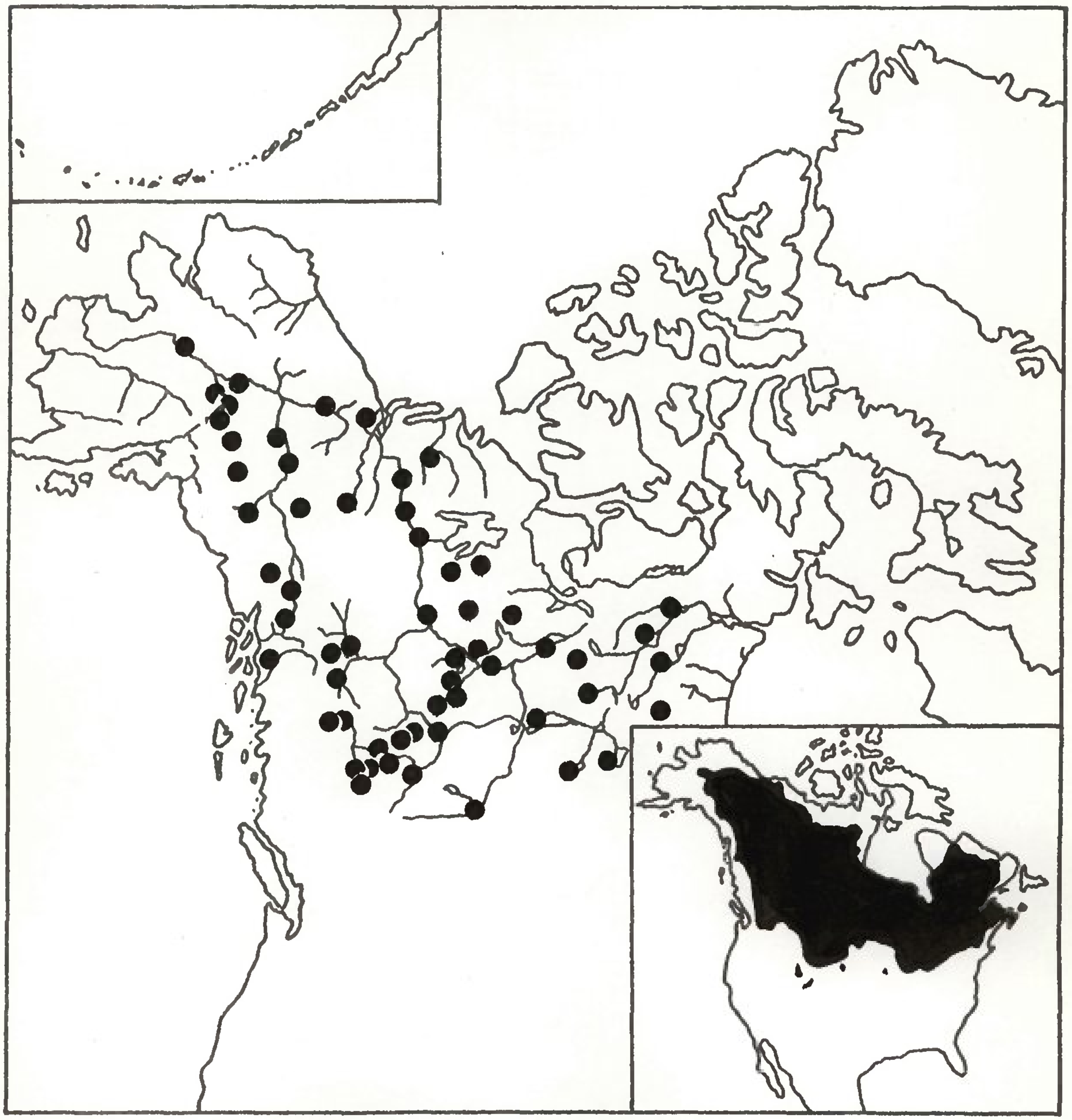


Fig. 35. Northern distribution of H. plumbea (inset total distribution). Circles indicate specimens examined, and squares literature records.

two unglaciated areas: the Bering, and the Mississippi Refugia. In the Columbia system the lake chub extends almost to the southern limit of glaciation. The isolated populations of *H. plumbea* in the Missouri and Mississippi systems suggest that the lake chub was wide spread in the Mississippi Refugium during the Wisconsin glaciation.

The number of lateral line scales, scales around the caudal peduncle, and the number of vertebrae were compared over the entire range of *H. plumbea*. In both the number of caudal peduncle scales and the number of vertebrae (Tables VII and VIII) the populations in the Columbia, Fraser, and upper Peace systems differ significantly ($p < 0.001$) from other populations. The existence of a morphologically distinct form west of the Continental Divide suggests *H. plumbea* may also have survived glaciation in the Pacific Refugium. The present absence of the lake chub from the middle Columbia system is probably due to postglacial climate changes. Figure 36 presents the distribution of the Pacific and Mississippi forms of *H. plumbea*. Both forms occur in northern North America.

Mylocheilus caurinum (Richardson) - Peamouth.

Range - Western North America: Columbia system (except the upper Snake River) to the Nass, upper Peace, and Athabasca Rivers (Fig. 37).

Northern records - Specimens examined: 228, 295, 306, 320; literature records: none for which the specimens have not been examined.

Table VII. Comparison of caudal peduncle scales in

Hybopsis plumbea.

Locality	18	19	20	21	22	23	24	25	N	Mean
Yukon system										
Old Crow			1		2	4	2	1	10	22.9
White R.				4	3	2		1	10	22.1
Kooksatoon L.			1	2	4	2	1		10	22.0
Stewart R.			1			1	2	1	5	23.1
Birch Cr.					1	1	2	1	5	23.6
Warm Bay					1	2	1	1	5	23.4
Niggerhead L.			1	2	3	2	1		9	22.1
Mackenzie system										
Peel R.				1	2	4	2	1	10	23.0
Lac La Martre				1	3	6	4	1	15	22.4
Muskwa R.				1	2	3	2		8	22.8
Kakisa L.			3	4	2	2	1		12	21.5
Athabasca R.			1	3	1	1	1	1	8	22.2
Keg R.			1	1	2	3	2	2	11	22.9
Thelon system										
Whitefish L.				2	2	4	1	1	10	22.7
Dubawnt system										
Dubawnt L.			1	2	1	2	2	1	9	22.3
Peace system below Canyon										
Pouce Coupe R.			1		3	3	2	1	10	22.8
Lynx Cr.			1	2	2	4	1		10	22.2
Peace system above Canyon										
Wolverine Cr.		3	5	3	1				12	20.2
Fraser system										
Middle R.	3	4	3	2					12	19.3
Dragon L.	6	6	4						16	18.8
Crystal L.		2	1	4	3				10	20.8
Fleming L.	1	5	4	3					13	19.7
Columbia system										
Prather L.	1	6	2	1					10	19.3
Jewel L.	3	5	4						12	19.1
Deep Cr.	3	5	2	1					10	19.2
Missouri system										
Broadview					1	3	4	2	10	23.7
Little Missouri				3	3	4	2		12	22.4
Great Lakes					4	8	8	2	22	23.4
New England				1	2	5	2		10	22.8

Table VIII. Comparison of vertebrae in *Hybopsis plumbea*.

Locality	39	40	41	42	43	44	N	Mean
			Vertebrae					
Yukon system								
Old Crow			5	3	2		10	41.7
Stewart R.			2	3	4	1	10	42.4
Mackenzie system								
Peel R.		1	1	6	1		9	41.8
Keg R.		1	2	4	3		10	41.9
Thelon system								
Whitefish L.			5	6	1		12	41.6
Dubawnt system								
Dubawnt L.			1	5	4		10	42.3
Peace system								
Lynx Cr.		2	4	8	1		15	41.5
Fraser system								
Dragon L.	1	9	9	3			22	40.6
Crystal L.		3	7				10	40.7
Fleming L.	1	4	3	2			10	40.6
Columbia system								
Jewel L.	1	6	5	1			13	40.5
Deep Cr.		5	4	1			10	40.6
Missouri system								
Broadview			4	5	1		10	41.7
Little Missouri			4	4	1		9	41.7
Great Lakes		2	3	5	1		11	41.6
New England			2	2	3		7	42.1

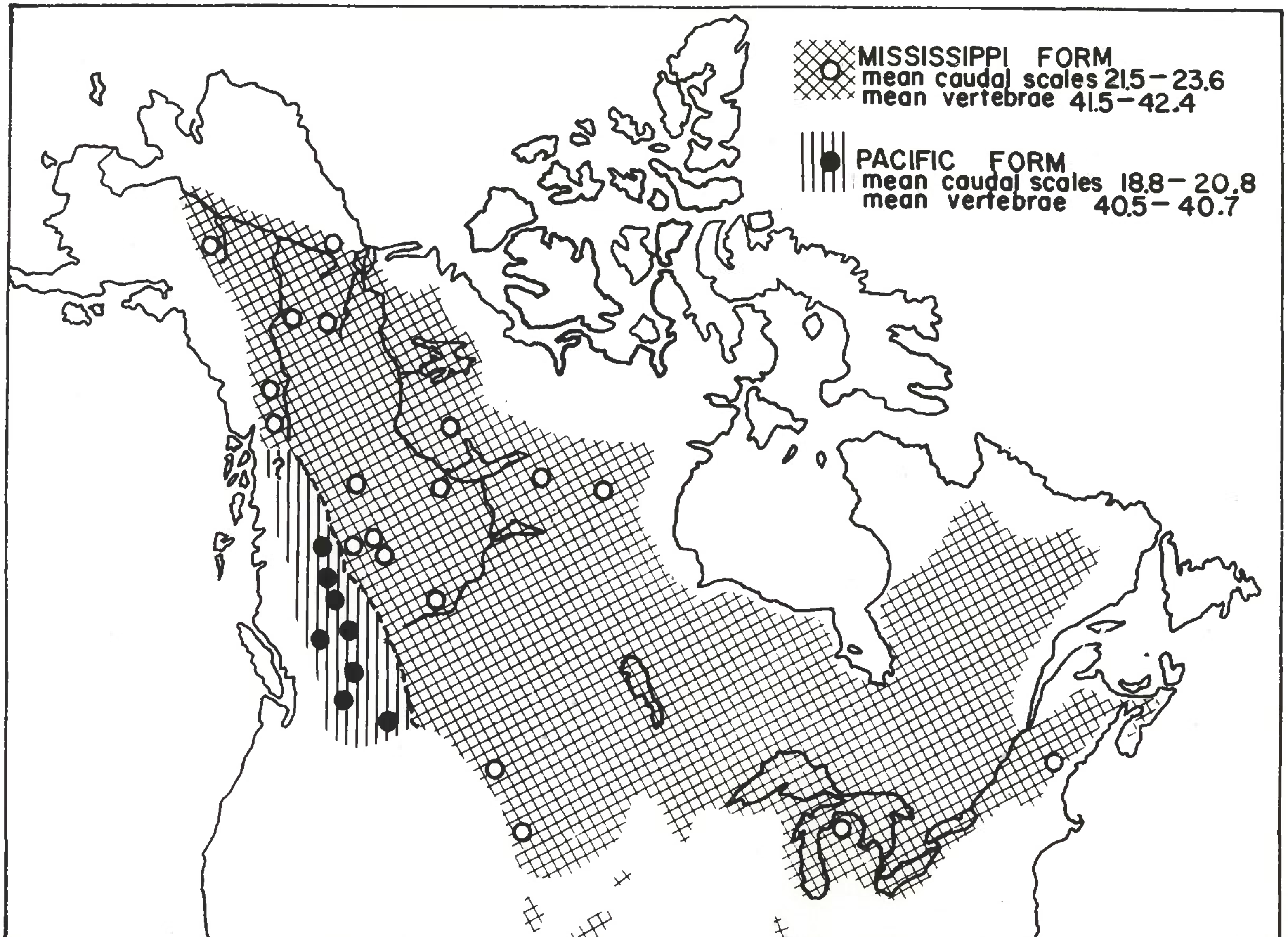


Fig. 36. Geographic variation in the number of caudal peduncle scales and vertebrae in _Hybopsis plumbea_.

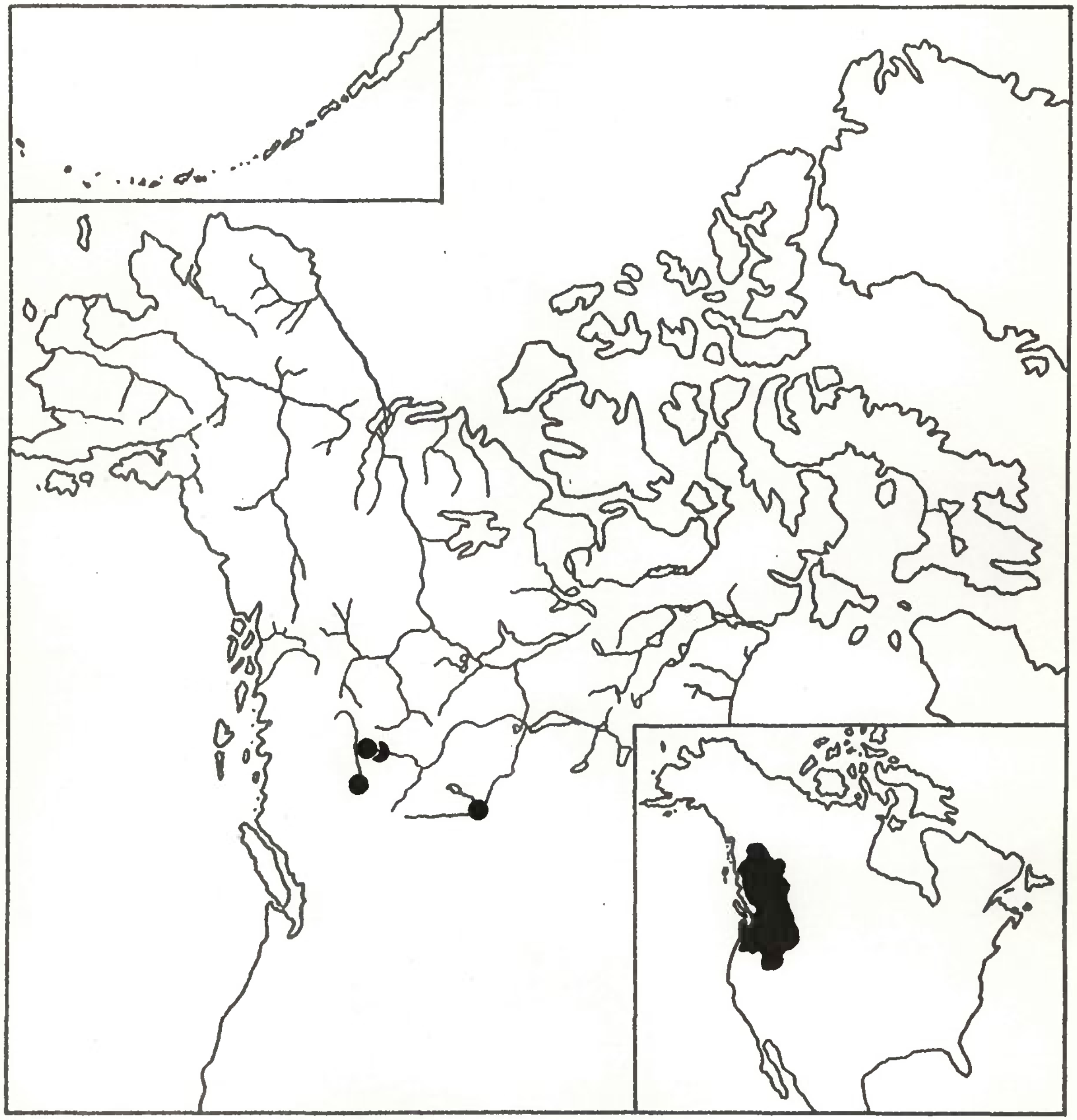


Fig. 37. Northern distribution of M. caurinum (inset total distribution). Circles indicate specimens examined, and squares literature records.

Glacial refugia - The distribution pattern of _M_. _caurinum_ (inset, Fig. 37) indicates survival in the Pacific Refugium.

Notropis atherinoides Rafinesque - Emerald shiner.

Range - Central North America: from the Trinity River, Texas, to the Liard River, British Columbia (Fig. 38).

Northern records - Specimens examined: 236, 253, 275, 277, 387; literature records: 39.

Glacial refugia - Bailey and Allum (1962) synonymize _Notropis percobromus_ with _Notropis atherinoides_. However, the two forms occur sympatrically (Hubbs, 1945), and it is questionable whether the synonymy is valid. The present discussion deals only with _N_. _atherinoides_ (_sensu stricto_). The distribution pattern of _N_. _atherinoides_ (inset, Fig. 38) indicates survival in the Mississippi Refugium.

Notropis hudsonius (Clinton) - Spottail shiner.

Range - North America: from the upper Mississippi north to Ft. Good Hope, N.W.T., and on the Atlantic Coast from the Hudson River south to the Ocmulgee River, Georgia (Fig. 39).

Northern records - Specimens examined: 232, 234, 236, 239, 253, 348, 372, 375, 378, 388, 391, 404, 449, 468; literature records: 39.

Glacial refugia - The range of _N_. _hudsonius_ includes two unglaciated areas: the Mississippi, and the Atlantic Refugia. The spottail shiner is widely distributed in these

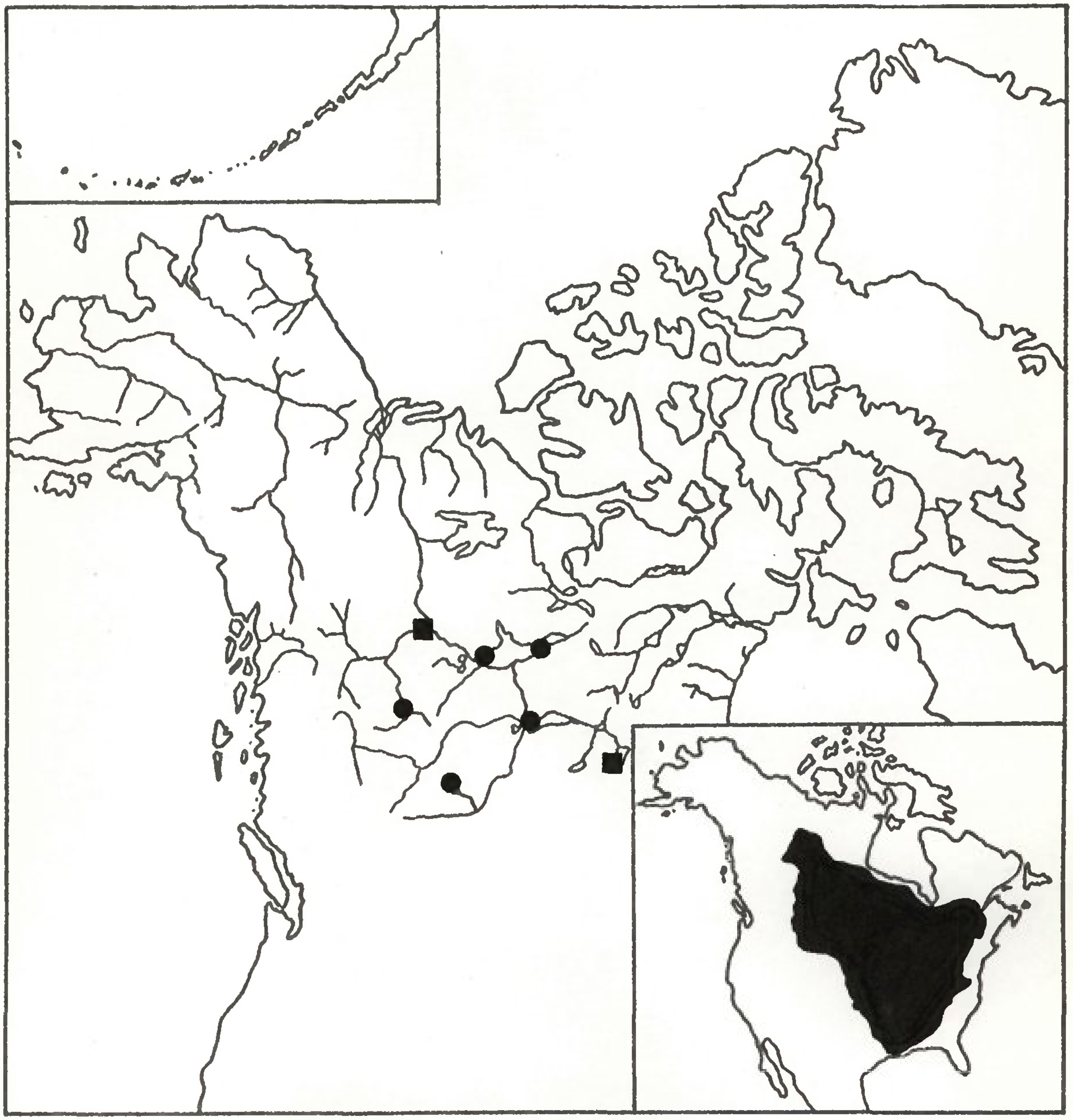


Fig. 38. Northern distribution of N. atherinoides (inset total distribution). Circles indicate specimens examined, and squares literature records.

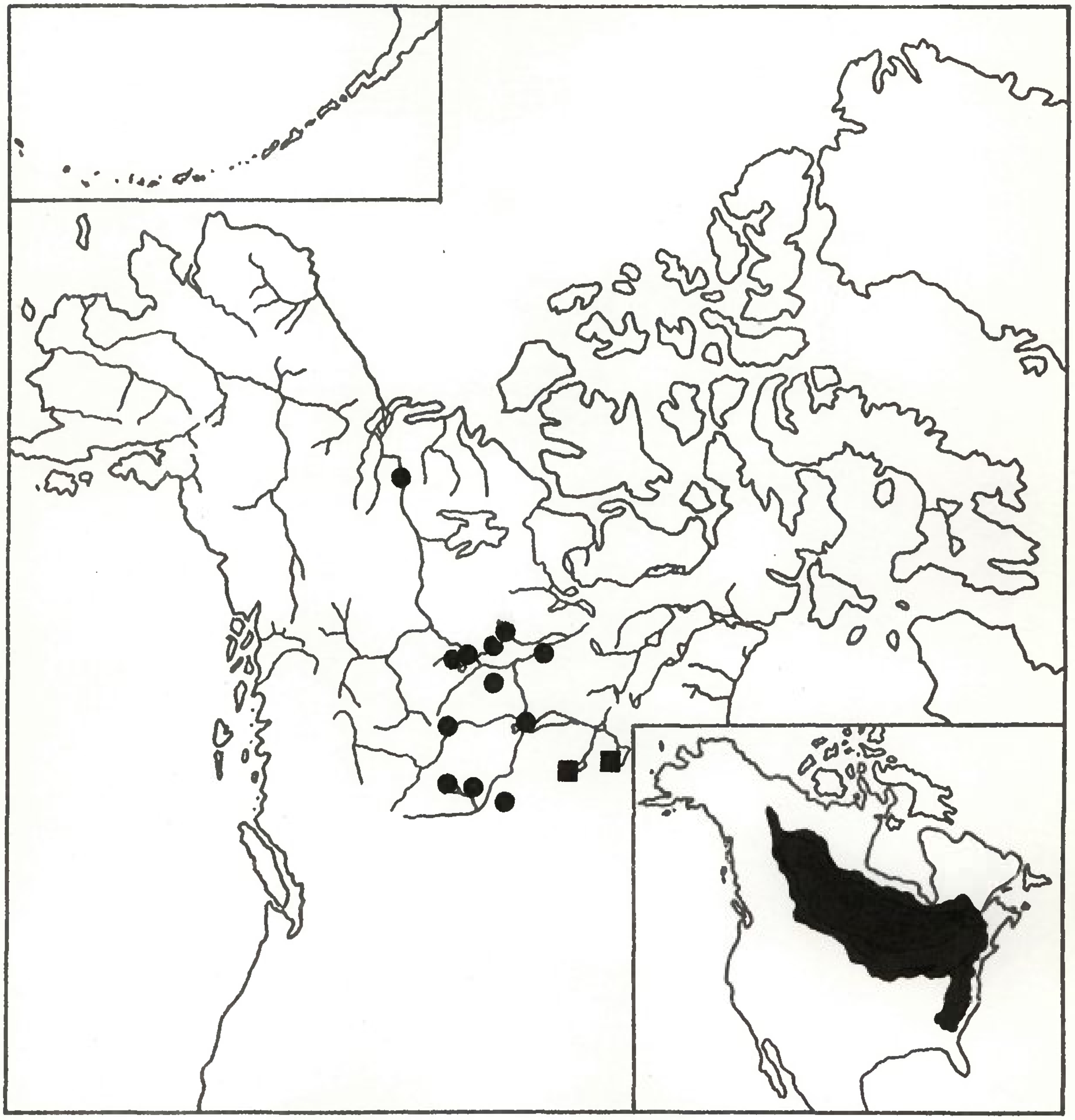


Fig. 39. Northern distribution of N. hudsonius (inset total distribution). Circles indicate specimens examined, and squares literature records.

areas, and probably survived glaciation in both refugia. The distribution of N. hudsonius in northern North America is probably due to postglacial dispersal from the Mississippi Refugium.

Pimephales promelas Rafinesque - Fathead minnow.

Range - North America: from the Rio Grande and Rio Yaqui systems, Mexico, north to the Hole Lakes, N.W.T.; isolated populations in Oklahoma,(Fig. 40).

Northern records - Specimens examined: 233, 381, 397; literature records: 31.

Glacial refugia - The distribution pattern of P. promelas (inset Fig. 40) indicates survival in the Mississippi Refugium. An early postglacial (about 10,000 B.P.) subfossil is known from southern Saskatchewan (R. R. Miller, pers. comm.).

Ptychocheilus oregonensis (Richardson) - Northern squawfish.

Range - Western North America: Columbia system (except the upper Snake River) to the Nass and upper Peace Rivers (Fig. 41).

Northern records - Specimens examined: 296, 307, 311, 320; literature records: none for which the specimens have not been examined.

Glacial refugia - The distribution pattern of P. oregonensis (inset, Fig. 41) indicates survival in the Pacific Refugium.

Richardsonius balteatus (Richardson) - Redside shiner.

Range - Western North America: Columbia system to

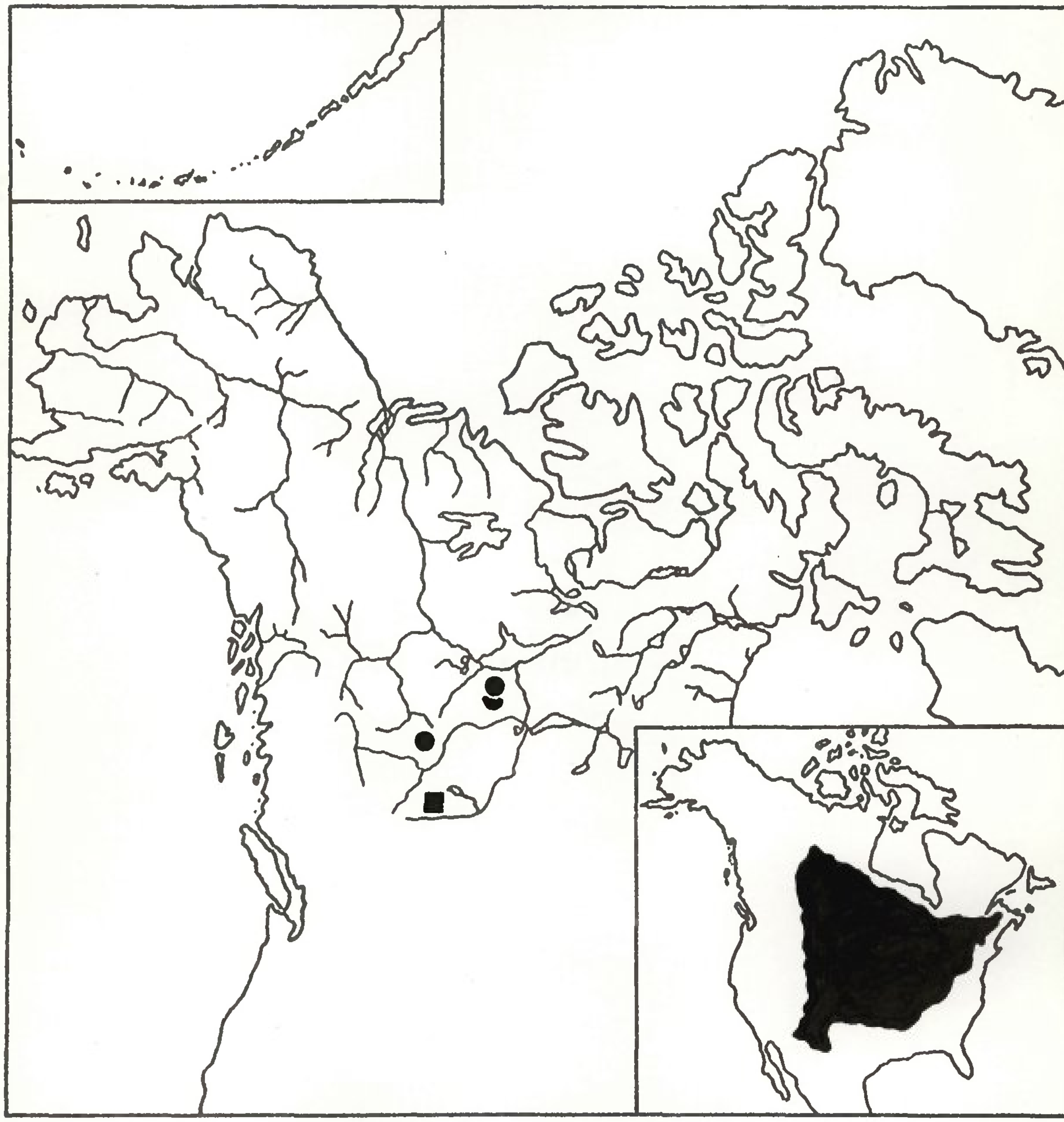


Fig. 40. Northern distribution of P. promelas (inset total distribution). Circles indicate specimens examined, and squares literature records.

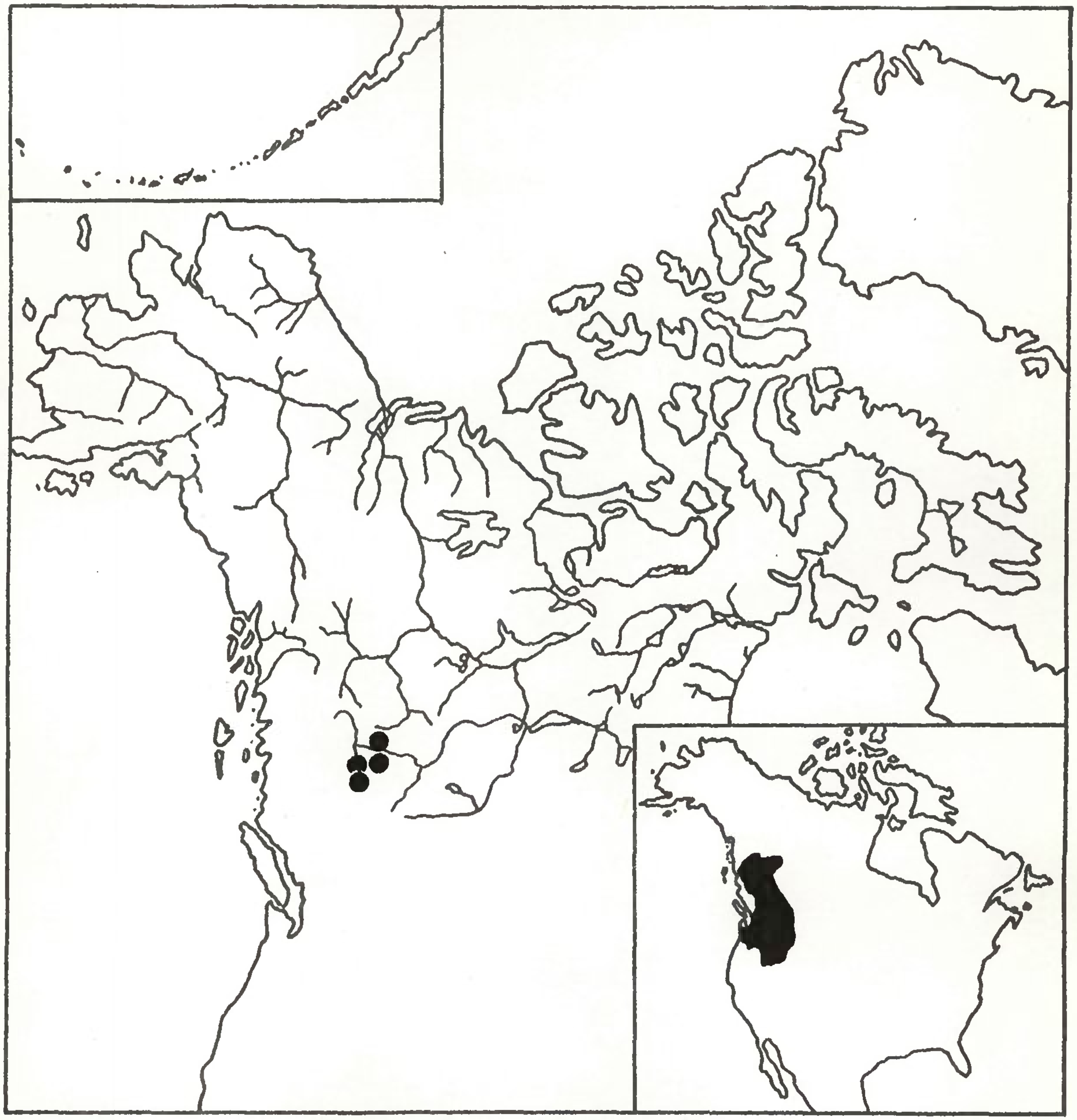


Fig. 41. Northern distribution of P. oregonensis (inset total distribution). Circles indicate specimens examined, and squares literature records.

the upper Peace River (Fig. 42).

Northern records - Specimens examined: 262, 263, 265, 266, 275, 280, 283, 288, 296, 298, 306, 307, 311, 313, 320, 323, 328; literature records: none for which the specimens have not been examined.

Glacial refugia - The distribution pattern of *R. balteatus* (inset, Fig. 42) indicates survival in the Pacific Refugium.

Rhinichthys cataractae (Valenciennes) - Longnose dace.

Range - North America: Rio Grande system, Mexico, to the Mackenzie Delta, and from Oregon to North Carolina (Fig. 43).

Northern records - Specimens examined: 239, 247, 248, 257, 262, 265, 266, 277, 285, 289, 295, 297, 301, 305, 306, 307, 311, 388, 393; literature records: 31.

Glacial refugia - The wide range of *R. cataractae* suggests survival in multiple refugia. Its range includes three unglaciated areas: the Pacific, the Mississippi, and the Atlantic Refugia. The longnose dace is widely distributed in these areas, and probably survived glaciation in all three refugia. No attempt was made to analyze geographic variation in *R. cataractae*.

It is unlikely that the Atlantic Refugium contributed to the northern distribution of *R. cataractae*. The presence of *R. cataractae* in northern North America probably due to post-glacial dispersal from both the Pacific and the Mississippi Refugia.

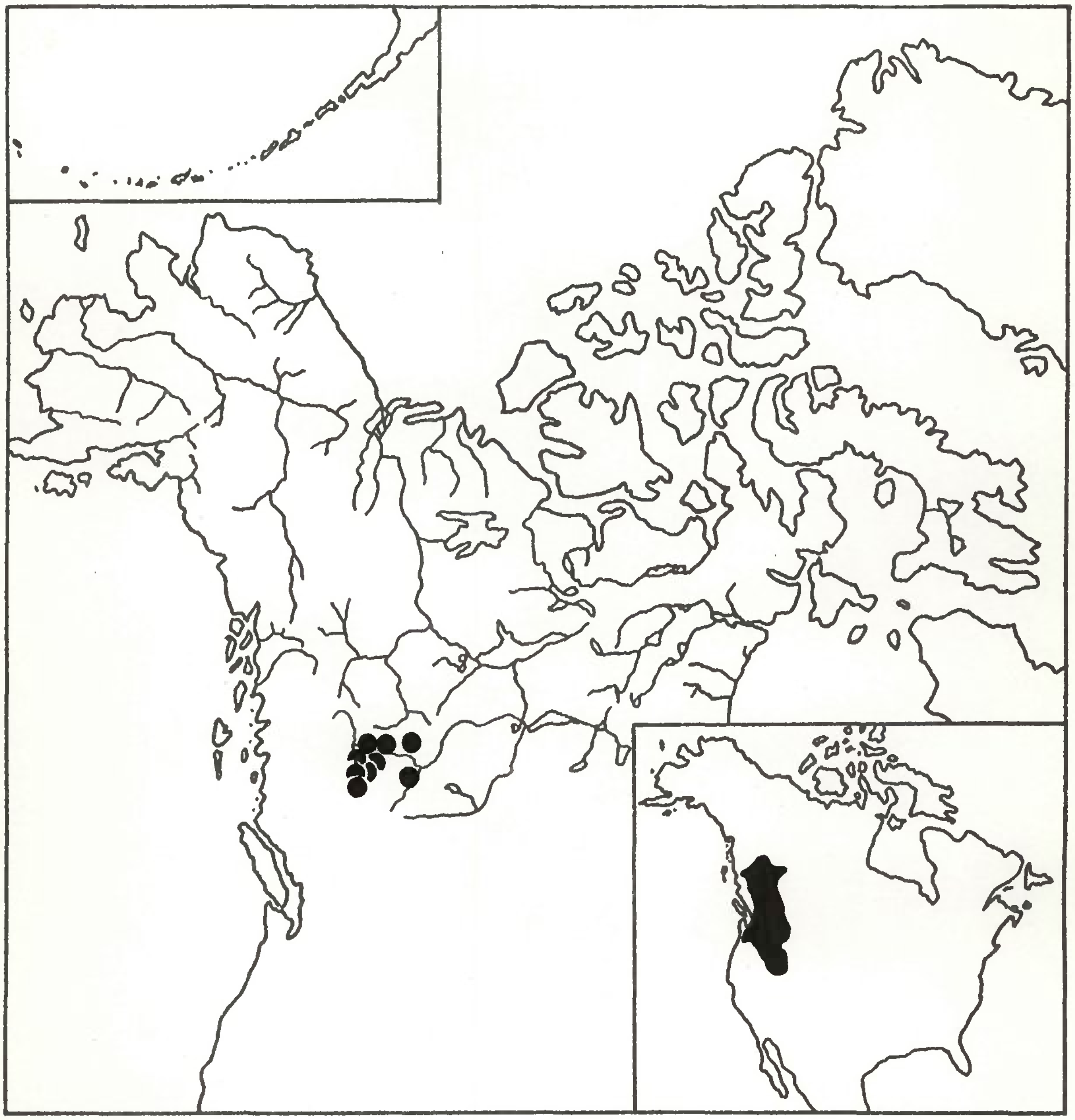


Fig. 42. Northern distribution of R. balteatus (inset total distribution). Circles indicate specimens examined, and squares literature records.

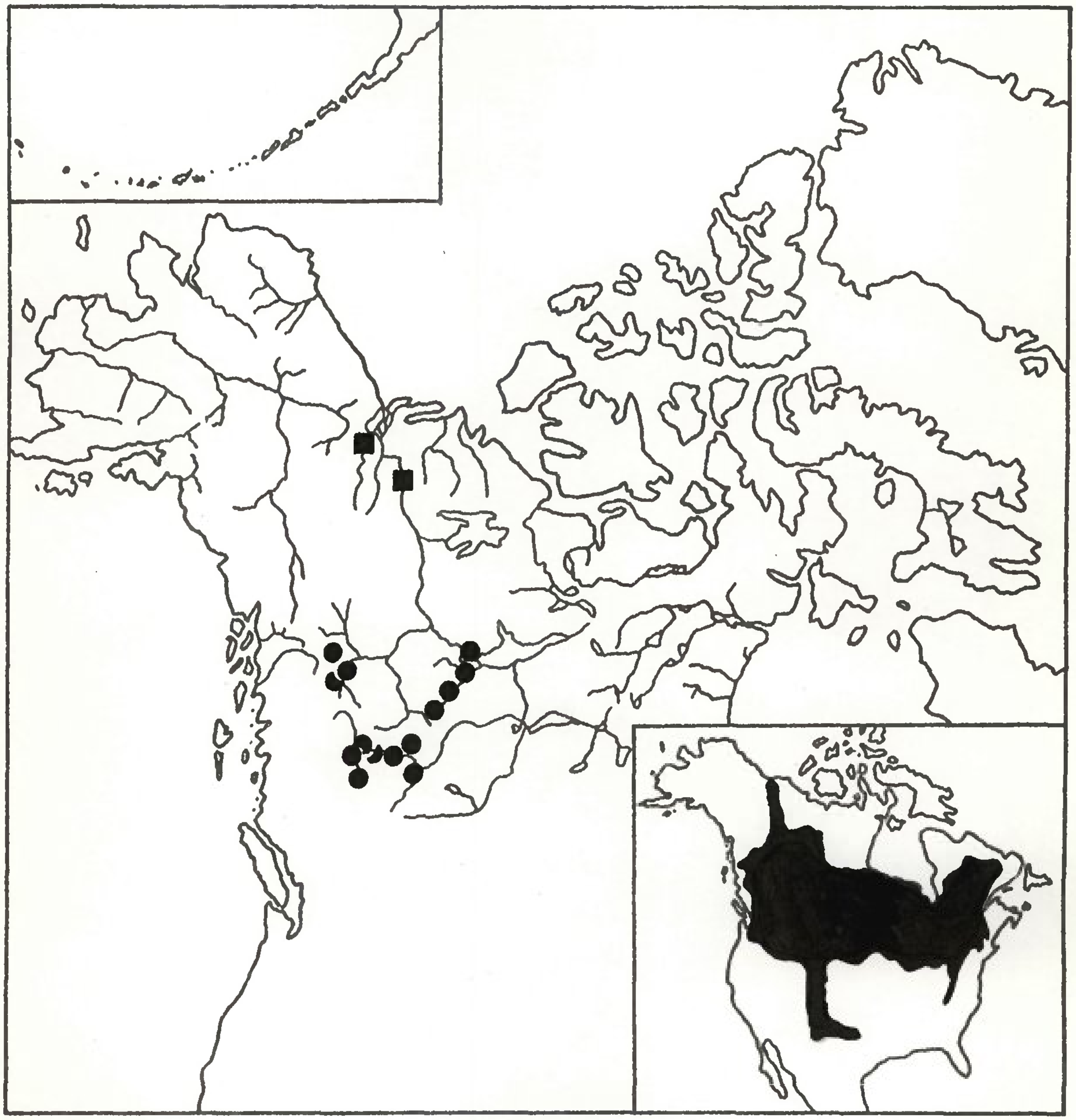


Fig. 43. Northern distribution of R. cataractae (inset total distribution). Circles indicate specimens examined, and squares literature records.

Semotilus _margarita_ (Cope) - Pearl dace.

Range - North America: Missouri system north to the lower Sass River, N.W.T., and through the Great Lakes to the Atlantic Coast; on the Atlantic Coast from Gaspe south to Virginia; relict populations in South Dakota and Nebraska (Fig. 44).

Northern records - Specimens examined: 240, 258, 273, 282, 317, 381, 418; literature records: 31.

Glacial refugia - There are two recognized subspecies of pearl dace: _S_. _margarita_ _margarita_ of the Atlantic Coastal Plain, and _S_. _margarita_ _nachtreibi_ the northern pearl dace (Bailey and Allum, 1962). Only _S_. _m_. _nachtreibi_ enters northern North America.

The distribution pattern of _S_. _m_. _nachtreibi_ (inset, Fig. 44) indicates survival in the Mississippi Refugium.

Dallia _pectoralis_ Bean - Alaska blackfish.

Range - Lowlands in Alaska and the Chukchi Peninsula, Siberia (Fig. 45).

Northern records - Specimens examined: 4, 5, 15a, 42, 56, 105, 107, 111, 122, 133, 143, 145, 149, 150, 170, 189, 203, 204; literature records: 5, 7, 33, 35.

Glacial refugia - The range of _D_. _pectoralis_ is almost restricted to the Bering Refugium. _Dallia_ is present on St. Lawrence and St. Matthew Islands (both remnants of the Bering Land Bridge). Since _Dallia_ is stenohaline it must have been present in the Bering Refugium before the late glacial rise in sea level.

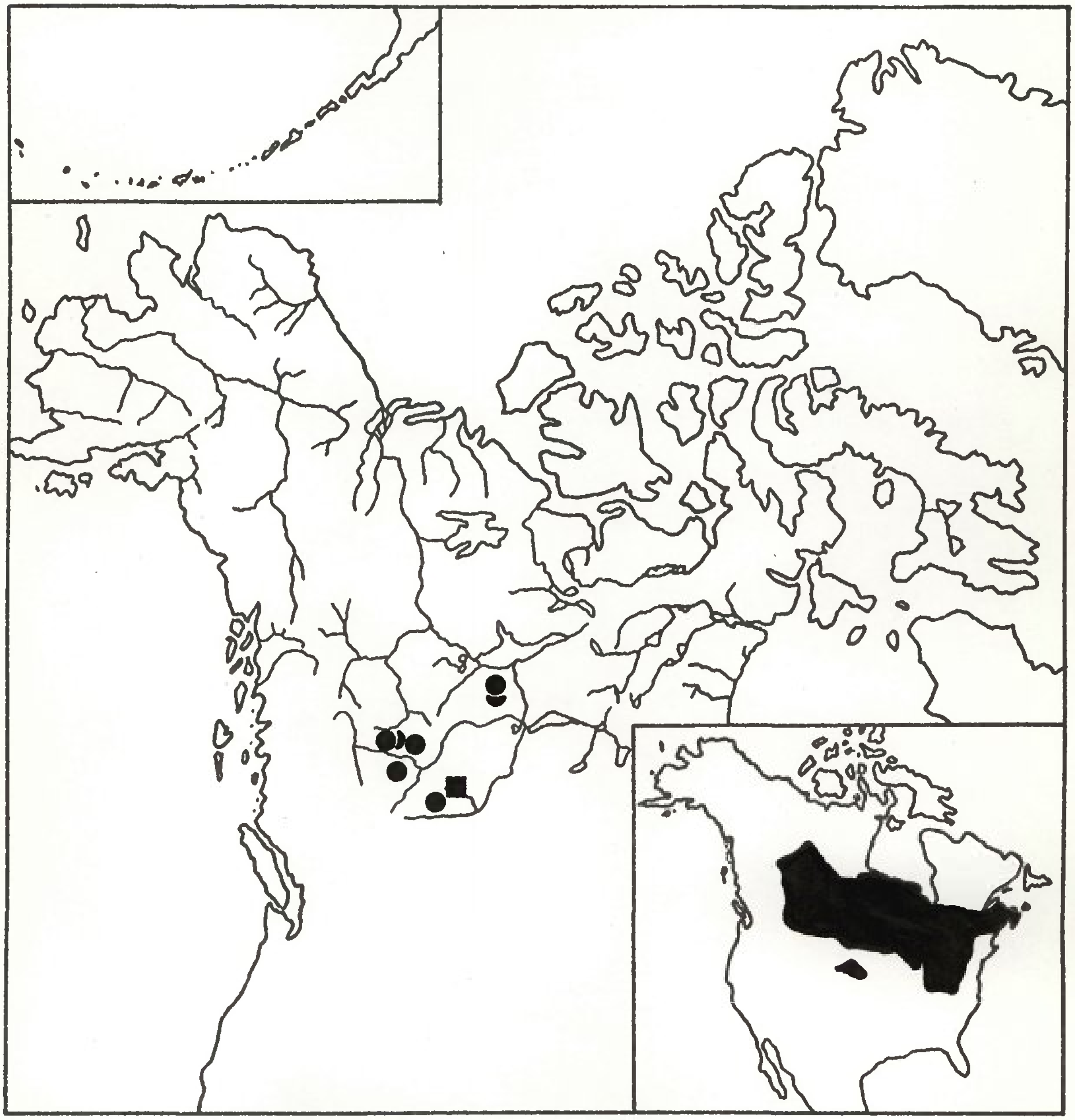


Fig. 44. Northern distribution of S. margarita (inset total distribution). Circles indicate specimens examined, and squares literature records.

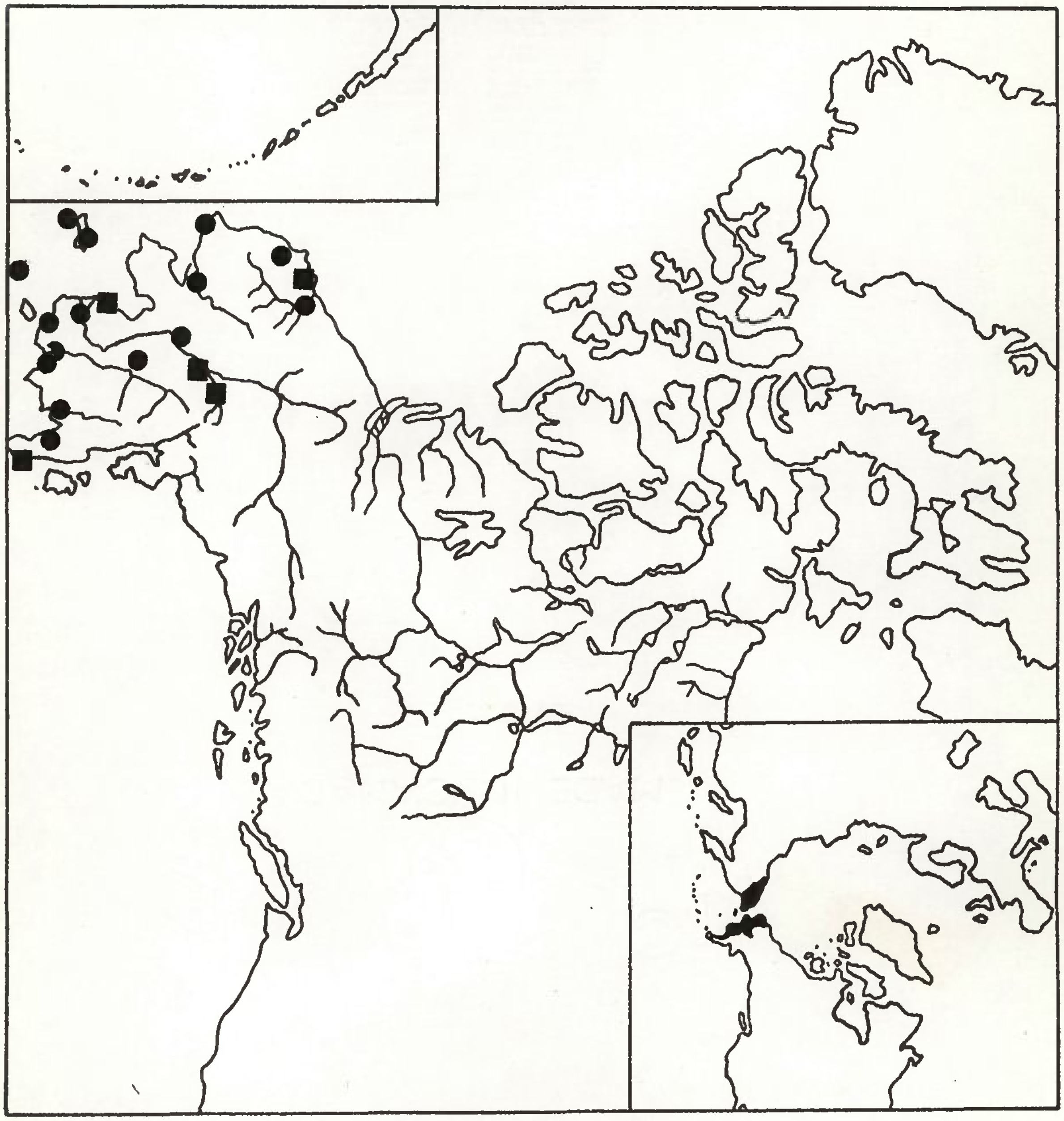


Fig. 45. Northern distribution of D. pectoralis (inset total distribution). Circles indicate specimens examined, and squares literature records.

Esox lucius Linnaeus - Northern pike.

Range - Europe, Asia, and North America; in North America from the upper Mississippi to the Mackenzie Delta, and from Alaska to Labrador (Fig. 46).

Northern records - Specimens examined: 4, 5, 6, 9, 18, 19, 31, 38, 101, 105, 112, 113, 116, 120, 124, 138, 147, 184, 189, 194, 201, 230, 231, 239, 244, 245, 249, 253, 256, 261, 265, 276, 285, 286, 291, 293, 298, 301, 326, 332, 334, 335, 336, 341, 346, 347, 352, 360, 374, 375, 376, 385, 387, 388, 390, 393, 394, 402, 404, 409, 414, 422, 432, 435, 440, 441, 449, 455, 457, 461, 465, 466, 467, 474, 475, 495, 505, 506, 510, 511, 515, 516, 524; literature records: 1, 4, 6, 10, 30, 31, 33, 37, 39, 53.

Glacial refugia - The range of E. lucius includes two unglaciated areas: the Bering, and the Mississippi Refugia. The northern pike is widely distributed in these areas, and probably survived glaciation in both refugia.

The number of branchiostegal rays, gill rakers, and vertebrae were compared over the North American range of E. lucius. Only the number of vertebrae suggests two morphological forms (Table IX). Vertebral count differs significantly ($p < 0.001$) between the Yukon River and the Mackenzie River at approximately the same latitude, while there is no significant difference ($p > 0.10$) in vertebrae number between Mackenzie River and Great Lakes E. lucius. This suggests that the vertebral differences are not phenotypic, and there are probably two genetic forms of

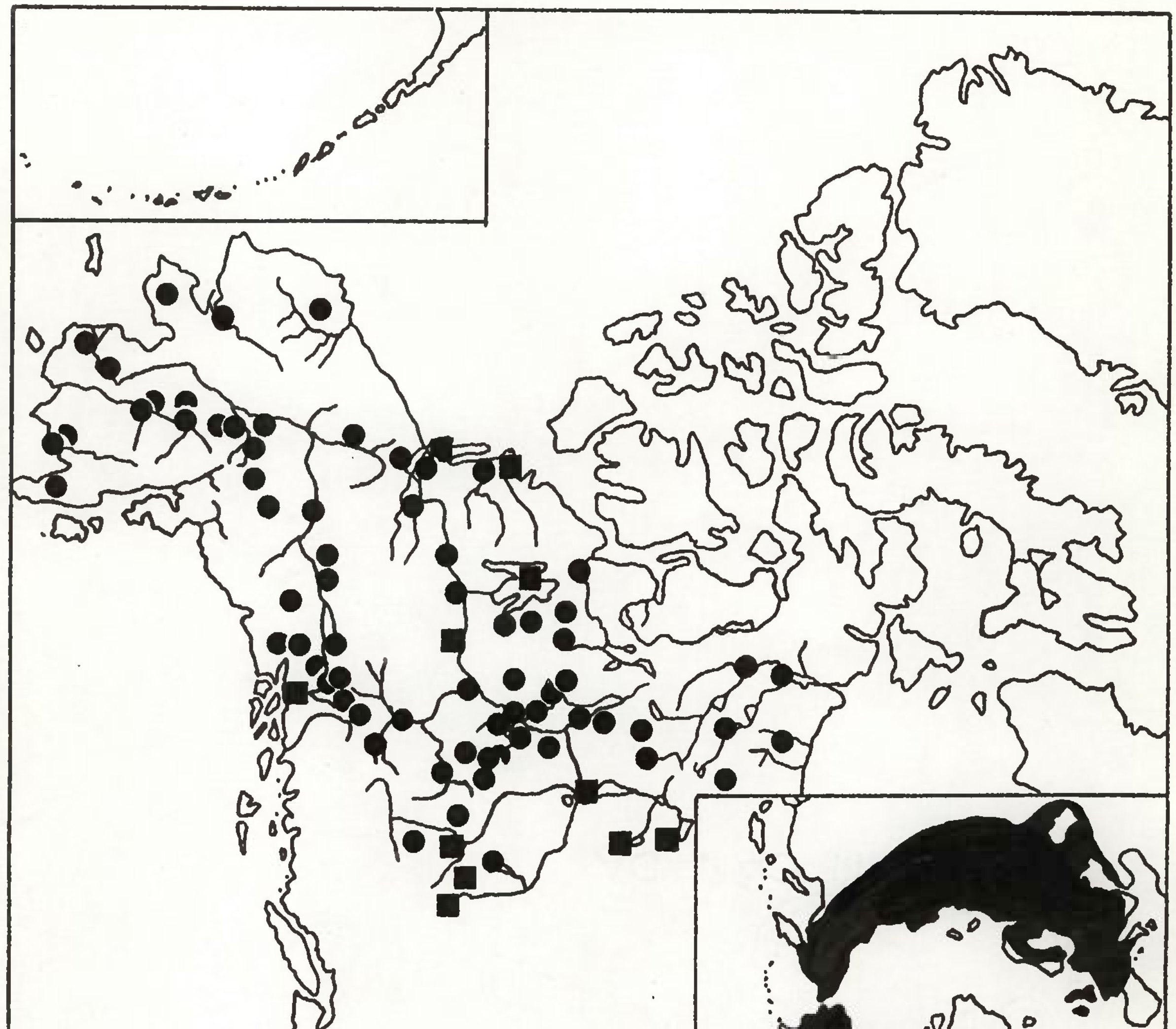


Fig. 46. Northern distribution of E. lucius (inset total distribution). Circles indicate specimens examined, and squares literature records.

Table IX. Comparison of vertebrae in North American *Esox lucius*.

Locality	Vertebrae 57	58	59	60	61	62	63	64	N	Mean
Yukon system				1	5	6	3	1	16	61.89
Aleknagik				1	2	5	1	1	10	61.90
Liard R. (above canyon)							1		1	
Muskawa R.			1	2					3	59.66
Great Slave L. (tributary)		1	3	3	3	2			12	60.01
Hay R.		2	4	2	2				10	59.40
Whitefish L.				2					2	60.00
Knowlton L.# Ontario	2		1	2	6				11	59.98

Data courtesy of E. J. Crossman, Royal Ontario Museum.

E. lucius in North America.

Figure 47 presents the probable distribution of the two forms of *E. lucius* in North America. Both forms occur in northern North America.

Lota lota (Linnaeus) - Burbot.

Range - Europe, Asia, and North America; in North America from the Missouri and upper Mississippi to the Mackenzie Delta, and from Alaska across Canada to Labrador, and south to the New England States (Fig. 48).

Northern records - Specimens examined: 4, 5, 6, 8, 9, 10, 11, 38, 41, 42, 44, 55, 69, 98, 113, 118, 121, 131, 135, 145, 149, 155, 157, 184, 195, 211, 243, 245, 253, 262, 277, 298, 304, 309, 321, 326, 330, 332, 335, 337, 339, 343, 346, 347, 352, 360, 363, 372, 384, 385, 386, 388, 402, 407, 408, 414, 422, 423, 424, 425, 435, 441, 449, 453, 454, 455, 458, 461, 462, 465, 467, 474, 483a, 494a, 511, 522; literature records: 1, 12, 14, 16, 18, 23, 31, 32, 33, 37, 39, 49.

Glacial refugia - The North American range of *L. lota* includes two unglaciated areas: the Bering, and the Mississippi Refugia. The burbot is widely distributed in both areas. Hubbs and Schultz (1941) named a subspecies of burbot (*L. l. leptura*) from Alaska. These authors distinguished *L. l. leptura* from *L. l. lacustris* of central North America on the basis of a ratio of caudal peduncle length to caudal peduncle height. However, Lindsey (1956) demonstrates a north-south and east-west cline in this character, and suggests

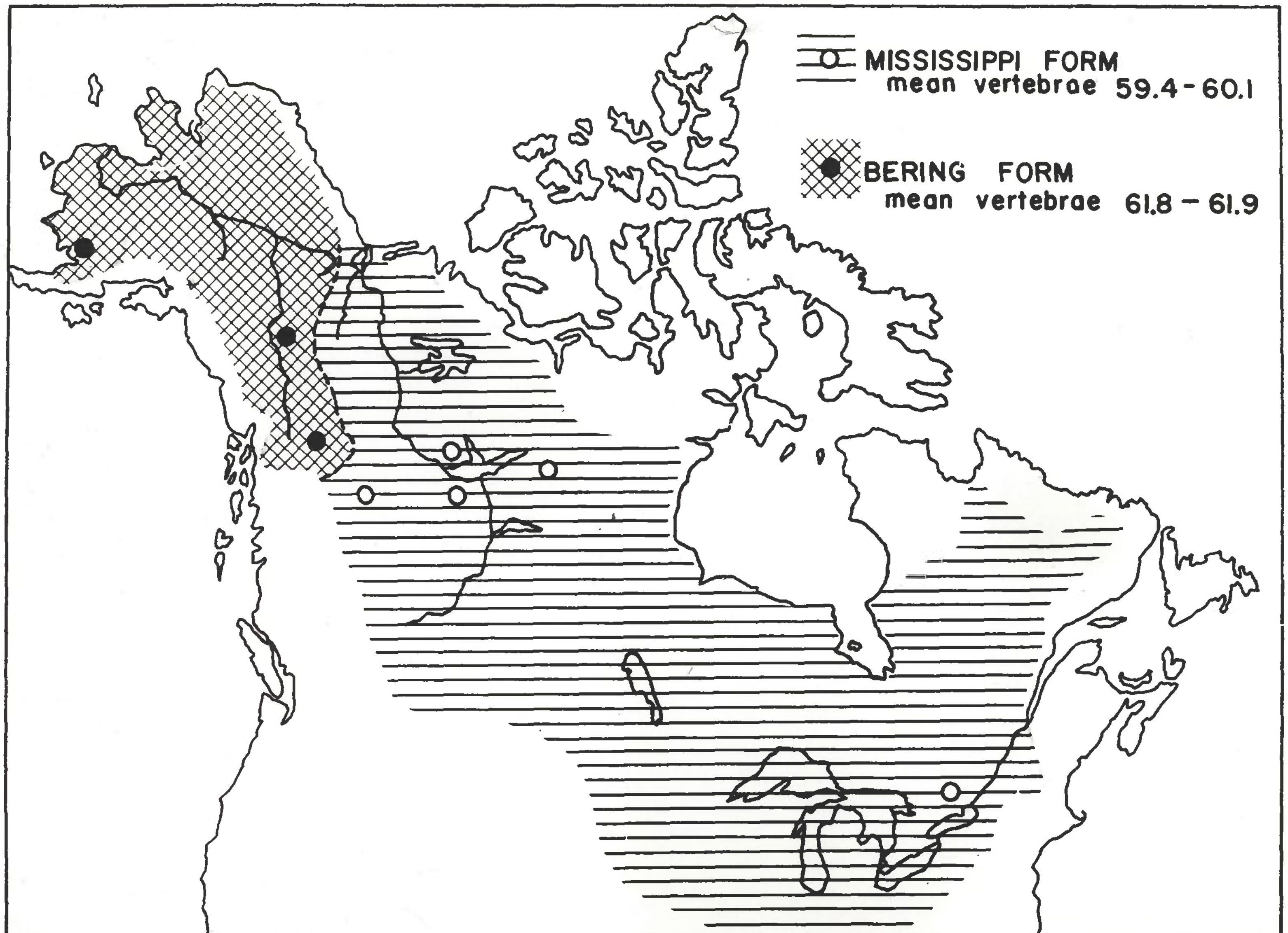


Fig. 47. Geographic variation in the number of vertebrae in Esox lucius.

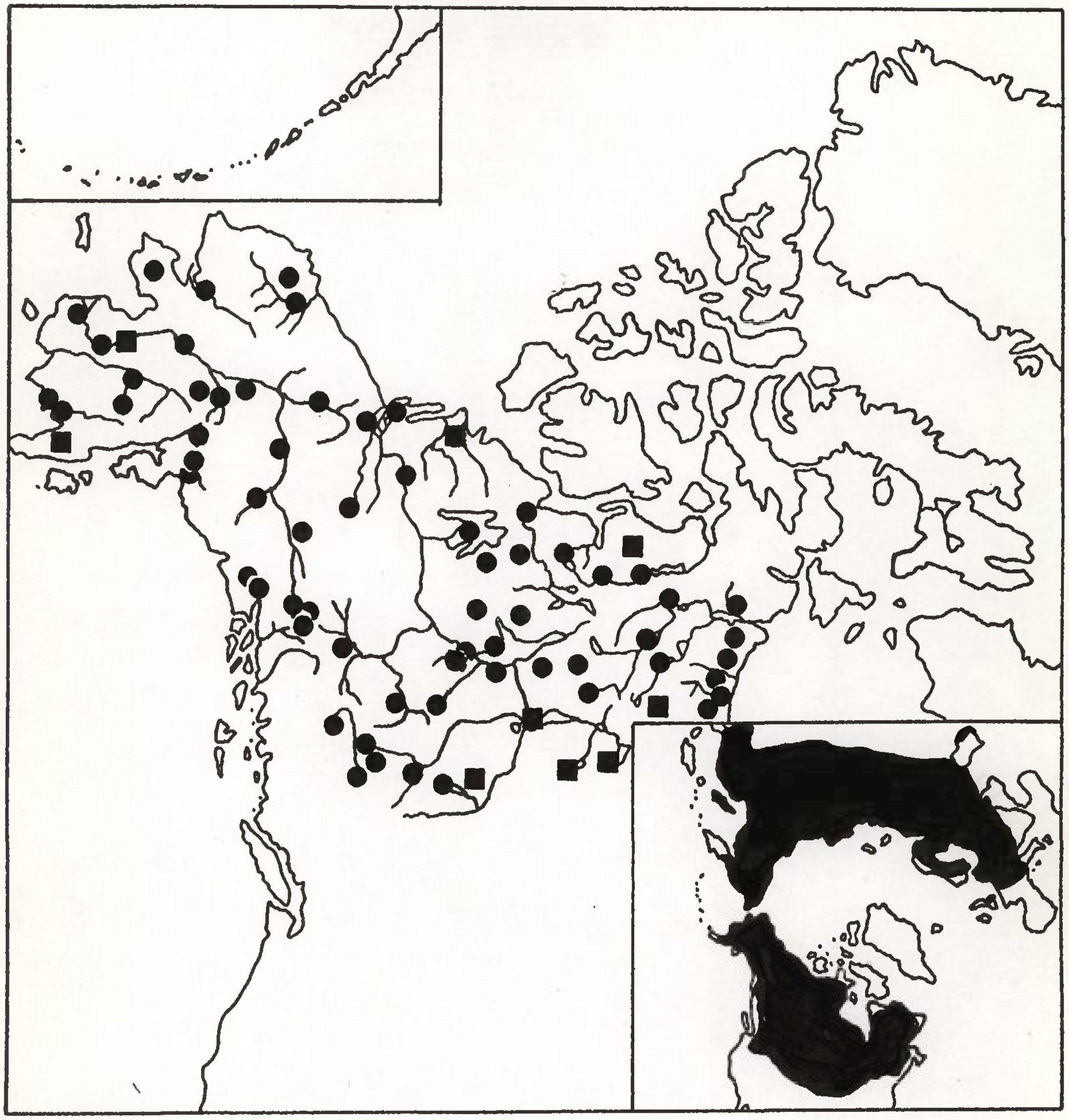


Fig. 48. Northern distribution of L. lota (inset total distribution). Circles indicate specimens examined, and squares literature records.

subspecific recognition of the Alaskan form is not warranted.

In the present study the number of gill rakers and pyloric caeca were compared over the North American range of L. lota (Tables X and XI). In both characters Lota from the Yukon system and other Alaskan rivers differ significantly ($p < 0.001$) from all other North American populations. This suggests the presence of two allopatric forms of L. lota in North America. The distribution of these forms (Fig. 49) indicates the northern form survived glaciation in the Bering Refugium, and the southern form in the Mississippi Refugium. Both forms occur in northern North America.

Culea inconstans (Kirtland) - Brook stickleback.

Range - Central North America: from the Missouri, upper Mississippi, and Ohio Valleys north to small tributaries on the south shore of Great Slave Lake (Fig. 50). Koster (1957) reports an isolated population from New Mexico.

Northern records - Specimens examined: 229, 230, 233, 235, 247, 273, 303, 317, 365, 381, 389, 418, 426; literature records: 31.

Glacial refugia - The distribution pattern of C. inconstans (inset, Fig. 50) indicates survival in the Mississippi Refugium. The restricted distribution of C. inconstans in the Atlantic Refugium was probably attained postglacially.

Gasterosteus aculeatus Linnaeus - Threespine stickleback.

Range - Amphiboreal in Eurasia and North America; North American range disjunct: Southern California to Bristol

Table X. Comparison of gill rakers in North American *Lota lota*.

River system	7	8	9	10	11	12	N	Mean
Kuzitrin				1			1	
Yukon		1	5	12	2	2	22	9.9
Copper				1	3		4	10.7
Wood			1	1			2	9.5
Mackenzie	3	12	7	6	2		30	8.7
Coppermine	1	4	5	2			12	8.7
Back			1				1	8.7
Thelon	4	6	6	3	1		20	8.5
Dubawnt		3	6	1			10	8.8
Kazan		2	3	1			6	8.8
Tha-ane		1	6	2	1		10	9.3
Churchill	1	3	4	2			10	8.7
Nelson	2	8	7	7	2		26	9.0
St. Lawrence	1	9	7	1			18	8.5
Mississippi	1	7	2				10	8.1
Connecticut	4	5	7				16	8.2
Missouri	1	2	1	1	1		6	8.8
Fraser	1	16	16	6	1		40	8.7
Columbia	1	12	9	6	2		30	8.9

Table XI. Comparison of pyloric caeca in North American *Lota lota*.

River system	31-40	41-50	51-60	61-70	71-80	81-90	91-100	101-110	111-120	121-130	131-140	141-150	N	Mean
Kuzitrin											1		1	
Yukon						3	1	2	4	2		5	17	118.0
Copper									3		1		4	117.6
Wood					1		1		1				3	96.4
Mackenzie	1		1	4	6	3	4	1	2	1			23	83.6
Coppermine			1	1	2	2	2	1					9	82.1
Back							1						1	
Thelon			5	5	3		1						14	68.2
Dubawnt		1			1		1						3	66.0
Kazan				2	2	1							5	68.5
Tha-ane			1	2	4		1						8	68.6
Churchill		1		1	2		2						6	71.7
Nelson	1	3	4	1		2	3						14	65.4
St. Lawrence	2	7	1			1							11	46.1
Mississippi				2		1		1					4	75.7
Connecticut		1			2	1	2		1				7	75.9
Missouri			1		2	1							4	76.6
Fraser		5	3	4			1						13	58.4
Columbia	1	2		2	3	1		1					10	67.8

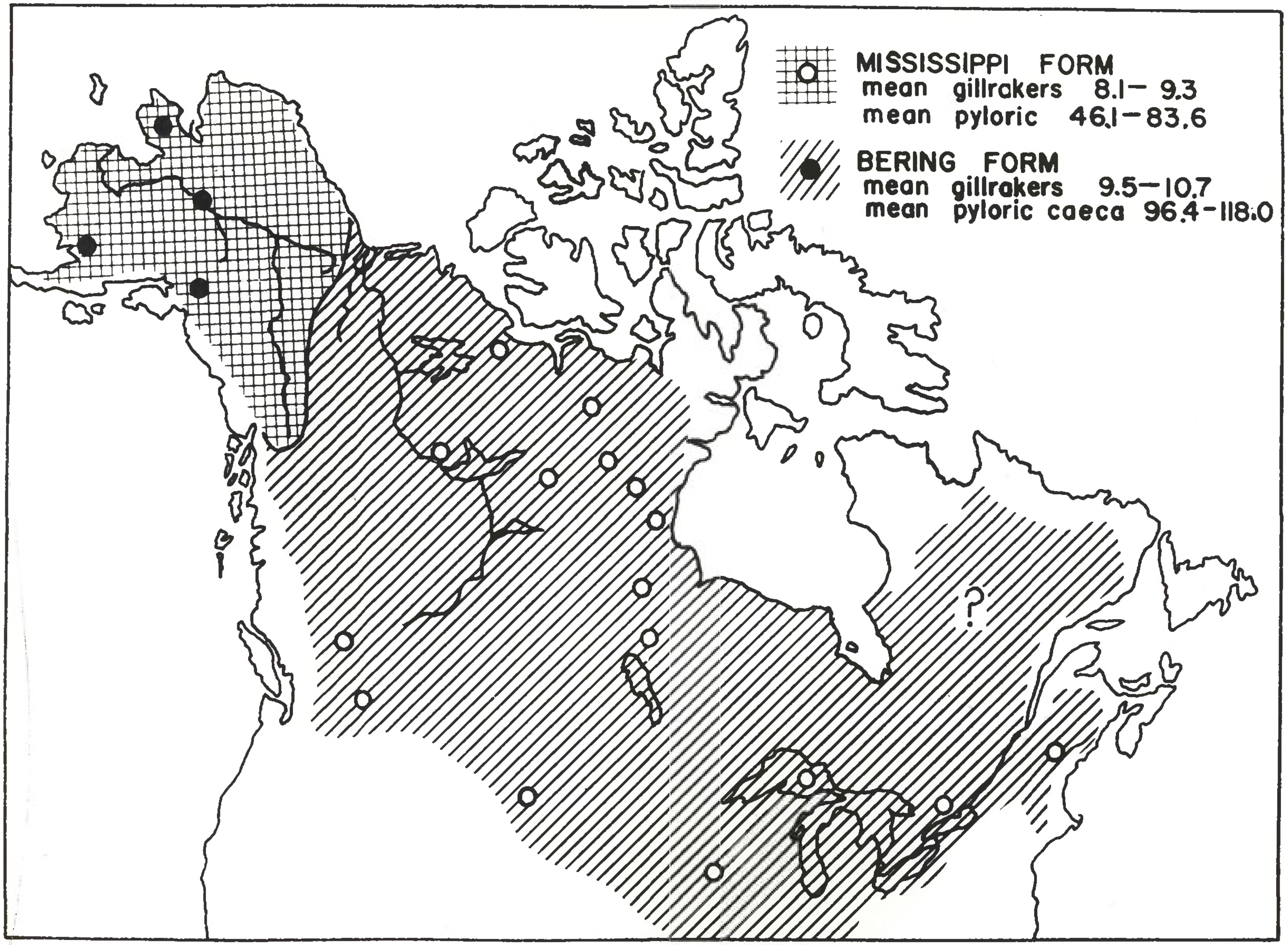


Fig. 49. Geographic variation in the number of gill rakers and pyloric caeca in *Lota lota*.

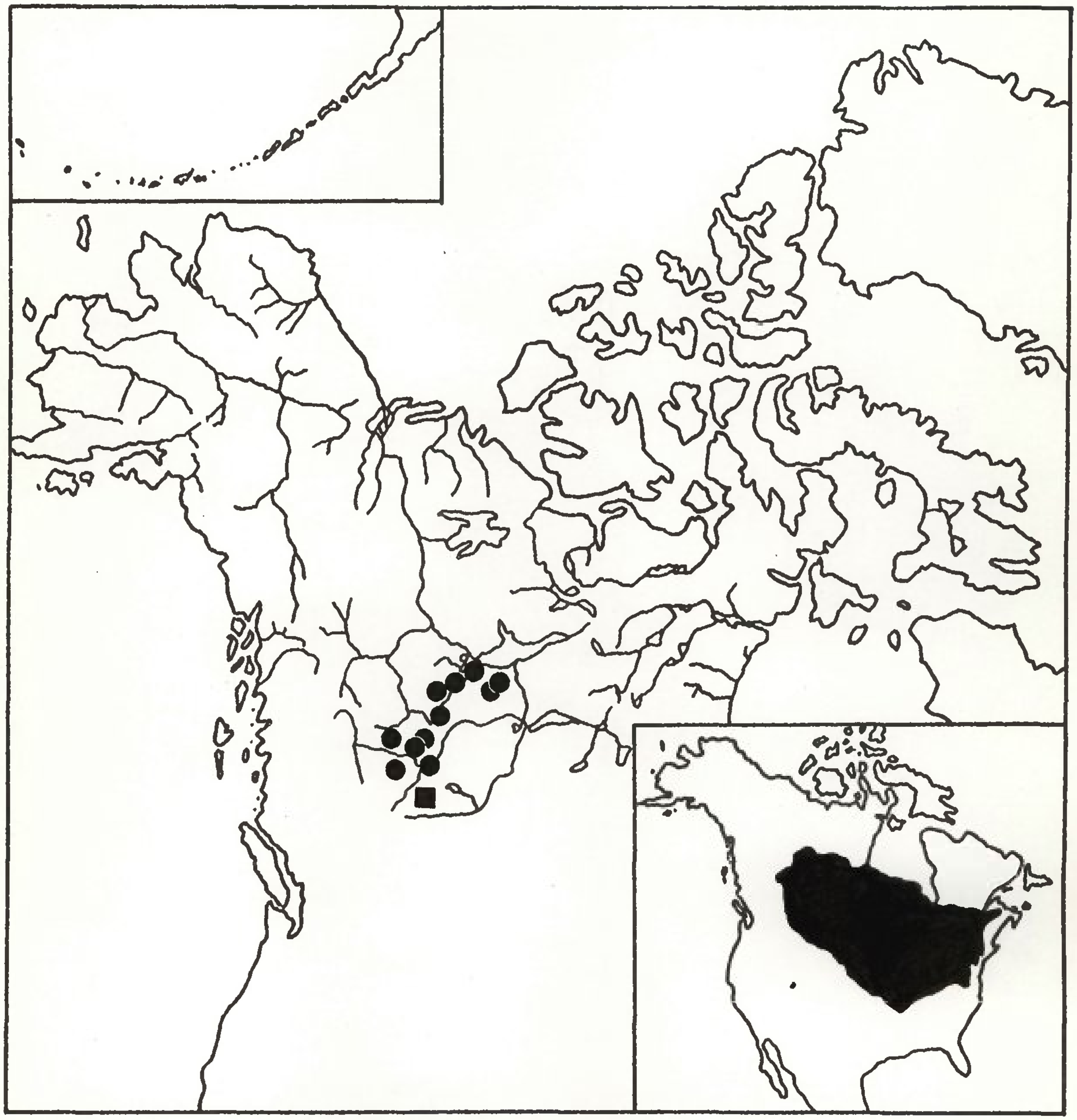


Fig. 50. Northern distribution of C. inconstans (inset total distribution). Circles indicate specimens examined, and squares literature records.

Bay, Alaska, and Chesapeake Bay to Cumberland Sound, Baffin Island. There are relict populations in Baja California (Fig. 51).

Northern records - Specimens examined: 23, 26, 28, 29, 34, 36, 46, 52, 58, 68, 71, 83, 85, 89, 93, 95, 101, 115, 119, 132, 133, 153, 154, 156, 166, 168, 170, 172, 175, 178, 179, 181, 199, 205, 208, 215, 224, 227, 344, 354, 356, 368, 384, 402, 412, 415, 423, 431; literature records: 3, 11, 14, 45.

Glacial refugia - In North America there are two totally allopatric populations of G. aculeatus. These populations are separated by 2500 miles (inset, Fig. 51). Geographic variation in the number of gill rakers and the number of lateral plates was examined. No consistent pattern was apparent.

The western population is widely distributed in the unglaciated coastal portions of the Pacific Refugium, and there are relict populations in Baja California. The western population probably survived Wisconsin glaciation in the Pacific Refugium.

A fossil threespine stickleback is known from the late glacial Champlain Sea deposits. The range of the eastern population includes the Atlantic Refugium, and G. aculeatus probably also survived glaciation in this area.

Pungitius pungitius (Linnaeus) - Ninespine stickleback.

Range - Circumpolar; in North America from Cook Inlet, Alaska, to New Jersey (Fig. 52).

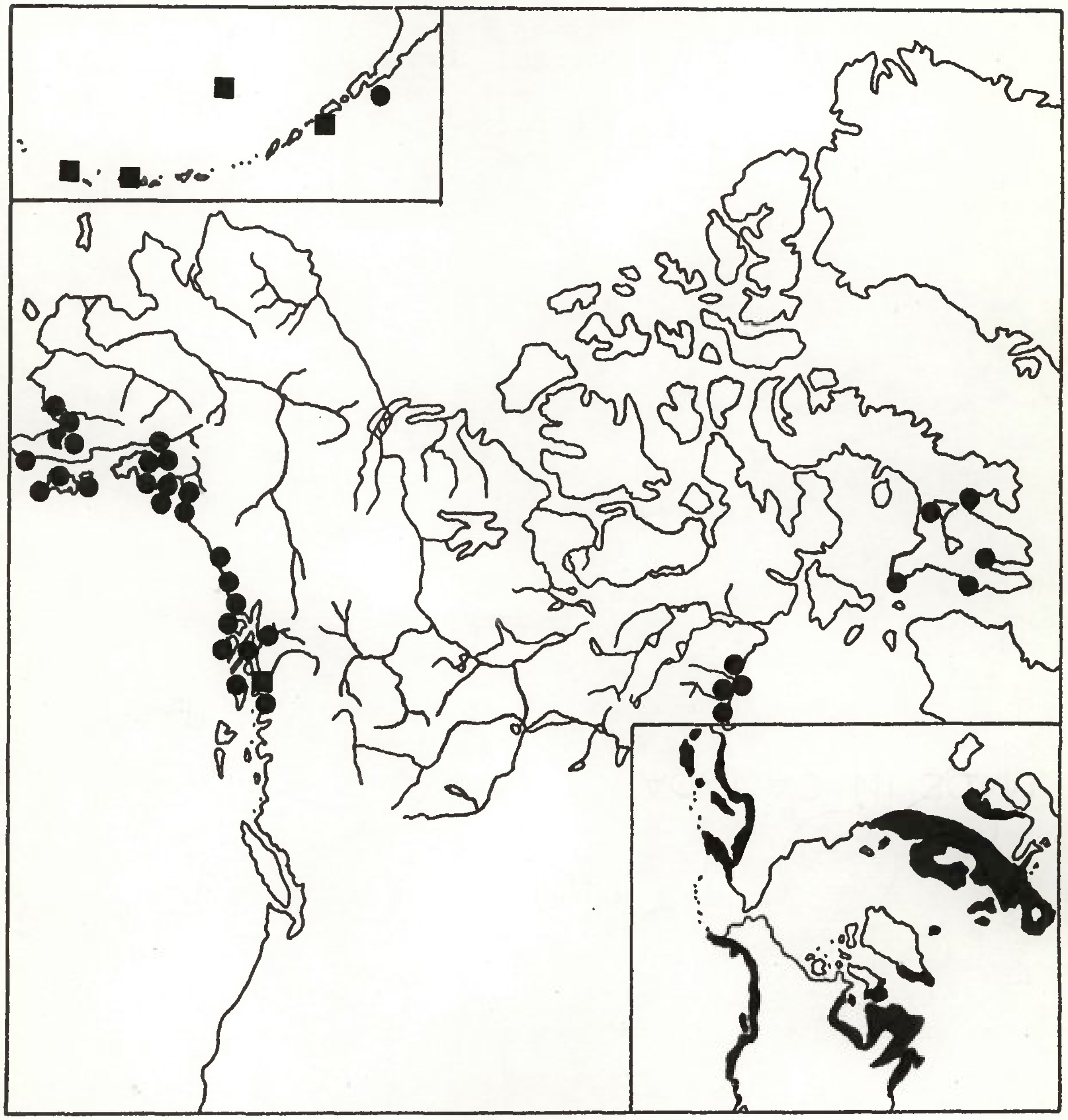


Fig. 51. Northern distribution of G. aculeatus (inset total distribution). Circles indicate specimens examined, and squares literature records.

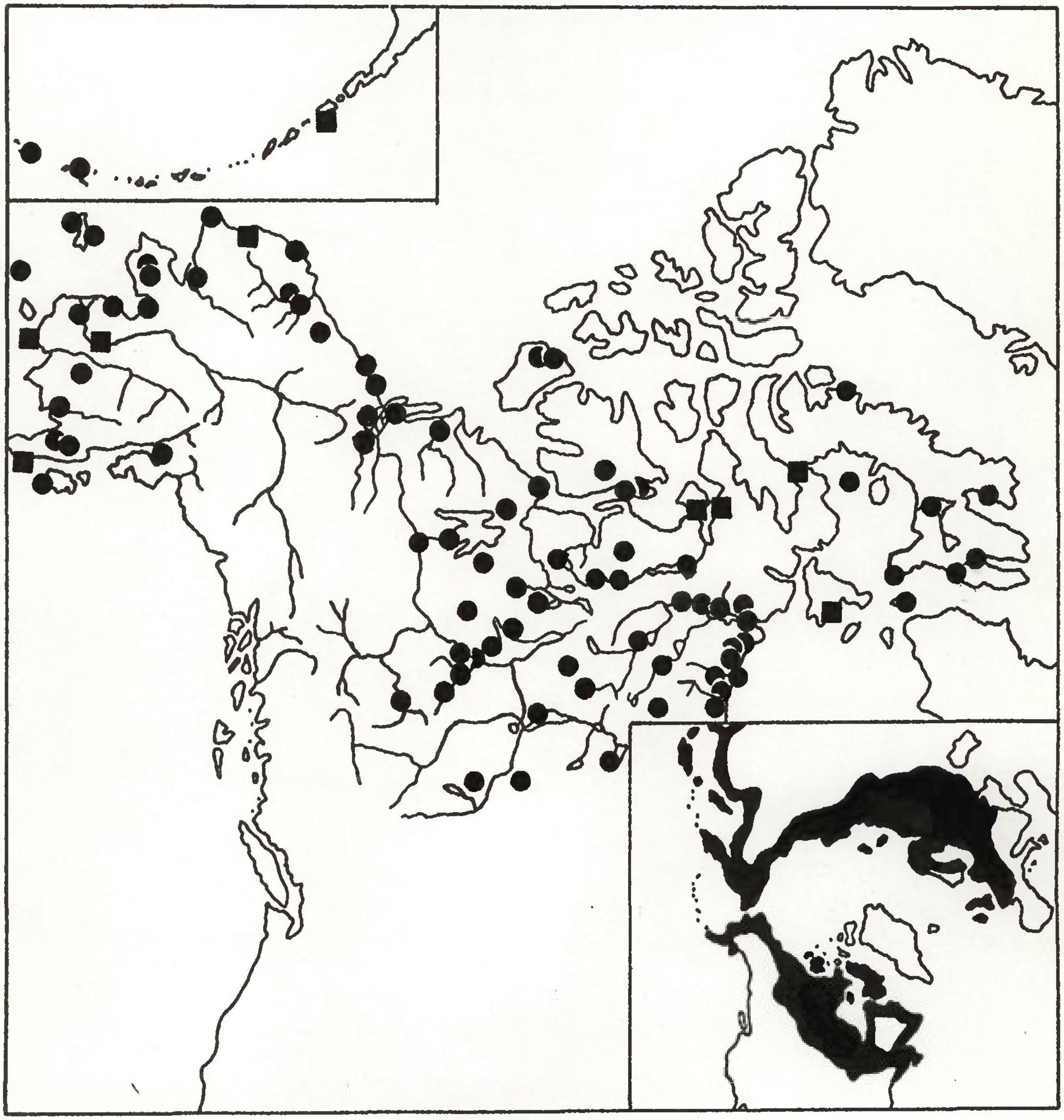


Fig. 52. Northern distribution of P. pungitius (inset total distribution). Circles indicate specimens examined, and squares literature records.

Northern records - Specimens examined: 4, 5, 6, 13, 42, 49, 79a, 94, 99, 101, 107, 109, 133, 150, 164, 170, 171, 174, 181, 203, 205, 211, 212, 236, 264, 331, 332, 335, 337, 339, 341, 343, 344, 345, 346, 347, 349, 353, 354, 355, 357, 359, 362, 363, 364, 367, 368, 370, 374, 376a, 379, 382, 388, 392, 393, 401, 402, 405, 407, 414, 415, 419, 422, 423, 424, 425, 428, 429, 431, 433, 434, 436, 437, 444, 446, 449, 450, 457, 462, 463, 465, 466, 467, 468, 470, 471, 472, 488; literature records: 3, 9, 13, 14, 21, 33, 36, 37, 39, 42.

Glacial refugia - McPhail (1963) suggests two allopatric forms of _P. pungitius_ in North America, distinguished by gill raker and dorsal spine number. The distribution of these forms is presented in Fig. 53. Both forms are relatively uniform throughout their ranges, and appear to intergrade wherever they come in contact.

The presence of two allopatric forms of _P. pungitius_ in North America implies two refugia. The northern form is widely distributed within the Bering Refugium and probably survived glaciation in this area. The distribution of the southern form suggests survival in the Mississippi Refugium. Both forms occur in northern North America.

Percopsis omiscomaycus (Walbaum) - Trout-perch.

Range - Central North America: from the Missouri, upper Mississippi, and Ohio Valleys north to the Mackenzie Delta, and in the Porcupine and Yukon Rivers downstream to the mouth of the Andreafsky River (Fig. 54).

Northern records - Specimens examined: 9, 41, 55,

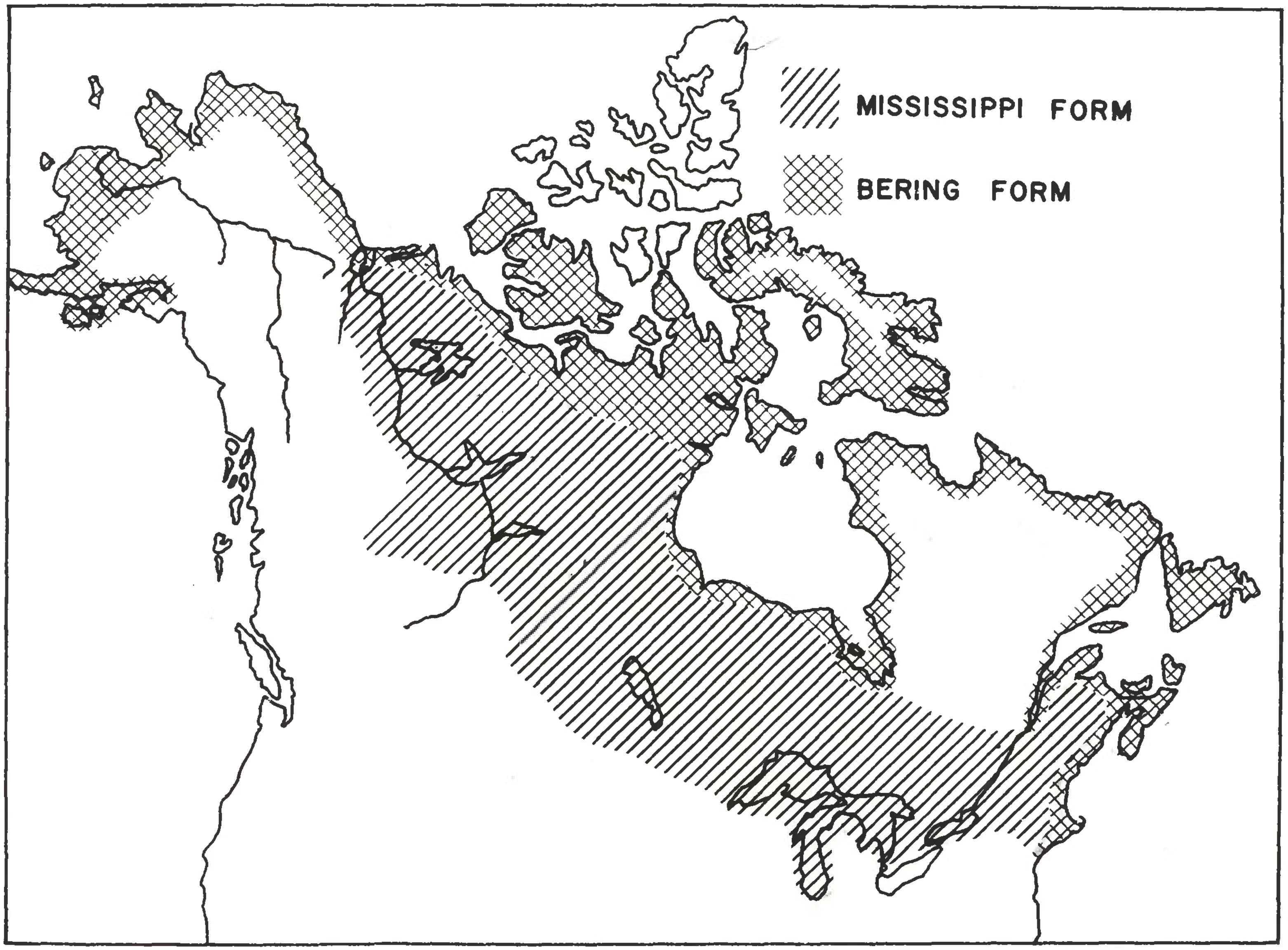


Fig. 53. Distribution of the morphological forms of Pungitius pungitius in North America (after McPhail, 1963).

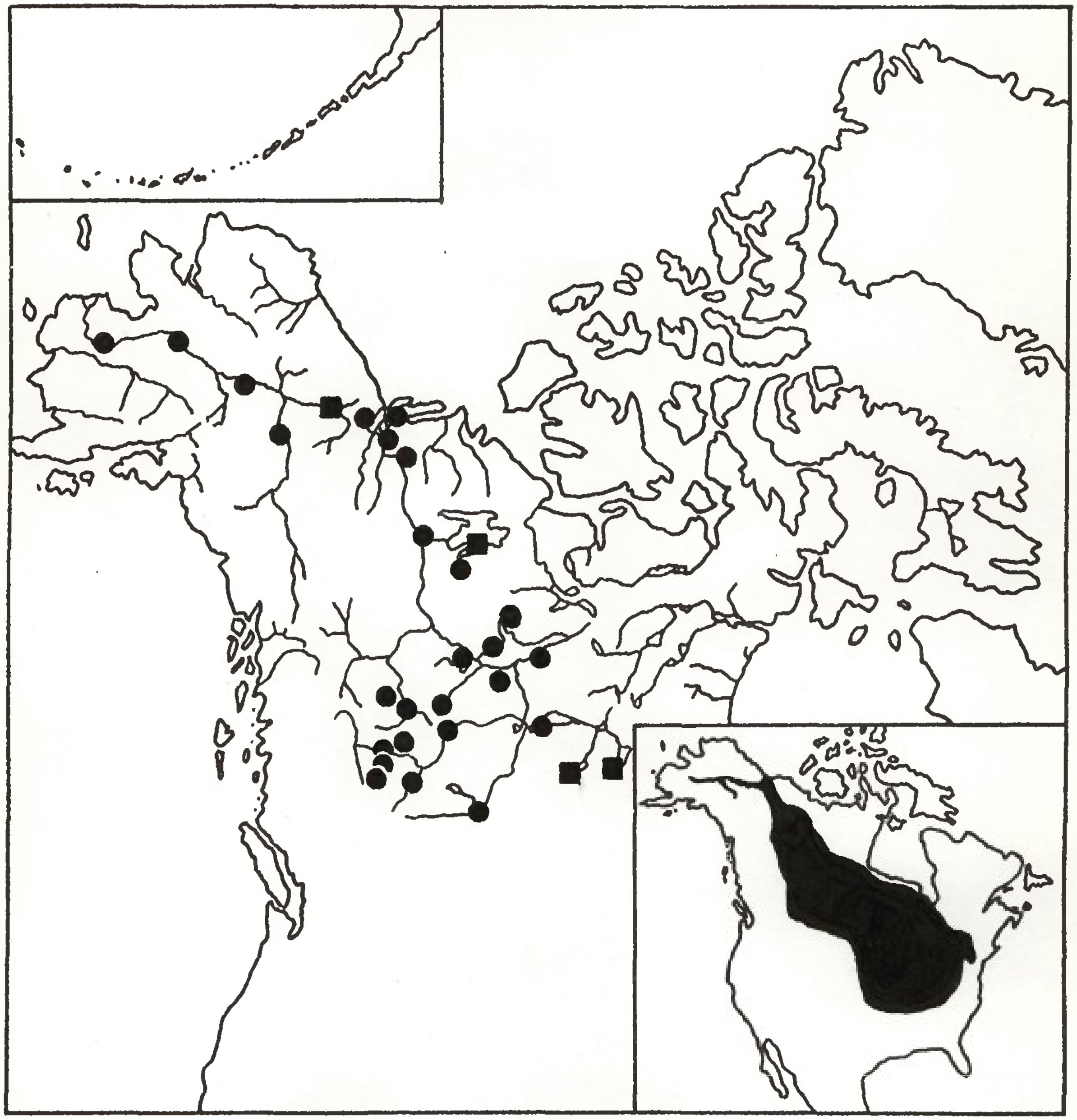


Fig. 54. Northern distribution of P. omiscomaycus (inset total distribution). Circles indicate specimens examined, and squares literature records.

146, 228, 239, 245, 246, 262, 265, 289, 298, 301, 307, 308, 311, 332, 352, 372, 374, 375, 385, 388, 403, 404, 435, 451, 466; literature records: 31, 39, 54.

Glacial refugia - The distribution pattern of P. omiscomaycus (inset, Fig. 54) indicates survival in the Mississippi Refugium. The restricted distribution of P. omiscomaycus in the Bering and the Atlantic Refugia is probably due to postglacial dispersal from the Mississippi Refugium.

Perca flavescens (Mitchill) - Yellow perch.

Range - North America (the Eurasian P. fluviatilis may be conspecific): from the upper Mississippi and Ohio Valleys north to Great Slave Lake, and on the Atlantic Coast from Nova Scotia to South Carolina (Fig. 55).

Northern records - Specimens examined: 232, 253; literature records: 31, 38, 39, 44.

Glacial refugia - The range of P. flavescens includes two unglaciated areas: the Mississippi, and the Atlantic Refugia. Radforth (1944) suggests the yellow perch survived glaciation in both areas. The yellow perch probably attained its present northern distribution by postglacial dispersal from the Mississippi Refugium.

Stizostedion vitreum (Mitchill) - Walleye.

Range - Central North America: from the upper Mississippi and Ohio Valleys north to the Mackenzie Delta; on the Atlantic Coast native only in North Carolina (Fig. 56).

Northern records - Specimens examined: 239, 277,

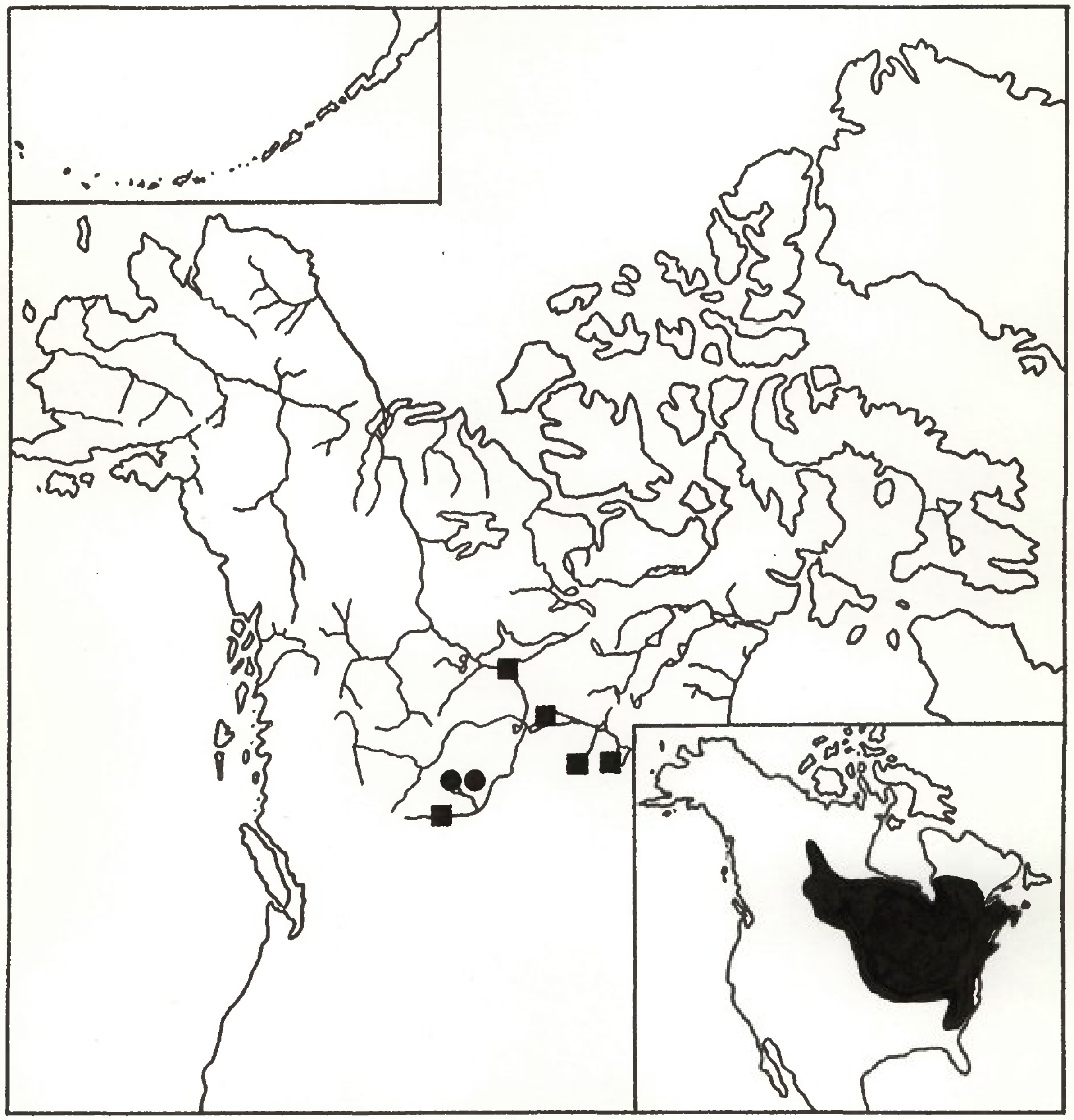


Fig. 55. Northern distribution of P. flavescens (inset total distribution). Circles indicate specimens examined, and squares literature records.

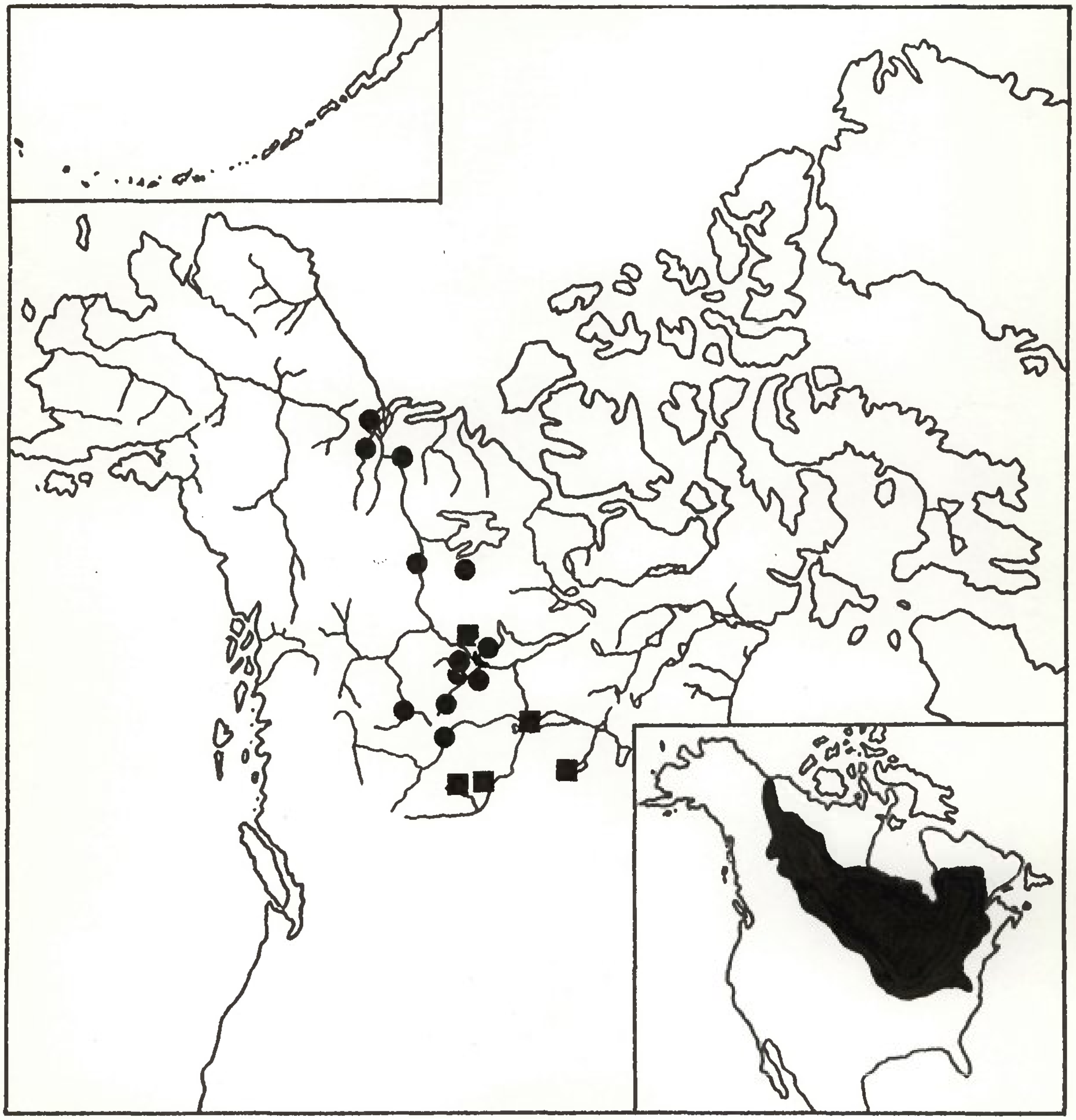


Fig. 56. Northern distribution of S. vitreum (inset total distribution). Circles indicate specimens examined, and squares literature records.

278, 288, 293, 332, 372, 404, 409, 432, 436, 454; literature records: 24, 31, 37, 39.

Glacial refugia - The distribution pattern of S. vitreum (inset, Fig. 56) indicates survival in the Mississippi Refugium.

Cottus aleuticus Gilbert - Coastrange sculpin.

Range - Western North America: from San Luis Obispo Co., California, to Bristol Bay, Alaska[3] (Fig. 57).

Northern records - Specimens examined: 2, 6, 17, 21, 22, 23, 32, 43, 58, 60, 68, 76, 95, 98?, 101, 104, 114, 115, 133a, 156, 169, 177, 178, 190, 213, 221, 223, 329; literature records: 3, 11, 42.

Glacial refugia - The distribution pattern of C. aleuticus (inset, Fig. 57) indicates survival in the Pacific Refugium.

Cottus asper Richardson - Prickly sculpin.

Range - Western North America: Ventura River, California, to the Kenai Peninsula, Alaska (Fig. 58).

Northern records - Specimens examined: 47, 96, 156, 175, 177, 223, 281, 323; literature records: 11, 34.

Glacial refugia - The distribution pattern of C. asper (inset, Fig. 58) indicates survival in the Pacific Refugium.

Cottus cognatus Richardson - Slimy sculpin.

Range - Northeastern Siberia and North America.

[3] A single specimen (UMMZ156990) is known from the Kobuk River, Alaska. Since C. aleuticus was not taken in the Kuskokwim or Yukon systems by the author, this record is considered questionable.

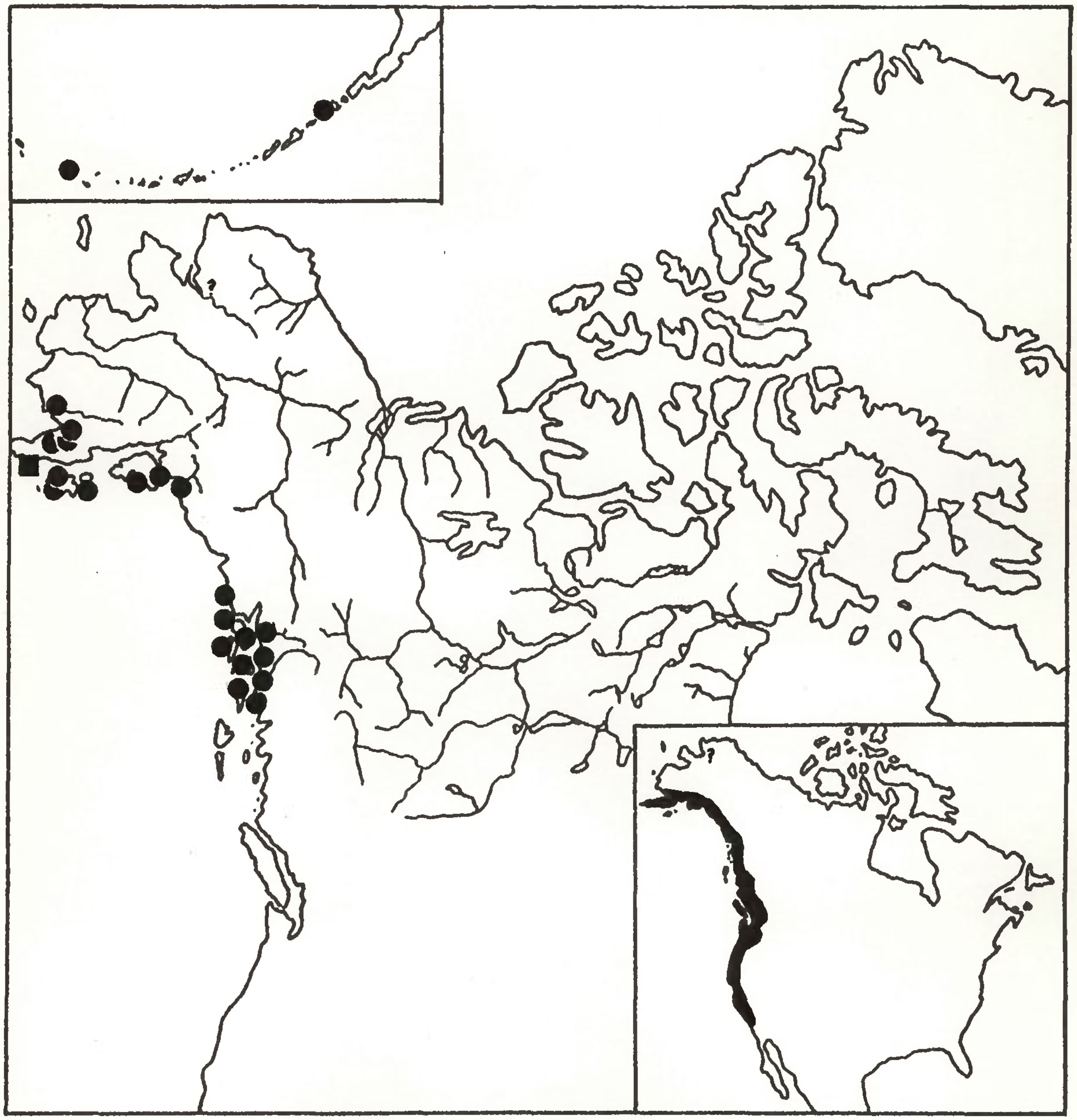


Fig. 57. Northern distribution of C. aleuticus (inset total distribution). Circles indicate specimens examined, and squares literature records.

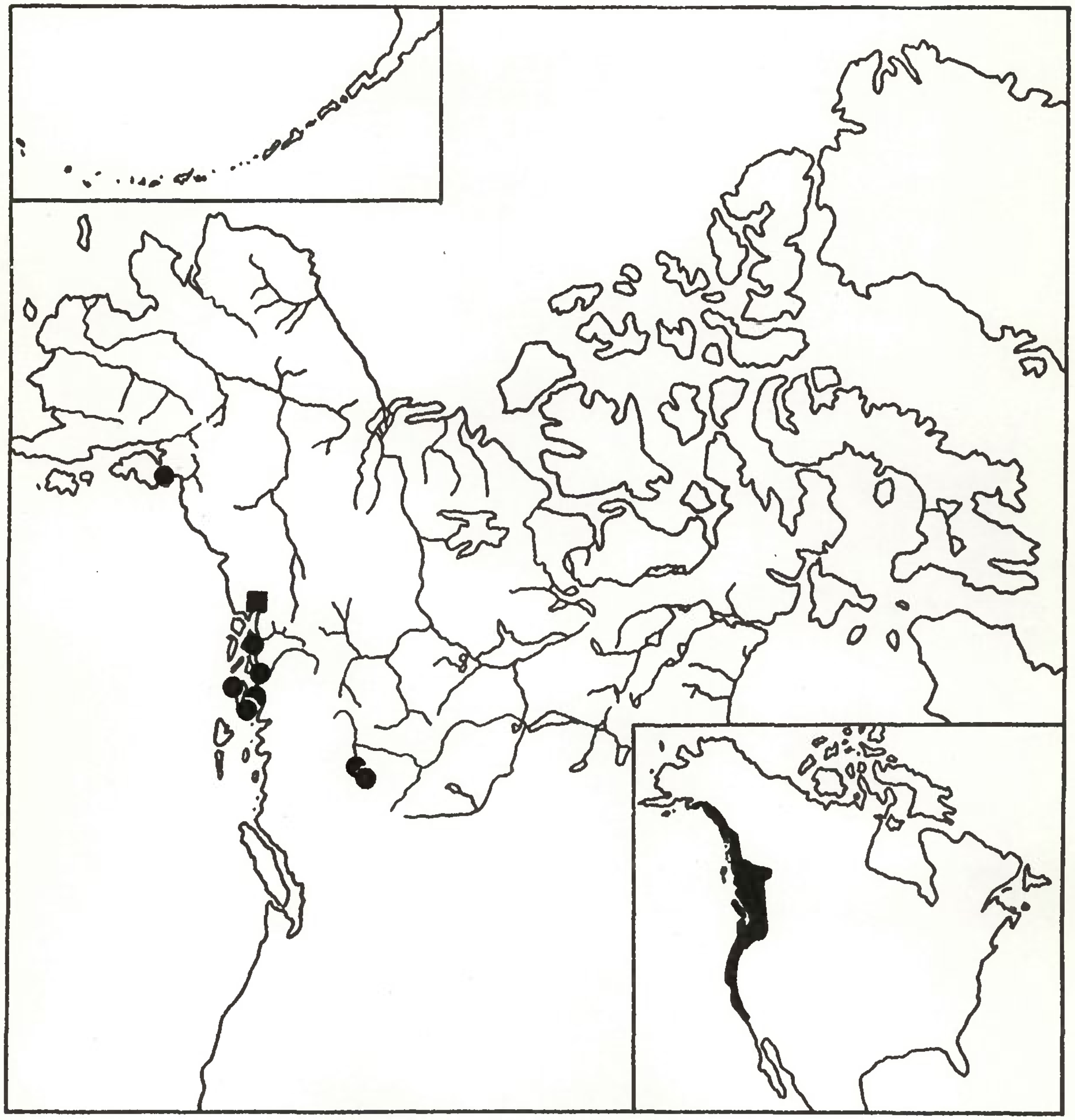


Fig. 58. Northern distribution of C. asper (inset total distribution). Circles indicate specimens examined, and squares literature records.

In North America from the Columbia system north to Alaska and east to the Great Lakes, on the Atlantic Coast from Labrador to New York; relict populations in Virginia and Iowa (Fig. 59).

Northern records - Specimens examined: 3, 6, 8, 10, 11, 14, 18, 19, 22, 28, 31, 33, 41, 42, 44, 48, 54, 60, 61, 63, 69, 79, 90, 101, 102, 115, 121, 127, 130, 131, 133, 135, 147, 153, 157, 158, 174, 180, 184, 185, 189, 195, 196, 197, 200, 201, 202, 202a, 203, 215, 218, 219, 222, 262, 272, 277, 283, 287, 295, 298, 304, 305, 306, 308, 310, 318, 321, 326, 335, 337, 343, 346, 347, 358, 362, 363, 367, 378, 384, 385, 386, 388, 402, 407, 411, 414, 419, 422, 423, 441, 449, 450, 453, 462, 465, 467, 471, 473, 474, 479, 480, 483, 483a, 486, 489, 490, 492, 494, 494a, 498, 501, 502, 503, 509, 510, 511, 514, 515, 516, 518, 519, 520, 522; literature records: 1, 6, 11, 13, 18, 24, 31, 34, 36, 39, 52.

Glacial refugia - The wide range of C. cognatus implies survival in multiple refugia. The presence of C. cognatus in northeastern Siberia and on St. Lawrence Island indicates the slimy sculpin was present in the Bering Refugium during glaciation. The occurrence of C. cognatus in the Columbia system, and the relict populations in Iowa and Virginia suggest the Pacific, the Mississippi, and the Atlantic Refugia were also used.

McAllister and Lindsey (1961) suggest three allopatric forms of C. cognatus in North America, distinguished

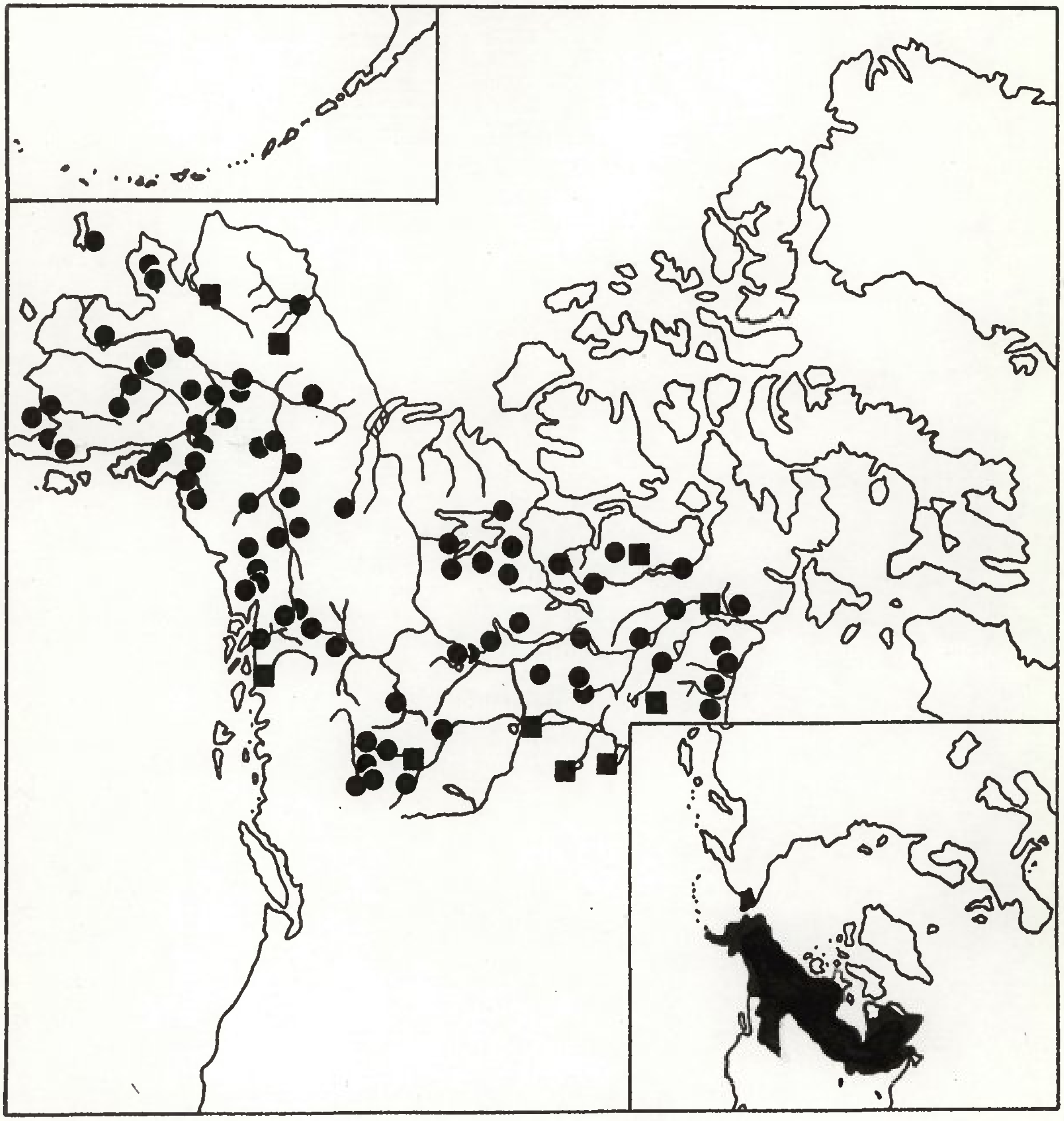


Fig. 59. Northern distribution of C. cognatus (inset total distribution). Circles indicate specimens examined, and squares literature records.

by the number of pelvic rays and the branching of the last anal ray. Each form is relatively uniform throughout its range. The distribution of these forms (Fig. 60) implies survival in the Bering, the Pacific, and the Mississippi Refugia. All three forms occur in northern North America.

Cottus ricei (Nelson) - Spoonhead sculpin.

Range - Central North America: Great Lakes Basin to the Mackenzie Delta (Fig. 61).

Northern records - Specimens examined: 228, 253, 255, 277, 301, 332, 346, 378, 388, 403, 459, 460; literature records: 39.

Glacial refugia - The distribution pattern of *C. ricei* (inset, Fig. 61) indicates survival in the Mississippi Refugium.

Myoxocephalus quadricornis (Linnaeus) - Fourhorn sculpin.

Range - Circumpolar in marine and fresh waters, only freshwater populations are considered. In North America in the Great Lakes, Lake Nipigon, Torch Lake, Lac La Plonge, Wollaston Lake, Lac La Ronge, Reindeer Lake, Great Slave Lake, Lac La Martre, Keller Lake, and the following lakes on Victoria Island: Ferguson Lake, Washburn Lake, Surrey Lake and Zeta Lake (Fig. 62).

Northern records - Specimens examined: 370, 387, 409, 414, 452, 464, 469; literature records: 39.

Glacial refugia - McAllister (1961) recognizes the freshwater form of *Myoxocephalus* in North America as a distinct species, *Myoxocephalus thompsonii*. He postulates *M. thompsonii*

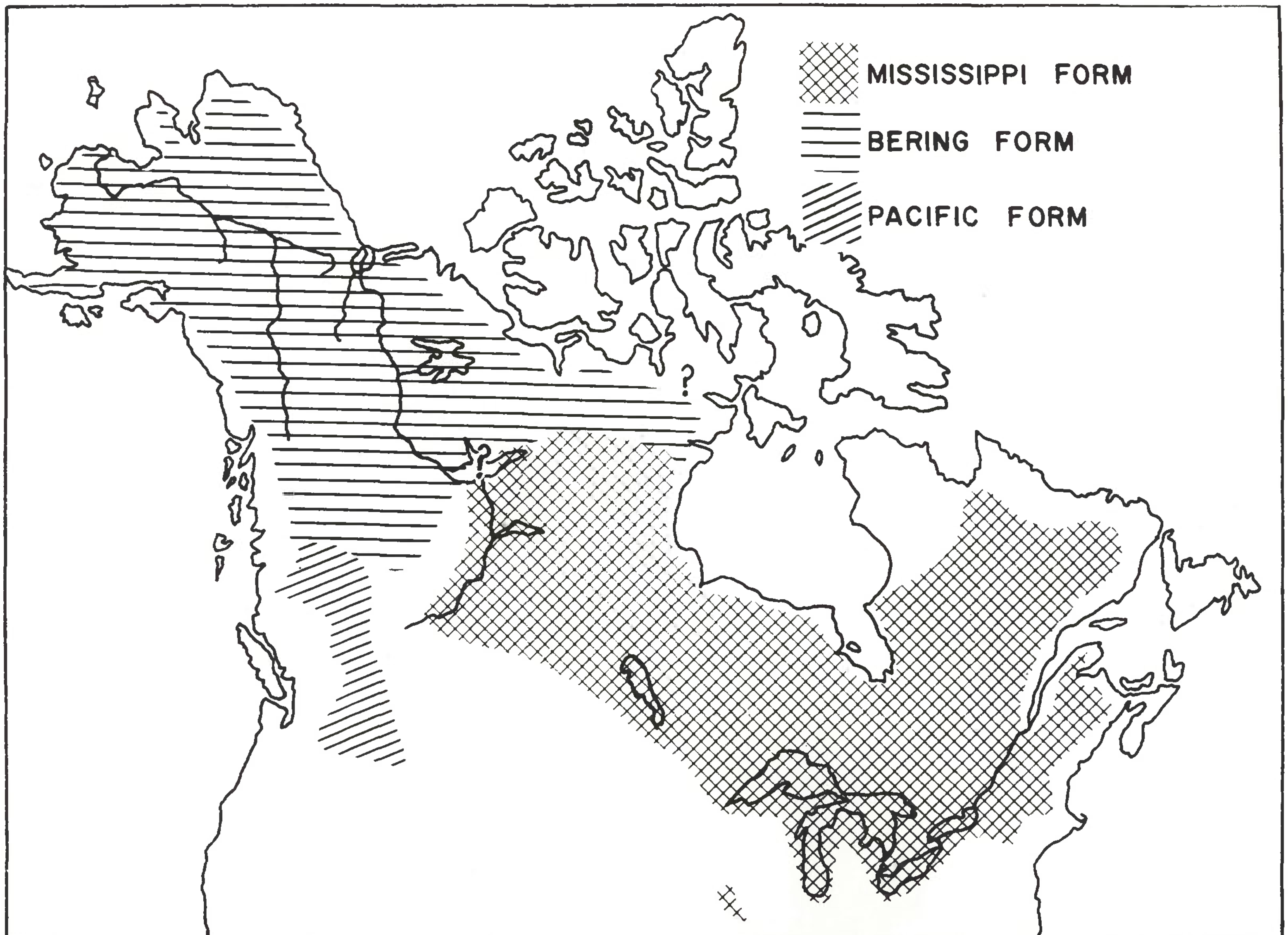


Fig. 60. Distribution of the morphological forms of <u>Cottus cognatus</u> in North America (after McAllister and Lindsey, 1961).

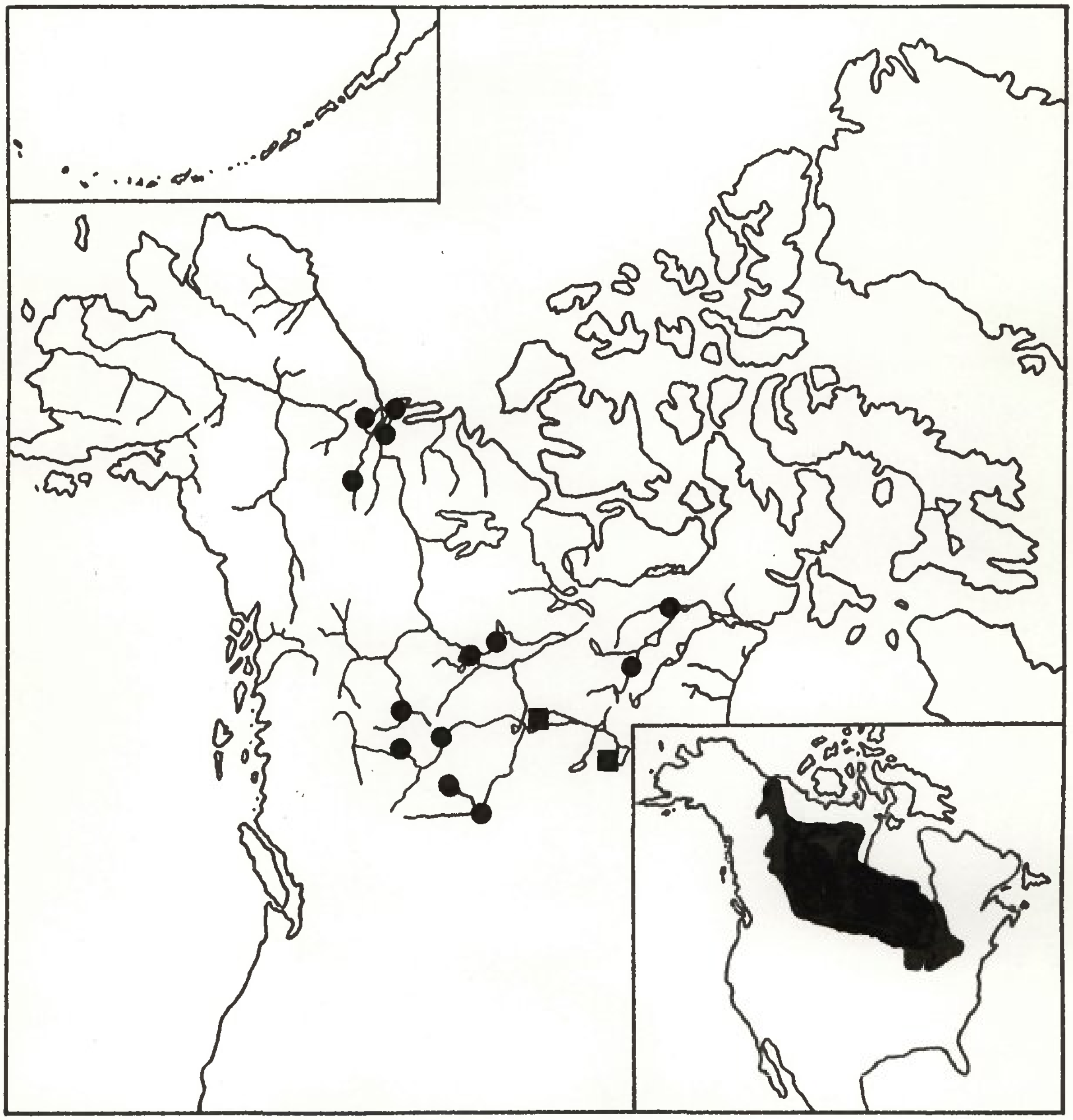


Fig. 61. Northern distribution of C. ricei (inset total distribution). Circles indicate specimens examined, and squares literature records.

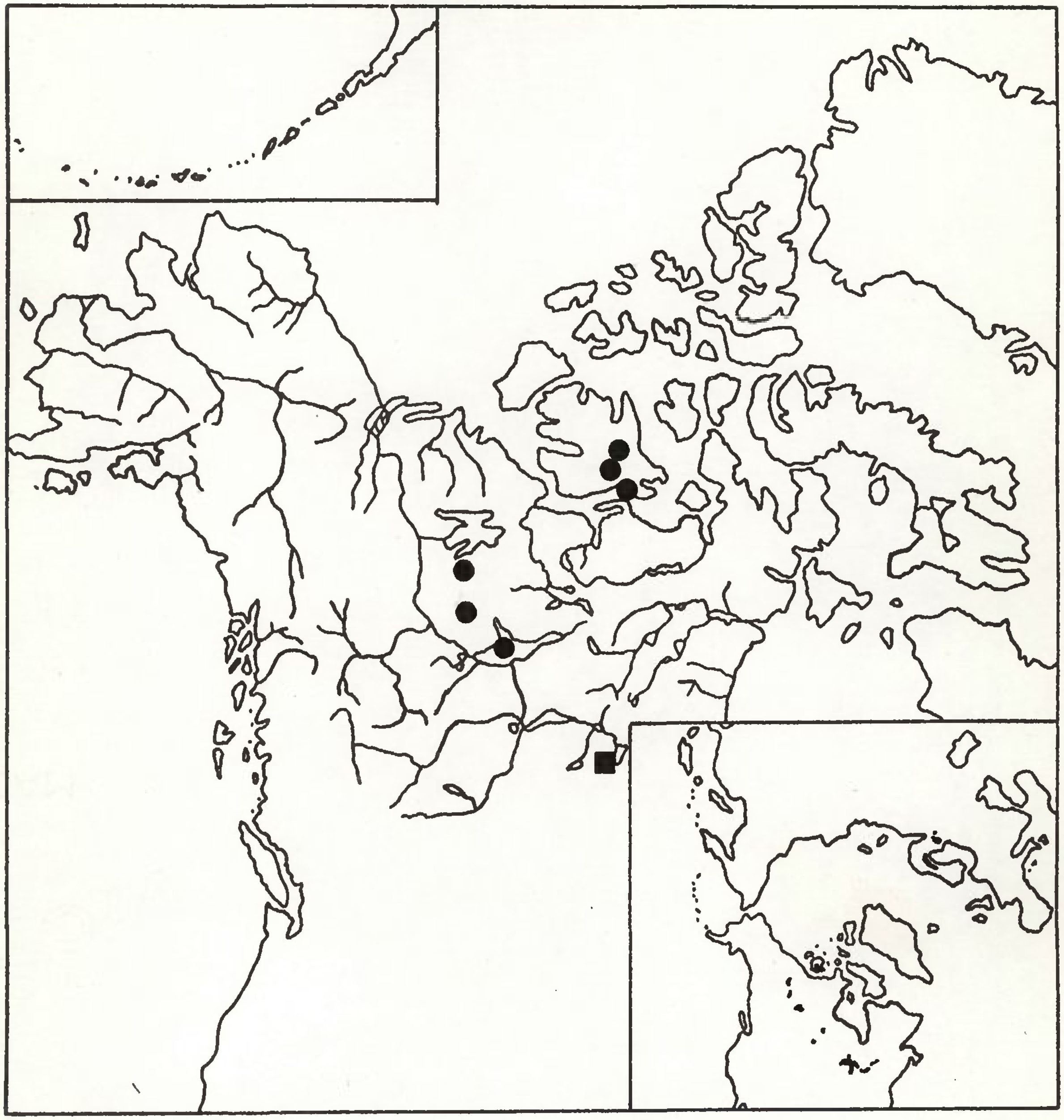


Fig. 62. Northern distribution of freshwater populations of M. quadricornis (inset total distribution). Circles indicate specimens examined, and squares literature records.

evolved in proglacial lakes in front of the Laurentide icesheet, and then dispersed through the lakes formed by the retreating icesheets.

Recently, freshwater populations of Myoxocephalus were discovered in lakes on Victoria Island, N.W.T. These populations are intermediate between M. quadricornis and M. thompsonii in preopercular spine length, like M. thompsonii in the absence of tubercles below the lateral line, and like M. quadricornis in the number of pyloric caeca (Table XII).

McAllister (1961) based the separation of M. thompsonii, as a distinct species, on the absence of other freshwater populations of M. quadricornis in North America, and the complete morphological separation of M. quadricornis and M. thompsonii. The freshwater populations of Myoxocephalus on Victoria Island negate both points. Further, all freshwater populations of M. quadricornis (North American and European) differ from marine populations in the same way (reduction in the number and length of spines, and reduction in the number of tubercles), and differ from one another only in the degree of reduction. The present author doubts that M. thompsonii warrants specific recognition.

The Victoria Island freshwater populations are probably not derived from mainland freshwater populations of Myoxocephalus. All of the known Victoria Island populations are in, or near, areas of postglacial marine submergence. This suggests that the Victoria Island populations are postglacial marine relicts. Freshwater populations of

Table XII. Comparison of marine and freshwater populations of *Myoxocephalus quadricornis* in North America (size range, 42-90 mm).

	Pyloric caeca range	Pyloric caeca mean	Tubercles below lateral line range	Tubercles below lateral line mean	Preopercle spine/ standard length (%) range	Preopercle spine/ standard length (%) mean
Marine population						
Cambridge Bay (15 specimens)	7-10	8.53	0-14	4.46	5.7-9.8	8.5
Freshwater populations						
Lake Superior (15 specimens	5-8	5.33	0	0	2.2-4.1	3.2
Ferguson Lake, Victoria Is. (10 specimens)	7-9	8.00	0	0	3.8-5.8	5.1

M. quadricornis have apparently independently evolved at least twice in North America, and probably twice in Europe (Svärdson, 1961).

DISCUSSION

Postglacial Dispersal

The northern half of North America was glaciated several times during the Pleistocene (Flint, 1957). Little is known about the earlier glaciations. The last glaciation, the Wisconsin, obliterated most traces of previous glacial events except in peripheral areas. The present discussion deals only with Wisconsin and postglacial events.

With the retreat of the Wisconsin icesheets freshwater fishes dispersed into the glaciated portions of northern North America. The present freshwater fish fauna of this area is derived from five sources: the Pacific Refugium, the Bering Refugium, the Mississippi Refugium, the Atlantic Refugium, and the Arctic Ocean. Figure 1 illustrates these glacial refugia with the Wisconsin icesheets at their maxima.

There were two main avenues of dispersal into northern North America: coastal dispersal by way of the sea, and inland dispersal through drainage changes. Both routes were controlled by the pattern of deglaciation. The following paragraphs outline Wisconsin deglaciation in North America and its effects on postglacial dispersal routes.

Deglaciation in the Great Lakes area is better documented than elsewhere. The following summary is mainly from Flint (1957) and Hough (1958). Flint (1957) indicates that the Wisconsin Laurentide icesheet was at its maximum in the Great Lakes region about 18,000 B.P. By 13,000 B.P. parts of the basins of Lakes Michigan, Huron, Erie, and Ontario were exposed. Large glacial lakes formed in these basins, and drained south into the Mississippi system and east into the Susquehanna River. This period culminated in a slight readvance, the Mankato (or Port Huron?) maximum. During the next 1,000 years (Two Creeks interval) the ice retreated further north, and glacial Lake Keweenaw formed in the exposed portion of the Lake Superior basin.

The Two Creeks interval was followed by a major readvance, the Valders maximum. During the Valders maximum the Lake Superior and Lake Ontario basins were covered by ice, and the glacial lakes in the other Great Lakes basins were considerably reduced. Drainage was mainly south into the Mississippi system.

After the Valders maximum the ice retreated steadily, and by about 8,000 B.P. most of the Great Lakes area was ice free. At this time drainage was south into the Mississippi system and east into the Hudson River. The ice retreated beyond the Hudson Bay drainage divide before 7,000 B.P., and Lake Barlow-Ojibway was formed. Lake Barlow-Ojibway first drained to the southeast into the St. Lawrence system, and later to the northwest into Hudson Bay. A minor readvance may have later covered part of the Lake Barlow-Ojibway basin. Differential uplift in the northern part of the Great Lakes region resulted in the Nipissing Great Lakes about 4,000 B.P. At this time drainage was south into the

Mississippi system and northeast into the St. Lawrence River. The present drainage was established with the closure of the last outlet to the Mississippi system about 2,000 B.P.

Deglaciation on the Atlantic Coast was earlier and more rapid than in the Great Lakes region. Newman and Fairbridge (1960) note that the initial ice retreat in the Long Island Sound area began about 30,000 B.P. By the Mankato maximum the ice had retreated to the Boston area (Ogden, 1959), and most of Nova Scotia was ice free by 10,000 B.P. (Hickox, 1960; Livingstone and Livingstone, 1958). Ives (1959, 1960) indicates that the coastal areas of Labrador were also ice free by about 10,000 B.P., but a residual ice mass remained in the Schefferville area until about 6,000 B.P.

On the Atlantic Coast deglaciation was followed by marine submergence, and the sea flooded the St. Lawrence lowlands forming the Champlain Sea. The Champlain Sea was probably contemporary with the Two Creeks interval (Terasmae, 1959).

On the Great Plains the Laurentide icesheet extended in a northeasterly direction from Illinois to the Rocky Mountains. At the Wisconsin maximum drainage was south into the Missouri and Mississippi Rivers. With the ice retreat after the Mankato maximum Lake Agassiz I was formed in southern Manitoba and North Dakota. Lake Agassiz I drained south into the Mississippi system, and perhaps at a later date east into the Lake Superior basin (Elson, 1957). During the Two Creeks interval crustal upwarping opened lower outlets and Lake

Agassiz I drained.

The Valders ice advance formed Lake Agassiz II in the same area. Lake Agassiz II drained south by the Warren River into the Mississippi system, and then east through several outlets into the Lake Superior basin. The final drainage of Lake Agassiz II was north into Hudson Bay.

Ice retreat on the western Great Plains was in a northeasterly direction (Gravenor and Bayrock, 1961). Southern Alberta and southwestern Saskatchewan became ice free relatively early in deglaciation. The numerous glacial lakes in this area were relatively small and short lived (Gravenor and Bayrock, 1961). Drainage was south into the Missouri River, and later east into Lake Agassiz.

The regional slope north of Edmonton is to the northeast. When the ice retreated to this area a series of large proglacial lakes were formed; the most important were: Lake Edmonton, Lake Peace, and Lake Tyrrell (Taylor, 1960). These lakes drained to the southeast into Lake Agassiz II. Later in deglaciation a large glacial lake was formed in the Great Slave-Great Bear basin and drained south into Lake Agassiz II until isostatic readjustment established the present northern drainage.

Along the Arctic Coast the ice retreated in a southeasterly direction (Craig and Fyles, 1960; Craig, 1960). The Arctic Coast was ice free to Coronation Gulf by 10,000 B.P. (Craig, 1960), and to the Gulf of Boothia by 8,000 B.P. (Craig, 1961). After deglaciation much of the Arctic Coast of Canada was submerged.

In the final stages of deglaciation the Laurentide icesheet split into two separate ice masses, and withdrew into Keewatin and Labrador. The division of the icesheet was caused by the entry of the sea into Hudson Bay, and Lee (1960) dates the maximum postglacial submergence in the Hudson Bay area at 7,000 to 8,000 B.P. The sea must have penetrated through Hudson Strait into Foxe Basin and Hudson Bay somewhat earlier. The residual ice masses in Keewatin and Labrador disappeared about 6,000 B.P.

Little is known about the deglaciation of the Cordilleran icesheet; apparently most of the coastal area became ice free relatively early in deglaciation. Crandell et al. (1958) indicate the ice retreated from the Seattle area prior to 14,000 B.P., and Armstrong (1956) notes a readvance in the Fraser Valley about 11,000 B.P. Some coastal areas as far north as Juneau were ice free by 10,000 B.P. (Olson and Broecker, 1959), and glaciated parts of the Kenai Peninsula by 9,600 B.P. (Broecker et al., 1956). The northern Pacific Coast is still not completely ice free, but dispersal along the coast was probably possible by about 9,000 B.P.

The general pattern of deglaciation in North America, and the resulting drainage changes are summarized in Fig. 63. Zoogeographically, the most important aspects of deglaciation were the early retreat of the ice from coastal regions, and the rapid northeasterly retreat of the ice on the Great Plains.

There are 50 species of freshwater fishes native to

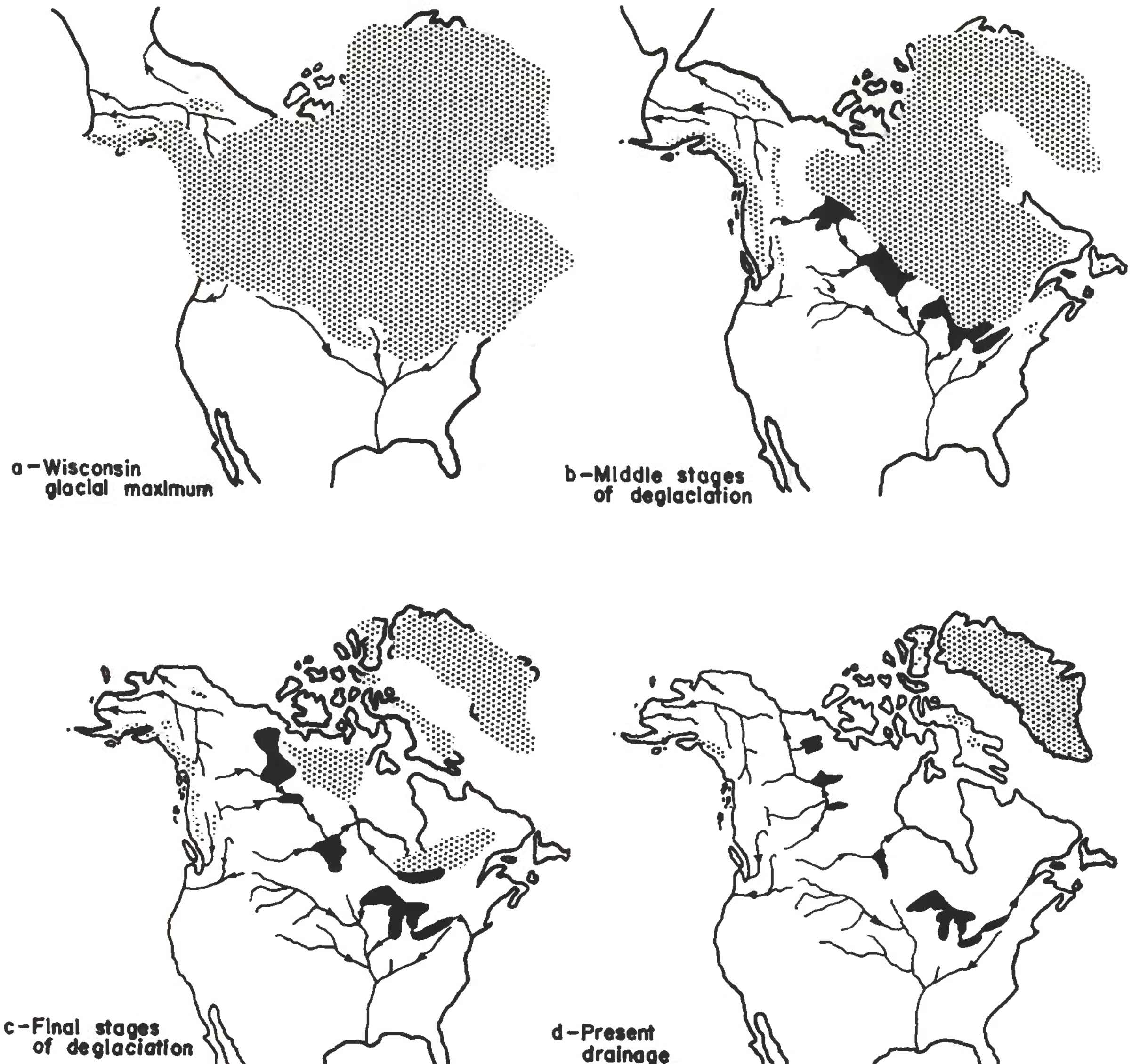


Fig. 63. General pattern of deglaciation in North America. Drainages are indicated by arrows, and major lakes are blacks. Not all events shown are synchronous.

northern North America (as here defined). Of these, 16 species originated in the Pacific Refugium, 6 species in the Bering Refugium, and 16 species in the Mississippi Refugium. The remaining 12 species entered the area from multiple refugia.

A. Dispersal from the Pacific Refugium.

The Pacific Refugium includes the Pacific watershed south of the Cordilleran icesheet, and perhaps part of the Great Basin. Most of the fishes that survived glaciation in the Pacific Refugium were probably present in the Columbia system.

Sixteen species entered northern North America from the Pacific Refugium only. They are:

Entosphenus tridentatus
Lampetra ayresii
Acipenser medirostris
Acipenser transmontanus
Salmo clarki
Salmo gairdnerii
Prosopium coulteri
Prosopium williamsoni
Spirinchus thaleichthys
Thaleichthys pacificus
Catostomus macrocheilus
Mylocheilus caurinum
Ptychocheilus oregonense

Richardsonius balteatus

Cottus aleuticus

Cottus asper

Eleven of these species are euryhaline. The distributions of seven of the euryhaline species (E. tridentatus, L. ayresii, A. medirostris, A. transmontanus, S. clarki, S. thaleichthys, T. pacificus, and C. aleuticus) are restricted, in northern North America, to coastal regions. These species probably dispersed north along the coast.

Two of the euryhaline species (S. gairdnerii, and C. asper) are found, in northern North America, mainly in coastal regions but also have restricted distributions in the upper Peace River (C. asper, and S. gairdnerii) and the upper Athabasca River (S. gairdnerii), suggesting that they dispersed north by both coastal and inland routes.

The remaining euryhaline species (M. caurinum) does not enter the sea as readily as the others. The northern distribution of M. caurinum is restricted to the upper Peace and Athabasca Rivers, and is probably entirely due to inland dispersal.

Five of the Pacific species in northern North America are stenohaline, and must have dispersed through fresh water. The northern North American distribution of three species (C. macrocheilus, R. balteatus, and P. oregonense) is restricted to the upper Peace system, and one species (P. williamsoni) is found only in the Athabasca, Peace, Liard, and Stikine Rivers. The remaining species (P. coulteri) has a wide but scattered distribution in northern North America. It is recorded from the Peace, Liard, Yukon, and Alsek systems, and also from Bristol Bay drainages in Alaska.

The main inland dispersal route north from the Pacific Refugium was through the Columbia system into the Fraser River, and then into the Peace River. The Columbia and Fraser Rivers were connected by glacial lakes in the Kamloops region (Matthews, 1958), and the Fraser and Peace Rivers by glacial lakes in the Prince George region (Armstrong and Tipper, 1948). There was also a connection between the Fraser and Athabasca Rivers (Taylor, 1960). These connections probably account for the Pacific species in the upper Peace and Athabasca Rivers.

The two Pacific species (P. coulteri, and P. williamsoni) in the Liard system most likely entered from the Finlay River (Peace system) or the Stikine River. The Glacial Map of Canada (Wilson et al., 1958) indicates drainage connections in both areas. Prosopium coulteri probably entered the upper Yukon and Alsek systems from the Liard River, and then dispersed north to the Bristol Bay region.

B. Dispersal from the Bering Refugium.

The Bering Refugium includes the unglaciated regions of Alaska, the Yukon Territory, and adjacent parts of Siberia. Walters (1955) treats the arctic slope of Alaska and the Yukon Valley as separate refugia, but during the Wisconsin these areas were probably less isolated from one another than they are today (Fig. 63a), and it seems unlikely that they operated as separate refugia. Karlstrom (1961) indicates that parts of Kodiak Island and the Cook Inlet area were ice free during the Wisconsin. These areas are included in the Bering Refugium, although Kodiak Island may have functioned as a separate refugium for S. alpinus. Freshwater fishes probably did not survive in the supposedly unglaciated highland areas suggested as plant refugia by Heusser (1960).

Six species dispersed into the glaciated regions of northern North America from the Bering Refugium only. These are:

Entosphenus lamottenii
Prosopium cylindraceum
Stenodus leucichthys
Hypomesus olidus
Osmerus eperlanus
Dallia pectoralis

Four of these species (E. lamottenii, S. leucichthys, H. olidus, and O. eperlanus) commonly occur in the sea, and distribution in northern North America is no doubt largely due to coastal dispersal. Entosphenus lamottenii, H. olidus, and O. eperlanus dispersed in two directions from the Bering Refugium: south into the Gulf of Alaska region, and east along the Arctic Coast. Stenodus leucichthys dispersed only to the east along the Arctic Coast. Both E. lamottenii and S. leucichthys moved up the Mackenzie system to Great Slave Lake. Hypomesus olidus dispersed up the Mackenzie River as far as

Great Bear Lake, but *O. eperlanus* is not recorded above the Mackenzie Delta.

Of the Bering species only *D. pectoralis* is stenohaline. *Dallia* probably has not greatly expanded its range postglacially, but it is present in the Chignik River (on the south side of the Alaska Peninsula). This distribution is probably due to a postglacial exchange between the Chignik system and a Bristol Bay drainage.

The remaining Bering species (*P. cylindraceum*) dispersed in two directions: south into the Liard River and Pacific drainages to the Taku River, and east into the Mackenzie system and across the Barren Grounds. *Prosopium cylindraceum* is a headwater form, and dispersal in both directions was probably by inland routes.

C. Dispersal from the Mississippi Refugium.

The Mississippi Refugium includes the unglaciated portions of the upper Missouri, the upper Mississippi, and the Ohio River Valleys. Twice during the early Wisconsin the Missouri River was diverted by the James icelobe, and drained south across Nebraska into the Platte River (Simpson, 1960). This resulted in the partial isolation of the upper Missouri and the upper Mississippi Rivers, and it is possible that the upper Missouri functioned as a separate refugium for some species. The Missouri was not diverted during the Mankato or later advances, and many species were probably continuously distributed from the upper Missouri system to the Ohio Valley at this time.

Sixteen species entered northern North America from the Mississippi Refugium only. These are:

Hiodon alosoides

Salvelinus namaycush

Catostomus commersonii

Chrosomus eos

Chrosomus neogaeus

Hybognathus hankonsoni

Hybopsis gracilis

Notropis atherinoides

Notropis hudsonius

Pimephales promelas

Semotilis margarita

Culea inconstans

Percopsis omiscomaycus

Perca flavescens

Stizostedion vitreum

Cottus ricei

The present distribution of eight species (*C. commersonii*, *C. eos*, *C. neogaeus*, *H. hankonsoni*, *N. atherinoides*, *P. promelas*, *S. margarita*, and *C. inconstans*) suggests they were widespread in the Mississippi Refugium during the Wisconsin. Five of these species (*C. commersonii*, *H. hankonsoni*, *N. atherinoides*, *P. promelas*, and *C. inconstans*) are widely distributed in the upper Missouri and upper Mississippi systems, and probably dispersed north from both regions. However, because of the pattern of deglaciation they probably entered northern North America from the upper Missouri system.

In northern North America *Hybognathus hankonsoni*, *N. atherinoides*, *P. promelas*, and *C. inconstans* are restricted to the Mackenzie system, but *C. commersonii* is also present in both the Mackenzie system and the upper Dubawnt River. *Catostomus commersonii* probably entered the Dubawnt from the Mackenzie system. The presence of *H. hankonsoni* in the upper Peace and Fraser systems is likely due to postglacial dispersal from the Missouri River. The brassy minnow probably dispersed north from the upper Missouri into the Saskatchewan system, and from there into the Peace River. There were numerous postglacial drainage connections between these systems. At present *H. hankonsoni* is not recorded from the Saskatchewan or the Mackenzie system in Alberta, but the area is poorly collected.

The remaining three species (*C. eos*, *C. neogaeus*, and *S. margarita*) are present (but not widely distributed) in both the upper Missouri and upper Mississippi systems, and were continuously distributed in the Mississippi Refugium during the Wisconsin. *Chrosomus eos* and *S. margarita* dispersed north from both the Missouri and the upper Mississippi, but because of the pattern of deglaciation they entered the Mackenzie system from the upper Missouri.

Underhill (1957) notes that *C. neogaeus* is absent from the upper Mississippi and St. Croix Rivers in Minnesota, although apparently suitable habitat exists. Underhill explains the absence of C. neogaeus from the St. Croix River by postulating postglacial dispersal from some eastern refugium (the Atlantic Refugium?). There is no other evidence to suggest an eastern refugium for C. neogaeus and its absence from the St. Croix River can be explained by postglacial dispersal from the Missouri system.

Relict populations in South Dakota and Nebraska imply that C. neogaeus was present in the Missouri system during glaciation. From the upper Missouri C. neogaeus probably dispersed into the Saskatchewan system, and from there north to the Mackenzie system, and east into Lake Agassiz II. The absence of the finescale dace from the Minnesota and Red Rivers indicates that C. neogaeus reached Lake Agassiz II after the Warren River outlet ceased to function. Dispersal to the Great Lakes was through the eastern outlets of Lake Agassiz II into glacial Lake Duluth after the St. Croix outlet closed. From Lake Duluth C. neogaeus dispersed through the glacial Great Lakes, and then to the upper Hudson River through the Rome outlet of Lake Iroquois. The isolated populations of C. neogaeus in central Wisconsin (Greene, 1935) may represent relicts that failed to expand, or they may have dispersed south from the Great Lakes region postglacially.

Two Mississippi species (Hiodon alosoides, and Hybopsis gracilis) dispersed north only from the Missouri system. Hiodon alosoides is widespread in the Missouri and the lower Mississippi, but is absent from the Great Lakes.

The presence of *H. alosoides* in Sandy Lake and Lake Abitibi, northern Ontario, indicate dispersal through the final stages of Lake Agassiz II. Antevs (1931) suggests Lake Barlow-Ojibway was contemporary with the final stages of Lake Agassiz, and that both lakes drained into Hudson Bay through the same area. Lake Abitibi occupies part of the former basin of Lake Barlow-Ojibway, and Sandy Lake is within the area of Lake Agassiz II.

If the goldeye dispersed into northern Ontario through Lake Agassiz II it was after the eastern outlets from Lake Agassiz II to the Great Lakes ceased to operate. Since the Warren River outlet to the Mississippi was abandoned before the closure of the eastern outlets, *H. alosoides* must have entered Lake Agassiz II from the west. As noted earlier, there were numerous postglacial connections between the Missouri and the Saskatchewan systems. It is suggested the goldeye dispersed north from the Missouri into the Saskatchewan system, and from there east through Lake Agassiz II to Lake Barlow-Ojibway, and north through glacial Lake Tyrrell to the Mackenzie system.

Hybopsis gracilis is abundant in the upper Missouri, but is absent from the upper Mississippi system and the Great Lakes. This suggests that the flathead chub dispersed north from the Missouri system after the closure of the Mississippi and Great Lakes outlets of Lake Agassiz II.

Four Mississippi species (*N. hudsonius*, *P. omiscomaycus*, *P. flavescens*, and *S. vitreum*) are abundant in the upper Mississippi system, but are apparently absent from the upper Missouri. In northern North America *N. hudsonius*, *P. flavescens*, and *S. vitreum* are restricted to the Mackenzie system. These species probably dispersed from the upper Mississippi system into Lake Agassiz II by way of the Warren River outlet, and from there north into the Mackenzie system. *Percopsis omiscomaycus* dispersed in a similar manner, but is also present in the Yukon system. The distribution of *P. omiscomaycus* in the Yukon River (particularly its absence from the Tanana and upper Yukon Rivers) suggests the trout-perch recently entered the Yukon system from the Peel River (Mackenzie system), and is still dispersing within the Yukon system.

The two remaining Mississippi species (*S. namaycush*, and *C. ricei*) also dispersed only from the upper Mississippi Valley. *Salvelinus namaycush* is absent from the upper Missouri and only present in the most northern waters of the upper Mississippi. *Salvelinus namaycush* is widespread in northern North America. The lake trout probably followed the retreating icesheets closely, and used temporary drainage connections to enter the Yukon system and disperse throughout Alaska. Walters (1955) noted *S. namaycush* is euryhaline, and very likely dispersed to the Arctic Archipelago through the sea.

Cottus ricei is absent from both the Missouri and the upper Mississippi systems, but its presence in the Great Lakes and Saskatchewan systems suggest dispersal from the upper Mississippi Valley through Lake Agassiz II. *Cottus ricei* is present in the Mackenzie and Thelon systems. The headwaters of these rivers interdigitate in low tundra areas, and *C. ricei* probably entered the Thelon River from the Mackenzie system.

D. Dispersal from multiple refugia.

Twelve species entered northern North America from more than one refugium. These are:

Salvelinus alpinus
Salvelinus malma
Thymallus arcticus
Catostomus catostomus
Hybopsis plumbea
Rhinichthys cataractae
Esox lucius
Lota lota
Pungitius pungitius
Gasterosteus aculeatus
Cottus cognatus
Myoxocephalus quadricornis

Salvelinus alpinus entered northern North America from the Bering and the Atlantic Refugia. In the Bering Refugium *S. alpinus* appears to have survived in two areas: the unglaciated portion of Kodiak Island, and the main Bering Refugium. From Kodiak Island *S. alpinus* dispersed north into the Bristol Bay region, and from the Bering Refugium *S. alpinus* dispersed east along the Arctic Coast. From the Atlantic Refugium *S. alpinus* dispersed north along the Labrador Coast, and then west into Hudson Bay and the Arctic Archipelago. The Bering and Atlantic forms of *S. alpinus* apparently intergrade along the Arctic Coast.

Salvelinus malma entered northern North America from the Pacific and the Bering Refugia. Pacific *S. malma* dispersed north by both inland and coastal routes. The Pacific form of *S. malma* is present in the upper Athabaska, Peace, Liard, and Yukon Rivers as well as in coastal drainages north to the Alaska Peninsula. The Bering form of *S. malma* occurs as scattered populations within the Bering Refugium, and apparently did not expand its range postglacially.

Thymallus arcticus probably entered northern North America from both the Bering and the Mississippi Refugia. The grayling of the Mackenzie system and the Barren Grounds appear to be the Mississippi form (F. M. Atton, pers. comm.), and probably dispersed north from the upper Missouri River. The Bering form of *T. arcticus* is apparently restricted to the Bering Refugium, but may have dispersed south into the upper Liard River and Pacific drainages south to the Taku River.

Catostomus catostomus entered northern North America from the Bering and the Mississippi Refugia. The Bering form of *C. catostomus* dispersed south into Pacific drainages and the upper Liard River. From the upper Liard River Bering *C. catostomus* entered the upper Peace River and the Fraser system. The longnose suckers in the northern Columbia system appear to be intergrades between the Bering and Pacific forms of C. catostomus. The Mississippi form of C. catostomus ranges north to the Mackenzie Delta, and is present in most of the large rivers on the Barren Grounds. Catostomus catostomus is present in both the upper Missouri and the upper Mississippi systems, but because of the pattern of deglaciation the Mississippi form of C. catostomus is assumed to have entered northern North America from the upper Missouri River.

Hybopsis plumbea entered northern North America from the Pacific and the Mississippi Refugia. The Pacific form of H. plumbea is found in the upper Peace River, and probably also entered the upper Liard and Stikine Rivers. The Mississippi form of H. plumbea ranges north to the Yukon, Mackenzie, Anderson, Thelon, Dubawnt, and Kazan Rivers. The lake chub probably entered the Yukon system in the same manner as P. omiscomaycus. Barton and Broscoe (1961) describe the piracy of a Mackenzie tributary by the Anderson River. This may account for the presence of H. plumbea in the Anderson River. Headwaters of the Mackenzie, Thelon, Dubawnt, and Kazen Rivers interdigitate in flat muskeg areas, and drainage connections likely occur during floods. The lake chub probably entered the Thelon, Dubawnt, and Kazen Rivers from the Mackenzie system.

Relict populations of H. plumbea in Iowa, North Dakota, South Dakota, Wyoming, and Colorado indicate that the lake chub was widespread in the Mississippi Refugium during the Wisconsin. Underhill (1957) notes that _H_. _plumbea_ is absent from the upper Mississippi and St. Croix Rivers in Minnesota, although suitable habitat is apparently present. Underhill explains the absence of _H_. _plumbea_ from the St. Croix River by postulating postglacial dispersal from the same eastern refugium suggested for _C_. _neogaeus_. There is no other evidence to suggest an eastern refugium for _H_. _plumbea_, and its absence from the St. Croix River can be explained by postglacial dispersal from the Missouri system in the same manner as _C_. _neogaeus_. The isolated population of _H_. _plumbea_ in northeastern Iowa may represent a relict population that failed to expand postglacially, or it may have dispersed there postglacially through the Des Plaines River outlet (the last outlet of the Great Lakes to the Mississippi system).

Rhinichthys _cataractae_ entered northern North America from the Pacific and the Mississippi Refugia. The populations of _R_. _cataractae_ in the upper Peace River probably represent a Pacific form, and those in the Mackenzie system a Mississippi form. _Rhinichthys_ _cataractae_ is widespread in the upper Missouri and Mississippi systems, and probably dispersed north from both areas. Because of the pattern of deglaciation _R_. _cataractae_ is assumed to have entered the Mackenzie system from the upper Missouri.

Esox _lucius_ probably entered northern North America from both the Bering and the Mississippi Refugia. The Bering population apparently dispersed south into the upper Liard system and the Pacific drainages south to the Taku River. Esox lucius is absent from the upper Missouri system, and the Mississippi form probably dispersed north from the upper Mississippi Valley through Lake Agassiz II. In northern North America the Mississippi form of E. lucius is present in the Mackenzie, Anderson, Coppermine, Thelon, Dubawnt, and Kazen Rivers. This distribution was apparently attained by headwater exchanges between the Mackenzie and the other rivers.

Lota lota entered northern North America from the Bering and the Mississippi Refugia. Bering L. lota dispersed south into the upper Liard River, and the Pacific drainages south to the Alsek River. Lota lota is present in the upper Missouri and the upper Mississippi systems, and the Mississippi form probably dispersed north from both areas. Because of the pattern of deglaciation the Mississippi form of L. lota is assumed to have entered northern North America from the Missouri system. Mississippi Lota are present in all major rivers on the Barren Grounds.

Pungitius pungitius entered northern North America from the Bering and the Mississippi Refugia. The Bering population dispersed in two directions: south to the Gulf of Alaska region, and east along the Arctic Coast to Hudson Bay and the Atlantic Coast. The Bering form of P. pungitius is euryhaline, and dispersed through coastal waters. The Mississippi form of P. pungitius appears to be less tolerant of seawater, and dispersed only through inland routes. The Mississippi form dispersed north from the upper Mississippi system through Lake Agassiz II to the Mackenzie system. From the Mackenzie system the Mississippi form entered the Anderson, Coppermine, Thelon, Dubawnt, and Kazen Rivers. The Bering and Mississippi forms of P. pungitius appear to intergrade on the Mackenzie Delta and in the Back River.

Gasterosteus aculeatus entered northern North America from the Pacific and the Atlantic Refugia. Pacific G. aculeatus dispersed north along the Pacific Coast to the Bristol Bay region and the Atlantic form dispersed north along the coast of Labrador to Hudson Bay and Baffin Island.

Cottus cognatus entered northern North America from the Pacific, the Bering, and the Mississippi Refugia. The populations in the upper Peace River may represent a Pacific form of C. cognatus (McAllister and Lindsey, 1961). The Bering form of C. cognatus dispersed in two directions: south to the Liard River and Pacific drainages to the Stikine River, and east into the lower Mackenzie River and the northern Barren Grounds. Dispersal in both directions was probably through inland routes.

The Mississippi form of C. cognatus dispersed north from the upper Mississippi system through Lake Agassiz II into the upper Mackenzie, Thelon, Dubawnt, and Kazen Rivers. The Bering and Mississippi forms of C. cognatus apparently intergrade in Great Slave Lake, and in the Maguse and Tavani systems.

The freshwater populations of Myoxocephalus quadricornis in northern North America are derived from two sources: the Mississippi Refugium and the Arctic Ocean. Those derived from the Mississippi Refugium dispersed north in the series of large proglacial lakes formed by the retreating Laurentide icesheet. The populations of M. quadricornis on Victoria Island are postglacial marine relicts.

Summary of Postglacial Dispersal

The preceding discussion outlines, in detail, the postglacial dispersal of freshwater fishes into northern North America. Figure 64 summarizes the dispersal routes derived from this discussion. Dispersal from the Pacific Refugium (Fig. 64a) was by two main routes: north along the coast through the sea, and north through inland drainage connections between the Columbia, Fraser, and Peace Rivers.

Dispersal from the Bering Refugium (Fig. 64b) was by way of two routes: to the south and east along the coasts, and south into the upper Liard and Pacific systems through inland drainage connections. Two Bering species (Prosopium cylindraceum and Cottus cognatus) dispersed to the east through inland routes. Both species are headwater forms.

Dispersal north from the Mississippi Refugium (Fig. 64c) was through two inland routes: one from the upper Missouri system through drainage changes connected with proglacial lakes in Alberta, and the other from the upper

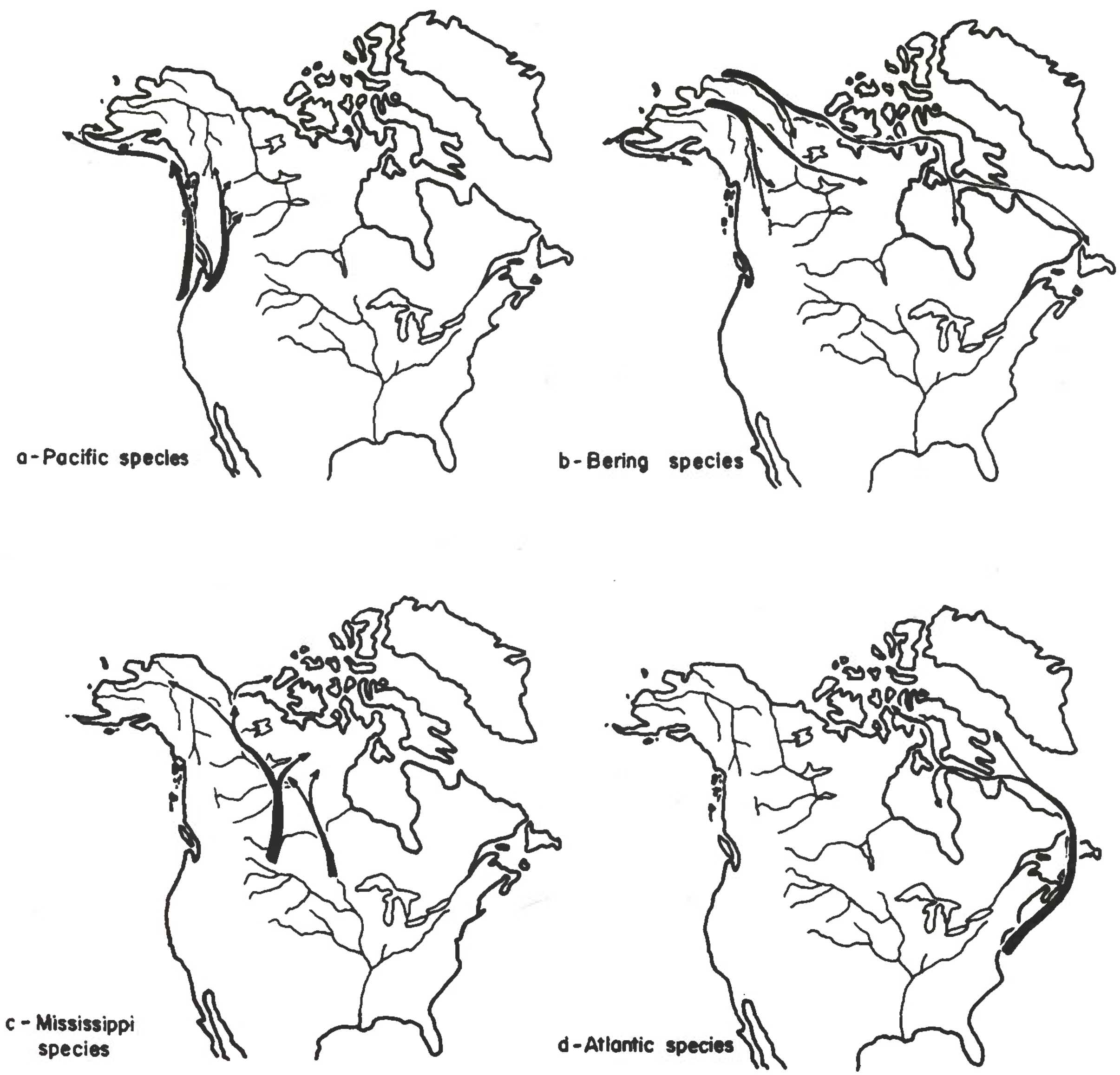


Fig. 64. Postglacial dispersal routes into northern North America.

Mississippi system through Lake Agassiz II. The upper Mississippi and the upper Missouri probably acted as separate refugia for some species, but the majority of Mississippi species dispersed north from both regions. However, the ice retreated from the Great Plains earlier than from the Great Lakes region, and this resulted in the upper Missouri being the main source of Mississippi forms in northern North America.

Dispersal from the Atlantic Refugium (Fig. 64d) was north along the Labrador Coast.

Present Distribution

The present distribution of freshwater fishes in northern North America is not static. Some species are expanding, and other species contracting their ranges. Lindsey (1956) suggests that the Pacific species in the upper Peace River are still in the process of dispersal. In contrast, some minnows (C. eos, C. neogaeus, P. promelas, and S. margarita) are discontinuously distributed in the Mackenzie system, and may have been more widespread in the past.

Probably no individual factor (except topographic barriers) limits the present distribution of freshwater fishes in northern North America. However, a complex of geological, physical, and biological factors influence present distribution. Some of these factors are discussed below.

The most important factor is the glacial history of the region, which controlled the dispersal routes. The absence of species from large areas of mainland northern

North America is probably more often due to a lack of dispersal routes than to ecological or physiological barriers.

However, not all species present in a particular refugium used all of the available dispersal routes. The ability of a species to use an available dispersal route no doubt depended on ecological and physiological factors. Coastal dispersal routes were open only to euryhaline species, and dispersal routes in mountainous areas only to headwater forms. Many species that dispersed through inland routes were probably unable to follow the retreating icesheets closely. The proglacial lakes, when first impounded by the retreating icesheets, were relatively barren and probably ecologically unsuitable for many species. They may have resembled many contemporary northwestern lakes associated with glaciers. These lakes are cold, extremely turbid in the summer, often lack rooted aquatic plants, and have barren silt bottoms. Yet, such lakes usually support fish populations, particularly salmonids.

As the icesheets retreated many of the proglacial lakes became very large. In their final stages conditions along the lake margins farthest from the ice were probably suitable for most of the species now present in northern North America.

Larkin (1956) indicates that northern freshwater fishes are flexible in their ecology. They normally have a wide tolerance of habitat type, and share many resources of their environment with other species. Therefore, interspecific competition is probably unimportant in limiting the distribution of freshwater fishes in northern North America. However, the distributions of some species are apparently restricted by habitat requirements. As noted earlier, *C. eos*, *C. neogaeus*, *P. promelas*, and *S. margarita* are discontinuously distributed in the Mackenzie system. This is probably due to ecological factors. These species are usually found in muskeg lakes and bogs (where they are often abundant), and are taken only occasionally in large rivers. Taylor (1960) indicates that the upper Mackenzie region is draining rapidly, and the amount of habitat suitable for these species is probably decreasing.

According to Radforth (1944), the distribution of some fishes is limited by temperature. She found that the northern limits of one group of species in Ontario approximated the July 70°F isotherm, and another group the July 65°F isotherm. Two species in the latter group (*C. eos* and *S. margarita*) are present in the area studied, where they occur at least 600 miles north of the July 65°F isotherm. Underhill (1957) notes that water temperature depends on a number of factors other than air temperature, and that it is difficult to relate air and water temperatures. This is particularly true in northern North America where many of the larger rivers rise far to the south and carry large volumes of warm water northwards.

Macan (1961) indicates that aquatic organisms are barred from colder waters if the temperature reaches a lethally low level at some time of year, and if the threshold temperature for development or some other activity is never exceeded or not exceeded for long enough. Since fresh waters rarely go below 0°C without freezing lethally low temperatures are probably rare.

Radforth (1944) suggests the northern limits of some species are controlled by the requirement of certain maximum water temperatures necessary for breeding and growth. Little is known about the effects of temperature on the breeding of northern fishes. However, Fabricius (1950) indicates there is no absolute threshold spawning temperature for the pike (E. lucius), but that rising temperatures are important. The same is probably true for other northern fishes.

The length of the open water season may limit the northern distribution of some species. The threespine stickleback (G. aculeatus) reaches Hudson Bay and southern Baffin Island; it is short lived, and most adults die after spawning (Greenbank and Nelson, 1959). In such a species unsuccessful spawning (due to ice conditions) for two consecutive years could eliminate the entire population.

Oceanographic conditions also appear to influence the distribution of some species in northern North America. Many euryhaline species dispersed through the sea; such species often spend most of their lives in brackish or marine waters. Along the Arctic Coast of Canada most of the euryhaline Bering Refugium species are restricted to coastal areas where the marine waters are subarctic (as defined by Dunbar, 1953).

A number of topographic barriers restrict distribution in northern North America. The most important of these is the drainage divide between the Yukon and Mackenzie Rivers. A number of species (H. alosoides, C. commersonii, H. gracilis, N. hudsonius, R. cataractae, S. vitreum, and C. ricei) occur in the middle and lower Mackenzie system, but are absent from the Yukon system. At least two of these species (H. gracilis, and C. ricei) occur in the Peel River close to headwaters of the Yukon. The Yukon system is apparently ecologically suitable for these species, and their absence is probably due to lack of a dispersal route.

Other important topographic barriers restricting the distribution of fishes in northern North America are the rapids on the Peace River above Hudson Hope, the rapids on the Liard River near the first Alaska Highway crossing, and the rapids on the Slave River at Ft. Smith. Each of these barriers prevents the upstream dispersal of some fishes. The narrow strait of saline water between the Arctic Archipelago and the mainland is a barrier to the northward dispersal of stenohaline species.

Glaciation and Evolution in Northern Freshwater Fishes

Rand (1948) suggests that glaciation was the geographic isolating factor involved in the evolution of some species of northern birds. The same appears true in some northern freshwater fishes. McPhail (1961) indicates that Salvelinus alpinus and Salvelinus malma evolved when a circumpolar ancestral stock was divided by glaciation. However, most of the present species of northern freshwater fishes probably existed before the first (Nebraskan) glaciation (Shtylko, 1934; Smith, 1962). Most of the evolution in northern freshwater fishes during the Pleistocene was at an infraspecific level.

Northern freshwater fishes are notoriously variable; this variability may be a reflection of the variable environment. The physical nature of the northern freshwater environment fluctuates seasonally, and also over longer periods of time. The Pleistocene Epoch in North America was characterized by alternating glacial and warm interglacial periods. The expanding and contracting icesheets disrupted the fauna at least four times.

Fishes living in such an environment face special problems. Seasonal fluctuations require a wide range of tolerance in individuals. Sheppard (1958) indicates that short-term environmental fluctuations select for genotypes with phenotypic flexibility. However, long-term fluctuations, such as climate changes, require genetic variability. If the gene complex of a species becomes too rigidly adapted to a particular environment the species may become extinct if conditions change. Therefore, northern freshwater fishes must maintain a gene complex in which the majority of individuals are approximately adapted to existing conditions, but with a large enough reservoir of variability to ensure continued existence in a fluctuating environment. A recent study (Lindsey, 1962) indicates that a single population of the ninespine stickleback (P. pungitius) contains a number of genotypes with slightly different morphological and physiological characteristics. This suggests that variability in northern freshwater fishes is both phenotypic and genotypic.

During the Wisconsin glaciation the environments in the various glacial refugia probably differed. The Bering Refugium was mainly tundra while the other refugia probably contained only narrow tundra zones near the ice margin (Dillon, 1956). The Pacific, the Bering, and the Atlantic Refugia were also in contact with the sea while the Mississippi Refugium was landlocked. For species isolated in several refugia these environmental differences probably resulted in the selection of slightly different gene complexes in the different refugia.

Whether these different gene complexes warrant subspecific recognition is debatable. Hubbs (1943) suggests that much more than half of a given form should be distinguishable in order to warrant subspecific recognition. Bailey, Winn, and Smith (1954) suggest at least 93 per cent of the individuals should be distinguishable. In the present study usually less than 20 per cent of the individuals in the different forms are separable by any single character. However, the number of distinguishable individuals can be increased by combining characters.

Less than 20 per cent of the two forms of Prosopium cylindraceum are separable using the best single character (gill raker count), but over 35 per cent of the individuals are distinguishable when gill raker, pyloric caeca, and caudal peduncle scale counts are combined in a discriminant function. The percentage of separable individuals could probably be increased by including more characters in the discriminant function. However, most of the allopatric forms differ significantly only in two or three characters, and it is unlikely that more than half of the individuals could be separated.

Although the morphological differences between the various forms are slight, populations can usually be distinguished. In the present study 80 to 100 per cent of the populations of the different forms are separable on the basis of mean characters. Hubbs (1943) suggests that forms separable only by mean characters should be excluded from the nomenclatorial system. Since the morphological forms in the present study can only be separated by mean characters they are not given subspecific status.

SUMMARY

The present study outlines the distributions of the fifty species of freshwater fishes in northern North America, and attempts to determine the glacial refugia and postglacial dispersal routes used by these species. The study is based on over 8,000 specimens from 542 northern localities. The freshwater fish fauna of this area is derived from five sources; the Pacific Refugium, The Bering Refugium, the Mississippi Refugium, the Atlantic Refugium, and the Arctic Ocean. Thirty-eight species dispersed into northern North America from single refugia: of these sixteen species entered from the Pacific Refugium, six from the Bering Refugium, and sixteen from the Mississippi Refugium. Twelve species entered the area from multiple refugia.

Intraspecific variation in some widespread species suggests they are divisable into allopatric morphological forms. These morphological forms are relatively constant over wide geographic areas, and apparently intergrade wherever they come in contact. The distributions of these forms indicate postglacial dispersal from different refugia, and they probably represent different gene complexes evolved during isolation in separate refugia.

There were two main avenues of dispersal into northern North America: coastal dispersal by way of the sea, and inland dispersal through drainage changes. Dispersal from the Pacific Refugium was northwards along the coast, and also through inland drainage connections between the

Columbia, Fraser, and Peace Rivers. Dispersal from the Bering Refugium was south and east along the coasts, and south and east through inland drainage changes. Dispersal from the Mississippi Refugium was through two inland routes: one from the upper Missouri system through drainage changes connected with proglacial lakes in Alberta, and the other from the upper Mississippi system through Lake Agassiz II. Dispersal from the Atlantic Refugium was north along the Atlantic Coast.

Postglacial dispersal was controlled by the pattern of deglaciation, and the absence of species from large areas of mainland northern North America is more often due to a lack of dispersal routes than to ecological or physiological barriers.

LITERATURE CITED

Antews, E. 1931. Late glacial correlations and ice recession in Manitoba. Geol. Sur. Canada, Memoir 168, pp. 1-76.

Armstrong, J. E. 1956. Mankato drift in the lower Fraser Valley of British Columbia, Canada. Bull. Geol. Soc. Am. 67: 1666-1667.

Armstrong, J. E. and H. W. Tipper. 1948. Glaciation in north central British Columbia. Am. J. Sci. 246: 283-310.

Atton, F. M. 1962. Pers. comm.

Bailey, R. M. 1945. Review of: Some considerations on the distribution of fishes in Ontario. Copeia 1945(2): 125-126.

Bailey, R. M., et al. 1960. A list of common scientific names of fishes from the United States and Canada. Am. Fish. Soc., Special Publ. No. 2, 2nd Ed., 102 pp.

Bailey, R. M. and O. M. Allum. 1962. Fishes of South Dakota. Misc. Publ. Mus. Zool., Univ. Michigan, No. 119, 131 pp.

Bailey, R. M., H. E. Winn and C. L. Smith. 1954. Fishes from the Escambia River, Alabama and Florida, with ecological and taxonomic notes. Proc. Acad. Nat. Sci., Philadelphia, 106: 109-164.

Barton, R. H. and A. J. Broscoe. 1961. Potential stream recapture in the Tieda and upper Iroquois drainage systems, N.W.T., Canada. J. Alta. Soc. Petr. Geologists, 9(8): 245-247.

Black, R. F. 1962. Pers. comm.

Broecker, W. S., *et al*. 1956. Lamont natural radiocarbon measurements III. Science 124: 154-165.

Craig, B. G. 1960. Surficial geology of north-central district of Mackenzie, Northwest Territories. Geol. Surv. Canada, Paper 60-18, 18 pp.

Craig, B. G. 1961. Surficial geology of northern district of Keewatin, Northwest Territories, Geol. Surv. Canada, Paper 61-5, 8 pp.

Craig, B. G. and J. G. Fyles. 1960. Pleistocene geology of arctic Canada, Geol. Surv. Canada, Paper 60-10, 21 pp.

Crandell, D. R., *et al*. 1958. Pleistocene sequence in southeastern part of the Puget Sound lowland, Washington. Am. J. Sci. 256: 384-397.

Creaser, C. W. and C. L. Hubbs. 1922. A revision of the Holarctic Lampreys. Occ. Papers Mus. Zool. Univ. Mich., No. 120, 14 pp.

Dillon, L. S. 1956. Wisconsin climate and life zones in North America. Science 123: 167-176.

Dunbar, M. J. 1953. Arctic and subarctic marine ecology: immediate problems. Arctic 6(2): 75-90.

Dymond, J. R. 1943. The Coregonine fishes of northwestern Canada. Trans. Roy. Canadian Inst. 24, pt. II: 171-231.

Elson, J. A. 1957. Lake Agassiz and the Mankato-Valders problem. Science 126: 999-1002.

Eschmeyer, P. H. and R. M. Bailey. 1955. The pygmy whitefish, Coregonus coulteri, in Lake Superior. Trans. Am. Fish. Soc., 84: 161-199.

Fabricius, E. 1950. Heterogeneous stimulus summation in the release of spawning activities in fish. Rep. Inst. Freshwater Res. Drottningholm, No. 31: 57-99.

Flint, R. F. 1957. Glacial and Pleistocene Geology. 2nd. Ed., John Wiley and Sons, New York. 553 pp.

Gilbert, C. H. and B. W. Evermann. 1894. A report upon investigations in the Columbia River basin with descriptions of four new species of fish. Bull. U.S. Fish. Comm. 14: 169-207.

Greenbank, J. and P. R. Nelson. 1959. Life history of the three-spine stickleback Gasterosteus aculeatus Linnaeus in Karluk Lake and Bare Lake, Kodiak Island, Alaska. U.S. Fish and Wildlife Service, Fish. Bull. 153, Vol. 59: 537-559.

Greene, C. W. 1935. The distribution of Wisconsin Fishes. Wisc. Cons. Comm., Madison, 235 pp.

Gravenor, C. P. and L. A. Bayrock. 1961. Glacial deposits of Alberta. Soils in Canada. Roy. Soc. Canada, Special Publ., No. 31: 33-50.

Heusser, C. J. 1960. Late-Pleistocene environments of North Pacific North America. Am. Geogr. Soc., Special Publ. No. 35, 265 pp.

Hickox, C. F. 1960. Late Pleistocene ice cap centered on the Nova Scotian Peninsula. Geol. Soc. Am. Bull. 71: 1887.

Holt, R. D. 1960. Comparative morphometry of the mountain whitefish, Prosopium williamsoni. Copeia 1960(3): 192-200.

Hough, J. L. 1958. Geology of the Great Lakes. University of Illinois Press, Urbana, 313 pp.

Hubbs, C. L. 1943. Criteria for subspecies, species and genera, as determined by researches on fishes. Ann. New York Acad. Sci., 44(2): 109-121.

Hubbs, C. L. 1945. Corrected distributional records for Minnesota Fishes. Copeia 1945(1): 13-22.

Hubbs, C. L. and K. F. Lagler. 1958. Fishes of the Great Lakes region. 2nd Ed., Cranbrook Inst. Sci., Bull. 26, 213 pp.

Hubbs, C. L. and R. R. Miller. 1948. The Great Basin. II- The Zoological Evidence. Bull. Univ. Utah 38(20): 17-144.

Hubbs, C. L. and L. P. Schultz. 1941. Contribution to the ichthyology of Alaska with descriptions of two new fishes. Occ. Papers Mus. Zool. Univ. Michigan, No. 431, 31 pp.

Hussakof, L. 1916. Discovery of the Great Lake trout, <u>Cristivomer namaycush</u>, in the Pleistocene of Wisconsin. J. Geol. 24: 685-689.

Ivanova, E. I. 1952. On finding smallmouth smelt in northern Europe. Trudi Gidrobiol. Obshch. 4: 252-259 (In Russian).

Ives, J. D. 1959. Glacial drainage channels as indications of late-glacial conditions in Labrador-Ungava. Cahiers de Geog. de Quebec 5: 57-72.

Ives, J. D. 1960. The deglaciation of Labrador-Ungava: an outline. Cahiers de Geog. de Quebec, Anne 4(8): 323-343.

Karlstrom, T. N. V. 1961. The glacial history of Alaska: its bearing on paleoclimatic theory. Ann. N.Y. Acad. Sci. 95(1): 290-340.

Koster, W. J. 1957. Guide to the fishes of New Mexico. University of New Mexico Press, Albuquerque, 116 pp.

Krassikova, V. A. 1960. Morphological characteristics of the nelma (Stenodus leucichthys nelma Pallas) of the Enissei River. Zh. Zool. 39(7): 1103-1106 (In Russian).

Larkin, P. A. 1956. Interspecific competition and population control in freshwater fishes. J. Fish. Res. Bd. Canada, 13(3): 327-342.

Lee, H. 1960. Late glacial and postglacial Hudson Bay sea episode. Science 131: 1609-1611.

Lindsey, C. C. 1956. Distribution and taxonomy of fishes in the Mackenzie drainage of British Columbia. J. Fish. Res. Bd. Canada, 13(6): 759-789.

Lindsey, C. C. 1962. Observations on meristic variation in ninespine sticklebacks, Pungitius pungitius, reared at different temperatures. Canadian J. Zool., 40(7): 1237-1247.

Livingstone, D. A. and B. G. R. Livingstone. 1958. Late glacial and postglacial vegetation from Gillis Lake, Richmond Co., Cape Breton Island, N.S., Am. J. Sci. 256(5): 341-359.

Macan, T. T. 1961. Factors that limit the range of fresh-water animals. Biol. Reviews 36: 151-198.

Mather, V. G. 1926. The velar apparatus of Entosphenus tridentatus. Anat. Rec. 34(1): 55-60.

Matthews, W. H. 1958. Glacial map of British Columbia. Victoria, British Columbia.

Mayr, E. 1942. Systematics and the origin of species. Columbia University Press, New York, 334 pp.

McAllister, D. E. 1961. The origin and status of the Deepwater Sculpin, Myoxocephalus thompsonii, a Nearctic glacial relict. Nat. Mus. Canada, Bull. 172: 44-65.

McAllister, D. E. 1963. A preliminary revision of the smelts, Osmeridae. Nat. Mus. Canada. In Press.

McAllister, D. E. and C. C. Lindsey. 1961. Systematics of the freshwater sculpins (*Cottus*) of British Columbia. Nat. Mus. Canada. Bull. 172: 66-89.

McPhail, J. D. 1961. A systematic study of the *Salvelinus alpinus* Complex in North America. J. Fish. Res. Canada, 18(5): 793-816.

McPhail, J. D. 1963. Geographic variation in North American Ninespine sticklebacks, *Pungitius pungitius*. J. Fish. Res. Bd. Canada, 20(1), in press.

Miller, R. R. 1962. Pers. comm.

Needham, P. R. and R. Gard. 1959. Rainbow trout in Mexico and California. Univ. Cal. Publ. Zool., 67(1): 1-124.

Newman, W. S. and R. W. Fairbridge. 1960. Glacial lakes in Long Island Sound. Bull. Geol. Soc. Am. 71: 1936.

Ogden, J. G. 1959. A late-glacial pollen sequence from Martha's Vineyard, Massachusetts. Am. J. Sci. 257: 366-381.

Olson, E. A. and W. S. Broecker. 1959. Lamont natural radiocarbon measurements V. Am. J. Sci. 257: 1-28. (Radiocarbon supplement 1: 1-28.)

Olund, L. J. and F. B. Cross. 1961. Geographic variation in the North American cyprinid fish, Hybopsis gracilis. Univ. Kans. Publ. Mus. Nat. Hist., 13: 323-348.

Qadri, S. 1959. Some morphological differences between the subspecies of cutthroat trout, Salmo clarkii clarkii and Salmo clarkii lewisi, in British Columbia. J. Fish. Res. Bd. Canada, 16(6): 903-927.

Radforth, I. 1944. Some considerations on the distribution of fishes in Ontario. Contr. Roy. Ontario Mus. Zool., No. 25, 116 pp.

Rand, A. L. 1948. Glaciation as an isolating factor in speciation. Evolution 2(4): 314-321.

Sheppard, P. M. 1959. Natural selection and Heredity. Hutchinson University Library, London, 212 pp.

Shtylko, B. A. 1934. A Neogene fauna of freshwater fishes from western Siberia. Un. Geol. Prosp. Serv. U.S.S.R., Trans. 359: 82-91 (In Russian).

Simpson, H. E. 1960. Geology of the Yankton area South Dakota and Nebraska. U.S. Geol. Surv. Prof. Paper 328, 124 pp.

Sinclair, W. J. 1904. Univ. Calif. Publ. Am. Archae. Ethnol. 11: 127.

Smith, C. L. 1962. Some Pliocene fishes from Kansas, Oklahoma and Nebraska. Copeia 1962(3): 505-520.

Stanley, J. 1962. The discriminant function, a mathematical method for the taxonomic separation of species. Mimeo., McGill University, 10 pp.

Svärdson, G. 1961. Young sibling fish species in northwestern Europe. In, Blair, W. F. Vertebrate Speciation. University of Texas Press, Austin: 498-513.

Taylor, R. S. 1960. Some Pleistocene lakes of northern Alberta and adjacent areas. J. Alb. Soc. Petr. Geol. 8(6): 167-185.

Terasmae, J. 1959. Notes on the Champlain Sea episode in the St. Lawrence lowlands, Quebec. Science 130: 334-336.

Underhill, J. C. 1957. The distribution of Minnesota minnows and darters in relation to Pleistocene glaciation. Occ. Pap. Minn. Mus. Nat. Hist. No. 7, 45 pp.

Vladykov, V. D. 1949. Quebec lampreys. Quebec Dept. Fisheries Contr. No. 26, 67 pp.

Walters, V. 1955. Fishes of western Arctic America and eastern Arctic Siberia. Bull. Am. Mus. Nat. Hist., 106(5): 255-368.

Wilimovsky, N. J. 1962. Pers. comm.

Wilson, J. T., *et al*. 1958. Glacial map of Canada. Geol. Assoc. Canada, Toronto.

Wynne-Edwards, V. C. 1947. Northwest Canadian fisheries survey. Bull. Fish. Res. Bd. Canada, No. 72. Ch. 2, The Yukon Territory: 6-20.

Zenkevitch, L. A. 1957. Caspian and Aral Seas. Geol. Soc. Am. Mem. 67, Vol. 1: 891-916.

APPENDIX I

Specimens examined; the numbers preceding the localities are referred to in the "results" section.

		North latitude	West longitude
Alaska			
1	Adak Is.	52°00'	176°80'
2	Admiralty Is.	57°22'	134°25'
3	Ahtel Cr.	62°43'	143°59'
4	Alakanuk	62°50'	164°40'
5	Alaktak	70°55'	155°00'
6	Aleknagik L.	59°12'	158°35'
7	Alexander L.		
8	Andreafsky R.	62°10'	163°01'
9	Andreaksky	62°05'	163°00'
10	Aniak L.	60°30'	159°12'
11	Aniak R.	61°35'	159°40'
12	Atka Is.	52°02'	174°08'
13	Barter Is.	70°05'	143°40'
14	Baxter L.		
15	Bear Cr.	63°37'	144°00'
15a	Bethel	60°50'	161°30'
16	Big L.	61°30'	150°00'
17	Big Kitoi L.	58°11'	152°25'
18	Birch Cr.	65°42'	144°22'
19	Birch Cr.	64°18'	146°42'
20	Birch L.	64°18'	146°40'
21	Bostwick Bay	55°13'	131°42'
22	Boundry Cr.	58°35'	133°40'
23	Boussole Bay	58°15'	137°00'
24	Boxer Bay	64°40'	171°30'
25	Bristol Bay	58°00'	158°00'
26	Brooks L.	58°22'	156°00'
27	Cantwell (a nearby lake)	63°20'	149°07'
28	Canyon Is.	58°34'	133°40'
29	Cape St. Elias	59°50'	144°40'
30	Chandler R.	68°15'	153°00'
31	Chatanika R.	65°12'	147°16'
32	Chatham In.	57°25'	134°30'
33	Chenan L.	61°32'	144°26'
34	Chichagof Is.	57°45'	136°00'
35	Chief Cr.	63°38'	144°02'
36	Chignik R.	56°28'	158°51'
37	Chilkat R.	59°35'	136°10'
38	Chisana R.	63°00'	141°49'
39	Chistochina R.	62°36'	144°38'
40	Chuckchi Sea	68°25'	167°55'
41	Circle	65°50'	144°04'
42	Colville R.	70°15'	151°00'

		North latitude	West longitude
Alaska			
43	Cooper L.	60°23'	149°45'
44	Copper R.	62°30'	144°48'
45	Copper R. mouth	60°30'	145°00'
46	Cordova Bay	55°00'	132°30'
47	Dall Is.	55°00'	135°00'
48	Daniel Vincent L.		
49	Dease Inlet	71°00'	155°30'
50	Dennison R.	63°55'	142°08'
51	Dickie L. (Copper syst.)		
52	Dixon Hbr.	58°20'	136°51'
53	Douglas Is.	58°10'	134°30'
54	Dry Cr.	63°41'	144°42'
55	Eagle	64°47'	141°11'
56	East Omalik	70°00'	155°30'
57	Elson Lagoon	71°12'	156°40'
58	Eshany L.	60°08'	149°02'
59	Esther Is.	57°51'	136°26'
60	Eyak L.	61°42'	145°42'
61	Faith Cr.	65°17'	146°23'
62	Fern L.	58°11'	152°25'
63	Fielding L.	63°10'	145°38'
64	Fish Cr.	63°23'	148°23'
65	Fish L. (Copper syst.)		
66	Flannigan Sl.	58°35'	133°39'
67	Forty Mile R.	64°05'	141°57'
68	Fraser L.	57°15'	154°10'
69	Gakona R.	62°18'	145°17'
70	Gambell	63°50'	171°40'
71	Gastineau Ch.	58°40'	134°11'
72	Gene's L. (Kenai Pen.)		
73	Glacier Cr.	60°56'	149°56'
74	Goodpaster R.	64°08'	145°28'
75	Grant Cr.	60°27'	149°21'
75a	Grantley Hbr.	65°05'	166°10'
76	Grindstone Cr.	58°12'	134°10'
77	Grosvenor L.	60°58'	155°01'
78	Gulf of Alaska	59°12'	146°15'
79	Gunn Cr.	63°10'	145°32'
79a	Gulkana R.	62°18'	145°18'
80	Haggard Cr.	62°42'	145°26'
81	Hanus Bay	57°25'	135°02'
82	Hansen Cr.	59°12'	158°35'
83	Herbert R.	58°31'	134°48'
84	Hidden Cr.	59°15'	158°35'
85	Hinchenbrook Is.	60°15'	146°21'
86	Holy Cross	62°08'	159°55'
87	Hooper Bay	61°55'	166°05'
88	Hot R.	69°34'	144°55'
89	Icy Bay	60°00'	141°20'
90	Idaho Cr.	65°20'	146°10'

		North latitude	West longitude
Alaska			
91	Idavain L.	58°45'	156°00'
92	Iguishik	58°43'	158°49'
93	Iliamna L.	59°45'	155°00'
94	Itkillik R.	70°00'	150°55'
95	Karluk L.	57°23'	154°09'
96	Karta Bay	55°34'	132°34'
97	Kenai R.	60°28'	151°24'
98	Kiana	66°59'	160°30'
99	Kikiakrorak R.	70°00'	151°40'
100	King Cove	55°03'	162°19'
101	King Salmon Cr.	58°10'	157°20'
102	King Solomon Cr.	64°32'	141°15'
103	Kisaralik L.	60°28'	159°20'
104	Kiska Is.	52°00'	178°30'E
105	Kobuk R.	66°57'	160°32'
106	Kokhanok L.	59°30'	154°02'
107	Kongii Stl.	63°10'	173°40'
108	Koozata Lagoon	63°20'	173°42'
109	Kotzebue Snd.	65°55'	163°00'
109a	Kruzof Is.	57°00'	135°40'
110	Kuichak Bay	58°30'	157°30'
111	Kuskokwim R. at mouth	60°40'	162°00'
112	Kuskokwim R. at Aniak	61°45'	159°40'
113	Kuzitrin R.	63°22'	164°00'
114	Letnik R.	58°10'	153°08'
115	Little Campbell Cr.	61°09'	149°52'
115a	Little Kitoi Str.	58°09'	152°21'
116	Livengood (stream 20 miles south)	65°27'	148°43'
117	Long L. (Copper R.)	61°25'	143°20'
118	Louise L.	62°19'	146°32'
119	MacDonald L.	58°09'	152°20'
120	McGrath	63°55'	153°38'
121	McLaren R.	63°13'	146°32'
122	Meade R.	70°30'	157°15'
123	Mentasta L.	63°01'	145°58'
124	Moon L.	63°23'	143°32'
125	Midarm L.	58°11'	152°23'
126	Mission	61°41'	161°27'
127	Moose Cr.	64°42'	147°08'
128	Moose L.	61°25'	143°33'
129	Mt. McKinley Pk.	61°10'	150°00'
130	Mud L.	60°32'	149°45'
131	Mukluk Slough	69°38'	158°00'
132	Nagai Is.	55°00'	160°00'
133	Naknek L.	58°39'	156°08'
133a	Naknek R.	58°39'	157°00'
134	Nelson Lagoon	55°55'	161°21'
135	Nenana R.	63°40'	148°51'
136	Nerka L.	59°25'	159°00'
137	Ninilichik	60°03'	151°40'

		North latitude	West longitude
Alaska			
138	Nixon Forks	63°56'	153°38'
139	Noluck L.	68°48'	160°00'
140	Nome Beach	64°31'	165°10'
141	Nome River	64°30'	165°08'
142	Nopaskik	60°55'	161°56'
143	Norohem		
145	Nulato	64°38'	158°00'
146	Nulato, ¼ mile below town	64°38'	158°00'
147	Nulato R.	64°37'	158°00'
148	Nunivak Is.	60°00'	166°00'
149	Nushagak R.	59°00'	158°00'
150	Oamolik	70°00'	155°30'
151	Oldman L.	62°10'	146°36'
152	Oliktok	70°22'	149°58'
153	Orca Is.	60°30'	146°00'
154	Otter Cr.	60°52'	150°52'
155	Paxson L.	62°56'	145°31'
156	Peterson Cr.	58°27'	132°13'
157	Phelan Cr.	63°16'	145°43'
158	Pilgrim R.	65°00'	162°40'
159	Pt. Barrow	71°10'	156°32'
160	Pt. Etches	60°19'	146°37'
161	Pt. Hope	68°25'	167°00'
162	Porcupine R. at Rampt.	67°04'	141°40'
163	Port Clarence	65°20'	167°00'
164	Port Hobron	57°10'	153°10'
165	Portland Is.	58°18'	135°14'
166	Potter Cr.	61°03'	149°47'
167	Pribiloff Is.	57°00'	170°00'W
168	Prince William Sound	60°30'	147°00'
169	Red R. (Kodiak)	57°12'	154°00'
170	St. Matthew Is.	60°15'	173°00'
171	St. Michael	63°38'	164°00'
172	St. Paul Is.	57°11'	170°18'
173	Salcha R.	64°28'	146°47'
174	Salmon L.	64°50'	165°00'
175	Seward (a lagoon)	60°05'	149°30'
176	Schrader L.	69°30'	145°00'
177	Seward (a stream)	60°05'	149°30'
178	Sheep Bay	60°28'	145°49'
179	Silver L.	58°11'	152°22'
180	Siona Cr.	62°36'	144°39'
181	Sitkalidak Is.	57°00'	151°15'
182	Situk R.	59°34'	139°31'
183	Skilak L.	60°25'	150°27'
184	Snag Pt.	59°06'	158°31'
185	Summit L.	63°08'	145°32'
186	Summit L.	60°37'	149°31'
187	Susitna L.	62°23'	147°23'
188	Susitna Trib.	63°06'	147°29'

		North latitude	West longitude
Alaska			
189	Takotna R.	62°58'	155°50'
190	Taku Hbr.	58°05'	134°00'
191	Taku R.	58°32'	133°51'
192	Tanana R. 20 miles above Fairbanks	64°33'	147°04'
193	Tanana R. 30 miles above Fairbanks	64°30'	146°58'
194	Tanana R. 40 miles above Fairbanks	64°20'	146°53'
195	Tanana R. at Delta R.	64°15'	146°21'
196	Tangle L.	62°58'	146°05'
197	Tangle L. trib.	62°58'	146°05'
198a	Tatlina R.	65°20'	148°19'
199	Taylor Bay	58°20'	136°31'
200	Tazlina R.	62°03'	145°26'
201	Tolovana R.	65°28'	148°19'
202	Tolstoi L	63°10'	157°45'
202a	Tolsona R.	62°06'	145°58'
203	Tomname	61°21'	169°00'
204	Topagoruk	70°48'	155°40'
205	Turnagain Arm	60°57'	149°21'
206	Turnagain Arm (a slough)	60°56'	149°20'
207	Twelvemile Cr.	65°22'	145°46'
208	Twin Glacier L.	58°32'	133°54'
209	Tyone L.	62°30'	146°48'
210	Ugashik	57°30'	157°41'
211	Umiat	68°20'	152°10'
212	Unalakleet R.	63°52'	160°55'
213	Unalaska Is.	53°53'	166°35'
214	Up-a-tree Cr.	58°22'	156°00'
215	Upper Trail L.	60°31'	149°24'
216	Wade Cr.	64°07'	141°33'
217	Wainwright	70°30'	160°00'
218	Washington Cr.	65°08'	147°53'
219	Wasilla L.	61°34'	149°52'
220	Wide Bay	57°28'	156°30'
221	Wilson R.	55°20'	130°40'
222	Wood R.	59°09'	158°30'
223	Wrangell	56°22'	132°28'
224	Yakatat	59°41'	139°50'
225	Yes Bay	55°54'	131°47'
226	Yukon R. 100 miles above mouth	61°55'	161°30'
227	Zachar Bay	57°32'	153°56'

		North latitude	West longitude
Alberta			
228	Athabasca (Town)	54°45'	113°15'
229	Bear R.	55°09'	118°48'
230	Boyer R.	58°17'	117°15'
231	Bush R.	58°35'	117°09'
232	Calling L.	55°16'	113°20'
233	Cardinal L.	56°18'	117°48'
234	Cold L.	54°40'	112°02'
235	East Hawk Hills	58°31'	117°37'
236	Ft. Chipewayan	58°31'	111°10'
237	Ft. McMurray	56°41'	111°20'
239	Ft. Vermilion	58°25'	116°00'
240	Fox Cr.	56°00'	119°54'
241	Goose Is.		
242	Grande Prairie	55°10'	118°50'
244	Hay R. at Indian Cabins	59°30'	117°09'
245	Hay R. mile 63	59°00'	117°49'
246	Hay R. mile 68	59°05'	117°50'
247	Highwood R.	55°40'	118°48'
248	Hotchkiss R.	57°06'	117°30'
249	Hutch L.	58°36'	117°05'
250	Jasper	52°46'	118°04'
251	Keg R.	57°42'	117°50'
252	Kemp R.	58°06'	117°20'
253	Lesser Slave L.	55°25'	115°00'
254	Lutose Cr.	58°42'	117°28'
255	Martin R.	55°30'	114°48'
256	Meander Cr.	58°35'	117°08'
257	Merkle R.	57°08'	117°31'
258	Obed L.	53°34'	117°10'
259	Peace R. at Dunvegan	55°58'	118°36'
260	Pyramid L.	52°47'	118°05'
261	Swan L.	55°31'	120°01'
262	Wapiti R. (Pipestone Cr.)	55°08'	119°00'
263	Wapiti R. (Big Mountain)	55°10'	119°01'
264	Wavey L. (near Athabasca L.)		
265	Whitemud R.	56°30'	117°34'
British Columbia			
266	Angusmac Cr.	54°34'	122°42'
267	Atlin L.	59°30'	133°43'
268	Atlin L. (Warm Bay	59°38'	133°42'
269	Azouzetta L.	55°23'	122°37'
270	Beaton R.	57°05'	122°34'
271	Carp L.	54°43'	123°21'
272	Centurion Cr.	55°50'	121°43'
273	Charlie L.	56°20'	120°00'
274	Coal R.	59°37'	127°00'
275	Davie L. (Parsnip system)		

		North latitude	West longitude
British Columbia			
276	Dease L.	58°40'	130°00'
277	Ft. Nelson	58°49'	122°30'
278	Ft. St. John	56°30'	120°46'
279	Gnat L.		
280	Haglen L.		
281	Hart L.	54°25'	122°37'
282	Hidden Cr.		
283	Hudson Hope	56°01'	121°55'
284	Hyland R.	59°58'	128°10'
285	Jackfish Cr.	58°34'	122°40'
286	Kelly L.		
287	Kelsall L.	59°40'	136°30'
288	Kerry L.	54°42'	122°30'
289	Kledo Cr.	58°50'	123°32'
290	Klua Lakes	58°07'	122°15'
291	Kotcho L.	59°02'	121°05'
292	Liard R. (Lower Post)	59°58'	128°30'
293	Liard R. (mile 496)	59°24'	126°05'
294	Liard Htsp.	59°24'	126°00'
295	Lynx Cr.	56°07'	121°44'
296	McLeod L.	54°54'	122°57'
297	Mill Cr.	58°40'	123°58'
298	Moberly L.	55°50'	121°40'
299	Moberly L. trib.	55°50'	121°42'
300	Muncho L.	59°00'	125°47'
301	Muskwa R.	58°47'	122°39'
302	Omineca R.	55°44'	124°40'
303	One Is. L.	55°30'	120°01'
304	Paquette Cr.	55°50'	121°40'
305	Parsnip R.	55°06'	122°58'
306	Peace R. above Hudson Hope	56°01'	122°00'
307	Peace R. at Pine R.	56°08'	120°42'
308	Peace R. at Bridge	56°08'	120°41'
309	Peace R. 11 miles W of Bridge	56°08'	120°42'
310	Pine R. (headwaters)	55°32'	122°28'
311	Pouce Coupe R.	55°33'	120°39'
312	Rasberry Cr.	58°54'	123°19'
313	Redrocky L. (Parsnip system)		
314	Seltat Cr.	59°36'	136°27'
315	Simmons L.	59°16'	129°20'
316	Stikine R.	58°00'	131°00'
317	Stoddard Cr.	56°16'	120°55'
318	Stonehouse Cr.	59°39'	136°28'
319	Stuhini Cr.	58°37'	133°32'
320	Summit L.	54°17'	122°40'
321	Swan L. (Yukon)	59°53'	131°24'
322	Sylvester Cr.	55°26'	124°02'
323	Tacheeda L. (Parsnip system)		
323a	Tagish L.	59°47'	134°15'
198	Tanzilla R.	58°00'	135°00'

	North latitude	West longitude
British Columbia		
324 Tatsho L.	58°24'	130°09'
325 Telegraph Cr.	57°54'	131°10'
326 Teslin L.	59°50'	132°16'
327 Toad R.	58°49'	125°28'
328 Tydyah L. (Parsnip system)		
329 Winter Cr.	57°52'	131°20'
330 Wolverine Cr.	55°40'	124°26'
Northwest Territories		
331 Aberdeen L.	64°30'	99°00'
332 Aklavik	68°13'	135°00'
333 Alert	82°31'	62°05'
334 Anderson R.	69°45'	128°53'
334a Andrew R.	68°48'	128°57'
335 Angikuni L.	62°17'	99°36'
336 Arctic Red River	67°27'	133°45'
337 Armit L.	64°06'	91°32'
338 Axel Heiberg Is.	80°30'	92°00'
339 Back R.	67°15'	95°15'
340 Baillie Is.	70°31'	128°19'
341 Baker L.	64°17'	96°05'
342 Bathurst Inlet	66°50'	108°01'
343 Beechy L.	65°12'	106°28'
344 Belcher Is.	56°26'	78°49'
345 Bernard Hbr.	68°45'	114°45'
346 Beverly L.	64°35'	100°38'
347 Beaverlodge L.	64°39'	118°08'
348 Big Buffalo L.	60°52'	115°03'
349 Birch L. tributary	62°04'	106°43'
350 Blackstone R.	61°05'	122°55'
351 Bloody Falls	67°46'	115°19'
352 Buffalo L.	60°52'	115°03'
353 Cambridge Bay	69°07'	105°10'
354 Cape Dorset	64°14'	76°32'
355 Cape Lambert	68°31'	114°07'
356 Char fishing R.	63°50'	68°30'
357 Chesterfield Inlet	63°25'	90°45'
358 Clinton-Colden L.	63°50'	107°38'
359 Cockburn Pt.	68°52'	115°00'
360 Coppermine R.	67°49'	115°04'
361 Creswell Bay	72°45'	94°06'
362 Dismal L.	67°13'	116°32'
363 Dubawnt L.	62°43'	102°31'
364 East Meliadine L.	63°05'	92°25'
365 Ekalluk	69°48'	104°35'
366 Eleanor L.	75°24'	93°54'
367 Ellice L.	65°43'	106°00'
368 Eskimo Pt.	61°07'	94°03'
369 Eureka	80°09'	86°00'
370 Ferguson L.	69°28'	104°22'

		North latitude	West longitude
Northwest Territories			
370a	Fish L.	71°50'	124°38'
371	Ft. Franklin	65°11'	123°26'
372	Ft. Good Hope	66°15'	128°38'
373	Ft. McPherson	67°26'	134°53'
374	Ft. Norman	64°54'	125°36'
375	Ft. Resolution	61°10'	113°40'
376	Ft. Simpson	61°52'	121°23'
377	Ft. Smith	60°00'	111°53'
378	Frank Channel	62°48'	115°56'
379	Franklin Bay	70°11'	127°03'
380	Frobisher Bay	62°51'	67°21'
381	Fuller L. (Wood Buffalo Park)		
382	Garry L.	66°00'	100°00'
383	Gjoa Haven	68°38'	95°40'
384	Godamit L.	62°25'	93°31'
385	Gordon L.	63°05'	113°10'
386	Great Bear L.	66°00'	120°00'
387	Great Slave L.	61°23'	115°38'
388	Great Slave L. at outlet	61°21'	117°35'
389	Great Slave L. stream entering S side	61°00'	116°28'
390	Great Slave L. 25 miles NW of Yellowknife	62°34'	115°08'
391	Gros Cap	61°51'	121°17'
392	Greiner L.	69°07'	105°00'
393	Hay R. near Great Slave	60°52'	115°46'
394	Hay R. 20 miles above Alexandra Falls	60°30'	116°25'
395	Hay R.	60°51'	115°43'
396	Hazen L.	81°50'	71°00'
397	Hole L. (Wood Buffalo Park)		
398	Hornaday R.	69°23'	123°55'
399	Horton R.	69°55'	126°46'
400	Hungry Bay, Devon Is.	76°37'	96°25'
401	Husky Lakes	68°10'	135°06'
402	Hyde L.	60°45'	95°21'
403	Inuvik	68°28'	134°30'
404	Kakisa L.	60°55'	117°40'
405	Kakisa R.	61°03'	117°10'
406	Kamilukuak R.	62°43'	101°03'
407	Kathawachage L.	66°12'	111°08'
408	Kazen R.	64°02'	95°30'
409	Keller L.	63°55'	121°35'
410	Kellett R.	72°05'	125°42'
411	Kendall R.	67°07'	116°02'
412	Kingva Fiord (Cumberland Sd.)		
413	Kittigasuit	69°21'	133°41'
414	Lac La Martre	63°10'	117°20'
415	Lake Harbour	62°51'	69°53'
416	Liverpool Bay	69°49'	130°19'

		North latitude	West longitude
Northwest Territories			
417	Long L.	69°09'	104°38'
418	Lower Sass R.	60°10'	112°53'
419	MacDougall L.	65°59'	98°34'
420	Mackenzie R. mouth	69°30'	135°30'
421	McKinley Pt.	72°14'	111°33'
422	Maguse L.	61°24'	94°24'
423	Maze L.	62°23'	93°25'
424	McConnell R.	60°49'	94°23'
425	Meliadine L.	63°02'	92°23'
426	Mink Cr.	60°02'	117°00'
427	Mould Bay	76°14'	119°25'
428	Mt. Oosaalin (Cumberland Sd.)		
429	Namaycush L.	70°45'	108°33'
430	Nelson L.	62°13'	111°38'
431	Nettilling L.	66°30'	70°40'
432	Norman Wells	65°17'	126°52'
433	Nottingham Is.	63°06'	78°00'
434	Nueltin L.	60°30'	99°30'
435	Peel Channel	68°13'	135°00'
436	Peel R.	67°42'	134°32'
436a	Pelly L.	65°49'	102°02'
437	Pond Inlet	72°41'	78°00'
438	Pt. Radium	66°05'	118°02'
439	Raddi L.	71°42'	123°42'
440	Rae, a small stream	62°50'	116°03'
441	Redrock L.	65°29'	114°26'
442	Reindeer Stn.	68°42'	134°06'
443	Resolute	74°41'	94°54'
444	Rowley Is.	69°08'	77°15'
445	Sachs Hbr.	71°59'	125°14'
445a	Shingle Pt.	69°00'	137°26'
446	Sylvia Grinnell R.	63°43'	68°32'
447	Simpson Pt.	68°34'	88°45'
448	Southampton Is.	64°20'	84°40'
449	Stagg R.	62°34'	115°29'
450	Starvation L.	64°54'	112°45'
451	Stock L.	62°28'	114°24'
452	Surrey L.	69°42'	107°17'
453	Taltson R.	61°23'	112°45'
454	Tathlina L.	60°32'	117°32'
455	Tazin R.	60°26'	110°45'
456	Teklani R.		
457	Term Pt.	62°08'	92°28'
458	Thelon R.	64°16'	96°05'
459	Thelon R.	64°00'	104°64'
460	Thomson R.	74°08'	119°35'
461	Tuktoyaktuk	69°27'	132°58'
462	Vaillant L.	66°12'	114°29'
463	Walker Bay	71°33'	118°15'
464	Washburn L.	70°02'	107°15'
465	Whitefish L.	62°37'	106°45'

		North latitude	West longitude
Northwest Territories			
466	Whitefish Stn.	69°23'	113°35'
467	Wholdaia L.	60°45'	104°30'
468	Yellowknife Bay	61°40'	114°00'
469	Zeta L.	71°00'	106°38'
Saskatchewan			
470	Cree L.	57°30'	107°00'
471	Lake Athabasca	59°00'	109°00'
472	Wollaston L.	58°00'	103°00'
Yukon Territory			
473	Aishikik R.	60°51'	137°05'
474	Big Joe Cr.	67°35'	139°51'
475	Brachbaum L.	60°46'	135°04'
476	Carmacks	62°07'	136°17'
479	Christmas Cr.	61°00'	138°14'
480	Clear Cr.	63°37'	137°37'
481	Collison Pt.	69°34'	138°50'
482	Crystal L.	63°14'	136°05'
483	Donjek R.	61°38'	139°44'
483a	Dezadeash L.	60°26'	137°00'
484	Fairchild L.	64°58'	133°43'
485	Firth R.	69°32'	139°22'
486	Flat Cr.	63°57'	138°37'
487	Foxe L.	61°14'	135°27'
488	Herschel Is.	69°34'	138°54'
489	Jarvis R.	60°45'	138°07'
490	Kathleen L.	60°33'	137°21'
491	King Pt. Hbr.	69°06'	131°54'
492	Klondike R.	64°01'	138°48'
493	Kluane L.	61°22'	138°59'
494	Kluane R.	61°34'	139°21'
494a	Klukshu L.	60°19'	136°59'
495	Koidern L.	61°58'	140°25'
496	Kookatsoon L.	60°40'	135°12'
497	Laberge L.	61°10'	135°05'
498	Lewes Dam	60°43'	135°03'
499	Little L. outlet	60°01'	134°15'
500	Little Rancheria	60°12'	129°34'
501	Louise L.	60°45'	135°08'
502	McQueston R.	63°33'	137°25'
503	Moose Cr.	63°30'	137°01'
504	Niggerhead L.	62°15'	140°40'
505	Nordenskiold R.	62°06'	136°19'
506	Old Crow	67°35'	139°50'
507	Partridge Cr.	60°00'	131°19'
508	Peel R.	67°42'	134°32'
509	Pelly R.	62°50'	136°36'

Yukon Territory

		North latitude	West longitude
510	Pickhandle L.	61°55'	140°19'
511	Pine L.	60°08'	130°55'
511a	Popcorn L.		
512	Rat R. (headwaters)	67°38'	134°52'
513	Sandpete Cr.	62°03'	140°40'
514	Slims R.	61°00'	138°31'
515	Squanga L.	60°28'	133°48'
516	Stewart R.	63°35'	135°52'
517	Swede Johnson Cr.	61°35'	139°24'
518	Takhanne R.	60°05'	136°59'
519	Takhini R.	60°37'	136°08'
520	Tatchun Cr.	62°17'	136°07'
521	Watson L.	60°06'	128°49'
522	White R.	62°22'	140°22'
523	Whitehorse Res.	60°22'	135°03'
524	Yukon R. at Dawson City	64°04'	139°26'
525	Yukon R. at Whitehorse	60°34'	134°42'
526	Mile 900 Alaska Highway	60°08'	133'00'

APPENDIX II

References containing literature records for areas from which specimens were not examined. The numbers preceding each are referred to in the "results" section.

1. Anderson, R. M. 1913. <u>In</u> Stefansson, V. My life with the eskimo. Macmillan Co., New York: pp. 450-455.

2. Bean, T. H. 1879. Fishes collected in Cumberland Gulf and Disko Bay. Bull. U.S. Nat. Mus. 15: 107-138.

3. Bean, T. H. 1881. A preliminary catalogue of the fishes of Alaskan and adjacent waters. Proc. U.S. Nat. Mus. 4: 239-272.

4. Bean, T. H. 1888. Fishes determined from photographs. <u>In</u> Dawson, G. M. Report on an exploration in the Yukon district, N.W.T. Rept. Geol. Survey Canada, 1887-1888, new ser., 3(1), app. 4: pp. 231B.

5. Blackett, R. F. 1962. Some phases in the life history of the Alaskan blackfish, <u>Dallia</u> <u>pectoralis</u>. Copeia 1962(1): 124-130.

6. Clarke, C. H. D. 1940. A biological investigation of the Thelon Game Sanctuary. Bull. Nat. Mus. Canada, 96, Fishes, pp. 112-117.

7. Dall, W. 1870. The food fishes of Alaska. Report of U.S. Comm. Agriculture, 1870: 375-392. There is no author's name with this paper but Bean (1890) credits it to W. H. Dall.

8. Dymond, J. R. 1943. The Coregonine fishes of northwestern Canada. Trans. Roy. Canadian Inst. 24, pt. II: 171-231.

9. Ellis, D. V. 1962. Observations on the distribution and ecology of some Arctic fish. Arctic 15(3): 179-189.

10. Evermann, B. W. 1905. Report on inquiry respecting food-fishes and fishing grounds. Rep. U.S. Comm. Fish. 1904: 81-162.

11. Evermann, B. W. and E. L. Goldsborough. 1907. Fishes of Alaska. Bull. U.S. Bur. Fish. 26, 1906: 221-360.

12. Fowler, H. W. 1905. Notes on some Arctic fishes, with a description of a new Oncocottus. Proc. Acad. Nat. Sci. Phila. 57: 362-370.

13. Fowler, H. W. 1948. Fishes of the Nueltin Lake expedition, Keewatin, 1947. Part I - Taxonomy. Proc. Acad. Nat. Sci. Phila. 100: 141-152.

14. Gilbert, C. H. 1895. The ichthyological collections of the steamer "Albatros" during the years 1890 and 1891. Rep. U.S. Comm. Fish. 1893, app. 6: 393-476.

15. Gilbert, C. H. and C. V. Burke. 1912. Fishes from the Bering Sea and Kamchatka. Bull. U.S. Bur. Fish. 30: 31-96.

16. Greenbank, J. 1954. Sport Fisheries Survey, Katmai National Monument. Administrative report, U.S. Dept. Interior, National Parks Service: 31 pp.

17. Gunther, A. 1877. Report on a collection of fishes made by C. Hart during the late Arctic Expedition. Proc. Zool. Soc., London, 1877: 475-477.

18. Hanson, H. C., P. Quenean and P. Scott. 1956. The geography, birds and man of the Perry River region. Spec. Publ. No. 3, Arctic Inst. N. A., App. 2, Miscellaneous zoological collections and observations, Fishes, page 91.

19. Harper, F. 1948. Fishes of the Nueltin Lake expedition, Keewatin, 1947, Pt. 2--Historical and Field notes. Proc. Acad. Nat. Sci. Phila. 100: 153-184.

20. Harper, F. and J. T. Nichols. 1919. Six new fishes from northwestern Canada. Bull. Am. Mus. Nat. Hist. 41(2): 263-270.

21. Henn, A. W. 1932. The exploration of Southampton Island, Pt. 2, Zoology, Sec. 3--Some fishes of Southampton Island. Mem. Carn. Mus. 12, pt. 2: 1-3.

22. Hildebrand, S. F. 1939. An annotated list of the fishes collected on several expeditions to Greenland, Foxe Basin region and the coast of Labrador by Captain R. A. Bartlet from 1925 to 1935. Medd. om Gronland, 125(1): 1-12.

23. Hunter, J. G. 1963. Pers. comm.

24. Kendall, W. C. 1920. An annotated list of a collection of fishes made by F. Harper in the Athabasca region in 1920. Cont. Canadian Biol., new ser., 1(23): 419-439.

25. Kennedy, W. A. 1949. Some observations on the Coregonine fish of Great Bear Lake, N.W.T. Bull. Fish. Res. Bd. Canada 82: 1-10.

26. Lindsey, C. C. 1957. Possible effects of water diversions on fish distribution in British Columbia. J. Fish. Res. Bd. Canada, 14(4): 651-668.

27. Manning, T. H. 1942. Notes on some fish of the eastern Canadian arctic. Canadian Field-Nat. 56: 128-129.

28. Manning, T. H. 1953. Notes on the fish of Banks Island. Arctic 6(4): 276-277.

29. Meehan, W. R. and D. B. Siniff. 1962. A study of the downstream migrations of anadromous fishes in the Taku River, Alaska. Trans. Am. Fish. Soc., 91(4): 399-407.

30. Miller, R. B. 1947. Northwest Fisheries Survey. Bull. Fish. Res. Bd. Canada 72, Ch. 4, Great Bear Lake: 31-44.

31. Miller, R. B. and M. J. Paetz. 1953. Preliminary biological surveys of Alberta watersheds (Volume 2). 1950-1952. A. Shnitka, Edmonton. 114 pp.

32. Murdoch, J. 1885. In, Report International Polar Exped., Point Barrow. Washington, 1885: 129-132.

33. Nelson, E. W. 1887. Fishes: In, Henshaw, H. W., Report upon natural history collections made in Alaska between the years 1877 and 1881 by E. W. Nelson. Washington, D. C.: 297-322.

34. Nichols, J. T. 1908. A small collection of Alaska fishes. Proc. Biol. Soc. Wash. 21: 171-173.

35. Ostdiek, J. L. and R. M. Nardone. 1959. Studies on the Alaskan Blackfish, Dallia pectoralis. I. Habitat, size, and stomach analysis. Am. Mid. Nat., 61(1): 218-229.

36. Pfaff, J. R. 1937. Fishes. In, Report of the 5th Thule Expedition 1921-1924, Vol. 2(7): 1-19.

37. Preble, E. A. 1908. A biological investigation of the Athabasca Mackenzie region. North American Fauna, No. 27, Fishes: 503-515.

38. Rawson, D. S. 1947. Northwest Fisheries Survey. Bull. Fish. Res. Bd. Canada 72, Ch. 6, Lake Athabasca: 69-85.

39. Rawson, D. S. 1959. Limnology and Fisheries in Cree and Wollaston lakes in northern Saskatchewan. Sask. Fisheries Rept. No. 4, 73 pp.

40. Richardson, J. R. 1823. Notice of the Fishes. In, Franklin, J. Narrative of a journey to the shores of the Polar Sea in the years 1819, 1820, 1821 and 1822. John Murray, London: 705-728.

41. Richardson, J. R. 1835. Salmones. In, Ross, J. C. Appendix to the narrative of a 2nd voyage in search of a north-west passage, and of a residence in the Arctic regions during the years 1829, 1830, 1831, 1832 and 1833. A. W. Webster, London: 55-58.

42. Roos, J. F. 1959. Feeding habitats of the Dolly Varden, Salvelinus malma at Chignik, Alaska. Trans. Am. Fish. Soc., 88(4): 253-260.

43. Scofield, N. B. 1899. List of fishes obtained in the waters of Arctic Alaska. In, Jordan, D. S. The fur-seals and fur-seal islands of the North Pacific Ocean. Report of the fur-seal investigations 1896-1897. Washington, D.C. Pt. 3, pp. 493-509.

44. Scott, D. C. 1956. Record of Perca flavescens from Great Slave Lake. Canadian Field-Nat. 70: 99.

45. Soper, J. D. 1928. A faunal investigation of southern Baffin Island. Bull. Nat. Mus. Canada 53, Fishes, pp. 116-117.

46. Sprules, W. M. 1952. The arctic char of the west coast of Hudson Bay. J. Fish. Res. Bd. Canada, 9(1): 1-15.

47. Stoney, G. M. 1899. Explorations in Alaska. Proc. U.S. Naval Inst., Annapolis, 25: 533-584, 799-849.

48. Townsend, C. H. 1887. Fishes. In, Report of the cruise of the Revenue Marine Steamer Corwin in the Arctic Ocean in the year 1885 by Capt. M. A. Healy. Washington, D.C., House Ex. Doc., First Session, Forty-ninth Congress (1885-1886), vol. 32: 95-96, 101-102.

49. Turner, L. M. 1886. Contributions to the natural history of Alaska, Pt. 4, Fishes. U.S. Army Signal Service, Arctic Series 2, Washington: 87-113.

50. Vladykov, V. D. 1933. Fishes from the Hudson Bay region (except Coregonidae). Contr. Canadian Biol. Fish., new series, 8(29): 13-61.

51. Walters, V. 1953. The fishes collected by the Canadian Arctic Expedition, 1913-1918, with additional notes on the ichthyofauna of western arctic Canada. Bull. Nat. Mus. Canada 128: 257-274.

52. Walters, V. 1955. Fishes of western arctic America and eastern arctic Siberia. Bull. Am. Mus. Nat. Hist., 106(5): 255-368.

53. Williams, M. Y. 1922. Biological notes along 1400 miles of the Mackenzie River system. Canadian Field-Nat. 36: 61-66.

54. Wynne-Edwards, V. C. 1947. Northwest Canadian fisheries survey. Bull. Fish. Res. Bd. Canada 72, Ch. 2, The Yukon Territory, pp. 6-20.

55. Wynne-Edwards, V. C. 1952. Freshwater vertebrates of the Arctic and Subarctic. Bull. Fish. Res. Bd. Canada 94. Fishes, pp. 5-24.

APPENDIX III

Correlation of taxonomic characters on standard length.

Species	Character	N	Correl. coeff.	P	Significance
E. lamottenii	myotomes	30	.280	>0.10	non sign.
	velar tentacles	30	.173	>0.10	non sign.
P. coulteri	caudal peduncle scales	30	.162	>0.10	non sign.
P. cylindraceum	gill rakers	30	.091	>0.10	non sign.
	pyloric caeca	30	.154	>0.10	non sign.
O. eperlanus	pyloric caeca	30	.063	>0.10	non sign.
C. catostomus	gill rakers	30	.290	>0.10	non sign.
H. plumbea	caudal peduncle scales	30	.157	>0.10	non sign.
	vertebrae	30	.183	>0.10	non sign.
E. lucius	vertebrae	22	.292	>0.10	non sign.
L. lota	gill rakers	30	.146	>0.10	non sign.
	pyloric caeca	30	.233	>0.10	non sign.
M. quadricornis	pyloric caeca	15	.360	>0.10	non sign.
	tubercles below lateral line	15	.310	>0.10	non sign.
	preopercle spine/ standard length	15	.620	<0.01	significant

APPENDIX IV

Sexual dimorphism.

Species	Character	No. males	No. females	t	P	Significance
E. lamottenii	myotomes	20	20	1.50	>0.10	non sign.
	velar tentacles	20	20	1.45	>0.10	non sign.
P. coulteri	caudal peduncle scales	30	30	1.26	>0.10	non sign.
P. cylindraceum	gill rakers	30	30	1.11	>0.10	non sign.
	pyloric caeca	30	30	1.23	>0.10	non sign.
O. eperlanus	pyloric caeca	30	30	1.06	>0.10	non sign.
C. catostomus	gill rakers	30	30	1.30	>0.10	non sign.
H. plumbea	caudal peduncle scales	30	30	1.15	>0.10	non sign.
	vertebrae	18	20	1.43	>0.10	non sign.
E. lucius	vertebrae	15	20	1.22	>0.10	non sign.
L. lota	gill rakers	30	30	1.36	>0.10	non sign.
	pyloric caeca	30	30	1.48	>0.10	non sign.
M. quadricornis	pyloric caeca	15	15	1.14	>0.10	non sign.
	tubercles below the lateral line	15	15	1.35	>0.10	non sign.
	preopercle spine/ standard length	15	15	1.53	>0.10	non sign.