FISHES OF WESTERN ARCTIC AMERICA AND EASTERN ARCTIC SIBERIA

TAXONOMY AND ZOOGEOGRAPHY

VLADIMIR WALTERS

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OF THE

AMERICAN MUSEUM OF NATURAL HISTORY
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DISSERTATION IN THE DEPARTMENT OF BIOLOGY SUBMITTED TO THE FACULTY OF THE GRADUATE SCHOOL OF ARTS AND SCIENCE IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY AT NEW YORK UNIVERSITY

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INTRODUCTION

THE ICHTHYOFAUNA of western Arctic America has been studied the least of any major sector of the northern polar regions, and that of Arctic Alaska the least of any equally great area of North America. Arctic Alaska is here considered to include all land drained by streams flowing into the Arctic Ocean from Cape Prince of Wales on Bering Strait north and east to the Canadian border, and all coastal salt waters north of Cape Prince of Wales from longitude 169° W. (between Big Diomede Island, Siberia, and Little Diomede Island, Alaska) east to 141° W. (Alaska-Yukon Territory border).

Aside from casual reports of fishes seen by early travelers (accounts that are mostly of historic interest owing to unreliable identifications and fragmentary descriptions which more often alluded to the gastronomic rather than the taxonomic attributes), the history of Arctic Alaskan ichthyology may be briefly summarized as follows:

Lay and Bennett (1839) were the first to give a scientific account of a fish caught north of Bering Strait; *Ophidium stigma* was described from Kotzebue Sound.

In a series of papers T. H. Bean (1882a-1890) greatly increased our knowledge of Arctic Alaskan fishes. In 1882b he published a catalog of fishes from Alaska and adjacent waters; many were listed from north of Bering Strait. In 1883 a more complete listing of fishes known from north of Bering Strait appeared. Bean named several fishes from Arctic Alaskan waters: Stichaeus rothrocki from Cape Lisburne (1882a), Notogrammus (based on S. rothrocki) (1882a), Cottus humilis from Eschscholtz Bay (1882a), Coregonus laurettae from Point Barrow (1882a), Coregonus pusillus from Kobuk River (1889), and possibly Aspidophoroides guntheri (1886) which may have been taken north of Bering Strait, though the exact type locality is unknown.

Murdoch (1885a, 1885b) reported on the fishes collected by the International Polar Expedition to Point Barrow. No new forms were named.

Townsend (1887) collected fishes in Kotzebue Sound and the Kobuk River. No new forms were named. Nelson (1887) made a few references to Kotzebue Sound fishes, though he was concerned more with the Bering Sea country of Alaska. No new forms were named.

Scofield (1899) published notes on fishes found by him in Arctic Alaska. Argyrosomus alascanus was named from Point Hope, though the description appeared first in Jordan and Evermann (1898) under Scofield's name.

Stoney (1899) published an account of his travels in Arctic Alaska. A few references to fishes were made, though no new forms were named.

Fowler (1904, 1905a, 1905b) reported on a small collection of fishes from Point Barrow and the Meade River. *Oncocottus hexacornis gilberti* was named from Point Barrow (1905b).

Evermann and Goldsborough (1907) listed a few new locality records from Arctic Alaska. No new forms were named.

Anderson (1913) published notes on fishes of Arctic Alaska, though most of his discussion pertains to Arctic Canada.

Andriashev (1937b) described the fishes collected by Russian expeditions into the Bering and Chukchi seas. In the same paper, Taranetz and Andriashev named Lycodes raridens from Cape Thompson, and other localities.

Hubbs and Schultz (1941) named *Lota lota leptura* from the Kobuk River.

Walters (1953a) listed Arctic Alaska localities for several fishes in a paper concerned primarily with western Arctic Canada.

Wohlschlag (1953) conducted an ecological study of fishes in an Arctic Alaskan lake. These studies were extended by Cohen (1954) and Wohlschlag (1954).

In addition to the above-mentioned papers, references to Arctic Alaskan fishes are scattered through a considerable volume of literature. Most of these contain restatements of findings reported in the above papers, or are concerned with taxonomic problems and thus Arctic Alaskan individuals of the species are discussed.

Concerning the zoogeography of western Arctic American fishes, the literature is extremely sparse. Nothing has appeared that

deals directly with Arctic Alaska, and there is little more that deals directly with western Arctic Canada. Wynne-Edwards (1947a, 1947b, 1952) offered some suggestions to explain distributions of fishes in the arctic and subarctic fresh waters of western Canada. Western Arctic America has entered several recent discussions in a roundabout manner. In discussing the distributions of marine fishes of Hudson Bay, Vladykov (1933, 1934a) concluded that some were of Pacific origin, thereby implying that they migrated to Hudson Bay along the Arctic Alaskan and western Arctic Canadian coastlines. While considering the distribution of Siberian freshwater fishes, Berg (1933, 1949) commented that the similarities in the Siberian and Alaskan faunas are a reflection of the former land connection between the two continents. Andriashev (1939a) and Shmidt (1948, 1950) discussed the zoogeography of the North Pacific and Arctic oceans; however, their knowledge of the western Arctic American fish fauna was meager. Radforth (1944) derived several Ontario fresh-water fishes from northwestern North America. Carl and Clemens (1953) derived several British Columbia fresh-water fishes from the Yukon and Mackenzie valleys.

The present study is divided into two parts. In the first part the fresh-water and marine fishes of eastern Arctic Siberia, Arctic Alaska, and western Arctic Canada are enumerated, and the ranges of the various subspecies and species are delimited. In the second part, the distribution patterns are analyzed in the light of our knowledge of the last glacial period.

Specimens collected by early travelers into Arctic Alaska have been reëxamined so far as possible; many of these have not been mentioned in the literature. Some of Scofield's specimens, which were deposited in Stanford University, were probably destroyed during the San Francisco earthquake, and others cannot be located.

In addition, a considerably greater volume of recently collected material (1947 to 1953) was examined. This consists of collections made by the writer on the Arctic Slope of Alaska during 1948 and 1949, the great number of marine fishes collected by Professor and Mrs. G. E. MacGinitie in the vicinity of

Point Barrow, and material collected by individuals too numerous to mention here by name. The writer is also most grateful to Mr. N. J. Wilimovsky of Stanford University, who has generously supplied information regarding fishes collected by him during 1951–1953.

Some time was also spent in studying the fauna of western Arctic Canada (Walters, 1953a, 1953b), and in 1953 the writer went on a brief expedition to the North-West Territories. The results of the 1953 trip, which centered on Coronation Gulf, are incorporated in the present study.

Great indebtedness is owed to many individuals and institutions. The data were gathered and the thesis was prepared under the guidance of Dr. C. M. Breder, Jr., of the American Museum of Natural History, and Prof. H. W. Stunkard of New York University: Drs. Per F. Scholander of the Woods Hole Oceanographic Institution and Laurence Irving of the Arctic Health Research Center encouraged the development of an interest in arctic fishes while the writer was working on the physiology program of the United States Naval Arctic Research Laboratory (Office of Naval Research) at Point Barrow; Drs. F. J. Alcock and L. S. Russell of the National Museum of Canada stimulated interest in the fishes of western Arctic Canada; Mr. Ralph Friedman of New York City arranged for the acquisition by the American Museum of a fish collection made in Spitsbergen, the Barents Sea, and northern Norway, and Dr. H. M.-K. Lund of the Tromsø Natural History Museum supervised the making of the collection; Mr. H. C. Sykes of Englewood, New Jersey, made arrangements with Canadian authorities and sponsored the American Museum's 1953 expedition to Great Slave Lake, Great Bear Lake, and Coronation Gulf; Drs. W. A. Clemens of the University of British Columbia and G. C. Carl of the British Columbia Provincial Museum provided information regarding the fishes of that province; Dr. Richard H. Backus of the Woods Hole Oceanographic Institution, Mr. Malcolm S. Gordon of Yale University, Dr. Henry H. Hildebrand of the University of Texas, and Mr. Norman J. Wilimovsky of Stanford University offered stimulating comments and generously shared

their knowledge of the arctic ichthyofauna; Mr. Wm. D. Clarke of the American Museum and Dr. M. K. Hecht of Queens College offered criticisms on the general aspects of taxonomy and zoogeography; Miss Francesca LaMonte and Mr. J. T. Nichols of the American Museum gave advice and information concerning many phases of this study; Drs. L. P. Schultz and E. A. Lachner of the United States National Museum, Dr. Yngve H. Olson of Yale University, Dr. G. S. Myers of Stanford University, and Mr. S. P. Bleakney of the National Museum of Canada arranged for the loan of specimens; Miss Hazel Gay and her staff at the Library of the American Museum were most helpful in

hunting down obscure references and in permitting certain Russian publications to be withdrawn from the Museum for translation: the writer's father, Mr. Walter J. Walters. spent many long hours in translating into English what certainly must have been the driest Russian literature he had ever read (copies of the longer translations have been deposited with the Library); and finally deepfelt appreciation is due to all the many individuals, both whites and Eskimos, who accompanied the writer in the field in Alaska and in Canada and who forwarded extremely valuable specimens they collected, but lack of space prohibits mentioning every one by name.

THE ICHTHYOFAUNA

AREA COVERED

MARINE FISHES: All marine fishes are included that have been found in coastal waters between Cape Cheliuskin on the Taimyr Peninsula, Siberia, in the west and longitude 105° W. in the east (somewhat east of Bathurst Inlet, Canada), and from a line drawn between Cape Prince of Wales on the Seward Peninsula, Alaska, and Mys Nunyagmo on the Chukchi Peninsula, Siberia, in the south, north to the pole. (See map 1.)

The inclusion of most of the polar basin in this study is for convenience in the delimitation of the area. Fish have never been reported from most of the basin, especially within several hundred miles of the North Pole.

There are several reasons for having selected the particular eastern and western marine limits. The eastern limit, longitude 105° W., marks a convenient meridian of reference; it lies only slightly east of Bathurst Inlet, the easternmost locality in western Canada of which the fauna may be considered to be at least fairly well known. The area east of Bathurst Inlet and west of Hudson Bay, notably Queen Maude Gulf and the Gulf of Boothia, is poorly explored, and to include it in the present study would serve mainly to add only additional blank areas to the sector of the Arctic covered.

Cape Cheliuskin was chosen as the western limit because it separates the Laptev and seas to the east (which largely escaped glaciation) from the Kara and seas to the west which had been completely glaciated. In the Kara Sea there are several species, common westward but absent eastward, which are indicative of a strong North Atlantic influence in the marine fauna. It would be entirely

a library task to delimit the faunal differences between the seas east and west of the Taimyr Peninsula, because the present world situation makes it impossible to obtain specimens from or do field work in the Soviet European Arctic, and it is most probable that only a trickle of the literature on the Soviet Arctic is reaching our shores. Finally, any discourse on the faunal differences east and west of the Taimyr Peninsula should be a separate study in itself.

FRESH-WATER FISHES: All fresh-water species known to occur in the drainages of the east Siberian and Chukchi seas of Siberia, the drainages of the Chukchi and Beaufort seas of Alaska, and the Arctic watershed of Canada east to 105° W. are included (map 1). Canadian fishes that are not known to range north of Arctic Red River in the Mackenzie Valley have been excluded but are considered in the zoogeographic discussion below. The life zone criterion has not been employed in this study, because it is not certain that the landscape zones of the Soviet Union, as delimited by Berg (1950), are strictly comparable to the life zones of North America as recently revised by Muesebeck et al. (1951).

For fresh-water species (other than white-fishes) known only from Siberia, the range given is only that part that actually lies within the area under discussion. It would be a waste of space to repeat the complete range for each form, if there is nothing new to add. The fourth edition of Berg's comprehensive treatise on the fresh-water fishes of the Soviet Union and neighboring waters (1948–1949) gives complete distributional data for these fishes.

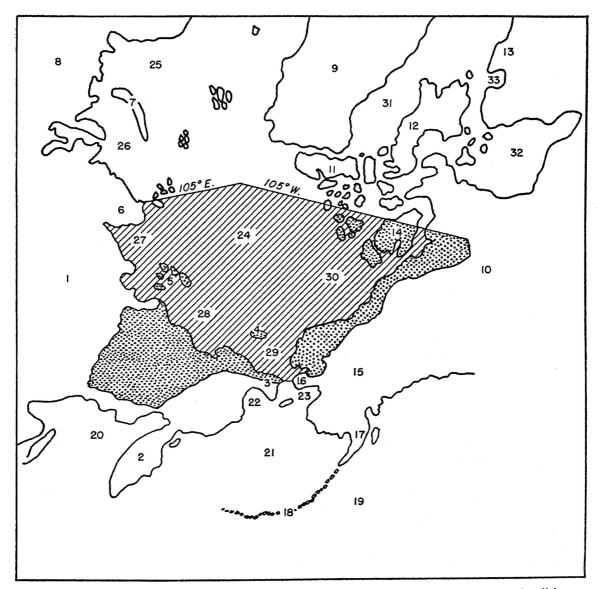
METHODS OF COUNTING AND MEASURING

Except as noted below, all counts and measurements have been carried out according to the methods suggested by Hubbs and Lagler (1947, pp. 8-15).

FIN RAY COUNTS: Except for the Zoarcidae and Liparini, where all elements are counted, the posteriormost element of each soft-rayed

dorsal and anal fin has been deleted from the count. All elements are counted in the Liparini, and in the Zoarcidae half the caudal rays have been included in the dorsal and anal counts.

STANDARD LENGTH: In the Gadidae there might be some misunderstanding regarding



MAP 1. North polar projection of the area covered in the present study. Fresh-water localities are stippled; marine localities are shaded. 1. Siberia. 2. Kamchatka, 3. Chukchi Peninsula. 4. Wrangel Island. 5. New Siberian Islands. 6. Taimyr Peninsula. 7. Novaya Zemlya. 8. Europe. 9. Greenland. 10. Canada. 11. Ellesmere Island. 12. Baffin Island. 13. Labrador. 14. Victoria Island. 15. Alaska. 16. Seward Peninsula. 17. Alaska Peninsula. 18. Aleutian Islands. 19. North Pacific Ocean. 20. Sea of Okhotsk. 21. Bering Sea. 22. Gulf of Anadyr. 23. Norton Sound. 24. Arctic Ocean. 25. Barents Sea. 26. Kara Sea. 27. Laptev Sea. 28. East Siberian Sea. 29. Chukchi Sea. 30. Beaufort Sea. 31. Baffin Bay. 32. Hudson Bay. 33. Ungava Bay.

the location of the base of the caudal fin; the writer measured to the tip of the lancet, i.e., to the bases of the middle caudal rays.

INTERORBITAL WIDTH: In all cases the least bony width was measured.

DIAMETER OF EYE: In all cases this refers to the horizontal diameter of the eyeball. As the dividers close down on the eyeball the cornea wrinkles; the dividers are then spread until the wrinkling just disappears, and the distance between the tips is the eye diameter.

WIDTH OF VOMERINE TOOTH PATCH: This measurement is the straight line distance between extreme right and extreme left teeth

of the vomer.

Other measurements used in the text and not mentioned by Hubbs and Lagler are self-explanatory.

THE NOMENCLATORIAL SYSTEM

For the most part the suprageneric classification follows Berg (1940).

For categories of generic rank or lower the following "definitions" are offered. These are not definitions in the true sense of the word, for there is little agreement among systematists regarding the limits of taxonomic categories.

The phenotype of an individual is the result of the interaction of genotype and environment. Therefore all phenotypes are genetically (and environmentally) determined. Among sexually reproducing organisms it is highly improbable that any two individuals have identical genotypes. It is obvious therefore that genetic differences between taxonomic categories are differences of degree. ranging from the differences between individuals of the same population to the differences between kingdoms. It should be borne in mind that the nomenclatorial system is inherently two-dimensional and cannot portray all the nuances of evolutionary relationships (spatial and temporal) between one form or group of forms and all its relatives, past and present.

MORPHA: The morpha is a phenotype resulting from certain environmental conditions acting upon the genotype and appears whenever the organism is subjected to those conditions. (From genetics we have numerous examples of one genotype's producing different phenotypes under different environmental conditions.) Thus there is no geographical range for the morpha, because it may appear here and there throughout the range of the organism, whenever the necessary environmental conditions are satisfied. The morpha is not recognized taxonomically. For example, the Atlantic salmon (Salmo salar) produces the morpha sebago when landlocked in Europe and North America: the sea trout (Salmo trutta) produces the morpha fario when prevented from running into the sea from rivers; and the sea lamprey (Petromyzon marinus) produces a dwarf morpha when landlocked. Other examples of morphas, in particular concerning river fishes that enter lakes, lake fishes that enter ponds, and others, are discussed by Berg (1948).

RACE: A race is a population or group of populations that differs slightly from other populations. The differences may be in scale or vertebral number, spawning season, spawning place, growth rate, size attained, or other characters. Unless the place of origin of the specimens is known, most of the members of the race cannot be distinguished from the members of other races. The race is not recognized taxonomically. Soviet workers recognize a host of categories higher than the race but lower than the subspecies. These include the infrasubspecies, natio, infranatio, subnatio, and others. To accept the practice of naming each local form would lead to confusion. It is not even certain that some of these sub-subspecific categories exist for more than one or a few seasons in nature, or perhaps they do not even exist beyond the confines of the ichthyologist's specimen jars; most taxonomic studies concerning these splinter categories have been based on limited samples.

Subspecies: A subspecies is a group of populations of a species, most (ca. 80%-90%) of the members of which are distinguishable from most other individuals of the species. This category is referred to by means of a trinomial. The subspecies has a definite geographic range. Ideally, individuals living at or near the periphery of the range closely resemble individuals of the neighboring subspecies. Thus when the range of the species is essentially continuous, its subspecies typically "blend" into one another, the intermediate individuals being known as intergrades. The subspecies, as its name implies, is morphologically almost a species; as such it is distinguishable on the basis of two or more separate characters, and all the characters show the intermediate condition in the intergradation zones. The intergradation zone is actually the

area of mass hybridization between subspecies; usually it is found wherever subspecies meet, but cases are known where a subspecies may behave as a true species at one end of its range and as a subspecies at the other. The practice of using trinomials in designating subspecies has been severely criticized by Wilson and Brown (1953). In the present writer's opinion the current confusion regarding the subspecies is not the fault of the trinomial system but rather of some of the people who have used it. Many forms called subspecies are little more than races. It has been pointed out that the nomenclatorial system, whether mono-, bi-, tri-, or othernomenal, cannot portray faithfully the varying shades of evolutionary relationships between different organisms. The primary function of the systematist is to give the organism a name so that it may be referred to conveniently; any other function is secondary. No one can deny that the use of a trinomial in designating an organism is ever so much more convenient than a return to the almost pre-Linnaean method of describing the organism in several lines of text, as has been recommended by Wilson and Brown.

Species: A species is a group of populations, most (ca. 95%-100%) of the members being distinguishable from all other species.

Subgenus: One or a group of species that, possessing one or two "generic" characters in common, differs from other species of the genus. The subgenus is a subjective category. It is the present writer's opinion that, as in the relation of the subspecies to the species, most of the species in the subgenus should be sharply distinguishable from other subgenera but intermediate conditions will be found in some of the species.

GENUS: A group of species possessing several characteristics in common, and which closely related genera do not possess. The genus is a subjective category. The present writer believes that a genus should be sharply distinguishable from related genera.

KEY TO MARINE FISHES OF EASTERN ARCTIC SIBERIA AND WESTERN ARCTIC AMERICA, AND TO FRESH-WATER FISHES OF ARCTIC ALASKA

The key on the following pages is dichotomous; each numbered entry consists of two alternate descriptions (a and b), one of which will fit the unknown fish. At the end of each alternate is the number of the next pair of alternates. By starting with the first pair of choices (1a and 1b) and continuing from one pair to the next as directed, the reader will finally arrive at an alternate giving the name of the fish.

The key was constructed primarily for the identification of Arctic Alaskan fishes but may be used for marine fishes from western

Arctic Canada and eastern Arctic Siberia.

The key is intended for the identification of older juvenile and adult fishes; it cannot be used to identify larval stages or, in most cases, small juveniles. The morphology of many species changes so rapidly and so profoundly in passing from the larval to the larger juvenile form that it would be necessary to construct a separate key for each size group. It is also sad but true that the larval, postlarval, and small-juvenile stages of some species in the key are unknown.

1a. Jaws absent, mouth surrounded by a sucking disc in adults and by a hood in larvae. Gills open to
outside by seven separate pairs of oill openings. Paired fins absent
Petromyzonidae (Lampreys), Lampetra japonica (Arctic Lamprey)
1b. Taws present Gills covered by an operculum. Paired fins present
20. Caudal for externally beterocercal Mouth inferior, snout with four long barbels, body with live
rows of large hony plates Acidenseridae (Sturgeons), Acidenser oderi (Siberian Ocean)
2h Caudal fin not externally heterocercal. Mouth may be interior and shout may have barbers but
then hody is completely covered by hony plates
3a. Pointed, posteriorly directed fleshy appendage just above base of each pelvic fin; this may be
inconspicuous in small fish

¹ There is no sturgeon definitely known from Arctic Alaska, though the Eskimos tell of such a fish on the Arctic Slope. If a sturgeon does occur, it is probably A. baeri.

¹⁷b. Anal fin with fewer than 12 branched rays. Vomerine teeth variable in distribution, but shaft is

1 Not known to occur west of the Mackenzie, though possibly it may be found replacing *C. lavaretus pidschian* in easternmost Arctic Alaska.

	never toothed. Fishes usually with light spots equal to or smaller than eye in size, on sides of body
	and sometimes also on the back and dorsal, caudal, adipose, and pectoral fins
40	A figure Compile 11 to the back and dorsal, caudal, adipose, and pectoral fins
18a.	Adipose fin with light spots
18b.	Adipose fin without light spots Salvelinus alpinus complex (Arctic Charrs)
19a.	Scales in first row above lateral line more than 170. Black spots on both lobes of caudal fin large
	and elongate. Gill rakers more than 26 Oncorhynchus gorbuscha (Hump-back Salmon)
10h	Scales in first row above lateral line fewer than 155. No large black spots on back or caudal fin
1750	Gill rakers fewer than 26
20.	Gill takels lewel than 20
zua.	Dorsal fins one or two, not preceded by a number of free spines which can lock upright. If two
	dorsal fins (first may be fleshy and keel-like), then a sucking disc present on ventral surface of
	body. Body not completely covered by bony plates
20b.	Dorsal fins one or more, or dorsal fin preceded by a number of free spines which can lock upright.
	If one dorsal fin, then body completely covered by non-overlapping bony plates. No sucking
	disc on ventral surface of body
01-	Description and the state of body
21a.	Dorsal fin with six to 12 free short spines which can lock upright
	Gasterosteidae (Sticklebacks), Pungitius pungitius pungitius (Stickleback)
21b.	Dorsal fin(s) not preceded by six to 12 free spines
22a.	Dorsal fins one or two in number; if two, then the second has fewer than 50 rays
22h	Dorsal fins two or three in number; if two, then the second has more than 50 rays
220.	
00	D. 1. C. 1.1. Saulus (Counsiles)
23a.	Dorsal fins two, anal fin single, caudal fin rounded Lota lota leptura (Burbot)
23b.	Dorsal fins three, anal fins two, caudal fin not rounded
24a.	Mouth terminal, lower jaw equal to or longer than upper. Lateral line consists entirely of un-
	connected tubes
24h	Mouth inferior, lower jaw shorter than upper. Lateral line continuous beneath first two dorsal fins
ZIU.	and consists of unconnected tubes beyond second dorsal fin
~=	and consists of unconnected tupes beyond second dorsal in
25a.	Palatine teeth present. Gill rakers 32-34. Body covered by overlapping scales which do not bear
	bony tubercles
25Ъ.	bony tubercles
260	Bony interorbital width contained 6.3-8.7 times in head length; head length contained less than
zva.	2.6 times in the distribution of the state o
	3.6 times in standard length Arctogadus pearyi (American Arctic-Cod)
26b.	Bony interorbital width contained 4.8-5.7 times in head length; head length contained more than
	3.6 times in standard length Arctogadus borisovi (Siberian Arctic-Cod)
27a.	Length of mental barbel about equal to eye diameter. Parapophyses not hollow and club-shaped,
	and swim bladder does not send diverticula to them. Peritoneum uniformly black
271	Togeth of granted best allow they grant dismeter Demonstrates also changed and hollow and ewim
21D.	Length of mental barbel less than pupil diameter. Parapophyses club-shaped and hollow, and swim
	bladder sends diverticula to them. Diverticula may be seen by slitting swim bladder open.
	Peritoneum silvery with black flecks Eleginus navaga navaga (Saffron Cod)
28a.	Body completely covered by non-overlapping bony plates Agonidae (Sea-Poachers) 29
28b	Body not completely covered by non-overlapping bony plates Cottidae (Sculpins) 30
200.	Dorsal fin single, composed entirely of rays. No barbels on under side of snout
27a.	Dolsai in single, composed entirely of lays. No barbles on under size of size of control of the size of size o
	Aspidophoroides olriki (Arctic Sea-Poacher)
29b.	Dorsal fins two, first spinous and second rayed. Several barbels on under side of snout
	Agonus acipenserinus (Sturgeon Sea-Poacher)
30a.	Skin on sides of body below lateral line has diagonal folds. More than 20 anal rays
	Triglops pingeli (Ribbed Sculpin)
30h	Skin not in diagonal folds below lateral line. Fewer than 20 anal rays
300.	Skill not in diagonal folds below lateral lines between the course days of spinous bony
SIA.	In fish over about 35 mm. in standard length, lateral line covered by single row of spinous bony
	plates. In addition a straight row of spinous bony plates running above lateral line from gill
	opening to base of caudal fin in fish over 20 mm. in standard length
31b.	Lateral line not covered by single row of spinous bony plates. Scattered prickly tubercles may occur
	above lateral line but these not arranged in a straight row
32-	Bony plates along lateral line have microscopic spines on posterior edges below lateralis pores in
oza.	Doing places along lateral line have introscopic spines on posterior eagle set.
	fish over about 40 mm. in standard length. Lateral line usually incomplete. In males, terminal
	portion of urinogenital papilla about twice the length of basal portion and not closely applied to
	basal portion

32b.	Bony plates along lateral line do not have microscopic spines on posterior edges below lateralis pores in fish over about 40 mm. in standard length. Lateral line complete. In males, terminal portion of urinogenital papilla much shorter than basal portion and closely applied to basal portion.
220	Vomerine teeth present, palatine teeth present or absent. Upper preoperculor spine typically un-
osa.	branched, but if branched all points radiate from same focus
22h	Vomerine and palatine teeth absent. Upper preopercular spine with one to five points arranged in
JJD.	antler fashion, the number increasing with size of fish. Some points may be buried in flesh and
	must be dissected out
3/10	Three pairs of blunted spines behind pair of frontal spines on top of head. Males have club-shaped
J u a.	filaments (pistillae) in axillary region Gymnocanthus pistilliger (Pistillate Sculpin)
3/h	No blunted spines behind frontal spines. Males do not have club-shaped filaments in axillary region
JTU.	Two brunted spines beaming frontal spines. Males do not have club-singled manners in axinally region.
350	Gymnocanthus tricuspis (Stag-Horn Sculpin) Gill membranes broadly joined to isthmus and do not form a free fold across it. Pectoral rays 13-14.
JJa.	Fresh-water species
35h	Gill membranes united and free of isthmus or forming a broad fold across it. Pectoral rays seldom
555.	14, usually 15 or more. Marine, one species (Myoxocephalus quadricornis) regularly entering
	fresh water
362	Palatine teeth absent. Maxillary barbel absent. Pectoral rays 14–19
	Palatine teeth absent. Maxillary barbel present. Pectoral rays usually 20 or more
	Cirri present along lateral line and between dorsal fins and lateral line. Upper head surface rough-
Jia.	ened by many small papillae and cirri Artediellus scaber (Rough Hook-eared Sculpin)
37h	Cirri absent from lateral line and from between dorsal fins and lateral line. Upper head surface
570.	relatively smooth Artediellus uncinatus (Smooth Hook-eared Sculpin)
382	Width of vomerine tooth patch well exceeds width of interorbital space
ooa.	
38b.	Width of vomerine tooth patch less than width of interorbital space
39a.	Bony interorbital space contained less than five times in head length. Interorbital width 1.2 to 1.5
o, u.	times eye diameter. In adults, lower jaw projects
	Myoxocephalus platycephalus (Flat-headed Sculpin)
39b.	Bony interorbital space contained six or more times in head length. Interorbital width equal to or
	less than eye diameter. In adults, lower jaw does not project
40a.	In fish over 40 mm. in standard length, peritoneum is dusky dorsad. Lateral line diminishes to
	thread-like line on caudal peduncle Myoxocephalus quadricornis (Four-horned Sculpin)
40b.	Peritoneum pink, with some scattered melanophores. Lateral line does not alter in appearance on
	caudal peduncle
41a.	Pectoral rays (16) 17-18. Frontal and parietal spines develop stout accessory spines at their bases,
	which become more evident in larger fishes. Interorbital space and nape have some rounded
	warty prominences
41b.	Pectoral rays (14) 15-16. Frontal and parietal spines are incipient, do not develop stout accessory
	spines at their bases, and remain covered by a thick skin. Interorbital space and nape roughened
	by presence of numerous sharp-tipped warty prominences
42a.	Dorsal fin single, short, composed entirely of rays. No sucking disc on ventral surface 43
42 b.	If only one dorsal fin, it is long (base extends from head or nape to caudal peduncle or caudal fin)
	and has more than 30 elements; if two dorsal fins, then a sucking disc is present on ventral sur-
	face of body
43a.	Anal fin lies beneath dorsal fin. Mouth terminal
43b.	Anal fin lies behind dorsal fin. Mouth inferior
44a.	Caudal fin rounded in outline. Appressed pelvic fins overlap anal fin
	Dalliidae (Blackfishes), Dallia pectoralis (Blackfish)
44b.	Caudal fin emarginate. Appressed pelvic fins do not reach anal fin
	Esocidae (Pikes) Esoc lucius (Pike)
45a.	A rounded sucking disc on ventral surface of body
	· · · · · · · · · · · · · · · · · · ·
45b.	No rounded sucking disc on ventral surface of body

46a. Body form tadpole-like. Dorsal fin long, extending from near nape to base of caudal fin
46b. Body form globose anterior to anus, compressed posterior to anus. Dorsal fins two in number; the first may be encased in flesh and appear like a keel Cyclopterini (Lumpsuckers) 49
47a. Peritoneum black
47b. Peritoneum pink, with a few scattered melanophores
to middle of fin
48b. Dorsal and anal fins joined to caudal for about one-third of its length. Highest anal rays are before middle of fin
49a. First dorsal fin covered by flesh and muscle, appearing like a keel. Bony tubercles absent from chin and frequently also from bases of pectoral fins. Barbel-like cirri absent from chin. No bony tubercles on body in contact with base of first dorsal fin
49b. First dorsal fin not covered by flesh and muscle in most fish. Chin and pectoral fin bases covered with bony tubercles. Chin with barbel-like cirri. Some bony tubercles on body in contact with base of first dorsal fin
50a. Both eyes on same side of head. Eved side of body more heavily pigmented than blind side
50b. Both eyes not on same side of head. Both sides of body equally pigmented
51a. Mouth symmetrical on both sides of head (jaws of equal length and shape). Teeth equally well developed on both sides of head Hippoglossoides elassodon robustus (Flat-headed Sole)
51b. Mouth asymmetrical on right and left sides. Teeth stronger and more numerous on blind side of head
52a. Lateral line with an almost semicircular arch over pectoral area. Lateral line scaled. Dorsal and anal fin bases with a dark line
52b. Lateral line with a very slight arch over pectoral area. Lateral line scaleless. No dark line along
bases of dorsal and anal fins
Dorsal and anal fins black-banded Pleuronectes stellatus (Starry Flounder)
53b. No stellate bony tubercles on body, only scales. Dorsal and anal fins either clear or with rounded dark spots
54a. Dorsal, caudal, and anal fins not continuous with one another, or they are set off from one another by notches so that limits of fins are readily seen
54b. Dorsal, caudal, and anal fins continuous, without any evident demarcations between them
55a. Pelvic fins present. Snout overhangs mouth. Gill opening extends all the way down base of pectoral
fin
down base of pectoral fin
56a. Scales absentGymnelis viridis56b. Scales presentOphidium stigma
57a. Anterior part of lowermost lateral line does not pass below midline of body. Body naked, partially
scaled, or completely scaled in some very large individuals
58a. D plus 1/2 C 99-103, A plus 1/2 C 78-83 Lycodes jugoricus (Jugorsky Shar Eelpout)
58b. D plus 1/2 C 87–95. A plus 1/2 C 68–76
59a. Posteriormost premaxillary tooth lies at about level of last vomerine or first palatine teeth. Length of band of premaxillary teeth on each side equal to about half of length of band of mandibular teeth on each side
59b. Last premaxillary tooth lies at level just anterior to last palatine tooth. Length of band of premaxillary teeth about equal to band of mandibular teeth
¹ Lycodes raridens and L. knipowitschi are not included in the key, although they have been reported from the Chukchi Sea by Russian workers.
² Not reported from the area covered but included here because of its great superficial resemblance to L. turneri.

60a.	Peritoneum densely black-flecked or dusky in color. Cartilaginous combs beneath chin rounded at
	their tips and do not extend anterior to tip of chin Lycodes pallidus (Pale Eelpout)
60b.	Peritoneum creamy to pink in color. Cartilaginous combs beneath chin sharp-tipped and extend
	as far as or beyond tip of chin Lycodes palearis arcticus (Wattled Eelpout)
61a.	Lower jaw ends in rod-like projection. About 150 diagonal folds of skin along sides of body
	Ammodytidae (Sand Lances), Ammodytes hexapterus (Sand Lance)
61b.	Lower jaw does not end in rod-like tip, and skin is not folded
62a.	Gill membranes broadly joined to isthmus, without a free fold. Maxillary ends below or behind
	vertical of rear of orbit . Anarhichadidae (Catfishes), Anarhichas denticulatus (Blue Catfish)
62b.	Gill membranes separate, or united but free from isthmus. Maxillary ends before vertical of rear of
	orbit
63a.	Dorsal spines fewer than 55 Stichaeidae (Snakeblennies) 65
63Ъ.	Dorsal spines more than 55 Lumpenidae (Eelblennies) 64
64a.	Posterior anal rays notably longer than anterior anal rays; last anal ray reaches beyond base of
	caudal fin. Pectoral rays (12) 13-14 (15). Body depth less than 10 times in standard length
64b.	Posterior anal rays not notably longer than anterior anal rays; last anal ray does not reach or barely
	reaches base of caudal fin. Pectoral rays 15-16 (17). Body depth more than 10 times in standard
	length Lumpenus fabricii (Slender Eelblenny)
65a.	Lateral line single, high, incomplete Stichaeus punctatus (Spotted Snakeblenny)
65b.	Lateral lines four in number, the second from top being complete
	Eumesogrammus praecisus (Four-lined Snakeblenny)
	2 out mile onancoichity)

ANNOTATED LIST OF FISHES

On the following pages under Previous Records are listed only published records of fishes from Arctic Alaska, and under Specimens Seen are listed only those specimens examined that had been collected in the waters of Arctic Alaska.

PETROMYZONIDAE

LAMPREYS

Only one lamprey has any appreciable range in arctic waters. *Petromyzon marinus* barely enters the Arctic (Davis Strait, Greenland), and previous records of *Petromyzon fluviatilis* (= Lampetra fluviatilis) from Greenland are due to errors in labeling (Jensen, 1941).

Lampetra japonica (Martens)

ARCTIC LAMPREY

RANGE: In arctic regions, from Vyg River in Europe (White Sea) east to the Mackenzie River and Great Slave Lake in Canada. In the Pacific south to Fusan (Korea) in the west and the Yukon River (Alaska) in the east. In salt and fresh waters.

Previous Records: None.

Specimens Seen: U.S.N.M. No. 152896 (Point Barrow).

Notes: Berg (1948) recognized Lampetra

japonica japonica (Martens) and L. japonica kessleri (Anikin); the former includes L. japonica septentrionalis Berg as a synonym. Lampetra j. japonica is a migratory fish; L. j. kessleri, a dwarf that never goes to sea. A similar situation is found in the sea lamprey, Petromyzon marinus, which has dwarf native landlocked populations in Lake Champlain, Lake Ontario, and tributary lakes in eastern North America, but in this case the dwarfs are not given the status of subspecies. Lampetra j. kessleri is probably a morpha and should not be distinguished from L. j. japonica.

Professor G. E. MacGinitie found a 355-mm. female washed ashore at Point Barrow on October 17, 1949, the first record of a lamprey from Arctic Alaska. Hildebrand (1948) reported *Entosphenus japonicus* (prov.) from Aklavik, and Walters (1953a) recorded ammocoetes of *L. japonica* from the Mackenzie Delta.

Berg (1931) suggested that Richardson's (1823) record of *Petromyzon fluvialis* from Great Slave Lake may have been *L. j. kessleri*, but Dymond (1947) and Rawson (1951) listed it as *Entosphenus japonicus septentrionalis* (Berg) (= *L. j. japonica*). It has not been shown that the Great Slave Lake fish migrates into the lake from the sea for

spawning. Great Slave specimens examined by the present writer were of the dwarf form; the Great Slave fish is *L.j. kessleri*. Lampreys are said to occur in Artillery Lake which empties into Great Slave Lake by waterfalls. They apparently spawn in Artillery Lake and Great Slave Lake in July, because clusters of adults have been noted in shallow water during this month.

ACIPENSERIDAE

STURGEONS

Acipenser baeri Brandt

SIBERIAN OCETR

RANGE: Kolyma River basin of Siberia and westward, in fresh and brackish waters.

Notes: No sturgeon is listed from western Arctic America; Acipenser fulvescens ranges westward to the Churchill and Nelson systems of Manitoba (Wynne-Edwards, 1952). However, Bob Brower said that at Half Moon Three (about 40 miles east of Point Barrow, on the Alaktak River) fish about 3 feet long with whiskers and with big bones in the skin are sometimes caught. During 1948 and 1949 none were caught. If a sturgeon occurs on the Arctic Slope of Alaska it may be Acipenser baeri, the only known one from near-by arctic waters.

CLUPEIDAE

HERRINGS

Clupea harengus pallasi Cuvier and Valenciennes Arctic Herring

RANGE: Salt, brackish, and, in some places, fresh water. White Sea of Europe east to Bathurst Inlet, Canada, in arctic waters, and south to Korea and San Diego, California, in the North Pacific. In all seas of the North Pacific.

Previous Records: None. Specimens Seen: None.

Notes: Mr. N. J. Wilimovsky (in litt.) has collected this fish among ice floes off Point Barrow and in Admiralty Bay, these being the first authentic records from Arctic Alaska. The occurrence of herring in western Arctic Canada is well known. Richardson (1823) reported it from Bathurst Inlet; Anderson (1913), from Cape Bathurst; Hildebrand (1948), from Mackenzie Delta; and

Walters (1953a), from Cape Bathurst and Mackenzie Delta.

The subspecies is known from the White Sea of Europe and east to the northern part of Ob' Gulf, where it is considered to exist as two natios, maris-albi and suworowi (Svetovidov, 1952). Svetovidov also identified the Atlantic herring, C. harengus harengus, as ranging throughout the White and Barents seas. Clupea harengus pallasi has recently been reported from the central Siberian Arctic, as follows: off the Lena Delta and in Olenek Bay, both in the Laptev Sea (Berg, 1949, p. 1320); most likely it occurs off the mouth of the Indigirka River in the East Siberian Sea, but previous reports for Lyakhov Island (New Siberian group) and Chaun Bay (East Siberian Sea) are not reliable (Svetovidov, 1952, p. 151, footnote 3).

Although it is now known that C. h. pallasi is broadly distributed in the Arctic, there are no records of any herring from the following areas which are fairly well explored: Hudson Bay and Ungava Bay, east to but not including West Greenland; southern Chukchi Sea; Bering Sea north of Anadyr Gulf and Port Clarence. The distributional gaps appear to be real rather than indicative of poor collecting, because the herring has been reported from some of the poorestknown parts of the Arctic, and the reports go back to the early 1800's. It is possible that careful study of herrings from the Arctic will reveal differences from the herrings of the North Pacific.

SALMONIDAE

SALMONS, TROUTS, AND WHITEFISHES SUBFAMILY SALMONINI

Oncorhynchus keta (Walbaum)

Dog Salmon

RANGE: In Arctic drainages, from the Lena River (Siberia) east to the Mackenzie system (Canada); south in the Pacific to Fusan (Korea) and San Francisco (California). In fresh and salt waters.

Previous Records: Cape Lisburne (Bean, 1882b, 1883, Salvelinus malma); Kotzebue Sound (Bean, 1883, 1885, O. keta); Kowak (Kobuk) River (Townsend, 1887, O. keta); lake near Point Barrow (Wohlschlag, 1953, O. keta).

Specimens Seen: U.S.N.M. Nos. 27569 (Cape Lisburne), 38902, 38904, 38911, 38912, 38915, 38916 (Kobuk River).

Notes: Dog salmon occur all along the coast from Bering Strait north to Point Barrow and east to the Mackenzie; there are no published records for east of the Mackenzie. According to Townsend (1887) this is the prevailing salmon in the Kobuk River. It ascends far upstream (to headwater lakes of the Yukon system), and Dr. Laurence Irving (in litt.) reported that an adult male was taken in the headwaters of the Anaktuvuk River (Colville system) in Anaktuvuk Pass, Brooks Range, on August 7, 1951. Dymond (1940) reported O. keta from the Mackenzie system upstream to just below Fort Smith on the Slave River.

Along the Siberian Arctic coast this species is found in the Kolyma, Indigirka, Yana, and Lena rivers (Berg, 1948); it is of sufficient abundance in the lower Lena that a commercial salmon fishery exists there (Shmidt, 1948, p. 117).

Oncorhynchus gorbuscha (Walbaum)

HUMP-BACK SALMON

RANGE: In Arctic drainages, from the Lena River (Siberia) east to the Mackenzie system (Canada); south in the Pacific to the Gulf of Peter the Great in the west and the Sacramento River in the east. In fresh and salt water.

Previous Records: As O. gorbuscha north along coast to Colville River (Bean, 1883, 1885); east to Mackenzie River (Bean, 1890); Elson Lagoon (Murdoch, 1885a, 1885b), Kobuk River (Townsend, 1887).

Specimens Seen: U.S.N.M. Nos. 38356, 38933 (Kobuk River).

Notes: Hump-back salmons were seen being caught by Eskimos at Half Moon Three (about 40 miles east of Point Barrow). Bean (1890) and Dymond (1940) reported this species from the Mackenzie system in Canada. This species does not ascend so far upstream as the preceding species.

In Siberia it is found in the Kolyma, Indigirka, Yana, and Lena rivers (Berg, 1948).

Only two of the six species of Oncorhynchus have been found in the Arctic. Unreliable sight reports identify O. tschawytscha from Point Barrow (Evermann and Goldsborough, 1907) and O. nerka questionably from the Mackenzie (Preble, 1908) and Point Barrow (Murdoch, 1885b), but there are no Arctic specimens of these fishes.

Salvelinus alpinus complex

ARCTIC CHARRS

RANGE: Throughout the Arctic in fresh and salt water. Close relatives are found in temperate regions of the Northern Hemisphere.

Previous Records: As S. malma, Colville River mouth and Point Barrow (Murdoch, 1885a, 1885b), Kobuk River (Townsend, 1887), Point Hope (Scofield, 1899), Hulahula River (Anderson, 1913); as Col-lic-pic, Chandler Lake (Stoney, 1899); Hot River (tributary of Sadlerochit River), and Collinson Point (Walters, 1953a, S. alpinus).

Specimens Seen: Stanford No. 5607 (Point Hope); U.S.N.M. Nos. 33953 (Point Barrow), 38361, 38928, 38930 (Kobuk River), 74249 (Firth River), 111653, 111697 (Alaktak River, Chipp system), 111672, 111688, 111689 (Anaktuvuk Pass, headwaters Anaktuvuk River); A.M.N.H. Nos. 1887, 2941 (Hulahula River), 9071 (Sadlerochit River); specimens in National Museum of Canada from Sadlerochit River and Collinson Point; uncatalogued specimens from Kanayuk Lake in the Brooks Range (Willow Creek headwaters), stream emptying into Schrader Lake in the Brooks Range (Sadlerochit River headwaters).

Notes: The various forms of charr allied to Salvelinus alpinus (Linnaeus) present as confused a picture to the systematist as does Coregonus. A myriad of forms, described and undescribed, exist. At present it is impossible to determine which are morphas and which are not, and of the latter group it is impossible to decide which deserve recognition as subspecies or perhaps even full species.

The present writer follows Hildebrand (1948), Dunbar and Hildebrand (1952), Backus (1953), and others in calling all alpinoid charrs Salvelinus alpinus until sufficient material has been collected to permit a thorough study of the group. Berg (1948, 1949) recognized 16 forms of alpinoid charrs in the Soviet Union and adjacent countries.

It is questionable how sound most of these Eurasian forms are.

One form of alpinoid charr stands out from all others in Arctic Alaska; this is the fish called by the Eskimos Angayukaksurak ("old man fish"). Angayukaksuraks have been examined from: springs feeding into Tolugak Lake, headwaters of Anaktuvuk River, in Anaktuvuk Pass (Brooks Range); headwaters of the Hulahula River, also in the Brooks Range; Kanayuk Lake, headwaters of Willow Creek (Brooks Range); and Ikiakpuk Creek, headwaters John River (Yukon system), Brooks Range. Mr. Frits Johansen (MS) examined similar fishes from the upper Hulahula River.

So far as the locality records indicate, the Angayukaksurak is limited to headwaters situations in the Brooks Range. This is a dwarf, measuring at most about 250 mm. in standard length. Normal-sized arctic charrs occur in the same localities as the dwarfs, and the parrs of the normal charrs reach 200 mm. in length, while the adults grow to 500 mm. or so. The dwarfs are recognizable not only because of their small size but because they are stocky in appearance, like Salvelinus fontinalis of eastern North America. In addition the adult dwarfs are almost black. A similar color pattern exists in some Iceland charrs, though these do not have the S. fontinalis body form.

The Angayukaksurak may represent either a morpha or a distinct species of Salvelinus. It seems closest to the palias of Eurasia (Salvelinus lepechini and relatives).

Salvelinus namaycush (Walbaum)

LAKE TROUT, SALMON-TROUT

RANGE: Primarily in lakes but entering rivers and coastal waters in the Arctic. Present on the southern islands of the Canadian Archipelago; found throughout arctic and subarctic continental North America, from Bering and Chukchi Sea drainages in the west to the Labrador Peninsula in the east, and south to New England, the Great Lakes basin, deep lakes of northern Wisconsin and Minnesota, and lakes in the Fraser and Skeena systems of the Pacific coast. Apparently absent from the Columbia system and Vancouver Island.

PREVIOUS RECORDS: Lake at headwaters

of Kobuk River (Townsend, 1887, Salvelinus namaycush), Chandler Lake (Stoney, 1899, Col-lick-puk), northern foothills of Endicott Mountains (Anderson, 1913, Cristivomer namaycush).

Specimens Seen: U.S.N.M. No. 38365 (Kobuk River source); A.M.N.H. No. 1898 (lake near headwaters of Kuyula River, north slope of Endicott Mountains); two specimens from Chandler Lake, headwaters of Chandler River (Colville system).

Notes: Two fish were caught in Tolugak Lake, Anaktuvuk Pass, but because they were too large to take to Point Barrow in the airplane, they were eaten. Dr. P. F. Scholander reports that lake trout were caught by him in Schrader Lake (headwaters of Sadlerochit River, Romanzoff Mountains). The lake trout appears to occur in all suitable lakes in the Brooks Range. It also gets into rivers; heads of two fish from the Colville River at Umiat were seen.

Wynne-Edwards (1952) stated that the lake trout is never known to descend to the sea. Dunbar and Hildebrand (1952) acknowledged a few records from brackish and salt water in Ungava Bay and Labrador. Walters (1953a) mentioned records of lake trout caught in brackish water of Hudson Bay and in river mouths near Coronation Gulf. In July, 1953, lake trout were seen being removed from Eskimo gill nets set near the mouth of the Burnside River in Bathurst Inlet; the water was definitely brackish in taste and capelins (Mallotus villosus), cods (Eleginus navaga), and flounders (Pleuronectes stellatus, Liopsetta glacialis) were caught near by.

In recent years the lake trout has been reported from several of the southern Arctic islands. These are Victoria Island (Wynne-Edwards, 1952; Walters, 1953a), King William Island (Pfaff, 1937), Southampton Island and possibly Baffin Island (Manning, 1942), and possibly Banks Island (Manning, 1953).

Eskimo legend credits the lake trout with a tremendous size and appetite. Stoney (1899), in speaking of the fishes of Chandler Lake (headwaters Colville system) mentioned that the *Col-lick-puk* (lake trout) is said to grow over 50 feet long and can swallow a deer (caribou), antlers included.

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Hucho taimen (Pallas)

TAIMEN

RANGE: Fresh waters; in Arctic drainages, from the Indigirka system westward. Absent from the Kolyma, Anadyr, and Penzhina systems and rivers of Kamchatka.

Notes: This species is a solitary giant (weight to 80 kilograms) which prefers cold water and avoids the sea, though in the Yenisei and Lena systems it is distributed north to the deltas. (From Berg, 1948.)

Brachymastax lenok (Pallas)

LENOK

RANGE: Fresh waters; in Arctic Ocean drainages, from the Kolyma system westward; absent from northeastern Siberia, including the Penzhina and Anadyr systems and waters of Kamchatka.

Notes: There are no New World representatives. A solitary non-migratory fish prefering mountain waters, never entering even slightly saline waters. Said to be intermediate between the Salmonidae and Thymallidae, being most similar to the salmonid Salmothymus obtusirostris of Dalmatia (from Berg, 1948).

SUBFAMILY COREGONINI

WHITEFISHES

The taxonomy of this group has been particularly confusing. The classification used here follows that of Berg (1948) which is the most recent comprehensive systematic treatment of the group in Eurasia.

As with the arctic charrs (Salvelinus alpinus complex), whitefishes range widely in country inhabited by few people, and it is therefore difficult to get material from the areas of greatest whitefish abundance. In our area these are primarily river and bay fishes. All but one of the species regularly enters brackish or salty coastal waters.

Natural hybridization between species and genera is known to occur, but the hybrids are never very common. Berg (1948) and Dymond (1943) list alleged hybrids known from our area. In some places the local residents give common names for the product of each kind of cross. It is interesting that Stenodus and Coregonus (both subgenera) hybridize, but there seems to be no mention

of natural hybrids involving *Prosopium* and the other genera.

Whether the hybrids are fertile is not known. Berg (1948, p. 342) mentioned that Coregonus autumnalis × C. muksun had been found with running sexual products, but this does not indicate that the gametes were viable or fertile. From an evolutionary standpoint the hybrids should be inferior to the parentals with regard to fertility, viability, or ability to compete for feeding and spawning grounds. Otherwise the hybrids would increase in numbers and eventually replace the parental species.

Stenodus leucichthys nelma (Pallas)

SHEE

RANGE: Fresh and brackish waters. Entering rivers from the White Sea in Europe (Mezen River) eastward to Cape Bathurst in Canada, in Arctic Ocean drainages. Southward in the Bering Sea to the Bay of Korf in the west and the Kuskokwim River (Alaska) in the east.

PREVIOUS RECORDS: Kobuk River (Townsend, 1887, Stenodus mackenzii; Stoney, 1899, See), Ikpikpuk River (Stoney, 1899, S. Mackenzie).

SPECIMENS SEEN: U.S.N.M. Nos. 38360, 38914 (Kobuk River).

Notes: This fish is a notable migrator, undertaking journeys of upward of 1500 miles (2500 km.) in Siberia. It reaches the headwaters lakes of the Yukon system in the Yukon Territory and British Columbia but does not migrate above the first big rapids in any river; it is not found above the rapids at Fort Smith on the Slave River, which marks the extent of penetration into the North American interior (Wynne-Edwards, 1952).

In large rivers of Siberia and probably also in America, there are races that migrate downstream but never reach the sea, while in the same rivers there are races that migrate upstream from the sea. These races also spawn in different parts of the rivers. There is evidence that in the larger lakes (such as Great Slave) landlocked races have developed. The shee varies in size from river system to river system. Lena River fish reach a size of 35 kilograms, Ob' fish reach 10.5 kilograms (Berg, 1932); a fish of 63 pounds was caught in the Mackenzie Delta,

	TABLE 1	
Scale and Gill Raker	Counts of American	Stenodus leucichthys nelma

Drainage System	Gill Rakers	Scales	Sample	Authority
Lower Mackenzie	19–22	97–103	3	Dymond, 1943
Mackenzie Delta	22	101	1	Walters, 1953a
Mackenzie Delta	24	100	1	Gilbert, 1895
Mackenzie mouth	22	103	3	Scofield, 1899
Yukon near Dawson	20	99	1	Dymond, 1943
Slave River, Canada	19-23 ^a	100-107	11	Dymond, 1943
Kobuk River, Alaska	21	104–110	2	
Total variation in American fishes	19–24	97–110		
Total variation in Eurasian fishes	18-24	87–118		Berg, 1948

^a Ten specimens.

while at Dawson, Yukon Territory, on the Yukon River the largest size seems to be about 14 pounds (Dymond, 1943).

Walters (1953a) showed that there is no significant difference between American and Siberian shees regarding gill raker or scale counts, and therefore the American fish should be designated as S. l. nelma instead of S. l. mackenzii.

Dymond (1943) observed that fishes from Great Slave Lake and the tributary Slave River seem to average more scales than those from the Yukon and lower Mackenzie rivers and considered them to belong to a "population" different from that of the lower Mackenzie and Yukon. Gill raker and scale counts for some American shees are given in table 1. The two Kobuk River fish have higher scale counts than most Canadian fish, and the Kobuk River fish could probably be shown to belong to a different population than those of other rivers. Whitefishes are notorious for developing numerous local races, and it is of no particular value to assign a different name to the race of each river system or part thereof.

GENUS COREGONUS

It is impossible to retain Leucichthys as a distinct genus in our area. According to Hubbs and Lagler (1947), the premaxillaries of Leucichthys are never retrorse. The genotype of Leucichthys Dybowsky is Salmo omul Pallas (= C. autumnalis). The premaxillaries of C. autumnalis are at times so markedly retrorse that the fishes are easily mistaken

for small *C. clupeaformis* or *C. lavaretus* pidschian. With regard to gill raker count there is no difference between the two subgenera; *C. clupeaformis* has 24–33 gill rakers, *C.* (*L.*) tugun has 25–33, and *C. muksun* has 44–72, while *C.* (*L.*) peled has 49–68.

In the subgenus Coregonus the premaxillaries are always retrorse and the maxillary usually ends before the vertical of the anterior edge of the pupil, while in the subgenus Leucichthys the premaxillaries are antrorse, vertical, or retrorse and the maxillary usually ends beneath the pupil.

In a recent series of extremely interesting papers an attempt has been made to apply modern systematic concepts to Swedish whitefishes (Svärdson, 1949-1953). Evidence from parasitology, cytology, glacial geology, history, taxonomic studies, and information from experiments in which sea-running fishes were placed in lakes and lake-dwelling fishes were moved to different lakes has been considered by Svärdson. It is vexing that he has not referred to any Latin names, but he remarked that at present the common names are more stable than the scientific. Svärdson's discussions are based on the concepts of the superspecies (polytypic species), sibling species, primary and secondary intergradation, sympatry, and allopatry. At first his results appear incredible, but a careful reading of his arguments reveals a better grasp of the problem of coregonine evolution and systematics than has hitherto been evidenced by other workers.

Svärdson (1951-1953) reviewed the Euro-

pean literature on hybridization in Coregonus; isolating mechanisms between species in a lake break down occasionally, with a resulting mass introgressive hybridization. There is no evidence of such an occurrence in our area; hybrids are known (see above under Subfamily Coregonini), but mass hybridization has not been detected. Mass hybridization may indeed be a phenomenon of glaciated areas, where the species have been "thrown" together recently, following the withdrawal of the ice sheets, and isolating mechanisms have not become stabilized. In eastern Siberia and Arctic Alaska (plus the Yukon Valley) the ice sheets were insignificant in extent, and the whitefishes of these areas have been resident for a very long time. Thus the whitefishes of our area (excluding Canada) have had a long period of time in which to stabilize their isolating mechanisms with the environment, whereas the fishes of formerly glaciated areas have had only a short time in which to do so.

Dymond (1943), Svärdson (1951, 1952), and the present writer concur that the gill rakers offer the most stable character for a study of whitefishes. Dymond's conclusions, as well as the present writer's, were reached by a study of material from wild populations. Svärdson's conclusions were based on experiments in which fishes were transferred from one body of water to another. Because the present writer's separation of whitefish species is based primarily on gill raker characters, Svärdson's results are summarized below.

The following characters employed in coregonine systematics were found by Svärdson (1951) to be highly plastic and experimentally modifiable by temperature, salinity, amount of food available per fish, and undefined characteristics of the particular body of water: rate of growth, maximum size, snout length, head size, eye size, and number of scales along the lateral line. Thus within the same species fishes living in salt water do not grow so fast as those in fresh water; faster-growing fishes have relatively smaller heads; larger individuals have proportionately longer snouts; among fish of the same size the slowergrowing fish has the longer snout; among fish of the same size and with the same growth rate the sea-run individual has a longer snout than the lake dweller; slower-growing fishes

have relatively larger eyes; the number of lateral line scales is influenced by water temperature and perhaps also by the size of the parent fish and consequently the size of the egg from which the individual was hatched; and gill raker count, although somewhat modifiable by transplanting fish to another body of water, is the most stable character studied.

In discussing the transplantation of two lake-dwelling species into lakes that had not had whitefishes, Svärdson (1950) reported that in the storsik, the gill raker mean shifted from 19.0 to 20.5 and 23.2 and in the aspsik from 45.3 to 44.5 and 39.1; in neither case did the new mean lie outside the old range, since the range for the storsik is 16-28 (Svärdson, 1949, 1951) and for the aspsik 38-51 (Svärdson, 1949). Sea-run whitefish, mean 28.5, were transplanted into two lakes and the new means became 29.6 in both; the range was essentially unchanged (Svärdson, 1951). This latter case is of interest in connection with the present writer's comments on lake and river forms of Coregonus lavaretus pidschian in Siberia (which see).

With regard to gill raker number, Svärdson (1952) concluded that variation in gill raker number is the only character so far used in whitefish taxonomy of which the variation is proved to have a genetic basis. The capacity for environmental non-genetic modification is very slight or non-existent. In 12 cases of transplantation the mean gill raker count remained unchanged ordiverged from that of the parental stock, on the average, less than two units. The number of scales, on the other hand, sometimes shows a decided divergence on transplantation; in one case there was a drop of 11 units in scale count.

The northern limits of whitefish distribution are not accurately known. All American records have previously been from the continental mainland or near-by localities, but a specimen taken by T. H. Manning from Castel Bay on the north coast of Banks Island, referred to *C. sardinella* by the present writer, indicates whitefishes are widespread in the southern islands of the Canadian Archipelago. The Banks Island record appears to be the farthest north that a whitefish has been taken in North America (north of latitude 74° N).

SUBGENUS LEUCICHTHYS

LAKE HERRING

Coregonus sardinella Valenciennes

LEAST HERRING

RANGE: Fresh and brackish waters. White Sea (Europe) eastward to Bathurst Inlet in Canada, in Arctic Ocean drainages; in Bering Sea, south to Bay of Korf in the west and the Yukon River in the east. Northern limit not known; a head of a fish, probably this species, was obtained at Castel Bay, northern coast of Banks Island, by T. H. Manning on July 21, 1953.

Previous Records: Kotzebue Sound and Kobuk River (Bean, 1883, 1884; Townsend, 1887, Coregonus merkii subsp.; Bean, 1889, Coregonus pusillus); Barter Island (Scofield, 1899, Argyrosomus pusillus); Meade River (Fowler, 1905b, A. pusillus); lake near Point Barrow (Wohlschlag, 1953, Leucichthys sardinella; Cohen, 1954; Wohlschlag, 1954, Coregonus sardinella).

Specimens Seen: U.S.N.M. Nos. 38919, 38929 (Kobuk River); 38366 (Kobuk River, C. pusillus type); 33945-33947, 111691, 111714, 152890 (Point Barrow and Elson Lagoon); 111670, 111696, 111699, 111711 (Alaktak River, Chipp system); 111666, 111684 (headwaters of Anaktuvuk River, Brooks Range).

Notes: Dymond (1943) showed Coregonus pusillus Bean to be conspecific with Leucichthys sardinella (Valenciennes). This is a widely ranging species which breaks up into numerous local forms. Recognition characters are that the tip of the lower jaw lies in front of the tip of the upper jaw (chin projects), the tips of the pectoral pelvic and anal fins are black, and the dorsal fin is falcate. The head is usually dark-spotted on top.

Dymond (1943) and Wynne-Edwards (1952) believed that Coregonus (Leucichthys) autumnalis (=L. laurettae) is closest to C. (L.) artedi. This viewpoint is not shared by Russian workers, who regard C. artedi to be closely related to C. sardinella and C. albula (western Europe), and who regard C. autumnalis as a member of the C. tugun-C. peled group.

In Alaska and in the Yukon Territory C. sardinella is the only lake herring that ascends into the headwaters of rivers, yet

in the Mackenzie it has not been identified above Camsell Bend (Wynne-Edwards, 1952), while *C. artedi* is found replacing it in Great Bear Lake and farther south. *Coregonus sardinella* and *C. artedi* are allopatric; *C. artedi* enters coastal salt waters in Hudson Bay but seems not to enter coastal salt water in the range of *C. sardinella*. The problem bears looking into, for *C. sardinella* and *C. artedi* may be conspecific.

Coregonus autumnalis (Pallas)

SALMON-HERRING

RANGE: Fresh and brackish waters. In Arctic Ocean drainages, from the White Sea (Europe) eastward to Bathurst Inlet (Canada); in Pacific Ocean drainages, south to the Alaska Peninsula (Bering Sea) in the east and probably the Penzhina River (Sea of Okhotsk) in the west, but unknown from Bering Sea shores of Siberia.

PREVIOUS RECORDS: Point Barrow (Bean, 1882a, C. laurettae), Meade and Kuaru rivers and Elson Lagoon (Murdoch, 1885a, 1885b, C. laurettae), Point Hope (Scofield, 1899, Argyrosomus alascanus), Marsh River, Collinson Point (Walters, 1953a, Leucichthys autumnalis).

SPECIMENS SEEN: U.S.N.M. Nos. 33943–33944 (Meade River), 27695 (Point Barrow, types of *C. laurettae*), 29940 (Point Barrow), 29935, 29947 (Kotzebue Sound); Collinson Point specimens in National Museum of Canada.

Notes: Dymond (1943) showed that Leucichthys laurettae (Bean) is conspecific with Leucichthys autumnalis (Pallas). The salmonherring, or omul, has a spawning run of 1500 kilometers (930 miles) in the Yenesei River, but it has a short run in other rivers, and in the Piasina and Kara systems spawning is believed to take place in brackish water (Berg et al., 1949).

Berg (1948) regarded Coregonus autumnalis migratorius (Georgi) of Lake Baikal and C. subautumnalis Kaganowsky as the closest relatives of C. autumnalis of the Arctic Ocean. Coregonus subautumnalis, described by Kaganowsky in Berg (1932), is known from one specimen taken at Penzhina near the headwaters of the Penzhina River (Sea of Okhotsk). A comparison of some proportions and counts given by Kaganowsky for C.

TABLE 2 COMPARISON OF TWO FORMS OF Coregonus

Character	Coregonus subautumnalis Data from Kaganowsky	Coregonus laurettae U.S.N.M. No. 27965, 4 Point Barrow types		
	(in Berg, 1932)	Range	Mean	
Eye as per cent of interorbital width	67.5	73.8–77.8	74.2	
Interorbital width as per cent of head length	27.1	27.7-30.3	28.8	
Upper jaw length as per cent of head length	29.3	32.4-33.4	32.6	
Upper jaw length as per cent of interorbital width	108	111-117	114	
Scales	83	80-93	<i>85.5</i>	
Gill rakers	4 5	33-43	<i>37</i>	

subautumnalis with similar data taken from the four Point Barrow types of C. laurettae Bean indicates that C. laurettae and C. subautumnalis are probably conspecific (see table 2); in both the upper jaw length exceeds the interorbital width, which Kaganowsky considered to be the diagnostic character for C. subautumnalis.

Dymond (1943) considered Argyrosomus alascanus Scofield (1898) as probably synonymous with Leucichthus laurettae (Bean), which in turn is conspecific with L. autumnalis. Dymond was unable to locate the types of Scofield's species. These are in the collections of Stanford University. Mr. Adair Fehlmann was kind enough to examine the Point Hope holotype of A. alascanus (S.U. No. 5611). This has 82 scales along the lateral line (Scofield counted 85), 34 gill rakers, and measures 234 mm. in standard

TABLE 3 MERISTIC VARIATION IN AMERICAN Coregonus autumnalis

Locality	Scales Along Lateral Line			Gill Rakers		
Locality	Range	Mean	Sample	Range	Mean	Sample
Kotzebue Sound, Alaska	83	83	2	-		
Point Hope, Alaska ^a	82	<i>82</i>	1	34	<i>34</i>	1
Meade River, Alaska	92-93	92.5	2	40-43	41.5	2
Point Barrow, Alaska ^b	8093	85.5	4	33-43	37.0	4
Collinson Point, Alaska	84-94	89.3	3	42-43	42.8	4
Herschel Island and Kamakok,						
Canada	82-94	87.8	4	39-45	41.3	4
Mackenzie Delta, Canadac		<i>87</i>	10		42	10
Lower Mackenzie and Delta,						
Canadac	8499	92	5	39-46	42	5
Arctic Red River, Canadac	88-93	91	6	40-50	43.6	6
Cape Bathurst, Canada	93	93	1	40-43	41.5	6
Bernard Harbour, Canada	85	<i>85</i>	1	42	42	1
Bathurst Inlet, Canada		*****	-	42-45	43.4	5
Total variation in American fishes	8099			33-50		
Total variation in Eurasian fishes ^d	86-111			35-51		

^a Counts made by A. Fehlmann on type of A. alascanus. ^b Four types of C. laurettae.

Data from Dymond, 1943.

^d Data from Berg, 1948.

length. The dorsal fin is as in *Coregonus autumnalis*, i.e., it is low and when depressed the first branched ray does not reach farther back than does the last. *Argyrosomus alascanus* is considered to be conspecific with *C. autumnalis*. Meristic variation in American fishes is given in table 3.

Coregonus peled (Gmelin)

PELED, SIROK

RANGE: Fresh waters. Mezen River (White Sea) eastward to the Kolyma.

Notes: Not known from the New World. Its closest relatives are the omul and the tugun, from which it is readily distinguished by its high number of gill rakers (49–68 instead of 25–51), and the greater number of branched rays in its anal fin (usually 12–16 instead of 10–12).

The sirok is a fish of lowland fresh waters, but does not enter saline waters (from Berg, 1948).

TULLIBEES

Anderson (1913) listed Argyrosomus tullibee from the Mackenzie Delta but brought none back, the identification being based on his impression of the fishes' appearance. Walters (1953a) suggested that these may have been Coregonus nasus, Leucichthys sardinella, or both. Anderson mentioned that the tullibee was probably the same as the Eskimo *Pi-kok-tok*, which in turn resembles the An-Ark'-hlirk but is not so fat as the latter. People who speak Eskimo told the present writer that the Alaskan Eskimo "k" sound is substituted by the German "ch" in the Coronation Gulf area. This was found to hold true for fish names. Thus Anaklik in Alaska (Point Barrow) is pronounced Anah'lih' (present writer's spelling) at Coppermine and at Bathurst Inlet, which is similar to An-Ark-'hlirk of the Mackenzie Delta (Anderson's spelling). Because Eskimo has no written language, word spellings vary with the author concerned. Anaklik refers to the broad whitefish, Coregonus nasus. Pi-kok-tok probably refers to the hump-backed whitefish, C. lavaretus pidschian in Alaska and C. clupeaformis in Canada. Anderson did not list any true whitefishes in his report, and it is reasonable to conclude that his "Argyrosomus tullibee" consisted of one or two

species of Coregonus (sensu stricto). Dymond (1943) considered Anderson's tullibee to be Leucichthys autumnalis and L. sardinella. This could not be the case, because C. sardinella is called Kalushak by the Eskimos, and C. autumnalis is known as Kaktak. Anderson's L. lucidus (Kaktak) was indicated by Walters (1953a) to have been probably C. autumnalis.

Another report for Argyrosomus tullibee in western Arctic Canada was given by Pfaff (1937), who listed it from King William Island and Danish Island (north of Vansittart Island, northern Hudson Bay). Dunbar and Hildebrand (1952) suggested that Pfaff's specimens may have been Leucichthys artedi, and Walters (1953a) commented that their identity remains problematical. Pfaff described a projecting lower jaw, the eye as equal to the snout, and about 70 scales along the lateral line. The jaw character restricts the identification to Coregonus artedi and C. sardinella. The large eve indicates that the fish may be C. sardinella, but it would be unwise to base any definite statement on Pfaff's report.

Reports of tullibees by early travelers in western Arctic America had best be regarded not as records for *Coregonus tullibee* but simply as records for deep-bodied individuals of any or all of five species: C. sardinella, C. autumnalis, C. nasus, C. lavaretus pidschian, C. clupeaformis.

SUBGENUS COREGONUS

TRUE WHITEFISHES

Coregonus nasus (Pallas)

Broad or Round-nosed Whitefish

RANGE: Fresh and brackish waters. Pechora River (Russia) east to Bathurst Inlet (Canada), in Arctic drainages. In Pacific drainages: south to the Yukon River in the east and to the Bay of Korf (latitude 60° N.) in the west of the Bering Sea; also in the Penzhina River (Sea of Okhotsk).

Previous Records: Rivers near Point Barrow (Murdoch, 1885a, 1885b, C. kennicotti), Kobuk River (Townsend, 1887, C. kennicotti), Barter Island (Scofield, 1899, C. kennicotti), Meade River and Point Barrow (Fowler, 1904, C. nelsoni; 1905a, 1905b, C. kennicotti), lake near Point Barrow (Wohl-

schlag, 1953, Prosopium cylindraceum; Cohen, 1954, C. nasus kennicotti).

Specimens Seen: U.S.N.M. Nos 33941-33942 (Meade River), 38357, 38459, 38906 (Kobuk River), 111659 (Colville River), 111671, 111698, 111706 (Alaktak River, Chipp system), head from Teshekpuk Lake.

Notes: The identifying features of this species have recently been discussed and illustrated by Wynne-Edwards (1952). The short gill rakers are characteristic; the longest are less than the diameter of the pupil, and except for the two or three of the upper and lower ends of the arch all are of about the same length. Dymond (1943) did not distinguish between this species and C. clupeaformis. His series from Kittigasuit, Peel River, and Yukon River near Dawson, Yukon Territory, probably contained both species. Mixture is indicated by the low gill raker means for these localities (22-22.8) and also by Dymond's data on gill raker lengths of Kittigasuit fishes. Table 4 indicates relative gill raker lengths for C. lavaretus pidschian, C. clupeaformis, C. nasus, and the Kittigasuit fishes. In 39 C. clupeaformis from various localities and ranging from 113 to 455 mm. in standard length, the longest gill raker is contained in the standard length 40 to 66 times; in five C. nasus measuring 167 to 477 mm. in standard length the value is 77 to 100; in five C. lavaretus pidschian (Alaska) 311 to 406 mm. in standard length the value is 60 to 63. Dymond's Kittigasuit series (11 fish) may be divided into two groups, one in which gill raker length is contained in standard length 35 to 39 times (seven fish) and the other in which the value is 77 to 95 (four fish); the groups correspond in gill raker length to Coregonus clupeaformis and Coregonus nasus, respectively.

Wynne-Edwards (1952) stated that *C. nasus* is found in the Mackenzie as far upstream as Camsell Bend; Gilbert (1895) listed the species for Great Bear Lake (as *C. kennicotti*). Peel River and Kittigasuit are in the Mackenzie system, and both lie within the range of *C. nasus*. The species is known to occur in the Yukon system. Therefore Dymond probably had the two species confused in his samples.

Wynne-Edwards (1952) regarded Amer-

ican fishes to be *C. nasus kennicotti* but gave no reason for this decision. There are no apparent significant differences in gill raker or scale counts between Eurasian and American *C. nasus*, and there seems to be no reason to recognize an American subspecies of this fish (table 5).

Coregonus clupeaformis (Mitchill)

HUMP-BACKED WHITEFISH

RANGE: Fresh and brackish waters in the north; restricted to lakes in the south. Labrador Peninsula and Ungava Bay south to New York and Michigan, west to Montana and northward to the Arctic coast of Canada; found on both sides of Hudson Bay; not known from Alaska, though present in the headwaters of the Yukon system (Squanga Lake, Yukon Territory, and apparently Teslin Lake, British Columbia) and in the Skeena and Fraser systems of British Columbia.

Notes: Whether Coregonus clupeaformis is conspecific with C. lavaretus of Europe. Asia, and Alaska or not cannot be determined at present. The two are evidently members of the same species group. Dymond (1943) concluded that C. clupeaformis is derived from C. nasus. This viewpoint is unacceptable, because C. lavaretus pidschian of Alaska is almost identical in appearance to C. clubeaformis of western Arctic Canada. The only reliable criterion known thus far for distinguishing between the two is gill raker count. On the other hand, C. clupeaformis differs from C. nasus in several important characters such as length and shape of the maxillary, length and structure of the gill rakers (short and fairly smooth in C. nasus, long and spiny in C. clupeaformis), and breeding season (C. nasus in early summer, C. clupeaformis in autumn).

Bean (1884) mentioned that on April 14, 1877, 409 European *Coregonus lavaretus* were put into Lake Gardner, Otsego County, Michigan. The subsequent fate of these fishes seems to be unknown, and Koelz (1929, 1931) made no mention of the experiment.

Gill raker counts for *C. clupeaformis* from various localities are given in table 6. Dymond's (1943) data for Kittigasuit, Peel River, and Yukon River near Dawson, Yukon Territory, are not included, because

TABLE 4 RELATIVE LENGTHS OF THE GILL RAKERS IN SOME AMERICAN WHITEFISHES

	Longest Raker in Standard Length					
Locality	Range	Mean	Length of Fish in Mm.	Sample		
Coregonus lavaretus pidschian						
Meade River, Alaska	60-63	60.8	311-406	5		
Coregonus clupeaformis						
Lake Ontario ^a	43-65	50.3	327-435	10		
Lake Nipigon ^a	47-62	<i>54.0</i>	328-363	9		
Baker Lake, Canada ^a	52-66	<i>58.0</i>	337-455	8		
Arctic Red River, Canadaa	46-56	51.6	370-426	5		
Great Slave Lake	49-54	51.5	380-390	2		
Coppermine, Canada	40-47	44.6	113-202	5		
Coregonus nasus (C. kennicotti)						
Fort Good Hope, Mackenzie River (type)a	7895		477 (skin)	1		
Bathurst Inlet, Canada	84-100	88.5	167–219	4		
? Coregonus nasus ^{a,b}	77–95°	-		4		
?Coregonus clupeaformis ^{a,b}	35-69°		all controls	7		

^a Calculated from data given by Dymond, 1943.

TABLE 5 MERISTIC VARIATION IN AMERICAN Coregonus nasus

T 1	Scales a	long Later	al Line	Gill Rakers			
Locality	Range	Mean		Range	Mean	Sample	
Saint Michael's, Alaska (Bering							
$Sea)^a$	85	<i>85</i>	1	22	22	1	
Kobuk River, Alaska	83-88	<i>85.7</i>	3	20-22	20.7	3	
Meade River, Alaska	83-86	84.5	2	20	20	1	
Meade River-Point Barrow, Alaska ^b	80-81		4	20	20	4	
Alaktak River, Alaska	82-88	84.5	4	20-23	21.5	4	
Teshekpuk Lake, Alaska				22	22	1	
Colville River, Alaska	78-84	80.3	3	19–21	20	3	
Barter Island, Alaska ^c	86	8 6	1	21-22	21.5	1	
Mackenzie Delta, Canadad				21	21	1	
Mackenzie River, Canadae	90	90	1	21	21	1	
Tree River mouth, Canadaf	91	91	1	21	21	1	
Bathurst Inlet, Canada			-	19–21	20	4	
Teslin Lake (Yukon headwaters),							
Canada				23-25	23.8	12	
Total variation in American fishes	78-91			19–25			
Total variation in Eurasian fishesh	76-106			18-27			

^a From Dymond, 1943 (C. kennicotti).

^b Series from Kittigasuit, Mackenzie Delta.

^c Values for 11 specimens of "Coregonus clupeaformis," here considered to belong probably to two species, are as follows: 35, 44, 46, 47, 55, 69, 69, 77, 82, 91, 95.

^b From Fowler, 1904 (C. nelsonii).
^c From Scofield, 1899 (C. kennicotti); gill rakers on both sides counted.
^d From Gilbert, 1895 (C. kennicotti).

From Dymond, 1943 (C. kennicotti type).

From Walters, 1953a.
From W. A. Clemens (in litt.).

^h From Berg, 1948, p. 354, text and footnote.

he probably had a mixture of *C. clupeaformis* and *C. nasus* from these localities (see *C. nasus*).

The gill raker counts of C. clupeaformis indicate no apparent tendency for the number to be higher or lower in the north, south, east, or west. Means vary from 25 to 32, which may be indicative of local raciation, because high values are found in both the north and south (32 in Gulliver Lake, Michigan, 28.3 in Lake Nipigon, Ontario, 28 in Squanga Lake, Yukon Territory), and low values are found in the north and south (25 in Arctic Red River, Yukon Territory, 25 in Simcoe Lake, Ontario, 25.9 for Maine C. c. stanleyi). Throughout the entire range of the species, individuals with fewer than 24 gill rakers are rare; of 1226 fish examined by Koelz (1929, 1931) one had 22 and one had 23 gill rakers, indicating a frequency of 0.0008 each for these counts. Coregonus clupeaformis may be characterized as having 24 to 33 gill rakers.

Walters (1953a) reported that a 63-mm. C. clupeaformis from Horton River, North-West Territories had 21 gill rakers. The small size of the specimen may have caused a few stubs to be overlooked, or all gill rakers may not have been formed, or it may be that the specimen was actually Coregonus lavaretus pidschian. It is now realized that the specimen was too small to be identified as to species. At the time, the writer's ideas concerning hump-backed whitefishes had not crystallized, and the specimen was automatically identified as C. clupeaformis.

Coregonus lavaretus pidschian (Gmelin)

HUMP-BACKED WHITEFISH, PIDSCHIAN

RANGE: Fresh and brackish waters; typically in rivers, not lakes. Lower portion of the Ob' system eastward across all of Siberia, except possibly the Piasina system on the Taimyr Peninsula; in Bering Sea drainages of Siberia south to the Bay of Korf (latitude 60° N.) and also present in the Penzhina system of the Sea of Okhotsk; Bering, Chukchi, and Beaufort Sea drainages of Alaska; not known from Canada. Probably intergrading with other forms of the polytypic Coregonus lavaretus, upstream and westward from the mouth of the Ob', in Lake Baikal, and possibly also in the Piasina basin; it is

not established whether or not intergradation takes place with the American representative of the *C. lavaretus* complex, *C. clupeaformis*.

Previous Records: All as *C. nelsoni;* rivers near Point Barrow (Murdoch, 1885a, 1885b), Kobuk River (Townsend, 1887), Point Barrow (Fowler, 1905b).

Specimens Seen: U.S.N.M. Nos. 33936–33940 (Meade River), 38365, 38926, 38935 (Kobuk River), 37970 (Kotzebue Sound), 111659 (Colville River), 111670, 111695, 111698, 111710 (Alaktak River, Chipp system).

Notes: The hump-backed whitefish of Alaska, named Coregonus nelsoni by Bean (1884), was judged by Dymond (1943) to be identical to C. clupeaformis. Dymond based his conclusion on a supposed cline for gill raker number in C. clupeaformis; gill raker count was said to increase southeastward across North America. It has already been demonstrated that there is no such cline for gill raker number in C. clupeaformis.

Another factor that has led to confusion regarding the identity of the hump-backed whitefish of Alaska is that the type description of C. nelsoni reported the species to have about 26 gill rakers (Bean, 1884). None of the specimens examined and no other published reports indicate a count in excess of 23 gill rakers for Alaskan fishes. The following is a portion of a letter dated September 23, 1953, from Dr. Ernest A. Lachner concerning the type specimen of Coregonus nelsoni Bean (U.S.N.M. No. 29903): "We are sorry but we cannot find the type of Coregonus nelsoni Bean. It has never been recorded in our file cards of types. However it is listed in our catalogue book but not indicated as a type. It was often a practice in the early days to assign a U.S.N.M. number but sometimes the specimen never got here. This one may be here in our numerous uncatalogued crocks but it would be a hopeless task going thru them. Our catalogue book contains the following data under No. 29903, Coregonus nelsoni, which may be of some value to you: Original number 249, scales 10-86-9; gill rakers 6-16."

According to Lachner's letter, the type of *C. nelsoni* was counted to have 22 instead of "about 26" gill rakers as reported by Bean (1884). This new figure is in agreement

TABLE 6
GILL RAKER COUNTS OF Coregonus clupeaformis^a

Locality	Mean	Range	Sample	Authority
Northeast America ^b	27.4	24-33	602(604)°	Koelz, 1931 ^d
Lake Nipigon	28.3	27-30	32 (33)°	Koelz, 1929 ^d
Lake Superior	27.4	25-30	109	Koelz, 1929^d
Lake Michigan	27.0	25-29	149(151)°	Koelz, 1929 ^d
Lake Huron	27.1	25-31	192(193)°	Koelz, 1929 ^d
Lake Erie	27.6	25-30	100	Koelz, 1929 ^d
Lake Ontario	27.6	26-30	34 (36)¢	Koelz, 1929 ^d
Kerr Lake, New Brunswick	26.7	25-28	21	Smith, 1952 ^d
Lake Opeongo, Ontario	25.4-27.7		171	Kennedy, 1943
Hudson and James bays	27	26-29	66	Dymond, 1933
Labrador	26.5	24-29	17	Backus, 1953 ^d
Ungava Bay	26.1	25-27	9	Dunbar and Hildebrand, 1952d
Clear Lake, Manitoba	26.2	24-29	10	Bajkov, 1930 ^d
Churchill, Manitoba		28	1	Fowler, 1948
Northern Manitoba	25.6			Bajkov, 1933
Athabaska Lake, river	26.8	25-28	5	Kendall, 1924^d
Beauvert Lake, Alberta	26-27			Bajkov, 1927
Beauvert Lake, Alberta		26	1	Dymond, 1943
Baker Lake, North-West Terri-				
tories	25.8		8	Dymond, 1943
Squanga Lake, Yukon Territory	28	26-30	6	Dymond, 1943
Great Slave Lake	27.5	27-28	2	
Mackenzie River		28	1	Kendall, 1924
Arctic Red River, Yukon Terri-				
tory	25		5	Dymond, 1943
Coppermine, North-West Terri-				
tories	27.2	26-28	5	
Teslin Lake, British Columbia	24.8	23-26	12	W. A. Clemens (in litt.)

^a Including all forms considered by Dymond (1943) to be *C. clupeaformis* except *C. kennicotti* and Alaskan *C. nelsoni*; identical to *C. nelsoni* plus the squanga of Wynne-Edwards (1952).

b Koelz's data for all localities have been consolidated as "Northeast America"; seven subspecies, distributed haphazardly through one another's ranges, were recognized. His data (1931, table 38) have been used to calculate the means of various whitefish populations. The range in means of populations is 25.0 (3 C. c. neo-hantoniensis, Simcoe Lake, Ontario) to 32.0 (5 C. c. gulliveri, Gulliver Lake, Michigan). The range in means for the subspecies is 25.9 (C. c. stanleyi) to 32.0 (C. c. gulliveri). Koelz's material came from Maine, New Hampshire, New York, Ontario, Upper and Lower Michigan peninsulas, Wisconsin, Minnesota, Saskatchewan, and Montana.

^c Mean calculated from sample size indicated in parentheses. In these the series are so large that "extreme" classes with only one individual have been discarded by the present writer in the column indicating the range in gill raker count.

d Mean calculated from the data given.

It is possible that the low count reflects mixture of some C. lavaretus pidschian in the sample.

with data for two topotypes of *C. nelsoni* (U.S.N.M. Nos. 29898 and 29900 from Nulato, Yukon River, Alaska), which have 21 and 23 gill rakers.

Gill raker counts for Alaskan hump-backed whitefishes are given in table 7; the range for 46 fish is 16-23, the mean 20.5. In *C. clupeaformis* of the United States and Canada (including Arctic coast localities) the range

is 24-33, with a mean of not less than 25 (see table 6).

According to Wynne-Edwards (1952), Coregonus nelsoni of the Mackenzie system has 25–28 gill rakers. This range does not differ from that for C. clupeaformis, but it does differ from the range of C. nelsoni of Alaska. Because C. nelsoni was named from Alaska, Wynne-Edwards' fish must be iden-

TABLE 7

GILL RAKER COUNTS OF ALASKAN HUMP-BACKED WHITEFISHES, "Coregonus nelsoni"a

Locality		18	19	20	21	22	23	Authority
Nulato, Yukon River		_	_	_	1	1 ^b	1	Writer and E. A. Lachner
Port Clarence and Grantley Harbor		3	1	2	4	2		Scofield, 1899
Kobuk River and Kotzebue Sound		_	1	1	1	1	_	•
Meade River		-	_	_	1	1	1	Fowler, 1905b
Meade River		_	_	_	3	2	_	R. Kanazawa
Alaktak River		_	_	1	2	3	_	
Colville River		-	-	-	1	1	-	
Total Mean	20.7	3 -	2	4	13	11	2	

^a Mr. N. J. Wilimovsky (in litt.) found 11 specimens from Dease Inlet, Elson Lagoon, Meade River, and Colville River to have 16–23 gill rakers, mean 20.0. Combined with the data for 35 fish in the table, the range for 46 Alaskan hump-backs is 16–23, mean 20.5.

^b Type specimen, U.S.N.M. No. 29903.

tified as C. clupeaformis. As yet there is no positive evidence that C. nelsoni and C. clupeaformis overlap in range; the Teslin (British Columbia) population of C. clupeaformis has a somewhat low count, indicating possible mixture with C. nelsoni. According to Wynne-Edwards (1952) two kinds of hump-backs are found in Squanga Lake, Yukon Territory (Yukon system), which is close to Teslin Lake. The squanga is C. clupeaformis (which see), but Wynne-Edwards did not give gill raker counts for the other kind, and it is uncertain what this other fish may be. Walters (1953a) listed C. clupeaformis from Horton River, North-West Territories; this was a small individual (63 mm. standard length) with 21 gill rakers. It is possible that this individual may have been C. nelsoni (see C. clupeaformis for further comment).

Since gill raker count indicates that *C. nelsoni* of Alaska is distinct from *C. clupea-formis* of Canada and the United States, the question that next arises is, to what form of whitefish is *C. nelsoni* most closely related?

Coregonus lavaretus is distributed in profuse variety throughout northern Europe and Asia. The similarity of the American C. clupeaformis to C. lavaretus has been mentioned by many authors, most recently by Wynne-Edwards (1952). If we were to consider C. clupeaformis as a member of the C. lavaretus group, the distribution of the

C. lavaretus group would then be comparable to the distributions of certain other freshwater fishes such as the pike (Esox lucius), burbot (Lota lota), and stickleback (Pungitius pungitius). However, for the time being it is best to regard C. clupeaformis as closely related to C. lavaretus but not yet demonstrated to be conspecific with it.

Wynne-Edwards (1952) considered the Mackenzie River hump-back as closest to Coregonus lavaretus pidschian. Coregonus clupeaformis is undoubtedly related to C. lavaretus pidschian, but gill raker counts indicate that the Alaskan hump-back (C. nelsoni) is more closely related to C. l. pidschian.

It is pointed out above in the discussion of the genus *Coregonus* that gill raker count is the most stable of the taxonomic characters employed in a study of whitefishes. Other characters, such as scale count and body proportions, are highly plastic. The mean gill raker count varies only within fairly narrow limits from population to population; the table of gill raker counts for *Coregonus clupeaformis* offers an example of this (table 6).

The gill raker counts for *C. nelsoni* of Alaska indicate the range to be 16-23, the mean 20.5 (table 7). *Coregonus lavaretus pidschian* has a range of 16-23 gill rakers over most of its range. Berg (1948) recognized 13 forms of *C. l. pidschian*, distributed from

northern Scandinavia eastward across northern Europe and Siberia and south into Bering Sea and Sea of Okhotsk drainages; the over-all gill raker range for the 13 forms is 16–29. In the present writer's opinion, some of these 13 forms represent intergrades between C. l. pidschian and other forms of C. lavaretus, and some may not even be C. l. pidschian. Five forms are considered to be C. l. pidschian; these are "typical" pidschian, natio brachymastax, natio fluviatilis, natio jucagiricus, and natio anaulorum.

The distributions and gill raker counts of the 13 forms of *C. l. pidschian* recognized by Berg are given in table 8.

An examination of the geographical distribution of gill raker counts in Eurasian C. l. pidschian reveals certain interesting items. First, fishes with a gill raker range similar to Alaskan hump-backs (C. nelsoni) are found throughout Siberia east of the Ob' system, from Gydan Bay east. The only exceptions are fishes of lakes in the Piasina basin (Taimyr Peninsula) and the population living in Lake Baikal. Otherwise, the gill raker range for Gydan Bay, the Yenesei system, Lena system, Kolyma system, Ana-

dyr system, and Penzhina system is 16-23.

Fishes of the lower Ob' have slightly more gill rakers (18-25), and both upstream and westward from the mouth of the Ob' gill raker count increases rapidly. This increase is indicative of intergradation between C. 1. pidschian and the complex of forms of C. lavaretus in European Russia and neighboring countries (Berg, 1948, recognizes 31 forms of C. lavaretus, exclusive of C. l. pidschian, in Soviet Europe). Russian workers show no indication of adhering to the concept of intergradation between subspecies; each local variant is given a name, and the categories employed below the subspecies are variously designated as infrasubspecies, natio, subnatio, infranatio, race, and so forth. This practice results in a confusing array of taxonomic units, and the student is very apt to lose sight of the forest because of the trees.

In similar manner, Lake Baikal has an endemic subspecies of *C. lavaretus*, *C. l. baicalensis*. *Coregonus l. pidschian* in the Yenesei and Lena systems, which are the two rivers closest to Lake Baikal, has 16–23 gill rakers. *Coregonus l. baicalensis* has 25–33 gill rakers, the mean being 29. It is interesting

TABLE 8
FORMS OF Coregonus lavaretus pidschian: FROM BERG (1948)

Form	Gill Rakers		Distribution			
Form	Range	Mean	Distribution			
Natio pidschianoidesa	21-33	25–26	Murman coast, White Sea basin, Pechora River			
Natio pidschianoides ^a Natio pidschianoides,	20–28	Various	Lakes and rivers of the Kola Peninsula			
subnatio soldatovia	20-27	23	Kildin Lake, Kola system			
Natio bergiellusa	20-29	23.5	Sibircha and Kara rivers, Kara Gulf			
Natio smittia	24-25		Upper Ob' system and Telets Lake			
Natio mokschegorb	20-27	24.1	Lakes of Piasina basin			
Natio ajakliensisa	19-24	21.8	Lakes of Piasina basin			
Natio norilensisa	18-25	20.9	Lakes of Piasina basin			
Natio bargusinia	18-26	22.2	Lake Baikal			
Typical pidschiana	18-25	22-23	Lower Ob' system, Ob' Gulf north to latitude 71° 30' N.			
Typical pidschian	17-23	19.8	Gydan Bay, between Ob' and Yenesei mouths			
Natio brachymastax	16-22	18.2	Lower Yenesei system and Lena system			
Natio fluviatilis	18-23		Upper Yenesei system			
Natio jucagiricus	17-21		Kolyma system			
Natio anaulorum Same as brachy- mastax			Anadyr and Penzhina systems			

^a Considered to be intergrades by present writer.

^b Considered not to be C. l. pidschian by present writer.

that C. l. pidschian of Lake Baikal (natio bargusini) has 18-26 gill rakers, mean 22.2, i.e., higher than in the Yenesei and Lena. It is also interesting that Berg recognizes a natio of C. l. baicalensis with a gill raker count intermediate between natio bargusini and typical baicalensis; the range for natio dybowskii is 22-31, mean 25.6. The Lake Baikal situation looks suspiciously like intergradation between C. l. pidschian and C. l. baicalensis, the intermediates being known as natios bargusini and dybowskii.

In the Piasina River system gill raker count is high, but there is no other form of *C. lavaretus* recognized from the Piasina. Instead Berg lists three natios, *norilensis*, *ajakliensis*, and *mokschegor*, with mean gill raker counts of 20.9, 21.8, and 24.1, respectively. The three natios are said by Berg to be lake-dwellers that enter rivers to spawn, whereas *C. l. pidschian* throughout the area of low gill raker counts is a fish of rivers and coastal salt waters. The three Piasina natios may represent a relict lake-dwelling white-fish of the *C. lavaretus* group plus intergrades between this form and the migratory riverdwelling *C. l. pidschian*.

Coregonus nelsoni Bean (1884) is identical with C. lavaretus pidschian (Gmelin, 1788). Coregonus nelsoni of Alaska and C. l. pidschian east of the Ob' are typically hump-backed in appearance. Both are characteristically found in brackish or salt water for at least part of the life cycle (populations far upstream in large Siberian rivers do not migrate to the sea). Both are typically river rather than lake fishes. In both the gill rakers are long. In both the gill raker number is usually lower than 23. In consideration of the fact that other whitefishes, Stenodus leucichthys nelma, Coregonus nasus, Coregonus autumnalis, Coregonus sardinella, and Prosopium cylindraceum, occur in Siberia as well as in Alaska, it is not surprising to find that C. lavaretus pidschian is also found in the two places. Coregonus lavaretus pidschian is regarded by Berg (1948) and other Russian authors to be the most distinctive form of the species; it has a greater range than any other member of the Coregonus lavaretus group, with the possible exception of C. clupeaformis of North America.

Sometimes the type locality for a sub-

species lies near the periphery of the range, and the taxonomically "typical" individuals are not at all typical of the subspecies. The present subspecies is an example. Over the greater portion of its range, from Gydan Bay eastward into Alaska, except for a few cases which have already been discussed, C. l. pidschian has an extreme range in gill raker count of 16 to 23. By way of contrast. the "typical" fishes of the lower Ob' have 18 to 25 gill rakers, and the count rises upstream and westward from the Ob' mouth. In other words, the type locality for C. l. pidschian lies close to, or in, the presumed zone of intergradation between this and other forms of C. lavaretus.

Coregonus muksun (Pallas)

Muksun

RANGE: Fresh and brackish waters. Pechora River east to the Kolyma River. Notes: Not known from the New World. The humped back and high gill raker count (44-72) identify this fish (from Berg, 1948).

Wynne-Edwards (1952) drew comparisons between the lakelocked Finno-Karelian C. muksun aspius and the squanga of Squanga Lake, Yukon Territory. The latter, however, has 26-29 (30) gill rakers and is a form of C. clupeaformis (which see). Berg (1949, p. 1324) transferred the Finno-Karelian fish from C. muksun to C. lavaretus and reduced it to a natio of C. lavaretus pallasi. Thus again C. clupeaformis is indicated to be similar to C. lavaretus.

Prosopium cylindraceum (Pallas)

ROUND WHITEFISH

RANGE: Fresh and brackish waters, abundant in headwaters. Arctic Ocean drainages: from the eastern branches of the Yenesei system in Siberia east to Bathurst Inlet in Canada; also present in drainages of the east and west shores of Hudson Bay and the Quebec-Labrador Peninsula north to Ungava Bay. Bering Sea drainages: south to Alaska Peninsula in the east and Bay of Korf in the west. Sea of Okhotsk drainages: Penzhina River and neighboring streams. In North America from the Yukon River southeast to the Great Lakes (except Erie) and New England, except northern and western On-

TABLE 9

VARIATION IN NUMBER OF SCALES IN Prosopium cylindraceum

Locality	Range	Mean	Sample	Authority
Siberia	86–106	97		Berg et al., 1949
Arctic Alaska	89-101	95	24	
Great Bear Lake, North-West Territories	90-100	95	4	Dymond, 1943
Baker Lake, North-West Territories	86-99	92	6	Dymond, 1943
Great Slave Lake, North-West Territories	85-97	90.6	8	a
Labrador	79–93	86.7	21	Backus, 1953 ^b
Lake Superior	7 4 –98	89.7	69	Koelz, 1929 ^b
Lake Michigan	84-100	91.9	65	Koelz, 1929b
Lake Huron	8095	88.1	64	Koelz, 1929b
Lake Ontario	86-93	90	6	Koelz, 1929 ^b
Lake Ontario		<i>86</i>	10	Dymond, 1943
Restigouche River, New Brunswick		<i>87</i>	3	Dymond, 1943
Northeast United States	79–98	83.1 - 89.7	-	Koelz, 1931°

^a Five specimens from Taltheilei Narrows collected by the present writer plus three from Rutledge River reported by Dymond, 1943.

^b Means calculated from the data given.

tario, Manitoba interior, Saskatchewan, and Alberta. Pacific Ocean drainages: Alsek River (Wynne-Edwards, 1952) and possibly Kodiak Island (Bean, 1884, 1885, Coregonus quadrilateralis).

Previous Records: Kobuk River (Townsend, 1887, Coregonus quadrilateralis).

SPECIMENS SEEN: U.S.N.M. Nos. 38362, 38920, 38936 (Kobuk River), 111663, 111677, 111680 (Colville River), 111673, 111683 (Anaktuvuk River headwaters, Brooks Range).

Notes: Russian workers regard *Prosopium* to be a subgenus of *Coregonus*. This viewpoint is not acceptable, because juvenile *Prosopium* have parr marks (absent in *Coregonus*) and there is a single flap between the nostrils (double in *Coregonus*); additional species of *Prosopium* are found in North America. *Prosopium* is not known to hybridize with either *Stenodus* or *Coregonus*.

In the appendix of his book, Berg (1933) reduced *Prosopium quadrilaterale* (Richardson) to a subspecies of *Coregonus (Prosopium) cylindraceus*, and identified *C. cylindraceus quadrilateralis* from the Anadyr River because a single specimen had 86–88 scales. The normal range for the species in Siberia was

given by Berg to be 89–106. In the present writer's opinion it is dangerous to assign a fish to subspecies if only one specimen is available, if the subspecies had not previously been listed from the continent.

Dymond (1943) suggested that the separation of *P. cylindraceum* into subspecies is arbitrary, because there is a cline for gill raker and scale counts from Siberia southeast across North America. Scale counts of Arctic Alaskan fishes are given in table 9, together with data from other localities. Samples of fewer than three individuals are not included, in order that the means may be more comparable.

The table cannot be used to refute the idea of a cline in scale count for *Prosopium cylindraceum*, because there are no data available for the area between the Great Lakes, Great Slave Lake, and Baker Lake. The cline, however, if it be such, seems quite unsteady.

Recently Wohlschlag (1953) studied the biology of "Prosopium cylindraceum" in a lake near Point Barrow. According to Mr. N. J. Wilimovsky (in litt.) the specimens were misidentified and are actually Coregonus nasus.

^c Means calculated for *P. quadrilaterale*. Samples of one to 20 individuals from lakes in Maine, New Hampshire, and New York. The lowest mean is for 20 Chazy Lake (New York) fish, the highest for three fish from a lake in the Adirondack Mountains of New York. *Prosopium q. minor* is not distinguished as a subspecies in the present table.

THYMALLIDAE

GRAYLINGS

Thymallus arcticus signifer (Richardson) SAILFIN GRAYLING

RANGE: Fresh waters, straying into brackish waters. In Arctic Ocean drainages: possibly the lower Yenesei system, otherwise from the Piasina system (Taimyr Peninsula) east to the western shore of Hudson Bay (no records from Melville Peninsula north of Danish Island). In Bering Sea drainages: all of Siberia and North America. In Sea of Okhotsk drainages: the Penzhina River fish may belong to this subspecies. In Pacific Ocean proper drainages: Alsek River and Stikine system probably as a result of headwaters capture. Southern limit: in Siberia, headwaters of the rivers concerned; in North America, headwaters of drainages concerned and south along the west shore of Hudson Bay to just north of the Nelson system of Manitoba.

Replaced by: T. a. arcticus in the Ob' and Yenesei systems; T. a. baicalensis of the Baikal basin; T. a. grubei of the Okhotsk (except Kamchatka and possibly Penzhina River) basin, Sea of Japan basin, Yellow Sea basin (Yalu River); T. a. tricolor of the Missouri River headwaters in the Rocky Mountains and formerly of the southwestern Great Lakes basin.

Previous Records: To northern limit of Alaska (Bean, 1885, T. signifer), Kobuk River and all fresh waters (Townsend, 1887, T. signifer), Chandler Lake (Stoney, 1899, Su-luk-pow-wuk), Meade River (Fowler, 1905b, T. signifer), numerous sight records (in Evermann and Goldsborough, 1907, T. signifer); Hulahula and Chandler rivers (Anderson, 1913, T. signifer); Sadlerochit River (Walters, 1953a, T. arcticus).

SPECIMENS SEEN: U.S.N.M. Nos. 38364, 38924–38925, 38927, 38931 (Kobuk River), 74248, 143272 (Firth River), 111649, 111658, 111675, 111676, 111679, 111681 (Colville River), 111705 (Alaktak River, Chipp system), 111655, 111674, 111682, 111690 (Tolugak Lake, Anaktuvuk Pass); A.M.N.H. No. 1877 (Hulahula River); specimen in National Museum of Canada from Sadlerochit River; uncatalogued United States National Museum material from Chandler Lake, head-

waters of Chandler River and Nigu Lake, headwaters of Nigu River (Etivluk system); uncatalogued material in the American Museum from Kanayuk Lake, Willow Creek headwaters.

Notes: Thymallus signifer (Richardson) is conspecific with T. arcticus (Pallas) (Berg, 1948; Svetovidov in Berg et al., 1949; Wynne-Edwards, 1952; Walters, 1953a). It is now desirable to determine to which form or forms of Thymallus arcticus the American fish is most closely related.

Svetovidov (1936) divided Thymallus arcticus into the following Old World forms (ranges generalized): T. a. arcticus (Ob' and Yenesei systems), T. a. baicalensis (Baikal basin), T. a. baicalensis infrasubspecies brevipinnis (Baikal basin), T. a. pallasi (Arctic Siberia east of Yenesei to Kolyma system), T. a. grubei (Amur basin and near by), T. a. grubei natio mertensi (Anadyr River and Kamchatka).

Three of the forms recognized by Svetovidov have the pelvic fins longer than the pectorals (adults), and the dorsal fin base is more than 20 per cent of the body length, as in the American fish; these are T. a. pallasi, T. a. grubei, and T. a. grubei natio mertensi (significantly, the three forms of northeasternmost Asia). The Amur grayling (T. a. grubei) differs from the three other fish in the form of its dorsal fin; in this the posterior rays are not excessively lengthened, and the spots in the rear of the fin are not elongated. In the American fish and in T. a. pallasi and T. a. grubei natio mertensi the posterior dorsal rays are excessively lengthened in the adult (when depressed they may reach to the adipose fin or even the caudal fin), and the spots in the rear of the fin are elongated. No other gravling has such a well-developed dorsal fin.

In addition to fin development, Svetovidov (1936) also distinguished between T. a. grubei (including natio mertensi) and T. a. pallasi on the basis of maxillary length. In T. a. grubei the maxillary is 5.5-6.9 per cent of the head length and ends beneath the middle of the pupil, while in T. a. pallasi the value is 4.5-5.8 per cent and the maxillary ends beneath the anterior edge of the pupil. Svetovidov's samples were of a limited nature: he examined only 23 Kolyma River

TABLE 10

Lateral Line Scales in American Thymallus arcticus signifera

77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97
1		1	6	1	9	10	6	10	6	3	2	3	2	3	3	1	1			1
^a Fishe	es fro	m the		wing		ities:							op sys					1 15		
	eat Si					5 2						Will	ktuvi ow C	reek				16 1		
Ho	rton 1	River		ric Ai	LASK	1						Hula	eroch thula h Riv	Rive				1		
	buk I vluk			dwate	ers	5 18						1.11.61	ı Kıv	C1				 69 sp	ecim	ens

T. a. pallasi, 11 Amur River T. a. grubei, and used data provided by Kaganowsky for T. a. grubei natio mertensi. Therefore it is possible that the maxillary differences may be characteristic of the race living in a particular river system rather than of the subspecies as a whole. In adult Great Slave Lake fishes the maxillary ends beneath or beyond the middle of the pupil, in Great Bear Lake fishes of similar size it ends before the middle of the pupil, and in some Arctic Alaskan fishes of similar size it ends beneath the anterior edge of the pupil. Maxillary length was not measured in American fishes because it was observed to be so variable.

There is doubt as to the status of natio mertensi; Svetovidov (in Berg et al., 1949) referred it to T. a. grubei, but Berg (1948) wrote that it may very well be a form of T. a. pallasi.

Svetovidov (1936) and subsequent authors separate natio mertensi from T. a. pallasi on scale count. Natio mertensi has 75-86 scales and T. a. pallasi from the Khatanga, Lena, and Kolyma rivers has an over-all range of 82-107 scales (figures from Berg, 1948). Scale counts for 69 American graylings are given in table 10; the range is (77) 79-94 (97). Thus the American grayling bridges natio mertensi and T. a. pallasi in number of scales along the lateral line.

Because American, graylings are identical to T. a. pallasi and T. a. grubei natio mertensi with regard to dorsal fin development, because they bridge the two forms in scale count, and because maxillary length varies from locality to locality, all three graylings belong to the same subspecies. As Richardson

named the American fish in 1823 and Valenciennes did not name the Siberian fishes until 1848 (fide Svetovidov, 1936), the sailfin grayling should be called *Thymallus arcticus signifer* (Richardson, 1823).

The range given for the subspecies in Siberia is based on information given by Berg (1948) and in America by Preble (1908), Kendall (1924), Bajkov (1927), Hinks (1943), Dymond (1947), Wynne-Edwards (1952), and Carl and Clemens (1953).

OSMERIDAE

SMELTS

Osmerus eperlanus dentex Steindachner

RAINBOW SMELT

RANGE: Shallow coastal waters, entering fresh water to spawn. White Sea (Europe) east to Cape Bathurst (Canada) (specific Arctic records listed below) south in the Pacific to Yakutat Bay (Alaska) in the east and to Hakkodate (Japan) and Chinnampo (Korea) in the west, known thus from the Yellow Sea, Sea of Japan, Sea of Okhotsk, Bering Sea, and North Pacific Ocean proper.

PREVIOUS RECORDS: Ku (Kuk) River at Wainwright (Murdoch, 1885a, 1885b, O. dentex), Kotzebue Sound (Bean, 1882b, 1883, O. spirinchus; Nelson, 1887, O. dentex).

SPECIMENS SEEN: U.S.N.M. Nos. 27558 (Kotzebue Sound), 33927–33933 (Kuk River).

Notes: The eastern limit is Cape Bathurst, North-West Territories (Anderson, 1913, O. dentex), where one specimen was caught; this has disappeared from the collections of the American Museum of Natural History (Walters, 1953a). The next locality, west-

ward, is the Mackenzie River system, where Evermann and Goldsborough (1907, O. dentex), Preble (1908, O. dentex), Hildebrand (1948, O. dentex), and Wynne-Edwards (1952, O. e. dentex) report it as far upstream as Arctic Red River. In Alaska, Mr. N. J. Wilimovsky (in litt.) found it from Pitt Point (about 100 miles east of Point Barrow) west and south to Point Lay (about 200 miles southwest of Point Barrow). It is known from the Kuk River (ca. 150 miles southwest of Point Barrow) and also from Kotzebue Sound in Alaska (material from the latter two localities was examined).

In Arctic Siberia and Europe, according to Berg (1948) this form occurs on the Chukchi Peninsula, Yana Bay, delta of and lower Lena River, Khatanga Bay, lower 1000 kilometers of Yenesei River, Ob' system, and Kara Bay and River. It has not been found in the Kolyma River, but smelts are known close by on both sides (Yana Bay, Chukchi Peninsula). The smelts found west of Kara Bay, in the southwestern Barents and White seas, are identified as O. e. dentex natio dvinensis.

Hypomesus olidus (Pallas)

POND SMELT

RANGE: Brackish coastal waters, entering lakes to spawn; often landlocked. In the Arctic Ocean, from the Kara Sea east to the Mackenzie River in Canada; in the Pacific, south to Gensan (Korea) and northern Japan in the west and to California in the east.

PREVIOUS RECORDS: None.

Specimens Seen: U.S.N.M. No. 38921 (Kobuk River).

Notes: Hypomesus olidus is divided into three subspecies (Berg, 1948), as follows: H. o. olidus, south of Bering Strait; H. o. bergi Taranetz, a lake on Sakhalin (Sea of Okhotsk); H. o. drjagini Taranetz, Arctic Ocean. In H. o. drjagini the pectoral fin length is 40-60 per cent of the distance between the bases of the pectoral and pelvic fins; in the two other subspecies the figure is 61-80 per cent.

Three Kobuk River fishes have the pectoral fin 55-59 per cent of the pectoral-pelvic distance; hence they are *H. o. drjagini*. Wynne-Edwards (1952) listed the fish taken

in the Peel River (Yukon Territory) only as H. olidus and gave no measurements. The Peel River (Mackenzie system) fishes are probably H. o. drjagini, as no other form is known from the Arctic.

In Siberia, Berg (1948) gave the following Arctic locality records for the pond smelt: Chukchi Peninsula, Kolyma River, Alasei River, and Kara Gulf (west of the Ob').

The pond smelt will probably be found widely distributed in the Arctic. All the Arctic records thus far have been from fresh water.

Mallotus villosus (Müller)

CAPELIN

RANGE: Salt water. Northern limit not known over most of the range; to latitude 76° 19′ N. in Greenland (Jensen, 1939) and to latitude 75° N. in the Kara Sea (Berg, 1949, p. 1325). Recent records indicate the distribution to be circumpolar. South in the Atlantic to Gulf of Maine in the west and Oslo Fjord, Norway, in the east. In the Pacific, south to latitude 40° N. (Korea) in the west and Juan de Fuca Strait (Washington-British Columbia border) in the east.

PREVIOUS RECORDS: Bering Strait, Cape Lisburne, Point Belcher (Bean, 1882b, 1883), Point Barrow (Murdoch, 1885a, 1885b).

Specimens Seen: U.S.N.M. Nos. 24038 (Bering Strait), 27555 (Point Belcher), 27572 (Cape Lisburne), 32424-32425, 111619, 111712, 152608-152609 (Point Barrow); A.M.N.H. Nos. 4538 (Point Barrow), 17861 (mouth of Kotzebue Sound).

Notes: The capelin is well known in North America from Hudson Bay and farther east. There are few records between Point Barrow and Hudson Bay; these are (west to east) Herschel Island, Yukon Territory (Walters, 1953a), Bathurst Inlet (Richardson, 1823, Salmo groenlandicus), and possibly Chantrey Inlet. In the latter place, Simpson (1843, p. 365) found little fishes left on shore by the tide near the mouth of Back's Great Fish River on August 10; his comments suggest that they were capelins. Hildebrand (1948) listed the species from King William Island. The present writer collected capelins at Bathurst Inlet and also saw them on the beach at Coppermine. Mr. N. J. Wilimovsky (in litt.)

found the species from Cape Lisburne (Alaska) north and east to Herschel Island, Yukon Territory.

Until recently there was no record for the capelin from Siberia between Novaya Zemlya and Bering Strait, but on September 1, 1945, a specimen was found at Cape Mastakh near Lena River Delta (Berg, 1948), more than 1500 miles east or west of the next nearest localities.

Rass (1933) described spawning in capelins at depths down to 100 meters in the Barents Sea although this fish is usually thought of as a beach spawner. It is possible that deepwater spawning may often be resorted to in the Arctic, because it is known that the shoals do not run onto the beaches every summer. Murdoch (1885b) reported schools on the beaches at Point Barrow in 1882, but none were seen in 1883. Adult *Mallotus* were found in the stomach of an Arctic charr (U.S.N.M. No. 33953) caught at Point Barrow on August 17, 1883. Therefore, capelins were present at Point Barrow that summer but did not run onto the beaches.

Rass (1933) found that salinity is important in the determination of whether or not spawning will occur; in the Barents Sea, capelins spawn at salinities of 32–34 parts per mille (Dunbar and Hildebrand, 1952, point to discrepancies in the literature regarding thermal requirements for spawning in eastern North America but do not consider salinity requirements). The high salinity necessary for spawning may explain the apparent absence of capelins from most of Siberia, because the coastal salinities are low.

The time of appearance of the schools on the beaches and the length of the apparent spawning season vary from year to year. At Point Barrow the inclusive dates for several years are:

> 1882 July 20-July 25 (Murdoch, 1885b) 1948 August 6

1949 August 1–August 13

Males usually outnumber females on the beaches; sex ratios for various dates at Point Barrow were determined (table 11).

A few individuals are sometimes caught at Point Barrow after the spawning runs have ended. Murdoch (1885b) reported a female

TABLE 11
SEX RATIOS IN Mallotus villosus Taken on the Beach at Point Barrow, Alaska

Date	Ratio of Males to Females	Sample Size		
August 6, 1948	0.4	25		
August 1, 1949	2.6	465		
August 2, 1949	10.9	83		
August 4, 1949	7.6	458		
August 5, 1949	17.0	72		

caught September 5, 1882. In 1949, five males washed ashore September 12; a female, September 14; and two males and one female, September 21 (this latter female is full of roe and had evidently not taken part in the spawning activities of August 1–13).

Two subspecies of the capelin are recognized. Mallotus villosus villosus (Müller) is found in the North Atlantic and near-by parts of the Arctic. Mallotus villosus socialis (Pallas) (= M. catervarius) is found in the North Pacific. The subspecific affiliations of Arctic capelins cannot be determined until sizable series from many localities are collected. If the situation in the Barents Sea is typical (Rass, 1933), it is to be expected that two or more races will be found inhabiting each part of the Arctic. Caution must be used in recognizing additional species or subspecies because the differences may be only racial.

MYCTOPHIDAE

Lantern-Fishes

Benthosema glaciale (Reinhardt)

GLACIAL LANTERN-FISH

RANGE: Bathypelagic. In our area known from Point Barrow, Alaska. Widely distributed in the North Atlantic and adjacent parts of the Arctic.

Previous Records: None. Specimens Seen: None.

Notes: Mr. N. J. Wilimovsky (in litt.) found this species at Point Barrow. Because the myctophids are primarily a bathypelagic group, they are not considered in the zoogeographic discussion below.

DALLIIDAE

BLACKFISH

Dallia pectoralis Bean BLACKFISH

RANGE: Lowland fresh waters. Siberia, Chukchi Peninsula (east of the Kolyma basin) south to St. Lawrence and Mechigmen Bays; St. Lawrence Island (Alaska), south of Bering Strait; Alaska, Kuskokwim River system north to but not including Point Barrow, then east to the Ikpikpuk River system.

Previous Records: Kotzebue Sound (Nelson, 1887).

Specimens Seen: U.S.N.M. Nos. 38917–38918 (Kobuk River), 111645, 111652, 111669, 111702 (lakes and ponds near Alaktak River, Chipp system), 152897 (lake 5 miles east of Topagoruk River mouth, Dease Inlet), 152899 (lake near East Oumalik, about 100 miles southeast of Point Barrow, in Ikpikpuk watershed).

Notes: In addition to the specimens listed above, the present writer saw a blackfish in a lake about 4 miles inland from Icy Cape (halfway between Point Barrow and Cape Lisburne) in July, 1948. Mr. N. J. Wilimovsky (in litt.) reports this fish from backwaters of the Meade River.

This is a fish of lowland waters. The farthest inland record appears to be at the junction of the Yukon and Tanana rivers.

In summer the blackfish frequents sluggish, weed-infested waters. It is amazingly rapid in its actions when alarmed, and darts away in a flash. The effect on the observer is similar to having a frog jump out from under foot. The blackfish is reported to survive being frozen solid. This tale was initiated by Nordenskiöld (1882) and Turner (1886) and has been repeated by various authors since, most recently by Berg (1948) and Wynne-Edwards (1952).

Nordenskiöld (1882, pp. 442-444) related that the fishes (Dallia delicatissima = D. pectoralis) were found in a fresh-water lagoon on the Chukchi Peninsula, a lagoon that is shut off from the sea and freezes to the bottom. Later in his account, Nordenskiöld modifies the statement to mean that the lagoon apparently freezes to the bottom.

Turner's statements provide the basis for

the misconception, and are quoted in part (1886, p. 101): "... The mass of fish in each basket is frozen in a few ninutes; and when required to take them out they have to be chopped out with an ax or beaten with a club to divide them into pieces of sufficient size to be fed to the dogs. . . . They will remain in those grass-baskets for weeks and when brought into the house and thawed out they will be lively as ever. The pieces which are thrown to the ravenous dogs are eagerly swallowed; the animal heat of the dog's stomach thaws the fish out, whereupon its movements soon cause the dog to vomit it up alive. This I have seen, but have heard some even more wonderful stories of this fish."

As field observations go, Turner's story is credible. But he did not actually offer proof that the fishes were frozen solid; it is possible that the watery film about each fish had frozen, but it is not proved that the body tissues themselves had frozen.

The first researcher to become disillusioned regarding the cold resistance of *Dallia* was Borodin (1934). He found that *Dallia* survives 30 to 35 minutes of exposure to -20° C., but an hour's exposure is fatal. Also, freezing the fish in a block of ice results in the death of the fish.

Dr. P. F. Scholander and his associates at Point Barrow were similarly unable to freeze Dallia successfully and have the fish live afterward; freezing of only a part of the body resulted in necrosis of the part (Scholander, Flagg, Hock, and Irving, 1953).

Another observation indicates that Dallia cannot survive being frozen in nature. Several fish were placed in a shallow pond containing plenty of insect and crustacean life at Point Barrow in the summer of 1947. The pond had no inlet or outlet; thus the fish could not have escaped. The depth of water at most was about 2 feet. The pond froze solid to the bottom during the winter. During 1948, although repeated collecting trips were made to the pond, not a single fish was found. It is possible that seagulls or jaegers may have taken the fish out, but the absence of Dallia from the pond the following season certainly does not indicate that the fish can survive freezing.

Blackfishes exhibit two color phases. Juveniles are chestnut brown, with white

bellies and dark brown bars on the sides; adults are barred with black and grayish white. In males the dorsal fin when depressed reaches the base of the caudal fin, while in females it does not.

ESOCIDAE

PIKES

Esox lucius Linnaeus

PIKE

RANGE: Circumpolar in fresh water. In Arctic drainages, from Scandinavia eastward to Labrador; absent from Greenland and Iceland. American subspecies not yet analyzed.

Previous Records: Kobuk River (Townsend, 1887).

Specimens Seen: U.S.N.M. Nos. 38367-38368, 38913 (Kobuk River), 111654 (Alaktak River, Chipp system).

Notes: In addition to the Arctic Alaskan records listed above, pike were seen at Umiat on the Colville River, and the species was found in the Ikpikpuk River by members of the United States Geological Survey.

Esox lucius is present in the Anadyr and Penzhina systems of Siberia but is absent from Kamchatka and most of the drainages emptying into the Sea of Okhotsk. In the Amur system and near-by waters it is replaced by Esox reicherti, a black-spotted species similar to the muskellunge (Esox masquinongy) of southeastern Canada and the United States.

The range of *E. lucius* appears to be interrupted in Arctic America; it ranges east to Bathurst Inlet, where a fish that had been caught in the Burnside River was seen, but it is apparently absent from the North-West Territories east of the Burnside River and north of the Churchill River.

The pike of Siberia is now regarded as subspecifically different from E. l. lucius of Europe. Berg (1949, p. 1325) identified the pike of the Ob' system and all of Siberia as Esox lucius baicalensis Dybowsky. Not enough Alaskan material has been seen to determine whether or not E. l. baicalensis ranges into North America, although there are several "Siberian" forms which do occur in Alaska and western Arctic Canada. It would be well to investigate the possibility

that two or more subspecies of Esox lucius occur in North America.

CATOSTOMIDAE

SUCKERS

Catostomus catostomus rostratus (Tilesius)

SIBERIAN RED SUCKER

RANGE: Fresh and brackish waters. Siberia: Yana, Indigirka, Alasei, Chukocha, Kolyma, and Anadyr systems, absent from lower Anadyr (Berg, 1949). North America: rivers emptying into Bering, Chuchi, and Beaufort seas east at least as far as the Coppermine in Canada. Replaced by other subspecies somewhere in northwestern Canada.

PREVIOUS RECORDS: Brackish waters and streams flowing into Kotzebue Sound (Nelson, 1887, Catostomus longirostrum), upper Kobuk River (Townsend, 1887, C. longirostris), Colville River (Anderson, 1913, C. catostomus).

Specimens Seen: U.S.N.M. Nos. 29905 (Kobuk River), 38363, 38368, 38932, 38934 (Kotzebue Sound), 111678 (Colville River); A.M.N.H. No. 4449 (Colville River).

Notes: The red sucker is abundant at times in brackish water around river mouths. The common name is derived from the presence of a red stripe on the forward half of the body in the male. Both sexes are covered with a copious mucus, thicker towards the head, which obscures the scales and the lateral line in the forward half of the body. The scales in the forward half of the body are very small and in fish under 200 mm. standard length they are scarcely distinguishable one from the other. Scales are difficult to count even in large fish. Peritoneum color is variable from river system to river system; in the Colville it is jet black (as in Siberia), in the Coppermine it is leaden to sooty, and in Kotzebue Sound it is black-flecked.

All the western Arctic American fishes examined fit the Siberian subspecies regarding scale and gill raker counts and are identified as this subspecies (table 12). It may be that this fish is not really subspecifically different from the red sucker of the eastern American Arctic, but not enough information is available for a decision to be made.

TABLE 12

MERISTIC VARIATION IN THE RED SUCKER, Catostomus catostomus^a

Character	Siberia ^b	Kotzebue Sound¢	Colville River ^d	Coppermine ^e	Labrador [,]
Scales along lateral line	109–127	104-121	115	108–116	92–107
Gill rakers	23-27	24-28	28	24–28	

- ^a Evermann and Goldsborough (1907) give the number of scales for fishes from Watson Creek near Caribou, Yukon Territory (Yukon system), as 110–120. This is in line with counts for *C. c. rostratus* from western Arctic America.
 - b Data from Berg (1949), for C. c. rostratus.
 - * Catostomus c. rostratus; scale count based on four fish, gill raker count on five fish.
 - d Catostomus c. rostratus; scale count based on one fish, gill raker count on two fish.
 - e Catostomus c. rostratus; scale count based on four fish, gill raker count on 16 fish.
 - Data from Backus (1953); 21 individuals of C. c. catostomus.

Catostomus commersoni (Lacépède)

GRAY SUCKER

RANGE: Fresh waters. From Arctic Red River in the Mackenzie system southward and eastward across North America, including the Labrador Peninsula, to Georgia, Arkansas, and Oklahoma.

Notes: Preble (1908) listed large-scaled suckers as Moxostoma lesueuri, and Walters (1953a) tentatively identified Preble's fish as Moxostoma aureolum, from Arctic Red River. The only large-scaled sucker positively known from Great Slave Lake and the Mackenzie River is Catostomus commersoni; it is probable that Preble's and Walters' identifications are referable to this species. Wynne-Edwards (1952) credits this species in the Mackenzie north to Fort Good Hope, but Preble's remarks indicate that it ranges to Arctic Red River, almost in the Arctic Life Zone.

CYPRINIDAE

Minnows

Couesius plumbeus (Agassiz)

LAKE CHUB, NORTHERN SHINER

RANGE: Fresh waters. Arctic and subarctic America, westward to the upper parts of the Yukon system in Canada and north to the Mackenzie Delta (from Wynne-Edwards, 1952).

Notes: The lake chub is just barely able to survive arctic life and has not been found in Arctic Alaska.

Leuciscus leuciscus baicalensis (Dybowski)

SIBERIAN ELETZ

RANGE: Fresh waters. In our area from the Kolyma River system westward; in the Kolyma it is found from the delta to the headwaters (from Berg, 1949).

Phoxinus percnurus (Pallas)

LAKE GOLYAN

RANGE: Fresh waters. In our area in lakes of the Kolyma basin and westward; it is found chiefly south of the Arctic Circle (from Berg, 1949).

Phoxinus czekanowskii czekanowskii Dybowski

CZEKANOVSKY'S GOLYAN

RANGE: Fresh waters. In our area from the Kolyma River system westward; it is rare in the Kolyma, being known from the lower currents of the river (from Berg, 1949).

Phoxinus phoxinus (Linnaeus)

GOLYAN

RANGE: Fresh waters. In our area from the Kolyma system westward; it also occurs in the Anadyr River, being the only minnow that is found in that river (from Berg, 1949).

Notes: The presence of the golyan in the Anadyr and Kolyma systems indicates that it may also occur in some of the smaller rivers lying to the east of the Kolyma.

Carassius auratus gibelio (Bloch) SILVER KARAS

RANGE: Fresh waters. In our area from the Kolyma River basin and westward (from Berg, 1949).

COBITIDAE

LOACHES

Nemachilus barbatulus toni (Dybowski)

SIBERIAN GOLETZ

RANGE: Fresh waters. In our area from the Kolyma River basin and westward (from Berg, 1949).

GADIDAE

CODFISHES

Lota lota (Linnaeus)

NALIM

RANGE: Fresh and brackish waters of northern Europe and northern Asia; in Arctic Siberia east to the Lena River; may occur in the Yana and Indigirka rivers; replaced farther east by Lota lota leptura.

NOTES: The nalim ranges southward in eastern Asia to the Sea of Okhotsk drainages, being found even on Sakhalin and the Shantar Islands of that sea, but it is absent from the Penzhina system, where *Lota lota leptura* is found instead. The species is absent from Kamchatka.

The nalim enters brackish water in the Gulf of Finland and presumably also in Asia. According to Svetovidov (1948) and Berg (1949) the fish of the Yana and Indigirka rivers may be either this subspecies or *Lota lota leptura*.

Lota lota leptura Hubbs and Schultz

BURBOT

RANGE: Fresh and brackish waters. Possibly in the Yana and Indigirka rivers of Siberia (see preceding subspecies), otherwise from the New Siberian Islands and the Kolyma system eastward in Arctic drainages to northwestern Canada; in Bering Sea drainages of Siberia (south to the Bay of Korf, latitude 60° N.) and North America; absent from Kamchatka but present in the Penzhina system of the Sea of Okhotsk; Kodiak Island, Alaska. The limits of the area of intergradation between this subspecies and

Lota lota lacustris (= L. lota maculosa, see Speirs, 1952) of North America have not been determined.

Previous Records: As Lota maculosa, Meade and Kuaru rivers (Murdoch, 1885a, 1885b); Ikpikpuk River (Stoney, 1899); Meade River (Fowler, 1905b); as Lota lota leptura, Kowak (Kobuk) River (Hubbs and Schultz, 1941, type locality).

SPECIMENS SEEN: U.S.N.M. Nos. 38901, 38905 (Kobuk River, paratypes), 111648, 111660 (Colville River), 111709 (Alaktak River, Chipp system).

Notes: Burbot were seen but not collected by the present writer in Tolugak Lake at the headwaters of the Anaktuvuk River in Anaktuvuk Pass (Brooks Range). Berg (1949) gave no reasons for considering this a natio of *Lota lota lota*, and therefore the classification used by Svetovidov (1948) is followed here.

Although widely distributed in Arctic Alaska the burbot is not well represented in collections owing to the large size of most specimens. Fish at least 3 feet long were seen caught in the Colville River at Umiat, and similar-sized fishes were seen at Anaktuvuk Pass and in the Alaktak River (about 40 miles east of Point Barrow). According to the Eskimos, some burbots are almost as long as a man is high (about 5 feet). The burbot is of general distribution from brackish water near river mouths up to the mountain lakes; none were taken in the Point Barrow area, no doubt owing to the absence of rivers.

This subspecies frequently enters the sea. Anderson (1913) reported it (as Lota maculosa) to be universal in fresh and brackish water of Alaska and Canada. Simpson (1843) found these fish coming in from the sea with the rising tide a short distance west of the Mackenzie mouth, and found them near the Coppermine River mouth. The present writer collected a burbot in brackish water at the mouth of the Coppermine (North-West Territories) in 1953. Preble (1908) commented that this fish is found in the Arctic Ocean. Despite its maritime tendencies, there is no record of its occurrence on the Canadian Archipelago, and along the Arctic coast of North America it is definitely known eastward only as far as the Coppermine system, although there are reliable reports for its occurrence in the Burnside system at Bathurst Inlet.

The range of Lota lota leptura in Canada has not been determined. The specimen caught at Coppermine, a fish 315 mm. in standard length, fits Lota lota leptura in the key given by Svetovidov (1948).

Wynne-Edwards (1952) remarked that contrary to the anticipation of Hubbs and Schultz (1941) the burbots of northwestern Canada are not intermediate between the Alaskan and eastern American forms; unfortunately he neglected to say what the Canadian fishes are.

Gadus morhua ogac Richardson

OGAC

RANGE: Coastal brackish and salt waters. West Greenland (absent from East Greenland) south to Miramichi Bay in the Gulf of St. Lawrence and west to Point Barrow, Alaska. In the White Sea (Europe) a similar fish is known as G. morhua maris-albi.

Previous Records: None. Specimens Seen: None.

Notes: Two recent studies of cods are by Jensen (1948) on Greenland fishes and Svetovidov (1948) on the cods of the world. The North Atlantic commercial cod is called Gadus m. morhua Linnaeus by Svetovidov, whereas Jensen considers the fish to be G. callarias Linnaeus. Svetovidov claims that the cod of the Baltic Sea is Gadus morhua callarias, that of the Atlantic G. m. morhua.

Jensen concluded that the ogac is a species distinct from G. callarias (= G. m. morhua) and should be called Gadus ogac. Svetovidov concluded that the ogac is very similar to Gadus morhua maris-albi of the White Sea which cannot always be distinguished from G. m. morhua, and therefore the ogac should be regarded as a subspecies of G. morhua. Svetovidov's viewpoint is followed here and, as is shown below, G. morhua maris-albi is probably a synonym of G. morhua ogac.

Mr. N. J. Wilimovsky (in. litt.) has collected Gadus morhua ogac in Arctic Alaska, between Point Barrow and Smith Bay. The first record for this fish west of Hudson Bay was reported by Ross (1835) as Gadus callarias from the west side of Boothia Peninsula; the mental barbel was described as

being large and the fish themselves as small (14 inches to a foot and a half in length). The ogac was listed from several western Arctic Canada localities by Pfaff (1937) and Walters (1953a) as *Gadus ogac*. Hildebrand (1948) indicated several sight records for *G. ogac* between the Mackenzie and Hudson Bay.

Vladykov (1933) was the first to comment on the marked similarity of the European Gadus callarias maris-albi Derjugin to the American Gadus ogac Richardson. In a key to the forms of Gadus morhua, Svetovidov (1948) separated G. m. maris-albi from G. m. ogac as follows: in G. m. maris-albi the anterior horns of the swim bladder are long, curving mediad proximally and laterad distally, while in G. m. ogac the horns are short and curve mediad. The horns of small G. m. maris-albi (169 mm.) are similar in form to those of G. m. ogac (260 mm.), according to Svetovidov's figures (1948, figs. 27k, o). The swim-bladder horns of two adult female G. m. ogac (345, 349 mm.) from Chaleur Bay, Gulf of St. Lawrence, were found to be of the same relative size and form as those of a 346-mm. G. m. maris-albi illustrated by Svetovidov (1948, fig. 27j); the horns are long, curving mediad proximally and laterad distally. It is evident therefore that Svetovidov's "key" distinction between the two cods is not valid; he did not compare similarsized fishes.

Svetovidov (1948, p. 179) considered that G. m. ogac and G. m. maris-albi, although morphologically and ecologically analogous, differ in eye size, snout and jaw length, and size and form of the swim-bladder horns. It has been shown that there is no difference in the swim-bladder horns. Body proportions of G. m. maris-albi and G. m. ogac are compared in table 13; there is no difference in eye size. The ogac appears to break up into local races, one of which may be the short-jawed G. m. maris-albi of the White Sea.

Jensen (1948) confirmed Williamson's (1908) discovery that the interiors of the ovaries of the ogac are black; according to Jensen the linings are lead-black to jet-black and the interiors are black-violet, partly violet, or bluish mottled with black chromatophores. However, the ovaries of two adults from Chaleur Bay, Gulf of St. Lawrence, had no dark pigment within the glands; the

			TAI	BLE	13			
COMPARISON	OF	Gadus	morhua	ogac	AND	Gadus	morhua	maris-albi

Character	G. m. ogac ^a	G. m. maris-albi ^a	Chaleur Bay ⁸	Miramichi Bay ^e	Bathurst Inlet ^d
Eye contained in head length	21.4-23.1%	16.2-20.2%	18.6-20.0%	13.3-16.1%	13.9-14.4%
Upper jaw in head length	44.0-46.6	40.2-44.5	44.3-44.7	45.0-45.1	

- ^a Data from Svetovidov (1948).
- ^b Three adults.
- ^c Calculated from data in McKenzie (1952); two adults.
- d Calculated from data in Johansen (MS); two adults.

linings are dusky, but the interiors are white. These fish are fully mature, measuring 345 and 349 mm. in standard length, they were collected in early February, 1953, and the ovaries almost fill the body cavity. The differences in ovarian pigmentation between Greenland and Gulf of St. Lawrence fishes indicates that G. m. ogac is broken up into local races. This is further indicated by the color pattern of the Chaleur Bay fishes; in addition to the blue-black spot at the base of the pectoral fin noted by Jensen in Greenland fishes, the Chaleur Bay specimens (three) have a blue-black spot on the opercle and a blue-black mediolateral band running almost the entire length of the body. Jensen made no mention of these additional marks in Greenland fishes.

Eleginus navaga navaga (Pallas)

SAFFRON COD

RANGE: Coastal salt and brackish waters, readily entering fresh water. In the Arctic Ocean only, from Kola Bay east to Ob' Lip (i.e., in White, Barents, and Kara seas) and from northeastern Siberia east to Bathurst Inlet in Canada, probably east to Simpson Strait; not known from the Laptev and East Siberian seas. Replaced by E. n. gracillis (Tilesius) in the Bering, Okhotsk, Japan, and Yellow seas of the North Pacific, which ranges south to Sitka, Alaska.

PREVIOUS RECORDS: Locally abundant along the coast (Walters, 1953a, Eleginus sp.).

SPECIMENS SEEN: U.S.N.M. Nos. 29927, 29946 (Kotzebue Sound), 152894 (Point Barrow).

Notes: The saffron cod is of widespread distribution in Arctic America. In Canada, Pfaff (1937) listed it from Simpson Strait or possibly eastern Coronation Gulf; Hildebrand (1948) and Wynne-Edwards (1952) recorded Eleginus navaga from the Mackenzie Delta: Walters (1953a) reported Eleginus sp. from Bathurst Inlet and other localities along the Alaskan and Canadian coasts, and suggested that Anderson's (1913) records of Microgadus proximus be referred to this genus. In a revision of Greenland cods, Jensen (1948) made no reference to Eleginus in Greenland waters, but Williamson (1908) illustrated a fish, definitely of this genus, as Gadus navaga from Greenland. Williamson probably had inaccurate data, because Eleginus has never since been reported from the Eastern Arctic.

The Arctic American cod is meristically intermediate between *E. navaga* of Europe and *E. gracilis* of the North Pacific. The two are distinguished as species by Svetovidov (1948), Berg (1949), and Berg et. al. (1949) in meristic characters. As Arctic American fishes "bridge" the differences between the two, the Pacific fish should be considered a subspecies of the Arctic fish. Meristic variation in *Eleginus navaga* is given in table 14.

Although the Arctic American fish is meristically intermediate between the two subspecies, it is considered to be closer to the European than to the Pacific fish for the following reasons:

1. The tips of the parapophyses are greatly enlarged in *E. n. navaga*, but in *E. n. gracilis* they are only slightly enlarged (Svetovidov,

TABLE 14
MERISTIC VARIATION IN Eleginus navaga

Character	Arcti Range	c Europe ^a Mean	Arctic A Range	merica ^b Mean	North I Range	Pacific ^e Mean
Vertebral count Gill raker count	55–60 23–28	57.5-57.8 25.6	58-60 19-23	59.0 21.3	57-64 14-23	<u> </u>
Vertebral number of first expanded parapophysis	6		7–10	7.9	9	19
Pairs of normal parapophyses be- fore first expansion	1		2-5	2.9	4	

^o From Svetovidov (1948) for *Eleginus navaga*; vertebral and gill raker counts taken from his footnote on the species.

^b Counts as follows: vertebrae, three Point Barrow and two Kotzebue Sound fish; gill rakers, three Point Barrow, two Kotzebue Sound, one Coppermine, and nine Bathurst Inlet fish; parapophyses, three Point Barrow, two Kotzebue Sound, and six Bathurst Inlet fish.

^c Vertebral and gill raker counts taken from Berg (1949) for *Eleginus gracilis*. Svetovidov mentioned some of these data in a footnote of his 1948 work, but his text figures are different; Berg corrected the discrepancy. The rest of the data are from Svetovidov (1948) for *E. gracilis*.

1948, figs. 34a-b, pls. 71, 6, and 72, 1). In Arctic American fishes the tips of the parapophyses are greatly enlarged (specimens examined from Point Barrow and Bathurst Inlet).

2. Svetovidov's figures (loc. cit.) indicate that in E. n. navaga the expanded parapophyses are directed almost laterad from the vertebrae, while in E. n. gracilis they are directed slightly ventrad and caudad. In Point Barrow and Bathurst Inlet fishes the parapophyses are directed almost as in E. n. navaga, hardly as in E. n. gracilis.

3. Svetovidov's figures (loc. cit.) indicate that in E. n. navaga the first haemal arch has a pair of angular expansions representing expanded parapophysis tips, while in E. n. gracilis these are hardly developed. In Bathurst Inlet and Point Barrow fishes the first haemal arch has a pair of angular expansions as in the European fish.

4. The coloration of living Bathurst Inlet adults was noted during the summer of 1953 to be as follows: eye with pupil black, iris brassy, lower outer border of iris red; body saffron yellow with a dark overcast dorsad; dorsal fins dusky with yellow tips; anal fins yellow; upper lobe of caudal fin dusky, lower lobe yellow, distal edge white; pectoral fins dusky yellow; pelvic fins yellow with white tips; lateral line pink; the adult body lacks spots, bands, or other markings.

The color of living Bathurst Inlet cods

(adults) compares favorably with that of European E. n. navaga as shown in a plate drawn from a living fish (Berg et al., 1949, atlas). In E. n. gracilis the iris is dark-colored, there is no yellow overcast to the body, the pelvic fins are dark-tipped, and the dorsal fins are white-edged; a colored figure is given by Berg et al. (1949, atlas). Turner (1886) described the color of fresh Tilesia gracilis (=E. n. gracilis) from Norton Sound, and Scofield (1899) described the coloration of E. navaga (=E. n. gracilis) from Port Clarence, both in Bering Sea.

Rendahl (1931a) named Gadus gracilis forma vegae from northeastern Siberia. Svetovidov (1948) considered this to be a synonym of the Pacific fish. Rendahl's was the only record of Eliginus in the Arctic outside the Barents, White, and Kara seas of which Svetovidov was aware, and it is understandable that he should consider the northeast Siberian fish identical to the Pacific form. It is possible that the cods of the southern Chukchi Sea may be E. n. gracilis rather than E. n. navaga, but the question cannot be settled at present.

GENERA ARCTOGADUS AND BOREOGADUS

The two genera are similar in the following characters: there are three dorsal and two anal fins; the caudal fin is notched; the tip of the lower jaw lies at the level, or in front, of the tip of the upper jaw; the maxillary ends beneath or beyond the posterior edge of the pupil; the lateral line is the same color as the body, it is wavy, and it is completely disrupted into short tubes; there are no lateral line pores on the head; the peritoneum is dark-colored.

The two genera differ in the following characters:

- 1. Arctogadus has an irregular double row of well-developed palatine teeth on each side; palatine teeth are absent in Boreogadus.
- 2. Arctogadus has elliptical overlapping scales, none of which bear bony tubercles; Boreogadus has circular, non-overlapping scales, many of which (all but the smallest individuals) have a bony tubercle and which give the skin the texture of coarse sand-paper.
- 3. Arctogadus has 32-34 gill rakers; Boreogadus has 37-47.
- 4. In intact specimens of Arctogadus the length of the mental barbel exceeds the diameter of the pupil and may almost equal the eye; in Boreogadus the barbel is always less than the pupil. The barbel character, however, is not so reliable, because the barbel is frequently destroyed in specimens of Arctogadus.
- 5. According to Popov (1933) young Arctogadus have no large chromatophores along the back, and there are about seven dark vertical bands on the body. In small Boreogadus the chromatophores are larger and more numerous along the back, and the body is not banded.

At present there is one recognized species of *Boreogadus* and three of *Arctogadus*. The present writer believes that the three species of *Arctogadus* may yet be shown to be one widely ranging species (in which case it should be called *A. glacialis*).

Boreogadus saida (Lepechin)

Polar Tomcod, Sayka

RANGE: Circumpolar in salt water, entering fresh waters. Throughout the Arctic and ranging southward to the Gulf of St. Lawrence in the Atlantic and the northern Bering Sea in the Pacific; absent from the Sea of Okhotsk.

Previous Records: All as B. saida: Cape Lisburne and latitude 66° 45′ N., longitude 166° 35′ W. (Bean, 1882b, 1883); Point

Barrow (Murdoch, 1885a, 1885b; Scofield, 1899; Fowler, 1905b); Collinson Point and Barter Island (Walters, 1953a).

Specimens Seen: U.S.N.M. Nos. 27570 (Cape Lisburne), 32426-32439, 33950, 111614, 111630, 111637, 111642, 152601-152607, 152891, 154061 (Point Barrow); specimens in National Museum of Canada from Collinson Point and Barter Island.

Notes: Svetovidov (1935) resurrected Gadus agilis Reinhardt as a species of Boreogadus distinct from B. saida. In 1948 the same author opined that B. agilis may be only a subspecies of B. saida, and, if so, then B. agilis must be called B. saida polaris (Sabine), which has priority over Reinhardt's name. Berg (1949) referred to the cod of Greenland and North America as B. saida polaris. Jensen (1948) examined Reinhardt's specimens of Gadus agilis (Greenland) and found them to be the same as Greenland B. saida. However, B. saida was named from the White Sea, not Greenland, and therefore Jensen did not dismiss the possibility that there is a Greenland-North American subspecies of B. saida.

The principal characteristic of B. saida polaris (B. agilis) is that the length of the base of the third dorsal fin is equal to or less than the length of the base of the second dorsal fin (Svetovidov, 1948). In order to determine whether Alaskan fishes were B. saida polaris or not, the fin bases of 10 Point Barrow adults (153-226 mm. in standard length) were measured. The third dorsal fin base is 3-5 mm. longer than the second in six fish, 1 mm. longer in three fish, and equal to the second in one fish. This compares favorably with a series of 10 cods from latitude 78° 15.5' N., longitude 12° 29.5' E. (Spitsbergen), ranging from 119 to 197 mm. in standard length. In the Spitsbergen cods, the third dorsal base is 7 mm. longer than the second in one fish, 3-5 mm. longer in seven fish, and 0.5-1 mm. longer in two fish. Alaskan fishes therefore do not differ from European individuals in any significant manner and belong to the subspecies B. s. saida.

Although Jensen (1948) concluded that Greenland fishes are all one species, he mentioned (p. 139) that the third dorsal base is shorter than, equal to, or sometimes longer than, the second. It therefore is still within

the realm of possibility that a valid Greenland subspecies of *Boreogadus saida* exists.

Thirty-seven Point Barrow fishes were found to have 38-47 (mean 42.2) gill rakers. This is in close agreement with 70 Barents Sea specimens reported in 1948 by Svetovidov (37-46, mean 41.4).

This cod is usually associated with ice floes but is known to range down to 320 meters in depth in the Barents Sea and 930 meters in Greenland.

Arctogadus borisovi Drjagin

SIBERIAN ARCTIC-COD

RANGE: Fresh (river mouths), brackish, and salt waters. Cape Sterlegov (Kara Sea, Siberia) east to Point Barrow, Alaska; known from the Arctic Ocean only, and north to latitude 77° 26′ 30″ N., longitude 138° 47′ E.

Previous Records: None.

SPECIMENS SEEN: None.

Notes: Mr. N. J. Wilimovsky (in litt.) has collected Arctogadus borisovi in the ice off Point Barrow. Because this species has been collected in fresh water at the mouths of the large Siberian rivers, it should be expected to occur near the mouths of larger rivers of Arctic America. The easternmost locality for A. borisovi is Point Barrow, the westernmost for A. pearyi is off the west shore of Melville Island. The two cods undoubtedly overlap in range. Arctogadus borisovi differs from A. pearyi in proportions (see table 15), but these differences may be due to the larger size of specimens of A. borisovi.

Arctogadus pearyi (Nichols and Maxwell) American Arctic-Cod

RANGE: Marine fish; salinity preferences not known, but probably the same as for A. borisovi. Described from Lincoln Bay, northern Greenland; southwest to Coronation Gulf (North-West Territories) and west to the west shore of Melville Island (North-West Territories). This or a similar species is probably found in Fury and Hecla Strait, North-West Territories, which would extend the southern range eastward to the longitude of Hudson Bay.

Notes: The first mention of what may be a species of Arctogadus was made by Sabine

(1821), who found three specimens of Merlangus? frozen in the ice at Winter Harbor, Melville Island. The fishes were about 15 inches long and in poor condition, but the lower jaw was noted to extend beyond the upper. Ross (1835) considered Sabine's specimens to be "Gadus callarias" (=G.morhua ogac) but overlooked the jaw characters. Sabine's material was either Boreogadus or Arctogadus. The large size and the large number of rays in the second dorsal and anal fins (19 and 20) reported by Sabine are indicative of Arctogadus (Boreogadus generally has fewer rays, though there is some overlap). Arctogadus pearvi has been reported from Melville Island (Walters, 1953a).

Nichols and Maxwell (1933) described Boreogadus pearyi from Lincoln Bay, Greenland; the types (A.M.N.H. No. 9699) were collected by R. E. Peary on September 1, 1905. A third specimen (A.M.N.H. No. 12131) was taken by Peary on the same day and in the same locality and may be designated a paratype.

Drjagin (1932) referred Gadus glacialis Peters (1874), described from Sabine Island on the east coast of Greenland, to Arctogadus, because palatine teeth are present. Schultz and Welander (1935) placed B. pearyi in Arctogadus but made no mention of A. glacialis. Svetovidov (1948) said that A. pearyi and A. glacialis are apparently identical but listed A. pearyi as a valid species. Jensen (1948) named a new genus and species of codfish from localities north and south of the type locality for Gadus glacialis. Because Jensen's description of the "new" species differs somewhat from A. pearyi, A. glacialis is for the moment regarded as a species distinct from A. pearyi.

Arctogadus borisovi, A. pearyi, and A. glacialis are compared in table 15.

Arctogadus glacialis (Peters)

GREENLAND ARCTIC-COD

RANGE: Waters of northeast Greenland and northern Baffin Bay.

Notes: Jensen (1948) described a new genus, *Phocaegadus*, from northeast and northwest Greenland, which is identical to *Arctogadus* Drjagin (1932). Both have palatine teeth, and in both, the scales are imbri-

	TABI	E	15	
COMPARISON OF	F FORMS	OF	Arctogadus	Drjagin

Character	A. borisovia	A. pearyi	A. glacialis ^c
1st D rays	11–12	11–12	10–13
2d D rays	18-21	16–19	15-20
3d Darays	21-24	19–23	18-24
1st Arays	20-24	18-22	17–20
2d A rays	20-23	18-21	18-21
Gill rakers	32-34	32–34	
Pyloric ceca		42	
Vertebrae	59		54-58
Head in standard length	3.7-4.1	3.3-3.5	3-3.3
Barbel	Exceeds pupil	Obsolete or exceeds pupil	Obsolete or rudimentary
Eye in head	3.9-5.3	3.3-4.2	3-3.3
Interorbital in head	4.8-5.7	6.3-8.7	5–6
Pelvic fins	Not to anus	To anal origin in some but sex not determi- nable	To anal origin in males but not in females
Maximum size	Over 550 mm.	225 mm.	310 mm.

From Svetovidov (1948).

From Jensen (1948) for Phocaegadus megalops.

cate, the lower jaw projects, and the lateral line is completely disrupted into short tubes. Jensen made no mention of Drjagin's genus.

Arctogadus megalops (Jensen, 1948) is identical to A. glacialis (Peters); both occur in northeast Greenland waters. Jensen considered Peters' fish a synonym of Boreogadus saida, even though Peters mentioned that his fish has palatine teeth. Specimens of A. glacialis have not been available for comparison with A. pearyi, but the two will probably prove to be identical, and in turn these may prove to be identical to A. borisovi, in which case Arctogadus glacialis (Peters) will have priority over all other names for the species.

The three forms of Arctogadus are compared in table 15.

GASTEROSTEIDAE

STICKLEBACKS

Gasterosteus aculeatus does not range north of Bering Strait in the Pacific; it is not circumpolar in distribution. Berg (1949) distinguishes six species and subspecies of Pungitius in Eurasia; only one form enters the Arctic.

Pungitius pungitius (Linnaeus) STICKLEBACK

RANGE: Circumpolar in cool fresh waters, often entering the sea in Europe, Asia, and North America; typical of lowlands in our area (not known from mountain headwaters). In virtually all Arctic drainages of Eurasia and North America (even east of Hudson Bay) but absent from Greenland and Iceland. South in the Pacific to Kamchatka (where it intergrades with P. p. sinensis) in the west and the Alaska Peninsula in the east: south in the Atlantic to New Jersey in the west and central Europe in the east. Northern limit not accurately known; North American records include Cumberland Gulf (Bean, 1879a), Fury and Hecla Strait (Pfaff, 1937), and Point Barrow (present report); probably on most southern islands of the Canadian Archipelago.

PREVIOUS RECORDS: Kotzebue Sound and near Icy Cape (Bean, 1882b, 1883, Gasterosteus pungitius brachypoda), rivers near Point Barrow (Murdoch, 1885b, Gasterosteus pungitius brachypoda), ? Barter Island (Walters, 1953a, Pungitius pungitius), lake near Point

^b Three types (A.M.N.H. Nos. 9699, 12131); two Coronation Gulf fish; one Borden Island fish (latter examined by Mr. W. T. Leapley).

Barrow (Wohlschlag, 1953, Pungitius pungitius).

SPECIMENS SEEN: U.S.N.M. Nos. 27587 (Icy Cape); 27590 (Kotzebue Sound), 33951 (Meade River), 111646–111647 (Colville River), 111650, 111667, 111656 (Point Barrow), 111651, 111668, 111703–111704, 111708 (Alaktak River, Chipp system), 111662, 111664 (Colville River), 152898–152899 (about 100 miles southeast of Point Barrow-Ikpikpuk system); specimens in National Museum of Canada from Meade River, ?Barter Island, and latitude 69°40′ N., longitude 141° W.

Notes: Breeding fishes and, later, their young were collected in a tundra stream near Point Barrow during the summer and fall of 1948. The stream was visited on several occasions during 1949, but not a single fish was observed. Evidently the 1948 fishes entered from the Chukchi Sea to spawn and, at the end of the season, re-entered the ocean. Point Barrow adults are the largest individuals of this species examined from Arctic America; the smallest measured 45 mm. in standard length, the largest 85 mm. (female), while the average standard length for 18 individuals is 64.5 mm. Adults from other localities average about 45 mm. in standard length. The Point Barrow fishes also have the highest modal and mean dorsal spine count yet given for Arctic American fishes, with the possible exception of the small Baffin Island series.

It was observed that the fishes in the stream were very lively when water temperature was high in August (10° C.), but in September, when ice was forming almost nightly and daytime water temperature had dropped to 3.2° C., the fishes (including adults) were sluggish and easy to scoop up by hand. On September 2, three young were placed in each of six vials of stream water and the vials were treated as follows:

- a. 1 vial was placed on the laboratory porch, where air temperature ranged from 10° to 15° C., to serve as a control.
- b. 3 vials were placed outside the laboratory, where air temperature ranged from 1.5° to 5° C.; after 8 hours, two vials were placed in the refrigerator (-11° C.).

 c. 2 vials were placed directly in the refrigerator (-11° C.).

After 18 hours, one of the vials of group b that had been placed in the refrigerator and one vial of group c were brought inside and thawed slowly over a period of four hours. The remaining vial of group b that had been placed in the refrigerator and the other vial in group c were thawed over a period of two hours.

The results are summarized below:

	Vial kept at 10° to 15° C.	All survived
2.	Vial kept at 1.5° to 5° C.	All survived
3.	Vial kept at 1.5° to 5° C. for 8	
	hours, then frozen to -11° C.,	
	then thawed in 2 hours	All died
4.	Same as (3), but thawed in 4	
	hours	All died
5.	Vial frozen to -11° C. im-	
	mediately, then thawed in 2	
	hours	All died
6.	Same as (5), but thawed in 4	
	hours	All died

The results indicate that *Pungitius* cannot survive being frozen, even when individuals were tested of which the habitat was being subjected to freezing temperature almost nightly.

Table 16 indicates variation in number of dorsal spines in some American sticklebacks. Localities represented by only one or a few specimens are not included. An inspection of the data reveals a tendency, in proceeding from colder to warmer climates, for lower spine counts to appear, higher spine counts to disappear, and for the mode and mean to shift downward. However, this is not accomplished by a uniform shifting of the curve, because the larger series (Bernard Harbour, Meade River, Great Slave Lake) in particular show a marked skewness in the spine counts. It appears as though some factor in the environment were selectively eliminating those individuals with spine counts not adaptive to the locality. Thus at Great Slave Lake three fish had six or seven spines, but none of the 256 had more than 10 spines, while at Meade River and Bernard Harbour (combined) out of 510 individuals none was found with fewer than eight spines, and 45 had 11 or 12 spines.

TABLE 16	
VARIATION IN NUMBER OF DORSAL SPINES IN Pungitius pungitius pun	gitius

Locality	VI	VII	VIII	IX	X	XI	XII	Sample	Mean	Mode
Mt. Ooscooadlin, Baffin Islanda				2	2	4		8	10.3	11
Point Barrow, Alaska				4	8	8	1	21	10.3	10.5
Bathurst Inlet, North-West										
Territories	_			2	8	3		13	10.1	10
Hudson Bay ^b				5	23	3		31	9.9	10
Oumalik, Alaska	_			4	12	1		17	9.8	10
Umiat, Alaska			_	5	8	2		15	9.8	10
Bernard Harbour, North-West										
Territories ^c			4	97	207	29	1	338	9.8	10
Meade River, Alaska			5	50	102	15		172	9.7	10
Half Moon Three, Alaska			2	17	24	5	_	4 8	9.7	10
Lake Athabaska, Albertad			1	10	5	_		16	9.3	9
Lake Nipigon, Ontariob			4	10	5	1		20	9.2	9
Great Slave Lake, North-West										
Territories	1	2	24	173	56	_	_	256	9.1	9

- ^a From Bean (1879a) for Gasterosteus pungitius brachypoda.
- ^b From Vladykov (1933).
- From Walters (1953a).
- d From Kendall (1924).

PERCOPSIDAE

TROUTPERCHES

Percopsis omiscomaycus (Walbaum)

TROUTPERCH

Range: Fresh waters of North America. Quebec south to the Potomac River on the Atlantic coast and south to Kansas, Missouri, and Kentucky in the Mississippi Valley. Northwestward to Great Bear Lake, Fort Good Hope (Mackenzie River), and the Porcupine River at Old Crow, Yukon Territory (Yukon system).

Notes: The troutperch has not been found in the Arctic, but its range indicates that it occurs in the Mackenzie northward to the Delta, as it is present in Great Bear Lake and in the Porcupine River (evidently it entered the Yukon system here as a result of headwaters capture). Wynne-Edwards (1952) gave the Porcupine River and other records for this highly interesting fish, and suggested the headwaters capture theory (involving the Mackenzie near its mouth).

PERCIDAE

PERCHES

Perca fluviatilis Linnaeus

YELLOW PERCH, OKUN

RANGE: Fresh waters; within our area found in the Kolyma basin and other rivers to the west (from Berg, 1949).

Notes: According to the Russian workers the American perch is a subspecies of the Eurasian perch; the fishes of the Kolyma River are intermediate between the two (Berg, 1949, p. 1035). If this be true, the yellow perch offers an interesting example of discontinuous distribution in fresh-water fishes, for there are no records between the Kolyma River in Siberia and Lesser Slave Lake in Alberta.

Acerina cernua (Linnaeus)

YERSCH

RANGE: Within our area in the Kolyma and other Arctic drainages to the west; in lakes, slow rivers, river mouths, bays, and coastal salt waters (Berg, 1949).

Stizostedion vitreum (Mitchill) WALLEYED PIKE

RANGE: Fresh waters; within the Arctic only in the Mackenzie River, where it ranges north to the Delta (Wynne-Edwards, 1952).

Notes: The walleyed pike just manages to enter the Arctic. It is of widespread distribution in North America southward and eastward from the Mackenzie system.

ANARHICHADIDAE

CATFISHES OR WOLFFISHES

Fishes of this family are often stated to lack a lateral line (e.g., Jordan and Evermann, 1896–1900; Jordan, 1929; Clemens and Wilby, 1946), although there are numerous figures indicating lateral lines to be present. For example, Turner (1886) indicated two lateral lines in *Anarhichas lepturus* (=A. orientalis)—an incomplete dorsolateral structure and a complete mediolateral structure.

The figure of A. lupus in Berg et alii (1949, atlas) indicates a single complete medio-lateral structure. Small- to medium-sized (ca. 600 mm.) individuals examined by the present writer show three lateral lines as follows: the uppermost is dorsal in position and ends at the origin of the dorsal fin; the next is dorsolaterally located and ends at the vertical of the origin of the anal fin; the lowermost is mediolateral and complete—it gradually descends to the midline at the level of the anal origin and courses straight back to the end of the body.

The figure of A. minor given by Berg et alii (1949, atlas) shows no lateral line. Specimens larger than about 300 mm. that the present writer examined fail to show any lateral line, but smaller individuals have the same lateral line pattern as small A. lupus.

The figure of A. latifrons (=A. denticulatus) given by Berg et alii (1949, atlas) shows two incomplete lateral lines, one dorsolateral and the other mediolateral. A figure of A. latifrons, reproduced by Gill (1911), indicates three incomplete lateral lines, one dorsolateral, one medial lateral, and one ventral. A large individual of A. denticulatus from Prince Patrick Island examined by Walters (1953b) had no lateral line, which led this author to suggest that lateral lines shown in figures of

the species may be artifacts. Another large individual of A. denticulatus, of the same form as the Prince Patrick Island fish but from Spitsbergen, has no lateral lines.

It is possible that the lateral line system becomes obscured in large individuals of *Anarhichas*, though it is well developed in smaller individuals. The only other species of this family, *Anarrhichthys ocellatus*, is said by Clemens and Wilby (1946) to lack a lateral line.

Anarhichas denticulatus Krøyer Blue Catfish

RANGE: Deep salt waters. Prince Patrick Island east to Novaya Zemlya. Absent from the North Pacific. South to the Newfoundland Banks (Banquereau) in the Atlantic.

Notes: Unknown from Alaskan waters. In describing the Prince Patrick Island specimen, Walters (1953b) indicated that two forms are currently assigned to this species. The nomenclature of the North Atlantic catfishes has recently been reviewed by Jensen (1948), who questionably included Lycichthys fortidens Gill as a synonym of A. denticulatus. The Prince Patrick Island fish was considered by Walters closely to resemble Goode and Bean's (1895) Banquereau specimen of A. latifrons. Goode and Bean's Banquereau specimen was selected by Gill (1911) as the type of Lycichthys fortidens. It is possible that Gill's is a good species, but until sufficient material is available for study Jensen's nomenclature is followed.

STICHAEIDAE

SNAKEBLENNIES

Eumesogrammus praecisus (Krøyer)

FOUR-LINED SNAKEBLENNY

RANGE: Coastal salt waters. West side of Victoria Island, North-West Territories, east to the west coast of Greenland (north to latitude 73° N.), then south to Belle Isle Strait, between Labrador and Newfoundland; also in colder portions of the Sea of Okhotsk and western Bering Sea.

Notes: Unknown from the waters of Arctic Alaska. Walters (1953a) listed this species from Victoria Island, the westernmost North American record. The information on the Greenland range is from Jensen (1944a),

that on Labrador from Backus (1951).

It has been suggested (most recently by Walters, 1953a) that the absence of this species from the Arctic coasts of Siberia and Alaska may be due to the shallowness of the seas. This suggestion is now considered unlikely. In the southern part of its range (Labrador) the four-lined snakeblenny is most often caught in 10–18 fathoms of water (Backus, 1951, 1953), although it has been caught as deep as 400 meters in Greenland (Jensen, 1944a). Depths of up to 60 meters are frequently found in the seas of Siberia and Alaska.

Stichaeus punctatus (Fabricius)

SPOTTED SNAKEBLENNY

RANGE: Coastal salt waters. West coast of Greenland from latitude 73° N. south to Belle Isle Strait (Labrador-Newfoundland) and west to Hudson Bay; unknown between Hudson Bay and Smith Bay; Smith Bay (70 miles southeast of Point Barrow) westward into the Chukchi Sea and southward into the Bering Sea and Sea of Okhotsk. Not known from Arctic Eurasia.

Previous Records: Cape Lisburne (Bean, 1882a, 1882b, Stichaeus? rothrocki; Bean, 1883, Notogrammus rothrocki).

Specimens Seen: U.S.N.M. No. 112750 (Cape Lisburne; *Notogrammus rothrocki* paratypes); A.M.N.H. No. 17859 (mouth of Kotzebue Sound). Mr. N. J. Wilimovsky (*in litt.*) has taken the species at Smith Bay.

Notes: Taranetz (1935) separated Okhotsk fishes as S. punctatus pulcherrimus, because they have 60–73 lateral line pores, whereas Bering Sea fishes have "72–86" pores. Jensen (1944a) gave the pore count for six Greenland fishes as 56–72. It is evident that the Okhotsk Sea "subspecies" is not different from the typical (Greenland) form, and therefore the Okhotsk Sea "subspecies" cannot be maintained. Taranetz must have had unusual Bering Sea material of Stichaeus punctatus.

LUMPENIDAE

EELBLENNIES

Lumpenus gracilis was recorded from Point Belcher, Alaska, by Bean (1882b, 1883) as L. anguillaris. The specimen (U.S.N.M. No. 27554) was very small and

has since been destroyed, according to United States National Museum records. This is the only record for *L. gracilis* in Arctic waters. Recent collecting in the Chukchi Sea has yielded two species of *Lumpenus*, both well known from Arctic waters, but has failed to produce *L. gracilis*. Bean's specimen was probably misidentified.

Lumpenus fabricii (Cuvier and Valenciennes)

SLENDER EELBLENNY

RANGE: Coastal salt waters. Often considered circumpolar in distribution but not known from Spitsbergen or the Kara, Laptev, East Siberian, and Beaufort seas, the east coast of Greenland, or Labrador. In our area known only from the Chukchi Sea. Well known from the Pacific, where it occurs in western Bering Sea and the Sea of Okhotsk.

PREVIOUS RECORDS: None.

Specimens Seen: U.S.N.M. Nos. 111638, 152596-152600 (Point Barrow); A.M.N.H. Nos. 8985, 17352, 17862 (Kotzebue Sound).

Notes: Twenty-four Arctic Alaskan L. fabricii have been examined. These agree with characterizations given by Rass (1936), Taranetz (1937), and Jensen (1944a). The material ranges from 39 to 134 mm. in standard length, permitting observations regarding morphological changes with increase in body size.

The following characters were observed to be constant for the entire size range of 39 to 134 mm.: snout length exceeds eye diameter; vomerine and palatine teeth are absent; the maxillary ends beneath the anterior edge of the pupil; the posterior anal rays are not notably longer than the rays in the rest of the fin and do not reach farther back than the base of the caudal fin; and a row of large dark spots is found along the middle of the body (on the lateral line).

Meristic variation: dorsal spines 61-65 (mean 63.1), nine specimens; anal 1, 37-42 (mean 1, 40.0), seven specimens; pectoral 15-16 (mean 15.4), seven specimens; gill rakers 13-15 (mean 13.8), five specimens.

In standard length: body depth is contained 10-12 times, head length 4.5-5.0 times for fishes 39-58 mm. in standard length; body depth is contained 11-13 times, head length 5.1-6.1 times for fishes 89-134 mm. in standard length.

Scales are present in fishes 42 mm. or more long.

The snout profile is deeply concave in specimens 39-45 mm. long, shallowly concave in those 46-48 mm. long, convex in those 50-134 mm. long.

The dorsal and anal fins are adnate to caudal in most specimens, free from caudal in one 129-mm. fish. The dorsal is more strongly joined to the caudal than is the anal.

COLOR PATTERN

Postlarvae: In specimens 39-50 mm. in standard length a series of pinhead-sized black spots (9 or 10) is present on either side between the pectoral fin base and the anus. These are absent in larger fishes. The postlarvae show indications of the adult color pattern in having a row of large dark spots along the lateral line.

Larger specimens: Each dorsal spine has a dark spot at its tip and another dark spot along the middle of its length; the dorsum has a row of elongate dark spots along the base of the dorsal fin, but these do not form a dark line as in *L. gracilis*. The head and dorsum are marbled. A row of large dark spots along the lateral line alternates with a row of smaller spots below the lateral line; the spots in the two rows coalesce with one another caudad. The anal fin is without dark pigment.

Lumpenus medius Reinhardt

STOUT EELBLENNY

RANGE: Coastal salt water. Not likely to be circumpolar in distribution, being unknown from the East Siberian and Beaufort seas and Hudson and Ungava bays. South to the western Bering Sea and Sea of Okhotsk in the Pacific, and to latitude 52° 15′ N. (Labrador) in the Atlantic.

Previous Records: None. Specimens Seen: None.

Notes: Mr. N. J. Wilimovsky (in litt.) has collected this species in the waters of Arctic Alaska.

ZOARCIDAE

EELPOUTS

SUBFAMILY GYMNELINI

Gymnelis viridis (Fabricius)

RANGE: Marine. Circumpolar; south in the

Atlantic to Nova Scotia, in the Pacific to the Aleutian Islands and the Sea of Okhotsk.

PREVIOUS RECORDS: Point Barrow (Murdoch, 1885b).

Specimens Seen: U.S.N.M. Nos. 33948, 152613 (Point Barrow); A.M.N.H. No. 18780 (Bering Strait); specimen in National Museum of Canada from Kotzebue Sound.

Notes: Several species, related to Gymnelis viridis, occur in the North Pacific. Walters (1953a) questionably listed G. viridis from western Arctic Canada because of the possible occurrence of other closely related eelpouts, and the specimens were in very poor condition. To date, the only other eelpout similar to G. viridis known from the Arctic is Ophidium stigma, listed below; this is known only from one specimen which was subsequently lost.

Ophidium stigma Lay and Bennett

RANGE: Marine. Described from Kotzebue Sound, probably identical to one of the species of the Sea of Okhotsk and Bering Sea.

PREVIOUS RECORDS: Kotzebue Sound (Lay and Bennett, 1839, Ophidium stigma).

SPECIMENS SEEN: None.

Notes: Current authors consider Ophidium stigma a synonym of Gymnelis viridis. Lay and Bennett (1839) described this fish as having scales, a character that removes it from Gymnelis as the genus is understood at the present time. Lay and Bennett's fish seems to have been a species of Gymnelopsis.

SUBFAMILY LYCODINI

Lycodes jugoricus Knipowitsch

JUGORSKY SHAR EELPOUT

RANGE: Estuarine zone. In the Arctic Ocean only, from the White Sea (Europe) east to the Chukchi Sea, and possibly in Arctic Canada.

Previous Records: None. Specimens Seen: None.

Notes: Recently Andriashev (1939b) compared adult *L. jugoricus* with *L. polaris* (here called *L. turneri* for reasons given below). Andriashev listed several morphological differences, but only three are considered here.

According to Andriashev adult *L. jugoricus* have a yellow ground color, with eight or nine blackish brown bands; the bands are narrower than the yellow interspaces and are broader dorsad. A color pattern similar to

this is shown by the small stages of *L. turneri*, but is replaced by the adult color pattern (chocolate-brown ground color with 10 to 12 narrow cream-colored bands) at a length of 100–130 mm. in Point Barrow individuals.

Lycodes jugoricus has 99 to 103 dorsal rays and 78 to 83 anal rays; L. turneri has 87 to 95 dorsal rays and 68 to 76 anal rays (counts include one-half of the caudal fin each).

Mr. N. J. Wilimovsky (in litt.) has collected what appears to be L. jugoricus in the Chukchi Sea. It is possible that Sabine (1821) had this species when he described Blennius polaris from Arctic Canada. Sabine's specimen was 7 inches long, scaleless, and had the following color pattern: yellow with 11 saddle-shaped brown markings across the back; dorsal and anal fin counts were not given. The large size of Sabine's specimen, which was still in the "juvenile" phase of coloration, is indicative of Lycodes jugoricus rather than L. turneri or L. mucosus.

Lycodes mucosus Richardson RICHARDSON'S EELPOUT

RANGE: Marine. Known only from the eastern American Arctic.

Notes: This species is included here because of its similarity to L. turneri and L. jugoricus. Vladykov and Tremblay (1936) regarded L. mucosus as differing from L. turneri in color pattern. Some Point Barrow L. turneri have the "mucosus" pattern, and thus color pattern differences cannot be accepted as diagnostic.

Richardson (1855, pl. 26) illustrated the dentition of *L. mucosus*, and Bean (1879a) said that a second specimen examined by him had the same dentition. In *L. mucosus* the last premaxillary tooth lies almost as far back as the last palatine tooth, and the length of the premaxillary tooth band almost equals the length of the mandibular tooth band; in *L. turneri* (15 Point Barrow fish, 75 to 495 mm., both sexes) the last premaxillary tooth lies as far back as the last vomerine or first palatine tooth, and the length of the band of premaxillary teeth is about half of the length of the band of mandibular teeth.

Richardson's species was listed from Etah, northwest Greenland, by Nichols (1918) as *Lycodalepis mucosus*. The specimen (A.M.N.H. No. 17448) is hardly recognizable

now, but its dentition is of the Lycodes turneri pattern.

On the basis of color pattern, Jensen (1952a) identified several fishes from Thule, northwest Greenland, and one from northern Ellesmere Island as *L. mucosus*. Dentition was not mentioned.

Lycodes turneri Bean Polar Eelpout

RANGE: Marine. Kara Sea east to West Greenland, south to the Gulf of St. Lawrence in the Atlantic and northern Bering Sea in the Pacific.

Previous Records: Point Barrow (Murdoch, 1885b, as L. turneri and L. coccineus; Scofield, 1899, as Lycodalepis turneri).

SPECIMENS SEEN: U.S.N.M. Nos. 33922-33926, 111621, 152592-152595, 152889, 152893 (Point Barrow).

Notes: This is called Lycodes (Lycodalepis) polaris by some authors. Sabine (1821) named Blennius polaris from North Georgia (Canada); the description is incomplete, no figure was given, and Richardson (1855) said the type specimen could not be found. Vladykov and Tremblay (1936) considered Blennius polaris a nomen nudum. Of three Arctic species of naked Lycodes, Sabine's description best fits L. jugoricus (which see), but until fishes fitting the original description are collected at or near the type locality, Sabine's name had best not be used.

Lycodes turneri Bean (1879b) was discussed at length by Vladykov and Tremblay (1936). In the main their conclusions are accepted, but the division into the subspecies L. t. turneri, L. t. agnostus, and L. t. atlanticus is not followed. Their eastern American form, L. turneri atlanticus, was based chiefly on differences in fin ray counts between Siberian, Alaskan, and eastern American fishes. However, they did not include half of the caudal fin in counting dorsal and anal rays, a procedure followed by some workers. In table 17 the fin ray counts of the three forms are compared. There are no discernible differences.

According to many workers this species is scaleless. Among the Point Barrow specimens examined, numerous scales are present in a male more than 465 mm. long (U.S.N.M. No. 33926), and scales are present in varying numbers in individuals as small as 130 mm.

TABLE 17
Fin Ray Counts of Lycodes turneri

	Siberia ^a	Point Barrow ^b	Labrador	Gulf of Saint Lawrence ^d
Dorsal	90–93	89–95	87–92	87–94
Anal	70–75	68-75	69-76	72-75
Pectoral	16–17	16–18	16-19	16-18

^a Twenty-seven specimens of *L. agnostus* from the Kara and Laptev seas; data from Jensen (1904). Dorsal and anal counts each include half of the caudal.

^b Ten specimens of L. turneri. Dorsal and anal counts each include half of the caudal.

^c Nine specimens of *L. turneri atlanticus*; data from Backus (1953). The original dorsal and anal counts do not include half of the caudal fin, and therefore five rays have been added to the upper and lower limits of each because caudal rays average 10 in *Lycodes*.

d Ten specimens of *L. turneri atlanticus*, including two of the morpha squamosa; data from Vladykov and Tremblay (1936). The original dorsal and anal counts do not include half of the caudal fin, and therefore five rays have been added to the upper and lower limits of each because caudal rays average 10 in *Lycodes*. There is an evident typographical error in Vladykov and Tremblay's paper; in the text they give the range in dorsal count as 82–89, whereas on table 14 the range is given as 89–92. The text range has been chosen for the present table, because on the page following table 14 the authors give the count for morpha squamosa as 83 dorsal rays.

(U.S.N.M. No. 152592); some may have as few as a half dozen scales. In the southern portions of the range, numerous scales may develop at smaller body lengths. In the Gulf of St. Lawrence the scaled form is called morpha squamosa and in the Bering Strait it was originally named as a distinct species, Lycodes coccineus Bean.

In Point Barrow fishes 75 mm. or more long, there are three lateral lines on each side; none were found in a 50-mm. juvenile. The uppermost line extends from the occiput to the origin of the dorsal fin. The next extends from the gill opening, rising to a dorso-lateral position, and consists of a series of widely separated pores. The lowermost extends from the gill opening, descending to the midline and then coursing straight back; it does not descend below the midline. The lateral lines are almost impossible to trace very far back in fishes over 250 mm. long, unless the material has been well preserved.

Lycodes knipowitschi Popov Knipowitsch's Eelpout

RANGE: Marine. Okhotsk, Bering, and southern Chukchi seas.

Previous Records: None. Specimens Seen: None.

Notes: This was stated by Andriashev (1937b, 1939a) to be closely related to Lycodes coccineus Bean (one of the synonyms

of *L. turneri*). He reported it from the Siberian portion of the Chukchi Sea, at latitude 66° 45′ N., longitude 169° 35′ W. (1937b).

It is possible that *L. knipowitschi* is the scaled Okhotsk representative of *L. turneri* and that intermediate individuals occur in the Bering and Chukchi seas.

Lycodes raridens Taranetz and Andriashev BIG-TOOTHED EELPOUT

RANGE: Marine. Okhotsk, Bering, and southern Chukchi seas.

Previous Records: Cape Thompson (Lycodes raridens, Andriashev, 1937b).

SPECIMENS SEEN: None.

Notes: It is possible that U.S.N.M. No. 33926, a Point Barrow male over 465 mm. long (snout distorted, preventing more accurate measurement), may be this species, although it agrees well with *Lycodes turneri*. The trunk, tail, and vertical fins are liberally scaled.

Lycodes palearis arcticus Taranetz and Andriashev

ARCTIC WATTLED EELPOUT

RANGE: Marine. Chukchi Sea and northern Bering Sea. The species *L. palearis* occurs in the Chukchi, Bering, Okhotsk, and northern Japan seas, and along the Pacific coast of North America south to Puget Sound.

Previous Records: None. Specimens Seen: None.

Notes: Mr. N. J. Wilimovsky (in litt.) has collected what appears to be this species in Arctic Alaska. Soviet ichthyologists recognize four subspecies of the wattled eelpout (for reviews, see Andriashev, 1937b, and Shmidt, 1950).

Lycodes pallidus Collett

PALE EELPOUT

RANGE: Marine. Circumpolar; in the Atlantic, south to Labrador; unknown from the Pacific.

Previous Records: None.

SPECIMENS SEEN: None.

Notes: Mr. N. J. Wilimovsky (in litt.) has identified this species in his collections from Arctic Alaska. Previous records from this sector of the Arctic are: Laptev Sea (Popov, 1933; Andriashev, 1939b; Esipov, 1940), East Siberian Sea (Popov, 1933), Beaufort Sea (Walters, 1953b). Andriashev (1939b) considered L. attenuatus Knipowitsch a synonym of L. pallidus.

Lycodes soldatovi Taranetz and Andriashev BLACK EELPOUT

RANGE: Marine. Positively known only from the Sea of Okhotsk, in deep waters.

Notes: When this species was named, it was noted that all specimens for which locality data were reliable come from the Sea of Okhotsk (Taranetz and Andriashev, 1935). Andriashev (1937b, 1939a) in discussing the fishes of the Bering and Chukchi seas mentioned *L. soldatovi* as possibly being a member of the ichthyofauna, although reliable locality records are lacking. Therefore Shmidt (1950, p. 323) should not have listed this species as entering the Chukchi Sea.

AMMODYTIDAE

SAND LANCES

Most workers have overlooked Lindberg's (1937) study of the North Pacific Ammodytes hexapterus Pallas (1826); Pallas' species is identical to a sand lance of the North Atlantic, A. marinus Raitt. In a recent account by Rass (in Berg et al., 1949) an attempt to treat the entire group has been made. Rass' system is followed here.

Ammodytes hexapterus Pallas

SAND LANCE

Range: Marine. Baltic, White, Barents, East Siberian, Chukchi, Bering, Okhotsk, and northern Japan seas; also in Beaufort Sea, West Greenland, and possibly in Hudson Bay and Labrador.

Previous Records: Point Belcher (Bean, 1882b, 1883, A. americanus; Evermann and Goldsborough, 1907, A. alascanus).

Specimens Seen: U.S.N.M. Nos. 27556 (Point Belcher), 111634 (Point Barrow); A.M.N.H. No. 18779 (Bering Strait).

Notes: Rass considered the Arctic sand lance to be A. hexapterus. Thus the identification of A. tobianus given by Walters (1953a) for Langton Bay and Bernard Harbour, North-West Territories, should be changed.

Rass recognized two subspecies of A. hexapterus, but not enough material is available to permit a determination of the affinities in Arctic American individuals. The species appears to be circumpolar in distribution.

Sand lances occur in Hudson Bay (Vladykov, 1933, A. dubius hudsonius; Pfaff, 1937, A. lancea). The two species that would be expected there are A. hexapterus (=A.marinus) and A. dubius. These cannot be distinguished by fin count, as dorsal count is 60-68 in A. dubius (Jensen, 1944b) and 57-65 in A. hexapterus (Rass), and anal count is 30-36 in A. dubius and 28-36 in A. hexapterus. The two differ in vertebral count, A. dubius having 73-80 (Jensen, 1944b) and A. hexapterus 66-74 (Rass; Jensen, 1944b). The dorsal and anal counts for Hudson Bay fishes are 57-65 and 28-37, respectively. Thus Hudson Bay sand lances may be either or both species; information on vertebral counts is lacking.

Backus (1953) listed A. dubius from Labrador, with 71-75 vertebrae, mean 73.2 (13 specimens). Some or all of these may have been A. hexapterus.

COTTIDAE

SCULPINS

Wishing not to become involved in a discussion concerning the limits of this family, the present writer follows the classification used by Shmidt (1950) instead of Berg

(1940). The genera and species are listed alphabetically rather than phylogenetically.

Artediellus scaber Knipowitsch

ROUGH HOOK-EARED SCULPIN

RANGE: Coastal salt and brackish waters. Kara Sea east to Chukchi Sea in the Arctic, thence south into northern Bering Sea.

Previous Records: Between Cape Sabine and Icy Cape (Walters, 1953a).

Specimens Seen: A.M.N.H. Nos. 8977 (15 miles north of the Diomede Islands), 17860 (Kotzebue Sound).

Notes: This is a euryhaline species, according to Andriashev (1939b).

Artediellus uncinatus (Reinhardt)

SMOOTH HOOK-EARED SCULPIN

RANGE: Possibly circumpolar, in strictly salt waters. (See below for comments.)

Previous Records: None.

Specimens Seen: U.S.N.M. No. 152901 (Point Barrow).

Notes: The most recent revision of North Atlantic Artediellus was performed by Jensen (1952b), but his treatment of the genus cannot be relied upon for waters beyond Greenland. For example, A. uncinatus is said to be known only from Greenland waters, and A. atlanticus (=A. europaeus) from Greenland east to Arctic Europe and south to Labrador and Cape God in North America. Nybelin (1941) considered A. europaeus and A. uncinatus conspecific. Backus (1953) identified all Labrador individuals as A. uncinatus, and his data fit this species better than they do A. atlanticus, if Jensen's diagnoses are followed.

Two small individuals, collected by the Canadian Arctic Expedition in the North-West Territories (Dolphin and Union Strait), were dubiously listed by Walters (1953a) as A. dydymovi. The specimens were not seen, the identification being based on F. Johansen's unpublished account. According to Johansen the fishes had 13 to 15 rays in the second dorsal fin (12 and 14, if the method followed in this work is used), which is the range for A. atlanticus as given by Jensen. Johansen did not count lateral line pores, and the specimens were too small to show secondary sexual characters (35 and 40 mm. in standard length). Therefore, the North-

West Territories specimens may have been A. atlanticus, if Jensen's scheme is followed.

The Point Barrow fish, a female 35 mm. in standard length, has 11 rays in the soft dorsal fin (12, in Jensen's method) and 23 lateral line pores. Thus it fits neither A. uncinatus nor A. atlanticus of Jensen. Instead the fish seems to fit accounts of A. dydymovi in Soldatov and Lindberg (1930) and Taranetz (1937).

Shmidt (1950) considered A. uncinatus, A. europaeus (A. atlanticus of Jensen), and A. dydymovi to be closely related. The problem warrants further study, and for the present the present writer prefers referring to the Arctic Ocean fishes as A. uncinatus.

Cottus cognatus Richardson

SLIMY MUDDLER

RANGE: In fresh and brackish waters. Ungava Bay and Labrador south to New York and West Virginia, west to Minnesota and Iowa, then northward to the Bering Sea and Arctic Ocean drainages of Alaska and Canada, and the Pacific drainages of British Columbia. Cottus kaganowskii of eastern Siberia is probably identical to C. cognatus.

PREVIOUS RECORDS: None.

SPECIMENS SEEN: U.S.N.M. Nos. 38913 (Kobuk River; in stomach of *Esox lucius* bearing this number), 111655, 111657, 111661 (Colville River), 111685–111687 (headwaters of Anaktuvuk River, Anaktuvuk Pass); uncatalogued specimens from Willow Lake, headwaters of Willow Creek (Colville system).

Notes: Dunbar and Hildebrand (1952) report this species from tide pools in Ungava Bay. Arctic Alaskan material compares favorably with Berg's (1949) characterization of Cottus kaganowskii but is identified as C. cognatus, because Mr. N. J. Wilimovsky (in litt.) examined material of C. kaganowskii and considers it and C. cognatus identical. Dr. C. Richard Robins of Cornell University is of similar opinion (personal communication).

Anderson (1913) listed as Cottus punctulatus a specimen caught February 23, 1909, in the upper "Chandlar" River (Brooks Range). The locality name is incorrectly spelled. During the time in question, Anderson visited the Chandalar, not the Chandler, River. The Chandalar is in the Yukon sys-

TABLE 18

MERISTIC VARIATION IN ARCTIC ALASKAN

Cottus cognatus

Character	Range	Mean	Sample
1st D spines	8–9	8.3	12
2d D rays	15-17	15.5	12
A rays	10-12	11.3	12
P ₁ rays	13-14	13.3	13
P ₂ rays	I. 4	I, 4	13
Caudal vertebrae	21-22	21.7	9

tem, the Chandler in the Colville system. In addition, Anderson's specimen was incorrectly identified. The fish (A.M.N.H. No. 1850), though now in poor condition, is neither *C. punctulatus* nor *C. bairdi* (generally considered close to *C. punctulatus*), because palatine teeth are absent. The specimen compares favorably with Arctic Alaskan specimens of *C. cognatus*.

Meristic variation in Arctic Alaskan fishes is given in table 18.

Cottus poecilopus Heckel Muddler

RANGE: Fresh waters of northern Europe and Asia. In Arctic Ocean drainages east to the Kolyma system; present in Okhotsk Sea drainages (from Berg, 1949).

Cottus ricei Nelson Spoonhead Muddler

RANGE: Fresh waters. Great Lakes northward along the western shore of Hudson Bay, westward to the Saskatchewan system, Lake Athabaska, Lesser Slave Lake, and the Mackenzie River north to the Delta.

Notes: Wynne-Edwards (1952) gave locality records north and west of the Saskatchewan. He erroneously included southeastern Alaska in the range, giving as a reference Evermann and Goldsborough (1907, p. 306). A perusal of this work fails to reveal any mention of *Cottus ricei*, and on page 306 *C. asper* and *C. gulosus* are discussed. Neither of these is identical to *C. ricei*.

Wynne-Edwards considered *C. ricei* to be closest to the Asiatic *C. sibiricus*. He stated that *C. sibiricus* is present in the Kolyma system, although Berg (1949) distinctly no-

ted that C. sibiricus does not occur east of the Yana River.

Gymnocanthus pistilliger (Pallas)

PISTILLATE SCULPIN

RANGE: Coastal salt waters. In the Arctic, from northeastern Siberia east to Dolphin and Union Strait, Canada; south in the Pacific to the Bering, Okhotsk, and Japan seas.

PREVIOUS RECORDS: Point Belcher (Bean, 1882b, 1883, Gymnacanthus pistilliger).

Specimens Seen: None that are positively this species.

Notes: The three Point Belcher specimens listed by Bean (U.S.N.M. No. 27592) are only about 25 mm. long and at the present time cannot be reliably identified more accurately than to genus.

Smitt (1892–1895) described and illustrated this species (both sexes) from Najtschkaj in northeastern Siberia. Rendahl (1931a) identified these as G. pistilliger pistilliger. Walters (1953a) listed the species from the North-West Territories.

Gymnocanthus tricuspis (Reinhardt)

STAGHORN SCULPIN

RANGE: Coastal salt waters. Circumpolar; south to Avacha Bay (Bering Sea) in the North Pacific and to Maine in the North Atlantic.

Previous Records: As Gymnacanthos galeatus; off Cape Sabine (Bean, 1882b, 1883), Point Barrow (Scofield, 1899).

Specimens Seen: U.S.N.M. Nos. 27595 (off Cape Sabine), 33925 (Point Barrow; in stomach of *Lycodes turneri*), 111618, 111626, 111629, 111640, 152584, 152588, 152895, 152903, 152904, 152906 (Point Barrow); A.M.N.H. No. 17857 (mouth of Kotzebue Sound).

Notes: Aside from old records from the Chukchi Sea coast of Alaska, Gymnocanthus galeatus has been reported only once from the Arctic; it is otherwise a species of the Bering Sea and Pacific Ocean proper off Alaska, being unknown from the Sea of Okhotsk (Shmidt, 1950). Vladykov (1933) identified a mature male Hudson Bay fish as G. galeatus.

According to Bean's original description (1882a), and according to Taranetz (1937) and Shmidt (1950), G. galeatus has the entire

interorbital space covered by bony granulations. In *G. tricuspis* bony granulations are often absent from the interorbital space but when present they are confined to its middle. Only juvenile material has been seen from Arctic Alaska (largest specimen 56 mm. in standard length). Most specimens have a naked interorbital space, but in those that have prickles evident, the prickles are confined to the middle. Adults from North-West Territories fit current descriptions of *G. tricuspis*, not *G. galeatus. Gymnocanthus tricuspis* is common at Point Barrow; depths of capture ranged from 25 to 453 feet.

Vladykov's (1933) account of the Hudson Bay G. galeatus did not mention whether or not the entire interorbital space was covered by bony granulations. It is possible that the specimen was an extreme G. tricuspis, although the very broad interorbital space (13.3% of head length) is indicative of G. detrisus of western Bering Sea and Sea of Okhotsk (Andriashev, 1937b, 1939a).

Icelus bicornis Reinhardt Two-Horned Sculpin

RANGE: Circumpolar in salt water. See Notes for distributional records. This fish ranges as far north as sculpins have been discovered (northern end of Ellesmere Island); absent from the Pacific; in the Atlantic south to Ungava Bay in North America and to Sweden in Europe.

Previous Records: None. Specimens Seen: None.

Notes: Prior to 1937 this fish was considered circumpolar in distribution, but in that year Andriashev showed that it had been long confused with Icelus spatula, and I. bicornis was definitely known to range only from Greenland eastward to the Kara Sea. Jensen (1949) accepted Andriashev's conclusions and found additional characters to separate the two species; he identified I. bicornis from Ellesmere Island. Recent records of I. bicornis are: Dunbar and Hildebrand (1952), Ungava Bay; Walters (1953b), northern Ellesmere Island, Prince Patrick Island, and possibly Dolphin and Union Strait. Mr. N. J. Wilimovsky (in litt.) found the species in shallow water north and east of Point Barrow, Alaska. Esipov (1940) identified I. bicornis (and I. spatula) from the Laptev Sea, and Gorbunov (1946) listed

I. bicornis (and I. spatula) from the East Siberian Sea.

Icelus spatula spatula Gilbert and Burke

TWO-HORNED SCULPIN

RANGE: Coastal salt waters. In the Arctic; from the Kara Sea eastward to West Greenland and south to Labrador and Cape Cod in the North Atlantic. In the Pacific Ocean, only in Bering Sea. Not known from East Greenland or European waters.

Previous Records: None. Specimens Seen: None.

Notes: This species has been reported from all seas of Arctic Siberia and was said by Andriashev (1937a, 1937b) to occur in the Chukchi Sea. Walters (1953b) showed that his (1953a) record of *I. bicornis* from Dolphin and Union Strait in Canada was probably mostly this species, although the adults have disappeared. Jensen (1949) recorded *I. spatula* from West Greenland; Dunbar and Hildebrand (1952) found it in Ungava Bay; Backus (1953) extended the range to include Labrador and south to Cape Cod. This species ranges much farther south than *I. bicornis*, which seems absent from the Atlantic coast south of Ungava Bay.

Shmidt (1950) listed three forms of *Icelus* spatula: I. s. bispinis and I. s. ochotensis, both in the northern Sea of Okhotsk, and I. s. spatula of the Bering Sea and Arctic Ocean.

Myoxocephalus jaok (Cuvier and Valenciennes) Northern Daddy Sculpin

RANGE: Coastal salt waters. Sea of Japan, Sea of Okhotsk, Bering Sea, Chukchi Sea; in the Aleutian Islands and probably at Kodiak Island.

Previous Records: Cape Lisburne (Bean, 1882b, Cottus polyacanthocephalus), Kotzebue Sound (Bean, 1882a, Cottus humilis), Kotzebue Sound and Point Belcher (Bean, 1883, Cottus humilis), Cape Prince of Wales (Townsend, 1887, Cottus humilis), Point Belcher, Kotzebue Sound, Cape Prince of Wales records as M. jaok in Evermann and Goldsborough (1907).

SPECIMENS SEEN: U.S.N.M. Nos. 27553, 27557 (Point Belcher), 27972 (Kotzebue Sound, *C. humilis* type), 38354 (Cape Prince of Wales).

Notes: The record of Cottus polyacan-

thocephalus from Cape Lisburne (Bean, 1882b) was based on U.S.N.M. No. 27571, which can no longer be found; according to the catalogue records at the National Museum it was a very small specimen. Small individuals of M. jaok and M. polyacanthocephalus are similar in appearance. Because no large individuals identifiable as M. polyacanthocephalus have been found in the Arctic, it is probable that Bean's record was for juvenile M. jaok. Meristic variation in Arctic Alaskan fishes is given in table 19.

Myoxocephalus platycephalus (Pallas)

FLATHEAD SCULPIN

RANGE: Coastal waters. Northern Sea of Japan, Sea of Okhotsk, Bering Sea, Chukchi Sea.

Previous Records: Point Belcher (Bean, 1882b, 1883, Cottus taeniopterus; Evermann and Goldsborough, 1907, Megalocottus laticeps), Point Barrow (Scofield, 1899, Oncocottus sp. incog.).

SPECIMENS SEEN: U.S.N.M. Nos. 28004 (Point Belcher), 29923, 29925 (Eschscholtz Bay, Kotzebue Sound), 111615 (Point Barrow).

Notes: This sculpin differs from all others in our area by having a projecting lower jaw and a broad interorbital space (about 1.5 times the eye diameter). It is likely that Scofield (1899) had the young of this fish before him when he compared them as Oncocottus sp. incog. with similar-sized Oncocottus hexacornis (=M. quadricornis) from Point Barrow. Scofield mentioned the broad interorbital space and projecting lower jaw of his specimens.

There is no agreement regarding the ranges of subspecies in this fish. Taranetz (1937) recognized M. laticeps in eastern Bering Sea, M. p. platycephalus in western Bering Sea

TABLE 19

Meristic Variation in Arctic Alaskan

Myoxocephalus jaok

Character	Range	Mean	Sample
1st D spines	8–10	9	3
2d D rays	13–15	13.7	3
A rays	12-14	13	3
P ₁ rays	16–18	17.3	3

TABLE 20

MERISTIC VARIATION IN ARCTIC ALASKAN

Myoxocephalus platycephalus

Character	Range	Mean	Sample
1st D spines	8–9	8.3	4
2d D rays	13	13	4
A rays	11-12	11.3	4
P ₁ rays	17	17	4

and Sea of Okhotsk, and M. p. taeniopterus in northern Japan Sea and the Amur Delta in the Sea of Okhotsk. Berg (1949) listed M. p. platycephalus from the Chukchi, Bering, and Okhotsk seas, and M. p. taeniopterus from Sea of Japan. Shmidt (1950) recognized M. p. platycephalus of the Japan and Okhotsk seas and M. p. laticeps of the Okhotsk, Bering, and Chukchi seas. It is the present writer's opinion that, since the ranges differ according to the worker, there may be no distinct subspecies of this fish.

Meristic variation in Arctic Alaskan specimens is given in table 20.

Myoxocephalus quadricornis (Linnaeus)

FOUR-HORNED SCULPIN

RANGE: Preferring brackish coastal waters and commonly ascending far up river. Circumpolar, the southern limits of the marine form being northern Bering Sea (Norton Sound, Anadyr Gulf) in the Pacific and, in the Atlantic, the Baltic Sea in the east and latitude 56° 32′ N. (Labrador) in the west. Landlocked, fresh-water glacial relicts, closely related to this species, are known from lakes of Sweden, Finland, European Russia, the United States, and Canada.

PREVIOUS RECORDS: Point Barrow and Meade River (Murdoch, 1885b, Cottus quadricornis), Point Barrow (Scofield, 1899, Oncocottus hexacornis), Point Barrow (Fowler, 1905b, Oncocottus hexacornis and O. hexacornis gilberti), Point Barrow, Martin Point, Collinson Point (Walters, 1953a, M. quadricornis hexacornis).

Specimens Seen: U.S.N.M. Nos. 27588 (Kotzebue Sound), 32445–32450 (Point Barrow), 33921 (Meade River), 38907 (Kotzebue Sound), 111622, 111631, 111633, 111636, 111692, 111693, 111713, 152587 (Point Barrow); A.M.N.H. No. 9202 (Martin Point);

specimens in National Museum of Canada from Meade River, Point Barrow, Martin Point, Camden Bay, Collinson Point.

Notes: In addition to the Alaskan specimens, material from the following places in Canada has been examined: Alert, Ellesmere Island; Mould Bay, Prince Patrick Island; Prince of Wales Strait, Victoria Island; Pond Inlet, Baffin Island; Bernard Harbour (Dolphin and Union Strait), North-West Territories; Bathurst Inlet, North-West Territories; Nain, Labrador.

Records of this species from the British Isles were shown by Bruun (1941) to be the young of Acanthocottus lilljeborgi. Backus (1953) referred all previous Labrador records for this species to M. scorpius and then reported M. quadricornis from Labrador. The Kodiak Island record of Oncocottus hexacornis by Evermann and Goldsborough (1907) is indicated to be M. jaok by the cranial armaments, body tubercles, and size of the specimen (2 feet long, about 2.5 times as large as the largest four-horned sculpin seen by the present writer).

The four-horned sculpin is characteristic of coastal waters of low salinity and of fresh waters (lower parts of rivers) in western Arctic America. It is seldom found in water of high salinity; one specimen was washed ashore off Point Barrow, and this may have been in full strength sea water. The species has been frequently reported from considerable distances upstream from river mouths. According to Murdoch (1885b) the Meade River specimens were caught 80 to 90 miles from the sea. In the Mackenzie, Preble (1908, p. 514) reported it from Arctic Red River. One of the Meade River fishes (U.S.N.M. No. 33921) is an adult with welldeveloped cranial clubs, identical in appearance to adult coastal fishes from Point Bar-

A review of the forms of *Myoxocephalus quadricornis* was published by Berg and Popov (1932). Berg (1949) reclassified the forms, but the changes involved only the relict fresh-water populations; three coastal subspecies are still recognized. Their names, characteristics, and ranges are:

M. q. quadricornis (Linnaeus). Head flattened; frontal spines higher than parietal spines; caudal peduncle comparatively high. Baltic Sea. M. q. hexacornis (Richardson). Head usually more or less compressed; frontal spines usually lower than parietal spines; caudal peduncle usually low. Northern Bering Sea and Arctic Ocean from Chukchi Peninsula east to the Coppermine River (Canada).

M. q. labradoricus (Girard). Instead of having club-shaped spines atop the head (as in the preceding two forms) there are low combs or poorly developed spongy lumps; the frontal pair is as high as or lower than the parietal pair. Bony tubercles are poorly developed, there generally being none at the base of the anal fin. The head is compressed. Arctic Ocean, from Hudson Bay and Greenland eastward to the Kolyma River of Siberia.

Nice as the separation into subspecies may seem, there is no indication that *M. quadricornis* breaks up into units similar to those recognized by Soviet ichthyologists.

First of all, the head compression character is invalid. Fishes belonging to the "subspecies" hexacornis, collected by the present writer at Point Barrow and at Bathurst Inlet, had a flattened head when alive. Most of the American material exhibits a flattened head. The only specimens in which the head is not flattened are those that were crammed into their specimen jars; in these the head has become distorted from crowding and looks compressed.

The second major character employed in separating the subspecies, namely, whether the frontal spines are higher or lower than the parietal spines, seems to be sexually influenced in American fishes. Thus in seven Point Barrow and 10 Bernard Harbour (North-West Territories) males the frontal spines average 1.06 and 1.20 times as high as the parietal spines, respectively (over-all range 0.7-1.5). In eight Point Barrow, six Collinson Point, and 17 Bernard Harbour females the frontal spines average 0.87, 0.92, and 0.99 times as high as the parietal spines, respectively (over-all range 0.5-1.3). Thus males qualify as M. q. quadricornis, females as M. q. hexacornis. It is evident that relative spine height is not valid for separating subspecies.

The third major character, whether the frontal and parietal spines are high and clublike or low and not club-like, varies from

TABLE 21

MERISTIC VARIATION IN Myoxocephalus quadricornis OF WESTERN ARCTIC AMERICA

Dorsal fins	VI	VII	VIII	IX	X	11	12	13	14	15
Prince Patrick Island, North-										
West Territories ^a		2	20	1		1	5	10	7	_
Bernard Harbour, North-West		_					_			_
Territories ^b	_	8	22	11			5	16	16	2
Arctic Alaska ^c	2	13	29	7	1	2	21	19	10	
Totals	2	23	71	19	1	3	31	45	33	2
Anal fin	12	13	14	15	16					
Prince Patrick Island, North-										
West Territories ^a	1	6	13	3	_					
Bernard Harbour, Northwest		20								
Territories ^b	5	20	14	1 7	_					
Arctic Alaska ^c	5	9	26	7	1					
Totals	11	35	53	11	1					
Pectoral fin	15	16	17	18						
Prince Patrick Island, North-										
West Territories ^a	7	13	3							
Bernard Harbour, North-West										
Territories ^b	4	28	3							
Arctic Alaska ^c	1	19	23	7						
Totals	12	60	29	7						

From Walters (1953b).

locality to locality. In Labrador fishes (supposedly typical for M. q. labradoricus) there is considerable variation, from "quadricornis" and "hexacornis to "labradoricus" spines; most specimens are of the "quadricornis" or "hexacornis" type. Fishes from Collinson Point, Alaska (about midway between Point Barrow and Bernard Harbour), have the "labradoricus" condition more frequently than the "hexacornis" or "quadricornis" condition, and Berg and Popov (1932) stated that Anadyr River "hexacornis" are not distinct from "labradoricus." The height of the frontal spines was measured in fishes from various localities; it is contained in standard length 27-83 times (mean 44.1) in 15 Point Barrow fish, 31-113 times (mean 64.5) in six Collinson Point fish, and 22-48 times (mean 32.9) in 27 Bernard Harbour fish.

The next character used by Berg and Popov, the relative depth of the caudal pe-

duncle, is expressed in subjective terms by them. In 40 adults from Arctic Alaska and the North-West Territories, the caudal peduncle depth is contained in standard length 19-30 times, most often 24 or 25 times.

The final character used by Berg and Popov, the poor development of the tubercles on the body of "labradoricus," was shown by Backus (1953) to be invalid for Labrador fishes. "Labradoricus" is said typically to lack tubercles along the base of the anal fin; Backus found nine Labrador fishes to vary uniformly over a range of six to 27 tubercles.

Even though all the characters employed by Berg and Popov (1932) and by Berg (1949) to separate the three marine "subspecies" of M. quadricornis are subject either to considerable local variation or to sexual dimorphism, some authors may still wish to recognize subspecies. In this event, it should be noted that Backus (1953) showed Acanthocottus labradoricus Girard to be a synonym

^b From Walters (1953a).

e Specimens from Point Barrow, Camden Bay, Collinson Point, Meade River, and Kotzebue Sound.

of M. scorpius; Walters (1953b) showed that Cottus polaris Sabine is a synonym of M. quadricornis. Sabine's name (1821) antedates Cottus hexacornis Richardson (1823) and other North American synonyms. If an American subspecies is recognized, it must be called M. quadricornis polaris (Sabine, 1821).

There exist several landlocked glacial relicts which are evidently closely related to M. quadricornis. In North America these are called Triglopsis thompsoni. Whether T. thompsoni is actually conspecific with M. quadricornis or not cannot be determined at present. It is not doubted, however, that Triglopsis thompsoni and M. quadricornis are congeneric. Triglopsis is the fresh-water morpha of the marine Myoxocephalus, and the name should not be used as it does not have priority. Recent reviews of the subject were given by Berg and Popov (1932), Lönnberg (1932a, 1932b, 1939), and Vladykov (1933, 1934b).

Meristic variation in *M. quadricornis* of western Arctic America is given in table 21.

M. scorpioides

Pectoral fin with 14-16 rays

Top of head roughened by numerous hard and sharp-tipped warty protuberances

Frontal and parietal spines weakly developed, covered by thick skin in adults

Stout cirrus present on each frontal and parietal spine

Caudal peduncle relatively longer and slenderer

Myoxocephalus scorpioides (Fabricius)

FALSE SEASCORPION

RANGE: Coastal salt waters. In the Arctic, from Chaun Bay (East Siberian Sea) east to Greenland; south to northern Bering Sea in the Pacific and the Gulf of St. Lawrence in the Atlantic.

Previous Records: None. Specimens Seen: None.

Notes: Mr. N. J. Wilimovsky (in litt.) has collected M. axillaris (syn. M. scorpioides) in Arctic Alaska.

Eastern and western Arctic America each

have a pair of sibling species of Myoxocephalus. These are M. scorpius groenlandicus and M. scorpioides in the east and M. verrucosus and M. axillaris in the west. Myoxocephalus axillaris and M. scorpioides are the more Arctic members of the pairs (see Range above).

Not only are the two species pairs analogous in general distributions, but the members of each pair differ in the same characters and in the same direction for each character.

The eastern pair is discussed first. Comparisons of *M. scorpius groenlandicus* and *M. scorpioides* are available for localities covering a considerable portion of the common range (e.g., Greenland, Nichols, 1918; Hudson Bay, Vladykov, 1933; Ungava Bay, Dunbar and Hildebrand, 1952; Labrador, Backus, 1953; North-West Territories, Walters, 1953a). In addition material of both species from North-West Territories, Greenland, and Labrador has been examined. The following differences appear constant for all localities:

M. scorpius groenlandicus

Pectoral fin rays usually 17-18, seldom 16

Top of head relatively smooth; warty protuberances not numerous

Frontal and parietal spines well developed, blunted, frequently with 1 or more smaller accessory spines at their bases

Cirri often absent in adult fish; when present, short and slender

Caudal peduncle relatively shorter and stouter

The writer examined *M. verrucosus* from Point Barrow (measuring up to 233 mm. in standard length). The characters for *M. verrucosus* are based on these specimens plus descriptions and figures of the species by Jordan and Gilbert (1899), Soldatov and Lindberg (1930), Rendahl (1931a), Taranetz (1937), and Shmidt (1950). The characters for *M. axillaris* are based on descriptions and figures in Jordan and Gilbert (1899), Scofield (1899), Soldatov and Lindberg (1930), Rendahl (1931a), and Taranetz (1937).

M. axillaris

Pectoral rays 15-16

Top of head roughened by numerous hard warty protuberances

Frontal and parietal spines incipient, skin-covered

Frontal and parietal spines each with well-developed cirrus

Caudal peduncle relatively longer and slenderer

Myoxocephalus axillaris differs from M. verrucosus in the same manner and same degree as M. scorpioides differs from M. scorpius groenlandicus. There seem to be no important differences between M. verrucosus of Point Barrow and M. scorpius groenlandicus of the North-West Territories, Greenland, Labrador, and some localities in Maine (see M. scorpius groenlandicus for additional comparisons). Myoxocephalus verrucosus (Bean) is identical to M. scorpius groenlandicus (Cuvier and Valenciennes); M. axillaris (Gill) is identical to M. scorpioides (Fabricius).

Myoxocephalus scorpius groenlandicus (Cuvier and Valenciennes)

SEASCORPION

RANGE: Coastal salt waters. Throughout the Arctic in the lower latitudes, from the Kara Sea east to Greenland. In the Pacific, throughout Bering Sea and Sea of Okhotsk, south to the northern Kurile Islands and Sitka (Alaska). In the Atlantic, south to New York.

Previous Records: Point Barrow (Murdoch, 1885b, Cottus decastrensis; Evermann and Goldsborough, 1907, M. stelleri), near Icy Cape and between Icy Cape and Cape Sabine (Walters, 1953a, M. scorpius).

SPECIMENS SEEN: U.S.N.M. Nos. 32440—32444, 33920, 111623, 111627, 111628, 111632, 111635, 111641, 111715, 152585, 152589, 152895—152896, 152900, 152902, 152906 (Point Barrow); specimens in National Museum of Canada from latitude 69° 35′ N., longitude 163° 27′ W. and latitude 70° 24′ N., longitude 161° 25′ W.

NOTES: An examination of 29 Point Barrow fishes ranging from 31 to 233 mm. in

M. verrucosus

Pectoral rays 17-18, seldom 16

Top of head with some warty protuberances

Frontal and parietal spines well developed, usually with 1 or more smaller accessory spines at their bases

Frontal and parietal cirri small, often absent in adults

Caudal peduncle relatively shorter and stouter

standard length revealed no trenchant differences between these and specimens from the North-West Territories, Greenland, Labrador, and Casco Bay in Maine. The Alaskan fishes agree well with *M. verrucosus*, which is regarded here as a synonym of *M. scorpius groenlandicus*.

Vladykov (1933), Shmidt (1950), and Dunbar and Hildebrand (1952) have expressed the opinion that Myoxocephalus stelleri Tilesius is the Pacific representative of M. scorpius. The figure of M. stelleri in Jordan and Evermann (1896-1900) and Evermann and Goldsborough (1907) resembles Point Barrow adults very closely. However, the figure is not of M. stelleri. Jordan and Gilbert (1899) illustrated M. stelleri, which is a different fish; their figure of M. verrucosus is similar to Point Barrow individuals. Jordan and Gilbert's account of M. stelleri is in agreement with other accounts of this species (Soldatov and Lindberg, 1930; Taranetz, 1937; Berg, 1949; Shmidt, 1950), and agrees with a specimen (A.M.N.H. No. 936), 168 mm. in standard length, collected at Vladivos-

Myoxocephalus stelleri is restricted to the western Bering Sea, Sea of Okhotsk, and Sea of Japan, according to recent Russian accounts. Murdoch (1885b) identified Point Barrow fishes as Cottus decastrensis, which was referred to M. stelleri by Evermann and Goldsborough (1907). Vladykov (1933) recognized an Okhotsk subspecies, M. stelleri ochotensis. Shmidt (1950) regarded the Okhotsk fish as, at best, a subspecies of M. verrucosus. It is evident that until recently M. stelleri had been confused with M. verrucosus

Russian ichthyologists consider M. scorpius

distinct from *M. verrucosus*; the former is regarded as ranging east to the Kara Sea in the Arctic, the latter from the mouth of the Yenesei River eastward. *Myoxocephalus scorpius* from Norway and Spitsbergen appear different from most American fishes, which may account for the Soviet attitude. Some of the differences are:

NORWEGIAN AND SPITSBERGEN SPECIMENS

Body weakly armored; no large cancellous tubercles above lateral line, only small ctenoid plates Interorbital space narrower, vomer width equals or exceeds interorbital

Frontal and parietal spines sharp-tipped, directed backward, without accessory spines

Upper head surface relatively rough, many warty protuberances present

Pectoral rays 15-17

The "American" M. scorpius came from the following localities; Point Barrow (Alaska), Bernard Harbour (North-West Territories), Greenland, Labrador, and Casco Bay (Maine). Sculpins from Penobscot Bay (Maine) exhibit all the characters of the European fish except for number of pectoral rays, in which the count is 17–18 for five specimens.

Myoxocephalus scorpius admittedly is highly variable. In the early days of Arctic research the American fish was considered a separate species, M. groenlandicus. At present the tendency is to call the European and American fishes M. scorpius without reference to subspecies. It is likely that there are two subspecies: M. s. scorpius of Europe and the European Arctic, and M. scorpius groenlandicus (which has priority over other names) of Siberia and North America.

At Point Barrow this fish is the most com-

TABLE 22

MERISTIC VARIATION IN ARCTIC ALASKAN

Myoxocephalus scorpius groenlandicus

Character	Range	Mean	Sample	
1st D spines	9–11	10.4	29	
2d D rays	14-16	15.1	27	
A rays	11-14	11.8	25	
P ₁ rays	16–18	17.4	29	

mon resident of fully salt water. Of Arctic Alaskan specimens for which depth data are available, 24 of 25 were taken between 33 and 151 feet down; only one was taken in shallower water.

Point Barrow individuals of less than 60 mm. standard length have the body naked; there are leathery circular scales above the

AMERICAN SPECIMENS

Body well armored; many large cancellous tubercles above lateral line

Interorbital space broader, vomer width markedly less than the interorbital

Frontal and parietal spines blunted, vertical, often with accessory spines

Upper head surface relatively smooth, few warty protuberances present

Pectoral rays most often 17-18, seldom 16

lateral line at 61–120 mm.; at 162–233 mm. there are one or two irregular rows of large cancellous tubercles (developed from the circular scales?) above the lateral line and numerous sharp-tipped, backward-pointing spines (with one to several points) below the lateral line (developed from the warty protuberances present in smaller fishes?).

Meristic variation in Arctic Alaskan fishes is given in table 22.

Triglops pingeli Reinhardt

RIBBED SCULPIN

RANGE: Circumpolar in salt water. See below for comments.

PREVIOUS RECORDS: None.

SPECIMENS SEEN: None.

Notes: Mr. N. J. Wilimovsky (in litt.) has collected this species north and east of Point Barrow. Gorbunov (1946) listed the species from deep water in the polar basin. It is now well known from the Siberian Arctic, and Walters (1953a) listed it from Dolphin and Union Strait in western Canada. The southern limit for T. pingeli is Puget Sound in the Pacific and Cape Cod in the Atlantic.

Rendahl (1931a) identified T. p. beani from northeastern Siberia, and subsequent records from Arctic Siberia have been identified as this subspecies. Vladykov (1933) reported T. p. beani from Hudson Bay. Jensen (1944a) considered the range of T. p.

pingeli to be East and West Greenland and Baffin Island, but did not mention T. p. beani. Shmidt (1950) considered T. p. beani of the North Pacific identical with T. p. pingeli of Greenland.

AGONIDAE

SEA-POACHERS

Pallasina barbata was indicated for the Arctic by Popov (1933); this record was based on the collections made by the Vega Expedition. Rendahl's (1931a) report on the Vega collections listed P. barbata from the Bering Sea only. Therefore P. barbata should be stricken from the Arctic fauna.

Agonus acipenserinus Tilesius Sturgeon Sea-Poacher

RANGE: Coastal salt water. Puget Sound north to Point Barrow, absent from Sea of Okhotsk.

PREVIOUS RECORDS: Cape Lisburne (Bean, 1882b, 1883, *Podothecus acipenserinus*).

SPECIMENS SEEN: None.

Notes: Bean's specimen (U.S.N.M. No. 27574) has been destroyed, and the identification cannot be verified; it was a small individual measuring 1.1 inches in length and lacking snout barbels. Mr. N. J. Wilimovsky (in litt.) collected this species at Barrow.

Aspidophoroides olriki Lutken

ARCTIC SEA-POACHER

RANGE: Salt water. South to Newfoundland in the Atlantic and to the northern Bering Sea in the Pacific. Arctic records listed below.

PREVIOUS RECORDS: None.

SPECIMENS SEEN: U.S.N.M. Nos. 87673 (Kotzebue Sound), 111624, 149947, 152591, 152905, 152906 (Point Barrow); A.M.N.H. No. 17858 (Kotzebue Sound).

Notes: Rendahl (1931a) synonymized A. guntheri Bean with A. olriki. Jensen (1942) listed A. olriki from the following areas: Hudson Bay and West Greenland (absent from East Greenland) south to Newfoundland, east to the White, Barents, and Kara seas. The species is known also from the Laptev Sea (Andriashev, 1939b; Esipov, 1940), East Siberian Sea (Popov, 1933) and Chukchi Sea (present records); there are many northern Bering Sea records. There is no record

TABLE 23

MERISTIC VARIATION IN ARCTIC ALASKAN

Aspidophoroides olriki

Character	Range	Mean	Sample	
D rays	5–6	5.6	5	
A rays	5-6	5.3	4	
P ₁ rays	14-15	14.3	5	
C rays	10	10	3	
Body plates	36-38	37.2	5	

for the Beaufort Sea, but the species is undoubtedly found there. There are no records for the Sea of Okhotsk.

Arctic Alaskan specimens were collected between 80 and 295 feet in depth, except for one specimen washed ashore (at Point Barrow).

Meristic variation for Arctic Alaskan specimens is given in table 23.

CYCLOPTERIDAE

LUMPSUCKERS AND SEASNAILS SUBFAMILY CYCLOPTERINI

LUMPSUCKERS

A review of the status and characters of the species of *Eumicrotremus* occurring in the Arctic Ocean was published by Walters (1953b).

Eumicrotremus derjugini Popov

LEATHER-FIN LUMPSUCKER

RANGE: Salt water, from Hudson Bay and Greenland east to the Laptev Sea, also in Sea of Okhotsk; not recorded from the East Siberian, Chukchi, and Beaufort seas. Notes: Unknown from Alaskan waters.

Eumicrotremus spinosus (Müller)

SPINY LUMPSUCKER

RANGE: Salt water, from Prince Patrick and Banks Islands, North-West Territories, east to Barents and possibly Kara seas; not recorded from Laptev, East Siberian, or Chukchi seas; absent from the North Pacific.

Notes: Unknown from Alaskan waters. Mr. N. J. Wilimovsky (in litt.) found this species at Banks Island.

SUBFAMILY LIPARINI

SEASNAILS

Careproctus reinhardti was thought by An-

driashev (1939b) to occur in the Laptev Sea, but in the absence of published records this species is not included here.

Liparis koefoedi Parr

GELATINOUS SEASNAIL

RANGE: Circumpolar in salt water. All major seas of the Arctic except the Chukchi Sea. Not known from the North Pacific. South in the Atlantic to Labrador.

Previous RECORDS: Collinson Point (Walters, 1953a, ?Liparis koefoedi).

Specimens Seen: Collinson Point individual in National Museum of Canada.

Notes: The Collinson Point specimen is a post-larva which was identified by F. Johansen (MS) as L. fabricii on the basis of color pattern when it was alive. Walters listed this specimen questionably as L. koefoedi, because Johansen's (1912) L. fabricii had been shown by Parr (1932) to be L. koefoedi, and fin counts fitted the species. It is now safe to assume that the Collinson Point specimen is L. koefoedi, because Mr. N. J. Wilimovsky (in litt.) has collected the species in deep water north of the mouth of the Colville River.

Walters (1953a) gave the longitudinal range for this species as Beaufort Sea east to the Laptev Sea; Gorbunov's (1946) inclusion of this species in the East Siberian Sea fauna was overlooked.

Liparis laptevi Popov

LAPTEV'S SEASNAIL

RANGE: Salt water, known only from the Laptev Sea.

Notes: Since Popov named this form (1933) it has not been found again.

Liparis liparis complex Linnaeus

NORTHERN SEASNAIL

RANGE: Specimens referable to the Liparis libaris complex have been taken throughout the Arctic. See below for comments.

Previous Records: Point Barrow (Murdoch, 1885b, L. gibbus; Evermann and Goldsborough, 1907, L. agassizii).

SPECIMENS SEEN: U.S.N.M. Nos. 33949, 111617, 149949, 152612, 152590 (Point Barrow); A.M.N.H. No. 8976 (mouth of Kotzebue Sound); Collinson Point post-larva in National Museum of Canada.

Notes: U.S.N.M. No. 33949, the specimen of L. gibbus reported from Point Barrow by Murdoch (1885b), has been skeletonized.

The largest Arctic Alaskan specimen examined is 89 mm. in standard length. It is possible that more than one kind of seasnail has been included under the designation "L. liparis." Dunbar and Hildebrand (1952) have recently commented on the taxonomic confusion regarding Liparis liparis Linnaeus and Liparis tunicatus Reinhardt: to this might be added Liparis herschelinus Scofield which Walters (1953a) regarded as at best a subspecies of Liparis liparis.

The Arctic Alaskan material best fits L. herschelinus, following Burke (1930), yet F. Johansen identified a post-larva from Collinson Point as L. liparis because it agreed well with Greenland L. liparis as to coloration when alive (Johansen, 1912). Arctic Alaskan fishes have 40-43 dorsal elements and 34-37 anal elements (six specimens).

PLEURONECTIDAE

FLOUNDERS

Hippoglossoides elassodon robustus Gill and Townsend

FLAT-HEADED SOLE

RANGE: Marine, does not enter brackish waters. Bering and Okhotsk seas south to Japan; strays into the Chukchi Sea.

Previous Records: None. SPECIMENS SEEN: None.

Notes: The flat-headed sole was recorded by Andriashev (1937b) from the southern Chukchi Sea; only small stages were found.

Limanda aspera (Pallas)

YELLOW-FIN SOLE

RANGE: Coastal salt waters. North Pacific: in the east, northward from northern British Columbia; in the west, from Hokkaido (Japan) and Fusan (Korea) northward. Throughout the Bering Sea and Sea of Okhotsk. Straggles into the Chukchi Sea along the Alaskan coast, north to Point Barrow.

Previous Records: Kotzebue Sound (Townsend, 1887, Limanda aspera).

Specimens Seen: U.S.N.M. Nos. 38353 (Kotzebue Sound), 111616, 111620, 111639, 149948, 152610, 152611 (Point Barrow).

Notes: Only two specimens large enough so that the characters diagnostic for the species are apparent were examined; one measures 155 mm. (standard length) from Kotzebue Sound, the other 72 mm. from Point Barrow. The nine others, all from Point Barrow, measure 31–40 mm. in standard length.

The lateral line is of the typical Limanda form, and there is a dark line along the dorsal and anal fin bases in all specimens. The weak postorbital ridge is developed on the opercle, and the snout is convex only in the two largest fish. The vertical fins are darkspotted in all but the largest specimen (155 mm.). The caudal peduncle is square in lateral aspect in the 72- and 155-mm. fish; it is barely present in 39-40-mm. fish; in 31-39mm. fish there is no caudal peduncle (dorsal and anal fins adnate to caudal). The 31-40mm. specimens average 63.3 dorsal rays (range 60-67); the two larger ones have 69 and 70 dorsal rays. The 31-40-mm. specimens average 47.3 anal rays (range 45-51); the two larger ones have 52 and 54 anal rays. The difference in fin counts between small and large individuals is interpreted to mean that as the caudal peduncle lengthens the dorsal and anal fins complete their development. Scales are absent in 31–40-mm. fish but are present in full number in the two larger individuals. The scales of the eyed side have one or two (rarely three) ctenii each. There are 76 and 80 scales along the lateral line. The teeth of 31–40-mm. fish are needle-like and well separated; in the two larger fish the teeth are blunted, conical, and set close together.

Liopsetta glacialis (Pallas)

ARCTIC FLOUNDER

RANGE: Brackish coastal waters and the lower parts of rivers; avoids fully salt water. Arctic Ocean, from the White Sea (Europe) east to Bathurst Inlet and possibly Queen Maude Gulf (Canada); south along the east shore of the Bering Sea to the Alaska Peninsula; absent from western Bering Sea and Sea of Okhotsk.

Previous Records: Kotzebue Sound (Bean, 1882b, 1883, Pleuronectes glacialis).

Specimens Seen: U.S.N.M. Nos. 27947, 29913, 29928 (Kotzebue Sound).

Notes: The possible Queen Maude Gulf record was indicated by Hildebrand (1948). According to Shmidt (1950) L. glacialis is not found in the Sea of Okhotsk.

The marked sexual dimorphism of Liopsetta is well known. Arctic American L.

TABLE 24

MERISTIC VARIATION IN ARCTIC AMERICAN Liopsetta glacialis

Character	Range	Mean	Sample
Dorsal rays			
Kotzebue Sound, Alaska	51–59	<i>54.8</i>	15
Herschel Island, Yukon Territory ^a	55-62	<i>58.7</i>	3
Bathurst Inlet, North-West Territories	54-60	<i>57.4</i>	5
Bathurst Inlet, North-West Territories ^b	57		1
Anal rays			
Kotzebue Sound, Alaska	34–43	39.7	15
Herschel Island, Yukon Territorya	40-47	43.7	3
Bathurst Inlet, North-West Territories	39-43	40.8	5
Bathurst Inlet, North-West Territories ^b	42		1
Gill rakers			4 7
Kotzebue Sound, Alaska	10–13	11.3	15
Bathurst Inlet, North-West Territories	11–12	11.4	5

^a From Walters (1953a).

^b From Richardson (1854); one element dropped from count.

TABLE 25
Meristic Variation in Arctic American Pleuronectes stellatus

Character	Range	Mean	Sample
Dorsal rays			
Kotzebue Sound, Alaska	47-51	49.0	2
Langton Bay, North-West Territories ^a	56		1
Coppermine, North-West Territories ^b	54-56	<i>55.0</i>	2
Port Epworth, North-West Territories	49-58	52.8	5
Bathurst Inlet, North-West Territories	49-58	53.6	21
Anal rays			
Kotzebue Sound, Alaska	33-35	34.0	2
Langton Bay, North-West Territories ^a	38		1
Coppermine, North-West Territories ^b	40-42	41.0	2
Port Epworth, North-West Territories ^c	36-40	37.7	7
Bathurst Inlet, North-West Territories	35-41	37.5	20
Gill rakers			
Kotzebue Sound, Alaska	10-11	10.5	2
Bathurst Inlet, North-West Territories	7–12	10.0	21

^a From Walters (1953a).

^b Count for one individual taken from Richardson (1854); one element dropped from Richardson's counts.

Some of the counts were given by Walters (1953a).

glacialis show the following:

Male: In individuals as small as 99 mm. in standard length, the lateral line is complete, the head is completely covered by ctenoid scales, and the eyed side of the body is covered by slightly overlapping ctenoid scales.

Female: In individuals as large as 172 mm. in standard length, the lateral line is an open groove in the posterior portion of the body, the head has a few scattered cycloid scales, and the body has scattered, non-overlapping, cycloid scales on the eved surface.

TABLE 26

ESTIMATE OF MINIMUM PROBABLE FREQUENCY OF SINISTRAL INDIVIDUALS IN NORTH-WEST
TERRITORIES Pleuronectes stellatus

(Based upon 50 fish from Langton Bay, Coppermine, Port Epworth, and Bathurst Inlet.)

Observed Values Predicted Values		Observed Values Predicted Values		ed Values			
Per Cent of Population Sinistral	Number of Sinistral Individuals	Per Cent of Population Sinistral	Number of Sinistral Individuals	D	SEr	D/SEr	
100	50	70	35	15	3.24	4.6	
100	50	80	40	10	2.83	3.5	
100	50	90	45	5	2.12	2.4	
100	50	92.5	46.25	3.75	1.86	2.0	
100	50	95	47.5	2.5	1.54	1.6	

D, deviation or the numerical difference between the observed and predicted numbers of sinistral individuals.

SEr, standard error of the ratio or $\sqrt{C_1 \cdot C_2/N}$ where C_1 is the predicted frequency of sinistrality, C_2 the predicted frequency of dextrality, and N the total number of dextral and sinistral individuals.

D/SEr, deviation/standard error of the ratio; if the quotient is 2 or less, there is no significant difference between the observed and the predicted values.

TABLE 27
GEOGRAPHICAL VARIATION IN FIN RAY COUNTS OF Pleuronectes stellatus

Locality	Range	Mean	Authority
Dorsal fin rays			
Arctic America	47-58	<i>53.4</i>	Table 25 above
Bering Sea	50-60	53.8	Rendahl, 1931ba
Shantar Islands, Okhotsk Sea	53-64		Berg, 1949 (four fish, no mean given)
Southern Alaska	5566	60.6	Townsend, 1936
Japan	52-66	<i>58.6</i>	Hubbs and Kuronuma, 1942
Washington State	52-65	58.5	Townsend, 1936
Monterey Bay, California	52-64	58.5	Orcutt, 1950
Anal fin rays			
Arctic America	33-42	37.6	Table 25 above
Bering Sea	37-42	38.9	Rendahl, 1931ba
Shantar Islands, Okhotsk Sea	37-45		Berg, 1949 (four fish, no mean given)
Southern Alaska	39-47	42.9	Townsend, 1936
Japan	36-48	42.0	Hubbs and Kuronuma, 1942
Washington State	38-46	42.1	Townsend, 1936
Monterey Bay, California	38-47	42.5	Orcutt, 1950

^a Mean calculated by present writer; Rendahl had nine fish from Port Clarence, Alaska; Avacha Bay, Kamchatka; Bering Island, Commandorskie group.

The variation in number of fin rays and gill rakers of Arctic American *L. glacialis* is shown in table 24.

Pleuronectes stellatus Pallas

STARRY FLOUNDER

RANGE: Brackish coastal waters and the lower sections of rivers. In the Arctic Ocean, possibly from Queen Maude Gulf but definitely from Bathurst Inlet (Canada) west and south along the American coast into the Bering Sea, but unknown from the Siberian Arctic. In the Pacific, throughout Sea of Okhotsk and Bering Sea; south to Fusan (Korea) and Tokyo in the west and Santa Barbara County, California, in the east.

PREVIOUS RECORDS: Kotzebue Sound (Bean, 1883; Townsend, 1887, Pleuronectes stellatus).

SPECIMENS SEEN: U.S.N.M. Nos. 38351—38352 (Kotzebue Sound).

Notes: There are two schools of thought regarding the correct generic designation for this form and the closely related river flounder of Europe (P. flesus Linnaeus). American authors and Norman (1934) refer both to Platichthys Girard, 1854 (type P. rugosus = P. stellatus). Berg (1933, 1949) and

other authors regard P. flesus as the genotype of Pleuronectes Linnaeus, 1758. Norman was the first to place P. flesus in Platichthys; he regarded P. platessa as the genotype of Pleuronectes. According to Berg, Cuvier in 1817 selected P. platessa as the genotype of Platessa. Thus Pleuronectes of Norman corresponds to Platessa of Berg; Platichthys of Norman corresponds to Pleuronectes of Berg. Berg does not accord recognition to Platichthys, and Norman does not recognize Platessa. The present writer has decided to follow the Russian school and use Pleuronectes for these flounders.

The starry flounder is common in the North-West Territories, where Hildebrand (1948) indicated it as far east as Queen Maude Gulf. Table 25 indicates meristic variation in Arctic American fishes.

All Arctic American fishes seem to be sinistral, but there are data for only 52 fish, and it is possible that dextral individuals, if scarce, may have been overlooked by collectors. Fifty fish have been taken in the North-West Territories; the data for these are treated in table 26. The standard error of the ratio has been used to estimate the lowest probable frequency of sinistral individuals in

TABLE 28
GEOGRAPHICAL VARIATION IN OBSERVED FREQUENCIES OF SINISTRAL Pleuronectes stellatus

Locality	Frequency	Sample	Authority
Arctic America	100%	52	
Bering Sea	70	10	Rendahl, 1931ba
Alaska Peninsula, Kodiak Island	68.0	5129	Hubbs and Kuronuma, 1942
Southeastern Alaska	58.2	2498	Hubbs and Kuronuma, 1942
Washington State	52	9219	Hubbs and Kuronuma, 1942a
Puget Sound	47.6-52.7	8416	Hubbs and Hubbs, 1945
Oregon	58	290	Hubbs and Kuronuma, 1942a
Monterey Bay, California	59.5	1 4 39	Orcutt, 1950
California	55.2	509	Hubbs and Kuronuma, 1942
Japan	100	476	Hubbs and Kuronuma, 1942

^a Recalculated.

a mixed population that would permit a random sampling of 50 individuals to be entirely sinistral. It is probable that sinistral individuals constitute no less than 92.5 per cent of the North-West Territories population. No estimate can be given for Arctic Alaska, because only two specimens from the area were examined.

The geographical distribution of sinistrality for *P. stellatus* is shown in table 28. Of the localities reported, only Japan seems to have as high a frequency of sinistrality as, or one higher than, that found in Arctic America. The flounders of the American Pacific coast south of the Bering Sea are 47.6–68.0 per cent sinistral, which is considerably lower than in flounders of Japan and the Arctic. Adequate data are lacking for those of the Chukchi Sea and the Sea of Okhotsk. Information given by Rendahl (1931b) for 10 Bering Sea fishes indicates

70 per cent sinistrality, but the sample is small. The significance of high or low sinistrality is not understood; Hubbs and Hubbs (1945) suggested that dextral individuals of *P. stellatus* are selected for in Puget Sound.

The data on fin ray counts (table 27) are far from adequate, but Bering Sea flounders seem more closely related to the Arctic fishes than to those of the rest of the Pacific. Bering Sea and Arctic fishes average about 38 anal fin rays compared to 42-43 in the rest of the Pacific. Bering Sea and Arctic fishes average 53-54 dorsal fin rays compared to 58-61 in the rest of the Pacific. There are virtually no data available for the Sea of Okhotsk, but the four individuals mentioned by Berg (1949) range much higher in fin counts than do Bering Sea and Arctic fishes, and the Okhotsk fishes therefore are indicated to be closer to the fishes of Japan, southern Alaska, Washington, and California.

DISCUSSION

THE SECTION of the Arctic under discussion (map 1) includes the coastal salt waters from Cape Cheliuskin on the Taimyr Peninsula of Siberia (longitude 105° E.) east to longitude 105° W. in Canada, and south to Mys Nunyagmo and Cape Prince of Wales on both sides of Bering Strait (latitude 65° 40' N.), and the fresh waters draining into the East Siberian, Chukchi, and Beaufort seas east to longitude 105° W. The entire Arctic watershed is included for Siberia, Alaska, and Canada except that the Mackenzie Valley south of Arctic Red River is excluded. The area from the New Siberian Islands east to the Alaska-Yukon Territory border is called the "Beringian Arctic," characterized by its largely having escaped ice coverage during the last glacial period, and by having constituted the Arctic Slope of the Bering Strait land bridge.

The salt waters delimited above lie entirely within the limits of the "Circumpolar-Arctic Zone" (Andriashev, 1939a) or the

"Polar-Arctic Subregion" (Ekman, 1953). Andriashev is followed in considering the Arctic Zone for marine fishes to lie almost entirely north of Bering Strait, with a slight southward extension into the Gulf of Anadyr and Norton Sound in Bering Sea; the Bering, Okhotsk, and Japan seas are primarily boreal. Ekman considered the western Bering Sea, most of the Sea of Okhotsk, and parts of the Sea of Japan to belong to the "Northwest Pacific Seas Arctic Subregion." Ekman based this subregion on the distributions of water temperatures, stating that the distributions of the animals are not sufficiently known internationally. Andriashev noted that certain parts of these seas closely approach the Arctic Ocean in physical conditions, but their faunas cannot be considered Arctic; rather, there has been a separate evolution of a fauna of arctic type from boreal elements. Shmidt (1948, 1950) termed the Okhotsk fauna "prearctic" rather than "Arctic."

CLIMATIC CHANGES

It is likely that the area has experienced marked climatic changes, but there is little information available.

In a consideration of past climates, it is unnecessary to go back farther than the last (Fourth, Würm, or Wisconsin) glaciation. Any warm-water fishes that may have dwelt in the region prior to that time were eliminated by the cold. The present fauna consists of fishes that have lived there since the last glaciation in addition to those that have entered the area post-glacially.

In temperate latitudes the mean annual (air) temperature seems to have varied not more than 10° C. during the Pleistocene epoch (Flint, 1952). During the four Pleistocene glaciations mean temperature was about 8° C. lower, and during the interglacial periods it was about 2° C. higher, than at present. The present climate is warmer than that during glacial times, 30,000 and more years ago, but is colder than the "Climatic Optimum" of 4000 to 6000 years ago when sea temperatures in northern Europe were

as much as 2.5° C. higher than those of today (Flint, 1947, ch. 21). Radiocarbon measurements for Alaskan localities indicate that 450 years ago the climate was like that of the present, but the climate was warmer 3750, 4200, 8350, and 13,600 years ago; the 8350-year old sample is underlain by a deposit indicative of a climate cooler than that of the present time (Kulp, Tryon, Eckleman, and Snell, 1952).

If a fish required a post-glacial warm period in order to enter the Arctic it must now be limited to the warmest pockets in the Arctic; in other words, its range must not include the colder portions. Some marine fishes stray through Bering Strait into the Chukchi Sea from the Bering Sea during warm spells, but they are eliminated when the climate again becomes rigorous (cf. Andriashev, 1937b, Hippoglossoides robustus).

Although the climate in temperate latitudes may have been about 8° C. lower during the Wisconsin glaciation, it is likely that water temperatures in high latitudes

were not too different from those of the present time, because the present temperatures are only slightly above freezing most of the year. Marine fishes which today live at the highest latitudes were not eliminated from the Arctic during the recent glaciation; instead, as water temperatures dropped in the south they expanded their ranges. Wherever rivers continued to flow, brackish coastal and fresh-water fishes were able to

survive in the Arctic during the Wisconsin glaciation; the rivers exerted a warming influence on the near-by salt waters and sustained "oases" of elevated temperature. In the Beringian Arctic, owing to the large area of land exposed by the drop in sea level during the last glaciation, the rivers had either the same or greater volumes than those of the present day.

WATER TEMPERATURE AND SALINITY

In nature a fish cannot thrive at temperatures below the freezing point of its body fluids. The celebrated ability of the freshwater Dallia pectoralis to survive being frozen solid was shown to be a myth by Borodin (1934) and by Scholander, Flagg, Hock, and Irving (1953). The freezing point of water varies with its salinity; fresh water begins to freeze at 0° C., full-strength sea water at about -2° C. The blood of marine teleosts is said to freeze at from -0.77° to -1.05° C. (Heilbrunn, 1943, p. 113; Mitchell, 1948, p. 469), but some Arctic marine teleosts are often found in water of -1° C. to -1.9° C. Obviously something interesting must happen to keep the body fluids of these fishes from freezing; Dr. P. F. Scholander, Woods Hole Oceanographic Institution, is studying the problem.

It is likely that the freezing point of the body fluid limits the distribution and dictates the behavior of some arctic fishes. It is suggested that among arctic fishes, unless the freezing point of the body fluid is, or can be adjusted to be, at or below the winter temperature of the surrounding water. the habitat should shift towards lower salinities as the high-salinity waters grow cold. It is possible that marine fishes that have low osmotic concentrations and that cannot tolerate low salinities can survive only in the warmest sectors of the Arctic. Even though the freezing point of the body fluid may be low enough, other physiological disturbances that might occur at very low temperatures could be avoided by entry into low-salinity water. For example, Fry (1947) considered that for some marine fishes the lethal effect of low temperature results from the metabolic load imposed by the osmoregulatory function. It is possible that the movement of a euryhaline marine species into water isotonic to its body fluid would reduce osmoregulatory labor.

In high latitudes fishes that require low salinities can find these during winter only near river mouths. In summer brackish water exists in many other places, but ice formation causes a rise in salinity, and during winter only the flowing rivers can maintain the brackish water. In addition winter river water has a temperature of 0° C. or higher, while winter salt water has negative temperatures; thus in high latitudes river mouths act as a warming influence on the neighboring salt water.

Scholander, Flagg, Walters, and Irving (1953) showed that among aquatic poikilotherms (crustaceans, fishes) there is considerable though incomplete metabolic adaptation to the Arctic environment. Owing to technical difficulties, these authors did not investigate subzero metabolism of marine forms, but it would seem that, because the fishes are exposed to temperatures at or only slightly above freezing (subzero) during winter, life is being carried on near its lower thermal limit and a matter of perhaps only tenths of a degree in water temperature may mean the difference between survival and extinction. Marine fishes such as Gadus morhua ogac and Eleginus n. navaga, which spawn in brackish water in mid-winter, and coastal fishes such as Salvelinus alpinus, the whitefishes, and Osmerus sperlanus dentex, which run up rivers or into lakes for the winter, may be escaping high salinities and possibly lethal low temperatures. The diadromous habit (Myers, 1949) is therefore indicated to be of positive selective value

among Arctic fishes, if the sojourn in freshened water occurs during winter.

So far as the fishes are concerned there are two kinds of fresh waters in the Arctic, those that freeze from top to bottom in winter and those that do not. The former cannot support permanent fish populations, but the latter may. The only fresh waters that can harbor a permanent fish fauna are rivers, large streams, lakes more than about 6 feet deep (depth of ice formation, Johansen, 1922), and springs. Nevertheless many shallow lakes and ponds contain fishes during the summer months; these either enter from streams or are deposited by flood waters. Fishes deposited by flood in shallow waters lacking communication with non-freezing water bodies are doomed to death during the ensuing winter.

There is a forced movement of fresh-water

fishes into waters that do not freeze in winter. With the onset of winter the supply of surface water for streams diminishes as the ground freezes. Eventually the shallow lakes and small streams freeze completely, and the lower portions of streams suffer a reduction in flow; some streams dry up. There is a corresponding decrease in river volumes, because many tributaries cease functioning. Zaykov (1936) estimated that 85 to 95 per cent of the annual flows of Laptev and East Siberian Sea drainages occurs during the four to six warmest months. Ray (1885) reported that the Meade River of Alaska ceases flow altogether in winter, and it is likely that many smaller river systems of the Arctic do likewise: however. Ray caught fishes in the quiescent Meade, in deep holes between the bars of ice.

INVASION OF NEW AREAS

A species tends to expand its range into all localities having suitable habitats provided they lie within the radius of dispersal from localities where the species occurs. By radius of dispersal is meant the distance across unfavorable territory that may be successfully traversed by the species. The radius varies with the life history stage of the particular species, with the geographical peculiarities of the area, and with changes in the environment. Certain groups of sedentary, bottom-dwelling, littoral and sublittoral fishes such as blennioids, eelpouts, and many sculpins were considered by Andriashev (1939a) to be of greater significance in zoogeography than free-swimming types such as herrings and cods. Andriashev

overlooked the fact that most bottomdwellers have pelagic life history stages that are carried about by the ocean currents. Thus a basic zoogeographic distinction between bottom-dwelling and free-swimming groups is invalid.

A species may be unable to establish itself in an area unless it can compete successfully with the species already present. In effect, if the ecological requirements differ for the various life history stages, then each stage represents a separate "species" which may or may not be able to survive in the new area. Permanent breeding populations cannot be established unless the area is suitable for the survival of all life history stages.

AVENUES OF DISPERSAL

FRESH WATERS

Five likely avenues are apparent: headwaters transfer, confluence, lowlands transfer, flooding, and low-salinity bridges. In addition, Lampetra japonica, Oncorhynchus spp., and the Salvelinus alpinus complex are able to enter high-salinity waters and can therefore disperse along fully marine avenues. Many other fresh-water fishes enter coastal waters but avoid high salinities.

HEADWATERS TRANSFER

This avenue is open only to species that enter headwaters situations, such as Oncorhynchus keta (not a headwaters form in the south, but ascends to the headwaters of the Yukon and other streams in the north), the Salvelinus alpinus complex, Salvelinus namaycush, Prosopium cylindraceum, Thymallus arcticus signifer, Lota lota subsp., and Cottus cognatus. Certain species are unable to

utilize headwaters transfer in expanding their ranges, because they do not enter the upper parts of river systems; examples are Oncorhynchus gorbuscha, Osmerus eperlanus dentex, Hypomesus olidus drjagini, Dallia pectoralis, and Pungitius pungitius pungitius.

Headwaters transfer may be accomplished either by the piracy of a segment of the headwaters of one river system by a neighboring system (cf. von Engeln, 1942) or by the temporary diversion of part of the headwaters of one river system into another, resulting from blockage by glacial ice or other agency. The latter phenomenon as it affects fishes in western Arctic America was discussed by Wynne-Edwards (1947a, 1952). In formerly glaciated areas, where the lower reaches of rivers were impounded by the ice sheets, large glacial lakes formed and altered the drainage patterns. The greater part of the sector of the Arctic under discussion did not experience any extensive glaciation and probably had insignificant glacial lake formation; extensive glacial lake production occurred to the east and west.

CONFLUENCE

Confluence as an avenue of dispersal is open to species that inhabit the lower parts of river systems. In western Arctic America none of the fresh-water species is limited to headwaters situations; all occur in the lower parts of rivers. A river, during its meandering over a coastal plain, may run into neighboring streams, the two systems becoming one as a result of confluence (cf. von Engeln. 1942). Thus confluence reduces the number of drainage systems flowing across a coastal plain. However, if sea level rises to submerge the coastal plain, then many of the formerly confluent systems become independent drainages (junctions submerged). The Arctic, as the rest of the earth, has experienced a considerable post-glacial rise in sea level. Many drainages that are now separate were confluent when sea level was low.

When confluence occurs the fishes of one drainage system are able to move into the other component. When the component systems become separated by the rise in sea level, the fishes may remain in both systems if the environments are satisfactory. All species that inhabit the lower parts of rivers

are able to disperse into new drainage systems by confluence. Dallia pectoralis is the only strictly lowland fish in the area that seems to avoid saline waters (some additional examples may exist among the Siberian minnows); its occurrence in Alaska and Siberia may be attributable to former confluence between streams of the two continents, to lowlands transfer (below), or to flooding (below) of land between closely adjoining Siberian and Alaskan rivers when sea level was low.

LOWLANDS TRANSFER

In the marshy, lake-stream country along the coast, as streams develop and capture lakes and ponds, smaller segments of the countryside may be drained first by one river system, then by a neighboring system. Low-land fishes may thus be transferred along a coastal plain from one system to another, in "bucket brigade" fashion. Dallia pectoralis, the home of which is in such country, has undoubtedly spread over part of its range by this method.

FLOODING

During the summer thaw the tundra becomes a virtually continuous sheet of water near the coast. It is likely that some fishes may spread from river system to river system through this water layer. It is not unusual to find isolated puddles, an inch or so deep, containing Dallia pectoralis or Pungitius pungitius, on the coastal plain of Arctic Alaska. These fishes evidently were stranded in the puddles by the recession of the summer flood waters, because they cannot possibly survive the Arctic winter under such conditions.

LOW-SALINITY BRIDGES

In the vicinity of large rivers the freshening effect on the sea is profound, and the salinity of near-by coastal waters may never rise high. For great stretches off the Siberian Arctic coasts the salinity is only 15 to 23 per mille on the sea bottom, which is definitely in the brackish range (Ekman, 1953) and salinities of less than 3 per mille (fresh water) occur up to 60 miles away from the Lena Delta (Sverdrup, 1950). Similar, though by no means as striking, conditions prevail in western Arctic America wherever larger

rivers debouche (Goodman et al., 1942; Tully, 1952).

The ice of the Arctic Ocean serves to accentuate the freshening of coastal waters, even in the vicinity of relatively insignificant rivers and streams. In the Beringian Arctic the land begins to thaw before the sea ice drifts away from shore; in fact the warmed water running off the land surface is of importance in eroding the grounded sea ice until it lifts free of the bottom and drifts away (Goodman, Lincoln, Thompson, and Zeusler, 1942). Thus fresh water coming off the tundra pours into the ice-choked coastal waters to accumulate between the offshore ice and the coastline. Being lighter, the "warm" fresh water displaces the cold salt water. In addition the melting sea ice contributes to the volume of the low-salinity water. Thus low-salinity bridges between river mouths may exist for varying lengths of time during the summer months, particularly during years when the sea ice stays close to shore for extended lengths of time. When the sea ice drifts off, coastal salinities rise and temperature may drop owing to upwelling.

Only one species of Arctic Alaskan freshwater fish, Dallia pectoralis, has not been reported from saline waters somewhere in its range. The formation of low-salinity bridges between river mouths therefore constitutes a real avenue for the dispersal of many freshwater forms. True, some (e. g., Thymallus arcticus signifer, Esox lucius) seldom enter coastal waters in numbers, but others (e. g., Oncorhynchus spp., the Salvelinus alpinus complex, whitefishes) enter coastal waters in droves, and yet other species, considered strictly fresh-water in lower latitudes, enter coastal waters with ease in high latitudes (e.g., Salvelinus namaycush, Catostomus catostomus, Lota lota).

MARINE WATERS

Knowledge concerning the physical oceanography of large areas of the seas of this sector of the Arctic is poorly advanced. Gorbunov (1946) cautioned against the blind use of "episodic" hydrological information; many hydrological determinations performed in high latitudes are limited to a few hours' to a few days' observations at any one locality. The information therefore is apt to be misleading, because the annual cycle and amplitude of variation for each factor at the particular locality are unknown. The hydrological determinations may have been made at a time when conditions were far from normal, such as during summer. In view of the ignorance regarding the physical oceanography of most of the region, a discussion of avenues of marine dispersal in the Beringian Arctic must be limited to generalities.

There is a pronounced northward flow of the water through Bering Strait (Goodman, Lincoln, Thompson, and Zeusler, 1942) which thus provides a highway to the Arctic for Bering Sea fishes. Certain fishes are able to stray into the Chukchi Sea, but unless they can withstand the harsh winter conditions they cannot survive long north of Bering Strait.

In the absence of detailed information concerning the currents of much of the area, the absolute importance of such currents in distributing planktonic and nektonic life history stages of fishes cannot be properly evaluated. the northward flow through Bering Strait is well established. For the rest of the Beringian Arctic it is assumed that pelagic stages may be carried anywhere, and any mass deviation of species from a cosmopolitan distribution in waters of arctic type should command attention.

THE ICHTHYOFAUNA

FRESH-WATER FISHES

The forms listed below occur in drainages emptying into the East Siberian, Chukchi, and Beaufort seas (east to longitude 105° W.); Canadian records are for the Arctic Life Zone and south to Arctic Red River in the Mackenzie Valley. All spawn in fresh water.

Lampetra japonica¹ Acipenser baeri Oncorhynchus gorbuscha¹ Oncorhynchus keta¹ Salvelinus alpinus complex¹ Salvelinus namaycush¹

¹ Occurs in Arctic Alaska. *Cottus kaganowskii* is considered identical to *C. cognatus*.

Hucho taimen Brachymastax lenok Stenodus leucichthys nelma1 Coregonus sardinella1 Coregonus autumnalis1 Coregonus peled Coregonus nasus1 Coregonus clupeaformis Coregonus lavaretus pidschian1 Coregonus muksun Prosobium cvlindraceum1 Thymallus arcticus signifer¹ Osmerus eperlanus dentex1 Hypomesus olidus drjagini¹ Dallia pectoralis1 Esox lucius1 Catostomus catostomus¹ Catostomus commersoni Couesius plumbeus Leuciscus leuciscus Phoxinus percnurus Phoxinus czekanowskii Phoxinus phoxinus Carassius auratus gibelio Nemachilus barbatulus toni Lota lota lota Lota lota leptura1 Pungitius pungitius1 Percopsis omiscomaycus Perca fluviatilis Acerina cernua Stizostedion vitreum Cottus cognatus1 Cottus poecilopus Cottus ricei

MARINE FISHES

The following occur in the Laptev, East Siberian, Chukchi, and Beaufort seas (east to longitude 105° W.). The bathypelagic Benthosema glaciale, known from Point Barrow, is omitted. All spawn in salt or brackish water.

Clupea harengus pallasi¹ Mallotus villosus¹ Gadus morhua ogac¹ Eleginus n. navaga¹ Boreogadus saida¹ Arctogadus spp.¹

Anarhichas denticulatus Eumesogrammus praecisus Stichaeus punctatus1 Lumpenus fabricii1 Lumpenus medius¹ Gymnelis viridis1 Ophidium stigma¹ Lycodes jugoricus1 Lycodes turneri1 Lycodes knipowitschi Lycodes raridens1 Lycodes palearis1 Lycodes pallidus1 Ammodytes hexapterus1 Artediellus scaber1 Artediellus uncinatus1 Gymnocanthus pistilliger² Gymnocanthus tricuspis1 Icelus bicornis¹ Icelus spatula spatula2 Myoxocephalus jaok1 Myoxocephalus platycephalus1 Myoxocephalus quadricornis1 Myoxocephalus scorpioides1 Myoxocephalus scorpius groenlandicus1 Triglops pingeli1 Agonus acipenserinus1 Aspidophoroides olriki1 Eumicrotremus derjugini Eumicrotremus spinosus Liparis koefoedi¹ Liparis laptevi Liparis liparis complex¹ Hippoglossoides elassodon robustus Limanda aspera1 Liopsetta glacialis1 Pleuronectes stellatus1

Certain marine fishes must be omitted from further consideration, because either they are known only from the type description or their taxonomic status is open to too much question. The following are not considered further:

Ophidium stigma, known only from original description

Ammodytes hexapterus, taxonomic status uncertain Artediellus uncinatus, taxonomic status uncertain Gymnocanthus pistilliger, taxonomic status uncertain

Liparis laptevi, known only from original description

Liparis liparis complex, taxonomic status uncertain

² Probably occurs in Arctic Alaska.

¹ Occurs in Arctic Alaska. Cottus kaganowskii is considered identical to C. cognatus.

GEOLOGY AND ZOOGEOGRAPHY

In order to interpret distributional patterns in this sector of the Arctic it is necessary to consider the probable history of the region from the Wisconsin glacial period up to the present. During this time there occurred pronounced dwindling in the size of glaciers, local changes in land elevations, and a worldwide or eustatic rise in sea level. Climatic changes are considered above.

The story of the last glacial period in the Arctic is imperfectly known. In particular, details for Siberia are of a sketchy nature. Two recent Russian papers have not been seen. They were referred to by Berg (1949) and seem to be of great importance. They could not be located by the Library of Congress, and neither is listed in the "Arctic bibliography." For workers who may be fortunate to locate the papers, the references are:

SAKS, V. N.

1945. Morya sovetskoy Artiki v Chetvertichniy period. Dokl. Yubil. sessii Arktich. inst., 11 pp. Leningrad.

1948. Chetvertichniy period v Sovetskoy Arktike. Tr. Arkt. Inst., vol. 201, 134 pp., maps. Moscow.

DISTRIBUTION OF PERENNIAL ICE AND SNOW

At the present time perennial ice and snow are scarce, disregarding the sea's pack ice. In the American portion perennial snow fields or glaciers occur only on Melville and Lougheed Islands of the western Canadian Archipelago (Washburn, 1947), and a few glaciers, too small to be shown on a map, are found in the Brooks Range of Alaska (Flint, 1947). On the mainland of the Siberian portion glaciers when present are small and confined to mountains; of the Arctic Islands only Severnaya Zemlya and the DeLong group have glaciers today (Flint, 1947).

During the Fourth or Wisconsin glacial period this sector of the Arctic had greater areas of perennial ice and snow, but the coverage was neither so extensive nor so heavy as in adjoining regions. For many places the reports have not distinguished between the different glacial periods, and thus the precise distributions of former Wisconsin glaciers are not known.

NORTH AMERICA

The western Canadian islands south of Viscount Melville Sound, with the possible exception of northern Banks Island, were covered by an ice sheet continuous with that covering the mainland to the south¹; on the western islands north of Viscount Melville Sound the highest elevations may have been glaciated, but the ice if present was not continuous with that to the south (Hobbs, 1945; Jenness, 1952).

On the mainland, the Brooks Range of Alaska was covered by the Cordilleran Glacier Complex which was coalescent with the Laurentide Ice Sheet to form a continuous ice cover to the east. Glacial ice formerly covered the entire Canadian mainland portion of the Arctic: the ice extended east to the Atlantic coast and south to the United States. In the Alaskan portion (and part of the Yukon Territory) glacial ice was less widely distributed. Virtually all of the Arctic Slope of Alaska, most of the area around Kotzebue Sound (except the Kobuk Valley), and most of the valleys of the Bering Sea drainages of Alaska and the Yukon Territory were not ice covered; in addition the islands in the Bering Sea north of the Alaska Peninsula and Aleutian Islands escaped glaciation (Flint et al., 1945).²

SIBERIA

The information has been taken from Flint (1947, ch. 17). Except where noted the conditions reflect the maximum extent of glaciation, probably for the Third glacial period; ice was less extensive during the Fourth glacial period.

- ¹ Northerly Prince of Wales Island and Somerset Island also seem to have escaped glaciation, but these lie east of our area.
- ² After this manuscript was completed a paper appeared which is based upon recent echo-soundings made in the Arctic regions (Carsola, A. J., 1954). According to Carsola, the continental shelf in the Chukchi Sea and most of the Beaufort Sea, which extends seaward to a depth of approximately 210 feet, was not covered by continental ice sheets. On the present-day continental shelf only the Amundsen Trough, lying between Banks Island and the mainland, and possibly the Mackenzie Seavalley, lying off the Mackenzie mouth, mark the courses either of local glaciers or of lobes of the continental ice sheet which extended across the Pleistocene coastal plain.

Wrangel Island had a small ice sheet which never reached south to the mainland. The Novosiberian Islands had an ice sheet which reached south to the mainland between the Yana and Indigirka rivers but which never coalesced with the ice moving north out of the mainland mountains (below); the DeLong Islands, northeast of the Novosiberian group, were probably glaciated. The Severnaya Zemlya group had an ice sheet which coalesced with sheets from the west and south to form the Siberian Ice Sheet, mentioned below.

The coalescence of mountain glaciers on the mainland produced a system similar to the Cordilleran Glacier Complex of western North America. The ice extended, in the mountains, from the eastern side of the Lena basin east to Bering Strait. The Chukchi Peninsula was largely covered by glacial ice. The lower Kolyma, Indigirka, Yana, and other rivers west to the Taimyr Peninsula, and the broad adjoining lowlands, were never glaciated.

There was a continuous ice cover to the east (Laurentide Ice Sheet, above) and another to the west. The Siberian Ice Sheet of the Fourth glacial period extended south to latitude 64° N. between the Ob' and Yenesei basins, but its eastern face turned northward so that only the lower portion of the mouth of the Yenesei was glaciated; the ice sheet then continued northeastward across the northern Taimyr Peninsula to join the Severnaya Zemlya sheet. An additional, smaller, ice sheet occurred in the Putorana Mountains during the Fourth glacial period. Ice-free areas of Arctic Siberia during the last glacial period therefore included the Yenesei Valley above its mouth and all major river valleys (at least in the lower portions) from the Khatanga in the west to at least the Kolyma in the east.

EUSTATIC RISE IN SEA LEVEL

As the total world mass of ice increases during a glacial period there is a world-wide or eustatic drop in sea level, because water is prevented from returning to the sea. As the glaciers melt, sea level rises. During the Wisconsin glacial period there was a drop in sea level of about 220 to 300 feet, a conservative estimate (Daly, 1942; Flint, 1947; Kuenen,

1950). This drop was more than sufficient to establish a terrestrial connection between North America and Asia.

The average depth of the ocean is about 13,000 feet; the average salinity 34 to 35 per mille. A sea level drop of 300 feet (by ice accumulation) would remove about 2 per cent of the ocean volume, causing a slight rise in salinity (to less than 36 per mille). The estimates are rough but indicate that worldwide salinity changes caused by rise and fall of sea level probably had slight effects, if any, on the inhabitants of the oceans.

LOCAL CHANGES IN LAND ELEVATION

The weights of glaciers cause the underlying earth's crust to become depressed. The depression is greatest beneath the largest ice masses. In the Hudson Bay region of eastern North America, the Laurentide Ice Sheet was about 3.8 miles deep and caused a sagging of about 3000 feet in the earth's crust (Lougee, 1953). As the glaciers melt the depressed land begins to rise (upwarping). However, during the early stages of deglaciation the sea level rises more rapidly than can the land and, in coastal areas, the sea transgresses the depressed land surface. Later on, the land rises out of the sea. Upwarping is still going on in many places.

In the sector of the Arctic under discussion, post-glacial marine submergence is indicated for the following coastal areas.

NORTH AMERICA

As a whole the Canadian Archipelago underwent post-glacial marine submergence of 400 to 500 feet or more, that is to say, the post-glacial sea was 400 to 500 feet deeper (Jenness, 1952). The Canadian mainland coast similarly experienced post-glacial marine submergence and then emergence, but the magnitude diminished westward until, for the Arctic Alaskan coast, there is no positive evidence for post-glacial marine submergence (Richards, 1950). Similarly the Bering Sea coast of Alaska has had little or no postglacial upwarping (Flint, 1952). In the vicinity of Bering Strait in Alaska there is no evidence for upwarping, as the marine strand lines both above and below sea level are horizontal (Flint, 1947, pp. 444, 459); the higher strand lines reflect pre-Wisconsin (interglacial) high sea levels.

SIBERIA

The northern Taimyr Peninsula, Severnaya Zemlya, and apparently also the Novosiberian Islands underwent post-glacial

marine submergence (Berg, 1950, pp. 11–12, 349), and upwarping is still in process. In Siberia as in North America, coastal areas formerly covered by large ice masses were submerged post-glacially and are now emerging.

EXISTENCE AND DISAPPEARANCE OF BERING STRAIT LAND BRIDGE

With information on distributions of glaciers, eustatic sea level changes, local changes in land elevation, and the topography of the sea bottom (below), it is possible to depict roughly the changes in the Beringian Arctic from the last glacial period to the present, and to discuss the effects on its ichthyofauna.

STAGE 1, THE LAND BRIDGE

The suggested appearance of the Beringian Arctic during the last glacial period is shown in map 2; sea level is considered to have been 180 feet (rather than 220 to 300 feet) lower than it is at present, and any greater drop would not appreciably alter the map.

Sea level has been rising since the ice masses of the Fourth glacial period began melting. In areas of no or only slight post-glacial upwarping, the sea bottom to depths of 180 (or 200 to 300) feet was dry land during the last glacial period; areas that evidence significant post-glacial marine submergence (hundreds of feet), as in western Siberia and Canada, did not have the adjacent sea floor exposed.

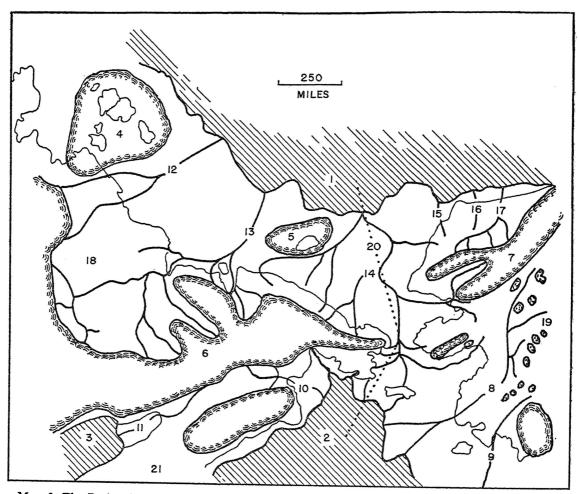
The Laptev, East Siberian, Chukchi, and northern and eastern Bering seas are remarkable for their shallowness; over most of this area the depth is less than 180 feet. These shallow seas border areas that exhibit no or only slight post-glacial crustal movements, and it is assumed that the bottoms of these for the most part have neither been uplifted nor depressed since the Fourth glacial period (some uplift has occurred in the Novosiberian Islands and in western Laptev Sea); areas of volcanic or other orogenic activity lie well south of the Beringian Arctic.

The suggested courses of the rivers shown on map 2 follow the depressions in the pres-

ent-day sea bottoms; some of the Alaskan and Siberian rivers of today represent the upper parts of former drainage systems of much larger size.

The Kolyma system is suggested to have flowed west rather than east of the Wrangel Ice Sheet; the absence of Dallia from the Kolyma indicates that this river was not a component of the "Chukchi Complex" (term introduced as new by the present writer). The Chukchi Complex included all Chukchi Sea drainages of Siberia and Alaska south of the Kuk River, south in the Bering Sea to St. Lawrence Island, Mechigmen Bay, and Norton Sound. In map 2 the ice sheets are probably portrayed as being larger than they actually were during the last glacial period. In addition because sea level was probably much more than 180 feet lower during the last glacial period, the ice masses on and near the land bridge may have dwindled considerably by the time sea level rose to the stage depicted in the map.

It should be noted that according to the map the Anadyr and Yukon systems were not confluent and were not integral components of the land bridge. The zoogeographically functional part of the land bridge was its Arctic Slope. All fresh-water and terrestrial organisms that used the land bridge to cross from one continent to the other during the last glacial period were obliged to enter the Arctic Slope and pass north of the "Siberian Mountain Glacier Complex." The ice sheets descended close to the shores of the Sea of Okhotsk and also covered most of the Kamchatka Peninsula (not shown on map). In addition the complicated pattern of Siberian mountain ranges south of the Arctic Slope (cf. Berg, 1950) makes any other route practically impossible



MAP 2. The Bering Strait land bridge, being the probable appearance of the Beringian Arctic and adjoining regions during the last glacial period. Continental outlines reflect a sea level drop of 180 feet, based on soundings in United States Navy Hydrographic Office Map 2560 (June, 1948, ed.). Distributions of ice sheets and smaller glacial masses based on Flint et al. (1945) and Flint (1947). Shaded areas are seas; present-day continental outlines indicated by thinnest lines. 1. Arctic Ocean. 2. Bering Sea. 3. Sea of Okhotsk. 4. Novosiberian Ice Sheet. 5. Wrangel Ice Sheet. 6. Siberian Mountain Glacier Complex. 7. Cordilleran Glacier Complex. 8. Yukon system. 9. Kuskokwim system. 10. Anadyr system. 11. Penzhina system. 12. Alasei-Indigirka Complex. 13. Kolyma Complex. 14. Chukchi Complex. 15. Kuk system. 16. Meade system. 17. Colville system. 18. Siberia. 19. Alaska. 20. International Date Line. 21. Kamchatka (glaciers omitted).

except for alpine terrestrial forms, even in the complete absence of glaciers. This may account for the lesser faunal similarities between most of the Okhotsk region, Kamchatka, and Alaska than between the Siberian Arctic Slope and Alaska. It is also apparent that the land bridge of the last glacial period was usable only by organisms capable of surviving in the Arctic.

Because the climate of the Beringian Arctic during the Fourth glacial period was probably cooler than that of the present time, one may ask whether the rivers flowed all year round at that time. Even today some Alaskan rivers do not flow in winter, although fishes survive in the deeper, non-freezing portions. During the land bridge stage the rivers had longer courses (over the floors of the present

East Siberian and Chukchi seas) and, though some headwaters were glaciated, the river volumes of the land bridge were considerable. Confluence occurred, thus further increasing river volumes. Notwithstanding the probably cooler climate of the land bridge, at least some of the rivers had a winter flow.

The high-salinity waters probably remained close to freezing throughout the year, as no "warm" salt water entered the Arctic from Bering Sea. It is likely that the sea north of the land bridge was no warmer than the present seas off central Arctic Siberia and central Arctic America.

MARINE ARCTIC FAUNA OF LAND BRIDGE

Six marine species undoubtedly have been present since land bridge times, for the following reasons: they are now circumpolar in distribution and occur in the highest latitudes from which fish have been reported, which indicates that they would have survived north of the land bridge even if conditions had been as rigorous as they are now between latitudes 78° N. and 83° N. Further, if they had entered the Beringian Arctic post-glacially from the North Pacific, they should now be found in the Arctic portions of the Sea of Okhotsk, but their absence indicates they did not live south of the land bridge during the last glacial period. The six are:

Boreogadus saida Lycodes pallidus Gymnocanthus tricuspis Icelus bicornis Myoxocephalus quadricornis Liparis koefoedi

Four circumpolar Arctic species (Mallotus villosus, Gymnelis viridis, Myoxocephalus scorpius, Triglops pingeli) are widespread in the North Pacific (and North Atlantic) and conceivably could have entered the Beringian Arctic post-glacially from the North Pacific (and North Atlantic) to make the present range secondarily circumpolar. However, two range as far north as the six above listed, indicating they could have survived north of the land bridge:

Gymnelis viridis Triglops pingeli

Clupea harengus pallasi may have been pre-

sent since land bridge times. It is unknown from the best-explored and warmest part of the Beringian Arctic, i.e., Chukchi Sea and the neighboring northernmost Bering Sea, but occurs in very cold parts of the Arctic such as off the Lena Delta. The apparently disrupted range suggests that a cold-adapted race of the herring could have survived glacial times north of the land bridge.

Eleginus navaga navaga has probably been present since land bridge times. It is represented in the North Pacific by another subspecies (E. n. gracilis). There are no records from between the Ob' and the Chukchi Peninsula, but the present writer suspects that this cod has been overlooked by Siberian explorers. It is tolerant of low salinities and could have survived the glacial period by remaining in the vicinity of rivers.

Arctogadus species have probably been present since land bridge times. The genus is absent from the North Pacific, from Europe (including Spitsbergen), and from eastern North America save for northern Greenland, and is present in all parts of our area. It ranges as far north as fishes go and is tolerant of low salinities.

Lycodes jugoricus has probably been present since land bridge times. The bulk of its range lies in our area, and it is absent from the Atlantic and Pacific oceans. According to Andriashev (1939b) this is an estuarine fish; the only rivers that existed in the Arctic during the last glacial period were in our area.

Lycodes turneri has probably been present since land bridge times. Its range is almost circumpolar, and it is absent from the Sea of Okhotsk.

Artediellus scaber has probably been present since land bridge times. It is almost restricted to our area.

Icelus spatula spatula has probably been present since land bridge times. It is represented by two other subspecies in the Sea of Okhotsk, which indicates that it may have been absent from the North Pacific until recently. Backus (1953) remarked that 16 of the 22 collections in Labrador were taken in water of -1.0° C. to -1.85° C., and only once was the species taken in water warmer than 1° C. This fish thus seems to seek the coldest water, which is indicative of a true Arctic form.

Aspidophoroides olriki has probably been present since land bridge times. It is absent from the Sea of Okhotsk, which indicates that it has entered Bering Sea post-glacially.

Liopsetta glacialis has probably been present since land bridge times. It is almost continuously distributed in the Arctic, from the White Sea east to Bathurst Inlet and possibly Queen Maude Gulf, but is absent from the Eastern Arctic. According to Shmidt (1950) it is absent from the Sea of Okhotsk and in the Bering Sea is found only along the Alaskan shore. This flounder avoids high salinities, and its presence in the Arctic is strong evidence that continual brackish water was available along the Arctic coast during the last glaciation, which in turn is indirect evidence that at least a few rivers did not cease flowing in winter time during the land bridge stage.

Pleuronectes stellatus may have been absent until recently. It has not been reported from the seas of Arctic Siberia. It is broadly distributed in the North Pacific. However, there is indication that the Arctic American and perhaps Bering Sea flounders are not exactly identical to those from the rest of the North Pacific.

The marine fishes that could have dwelt in the Beringian Arctic since land bridge times are listed in phylogenetic order:

Clupea harengus pallasi Eleginus navaga navaga Boreogadus saida Arctogadus spp. Gymnelis viridis Lycodes jugoricus Lycodes turneri Lycodes pallidus Artediellus scaber Gymnocanthus tricuspis Icelus bicornis Icelus spatula spatula Myoxocephalus quadricornis Triglops pingeli Aspidophoroides olriki Liparis koefoedi Liopsetta glacialis

FRESH-WATER ARCTIC FAUNA OF LAND BRIDGE

During the land bridge stage fresh-water fishes were found only in non-glaciated areas, which even with today's high sea level constitute a large portion of the Beringian Arctic. Because fresh waters were available the year round (even though some streams probably ceased flowing in winter), the unglaciated areas of the Arctic were inhabitable.

As there are no strictly headwaters fishes in the Beringian Arctic (except possibly in the Kolyma system and west in Siberia), the existence of the land bridge with its lengthened rivers and close proximity or confluence between Siberian and Alaskan systems enabled all fresh-water fishes living on the Arctic Slope of the land bridge to become distributed on both continents (map 2). The numerous avenues of dispersal available to Arctic fresh-water fishes virtually guaranteed that all forms became distributed on both continents. As the land bridge was being drowned by the rising sea, the Chukchi Complex (map 2) was replaced by the "Chukchi Embayment" (map 3) (both terms introduced by the present writer as new). At a sea level 120 feet below the present height, the Chukchi Embayment was no more than 75 feet deep and was probably of low salinity owing to the fact that large volumes of fresh water poured in from the retreating ice sheets and from the former components of the Chukchi Complex. Freshwater fishes tolerant of low salinities could utilize the shallow, brackish Chukchi Embayment to travel freely between Siberia and Alaska. Fresh-water fishes that have lived in the Beringian Arctic since land bridge times therefore are distributed in both Asia and North America; however, some "bicontinental" fishes probably entered the Arctic post-glacially.

Lampetra japonica has probably been present since land bridge times. Its range, from the White Sea east to the Mackenzie, so indicates. The sea-running form has not been observed in eastern Arctic Siberia, which has the landlocked dwarf. If the glacial seas were too cold for the sea-run form during the land bridge stage, the fresh-water dwarf could have survived.

Oncorhynchus gorbuscha and Oncorhynchus keta, aside from the Arctic charrs, are undoubtedly the strongest swimmers of the fresh-water fishes of our area capable of living in high-salinity water (whitefishes avoid fully salt water). Both salmons range from the

Lena system east to the Mackenzie system. It is likely that both invaded the Arctic post-glacially through the sea by way of Bering Strait. Oncorhynchus gorbuscha does not enter headwaters, eliminating the possibility that these attain their present range entirely by headwaters transfer. If they lived on the Arctic Slope of the land bridge their present longitudinal range in the Arctic would probably have been much greater.

Salvelinus alpinus complex has been present since land bridge times. If any freshwater fishes were present in the Arctic this fish certainly was; it ranges farther north than any other fresh-water fish.

Stenodus leucichthys nelma, Coregonus sardinella, C. nasus, C. lavaretus pidschian, and Prosopium cylindraceum have been present since land bridge times; all have much more extensive ranges in the Arctic than Oncorhynchus, and their distributions in Pacific drainages are limited almost entirely to Bering Sea systems. Whereas Prosopium coulteri has spread along the Pacific coast from the Columbia Valley north to southern Bering Sea drainages and P. williamsoni has spread from the Columbia north to the Nass (British Columbia), none of the land bridge whitefishes appears to have moved farther south than Kodiak Island along the Pacific coast. The occurrence of P. cylindraceum in Pacific coast drainages (Alsek) is attributable to headwaters transfer from Bering Sea drainages (Yukon).

Thymallus arcticus signifer has been present since land bridge times. Its range is much more extensive than that of Oncorhynchus in the Arctic; it is limited in the North Pacific almost entirely to Bering Sea drainages.

Hypomesus olidus drjagini and Osmerus eperlanus dentex seem to have been present since land bridge times. The ranges of both greatly exceed the range of Oncorhynchus in the Arctic. The range of H. olidus is most interesting; in North America there are no records between northern California (Hubbs, 1925) and Alaska; it may have a relict distribution. The fact that H. olidus and not its close relative H. pretiosus occurs in the Arctic may be explainable on the basis of salinity requirements versus thermal tolerances. Where their ranges overlap the two often

school together in brackish coastal waters (Berg et al., 1949), but, whereas H. olidus spawns in fresh water and is frequently landlocked, H. pretiosus spawns in salt water. seldom if ever enters fresh water, and does not become landlocked. Thus H. olidus can stay permanently in fresh water, which is warmer than Arctic salt water, whereas H. pretiosus cannot. The absence of records between Alaska and California indicates that H. olidus has been unable to invade British Columbia post-glacially from either the north or the south, a distance that is considerably shorter and a route that is considerably warmer than that between the Kara Sea and Bering Strait or even that between Bering Strait and the Mackenzie. The indications are that H. olidus survived, landlocked, on the Arctic Slope of the land bridge.

Dallia pectoralis has been present since land bridge times. An apparent unwillingness to enter saline coastal waters may account for its small longitudinal range (Chukchi Peninsula east to Ikpikpuk River). It may be that Dallia was absent from the Bering Sea slope of the land bridge because it is absent from Bering Sea drainages of Siberia; its presence along the Bering Sea shores of Alaska may be due to the presence of extensive marshy lowlands (ideal for flood dispersal) which it could have entered from the north as the land bridge was being drowned. The presence of cyprinids and some other "fringe" elements in the Kolyma system of Siberia may be keeping Dallia from spreading westward, or the presence of Dallia on the Chukchi Peninsula may be keeping some "fringe" elements from spreading eastward. The fresh-water fauna of the Chukchi Peninsula is not very well known, and it is possible that Dallia does coexist with some of the "fringe" elements. However, the "competition" hypothesis does not account for the restricted range of Dallia in Arctic Alaska, and the present writer therefore does not subscribe to it.

Esox lucius, Catostomus catostomus rostratus, Lota lota leptura, and Pungitius pungitius have probably been present since land bridge times. Their extensive distributions in the Arctic and restricted distributions in the North Pacific drainages indicate this.

Cottus cognatus has probably been present since land bridge times. Cottus kaganowskii, here considered a probable synonym, is found in lakes near St. Lawrence Bay on the east end of the Chukchi Peninsula (Berg, 1949) and is the only form of its genus known from east of the Kolyma in Siberia.

In summary, 17 of the 19 fresh-water fishes common to Arctic Alaska and Arctic Siberia have probably been present since land bridge times:

Lambetra jabonica Salvelinus alpinus complex Stenodus leucichthys nelma Coregonus sardinella Coregonus autumnalis Coregonus nasus Coregonus lavaretus pidschian Prosopium cylindraceum Thymallus arcticus signifer Osmerus eperlanus dentex Hypomesus olidus drjagini Dallia pectoralis Esox lucius Catostomus catostomus rostratus Lota lota leptura Pungitius pungitius pungitius Cottus cognatus

STAGE 2, DROWNING OF LAND BRIDGE

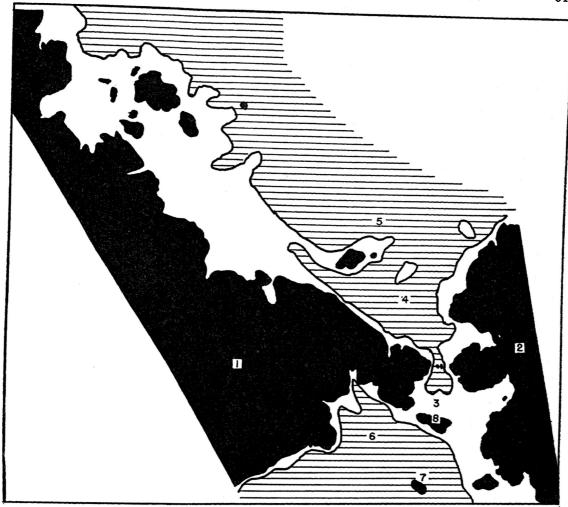
After sea level had risen sufficiently (as glacial ice masses dwindled) the isthmus connecting Alaska and Siberia was inundated. The North Pacific and Arctic oceans became continuous as North America and Asia became separated. If sea level were to drop now, the land bridge would probably be a reality after 120 feet of water had been abstracted (map 3), but this seems to represent the minimal drop necessary to establish the bridge. Radiocarbon measurements afford a guide as to how long ago the land bridge may have been swamped: a Bermuda cedar forest now 60 to 90 feet below sea level was drowned about 11,500 years ago (Kulp, Feely, and Tryon, 1951), a Mississippi Delta shell from 73 feet down was found to be 8700 to 9000 years old, and Mississippi Delta wood from 273 feet down was found to be more than 30,000 years old (Kulp, Tryon, Eckelman, and Snell, 1952). These figures indicate that the land bridge, which existed until sea level had risen to within about 120 feet of its present height, was destroyed more than 11,000 years ago.

Thus the "Climatic Optimum" of 4000 to 6000 years ago, when climate was markedly warmer than that of today, occurred after the land bridge had been destroyed. The mild Alaskan climate of 13,600 years ago either occurred when the land bridge was in its final stages or after it had been drowned.

Recent estimates indicate the last glacial period ended about 11,000 years ago (Kulp, Feely, and Tryon, 1951); this figure is based on radiocarbon measurements of several localities in Europe and North America. The last major advance of the Laurentide Ice Sheet in the United States (the Mankato Substage; Flint et al., 1945; Flint, 1947) occurred about 11,000 years ago; the radiocarbon age of the peat underlying the glacial drift is about that old (Flint, 1952). The melting of the Laurentide Ice Sheet was generally concentric, with the main body persisting longest in the vicinities of Hudson Bay and the highlands of Quebec and Labrador (Flint, 1952). In other words the Bering Strait land bridge had drowned while eastern North America and Europe were still largely covered by glacial ice.

In a consideration of what the seas may have been like during and shortly after the drowning of the land bridge, attention is here first directed to the Bering Strait region. The coastal salinities must have been lower than today's values, because volumes of fresh water were pouring into the sea from the melting ice masses and the longer river courses in the vicinity of Bering Strait. When the land bridge became submerged, the water covering it was in all probability fairly fresh. As sea level rose more Bering Sea salt water began flowing through Bering Strait into the Arctic Ocean. Even today the water in the Alaskan part of Bering Strait is fresher than in the Siberian part, owing to the strong influence of the Yukon River (Goodman, Lincoln, Thompson, and Zeusler, 1942).

The Arctic seas remained brackish for some time after the land bridge drowned. The seas of Arctic Siberia today are of low salinity. Marine fossils from western Arctic Canada indicate that the post-glacial sea was cold and of low salinity, much like that near the Mackenzie Delta today (Richards in Wash-



MAP 3. Bering Strait land bridge. Continental outlines reflect sea level 120 feet lower than at the present time. Based on soundings in United States Navy Hydrographic Office Map 2560 (June, 1948, ed.). Glaciers and rivers not shown. Present-day land features are solid black; land now submerged is white; seas are shaded. 1. Siberia. 2. Alaska. 3. Land bridge. 4. Chukchi Embayment. 5. Arctic Ocean. 6. Berng Sea. 7. St. Matthew Island. 8. St. Lawrence Island.

burn, 1947; Richards, 1950).

It is unlikely that any additional freshwater fishes (with the possible exception of Oncorhynchus spp.) invaded the Beringian Arctic until some time after the land bridge had been submerged and Bering Strait salinities had reached high values (see discussion under Salvelinus namaycush in the following section). Oncorhynchus gorbuscha and O. keta could have moved from Bering Sea drainages soon after the land bridge drowned.

So far as marine fishes are concerned, the first to enter the Arctic post-glacially came from the North Pacific (the land bridge was destroyed by the time European and eastern North American ice sheets began their final retreat). The first invaders from the south were species tolerant of low salinities. Two marine species may have entered from the Bering Sea soon after the land bridge was inundated:

Myoxocephalus platycephalus Pleuronecies stellatus Unless P. stellatus was present along the Arctic shore of the land bridge, it entered the Arctic soon after the land bridge drowned because it has made an extensive penetration of Arctic America; for some unknown reason it has not been reported from Arctic Siberia. Myoxocephalus platycephalus may have entered at an early date though it has not managed to extend its range beyond the Chukchi Sea.

STAGE 3, DISAPPEARANCE OF THE ICE SHEETS

As the ice sheets dwindled in area, fishes quickly moved in to populate the newly available habitats. The sequence of the deglaciation is practically unknown for western Arctic America and Siberia. Therefore the following discussion must be considered highly speculative. Fresh-water fishes are considered first, then marine fishes.

FRESH WATERS SIBERIA

Being concerned principally with the American portion of the Arctic, we limit the discussion of Siberian problems to those most pertinent to Arctic American zoogeography.

The amelioration of climate and disappearance of the ice sheets enabled "warm" freshwater fishes to invade river systems that had until then been inaccessible or uninhabitable. Large Arctic drainages that extend far south (Ob', Yenesei, Lena) and were scarcely glaciated undoubtedly served as sources for the invasion of smaller Arctic drainages. In particular the Lena was the major source for warm-water fishes spreading eastward into the Beringian Arctic. The Indigirka and Kolyma valleys probably lacked warm elements during the land bridge stage because their upper (southern) portions were glaciated, and none of the warm elements has reached Alaska.

One warm species has apparently spread farther east than the others. *Phoxinus phoxinus* presumably lives on the Chukchi Peninsula, as it exists in the Kolyma and Anadyr systems. However, its absence from Alaska (which has no minnows) indicates that it attained its present range after all fresh-water links between Siberia and Alaska

had been severed. It is presumed able to coexist with *Dallia* on the Chukchi Peninsula.

The 14 Siberian "fringe" elements (listed below) apparently spread east from the Lena more recently; Hucho taimen and Lota lota lota have not reached the Kolyma Valley, but the others have. A sharp faunal change takes place in drainages between the Lena system and the Chukchi Peninsula, evidenced by a rapid disappearance of Siberian fishes accompanied by an increase in the number of forms common to Arctic Alaska. For example, Catostomus catostomus is met with in the Yana system and streams to the east; Lota lota lota is replaced by Lota lota leptura in the New Siberian Islands and farther east; Dallia pectoralis and Cottus cognatus make their appearance on the Chukchi Peninsula.

Siberian "fringe" elements living in the Indigirka and/or Kolyma systems but absent from Chukchi Peninsula, Anadyr system, Kamchatka, and Penzhina system (Sea of Okhotsk):

Acipenser baeri
Hucho taimen
Brachymastax lenok
Coregonus peled
Coregonus muksun
Leuciscus leuciscus
Phoxinus percnurus
Phoxinus czekanowskii
Carassius auratus gibelio
Nemachilus barbatulus toni
Lota lota lota
Perca fluviatilis
Acerina cernua
Cottus poecilopus

Until the former Novosiberian ice sheet (which reached south to between the Yana and Indigirka systems) had dwindled considerably it was a barrier to the dispersal of some fresh-water fishes. This may account for the rapid transition from a predominantly Siberian fauna west of the Indigirka system (other Siberian species make their appearance in the Yana system and westward) to a predominantly Beringian fauna east of the Kolyma system. The "fringe" elements most likely took advantage of the "Climatic Optimum" to spread east of the Lena, and some may have spread through low-salinity coastal waters.

NORTH AMERICA

Generally speaking, as western Arctic America became deglaciated it lay open to invasion by fresh-water fishes coming from four areas: the Arctic Slope of Alaska, the Pacific Slope, the Mississippi Valley, and the Yukon Valley. Some species have entered by more than one route. Some fishes may have entered western Canada (i.e., west of longitude 105° W.) from the direction of Hudson Bay. Because Hudson Bay was among the last areas to become deglaciated, its contribution to the western fresh-water fauna has probably been meager; Salvelinus alpinus and Pungitius pungitius may have entered some parts of western Canada from Hudson Bay.

INVASION FROM ARCTIC ALASKA

As the Laurentide Ice Sheet withdrew, fresh-water species that tolerate coastal water were able to travel eastward from the Arctic Slope of Alaska along the Canadian Arctic coast, colonizing suitable waters along the way. Today many Canadian rivers have waterfalls or rapids near the coast which are insurpassable barriers for some fishes, but during the postglacial marine submergence some of the falls and rapids were non-existent and others were of much lower elevation above sea level.

The 17 fishes of the Arctic Slope of the land bridge plus the two salmons that entered Arctic Alaska post-glacially were potential invaders of Canada. Dallia pectoralis is absent from Canada, perhaps owing to its aversion to coastal waters. The euryhaline Coregonus lavaretus pidschian seems absent from Arctic Canada; perhaps it cannot coexist with C. clupeaformis. The remaining 17 forms are listed individually.

Lampetra japonica is eurhyaline and has penetrated east to the Mackenzie and south to Great Slave and perhaps Artillery lakes.

Oncorhynchus gorbuscha is euryhaline and has penetrated east to the lower Mackenzie system.

Oncorhynchus keta is eurhyaline and has penetrated east to the Mackenzie system and south to just below Fort Smith on the Slave River (i.e., as far upstream as Stenodus).

Salvelinus alpinus complex is euryhaline and occurs in virtually all Arctic fresh waters having present or past access to the sea.

Arctic charr range south in the Mackenzie system to Fort Good Hope (Wynne-Edwards, 1952). Nothing is known regarding possible landlocked populations of this fish in the myriad lakes of western Arctic Canada; landlocked populations exist in lakes along the west shore of Hudson Bay (Sprules, 1952). Arctic charr occur in every larger Arctic coastal stream that has been investigated, and have been found north to the extremities of land. Sea-running charr are known from the west shore of Hudson Bay as far south as the Churchill system, with unauthenticated reports for the Nelson River (Sprules, 1952). The Eastern Arctic charrs probably came from an eastern North American refuge, as there are landlocked forms in the lakes of New England.

Stenodus leucichthys nelma is euryhaline and ranges east to the Anderson system (ca. 200 miles east of the Mackenzie Delta) and Cape Bathurst and south in the Mackenzie Valley to Fort Smith on the Slave River (between Great Slave Lake and Lake Athabaska).

Coregonus sardinella is euryhaline and ranges east to Bathurst Inlet and south to Camsell Bend on the Mackenzie. It is absent from Great Bear and Great Slave lakes.

Coregonus autumnalis is euryhaline and has the same range as C. sardinella.

Coregonus nasus is euryhaline and has the same range as the two preceding species, though it does enter Great Bear Lake.

Prosopium cylindraceum is euryhaline and may range all along the Arctic coast, though there are no reports for the little-known area between Bathurst Inlet and Wilson River on the west shore of Hudson Bay (latitude 62° N.).

Thymallus arcticus signifer is not prone to enter coastal waters in any numbers, and therefore it is not likely that Arctic Slope of Alaska stocks made much headway to the east by way of the sea.

Osmerus eperlanus dentex is euryhaline and ranges east to Cape Bathurst and south to Arctic Red River in the lower Mackenzie system.

Hypomesus olidus drjagini is eurhyaline and ranges east to the Mackenzie system where it is known from the lower part (Peel River).

Esox lucius seldom enters coastal waters. The Arctic Alaska stocks probably did not invade eastward.

Catostomus catostomus rostratus readily enters coastal waters. It ranges east to the Coppermine, but its southern limit in Canada is unknown.

Lota lota leptura readily enters coastal waters and ranges east to the Coppermine along the Arctic coast, but its eastern and southern limits in Canada are unknown.

Pungitius pungitius is euryhaline and probably occurs all along the mainland coast and in the southern islands of the Archipelago; Arctic Alaska stocks have probably met and mingled with fishes coming from the Mississippi Valley.

Cottus cognatus probably occurs all along the Arctic coast, though few collectors have gotten this species. In Ungava Bay Dunbar and Hildebrand (1952) reported it from tide pools, which indicates the possibility that this species could have dispersed east from Arctic Alaska by way of coastal waters.

INVASION FROM PACIFIC SLOPE

Four species, typical of Pacific Slope or western drainages, are of limited distribution in the Arctic watershed, though none actually enters the area we are concerned with. Prosopium williamsoni occurs in the upper Saskatchewan and Athabaska rivers (Bajkov, 1927; Schultz, 1936), and P. oregonium has been identified from Lesser Slave Lake (Dymond, 1943). The minnow Richardsonius balteatus and the sculpin Cottus asper have been reported from a tributary of the Crooked River, Peace-Mackenzie system, in British Columbia (Carl and Clemens, 1953).

The presence of these western fishes in the Arctic watershed, though their distribution is limited, suggests that some other fishes which are now widely distributed in the Arctic watershed may owe a small part of their present range to headwaters transfer from western drainages. In particular the following, though they probably entered some Pacific Slope streams by headwaters transfer from the Arctic watershed, may have secondarily reëntered the Arctic watershed from the Pacific Slope:

Salvelinus namaycush Catostomus catostomus subsp.

Couesius plumbeus Rhinichthys cataractae Lota lota subsp.

The presence of so many species and genera of fishes peculiar to Pacific slope and western drainages indicates that the Arctic watershed has received no important contributions to its ichthyofauna from this source.

INVASION FROM UPPER MISSISSIPPI VALLEY

As the Laurentide Ice Sheet withdrew, rivers that had their lower courses blocked by the ice wall backed up and formed extensive glacial lakes. Where the post-glacial sequence has been well studied, it is apparent that drainage patterns changed more than once, and glacial lakes formed, drained, and formed again. The sequence for eastern North America, as it has influenced fish distributions, was given by Radforth (1944). The geological sequence for eastern North America has recently been reviewed by Lougee (1953).

The retreat of the ice sheet west of the Great Lakes basin appears to have progressed from the southwest towards the north and northeast (cf. Flint, 1947, fig. 57). There is no detailed information concerning changes in post-glacial drainage patterns for northwestern Canada, but it is likely that a series of glacial lakes resulted as the ice sheet withdrew. The former glacial Lake Agassiz, survived now by Lakes Winnipeg, Winnipegosis, and others, was as large as the combined areas of the present Great Lakes, extended from Saskatchewan and northern Manitoba to North Dakota and Minnesota, and spilled over into the Mississippi Valley. According to the map prepared by Flint et alii (1945) the present lakes of Great Bear, Great Slave, Athabaska, Wollaston, Cree, and Reindeer were formerly larger than they are today and lie in a generally northwest-southeast line between the Mackenzie Delta and the former Lake Agassiz; connections between all these lakes and the bed of Lake Agassiz now exist. Some fishes moving northwestward from the Mississippi Valley followed the chain of glacial lakes and occupied deglaciated country as soon as it became inhabitable; they are broadly distributed in northwestern Canada. Others, moving northwestward at a later date, were not able to spread very far beyond the Mackenzie Valley as drainage

patterns assumed their present picture.

Twenty-one or 22 species living in the North-West and Yukon Territories may have come in post-glacially from the direction of the upper Mississippi Valley; only a few have spread into the Arctic. Prosopium hearnei and Leucichthys nueltinensis, recently named by Fowler (1948) from Nueltin Lake, North-West Territories, on the Manitoba and North-West Territories border, are not included in the discussion because they are known only from the original descriptions.

Amphiodon alosoides ranges northwest to Great Slave Lake and the Mackenzie River but does not enter the Arctic. It entered from the Mississippi Valley.

Salvelinus namaycush ranges from the islands of the Canadian Archipelago south to the upper Mississippi Valley, the Great Lakes basin, and New England; and from British Columbia and Alaska east to Labrador. In common with other cold-water fishes, the lake trout is restricted to lakes in the south, but in the far north it also lives in rivers and coastal waters.

Although Radforth (1944) and Wynne-Edwards (1952) believed the fish resided in the northwest (lower Yukon Valley) during the glacial period, the present writer considers this viewpoint untenable. Otherwise, the lake trout would have had access to Siberia via either the land bridge or the freshened seas that resulted after the land bridge drowned. Of the 20 species of fresh-water fishes found in Siberia east of the Kolyma Valley, only the minnow (Phoxinus phoxinus) is absent from Alaska, and except for S. namaycush every Arctic Alaskan fresh-water fish occurs in Siberia; it is improbable that the lake trout has been kept out of Asia by a small minnow. Hucho taimen, the only northeast Siberian fish that might possibly compete with the lake trout, does not occur east of the Indigirka system. If S. namaycush had lived in the northwest during glacial times, it may have been prevented from colonizing Siberia by the rigorous climate, but this is not likely because the lake trout ranges as far north as any other North American fresh-water fish other than S. alpinus, which indicates that it is well adapted for arctic life. The lake trout can disperse across saline water. There is no other way to explain its presence on the Arctic islands, because if anything the islands are now separated from one another and the mainland by the narrowest gaps since the withdrawal of the glaciers, and the sea of early post-glacial time was of lower salinity than it is today. If the lake trout had lived in Arctic Alaska and/or the Yukon Valley during the last glacial period, it would have been able to colonize Siberia and should be present in the Kolyma, Anadyr, and other river valleys today.

The foregoing reflections suggest that the lake trout, until recently, had been absent from the northwest. During the last glacial period it lived south of the Laurentide Ice Sheet, where arctic to boreal conditions obtained. The species was present in what is now the United States prior to the last glacial period; Hussakof (1916) found fossil remains in interglacial clays from Wisconsin. Radforth (1944) doubted whether suitable habitats were available south of the ice sheet. but surely there must have been at least one suitable water body for the species in the thousands of miles between the Rockies and the Atlantic Coast; also it is likely the fish was not restricted to lakes.

As the present writer visualizes the situation, S. namaycush followed the retreating ice border northward from glacial refugia in the United States, utilizing the chain of glacial lakes (beginning with Lake Agassiz) and the Mackenzie to sweep northwestward to the Arctic Coast; it also traveled northeastward up the Quebec-Labrador Peninsula, but probably much later (owing to the persistence of the ice sheet). The low salinities of the postglacial sea permitted it, on reaching the Arctic coast, to travel northward to colonize the southern islands of the Canadian Archipelago. The fish was also able to move westward from the Mackenzie Delta and invade the Arctic Slope of Alaska. However, it was unable to reach Bering Strait (if it has done so at all), until salinities in the strait and adjoining seas had reached high values, thereby preventing it from reaching Siberia. It is also most probable that the lake trout entered the Yukon, Skeena, and Fraser valleys at several points from the Mackenzie Valley by headwaters transfer. Owing to its lake-dwelling habits it would have been among the first to cross a divide when a stream, dammed by glacial activity, spilled into a neighboring drainage. Once in the Yukon system the fish could have emigrated downstream, ascending tributaries along the way, and now and then transferred to adjoining systems through the headwaters. Its presence in the Kobuk system of Kotzebue Sound may be attributable to transfer from either the Yukon or Colville systems.

Salvelinus namaycush is the only fresh-water fish indicated to have invaded Arctic Alaska post-glacially from Canada; some others may have done so, but as yet there is no evidence that they have.

Coregonus artedi ranges northwestward to Great Bear Lake but is unknown from Arctic Canada west of Hudson Bay; in addition it is absent from the Yukon system and from the interior of the Yukon Territory. It is replaced northward and westward by C. sardinella. Its absence from unglaciated parts of northern Canada and Alaska and its widespread distribution through Canada on both sides of Hudson Bay (absent from Labrador) south to the upper Mississippi Valley, the Great Lakes basin, and the upper Hudson Valley in New York suggest that during glacial times C. artedi was distributed in cold waters south of the Laurentide Ice Sheet. It followed the retreating glaciers and drew its southern limit northward as the climate warmed.

Coregonus nigripinnis. Rawson (1947a) listed lake herrings of the "Leucichthys nigripinnis" type for Great Slave Lake. If this species occurs, it must have entered from the direction of the Mississippi Valley; it is otherwise known from Late Athabaska southeastward to Lake Ontario. Rawson also indicated "tullibee" for Great Slave Lake, but in the absence of more specific information nothing can be said about it here.

Coregonus clupeaformis ranges from the Mackenzie Delta east to Ungava Bay and Labrador, south to New England and the Great Lakes basin and west to Montana. It is absent from the Mississippi Valley and also from the Arctic Slope of Alaska and the lower Yukon Valley. Although the fish was probably eliminated from the southern part of its range by the warming post-glacial climate, this does not account for its absence from the north, where other species of the genus abound today. It probably passed the last glacial

period south of the Laurentide Ice Sheet and extended its range northward as the ice withdrew. Its present occurrence in the south is limited to waters still having an arctic or subarctic character. It has reached the Arctic coast in Canada but seems not to overlap the range of *C. lavaretus pidschian* farther west except perhaps in the upper Yukon Valley. *Coregonus clupeaformis* lives in some lakes in the upper Yukon Valley of British Columbia and the Yukon Territory, and in the Skeena and Fraser systems of British Columbia (it has been introduced elsewhere); headwaters transfer from the Mackenzie Valley seems to have taken place.

Prosopium cylindraceum may have entered part of its range in the western Arctic watershed from the upper Mississippi Valley, but a great distributional gap is indicated. The species is missing from northern and western Ontario (Radforth, 1944), and in Manitoba it is known only from waters close to Hudson Bay (Hinks, 1943); it is absent from lakes that are remnants of the former Lake Agassiz (notably Winnipeg and Winnipegosis). There seem to be no definite records from Saskatchewan or Alberta. Harper and Nichols (1919) had a Prosopium parr from Thluicho northern Saskatchewan. (1924) had three small Prosopium parrs from Lake Athabaska. Rawson (1947b) listed "round whitefish" from Lake Athabaska. All these could be P. cylindraceum, P. oregonium, or possibly P. williamsoni, as all three occur in the Mackenzie Valley, and the last two are known from waters tributary to Lake Athabaska. They may also be the littleknown P. hearnei Fowler (1948). In addition, P. cylindraceum has not been recorded from the Mackenzie Valley in British Columbia. The species occurs in the Yukon and rivers of Arctic Alaska from their lower parts to their headwaters, which means that if it had come into northwestern Canada from the Mississippi Valley its range should include all suitable waters along the way. Instead it is unknown from interior waters between the North-West Territories and the Great Lakes; the fishes of Hudson Bay drainages in Manitoba may have come in recently from the north, by way of the sea. On the other hand the round whitefish occurs in the Great Lakes, lakes of New York and New England,

and apparently throughout the Quebec-Labrador peninsula; these eastern American stocks were probably derived from a glacial refugium east of the Mississippi Valley.

Esox lucius has probably entered some of northwestern Canada from the direction of the Mississippi Valley. It seems to occur in all suitable waters save for a poorly explored gap between Bathurst Inlet and the Churchill system of Manitoba.

Catostomus catostomus subsp. probably entered some of northwestern Canada from the direction of the Mississippi Valley.

Catostomus commersoni ranges northwestward to Arctic Red River in the Mackenzie system. It entered from the Mississippi Valley.

Pfrille neogaea ranges northwestward to Fort Good Hope on the Mackenzie. It entered from the Mississippi Valley.

Rhinichthys cataractae ranges northwestward to Fort Good Hope and Peel River of the Mackenzie system. It probably entered from the Mississippi Valley.

Couesius plumbeus, the only minnow known from the Yukon system, occurs in the upper portions of the valley. In the Mackenzie system it is distributed from the delta southward and ranges east to the Atlantic coast. It probably entered from the Mississippi Valley and is the only minnow known from the western Arctic.

Platygobio gracilis ranges northwest to Fort Good Hope on the Mackenzie. It entered from the Mississippi Valley.

Notropis hudsonius ranges northwestward to Fort Good Hope on the Mackenzie. It entered from the Mississippi Valley.

Notropis atherinoides ranges northwestward to Fort Simpson on the Mackenzie. It entered from the Mississippi Valley.

Lota lota lacustris probably occurs in the western Arctic watershed. Wynne-Edwards (1952), noting that Mackenzie and Yukon fishes are not intermediate between L. l. leptura and L. l. maculosa (=L. l. lacustris), neglected to say what the Mackenzie and Yukon fishes are. The Columbia system has L. l. lacustris.

Pungitius pungitius seems to have traveled northwestward from the direction of the Mississippi Valley. It is absent from the Mississippi Valley today, which may be because of lack of suitable habitats. The species is otherwise continuously distributed northwestward from the Great Lakes basin to the Mackenzie Delta, in the lower elevations; it is absent from the Rockies. Much of its range in eastern North America is attributable to post-glacial marine transgressions which have left isolated inland fresh-water populations of the species as relicts, in addition to populations in rivers and lakes having direct communication with the sea today. However, this does not account for the populations of the Great Lakes basin above Niagara Falls. Possibly *Pungitius* may have spread south to the Great Lakes from the northwest post-glacially, as suggested by Radforth (1944). But this seems unlikely, because it is difficult to visualize the little stickleback conquering waterfalls and rapids (such as the obstacles at Camsell Bend on the Mackenzie and Fort Smith on the Slave River) which have held back more powerful swimmers such as Coregonus nasus, Oncorhynchus keta, and Stenodus. The stickleback has not even been able to invade the upper Yukon, and it is absent from Arctic Alaskan streams above the first big rapids. It is most likely that Pungitius spread downstream from the Mississippi Valley into the northwest, meeting its species near the coast, rather than having spread upstream from the northwest to the Great Lakes. The upper Great Lakes populations represent pre-Wisconsin relicts.

Percopsis omiscomaycus ranges northwestward to the upper Yukon system. It entered from the Mississippi Valley, getting into the Yukon by headwaters transfer from the Mackenzie.

Stizostedion vitreum ranges northwestward to the Mackenzie delta. It entered from the Mississippi Valley.

Cottus cognatus is very broadly distributed, from tide pools to headwaters mountain springs, from Siberia east to Labrador and south to Iowa and Virginia. It is likely that the species has invaded some of the Arctic watershed from the direction of the Mississippi Valley.

Cottus ricei ranges northwestward to the Mackenzie Delta. It entered from the direction of the Mississippi Valley.

Myoxocephalus (Triglopsis) thompsoni was listed by Rawson (1951) from Great Slave

Lake. The species is otherwise known from all five of the Great Lakes, Lake Nipigon, and Torch Lake in Michigan. This is the freshwater representative of Myoxocephalus quadricornis. The marine form is not a strong migrator and is not known above the lower Mackenzie (Arctic Red River, Preble, 1908); there is no evidence that the Mackenzie Valley (including Great Slave and Great Bear Lakes) has experienced post-glacial marine submergence (Flint et al., 1945; Richards, 1950). The fresh-water relict probably came north via the chain of glacial lakes, and will probably be found in many interior lakes that had been part of the chain (i.e., Great Bear, Artillery, Athabaska, etc.). The presence of the relict in Lake Ontario may be attributable to post-glacial marine submergence (cf. Lougee, 1953), though the marine fish is not known south of northern Labrador today (Backus, 1953).

INVASION FROM YUKON VALLEY

The fact that much of the Yukon Valley escaped glaciation has been used by zoogeographers to relegate certain species to a Yukon glacial refugium, the species spreading out over their present ranges via the Mackenzie Valley as the ice sheets withered away. So far as the ichthyofauna is concerned, the only direct way to enter the Mackenzie Valley from the Yukon Valley is by headwaters transfer. An indirect route, from the Yukon mouth to the Mackenzie mouth via Arctic Alaska is possible and is discussed above under the headings Stage 2, Drowning of Land Bridge and Invasion from Arctic Alaska.

It is obvious that the only species capable of entering the Mackenzie through headwaters transfer from the Yukon are those that enter the upper parts of the Yukon system. Species that do not exist in the upper Yukon could not have entered the Mackenzie (where they occur today) by headwaters transfer. They entered the Mackenzie from Arctic Alaska via the sea. These are:

Oncorhynchus gorbuscha
Salvelinus alpinus complex
Coregonus autumnalis
Osmerus eperlanus dentex
Hypomesus olidus drjagini
Pungitius pungitius pungitius

One species enters the upper Yukon but is absent from the Mackenzie and also from Arctic Alaska: Oncorhynchus tschawytscha.

One species may enter the upper Yukon but is absent from the Mackenzie though it occurs in Arctic Alaska: Coregonus lavaretus bidschian.

One species, widespread in the Yukon and in Arctic Alaska, was shown to have entered the northwest from the direction of the upper Mississippi Valley: Salvelinus namaychush.

Three species, common to the Mackenzie and Yukon systems but absent from Arctic Alaska, indicate that headwaters transfer has taken place. These are distributed throughout the Mackenzie system north to the delta, they are widely distributed over the rest of North America, but in the Yukon system they are known only from its upper parts. It seems most reasonable that they entered the Yukon from the Mackenzie, and their home during the last glacial period was located south of the ice sheets. If they had used the Yukon Valley as a glacial refugium, we would expect them to be at least fairly broadly distributed in the unglaciated portions, which is not the case. These three are:

Coregonus clupeaformis Couesius plumbeus Percopsis omiscomaycus

Coregonus sardinella and C. nasus occur in the upper Yukon but are limited to the lower Mackenzie. They seem to have entered the Mackenzie from the sea rather than from the Yukon.

Nine fishes remain to be considered. Each ranges widely in the Yukon to its upper parts, and each is distributed in the Mackenzie system south at least to Great Slave Lake. These nine fishes could have entered the Mackenzie by headwaters transfer from the Yukon, although some also entered from the Arctic Slope of Alaska through the Mackenzie mouth and some also entered from the upper Mississippi Valley.

Lampetra japonica may have entered the Mackenzie system from the Yukon, although its sea-running form also came into Canada from the Arctic Slope of Alaska by way of river mouths. Wynne-Edwards (1952) reported it from the upper Yukon.

Oncorhynchus keta may have entered the

Mackenzie from the Yukon, although its ability to enter coastal waters strongly indicates that it entered Canada from Arctic Alaska via the sea. Dymond (1940) listed the species from the Slave River, 5 miles below Fort Smith. The upstream penetration of this species is identical to that of Stenodus, another notable migrator. It is unlikely that O. keta came into the Mackenzie from the Yukon by headwaters transfer, because the capture of salmon above the lower portions of the Mackenzie is a noteworthy event; evidently the Mackenzie Valley south to the rapids of the Slave River at Fort Smith is penetrable by any strong migrator coming in from the sea. This suggests that Stenodus (below) and perhaps others may have been able to go south to Great Slave Lake and Fort Smith from the Mackenzie Delta, instead of having to rely on headwaters transfer from the Yukon to get into the upper Mackenzie system.

Stenodus leucichthys nelma may have entered the Mackenzie from the Yukon, although the tendency to enter salt waters indicates that it also entered Canada from Arctic Alaska via river mouths. It is a notable migrator and may have attained its entire Mackenzie range from the sea (see Oncorhynchus keta, above).

Prosopium cylindraceum may have entered the Mackenzie system from the Yukon, although its ability to enter coastal waters indicates that it also entered Canada from Arctic Alaska by way of river mouths. It is unlikely that it invaded the western Arctic from the Mississippi Valley.

Thymallus arcticus signifer seems most likely to have entered the Mackenzie from the Yukon. It occurs on the Arctic Slope of Alaska, but its weak tendency to enter coastal waters indicates that little colonization of Canada has taken place by fishes coming in through river mouths and coastal waters. The grayling ranges east to the drainages of the western shore of Hudson Bay south to just north of the Nelson system, and to the upper reaches of the western Arctic watershed. Thymallus arcticus tricolor of the upper Missouri Valley (Mississippi drainage) and formerly of the southwestern Great Lakes basin is absent from Canada (cf. Dymond, 1947), indicating that the Mississippi Valley has not supplied grayling stock to the western Arctic.

Esox lucius occurs in headwaters lakes of the Yukon and could therefore have entered the Mackenzie, but the western Arctic watershed has also received stocks from the Mississippi Valley. Because the species is not prone to enter coastal waters, Arctic Alaska seems not to have contributed E. lucius to Canada.

Castostomus catostomus subsp. could have entered the Mackenzie from the Yukon; it also entered western Arctic Canada from Arctic Alaska and from the upper Mississippi Valley.

Lota lota leptura could have entered the Mackenzie system from the Yukon, if it occurs in the Mackenzie above the lower stretches; it also entered Canada from Arctic Alaska.

Cottus cognatus could have entered the Mackenzie from the Yukon; it also entered from the Mississippi Valley and probably also from Arctic Alaska.

In addition to its contributions to the Mackenzie, the Yukon system may have contributed fishes to Arctic Alaska. After the land bridge drowned, Oncorhynchus gorbuscha and O. keta invaded the Arctic drainages through Bering Stratit; the Yukon and also the Anadyr (Siberia) were in all likelihood the immediate sources for the Arctic emigrants. The presence of Salvelinus namaycush in the Kobuk system of Kotzebue Sound may be due to headwaters transfer from either the Yukon or Colville systems.

MARINE WATERS

When Bering Strait salinites had risen sufficiently, a number of Bering Sea forms were able to spread northward into the Arctic. With one exception all of these occur also in the Sea of Okhotsk, which indicates that they did live south of the land bridge; the exception, Agonus acipenserinus, ranges southward to Puget Sound along the Pacific coast of North America (as does Lycodes palearis). The restriction of these fishes principally to the Chukchi Sea in our area (which had been dry land not long previously) is considered evidence that they did not survive the glacial period north of the land bridge:

Stichaeus punctatus Lumpenus fabricii Lumpenus medius (also entered our area from Europe)
Lycodes knipowitschi
Lycodes raridens
Lycodes palearis
Myoxocephalus jaok
Agonus acipenserinus
Hippoglossoides elassodon robustus
Limanda aspera

Some of the above are also found in the North Atlantic and together with many more forms that do not enter our area constitute the "discontinuous circumboreal" group of Ekman (1953) (= the "amphiboreal" group of Soviet students). The probable causes of discontinuous circumboreal distributions were discussed ably and in great detail by Andriashev (1939a), and it is unnecessary to delve into the subject here, because the phenomenon is one of boreal rather than arctic waters and reflects pre-Wisconsin distribution patterns. Future explorations may reveal that some of the above 10 species are distributed considerably beyond the confines of the Chukchi Sea, but in the light of present information we can do nothing but consider these, together with Myoxocephalus platycephalus, as "fringe" elements of North Pacific derivation.

As the ice sheets disappeared, marine areas were colonized by fishes coming from many directions. Most likely the first fishes to move into deglaciated areas were brackish-water forms and could follow close to the retreating ice walls; high-salinity forms came in later. The course of the deglaciation in marine areas of the Arctic is unknown, and therefore the following discussion must be the least definite of all thus far.

Two species, continuously distributed across the Arctic today, may have been absent during the land bridge stage. They had glacial refugia in the North Atlantic and North Pacific, and, with the disappearance first of the land bridge and later of the ice sheets, they could have quickly entered the Arctic from both oceans, spreading eastward and westward as opportunity permitted. The North Atlantic and North Pacific stocks met to produce a circumpolar distribution.

Mallotus villosus is broadly distributed in the North Atlantic and North Pacific oceans. It is circumpolar, but the range has moved northward considerably in Greenland during the years of "warm" climate, as shown by Jensen (1939). The Greenland observations indicate that a sufficient deterioration of the climate might eliminate capelin from the Arctic and cause the species to have a discontinuous circumboreal distribution.

Myoxocephalus scorpius is circumpolar in distribution and as with the capelin its abundance diminishes northward. In the range of M. quadricornis this species appears to seek deeper habitats than those farther south. This is contrary to the general rule that in the northern portion of its range a northern species occurs in shallower waters. The European M. s. scorpius becomes replaced by the Asiatic-American M. s. groenlandicus in the eastern part of the Kara Sea.

The distributions of five high-salinity forms indicate recent penetration from the North Atlantic. The easternmost penetration from Europe has reached the Laptev Sea, from which Lumpenus medius and Eumicrotremus derjugini are known; the former also entered the Chukchi Sea from the North Pacific (mentioned above). The westernmost penetration from eastern North America for high-salinity forms is made by Anarhichas denticulatus (Lycichthys fortidens), Eumesogrammus praecisus, and Eumicrotremus spinosus which are known from the western members of the Canadian Archipelago (Prince Patrick, Banks, and western Victoria Islands).

In addition, two euryhaline species appear to have spread westward from eastern Arctic America. Gadus morhua ogac ranges west to Point Barrow, and Myoxocephalus scorpioides ranges west to Chaun Bay in Siberia. In view of the absence of records for these fishes from most or all of Siberia and Europe (if G. morhua maris-albi is not identical to G. m. ogac), it is unlikely that they lived in the Beringian Arctic during land bridge times. The White Sea codfish may represent a separate European population that has entered the Arctic post-glacially.

We turn now to the influence of the Beringian Arctic in the enrichment of the marine fauna of deglaciated portions of Arctic America (Siberia is here not considered further).

Four marine fishes occur in western Canada which are absent from Labrador, Greenland,

and the northern islands of the Archipelago; all are broadly distributed to the west. They could have come into deglaciated localities only from the west. These are:

Clupea harengus pallasi Eleginus n. navaga Liopsetta glacialis Pleuronectes stellatus

All are definitely known to range as far east as Bathurst Inlet. Three (Eliginus, Liopsetta, Pleuronectes) are believed to range into Queen Maude Gulf, but their absence from Hudson Bay and the rest of the Eastern Arctic may be considered real. Two have close relatives in the North Atlantic (Clubea harengus harengus and Liopsetta putnami), but these are absent from Hudson and Ungava Bays, according to Vladykov (1933) and particularly Dunbar and Hildebrand (1952). All four species can survive in water of low salinity; they probably followed the retreating ice wall at not too great a distance, keeping close to the mainland coast (none is known from the Archipelago, though they may be expected among the southern islands). The occurrence of these fishes in western Arctic Canada should not be interpreted as being indicative of an influence of Pacific water (Dunbar, 1947, 1951, has taken the herring to indicate this), because Eleginus and Liopsetta and probably also Clupea appear to have lived in the Arctic since the land bridge stage; all three range west to the White Sea in Europe. It is also interesting that euryhaline fresh-water fishes, which entered western Canada only via the sea from Arctic Alaska and from no other source, have seemingly been unable to reach Hudson Bay; examples are Oncorhynchus gorbuscha, Coregonus sardinella, C. autumnalis, C. nasus, Osmerus eperlanus dentex, and Hypomesus olidus drjagini.

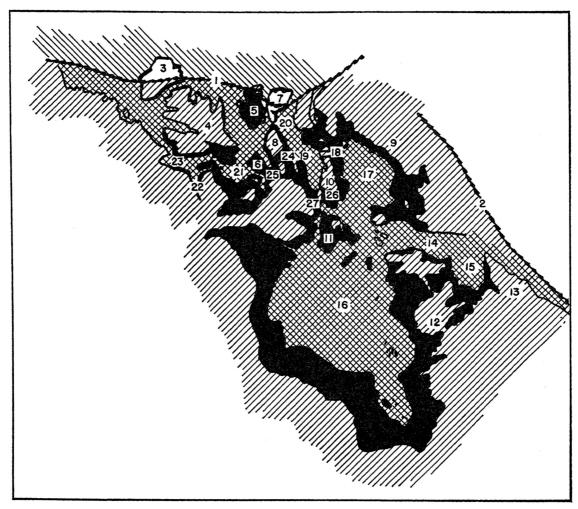
The evident inability of euryhaline western elements, both fresh-water and marine, to invade Hudson Bay through coastal waters is in contrast to certain euryhaline Eastern Arctic marine fishes (Gadus morhua ogac, Myoxocephalus scorpioides) which have gone west to Point Barrow, Siberia, and northern Bering Sea. A possible explanation for this lies in the sequence of deglaciation and postglacial uplift in the Arctic.

As shown in map 4, at present the most southern connection between Hudson Bay and the sea to the west is Fury and Hecla Strait (about latitude 70° N.) which leads from Foxe Basin into the Gulf of Boothia, but post-glacially there were two other straits across the Melville Peninsula (about latitude 67° N.) connecting Hudson Bay proper with the Gulf of Boothia. At present the most southern connection between the Gulf of Boothia and the sea to the west is Bellott Strait (about latitude 72° N.), but formerly there was one connection immediately south of Bellott Strait, a second across Boothia Peninsula at about latitude 69° 30' N., and a third across Boothia Peninsula at about latitude 68° 30′ N. (map 4).

Today, any fish moving between Hudson Bay and, say, Queen Maude Gulf must go north to latitude 72° N. to use Bellott Strait and to 70° N. to use Fury and Hecla Strait. This route may not be favorable for many fishes, owing to its high latitude and absence of near-by large rivers to supply "warmth" and low salinities in winter.

After the ice sheet withdrew, however, the marine submergence permitted a route farther south; fishes could utilize the strait across Boothia Peninsula (at latitude 68° 30' N.) and the strait across Melville Peninsula (at latitude 67° N.). This southern (postglacial) route lay close to large mainland rivers, and the retreating ice sheet provided great volumes of "warm" fresh water to assure low salinities. The absence of euryhaline western fishes from Hudson Bay is puzzling in view of the former existence of a more southerly, probably more favorable, marine route to Hudson Bay.

Perhaps a residual ice mass lying west of Bathurst Inlet (between the mainland and Victoria Island) prevented western euryhaline fishes, unable to pass north of Victoria Island, from traveling eastward until sufficient uplift had taken place to close the southern marine route to Hudson Bay. This suggestion (neither supported nor negated by geological evidence) of a lingering ice barrier west of Bathurst Inlet would explain the distributions of Gadus morhua ogac and Myoxocephalus scorpioides, which were able to get west of Hudson Bay by the southern route but were stopped on the east side of the bar-



MAP 4. Distribution of the Laurentide Ice Sheet and areas of post-glacial marine submergence in Arctic Canada. Islands north of Viscount Melville Sound, Barrow Strait, and Lancaster Sound omitted. Limit of ice sheet west of Baffin Island based on Hobbs (1945) and Jenness (1952); areas of marine submergence based on Flint et al. (1945). Areas of marine submergence, now dry land, shown in solid black; margins of ice sheet shown by serrated line; glaciated areas shaded by lines ascending to the right; seas shaded by lines descending to the right. 1. Northern edge of ice sheet. 2. Hypothetical eastern edge of ice sheet. 3. Banks Island. 4. Victoria Island. 5. Prince of Wales Island. 6. King William Island. 7. Somerset Island. 8. Boothia Peninsula. 9. Baffin Island. 10. Melville Peninsula. 11. Southampton Island. 12. Quebec. 13. Labrador. 14. Hudson Strait. 15. Ungava Bay. 16. Hudson Bay. 17. Foxe Basin. 18. Fury and Hecla Strait. 19. Gulf of Boothia. 20. Bellott Strait. 21. Queen Maude Gulf. 22. Bathurst Inlet. 23. Coronation Gulf. 24. Former post-glacial marine passage. 25. Former post-glacial marine passage. 26. Former post-glacial marine passage.

rier; when the barrier disappeared they then moved west to Point Barrow, Bering Sea, and eastern Siberia.

Our discussion thus far has indicated that there are no distinctly western euryhaline elements that entered Hudson Bay by way of the sea (*Prosopium cylindraceum* probably came in via headwaters transfer and glacial lakes from the Yukon Valley, together with *Thymallus arcticus signifer*). However, certain fishes that lived in the Beringian Arctic during land bridge times are present in

Hudson Bay, but they have not necessarily entered Hudson Bay from the west. They probably had glacial refugia in several places; there is no reason to suggest that they had a refuge only in the Beringian Arctic. Some species most likely existed north of the ice sheets (which in the Western Arctic reached to about latitude 74° N.), some were most likely found in Baffin Bay and the Labrador Sea, and some seem to have ranged south to the United States along the Atlantic coast. Thus as the ice sheets dwindled Hudson Bay lay open to colonization from the west, north, and east; there is no evidence in the ichthyofauna that it had been colonized by marine fishes coming from the south via a postulated post-glacial marine connection with the Gulf of St. Lawrence. It seems most likely that virtually all the marine fauna came into Hudson Bay from the east, through Hudson Strait, which accounts for its great affinity with the Atlantic fauna. Some high arctic forms may also have come from the north through Fury and Hecla Strait. Vladykov (1934a) considered that four marine fishes reflect an association between Hudson Bay and the Bering Sea in the west via the Arctic Ocean: Lycodes ?turneri (Lycodalepis sp., probably polaris), Gymnocanthus galeatus, Triglops pingeli beani, and Liparis cyclostigma.

The Pacific Triglops pingeli beani is now considered identical to T. p. pingeli of Greenland (Shmidt, 1950); the Hudson Bay fish most likely entered from the east through Hudson Strait. Naked species of Lycodes (Lycodalepis) are typical of Arctic waters, the species L. turneri ranging from the Kara Sea east to West Greenland and south to the Gulf of St. Lawrence and northern Bering Sea; the Hudson Bay fish most likely entered from the east through Hudson Strait (the other naked Arctic species, L. jugoricus and L. mucosus, are absent from the Pacific; two naked species, L. bathybius and L. heinemanni, occur in the Pacific but are known only from the Sea of Okhotsk).

Vladykov's Gymnocanthus galeatus may have been G. detrisus, but in either case, the species is otherwise unknown outside the

North Pacific; similarly, Liparis cyclostigma is otherwise known only from Bering Sea. A number of high-salinity fishes range into the Chukchi Sea from the Bering Sea but have never been reported from Hudson Bay: e.g., Lycodes knipowitschi, L. raridens, L. palearis, Myoxocephalus jaok, Agonus acipenserinus, Hippoglossoides elassodon robustus, and Limanda aspera. In view of the fact that North Pacific forms that do enter the Arctic Ocean are absent from Hudson Bay while North Pacific forms that do not enter the Arctic Ocean are present in Hudson Bay, the present writer is inclined to regard the Hudson Bay records of "Gymnocanthus galeatus" and Liparis cyclostigma as indicative of discontinuous circumboreal distributions, if the specimens really are these species. There is no satisfactory evidence that any high-salinity forms have entered Hudson Bay postglacially from the west. Dunbar and Hildebrand (1952) regarded the occurrence of Eumesogrammus praecisus and Icelus spatula in Ungava Bay as possible evidence of an affinity with the North Pacific. The ranges of both species are now known to be more extensive in North America than those authors believe, thanks to the research of Backus (1953); E. praecisus ranges south to Belle Isle Strait (between Labrador and Newfoundland), and I. spatula ranges south to Cape Cod. Eumesogrammus praecisus is almost certainly of discontinuous circumboreal distribution, together with other blennies, such as Stichaeus punctatus, Pholis fasciatus, Lumpenus fabricii, Lumpenus maculatus, and Lumpenus medius. Their distributions reflect pre-Wisconsin patterns of continuous ranges in the Arctic and do not indicate that any post-glacial exchanges between the Atlantic and Pacific have occurred. It has been shown elsewhere that Icelus s. spatula appears to have entered the North Pacific post-glacially from the Arctic Ocean; its presence in the Eastern Arctic could be interpreted to mean that during the last glacial period this fish had a refugium off eastern North America as well as along the Arctic coast of the land bridge.

ARCTIC VERSUS SUBARCTIC

At present the matter of delimiting arctic salt waters from subarctic salt waters is purely academic, because the major part of the polar basin, off Siberia and western North America, has been poorly explored. Our knowledge of the fauna is practically limited to the rim of the Arctic Ocean in this area. In addition, the less well known a locality, the more likely it is to be considered "high arctic." There is a general dropping out of species northward, to be sure, but the fauna in many localities is undoubtedly much richer than the literature indicates. As the relatively inaccessible parts become better explored many localities are placed farther and farther away from "high arctic" on the arctic-to-subarctic scale; witness the recent finds of Clupea and Mallotus in the central Siberian Arctic, in the case of Mallotus over 1500 miles removed from the next nearest locality to the east or west.

Fish distribution patterns in the north are highly dependent upon geological events since the last glacial period. In addition it had been pointed out earlier that salinity tolerance, temperature tolerance, freezing point of the body fluid, metabolic demands of osmoregulation, migratory behavior, and other factors enter the picture to determine where a fish can live. During the Arctic winter fresh water cannot become as cold as brackish water and brackish water cannot become as cold as fully salt water, regardless of the latitude of the locality, provided that ice formation takes place; this is a fundamental physical relationship. Therefore an animal the habitat of which is typically in brackish water (e.g., Myoxocephalus quadricornis, Liopsetta glacialis) cannot be compared with one with a habitat typical of high salinities (e.g., Triglops pingeli, Liparis koefoedi). Fishes living in different salinities live in different "worlds," so to speak.

This discussion brings us to the subject of

"indicator species" for use in delimiting arctic from subarctic. Myoxocephalus quadricornis is considered to be an "arctic indicator" (Dunbar, 1947, 1951). Wherever it occurs, the water is "arctic." But M. quadricornis is practically restricted to coastal waters of reduced salinity, seldom entering fully salt water in the arctic (if fresh-water relicts are ignored). The "arctic" for this fish is therefore restricted to the peripheries of land masses, and so far as it is concerned the fully salt water of the polar basin is not arctic. This species may be used to delimit arctic waters, but only of the brackish coastal type. Incidentally this fish is tolerant of fairly warm waters; most survived 20° C. in experiments at Point Barrow (Scholander, Flagg, Walters, and Irving, 1953), and the present writer collected juveniles and adults at Bathurst Inlet in water measuring 14° C. to 15° C.

In a given area no two species of fish have identical ecological requirements, or, in other words, no two species in an area occupy the same ecological niche. The converse of this is that no two species (of fishes) have identical distribution patterns, unless some barrier such as a land mass imposes a limit to marine distributions. Because no two marine fishes have identical distributions, if we wish to select "indicators" for arctic and subarctic waters the fewer species selected the better. Otherwise the limits of the Arctic become quite nebulous. For example, the following meet their southern limits along the Atlantic coast (Ungava Bay and south) as follows: Arctogadus, absent; Icelus bicornis, Ungava Bay; Myoxocephalus quadricornis, Nain (Labrador); Liparis koefoedi, Goose Bay (Labrador); Boreogadus saida, Gulf of St. Lawrence; Gymnelis viridis, Nova Scotia; Triglops pingeli, Cape Cod. Each of these ranges north to northernmost Greenland or Ellesmere Island, or farther in the polar basin.

SUMMARY

- 1. The ichthyofauna is delimited for the following sector of the Arctic (map 1): coastal waters, from Cape Cheliuskin (longitude 105° E.) east to longitude 105° W. in Canada and south to latitude 65° 40′ N. in Bering Strait; fresh waters, Arctic watershed from the New Siberian Islands east to longitude 105° W. but excluding the Mackenzie Valley south of Arctic Red River. The term "Beringian Arctic" is introduced to cover the area from the New Siberian Islands east to the Alaskan-Yukon Territory border and south to Bering Strait; this constituted the Arctic Slope of the recent Bering Strait land bridge.
- 2. The following nomenclatorial changes are introduced:

Coregonus subautumnalis Kaganowsky is probably a synonym of C. autumnalis (Pallas).

Coregonus kennicotti Milner is identical to C. nasus (Pallas).

Coregonus nelsoni Bean is identical to C. lavaretus pidschian (Gmelin).

Thymallus arcticus pallasi Valenciennes and T. a. grubei n. mertensi Valenciennes are identical to T. a. signifer (Richardson).

Eleginus gracilis (Tilesius) is changed to E. navaga gracilis.

Phocaegadus Jensen is identical to Arctogadus Drjagin.

Phocaegadus megalops Jensen is identical to Arctogadus glacialus (Peters).

Stichaeus punctatus pulcherrimus Tarenetz is identical to S. punctatus (Fabricius).

Ophidium stigma Lay and Bennett is resurrected; its proper generic affiliation has not been determined.

Lycodes turneri agnostus Jensen, L. t. atlanticus Vladykov and Tremblay, and L. t. atlanticus m. squamosa Vladykov and Tremblay are synonyms of L. turneri Bean.

Myoxocephalus quadricornis hexacornis (Richardson) and "M. q. labradoricus" (non Girard) are identical to M. quadricornis (Linnaeus).

Myoxocephalus axillaris (Gill) is identical to M. scorpioides (Fabricius).

Myoxocephalus verrucosus (Bean) is identical to M. scorpius groenlandicus (Cuvier and Valenciennes).

- 3. The sector of the Arctic herein discussed probably experienced marked climatic changes since the last glacial period, but there is no factual information on the chronological sequence of such changes. It is assumed that the climate now is warmer than during the last glacial period.
- 4. Salinity preferences, blood freezing point, thermal tolerances, migratory behavior, and other factors determine which fishes may live in the Arctic and also determine where they may live. The diadromous habit is of positive selective value, if the sojourn in freshened or fresh waters occurs during winter. There is a forced winter migration of fresh-water fishes into waters that do not freeze; the size of the population is limited by the mid-winter volume of water, which is considerably less than the summer volume.
- 5. Fresh-water species may use five dispersal avenues other than passage through fully salt water (which a few are able to do): headwaters transfer by stream piracy or temporary damming and diversion through glacial activity (this sector had insignificant glacial lake formation), confluence of adjoining river systems, lowlands transfer, flooding of coastal areas, and low salinity bridges between river mouths. Marine species are considered, in the absence of sufficient knowledge concerning the physical oceanography of the area, potentially able to disperse anywhere.
- 6. With information on past distributions of ice sheets, eustatic rise in sea level, postglacial upwarping, and the topography of the sea floor, the probable characteristics of the Beringian Arctic during the last glacial period are depicted. This constituted the Arctic Slope of the Bering Strait land bridge (map 2). River volumes probably were considerable; confluence between Siberian and Alaskan streams probably occurred. The presence of rivers permitted certain freshwater and euryhaline marine fishes to survive the glacial period in the Arctic. High-salinity fishes which today range into the highest latitudes could have survived north of the land bridge. The Beringian Arctic fauna during land bridge times could have included the following:

FRESH-WATER

Lampetra japonica Salvelinus alpinus complex Stenodus leucichthys nelma Coregonus sardinella Coregonus autumnalis Coregonus nasus Coregonus lavaretus pidschian Prosopium cylindraceum Thymallus arcticus signifer Osmerus eperlanus dentex Hypomesus olidus drjagini Dallia pectoralis Esox lucius Catostomus catostomus rostratus Lota lota leptura Pungitius pungitius pungitius Cottus cognatus

MARINE

Clupea harengus pallasi Eleginus navaga navaga Boreogadus saida Arctogadus spp. Gymnelis viridis Lycodes jugoricus Lycodes turneri Lycodes pallidus Artediellus scaber Gymnocanthus tricuspis Icelus bicornis Icelus spatula spatula Myoxocephalus quadricornis Triglops pingeli Aspidophoroides olriki Liparis koefoedi Liopsetta glacialis

- 7. By the time the ice sheets began their final retreat in Europe and eastern North America, the land bridge had drowned. The water covering the land bridge was at first fairly fresh, but with a further rise in sea level high-salinity water began flowing through Bering Strait, preventing exchange between Siberia and Alaska of fishes intolerant of fully salt water. The Arctic seas remained brackish for some time after the land bridge drowned. After the land bridge drowned, the euryhaline fresh-water Oncorhynchus gorbuscha and O. keta and the euryhaline marine Myoxocebhalus platycephalus and Pleuronectes stellatus could have entered the Arctic from Bering Sea.
- 8. As the ice sheet dwindled, fishes quickly moved into deglaciated areas. In Siberia,

Phoxinus phoxinus colonized the Chukchi Peninsula from the Lena Valley; other freshwater species spread out from the Lena Valley but none have gone east of the Kolyma system:

Acipenser baeri
Hucho taimen
Brachymastax lenok
Coregonus peled
Coregonus muksun
Leuciscus leuciscus
Phoxinus percnurus
Phoxinus czekanowskii
Carassius auratus gibelio
Nemachilus barbatulus toni
Lota lota lota
Perca fluviatilis
Acerina cernua
Cottus poecilopus

Accompanying the diminution in number of Asiatic elements east of the Lena system is an increase in the number of elements common to Siberia and Alaska. Catostomus catostomus occurs in the Yana and streams to the east, Lota lota leptura replaces L. l. lota in the New Siberian Islands and eastward, and Dallia pectoralis and Cottus cognatus appear on the Chukchi Peninsula. This transition in the fresh-water fauna indicates that until recently the Novosiberian Ice Sheet was a barrier to the dispersal of some fresh-water fauna.

Arctic Alaska received only one fresh-water fish in recent times: Salvelinus namaycush, which came from the upper Mississippi Valley. Seventeen fresh-water fishes were present since land bridge times (see 6, above), and two entered via Bering Strait soon after the land bridge drowned (see 7, above).

Arctic Canada west of the 105th meridian received fresh-water fishes from several directions: (a) Arctic Alaska via the sea; (b) the upper Mississippi Valley via glacial lakes and the Mackenzie Valley; (c) the Yukon Valley by headwaters transfer; (d) from more than one direction, for some fishes.

- (a) Seven entered from Arctic Alaska: Oncorhynchus gorbuscha, Salvelinus alpinus complex, Coregonus sardinella, Coregonus autumnalis, Coregonus nasus, Osmerus eperlanus dentex, and Hypomesus olidus drjagini.
- (b) Seven entered from the upper Mississippi Valley: Salvelinus namaycush, Coregonus

clupeaformis, Catostomus commersoni, Couesius plumbeus, Percopsis omiscomaycus, Stizostedion vitreum, and Cottus ricei.

(c) One entered from the Yukon valley:

Thymallus arcticus signifer.

(d) Nine could have entered by more than one route. The possible sources are (1) Mississippi Valley, (2) Arctic Alaska, and (3) Yukon Valley:

Lampetra japonica (2, 3)
Oncorhynchus keta (2, 3)
Stenodus leucichthys nelma (2, 3)
Prosopium cylindraceum (2, 3)
Esox lucius (1, 3)
Catostomus catostomus subsp. (1, 2, 3)
Lota lota subsp. (1, 2, 3)
Pungitius pungitius pungitius (1, 2)
Cottus cognatus (1, 2, 3)

9. When Bering Strait salinities had risen sufficiently, additional marine fishes could enter the Arctic from the North Pacific. The following entered the Chukchi Sea from Bering Sea:

Stichaeus punctatus
Lumpenus fabricii
Lycodes knipowitschi
Lycodes raridens
Lycodes palearis
Myoxocephalus jaok
Agonus acipenserinus
Hippoglossoides elassodon robustus
Limanda aspera

Lumpenus medius entered the Chukchi Sea from Bering Sea and also entered the Laptev Sea from Europe.

- 10. Mallotus villosus and Myoxocephalus scorpius entered the Arctic from several sources and spread eastward and westward across the Eurasian and North American continents to become circumpolarly distributed.
- 11. Lumpenus medius and Eumicrotremus derjugini entered the Laptev Sea from Europe. Anarhichas denticulatus, Eumesogrammus praecisus, and Eumicrotremus spinosus spread from the eastern American Arctic to the western Canadian Islands.
- 12. Two euryhaline marine fishes have spread west from the Eastern Arctic to Point Barrow, northern Bering Sea, and eastern Siberia: Gadus morhua ogac, Myoxocephalus scorpioides. Thus the eastern American influence in the euryhaline marine fauna dis-

appears west of the Chukchi Peninsula in Siberia.

- 13. Clupea harengus pallasi, Eleginus n. navaga, Liopsetta glacialis, and Pleuronectes stellatus are absent from Labrador, Greenland, and the northern Canadian islands. These entered Arctic Canada from Arctic Alaska. Being euryhaline, their ranges indicate the maximal penetration of Canada from the Western Arctic, as they could have followed the retreating ice sheets at a close distance. All four range east to Bathurst Inlet and perhaps farther, but none have been detected in Hudson Bay or farther east. Thus the western influence in the euryhaline marine fauna disappears west of Hudson Bay. No fresh-water fishes that entered Canada solely via the sea from Arctic Alaska occur in Hudson Bay, though several range east to Bathurst Inlet (8a, above; Salvelinus alpinus occurs in Hudson Bay, but it also had a glacial refugium in the east).
- 14. The unequal dispersal of eastern and western euryhaline elements across Arctic America is difficult to explain, because there were more southerly, probably more favorable, post-glacial marine routes between Hudson Bay and the west. It is suggested that a residual glacial mass persisted between Victoria Island and the mainland until post-glacial upwarping west of Hudson Bay closed the southern marine routes. Thus western fishes were held back until the ice barrier disappeared, while eastern fishes could move west to the ice barrier, utilizing the southern routes before they were destroyed.
- 15. There is no satisfactory evidence that any high-salinity fishes have entered Hudson Bay from the west post-glacially. Examples reported in the literature are either of almost circumpolar or discontinuous circumboreal distribution.
- 16. Any delimitation of arctic from subarctic salt waters in the sector under discussion is academic, because the major portion of the polar basin has been poorly explored. Lack of sufficient exploration results in labeling as "high arctic" many localities that probably have a much richer fauna than the literature indicates.
- 17. Fish distribution patterns are dependent on many factors, not the least important of which are the geological history of the

region and the salinity requirements of the species. Provided ice formation occurs, low-salinity water cannot become so cold as high-salinity water and fresh water cannot become so cold as either of the two. Therefore the distributions of fishes that dwell in different

salinities cannot be compared. Thermally there is no difference between winter habitats in the Arctic, regardless of latitude, if salinities are identical. If certain species are selected as "indicators," their salinity preferences must be kept in mind.

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APPENDIX

Six studies came to the present writer's attention too late to be incorporated in the text. These are discussed briefly in chronological order.

KELEHER, J. J.

1952. The subspecific name of the Great Slave Lake burbot. Ann. Rept. Central Fish. Res. Sta. 1952, Fish. Res. Board Canada, pp. 62-63.

Appreciation is expressed for Keleher's permission to comment on his study, which has not yet been released for general distribution. Burbots were examined from the vicinity of Hay River, on the southern side of the lake. It was concluded that Lota lota leptura is the proper designation for the Great Slave Lake population. Added to previous knowledge concerning the species in western North America, this finding indicates that Lota lota leptura is the only subspecies occurring in Alaska, the Yukon and North-West Territories, and northern British Columbia. There is no indication that western Arctic America has been colonized by Lota lota lacustris.

Andriashev, A. P.

1954. Ryby severnykh morei SSSR. Zool. Inst. Akad. Nauk SSSR, 566 pp., Moscow, Leningrad.

Excluding those forms considered to be of doubtful specific distinction from others already known from longitude 105° E. east to longitude 105° W., Andriashev lists eight additional marine species from Siberia east of the 105th meridian. All are known from the Laptev Sea only, in this region. All are inhabitants of moderately deep to very deep waters, and all are also known from the seas west of the Laptev:

Zoarcidae

Gymnelis retrodorsalis Danois Lycodes reticulatus Reinhardt Lycodes frigidus Collett

Cottidae

Triglops nybelini Jensen Cottunculidae

Cottunculus sadko Essipov

Agonidae

Leptagonus decagonus (Bloch and Schneider) Cyclopteridae

Liparini

Careproctus reinhardti Kröyer Rhodichthys regina Collett As the deeper waters north of eastern Siberia and western North America become explored more fully, it is likely that many additions to the list of fishes known from the region will be made. Thus far the majority of deep-water marine fishes that have been collected in these seas are unknown from even the coldest portions of the North Pacific. This apparent trend in the fauna is in keeping with the fact that the deep waters of the Arctic Ocean are isolated from those of the North Pacific Ocean by the broad and high shelf between Siberia and Alaska.

Wilimovsky, N. J.

1954. List of the fishes of Alaska. Stanford Ichthyol. Bull., vol. 4, no. 5, pp. 279-294.

Some of the identifications and nomenclatorial changes used by Wilimovsky were obtained from the present writer. Unfortunately the list of fishes found in Arctic Alaska is incomplete; the following were either omitted from the Alaskan fauna or are not indicated by Wilimovsky to occur in Arctic Alaska:

Gadus morhua ogac Arctogadus borisovi Gymnelopsis stigma (Ophidium stigma) Artediellus scaber Triglops pingeli (T. beani) Podothecus acipenserinus (Agonus acipenserinus) Limanda aspera

Wilimovsky erroneously lists two species from Arctic Alaska. Because there are no authenticated reports for either, *Leptoclinus maculatus* and *Eumicrotremus derjugini* should be stricken from the faunal list.

A personal communication revealed that Wilimovsky's earlier determinations of Lycodes jugoricus and Icelus bicornis from Arctic Alaska were in error. In the present study these species are erroneously listed from the waters of Arctic Alaska. These species have not been collected in Arctic Alaskan waters and their longitudinal ranges at the present time are:

Lycodes jugoricus, White Sea east to the New Siberian Islands

Icelus bicornis, Prince Patrick Island and possibly Dolphin and Union Strait, North-West Territory, east to the East Siberian Sea Wilimovsky lists Dallia pectoralis from St. Matthew Island in the Bering Sea. It was suggested on page 339 of the present study that Dallia may have been absent from Bering Sea drainages during most of the time the land bridge was in existence, having entered the Bering Sea drainages of Alaska while the land bridge was being drowned. However, the presence of Dallia on St. Matthew Island indicates the fish was probably present on the Bering Sea slope as well as on the Arctic slope on the land bridge, because this island became separated from the mainland some time before the land bridge was destroyed (see map 3).

Finally, Wilimovsky lists one species from Arctic Alaska which is new to the ichthyofauna: *Eumesogrammus praecisus*. The distribution pattern of this fish is still indicative of a species that may have reëntered the Arctic recently.

WEBSTER, C. J.

1955. The Soviet expedition to the Central Arctic, 1954. Arctic, vol. 7, no. 2, pp. 59-80.

LAFOND, E. C.

1955. Physical oceanography and submarine geology of the seas to the west and north of Alaska. Arctic, vol. 7, no. 2, pp. 93-101.

METCALF, W. G.

1955. A note on Arctic oceanography and the Lomonosov Range. Arctic, vol. 7, no. 2, pp. 108-109.

These papers are discussed together because each overlaps the others. In 1948 Soviet explorers discovered a submerged mountain system extending across the floor of the Arctic Ocean and named it the Lomonosov Range. The Russians now claim that it extends over 1100 miles from the New Siberian Islands across the top of the world to Greenland and Ellesmere Island. American studies have confirmed the existence of the Lomonosov Range, and the Americans have studied it near Ellesmere Island. However, the true topographic features of the range are still a matter of speculation.

The Lomonosov Range divides the polar basin into the Central Arctic Basin on the European side of the mountains, and the Eastern Basin on the Alaskan side of the mountains. The hydrological picture differs in the two basins. What bearing the Lomonosov Range may have on the zoogeography of fishes remains to be seen. It is suspected that it may be influential in the zoogeography of deep-water, bottom-dwelling fishes, but it may be of little or no importance in the zoogeography of bathypelagic and surface fishes. At the present time there is little information concerning the deep-water fauna of the Eastern Basin.

A comparison of the drainage patterns on the Arctic Slope of the Bering Strait land bridge (map 2 of the present work) with the "Bathymetric Map of the Central Arctic Basin" published by the Russians in 1954 and reproduced in Webster's article (p. 72, fig. 13) reveals that the land bridge river mouths lie close to sea valleys. The valley located near longitude 162° E. is close to the mouth of the Alasei-Indigirka Complex: the mouth of the Kolyma Complex is close to the valley near longitude 169° E.; the mouth of the Chukchi Complex is close to two valleys, one near longitude 171° W. and the other near longitude 174° W. (the Chukchi Complex may have been two separate river systems with their mouths only a few miles apart rather than two systems which became confluent a short distance before emptying into the sea). Two other sea valleys are indicated on the map, one north of the New Siberian Islands and the other north of Wrangel Island; these may have been associated with streams issuing from the Novosiberian and Wrangel ice sheets. The relatively small sizes of the Alaskan Beaufort Sea drainages may account for the absence of sea valleys from the Alaskan part of that sea. Of the Chukchi Sea drainages of Alaska, most were members of the Chukchi Complex which has already been mentioned; the Kuk system seems to have been associated with the Barrow Sea Valley (LaFond's article, fig. 2, shows the valley northwest of Point Barrow). Two lesser valleys, between the eastern valley of the Chukchi Complex and the Barrow Sea Valley, may indicate Alaskan rivers which had existed on the land bridge but are now drowned.