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Systematics of the Northern Hemisphere Cod Genus Gadus

Linnaeus, 1758 (Gadiformes: Gadidae)

Claude B. Renaud

Thesis presented to the School of Graduate Studies and
Research, in partial fulfilment of the requirements for the
degree of Ph.D. in Biology

University of Ottawa

Supervisor: Dr. Don E. McAllister

Co-supervisor: Prof. Sami U. Qadri



Claude B. Renaud, Ottawa, Canada, 1989

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ABSTRACT

Based on a study of topotypic adult specimens for all six nominal subspecies of Gadus morhua recognized by Svetovidov (1948), the last reviser of the genus, as well as non-topotypic adult specimens believed to adequately reflect the geographic distribution of the marine cod genus Gadus, the following three species are recognized: the Atlantic cod, G. morhua Linnaeus, 1758; the Pacific cod, G. macrocephalus Tilesius, 1810; and the ogac, G. ogac Richardson, 1836. The subspecies Gadus morhua callarias Linnaeus, 1758; G. m. kildinensis Derjugin, 1920; and G. m. marisalbi Derjugin, 1920 are synonymized with the monotypic species G. morhua Linnaeus, 1758, and therefore, no subspecies of G. morhua is recognized. The presence of nuptial tubercles in members of the genus is proposed as a synapomorphy to support the monophyly of Gadus. Likewise, the presence of nuptial tubercles in members of the genus Boreogadus, which are nonhomologous with those found in Gadus, is proposed as a synapomorphy to support the monophyly of that genus. G. morhua is the sister group to the G. macrocephalus - G. ogac lineage. The G. macrocephalus - G. ogac clade is supported by two synapomorphies.

RESUME

Selon une étude de spécimens topotypiques adultes appartenant aux six sous-espèces nominales de Gadus morhua reconnues par Svetovidov (1948), le dernier réviseur du genre, de même que des spécimens adultes non-topotypiques qui croit-on représentent adéquatement la répartition géographique du genre marin de morue Gadus, les trois espèces suivantes sont reconnues: la morue franche, G. morhua Linnaeus, 1758; la morue du Pacifique, G. macrocephalus Tilesius, 1810; et l'ogac, G. ogac Richardson, 1836. Les sous-espèces Gadus morhua callarias Linnaeus, 1758; G. m. kildinensis Derjugin, 1920; et G. m. marisalbi Derjugin, 1920 sont synonymisées avec l'espèce monotypique G. morhua Linnaeus, 1758, et par conséquent, aucune sous-espèce de G. morhua est reconnue. La présence de tubercules nuptiaux chez les membres du genre est suggérée comme étant une synapomorphie appuyant la monophylie de Gadus. De même, la présence de tubercules nuptiaux chez les membres du genre Boreogadus, qui sont nonhomologues avec ceux que l'on retrouvent chez Gadus, est suggérée comme étant une synapomorphie appuyant la monophylie de ce genre. G. morhua est le groupe frère de la lignée G. macrocephalus - G. ogac. Le clade G. macrocephalus - G. ogac est appuyé par deux synapomorphies.

INTRODUCTION

The genus Gadus Linnaeus, 1758 belongs to the monophyletic subfamily Gadinae. Although Svetovidov (1948) and Markle (1982) differ in their interpretations of the generic constituents of some of the subfamilial groupings in the family Gadidae, both are in agreement with regards to the genera which make up Gadinae. Three of the characters used by Svetovidov (1948) to define this subfamily namely, the presence of three dorsal fins, two anal fins, and eggs without an oil globule, were interpreted by Markle (1982) as being synapomorphic, thereby supporting its monophyletic status.

The marine cod genus Gadus is of enormous historical and economic importance to Canada. It was probably the search for new cod fishing grounds to feed Catholic Europe that brought European fishermen to Canada's Atlantic waters, notably off the coasts of Newfoundland and Labrador, as early as 1454 (80 years before Cartier), and certainly by 1497 (Tuck and Grenier 1981; Lacoursière and Bizier 1983a, b; Thurston 1983). All through the 16th century, Basque, Dutch, English, French (Breton), Portuguese, and Spanish fishing fleets came yearly to the Newfoundland banks, to catch cod to sell on the European market (Lacoursière and Bizier 1983a, b).

The cods (Gadidae), Gadus morhua especially, are second only to the herrings (Clupeidae) in economic importance

worldwide (Joensen and Tåning 1970, Berra 1981). The Atlantic cod is Canada's most important commercial fish species in terms of landed value; a catch of 463 100 t valued at \$168 600 000 in 1984 (Scott and Scott 1988). The Pacific cod is the most important of the bottom fishes of British Columbia; landings in 1970 amounted to 2270 t (Hart 1973).

Despite the enormous economic importance of some of its members, the genus Gadus requires a systematic revision. Bélanger-Steigerwald and McAllister (1982) have stated that "Properly managing fisheries means correctly naming, identifying, and regulating each species in the catch" and as a corollary that "Stocks cannot be properly regulated unless catches are correctly identified."

There is some confusion in the literature, at least up to 1970, concerning the proper scientific name for the common Atlantic cod; many authors using the specific epithet callarias instead of morhua. The root of the problem stemmed from the fact that Linnaeus (1758) described both cods on the same page (p. 252). According to Cohen (1959) and McAllister (1960), the first reviser recognized the two forms as being conspecific and chose morhua as the name to be applied to the species in accordance with article 24(a) of the International Code of Zoological Nomenclature (1985). Furthermore, Gadus morhua is the only member of the genus placed in the Official Lists and Indexes of Names and Works in Zoology (1987) as specified by direction 57.

In the last comprehensive systematic study of Gadus, Svetovidov (1948) recognized a single species, G. morhua, divided into the following six subspecies on the basis of morphological and pigmentary characters: the Atlantic cod, G. m. morhua Linnaeus, 1758, from the North Atlantic and Arctic oceans; the Baltic cod, G. m. callarias Linnaeus, 1758, from the Baltic Sea; the Pacific cod, G. m. macrocephalus Tilesius, 1810, from the North Pacific Ocean; the ogac, G. m. ogac Richardson, 1836, from the Arctic and North Atlantic oceans; the Kil'din cod, G. m. kildinensis Derjugin, 1920, from Kil'din Island, in the Barents Sea; and the White Sea coastal cod, G. m. marisalbi Derjugin, 1920, from the White Sea. In the original description of marisalbi, Derjugin (1920) incorrectly spelled it Maris-Albi. According to articles 5(b) and 32(d)(i) of the International Code of Zoological Nomenclature (1985), it should be correctly emended to marisalbi. Because of lack of sufficient material, Derjugin (1920) only conditionally proposed the subspecific distinctiveness of marisalbi. Nevertheless, according to article 15 of the ICZN (1985), it is an available name.

Reports of sympatric occurrences for three pairs of the above nominal subspecies called into question the appropriateness of the subspecific designation for these forms, especially in the absence of any reported intergradation between members of these pairs. The three

sympatric pairs were: morhua-callarias (Svetovidov 1948), morhua-marisalbi (Il'in and Pevzner 1939, Svetovidov 1948), and morhua-ogac (Jeffers 1932; Vladykov 1933, 1945; Jensen 1948; Dunbar and Hildebrand 1952; Scott 1952; Backus 1957; McKenzie 1959; McAllister 1960; Legendre 1961; Sick 1965; Leim and Scott 1966; Drainville 1970; Markle 1982; Hunter et al. 1984; Vladykov et al. 1985; Renaud et al. 1986; McAllister et al. 1987; Scott and Scott 1988; Renaud 1989).

In "Pacific Fishes of Canada", Hart (1973) treated macrocephalus as a distinct species and in "Fishes of the Atlantic Coast of Canada", Leim and Scott (1966) treated morhua and ogac as distinct species, as did Scott and Scott (1988) in their "Atlantic Fishes of Canada". These faunal accounts however, did not involve a comparison of all nominal subspecies within the genus, nor an analysis of taxonomic characters or a search for possible intermediates.

The purpose of this study is to determine how many species and subspecies are present within the genus, the appropriate nomenclature, and to establish whether or not Gadus is monophyletic.

INTRAGENERIC STUDY OF Gadus

PILOT STUDY

INTRODUCTION

The purpose of this pilot study was twofold: 1- determine how many species and subspecies are present within the genus, and 2- extract a small number of diagnostic characters out of 84 surveyed (48 morphometric, 17 meristic, 12 pigmentary, and 7 miscellaneous: see Methods), for distinguishing these taxa.

The material studied consisted of 110 adult Gadus specimens equal to or greater than 100 mm in standard length selected from across the range of the genus. Each specimen was given a two-letter label. The first letter refers to the a priori taxonomic identification as determined using the key and descriptions of the six nominal subspecies of Gadus morhua recognized by Svetovidov (1948) (Table 1). The only taxon discussed in Svetovidov (1948) and not represented in the pilot study is G. m. kildinensis Derjugin, 1920, a form endemic to Lake Mogil'noye on Kil'din Island, in the Barents Sea, USSR. A single specimen of this form became available only after the pilot study had been virtually completed and it was therefore only incorporated in the latter part of the study. In his key, Svetovidov (1948) used eight diagnostic characters (least bony interorbital width, length and arrangement of the horn-like processes of the gas bladder, body pigmentation, length of the pectoral fin's longest fin

Table 1. Code used for the six nominal subspecies of Gadus morhua recognized by Svetovidov (1948) and their numerical representation in the pilot study.

Taxon	Code (1st letter of label)	N
<u>G. m. morhua</u> Linnaeus, 1758	A	29
<u>G. m. callarias</u> Linnaeus, 1758	C	10
<u>G. m. macrocephalus</u> Tilesius, 1810	P	43
<u>G. m. ogac</u> Richardson, 1836	O	24
<u>G. m. kildinensis</u> Derjugin, 1920	K	0
<u>G. m. marisalbi</u> Derjugin, 1920	W	4

ray, first principal pelvic fin ray length, chin barbel length, and least caudal peduncle depth). These were also used in the pilot study, except for the length and arrangement of the horn-like processes of the gas bladder, which were evaluated in a small number of specimens in a parallel study (see appropriate section) because these are characters which require extensive dissection to be assessed and also because Svetovidov (1948) stated that "... fishes measuring to 30 cm are not distinguishable on this character, inasmuch as their horn-like processes are shortened and have the same appearance as in adult Pacific Ocean cods." Type material was not available for comparative purposes but broadly topotypic specimens were included for the five putative taxa represented, as follows: Gadus morhua morhua - European seas (type material lost, Mr. A. Wheeler, in litt. 14 May 1986); G. m. callarias - European seas and Baltic Sea (one syntype extant, Wheeler (1985)); G. m. macrocephalus - Bering Sea, off Kamchatka Peninsula (whereabouts of type material unknown); G. m. ogac - off west Greenland (type material lost, Dr. J. Nielsen, in litt. 9 July 1986); and G. m. marisalbi - White Sea (whereabouts of type material unknown). The second letter in the label refers to the geographic locality. The marine zoogeographic regions and provinces designated by Briggs (1974) were used. According to the literature (Svetovidov 1948; Phillips 1950, 1951, 1953, 1958; Pinkas 1967; Fitch and Schultz 1978), the genus

Gadus is found in 11 of the zoogeographic areas designated by Briggs (1974) (Table 2). Specimens were available for nine of the areas (Table 2). Two specimens of G. m. macrocephalus from the San Diego Province of the California Region became available only after the pilot study had been virtually completed and were therefore only incorporated in the latter part of the study. The absence of specimens from the Lusitania Province and the poor representation from the Japan Region (1 specimen) and the San Diego Province (2 specimens) is probably due to the fact that these are the only areas in the range of the genus which are classified under warm-temperate regions and is thereby a reflection of a lower water temperature preference for the genus. Furthermore, a thorough survey of museums throughout the Northern Hemisphere failed to produce any other specimens from these areas. Because the apparent gaps represent marginal habitat, the sample of specimens studied is believed to adequately reflect the geographic distribution of the genus.

Table 2. Code used for the marine zoogeographic areas and number of specimens of Gadus in the pilot study according to these marine zoogeographic areas (following Briggs (1974)).

Marine zoogeographic area	Code (2nd letter of label)	N	Specimen label
1- Northern Hemisphere Warm-Temperate Regions			
a- Mediterranean-Atlantic Region			
i- Lusitania Province	K	0	-
b- Japan Region	A	1	PA1
c- California Region			
i- San Diego Province	J	0	-
2- Northern Hemisphere Cold-Temperate and Arctic Regions			
a- Western Atlantic Boreal Region	B	18	AB1-8, OB1-10
b- Eastern Atlantic Boreal Region	C	23	CC1-10, AC1-13
c- Western Pacific Boreal Region			
i- Oriental Province	D	8	PD1-8
ii- Okhotsk Province	E	3	PE1-3
iii- Kurile Province	F	11	PF1-11
d- Eastern Pacific Boreal Region			
i- Oregon Province	G	5	PG1-5
ii- Aleutian Province	H	15	PH1-15
e- Arctic Region	I	26	AI1-8, OI1-14, WI1-4

MATERIAL

The following are the codes of the repository institutions for the specimens studied:

ANSP = Academy of Natural Sciences of Philadelphia,
Philadelphia, Pennsylvania, USA;

BM(NH) = British Museum (Natural History), London, UK;

CAS-SU = California Academy of Sciences-Stanford
University Collections, Department of
Ichthyology, San Francisco, California, USA;

CU = Cornell University, Ichthyological Collection,
Ithaca, New York, USA;

ISH = Institut für Seefischerei, Zoologisches Institut
und Museum, Universität Hamburg, Aussenstelle
Ichthyologie, Hamburg, GFR;

LACM = Los Angeles County Museum of Natural History,
Section of Fishes, Los Angeles, California, USA;

MNHN = Muséum National d'Histoire Naturelle, Ichthyologie
Générale et Appliquée, Paris, France;

NMC = National Museums of Canada, National Museum of
Natural Sciences, Ichthyology Section, Ottawa,
Ontario, Canada;

NRM = Swedish Museum of Natural History, Stockholm,
Sweden;

RMNH = Rijksmuseum van Natuurlijke Historie, Leiden,
The Netherlands;

ROM = Royal Ontario Museum, Department of Ichthyology

and Herpetology, Toronto, Ontario, Canada;

UMMZ = University of Michigan Museum of Zoology,

Division of Fishes, Ann Arbor, Michigan, USA;

USNM = National Museum of Natural History (Smithsonian

Institution), Division of Fishes, Washington, DC,

USA;

ZIL = Zoological Institute, Academy of Sciences,

Leningrad, USSR;

ZMA = Zoölogisch Museum Universiteit van Amsterdam,

Department of Ichthyology, Amsterdam, The

Netherlands;

ZMH = Zoologisches Institut und Museum, Universität

Hamburg, Abteilung Ichthyologie, Hamburg, GFR;

ZML = Museum of Zoology and Entomology, Lund University,

Lund, Sweden;

ZMUU = Zoologiska Museet, Uppsala Universitet, Uppsala,

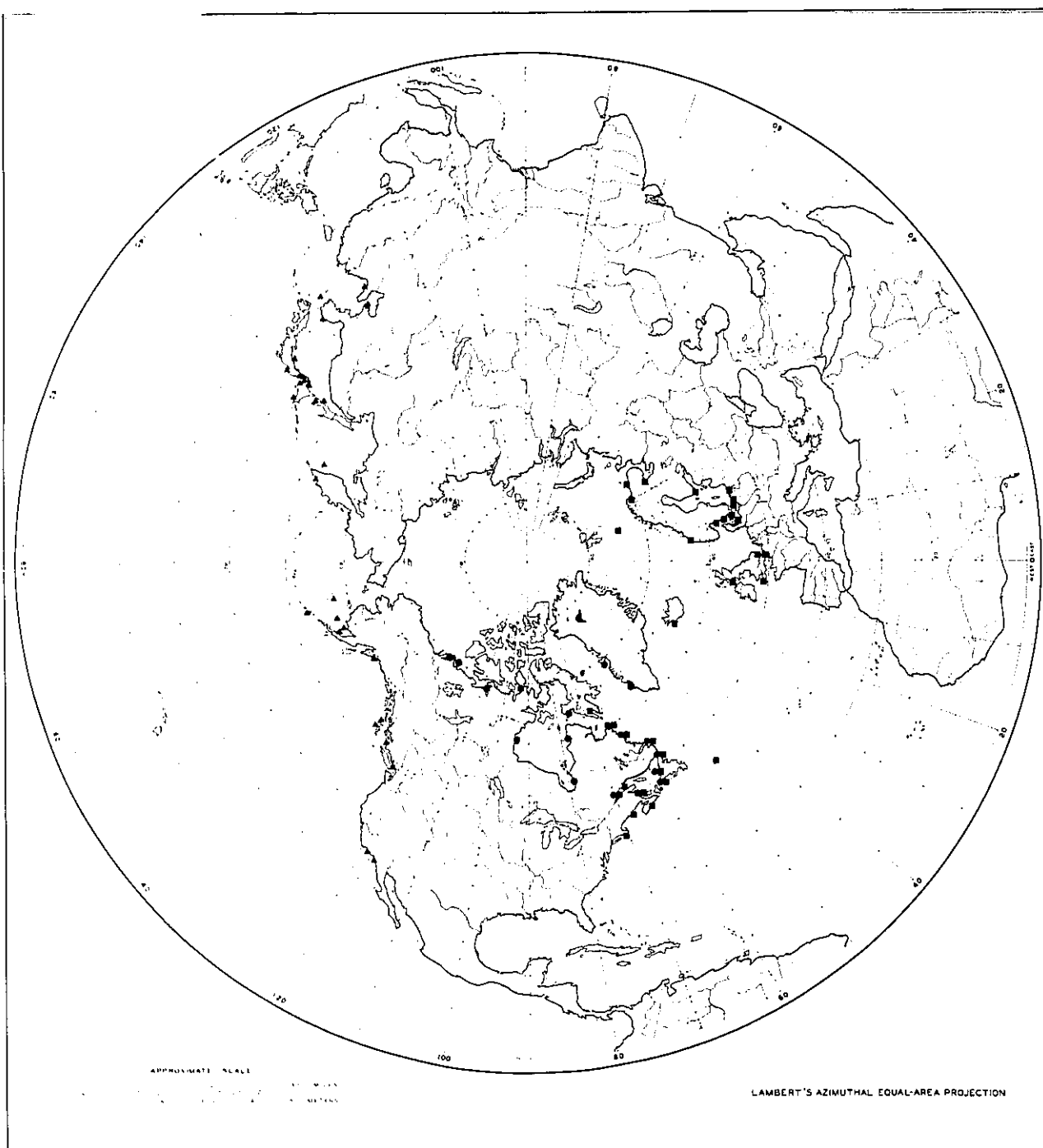
Sweden.

Collection data, when available, are as follows: catalog number; number of specimens; locality; geographic coordinates; collector(s); collection date; depth of capture; nature of substrate; water temperature at level of capture; water salinity at level of capture; method of capture. The following collections appear on a spot distribution map (fig. 1).

Gadus morhua

1- MNHN1974-291; 1; UK: off west Cornwall County, England;

Fig. 1. Distribution map of the collections of the genus Gadus studied. ■ = G. morhua; ▲ = G. macrocephalus; ● = G. ogac. One symbol may represent more than one collection.



- approx. 50°30'N 5°0'W; C. Roux.
- 2- MNHN1898-895; 1; France: North Sea, at Dunkerque; 51°4'N 2°21'E; E. Moreau.
 - 3- MNHNA.3995; 2; Norway: Varanger Fjord, at Nesseby, Finnmark County; 70°9'N 28°54'E; 1881.
 - 4- USNM163475; 1; USA: 84-167 air km off coast of Rhode Island; approx. 40°30'N 70°30'W; G. Sundstrom; 1954.
 - 5- USNM92096; 2; Iceland: off Reykjavík; 64°10'N 22°0'W; McMillan; 25 July 1930.
 - 6- USNM28596; 1; France: Strait of Dover, at Pas de Calais; 50°58'N 1°50'E.
 - 7- NMC66-127; 1; Canada: Grandy Sound, Cabot Strait, 19 km east of Channel-Port aux Basques, Newfoundland; 47°36'20"N 58°50'30"W; D.E. McAllister and W.H. van Vliet; 8-9 June 1966; gill net.
 - 8- BM(NH)1931.6.25.2; 1; Norway: off Bear Island, Svalbard Archipelago, Barents Sea; 74°20'N 18°50'E; Robertson.
 - 9- CU43110; 1; USA: 5 km east of Small Point, Maine; 43°42'N 69°46'W; R.V. Miller; 29 July 1962.
 - 10- BM(NH)1888.5.23.14; 1; UK: Firth of Lorne, Scotland; 56° 20'N 5°35'W; Murray; May; 46 m.
 - 11- BM(NH)1971.2.16.628-633; 2; UK: Crouch River estuary, at Burnham on Crouch, Essex County, England; 51°37'N 0°49'E; A.C. Wheeler; 2 Nov. 1960.
 - 12- BM(NH)1971.2.16.637-638; 2; UK: Crouch River estuary, at Burnham on Crouch, Essex County, England; 51°37'N 0°49'E;

- A.C. Wheeler; 21 March 1963.
- 13- ZMA119.721; 1; UK: Firth of Clyde, Scotland; 55°10'N 5°15'W; F.P. Vermeulen; July 1932.
- 14- NRMLÖN/1924.989.3798; 1; Sweden: Skagerrak, off Lysekil, Goteborg och Bohus County, Bohuslän Province; 58°18'N 11°26'E; E. Lönnberg; summers of 1923-25.
- 15- NMC81-891; 4; Canada: Gulf of St. Lawrence, at Baie-Trinité, Saguenay County, Québec; 49°25'N 67°25'W; A. Lesage, L. Caron, and B. Marcil; 24 June 1981; sand; gill net.
- 16- NMC84-150; 1; Canada: Western Arm, Red Bay, Strait of Belle Isle, Labrador, Newfoundland; 51°43'N 56°27'W; R. Chan; 5 Aug. 1982; 18 m; jigging.
- 17- NMC83-100; 3; Canada: Sipukat Lake, north of Okak Bay, Labrador, Newfoundland; 57°33'N 62°22'W; J.G. Hunter; 25-31 Aug. 1964; 1-9 m; sand and rocks; gill net.
- 18- NMC83-99; 4; Canada: Christopher Inlet, at Port Burwell, Killinek Island, Ungava Bay, District of Franklin, Northwest Territories; 60°24'N 64°51'W; G. Gleno; 5-13 Aug. 1967; large trap.
- 19- ZMH12938; 1; GFR: Neustadt Bay, Schleswig-Holstein State, Baltic Sea; 54°6'N 10°49'E; Duncker; 12 Oct. 1892.
- 20- NMC64-763; 3; off Canada: Grand Banks, about 370 air km southeast of Cape Race, Newfoundland; 45°6'30"N 49°1'0"W; J. Hannan; 14 Oct. 1964; bottom trawl.
- 21- NMC67-762; 1; Canada: Saguenay River Fjord, about 21 air

km east of Chicoutimi, Chicoutimi County, Québec; 48°25' 15"N 70°47'0"W; "Les Jeunes Explorateurs"; 1 July 1963; 50 m; mud; gill net.

- 22- NMC70-31; 1; Canada: Saguenay River Fjord, near Cap Jaseux, Chicoutimi County, Québec; 48°25'12-42"N 70°47-48'30"W; G. Drainville and P. Brunel; 22 June 1962; 73-92 m; sand and mud; bottom trawl.
- 23- NMC67-581; 1; Canada: Saguenay River Fjord, north of Petit Saguenay River mouth, Chicoutimi County, Québec; 48°15'46"N 70°5'55"W; "Les Jeunes Explorateurs"; 15 Aug. 1962; 22 m; rocks; gill net.
- 24- NMC86-229; 2; Canada: Miramichi Bay, Gulf of St. Lawrence, New Brunswick; 47°8'N 64°58'W; 25 Feb. 1982; smelt trap.
- 25- NMC81-61; 2; Canada: Humber Arm, at Curling, Newfoundland; 48°57'42"N 58°0'6"W; J.N. Bowlby; 21 May 1978; 4-7 m; mud and detritus; gill net.
- 26- NMC66-604; 2; Canada: Aspotogan Harbour and Northwest Cove, Lunenburg County, Nova Scotia; 44°28-31'N 64°3-10' W; R.M. Rankin; 25 July 1965; 7-8 m; gravel and rocks; 13.3°C; baited hook and line.
- 27- NMC61-169; 2; Canada: Northwest Arm, Halifax, Nova Scotia; 44°38'N 63°36'W; R.M. Rankin and P. Coady; 26 July 1960; 5-6 m; shells, mud, stones, and rocks; 12°C; baited hook and line.
- 28- ISH1023/82; 2; Canada: Labrador Sea, off Labrador,

- Newfoundland; 54°4'30"N 55°5'30"W; M. Kerstan; 5 Nov. 1982; 169 m; -0.67°C; 33.32‰/‰; bottom trawl.
- 29- RMNH15452; 1; Norway: Trondheims Fjord, at Trondheim; 63° 26'N 10°25'E; C.F. Milo; 12 Aug. 1935.
- 30- NMC87-90; 4; Canada: Ogak Lake, Baffin Island, District of Franklin, Northwest Territories; 62°52'N 67°21'W; 25 March 1987; jigging.
- 31- ZMLL960/3252; 1; Sweden: Laholmsbukten, Kattegat Strait, off Trönninge and Laxvik, Halland County; 56°36'40"N 12° 54'32"E; H. Hallander; 17 Aug. 1960.
- 32- ZMLL962/3318; 1; Sweden: Öresund Strait, off Ven Island; 55°54'5"N 12°43'6"E; F. Karlbrink; 18 April 1962.
- 33- NRMA75/1975.257.1401; 1; Norway: Varanger Fjord, in front of Nesseby church, Finnmark County; 70°9'N 28°54'E; G. Frisk; 22-27 June 1975; 5-10 m.
- 34- ZIL38915; 1; USSR: Lake Mogil'noye, Kil'din Island, Murmanskaya Oblast'; 67°50'N 37°22'E; R.Ya. Tzeb; June 1968.
- 35- USNM272360; 2; USSR: Gulf of Kandalaksha, near Kandalaksha, White Sea, RSFSR; 67°8'N 32°26'E; 21 June 1972.
- 36- BM(NH)1932.8.2.6-7; 1; USSR: Gulf of Kandalaksha, White Sea, RSFSR; 66°30'N 34°0'E; A.N. Svetovidov.
- 37- BM(NH)1938.8.2.8; 1; USSR: Gulf of Kandalaksha, White Sea, RSFSR; 66°30'N 34°0'E; A.N. Svetovidov.
- 38- BM(NH)1924.5.19.9; 1; USSR: Gulf of Kandalaksha, White

Sea, RSFSR; 66°30'N 34°0'E; A.N. Svetovidov; 13 Nov.
1923.

- 39- NMC87-165; 2; USSR: Strait of Velikaya Salma, Gulf of
Kandalaksha, White Sea, Karel'skaya ASSR; 66°31'N 33°22'
E; R.V. Kvartsit, Sev PINRO; 9 Oct. 1986; gill net.
- 40- NMC87-166; 3; USSR: Strait of Velikaya Salma, Gulf of
Kandalaksha, White Sea, Karel'skaya ASSR; 66°31'N 33°22'
E; R.V. Kvartsit, Sev PINRO; 9 Oct. 1986; gill net.
- 41- NMC87-167; 2; USSR: Strait of Velikaya Salma, Gulf of
Kandalaksha, White Sea, Karel'skaya ASSR; 66°31'N 33°22'
E; R.V. Kvartsit, Sev PINRO; 9 Oct. 1986; gill net.
- 42- NMC87-168; 4; USSR: Strait of Velikaya Salma, Gulf of
Kandalaksha, White Sea, Karel'skaya ASSR; 66°31'N 33°22'
E; R.V. Kvartsit, Sev PINRO; 9 Oct. 1986; gill net.
- 43- NMC87-169; 3; USSR: Strait of Velikaya Salma, Gulf of
Kandalaksha, White Sea, Karel'skaya ASSR; 66°31'N 33°22'
E; R.V. Kvartsit, Sev PINRO; 9 Oct. 1986; gill net.
- 44- NMC87-170; 2; USSR: Strait of Velikaya Salma, Gulf of
Kandalaksha, White Sea, Karel'skaya ASSR; 66°31'N 33°22'
E; R.V. Kvartsit, Sev PINRO; 9 Oct. 1986; gill net.
- 45- NMC77-504; 1; Finland: off Hangö, Gulf of Finland, Baltic
Sea; 59°45'N 22°40'E; T. Bergman; 5 Aug. 1976.
- 46- NMC85-80; 3; Poland: Gdańsk Bay, northeast of Gdynia,
Baltic Sea; 54°38'N 18°55'E; Sea Fisheries Institute,
Gdynia; 23 Nov. 1984; 60 m.
- 47- ZMUU27.5.1906; 3; Denmark: off Bornholm Island, Baltic

Sea; approx. 55°N 15°E; A. Appellöf and L. Johansson; 27 May 1906.

- 48- NMC79-580; 2; Finland: off Airisto, near Turku, Baltic Sea; 60°27'N 22°17'E; M. Himberg; 20 Oct. 1977.
- 49- NMC79-579; 1; Finland: off Stenskär, near Pargas, Baltic Sea; 60°18'N 22°21'E; K.J. Lehtinen; 23 Sept. 1977.
- 50- NMC87-94; 4; Poland: Gulf of Gdansk, Baltic Sea; 54°42'N 19°40'E; J. Wiktor; 10 Jan. 1986.
- 51- NMC87-93; 1; Poland: Baltic Sea; 54°50'N 16°51'E; B. Szelwicki; 20 April 1986.

Gadus macrocephalus

- 52- USNM161480; 1; USSR: Aniva Gulf, at Korsakov, Sakhalin Island, RSFSR; 46°30'30"N 142°43'30"E; Albatross station no. D5010, field no. TT4125; 24 Sept. 1906; 38-59 m; green mud and sand; beam trawl.
- 53- USNM150368; 1; Japan: Uchiura Bay, at Muroran, Hokkaidō; 42°18'N 141°1'E; F. Wilke; 30 April 1949.
- 54- USNM48174; 1; Japan: Tsugaru Strait, at Hakodate, Hokkaidō; 41°46'N 140°47'E; S. Nozawa; April 1889.
- 55- USNM160632; 1; Japan: Ishikari Bay, at Otaru, Hokkaidō; 43°12'N 141°3'E; Albatross field no. TT4021; 21 Sept. 1906.
- 56- USNM149850; 2; Japan: off the southern coast of Hokkaidō; 42°16'30"N 142°4'0"E; Albatross station no. D5041; 3 Oct. 1906; 112-256 m; brown mud, fine black sand, coral, and

- sand; 5.1°C; beam trawl.
- 57- USNM149852; 1; Japan: off the southern coast of Hokkaidō; 42°17'30"N 142°7'30"E; Albatross station no. D5042; 3 Oct. 1906; 112 m; brown mud, fine black sand, coral, and sand; 9.9°C; beam trawl.
- 58- USNM160634; 1; Japan: off Kinkazan Island, Honshū; 38°9'24"N 141°52'30"E; Albatross station no. D5048, field no. TT4278; 10 Oct. 1906; 236 m; dark gray sand and broken shells; 4.8°C; beam trawl.
- 59- USNM160635; 1; Japan: off Kinkazan Island, Honshū; 38°12'N 142°2'E; Albatross station no. D5049, field no. TT4285; 10 Oct. 1906; 333 m; dark gray sand, broken shells, Foraminifera; 3.2°C; beam trawl.
- 60- USNM149851; 1; South Korea: off Cape Clonard, eastern coast of South Korea, Sea of Japan; 36°17'N 129°41'E; Albatross station no. D4859; 31 July 1906; 170 m; green mud; 2.1°C; beam trawl.
- 61- USNM161482; 1; Japan: off the southern coast of Hokkaidō; 42°16'30"N 142°4'0"E; Albatross station no. D5041, field no. TT4248; 3 Oct. 1906; 112-256 m; brown mud, fine black sand, coral, and sand; 5.1°C; beam trawl.
- 62- USNM160633; 1; USSR: Aniva Gulf, off Dal'nyaya, Sakhalin Island, RSFSR; 46°4'40"N 142°27'30"E; Albatross station no. D5005, field no. TT4107; 24 Sept. 1906; 77-79 m; green mud and fine gray sand; beam trawl.
- 63- USNM161493; 1; USSR: Aniva Gulf, west of Novikovo,

- Sakhalin Island, RSFSR; 46°18'30"N 143°5'40"E; Albatross station no. D5011, field no. TT4157; 25 Sept. 1906; 77 m; green mud; 1.1°C; beam trawl.
- 64- NMC80-1114; 1; People's Republic of China: off Qingdao (also Tsingtao, or Ch'ing-tao), Shandong Province, Yellow Sea; 36°4'N 120°19'E; 28 May 1980.
- 65- NMC84-157; 1; USA: off Seward Marine Center dock, Seward, Resurrection Bay, Gulf of Alaska, Alaska; 60°7'N 149°27' W; C.B. Renaud and T.A. Edge; 28 July 1983; 23-26 m; 13.5°C; 23.5‰; gill net.
- 66- NMC84-275; 6; USA: south of Unalaska Island, Aleutian Islands, Alaska; 53°18'12-30"N 166°38-40'12"W; H. Zenger, Ocean Harvester cruise no. 82-1, haul no. 91; 22 March 1982; 163-168 m.
- 67- USNM161481; 1; USSR: Tatar Strait, west of Sakhalin Island, RSFSR; 47°32'30"N 141°45'0"E; Albatross station no. D5003, field no. TT4091; 23 Sept. 1906; 64-70 m; fine gray sand and green mud; 5.8°C; beam trawl.
- 68- CAS-SU3035; 1; USA: Bristol Bay, northwest of Stroganof Point, Alaska, Bering Sea; 56°58'30"N 159°11'0"W; Albatross station no. D3291; 18 July 1890; 48 m; black sand and gravel; 5.1°C; large beam trawl.
- 69- CAS-SU23804; 2; Japan: Tsugaru Strait, at Hakodate, Hokkaido; 41°46'N 140°47'E; D.S. Jordan and J.O. Snyder; 1900.
- 70- CAS-SU20152; 1; People's Republic of China: Korea Bay, at

Lüshun (= Port Arthur), Liaoning Province; 38°48'N 121°16'E; Abbott.

- 71- ANSP136732; 1; People's Republic of China: off Qingdao (also Tsingtao, or Ch'ing-tao), Shandong Province, Yellow Sea; 36°4'N 120°19'E; T.J. Tu; March 1932.
- 72- UMMZ167441; 1; People's Republic of China: off Qingdao (also Tsingtao, or Ch'ing-tao), Shandong Province, Yellow Sea; 36°4'N 120°19'E; T.J. Tu; March 1932.
- 73- CAS-SU17552; 1; Korea Strait, southeast of Cheju Island (= Quelpart Island), South Korea and west of Kyūshū, Japan; approx. 33°N 127°E; F.B. Steiner; Dec. 1971; 80 m.
- 74- UMMZ142768; 1; Japan: off Kushiro, Hokkaidō; 42°58'N 144°26'E; S. Tanaka; 1922.
- 75- UMMZ142767; 1; Japan: off Niigata Prefecture, Honshū, Sea of Japan; approx. 38°N 139°E; Noo Fisheries School; 1922.
- 76- NMCB4-163; 1; USA: off Seward Marine Center dock, Seward, Resurrection Bay, Gulf of Alaska, Alaska; 60°7'N 149°27'W; C.B. Renaud and T.A. Edge; 29 July 1983; 7-9 m; gill net.
- 77- NMCB4-161; 1; USA: off Seward Marine Center dock, Seward, Resurrection Bay, Gulf of Alaska, Alaska; 60°7'N 149°27'W; T.A. Edge and C.B. Renaud; 29 July 1983; 16-17 m; boulders.
- 78- NMCB4-155; 5; USA: off Seward Marine Center dock, Seward, Resurrection Bay, Gulf of Alaska, Alaska; 60°7'N 149°27'W; C.B. Renaud and T.A. Edge; 28 July 1983; 18-22 m;

- boulders; 15°C; 22.5‰/‰; gill net.
- 79- NMC66-285; 2; Canada: about 16 km in on south side of Rennell Sound, west coast of Graham Island, Queen Charlotte Islands, British Columbia; 53°22'N 132°37'W; W. H. van Vliet; 9 Sept. 1966.
- 80- NMC68-1795; 1; Canada: Smith Inlet, off Indian Island, Smith Sound, British Columbia; 51°15'N 127°16'W; G. Cowan and F.K. Sandercock; 28 July 1964; 146-161 m; 7.3°C; bottom trawl.
- 81- NMC66-258; 1; Canada: Dixon Entrance, off Naden Harbour, north coast of Graham Island, Queen Charlotte Islands, British Columbia; 54°6'N 132°29'W; W.H. van Vliet; 30 Aug. 1966; 249 m; sand; 5.8°C; trawl.
- 82- NMC68-1730; 1; Canada: Swanson Channel, east of south end of Vancouver Island and west of North Pender Island, British Columbia; 48°47'N 123°20'W; G. Cowan; 4 Oct. 1963; 82-91 m; sand and mud; otter trawl.
- 83- NRMSBM/1922.353.3110; 1; USSR: off Petropavlovsk-Kamchatskiy, Kamchatka Peninsula; 53°1'N 158°39'E; S. Bergman et al., Swedish Kamchatka Expedition; 30 Aug. 1922.
- 84- LACM37172-1; 1; USA: off San Diego County, California; approx. 32°43'N 117°10'W.
- 85- LACM6909-1; 1; USA: Santa Monica Bay, about 1.5 km offshore, California; 33°59'30"N 118°30'0"W; J. Gagliano; 15 March 1966; 12 m; hook and line.

- 86- NMC61-118; 5; USA: cove on east side of Puget Bay, Prince William Sound, Gulf of Alaska, 45 air km east of Seward, Alaska; 60°0'N 148°29'W; D.E. McAllister, E.L. Bousfield, and J.W. Scoggan; 8 July 1961; 9 m; stones; jigging.
- 87- NMC68-1823A; 2; USA: North Pacific Ocean, south of Oagli Point, Unalaska Island, Alaska; 53°7'N 167°6'W; G. Cowan and F.K. Sandercock; 15 Aug. 1964; 179-186 m; 4.8°C.
- 88- NMC68-1880; 1; USA: Bristol Bay, Bering Sea, about 70 air km southwest of Cape Constantine, Alaska; 58°0'N 160°0'W; N.E. Okerstrom and C.J. Bresee; 16 July 1965; 48 m.
- 89- NMC68-1883; 1; USA: Bering Sea, about 100 air km northeast of St. Paul Island, Alaska; 57°45'N 168°45'W; C.J. Bresee and N.E. Okerstrom; 1 Aug. 1965; 69 m.
- 90- NMC68-1645; 1; USSR: Okhotsk Sea; 52°43'N 155°41'E; Myoyo Maru; 27 Sept. 1961; 58 m; otter trawl.
- 91- NMC68-1888; 1; USA: Bering Sea, about 200 air km southwest of Cape Newenham, Alaska; 57°45'N 164°45'W; C. J. Bresee and N.E. Okerstrom; 16 Aug. 1965; 49 m; 7.8°C.

Gadus ogac

- 92- NMC66-127; 1; Canada: Grandy Sound, Cabot Strait, 19 km east of Channel-Port aux Basques, Newfoundland; 47°36'20" N 58°50'30"W; D.E. McAllister and W.H. van Vliet; 8-9 June 1966; gill net.
- 93- CAS-SU24065; 1; Greenland: off Disko Island, west Greenland; approx. 69°15'N 53°32'W; US Fish Commission.

- 94- NMC84-277; 9; Canada: The Harbour, Red Bay, Strait of Belle Isle, Labrador, Newfoundland; 51°44'N 56°25'W; R. Chan; 27 Sept. 1982; 8-9 m.
- 95- NMC93-97; 2; Canada: Okak Bay, about 20 km southeast of Sipukat Lake, Labrador, Newfoundland; 57°30'0"N 62°15'3"W; J.G. Hunter; 29 Aug.-1 Sept. 1964; 1 m; sand and rocks; gill net.
- 96- NMC62-449; 3; Canada: Cape Parry harbor, Amundsen Gulf, District of Mackenzie, Northwest Territories; 70°7'N 124°39'W; M.V. Salvelinus; 23 Aug. 1962; 6 m; rocks; bottom dredge.
- 97- NMC83-104; 8; Canada: Bathurst Inlet, at the mouth of Arctic Sound, off Chapman Islands, about 4 km northeast of Kater Point, District of Mackenzie, Northwest Territories; 67°43'30"N 108°55'0"W; J.G. Hunter; 6-7 Sept. 1969; 0-9 m; 1.03-4.53°C; 24.84-26.92‰; gill net.
- 98- ROM9778; 1; Canada: Baie du Vieux Comptoir, James Bay, Territoire du Nouveau-Québec, Québec; 52°36'N 78°45'W; F. Johansen; 11-12 Sept. 1920.
- 99- ROM9779; 1; Canada: Baie du Vieux Comptoir, James Bay, Territoire du Nouveau-Québec, Québec; 52°36'N 78°45'W; F. Johansen; 11-12 Sept. 1920.
- 100- ROM9702; 1; Canada: Christopher Inlet, at Port Burwell, Killinek Island, Ungava Bay, District of Franklin, Northwest Territories; 60°25'N 64°50'W; 1927.

- 101- ISH290/59; 2; Greenland: Davis Strait, off west coast of Greenland; 63°50'N 53°0'W; H. Koops; 29 Dec. 1959; 260 m.
- 102- ISH1024/82; 1; Canada: Labrador Sea, off Labrador, Newfoundland; 54°16'N 55°24'W; M. Kerstan; 6 Nov. 1982; 176 m; -0.65°C; 33.25‰; bottom trawl.
- 103- NMC77-1207; 3; Canada: outlet of Eskimo Lakes, about 18 km west of Campbell Island, southern Liverpool Bay, District of Mackenzie, Northwest Territories; 69°34'48"N 131°15'0"W; Arctic Biological Station, Ste-Anne-de-Bellevue; 26 July 1971; 23 m; mud; bottom trawl.
- 104- NMC61-229; 3; Canada: bay at Eskimo Point, northwest Hudson Bay, District of Keewatin, Northwest Territories; 61°7'N 94°2'W; S.D. MacDonald; 24-25 July 1960; 0-2 m; gill net.
- 105- NMC63-167; 3; Canada: off Fovungnituk, northeast Hudson Bay, Territoire du Nouveau-Québec, Québec; 60°2'N 77°16'W; J.G. Robertson; 23 Aug. 1963; 3-12 m; rocks; lure and line.
- 106- NMC67-767; 1; Canada: Saguenay River Fjord, about 21 air km east of Chicoutimi, Chicoutimi County, Québec; 48°25'15"N 70°47'0"W; "Les Jeunes Explorateurs"; 11 July 1963; 50 m; mud; gill net.
- 107- NMC67-528; 1; Canada: Saguenay River Fjord, about 40 air km northwest of mouth, Chicoutimi County, Québec; 48°16'6"N 70°11'50"W; L. Brassard; 15 Aug. 1959; 18 m; rocks; gill net.

- 108- NMC67-529; 1; Canada: Saguenay River Fjord, about 40 air
km northwest of mouth, Chicoutimi County, Québec; 48°15'
36"N 70°11'12"W; L. Brassard; 18 Aug. 1959; 18 m; rocks;
gill net.
- 109- NMC74-260; 3; Canada: Spence Bay, southwest Boothia
Peninsula, District of Keewatin, Northwest Territories;
69°31'52"N 93°31'30"W; D.E. McAllister; 6 Aug. 1974; 6-12
m; boulders; 8°C; jigging.
- 110- NMC64-330; 1; Canada: Tellik Inlet, Cape Dorset, south
Baffin Island, District of Franklin, Northwest
Territories; 64°17'N 76°45'W; A.E. Peden and J.D.
McEachran; 27 Aug. 1960; 15 m.
- 111- NMC86-229; 3; Canada: Miramichi Bay, Gulf of St.
Lawrence, New Brunswick; 47°8'N 64°58'W; 25 Feb. 1982;
smelt trap.
- 112- NMC81-61; 2; Canada: Humber Arm, at Curling,
Newfoundland; 48°57'42"N 58°0'6"W; J.N. Bowiby; 21 May
1978; 4-7 m; mud and detritus; gill net.

METHODS

The methodology used for counting and measuring characters follows Hubbs and Lagler (1964) with some modifications and additions. The morphometric, meristic, pigmentary, and miscellaneous characters were assessed on the left side of a specimen unless that side was damaged. Adults equal to or greater than 100 mm in standard length and preserved either in a 45-60% aqueous solution of isopropanol or in a 70-75% aqueous solution of ethanol were studied.

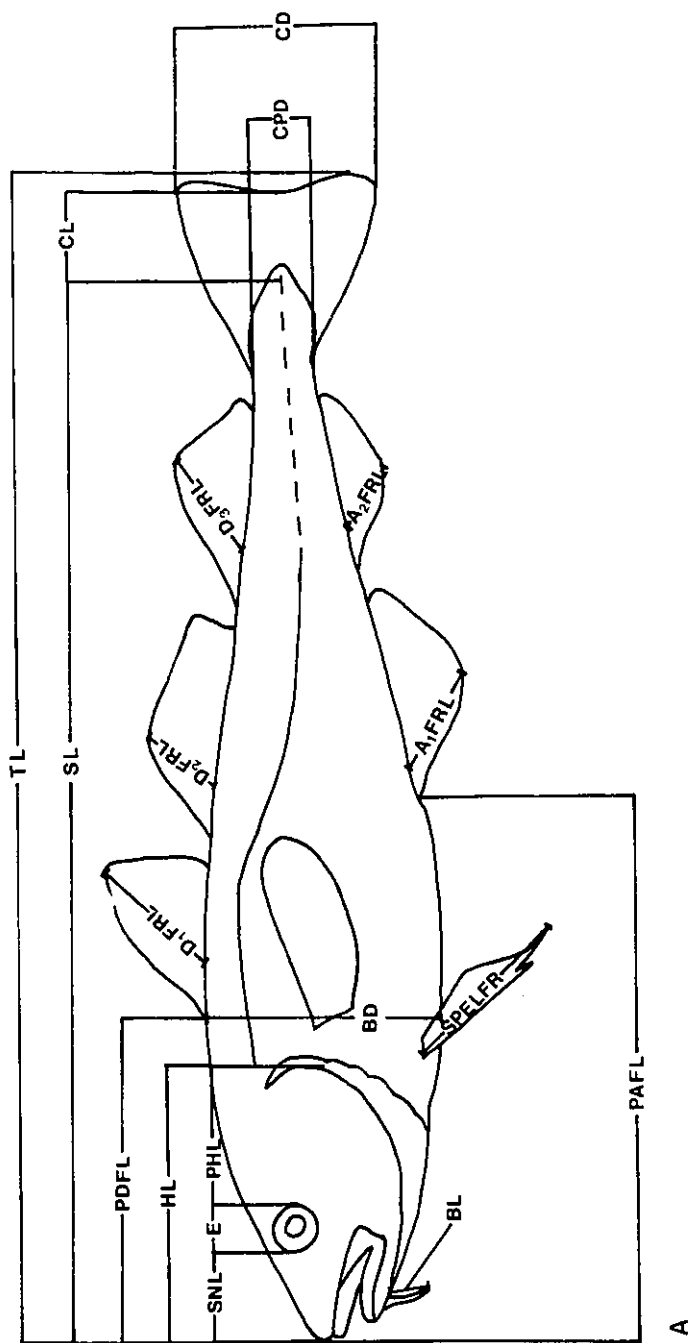
Morphometrics

Total length, standard length, and preanal fin length (in the few cases it exceeded 300 mm) were measured to the nearest millimetre using a wooden measuring board; body girth was taken with a string, the length of which was determined using the measuring board. The rest of the 48 morphometrics were measured to the nearest 0.1 mm with a pair of 300 mm long Limnoterra electronic calipers interfaced to a Hyperion (TM of Dynalogic Info-Tech Corp.) microcomputer. In taking measurements on a contorted specimen, efforts were made to make it assume a "normal" position. Fig. 2A-B illustrates some of the morphometrics measured.

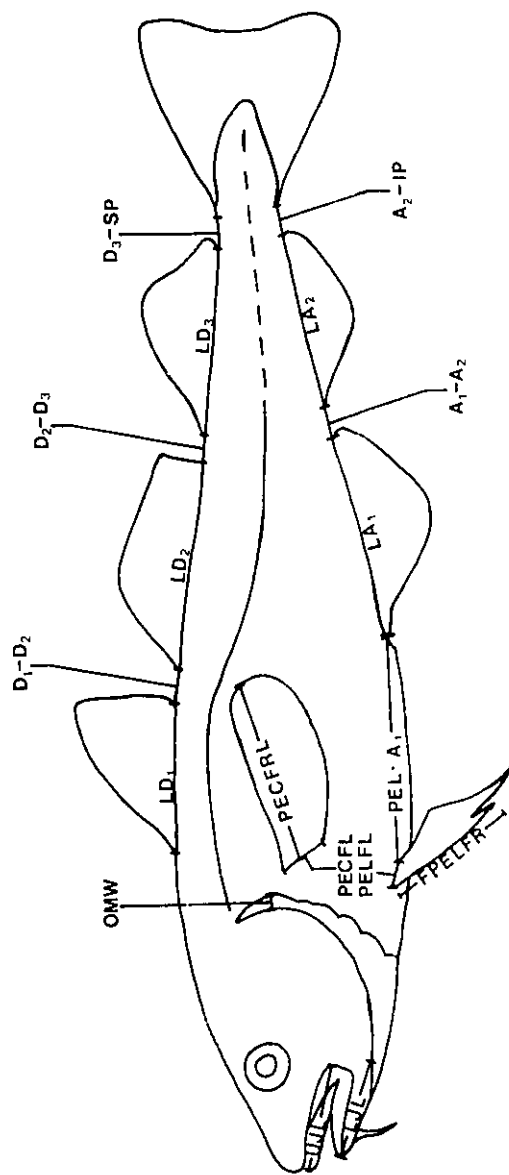
Total Length (TL): The length from the tip of the snout to the posteriormost tip of the caudal fin.

Standard Length (SL): The length from the tip of the snout to the caudal flexure; at the bottom of the

Fig. 2A-B. Schematic drawings of a cod showing some of the morphometrics measured. See the text (Methods) for the meaning of the character mnemonics.



A



B

crease.

Predorsal Fin Length (PDFL): The length from the tip of the snout to the origin of the first dorsal fin.

Head Length (HL): The length from the tip of the snout to the posteriormost edge of the bony operculum taken at the level of the eye.

Opercular Membrane Width (OMW): The width from the posteriormost edge of the operculum to the posteriormost edge of the opercular membrane taken at the level of the eye.

Snout Length (SNL): The length from the tip of the snout to the anteriormost edge of the fleshy orbit.

Nasal Flap Length of Incurrent Nostril (NFL): The length from the base of the nasal flap to its tip.

Horizontal Eye Diameter (E): The diameter of the fleshy, as opposed to the bony orbit.

Postorbital Head Length (PHL): The length from the posteriormost edge of the fleshy orbit to the posteriormost edge of the operculum.

Upper Jaw Length (UJL): The length from the premaxillary symphysis to the posteriormost edge of the maxillary.

Lower Jaw Length (LJL): The length from the dentary symphysis to the posteriormost edge of the angular. This measurement includes the three following bones: the dentary, the articular, and the angular.

Chin Barbel Length (BL): The length from its base to its tip taken posteriorly.

Preal Anal Fin Length (PAFL): The length from the tip of the snout to the origin of the first anal fin.

Distance Between Dentary Symphysis and Angle of Branchiostegal Membrane (DSBM): This measurement was taken along the ventral surface from the dentary symphysis to the lower end of the gill slit.

First Dorsal Fin Length (LD_1): The length along its base from the origin to the insertion.

The lengths of the second dorsal fin (LD_2), third dorsal fin (LD_3), first anal fin (LA_1), second anal fin (LA_2), pectoral fin (PECFL), and pelvic fin (PELFL) were measured as was the first dorsal fin length.

Length of D_1 - D_2 Interspace (D_1 - D_2): The length of the interspace between the insertion of the first dorsal fin and the origin of the second dorsal fin.

Length of D_2 - D_3 Interspace (D_2 - D_3): The length of the interspace between the insertion of the second dorsal fin and the origin of the third dorsal fin.

Distance Between Insertion of D_3 and Insertion of the Superior Procurrent Caudal Fin Rays (D_3 -SP): The length of the interspace between the insertion of the third dorsal fin and the insertion of the superior procurrent caudal fin rays. The superior

procurrent caudal fin rays are hidden in the flesh but a sharp angle marks the place where the first superior procurrent caudal fin ray lies.

Length of A_1 - A_2 Interspace (A_1 - A_2): The length of the interspace between the insertion of the first anal fin and the origin of the second anal fin.

Distance Between Insertion of A_2 and Insertion of the Inferior Procurrent Caudal Fin Rays (A_2 -IP): The length of the interspace between the insertion of the second anal fin and the insertion of the inferior procurrent caudal fin rays. The inferior procurrent caudal fin rays are hidden in the flesh but a sharp angle marks the place where the first inferior procurrent caudal fin ray lies.

Pelvic Fin to A_1 Length (PEL- A_1): The distance between the insertion of the pelvic fin and the origin of the first anal fin.

Length of the First Dorsal Fin's Longest Fin Ray

(D_1 FRL): The length of the longest fin ray from the base of the fin and along that ray up to its tip.

The lengths of the second dorsal fin's longest fin ray (D_2 FRL), third dorsal fin's longest fin ray (D_3 FRL), first anal fin's longest fin ray (A_1 FRL), second anal fin's longest fin ray (A_2 FRL), and pectoral fin's longest fin ray (PECFRL) were measured as was the length of the first dorsal fin's longest fin ray.

First Principal Pelvic Fin Ray Length (FPELFR): The length of the first principal pelvic fin ray from its base to its tip.

Second Principal Pelvic Fin Ray Length (SPELFR): The length of the second principal pelvic fin ray from its base to its tip.

Caudal Fin Length (CL): The length of the caudal fin from the caudal flexure to the posteriormost tip of the median caudal fin rays.

Body Depth (BD): The body depth was taken at the level of the origin of the first dorsal fin.

Caudal Peduncle Depth (CPD): Least depth of the caudal peduncle was taken.

Caudal Fin Depth (CD): The maximum depth of the caudal fin taken at the posteriormost tips of the first principal fin rays (see below about the difficulty in locating these) on the superior and inferior lobes of the caudal fin.

Least Internarial Width (INW): The least distance between the two incurrent (innermost) nostrils.

Mouth Gape (MG): The transverse distance across the closed mouth taken at the commissures.

Least Bony Interorbital Width (IOW): The least distance across the skull between the bony rims of the orbits.

Head Width (HW): This measurement was taken at the

posteriormost edges of the opercles at the level of the eyes.

Interinsertions of Pectoral Fins (IPEC): The width of the interspace between the insertion of the left and right pectoral fins.

Interinsertions of Pelvic Fins (IPEL): The width of the interspace between the insertion of the left and right pelvic fins.

Length of Longest Gill-raker on Outer Side of First Gill Arch (LOGR)

Length of Longest Gill-raker on Inner Side of First Gill Arch (LIGR)

Body Girth (BG): The body circumference taken at the level of the origin of the first dorsal fin, excluding the pectoral and pelvic fins which are lifted. A string was used to make this measurement.

Meristics

Infraorbital Pores (IOP)

Preoperculo-mandibular Pores (PMP)

Lateral Line Pores (LLPD): The first pore counted was the one that was at or immediately posterior to the junction of the cephalic and supratemporal branches of the lateral line system. The last pore counted was the one that was on or immediately anterior to

the caudal flexure. Water was squirted abundantly with a wash bottle over the specimen, and then a fine pair of forceps were run along the canal to extrude the water and thus reveal the pores. When two pores were placed parallel to each other (one directly above the other) only one was counted. Pores on side branches of the main lateral line canal, when they occurred, were not counted.

Branchiostegal Rays (BR)

First Dorsal Fin Rays (D_1 FRN): In Gadus, it is difficult to determine where the first principal fin ray begins since the rudimentary ones smoothly grade with the principal ones. Therefore, the total count of rudimentary and principal rays was made. Furthermore, in Gadus every dorsal and anal fin ray articulates with its own set of pterygiophores (radial bones) so that each ray is counted as one. The investing membrane of the fin was not dissected anteriorly to ascertain the presence of rudimentary fin rays but a 100 W lightbulb was shone through the fin to permit their detection.

The second dorsal fin rays (D_2 FRN), third dorsal fin rays (D_3 FRN), first anal fin rays (A_1 FRN), and second anal fin rays (A_2 FRN) were counted as were the first dorsal fin rays.

Pectoral Fin Rays (PECFRN): Only the principal rays were

counted.

Pelvic Fin Rays (PELFRN): Only the principal rays were counted.

Caudal Fin Rays (CFR): In Gadus, it is difficult to determine where the principal caudal fin rays begin since the rudimentary ones smoothly grade with the principal ones. Therefore, the total count of rudimentary and principal rays was made. The caudal fin ray counts are made from radiographs to avoid extensive and time-consuming dissections.

Primary Caudal Fin Rays (PCFR): The number of caudal fin rays that articulate with hypurals 3 to 5 as defined by Markle (1982).

Gill-rakers on Outer Side of First Gill Arch (NOGR): The gill-rakers counted were those on the upper and lower limbs of the first branchial arch combined, and included the rudimentary ones. In counting gill-rakers, particularly in the smaller fishes, the gill arch often had to be cut at its base and stretched outward.

Gill-rakers on Inner Side of First Gill Arch (NIGR): counted as were the gill-rakers on the outer side of the first gill arch.

Precaudal Vertebrae (PV): The vertebrae were counted from radiographs. The count begins with the atlas and proceeds posteriorly up to the last centrum

with pleural ribs. Except for two ribless vertebrae anteriorly, all precaudal vertebrae have pleural ribs.

Caudal Vertebrae (CV): The vertebrae were counted from radiographs. Included in this count were the vertebrae with hemal spines and the hypural plate (urostyle) which was counted as one.

Pigmentation

Chin Barbel Pigmentation (CBP): A score of 1 was given if the chin barbel was unpigmented; 2 if its anterior face was at least partly pigmented; and 3 if pigmentation was present all around the barbel but not necessarily to its tip.

Lateral Line Pigmentation (LLPI): A score of 1 was given if the strip of skin along the lateral line was lightly pigmented from the level of the cleithrum and along its entire course, sharply contrasting with the heavily pigmented adjacent areas; 2 if it was heavily pigmented up to the middle of the first or second dorsal fin, blending in with adjacent areas and posteriorly it was lightly pigmented, in sharp contrast to adjacent areas; and 3 if it was heavily pigmented along its entire course, blending in with adjacent areas.

Body Pigmentation (BP): A score of 1 was given if the

body had a uniform brownish pigmentation which became progressively lighter as one proceeded ventrally; 2 if dark spots were present on the dorsal surface, upper and mid flanks on a lighter background and the lower flanks and ventral surface had fine dark speckling which may be more sparsely distributed on the ventral surface compared to the lower flanks; 3 if the dorsal surface, the upper and mid flanks had lightly pigmented vermiculations, the lower flanks had fine dark speckling and the ventral surface was very sparsely speckled; 4 if the dorsal surface was uniformly darkly pigmented, the upper and mid flanks had lightly pigmented vermiculations, and the lower flanks and ventral surface had fine dark speckling which may be more sparsely distributed on the ventral surface compared to the lower flanks. The vermiculations may extend to the lower flanks. A score of 5 was given if the dorsal surface, upper and mid flanks were darkly pigmented with dark spots being hardly if at all discernible and the lower flanks and ventral surface had fine dark speckling.

First Dorsal Fin Pigmentation (D₁F): A score of 1 was given if the posterior edge of the first dorsal fin was unpigmented or much more lightly pigmented than

the rest of the fin was, and 2 if the whole fin was uniformly darkly pigmented. The unpigmented or lightly pigmented edge when present, although readily discernible, may be quite narrow. Only in the case of D_1P can the unpigmented or lightly pigmented edge be discontinuous. In such a case, a score of 1 was given.

The pigmentation of the second dorsal fin (D_2P), third dorsal fin (D_3P), first anal fin (A_1P), second anal fin (A_2P), and caudal fin (CFP) was scored as was the first dorsal fin pigmentation.

Pelvic Fin Pigmentation (PELP): A score of 1 was given if the membrane investing the first two principal fin rays only was unpigmented; 2 if the membrane investing the first fin ray and the trailing part of the second ray only was unpigmented; 3 if the membrane investing the trailing parts of the first two rays only was unpigmented; 4 if the membrane investing the trailing part of the first ray only was unpigmented; and 5 if the whole fin was pigmented, with the trailing parts of the first two rays being at least partly pigmented. This character was assessed on the ventral aspect of the pelvic fin which faces towards the midline when the fin is erect.

Peritoneal Pigmentation (PP): A score of 1 was given if

the peritoneum was unpigmented save for some sparsely distributed black melanophores; 2 if it was uniformly speckled with conspicuous dark brown or black melanophores on a grayish brown background; 3 if it had grayish brown or grayish black mottling with conspicuous dark brown melanophores in the light areas; and 4 if it was uniformly dark brown or jet black with melanophores hardly distinguishable with the naked eye. The silvery pigmented inner layer of the peritoneum may show up through the pigmented outer layer. This character was assessed on the ventral surface of the body cavity near the ventral midline.

External Pigmentation of Ovaries (EPO): A score of 1 was given if the ovaries were yellowish or pinkish with no melanophores; 2 if brown melanophores were sparsely distributed over the anterior half to two-thirds of the ovaries; 3 if dark brown or grayish black mottling covered the ovaries entirely; and 4 if dark brown or jet black melanophores uniformly covered the entire ovaries. A missing datum value was given when an immature specimen or a male were being assessed.

Miscellanea

Sex (S): A score of 1 was given for males; 2 for

females; and 3 if the sex could not be determined because the specimen was too immature.

Nuptial Tubercles (NT): A score of 1 was given if tubercles were absent, and 2 if they were present. The presence or absence of tubercles was ascertained with the naked eye. Care was taken not to mistake lifted scales for tubercles.

Lateral Line Shape (LLS): A score of 1 was given if the lateral line decurved smoothly, and 2 if it decurved sharply at the level of the D_1 - D_2 interspace. The lateral line was said to be smoothly decurving if the angle of decurvature with the horizontal at the level of the D_1 - D_2 interspace was less than 30° and it was said to be sharply decurving if it was 30° or more.

Lateral Line Interruption Point (LLIP): A score of 1 was given if the lateral line was interrupted under the first dorsal fin; 2 if it became so under the second dorsal fin; 3 if it became so under the D_2 - D_3 interspace; 4 if it became so under the third dorsal fin; and 5 if it became so posteriorly to the insertion of the third dorsal fin.

Origin of First Anal Fin Relative to Dorsal Fins (OA_1): A score of 1 was given if the origin of the first anal fin was at or anterior to the insertion of the first dorsal fin; 2 if it was in the D_1 - D_2

interspace; and 3 if it was at or posterior to the origin of the second dorsal fin.

Origin of Second Anal Fin Relative to Dorsal Fins (OA₂):

A score of 1 was given if the origin of the second anal fin was at or anterior to the insertion of the second dorsal fin; 2 if it was in the D₂-D₃ interspace; and 3 if it was at or posterior to the origin of the third dorsal fin.

Caudal Fin Shape (CFS): A score of 1 was given if the caudal fin was truncate, and 2 if it was emarginate. In both cases, the posteriormost edges of the superior and inferior lobes of the caudal fin were rounded.

Three statistical software packages were used for data analysis: S199 (Wolynetz and Thompson 1977) for computation of the g_1 , g_2 statistics; SAS (SAS Institute Inc. 1982) for computation of the residuals, the ANOVA, the correlation coefficients, and the canonical discriminant analysis; and S075 (Lefkovitch 1981) for the principal coordinates analysis. These analyses were carried out on the University of Ottawa mainframe, an Amdahl V360, using double precision. The raw data have been deposited in the Ichthyology Section, National Museum of Natural Sciences, Ottawa.

In the principal coordinates analyses, only group percentage separations above 85% were analyzed. These group

percentage separations are ones in multivariate space and were used to identify principal coordinates axes of discriminatory value between groups. Once one or more axes were identified, all univariate characters with heavy loadings on these particular axes were investigated for their discriminatory value between the groups. Characters with heavy loadings were defined as ones having an absolute correlation ≥ 0.50 between their transformed values (transformation procedure is given in Results and Discussion) and the coordinates of the specimens along a particular principal coordinates axis. If two groups exhibited 100% separation (i.e.: non-overlap) based on one or more untransformed univariate characters (except for morphometric characters which were expressed as ratios of standard length), indicating the absence of gene flow, these were said to represent distinct species. If two groups exhibited at best between 90 and 99% non-overlap based on one or more untransformed univariate characters, these were said to represent distinct subspecies. If no untransformed univariate characters (out of at least 30 investigated) could be found that gave at least 90% separation between two groups then these groups were not recognized as belonging to distinct species or subspecies.

RESULTS AND DISCUSSION

The samples for each of the five groups available were determined to be rectilinear in their relative growth patterns. No inflection points could be detected following visual inspection of $\ln X \ln$ plots of the 47 morphometric characters against the standard length, indicating that only one growth stanza was involved in the size range studied and therefore, that we are dealing with morphometrically comparable semaphoronts (see Wiley 1981). Visual inspection was deemed a sufficient criterion of rectilinearity because I was looking for the type of marked shift in growth pattern one finds when an organism changes life stages.

The raw data for the 48 morphometrics were tested for normality for each of the five groups by performing a two-tailed Student's t -test on the g_1 and g_2 statistics as outlined in Sokal and Rohlf (1969), where $H_0: g_1, g_2 = 0$ and $H_1: g_1, g_2 \neq 0$. The level of significance used was $\alpha = 0.05$.

A number of null hypotheses were rejected and therefore a logarithmic transformation ($\ln(x + 1)$, where $x =$ morphometric characters 1-48) was made on the data as suggested by Sokal and Rohlf (1969) in order to reduce the skewness and kurtosis of the variable distributions. On the average, the logarithmic transformation substantially lessened the skewness but the kurtosis remained unchanged.

Two characters (OA_1 and OA_2) were removed from future analysis because they are invariable. These characters were

therefore useful to characterize the genus but could not be used as diagnostic characters for the species within it. The data for the remaining 82 characters were standardized to

zero mean and unit standard deviation in order that the various characters be expressed on a comparable scale.

Furthermore, each morphometric character was regressed against the standard length. The residuals of the pooled regression lines were then extracted for each morphometric character. Analysis of the g_1 and g_2 statistics on the standardized residuals showed them to be much more skewed on average compared to when only the logarithmic transformation had been done, but less so compared to when the raw data were being evaluated. Also, they exhibited much less kurtosis on average than either the logarithmic transformed or raw data. The use of residuals was chosen over other transformation procedures, because it is one of two equally effective methods to remove the effect of size in organisms with indeterminate growth (Reist 1985, 1986), such as is the case here. Furthermore, of the various univariate transformations compared by Reist (1985) for removal of the size effect, residuals least affected the covariance relationships between the morphometric characters.

These transformed data (82 characters) were subjected to an ordination technique, principal coordinates analysis (PCO). PCO was chosen over principal components analysis (PCA) because 77.3% of the specimens had one or more missing data cells. The maximum amount of data missing for a single specimen was 24.4%, the average being 4.0%. In contrast to PCA, PCO does not require estimation of missing data for the

computation of a complete association matrix (Neff and Marcus 1980). The reason for this is that PCO operates on an OTU (operational taxonomic unit) X OTU matrix (Q-mode analysis) instead of a character X character matrix (R-mode analysis) like PCA (Blackith and Reyment 1971). The Gower dissimilarity (= distance) coefficient was used because it is made to handle a matrix composed of mixed characters (Lefkovitch 1981).

A plot of the 110 adult specimens of Gadus using principal coordinate axes 1 and 2 (fig. 3) revealed two non-overlapping homogeneous groups, ogac and macrocephalus, readily distinguishable from the taxonomically heterogeneous group made up of morhua, callarias, and marisalbi. Plots of principal coordinate axes 1 and 3 (fig. 4) and principal coordinate axes 2 and 3 (fig. 5) did not further resolve the morhua-callarias-marisalbi group. The first three axes accounted for only 22.49% of the total variance and is an indication that the residuals were effective in removing the effect of size; the first axis accounting for only 9.49% of the variance. Forty-two axes were required to account for 75.32% of the variance, the amount of variance explained with each successive axis after axis 3 never exceeding 3.34% .

A second principal coordinates analysis was conducted on the heterogeneous group alone in order to remove any noise associated with the ogac and macrocephalus groups. However, this procedure did not break up the heterogeneous group into distinct groupings nor could one definitely establish that a

Fig. 3. Plot of principal coordinate axes 1 and 2 for the 110 adult specimens of Gadus used in the pilot study. O = morhua; Δ = callarias; $\square$ = kildinensis; $\bullet$ = ogac; $\blacktriangle$ = macrocephalus; $\blacksquare$ = marisalbi. The symbol $\square$ only appears in figs. 9-11. Two of the macrocephalus symbols are so close to each other that the resolution of this graph does not permit their separation.

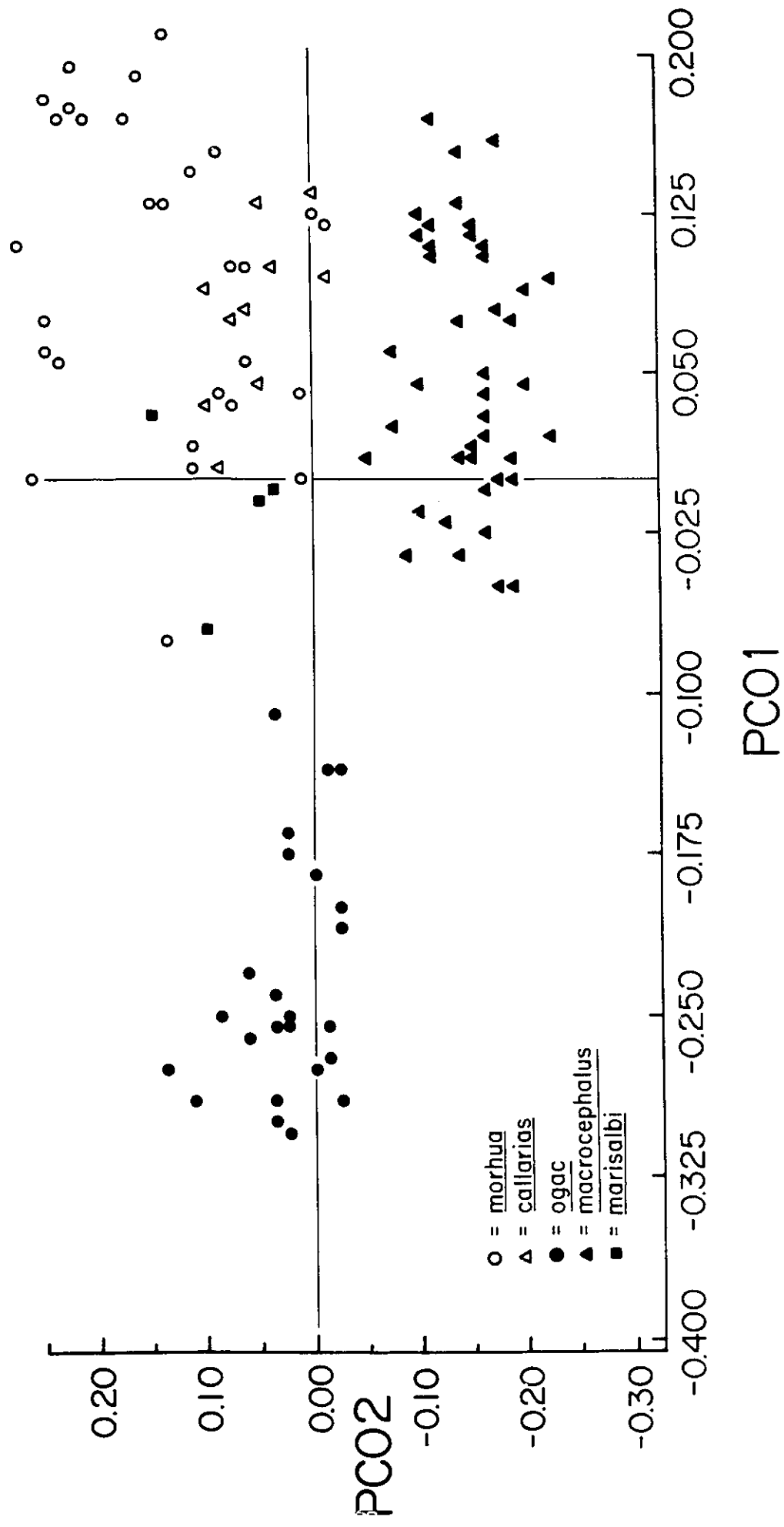


Fig. 4. Plot of principal coordinate axes 1 and 3 for the 110 adult specimens of Gadus used in the pilot study. Refer to Fig. 3 for meaning of symbols. A pair of ogac symbols, two pairs of macrocephalus, and one morhua and one macrocephalus are so close to each other that the resolution of this graph does not permit their separation.

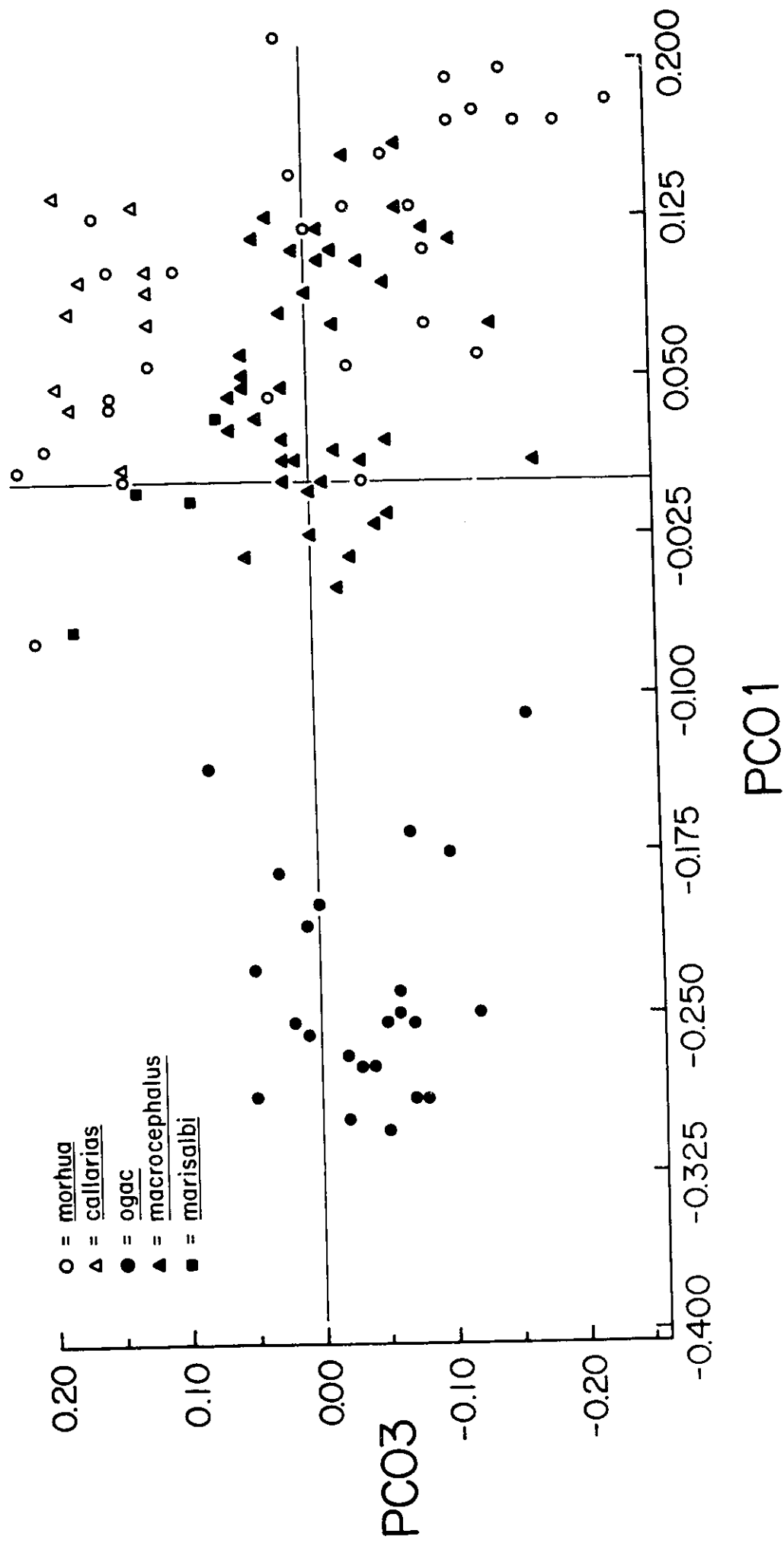
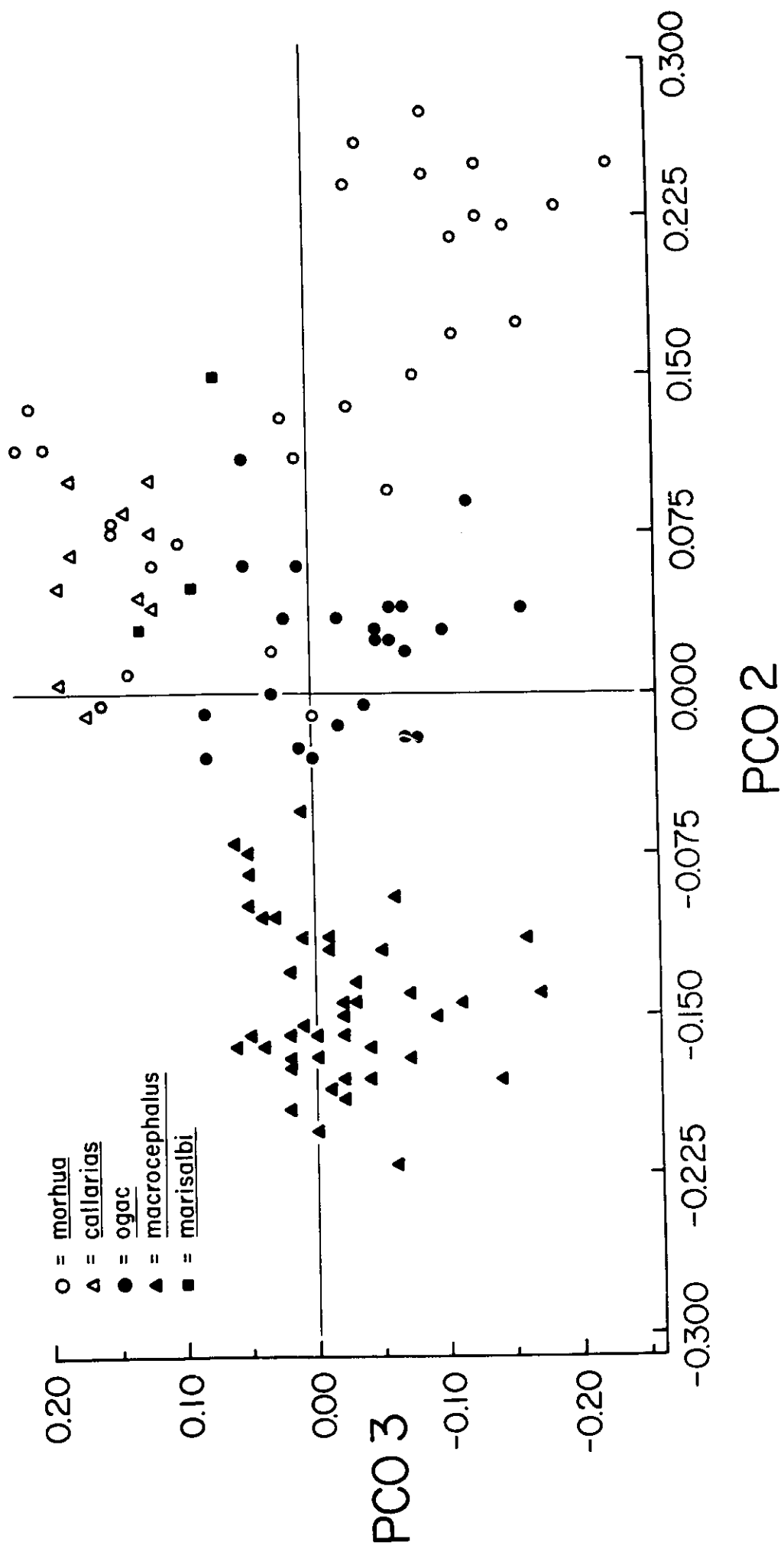


Fig. 5. Plot of principal coordinate axes 2 and 3 for the 110 adult specimens of Gadus used in the pilot study. Refer to Fig. 3 for meaning of symbols. A pair of morhua symbols, a pair of macrocephalus, one morhua and one ogac, and one morhua and one marisalbi are so close to each other that the resolution of this graph does not permit their separation.



single group was involved (figs. 6-8). The first three axes accounted for only 24.23% of the total variance and is an indication that the residuals were effective in removing the effect of size; the first axis accounting for only 11.34% of the variance. Twenty-two axes were required to account for 75.31% of the variance, the amount of variance explained with each successive axis after axis 3 never exceeding 4.56% .

The degree of separation generally accepted for subspecific recognition is 90-93% (Bailey et al. 1954, Mayr 1969). The percentage separation between all pairs of the three putative subspecies along the first three principal coordinate axes (figs. 6-8) varied between 59.0 and 92.9% . Out of nine possible pair combinations, only two pairs of putative subspecies exhibited a percentage separation greater than 78.6%, namely, callarias-marisalbi along principal coordinate axis 2 with 92.9% separation and morhua-marisalbi along principal coordinate axis 3 with 90.9% separation. However, in view of the fact that a shift of a single specimen in either of these cases changed the percentage separation from highly significant to nonsignificant, it was decided that a larger sample of specimens representative of each component of the morhua-callarias-marisalbi group was desirable to test its homogeneity. Therefore, one could only conclude that the genus Gadus was comprised of at least three groups: ogac, macrocephalus, and an unresolved morhua-callarias-marisalbi group.

Fig. 6. Plot of principal coordinate axes 1 and 2 for 43 adult specimens of Gadus used in the pilot study. Refer to Fig. 3 for meaning of symbols.

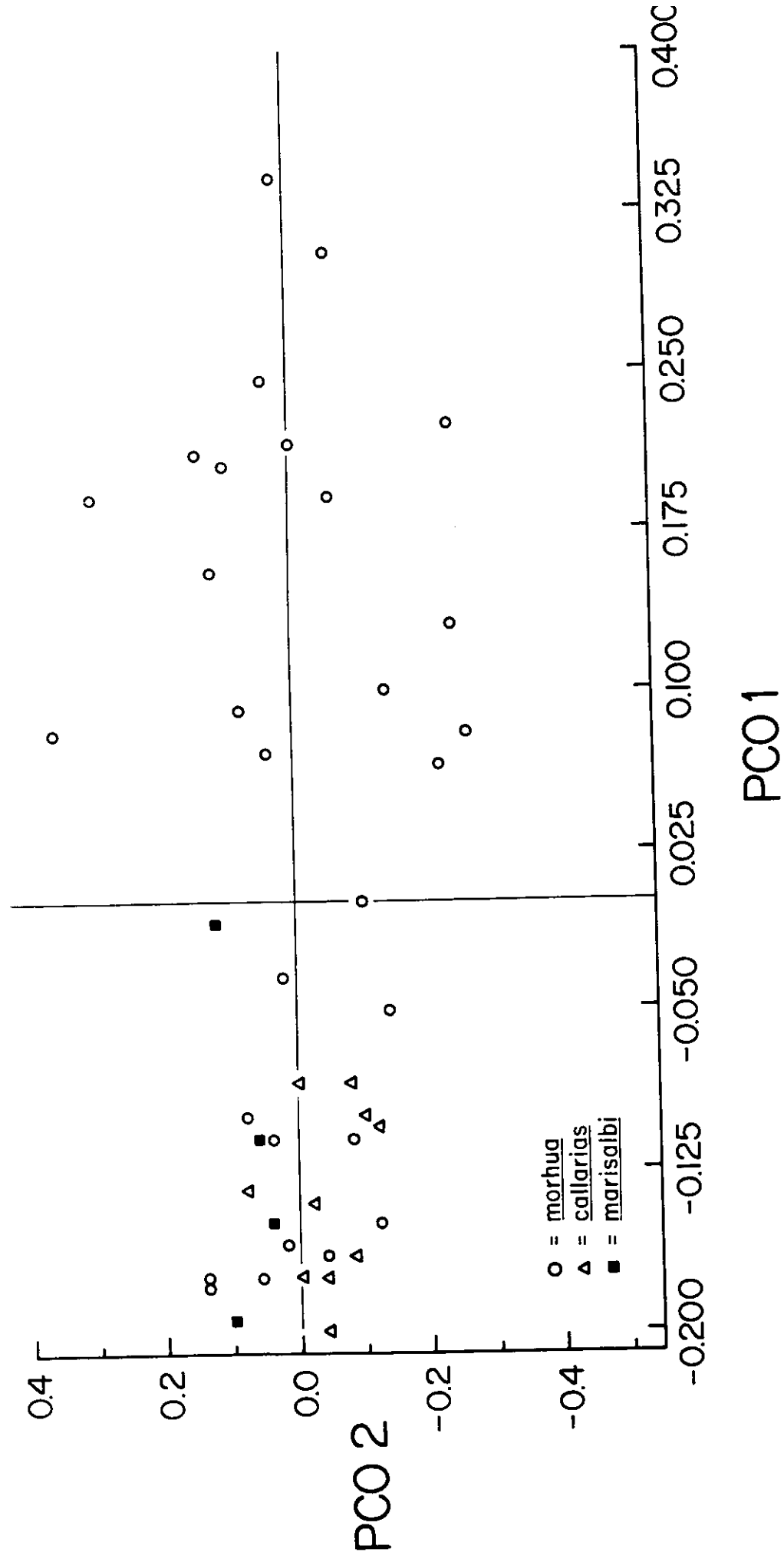


Fig. 7. Plot of principal coordinate axes 1 and 3 for 43 adult specimens of Gadus used in the pilot study. Refer to Fig. 3 for meaning of symbols.

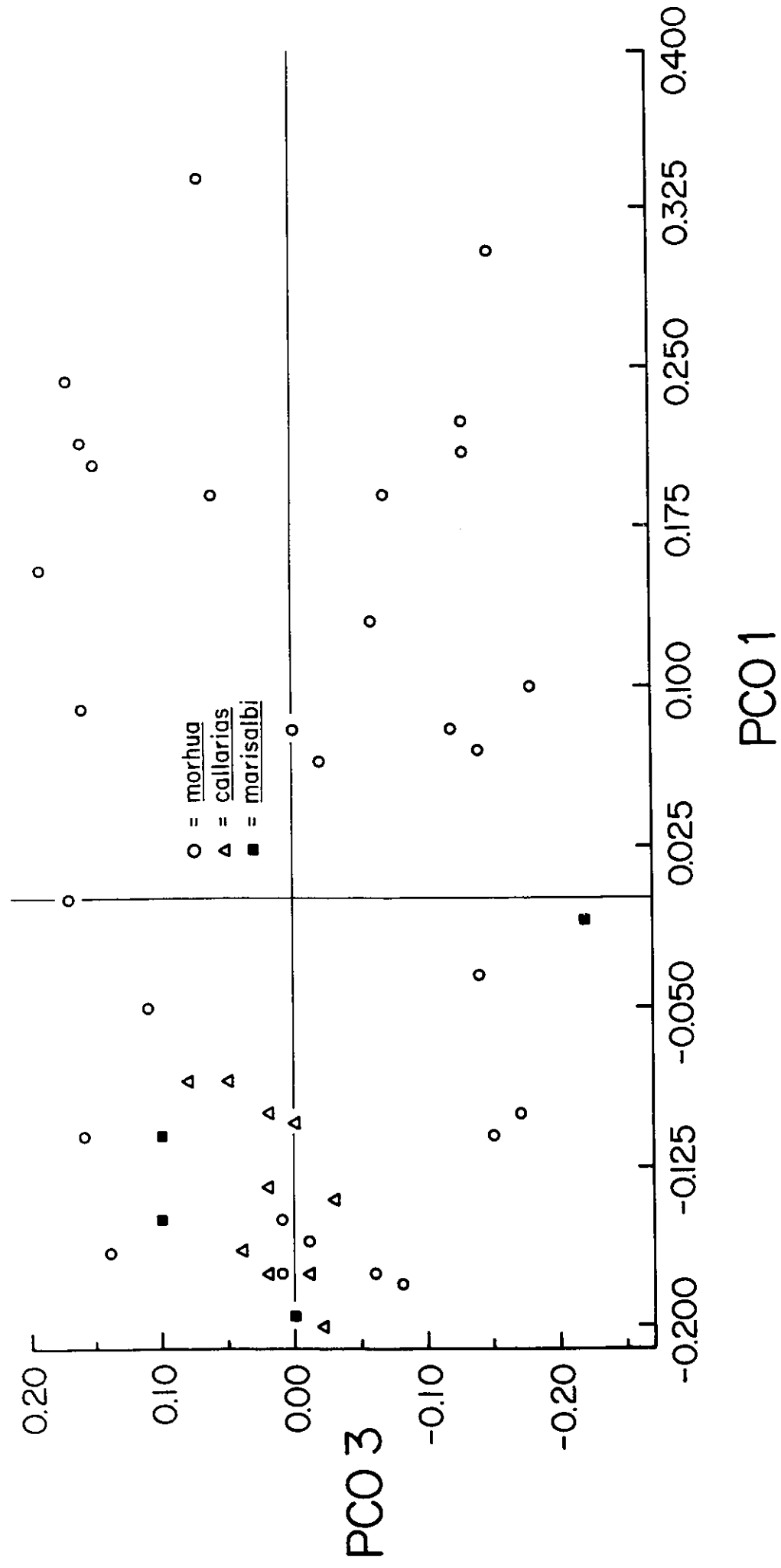
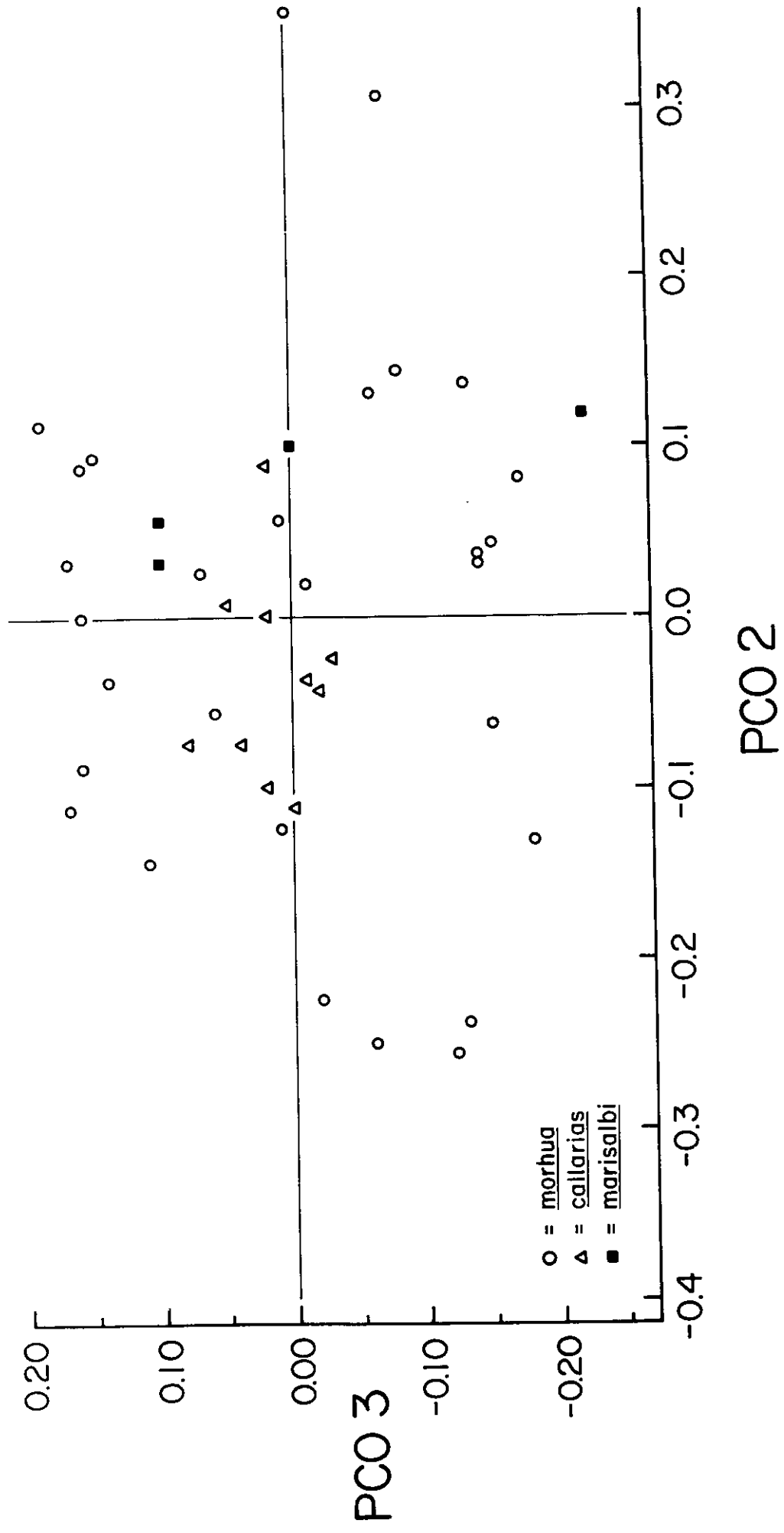


Fig. 8. Plot of principal coordinate axes 2 and 3 for 43 adult specimens of Gadus used in the pilot study. Refer to Fig. 3 for meaning of symbols.



Since the number of groups within the genus was not definitely resolved, one could not proceed to perform an ANOVA in order to remove those characters which were of no value in discriminating between the groups. A more conservative approach was therefore adopted. The a priori identifications of morhua, callarias, and marisalbi were provisionally assumed to represent distinct groups. The transformed data for each of the characters except for the five multistate unordered ones (BP, PELP, PP, EPO, and S) were subjected to an ANOVA utilising as groups those collections made up of two or more individuals of a given putative subspecies from a given locality and a given time. This subsample amounted to 20 groups and comprised 68 specimens belonging to the five putative subspecies represented in the pilot study (Table 3). The level of significance chosen was $P \leq 0.005$ and consequently, the following 31 characters were rejected: OMW, SNL, NFL, LD₂, LA₁, LA₂, PECFL, E, D₁FRL, D₂FRL, A₁FRL, BD, D₁-D₂, D₃-SP, A₁-A₂, PEL-A₁, IPEL, CD, LOGR, LIGR, IOP, BR, D₁FRN, A₁FRN, PELFRN, PECFRN, NOGR, PV, CV, CFS, PCFR. The 51 characters retained for future analyses are given in Table 4.

This reduced character suite was examined in an additional 90 adult specimens of Gadus, bringing the total number studied to 200, distributed as follows: 55 morhua (100-765 mm SL), 15 callarias (114-404 mm SL), 57 macrocephalus (133-662 mm SL), 51 ogac (149-526 mm SL), 1

Table 3. Groups used in the ANOVA.

Group code	Specimen label	Locality	N
A	AB2-5	Canada: Gulf of St. Lawrence, at Baie-Trinité	4
B	AC3-4	Norway: Varanger Fjord, at Nesseby	2
C	AC5-6	Iceland: off Reykjavík	2
D	AC10-11	UK: Crouch River estuary, at Burnham on Crouch	2
E	AC12-13	UK: Crouch River estuary, at Burnham on Crouch	2
F	AI1-3	Canada: Sipukat Lake, north of Okak Bay	3
G	AI4-7	Canada: Ungava Bay, at Port Burwell	4
H	CC2-4	Denmark: Baltic Sea, off Bornholm Island	3
I	CC6-7	Finland: Baltic Sea, off Airisto	2
J	CC8-10	Poland: Gdańsk Bay, northeast of Gdynia	3
K	WI1-2	USSR: Gulf of Kandalaksha, White Sea	2
L	OB1-7,9-10	Canada: Red Bay, Strait of Belle Isle	9
M	OI1-2	Canada: Okak Bay	2
N	OI3-5	Canada: Cape Parry harbor, Amundsen Gulf	3
O	OI6-13	Canada: Bathurst Inlet	8
P	PH3-7	USA: Resurrection Bay, at Seward	5
Q	PH9-14	USA: south of Unalaska Island	6
R	PF7-8	Japan: off southern coast of Hokkaidō	2
S	PF10-11	Japan: Tsugaru Strait, at Hakodate	2
T	PG1-2	Canada: Rennell Sound, Queen Charlotte Islands	2

Table 4. Characters retained as potentially diagnostic for members of the genus Gadus.

Character no.	Character mnemonic	Character no.	Character mnemonic
1	TL	34	CPD
2	SL	35	INW
3	PDFL	37	D ₂ -D ₃
4	HL	40	A ₂ -IP
8	LD ₁	43	IPEC
10	LD ₃	44	CL
14	PELFL	48	BG
16	UJL	49	LLPO
17	LJL	51	FMP
18	MG	54	D ₂ FRN
19	DSBM	55	D ₃ FRN
22	D ₃ FRL	56	CFR
24	A ₂ FRL	58	A ₂ FRN
25	PECFRL	62	NIGR
26	PAFL	65	CBP
27	IOW	66	LLPI
28	BL	67	BP
29	HW	68	D ₁ P
30	PHL	69	D ₂ P
31	FPELFR	70	D ₃ P
32	SPELFR	71	A ₁ P

Table 4 cont...

Character no.	Character mnemonic	Character no.	Character mnemonic
72	A ₂ P	77	S
73	PELP	78	NT
74	PP	79	LLS
75	LLIP	83	OFF
76	EPO		

kildinensis (358 mm SL), and 21 marisalbi (122-329 mm SL). A priori identifications were made according to the key and descriptions by Svetovidov (1948). This expanded data set was submitted to another principal coordinates analysis. However, the principal coordinates analysis program in S075 (Lefkovitch 1981) has an upper limit of 199 OTUs and therefore, one of the specimens had to be removed from the analysis. The specimen removed was one that had been used at the beginning of the pilot study (PF7; USNM149850) and came from a collection with two representatives.

The character loadings (i.e.: eigenvectors) are not computed for each axis in principal coordinates analysis as they are in principal components analysis. Instead, correlations between the values for each transformed character for all specimens and their coordinates along each of the principal coordinates axes were computed and give a weighting for the characters on the various axes (Prof. J. McNeill, pers. comm.). Only the characters having an absolute correlation ≥ 0.50 were retained (Table 5). All these were significant at $P \leq 0.0001$.

The first three axes accounted for only 25.19% of the total variance and is an indication that the residuals were effective in removing the effect of size; the first axis accounting for only 11.96% of the variance. The fact that only 9 out of 16 characters having the highest loadings on the first principal coordinate axis were morphometric (Table

5), further indicates the effectiveness of residuals. Furthermore, the correlation coefficients between the values for all specimens of the transformed character total length (TL) and the PCO coordinates along axes 1, 2, and 3 are respectively only 0.10 ($P = 0.1519$), -0.35 ($P = 0.0001$), and 0.20 ($P = 0.0031$). Forty-

Table 5. Correlation coefficients (in parentheses) for characters along the first three principal coordinate axes. All correlations are significant at $P \leq 0.0001$.

Principal coordinate axes		
1	2	3
PDFL (-0.62)	LD ₁ (-0.50)	D ₁ P (0.61)
LD ₃ (0.53)	A ₂ FRL (-0.50)	D ₂ P (0.58)
UJL (-0.67)	PECFRL (-0.50)	D ₃ P (0.57)
LJL (-0.57)	FPELFR (-0.59)	CFP (0.58)
PECFRL (-0.53)	SPELFR (-0.61)	
PAFL (-0.53)	D ₂ -D ₃ (0.59)	
IDW (-0.74)	CL (-0.66)	
BL (-0.72)	CBP (-0.62)	
INW (-0.58)		
LLPI (-0.82)		
BP (-0.61)		
FELP (-0.55)		
PP (-0.59)		
LLIP (0.56)		
EPD (-0.63)		
NT (-0.52)		

six axes were required to account for 75.41% of the variance, the amount of variance explained with each successive axis after axis 3 never exceeding 3.99%.

Figure 9 shows ogac (fig. 10) and macrocephalus (fig. 11) as fairly cohesive groups best separated along principal coordinate axis 2 with 98.15% separation. Axis 1 gives an 86.11% separation (fig. 9). A comparison of the percentage separation for the characters with the greatest loadings on axes 1 and 2 (Table 5) was made between the two groups (Table 6). In decreasing order of discriminatory power we have FELF with 97% separation, CBF with 94%, FPELFR/SL% with 89%, PECFRL/SL% with 88%, LD₁/SL% with 86%, and EPO with 85% separation.

The known distributions of macrocephalus and ogac are allopatric. At best, they are separated by 2000 kilometers via the shortest sea route, the distance between a spot roughly halfway between St. Lawrence Island, Alaska and the Bering Strait for macrocephalus (Sample and Wolotira 1985) and the Eskimo Lakes and Liverpool Bay, Northwest Territories for ogac (Hunter et al. 1984). The report by Walters (1955) of ogac occurring between Point Barrow and Smith Bay, Alaska is dismissed for lack of evidence (i.e.: no voucher specimen originally and no confirmatory record since). Even if accepted, the gap between the distributions would still be considerable (i.e.: 1000 km).

To test whether macrocephalus and ogac represent

Fig. 9. Plot of principal coordinate axes 1 and 2 for 199 adult specimens of Gadus. Refer to Fig. 3 for meaning of symbols. A pair of callarias symbols, five pairs of macrocephalus, and one morhua and one marisalbi are so close to each other that the resolution of this graph does not permit their separation.

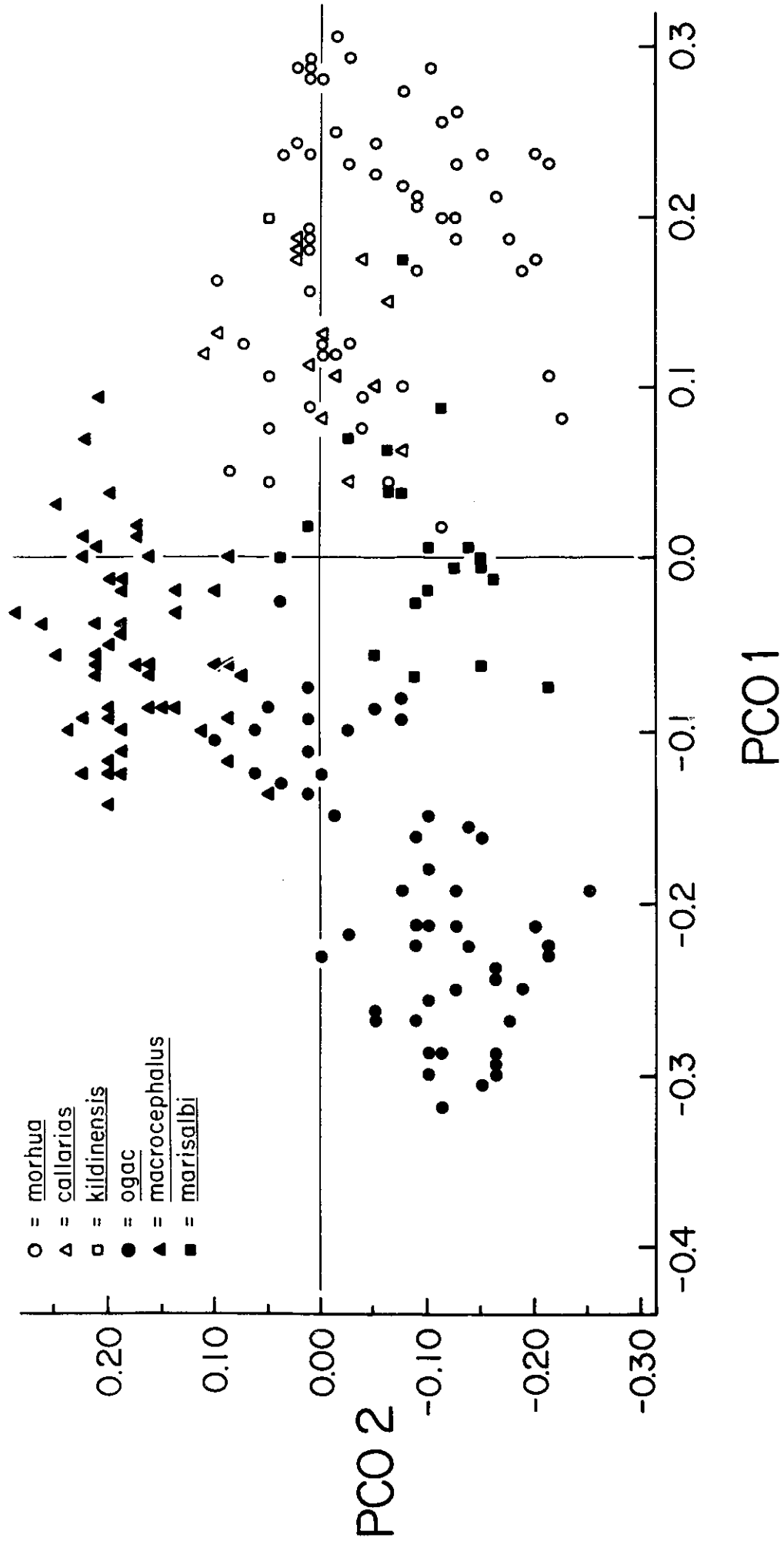


Fig. 10. Side-view of Gadus ogac Richardson, 1836 (NMC84-214, 374 mm SL). This specimen was collected sympatrically with the specimen of G. morhua in fig. 18. Drawing by C.H. Douglas.

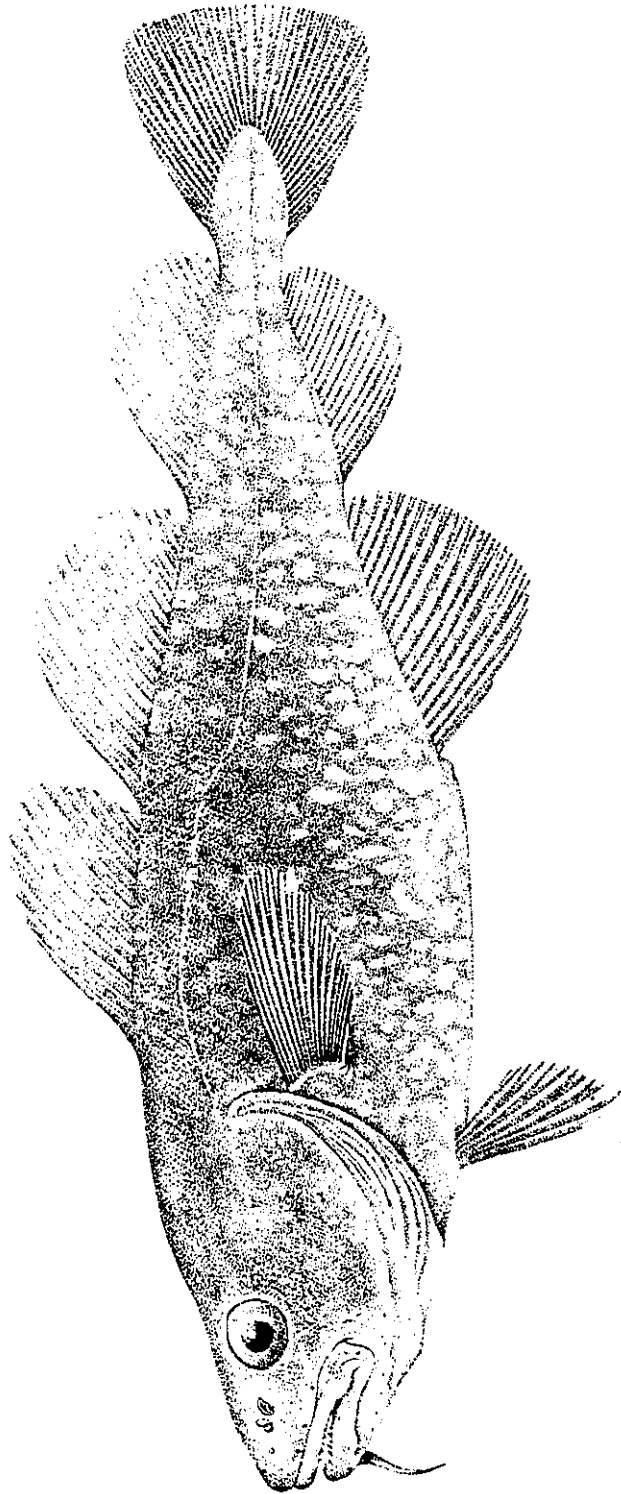
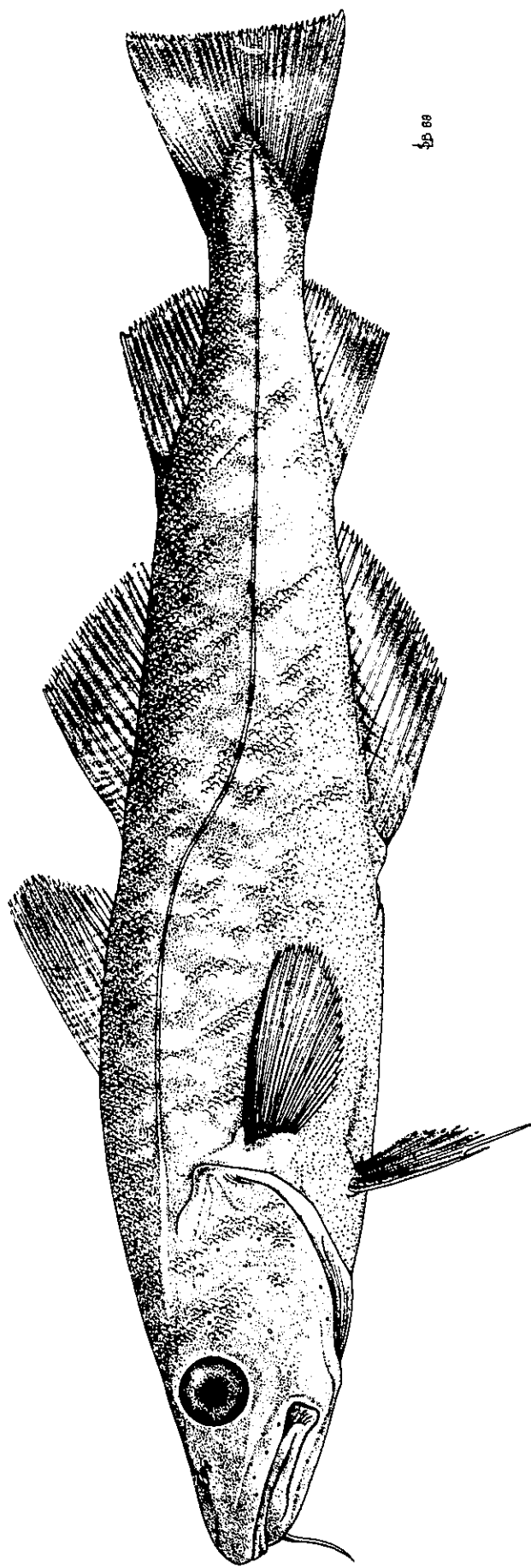


Fig. 11. Side-view of Gadus macrocephalus Tilesius, 1810 (NMC
84-155, 269 mm SL). Drawing by Susan Laurie-Bourque.



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Table 6. Percentage separation between the macrocephalus and ogac groups according to the characters with the greatest loadings along principal coordinate axes 1 and 2.

Character	<u>macrocephalus</u>				<u>ogac</u>				Percentage separation
	N	Range	$\bar{X}$	SD	N	Range	$\bar{X}$	SD	
PELP*	49	1-4	-	-	50	3-5	-	-	97
CBP	50	2-3	2.10	0.30	50	2-3	2.98	0.14	94
FPELFR/SL%	57	8.9-12.9	10.94	0.74	51	10.4-14.8	12.79	1.03	89
PECFRL/SL%	57	12.6-16.0	14.20	0.86	51	13.7-19.3	16.56	1.21	88
LD ₁ /SL%	57	11.3-15.2	13.35	0.86	51	11.8-19.0	15.39	1.32	86
EPO*	23	1-4	-	-	32	2-4	-	-	85
NT	55	1-2	1.09	0.29	50	1-2	1.76	0.43	84
SPELFR/SL%	57	11.3-15.5	13.38	1.08	51	12.7-18.2	15.78	1.36	83
A ₂ FRL/SL%	56	9.1-13.4	11.21	0.93	51	8.7-14.2	12.47	1.06	76
CL/SL%	57	7.2-10.9	9.32	0.84	51	8.8-12.6	10.58	0.86	75
UJL/SL%	57	11.8-13.9	12.73	0.53	51	11.1-15.5	13.62	0.84	75
LLIP	49	2-5	3.35	0.90	50	1-4	2.42	0.95	74
PAFL/SL%	57	47.0-58.0	51.67	2.52	51	47.2-62.1	55.30	2.97	74
BL/SL%	57	2.6-7.0	5.33	0.91	51	5.2-8.2	6.45	0.70	73
D ₂ -D ₃ /SL%	57	1.7-7.1	4.55	1.08	51	1.9-5.0	3.31	0.74	73
LJL/SL%	57	13.6-16.5	15.12	0.72	51	13.8-17.7	15.96	0.87	71
PDFL/SL%	57	32.2-38.9	35.72	1.31	51	32.1-40.4	36.76	1.57	69
IDW/SL%	57	5.0-9.5	6.94	0.77	51	6.0-8.6	7.42	0.70	63
LD ₃ /SL%	57	11.8-16.9	14.94	1.11	51	11.5-17.6	14.67	1.21	61

Table 6 cont...

Character	N	<u>macrocephalus</u>			N	<u>ogac</u>		Percentage	
		Range	$\bar{X}$	SD		Range	$\bar{X}$	SD	separation
BP*	48	1,3-4	-	-	45	1,3-4	-	-	60
INW/SL%	55	4.2-6.0	5.24	0.40	51	4.2-6.2	5.31	0.44	58
PP*	53	2-4	-	-	49	2-4	-	-	53
LLPI	50	2-3	2.96	0.20	50	3	3.00	0.00	2

* The mean and standard deviation were not calculated for multistate unordered characters.

distinct species and not merely a single widely distributed and clinally variable species, a canonical discriminant analysis was performed. The analysis was based upon 49 of the 51 characters in the reduced character suite (Table 4). Body pigmentation and external pigmentation of ovaries were the two characters omitted. Canonical discriminant analysis requires that groups be designated a priori and since body pigmentation was the prime character for distinguishing the various nominal subspecies, it had to be removed to prevent circularity in reasoning. External pigmentation of ovaries was omitted in order that both the sexes be represented in the analysis. Indeed, canonical discriminant analysis requires a full association matrix to proceed and males were scored a missing datum value for this character. Besides, both these characters were of relatively limited discriminatory value for the two taxa under consideration (Table 6). Mean canonical axis 2 scores were plotted on a map (fig. 12) since these two groups separate best (100% separation) along that axis. The distribution of macrocephalus runs from south to north along the west coast of North America (California to Alaska) and that of ogac runs from east to west along the Labrador and Arctic coasts of Canada (Labrador to almost reaching Alaska). If we are dealing with a single clinally variable species one would expect the canonical variate scores to approach one another numerically as the populations approach one another

Fig. 12. Map of mean canonical axis 2 scores for specimens of Gadus macrocephalus (▲) and G. ogac (●). Number in parentheses represents the number of specimens. If no parentheses are present, a single specimen is implied.



geographically. If on the other hand we are dealing with distinct species, no such trend would be observed. The correlation coefficient between the mean canonical axis 2 scores and latitude for eight populations (15 specimens) of macrocephalus from along the west coast of North America ($32^{\circ} 43' - 60^{\circ} 7' N$) is 0.16 with a $P > 0.72$. On the other hand, the correlation coefficient between the mean CAN2 scores and longitude of eight populations (21 specimens) of ogac from along the Labrador and Arctic coasts of Canada ($55^{\circ} 24' - 131^{\circ} 15' W$) is 0.13 with a $P > 0.77$. Furthermore, there is no overlap between the mean CAN2 scores of the two groups with -7.82 to -5.01 for the macrocephalus populations and 0.40 to 4.41 for the ogac populations. In fact, the variation between groups (5.41) is greater than the variation within groups (2.81-4.01). These analyses support the hypothesis that G. macrocephalus and G. ogac are distinct species.

A single adult of kildinensis (fig. 13) was available for study. Examination of the plots of principal coordinate axes 1 X 2 (fig. 9), 1 X 3 (fig. 14), and 2 X 3 (fig. 15) shows that it is not specifically and probably not subspecifically distinct from the morhua group and hence, I synonymize Gadus morhua kildinensis Derjugin, 1920 with Gadus morhua Linnaeus, 1758. The translation of the original description of kildinensis by Derjugin (1920) became available only in the final stages of this analysis. Derjugin (1920) used four diagnostic characters to

Fig. 13. Side-view of nominal Gadus morhua kildinensis
Derjugin, 1920 (ZIL38915, 358 mm SL). Insect pins
were inserted in the first and second dorsal fins so
they would be erect. Photographed by G. Ben-
Tchavtchavadze.



Fig. 14. Plot of principal coordinate axes 1 and 3 for 199 adult specimens of Gadus. Refer to Fig. 3 for meaning of symbols. A pair of morhua symbols, four pairs of ogac, nine pairs of macrocephalus, a pair of marisalbi, one morhua and one marisalbi, and one ogac and one macrocephalus are so close to each other that the resolution of this graph does not permit their separation.

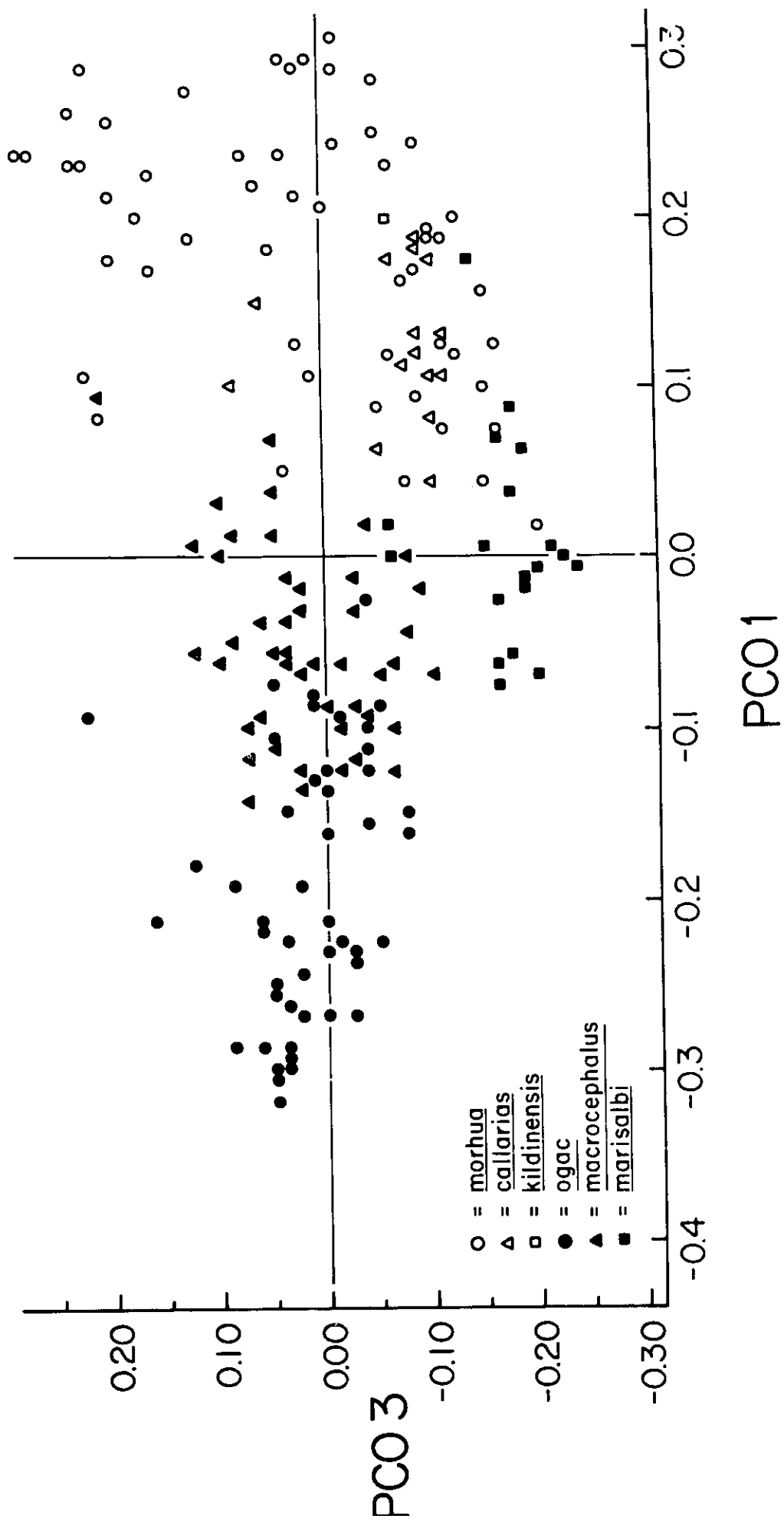
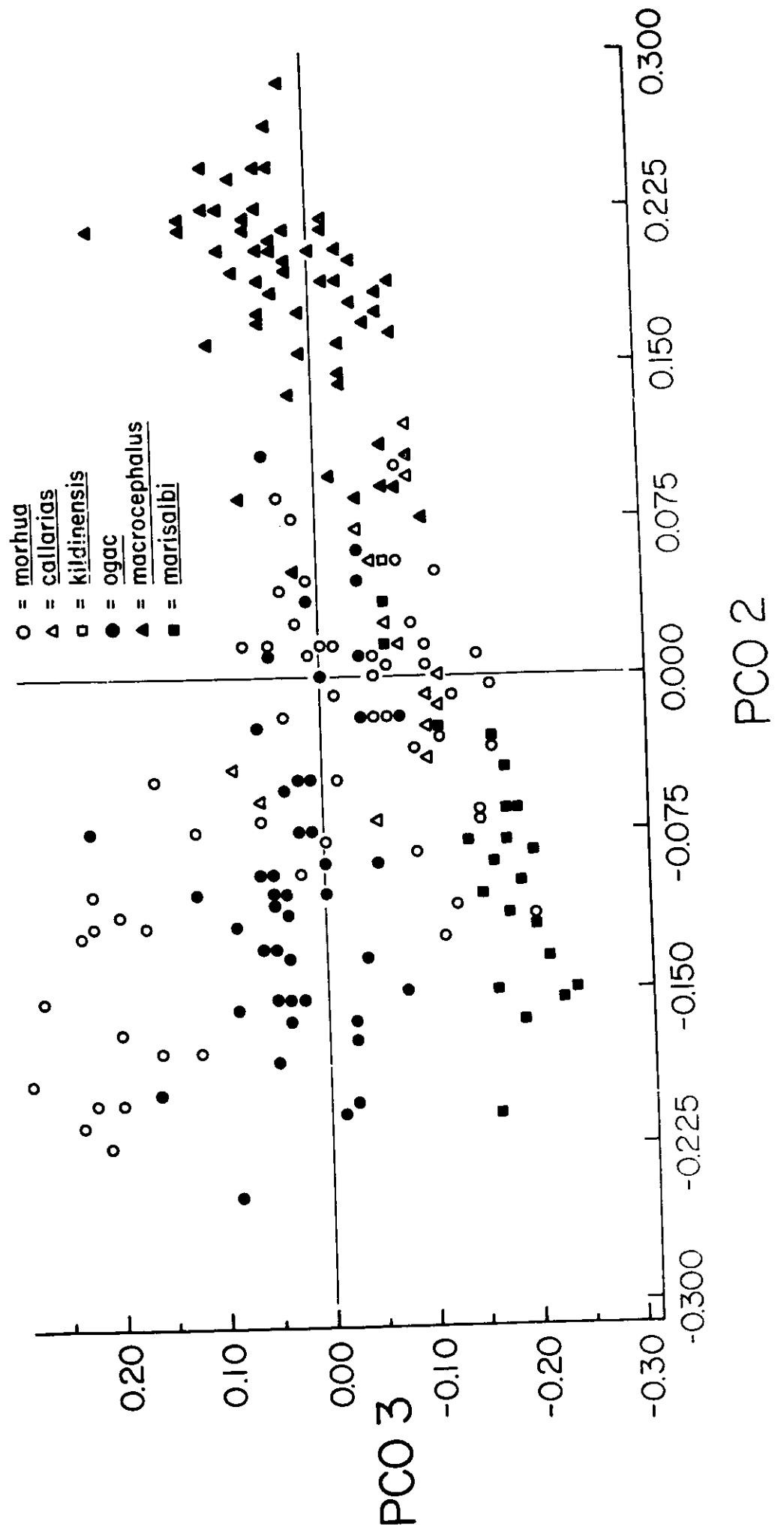


Fig. 15. Plot of principal coordinate axes 2 and 3 for 199 adult specimens of Gadus. Refer to Fig. 3 for meaning of symbols. A pair of morhua symbols, three pairs of ogac, a pair of macrocephalus, three morhua and three callarias, and one morhua and one ogac are so close to each other that the resolution of this graph does not permit their separation.



distinguish kildinensis from morhua from the Barents Sea, two of which, caudal peduncle length and eye diameter, were not part of the reduced character suite studied herein (Table 4). However, Tzeb and Astafyeva (1975) examined 25 morphometric characters (including the two mentioned above) and seven meristic characters on between 56 and 128 adult specimens of kildinensis and in 100 to 140 adult specimens of morhua from the Barents Sea. Tzeb and Astafyeva (1975) analysed their morphometric data using the coefficient of difference (CD). According to Mayr (1969), a CD of 1.28 corresponds to a 90% non-overlap between two groups and is the minimum criterion for subspecific recognition. The morphometric characters that gave the best separation between the two groups had CD's between 0.23 and 0.79; well below the 1.28 threshold value (Tzeb and Astafyeva 1975). The other two characters suggested by Derjugin (1920) to be diagnostic, caudal peduncle depth and postorbital head length, were part of the reduced character suite studied herein (Table 4) but did not reveal themselves as diagnostic; and the latter one was also rejected by Tzeb and Astafyeva (1975). In view of this, the decision to synonymize kildinensis with morhua was maintained.

Examination of the plots of principal coordinate axes 1 X 2 (fig. 9), 1 X 3 (fig. 14), and 2 X 3 (fig. 15) shows that callarias (fig. 16) is also not specifically or subspecifically distinct from the morhua group and hence, I

Fig. 16. Side-view of nominal Gadus morhua callarias

Linnaeus, 1758 (ZMUU27.5.1906, 253 mm SL). Photographed
by G. Ben-Tchavtchavadze.



synonymize Gadus morhua callarias Linnaeus, 1758 with Gadus morhua Linnaeus, 1758. The heterospecificity of callarias and morhua is likewise not supported by electrophoretic data (Grant and Ståhl 1988, Mork et al. 1985, Renaud et al. 1986) and testicular lobe morphology (Renaud 1989).

Svetovidov (1948) stated that some large cod occasionally found in the Gulf of Finland are presumed to be Atlantic cod that have strayed into the Baltic Sea.

The taxonomic status of the White Sea coastal cod, marisalbi, has been variously interpreted. In the original description, Derjugin (1920) treated it as a subspecies of callarias (= morhua) from the Barents Sea. Il'in and Pevzner (1939) also compared marisalbi with callarias (= morhua) from the Barents Sea as well as White Sea callarias (= morhua) and determined that marisalbi and morhua were specifically distinct. Finally, Walters (1955), based solely on the description of marisalbi in Svetovidov (1948), judged it to be a synonym of G. morhua ogac. Each of these hypotheses will be tested.

Marisalbi (fig. 17) separates equally well from ogac (fig. 10) along principal coordinate axes 1 (fig. 9) and 3 (fig. 14) with 97.22% separation. A comparison of the percentage separation for the characters with the greatest loadings on axes 1 and 3 (Table 5) was made between the two groups (Table 7). In decreasing order of discriminatory power we have EPD with 100% separation, BP with 98%, LLPI

Fig. 17. Side-view of nominal Gadus morhua marisalbi
Derjugin, 1920 (BM(NH)1938.8.2.8, 263 mm SL).
Photographed by G. Ben-Tchavtchavadze.



Table 7. Percentage separation between the ogac and marisalbi groups according to the characters with the greatest loadings along principal coordinate axes 1 and 3.

Character	N	<u>ogac</u>			N	<u>marisalbi</u>			Percentage separation
		Range	$\bar{X}$	SD		Range	$\bar{X}$	SD	
EPQ*	32	2-4	-	-	10	1	-	-	100
BF*	45	1,3-4	-	-	21	2,4-5	-	-	98
LLPI	50	3	3.00	0.00	21	1-3	2.10	0.54	94
LD ₃ /SL%	51	11.5-17.6	14.67	1.21	21	15.4-19.1	17.04	0.96	88
PDFL/SL%	51	32.1-40.4	36.76	1.57	21	31.3-36.9	34.31	1.48	82
NT	50	1-2	1.76	0.43	21	1-2	1.10	0.30	80
PECFRL/SL%	51	13.7-19.3	16.56	1.21	21	14.3-15.9	15.04	0.44	79
LLIP	50	1-4	2.42	0.95	20	2-5	4.05	1.05	77
FP*	49	2-4	-	-	21	2-4	-	-	76
IOW/SL%	51	6.0-8.6	7.42	0.70	21	5.1-7.5	6.34	0.69	74
LJL/SL%	51	13.8-17.7	15.96	0.87	21	13.8-16.5	15.20	0.80	69
UJL/SL%	51	11.1-15.5	13.62	0.84	21	12.2-14.0	13.00	0.48	68
PAFL/SL%	51	47.2-62.1	55.30	2.97	21	44.9-54.8	52.06	2.53	68
BL/SL%	51	5.2-8.2	6.45	0.70	21	4.0-6.8	5.75	0.68	63
INW/SL%	51	4.2-6.2	5.31	0.44	21	4.3-5.3	4.91	0.27	58
FELP*	50	3-5	-	-	21	1-2,5	-	-	52
CFP	50	1-2	1.18	0.39	20	1	1.00	0.00	13
D ₁ F	51	1-2	1.06	0.24	21	1	1.00	0.00	4
D ₂ F	51	1-2	1.02	0.14	21	1	1.00	0.00	1

Table 7 cont...

Character	N	<u>ogac</u>			N	<u>marisalbi</u>			Percentage separation
		Range	$\bar{X}$	SD		Range	$\bar{X}$	SD	
D ₃ P	50	1	1.00	0.00	21	1	1.00	0.00	0

* The mean and standard deviation were not calculated for multistate unordered characters.

with 94%, and LD₃/SL% with 88% separation. Therefore, Walters' (1955) hypothesis that marisalbi and ogac are synonyms is rejected.

Marisalbi (fig. 17) separates best from morhua (fig. 18), with which it is said to be sympatric in the White Sea during the autumn (Svetovidov 1948) and with no apparent hybridization (Il'in and Fevzner 1939), along principal coordinate axis 1 with 93.48% separation (fig. 9). Axis 3 gives a 90.22% separation (fig. 14). In the count of morhua is now included the kildinensis and the callarias, giving a total of 71 specimens. A comparison of the percentage separation for the characters with the greatest loadings on axes 1 and 3 (Table 5) was made between morhua and marisalbi (Table 8). In decreasing order of discriminatory power we have BP with 91% separation, PELP with 88%, and PP with 85% separation. Upon closer scrutiny, one finds a correlation between type of body pigmentation and body size in marisalbi. Smaller marisalbi (N = 7, Range: 122-263 mm, $\bar{X}$ = 182.4, SD = 49.4) have the typical morhua body pigmentation (i.e.: dark spots on a light background, fig. 17), intermediate-size marisalbi (N = 7, Range: 190-267 mm, $\bar{X}$ = 224.0, SD = 25.3) exhibit a body pigmentation intermediate between the typical morhua and typical marisalbi pigmentations (i.e.: dark spots barely visible on a dark background), and finally, larger marisalbi (N = 6, Range: 200-329 mm, $\bar{X}$ = 254.0, SD = 42.2) possess the typical marisalbi body pigmentation (i.e.:

Fig. 18. Side-view of Gadus morhua Linnaeus, 1758 (NMC84-150,
261 mm SL). Drawing by C.H. Douglas.

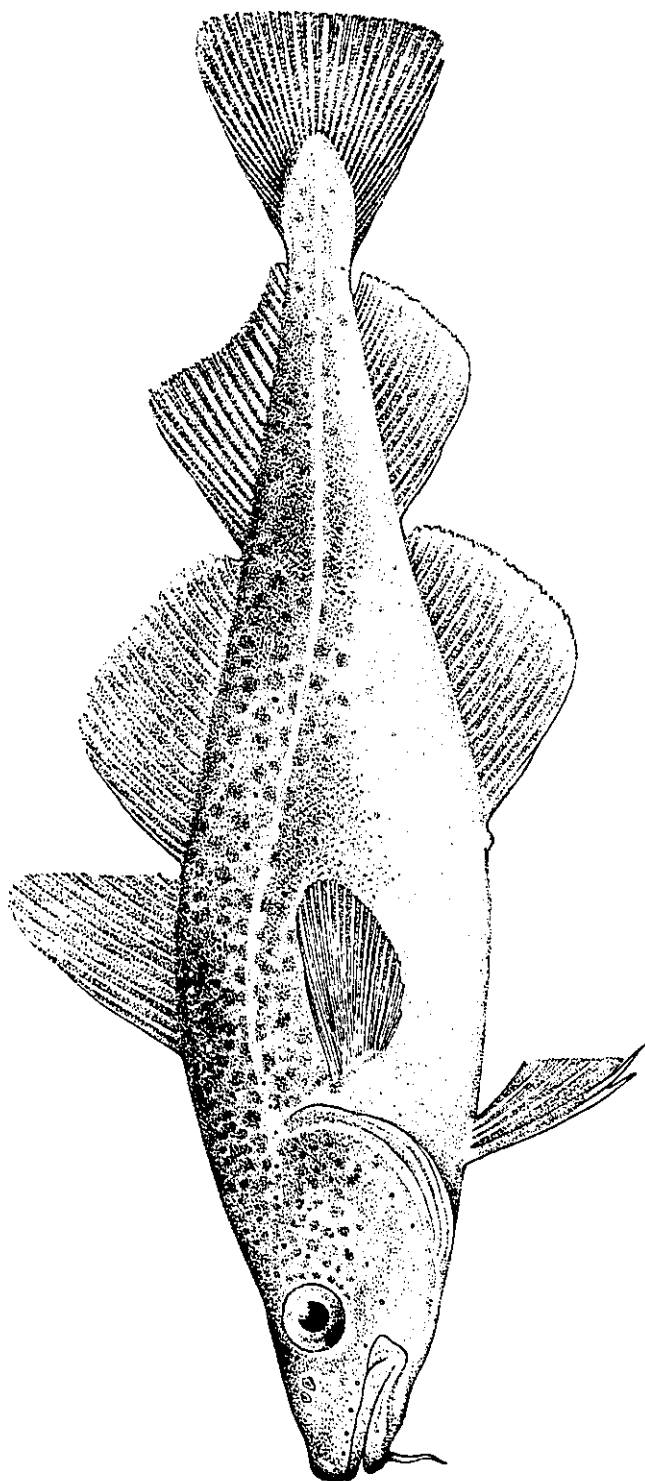


Table 8. Percentage separation between the morhua and marisalbi groups according to the characters with the greatest loadings along principal coordinate axes 1 and 3.

Character	N	<u>morhua</u>			N	<u>marisalbi</u>			Percentage separation
		Range	$\bar{X}$	SD		Range	$\bar{X}$	SD	
BP*	60	1-3	-	-	21	2,4-5	-	-	91
PELP*	69	1-5	-	-	21	1-2,5	-	-	88
PP*	71	2-4	-	-	21	2-4	-	-	85
BL/SL%	69	2.4-6.6	4.60	0.78	21	4.0-6.8	5.75	0.68	76
LJL/SL%	70	12.6-16.8	14.66	0.94	21	13.8-16.5	15.20	0.80	74
LLPI	66	1-3	1.45	0.61	21	1-3	2.10	0.54	68
UJL/SL%	71	10.8-13.8	12.20	0.74	21	12.2-14.0	13.00	0.48	67
LLIP	62	2-5	4.11	0.75	20	2-5	4.05	1.05	65
PDFL/SL%	71	30.1-36.7	34.03	1.62	21	31.3-36.9	34.31	1.48	65
PECFRL/SL%	70	12.5-16.1	14.46	0.85	21	14.3-15.9	15.04	0.44	58
IDW/SL%	71	4.1-7.3	5.92	0.65	21	5.1-7.5	6.34	0.69	54
PAFL/SL%	71	45.2-55.8	51.14	2.35	21	44.9-54.8	52.06	2.53	52
CFP	63	1-2	1.25	0.44	20	1	1.00	0.00	43
INW/SL%	70	4.1-6.0	4.78	0.40	21	4.3-5.3	4.91	0.27	43
LD ₃ /SL%	71	14.0-18.9	16.68	1.23	21	15.4-19.1	17.04	0.76	42
D ₁ P	69	1-2	1.20	0.41	21	1	1.00	0.00	39
D ₃ P	70	1-2	1.20	0.40	21	1	1.00	0.00	39
D ₂ P	70	1-2	1.17	0.38	21	1	1.00	0.00	36
NT	70	1-2	1.12	0.32	21	1-2	1.10	0.30	31

Table 8 cont...

Character	N	<u>morhua</u>			N	<u>marisalbi</u>			Percentage separation
		Range	$\bar{X}$	SD		Range	$\bar{X}$	SD	
EPO*	32	1	-	-	10	1	-	-	0

* The mean and standard deviation were not calculated for multistate unordered characters.

uniform dark pigmentation with no discernible dark spots). The intermediate-type and the marisalbi-type body pigmentations were given identical scores for the PCO analysis (see Methods). Both males and females were represented in the three groups thus sexual dimorphism was ruled out to explain this phenomenon. One specimen (WI4) was removed from this particular analysis of body pigmentations because it defied classification into one of the above body pigmentation categories. In fact, its body pigmentation is that of a typical macrocephalus or ogac. It is neither of these and belongs to the morhua group however because its ovaries are unpigmented and its lateral line is only partly pigmented.

The translation of the original description of marisalbi by Derjugin (1920) became available only in the final stages of this analysis. Derjugin (1920) used three diagnostic characters to distinguish marisalbi from morhua from the Barents Sea, one of which, body depth, was not included in the reduced character suite studied herein (Table 4). However, this character had already been dismissed as non-diagnostic in the anova. Furthermore, Il'in and Pevzner (1939) compared the body depth expressed as a percentage of standard length in 136 marisalbi and 16 morhua collected sympatrically in the White Sea (Kalgalakshskaya, Por'ya, and Sosnovka bays). A coefficient of difference of 0.20 was calculated using data from Table 1 in Il'in and Pevzner

(1939). This is well below the 1.28 threshold value for subspecific recognition. Besides, Il'in and Pevzner (1939) stated that a positive correlation exists between body depth and standard length. Specimens belonging to the marisalbi sample were longer on average ($\bar{X} = 285$ mm SL, SD = 184) than those of the morhua sample ($\bar{X} = 236$ mm SL, SD = 139). Hence, the greater body depth expressed as a percentage of standard length in the marisalbi ($\bar{X} = 22.3\%$, SD = 7.1) compared to that in the morhua ($\bar{X} = 20.0\%$, SD = 4.5) would be partly due to a size factor. Secondly, Svetovidov (1948) stressed the fact that the body depth is related to the fullness of the stomach and because of this, he did not use it in his comparisons. The other two characters suggested by Derjugin (1920) to be diagnostic, interorbital width and body pigmentation, were part of the reduced character suite studied herein (Table 4). The interorbital width was dismissed as being non-diagnostic (Table 8). Furthermore, Il'in and Pevzner (1939) compared the interorbital width expressed as a percentage of head length in the same samples of marisalbi and morhua as discussed above for body depth. A coefficient of difference of 0.12 was calculated using data from Table 1 in Il'in and Pevzner (1939). Again, this is well below the 1.28 threshold value for subspecific recognition. Body pigmentation, on the other hand, was retained as a character of potential discriminatory value.

Karpov et al. (1984) compared allelic frequencies in

three polymorphic loci from blood and white muscle tissues in 1020 to 2300 specimens of morhua and marisalbi from nine localities in the White Sea (eight of them in the Gulf of Kandalaksha, the locality from which came all 21 White Sea cod specimens available in this study). The three polymorphic loci studied were hemoglobin I, transferrin, and glyceraldehydephosphate dehydrogenase II. Karpov et al. (1984) first compared allelic frequencies of inshore summer samples (only marisalbi present) with those of inshore autumn samples (mixture of morhua and marisalbi) and did not find significant ($\alpha = 0.05$) deviations from the theoretical phenotypes predicted by the Hardy-Weinberg Law for a single panmictic population. Furthermore, Karpov et al. (1984) also separated the samples into two groups based on morphology (specimens with shorter preanal distance and narrower interorbital width and specimens with longer preanal distance and wider interorbital width) and compared their allelic frequencies for the three polymorphic loci and again found no significant departures from the expected values predicted by the Hardy-Weinberg Law for a single interbreeding population.

It appears from Il'in and Pevzner (1939) that the change from small specimens with a morhua-type body pigmentation (i.e.: dark spots on a light background) to larger specimens with a marisalbi-type body pigmentation (i.e.: uniform dark pigmentation with no discernible dark spots) is correlated with the presence of algae. Il'in and Pevzner (1939)

analysed stomach contents in 161 specimens of marisalbi from under 100 to greater than 400 mm in standard length and found small amounts of algae (without specifying which type) only in specimens greater than 300 mm SL. Furthermore, Il'in and Pevzner (1939) stated that marisalbi spawns over a stony substrate overgrown with seaweed. It may be that the association with algae is not a cause and effect relationship but an incidental one since Winkler (1988) demonstrated experimentally that the environmentally induced color polymorphism (i.e.: green, brown, and red morphs) in the penpoint gunnel, Apodichthys flavidus, is due to the availability and quantity of light received at a given depth and not to the color of the algae present at that depth. Unfortunately, I am not aware of any data relating to the depth distribution of morhua and marisalbi in the White Sea other than the fact that the marisalbi are found inshore throughout the year whereas the morhua are found offshore during the summer and move inshore during the autumn (Svetovidov 1948). Therefore, the marisalbi usually occur in shallower waters than the morhua do. Love (1974) kept some large cod in laboratory (Gadus morhua, 690-960 mm in length) from two localities (Faroe Bank from a depth of around 100 m and Aberdeen Bank from a depth not stated) for a period of 8½ months and observed a darkening of the skin color of the lighter Faroe cod but never reaching the intensity found in the Aberdeen cod. He concluded that in order to determine

whether the range in pigment movement genetically characterizes a fish stock or becomes fixed at some developmental stage in response to the environment can only be answered by artificially rearing eggs and larvae of fishes from two grounds under identical conditions to a size where the body pigmentation can be studied.

It is most significant that Il'in and Pevzner (1939) did not collect any spawning or even sexually mature morhua in the White Sea, but that they collected at least 20 sexually mature or spawning marisalbi, 248-438 mm SL, and 4+ - 5+ years old. This being the case, it is unlikely that the intermediate-size marisalbi with the intermediate body pigmentation represent hybrids between morhua and marisalbi. Furthermore, Il'in and Pevzner (1939) determined the ages of 95 marisalbi and 15 morhua collected sympatrically in Por'ya and Sosnovka bays (Table 9). They determined that 86.7% of the morhua were 2+ years old or younger whereas 84.2% of the marisalbi were 3+ years old or older. No morhua above 3+ years of age were ascertained. The above two observations corroborate the hypothesis put forth in this study, namely, that the so-called marisalbi of the White Sea are simply the larger and older morhua that have become melanistic. As an alternative and equally viable hypothesis, Il'in and Pevzner (1939) surmised that the morhua enter the White Sea as fry and remain there for two or three years after which they either return to the Barents Sea or die off. The latter

hypothesis requires a migration or dying off; neither of which has been confirmed. The former one requires the presence in the White Sea of uniformly darkly

Table 9. Percentage representation according to age of the morhua and marisalbi forms sympatric in Por'ya and Sosnovka bays, White Sea. Data taken from Il'in and Pevzner (1939).

Nominal taxon	N	Age (years)			
		1+	2+	3+	4+
<u>morhua</u>	15	20.0	66.7	13.3	0.0
<u>marisalbi</u>	95	2.1	13.7	53.7	30.5

pigmented cod, which has been independently confirmed by a number of investigators (Derjugin 1920, Il'in and Pevzner 1939, Svetovidov 1948, this study). The data available cannot be used to reject either one of the hypotheses and therefore, I synonymize Gadus morhua marisalbi Derjugin, 1920 with Gadus morhua Linnaeus, 1758 pending further data to properly test the hypotheses.

Morhua (fig. 18) separates best from ogac (fig. 10), with which it is broadly sympatric from off west Greenland at 72°45'N to 46°2'N in Nova Scotia (Jeffers 1932; Vladykov 1933, 1945; Jensen 1948; Dunbar and Hildebrand 1952; Scott 1952; Backus 1957; McKenzie 1959; McAllister 1960; Legendre 1961; Sick 1965; Leim and Scott 1966; Drainville 1970; Markle 1982; Hunter et al. 1984; Vladykov et al. 1985; Renaud et al. 1986; McAllister et al. 1987; Scott and Scott 1988; Renaud 1989), along principal coordinate axis 1 with 98.60% separation (fig. 9). Jensen (1948) rejected an earlier record of ogac occurring sympatrically with morhua at Angmagssalik on the east coast of Greenland. In this study, specimens of morhua and ogac occurring sympatrically were available from nine Canadian localities between latitudes 47° 8' and 60°25'N (Table 10). In the count of morhua is now included the marisalbi, in addition to the kildinensis and the callarias, giving a total of 92 specimens. A comparison of the percentage separation for the characters with the greatest loadings on axis 1 (Table 5) was made between morhua

Table 10. Canadian localities for which sympatric specimens of morhua and ogac were available in this study.

Locality	Lat. N	Long. W	N	
			<u>morhua</u>	<u>ogac</u>
Ungava Bay, at Port Burwell, Northwest Territories	60°24-5'	64°51'	4	1
Sipukat Lake and Okak Bay, Labrador, Newfoundland	57°30-3'	62°15-22'	3	2
Labrador Sea, off Labrador, Newfoundland	54°5-16'	55°6-24'	2	1
Red Bay, Strait of Belle Isle, Labrador, Newfoundland	51°43-4'	56°25-7'	1	9
Gulf of St. Lawrence, at Baie- Trinité, Québec	49°25'	67°18-25'	4	1*
Humber Arm, Newfoundland	48°58'	58°0'	2	2
Saguenay River Fjord, Québec	48°16-26'	70°6-49'	3	3
Grandy Sound, Newfoundland	47°36'	58°50-1'	1	1
Miramichi Bay, New Brunswick	47°8'	64°58'	2	3

* Although not included in this study, a specimen of ogac was studied electrophoretically in Renaud et al. (1986) and gives an additional locality for the sympatric occurrence of morhua and ogac.

and ogac (Table 11). In decreasing order of discriminatory power we have EPO with 100% separation, BP with 98%, LLPI with 94%, PECFRL/SL% with 86%, and LLIP and IDW/SL% both with 85% separation. Therefore, Gadus morhua Linnaeus, 1758 and Gadus ogac Richardson, 1836 represent distinct species.

Morhua (fig. 18) separates best from macrocephalus (fig. 11) along principal coordinate axis 2 with 95.93% separation (fig. 9). As above, the count of morhua also includes the marisalbi, the kildinensis, and the callarias. A comparison of the percentage separation for the characters with the greatest loadings on axis 2 (Table 5) was made between morhua and macrocephalus (Table 12). In decreasing order of discriminatory power we have D_2-D_3 /SL% with 88% separation and CBP with 85% separation. Three even better diagnostic characters, EPO, LLPI, and BP, with heavy loadings on axis 1 (Table 5), were not revealed by the principal coordinates analysis possibly because of a swamping effect by other characters of low discriminatory value for the two groups along the same axis. EPO gave a 95% separation, followed by LLPI with 93% and BP with a 90% separation (Table 13). The evidence presented indicate that morhua and macrocephalus are at least subspecifically distinct. Nuptial tubercle morphology as well as karyological and electrophoretic data however, support the hypothesis that G. morhua and G. macrocephalus represent distinct species (Renaud 1989).

Svetovidov (1948) stated that reddish or orangish

Table 11. Percentage separation between the morhua and ogac groups according to the characters with the greatest loadings along principal coordinate axis 1.

Character	<u>morhua</u>				<u>ogac</u>				Percentage separation
	N	Range	$\bar{X}$	SD	N	Range	$\bar{X}$	SD	
EPD*	42	1	-	-	32	2-4	-	-	100
BP*	81	1-5	-	-	45	1,3-4	-	-	98
LLPI	87	1-3	1.61	0.65	50	3	3.00	0.00	94
PECFRL/SL%	91	12.5-16.1	14.59	0.81	51	13.7-19.3	16.56	1.21	86
LLIP	82	2-5	4.10	0.83	50	1-4	2.42	0.95	85
IQW/SL%	92	4.1-7.5	6.01	0.68	51	6.0-8.6	7.42	0.70	85
NT	91	1-2	1.12	0.33	50	1-2	1.76	0.43	84
PDFL/SL%	92	30.1-36.9	34.10	1.58	51	32.1-40.4	36.76	1.57	83
BL/SL%	90	2.4-6.8	4.87	0.90	51	5.2-8.2	6.45	0.70	81
FP*	92	2-4	-	-	49	2-4	-	-	80
PELP*	90	1-5	-	-	50	3-5	-	-	80
LD ₃ /SL%	92	14.0-19.1	16.76	1.18	51	11.5-17.6	14.67	1.21	80
UJL/SL%	92	10.8-14.0	12.38	0.77	51	11.1-15.5	13.62	0.84	77
PAFL/SL%	92	44.9-55.8	51.35	2.41	51	47.2-62.1	55.30	2.97	77
LJL/SL%	91	12.6-16.8	14.78	0.93	51	13.8-17.7	15.96	0.87	76
INW/SL%	91	4.1-6.0	4.81	0.37	51	4.2-6.2	5.31	0.44	69

* The mean and standard deviation were not calculated for multistate unordered characters.

Table 12. Percentage separation between the morhua and macrocephalus groups according to the characters with the greatest loadings along principal coordinate axis 2.

Character	N	<u>morhua</u>			N	<u>macrocephalus</u>			Percentage separation
		Range	$\bar{X}$	SD		Range	$\bar{X}$	SD	
D ₂ -D ₃ /SL%	92	0.5-4.8	2.50	0.80	57	1.7-7.1	4.55	1.08	88
CBF	87	1-3	2.79	0.46	50	2-3	2.10	0.30	85
CL/SL%	91	8.1-13.1	10.65	0.91	57	7.2-10.9	9.32	0.84	80
SPELFR/SL%	91	11.5-17.5	14.74	1.37	57	11.3-15.5	13.38	1.08	72
A ₂ FRL/SL%	92	9.3-14.3	12.15	1.10	56	9.1-13.4	11.21	0.93	70
LD ₁ /SL%	92	11.2-17.6	14.42	1.24	57	11.3-15.2	13.35	0.86	69
FPFLFR/SL%	91	9.3-13.4	11.76	0.97	57	8.9-12.9	10.94	0.74	69

Table 13. Percentage separation between the morhua and macrocephalus groups according to some characters with heavy loadings on principal coordinate axis 1.

Character	N	<u>morhua</u>			N	<u>macrocephalus</u>			Percentage separation
		Range	$\bar{X}$	SD		Range	$\bar{X}$	SD	
EPO*	42	1	-	-	23	1-4	-	-	95
LLPI	87	1-3	1.61	0.65	50	2-3	2.96	0.20	93
BP*	81	1-5	-	-	48	1,3-4	-	-	90

* The mean and standard deviation were not calculated for multistate unordered characters.

appears to be the most common color variant in Atlantic cod. Joensen and Tåning (1970) also reported the presence of red-colored G. callarias (= morhua) from the Faroes and Love (1974) reported red and even golden G. morhua from off Norway. Six adult specimens with reddish body pigmentation and belonging to two collections were included in this study. Five of these, 177-219 mm SL, from the Gulf of Alaska (NMC61-118), were closest to the centroid of the macrocephalus cloud (fig. 9) and were identified as such. The other specimen, 373 mm SL, from Varanger Fjord, Norway (NRMA75/1975.257.1401), was closest to the centroid of the morhua cloud (fig. 9) and was identified as such. Both collections were made at comparable depths; 5-10 m for the G. morhua and 9 m for the G. macrocephalus. The distance between the PC01 X PC02 coordinates (fig. 9) for the G. morhua from Varanger Fjord (0.1888, -0.1236) and the centroid for the five G. macrocephalus from the Gulf of Alaska (-0.0639, 0.1830) was greater than the distance between the centroid for the morhua cloud (N = 92 and includes the kildinensis, callarias, and marisalbi; 0.1323, -0.0333) and the one for the macrocephalus cloud (N = 56; -0.0523, 0.1795). Since the red-colored specimens were identified as belonging to two distinct species of cod and they were not significantly different from the species to which they were assigned, the red body pigmentation was not deemed to be useful in the diagnosis of species in Gadus. Both Svetovidov (1948) and

Joensen and Tåning (1970) drew attention to the positive correlation between the red body pigmentation and the association with brown algae (Laminaria) or red algae (type not stated), respectively. Although G. callarias (= morhua) is found from the surface to depths over 400 m around the Faroes, small and large red morph cod are encountered only in the seaweed zone which extends to a maximum depth of about 20 m (Joensen and Tåning 1970). Svetovidov (1948) stated that the red pigmentation is quite labile, disappearing once the red cod are removed from their natural habitat. Whether the red cod have a red body pigmentation because of the depth at which they live, as demonstrated for another polychromatic marine fish species by Winkler (1988), or because of ingestion of algae, or background-matching effect (fish adjusting chromatophores to background) requires experimental verification.

There is at least one other case of a permanent lacustrine population of cod besides the one in Lake Mogil'noye (67°50'N 37°22'E), on Kil'din Island, in the Barents Sea, USSR, and it is the one reported from Ogak Lake (62°52'N 67°21'W), on Baffin Island, Northwest Territories by Kennedy (1953), Dunbar (1958), and Patriquin (1967). Four adult cod specimens from Ogak Lake (NMC87-90) were available in this study. These specimens, 472-765 mm SL, have a centroid on the PC01 X PC02 plot (fig. 9) of 0.2349, -0.1733, which is closest to the centroid of the morhua cloud. They

were thus identified as being morhua. Despite its name and despite a number of biological surveys, notably by Kennedy (1953) and Patriquin (1967), no G. ogac have been reported from Ogak Lake. "Ogak", or a variant spelling thereof, is simply the Inuit word for cod (Legendre 1961, McAllister et al. 1987). Both the Ogak Lake and Lake Mogil'noye populations of G. morhua live under similar unusual ecological conditions. Ogak Lake is about 1.5 km in length (Kennedy 1953, Dunbar 1958) and Lake Mogil'noye about 0.5 km in length (Guryevitsch 1975). The former has a maximum depth slightly over 60 m (Kennedy 1953, Dunbar 1958) and the latter a maximum depth of 14 m (Guryevitsch and Shirokolobov 1975). Both lakes are meromictic (Patriquin 1967, Guryevitsch 1975) and possess a salinity stratification from fresh at the surface to 28‰ at a depth of 20 m in the case of Ogak Lake (Patriquin 1967), and from fresh at the surface to 30.9‰ at the bottom in the case of Lake Mogil'noye (Guryevitsch and Shirokolobov 1975). Both lakes have an anaerobic bottom layer of stagnant water rich in hydrogen sulphide (Dunbar 1958, Tzeb 1975), which begins at a depth between 20 and 27 m in Ogak Lake (Patriquin 1967), and between 8 and 13 m in Lake Mogil'noye (Derjugin 1920, Tzeb and Pozdnyakov 1975). The cod generally occur at depths between 5 and 20 m in Ogak Lake (Patriquin 1967), and between 3 and 13 m in Lake Mogil'noye (Derjugin 1920, Tzeb 1975). Kennedy (1953) suggested that the cod population in Ogak Lake has been isolated for 1000 to

4000 years and Guryevitsch (1975) simply stated that Lake Mogil'noye was thousands of years old. During the spring high tides and at least until August 6, there is some influx of salt water from Frobisher Bay into Ogak Lake (Kennedy 1953, Dunbar 1958), which potentially could result in Atlantic cod moving into the lake. However, Gadus morhua has never been reported from Frobisher Bay whether as eggs, larvae, or adults (Kennedy 1953, Patriquin 1967).

ALLOZYMES

Sick (1965) studied hemoglobin types in 2282 specimens of G. m. morhua from the North Sea (nine localities), and coastal waters of the Faroes (three), Iceland (three), west Greenland (four), eastern Canada (one), and eastern United States (two) and compared them with those of 207 G. m. ogac from the coastal waters of west Greenland (one) and 77 G. m. macrocephalus from Puget Sound (one). G. m. ogac and G. m. macrocephalus were indistinguishable from each other and they differed from G. m. morhua "... by the extreme weakness and much slower migration of ..." the HbII band. Furthermore, G. m. morhua and G. m. ogac populations studied were sympatric at one of the west Greenland localities (near Godthåb).

Mackie and Ritchie (1981) compared white skeletal muscle proteins of G. m. morhua and G. m. macrocephalus using electrophoresis and isoelectric focusing. The G. m. morhua were collected in the North Sea, off Aberdeen, Scotland, and the G. m. macrocephalus came from the Aleutian Islands, Alaska, and the coastal waters of British Columbia. They suggested that the differences observed between the two forms using either technique "... are of the order of those found between separate species rather than variants of a single species."

Grant (unpublished observations, 1982), Grant, Zhang, and Kobayashi (unpublished observations, 1982), and Grant and Ståhl (unpublished observations, 1982) examined 41 loci, 23

of which were polymorphic at the 99% criterion level, from white skeletal muscle, vitreous fluid of the eye, heart, and liver, in 50 adult G. m. callarias from the Baltic Sea (one locality), 80 adult G. m. morhua from Georges Bank (one), and 783 adult G. m. macrocephalus from the Yellow Sea (one), the Sea of Japan (one), the Bering Sea (three), the Aleutian Islands (two), the Gulf of Alaska (two), Alexander Archipelago (one), and the Strait of Georgia (one). The mean genetic distance (Nei 1972) between G. m. callarias and G. m. morhua based on 41 loci was 0.03; no loci were fixed for alternate alleles in the two, and Grant and Ståhl (unpublished observations, 1982) treated them as conspecifics. However, nine loci (Aat-1, Acon-1, Acon-2, Ck-1, Gapdh-1, Gda, Gl-2, Idh-1, and Tat) were fixed for alternate alleles in G. m. callarias - G. m. morhua versus G. m. macrocephalus. The mean genetic distance between G. m. callarias - G. m. morhua and G. m. macrocephalus based on 41 loci was 0.39 and Grant and Ståhl (unpublished observations, 1982) treated the two groups as separate species.

Mork et al. (1985) studied 19 loci, ten of which were polymorphic at the 99% criterion level, from white skeletal muscle and liver, in 99 G. m. callarias from the Baltic Sea (one locality) and in 781 G. m. morhua from the Barents Sea (one), the coastal waters of Norway (three), the North Sea (one), Iceland (one) west Greenland (one), and eastern United States (one). The mean genetic distance between G. m.

callarias and G. m. morhua based on ten polymorphic loci was 0.01, they were not fixed for alternate alleles at any locus, and Mork et al. (1985) treated them as conspecifics.

Renaud et al. (1986) examined 21 loci, ten of which were polymorphic at the 99% criterion level, from white skeletal muscle and liver, in 12 adult G. m. callarias from the Baltic Sea (one locality), 25 adult G. m. morhua from the Strait of Belle Isle (one), 20 adult G. m. ogac from the Strait of Belle Isle (1), and the Gulf of St. Lawrence (one), and 30 adult G. m. macrocephalus from the Aleutian Islands (one) and the Gulf of Alaska (one). The results showed two biochemically distinct groups: a G. m. callarias - G. m. morhua group and a G. m. ogac - G. m. macrocephalus one. The two groups were fixed for alternate alleles at the following loci: Aat-1, Ck-1, Est-1, Est-2, Est-4, G3pdh-2, and Mdh-3. Given that G. m. morhua and G. m. ogac were sympatric in the Strait of Belle Isle samples and seven loci were fixed for alternate alleles in the two indicate that they are reproductively isolated and ipso facto are distinct species. The mean genetic distance between G. m. callarias - G. m. morhua and G. m. ogac - G. m. macrocephalus based on 13 loci was 0.48. The within-group subspecies could not be distinguished on the basis of fixation for alternate alleles and the mean genetic distance within-groups being 0.00, the hypothesis that members in each pair of nominal taxa are conspecific, could not be rejected.

In Renaud (1989), 12 adult G. m. morhua from Passamaquoddy Bay, New Brunswick, and four adult G. m. ogac from Baie des Chaleurs, New Brunswick, were examined electrophoretically. Eight of the loci surveyed by Renaud et al. (1986) were investigated in these specimens (Ck-1, Gpi-1, Gpi-2, Ldh-2, Mdh-2, Mdh-3, Me-1, and Me-2). The allelic patterns of these two samples matched the ones of their respective conspecifics in Renaud et al. (1986). Indeed, they were fixed for alternate alleles at Ck-1 and Mdh-3.

Renaud (1989) further compared G. m. ogac and G. m. macrocephalus by assaying the enzyme SOD in heart and liver tissues in the two, using the buffer described by Ridgway et al. (1970). The 11 adult G. m. ogac were from the Strait of Belle Isle and the seven adult G. m. macrocephalus were from the Aleutian Islands. In addition to the monomorphic locus expressed in white skeletal muscle reported by Grant (unpublished observations, 1982), Mork et al. (1985), and Renaud et al. (1986), a second monomorphic anodally migrating locus termed Sod-2 and expressed in both heart and liver tissues was identified in the two nominal subspecies. This new locus could therefore also not be used to reject the hypothesis of conspecificity between G. m. ogac and G. m. macrocephalus.

Out of 45 loci investigated in G. m. callarias and G. m. morhua (Grant, unpublished observations, 1982; Grant and Ståhl, unpublished observations, 1982; Mork et al. 1985;

Renaud et al. 1986) there is no fixation for alternate alleles in the two forms and likewise in 24 loci surveyed in G. m. ogac and G. m. macrocephalus (Sick 1965; Renaud et al. 1986; Renaud 1989).

In summary, the biochemical data indicate that there are at least two species in the genus. Using the molecular clock hypothesis and the calibration of Vawter et al. (1980) (a mean genetic distance of 1 = 16.4 million years) derived from marine fish data, the mean genetic distance between G. m. callarias - G. m. morhua and G. m. macrocephalus, estimated by Grant and Ståhl (unpublished observations, 1982), suggests a time of divergence for the two groups of 6.4 million years, whereas that of Renaud et al. (1986) between G. m. callarias - G. m. morhua and G. m. ogac - G. m. macrocephalus suggests a time of separation of 7.9 million years.

NUPTIAL TUBERCLES

The presence of roughening structures or nuptial tubercles in Gadus has already been dealt with in Vladykov et al. (1985) and Renaud (1989). The purpose of this section is to detail the frequency of occurrence of the nuptial tubercles between the three species herein recognized and between the sexes within each of the species.

Out of 91 specimens of G. morhua (13 sex undetermined: 33 ♂ : 45 ♀) measuring 100 to 765 mm SL, nuptial tubercles were ascertained with the naked eye in only 11 specimens (12%) measuring 230-527 mm SL. Of these, five were male (329-458 mm SL) and six were female (230-527 mm SL). Therefore, the presence of nuptial tubercles is not sexually dimorphic in G. morhua. Of the tuberculate specimens, two had been identified a priori as callarias and two as marisalbi.

Out of 55 specimens of G. macrocephalus (5 sex undetermined: 26 ♂ : 24 ♀) measuring 133 to 662 mm SL, nuptial tubercles were ascertained with the naked eye in only five specimens (9%) measuring 426-662 mm SL. Of these, two were male (426-560 mm SL) and three were female (487-662 mm SL). Here again, the presence of nuptial tubercles is not sexually dimorphic in G. macrocephalus.

Out of 50 specimens of G. ogac (18 ♂ : 32 ♀) measuring 149 to 526 mm SL, nuptial tubercles were ascertained with the naked eye in 38 specimens (76%) measuring 222-526 mm SL. Of

these, 11 were male (268-475 mm SL) and 27 were female (222-526 mm SL). As in the two previous species, the presence of nuptial tubercles is not sexually dimorphic in G. ogac.

In the three species, tubercles are found in both the sexes at comparable sizes. In both G. morhua and G. ogac, tubercles may be present in individuals of very small sizes (230 and 222 mm SL respectively), indicating that sexual maturity need not be attained for tubercles to occur. Unlike the situation in G. macrocephalus and G. ogac where the largest specimens were tuberculate, in G. morhua the largest specimens did not have tubercles which may indicate that these are gradually lost, at least in that species.

TESTICULAR LOBES

The morphology of the testicular lobes in Gadus has already been addressed in two papers (Vladykov 1972; Renaud 1989). The aim of this section is to present additional data from a wider range of localities for the three species herein recognized.

Vladykov (1972) provided a photograph and described the contour of testicular lobes in three specimens of G. ogac from Cambridge Bay, Northwest Territories and the Gulf of St. Lawrence, Québec as being scalloped (crenate). Renaud (1989) confirmed this in eight specimens measuring 276 to 403 mm SL from Bathurst Inlet, Northwest Territories and three localities along the coast of Labrador. In the present study, ten additional specimens, measuring 244 to 475 mm SL, from James Bay, eastern Hudson Bay, Boothia Peninsula and south Baffin Island, Northwest Territories, off west Greenland, Humber Arm, Newfoundland, and Miramichi Bay, New Brunswick also had the same testicular lobe morphology. Therefore, in a total of 21 specimens encompassing most of G. ogac's wide ranging distribution, the lobes were invariably scalloped.

In the original description of G. macrocephalus, Tilesius (1810) included a drawing of the testes (Plate XVII, fig. 2) in which the testicular lobes have a distinct serrated edge. This condition is different from that described and illustrated in Renaud (1989) for G.

macrocephalus from the southwest coast of Vancouver Island, and may have been brought about by dessication of Tilesius's specimen. As evidence for this interpretation, Plate XVI, fig.1, in Tilesius (1810) depicting a side-view of an adult G. macrocephalus, shows a dessicated specimen notably in the head region where features of the underlying cranium are clearly visible and the rays of the two pelvic fins are shriveled up. In three specimens of G. macrocephalus measuring 566 to 606 mm SL from the southwest coast of Vancouver Island, Renaud (1989) found the testicular lobes to be smooth (unindented). The same condition was also found in the present study in one specimen 322 mm SL from the Bering Sea off the Kamchatka Peninsula (type-locality), one specimen 560 mm SL from the Bering Sea off Alaska, and two specimens 522 and 543 mm SL from off southern California. Although dessication may be invoked to explain the serrated aspect of the testes figured in Tilesius (1810), it is clear that additional ripe samples, especially from the western North Pacific, are required to further test this hypothesis.

Vladykov (1972) illustrated and described the shape of testicular lobes in four specimens of G. morhua from east of Newfoundland and off Nova Scotia as smooth. However, Renaud (1989) determined that two males, 458 and 477 mm SL, out of three from Sipukat Lake, Labrador and two males, 566 and 589 mm SL, from off Nova Scotia had scalloped lobes. The other male, 567 mm SL, from Sipukat Lake had smooth lobes. In this

study, another specimen, 472 mm SL, from Ogak Lake, Baffin Island, Northwest Territories was found to have scalloped lobes. Renaud (1989) also studied the testicular lobes in two specimens identified a priori as G. callarias from off Bornholm Island, Denmark, and found both specimens, 211 and 220 mm SL, had smooth lobes. In this study, three more specimens of G. callarias, 278-384 mm SL, from the Gulf of Gdańsk, Poland, were also found to possess smooth lobes. No justification could be made for callarias being specifically or subspecifically distinct from morhua and the two groups were combined. Furthermore, in eight specimens identified a priori as G. marisalbi from the Gulf of Kandalaksha, USSR, five were found to have smooth lobes and three were found to have scalloped lobes. The testicular lobe morphologies were grouped according to the three following body pigmentations: morhua-type, one specimen (203 mm SL) scalloped; intermediate between morhua and marisalbi, two specimens (240, 267 mm SL) smooth; marisalbi-type, three specimens (237, 250, 260 mm SL) smooth and two specimens (248, 329 mm SL) scalloped. No pattern could be detected between body pigmentation or body size and testicular lobe morphologies. Therefore, no justification could be made for marisalbi being specifically or subspecifically distinct from morhua and the two groups were combined. In summary, 23 specimens of G. morhua from across its wide range gave proportions of 65% smooth and 35% scalloped testicular lobes.

THE GAS BLADDER AND ITS ASSOCIATED MUSCLES

The variation in three structures associated with the gas bladder will be evaluated in this section. Firstly, the length and arrangement of the horn-like processes of the gas bladder will be examined, then the drumming muscles, and finally, the retractor dorsalis muscles.

GAS BLADDER HORNS

The length and the arrangement of the horn-like processes of the gas bladder (figs. 19-20) are two of the eight diagnostic characters Svetovidov (1948) used in his key to members of the genus Gadus. Svetovidov (1948) stated that "... fishes measuring to 30 cm are not distinguishable on this character, inasmuch as their horn-like processes are shortened and have the same appearance as in adult Pacific Ocean cods." Schultz and Welander (1935) had previously made a similar observation: "Apparently the anterolateral horns of the air-bladder become more highly developed with age in the larger morhua, because in the young of that species, about six inches (150 mm) in length, the horns differ but little from those of Pacific cod 18 to 24 inches (450-600 mm) in length." Using the criterion of ontogeny for character polarity (Wiley 1981), the preceding statements suggest that short gas bladder horns represent the plesiomorphic condition and long ones the apomorphic condition.

The 13 specimens listed in fig. 20 (two G. morhua, eight

Fig. 19A-B. Ventral view of the gas bladder and its associated muscles in two species of Gadus. A. G. macrocephalus, NMCB4-157, ♀, 276 mm SL; B. G. ogac, NMC 66-127, ♀, 247 mm SL. The peritoneum was removed in A B in order to expose the drumming muscles. Both bar scales represent 10 mm. Photographed by G. Ben-Tchavtchavadze.



RETRACTOR
DORSALIS
MUSCLES

GAS BLADDER
HORNS

DRUMMING
MUSCLES

GAS BLADDER

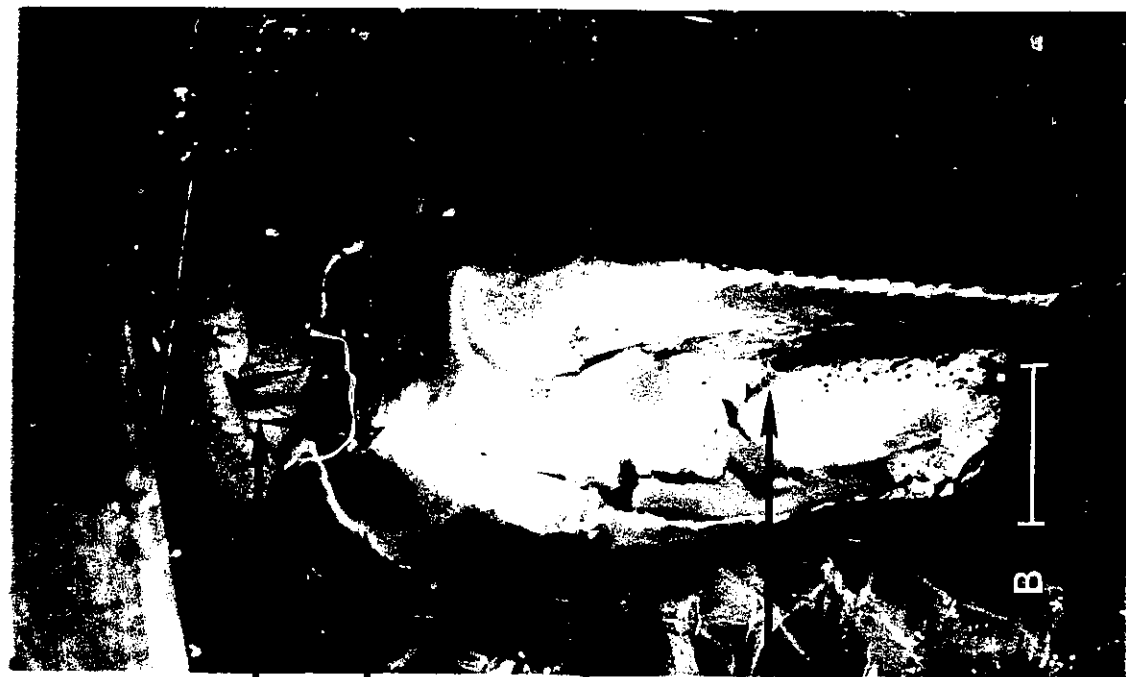
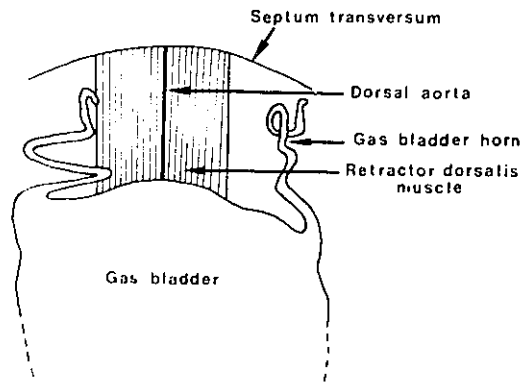
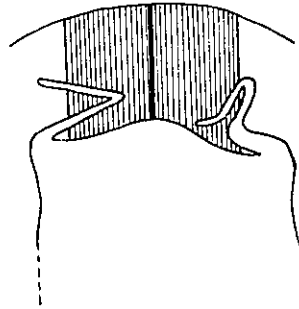


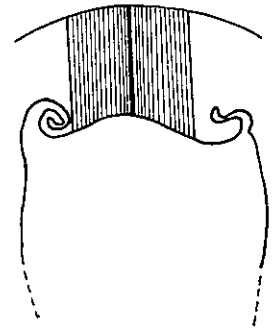
Fig. 20A-M. Schematic drawings of the anterior part of the gas bladder seen in ventral view in the three species of Gadus. A-B. G. morhua: A. NMC84-144, ♂, 529 mm SL; B. NMC84-142, ♀, 438 mm SL; C-J. G. macrocephalus: C. NMC84-275, ♂, 599 mm SL; D. NMC84-275, ♀, 701 mm SL; E. NMC84-275, ♂, 326 mm SL; F. NMC84-276, ♀, 343 mm SL; G. NMC84-276A, ♀, 441 mm SL; H. NMC84-276A, ♂, 319 mm SL; I. NMC84-276A, ♂, 630 mm SL; J. NMC84-276A, ♀, 913 mm SL; K-M. G. ogac: K. NMC84-277, ♂, 403 mm SL; L. NMC84-277, ♀, 512 mm SL; M. NMC85-246, ♀, 276 mm SL. No scale is included. These drawings were made simply to show the shapes and the relationships between the various structures.



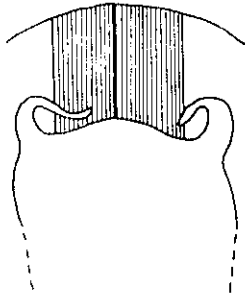
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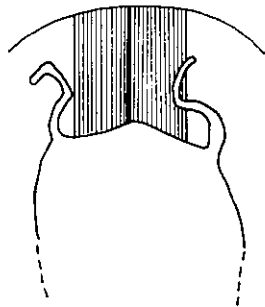
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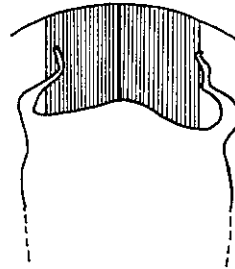
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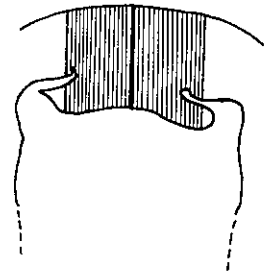
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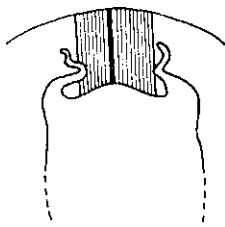
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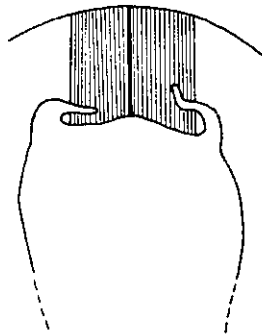
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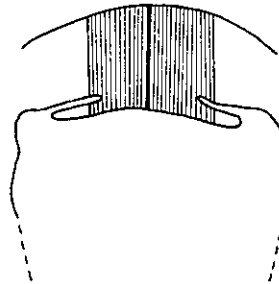
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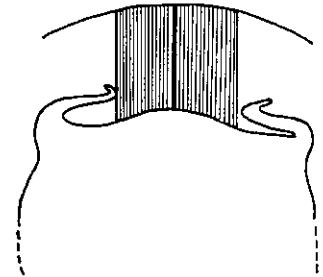
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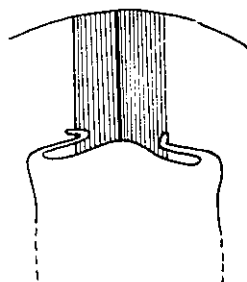
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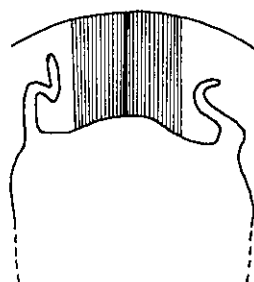
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M

G. macrocephalus, and three G. ogac) had their gas bladder horns studied. The two G. morhua were collected sympatrically with two of the G. ogac. Two general comments apply to all three taxa examined. The gas bladder horns are most often not arranged symmetrically (figs. 19-20) and they never reach the septum transversum (fig. 20); hence, there is no otophysic connection in Gadus. The extended length of the horns was measured to the nearest millimetre from the inside base of the horn to its anteriormost tip. Only specimens above 300 mm in total length were studied. The absolute lengths of the left and right gas bladder horns were compared in all three taxa combined. A two-tailed Student's t-test indicated no significant difference in length between the left and right horns ($0.8 > P > 0.7$). Although there is quite a bit of overlap in the absolute lengths of the horns, those in G. morhua are roughly twice as long on average as those in G. macrocephalus and G. ogac (Table 14). When expressed as a ratio of standard length, the gas bladder horns show no overlap between G. morhua and G. macrocephalus, slight overlap between G. morhua and G. ogac, and considerable overlap between G. macrocephalus and G. ogac (Table 14). The anterior end of the gas bladder, excluding the horns, extends medially up to the level of the third or fourth centrum in the two G. morhua examined; up to the level of the third, fourth, or fifth centrum in the eight G. macrocephalus examined; and up to the level of the second or

Table 14. Gas bladder horn lengths in three species of Gadus.

Species	SL (mm)			No. of horns	Horn length (mm)			Horn length/SL (%)		
	N	$\bar{X}$	Range		$\bar{X}$	Range	$\bar{X}$	$\bar{X}$	Range	Range
<u>G. morhua</u>	2	483.5	438-529	4	45.8	26-65	9.3	9.3	5.9-12.3	
<u>G. macrocephalus</u>	8	534.0	319-913	16	22.3	10-40	4.3	4.3	2.3-5.7	
<u>G. ogac</u>	3	397.0	276-512	6	20.0	13-26	5.2	5.2	3.7-6.9	

third centrum or the intervertebral disc between centra three and four in the three G. ogac examined.

Svetovidov (1948) categorized the six subspecies of Gadus morhua he recognized, into the following three gas bladder horn morphology types: a) gas bladder horns long, bent at the base towards the midline, then forward, and finally outwards (G. m. morhua and G. m. marisalbi); b) horns even longer, and the whole horn is coiled into a ball (G. m. callarias and G. m. kildinensis); c) horns short, bent at the base towards the midline and then, slightly bent outwards at the tips (G. m. macrocephalus and G. m. ogac). These types apply only to adults greater than 300 mm in total length (Svetovidov 1948). Svetovidov's (1948) descriptions of the gas bladder horns in morhua, macrocephalus, and ogac are identical to those in Schultz and Welander (1935).

Svetovidov (1948) cautioned that the length and arrangement of the horns vary greatly but added that each of the nominal subspecies generally falls within one of the three categories outlined above. In his fig. 27, Svetovidov (1948) illustrated the anterior part of 15 gas bladders. Only eight of these were from specimens greater than 300 mm in total length; the rest were used to demonstrate the underdevelopment of the horns in smaller specimens.

However, Brawn (1961) described the gas bladder horns in G. callarias (= morhua) from the North Sea, near Blyth, Northumberland, England as coiled. Furthermore, Tzeb and

Astafyeva (1975) studied the morphology of gas bladder horns in a total of 100 specimens of kildinensis from Lake Mogil'noye and of morhua from the Barents Sea, and illustrated the most characteristic of these (23 kildinensis and 26 morhua measuring between 350 and 660 mm in total length) in their fig. 71. They found that aside from the usual immediate bend towards the midline, the arrangement of the horns was most variable. Their observation was confirmed in this study (figs. 19-20) for morhua, macrocephalus, and ogac. Tzeb and Astafyeva (1975) also underlined the general lack of symmetry between the left and right horns in both the morhua and the kildinensis. In looking at fig. 71 in Tzeb and Astafyeva (1975), we find that a significant proportion (54.3%) of the horns in the kildinensis are not coiled into balls, and in the remainder that are, often only the extremity of the horn is involved (52.4%). Additionally, in the morhua, 84.6% of the horns are not coiled into balls, and in the remainder that are, often only the extremity of the horn is involved (62.5%). On the other hand, 26.1% of the horns in the kildinensis compared to 26.9% in the morhua were of the morphological type described for G. morhua morhua by Svetovidov (1948). Besides, Tzeb and Astafyeva (1975) state that some (without specifying a number) of the Barents Sea morhua have horns as long as those in the kildinensis.

DRUMMING MUSCLES

Drumming muscles are sonic or sound producing muscles which are either intrinsically or extrinsically associated with the gas bladder (Tavolga 1971, Winterbottom 1974). Contraction and relaxation of these muscles causes the gas bladder to vibrate, thereby causing movement of the inside gases. A deep, grunting noise is produced in Gadus by these gases oscillating through the two narrow lumina at the junction of the main gas bladder chamber and the horns (Brawn 1961).

In Gadus, the intrinsic drumming muscles present themselves as two thin sheets of muscle, one on each side of the gas bladder, and intimately attached to the external surface of the bladder close to the gas bladder horn base (fig. 19). Their fibers are oriented perpendicularly, or nearly so, to the longitudinal axis of the bladder. The presence of intrinsic drumming muscles was ascertained in one specimen of G. callarias from the Gulf of Finland, Baltic Sea, a male, 185 mm SL, two specimens of G. macrocephalus respectively from the Gulf of Alaska, a female, 276 mm SL and from Chatham Sound, British Columbia, a female, 537 mm SL, and one specimen of G. ogac from Grandy Sound, Newfoundland, a female, 247 mm SL. Brawn (1961) reported the presence of intrinsic drumming muscles in G. callarias (= morhua) from the North Sea, near Blyth, Northumberland, England.

So far, within the genus, only G. morhua has been

confirmed as a sound producer (Brawn 1961). However, given the presence in G. macrocephalus and G. ogac, the only other species recognized herein, of intrinsic drumming muscles and of moderately well developed gas bladder horns, it is likely that they too can produce gas bladder generated sounds.

RETRACTOR DORSALIS MUSCLES

These muscles (figs. 19-20) have had a varied nomenclature: pharyngeal bone muscles (Hagman 1921), retractor arcuum branchialium muscles abbreviated RAB (Holstvoogd 1965, Rosen 1973), and retractor dorsalis muscles (Winterbottom 1974). The retractor dorsalis muscles were studied in the same specimens as were the gas bladder horns (fig. 20a-m). In Gadus, these muscles present themselves as a pair of spindle-shaped striated muscles lying side by side under the vertebral column. The dorsal aorta lies between the paired retractor dorsalis muscles and directly ventral to the vertebral column. One must push aside the two muscles in order to expose it.

In G. morhua, each retractor dorsalis muscle inserts anteriorly on one of the dorsal or upper pharyngeal plates, each of which consists of three bones, and posteriorly each originates on the ventral surfaces of the basioccipital and vertebral centra one to six inclusively. This statement refers to the full range of sites of origin observed in G. morhua. The same will apply to the taxa discussed below.

Additionally, the left and right retractor dorsalis muscles may not be symmetrical as far as their sites of origin in a given specimen. In G. morhua, the gas bladder attaches to the ventral surface of the sixth centrum via two ligaments at the same points as the posteriormost sites of origin of the retractor dorsalis muscles.

In G. macrocephalus, each retractor dorsalis muscle inserts anteriorly on one of the dorsal pharyngeal plates and posteriorly each originates on the ventral surfaces of the basioccipital and vertebral centra one to seven inclusively. The gas bladder attaches to the ventral surface of the sixth or seventh centrum via two ligaments at the same points as the posteriormost sites of origin of the retractor dorsalis muscles.

In G. ogac, each retractor dorsalis muscle inserts anteriorly on one of the dorsal pharyngeal plates and posteriorly each originates on the ventral surfaces of the basioccipital and vertebral centra one to six inclusively. The gas bladder attaches to the ventral surface of the fifth or sixth centrum via two ligaments at the same points as the posteriormost sites of origin of the retractor dorsalis muscles.

The close association between the retractor dorsalis muscles and the gas bladder via two ligaments, as found in all three taxa studied, leads me to suggest that, in addition to assisting in the swallowing process (Rosen 1973), the

retractor dorsalis muscles may function as extrinsic drumming muscles in addition to the intrinsic drumming muscles discussed above. The drumming muscles are derived from the retractor dorsalis muscles in diodontids (Winterbottom 1974).

In summary, the relative length of the gas bladder horns is useful to separate G. morhua from G. macrocephalus and from most G. ogac. G. macrocephalus and G. ogac could not be distinguished on the basis of gas bladder horn length. The gas bladder horn arrangement and characters pertaining to the drumming and retractor dorsalis muscles were not found to be taxonomically useful, at least at the specific level. A review of the literature data did not support the subspecific recognition of Gadus morhua callarias Linnaeus, 1758, Gadus morhua marisalbi Derjugin, 1920, and Gadus morhua kildinensis Derjugin, 1920, and they were synonymized with Gadus morhua Linnaeus, 1758.

MATERIAL

Gadus morhua: NMC77-504; 1; Finland: off Hangö, Gulf of Finland, Baltic Sea; 59°45'N 22°40'E; T. Bergman; 5 Aug. 1976. NMC84-142; 1; Canada: Strait of Belle Isle, off Barge Point, Labrador, Newfoundland; 51°47'24"N 56°12'0"W; C.B. Renaud and crew of the M.V. Lady N; 3 Aug. 1982; 12-17 m; stones; 3.5°C; 25‰; codtrap. NMC84-144; 1; Canada: Barge Bay, Strait of Belle Isle, Labrador, Newfoundland; 51°48'18"N 56°12'3"W; crew of the M.V. Lady N; 3 Aug. 1982; 27-28 m;

stones; gill net.

Gadus macrocephalus: NMC84-275; 3; USA: south of Unalaska Island, Aleutian Islands, Alaska; 53°18'12"-30"N 166°38'-40'12"W; H. Zenger; Ocean Harvester cruise no. 82-1, haul no. 91; 22 March 1982; 163-168 m. NMC84-276; 1; USA: southeast of Lance Point, Unalaska Island, Aleutian Islands, Alaska; 53°16'12"-54"N 166°47'12"-49'12"W; H. Zenger, Ocean Harvester cruise no. 82-1, haul no. 93; 22 March 1982; 133-134 m. NMC84-276A; 4; USA: Bering Sea, east of Cape Shaw, Atka Island, Aleutian Islands, Alaska; 52°26'0"-6"N 173°50'42"-52'54"W; H. Zenger, Ocean Harvester cruise no. 82-1, haul no. 113; 27 March 1982; 152 m. NMC84-157; 1; USA: off Seward Marine Center dock, Seward, Resurrection Bay, Gulf of Alaska, Alaska; 60°7'N 149°27'W; C.B. Renaud and T.A. Edge; 28 July 1983; 23-26 m; 13.5°C; 23.5‰; gill net. NMC65-174; 1; Canada: Chatham Sound, north of Stephens Island, British Columbia; 54°13'N 130°20'W; D.E. McAllister; 12-13 June 1965; jigging.

Gadus ogac: NMC84-277; 2; Canada: The Harbour, Red Bay, Strait of Belle Isle, Labrador, Newfoundland; 51°44'N 56°25'W; R. Chan; 27 Sept. 1982; 8-9 m. NMC66-127; 1; Canada: Brandy Sound, Cabot Strait, 19 km east of Channel-Port aux Basques, Newfoundland; 47°36'20"N 58°50'30"W; D.E. McAllister and W.H. van Vliet; 8-9 June 1966; gill net. NMC85-246; 1; Canada: Gulf of St. Lawrence, at Baie-Trinité, Saguenay County, Québec; 49°25'N 67°18'W; F. Caron; 18 Oct. 1982; 3-5 m; gill net.

CONCLUSION

This study is based upon the examination of topotypic adult specimens for all six nominal subspecies of Gadus morhua recognized by Svetovidov (1948), the last revisor of the genus, as well as non-topotypic adult specimens believed to adequately reflect the geographic distribution of the genus.

The allopatric macrocephalus and ogac are recognized as distinct species based upon differences in pelvic fin and chin barbel pigmentations (this study), length and shape of nuptial tubercles (Vladykov et al. 1985), and testicular lobe morphology (Renaud 1989, this study). The allopatric morhua and kildinensis are synonymized because they cannot be distinguished on the basis of morphometric characters (Tzeb and Astafyeva 1975, this study), meristic and pigmentary characters (this study), or gas bladder horn length and arrangement (Tzeb and Astafyeva 1975). The sympatric morhua and callarias (Svetovidov 1948) are synonymized because they cannot be distinguished on the basis of morphometric, meristic, and pigmentary characters (this study), testicular lobe morphology (Renaud 1989, this study), type of drumming muscles (Brawn 1961, this study), and protein electrophoresis (Mork et al. 1985, Renaud et al. 1986, Grant and Ståhl 1988). The sympatric morhua and marisalbi (Il'in and Pevzner 1939, Svetovidov 1948) are synonymized because they cannot be distinguished on the basis of morphometric and meristic

characters (this study), testicular lobe morphology (this study), protein electrophoresis (Karpov et al. 1984), and karyotype (Nygren et al. 1974, Vasil'yev 1980). Although marisalbi could be at least partly distinguished from morhua on the basis of body pigmentation (91% separation), this character was hypothesized to be environmentally controlled and therefore, could not be used for specific or subspecific recognition (this study). The sympatric morhua and ogac (see this study p. 104 for references) are recognized as distinct species based upon differences in the external pigmentation of ovaries, body pigmentation, and lateral line pigmentation (this study), length and shape of nuptial tubercles (Vladykov et al. 1985), length of the gas bladder horns (Schultz and Welander 1935, Svetovidov 1948, this study), and protein electrophoresis (Sick 1965; Renaud et al. 1986; Renaud 1989). The allopatric morhua and macrocephalus are recognized as distinct species based upon differences in the external pigmentation of the ovaries (this study), length and shape of the nuptial tubercles (Vladykov et al. 1985), length of the gas bladder horns (Schultz and Welander 1935, Svetovidov 1948, this study), protein electrophoresis (Sick 1965, Mackie and Ritchie 1981, Renaud et al. 1986, Grant and Ståhl 1988), and karyotype (Nygren et al. 1974, Ishii and Yabu 1985).

In summary, the three following monotypic species of Gadus are recognized: G. morhua Linnaeus, 1758; G.

macrocephalus Tilesius, 1810; and G. ogac Richardson, 1836.

The subspecies Gadus morhua callarias Linnaeus, 1758; G. m. kildinensis Derjugin, 1920; and G. m. marisalbi Derjugin, 1920 recognized by Svetovidov (1948) are synonymized with the monotypic species G. morhua Linnaeus, 1758. A formal albeit partial synonymy for the three species of Gadus herein recognized follows:

Gadus morhua Linnaeus, 1758

Gadus Morhua Linnaeus, 1758: 252 (European seas)

Gadus Callarias Linnaeus, 1758: 252 (European seas and Baltic Sea)

Gadus callarias Kildinensis Derjugin, 1920: 2 (Lake

Mogil'noye on Kil'din Island, in the Barents Sea)

Gadus callarias Maris-Albi Derjugin, 1920: 2 (White Sea)

Gadus macrocephalus Tilesius, 1810

Gadus macrocephalus Tilesius, 1810: 350 (Bering Sea, off Kamchatka Peninsula)

Gadus ogac Richardson, 1836

Gadus ogac Richardson, 1836: 246 (off west Greenland)

At this point, it is important to demonstrate that the scientific nomenclature I use for the Atlantic cod, the Pacific cod, and the ogac applies to the same species as Linnaeus (1758), Tilesius (1810), and Richardson (1836) respectively, intended it for. In the absence of any type

material, one must rely solely on the original descriptions.

Linnaeus (1758) stated the characteristics of the genus Gadus as follows: jugular pelvic fins, branchiostegal membrane with seven rays, deciduous scales, mouth with barbel, and dorsal fins divided. All three species herein recognized fit this generic description.

Linnaeus (1758) described Gadus morhua as follows: three dorsal fins, two anal fins, the first ray of the caudal fin is spinous, the first ray in the two anal fins is spinous, a fecundity equal to 9 344 000 eggs, and distributed in the European seas. Linnaeus (1758) adds the following fin formula: first dorsal with 15 rays, second dorsal with 20 rays, third dorsal with 16 rays, first anal with 21 rays, second anal with 16 rays, pectoral with 20 rays, and pelvic with six rays.

The possession of three dorsal fins and two anal fins places the species within the subfamily Gadinae. The presence of a spine in the caudal fin and in the two anal fins is interpreted as an error since by definition gadines do not have spines. A survey of Svetovidov (1948) gives the following maximum fecundities (in thousands of eggs) for the gadine taxa for which data are available: Eleginus gracilis - 210; E. navaga - 90; Gadus morhua macrocephalus - 5722; G. m. marisalbi - 840; G. m. morhua - 9300; Microgadus tomcod - 40; and Pollachius virens - 4000. Gadus morhua is the only gadine which reaches the high fecundity reported by Linnaeus

(1758) in his original description. I therefore feel confident that the scientific name I ascribe to the Atlantic cod is the one Linnaeus (1758) intended for it. Furthermore, the fin formula given in Linnaeus (1758) is consistent with my unpublished results.

Tilesius (1810) described Gadus macrocephalus as follows: collected in the Bering Sea, off the Kamchatka Peninsula, three dorsal fins, one to two feet long (305-610 mm), large head, large mouth, intestine with innumerable worms, caught in great numbers between the end of July and the beginning of August, related to Gadus callarias but with a larger head, with the second ray of the pelvic fin long and curved, body not spotty, branchial opening large, and branchiostegal membrane with six rays on both sides. In addition to the written description above, Tilesius (1810) provided four plates depicting G. macrocephalus. These consist of the following: Plate XVI, fig. 1 is a side-view of a whole specimen, figs. 2 and 3 represent jaw bones; Plate XVII, fig. 1 is a ventral view of a whole specimen with its internal anatomy exposed, fig. 2 depicts a pair of testes, and fig. 3 a pair of oviducts; Plate XIX, fig. 1 shows the stomach, pyloric caeca and intestine in detail, figs. 2-10 show different types of intestinal worms, and figs. 11-13 depict worms found to be closely associated with the vertebrae and ribs; Plate XX, fig. 1 is a ventral view of a partial specimen showing the position of the worms associated

with the vertebrae and ribs, and fig. 2 depicts a pair of ovaries.

The specimen in Plate XVI, fig. 1 exhibits three dorsal fins and two anal fins which places it within the subfamily Gadinae. From the present study, we know that G. macrocephalus attains at least 610 mm in length. Tilesius (1810) did not quantify what he meant by large head and large mouth but a study of the specimen in Plate XVI, fig. 1 reveals the following: the head length expressed as a percentage of the standard length equals approximately 43.5% and the posteriormost edge of the maxillary reaches the level of the middle of the eye. In the present study, the specimen of G. macrocephalus with the largest head attains a HL/SL ratio of only 31.3% . This large discrepancy in relative head length between Tilesius's (1810) specimen and my specimens is I believe explained by the fact that the drawing in Tilesius (1810) is highly stylized and although it depicts the essential features of the fish, it does not adequately reflect all of the various body proportions. As in Tilesius's (1810) specimen, the posteriormost edge of the maxillary reaches the level of the middle of the eye in the specimen of G. macrocephalus illustrated in this study (fig. 11). In the present study, G. macrocephalus was not found to have a significantly greater head length or head width compared to G. callarias (= morhua) as stated by Tilesius (1810). Furthermore, the second ray of the pelvic fin is

shorter on average not longer than in G. callarias (= morhua) (Table 12). As far as the curvature of this fin ray, dessication has been invoked to explain this condition. Indeed, Plate XVI, fig. 1, in Tilesius (1810) shows a dessicated specimen notably in the head region where features of the underlying cranium are clearly visible and the rays of the two pelvic fins are shriveled up. As further evidence for this interpretation, Tilesius (1810), in the same article, described another species of Gadinae, Gadus gracilis (= Eleginus gracilis) and in his Plate XVIII depicting this species, the pelvic fin rays of both fins are likewise curled up. In the present study, body pigmentation was also found to be a very important character to distinguish G. macrocephalus from G. callarias (= morhua); the former lacking spots and the latter having them (Table 13, figs. 11 and 18). Examination of 43 specimens of G. macrocephalus in the present study revealed that six branchiostegal rays was not the normal count for this species. Only three specimens had a count of six, the remaining 40 having a count of seven. Vladykov (1972) described and provided photographs of the testes for six of the 12 genera within the Gadinae. These included Arctogadus, Boreogadus, Eleginus, Gadus, Melanogrammus, and Microgadus. Comparison of these with Plate XVII, fig. 2, in Tilesius (1810) and with fig. 1 in Renaud (1989) confirms the identity of the specimens used in the present study as belonging to the genus Gadus. Of the

six genera of Gadinae not covered by Vladykov (1972), only Theragra is present in the Pacific Ocean. However, it may be distinguished from G. macrocephalus by the presence of a small chin barbel and of a lower jaw projecting beyond the upper jaw whereas in Plate XVI, fig. 1 in Tilesius (1810) and in this study (fig. 11), a very prominent chin barbel and an upper jaw projecting beyond the lower jaw is found in G. macrocephalus. Tilesius (1810) did not provide any characters to distinguish G. macrocephalus from G. ogac but since G. macrocephalus is the only species in the genus to be found in the Pacific Ocean, I take G. macrocephalus as the scientific name to be ascribed to the Pacific cod.

Richardson (1836) described Gadus ogac as follows: rarely exceeds 18 inches (458 mm) in length, no dark spots at the base of the pectorals, spawns among the seaweeds under the ice in February or March, keeps nearer the bottom than does Gadus callarias, distributed off west Greenland, seven branchiostegal rays. Richardson (1836) adds the following fin formula: first dorsal with 15 rays, second dorsal with 17 rays, third dorsal with 16 rays, first anal with 22 rays, second anal with 17 rays, pectoral with 18 rays, pelvic with six rays, and caudal with 32 rays. Richardson (1836) further stated that since the name given to a particular fish (owak or owuk) by the Inuit of Boothia Peninsula, Northwest Territories is virtually identical to the name the Inuit of west Greenland give G. ogac, namely ogak or ovak, it is

probable that they refer to the same species.

The presence of three dorsal fins and two anal fins places the species within the subfamily Gadinae. According to Svetovidov (1948) and Nielsen and Jensen (1967), only the seven following species of Gadinae are found off west Greenland: Arctogadus borisovi, A. glacialis, Boreogadus agilis, B. saida, Gadus morhua, G. ogac, and Pollachius virens. Arctogadus borisovi can be rejected as the species Richardson (1836) was alluding to in his description of Gadus ogac, since according to Nielsen and Jensen (1967), A. borisovi has 10-13 rays in the first dorsal fin, 19-23 rays in the third dorsal fin, and 19-23 rays in the second anal fin. Likewise, A. glacialis can be rejected, since according to Nielsen and Jensen (1967), its maximum recorded standard length is 325 mm, it leads a pelagic mode of life in the adult stage, it has 20-24 rays in the third dorsal fin, and 17-24 rays in the second anal fin. Boreogadus agilis can be rejected, because according to Svetovidov (1948), its maximum recorded total length is 370 mm, it leads a cryopelagic mode of life in the adult stage, it has 13-14 rays in the first dorsal fin, 16 rays in the second dorsal fin, 19-20 rays in the third dorsal fin, 18-19 rays in the first anal fin, and 19-22 rays in the second anal fin. B. saida can be rejected, because according to Svetovidov (1948), its maximum recorded total length is 321 mm, it leads a cryopelagic mode of life in the adult stage, it has 12-17 rays in the second dorsal

fin, 17-23 rays in the third dorsal fin, 14-20 rays in the first anal fin, and 18-24 rays in the second anal fin.

Pollachius virens can be rejected, because according to Svetovidov (1948), its maximum recorded total length is 1200 mm, it has 13-14 rays in the first dorsal fin, 20-22 rays in the second dorsal fin, 20-24 rays in the third dorsal fin, 25-28 rays in the first anal fin, and 19-23 rays in the second anal fin. Gadus morhua can be rejected, because according to Svetovidov (1948), its maximum recorded total length is 1800 mm. Furthermore, this species is not known from Boothia Peninsula (Hunter et al. 1984) and therefore, cannot be used to support the ethnozoological inference of Richardson (1836) as to the geographic distribution of the ogac. The specimens I call G. ogac in the present study, fit Richardson's (1836) original description as far as length, the absence of a dark spot at the base of the pectoral fins, their benthic habit, the presence of seven branchiostegal rays, the inferred geographic distribution, and in all the fin ray counts he listed, except for two. None of my G. ogac specimens have more than 21 rays in the first anal fin. However, Svetovidov (1948) gives a range up to 23. Secondly, I obtained a range of 44-53 in the number of caudal fin rays. This discrepancy is almost certainly attributable to my counts being made using radiographs and therefore, my being able to count all procurrent fin rays. In conclusion, I take Gadus ogac as the scientific name to be ascribed to the ogac.

Key to Adults (≥ 100 mm SL) of the Genus Gadus

- 1a. Dark spots present on the dorsal body surface, upper and mid flanks on a lighter background or the dorsal surface, upper and mid flanks darkly pigmented with dark spots hardly if at all discernible; strip of skin along the lateral line lightly pigmented from the level of the cleithrum and along its entire course, sharply contrasting with the heavily pigmented adjacent areas or heavily pigmented up to the middle of the first or second dorsal fin, blending in with adjacent areas and posterior to that lightly pigmented, in sharp contrast to adjacent areas; nuptial tubercles, when present, horn-shaped and of medium length (2.81-5.71% of scale length); no melanophores on ovaries; gas bladder horn length/SL between 5.9 and 12.3%
 Atlantic cod - G. morhua Linnaeus, 1758
 western and eastern North Atlantic Ocean and Arctic Ocean and their adjacent seas from the coast of USA at Cape Hatteras and northward to the Gulf of St. Lawrence, off the east coast of Newfoundland, up the Labrador coast to Baffin Island and across to west Greenland, south around to east Greenland, then to Iceland, to the British Isles, south to the Bay of Biscay, in the North Sea, the Baltic Sea, north to the Norwegian Sea, Barents Sea from Spitsbergen to Novaya Zemlya, and south to the White Sea

- b. Dorsal body surface uniformly darkly pigmented, the upper and mid flanks with lightly pigmented vermiculations (sometimes the lightly pigmented vermiculations also occur on the dorsal surface and on the lower flanks); skin along the lateral line heavily pigmented, blending in with adjacent areas; nuptial tubercles, when present, either club-shaped and long (5.95-9.42% of scale length) or hillock-shaped and very short (0.72-1.79% of scale length); melanophores cover anterior half to entire surface of ovaries; gas bladder horn length/SL between 2.3 and 6.9% 2
- 2a. Only the membrane investing the first two principal pelvic fin rays, or the first principal ray and the trailing part of the second ray or the trailing parts of the first two principal rays is unpigmented; only anterior face of the chin barbel is at least partly pigmented; first principal pelvic fin ray length/SL% = 8.9-12.9 (usually 8.9-11.9); pectoral fin's longest fin ray/SL% = 12.6-16.0 (usually 12.6-15.4); first dorsal fin length/SL% = 11.3-15.2 (usually 11.3-14.4); nuptial tubercles, when present, hillock-shaped and very short (0.72-1.79% of scale length); testicular lobes smooth; brown melanophores are typically sparsely distributed over anterior half to two-thirds of ovaries
Pacific cod - G. macrocephalus Tilesius, 1810
 western and eastern North Pacific Ocean and adjacent seas

from the People's Republic of China and North and South Korea, Japan, the USSR nearly up to the Bering Strait, across to Alaska and southward along the coasts of Canada and the USA down to southern California

- b. Only the membrane investing the trailing part of the first principal pelvic fin ray is unpigmented or the whole pelvic fin is pigmented, with the trailing parts of the first two principal rays being at least partly pigmented; pigmentation present all around the chin barbel but not necessarily to its tip; first principal pelvic fin ray length/SL% = 10.4-14.8 (usually 12.0-14.8); pectoral fin's longest fin ray/SL% = 13.7-19.3 (usually 15.5-19.3); first dorsal fin length/SL% = 11.8-19.0 (usually 14.5-19.0); nuptial tubercles, when present, club-shaped and long (5.95-9.42% of scale length); testicular lobes crenated (scalloped); entire surface of ovaries covered by dark brown or grayish black mottling or uniformly covered by dark brown or jet black melanophores ogac - G. ogac Richardson, 1836 Canadian Arctic coast from the Eskimo Lakes, Northwest Territories, to west Greenland and including Hudson and James Bay, south along the Labrador coast, into the Gulf of St. Lawrence, and in Bras d'Or Lake, Nova Scotia

RELATIONSHIPS WITH OTHER GADINES

Only monophyletic groups (i.e.: ones that comprise all and only the descendants of a common ancestor) are used in a cladistic study. These groups are based upon the possession of shared derived characters (synapomorphies). For a comprehensive discussion of the cladistic method, the reader is referred to Wiley (1981).

In a cladistic analysis conducted by Dunn (1989) including 11 of the 12 genera (Arctogadus was excluded for lack of material) in the subfamily Gadinae as understood by Svetovidov (1948) and Markle (1982), and based upon the examination of 42 almost exclusively osteological characters of early life history and adult stages, no single synapomorphy was found to establish the monophyly of Gadus. However, as found in this study, the presence of nuptial tubercles in Gadus provides the synapomorphy necessary to establish its monophyletic status. In the following discussion, the expression nuptial tubercles is used in lieu of the terms breeding tubercles and contact organs, because it is the general term used by Wiley and Collette (1970) and Collette (1977) when referring to roughening structures whose origin (i.e.: epidermal or dermal) has not yet been determined.

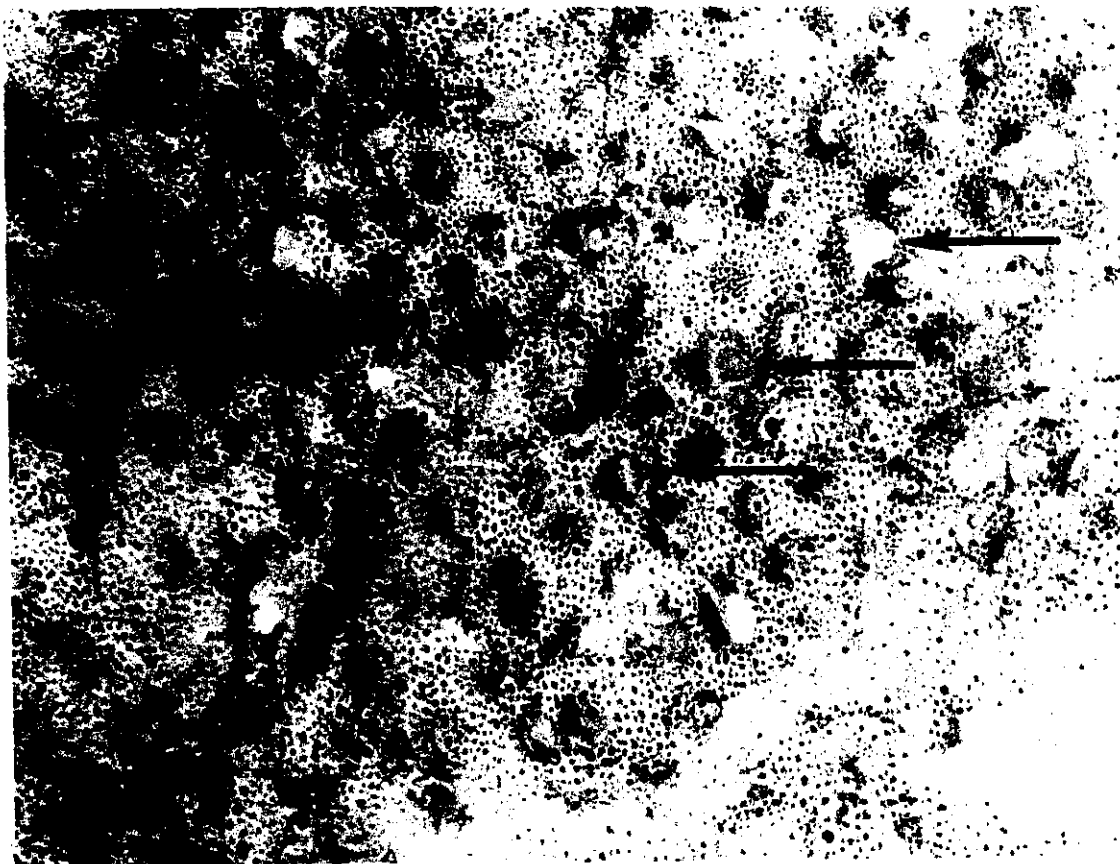
Vladykov et al. (1985) reported the presence and provided photographs of "breeding tubercles" on the scales of Gadus. Their use of the term "breeding tubercle" infers

structures of epidermal origin as explained in Wiley and Collette (1970) and Collette (1977) although Vladykov et al. (1985) did not conduct a histological examination to confirm this. Boreogadus is the only other gadine in which nuptial structures have been reported (Svetovidov 1948, Walters 1955, Andriyashev et al. 1980). However, these authors did not provide photographs of these structures. Svetovidov (1948) described the nuptial tubercles in Boreogadus saida and B. agilis as "... small hard protuberances or tubercles scattered on sides of body, head, and fins." Walters (1955) described the nuptial structures in B. saida as "... bony tubercles" on some of the scales and Andriyashev et al. (1980) stated that "... in addition to the ordinary scales, the body bears numerous small bony plates, each of which carries a spinule with a blunt tip directed upward and posteriorly" and further, described the development of these structures as follows: "An alizarin preparation of skin from Boreogadus saida clearly shows all the stages of development of the prickly plates, beginning with the formation on the posterior margin of an ordinary scale of the minute spinule which, as it gradually develops, forms a separate basal plate with a spine, outwardly resembling a small placoid scale." From the above descriptions, it would appear that the nuptial structures in Boreogadus are of dermal origin and would be termed contact organs according to the nomenclature of Wiley and Collette (1970) and Collette (1977). According to Wiley

and Collette (1970) no pelagic or epipelagic marine fishes are known to develop nuptial tubercles. Boreogadus therefore becomes the first reported case of a pelagic marine fish with nuptial tubercles. Andriyashev (1970), McAllister (1977), and Andriyashev et al. (1980) point out however, that Boreogadus saida is often associated with the ice ceiling habitat, which has been likened to an inverse benthos (McAllister 1977).

Study of the tubercles in an adult female of Boreogadus saida (fig. 21) measuring 243 mm SL and from the southeast coast of Baffin Island, Northwest Territories, indicated they were pale yellow, hard protuberances, resembling a very coarse grain of sand and that they originated from under the scales and extended beyond the posterior edge of the scales rather than as darkly pigmented dorsal extensions (horn-, club-, or hillock-shaped) of the posterior edge of the scales as in Gadus (Vladykov et al. 1985; fig. 4). The same type of tubercles were found in two more adult specimens of B. saida of undetermined sex (the gonads had been removed), measuring 221 and 268 mm SL and from the same general locality as the one above. Furthermore, the tubercles in Boreogadus and Gadus reacted differently to treatment with the bone specific stain alizarin Red S. In a specimen of B. saida (NMC64-466), the tubercles stained whereas in two specimens of G. morhua (NMC86-229) and in one specimen of G. ogac (ROM26823), the tubercles did not accept the stain.

Fig. 21. Skin of Boreogadus saida (NMC64-466) taken from the upper flank between the second and third dorsal fins. Arrows point to nuptial tubercles. Bar scale represents 1 mm. Photographed by G. Ben-Tchavtchavadze.



I

Twenty-one out of 24 families which possess roughening structures (= nuptial tubercles) belong to groups of fishes with cycloid scales and only three belong to families which usually have ctenoid scales (Wiley and Collette 1970, Collette 1977). Collette (1977) omitted Gadidae in his count of fish families with nuptial tubercles and therefore a readjustment of his numbers would make it 22 out of 25 since gadids have cycloid scales. This observation led Wiley and Collette to revive the following hypothesis proposed by Newman (1907): "... ctenoid scales may have evolved in higher fishes to permanently replace the contact organs and breeding tubercles found during the breeding season in lower fishes." By implication, the following two transformation series from primitive to derived are suggested: 1. naked cycloid scale -----> cycloid scale with breeding tubercle and 2. naked cycloid scale -----> cycloid scale with contact organ. It follows therefore that gadine genera with naked cycloid scales possess the plesiomorphic condition and those with nuptial structures the apomorphic one. The nuptial tubercles in Gadus and Boreogadus do not constitute homologous characters. As described above, they differ in their color, shape, and position. Furthermore, only those in Boreogadus stain with alizarin. However, a histological study of the tubercles in these two genera will have to be made to determine their developmental origin (i.e.: epidermal or dermal). Incidentally, the presence of contact organs and

breeding tubercles within the same family is not without precedent: Characidae have both (Collette 1977). The tubercles in Gadus and Boreogadus being nonhomologous apomorphic characters, they individually confirm the monophyletic status of each genus but cannot be used to relate them.

MATERIAL

Boreogadus saida: NMC80-426; 2; Canada: Frobisher Bay, about 6 km east of Peale Point, southern Baffin Island, District of Franklin, Northwest Territories; 63°44'N 68°33'W; Arctic Biological Station, Ste-Anne-de-Bellevue; 16 June 1979; jigging. NMC64-466; 1; Canada: Winton Bay lagoon, Beekman Peninsula, southeast Baffin Island, District of Franklin, Northwest Territories; 63°24'N 64°40'W; M. Freeman; Aug. 1964; sand and rocks.

Gadus morhua: NMC86-229; 2; Canada: Miramichi Bay, Gulf of St. Lawrence, New Brunswick; 47°8'N 64°58'W; 25 Feb. 1982; smelt trap.

Gadus ogac: ROM26823; 1; western Greenland; A.T. Cameron; Sept.-Oct. 1967.

PHYLOGENETIC RELATIONSHIPS WITHIN THE GENUS Gadus

According to Dunn's (1989) cladogram of Merluccius and 11 of the 12 gadine genera sensu Svetovidov (1948) (only Arctogadus missing), Gadus belongs to a clade together with Theragra, Boreogadus, and Micromesistius which is characterized by two synapomorphies. Dunn (1989) did not find a synapomorphy to characterize Gadus but he gave two to characterize the Theragra-Boreogadus-Micromesistius subclade and this lineage was used as the sister group to Gadus (fig. 22). Table 15 gives a list of the characters used in the cladogram and the polarity of their character states. Table 16 is a Wagner matrix of the characters used in the cladogram and their character states as they pertain to the three recognized species of Gadus.

Characters 1-4 are taken from Dunn (1989). Characters 1 and 2 were used to root the cladogram and characters 3 and 4 were used to define the sister group to Gadus.

Character 5: Presence or absence of nuptial tubercles. As discussed in the section Relationships With Other Gadines (p. 146-52), the presence of nuptial tubercles in Gadus is interpreted as a synapomorphy that supports the monophyly of that genus. Comparison with the sister group shows that only Boreogadus possesses tubercles but that these are nonhomologous with those in Gadus based on differences in color, shape, position, and acceptance of alizarin. However,

Fig. 22. Cladogram of the species of Gadus. Numbers refer to characters listed in Table 15. Only apomorphic character states are indicated on the cladogram.

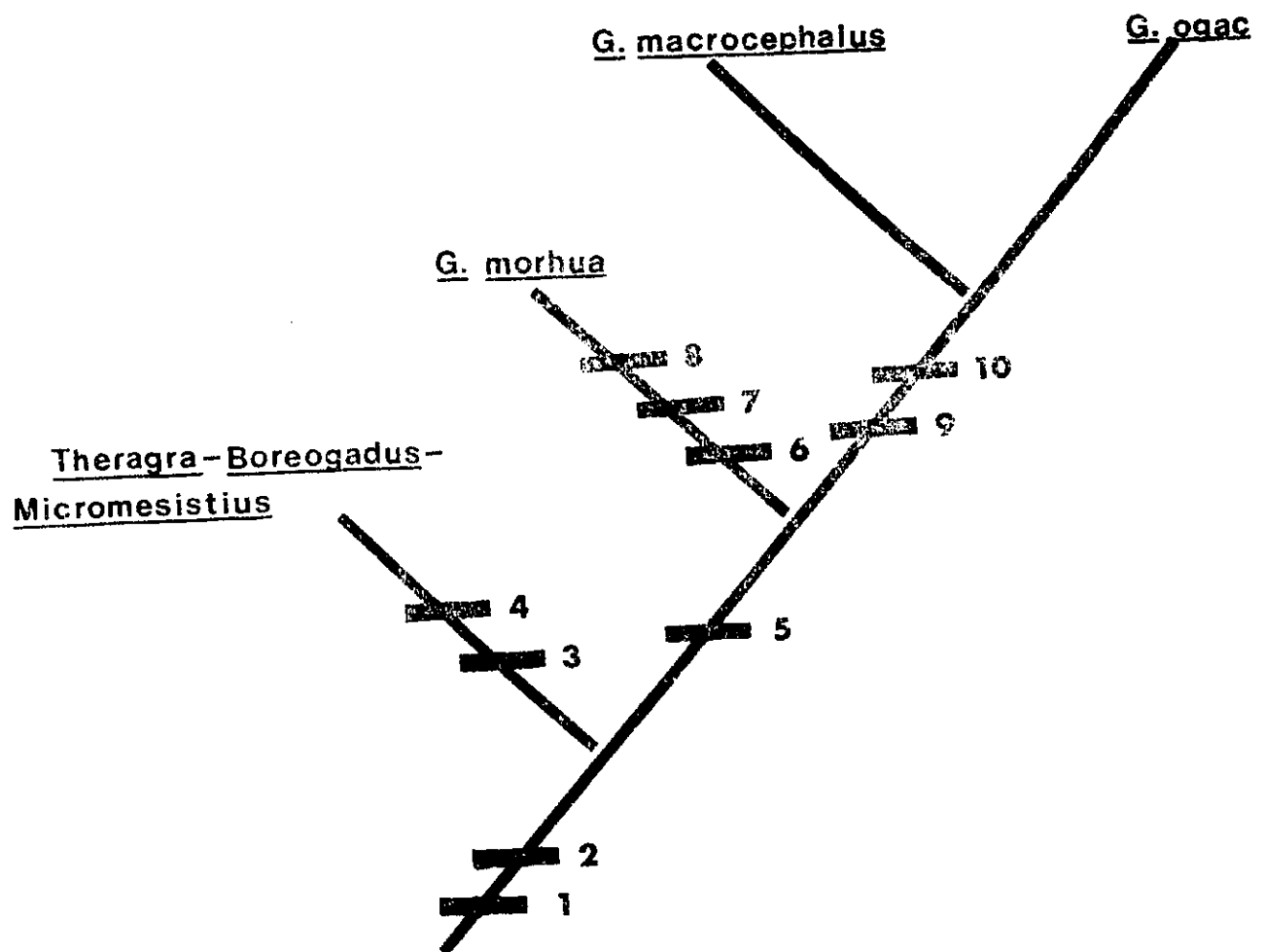


Table 15. List of characters used in the cladogram and the polarity of their character states. The first four characters are taken from Dunn (1989).

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1. Relationship of sphenotic to pterotic. Plesiomorphic condition: shelf of sphenotic barely touches the pterotic shelf. Character states: 0 (barely touches), 1 (overlaps), 2 (does not touch). On the cladogram, character 1 represents a lost character since it has reverted to the plesiomorphic state.
 2. Presence or absence of ribs on opercle. Plesiomorphic condition: present. Character states: 0 (present), 1 (absent).
 3. Length of postcleithrum. Plesiomorphic condition: moderate. Character states: 0 (moderate), 1 (long), 2 (short). On the cladogram, character 3 represents a lost character since it has reverted to the plesiomorphic state.
 4. Distance between the first and second dorsal fins. Plesiomorphic condition: close. Character states: 0 (close), 1 (moderate), 2 (wide).
 5. Presence or absence of nuptial tubercles. Plesiomorphic condition: absent. Character states: 0 (absent), 1 (present).
 6. Length of gas bladder horns. Plesiomorphic condition: short. Character states: 0 (short), 1 (long).
-

Table 15 cont...

-
7. Est-1 locus. Plesiomorphic condition: allele 110.
Character states: 0 (allele 110), 1 (allele 100).
8. Lateral line pigmentation. Plesiomorphic condition:
heavily pigmented. Character states: 0 (heavily
pigmented), 1 (lightly pigmented).
9. Est-2 locus. Plesiomorphic condition: allele 100.
Character states: 0 (allele 100), 1 (allele 110).
10. Mdh-3 locus. Plesiomorphic condition: alleles 110, 120.
Character states: 0 (alleles 110, 120), 1 (alleles 90,
100).
-

Table 16. Wagner matrix of the characters used in the cladogram and their character states for the three species of Gadus. Character numbers refer to those listed in Table 15. 0 = plesiomorphic character state; 1 = apomorphic character state.

Character number	Taxa		
	<u>G. morhua</u>	<u>G. macrocephalus</u>	<u>G. ogac</u>
5	1	1	1
6	1	0	0
7	1	0	0
8	1	0	0
9	0	1	1
10	0	1	1

even if a histological study demonstrates that the nuptial tubercles in Gadus and Boreogadus originate from the same embryological layer, Dunn's (1989) cladogram shows that Boreogadus is the sister group to Micromesistius (supported by two synapomorphies) and therefore, the most parsimonious hypothesis is that the tubercles in Gadus and Boreogadus represent a homoplasy.

Character 6: Length of gas bladder horns. Both Schultz and Welander (1935) and Svetovidov (1948) have stated that there is an ontogenetic progression of short to long gas bladder horns in G. morhua. Both G. macrocephalus and G. ogac have short gas bladder horns. Long gas bladder horns are therefore interpreted as an autapomorphy that characterizes G. morhua within the genus. Comparison with the sister group was uninformative as far as confirming the polarity of this character because the only genus examined, Boreogadus (NMC64-466), does not possess gas bladder horns.

Character 7: Est-1 locus (Enzyme Commission no. 3.1.1.1). Two alleles are expressed in Gadus. G. morhua is fixed for allele 100, whereas G. macrocephalus and G. ogac are fixed for allele 110 (Renaud et al. 1986). Comparison with the sister group shows that Theragra is fixed for allele 110 (Renaud 1989) and therefore, allele 100 is interpreted as an autapomorphy that characterizes G. morhua within the genus.

Character 8: Lateral line pigmentation. A heavily

pigmented lateral line is found in G. macrocephalus and G. ogac, whereas a lightly pigmented lateral line occurs in G. morhua. Comparison with the sister group shows that both Boreogadus (NMC64-466, 80-426) and Theragra (NMC84-165, 84-166) have heavily pigmented lateral lines and therefore, a lightly pigmented lateral line is interpreted as an autapomorphy that characterizes G. morhua within the genus.

Character 9: Est-2 locus (Enzyme Commission no. 3.1.1.1). Two alleles are expressed in Gadus. G. morhua is fixed for allele 100, whereas G. macrocephalus and G. ogac are fixed for allele 110 (Renaud et al. 1986). Comparison with the sister group shows that Theragra is fixed for allele 100 (Renaud 1989) and therefore, allele 110 is interpreted as a synapomorphy that supports the G. macrocephalus - G. ogac lineage.

Character 10: Mdh-3 locus (Enzyme Commission no. 1.1.1.37). Four alleles are expressed in Gadus. G. morhua is fixed for alleles 110 and 120, whereas G. macrocephalus and G. ogac are fixed for alleles 90 and 100 (Renaud et al. 1986). Comparison with the sister group shows that Boreogadus is fixed for allele 110 and Theragra is fixed for allele 120 (Renaud 1989) and therefore, alleles 90 and 100 are interpreted as a synapomorphy that supports the G. macrocephalus - G. ogac lineage.

In summary, the genus Gadus is monophyletic (supported by one synapomorphy) and G. morhua is the sister group to the

G. macrocephalus - G. ogac lineage. The G. macrocephalus -
G. ogac clade is supported by two synapomorphies.

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APPENDIX 1. Alphabetical list of characters used in this study.

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1. A_1-A_2 : Length of A_1-A_2 interspace
 2. A_1FRL : Length of the first anal fin's longest fin ray
 3. A_2FRL : Length of the second anal fin's longest fin ray
 4. A_1FRN : Number of rays in the first anal fin
 5. A_2FRN : Number of rays in the second anal fin
 6. A_2-IP : Distance between insertion of A_2 and insertion of the inferior procurent caudal fin rays
 7. A_1P : First anal fin pigmentation
 8. A_2P : Second anal fin pigmentation
 9. BD : Body depth
 10. BG : Body girth
 11. BL : Chin barbel length
 12. BP : Body pigmentation
 13. BR : Number of branchiostegal rays
 14. CBP : Chin barbel pigmentation
 15. CD : Caudal fin depth
 16. CFP : Caudal fin pigmentation
 17. CFS : Caudal fin shape
 18. CFR : Number of caudal fin rays
 19. CL : Caudal fin length
 20. CPD : Caudal peduncle depth
 21. CV : Number of caudal vertebrae
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APPENDIX 1 cont...

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- 22. D_1-D_2 : Length of D_1-D_2 interspace
 - 23. D_2-D_3 : Length of D_2-D_3 interspace
 - 24. D_1FRL : Length of the first dorsal fin's longest fin ray
 - 25. D_2FRL : Length of the second dorsal fin's longest fin
ray
 - 26. D_3FRL : Length of the third dorsal fin's longest fin ray
 - 27. D_1FRN : Number of rays in the first dorsal fin
 - 28. D_2FRN : Number of rays in the second dorsal fin
 - 29. D_3FRN : Number of rays in the third dorsal fin
 - 30. D_1P : First dorsal fin pigmentation
 - 31. D_2P : Second dorsal fin pigmentation
 - 32. D_3P : Third dorsal fin pigmentation
 - 33. $DSBM$: Distance between dentary symphysis and angle of
branchiostegal membrane
 - 34. D_3-SP : Distance between insertion of D_3 and insertion
of the superior procurrent caudal fin rays
 - 35. E : Horizontal eye diameter
 - 36. EPO : External pigmentation of ovaries
 - 37. $FPELFR$: First principal pelvic fin ray length
 - 38. HL : Head length
 - 39. HW : Head width
 - 40. INW : Least internarial width
 - 41. IOP : Number of infraorbital pores
-

APPENDIX 1 cont...

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|---------------------|--|
| 42. IOW | : Least bony interorbital width |
| 43. IPEC | : Interinsertions of pectoral fins |
| 44. IPEL | : Interinsertions of pelvic fins |
| 45. LA ₁ | : First anal fin length |
| 46. LA ₂ | : Second anal fin length |
| 47. LD ₁ | : First dorsal fin length |
| 48. LD ₂ | : Second dorsal fin length |
| 49. LD ₃ | : Third dorsal fin length |
| 50. LIGR | : Length of longest gill-raker on inner side of
first gill arch |
| 51. LJL | : Lower jaw length |
| 52. LLIP | : Lateral line interruption point |
| 53. LLPI | : Lateral line pigmentation |
| 54. LLPO | : Number of lateral line pores |
| 55. LLS | : Lateral line shape |
| 56. LOGR | : Length of longest gill-raker on outer side of
first gill arch |
| 57. MG | : Mouth gape |
| 58. NFL | : Nasal flap length of incurrent nostril |
| 59. NIGR | : Number of gill-rakers on inner side of first
gill arch |
| 60. NOGR | : Number of gill-rakers on outer side of first
gill arch |
-

APPENDIX 1 cont...

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- 61. NT : Nuptial tubercles
 - 62. OA₁ : Origin of first anal fin relative to dorsal fins
 - 63. OA₂ : Origin of second anal fin relative to dorsal
fins
 - 64. OMW : Opercular membrane width
 - 65. PAFL : Preanal fin length
 - 66. PCFR : Number of primary caudal fin rays
 - 67. PDDL : Predorsal fin length
 - 68. PECFL : Pectoral fin length
 - 69. PECFRL : Length of the pectoral fin's longest fin ray
 - 70. PECFRN : Number of pectoral fin rays
 - 71. PEL-A₁ : Pelvic fin to A₁ length
 - 72. PELFL : Pelvic fin length
 - 73. PELFRN : Number of pelvic fin rays
 - 74. PELP : Pelvic fin pigmentation
 - 75. PHL : Postorbital head length
 - 76. PMP : Number of preoperculo-mandibular pores
 - 77. PP : Peritoneal pigmentation
 - 78. PV : Number of precaudal vertebrae
 - 79. S : Sex
 - 80. SL : Standard length
 - 81. SNL : Snout length
 - 82. SPELFR : Second principal pelvic fin ray length
-

APPENDIX 1 cont...

83. TL : Total length

84. UJL : Upper jaw length
