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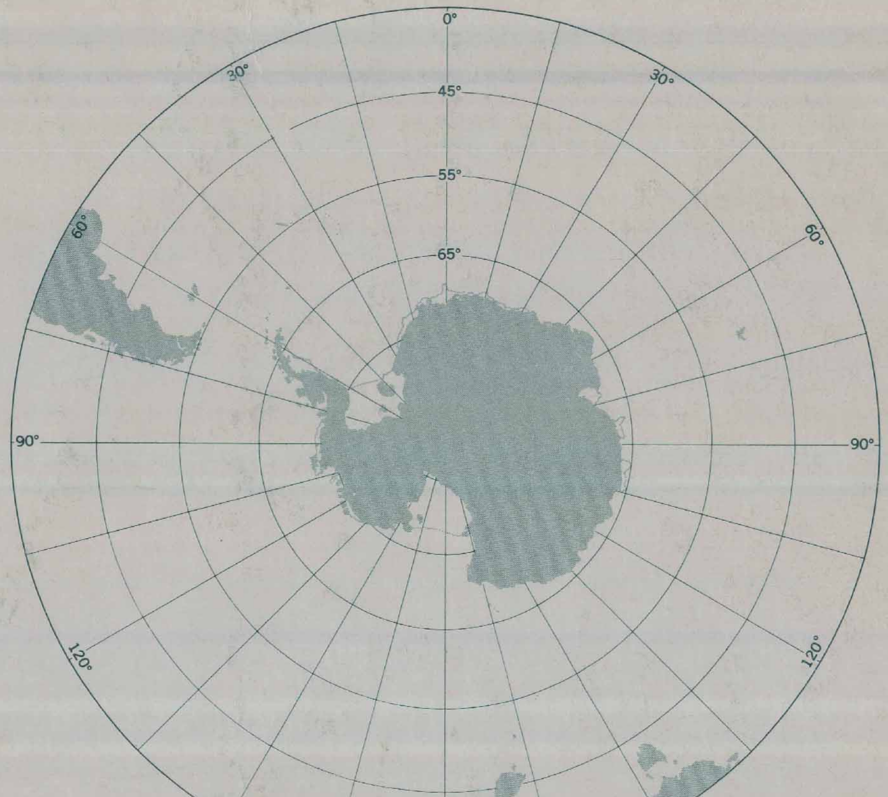
Coastal and Deep-Water Benthic Fishes of the Antarctic

Hugh H. DeWitt



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Coastal and Deep-Water Benthic Fishes of the Antarctic[1]

Hugh H. DeWitt[2]

Introduction

The following account and the accompanying maps have been compiled mainly from a study of the literature through about June of 1970. More will be learned about the distribution of Antarctic fishes when the large amount of material being amassed by post-IGY expeditions into the Antarctic, especially those of the United States and Russia, has been studied. Enough information has accumulated from the collections of the various Antarctic expeditions, beginning with that of Ross with the *Erebus* and *Terror* in 1839–1843, that we have a good picture of the species composition of the bottom forms and can make a number of generalizations about distributions and their patterns. It is also possible to delimit zoogeographic regions based upon distribution and occurrence patterns, and by examining the interrelationships among the species, to indicate the origins of some of the faunas.

History of Antarctic Ichthyogeography

The first fishes collected from Antarctica showed that the waters about the Antarctic continent harbored a fish fauna peculiar to those waters. Yet ideas concerning the limits of the region properly called the Antarctic based upon fish distribution have changed considerably since the last century. Boulenger (1902) implied that the Antarctic region included the islands south of New Zealand. Dollo (1904) used the Antarctic Circle as the limits of the true Antarctic region. Lönnberg (1905) was the first to attempt a definition based upon physical evidence. "A sea where the temperature in the summer from the surface to the bottom in a depth of 1450 m shows a temperature below zero of the Centigrade deserves to be termed 'Antarctic'." Thus he included the Antarctic Peninsula and the South Shetland Islands within the Antarctic Zone, although they extend north of the Antarctic Circle. Lönnberg also recognized that South Georgian fishes had their greatest affinities with Antarctic species to the south rather than with those of Tierra del Fuego to the west. Vaillant (1907) extended the Antarctic region to include areas lying south of the 7°C surface isotherm. This encompassed the Magellanic region of South America and the isolated southern islands (Prince Edward, Crozet, Kerguelen and Macquarie Islands, etc.). Vaillant also differentiated an Antarctic subregion lying within the limits of pack ice, which included South Georgia and the islands to the south along the Scotia Ridge. Regan (1914) defined the Antarctic Zone as including the coasts of Antarctica and the waters and islands lying south of the 6°C surface isotherm, with the possible exception of Macquarie Island.

Regan's conclusions, as far as they went, have agreed well with the additional information accumulated since the *Terra Nova* expedition. The Antarctic Convergence, first described by Meinardus in 1923, was quickly recognized as a major natural boundary and was substituted for the 6°C surface isotherm as the northern limit of the Antarctic Zone (Deacon, 1964). Discussions of the Antarctic Convergence have been given by Sverdrup, *et al.*, 1942; Picard, 1963; Ostapoff, 1965; Gordon, 1967; as well as Deacon, 1964, and others. It is a credit to Regan's acuity that the 6°C isotherm, which he recognized as a region of faunal change, closely follows the Antarctic Convergence, a physical feature of which he had no knowledge. Norman (1938) defined the Antarctic Zone as bounded to the north by the Antarctic Convergence and thought that Macquarie Island was definitely associated with the Antarctic. This general definition has been used, either explicitly or implicitly, by all subsequent workers who have published on the zoogeography of the Antarctic ichthyofauna, but there have been divided opinions about the affinities of the isolated southern islands, which lie on or close to the Convergence.

Regan (1914) further divided the Antarctic Zone into Glacial and Kerguelen districts. The first encompassed the coasts of the continent and neighboring islands, including those of the Scotia Ridge northward to South Georgia. The second comprised the Prince Edward, Crozet, Kerguelen and Heard Islands. Norman (1938) added Macquarie Island to the Kerguelen District. Nybelin (1947, 1951, 1952) removed the Kerguelen–Macquarie District from the Antarctic Zone, and further divided the remaining Antarctic Zone. He recognized a "High Antarctic Region" consisting of the coasts of the continent and nearby islands, and a "Low Antarctic Region" consisting of South Georgia and Shag Rocks. The island chain along the Scotia Ridge between the continent and South Georgia was considered a transitional zone. Within the "High Antarctic," Nybelin identified an "East Antarctic Subregion" extending from the Ross Sea westward about the continent to the Weddell Sea, and a "West Antarctic Subregion" comprising the coasts of the Antarctic Peninsula and nearby islands. Ekman (1953) used Nybelin's scheme in all respects. Andriashev and Tokarev (1958), Marshall (1964), and Andriashev (1965) followed Nybelin except that the Kerguelen–Macquarie Province or Subregion was again considered Antarctic rather than Subantarctic.

Most general reviews of Antarctic zoogeography have identified the Antarctic Convergence or a comparable feature as the northern boundary of the Antarctic Zone. Murphy (1928), possibly following Regan (1914), used the 6°C surface isotherm; Ekman (1953) and Knox (1960) implied that the Antarctic Convergence is the boundary; Broch (1961), Knox (1968) and Hedgpeth (1969a, 1970) all defined the Antarctic Zone as lying south of the Antarctic Convergence. The papers by Ekman (1953), Knox (1960), Broch (1961) and Hedgpeth (1969a) contain execellent lists of references pertaining to southern biogeography.

Limits of Coverage

The fishes which are considered in this review comprise all the benthic species which have been recorded from beneath or to the south of the Antarctic Convergence, together with those species recorded from the isolated islands lying near it. Broch (1961) emphasizes that the Antarctic Convergence is not important in the distributions of deep-sea benthic faunas, and this is confirmed by examples included here. Yet, for shallow-water faunas, the Antarctic Convergence seems to have a marked effect on fish distribution, for there are very few littoral or sublittoral species which are found on both sides of it (Knox, 1968). The great isolation of the various landmasses and their associated shallow waters probably accentuates the distinctness of the Antarctic faunas.

In addition to the benthic fishes, I have included a few pelagic species which belong to families whose members are nearly all benthic. These are *Pleuragramma antarcticum* of the family Nototheniidae, *Melanostigma gelatinosum* and *M. bathium* of the family Zoarcidae and *Cynomacrurus piriei* of the family Macrouridae. The family Nototheniidae, with 31 species described from our area, forms the largest and most characteristic element of the bottom fish fauna. Although several

[1] Contribution No. 31 from the Darling Center for Research, Teaching and Service, University of Maine.
[2] University of Southern California, and University of South Florida, when maps were compiled; text written while at the Darling Center.

species of the family are pelagic during part of their lives, or occasionally leave the bottom to feed, only the one species listed above appears to be wholly pelagic. The family Zoarcidae, known from both hemispheres, contains both shallow and bathyal species. The genus *Melanostigma* contains the only pelagic representatives of the family, with species in both hemispheres. The Macrouridae constitute the most characteristic element of the bottom fish fauna in the deep waters of the world ocean. *Cynomacrurus* is one of the two or three pelagic genera known in the family.

The Antarctic Fish Fauna

Most of the bottom fishes found within our defined area can be divided into two groups, with respect to both habitat and relationships, which we may call deep-sea fishes and coastal fishes, a distinction which can probably be made along any coast fronting the open ocean. The pattern is not a simple one in the Antarctic, however. Andriashev and Tokarev (1958) and Andriashev (1965), among others, have noted the presence within the continental shelf of deep trenches or regions, with depths as great as 1600 m. Adie (1964b) and Rutford, *et al.* (1968) as well as the previous authors, have also noted that the depth of the continental shelf about the continent is unusually deep, averaging between 500 and 750 m, compared to a world average of about 132 m. Adie (1964b) explains these greater depths as a result of the depression of the entire Antarctic continent and associated shelf region due to the weight of accumulated ice during the Pleistocene, and he presents a correlation of shelf depth with latitude. Thus South Georgia, with an average shelf depth of about 120 m, has not been affected, but the South Orkney Islands (shelf depth about 230 m), South Shetland Islands (about 250 m) and the southern part of the Antarctic Peninsula (about 450 m) show increasing depth with increasing latitude. Another result of this depression is that where the shelf is very broad, as in the Ross Sea, the greatest depths are close to the southern shores. The southwest basin in the Ross Sea has depths of slightly more than 1000 m, whereas the shelf edge is everywhere less than 600 m. For this reason, many typical shelf species have the aspect of deep-sea fishes, and have been called pseudoabyssal forms (Andriashev, 1953, 1965; Andriashev and Tokarev, 1958), as distinct from true abyssal forms derived from worldwide deep-sea groups.

The boundaries of the two faunas, then, cannot be described by depth, but rather by topography. About the continent proper, the edge of the continental shelf and the upper part of the continental slope seem to be the areas of overlap of the two faunas. Farther north, along the Scotia Ridge, the few data available to me indicate that a characteristically Antarctic fauna extends to a relatively greater depth, at least with respect to the shelf edge. In the Ross Sea, this change in fauna is probably associated with a relatively rapid change in temperature as one moves from the shelf edge down the continental slope (Countryman and Gsell, 1966; DeWitt, 1970a).

The characteristic Antarctic deep-sea fishes are members of the families Synaphobranchidae, Halosauridae, Brotulidae, and Macrouridae. The first two families comprise elongate, rather eel-like forms found only at bathyal and abyssal depths. Two species, one from each family, are known from our area: *Histiobranchus bathybius* and *Aldrovandia macrochir* (Map 2). The Brotulidae are a diverse group found from shallow near-shore regions of warm seas to the greatest depths for which fishes have been recorded. Most are found at abyssal depths, and are soft-bodied, rather elongate forms, although not eel-like. In the area discussed, one deep-water form has been described, *Bassogigas brucei* (Map 2). The fourth family, the Macrouridae, or rat tails, constitutes the most common and widespread family of fishes found at abyssal depths. Long considered as deep-sea relatives of the codfishes, they are elongate fishes with large heads and eyes, covered with spiny scales, and have a very long and attenuated posterior body with often no recognizable caudal fin. Seven species have been recorded from our area, one of which, *Cynomacrurus piriei*, is pelagic rather than benthic (Map 5).

The remaining species can be called coastal fishes, even though some are known from depths as great as some of the deep-sea forms. The families Moridae, Zoarcidae (eel pouts) and Liparidae (snailfishes), especially, contain numerous species from deep water. As opposed to the truly abyssal forms, the deep-water species of these families are found on continental slopes and submarine ridges. Compare, for example, the distributions of the deep-water groups mentioned above with the species *Lycenchelys* of the family Zoarcidae (Map 3) or with the morids *Antimora rostrata* and *Halargyreus johnsonii* (Map 2; Fig. 1).

The coastal fishes comprise a diverse group, including representatives of fourteen families. Four of these families, the Nototheniidae (Antarctic cods), Harpagiferidae (plunder fishes), Bathydraconidae (dragon fishes) and Channichthyidae (ice fishes), all belonging to the suborder Notothenioidei, may be termed the "...ancient autochthonic elements..." of the fish fauna (Andriashev, 1965). They include over 60% of the species found in the Antarctic and over 90% of the individuals. Table 1 shows the relative numbers, expressed as percents, of the fishes collected with bottom trawls in the area of the Ross Sea during *Eltanin* Cruise 27, in January and February of 1967. These figures include data from hauls made on the continental slope as well as on the shelf of the Ross Sea. The figures would be weighted still more heavily toward the Notothenioids if the slope data were omitted. Note the dominance of the family Nototheniidae, to which nearly 60% of the specimens belong.

TABLE 1. Relative numbers of specimens collected in Blake trawls in the Ross Sea area during *Eltanin* Cruise 27 in 1967. The total number of specimens for all groups is 614.

	Family		Percent
Notothenioidei	Nototheniidae	92.4%	58.0
	Harpagiferidae		10.1
	Bathydraconidae		17.6
	Channichthyidae		6.7
	Muraenolepidae		1.1
	Zoarcidae		2.4
	Rajidae		0.2
	Liparidae		1.8
	Macrouridae		2.1

The Notothenioidei are a diverse group of some 90 to 100 species, of which 75 are known from the Antarctic. At various times they have been placed with the percoid fishes (Regan, 1913; Berg, 1940), in a separate suborder of the perch-like fishes (Greenwood, *et al.*, 1966), or with the blenny-like fishes (Gosline, 1968). Their diversity in habit and structure, together with the uncertainty of their relationships and their southern distribution, argue strongly for an independent evolution in the cool waters of the southern hemisphere throughout at least most of the Tertiary. Their fossil record is too meager for any indication of relationships or prior distribution.

The Nototheniidae form the largest assemblage of Antarctic fishes, and are the most diverse family in structure, habit and distribution (Maps 7–20). Most are rather sedentary bottom forms, which feed on a variety of invertebrates, and in some cases algae (Arnaud and Hureau, 1966). Some have become specifically adapted to living in and about the undersurface of sea ice (*Trematomus borchgrevinki, T. brachysoma* and probably *Pagothenia antarctica*, Maps 18 and 20). One is entirely pelagic in habit (*Pleuragramma antarcticum*, Map 20). *Pleuragramma* has become the dominant midwater fish over the continental shelf, at least in the Ross Sea (DeWitt, 1970a).

The Harpagiferidae (Maps 21–23) are similar to the Nototheniidae in general appearance, but lack scales and have a larger head. All but one have a mental barbel and a rounded hook on the operculum. These are all bottom fishes, most from fairly deep water. The most widespread form, however, *Harpagifer bispinis* in its various subspecies, is often found in the littoral zone under rocks in the more temperate parts of its range (Map 22).

The Bathydraconidae (Maps 24–26) are distinguished by their elongate form and the absence of a spinous anterior dorsal fin. This is a more diverse group than the last, some having only a few scales and others developing pointed snouts and large canine teeth (*Gymnodraco acuticeps*, Map 25). The genus *Bathydraco* includes two species inhabiting abyssal depths: *B. antarcticus* and *B. scotiae.* This family is the most Antarctic of the Notothenioidei, being restricted to the coasts of the continent and the Scotia Ridge northward to South Georgia, with one deep-water species found on the Kerguelen Plateau (Map 26).

The Channichthyidae (Maps 28–31) are recognized by their nearly complete lack of scales, the presence of an anterior spinous dorsal fin, and a very large, often spiny, head with a produced and flattened snout. They also lack an oxygen-carrying pigment in their blood, which appears pale whitish. Most are probably sedentary predators, feeding on fishes and larger crustaceans (Robilliard and Dayton, 1969), but some, such as *Neopagetopsis ionah* and *Champsocephalus gunnari* may be at least partly pelagic.

Andriashev (1965) included the Muraenolepidae as an element of the original, or ancient, fish fauna. It seems better, however, to consider this small and peculiar family of Gadoid fishes (Map 2) as a more recent invader into the Antarctic. The two species found near the continent are taken primarily on the continental slope, and not on the inner, or southern, parts of the continental shelf. This was clearly evident from the trawl catches obtained during *Eltanin* Cruise 27 into the Ross Sea,

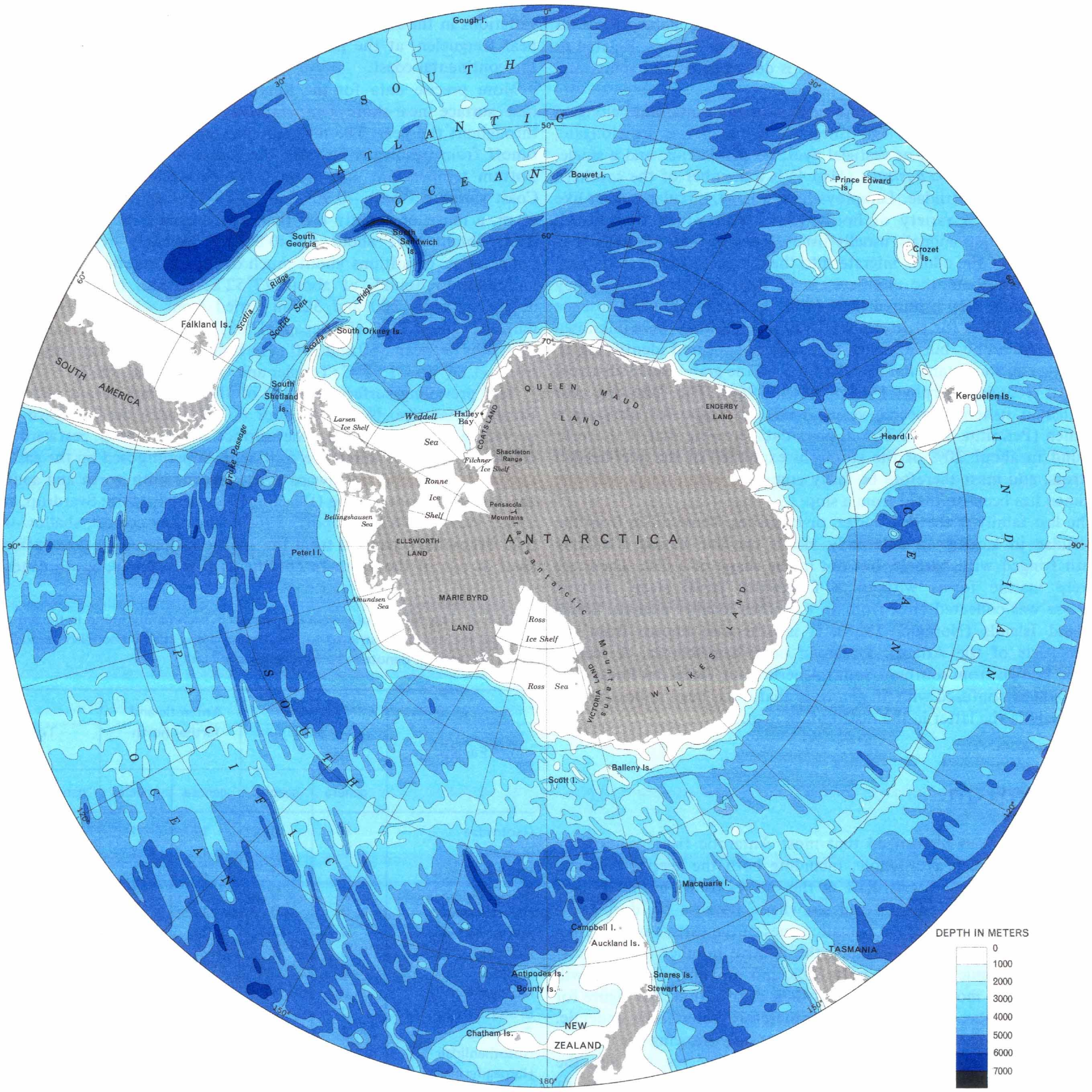
SOUTH ATLANTIC OCEAN
INDIAN OCEAN
SOUTH PACIFIC OCEAN
ANTARCTICA
Gough I.
Bouvet I.
Prince Edward Is.
Crozet Is.
Kerguelen Is.
Heard I.
South Georgia
South Sandwich Is.
Scotia Ridge
Scotia Sea
South Orkney Is.
Falkland Is.
SOUTH AMERICA
South Shetland Is.
Drake Passage
Larsen Ice Shelf
Weddell Sea
Halley Bay
COATS LAND
QUEEN MAUD LAND
ENDERBY LAND
Shackleton Range
Filchner Ice Shelf
Ronne Ice Shelf
Pensacola Mountains
Bellingshausen Sea
ELLSWORTH LAND
Peter I I.
Transantarctic Mountains
Amundsen Sea
MARIE BYRD LAND
Ross Ice Shelf
Ross Sea
VICTORIA LAND
WILKES LAND
Balleny Is.
Scott I.
Macquarie I.
Campbell I.
Auckland Is.
Antipodes Is.
Bounty Is.
Snares Is.
Stewart I.
Chatham Is.
NEW ZEALAND
TASMANIA
0°
30°
50°
60°
70°
90°
120°
150°
180°
DEPTH IN METERS
0
1000
2000
3000
4000
5000
6000
7000

Fig. 1. Submarine topography in the region south of 35°S. (Generalized from a map prepared by Bruce Heezen for Folio 16 of the Antarctic Map Folio Series.)

when 35 tows were made with Blake trawls on the shelf and on the slope to the north. Muraenolepids were taken at five stations, all at the edge of the shelf or on the upper continental slope, at depths ranging between 351 and 1230 m. Such a pattern indicates a species not adapted to the colder Ross Sea bottom water found farther south. I consider the Muraenolepidae to form part of a second group of fishes which have more recently entered the Antarctic Zone.

This second group is much less important in terms of numbers of specimens and species, yet it is formed by a surprisingly diverse array of unrelated forms. With the exception of the Muraenolepidae and Congiopodidae, all belong to families with wide distributions throughout the world. The most important of these groups is the family Zoarcidae or eel pouts (Maps 3 and 4), which may be encountered nearly everywhere in the Antarctic, occasionally in large numbers. These elongate, eel-like fishes may be underrepresented in trawl catches, and perhaps are more common than our data admit, for at times large numbers of them have been taken by means of traps (DeWitt, 1962). They have also evolved into several genera and a number of species endemic to the Antarctic, evidence that they have inhabited the region for a considerable time. *Lycenchelys antarcticus* (Map 3) is found in very deep water, and the genus *Melanostigma* (Map 4) is pelagic.

The next group, in terms of numbers of species, is the Liparidae, or snailfishes (Map 6). These are sedentary, heavy-bodied, gelatinous fishes, sometimes with a ventral sucker. Some are beautifully colored: purple-brown, red-orange, pink, or transparent white. They are found virtually everywhere, in shallow as well as deep water, and from all regions of the continental shelf, though they are nowhere common.

The remaining groups form only a very minor part of the fish fauna, and most do not occur in the southernmost portions of the Antarctic Zone. The Rajidae, or rays (Map 1), extend southward into the region of the Antarctic Peninsula, and some unreported specimens have been taken from the edge of the continental shelf of the Ross Sea (*Eltanin* Cruise 27), but they are best known from South Georgia and the Kerguelen Islands. The Moridae, or moras (Map 2), are close relatives of the codfishes, and penetrate only into the periphery of the Antarctic, reaching South Georgia and the South Sandwich Islands. Two species are recorded: *Antimora rostrata* and *Halargyreus johnsonii*, both well known from the North Atlantic. The Gadidae, or true cods (Map 2) are represented by one species, *Micromesistius australis*, which migrates during the summer into the Scotia Sea as far south as Clarence and Elephant Islands off the tip of the Antarctic Peninsula. In the Antarctic it behaves as a pelagic fish, feeding upon krill (Merrett, 1963; Permitin, 1970), but off South America, it is considered demersal. The flatfish family Bothidae, or lefteye flounders (Map 27), also penetrate only into the peripheral parts of the Antarctic. The records for *Mancopsetta maculata* refer to bottom catches of metamorphosed individuals; those for *M. slavae* are based upon small pelagic specimens which had metamorphosed but not migrated to the ocean floor. Since no adult or bottom-living flatfishes have been taken on the Antarctic continental shelf, it is possible that the pelagic records represent specimens which had strayed far south of their normal range. It may be that the specimens described as *M. slavae* are the young of a species previously described from farther north, perhaps *M. maculata*. Unfortunately, we

know very little about these southern flatfishes. The Congiopodidae, variously called horsefishes or pigfishes, etc. (Map 6), are a small family of mainly south-temperate distribution. One species, *Zanclorhynchus spinifer*, is endemic to the Kerguelen and Macquarie Islands. Related to the rockfishes and sculpins, this species is deep-bodied and spiny, and lacks scales.

The two remaining families represented in the Antarctic belong to the class Agnatha, the jawless fishes. All living species are elongate, eel-like fishes with small or vestigial eyes, no paired fins, and a single, median nostril. *Geotria australis* (Map 1) is a member of the southern lamprey family Geotriidae. Lampreys have a large, circular, sucker-like mouth, set with a variety of horny teeth, with which they attach themselves to other animals, usually fishes. Much of their life is spent in fresh water, but the adults migrate into the ocean. Unfortunately, very little is known about the marine stage of their life history, and they have only rarely been captured there (note the nearly complete absence of marine localities for *G. australis*). Until recently they were unknown from the Antarctic, but in 1964 two reports appeared identifying *G. australis* as an important item in the food of the gray-headed albatross at South Georgia (Murphy, 1964; Tickell, 1964). The following year the Russian fisheries research vessel *Academic Knipovich* obtained a specimen (Permitin, 1966). Tickell gives data showing that *G. australis* is found in about 20% of the stomachs examined of the gray-headed albatross, and must therefore be fairly common, even though only one specimen has been captured from a ship.

The last family is the Myxinidae, or hagfishes. These differ from the Geotriidae in lacking an externally visible eye and having a sucking mouth fringed with barbels, but not in the shape of a disc. These are entirely marine forms without a freshwater larval stage. *Myxine glutinosa* was collected once from an unknown locality near the South Shetland Islands (Norman, 1938). It is otherwise known from the cooler parts of the Atlantic Ocean in both hemispheres. A second species, known from southern South America and Tierra del Fuego, has so often been confused with *M. glutinosa* that it has been impossible for me to include the latter in the distribution maps.

Endemism

It has long been recognized that most Antarctic fish species exist nowhere else. Taken as a whole, including both the deep-sea, coastal and associated pelagic forms, 83% of the species found in our defined region have not been encountered elsewhere. Because the deep sea is less affected by the latitudinal climatic zones of the earth's surface than are the surface and coastal waters, the relative number of Antarctic deep-water endemic species is only 50%, and probably the figure will become lower as more is learned about their distribution. The figure for the species of the coastal families is therefore about 86% endemic. Table 2 presents the data for each family, not only showing the number and percents of endemic and more widespread species, but also the importance of the Notothenioidei, which account for 79 species, or more than 65% of the total fish fauna. Table 2 also summarizes similar data for genera. Note again that over 50% of the genera are found in the four notothenioid families. More important, about 86% of the genera endemic to the Antarctic belong within the Notothenioidei.

The causes of the unusually high endemic percentages are easily observed. The Antarctic continent and its associated islands are isolated from the rest of the world geographically, environmentally, and through prevailing ocean currents. South America, the closest landmass to the north, is approximately 500 nautical miles from the South Shetland Islands off the northwest coast of the Antarctic Peninsula. New Zealand, Tasmania and Africa are much more distant. In every instance a deep ocean separates Antarctica from its northern neighbors (Fig. 1). Although a submarine ridge connects South America (Tierra del Fuego) with the Antarctic Peninsula, in three places the ridge falls away to depths over 3000 m. A much less well-defined ridge system extends northward toward New Zealand and Tasmania.

The environment of Antarctica and the associated region lying south of or near the Antarctic Convergence is more limiting than those of more northerly regions to a significant degree. Not only are temperatures lower in the Antarctic Zone, as would be expected, but they are more uniformly low. Average surface temperatures near Tierra del Fuego in February (the southern summer) range between about 8° and 10°C; corresponding winter (August) temperatures are about 3° to 6°C. The average annual variation is therefore about four to five degrees. South Georgia, situated at about 54°S, the same as Tierra del Fuego, has average summer and winter temperatures between 1.7° and 3.1°C, and −1.1° and 0.3°C, respectively. Similar temperatures for other regions are: Antarctic Peninsula, −1.1° to 0.3°C and below −1.1°C; coasts of the remainder of Antarctica, less than −1.1°C at all times. The Kerguelen Islands, which lie slightly north of the Antarctic Convergence at about 49°S, have average summer temperatures of just over 4.4°C and winter temperatures between 1.7° and 3.1°C (temperature data from U.S. Navy Hydrographic Office, 1957). The average annual variations in the Antarctic Zone therefore range from about 1° to 3°C near Kerguelen, at the periphery, to almost none at all along most of the continental coast.

More precise data for the Kerguelen Islands (Hureau, 1970) show that surface near-shore temperatures vary between 1.5° and 7.7°C throughout the year. The high summer temperatures are caused by the runoff from freshwater streams, the waters of which may reach 14°C. Bottom temperature data from Géologie Archipelago on the Adélie Coast varied between −0.90° and −1.88°C at depths of 30 and about 60 m, a range of slightly less than one degree (Hureau, 1970). These data, obtained at about 66°40′S, are probably representative of temperature conditions about much of East Antarctica. Farther south in McMurdo Sound, at about 77°52′S, bottom temperatures from depths between 200 and 300 m varied from −1.81° to −2.02°C, a range of only 0.21°C (Littlepage, 1965). The annual temperature range at depths between 560 and 590 m in McMurdo Sound was only 0.07°C, from −1.86° to −1.93°C (Tressler and Ommundsen, 1962).

The prevailing surface currents of the southern oceans also act to isolate Antarctica. North of about 65° S, under the influence of the prevailing westerly winds, the surface waters move eastward in a clockwise direction about the continent. Superimposed on the eastward cycling is a general northward drift, present both north and south of the Antarctic Convergence (Deacon, 1937, 1964, 1965; Sverdrup, *et al.*, 1942; Picard, 1963; Ostapoff, 1965). Thus any coastal, shallow-water fish, becoming separated from the southern portion of the continental shelf of one of the southern continents (for example, South America), would tend to drift northeastward, away from Antarctica. This is most important for larvae or juveniles which, sometimes leaving the bottom to feed on plankton, have the greatest tendency to drift away from shelf regions.

TABLE 2. The number of genera and species in each family found in the Antarctic, showing the number restricted to the Antarctic and the number also found farther north. An asterisk denotes a bathyal or abyssal family.

Family	Antarctic only		Antarctic and farther north		Totals	
	genera	species	genera	species	genera	species
Geotriidae	0	0	1	1	1	1
Myxinidae	0	0	1	1	1	1
Rajidae	0	3	2	1	2	4
*Synaphobranchidae	0	0	1	1	1	1
*Halosauridae	0	0	1	1	1	1
Muraenolepidae	0	2	1	1	1	3
Moridae	0	0	2	2	2	2
Gadidae	0	0	1	1	1	1
*Macrouridae	0	4	5	3	5	7
*Brotulidae	0	1	1	0	1	1
Zoarcidae	3	8	3	3	6	11
Nototheniidae	4	31	2	3	6	34
Harpagiferidae	4	14	1	1	5	15
Bathydraconidae	8	15	0	0	8	15
Channichthyidae	9	15	1	0	10	15
Congiopodidae	1	1	0	0	1	1
Liparidae	0	5	3	0	3	5
Bothidae	0	1	1	1	1	2
TOTALS						
All families	29	100	27	20	56	120
All but abyssal families		95		15		110

The unusually high proportion of endemic genera and species in the Antarctic fish fauna indicates that the region has been isolated both physically and climatically for a long time. Recent evidences of continental drift demonstrate that Antarctica was clearly a part of the supercontinent of Gondwanaland (Adie, 1963, 1970; Colbert, 1970; Craddock, 1970; Denton, *et al.*, 1970; Dietz and Sproll, 1970; Frakes and Crowell, 1970; Hamilton, 1963; Hayes and Pitman, 1970; King, 1958; Schopf, 1970; Wilson, 1963). While there is some question as to timing of the events, the evidence indicates that Antarctica was last contiguous with Australia, and that the final separation occurred in the Cretaceous or very early Cenozoic. Antarctica was probably close to its present position in the early Cenozoic and has moved only slightly since that time; the major movement has been that of Australia, to the north. Thus isolation has been a factor for at least 65 million years.

In a review of island ages and endemism, Briggs (1966) concluded that the highly endemic faunas of the South Atlantic and Antarctic islands were a result of less severe temperature changes during the Pliocene and Pleistocene, and that the southern waters of all oceans had been cold for a long time. There is now considerable evidence that the Antarctic climate has been cold for a much greater length of time than previously thought. Several workers believe that large-scale glaciation existed from three to seven million years ago (Craddock, 1970; Denton, *et al.*, 1970; Hays, 1970; Rutford, *et al.*, 1968), that is, beginning in late Miocene or Pliocene times. Other evidence, both marine and continental, indicates that some glaciation was present much earlier. Denton, *et al.* (1970) postulate local glaciation as early as the Eocene. Tanner (1968) believes that the ice sheet developed more than 24 million years ago, and that the development may have required a few tens of millions of years. This means that one-third to one-half of the Tertiary may have been a period of large-scale glaciation. Le Masurier (1970) suggests that an ice sheet existed as early as the Eocene.

The glacial history is corroborated by fossil faunas and floras, which show that by late Oligocene to early Miocene times the climate had cooled considerably from earlier times, although there is also some evidence for temperate biotas in the Antarctic Peninsula and the Ross Sea area as late as the early Miocene (Adie, 1964a, 1970; Brooks, 1951; Denton, *et al.*, 1970; Durham, 1952, 1959; Harris, 1950; MacGinitie, 1958). Kennett and Fillon (1970), and Harris (1950) find evidence of cooling during Eocene and Oligocene times, with subsequent warming during early and middle Miocene, which perhaps explains the presence of temperate biotas during the latter epoch. The presence of cool southern oceans as early as the Eocene allowed ample time for the development of a peculiar cold-adapted fauna. During the early two-thirds of the Miocene this cool-water fauna was probably restricted to the immediate coasts of the Antarctic continent, and may not have been present along part of the Antarctic Peninsula (Durham, 1959; Emiliani, 1954). The cooling which resulted in the extreme Pliocene and Pleistocene glaciations occurred in the late Miocene and is corroborated by the appearance of cold-water faunas in New Zealand during late Miocene and Pliocene times (Adie, 1970; Brooks, 1951; Kennett, 1967, 1968; Kennett and Fillon, 1970; Kennett, *et al.*, 1971; Fleming, 1962, 1963). The cooling was associated with a significant drop in sea level, indicative of large-scale glaciation. The fall in temperature of polar water was probably on the order of 7° to 8° C (Brooks, 1951; Emiliani, 1954, 1961).

During warm periods (Eocene and earlier, and probably early Miocene) the Antarctic Convergence probably retreated far to the south or perhaps did not exist (Emiliani, 1954). Kennett (1968), however, presents evidence that during the Pliocene and the end of the Miocene the Convergence zone moved northward to latitudes of the present North Island of New Zealand (39° S). With post-Pleistocene warming, the Convergence has moved south again to its present position, a total of 18° of latitude, or about 2100 km. If the Antarctic Convergence did migrate northward as far as New Zealand, the spread of the cold water faunas mentioned above would have been greatly facilitated.

In summary, there is ample evidence that the Antarctic continent has been isolated and bathed by a cool ocean for a considerable period of time, perhaps 40 million years or more. Since most of the modern percoid ("spiny-rayed") fish families for which there are fossil records first appear in the Eocene (Romer, 1966), it is reasonable to conclude that 40 million years is adequate for the development of the five families which comprise the suborder Notothenioidei, a group which almost certainly originated on the shores of the Antarctic continent and which now dominates the fish fauna there. In addition, for a shallow-water organism to colonize the Antarctic from the north, it must pass through adverse ocean currents, a drop in temperature to or toward the minimal extreme, and long distances over deep water. It is therefore not strange that the Antarctic fish fauna is characterized by the absence of northern types, the dominance of peculiar groups, very high percentages of endemic genera and species, and one endemic family (Bathydraconidae). Regan's statement (1914), based upon the peculiarities of Antarctic fishes, that "...Antarctica may have long been isolated and that its coasts may have been washed by a cold sea for a long time, probably throughout the Tertiary Period..." has certainly been demonstrated in large measure, even though at the time he believed he was presenting evidence against continental drift.

Patterns of Distribution

Antarctic demersal fishes can be arbitrarily divided into two groups: those found only within our defined region (Antarctic endemics) and those found as well in regions farther north. If we look first at the latter group, we can further identify species which are found primarily in more northern regions and which penetrate to varying degrees into the Antarctic Zone. These are species which, in most cases certainly, and probably in the remainder, evolved outside the Antarctic and have moved southward in relatively recent times, probably since the Pleistocene.

Table 3 lists, of these species, those found on continental slopes and shelves, together with the numbers of the maps on which their distributions are plotted. It will be noted that all species but one have probably entered the Antarctic via South Georgia and the Scotia Ridge (Fig. 1). Ten of the fourteen species have been taken in the vicinity of South Georgia, and three of the remaining four are known from the South Shetland or South Sandwich Islands, part of the Scotia Ridge system. The one exception is *Notothenia microlepidota,* which is found only in the New Zealand region and Macquarie Island to the south.

Only three species have reached the coastal waters of the Antarctic continent elsewhere than the peninsular region, and these three species are all pelagic, at least in the Antarctic portions of their ranges. *Melanostigma gelatinosum* and *Cynomacrurus piriei* are wholly pelagic, the former apparently restricted to waters adjacent to continents or submarine ridges, while the latter is an open ocean inhabitant. The distributions of these two species seem to reflect their probable derivation. *Melanostigma* belongs to the family Zoarcidae, a group which is known from both hemispheres and from intertidal regions down to depths of close to 5000 m. Nearly all species are benthic, and even the deepest-living species are found on or adjacent to continental slopes and submarine ridges. Although pelagic in habit, *Melanostigma* seems to be similarly restricted in distribution. *Cynomacrurus piriei,* on the other hand, is broadly distributed in the South Atlantic and probably will be eventually found throughout most of the other southern oceans (note the record east of the Kerguelen Islands). Its family, the Macrouridae, is nearly cosmopolitan in distribution, forming the characteristic element of the abyssal fauna of all oceans except the Arctic (Andriashev, 1954; Grey, 1956).

Notothenia magellanica has been known until recently as an inhabitant of shallow, rocky, coastal waters, mostly in protected bays and channels, living amongst kelp. Its essentially circumpolar distribution in the Subantarctic and peripheral Antarctic has probably been attained by means of its pelagic juvenile stage, which has been collected at the surface from oceanic waters (Hart, 1946). Now, however, it has been taken at South Georgia and the southern Scotia Sea near the South Orkney Islands, as well as in the Ross Sea (DeWitt, 1970b; Permitin, 1966, 1969, 1970). In these regions it behaves as a pelagic schooling fish. Other species which undergo similar behavioral changes in the southern parts of their ranges are *Micromesistius australis* and *Dissostichus eleginoides.* All three assume a pelagic mode of life in order to feed upon the rich concentrations of krill (*Euphausia*) which appear during the Antarctic summer. *M. australis* is known to make yearly migrations from the continental shelf off Patagonia into the Scotia Sea and back again. It is probable that the same is true for *N. magellanica* which is known to spawn in the Subantarctic and at Kerguelen, and for *D. eleginoides,* although little is known about the life history of the latter (Hart, 1946; Merrett, 1963; Permitin, 1970).

The appearance of *Breviraja griseocauda* off the South Shetland Islands as well as on the continental shelf off Patagonia is surprising since rays are normally considered as strictly benthic in habit, not exhibiting tendencies toward pelagic behavior. Permitin (1970), however, has found krill in the stomachs of 23% of young *Raja georgiana,* good evidence that they leave the bottom to feed. Probably *B. griseocauda* has extended its range through the agency of pelagic juveniles. *Mancopsetta maculata* also has probably attained its broad and disjunct distribution by means of pelagic young since nearly all species of the family Bothidae for which life histories are known pass through a pelagic juvenile stage (Norman, 1934; Bertin and Arambourg, 1958).

On the other hand, it is more likely that *Antimora rostrata, Halargyreus johnsonii* and *Lycodapus australis* entered the Antarctic Zone along the bottom via the Scotia Ridge (Fig. 1). The first two have

TABLE 3. Shelf, slope, and related fishes which have penetrated into the Antarctic during the recent past from the Subantarctic.

Species	Map No.
Geotria australis	1
Myxine glutinosa	(not mapped)
Breviraja griseocauda	1
Antimora rostrata	2
Halargyreus johnsonii	2
Micromesistius australis	2
Coelorhynchus marinii	5
Cynomacrurus piriei	5
Notothenia magellanica	10
Notothenia microlepidota	11
Dissostichus eleginoides	19
Melanostigma gelatinosum	4
Melanostigma bathium	4
Lycodapus australis	3
Mancopsetta maculata	27

been captured from deep water, down to 2600 and 1300 m, respectively, and they may have followed the ridge westward from Tierra del Fuego or the Burdwood Bank to South Georgia. Since *A. rostrata* is known also from several widely spaced localities about the continent (always on a ridge, however), some other dispersal mechanism is indicated as well. The genus *Lycodapus* is best known from the North Pacific Ocean, *L. australis* being the sole southern species (Norman, 1966; Clemens and Wilby, 1961). Probably representatives of the genus will eventually be found along the west coasts of Central and South America in rather deep water. Because of the generally northern distribution of the genus it is probable that *L. australis* has entered the Antarctic from the Magellanic region along the Scotia Ridge.

In addition to the above, there are four deep-water, or abyssal, species which penetrate into the peripheral parts of our region: *Histiobranchus bathybius* (Map 2), *Aldrovandia macrochir* (Map 2), *Nematonurus armatus* (Map 5) and *Lionurus filicauda* (Map 5). The first three are known from widely scattered localities in both hemispheres. The last has been taken from the southern parts of the three major oceans. There is little doubt that they have originated outside the Antarctic, and their presence in our defined region raises a question as to the reality of a distinct Antarctic region at abyssal depths. Unfortunately, very little is known about abyssal fishes in our region.

There remain two species which, from their distributions, possibly moved northward from the Antarctic. These are *Muraenolepis microps* (Map 2) and *Harpagifer bispinis* (Map 22). The first has been collected from rather widely separated localities along the Scotia Ridge and off the coasts of the continent, and is also known from the southern Magellanic region. Probably *M. microps* is Circumantarctic, and this broad distribution, coupled with the restricted Subantarctic range, indicates an Antarctic origin. *Harpagifer bispinis*, in its several subspecies, is known from many localities along the Scotia Ridge and from many of the Antarctic islands as well as the Magellanic region. Since the family Harpagiferidae is entirely Antarctic except for this species, I postulate an origin in the Antarctic Peninsula–Scotia Ridge region. Probably dispersal was eastward about the continent to the Antarctic islands and thence to South America. This route is consistent with the general circulation patterns of the surface waters as outlined earlier, and is paralleled by the distribution patterns of other groups of species.

ANTARCTIC ENDEMIC SPECIES

Antarctic endemics may be arbitrarily divided into a number of distributional groups: bathyal and abyssal species, island endemics, Circumantarctic species, West Antarctic species, and East Antarctic species.

Bathyal and abyssal species. This group includes species found at depths greater than 2000 m, although some have been taken from shallower areas as well. Most have been captured only rarely (two species are known from a single specimen each), and only one, *Chalinura whitsoni*, can be considered at all "common." Table 4 lists these species together with the numbers of the maps on which their distributions have been plotted and their known depth ranges. Nearly all appear to be continental slope or near slope forms, with only two species, *Chalinura whitsoni* and *Nematonurus lecointei* found in mid-ocean regions and even these, it would seem, tend to follow features such as the Mid-Atlantic Ridge (Fig. 1). *Bassogigas brucei* and *Lycenchelys antarcticus* are both known from deep water just south of, or at the base of, the Scotia Ridge. The remainder are from the Antarctic continental slope. Since so little deep-water trawling has been done in the southern oceans it is premature to say that some of these species will not be found from more northerly localities. This is particularly true for *Bassogigas brucei* and *Lycenchelys antarcticus*. I would expect that the two Bathydracos are restricted to slopes or ridges (compare with Fig. 1), and that they are more widely distributed (unpublished *Eltanin* data confirm this). I also suspect that the Antarctic faunal boundary for benthic abyssal forms will be found to be close to the base of the continental slope, with perhaps northward extensions along the major submarine ridges.

Island endemics. This heading includes fishes which are found exclusively at one or more of the isolated islands and at South Georgia and the South Sandwich Islands. Table 5 lists the species according to island or island groups, together with their respective map numbers. It should be noted that South Georgia has been sampled most extensively, with Kerguelen next, and this may explain, at least in part, why they have such relatively large numbers of endemic species. The other islands are very poorly sampled, with the possible exception of Macquarie. Recent trawling by the *Eltanin* shows that our knowledge about the fishes of Macquarie is very incomplete, but the material collected is as yet unworked.

Deferring until later a discussion of the relationships of these island faunas to other regions, one still should note the preponderance of the Notothenioidei at nearly all the islands, and especially at the two that are best known. Note also that whereas four of the species from South Georgia belong to the families Liparidae and Zoarcidae, these groups are not found at Kerguelen. The absence of the Zoarcidae at Kerguelen is probably related to the benthic habit and lack of a pelagic period in the lives of nearly all species, and to their tendency to remain associated with continental slopes and associated ridges. The same is probably true for the Liparidae, for they are also primarily benthic and no young have been collected in plankton tows, although a few are partly or entirely pelagic as adults (Burke, 1930). Some species of the genus *Liparis* have been found floating with algae, and perhaps *L. steineni* was rafted to South Georgia in a similar manner. *Paraliparis*, *Careproctus* and *Lycenchelys* are deep-water genera and have probably moved south along the Scotia Ridge. The two deepest dwelling genera, *Paraliparis* and *Lycenchelys* are also found about the Antarctic continent whereas *Careproctus* and the much shallower *Liparis* are absent there, which also indicates the Scotia Ridge as the migratory route.

Circumantarctic species. Many workers have emphasized that the Antarctic fauna is largely circumpolar in distribution. Fishes seem to be no exception, and a significant number are either known to have, or can be assumed to have, circumpolar distributions. Several species are known from so few localities that they are included here only on the assumption that eventually they will be found elsewhere about the continent. In particular, if a species has been taken once from the region of the Antarctic Peninsula and again from somewhere along the coasts of East Antarctica, from the Ross Sea to the Weddell Sea, it is considered Circumantarctic. I am certain that with further sampling about the continent many more species will come to be placed in this category.

Twenty-five species, or 20.8% of the fishes discussed here, are presently considered circumpolar (Table 6). The distributions for all, however, show one important blank area: the southern and western parts of the Weddell Sea. This is perhaps the most inaccessible region of the Antarctic, and I believe that all of the species grouped here do occur there, but trawling has simply not been possible. The Bellingshausen and Amundsen Seas are two other regions difficult of access, and many species are unknown there for probably the same reason. The species for which evidence is weakest are *Aethotaxis mitopteryx*, *Pogonophryne marmoratus*, *Austrolycichthys concolor* and *A. brachycephalus*. The first three have been taken from the peninsular region and one locality on the coast of East Antarctica; the fourth has been collected in two general regions of East Antarctica in addition to the peninsular region. Note that although several species of *Trematomus* are Circumantarctic, only three species of *Notothenia* are included with this group. One of the latter, *N. rossii*, is circumpolar only in the sense that it occurs at some of the isolated Antarctic islands (in this sense *N. magellanica* is even more nearly circumpolar). *Notothenia neglecta* has been found from South Georgia south and westward to the Adélie Coast. I am least sure of the circumpolar distribution of this species, however, since it is a shallow inhabitant and is normally easily caught. The distribution pattern of *N. kempi* is rather peculiar in that it is found at shallow and peripheral localities about the continent, for example, Scott and Balleny Islands.

East and West regions. Nybelin (1947) first divided the Antarctic continent into two subregions on the basis of fish distributions. The limits separating the two were the Weddell and Ross Seas (Nybelin, 1952). West Antarctica included the Antarctic Peninsula and the areas on the peninsular sides of the two seas. East Antarctica made up the remainder of the continent, including the two seas. Unfortunately the Weddell Sea and the coast between the Antarctic Peninsula and the Ross Sea are very little known, and it is not possible to state precisely where the boundaries lie, if such distinct boundaries do, in fact, exist. It is likely, as I have stated earlier, that a number of species presently known only from East Antarctica will prove to have circumpolar distributions. As Tables 7 and 8 show, however, there are a great number of species found solely in one or the other of the regions, and I believe that this is a reflection of real differences in habitat. Andriashev (1965) pointed out that as one moves from East Antarctica to South Georgia the size and extent of the continental shelf decreases, the environmental conditions become less severe, and the number of species decreases. The difference in areal extent of the shelf is obvious from any chart of the Antarctic; the numbers of species found in each of the regions can be obtained from the several tables of distribution. That the environment becomes less severe is not as obvious. Data on water temperatures from the Ross Sea, McMurdo Sound and the Adélie Coast, however, show clearly that bottom temperatures close to the continent are always less than 0° C, and are normally −1.0° C or less (Tressler and Ommundsen, 1962; Littlepage, 1965; Countryman and Gsell, 1966; Jacobs and Amos, 1967; Hureau, 1970). Throughout most of the Ross Sea, bottom temperatures are less than −1.0°C, and only at the outer edge of the shelf may they rise to 0° or 0.5°C. On the other hand, summer temperatures in the peninsular region may vary from less than −1.5°C

in the deeper parts of the Bransfield Strait to above 1°C southwest of the Strait. The bottom along the whole of the northwest edge may be warmer than 0° C, including the waters surrounding the South Shetland Islands (Friedman, 1964). The ocean is free of ice for significantly longer periods during the summer (U.S. Navy Hydrographic Office, 1957), and much of the shelf about the Antarctic Peninsula and the nearby islands is less than 200 m in depth, considerably shallower than nearly all of the Ross Sea and much of the remainder of the Antarctic continental shelf.

Characteristic of West Antarctica are several species of *Notothenia,* three of which are found only there and at South Georgia. Two species, *N. neglecta* and *N. kempi,* have also been found in East Antarctica. Note, however, that the latter is found in peripheral areas where there are shallow shelves (such as at Scott Island) or warmer temperatures (edge of the Antarctic continental shelf). Abe and Arai (1968) have found *N. larseni* at the Balleny Islands, but their paper was seen too late for the locality to be included in the distribution maps. The fishes known from these islands are therefore *Trematomus loennbergii, T. scotti* and *Notothenia larseni,* all species which are found in West Antarctica, and the combination gives to the Balleny Islands the character of the peninsular region. *Notothenia kempi* is the only species so far recorded from Scott Island, and again the relationship is with the Antarctic Peninsula fishes. It is curious that islands so close to the eastern portion of the continent should harbor only species which are also found about the Antarctic Peninsula, and that the large East Antarctic endemic fauna is absent. It would be worth investigating whether the island populations of the two *Trematomus* species are more similar to those at the Peninsula or to those in the Ross Sea to the south.

The most characteristic genus of East Antarctica is *Trematomus,* of which there are five endemic species. There are also several species of the genera *Pogonophryne* and *Bathydraco* which have been captured nowhere else. Several of these distributions will be extended, however, when current work on *Eltanin* collections is completed. Many of the species may be truly restricted to East Antarctica by reason of the differences mentioned above. It will be interesting to eventually determine the boundaries, or more likely the areas of intermingling, of the two faunal regions.

DEPTH DISTRIBUTIONS

Nybelin (1947) was the first to attempt a classification based upon depth distribution. He recognized four major patterns: (1) Stenobath shallow-water species from the shore down to about 40–60 m; (2) Eurybath shallow-water species with an upper limit of 0–40 m; (3) species from intermediary depths; (4) deep-water species. Andriashev (1965) reviewed this scheme and emphasized that the depth patterns usual for the world were not applicable to the Antarctic because of the presence of ice in littoral areas and the greater depth of much of the continental shelf about the continent. Andriashev was the first to note the suppression of shallow-living forms and to show that the greatest numbers of species were found between 200 and 600 m. He also pointed out that some species are taken at depths which would ordinarily be considered bathyal but which, in the Antarctic, are all from the continental shelf. He noted that many species tend to have large depth ranges, encompassing 500 to 700 m.

During *Eltanin* Cruise 22 I independently came to a similar conclusion concerning the depths at which the greatest number of species occurred; the suppression of numbers of shallow-living forms was made even more apparent during Cruise 27 into the Ross Sea. Not only were the numbers of species obtained between 300 and 600 m greater than at shallower depths, but the numbers were greater to depths between 800 and 900 m. More striking was the difference in species composition between the near-shore shallow collections and those taken on the floor of the continental shelf. The dominant shallow species were almost never taken with species inhabiting the shelf floor.

While gathering the data for the distribution maps presented here, I noticed that some of the species which I recognized as shallow near-shore fishes had considerable depth ranges, often overlapping those of species found on the shelf floor. It occurred to me that the near-shore species were not necessarily shallow inhabitants, but were species living on the "first slope" (Hart, 1946) extending from the shore to the continental shelf. The broad depth distributions are explained by the depression of the Antarctic continent and the associated shelf, causing the greatest shelf depths to be adjacent to the continent. For example, the deepest parts of the Ross Sea, about 1000 m, are found in the southwest corner only a few miles from Ross Island and McMurdo Sound. The sea floor drops rapidly to relatively great depths close to the continent. The best example of this distribution type is *Trematomus bernacchii,* which lives at depths from 1 to 732 m, yet is closely associated with the continental shores (Map 17). We never obtained *T. bernacchii* in the Ross Sea except in McMurdo Sound and adjacent to Franklin Island.

Grouping all near-shore, first-slope species together makes sense biologically, but it unites species with widely varying depth ranges. Much of this is explained by the varying depths of the continental shelves in the Antarctic. Those species inhabiting shelves and upper-slope regions reflect the depth differences more strongly. Compare, for example, *Notothenia mizops* from Kerguelen (20–219 m), *Trematomus vicarius* from South Georgia (20–235 m), and *T. loennbergii* from the Antarctic continent (65–832 m). All of these are first-slope (sublittoral) and continental-shelf forms.

In general, the following groups can be recognized, excluding non-benthic and wholly pelagic species: (1) near-shore (sublittoral) species (Table 9); (2) near-shore (sublittoral) onto continental shelf species (Table 10); (3) continental-shelf and upper-continental-slope species (Table 11); (4) continental-slope (bathyal) and abyssal species (Table 12). These groups are comparable to those distinguished by Nybelin, but emphasize the relationships to bottom topography.

The two largest groups (Tables 11 and 12) overlap broadly on the continental shelves and together cause the preponderance of species found there. This is shown graphically in Figure 2. In East Antarctica the greatest numbers occur between 250 and 600 m, with the largest changes falling on each side of the region between 350 and 550 m. The increase in species with depth is much less in West Antarctica (the fall in species between 50 and 200 m is probably due to lack of sampling at those depths), and peak abundances occur between 150 and 400 m. *Harpagifer bispinis,* a species considered truly intertidal, makes its appearance in West Antarctica. The curve for South Georgia shows a significantly larger number of shallow-living species, a lesser increase in numbers of species with depth, and the depth of peak abundance is the shallowest. In addition to *Harpagifer bispinis,* two other intertidal species are found at South Georgia: *Notothenia angustifrons* and *Liparis steineni.*

Further indication that the depth of the continental shelf affects the depth ranges of many species arises from comparisons between the ranges from East and West Antarctica for species occurring in both. Most species, but not all, are found in significantly deeper water in East Antarctica (Table 13).

Interrelationships of Regions

The only real controversy that has arisen regarding the affinities of zoogeographical regions is whether the isolated Antarctic islands (Kerguelen–Macquarie District) should be considered Antarctic or Subantarctic. This district includes the Prince Edward, Crozet, Kerguelen, Heard, McDonald and Macquarie Islands. Nybelin (1947, 1951, 1952) considered these islands Subantarctic because no species found near them could be said to exist in an identical form in the true Antarctic (South Georgia). Those species which were found in identical form elsewhere, such as *Notothenia magellanica* and *Mancopsetta maculata,* were primarily Subantarctic. Nybelin did admit, however, that the closest relations of most species were found at South Georgia and the West Antarctic Subregion. Andriashev (1965) reviewed the evidence and concluded that the relationship was mainly Antarctic: five species also at South Georgia in some form, and six others, showed relationships with West Antarctica. I have examined the relationships of the fishes of the Kerguelen Islands in some detail (DeWitt, 1971) and

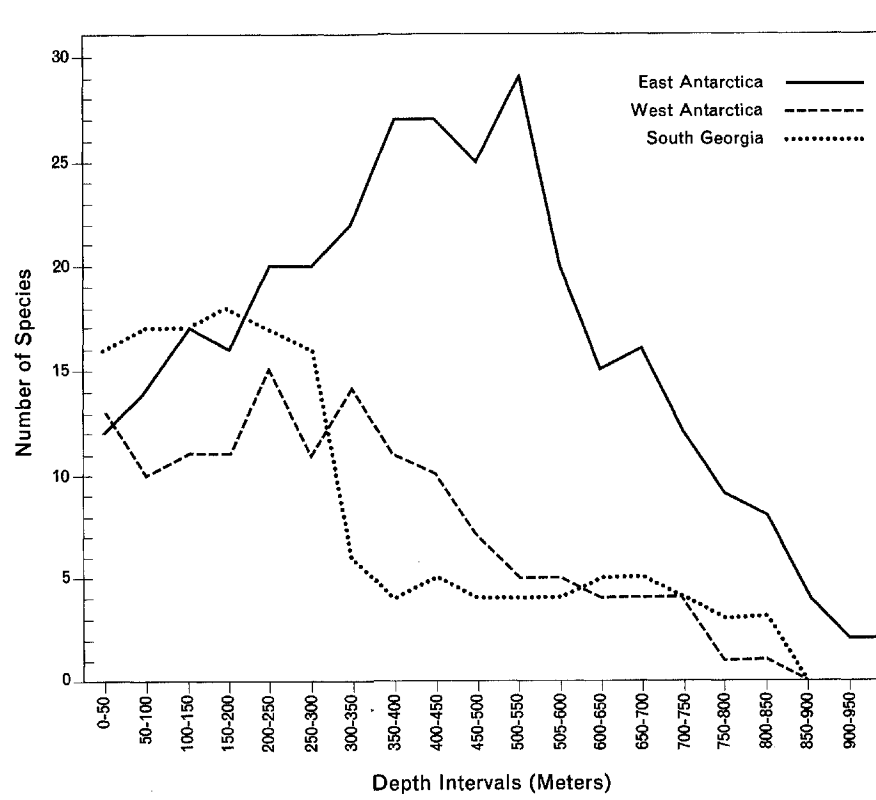

Fig. 2. Variation, with depth, in numbers of species collected in three coastal regions of Antarctica.

As the fish fauna of South Georgia is more thoroughly sampled, it becomes increasingly clear that Nybelin's characterization of it as a low Antarctic or transitional region is correct. Of the 33 species captured near it (Table 14), ten, or 30.3%, are endemic (including two endemic genera), eleven, or 33.3%, are of northern origin, and twelve, or 36.4%, have Antarctic affinities. Five of the endemic species have Antarctic affinities, while the other five belong to northern groups. The two endemic genera, *Psilodraco* and *Pseudochaenichthys,* both belong to Antarctic families. South Georgia is certainly the major point of entrance into the Antarctic for northern species.

TABLE 13. Comparison of depth ranges between East and West Antarctica (including Scotia Ridge islands) for species inhabiting both regions.

Species	Depth Range (m)	
	West Antarctica	*East Antarctica*
Muraenolepis microps	18-450	315-830
Notothenia kempi	160-650	670-830
Notothenia neglecta	0-160	0-20
Trematomus newnesi	2-150	0-110
Trematomus bernacchii	1-80	3-732
Trematomus hansoni	17-344	5-549
Trematomus loennbergii	0-65	366-832
Trematomus scotti	130-411	70-655
Trematomus eulepidotus	160-344	70-441
Dissostichus mawsoni	20-30	20-219
Artedidraco skottsbergi	40-203	5-379
Artedidraco loennbergi	230	289-578
Dolloidraco longedorsalis	230	415-860
Pogonophryne marmoratus	490-849	430-540
Gerlachea australis	450-460	415-655
Racovitzia glacialis	369-512	219-595
Racovitzia infuscipinnis	769	560-750
Prionodraco evansii	244-344	70-440
Pagetopsis macropterus	230	100-655
Cryodraco antarcticus	177-450	110-549
Austrolycichthys concolor	391	534-549

TABLE 14. Fishes obtained from the sea around South Georgia. An E denotes an endemic species; N denotes a northern origin; S denotes a species also found farther south.

Species	Symbol
Geotria australis	N
Raja georgiana	E
Muraenolepis microps	S
Antimora rostrata	N
Halargyreus johnsonii	N
Micromesistius australis	N
Coelorhynchus marinii	N
Cynomacrurus piriei	N
Notothenia angustifrons	S
Notothenia gibberifrons	S
Notothenia kempi	S
Notothenia larseni	S
Notothenia nudifrons	S
Notothenia neglecta	S
Notothenia rossii	S
Notothenia magellanica	N
Trematomus vicarius	E
Trematomus hansoni	S
Dissostichus eleginoides	N
Artedidraco mirus	E
Harpagifer bispinis	S
Parachaenichthys georgianus	E
Psilodraco breviceps	E
Champsocephalus gunnari	S
Pseudochaenichthys georgianus	E
Chaenocephalus aceratus	S
Lycenchelys bellingshauseni	E
Melanostigma gelatinosum	N
Lycodapus australis	N
Liparis steineni	E
Paraliparis gracilis	E
Careproctus georgianus	E
Mancopsetta maculata	N

Notes on Nomenclature

The following nomenclatural changes have been made in the tables and distribution maps. They are based upon my own observations and since they have not been published previously they require comment.

Notothenia normani Nybelin (1947) is considered a synonym of *N. cornucola* Richardson (1844), a species occurring only in the Magellanic region of South America. I have carefully examined the two types of the former and can find no essential differences from authentic South American material. It is my belief, although I have no proof, that the locality data are incorrect. It seems significant that all of the material reported upon by Nybelin except the two types of *N. normani* have detailed locality data with them; the latter are simply said to be from South Georgia.

Bathydraco wohlschlagi DeWitt and Tyler (1960) is a synonym of *B. nudiceps* Waite (1916). I have examined the holotype of the latter and have found that Waite's description is in gross error for several important characters (numbers of branchiostegal and fin rays, and scale characteristics). Waite's paper contains many other such errors.

Chionodraco markhami Miller and Reseck (1961) is considered a synonym of *C. myersi* DeWitt and Tyler (1960). Although I have not examined the types of *C. markhami* closely, there is little doubt that the two names represent but one species.

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In doing the literature search which forms the basis of this paper I have been greatly aided by lists of collection localities for most of the species which were compiled by Professor Orvar Nybelin of the Natural History Museum in Göteborg, Sweden. Professor Nybelin had planned to write a general work on the distribution of Antarctic fishes, but when I visited him in 1965 he gave the lists to me because he believed he would not be able to finish it. I am much indebted to Professor Nybelin for this kindness, for although I have rechecked the literature myself and am responsible for any errors which may be detected, the lists made the work much easier.

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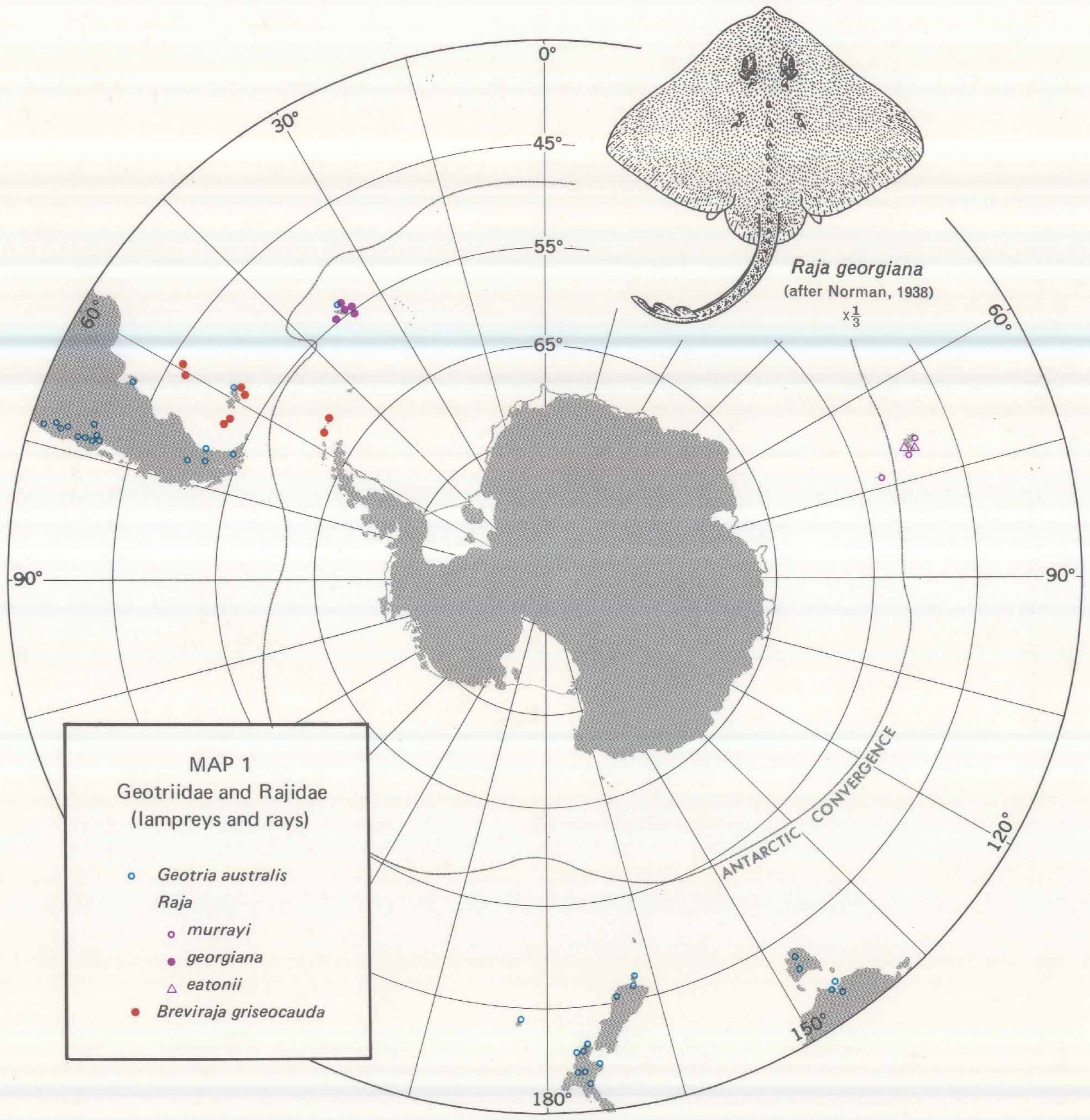

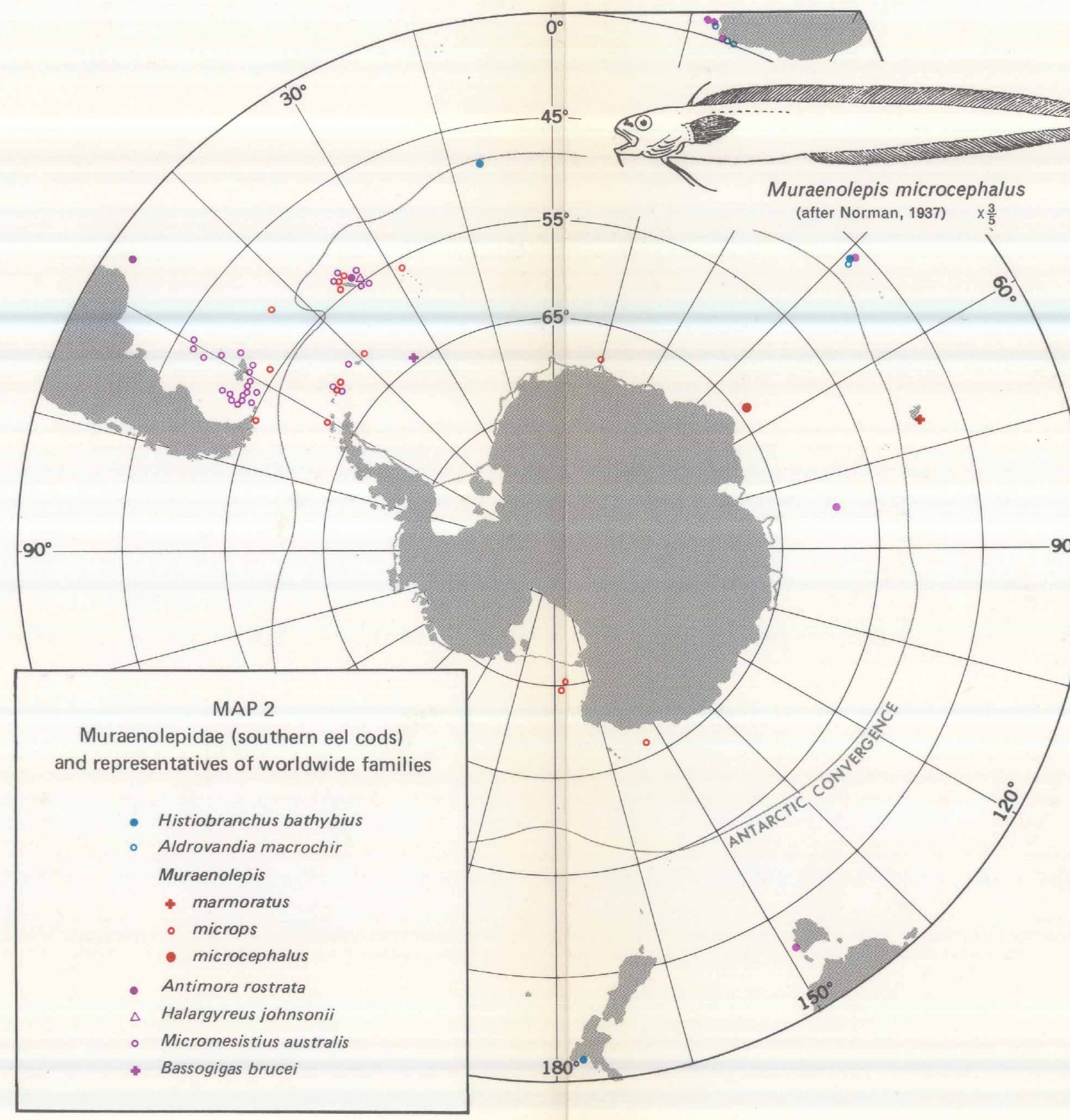

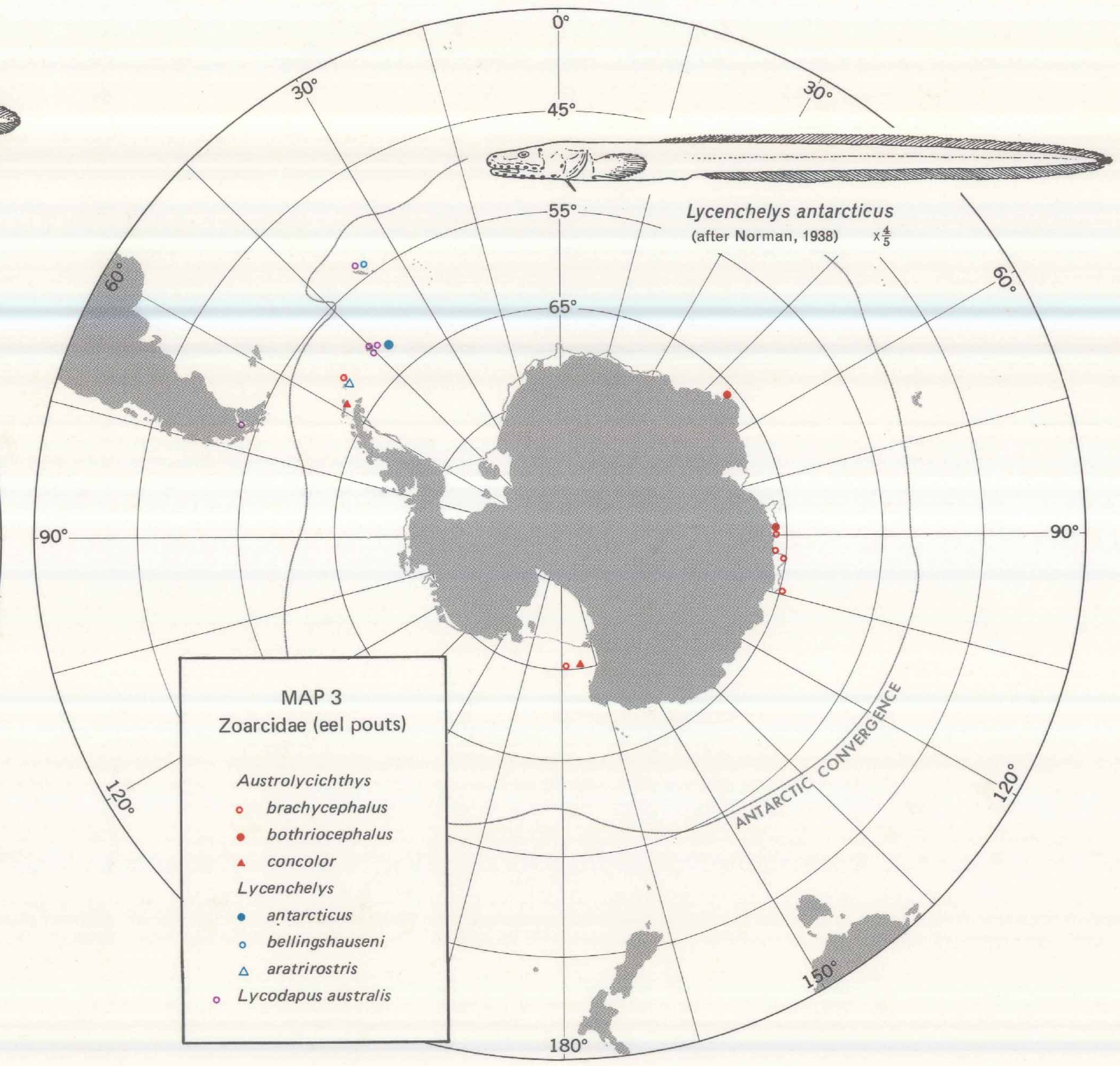

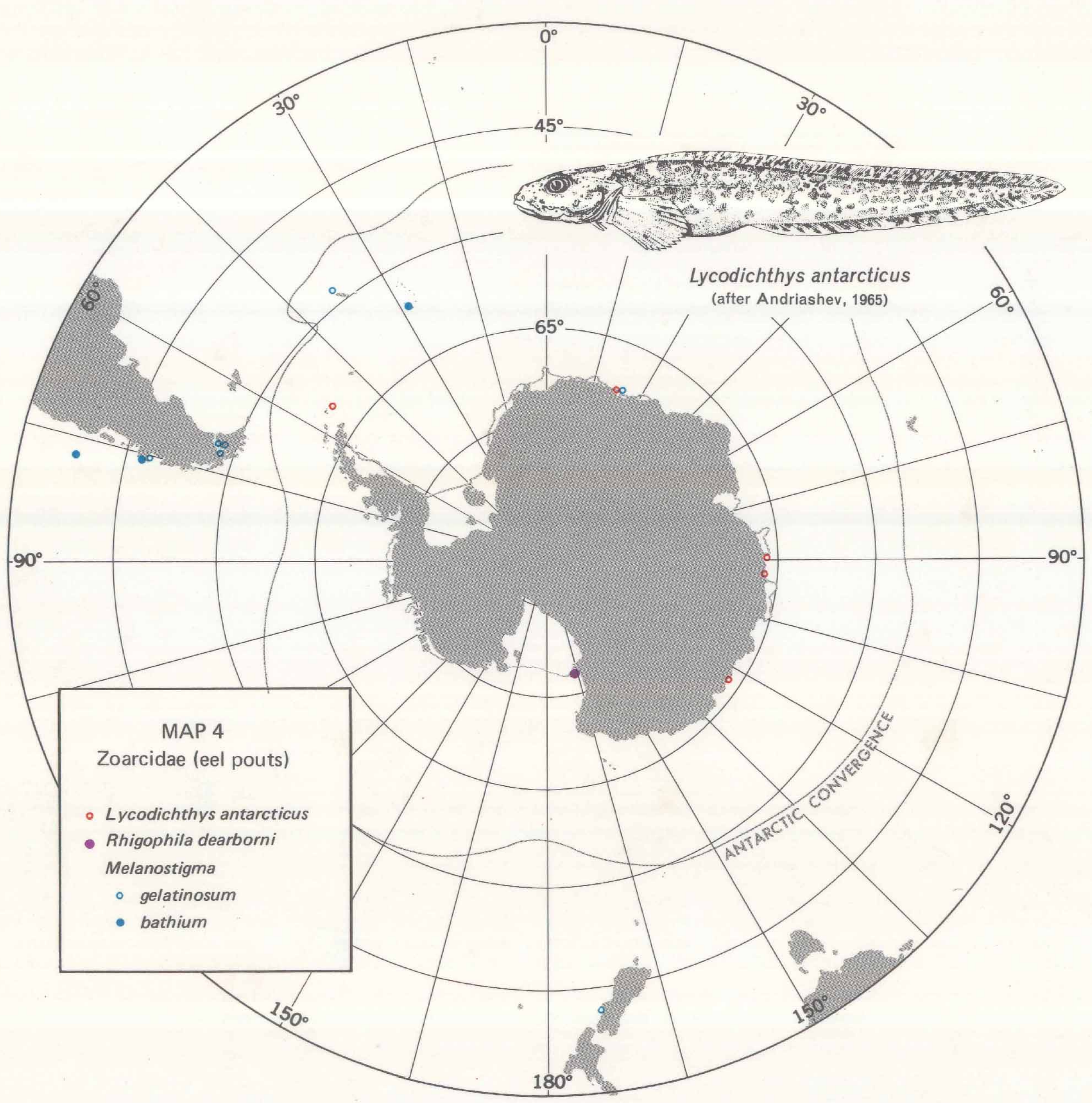

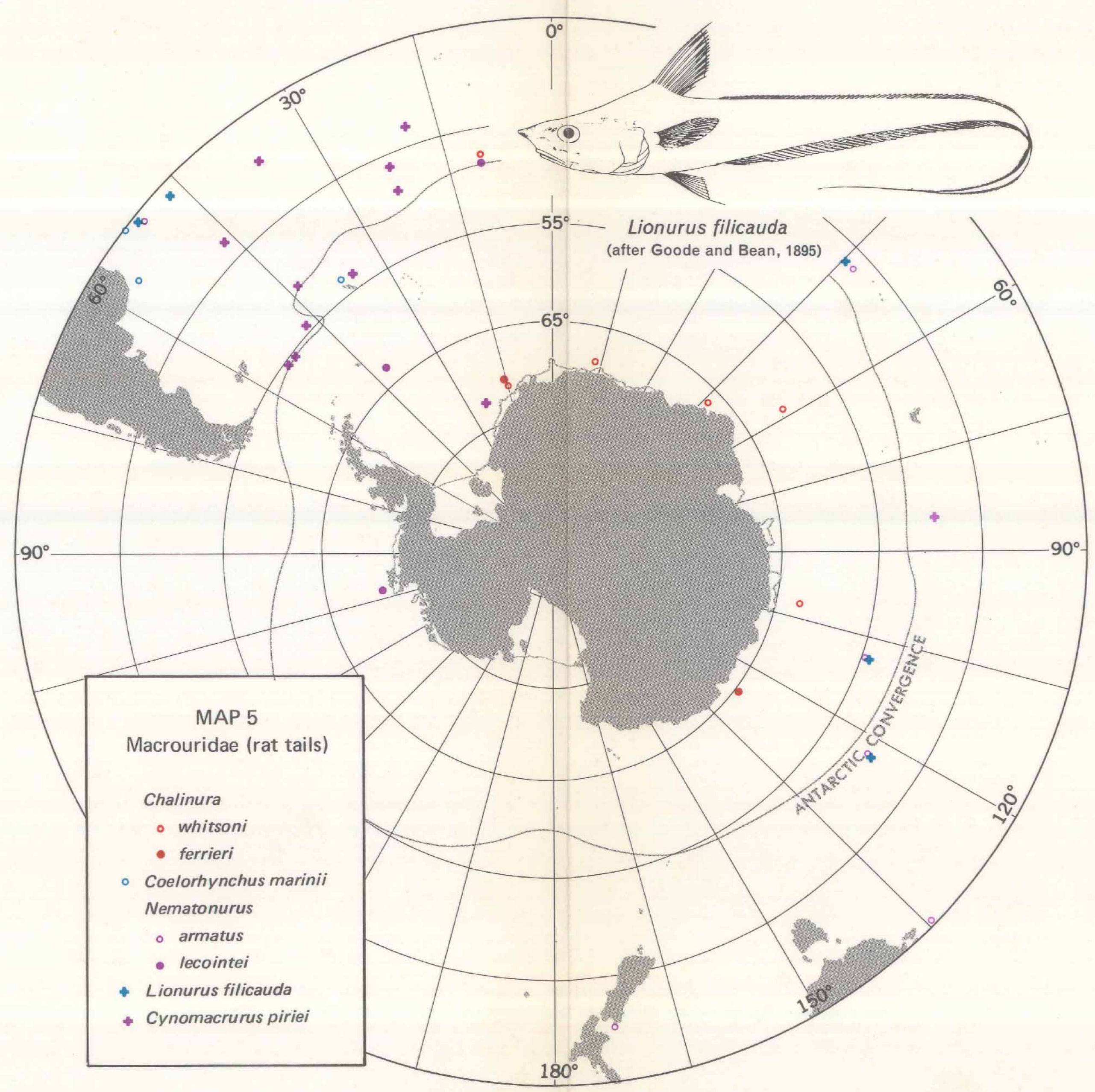

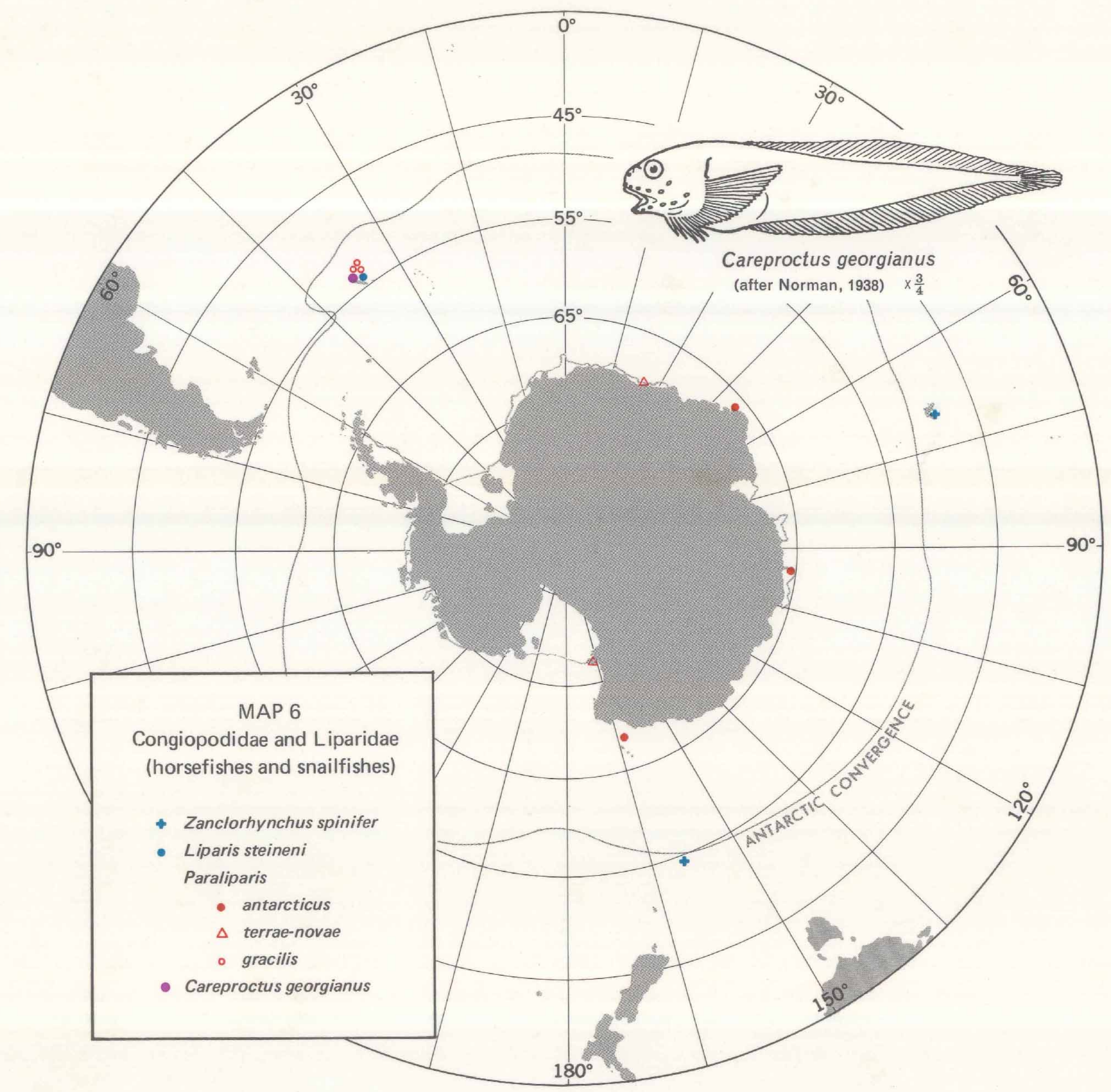

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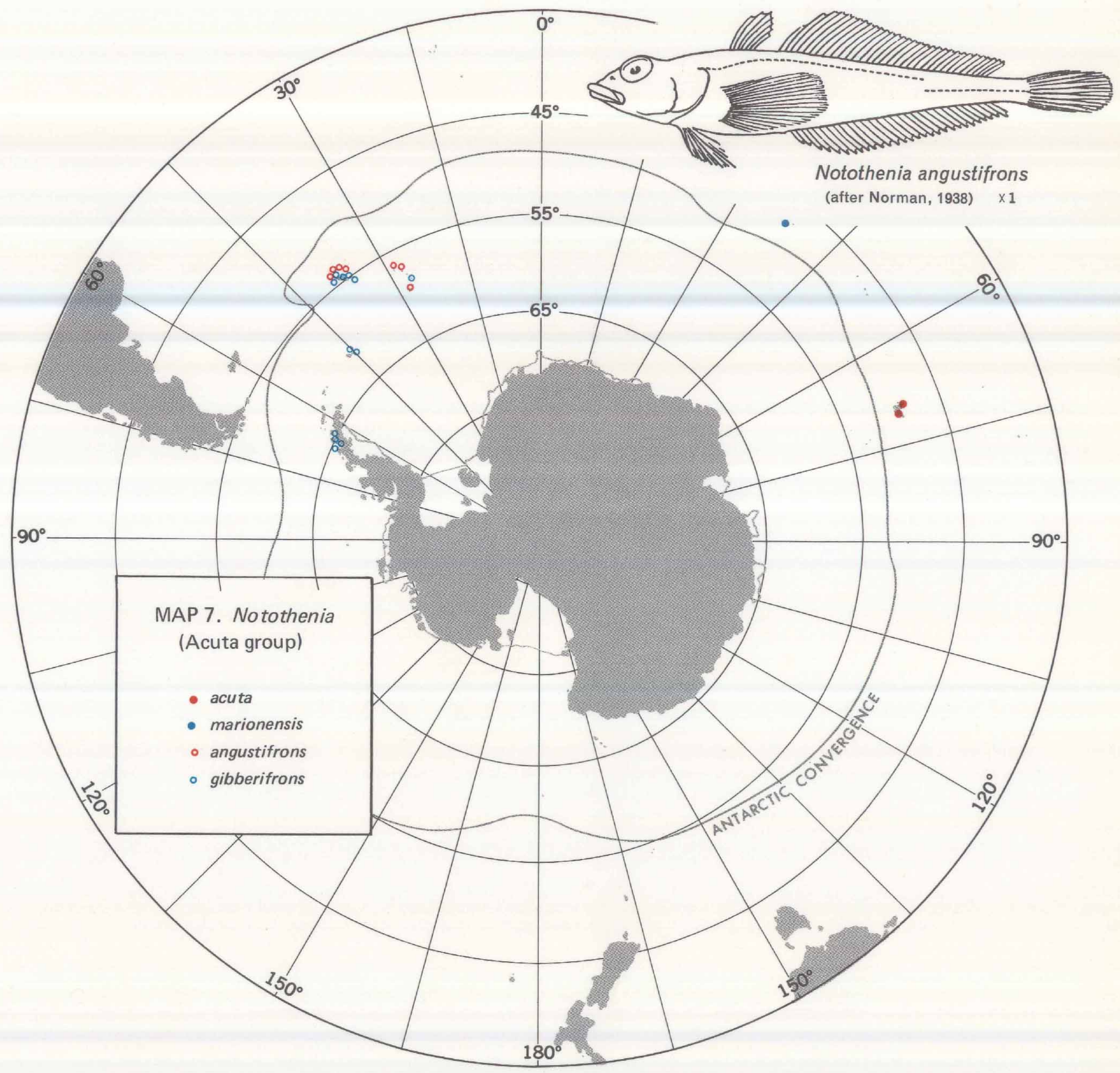
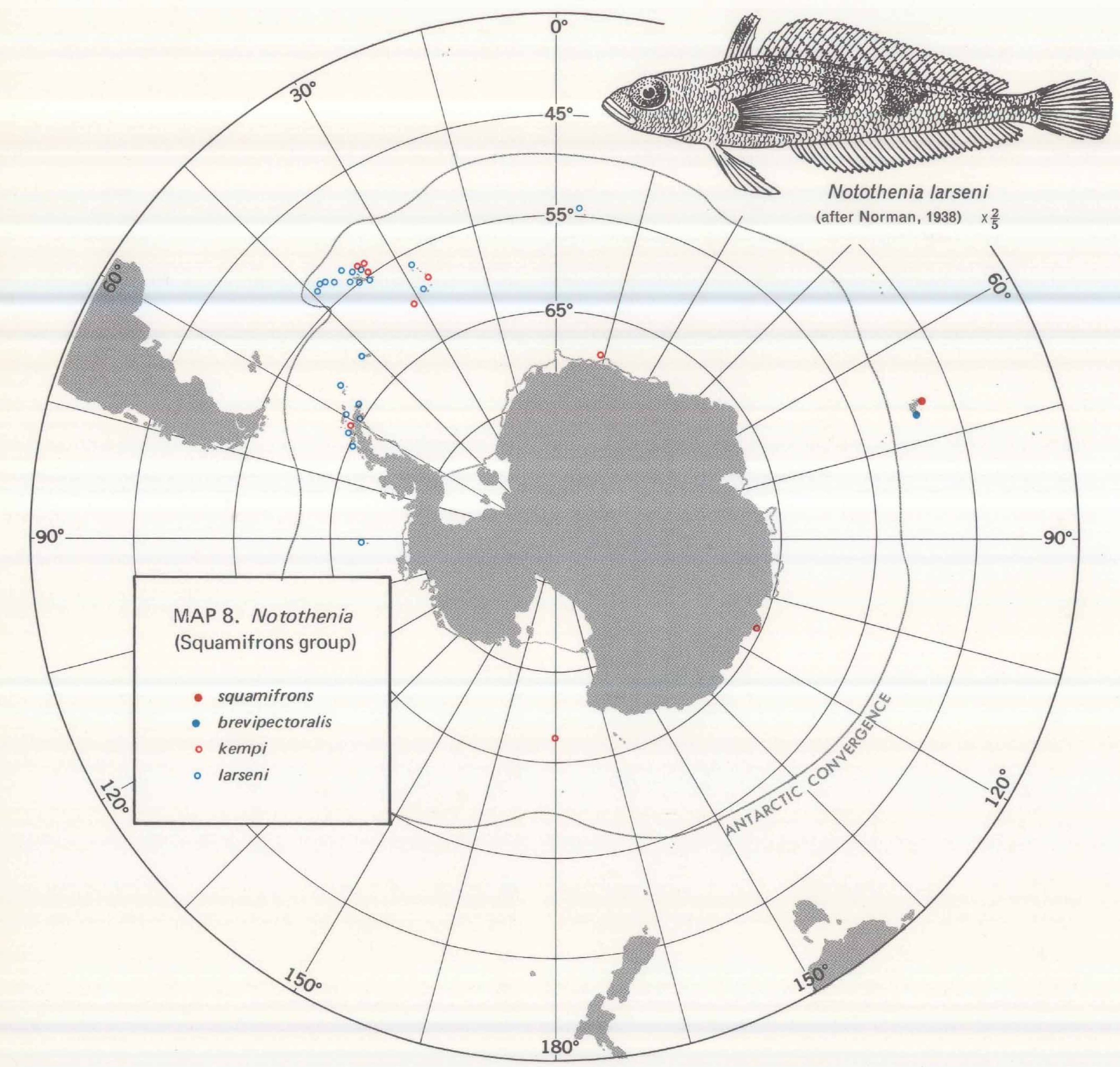

Nototheniа angustifrons
(after Norman, 1938) x 1
MAP 7. Notothenia
(Acuta group)
acuta
marionensis
angustifrons
gibberifrons
ANTARCTIC CONVERGENCE
0°
30°
45°
55°
60°
65°
90°
90°
120°
120°
150°
150°
180°


Notothenia larseni
(after Norman, 1938) x 2/5
MAP 8. Notothenia
(Squamifrons group)
squamifrons
brevipectoralis
kempi
larseni
ANTARCTIC CONVERGENCE
0°
30°
45°
55°
60°
65°
90°
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120°
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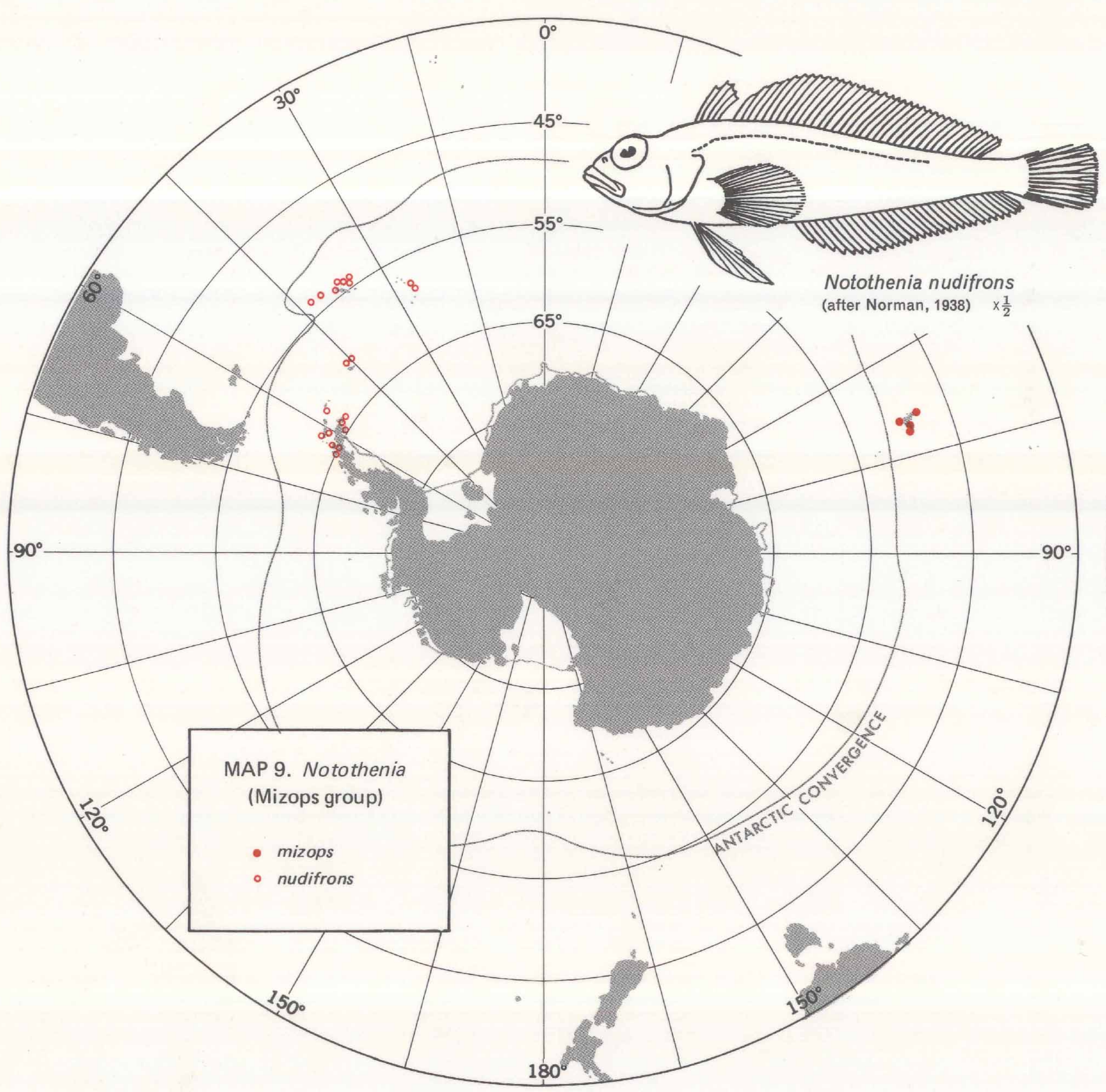
Notothenia nudifrons
(after Norman, 1938) x 1/2
MAP 9. Notothenia
(Mizops group)
mizops
nudifrons
ANTARCTIC CONVERGENCE
0°
30°
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60°
65°
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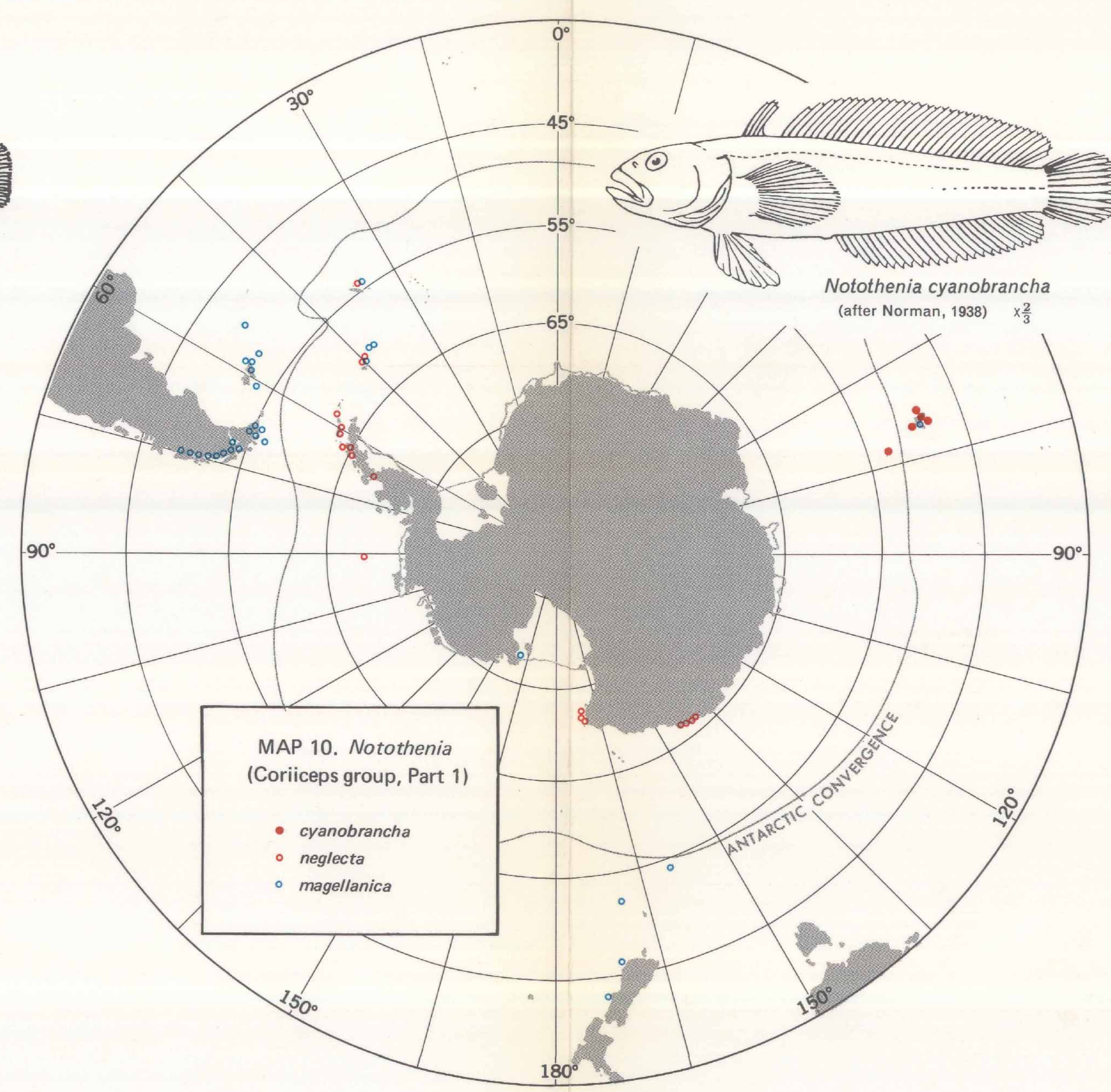
Notothenia cyanobrancha
(after Norman, 1938) x 2/3
MAP 10. Notothenia
(Coriiceps group, Part 1)
cyanobrancha
neglecta
magellanica
ANTARCTIC CONVERGENCE
0°
30°
45°
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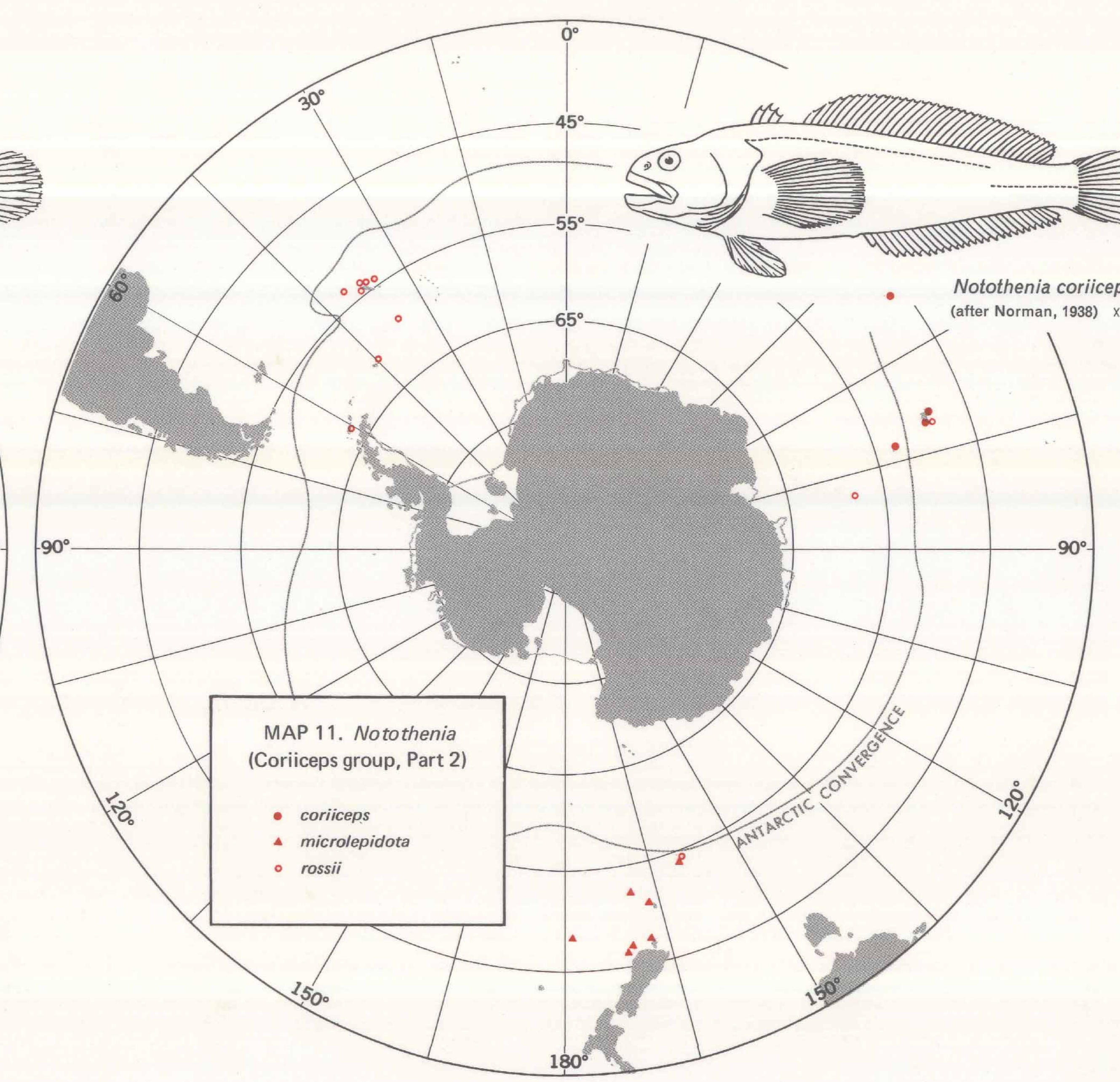
Notothenia coriiceps
(after Norman, 1938) x 1/5
MAP 11. Notothenia
(Coriiceps group, Part 2)
coriiceps
microlepidota
rossii
ANTARCTIC CONVERGENCE
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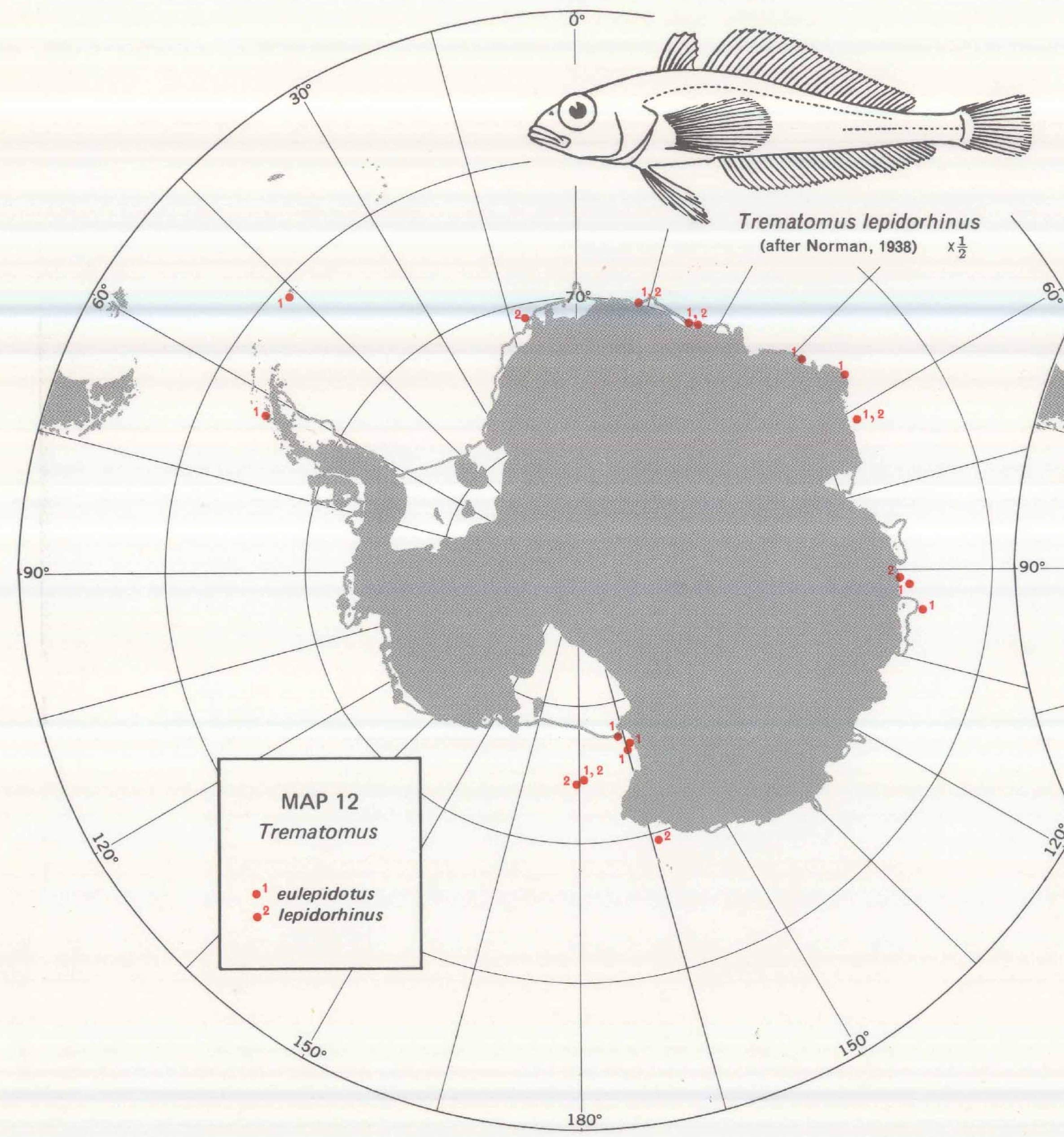
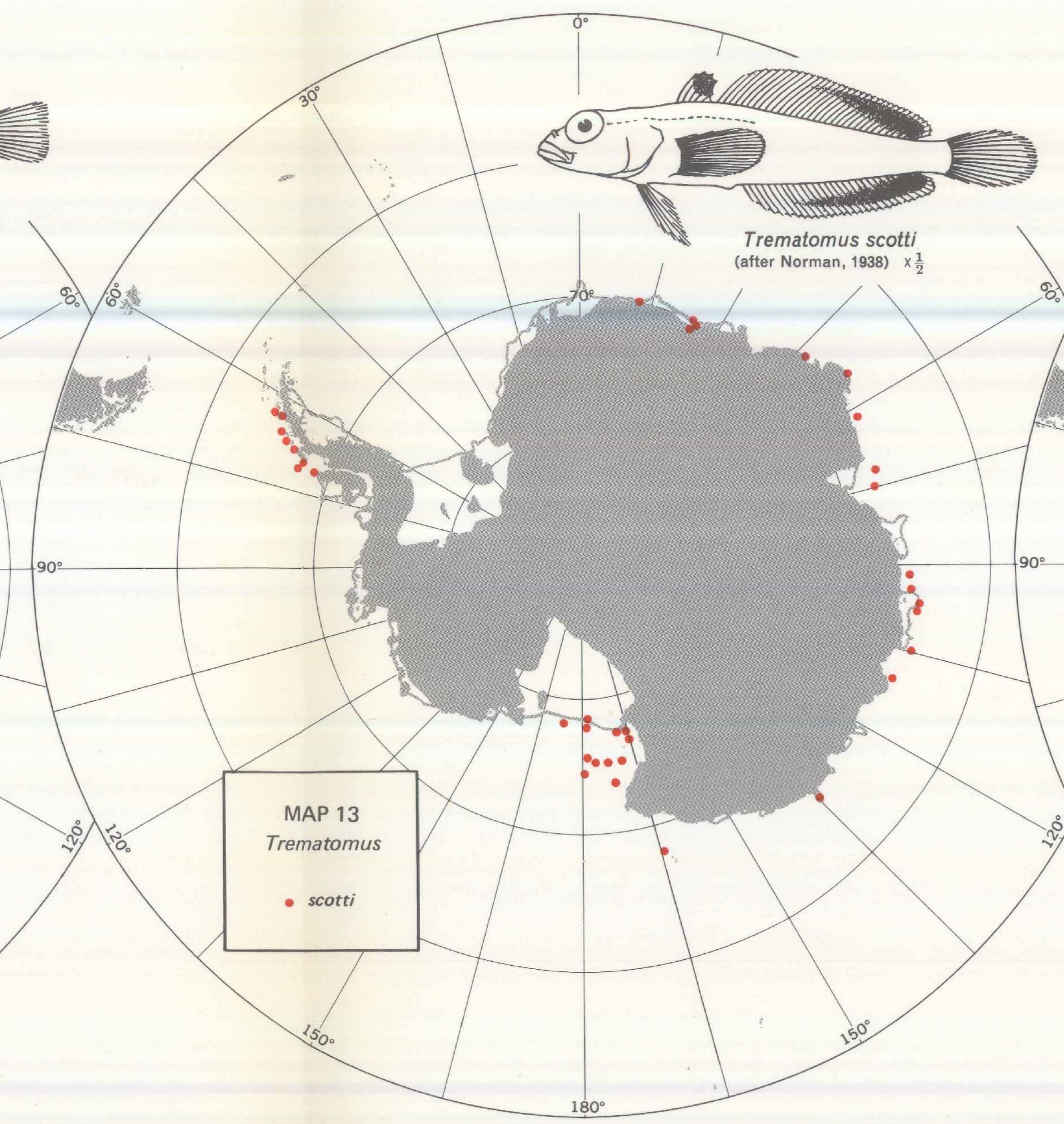
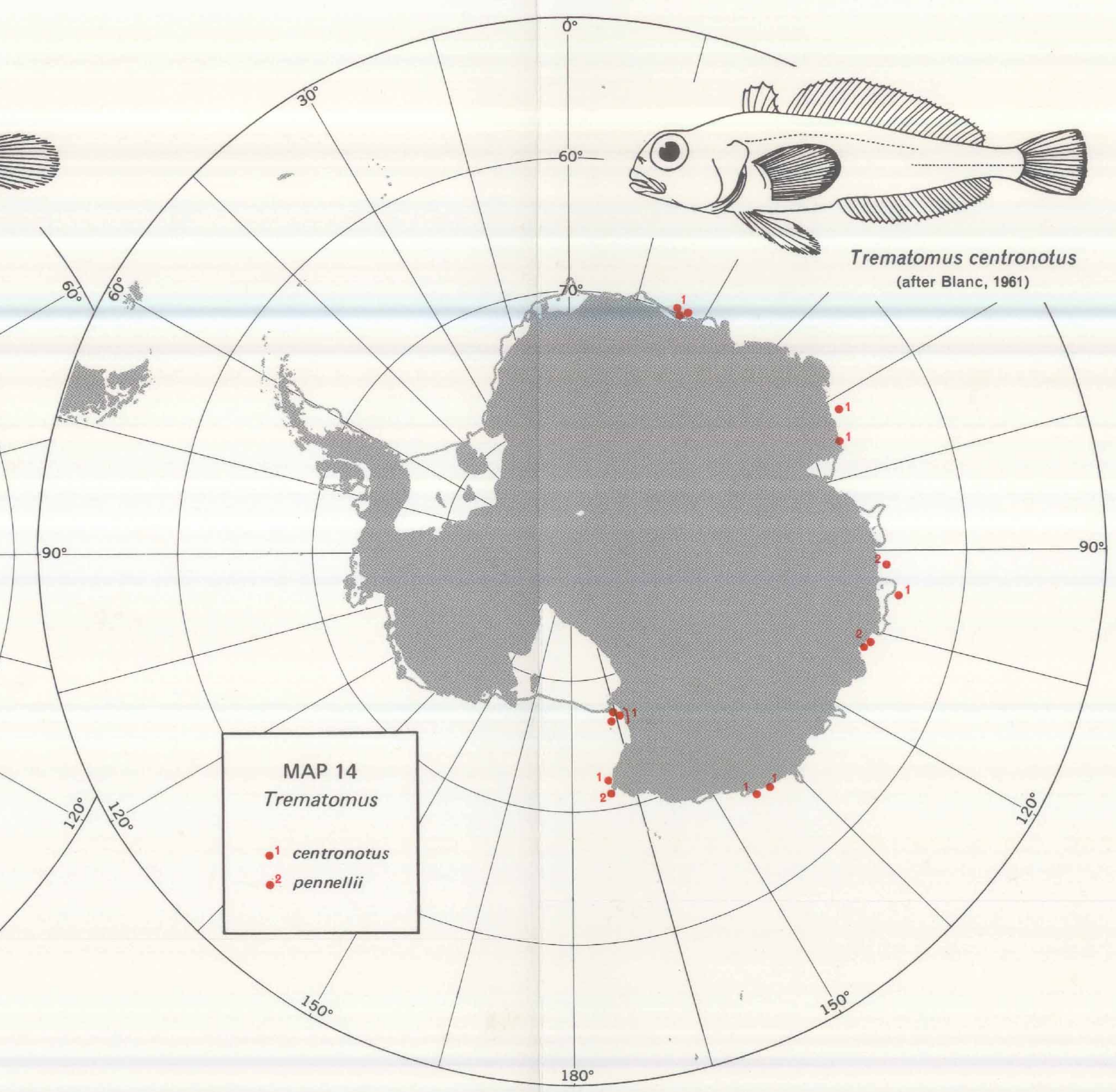
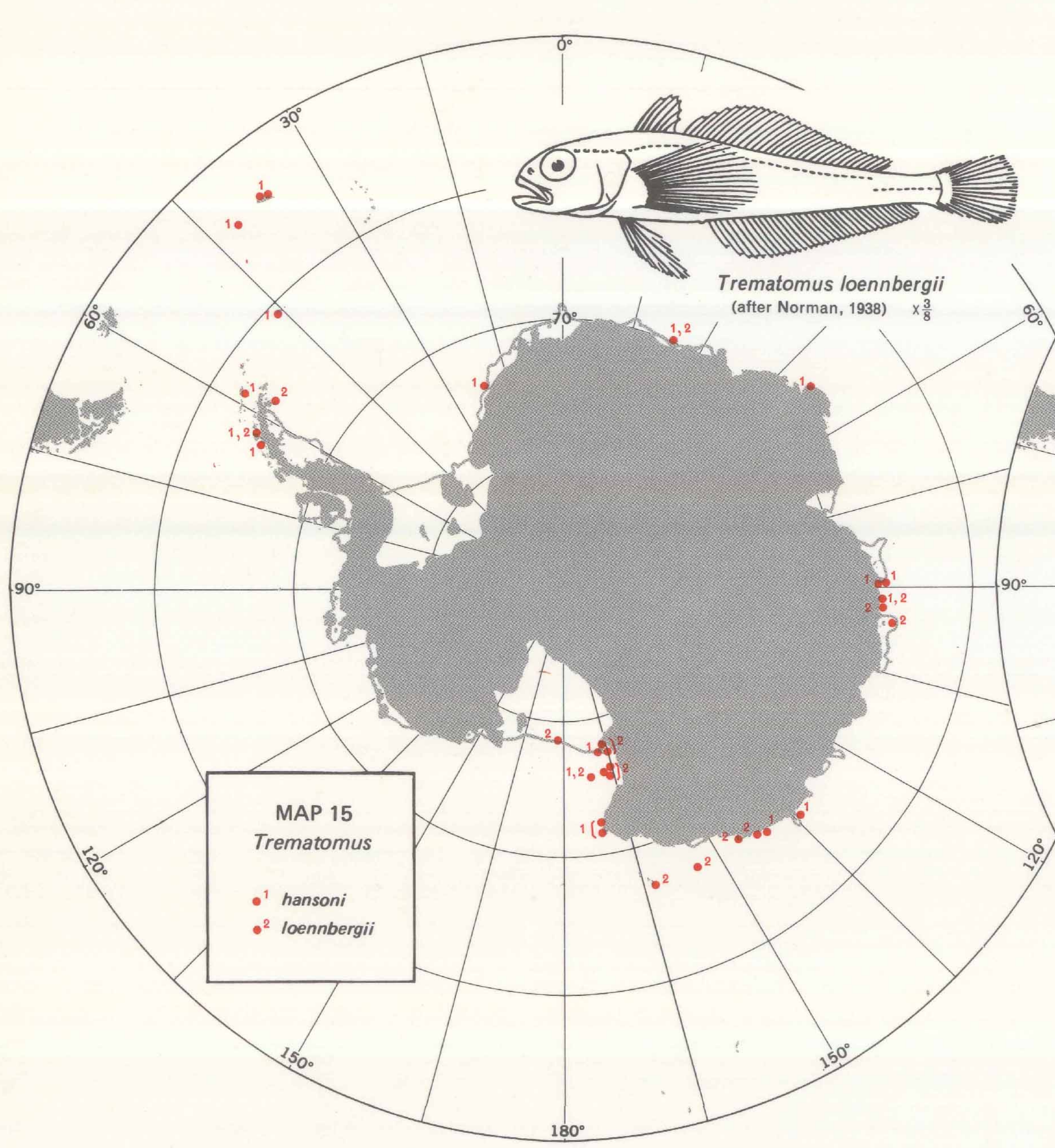
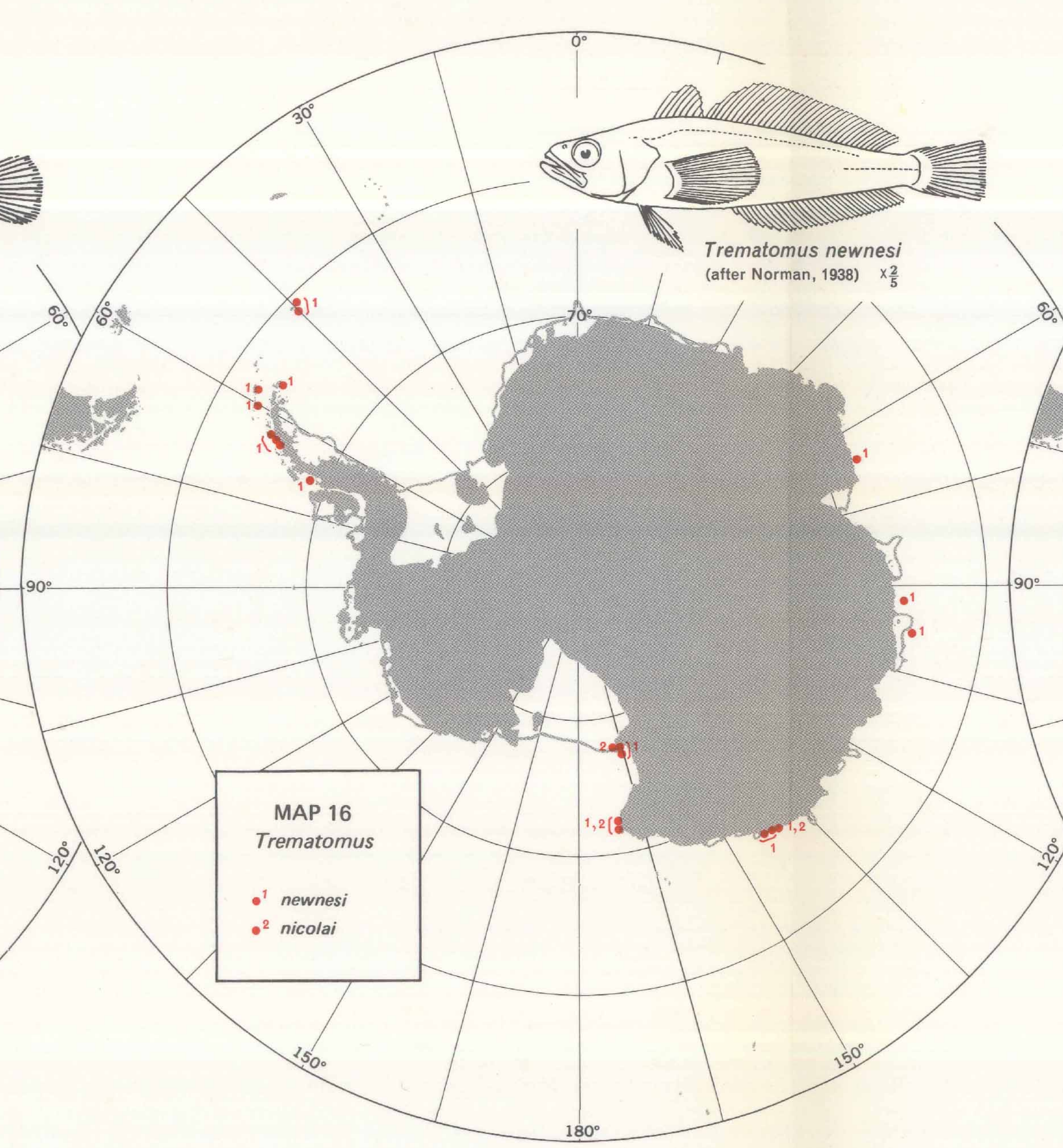
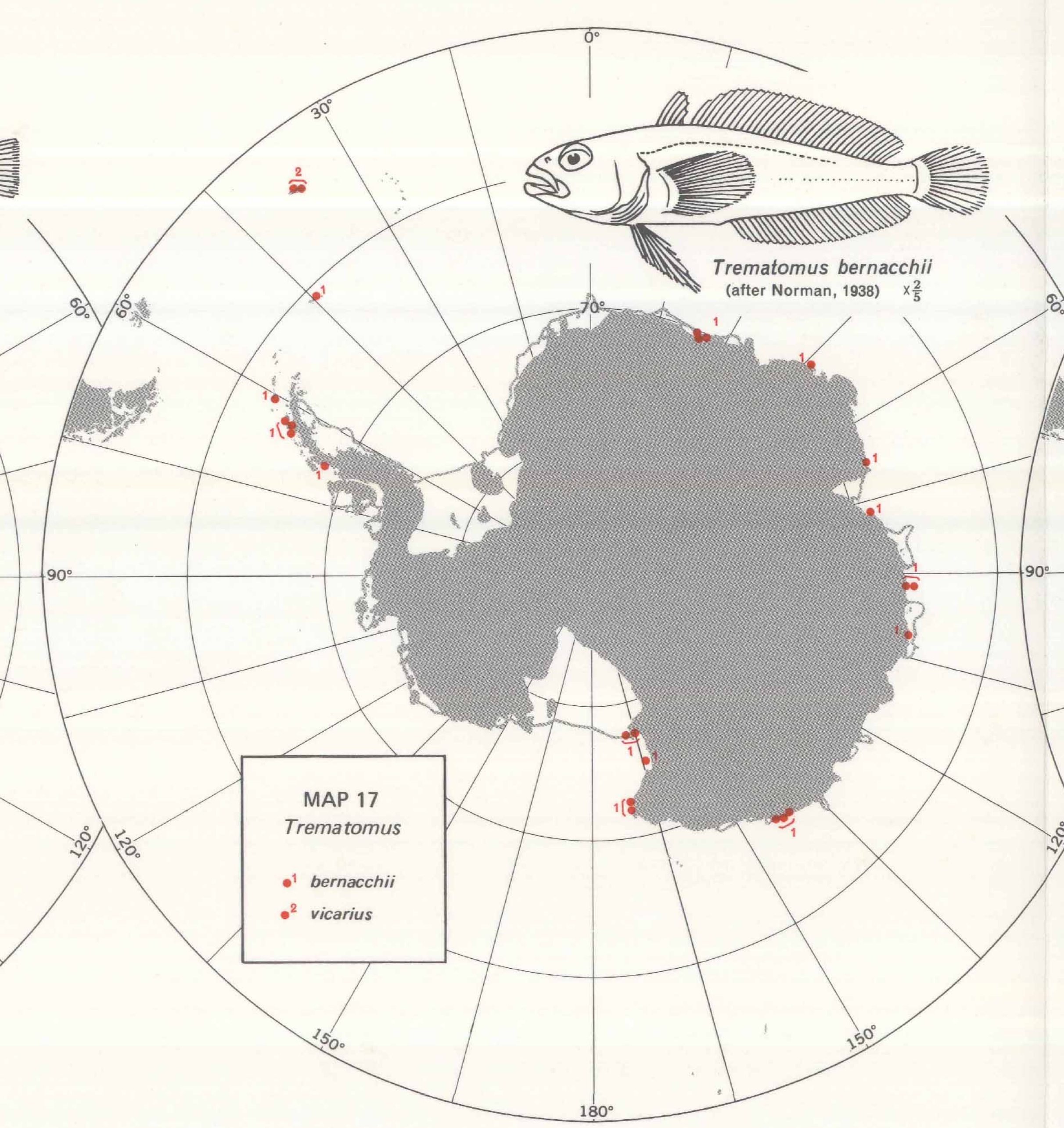

Trematomus lepidorhinus
(after Norman, 1938) x 1/2
MAP 12
Trematomus
1 eulepidotus
2 lepidorhinus

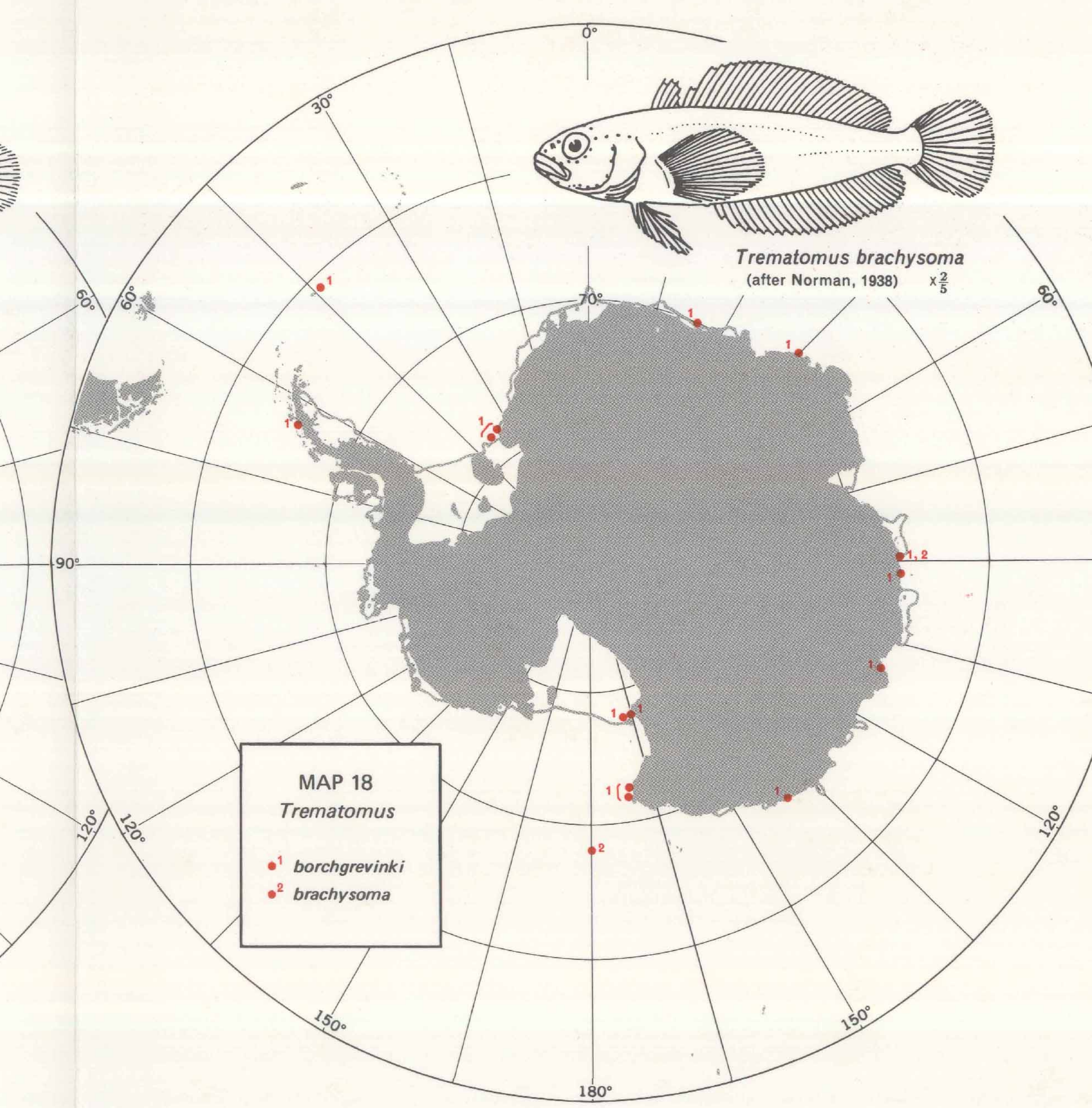

Trematomus scotti
(after Norman, 1938) x 1/2
MAP 13
Trematomus
scotti

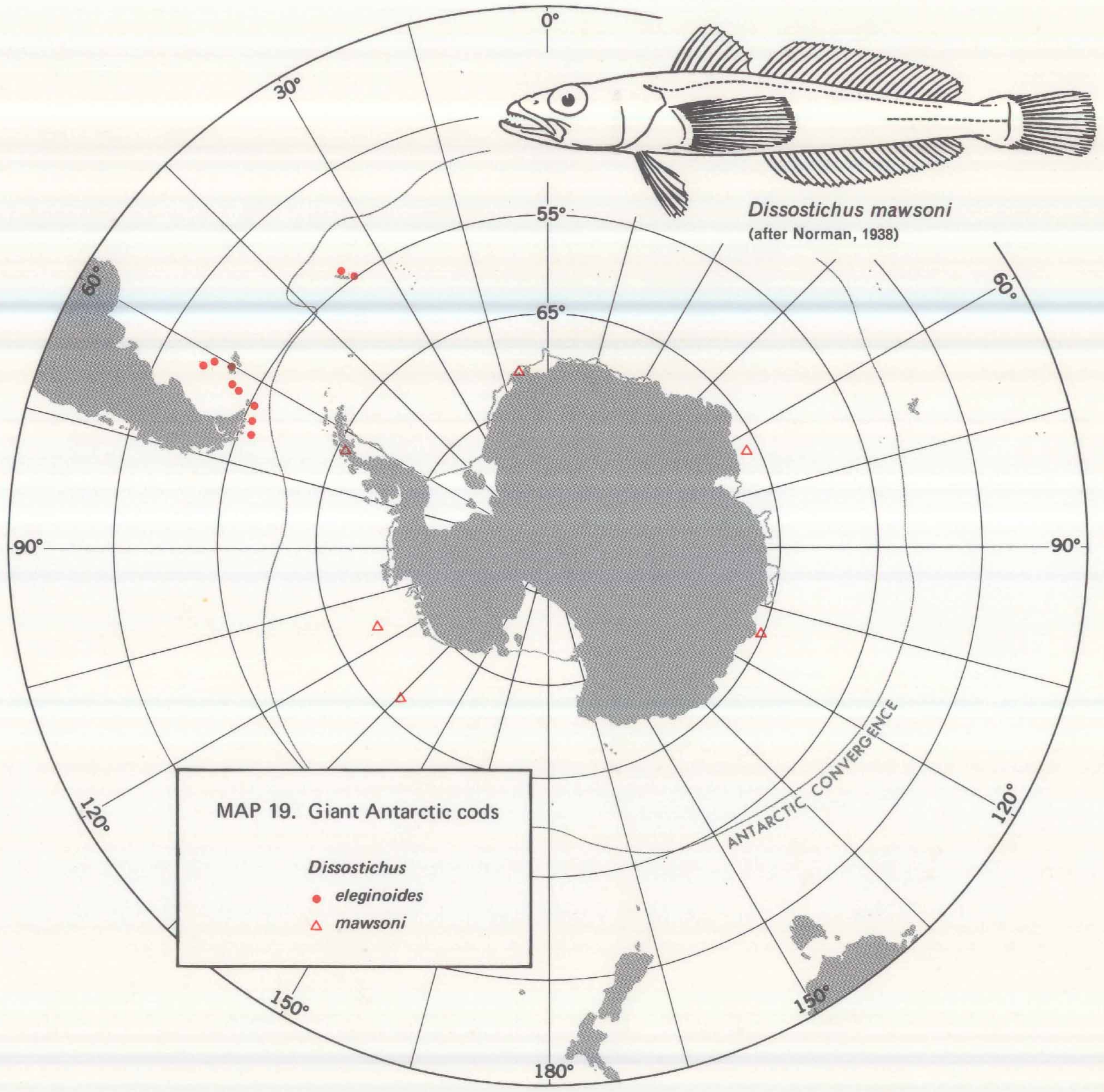

Trematomus centronotus
(after Blanc, 1961)
MAP 14
Trematomus
1 centronotus
2 pennellii


Trematomus loennbergii
(after Norman, 1938) x 3/8
MAP 15
Trematomus
1 hansoni
2 loennbergii


Trematomus newnesi
(after Norman, 1938) x 2/5
MAP 16
Trematomus
1 newnesi
2 nicolai


Trematomus bernacchii
(after Norman, 1938) x 2/5
MAP 17
Trematomus
1 bernacchii
2 vicarius


Trematomus brachysoma
(after Norman, 1938) x 2/5
MAP 18
Trematomus
1 borchgrevinki
2 brachysoma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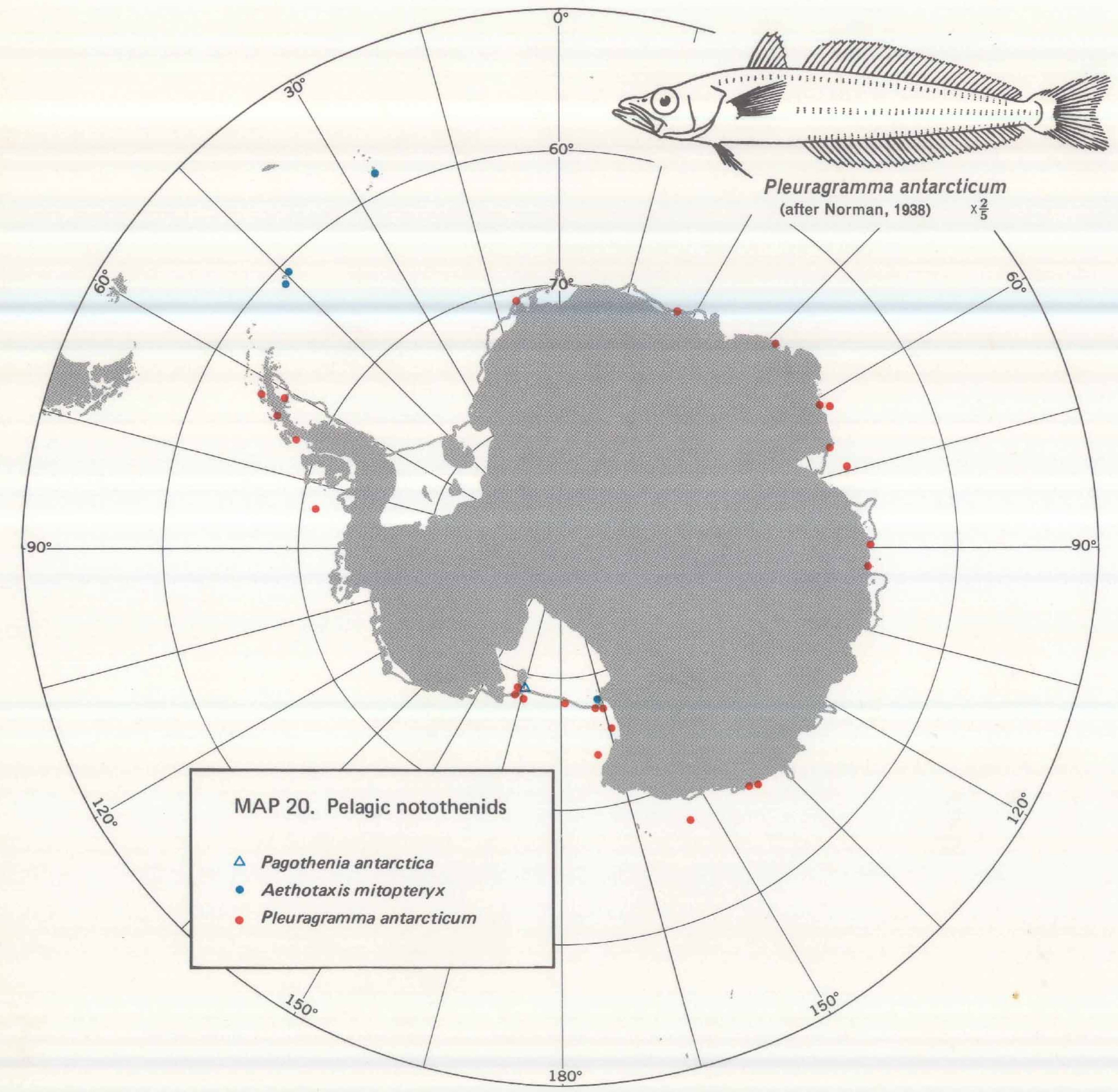
ANTARCTIC CONVERGENCE
Dissostichus mawsoni
(after Norman, 1938)
MAP 19. Giant Antarctic cods
Dissostichus
eleginoides
mawsoni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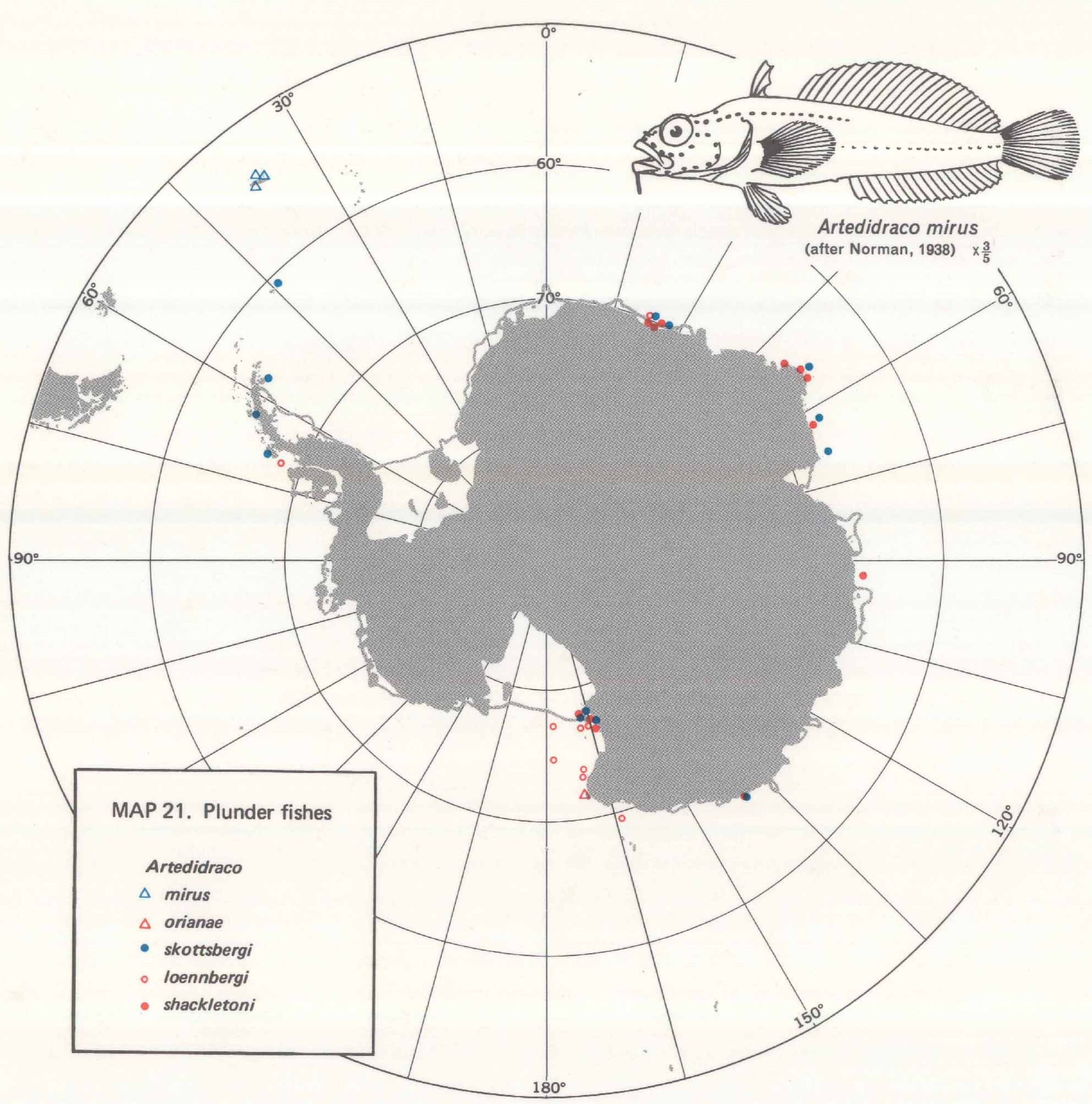
Pleuragramma antarcticum
(after Norman, 1938)
MAP 20. Pelagic notothenids
Pagothenia antarctica
Aethotaxis mitopteryx
Pleuragramma antarcticum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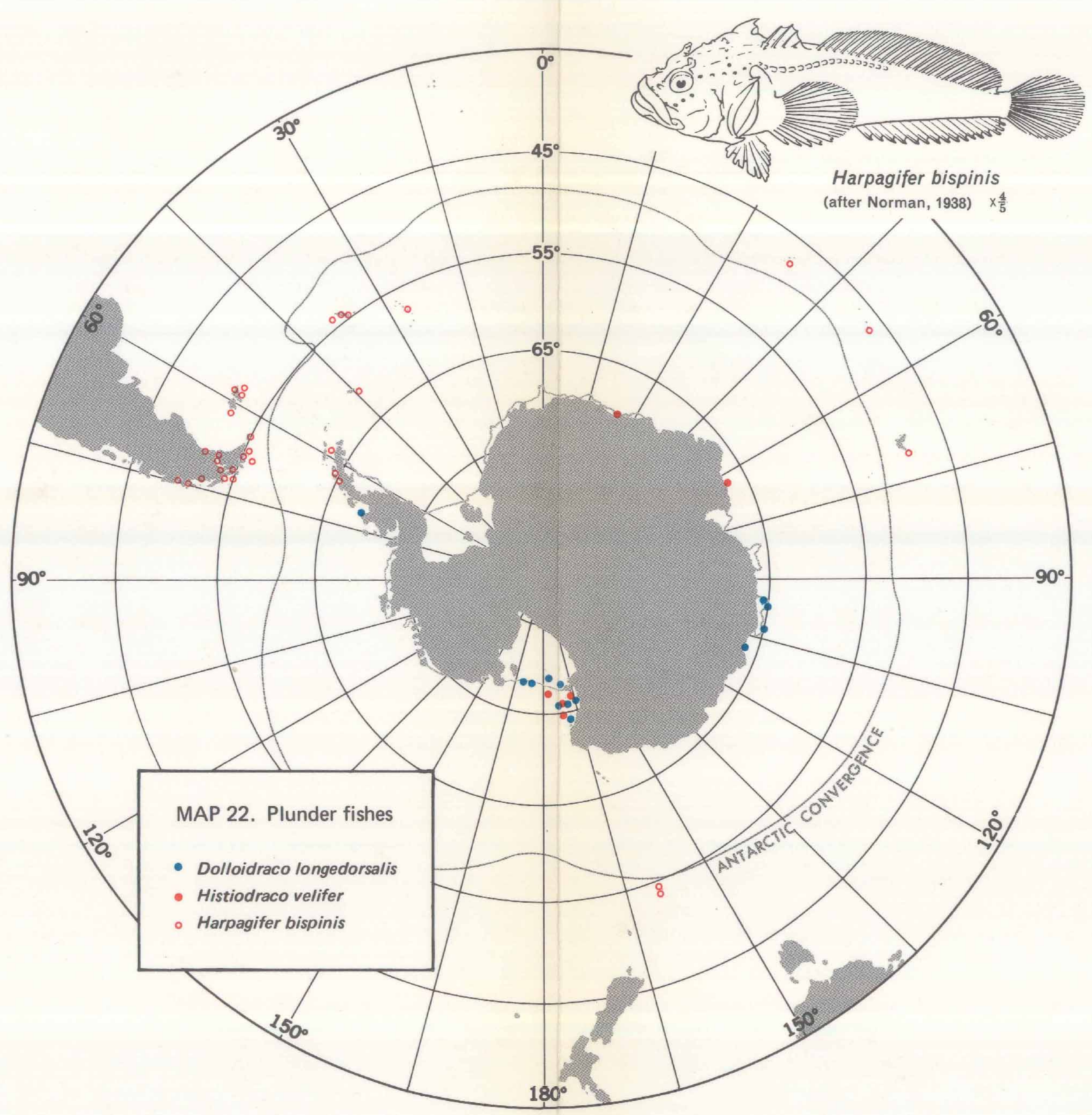
Artedidraco mirus
(after Norman, 1938)
MAP 21. Plunder fishes
Artedidraco
mirus
orianae
skottsbergi
loennbergi
shackletoni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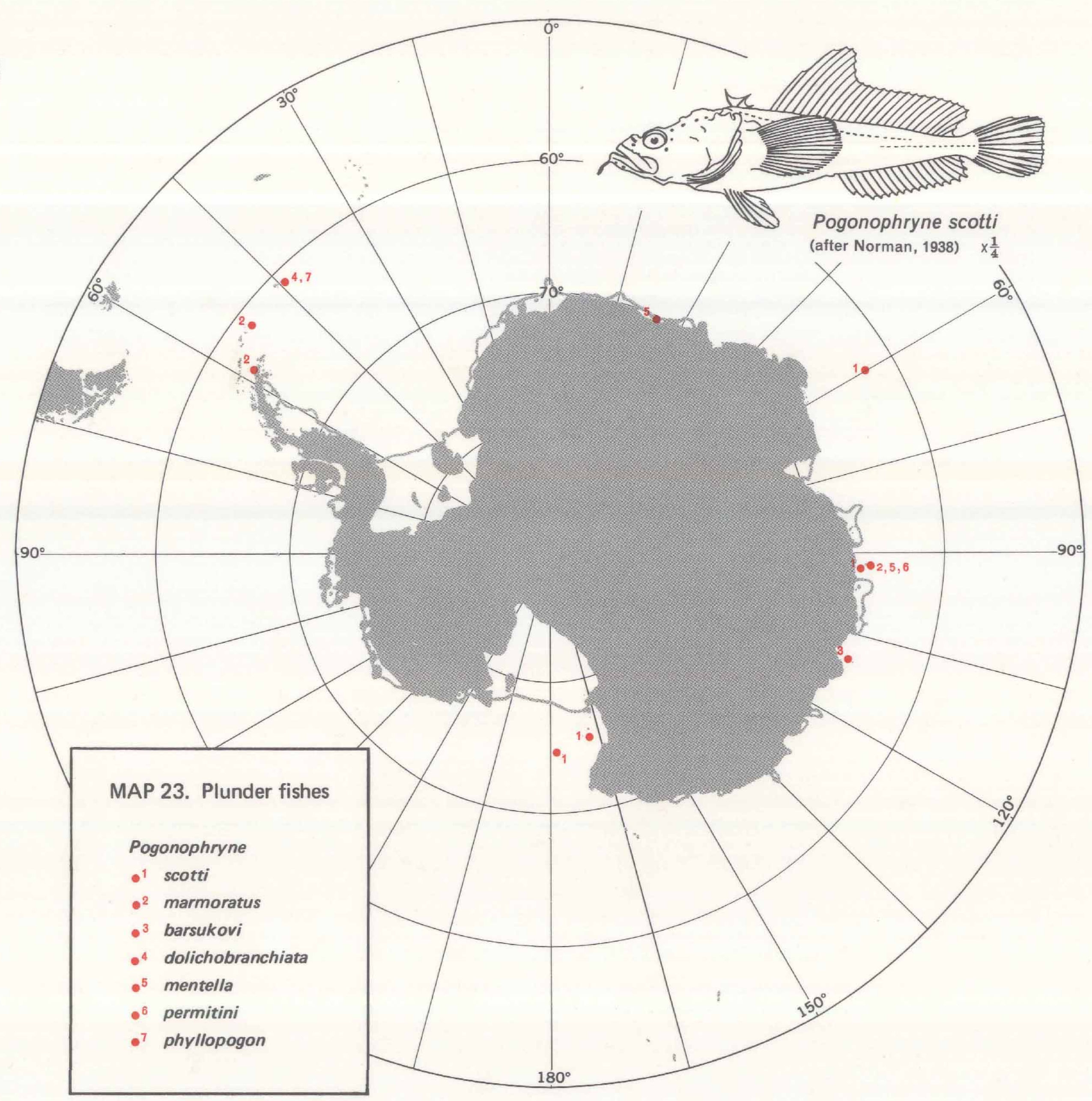
ANTARCTIC CONVERGENCE
Harpagifer bispinis
(after Norman, 1938)
MAP 22. Plunder fishes
Dolloidraco longedorsalis
Histiodraco velifer
Harpagifer bispinis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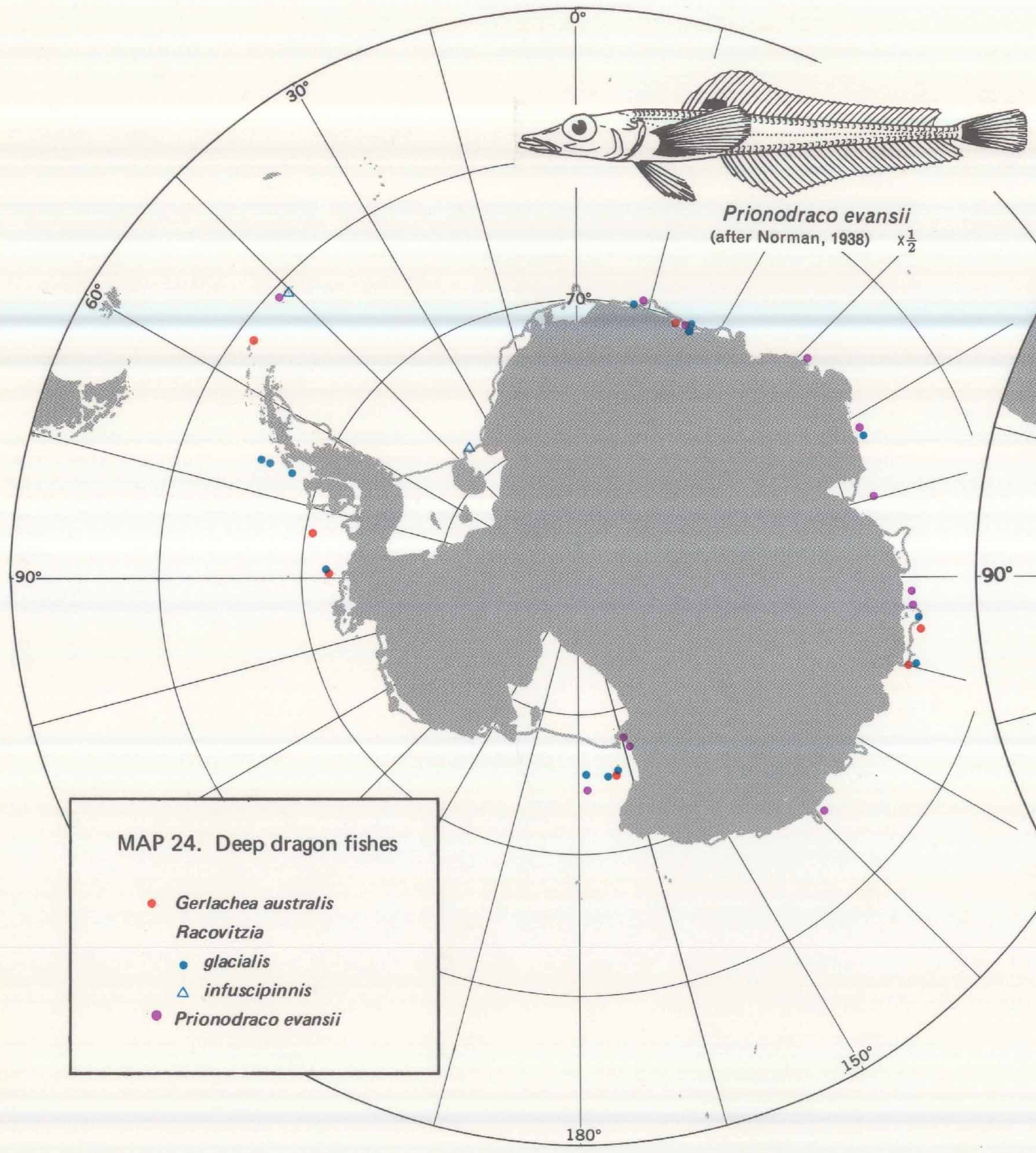
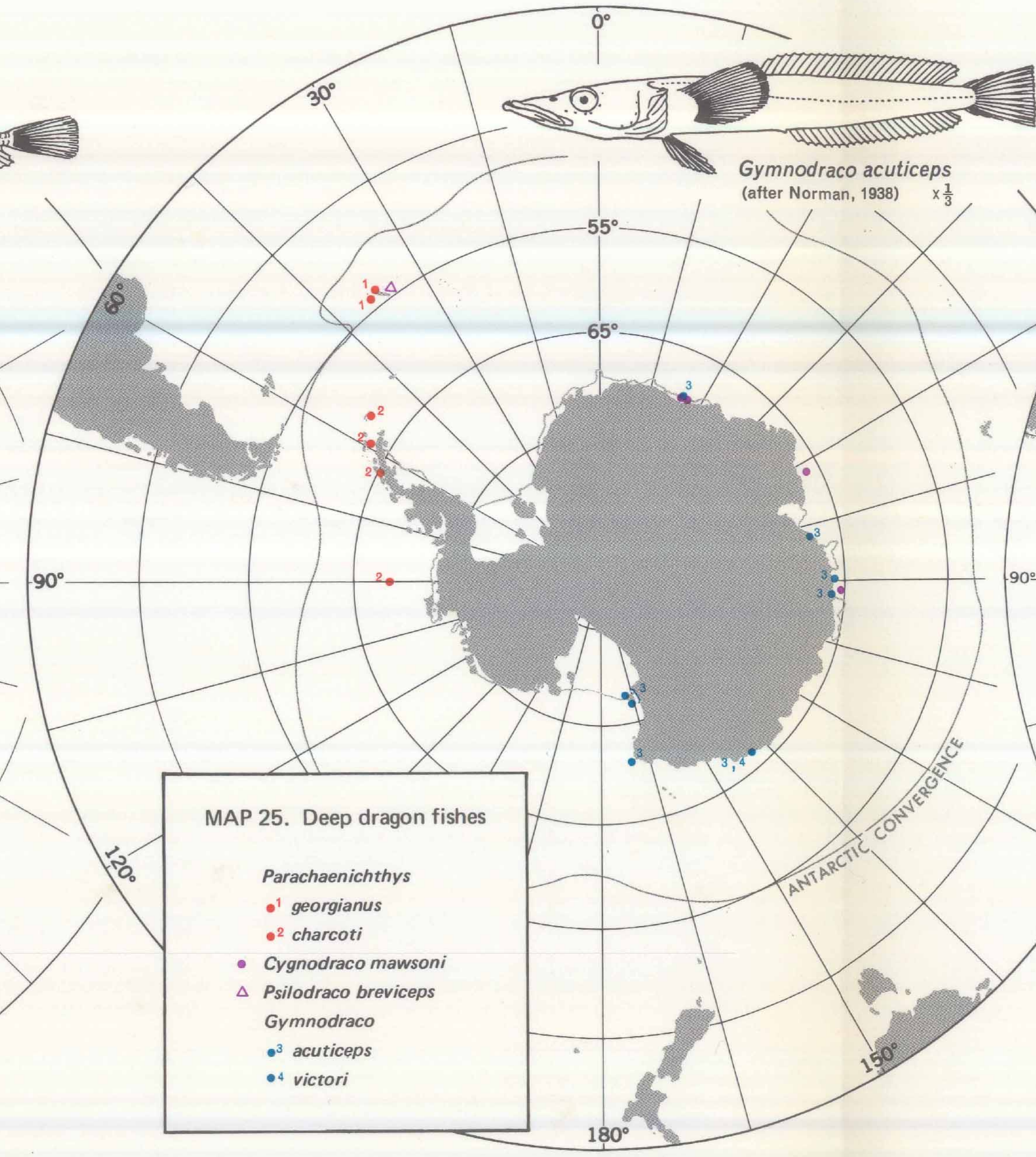
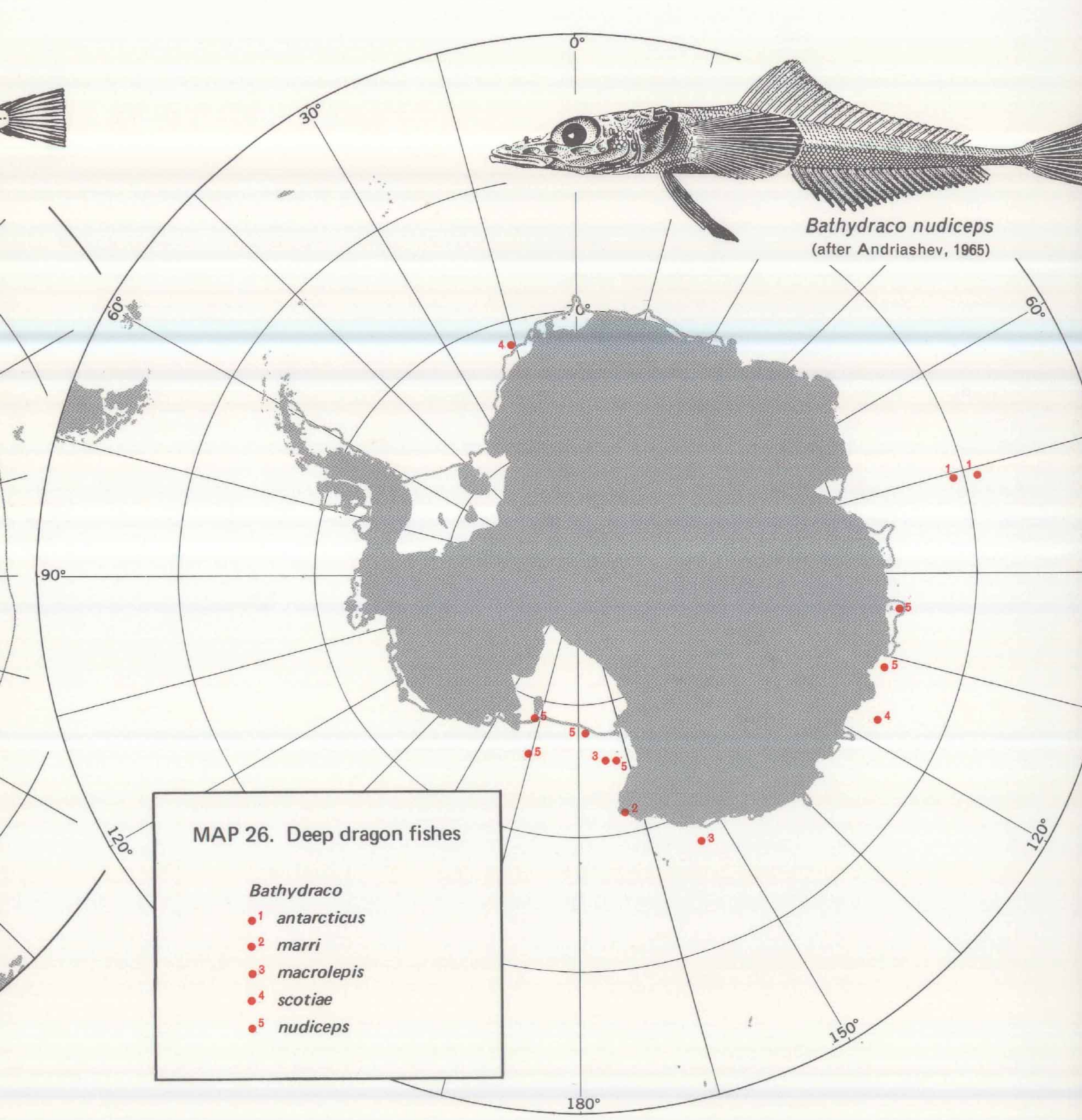
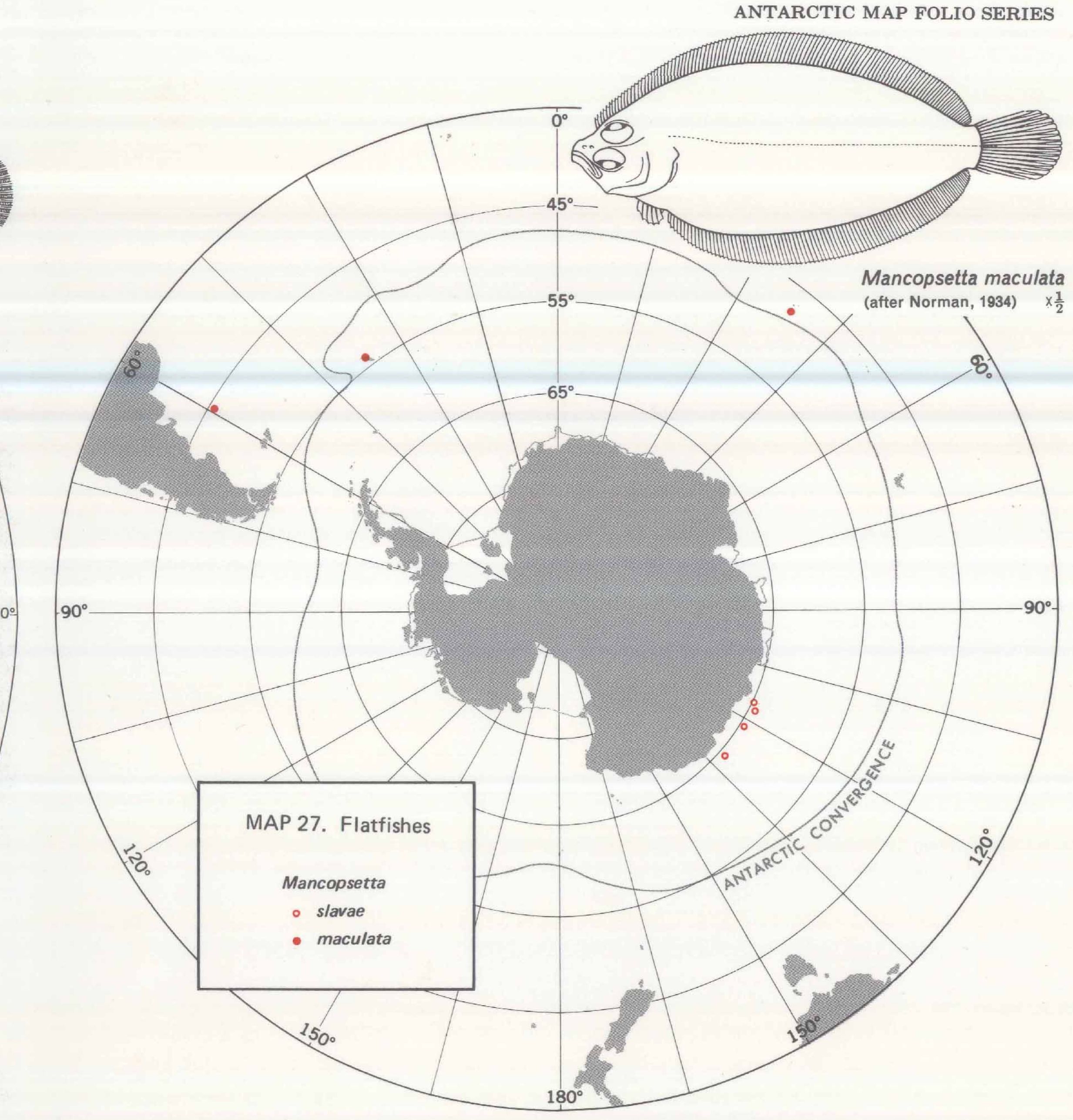
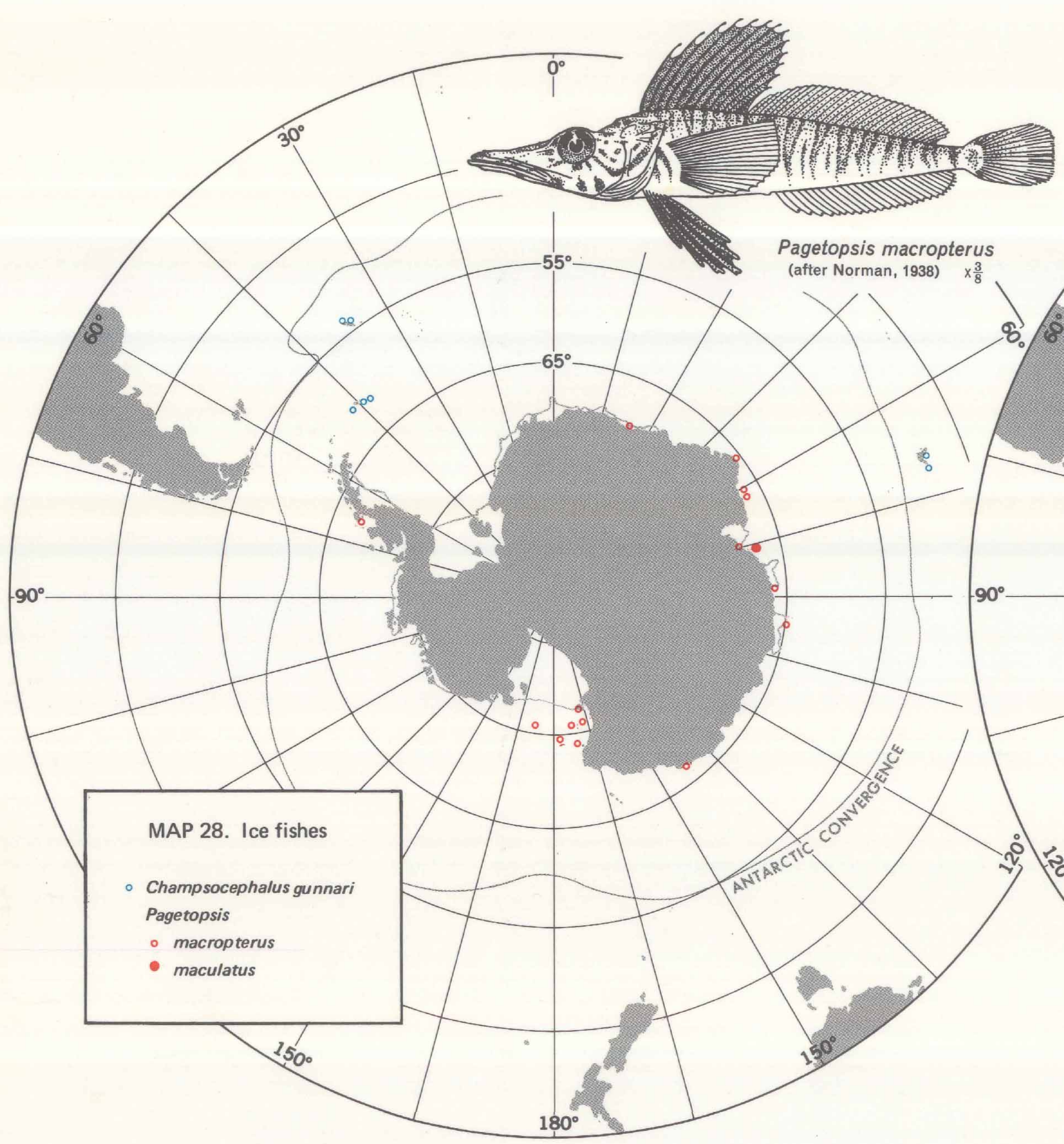
Pogonophryne scotti
(after Norman, 1938)
MAP 23. Plunder fishes
Pogonophryne
1 scotti
2 marmoratus
3 barsukovi
4 dolichobranchiata
5 mentella
6 permitini
7 phyllopogon

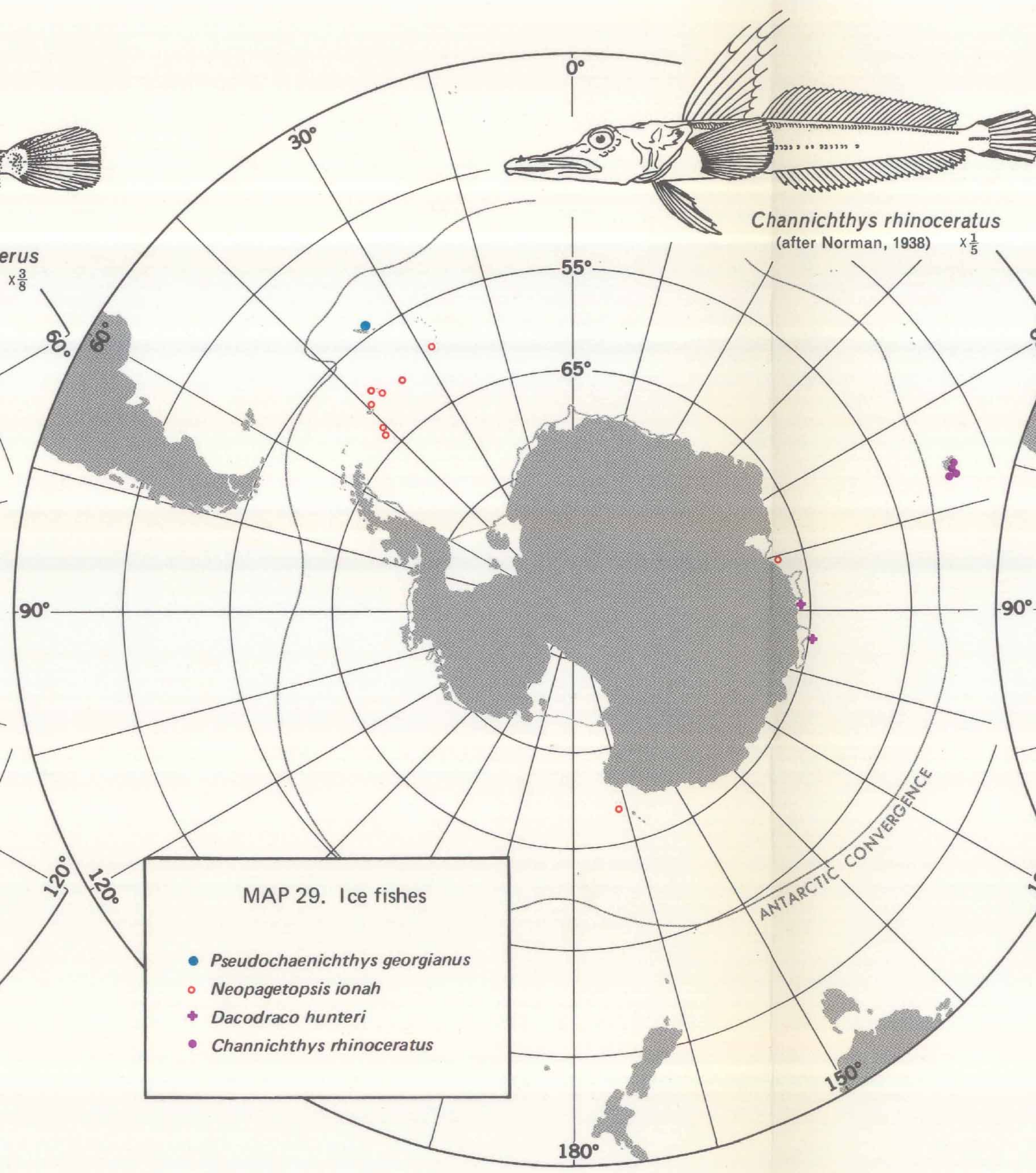


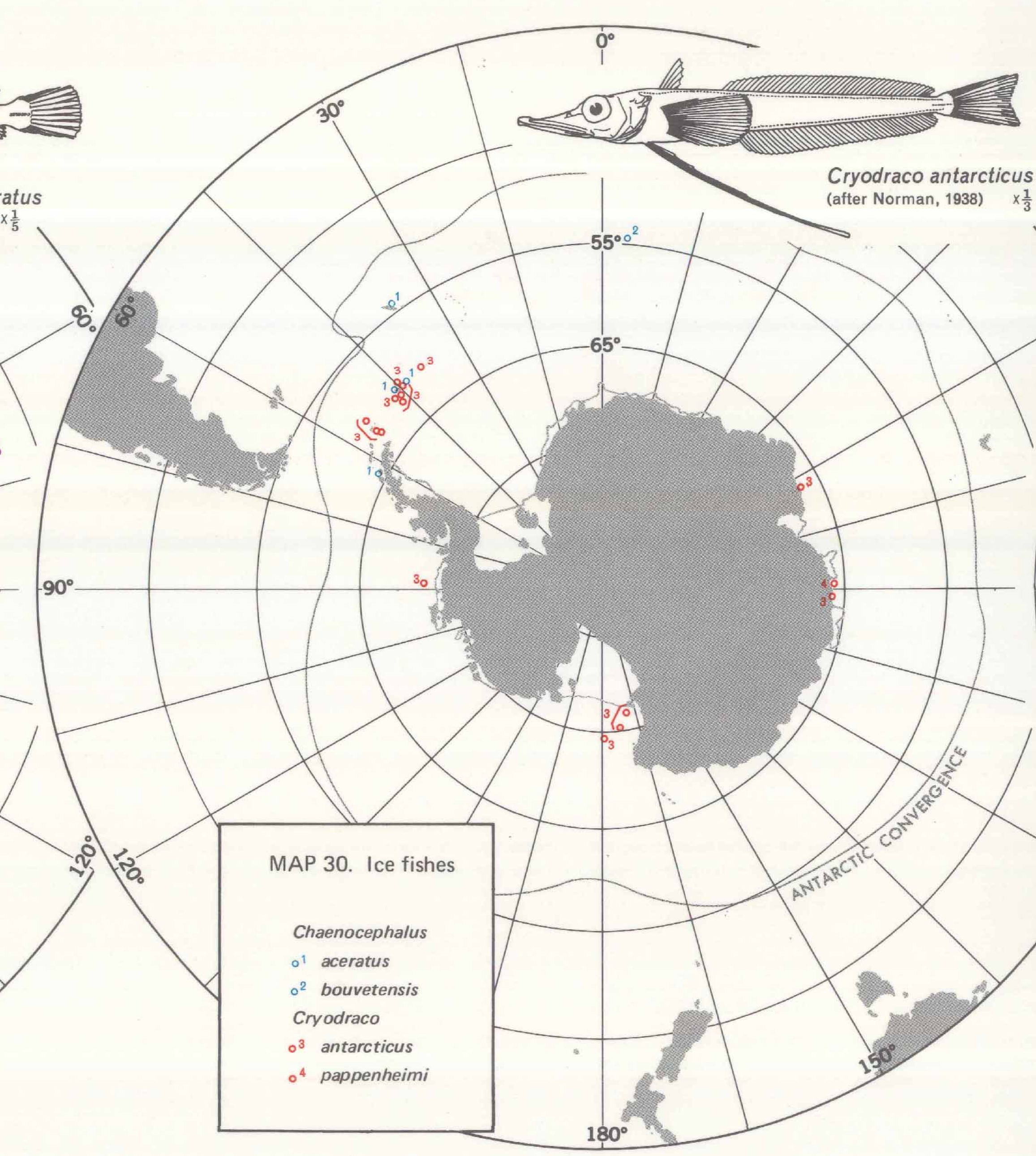


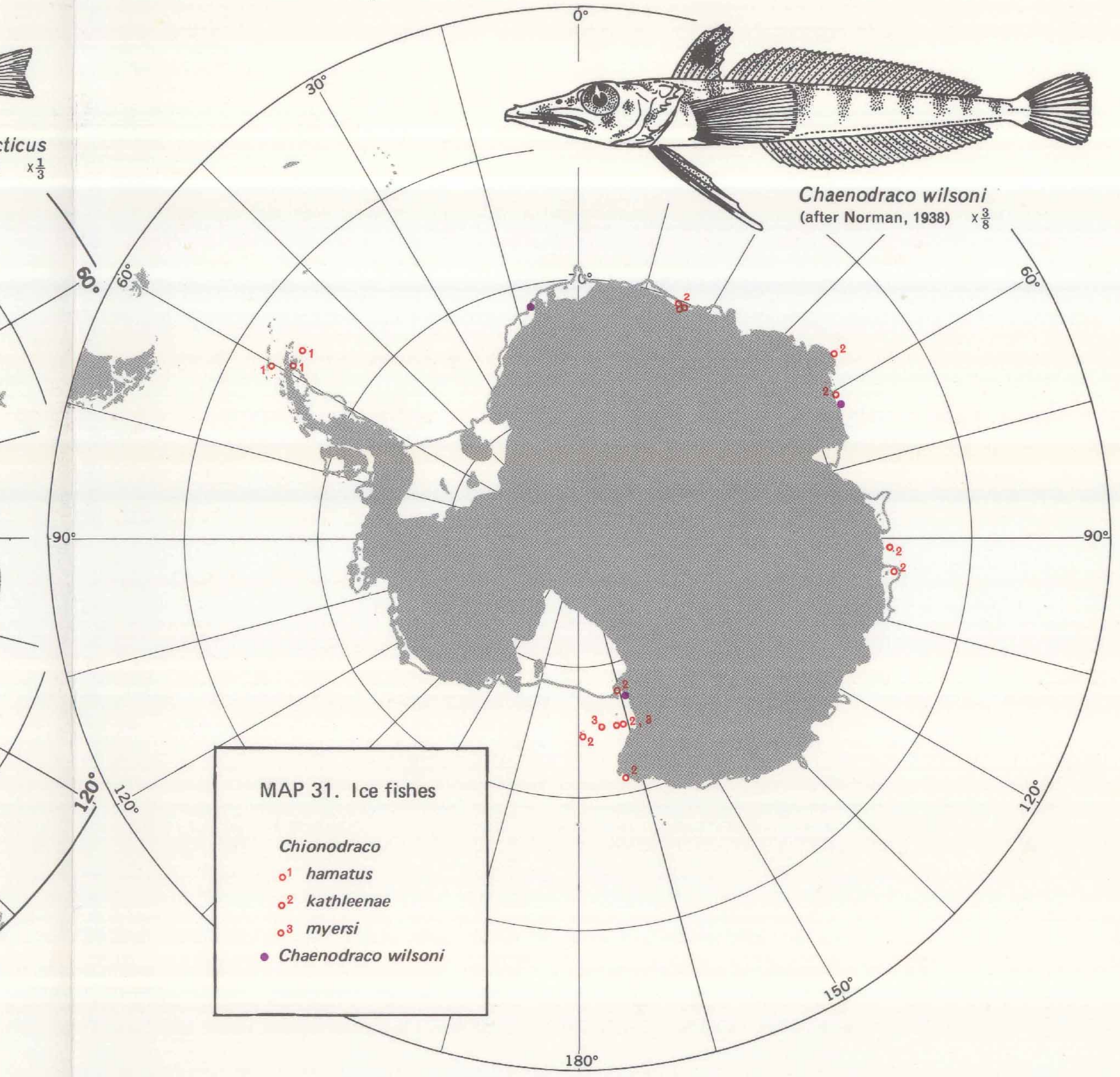












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