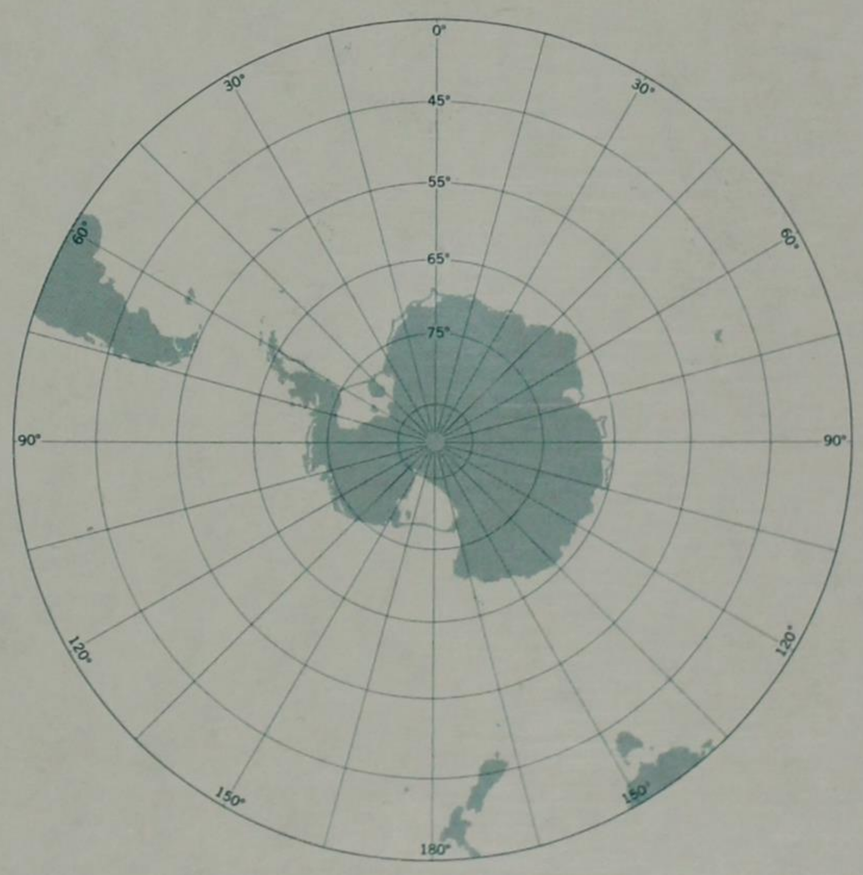
Antarctic Map Folio Series

FOLIO 11

Distribution of Selected Groups of Marine Invertebrates in Waters South of 35°S Latitude

A. W. H. Bé; H. Boschma and T. P. Lowe;
J. S. Bullivant; E. W. Dawson;
J. H. Dearborn and J. A. Rommel; R. K. Dell;
S. J. Edmonds; H. B. Fell and S. Dawsey;
H. B. Fell, T. Holzinger, and M. Sherraden;
M. W. Foster; S. R. Geiger and C. Brahm;
J. W. Hedgpeth; N. S. Hillman; D. E. Hurley;
V. M. Koltun; P. Kott; D. L. Pawson;
A. Ross and W. A. Newman; D. F. Squires



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GEOGRAPHICAL SOCIETY

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Antarctic Map Folio Series

VIVIAN C. BUSHNELL, Editor
JOEL W. HEDGPETH, Coeditor of Folio 11

The objective of the Antarctic Map Folio Series is to summarize in a succinct manner the present knowledge of the Antarctic; the Series will consist of some twenty folios, each devoted to one subject or scientific discipline. The areal extent of the coverage will vary from one folio to another. For example, folios dealing with atmospheric and oceanographic parameters will present data north of what is usually considered the Antarctic in order to furnish a meaningful picture, whereas studies of the ice sheet will necessarily be limited to Antarctica.

In planning the content of the Antarctic Map Folio Series, the advice of numerous scientists with many fields of interest has been sought with a most gratifying response. Much helpful guidance has also been furnished by the scientists on the staff of the Office of Antarctic Programs at the National Science Foundation.

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Editor's note:
The Antarctic Convergence line shown on the plates is taken chiefly from Mackintosh. However, between 10°W and 270°W Gordon's mean value, which incorporates new data, is used (A. Gordon, 1967, Folio 6, Antarctic Map Folio Series); between 60°E and 90°E the position is approximated according to information from R. Delépine (personal communication) that the Convergence is found between the Kerguelen Islands and Heard Island.

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Distribution of Selected Groups of Marine Invertebrates in Waters South of 35°S Latitude

Introduction to Antarctic Zoogeography

J. W. Hedgpeth[1]

THE OCEANOGRAPHIC SETTING

From the viewpoint of the distribution of marine organisms, the Antarctic Ocean is a system of concentric rings of water, moving slowly westward and downward near the roughly circular landmass of Antarctica, and eastward at the surface between the region of divergence at about 65°S (known as the Antarctic Divergence) and the great natural boundary of the Antarctic Convergence to the north (Deacon, 1937; Mackintosh, 1946). The region of divergence is roughly the limit of pack ice under present climatic conditions; during glacial periods the relationship between these two phenomena may have been different. This circulation pattern (Figure 1) corresponds roughly to latitude, and the water masses associated with it are more uniform in their temperature and salinity characteristics than around any other continent. The Antarctic Convergence, which lies at about 50°S in the Atlantic sector and 60°S in the Pacific sector, is an almost stationary, permanent boundary. In Folio 6 of this series this is termed the Polar Front (Gordon, 1967). Surface waters to the south have temperatures below 1°C in winter and 3.5°C in summer and salinities less than 34‰, while the Subantarctic Surface Water just north of the Convergence is around 2.0°C in winter and of higher salinity. Surface temperatures increase gradually and more or less regularly with latitude northwards to the Subtropical Convergence about 10° north of the Antarctic Convergence, where the temperature changes from about 10°C to 14°C in winter, and 14°C to 18°C in summer (Deacon, 1963). There is also a sharp increase in salinity in this region. The Subtropical Convergence is more variable in position than the Antarctic Convergence, and extends northward to North Island of New Zealand and towards 40°S along both sides of South America. Strictly speaking, the term 'Antarctic Ocean' should probably be confined to the waters south of the Antarctic Convergence. British and New Zealand workers prefer the less precisely defined concept of the 'Southern Ocean' (for example, Knox, 1960; Deacon, 1963; Brodie, 1965). It is usually understood as lying south of the Convergence, but may include parts of the Subantarctic, that broad region between the Antarctic and Subtropical Convergences.

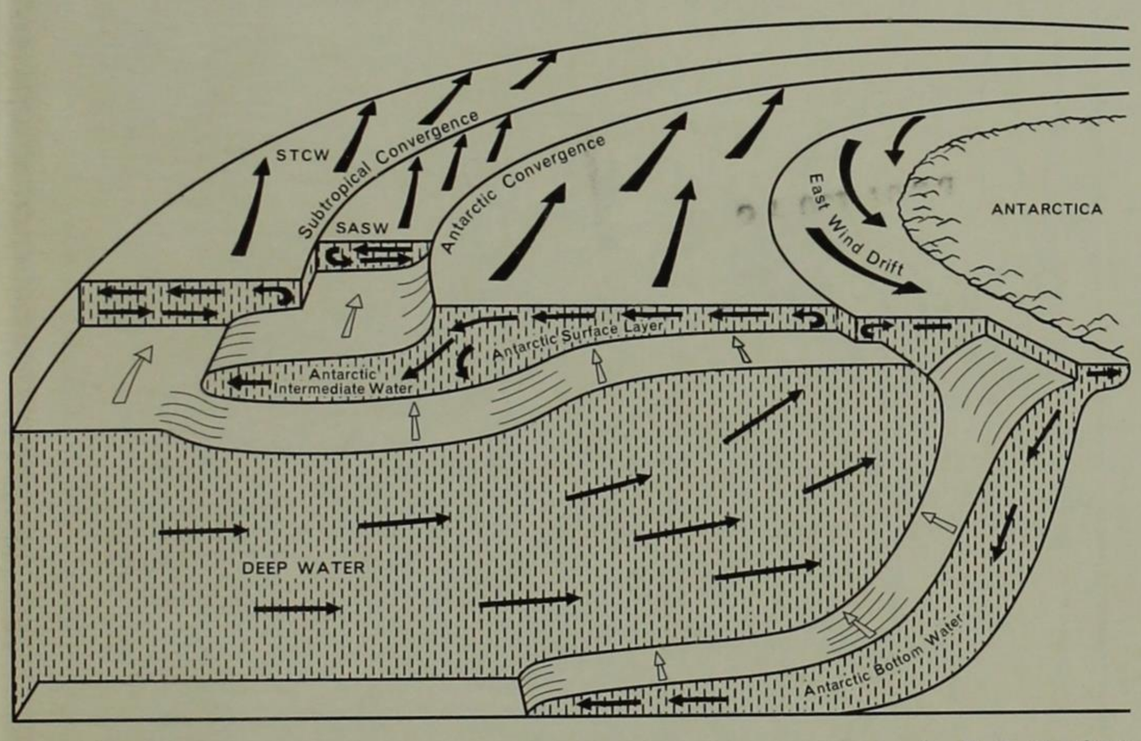


Fig. 1. The structure of Antarctic water masses (adapted from a diagram by R. I. Currie *in* David, 1965).

The surface waters of the 'Antarctic Ocean' form a layer about 200 m deep; at the Convergence this layer sinks below the warmer, lighter Subantarctic water. Near the continental shore the water is very cold and is more highly saline because of the ice cover. This cold, dense water, with temperatures below 0°C and salinities greater than 34.5‰, sinks northward from the shallow shelf regions as the Antarctic Bottom Water. Much of this water mass is formed in the Weddell Sea. The Antarctic Bottom Water moves northward and becomes mixed with the deep water of the Atlantic and Pacific Oceans, apparently without a gradient zone such as the surface convergences. Between the Bottom Water and the surface layers is the great intrusive mass of the warm Deep Water, originating in the Atlantic, Indian, and Pacific Oceans. Much of this water is derived from the Atlantic, and some of it by mixing with Antarctic Bottom Water.

Most of our information concerning the distribution of marine life is based on studies of the plankton of the upper layers and of the benthos; considerably less is known concerning the state of affairs in the deep waters of the bathypelagic regions.

Ekman's proposal (1953) to use the term 'Antiboreal' instead of 'Subantarctic' has not met with general acceptance, especially among oceanographers, who have declined to adopt the suggested change from Subtropical to Antiboreal Convergence. Some Soviet workers, for example, Vinogradova (1962), Andriashev (1962, but not 1965), and Lomakina (1964) have used the term 'notal' as the equivalent of Subantarctic (between the Convergences). In English, at least according to Webster III, this means 'pertaining to the back or dorsum,' and the word 'notalian' (which I have not encountered anywhere outside the dictionary), is defined by this august authority as the 'south temperate marine biogeographic realm that is bounded by the southern isocrymes of 68° and 44°F.' Fleming (1963) suggests that the terms 'Neoaustral' and 'Paleoaustral,' which he considers derived by false analogy to Nearctic and Palearctic, be replaced by the terms 'Neonotian' and 'Paleonotian' in paleontological usage. While one may be tempted by such a term as 'Paleonotian' for many discussions in this field, these and similar terms are subject to Fleming's criticism of false analogy, since they imply that the Southern Hemisphere is the back or dorsum of the globe. Most workers in this field have obviously found no objection to the use of the terms 'Antarctic' and 'Subantarctic' for the general biographic realms of what journalists often refer to as 'The Bottom of the World.'

PLANKTON DISTRIBUTIONS

The surface waters of the Antarctic comprise a relatively uniform biogeographic region, characterized by very high primary productivity which in turn is associated with a rich zooplankton population. El-Sayed (1968) estimates that the waters south of the Antarctic Convergence, which constitute about 5% of the world oceans, support a gross production in the order of 20% of the world oceans. On the basis of unit area, this means that the Antarctic is 400% more productive than the rest of the oceans. The dominant animal of the Antarctic is the krill *Euphausia superba* (Figure 2), which in the past supported the stocks of whales, and upon

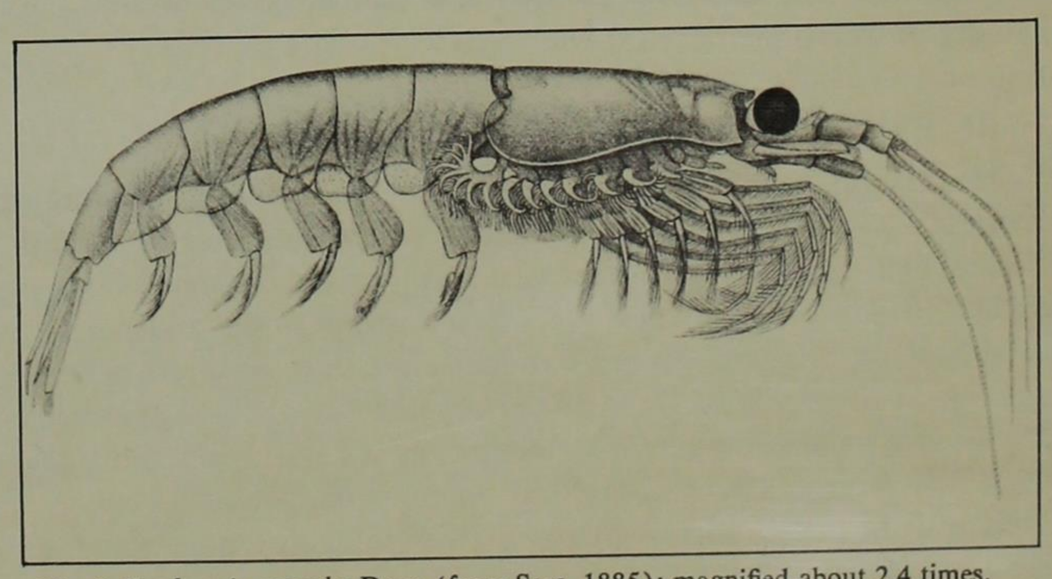


Fig. 2. *Euphausia superba* Dana (from Sars, 1885); magnified about 2.4 times.

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which several species of penguins, other sea birds, and many fishes depend (Marr, 1962). *Euphausia superba* is an Antarctic endemic, occurring, for the most part, south of the Antarctic Convergence (Figures 3, 4). Recent estimates of the total population of this single species vary rather widely, but suggest that the potential fishery for *Euphausia superba* might exceed that of all the other fisheries of the world combined. However, such a fishery would involve difficult processing problems.

This great productivity and the overwhelming abundance of this endemic species (along with other endemic zooplankton species of copepods, chaetognaths, and others) clearly set upper layers of the Antarctic Ocean apart as a separate and distinct region. Yet the regional abundance of this species indicates differences within the Antarctic Ocean itself. These differences are associated with the geographic conformation of the Antarctic continent. Most if not all zooplankton species are circumpolar in distribution, but they are not uniformly so, with the result that there are both qualitative and quantitative differences in the complex region of the South Atlantic, as well as the latitudinal differences south and north of the Antarctic Divergence. In the opinion of some workers, these differences merit recognition of sub-districts, such as 'high' and 'low' Antarctic zones (for example, Lomakina, 1964).

The Subantarctic waters do not comprise as discrete a zone for plankton as the waters south of the Antarctic Convergence. There are fewer endemic species, and most of the pelagic organisms are obviously derived from farther north, either as widely ranging species or closely related to warmer water species. David (1965) suggests that this colonization from the north is 'relatively recent' for chaetognaths; he believes that the fauna of the Antarctic waters are composed of 7 species, 3 of which are endemic, and that their basic distribution is circumpolar, the Antarctic and Subtropical Convergences acting 'to a greater or lesser extent as boundary regions for the fauna.' The occurrence of 4 species common to other regions suggests that, as far as oceanic distributions are concerned, the value of chaetognaths as 'indicator species' for specific water masses is moot. In any event, there is a tendency for zooplankton organisms to occur in latitudinal bands according to abundance.

The problem of latitudinal gradients has been discussed by a number of authors (see the review by Fischer, 1960), but perhaps without adequate emphasis on the population aspects. While it may appear, for example, that the total number of species in higher latitudes may be less than in the temperate or tropical regions, this diversity is apparently not as sharply marked with respect to populations. Such a diagram as Figure 5 shows the abundance, not of each species involved, but of all of them combined, and it does indicate that total numbers are greater in the Bering Sea than in the tropics. Several overlapping species of *Euphausia* occur in the Subantarctic seas (Figure 6), but this may be a misleading picture since it does not show relative abundances. According to Baker (1965), a single species tends to make up at least 50% of the total of all euphausiids in each ten degrees of latitude in the Indian Ocean, from the equator to from 60°S to 70°S. A further aspect of this problem is that of varying seasonal abundances of different species of the same genus.

According to Voronina (in press), for example, the three abundant mesoplankton copepods of the Antarctic have different cycles of development so that their maxima are spatially isolated. From these various considerations it is probably safe to assume that the overlapping distributions of planktonic organisms is more a reflection of the kinds of data at present available than of the actual situation in nature. When it is remembered that such distributions associated with different reproductive periods and rates may occur in an environment that is possibly as uniform as tropical waters are supposed to be, it is not difficult to suspect that as far as the plankton is concerned, the idea of latitudinal diversity, at least as simultaneous occurrence of more or less equally abundant species, may be overemphasized in the literature.

In any event, the broad picture drawn by Ekman (1953) of the pelagic zones of the southern regions is substantially correct, except that our knowledge of comparative abundances has increased greatly since his time, and the circumpolar distributions of many plankton species should be viewed as eccentric, represented by larger populations in the Atlantic sector (Scotia Sea and Weddell Sea) and thinner bands around the remainder of the Antarctic.

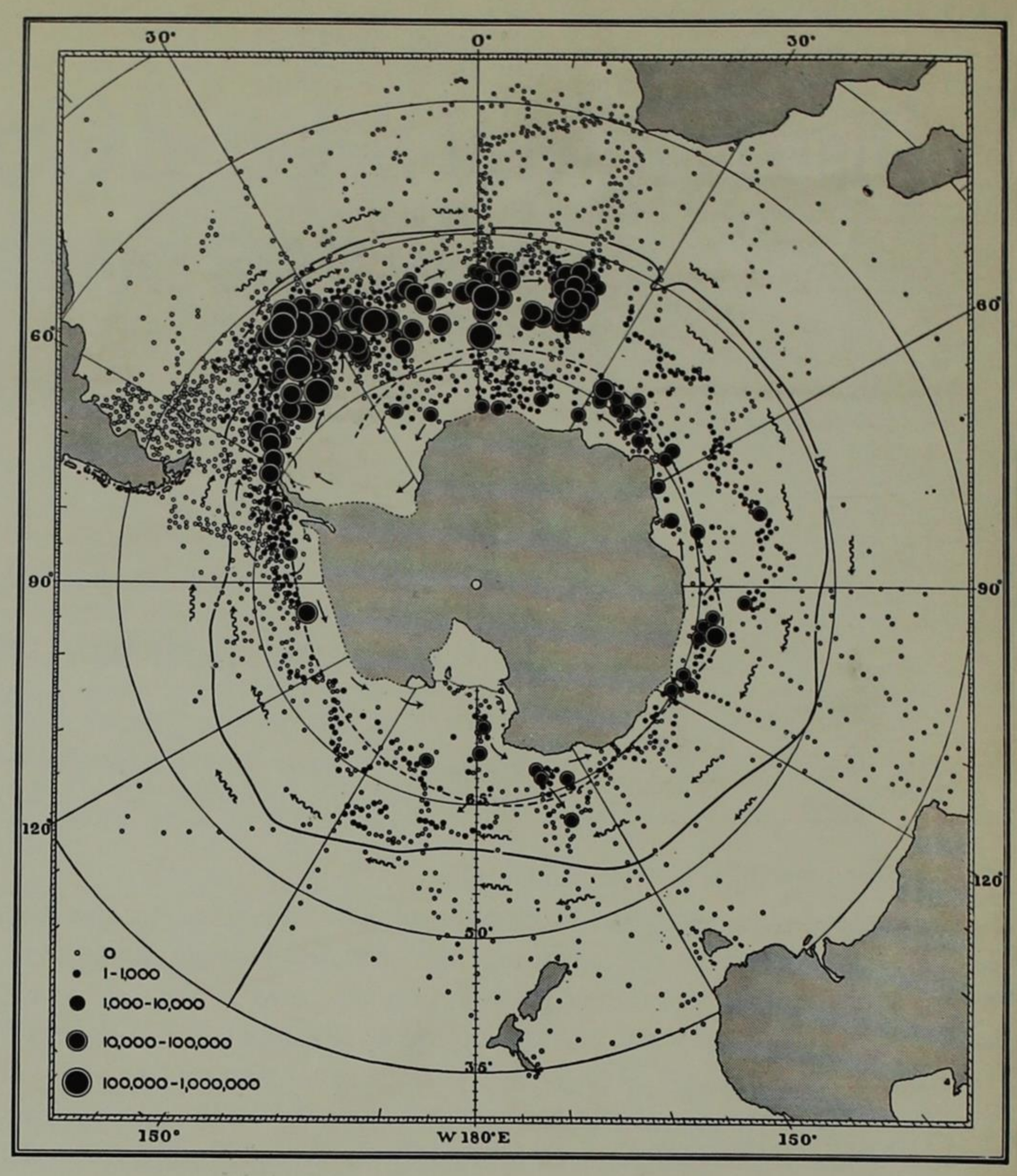


Fig. 3. Gross distribution of total euphausiid population (from Marr, 1962).

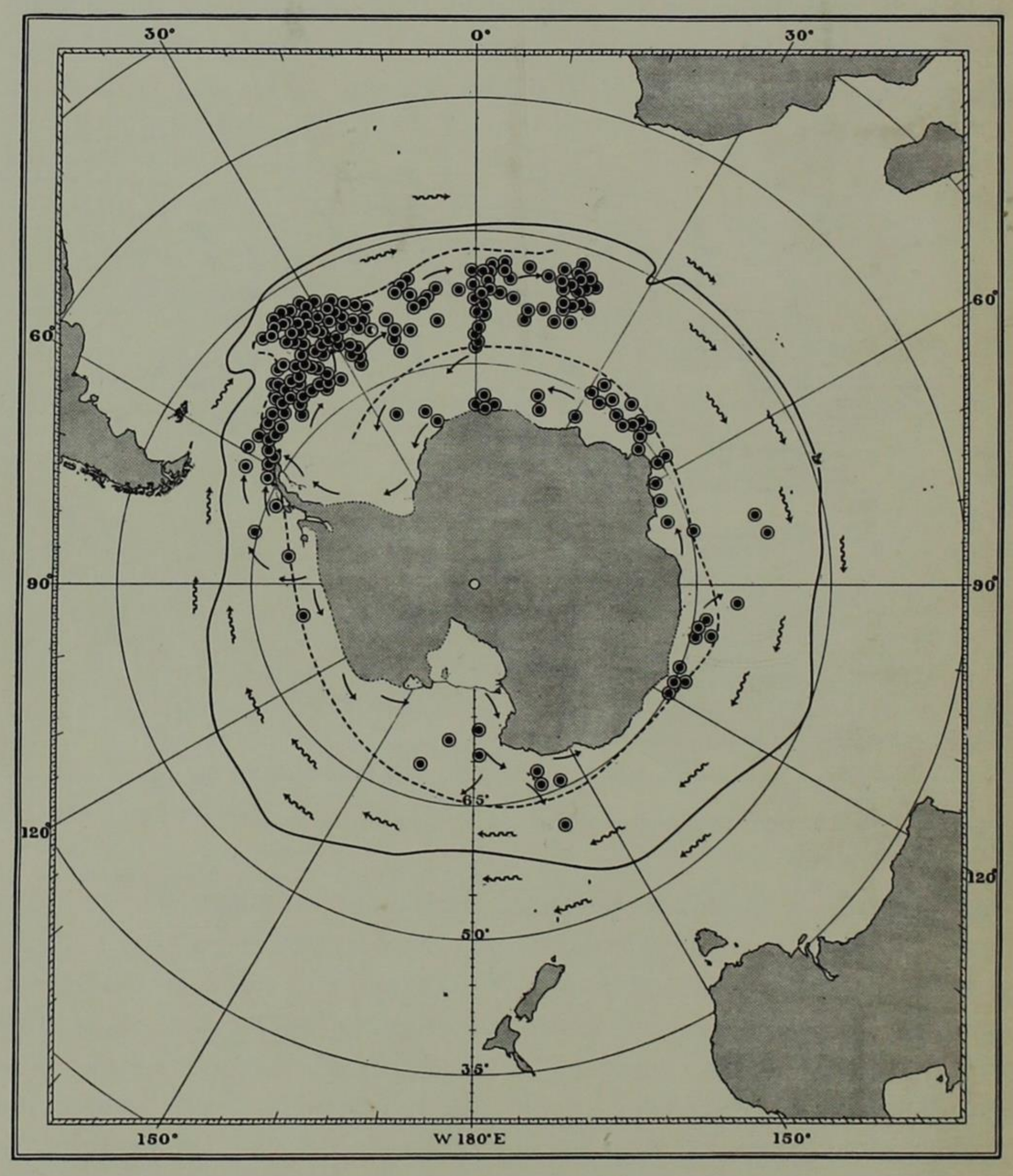


Fig. 4. Principal concentrations of *Euphausia superba* (from Marr, 1962).

THE BENTHOS

SUBLITTORAL ENVIRONMENTS. The near shore bottom of the Antarctic Ocean is a narrow region directly influenced by winter ice to a depth of 15 m to 30 m or more. This 'anchor ice' forms on the bottom as large crystals and in spring and summer is dislodged, rising to the undersurface of the annual ice, carrying entrapped organisms with it. As a result there is a bare region to a depth of 15 or 20 m occupied during the Antarctic summer by such vagile, foraging invertebrates as sea stars, echinoids, nemerteans, the isopod *Glyptonotus* and some pycnogonids (Dayton and Robilliard, in press). Below this is a zone consisting predominantly of sessile coelenterates, extending to 30 or 40 m, where it is replaced by a zone of sponges, bryozoans, ascidians, and numerous associated organisms. This zonal arrangement has been observed by divers in both McMurdo Sound and the Davis Sea (for example, Gruzov, Propp, and Pushkin, 1967); there appear to be some local differences due to slope or sediment types or ice action, but there are no significant differences in these widely separated areas, and the same pattern of zonal arrangement is probably circumpolar, at least in the near shore continental regions of the Antarctic.

Intertidal algae are absent from regions where the shore is ice bound for extended periods, but there is a well developed algal belt or region below extreme low tide, extending to about 37 m (Zaneveld, 1966). According to Zaneveld, this region can be subdivided into an upper belt or sublittoral fringe from low tide to 10 m, and a lower sublittoral belt down to 37 m. Below this is the elittoral or circalittoral region, extending from the sublittoral belt to the limit of macroscopic algae, which may be at a depth of several hundred meters in the Ross Sea. It is interesting to note that the

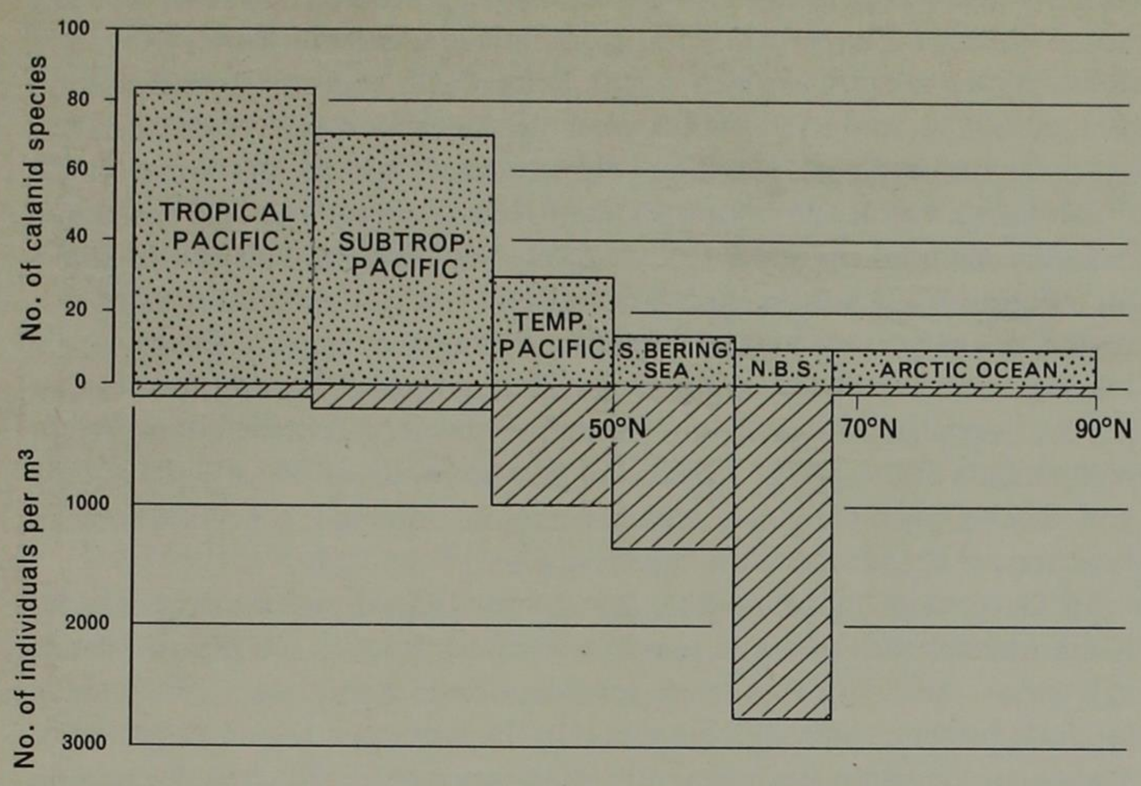


Fig. 5. Diversity gradient in pelagic calanoid copepods in the upper 50 m (adapted from a diagram by Brodsky *in* Fisher, 1960).

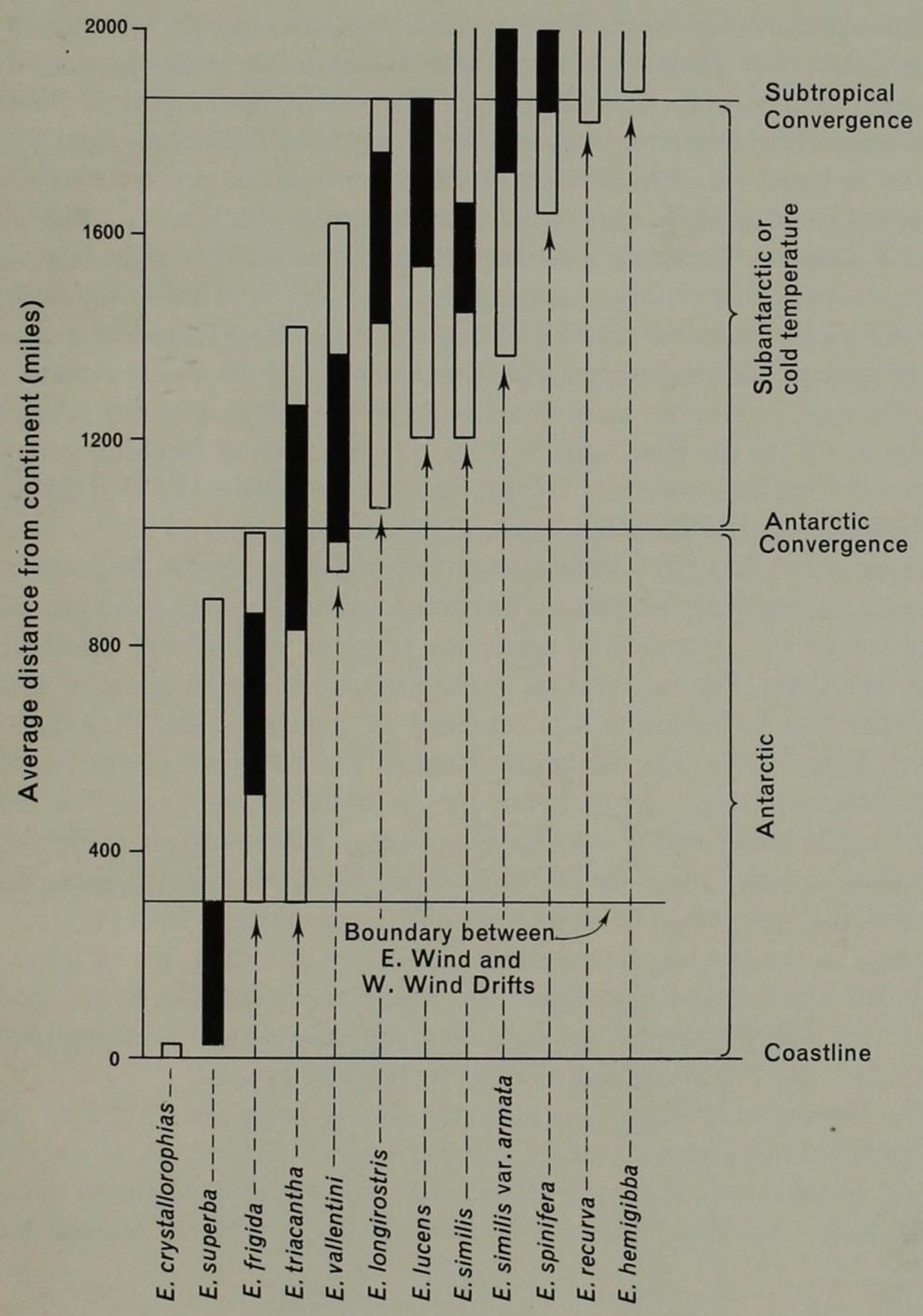


Fig. 6. Zonal distribution of species of *Euphausia;* the black parts indicate greatest concentrations (adapted from Mackintosh, 1960).

division at 10 m corresponds roughly to the region of unattached benthos observed by divers.

To the north, where the shore is free of ice for longer periods, algal growth increases, and on many of the Subantarctic islands there are abundant growths of macroscopic algae, especially *Durvillea*. This genus is not represented south of the Antarctic Convergence. However, two sublittoral brown algae are restricted to the south of the Convergence; these are *Phyllogigas grandifolias* from the South Shetlands to Cape Adare (or 73°S) and *Ascoseira mirabilis* on islands of the Scotia Ridge to the South Shetlands. *Macrocystis pyrifera* reaches its southern limits around South Georgia and the islands near the Antarctic Convergence from Prince Edward to Macquarie. For further information on the distribution of Antarctic macroscopic algae, see Neushul (1968) and Zaneveld (1968) in Folio 10 of this series.

THE ROSS SEA BENTHOS. The deeper parts of the Ross Sea, from 200 m to 400 m, are rich in assemblages of invertebrates; Bullivant (1967) recognizes three major assemblages of larger invertebrates associated with different types of bottom on the basis of qualitative samples and photographs. The first of these he calls the Deep Shelf Mixed Assemblage, associated with a fine sediment with erratic boulders, consisting for the most part of tubiculous polychaetes, rooted bryozoa, various echinoderms, and mollusks. The second type is the Deep Shelf Mud Bottom Assemblage, occurring on mud or sandy mud bottom with erratic boulders; tubiculous polychaetes are abundant here, along with sipunculids, a foraminifer and ophiuroids. The third assemblage is that associated with a bottom of cobbles embedded in muddy sand, consisting for the most part of hard bottom animals such as bryozoa, gorgonaceans, stylasterine corals and tunicates, several species of ophiuroids and pycnogonids. A number of minor assemblages were noted, including the McMurdo Sound glass sponge assemblage in depths of 69 m to 180 m, on a bottom of 'unsorted rock debris.' Some of these assemblages are not well defined quantitatively.

Taken as a whole the Ross Sea benthos consists primarily of sessile, filter-feeding, or fine particle-feeding invertebrates attached to numerous rocks, and cannot be compared with the shallow, soft, or level bottom communities of European waters. The nearest analogue seems to be the assemblage associated with cobble bottoms off Point Barrow. In deeper water where sediments are finer, sessile organisms are less abundant, and polychaetes, crustaceans, echinoderms, and mollusks are relatively more numerous.

It seems probable that similar assemblages occur all around the Antarctic, but comparable quantitative data of the sort that has been obtained for the infaunal bottom communities of northern latitudes will be very difficult to obtain for these essentially epifaunal assemblages. As Bullivant remarks, many of the common organisms making up these assemblages are circumpolar in distribution.

SEDIMENTS. Antarctic bottom sediments consist for the most part of glacial or 'iceberg' sediments brought from the continent by ice action. These are not deposited immediately near the shore but are carried out to the outer shelf and slope; they consist of muds, fine and coarse sand, and boulders; the finer sediments are greenish gray in color (Brodie, 1965). The region of glacial sediments corresponds roughly with the limit of pack ice; north of this region the predominant sediment is creamy yellow diatom ooze with patches of recent volcanics and foraminifera. These sediments are replaced farther north by foraminiferal ooze and large areas of red clay in deeper parts of the Pacific sector. Near shore the abundant filter-feeding animals of the bottom assemblages suggest low rates of sedimentation. It is possible that sedimentation may be comparatively light under the present climatic regime.

PATTERNS OF DISTRIBUTION. Ekman (1953) divided the benthic faunas of the shelf and near island bottoms into Antarctic and Antiboreal regions. For the Antarctic he recognized a high Antarctic subregion, in turn divided into the West Antarctic, including the Weddell Sea and Antarctic Peninsula, and the East Antarctic, including the Ross Sea. He considered the low Antarctic region to include South Georgia. He divided the Antiboreal region into a South American subregion with a strong Antarctic component, a region of oceanic islands, and a Kerguelen region. These generalizations were based, for the most part, on information from the first intensive era of Antarctic exploration and collecting before 1914; since then systematic work with many groups has been reappraised, and new information has become available. It should be noted that Ekman (or his translator) is not precise about such terms as 'region' and 'province' and indeed uses them interchangeably.

While many recent workers, including most of the contributors to this folio, do not find clear evidence of distinct East and West subregions, Koltun, in this folio, notes differences in the sponge genera of East Antarctica, including McMurdo Sound, and West Antarctica and believes that this cannot be explained on the usual grounds of inadequate collections. Kussakin (1967) designates as the East Antarctic province for isopods the region from somewhere in the Weddell Sea around the entire continent to 90°W in the Bellingshausen Sea, this is almost circumpolar (270°) and leaves the Antarctic Peninsula and nearby islands, with the exception of South Georgia, as his West Antarctic province. South Georgia is considered a separate province in this scheme. On the basis of fishes, Andriashev recognizes a Continental Province with East Antarctic and West Antarctic districts.

Except for the different uses of 'subregion' and 'province,' the divisions proposed by Andriashev and Kussakin are essentially the same. The East Antarctic of these distribution schemes is the continental near shore, or 'high' Antarctic, of Ekman and many authors following him, but Ekman's 'low' Antarctic included South Georgia, which, according to some systematists, merits recognition as a separate region or province. The South Georgian Province proposed for ascidians by Kott in this folio includes the islands of the Scotia Ridge and the Antarctic Peninsula, however. A number of the contributors to this folio suggest that the fauna of the Antarctic Peninsula and island arc is somewhat different in composition from the 'high' Antarctic region, and especially that it shows strong affinities with that of South America. The groups involved in such a distribution pattern include the Bryozoa, Brachiopoda, Mollusca and many echinoderms. Groups represented mainly by deeper water species, including the various types of corals, sipunculids, and echiurids do not show such a regionalization, and are more closely related to the Convergences than to continental and island configurations.

In a recent review of benthic faunas, Dell (1968) recognizes four main groups of mollusks according to distribution. These are:

(1) Species found around Antarctica

(2) Species found in Antarctica but only in the regions of the Weddell Sea, the Antarctic Peninsula and the Bellingshausen Sea, that is, the region immediately adjacent to the Scotia Ridge

(3) Species confined to the Scotia Ridge

(4) Species characteristic of the Subantarctic islands[2]

Dell also notes that many Antarctic mollusks have very wide bathymetric ranges (a circumstance also applicable to sponges and pycnogonids); 48 species have ranges exceeding 500 m, and 5 have ranges greater than 1,000 m.

All of the Antarctic islands have littoral species in common with New Zealand, South America, and South Africa in varying degrees (Figure 7). This indicates that the source of colonizing species tends to be the nearest neighbor to the west (especially in the case of Tristan da Cunha

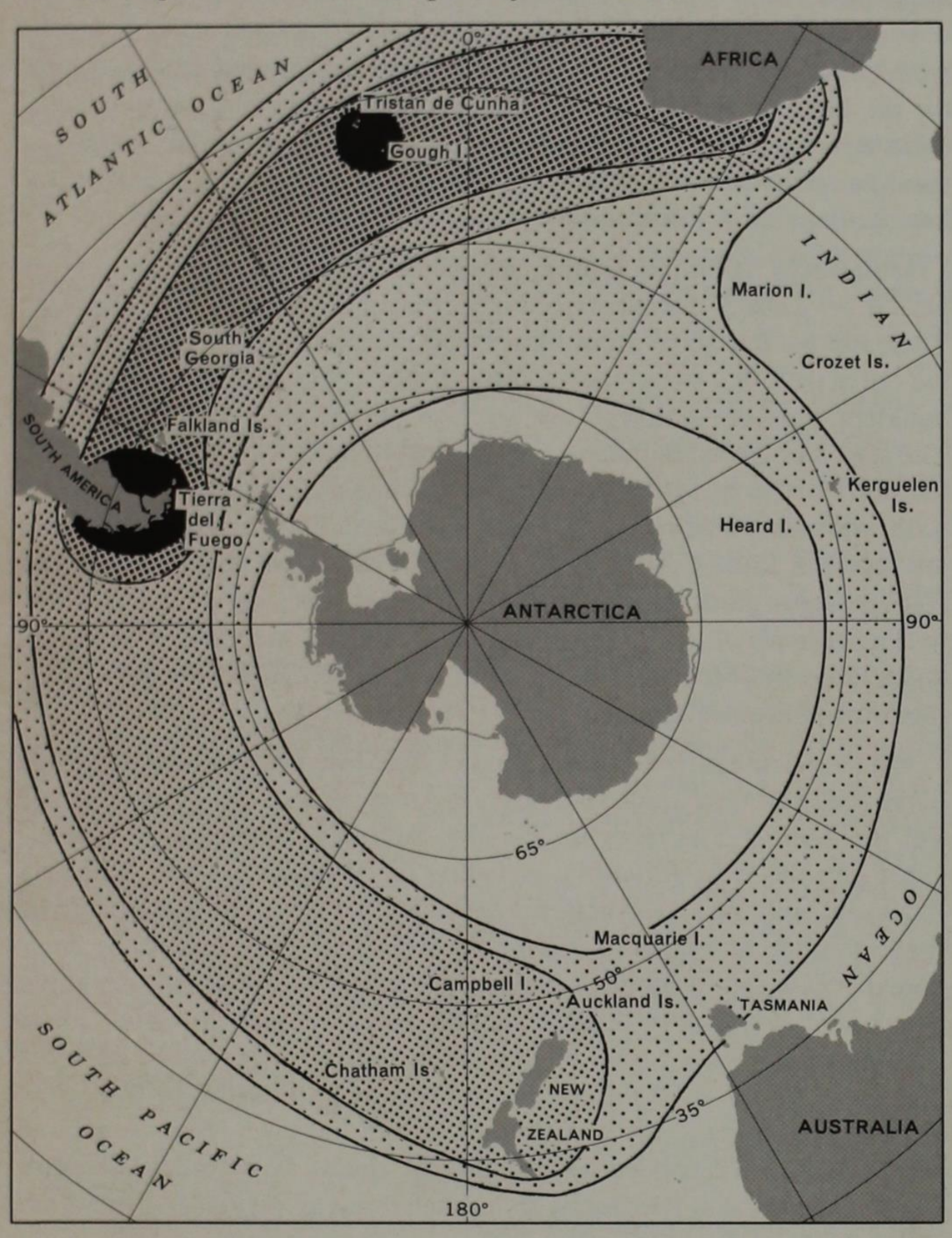


Fig. 7. Distribution of marine fauna of the Subantarctic islands and southern continents (adapted from Holdgate, 1960).

and South America), and that the distribution of these species is apparently influenced by the West Wind Drift or prevailing eastward surface current of these latitudes. Fell (1967) postulates that the New Zealand region is an area of active speciation, sending its colonists eastward, so to speak. However, it should be pointed out that New Zealand stands astride the cold temperate and subtropic seas and accordingly provides a broader range of environments, whereas the similar extent of South America lies well within cold temperate or Subantarctic conditions, so it should be expected that eurythermal New Zealand species might gain footholds in South America. Further, the Subantarctic islands by their nature as small, stenotopic environments, have proportionately fewer species to contribute to the eastward trend. It does not seem necessary to invoke rates of evolution or the Coriolis effect to account for this pattern. Fell also suggests that this evolutionary pattern could be traced in the opposite direction in the tropics; this idea has been criticized with respect to insular speciation by Briggs (1967). To say that such trends in speciation may be related to the Coriolis parameter is to say little more than this is what might happen on a spherical rotating body such as the earth.

Although fishes would be expected to conform to the general distribution patterns recognized for invertebrates, the distribution of penguins, when related to their nesting sites, is surprisingly similar, and follows systematic divisions rather closely. The Antarctic group includes the Emperor, which nests only on ice on the continental ledge, and the Adélie and Ringed penguins which nest on outlying Antarctic islands but not South Georgia. The Subantarctic group includes the Macaroni, King, and Rockhopper penguins which occur from South Georgia to Macquarie Island, that is, on the islands between the Antarctic Convergence and the northern limit of pack ice. The cold temperate species overlap with the Subantarctic species on islands south of New Zealand. The cold temperate category includes the species of southern New Zealand and South America (Figure 8). Antarctic and Subantarctic species spend more than half their lives as pelagic animals, and their ranges at sea are incompletely known, but are probably not greatly different from the broad distribution patterns suggested in the figure. Hence they must be considered important components of the pelagic regions of the Antarctic, especially the Adélie and Rockhopper penguins, which occur in observed concentrations of hundreds of thousands at the breeding sites.

In the general biogeographic scheme for littoral regions proposed by Knox (1960) the Antarctic province includes Bouvet and Heard Islands as well as the South Sandwich Islands; South Georgia is considered a separate province although lying within the Antarctic region (Figure 9). The Antarctic Peninsula and Scotia Ridge are considered to be the Scotian Subprovince; a separate Rossian Subprovince is recognized for the Ross Sea and adjacent regions. In the Subantarctic or cold temperate regions, the scattered islands of Prince Edward and Marion, Crozet, Kerguelen, and Macquarie comprise the Kerguelenian Province, and the Subantarctic islands near New Zealand, but not the shore of South Island proper, are regarded as the Antipodean Province. The southernmost part of South America and the Falkland Islands make up the Magellanic Province. This scheme is based on consideration of information about plants as well as many groups of animals, but is concerned primarily with littoral or shallow water organisms. Therefore it does not take into consideration the benthos of depths below the limits of algal growth. Most of our information for the benthos concerns the animals of this lower region and includes a number of groups showing strong affinities with the tip of South America. Furthermore, it does not seem possible to defend independent or subprovincial status for the Ross Sea; as work progresses on group after group, supposed Ross Sea endemics fall by the wayside. Dell (1968) does not recognize a separate Ross Sea region for mollusks.

There is no clear agreement among biogeographers as to the limits or comparative ranking of regions, provinces, or other biotic subdivisions. As noted above, even Ekman used such terms as 'region' and 'province' interchangeably. For the purposes of this folio, the major divisions, that is, Antarctic and Subantarctic, are regarded as 'regions' rather than 'provinces' (Figure 10). The Antarctic Region, including all of the Scotia Ridge and the pelagic waters below the Antarctic Convergence, has two major subdivisions which may be regarded as subregions or provinces, according to taste. These are the 'high' Antarctic or continental Antarctic, south of the Antarctic Divergence, roughly equivalent to East Antarctic of some workers, and the 'western' Antarctic including the Antarctic Peninsula and Scotia Ridge. From this broad viewpoint it does not seem that South Georgia should be regarded as an independent biogeographic entity, but may rate status as a 'district' or subprovince.

The Subantarctic Region includes the vast oceanic area south of the Subtropical Convergence (except that the limits of this region on the two sides of South America are not yet defined), and the shallow waters of the tip of South America. Although the southern part of New Zealand lies

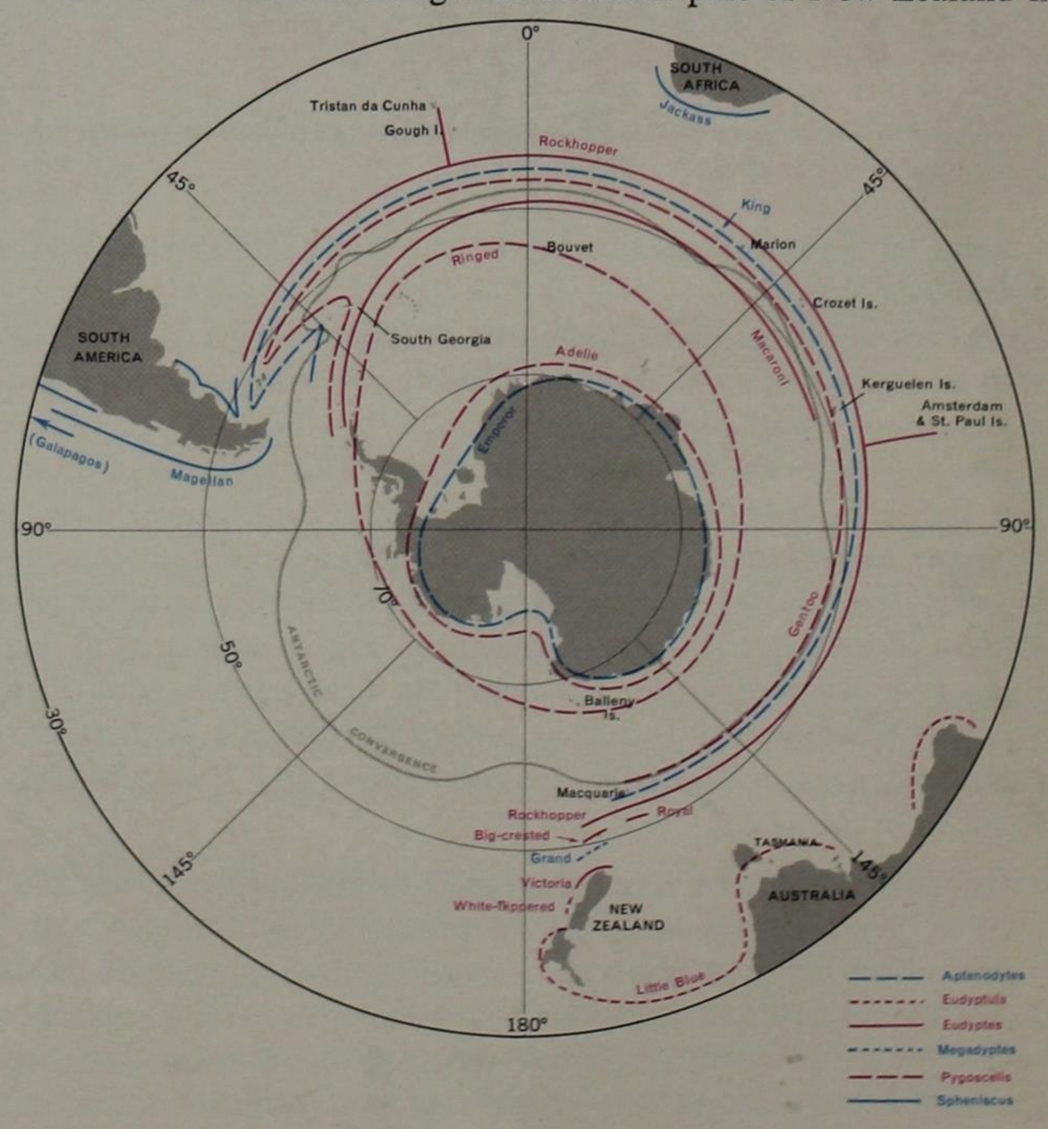


Fig. 8. Distribution of penguins in the Antarctic and Subantarctic regions (adapted from Mackintosh, 1960).

[2]The somewhat different categories in Dell's contribution to this folio are based primarily on origin rather than present distribution, but are essentially the same.

within the Subtropical Convergence, the biota is not regarded as 'Subantarctic' but 'cold temperate.' There is certainly less evidence of interchange at this time between South America and the Antarctic regions. There are some faunal similarities between New Zealand and South America, as there are between South America and Tristan da Cunha and Gough Islands. This distribution pattern is usually associated with the West Wind Drift, the prevailing eastward current of these latitudes. A similar eastward distribution pattern has been recognized for the islands near the Antarctic Convergence from Kerguelen to Macquarie. These islands are usually regarded as comprising a Kerguelen subregion, province, or district. The status of such isolated islands as Bouvet and Heard is uncertain because of inadequate information, but they appear to be more Antarctic than Subantarctic.

It is possible that some of the faunal relationships between various Subantarctic islands and such mainland regions as New Zealand and South America may be due to past connections of shallow 'highways' which might have been available in late Cretaceous or early Tertiary times. The situation on the Chatham Islands, less than 1000 km from New Zealand, emphasizes the difficulties faced by many marine invertebrates in crossing marine barriers (algae seem to be more able to cross such barriers). The fauna of the Chatham Islands is an interesting mixture of elements from North and South Islands of New Zealand that may have been established since post Pliocene times (see Knox, 1954), yet certain common New Zealand intertidal genera and species have been unable to establish themselves. It is hardly surprising, in the light of this example, that there are no barnacles, prosobranch limpets, littorines, or mussels in the upper intertidal zone of Macquarie Island (Kenny and Haysom, 1962).

There seems to be only slight evidence that the Kerguelen-Gaussberg Ridge and the Macquarie Rise serve as migration routes, even for eurybathic species. The principal migration or transfer route at this time is the region of the Scotia Ridge, but here, as Dell (1968) points out, the situation is much more complex because of the various island groups and the shallow regions between them.

BIPOLARITY

Much has been written about bipolarity, the occurrence of identical or similar species in Arctic and Antarctic waters (see Ekman, 1953, pp. 244–263), as an indication of a previous continuous distribution of polar faunas. The basic argument set forth by D'Arcy W. Thompson (1898) still holds, however, namely that the phenomenon is comparatively insignificant in terms of actual numbers of authentically bipolar species, and that many supposedly bipolar species will fall under critical systematic reappraisal. Very few examples of species with completely discontinuous distribution are cited by the contributors to this folio. In the sponges, for example, Koltun mentions 4 such species in a total of 300 Antarctic and 200 Arctic species, and several others whose occurrences while essentially bipolar are nevertheless found in lower latitudes, especially in the Northern Hemisphere (see Plate 4). As with many other groups, the general facies of the fauna is remarkably different, and the large distinctive species of the family Rossellidae are charcteristic; this family is not represented at all in Arctic waters.

There appear to be no bipolar or even antitropical species of stylasterine corals, and the species of this group form a zoogeographic unit in Antarctic and Subantarctic waters. The information for the scleractinian corals suggests a similar distribution. Of the 16 species of brachiopods from Antarctic waters, 11 are endemic, and the others are widespread deeper water forms. Most of the 130 species of the Bryozoa occurring in the Antarctic and elsewhere are Southern Hemisphere species, and only a single species is noted as occurring in the Arctic at all.

Much of the original emphasis on bipolarity was based on the similarity of species in the group formerly known as 'Gephyrea,' an unconvincing assemblage of sipunculids, echiurids and priapulids. It is interesting to note that Edmonds (in this folio) lists 7 sipunculids as bipolar but cautions that some of these may turn out to be more widely distributed than previously thought. As for the echiurids, 2 species are claimed as bipolar, but the records are admittedly inadequate; for 1 species, 3 specimens are known (1 of them fragmentary) and for the other a single slightly damaged specimen is known, all of them from the South Shetland Islands.

The classic bipolar example, at least in the past, has been that of *Priapulus caudatus,* and one may still find references to this species as 'known only from the north and the south, particularly in the polar regions' (Hardy, 1967). However, Lang (1951) convincingly demonstrated that the Antarctic–Subantarctic form *tuberculato-spinosus* is a separate species, and Murina and Starobogatov (1961) recognized *Priapulus tuberculatospinosus* as one of the forms of a widely distributed deepwater species found as far north as Kamchatka and deeper waters of the north-

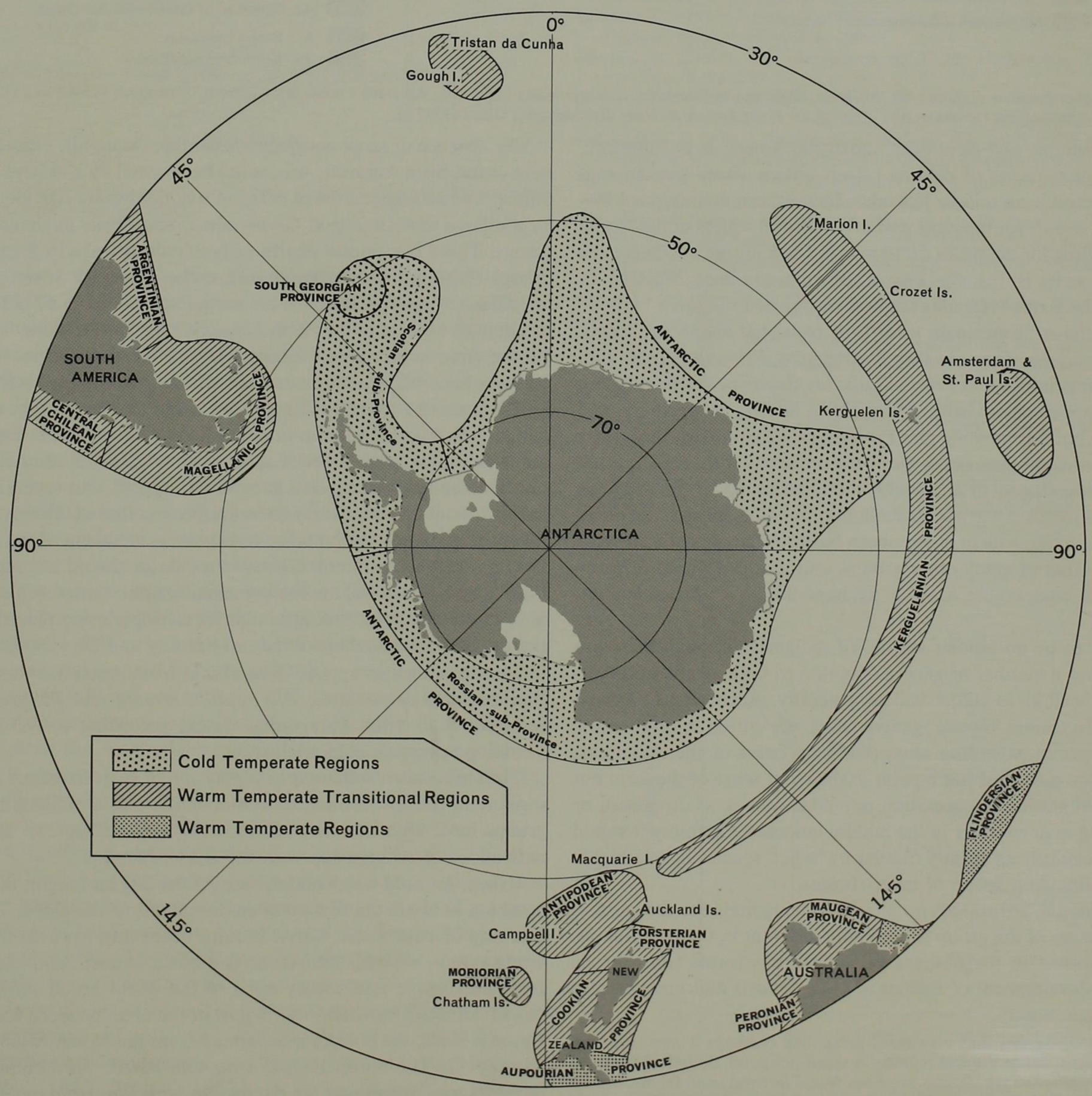


Fig. 9. Proposed biogeographic division of the southern temperate and Antarctic regions according to Knox (1960).

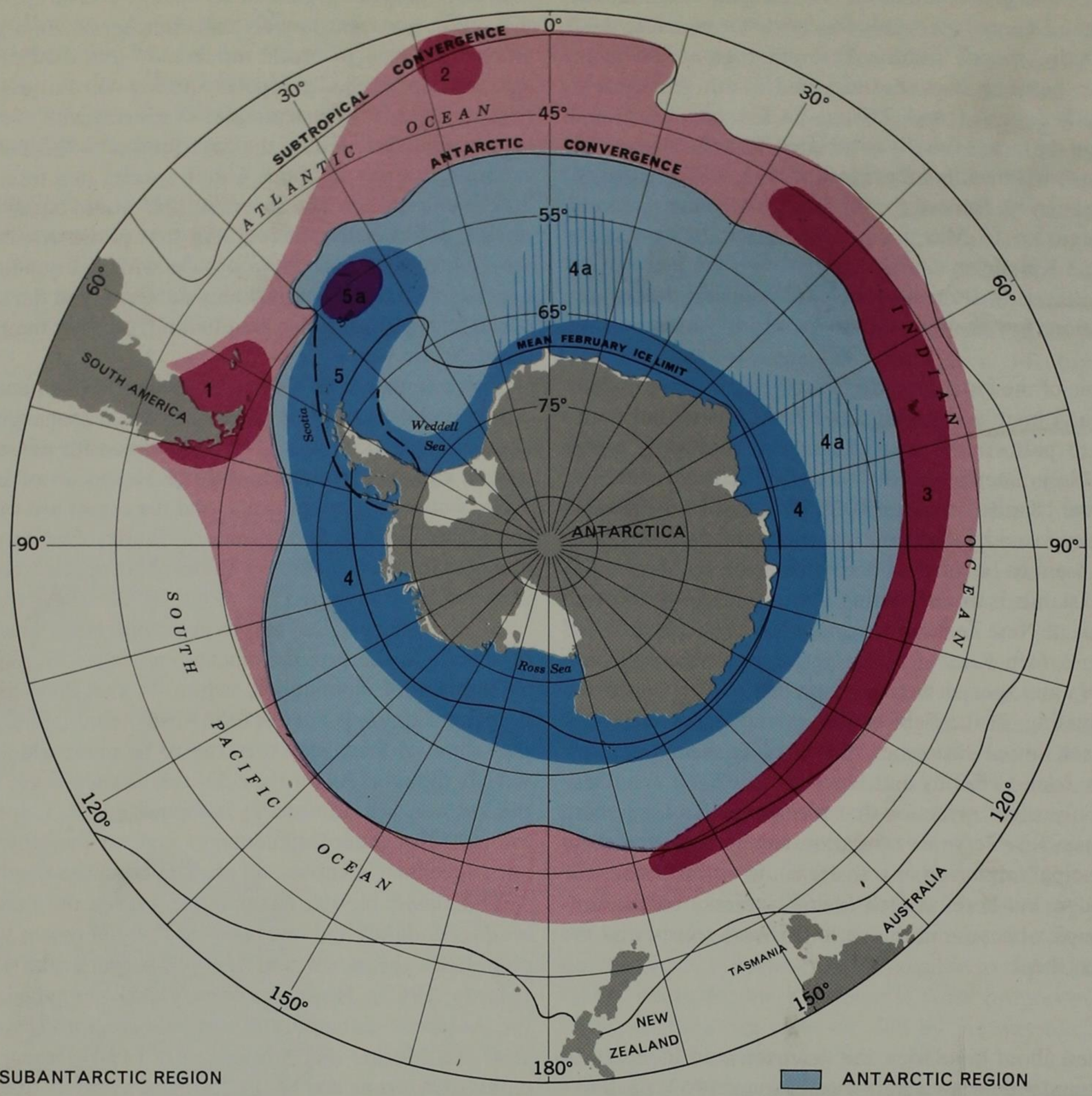


Fig. 10. Biogeographic divisions proposed for this folio. [Subtropical Convergence is according to Deacon; Antarctic Convergence is from Mackintosh (1946) and Gordon (1967); mean February ice limit is from *Oceanographic Atlas of the Polar Seas*, U.S. Navy Hydrographic Office (1957)]

eastern Pacific basin as well as in deep equatorial waters. It is, therefore, a widely distributed species of cold and deep waters whose pattern suggests deep submergence in middle latitudes. Its northern counterpart, *Priapulus caudatus,* occurs for the most part in sublittoral waters of the Arctic but there are records for depths of 2670 m and 1425 m; the southernmost record for this species is Tomales Bay, California, at about 38°10′N. In all, 7 species of the genus *Priapulus* are now recognized (Figures 11, 12). Of these, 3 are known from single records or restricted deepwater localities. The genus may be separated into 2 subgenera, *Priapulus* s. str. with a single caudal appendage and *Priapulopsis,* for those species having two tails or caudal appendages. Both groups have species in northern and southern waters, but it is possible that *Priapulus atlantisi* should not really be considered in this subgenus because of the markedly different structure of the caudal appendages. In any event, the distribution of the genus as a whole indicates that it is a group of shallow cold-water species and deep-water species occurring widely in the ocean basins.[3] This distribution pattern is similar to that of many other groups, and that of *Priapulus tuberculatospinosus* is comparable to such pycnogonids as *Colossendeis angusta.*

There appear to be no bipolar species of mollusks although there are many families and a number of genera common to both Arctic and Antarctic waters as well as to colder waters generally. According to Powell (1965), there are several 'bipolar' genera which are currently represented by cold-water species extending along the west coast of the Americas; such a distribution pattern is not bipolar in the strict sense of the term but suggests active migration or speciation in colder waters, as do genera or species occurring in deep water in the middle latitudes. Certainly it would be difficult to demonstrate strictly bipolar or 'relict' species in this highly successful and abundant group of invertebrates.

Among the benthic arthropods no bipolar pycnogonids are recognized, and the entire facies of the group is markedly different in the two regions. This is most marked in the absence of polymerous forms from Arctic waters and the development of species of *Colossendeis* and large ammotheids in Antarctic waters.

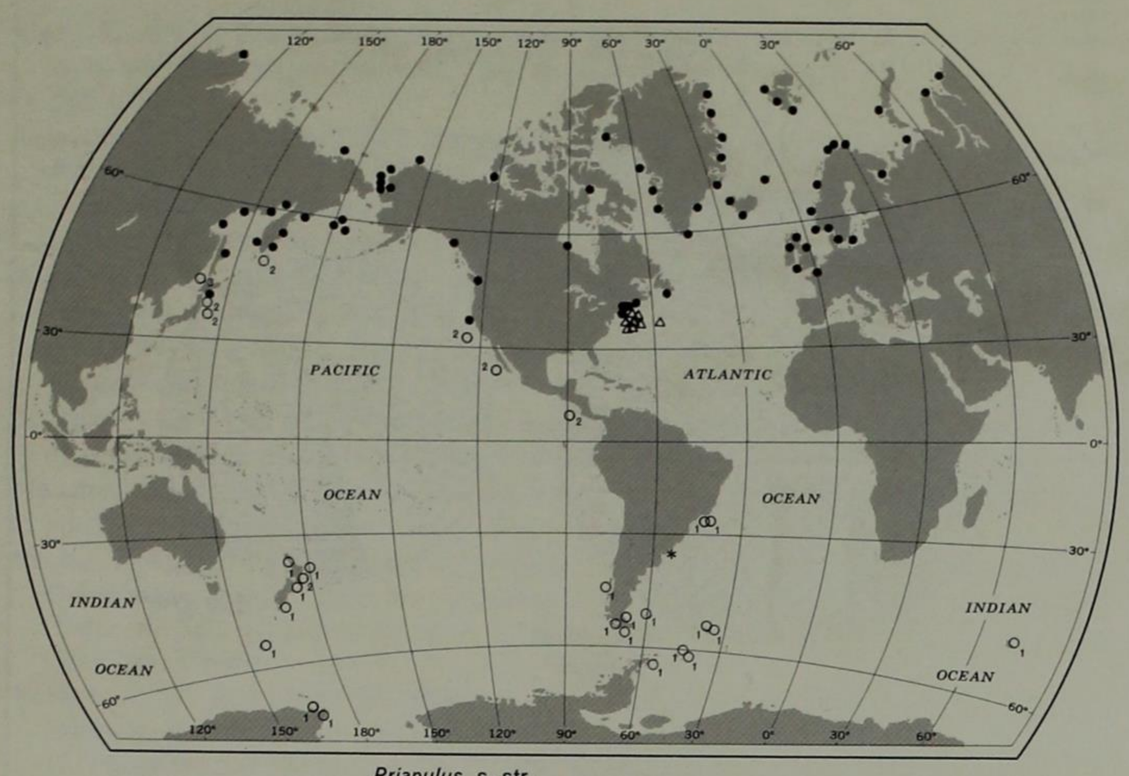
[3]Recent information suggests that very small priapulids (perhaps 2 mm or 3 mm long) may be widespread in tropical regions. A small priapulid, described from the larval stages as *Tubiluchus corallicola,* has been found in coral sand from Curaçao (van der Land, 1968), and is evidently similar to a form found in shallow sandy bottom in the Red Sea at Al Gardaqah.

The absence of large conspicuous benthic decapods, especially brachyuran crabs, from Antarctic waters has been noted by Yaldwyn (1965) and others. The ecological role of crabs in warmer waters is evidently assumed by the large idoteid isopod *Glyptonotus antarcticus* in shallow Antarctic waters. There is a similar dearth of brachyuran crabs in Arctic waters although there are several anomuran crabs. Recently Soviet investigators identified several specimens of an anomuran crab from 67°23′S, 179°53′E at a depth of 500 m to 900 m as *Paralomis spectabilis,* a species previously known from southeastern Greenland and Iceland waters (Birstein and Vinogradov, 1967). Another species of this genus is known from southern South America and the Falkland Islands, but this seems to be the first *bona fide* record of an anomuran crab from Antarctic waters proper although one would like more material to be certain of the identity of the species. The distribution of the genus as a whole suggests that several species may have wider distributions but have not been collected. In any event, crabs of any kind do not appear to be conspicuous members of the Arctic fauna and, as with the Antarctic *Glyptonotus,* large idoteid isopods *(Mesidotea sibirica* and *M. sabini)* are the principal benthic crustacean scavengers. It is of interest to note that although these isopods are placed in different genera, they are members of the same family and are superficially similar.

Stomatopods also appear to be absent from Antarctic waters, although *Heterosquilla polydactyla, Pterosquilla armata* and *Pt. gracilipes* have been recorded from Patagonian waters according to Dr. Raymond B. Manning (personal communication).

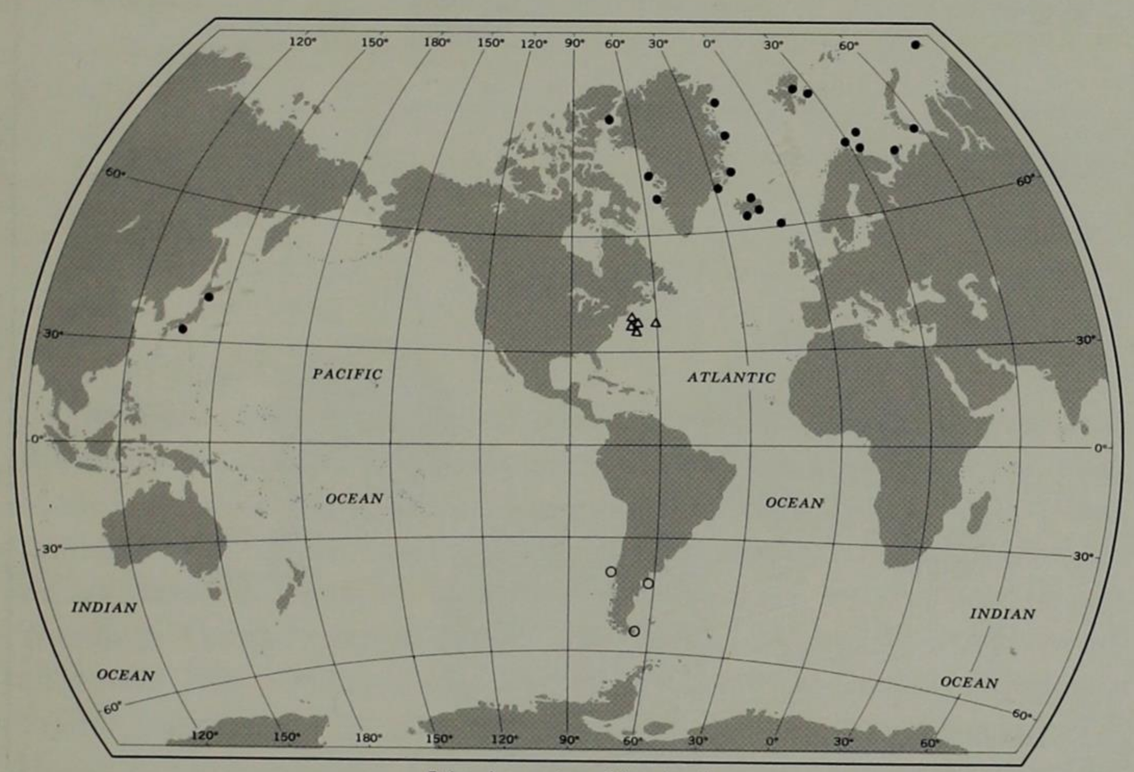
The enthusiastic adherent of bipolarity (if such remains) can find little support in the distribution of echinoderms and ascidians; both of these groups have high numbers of Antarctic endemic species and show few indications of relationship with the Arctic fauna.

Except for cold water and the long polar day and night, there is little in common between the two polar environments of the globe. The Antarctic is a ring of cold water with a bottom deepening towards the rest of the world ocean, whereas the Arctic is a basin almost completely closed off from the Pacific and widely open to the world ocean only through the North Atlantic. Furthermore, in part of the area, between Iceland and the Faroe Islands, the bottom is separated from the North Atlantic proper by the Wyville-Thompson Ridge, a notable barrier for benthic organisms. Several large rivers enter the Arctic, but none flow from the Antarctic continent.



Priapulus s. str.
- *caudatus* Lamarck
- *tuberculatospinosus*
  - O_1 *tuberculatospinosus* Baird
  - O_2 *abyssorum* Menzies
  - O_3 *japonicus* Murina and Starobogatov
- * *horridus* Theel
- △ *profundus* Sanders and Hessler

Fig. 11. Distribution of *Priapulus* s. str. (from various sources, including H. L. Sanders, personal communication).



Priapulus subg. *Priapulopsis*
- ● *bicaudatus* Danielssen
- ○ *australis* (de Guerne)
- △ *atlantisi* Sanders and Hessler

Fig. 12. Distribution of *Priapulus* subg. *Priapulopsis* (from various sources, including H. L. Sanders, personal communication).

When one views the composition of the biota, both qualitatively and quantitatively, the differences between the Antarctic and the Arctic are even more pronounced (Figures 13, 14). On the basis of Soviet investigations of the benthos of various regions of both polar seas, it appears that the average biomass at comparable depths is from several times to an order of magnitude greater in the Antarctic. More significant is the percentage composition of the more common invertebrates of the benthos (Figure 14). While there is in the Barents Sea a bottom assemblage consisting for the most part of sponges, the Arctic does not have the dense sponge–Bryozoa associations of the Antarctic. Conversely, the Antarctic lacks the well developed bivalve-ophiuroid assemblages of shallow Arctic waters, although at least one ophiuroid, *Ophiacantha antarctica,* may make up at least a third of the biomass in localities in the Ross Sea according to Fell's (1961) estimate based on photographs and collection records. As emphasized by Bullivant (1967) the benthos of the shallow Antarctic shelf is primarily an epifaunal or hard bottom assemblage and has little in common with the Arctic infaunal assemblages. Unfortunately quantitative bottom sampling on a scale comparable to Soviet work in the Arctic has not been carried out in the Antarctic except for the limited area near Mirny Station. Thus it is impossible to document by quantitative data the impression that the distribution of bottom communities or recurrent combinations of species has more of the pattern of a mosaic in the Arctic. Furthermore, the most significant aspect of the shallow bottom life of the Antarctic, the comparative rate of turnover or replacement as contrasted with that of the Arctic, remains to be determined, although the example of sea stars discussed by Pearse (1965) suggests a similar rate of reproduction in both polar regions at least for asteroids. It seems possible that the rate of turnover may actually be very slow and the dense sponge mats, accumulations of shells, and barnacle plates represent the production of many years.

There is a pronounced latitudinal discontinuity in many plankton species, for which the term 'antitropical' has been suggested in preference to 'bipolar' (Hubbs, 1952; Brinton, 1962). In discussing such distribution patterns in relation to euphausiids, Brinton uses the term 'biantitropical.' He further notes that these species are also panoceanic, occurring in similar latitudes on both Pacific and Atlantic Oceans. During warm times these species would tend to be more widely separated (thus more nearly 'bipolar,' although there are no strictly bipolar euphausiids at this time), and during periods of cooling, the populations would tend to move closer to the equator and be continuous, thus making exchange of genetic material possible. Examples of such antitropical distributions are given in Figure 15. Such distribution patterns do not, of course, support a concept of original continuity of identity of the polar biota, or continuity of the bottom fauna. Some of the populations of species involved in these antitropical distribution patterns may presently be able to exchange genetic material by submergence beneath the tropics.

If we accept Dunbar's (1968) concept of the polar biota as evolving systems subject to natural selection, it would appear that the different biotas have responded to different selective pressures. According to geological opinion (Adie, 1963), the Antarctic continent has been separated from other landmasses since possibly Jurassic times. This implies that the Antarctic Ocean as such may have been in existence before the present cycle of glaciation (whether one equates this with the Pleistocene or suggests that the Pleistocene began in the Miocene). This would suggest that the marine fauna of the Antarctic has had more time to evolve than that of the Arctic, since the ocean of the Antarctic regions has been continuous whereas the Arctic has been ice-covered or landlocked during times since the Tertiary.

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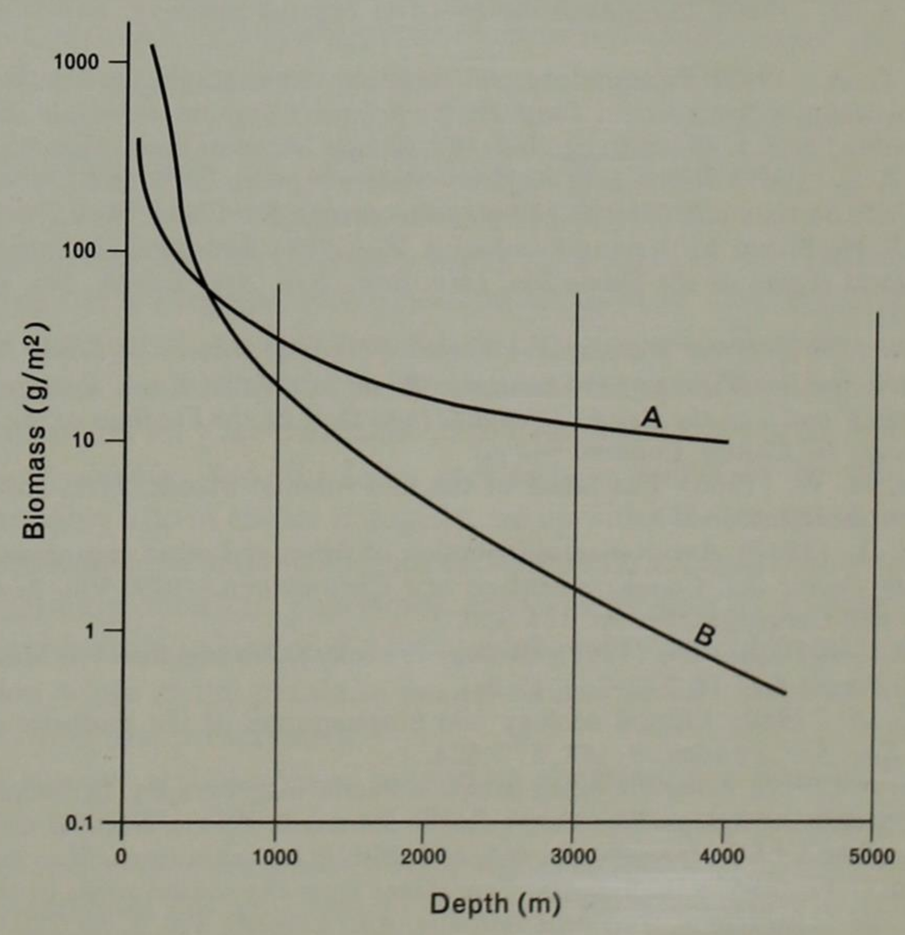


Fig. 13. Comparative benthic biomass for the Bering Sea (A) and the Antarctic in the Davis Sea (B) (adapted from Ushakov, 1963).

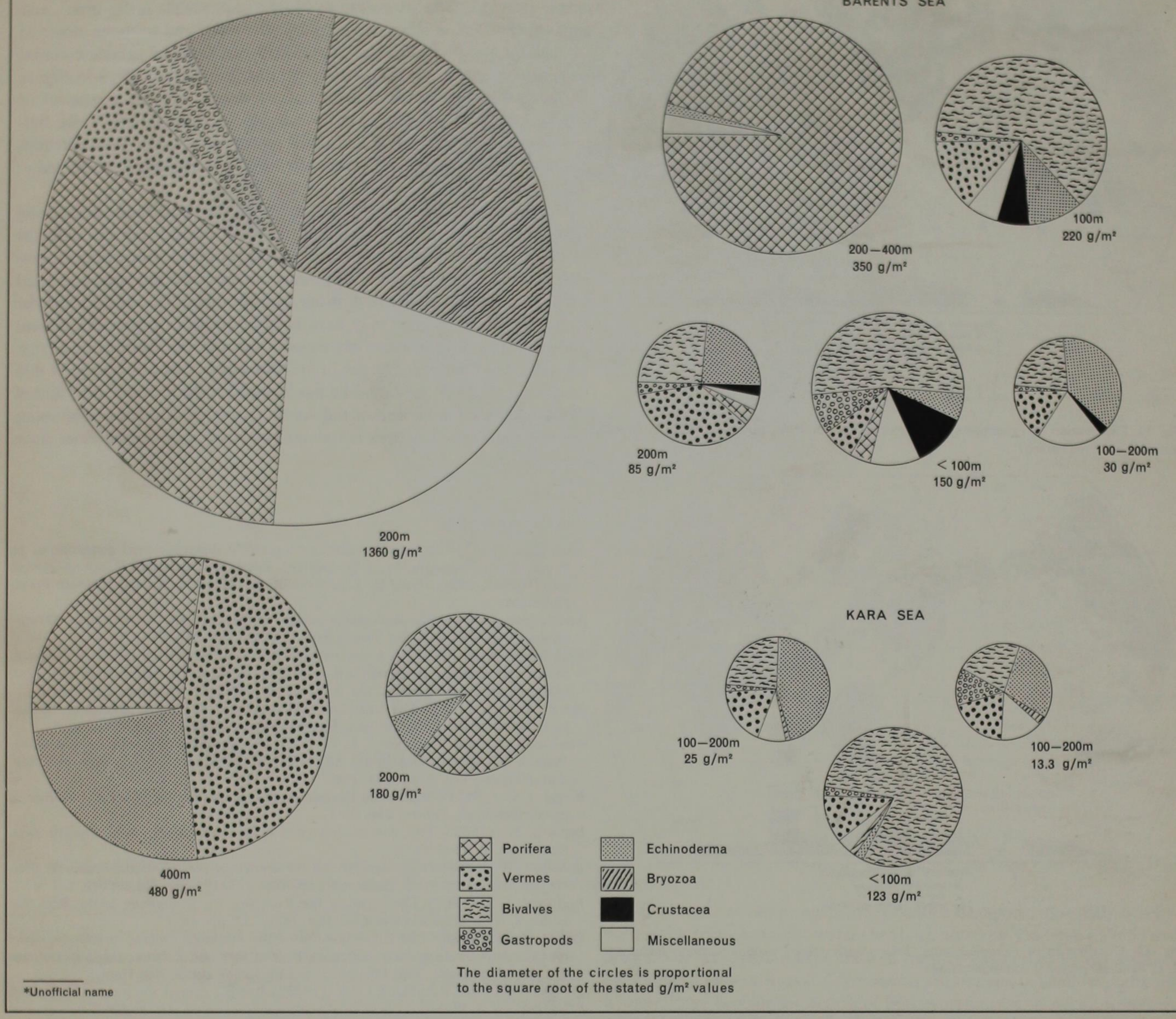


Fig. 14. Percentage composition of the common elements of the bottom communities of Antarctic and Arctic waters (compiled from Ushakov, 1963, and Zenkevitch, 1963).

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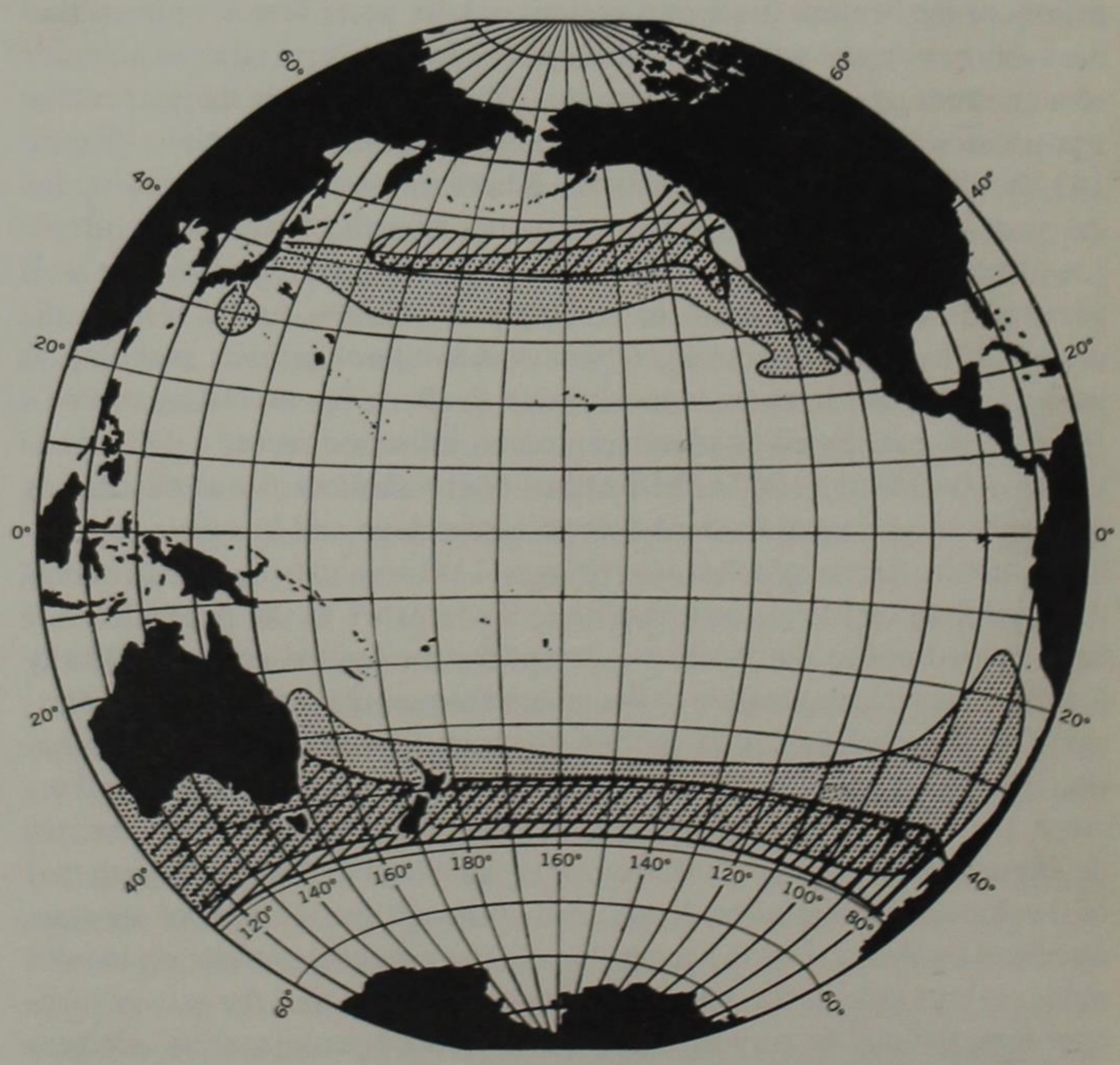


Fig. 15. Antitropical distribution of euphausiid species (adapted from Brinton, 1962).

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Planktonic Foraminifera[1]

Allan W. H. Bé[2]

INTRODUCTION

There are about 30 species of planktonic Foraminifera, as contrasted with the more than 4200 benthic species in the oceans of the world. Most of the planktonic species belong to the families Globigerinidae and Globorotaliidae. Of the 30 species, 9 occur in Antarctic[3] and Subantarctic[4] waters; however, none of these cold-water species are restricted to the 'Southern Ocean,'[5] except possibly the newly recognized *Globorotalia cavernula* (Bé, 1967b). These species are distributed in broad zones of similar temperature in both the Northern and Southern Hemispheres. Hence, it is not possible to refer to these species as endemic to the Antarctic or Subantarctic, although some of them do appear in very high concentrations of 10 specimens/m^3 or more in the Antarctic regions. The species inhabiting the major distributional zones in the world's oceans (Figure 1) are listed in Table 1. It is noteworthy that the highest species diversity occurs between latitudes 40°N and 40°S in regions where surface temperatures are greater than 18°C.

Most planktonic Foraminifera live in the euphotic zone during their early stages; they descend to deeper water as adults and secrete thick, calcite tests. Other species prefer to live in deep water; for example, *Globorotalia scitula* is most commonly encountered between depths of 500 m and 1000 m. Spinose *Globigerinoides* and *Globigerina* are generally epipelagic, whereas the nonspinose *Globorotalia* and *Globoquadrina* have a greater range of depth habitats.

The plankton samples upon which the accompanying maps are based were collected between 1960 and 1965 on the research vessels *Eltanin* of the National Science Foundation (U.S. Antarctic Research Program), and *Vema* and *Conrad* of the Lamont Geological Observatory (Table 2). All surface (0 m to 10 m) and vertical (0 m to 300 m) tows were obtained with plankton nets of uniform mesh size and material (NITEX 202 = 202 μ mesh-aperture width) and were provided with flowmeters for quantitative readings of amounts of water filtered. The locations of the stations from which plankton samples have been examined are shown in Map 1, Plate 1.

Investigations of living planktonic Foraminifera in the Antarctic and Subantarctic are comparatively few. Boltovskoy (1959a, 1959b, 1959c, 1961, 1962, 1966a) has studied the distribution of modern species in the western South Atlantic between Cape Horn and Porto Alegre. Using Foraminifera as indicator species for differentiating between the Malvin (Falkland) Current and the Brazilian Current, he was able to locate the 'Subtropical–Subantarctic Convergence Zone'[6] off Argentina. Its southern and northern boundaries are located, respectively, at 47°45′S and 29°30′S in winter and at 49°S and 35°30′S in summer (Boltovskoy, 1966a).

Parker (1960) has delineated the distribution patterns of planktonic Foraminifera from the equatorial and southeast Pacific as far south as 46°S latitude using 81 plankton samples collected between October 1957 and February 1958. Her tows were obtained with considerably coarser nets (mesh-aperture width of 650 μ) than those used in our study, and they consequently allowed the escape of a large fraction of Foraminifera. Comparison of Parker's results with ours is possible for the larger species only. Bradshaw's (1959) comprehensive work in the North and equatorial Pacific does not consider distribution south of 20°S. Boltovskoy's (1966b) distributional study, based on three *Eltanin* cruises in the South Pacific sector of the Antarctic waters, agrees generally with our results.

Uchio (1960) described the planktonic Foraminifera in two plankton tows and eleven bottom samples from the southern Indian Ocean. Belyaeva (1964) has made an extensive comparison of the distribution of living and dead assemblages of planktonic Foraminifera in 400 plankton and 286 bottom samples in the Indian Ocean. Her observations on the fossil distributions covered the entire Indian Ocean to Antarctica, but her study of living species was limited to the region north of 40°S latitude.

The dead assemblages of planktonic Foraminifera in South Pacific sediments have been studied by Parker (1962), whose definitive taxonomic survey of 34 species included their gross geographic distributions. Blackman (1966) also investigated planktonic foraminiferal assemblages in sediment cores from the southeastern Pacific, including the Albatross Cordillera. Kustanowich (1963) recorded the distributions of 26 species in sediments from the New Zealand region between 18°S and 54°S latitude. Blair's (1965) and Kennett's (1968) investigations of planktonic foraminiferal assemblages in sediments of the Scotia Sea and the South Pacific are particularly pertinent, and correlatable to our study, because their core samples and our plankton tows were obtained on the same expeditions (*Eltanin* Cruises 3 to 15).

DISTRIBUTION IN THE UPPER 300 M (PLATES 1 AND 2)

MAPS 2 AND 3: *Globigerina quinqueloba* Natland

This species occurs commonly along both sides of the Antarctic Convergence but is perhaps more abundant south of it. The typical form has a final chamber that extends as a lobe over the umbilicus and constricts the aperture. Unfortunately, this prominent feature is lacking in the earlier stages, and they are then difficult to distinguish from juvenile *Globigerina pachyderma*. Since the latter species lacks spines in the adult stages and probably also in earlier ontogeny, we consider the possession of spines by *G. quinqueloba* and the absence thereof on *G. pachyderma* as the major distinguishing criterion. This is not always as obvious as it seems because the very delicate spines of *G. quinqueloba* can be readily rubbed off by abrasion while in the plankton net or sample jar or dissolved by inadequately buffered preservative.

The regions and seasons of maximum abundance of *Globigerina quinqueloba* coincide with those of *Globigerina pachyderma* (Maps 4 and 5), but the former decreases toward the pole and is absent in the southernmost stations (Maps 2 and 3). It occurs less abundantly in Subantarctic waters and has a northern limit in the Southern Hemisphere at approximately 40°S latitude.

[1]Contribution No. 1223, Lamont Geological Observatory of Columbia University
[2]Lamont Geological Observatory, Palisades, New York
[3]Waters south of the Antarctic Convergence (sometimes called Antarctic Polar Front)
[4]Waters between the Antarctic Convergence and the Subtropical Convergence
[5]Roughly, all oceans south of the Subtropical Convergence
[6]Roughly equivalent to the region of the Subtropical Convergence

Blair (1965) noted that *G. quinqueloba* constitutes less than 10% of the total planktonic Foraminifera in Recent sediments in the Drake Passage and the South Pacific and that it appeared in larger numbers and at more stations north of the Antarctic Convergence than south of it. Kustanowich (1963) found it a rare but widespread species in the surface sediments around New Zealand and south of it.

Globigerina quinqueloba occurs predominantly in waters colder than 12°C, and in the Antarctic region it is most frequently found in water temperatures between 1°C and 6°C.

MAPS 4, 5, AND 6: *Globigerina pachyderma* (Ehrenberg)

This species, particularly the left-coiling variety, is the most cold-tolerant of the planktonic Foraminifera and is abundant in Antarctic and Subantarctic as well as in Arctic and Subarctic waters. In Subantarctic waters it is especially common over the Argentine continental shelf. The species is very rare, or absent, in subtropical waters.

Juveniles of *G. pachyderma* have 4.5 to 5 hemispherical chambers per whorl, a large aperture, an open umbilicus, and a thin-walled test that looks considerably different from the compact, thick-walled adult test with 4 coalescing chambers per whorl, a reduced final chamber, and a constricted aperture. The typical adult form of *G. pachyderma* is attained by crystalline thickening (Bé, 1960b).

The young forms of *Globigerina pachyderma* are difficult to separate from *G. quinqueloba* Natland, as we have discussed previously. Spinosity may or may not prove to be a real distinguishing characteristic, since it has not yet been established whether *G. pachyderma* truly lacks spines in its earlier stages.

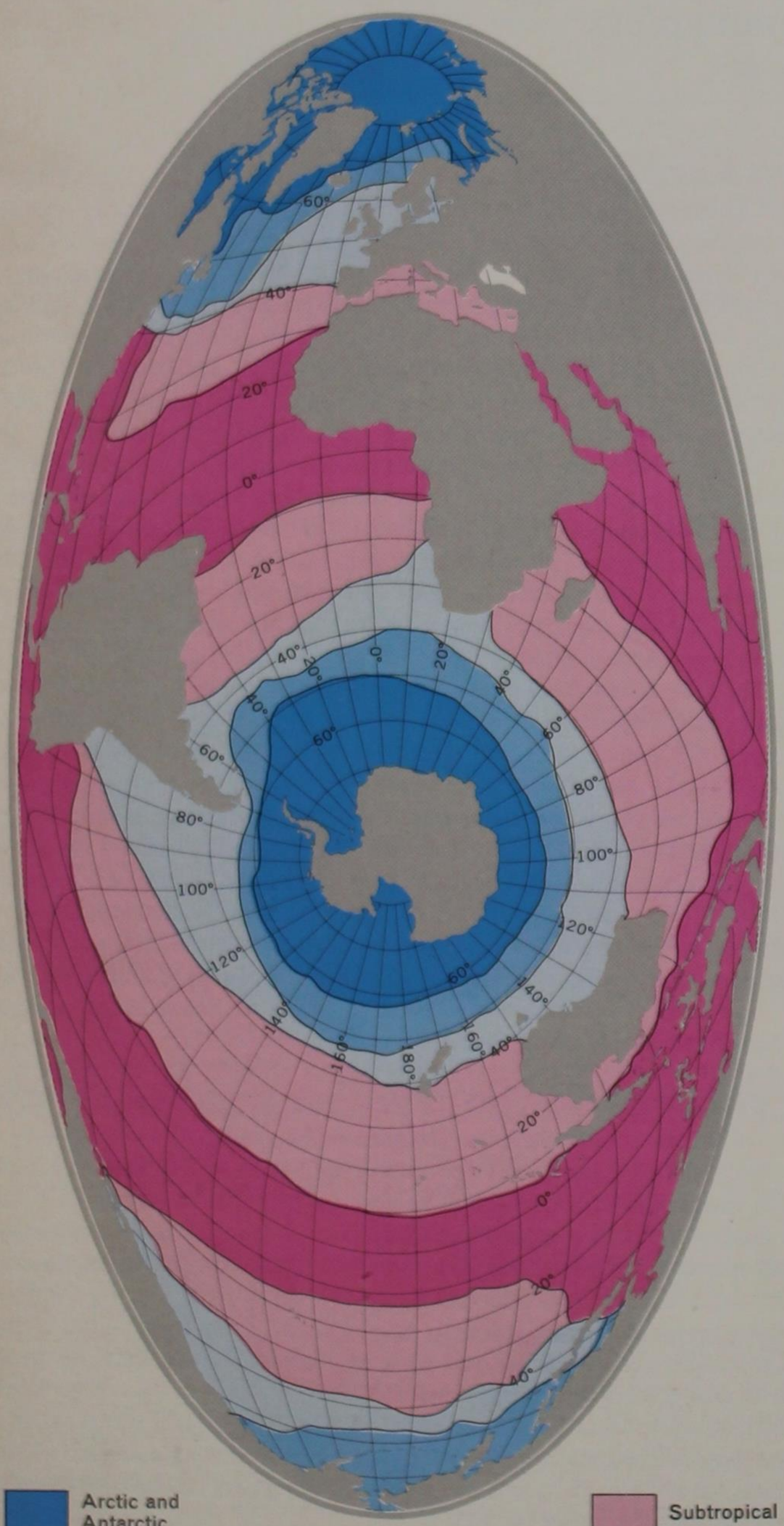


Fig. 1. World distributional zones of planktonic Foraminifera. Species that inhabit each zone are listed in Table 1.

There are several regions where either the right-coiling or the left-coiling variety is predominant (Map 6). One area where right-coiling specimens predominate is located over the Argentine continental shelf north of the Falkland Islands, where concentrations of *G. pachyderma* are exceptionally high for a region so far north of the Antarctic Convergence. Our plankton collections and those of Boltovskoy (1966a) both indicate a sharply defined boundary between predominantly left-coiling and right-coiling populations north of the Falkland Islands. Another region of mostly right-coiling forms is east and west of New Zealand (Jenkins, 1967). Because of the generally rapid decrease of *G. pachyderma* northwards and the lack of sample coverage in certain parts of the ocean, the actual extent of these regions cannot be readily ascertained. It should be noted, however, that the water is warmer in these areas than in regions inhabited by left-coiling forms. It may well be that dextral populations of *G. pachyderma* are distributed in a continuous belt north of their sinistral relatives in a manner reciprocal to that observed by Ericson (1959) in the North Atlantic. It is also possible that a gradual and nearly continuous genetic gradient exists from left-coiling to right-coiling populations of *G. pachyderma* and that the latter, in turn, grade into *Globoquadrina dutertrei*. Cifelli (1961), Parker (1962) and Zobel (1968) have noted strong morphological similarities between the two species.

The left-coiling variety occurs preponderantly in the colder Subantarctic and Antarctic waters. The percentage of sinistral forms increases southward as water temperature decreases. Ninety percent or more of *G. pachyderma* tests are sinistral south of the Antarctic Convergence. This agrees closely with Blair's (1965) and Kennett's (1968) observations of coiling ratios of *G. pachyderma* in Antarctic Recent bottom sediments. The 90% left-coiling isopleth of both investigators is based on fossil populations and runs north of the Antarctic Convergence, while our relative abundances of 90% for living forms generally follow the Antarctic Con-

TABLE 1. Species Composition of World Distributional Zones Shown in Figure 1

Zone	Species[1]
NORTHERN AND SOUTHERN COLD-WATER REGIONS	
Arctic and Antarctic zones	*Globigerina pachyderma* (left-coiling variety)
Subarctic and Subantarctic zones	*Globigerina pachyderma* (right-coiling variety) *Globigerina quinqueloba* *Globigerina bulloides* *Globigerinita uvula* *Globorotalia scitula* *Globorotalia cavernula*[4]
TRANSITION ZONES	
Northern and southern zones of transition between cold-water and warm-water regions	*Globorotalia inflata* Also, mixed occurrences of subpolar and tropical–subtropical species
WARM-WATER REGIONS	
Northern and southern subtropical zones	*Globigerinoides ruber* (pink variety in Atlantic Ocean only) *Globigerinoides conglobatus* (fall species) *Hastigerina pelagica* *Globigerinita glutinata* *Globorotalia truncatulinoides* (winter species) *Globorotalia hirsuta* (winter species) *Globigerina rubescens* *Globigerina falconensis* *Globigerinella aequilateralis*[2] *Orbulina universa*[2] *Globoquadrina dutertrei*[2] *Globorotalia crassaformis*
Tropical zones	*Globigerinoides sacculifer* [incl. "*Sphaeroidinella dehiscens*" (Parker and Jones)] *Globorotalia menardii* *Globorotalia tumida* *Pulleniatina obliquiloculata* *Candeina nitida* *Hastigerinella digitata* *Globoquadrina conglomerata*[3] *Globigerinella adamsi*[3] *Globoquadrina hexagona*[3] Most species from subtropical zones are also common in tropical zone

[1]Species are listed under the zone where their highest concentrations are observed, but they are not necessarily limited to these areas.

[2]Prefer outer margins of subtropical central water masses and fringes of the Transitional Zone.

[3]Restricted to the Indo-Pacific.

[4]Restricted to the Subantarctic.

TABLE 2. Plankton Collections Used in This Study

Ship and Cruise Number	Date of Collection	Number of Samples	Number of Stations
Eltanin			
8	April 14–June 12, '63	66	21
9	Aug. 12–Sept. 13, '63	63	16
10	Oct. 13– Nov. 29, '63	101	30
11	Dec. 28, '63–Feb. 13, '64	117	29
12	Mar. 13–April 18, '64	95	9
13	May 19–June 29, '64	127	16
14	Aug. 2–Sept. 5, '64	158	19
15	Oct. 11–Nov. 21, '64	175	24
16	Feb. 4–Feb. 18, '65	45	9
17	Mar. 25–April 30, '65	204	23
18	June 5–10, '65	26	3
19	July 13–Aug. 24, '65	147	11
Vema			
14	Jan. 8–April 5, '58	21	21
15	Feb. 24, '59	1	1
16	March 30–Apr. 16, '60	3	3
18	Feb. 28–May 15, '62	29	29
18	July 28–Aug. 7, '62	3	3
Conrad			
8	Feb. 18–April 1, '64	19	19
9	Mar. 8–April 14, '65	15	15

vergence or are located to the south of it. We believe this indicates that a southward shift of predominantly sinistral populations has taken place in the recent past.

Globigerina pachyderma occurs most abundantly during spring, summer and early fall (early October to late April); this coincides with the period of high phytoplankton production. The region of highest abundance, where *G. pachyderma* exceeds 10 specimens/m^3, lies between 60°W and 155°W and south of the Antarctic Convergence; a secondary area of high concentration is located off the Argentine shelf (Map 4). Low concentrations of *G. pachyderma* prevail during late fall and winter (May to September). The left-coiling populations are encountered at water temperatures between −1°C to 8°C, and reach highest concentrations at temperatures below 2°C. Dextral populations are found primarily between 9°C and 15°C.

MAPS 7 AND 8: *Globigerina bulloides* d'Orbigny

This is the most abundant species in Subantarctic waters, often reaching 80% to 90% of the total planktonic foraminiferal populations. It is next in importance to *G. pachyderma* as a cold-water indicator. The species occurs in a broad belt roughly between 40°S latitude and the Antarctic Convergence. Highest concentrations are generally observed during spring and summer, while sparse populations are usual in winter.

Globigerina bulloides is found to about 480 km south of the Antarctic Convergence, but the main decrease in numbers occurs within the first 160 km or so south of the Convergence. In addition, seasonal fluctuations of *G. bulloides* are responsible for southward invasions beyond the Convergence during summer and spring and northward retreats during late fall and winter.

The northern limit of abundant *G. bulloides* in the Southern Hemisphere is at approximately 40°S latitude coinciding roughly with the 18°C surface isotherm. *Globigerina bulloides* grades morphologically and zoogeographically into *G. falconensis* Blow. The latter inhabits the cooler edges of subtropical regions and differs from *G. bulloides* in having a smaller test, a more constricted low-arched aperture with a lip, and more elongate chambers (Bé, 1967a). We believe that the two forms belong to a cline.

Blair (1965) found that the 20% isopleth of fossil *G. bulloides* in Recent bottom sediments of the South Pacific is situated north of the Antarctic Convergence, whereas relative abundances of 20% for living *G. bulloides* are located about 160 km south of the Convergence. As is true in the comparison of fossil with living *G. pachyderma* populations, we infer that the present-day extension of *G. bulloides* south of the Convergence is due to a warming trend of waters in the recent geologic past.

Blackman (1966) observed that *G. bulloides* constituted from 39% to 73% of the total planktonic Foraminifera in Recent sediments of the Albatross Cordillera south of 40°S latitude. Kustanowich (1963) also observed the dominance of *G. bulloides* in Subantarctic sediments south of New Zealand. The species made up more than 40% of the total planktonic Foraminifera south of 40°S latitude.

Globigerina bulloides is encountered primarily in near-surface waters and decreases in number with depth. Its optimum temperature range lies between 2°C and 10°C.

MAPS 9 AND 10: *Globorotalia truncatulinoides* (d'Orbigny)

This species flourishes in Subantarctic waters during late fall and winter (May to October), but is rare during the remaining months of the year (Figure 2). The seasonal factor explains why this species is sparsely distributed during summer and early fall. If only late fall and winter samples are considered, the high densities found in the Subantarctic region may well be part of an extensive bloom of *G. truncatulinoides* over the middle latitudes of the southeastern Pacific. The northern extent of such a fall–winter bloom cannot be ascertained because of the paucity of samples in the southeastern Pacific.

Parker (1960) did not report any *G. truncatulinoides* south of 40°S latitude. However, on the Albatross Cordillera between 25°S and 45°S latitude, in Recent sediments, it is one of the dominant species, constituting more than 20% of the planktonic foraminiferal assemblages (Blackman, 1966). The absence of *G. truncatulinoides* in Parker's southern stations may be due to its very low concentration between October and February and is a further indication that it is a mid-latitude species which occurs most abundantly in late fall and winter in subtropical, transitional, and Subantarctic waters of the South Pacific.

In the North and South Atlantic *G. truncatulinoides* is also a winter species, occurring primarily between December and April in the Sargasso Sea and in July and August in the central South Atlantic (Bé, 1960a, and unpublished data). However, while it is restricted to subtropical waters in the Northern Hemisphere (Bradshaw, 1959; Bé, and Hamlin, 1967), *G. truncatulinoides* appears to have a wider temperature tolerance in the Southern Hemisphere, where it flourishes in Subantarctic as well as subtropical waters. In the Northern Hemisphere it does not occur in regions with surface temperatures below 14°C, but in the Southern Hemisphere this species is common in Subantarctic waters with temperatures as low as 4°C.

Blair (1965) reported that in bottom sediments the relative abundance of *G. truncatulinoides* tests are about 1% and 2% along the Antarctic Convergence in the South Pacific and about 1% to 5% in the Scotia Sea north of the Convergence. Although this seems considerably lower than the high percentages of living *G. truncatulinoides* along or north of the Convergence (Map 10), the lower frequencies in the sediments may reflect either the averaging effect of the strongly seasonal productivity of this species or the recency of the incursion of greater concentrations of *G. truncatulinoides* in the Subantarctic region.

Left-coiling tests of *G. truncatulinoides* greatly outnumber the right-coiling ones in Subantarctic waters.

MAPS 11 AND 12: *Globorotalia inflata* (d'Orbigny)

This is a good indicator species of transitional waters between the subtropical and Subantarctic regions in the South Atlantic, but in the South Pacific highest frequencies are found mainly in Subantarctic waters (Map 12). Whereas in the Atlantic highest relative abundances are encountered in regions where surface isotherms are between 13°C and 19°C, in the Pacific it is one of the dominant species of Subantarctic waters having surface temperatures between 2°C and 6°C.

Globorotalia inflata occurs predominantly during winter and spring (early August to early January) reaching a climax in October and November, when relative abundances up to 70% of the total population and absolute abundances of 10 specimens/m^3 or more are recorded. The seasonal distribution of *G. inflata* (Figure 2) shows its spring preference even more distinctly if *Conrad* Cruises 8 and 9 are disregarded, because they are mostly north of 50°S latitude. The high concentrations in the New Zealand region contrast with the relatively low densities to the south near the Antarctic Convergence; this difference can probably be attributed to the seasonal factor.

G. inflata is not common over the Argentine continental shelf, although the temperature–salinity conditions appear favorable for its development. Here right-coiling *Globigerina pachyderma* and *G. bulloides* are predominant among the planktonic Foraminifera.

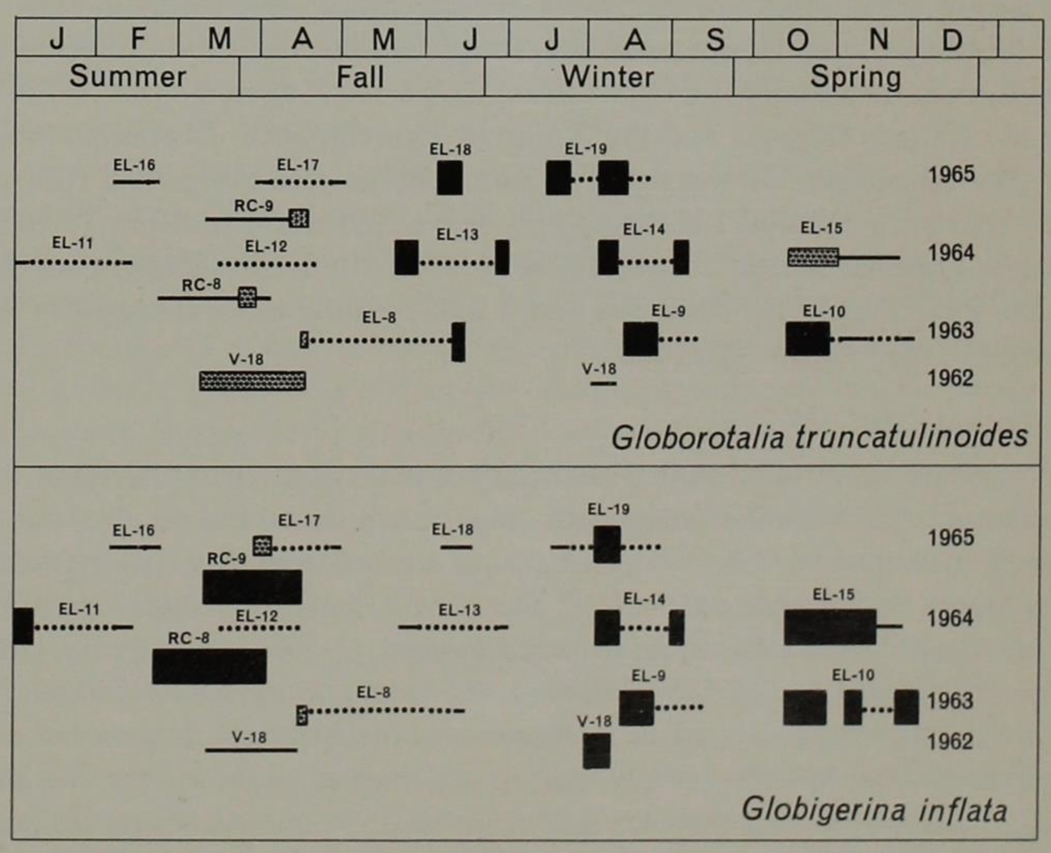


Fig. 2. Seasonal distributions of *Globorotalia truncatulinoides* and *G. inflata* according to various cruises.

Whether *G. inflata* is also abundant in the southeastern Pacific to the north of our present area of study is a matter of conjecture. Parker (1960) noted low relative abundances (<10%) in 2 out of 11 stations in this area, but her plankton samples were collected with coarse-meshed nets (0.65 mm mesh aperture) which in all likelihood allowed the escape of many Foraminifera. Blackman (1966) observed that *G. inflata* constituted more than 20% of the planktonic foraminiferal thanatocoenosis in the sediments south of 45°S latitude of this same area.

Blair (1965) reported relative abundances of *G. inflata* as high as 30% in the southeastern Pacific floor and up to 20% in the Drake Passage sediments north of the Antarctic Convergence. His 10% isopleth is also located north of the Convergence, whereas equivalent relative abundances for living *G. inflata* are generally south of the Convergence. This is interpreted as the result of a southward migration during the warming trend of the recent geological past. Blair's high relative abundances in the Scotia Sea are also reflected in the living populations which are transported eastward from the Pacific into the Scotia Sea.

MAPS 13 AND 14: *Globigerinita glutinata* (Egger)

This is a ubiquitous species that is found commonly in small numbers in Subantarctic waters. Its frequency is usually less than 5% of the total planktonic Foraminifera, although it sporadically increases to 10% or higher, as in the region west of the Drake Passage (Map 14). In the southeastern Pacific and the Atlantic sectors, reduced numbers of this species are able to cross the Antarctic Convergence. The species is absent in the southernmost stations, where surface temperatures drop below 1°C.

Globigerinita glutinata is an enigmatic species among planktonic Foraminifera. It ranges from Subarctic to tropical to Subantarctic waters, but it does not appear to have any distinct patterns or centers of maximum concentration. Bradshaw (1959) observed that it is more abundant in tropical than in Subarctic regions of the Pacific Ocean. Boltovskoy (1966a) considered it useless as an indicator species, because it inhabits Subantarctic as well as subtropical waters of the South Atlantic off Argentina. The general lack of diagnostic morphological features and the usual absence of the distinctive bulla in specimens from plankton tows make it difficult to determine whether cold-water Subantarctic or Subarctic populations belong to the same species complex as those from the tropical–subtropical regions.

Blair (1965) noted that this species is randomly distributed in frequencies up to 9% in the bottom sediments of the South Pacific and Scotia Sea north of the Antarctic Convergence.

UNMAPPED SPECIES

Globigerinita uvula (Ehrenberg)

This species is more frequent and abundant in Antarctic than in Subantarctic regions. It was present at 23 stations south of the Antarctic Convergence and at 18 stations north of it. *Globigerinita bradyi* Wiesner and *Globigerinoides* cf. *G. minuta* Natland of Bradshaw (1959) are considered conspecific with *Globigerinita uvula*. The tightly coiled, high-spired, nonspinose test frequently possesses a diagnostic bulla with infralaminal apertures. Because its maximum dimension is 190 μ or less, most specimens probably escape through the meshes of the plankton nets and our quantitative estimates are therefore unreliable. Blair (1965) reported a random distribution of *G. uvula* in bottom sediments from both sides of the Convergence and noted that its frequency rarely exceeded 1%.

Globorotalia scitula (Brady)

This is a Subantarctic, deepwater species which very rarely occurs in the epipelagic zone (0 m to 300 m). It appeared in the 500 m to 1000 m depth range at 4 *Eltanin* stations during the period August 12 to 21, 1963, north of South Georgia and the Antarctic Convergence. During October and November 1963, it was again encountered between 500 m and 1000 m at 3 stations north and 1 station south of the Convergence. Blair (1965) reported that *G. scitula* is rare or absent in the Antarctic sediments of the South Pacific and the Scotia Sea and it tended to be more frequent in his northern Subantarctic samples.

SUMMARY

Nine species of planktonic Foraminifera have been encountered in the Antarctic and Subantarctic waters. The only species that occurs abundantly in Antarctic waters is *Globigerina pachyderma*. Six species occur commonly in Subantarctic waters; these are *Globigerina bulloides, Globorotalia inflata, Globorotalia truncatulinoides, Globorotalia scitula, Globigerinita glutinata* and *Globorotalia cavernula*. *Globigerina quinqueloba* and *Globigerinita uvula* are more frequent in the Antarctic region, but are also ubiquitous in Subantarctic waters. All species show widely overlapping distributions, but their centers of maximum concentrations are generally located either in Antarctic or Subantarctic waters.

Two species have distinct seasonal occurrences. *Globorotalia truncatulinoides* is most abundant between early May and late October, while *Globorotalia inflata* proliferates between early August and early January.

In winter (June through September) the upper 100 m of water around Antarctica is comparatively barren of plankton (including Foraminifera) and the bulk of the planktonic populations inhabit the deeper waters between 250 m and 1000 m.

In comparing the fossil assemblages in surface sediments studied by Blair (1965) with living populations from the same regions, we have noted that the equivalent frequencies of *Globigerina pachyderma* (20%), *G. bulloides* (20%), *Globorotalia truncatulinoides* (5%), and *G. inflata* (10%) are all located north of the mean position of the Antarctic Convergence in the bottom sediments, whereas these frequencies for living populations are now south of the Antarctic Convergence. The southward retreat of Antarctic *G. pachyderma* and the advance of the three Subantarctic species indicate the extent of a warming trend since the deposition of the most recent sediments and their skeletal remains.

These findings agree with Hays' (1965) observations that the boundary between Antarctic and Subantarctic Radiolaria in bottom sediments is located 3° to 10° north of the mean position of the Antarctic Convergence. He noted also that north of the Convergence the radiolarian species in the thin top layer of cores are indicative of a recent warming period during the past few thousand years.

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Porifera

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INTRODUCTION

Sponges are the most primitive of multicellular animals; they are, for the most part, attached to the bottom or to hard objects and are immobile. The majority of sponges occur as distinct but irregularly shaped colonies, but some of them, especially the glass sponges (Hyalospongiae) and the calcareous sponges (Calcispongiae), may often be found in isolated forms. Sponges live by pumping water through the numerous openings and feed upon fine detrital particles and unicellular organisms from the water carried into the colony. Sponges reproduce both sexually and asexually. In the first case the fertilized egg develops into a free-swimming larva, which, having settled on the bottom, gradually turns into a young sponge. Asexual reproduction is by budding and the formation of gemmules.

Sponges are widely distributed in seas and oceans from tidal flats to depths of 8000 m–8500 m; however, they attain their greatest abundance and diversity on the continental shelf and in the upper part of the continental slope. An important factor in the distribution of sponges is the character of the sea bottom; as sedentary, attached forms they tend to favor boulders and cobbles.

Together with Bryozoa and Echinodermata, sponges are the most characteristic representatives of bottom fauna in Antarctica. It would probably be difficult to find another part of the world's oceans where sponges are found in such constant abundance over such a large area. A broad belt of sponge colonies extends virtually around the entire Antarctic continent. This wealth of sponges in Antarctica can doubtlessly be explained by favorable nutritional and hydrochemical conditions and by the presence of a large amount of terrigenous, stony bottom material that has been transported by glaciers and icebergs. Sponges are so abundant that, in many parts of the shelf, skeletal remains deposited on the bottom form a layer of interlocked spicules 65 cm thick (Koltun, 1966).

At present about 300 sponge species are known in the Antarctic, including the areas of the Scotia Ridge and the Prince Edward, Kerguelen, and Macquarie Islands. Many of them are stenothermal, cold-loving forms, well adapted to the extremely low water temperatures. A high percentage of endemic species is typical of Antarctic sponges; more than half the known Antarctic species are limited to Antarctic waters.

The Antarctic sponge fauna is marked by an almost complete absence of horny sponges and by poor representation of such families as the Geodiidae, Stellettidae, Theneidae, and Tethyidae (Burton, 1932). By contrast, there is an abundance of large glass sponges, especially those of the family Rossellidae. Some of these, for example, the barrel-shaped *Scolymastra joubini,* are gigantic, attaining heights of more than 100 cm.

Another distinctive feature of Antarctic sponges is the wide eurybathic range in which they occur. This is related to the predominance of mixed bottom sediments, which, together with other factors, provide relatively uniform conditions of life over a large part of the continental shelf and slope. However, the wide range in vertical distribution of Antarctic sponges is also promoted by other factors. First of all, because of the absence of a continental runoff, ocean waters extend all the way to the edge of the Antarctic continent, filling the shelf zone and bringing with them sponges from the bathyal depths and lower parts of the sublittoral to the shallower reaches. A characteristic example is provided by the glass sponges, typically oceanic forms that are usually found at depths of more than 100 m. In Antarctica, however, these sponges are abundant near the coast, sometimes at depths of as little as 10 m. On the other hand, the presence of bottom currents that flow from the coast seaward tends to promote a pattern of sponge settlement from the shelf down along the continental slope and even into abyssal depths. This tends to eliminate any vertical zonality in sponge distribution within a broad range of the shelf and slope, that is, between 100 m and 900 m.

Compared with a large number of endemic species, the number of endemic genera is extremely limited, as is true of most other benthic animals in the Antarctic. Of the 116 sponge genera found in Antarctica, only about 10 may be regarded as endemic. They include the *Scolymastra, Acanthorhabdus, Dolichacantha, Hoplakithara, Cercidochela, Bipocillopsis,* and some other mostly monotypic genera. Most of the Antarctic sponges belong to genera that are also well represented elsewhere in the world. They are: *Mycale* (8), *Tedania* (8), *Myxilla* (9), *Iophon* (6), *Isodictya* (9), *Anchinoë* (5), *Haliclona* (21), *Adocia* (6), *Hymeniacidon* (6), and several others. There are also species that belong to less widely distributed genera, which occur only in nearby water areas or in isolated parts of the Northern Hemisphere. These genera include *Monosyringa,* also known off New Zealand; *Cinachyra,* with several forms in the West Indies; *Axociella,* which has been observed off South America, Australia, and in the West Indies; and *Rossella,* primarily an Antarctic genus, found only in the Azores in the Northern Hemisphere.

Many Antarctic sponges are circumpolar in distribution. The most common are: *Rossella antarctica, R. racovitzae, Scolymastra joubini, Cinachyra antarctica, Tetilla leptoderma, Mycale tridens, M. acerata, Asbestopluma belgicae, Iophon radiatus, I. spatulatus, Acanthorhabdus fragilis, Cercidochela lankesteri, Tedania massa, T. oxeata, Axociella nidificata, Ectyodoryx ramilobosa, Eurypon miniaceum, Isodictya erinacea,* and *Microxina benedeni* (Koltun, 1964). In addition to this main group, the Antarctic sponges also include species with more limited areas of distribution. For example, the McMurdo Sound area is the only place in Antarctica where representatives of the genera *Stelletta, Jaspis, Penares, Geodinella, Hemiastrella, Rhabdermia, Chondropsis,* and *Dysidea* (Burton, 1929) have so far been found. Somewhat more widely distributed, but still within the limits of East Antarctica, are *Hoplakithara dendy, Plocamia gaussiana, Clathria pauper, Sphaerotylus schoenus, Dolichancantha macrodon, Desmacella vestibularis,* and *Monosyringa longispina.* Far fewer species are endemic in West Antarctica; among them are *Mycale macrochela, M. tylotornota, Isodictya toxiphila, Myxilla australis, M. pistillaris,* and *Hymeniacidon torquata.* This observed difference between the sponges of West and East Antarctica cannot adequately be explained simply on the basis of insufficient and uneven exploration and collecting.

An analysis of Antarctic sponges shows a close relationship with the sponges of the Falkland Islands and South America. Among the Demospongiae and the Hyalospongiae alone there are more than 50 common species in these areas. The link with New Zealand and Australia is weaker, with only 30 common species

The Antarctic sponge fauna is far richer and more diversified than its Arctic counterpart. The Arctic includes only about 200 species, and it should be borne in mind that the Arctic fauna is now almost entirely known while new species may still be found in Antarctica. Of great interest is the presence of the undoubtedly bipolar species *Sphaerotylus schoenus, Artemisina apollinis, Suberites montiniger,* and others in both Arctic and Antarctic faunas. These are primarily ancient forms that have undergone little change and are now found only in these widely separated parts of the Northern and Southern Hemispheres.

The sponge fauna of the abyssal depths of the southern oceans has been studied only to a slight extent; it includes about 30 deep-sea species, most of them endemic and belonging to the genera *Caulophacus, Malacosaccus, Holascus, Aulocalyx, Hyalonema, Asbestopluma, Cladorhiza,* and others.

THE MAPS (PLATES 3 AND 4)

MAP 1: Family Rossellidae

The Rossellidae are extremely characteristic of Antarctic waters. It is these glass sponges, found frequently and reaching large size (50 cm or more high), that give the Antarctic sponge fauna its distinctive and specific character. Like the other glass sponges, the Rossellidae are oceanic forms that usually occur on the shelf and continental slope at depths greater than 100 m. In Antarctica, however, in contrast to other parts of the world, they are found mainly on the shelf and may rise to the upper sections of the sublittoral, developing abundantly even at a depth of 10 m. To be sure, the Rossellidae also include a genuine abyssal genus, *Bathydorus,* known from depths of 717 m to 4792 m.

Rossella, the typical genus of this family, is limited in distribution to the Antarctic and Subantarctic, with the single exception of *R. nodastrella,* which is found in the Azores. This genus reaches its greatest diversity along the Antarctic coast. In the North Pacific *Rossella* is replaced by the closely related genus *Acanthascus,* which is represented in Antarctica by *A. australis,* found only once in the Bellingshausen Sea. It is characteristic that both *Rossella* and *Acanthascus* are completely absent in the Arctic.

Map 1 shows the distribution of *Rossella, Bathydorus,* and *Acanthascus;* it should be noted that *Acanthascus* also includes the genera *Rhabdocalyptus, Staurocalyptus,* and *Acanthasaccus,* which are here regarded as synonyms.

MAP 2: Rossellinae

In Antarctic waters, 24 representatives of *Rossella* have been identified, and Burton (1929) has assigned them quite properly to 4 species: *R. antarctica, R. racovitzae, R. nuda,* and *R. villosa.* Antarctica also includes *Scolymastra joubini* and *Anoxycalyx ijimae,* the former being one of the gigantic glass sponges, reaching a height of 100 cm or more. All these species are circumpolar, and 3 of them—*R. antarctica, R. racovitzae,* and *R. nuda*—extend beyond Antarctica to the Patagonian coast and the Falkland Islands.

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MAP 3: Tetractinellida

The Tetractinellida, a basically warmth-loving sponge group, is represented in Antarctica by 19 species. As a whole this group is related more closely to the Australia–New Zealand fauna than to the Falkland Islands–South American sponges. Most of them are rare; 5 species have been found only in the Ross Sea and off New Zealand *(Stelletta crater, S. maori, Jaspis novaezealandiae, Penares tylotaster,* and *Geodinella vastigifera).* Nevertheless, several species are rather widely distributed in the Antarctic and are quite characteristic of the Antarctic fauna. They are *Monosyringa longispina, Tetilla leptoderma, Cinachyra antarctica, C. barbata,* and *Plakina trilopha.* Except for the cosmopolitan genus *Tetilla,* all the others have a more limited distribution. For example, *Monosyringa* is represented by only 1 additional species, *M. mortenseni,* off New Zealand; *Cinachyra* is also known in the West Indies, Australia, Malaysia, and India, and the genus *Plakina* is found in the North Atlantic, in the Mediterranean, and off Japan. *Monosyringa longispina* has been found only in East Antarctica, but the other more common *Tetractinellida* are circumpolar in distribution, *Cinachyra antarctica* being the only endemic species. It is noteworthy that the genus *Thenea,* very characteristic of shallow waters in many areas of the Northern Hemisphere, is not represented on the Antarctic shelf. However, *Thenea delicata* (2926 m–3400 m) and the closely related *Cladothenea andriashevi* (3000 m) have been found at abyssal depths in the Antarctic.

MAP 4: Clavaxinellida

The Clavaxinellida play a rather modest role in the sponge fauna of Antarctica; like the Tetractinellida, they are more typical of the temperate and warm oceans. The Antarctic includes about 25 species of this sponge group, mostly belonging to the genera *Latrunculia, Stylocordyla, Suberites, Polymastia, Sphaerotylus, Axinella, Rhizaxinella,* and others. It is interesting that the percentage of endemic species is relatively low (35%) in this group and that it includes the most probable bipolar species, among them *Suberites montiniger, Sphaerotylus schoenus, S. borealis (S. antarcticus).*

The Clavaxinellida are found mainly on the shelf and only partly on the slope. Some species of the family Polymastiidae may descend to the ocean floor and are found at a depth of 5000 m. Other deep-sea sponges that have recently been found in the Antarctic (Koltun, 1964) are *Atergia acanthoxa* (north of the Ross Sea at 3400 m) and *Protelaia burtoni* (north of the Balleny Islands at 3000 m).

Map 4 shows the distribution of the most common Antarctic species of Clavaxinellida, except for the bipolar species, which have been mapped separately on Map 8.

MAP 5: Haplosclerida

The Antarctic sponge fauna includes about 50 species of Haplosclerida. This is a widely distributed eurybiontic (wide-ranging) sponge group, found mainly on the shelf and only partly in the upper part of the continental slope. The most numerous genus of these sponges—*Haliclona*—is represented in Antarctica by 20 species, and the closely related genus *Adocia* by 7 species. It is noteworthy that certain genera, such as *Halichondria* and *Hymeniacidon,* which are characteristic of Arctic and northern temperate waters, are very rarely found off Antarctica.

Other common Haplosclerida, in addition to those mapped on Map 5, are *Haliclona bidens, H. phakelloides,* and *Adocia cucurbitiformis.*

MAPS 6 AND 7: Poecillosclerida

The Poecillosclerida is the largest and most diversified group of contemporary sponges, occurring from tidal flats to ultra-abyssal depths. It includes 124 Antarctic species, belonging to 47 genera. Most of them are cosmopolitan mass genera represented in the Antarctic by many species. They are the genera *Mycale* (8), *Asbestopluma* (6), *Esperiopsis* (4), *Isodictya* (9), *Myxilla* (8), *Lissodendoryx* (4), *Iophon* (6), *Tedania* (8), *Hymedesmia* (6), *Clathria* (3), *Artemisina* (4), *Ectyodoryx* (4), *Anchinoë* (5), and others. Among the endemic and monotypic genera are *Hoplakithara, Cercidochela, Acanthorhabdus,* and *Bipocillopsis.* As in other oceans, the Poecillosclerida are most abundant in the Antarctic on the shelf and in the upper part of the slope; however the following species have been found at greater depths and on the ocean floor: *Mycale profunda* (3000 m), *Asbestopluma obae* (2250 m), *Cladorhiza tridentata* (2880 m), *Cladorhiza mani* (3700 m), *Cladorhiza moruliformis* (3568 m), *Meliiderma stipitata* (2928 m), *Chondrocladia antarctica* (2450 m), *Esperiopsis profunda* (2928 m), and *Esperiopsis scotiae* (2560 m). Of special interest among the genera found at abyssal depths are *Asbestopluma, Chondrocladia,* and *Cladorhiza,* which, together with some glass sponges (*Hyalonema* and *Caulophacus*), may occur in oceanic depressions as deep as 8500 m.

Maps 6 and 7 show the distribution of the more common Antarctic species of Poecillosclerida. Other species that are found relatively often in bottom samples are *Mycale gaussiana, Asbestopluma belgicae, Amphilectus rugosus, Hoplakithara dendyi, Myxilla asigmata, Kirkpatrickia variolosa, Iophon radiatus, Iophon aceratus, Tedania charcoti, Artemisina plumosa, Myxodoryx hanitschi,* and a few others. Most of the Antarctic species of Poecillosclerida are circumpolar and are related to the sponge fauna of the Falkland Islands–South America area.

MAP 8: Bipoiar distribution of some sponges

The Antarctic sponge fauna includes more than 10 species that can be regarded as bipolar in distribution. The more important are: *Sphaerotylus schoenus, S. borealis (=S. antarcticus), Suberites montiniger, Artemisina apollinis, Hymedesmia simillima,* and *Hymedesmia longurius.* The morphologically similar populations of these species are found in widely separated areas of the Arctic and the Antarctic and extend only in part into nearby water areas. A somewhat different distribution is found for the bipolar species *Plakina monolopha, Plakina trilopha, Esperiopsis villosa,* and *Desmacidon fruticosa,* which, especially in the Northern Hemisphere, are more typical of temperate and subtropical waters. Other species that may be regarded as bipolar are *Stylocordyla borealis, Amphilectus fucorum, Adocia flagellifer, Aplysilla sulphurea,* and *Halisarca dujardini.* However, any zoogeographic evaluation of most of these species should be made cautiously since the composition of the sponge fauna of the tropical zone has not been fully studied.

Map 8 shows the distribution of *Suberites montiniger, Sphaerotylus schoenus, S. borealis,* and *Artemisina apollinis,* all undoubtedly bipolar in character.

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Stylasterina

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INTRODUCTION

There are two orders of hydrozoan corals, the Milleporina and Stylasterina. The Milleporina are confined to the tropical regions, whereas the Stylasterina are nearly worldwide in distribution. According to present knowledge they are most abundant in the North Pacific, Japan, the East Indies, and the West Indies, but this distribution may reflect collecting effort. Our knowledge of the Stylasterina of the Antarctic and Subantarctic regions has increased enormously on the basis of material collected in the last ten or fifteen years.

Stylasterina form calcareous skeletons supporting three forms of polyps —gastrozooids, dactylozooids, and gonophores. Gastrozooids are feeding polyps of the colony, and are housed in skeletal pores called gastropores. They are short, cylindrical structures bearing a conical hypostome with a four-cornered mouth and generally have a whorl of filiform tentacles. Gastrozooids of some genera are not tentaculate. Dactylozooids, simple, hollow finger-like polyps with no mouth or tentacles, are housed in skeletal pores called dactylopores. They are smaller and much more numerous than the gastrozooids and evidently have a tentacular function. Gonophores, the reproductive individuals of the styloid polyp stage, are housed in small cavities of the skeleton called ampullae. Fertilization of the female gonophores results in microscopic planula larvae which develop in the ampullae. After release from the ampullae, the larvae settle on hard substrates such as pebbles, rock, and shells. Neither the pelagic life nor the settlement of released larvae is known. Stylasterine colonies generally are dioecious, but monoecious species are known among the genera *Distichopora* and *Stylaster.* Anatomically Stylasterina differ from Milleporina, which have capitate tentacles on the dactylozooids and gonophores which produce sexual, free-swimming medusae.

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DISTRIBUTION (PLATE 5)

Some 20 rather ill-defined fossil species and about 165 Recent species of Stylasterina are recognized; most of the latter are restricted to the tropical and subtropical regions, but 2 species, *Stylaster gemmascens* and *Allopora norvegica,* have their northernmost distribution off the coast of Norway within the Arctic Circle, and, in the course of time, nearly 20 species have been reported from the Antarctic and Subantarctic regions. *Errina antarctica* and *Errina fissurata* were the first 2 species described from these regions (Gray, 1872); additional species were not reported until 1903 when von Marenzeller discovered *Errina gracilis*. Broch, in his 1942 review of the distribution of Stylasterina, noted that the genus *Errina* was the only one penetrating southward into the Subantarctic region. He gave more precise information from additional records in 1950; his map included 9 Antarctic and Subantarctic localities of *Errina antarctica* (including *Errina gracilis*), while the text mentioned the localities near the Falkland Islands of *Errinopsis reticulum* and *Errina spongiosa* (now regarded as a synonym of *E. antarctica*). The type locality of *Conopora pauciseptata* is, as Broch noted, in the subtropical region; the species is now also known to inhabit the Antarctic. In later years a few more localities of Stylasterina from the eastern side of the Antarctic continent and from the Ross Sea have become known (Eguchi, 1964; Boschma, 1966), while investigations by Lowe have added many new localities for known species and several records of as yet undescribed species from the Drake Passage region.

Our present knowledge of the distribution of the Stylasterina shows that the Antarctic and Subantarctic regions form a zoogeographical unit. More than half the species found here are endemic to the region; the others are known also from a few surrounding localities. (*Errina aspera* extends as far north as the Mediterranean.) In the eastern sector of the southern oceans, the boundaries of the Antarctic–Subantarctic zoogeographical unit extend only as far north as the coastal waters of New Zealand and the Kerguelen Islands. In the western sector, these faunal elements occur much farther to the north, off the South American coasts including the locality of Station 320 of the *Challenger* Expedition, at 37°17′S, 53°52′W, off the mouth of the Rio de la Plata, at a depth of 1097 m (600 fms). Four of the 5 species of Stylasterina obtained at this locality were also found to live farther south, in the Subantarctic or even the Antarctic region.

The Stylasterina of the regions surrounding the Subantarctic consist almost entirely of groups of species completely different from the Antarctic–Subantarctic ones. In the waters surrounding New Zealand, a number of apparently endemic species of *Errina,* some species of *Stylaster,* and 1 of *Stenohelia* have been recorded[3]. The only representative of the genus *Stylaster* in the Subantarctic region is *S. densicaulis*. *Sporadopora mortenseni,* described from off the Three Kings Islands, north of New Zealand, is now known to occur also in the Queen Maud Land area of Antarctica; this is the only New Zealand species known to occur in the Antarctic. There is not a single record of a species from Australia that has also been found in the Antarctic–Subantarctic area, but the data from Australia are scanty. The type locality of *Conopora tenuis* is Station 170 of the *Challenger* Expedition, off the Kermadec Islands, in the border region of the Subantarctic. The species has later been recorded from several other widely-scattered localities as far north as Japan and as far west as Mauritius. The Stylasterina from off the coast of South Africa appear to form a group of species restricted to the area; none of the species have been reported from other localities.

When attention is paid to the occurrence of the species in the Antarctic–Subantarctic region (also including Station 320 of the *Challenger* Expedition, off the mouth of the Rio de la Plata), it becomes evident that most of these species are endemic. This holds for the single species of *Stylaster* and the 3 species of *Allopora*. Of *Conopora pauciseptata* most of the localities are in the Antarctic–Subantarctic region, only 1 being subtropical.

[3]The manuscript of the present text was completed in 1967; the data on some new species from the New Zealand region, published in 1968, are not taken into consideration here.

In their distribution 4 species of the genus *Errina* (*antarctica, fissurata, laterorifa,* and an as yet undescribed species) are entirely confined to the Antarctic–Subantarctic region. *Errina gracilis* has only 1 locality outside this region, Tristan da Cunha; the same holds true for *Errina labiata,* fairly common in the region, but occurring also off Providence Island in the western Indian Ocean. *Errina aspera* was originally known only from the Mediterranean; later doubtful records for the Azores and the West Indies were published for the species, and a subspecies was described from Mauritius. The species has now become known from a number of localities in the Drake Passage region.

The 2 species of the genus *Errinopsis* are known only from the Drake Passage region. A representative of an as yet undescribed genus occurs farther north in the vicinity of the mouth of the Rio de la Plata as well as near Cape Horn. It is very interesting that the genus *Errinopora,* which until recently was known only from the North Pacific area, also proved to have a species (as yet undescribed) in the Drake Passage region.

Three species of the genus *Sporadopora* occur in the Antarctic–Subantarctic region; only 1 of these *(mortenseni)* is also known from a locality outside the area (north of New Zealand).

In summary we can say that of the 19 species of Stylasterina occurring in the Antarctic–Subantarctic region, 15 are strictly endemic, 3 (*Conopora pauciseptata, Errina labiata,* and *Sporadopora mortenseni*) each have, besides localities in the region, 1 record outside, while 1 (*Errina aspera*) occurs in as widely distant localities as the Mediterranean, Mauritius, and the Drake Passage region.

As far as their vertical distribution is concerned, all the Antarctic–Subantarctic Stylasterina occur in depths between 200 m and 1300 m; only a comparatively few species have been found in shallower or in deeper water. In the coastal region of South America, *Errina antarctica* has been obtained from depths of 3.5 m to 18 m; in other areas there are records of the species from 55 m to 200 m. Of *Errina laterorifa* there are 2 localities at depths of 46 m and 80 m; of *Errina gracilis* there is 1 locality at a depth of 100 m. Five species that are rather commonly found in the region between 200 m and 1300 m occur also at greater depths. The greatest known depth of *Sporadopora dichotoma* is 1501 m, of *Errina labiata,* 1879 m to 1886 m and of *Stylaster densicaulis,* 1904 m. Most of the records of *Conopora pauciseptata* are from depths between 300 m and 1300 m; the species has also been obtained from 1879 m to 1886 m and at a depth of 5845 m in 1 locality. It is interesting to note that Vaughan and Wells (1943), in their table of bathymetric ranges of deep-sea Madreporaria, record but a single genus from a comparable depth, namely *Fungiacyathus,* with a maximum depth of 5872 m.

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Scleractinia

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INTRODUCTION

The Scleractinia include the conspicuous and well-known stony corals of the tropics and the less well-known 'simple' corals of the cold and deep waters. Since the early 1800's it has been known that corals occur in the Antarctic, but knowledge of their distribution and the composition of the fauna was based mainly on the meager early collections. Though modern collections are from more widely distributed locations and contain numerous specimens, it has been only during the last decade that the study of these corals has advanced. Unfortunately, knowledge is still superficial, particularly in such Subantarctic areas as the shallow waters surrounding the islands of the southern Indian Ocean and the South Atlantic. Understanding of the distribution of the deepwater corals is also in an extremely fragmentary state.

Present information suggests that the corals of the Subantarctic and the Antarctic comprise a biogeographic unit, the 'southern ocean' fauna, composed of the corals which inhabit the southern portions of the Indian, Pacific, and South Atlantic Oceans, as well as the Antarctic waters. In general, this area extends as far north as the Subtropical Convergence.

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CHARACTERISTICS OF 'SOUTHERN OCEAN' CORALS

Corals inhabiting the 'southern ocean' may be characterized as ahermatypic by morphological features and by their ecology. They are often incorrectly called 'simple' corals. Wells (1933, p. 27, footnote) made this definitive statement:

> The term 'deep-sea' corals is unfortunate, because there is no real distinction between corals found in the bathyal and neritic environments, with the exception of the true reef corals which are exclusively neritic. The term 'hermatypic,' from *herma,* a reef, is therefore proposed to describe corals of the reef-building type, the living species of which possess symbiotic zooxanthellae within their tissues. In contrast to this term, 'ahermatypic' is proposed to describe the corals of the non-reef building type, the living forms of which do not possess zooxanthellae and which live under greatly varying conditions of depth, temperature, and light. The use of these eliminates the inaccurate expression 'deep-sea corals.' Ahermatypic corals include both the deep (bathyal) and shallow (neritic) water forms which do not build reefs.

Reefs are difficult to define in structural terms or in relation to assemblages of species, particularly in the geographic margins where the complex associations of the tropics may give way to simpler polyspecific groupings, or indeed, monospecific structures in some areas ecologically replaced by kelp beds (Squires, 1959). A clear faunal demarcation may be drawn vertically, but as knowledge of deepwater coral structures increases (Teichert, 1958; Stetson, Squires, and Pratt, 1962), the boundary may become increasingly complex. Aggregations of coral in the marginal regions of the 'southern ocean' may form thickets, coppices, or banks (Squires, 1965).

The term 'ahermatypic' does not preclude colonial forms, but the distinction between colonial and solitary becomes arbitrary in the attempt to segregate those species which reproduce asexually and those which do not. Species which reproduce asexually are generally capable of generating a bewildering variety of colonial growths. Hermatypic corals, through the mechanism of intratentacular budding (a method not employed by the ahermatypic corals), produce a complex polyp which is, in many respects, an individual having an extensive ability to adapt the form of its skeleton in response to the external environment. On the other hand, ahermatypic corals are usually individuals distinguished by a single mouth encircled by one or more circlets of tentacles and which possess a rather simple cup-like corallum. Some species produce colonies of an arborescent appearance, due to extratentacular budding in which the young are produced from the portion of the polyp outside the tentacular ring, the new polyps often being placed alternately on the branches. Colonial corals are not found in waters of the Antarctic shelf. *Solenosmilia variabilis* and *Lophelia prolifera* are found in outlying islands in both the South Atlantic and southern Indian Oceans. *Madrepora vitiae* and *Solenosmilia variabilis* penetrate into the 'southern ocean' as far south as Macquarie Island along the Macquarie Rise; this is the most southerly occurrence of colonial corals.

Solitary corals are characteristic of cold-water regions, and many of them have a broad geographic range which is associated with their wide temperature tolerance and bathymetric range. Antarctic corals are morphologically similar to deepwater corals in tropical regions, but whereas the deepwater tropical species are generally small, Antarctic species include some of the largest of the solitary corals. The size of these corals is exceeded only by that of representatives of the shallow tropical reef species of Fungiidae.

The Antarctic corals are as yet inadequately known. The appellation 'simple,' connoting lack of structural complexity, has resulted in broad definitions of species and attribution of cosmopolitan distribution. Recent studies of populations (for example, Squires, 1961, 1962a, and Squires and Keyes, 1967) have resulted in refinements and narrowing of ranges so that patterns of distribution among those species considered are not unlike those of other benthic organisms possessing similar mechanisms for dispersal. Unfortunately all too few species have been considered in detail, and many of those mentioned in the following text are, in reality, 'form' genera and species.

Distribution patterns of 'southern ocean' corals are very uneven, both locally and regionally. Most characteristic is the large number of individuals in contrast to the low diversity of species taken in a single locality (Squires, 1964b, p. 448), a pattern well known among other organisms from high latitudes (Wallace, 1878; Fischer, 1960). Distribution data accumulated solely by dredging can be misleading, but patterns ascribed to corals have been confirmed by undersea photographs. These show that when corals occur, they are, in fact, frequently present in great numbers of individuals, but such groups may be separated by broad areas of very low density. This arrangement results from many factors, paramount among which is the apparently limited dispersal capacity of 'southern ocean' corals. The author (Squires, 1962a and unpublished notes) found highly advanced free larvae within adult corals and in 1965 (unpublished data) was able to maintain larvae in an aquarium until they reached the settling stage. Although a maximum of twenty days passed between release and settlement (subject to introduced error caused by premature larval release), larvae were at no time motile. Apparently larvae of Antarctic corals mature principally within the adult and settle shortly after release. The high percentage of settlement of young corals upon adult coralla suggests that many are not moved from the parent population site, although the larvae could be drifted by bottom currents.

These examples of planulation have been observed in adult corals collected by dredging and then maintained for short periods in aquaria at appropriate temperatures and salinities but without pressurization. These observations are of behavior which may result entirely from the traumatic experiences related to environmental changes during the process of collection, and must be verified by further study.

It has been the writer's thesis (Squires, 1965) that since distribution of sediment type was extremely patchy, distribution of those species having a high specificity for sediments of certain types would also be patchy, based on the premise that many species require materials of a certain size for settlement of larvae (Squires, 1961).

In summary, the characteristics of the 'southern ocean' corals, particularly those of the shallower waters are:

(1) Predominance of solitary forms, colonial corals being found only on the northern fringes of the region.
(2) Contagious distribution of species, reflecting the characteristics of larval distribution and patchiness of sediment type distribution.
(3) Abundance of individuals at a site, but a limited number of species in any association.
(4) Large size of individuals, particularly from the Antarctic shelf.

REGIONAL DISTRIBUTION

Although it is a surface feature of the upper oceanic layers, the Subtropical Convergence (Figure 10, p. 6, this folio) can be taken as the northern boundary of the coral fauna of the 'southern ocean.' This feature lies south of the shallow-water faunas of Australia and South Africa (see Plate 6); however New Zealand and South America lie astride the Subtropical Convergence and have faunas of mixed type.

SOUTH ATLANTIC OCEAN. In the South Atlantic, Tristan da Cunha, north of the Subtropical Convergence, is characterized by species with northern affinities, including *Lophelia prolifera, Solenosmilia variabilis,* and *Caryophyllia profunda.* A short distance to the south of the Convergence is Gough Island with only one known coral, *Caryophyllia profunda* (= *C. cyathus* Gardiner, 1939). Still farther to the south is Bouvet Island from which only one species is known—*Caryophyllia antarctica,* a true Antarctic species.

INDIAN OCEAN. In the southern Indian Ocean there are several major island groups, but little is known of their fauna. The principal gap is in the region of Kerguelen, McDonald, and Heard Islands, from which there are no records. From the Prince Edward Islands, south of the Subtropical Convergence, *Flabellum apertum,* a Subantarctic species occurring as far east as the Macquarie Rise, has been recorded. No shallow-water corals have been taken from the Crozet Islands, although deepwater stations have been made in the vicinity. Farther east, the corals collected by the Deutsche Tiefsee Expedition in 1901–1903 from Amsterdam and Saint Paul were *Solenosmilia variabilis, Lophelia prolifera, Desmophyllum cristagalli, Caryophyllia profunda,* and a species recorded as *Stenocyathus vermiformis.* This assemblage is of northern affinities.

SOUTH AFRICA. The South African coral fauna has not been studied as a unit. The only listings of the coral species occurring there are the uncritical lists of Wells (1958) and Squires (1961). These give a total of 32 species of which only *Solenosmilia variabilis* and possibly *Desmophyllum capense*[2] are related on the species level to forms occurring in the Antarctic.

SOUTH AUSTRALIA. The South Australian fauna has long been known to contain a high proportion of autochthonous endemic types, both at a generic and a specific level. Lists of the 41 species occurring there, both uncritical, are given by Wells (1958) and Squires (1961). The South Australian fauna is mainly ahermatypic, although some elements of the hermatypic fauna apparently extend all the way around the continent (Squires, 1966). This is the most southerly occurrence of hermatypic corals. Few of the species occurring in Australia have close relationships to the corals of New Zealand (Squires and Keyes, 1967), and none are in common with the true 'southern ocean' fauna, as presently understood. At least one species of the Australian fauna, *Ceratotrochus recidivus,* has been found on the Macquarie Rise.

NEW ZEALAND. The shallow water fauna of two northern landmasses, South America and New Zealand, are interjected into the 'southern ocean.' Both regions are connected by nearly continuous, shallow, submarine ridges to the Antarctic. These ridges are potential migration routes to and from the Antarctic, but it appears that the connection from South America has served primarily as an emigration route to the Antarctic waters for

[2] *D. capense* is apparently restricted to South Africa, for records of this species as given by Gardiner (1939) on the Argentine Shelf are erroneous and represent an undescribed species.

corals in recent times, whereas the New Zealand region has been invaded from the Antarctic in the past and has a number of relict species. In the more recent past, faunal elements from New Zealand waters have moved southwards. The New Zealand fauna has been reviewed extensively in a number of publications, principally those of Ralph and Squires (1962), Squires (1963, 1964a, 1966), and Squires and Keyes (1967), but it is still not fully known. The most recent list (Squires and Keyes, 1967) gives 25 species, almost half of which are endemic, the others displaying relationships to species both to the north and south.

SOUTH AMERICA. Although very important to the study of the Antarctic, the faunas of the coasts of South America have not been as intensively studied as is warranted. The rather striking difference between the Chilean and Argentine coasts has been only partially documented, and the corals from both regions are only sketchily recorded. Squires (1961) reported on the corals from the Argentine shelf, summarizing the work of Gardiner (1939), which badly needs review and expansion, and that of earlier workers. From the Argentine shelf 5 species are recorded, a number enlarged in subsequent studies (unpublished) to 14. When recent findings are complemented by records of species occurring off the Chilean coasts, a total of 15 species may be expected. Most of these are closely related to Antarctic species, and Antarctic species do occur on the slopes of the South American coast. There is an apparent difference between the coral fauna of the Chilean and Argentine shelves, but one which may not be real, for collections are not yet comparable in the two areas. Missing from the Chilean region are the species of *Flabellum* which dominate the Argentine shelf: *Flabellum curvatum* and *Flabellum thouarsii*. Except for one occurrence of *Flabellum patagonichum* off the Rio de la Plata, this species is apparently confined to the Chilean coast, a pattern followed by *Solenosmilia variabilis* in more limited occurrences. Large colonies of *Desmophyllum ingens* are typical of the deeps off the Chilean coast, and although the same species is found on the eastern side of the continent, it does not reach the same magnificent proportions there. *Balanophyllia malouinensis,* the ubiquitous species of Cape Horn and the Falkland Islands is apparently absent from Chilean waters.

Relationships with the Antarctic are even less clear-cut. At first, there appeared to be a distinct gap between the South American faunas and those of the Antarctic Peninsula (Squires, 1961), but more recent intensive collecting efforts have yielded collections demonstrating that the differences are not as great as supposed. It now appears that *Flabellum impensum, Caryophyllia antarctica,* and *Caryophyllia* sp.A all occur on the slopes and outer shelf of South America. The former species is closely related to the *Flabellum thouarsii* and *F. curvatum* complex and is interpreted as being of modern origin (Squires, 1962a).

ANTARCTICA. Seven species of coral are known from Antarctica, of which 1, *Fungiacyathus symmetricus,* is a cosmopolitan deepwater species. The remaining 6 are composed of 4 endemic species *(Gardineria lillei, G. antarctica, Flabellum antarcticum, Balanophyllia chnous)* and 2 species which range into the South American region *(Flabellum impensum* and *Caryophyllia antarctica).* The ancestral relationships of the *Gardineria* are not known although the genus occurs in the West Indies, off Brazil, and off the Hawaiian and Philippine Islands. *Balanophyllia chnous* is endemic, without well-understood affinities, although Squires (1962a) recognized similarities between this species and *B. alta* from New Zealand. As yet the species has been recorded only from the Ross Sea. *Flabellum antarcticum* is a member of the *'rubrum'* group of this genus (Squires 1962b) but is of more distant relationships than *F. impensum. Caryophyllia* species belong to a great and as yet unresolved complex which is not well understood and which is burdened by a plethora of poorly described species.

The Antarctic Peninsula forms the most logical transition between the faunas of South America and those of the Antarctic. Collections from this region show a rich and large fauna of typical Antarctic species extending to South Georgia and Shag Rock, and indeed beyond, into the deeper waters of the Drake Passage.

SUMMARY. Antarctic corals are few in number and rather clearly demarcated from faunas of neighboring regions, particularly in the case of species occurring in shallow waters. Existing possible migration routes seem to have been active both now and in the recent past. Close affinities exist between species of *Flabellum* from both South America, New Zealand, and the Antarctic, with the genetic source presumed to be the Eastern South American continental shelf. This hypothesis is to a large extent based on as yet unpublished paleontological data and upon premises of the geologic history of the Scotia Ridge. Similarities with New Zealand, through the Macquarie Rise route, are believed to be of historic rather than modern significance, and the evidence is that corals are penetrating more deeply into the Antarctic waters along both routes, with passage of time. Other 'southern ocean' regions show rather strong segregation of faunas with the coral species being endemic or related to those of northern regions. Australian corals are the most autochthonous, while those of New Zealand are less so, having some strong relationships with northern species, possibly through modern immigration (Squires and Keyes, 1967). The northern boundary of the 'southern ocean' region may be conveniently marked by the Subtropical Convergence although this is not thought to be the limiting mechanism in the distribution of the species of the 'southern ocean.' Those islands occurring south of the Convergence have a fauna of southern affinities while those to the north have corals related to those occurring in similar regions yet farther to the north. Although all regions are very scantily represented in existing collections, a clearer definition appears to exist at the Subtropical Convergence than is found at the Antarctic Convergence.

Isolating mechanisms are not well understood since detailed knowledge of the biology of most species is rudimentary. Although existing evidence suggests that coral larvae are short-lived, later data tend to suggest the contrary, and more information is required. Patterns of sediment selectivity suggest that this may be as important a causal factor in contagious distribution patterns as larval behavior.

THE MAPS (PLATE 6)

MAP 1. Caryophylliid corals are among the most important of the ahermatypic corals in numbers of species, distribution, and evolutionary attainments. The 6 most common of the 19 caryophylliid corals of the 'southern ocean' are represented on this map. Species not represented are known from too few records to be significant, or are 'form,' or nominal, species badly needing taxonomic revision.

Caryophyllia antarctica had been thought to be restricted to the Antarctic, but recent collections show it to occur off the Chilean coast, the Falkland Islands, and Bouvet Island. Its distribution in the Antarctic reflects the distribution of collecting effort, with most numerous occurrences being in the Antarctic Peninsula and the Ross Sea. Its circumpolar distribution is, however, apparent. *Caryophyllia* sp.A is a closely related species as yet undescribed, differing in the character of pali and septal spination. Its distribution is particularly interesting as it is widely distributed around New Zealand and less commonly off South America and at the northern tip of the Antarctic Peninsula. It is presumed that this species is a derivative of *C. antarctica,* and the occurrences in South America may reflect the need for careful consideration of the status of the species. *Caryophyllia profunda* is a broadly defined species which has circumpolar distribution outside the Antarctic. In general, it is the name applied to attached *Caryophyllia,* and review of the species may reveal a more complex clonal situation. Two species of *Desmophyllum* are shown: *D. ingens* and *D. cristagalli.* The former was originally described from the Chilean deeps where it is large, robust, and common. Similar forms are found sparingly on the eastern coast of South America but are not recorded elsewhere. *D. cristagalli,* on the other hand, is a 'form' species including most *Desmophyllum* not taxonomically placed elsewhere. The type locality of *D. cristagalli* is the Gulf of Gascony, but the name is applied equally to specimens from all parts of the world and, indeed, through the Tertiary record of the genus. Although study of the New Zealand fauna has been under way for nearly a decade, there has not been occasion to definitively examine the relationships between *D. ingens* and the coral referred to as *D. cristagalli* from that country. This absence of critical work results from inconclusive understanding of the biology of the coral with consequent absence of critical selection of species characteristics. *Sphenotrochus,* a small turbinoliid coral, is commonly found in South African, South American, and northern New Zealand waters. Distribution of a South American species, *Sphenotrochus gardinieri,* is shown to indicate how localized a coral species may be.

MAP 2. This map illustrates distribution of a variety of corals rather arbitrarily grouped together for convenience. Distributions of 2 species of deepwater corals, neither common, are shown to illustrate the presumed cosmopolitan occurrences of deepwater corals of the 'southern ocean.' *Leptopenus discus* is rare, known only from 5 specimens, but is quite distinctive. Its rarity may result either from its extreme fragility, or the probable tendency for its skeletal material to dissolve upon the death of the animal in the deep waters it inhabits. *Fungiacyathus symmetricus* is a ubiquitous species in deep waters, but revision will be required to ascertain if this distribution is actual.

Shallow-water corals include species from a number of families. *Goniocorella dumosa* is included to demonstrate the interesting pattern of distribution of several species from New Zealand (see Squires and Keyes, 1967). *G. dumosa* is a northern species, occurring in the Malayasian region but also common in New Zealand on the eastern side of South Island. Its distribution probably reflects the warming effects of currents on the eastern coast, but its ability to survive in abundance on the Campbell Plateau indicates that it is not stenothermal. On the plateau it is the sediment-forming constituent of deepwater coral banks (Squires, 1966). *Stenocyathus decamera* is also restricted to New Zealand, but in this instance, largely to the southern region, and is widely distributed on the Campbell Plateau. *Gardineria antarctica* and *G. lillei* are 2 species of unknown origin but characteristic of the Antarctic. The genus is found in the West Indies, off Brazil, and in the Hawaiian and Philippine Islands, but not anywhere in close relation to the Antarctic. The distribution of *G. antarctica* is cir-

cumpolar, but *G. lillei,* less well known, appears to be restricted to the Antarctic Peninsula except for the single Ross Sea occurrence.

Solenosmilia variabilis is mapped, not because its distribution is of a significant pattern, but rather because its occurrence at Macquarie Island is the most southerly known for a colonial coral; a second colonial coral, *Madrepora vitiae,* is known from the somewhat more northerly New Zealand waters.

Two species of dendrophylliid corals are shown: *Balanophyllia chnous,* because it is the only dendrophylliid to occur in the Antarctic (one locality in the Ross Sea) and *Balanophyllia malouinensis* because it is restricted to the Argentine shelf where it is a particularly conspicuous and abundant form. A balanophylliid coral known from a single record at Gough Island is thought to be *B. malouinensis,* but there are many difficulties in identifying the single specimen. Such an occurrence would be possible if larvae could be carried for such large distances, but nothing is known of the breeding of this species.

MAPS 3 AND 4. Corals of the genus *Flabellum* are among the most important in the 'southern ocean' in numbers of specimens and for documentation of the faunal history of the shallow water areas in the 'southern ocean.' Three general groups may be recognized: (1) the *'rubrum'* group (Squires, 1962b) includes *Flabellum rubrum* (a New Zealand species); *F. impensum, F. antarcticum* (Antarctic species); *F. thouarsii, F. curvatum* (eastern South America); and *F. serpuliforme* and *F. gracile* (Atlantic); (2) the lacerate corals including those forms in which the upper margin of the calice is notched or scalloped, such as *F. apertum* and *F. patagonichum;* and (3) broadly flabellate *Flabellum* with a normal epitheca including *F. knoxi.* The first group is widely distributed through the 'southern ocean' with only 2 species being found in the Atlantic north of the region of the Subtropical Convergence, and *F. rubrum* which is widely distributed around New Zealand. Lacerate flabellids are found from pole to pole and are not, as yet, a well-defined group of corals. They are more abundant and more diversified in the Pacific than the Atlantic and extend only marginally into the 'southern ocean.' The flabellate *Flabellum* are also more typical of the tropical regions and in the Subantarctic they are found only on the Campbell Plateau.

Those species of the *rubrum* group occurring in the 'southern ocean' are indicated. *F. rubrum* has been discussed elsewhere (Squires, 1962b) and is believed to be a relict of an earlier wider dispersal of this group through the Antarctic. *F. antarcticum* and *F. impensum* display a circumpolar distribution occurring at almost every site from which corals have been collected. *F. impensum* is particularly common in the Antarctic Peninsula region where it reaches very large sizes and is quite abundant. It apparently extends its range across the Drake Passage onto the outer slopes of the Argentine Shelf where it meets the complex of *F. thouarsii* and *F. curvatum.* The latter species is apparently a northern extension of *F. thouarsii,* and *F. impensum* is a southern member. In discussing the distribution of corals on the Argentine Shelf, I postulated (Squires, 1961) that *F. thouarsii* was dependent in its distribution on the occurrence of pebbles on the Argentine Shelf. Greater distribution of this species in the past is borne out by its fossil occurrence in sediment cores from much more northern localities (also associated with pebbles) than at present. The boundary between the occurrence of *F. thouarsii, F. curvatum,* and *F. impensum* is much more uneasy than depicted on the map. Many collections of the *William Scoresby* were poorly recorded and identified by J. S. Gardiner (1939), and until this material is carefully reconsidered, the degree of intermingling of the species will not be certain. Discrimination is difficult but important, for it is one of the keys to the history of the migration of this important species complex.

F. apertum, a member of the lacerate group, is found in the southern Indian Ocean and more recently along the Macquarie Rise. This species is believed to be restricted to the Subantarctic waters. *F. patagonichum* resembles *F. apertum,* but apparently is not related. *F. patagonichum* is widely distributed around the South American continent but is not abundant, and its relationships with other species of this group to the north in the Atlantic is not known.

F. knoxi is the only member of the flabellate group to be mapped, for members of this group do not occur commonly in the 'southern ocean' except in the vicinity of New Zealand. This species shows the distribution peculiar to many corals occurring in New Zealand, in which there is a broad distribution on the Campbell Plateau and to the east of New Zealand along the Chatham Rise. This species is further discussed in Squires and Keyes (1967).

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Nemertea

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INTRODUCTION

Nemerteans, popularly known as ribbon-worms, are characterized by elongated, soft, extensible, ciliated bodies without external signs of segmentation. When alive, they may be brightly colored, especially with shades of red, orange, yellow, green, or brown. Development may be direct, leading to the formation of a larva similar to the adult, or in many heteronemerteans such as *Cerebratulus,* it may be indirect, with a free-swimming ciliated larva of complicated form known as a pilidium. The young worm develops by metamorphosis within the pilidium. All nemerteans are carnivorous, feeding on protozoans, and various kinds of worms, mollusks, crustaceans, and larval invertebrates.

Nemerteans are found along all the sea coasts of the world and offshore to depths of hundreds of meters. Some of the northern species appear to be circumpolar, extending southward along the coasts as far as Madeira, southern New England, California, and Japan. A few species live in both the Northern and Southern Hemispheres. Some are limited to the polar seas and others to the tropics. Some of the bathypelagic species live at depths of 1000 m to 2000 m or more, and populations may be carried for thousands of miles by deep ocean currents, reproducing generation after generation in their endless circuits throughout the great oceans.

At the present time the principal difficulty in the study of the Nemertea is in obtaining adequately preserved and documented collections. Nemerteans are difficult animals to collect and preserve in a useful condition. Many species contract and fragment violently when placed in preserving fluid and considerable patience must be used to relax them.

Estimates of the number of validly described species of Nemertea vary from 550 to 750. Of these, nearly 200 species have been recorded from the coasts of Europe, 100 from the Pacific coast of North America, and 53 from the Atlantic coast. An analysis of the situation up to about 1943 (Coe, 1943) showed that 11 species were common to both sides of the Atlantic and 11 occurred on both Atlantic and Pacific coasts of North America. The 98 species of Pacific North America shared 7 species with the 21 of Pacific South America, 16 with Japan, and 5 with the 13 species known from South Africa which, in turn, shared 8 with the European fauna. Since that analysis, nearly 100 new species have been described from localities throughout the world, including 37 from Japan, 38 from eastern South America (mainly from Brazil), 7 from eastern Africa and 7 from Europe. The 67 species of bathypelagic nemerteans recorded by

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Coe (1954) have now been increased by the 11 new species from the southern oceans described by Korotkevich (1963).

The nemerteans known at present from the Antarctic and the Falkland Islands consist of 39 species within the following genera: *Carinina* (2), *Baseodiscus* (1), *Cerebratulus* (2), *'Lineus'* (4), *Parapolia* (1), *Nemertopsella* (1), *'Amphiporus'* (10), *'Tetrastemma'* (13), *Cratenemertes* (1), *Obnemertes* (4).

A general outline of distributions and references to the literature of each species, except the 5 pelagic forms described by Korotkevich (1960, 1962, 1963), has already been given by Dawson (1967). Therefore, only major bibliographic data sources for the benthic forms are given here.

Published records up to 1967 show that of the 39 'Antarctic' species, 14 species have been recorded only once, 3 have been recorded twice, and 4 recorded three times. The number of sparsely known species is therefore 21, or 53.8% of the known fauna. Another 10 species, or 25.6%, have been recorded between 4 and 9 times. Only 8 species, or 20.5%, have been recorded more than 10 times (but one, *Lineus corrugatus* McIntosh, has been recorded over 70 times).

The locations where Nemertea have been collected in the map area of Plate 7 are shown on Figure 1. Names of the expeditions are given in Table 1.

BENTHIC NEMERTEA

Of the 34 benthic 'Antarctic' species, 6 are known from only 1 specimen, 7 from less than 5 specimens, 7 from less than 10, 4 from between 10 and 30, and 8 from up to 100 specimens. Only 2 species, *Lineus corrugatus* McIntosh and *Tetrastemma validum* Bürger, are known in great abundance, but *Amphiporus moseleyi* Hubrecht and *Tetrastemma hansi* Bürger are probably much more common than collection figures show.

PALAEONEMERTEA. This order is said to be represented in the Antarctic by 2 species of the genus *Carinina*. However, Müller (1965) has recently reviewed the genus, which contains 11 described species, and has shown that among the 3 doubtful species attributed to this genus are the 2 Antarctic representatives, *C. antarctica* Bürger and *C. mawsoni* Wheeler.

Since the true status of these species must await the collection and examination of new material, no collection localities have been shown on the maps.

HETERONEMERTEA. This order is represented by the genera *Baseodiscus, Parapolia,* and *'Cerebratulus'* and *'Lineus'* in the broad sense. Both

TABLE 1. Expeditions Which Have Collected Nemertea in the Region South of 35°S Latitude

PUBLISHED RECORDS

Britain, Australia, and New Zealand

1. Voyage of H.M.S. *Challenger*, 1873–1876
2. British Antarctic Expedition *(Southern Cross)* 1898–1900; British National Antarctic Expedition *(Discovery)*, 1901–1904
3. Scottish National Antarctic Expedition, 1902–1904
4. British Antarctic *(Terra Nova)* Expedition, 1910–1913
5. *Discovery* Investigations, 1925–1931
6. Australasian Antarctic Expedition, 1911–1914; British–Australian–New Zealand Antarctic Research Expedition, 1929–1931; Australian National Antarctic Research Expeditions, 1947–1962 (Macquarie Island)

Germany

7. German Transit of Venus Expedition, 1874–1876
8. German group of the International Polar Year Investigations, 1882–1883
9. Hamburg Magellanic Expedition, 1892–1893
10. German South Polar Expedition *(Gauss)*, 1901–1903
11. Plate collections, Chile, 1896
12. Schauinsland's Pacific journey, 1896

United States

13. United States Exploring Expedition, 1838–1842
14. United States Antarctic Service expedition, 1939–1941
15. United States Navy Operation Windmill, 1947–1948

France

16. Expedition led by Capt. Dumont D'Urville, 1837–1840
17. French Antarctic Expedition (led by Charcot) 1903–1905
18. Second French Antarctic Expedition (led by Charcot) 1908–1910

Russia

19. Soviet Antarctic Expeditions, 1955–1964

Others

20. Austrian voyage in the *Novara*, 1857–1859
21. Lund University Chile Expedition, 1948–1949
22. Belgian Antarctic Expedition, 1897–1899
23. Argentine Antarctic Institute expeditions

UNPUBLISHED RECORDS

24. New Zealand Oceanographic Institute, D.S.I.R., Wellington
25. Lamont Geological Observatory, Research Vessel *Vema*
26. Stanford University Biological Laboratory, McMurdo Sound
27. Royal Society Expedition to Southern Chile, 1958–1959
28. Australian Museum, Sydney

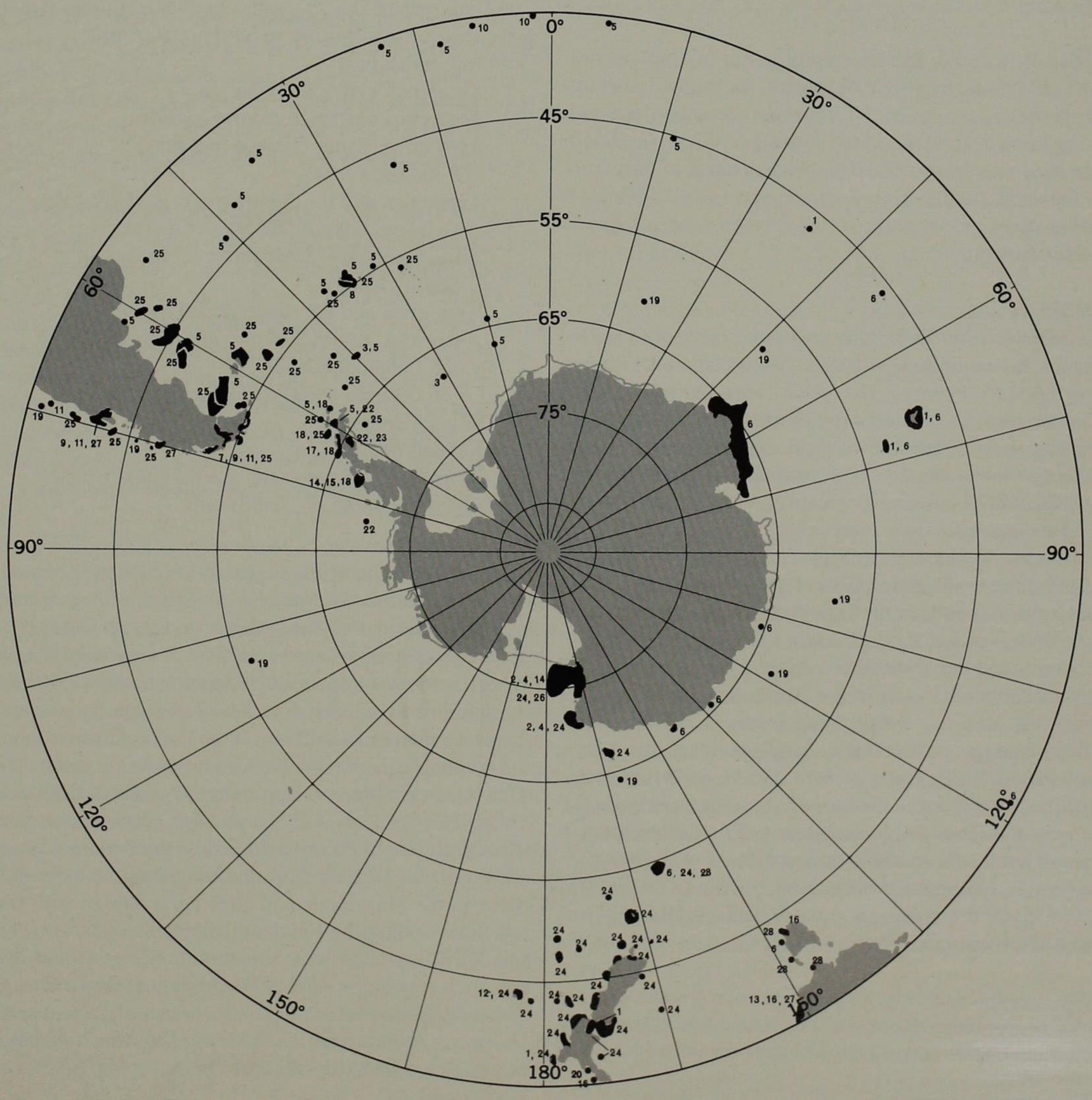


Fig. 1. Locations where Nemertea have been collected south of 35° S latitude. Numbers designate expeditions listed in Table 1.

of the last named genera contain a great number of species in the world fauna and present many taxonomic difficulties. However, some progress has been made on better definitions of genera and species by Friedrich (1960), and others more recently. *Parapolia* is represented by only 1 relatively little known species *(P. grytvikensis)* from South Georgia and East Antarctica (70°E to 85°E) and is not shown on the maps.

Baseodiscus (Map 1, Plate 7) has 1 species known from the Antarctic. Over 25 species of *Baseodiscus* are known in the world fauna, 10 of which occur within the Central to South American region according to Corrêa's list (1955, pp. 4–5).

Cerebratulus (Map 1, Plate 7) is a large genus by nemertean standards with perhaps 90 recognized species, of which only 2, *C. larseni* and *C. magelhaensicus,* occur in the Antarctic. *C. larseni* also occurs at Macquarie Island and at South Georgia. *C. malvini* is circumpolar on the Subantarctic islands, but other species within the map area have a more northerly distribution.

Lineus (Map 2, Plate 7) contains over 60 species throughout the world, many of which are now being found to belong more properly to new genera. *Lineus corrugatus* McIntosh, a large and conspicuous nemertean, which has figured notably in underwater photographs of the benthos of the Antarctic (see Peckham, 1964), is truly circumpolar in distribution and is, as Coe (1950, p. 56) has stated, 'evidently most abundant and most widely distributed of all Antarctic species.'

The second species shown on the map, *Lineus longifissus* (Hubrecht), is known from Marion Island, the South Orkney Islands, Kerguelen Island, Macquarie Island, and along the Kemp Coast in East Antarctica.

HOPLONEMERTEA. Benthic genera of this order reported from the map region are *Nemertopsella, Amphiporus,* and *Tetrastemma.*

Nemertopsella marri (not shown on the maps) was described by Wheeler (1940a) from intertidal specimens collected at Kerguelen Island, and recent records of its occurrence at Macquarie Island have been published by Kenny and Haysom (1962).

Amphiporus (Map 3, Plate 7) is a worldwide genus containing approximately 100 described species. *Amphiporus spinosus* Bürger is perhaps the most abundant species of *Amphiporus* in the Antarctic, occurring at many stations in and around South Georgia, the Ross Sea, and elsewhere. The genus is particularly well represented at South Georgia by the presence of 5 species. *Amphiporus moseleyi* Hubrecht is another common species, especially in King Edward Cove at Grytviken, but several species of *Amphiporus* are known from only 1 or a few specimens. Further details of distribution of the Antarctic *Amphiporus* species were given by Dawson (1957).

Tetrastemma (Map 4, Plate 8), the other large genus of Hoplonemertea, is known in the world fauna by about 90 species. Germany, for example, has about 10 recorded species, and 12 species occur in the South American region. The known Antarctic fauna consists of 12 species. South Georgia is the home of at least 10 species, 6 of which are known only from this location. The Falkland Islands have 4 known species, 1 of which is not known elsewhere. Other species occur in the Ross Sea and off several parts of the Antarctic continent.

PELAGIC NEMERTEA

The world fauna of polystyliferous hoplonemerteans, more often called the pelagic nemerteans, now numbers 78 species, 21 of which are known south of the equator (Map 5, Plate 8). No species were known from the Antarctic before the collections of the Soviet Antarctic expeditions, although the type locality of the first described species of pelagic nemertean, *Pelagonemertes rollestoni* Moseley, 1875, is 'near the southern verge of the South Australian Current' (between Kerguelen and Macquarie Islands) at 3300 m. Now, 15 species have been recorded by Korotkevich (1963) from the southern oceans, of which 5 are truly Antarctic in distribution. Four of these species belong to the genus *Obnemertes* Korotkevich, 1960, and only 1 of them has been found north of the Antarctic Convergence, in an area of mixed waters. None of the well-known widespread genera of more northerly regions, such as *Planktonemertes, Nectonemertes,* and *Pelagonemertes,* have been found south of the Antarctic Convergence.

The fourth species of Antarctic pelagic nemertean is *Cratenemertes pelagica* Korotkevich[2], belonging to the family Amphiporidae. The pelagic nemertean fauna of the Antarctic has therefore developed in two ways, from the Amphiporidae, belonging to the monostyliferous hoplonemerteans and from the polystyliferous hoplonemerteans. This information is particularly interesting because it confirms the hypotheses of the polyphyletic origin of the pelagic Nemertea proposed by Bürger (1897–1907) and Korotkevich (1955) and considered in more detail by Korotkevich (1962) in opposing the monophyletic origin supported by Brinkmann (1917).

Before Korotkevich's work from the *Ob'*, pelagic nemerteans had not been taken at depths of less than 300 m. The Soviet records extend from the surface to 200 m, in an optimum salinity of approximately 34 ‰ and at temperatures of 0°C or warmer. Korotkevich (1963) concluded that '. . . it can be assumed that they do not move beyond the intermediate water masses of the Antarctic, which, in contrast to the surrounding waters, have positive temperatures. Thus, it can be assumed that the boundaries of the intermediate water masses are also the boundaries of the distribution of pelagic nemerteans.'

[2]Now *Korotkevitschia pelagicus* (Korotkevich, 1961). The new genus *Korotkevitschia* was proposed by Friedrich (1968).

BOTTOM CONDITIONS AND DEPTH RANGES

Intertidal collections from various Antarctic and Subantarctic localities show that nemerteans may be commonly found underneath stones, in crevices, and especially in kelp holdfasts.

Recent collections at the Balleny Islands and in Robertson Bay off Cape Adare have shown the abundance of both numbers and species of nemerteans in an organically rich mud bottom.

In the Ross Sea, New Zealand Oceanographic Institute and Stanford University investigations from 1958 to 1961 showed that nemerteans were particularly abundant in the 'Deep Shelf Mixed Assemblages' and 'Deep Shelf Mud Bottom Assemblages' (Bullivant and Dearborn, 1967). Scuba diving (Peckham, 1964) has shown that *Lineus corrugatus,* at least, occurs in great abundance in the rich shallow-water fauna close to the biological laboratories at McMurdo Station. Thus, an animal suitable for the study of several physiological and ecological problems is very conveniently situated.

A number of species, notably *Cerebratulus larseni, Antarctolineus scotti,* and *Amphiporus spinosus,* have been taken from the shore to 500 m and deeper. Other species seem to be more depth restricted but this may be merely an indication of inadequate collecting of these particular species. The table on Plate 7 presents depth ranges of the Antarctic Nemertea and type of substrate when known.

SUMMARY

It is difficult to assess, at this stage of knowledge of distribution and systematics, what proportion of the nemertean fauna of the world is endemic to the Antarctic. A substantial increase in our knowledge of the distribution of nemerteans is to be expected when reports are available on new collections from the Ross Sea and southern New Zealand, South American material from the Royal Society Expedition to southern Chile, and material from *Eltanin* and *Vema* cruises. These collections may provide new data on many species mapped here and doubtless on new species as well—especially from the deepwater stations.

An analysis of the 39 species known from the 'Antarctic' in the broad sense shows the following geographic allocation:

Antarctica only	9 species
Antarctica and South Georgia	6 species
Antarctica and the Falkland Islands	4 species
Antarctica, South Georgia and the Falkland Islands	3 species
Antarctica and the Subantarctic, excluding the Falkland Islands and South Georgia	2 species
Antarctica and the Subantarctic, including South Georgia	1 species
Antarctica and the Magellanic Province	1 species
Antarctica, the Magellanic Province, and the Falkland Islands	1 species
South Georgia and the Falkland Islands only	1 species
South Georgia only	6 species
Falkland Islands only	3 species
Magellanic Province and the Falkland Islands	1 species
Other Subantarctic islands only	1 species
	39 species

The 9 Antarctic species include the 5 pelagic nemerteans, 1 species of benthic nemertean known from a single specimen from Shag Rocks (halfway between the Falkland Islands and South Georgia) and the 2 species doubtfully placed in *Carinina.* This leaves only *Amphiporus schollaerti* Wheeler, known from a single specimen collected at 278 m to 500 m in the Schollaert Channel, Antarctic Peninsula, to be considered as a strictly Antarctic benthic nemertean. If the Falkland Islands are considered within the Antarctic, then 38 of the Antarctic species can be considered endemic. This number represents approximately 5% of the world species.

Corrêa (1955, pp. 4–11) listed 115 species of nemerteans from Central to southern South America, including the Falkland Islands. Of these, 25% are known so far only from the Magellanic Subregion[3] and another 8% occur in the Magellanic and elsewhere. Shared with the Magellanic Subregion, including the Falkland Islands, is 25.6% of the Antarctic fauna, and 7.7% is shared with Subantarctic islands other than Magellanic. Of the Antarctic fauna, 40% is found only at South Georgia while 30.8% is recorded from the Scotian Subregion only. No species are at present known to be restricted to the Ross Sea which is the other region most extensively sampled in Antarctica.

[3]See Figure 10, p. 6, this folio.

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Brachiopoda

M. W. Foster[1]

INTRODUCTION

Brachiopods are lophophorate animals that produce a bivalved shell of upper and lower valves. The majority of brachiopods are epifaunal animals and are anchored to the substratum by a fleshy stalk, the pedicle, which emerges from one valve. Most brachiopods attach to hard substrates such as rock or scattered stones, the shells of living or dead mollusks, bryozoans, coelenterates with a stony skeleton, kelp holdfasts, or other brachiopods. They are rare on soft bottoms which lack scattered hard objects for attachment. Some brachiopods attach to the parchment-like tubes of *Phyllochaetopterus* (a polychaete) emerging from a fine sediment substrate. The brachiopod species *Chlidonophora chuni* has a finely branched pedicle with rootlets that penetrate the tests of Foraminifera on fine ooze bottoms. The pedicle is very adaptable in many articulate brachiopods so that one species may attach to quite a few different hard substrates. Some species are known to attach to soft substrates such as worm tubes as well as to hard substrates. Some brachiopods of the class Inarticulata burrow into soft substrates, but such infaunal brachiopods have not been reported from Antarctic waters.

Brachiopods tend to live in clumped aggregations, and one locality may have hundreds of individuals, while other apparently suitable localities have no brachiopods at all. This sort of distribution may be related to the very brief planktonic larval stage, especially of articulate brachiopods. Brooding of young occurs in some brachiopods, but not in others. Where a larval stage is known, it appears to have a planktonic life of only a few hours and does not move far from the bottom. On the other hand, the larvae of inarticulates such as *Lingula* and *Discinisca*, which have a longer planktonic life, have been found in surface waters. Most brachiopods occur in depths of less than a few hundred meters; therefore, because of the short planktonic stage of most brachiopods, deepwater areas are barriers to distribution.

The inarticulate brachiopods dredged from waters off Antarctica have all been attached to loose stones or boulders, at least insofar as their attachment can be ascertained. The articulate brachiopods, on the other hand, are known to be attached to stones, mollusk and brachiopod shells, calcareous worm tubes, bryozoans, and coelenterates. No brachiopod species known from more than one area is restricted to any one substrate. The available information suggests that Antarctic brachiopods are found only where there are hard objects on the sea floor. Those Antarctic species collected in localities where the bottom is reported to consist of only fine sediment were probably attached to worm tubes or other firm objects not mentioned in the general bottom description. The preference of brachiopods for attachment to firm objects is reflected in their geographic distribution, which is largely confined to continental shelves, slopes, and sea mounts.

In Paleozoic times brachiopods apparently dominated the benthic fauna of the seas in number of species and in diversity of form. Although the modern brachiopod fauna is much reduced in both respects from the level maintained in this era, it still appears to equal or outnumber the late Mesozoic and Cenozoic faunas. Brachiopods are an important, perhaps a dominant, group in a number of localities today. Recent brachiopods are most numerous and diverse in cool-water areas, although abundance and variety do not appear to be directly related to temperature. The diversity of the Antarctic fauna (16 species) compares favorably with that of the faunas off other landmasses in the Southern Hemisphere. For example, there are 17 species off southern Australia, 10 off New Zealand, 16 off South Africa and 11 off South America. The Antarctic fauna is rather small in number of species when compared with that found off the coast of Japan (50 species) or western North America (31 species). However, it should be remembered that the Antarctic fauna is still incompletely sampled, and future collections may bring more species to light.

DISTRIBUTION (PLATE 9)

The present pattern of distribution of brachiopods around Antarctica is more an artifact of limited dredging than of actual distribution. It does appear, however, that there are at least two circumpolar species, *Aerothyris joubini* (Map 3) and *Compsothyris racovitzae* (Map 1).

At least 11 of the 16 species off Antarctica are endemic to this region. Only the genus *Compsothyris* (Map 1) is endemic to Antarctica. The degree of endemism on both the specific and generic levels is much less than that of New Zealand and only slightly greater than that of South America.

It is possible to make some generalizations concerning the relationships of the Antarctic fauna to that of other parts of the world. Detailed discussion of most of the available information can be found in Thomson (1918) or Elliott (1951).

The inarticulate brachiopods (Map 1) occurring around Antarctica may be very widespread, such as the deepwater species *Pelagodiscus atlanticus* (Map 1), or they may be endemic species of widespread genera such as *Crania lecointei* (Map 1). The articulate brachiopods yield more information concerning zoogeographic relationships.

The living articulate brachiopod fauna of Antarctica has more similarities with that of southernmost South America than with that of any other continental area. The dallinid genus *Macandrevia* (Map 2) is represented in the Southern Hemisphere only off South America and Antarctica. The deepwater species *Macandrevia diamantina* (Map 2) occurs off Panama, Peru, and Antarctica. Thomson (1918) suggested that this genus had migrated to southern South America and Antarctica in post-Miocene times since it does not occur in the Tertiary deposits of Patagonia. Smooth terebratelline species with a magellaniiform loop occur off Macquarie Island, Antarctica, and South America (Map 3). Species from the first two localities have been assigned by Allan (1939) to the genus *Aerothyris* even though species from the last two localities are more similar to each other. The terebratulid species *Liothyrella uva* has been reported only off South America and Antarctica (Map 1). The other Antarctic species of *Liothyrella* are all much more like the South American species than the New Zealand species.

The living Antarctic brachiopod fauna has no identity with those of Australia or South Africa at either generic or specific levels. New Zealand shares two genera, *Amphithyris* and *Liothyrella*, with Antarctica. The genus *Magellania*, which occurs only in Australia, is quite similar to *Aerothyris* in Antarctica except that it has radial ornament. From South African

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waters there is only one highly questionable record of a species of the characteristic Southern Hemisphere family Terebratellidae. The other Southern Hemisphere areas have two or more unquestioned representatives of this family. The other Antarctic family in South Africa, Cancellothyridae, is essentially cosmopolitan.

Cenozoic fossil brachiopods have been found off the Antarctic Peninsula. This fauna is most similar to the Cenozoic fauna of South America and suggests possibly better connections between the two areas at that time, or earlier, than at present. The fauna shows more similarity to the fossil faunas of New Zealand and Australia than does the Recent Antarctic fauna to the Recent New Zealand and Australian faunas. The fossil Antarctic fauna is slightly closer to the fossil fauna of New Zealand than to that of Australia. The details of this similarity remain questionable because of taxonomic uncertainties. In any event, the similarity seems no closer than the generic level. The similarities of most of the Australian and New Zealand Recent and Cenozoic brachiopod faunas, and some elements of the South American fauna with the Antarctic fauna, are probably due to their retention of common pre-Cenozoic elements, as pointed out by Allan (1949).

TABLE 1. Species Reported From Only One Unquestioned Locality in the World

Species	Location	Depth (m)
Discina? joubini	65°20′S, 95°27′E	439
Crania roseoradiata	Saldanhabaai (Saldanha Bay), South Africa	82
Crania valdivae	38°40′S, 77°38′E	672
Liothyrella neozelanica	Cook Strait, off Wellington, New Zealand	366
Liothyrella winteri	38°40′S, 77°38′E	1230
Compsothyris? valdivae	38°40′S, 77°38′E	672
Valdiviathyris quenstedti	38°40′S, 77°38′E	672
Argyrotheca australis	Cape Willoughby, Kangaroo Island, Australia	37
Argyrotheca mayi	Schouten Island, east coast of Tasmania	145
Amphithyris buckmani	Cook Strait, off Wellington, New Zealand	366
Gyrothyris mawsoni	South end of Macquarie Island	
Kraussina crassicostata	Valsbaai (False Bay), South Africa	42
Kraussina cognata	Cape of Good Hope, South Africa	
Macandrevia lata	65°06′S, 96°13′E	594
Magellania australis	Western Port, Victoria, Australia	
Magellania wyvillei	33°31′S, 74°43′W	4320
Megathiris capensis	Saldanhabaai (Saldanha Bay) South Africa	82
Megerlina davidsoni	St. Paul Island, Madagascar	
Neothyris ovalis	Farewell Spit New Zealand	
Pumilus antiquatus	Littleton harbor (intertidal), Christchurch, New Zealand	
Pumilus antiquatus	Portobello Station, Dunedin, New Zealand	
Terebratella mayi	Cape Pillar, Tasmania	180
Terebratella rubiginosa	? Simons Bay, Cape of Good Hope, South Africa	

The present evidence strongly suggests that genera with a wide bathymetric range such as *Macandrevia* (Map 2) and *Liothyrella* (Map 1) have migrated in the late Cenozoic and/or are now migrating from South America to Antarctica. The absence of migrants from the New Zealand–Australia area may be due to the absence of forms with a wide bathymetric range in these areas.

Most of the known brachiopod localities south of 35°S latitude and from South Africa are represented on Plate 9. The remaining species, which have been reported from only one locality in the world, have not been placed on the maps and are listed in Table 1. Where several localities for the same species occur in a restricted geographic area, only one symbol is used.

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Bryozoa

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INTRODUCTION

The Bryozoa are less well known than most other groups of the Antarctic benthos. Although bryozoans often make up a significant bulk of the benthos, several collections from early expeditions remain unstudied. Thus, only the Stenolaemata from the Swedish Antarctic Expedition, 1901–1903, and the cellularine Bryozoa from several British expeditions have been described. The distribution and affinities of the Antarctic Bryozoa have been discussed by Waters (1904), Hastings (1943), Borg (1944), and also by Rogick (1965), who lists the earlier studies.

The Bryozoa form sessile colonies, either erect or encrusting, which may attach to a variety of substrates such as stone, mollusk shells, arthropods, seaweeds, wood, and the bottoms of ships. Some species are able to live on muddy or sandy bottoms anchored by rootlets, or growing in a disc- or cone-shaped colony lying free on the bottom. Bryozoa feed on suspended flagellates, small diatoms, other protozoa, and possibly bacteria.

In most species the ciliated motile larva does not feed and settles after the first few hours of life. A few species have a feeding larva known as a cyphonautes, which may spend two months in the plankton.

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A total of 310 species and subspecies of Bryozoa have been recorded from south of the Antarctic Convergence. It appears that 180 (58%) of these species and subspecies are confined to the Antarctic region.

Of the 130 species which have been reported from other regions as well as from the Antarctic, the majority are confined to the Southern Hemisphere. A greater number of Antarctic species are found in the southern South America–Falkland Island region (about 44) than in the Australia–New Zealand region (about 15). These totals include about 8 Antarctic species found in both regions.

Waters (1904) lists *Micropora coriacea, Hippothoa divaricata, Hippothoa distans, "Smittia" reticulata, Idmonea atlantica,* and *Entalophora proboscidea* as cosmopolitan species which occur in the Antarctic. There is doubt as to the validity of Waters' identification of *"Smittia" reticulata* (Rogick, 1956) and *Idmonea atlantica* (Borg, 1944), and it is believed that his *Entalophora proboscidea* may be a subspecies (Borg, 1944). These examples are given to show that until the taxonomy of the Antarctic Bryozoa has reached a more refined state and until detailed and accurate descriptions are available for all species, any study of distributions is tentative.

In a recent summary list of the Bryozoa collected during the Belgian Antarctic Expedition, 1959–1960, Redier (1965) lists *Bugula neritina* from the coast of Queen Maud Land. Although Redier does not include it in his list of first records, this seems to be the first time *B. neritina* has been taken in the Antarctic. *B. neritina* is a cosmopolitan shallow-water species readily distributed on the bottoms of ships. It is interesting to speculate whether this is a recent introduction into Antarctic waters and, if so, whether the species will now spread around the continent.

About 17 other species which occur in the Antarctic have been reported from the Northern Hemisphere, including 6 reported by Redier (1965). Perhaps the most interesting of these records is *Lichenopora canaliculata* which Osburn (1953) reported from Point Barrow, Alaska.

THE MAPS (PLATE 10)

The accompanying maps are designed to show the distribution of representative Antarctic Bryozoa. Species from a single locality and doubtful records are not included.

MAPS 1 AND 2: Family Smittinidae

The smittinids attach to hard substrates, forming encrusting layers or erect bilamellar plates. The 34 species and subspecies of the family collected in the Antarctic have all been taken at depths of less than 650 m. Of the 8 genera represented, *Emballotheca,* with 9 species, and possibly *Smittinella,* with 1 Recent species, are confined to the Southern Hemisphere (Rogick, 1955, 1956).

MAP 3: Family Bicellariellidae

Bassler (1953) lists 51 genera in the division *Cellularina,* including *Bugula* and other branching chitinous forms. Hastings (1943) found 14 genera of cellularine Bryozoa with representatives in the Antarctic region. Three of these genera, *Tricellaria, Bugula,* and *Menipea* have a predominantly northern distribution; the affinities of 3 genera are not clear; and 8 genera, *Amastigia, Notoplites, Farciminellum, Cornucopina, Himantozoum, Camptoplites, Beania* and *Caberea* have a predominantly southern distribution.

In the family Bicellariellidae, 3 genera and 9 species occur in the Antarctic. The distribution of 7 species is shown. Cellularine Bryozoa may occur at considerable depth, which could explain their spread into the Subantarctic. Three species of *Cornucopina* occur below 1800 m.

MAP 4: Family Sclerodomidae

The family Sclerodomidae comprises 3 genera: *Sclerodomus,* which is found in the South Atlantic; *Cellarinella,* represented by 10 species, 9 of which are confined to the Antarctic region; and *Systenopora,* with 1 species, which is also confined to the Antarctic region.

These examples show that there is a distinct Antarctic bryozoan fauna which has affinities with the Subantarctic Islands and South America and, in the southern temperate region, with Australia and New Zealand. This fauna is largely coastal and appears to be circum-Antarctic. The fact that the fauna is not divisible into provinces along the very long coastline may possibly be attributed to the uniform physical conditions of the coastal Antarctic regions.

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Sipuncula and Echiura

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SIPUNCULA (MAPS 1, 2, AND 3, PLATE 11)

Sipunculids are a group of worm-like marine invertebrates that live in tropical, temperate, and polar waters. The body or trunk of an adult animal is cylindrical, flask- or sausage-shaped, and from its anterior region a highly retractile introvert is extended from time to time. Sipunculids are soft-bodied and normally live in protected places. They are often found under stones, in the holdfasts of algae or roots of marine angiosperms, and in the empty shells of some mollusks. They are also found burrowing in sand, mud, or gravel, and sometimes in holes which they have bored in rocks and coral. Their bathymetric range is wide. They are collected between tide-marks along the shore, they are sometimes dredged from the ocean floor, and they also are known to live in the abyssal depths. The gut of sipunculids usually contains sand, mud, fragments of shells, pieces of coral, and frustules of diatoms, and it is thought that the animals are detritus feeders. The sexes are separate. Ripe eggs and sperms are shed into the sea where fertilization takes place. The zygote quickly develops into a trochophore larva. After swimming freely in the water (for about a month in the case of *Sipunculus nudus*), the larva sinks to the floor of the sea and develops into an adult. Larval sipunculids are sometimes found in samples of plankton.

Most of the sipunculids known from the Antarctic and the Subantarctic have been collected, usually by dredging, from the Ross Sea, Graham Land, and a few other widely separated localities along the coast of Antarctica, and from South Georgia, the Falkland Islands, and Kerguelen Island. A study of the records shows that species belonging to only two genera, *Golfingia* and *Phascolion,* have been found in the Antarctic and Subantarctic, and that by far the greater number of species fall into the genus *Golfingia. Golfingia,* however, is not restricted to the polar regions but is well known in tropical and temperate seas. Sipunculids of the world-wide genus *Phascolion* usually inhabit the abandoned shells of mollusks like *Dentalium* and *Turritella.* Why such well-known genera as *Sipunculus, Siphonosoma, Phascolosoma,* and *Themiste* have not been found in Antarctic waters is not known. The most common Antarctic and Subantarctic species are *Golfingia margaritacea capsiformis, G. anderssoni, G. mawsoni, G. ohlini, G. nordenskjoldi,* and *Phascolion strombi.* Many of the sipunculids from southern Australia, South America, and New Zealand are warmer-water species, and their ranges do not extend to Antarctica.

There seems to be little doubt that many of the Antarctic sipunculids are identical to, or subspecies of, forms that are also found in the Arctic and Subarctic regions. Théel (1911), Fischer (1922), Stephen (1941), and

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Wesenberg-Lund (1955) have reported that some species of sipunculids are bipolar. In addition, Murina (1964) has shown that a number of species regarded by previous writers (Stephen, 1941) as being truly Antarctic also occur in the northern cold-water regions of the Pacific Ocean. Also it is possible that some of the so-called 'bipolar' species, for example, *Golfingia margaritacea* and *Phascolion strombi,* are more widely distributed than was previously thought.

The species shown on the maps can be divided into four groups.

(1) Species restricted to the Antarctic and Subantarctic

Golfingia benhami
Golfingia charcoti
Golfingia nordenskjoldi

(2) Species known from cold-water regions in both the Arctic and the Antarctic (bipolar species)

Golfingia anderssoni
Golfingia eremita australis
Golfingia improvisa
Golfingia intermedia
Golfingia mawsoni
Golfingia minuta
Phascolion lutense

(3) Species known to be more widely distributed

Golfingia margaritacea capsiformis[2]
Golfingia muricaudata
Golfingia ohlini
Golfingia pudica
Phascolion strombi

(4) Species which are tropical or temperate and whose range does not extend to the Antarctic

Golfingia cantabriensis
Golfingia catharinae
Golfingia depressa
Golfingia novaezealandiae
Golfingia schuttei
Golfingia tasmaniensis
Phascolosoma annulatum
Phascolosoma nigrescens
Phascolosoma noduliferum
Phascolosoma scolops
Sipunculus angasii
Themiste[3] *cymodoceae*
Themiste fisheri
Themiste fuscum
Themiste huttoni
Themiste petricolum
Themiste rosaceum
Themiste signifer
Xenosiphon mundanum

Very little is known about the ecology and physiology of the Antarctic sipunculids. Many of the animals were dredged, sometimes from great depths where the temperature of the sea is below 0°C. The specimens of *Golfingia margaritacea capsiformis* and *G. anderssoni* collected in the New Zealand expedition to the Ross Sea were obtained at depths of between 363 m and 752 m where the water temperatures were −1.6°C to −2.0°C (Edmonds, 1965). Even under these conditions specimens of *G. margaritacea capsiformis* weighing 35 g were collected. *Golfingia muricaudata* was dredged at 2960 m (Fischer, 1922), *Phascolion lutense* at 4540 m (Murina, 1961), and *G. nordenskjoldi* at 2000 m (Murina, 1964).

ECHIURA (MAP 4, PLATE 11)

Echiurids comprise a small group of unsegmented marine worms related to the Annelida and Sipuncula. Like the latter they live for most of their lives in sheltered places such as sand and mud or in coral and rock. They are soft-bodied animals and consist of a cylindrical, sac-like or flask-shaped trunk and a highly extensible and fleshy proboscis which helps the animal in obtaining food. Echiurids are largely detritus feeders. They are not uncommonly collected in tropical and temperate waters, but only a few species are known from the Antarctic and Subantarctic.

The phylum consists of three chief families, the Echiuridae, the Bonelliidae, and the Urechidae. Species belonging to all three families have been recorded south of latitude 35° although there is no evidence that *Anelassorhynchus adelaidensis, Bonellia gigas,* known from southern Australia, and *Urechis novaezealandiae* from New Zealand extend their range into Subantarctic waters. The species recorded fall into three groups.

(1) Species which have been found in the Antarctic and Subantarctic

Echiurus antarcticus
Maxmulleria verrucosum
Thalassema antarcticum
Urechis chilensis (from Chile and Patagonia)

(2) Species which it is claimed are bipolar (Stephen, 1941, p. 243)

Hamingia arctica
Maxmulleria faex

(3) Species which have been found only in temperate waters

Anelassorhynchus adelaidensis
Bonellia gigas
Urechis novaezealandiae

The records of the 'bipolar' species, however, are few. The identification of the southern specimens of *M. faex* is based on an examination of one fragmentary and two complete specimens from the South Shetland Islands and that of *H. arctica* on one slightly damaged specimen also from the South Shetlands.

Most of the literature on the southern forms of Echiura is purely taxonomic, and very little is known about their physiology and ecology. The best studied echiurid is *Urechis caupo,* a Californian species. This animal lives in a U-shaped burrow which it digs with the aid of its proboscis and setae and through which a current of fresh water is pumped by means of a series of peristaltic movements of its body. *U. caupo* feeds by straining water through a fine mucous tube or funnel which it secretes from a zone of superficial mucous glands. When sufficient food accumulates, the tube is swallowed. How closely the burrowing, feeding, and respiratory habits of *U. chilensis* and *U. novaezealandiae* resemble those of *U. caupo* is not known.

[2]I have used the name *Golfingia margaritacea capsiformis* to denote a number of Antarctic and Subantarctic species considered by several authors (Théel, 1911; Stephen, 1941; Wesenberg-Lund, 1954) to be synonymous with *G. margaritacea* (Sars, 1851).

[3]Stephen (1965) has shown that the name *Themiste* Gray 1828 must replace *Dendrostomum* Grube 1859 and other authors.

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Benthic Mollusca

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The limits of the Antarctic molluscan faunal area cannot be clearly defined on geographical, climatic, or hydrological evidence. The Antarctic and Subantarctic faunas occur around the Antarctic continent, along the islands of the Scotia Ridge, into the Falkland Islands and southern South America, and through Bouvet, Crozet, Prince Edward, Marion, Kerguelen, Heard, and Macquarie, the scattered islands of the southern oceans. On a faunal basis there appear to be fairly definite Antarctic and Subantarctic faunas, but there is no hard and fast geographical boundary between them, and in certain areas they intermingle to some extent. Some elements of the Antarctic fauna do extend in varying degrees to the north through the islands of the Scotia Ridge, and some forms are represented in the Subantarctic islands. Some northern species appear to extend in the reverse direction into the Antarctic region from southern South America through the Scotia Ridge.

It is difficult to make comparisons between the Antarctic and Subantarctic molluscan faunas since that of the Antarctic is composed essentially of deepwater species derived from adjacent abyssal basins, whereas the Subantarctic fauna is predominantly littoral in origin. Almost nothing is known of the deepwater molluscan fauna in the South Atlantic, South Pacific, and South Indian Oceans, but it is probable that Antarctic representatives of such families as the Nuculanidae, Malletidae, Limopsidae, Lyonsidae, Verticordiidae, Cuspidariidae, Eulimidae, Cancellariidae, Turridae, and many others have come from these regions.

The Antarctic molluscan fauna consists essentially of those species which occur around the Antarctic continent and along the Scotia Ridge to the general area of South Georgia, with the proviso that, as mentioned above, some considerable interchange of species takes place both to the north and to the south. The fauna of South Georgia itself contains a surprising number of endemic elements.

The major elements in the Antarctic fauna can be characterized as follows:

(1) A small group of 'old' Antarctic forms of uncertain derivation which are widely distributed and which are presumed to have survived the last glaciation either in the Antarctic itself or in areas close to it.

(2) A group derived from contiguous deepwater basins in the South Atlantic, South Pacific, and South Indian Oceans.

(3) A group derived from southern South America through the Scotia Ridge. Some of this group have established themselves on the Antarctic continent and have subsequently spread around its shores; others have established themselves only on the southern islands of the Scotia Ridge, for example, the South Shetland and South Orkney Islands, the shores of the Palmer Archipelago, and the Weddell and Bellingshausen Seas.

(4) A group of established Antarctic forms which have spread northwards to varying degrees along the Scotia Ridge and may have reached some of the Subantarctic islands.

Many of the species known from around the Antarctic continent are widely distributed. There are still enormous gaps in our knowledge of geographical distribution in the area, but on the present evidence at least 40 percent of these species appear to be circum-Antarctic. The two wide areas along the shores of the Antarctic continent from which no benthic material has been collected are from 90°W to 150°W and from 10°W to 50°E. Some of the gaps in the distribution maps indicate this lack of sampling. Similarly the fauna of the Crozet Islands is virtually unknown and the shallow-water faunas of Bouvet, Prince Edward, Marion, and Heard Islands have been very sketchily sampled.

The molluscan fauna of the Antarctic is relatively impoverished. Many families which form important elements in the faunas of most other parts of the world do not reach Antarctic waters. The only effective shallow-water migration route in existence today is through the islands of the Scotia Ridge from southern South America, and this has probably been the only route for a considerable period in the geologic past. The extent to which some molluscan families have invaded the Scotia Ridge is shown in Figure 1.

Disregarding the area comprising the Bellingshausen Sea, the Palmer Archipelago, and the Weddell Sea, the faunas of which may well have been influenced by recent migrations, the benthic mollusca known from the waters surrounding the Antarctic continent are contained in 91 families with 154 genera and 309 species (see Table 2). Fifty of these families have only 1 species. Five families are represented by more than 11 species, the average per family in New Zealand. Many of the families are represented by minute, anomalous, or deepwater genera; the Mytilidae have only the deepwater genus *Dacrydium* and the Arcidae is represented by *Bathyarca*. Many of the species are as yet known only from a single locality or from very restricted areas. Some of the common species are, however, known from widely separated areas. The distribution of some of these commoner Antarctic forms is shown in Map 1, Plate 12.

More detailed distribution maps have been given for two restricted

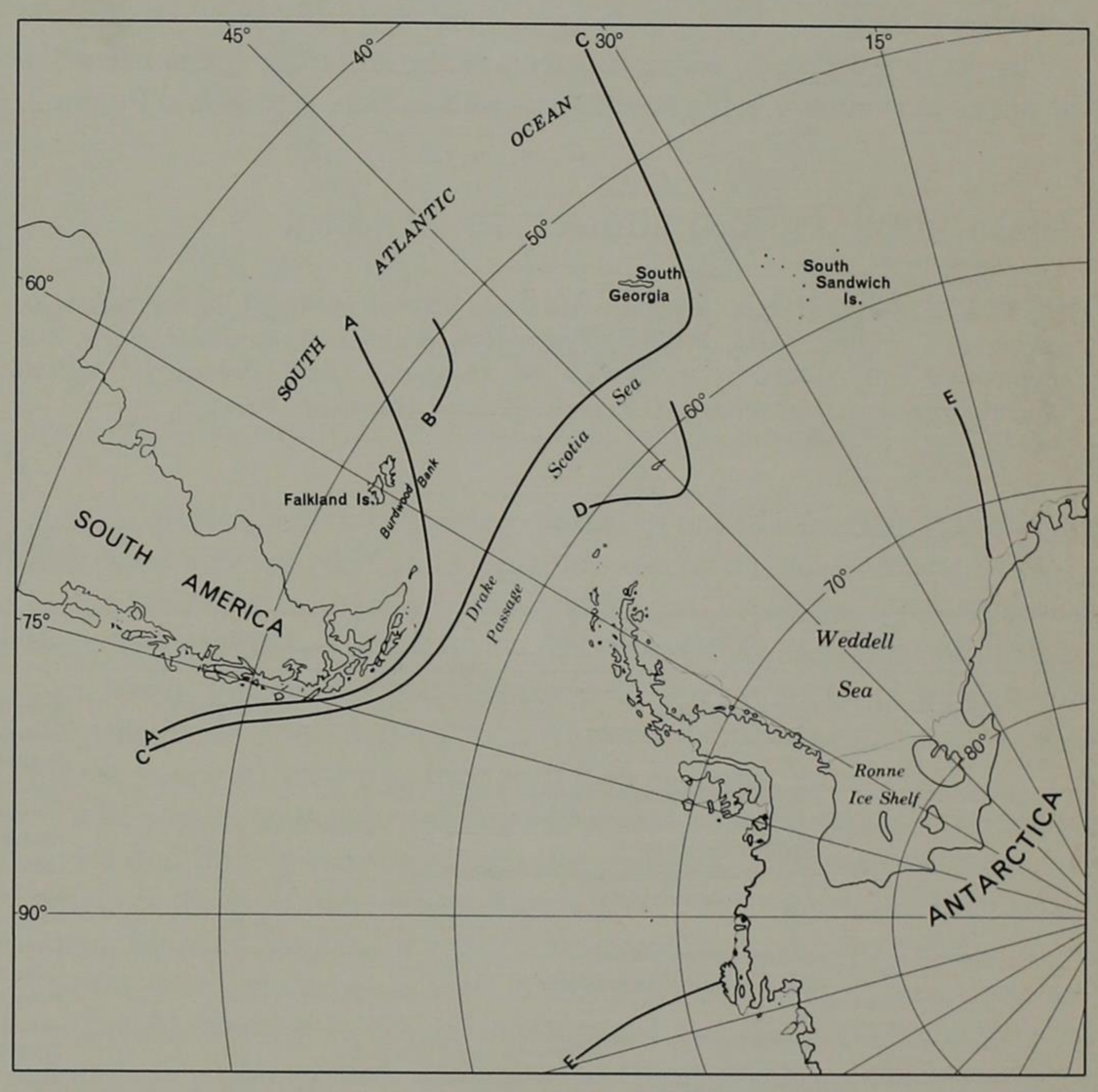


Fig. 1. The disappearance of molluscan families from South America through the Scotia Ridge to the Antarctic continent (see Table 1 for explanation).

TABLE 1

Southern Limit	Family	Southern Limit	Family
Curve A	Chitonidae	Curve B	Olividae
	Acanthochitonidae		
	Anomiidae	Curve C	Veneridae
	Cardiidae		Tellinidae
	Mactridae		Hiatellidae
	Condylocardiidae		Calyptraeidae
	Lucinidae		Retusidae
	Solenidae		
	Corbulidae	Curve D	Chaetopleuridae
	Myidae		
	Pandoridae		
	Teredinidae	Curve E	Hanleyidae
	Acmaeidae		Ischnochitonidae
	Nassariidae		Mopaliidae
			Gaimardiidae
			Patellidae

TABLE 2. Comparative Figures for the Faunas of Antarctica, the Magellanic Region, and New Zealand.

	Families	Genera	Species
BENTHIC MOLLUSCA			
Antarctica	91	154	309
Magellanic Region	114	280	667
New Zealand	160	552	1759
BIVALVES			
Antarctica	25	36	66
Magellanic Region	39	89	175
New Zealand	44	142	400
Arctic Region	31	51	118

[1]Dominion Museum, Wellington, New Zealand

groups. The bivalve genus *Limopsis* has 6 species represented in Antarctic and Subantarctic waters (Map 2, Plate 12). *Limopsis marionensis* has an apparently circum-Antarctic distribution extending through the islands of the Scotia Ridge (except for South Georgia) to southern South America and also to Kerguelen and Marion Islands. Of the 2 closely allied forms *L. lilliei* and *L. hirtella,* the former extends around most of the continent and to Bouvet Island and South Georgia, while *L. hirtella* is confined to southern South America and the Falkland Islands. Forms of an intermediate type are known from South Georgia. One species, *L. scabra,* is known only from a small area off Enderby Land.

The scaphopod fauna of Antarctica is small (Map 3, Plate 12). Two species, *Dentalium (Fissidentalium) majorinum* and *Cadulus (Polyschides) dalli antarctica,* are circum-Antarctic in distribution; the *Fissidentalium* extends to southern South American waters. *Cadulus dalli antarcticus* extends no further north than the South Orkney Islands, but is represented in the Magellanic region by the subspecies *C. dalli dalli.* Another species, *Cadulus thielei,* is known from two widely separated areas in eastern Antarctica while 2 species, *Siphonodentalium minimum* and *Dentalium eupatrides,* are both known from single localities. Several species have also been recorded from the Magellanic region, and *Dentalium aegeum* was described from Kerguelen.

A number of cephalopods are common in the Antarctic; 12 species of eledonid octopods are recognized in Antarctic waters. Most of these are small, but *Megaledone senoi* reaches a total length of at least 460 mm. Two other species of octopods and several squid have been described from Antarctic waters.

The varying degree to which members of the Antarctic fauna extend to the north, particularly in the South American section, is shown in Figure 2.

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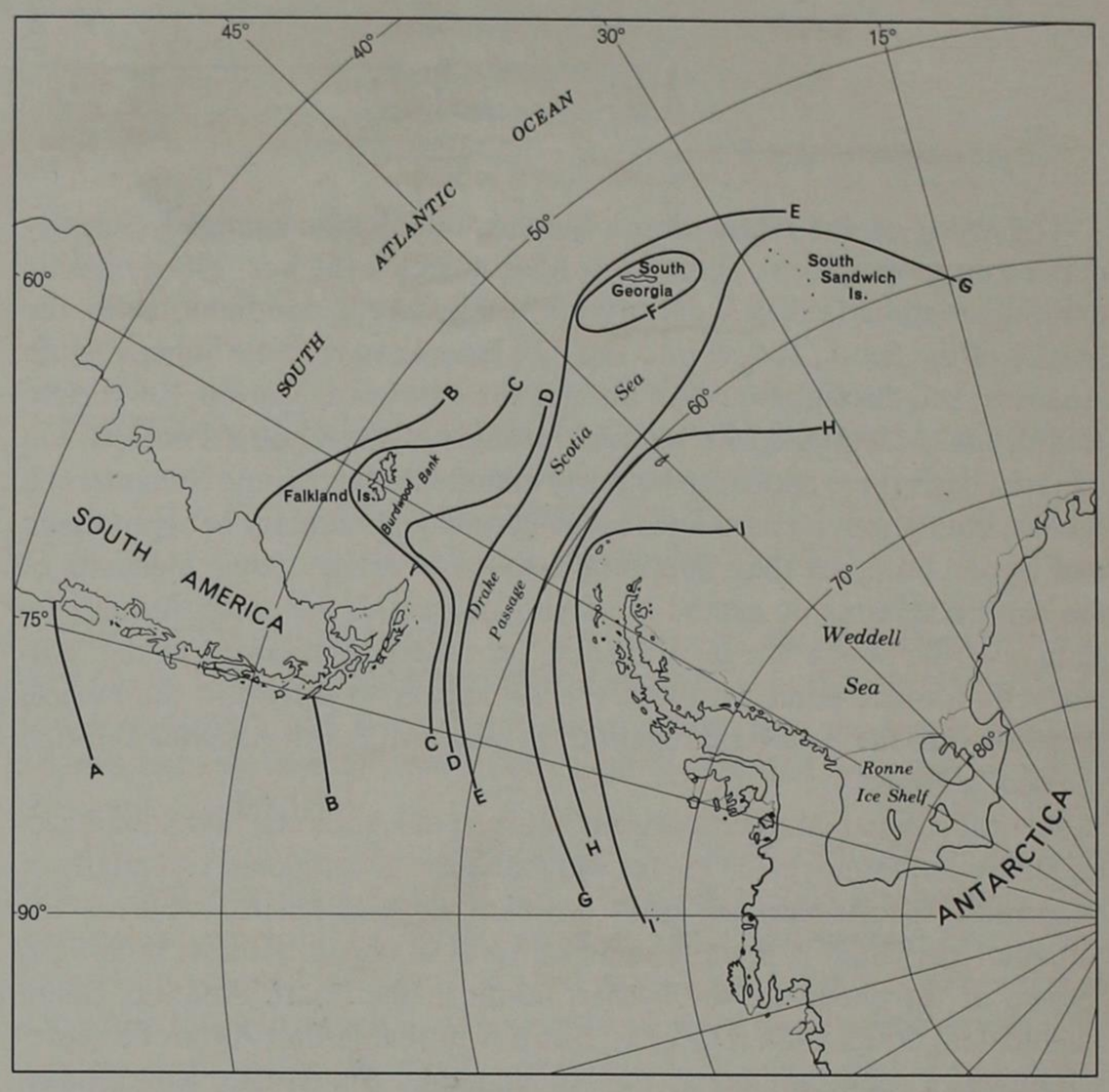


Fig. 2. Northern limits of some elements of the Antarctic molluscan fauna in the South American sector (see Table 3 for explanation).

TABLE 3

Northern Limit	Genus or Species	Northern Limit	Genus or Species	Northern Limit	Genus or Species
Curve A	*Cyamiomactra*	Curve E	*Adacnarca*	Curve F	*Venustatrochus*
	Limopsis marionensis		*Pseudokellya*		*Promargarita*
			Propeleda		*Chlanidotella*
Curve B	*Yoldia (Aequiyoldia) eightsi*		*Limatula hodgsoni*		*Cavineptunea*
	Lepidopleurus kerguelensis		*Limopsis lilliei*		
	Callochiton gaussi		*Philobrya sublaevis*	Curve G	*Neobuccinum eatoni*
	Dentalium (Fissidentalium) majorinum		*Lissarca notorcadensis*		*Philine alata*
	Thracia meridionalis		*Cyclocardia astartoides*		
			Laternula elliptica	Curve H	*Cadulus (Polyschides) dalli antarctica*
Curve C	*Nuttalochiton mirandus*		*Cuspidaria infelix*		*Subnoba fraudulenta*
	Cyamiomactra laminifera		*Cuspidaria tenella*		*Adamussium colbecki*
			Patinigera polaris		
Curve D	*Schizotrochus euglyptus*		*Laevilacunaria*	Curve I	*Prosipho madigani*
	Pellilitorina pellita		*Trichoconcha*		*Balcis solitaria*
	Balcis antarctica		*Chlanidota*		*Falsimargarita gemma*
	Paradmete fragillima		*Neacteonina*		*Antimargarita dulcis*
					Acteon antarcticus
					Toledonia major

Pycnogonida

J. W. Hedgpeth[1]

INTRODUCTION

The Pycnogonida are, for the most part, holobenthic arthropods, living on the ocean bottom throughout their life cycles. The larvae are either nonmotile or capable of very limited locomotion; many of them are parasites of coelenterates in which they may form galls or cysts. The adults are slow moving, somewhat clumsy animals with limited capacity for dispersal. Because of their large surface to volume ratio associated with the reduced body and long slender legs, some of the larger species may be moved about somewhat by near-bottom currents. One exception to the predominantly holobenthic habit of the group is *Pallenopsis calcanea,* which is apparently bathypelagic, possibly associated with a species of jellyfish. It has been found in widely scattered localities, suggesting a cosmopolitan distribution at depths of 650 m to 2000 m (Hedgpeth, 1962). One North Pacific species, *Achelia alaskensis,* has been found as juveniles in the hydrozoan medusa *Polyorchis,* a medusa for which the hydroid stage is as yet undetermined. Some shallow-water species of pycnogonids have been taken in plankton tows; whether they rise to the surface for breeding or are simply carried to the surface by water movements is unknown. In any event, the Pycnogonida as a group do not have free-swimming larvae and, for the most part, may be distributed either by walking or by riding on some other organism. The eggs are carried about by the males until hatching, at least in those species of which something is known of the life cycle. Nothing is known of eggs or larval stages of the cosmopolitan, deepwater Colossendeidae.

The specific diversity of Pycnogonida in Antarctic waters has been

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known since the first inflorescence of Antarctic exploration at the beginning of the century; while more critical systematic studies have suggested the consolidation of some of the previously described species, it is certain that a very large percentage of species of some genera are endemic to the regions south of the Antarctic Convergence. Two aspects of the Antarctic pycnogonid fauna are especially noteworthy. The first is the gigantism of certain species, and indeed of genera; with the exception of the cosmopolitan deep-sea species of *Colossendeis,* Antarctic pycnogonids include the largest forms known, occurring in several distinctly different families. The second aspect is the occurrence of 3 ten-legged and 2 twelve-legged forms in Antarctic waters. Elsewhere this phenomenon is found only in the American–Atlantic tropics, where there are 2 polymerous forms. The nature of these polymerous forms is not understood, but the phenomenon is unique among the Arthropoda; they are possibly phases or polyploid forms of ordinary or octopodous species. The Antarctic is a region inhabited not only by giant and polymerous species, but also by numerous, very small forms; in fact, some of the smallest pycnogonids known are endemic to the Antarctic region. Thus, there is not only a large variety of species and range of sizes, but also evidently large populations of many of them. Although Fry (1964) has pointed out that collection records indicate that pycnogonids may attain very large populations in various parts of the world, nevertheless, it does appear that, in general, there may be a somewhat higher level of populations in the Antarctic.

Pycnogonids are often abundant in Arctic waters although there are not as many species there as in the Antarctic. The facies of the Arctic fauna is notably different because of the absence of giant and polymerous forms. There are, incidentally, no known bipolar pycnogonids, and only one species, *Colossendeis angusta,* a predominantly deepwater species, occurs from Arctic to Antarctic waters. It appears that of the 500 or 600 known species of pycnogonids, at least half are stenothermic, cold-water species, occurring either in the polar regions or in the deeper waters of the ocean. Pycnogonids appear to be scarce in tropical waters, and most of the warm-water species described are known only from single specimens or from small series.

It is, therefore, not surprising to find in such a cold-stenothermal group that the Antarctic is evidently a region of active speciation and evolutionary development. Some of this may be attributed to migration and subsequent isolation, as Stock (1957) suggests for the genus *Austrodecus.* It is probably also associated with the rich benthos and abundant detritus found on the bottom in many areas of the Antarctic shelf. Pycnogonids are feeders principally upon such soft-bodied invertebrates as coelenterates and sponges, and some of the very small ones are admirably adapted for feeding upon such organisms as Bryozoa (Fry, 1965).

Yet, in spite of this active speciation, which accounts for almost half of the known species in some genera and for at least a fifth of all described species, there are surprisingly few endemic genera in Antarctic waters. Most of the genera represented abundantly in the Antarctic are also represented by species in other oceans; some are worldwide. Of the 6 polymerous genera—although there is some question whether these are actually valid genera—the following representatives are found in the American–Atlantic tropics: (1) the monospecific *Pentacolossendeis* in the Straits of Florida, and (2) *Pentapycnon geayi* in French Guiana and Puerto Rico. The other polymerous genera, *Pentanymphon, Sexanymphon, Decolopoda,* and *Dodecolopoda* are so far known only south of the Antarctic Convergence. As collection records increase, genera or species complexes thought to be characteristically Antarctic turn out to have representatives in other parts of the world. *Austrodecus,* a genus consisting of 19 species (Stock, 1957), is confined for the most part to the Antarctic Region and Magellanic Subregion, but species also occur on Tristan da Cunha and Gough Islands, the Three Kings Islands north of New Zealand, and a single species (based on a single specimen) has been recognized from Sagami Bay, Japan (Figure 1). A similar distribution pattern has been recognized for the species of the generic complex *Ammothea, sensu lato.* The species of this complex are the largest pycnogonids of this family and are commonly taken in Antarctic collections. With the single exception of a species from deep water near the Kurile Islands, all other representatives of this group occur south of 33°S, and most of them are confined to the region south of the Antarctic Convergence. Certain other genera which appear to be endemic to the Antarctic, for example, *Austroraptus* and *Austropallene,* are not taxonomically very different from other genera in their respective families. These families, Ammotheidae and Callipallenidae, contain groups of genera separated on the basis of minor characters, and critical reappraisal may result in their inclusion with other genera.

With the exception of gigantic forms and a high incidence of polymerous species, the Antarctic species are not notably different from the general aspect of pycnogonids in other seas. Antarctic representatives of the largest genus of pycnogonids, *Nymphon,* do not look much different from their congeners in other oceans; of the 110 or 125 described species of *Nymphon,* some 30 are confined to Antarctic waters. This genus is characteristic of deeper and colder waters; there are no true intertidal species. Proportionately, the Arctic is equally well represented with approximately 25

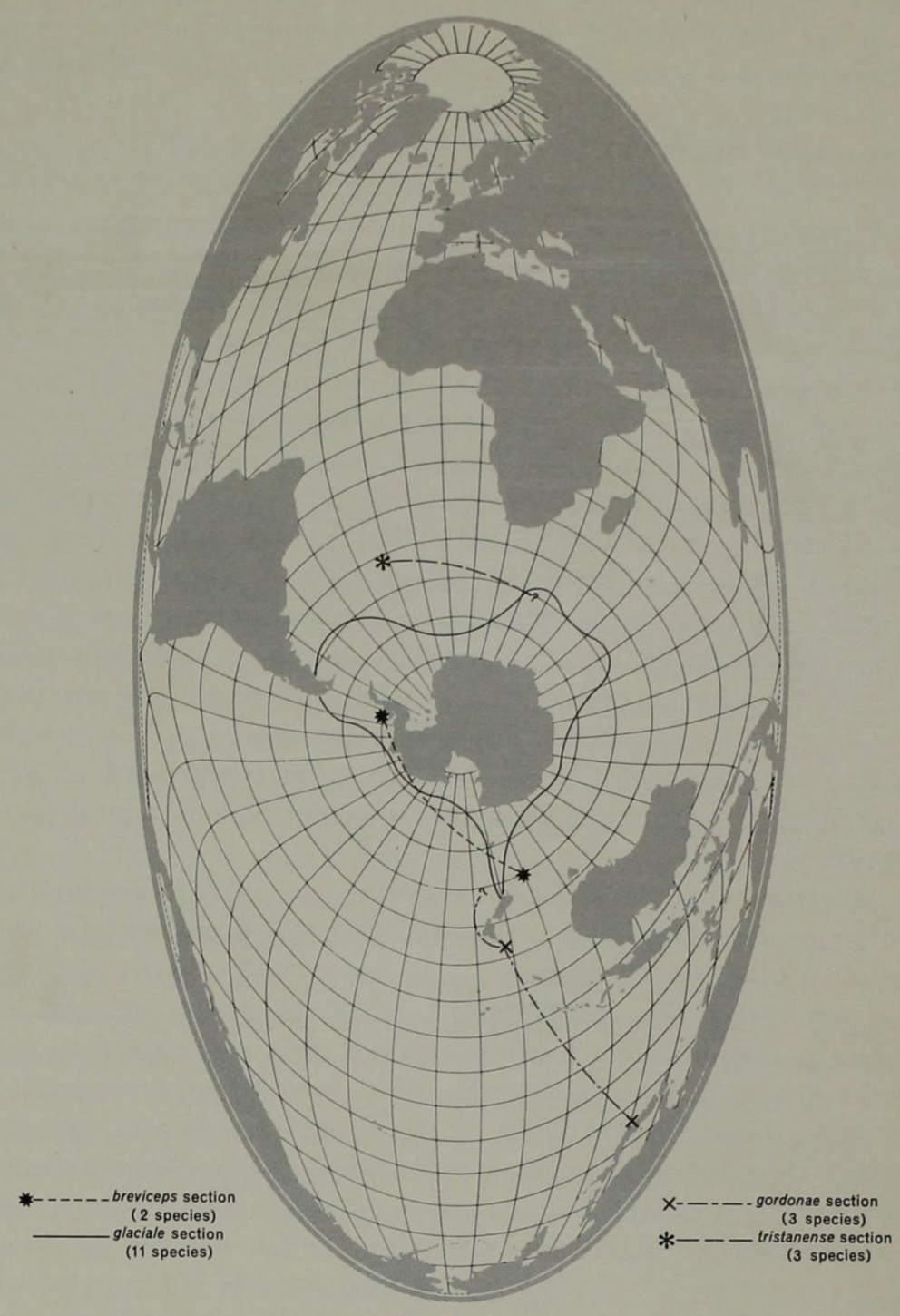


Fig. 1. Worldwide distribution of *Austrodecus* by sections (according to Stock, 1957).

species, a few of which extend into boreal waters. An interesting biological difference between Arctic and Antarctic species has been noticed by Hedgpeth (1963) on the basis of preserved material. In several Arctic species the young are carried about by the males until they are a third of the adult size; so far, this has not been observed for any Antarctic *Nymphon.* Possibly the food resources of the rich Antarctic benthos make it unnecessary for the young to remain so long with their parents.

When we examine the pycnogonid fauna of the Antarctic regions *per se,* we find little indication of separate regions of development within the waters of the shelf region. The Ross Sea is obviously not a distinct faunal region for pycnogonids since no endemic species have been demonstrated, and the circumpolar species are the largest component of any Antarctic shelf region studied so far. It is anticipated that further collections in regions from which we have inadequate records will confirm the circumpolar distribution of most of the Antarctic shelf species. So far, all records from the Weddell Sea, for example, are of circumpolar Antarctic species.

The Magellanic Subregion comprises, as far as Pycnogonida are concerned, another faunal area, with at least a dozen endemic species. Some of these suggest migration from southern South America; one of these, *Achelia sufflata,* indicates possible migration southward across the Drake Passage; others suggest dispersion northward from Antarctic waters, for example, species of *Austrodecus.* Species of this genus (see Plate 14) also indicate possible dispersion from other parts of the Antarctic shelf to Kerguelen and to other Subantarctic islands, and perhaps from there to New Zealand; but there is no suggestion of emigration from Australian areas including New Zealand to the Magellanic Subregion. The morphologically similar species of *Ammothea, A. magniceps* of Australasia, and *A. minor* and *A. clausi* of Antarctic waters suggest that migration may have occurred along the West Wind Drift. In all, however, there are comparatively few indications of faunal migrations to or from Antarctica, except possibly those of species of *Colossendeis* along the sea bottom itself.

THE MAPS (PLATES 13 AND 14)

MAP 1. Colossendeidae

The Colossendeidae are a family of deep-sea and cold-water forms, occurring throughout the major ocean basins in depths to at least 5000 m. They have not been found in the deep trenches; however, this may simply be an artifact of collecting. One of the cosmopolitan deepwater species, *Colossendeis colossea,* is the largest pycnogonid known, with a leg span of more than 50 cm. Three polymerous forms are included in this family. The 2 ten-legged forms are *Decolopoda australis* (first described by James Eights in 1834), a relatively common Antarctic species found at South Georgia, in the Ross Sea, and at Heard Island from the shore to depths of more than 1000 m, and *Pentacolossendeis reticulata,* found south of the

Florida Keys at depths of approximately 200 m. The most massive pycnogonid is the twelve-legged *Dodecolopoda mawsoni,* so far known from only 2 specimens, 1 from the Ross Sea (549 m) and 1 from off Enderby Land (219 m).

More than 30 species of 'normal' or octopodous colossendeids have been described; 2 species from East Indian waters have been assigned to the genus *Rhopalorhynchus,* which is probably not a valid genus. Some of the species described under *Colossendeis* are probably synonyms, but revisionary studies have so far been made only on Antarctic material (Fry and Hedgpeth, 1969?). At least 10 species are restricted to waters south of 45° S, and the most common species of Antarctic waters, *Colossendis megalonyx,* extends, in deeper water, as far north as Madagascar. Thus, the Antarctic component of this genus comprises at least 30% of the known species, in striking contrast to the Arctic where there is only a single endemic species, *Colossendeis proboscidea.* As collection records increase, it appears that many, if not most, of the Antarctic species are circumpolar, whereas the Arctic *C. proboscidea* is restricted to the area north of the Wyville Thomson Ridge and the Atlantic and eastern American regions of the Arctic; therefore, it is apparently not a circumpolar species. It is also noteworthy that such widely distributed deepwater species as *Colossendeis colossea, C. angusta,* and *C. macerrima* are rarely found south of 50°S, although there is 1 Antarctic record for *C. colossea* and several for *C. macerrima.*

The Antarctic shelf species of *Colossendeis* have well-developed if not always pigmented eyes, whereas the eyes of deep-sea species tend to be absent, reduced, or weakly pigmented. As Fry (1964) suggests, this character, together with the stenothermal habit of the genus, indicates that *Colossendeis* originated on some continental shelf in very cold water from which the species radiated into deeper water; in addition, the number of species in the Antarctic would support the further idea that the Antarctic continental shelf is the original center for the evolution of these species. In this context it is of interest to note that the single endemic Arctic species is blind although it occurs in relatively shallow water in the Arctic basin.

MAP 2. *Colossendeis*

Of the 11 species of *Colossendeis* known to be endemic or predominantly Antarctic in distribution, 8 are represented by adequate records; the others are represented by 1 or 2 records each. These distributions, with the possible exception of that of the widespread *Colossendeis megalonyx* and subspecies, are typical of many pycnogonids of the Antarctic regions in such genera as *Nymphon* and *Pallenopsis* occurring in moderately deep water. All are essentially circumpolar and their distribution records reflect the intensity of bottom sampling in various parts of the Antarctic. As Antarctic research continues we can expect many more records of these species from the regions at present sparsely represented.

MAP 3. *Austrodecus* (*glaciale* section)

Pycnogonids of the genus *Austrodecus* are small animals, only 3 mm to 4 mm in total length, with extremely long, delicate, slender proboscides. With the exception of *Austrodecus profundum,* which was taken from a depth of about 1000 m, the species are essentially sublittoral or shallow shelf species from near surface to 640 m, with most of the records from depths of less than 400 m. Apparently, they feed by suction of the proboscis on such things as bryozoan polypides. Stock (1957) recognized 17 species in this genus, most of them confined to Antarctic regions. He has further recognized 4 species groups or sections. Most of the species (11) belong to what he terms the *glaciale* section, which is represented in the Antarctic and Subantarctic regions with a record from New Zealand (South Island) and a dubious or uncertain record from Tasmania. The species of this section may further be divided according to the length of the eye tubercle and other characters.

Austrodecus glaciale is the most common species, occurring on the shallow shelf areas of the Antarctic continent; it is apparently circumpolar. There is a dubious record from *Discovery* Station 113 near Tasmania which may be due to net contamination. Along the coast of East Antarctica between 30°E and 140°E, this species occurs with *Austrodecus fagei.* Stock's (1957) explanation of this sympatric distribution is that *Austrodecus fagei* has features which suggest that it is more closely related to *A. simulans* of Kerguelen Island than to the parent species, *A. glaciale; A. simulans* arose by isolation in Kerguelen, and from that species the stock which gave rise to *A. fagei* reinvaded the Antarctic continent. This hypothesis does not allow for the possibility that *A. simulans* did not remigrate to the Antarctic shelf, but it may suggest that *A. fagei* represents another phase of speciation, perhaps by ecological rather than geographical isolation.

Be that as it may, there is evidently a complex of closely related forms of species of these curious small pycnogonids, which suggest evolutionary change resulting from isolation of one kind or another and migration from the parent Antarctic stock. It is interesting to note that the 'short eyed' section is not found on the Antarctic shelf, but has several distinct species or forms scattered on the Antarctic islands and in southern South America. This suggests that this group represents an earlier wave of migration from the Antarctic shelf regions.

MAP 4. Pycnogonidae

The family Pycnogonidae includes 2 genera, *Pycnogonum* and *Pentapycnon.* There are some 25 species of *Pycnogonum* and 2 of *Pentapycnon.* Species of *Pycnogonum* are found in most parts of the world except the Arctic basin; often there are 2 species occurring sympatrically. There are no clear trends of relationship between these various species, and it is not possible, with the data available at present, to draw inferences concerning biogeographic relationships between one area and another because of morphology. Most of the species of which we have life history knowledge are ectoparasites as adults on sea anemones. Most of the species are littoral or sublittoral; none are taken in abyssal or hadal depths.

The common Antarctic species appears to be *Pycnogonum gaini,* an apparently circumpolar species occurring from the upper sublittoral region to 2495 m; large adults may be more than 2 cm in length from the tip of the proboscis to the abdomen. *P. gaini* has rather long legs for a member of this genus. *Pycnogonum rhinoceros* is a large, lumpy looking pycnogonid whose known distribution includes South Georgia, the Antarctic Peninsula, and the Weddell Sea from depths of 154 m to 1115 m; so far it has not been collected from the Ross Sea. In several anatomical features *Pycnogonum rhinoceros* appears to be related to the ten-legged *Pentapycnon charcoti.* It is interesting, therefore, to note that most of the records for *Pentapycnon charcoti* are from the Antarctic Peninsula, the apparent population center for *Pycnogonum rhinoceros*—if a dozen or so specimens may be so loosely interpreted. Two specimens of *Pentapycnon charcoti,* however, have been collected from the Ross Sea. The bathymetric range of the polymerous form is 240 m to 1420 m.

The problem of the Magellanic and Subantarctic island species of this genus is a good example of the type of problem faced by the biogeographer when he has inadequate material. A number of specimens collected from the southern part of South America and the Falkland Islands have been identified as *Pycnogonum platylophum.* This range also coincides with that of other specimens identified as *Pycnogonum magellanicum,* which may in turn also be identical with *Pycnogonum magnirostre* from Kerguelen and Crozet Islands. *Pycnogonum platylophum* has also been identified from the Macquarie Islands, and there is one Antarctic shelf record from about 71°E, directly south of Kerguelen Island. Perhaps all of these forms will prove to be the same species. There is a related but distinctly different species, *Pycnogonum sivertseni,* from Tristan da Cunha and Gough Islands. Whatever the final systematic judgment, we are apparently dealing with a complex of related forms which may be differentiating from a basic stock by geographic isolation.

MAP 5. *Achelia*

Achelia is a genus of small, sluggish species usually associated with some coelenterate. Many of them are probably parasitic in their larval stages on the same organism on which they feed as juveniles and adults. Therefore, the chances for dispersal are not many, although species may be transported on drifting material or within hydrozoan medusae. Many species occur along considerable distances of shore line. Many 'forms,' 'abnormal specimens,' and 'varieties' have been described for species in this genus; this suggests that the various species may have morphological clines, although we do not have extensive enough material to document this supposition for any species.

Several distinct groups of species may be recognized in the Southern Hemisphere, and may be referred to as 'morphogroups.' Of these groups, one is characteristically Antarctic, including species occurring in the Falkland Islands, along the Scotia Ridge and the Antarctic shelf to the east of Cape Adare, with a disjunct representation in East Antarctica. This Antarctic morphogroup includes 4 species.

A second group consists of 4 species distributed principally around the shore of South America, including Juan Fernandez Islands, but with one Antarctic representative, *Achelia sufflata,* which is known only from a few records in the east Antarctic region.

A third group, the southern south temperate morphogroup, includes 3 species, of which 1, *Achelia assimilis,* occurs in New Zealand and southern Chile.

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Halocypridae[1]

N. S. Hillman[2]

INTRODUCTION

All members of the Halocypridae are planktonic in each of their stages, and the family is of worldwide occurrence; most of the species are tropical or subtropical, however. The most important genus in this family is *Conchoecia,* with more than 100 described species. This genus alone accounts for about 6 percent of all the described species of Ostracoda. Other halocyprid genera, such as *Halocypris, Euconchoecia,* and *Archiconchoecia,* are comparatively insignificant as compared with *Conchoecia.*

Five species of halocyprids are restricted principally to the waters south of the Antarctic Convergence. Approximately 17 other species occur in the southern oceans, raising the complement of Antarctic species to more than 20, but only 11 of these are regularly taken in plankton tows. Large bathypelagic species, at one time collected infrequently, are now appearing often in Isaacs–Kidd Midwater Trawl samples. Among these is the gigantic bathypelagic cypridinid *Gigantocypris mulleri,* which attains a size of 15 mm to 23 mm as compared with the typical *Conchoecia* of about 2 mm. Although it is often mentioned in the literature, little is known about *Gigantocypris.*

Antarctic halocyprids are apparently circumpolar, but since distribution records are incomplete for many species, especially in the Indian Ocean sector of the Antarctic, it is not certain that all species are circumpolar. Little is known of diurnal or seasonal vertical migration of planktonic Ostracoda in the Antarctic; the statement by Mackintosh (1937, p. 390) that *Conchoecia hettacra* is able to accomplish diurnal vertical migrations is not substantiated by the data he presents. Therefore, it is still uncertain how these organisms maintain their populations in the extreme southern waters in the presence of the prevailing northward component of the current in the upper water layers.

The distribution maps are based on reports from seven major Antarctic expeditions and the collections from the USNS *Eltanin.* No significant report on Antarctic planktonic Ostracoda with station data has been published since 1935. In all, Ostracoda have been identified from 103 stations made by these earlier expeditions, and information has been added from 111 *Eltanin* stations occupied in 1963 and 1964 in the Scotia Sea and the Pacific sector of Antarctic waters. Several stations of the Deutsche Südpolar-Expedition, the *Belgica* expedition, and the *Terra Nova* expedition are not shown on the maps because they are too close together at this scale, and nine *Terra Nova* stations in McMurdo Sound have been designated as a single locality on the maps. Twenty-two *Discovery* stations are not indicated on the maps because only one species, *Conchoecia hettacra,* was identified in the samples, and other species present were not identified (Mackintosh, 1937). These stations are between 78°W and 81°W and 55°S and 64°S; records from this region are available from *Eltanin* collections. However, 22 additional *Discovery* stations around South Georgia and in the area between South Georgia and the Falkland Islands (Hardy and Gunther, 1935) have been included on the maps.

Of the approximately 23 species occurring in Antarctic waters, the distribution of 12 commonly collected and 3 less frequently collected species is indicated on the maps. The remaining 8 species are of minor importance and have seldom been recorded.

THE PLATES

PLATE 15. Distribution of Antarctic species of Halocypridae

These are species confined primarily to the Antarctic regions, and their northern limit usually is the region of the Antarctic Convergence.

The most common species south of the Convergence is *Conchoecia hettacra* Müller (Map 4), which is most often identified as a component of the Antarctic plankton (Mackintosh, 1937; Hardy and Gunther, 1935; Baker, 1954) and is the only species truly demonstrated to be circumpolar (Baker, 1954). This species occurs well within the region of pack ice and probably as far south as the continent in some localities. It has been collected very close to the land by the Deutsche Südpolar-Expedition in the Indian Ocean sector of the Antarctic (Müller, 1908), by the Swedish Antarctic Expedition in the Weddell Sea (Skogsberg, 1920), by the British Antarctic Expedition in the Ross Sea (Barney, 1921), and by the USNS *Eltanin* in the Bellingshausen Sea. In some areas there are no stations from which the northern limit of distribution might be determined.

Conchoecia borealis Sars *antipoda* Müller (Map 2) is a relatively large (2.8 mm to 2.9 mm) and distinct species. Müller (1906a) records it as far north as 1°S. *C. borealis antipoda* is a deepwater species, primarily inhabiting depths greater than 250 m. Presumably the species could be transported north by the action of the Subantarctic Intermediate Water, but since the species is far more abundant south of the Convergence (*Eltanin* samples), the Antarctic is considered its principal habitat. There is no certainty that this species extends to the continent at all points, but Müller (1908) did find it in samples taken somewhat south of 65°S during the Deutsche Südpolar Expedition. It is recorded in the Bellingshausen Sea (*Eltanin* samples) at a little over 70°S, but is not found in the *Belgica* samples in the same area. Barney (1921) recorded this species in McMurdo Sound.

Conchoecia belgicae Müller (Map 5) is the most southerly distributed species, found quite close to the continental landmass. Data are scarce and are recorded only from stations near or in the pack ice. Skogsberg (1920) states that the distribution of this species is south of 64°S.

Conchoecia brachyaskos Müller (Map 5) is not common in plankton samples. The available data indicate an unusual distribution. The species is found in the true Antarctic, south of the Antarctic Convergence and very near the continent (Müller, 1908). It has also been reported in tropical regions of the Atlantic and Indian Oceans (Müller, 1906a); however, few catches are recorded between these two regions.

Conchoecia isocheira Müller (Map 3) is the smallest of Antarctic Halocypridae. Samples from the *Eltanin* cruises containing this species have been collected as far as 70°S, and data from the *Belgica* expedition record *C. isocheira* to at least 71°S in the Bellingshausen Sea. These southern locations are farther south than the 66°S limit stated by Skogsberg (1920), indicating that there is probably no southern limit based on latitude but that the limit is the Antarctic continent itself.

PLATE 16. Distribution and southern limits of 'warm-water' Halocypridae found in Antarctic waters

The species represented here are not true Antarctic species, for they inhabit the tropical, subtropical, and Subantarctic areas. A few are common well into the Northern Hemisphere. The southern limit of several species is in the area of the Antarctic Convergence; other species extend somewhat south of the Convergence. Species illustrated in Maps 6 to 9 are primarily found in the upper 250 m but are also found in smaller numbers to at least 1000 m.

Conchoecia serrulata Claus (Map 6) is probably one of the most common species in the upper 100 m between 40°S and the Antarctic Convergence. In the *Eltanin* samples it often occurred in prodigious numbers compared with other species, at times comprising 100 percent of the Ostracoda present in the samples. This species is primarily found in the upper 100 m, and its numbers drop off rapidly below that depth.

Conchoecia chuni Müller (Map 7) is an elongate species rarely found south of the Convergence. It has been recorded as far north as 2°S (Müller, 1906a), but is principally located between 26°S and 64°S.

Conchoecia obtusata Sars (Map 8) has been combined with *Conchoecia obtusata* Sars var. *antarctica* Müller for the purposes of the map. According to Skogsberg (1920), *C. obtusata* occurs primarily north of 60°N latitude, but it is also found alongside the Antarctic form, whose distribution he gives as 26°S to 53°S. *Eltanin* samples have frequently yielded both types together in Antarctic waters.

Conchoecia rotundata Müller (Map 9) has the most irregular southern distribution of the species considered. In the Indian Ocean this species was found near the Antarctic continent (65°S latitude) by the Deutsche Südpolar-Expedition (Müller, 1908). In the Bellingshausen Sea it was again found close to the continent at 70°S (*Eltanin* samples). In other localities the southern limits do not approach the continent, but it is not certain whether this indicates some unknown limiting factors or is an artifact of inadequate data.

The following species (Maps 10 to 14) principally inhabit depths greater than 250 m in southern waters. A large number of species in the Antarctic inhabit depths greater than 250 m, and several shown on these maps are not common above 500 m. *Gigantocypris* and such large representatives of the genus *Conchoecia* as *C. valdiviae* occur at depths greater than 250 m. The carapace of these deepwater species is often the reddish color typical of so many bathypelagic crustacea.

Not only giants, however, live in the deep water; the small species indicated in Maps 6 to 9 can also be found below 250 m, along with such distinctive species as *Archiconchoecia cucullata* Müller (Map 14), whose carapace has a shape unlike that of any other halocyprid.

Conchoecia elegans Sars (Map 10) is probably a truly cosmopolitan species; in the Pacific it is known from 79°N to 64°S. It is one of the most commonly collected species and is found almost anywhere and at any time.

Conchoecia symmetrica Müller (Map 12) can be found as far north as the equator (Müller, 1906a). In Antarctic waters it is most abundant below 500 m, but in the Subantarctic it rises near the surface.

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[1]Contribution No. 1277 from Lamont Geological Observatory of Columbia University, Palisades, New York.

[2]Lamont Geological Observatory

Conchoecia edentata Müller (Map 13) is not reported often, though it occurs frequently in the *Eltanin* samples. It is most abundant at depths greater than 500 m. It is apparently one of the bathypelagic species having a very wide distribution; Rudjakov (1962) found *C. edentata* in the northwestern Pacific.

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Cirripedia[1]

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INTRODUCTION

The subclass Cirripedia, consisting of nearly 1000 species, is usually divided into the orders Ascothoracica, Rhizocephala, Acrothoracica, and Thoracica. The greatest diversity of species occurs in the warm and tropical seas of the world, in intertidal regions, and in relatively shallow water. The region south of the Antarctic Convergence is relatively depauperate, with 1 Recent ascothoracican, 1 rhizocephalan, 1 fossil acrothoracican, and 29 Recent and 5 fossil thoracicans.

LIVING BARNACLES

The Ascothoracica are commensal or wholly parasitic on coelenterates and echinoderms and are widely distributed both geographically and bathymetrically (Wagin, 1964). At present, only one ascothoracican, *Ascothorax bulbosus* Heegaard, an endoparasite of the ophiuroids *Amphiura belgica* Koehler and *A. microplax* Mortensen, is known from Antarctic waters. This parasite was dredged from shallow waters (100 m to 175 m) in the vicinity of South Georgia. It is probably to be expected that other species will be found in the deeper waters bounding Antarctica owing to the great abundance of potential echinoderm and coelenterate hosts.

The Rhizocephala are wholly parasitic, for the most part on decapod crustaceans. They occur most commonly on the continental shelf, although some species are known from deeper waters. Examples are *Sacculina abyssicola* Guérin-Ganivet at 3975 m in the Azores, on *Ethusina abyssicola* Smith and *Triangulopsis abyssorum* Guérin-Ganivet at 4255 m, between the Azores and Rochefort, on *Orophorhynchus parfaiti* Milne Edwards (see Guérin-Ganivet, 1911). The single Antarctic species is *Briarosaccus callosus* Boschma on *Lithodes* spp. and *Paralomis* sp. (see Map 4, Plate 17). The reason for the scarcity of rhizocephalans correlates with the relative scarcity of decapod hosts south of the Antarctic Convergence.

The Acrothoracica are burrowers in a wide variety of calcareous substrata, including corals and mollusk shells. The order is predominantly tropical and is so far known only from shallow waters. *Cryptophialus* has representatives in New Zealand, the southern extremities of South America and Africa, and around the perimeter of Subantarctic waters. Although the order was represented during the Cretaceous, no Recent Antarctic species are known.

The Thoracica, the largest and most diverse group of the Cirripedia, is relatively well represented in the Antarctic. Members are distinguished from other Cirripedia and from nearly all other Crustacea by a calcareous shell that is not molted during life. Consequently, they have a well-documented fossil record dating from Silurian times.

The order Thoracica contains three extant suborders: the Lepadomorpha, Verrucomorpha, and Balanomorpha. The Lepadomorpha, or stalked barnacles, are considered the most primitive. They also have the greatest bathymetric range—from the high intertidal regions to depths greater than 5000 m (Nilsson-Cantell, 1950). In the Antarctic the lepadomorphs are the most significant group of cirripeds, and the two principal families are both represented. The more significant is the holobenthic Scalpellidae. The other, the Lepadidae, can be divided into two major groups: those that are epizoic on whales and other marine vertebrates, and those that are carried about on floating objects by surface currents. The former are cosmopolitan forms because of the migratory habits of their hosts. The latter is represented by a single endemic species whose distribution is correlated with the West Wind Drift.

The Verrucomorpha, or wart barnacles, are sessile forms, descended from an earlier line than that which gave rise to the true sessile barnacles or Balanomorpha. They are widely distributed geographically and bathymetrically; the majority of the known species are found in relatively deep water, to 4630 m (Nilsson-Cantell, 1950). At present only 1 species is known to occur south of the Antarctic Convergence.

The Balanomorpha, or acorn barnacles, are divided into 2 families, the Chthamalidae and Balanidae. Both families are widely distributed, primarily in the shallow seas of the world. The Chthamalidae is morphologically and paleontologically more primitive, and its members occupy the highest reaches of the intertidal zone and extend to depths greater than those reached by the Balanidae. Two deepwater chthamalids occur south of the Antarctic Convergence. Although littoral balanids at one time inhabited the Antarctic, the only ones presently found there are forms occurring on whales; therefore, they are not members of the Antarctic fauna in the strict sense.

The life cycle of many shallow-water thoracicans begins with eggs that are fertilized and brooded within the so-called mantle cavity of the female or hermaphrodite; the larvae are then released as free swimming nauplii. In some species the naupliar stages are passed in the egg, and the larva is released as a cyprid. Ordinarily, during approximately two weeks of planktonic development, the nauplius feeds and progresses through six naupliar stages of increasing size and complexity before metamorphosis into the bivalved, cyprid stage. The cyprid stage, of which there is only one, is relatively weak-swimming and non-feeding. It selects the site of permanent attachment, where it will develop into a female, a hermaphrodite, or a reduced male attached to an individual that will act as a female.

Methods of dispersal are of great importance to the biogeographer. The adult stages of most thoracic cirripeds are generally not considered in problems of dispersal because, for the most part, they attach to fixed substrate. Exceptions are found with fouling forms and those attached to floating objects or motile invertebrates and vertebrates. Ordinarily, the naupliar stage is considered the usual dispersal agent. However, in a number of species the naupliar stage is entirely passed through in the egg as it develops within the mantle cavity, and only the weak-swimming cyprid enters the plankton. Species in which the planktonic phase of the life-cycle has been suppressed through elimination of the nauplius might be expected to show relatively restricted patterns of distribution, or endemism. However, in the few warm-water forms without nauplii, this is not the case. Indeed, release of non-feeding, advanced larvae may be related to the lack of suitable food available in the plankton, or to maintaining a population in a particular habitat, such as on off-shore islands.

FOSSIL BARNACLES

Thirty-seven nominate taxa are known from south of the Antarctic Convergence. Of these, 6 are fossil, representing 2 of the 4 cirriped orders, the Acrothoracica and Thoracica. With the exception of the balanomorphs (Order Thoracica), all of the fossils are from Cretaceous deposits, and represent extinct species (Table 1).

The single acrothoracican found in Antarctic waters was recognized by its burrows in belemnite shells and has been assigned to the extinct genus

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Brachyzapfes. A closely related species occurs in France in early Cretaceous sediments (Taylor, 1965).

The fossil lepadomorphs (Order Thoracica) are represented by 1 extant and 2 extinct genera. *Euscalpellum,* with more than one-half of the 15 known species extinct, is represented by *E. antarcticum.* While other extinct species of *Euscalpellum* are found in New Zealand, Australia, and Tierra del Fuego, extant species are not known to occur higher than the 40th parallel in either hemisphere (Withers, 1951). The extinct genera *Zeugmatolepas* and *Cretiscalpellum,* otherwise known only in European Cretaceous sediments, are each represented in Antarctica by a single species (Withers, 1947; Taylor, 1965).

The balanomorphs (Order Thoracica) were better represented in Antarctica in the past than they are today. Fossil records for the extant chthamalid, *Hexelasma antarcticum,* are apparently restricted to Pleistocene or sub-Recent deposits (Speden, 1962). A closely related extinct species, *H. aucklandicum,* is known from the Miocene of New Zealand, while the extant *H. hirsutum* is known from the northeast Atlantic at depths to 2000 m. On the other hand, all of the Antarctic balanids are extinct, having been represented by *Balanus (Austrobalanus) flosculus sordidus* Darwin and an undetermined species of *Balanus* (Fletcher, 1938; Hennig, 1911). The extant austrobalanids, as their name implies, are widely distributed in the Southern Hemisphere except for South Africa.

TABLE 1. Collection Localities and Ages of Fossil Barnacles

Species	Locality	Age and Elevation Above Mean Sea Level
Acrothoracica		
Brachyzapfes elliptica var. *gigantea* Taylor	East coast Alexander Island 73°S, 68°W (approx.)	Early Cretaceous (Aptian)
Thoracica (Lepadomorpha)		
Euscalpellum antarcticum Withers	Antarctic Peninsula 63°55′S, 57°30′W 63°59′S, 57°25′W	Late Cretaceous (Senonian)
Zeugmatolepas georgiensis Withers	Annenkov Island 54°29′S, 37°05′W	Early Cretaceous (Aptian)
Cretiscalpellum aptiensis var. *antarcticum* Taylor	East coast Alexander Island 73°S, 68°W (approx.)	Early Cretaceous (Aptian)
Thoracica (Balanomorpha)		
Hexelasma antarcticum Borradaile	78°04′S, 167°60′E	Pleistocene 100–200 feet
	78°28′S, 165°50′E	Pleistocene or younger 3–10 feet
Balanus (Austrobalanus) floculus var. *sordidus* Darwin	Kerguelen Island 53°S, 108°E (approx.)	Late Cenozoic 750 feet
Balanus sp.	Cockburn Island 64°20′S, 56°50′W	Late Cenozoic

THE MAPS (PLATE 17)

MAP 1: Worldwide records

The Recent Antarctic cirriped fauna, like some other invertebrate faunas of the region, is highly endemic. Many species are known from one or more localities within the Antarctic, and many also occur or have their closest relatives to the north. *Coronula, Conchoderma,* and *Xenobalanus* (Order Thoracica) are wide ranging because they are epizootic on whales. The pelagic lepadomorphs (*Lepas:* Order Thoracica) are widely distributed by surface currents. The benthonic *Arcoscalpellum* (Order Thoracica) are known from only a few records, and consequently little information can be advanced regarding their occurrence other than to point out that they are generally not limited in their distribution.

MAP 2: Scalpellidae

The Scalpellidae is the oldest known family of the Lepadomorpha, with a fossil record dating from Carboniferous times. Of the 17 known genera, 11 are extant. Scalpellids range in size from a few millimeters to more than 15 cm in length. Bathymetrically, the scalpellids range from the littoral to the hadal region, but the greatest diversity in terms of recognized genera occurs on the continental shelves. Scalpellids occur on a wide variety of substrate, including rocks, worm tubes, arborescent invertebrates, echinoderms, and pycnogonids. However, no strict associations have been observed, even though the names of many of the species may imply such an association.

Only two Recent genera of the Scalpellidae, *Scalpellum* and *Arcoscalpellum,* are known from the region south of the Antarctic Convergence. Both of these genera are widely distributed in all seas. At least 1 species, *Arcoscalpellum gruvelianum* (Pilsbry), is reported in both hemispheres and occurs in deeper water in the tropics than at high latitudes (Krüger, 1940). However, no truly Antarctic species are recognized as having a comparable distribution.

Scalpellum, with approximately 15 species, is represented in Antarctic waters by *S. vanhoffeni* Gruvel and, like most representatives of this genus, it occurs on the shelf. Such species as *S. ornatum* (Gray) (South Africa), and *S. gibberum* Aurivillius (southern extremity of South America) occur in Subantarctic regions. Both of these species range from relatively shallow water to the edge of the continental shelf (*S. ornatum,* 66 m to 266 m; *S. gibberum,* 0 m to 253 m).

Arcoscalpellum is by far the largest genus of the family with approximately 160 species, of which a proportionately large number occur in the Antarctic. Of the 19 species known from this region, 8 have been recovered from more than one locality, and all except 2 have been taken from between 90 m and 550 m. Two other species represented by single collections are from the abyss. From published data it appears there is an absence of barnacles between the shelf and the abyss, but this could be due simply to a lack of sampling at the intervening depths. A preliminary examination of the specimens taken in Antarctic waters by the USNS *Eltanin* between 1962 and 1965 indicates that this is the case.

Arcoscalpellum compactum (Borradaile) and *A. discoveryi* (Gruvel) appear to be amphipolar. The apparent amphipolarity of these 2 species could be related to environmental conditions associated with the East Wind Drift and concomitant planktonic factors (Marr, 1962). On the other hand, it could simply be due to lack of adequate collections in the intervening areas; they could be actually circumpolar with high population densities in the Weddell and Ross Sea areas. A further complication in interpretation arises in this and related problems because young stages of different species are very similar among themselves but are markedly different morphologically from their adult forms. Many of the single collections could be of young stages of these or other widely distributed species, but this cannot be resolved at present.

Arcoscalpellum convexum (Nilsson-Cantell) has been taken off South Georgia and the South Shetlands Islands, and *A. magnaecarinae* (Nilsson-Cantell) has been dredged twice off the South Shetland Islands. Neither of these species has appeared in the numerous collections from comparable depths in the vicinity of the Ross Sea or off Wilhelm II Coast (*Gauss* winter station). Based on the present data, these 2 species must be considered regional in distribution.

The preliminary evidence suggests that there are both circumpolar and regionally distributed species. Presently there are no conclusive data on means of, or limitations on, dispersal, nor are there sufficient paleogeographical data that would seem to account for the meager distributional patterns of these shallow-water species. Evidence derived from the fossil record indicates a more diverse scalpellid fauna during the Cretaceous than exists today.

MAP 3: Lepadidae

The family Lepadidae is an oceanic complex containing 3 principal genera: *Lepas* (on floating objects or floats of its own), *Alepas* (on large scyphomedusae), and *Conchoderma* (on marine vertebrates and other objects not strictly associated with the shore). Only *Lepas* and *Conchoderma* are known from the Antarctic.

Of the 10 recognized species of *Lepas* in the world, only 2 occur in the Antarctic. One, *L. hillii* Leach, is known from a single record. The other *L. australis* Darwin, is a circumpolar species that ranges as far north as Valparaíso, Chile; Cape of Good Hope, South Africa; Tasmania; Auckland, New Zealand; and as far south as the South Shetland Islands. The majority of the circumpolar records for *L. australis* are scattered around the 50th south parallel.

The genus *Conchoderma* contains 2 cosmopolitan species. *Conchoderma virgatum* (Spengler) usually attaches to a wide variety of floating objects or swimming organisms near or at the sea surface, yet it is infrequently encountered in polar waters, and at present there are no records from the Antarctic. *Conchoderma auritum* (Linnaeus) occurs on cetaceans, either on the associated sessile barnacles or on exposed hard parts of the whale such as the teeth or the baleen. Therefore, its distribution corresponds to the distribution of its hosts, which occur in large numbers in the vicinity of the South Shetland and South Georgia Islands.

MAP 4: Other Cirripedia

Verruca is the sole extant genus in the suborder Verrucomorpha. Of the more than 40 described species, only *V. gibbosa* Hoek occurs in the Antarctic. This species also occurs in the southern portion of the three great oceans at depths of 385 m to 3128 m. *V. quadrangularis* Hoek occurs in the south Atlantic at depths ranging from 2380 m to 3475 m, immediately north of the known range for *V. gibbosa.* Another species, *V. nitida* Hoek, occurs on the opposite side of the world in the southern Indian Ocean at depths of from 900 m to 1300 m, and thus occupies a comparable but more northern latitudinal position than that of *V. quadrangularis.*

The majority of the species of Verrucomorpha are bathyal and abyssal, but a few intertidal species are known in the world. Occurrence in the intertidal zone is apparently correlated with paleogeographical and biological factors rather than simply with temperature as a function of latitude, because representatives are found in tropical, temperate, and sub-Antarctic regions (Hawaii, *V. cookei* Pilsbry; England, *V. stromia* (Müller); Peru to Tierra del Fuego, *V. laevigata* Sowerby).

Two principal genera of the Chthamalidae occur in deep water. The morphologically more primitive of these, *Pachylasma,* with species scattered about the world, predominantly on the shelf to depths of about 400 m, has its greatest diversity in terms of species in Indo-Pacific waters. Three representatives are found in the Southern Hemisphere, 1 littoral and 1 in deep water in southeast Australia (*P. aurantiacum* Darwin and *P. scutistriata* Broch) and 1 littoral in South Africa (*P. giganteum* Philippi). *Pachylasma* has not been reported from the North Atlantic or from the Antarctic.

The bathyal genus *Hexelasma* is predominantly Indo-Pacific, as is *Pachylasma,* but it has representatives on both sides of the North Atlantic and in the Antarctic. No species are known from the Indian Ocean proper or from the eastern Pacific (from the Bering Straits to Tierra Del Fuego).

Two species of *Hexelasma* are recognized in the Antarctic. One, *H. corolliforme* (Hoek), has been reported from two localities on opposite sides of the Antarctic continent, just within the Antarctic Convergence, at approximately the same depths. The other species, *H. antarcticum* Borradaile, was first discovered as a fossil in a glacier about 9 m above sea level in the Ross Sea area. Living specimens were subsequently found at a depth of 157 m off the Adélie Coast (141° E) and at 790 m off the Princess Ragnhild Coast (33° E). Isolated shells have been dredged at a number of other localities. If the complete specimens and fragmentary fossil or subfossil materials are of the same species, *H. antarcticum* is apparently a circumpolar, bathyal species.

The only Recent representatives of the family Balanidae found in the Antarctic belong to the genera *Coronula* and *Xenobalanus,* forms found only on cetaceans. Their distribution, like that of *Conchoderma,* is determined by the migration of the whales on which they live, and thus they are not strictly members of the Antarctic fauna. It is not known, but it is inferred, that whale barnacles are not reproductively active during their sojourn on the whales in the Antarctic (Clarke, 1966).

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Amphipoda Hyperiidea

D. E. Hurley[1]

INTRODUCTION

The suborder Hyperiidea includes most pelagic amphipods. All species of this suborder are either pelagic themselves, or parasitic on or commensal with other pelagic animals, especially coelenterates. Planktonic amphipods of the suborder Gammaridea, notably species of *Synopia* (Family Synopiidae) and members of the *Cyphocaris* complex (Family Lysianassidae), may be taken in the open sea, but are quantitatively insignificant. (Benthic Gammaridea are, however, frequently found in shallow-water plankton.) The Gammaridea as a group are not considered here.

As with all Amphipoda, identification of hyperiids is complicated by the number of mouthparts and appendages to be examined, but, unlike the Gammaridea, most of the significant taxa are not difficult to identify, at least to generic level. Many species of hyperiids have some particularly distinctive features, for example, the 'winged' body of *Platyscelus armatus,* or the long grasshopper- or mantid-like head of the transparent *Phronima.* Using suitable illustrations, one can quickly recognize these with some degree of certainty. There are few larval forms to complicate identification or life histories[2]; most young are released from the parental brood pouch as miniatures of the adult. Because the full complement of spines or setae may not be developed, juvenile specimens are sometimes difficult to identify to species level, especially in genera like *Hyperia* which have a number of very similar species. Specimens from quantitative nets, particularly Clarke–Bumpus samplers, which selectively exclude larger animals, may therefore be difficult to identify, and the time involved may not be warranted because of the uncertain identification of these extremely small specimens.

Because of their pelagic nature, the Hyperiidea are a cosmopolitan group with few local endemic species. Thus, it is unlikely that there are many undiscovered species. A species which appears to be new is more likely to have been already described but to have been temporarily lost by having been subsequently treated as a synonym. This is partly because the systematics of the group have gone through at least two distinct phases and are now entering a third. Originally, specimens of many species were collected in small numbers, often in ones and twos from widely separated parts of the world, by the great historical expeditions (*Challenger, Siboga, Ingolf,* Deutsche Südpolar, Deutsche Tiefsee) and described as distinct species, only to be synonymized later as more material became available and differences previously considered specific were recognized as being due to age or sex. With some species, and some authors, particularly in the 1930's, this tendency may have been taken too far; modern workers (Bowman, 1960; Yang, 1960), examining large collections of individuals, are re-recognizing species previously consigned to synonymy.

For identification of Antarctic species, the most useful general publications are Stebbing (1888), Chevreux and Fage (1925), and Spandl (1927). There are useful keys in Pirlot (1929), Barnard (1940), and Hurley (1955). A checklist of species, now somewhat outdated but still useful, is given in Stephensen (1925).

DISTRIBUTION

I have taken 35°S as the northern boundary for this compilation (Plates 18 and 19); thus, the area treated includes Antarctic and Subantarctic waters. Within this region the distribution of Hyperiidea in the Southern Hemisphere appears to be conditioned by the major hydrological boundaries. Using the Subtropical Convergence and Antarctic Convergence boundaries and the mean limits of the pack ice (Deacon, 1937[3]; Mackintosh, 1946[3]), it is possible to separate the species in these waters into several groupings. This is necessarily an approximation of the true position, since these boundaries vary considerably throughout the year; the season and depth of capture of specimens have not been taken into consideration. In marginal instances an arbitrary decision on whether isolated

[1]New Zealand Oceanographic Institute, Wellington.

[2]Larval forms of *Cystisoma* are known (Barnard, 1932, p. 271; Spandl, 1927, p. 173; Spooner *in* Marine Biological Association, 1966).

[3]Despite the dates of these works, they were the only available comprehensive treatments of 'Southern Ocean' water mass boundaries at the time of writing.

transgressions of boundary should be disregarded has been made on the basis of the general distributional pattern as shown by all other records.

The Subtropical Convergence, according to Deacon (1937), lies mainly between 35°S and 47°S. Certain tropical species and even families, notably Oxycephalidae, are recorded a few degrees south of 35°S, but are not found south of the Subtropical Convergence; likewise, certain colder water species, notably *Parathemisto gaudichaudii,* the most common species, do not appear to go significantly north of the Convergence. Therefore, in compiling these maps, I have dealt only with those families represented south of the Subtropical Convergence; thus, the Oxycephalidae are omitted. However, where a family such as the Scinidae (Plate 18, Map 2) is definitely represented south of the Convergence, I have included all species recorded south of 35°S, even though some, such as *Scina incerta,* do not go south of the Convergence. This serves to illustrate both the cosmopolitan nature of species which transgress this boundary and the replacement of certain tropical and subtropical species by Subantarctic and Antarctic ones. Rare species have been included as well as common ones.

The pattern of distribution which emerges is one in which the greatest number of species are in the tropics, with the number decreasing southwards to the Antarctic; there are very few endemic species in the colder waters, and most of these are restricted to the area south of the Antarctic Convergence. Of the 20 families of Hyperiidea, 15 are known from south of the Subtropical Convergence, and are represented by 29 genera and 56 species.

Hyperiidea occurring below 35°S may be grouped as follows:

(1) **Tropical species** which extend from the equator no farther south than the Subtropical Convergence, for example, *Scina oedicarpus, Iulopis loveni, Streetsia challengeri,* and *Platyscelus serratulus.*

(2) **Cosmopolitan species** which extend from the equator to the Antarctic continent. This, surprisingly, is the largest group: *Archaeoscina steenstrupi, Mimonecteola beebei, Lanceola clausi*[4]*, Scypholanceola vanhoeffeni, Mimonectes sphaericus, Scina typhlops, S. borealis, S. spinosa, S. crassicornis, S. rattrayi* var. *keilhacki*[5]*, S. wolterecki, S. pusilla, Ctenoscina brevicaudata, Vibilia stebbingi, V. antarctica, Hyperia spinigera*[6]*, H. galba* (incl. *gaudichaudii*), *Phrosina semilunata, Primno macropa, Pegohyperia princeps,* and *Brachyscelus crusculum* (to pack ice only).

(3) **Near-cosmopolitan species** which extend from the equator to the Antarctic Convergence. This is also a large group: *Vibilia propinqua, V. armata, V. pyripes, Hyperia luzoni, Hyperoche mediterranea, Hyperioides longipes, Phronima sedentaria, P. atlantica, Anchylomera blossevillei, Paraphronima crassipes, Pseudolycaea pachypoda, Tryphana malmi, Brachyscelus rapacoides, Thamneus platyrhynchus, Parascelus typhoides, Platyscelus ovoides, Hemityphis rapax,* and *Tetrathyrus forcipatus.*

(4) **Antarctic species,** which fall into three groups:

(a) Those occurring from the Antarctic continent to the limits of the pack ice only. There are four species: *Paralanceola anomala, Mimoscina setosa, Hyperia antarctica,* and *Hyperia macronyx.*

(b) Those occurring from the Antarctic continent to the Antarctic Convergence. There are five species: *Lanceola loveni* var. *antarctica*[7]*, Cyllopus lucasii, Hyperiella dilatata, Hyperoche luetkenides,* and *Scina antarctica*[8].

(c) Those occurring from the Antarctic continent to the Subtropical Convergence. These are *Vibilia antarctica* and the two most common and characteristic cold-water species, *Cyllopus magellanicus*[9] and *Parathemisto gaudichaudii*[9].

A number of species do not fit into these patterns, perhaps because of misidentification or perhaps because there are insufficient records to indicate their full range. These include: *Vibilia antarctica* (from the edge of the pack ice to north of the Subtropical Convergence); *Hyperiella antarctica* (between the Subtropical Convergence and the edge of the pack ice); *Hyperoche medusarum*[6] (between the Antarctic continent and the Subtropical Convergence); *Parathemisto australis*[6] (Subtropical Convergence region, neritic around New Zealand and Tasmania); and *Parathemisto gracilipes*[6] (Subtropical Convergence region, mostly neritic around New Zealand and southern Australia); and *Chuneola parasitica* (2 southern records, 59°29′S, 97°08′E and 36°32′S, 160°38′E).

PROBLEMS IN DISTRIBUTION

WARM- AND COLD-WATER FAUNAS. The most striking faunal division in the Hyperiidea would appear to be the warm-water–cold-water division between tropical species and Subantarctic and Antarctic species. In very general terms, this division seems to be about 30°N and 30°S of the equator. North of 30°S one finds particularly, although not necessarily in great numbers, the families Oxycephalidae, Thaumatopsidae (Cystosomatidae), Dairellidae, Lycaeopsidae, and Pronoidae. No one family is found only south of 30°S, but the two most important genera here are *Cyllopus* and *Parathemisto;* and, according to Bowman (1960), members of *Parathemisto* 'overwhelmingly dominate the cool-water epipelagic fauna.'

The exact boundary is difficult to pinpoint. While it would appear to be about 30°S, it could be nearer 40°S, or it could be the entire intervening zone. In the open ocean there are insufficient records to define the planktonic boundaries; what evidence there is comes mainly from waters close to islands or continents, and even here faunal studies are insufficient for satisfactory correlations.

A good example of the difficulty of defining the exact boundary even within several degrees of latitude is found in the New Zealand region. Immediately north of New Zealand there is a 'Tropical Convergence' at about 30°S (Wyrtki, 1962; also 'Tropische Stromgrenzen' of Schott, 1935 and 'Tropical Front' in Hurley, 1960b, p. 288), which seems to be a major hydrological boundary between tropical and more southerly planktonic faunas. The author (Hurley, 1960b, p. 288) has previously suggested the possibility of a subtropical planktonic zone here between the 'Tropical Convergence' and the Subtropical Convergence. This may be an intermediate 'neutral' zone of mixed fauna. The existence of such a region is suggested by hydrological evidence that, on the west coast of New Zealand, the 'Tropical Convergence' and the Subtropical Convergence are quite distinct features, separated by a distinct hydrological regime (Wyrtki, 1962). An intermediate neutral zone is also suggested by limited planktonic information (Barnard, 1930; Hurley, 1960b) which indicates that around the Three Kings Islands[10] and the Cape Maria van Diemen area there are to be found tropical, cosmopolitan, and near-cosmopolitan species, but no species restricted to the area, and neither of the cold-water genera, *Cyllopus* and *Parathemisto.* On the east coast the hydrological situation is less clear. Oxycephalidae stray south to about 40°S (Fage, 1960), and the characteristic cool-water species *Cyllopus magellanicus* and *Parathemisto gaudichaudii* are not found significantly above the northern fringes of the Subtropical Convergence region, as defined by Burling (1961). It may be that at this point the northern Tropical Convergence boundary swings down to meet the Subtropical Convergence and that the 'neutral zone' is here non-existent. Thus, the supposed 'neutral zone' may be a purely local Tasman Sea phenomenon, but there appears to be an equally interesting situation in similar latitudes off South Africa (Grindley and Penrith, 1965; see also footnote 9).

GENERAL CONSIDERATIONS. Cosmopolitan species[11], which include many of the most common hyperiids, extend through a great latitudinal range, with its accompanying variations of physical environment, and should be valuable material for a study of microspecific, micromorphological, or physiological differences, particularly in relation to physical differences in their environment. One would like to know whether their recorded continuity is due to hauls from different depths at different parts of the range and, if so, if this is correlated with the varying depths of water masses at different latitudes. Many of the larger species are known from great depths, thus supporting the tantalizing possibility that their distribution may be continuous, although the depths at which they occur may vary from place to place.

In bipolar species there is little information regarding distribution in relation to depth between Northern and Southern Hemisphere populations. Is there, for example, in *Parathemisto gaudichaudii* (Bowman, 1960) some continuity of distribution at depth today? In this species it would seem unlikely, although if the two populations are identical, as claimed, there must have been some continuity between them in the past.

In general, the greater the sampling depth the larger the specimen, a circumstance apparently not entirely due to differences in gear. This is especially noticeable in the Parascelidae and Platyscelidae, where the normal 50 cm or 100 cm plankton net is likely to produce specimens of the 5 mm to 10 mm size range from surface and shallow hauls, but specimens from midwater trawls or from the stomachs of deep-ranging fish are likely to be in the 18 mm to 20 mm range. Does this indicate depth separation

[4]Includes *Lanceola clausi* sp. *gracilis,* from Ob' Sta. 36 (62°55′S, 118°52′E) where *L. clausi* was also recorded (Vinogradov, 1962).

[5]There is also an apparently anomalous record of *Scina rattrayi* (s. str.) from 64°29′S, 85°27′E (Vinogradov, 1964).

[6]This appears to be a neritic species.

[7]*Lanceola loveni* (s. str.) is not recorded south of 30°S (Vinogradov, 1964, Fig. 21).

[8]Wagler (1927, p. 105) has an anomalous record of one young male and one female from 27°18′S, 2°51′E which seems likely to be a misidentification.

[9]Except in the Indian Ocean to the east of South Africa where there are some records north of the Deacon–Mackintosh mean position of the Subtropical Convergence. In addition, Siegfried (1963) records *P. gaudichaudii* north of 25°S off the west coast of South-West Africa but comments that it is common and very abundant in the *cool neritic water* of the west coast (my italics).

[10]This is an area where cold water is known to upwell (Garner, 1959).

[11]Brodskij (1965) has a very relevant discussion on the validity of 'cosmopolitan distributions.'

of size ranges? If so, what separation factors are involved? Do none of the largest specimens come to the surface?

It is obvious that, while the number of species of Hyperiidea may not be greatly added to by present-day investigations, much—in fact, most—of their ecology and biology is still unknown.

CONCLUSIONS

In the 15 families represented south of the Subtropical Convergence, of 54 genera:

(1) 33 are represented south of 35°S

(2) 30 of these are found north of the Subtropical Convergence.

(3) 29 extend south of the Subtropical Convergence but only 3 are restricted to the south of this limit.

(4) 20 extend south of the Antarctic Convergence but only 3 are restricted to the south of this limit.

(5) 18 extend south of the pack ice limits but only 2 are restricted to the south of these limits.

In these 15 families, of 187 species:

(1) 71 are represented south of 35°S

(2) 58 of these are found north of the Subtropical Convergence.

(3) 56 extend south of the Subtropical Convergence but only 9 are restricted to the south of this limit.

(4) 36 extend south of the Antarctic Convergence but only 5 are restricted to the south of this limit.

(5) 32 extend south of the pack ice limits, but only 4 are restricted to the south of these limits.

The only family with all genera represented in southern waters is the monogeneric family Chuneolidae; the single species concerned is represented by only two records and is not found south of the Antarctic Convergence. Thus, there is no truly endemic Antarctic family nor even Subantarctic family; all found south of the Subtropical Convergence are also represented to the north.

The numbers of genera and species steadily decrease from warmer waters to Antarctic waters. It seems undeniable that, despite the large numbers of specimens found in southern waters, the Hyperiidea have their origin not in Antarctic waters, but in temperate or tropical waters, particularly if Briggs (1966) is correct in his conclusion that 'the Subantarctic seas are now influenced by their contact with the Antarctic ice pack and its zone of floating ice; this state of affairs also prevailed during the ice ages (although the ice pack was somewhat larger), so temperatures in that area have probably remained steady.'

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[12]Comprehensive bibliographies will be found in Barnard (1932) and Hurley (1955). The better-known expedition reports have been omitted here in favor of recent papers and the more obscure sources of data, which are asterisked.

Nebaliopsis typica[1]

S. R. Geiger[2] and C. Brahm[2]

The Nebaliacea are a group of malacostracan crustaceans. With the exception of *Nebaliopsis typica,* all the species are benthic. They are small- to medium-sized animals (up to about 10 mm), except for *Nebaliopsis,* which attains a maximum length of 56 mm. Some of the benthic species are intertidal in occurrence; others are found on the continental shelf and slope. *Nebaliopsis typica,* the only bathypelagic nebaliacean, occurs in most of the major oceanic regions of the world. It has been collected from Antarctic and Subantarctic waters, where it has been taken sparingly in about 10 percent of the bathypelagic hauls. Near the Antarctic Convergence it was collected at less than 1000 m but was not taken in more than 100 Isaacs–Kidd samples at 585 m and above in Antarctic and Subantarctic regions.

The adaptations of *Nebaliopsis* for planktonic life have been discussed by Cannon (1931, 1946) and Linder (1943); the digestive system and its associated musculature have been studied by Rowett (1943). Studies of the feeding structures suggest that nebaliaceans filter fine particles from the water; they also feed upon eggs in the plankton. Developing eggs and larvae are apparently held in the basket formed by the eighth pair of thoracic appendages, which remain small and poorly differentiated in the female until the animal is about 35 mm long. At this time the appendages become enlarged and develop marginal setae. Development apparently occurs within the basket until the larvae are about 5 to 10 mm long, when they are released as free-swimming post-larvae (Mancoidstadien).

[1]Distribution shown on Plate 20

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Crinoidea

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INTRODUCTION

Crinoids are stalked and sessile or unstalked and free-swimming echinoderms with radiating movable arms which bear food grooves. The stalked forms are called sea lilies. Members of the order Comatulidae, the unstalked motile species, are known as feather stars. Although capable of motion, comatulids are essentially benthic organisms. All extant crinoids are included in the subclass Articulata. None of the other 3 subclasses of Crinoidea survived the Paleozoic. There are approximately 615 living species of which about 75 are stalked forms (Fell, 1966). Crinoids occur in all seas mostly in depths of less than 2000 m.

The sexes are separate. The gonads develop on specialized genital pinnules, usually along the proximal portion of the arm. In the Antarctic genus *Notocrinus* the gonads occupy a unique position in the axils between the pinnules and arms. Sexual dimorphism is found only in certain Antarctic genera. In *Thaumatometra, Phrixometra, Isometra,* and *Notocrinus,* for example, the female genital pinnules are expanded to form marsupia or brood chambers for the developing larvae. In *Notocrinus* the testes are about twice as large as the ovaries. In comatulids for which development is known, the yolky eggs develop into free-swimming vitellaria-type larvae, armless and oval in shape with horizontal bands of cilia. Metamorphosis of the swimming larva results in a stalked pentacrinus stage. The pentacrinoid is initially sessile, attached to the substrate, algae, or another organism, frequently an adult crinoid. A stem of ossicles later grows out from the aboral pole. The calyx and crown of arms are eventually cast off, and once again the organism becomes free-swimming. The development of stalked crinoids is completely unknown but is presumably similar to that of comatulids except that the stalked phase persists (Fell, 1966).

The percentage of viviparous comatulids is very high in the Antarctic. Over 50% brood their young in some manner, and the figure may be even higher since 3 species are known only from single male specimens (John, 1938, 1939). Viviparous forms account for only about 1% of the more than 600 species of comatulids from all other seas. Comatulids may be distributed by planktonic larvae, by the attachment of pentacrinoid stages to movable objects, or by movements of adults themselves. For a large percentage of viviparous forms in high southern latitudes, dispersal is accomplished only by the adults. An important exception to the viviparous habit of Antarctic comatulids is the subfamily Heliometrinae which includes the 3 most abundant species of Antarctic crinoids, *Promachocrinus kerguelensis, Anthometra adriani,* and *Florometra mawsoni.*

Certain taxa of southern crinoids are poorly defined, and others are variously placed by different authors. One of the major problems for workers in this group is the fact that many species are known from only a very few specimens. In addition, the material that is available is frequently in very bad condition because of the delicate nature of the animals.

In the accompanying maps we have attempted to plot all valid published records for the species included. Where reasonable doubt exists concerning the specific identification of a specimen, the record has been omitted.

The information reported here is a compilation of the literature to date; however, there have been no major taxonomic reports on southern crinoids since the papers of John (1937, 1938, 1939). There exist at present large collections of Antarctic and Subantarctic crinoids yet to be reported on. This material has been taken by ships of the U.S. Antarctic Research Program, the New Zealand Oceanographic Institute, various Russian expeditions, and others, mostly after 1958. It is expected that the published results of studies of these collections will add much to the distribution data summarized here.

COMPOSITION OF THE ANTARCTIC FAUNA

There are 23 families of extant crinoids. Five of these families are stalked forms. Only 2 of the 23 families, the Notocrinidae and Antedonidae, occur on the Antarctic continental shelf and the outlying shelves of the surrounding oceanic islands of South Georgia, Bouvet, Heard, Kerguelen, Prince Edward, the Crozets, and Gough. Twenty-two species have been found in this region. Excluding the seas adjacent to New Zealand and Australia, an additional 16 species in the families Bathycrinidae, Hyocrinidae, Thalassometridae, Pentametrocrinidae, and Antedonidae are known from abyssal depths south of 35°S. Four of these species are stalked crinoids in the families Bathycrinidae (1 species) and Hyocrinidae (3 species) (Map 1, Plate 21). Both these families have widespread genera outside the Antarctic and Subantarctic.

The remaining 12 abyssal species and their bathymetric ranges are as follows: (Thalassometridae) *Thalassometra bispinosa,* 2926 m; *T. setosa,* 1005 m to 4862 m; (Pentametrocrinidae) *Thaumatocrinus renovatus,* 2330 m to 3303 m; (Antedonidae) *Tonrometra remota,* 2312 m to 3859 m; *Trichometra remota,* 2926 m; *Thaumatometra abyssorum,* 2926 m; *Bathymetra carpenteri,* 1832 m to 4853 m; *Florometra spinulifera,* 1266 m to 3073 m; *Eometra antarctica,* 2725 m; *E. weddelli,* 3257 m; *Isometra lineata* and *I. angustipinna,* 1097 m (see Map 3, Plate 21).

The crinoids of the Antarctic continental shelf and outlying oceanic islands are all comatulids. One family, the Notocrinidae, is endemic to this region and is of special interest because of peculiar reproductive modifications. Map 2 (Plate 21) shows the distribution of the 2 known species.

All remaining Antarctic and outlying shelf crinoids belong to 10 genera in the family Antedonidae, a cosmopolitan group of about 48 genera found from intertidal to abyssal depths. Of the 20 species that occur in the region, 8 are represented in the maps presented here. Thirteen of the 20 species are known from 5 or fewer specimens. Localities and bathymetric ranges of the 12 species not shown on the maps are: *Hathrometra exigua,* Marion Island, 92 m to 257 m; *Phrixometra longipinna,* off Argentina, South Georgia and on the Antarctic shelf, 18 m to 2000 m; *P. nutrix,* Bransfield Strait and Burdwood Bank, 143 m to 206 m; *P. rayneri,* South Georgia, 177 m; *Florometra goughi,* Gough Island, 183 m; *Kempometra grisea,* near Clarence Island, 830 m; *Eumorphometra aurora,* off Enderby Land and South Georgia, 177 m to 220 m; *E. fraseri,* off South Shetland Islands, 425 m; *E. marri,* near Clarence Island, 550 m; *E. hirsuta,* near Prince Edward Island, 257 m; *E. concinna,* off Gaussberg, 380 m to 400 m; *Anisometra frigida,* off Mac. Robertson Land, 219 m.

At present crinoids are not well enough known from the Antarctic and Subantarctic to be good indicators of any zoogeographic provinces. Only 5 species are known from 10 or more occurrences. These are *Notocrinus virilis, Promachocrinus kerguelensis, Florometra mawsoni, Anthometra adriani,* and *Isometra vivipara.* All are circumpolar in distribution except *Isometra vivipara,* which is found only off the Antarctic Peninsula and the eastern Patagonian shelf. The presence of a high shelf circumpolar element of the crinoid fauna seems established, but any other patterns of distribution remain ill-defined at present.

There are two views of the origin of the Antarctic shelf crinoids. John (1938) believes that this fauna originated from the southern tip of South America. Marr (1963), in a detailed account of the distribution of Antarctic comatulids, takes the view that the high-Antarctic forms originated on the Antarctic continental shelf itself. He cites as evidence the circumpolar distribution of certain endemic species, notably *Promachocrinus kerguelensis.* The vast amount of crinoid material presently being studied should provide the basis for a firm judgment on the matter.

THE MAPS (PLATE 21)

MAP 1. Stalked crinoids and the comatulid *Promachocrinus kerguelensis* (Antedonidae, Heliometrinae).

Four species of stalked crinoids are known from the Antarctic and Subantarctic. They all occur in deep water and are rare in existing collections. *Bathycrinus australis* (Family Bathycrinidae), the most frequently encountered stalked form, is known from 6 records, 3 of these near the Crozet Islands. Its bathymetric range is 2514 m to 4636 m. As defined by Gislén (1938) the family Bathycrinidae consists of 28 species in 4 genera. The family is nearly cosmopolitan in distribution, mostly in depths exceeding 1000 m. However, 1 Caribbean species, *Democrinus rawsonii,* occurs from 70 m to 650 m.

The remaining 3 stalked species belong to the family Hyocrinidae. This family comprises 7 species in 5 genera (Gislén, 1939). The bathymetric range of the family is 480 m to 4973 m. The Antarctic species shown here have the following bathymetric ranges: *Ptilocrinus brucei,* 3245 m to 4973 m; *P. antarcticus* ca., 480 m; *Hyocrinus bethellianus,* 2926 m to 4636 m. A third species of *Ptilocrinus, P. pinnatus,* is known from 2860 m off British Columbia. The remaining 3 species of hyocrinids are known from low latitudes as follows: *Calamocrinus diomedae,* off the Galapagos Islands and Panama, 705 m to 1410 m; *Gephyrocrinus grimaldii,* equatorial mid-Atlantic, Madeira, and the Canary Islands, 1790 m to 3380 m; *Thalassocrinus pontifer,* from the Moluccas, 2270 m.

Promachocrinus kerguelensis is by far the most abundant crinoid in the Antarctic and on outlying Subantarctic shelves. This is true both in terms of the total number of specimens taken and the number of occurrences (Marr, 1963). The bathymetric range is 10 m to 1080 m. This species is also the largest comatulid in high southern latitudes and the only polybrachiate form there. There are usually 10 rays and 20 arms. The arms of large specimens are up to 250 mm long (John, 1938).

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MAP 2. Notocrinidae and *Anthometra adriani* and *Florometra mawsoni* (Antedonidae, Heliometrinae).

The family Notocrinidae is endemic to the Antarctic. There are only 2 known species both referable to the type genus. The bathymetric ranges are as follows: *Notocrinus virilis,* 163 m to 649 m; *N. mortenseni,* 194 m to 603 m.

In terms of number of occurrences the second and third most abundant species of crinoids of the Antarctic Shelf are *Anthometra adriani* and *Florometra mawsoni* (Marr, 1963). Both species are circumpolar in distribution. Their bathymetric ranges are: *A. adriani,* 189 m to 917 m; *F. mawsoni,* 100 m to 917 m.

MAP 3. Family Antedonidae, subfamily Isometrinae, and *Solanometra antarctica,* subfamily Heliometrinae.

The subfamily Isometrinae contains 6 known species all referable to the type genus. They are all Antarctic or Magellanic in distribution. Because of the limited southern distribution of this subfamily, we have included for completeness 3 species known from single records only. *Isometra flavescens* is known from 12 specimens taken at *Discovery* Station 160 near Shag Rocks, at 177 m (John, 1938). *I. lineata* and *I. angustipinna* are known only from single specimens from 1097 m off northern Argentina. *I. vivipara,* the species of *Isometra* occurring over the widest range of latitude, is known from the Antarctic Peninsula and the Patagonian Shelf, especially in the vicinity of the Falkland Islands, at depths of 79 m to 350 m. The bathymetric ranges of the remaining 2 species are as follows: *I. graminea,* 194 m to 567 m; *I. hordea,* 117 m to 550 m. *I. graminea* is the only member of this subfamily with a known circumpolar distribution.

Solanometra antarctica is known from 137 m to 649 m.

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*This important new monograph is included here for reference. It was unavailable when we prepared our text.

Holothuroidea

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INTRODUCTION

The Holothuroidea occur in all seas and at all depths from the intertidal zone to 10,700 m in the deepest trenches. The bathymetric range of holothurians far exceeds that of other groups of echinoderms, and in abyssal depths they are especially conspicuous in some areas, where they represent more than 90% of the total biomass on the sea floor. Like other echinoderms, holothurians generally cannot tolerate waters of low salinity, but there are some notable exceptions. In the North Sea *Thyonidium pellucidum* can tolerate salinities of 20‰, while in the Philippines *Protankyra similis* inhabits brackish waters in mangrove swamps. Holothurians are adapted to live in a wide variety of habitats, including rock, mud, and the fronds of seaweed. Although they are generally sedentary or burrowing, a few species are capable of swimming for varying lengths of time, and a few seem to spend most of their lives as bathypelagic swimmers.

The sexes are usually separate, but hermaphroditic species are known, of which 2 common examples in the region shown on the maps of Plate 22 are *Pentactella laevigata* and *Cladodactyla crocea.* Many holothurians pass through a pelagic larval stage known as an auricularia, but others lack this stage completely. At least 15 species of Antarctic holothurians have large yolky eggs and brood their young, thus omitting the pelagic larval stage. The young of brooding holothurians are usually held on the external surface of the mother, either dorsally or ventrally, or are carried in specially developed pouches or pockets. This brooding habit is a conspicuous feature of Antarctic holothurians.

In the southern oceans, dispersal of holothurians can be effected by drift of larvae (uncommon), by spreading across the sea floor, or by rafting after attaching to floating seaweed. This latter phenomenon has been observed by Mortensen (1925), and is believed to be an important dispersal mechanism for those species which live within the influences of the West Wind Drift.

Holothurians are poorly represented as fossils. The earliest unequivocal holothurian fossil is known from the Ordovician. So far no fossil holothurian remains have been reported from the Antarctic region, and all speculations on the origin and affinities of the Antarctic holothurian fauna must be based on the extant fauna.

Our knowledge of the holothurians of the Antarctic is regrettably scanty. Since the works of Perrier (1905), Vaney (1906, 1909, 1914), and Ekman (1925), little has been published on the Antarctic holothurians, and several major collections still remain unidentified. Therefore, very few definite statements can be made about the distribution and relationships of Antarctic and Subantarctic holothurians, and broad generalizations may prove to be unreliable. The work of Ekman (1925), the most recent major work on the Antarctic species, is regarded as definitive. Unless there is proof to the contrary, I have taken his conclusions regarding the synonymy of certain holothurians to be valid.

In the following discussion one order of holothurians, the Elasipodida, is omitted. This group is almost exclusively restricted to the deep sea (the continental slope and beyond), and it is now known that a high percentage of the species are essentially cosmopolitan in distribution. Forty-four species of elasipodids are known to occur in the Antarctic and Subantarctic; as the fauna becomes better known, it is likely that several of these species will prove to be synonyms of their northern congeners.

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COMPOSITION OF THE ANTARCTIC FAUNA

COASTAL ANTARCTICA. Of the 38 species at present known from the coastal waters of Antarctica (excluding elasipodids), 28 are dendrochirotaceans, and of these the majority are psolids or cucumariids. Only 1 phyllophorid *Havelockia secunda,* is known, and the familes Sclerodactylidae, Placothuriidae, Vaneyellidae, and Rhopalodinidae are not represented. The deep-sea aspidochirotid family Synallactidae is represented by 8 species, but no representatives of the Holothuriidae or Stichopodidae are known. One molpadid *(Molpadia antarctica)* and 1 apodid *(Taeniogyrus contortus)* are known. It is evident that the fauna is of a specialized type, for such groups as molpadids and apodids are well represented in Subantarctic regions, but evidently do not flourish in Antarctic waters. The facility with which psolids and cucumariids appear to be able to adopt either a brood-protecting or viviparous habit may account for their predominance in the fauna.

Twenty genera are known, of which only 1, *Paracucumis* (monotypic, with the species *P. antarcticus*), is endemic. *Ekmocucumis* is of essentially southern distribution; 4 of its 6 species are endemic to the Antarctic region; 1 species occurs at South Georgia and the Falkland Islands, and the other only at South Georgia. The remaining 18 genera are more or less widespread in world seas. Thus, in spite of its isolation and the low ambient temperatures, Antarctica has a holothurian fauna which, in terms of the genera, is not unique.

At the species level the percentage of endemic forms is somewhat higher, as the following list of Antarctic holothurian species which occur at depths less than 1000 m shows.

Total number of species		38
Endemic species		22 (58%)
South Georgia only	5	
South America, South Georgia, Kerguelen Islands	8	
Kerguelen Islands only	1	
New Zealand and South America	2	
Total non-endemic species		16 (42%)

On the basis of the above figures, it might be postulated that the Magellanic Province (Figure 10, p. 6) is an important portal of entry into the Antarctic for migrating holothurians. Those species common to South America and Antarctica must be able to tolerate a temperature range of −2°C to +10°C. No close relationship exists between Antarctica and the Kerguelen Island or New Zealand regions.

As the fauna comprises 20 genera and 38 species, the average number of species per genus is approximately 2. Compared with the echinoids (approximately 4 species per genus if the monotypic genera are neglected), the species diversity of Antarctic holothurians is not pronounced.

SOUTH GEORGIA. There are 15 species in the South Georgia area of which 1 is endemic. Five are shared only with coastal Antarctica, 3 with Subantarctic areas, and the remaining 6 species occur both in coastal waters of Antarctica and in Subantarctic regions. The fauna is therefore mixed, derived in part from the Antarctic fauna and in part from a Subantarctic 'pool' of widespread species.

ORIGIN OF THE ANTARCTIC FAUNA

The only Subantarctic region which resembles the Antarctic in terms of its holothurian fauna is southern South America. In view of the diverse nature of the fauna at the generic level, it would appear that the Antarctic holothurian fauna has been built up piecemeal by immigration of species which can tolerate the low temperatures. There is some evidence to indicate that the fauna of Antarctica, like that of southern South America, may have received most of its immigrants from the Indo-Pacific region, probably with the aid of the West Wind Drift. The New Zealand sector of the South Pacific Ocean does not appear to have acted as a direct contributor to the fauna of Antarctica, but it appears that some species may have reached South America (and then perhaps Antarctica) via the New Zealand region.

COMPOSITION OF THE SUBANTARCTIC FAUNA

The fauna of the Subantarctic includes several circumpolar species (see Plate 22). It is believed that this distribution has been achieved through the agency of the West Wind Drift, and it is interesting to note that most of these circumpolar species are known to inhabit the holdfasts and fronds of large brown seaweeds such as *Macrocystis,* which can form substantial rafts.

SOUTHERN SOUTH AMERICA. The fauna comprises 32 species, of which approximately 50% are endemic. The unusual composition of the fauna (somewhat reminiscent of that of Antarctica) indicates origin from the west and possibly also the south. There is no evidence to suggest that the fauna was derived from farther north. Circumpolar elements include *Pseudocnus laevigatus* and *Trachythyone parva.*

KERGUELEN ISLAND REGION. Eighteen species are known, of which 5 are endemic. The remaining 13 species are shared generally with areas to the west, notably South America (7 species). No close relationships to the fauna of Antarctica are shown despite the existence of the Kerguelen–Gaussberg Ridge running south from Kerguelen Island toward Antarctica. Those species which occur both in Antarctica and in the Kerguelen area (with the exception of *Abyssocucumis abyssorum,* a deep-sea species) are also common in southern South America, and it appears far more reasonable to assume that these generally shallow-water species reached the Kerguelen Island area from the west rather than from the south, with the aid of the West Wind Drift.

SOUTHEAST AUSTRALIA. The holothurian fauna of this region is clearly of a generalized Indo-Pacific type, with no conspicuous Subantarctic elements. The Tasmanian fauna is closely related to that of southeast Australia but includes *Psolidella adhaerens,* representing an essentially Subantarctic genus.

SOUTHERN NEW ZEALAND AND ISLANDS OF THE CAMPBELL PLATEAU. It has been shown (Pawson, 1968) that Macquarie Island has a holothurian fauna which is closely related to that of the Subantarctic islands belonging to New Zealand, which fauna in turn is derived from that of southern New Zealand. From the New Zealand islands and Macquarie Island, 12 species of holothurians are recorded. Of these, 5 are endemic, 5 occur also in southern New Zealand and 2, *Psolus antarcticus* and *Pseudocnus laevigatus,* are of circumpolar distribution; *P. antarcticus* also occurs in the Antarctic fauna.

ORIGIN OF THE SUBANTARCTIC FAUNA

It is apparent from the present distribution patterns of the fauna and its composition that the Subantarctic fauna was derived mostly from the north rather than from the Antarctic. The Antarctic region may have contributed a few elements (for example, species of *Ekmocucumis,* Map 4, Plate 22) but it is believed that this influence is slight. The Subantarctic fauna resembles the Antarctic fauna in that it lacks representatives of certain large groups of holothurians, and, again, temperature is probably the restricting factor.

The writer believes that, as with other echinoderm groups (Fell, 1962), the West Wind Drift has played an important part in distributing the southern holothurians. The Subantarctic apodus holothurians are distributed in a way which leads to the suggestion that the group entered the Subantarctic region via Australasia. This same portal of entry is indicated for the other Subantarctic forms, particularly the dendrochirotids.

THE MAPS (PLATE 22)

MAP 1: Genera *Pseudocnus, Psolidiella,* and *Pseudopsolus*

Pseudocnus comprises approximately 20 species, is widespread in world seas, and is generally confined to relatively shallow water. In the southern oceans 5 species occur. *P. cornutus* is known from 1 record near the Straits of Magellan. Each of the 3 forms of *P. dubiosus* has its own distribution range. The *leoninus* form occurs in southern South America and the Falkland Islands; the *dubiosus* form is found along the eastern and western shores of South America; and the *jaegeri* form is limited to South Africa. The *leoninus* form is common; its bathymetric range is 0 m to 108 m, but most specimens have been collected at depths less than 20 m. *P. perrieri* occurs in 0 m to 197 m around southern South America and South Georgia. *P. laevigatus* has a depth range of 0 m to 990 m, but most specimens have been collected at depths of less than 100 m. This species is known from the Subantarctic islands between 30°E and 180°E; Bell (1908) reported specimens from McMurdo Sound, Antarctica, but the record is doubtful, and it is not known that this species actually occurs in the 'high' Antarctic. *P. leoninoides* is restricted to the Campbell Plateau south of New Zealand at depths of 0 m to 112 m.

The southern complex of species of the genus *Pseudocnus* appear to be closely interrelated, differences between them being slight. The distribution of the species probably reflects their living habits, for many have been found living on the fronds of brown seaweeds.

Psolidiella comprises only 3 species and is restricted to the southern oceans. From the map it can be seen that the genus is circumpolar in distribution. Since both *P. adhaerens* and *P. nigra* are known to live on a rocky substrate, and since they lack a pelagic larval stage, it is not known how the genus has achieved such a wide distribution.

Pseudopsolus macquariensis is a monotypic genus restricted to the intertidal zone of Macquarie Island. This genus closely resembles *Psolidiella* and *Cucumaria* in features of anatomy, and it appears likely that these 3 genera arose from some common source, perhaps in the Subantarctic region.

MAP 2: Genera *Cladodactyla, Cucumaria,* and *Hemioedema*

Cladodactyla has 2 species, *C. senegalensis* from West Africa and *C. crocea* from the southern oceans. *C. crocea* is a widespread brood-protect-

ing species, most common at depths of less than 20 m, but with a bathymetric range of 0 m to 3875 m. Many specimens have been found attached to the fronds and holdfasts of seaweeds. The species probably was dispersed by rafting or spreading across the sea floor.

Hemioedema is another small genus with 3 species, 2 of which occur in northwest Africa; the third, *H. spectabilis,* is known from the coast of Argentina and the Straits of Magellan, to depths of 60 m.

Cucumaria, as restricted by Panning (1949), is essentially cosmopolitan with about 20 species of which 7 occur in the southern oceans. *C. periprocta, C. perfida,* and *C. conspicua* are known from 1 record; all were described by Vaney (1909) from Scotia Bay in the South Orkney Islands. All of the remaining 4 species have been collected from depths of less than 400 m, and 1, *C. georgiana,* is widespread. There is some evidence to suggest that these *Cucumaria* species are closely related.

MAP 3: Families Ypsilothuriidae (excluding *Ekmocucumis,* which is on Map 4), Psolidae (excluding *Psolus* which is on Map 5), and the genus *Pentamera.*

The Ypsilothuriidae comprises 6 genera, all of which occur in the southern oceans. *Ekmocucumis* (Map 4) is restricted to the southern oceans, while the other genera are more or less widespread in world seas. It is probable that the deeper water members of this family (for example, *Echinocucumis hispida* at 50 m to 1400 m; *Ypsilothuria bitentaculata* at 250 m to 4000 m) occur elsewhere in the southern oceans.

Of the 15 species in the genus *Pentamera,* only 1, *P. chiloensis,* occurs in the southern oceans, where it is restricted to southern Chile at depths of 0 m to 140 m. This species is notable in that it is one of the very few phyllophorid holothurians to occur in higher southern latitudes.

Four of the 5 genera in the family Psolidae occur in the southern oceans. These are *Psolus* (Map 5), *Psolidium, Neopsolidium,* and *Theelia (Stolinus?). Psolidium* has 8 of its 25 species here, though 4 are known from only 1 record. Two, *P. incertum* (bathymetric range 100 m to 567 m) and *P. disciformis* (440 m to 448 m), are restricted to the Subantarctic. *P. gaini* (55 m to 380 m), is apparently circum-Antarctic and also occurs off South Georgia. *P. dorsipes* (10 m to 150 m) occurs in southern Chile and the Falkland Islands. Deichmann (1941) recorded this latter species from the Gulf of California; perhaps a richer material may show that this northern form represents a different species.

Neopsolidium convergens is common in southern Chile and the Falkland Islands at 0 m to 15 m. *Theelia porifera (Stolinus cataphractus?)* is known from Kerguelen Island at 37 m to 119 m; the same species or a near relative has been reported from western Australia.

As the greatest variety of the psolids are found in the vicinity of southern South America (Maps 3 and 5), it appears probable that this region serves as the portal of entry into Antarctica for psolids. Elsewhere in the southern oceans the psolid fauna is very sparse, nowhere as well developed as it is in southern South Africa.

MAP 4: Genus *Ekmocucumis* and southern representatives of the genus *Trachythyone*

Ekmocucumis comprises 6 species and is restricted to the Antarctic and Subantarctic regions. None have been collected from depths in excess of 400 m. It is probable that most of the high Antarctic representatives of the genus are circum-Antarctic in distribution. The present known distribution of the genus leads to the inference that the genus arose in the Antarctic seas and has dispersed northward to the Falkland Islands and South Georgia. This distribution pattern is unusual, for while most distribution patterns of holothurians in this region point to northern origin and southward dispersal, the present case suggests the opposite.

Trachythyone is essentially cosmopolitan, with 15 species, of which 5 occur in the area being considered. The most notable of these is *T. parva* (2 m to 385 m), which is widespread in the Subantarctic and Antarctic regions. *T. macphersonae* and *T. squamata* are both closely related to *T. parva.*

MAP 5: Southern representatives of the genus *Psolus.*

Psolus is cosmopolitan, comprising about 50 species, of which 15 occur in the southern oceans. Two species, *P. squamatus* and *P. operculatus,* are not restricted in distribution, the former also occurring in the eastern Pacific, the latter in the Atlantic Ocean. Seven are known from only 1 record. The remaining 6 species have varying patterns of distribution. *P. antarcticus,* formerly believed to be restricted to the Antarctic Peninsula–South America region has been recently discovered (Pawson, 1968) off Macquarie Island.

The methods by which psolid holothurians achieve their distribution are not clear. They are sedentary for the greater part of their lives; they lack a pelagic larval stage, and generally attach to a hard substrate. It remains a mystery how such a species as *P. antarcticus,* which broods its young, has achieved such a wide distribution.

MAP 6: Southern distribution of the apodous holothurian genera *Taeniogyrus, Chiridota,* and *Trochodota*

Taeniogyrus, with 8 species, is mostly Indo-Pacific, with species in Indonesia, South Africa, Hawaii, and eastern and western Australia. Two species occur in the area under consideration. *T. australianus* is restricted to the vicinity of Sydney, Australia. *T. contortus,* on the other hand, is widely distributed at 1 m to 570 m. Clearly, *T. contortus* is an immigrant into the southern fauna.

Chiridota is almost cosmopolitan, with 30 species, most of which have a limited bathymetric and geographic range. There are 6 southern species, none of which is widely distributed, although *C. gigas* occurs in eastern Australia and New Zealand.

Trochodota comprises 10 species, of which 3 occur off Japan, 1 is found in the Mediterranean, and 1 in the Torres Strait. The remaining 5 are of southern distribution, *T. allani* and *T. roebucki* in southeast Australia, *T. dunedinensis* and *T. dendyi* in New Zealand and the Campbell Plateau, and *T. purpurea* in southern South America and South Georgia.

The distribution patterns of the 3 genera discussed above are similar in that all genera are poorly represented in the South America–Antarctic Peninsula area, and all appear to have their origin in the Indo-Pacific region on the evidence of present day distribution of the species. How the few Subantarctic representatives of these genera reached the South American area remains a mystery. It may be noted here that in South America representatives of these genera occur mainly in the southern areas. Exceptions are *Chiridota rotifera* and *C. fernandensis;* the former species ranges from Florida to Brazil, and the latter is recorded from Juan Fernandez Island off the coast of Chile. Present day distribution patterns suggest that the Magellanic apodids were derived not from the north but from the west, perhaps from Australasia, through the agency of the West Wind Drift.

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Echinoidea

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INTRODUCTION

The Echinoidea are a cosmopolitan group of almost exclusively benthic echinoderms that live on a soft or hard substrate in all seas from low-tide level to depths in excess of 7000 m. Like most other echinoderms, echinoids generally cannot tolerate waters of low salinity, although one Subantarctic species, *Abatus cordatus* (Verrill), has been found in brackish water at Kerguelen Island (Mortensen, 1951). Echinoids usually possess a pelagic larval stage known as an echinopluteus, but in Subantarctic and Antarctic regions many species lack the echinopluteus stage and develop directly, thus spending no part of their lives adrift in the plankton. The sexes are separate and are indistinguishable except in those species which have large eggs (in which case the genital pores of the mature female are larger than those of the mature male), or which brood their young. The

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brooding habit is an especially notable feature of the Antarctic echinoderms in general and is prevalent among the echinoids. Some cidaroids brood their young on the peristome or in the vicinity of the periproct, while in spatangoids the eggs develop in the sunken dorsal petals of the female.

Because most echinoids are sluggish and slow-moving, the capacity for dispersal of those Antarctic species which lack a pelagic larval stage is somewhat limited. They can either spread across the sea floor or drift in the epiplankton attached to, or entangled in, masses of seaweed. This latter phenomenon has been observed by the author in the case of echinoids, and Mortensen (1925) has observed holothurians and asteroids being rafted in this way.

The echinoids have a long history. Fossils occur in early Paleozoic strata, and today over 700 species are extant, those of the tropical and subtropical areas being most diverse. Fossil echinoids are reported from a few Subantarctic localities. From the Antarctic continent proper, perhaps the most important collection of fossil echinoids known is that described by Lambert (1910) from Snow Hill and Seymour Islands, close to the Antarctic Peninsula.

Echinoids are among the best known groups of Antarctic and Subantarctic invertebrates. The first Antarctic echinoids known, *Abatus cavernosus* and *Tripylus excavatus,* were described by Philippi (1845). Our present knowledge of the southern representatives of the group is based largely on the research of Mortensen (1909, 1910, 1925, 1928, 1936), Koehler (1908) and Bernasconi (1953). The echinoids collected by most major Antarctic expeditions have now been described, but, in spite of the amount of work that has been done on this group, some of the more conspicuous taxa in the Antarctic fauna have not been clearly defined, and in the past there has been some confusion of names.

Where a locality is plotted for a species on the accompanying maps, I have tried to ensure that the species from the locality are correctly identified. Of course, it has not been possible to verify each identification, but doubtful records have been ignored, unless corrected by later authors. The conclusions drawn here on the basis of the known distribution of Antarctic and Subantarctic echinoids must be regarded as tentative. The immense collections now being amassed by research vessels of the U.S. Antarctic Research Program and others have yet to be reported on, and undoubtedly such studies will modify generalizations.

THE ANTARCTIC ECHINOID FAUNA

Only 6 of the more than 50 known families of echinoids are represented in the coastal waters of the Antarctic. Perhaps the most striking feature of this fauna is the absence of the superorders Diadematacea and Gnathostomata, and apart from the single genus *Sterechinus,* the absence of the vast assemblage of regular non-cidaroid echinoids comprising the superorder Echinacea. Another notable feature is the diversity of the cidaroid subfamily Ctenocidarinae and the spatangoid family Schizasteridae in Antarctic waters.

The small amount of data afforded by fossils (Lambert, 1910) indicate that several elements which existed in Antarctica in lower Tertiary and Cretaceous times have since vanished. These include the subfamily Cidarinae (represented in the upper Cretaceous of Snow Hill Island by *Cyathocidaris*), the family Cassidulidae (*Cassidulus* found in the Eocene of Snow Hill Island), and the family Holasteridae (*Holaster* in Upper Cretaceous at Snow Hill Island).

The suborder Hemiasterina, presently cosmopolitan and represented in the Antarctic by the genera *Abatus, Amphipneustes,* and *Tripylus,* was represented in the Upper Cretaceous of Snow Hill Island by *Hemiaster* and in the Eocene by *Schizaster*. The latter genus is closely related to the extant Antarctic representatives of the suborder.

Fifteen genera of echinoids have been collected in the region south of the Antarctic Convergence (Antarctic Region). Of these, 4 are restricted to the area, 6 are restricted to the Antarctic–Subantarctic region in the broad sense, and 5 occur in the Antarctic and elsewhere in the world. Of the 4 endemic genera, 3, *Rhynchocidaris, Homalocidaris,* and *Delopatagus,* are monotypic while the fourth, *Notocidaris,* has 6 species. The 5 genera which are known to occur elsewhere in the world are almost all bathyal forms. *Urechinus, Plexechinus,* and *Pourtalesia* are essentially cosmopolitan. *Aporocidaris* has been taken from the vicinity of Kerguelen Island and from two areas of the Pacific Ocean, and *Pilematechinus* is known only from Antarctica and Panama.

As is the case in several other groups of Antarctic invertebrates,the proportion of endemic genera of echinoids is quite small (25%) but it is notable that 66% of the genera found in the coastal regions of Antarctica are restricted to the Antarctic–Subantarctic region.

In the case of echinoids, there is as yet no positive evidence of equatorial submergence. *Aporocidaris,* with 2 species found elsewhere (Galapagos Islands and the Alaska–Kamchatka region) in depths greater than 1000 m, is represented around Antarctica by 2 species, 1 of which occurs in depths less than 1000 m, the other in depths greater than 2000 m. The 3 Antarctic–Subantarctic species of the genus *Pourtalesia* have bathymetric ranges which do not differ significantly from those of other species found in warmer northern waters. Other widespread genera are similar in this respect to the 2 cited as examples here. There is also no indication of bipolar distribution among the echinoids.

The echinoid fauna of coastal Antarctica comprises 44 species, of which 34 (77%) are endemic. Twenty-seven of the 34 endemic species are apparently restricted to depths of less than 1000 m. The bulk of the endemic species are representatives of the genera *Sterechinus* (3 species), *Abatus* (7 species), *Amphipneustes* (7 species), *Ctenocidaris* (5 species), and *Notocidaris* (6 species).

Since 15 genera and 44 species are known from coastal waters of the Antarctic Region, the average number of species per genus is 3. By comparison, the Australian echinoid fauna averages approximately 2 species to each genus. The figure for Antarctica would be 4 species per genus if the monotypic genera were neglected. Thus, species diversity, often regarded as a character of Antarctic invertebrate faunas in general, is certainly a conspicuous feature of the Antarctic echinoid fauna.

South Georgia, which is 'Antarctic' in the sense that it is south of the Antarctic Convergence, has a fauna of 10 species, of which 2 are endemic to South Georgia, 4 are found only around South Georgia and Antarctica, and 4 occur around South Georgia, Antarctica, and southern South America. Clearly, South Georgia is essentially Antarctic in the character of its echinoid fauna.

THE SUBANTARCTIC ECHINOID FAUNA

The echinoid fauna of the Subantarctic region presents many zoogeographical problems. It includes (1) some taxa which are essentially circumpolar in distribution (for example, *Pseudechinus,* Map 3, Plate 23), but derived from northern ancestors, (2) some taxa of presumably northern origin which have spread southwards, but which have a restricted distribution (for example, *Loxechinus* in Chile, *Evechinus* in New Zealand), and (3) taxa which have apparently arisen in the Antarctic region and spread to the north (for example, some Ctenocidarinae, Map 1, Plate 23). Thus, in essence, the faunas of Subantarctic landmasses may include endemic elements and elements derived from all three sources referred to above. The character of the fauna of each southern landmass is determined by its proximity to other landmasses and by the nature of the surrounding sea floor.

One of the most effective dispersal mechanisms available to Subantarctic echinoids is the West Wind Drift. The role of this phenomenon in the dispersal of echinoderms has been discussed by Mortensen (1925), Fell (1962a) and Pawson (1968). Of the 9 species known from the Kerguelen, Prince Edward, and Crozet Islands, 5 are endemic, 2 occur also in the Magellanic Province, and 2 occur around the Antarctic continent. The 2 Magellanic elements are *Pseudechinus magellanicus* and *Sterechinus diadema*. The Antarctic species, *Aporocidaris antarctica* and *Sterechinus neumayeri,* may have reached the island areas by migration across the Kerguelen–Gaussberg Ridge.

The fauna of southern South America is apparently derived from three main sources. The genera *Arbacia, Tetrapygus,* and *Loxechinus* were probably derived from farther north. The species of *Sterechinus, Abatus,* and *Tripylus* are probably derivatives of their Antarctic congeners. *Pseudechinus* and perhaps also *Dermechinus* species are circumpolar Subantarctic types. The fauna of the Falkland Islands is virtually identical to that of southern South America.

Only 1 echinoid, *Pseudechinus novaezealandiae,* is known from Macquarie Island. This species is also common on the Campbell Plateau and around the southern part of New Zealand. This area marks the southern limit of distribution of the genera *Apatopygus* (2 species, 1 in the New Zealand area and 1 in Australia), *Goniocidaris,* and *Spatangus.*

THE ECHINOID FAUNA OF SOUTHEASTERN AUSTRALIA

This area, just north of the Subantarctic region, is characterized by the presence of southern outliers of genera which are more diversified in warmer waters, but, among the echinoids, 2 genera occur there which are also found in Subantarctic areas. They are *Paramaretia* and *Pseudechinus;* the former genus is represented by 1 extant Australian species, the latter by 2.

PATTERNS OF DISTRIBUTION IN THE ANTARCTIC AND SUBANTARCTIC

Examination of the accompanying maps will show that some similar patterns of distribution are exhibited by different genera of echinoids. There appear to be four conspicuous patterns, as follows:

(1) Circumpolar or partly circumpolar distribution in the Subantarctic, but with no representatives in the Antarctic Region (except occasionally South Georgia). An excellent example of this pattern is *Pseudechinus,* which displays a typical 'West Wind Drift' distribution.

(2) Distribution circumpolar in the Antarctic only. Only 4 genera have this type of distribution, and 3 of these are mono-

typic. The environment of the Antarctic continental shelf appears to be of such a uniform nature that very often species are found to occur all around the continent.

(3) Distribution circumpolar in the Antarctic, but also with representatives in the Magellanic Province in the broad sense and perhaps also in the vicinity of Kerguelen Island. Such a distribution is found in the genera *Abatus, Sterechinus, Ctenocidaris,* and *Tripylus.*

(4) Genera restricted to coastal waters of a southern landmass and unknown elsewhere. Among the southern genera, *Loxechinus* is restricted to Chile, *Tripylaster* to the Magellanic Province in the broad sense (and at South Georgia), *Austrocidaris* to the Magellanic Province, *Evechinus* and *Ogmocidaris* to New Zealand.

RELATIONSHIPS AND ORIGIN OF THE ANTARCTIC FAUNA

The fossil record of the Antarctic echinoderms is too incomplete to support a discussion of the origin of the fauna. However, the composition and distribution of the present-day fauna permit some inferences to be made; these may of necessity be modified in the light of further fossil evidence.

The subfamily Ctenocidarina is virtually restricted to the Subantarctic–Antarctic region. Mortensen (1928) believed that the subfamily is an ancient one which arose in Antarctic seas and has remained there (apart from the 2 deep-sea Pacific species of *Aporocidaris*). What is believed to be a representative of the genus *Austrocidaris* is reported from the Eocene of Patagonia (Mortensen, 1928), but no other fossils of an earlier age are known.

The present-day distribution of the other genera in the Antarctic fauna also leads to the inference that these genera arose in the Antarctic, or at least in the Subantarctic, for 66% of the Antarctic genera are restricted to this broad area. There is no evidence to show that echinoid species have migrated from elsewhere into Antarctica; it seems more likely that Antarctica has been the source of several species (for example, species of *Abatus, Sterechinus,* and *Ctenocidaris*) which now live around Subantarctic landmasses.

THE MAPS (PLATE 23)

MAP 1: Southern representatives of the order Cidaroida, subfamily Ctenocidarinae

Twenty-one species are known in this subfamily, scattered through 7 genera. *Notocidaris* (6 species) and *Ctenocidaris* (6 species) are the largest of these genera. Two species of *Aporocidaris* are known from elsewhere in the Pacific Ocean — *A. milleri* from the vicinity of the Galapagos Islands and *A. fragilis* from near Alaska and Kamchatka. The remainder are more or less restricted to Antarctic and Subantarctic seas. Thirteen of the species are 'high' Antarctic forms, which have been recorded only south of latitude 60°S. Two, *Austrocidaris canaliculata* and *A. spinulosa,* are known only from the southern part of South America. One, *Ogmocidaris benhami,* is restricted to the New Zealand region. One, *Ctenocidaris nutrix,* is restricted to the vicinity of Kerguelen and Crozet Islands. *Ctenocidaris speciosa* is circum-Antarctic in high latitudes and is also common at South Georgia; *Aporocidaris antarctica* occurs near the Antarctic coast south of Kerguelen Island and is also known from the Crozet Islands. Seventeen of the 21 species have not been found in depths greater than 1000 m. The 2 northern species of *Aporocidaris* occur in depths in excess of 2800 m.

On present evidence, some species in the family appear to be widely distributed, while others are of a more restricted distribution. It is probable that all of the Antarctic continental shelf species are circumpolar.

MAP 2: Genus *Sterechinus*

Sterechinus, one of the more conspicuous echinoid genera in the Antarctic fauna, is composed of 5 species. *S. agassizi* is restricted to the southern part of South America, where it is known from latitudes higher than 35°S. It also occurs at Shag Rocks and South Georgia. *S. diadema* is known only from the vicinity of the Kerguelen Islands as are several other species of Subantarctic echinoids. *S. neumayeri* is circum-Antarctic, but occurs at the South Orkney Islands and South Georgia, while *S. antarcticus* and *S. dentifer* are strictly continental Antarctic species. The distribution of *Sterechinus* affords an excellent illustration of the nature of the fauna of South Georgia. *S. dentifer* is known from two localities in deep water (1266 m to 1566 m), and is probably widespread. The other species are restricted to depths of less than 700 m.

MAP 3: Genus *Pseudechinus*

Pseudechinus is a genus with a circumpolar distribution in essentially Subantarctic areas. Thirteen species are known, but only 9 are plotted here. Of the remaining 4, *P. woodsi* is a fossil species known from the Oligocene and lower Miocene of the River Murray and Aldinga Cliffs in southern Australia, and 3 species occur in latitudes lower than 35°S; *P. grossularia* and *P. variegatus* are known from the northern extremity of New Zealand, while *P. hesperus* has been recorded from Rottnest Island off Fremantle, Western Australia. *P. magellanicus* is the dominant echinoid in southern Chile, while *P. novaezealandiae* is particularly common around southern New Zealand and on the Campbell Plateau. Seven of the 12 extant species are apparently restricted to depths of less than 200 m. *P. novaezealandiae* occurs down to 306 m, *P. magellanicus* to 820 m, *P. flemingi* to 594 m, and *P. huttoni* to 540 m. None of the species has a circumpolar distribution, but all are very closely related and obviously derived from a common source.

The scanty fossil evidence (Fell, 1962a), coupled with our knowledge of the present-day distribution of the genus, indicates that *Pseudechinus* arose in Australasia, and has achieved its distribution through the agency of the West Wind Drift (Fell, 1962b; Pawson, 1968). Since the species have a planktonic larval stage, and since some species often live on the fronds of brown algae (Pawson, 1966), dispersal is facilitated by easterly drift of planktonic larvae and rafting adults.

It is interesting to note that the genus has not yet been found in the vicinity of South Georgia; possibly the generally lower temperature of the water about South Georgia has prevented colonization by *Pseudechinus.*

MAP 4: Genus *Abatus*

Abatus is essentially restricted to the Antarctic and Subantarctic, although 2 species, *A. philippi* and *A. cavernosus,* extend as far north as about 36°S, off Argentina. *A. cordatus* is known only from the vicinity of Kerguelen and Heard Islands; *A. bidens* is known from 2 records at South Georgia. The remaining 8 species of the genus are widely distributed, as can be seen on Map 4. The genus is unknown elsewhere in the world. No species have been taken from depths in excess of 700 m; in this respect, the vagility of the species is limited. In view of the present known distribution of the species, it seems probable that the genus arose in the Antarctic region, from which it has dispersed northward to South America and to Kerguelen Island.

MAP 5: Genus *Amphipneustes*

Amphipneustes, like *Abatus,* is conspicuous in the Antarctic echinoderm fauna, but *Amphipneustes* is more strictly Antarctic in character than is *Abatus. Amphipneustes koehleri* is known only from the vicinity of South Georgia, while all of the other species are apparently restricted to the coast of the Antarctic continent. The most widespread species appears to be *A. lorioli,* but further sampling should show that all of the continental species are more or less circum-Antarctic in distribution. The bathymetric range of *Amphipneustes* is 0 m to 645 m, but most species live in depths in excess of 100 m. The genus probably arose in the Antarctic region and, unlike *Abatus,* has not been able to adapt to warmer waters near more northern landmasses.

MAP 6: Spatangid genera *Paramaretia* and *Spatangus* and southern representatives of the family Schizasteridae (excluding *Abatus* and *Amphipneustes*)

Tripylus is the only genus shown here which extends into the 'high' Antarctic region where 2 species have been recorded from the Antarctic Peninsula area. The other species and genera are Subantarctic or warm temperate in distribution in the southern oceans, although the monotypic genus *Tripylaster* is known to occur at South Georgia. *Tripylus* is an exclusively southern genus, and *Tripylaster* occurs only in the area encompassed by Map 6. However, *Brisaster* has an almost bipolar distribution, with 4 southern species as shown here, and 4 northern species. These latter are *B. fragilis* from Norway, Iceland, and the east coast of North America (as far south as Florida) at 40 m to 1300 m; *B. townsendi* and *B. latifrons* from the west coast of North America (Alaska to the Gulf of Panama) 35 m to 1900 m; *B. owstoni* from the Sagami Sea and the Gulf of Tokyo, at 10 m to 530 m. In the southern oceans the species shown have the following bathymetric ranges: *Brisaster* sp. at 162 m to 821 m, *B. kerguelenensis* at 132 m to 216 m, and *B. moseleyi* at 72 m to 720 m. Further sampling may show that this suggested bipolarity is more apparent than real.

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Asteroidea

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INTRODUCTION

The Asteroidea are benthic echinoderms occurring in all seas (including waters of the Baltic which have salinites as low as 17‰), and from about mean sea level to depths of 7614 m. The deepest record in Antarctic waters is 5760 m for the species *Hymenaster densus* and *Freyella giardi*. A free larval stage is characteristic of many temperate and tropical species of asteroids, but direct development with brooding females is characteristic of Antarctic asteroids. Except for brooding females, the sexes are externally indistinguishable.

DISTRIBUTION IN THE ANTARCTIC AND SUBANTARCTIC REGIONS

There appear to be three conspicuous distribution patterns:

(1) Circumpolar, chiefly around Antarctica, but usually including South Georgia

(2) Circumpolar in the Antarctic generally, including the Magellanic region

(3) Circumpolar or incompletely circumpolar in the Subantarctic region

The circumpolarity of the first two distribution patterns may be attributed to shallow-water connections throughout the regions involved, permitting the animals to travel along the sea floor from one locality to another. The circumpolarity of the third pattern, however, is thought to be brought about by epiplanktonic dispersal on brown seaweed under the influence of West Wind Drift. Within the past few years collections have yielded sufficient specimens of asteroids to make possible the analysis of distribution patterns by several methods. That which gives the clearest picture is the one utilized in Figure 1, which illustrates 10 genera. The method of plotting is explained in the caption. The circular histogram for each genus tends to form a more or less attenuated triangle in which the base-line (maximum speciation) occurs at the western end with the apex (minimum speciation) at the eastern end. It may be inferred that for each of these genera the original source lies at the western end of its range and that the more easterly representatives are derived from the western stock. We are thus presented with a simple clockwise pattern in which generic stocks tend to move from west to east. The West Wind Drift supplies the only acceptable distributing mechanism (see also Fell, 1962b).

It seems probable that thermal tolerance also influences the distribution of Antarctic asteroids. Clark (1963) reports that only 13 of the 37 species from the Ross Sea extend into Subantarctic or south temperate zones.

THE MAPS (PLATES 24 AND 25)

Excluding Australasia, which is considered part of the Indo-Pacific ('Indo-West-Pacific,' Fell, 1962b), the known asteroid fauna south of 35°S comprises 87 genera and 232 species. Of these, 42 genera and 166 species have been mapped. All genera found south of the Antarctic Convergence have been mapped, except for those with a total distribution of fewer than 4 localities and those of universal distribution usually found at depths of over 1000 m. A few examples of entirely Subantarctic circumpolar distributions have also been plotted. The nomenclature follows W. K. Fisher (1940) and H. E. S. Clark (1963). The genera have been divided according to distribution pattern.

Maps 1 and 2 show shallow-water genera with an essentially Subantarctic circumpolar range and genera which are essentially circumpolar in the coastal waters of Antarctica. A few chiefly Subantarctic circumpolar genera have 1 or 2 records in the Antarctic. It is inferred that shallow-water, circumpolar Subantarctic genera have been distributed by the West Wind Drift. Shallow-water, circumpolar Antarctic genera, on the other hand, can have achieved circumpolarity by following the depressed continental shelf of Antarctica. Deepwater genera may similarly have traversed the deep sea floor.

Map 3 shows additional genera with circumpolar distribution chiefly on the Antarctic continent but extending also to South Georgia. Three of the genera are restricted to this area, and 3 more also extend to the Subantarctic islands.

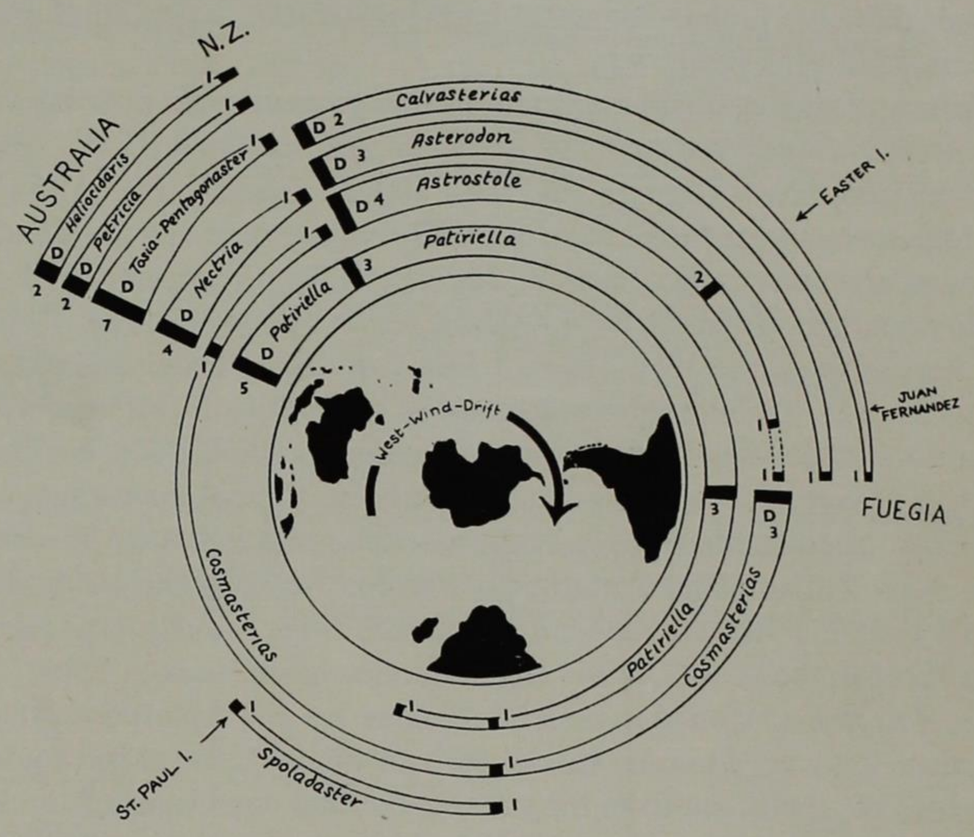


Fig. 1. Typical distribution patterns for benthal echinoderms with a southern circumpolar range. The length of radial co-ordinates for each genus is proportional to the number of species at the longitude indicated, and the number of species at each plot is indicated. Inferred donor areas are marked *D*. Australia is inferred to have been a major point of entry of Indo-Pacific elements into the Southern Hemisphere, by way of Indonesian landbridges; thereafter generic stocks are viewed as differentiating along clockwise circumpolar lines of movement, under the West Wind Drift. *Astrostole* is regarded as giving rise to *Meyenaster* on the Chilean coast, and *Pentagonaster* is grouped with *Tosia* as a single stock for the purpose of the survey (from Fell, 1962b).

Map 4 shows genera which enter the Antarctic and have Magellanic species but do not achieve circumpolar range in the Subantarctic region. These genera have presumably utilized the Scotia Ridge as a means of passage between Antarctica and South America and have not been dispersed by the West Wind Drift.

Maps 5, 6, and 7 show genera distributed which have a circumpolar distribution in the Antarctic and Subantarctic.

While most of the genera on Maps 3 and 4 are found only in the Antarctic and Subantarctic, most of the genera on Maps 5 and 6 are found elsewhere.

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Ophiuroidea

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INTRODUCTION

The Ophiuroidea, or brittle stars, comprise some 1900 extant species, referable to 230 genera. They occur in all oceans, and from the intertidal zone to approximately 8000 m. Many ophiuroids pass through a pelagic larval stage, but as Mortensen (1936) points out, echinoderms of the Antarctic region in particular tend to undergo direct development; at least 19% of Antarctic species are known to be viviparous. Of the 13% known to be oviparous, several have large yolky eggs, suggesting direct development of these also. Mortensen (1936) reports that among Antarctic ophiuroids there is a high incidence of hermaphroditism, a condition generally correlated with viviparity.

Temperature and depth are important factors governing the distribution of ophiuroids. A study was made of Antarctic species found off the Antarctic Peninsula, South Georgia, and the Falkland Islands (Fell, 1961). Some of the species were found to be markedly eurythermal and to tolerate the entire temperature range. Such species could tolerate the temperatures of the Subantarctic islands of New Zealand yet do not occur there. These islands have instead the very different fauna of Indo-Pacific derivation typical of the New Zealand submarine plateau as a whole. From these and other data it is concluded that the range of many ophiuroids is controlled by depth, and that shallow-water routes have been of great importance in the dispersal of echinoderms. No shallow-water route is known to exist between New Zealand and Antarctica, whereas between the Antarctic Peninsula and the Falkland Islands a submerged ridge occurs in the form of an arc through the South Orkney and South Sandwich Islands. Thus, for example, *Astrotoma* is found in both South America and Antarctica probably because it is a eurythermal species with an available migration route. The absence of *Astrotoma* from the suitable thermal conditions of southern New Zealand shelf waters is presumably due to the fact that no shallow-water route existed at any time between Antarctica and New Zealand.

Ophiuroids are one of the most common groups in the Antarctic marine fauna. One-third of the biomass of the Ross Sea benthos may be composed of brittle stars in some localities (Fell, 1961). On the basis of photographs taken between 75 m and 350 m, local maximum concentrations of ophiuroids are estimated to be 10^7 individuals per square kilometer. It should be recognized that some species are present in great numbers, while others are known from only a few specimens.

THE MAPS (PLATES 26 AND 27)

Most of the species of ophiuroids found south of 35°S are recorded on the maps of Plates 26 and 27. All endemic genera and their species are indicated, as well as the endemic species of cosmopolitan genera. In addition, Map 8 includes some deepwater cosmopolitan species. The species at the northern peripheries of the maps are plotted only if their range does not extend north of 35°S.

The maps attempt to show the complete ophiuroid fauna of the Antarctic and the Subantarctic islands. In the case of Australia, New Zealand, and South Africa, only those genera with Antarctic representatives are plotted. The maps include 178 species, 45 genera, and 10 families. The nomenclature follows Fell (1960b, 1962b).

The faunal relationships between different localities are shown in Table 1. From the table and the maps, it is clear that the island faunas are very largely derived from continental donor areas, particularly from South America and the Antarctic Peninsula–South Georgia region. The most probable mechanism for this dispersion of shelf fauna is the West Wind Drift discussed in the preceding section on asteroids. Tristan da Cunha lies at the northern edge of the Subantarctic region; its fauna is most closely allied to the more northerly faunas of South America and South Africa. The other Subantarctic islands seem to derive more of their faunas from the Antarctic Peninsula–South Georgia region, which lies completely within the Antarctic Convergence. Although some species appear to be endemic to certain islands, it seems likely that additional records will prove that distributions are broader than those presently known. The recent volcanic origin of the islands would seem to allow insufficient time for endemic species to have evolved.

The ophiuroid faunas of South Africa, Australia, and New Zealand are obviously only distantly related to those of more southern latitudes. Although the genera recorded from these areas are all found farther south, almost none of the individual species are shared. This is not surprising, because these regions lie mostly north of the Subtropical Convergence, and each region is populated by brittle stars from subtropical latitudes. The ophiuroid fauna of the New Zealand plateau is closely related to that of New Zealand (Fell, 1953a). Many ophiuroids have a circumpolar distribution on the Antarctic shelf, and it is probable that more intensive collecting will verify a greater number of circumpolar distributions. In particular, many species are common to the Antarctic Peninsula–South Georgia region, East Antarctica, the Ross Sea, and the area immediately west of the Antarctic Peninsula.

TABLE 1. Percentages of Genera (upper figure) and Species (lower figure) Which Are Shared by Each of the Main Regions.

	Patagonia and the Falkland Islands	Antarctic Peninsula and South Georgia	South Africa	East Antarctica	Australia	New Zealand	Ross Sea
Patagonia and the Falkland Islands (17 genera, 23 species)	100 100	82 57	53 9	41 22	24 0	41 4	47 22
Antarctic Peninsula and South Georgia (31 genera, 52 species)	45 25	100 100	36 2	58 35	16 0	36 2	55 40
Tristan da Cunha and Gough Islands (5 genera, 6 species)	80 33	80 0	60 33	40 0	40 0	80 0	40 0
Bouvet Island (3 genera, 3 species)	67 33	100 100	0 0	100 67	0 0	0 0	100 67
Marion and Prince Edward Islands (8 genera, 10 species)	63 40	100 60	50 20	75 40	13 0	25 10	75 40
Kerguelen and Heard Islands (12 genera, 14 species)	67 29	83 50	58 21	67 21	17 0	50 14	58 29
East Antarctica (23 genera, 38 species)	30 13	78 47	22 0	100 100	17 0	30 3	78 53
Ross Sea (22 genera, 32 species)	36 16	77 66	18 0	82 63	14 0	32 6	100 100
West Antarctica (12 genera, 13 species)	50 15	92 69	17 0	92 62	17 0	33 0	83 54

The close relationship between the fauna of the Palmer Archipelago and that of South America is particularly interesting because these regions are climatically separated by the Antarctic Convergence, but lie in close proximity. The Palmer Archipelago shows the greatest diversity and most intense speciation (31 genera and 52 species), suggesting considerable faunal exchange between South America and West Antarctica. When the brittle star fauna of the rest of the Magellanic region is better known, similar relationships may be expected.

Map 1 shows the distribution of the large and characteristically Antarctic genus *Ophiacantha*. It will be noted that circumpolar distribution occurs principally in those species having a southerly range. The species plotted on this map are not known to occur in deep water and therefore the circumpolarity is most easily explained by epiplanktonic dispersal in the path of the West Wind Drift. Species which occur in deeper water are shown on Map 8. When such forms exhibit a cosmopolitan (or circumpolar) distribution, the West Wind Drift is unlikely to be responsible. The wide distribution of such forms is better attributed to their ability to traverse deep ocean floors.

Maps 2 and 3 show the most frequent distribution of cosmopolitan genera in the southern latitudes; each genus is represented in most localities by a species endemic to that region, for example, *Monamphiura alternans* at South Georgia. However, within one genus, a number of species may be partially or totally circumpolar, for example, *Ophiuroglypha carinifera*. The distribution of the genus *Torporkovia* is bipolar.

The most obvious route of faunal exchange with Antarctica would seem to lie through South America, but Map 4 shows cosmopolitan genera which do *not* occur in the Magellanic region. Most of these are representatives of the family Amphiuridae. Amphiuridae are mainly small forms such as could be distributed by floating kelp. Probably these species have entered the Subantarctic and Antarctic regions by epiplanktonic means. *Hemilipis joubini* exemplifies a eurythermal species of a genus which is otherwise stenothermal.

Map 5 complements Map 4 by indicating the distribution of endemic species of cosmopolitan genera which occur in South America and elsewhere but not in Antarctica.

All endemic genera are recorded on Maps 6 and 7. Map 6 shows those endemic genera which occur chiefly on the Antarctic continent, and which do not necessarily have a circumpolar range. Map 7 illustrates endemic

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genera which have a characteristically circumpolar distribution. The morphology of some of these genera sometimes differs considerably from that of ophiuroids found elsewhere; for example, the basal discs of *Euvondrea* and *Ophiosteira* bear large skeletal excrescences. The genus *Astrotoma* is notably eurythermal (ranging through latitudes 42°S to 78°S), and in addition is circumpolar. *Ophioceres,* with 2 of its 3 species restricted to the New Zealand plateau, may be regarded as an Australasian stock which has contributed one circumpolar species to the Antarctic fauna. West Wind Drift dispersal would seem probable. The other genera (with the possible exception of *Ophiogona*) have a circumpolar range.

Map 8 presents the distribution of species which tend to inhabit deep water and are assumed to be stenothermal. Nineteen are cosmopolitan species, and 10 others seem to be restricted to particular regions, though they are of cosmopolitan genera. Although the means and rate of dispersal of these deepwater species are still unknown, it would seem probable that they can traverse deep ocean floors.

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Ascidiacea

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INTRODUCTION

The Ascidiacea, a class of the marine protochordate subphylum Tunicata, live from intertidal to abyssal depths in all oceans. The adults are benthic, fixed to rocks or rooted in the sand or mud of the ocean floor. Eggs develop into tailed larvae with a pelagic life that ranges from less than an hour in some species to about 24 hours in others. The phylogenetically primitive families Cionidae, Diazonidae, and Ascidiidae are exclusively oviparous and eggs are fertilized and develop after liberation from the parent. In more specialized families viviparity occurs, and progeny are liberated from the parent as tailed larvae. Asexual reproduction also occurs by various related budding mechanisms. However, no pelagic stage intervenes here between the parent and juvenile. The spread of species is therefore limited by the extent to which eggs and/or pelagic larvae are dispersed. As these stages are not of long duration, the rate of colonization by species of Ascidiacea is probably slow.

THE NATURE OF THE ANTARCTIC ASCIDIAN FAUNA

Hartmeyer (1911) estimated that 85% of all ascidians are found on continental shelves, and of these half occur at depths of 50 m or less where the variations in the environment provide the habitat for a wide diversity of species. In Antarctica, however, shallow waters of less than 50 m do not provide a particularly favorable environment for ascidians. Around the Antarctic continent there is no intertidal fauna, due to the scouring effect of ice which is present for a greater part of the year. In the Subantarctic certain species do extend into the intertidal area. However, in both the Antarctic and Subantarctic, species in shallow waters must survive not only low temperatures but also reduced salinity during periods of melting ice; the influence of seasonal changes extends to depths of 200 m. The ascidian fauna of Antarctic waters is more diverse than might be expected in an area where these physical conditions prevail, and 92 endemic species are recorded from shelf and slope regions. Of these, only 16 extend north of the Subtropical Convergence into the adjacent waters of Australia, New Zealand, South Africa, and South America. In addition, 21 species have been taken from depths of 2000 m to 6000 m of which only 6 are known from deepwater regions in other oceans. In contrast, only 47 species are known from Arctic waters and with few exceptions these extend into the boreal waters of western Europe and the eastern seaboard of North America. The diversity of the Antarctic ascidian fauna is further emphasized when compared with the number of species known from other more temperate seas in a wide range of environments. There are 114 species known in the eastern Pacific Ocean from the Arctic to the equator (Tokioka, 1963); 170 cold-water species are known from the North Atlantic and North Pacific Oceans (Millar, 1966b; Tokioka, 1963); in the varied conditions offered by the seas around Australia, only 200 species are known (Kott, 1952, 1957, 1962, 1963, 1964, 1966; Millar, 1966a); and 277 species are known from the seas around Japan (Tokioka, 1963).

The success of the class in the Antarctic may be due to certain adaptations which characterize this endemic fauna. These are (1) large populations of single species; (2) longevity and consequent increase in size (the largest simple ascidians known are the Antarctic *Molgula gigantea* and *Paramolgula gregaria*); (3) a greater abundance than usual of viviparous species and development in them of special mechanisms to insure viviparity (for example, orientation of gonoducts in relation to the atrial opening in Molgulidae, special closing mechanisms in Agnesiidae, large eggs and larvae retained in the parent colony in Polyclinidae); (4) toleration by most species of a wide range of depths from the shelf to the continental slope so that they may escape the effects of glaciation in shallow waters. The convergence of the external appearance of many species in many diverse families of Antarctic ascidians is noteworthy and probably represents a response to the environmental conditions encountered.

THE ORIGIN OF THE ANTARCTIC ASCIDIAN FAUNA

The following monotypic genera are endemic to the Antarctic: *Fungulus, Protoholozoa, Pharyngodictyon* (abyssal); *Xenobranchion* and *Tylobranchion* (sublittoral). Other endemic genera are represented by two or three species each: *Bathypera* (eurybathic) and *Caenagnesia* (sublittoral). The abyssal endemic genera are highly specialized for their deepwater environment, but with the exception only of *Fungulus* and *Bathypera,* they are phylogenetically primitive and are possibly derived from early unmodified sublittoral species. The sublittoral endemic genera are relatively unmodified representatives of primitive groups persisting as a relict fauna.

Other genera present in the Antarctic are represented by successfully adapted and widely flourishing species. There are only a few species, of limited distribution, whose presence suggests a recent origin. An example of possibly recent speciation is *Cnemidocarpa zenkevitchi* (Vinogradova, 1962), which has been found only in a brackish marine bay on the Knox Coast in the vicinity of Bunger Hills. In winter this bay is blocked by ice; in summer the surface water is freshened by melting ice, but at 2 m to 3 m the salinity remains high. The species is closely related to the circum-Antarctic *C. verrucosa* and may have derived from it in the isolation of this peculiar environment.

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The degree of specific and generic endemism (especially of primitive genera), the specialized nature of many of the species, and the widespread circumpolar distribution of species suggests that the Antarctic regions had been isolated for a long period and that a component of the fauna is a relict of a much older ascidian fauna. In contrast, generic endemism in the Arctic is not so pronounced nor is the fauna so isolated from that of adjacent regions. Of the genera which might be considered of Arctic origin, only *Rhizomolgula* has a distribution confined to the Arctic; *Corellopsis* and *Corelloides,* closely related to the deepwater *Corynascidia,* extend to the Aleutians; *Heterostigma* spp. are taken from the coast of New England; and *Dendrodoa,* closely related to the Antarctic *Styelopsis,* occurs off the English coast. Primitive unmodified relict genera such as *Tylobranchion, Xenobranchion,* and *Caenagnesia* do not occur in the Arctic.

FACTORS INFLUENCING GEOGRAPHIC DISTRIBUTION

The distribution of ascidians is influenced by hydrographic and sediment conditions on the ocean floor. Therefore, as Broch (1961) has pointed out, the deep benthic fauna of Antarctic waters is not limited sharply by the Antarctic and Subtropical Convergences. Around the Subantarctic islands the distribution is also affected by the protection afforded as well as the type of substrate available. Accordingly Kerguelen Island, with sheltered waters, supports a larger number of endemic species than Macquarie Island with its unfavorable, exposed coast line.

Species widely distributed in the Antarctic, and sometimes present in the Subantarctic as well, are found to depths of 400 m or more extending from the continental shelf onto the slope. Species of primarily Subantarctic distribution that are also found in the Antarctic extend to depths of only 200 m to 300 m. Those species with a limited geographic range in either of these regions also generally occur at lesser depths. This pattern of eurybathic distribution suggests that Antarctic species survived because of their ability to live at greater depths during periods of glaciation, whereas species unable to survive in deeper waters were progressively isolated in the north and became established as Subantarctic species. Subsequent submergence of land bridges further isolated these species from the Antarctic mainland and resulted in a Subantarctic fauna widely distributed in the shelf areas of isolated islands.

A number of species demonstrate tropical submergence in deeper waters north of the Subtropical Convergence: *Molgula pyriformis, Didemnum tenue, Ascidia meridionalis, Styela nordenskjoldi, Molguloides immunda, Didemnum studeri,* and *Bathypera splendens.*

ZOOGEOGRAPHIC DIVISIONS OF THE ASCIDIAN FAUNA

The following arrangement of biogeographic divisions is recognized:

(1) Antarctic—the region south of the Antarctic Convergence

(a) Continental Province—the circumpolar region near the continent. A few species are, so far, recorded only from the Victoria Land and Enderby Land quadrants and may represent an 'eastern district.'

(b) South Georgian Province—the Antarctic Peninsula and the Subantarctic islands along the Scotia Ridge to South Georgia.

(2) Subantarctic—the region between the Subtropical and Antarctic Convergences. Many of the species in this region also extend to South Georgia. The Guaitecas Islands, off the coast of Chile, represent the northern extent of Subantarctic species in the eastern Pacific. These islands have four species in common with New Zealand.

(a) Magellanic Province—the area from the Patagonian shelf to the Falkland Islands.

(b) Kerguelen Province—the region including Auckland, Campbell, Heard, and Macquarie Islands, in addition to the Kerguelen Islands.

(c) Antipodean Province—the region including New Zealand and the nearby Chatham Island. Despite the close geographic proximity of Macquarie Island, it is more closely related faunistically to Kerguelen Island than to New Zealand and Chatham Island. This may be a reflection of the isolated, unprotected environment of Macquarie Island, which has not permitted colonization by more temperate species from New Zealand.

THE MAPS (PLATES 28 AND 29)

MAPS 1 AND 2. The species plotted on these maps are widely distributed in the Antarctic. Generally they are taken from 100 m or less and extend to depths of 400 m to 1000 m. Only *Styela nordenskjoldi* (Map 2) and *Pyura squamata* (Map 1) are not endemic to the map region, and also occur (Map 7) off California *(S. nordenskjoldi),* and off eastern Australia and Japan *(P. squamata? > P. lepidoderma). Tylobranchion* is the only endemic genus.

MAPS 3 AND 4. The species shown are generally confined to the Antarctic region. Most have a wide circumpolar range and inhabit depths from less than 100 m to at least 400 m, extending beyond the edge of the continental shelf. The few species wtih a limited distribution in the South Georgian Province are generally taken from depths of less than 300 m, sometimes from 0 m to 20 m; however, with the exception of *Cnemidocarpa zenkevitchi,* those species with a limited distribution in the Continental Province tolerate greater depths on the continental shelf and do not extend into such shallow water. All the species are endemic to the Antarctic and *Caenagnesia* and *Bathypera* are endemic genera. Four species from the Antarctic Continental Province and 6 from the South Georgian Province, known from only a few records of single specimens, have not been included in the maps.

MAPS 5 AND 6. Species shown in these maps are generally confined to the Subantarctic region and are generally taken in depths from the immediate littoral to 300 m. Only *Aplidium irregulare* and *Didemnum studeri* (Map 6) are exceptional and extend beyond the edge of the Antarctic continental shelf and into the South Australian Basin, respectively. Most of the species concerned are endemic, but there are no endemic genera. *Agnesia glaciata* is closely related to, or identical with, species of this genus occurring off northeast Australia, Japan, and in the North Pacific. These species may represent relict populations (Van Name, 1945, p. 200).

MAP 7. Abyssal genera and species found in Antarctica and in other parts of the world are plotted on this map. *Bathypera* spp., *Styela nordenskjoldi, Pyura squamata, Molguloides immunda* and *Molguloides vitrea* are all recorded around the Antarctic continent both from waters of about 1000 m or less and from deeper waters. Farther to the north these species occur only in deeper waters except off northeastern Australia, Indonesia, the Philippines, and Japan, where identical or closely related species occur in shallower waters. None of the species indicated above are confined to Antarctica, and all lack the special modifications of the branchial sac characteristic of abyssal species. This peculiarity together with the pattern of their depth distribution suggests relict populations which have spread into deeper waters.

The genera *Culeolus, Abyssascidia, Megalodicopia* (and the closely related *Dicopia*), and *Corynascidia,* with the morphological characteristics associated with abyssal species, have been taken in the deep basins of both hemispheres. They also occur in waters of less than 1000 m off Indonesia or Japan, perhaps because of upwelling on the continental slope.

The distribution of 4 species of *Culeolus* closely related to *Culeolus murrayi* are presented on the map; *Bathyocus discoideus* and *B. minutus* (Herdman, 1886) from the abyssal North Pacific Ocean are not present in the Antarctic and have not been included on the map. Only the genera *Pharyngodictyon, Fungulus,* and *Protoholozoa* are confined to the abysses of the Antarctic waters. Ten of the world's abyssal genera are not represented in the Antarctic. A total of 40 species (Millar, 1959) have been described from waters of 3000 m or more throughout the oceans of the world, and only half of these have so far been recorded from Antarctic waters.

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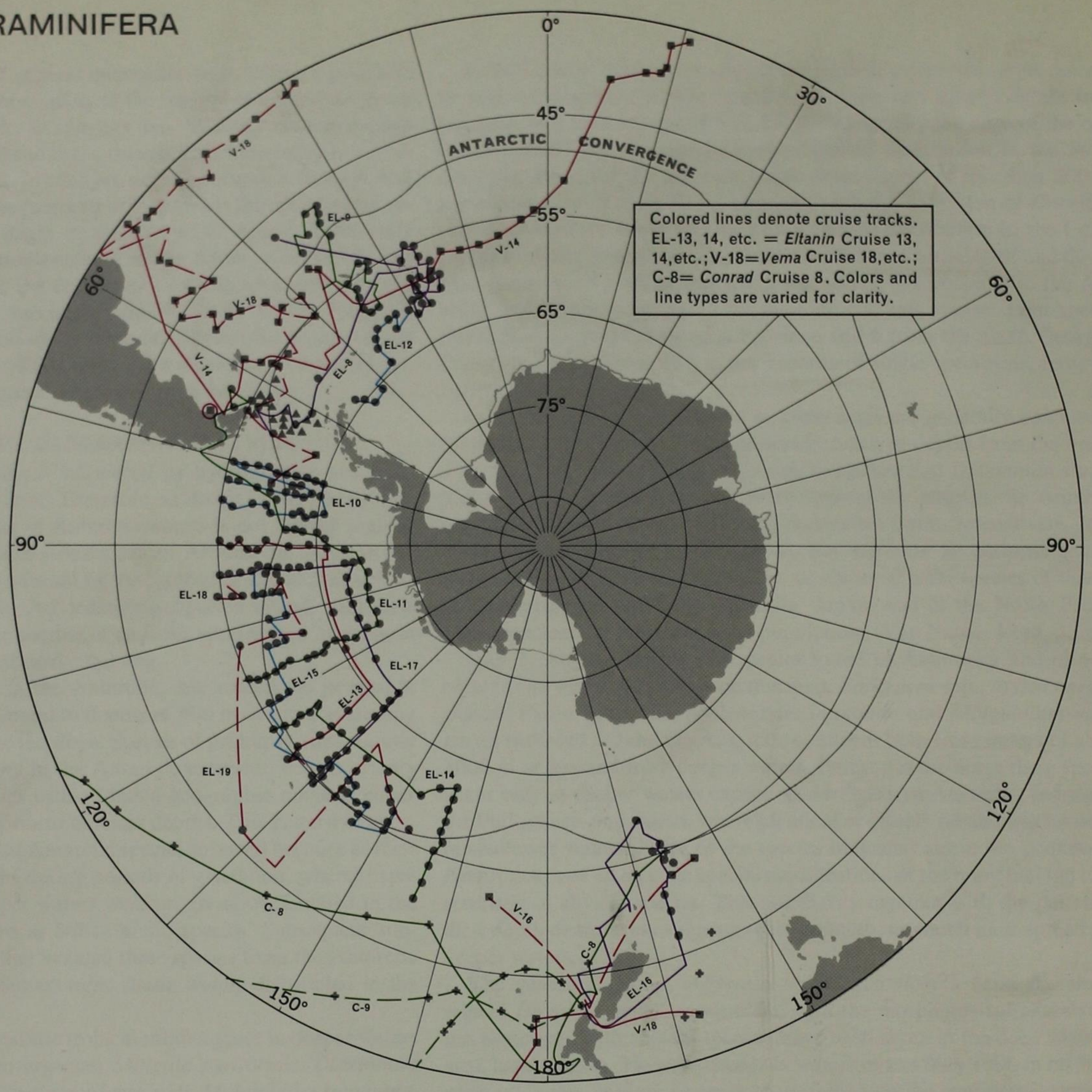
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PLANKTONIC FORAMINIFERA

SHEET 1

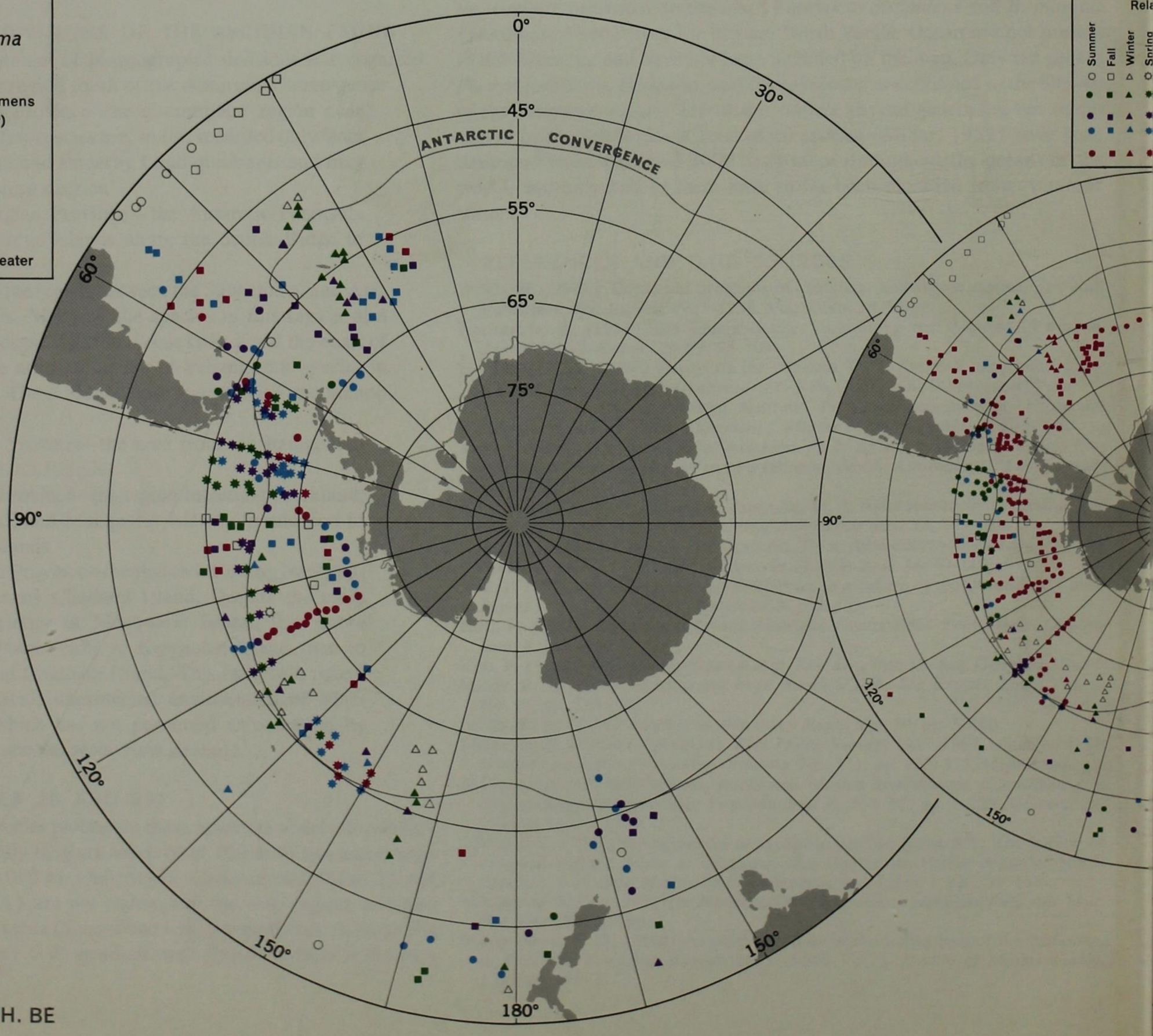
MAP 1
Station Map

- ● *Eltanin* cruises
- ■ *Vema* cruises
- ◆ *Conrad* cruises
- ▲ *Yelcho* cruises



MAP 4
Globigerina pachyderma
Absolute abundance

Summer	Fall	Winter	Spring	(no. of specimens per 1000m³)
○	□	△	☼	Absent
●	■	▲	✸	1-99
●	■	▲	✸	100-999
●	■	▲	✸	1000-9999
●	■	▲	✸	10,000 and greater



Austral seasons are indicated

COMPILED BY A. W. H. BE

PLATE 1

FOLIO 11— MARINE INVERTEBRATES

ANTARCTIC MAP FOLIO SERIES

MAP 2

Globigerina quinqueloba

Absolute abundance

(no. of specimens per 1000m³)

Summer	Fall	Winter	Spring	
○	□	△	☼	Absent
●	■	▲	✸	1-99
●	■	▲	✸	100-999
●	■	▲	✸	1000-9999
●	■	▲	✸	10,000 and greater

MAP 3

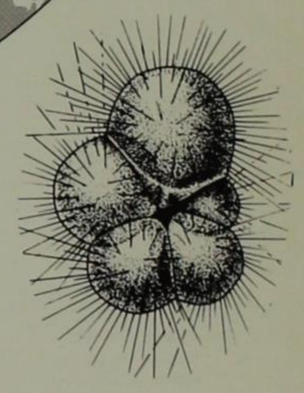
Globigerina quinqueloba

Relative abundance

(percent of total population)

Summer	Fall	Winter	Spring	
○	□	△	☼	Absent
●	■	▲	✸	0.1-4.9
●	■	▲	✸	5.0-9.9
●	■	▲	✸	10.0-19.9
●	■	▲	✸	20.0 and greater

ANTARCTIC CONVERGENCE



Globigerina quinqueloba
×93

MAP 5

pachyderma

abundance

percent of total population)

	Absent
	0.1-4.9
	5.0-9.9
	10.0-19.9
	20.0 and greater

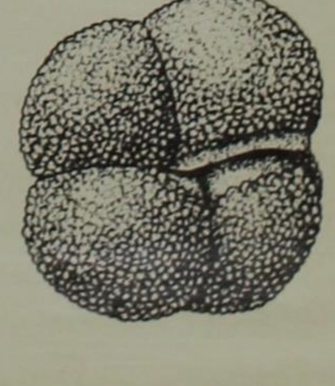
MAP 6

Globigerina pachyderma

Coiling percentages

Summer	Fall	Winter	Spring	(percent left-coiling)	
●	■	▲	✸	90-100	Left coiling dominant
●	■	▲	✸	50-89	Left coiling dominant
●	■	▲	✸	10-49	Right coiling dominant
●	■	▲	✸	0-9	Right coiling dominant

ANTARCTIC CONVERGENCE



Globigerina pachyderma
×120

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PLANKTONIC FORAMINIFERA

SHEET 2

ANTARCTIC CONVERGENCE

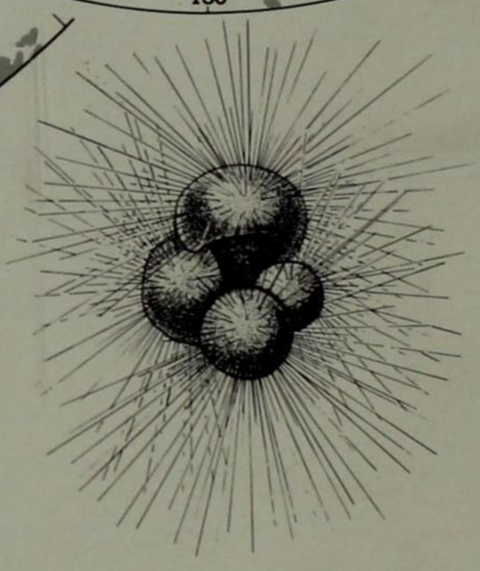
MAP 7

Globigerina bulloides

Absolute abundance

Summer	Fall	Winter	Spring	(no. of specimens per 1000m³)
○	□	△	☼	Absent
●	■	▲	✹	1-99
●	■	▲	✹	100-999
●	■	▲	✹	1000-9999
●	■	▲	✹	10,000 and greater

Globigerina bulloides
×42



MAP 8

Globigerina bul

Relative abunda

Summer	Fall	Winter	Spring	(percent popul
○	□	△	☼	Abs
●	■	▲	✹	0.1-
●	■	▲	✹	5.0-
●	■	▲	✹	10.0-
●	■	▲	✹	20.0 and

MAP 11

Globorotalia inflata

Absolute abundance

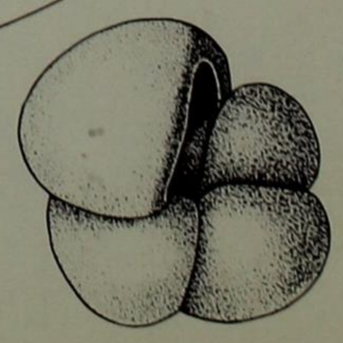
Summer	Fall	Winter	Spring	(no. of specimens per 1000m³)
○	□	△	☼	Absent
●	■	▲	✹	1-99
●	■	▲	✹	100-999
●	■	▲	✹	1000-9999
●	■	▲	✹	10,000 and greater

MAP 12

Globorotalia inflata

Relative abundance

Summer	Fall	Winter	Spring	(percent of total population)
○	□	△	☼	Absent
●	■	▲	✹	0.1-4.9
●	■	▲	✹	5.0-9.9
●	■	▲	✹	10.0-19.9
●	■	▲	✹	20.0 and greater



Globorotalia inflata
×68

Austral seasons are indicated

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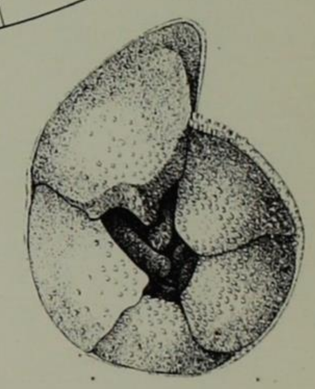
ANTARCTIC CONVERGENCE

MAP 10
Globorotalia truncatulinoides
Relative abundance

Summer	Fall	Winter	Spring	(percent of total population)
○	□	△	✡	Absent
●	■	▲	✸	0.1-4.9
●	■	▲	✸	5.0-9.9
●	■	▲	✸	10.0-19.9
●	■	▲	✸	20.0 and greater

MAP 9
Globorotalia truncatulinoides
Absolute abundance

Summer	Fall	Winter	Spring	(no. of specimens per 1000m³)
○	□	△	✡	Absent
●	■	▲	✸	1-99
●	■	▲	✸	100-999
●	■	▲	✸	1000-9999
●	■	▲	✸	10,000 and greater



Globorotalia truncatulinoides
×62

MAP 13
Globigerinita glutinata
Absolute abundance

Summer	Fall	Winter	Spring	(no. of specimens per 1000m³)
○	□	△	✡	Absent
●	■	▲	✸	1-99
●	■	▲	✸	100-999
●	■	▲	✸	1000-9999
●	■	▲	✸	10,000 and greater

MAP 14
Globigerinita glutinata
Relative abundance

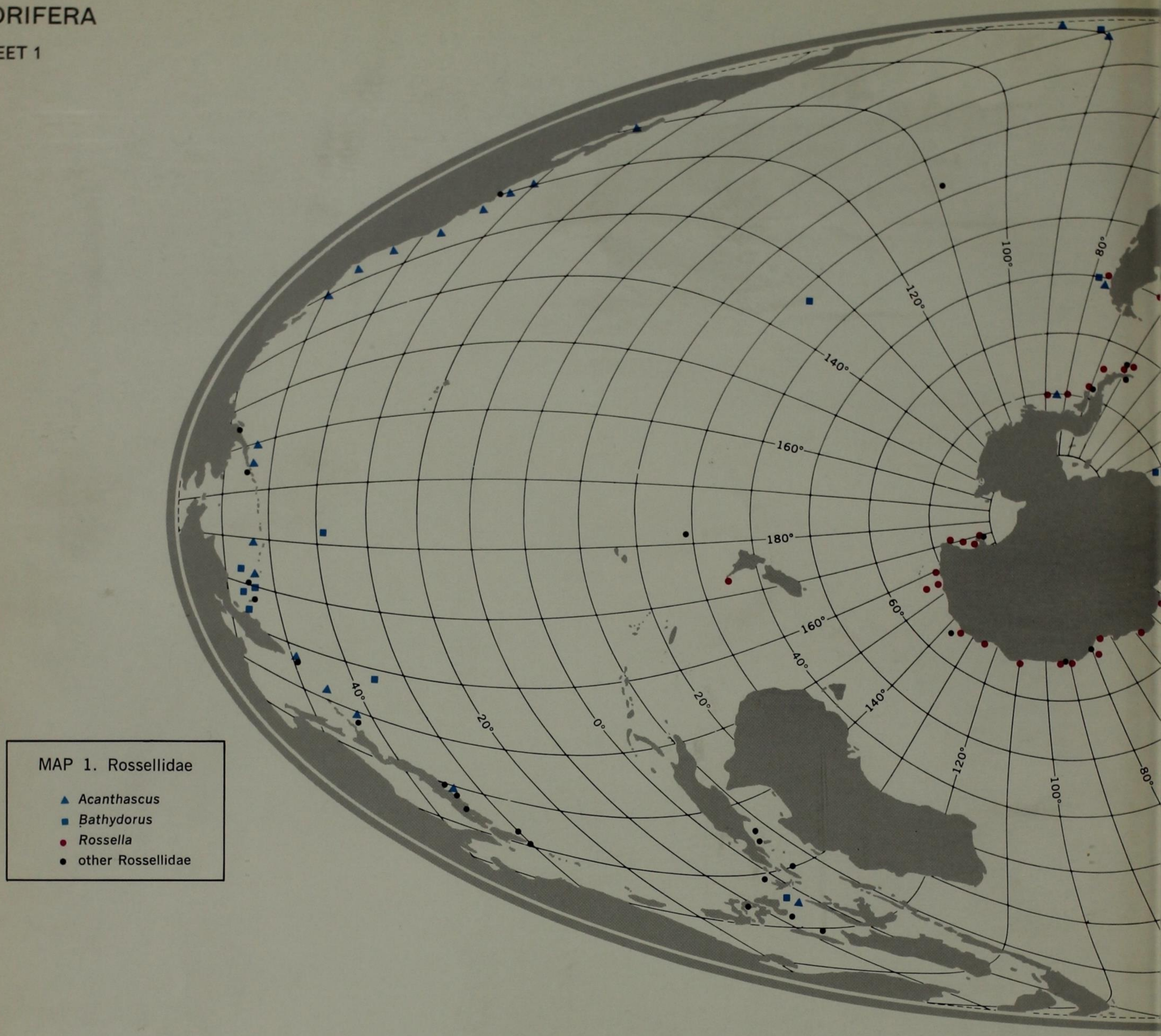
Summer	Fall	Winter	Spring	(percent of total population)
○	□	△	✡	Absent
●	■	▲	✸	0.1-4.9
●	■	▲	✸	5.0-9.9
●	■	▲	✸	10.0-19.9
●	■	▲	✸	20.0 and greater



Globigerinita glutinata
×71

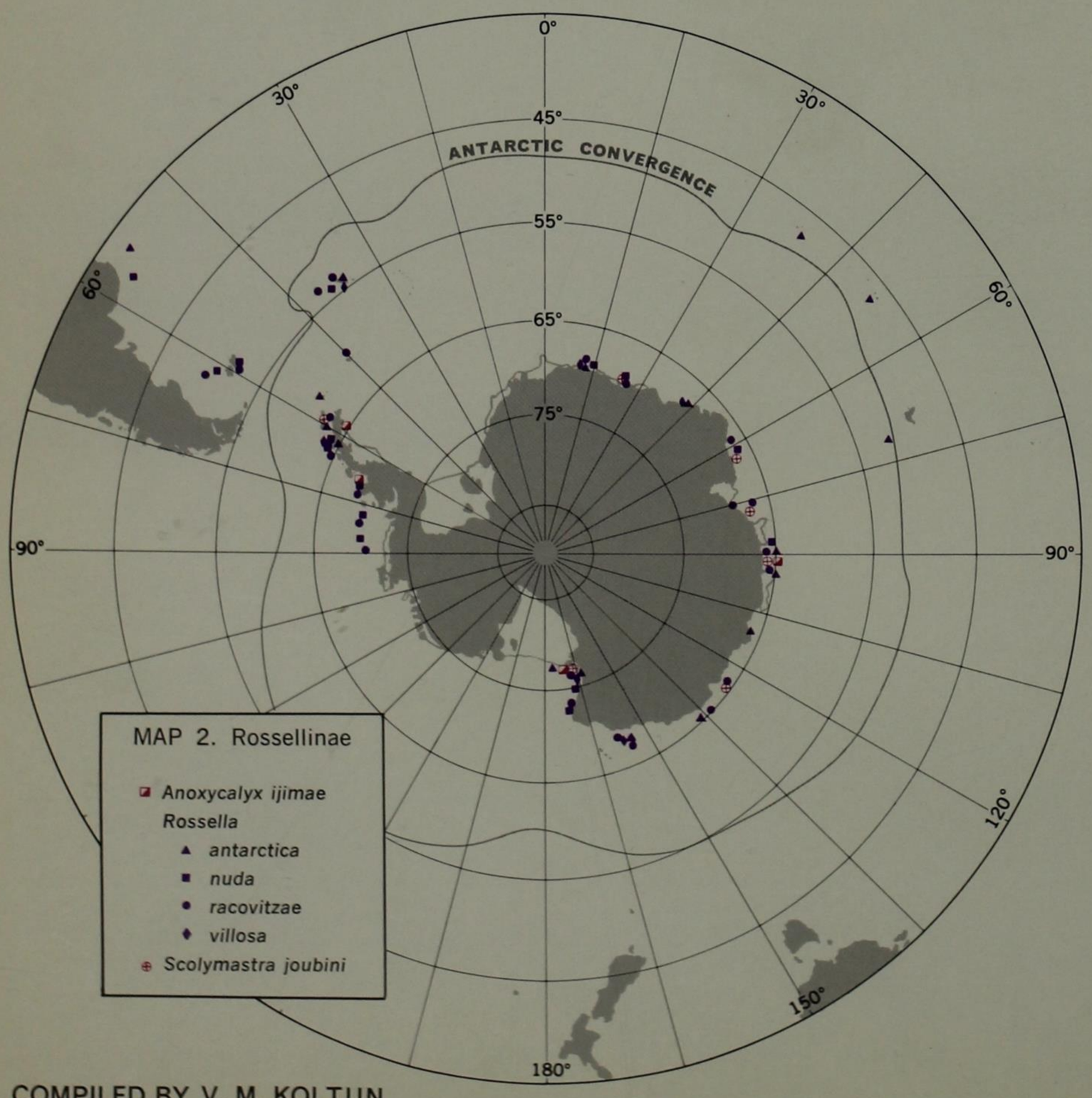
PORIFERA

SHEET 1



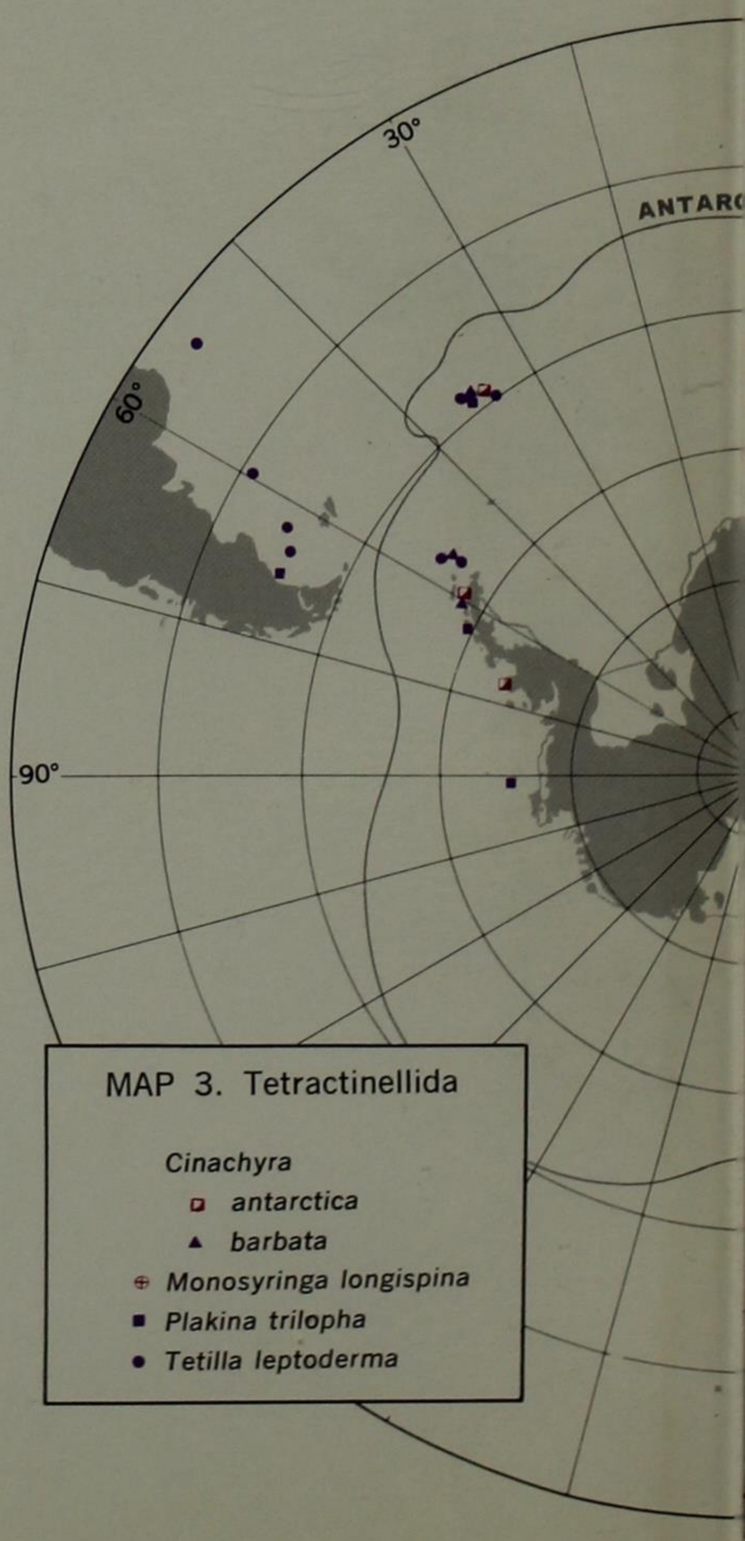
MAP 1. Rossellidae

- ▲ *Acanthascus*
- ■ *Bathydorus*
- ● *Rossella*
- ● other Rossellidae



MAP 2. Rossellinae

- ◪ *Anoxycalyx ijimae*
- *Rossella*
  - ▲ *antarctica*
  - ■ *nuda*
  - ● *racovitzae*
  - ♦ *villosa*
- ⊕ *Scolymastra joubini*

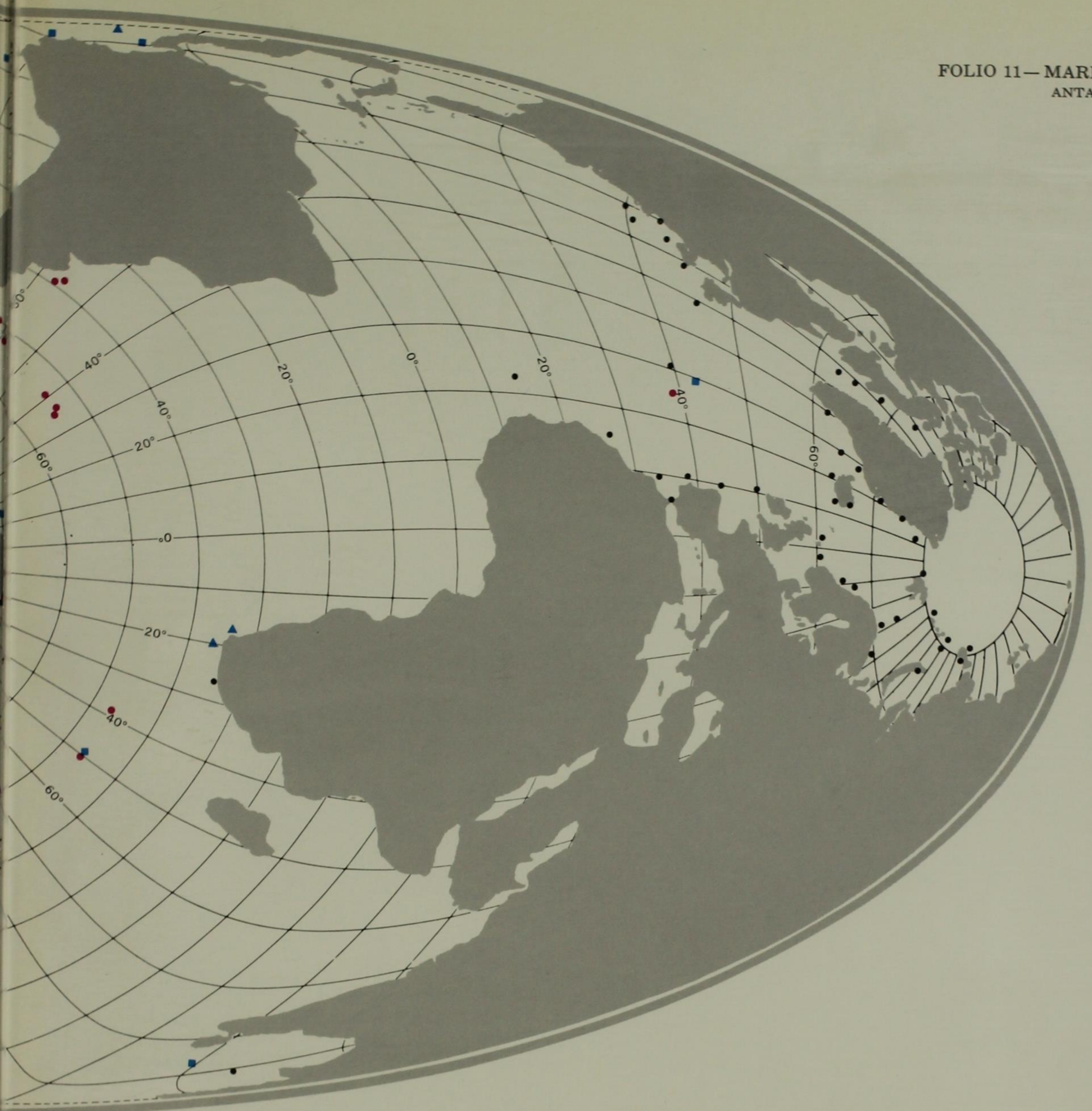


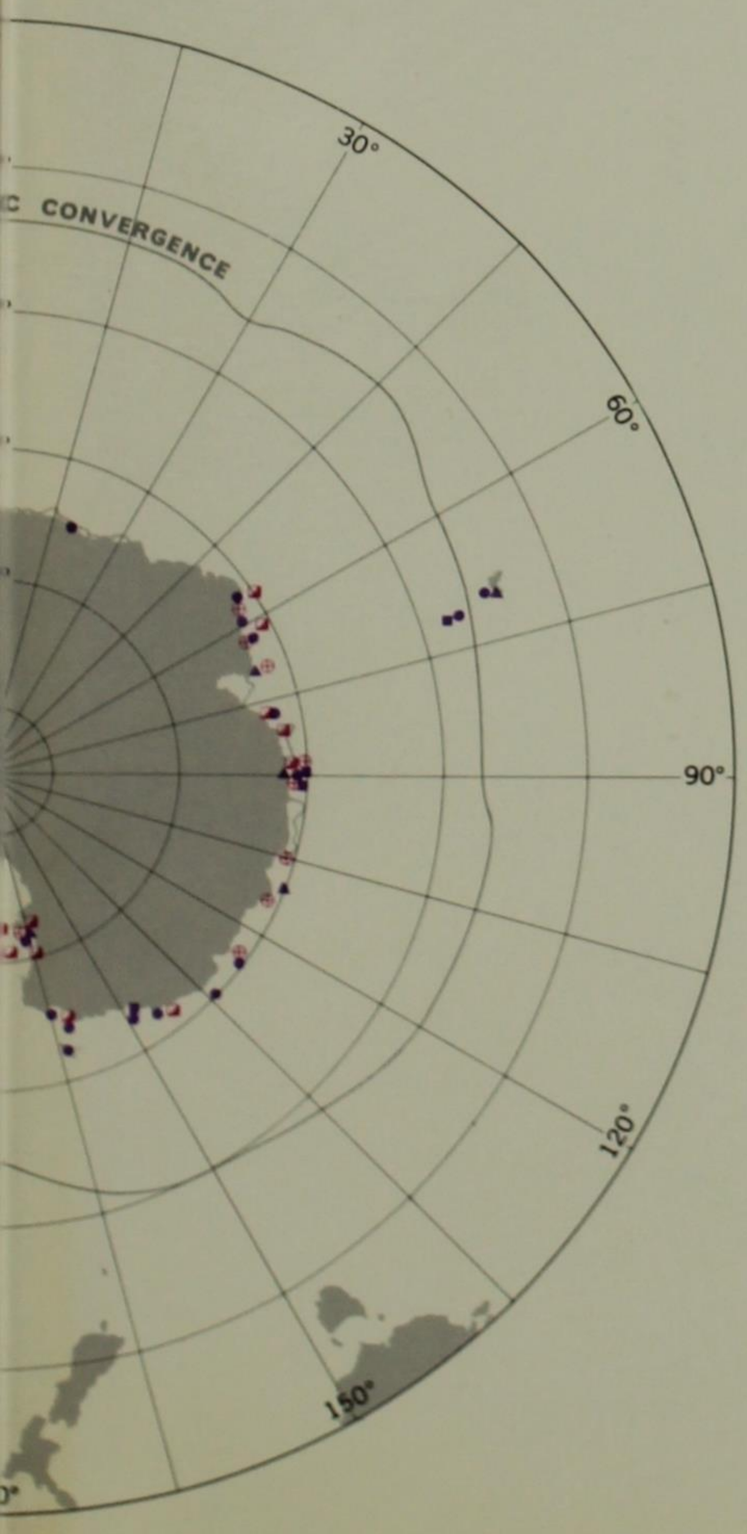
MAP 3. Tetractinellida

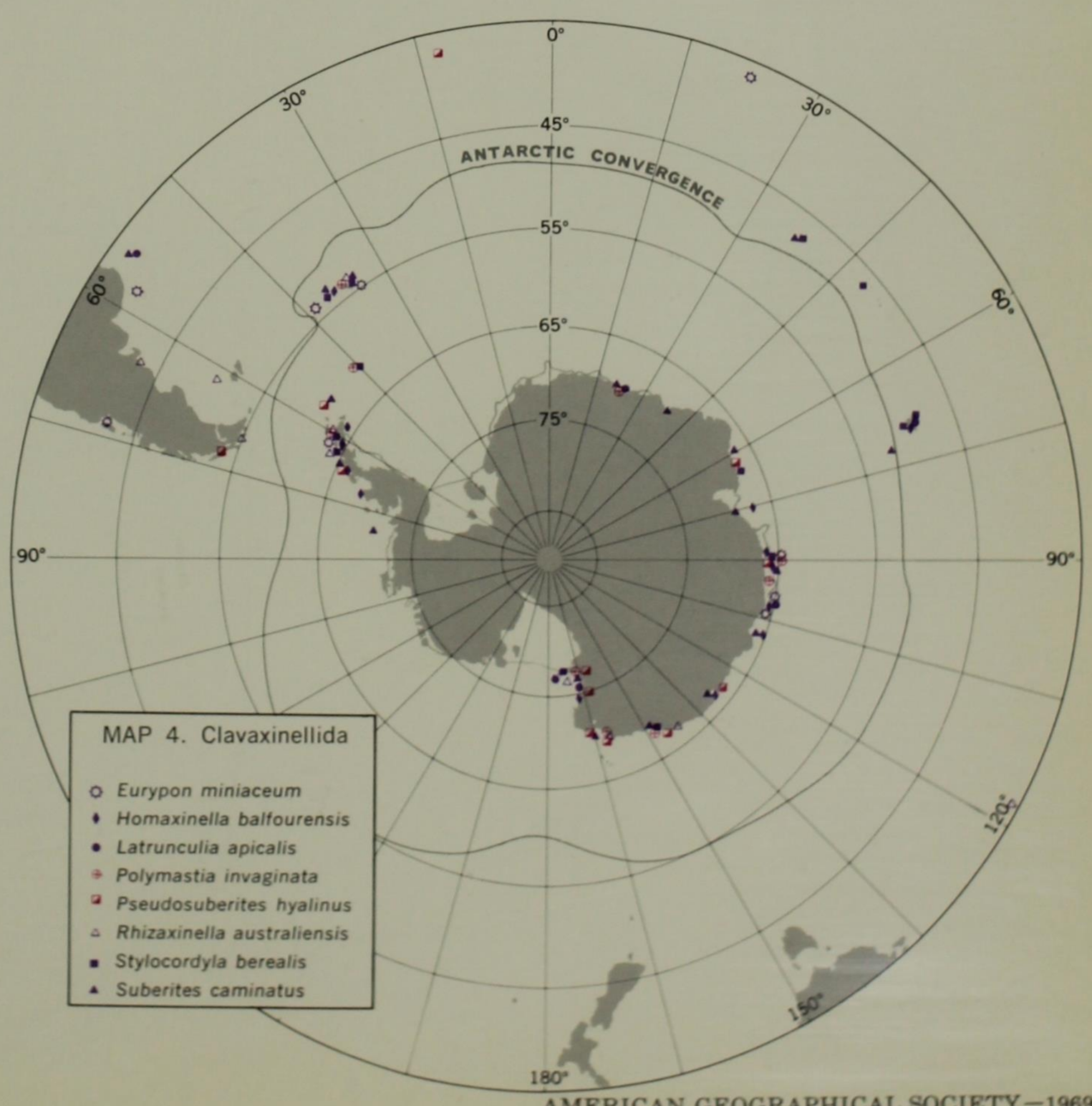
Cinachyra
- ◪ *antarctica*
- ▲ *barbata*

- ⊕ *Monosyringa longispina*
- ■ *Plakina trilopha*
- ● *Tetilla leptoderma*

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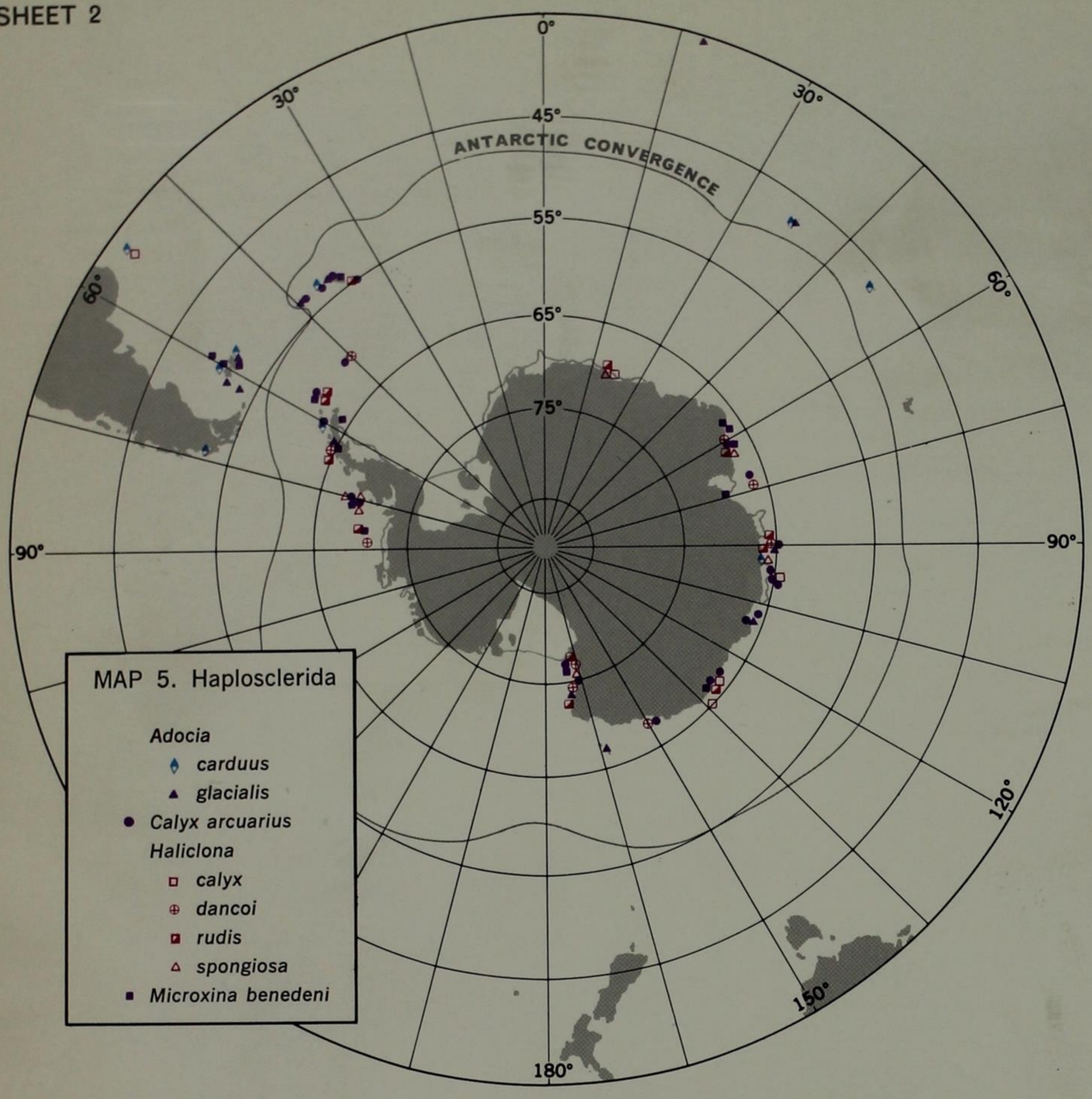
MAP 4. Clavaxinellida

- *Eurypon miniaceum*
- *Homaxinella balfourensis*
- *Latrunculia apicalis*
- *Polymastia invaginata*
- *Pseudosuberites hyalinus*
- *Rhizaxinella australiensis*
- *Stylocordyla berealis*
- *Suberites caminatus*

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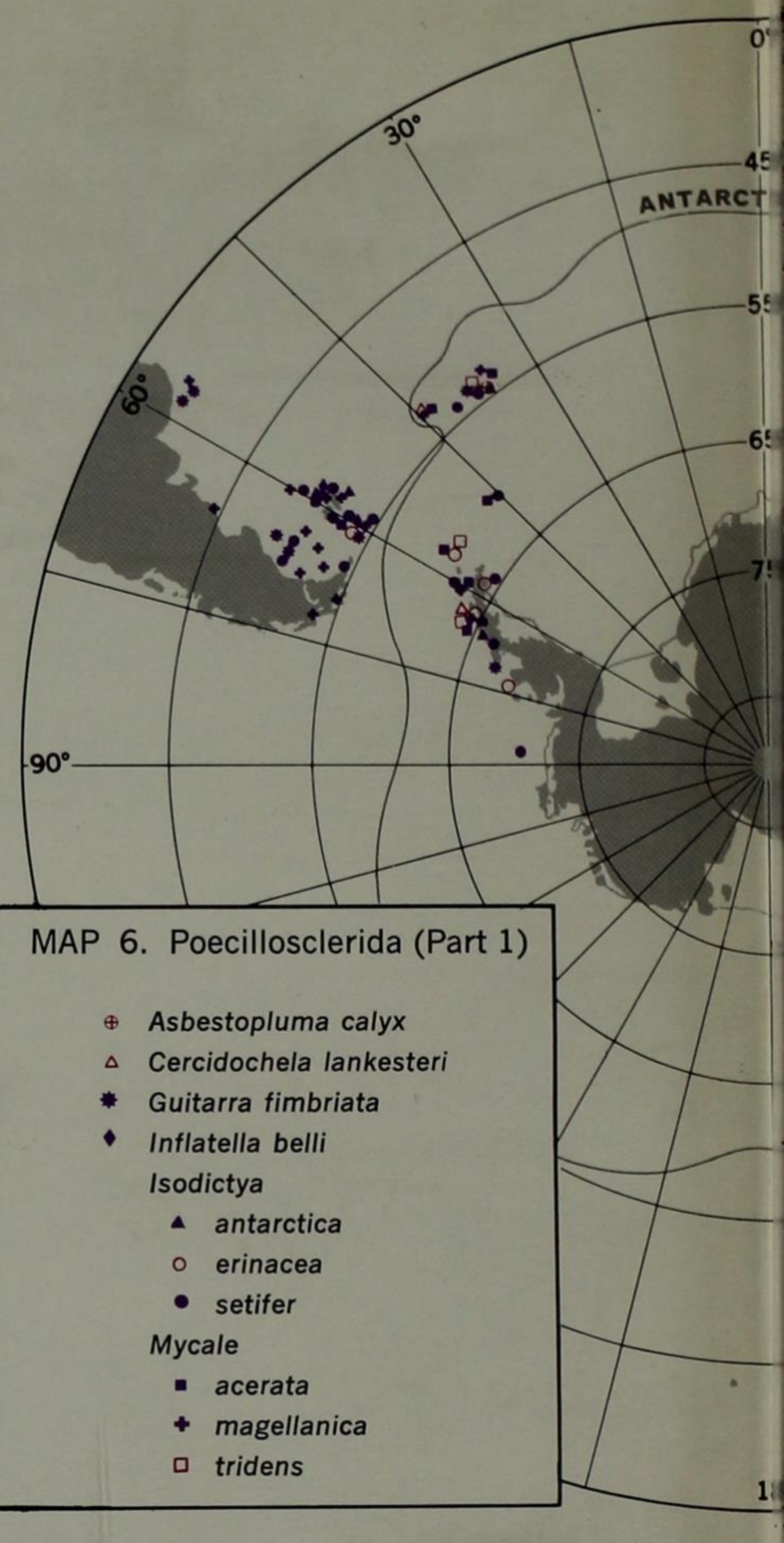
PORIFERA

SHEET 2



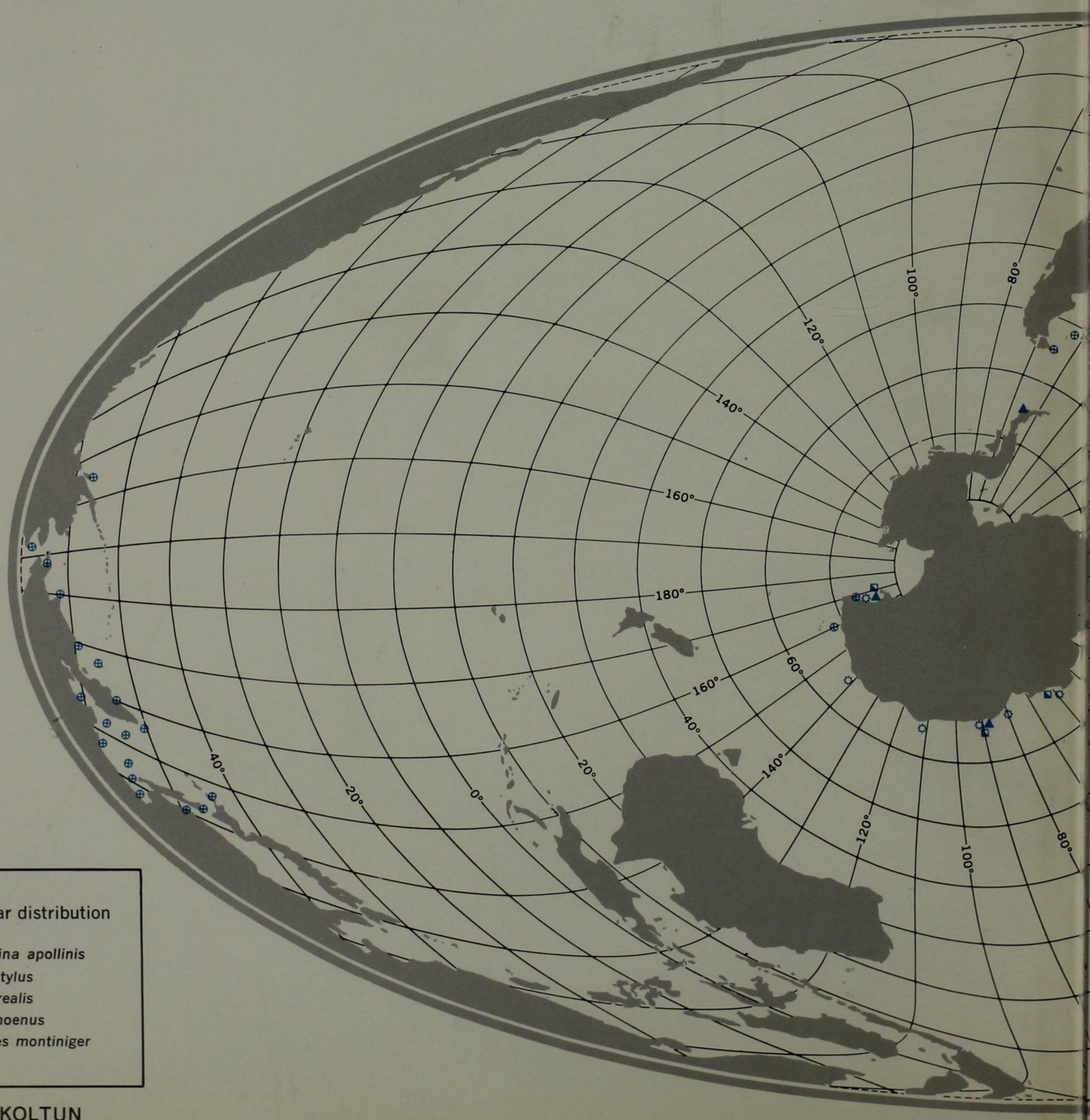
MAP 5. Haplosclerida

- *Adocia*
  - *carduus*
  - *glacialis*
- *Calyx arcuarius*
- *Haliclona*
  - *calyx*
  - *dancoi*
  - *rudis*
  - *spongiosa*
- *Microxina benedeni*



MAP 6. Poecillosclerida (Part 1)

- *Asbestopluma calyx*
- *Cercidochela lankesteri*
- *Guitarra fimbriata*
- *Inflatella belli*
- *Isodictya*
  - *antarctica*
  - *erinacea*
  - *setifer*
- *Mycale*
  - *acerata*
  - *magellanica*
  - *tridens*



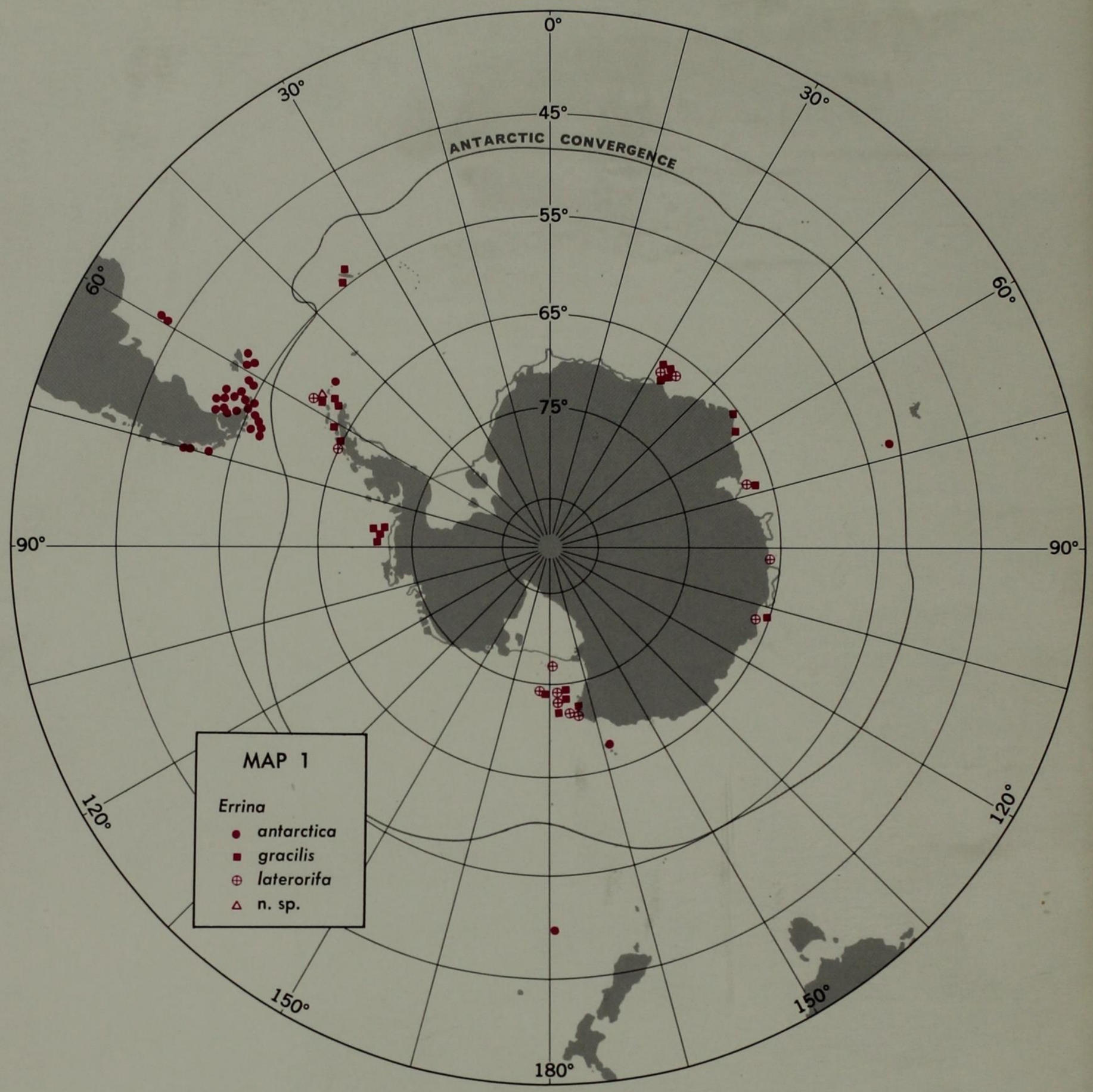
MAP 8. Bipolar distribution

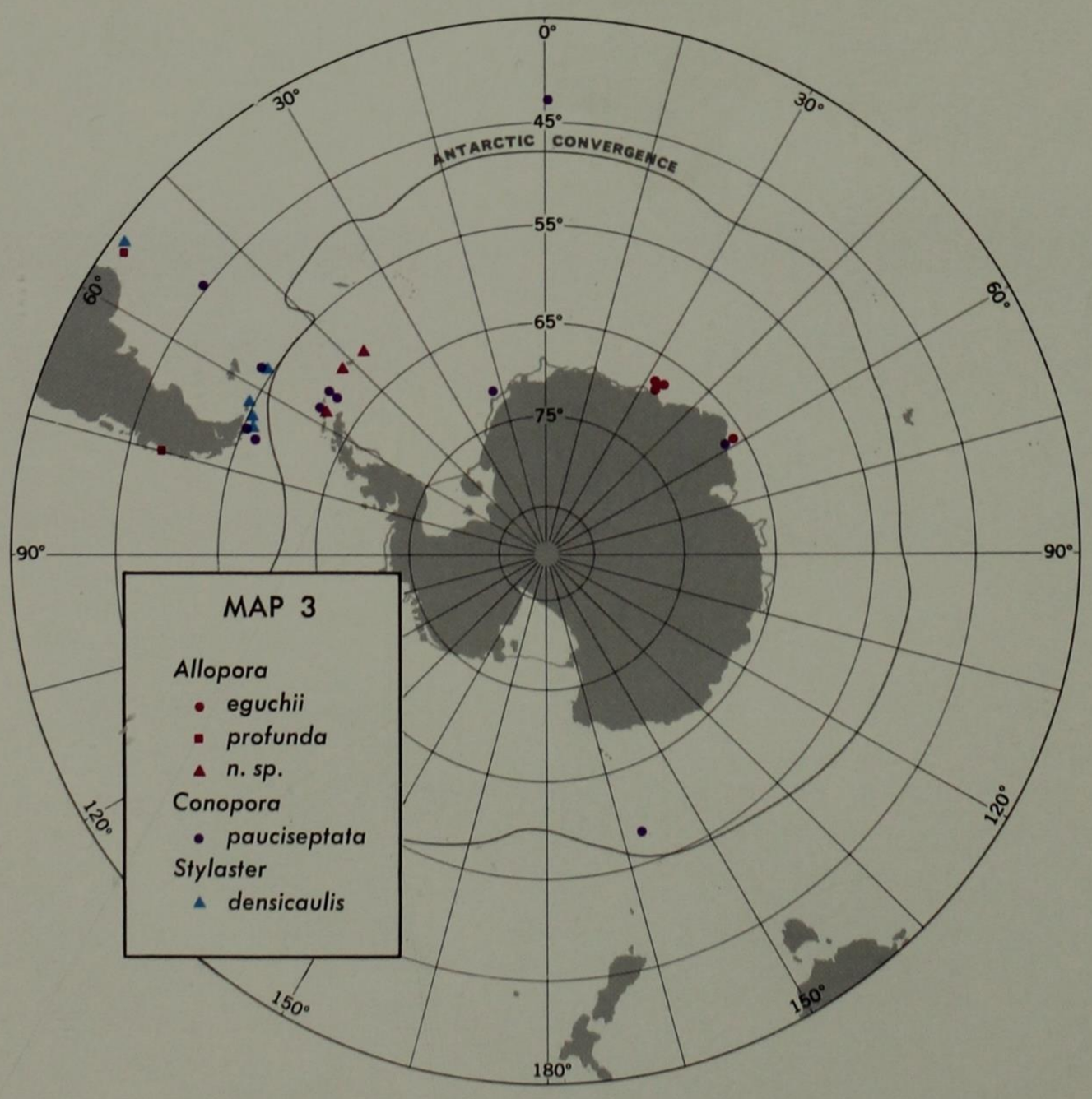
- *Artemisina apollinis*
- *Sphaerotylus*
  - *borealis*
  - *schoenus*
- *Suberites montiniger*

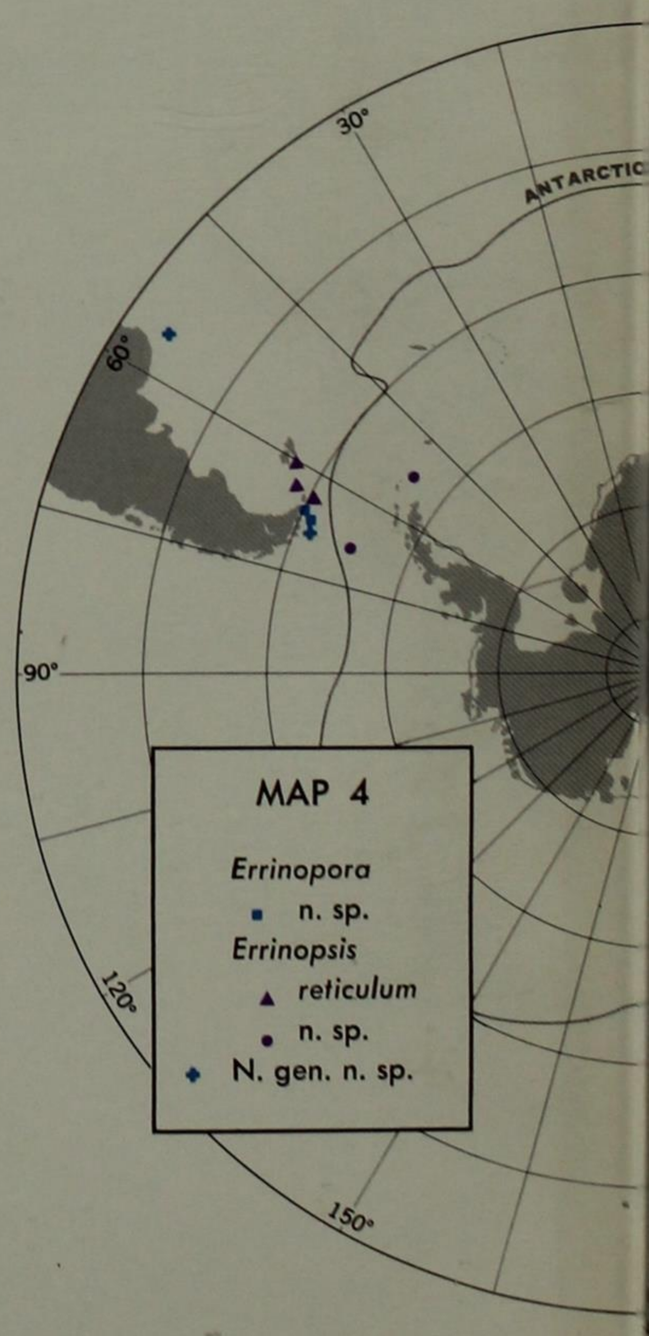
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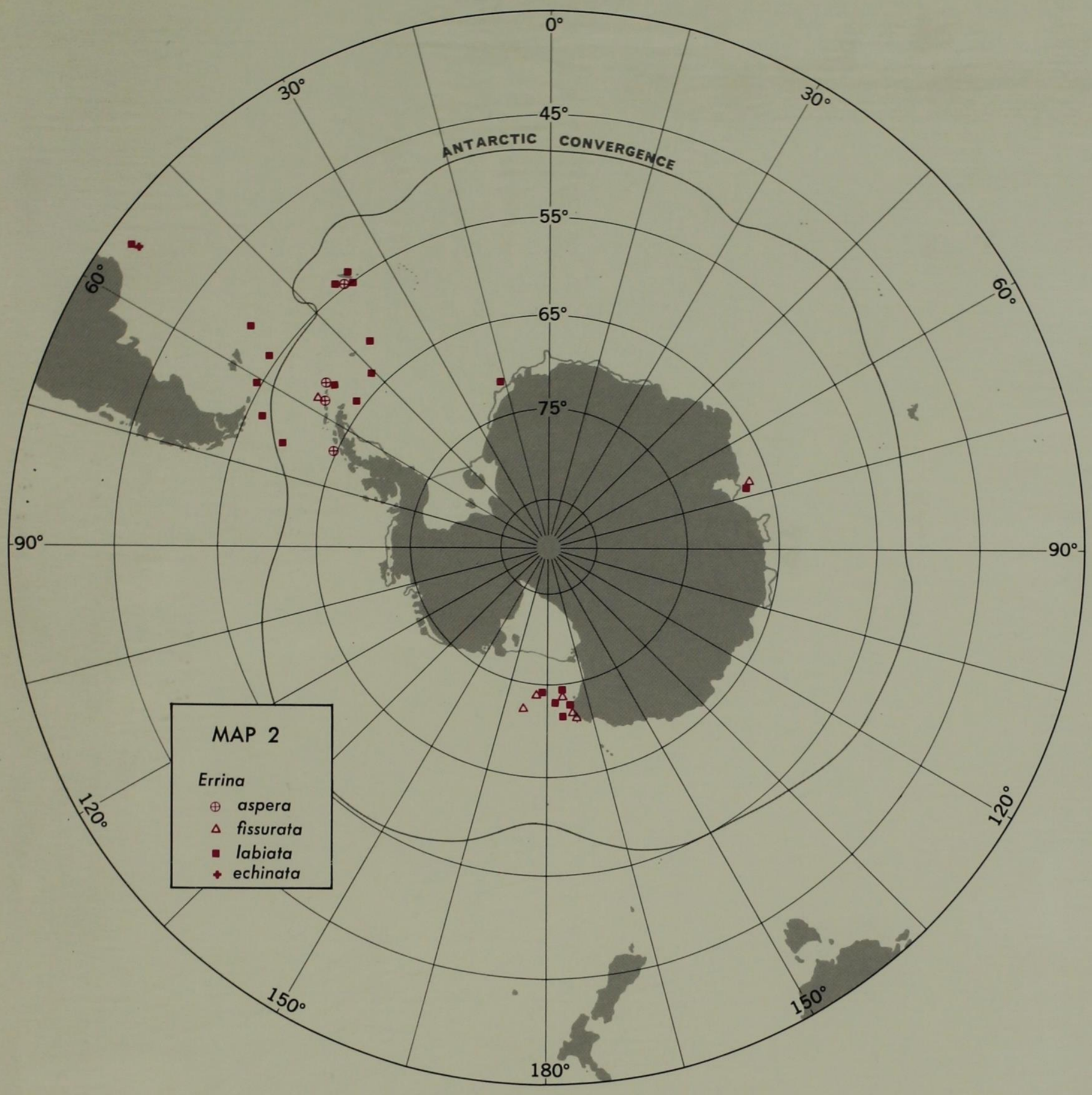
STYLASTERINA

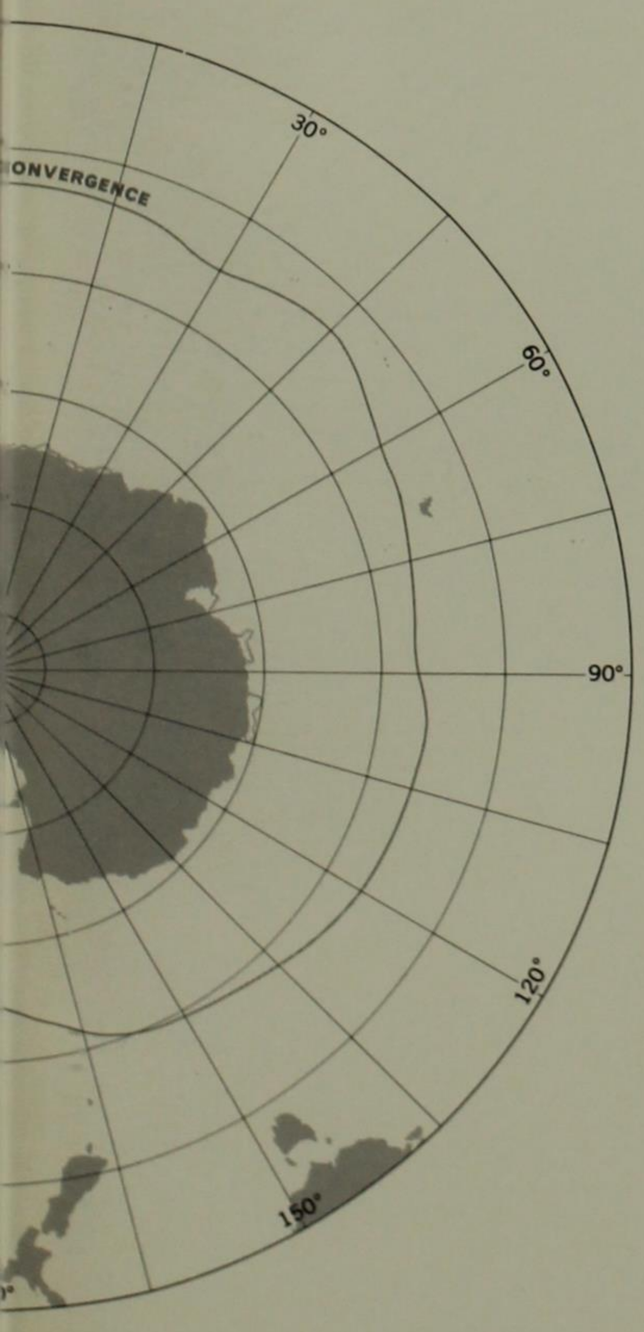


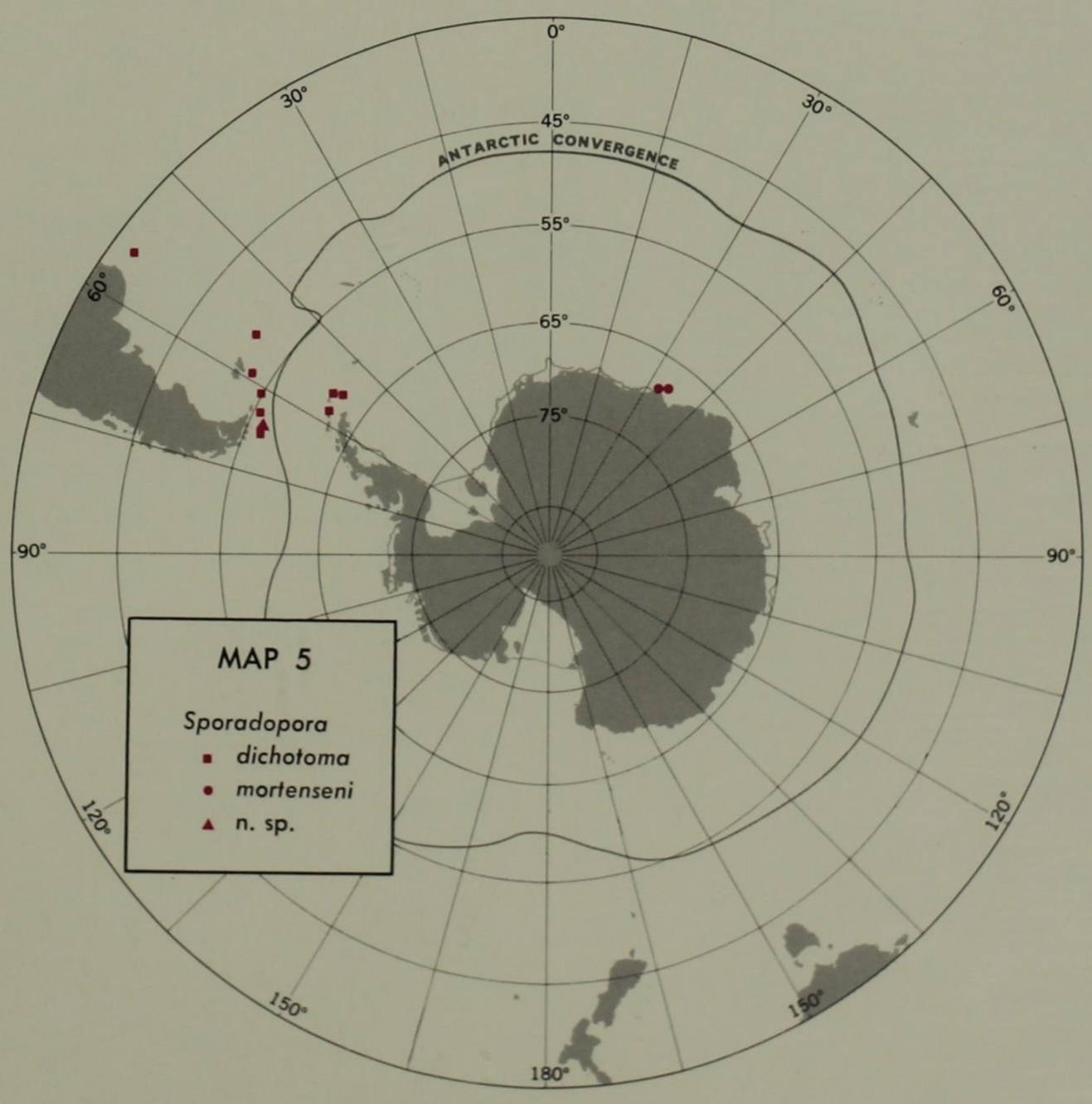




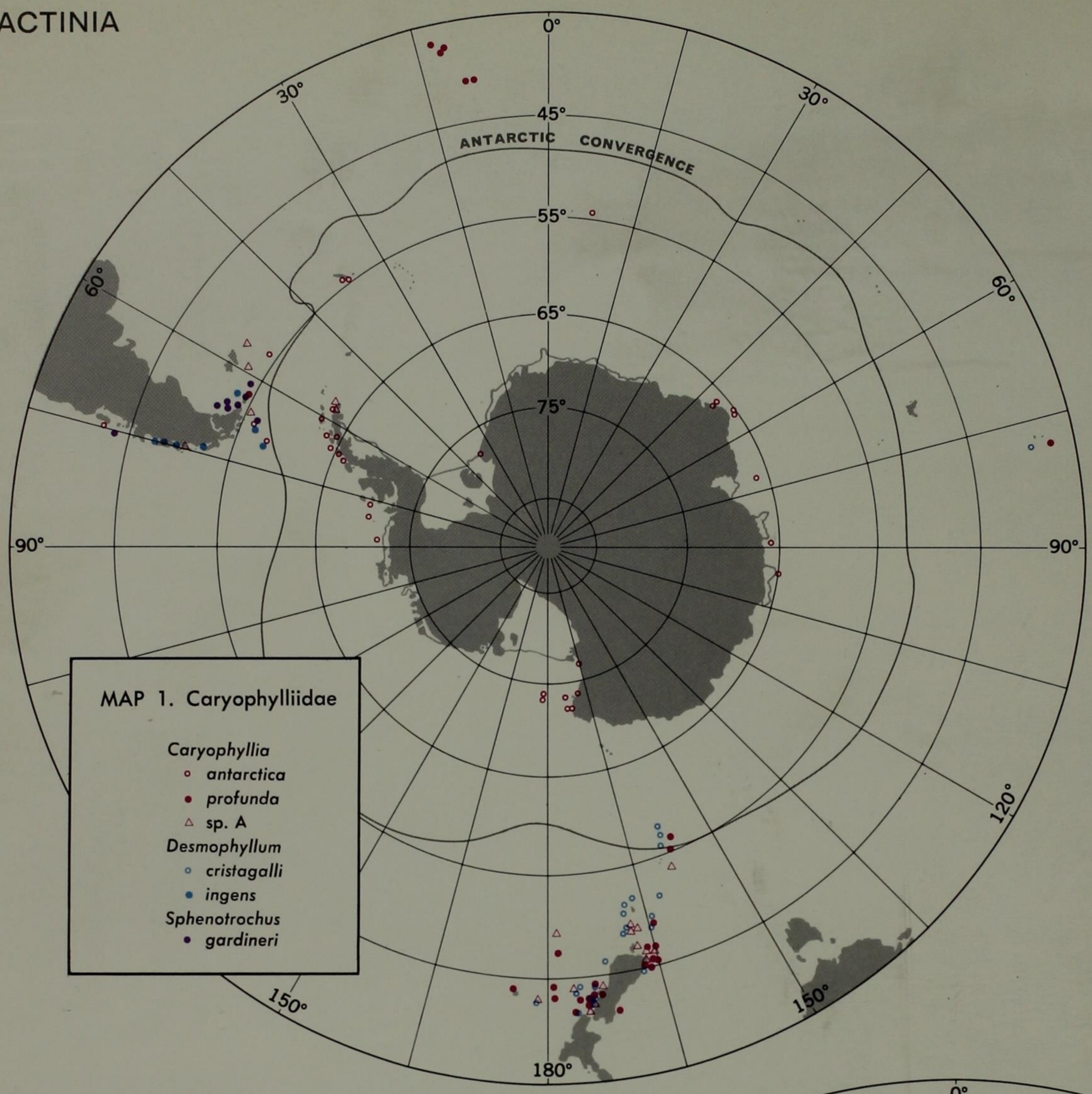
COMPILED BY H. BOSCHMA AND T. P. LOWE


0°
30°
30°
45°
ANTARCTIC CONVERGENCE
55°
60°
60°
65°
75°
90°
90°
120°
120°
150°
150°
180°
MAP 2
Errina
aspera
fissurata
labiata
echinata


ONVERGENCE
30°
60°
90°
120°
150°


0°
30°
30°
45°
ANTARCTIC CONVERGENCE
55°
60°
60°
65°
75°
90°
90°
120°
120°
150°
150°
180°
MAP 5
Sporadopora
dichotoma
mortenseni
n. sp.

SCLERACTINIA

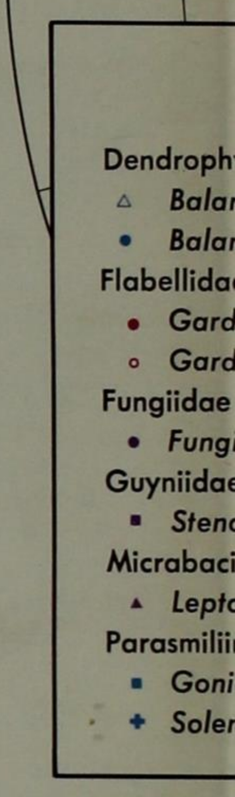


MAP 1. Caryophylliidae

Caryophyllia
- *antarctica*
- *profunda*
- sp. A

Desmophyllum
- *cristagalli*
- *ingens*

Sphenotrochus
- *gardineri*



Dendroph
- *Balan*
- *Balan*

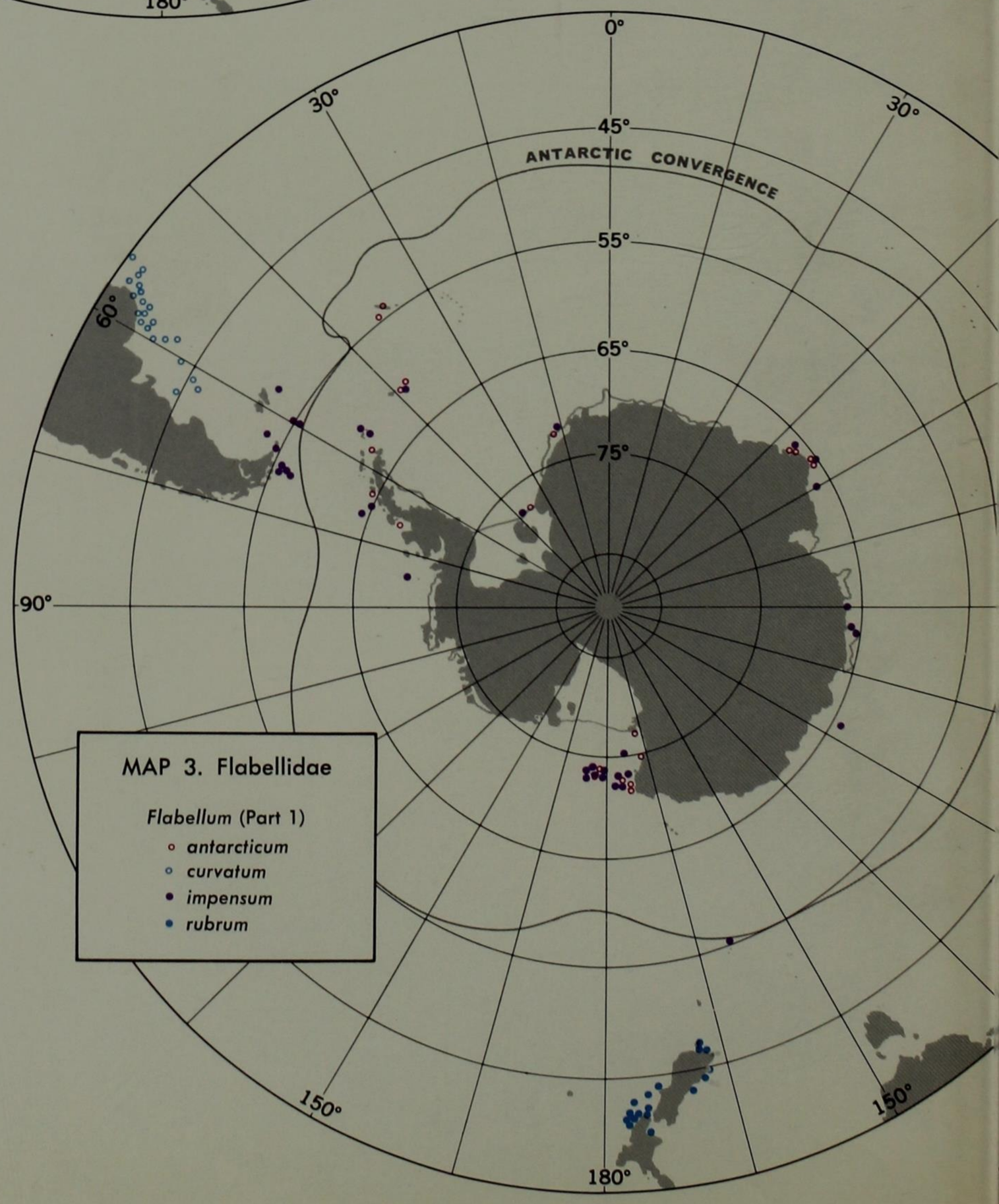
Flabellida
- *Gard*
- *Gard*

Fungiidae
- *Fungi*

Guyniidae
- *Stena*

Micrabaci
- *Lepto*

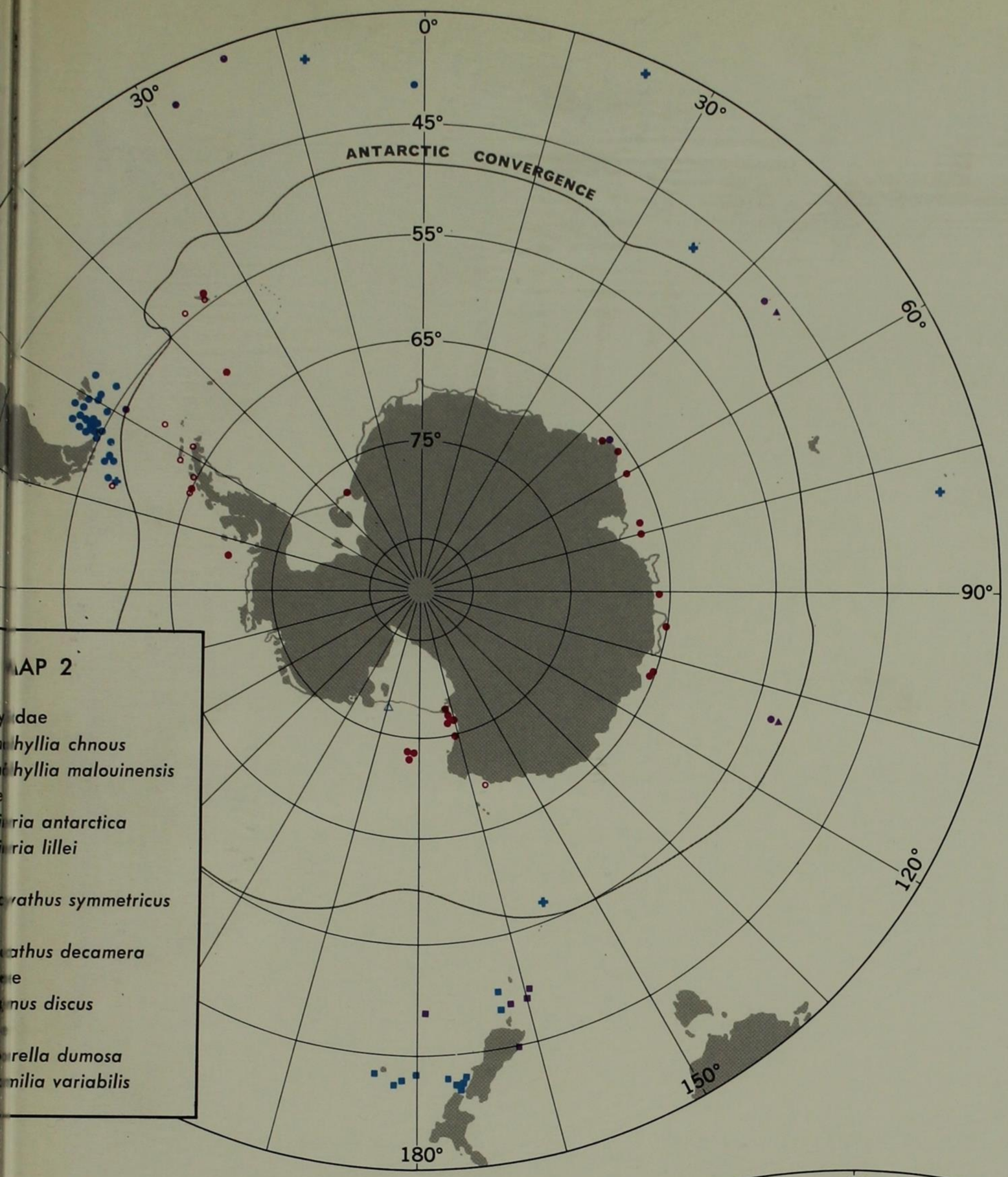
Parasmilii
- *Goni*
- *Soler*



MAP 3. Flabellidae

Flabellum (Part 1)
- *antarcticum*
- *curvatum*
- *impensum*
- *rubrum*

COMPILED BY D. F. SQUIRES



AP 2

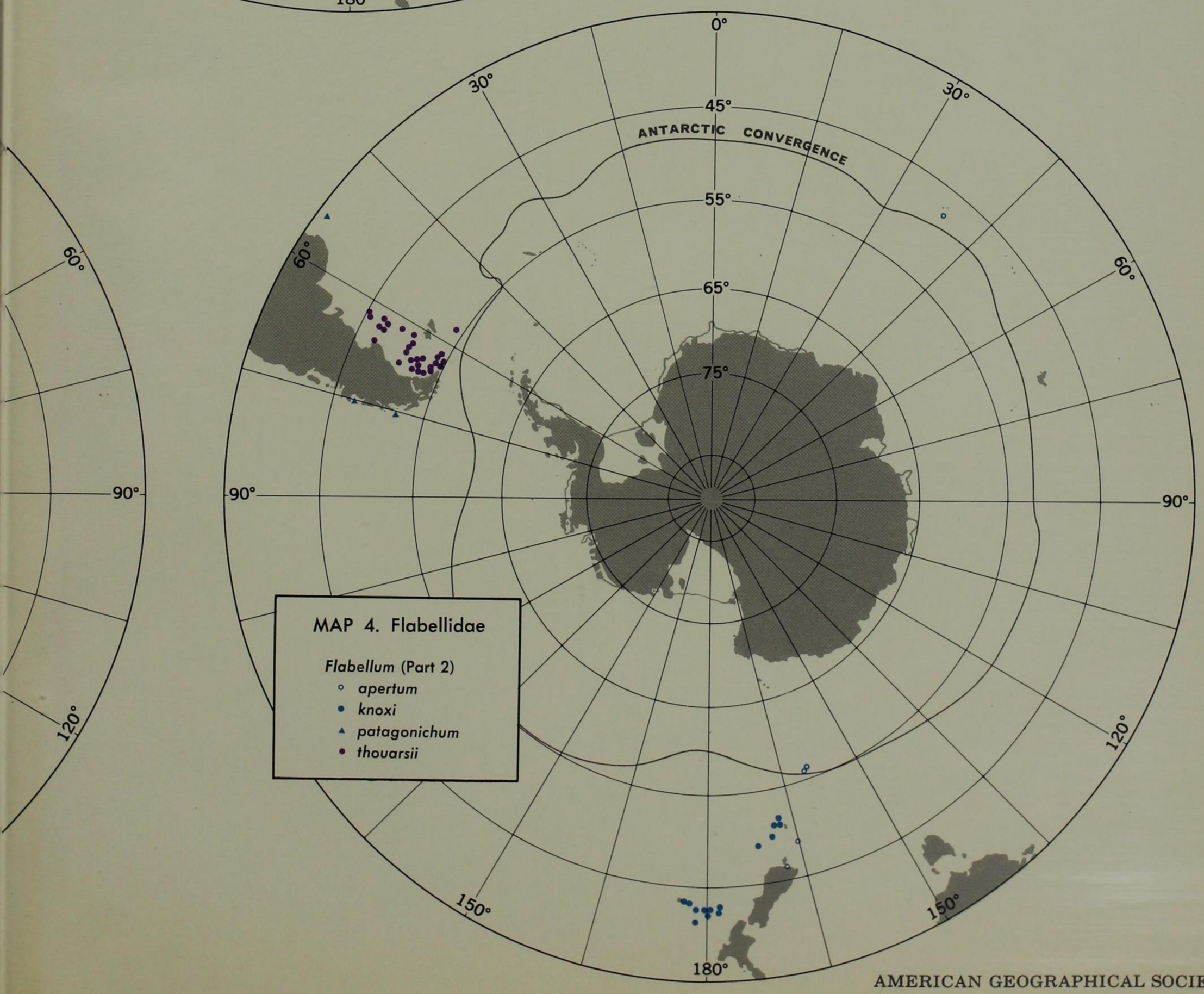
dae
hyllia chnous
hyllia malouinensis

ria antarctica
ria lillei

vathus symmetricus

athus decamera
e
nus discus

rella dumosa
milia variabilis



MAP 4. Flabellidae

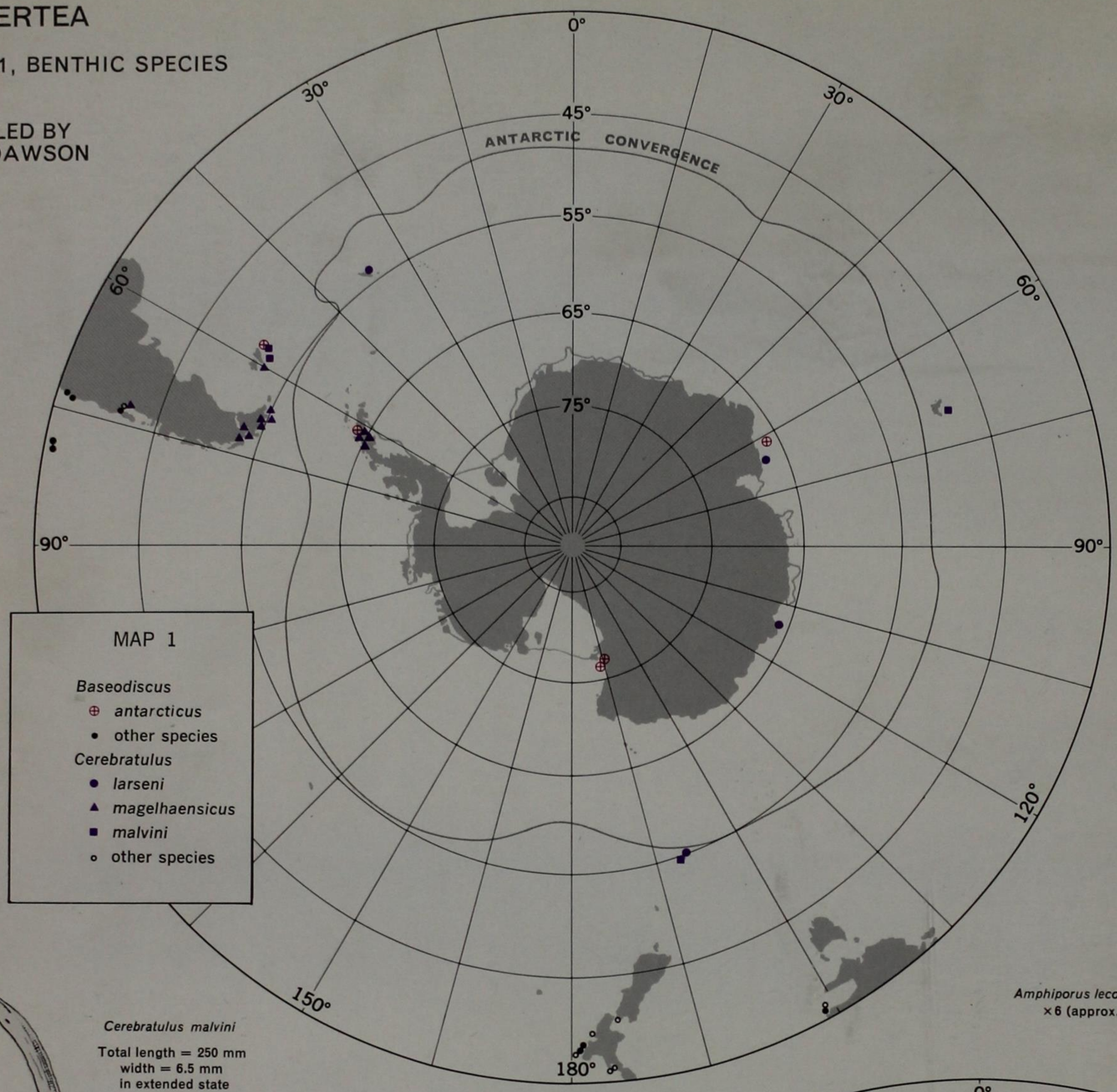
Flabellum (Part 2)
- *apertum*
- *knoxi*
- *patagonichum*
- *thouarsii*

AMERICAN GEOGRAPHICAL SOCIETY—1969

NEMERTEA

SHEET 1, BENTHIC SPECIES

COMPILED BY
E. W. DAWSON

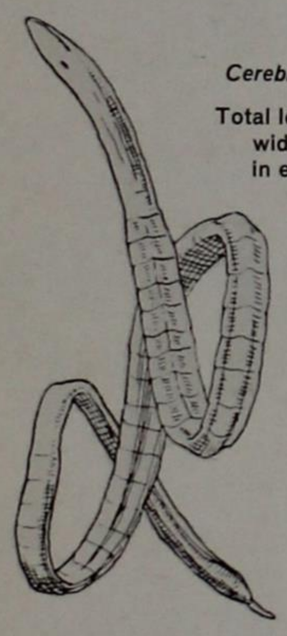


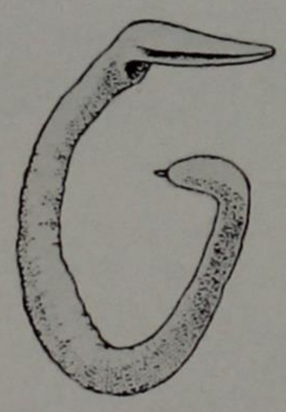
MAP 1

Baseodiscus
- ⊕ *antarcticus*
- • other species

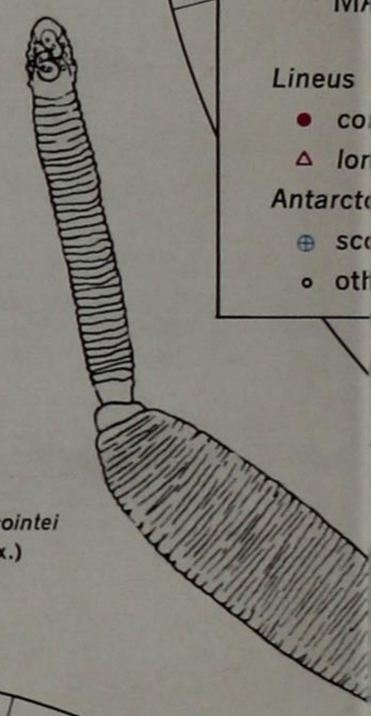
Cerebratulus
- ● *larseni*
- ▲ *magelhaensicus*
- ■ *malvini*
- ∘ other species

Cerebratulus malvini
Total length = 250 mm
width = 6.5 mm
in extended state

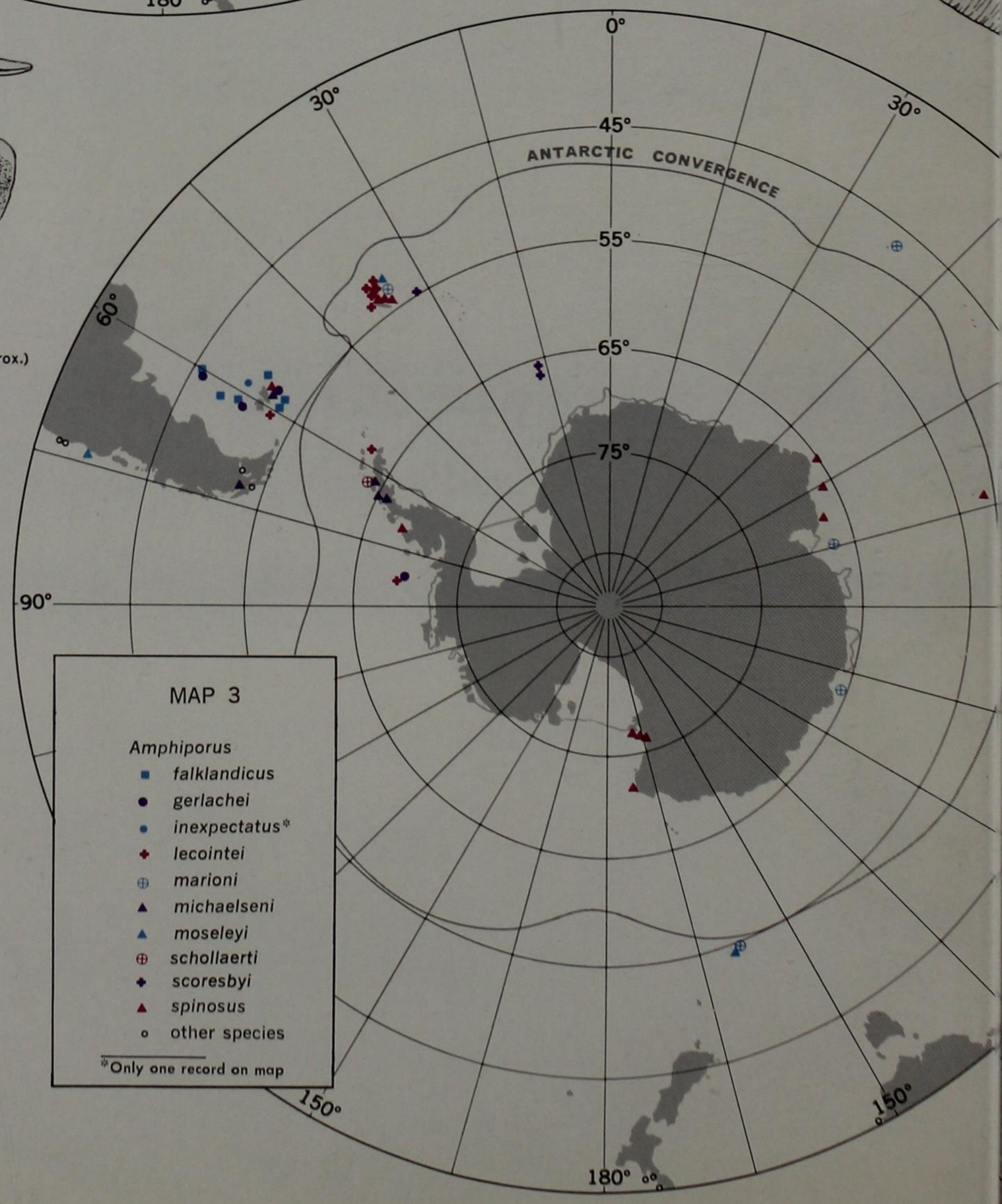




Cerebratulus larseni
Total length = 100 mm (approx.)



Amphiporus lecointei
×6 (approx.)



MAP 3

Amphiporus
- ■ *falklandicus*
- ● *gerlachei*
- • *inexpectatus**
- ✚ *lecointei*
- ⊕ *marioni*
- ▲ *michaelseni*
- ▲ *moseleyi*
- ⊕ *schollaerti*
- ✚ *scoresbyi*
- ▲ *spinosus*
- ∘ other species

*Only one record on map

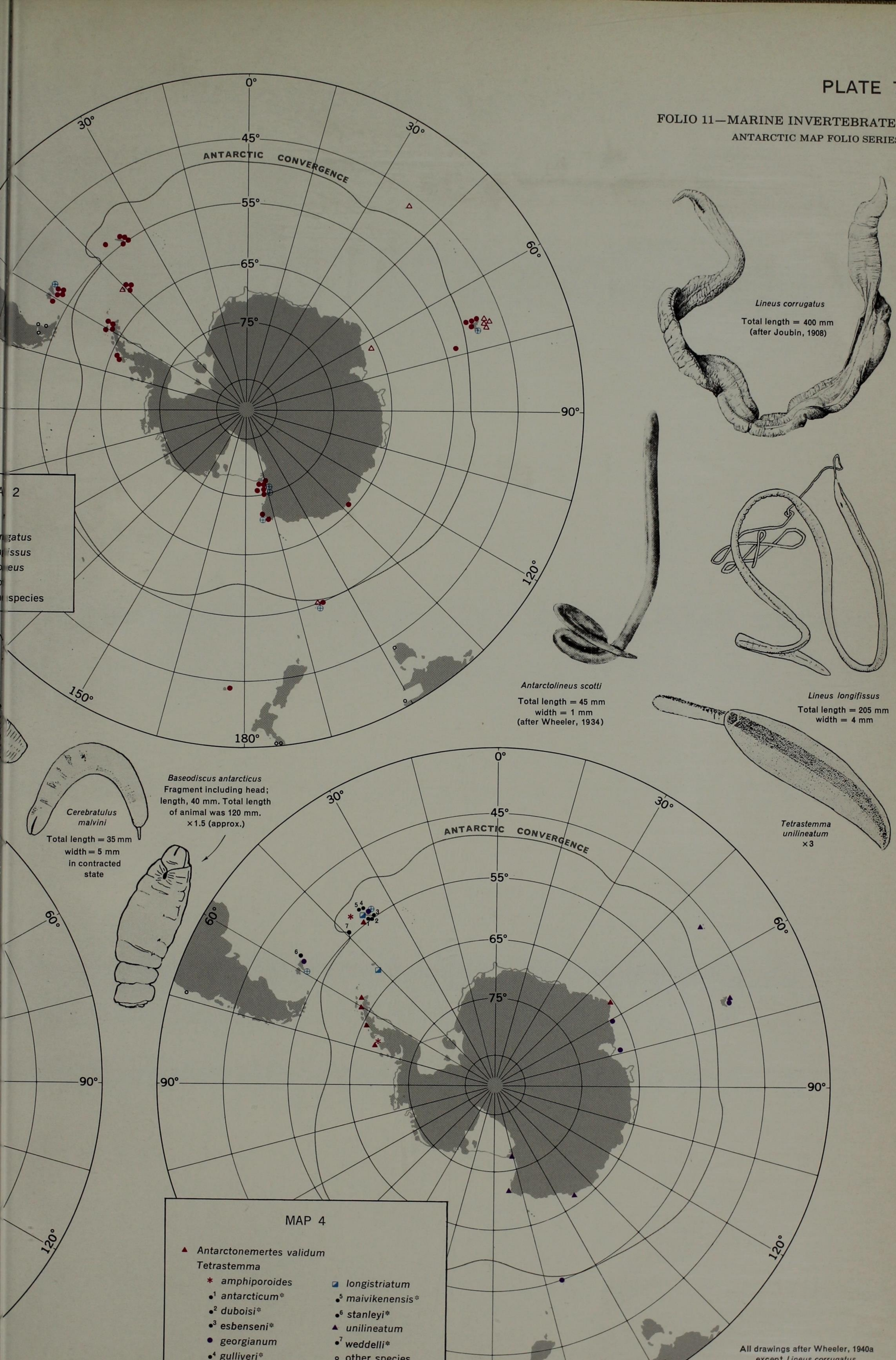
DEPTH RANGE AND SUBSTRATE CONDITIONS, ANTARCTIC BENTHIC NEMERTEA

*Letter symbols are for type of substrate: kh = kelp holdfasts, m = mud, mr = mud and rock, rs = rock and sand, st = under stones

PLATE 7

FOLIO 11—MARINE INVERTEBRATES

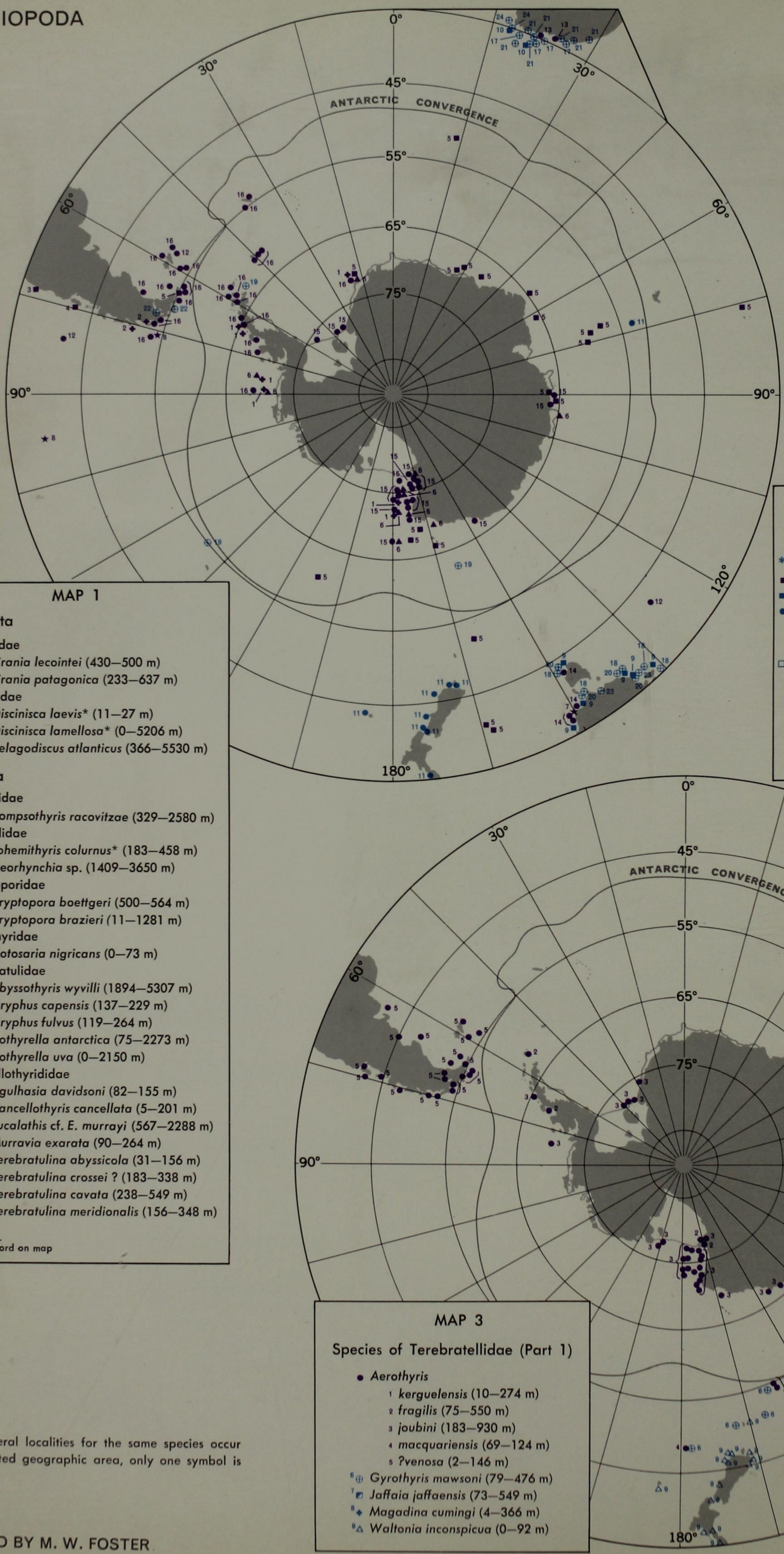
ANTARCTIC MAP FOLIO SERIES



All drawings after Wheeler, 1940a
except *Lineus corrugatus*
and *Antarctolineus scotti*

AMERICAN GEOGRAPHICAL SOCIETY—1969

BRACHIOPODA



MAP 1

Inarticulata

- Craniidae
  - 1 *Crania lecointei* (430—500 m)
  - 2 *Crania patagonica* (233—637 m)
- Discinidae
  - 3 *Discinisca laevis** (11—27 m)
  - 4 *Discinisca lamellosa** (0—5206 m)
  - 5 *Pelagodiscus atlanticus* (366—5530 m)

Articulata

- Frieleiidae
  - 6 *Compsothyris racovitzae* (329—2580 m)
- Basiliolidae
  - 7 *Eohemithyris colurnus** (183—458 m)
  - 8 *Neorhynchia* sp. (1409—3650 m)
- Cryptoporidae
  - 9 *Cryptopora boettgeri* (500—564 m)
  - 10 *Cryptopora brazieri* (11—1281 m)
- Hemithyridae
  - 11 *Notosaria nigricans* (0—73 m)
- Terebratulidae
  - 12 *Abyssothyris wyvilli* (1894—5307 m)
  - 13 *Gryphus capensis* (137—229 m)
  - 14 *Gryphus fulvus* (119—264 m)
  - 15 *Liothyrella antarctica* (75—2273 m)
  - 16 *Liothyrella uva* (0—2150 m)
- Cancellothyrididae
  - 17 *Agulhasia davidsoni* (82—155 m)
  - 18 *Cancellothyris cancellata* (5—201 m)
  - 19 *Eucalathis* cf. *E. murrayi* (567—2288 m)
  - 20 *Murravia exarata* (90—264 m)
  - 21 *Terebratulina abyssicola* (31—156 m)
  - 22 *Terebratulina crossei* ? (183—338 m)
  - 23 *Terebratulina cavata* (238—549 m)
  - 24 *Terebratulina meridionalis* (156—348 m)

*Only one record on map

Where several localities for the same species occur in a restricted geographic area, only one symbol is used.

COMPILED BY M. W. FOSTER

Species of Platidiid

- *1 *Amphithyris sp.* (392—641
- *2 *Platidia anomioides* (82—
- *3 *Aldingia willemoesi* (203—
- *Kraussina*
  - 4 *natalensis** (264 m)
  - 5 *rubra* (41—284 m)
- *Megerlina*
  - 6 *capensis** (183—220
  - 7 *lamarckiana* (0—201
  - 8 *pisum* (155—318 m)
  - 9 *striata* (58—264 m)

*Only one record on map

MAP 3

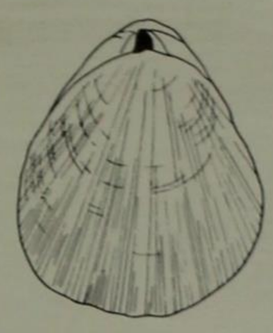
Species of Terebratellidae (Part 1)

- *Aerothyris*
  - 1 *kerguelensis* (10—274 m)
  - 2 *fragilis* (75—550 m)
  - 3 *joubini* (183—930 m)
  - 4 *macquariensis* (69—124 m)
  - 5 *?venosa* (2—146 m)
- 6 *Gyrothyris mawsoni* (79—476 m)
- 7 *Jaffaia jaffaensis* (73—549 m)
- 8 *Magadina cumingi* (4—366 m)
- 9 *Waltonia inconspicua* (0—92 m)

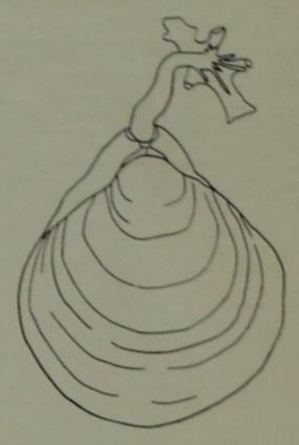
PLATE 9

FOLIO 11— MARINE INVERTEBRATES

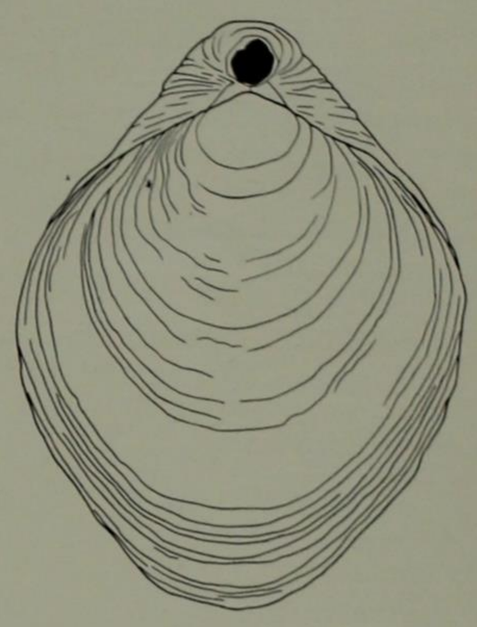
ANTARCTIC MAP FOLIO SERIES



Compsothyris racovitzae
(map 1)

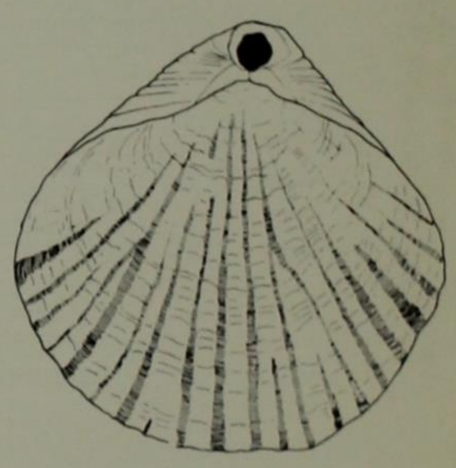


Liothyrella uva
(map 1)



Aerothyris joubini
(map 3)

All drawings
X2



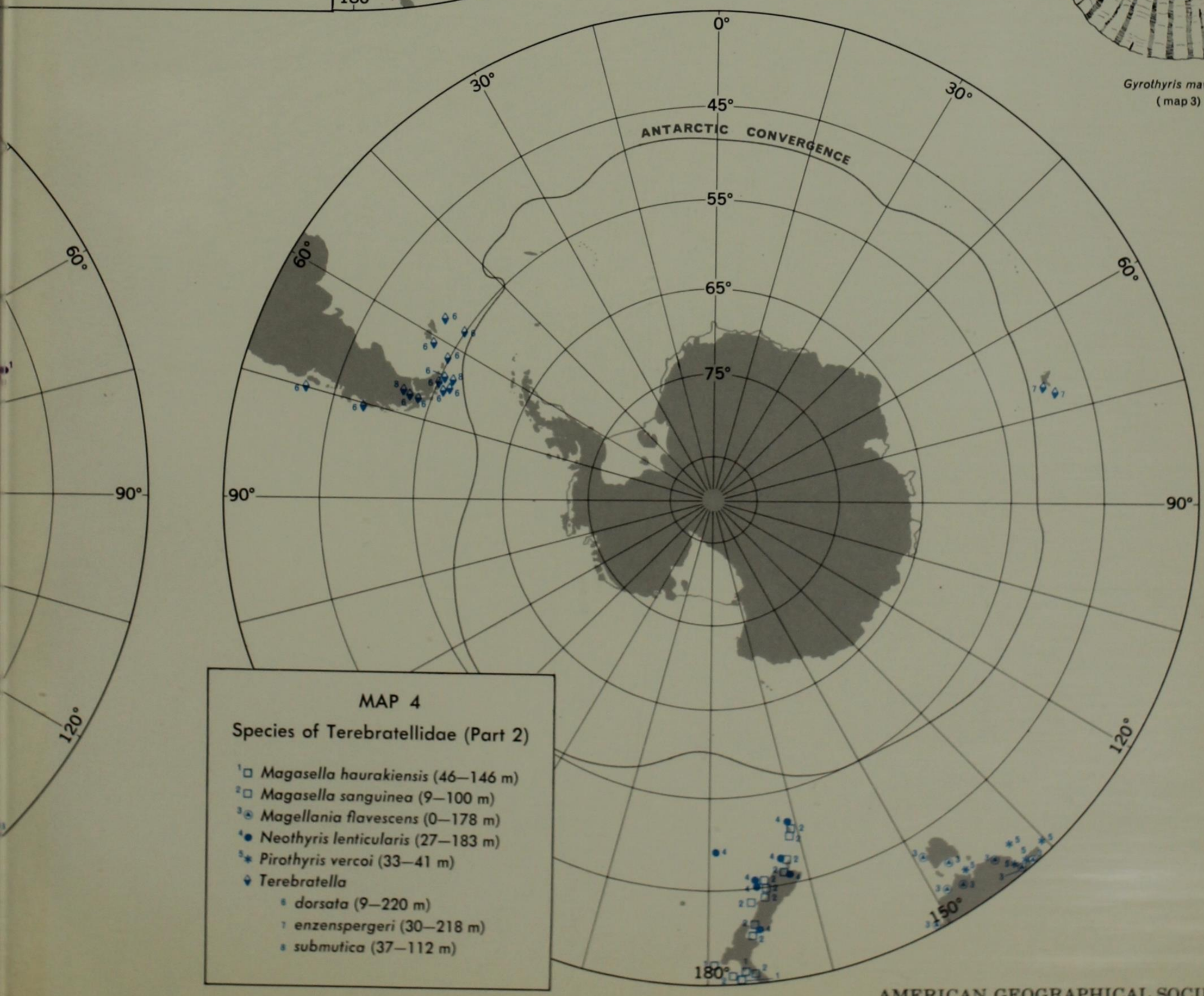
Gyrothyris mawsoni
(map 3)



MAP 2

, Kraussinidae, and Dallinidae

- *Campages furcifera* (203—265 m)
- *Macandrevia*
  - *americana* (223—4066 m)
  - *diamantina** (2580—4066 m)
  - *vanhoffeni* (385—930 m)



MAP 4

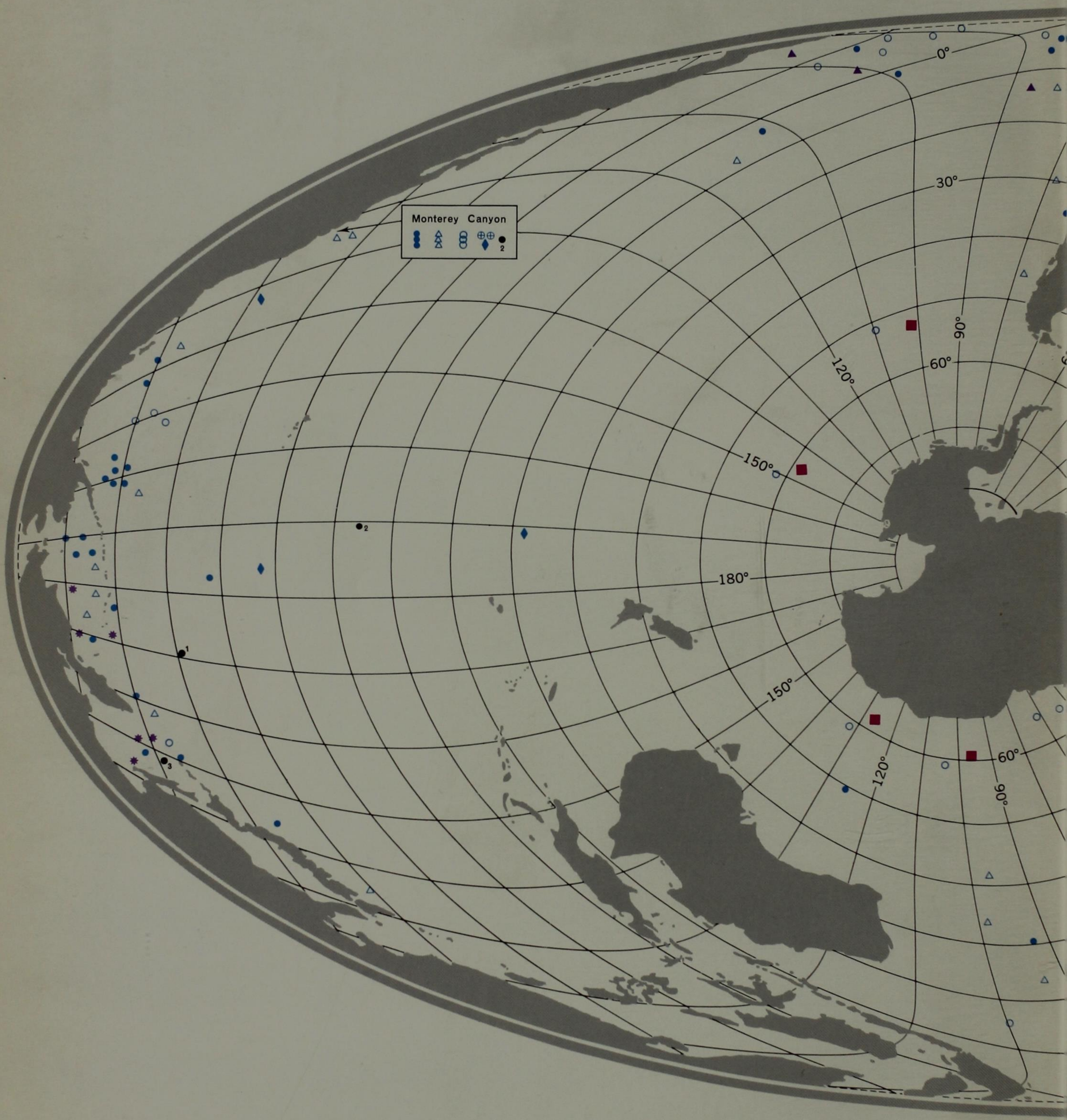
Species of Terebratellidae (Part 2)

- *Magasella haurakiensis* (46—146 m)
- *Magasella sanguinea* (9—100 m)
- *Magellania flavescens* (0—178 m)
- *Neothyris lenticularis* (27—183 m)
- *Pirothyris vercoi* (33—41 m)
- *Terebratella*
  - *dorsata* (9—220 m)
  - *enzenspergeri* (30—218 m)
  - *submutica* (37—112 m)

AMERICAN GEOGRAPHICAL SOCIETY—1969

NEMERTEA

SHEET 2, PELAGIC GENERA



Amphiporidae
- ☼ *Cratenemertes***

Nectonemertidae
- ⊕ *Chunianna*
- ▲ *Dinonemertes*
- △ *Nectonemertes*
- ○ *Planktonemertes*
- ●[1] *Plenanemertes**
- ●[2] *Tononemertes**
- ♦ *Tubonemertes*

Armaneriidae
- ■ *Armaneria*
- ✸ *Mesarmaneria*
- ●[3] *Proarmaneria**

Pelagonemertidae
- ■ *Obnemertes*
- ● *Pelagonemertes*

* Only one record on map

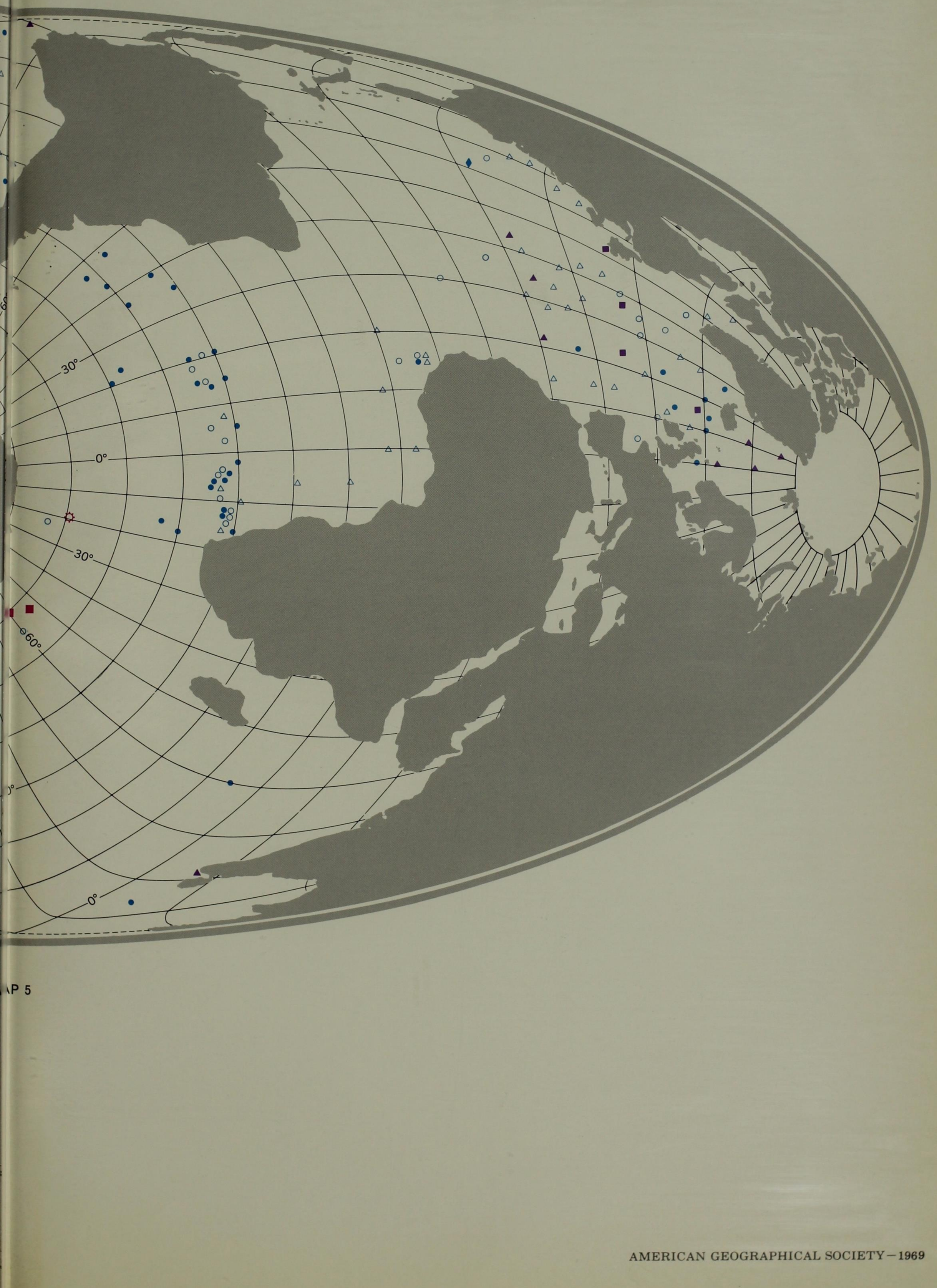
** Recently changed to *Korotkevitschia* (see Friedrich, 1968)

COMPILED BY E. W. DAWSON

PLATE 8

FOLIO 11—MARINE INVERTEBRATES

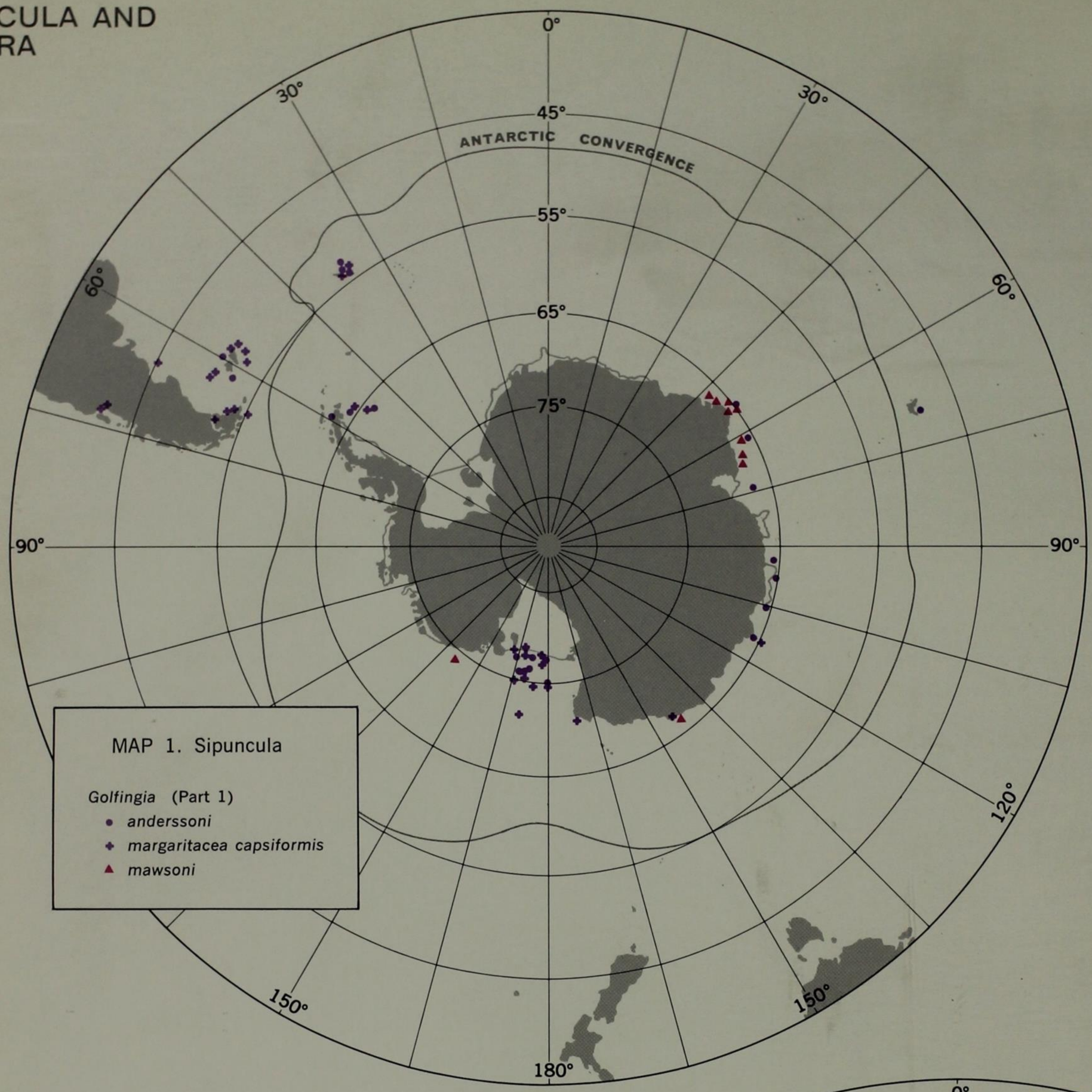
ANTARCTIC MAP FOLIO SERIES



AP 5

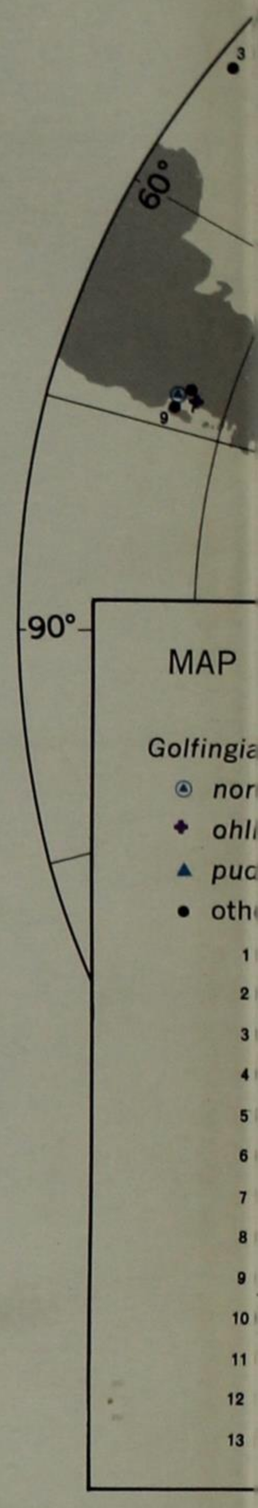
AMERICAN GEOGRAPHICAL SOCIETY—1969

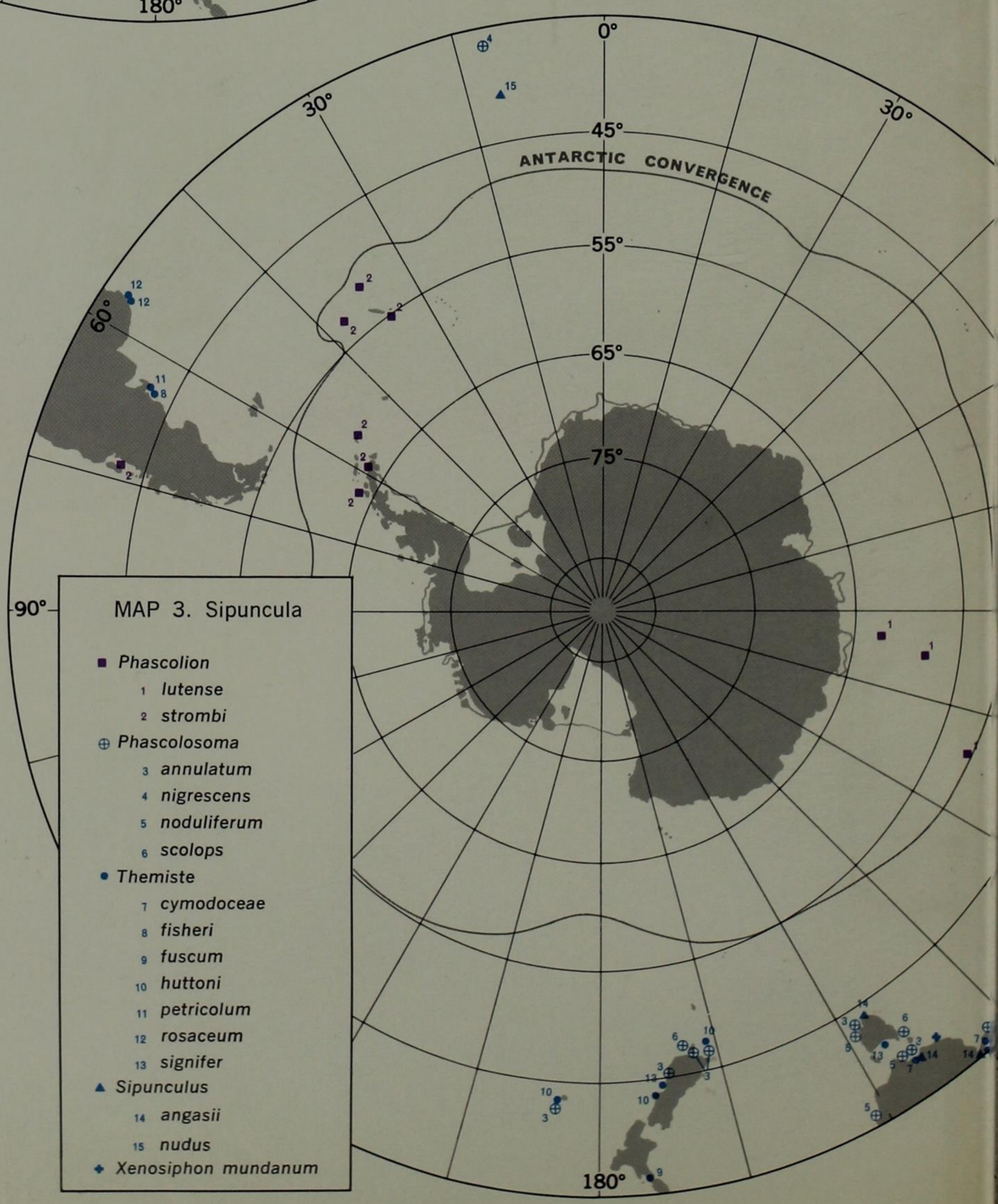
SIPUNCULA AND ECHIURA



MAP 1. Sipuncula

Golfingia (Part 1)
- *anderssoni*
- *margaritacea capsiformis*
- *mawsoni*

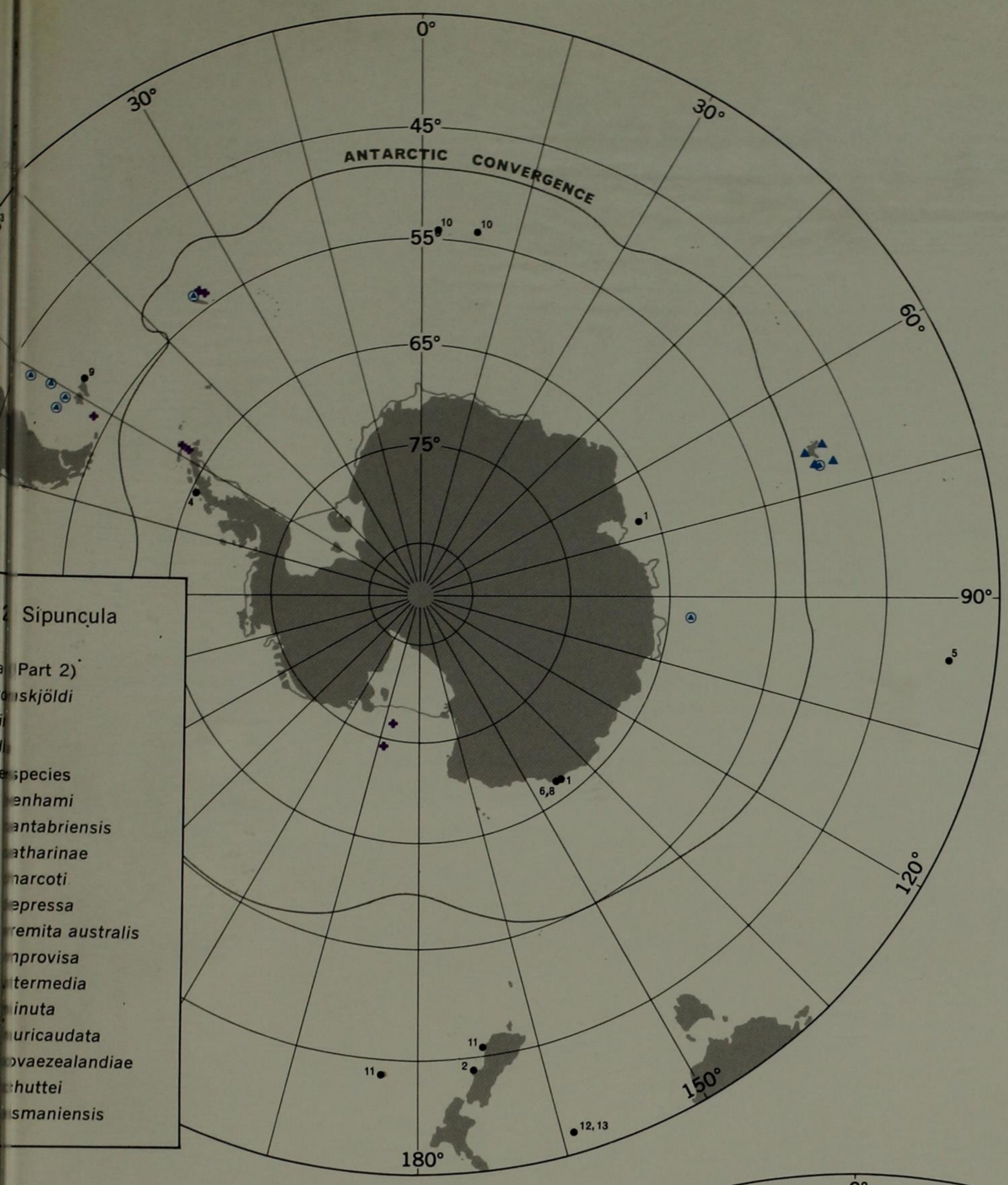




MAP 3. Sipuncula

- *Phascolion*
  - 1 *lutense*
  - 2 *strombi*
- ⊕ *Phascolosoma*
  - 3 *annulatum*
  - 4 *nigrescens*
  - 5 *noduliferum*
  - 6 *scolops*
- • *Themiste*
  - 7 *cymodoceae*
  - 8 *fisheri*
  - 9 *fuscum*
  - 10 *huttoni*
  - 11 *petricolum*
  - 12 *rosaceum*
  - 13 *signifer*
- ▲ *Sipunculus*
  - 14 *angasii*
  - 15 *nudus*
- ✚ *Xenosiphon mundanum*

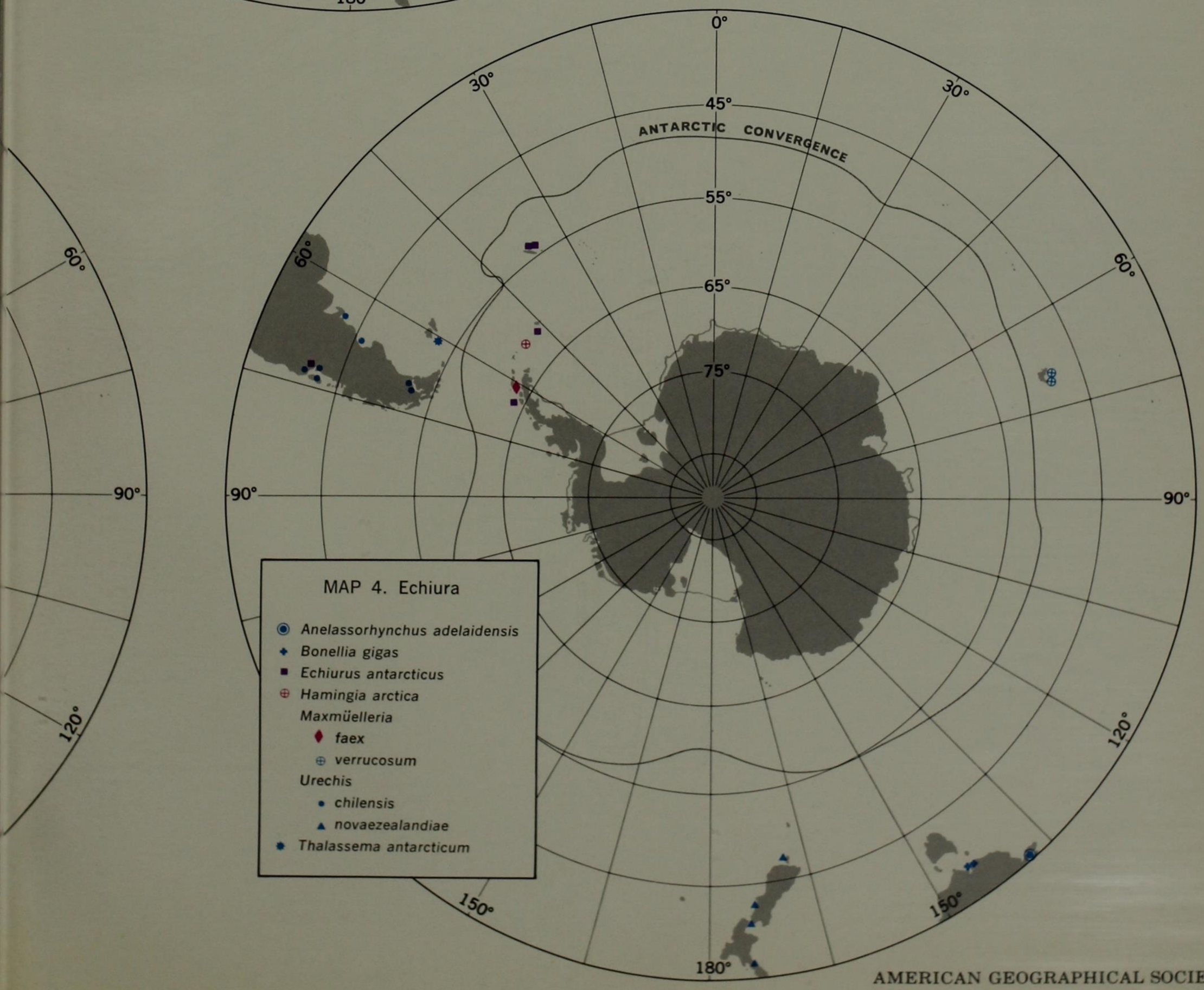
COMPILED BY S. J. EDMONDS



2 Sipuncula

(Part 2)
nskjöldi

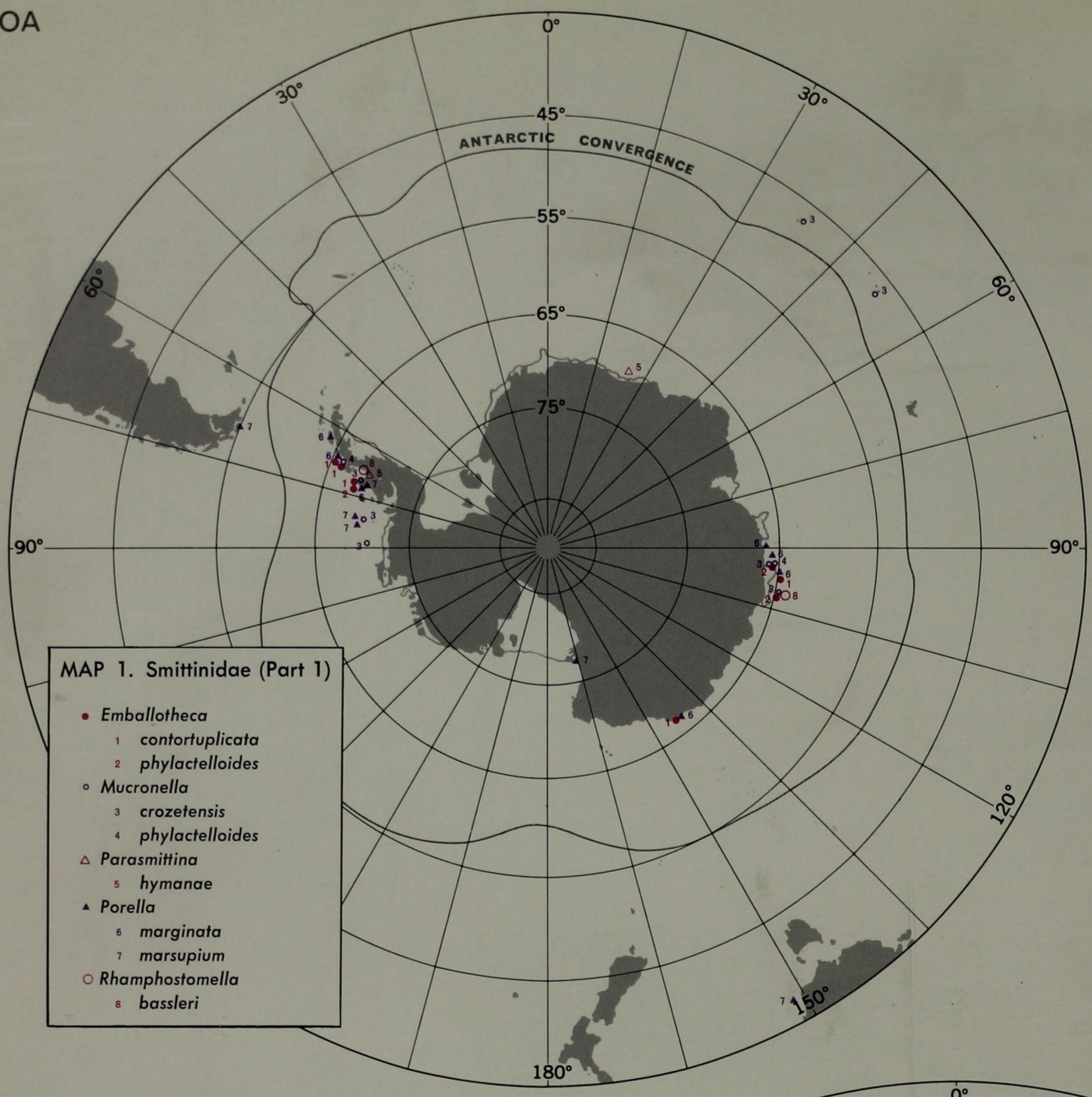
species
enhami
antabriensis
atharinae
narcoti
epressa
remita australis
mprovisa
termedia
inuta
uricaudata
ovaezealandiae
chuttei
smaniensis



MAP 4. Echiura

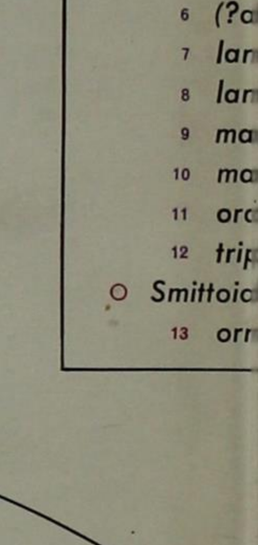
- *Anelassorhynchus adelaidensis*
- *Bonellia gigas*
- *Echiurus antarcticus*
- *Hamingia arctica*
- *Maxmüelleria*
  - *faex*
  - *verrucosum*
- *Urechis*
  - *chilensis*
  - *novaezealandiae*
- *Thalassema antarcticum*

BRYOZOA



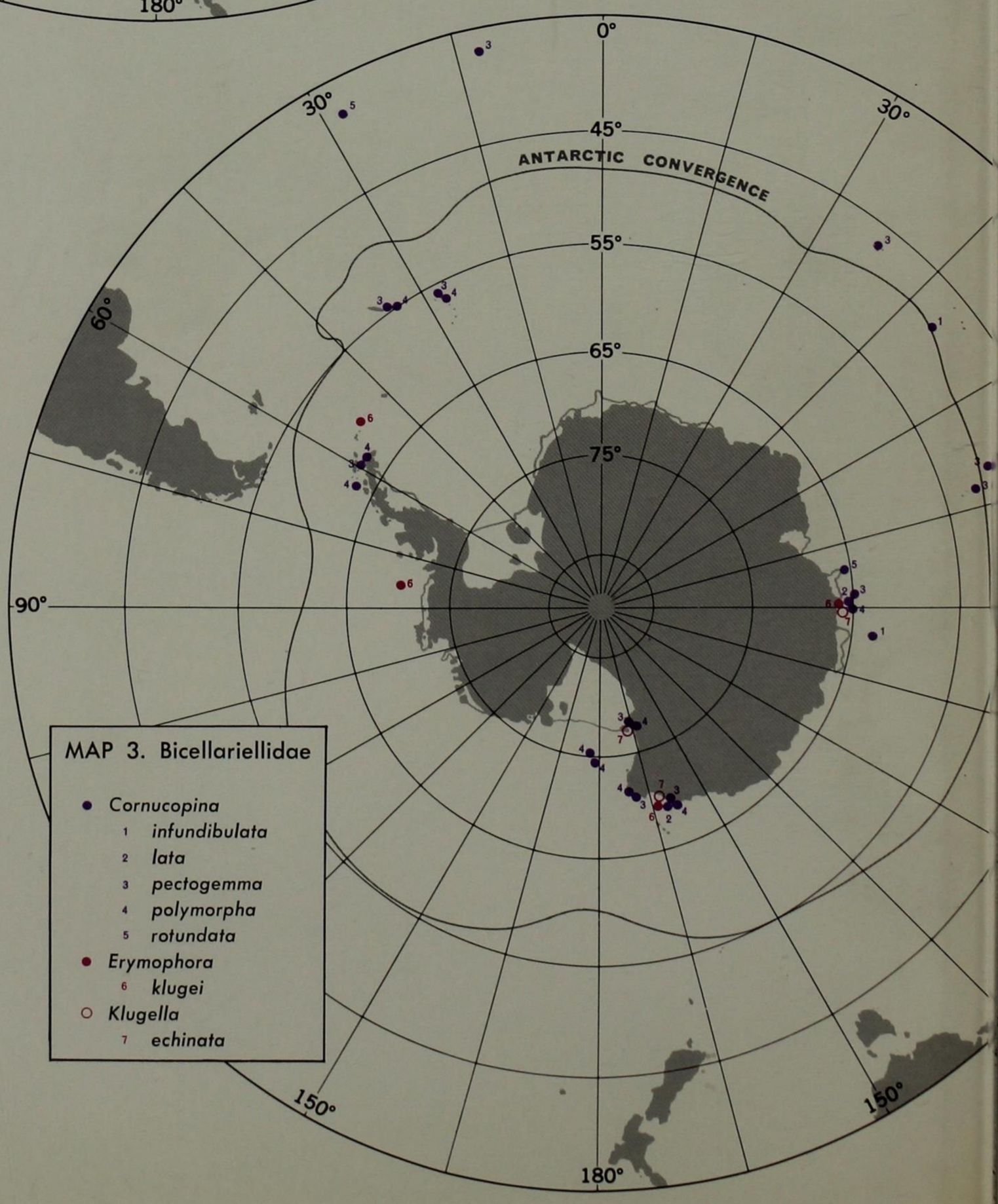
MAP 1. Smittinidae (Part 1)

- ● *Emballotheca*
  - 1 *contortuplicata*
  - 2 *phylactelloides*
- ○ *Mucronella*
  - 3 *crozetensis*
  - 4 *phylactelloides*
- △ *Parasmittina*
  - 5 *hymanae*
- ▲ *Porella*
  - 6 *marginata*
  - 7 *marsupium*
- ○ *Rhamphostomella*
  - 8 *bassleri*



MAP 2. Sm

- ● *Smittina*
  - 1 ab
  - 2 an
  - 3 ca
  - 4 cin
  - 5 co
  - 6 (?a
  - 7 lar
  - 8 lar
  - 9 ma
  - 10 ma
  - 11 orc
  - 12 trip
- ○ *Smittoic*
  - 13 orr



MAP 3. Bicellariellidae

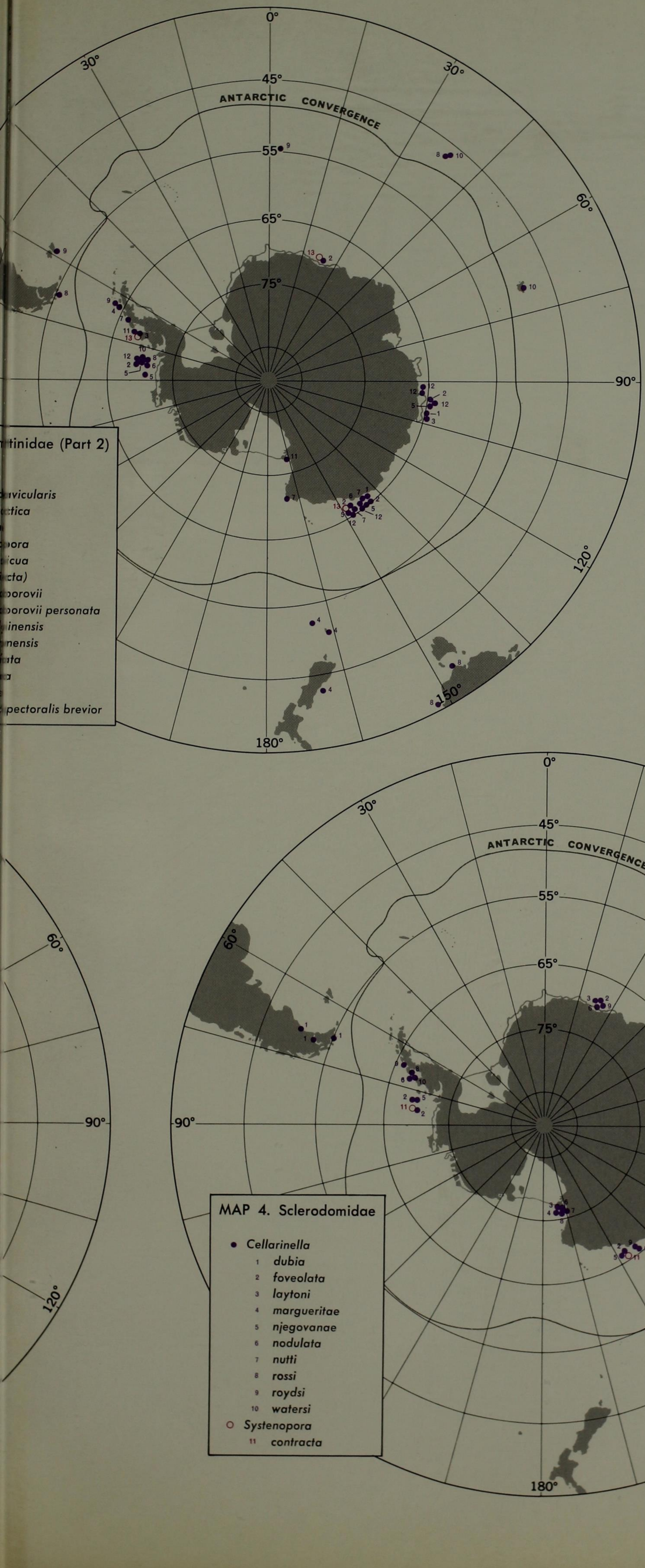
- ● *Cornucopina*
  - 1 *infundibulata*
  - 2 *lata*
  - 3 *pectogemma*
  - 4 *polymorpha*
  - 5 *rotundata*
- ● *Erymophora*
  - 6 *klugei*
- ○ *Klugella*
  - 7 *echinata*

COMPILED BY J. S. BULLIVANT

PLATE 10

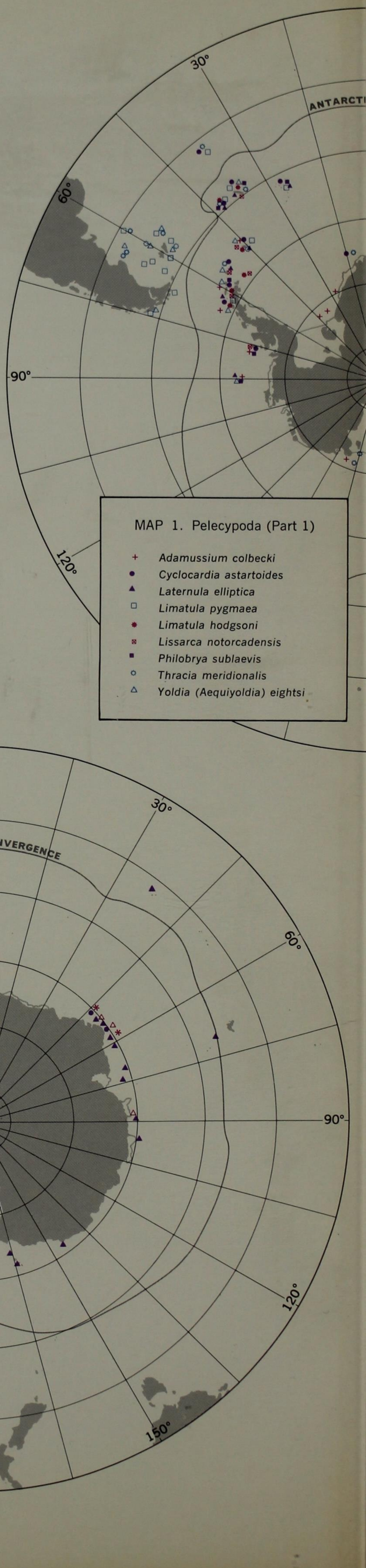
FOLIO 11—MARINE INVERTEBRATES

ANTARCTIC MAP FOLIO SERIES



AMERICAN GEOGRAPHICAL SOCIETY—1969

BENTHIC MOLLUSCA

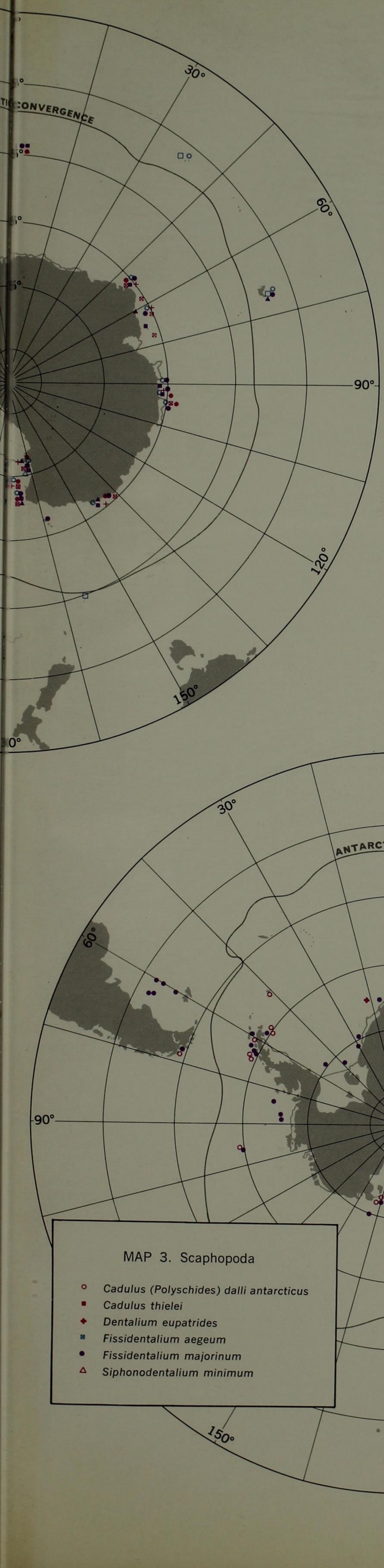


COMPILED BY R. K. DELL

PLATE 12

FOLIO 11—MARINE INVERTEBRATES

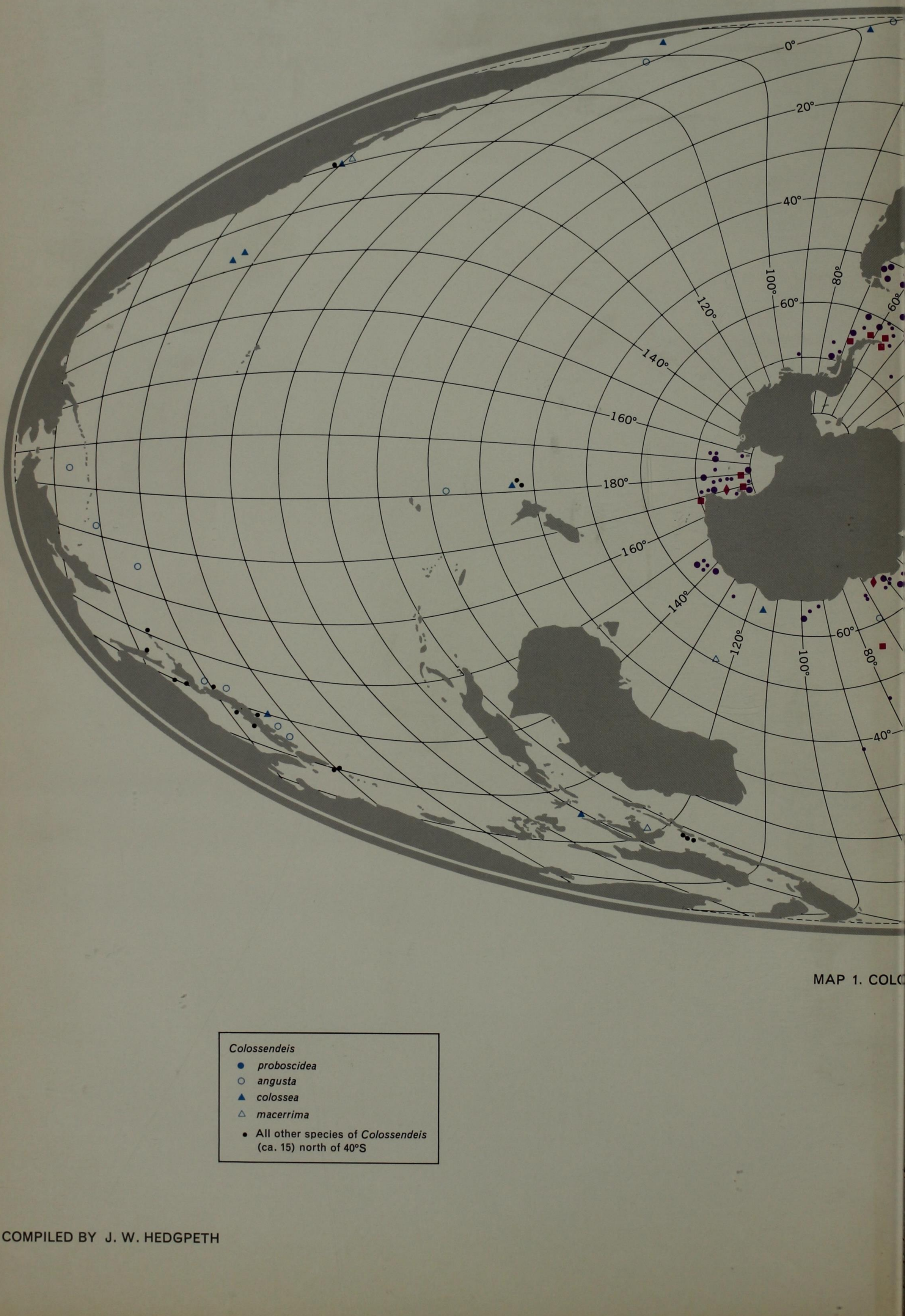
ANTARCTIC MAP FOLIO SERIES



AMERICAN GEOGRAPHICAL SOCIETY—1969

PYCNOGONIDA

SHEET 1



Colossendeis

- ● *proboscidea*
- ○ *angusta*
- ▲ *colossea*
- △ *macerrima*
- • All other species of *Colossendeis* (ca. 15) north of 40°S

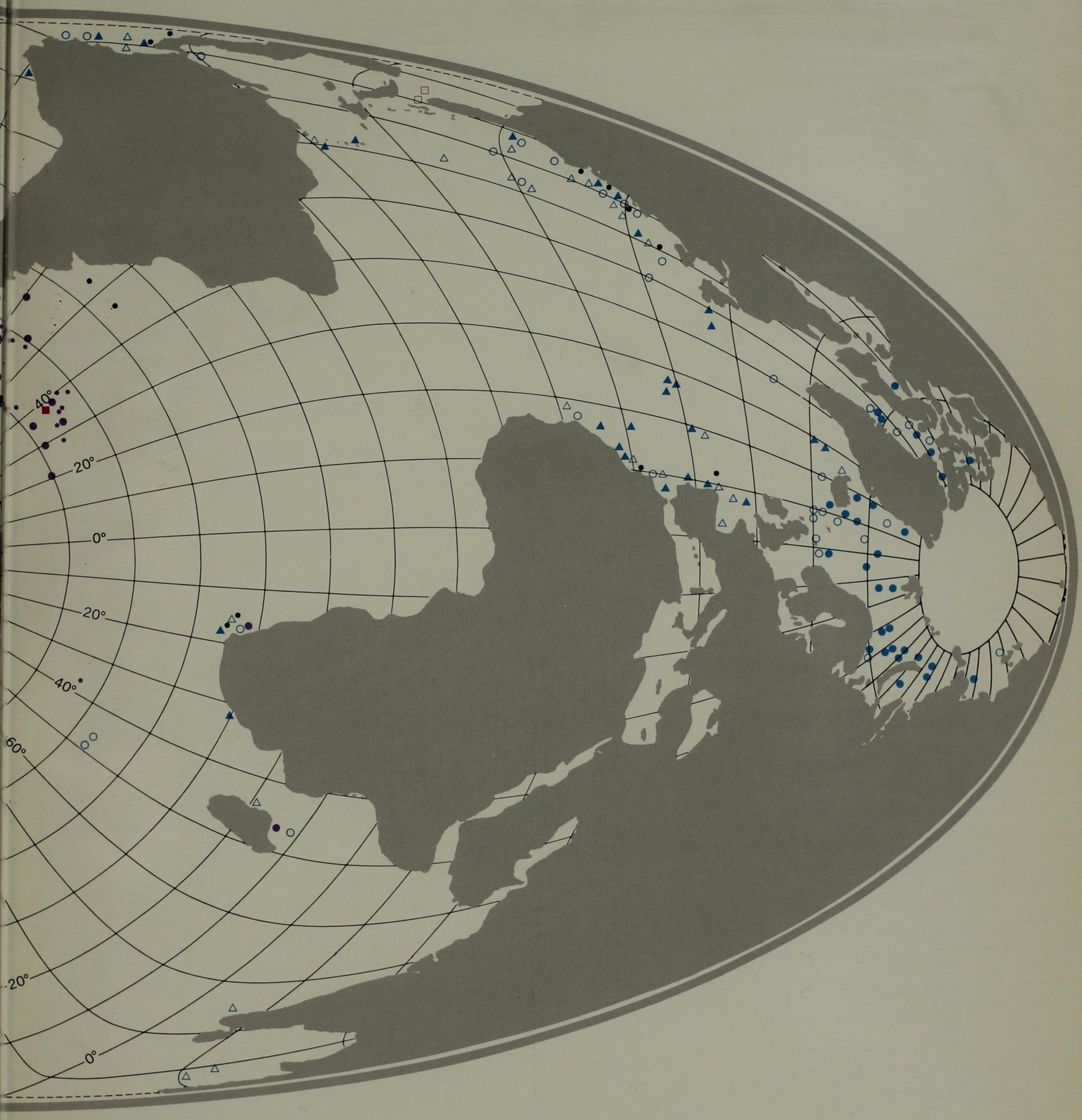
MAP 1. COLO

COMPILED BY J. W. HEDGPETH

PLATE 13

FOLIO 11 — MARINE INVERTEBRATES

ANTARCTIC MAP FOLIO SERIES



SENDEIDAE

- ● *Colossendeis megalonyx*
- • All other species of *Collosendeis* (ca. 10) S of 45°S

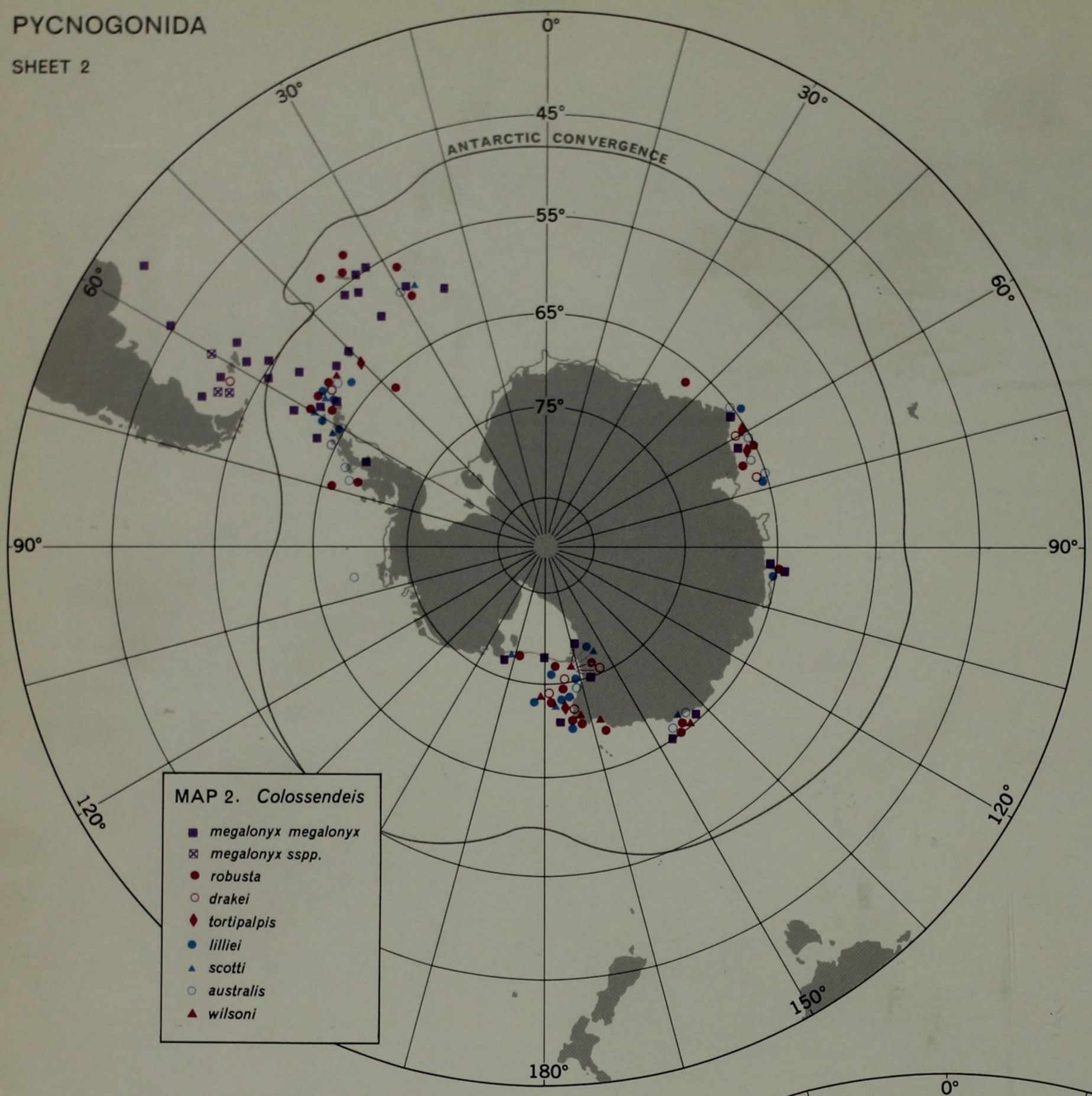
Polymerous Forms

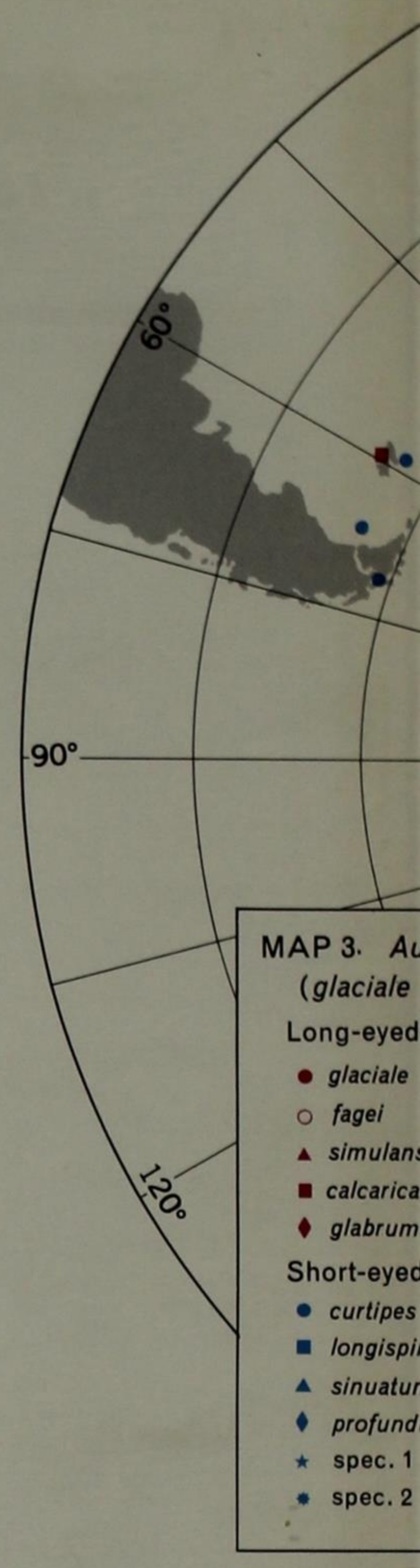
- ■ *Decolopoda australis*
- ♦ *Dodecolopoda mawsoni*
- □ *Pentacolossendeis reticulata*

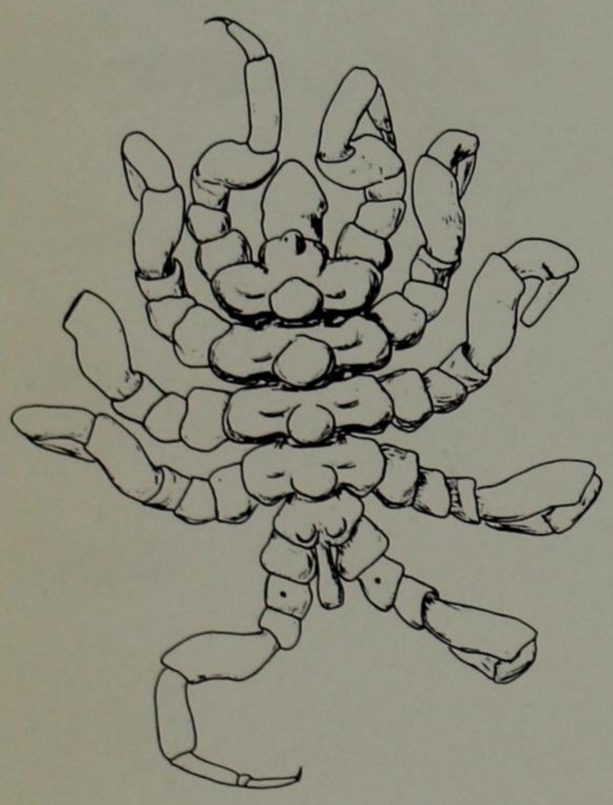
AMERICAN GEOGRAPHICAL SOCIETY — 1969

PYCNOGONIDA

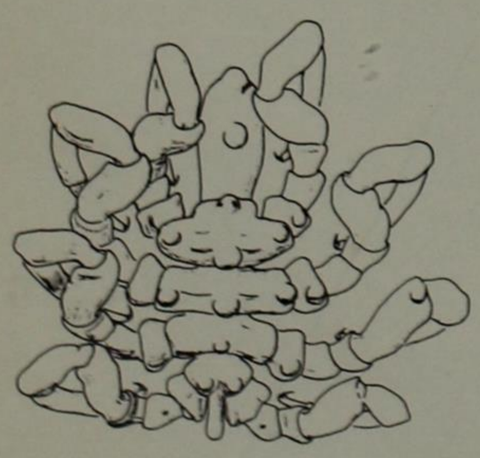
SHEET 2





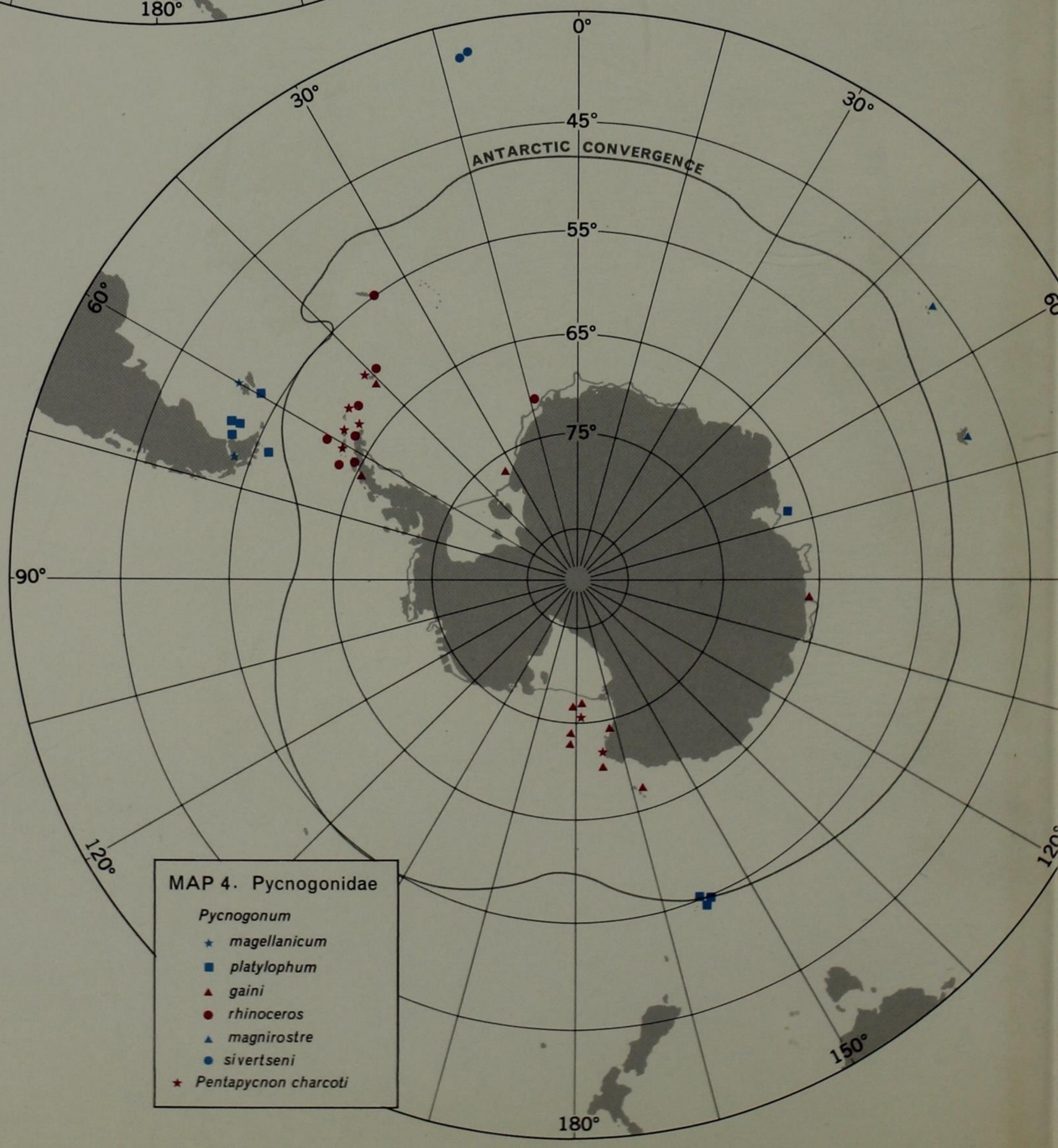


Pentapycnon charcoti
X 2.4

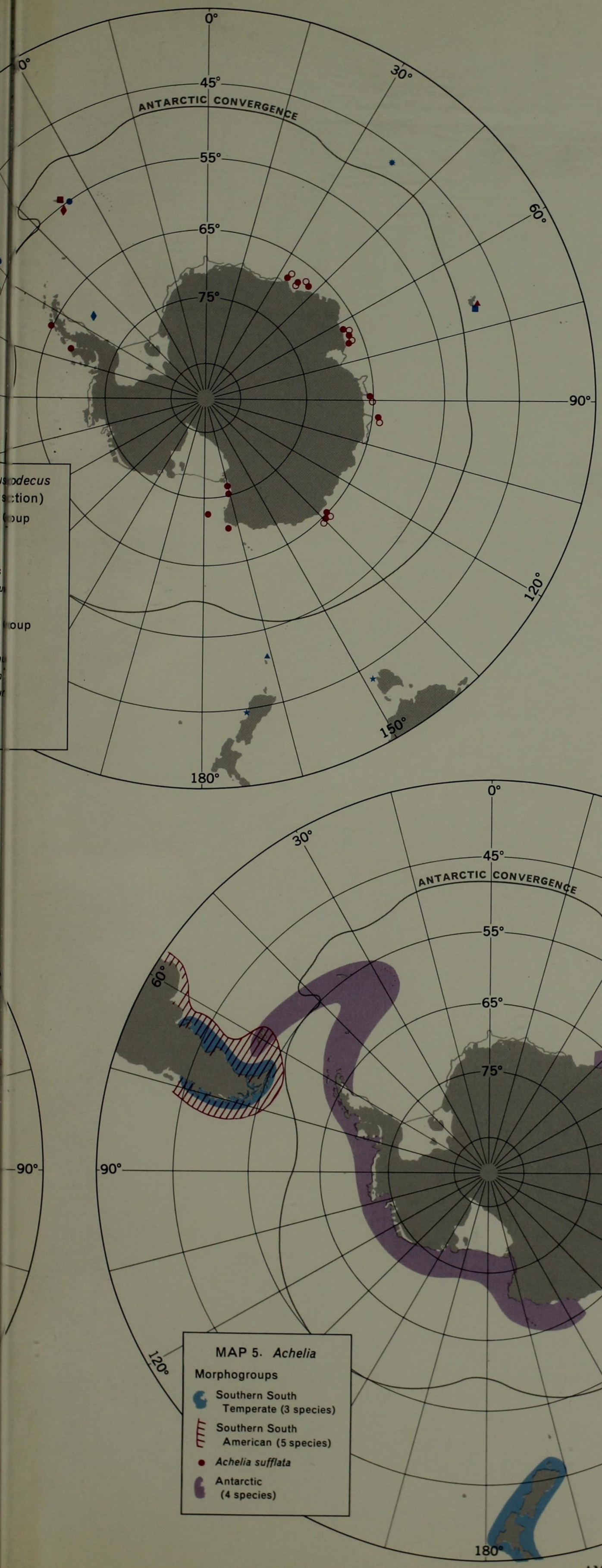


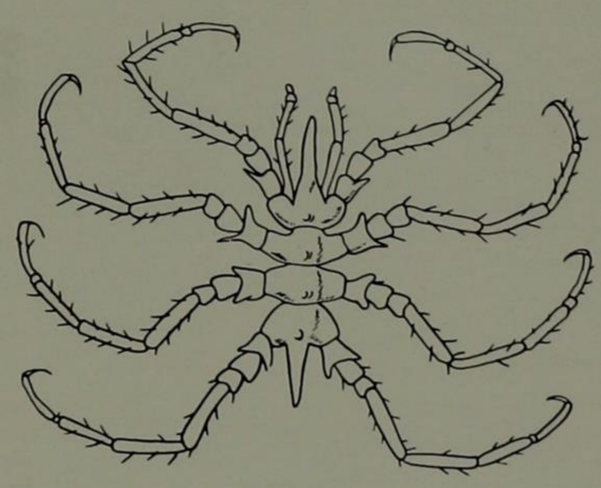
Pycnogonum rhinoceros
X 1.5

Drawings by author



COMPILED BY J. W. HEDGPETH

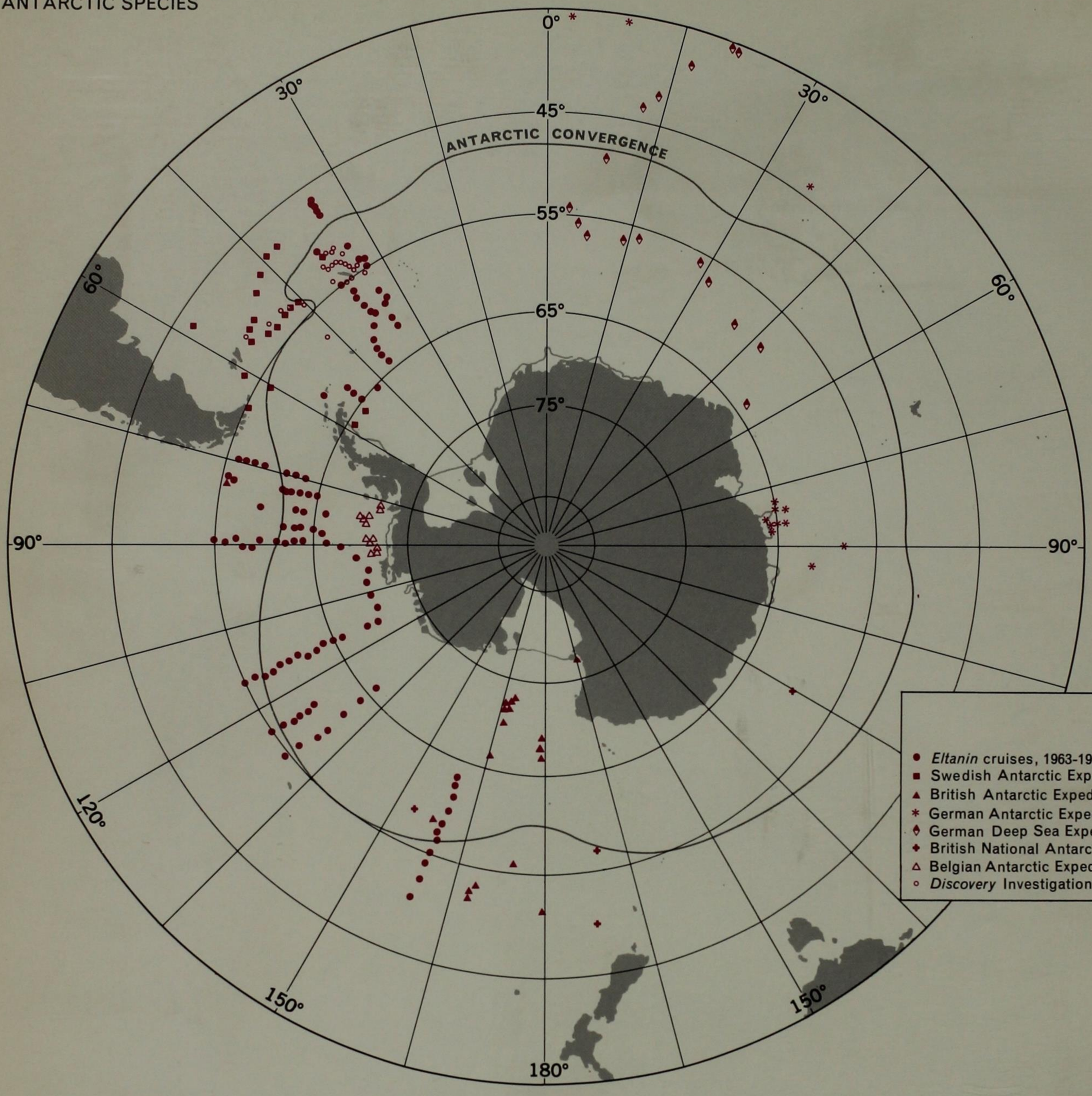




Austrodecus glaciale
X 14

PLANKTONIC OSCTRACODA (HALOCYPRIDAE)

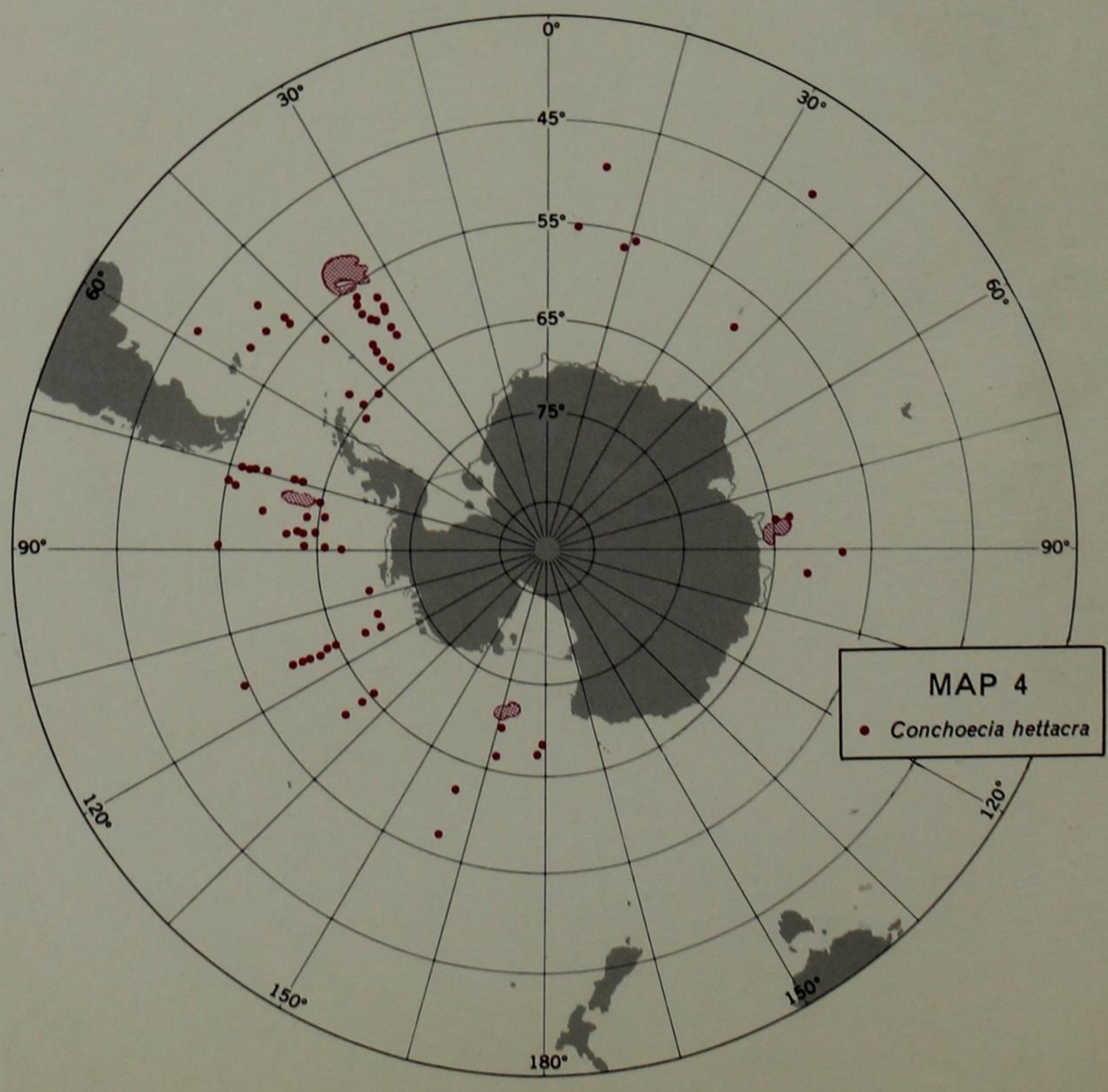
ANTARCTIC SPECIES



MAP 1
Station Map

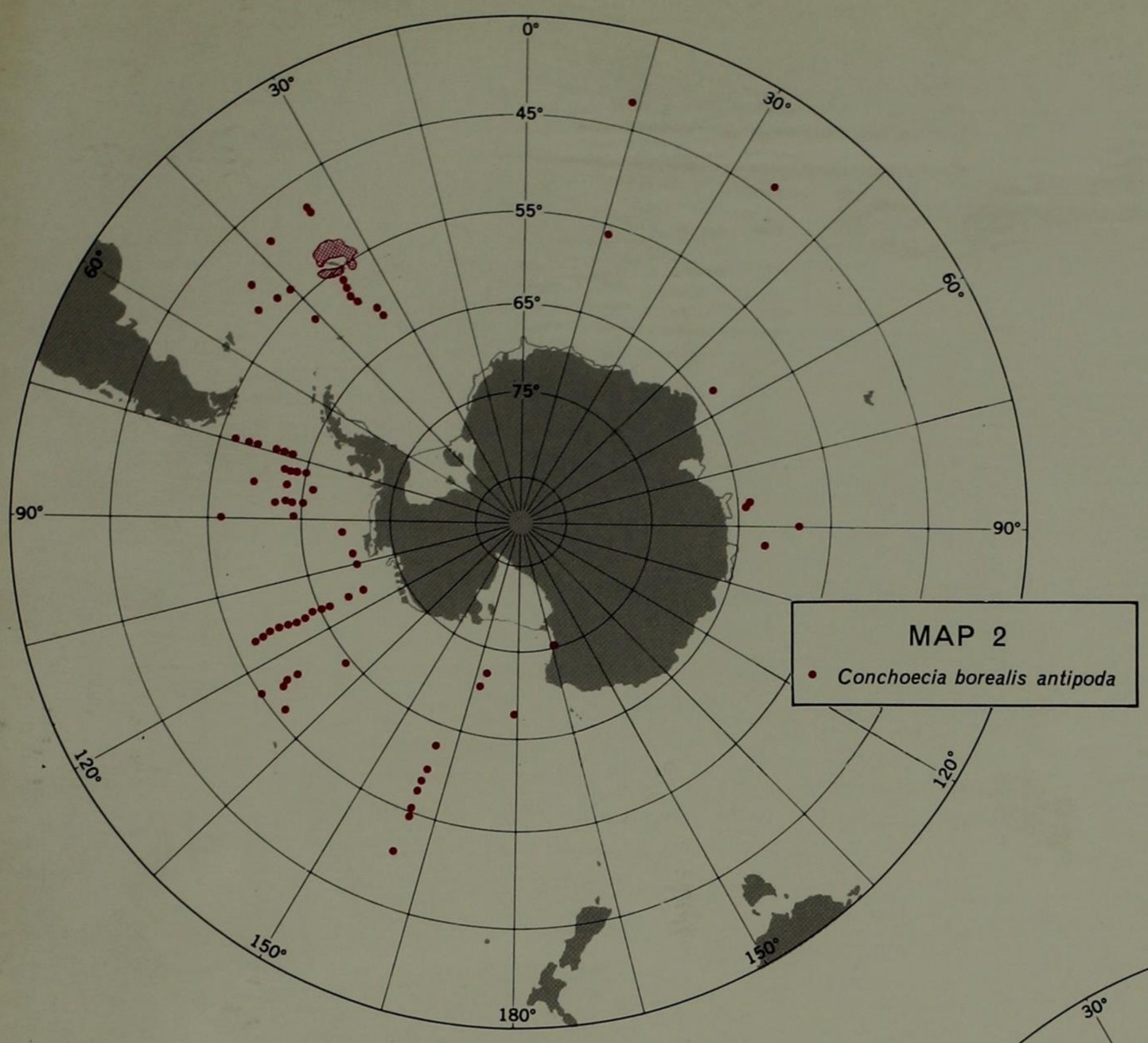
- ● *Eltanin* cruises, 1963-1964
- ■ Swedish Antarctic Expedition, 1901-1903
- ▲ British Antarctic Expedition, 1910-1913, i
- ✱ German Antarctic Expedition, 1901-1903,
- ♦ German Deep Sea Expedition, 1898-1899,
- ✚ British National Antarctic Expedition, 190
- △ Belgian Antarctic Expedition, 1897-1899, i
- ○ *Discovery* Investigations, 1926-1927

Reg
loc
to



MAP 4
● *Conchoecia hettacra*

COMPILED BY N. S. HILLMAN

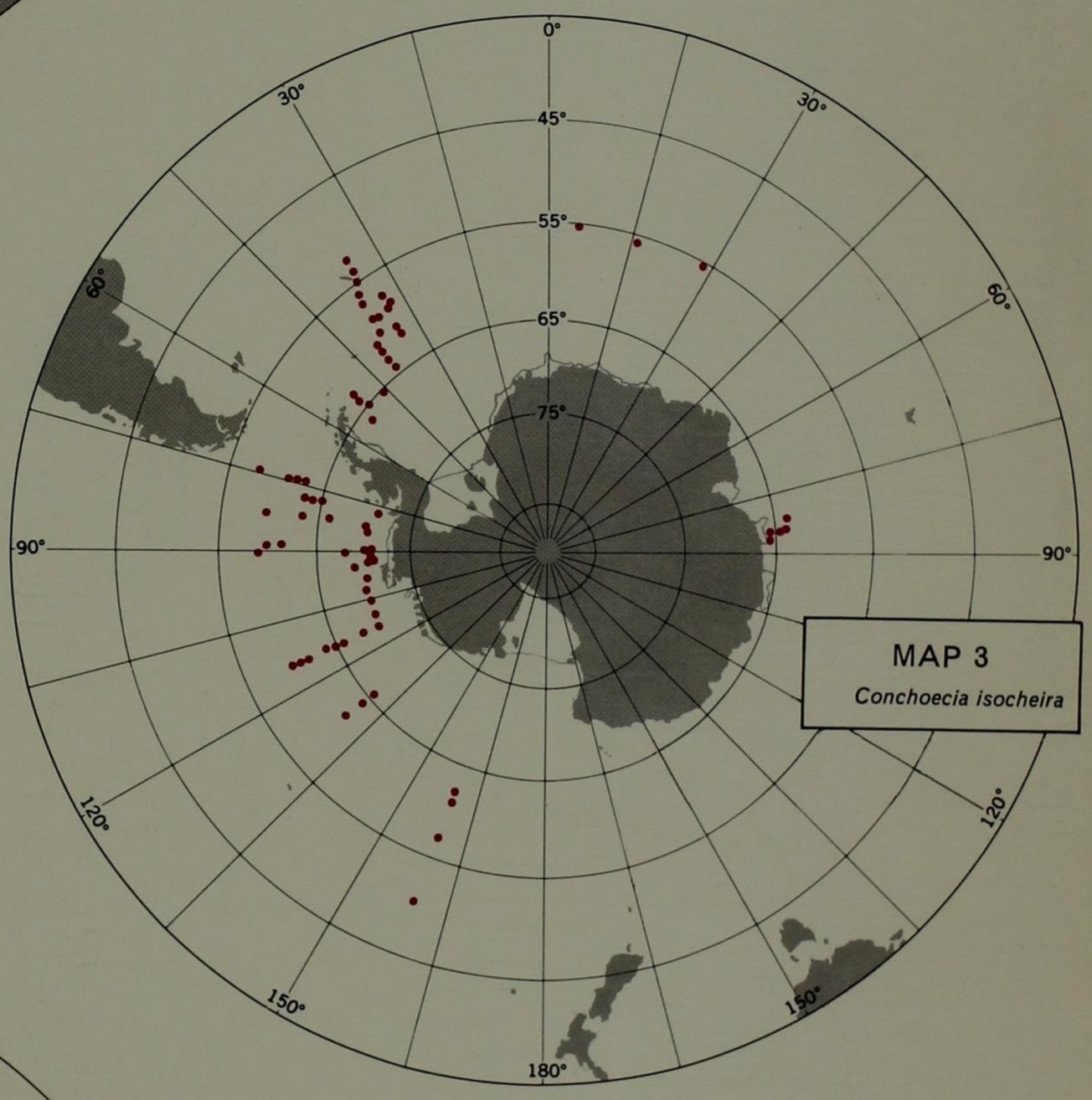


MAP 2

• *Conchoecia borealis antipoda*

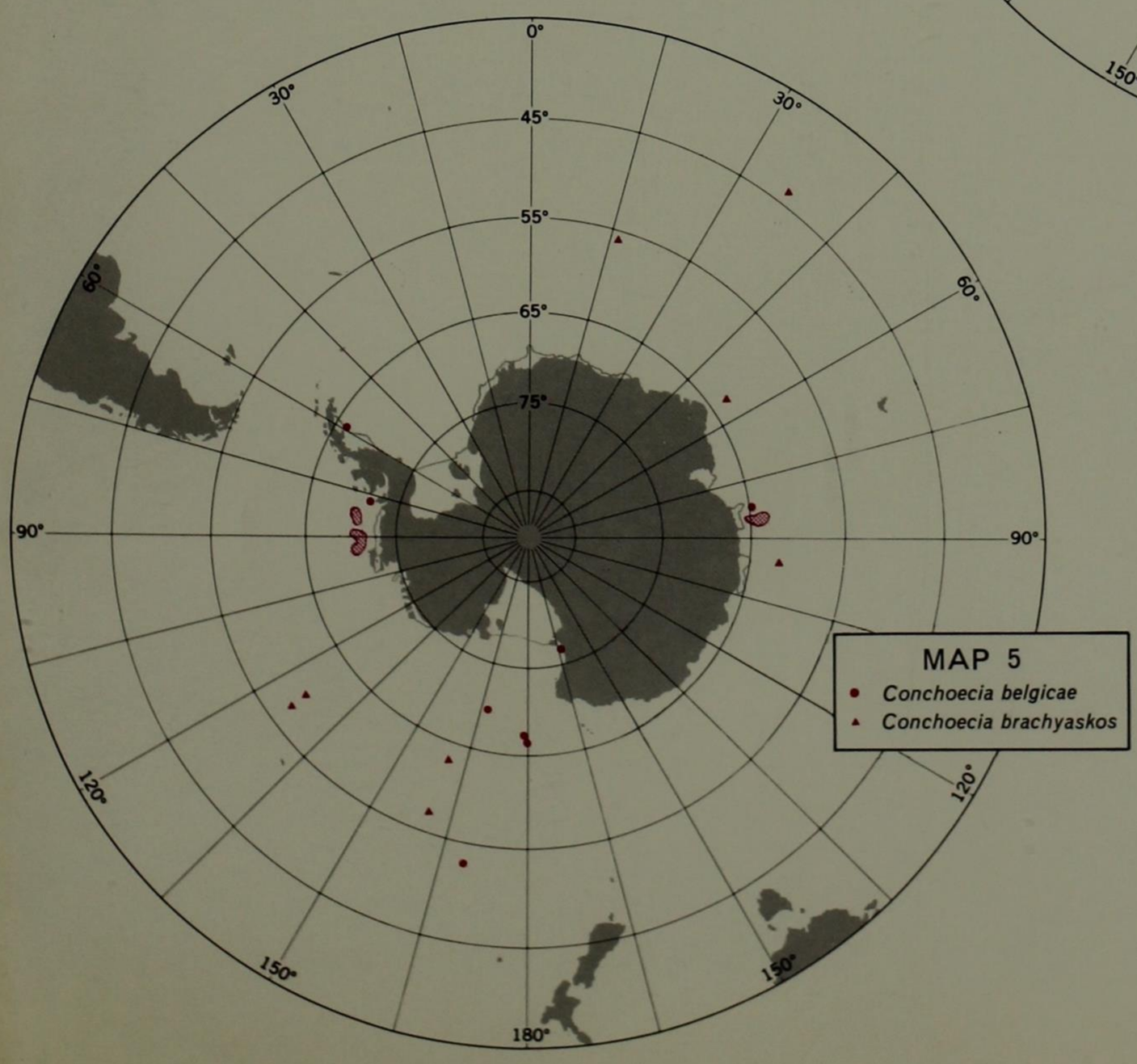
the *Antarctic*
ne *Terra Nova*
he *Gauss*
the *Valdivia*
904, in the *Discovery*
ne *Belgica*

where collection
es are too numerous
individually



MAP 3

Conchoecia isocheira



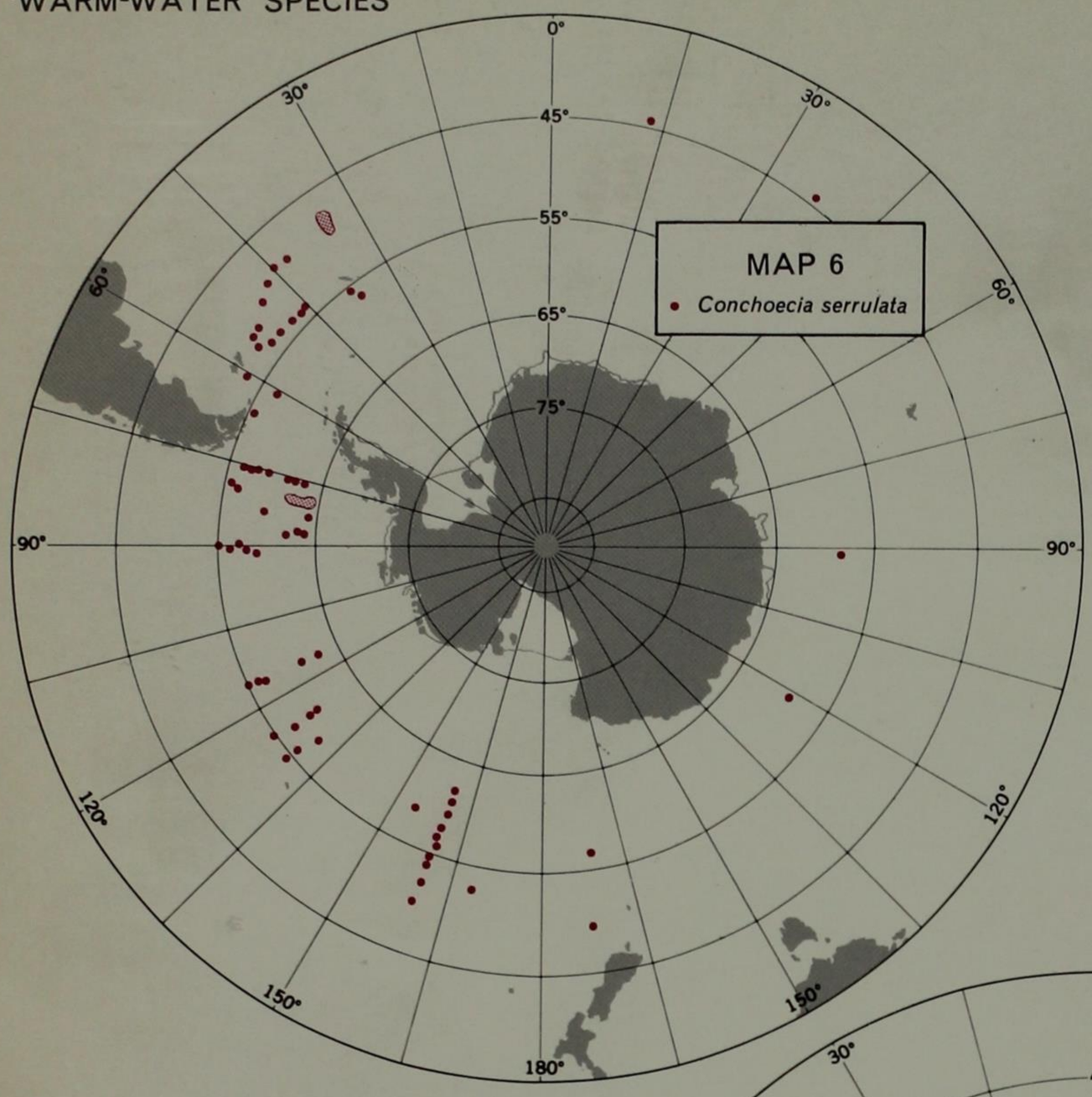
MAP 5

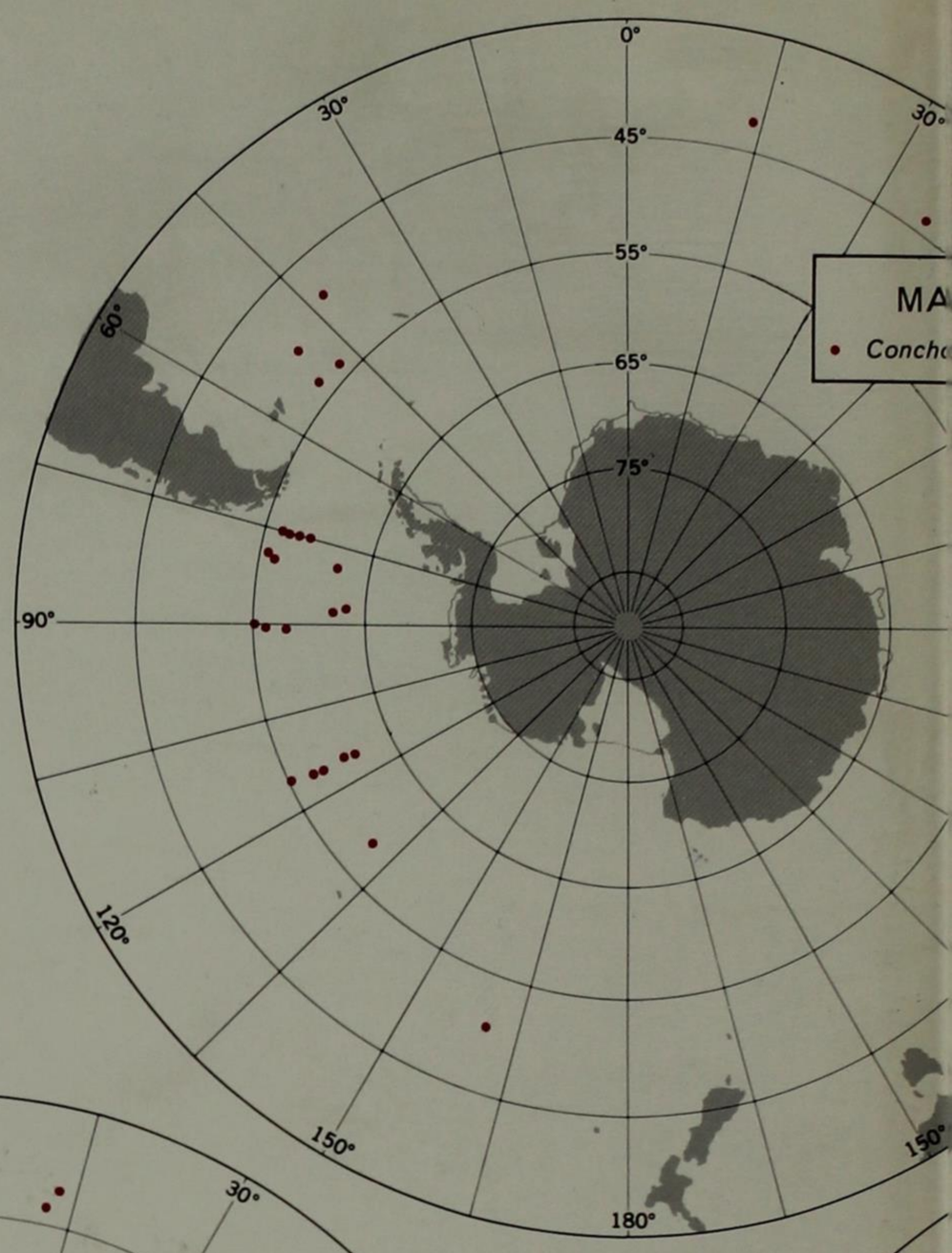
• *Conchoecia belgicae*

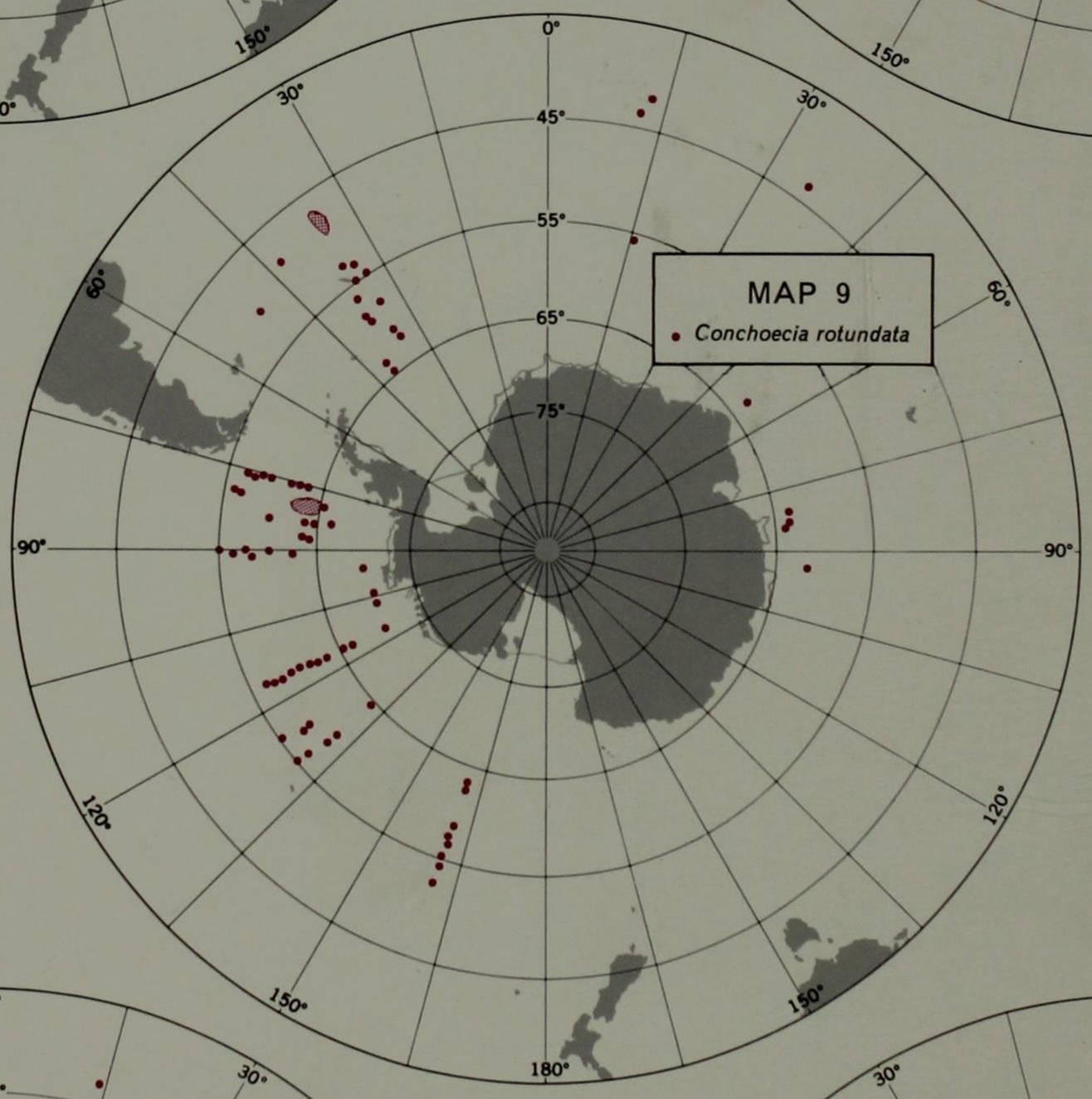
▲ *Conchoecia brachyaskos*

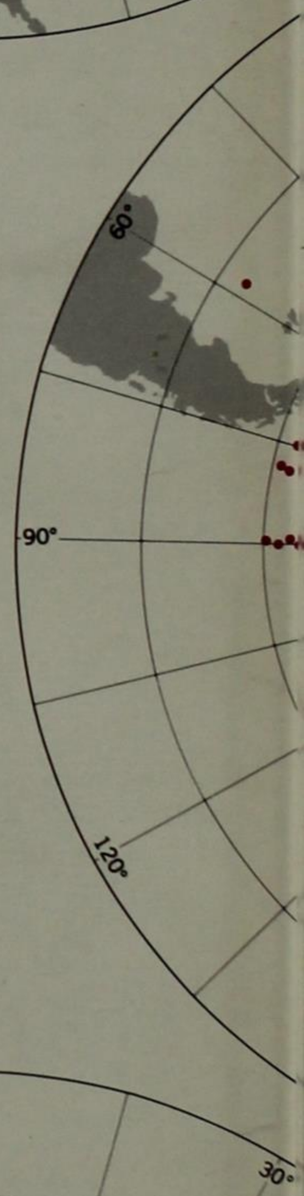
PLANKTONIC OSCTRACODA (HALOCYPRIDAE)

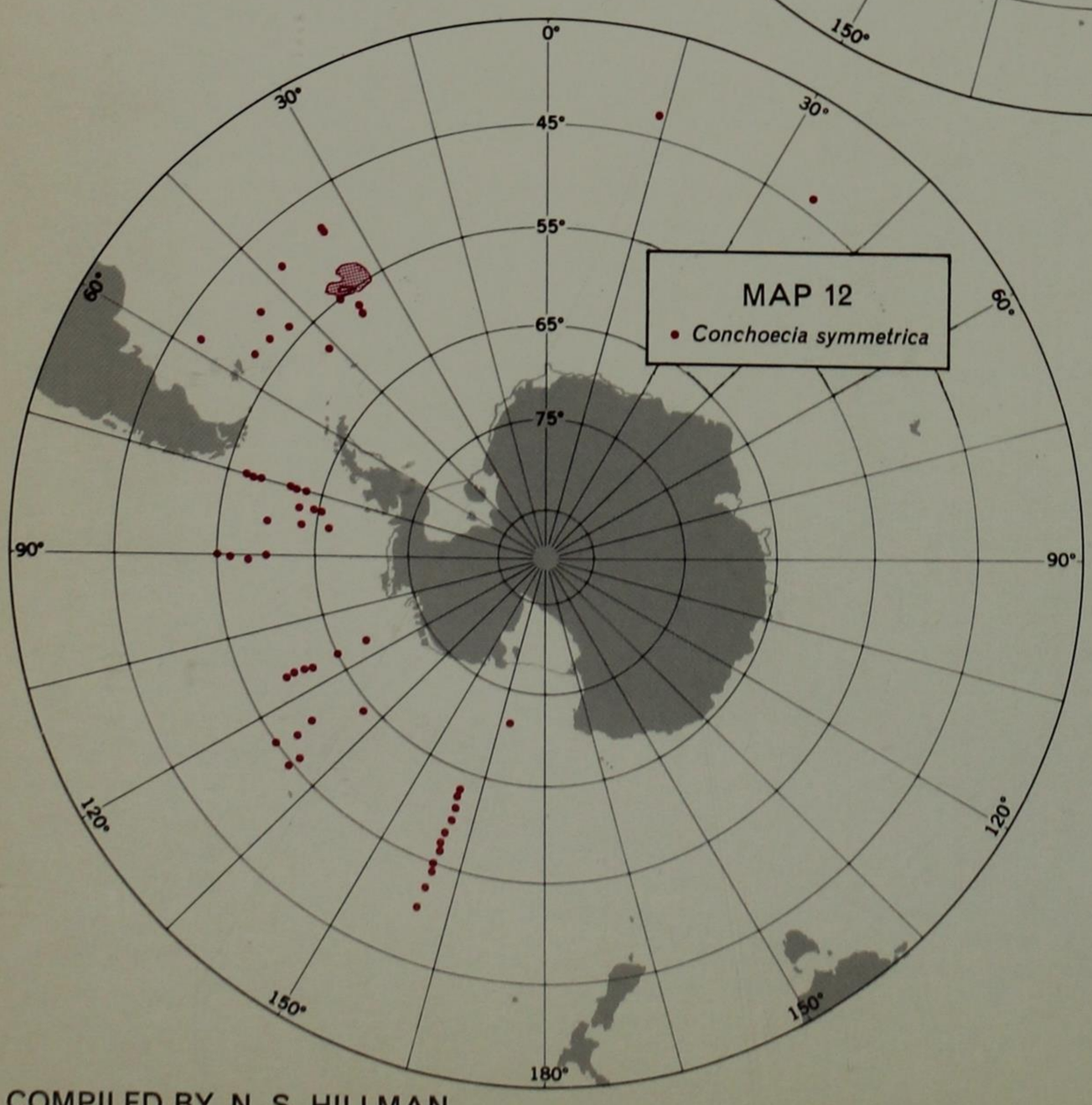
'WARM-WATER' SPECIES

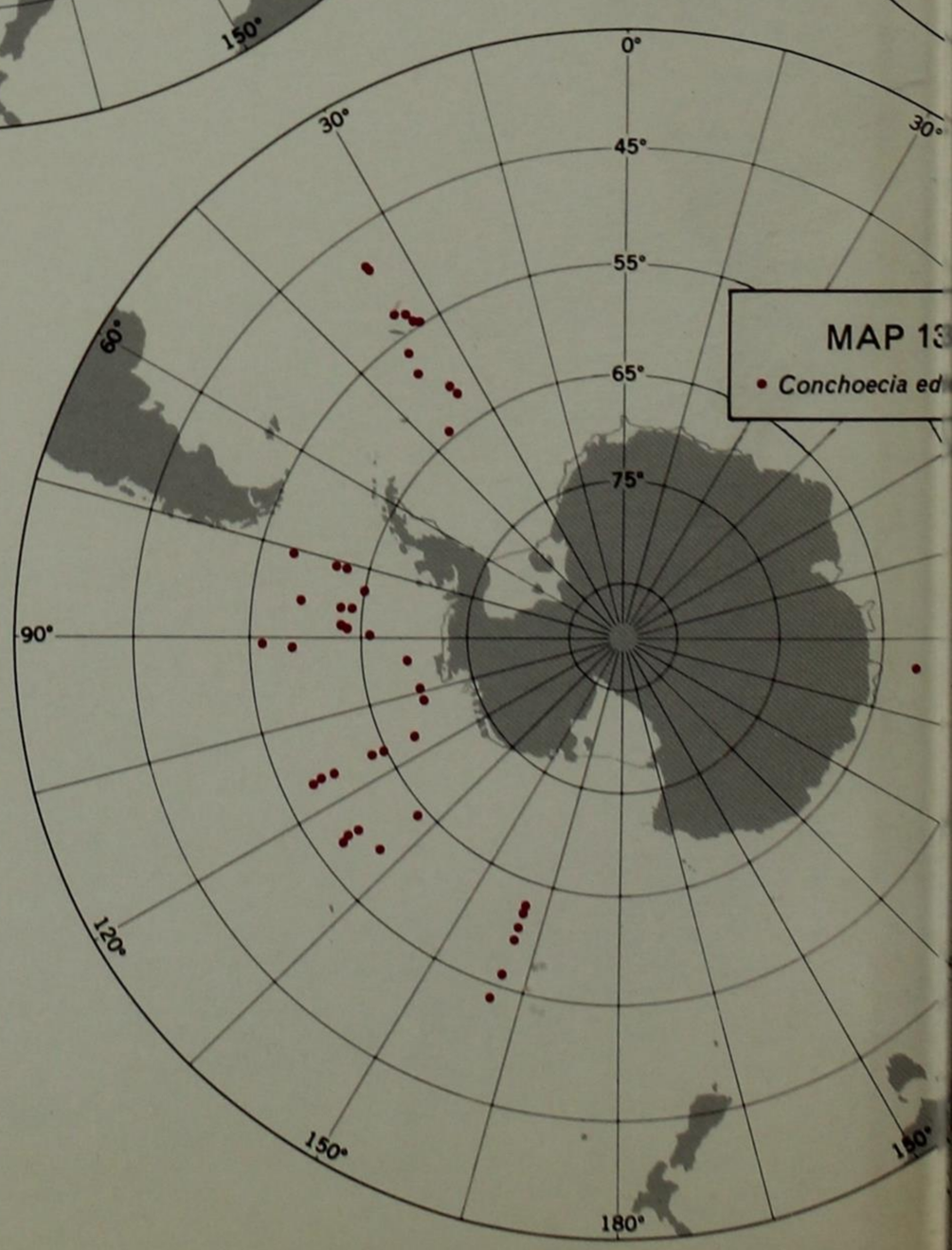




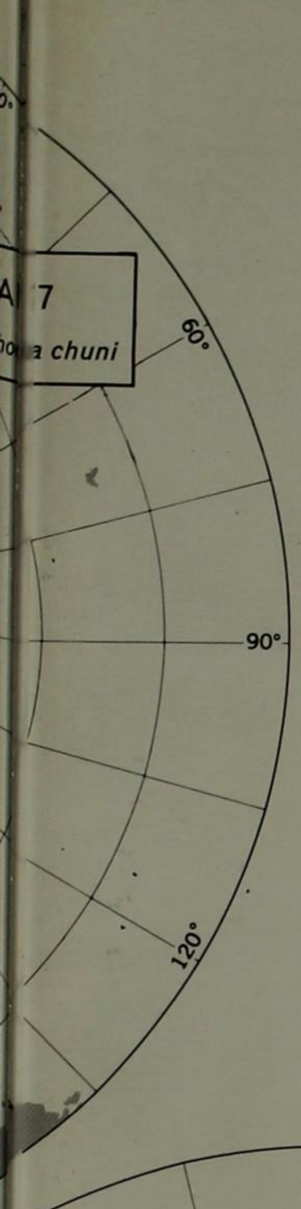


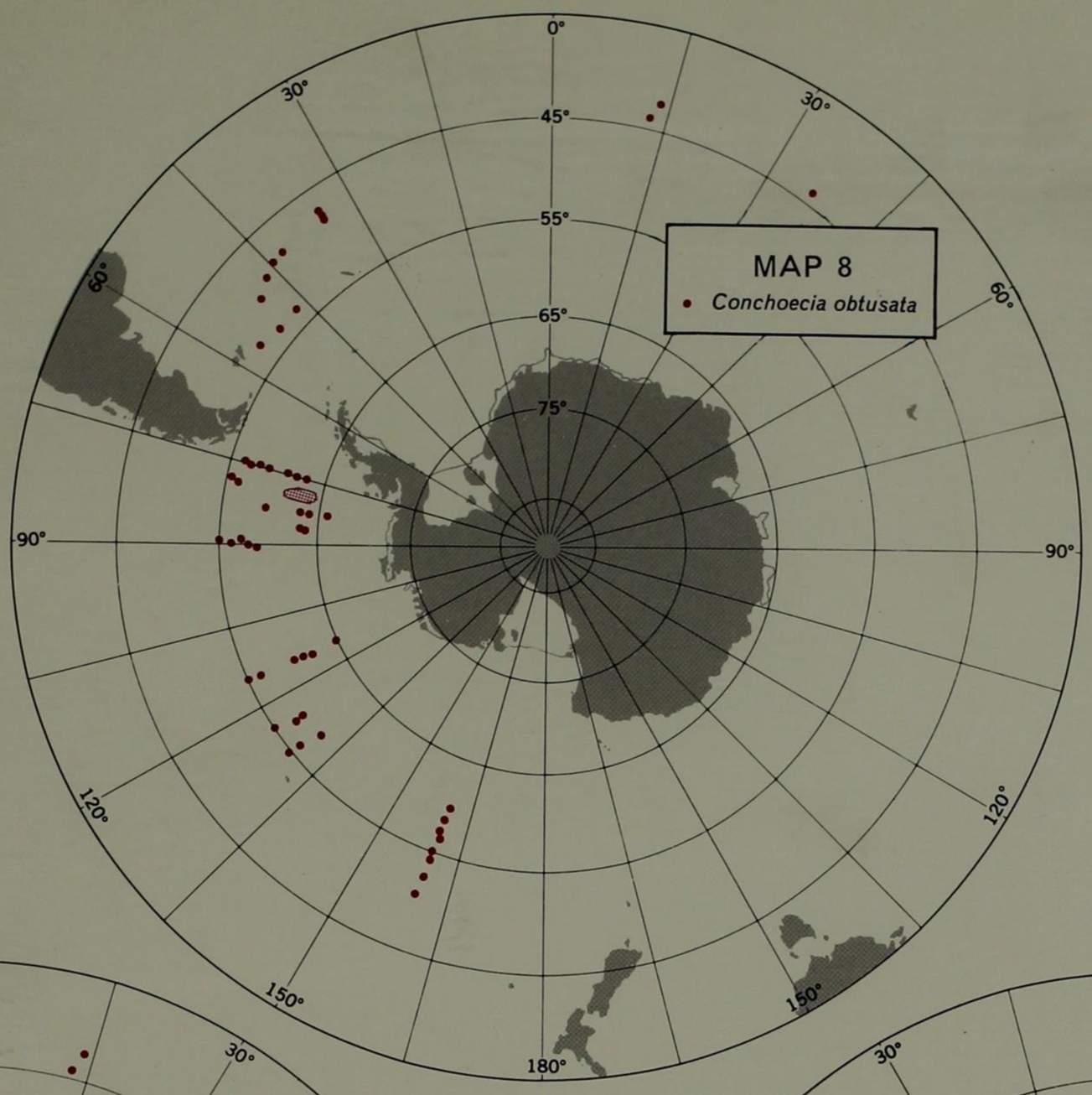


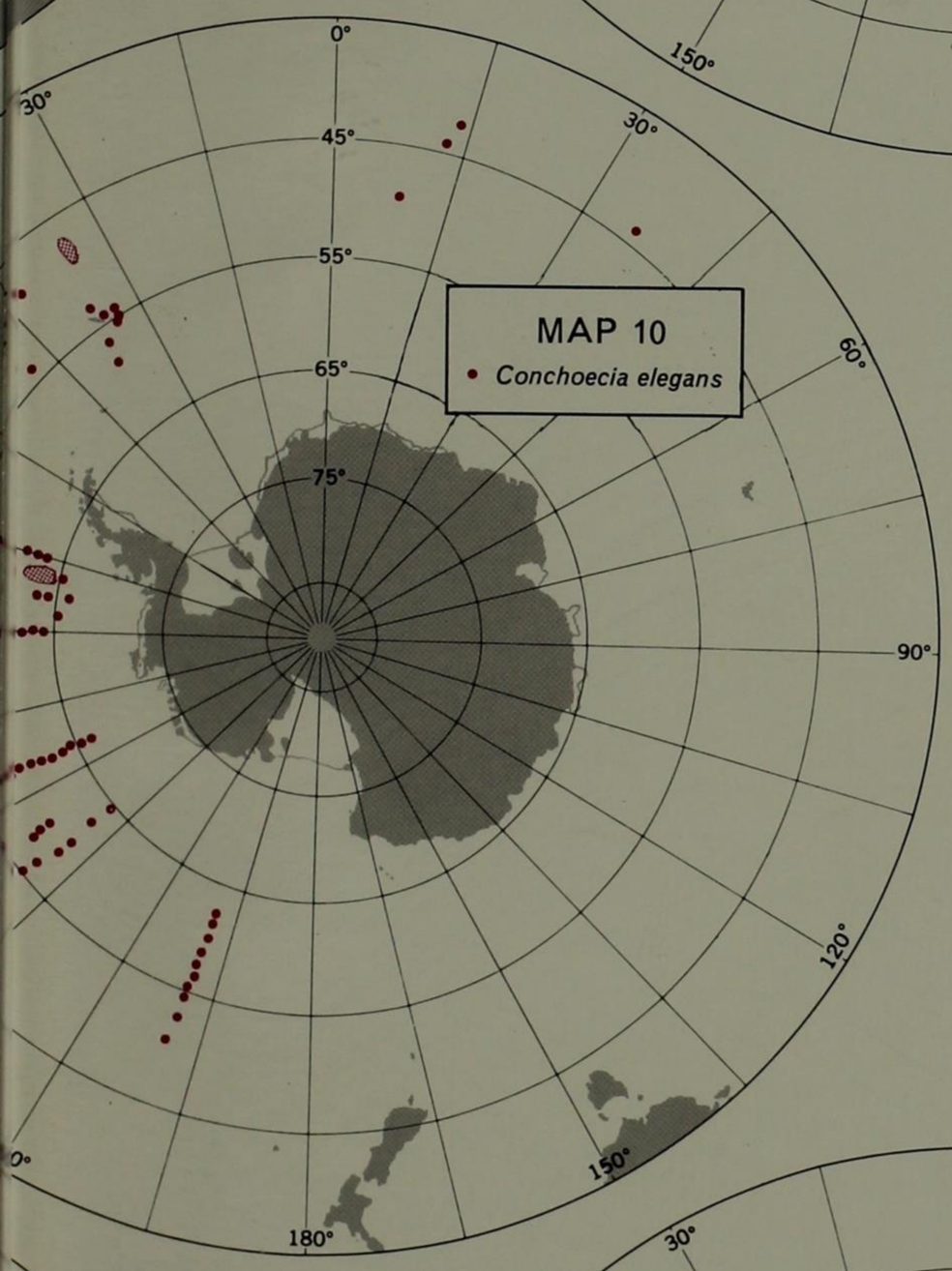


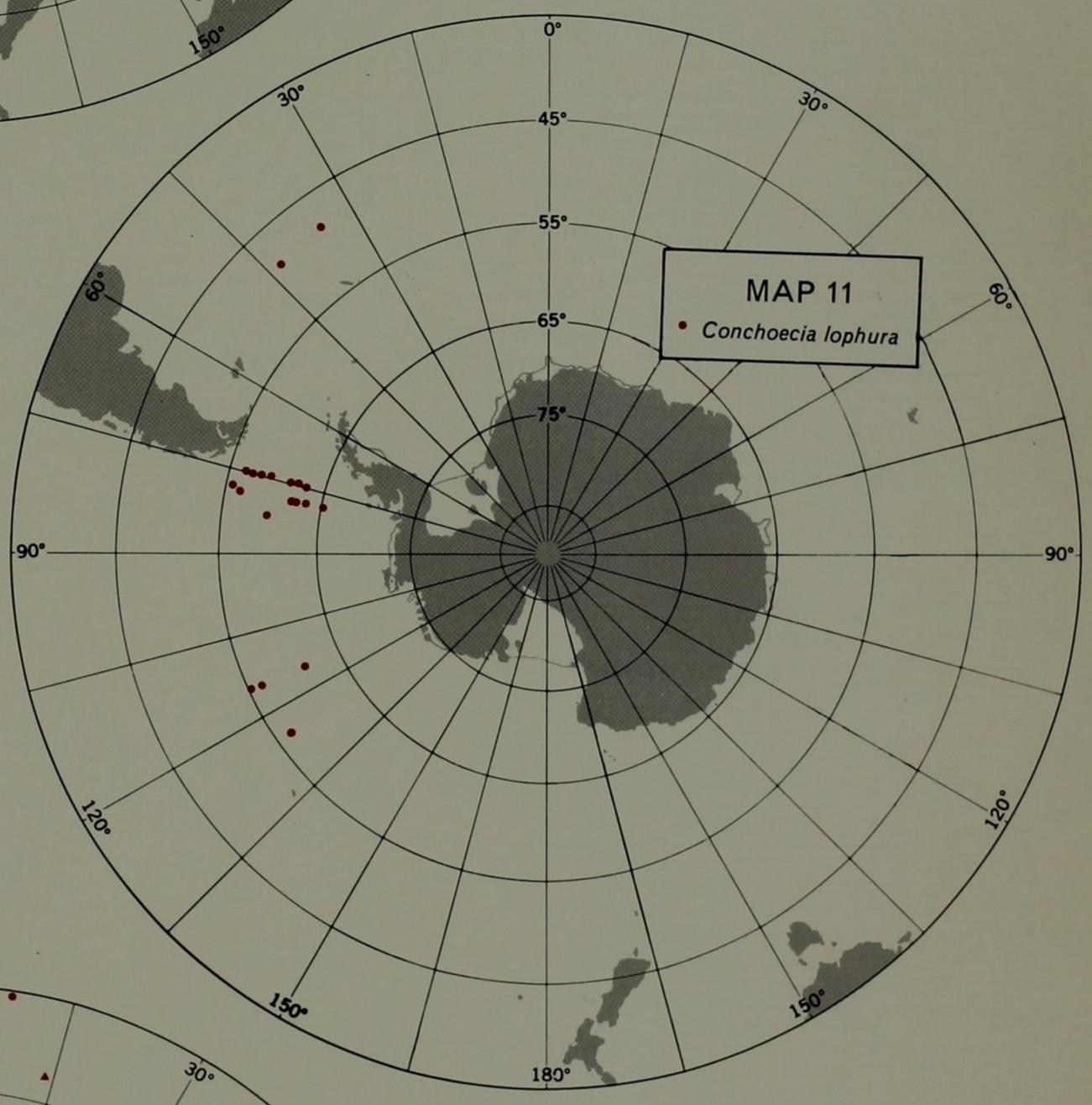


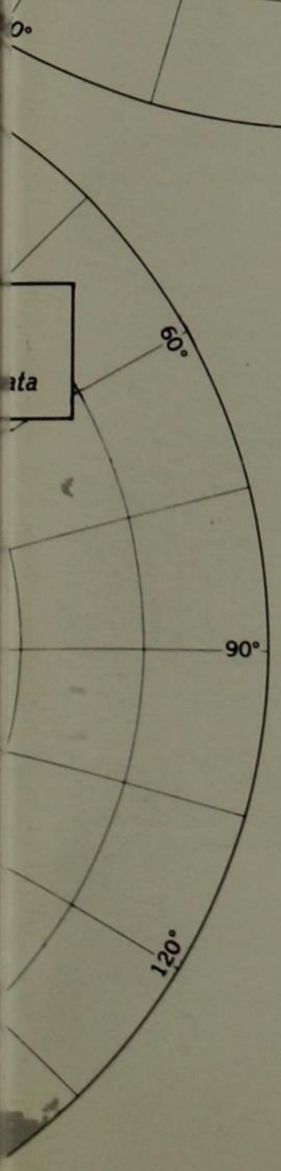
COMPILED BY N. S. HILLMAN

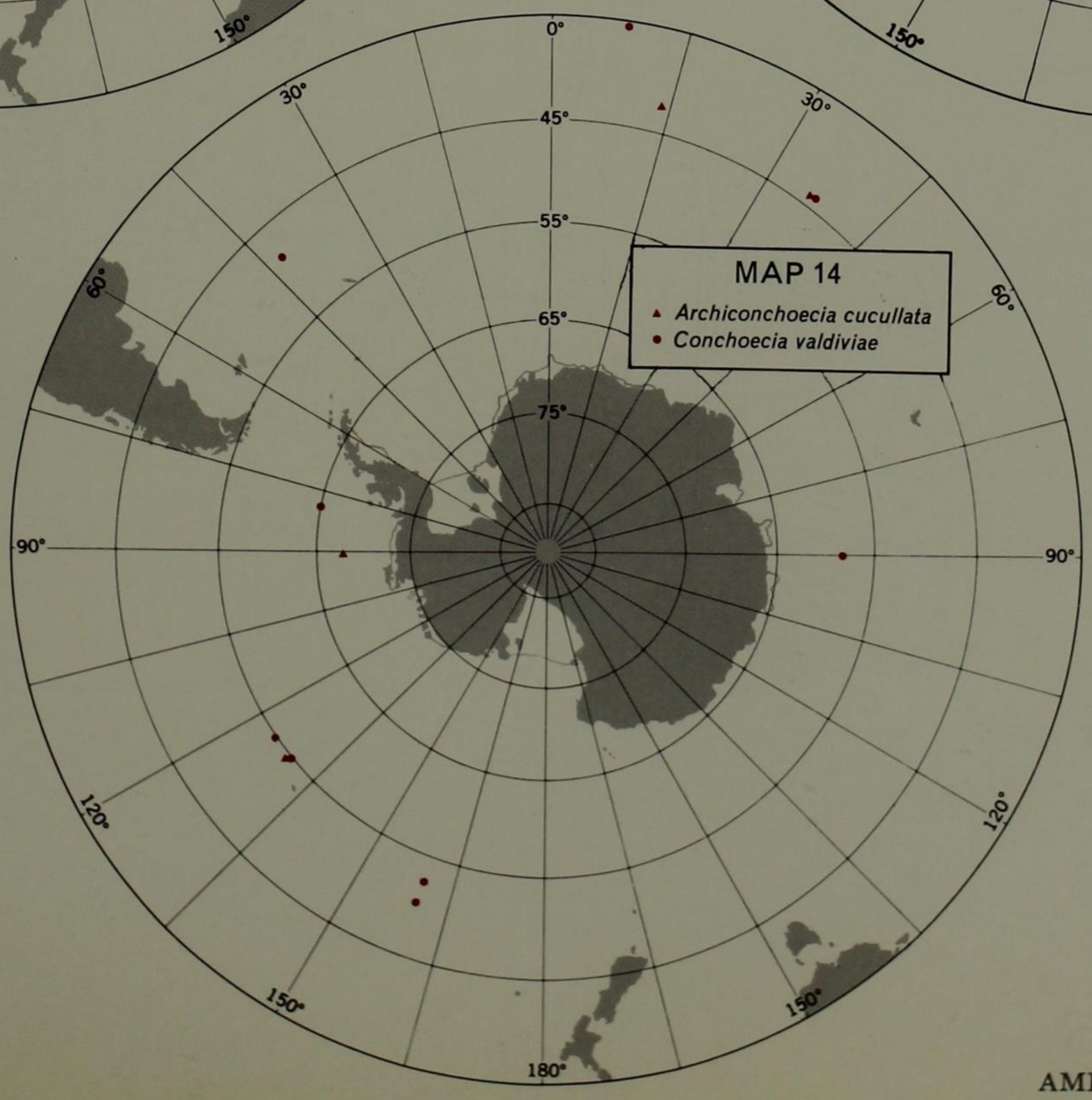










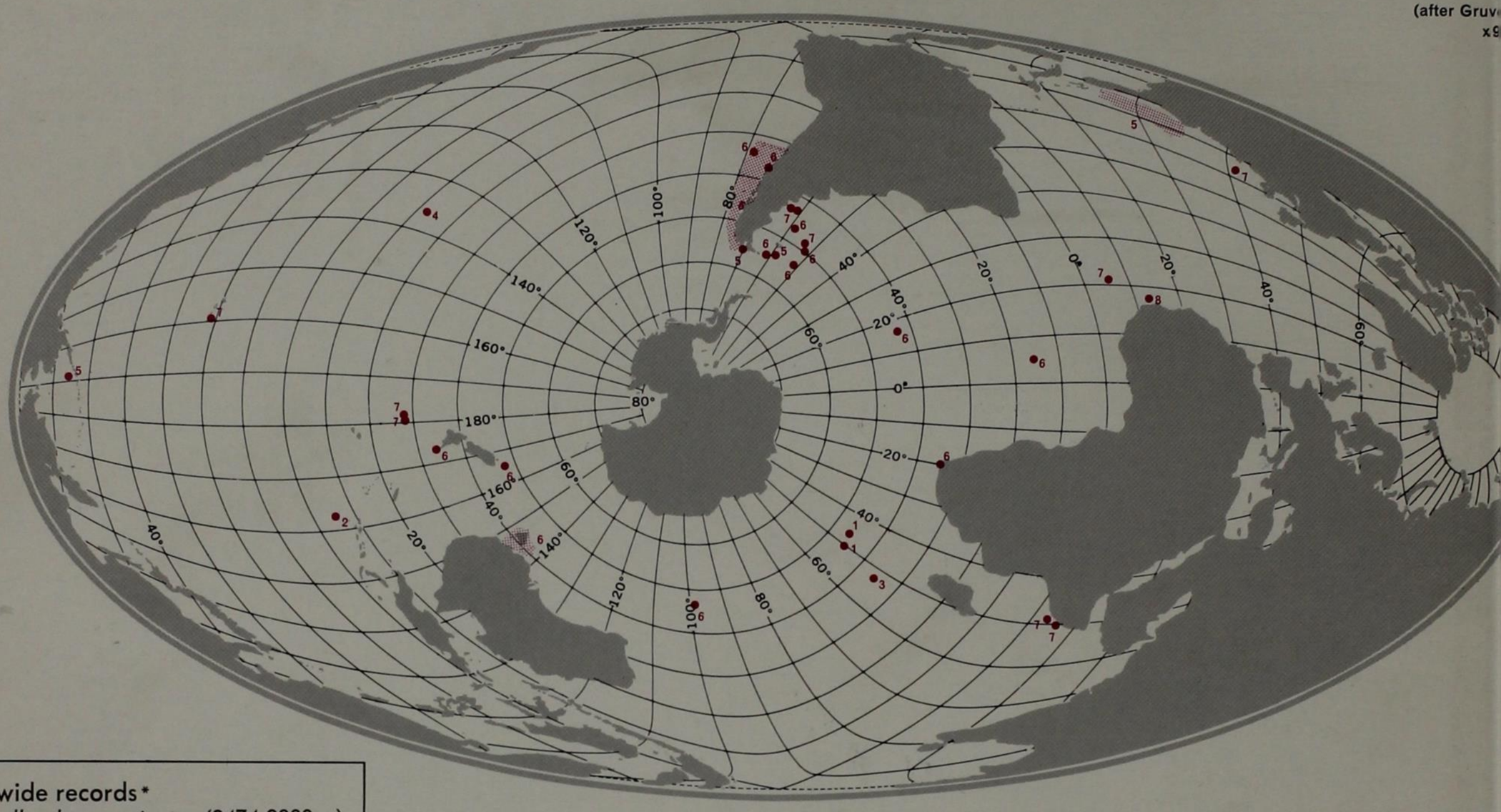


Maps 6-9
Species found primarily
at depths less than 250m

Maps 10-14
Species found primarily
at depths greater than 250m

Region where collection localities
are too numerous to plot individually

CIRRIPEDIA

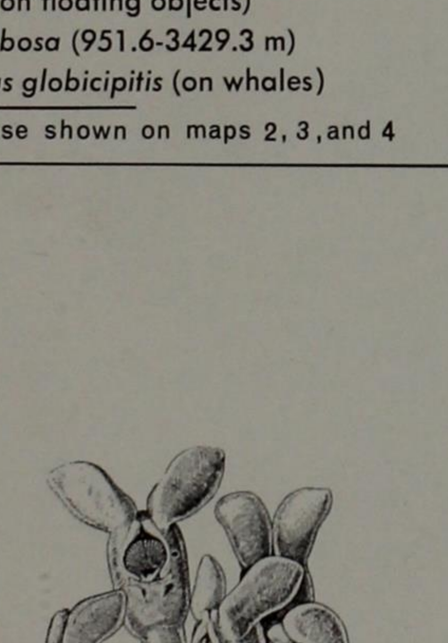


MAP 1. World wide records*

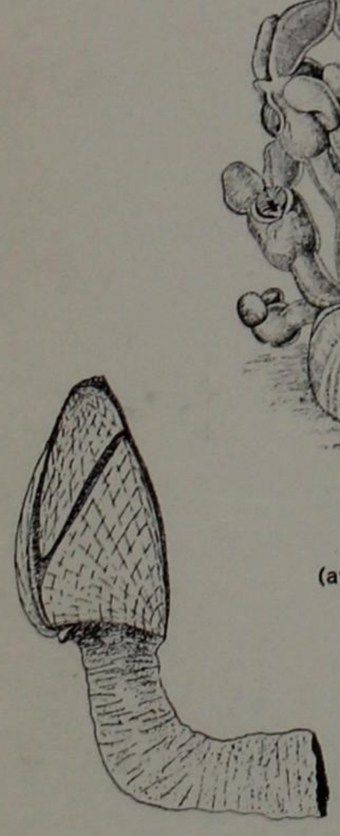
1 *Arcoscalpellum brevecarinatum* (2474-2880 m)
2 *Arcoscalpellum discoveryi* (292.8 m)
3 *Arcoscalpellum triangulare* (1080 m)
4 *Arcoscalpellum ventricosum* (2050 m)
5 *Briarosaccus callosus* (10.5-742 m)
Conchoderma auritum (on whales, fish, and floating objects)
Coronula diadema (on whales)
6 *Lepas australis* (on floating objects)
Lepas hillii (on floating objects)
7 *Verruca gibbosa* (951.6-3429.3 m)
8 *Xenobalanus globicipitis* (on whales)

*Other than those shown on maps 2, 3, and 4

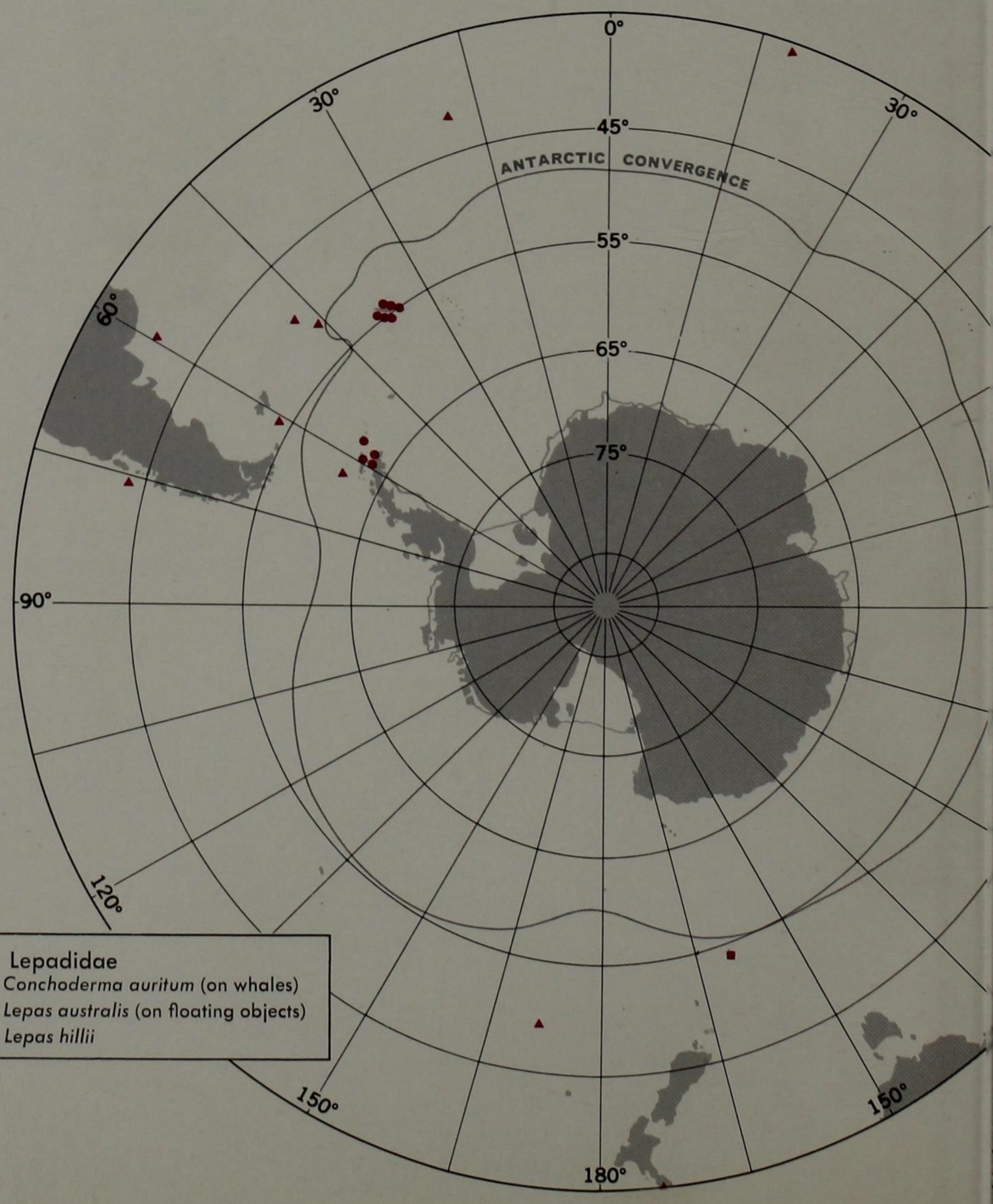
Regions where there are numerous undefined collection sites



Conchoderma auritum
on *Coronula diadema*
(after Tarasov and Zevina, 1957)
x 0.5



Lepas australis
(after Nilsson—Cantell, 1930)
x 0.75



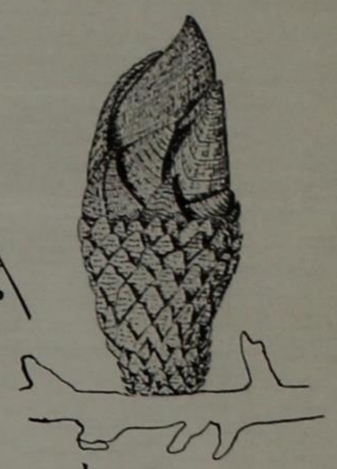
MAP 3. Lepadidae

- *Conchoderma auritum* (on whales)
- *Lepas australis* (on floating objects)
- *Lepas hillii*

Scalpellum v
(after Gruv
x9

COMPILED BY A. ROSS AND W. A. NEWMAN



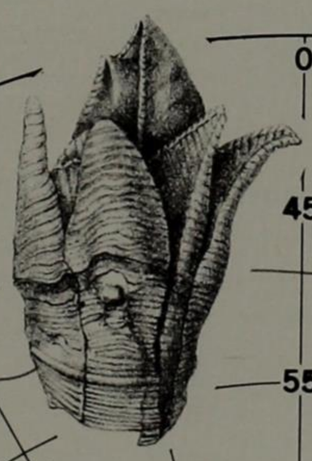


Arcoscalpellum liberum
(after Nilsson—Cantell, 1930)
x 3.75

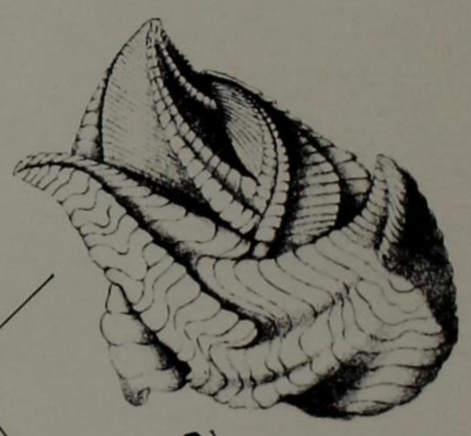
MAP 2. Scalpellidae

- ▲ *Scalpellum vanhoffeni* (350-385 m)
- ● *Arcoscalpellum*
  - 1 *angulare* (342 m)
  - 2 *antarcticum* (3065 m)
  - 3 *aurorae* (287 m)
  - 4 *berndti* (350 m)
  - 5 *bouveti* (40-45 m)
  - 6 *bouvieri* (18-550 m)
  - 7 *brevecarinatum* (515-4540 m)
  - 8 *compactum* (91-567 m)
  - 9 *convexum* (110-310 m)
  - 10 *discoveryi* (9-342 m)
  - 11 *gaussi* (380-385 m)
  - 12 *improvisum* (2305-4755 m)
  - 13 *liberum* (259 m)
  - 14 *magnaecarinae* (259-315 m)
  - 15 *nymphonis* (146 m)
  - 16 *recurvirostrum* (274 m)
  - 17 *triangulare*
  - 18 *ventricosum* (267 m)
  - 19 *weltneri* (280-385 m)

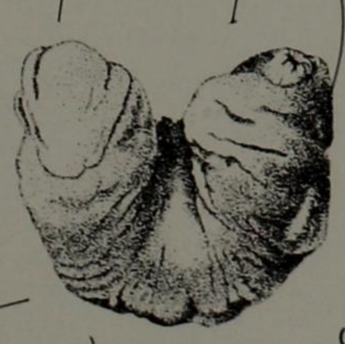
Arcoscalpellum gaussi
(after Gruvel, 1909)
x 9



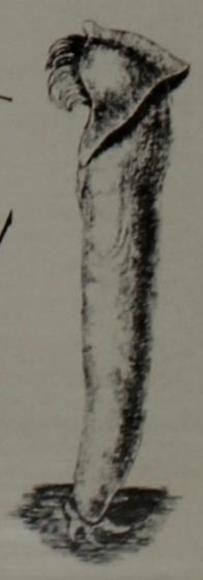
Hexelasma corolliforme
(after Hoek, 1883)
x 0.75



Verruca gibbosa
(after Hoek, 1883)
x 5



Briarosaccus callosus
(after Boschma, 1962)
x 0.75



Xenobalanus globicipitis
(after Darwin, 1854)
x 1.5

MAP 4. Other Cirripedia

- ● Chthamalidae
  - 1 *Hexelasma antarcticum* (9 m above sea level to 1592 m)
  - 2 *Hexelasma corolliforme* (200-280 m)
- △ Balanidae
  - 3 *Coronula diadema* (on whales)
  - 4 *Coronula reginae* (on whales)
  - 5 *Xenobalanus globicipitis* (on whales)

Verrucidae

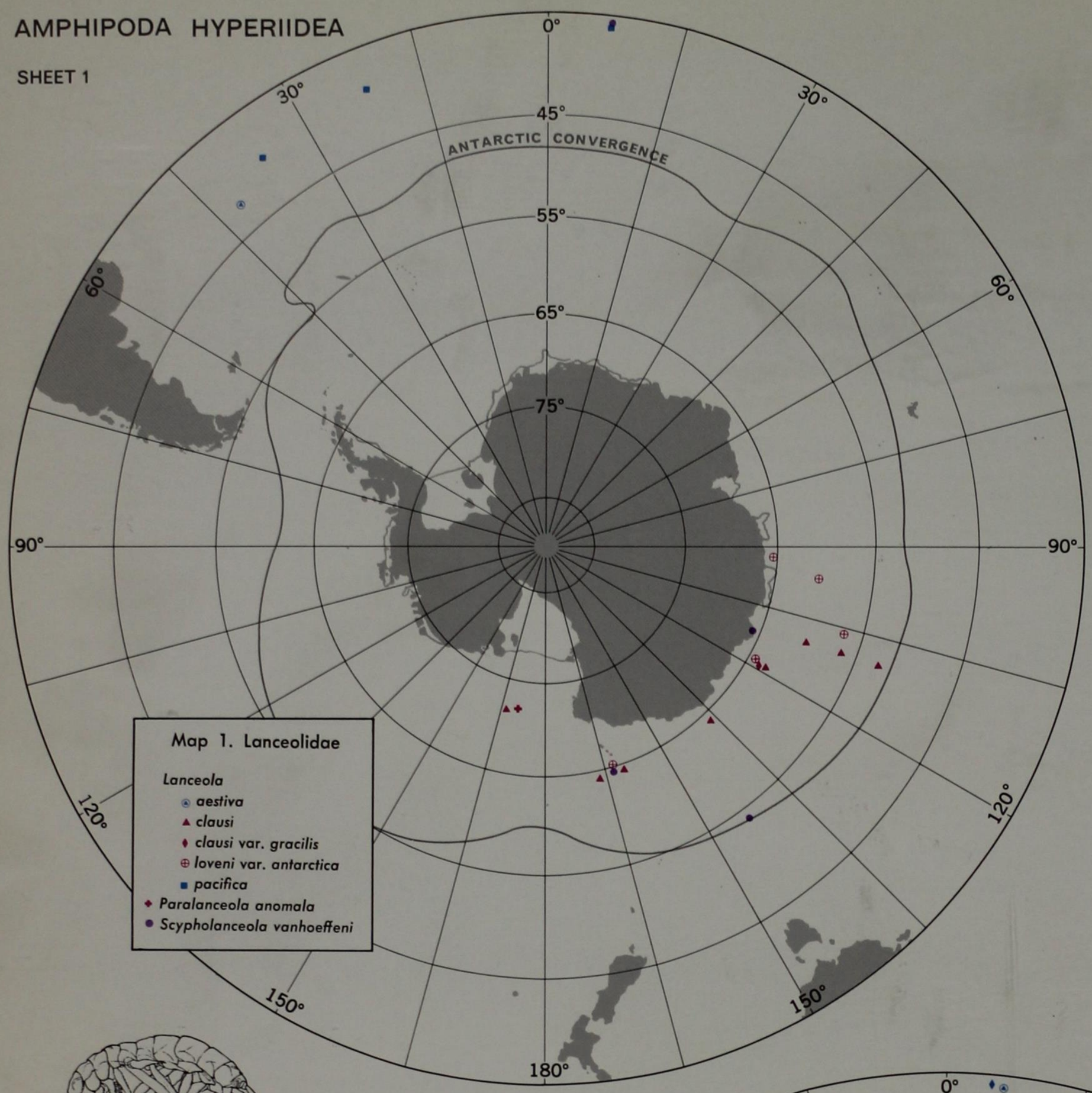
- ✸ *Verruca gibbosa (555—3056 m)*

Rhizocephala

- ◆ *Briarosaccus callosus* (13-728 m)

AMPHIPODA HYPERIIDEA

SHEET 1

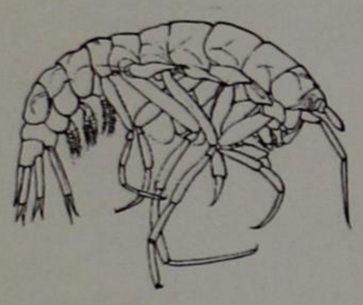


Map 1. Lanceolidae

Lanceola
- *aestiva*
- *clausi*
- *clausi* var. *gracilis*
- *loveni* var. *antarctica*
- *pacifica*

Paralanceola anomala

Scypholanceola vanhoeffeni



Lanceola pacifica

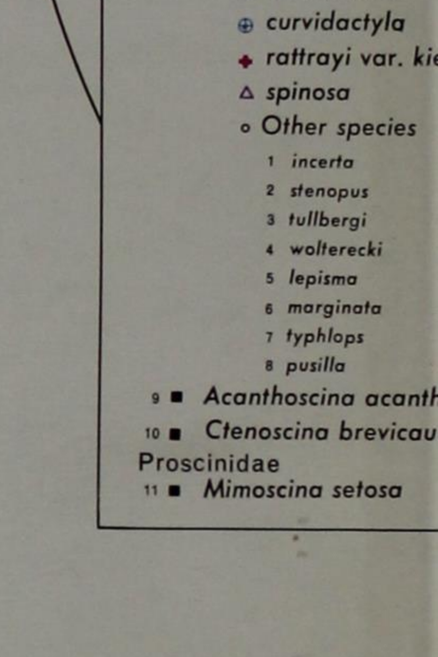
(after Stebbing, 1888)
X 3



Vibilia propinqua

(after Stebbing, 1888)
X 5

In tinted regions collection sites are too numerous to plot. Symbol or number adjacent to the area identifies species found there while number of localities is given in parentheses.

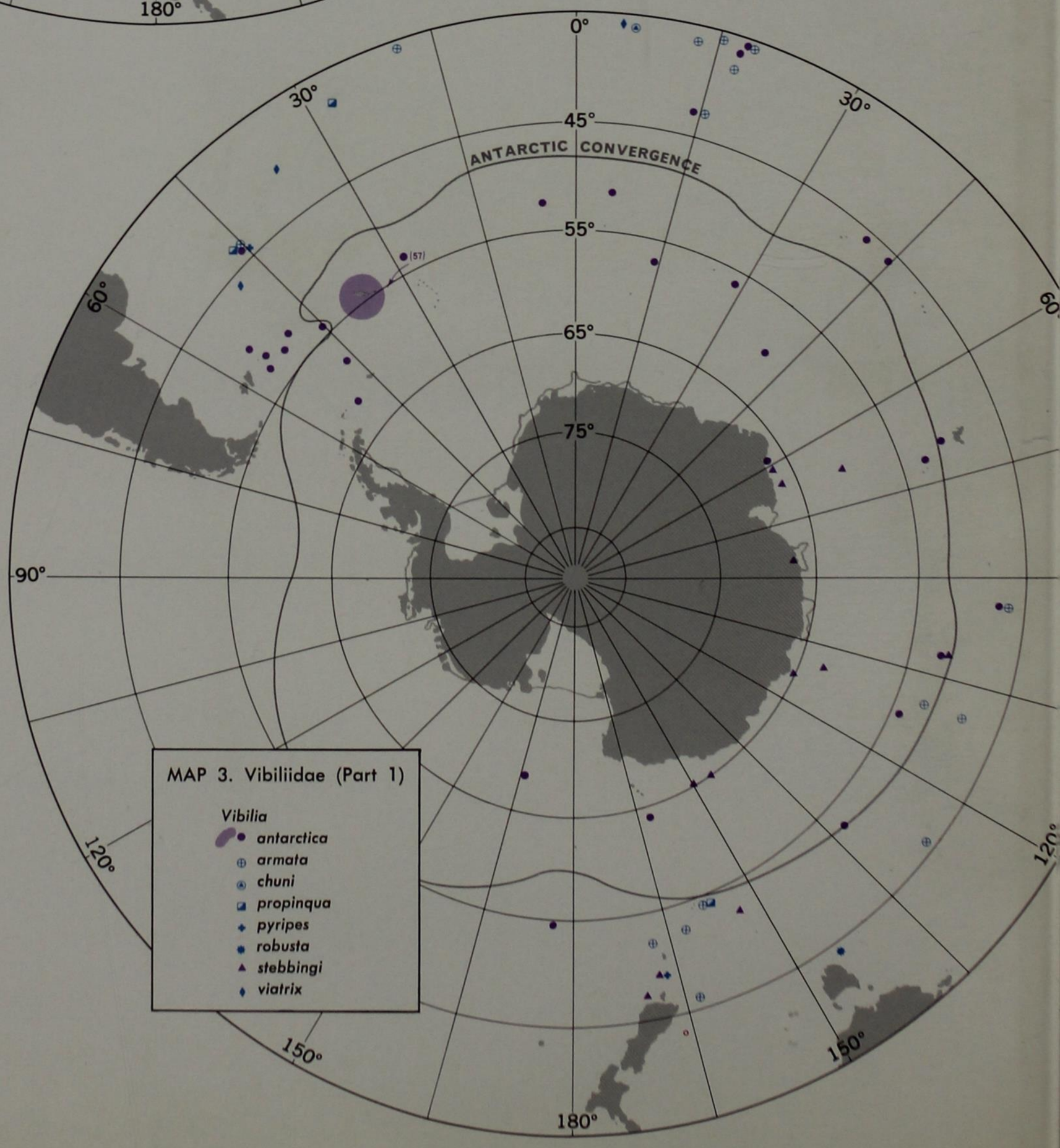


MAP 2.

Scinidae

Scina
- *antarctica*
- *borealis*
- *crassicornis*
- *curvidactyla*
- *rattrayi* var. *kie*
- *spinosa*
- Other species
  - 1 *incerta*
  - 2 *stenopus*
  - 3 *tullbergi*
  - 4 *wolterecki*
  - 5 *lepisma*
  - 6 *marginata*
  - 7 *typhlops*
  - 8 *pusilla*
- 9 *Acanthoscina acanth*
- 10 *Ctenoscina brevicau*

Proscinidae
- 11 *Mimoscina setosa*



MAP 3. Vibiliidae (Part 1)

Vibilia
- *antarctica*
- *armata*
- *chuni*
- *propinqua*
- *pyripes*
- *robusta*
- *stebbingi*
- *viatrix*

COMPILED BY D. E. HURLEY

PLATE 18

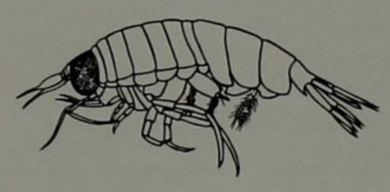
FOLIO 11—MARINE INVERTEBRATES

ANTARCTIC MAP FOLIO SERIES



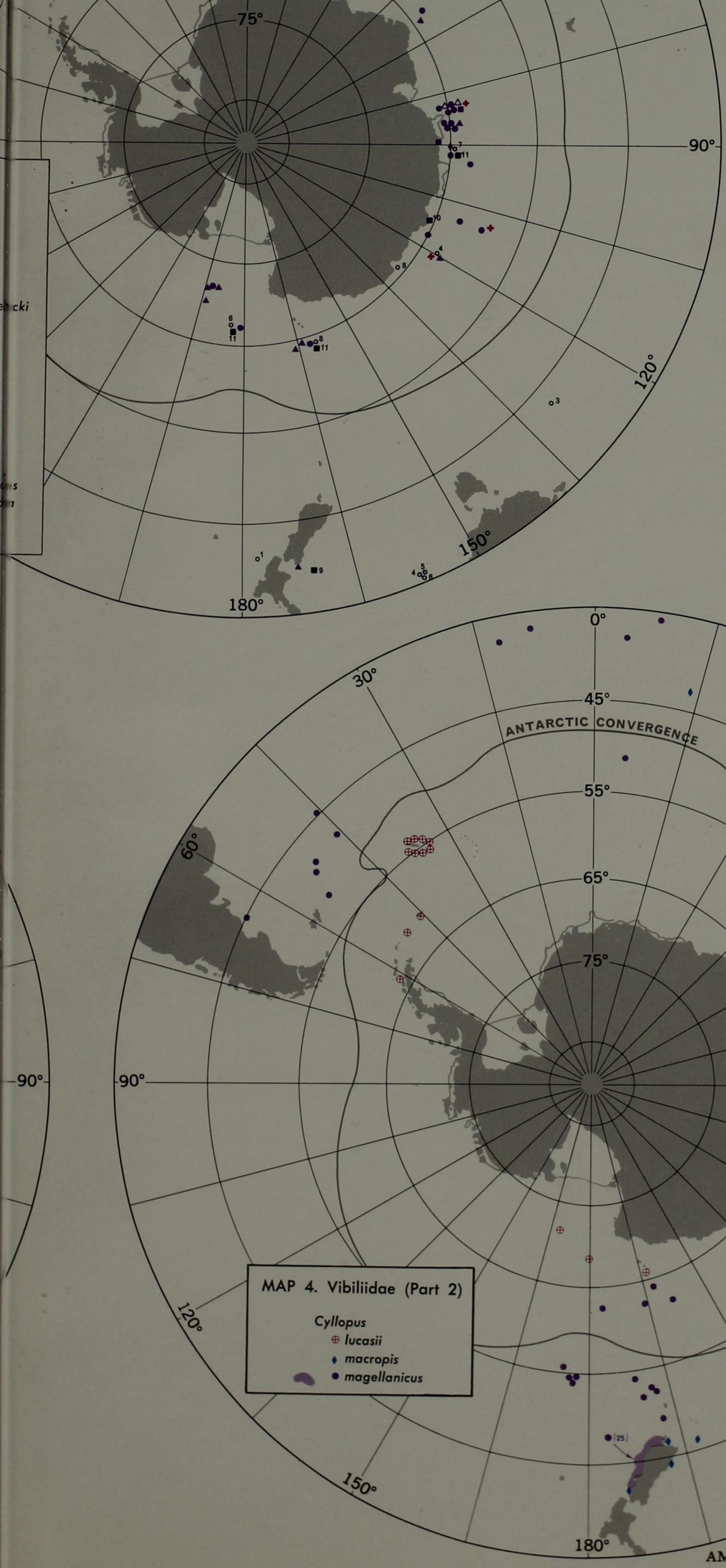
Scina typhlops

(after Wagler, 1926)
X 9



Cyllopus magellanicus

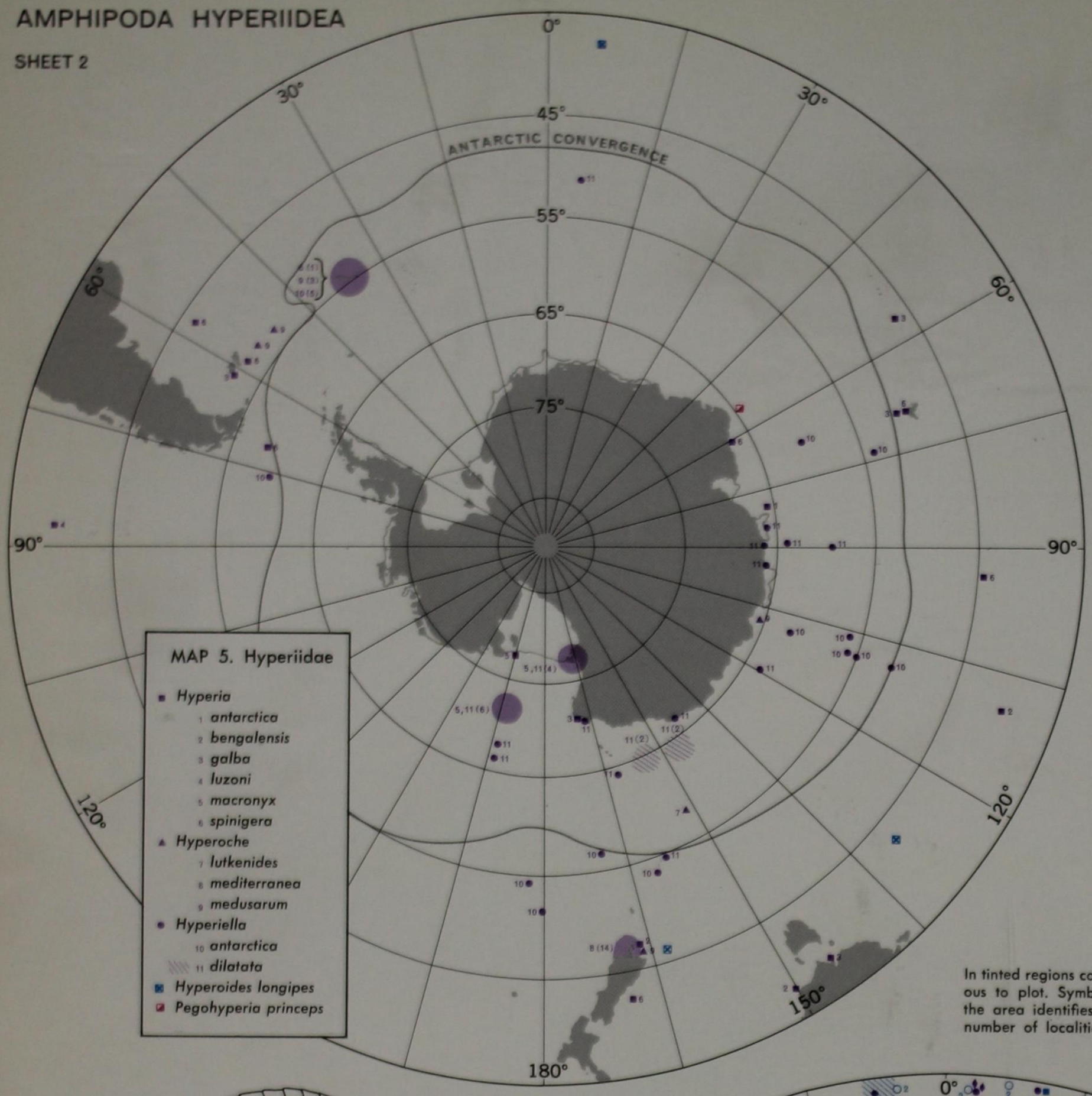
(after Hurley, 1955)
X 4



AMERICAN GEOGRAPHICAL SOCIETY—1969

AMPHIPODA HYPERIIDEA

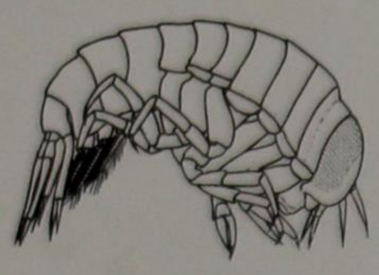
SHEET 2



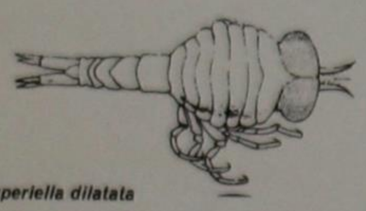
MAP 5. Hyperiidae

- *Hyperia*
  - 1 *antarctica*
  - 2 *bengalensis*
  - 3 *galba*
  - 4 *luzoni*
  - 5 *macronyx*
  - 6 *spinigera*
- *Hyperoche*
  - 7 *lutkenides*
  - 8 *mediterranea*
  - 9 *medusarum*
- *Hyperiella*
  - 10 *antarctica*
  - 11 *dilatata*
- *Hyperoides longipes*
- *Pegohyperia princeps*

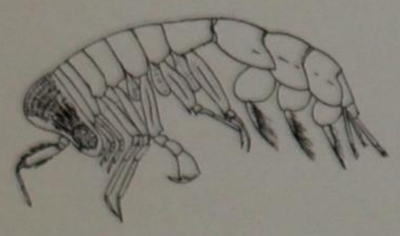
In tinted regions collection sites are too numerous to plot. Symbol or number adjacent to the area identifies species found there while number of localities is given in parentheses.



Hyperoche medusarum
(after Hurley, 1955)
X 7



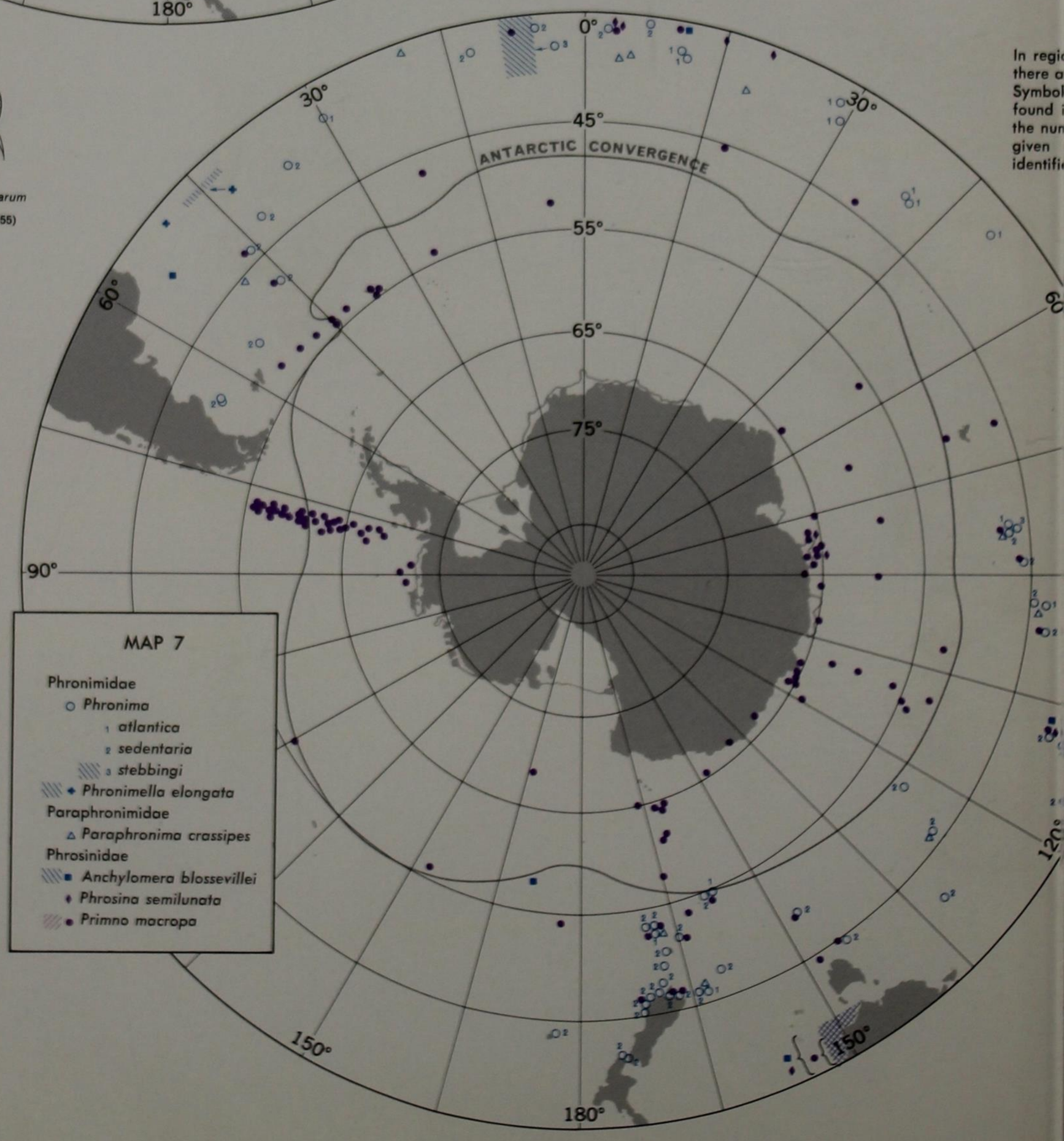
Hyperiella dilatata
(after Stebbing, 1888)
X 5



Phronima sedentaria
(after Chevreux and Fage, 1925)
× 2



Primno macropa
(after Chevreux and Fage, 1925)
X 7



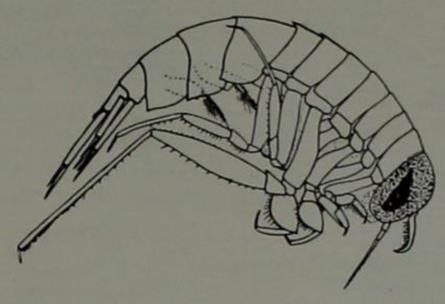
MAP 7

Phronimidae
- *Phronima*
  - 1 *atlantica*
  - 2 *sedentaria*
  - 3 *stebbingi*
- *Phronimella elongata*

Paraphronimidae
- *Paraphronima crassipes*

Phrosinidae
- *Anchylomera blossevillei*
- *Phrosina semilunata*
- *Primno macropa*

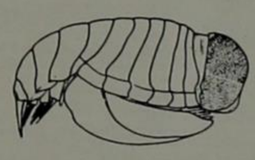
COMPILED BY D. E. HURLEY



Parathemisto gaudichaudii
(after Chevreux and Fage, 1925)
X 3



Brachyscelus crusculum
(after Stebbing, 1888)
×4



Platyscelus ovoides
(after Chevreux and Fage, 1925)
×2

designated by diagonal line pattern
collection sites at undefined locations.
numbers adjacent identify species
ne region of the line pattern. When
of collection localities is known it is
parentheses following the species
on number.

MAP 8

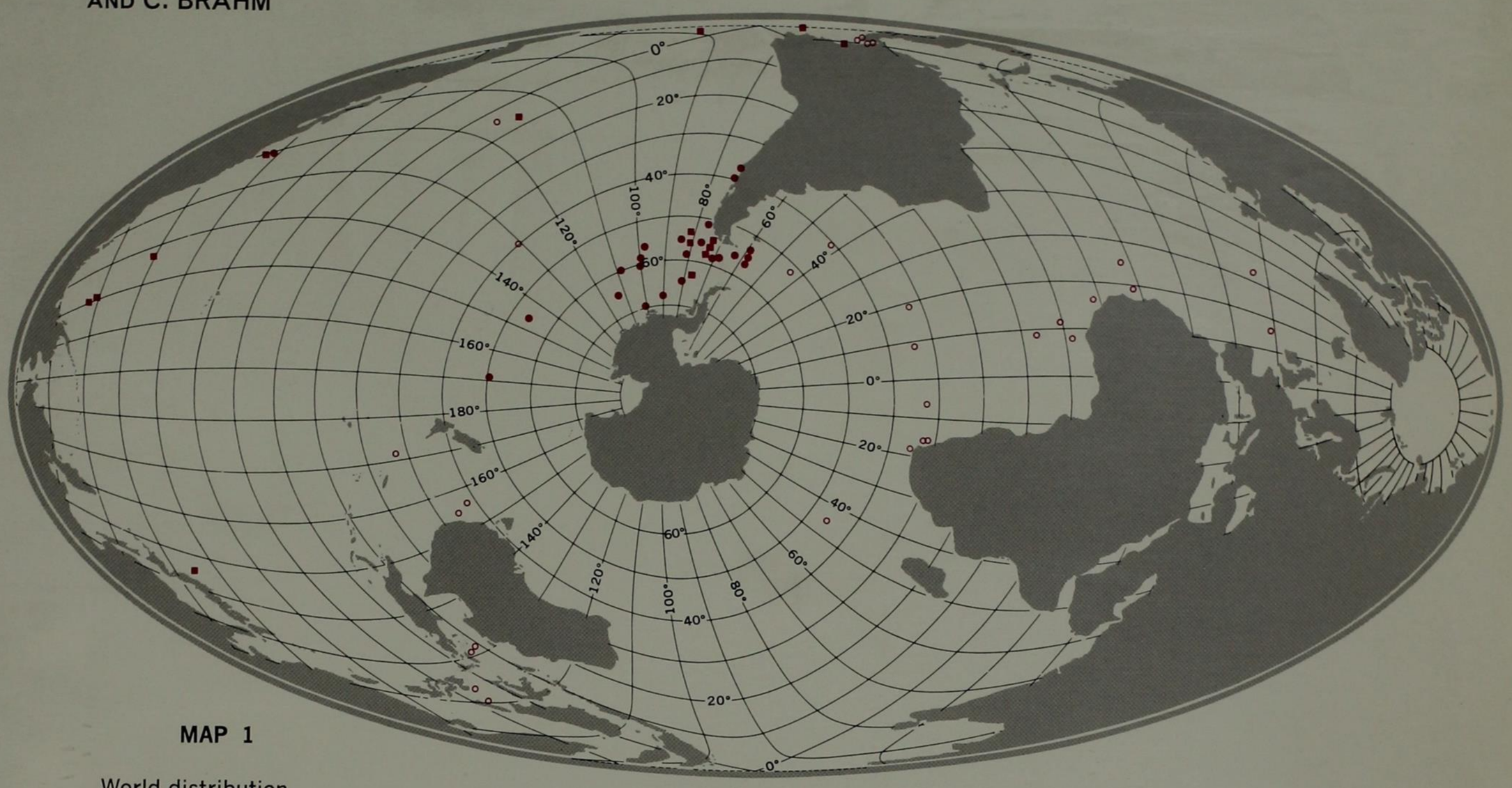
- Archaeoscinidae
  - 1 *Archaeoscina steenstrupi*
  - 2 *Mimonecteola beebei*
- Brachyscelidae
  - 3 *Brachyscelus rapacoides*
  - 4 *Brachyscelus crusculum*
  - 5 *Thamneus platyrhynchus*
- Chuneolidae
  - 6 *Chuneola parasitica*
- Lycaeidae
  - 7 *Pseudolycaea pachypoda*
  - 8 *Tryphana malmi*
- Mimonectidae
  - 9 *Mimonectes sphaericus*
- Parascelidae
  - 10 *Parascelus typhoides*
- Platyscelidae
  - 11 *Platyscelus ovoides*
  - 12 *Hemityphis rapax*
  - 13 *Tetrathyrus forcipatus*

NEBALIACEA

Nebaliopsis typica

FOLIO 11 — MARINE INVERTEBRATES
ANTARCTIC MAP FOLIO SERIES

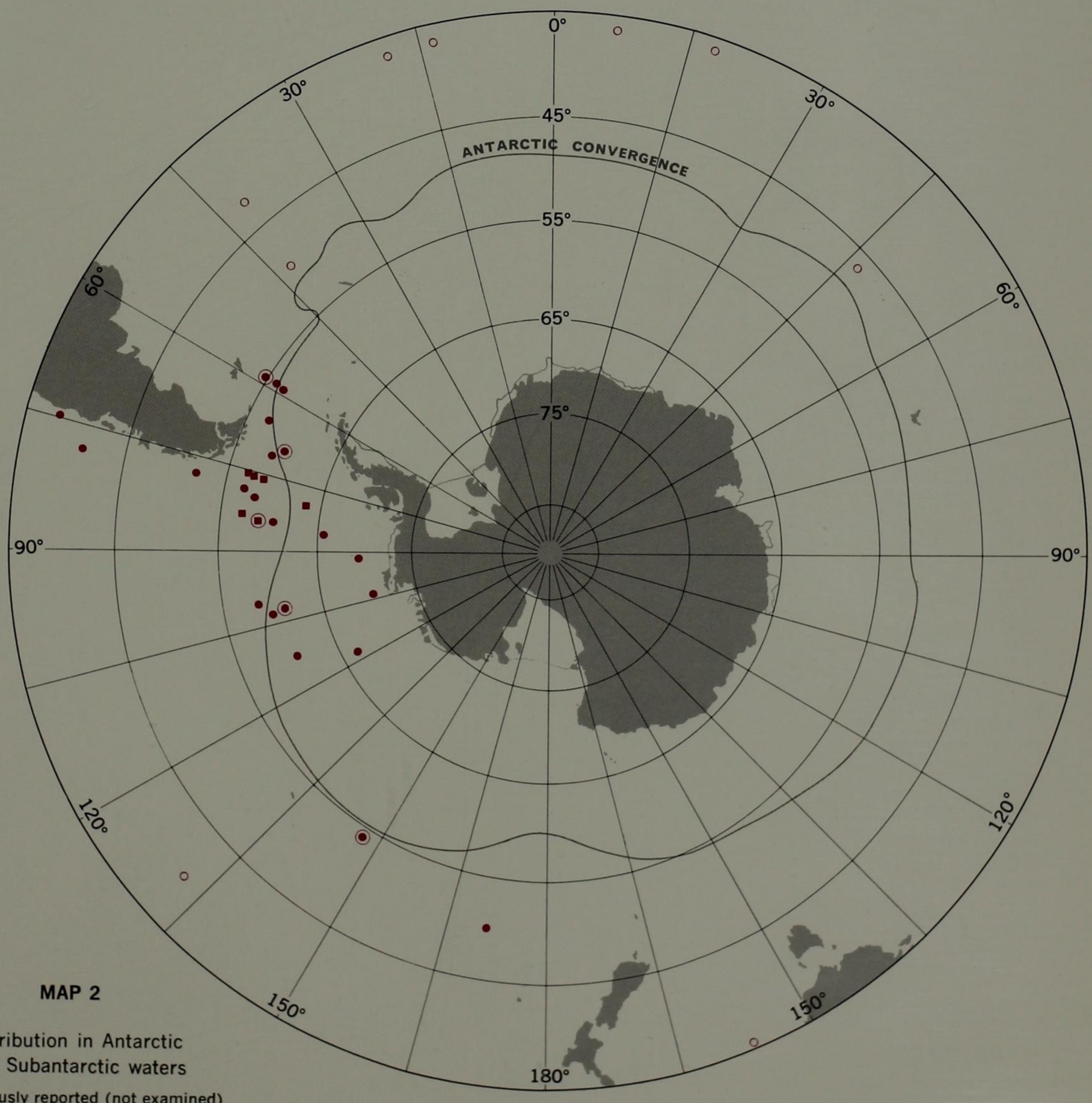
COMPILED BY S. R. GEIGER
AND C. BRAHM



MAP 1

World distribution

- ○ previously reported (not examined)
- ● previously reported (examined)
- ■ not previously reported



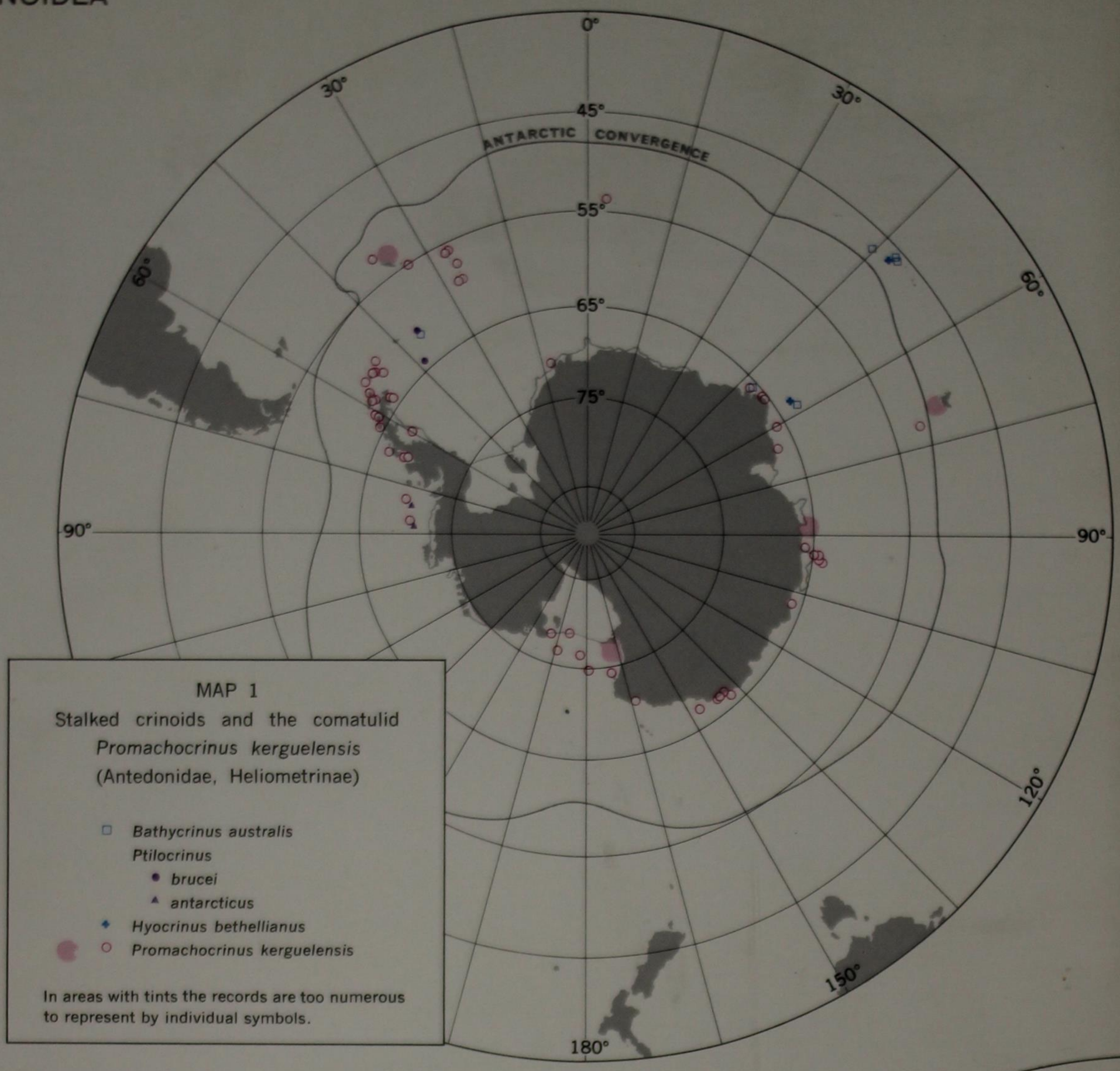
MAP 2

Distribution in Antarctic
and Subantarctic waters

- ○ previously reported (not examined)
- ● previously reported (examined)
- ■ not previously reported
- ◉◉ 0—1000 meters

AMERICAN GEOGRAPHICAL SOCIETY—1969

CRINOIDEA



MAP 1

Stalked crinoids and the comatulid *Promachocrinus kerguelensis* (Antedonidae, Heliometrinae)

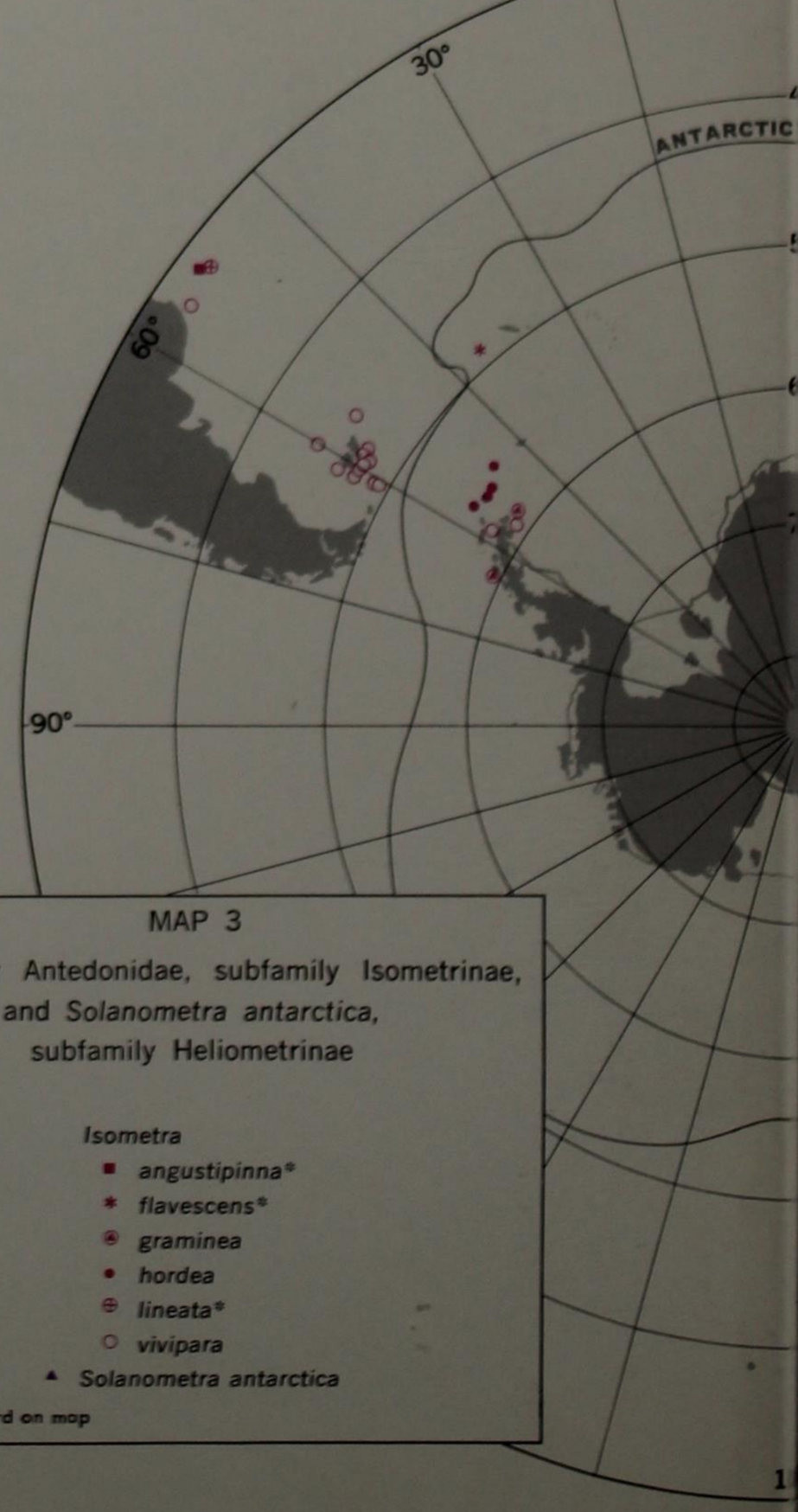
- *Bathycrinus australis*
- *Ptilocrinus*
  - *brucei*
  - *antarcticus*
- *Hyocrinus bethellianus*
- *Promachocrinus kerguelensis*

In areas with tints the records are too numerous to represent by individual symbols.



Bathycrinus

(after Thomson, 1876)
X2



MAP 3

The family Antedonidae, subfamily Isometrinae, and *Solanometra antarctica*, subfamily Heliometrinae

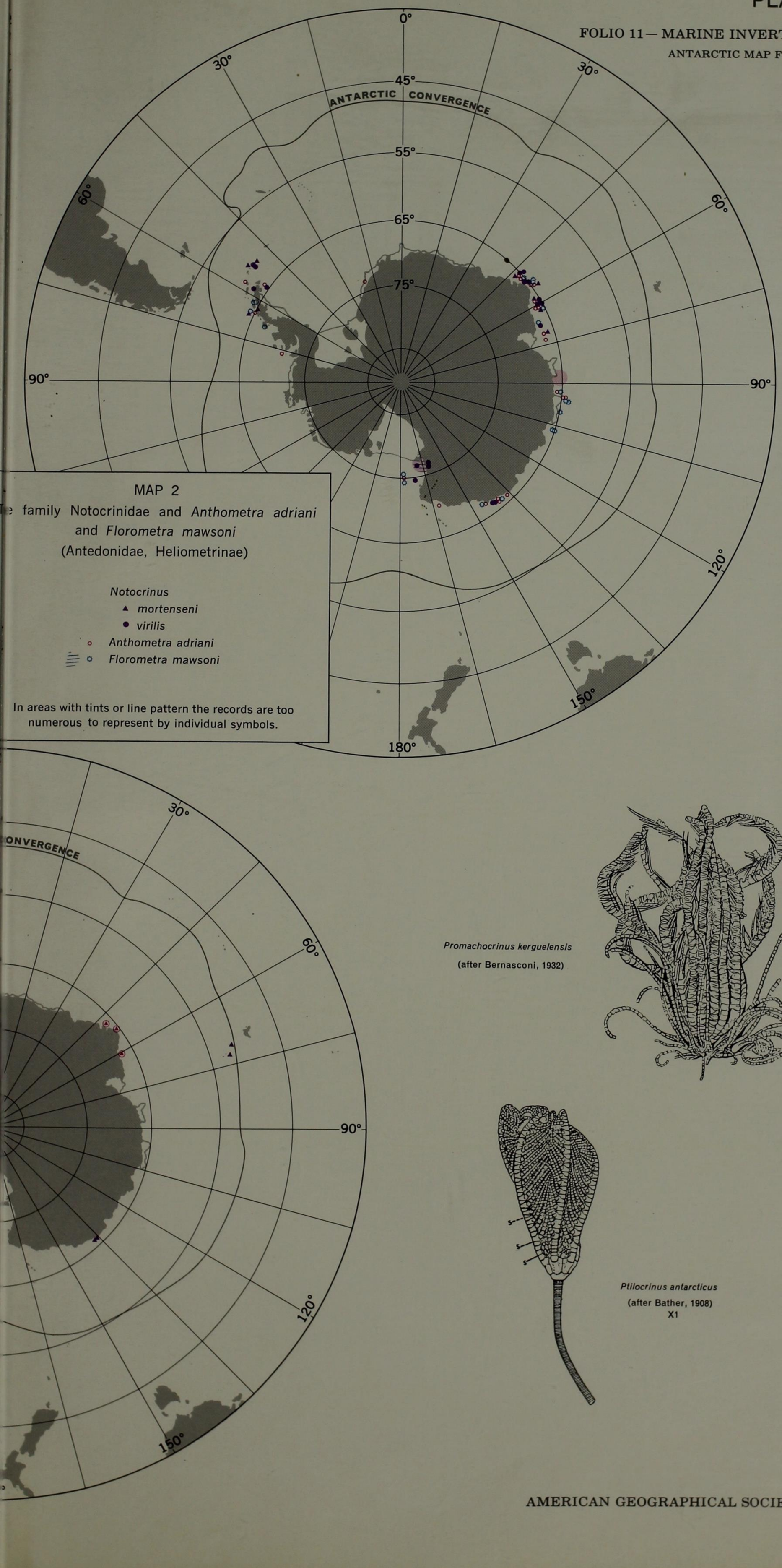
Isometra

- *angustipinna**
- *flavescens**
- *graminea*
- *hordea*
- *lineata**
- *vivipara*

Solanometra antarctica

*Only one record on map

COMPILED BY J. H. DEARBORN
AND J. A. ROMMEL



MAP 2

The family Notocrinidae and *Anthometra adriani* and *Florometra mawsoni* (Antedonidae, Heliometrinae)

Notocrinus
- ▲ *mortenseni*
- ● *virilis*

○ *Anthometra adriani*

○ *Florometra mawsoni*

In areas with tints or line pattern the records are too numerous to represent by individual symbols.

Promachocrinus kerguelensis
(after Bernasconi, 1932)

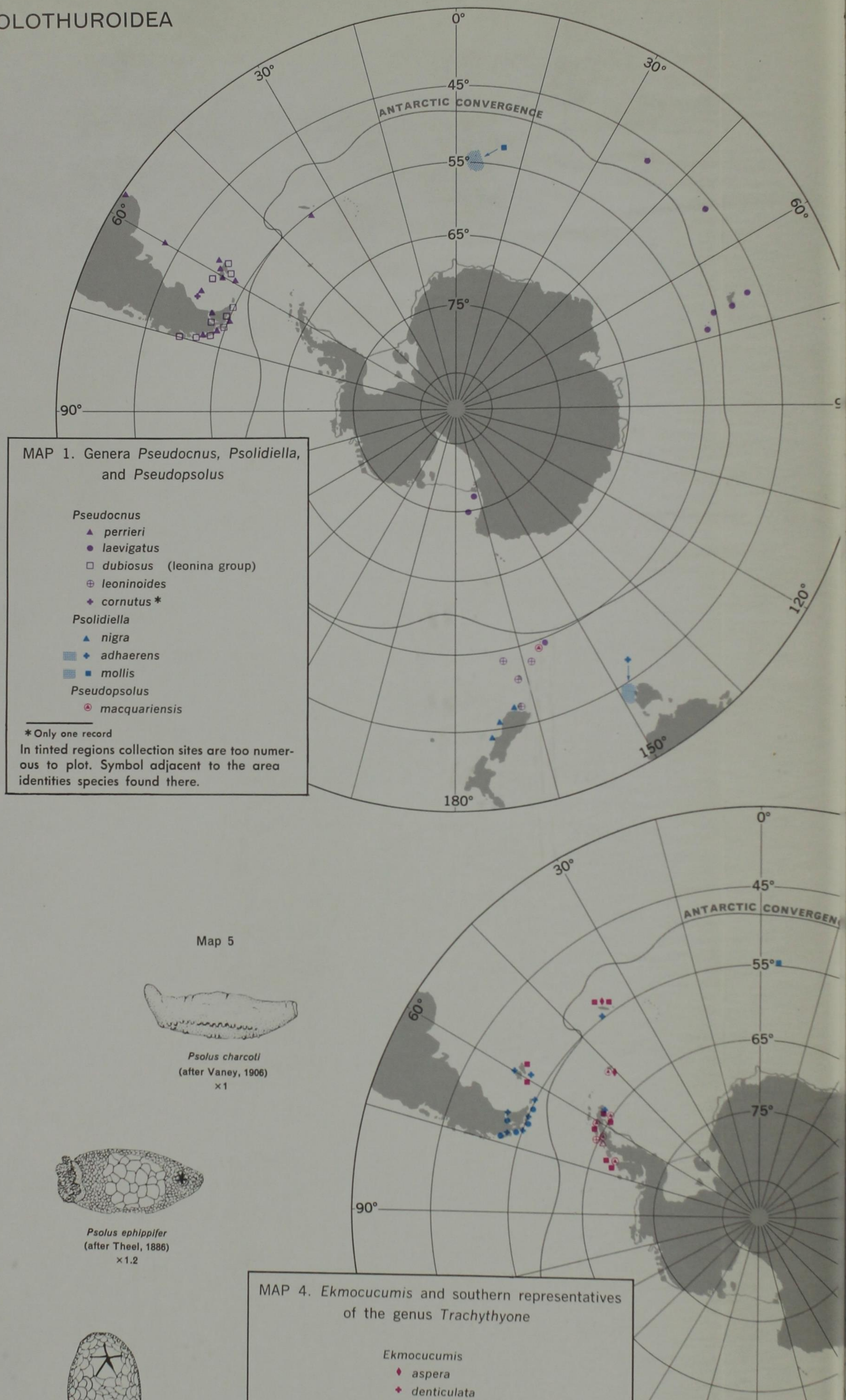
Ptilocrinus antarcticus
(after Bather, 1908)
X1

2

S

S

HOLOTHUROIDEA



MAP 1. Genera *Pseudocnus*, *Psolidiella*, and *Pseudopsolus*

Pseudocnus
- ▲ *perrieri*
- ● *laevigatus*
- □ *dubiosus* (leonina group)
- ⊕ *leoninoides*
- ✦ *cornutus* *

Psolidiella
- ▲ *nigra*
- ▩ ✦ *adhaerens*
- ▩ ■ *mollis*

Pseudopsolus
- ◉ *macquariensis*

* Only one record

In tinted regions collection sites are too numerous to plot. Symbol adjacent to the area identities species found there.

Map 5

Psolus charcoli
(after Vaney, 1906)
×1

Psolus ephippifer
(after Theel, 1886)
×1.2

Psolus antarcticus
(after Theel, 1886)
×1

MAP 4. *Ekmocucumis* and southern representatives of the genus *Trachythyone*

Ekmocucumis
- ♦ *aspera*
- ✦ *denticulata*
- ⊕ *irregularis*
- ◉ *spatha*
- ■ *steineni*
- △ *turqueti*

Trachythyone
- ● *lechleri*
- □ *macphersonae*
- ■ *mira*
- ✦ *parva*
- ⊕ *squamata* *

* Only one record

COMPILED BY D. L. PAWSON

MAP 2. Genera *Cladodactyla*, *Cucumaria*, and *Hemioedema*

Cladodactyla
- *crocea*

Cucumaria
- *ferrari*
- *psolidiiformis*
- *georgiana*
- *attenuata*
- *periprocta* *
- *perfida* *
- *conspicua* *

Hemioedema
- *spectabilis*

* Only one record

MAP 3. Families Ypsilot
see Map 4) and Psolida
and th

Abyssocucu
- *abyss*

Staurocucu
- *liouvil*

Ypsilocucur
- 1 *scotia*
- 2 *turrica*

Echinocucu
- *hispid*

Ypsilothuri
- *bitenta*

** Known from only one reco

MAP 5. Southern representatives of the genus *Psolus*

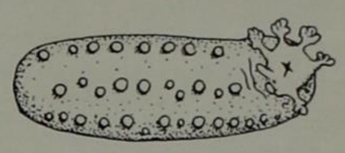
- *antarcticus*
- *charcoti*
- *ephippifer*
- *koehleri*
- *murrayi*
- *patagonicus*
- *punctatus*
- *squamatus*

PLATE 22

FOLIO 11— MARINE INVERTEBRATES

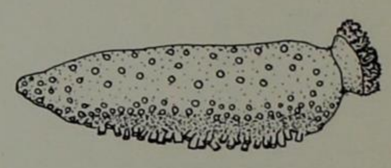
ANTARCTIC MAP FOLIO SERIES

Map 2

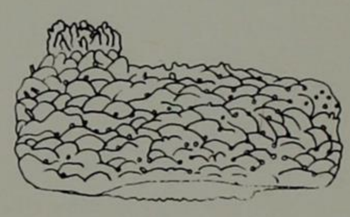


Cucumaria attenuata
(after Vaney, 1906)
×4.5

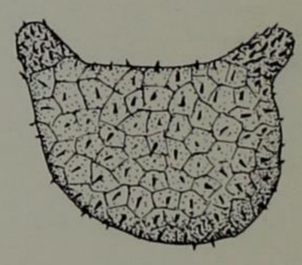
Map 3



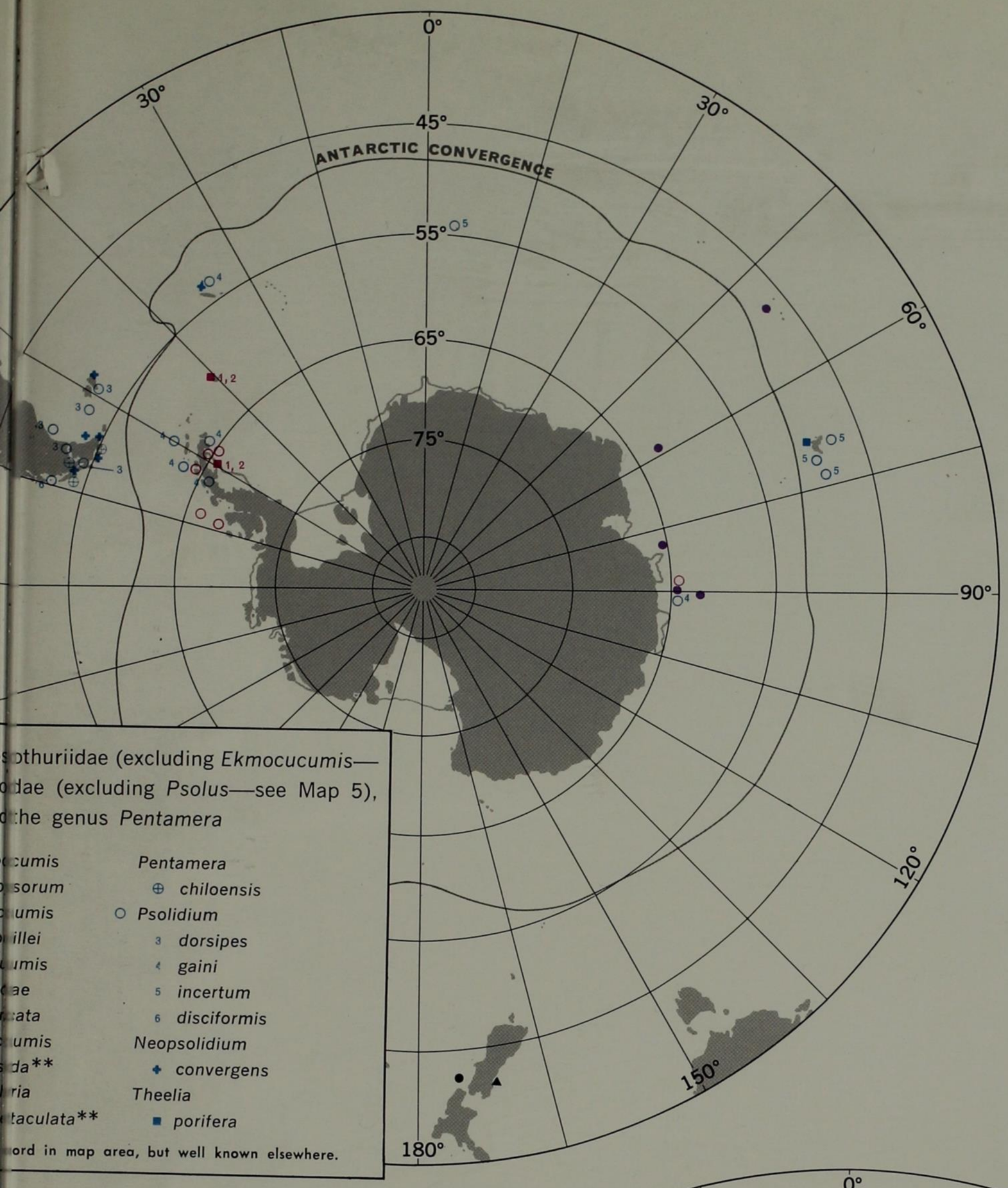
Neopsolidium convergens
(after Perrier, 1905)
×2



Psolidium dorsipes
(after Ekman, 1921)
×4.3



Ypsilothuria bitentaculata
(after Ludwig, 1894)
×2

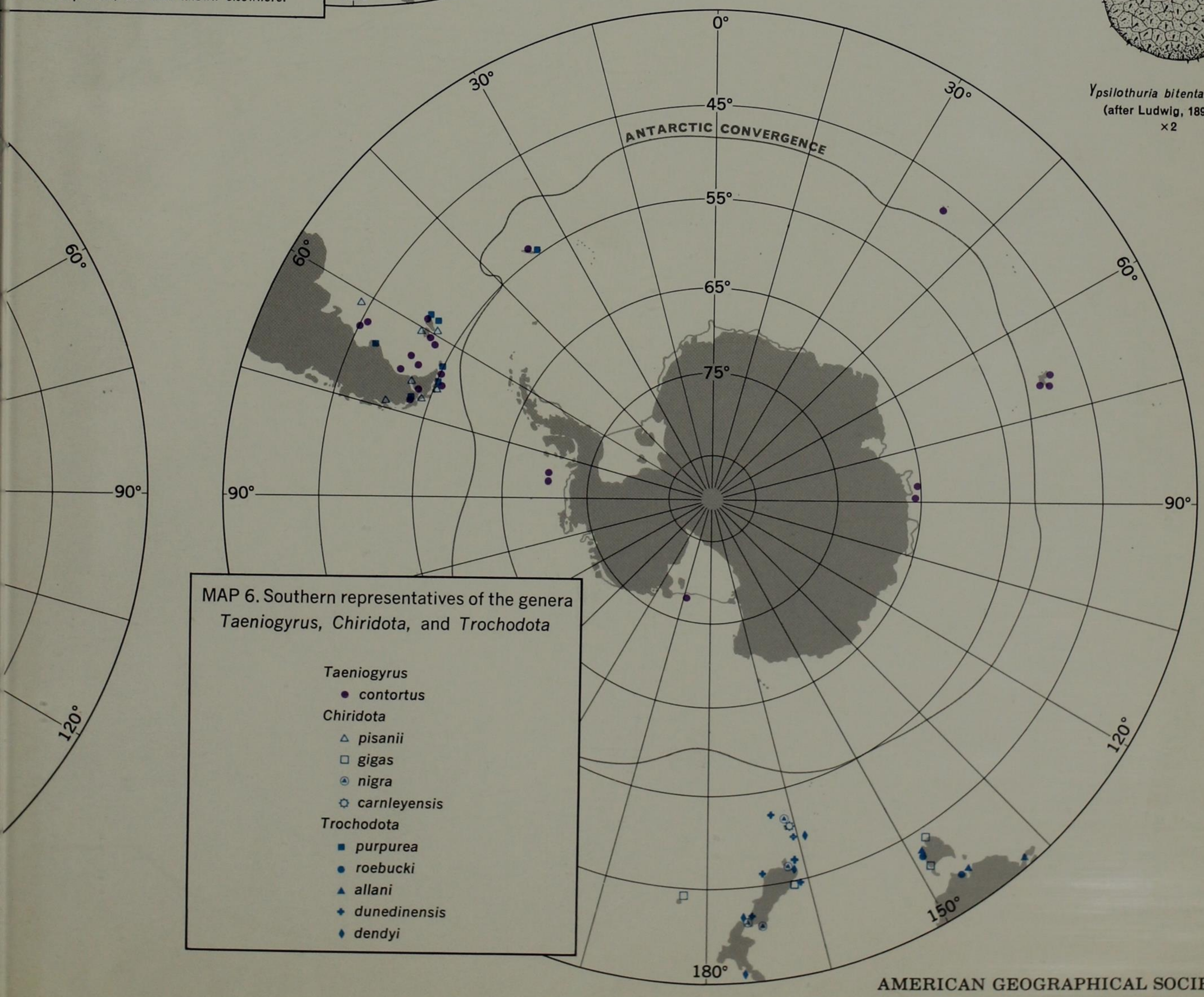


othuriidae (excluding *Ekmocucumis*—
dae (excluding *Psolus*—see Map 5),
he genus *Pentamera*

cumis
sorum
umis
illei
umis
ae
ata
umis
da**
ria
taculata**

Pentamera
⊕ *chiloensis*
○ *Psolidium*
3 *dorsipes*
4 *gaini*
5 *incertum*
6 *disciformis*
Neopsolidium
✤ *convergens*
Theelia
■ *porifera*

ord in map area, but well known elsewhere.



MAP 6. Southern representatives of the genera *Taeniogyrus*, *Chiridota*, and *Trochodota*

Taeniogyrus
● *contortus*
Chiridota
△ *pisanii*
□ *gigas*
◉ *nigra*
☼ *carnleyensis*
Trochodota
■ *purpurea*
● *roebucki*
▲ *allani*
✦ *dunedinensis*
♦ *dendyi*

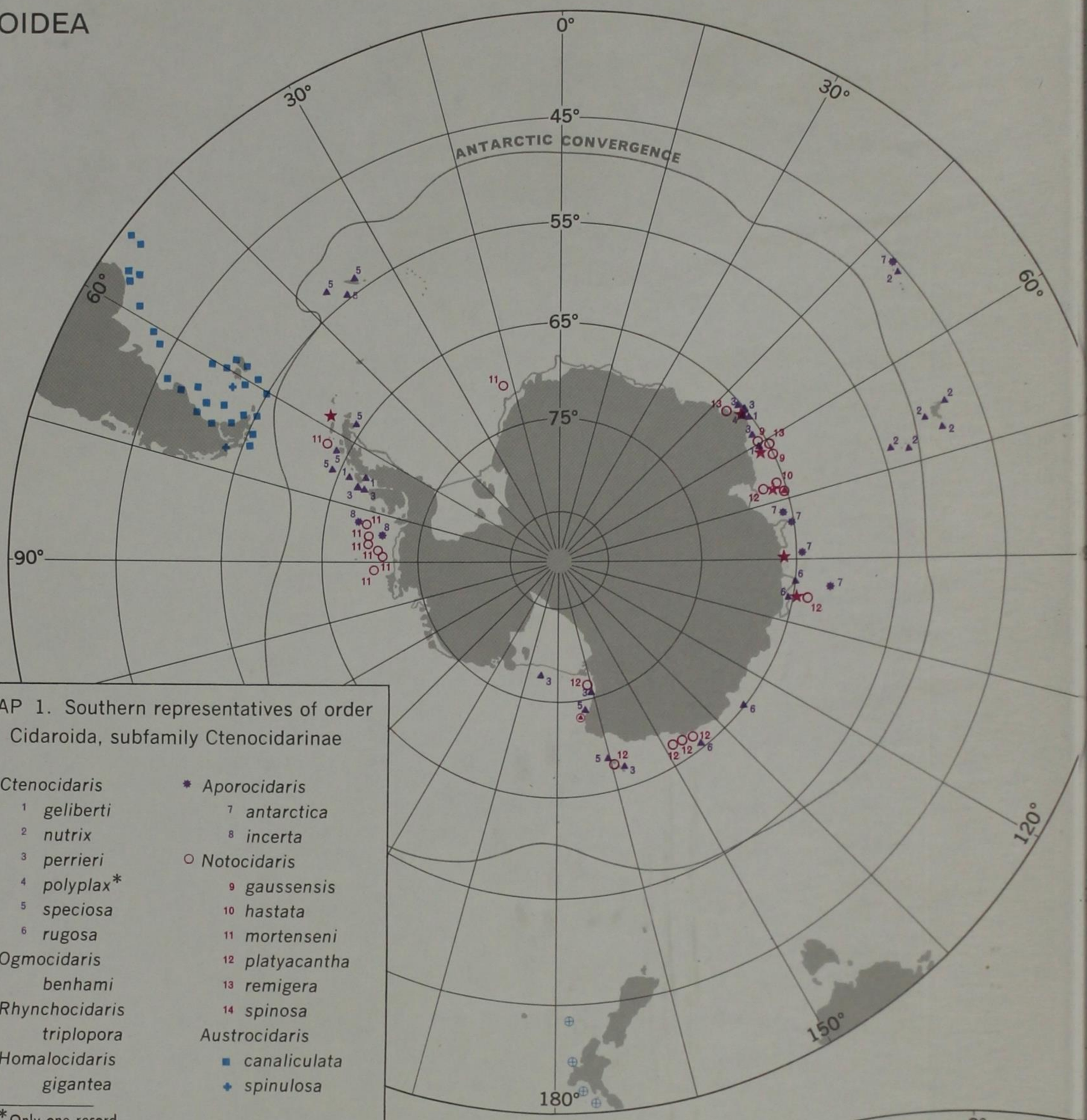
AMERICAN GEOGRAPHICAL SOCIETY—1969

3

ES

ES

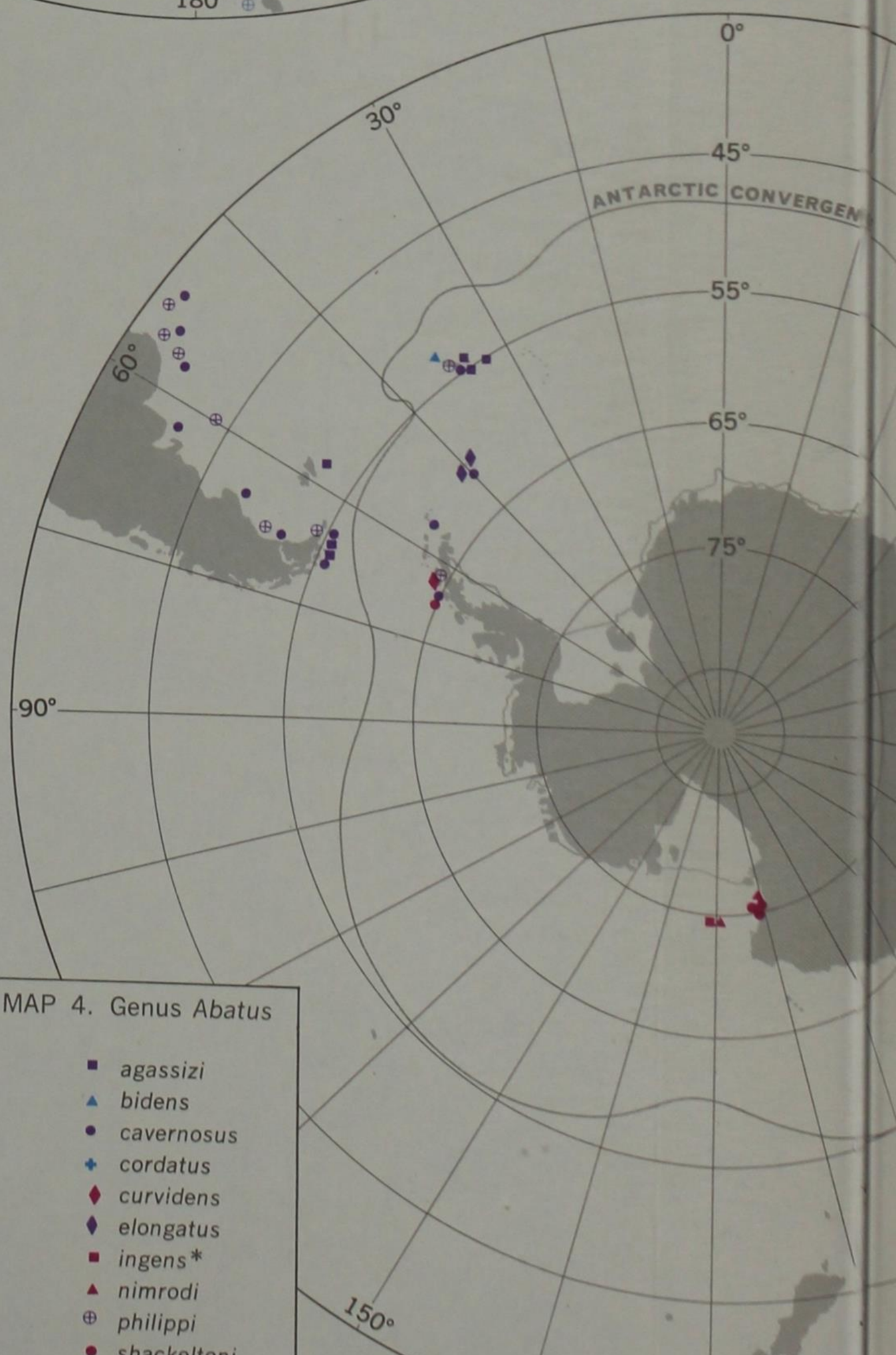
ECHINOIDEA



MAP 1. Southern representatives of order Cidaroida, subfamily Ctenocidarinae

- ▲ *Ctenocidaris*
  - 1 *geliberti*
  - 2 *nutrix*
  - 3 *perrieri*
  - 4 *polyplax**
  - 5 *speciosa*
  - 6 *rugosa*
- ⊕ *Ogmocidaris benhami*
- ★ *Rhynchocidaris triplopora*
- ◉ *Homalocidaris gigantea*
- ✸ *Aporocidaris*
  - 7 *antarctica*
  - 8 *incerta*
- ○ *Notocidaris*
  - 9 *gaussensis*
  - 10 *hastata*
  - 11 *mortenseni*
  - 12 *platyacantha*
  - 13 *remigera*
  - 14 *spinosa*
- *Austrocidaris*
  - ■ *canaliculata*
  - ◆ *spinulosa*

*Only one record



MAP 4. Genus *Abatus*

- ■ *agassizi*
- ▲ *bidens*
- ● *cavernosus*
- ✚ *cordatus*
- ♦ *curvidens*
- ♦ *elongatus*
- ■ *ingens**
- ▲ *nimrodi*
- ⊕ *philippi*
- ● *shackeltoni*

*Only one record

COMPILED BY D. L. PAWSON

MAP 2. Genus *Sterechinus*
(Bathymetric range of genus: 0 to 1566 m)

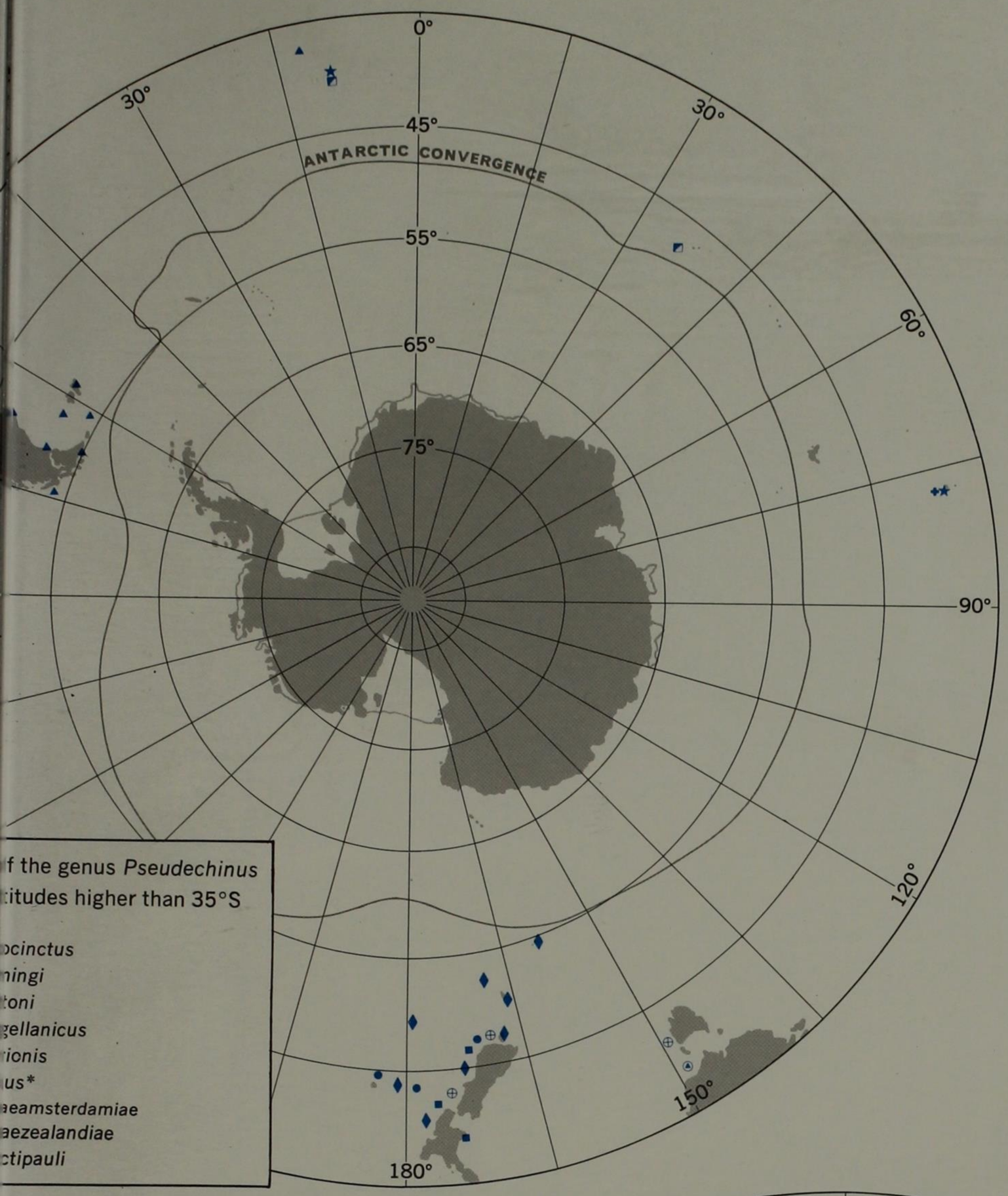
- ● *agassizi*
- ■ *antarcticus*
- ▲ *dentifer*
- ✚ *diadema*
- ⊕ *neumayeri*

MAP 3. Species
which occur in

- ■ *al*
- ● *fle*
- ⊕ *hu*
- ▲ *m*
- ◩ *m*
- ◉ *no*
- ★ *no*
- ♦ *no*
- ✚ *sa*

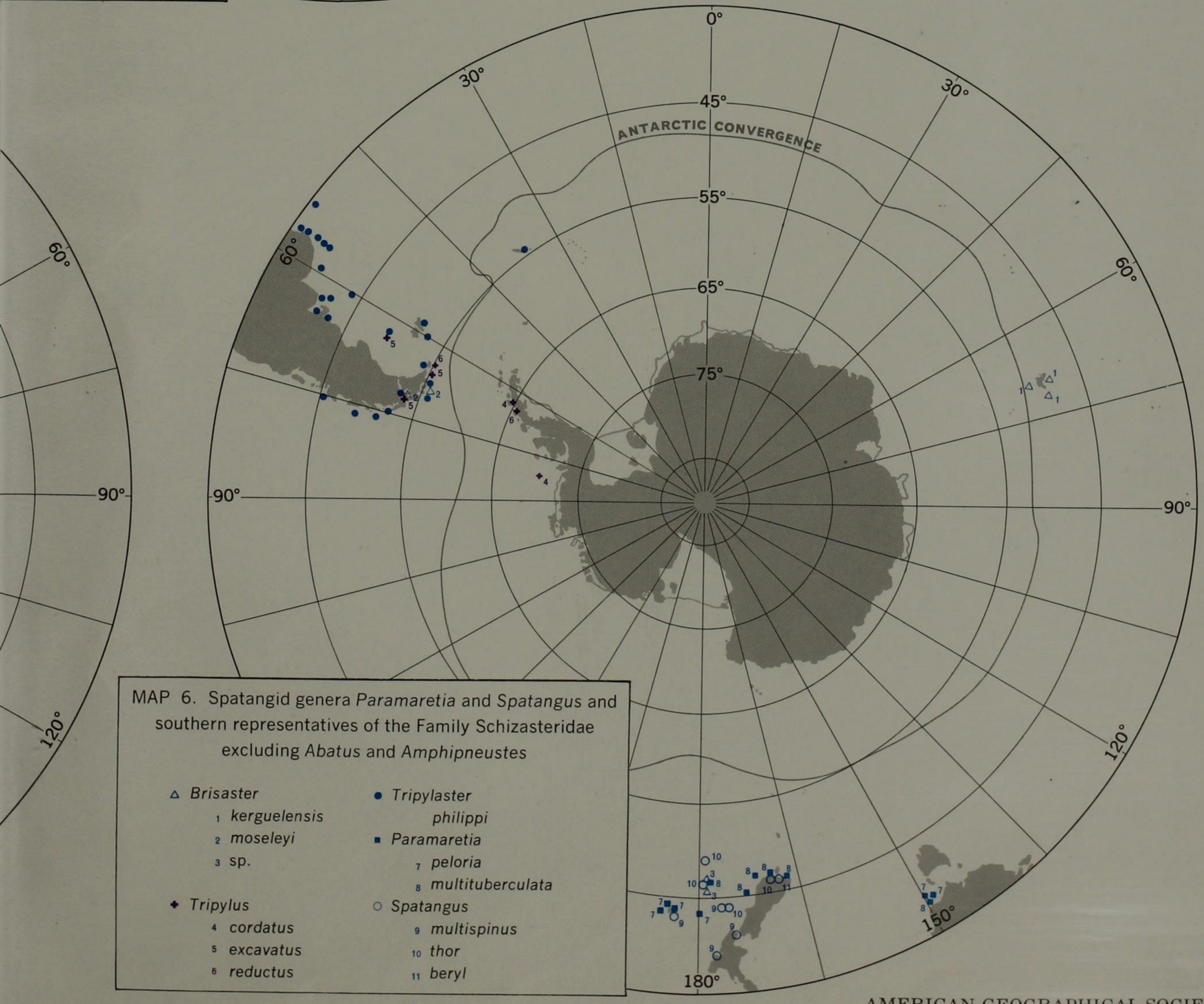
MAP 5. Genus *Amphipneustes*

- ● *bifidus*
- ⊕ *brevisternalis*
- ✚ *koehleri*
- ■ *lorioli*
- ◩ *marsupialis*
- ◉ *rostratus*
- ♦ *similis*
- ▲ *tumescens*



f the genus *Pseudechinus*
itudes higher than 35°S

- *ocinctus*
- *ningi*
- *toni*
- *gellanicus*
- *rionis*
- *us**
- *aeamsterdamiae*
- *aezealandiae*
- *ctipauli*

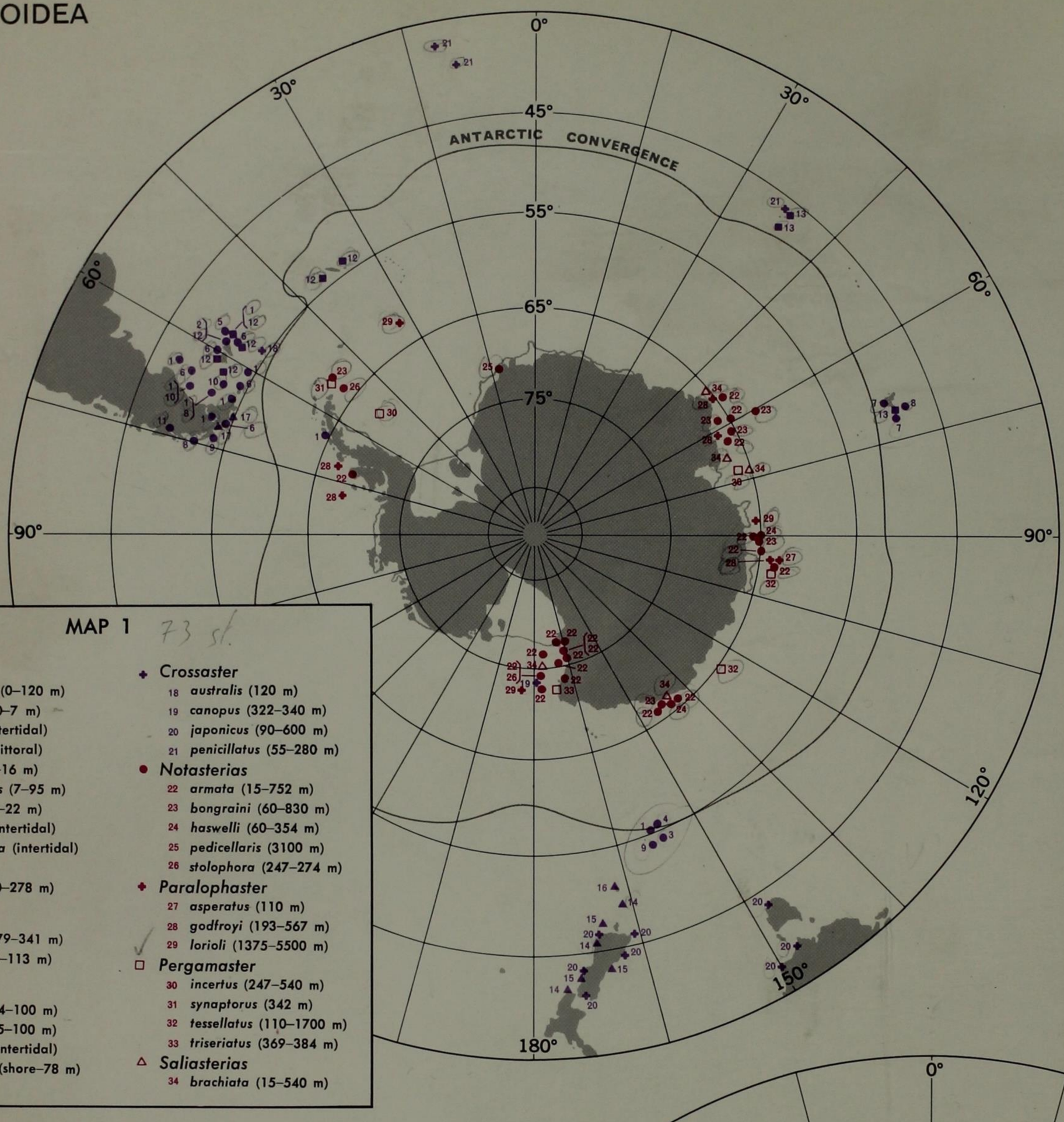


MAP 6. Spatangid genera *Paramaretia* and *Spatangus* and southern representatives of the Family Schizasteridae excluding *Abatus* and *Amphipneustes*

- △ *Brisaster*
  - 1 *kerguelensis*
  - 2 *moseleyi*
  - 3 sp.
- ✚ *Tripylus*
  - 4 *cordatus*
  - 5 *excavatus*
  - 6 *reductus*
- ● *Tripylaster philippi*
- ■ *Paramaretia*
  - 7 *peloria*
  - 8 *multituberculata*
- ○ *Spatangus*
  - 9 *multispinus*
  - 10 *thor*
  - 11 *beryl*

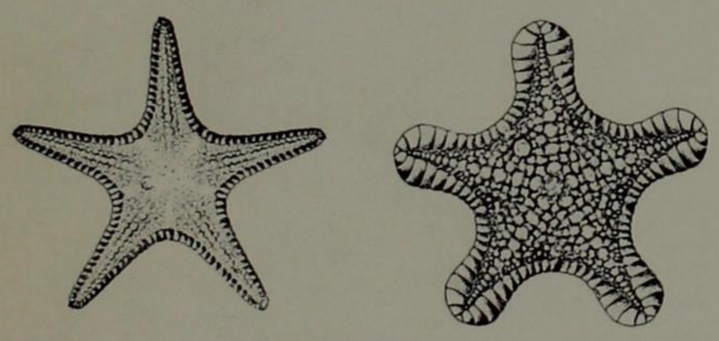
ASTEROIDEA

SHEET 1



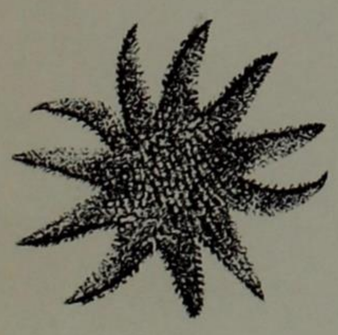
MAP 1

- ● *Anasterias*
  - 1 *antarctica* (0–120 m)
  - 2 *conferta* (0–7 m)
  - 3 *directa* (intertidal)
  - 4 *mawsoni* (littoral)
  - 5 *minuta* (0–16 m)
  - 6 *pedicellaris* (7–95 m)
  - 7 *perrieri* (0–22 m)
  - 8 *rupicola* (intertidal)
  - 9 *sphaerulata* (intertidal)
  - 10 *stolidota*
  - 11 *studeri* (50–278 m)
- ■ *Anteliaster*
  - 12 *australis* (79–341 m)
  - 13 *scaber* (22–113 m)
- ▲ *Asterodon*
  - 14 *dilatatus* (4–100 m)
  - 15 *miliaris* (35–100 m)
  - 16 *robustus* (intertidal)
  - 17 *singularis* (shore–78 m)
- ✚ *Crossaster*
  - 18 *australis* (120 m)
  - 19 *canopus* (322–340 m)
  - 20 *japonicus* (90–600 m)
  - 21 *penicillatus* (55–280 m)
- ● *Notasterias*
  - 22 *armata* (15–752 m)
  - 23 *bongraini* (60–830 m)
  - 24 *haswelli* (60–354 m)
  - 25 *pedicellaris* (3100 m)
  - 26 *stolophora* (247–274 m)
- ✚ *Paralophaster*
  - 27 *asperatus* (110 m)
  - 28 *godfroyi* (193–567 m)
  - 29 *lorioli* (1375–5500 m)
- □ *Pergamaster*
  - 30 *incertus* (247–540 m)
  - 31 *synaptorus* (342 m)
  - 32 *tessellatus* (110–1700 m)
  - 33 *triseriatus* (369–384 m)
- △ *Saliasterias*
  - 34 *brachiata* (15–540 m)



Asterodon

Arm-spread up to 5 in.



Crossaster

Arm-spread up to 7 in.

MAP 2

- ● *Coscinasterias*
  - 1 *africana* (0–40 m)
  - 2 *calamaria* (4–80 m)
  - 3 *candicans* (450–560 m)
  - 4 *eustyla* (200–300 m)
  - 5 *victoriae* (70 m)
- □ *Cosmasterias*
  - 6 *capensis* (120 m)
  - 7 *dyscrita* (230–400 m)
  - 8 *lurida* (0–690 m)
  - 9 *polygramma* (490 m)
  - 10 *tomidata* (90 m)
- ○ *Diplopteraster*
  - 11 *perigrinator* (254 m)
  - 12 *semireticulatus* (99–138
  - 13 *verrucosus* (75–205 m)

MAP 3

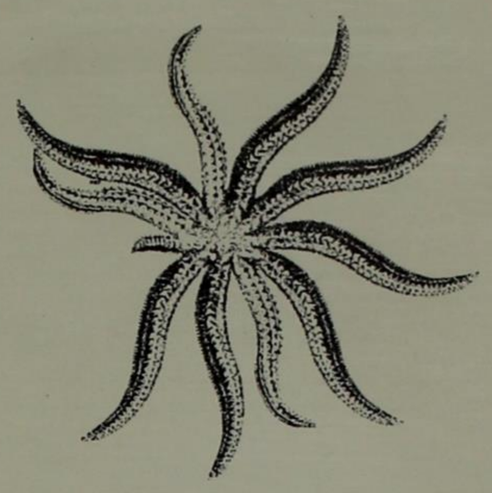
- □ *Cuenotaster*
  - 1 *involutus* (60–578 m)
- △ *Granaster*
  - 2 *nutrix* (1–250 m)
- ○ *Lysasterias*
  - 3 *adeliae* (24–578 m)
  - 4 *belgicae* (560 m)
  - 5 *chirophora* (450–560 m)
  - 6 *digitata* (163–300 m)
  - 7 *hemiora* (70 m)
  - 8 *heteractis* (342 m)
  - 9 *joffrei* (88–810 m)
  - 10 *perrieri* (0–708 m)
- ▲ *Myoraster*
  - 11 *antarcticus* (88–578 m)
  - 12 *incertus* (littoral)
  - 13 *tenuis* (110 m)
- ■ *Pedicellaster*
  - 14 *formatus* (120 m)
  - 15 *hypernotius* (93–450 m)
  - 16 *reticulatus* (156 m)
  - 17 *scaber* (40–50 m)
- ● *Perknaster*
  - 18 *aurantiacus* (75–254 m)
  - 19 *aurorae* (18–300 m)
  - 20 *charcoti* (132–235 m)
  - 21 *densus* (101–385 m)
  - 22 *fuscus* (3–362 m)
  - 23 *rallieri* (littoral)
  - 24 *sladeni* (120–500 m)

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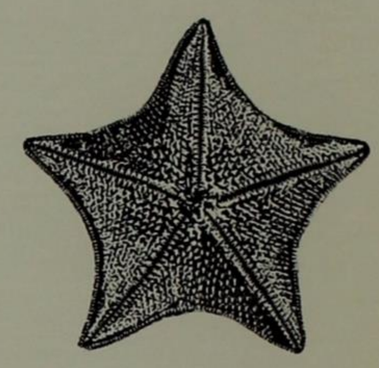
PLATE 24

FOLIO 11 — MARINE INVERTEBRATES

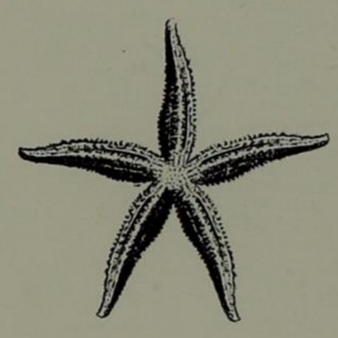
ANTARCTIC MAP FOLIO SERIES



Coscinasterias
Arm-spread up to 14 in.

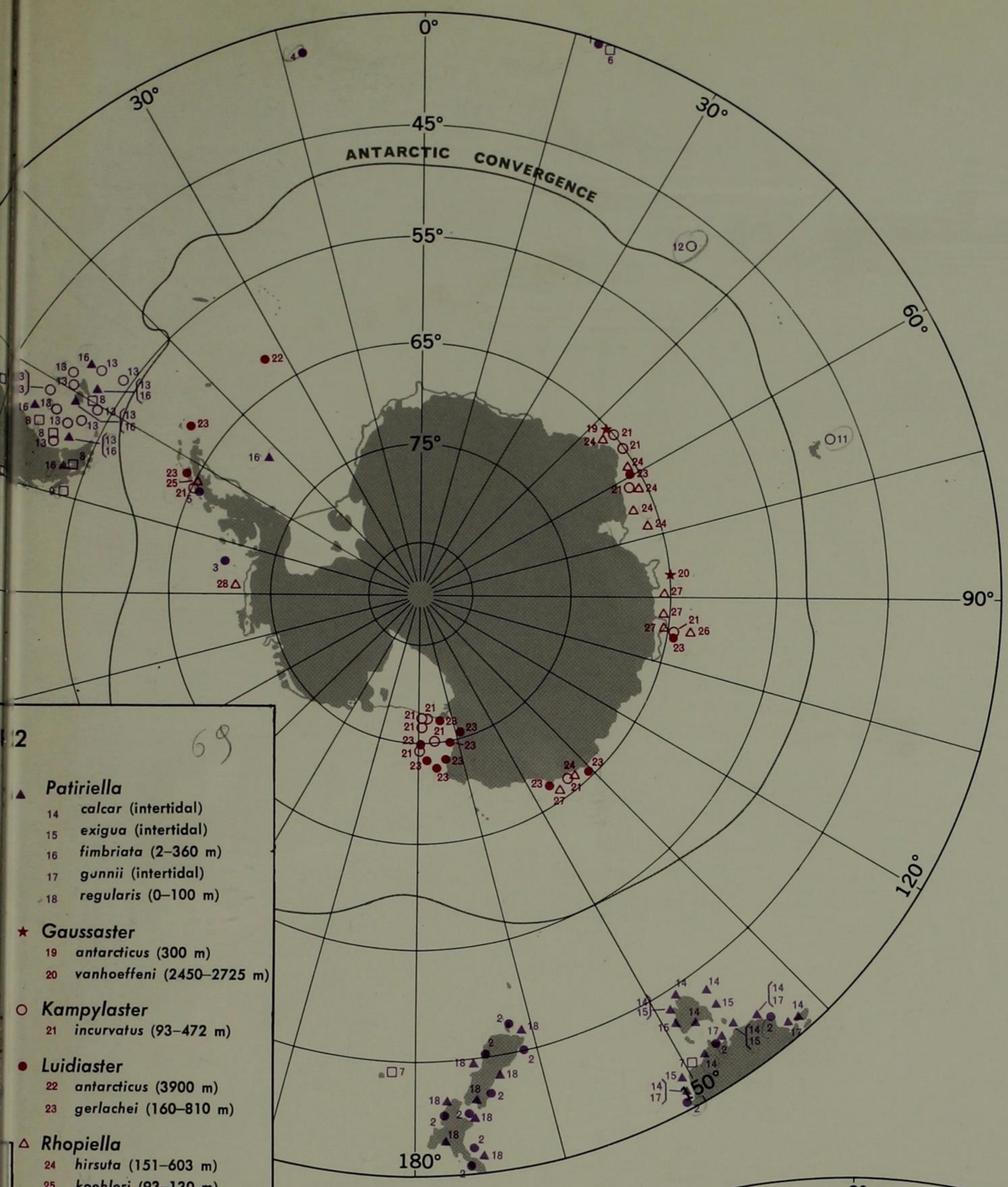


Patiriella
Arm-spread up to 3 in.



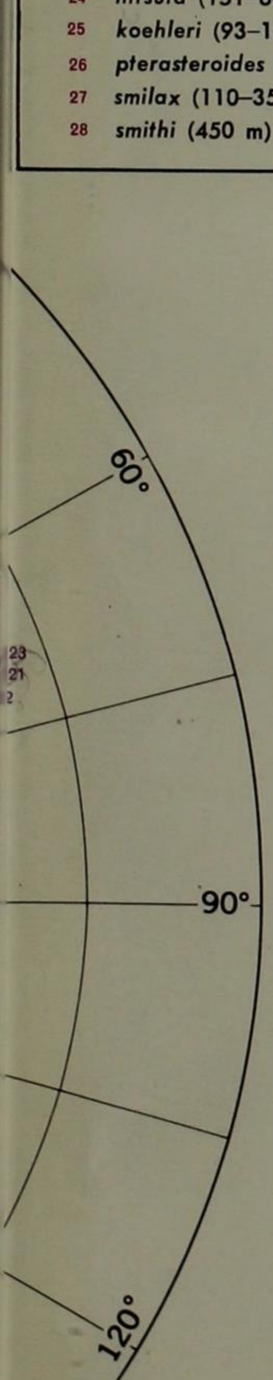
Cosmasterias
Arm-spread up to 8 in.

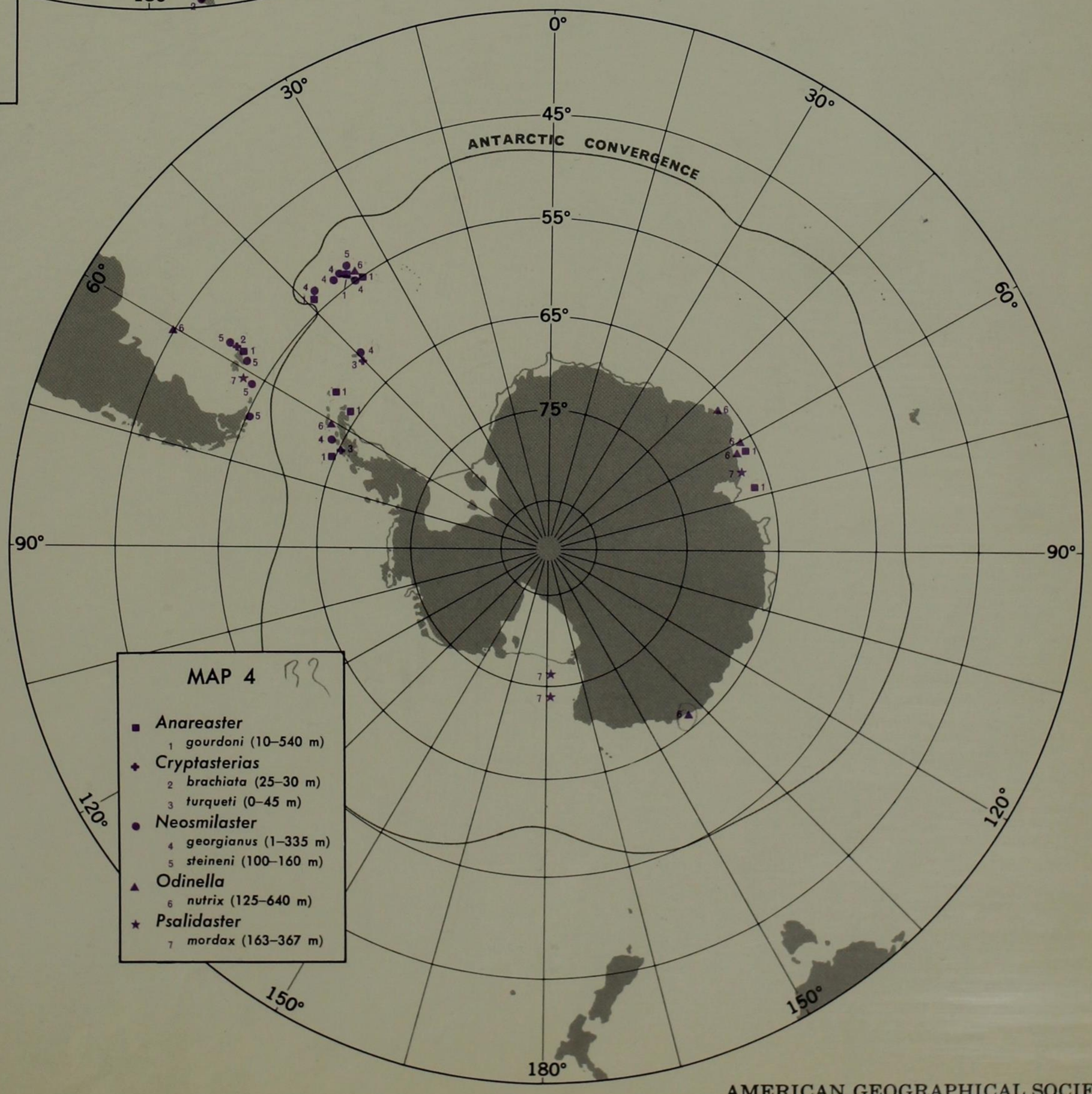
All drawings after Fell, 1962



MAP 2

- ▲ *Patiriella*
  - 14 *calcar* (intertidal)
  - 15 *exigua* (intertidal)
  - 16 *fimbriata* (2–360 m)
  - 17 *gunnii* (intertidal)
  - 18 *regularis* (0–100 m)
- ★ *Gaussaster*
  - 19 *antarcticus* (300 m)
  - 20 *vanhoeffeni* (2450–2725 m)
- ○ *Kampylaster*
  - 21 *incurvatus* (93–472 m)
- ● *Luidiaster*
  - 22 *antarcticus* (3900 m)
  - 23 *gerlachei* (160–810 m)
- △ *Rhopiella*
  - 24 *hirsuta* (151–603 m)
  - 25 *koehleri* (93–130 m)
  - 26 *pterasteroides* (358 m)
  - 27 *smilax* (110–350 m)
  - 28 *smithi* (450 m)





MAP 4

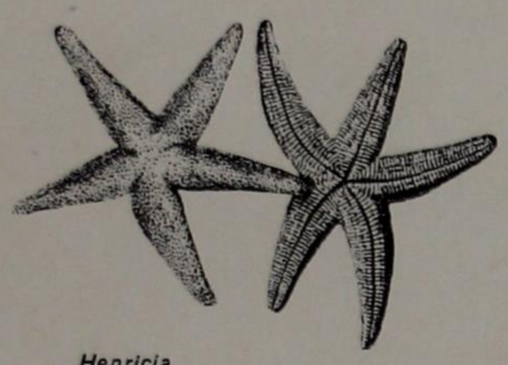
- ■ *Anareaster*
  - 1 *gourdoni* (10–540 m)
- ✦ *Cryptasterias*
  - 2 *brachiata* (25–30 m)
  - 3 *turqueti* (0–45 m)
- ● *Neosmilaster*
  - 4 *georgianus* (1–335 m)
  - 5 *steineni* (100–160 m)
- ▲ *Odinella*
  - 6 *nutrix* (125–640 m)
- ★ *Psalidaster*
  - 7 *mordax* (163–367 m)

AMERICAN GEOGRAPHICAL SOCIETY—1969

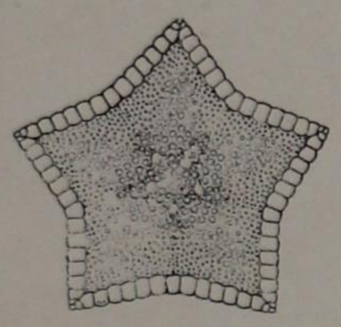
ASTEROIDEA

SHEET 2

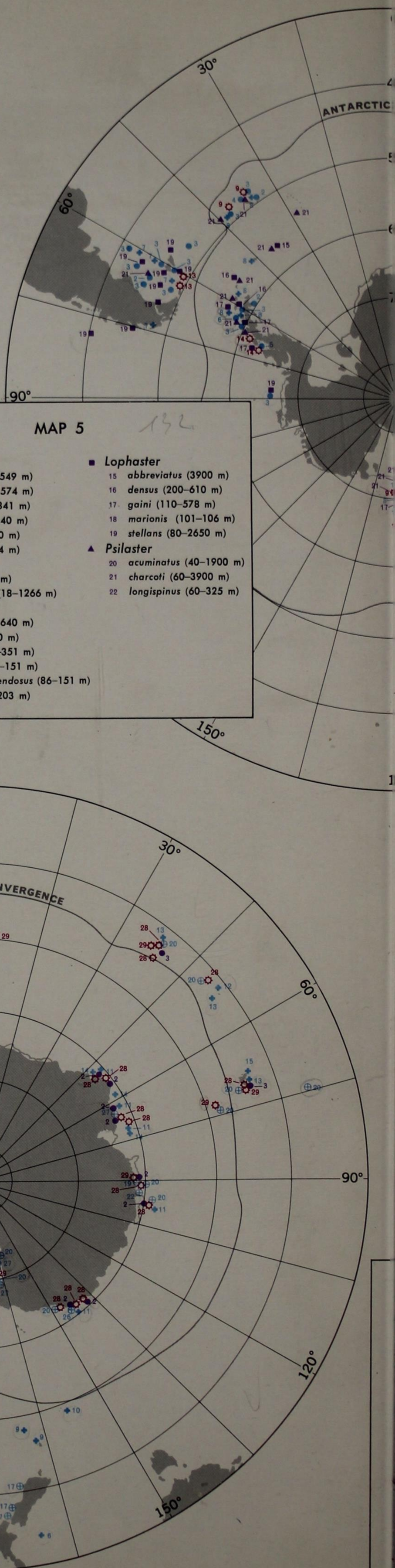
COMPILED BY H. B. FELL
AND S. DAWSEY



Henricia
Arm-spread up to 4 in.



Odontaster
Arm-spread up to 3 in.



MAP 5

- ● *Acodontaster*
  - 1 *capitatus* (163–549 m)
  - 2 *conspicuus* (25–574 m)
  - 3 *elongatus* (24–841 m)
  - 4 *hodgsoni* (25–540 m)
  - 5 *marginatus* (250 m)
  - 6 *waitei* (110–354 m)
- ◆ *Bathybiaster*
  - 7 *loripes* (0–490 m)
  - 8 *loripes obesus* (18–1266 m)
- ☼ *Leptychaster*
  - 9 *accrescens* (97–640 m)
  - 10 *antarcticus* (420 m)
  - 11 *flexuosus* (201–351 m)
  - 12 *kerguelensis* (0–151 m)
  - 13 *kerguelensis mendosus* (86–151 m)
  - 14 *magnificus* (5–203 m)
- ■ *Lophaster*
  - 15 *abbreviatus* (3900 m)
  - 16 *densus* (200–610 m)
  - 17 *gaini* (110–578 m)
  - 18 *marionis* (101–106 m)
  - 19 *stellans* (80–2650 m)
- ▲ *Psilaster*
  - 20 *acuminatus* (40–1900 m)
  - 21 *charcoti* (60–3900 m)
  - 22 *longispinus* (60–325 m)

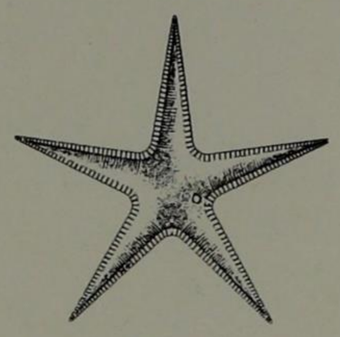
MAP 6

- ● *Diplasterias*
  - 1 *brandti* (0–450 m)
  - 2 *brucei* (5–752 m)
  - 3 *meridionalis* (1–234 m)
  - 4 *octoradiata* (8–55 m)
  - 5 *radiata* (160–177 m)
- ◆ *Henricia*
  - 6 *compacta* (550 m)
  - 7 *diffidens* (75–463 m)
  - 8 *hyadesi* (shore)
  - 9 *lukinsi* (0–30 m)
  - 10 *obesa* (24–490 m)
  - 11 *pagenstecheri* (17–610 m)
  - 12 *praestans* (420 m)
  - 13 *simplex* (0–610 m)
  - 14 *smilax* (163–603 m)
  - 15 *spinulifera* (4–47 m)
  - 16 *studeri* (75–341 m)
- ⊕ *Odontaster*
  - 17 *benhami* (40–600 m)
  - 18 *capitatus* (254 m)
  - 19 *gaussae* (380 m)
  - 20 *meridionalis* (shore–591 m)
  - 21 *penicillatus* (120–171 m)
  - 22 *pentagonalis* (120 m)
  - 23 *pilulatus* (110 m)
  - 24 *pusillus* (3830 m)
  - 25 *singularis* (shore)
  - 26 *tenuis* (25 m)
  - 27 *validus* (shore–941 m)
- ☼ *Porania*
  - 28 *antarctica* (4–3200 m)
  - 29 *glabra* (shore–1335 m)

PLATE 25

FOLIO 11—MARINE INVERTEBRATES

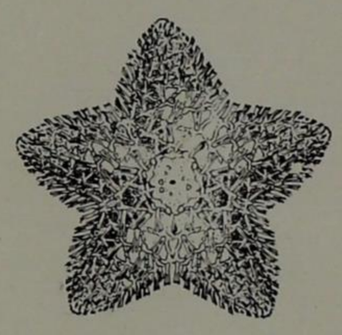
ANTARCTIC MAP FOLIO SERIES



Psilaster

Arm-spread up to 6 in.

All drawings after Fell, 1962



Peribolaster

Arm-spread up to 2 in.

MAP 7

- ● *Pteraster*
  - subgenus *Pteraster*
    - 10 *aculeatus* (325 m)
    - 11 *affinis* (0–603 m)
    - 12 *florifer* (1266–1700 m)
    - 13 *koehleri* (540 m)
    - 14 *lebruni* (0–740 m)
    - 15 *rugatus* (150–300 m)
  - subgenus *Retaster*
    - 16 *gibber* (210–490 m)
  - subgenus *Apterodon*
    - 17 *stellifer* (79–280 m)
    - 18 *tetracanthus* (180–300 m)
- ✚ *Smilasterias*
  - 19 *irregularis*
  - 20 *scalprifera* (79–267 m)
  - 21 *tririmus* (93–335 m)
- ○ *Solaster*
  - 22 *regularis* (118–603 m)

Cycethra
- 1 *cingulata* (16 m)
- 2 *macquariensis*
- 3 *verrucosa* (0–540 m)

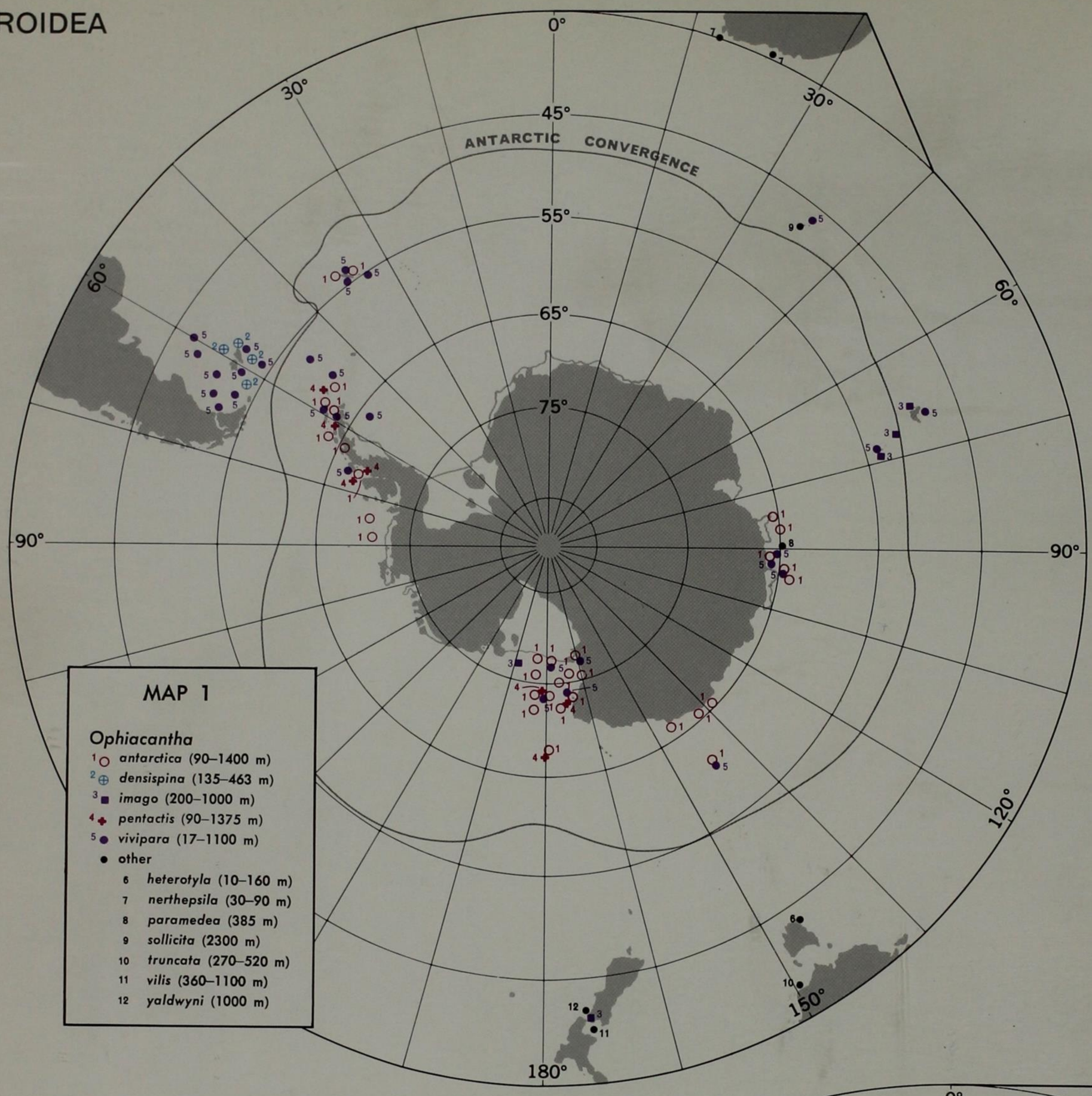
Labidiaster
- 4 *annulatus* (0–500 m)
- 5 *radiosus* (0–205 m)

Peribolaster
- 6 *folliculatus* (81–133 m)
- 7 *lictor* (260 m)
- 8 *macleani* (110–540 m)
- 9 *powelli* (201–1335 m)

AMERICAN GEOGRAPHICAL SOCIETY—1969

OPHIUROIDEA

SHEET 1



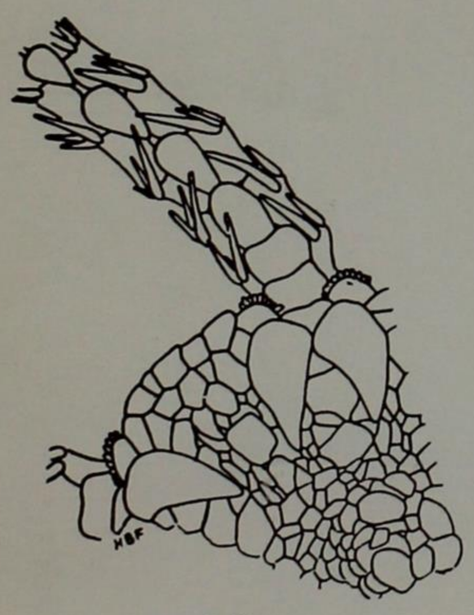
MAP 1

Ophiacantha
- 1 ○ *antarctica* (90–1400 m)
- 2 ⊕ *densispina* (135–463 m)
- 3 ■ *imago* (200–1000 m)
- 4 ✚ *pentactis* (90–1375 m)
- 5 ● *vivipara* (17–1100 m)
- ● other
  - 6 *heterotyla* (10–160 m)
  - 7 *nerthepsila* (30–90 m)
  - 8 *paramedea* (385 m)
  - 9 *sollicita* (2300 m)
  - 10 *truncata* (270–520 m)
  - 11 *vilis* (360–1100 m)
  - 12 *yaldwyni* (1000 m)

Ophioscolex
- 1 *dentatus* (280–390
- 2 *marionis* (99–113
- 3 *nutrix* (134–434 m)

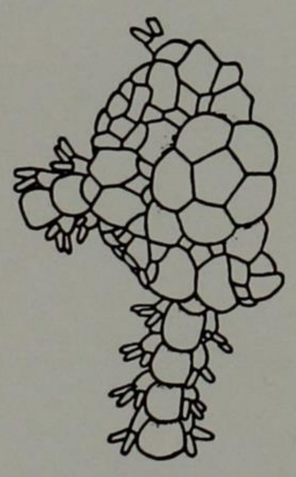
Ophiomitrella
- 4 *corynephora* (312–
- 5 *faulklandica* (40–4
- 6 *ingrata* (102–181

Icalia
- 7 *deficiens* (50–380
- 8 *dilatata* (178–220
- 9 *gaussi* (110–270 m)
- 10 *tomentosa* (20–120



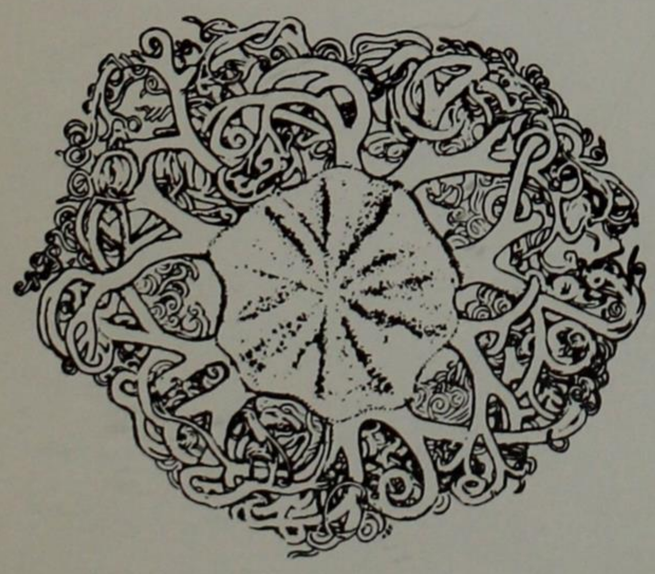
Ophiura

About 1 in. across the arms



Monamphiura

About ¾ in. across the arms



Gorgonocephalus

Arm-spread up to about 10 in.

MAP 3

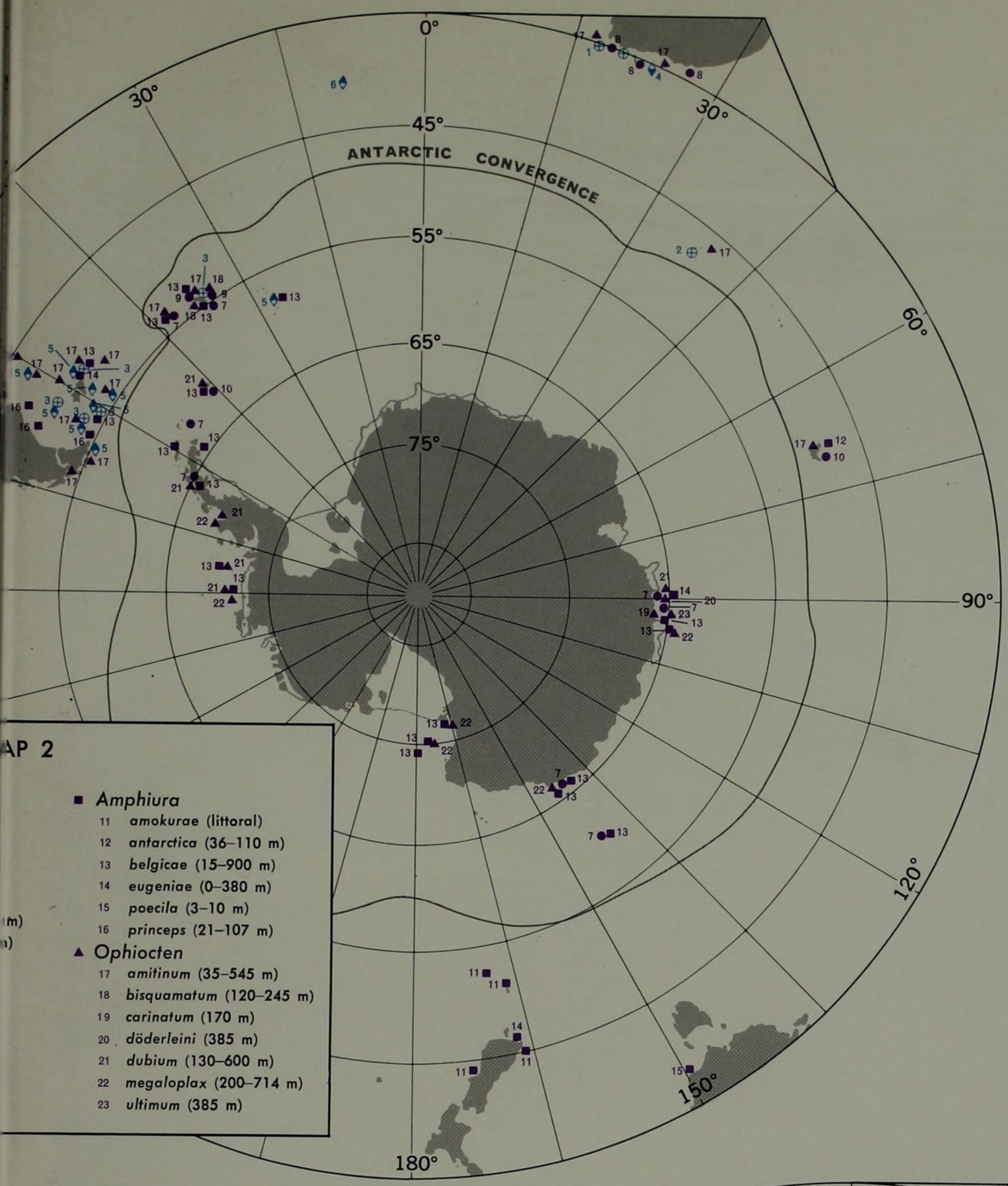
- ■ *Gorgonocephalus*
  - 1 *chilensis* (24–411 m)
  - 2 *novaezelandiae* (80–1100 m)
  - 3 *pectinatus* (350–860 m)
  - 4 *pourtalesii* (110–350 m)
- ● *Monamphiura*
  - 5 *alba* (5–90 m)
  - 6 *algida* (20–752 m)
  - 7 *alternans* (20–310 m)
  - 8 *annulifere* (littoral)
  - 9 *aster* (littoral)
  - 10 *capensis* (0–196 m)
  - 11 *constricta* (5–18 m)
  - 12 *heraldica* (320–700 m)
  - 13 *magellanica* (0–150 m)
  - 14 *microplax* (110–329 m)
  - 15 *praefecta* (1–40 m)
  - 16 *proposita* (200–314 m)
  - 17 *pusilla* (0–550 m)
  - 18 *spinipes* (10–150 m)
- △ *Torporkovia*
  - 19 *antarctica* (100–2450 m)
- ○ *Ophiuroglypha*
  - 20 *carinifera* (42–600 m)
  - 21 *lymani* (81–567 m)
- ▲ *Ophiura*
  - 22 *ambigua* (120–2450 m)
  - 23 *brevispinosa* (88–240 m)
  - 24 *chathamensis* (110–300 m)
  - 25 *costata* (170–460 m)
  - 26 *crassa* (322–342 m)
  - 27 *flexibilis* (80–472 m)
  - 28 *meridionalis* (0–2000 m)
  - 29 *serrata* (200–390 m)
  - 30 *trimeni* (262–1800 m)

COMPILED BY H. B. FELL,
T. HOLZINGER, AND M. SHERRADEN

PLATE 26

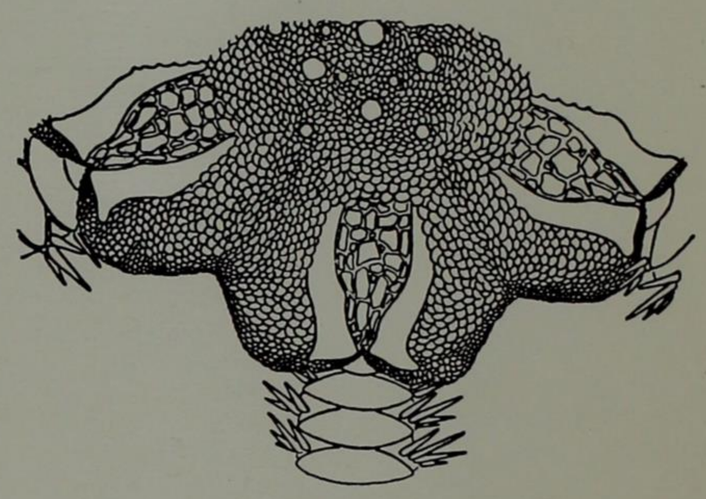
FOLIO 11— MARINE INVERTEBRATES

ANTARCTIC MAP FOLIO SERIES



MAP 2

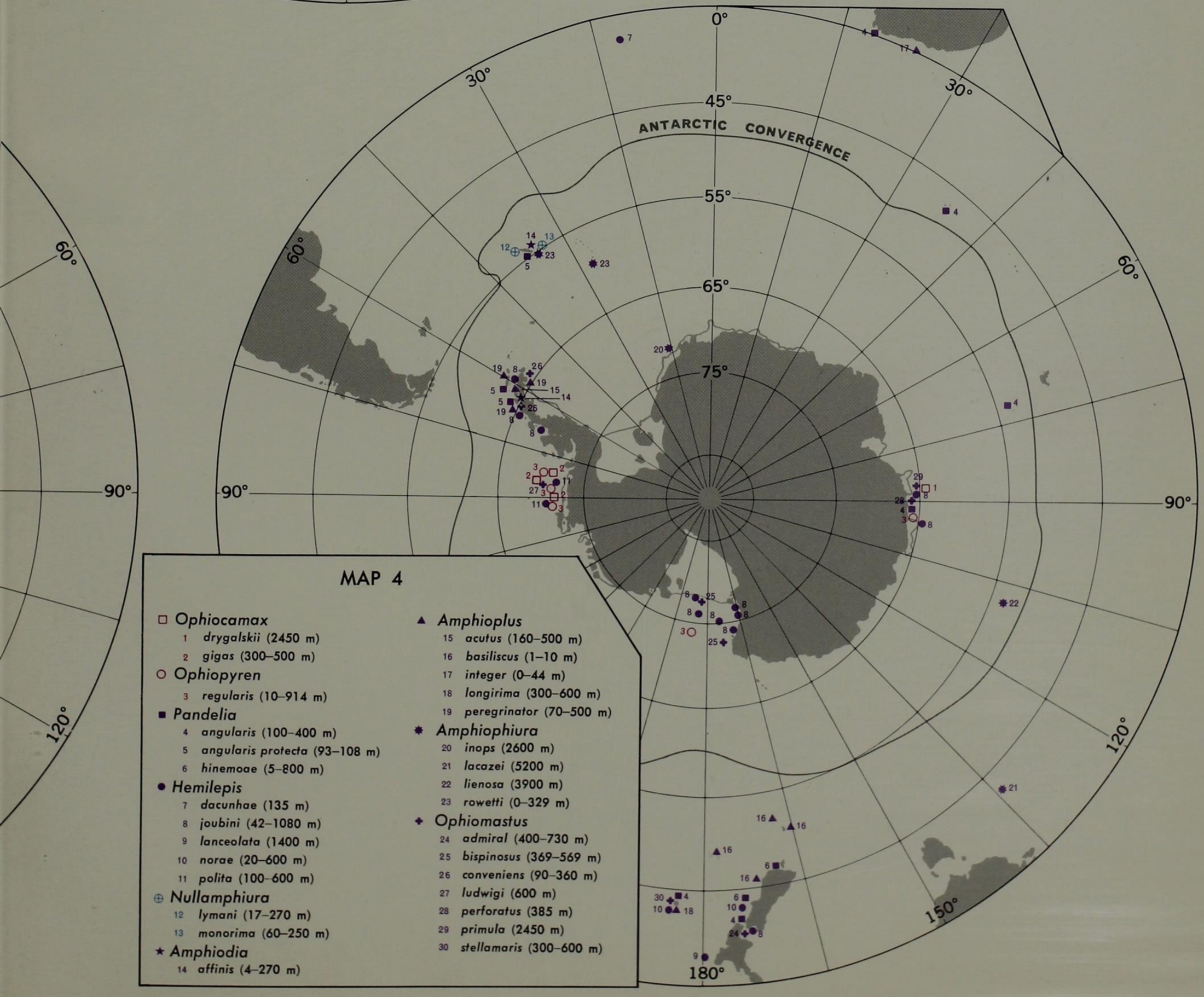
- ■ *Amphiura*
  - 11 *amokurae* (littoral)
  - 12 *antarctica* (36–110 m)
  - 13 *belgicae* (15–900 m)
  - 14 *eugeniae* (0–380 m)
  - 15 *poecila* (3–10 m)
  - 16 *princeps* (21–107 m)
- ▲ *Ophiocten*
  - 17 *amitinum* (35–545 m)
  - 18 *bisquamatum* (120–245 m)
  - 19 *carinatum* (170 m)
  - 20 *döderleini* (385 m)
  - 21 *dubium* (130–600 m)
  - 22 *megaloplax* (200–714 m)
  - 23 *ultimum* (385 m)



Amphiura

Disc up to ¾ in., arms 4 inches long

All drawings after Fell, 1962



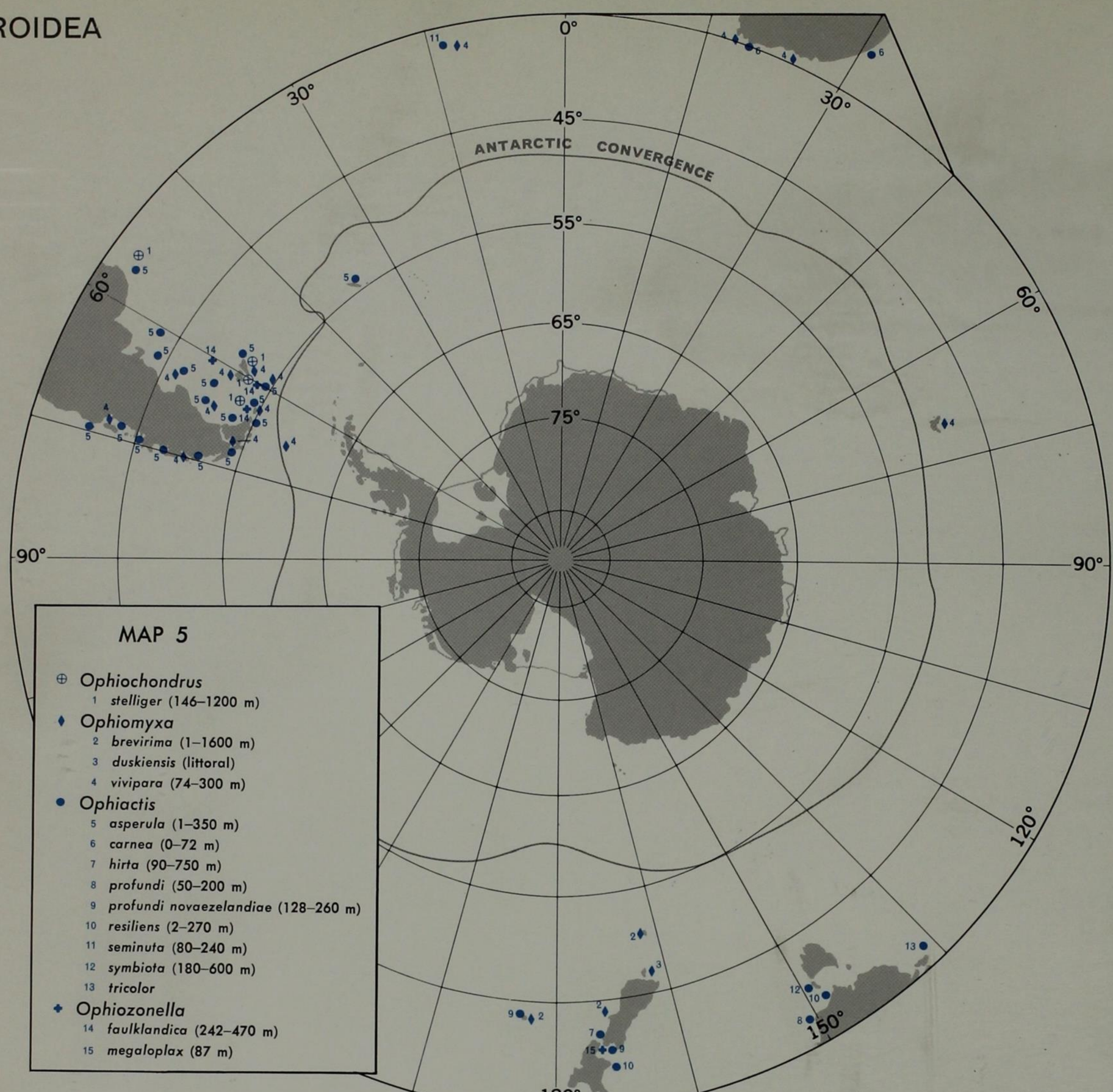
MAP 4

- □ *Ophiocamax*
  - 1 *drygalskii* (2450 m)
  - 2 *gigas* (300–500 m)
- ○ *Ophiopyren*
  - 3 *regularis* (10–914 m)
- ■ *Pandelia*
  - 4 *angularis* (100–400 m)
  - 5 *angularis protecta* (93–108 m)
  - 6 *hinemoae* (5–800 m)
- ● *Hemilepis*
  - 7 *dacunhae* (135 m)
  - 8 *joubini* (42–1080 m)
  - 9 *lanceolata* (1400 m)
  - 10 *norae* (20–600 m)
  - 11 *polita* (100–600 m)
- ⊕ *Nullamphiura*
  - 12 *lymani* (17–270 m)
  - 13 *monorima* (60–250 m)
- ★ *Amphiodia*
  - 14 *affinis* (4–270 m)
- ▲ *Amphioplus*
  - 15 *acutus* (160–500 m)
  - 16 *basiliscus* (1–10 m)
  - 17 *integer* (0–44 m)
  - 18 *longirima* (300–600 m)
  - 19 *peregrinator* (70–500 m)
- ✸ *Amphiophiura*
  - 20 *inops* (2600 m)
  - 21 *lacazei* (5200 m)
  - 22 *lienosa* (3900 m)
  - 23 *rowetti* (0–329 m)
- ✚ *Ophiomastus*
  - 24 *admiral* (400–730 m)
  - 25 *bispinosus* (369–569 m)
  - 26 *conveniens* (90–360 m)
  - 27 *ludwigi* (600 m)
  - 28 *perforatus* (385 m)
  - 29 *primula* (2450 m)
  - 30 *stellamaris* (300–600 m)

AMERICAN GEOGRAPHICAL SOCIETY—1969

OPHIUROIDEA

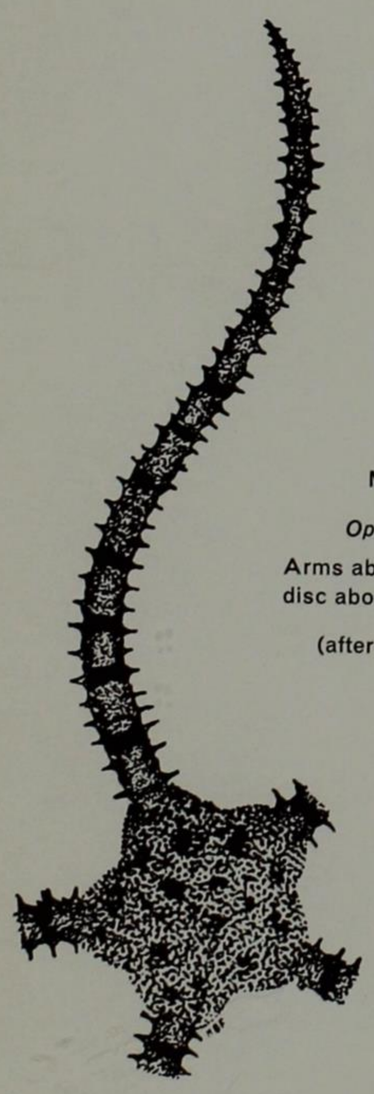
SHEET 2



MAP 5

- ⊕ *Ophiochondrus*
  - 1 *stelliger* (146–1200 m)
- ♦ *Ophiomyxa*
  - 2 *brevirima* (1–1600 m)
  - 3 *duskiensis* (littoral)
  - 4 *vivipara* (74–300 m)
- ● *Ophiactis*
  - 5 *asperula* (1–350 m)
  - 6 *carnea* (0–72 m)
  - 7 *hirta* (90–750 m)
  - 8 *profundi* (50–200 m)
  - 9 *profundi novaezelandiae* (128–260 m)
  - 10 *resiliens* (2–270 m)
  - 11 *seminuta* (80–240 m)
  - 12 *symbiota* (180–600 m)
  - 13 *tricolor*
- ✚ *Ophiozonella*
  - 14 *faulklandica* (242–470 m)
  - 15 *megaloplax* (87 m)

- ■ *Astrochlamys*
  - 1 *bruneus* (120–900 m)
  - 2 *sol* (342 m)
- △ *Astrohamma*
  - 3 *tuberculatum* (150–39 m)
- ▲ *Ophioperla*
  - 4 *koehleri* (70–1080 m)
- ✚ *Ophioplinthus*
  - 5 *grisea* (3500–4636 m)
  - 6 *medusa* (3500–4636 m)
- ○ *Ophiosteira*
  - 7 *antarctica* (25–752 m)
  - 8 *bullivanti* (460–835 m)
  - 9 *debitor* (314 m)
  - 10 *echinulata* (80–800 m)
  - 11 *rotundata* (480 m)

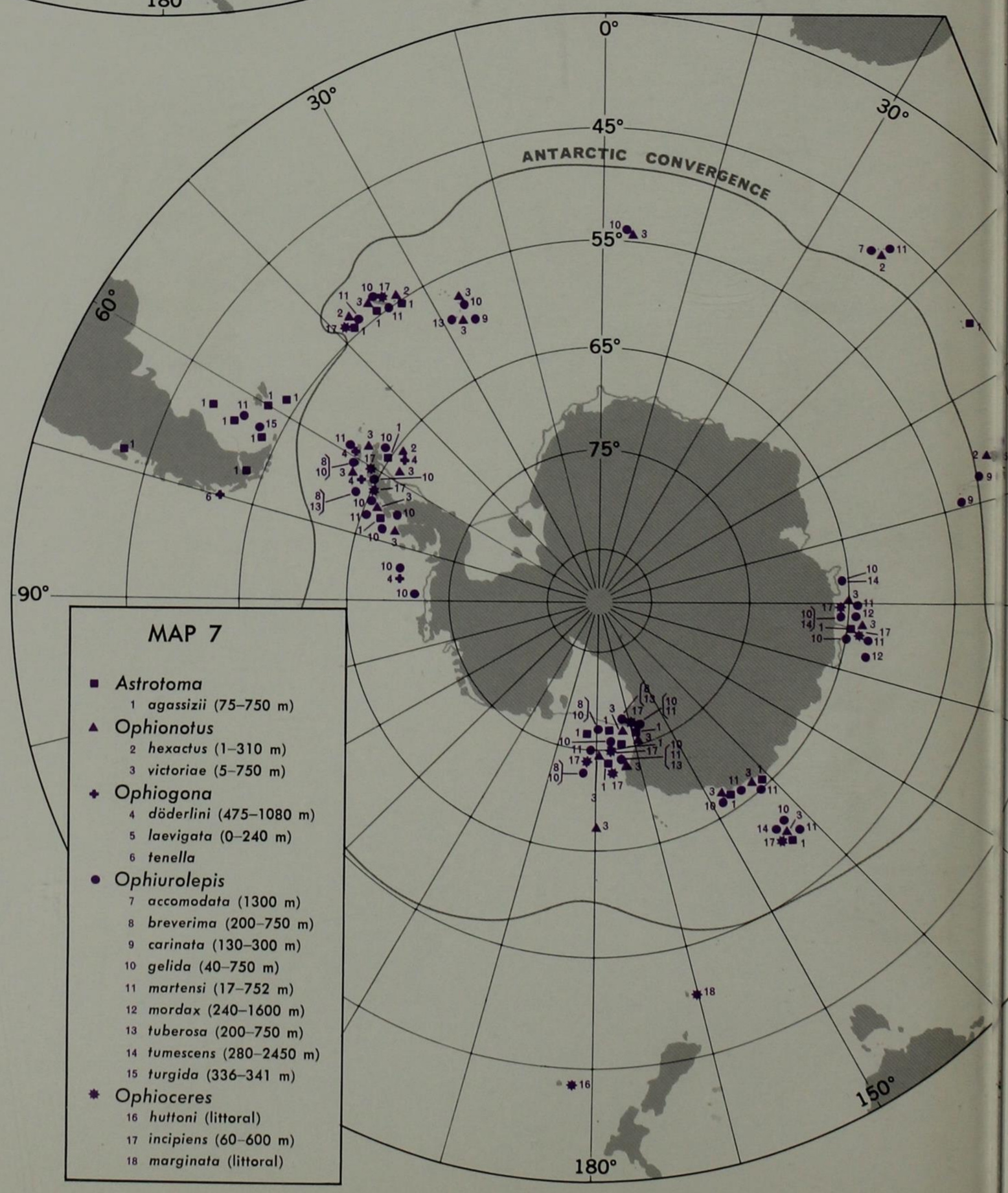


Map 5

Ophiomyxa

Arms about 3 in. long, disc about 1 in. across

(after Fell, 1962)



MAP 7

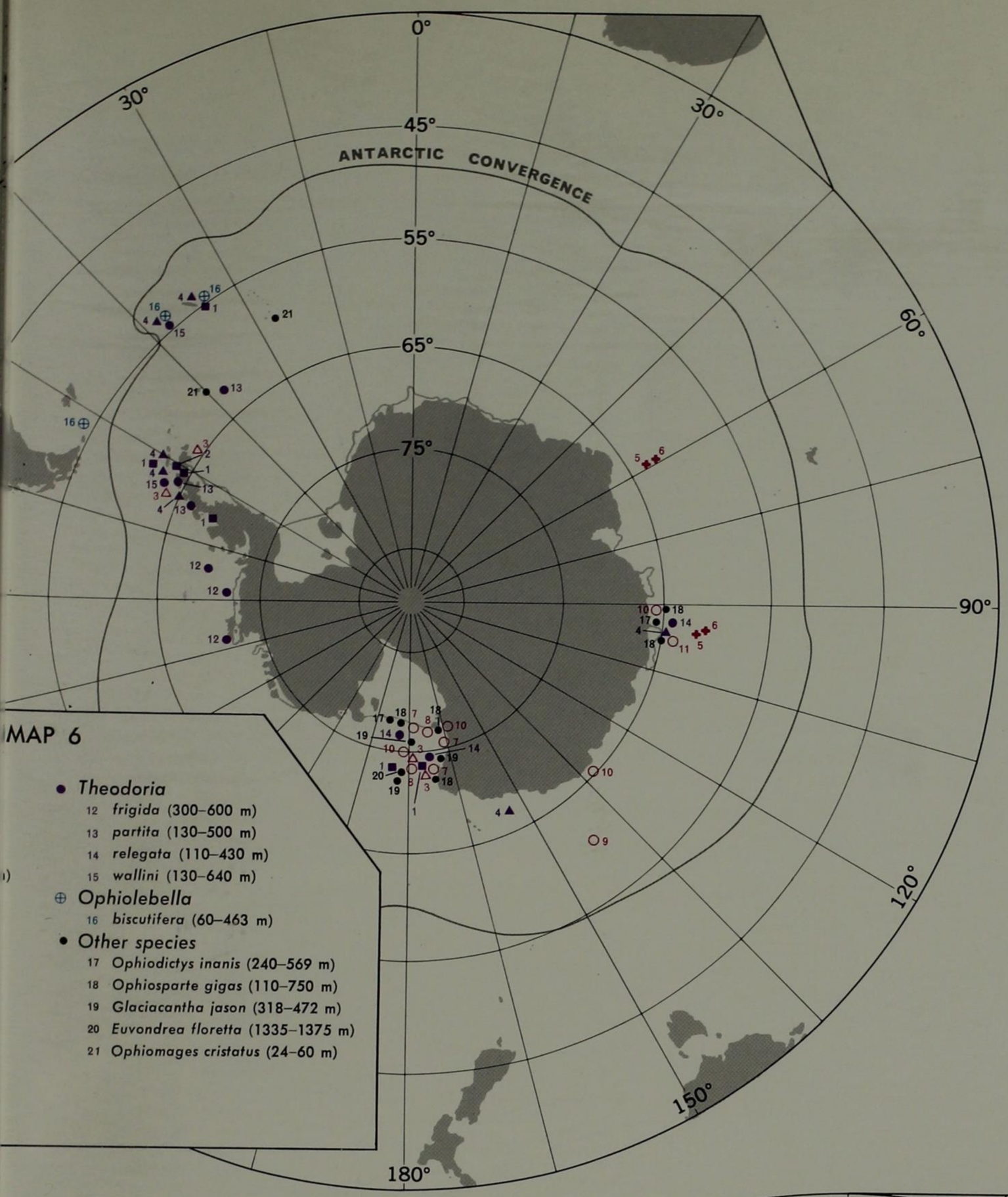
- ■ *Astrotoma*
  - 1 *agassizii* (75–750 m)
- ▲ *Ophionotus*
  - 2 *hexactus* (1–310 m)
  - 3 *victoriae* (5–750 m)
- ✚ *Ophiogona*
  - 4 *döderlini* (475–1080 m)
  - 5 *laevigata* (0–240 m)
  - 6 *tenella*
- ● *Ophiurolepis*
  - 7 *accomodata* (1300 m)
  - 8 *breverima* (200–750 m)
  - 9 *carinata* (130–300 m)
  - 10 *gelida* (40–750 m)
  - 11 *martensi* (17–752 m)
  - 12 *mordax* (240–1600 m)
  - 13 *tuberosa* (200–750 m)
  - 14 *tumescens* (280–2450 m)
  - 15 *turgida* (336–341 m)
- ✸ *Ophioceres*
  - 16 *huttoni* (littoral)
  - 17 *incipiens* (60–600 m)
  - 18 *marginata* (littoral)

COMPILED BY H. B. FELL,
T. HOLZINGER, AND M. SHERRADEN

PLATE 27

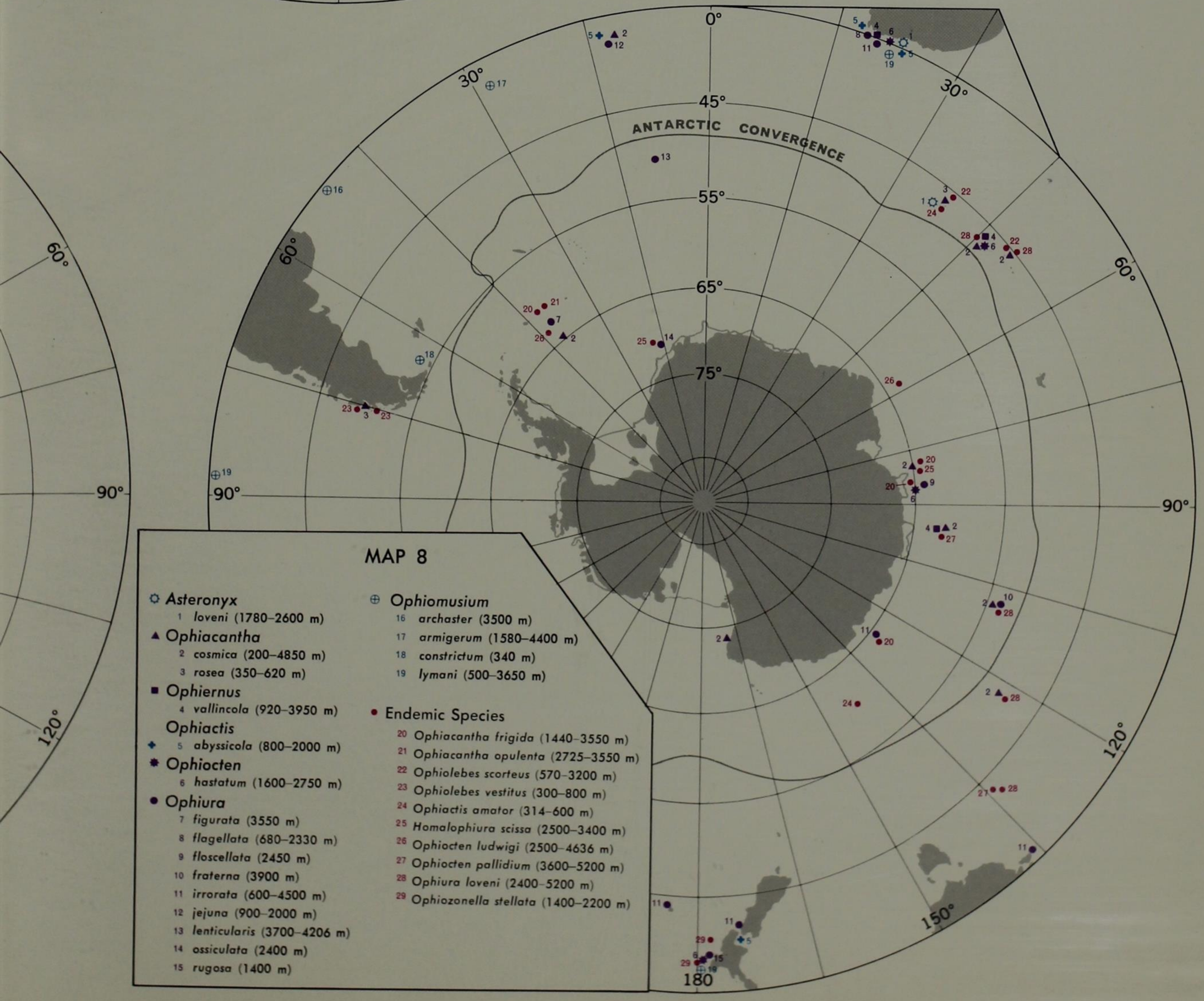
FOLIO 11—MARINE INVERTEBRATES

ANTARCTIC MAP FOLIO SERIES



MAP 6

- *Theodoria*
  - 12 *frigida* (300–600 m)
  - 13 *partita* (130–500 m)
  - 14 *relegata* (110–430 m)
  - 15 *wallini* (130–640 m)
- ⊕ *Ophiolebella*
  - 16 *biscutifera* (60–463 m)
- • *Other species*
  - 17 *Ophiodictys inanis* (240–569 m)
  - 18 *Ophiosparte gigas* (110–750 m)
  - 19 *Glaciacantha jason* (318–472 m)
  - 20 *Euvondrea floretta* (1335–1375 m)
  - 21 *Ophiomages cristatus* (24–60 m)



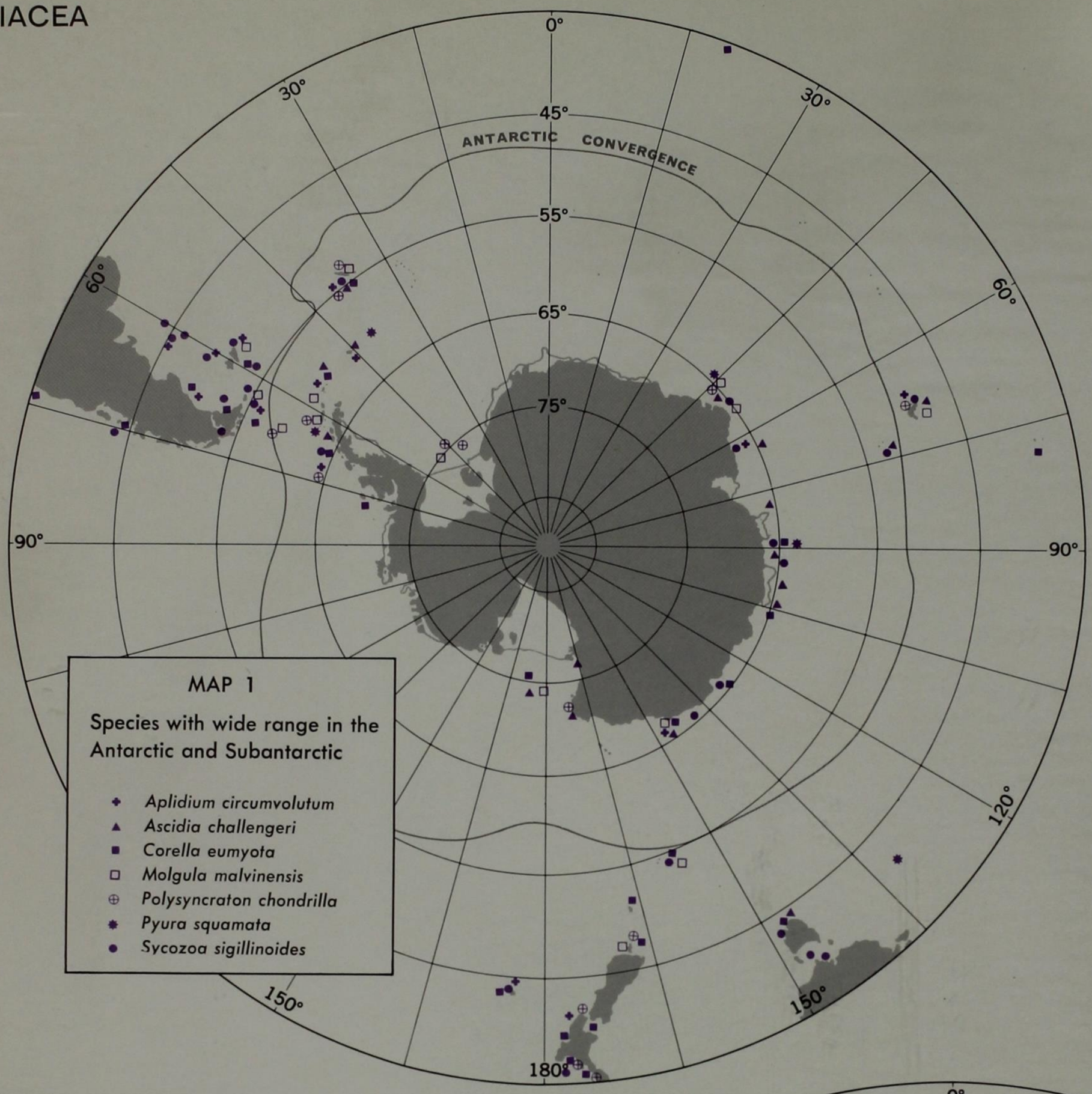
MAP 8

- ☼ *Asteronyx*
  - 1 *loveni* (1780–2600 m)
- ▲ *Ophiacantha*
  - 2 *cosmica* (200–4850 m)
  - 3 *rosea* (350–620 m)
- ■ *Ophiernus*
  - 4 *vallincola* (920–3950 m)
- *Ophiactis*
  - ✚ 5 *abyssicola* (800–2000 m)
- ✸ *Ophiocten*
  - 6 *hastatum* (1600–2750 m)
- • *Ophiura*
  - 7 *figurata* (3550 m)
  - 8 *flagellata* (680–2330 m)
  - 9 *floscellata* (2450 m)
  - 10 *fraterna* (3900 m)
  - 11 *irrorata* (600–4500 m)
  - 12 *jejuna* (900–2000 m)
  - 13 *lenticularis* (3700–4206 m)
  - 14 *ossiculata* (2400 m)
  - 15 *rugosa* (1400 m)
- ⊕ *Ophiomusium*
  - 16 *archaster* (3500 m)
  - 17 *armigerum* (1580–4400 m)
  - 18 *constrictum* (340 m)
  - 19 *lymani* (500–3650 m)
- • Endemic Species
  - 20 *Ophiacantha frigida* (1440–3550 m)
  - 21 *Ophiacantha opulenta* (2725–3550 m)
  - 22 *Ophiolebes scorteus* (570–3200 m)
  - 23 *Ophiolebes vestitus* (300–800 m)
  - 24 *Ophiactis amator* (314–600 m)
  - 25 *Homalophiura scissa* (2500–3400 m)
  - 26 *Ophiocten ludwigi* (2500–4636 m)
  - 27 *Ophiocten pallidium* (3600–5200 m)
  - 28 *Ophiura loveni* (2400–5200 m)
  - 29 *Ophiozonella stellata* (1400–2200 m)

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ASCIDIACEA

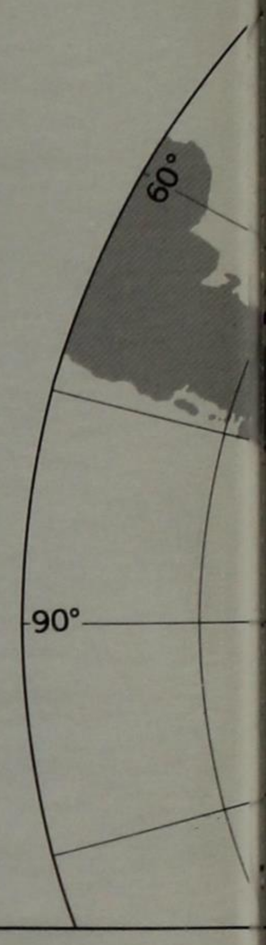
SHEET 1



MAP 1

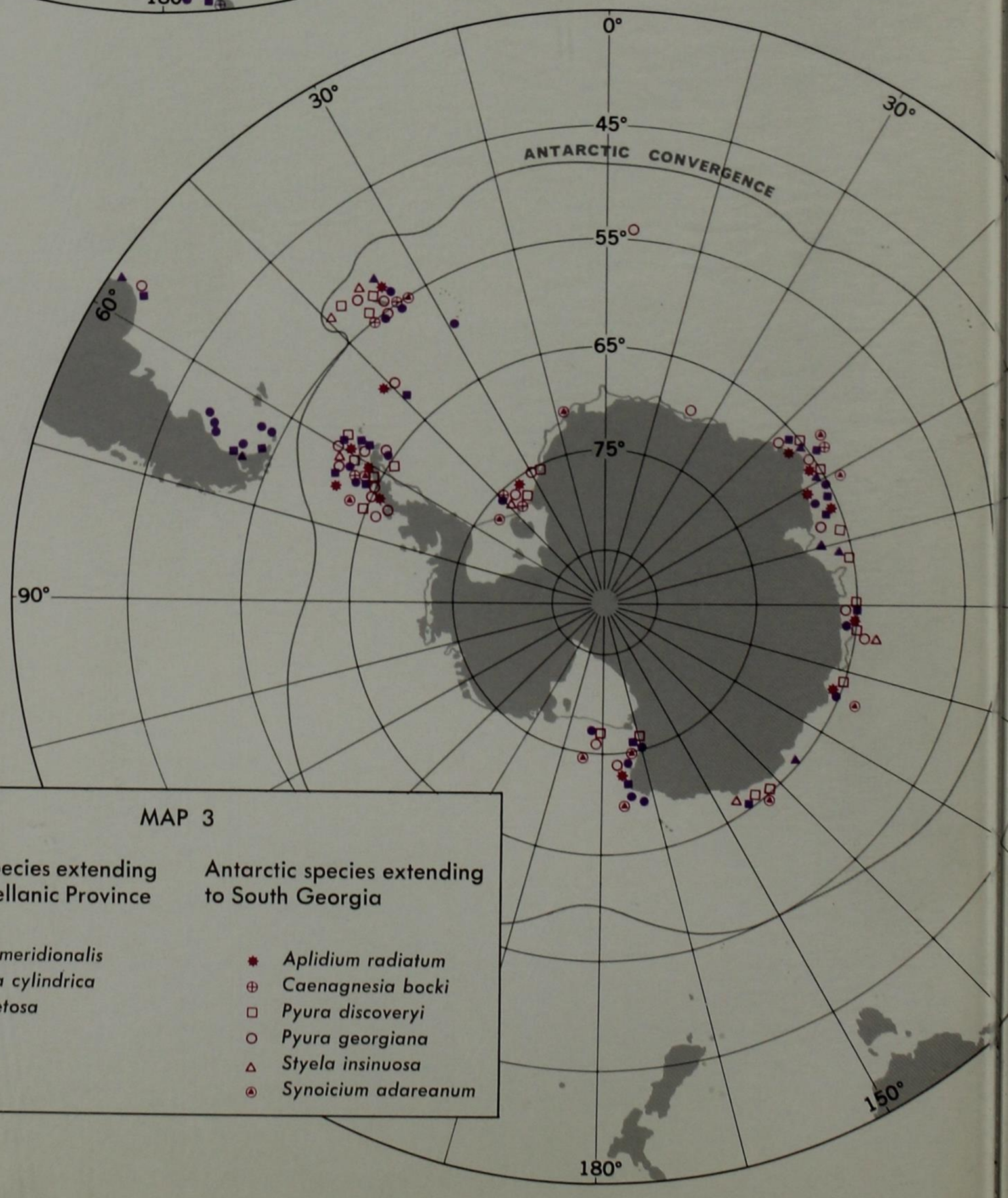
Species with wide range in the Antarctic and Subantarctic

- *Aplidium circumvolutum*
- *Ascidia challengeri*
- *Corella eumyota*
- *Molgula malvinensis*
- *Polysyncraton chondrilla*
- *Pyura squamata*
- *Sycozoa sigillinoides*



Antarctic species ex
to the Kerguelen an
Magellanic Province

- *Cnemidocarpa ve*
- *Styela nordenskj*
- *Tylobranchion sp*



MAP 3

Antarctic species extending to the Magellanic Province

- *Ascidia meridionalis*
- *Distaplia cylindrica*
- *Pyura setosa*

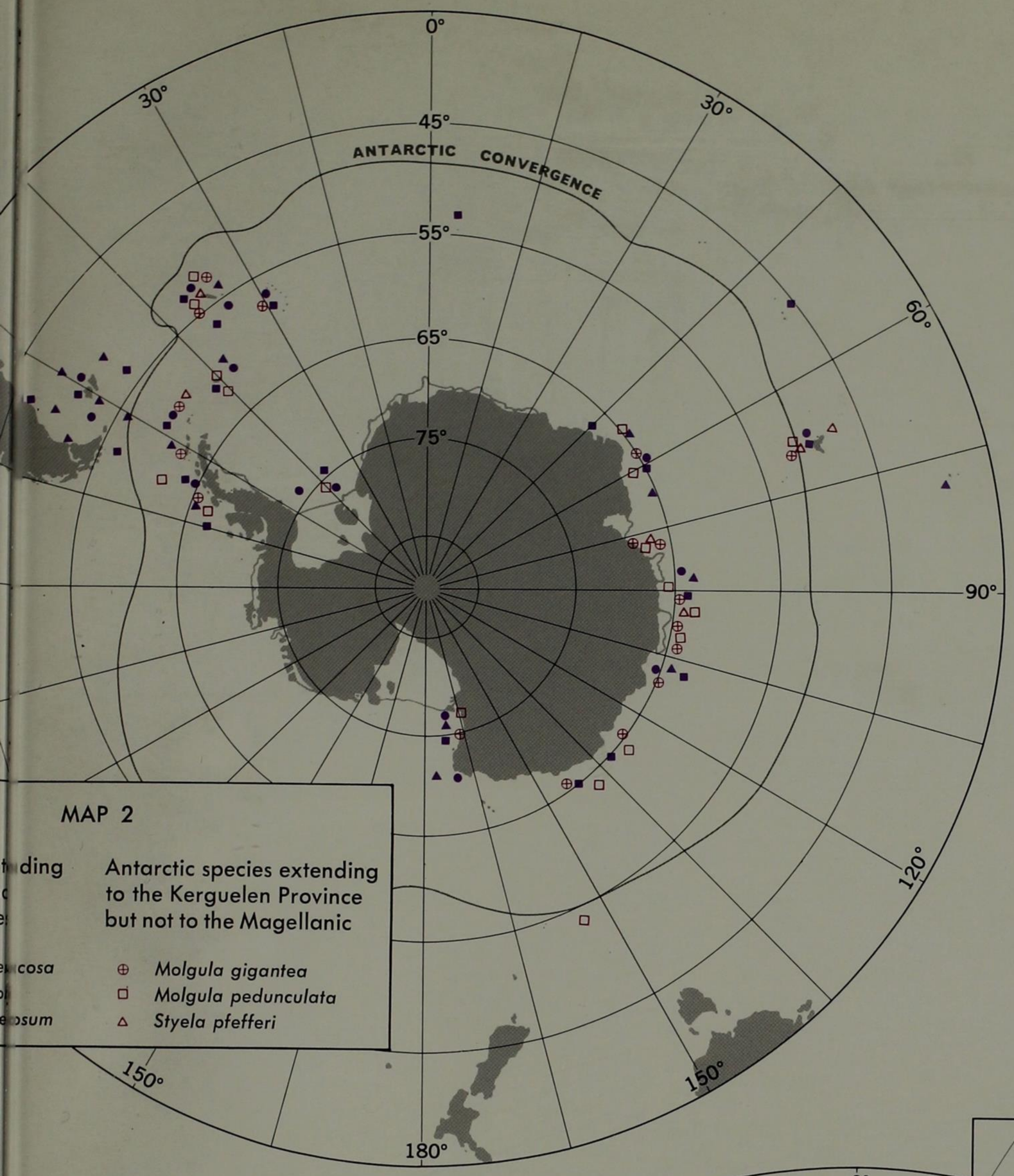
Antarctic species extending to South Georgia

- *Aplidium radiatum*
- *Caenagnesia bocki*
- *Pyura discoveryi*
- *Pyura georgiana*
- *Styela insinuosa*
- *Synoicium adareanum*

COMPILED BY P. KOTT

PLATE 28

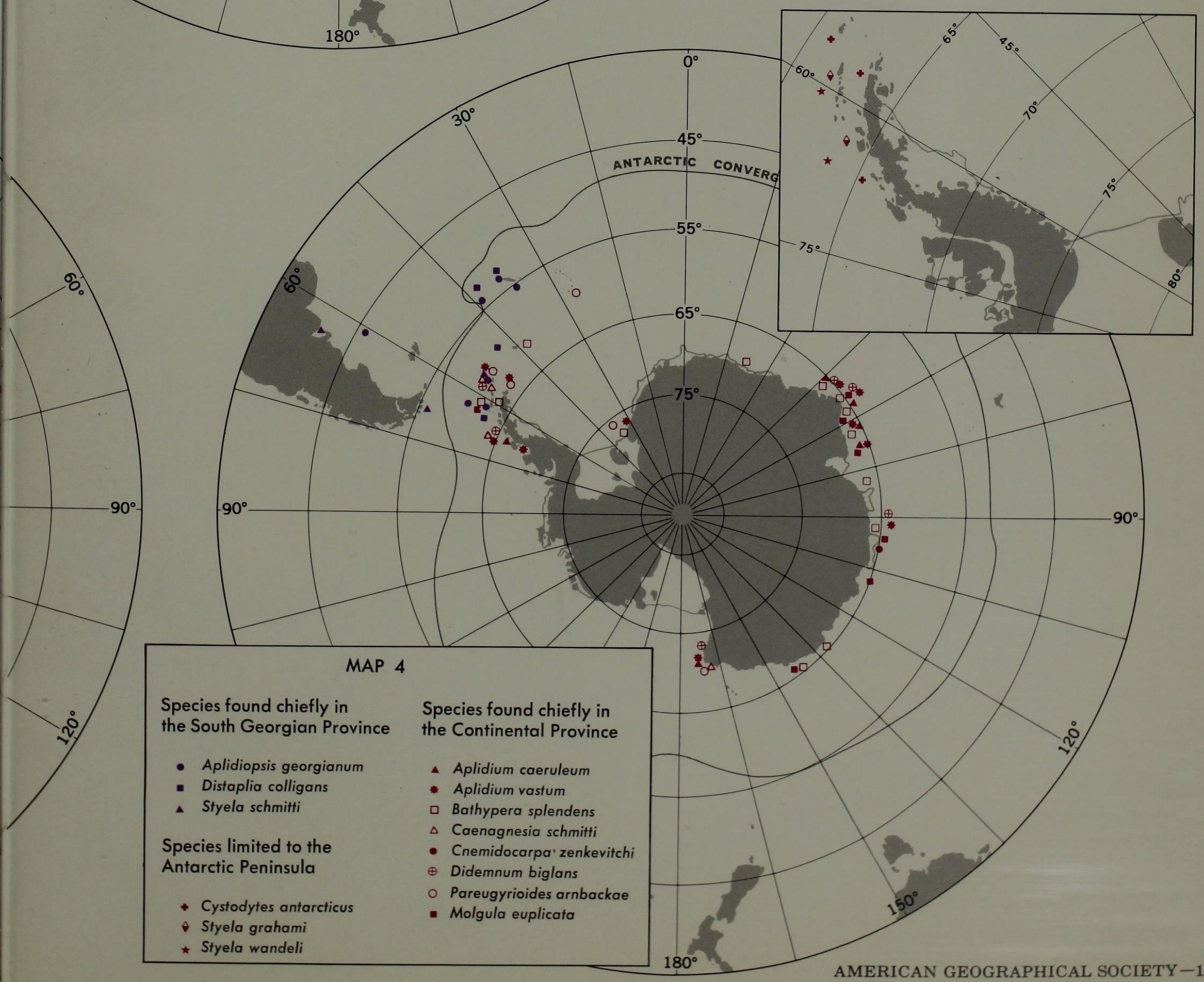
FOLIO 11— MARINE INVERTEBRATES
ANTARCTIC MAP FOLIO SERIES



MAP 2

ding — Antarctic species extending to the Kerguelen Province but not to the Magellanic

cosa — ⊕ *Molgula gigantea*
□ *Molgula pedunculata*
osum — △ *Styela pfefferi*



MAP 4

Species found chiefly in the South Georgian Province

- ● *Aplidiopsis georgianum*
- ■ *Distaplia colligans*
- ▲ *Styela schmitti*

Species limited to the Antarctic Peninsula

- ✦ *Cystodytes antarcticus*
- ♦ *Styela grahami*
- ★ *Styela wandeli*

Species found chiefly in the Continental Province

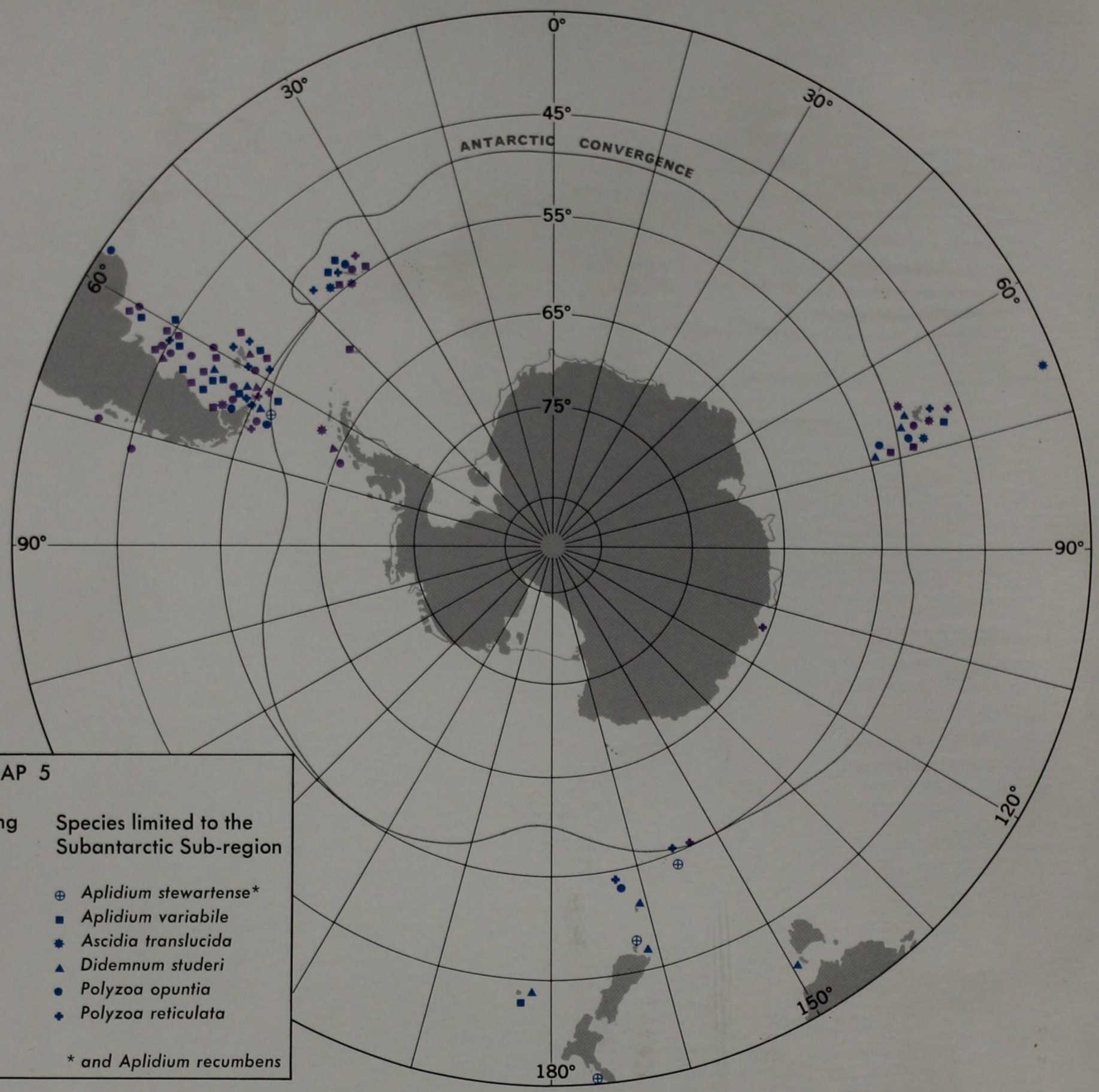
- ▲ *Aplidium caeruleum*
- ✸ *Aplidium vastum*
- □ *Bathypera splendens*
- △ *Caenagnesia schmitti*
- ● *Cnemidocarpa zenkevitchi*
- ⊕ *Didemnum biglans*
- ○ *Pareugyrioides arnbackae*
- ■ *Molgula euplicata*

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SHEET 2

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MAP 5

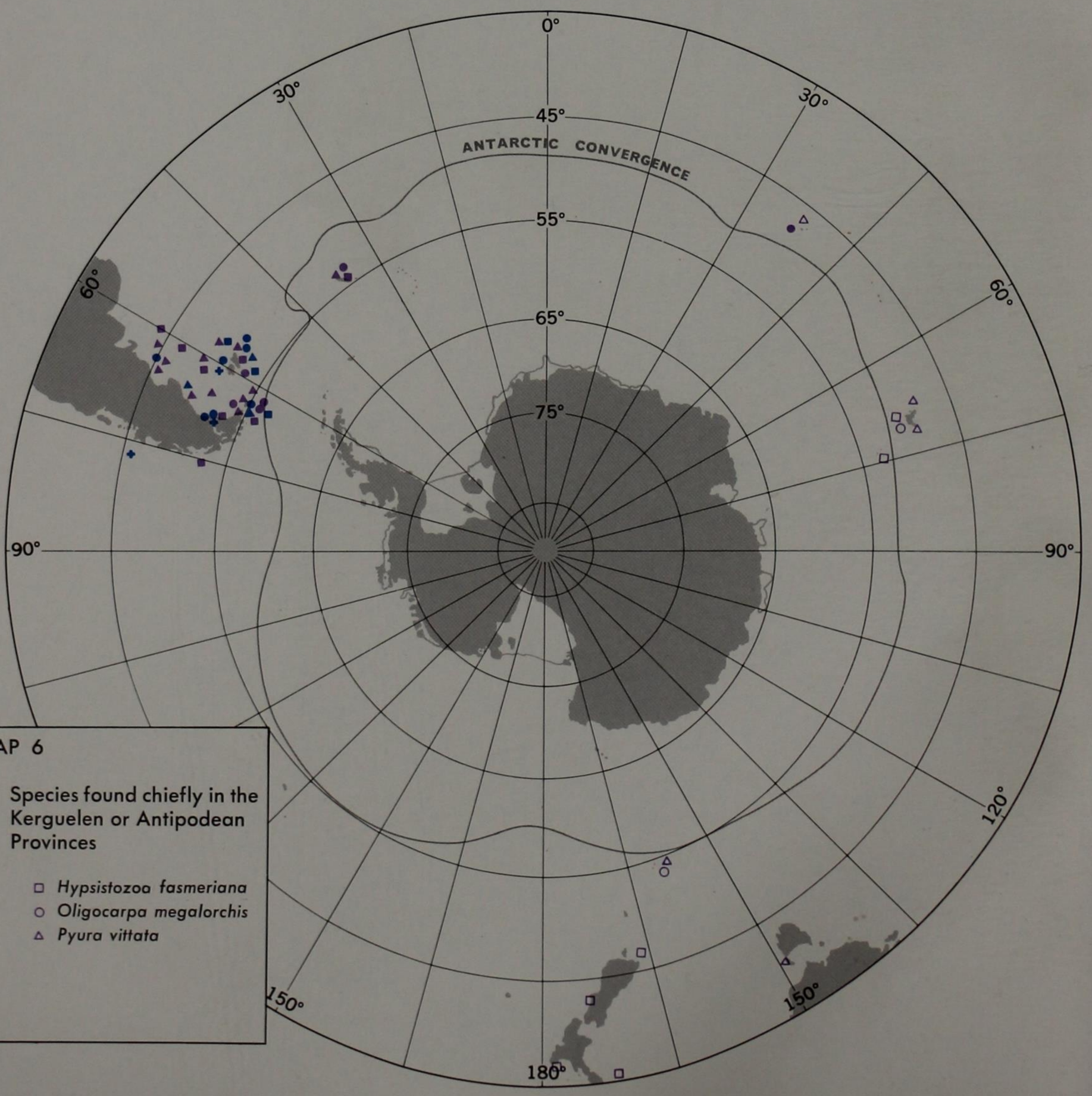
Subantarctic species extending into the Antarctic Sub-region

- ▲ *Agnesia glaciata*
- ● *Aplidium fuegiense*
- ■ *Aplidium irregulare*
- ✸ *Eugyra kerguelenensis*
- ✚ *Molgula pulchra*

Species limited to the Subantarctic Sub-region

- ⊕ *Aplidium stewartense**
- ■ *Aplidium variabile*
- ✸ *Ascidia translucida*
- ▲ *Didemnum studeri*
- ● *Polyzoa opuntia*
- ✚ *Polyzoa reticulata*

* and *Aplidium recumbens*



MAP 6

Species found chiefly in the Magellanic Province

- ■ *Alloeocarpa incrustans*
- ● *Molgula setigera*
- ▲ *Paramolgula gregaria*
- ● *Pyura legumen*
- ■ *Pyura paessleri*
- ▲ *Styela paessleri*
- ◆ *Tridemnum auriculatum*

Species found chiefly in the Kerguelen or Antipodean Provinces

- □ *Hypsistozoa fasmeriana*
- ○ *Oligocarpa megalorchis*
- △ *Pyura vittata*

MAP 7

Cosmopolitan abyssal genera and species found in the Antarctic

PRIMARILY ABYSSAL SPECIES

Cosmopolitan

1. *Corynascidia suhmi*
2. *Corynascidia sedens*
3. *Corynascidia herdmani*
4. *Megalodicopia hians*
5. *Dicopia fimbriata*
6. *Dicopia japonica*
7. *Culeolus murrayi*
8. *Culeolus* spp.
9. *Styella sericata*
10. *Abyssascidia wyvilli*
11. *Abyssascidia pediculata*
12. *Bathyoncus enderbyanus*

Antarctica

13. *Bathyoncus herdmani*
14. *Bathyoncus mirabilis*
15. *Protoholozoa pedunculata*
16. *Fungulus cinereus*
17. *Pharyngodictyon mirabile*

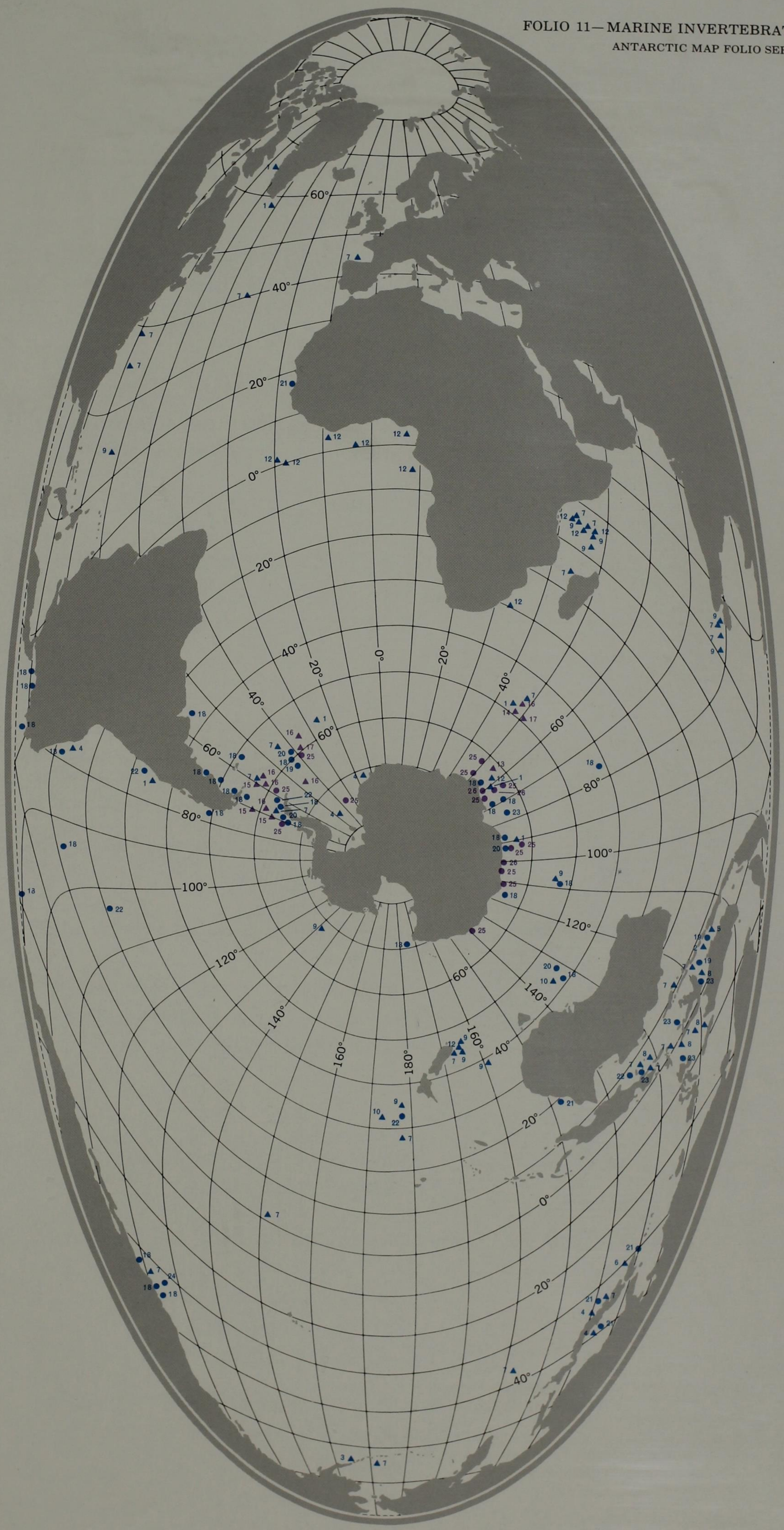
SECONDARILY ABYSSAL SPECIES

Cosmopolitan

18. *Styela nordenskjoldi*
19. *Styela orbicularis*
20. *Pyura squamata*
21. *Pyura lepidoderma*
22. *Molguloides immunda*
23. *Molguloides vitrea*
24. *Bathypera ovoida*

Antarctic

25. *Bathypera splendens*
26. *Bathypera hastaefera*



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