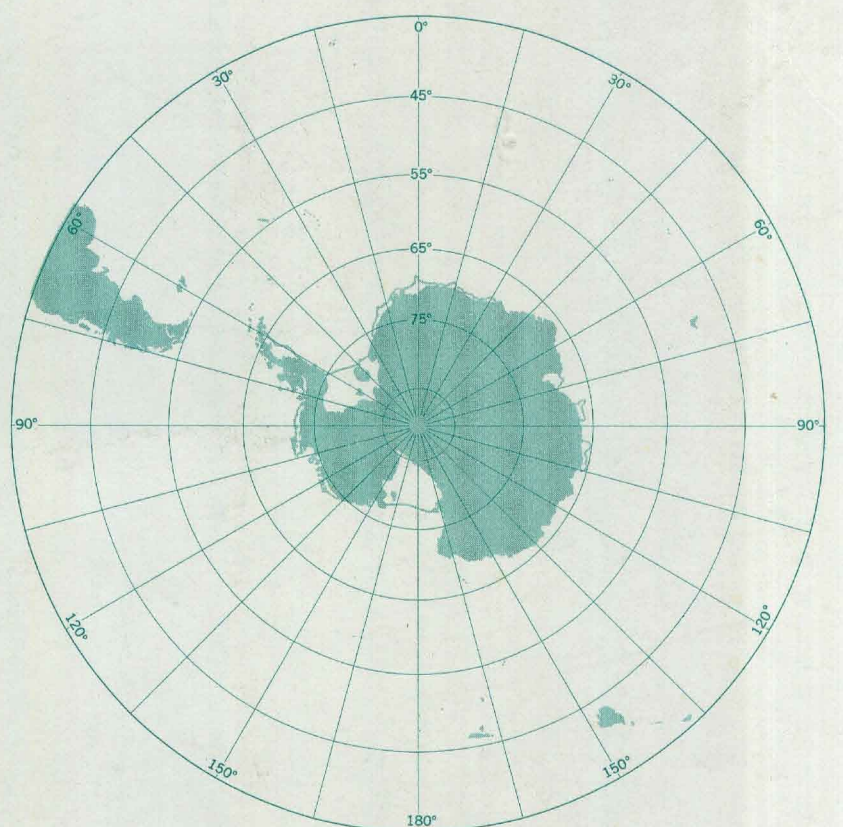


Antarctic Map Folio Series

Primary Productivity and Benthic Marine Algae of the Antarctic and Subantarctic

E. BALECH, S. Z. EL-SAYED, G. HASLE
M. NEUSHUL, AND J. S. ZANEVELD



AMERICAN
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Antarctic Map Folio Series

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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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Published under a contract with the
NATIONAL SCIENCE FOUNDATION

by the

AMERICAN GEOGRAPHICAL SOCIETY

Broadway at 156th Street
New York, New York 10032

Primary Productivity and Benthic Marine Algae of the Antarctic and Subantarctic

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*M. Neushul*⁴, and *J. S. Zaneveld*⁵

Introduction

Antarctic biological exploration dates back to the expedition of the *Erebus* and *Terror* under James Clark Ross (1839-1843) when the first plankton hauls in Antarctic waters were made. J. D. Hooker, botanist and surgeon on Ross's expedition, was the first to call attention to the fundamental importance of phytoplankton in the economy of the sea. Subsequent expeditions carried out investigations of a purely descriptive nature on the marine organisms of the Antarctic regions. The initiation of the *Discovery* Investigations in 1925 heralded a new phase which stressed the dynamic aspect of Antarctic biology. Although these investigations were primarily concerned with whales and whaling, studies of the factors influencing their migration, food, feeding habits, and breeding cycle have led to an intensive program of physical and biological oceanography resulting in the valuable '*Discovery Reports*.' Although other expeditions have followed, credit goes to the *Discovery* for initiating a continuous program. Since the International Geophysical Year (1957-1958), scientific investigation in the Antarctic waters has expanded and is still gaining momentum.

In the present folio, we are primarily concerned with the biological productivity and related aspects of Antarctic and Subantarctic waters. Maps showing the distribution and abundance of the phytoplankton standing crop, as well as primary productivity, are presented. The nutrient chemicals of these waters are also given in an effort to correlate the productivity with the distribution and concentration of the nutrient salts.

Of significance in productivity investigations is the study of the species composition and distribution of the two important components of the primary producers, the diatoms and the dinoflagellates. Maps of the distribution of selected species of these organisms have been included with brief discussions of their significance.

Because of the significance of marine benthic algae to organic production in coastal regions, we have included a section on the distribution of a few representative Antarctic species.

Primary Productivity

INTRODUCTION

The highly fertile waters surrounding Antarctica present a marked contrast to the cold, rugged, and hostile continent with its sparse vegetation. The special features of the southern waters that lead to their high fertility are the subject of discussion in this section.

It is well known that the food chains in Antarctic waters are simple and direct. Baleen whales, crab-eater seals, squid, fish, and winged birds as well as penguins thrive mainly on the shrimp-like organisms, *Euphausia superba*, commonly called krill, which are, in turn, supported by the planktonic algae. Thus the productivity of the Antarctic waters, like that of any other aquatic environment, depends primarily on the food-building activities of these minute plants which, through the agency of chlorophyll, utilize the energy of the sun to transform inorganic elements into living tissue.

Organic production in the ocean, as on land, varies from extremely fertile regions to ocean 'deserts.' These regional differences are due to the variation in the supply of nutrients such as phosphates, nitrates, silicates

and others. As a result of phytoplankton activity these nutrient salts are exhausted at the surface, but tend to accumulate at lower levels through the dissolution of the detrital matter by bacterial activity. Through the mechanism of vertical circulation in certain regions, the nutrient-rich deep waters are brought to the surface and a luxuriant plant growth results. This upwelling takes place in the coastal regions of Peru, Chile, California, southwest Africa, southeast Arabia, and Antarctica, among others. It is in some of these regions that many of the world's largest fisheries are located.

Since the explanation of the high productivity of the Antarctic waters lies in an understanding of the circulation of these waters, a brief summary of the hydrography of the region will be given here. (For more detailed accounts of the hydrography of the region, see Deacon, 1937, 1963; Gordon, 1967).

The waters surrounding Antarctica move generally eastward in what is known as the Antarctic Circumpolar Current, driven primarily by the westerly wind. Superimposed upon this eastward movement are north-south components that keep the southern waters in a state of flux. At the edge of the continent, very cold water sinks and moves northward (Figure 1). This dense 'Antarctic Bottom Water' spreads throughout major areas of the world oceans by lateral advection and diffusion. The cold 'Antarctic Surface Water,' which has a northward component of motion, on reaching the Antarctic Convergence sinks and contributes to the formation of the Subantarctic Intermediate Water. To replace these northerly moving water masses, waters high in salinity and rich in nutrient elements move southward to intermediate depths, rising close to the surface near Antarctica. Encircling the Antarctic waters as a belt is one of the dominant features in the hydrography of the southern waters, the Antarctic Convergence (Antarctic 'Polar Front' in the nomenclature of some oceanographers). The Antarctic Convergence is formed when the north-moving Antarctic Surface Water sinks beneath the more buoyant south-flowing Subantarctic Surface Water. It is a well-defined boundary between water masses of separate origins and as such it is of great significance in the distribution of life in the sea. Although probably not an impassable barrier to marine organisms, it prevents the dispersal of species which are adapted to the conditions on one side but cannot maintain themselves permanently in the conditions on the other side (Mackintosh, 1946).

The productivity of the sea can be measured by several methods. One of these is to measure the photosynthetic activity of the phytoplankton by the C^{14} uptake method. In this method the incorporation of a radioactive tracer (C^{14}) in the organic matter of the plankton algae is used as a measure of primary production. To estimate what marine biologists call the 'standing crop' of plankton algae (that is, the amount of living plant matter in a given place at a given time), the plant pigments are assayed. In this folio chlorophyll *a* will be used as a measure of the phytoplankton standing crop.

Plates 1-8 summarize what is known of the distribution of phytoplankton standing crop, C^{14} uptake, nutrient salts, and particulate and dissolved organic carbon in the Antarctic and Subantarctic waters. For such an enormous region, it is natural to expect regional variations in organic production. What is surprising about the data plotted in Plates 1 and 2 is the magnitude of these variations. For instance, the areas located to the east of the Weddell Sea are literally 'desert' regions compared to the Gerlache Strait. Geographic variations in productivity can best be explained by studying the physical and chemical factors which control the productivity in these waters. Some of the factors are:

(1) *Nutrient salts*. Published data for the Antarctic (Clowes, 1938; El-Sayed *et al.*, 1964, 1965) show that despite pronounced seasonal variations in concentration, the nutrient salts are always present in great abundance. It is unlikely that they are sufficiently sparse at any one time to become limiting factors to the growth of phytoplankton. This is in

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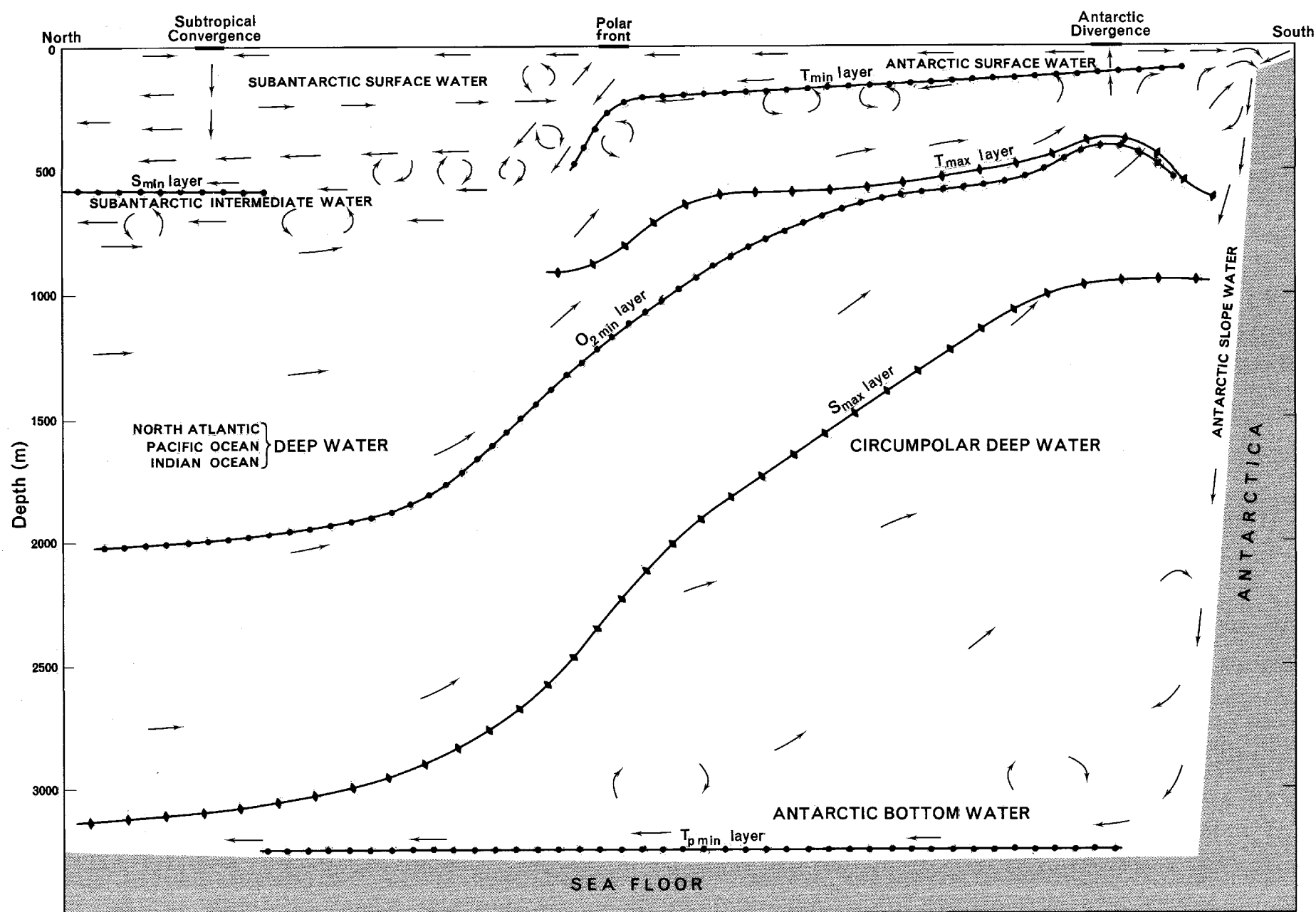


Fig. 1. Schematic representation of water masses in the Antarctic and Subantarctic (after Gordon, 1967).

marked contrast to the conditions in tropical and temperate regions where the nutrient salts are frequently limiting factors.

While the concentration of nutrient salts in Antarctic waters is never low enough to limit productivity, there is evidence that trace elements may, indeed, affect organic production in these waters. Volkovinsky's (1966) data showed direct correlation between manganese and molybdenum concentrations and primary production in the Scotia Sea.

(2) *Temperature.* Some conflicting views exist in regard to the effect of temperature on the metabolic activities of phytoplankton in Antarctic waters. Several investigators have indicated that because of their adaptation to the cold environment, phytoplankters are not inimically affected by extremely low temperatures. Others have attributed their low productivity in Antarctic waters to the effect of the near-freezing water temperature on the photosynthetic rate. The subject is thus wide open for more field and laboratory experiments in order to assess the effect of temperature on the metabolic activities of the primary producers in the Antarctic waters.

(3) *Light.* For a region which alternates between essentially complete darkness for half the year, and continuous daylight for the other half, the effect of light on primary productivity should be very important. Further, light penetration in Antarctic waters is determined not only by the intensity and angle of incidence of the light, surface reflectance, and absorption of suspended particles, but also by the presence of thick fast ice and pack ice which appreciably reduce the amount of submarine illumination. Our observations in the Bellingshausen Sea in February 1965 showed that 21% of the incident light penetrated through a layer of ice 1 m thick. The biological implication of this assumes great significance when it is realized that the areal extent of open surface waters south of the Antarctic Convergence is approximately halved by the extensive coverage of sea ice in winter (Mackintosh and Brown, 1956).

(4) *Stabilization of surface waters.* Another important factor which has great influence on phytoplankton production in Antarctic waters relates to the stability of surface waters. Two mechanisms relate stability to production. In a zone of favorable light intensity, high stability favors the maintenance of the phytoplankton population but restricts the vertical transfer of nutrients. Low stability, on the other hand, favors the vertical replenishment of nutrients in the euphotic zone, but could have a deleterious effect on phytoplankton growth by carrying these plants out of reach of light which is essential for their photosynthesis. Hasle (1956) attributes the low productivity in the Subantarctic zone and in the region of the Antarctic Convergence to the comparatively low stability of surface water. This was corroborated by the author's findings (see below) where, on several crossings of the Drake Passage, he found that the lowest productivity values coincided with the Antarctic Convergence where surface waters are sinking.

THE DATA

Data on the standing crop of phytoplankton, primary productivity, and nutrient salts in the Atlantic sector were collected during nine cruises aboard the Argentine vessels *Capitan Canépa*, *Commandante Zapiola*, and *General San Martín* in the course of a cooperative investigation between Texas A&M University and the Argentine Hydrographic Service. Chlorophyll *a* and C^{14} data collected during the International Weddell Sea Expedition (January to March 1968) have been used on the maps. Chlorophyll *a*, C^{14} uptake, nutrient salts, and dissolved and particulate organic carbon data from the Pacific sector were taken during USNS *Eltanin* Cruises 18 to 28 (except for Cruise 22 which was made in the Drake Passage and the Scotia Sea). The pertinent data collected (minimum, maximum, mean, standard deviation and number of observations) in the Atlantic and Pacific sectors are summarized in Table 1 and Table 2 respectively.

Primary production. The photosynthetic activity of the phytoplankton was measured by the C^{14} uptake method according to Steemann Nielsen (1952) with the modifications suggested by Strickland and Parsons (1960), and more recently by Steemann Nielsen (1964). Sampling was done with non-toxic samplers. Water samples were collected at five depths in the euphotic zone (that is, from the surface to the depth at which 1% of surface light intensity penetrated). These depths were selected by measuring with a submarine photometer the transmission of light in the water. In determining the rate of photosynthesis three 250-ml Pyrex glass bottles were filled with sea water; each bottle was inoculated with $4\mu\text{C}$ of $\text{NaHC}^{14}\text{O}_3$ and placed in an incubator with constant light intensity of approximately 1500 ft-candles. The incubation period was generally four hours. The C^{14} data have been corrected only for dark bottle uptake. Radioactivity of the samples was measured with a gas flow proportional counter, Nuclear Chicago Model D47, Scaler Model 186.

Chlorophyll a. In general, 2 to 3 liters of sea water were filtered with a 47 mm HA Millipore filter¹ (pore size $0.45\mu\pm 0.02$) after the addition of a small amount of MgCO_3 , and following the method of Richards with Thompson (1952) as modified by Creitz and Richards (1955). Estimation of the concentration of chlorophyll *a* was made using the revised equations given by Parsons and Strickland (1963).

Nutrient salts. Determinations of the amounts of phosphates, nitrates, nitrites, and silicates were made using, respectively, the methods of Robinson and Thompson (1948), Mullin and Riley (1955), Bendschneider and Robinson (1952), and Robinson and Thompson (1948).

Soluble and particulate organic carbon. The method for determining soluble organic carbon was that used by Menzel and Vaccaro (1964),

¹Registered trademark, Millipore Filter Corporation, Bedford, Massachusetts.

with some modifications. ‘Particulate organic carbon’ is defined as that fraction of the organic carbon which is retained by a 0.2 micron pore-size glass fiber filter. Duplicate 500-ml aliquots of water sample were passed through one-inch diameter glass fiber filters. The filters were then placed in individual 10-ml glass ampoules to which 10 ml of distilled water, 0.2 gm of potassium persulfate, and 0.25 ml of 6% phosphoric acid solution had previously been added. The contents of the ampoule were then purged of inorganic carbon components with purified oxygen for six minutes at a rate of 60 ml per minute, and then sealed. The ampoules were placed in a pressure vessel and heated to 175°C for twenty-four hours to convert the organic carbon to carbon dioxide. The carbon dioxide of each ampoule was determined by flushing the gaseous contents of the ampoules into a non-dispersive Beckman model 215 infrared analyzer. The signal from the analyzer was recorded on a strip chart recorder. The peak area was compared to a standard calibration curve and the organic carbon content of each ampoule determined after the subtraction of an appropriate reagent blank.

All the productivity and related data were processed with an IBM 7094 Fortran IV at the Texas A&M University.

THE MAPS

In presenting the distribution of the productivity parameters in Plates 1–8, two types of maps are used. In one, surface values are plotted; in the other, values are integrated through a column of water extending from sea surface to the depth of the euphotic zone (except for the nutrient salts collected in the Atlantic sector where their values are integrated from the surface to a depth of 150 m).

It should be noted, however, that the data plotted in both the Atlantic and Pacific sectors are primarily those collected by the author. Therefore the same techniques were used and the data may be compared with some confidence. However, no allowance has been made for seasonal or yearly changes.

Plate 1: Distribution of chlorophyll a. The distribution of chlorophyll *a* in the surface waters shows discernible regional variations. Relatively high chlorophyll *a* values were found off the coast of Argentina and over its continental shelf. In the northern and middle Drake Passage, the values were noticeably lower than those along much of the continental shelf. However, in the southern Drake Passage, higher values were again found in the region north of the South Shetland Islands. In the Weddell Sea, conspicuous regional variations in chlorophyll *a* were exhibited; high values were found between the South Orkney and South Sandwich Islands, especially in the vicinity northeast of the South Orkney Islands. In the eastern and southern Weddell Sea, the paucity of the phytoplankton was notable except in the region along the Edith Ronne and Filchner Ice

TABLE 1. Mean and extreme values of chlorophyll *a*, carbon¹⁴ uptake, and nutrient salts in the Atlantic sector of the Antarctic (Drake Passage, Cruises 1-9 of Argentine vessels).

	Min.	Max.	Mean	Standard deviation	Number of observations
*Ch1 <i>a</i> (mg/m ³)	0.01	18.35	0.89	1.31	518
*Ch1 <i>a</i> (mg/m ²)	0.72	81.38	15.94	14.17	79
*C ¹⁴ (mgC/m ³ /hr)	0.02	97.44	5.25	8.65	458
†C ¹⁴ (mgC/m ² /hr)	3.43	337.49	50.70	17.49	87
*PO ₄ (μg/L)	0.01	2.90	1.21	0.53	442
‡PO ₄ (mg/m ²)	38.22	437.95	225.66	69.58	173
*Si (μg/L)	0.1	100.0	29.1	21.5	385
‡Si (gr/m ²)	0.18	13.64	3.82	2.33	150
*NO ₃ (μg/L)	0.1	94.9	11.9	8.5	437
‡NO ₃ (g/m ²)	0.18	8.52	2.26	1.03	170
*NO ₂ (μg/L)	0.01	2.73	0.19	0.18	415
‡NO ₂ (mg/m ²)	1.50	71.75	22.80	10.35	170

* Surface values
† Integrated values for the euphotic zone
‡ Integrated values to a depth of approximately 150 m

TABLE 2. Mean and extreme values of chlorophyll *a*, carbon¹⁴ uptake, nutrient salts, and particulate and dissolved organic carbon (POC and DOC) in the Pacific sector of the Antarctic (*Eltanin* Cruises 18-21 and 23-28).

	Min.	Max.	Mean	Standard deviation	Number of observations
*Ch1 <i>a</i> (mg/m ³)	0.01	5.80	0.26	0.34	723
*Ch1 <i>a</i> (mg/m ²)	0.23	41.32	12.62	6.32	217
*C ¹⁴ (mgC/m ³ /hr)	0.03	22.50	1.22	1.69	656
†C ¹⁴ (mgC/m ² /hr)	3.54	194.73	32.01	23.93	213
*PO ₄ (μg/L)	0.01	4.66	1.09	0.46	350
†PO ₄ (mg/m ²)	0.84	457.00	42.98	37.01	146
*Si (μg/L)	0.1	79.9	13.5	13.5	368
†Si (g/m ²)	0.01	5.41	0.57	0.59	154
*NO ₃ (μg/L)	0.1	30.2	12.9	5.5	313
†NO ₃ (g/m ²)	0.01	2.93	0.63	0.41	161
*NO ₂ (μg/L)	0.01	1.23	0.18	0.11	296
†NO ₂ (mg/m ²)	0.6	33.8	10.7	6.7	146
*POC (mgC/L)	0.003	0.520	0.058	0.051	149
†POC (gC/m ²)	2.46	18.84	5.52	2.27	153
*DOC (mgC/L)	0.25	2.66	0.95	.27	156
†DOC (gC/m ²)	14.1	243.1	58.3	23.4	157

* Surface values
† Integrated values for the euphotic zone

Shelves, between 30°W and 40°W. The middle and southwestern Weddell Sea, on the other hand, showed markedly high chlorophyll concentration.

The region to the west of the Antarctic Peninsula showed extraordinarily rich phytoplankton populations; surface chlorophyll *a* values as high as 18.35 mg/m³ were recorded. In the Bellingshausen Sea, low values similar to those found in the Drake Passage were recorded.

In the Pacific sector, the phytoplankton standing crop in surface water samples was generally poor, with chlorophyll *a* values less than 0.50 mg/m³ except for isolated pockets ranging between 0.50 and 0.99 mg/m³. The waters of the Ross Sea and of coastal regions off New Zealand and Tasmania showed much higher chlorophyll *a* values than did oceanic areas.

The paucity of the data from the Indian Ocean sector makes it difficult to compare the productivity of this sector with those of the Atlantic and Pacific. A comparison is further complicated by the fact that different sampling methods were used by the investigators in the Indian Ocean. However, judging from the few scattered data available, it would seem that this sector is characterized by low phytoplankton standing crops.

Conspicuously high integrated pigment values were encountered in the Scotia Sea, in the southwestern Weddell Sea, in the Ross Sea, and in the waters west of the Antarctic Peninsula and surrounding New Zealand and Tasmania. Except for low phytoplankton standing crop in northern Drake Passage, the integrated chlorophyll data in the areas investigated were moderately rich.

Plate 2: Distribution of carbon¹⁴ uptake. The distribution of C¹⁴ uptake in surface water samples in the areas studied shows a picture more or less similar to that of phytoplankton standing crop. The average values of the Argentine continental shelf were found to be far greater than those of the Drake Passage. The values averaged 6.23 mgC/m³/hr for the Argentine shelf compared to 2.15 mgC/m³/hr for the Drake Passage. Relatively high photosynthetic rates were found in limited areas of the Weddell Sea. To the west of the Antarctic Peninsula, exceptionally high primary productivity values were recorded in the Bransfield and Gerlache Straits (11.83 and 13.13 mgC/m³/hr respectively). In the Bellingshausen Sea, primary production was low (1.46 mgC/m³/hr).

In the Pacific sector essentially all stations gave low rates of photosynthesis (<5.0 mgC/m³/hr); however, patches of relatively high photosynthetic rates were recorded between 170°W and 180°W longitude.

Data available from Japanese and Russian publications seem to indicate low productivity values in the Indian Ocean sector.

Primary production in the euphotic zone of the study areas shows relatively low photosynthetic activity in the Drake Passage, the eastern Weddell Sea, the Bellingshausen Sea, and in the Pacific sector between 75° and 150°W, except for isolated pockets of moderately rich photosynthetic activity. High carbon assimilation values were found southeast of Tierra del Fuego, in the vicinity of South Orkney Islands, in the southwestern Weddell Sea, in the Ross Sea, and in the waters west of the Antarctic Peninsula and those surrounding New Zealand and Tasmania.

The effect of the Antarctic Convergence on the distribution of chlorophyll *a* and C¹⁴ uptake is particularly noticeable in the Drake Passage where several crossings were made at various seasons in several years. El-Sayed *et al.* (1964) and El-Sayed and Mandelli (1965) have reported low phytoplankton standing crop and photosynthetic activity at the Antarctic Convergence. This seems to confirm the belief that the productivity of the surface layers is usually associated with stability and vertical mixing. At the Convergence, vertical mixing renders the formation of a shallow continuous layer impossible, and lack of such a layer is the initial factor militating against a heavy phytoplankton production (Hart, 1934).

Seasonal variations in the distribution of chlorophyll a and carbon¹⁴ uptake. The seasonal variations in the distribution of surface chlorophyll *a* and C¹⁴ uptake in the Drake Passage between March 1962 and March 1965 are shown in Figure 2. The Drake Passage was chosen to represent the Atlantic sector of the Antarctic primarily for want of data depicting the seasonal variation in other regions in that sector. It is clear from the above figure that there are discernible seasonal variations in the standing crop of phytoplankton and photosynthetic activity of phytoplankton in the Drake Passage during the period investigated. As expected, relatively high productivity values were encountered during the austral spring and summer cruises compared to fall and early winter values.

Figure 2 also shows the seasonal variations of surface productivity values during the nine *Eltanin* cruises in the Pacific sector. Initial increase in surface chlorophyll *a* and C¹⁴ uptake values is noted between Cruise 19 (July–Sept. 1965), Cruise 20 (Sept.–Nov. 1965) and Cruise 21 (Nov. 1965–Jan. 1966). This is followed by a marked decline during the two subsequent cruises; Cruise 23 (April–May 1966), and Cruise 24 (July–Sept. 1966). During the austral spring and summer, marked increases in phytoplankton standing crop and photosynthetic activity of the primary producers were noted on Cruises 26 (Nov.–Dec. 1966) and 27 (Jan.–Feb. 1967). However, it should be pointed out that the conspicuous rise in the productivity parameters during Cruise 27 is due, in part, to the collection of data in the relatively rich areas south of the Antarctic Convergence, as was mentioned before. Cruise 28, made during the austral fall (Mar.–May

1967) showed marked decline in productivity values.

In terms of the integrated productivity values in the Pacific sector (Figure 3), the picture very much resembles that of the seasonal distribution of the surface productivity parameters. Since integrated data are available for only three cruises in the Atlantic sector of the Antarctic, it is difficult to discuss their seasonal variation in a manner similar to that of the Pacific sector.

Latitudinal variations in chlorophyll a and carbon¹⁴ uptake. Since the areas covered by this investigation encompass large geographical regions which are bounded on the north by 40°S latitude and on the south by the coast of Antarctica, it is instructive to study the latitudinal variations in productivity in these vast regions. For this reason the data collected in surface waters in both the Atlantic and the Pacific sectors were averaged within 5° squares and are plotted in Figure 4. Figure 4 shows the regions between 60° and 65°S latitude in the Atlantic sector to be among the richest areas investigated (average surface chlorophyll *a*: 1.21 mg/m³). Unusually high phytoplankton standing crops were encountered between 70° and 75°S due mainly to an extraordinarily rich phytoplankton bloom off the Filchner Ice Shelf during the recent International Weddell Sea Oceanographic Expedition. In terms of carbon fixation, the areas between 35° and 40°S, and again between 60° and 65°S displayed higher values than any other area studied (C¹⁴ uptake: 9.22 mgC/m³/hr and 8.37 mgC/m³/hr, respectively). Integrated values of chlorophyll *a* and C¹⁴ uptake gave similar results to those of surface values.

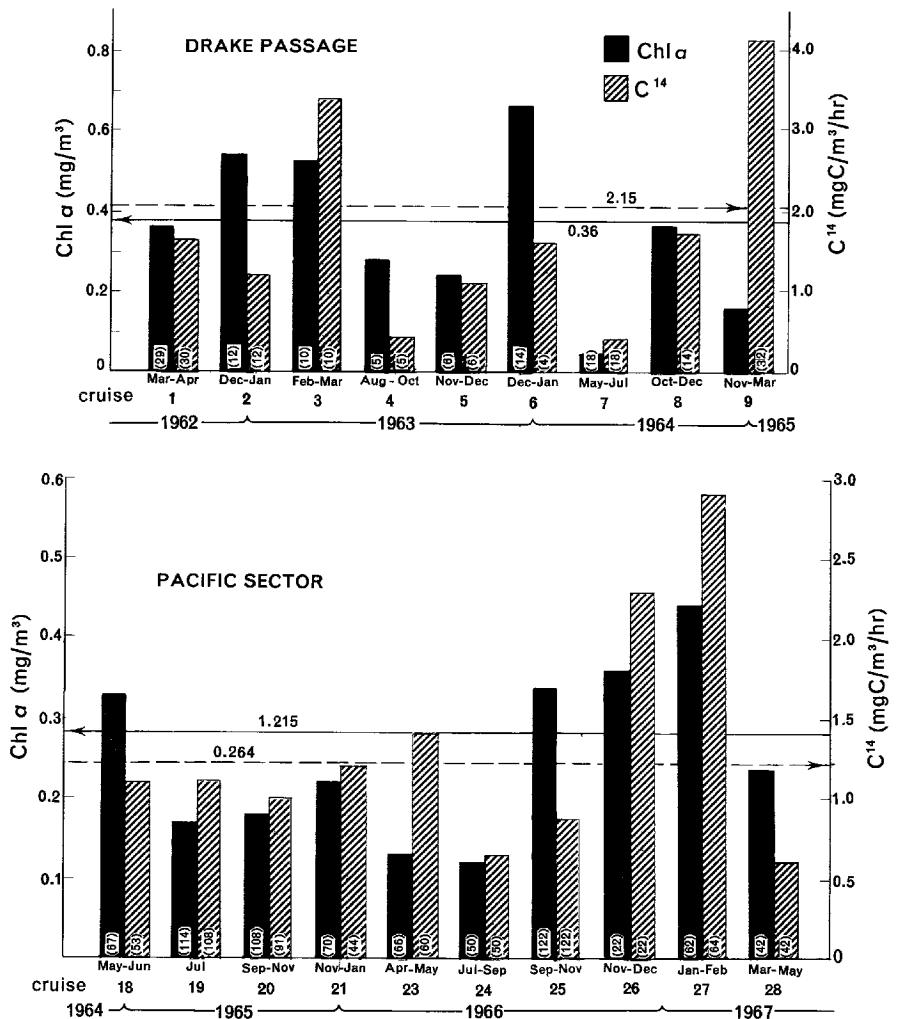


Fig. 2. Seasonal variations in chlorophyll *a* and carbon¹⁴ uptake (surface values) in the Atlantic¹ and Pacific² sectors of Antarctic waters³.

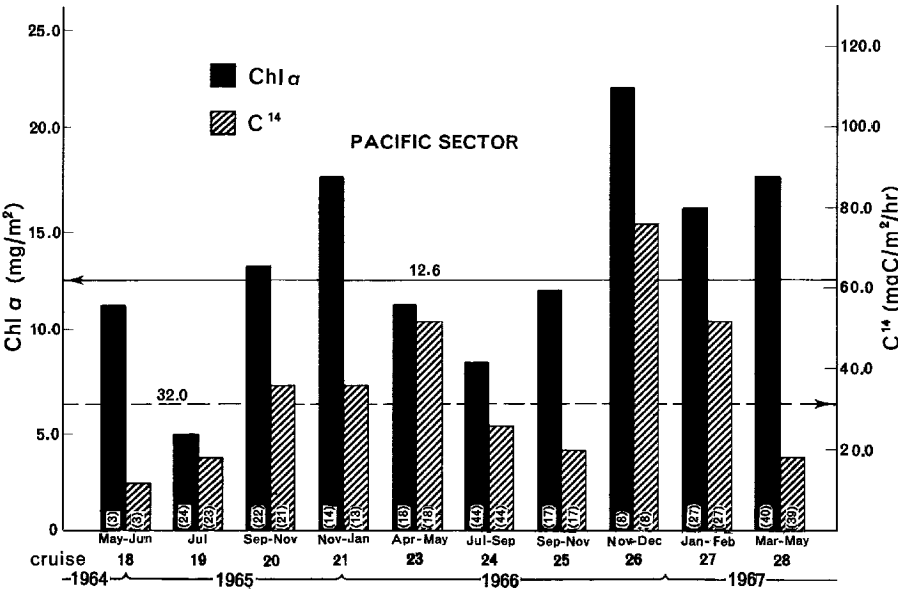


Fig. 3. Seasonal variations in chlorophyll *a* and carbon¹⁴ uptake (integrated through the euphotic zone) in the Pacific² sector of Antarctic waters³.

¹Argentinean Cruises 1–9 and International Weddell Sea Oceanographic Expedition
²*Eltanin* Cruises 18–28, except for Cruise 22
³Solid horizontal line indicates average value of chlorophyll *a*; dashed horizontal line indicates average value of carbon¹⁴ uptake

In the Pacific sector (Figure 4), the standing crop of phytoplankton in surface water samples between 30° and 60°S latitude is of the same magnitude. A slight increase in chlorophyll *a* concentration is found between 60° and 70°S, followed by a substantial increase between 70° and 80°S. It is interesting to note here that the concentration of the photosynthetic pigment in the region between 30° and 60°S latitude, in general, is below the overall average concentration of chlorophyll *a* (0.25 mg/m³) in the Pacific sector.

In terms of carbon fixation, the picture is more or less similar to that of the distribution of chlorophyll *a*, except that the photosynthetic activity of the phytoplankton in the region between 70° and 80°S is substantially higher than any other region studied.

Longitudinal variations in chlorophyll a and carbon¹⁴ uptake. The vast expanses of the Antarctic and Subantarctic waters in the Pacific sector made it necessary to average the productivity data collected during *Eltanin* Cruises 18–28 (excluding Cruise 22) within 10° squares in order to discern any longitudinal variations in productivity parameters. The data are plotted in Figure 5. It is clear from this figure that the western section of the Pacific sector between 140°E and 170°W (less 150° to 160°E) is conspicuously richer in chlorophyll *a* concentration than the central and eastern regions. It should be remembered, however, that the substantial increase in phytoplankton in the aforementioned region could be attributed to: (a) the proximity of the observation sites to New Zealand, Australia and Tasmania ('landmass effect', Doty and Oguri, 1956), and (b) the location of several of the stations in Antarctic waters, which, as noted before, are more productive than those of the Subantarctic. The low chlorophyll values encountered between 150°E and 160°E, in the Tasman Sea, are of the same order of magnitude found in the oceanic regions of the Pacific sector.

Since the longitudinal coverage in the Atlantic sector was not as extensive as in the Pacific, no attempt will be made here to compare the longitudinal variations in the productivity parameters in the former sector.

Vertical distribution of chlorophyll a and carbon¹⁴ uptake. The vertical distributions of chlorophyll *a* and C¹⁴ uptake in the euphotic zone at the stations occupied during Cruises 1–9 in the Atlantic sector of the Antarctic were discussed by El-Sayed (1968). A few stations representing the various areas studied during Cruise 9 are plotted in Figure 6. This figure shows that chlorophyll *a* values, by and large, tended to be higher at subsurface levels than at the surface. Carbon assimilation, on the other hand, showed higher values at or near the surface; these decreased gradually to minimum values at depths ranging between 7 m in the Gerlache Strait (Station 414) and 48 m in the Bellingshausen Sea (Station 258). The same figure shows that the shallower the euphotic zone, the greater the productivity. Thus at Station 368 (Bransfield Strait) and Station 414 (Gerlache Strait), which exhibited the highest primary production encountered during this cruise (5.26 gC/m²/day and 3.2 gC/m²/day), the depths of the euphotic zone at these stations were 8 m and 7 m respectively. On the other hand, at Station 258 in the Bellingshausen Sea where the euphotic depth is 47 m, the amount of organic production was much lower (0.15 gC/m²/day) than the Bransfield and Gerlache Straits.

In the Pacific sector of the Antarctic, the vertical distribution of the productivity parameters in some selected cruises will be discussed. *Eltanin*

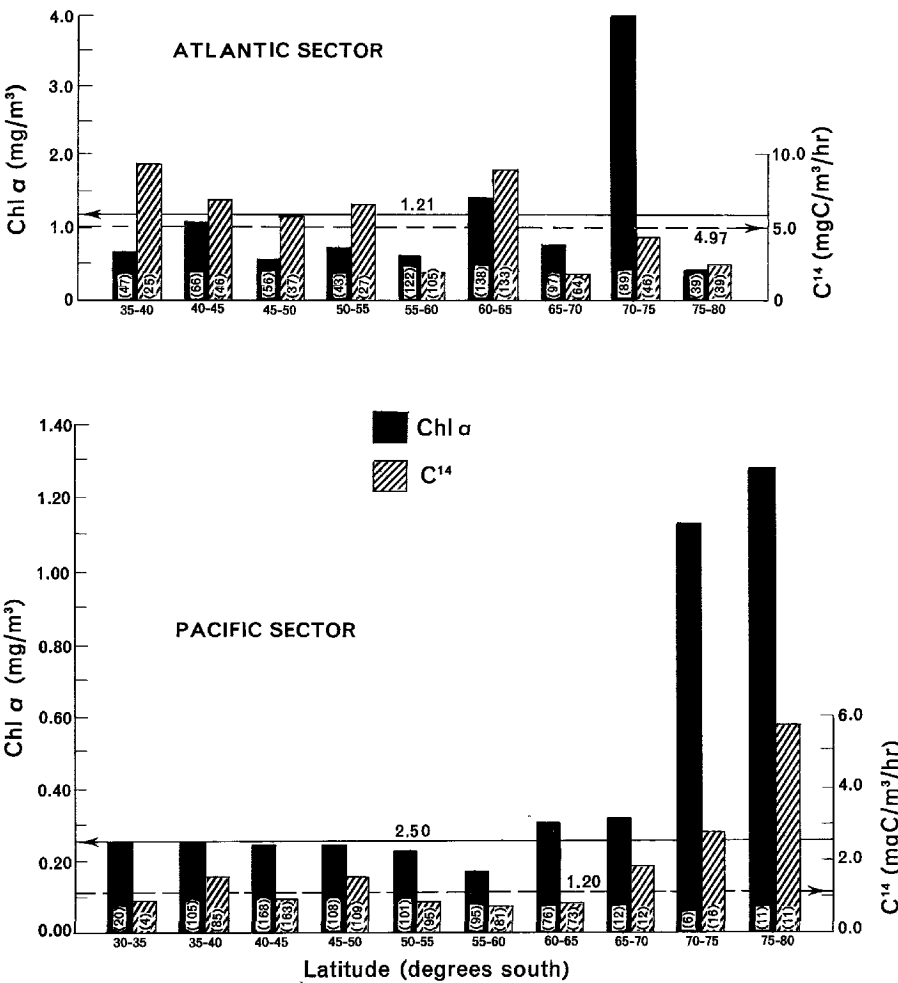


Fig. 4. Latitudinal variations of chlorophyll *a* and carbon¹⁴ uptake (surface values) in the Atlantic¹ and Pacific² sectors of Antarctic waters³.

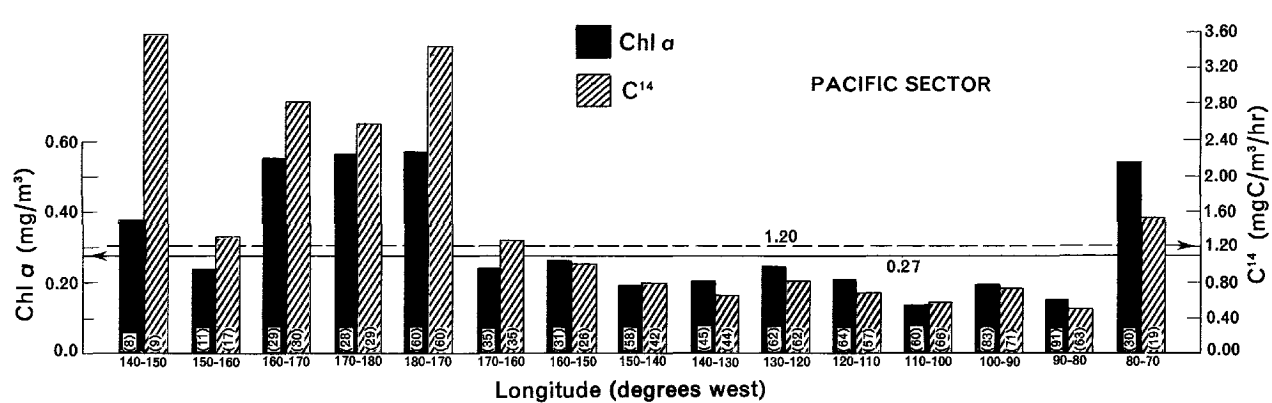


Fig. 5. Longitudinal variations of chlorophyll *a* and carbon¹⁴ uptake (surface values) in the Pacific² sector of Antarctic waters³.

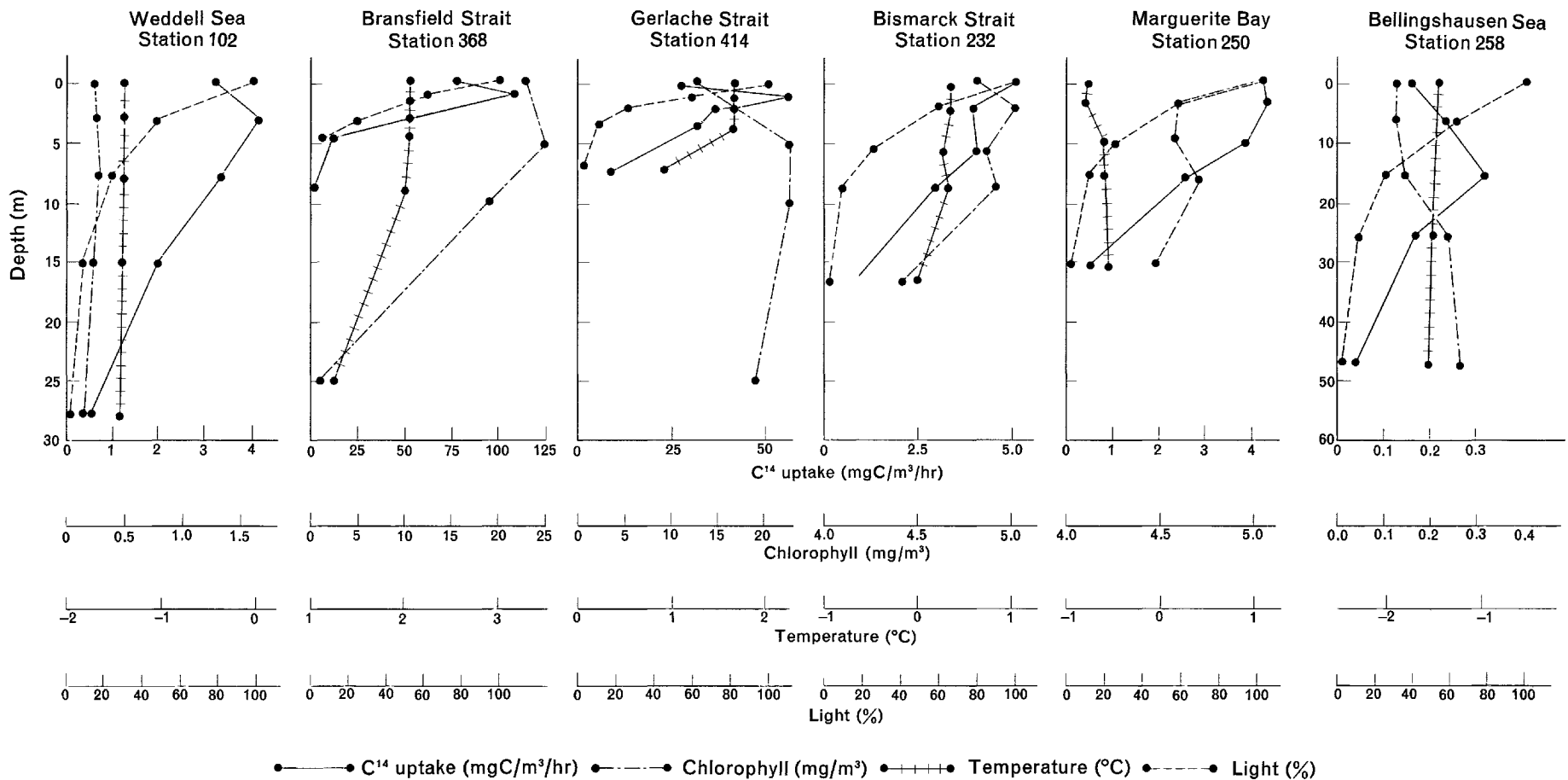


Fig. 6. Vertical distribution of chlorophyll *a*, carbon¹⁴ uptake, temperature, and light penetration at selected stations during *General San Martin* Cruise 9 (Atlantic sector).

Cruise 19 was selected because of its wide coverage of the Antarctic and Subantarctic waters between Chile and New Zealand; Cruise 27 was selected to represent conditions between Tasmania and the Ross Sea and Cruise 28 to represent the productivity parameters in the South Pacific (43°S latitude) between Australia and Chile. These are plotted in Figure 7. Distribution of chlorophyll *a* during Cruise 19 showed a more or less homogenous distribution in the euphotic zone; that of Cruises 27 and 28 showed a tendency to increase with depth. Carbon assimilation, on the other hand, exhibited high values at the surface for the three cruises; these decreased gradually to minimum values at depths ranging between 87 m (Cruise 19), and 45 m (Cruise 27). Primary production per square meter for Cruises 19, 27, and 28 were 19.3, 66.3, and 21.2 mgC/m²/hr, respectively.

Plates 3–6: Inorganic nutrient salts. The distributions of phosphate, silicate, nitrate, and nitrite concentrations are plotted on Plates 3–6. Despite marked variations in the distribution of the inorganic salts, their pattern of distribution in the Atlantic and Pacific sectors is more or less similar. By and large, low concentrations of these nutrients are found along the Argentine coast, in the northern Drake Passage, in the Bellingshausen Sea, in the Pacific waters north of the Antarctic Convergence and in the Tasman Sea. Moderately high values are found in the southern Drake Passage, west of the Antarctic Peninsula and south of Tasmania. Very high values of nutrient concentrations are located in the Bransfield Strait, the Weddell Sea, and to the north of the Ross Sea.

The effect of the Antarctic Convergence on the distribution of the nutrient elements is quite noticeable in the maps provided. In general, the nutrient distributions show higher concentrations south of the Convergence than north of it. However, it is interesting to note that although the concentration of the nutrient elements north of the Convergence is lower than in the Antarctic waters proper, even their lowest levels of concentrations are higher, in general, than the winter maximum of temperate regions.

The surface water of the Subantarctic zone has less nutrients than are found in the Antarctic surface waters. However, at a deeper level, between the northward movement in the Antarctic Intermediate Water and the southward movement in the more saline Deep Water, phosphate and nitrate appear to be regenerated, possibly because of a large mortality of sinking phytoplankton as indicated by abundant deposits of diatom ooze below

this region. The decomposition enriches the south-going deep waters and, in the Antarctic zone, the highest phosphate and nitrate concentrations are found in the warm Deep Water. Silicates are most abundant in the Antarctic Bottom Water, probably because of regeneration from the dissolution of the skeletons of diatoms near the bottom.

The vertical distribution of phosphates and silicates in a transect across the Drake Passage during a late summer cruise (March 1963) is shown in Figure 8. It is clear from this figure that substantial increase in surface phosphate and silicate values was noted as the Antarctic Convergence was crossed from north to south. Pronounced increases in the concentration of nutrient salts were also noted with increase in depth as shown by the high values of phosphates and silicates in the warm Deep Water and in the Antarctic Bottom Water (Figure 8).

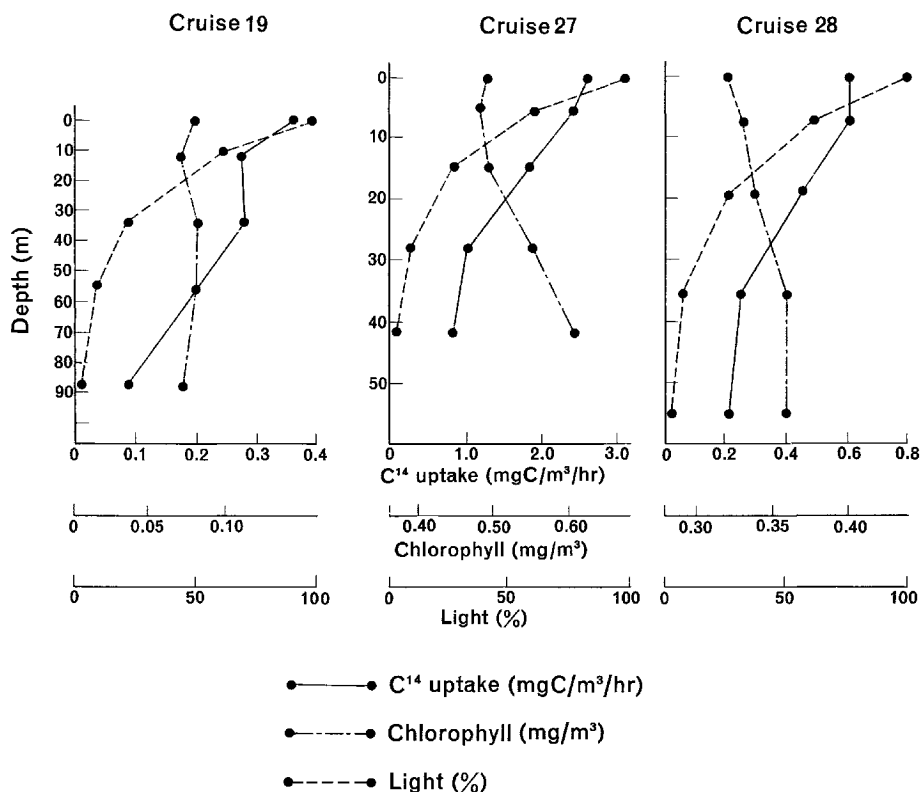


Fig. 7. Vertical distribution of average chlorophyll *a*, carbon¹⁴ uptake, and light penetration during *Eltanin* Cruises 19, 27, and 28 (Pacific sector).

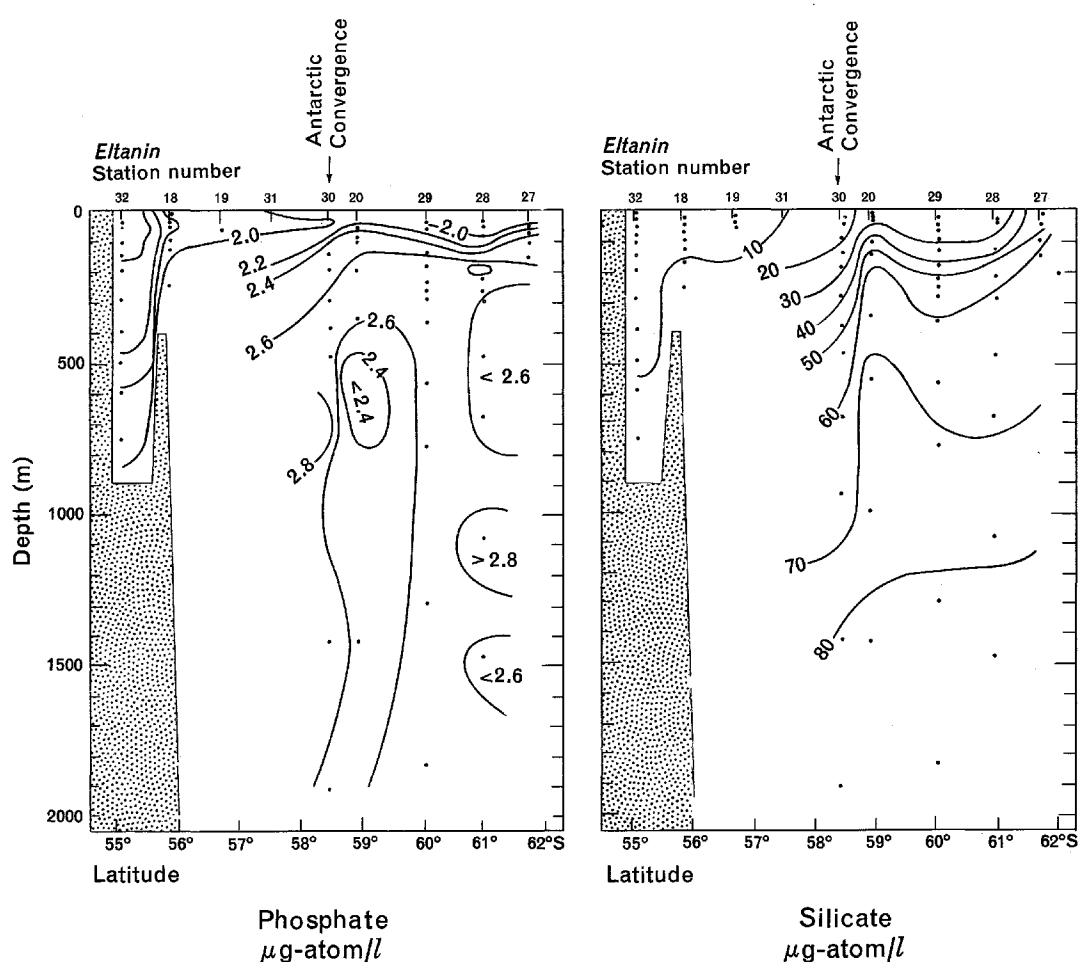


Fig. 8. Distribution of phosphates and silicates in a transect across the Drake Passage in March 1963 (after El-Sayed *et al.*, 1964).

Plates 7 and 8: Particulate and dissolved organic carbon. No clear-cut pattern in the distribution of particulate and dissolved organic carbon could be discerned in the Atlantic and Pacific sectors. Low values, however, were found in the Scotia Sea and in the region of the Antarctic Convergence in the Pacific sector. High values were found in the Tasman Sea, between 135°W and 150°W (north of the Antarctic Convergence) and between the Convergence and the Ross Sea.

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—S. Z. El-Sayed

Marine Diatoms

INTRODUCTION

The diatom flora of the Antarctic and Subantarctic include species peculiar to these regions and species common to other regions as well. Some species of the first type are distributed in both the Subantarctic and the Antarctic, such as *Chaetoceros criophilus* Castr., *Chaetoceros neglectus* Karsten and *Fragilariopsis kerguelensis* (O'Meara) Hust. Others appear only in the Antarctic, like *Chaetoceros flexuosus* Mangin and *Fragilariopsis sublinearis* (van Heurck) Heiden, and a small number appear only in the Subantarctic such as *Rhizosolenia curvata* Zacharias. The majority of the species present in more northerly waters as well as in the Antarctic and Subantarctic are found in both equatorial and cold-water regions of both hemispheres. They are regarded as cosmopolitan in their distribution even though they are sometimes absent from high latitudes. A number of these widely distributed species such as *Thalassionema nitzschioides* (Grun.) Hust. and *Nitzschia bicapitata* Cl. seem to have their southern limit at or close to the Antarctic Convergence (the boundary between the Subantarctic and Antarctic regions) while others, such as *Chaetoceros atlanticus* Cl., extend farther southward. In light of present knowledge, a few other species, for example *Fragilariopsis cylindrus* (Grun.) Krieger and *Thalassiosira antarctica* Comber, are regarded as bipolar in distribution.

A circumpolar distribution of the plankton of the southern oceans is generally assumed. At present there is no evidence to disprove this assumption for planktonic diatoms. For diatoms dependent upon the coast or upon pack ice during parts of their life, the situation may be slightly different.

The species whose distributions are shown on Plates 9 and 10 were selected as being representative of the approximately 100 species which are present in Antarctic and Subantarctic waters. About 40 data sources were used for mapping the species distribution; the most important of these are listed in the bibliography.

GENERAL COMPOSITION AND PHYSIOGNOMY OF THE ANTARCTIC AND SUBANTARCTIC DIATOM POPULATIONS

Since the first paper on Antarctic diatoms (Ehrenberg, 1844), which reported on the collections of J. D. Hooker in 1839-1843, more than 60 papers have been published containing information as to which marine diatom species are present in the Antarctic. Descriptions of new species are included in most of these papers, for example, Mangin's 1960 report, in which 123 species were recorded, 47 of them new to science. Concur-

rently, other authors have been able to reduce the number of species by elimination of duplication, as was pointed out by Kozlova (1966), who summarized information on the number of species recorded by various authors. However, the disparity between the numbers of species reported by the various investigators cannot be attributed entirely to the fact that more than one name has been assigned to the same species but must be partly explained by differences in quantities examined and in techniques employed. While some scientists examined hundreds or thousands of samples, others did a thorough examination of a small number. Further, while some made use of nets for sampling phytoplankton, others examined water samples, and still others obtained their samples from ice or bottom sediments. Because of these differences it is difficult to make a comparison between the number of Antarctic diatoms and the numbers present in other areas. Nevertheless we are able to arrive at some approximations using the data available. According to lists compiled by Allen (1963) for Pacific phytoplankton, more than 100 diatom species have been found in the waters of New Zealand and Australia. This number is comparable to that found in more temperate regions such as Puget Sound, where slightly fewer than 100 species have been recorded (Gran and Angst, 1931). Records from investigations in northern Canada (Bursa, 1961) and fjords of northern Norway (Gaarder, 1938) indicate that the numbers of species in the Arctic are somewhat lower.

The describing of new Antarctic diatom species, which has been going on for over 100 years, has often been done without a critical comparison with species already known from other areas. Therefore, it seems reasonable to assume that some of the species described from Antarctic material are, in reality, conspecific with species from other areas; however, it should be remembered that a number of Antarctic diatoms still remain undescribed.

Some diatom genera are particularly important in the region south of the Antarctic Convergence. Among these are the monospecific endemic genera *Charcotia* M. Per. and *Micropodiscus* Grun. Genera which, though not endemic, are apparently more abundant here than in other areas both in species and in individuals are the single-celled centric *Asteromphalus* Ehr., the single-celled pennate genus *Tropidoneis* Cl. and the chain-forming pennate *Fragilariopsis* Hust. Of the thirteen *Fragilariopsis* species known throughout the world, eleven occur south of the Antarctic Convergence. Nine of these seem to be endemic either to the Antarctic or to the Antarctic and Subantarctic. Each of the centric plankton genera *Chaetoceros* Ehr., *Rhizosolenia* (Ehr.) Brightw., and *Thalassiosira* Cl. are represented by ten or more species in the southern oceans. These waters are also rich in species of the centric genus *Coscinodiscus* Ehr. and the pennate genus *Nitzschia* Hass.; however, most of these genera are represented by a considerable number of species wherever they appear.

The author has examined water samples by the sedimentation technique which utilizes an inverted microscope. Estimates based on her findings indicate that the most abundant diatom species are the minute *Fragilariopsis pseudonana* Hasle and an extremely small form of *F. cylindrus*. Water samples from the South Pacific yield 500,000 to 1,000,000 cells per liter of these tiny plants; these species are recorded in great abundance in corresponding latitudes of the Northern Hemisphere also. Equally plentiful in the South Pacific are the three small species *Chaetoceros neglectus*, *Nitzschia prolongatoides* Hasle and *N. subcurvata* Hasle; however, these seem to be limited in distribution to the southern oceans. Some very large species also occur abundantly in these waters, for example, the pennate *Thalassiothrix antarctica* Schimper and *Synedra reinboldii* van Heurck, which are endemic here, and the centric *Corethron criophilum* Castr., whose geographic distribution is somewhat questionable. Water samples from the South Pacific which were examined by the author yielded 9,000 to 30,000 cells per liter of these three species.

Some genera in the southern oceans cover a wide size-spectrum. *Chaetoceros* species range in size from the tiny chain-forming *C. neglectus* with delicate setae to the large, single-celled *C. criophilus* with coarse, spiny setae. In *Rhizosolenia* the extremes are represented by *R. cylindrus* Cl., which may be about 5 μ long, and by *R. curvata* and *R. styliformis* Brightw., which may be as much as 1 mm long. *Fragilariopsis* species range from 4-20 μ for *F. pseudonana* in its greatest dimension, to 57-110 μ for *F. obliquecostata* (van Heurck) Heiden.

A great diversity in silicification is found in the Antarctic diatoms. Sometimes this diversity occurs among species of the same genus. For example, some of the *Fragilariopsis* species such as *F. kerguelensis* and *F. obliquecostata* are thick-walled and coarsely structured, while other species such as *F. cylindrus* and *F. pseudonana* are weakly silicified and very finely structured. In other cases the differences are within the same species. For example, some specimens of *Dactyliosolen antarcticus* Castr. have coarsely structured intercalary bands, while in other specimens the bands are so fine that their structure cannot be seen under a light microscope.

To a certain extent the composition and the physiognomy of the Antarctic and Subantarctic diatom populations are characterized by a great diversity of species and forms. Furthermore, endemism seems to be fairly high in these waters, although it is expected that the number of seemingly

endemic species will be reduced as examination of phytoplankton samples from the Antarctic as well as from other regions progresses.

THE MAPS (PLATES 9 AND 10)

Map 1: *Nitzschia bicapitata* Cl., *Nitzschia lecointei* van Heurck (see Hasle, 1964, for synonyms), *Rhizosolenia simplex* Karsten, and *Thalassionema nitzschioides* (Grun.) Hust.

Few observations have been recorded of the two *Nitzschia* species. Like *Thalassionema nitzschioides*, *Nitzschia bicapitata* has not been found in the Antarctic except by Kozlova (1962)¹. Both species have been found in equatorial waters as well as in cold waters in the Northern Hemisphere. *N. lecointei* has been found only in the Antarctic except for the northernmost record which is from the Kerguelen Islands, whose affinity to the Antarctic zone has been disputed (Delépine, 1963).

Rhizosolenia simplex has been observed at fairly northern localities, off the coast of southwest Africa, as well as in the Subantarctic and the Antarctic. Its normal range probably ends somewhere between the Antarctic Convergence and Antarctica.

Map 2: *Charcotia actinochilus* (Ehr.) Hust. (see Hustedt, 1958, for synonyms), and *Rhizosolenia curvata* Zacharias.

The records of *Rhizosolenia curvata* were compiled by Hart (1937) who concluded that the species was a typically Subantarctic oceanic planktonic diatom. Subsequent observations substantiate Hart's conclusion.

The distribution area of *Charcotia actinochilus* is restricted to the Antarctic. The record from St. Paul, north of 40°S, may be due to transport from the south or to an error in recording. Its greatest concentrations are found in coastal waters and regions of pack ice. Like *Nitzschia lecointei*, *Fragilariopsis cylindrus* and *Fragilariopsis sublinearis*, *Charcotia actinochilus* is a regular component of the Antarctic ice flora.

Map 3: *Fragilariopsis cylindrus* (Grun.) Krieger, *Fragilariopsis kerguelensis* (O'Meara) Hust. (see Hasle, 1965, for synonyms), and *Fragilariopsis sublinearis* (van Heurck) Heiden.

The distribution area of nine of the thirteen known *Fragilariopsis* species lies within the southern oceans. Of these nine species *F. kerguelensis* has been recorded most frequently. Records of several investigators indicate that it appears more frequently in open northerly waters than in coastal waters or regions of pack ice.

F. sublinearis is found in the Antarctic and does not extend into the Subantarctic region. *F. cylindrus* has occasionally been found in the Subantarctic, but most records are from far south in the Antarctic region. *F. cylindrus* also occurs abundantly in the high Arctic, while *F. sublinearis* is restricted to the Antarctic. Both species have been found in dense concentrations in Antarctic ice.

Map 4: *Chaetoceros criophilus* Castr., *Chaetoceros flexuosus* Mangin, and *Chaetoceros neglectus* Karsten.

The genus *Chaetoceros* is represented in the southern oceans by a great number of cosmopolitan species as well as by species peculiar to the map region. *C. criophilus*, *C. flexuosus*, and *C. neglectus* belong to the latter group.

The large single-celled *C. criophilus* is one of the most frequently recorded diatoms in the southern oceans. Like the small, chain-forming *C. neglectus*, *C. criophilus* has been recorded as far north as the coast of Africa and as far south as the pack ice. The densest concentrations of *C. criophilus* have been found far south in Antarctic waters late in summer, while *C. neglectus* has been observed in very great concentrations in the Subantarctic waters (Hasle, 1968?).

C. flexuosus belongs to the Antarctic region and, like *Nitzschia lecointei* and *Fragilariopsis sublinearis*, probably occurs chiefly in coastal waters or regions of pack ice.

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¹The records of *Thalassionema nitzschioides* and *Nitzschia bicapitata* between 90°W and 150°W originate from materials collected by the *Bratigg* Expedition, during which the position of the Antarctic Convergence was found to be fairly southerly (Midttun and Natvig, 1957; Hasle, 1968?).

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—G. Hasle

Dinoflagellates

INTRODUCTION

The maps of Plates 11 and 12 give some indication of our present knowledge of the distribution of dinoflagellates south of 35°S. I have chosen for mapping and discussion a rather small number of species which, in general, are well identified, were collected by at least two expeditions, and seem to be more or less significant in their distribution.

In plotting the maps, several taxonomic decisions have been necessary and must be explained in order that the maps be understood.

- (1) All species of *Phalacroma* are grouped under the name *Dinophysis* (Balech, 1967).
- (2) The name *Peridinium concavum* is used for the Antarctic species generally described under the name *Peridinium granii*. The Antarctic species certainly differs from the true *P. granii* and has been described by me as *P. petersi*; however I now am convinced that the Antarctic species is that described by Mangin under the name *P. concavum*.
- (3) *Dinophysis antarctica* Balech is used for the species sometimes referred to as *D. ovum*.
- (4) *Dinophysis acuminata* is used here in a rather broad sense. Despite the modern studies of Paulsen (1949) and Solum (1962), the status of this species is not yet clear. Therefore it seems best to use the oldest name available. (The records listed under *Dinophysis acuminata* include *D. laachmanni* and *D. borealis*.)
- (5) Under the heading *Ceratium pentagonum grandis*, I have included all the Subantarctic forms of *C. pentagonum*. Some authors recognize two Subantarctic subspecies of this cosmopolitan species. However, I have found it impossible to satisfactorily distinguish two subspecies because of the number of intermediate forms and therefore have used only one name, the first available and valid name assigned to a Subantarctic subspecies of *C. pentagonum*.

At present, information about dinoflagellates of the Southern Hemisphere is meager and, in some very large areas, even completely lacking. This is particularly true for the Subantarctic and the Antarctic between 30°E and 100°E and between 135°W and 180°W. The microplankton of most of the Subantarctic Atlantic between 45°W and 10°E is also little known. The reader is asked to keep this in mind when using the maps.

The paucity of data does not allow the construction of even a rough scheme showing vertical or seasonal differences of distribution. Similarly, it is impossible to present any quantitative data, not only because there is such a small amount in print, but also because the methods and units used by different authors are not comparable.

GENERAL COMPOSITION AND PHYSIOGNOMY OF THE ANTARCTIC DINOFLAGELLATE POPULATION

As far as we know, the truly Antarctic dinoflagellates all belong to only a few thecate genera, chiefly *Peridinium* and *Dinophysis*. Of the two,

Peridinium is by far the more abundant in species and also generally in individuals. Other genera present in Antarctic waters are: *Diplopeltopsis* (2 species), *Gonyaulax* (2 species), *Podolampas* (1 species), *Oxytoxum* (1 species), *Exuviaella* (1 species), and occasionally *Ceratium*.

The genus *Ceratium*, so prevalent in other seas, is generally absent from Antarctic waters. Most of the records indicate that in the Antarctic *Ceratium* is found either in surface waters relatively close to the Antarctic Convergence or in vertical hauls. Therefore, it seems likely that it is carried to the Antarctic by Subantarctic waters. As would be expected, two typical cold-water forms, *C. lineatum* and *C. pentagonum grandis* are those most often found in this realm. However, the reports of two authors supply information contrary to our assumption that all the *Ceratium* found in Antarctic waters are merely visitors. Hart (1934) found *C. pentagonum grandis* frequently and in relative abundance in Antarctic samples. Mangin (1926) in discussing the phytoplankton of the Scotia Sea reports *C. pentagonum grandis* and particularly *C. lineatum* in many Antarctic samples; even though these species always occur in very small numbers (from one to five individuals), we cannot disregard the findings. All the records of *C. petersi* in the Antarctic (Map 3) are (except for one individual) based on vertical hauls.

The naked dinoflagellates are probably not so rare in Antarctic waters as they seem; these fragile forms are often destroyed by fixation or are so distorted that they become unrecognizable. However, three species of *Gymnodinium* and two of *Gyrodinium* have been identified. *Pyrocystis pseudonociluca* is also reported. *Kofoidinium*, a genus generally regarded as typical of warm waters, has been recorded in Antarctic waters, but only rarely.

On the whole, the Antarctic phytoplankton is greatly dominated by the diatom population. Scattered among the diatoms are dinoflagellates and silicoflagellates (*Dictyocha speculum*); but since the flagellate numbers are small compared to the number of diatoms, the dinoflagellate biomass has generally been underestimated. Furthermore, Antarctic dinoflagellates are rather small and are protected by feeble and deformable thecae. It must be remembered that Antarctic phytoplankton studies have been devoted primarily to diatoms, and that in the process of cleaning them, dinoflagellates and other organic material have often been destroyed.

The Antarctic *Peridinium* are characterized by a relatively high number of small species; by species with long and sharp antapical spines which are widely separated from one another (*P. applanatum* and *P. obovatum*); and by species with abnormal plate patterns (*P. defectum*, *P. thulesense*, and *P. unipes*).

Most of the polar forms of *Dinophysis* in both hemispheres have striking protuberances. However, no Arctic *Dinophysis* has the highly developed excrescences that distinguish some Antarctic species.

As far as we know, the southern and northern polar waters have no species in common except for a very few which are cosmopolitan. The frequently mentioned *Peridinium pyriforme* of the Antarctic waters is almost certainly different from the northern form described by Paulsen (1905, 1949). The reported presence of the Arctic species *Gonyaulax alaskensis* and *G. spinifera* in the Antarctic is highly dubious. Nonetheless, there is a certain bipolarity of form. As mentioned previously, pronounced excrescences are known to be present in southern as well as in northern *Dinophysis*. *Peridinium bulbosum* Gaarder from the Newfoundland Banks is quite similar to *P. applanatum* Mangin and *P. defectum* Balech has a striking overall similarity to *P. minuscula* Pavillard (or *Minuscula bipes*) differing, however, in very important details of the plate pattern.

ENDEMISM OF ANTARCTIC DINOFLAGELLATES

Endemism is high in Antarctic waters. Species restricted to locations within the Antarctic boundaries are *Peridinium antarcticum*, *P. pseudo-antarcticum*, *P. archiovatum*, *P. concavum*, *P. thulesense*, *P. latistriatum*, *P. rosaceum*, *P. elegantissimum*, *P. raphanum*, *P. incertum*, *P. adeliense*, *P. nanum*, *P. metananum*, *P. defectum*, *P. charcoti*, *P. unipes*, *P. mediocre*, *Dinophysis cornuta*, *Deplopeltopsis granulosa*, *Gymnodinium frigidum*, *G. baccatum*, *Oxytoxum criophilum*, and *Podolampas antarctica*.

Several northern species have doubtless been incorrectly reported as found in the Antarctic and other reports are questionable. Up to the present, four northern species besides *Ceratium* seem to have been reliably reported in Antarctic seas. *Peridinium crassipes*, *P. monospinum*, and *P. solidicorne* have been found very close to the Antarctic Convergence, and *Diplopeltopsis minor* has been reported from Antarctic material.

The following Antarctic species are occasionally found in the Subantarctic: *Dinophysis tuberculata*, found close to the Antarctic Convergence, probably in mixed waters; *D. spinata*, found only by the *Meteor*; *P. turbinatum*, found in mixed waters; and *P. applanatum*, *P. variegatum*, *P. parvicollum*, *P. curtum*, and *P. incognitum*.

In explaining the occurrence, though rare, of Antarctic species in northerly Subantarctic waters, two possibilities must be considered: (1) either they are carried along with Antarctic Intermediate Water and appear on the surface in regions of upwelling, or (2) they are carried along with Antarctic surface waters. We are prone to accept the second

explanation, at least for the cases we studied in Argentina, though we cannot disregard the other possibility. On two occasions I found some Antarctic species in the Subantarctic waters off Argentina, far from the Antarctic Convergence. In both cases they were in waters where temperatures were significantly lower than in surrounding waters, with no indication of upwelling. The dinoflagellates studied were not isolated individuals in a Subantarctic community, but part of a mixed Antarctic—Subantarctic plankton with about 15 Antarctic species of diatoms, dinoflagellates, and tintinnids. Therefore, I believe that they were caught in some of the cold Antarctic Surface Water which was transported north of the Antarctic Convergence probably in outbreaks from eddies which form at the Convergence.

In summary, there is no other oceanic region where dinoflagellates attain such a high degree of endemism (80%-85%) as they do in the Antarctic. It is interesting to note that the tintinnids, a group of planktonic protists, are almost 100% endemic to the area.

SUBANTARCTIC DINOFLAGELLATES

As shown above, the endemism of the Antarctic population is very high. An almost reverse situation is encountered in Subantarctic waters. Only a few true Subantarctic species are known at present. Aside from some species studied by only one author (especially Wood or Balech), the only species of dinoflagellates almost unknown outside the Subantarctic boundaries are *Dinophysis truncata* and *Ceratium petersi*. A Subantarctic variety or subspecies is the previously mentioned *Ceratium pentagonum grandis*. However, both species of *Ceratium* are sometimes difficult to identify; furthermore, *C. pentagonum grandis* has been found rather frequently in the Antarctic.

Dinophysis operculata (Stein) as described by Balech (1962) is also probably a typical Subantarctic species, but we do not know very much about its distribution.

Peridinium obtusum seems to be a rather typical species of the Subantarctic. Although the validity of most of the records of this species in the Northern Hemisphere is questionable, and it seems to thrive best in the southern area, there are a few undisputed records from the Northern Hemisphere, especially in cool waters.

Ceratium lineatum is well known in cold waters of the Northern Hemisphere. However, it is also a very important component of the Subantarctic plankton, and it is one of the few species of *Ceratium* frequently cited from the Antarctic. In general, it delimits the Subantarctic waters rather well (see its distribution close to Argentina and to Australia, Map 5).

Dinophysis tripos has been found in several seas and in a great range of hydrographical conditions. However, in the Southern Hemisphere it seems to thrive well only in Subantarctic waters where it is often found with *Ceratium lineatum*, *C. pentagonum grandis*, and sometimes with *Dinophysis truncata*. The *Meteor* records (Kasler, 1938) indicate that it was encountered in high concentrations close to 40°W in two main areas, one south of South Africa and the other around 20°W. According to both the *Meteor* records and my findings, it occurs in somewhat lower concentrations near Tierra del Fuego.

Ceratium fusus, a cosmopolitan species, seems to prefer the proximities of the Subtropical Convergence where it has sometimes been found in great abundance.

Acknowledgments. The author is grateful to Mrs. G. Hasle and Miss P. Reinecke for some unpublished data.

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—E. Balech

Benthic Marine Algae

The Antarctic ice-continent accounts for 5 percent of the total world coastline. It is unique not only in being a large polar land mass, but also in being perhaps the most isolated of continents. The task of adequately charting the distribution of Antarctic benthic marine algae is complex. Collections of predominately sub-tidal marine flora are so scattered and generally so incomplete that conclusions concerning overall distribution patterns are extremely tenuous. It is also difficult to conclude from published works what taxa are most abundant. One can only hope that the distribution of the 10 species considered on Plates 14 and 15, which are common and (in the writer's experience) physiognomically important forms, will indicate phytogeographic patterns that will be confirmed when more complete collections and ecological surveys are made.

The most recent treatment of Antarctic biogeography and ecology (Van Oye and Van Mieghem, 1965) does not deal specifically with benthic marine algae. However, a catalog and bibliography of Antarctic and Subantarctic benthic marine algae, which includes distributional data, has been compiled by Papenfuss (1964). The reader is referred to this work for pertinent literature. Exploratory ecological work recently carried out is beginning to change many of our ideas about horizontal and vertical distributions of Antarctic marine plants (see Delépine, 1966; Delépine, Lamb, and Zimmermann, 1966; and Zaneveld, pp. 10—12 of this folio). It is particularly significant that the bulk of this new work is being done by botanists who are using diving techniques to collect and observe the plants *in situ*.

While it has been suggested by some that the Antarctic and Subantarctic be regarded as a single biogeographical province, Zinova (1958), Knox (1960), and others distinguish an Antarctic biogeographic region bounded on the north by the Antarctic Convergence. The present discussion considers mainly this Antarctic biogeographic region.

Tabulation of Antarctic zone species (based on type material listed by Papenfuss, 1964) suggests an even higher degree of endemism (35%) than that calculated by Zinova (1958) (25%).

- Antarctic algal distribution patterns can be distinguished as follows:
- (1) Species found only in the Antarctic Peninsula and the South Shetland Islands, such as *Cystosphaera jacquinotii* (Map 4, Plate 14). *Ascoseira mirabilis* is characteristic of the region but is also found in South Georgia (Map 2, Plate 14).
 - (2) Species found in the Antarctic Peninsula, the South Shetland Islands, and southern South America, but not in the main continent of Antarctica, such as *Adenocystis utricularis* (Map 1, Plate 14).
 - (3) Species found in Antarctica, except for the Antarctic Peninsula, and also in the Subantarctic islands and other regions between 50°S and 60°S, such as *Phyllophora* spp. (Map 9, Plate 15) and *Plocamium* spp. (Map 10, Plate 15).
 - (4) Species which are 'circumpolar' in Antarctica but which are not generally found north of 60°S: *Leptosomia simplex* (Map 7, Plate 15) and *Phyllogigas grandifolius* (Map 8, Plate 15).
 - (5) Species which are 'circumpolar' in Antarctica and are also

found between 50°S and 60°S, such as *Ballia callitricha*, (Map 3, Plate 14), *Desmarestia menziesii* (Map 5, Plate 14), and *Iridaea* spp. (Map 6, Plate 14).

Since such algae as *Phyllogigas*, *Ascoseira*, and *Desmarestia* are larger and more conspicuous than some of the other genera, it seems reasonable that their distribution patterns would be more accurate. *Cystosphaera* is also useful but presents some problems in that large quantities of attached specimens have yet to be encountered. A consideration of the distribution patterns raises several questions: (1) To what extent is the Antarctic flora unique? (2) Is the flora of the Antarctic Peninsula very different from that found elsewhere in the Antarctic? (3) What is the relationship between the flora of the Antarctic Peninsula and that of South Georgia and other more northerly Subantarctic regions?

At present it would appear that the flora of the Antarctic Peninsula bears considerable resemblance to that of South Georgia and other Subantarctic regions. Among the Phaeophyta, both *Phyllogigas* (Plate 14) and *Cystosphaera* occur in South Georgia which appears to represent an area of transition between the Antarctic and the Subantarctic regions. Further work in these areas will perhaps more clearly distinguish the two regions floristically. Collections to date suggest that the peculiar brown algal genera *Ascoseira*, *Cystosphaera*, and *Phaeurus* are confined to the Antarctic Peninsula region, while *Phyllogigas grandifolius* and *Desmarestia menziesii* are the most ubiquitous and conspicuous of the large, circumpolar brown algae. The distribution of *Phyllogigas* has been studied by Skottsberg and Neushul (1960).

The broad distribution patterns of Antarctic *Rhodophyta* and *Chlorophyta* suggest circumpolarity for all but two of the species shown. *Plocamium* and *Iridaea* were collected from Peter I Island by Dr. F. Beyer, Institute for Marine Biology, University of Oslo, in 1948, and constitute our only algal collection from the entire 90°W to 180°W quadrant.

There are no algal records as yet for the Antarctic coast from 72°W to 173°E and between 50°W and 40°E (exclusive of the South Orkney Islands). While these regions are still relatively unexplored, a lack of collections might be predicted on other grounds as well. An examination of the bathymetry indicates that in both of these regions either the ice extends down to depths below sea level and there is no rocky shore line present, or there is a permanent ice shelf that produces aphotic conditions. The characteristics of the Antarctic ice shelf are discussed in Folio 2 of this series (Bentley *et al.*, 1964). The Ross Ice Shelf, studied by Littlepage and Pearse (1962), ranges from 5 m thick at its margin to 70 m thick inland. It is possible that benthic plants might grow in ice shelf regions where thin ice, crevasses, or systems of cracks permit the penetration of adequate amounts of light (Zaneveld, 1966a).

A comparison of the Enderby Land collections discussed by Skottsberg (1953), the recent Adélie Coast studies of Delépine and Hureau (1963), and the collections made in the Antarctic Peninsula region (Neushul, 1965; Delépine, 1966; Delépine, Lamb, and Zimmermann, 1966) would seem to indicate that the floras of these regions are similar. Collections from all the regions were made largely at 60°S to 70°S.

In contrast to the apparent similarity of floras from the same latitudes are the variations that may occur as one proceeds southward along north-south coasts free of shelf ice such as the west coast of the Antarctic Peninsula and the coast of northern Victoria Land. The southernmost algal collection from the Antarctic Peninsula (Llaña, 1948) includes *Desmarestia menziesii* and *Adenocystis utricularis*, but is not complete enough to permit speculation on floristic modifications that might be associated with

latitude in this area. There is, however, suggestive evidence that the algal flora of the Victoria Land coast becomes more depauperate as one proceeds southward (Littlepage and Pearse, personal communication; Zaneveld, pp. 10–12, this folio), where *Iridaea obovata*, smaller red algae, and benthic diatoms predominate.

Vertical distribution patterns (Figure 1) were roughly described by Neushul (1965). Delépine and Hureau (1963), Delépine (1966), Delépine, Lamb, and Zimmermann (1966), Zaneveld (1966b) and Zaneveld (Plate 13 of this folio), also provide information on vertical distribution. These studies are in the 60°S to 70°S region. No one has yet described the plant communities found growing at lower photic-zone levels in any Antarctic region. Indeed it would seem at present that the limits of the photic zone will be difficult to define for several reasons. The abrasive action of ice and the anchor-ice rafting of rocks with attached vegetation most certainly transport plant material into deep water (Neushul, 1965). Plants capable of withstanding periods of darkness can undoubtedly survive for some time after being transported into deeper water. It has been suggested that some deep water plants are heterotrophic, although there is not yet any unequivocal evidence of this mode of nutrition in larger benthic algae.

The absence of a significantly diverse land flora in the Antarctic is frequently mentioned. In striking contrast, the surrounding waters contain large and spectacular submarine forests of brown and red algae which have only begun to be explored. As indicated above, there are many fascinating distributional and ecological problems to be solved in the study of the unique benthic marine flora of this most unique of continents.

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—M. Neushul

Benthic Marine Algae, Ross Island to Balleny Islands

INTRODUCTION

Field observations carried out along the coasts of Ross Island and Victoria Land, Antarctica (43,44,45) during the latter part of December 1963 and January and February 1964 revealed the presence of a widespread marine algal bottom vegetation at depths to 35 m. This vegetation was found from McMurdo station at 77°51'S, 166°39'E to Cape Hallett at 72°19'S, 170°13'E, near the entrance to the Ross Sea.

During the months of October, November, and December 1964, the same localities were checked again for the presence of algal beds. At this time of the year, most localities were covered by a 2-m to 6-m layer of shore-fast ice, extending 13 km to 37 km off the coast. Nowhere on the ice was the snow cover deeper than 5cm, and usually only traces were present. Even under these extreme conditions, a luxuriant sub-ice algal vegetation was observed (45). The collections, made by means of scuba diving down to 34 m, showed the presence of both adult and young specimens. The algae which were brought to the surface were fresh, they had their natural color and shape, and a number were fructifying.

At practically all localities visited, there were tidal cracks close to and parallel with the shore. In these cracks the ice is thinner, so this is where the Weddell seals often have breathing holes which they keep open

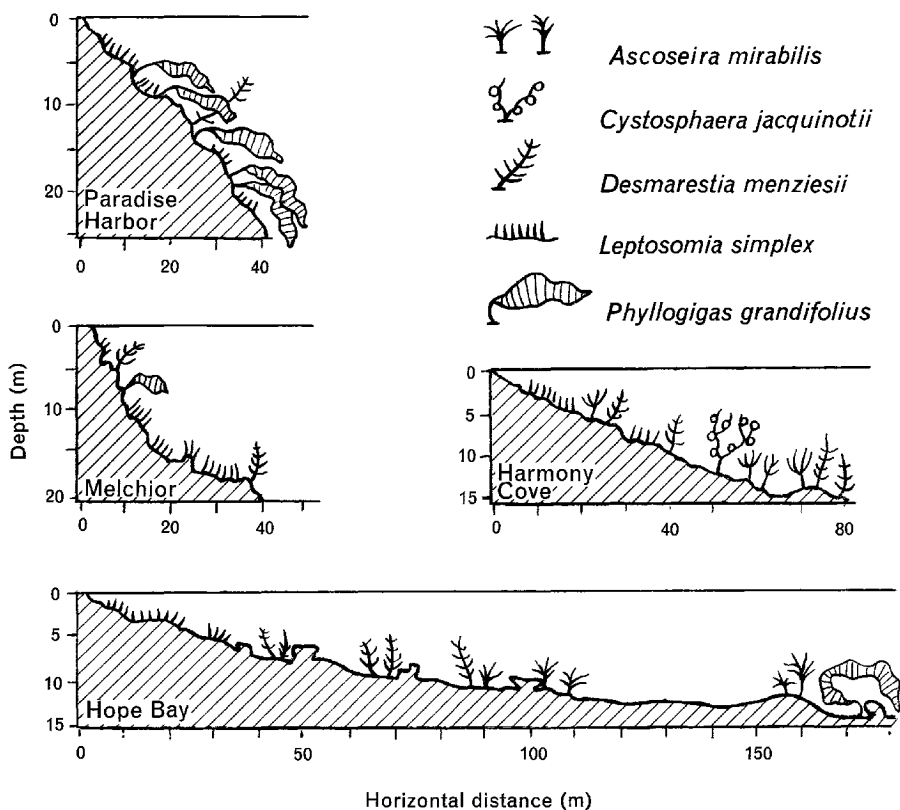


Fig. 1. Diagrammatic transects showing the vertical distribution of five common species of benthic marine algae at four locations in the Antarctic Peninsula.

continuously. When they were enlarged with an ice-axe and the slush was removed, these holes proved to be ideal entrances into the water for scuba diving under the ice. No problem was encountered by the presence of seals; they approached the divers out of curiosity, but never really bothered them. The thickness of the ice in the holes used was only 2 m so that leaving the water at high tide was possible, although somewhat difficult. At low tide, the ice wall of the hole above water level was as much as 1.5 m to 2 m, making it impossible to leave the water. As a result, diving was done only at high tide; tides in the western part of the Ross Sea are predominantly diurnal in character. The water salinity varies from 30‰ to 34‰ and the surface water temperature ranges from 0°C to -1.9°C.

During the period discussed, a total of 116 dives were made by Willard I. Simmonds, James M. Curtis, and Jack K. Fletcher; the dives lasted from 1 minute at a depth of 30 m to 21 minutes at depths less than 8 m.

From January 10 to March 4, 1965, while on board the icebreaker USCGC *Glacier*, we studied the occurrence of benthic algae around the islands in the western part of the Ross Sea, in Robertson Bay, around and on the Balleny Islands, and around and on Macquarie Island. Since Macquarie Island is located at 54°29'S, 158°58'E, just north of the Antarctic Convergence, the results of our algal studies around this island are not included here. Collections were made by means of scuba diving to a depth of 34 m and, from the ship, by conventional oceanographic equipment—grabs, dredges, and trawls—at depths to 729 m. While the divers were operating collection equipment, depths were recorded by the ship's sonar depth finder. Collections made during this period again showed a luxuriant growth, especially of red and brown algae. A number of specimens were still attached to their substratum, and they were often fructifying; therefore, growth at the collection depths cannot be disputed. Details regarding the type of collecting equipment used and the structure of the bottom at the localities visited are given in the table on Plate 13.

Subsequent investigations were carried out by the author during the austral winter of 1967. The sub-ice collections made during this period of total darkness showed the growth of two species of benthic Rhodophyta near Hut Point at 77°51'S, 166°38'E. The scuba divers, students L. L. Nero and D. M. Bresnahan, each used a 1000-watt, 115-volt AC light of 65,000 candle power (centerbeam). This light was found to be excellent for use under ice at this time of year. The duration of the dives was from 38 to 10 minutes at depths of 7 m and 36 m respectively. All specimens collected were fresh and some were fructifying, indicating that at least certain algal species can tolerate the extreme conditions of this biotope throughout the year. The two species of Rhodophyta collected were *Phyllophora antarctica* A. and E. S. Gepp and *Iridaea obovata* Kützinger. Several crustaceous and corallineous algae were also collected; identifications of these algae have not yet been made.

HORIZONTAL DISTRIBUTION

The horizontal distribution of the dominant species of algae collected are shown on Plate 13. Just outside the Ross Sea, in Robertson Bay, there are 11 species of algae. Inside the Ross Sea the number of species decreases as one proceeds southward. Around the Possession Islands there are also 11 species; south of Depot Island there are 7 species. Around Ross Island and as far south as 77°51'S, 166°40'E there are 4 dominant species, 1 belonging to the Chlorophyta (*Monostroma harti*) and 3 to the Rhodophyta (*Hildenbrandia lecanellieri*, *Phyllophora antarctica*, and *Iridaea obovata*).

It is interesting to note that the first macroscopic alga collected in the Ross Sea was *Iridaea obovata*. The fructifying specimen was collected on the ice between Black Island and White Island in 1902 during Scott's first Antarctic expedition.

Outside the Ross Sea, around the Balleny Islands, between 66°25'S and 67°24'S, 162°E and 165°E, again 11 attached algal species were collected. This island group is located south of the Antarctic Convergence, which forms a natural phycogeographical barrier. North of this Convergence, large brown algae such as *Macrocystis pyrifera* and *Durvillea* species are common; south of the Convergence, in the area investigated, there is only one giant species, *Phyllogigas grandifolius*.

Besides the green alga *Monostroma harti*, the Rhodophyta are best adapted to the waters of the Ross Sea. Without further *in situ* observations and laboratory cultures, it is difficult to say whether this is due to a greater tolerance of the constantly low temperature, the change in quantity and quality of light energy, the more severe ice conditions, the change in salinity, or a combination of two or more of these factors.

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The vertical distribution of the dominant algae occurring in the area under consideration is represented in Figure 1. The regions which can be distinguished are as follows:

- (1) Epilittoral (or supralittoral) region, above mean extreme high-water spring tide. Only two species are characteristic of

this region: *Ulothrix australis* Gain and *Prasiola crispa* (Lightf.) Menegh. spp. *antarctica* (Kütz.) Knebel f. *antarctica* Knebel. In order to survive in summer, these algae must be terrestrially adapted and must possess tolerances against low temperature, desiccation, and intensive radiant energy.

- (2) Littoral (or mediolittoral) region, between the mean extremes of high- and low-water spring tides. Both tide levels are characterized by a brown, diatomaceous layer. This region is destitute of algae because of the severe ice conditions.

- (3) Sublittoral (or infralittoral) region, between mean extreme low-water spring tide and a depth of 37 m. Within the sublittoral region two belts can be recognized:

(a) An upper belt reaching a depth of 10 m, which could best be named the sublittoral fringe. Algal growth is abundant here even under shore-fast ice 2 m to 3 m thick (45). The dominant species are *Monostroma harti* Gain, *Hildenbrandia lecanellieri* Hariot, *Phyllophora antarctica* A. and E. S. Gepp, and *Iridaea obovata* Kütz. *I. obovata* often grows in beds several kilometers long.

(b) A lower belt extending from 10 m to 37 m in depth. The dominant species growing in this belt can be seen in the maps of Plate 13. Some of these species have not been found south of 73°S (Table of Plate 13). The distribution in this belt is mainly controlled by light intensity and wave length.

- (4) Elittoral (or circalittoral) region, from 37 m down to the limit of attached macroscopic algal growth. The lower limit in the Ross Sea seems to be at a depth of 668 m. There is one species, *Ballia callitricha* (C. Ag.) Kütz., with an upper limit deeper than 37 m. This can be considered a true or steno-elittoral species. The main limiting factors in this region are light quantity and quality. Hydrostatic pressure could also be of importance since it might affect algal metabolism.

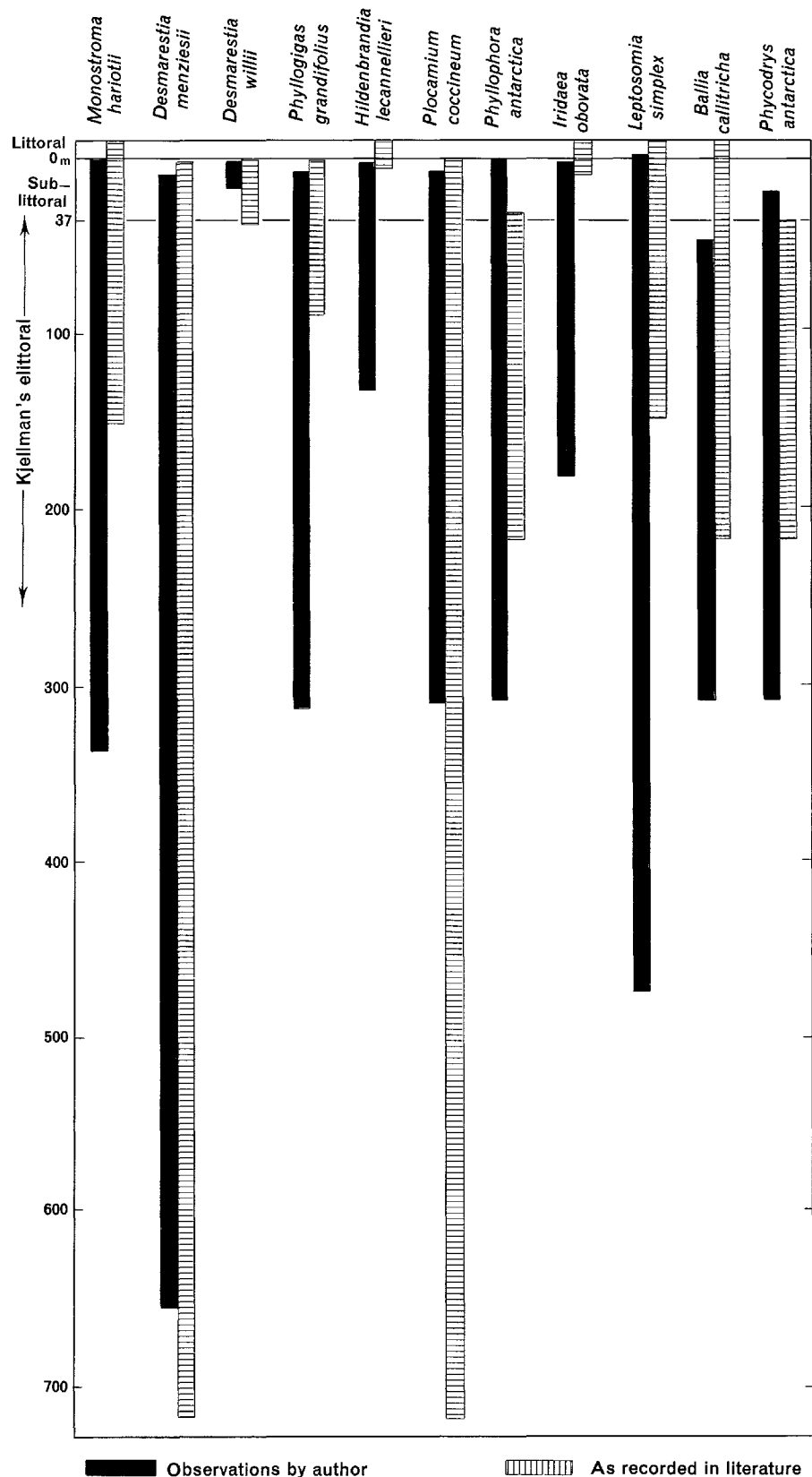


Fig. 1. Vertical distribution of the dominant species of benthic marine algae in the western part of the Ross Sea and around the Balleny Islands.

continuously. When they were enlarged with an ice-axe and the slush was removed, these holes proved to be ideal entrances into the water for scuba diving under the ice. No problem was encountered by the presence of seals; they approached the divers out of curiosity, but never really bothered them. The thickness of the ice in the holes used was only 2 m so that leaving the water at high tide was possible, although somewhat difficult. At low tide, the ice wall of the hole above water level was as much as 1.5 m to 2 m, making it impossible to leave the water. As a result, diving was done only at high tide; tides in the western part of the Ross Sea are predominantly diurnal in character. The water salinity varies from 30‰ to 34‰ and the surface water temperature ranges from 0°C to -1.9°C.

During the period discussed, a total of 116 dives were made by Willard I. Simmonds, James M. Curtis, and Jack K. Fletcher; the dives lasted from 1 minute at a depth of 30 m to 21 minutes at depths less than 8 m.

From January 10 to March 4, 1965, while on board the icebreaker USCGC *Glacier*, we studied the occurrence of benthic algae around the islands in the western part of the Ross Sea, in Robertson Bay, around and on the Balleny Islands, and around and on Macquarie Island. Since Macquarie Island is located at 54°29'S, 158°58'E, just north of the Antarctic Convergence, the results of our algal studies around this island are not included here. Collections were made by means of scuba diving to a depth of 34 m and, from the ship, by conventional oceanographic equipment—grabs, dredges, and trawls—at depths to 729 m. While the divers were operating collection equipment, depths were recorded by the ship's sonar depth finder. Collections made during this period again showed a luxuriant growth, especially of red and brown algae. A number of specimens were still attached to their substratum, and they were often fructifying; therefore, growth at the collection depths cannot be disputed. Details regarding the type of collecting equipment used and the structure of the bottom at the localities visited are given in the table on Plate 13.

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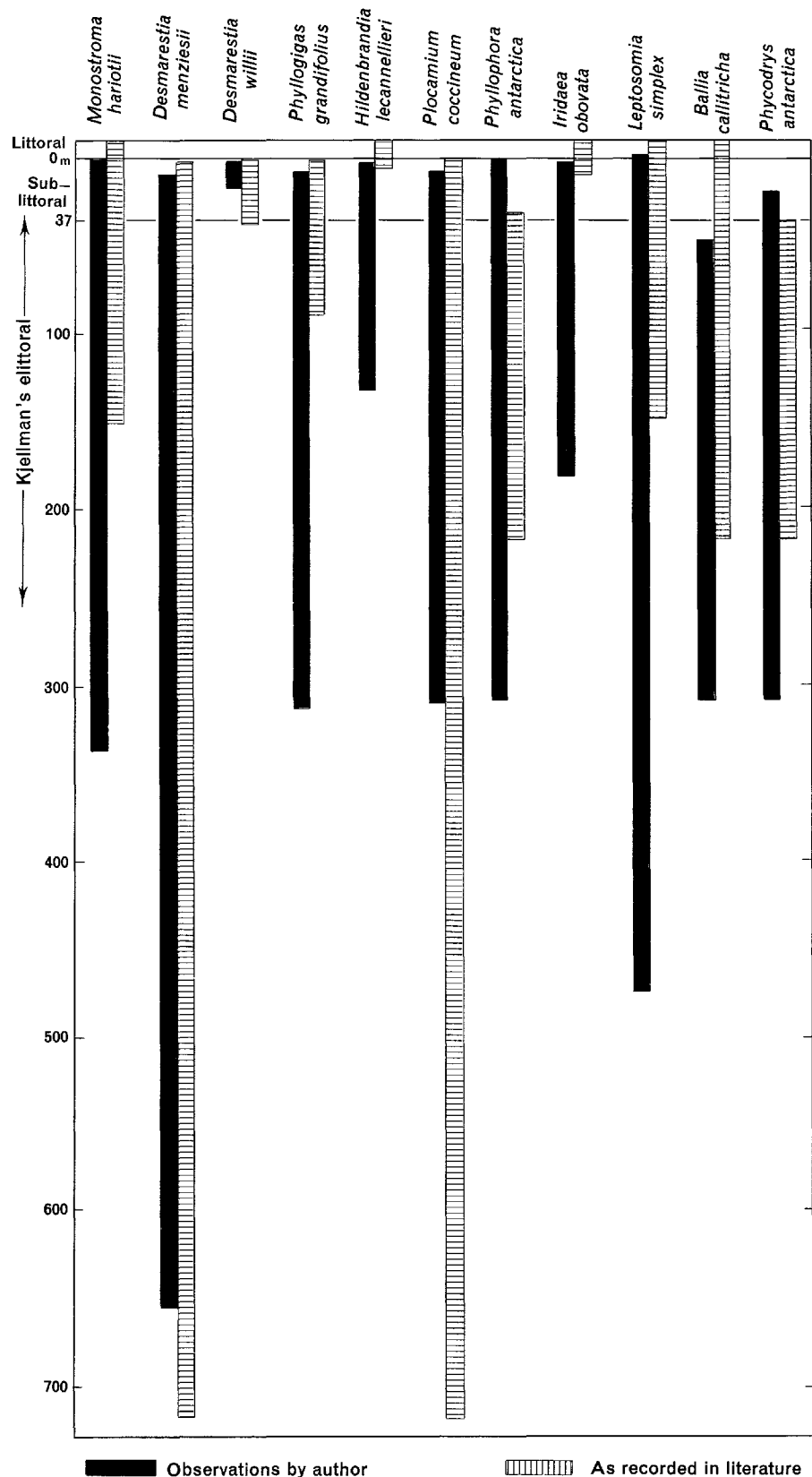


Fig. 1. Vertical distribution of the dominant species of benthic marine algae in the western part of the Ross Sea and around the Balleny Islands.

In checking the records of a number of former expeditions (references 9-27, 37-41, 46), I found that vertical distribution was reported for 353 species. Two hundred of these species (56.7%) are adapted to the shallow-water conditions of the littoral zone and to a depth of 10 m in the sublittoral region. For these species I propose the term 'steno-littoral.' The other 76 species occurring in these depths are eury-littoral. In the lower sublittoral region between 10 m and 37 m, there are 30 species (8.5%). These I shall call steno-sublittoral species. Below a depth of 37 m there are 23 species (6.6%); these are the steno-elittoral algae.

DISCUSSION

The term 'elittoral region' was introduced by Kjellman because of algal collections made with a dredge along the Murman Coast (25) and in the Skagerrak (26). Topographically, this region was defined by Kjellman as extending from the lower limits of the sublittoral region, that is, from 20 fathoms (36.58 m) downward as far as macroscopic algae will grow.

Since that time an increasing amount of benthic algae has been collected at great depths in many seas (2, 4, 5, 9, 10, 11, 12, 13, 31, 36, 37, 42, 45). Nevertheless, there have been several authors who did not recognize the existence of a separate elittoral algal flora (7, 23, 35, 40). Reasons for this skepticism were: (1) the lack of adequate depth measuring and recording devices; (2) the general acceptance of the theory that all deepwater algae had been transported by ice and subsequently deposited; (3) the absence of records of algae whose upper limit of growth was restricted to the lower limit of the rich sublittoral algal communities; (4) the belief that the low light intensity at such great depths would prevent photosynthesis.

During the present observations, particular attention was given to the problems listed above, for example:

(1) Special care was taken to obtain accurate depth records. While diving, depths were checked with a marked line and/or a calibrated Dacor wrist meter. On board the *Glacier* the ship's sonar depth finder was used.

(2) With regard to deepwater algal deposits, it cannot be denied that transport by ice might explain their presence at certain localities. My own observations, however, while camping along the coasts of Ross Island and Victoria Land, indicate that in many instances transportation by ice plays only a minor role in the distribution of bottom material over long distances. It was observed that the shape of a floating iceberg seldom remains the same for more than 24 hours during the austral summer. In the process of thawing, pieces drop off constantly from the circumference of the floating iceberg, thereby changing its center of gravity. The iceberg then turns partly over and other parts are exposed to the sun. Consequently, the attached bottom vegetation is returned to the sea floor much closer to the place from where it was picked up than has been suggested in the past.

(3) As mentioned above, during the field operations an abundance of macroscopic, deepwater algae was collected, much of which was still attached to its substratum. The majority of these algae were fresh, they had their natural color and shape, and they were often fructifying. All these factors strongly suggest that most of the algae collected were actively growing at the depths from which they were taken.

(4) Because deepwater algae were found growing so extensively, the reduced light intensity cannot be regarded as an important factor in limiting the growth depth of the algae in the clear seas of these high, southern latitudes. Laboratory studies by Brown and Richardson (5a) show that unicellular algae become increasingly independent of light intensity with an increase in the nutrient content of the growth environment.

Continuous 48-hour light intensity measurements by the author indicated an average scale reading of 53 μ amp in algal beds at a depth of 20 m, under a 6-m thick layer of ice. That is 1.39% of the incident light (45). These algal beds were found no farther than 3 km off shore in coastal regions, where the water is likely to be turbid. In the open sea, where the water is clear, light penetrates much deeper than in coastal regions; visibility measured in a horizontal direction in the open sea was often 90 m to 150 m.

Clarke (6) reports that daylight was detected at depths as great as 800 m in the Pacific and Indian Oceans. He also noted that luminescence is often produced in such high intensities that it must be of considerable ecological significance. Further discussion of the degree of penetration of light in oceanic depth is given by Clarke (6a).

It must not be overlooked that for a period of about eight months, temperature and light intensity are continuously very low. Low light

intensity, low temperature, and high hydrostatic pressure are known to reduce the rate of algal metabolism either directly or indirectly. According to Printz (33), respiration in algae is affected principally by decreasing temperatures. Consequently, there is an increase in the ratio of assimilation to respiration and hence an assimilation surplus. This might make survival of algae possible in the elittoral region during the austral winter period.

Bernard (3) and Kimball *et al.* (24) have recorded populations of photo-autotrophic micro-organisms at depths of 4000 m. They attribute the existence of these organisms to their adaptations to a heterotrophic mode of nutrition.

However, my own conclusion is that apart from the limitations imposed by the various substrates, the occurrence of elittoral macroscopic algae in the Antarctic does not need to be explained by an adaptation to a heterotrophic or mixotrophic physiology during a part of their life cycle.

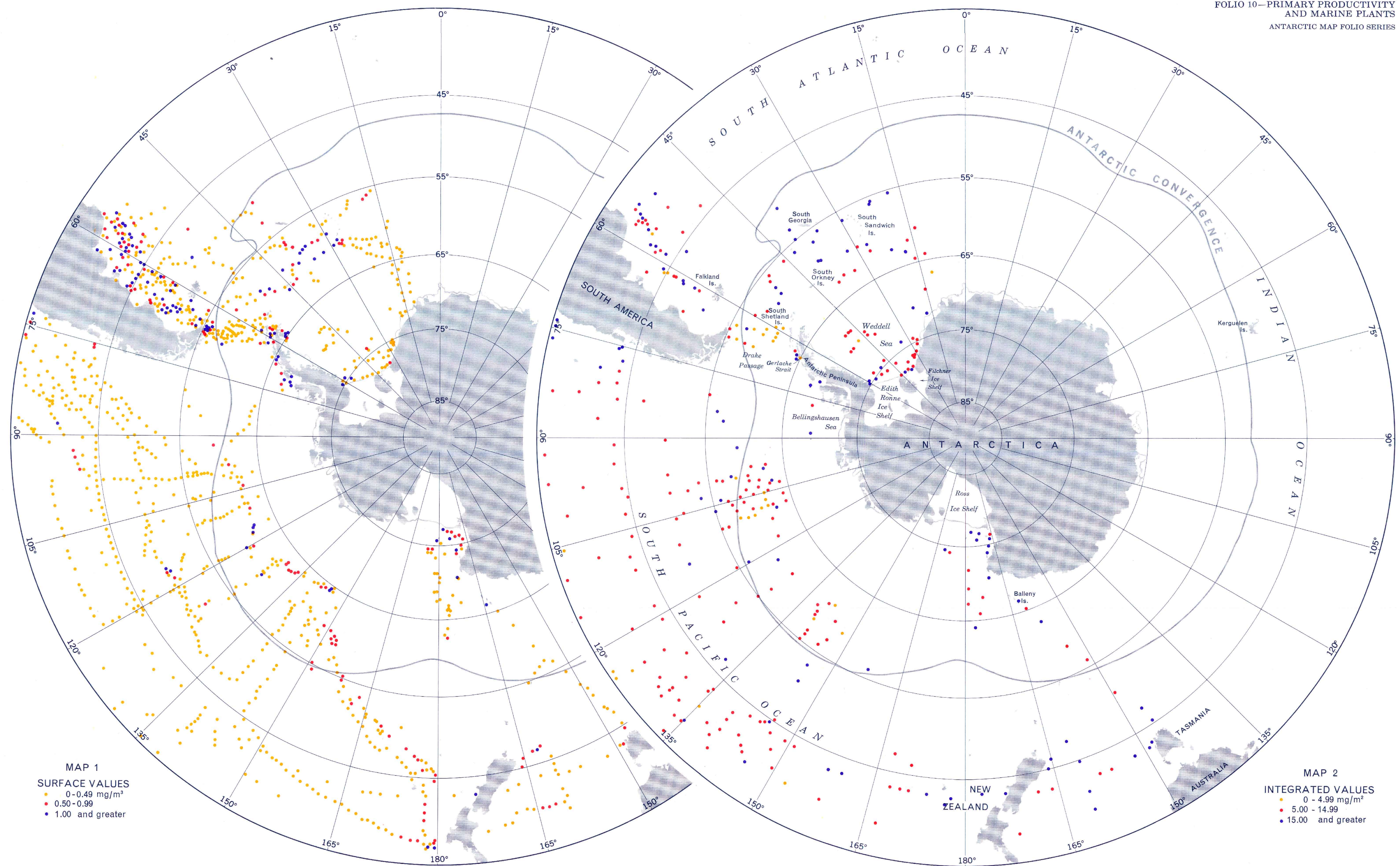
Acknowledgments. The author is indebted to his student, Miss Sarah C. Dickey, for the illustrations of the algae on Plate 13.

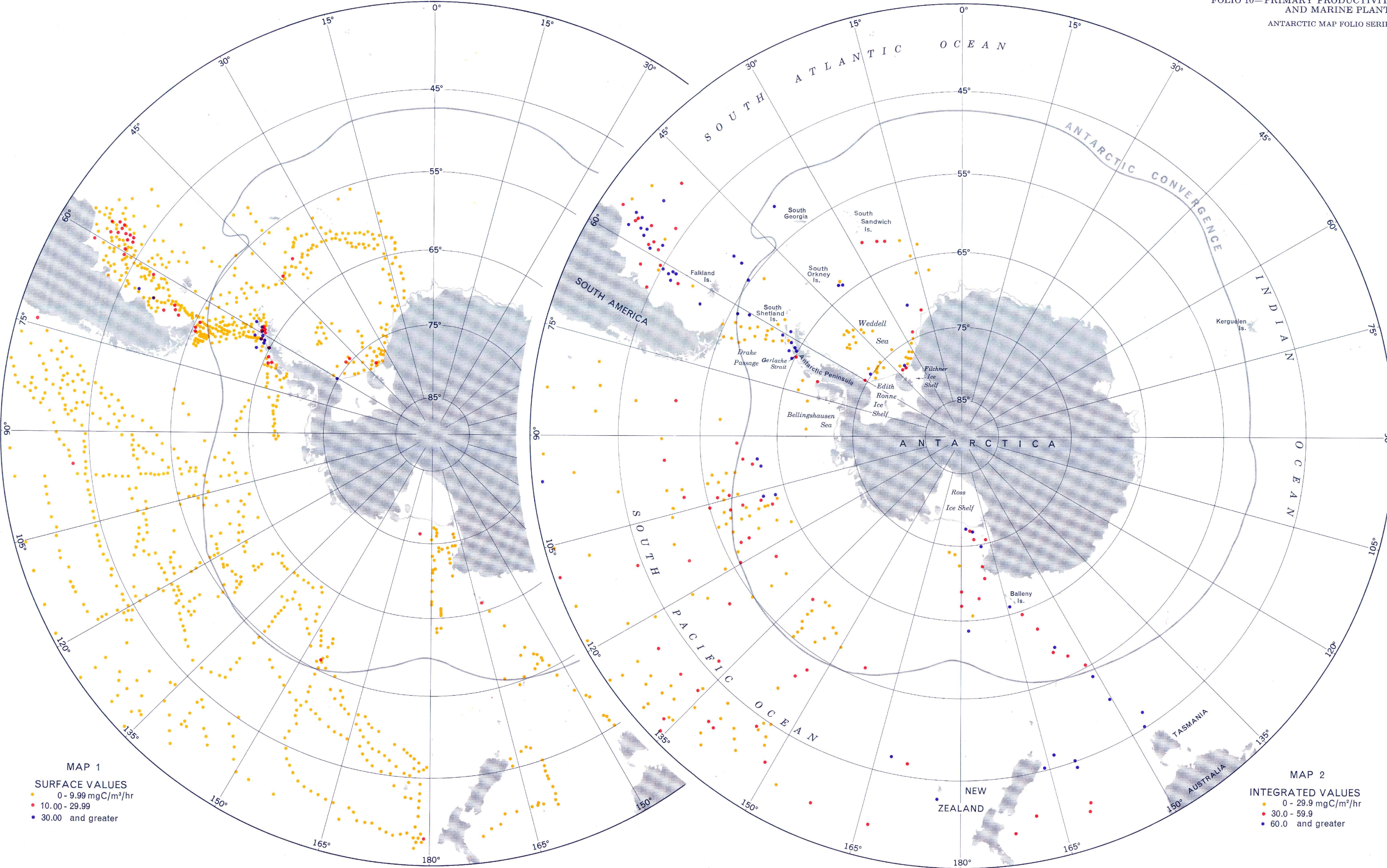
This study is part of an investigation of the benthic marine algae of the Ross Sea, which was supported by National Science Foundation grants.

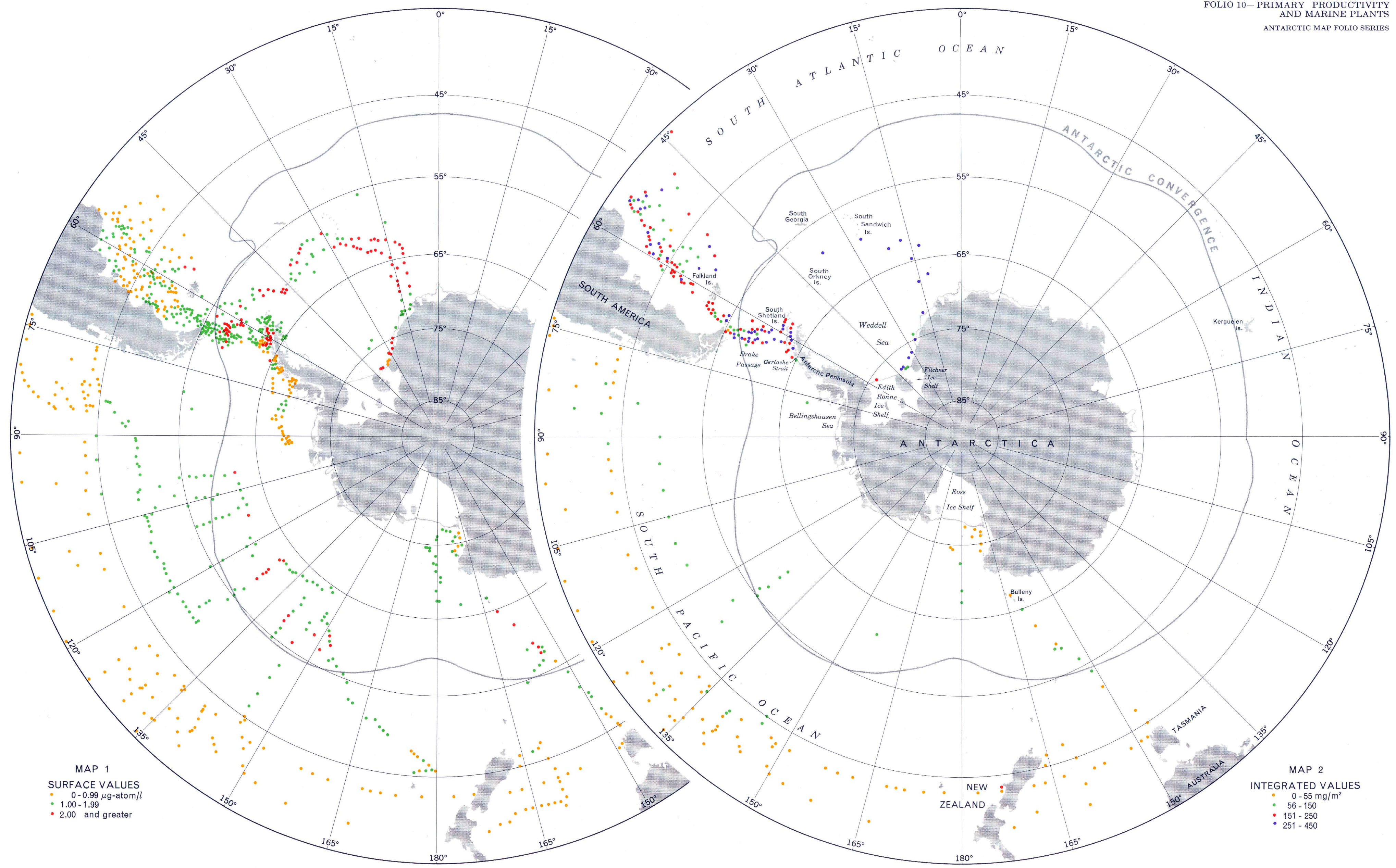
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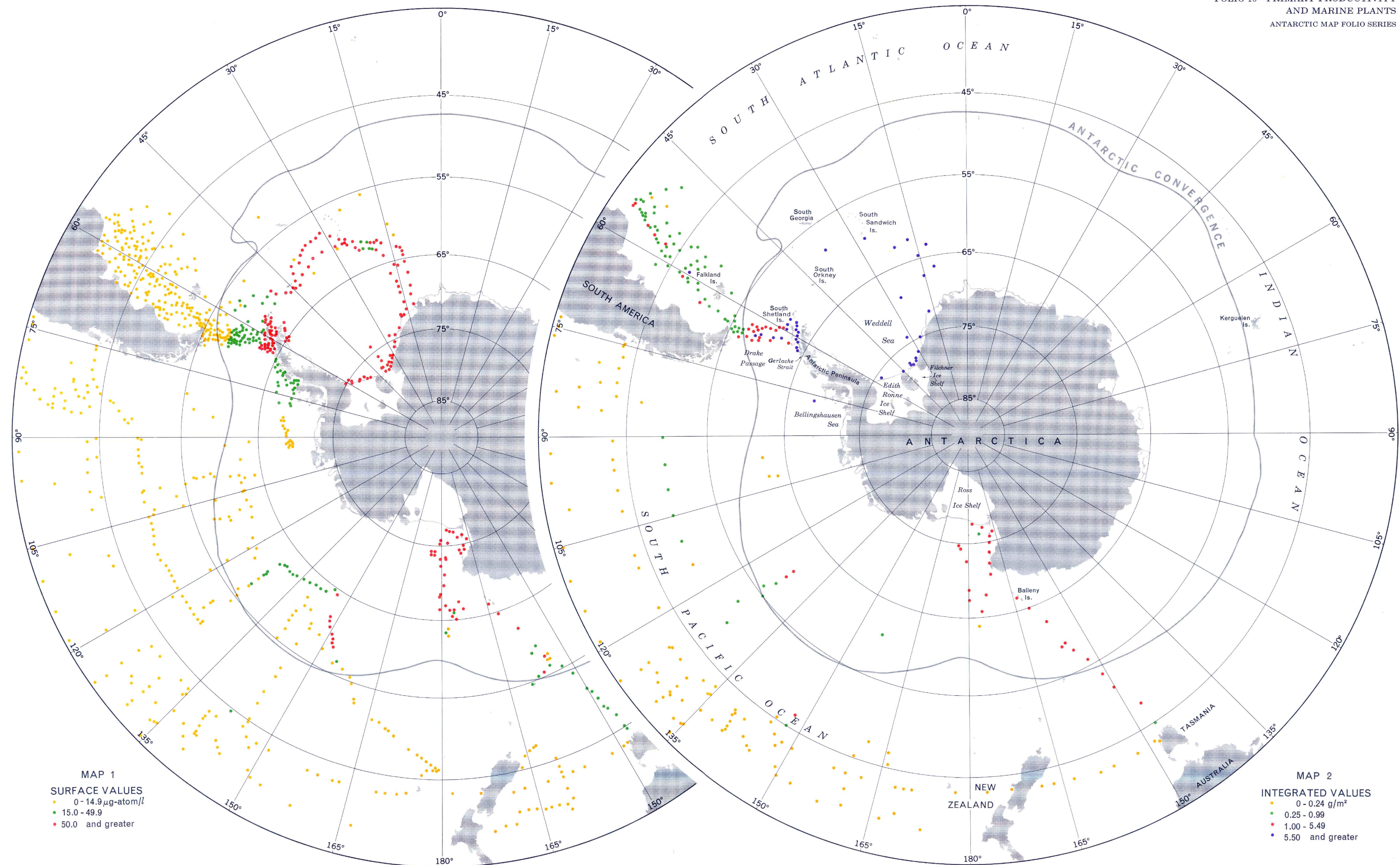
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—J. S. Zaneveld



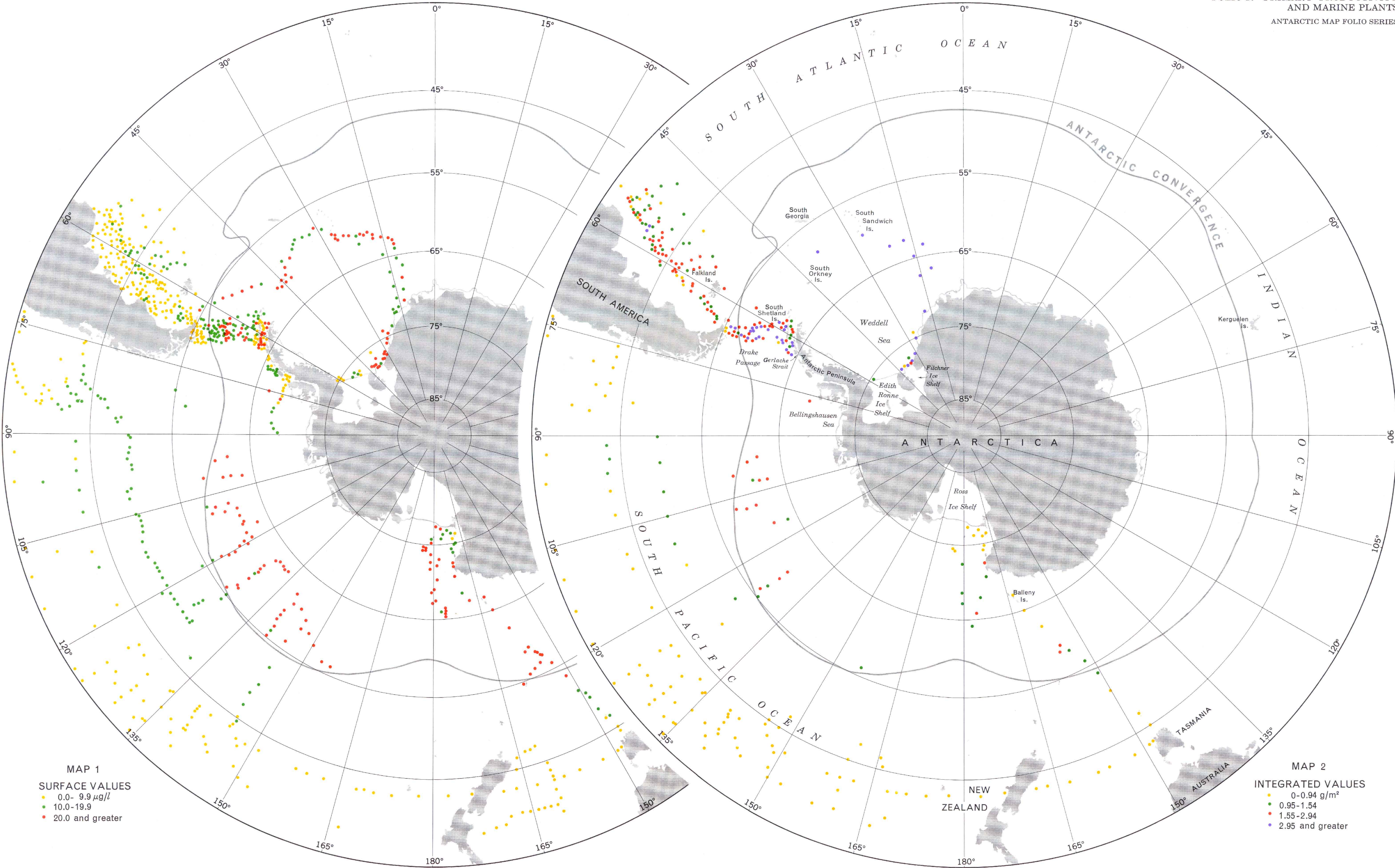


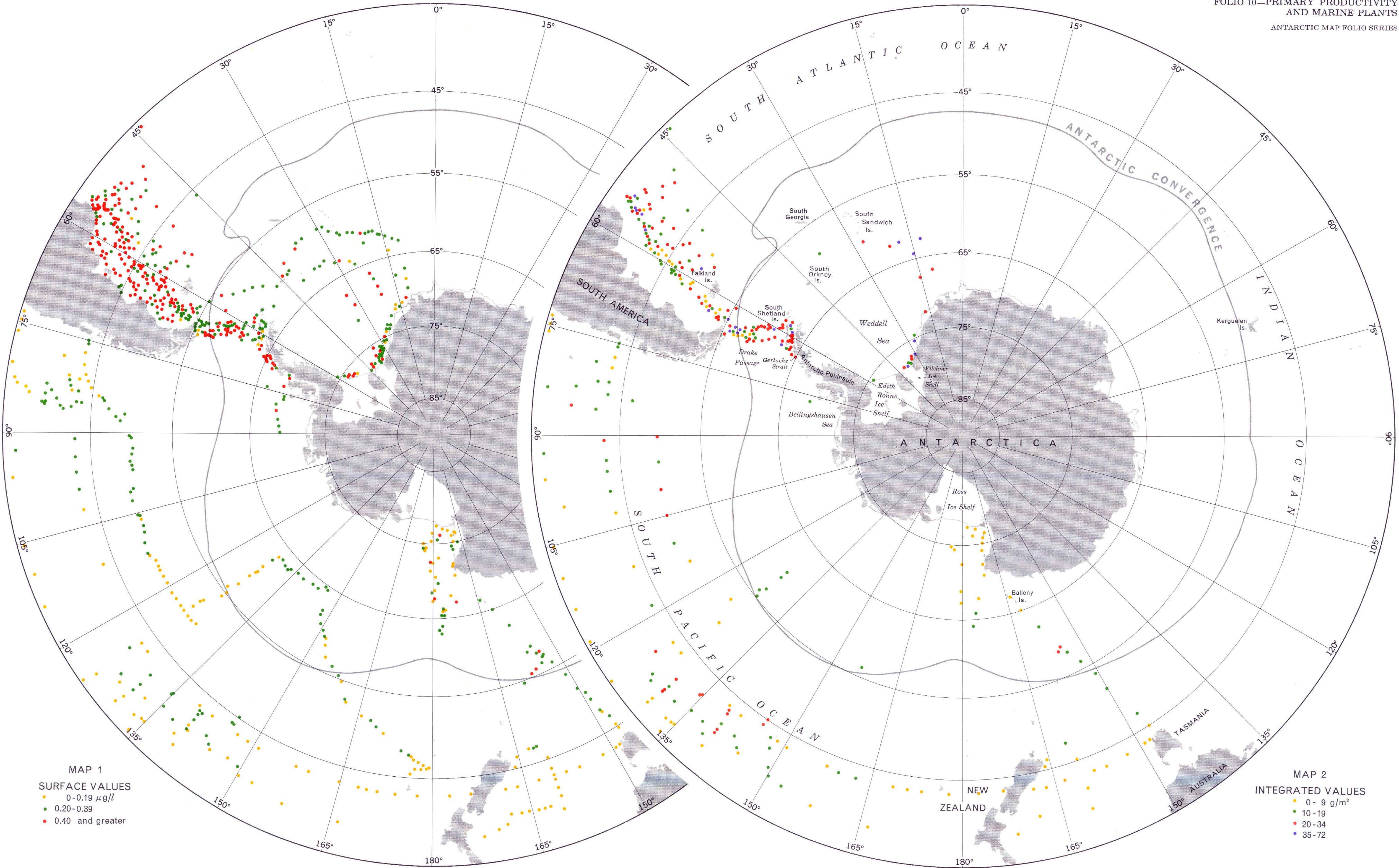


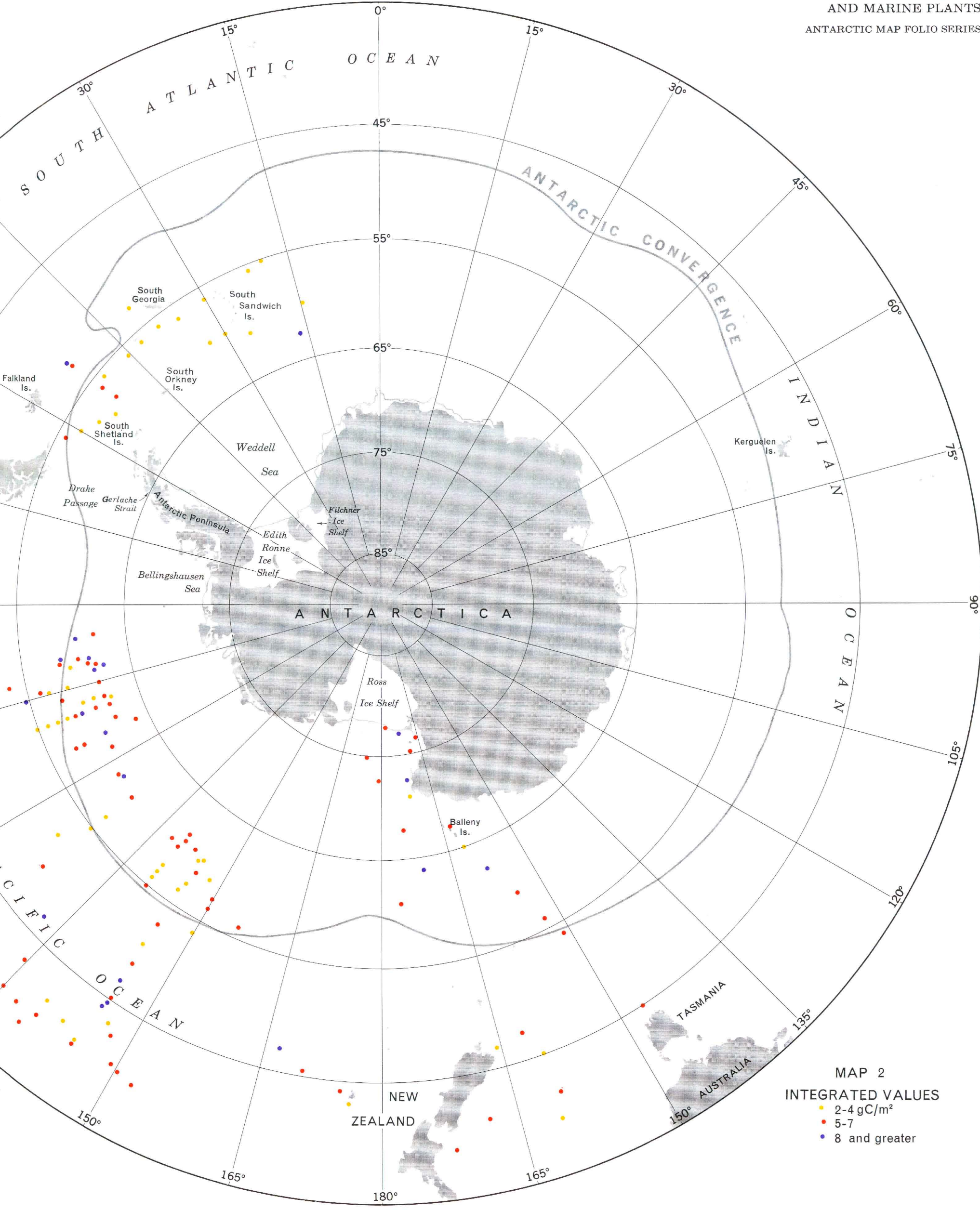
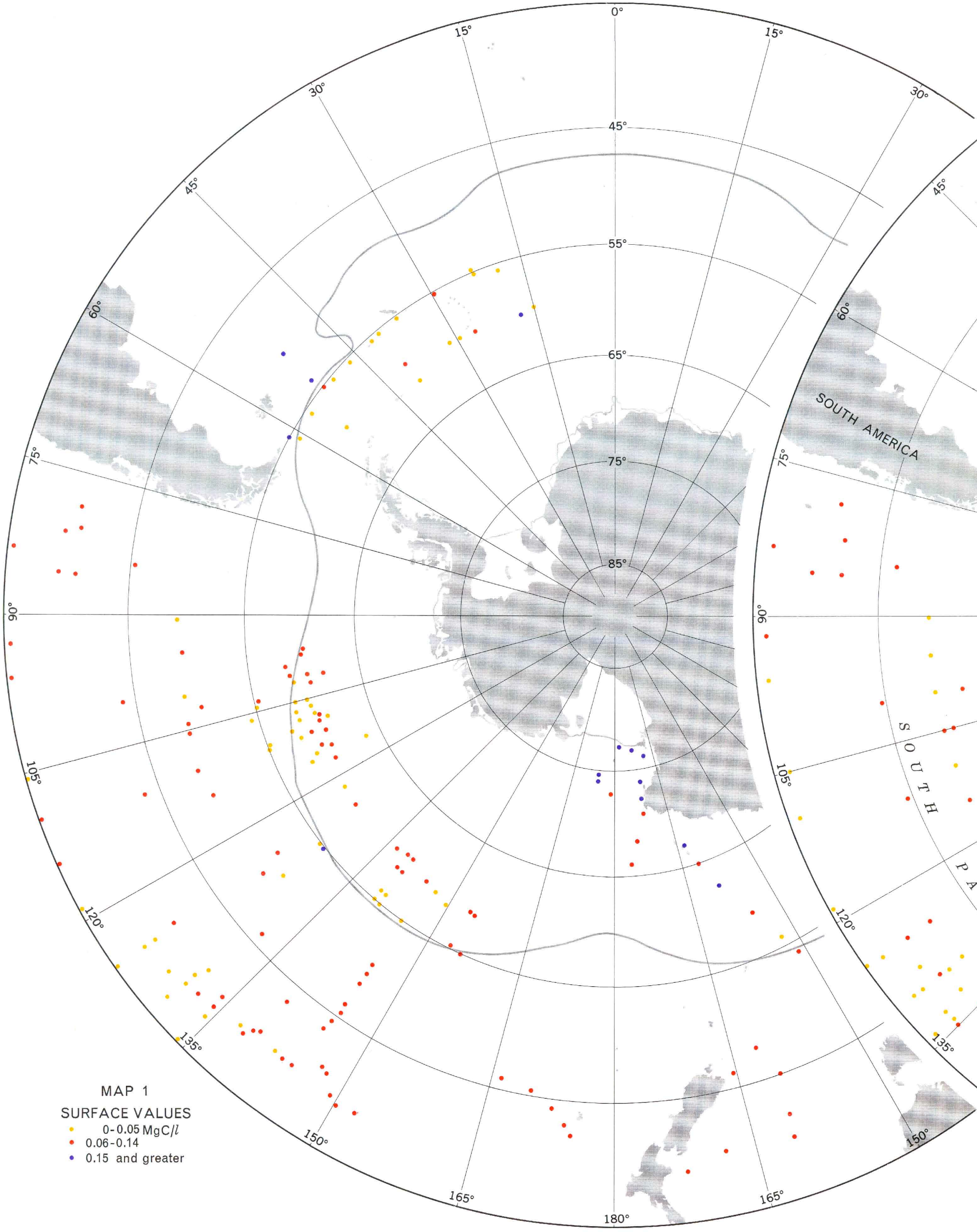


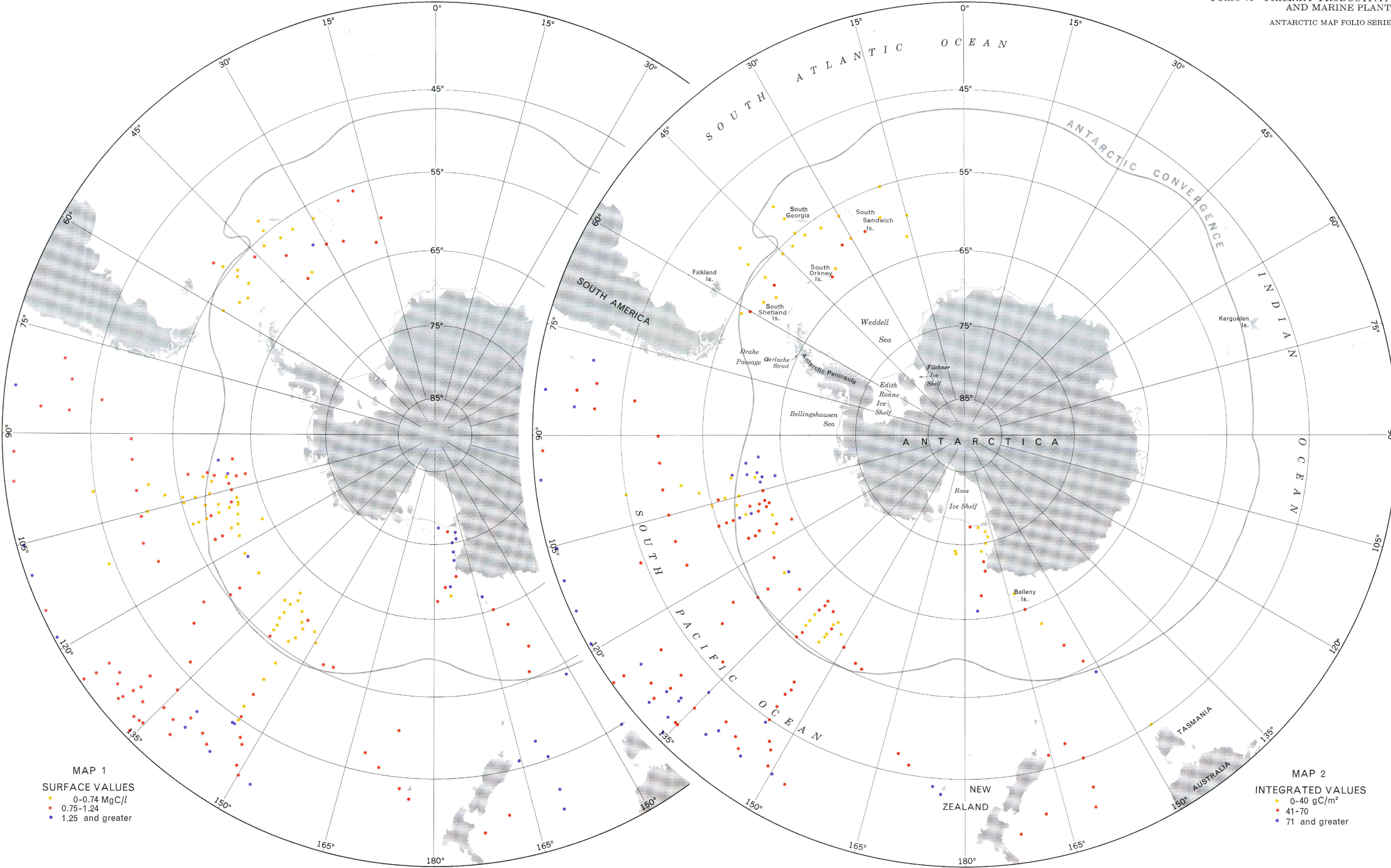
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SURFACE VALUES
● 0 - 14.9 µg-atom/l
● 15.0 - 49.9
● 50.0 and greater

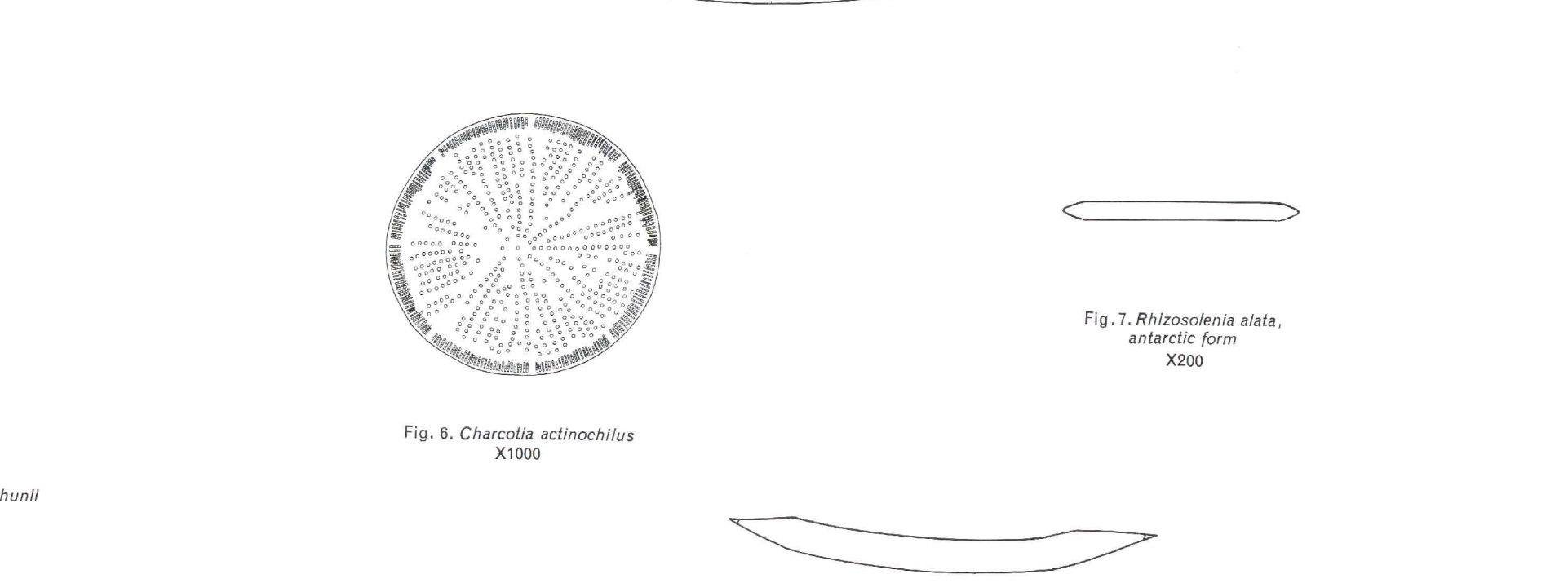
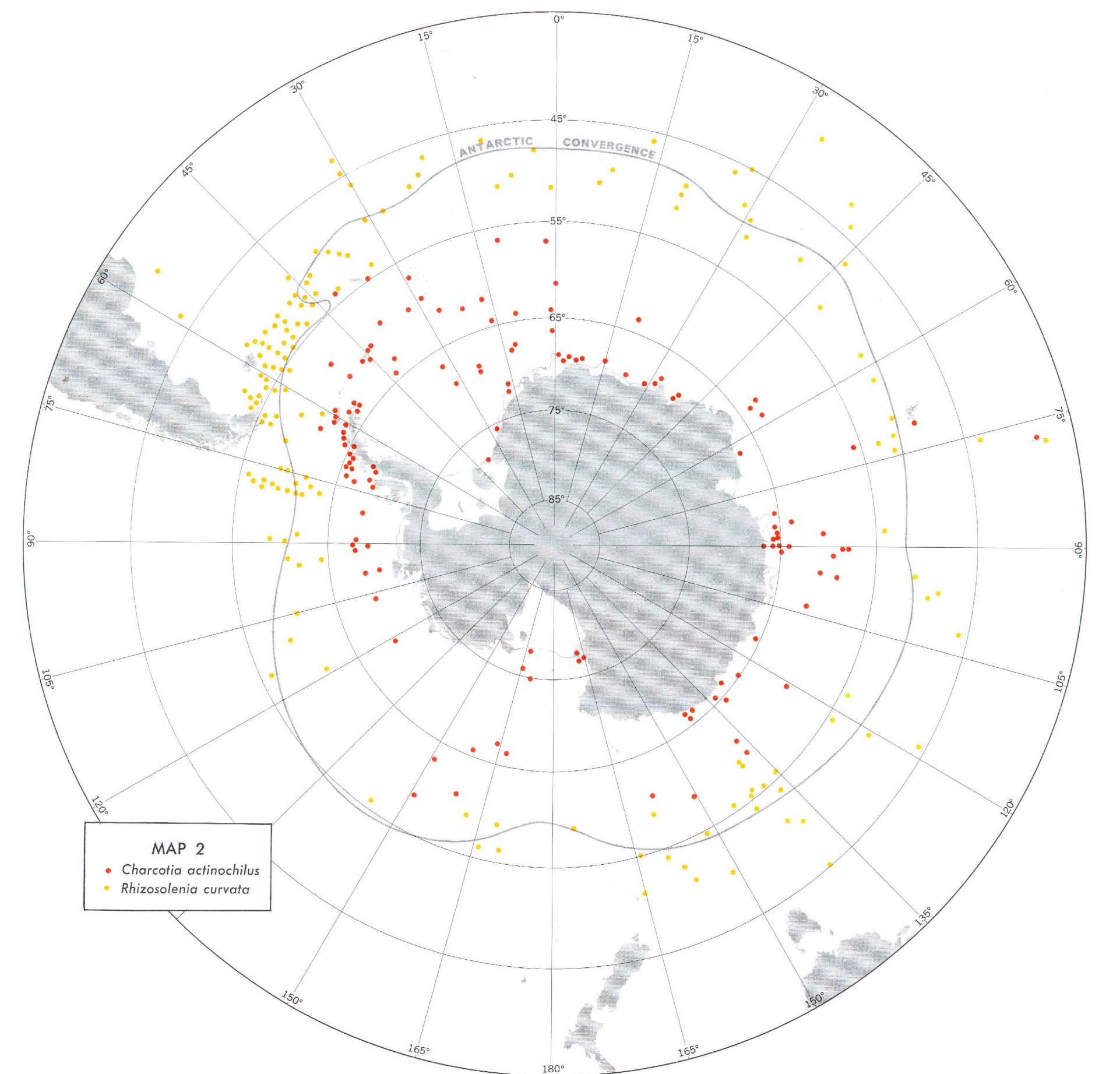
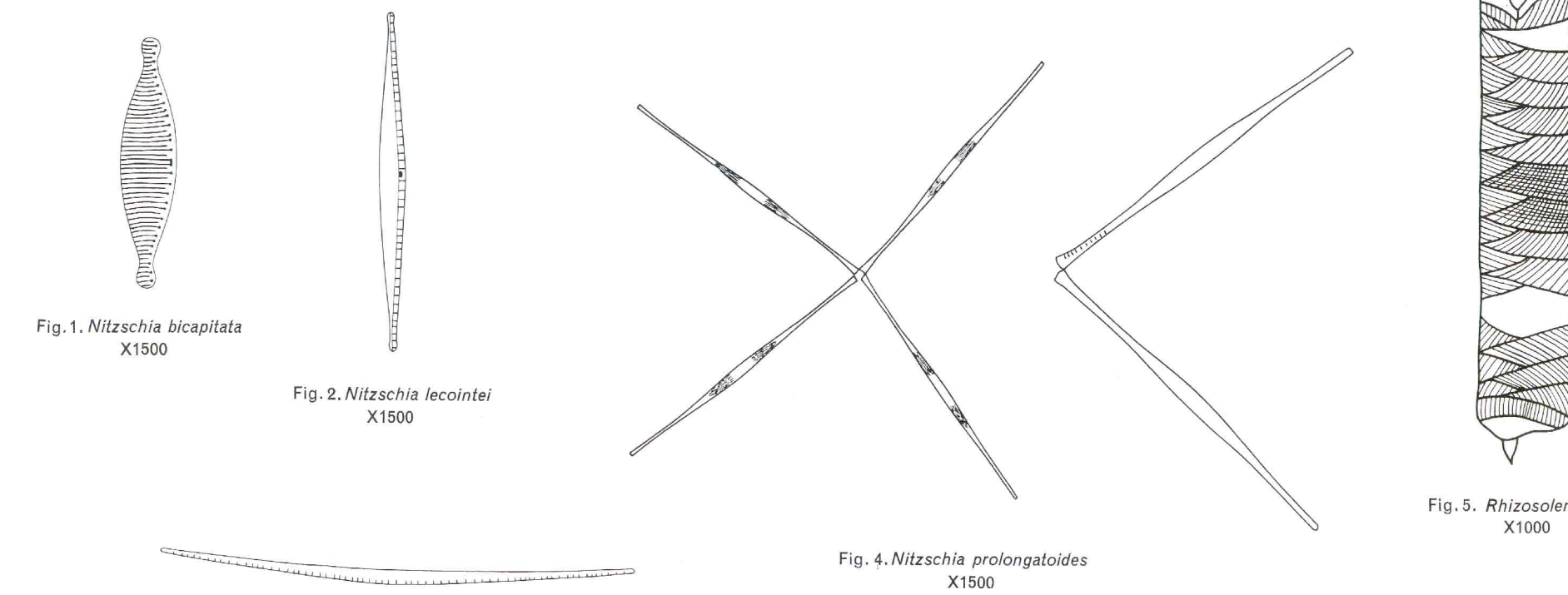
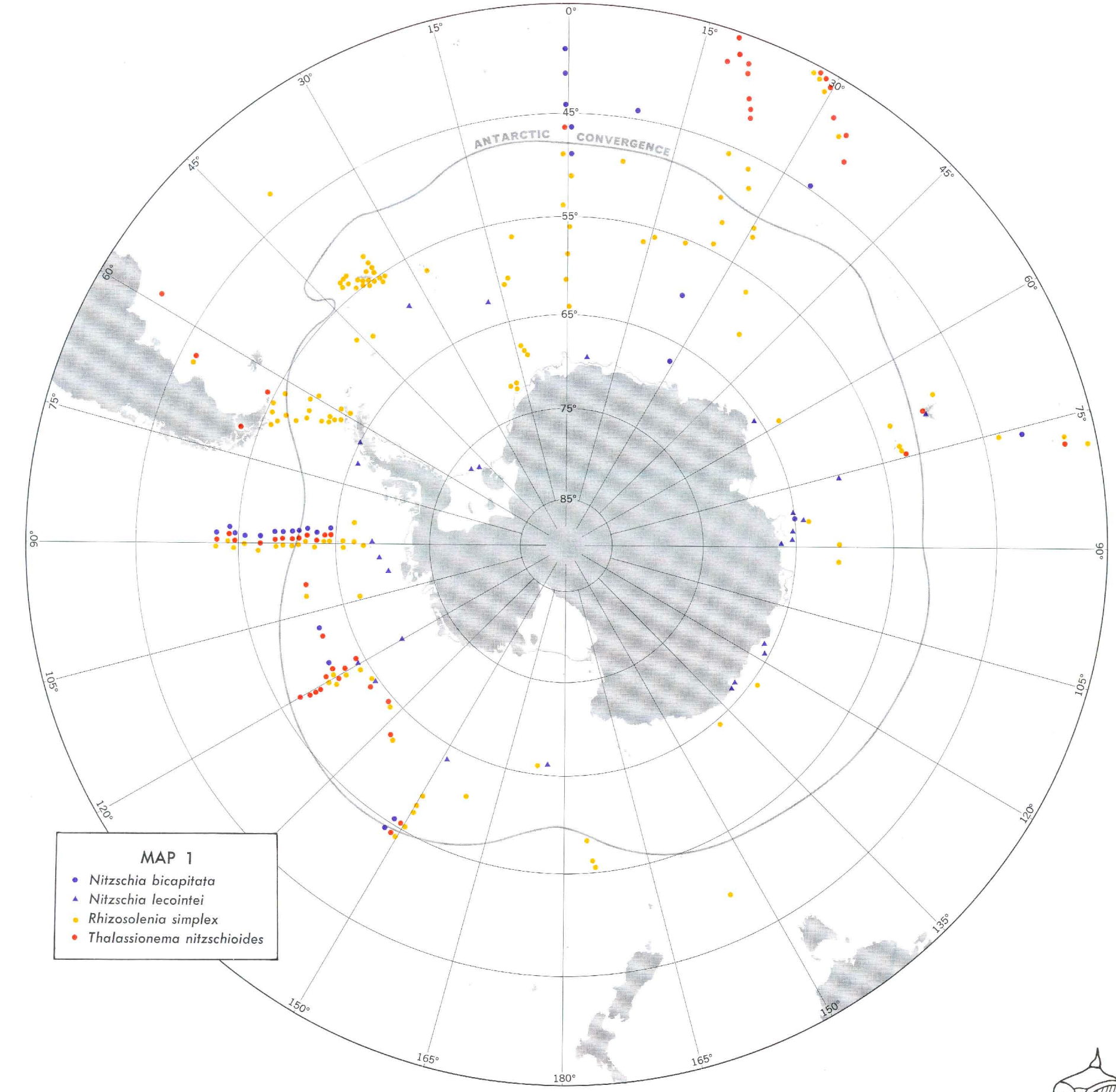
MAP 2
INTEGRATED VALUES
● 0 - 0.24 g/m²
● 0.25 - 0.99
● 1.00 - 5.49
● 5.50 and greater











Figures 1-3 are redrawn from original photomicrographs.
Figure 6 is from an original electron micrograph.
Figures 4, 5, 7, and 8 are original drawings made by camera lucida.

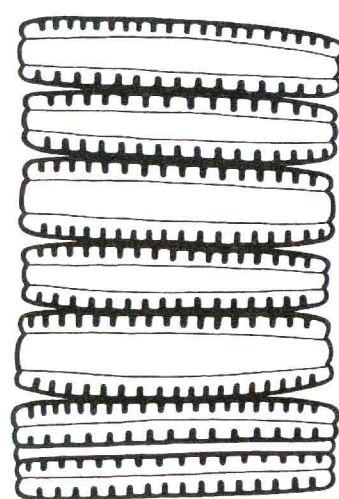
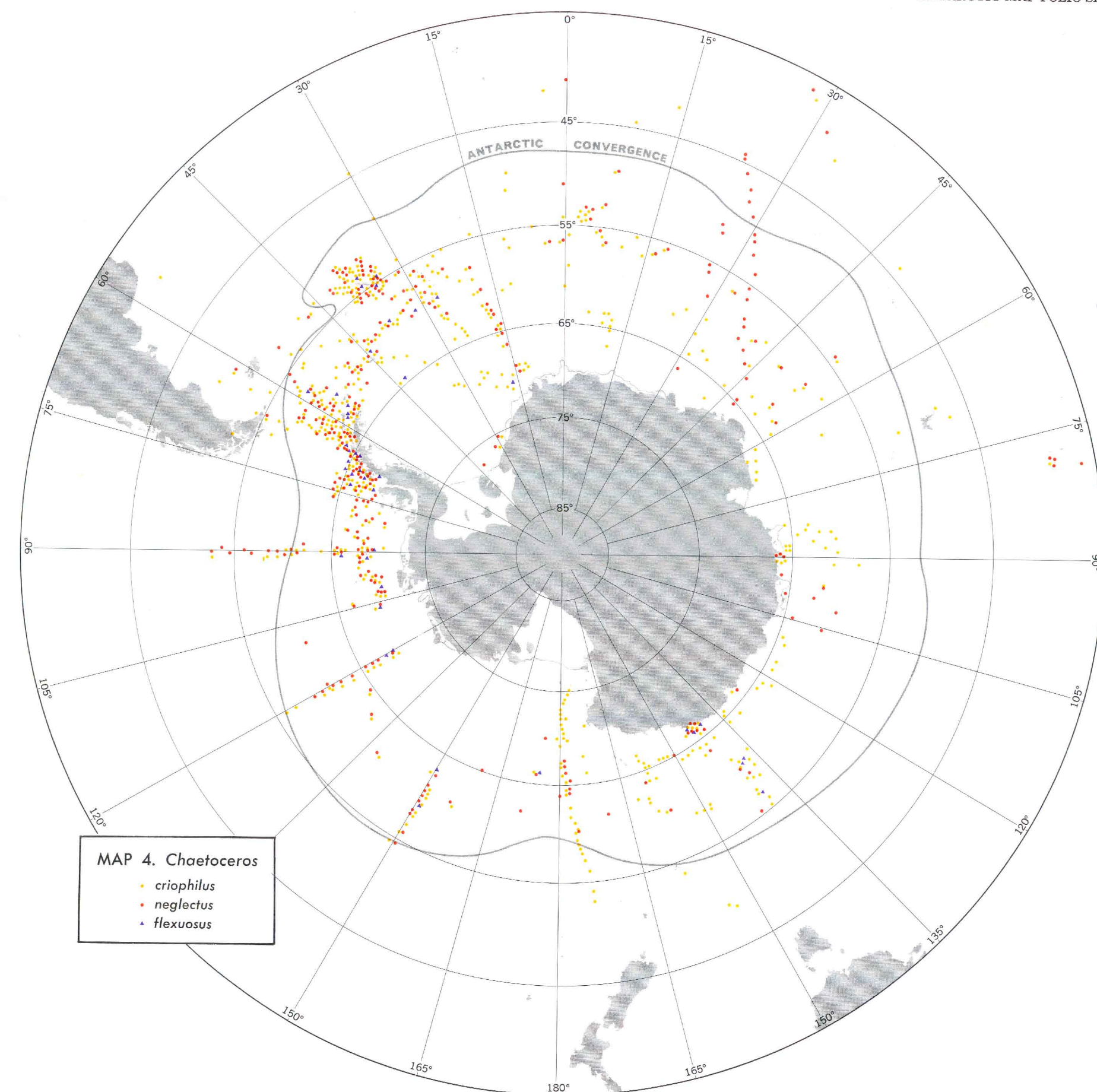
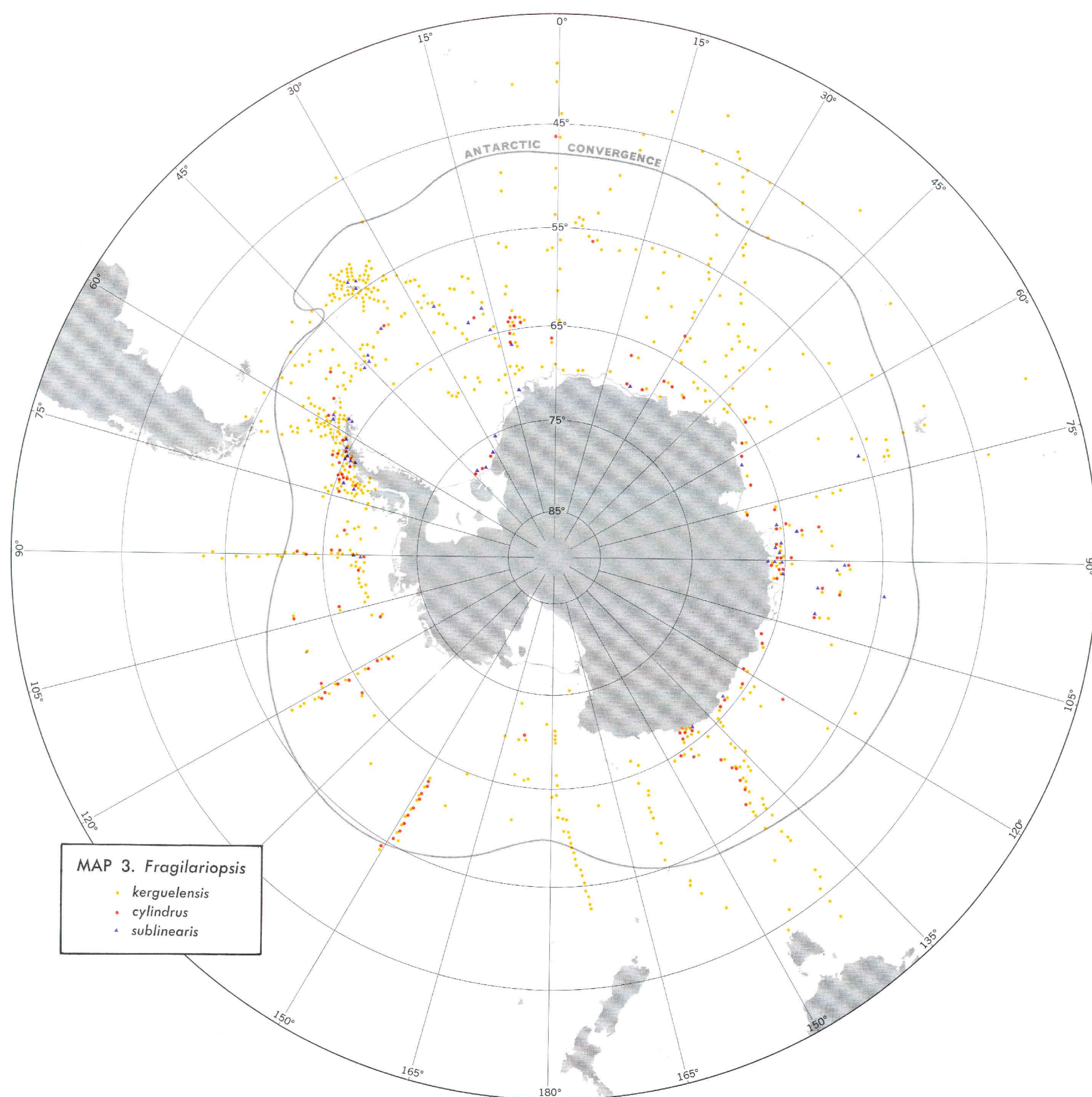


Fig. 9. *Fragilariopsis kerguelensis*
X1500



Fig. 10. *Fragilariopsis cylindrus*
X1500

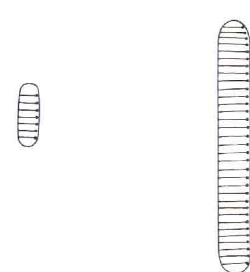


Fig. 11. *Fragilariopsis sublinearis*
X1500

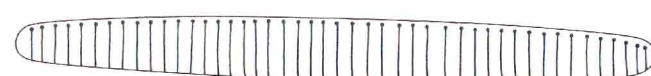


Fig. 12. *Chaetoceros criophilus*
X500

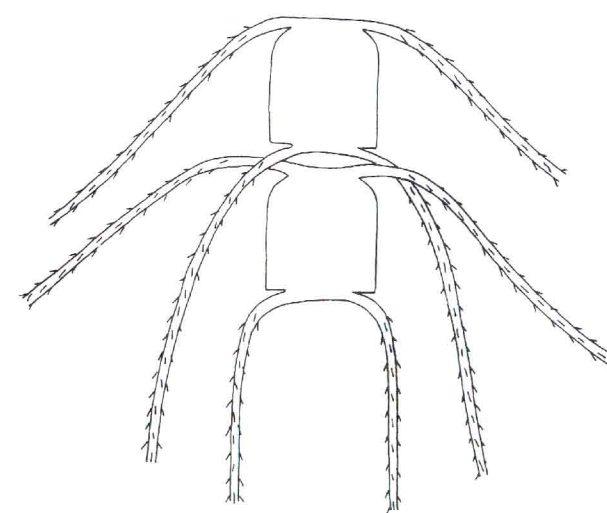


Fig. 13. *Chaetoceros neglectus*
X500

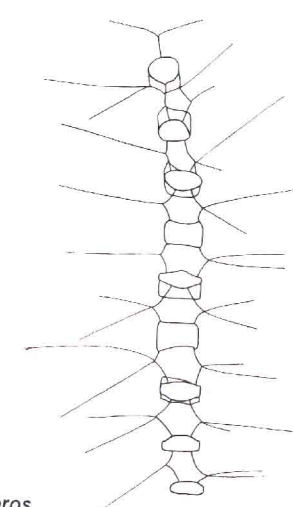


Fig. 14. *Chaetoceros flexuosus*
X500

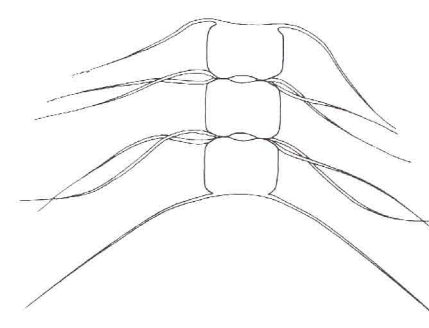
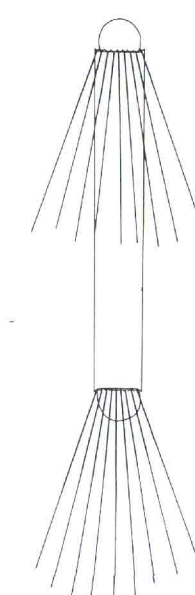
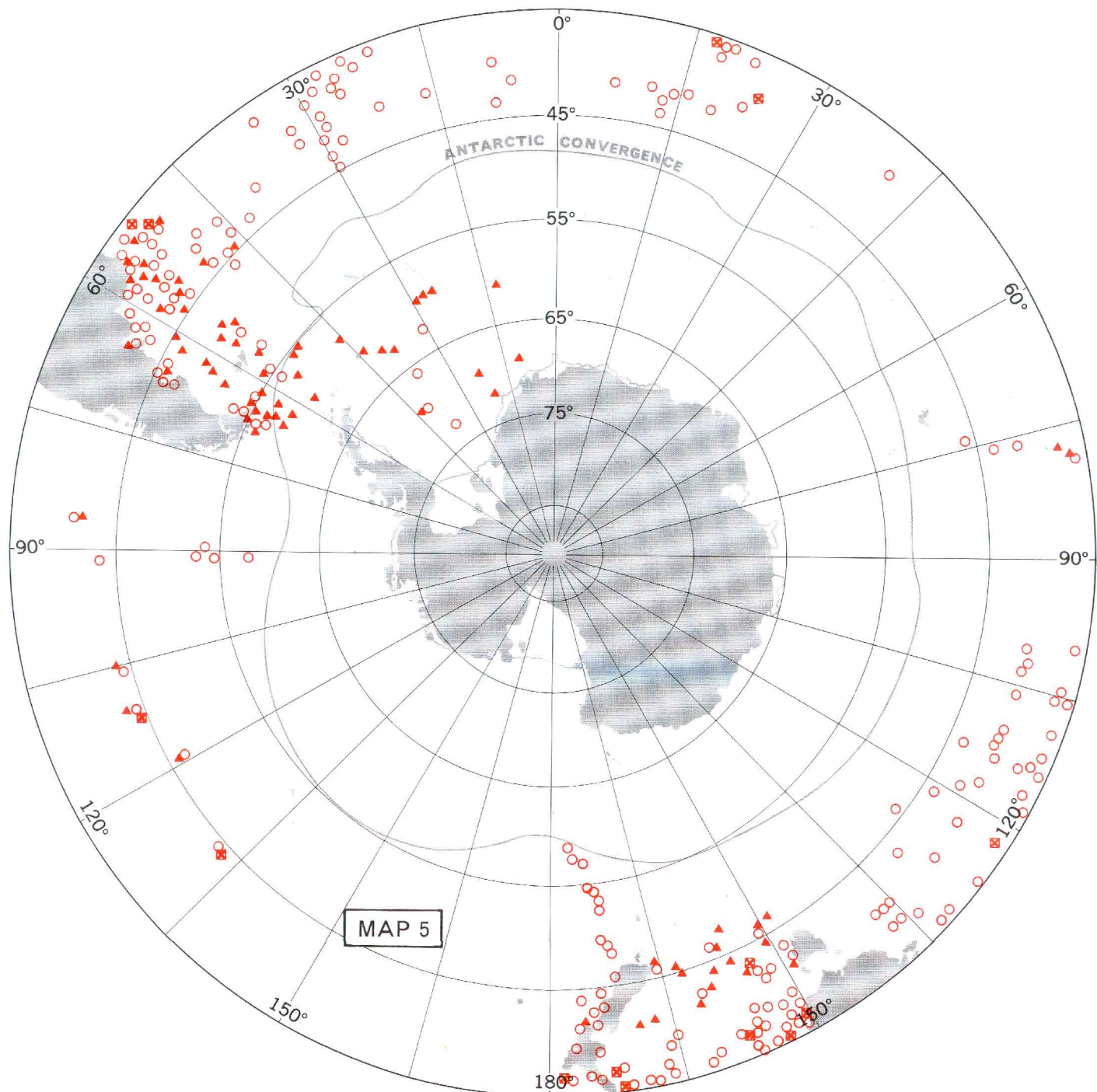
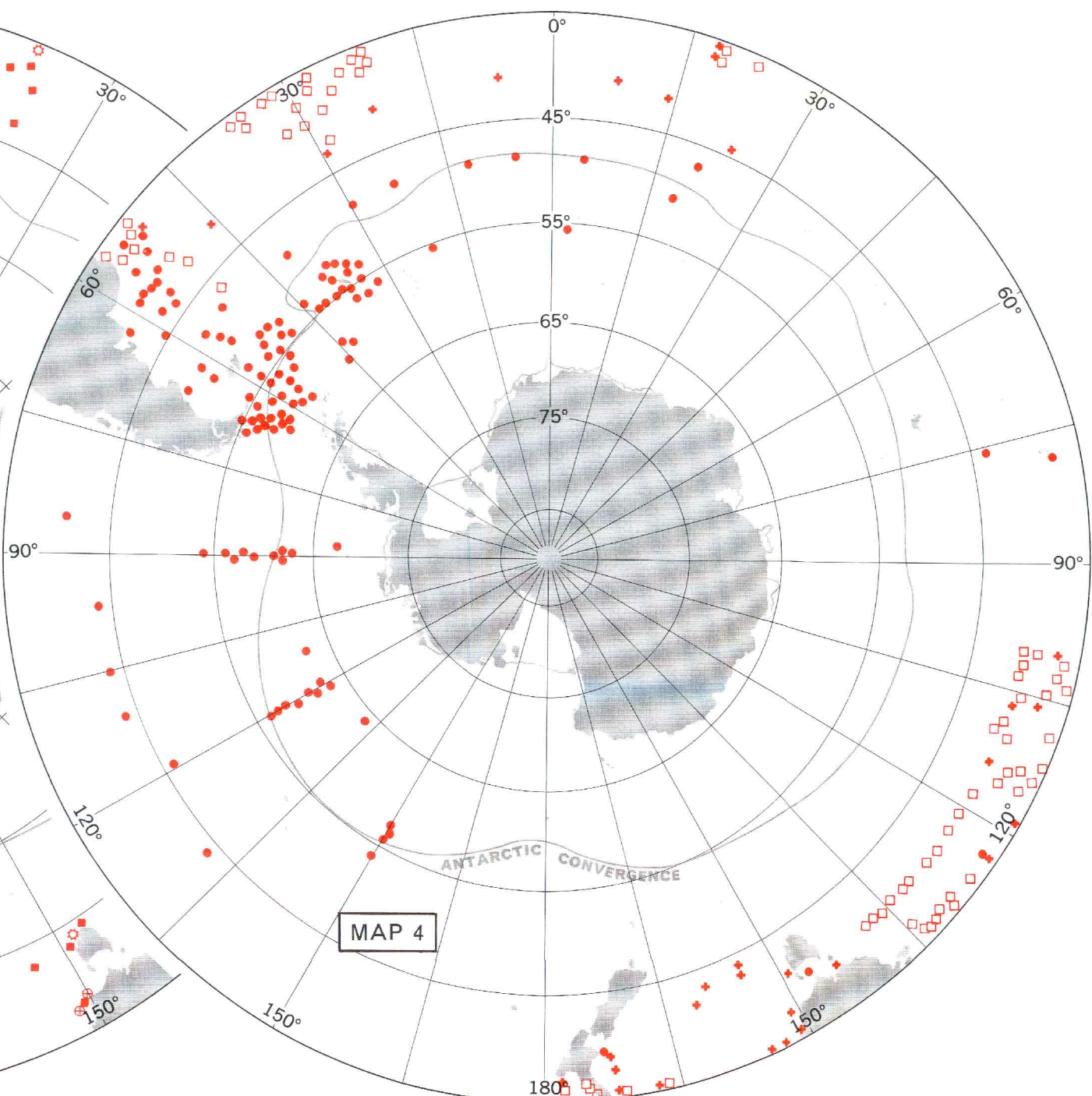
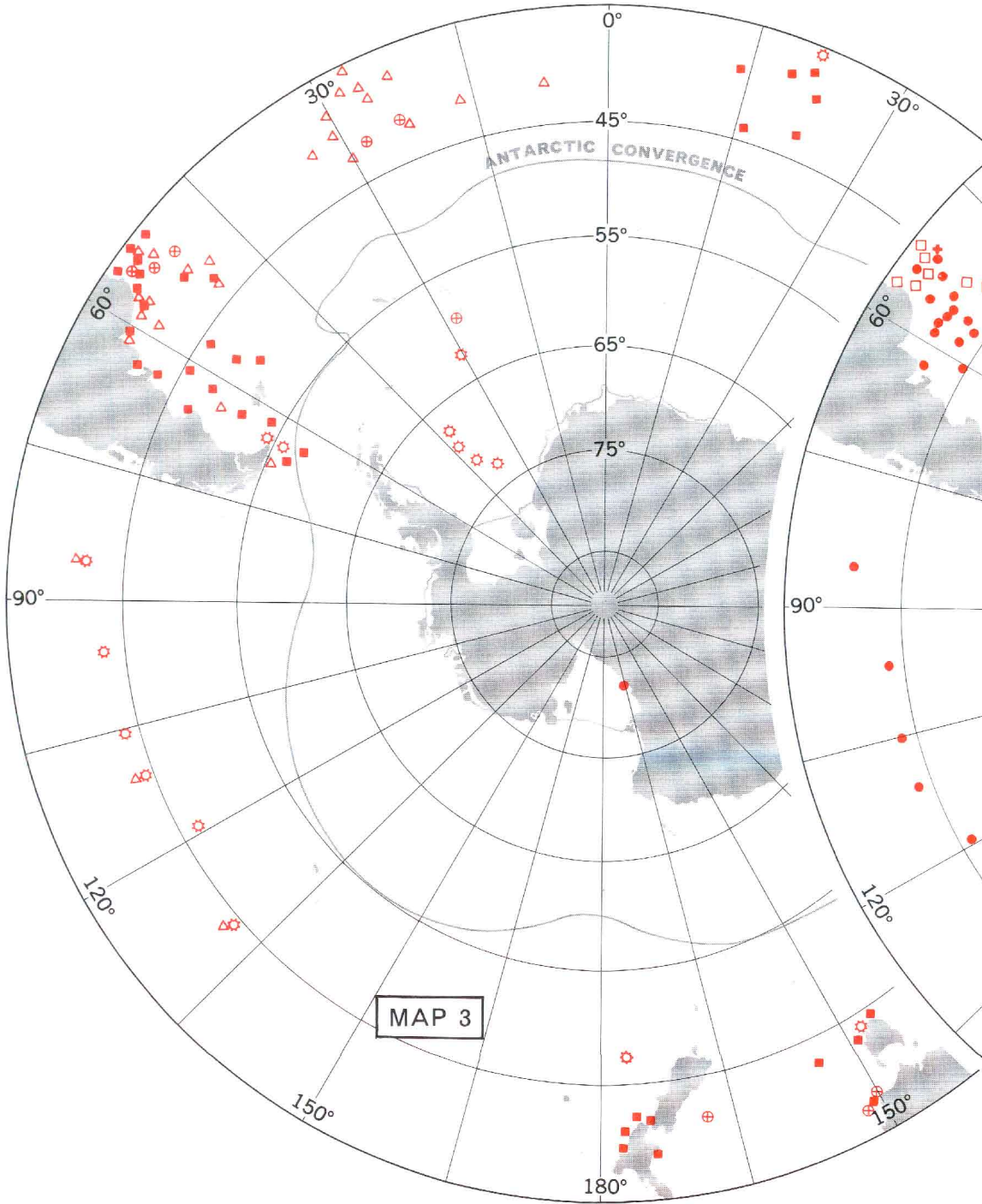
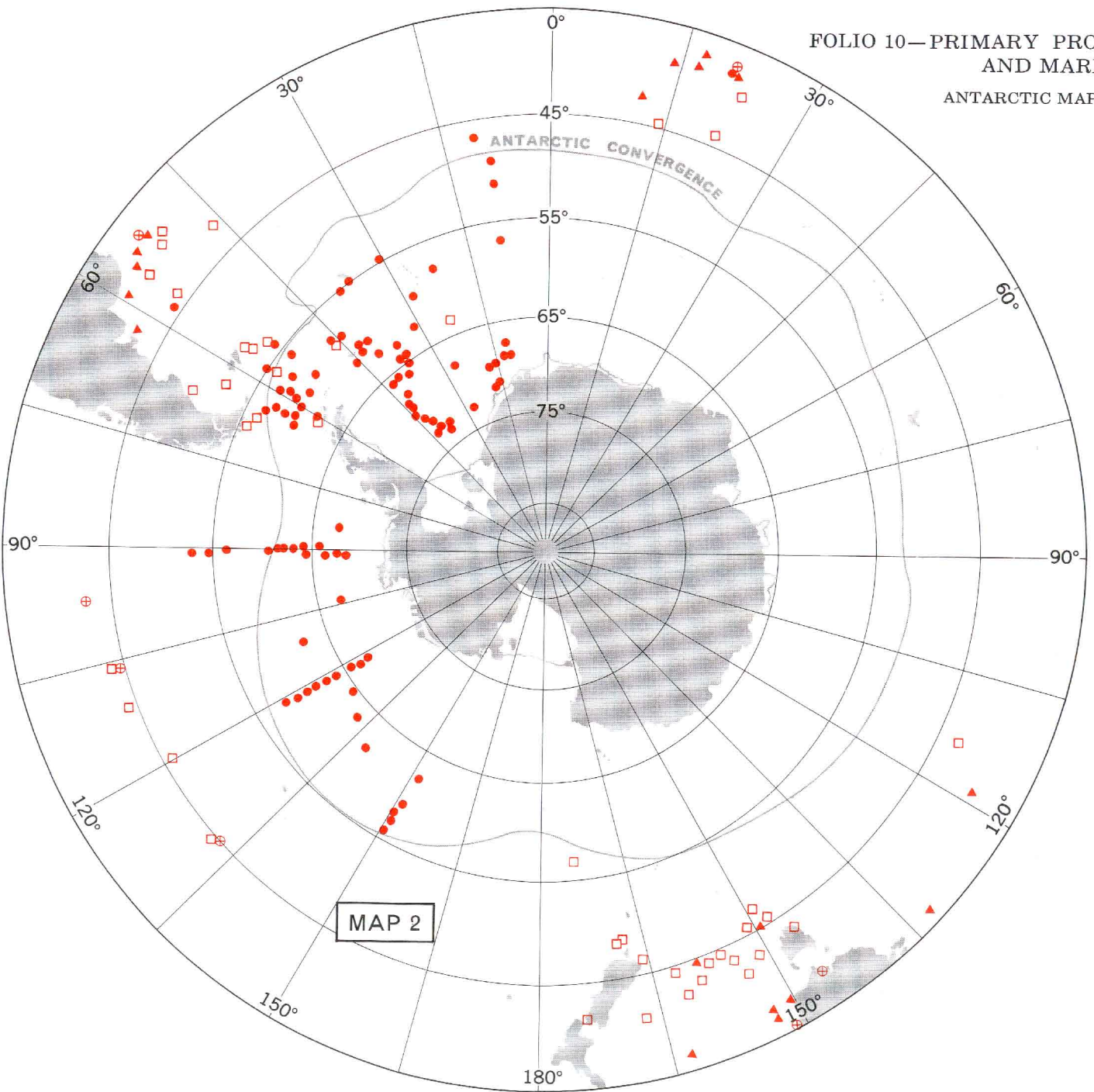
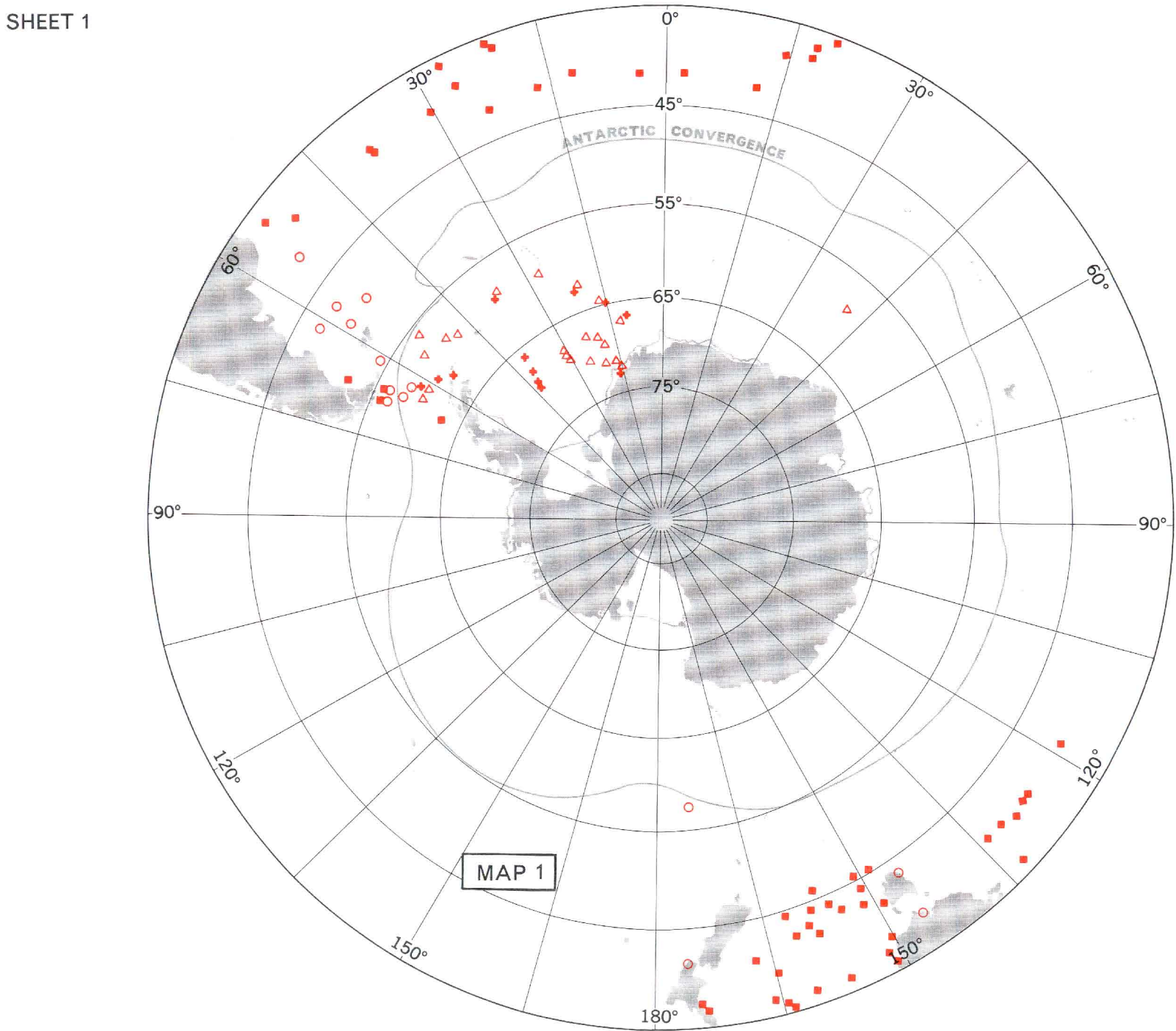
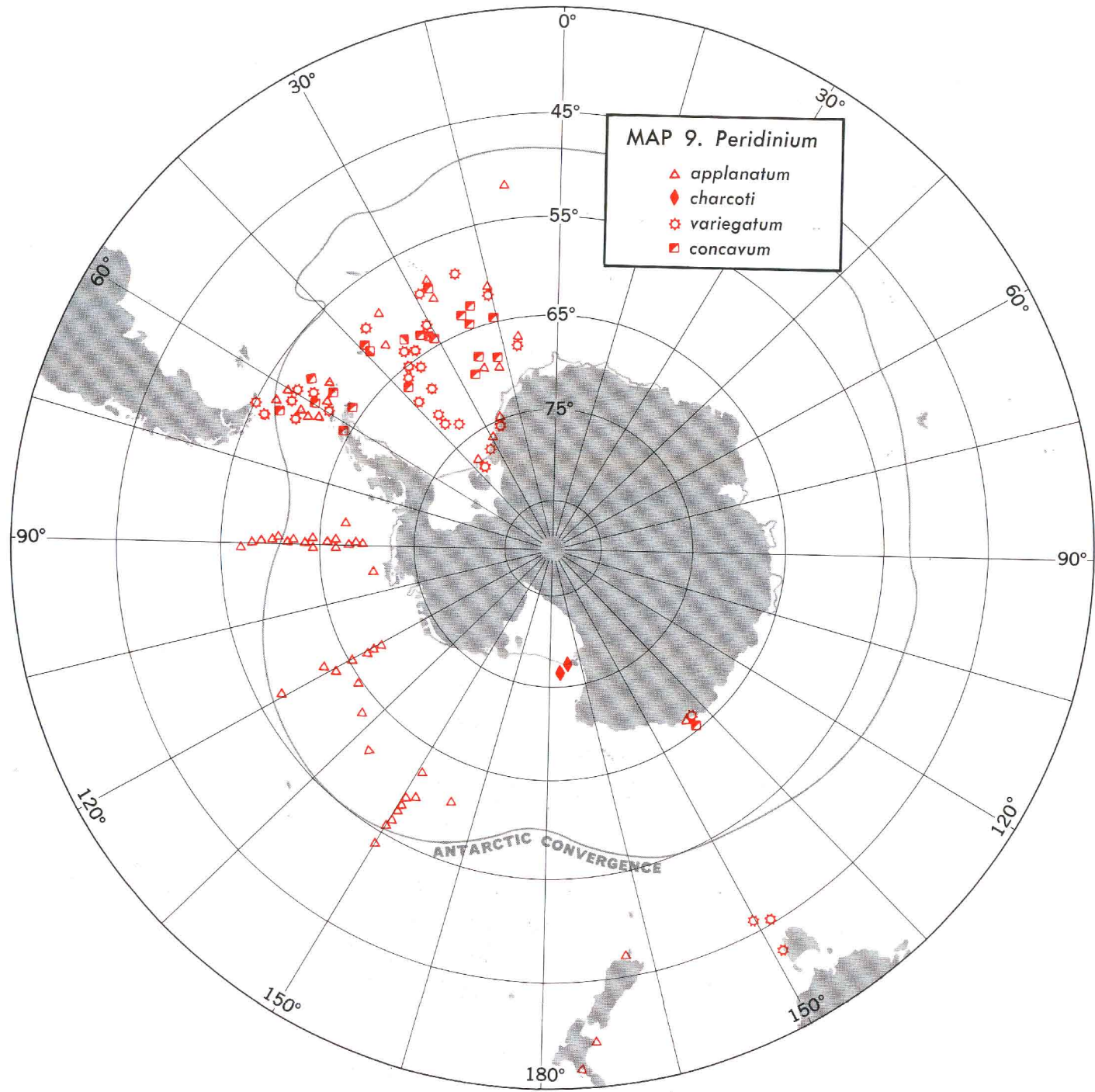
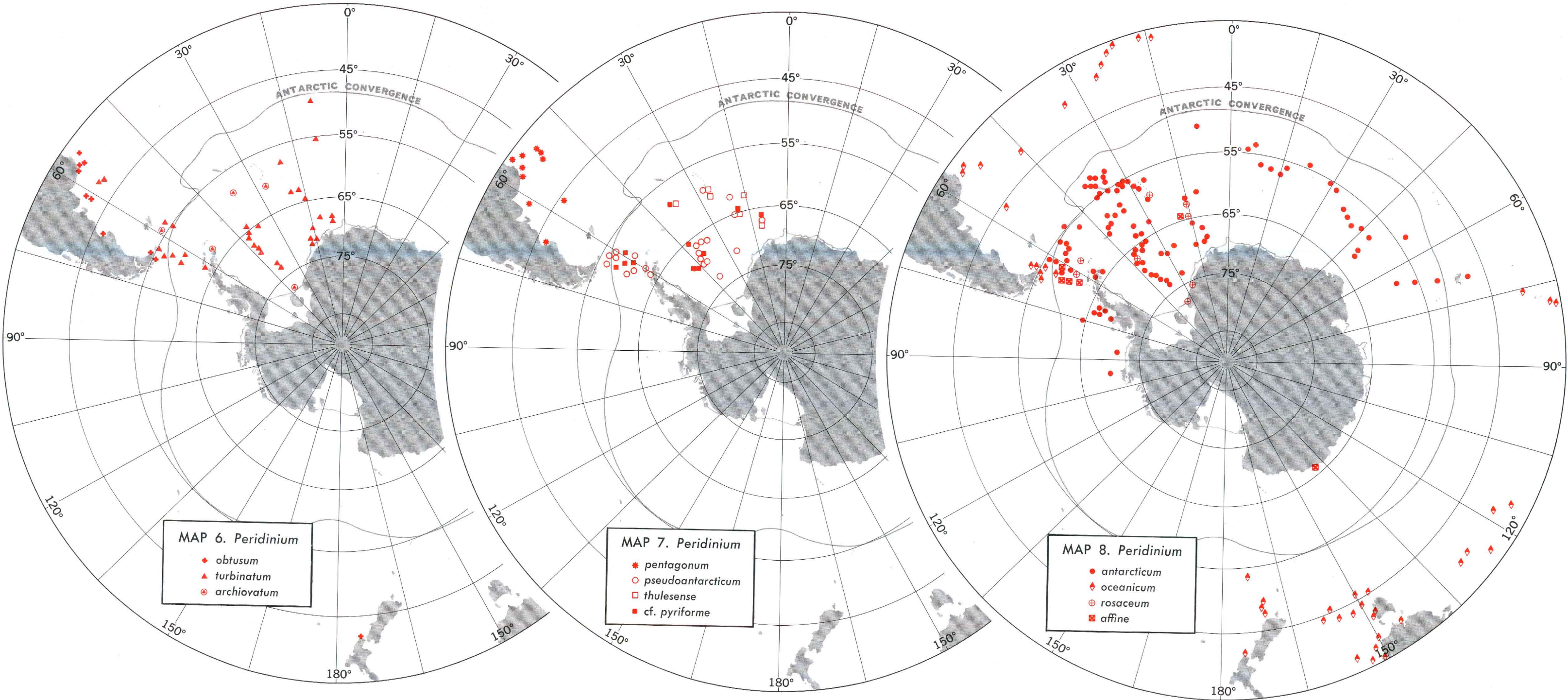


Fig. 15. *Corethron criophilum*
X250



Figures 9, 10, and 11 are redrawn from original photomicrographs.
Figures 12 and 15 are from Heney (1937).
Figures 13 and 14 are original drawings made by camera lucida.





IDENTIFICATION OF ANTARCTIC
THECATE DINOFLAGELLATES

The following concise descriptions and drawings are not intended as a key but rather as a simple guide to help distinguish the known species of Antarctic dinoflagellates. All drawings are of the same magnification (x400).

E. Balech

Dinophysis

D. antarctica Balech (Antarctic forms of *D. ovum*, auct.) Simplicity of contour, low epitheca, wide hypotheca, a narrow left sulcal list and a very short right one make this species easy to distinguish from the Antarctic congeners

D. cornuta Peters has a high epitheca with protuberances. Hypotheca narrow and irregular with a very ragged, irregular list along its sutural line in the dorsal and posterior parts. Left sulcal list very wide along the posterior rib.

subspecies *inermis* Balech. General contour like the typical subspecies. Epitheca and hypotheca without excrescences or with some, poorly developed, near the aboral end. Left sulcal list significantly narrower at the base.

D. tuberculata Mangin is the other species of low epitheca (*Dinophysis* type). It is larger than *D. antarctica*; the lateral outline is more elongated and generally furnished with irregular excrescences in the posterior part. Left sulcal list with a wide base. Highly variable.

D. spinata Peters. Very similar to *D. cornuta*; however its contour is different, especially in frontal view. Most of its excrescences are of a square type.

Diplopsalis

D. granulosa Balech. The high, elliptical form and strong sculpture are exceptional in this genus.

Podolampas

P. antarctica Balech is the only species of this genus found to date (1968) in the Antarctic. In general outline it is somewhat intermediary between *P. spinifer* and *P. palmipes* although its tabulation differs from both. Antapical membrane strongly sculptured.

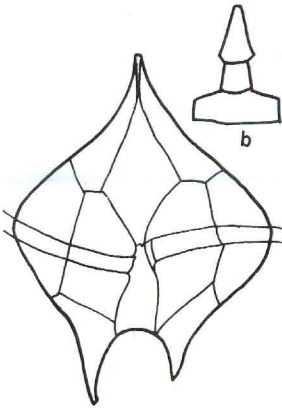
Oxytoxum

O. criophilum Balech. The only species of the genus known from the Antarctic. It is one of the very rare species of the genus with overhanging. It differs from *O. elegans* by the form of the epitheca and in its sculpture.

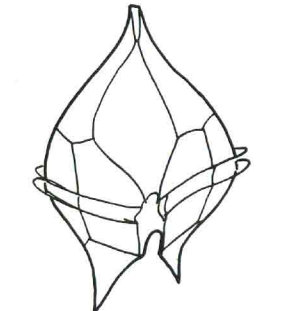
Peridinium

Fig. b. Epithecal plate pattern, dorsal view
Fig. c. The epitheca, apical view
Fig. d. Epithecal plate pattern, ventral view

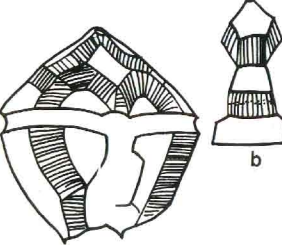
I. ORTHO
A. Quadra



P. antarcticum Schimper. The largest Antarctic species. This and the following species are the only Antarctic *Peridinium* with well-developed, hollow antapical horns. The protoplasm generally appears clear and contracted in fixed specimens.

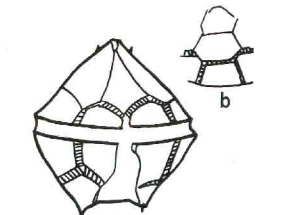


P. pseudoantarticum Balech. Somewhat smaller and narrower than *P. antarcticum*. Expansion at the girdle more gentle. Antapical horns more divergent; Plate 1' usually wider. Protoplasm generally opaque. The dorsal plate pattern similar to that of *P. antarcticum*.

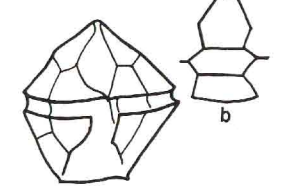


P. latistriatum Balech. Pentagonal outline. Sutures very wide; protoplasm dark.

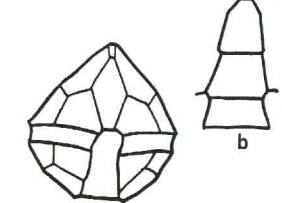
B. Hexa



P. rosaceum Balech. (Antarctic *P. subinermis*, auct.) Pentagonal contour. The lateral angles of 1' low. Lateral sutures of 3' prominent.



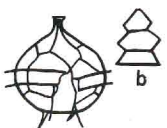
P. parvicollum Balech. Pentagonal outline. Plate 1' has a typical convexity at the right of the posterior angle. Plate 3' very high.



P. turbinatum Mangin. Pentagonal outline. Hypotheca is relatively low. Plate 1' is rather narrow; Plate 3' high. Lateral margins of 2' almost in a straight line with those of 3' and barely touching 3' and 5'.

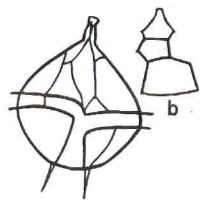
II. META

A. Hexa

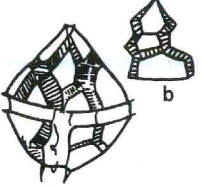


P. incertum Balech. The only Antarctic species with this plate pattern. It is a small species, probably referred to by some authors as *P. pelucidum*.

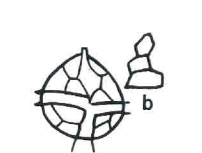
B. Penta



P. unipes Balech. Pear-shaped and has a rather long apical horn. Plate 1' narrow; Plate 7' very high. Its antapical plates are fused together; this is a character unique in the genus.



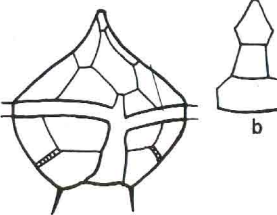
P. sp. cf. P. pyriforme Paulsen. Pear-shaped also. No apical horn. Short antapical spines and broad sutural bands.



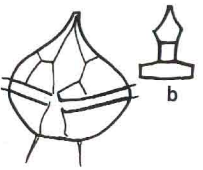
P. incognitum Balech. Much smaller than the other species in this group. Its shape is a broad oval. It has a very short apical horn.

C. Quadra

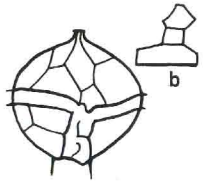
This is the division of the genus which contains the highest number of Antarctic species.



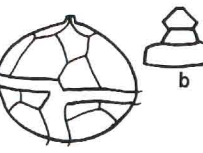
P. concavum Mangin. Rather large. Very short and attenuate apical horn. Two well-developed antapical spines, widely separated.



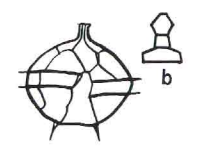
P. elegantissimum Balech. Very similar to *P. concavum*, but distinctly smaller. Details of the tabulation also differentiate the two species.



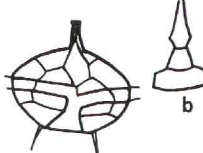
P. mediocre Balech. Wide ovoid, clumsy. Apical horn very short and steep. Antapical spines of medium size and closely set.



P. curtum Balech. Shorter than *P. mediocre*. It is wider than long. The cingulum has some overhanging. Antapical spines very small.



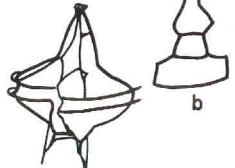
P. raphanum Balech. Small and short. Apical horn of medium size and emerges abruptly. Antapical spines rather short and widely separated.



P. applanatum Mangin. Shorter than the species described above. Long apical horn emerges abruptly and its long antapical spines are widely separated.



P. obovatatum Wood. Even shorter than *P. applanatum* and very flattened. It could be a variety of the former.



P. charcoti Balech. Very characteristic outline. The apical horn is preceded by a conical part of the epitheca. Antapical spines furnished with lists.



P. thulesense Balech. Short and pentagonal. Hypotheca very low. Typical plate pattern. Plate 1' touches one preangular at the left and two at the right (inverted meta). Cingulum has an excavated furrow.



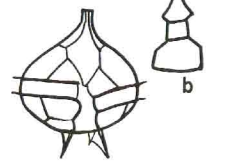
P. metananum Balech. Another pentagonal species but smaller. Epithecal sides convex in ventral view. Cingulum excavated.

III. PARA

A. Quadra



P. nanum Balech. The smallest Antarctic species. Its general contour is similar to that of *P. metananum*.

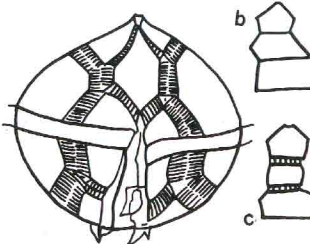


P. adelense Balech. Closely resembles *P. elegantissimum* in general outline and size; however its antapical spines are closer, and have lists. The left sulcal list forms a "third antapical."

B. Hexa

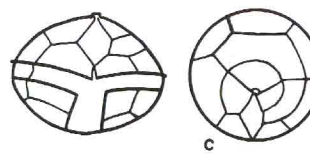


P. affine Balech. Rather closely resembles *P. adelense* in general outline, but is stouter with a short apical horn and shorter antapical spines.



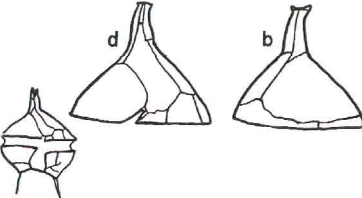
P. variegatum Peters. Somewhat wider than long. This is the larger *Peridinium* Para. Its apical horn and antapical spines are very short. Occasionally some quadra specimens are found.

IV. PERIDINIUM, SUBGENUS
Archaeoperidinium



P. archiovatum Balech. An "ovatum" form but has only two intercalaries plates. It is the only known Antarctic species belonging to this subgenus.

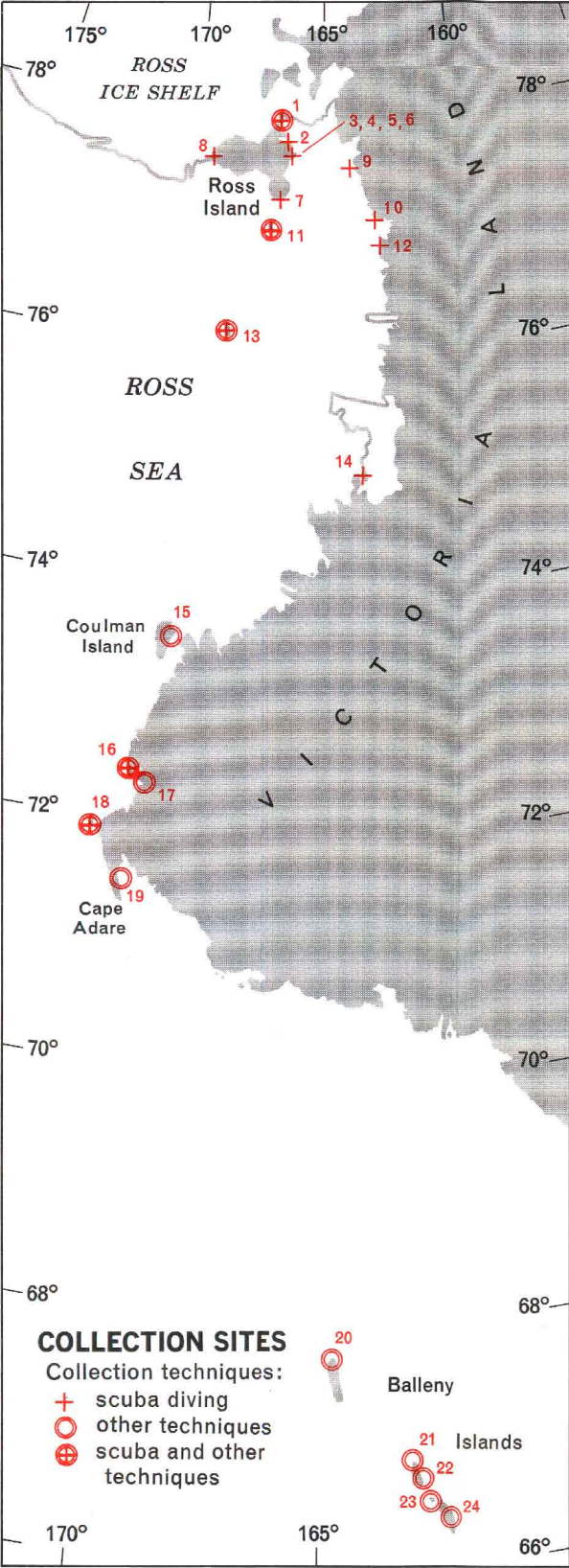
V. PERIDINIUM WITH QUITE ABNORMAL PLATE PATTERN



P. defectum Balech. A very small species with long and dissimilar antapical spines and a long apical horn. The very abnormal tabulation makes its inclusion in the genus contestable.

SEAWEEDS

SHEET 1 (ZANEVELD)



LIST OF COLLECTION SITES WITH DESCRIPTIVE DATA			
No.	Locality	Ice Cover	Bottom Composition
1	Cape Armitage	Ice covered	VoGRA, PEB, COB
2	Cape Evans	Ice covered	VoSAF, GRA, PEB, COB, BOUL
3	Backdoor Bay	Ice covered	VoSAF, GRA, PEB, COB, BOUL
4	Cape Royds	Ice covered	VoSAF, GRA, PEB, COB, BOUL
5	Blacksand Beach	Ice covered	VoSAF, GRA, PEB, COB, BOUL
6	Horseshoe Bay	Ice covered	VoSAF, GRA, BOUL
7	Cape Bird	Ice covered	VoSAF with shells, PEB, COB, BOUL
8	Cape Crozier	Ice covered	ScD, VoSAF, PEB, COB
9	Marble Point	Ice covered	ScD, GrGRA, BOUL
10	Granite Harbor	Ice covered	ScD, GrGRA, BOUL
11	Beaufort I.	Open water	ScD, TAC, TBL
12	Depot I.	Ice covered	ScD, VoGRA, PEB, COB, BOUL
13	Franklin I.	Open water	ScD, GH0, TAS, TBL
14	Inexpressible I.	Ice covered	ScD, VoSAM, GRA, BOUL
15	Coulman I.	Ice covered	DCM, GH0, TBL
16	Cape Hallett	Ice covered	ScD, DCM, TAC
17	Moubray Bay	Ice covered	DCM, TAC, TBL
18	Possession Is.	Open water	ScD, DCM, TAS, TBL
19	Robertson Bay	Open water	DCM, TBL
20	Sturge I.	Open water	DCM, TAS, TBL
21	Sabrina I.	Open water	TBL
22	Buckle I.	Open water	DCM, TAS, TBL
23	Borradale I.	Open water	DCM, TAS, TBL
24	Young I.	Open water	DCM, TAS, TBL

EXPLANATION OF SYMBOLS USED IN TABLE

Ice Cover

- Ice covered
- Open water
- Ice covered most of the time

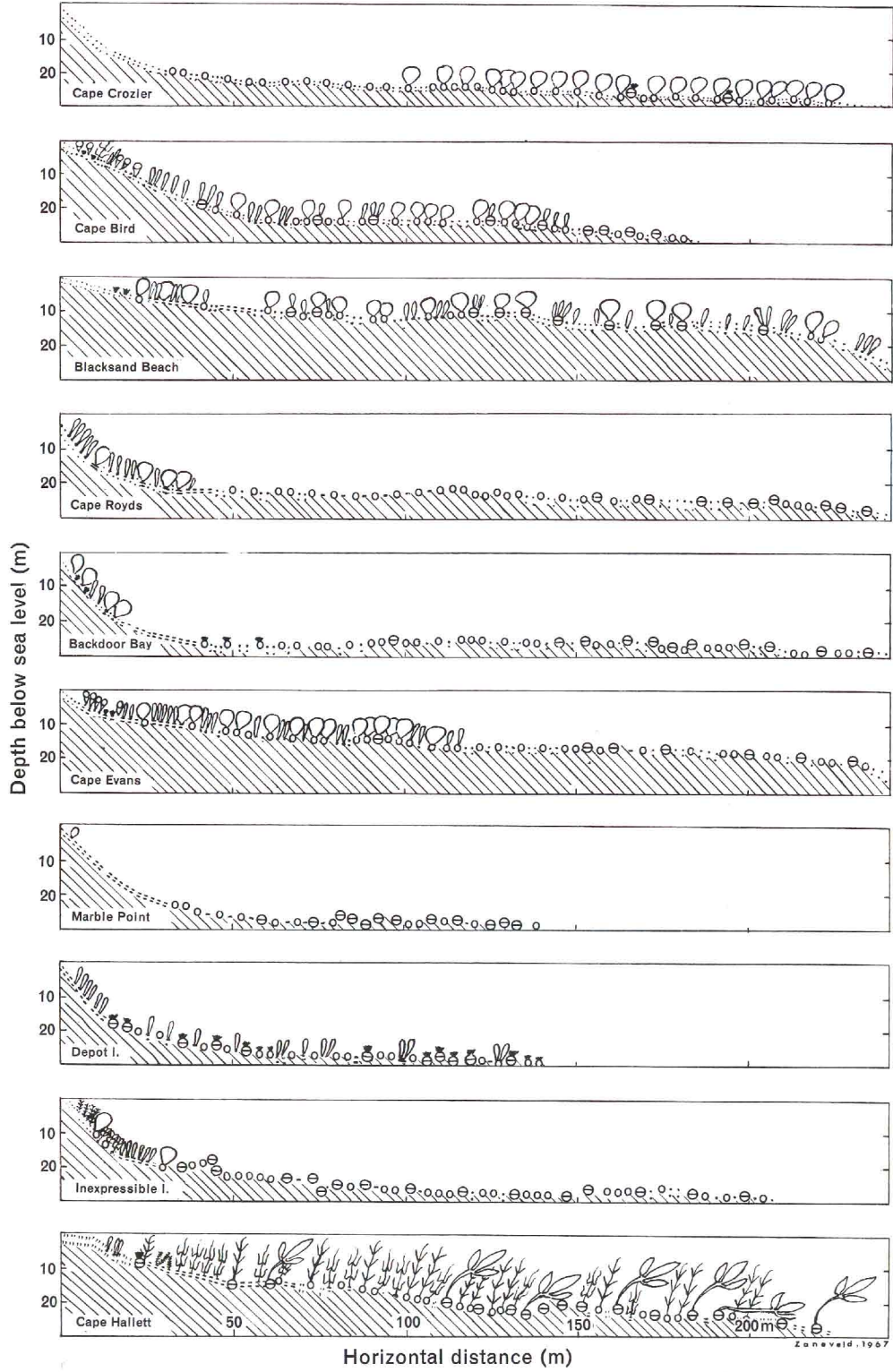
Collection technique

- DCM = dredge, cone shaped, medium
- GH0 = grab, orange peel
- ScD = scuba-diving
- TAS = Agassiz trawl, small
- TAC = Agassiz trawl, Caribbean
- TBL = Blake trawl, large

Bottom composition

- Vo = volcanic (basaltic)
- Gr = granite
- MUC = mud, clay
- MUS = mud, silt
- SAF = fine sand
- SAM = medium sand
- SAC = coarse sand
- GRA = gravel
- PEB = pebbles
- COB = cobbles
- BOUL = boulders

DIAGRAMMATIC PROFILES OF AREAS INVESTIGATED BY SCUBA DIVING

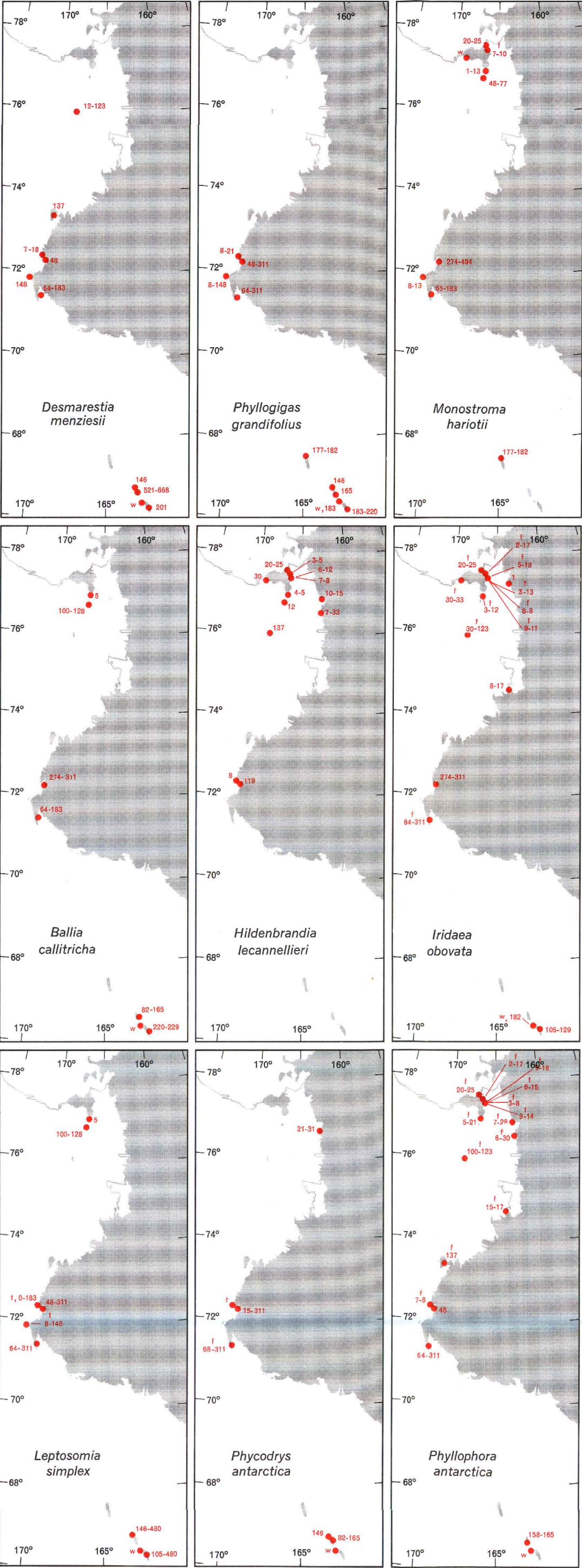


EXPLANATION OF PROFILES

- Algae depicted
- Desmarestia menziesii* J. Agardh
 - Phyllogigas grandifolius* (A. and E. S. Gepp) Skottsberg
 - Monostroma hariotii* Gain
 - Hildenbrandia lecanellieri* Hariot
 - Iridaea obovata* Kützing
 - Leptosomia simplex* (A. and E. S. Gepp) Kylin
 - Phycodrys antarctica* (Skottsberg) Skottsberg
 - Phyllophora antarctica* (A. and E. S. Gepp)
 - Plocamium coccineum* (Hudson) Lyngbye

Sediment size

- mud, 1/256 to 1/16 mm
- sand, 1/16 to 2 mm
- granules, 2 to 4 mm
- pebbles, 4 to 64 mm
- cobbles, 64 to 256 mm
- boulders > 256 mm



DISTRIBUTION OF DOMINANT SPECIES

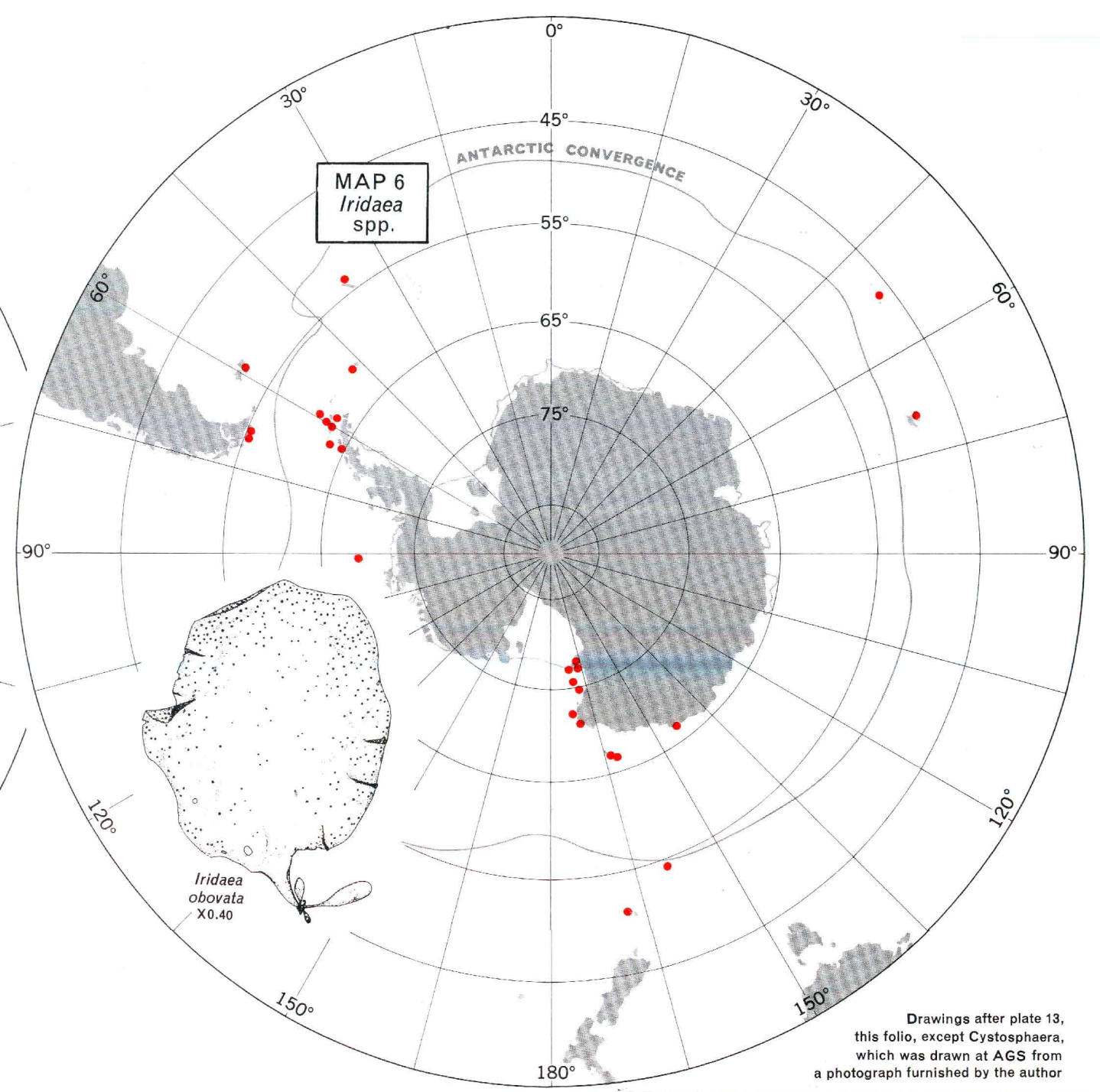
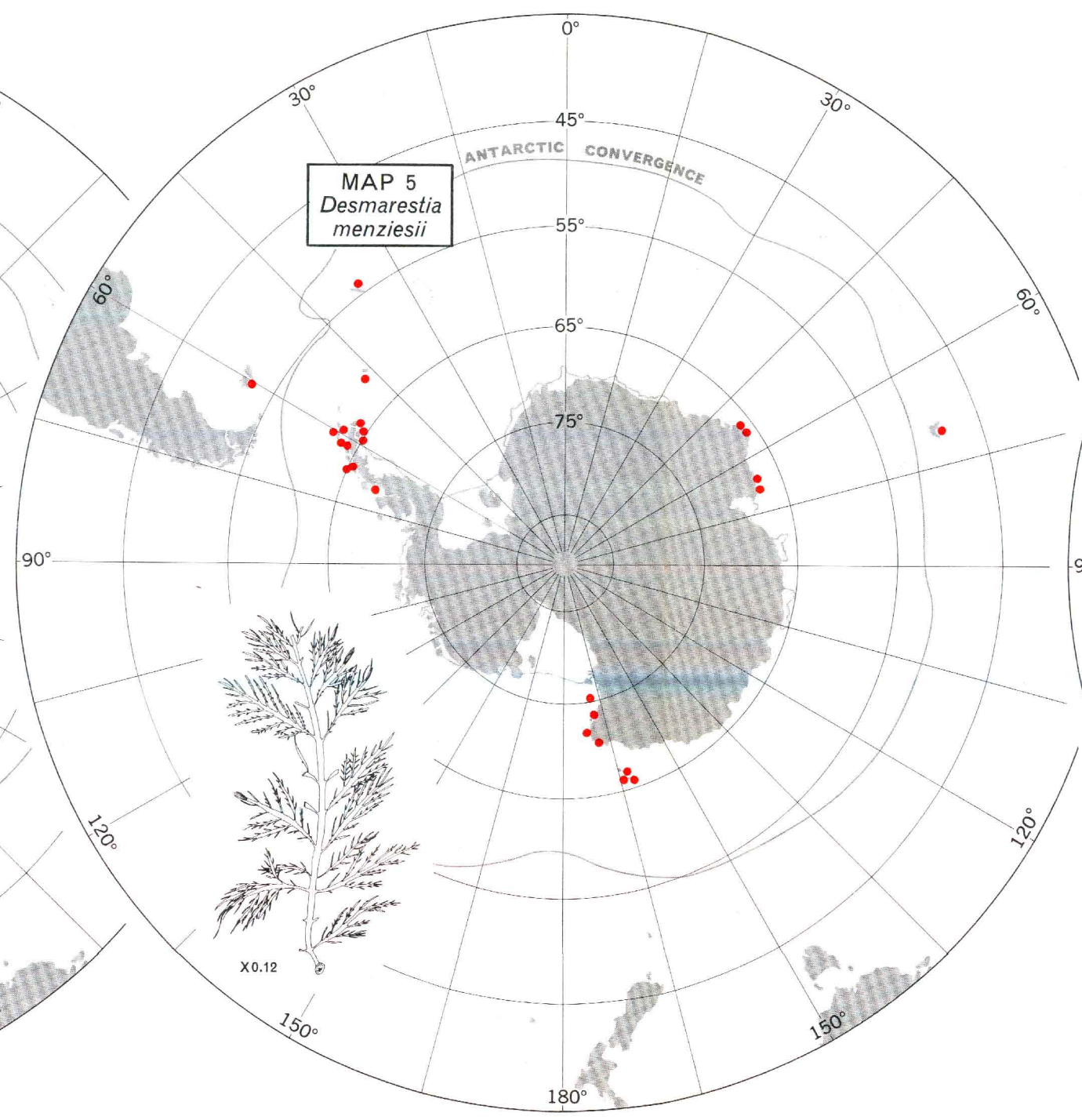
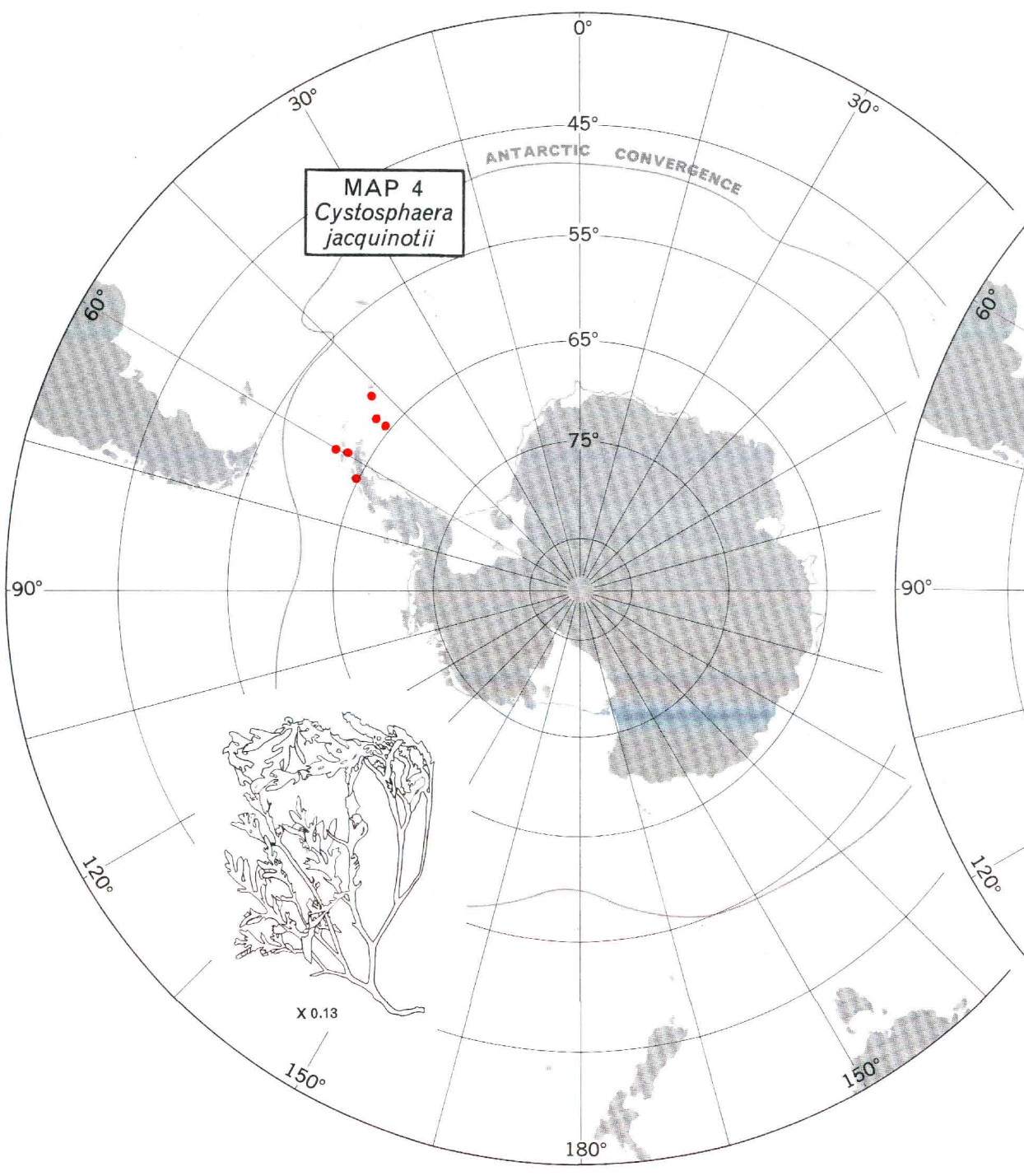
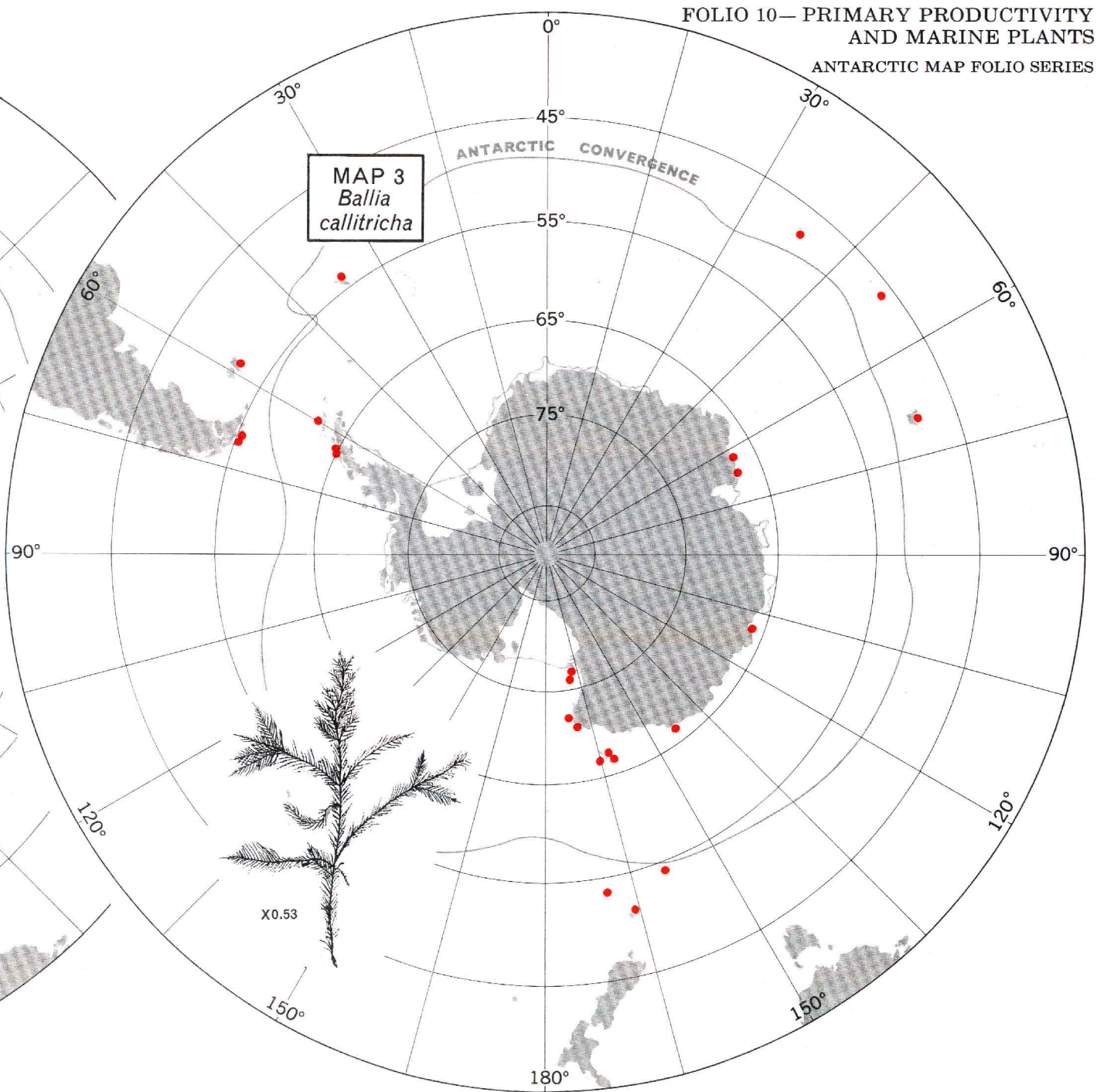
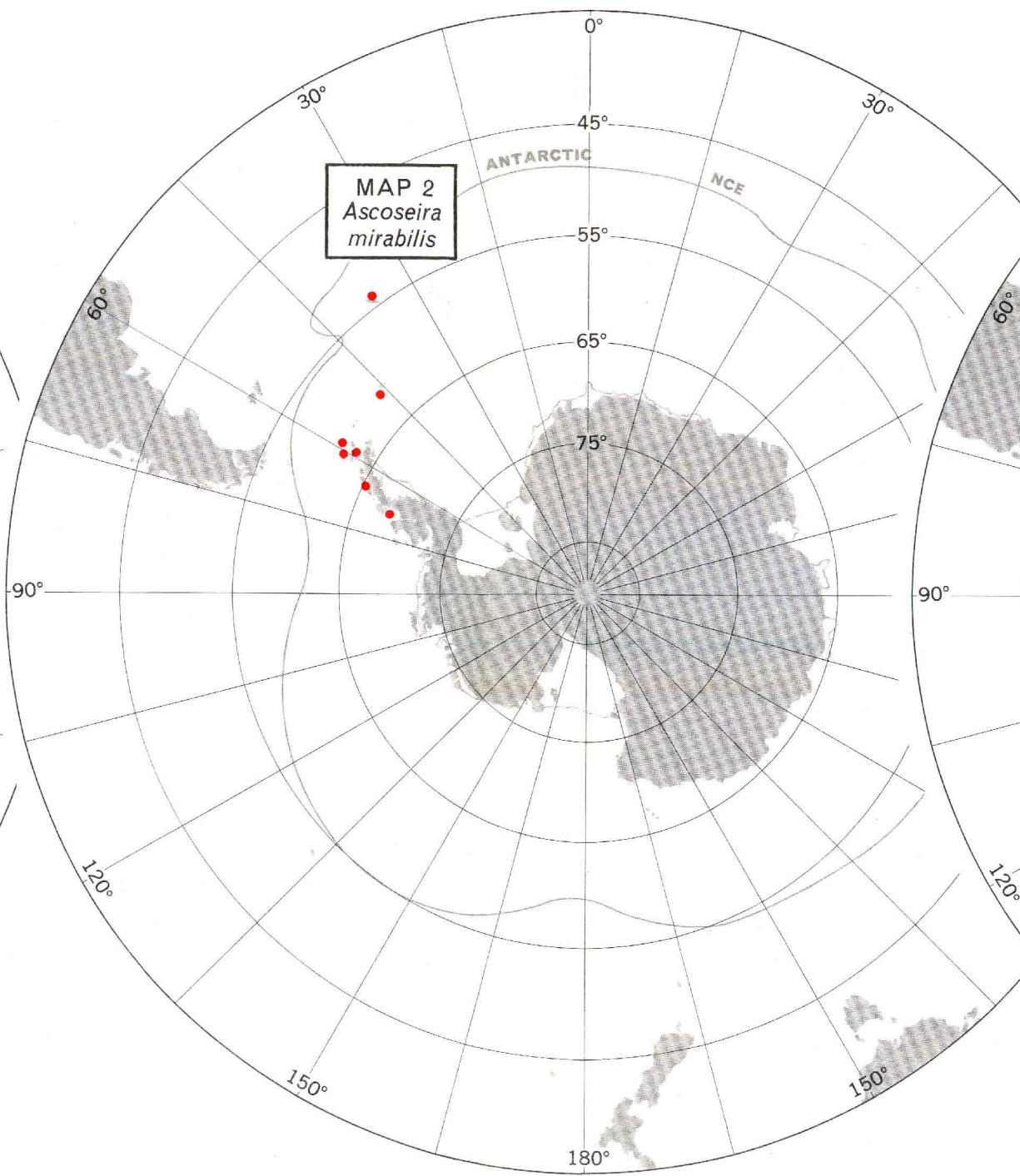
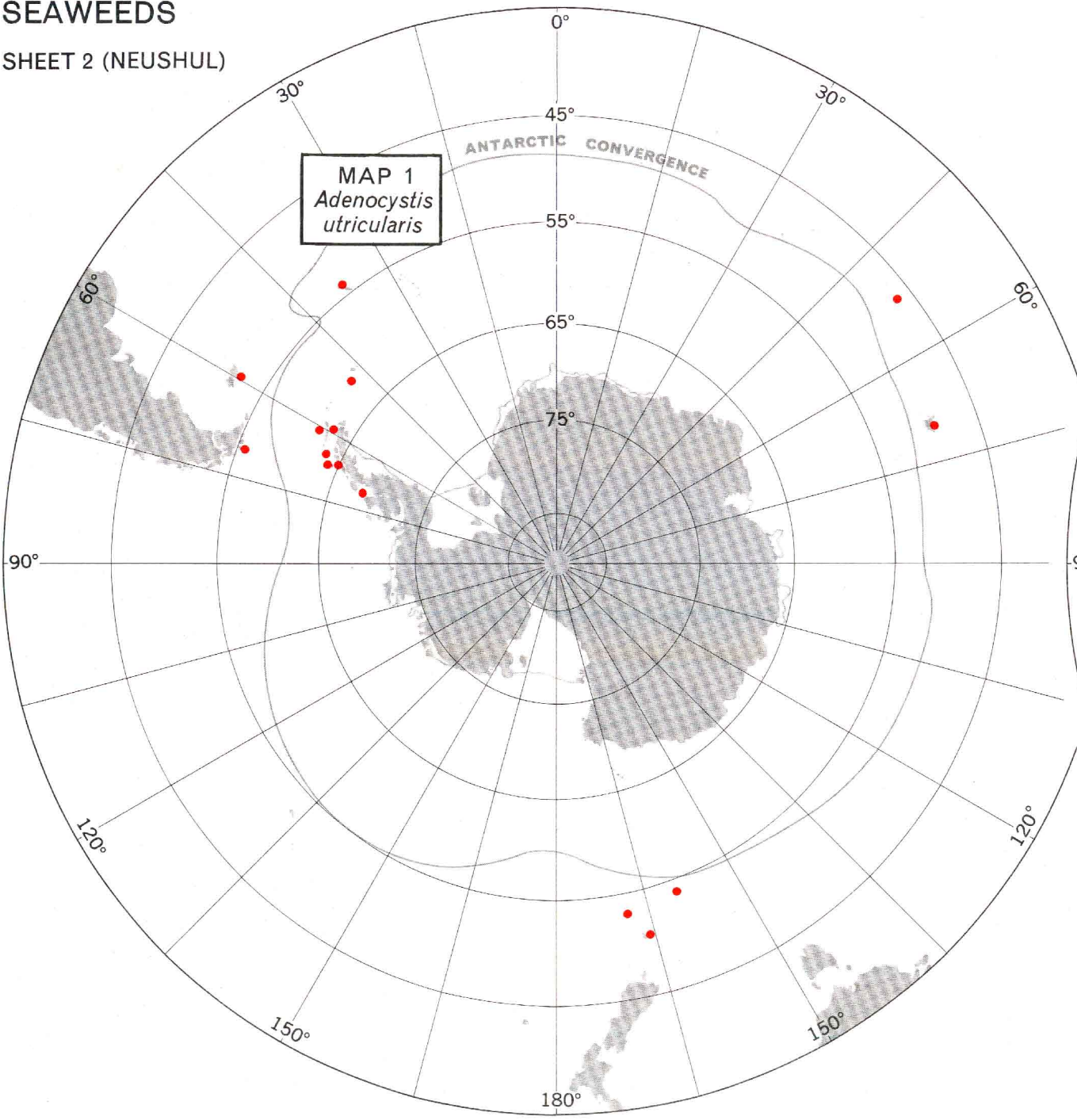
Site of collection record, with depth range in meters; f = fructifying, w = washed ashore, t = tide pool.

PLATE 13

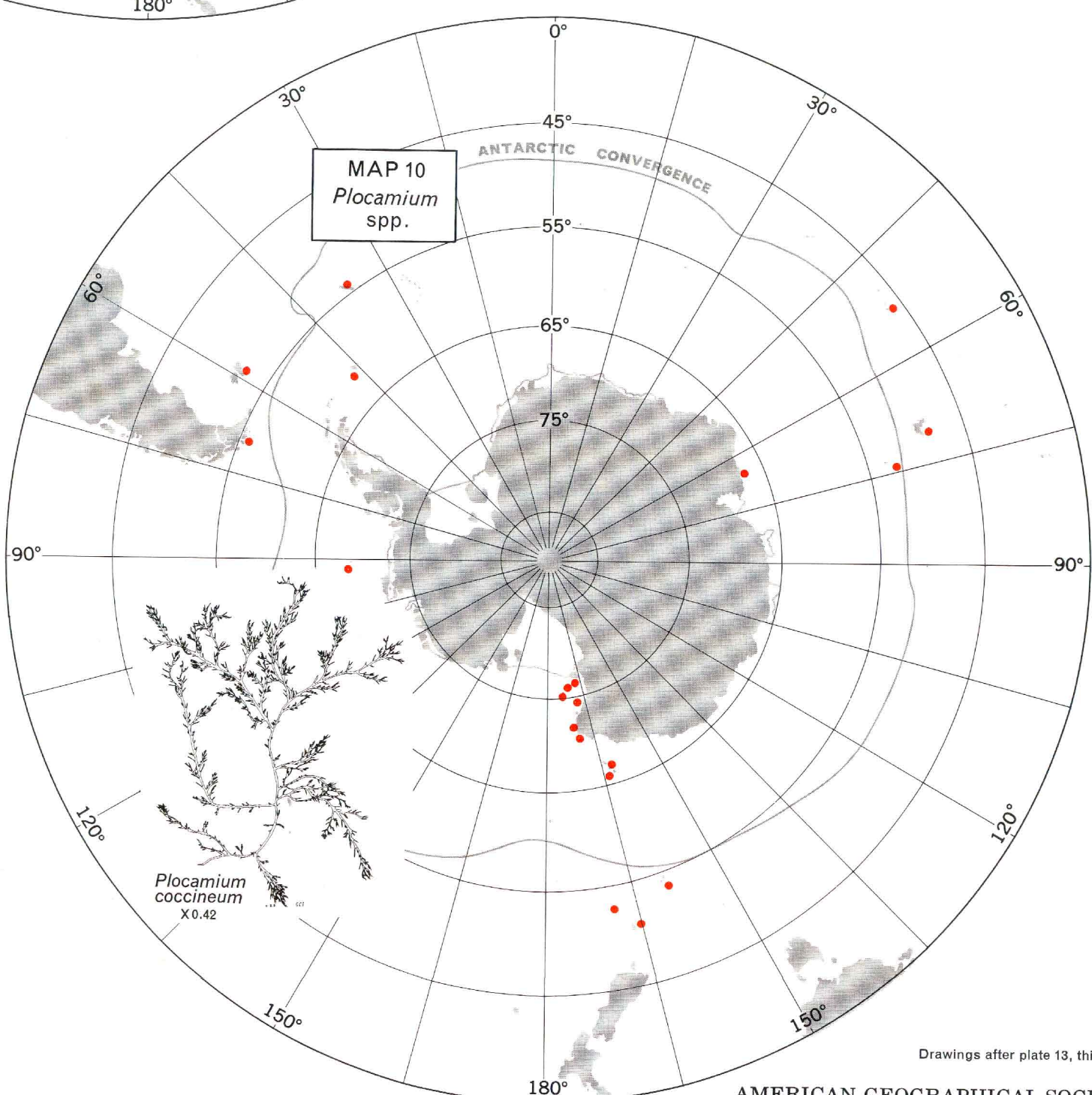
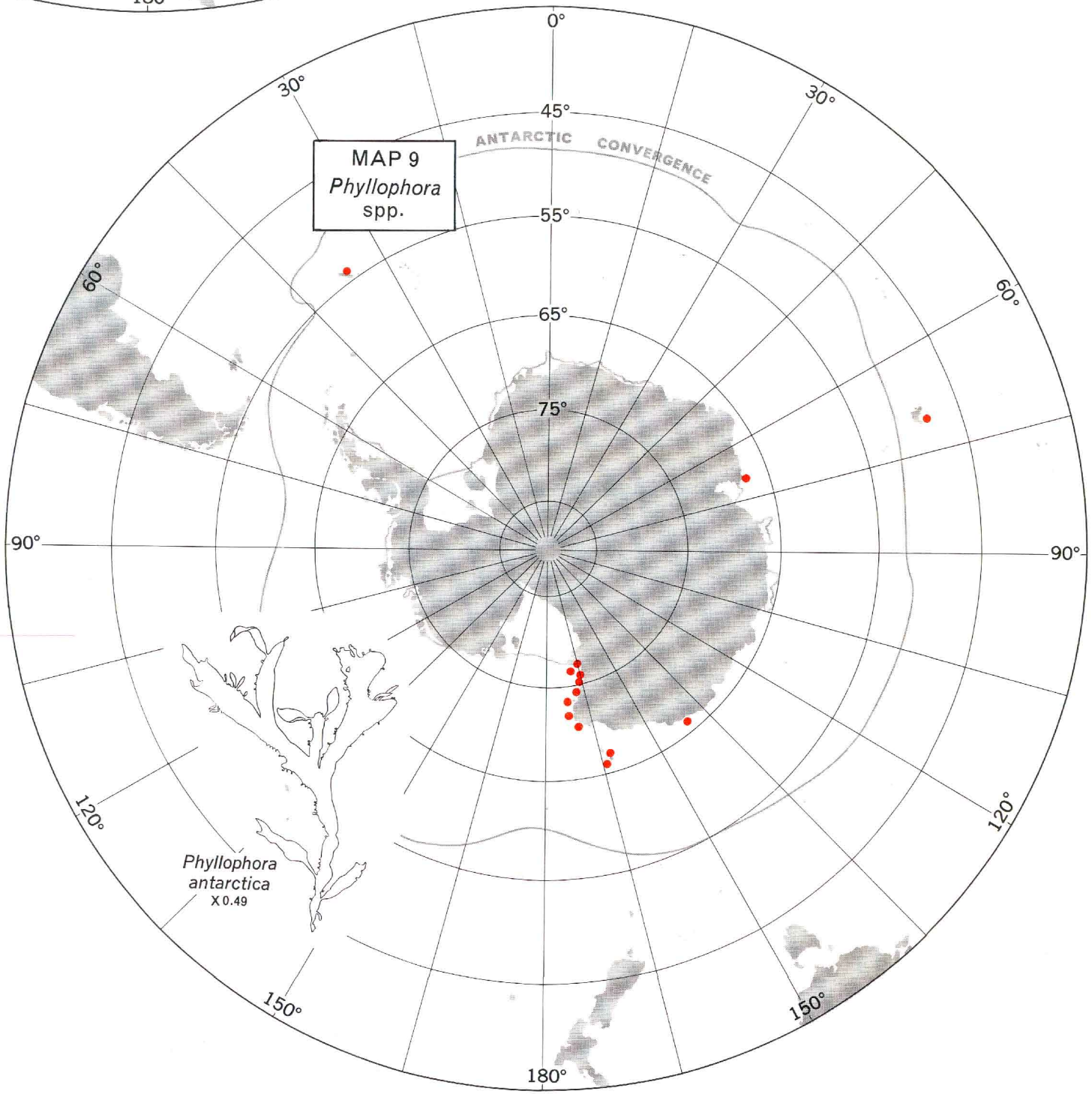
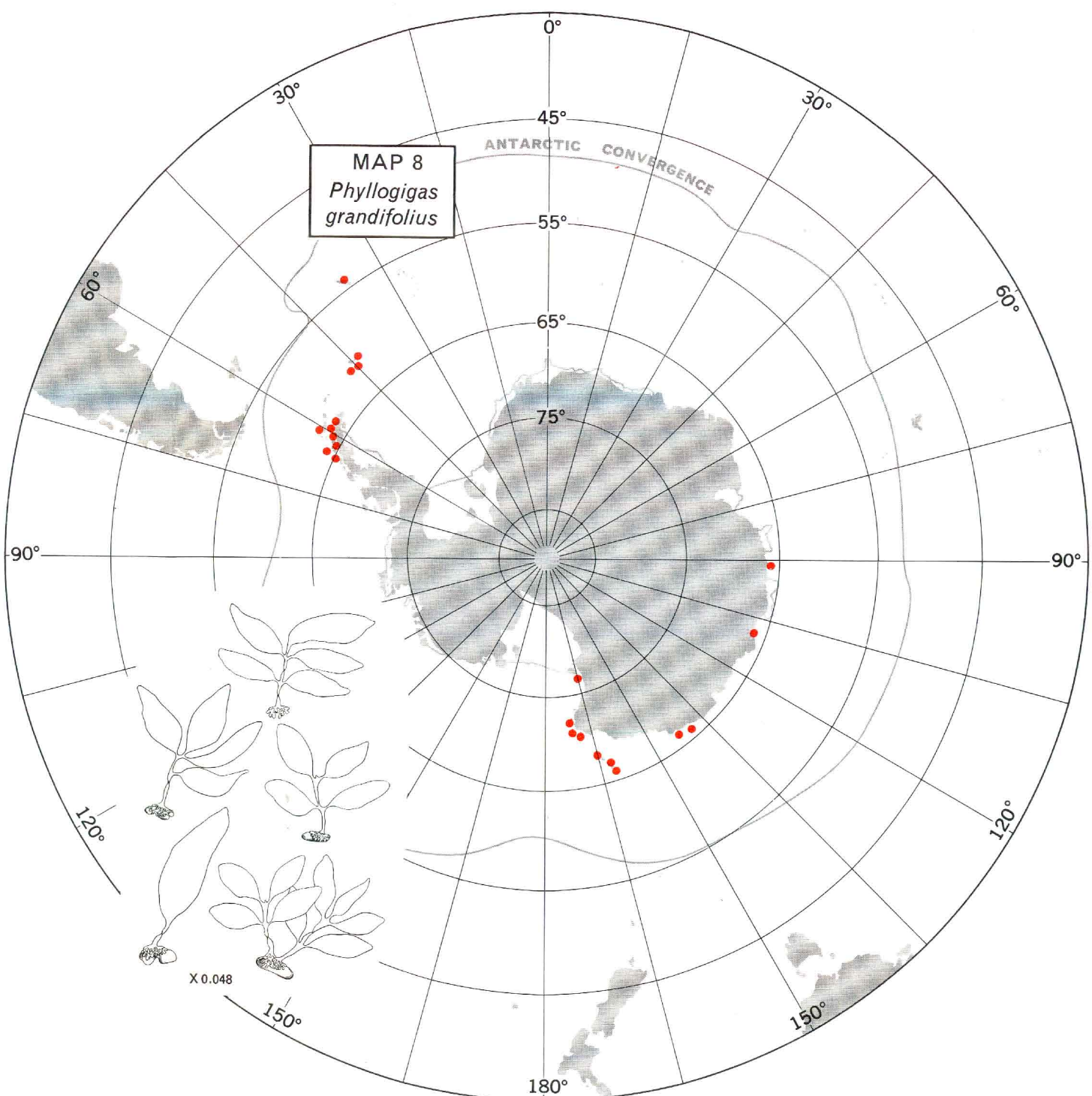
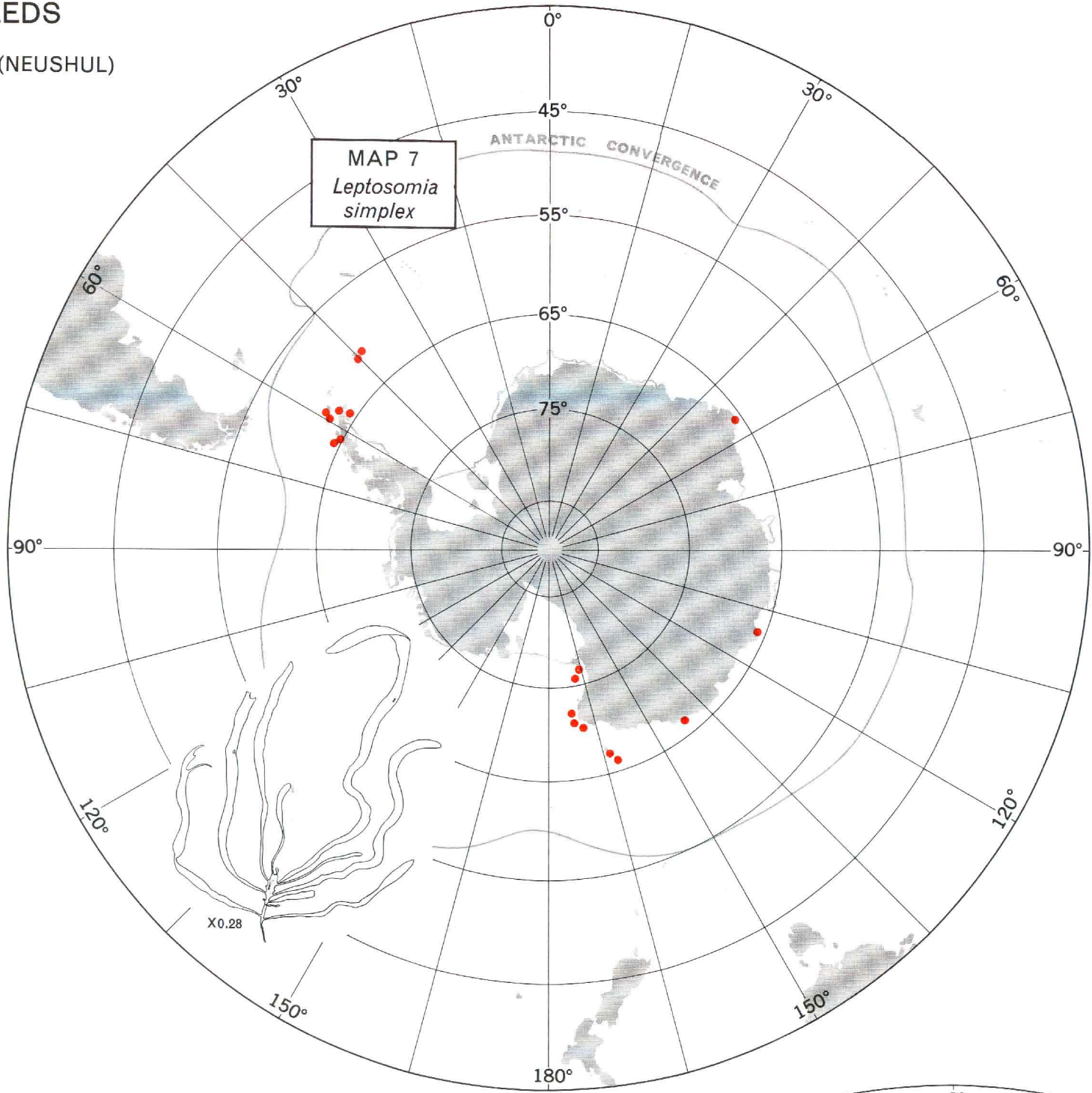
FOLIO 10— PRIMARY PRODUCTIVITY AND MARINE PLANTS

ANTARCTIC MAP FOLIO SERIES

Drawings by Sarah C. Dickey



Drawings after plate 13,
this folio, except *Cystosphaera*,
which was drawn at AGS from
a photograph furnished by the author



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Printed by Princeton Polychrome Press, Princeton, New Jersey