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Unstalked Crinoids of the Antarctic Continental Shelf. Notes on Their Natural History and Distribution

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UNSTALKED CRINOIDS OF THE ANTARCTIC CONTINENTAL SHELF. NOTES ON THEIR NATURAL HISTORY AND DISTRIBUTION

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[Plate 49]

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An account is given of the natural history, distribution and relative abundance of the comatulids of the Antarctic continental shelf. On the whole they form a distinctive geographical assemblage, that, cut off from northern influence, has evidently evolved in isolation since at least from the beginning of the Pleistocene or Quaternary Period. Where large enough numbers have been encountered the distribution of six of the seventeen known shelf species has been shown to be circumpolar, and at least one of the six, the largest and most mobile, appears to have spread, or perhaps even now is spreading, northwards to lower latitudes via the submarine ridges that radiate outwards from Antarctica.

Introduction

Within the last few years a number of well-equipped vessels have been working on the Antarctic continental shelf and many parts of it, for long unexplored or known only from a few scattered wire soundings, are now becoming targets for intensive surveying. In many instances these expeditions have sampled the bottom fauna, not only on the shelf itself but also in the deeper water beyond, and the results of this work, which is still going on, may be expected to appear shortly. Meanwhile, I have thought it worth while to review some aspects of the zoogeography of this region and I present here a study of the comatulids, a group represented in southern waters by a not unmanageably large number of species. I have also thought it worth while to give some account of my own experience of trawling and dredging in these high latitudes and of the gear that has been used with the most rewarding results.

A list of the gear in which the southern crinoids (stalked and unstalked) were collected, including some other bottom apparatus used by Antarctic expeditions, is given in table A of appendix I. In many instances precise information as to how this material was collected is lacking. I have been unable, for instance, to trace any detailed account of the apparatus used by the '*Belgica*' expedition. In the reports of this voyage it is true there are occasional references to the trawl (*chalut*), although it does not appear to have been used very often, and also to the *fauvert*, literally a mop or swab and evidently some form of tangle, as formerly used by the '*Challenger*' and other early expeditions, to trap small organisms, but now superseded by fine nets attached to the backs of dredges and trawls. My descriptions of the gear are very short and are presented mainly for the convenience of the reader who will find a shorter form of reference in the text, such as *DLH* for 'large heavy dredge', *DRR* for 'rectangular Russell dredge', *OTL* for 'large otter trawl', and so on. Fuller descriptions covering a wide variety of bottom apparatus will be found in Tizard, Moseley, Buchanan & Murray (1885), Kemp & Hardy (1929), Johnston (1937) and Mawson (1940).

In table B, of appendix I, I have tried to assess the relative catching capacity (in so far as the comatulids are concerned) of several types of gear for which 'time on the bottom' or 'minutes fishing' has been estimated.

Chronological lists of the occurrences of the coastal comatulids recorded by the major expeditions that have visited Antarctica from the time of the *Challenger* onwards are given in appendix II (tables C and D), table C dealing with the animals of the high continental platform (p. 330), table D with those from the shelves of the oceanic islands scattered about Antarctica and in the Southern Ocean. Both lists show how the specimens were collected (where this has been recorded), the number or numbers of the species taken at each station, and as much information as I have been able to trace about the environmental conditions, temperatures, depths, substrata and so on, at the points of collecting. The quality of the recording varies greatly from expedition to expedition, which is not surprising when we recall that most had geographical exploration as their main objective and had little time for oceanography. In some instances very full details are given, in others much that would have been of value to both ecology and zoogeography is lacking. However, enough has come down to permit us to build up a fairly accurate picture of the natural environment of the southern crinoids and to say something of how they occur and are distributed in the circumpolar sea. The best documented and best preserved collections are those of the vessels of the former Discovery Committee which, under the leadership of the late Stanley Kemp and his associates, dredged and trawled in many parts of Antarctica, on the Patagonian shelf and round the oceanic islands scattered about the

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southern continent.* This again is not surprising since these expeditions were primarily devoted to oceanography.

Appendix II in short presents the data upon which much of this paper, in so far as it concerns the comatulids of the south polar shelves, is based.

Table E in appendix II gives a corresponding list for the comatulids and other crinoids of the abyssal circumpolar sea. It is not arranged chronologically but in order of decreasing latitude north of 72° S.

Need for further sampling and taxonomic study

The trawling and dredging stations of the expeditions that have visited Antarctica and the circumpolar sea are shown in figure 3, the plotted positions referring exclusively to places where successful operations were conducted and the material obtained was examined for comatulids. They date from the time of the *Challenger* and include the observations of all vessels that came after her down to the time of the fifth and last pre-war commission of R.R.S. *Discovery II* in 1937–39. It will be seen that on the continental platform from the Ross Sea westwards to Enderby Land, and round the coasts of Graham Land, sampling has been reasonably good. There are, however, wide unsampled gaps, notably on the Atlantic side and again on the Pacific side. To seaward the abyssal sea, especially along the continental slope, is but poorly covered, so poorly in fact that I would hesitate even now to say whether the animals we repeatedly encounter on the shelf are truly shallow-dwellers or whether they range downwards into the deep ocean to abyssal or near-abyssal levels. On the Patagonian shelf, round South Georgia, the South Sandwich Islands, Bouvet, Gough, Tristan, Prince Edward and Marion, the Crozets, Kerguelen, Heard, Macquarie and Peter I Island, sampling is good or at any rate fair. Apart from some harbour dredging, however (p. 359), little has been done near the South Orkneys. Holdgate (1960), Mackintosh (1960), Darlington (1960), Knox (1960), and others, have all called attention to the need for further sampling in the southern field and for closer study of the taxonomy of species, Knox observing that too often new species had 'been erected on single specimens from one locality without reference to comparative material'. The gaps in the field that have yet to be filled can be seen at a glance in figure 3. Some of them in fact may already have been filled but the material obtained during the massive international operations of recent years has not yet been fully worked up. The need for large accumulations of comparative material cannot of course be overstressed, especially in so far as it affects the comatulids, the majority of which are represented in our collections by very few or single specimens. Other groups it is true are better represented, and in many instances we do in fact have a very considerable body of comparative material, especially among the collections of the former Discovery Committee. Much valuable taxonomic work on this has already been done, although as Knox suggests there is room perhaps for further study and revision. Obviously if in the long run we are to say that such and such a species is circumpolar we must be certain that our specimens, separated though they might be by thousands of miles of ocean, are in fact specifically identical, and not, as they could

* We must include here the records of the *Challenger* and *Valdivia* although both just failed to reach the high Antarctic continental platform. *Challenger*'s records are particularly valuable where the off-lying islands are concerned.

be, different species or at any rate racially distinct. The more specimens we can examine, therefore, and examine critically, the better. Even in the plankton of the seemingly boundless sea we find zoogeographical divisions for long unsuspected simply because in the past we did not look at enough material and taxonomic study had been inadequate. I refer particularly to the Subantarctic and Antarctic populations of the arrow worms, *Eukrohnia hamata* and *Sagitta gazellae*, which now, following the close examination of some hundreds of thousands of specimens, prove to be racially if not subspecifically distinct and to be separated by the Antarctic convergence (Marr 1936; David 1955). As Cragg (1960) has said: 'The biogeographer's units are made by the taxonomist' and since it is he alone who is equipped to deal with problems of relationship among groups of species it is on his verdict that the generalizations of the biogeographer must be based.

Description of the shelf

Zoogeographical divisions

In his *Zoogeography of the sea*, Ekman (1953) divides the shelf into two provinces, a *high-Antarctic* and a *low-Antarctic* province, the former including the shallow waters adjacent to the continental land,* together with those of the South Shetlands, the South Orkneys, the South Sandwich group and Bouvet, the latter the coastal waters of South Georgia including the Shag Rocks. In essence his high Antarctic shelf is the same as Regan's (1914) *Glacial District* for fishes, except that Regan includes South Georgia in his glacial zone. Here I use the terms 'high continental shelf' (or 'high shelf') to designate the coastal waters of Antarctica (including Graham Land with its adjoining islands), and 'outlying shelves' to designate the coastal waters of the South Orkneys, the South Sandwich Islands, South Georgia (with Shag Rocks), Patagonia (with Birdwood Bank), Bouvet, Gough, Tristan, Marion and Prince Edward Islands, the Crozets, Kerguelen, Heard and Macquarie (see figure 1). This, it is true, is an arbitrary division which may not hold good for other groups. In so far as the comatulids are concerned, however, it does in fact separate two provinces that (p. 339, table 1) seem to have little in common.

Width

The high shelf (figure 1) varies greatly in width and, even with its seaward limit based on the 1000 m line, is inclined in many places to be rather narrow. It is generally narrow off the long stretch of coastline that reaches from Cape Adare westwards to Coats Land, and very narrow indeed between Enderby Land and Coats Land. It is very wide in the Ross Sea where it extends up to nearly 400 miles out from the barrier coast, wide again at the head of the Weddell Sea and on the east side of Graham Land, and rather wide on the Pacific side except off Marie Byrd Land. Between Enderby Land and Coats Land, however, it is not in fact so narrow as it appears on many charts, for in most parts of this ice-bound coast, and for a long way to the west and south-west, the polar ice-cap pushes its perpendicular cliffs out to sea well beyond the underlying shore-line,† creating in many places *quasi*-pelagic coasts (Marr 1962) under which, owing to the absence of floating plant

* Or what seems to be the continental land. It now appears that, blanketed by the ice-cap, a deep channel connects the Ross with the Bellingshausen–Amundsen Seas (Bentley & Ostenso 1961).

† Brown, Mossman & Pirie (1906), Shackleton (1919), Filchner (1922), Christensen (1938), Swithinbank (1957*a*, *b*), Fuchs & Hillary (1958), and others.

life, the shelf fauna is probably not so rich and varied as in other parts of the coastal platform where there is a true shore-line and the ice-sheet does not protrude. Even so, without the seaward-thrusting ice-cap, the high shelf on the Atlantic side (Mackintosh 1960, fig. 74) would still be very narrow.

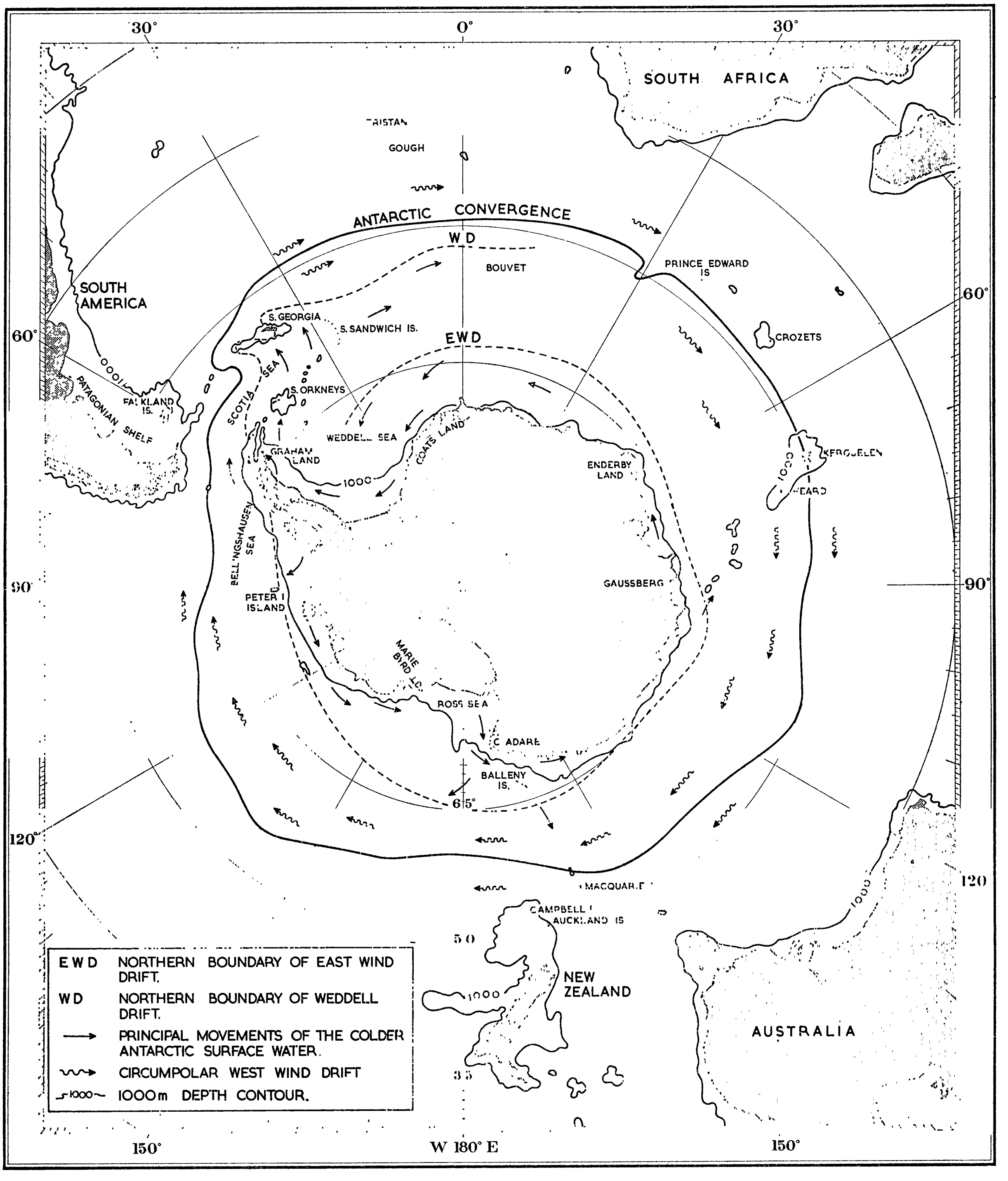

FIGURE 1. Map of Antarctica and its surrounding oceanic islands, with the seaward boundary of the shelf waters based on the 1000 m line, showing principal place names, hydrological boundaries, surface water movements and other features mentioned in the text, the hydrological boundaries and water movements following Deacon (1937) and Mackintosh (1946).

Isolation

Mackintosh (1960) calls attention to its isolation, noting that Antarctica is surrounded by a belt of deep, cold ocean, generally very wide, which constitutes a rather effective barrier to shelf-living organisms, suggesting, however, that submarine ridges radiating from the continent, notably the Scotia Arc and the Kerguelen–Gaussberg Ridge, may offer routes or stepping stones for dispersal. There is, however, no continuous connexion of the high continental shelf with the outlying shelves, and as Ekman has said, the zoogeographer 'runs here no risk of drawing an artificial boundary where nature has none', nature herself having drawn it 'with all desirable clarity'. He recalls too the old saying of Linnaeus, 'Natura non facit saltus' observing that in Antarctica she has in fact produced an exception not unwelcome to regional zoogeography.

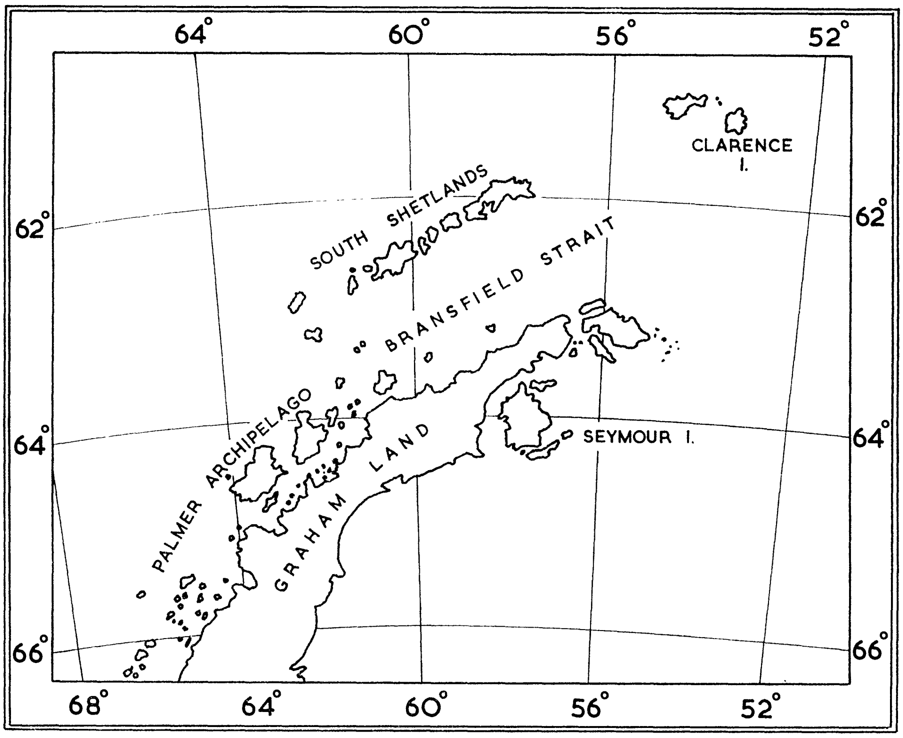

FIGURE 2. Map of the Graham Land region showing principal place names mentioned in the text.

Although, however, cut off in most parts from the other southern continents (and in parts from its own scattered oceanic islands) by a deep and generally wide abyssal sea, the high continental platform today, as Broch (1961) points out, is in free communication, through the archibenthal region, with the deep ocean, there being no sharply defined thermal or salinity boundaries, or major obstructions such as, for instance, are presented by the shallow Bering Strait, to prevent the free exchange (or dispersal) of benthic life between shelf and deeper levels, or vice versa.

Various estimates have been given as to how long Antarctica has remained isolated from the rest of the southern world. According to Wegener (1912) it would appear to have been cut off for only about a million years, since in fact from about the beginning of the Pleistocene. Both Regan (1914) and Ekman (1953), however, postulate a much longer isolation, Regan, in view of the highly successful speciation that has occurred among the Nototheniiformes, the dominant fish group of these far southern waters, suggesting that the south polar continent has stood remote from northern influence, its coasts 'washed by a cold sea', probably throughout the Tertiary Period. It is fair to add, however, that Couper (1960) finds that in the late Tertiary Antarctica had a temperate land fauna, and this, as Stephenson (1960) remarks, must have been associated with temperate-type littoral and sublittoral animals. From Regan's estimate, however, if it be true, the *Sechsten Erdteil* of Filchner (1922) would appear to have been isolated for approximately 60 times longer than the Wegener hypothesis would allow. In any case, even if Wegener is right, recent calculations by Cole (1961), based on the potassium–argon method, now put the Pleistocene as going back nearer two million rather than a million years.

Depth and seaward boundary

I take the edge of the shelf (figure 1) as the 1000 m line and there are several good reasons for choosing this at first sight very arbitrary limit. First, the high shelf, as continental shelves go, is rather deep, in many places distinctly deep. In general it varies between shoal depths and 500 m, but as Law (1961) points out the majority of the soundings lie in the range 300 to 500 m. It is distinctly deep in the Ross Sea, the greater part of which (Herdman 1948) has an average depth of some 600 m or more. And there are still deeper holes in this region, especially at the western end of the Ross Barrier and off the Victoria Land coast. Secondly, the high-shelf comatulids (p. 345, table 4) have a wide bathymetric range, *Promachocrinus kerguelensis*, for instance, having been recorded down to 1080 m and *Florometra mawsoni* and *Anthometra adriani* down to 917 m. Thirdly, and perhaps most important, the 1000 m line must lie very close to the seaward boundary recently proposed by Law (1961) who writes, 'I would like to suggest that maps and charts of Antarctic water delineate as accurately as possible the edge of the continental shelf, using as a criterion not some arbitrarily chosen depth (e.g. 400 fathoms) but the place, irrespective of small variations in depth, where the fairly level sea bed of the continental platform suddenly turns downward to plunge to great depths. This exact, rather than arbitrary, delineation would be of interest to many users of the charts'. He gives the following two examples of sudden plunging to abyssal levels. Both are from observations made while leaving the shelf:

480 to 1640 m and deeper in 5 miles of sailing;

380 to 2000 m and deeper in 7 miles of sailing.

Clearly my 1000 m line in most places must lie within a mile or two (often perhaps much less) of the line along which this sudden change takes place.

It follows from the above that the high continental platform, as designated here, will, along with a true shelf fauna, include the animals of the archibenthal (edge of shelf to 1000 m) zone. Ekman also includes this zone in his general survey of the shelf fauna.

In his recent survey of the zoogeography of the high continental platform Broch (1961), in view of the narrowness and relatively great depth of certain parts of it, concludes that 'the bottom only deserves the designation of a (continental) shelf in small and mostly well-separated localities. This is the case, for example, around the Balleny Is., around the South Shetlands Is., in the Ross Sea, and in scattered places elsewhere along the coasts of the

Antarctic Continent. On the other hand, it would be wrong to disregard the steep continental slopes of the mainland. Certainly the upper parts of them harbour a characteristic animal community with several typical neritic species, although even today, we must confess that the benthonic animal world of these shallower localities, and especially

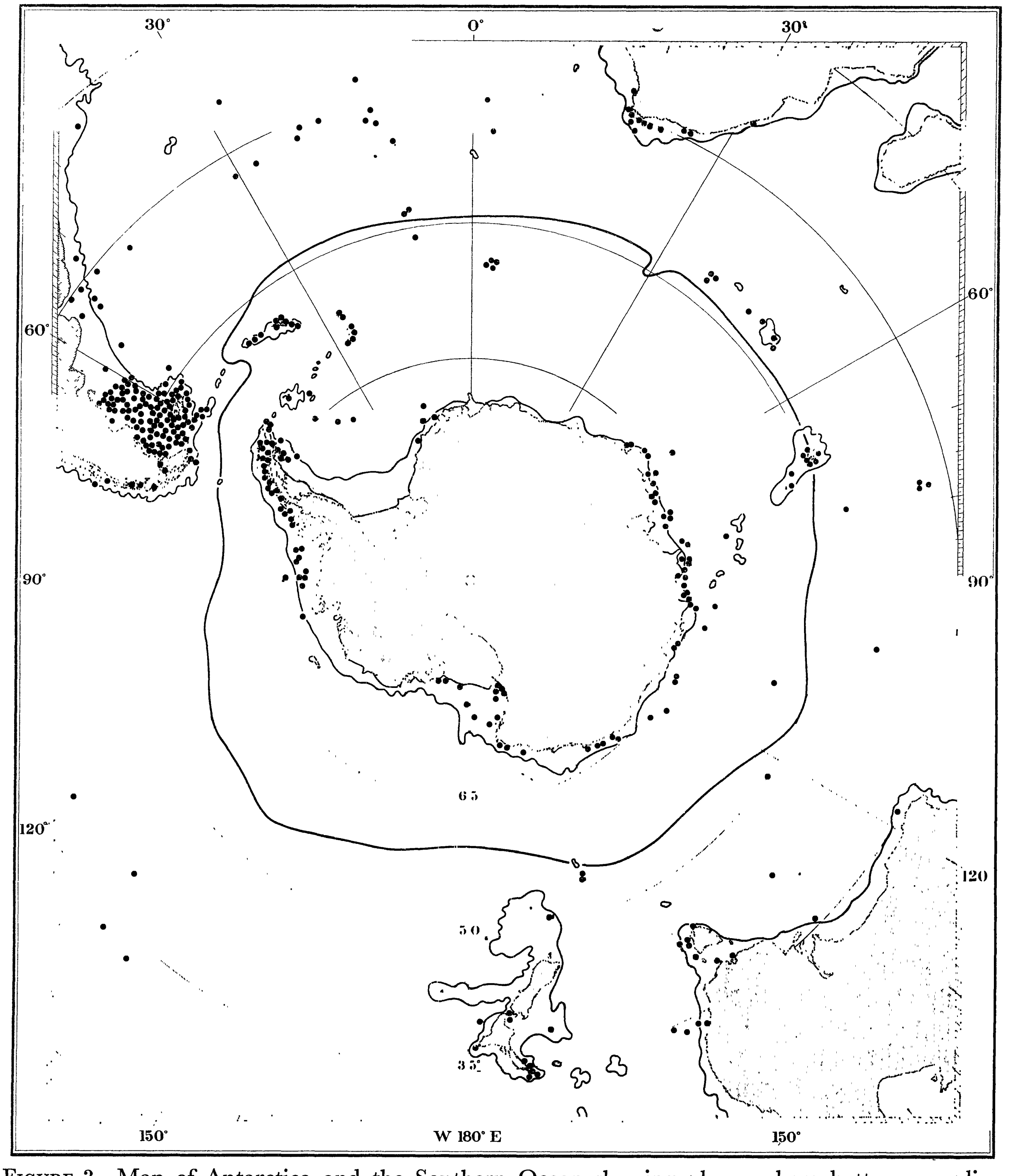

FIGURE 3. Map of Antarctica and the Southern Ocean showing places where bottom sampling (trawling and dredging) has been done. In addition to the positions shown there are hundreds of local inshore dredgings (see p. 359) which cannot be plotted on this scale. Local observations by fisheries and other laboratories on the coasts of South America, South Africa, Australia and New Zealand do not appear on this chart.

the fauna of the upper part of the slopes of the mainland have only been very scantily explored, if at all, the fringing pack ice presenting a great obstacle to the working of gear'. It will be seen, however (figure 3), that in certain places the high shelf, or what in Broch's opinion passes for it, has in fact been moderately well explored, especially round parts of Graham Land and along parts of the coast from the Ross Sea westwards to Enderby Land, although it is equally true that elsewhere there are wide unsampled gaps.

Temperature

The single dominating feature of the high-shelf environment is perennially low temperature, which, except apparently in the Bransfield Strait and in the Palmer Archipelago (figure 2), never rises above 0 °C. Even in the Graham Land region, however, the highest bottom temperature recorded, where comatulids are present, is only 0·55 °C and this was obtained not on the bottom itself but 15 m above it. In fact none of the positive values recorded from this, the most northerly part of the high shelf, was actually obtained from the bottom. Elsewhere round the continental platform the bottom temperature as a rule is below −1·00 °C, conspicuously (appendix II, table C) in the Ross Sea. It is perhaps largely owing to these frigid conditions, thought by some (p. 332) to have endured for a very long time, that a multi-speciated comatulid fauna in this coastal belt has evolved and flourished. Moreover, this frigid environment which has endured for so long is likely to persist for an immensely long time to come, for as Murphy (1962) has said of Antarctica: 'The site of a present-day ice age more stupendous than the northern Pleistocene glaciation, it thus far discloses no sign of a coming interglacial period. The effective double factors of isolation and insulation* seems to forestall that'. How different is the position on the outlying shelves, where positive temperatures prevail, and the comatulid fauna as a whole, especially (appendix II, table D and pp. 354 to 357) on the Patagonian shelf, is distinctly poor in species.

The high-shelf floor with notes on the behaviour of bottom gear

In many places round Antarctica the high continental platform (appendix II, table C) is known to be very muddy, especially where the great 'barrier snow plains', as Wilson (1907) has called them, thrust their perpendicular cliffs out to sea beyond the true shoreline, discharging a heavy load of finely divided terrigenous material. There are enormous areas of muddy ground, for instance, at the head of the Ross Sea and far south in the Weddell Sea, where immense barriers, or ice shelves as they are now called, discharge their glacial ooze. Muddy samples, too, have been obtained in many parts of the Australian–Indian Ocean sector. Other parts of the coastal platform seem to be rough and stony, or rocky, as for instance off Clarence Island, in the Bransfield Strait and along much of the Palmer Archipelago. The muddy substratum at times may be much encumbered with stones and erratic boulders which on occasion can play havoc with dredges and trawls. I recall a time off Enderby Land when I shot the 40 ft. otter trawl (*OTL*) in 209 m. Within 5 min it had hitched up round some major obstruction, probably an erratic boulder, and, with the dynamometer registering $2\frac{1}{2}$ tons, the $2\frac{1}{2}$ in. manilla stop holding the dynamometer to the warp parted like thread. The gear was hauled in badly damaged,

* He uses the term in the sense that meteorologically the south polar continent is buffered from the rest of the world by a permanently cold ocean and an overlying belt of circling winds.

with a 30 ft. rent in the belly. Yet, such was the profusion of benthic life at that place, the cod-end contained a rich and varied assortment of animals. Experiences such as this have been recorded by many Antarctic expeditions. In general, judging from the soundings, the shelf floor seems to be rather uneven. Indeed Lisitzin & Zhivago (1960) in places find it to be distinctly 'hillocky'.

In the Ross Sea, however, we get a somewhat different picture. In January 1936 we dredged on the muddy bottom there nineteen times (our total dredgings) without mishap, even using the large 40 ft. otter trawl with the most gratifying results. I got the distinct impression that the bottom there was inclined to be less uneven than elsewhere, to be little encumbered with stones or rocks, and apparently free from major obstacles such as large erratic boulders. And this could well be, for the water in these very high latitudes is intensely cold (−1·80 °C or less) from surface to bottom and I suspect that icebergs calved from the Ross Barrier may be passing clean over the coastal platform without dropping their erratics (if in fact they are carrying them at all) until they reach the deep oceanic water, with its warm (positive) layer, beyond. If this is so, I believe that from the purely collecting point of view extensive exploration of the Ross Sea floor, *with the right gear*, will prove to be more rewarding, and far easier to accomplish, than anywhere else round the continent. On the deep ooze of these very high latitudes we used one particular apparatus with conspicuous success. This was the iron frame and skids of the Russell bottom net to which we bent an ordinary rectangular dredge bag (appendix I, table A) instead of the usual stramin net. The Russell frame has a heavy chain footrope and this evidently stirs up the animals in the mud, or those that are creeping about above it, and they pass upwards into the net clean and undamaged, the fine ooze, which might otherwise have swamped and injured the specimens, escaping through the coarse meshes of the bag. The substratum, if wanted, can of course readily be sampled with the conical dredge (*DC*). I have never in fact seen benthic animals brought to the surface so nearly in their natural state as those we took with this modified gear (*DRR*) from the floor of the Ross Sea shelf. In spite of its raising skids the Russell bottom net, with dredge bag attached, has been used with marked success (appendix II, table C, Stations 1948 and 1952) on stony ground, bringing up quantities of boulders up to 6 in. in diameter along with fine specimens of comatulids in moderate to moderately large numbers.* Its heavy chain footrope I imagine must be largely responsible for this. I would recommend, too, in the apparently snag-free Ross Sea region, extensive use of the 40 ft. *OTL* and even the still larger commercial otter trawl (*OTC*), both with fine nets attached, for there seem to be fish about in plenty and with either apparatus enormous quantities of other material can be obtained in a most satisfactory condition. Suitable ground for such large apparatus may be found (although perhaps not very often) on other parts of the shelf, such as that, for instance, encountered (appendix II, table C) at *Discovery* (British, Australian, New Zealand) Station 107. Possibly modern echo-ranging (Stride 1961 *a*, *b*) and submarine photography will show shortly where such places are.

The same easy trawling conditions were encountered by H.M.N.Z.S. *Endeavour* in the Ross Sea in January and February 1959, Reseck (1961) noting that in view of the success

* I use the expression 'moderate to moderately large numbers' in a strictly relative sense. The vast majority of the comatulid samples from Antarctica (p. 340) are in fact very small.

with which he was using certain very small dredges and trawls 'gratifying results might be obtained from use of a large trawl specially designed for fish'.

Turning now to appendix I (table B) it will be seen that if we disregard the relatively enormous catch of comatulids obtained in an exceptionally lucky whole hour's fishing with the large 40 ft. otter trawl (*OTL*), the large heavy dredge (*DLH*) would appear to have been more successful in removing crinoids from the bottom, than have the several other gears for which 'fishing time' has been estimated. This is perhaps to be expected since with its heavy, biting, bevelled frame it digs deeply into the substratum, removing rocks and stones, and such animals as may be lurking between them, more readily than the modified Russell net (*DRR*), the Monegasque trawl (*TML*) or even the large otter trawl could be expected to do. However, it suffers from the great disadvantage that within a matter of minutes it fills itself up so completely with rubble that the specimens we are hoping to gather are not only excluded but such as may be taken are often so crushed and mangled that, having lost much of their original form and beauty, they prove in the long run to be a serious embarrassment to the taxonomist. It is for this reason that the otter trawl (*wherever trawlable ground is to be had*), the Monegasque trawl and above all the modified form of Russell's original bottom net are so strongly to be recommended.

Zoogeography of the shelf

Salient features

A general account of the zoogeography of the continental shelf has already been given by Ekman (1953), and I quote here from a summary of his major findings recently given by Mackintosh (1960).

'The fauna is rich in species compared with the Arctic, but the outstanding feature is its extreme independence. That is to say it has very few species in common with the shelf faunas of the more temperate coasts. Taking two of the better known groups, Ekman (1953) estimated that of the fishes no less than 90 % of species and 65 % of genera are endemic in the Antarctic, and that in the echinoderms the corresponding figures are 73 % and 27 %, which are also exceptionally high. Ekman also points out that the high proportion of endemic species, which is also observed in other groups, emphasizes the isolation of the fauna, and that the high proportion of endemic genera indicates isolation for a very long time.'

Having regard to the polar environments as we know them today it is somewhat surprising, as Ekman has noted, that the Antarctic shelf fauna should be so rich in species and its northern counterpart so relatively poor. The total area of shelf floor girdling the Arctic basin, for instance, is much greater than that of the narrow coastal platform surrounding Antarctica, and, moreover, whereas the Arctic shelf is in continuous connexion with the boreal faunas along two Atlantic and two Pacific continental coasts, the far southern continental platform is everywhere cut off from other lands by a deep, in most parts wide, abyssal sea. Both 'accidents of geography', as we may call them, suggest that the northern, rather than the southern, pole has for long offered the better conditions for speciation. Paradoxically, however, the converse is true and Ekman suggests that the main reason for this is that Antarctica has probably enjoyed a climate undisturbed by any major

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change from the end of the Cretaceous onwards. It is at any rate clear, he says, that its coastal platform has been a locus of development for marine animals over an immense period and this by itself he suggests might be enough to account for its wealth of species. Old, however, though it may be, the fauna of coastal Antarctica may not in fact be quite so ancient as Ekman postulates, nor need it have endured, and thrived in, the extreme cold in which we find it today for so long as he suggests is possible. For recently Couper (p. 333) has produced evidence that the southern continent had a temperate land fauna in the late Tertiary, Stephenson noting that this must have been associated with temperate-type littoral and sublittoral animals. Even so, allowing that the present-day climate of Antarctica does only go back to the beginning of the Quaternary, its shelf fauna would have enjoyed a stable unchanging climatic régime for a million years or more (but see p. 333).

In the Arctic the animals of the shallow sea have not, it seems, enjoyed the same stability of environment for so long. It is possible in fact, as Ekman suggests, that faunistic development, at least once, was arrested there, especially during the Quaternary Period when at the height of the glaciation the fall in temperature was maximal and the ice-sheet, like a 'lethal roof', extending far beyond its present limits, darkened the shallow sea. Moreover, according to Schott (1926) and Arldt (1919, 1921), during this period former land bridges, represented today by rises such as the Wyville Thompson Ridge and the shallow water of the Bering Strait, for thousands of years almost completely shut off the Arctic basin from the other oceans of the world, presenting a further limiting factor to the development of a rich and varied shelf fauna in these high latitudes.

Turning to the comatulids we find seventeen of them (p. 339, table 1) in the coastal waters of Antarctica, with more, as Clark (1937) has predicted, perhaps many more, to be discovered. On the Arctic shelf there are only two (Clark 1915). Taking the echinoderms as a whole Ekman reckons there are nearly five times as many shallow-living species in far southern waters as there are round the northern pole.* Broch (1961) too, quoting largely from Ekman, gives prominence to the wealth of echinoderm species girdling the southern continent and its surrounding oceanic islands, suggesting that this must spring from the fact that round the southern pole there has for long been 'uninterrupted intercommunication' between the neritic and deep-sea floors through the archibenthal region, the circumpolar sea having nothing to hinder the free dispersal of animals, in this or that direction, like such barriers as are presented by the Bering Strait or the North Atlantic Ridges.

The crinoids of the southern shelf and abyssal seas

As we have already seen seventeen comatulids are known from the high continental platform, a further five, recorded on the outlying shelves of South Georgia, Prince Edward and Gough (table 1), bringing the total so far discovered in the coastal waters of Antarctica and its scattered off-lying islands and island groups to 22†. Of these no less than fifteen

* He claims too that the Arctic shelf does not possess a single sea-urchin, but this is incorrect because I have often dredged up specimens of the common boreal form, *Strongylocentrotus dröbachiensis*, from the shoal water north of Spitsbergen, and between there and Franz Josef Land, in 79–82° N (Marr, 1927). Surprisingly Broch (1961), on the echinoids of the north polar shelf, repeats Ekman verbatim.

† A single specimen of *Florometra magellanica* taken by the *Challenger* in a west Patagonian channel (Carpenter 1888) has not been included in this table.

Table 1. List of the comatulids known from the high continental platform and from the coastal waters of the surrounding oceanic islands

species	high shelf	South Orkney	South Sand-wich	South Georgia	Bouvet	Heard	Kerguelen	Patagonian	Macquarie	Prince Edward	Crozets	Tristan Gough
		outlying shelves: south of Antarctic convergence						outlying shelves: north of Antarctic convergence				
Promachocrinus kerguelensis Carpenter	+	−	+	+	+	+	+	−	−	−	−	−
Florometra mawsoni A. H. Clark	+	−	−	−	−	−	−	−	−	−	−	−
F. goughi John[1]	−	−	−	−	−	−	−	−	−	−	−	+
Hathometra exigua Carpenter[2]	−	−	−	−	−	−	−	−	−	+	−	−
Anthometra adriani (Bell)	+	−	−	−	−	−	−	−	−	−	−	−
Solanometra antarctica (Carpenter)[3]	+	−	−	−	−	+	−	−	−	−	−	−
Eumorphometra aurora John[4]	+	−	−	+	−	−	−	−	−	−	−	−
E. fraseri John[5]	+	−	−	−	−	−	−	−	−	−	−	−
E. marri John[6]	+	−	−	−	−	−	−	−	−	−	−	−
E. hirsuta (Carpenter)[7]	−	−	−	−	−	−	−	−	−	+	−	−
E. concinna A. H. Clark[8]	+	−	−	−	−	−	−	−	−	−	−	−
Kempometra grisea John[9]	+	−	−	−	−	−	−	−	−	−	−	−
Anisometra frigida John[10]	+	−	−	−	−	−	−	−	−	−	−	−
Phrixometra longipinna var. *antarctica* John[11]	+	−	−	+	−	−	−	−	−	−	−	−
P. nutrix (Mortensen)[12]	+	−	−	−	−	−	−	+	−	−	−	−
P. rayneri John[13]	−	−	−	+	−	−	−	−	−	−	−	−
Isometra vivipara Mortensen	+	−	−	−	−	−	−	+	−	−	−	−
I. flavescens John[14]	−	−	−	+	−	−	−	−	−	−	−	−
I. graminea John	+	−	−	−	−	−	−	−	−	−	−	−
I. hordea John[15]	+	−	−	−	−	−	−	−	−	−	−	−
Notocrinus virilis Mortensen	+	−	−	−	−	−	−	−	−	−	−	−
N. mortenseni John	+	−	−	−	−	−	−	−	−	−	−	−

[1] Known only from two specimens taken near Gough Island.
[2] Known only from three specimens taken near Marion and Prince Edward Islands.
[3] Known only from eleven specimens taken off Heard Island and from eight specimens taken off Adélie Land.
[4] Known only from two specimens taken off Enderby Land and from one specimen taken near South Georgia (Shag Rocks).
[5] Known only from one specimen taken north of the South Shetland Islands.
[6] Known only from one specimen and fragments of another taken near Clarence Island.
[7] Known only from one specimen taken near Prince Edward Island.
[8] Known only from five specimens taken off Gaussberg.
[9] Known only from two specimens taken near Clarence Island.
[10] Known only from one specimen taken off MacRobertson Land.
[11] Known only from four specimens taken near Clarence Island and from one specimen taken off South Georgia.
[12] Known only from one specimen taken in the Bransfield Strait and from another taken on the Burdwood Bank.
[13] Known only from one specimen taken near South Georgia (Shag Rocks).
[14] Known only from twelve specimens taken near South Georgia (Shag Rocks).
[15] Known only from eight specimens taken near Clarence Island and from four specimens taken north of the South Shetland Islands.

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seem to be rare or very rare. We must remember, however, that with bottom-living animals the rarity we so often record may after all only be an appearance, since such as might chance to be in crevices of the rock or between large boulders might be beyond the reach of our dredges and trawls. In so far then as appearances go it is evident that of the high-shelf species alone as many as ten are rare or very rare and that only two, *Phrixometra nutrix* and *Isometra vivipara*, have been recorded north of the Antarctic convergence. *I. vivipara* might also be included among the rarer species. It has rarely been encountered on the high continental platform (only twice off Graham Land), and even more rarely on the Patagonian shelf, where its principal centre of abundance, if (pp. 354 to 357) we can call it such, seems to be, allowing that is for the relatively enormous scale of the trawling and dredging (pp. 354 to 357) that has been conducted there. There is some doubt too (p. 352) as to whether the Antarctic and Patagonian specimens of this species are in fact the same.

As mentioned in the introduction full particulars of the occurrence and natural environment of the southern crinoids are given in appendix II (tables C, D and E). In compiling this information authors have been consulted as follows:

Carpenter (1888)	Mortensen (1918)
Murray (1895)	Clark (1937)
Chun (1903)	Johnston (1937)
Bell (1908)	John (1938)
Bather (1908)	John (1939)
Wilton, Pirie & Brown (1908)	Vaney & John (1939)
Harmer & Lillie (1914)	Mawson (1940)
Clark (1915)	Madsen (1955)
Bell (1917)	

It will be seen that of the twenty-two known shelf species (table 1) the majority are confined to the high continental platform. Six of this far southern coastal group, *Promachocrinus kerguelensis*, *Solanometra antarctica*, *Eumorphometra aurora*, *Phrixometra longipinna* var. *antarctica*, *P. nutrix* and *Isometra vivipara* are known also from the outlying shelves, the last two as already said having been reported north of the Antarctic convergence. Besides *P. nutrix* and *I. vivipara* only three other species are known from island coasts north of the convergence. They are *Florometra goughi* from near Gough, *Hathometra exigua* from near Marion and Prince Edward Islands and *Eumorphometra hirsuta* from near Prince Edward Island. None of these three, however, has been recorded on the high continental platform, nor have the *Isometra flavescens* and *Phrixometra rayneri* of South Georgia. Altogether it would appear that taking the southern comatulids as a whole it is the coastal waters of continental Antarctica that have been the scene of the most successful speciation. From South Georgia, for instance, the South Sandwich Islands and the Patagonian shelf (including Burdwood Bank) only seven species are known in spite of the proximity and topographical connexion of these regions with the continental platform of Graham Land. It will be seen too (appendix II) that, Station 107 apart (p. 343), the southern comulatids have never been taken in large numbers. Of the 149 samples from shelf and abyssal water only 3 (2%) have between 50 and 100 specimens, only 22 (15%) 10 to 50 specimens, the vast majority (83%) having only 1 to 10 specimens. These low figures, however, should be regarded with caution, for they may simply be a measure of the inadequacy of our bottom gear which, it is possible (cf. plate 49), may be revealing fewer specimens than are actually present.

Taking first the high shelf (appendix II, table C), it will be seen that a characteristic group of species comprising some or all of the following—*Promachocrinus kerguelensis*, *Anthometra adriani*, *Florometra mawsoni*, *Notocrinus virilis*, *N. mortenseni* and *Isometra graminea** —has repeatedly been recorded all round Antarctica by every expedition from which there are records. I shall refer to this as the *Promachocrinus–Anthometra* complex. As a rule it is dominated by *P. kerguelensis*, but where this species is absent or scarce, which is not very often, the dominants may be *A. adriani*, *F. mawsoni* or *N. virilis*. Although further exploration of the slope and abyssal depths may lead me to qualify my opinion I believe this group to be peculiar to the high shelf, a unique community in fact that, *P. kerguelensis* excepted, does not extend to the outlying shelves (appendix II, table D), even where such are connected by submarine ridges, and is evidently absent from the abyssal sea. In fact it would appear (appendix II, table E) that immediately we go deeper than 1000 m we encounter a new world of crinoids.

Until much further exploration has been done, however, especially in the deep ocean, I hesitate to say whether the species recorded from both high and outlying shelves are in fact exclusively shallow-water forms or whether, as *P. kerguelensis* (p. 345, footnote †) would appear to do, they range downwards into the abyssal sea. Certainly such evidence as we have suggests they are exclusively shallow, and it may be very significant that a single but highly successful trawling with the large *TML* from the *Discovery* just over the high continental shelf in 1266 m (appendix II, table E) did not produce the characteristic *Promachocrinus–Anthometra* complex but a single (new) species, *Florometra spinulifera*, which has not been recorded from the continental platform.

Although she dredged widely on some of the outlying shelves, especially at Prince Edward, Marion, the Crozets, Kerguelen and Heard, the *Challenger* just failed to reach the high continental platform. The results of her deep-sea observations, however (appendix II, table E), together with those of the *Belgica*, *Valdivia*, *Scotia*, *Gauss*, *Aurora* and *Discovery* (Mawson) do help us to judge whether the species recorded from southern coastal waters are in fact, as they appear to be, true shallow-water forms or whether they range into the abyssal sea. Or shall we say they help us provisionally to judge, for as yet sampling in the deep ocean, especially just beyond the shelf (or shelves), is too scanty to permit us to decide what the true situation is.

Relative abundance

The relative abundance of the seventeen high-shelf species and of the eleven from the outlying shelves is shown in tables 2 and 3. *P. kerguelensis* is clearly dominant on the continental platform. Of fairly, but far less, common occurrence there, are *A. adriani*, *F. mawsoni* and *N. virilis* with *N. mortenseni* and *I. graminea* a long way behind. The remaining high-shelf species (always provided we can trust the evidence of our dredges and trawls) are manifestly scarcer, the majority of them in fact having been recorded only once or twice. On the outlying shelves *P. kerguelensis* is again a clear dominant with *I. vivipara* in some measure of abundance but still a long way behind. Nine low-shelf species are rare.

* I give these in the descending order of their abundance (see table 2) on the high shelf, not in their correct taxonomic order.

I do not of course claim that these lists are final or that they reveal the true position of the southern comatulids in so far as relative abundance goes. Further exploration, and perhaps submarine photography, may well show that at least some of the species that have so seldom been recorded are commoner than conventional apparatus lets us think.

TABLE 2. RELATIVE ABUNDANCE OF THE SEVENTEEN HIGH-SHELF COMATULID SPECIES BASED ON THE NINETY OCCURRENCES LISTED IN APPENDIX II (TABLE C)

species	total recorded	number of occurrences	% occurrence
Promachocrinus kerguelensis	435	63	70
Anthometra adriani	274	39	43
Florometra mawsoni	99	22	24
Notocrinus virilis	130	18	20
N. mortenseni	35	9	10
Isometra graminea	17	6	7
I. hordea	12	4	4
Eumorphometra concinna	5	4	4
Solanometra antarctica	6	2	2
Isometra vivipara	5	2	2
Eumorphometra aurora	2	2	2
Phrixometra longipinna var. *antarctica*	4	1	1
Eumorphometra marri	2	1	1
Kempometra grisea	2	1	1
Eumorphometra fraseri	1	1	1
Phrixometra nutrix	1	1	1
Anisometra frigida	1	1	1

TABLE 3. RELATIVE ABUNDANCE OF THE ELEVEN COMATULIDS OF THE OUTLYING SHELVES BASED ON THE FORTY-EIGHT OCCURRENCES LISTED IN APPENDIX II (TABLE D)

species	total recorded	number of occurrences	% occurrence
Promachocrinus kerguelensis	113	30	63
Isometra vivipara	68	13	27
Solanometra antarctica	11	2	4
Hathometra exigua	3	2	4
Isometra flavescens	12	1	2
Florometra goughi	2	1	2
Eumorphometra hirsuta	1	1	2
E. aurora	1	1	2
Phrixometra nutrix	1	1	2
P. rayneri	1	1	2
P. longipinna var. *antarctica*	1	1	2

Concentration on the bottom

From the data presented in appendix II it is evident that the high-shelf comatulids, although widely distributed round the continent, are never encountered in dense concentrations. They can never, I am sure, be packed so closely as are, for instance, certain ophiuroids which sometimes are brought up in their thousands in the fine nets attached to trawls, leaving one with the distinct impression that there must be many places where the shallow sea floor is literally carpeted with these gregarious animals. In the crinoids the catch-figures, even for what are evidently the commoner species, are without exception persistently low, so low in fact that one can hardly avoid the conclusion that these animals exist for the most part as solitary individuals more or less widely separated one from another.

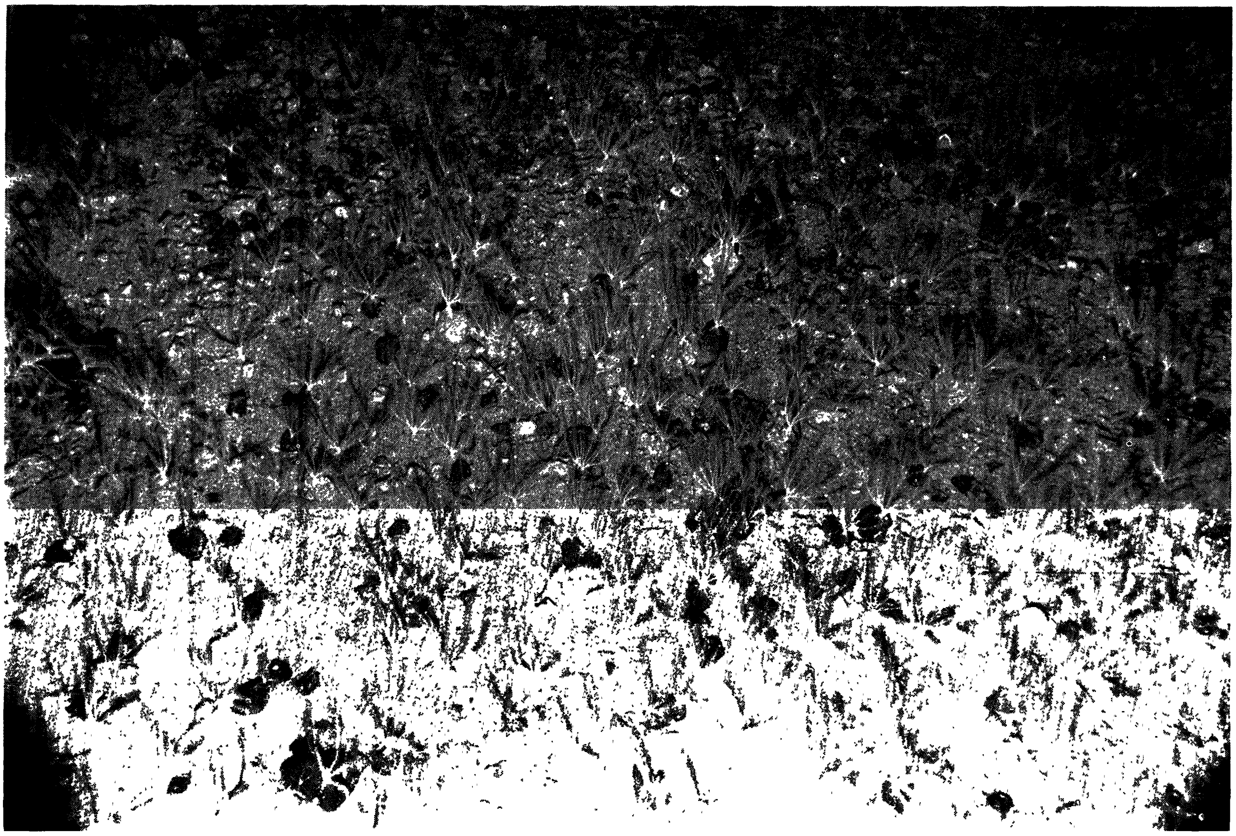

FIGURE 12. A photograph by Dr A. S. Laughton taken on the Galicia Bank in 651 m, 42° 40′ N, 11° 35′ W on 19 June 1958, showing part of a great field of comatulids evidently all belonging to the same, perhaps gregarious, species. Area of picture $1\frac{1}{2} \times 2\frac{1}{2}$ m.

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(*Facing p.* 343)

In other words, although mobile enough (p. 358) and therefore capable of congregating, they show little sign of being gregarious. Even the relatively enormous haul of *P. kerguelensis* and *A. adriani* obtained by the British, Australian, New Zealand expedition at Station 107 (appendix II, table C) does not necessarily indicate a particularly dense concentration, for this was the result of a whole hour's fishing with the large 40 ft. otter trawl which in that time may have covered up to as much as 4000 yards of ground (but see next paragraph).

At best, however, we can only judge from appearances, that is from the evidence provided by conventional bottom apparatus, dredges, trawls and so on, and while these, it is true, do not normally remain very long on the bottom some of them have in fact been large enough and been fished for long enough to have given at least some evidence of aggregation if the comatulids were naturally gregarious. Perhaps only submarine photography will reveal the true position. It has already provided clear evidence of gregariousness in certain ophiuroids (Hurley 1959; Czihak 1959) and on several occasions, once on the high shelf, has shown the comatulids to be solitary (Laughton 1959; Bullivant 1961). Laughton (1959) has photographed the sea floor on many occasions at abyssal depths. Some of these pictures show solitary crinoids, others loose aggregations of up to 5 per square metre. He has one remarkable series (unpublished) which shows a great field of comatulids, all apparently the same species, averaging out at about 6 per square foot over an area estimated to be about 1000 square feet. This was at 650 to 700 m on the Galicia Bank off northern Spain and it could have been a heavy local concentration such as this (see below, p. 344) that we chanced upon at Station 107. I am most grateful for his permission to publish one of this series in figure 12, plate 49. It shows that, contrary to what we have so far found on the Antarctic continental platform, the comatulids in certain places may in fact be gregarious.

I would conclude, too, that these animals are not only thinly spread but very unevenly spread, that they occur perhaps in weakly knit clusters, one separated from another by more or less barren gaps of ground. Let us look for instance (appendix I, table B and appendix II, table C) at the occurrences of the *Promachocrinus–Anthometra* complex and the gear in which it has been recorded. It will be seen that the relatively small *DLH*, *DRR* and *TML* quite often produce a distinctly better result than the much larger *OTL* does even when the latter has been up to six times as long on the bottom. This suggests a high degree of patchiness, for if the crinoids were merely thinly (but not unevenly) spread we should expect the apparatus with the largest catching capacity in general to produce the best result.

In the introduction to his report on the crinoids of the Australasian expedition of 1911–14 Clark (1937) wrote: 'Because of their dependence upon a definite and narrowly delineated range of conditions the Crinoidea are very locally distributed in all seas, and although they may be exceedingly abundant in a given region they will not be found unless one happens to hit upon one of the often very circumscribed areas in which they occur. So we may expect for some time to come, new crinoid types will continue to be found in the Antarctic seas, especially in the deeper waters'. While the records to date, it is true, do not suggest that the high-shelf comatulids are anywhere very abundant, they do provide unquestionable evidence of the circumscribed or local distribution that Clark has postulated.

Average scatter

Turning again to appendix II it will be seen that in many instances the smaller apparatus *DLH*, *DRR* and *TML*, remain on the bottom for only about 5 min. During this time, assuming a towing speed of, say, half-a-knot, or perhaps a little more, they would cover approximately 80 to 100 yards of ground. Under these conditions they sample the shelf comatulids, *when they strike them*, with moderate effect. At '*Discovery*' Investigations Station 170, for instance, twenty-eight individuals were captured in 5 min and if we assume them to have been strung out in line ahead evenly along the path of the net it could be argued that it had been striking one every 3 or 4 yards. On the same assumption '*Discovery*' (British, Australian, New Zealand) Station 40 gives one every 2 yards, '*Discovery*' Investigations Station 1952 one every 6 to 8 yards, and '*Aurora*' Station 1 one every 8 yards. These, however, I think are maximal figures, not representative of average scatter. For if we add up the total distance travelled by all the smaller gear, *BNR*, *DLH*, *DRR* and *TML*, for which estimated times of fishing are available, and divide it by the total crinoid catch, the figure for average scatter (towing at half-a-knot) works out at 23 yards. Locally, however, it seems it might not be so wide. At '*Discovery*' (British, Australian, New Zealand) Station 107, for instance, the large *OTL*, fishing for a whole hour, strangely without mishap, at 2 knots probably travelled some 4000 yards. It produced the handsome total of 342 comatulids, representing at the very lowest estimate one very 12 yards. Moreover, we have to allow for the possibility that this gathering was made not in a whole hour but perhaps in half an hour, perhaps, like so many of the specimens in the much smaller dredges and trawls, even in 5 min, and if this were so, we are presented here with a relatively enormously heavy local concentration.

It should be noted that these rough estimates are based on the assumption that the dredge or trawl is taking all the comatulids in its path, and this may be a wild assumption since some may be lurking between large stones or in rock crevices over which the gear is perhaps riding without effect.

Bathymetric range

It is clear from table 4 that the species inhabiting the rather deep coastal platform girdling the continental land have a wide bathymetric range, particularly pronounced in *P. kerguelensis*, *A. adriani*, *F. mawsoni*, *N. virilis* and *N. mortenseni* and probably true for the rarer species had we more observations to show it. The bathymetric range of the outlying species is naturally much narrower since the oceanic islands scattered round Antarctica have shelves of normal depth.

Optimum bathymetric range

The high shelf

The depths of occurrence of the two most commonly occurring forms, *P. kerguelensis* and *A. adriani*, are shown in table 5. In this presentation of the data I have regarded occurrences as having more significance than actual numbers, our dredges and trawls as a rule remaining for too short a time on the bottom to permit us to say whether the numbers we capture are indicative of the real measure of abundance or not. The frequency of occurrence of the other high-shelf comatulids in general is too low to warrant a similar treatment of the data and I have therefore dealt with them by groups showing (table 6) the depths of occurrence of the four commonest species combined, of the thirteen less common or rare species combined (for species in each instance see table 2) and of the total high-shelf comatulids. It will be seen that not one of the seventeen species has been recorded at depths of less than 50 m and that there is only one record (*P. kerguelensis*, one specimen) from between 50 and 100 m. It would seem therefore that on the high shelf at least these animals rarely occur at depths of less than 100 m and are absent from very shallow (inshore) water. In tables 5 and 6 I have expressed the number of occurrences at each

TABLE 4. BATHYMETRIC RANGE OF THE COMATULIDS OF THE HIGH CONTINENTAL SHELF AND OUTLYING SHELVES WITH THE AVERAGE DEPTH AT WHICH EACH SPECIES HAS BEEN RECORDED

	bathymetric range (m)		average depth (m)		number of records	
species	high shelf	outlying shelves	high shelf	outlying shelves	high shelf	outlying shelves
Promachocrinus kerguelensis	92–1080	18–303	383	143	63	32
Anthometra adriani	189–917	—	372	—	36	—
Florometra mawsoni	163–917	—	369	—	22	—
Notocrinus virilis	163–649	—	331	—	18	—
N. mortenseni	194–603	—	365	—	9	—
Isometra graminea	194–567	—	307	—	6	—
I. hordea	117–550	—	358	—	4	—
I. vivipara	150–200	79–350	175	167	2	13
Solanometra antarctica	288–649	137–275	468	206	2	2
Eumorphometra aurora	193–220	177	206	177	2	1
Phrixometra nutrix	206	143	200	143	1	1
P. longipinna var. *antarctica*	550	218	550	218	1	1
Eumorphometra concinna	380–400	—	388	—	4	—
E. marri	550	—	550	—	1	—
E. fraseri	425	—	425	—	1	—
Anisometra frigida	219	—	219	—	1	—
Kempometra grisea	830	—	830	—	1	—
Isometra flavescens	—	177	—	177	—	1
Phrixometra rayneri	—	177	—	177	—	1
Hathometra exigua	—	92–257	—	174	—	2
Eumorphometra hirsuta	—	257	—	257	—	1
Florometra goughi	—	183	—	183	—	1

depth interval as a percentage of the total samplings* at that interval and this shows clearly enough that, whether the species be treated as individuals or by groups, they occur in more or less equal abundance at all levels between 100 and at least 800 m. Below this the sampling begins to be rather poor and I hesitate to say whether the percentage figures for either the individual or grouped species in the 800 to 1000 m and 1000 to 2000 m horizons are reliable or not. There would seem, however, to be a marked falling off in abundance below 1000 m and complete absence from the abyssal sea.† Taking the shelf

* The figures given for 'number of samplings' in tables 5 and 6 are somewhat approximate since for a number of the southern expeditions there are no published station lists and details of the full extent of the trawling and dredging that was done in many instances are vague and hard to trace. However, I have obtained accurate figures for the bottom sampling done by the *Belgica*, *Scotia*, *Gauss*, *Antarctic*, *Terra Nova*, *Aurora*, *Discovery* (Mawson) and '*Discovery*' Investigations and these were the expeditions responsible for by far the greater part of the comatulid collecting on the high continental platform.

† There is, however, one record (appendix II, table C, '*Discovery*' Investigations Station 177) of a true shelf comatulid from what is in fact abyssal water, eight *P. kerguelensis* having been taken at a depth of 1080 m. Since, however, this record comes from the Bransfield Strait, it may rightly be regarded as belonging to the shelf and not to the abyssal sea.

fauna as a whole (table 6) the optimum bathymetric range would appear to lie between 200 and 400 m but many more samples are needed to confirm this.

Such evidence then as we have seems to show that the high-shelf comatulids tend to be rather deep-living animals, rarely found at depths of less than 100 m, and suggests that the optimum bathymetric range for the majority is between 200 and 400 m.

Table 5. Depths of occurrence of the two commonest high-shelf comatulids

bathymetric range (m)	no. of samplings	*P. kerguelensis* no. of occurrences	*P. kerguelensis* % occurrences/samplings	*A. adriani* no. of occurrences	*A. adriani* % occurrences/samplings
0–50	*	—	—	—	—
50–100	61	1	2	—	—
100–200	30	11	37	3	10
200–400	71	30	42	24	34
400–600	40	12	30	7	18
600–800	15	5	33	3	20
800–1000	6	2	33	1	17
1000–2000	6	1	17	—	—
below 2000	38	—	—	—	—

* The number is unknown but clearly (see text, p. 359) they run to many hundreds, not one of which seems to have produced a single comatulid (see however p. 360).

Table 6. Depths of occurrence of the high-shelf comatulids (for species see table 2)

bathymetric range (m)	no. of samplings	four commonest species: no. of occurrences	four commonest species: % occurrences/samplings	thirteen less common or rare species: no. of occurrences	thirteen less common or rare species: % occurrences/samplings	total high-shelf comatulids: no. of occurrences	total high-shelf comatulids: % occurrences/samplings
0–50	*	—	—	—	—	—	—
50–100	61	1	2	—	—	1	2
100–200	30	12	40	5	17	13	43
200–400	71	44	62	13	18	48	68
400–600	40	17	43	4	10	17	43
600–800	15	6	40	2	13	6	40
800–1000	6	2	33	1	17	2	33
1000–2000	6	1	17	—	—	1	17
below 2000	38	—	—	—	—	—	—

* See footnote below table 5.

The outlying shelves

The depths of occurrence of the species from the outlying shelves are shown in table 7 in which I deal individually only with *P. kerguelensis* and *I. vivipara*, the others being far too scarce (table 3) to merit individual treatment. As for the high shelf, however, I again show the depth distribution for the total comatulids. The occurrences only are shown, not expressed as percentages of the total samples, the comatulids of the outlying shelves having no continuity of distribution such as we find on the high continental shelf. *P. kerguelensis*, for example, although known from Kerguelen, Heard, Bouvet, the South Sandwich Islands and South Georgia, does not occur (or has not been recorded) on the heavily sampled Patagonian shelf and Burdwood Bank. Similarly, *I. vivipara*, the only other outlying species that might be said to be relatively common, is known only from the Patagonian region but from none of the other islands or island groups. Beyond the high shelf in fact the vast majority of the comatulids are known only as isolated occurrences of single individuals or from occurrences not exceeding two. It will be seen then that of the eleven outlying species, *P. kerguelensis* alone is found in very shallow water and that taking the outlying species as a whole they would seem to occur in more or less equal abundance at all levels between 50 and 300 m. There is, however, some slight indication of a maximum between 100 and 200 m, although again the sampling is much too scanty for this to be certain.

TABLE 7. DEPTHS OF OCCURRENCE OF THE COMATULIDS OF THE OUTLYING SHELVES

bathymetric range (m)	no. of occurrences		
	P. kerguelensis	*I. vivipara*	total comatulids
0– 50	3	—	3
50–100	8	4	13
100–200	10	5	18
200–300	8	3	12
300–400	1	1	2

Choice of substratum

The shelf comatulids do not appear to be particularly selective as to substratum. They have been recorded on rock, among stones, on sand and gravel and on (or in) deep terrigenous mud. But perhaps the overriding emphasis is on mud. The nature of the bottom, as appendix II shows, has been recorded in a wide variety of terms and since few have yet photographed or actually seen it* we must be careful how we interpret them. The most we can say is that these are the impressions we get from the contents and behaviour of dredges, trawls, sounding rods and so on and that they need not be conveying a true picture of what the bottom was actually like at the places where sampling was done. However, taken as they are, they can be grouped under three broad headings:

(1) Soft, muddy ground, sometimes mixed with stones, sand or gravel.
(2) Mainly level, sandy ground, sometimes mixed with shell, pebbles or gravel.
(3) Rough, stony, rocky ground.

In table 8 I have marshalled the occurrences of the high and outlying shelf species under these three categories, calling them for short, muddy, sandy and rocky bottoms. Disregarding for the moment the 100% occurrence of certain species on sandy ground, which in some 50 years of exploration has only once in fact been recorded on the high continental platform, it will be seen that there is a distinct tendency for the six apparently most abundant high-shelf species, *P. kerguelensis*, *A. adriani*, *F. mawsoni*, *N. virilis*, *N. mortenseni* and *I. graminea*, to occur on a muddy substratum. *P. kerguelensis*, however, would appear to be almost equally at home on rock or among stones and so, too, would *N. virilis* and *N. mortenseni*. *Isometra vivipara* has been taken on all three types of bottom, most frequently

* Except for very close inshore. Neushul (1961), working in the Graham Land area, has examined it down to depths of 80 ft. He saw an abundance of plants and animals there, many of them, he believed, being between rocks and stones, in positions inaccessible to the dredge. Recent photographs by the New Zealand Institute of Oceanography (Bullivant 1961) show clearly the dark muddy texture of the bottom at depths between 64 and 391 m in McMurdo Sound and north of Ross Island. They show, too, as I have for long suspected, that locally the substratum may be completely hidden by a veritable jungle of small-particle feeders, Polyzoa, sponges, gorgonians and the like.

TABLE 8. COMATULIDS OF THE HIGH AND OUTLYING SHELVES AND THE KIND OF BOTTOM ON WHICH THEY OCCURRED

(Bracketed numbers indicate percentages derived from insufficient data)

	high continental shelf						outlying shelves					
	muddy		sandy		rocky		muddy		sandy		rocky	
species	no. of occur-rences	% total samples	no. of occur-rences	% total samples	no. of occur-rences	% total samples	no. of occur-rences	% total samples	no. of occur-rences	% total samples	no. of occur-rences	% total samples
Promachocrinus kerguelensis	28	70	1	(100)	7	58	18	60	3	2	4	36
Florometra mawsoni	16	40	1	(100)	—	—	—	—	—	—	—	—
Hathometra exigua	—	—	—	—	—	—	—	—	2	1	—	—
Anthometra adriani	22	55	1	(100)	—	—	—	—	—	—	—	—
Solanometra antarctica	2	5	—	—	—	—	—	—	2	1	—	—
Eumorphometra aurora	3	8	—	—	—	—	—	—	—	—	—	—
E. marri	—	—	—	—	1	8	—	—	—	—	—	—
E. hirsuta	—	—	—	—	—	—	—	—	1	1	—	—
E. concinna	1	3	—	—	—	—	—	—	—	—	—	—
Kempometra grisea	—	—	—	—	1	8	—	—	—	—	—	—
Phrixometra longipinna var. *antarctica*	—	—	—	—	1	8	—	—	—	—	1	9
P. nutrix	1	3	—	—	—	—	—	—	—	—	1	9
P. rayneri	—	—	—	—	—	—	1	3	—	—	—	—
Anisometra frigida	—	—	1	(100)	—	—	—	—	—	—	—	—
Isometra vivipara	1	3	—	—	1	8	—	—	9	7	2	18
I. flavescens	—	—	—	—	—	—	1	3	—	—	—	—
I. graminea	5	13	1	(100)	—	—	—	—	—	—	—	—
I. hordea	—	—	—	—	3	25	—	—	—	—	—	—
Notocrinus virilis	11	28	1	(100)	3	25	—	—	—	—	—	—
N. mortenseni	6	15	1	(100)	2	17	—	—	—	—	—	—

on the sandy ground of the outlying Patagonian shelf. The nine occurrences there, however, represent only 7 % of the total sampling that was done. On the outlying shelves *P. kerguelensis* again seems to show a marked preference for muddy ground and is again seen to occur, not infrequently, on rock. For the rarer species the data, it will be seen, whether from the high or outlying shelves, are far too scanty to permit us to judge on what types of bottom they would be most likely to occur.

TABLE 9. LIST OF HIGH-SHELF SPECIES SHOWING CIRCUMPOLARITY IN SOME AND WHAT APPEARS TO BE MORE LOCALIZED DISTRIBUTION IN OTHERS

	Graham Land		Ross Sea to Enderby Land	
species	no. of specimens	no. of localities	no. of specimens	no. of localities
Promachocrinus kerguelensis	102	18	332	32
Anthometra adriani	13	4	263	26
Florometra mawsoni	11	4	84	18
Notocrinus virilis	40	4	90	14
N. mortenseni	10	4	25	5
Isometra graminea	6	2	14	4
I. hordea	12	4	—	—
I. vivipara	5	2	—	—
Eumorphometra fraseri	1	1	—	—
E. marri	2	1	—	—
Kempometra grisea	2	1	—	—
Phrixometra longipinna var. *antarctica*	4	1	—	—
P. nutrix	1	1	—	—
Solanometra antarctica	—	—	6	2
Eumorphometra aurora	—	—	2	2
E. concinna	—	—	5	1
Anisometra frigida	—	—	1	1

Turning now to the 100 % occurrences of certain high-shelf species on sandy ground I must emphasize here that the results obtained are based on a single observation, the exceptionally lucky one hour's trawling we were able to make with the large *OTL* from the *Discovery* (appendix II, table C) at Station 107. Here we must have struck one of the evidently rare patches of trawlable sandy ground that occur on the high continental platform, sampling it, it is true, with remarkable results. In fact all that this single observation shows is that the commonest of the Antarctic comatulids are equally at home on sandy as on muddy or stony ground.

Circumpolarity

As figure 3 shows, the most heavily sampled, in fact the only effectively sampled, parts of the high continental shelf lie round Graham Land and in the long stretch of shallow water that reaches from the Ross Sea westwards to Enderby Land. The comatulids known from these two widely separated regions are shown in table 9, from which it will be seen that of the 17 high-shelf species, six are common to both and I would conclude, despite the long unsampled gaps on the Atlantic and Pacific sides, that all six are circumpolar. This is strongly suggested by their distributional patterns (figures 4 to 9)* and also by the

* For the sake of clearness, figures 4 to 9, from which a circumpolar distribution in certain species can readily be inferred, are presented without place names or other annotation. For place names, hydrological boundaries, principal water movements and other relevant information the reader is referred to figures 1 and 2.

appearance off Coats Land, where there are two isolated stations, of *P. kerguelensis* (figure 4) and *Anthometra adriani* (figure 5), two examples of what appear to be the commonest of the Antarctic crinoids. It will also be seen that of the remainder seven have been recorded only from the Graham Land region and four only from the Ross Sea to Enderby Land region, and the animals in question would therefore *seem* at least not to be circumpolar. However, these

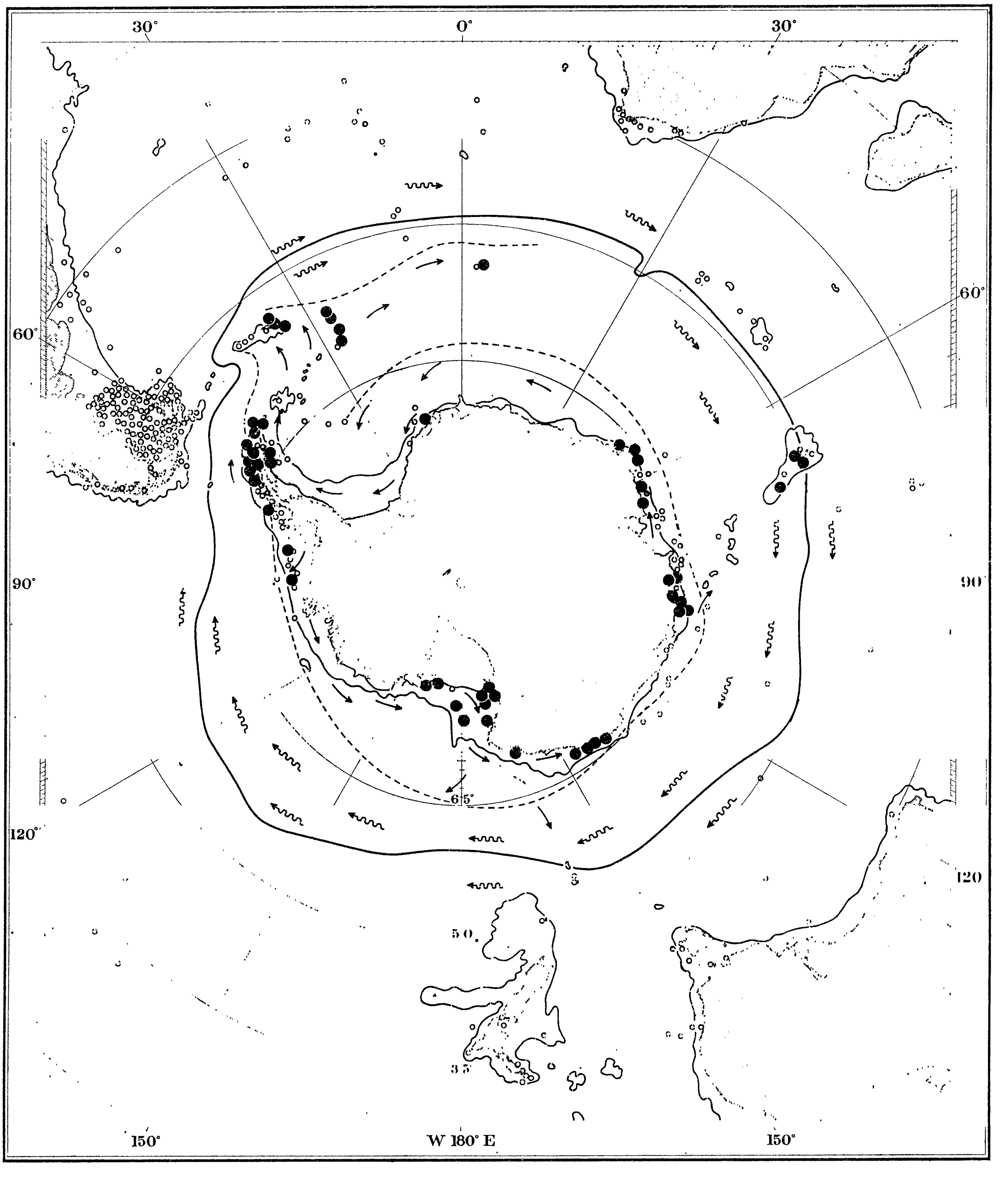

FIGURE 4. Antarctic comatulids. Distribution of *Promachocrinus kerguelensis* Carpenter. In this, as in figures 5 to 11 which follow, positive stations are represented by the larger solid black circles, negative stations by the smaller open circles.

eleven species are so poorly represented in the collections and have been recorded so rarely (seven of them only once, three of them only twice and one of them only four times) that I think it would be precipitate to take it that their distribution is as restricted as it appears. They might well not be circumpolar, or if they are, they would appear to be so widely scattered round the continental platform, that most of the southern expeditions have missed them. It is possible, for instance, that the rare *Eumorphometra aurora* John is circumpolar, two specimens having been recorded off Enderby Land and another near South

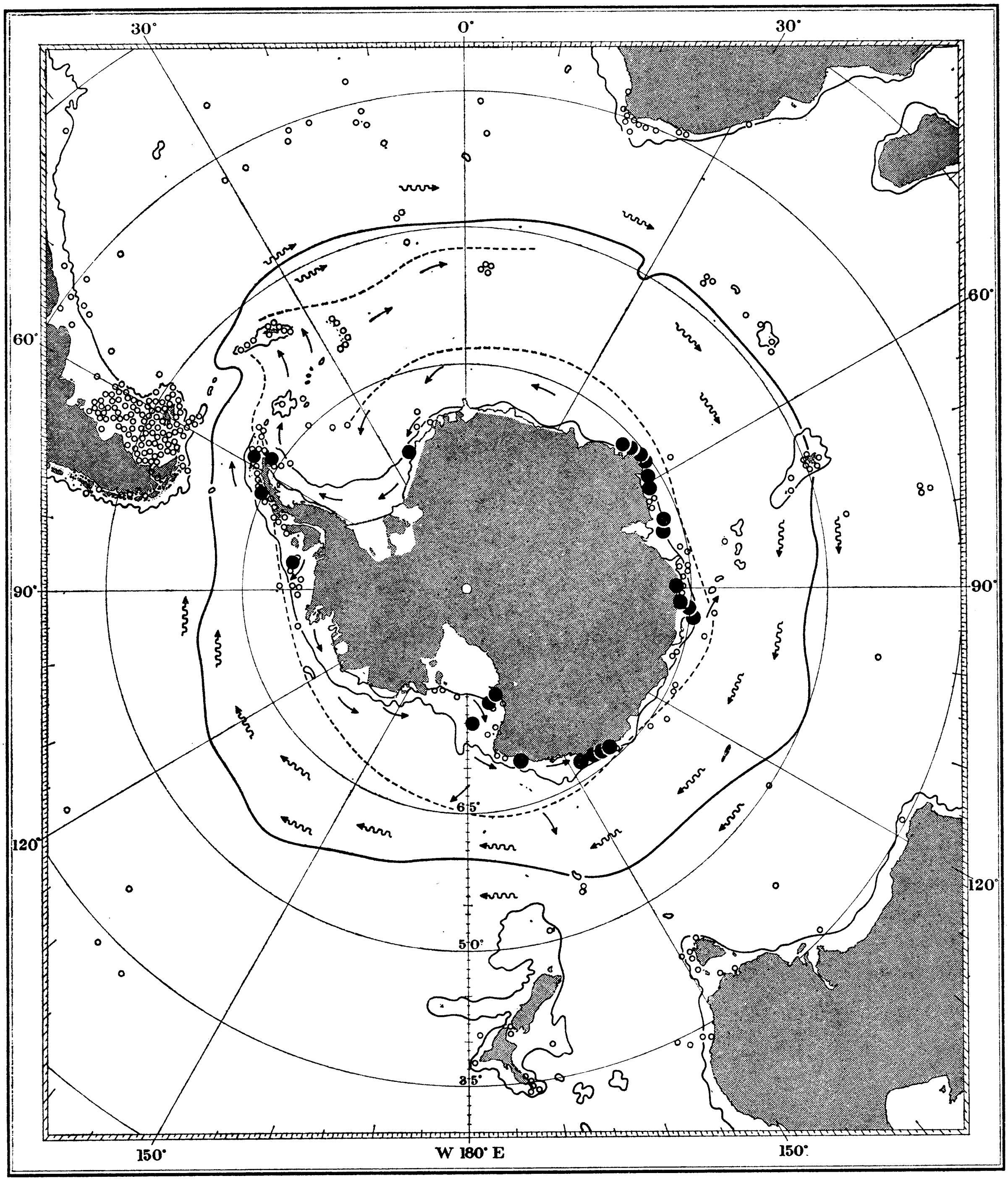

FIGURE 5. Antarctic comatulids. Distribution of *Anthometra adriani* (Bell).

Georgia (table 1). *Isometra vivipara*, I would say, is *not* circumpolar. From its distribution (figure 10) and the environmental conditions in which it is most commonly encountered (appendix II, table D) it would seem to be a relatively warm water species with a major centre of abundance on the Patagonian shelf, especially near the Falkland Islands. Round Graham Land, the only part of the high shelf from which it is known, it has been recorded only twice, John (1938) having described a single specimen from the Bransfield Strait and Mortensen (1918) four specimens from a station south of Seymour Island. There

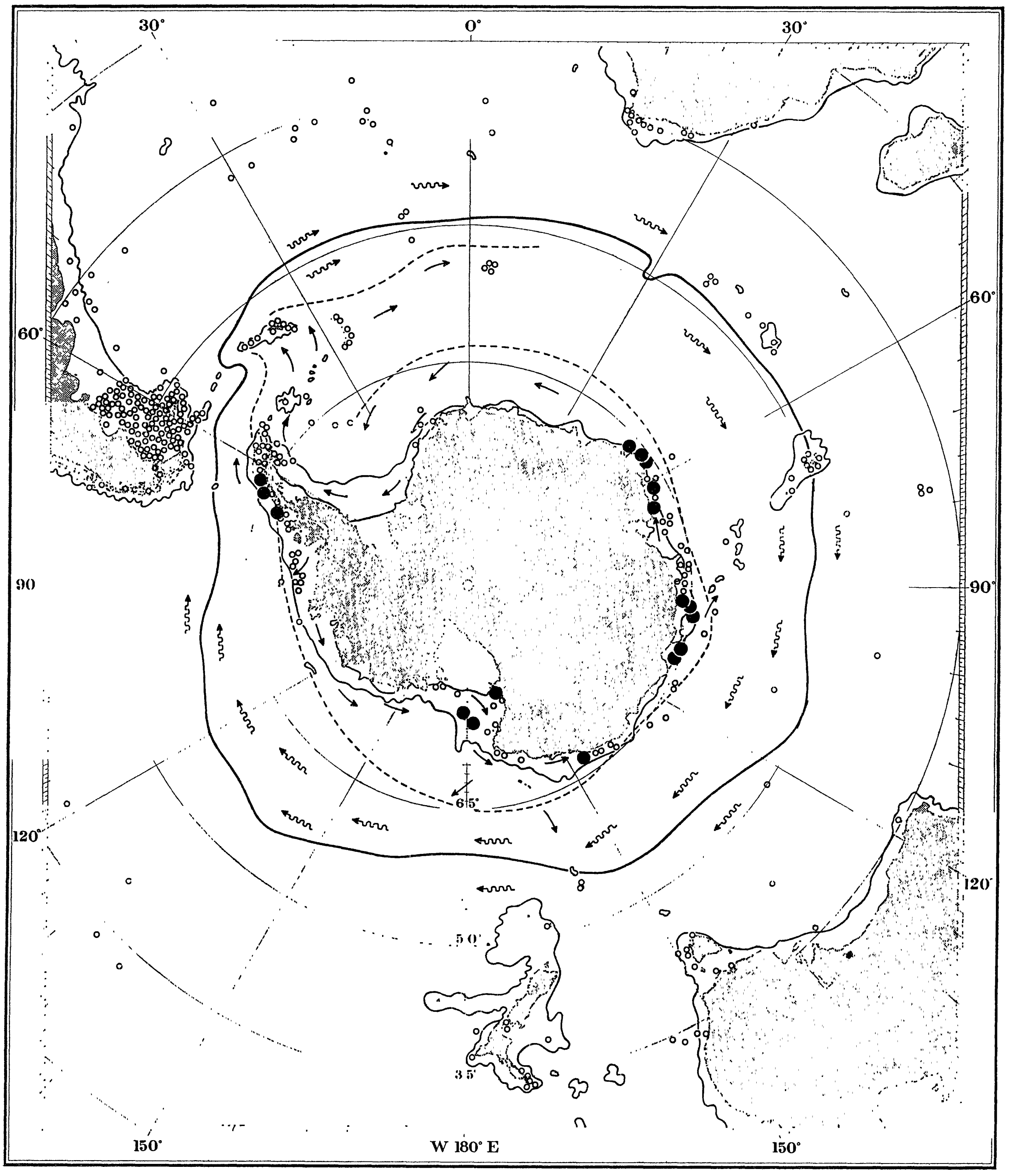

FIGURE 6. Antarctic comatulids. Distribution of *Florometra mawsoni* A. H. Clark.

seems, however, to be some question as to whether John's and Mortensen's Graham Land records refer to the same animal and also as to whether the specimens on the Patagonian shelf and from Graham Land are in fact identical. In his account of the Bransfield specimen John remarks, 'it differs in some ways from those described by Mortensen and from the remainder [i.e. the Patagonian specimens] of the present collection'. He notes four distinct points of difference but does not regard them as warranting specific or even variational distinction. I feel, therefore, that here perhaps we may have a case where closer

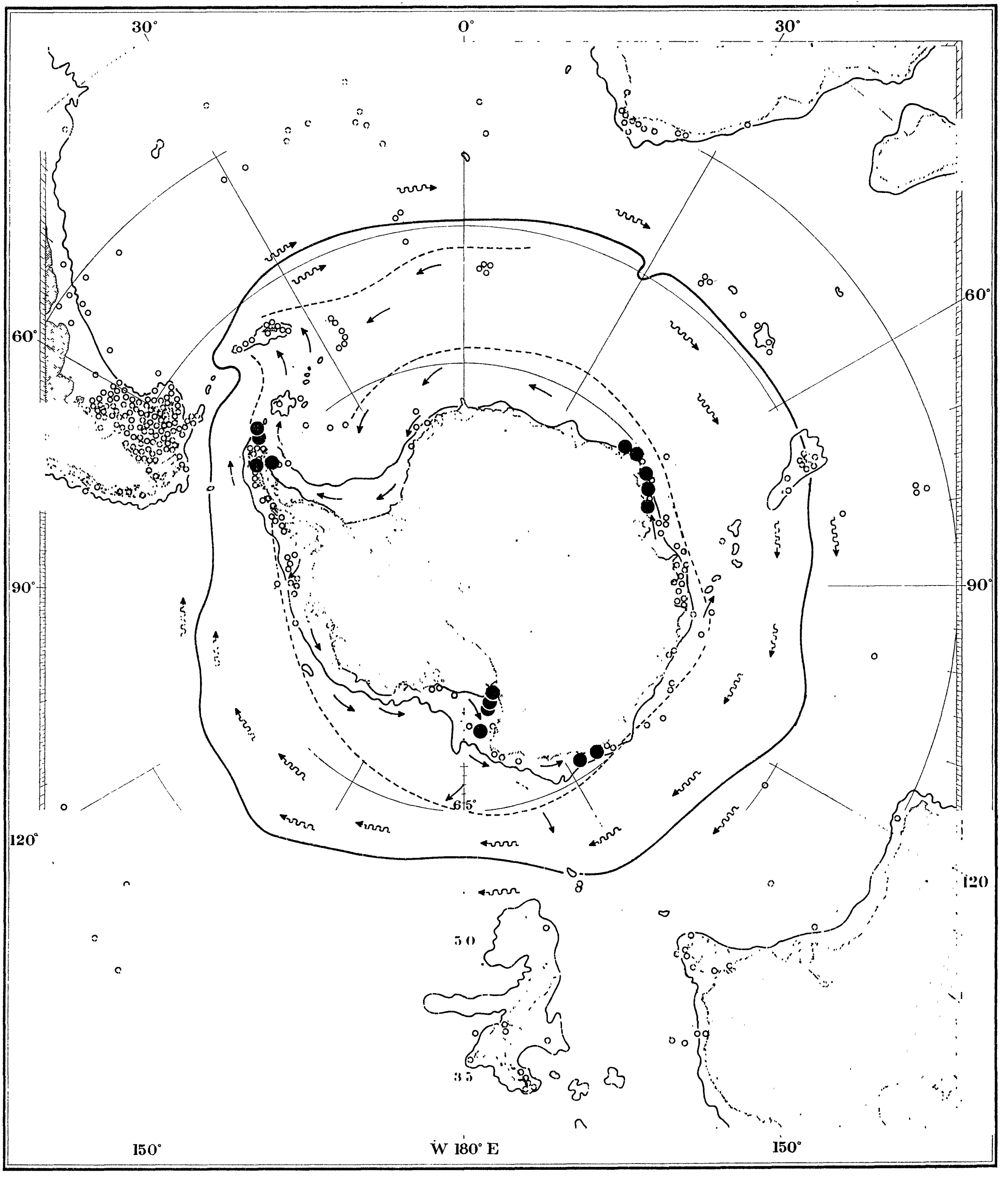

FIGURE 7. Antarctic comatulids. Distribution of *Notocrinus virilis* Mortensen.

taxonomic scrutiny of a much larger body of comparative material than is available at present may reveal racial, subspecific or even specific differences between the Patagonian and Graham Land forms. It seems likely, however, that it will be a long time before enough material comes to hand, for *I. vivipara* appears everywhere, even on the Patagonian shelf, to be exceedingly rare. And this I must emphasize is not for want of sampling, for in the shallow water round the Falkland Islands, and for a long way up the shelf to the north, we have in fact by far the most heavily sampled region of any that have been visited by

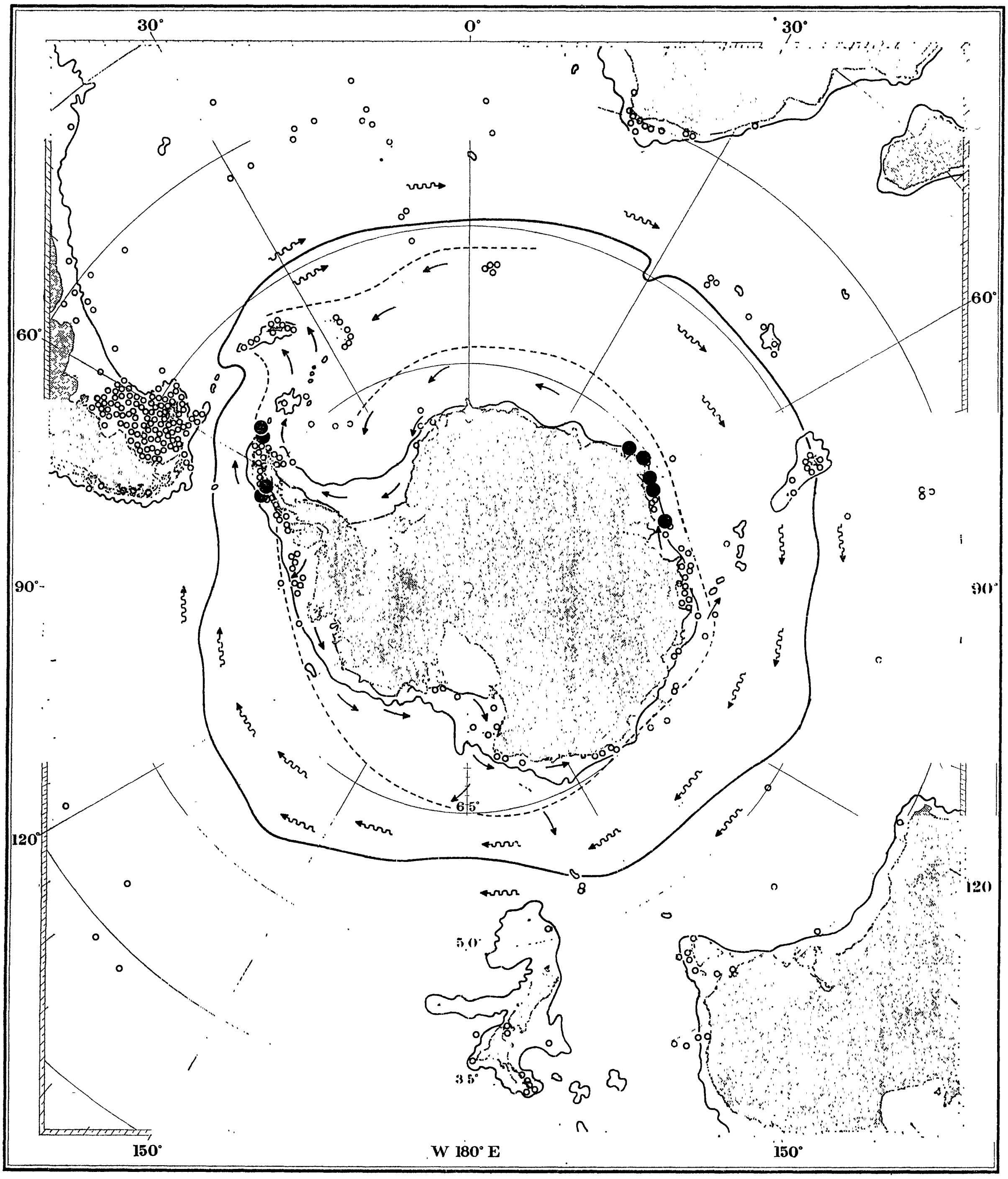

FIGURE 8. Antarctic comatulids. Distribution of *Notocrinus mortenseni* John.

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the southern expeditions. And not only has it been closely covered but covered repeatedly with an apparatus of enormous catching power, the 80 ft. commercial otter trawl. Between 1927 and 1932 we trawled successfully with this (with fine nets attached) no fewer than 165 times and the net result of this massive effort, representing 165 h fishing and covering some 500 to 600 miles of bottom, is a mere 27 *I. vivipara*, the only shallow-water comatulid in fact that has been recorded from this region. This is a meagre result indeed when compared with the 342 comatulids taken in a single hour's fishing with the 40 ft.

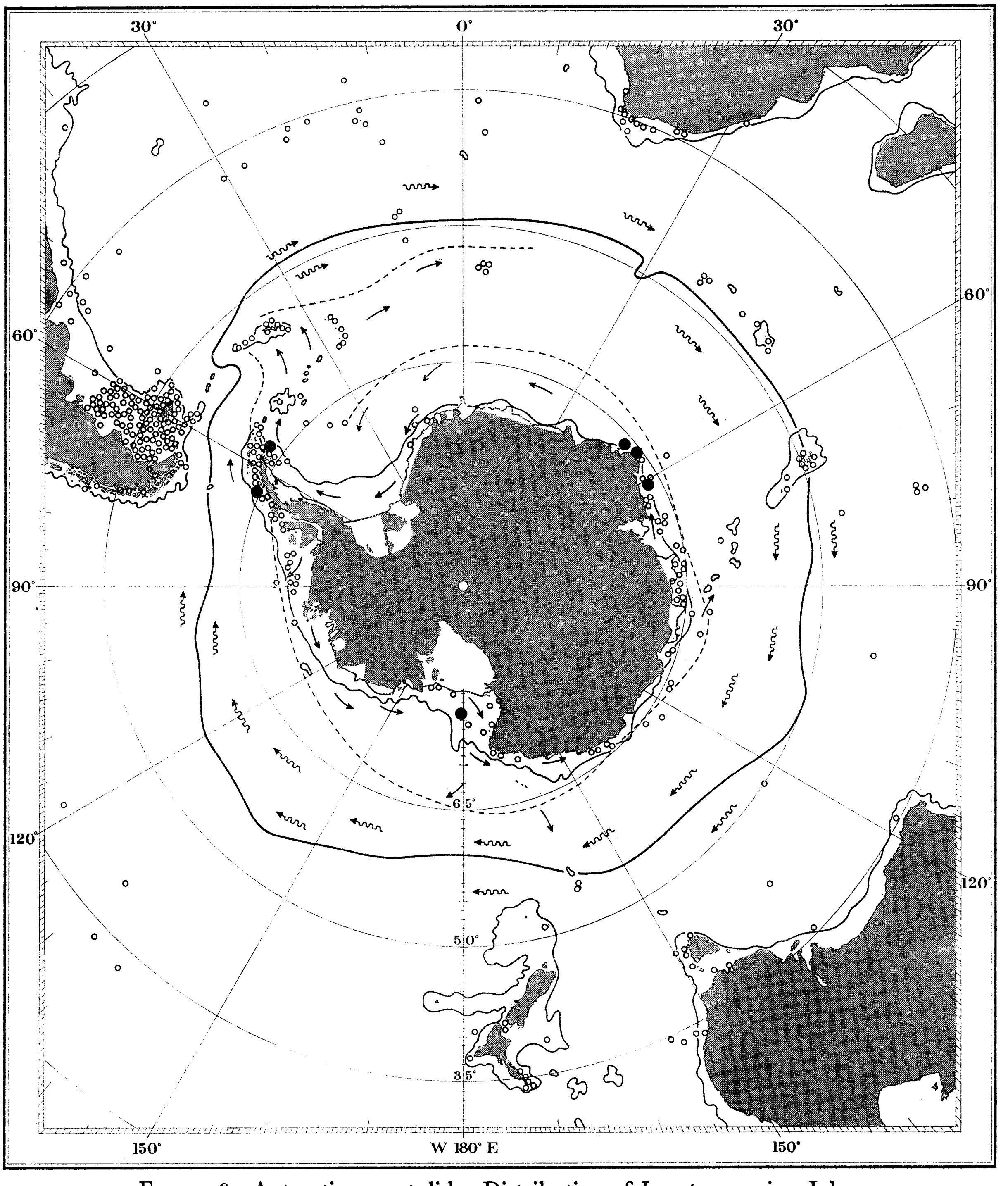

FIGURE 9. Antarctic comatulids. Distribution of *Isometra graminea* John.

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OTL (appendix II, table C) off MacRobertson Land in February 1931. Even the small dredges and Monegasque trawls, so widely used on the high continental platform, on occasion produce from a single station a distinctly better result than the total harvest from Patagonian waters, and this sometimes after only 5 or at most 30 min on the bottom.

Intensive exploration then has brought to light only one comatulid species on the Patagonian shelf,* and remarkably few indeed of that, and I think we may safely con-

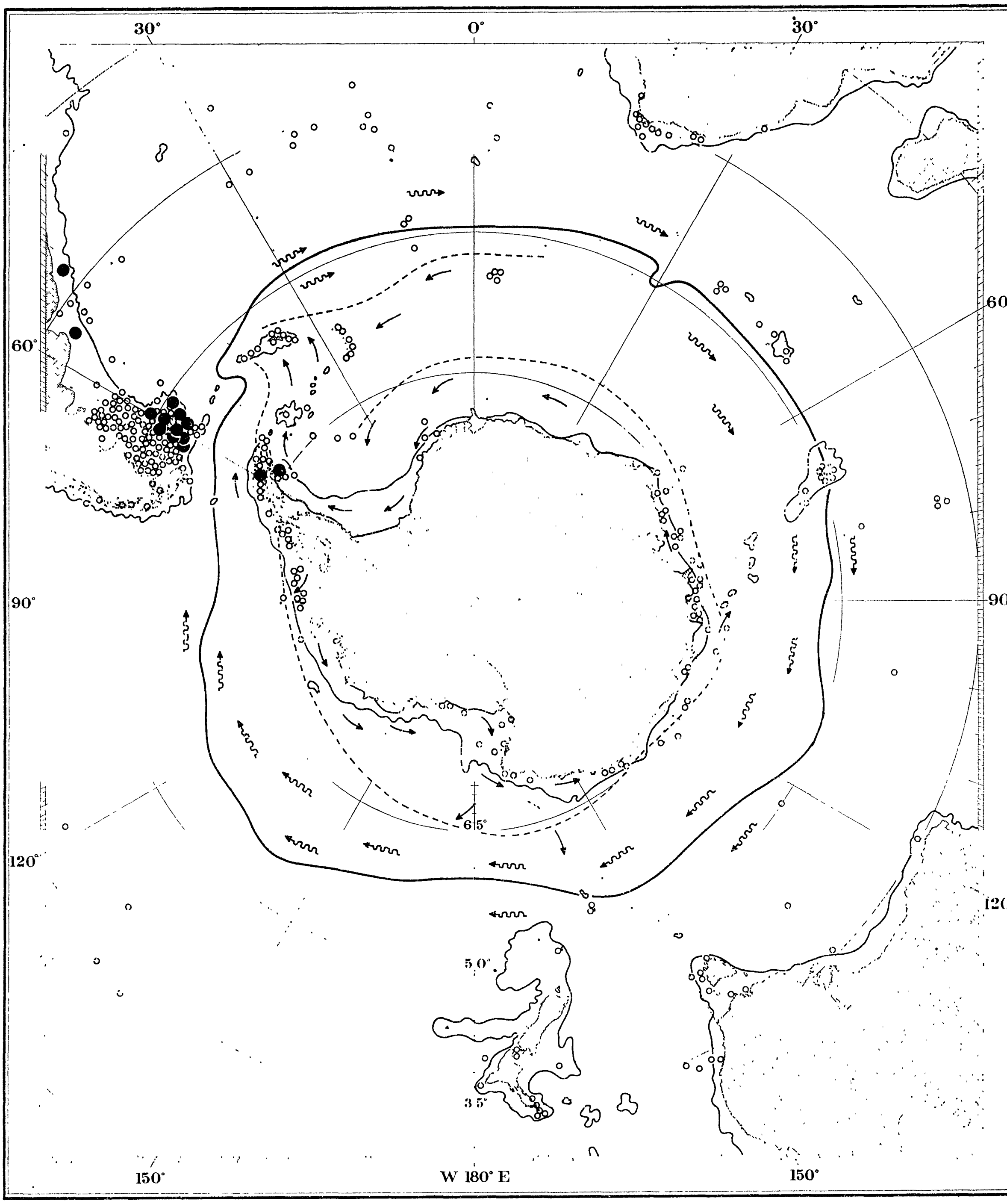

FIGURE 10. Antarctic comatulids. Distribution of *Isometra vivipara* Mortensen.

* I am excluding here the Burdwood Bank and the Patagonian channels.

clude that this wide, rather flat and sandy region, for some reason or another, is not a suitable ground for the development of a rich and varied crinoid fauna.

Circumpolarity, even though it can be postulated with reasonable certainty for only six of the species, is a remarkable thing, for it would seem itself to postulate: (1) that selection by the environment has been the same for all six all round the continent, (2) that conditions throughout this relatively narrow coastal platform are remarkably uniform, (3) that there has been parallel development all round Antarctica, or (4) that these species have gradually spread round the high shelf from some common source. Any or all of these factors might, I think, have contributed to this phenomenon although perhaps in (4) we might look for the most likely explanation. In fact I think we might expect that in a narrow coastal belt dominated by a west-going stream (figure 1) the bottom fauna, like the plankton, would be subject to westerly dispersal and ultimately girdle the continent. For even if the comatulids, like so many other bottom-living polar animals, have no pelagic larvae there is always the possibility that their young stages at least (see below) might occasionally get attached to floating objects. Moreover, if, as seems probable (p. 333), the high continental platform has been isolated for a million years or more this would allow plenty of time for slow circumpolar 'creep', even if attachment were a rare event. In his account of our '*Discovery*' Mollusca, Powell (1951) refers to the east wind drift as a 'present' factor responsible for the lateral dispersal of many animals.

Dispersal from the continental platform to lower latitudes

It would appear from figure 4 that there has been a northward spreading of at least one high-shelf comatulid (*P. kerguelensis*) and that this movement was (or is) most pronounced where there are islands set upon submarine ridges and evidently acting as stepping stones (Mackintosh 1960). It could of course be argued that this apparent movement had proceeded (or is proceeding) in the opposite direction. The principal objection to this argument, however, is that in a sense it would be paradoxical in that it would postulate a movement against the main trend of the surface and bottom currents. I do not of course suggest that the outlying shelves, as for instance at Kerguelen, Heard, Bouvet, the South Sandwich Islands and South Georgia, have been populated from the south *directly* through the agency of these currents, the high-shelf comatulids, so far as is known, having no pelagic larvae. Many of them in fact (Andersson 1904; Mortensen 1918; John 1938) are brood protecting. The currents, however, especially the surface currents, could at least indirectly be affecting dispersal, especially for instance if it should prove, as Burton (1932) suggested for the sponges, that the young crinoids occasionally get attached to floating objects.* It is perhaps significant in this connexion that it is at Kerguelen, Heard, Bouvet, the South Sandwich Islands and South Georgia, that *P. kerguelensis*, the commonest of the high-shelf species, is found, and that these are the very regions where surface outflow from the east wind drift and from the Weddell Sea is strong. The bottom current could also be imagined as an instrument of dispersal, especially where it runs strongly, as for instance (Marr 1962) below the Weddell Sea. On the Atlantic side, for example, it could be helping

* Among such objects seaweed, pack ice, and above all icebergs that had been in contact with the shallow shelf-sea floor, spring readily to mind. Floating ice in fact may well be a most potent instrument of dispersal.

(not at any rate hindering) a slow creeping of *P. kerguelensis* northwards and eastwards along the sea floor, the occurrence of this species on the remote and isolated shelf of Bouvet Island providing some evidence in favour of such an hypothesis. Although a shelf species, *P. kerguelensis* might well indeed be affected by the bottom water, deep though it be, for as we have seen (table 4) its known bathymetric range is distinctly wide. We must consider, too, the role of the east wind drift which dominates the continental platform. This could be contributing to the northward spread of life along the east side of Graham Land as well as to the phenomenon of circumpolarity which seems to crop up among so many animals of the shallow Antarctic sea.

A slow creeping along the sea bed, especially along the relatively shallow radiating ridges, from high to lower lattitudes would not, I believe, be incompatible with the habits of these animals, for some of them at least seem to be active enough to accomplish such a movement. I have seen, for instance, the large, many-hued *P. kerguelensis* swimming with remarkable grace and vigour (John 1938) in a tank on deck in *Discovery II*. I have seen, too, the exceedingly handsome *Heliometra glacialis*, of the Arctic, walk across the poop of a sailing ship quite rapidly (Worsley 1927). Other evidence of mobility comes from the *Zoological Log of the 'Scotia'* (Wilton *et al.* 1908). On 12 March 1904, while the *Scotia* was beset off Coats Land, it is recorded that in a large fish trap set in 161 fathoms (295 m) there was a crinoid, a specimen (unfortunately undescribed and now lost) which must have swum (or crawled) into the trap, successfully negotiating the entrance.

The distributional pattern presented in figure 4 does in fact then suggest that *P. kerguelensis* has spread northwards from the high shelf as far as Kerguelen, evidently along the Kerguelen–Gaussberg Ridge, and also as far as South Georgia, evidently via the winding course of the Scotia Arc. Clearly, however, we must conclude that in the course of its dispersal (or travelling) in the Falklands sector it has not yet reached the heavily sampled waters of the Patagonian shelf, or, if it has done so, has failed, because of high temperature or some other factor, to establish itself there. There are, of course, considerable gaps of rather deep water (3000 m or more) between the South Georgian shelf and the nearest adjacent shallow water to the west, the Burdwood Bank, and these may have presented a barrier to its further dispersal. However, since it seems to have negotiated successfully the even still deeper water between the South Sandwich Islands and South Georgia it may be that it is even now spreading westwards towards the South American mainland and may eventually turn up there. Its known bathymetric range (18 to 1080 m) as already mentioned is distinctly wide and further exploration of the abyssal sea, as yet so poorly sampled, may show that, like *Heliometra glacialis* and *Poliometra prolixa* of the Arctic, it can tolerate a still wider, perhaps far wider, range.* Here again its isolated occurrence near the remote Bouvet Island, which is separated from the high continental platform by over 950 miles of virtually unsampled abyssal bottom, may be of high significance. Let me quote here from Ekman on the zoogeography of the southern species of the echinoid genus *Abatus*. He writes:

'*Abatus* species are brood-protecting and thus lack pelagic larval stages; and they have no suckers on their feet and thus cannot be transported by oceanic currents [i.e. through

* *H. glacialis* has been recorded from 4 down to 1359 m and *P. prolixa* from 18 down to 1960 m (Clark 1915).

becoming attached to floating objects such as seaweed]. It has therefore been assumed that their occurrence in separated regions is a proof of fairly late land connexions or underwater ridges between these regions. Here the possibility of parallel development should be taken into account. But another explanation is more probable. Several *Abatus* species are found at archibenthal depths. Their occurrence at these depths makes it not improbable that they also tolerate abyssal surroundings; the most southern abyssal regions are not so well investigated that this possibility can be rejected. Under these circumstances it would be precipitate to deny the possibility of a present-day communication between the different populations and to suppose that the distribution and ecology of these species proves the existence of a closer Quaternary or late Tertiary geographical connexion between their present-day localities.'

Although it is apparent that *P. kerguelensis* has spread (or travelled) outwards from the high shelf in two widely separated regions where there are islands and submarine ridges offering, it seems, stepping stones for dispersal, it is a remarkable fact that the other common high-shelf species, *Anthometra adriani*, *Florometra mawsoni*, *Notocrinus virilis* and *N. mortenseni*, with which *Promachocrinus* has so often been found associated, have not, it would appear, moved outwards along the same relatively easy routes. It is difficult to account for this apparent anomaly but I would suggest that all four species are neither large enough nor active enough to accomplish such a movement or perhaps are intolerant of the abyssal sea. It might, however, be that the spreading of *P. kerguelensis* to the outlying shelves took place a very long time ago when Heard, Kerguelen, the South Orkneys, the South Sandwich Islands and South Georgia were in continuous connexion with the continental platform by shallow water; and if this were so it might perhaps be postulated that at that time the other species, today apparently exclusive to the high shelf, assuming equal opportunities and powers for dispersal, had not yet evolved and that now their bathymetric range does not permit them to bridge the deep gaps in the ridges that are found today.

Other instances of outward spreading, perhaps via the submarine ridges, are possibly provided by some of the rarer species, for instance (table 1), *Solanometra antarctica* (Adélie Land and Heard), *Eumorphometra aurora* (Enderby Land and South Georgia) and *Phrixometra longipinna* var. *antarctica* (Clarence Island and South Georgia). *Phrixometra nutrix* has been described from one specimen from the Bransfield Strait and from one (poorly preserved) specimen from the Burdwood Bank, but we need far larger quantities of this very rare form from many more localities before we can hazard even a guess at what this seemingly anomalous distribution implies. In other words, like *Isometra vivipara*, it provides a case for further taxonomic study of a large body of comparative material.

The occurrence of *P. kerguelensis* round Graham Land, at the South Sandwich Islands and at South Georgia would seem to postulate that its distribution was continuous throughout the whole of this large section of the Scotia Arc. Yet, anomalously, it has not been recorded from the South Orkneys. This, however, I think can simply be put down to inadequate sampling. There are in fact only two (negative) offshore stations in the shallow water there, and with a species inclined to be so sparsely, or at any rate unevenly, spread over the sea floor, from two negative samples only we cannot postulate absence. Extensive dredging it is true, was done by the Scottish expedition in the very shallow water (18 m or less) of Laurie Island's Scotia Bay, but this was singularly unproductive of crinoids,

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only one out of an enormous total of some 350 dredgings yielding 'feather-stars' which unfortunately have not been described. They could well, however, have been the missing and seemingly ubiquitous *P. kerguelensis* which as we have seen (appendix II, table D), is common enough in quite shallow water (20 to 50 m) in the fjords of Kerguelen and South Georgia. The virtually negative results of these many Scottish dredgings would therefore seem to indicate that at the South Orkneys at least this species rarely comes into water less than 10 fathoms deep. And this, I think, must be true for the Antarctic comatulids as a whole, for shallow dredging on a similar scale was also carried out by the Australasian ('*Aurora*') expedition in Commonwealth Bay (Mawson 1940) and by the '*Discovery*' expedition in McMurdo Sound (Hodgson 1907) without the reward of a single specimen.*

It will be noted that not one of the comatulids so often taken in the same haul on the continental platform (appendix II, table C) has yet been recorded from the nearby Balleny Islands (figures 4 to 9). There can be little doubt, however, that this is simply due to lack of observation and I feel sure that sooner or later some or all of these species will turn up there, the Ballenys being so close to the high shelf with which, moreover, they are connected by a ridge running out from Cape Adare. It will be seen, too, that although *P. kerguelensis* has been recorded from the relatively warm shelf waters of Heard Island and Kerguelen, it has not been recorded from Macquarie Island, Campbell Island, or from the Auckland Islands, all three localities where there has in fact been some sampling although mainly, I believe, at shore level. Here, as I have suggested for the Patagonian shelf, it may be temperature that is the limiting factor, or else the abyssal sea between the continental platform and these remote outliers is, and perhaps for long has been, much too deep to permit northward dispersal.

In so far then as this small group of animals is concerned there does not appear to have been any recent connexion with the north either by land or by shallow sea. On the contrary, the comatulids of the high continental platform appear to have developed independently for a very long time into a highly distinctive community, some members of which even now seem to be spreading not southwards but *northwards* to populate the shallow waters of the oceanic islands and island groups that encompass the polar continent. Du Rietz (1929) has expressed the view that the area of greatest specific differentiation of a genus is most likely to be that in which it originated. It might well, it seems, therefore be that it is from the shallow water girdling the Antarctic mainland, where (table 1) speciation has evidently been so successful, that the southern comatulids are now in fact spreading, or at any rate originally sprang.

John (1938) takes the opposite view. Referring to the anomalies presented by *I. vivipara* and *P. nutrix*, and believing them to provide evidence of a relationship between the shallow-water crinoid fauna of the Antarctic and of the east coast of the extreme south of South America, he is inclined to the view that the Antarctic comatulids *as a whole* are of Patagonian–Magellan origin. Mortensen (1910), for the littoral echinoids, Koehler (1912), for the littoral asteroids, ophiuroids and echinoids, and Ekman (1925), for the littoral holothurians, have arrived at the same conclusion.

* McMurdo Sound lies at the head of the Ross Sea at the extreme western corner, Commonwealth Bay in Australian Antarctic Territory in 143° E. The negative results in both instances were obtained in the inshore water of the high continental platform.

Circumpolarity and northward dispersal in other shelf-living animals

I have examined briefly the distribution of some other shallow-water Antarctic animals, selecting at random a sponge, a nemertean, a polychaete and three ascidians. The following systematic papers have been consulted.

Sponges

Poléjaeff (1883)	Kirkpatrick (1908)	Topsent (1917)
Schulze (1887)	Topsent (1908)	Dendy (1918)
Sollas (1888)	Jenkin (1908)	Dendy (1924)
Topsent (1901)	Topsent (1913)	Burton (1929)
Lendenfeld (1906)	Hentschel (1914)	Burton (1932)
Lendenfeld (1907)	Topsent (1915)	Burton (1934)
Kirkpatrick (1907)	Stephens (1915)	Burton (1938)

Nemerteans

Hubrecht (1887)	Joubin (1910)	Wheeler (1934)
Bürger (1904)	Joubin (1914)	Wheeler (1940*a*)
Bürger (1907, 1912)	Baylis (1915)	Wheeler (1940*b*)
Joubin (1908)		

Polychaetes

McIntosh (1885)	Ehlers (1912)	Monro (1930)
Willey (1902)	Ehlers (1913)	Augener (1932)
Gravier (1907)	Bergström (1916)	Monro (1936)
Ehlers (1908)	Benham (1921)	Fauvel (1936)
Gravier (1911)	Benham (1927)	Monro (1939)

Ascidians

Herdman (1882)	Hartmeyer (1912)	Ärnbäck-Christie-Linde (1950)
Herdman (1902)	Sluiter (1914)	Kott (1954)
Sluiter (1906)	Herdman (1923)	
Herdman (1910)	Ärnbäck-Christie-Linde (1938)	
Hartmeyer (1911)		

In all six species studied a circumpolar distribution is apparent. The ascidians, *Pyura setosa* (Sluiter) and *P. bouvetensis* (Michaelsen), like certain of the comatulids, seem to be confined, or mainly confined, to the high shelf, including in this instance the closely associated South Orkneys (*P. setosa*). The third ascidian, *P. discoveryi* (Herdman), like *Promachocrinus*, has evidently spread outwards via the Scotia Arc as far as South Georgia, the nemertean, *Lineus corrugatus* McIntosh, evidently by the same route as far as the Patagonian shelf and, again like *Promachocrinus*, up to Heard and Kerguelen. The sponge, *Mycale magellanica* (Ridley), has perhaps had a different zoogeographical history. Although circumpolar it has in fact rarely been encountered on the high continental platform, its principal centre of abundance, like that of *Isometra vivipara* (p. 356), appearing to be on the southern part of the Patagonian shelf, especially round the Falkland Islands, with perhaps another such centre round South Georgia. As John and others have postulated for the echinoderms, it might be that this is a species that does in fact spring from the Patagonian–Magellan region and has spread from there (or is now indeed spreading from there) to Antarctica.

Successful dispersal to the north from a high Antarctic centre is very pronounced in the circumpolar *Harmothoë spinosa* Kinberg, perhaps the commonest and most widely distributed polychaete of the far southern coastal seas. In the Falklands sector (figure 11) it has evidently spread all along the scattered islands of the Scotia Arc, successfully colonizing

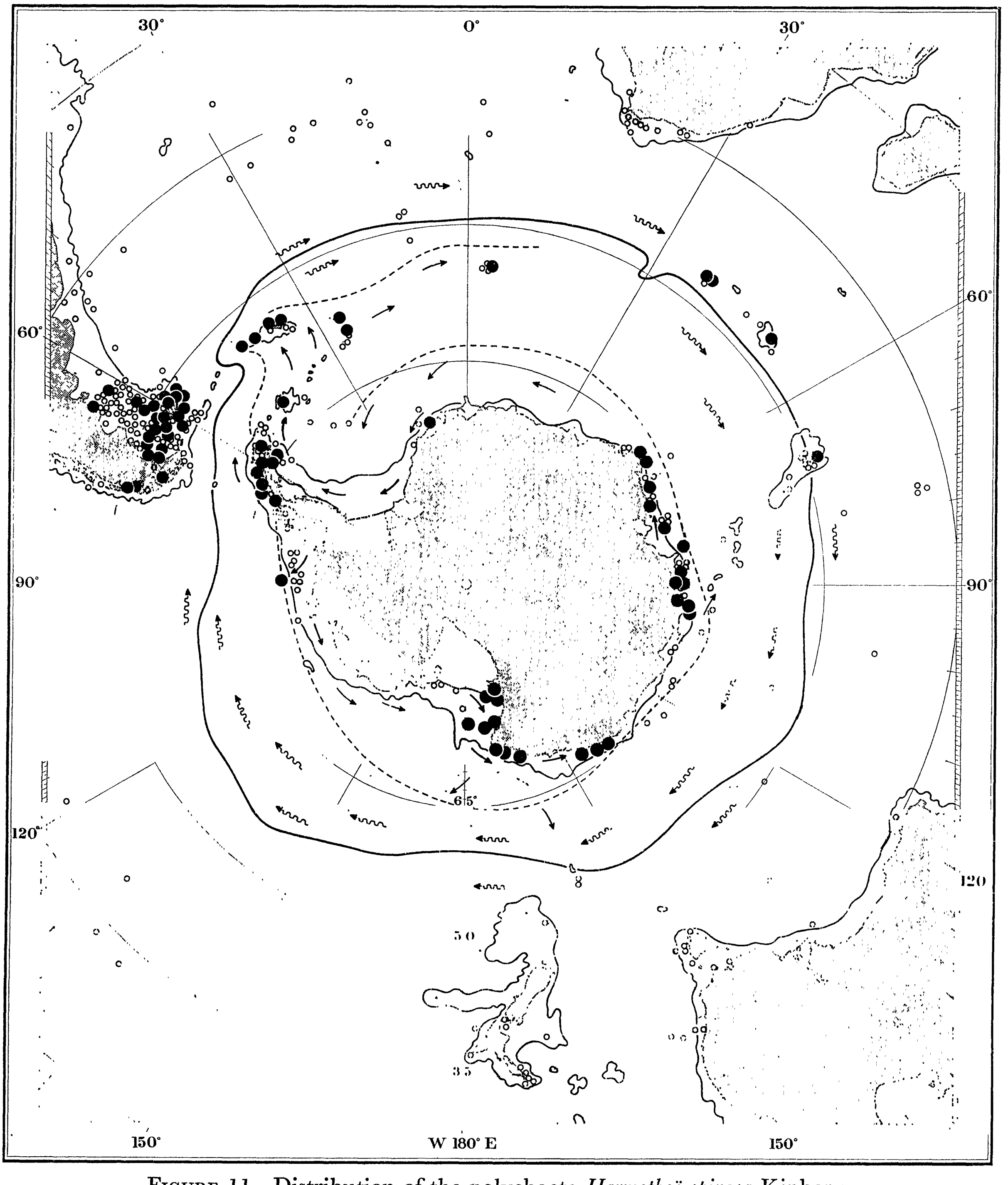

FIGURE 11. Distribution of the polychaete *Harmothoë spinosa* Kinberg.

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the southern part of the Patagonian shelf (including Burdwood Bank) and the Magellan channels. Again we may ask, is this a recent phenomenon or one long since accomplished at a time when the submarine ridges, which it has evidently used, offered easier pathways for dispersal than they do today? We may ask, too, especially in view of its widespread occurrence in the Patagonian–Magellan region, in what direction dispersal took place. In any case we may assume that it has been able to adapt itself to a much wider temperature range than for instance *P. kerguelensis* would seem to tolerate. Among the remoter islands of the circumpolar sea it has been recorded at Kerguelen, the Crozets, Marion, Prince Edward, Bouvet and Peter I Island. It has not, however, been reported from the abyssal sea and its presence near these isolated oceanic islands would seem to postulate that once they had a more solid connexion with Antarctica than they have today or that there has been something controlling, or responsible for, dispersal about which we are still in the dark. Ice transport however (p. 357, footnote *) might be an important factor.

Discussion and summary

Summing up the recent discussion on the biology of the southern cold temperate zone held at the Royal Society in December 1959 the leader, C. F. A. Pantin, F.R.S., remarked (Pantin 1960*b*) that a curious feature of this conference, and to him it seemed a rather healthy one, was that so much attention had been paid to the facts of distribution and ecology, and so little to hypotheses such as the Wegener drift theory. The majority of the speakers in fact who took part sought to explain present-day far southern distributional patterns in terms of what Holdgate (1960) has called 'natural and existing means of dispersal', laying particular emphasis on the efficacy of transport by birds and by the prevailing winds and currents. Stephenson (1960), for instance, pointed out that it was no longer necessary to postulate the existence of former land bridges to explain observed distributions, adding that the effectiveness of dispersal by birds, floating wood, seaweed, seeds and other objects had probably been underestimated. The small starfish, *Asterina exigua*, he said, had spread all over the Indo-West-Pacific region and had reached South Africa in the natural course of events. He would not, however, have expected it to spread to St Helena as it had no pelagic larva. Yet it had arrived there, apparently 'as adults attached to floating South African kelp'.* It would seem likely, too, that the viviparous and evidently shore-bound South African ophiuroid, *Amphiura capensis*, got carried to Tristan da Cunha by drifting weed (Mortensen 1946).

For the past sixty years Antarctic biogeography has been swamped in the flood of conjecture that has sprung from the hypothesis (Wegener 1912) of continental drift. On the one hand we have Wegener's disciples who believe that in the Eocene Australia, Antarctica and South America were in contact with each other as one super-continental land, or at farthest separated by narrow gaps of shallow water. This close association (or direct connexion), it is supposed, persisted throughout Tertiary times and it was not until about the beginning of the Pleistocene, say a million years ago,† that these three it was thought at

* In the *Zoological log of the 'Scotia'* (Wilton *et al.* 1908) there appears the following entry for 28 November 1903. '59° 43′ S., 48° 10′ W...hooked a piece of rotten kelp which was full of barnacles, some of which we bottled'.

† See, however, p. 333.

length drifted apart, their shelves becoming separated by an abyssal sea. This massive displacement of the earth's crust, they claim, lies at the roots of the distributional patterns found girdling the polar continent today. On the other, and now perhaps the stronger, side are ranged the sponsors of the simple and obvious, most of whom see in what is taking place today, in for example the prevailing winds and currents and the animate and inanimate objects they carry, a ready means of dispersal of plants and animals, to explain existing distributions in terms of former land connexions they say being an unwieldy and unnecessarily complex approach to what is in fact a simple problem. In other words they believe that the clue to what Pantin (1960*a*) has called the 'present and past biological history of the southern hemisphere round the Pole' is to be found in present-day meteorological and hydrological phenomena rather than in the rocks, although obviously the latter must also have their story to tell.

Today there are many subscribers to Holdgate's view. Holdgate himself (Holdgate 1960) argues that there is no element in the native fauna of the mid-Atlantic islands, Tristan and Gough, whose presence cannot plausibly be explained in terms of air- or sea-borne diffusion from the west. He points too to the work of Hafsten (1960) who finds there has been sporadic drift of pollen grains to these islands from Patagonia over the past 5000 years.* It is fair to add, however, as Holdgate does, that Brinck (1948) does not find such affinity among the Coeleoptera of Tristan and that Christophersen (1946) has expressed the view that neither the flowering plants of Tristan nor of Gough can be accounted for under present conditions. In the main, however, advocates of Holdgate's natural and existing means of dispersal are commoner than Wegener theorists. Among the former we find Regan (1914), Burton (1932), Stephenson (1932), Mortensen (1946), Ekman (1953), Skottsberg (1960), Falla (1960), Stephenson (1960), Cloud (1961) and Broch (1961). Regan and Broch are particularly sceptical of bridge-building geographers, the former remarking that if all their ancient land connexions were true the oceans would have been reduced 'to a few puddles'. Cloud is equally anti-Wegener, rejecting his hypothesis as 'unsatisfactorily documented and biogeographically unnecessary'.

Belief in continental drift, formerly popular although now perhaps on the wane, is by no means dead. At the close of the Royal Society discussion Lovis (1960) remarked that although two such eminent phyto-geographers as Professors Skottsberg and Du Rietz had both rejected the hypothesis, no one had mentioned the results of recent researches in palaeomagnetism. He called attention to the work of Irving & Green (1957) which indicated that although in the late Tertiary Australia and Antarctica occupied virtually the same positions relative to one another as they do today, in the early Tertiary both continents were adjacent. If further evidence of this sort were to accumulate he said 'then whether we like it or not, biologists will have to accept continental drift, and our theories concerning the origins of plant and animal distributions will have to conform to the geological facts'.

Of course as in all great clashes of conjecture there are some who steer a middle course, neither condemning Wegener nor seriously trying to vindicate him, and surely

* Perhaps the earliest mention of sea-borne diffusion as a factor in southern plant geography comes from Joseph Dalton Hooker who, when sailing with Ross in the Antarctic well over a century ago, called attention to the role of the West Wind drift as a carrier of Fuegian seeds to the east (Ross 1847).

it is with them that we should leave the verdict, at any rate until much further exploration has been done in the southern field, and we have gathered from the rocks and the sea a far larger body of information than is now available. In front stands the massive figure of Ekman (1953) who concludes that while the facts of southern zoogeography as we find them today do not disprove the existence of former land connexions, they do not on the contrary prove it. Stephenson (1932), for the microdrilid earthworms, expresses the same impartial view. Even Skottsberg (1960), anti-Wegener though Lovis has claimed him to be, ends on a cautious note. 'Migratory birds have their share in transportation, but I cannot find that they solve the problem of the diffusion of the Antarctic flora. Can we do without land connexions? The theory of a bridge between West Antarctica and South America is clearly indicated on the map and is supported by geologists. Submarine rises toward New Zealand and Tasmania and intervening islands, and a wide plateau and the long, shallow Kerguelen bank in the direction of Africa suggest early connexions or at least easier pathways, but they are rejected by the majority. Nobody denies that accidental overseas dispersal occurs. In areas which lost their entire higher flora during the glacial period there is no other alternative'. Broch (1961) too, without saying when, agrees that certain former connecting routes (or easier paths) must in fact have existed, which indeed is obvious enough from the bottom relief we see in Antarctica today, especially for instance (figure 3) between Gaussberg and Kerguelen and along the tortuous course of the Scotia Arc, or Southern Antilles as it used to be known, which most geologists are now agreed is all that remains of a former unbroken mountain range that (Matthews 1959) once linked the Andes with Graham Land. What is *not* clear, however, and has for long been a matter for conjecture, is whether this former land link, and obvious route for dispersal, led to the colonization of Antarctica from a northern faunistic centre such as we see today on the Patagonian shelf, or whether migration (or dispersal) took place in the opposite direction.

What inferences then may we draw, from the distribution of the comatulids, about the history of the Antarctic shelf fauna? Did they (the comatulids) spring from a shallow-living northern ancestral stock that once girdled the super-continent, the so-called Gondwanaland of Wegener, or did they evolve *in situ* in the cold coastal waters of present-day Antarctica, cut off from the other southern continents by an abyssal sea for a period variously estimated as having lasted, at its shortest for a million, at its longest for 60 million years or more? They form, it has been shown, a unique, and by Arctic standards, successful assemblage not one of which has been recorded from the coasts of Australasia, South Africa and South America.* This alone would seem to deny them a northern ancestry and to rule out the possibility of their having had recent association with the north. It seems to point on the contrary to their having evolved *where we find them today*, in complete isolation, possibly, as Regan suggests, since from as long ago as the dawn of the Tertiary Period. There is evidence, notably in the large and active *P. kerguelensis*, so abundant and widely spread on the high continental platform, of a northward dispersal to lower latitudes via the radial ridges, and this could be: (1) a recent phenomenon (perhaps still in fact going on), or (2) one perhaps that occurred when the more obvious routes for diffusion, the submarine ridges, offered easier paths (for supposedly shallow-living animals)

* I have disregarded here *Isometra vivipara* as there appears to be some doubt as to whether the Graham Land and Patagonian specimens are the same.

than they do today. Since the high-shelf comatulids, so far as is known, have no pelagic larvae we can only guess at how dispersal, both round and away from the continent, took, or is taking, place. As Burton (1932) did for the sponges, however, I have suggested the occasional attachment of the young stages to floating objects which might be carried along either by the bottom currents or in the surface drift, particularly where the latter is strong. I have suggested too, as Ekman does for *Abatus*, that in certain instances active migration by the adults over the sea, even the deep-sea, floor may sometimes take place.

The distribution of the comatulids then (and of such few other animals as have been studied) seems to postulate prolonged isolation of the Antarctic continental platform and to provide little to support the Wegener theory. Obviously, however, a much wider zoogeographical field has yet to be covered before we can say that the whole complex question of former land bridges and drifting continents is settled. Further researches in both field and laboratory may in the long run reveal the Gondwanaland of the Wegener geologists to be less speculative than it has so often been said to be. The winds, the currents, the birds, it is true, are active agents of dispersal, responsible for many distributional phenomena we see around us today. Often indeed, as Skottsberg remarked, they seem to be the only possible agents. It is equally true, however, as Pantin (1960*b*) has warned us, that there are certain faunistic and floristic relations round the southern pole which need former 'more solid', land connexions to explain them. Clearly such connexions would help us to understand how *Promachocrinus kerguelensis* for instance, otherwise confined to the high shelf, got to South Georgia and Kerguelen, and how *Harmothoë spinosa*, also a high-shelf species, got as far as Patagonia. It seems likely in fact that those who argue that everything can be explained in terms of natural and existing means of dispersal, the bridge-building biogeographers and believers in drifting continents, will all three in the end, as Pantin (1960*b*) said of Darwin and Hooker, each have given us part of the truth.

I conclude with a passage from Broch (1961), which, although basically in accord with recent opinion, suggests yet another avenue of approach to Antarctica's zoogeographical problem. 'Whereas in earlier days the "Bathybius"-theory was adhered to by a majority, it is generally accepted in our time that the cradle of animal life has been in the shallow waters of the sea where bottom animals are concerned. To a certain degree this has apparently paralyzed or hypnotized the chain of reasoning in many investigators so effectively that they always look for predecessors in the shallower waters. Nevertheless, many species among the shallcw-water animals certainly are descendants of species which have lived, or even live today, in the deeper regions of the oceans. This certainly holds good for a series of species of benthonic animals in the Antarctic Ocean, where no sudden break of temperature, salinity, etc., creates abrupt boundaries.* It is accordingly not out of place to say that the Antarctic fauna of the continental shelf has been derived without doubt from archibenthal as well as from shallow-water ancestors in neighbouring habitats'. Obviously this calls (p. 329) for much further exploration, not only of the high continental platform, but also of the adjoining archibenthal and abyssal sea.

* He was referring here to the seaward edge of the Antarctic continental shelf, not to the Antarctic convergence where there is in fact a marked thermal boundary.

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PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Appendix I

Table A. Types of collecting gear

distinguishing symbol	description
BNR	Russell's bottom townet. A 100 cm stramin net on a frame attached to skids which raise it clear of the bottom
BTC	'*Challenger*' beam trawl. Three sizes with beams 17, 13 and 10 ft. long; mesh *ca.* $\frac{1}{2}$ in.
BTS	small beam trawl. Beam 8 ft. long; mesh at cod-end $\frac{1}{2}$ in.
DC	conical dredge. Mouth 16 in. in diameter, with canvas bag
DL	large rectangular dredge. Light pattern, with mouth 4 ft. × 1 ft.; bag 4 ft. long, mesh 1 in.
DLH	large rectangular dredge. Heavy pattern, with mouth 4 ft. × 1 ft.; bag 4 ft. long, mesh 1 in.
DRC	large rectangular dredge used by *Challenger*, with mouth 5 ft. × 1 ft. 3 in.
DRR	an ordinary dredge bag, as used with *DLH*, attached to a Russell frame
DRS	small rectangular dredge. Light pattern with mouth 30 in. × 12 in., bag *ca.* 2 ft. long, mesh $\frac{3}{4}$ in.
N70V	fine-meshed townet, used vertically, which had inadvertently touched bottom
NCS-T	townet of coarse silk, with 16 meshes to the linear inch, attached to back of trawl
N7-T	net of 7 mm mesh attached to back of trawl
OTC	commercial otter trawl. Head rope 80 ft. long; mesh at cod-end $1\frac{1}{4}$ in.
OTL	large otter trawl. Head rope 40 ft. long; mesh at cod-end $1\frac{1}{4}$ in.
TA	Agassiz trawl
TML	Monegasque trawl. Essentially a large dredge with heavy steel rectangular frame 6 ft. 9 in. × 2 ft. 10 in.; bag *ca.* 15 ft. long, mesh 1 in.

Table B. Gatherings of total comatulids with four different types of gear for which times of fishing have been estimated

DLH		*DRR*		*TML*		*OTL*	
minutes fishing	total catch	minutes fishing	total catch	minutes fishing	total catch	minutes fishing	total catch
1	6	10	7	5	4	5	21
5	1	15	1	5	15	13	5
5	14	20	13	5	54	16	1
5	28	20	52	13	2	20	2
6	2	30	1	20	19	20	6
6	8	30	3	30	63	30	8
7	12	30	24	60	13	60	342
8	1	55	5	60	15		
10	14						
15	1						
15	8						
15	30						
20	12						

DLH			*DRR*			*TML*			*OTL*		
total fishing time	total catch	average catch per 30 min	total fishing time	total catch	average catch per 30 min	total fishing time	total catch	average catch per 30 min	total fishing time	total catch	average catch per 30 min
118	137	35	210	106	15	198	185	28	164	385	70

Appendix II

Table C. Comatulids of the high continental shelf

(For explanation of the symbols used to describe gear see appendix I, table A)

station	date	position	locality	sea temperature (° C) surface	sea temperature (° C) bottom	gear	estimated time on bottom (min)	depth (m)	species recorded	no. of speci-mens	nature of bottom
					'*Belgica*' (Belgian)						
station numbers apparently not used	11 v 98	71° 09′ S, 89° 15′ W	Bellingshausen Sea	—	—	—	—	460	*Promachocrinus kerguelensis*	3	not recorded
	8 x 98	70° 23′ S, 82° 47′ W	Bellingshausen Sea	—	—	—	—	480	*Anthometra adriani*	1	
	18 x 98	70° 00′ S, 80° 48′ W	Bellingshausen Sea	—	—	—	—	460	*Promachocrinus kerguelensis*	1	
					'*Antarctic*' (Swedish)						
5	16 i 02	64° 20′ S, 56° 38′ W	east coast of Graham Land	—	—	—	—	150	*P. kerguelensis*	14	stones, gravel
									Isometra vivipara	4	
									Notocrinus virilis	15	
6	20 i 02	64° 36′ S, 57° 42′ W	east coast of Graham Land	—	—	—	—	125	*Promachocrinus kerguelensis*	1	stones, gravel
8	—	64° 03′ S, 56° 37′ W	east coast of Graham Land	—	—	—	—	?360	*P. kerguelensis*	1	not recorded
									Anthometra adriani	1	
					'*Gauss*' (German)						
station numbers apparently not used	18 iii 02	66° 02′ S, 89° 38′ E (approx.)	off Gaussberg, Kaiser Wilhelm Land*	—	—	—	—	385	*Promachocrinus kerguelensis*	1	terrigenous mud
	20 iii 02			—	—	—	—	385	*Anthometra adriani*	1	
	4 iv 02			—	—	—	—	350–400	*Promachocrinus kerguelensis*	1	
	17 iv 02			—	—	—	—	385	*Eumorphometra concinna*	1	
	1 v 02			—	—	—	—	350–400	*Promachocrinus kerguelensis*	1	
	6 v 02			—	—	—	—	172	*P. kerguelensis*	1	
	20 vi 02			—	—	—	—	385	*P. kerguelensis*	2	
									Anthometra adriani	1	
	29 xi 02			—	—	—	—	385	*A. adriani*	1	
	2 xii 02			—	—	—	—	385	*Promachocrinus kerguelensis*	1	
	3 xii 02			—	—	—	—	385	*Anthometra adriani*	1	
	12 xii 02			—	—	—	—	385	*A. adriani*	1	
									Eumorphometra concinna	1	
	13 xii 02			—	—	—	—	385	*Promachocrinus kerguelensis*	1	
	3 i 03			—	—	—	—	380	*P. kerguelensis*	1	
	8 i 03			—	—	—	—	380	*P. kerguelensis*	1	
	26 i 03			—	—	—	—	380	*P. kerguelensis*	1	
	28 i 03			—	—	—	—	380	*P. kerguelensis*	2	
	31 i 03			—	—	—	—	380	*Eumorphometra concinna*	1	
	7 ii 03			—	—	—	—	350	*Anthometra adriani*	1	
	8 ii 03			—	—	—	—	350	*Promachocrinus kerguelensis*	1	
	8 ii 03			—	—	—	—	400	*Anthometra adriani*	1	
	15 ii 03			—	—	—	—	400	*Promachocrinus kerguelensis*	3	
									Anthometra adriani	9	
									Eumorphometra concinna	2	
					'*Discovery*' (British)						
station numbers apparently not used	on various dates between 1902 and 1904	off Coulman Island	Ross Sea	—	—	*TA*	—	183	*Promachocrinus kerguelensis*	4	not recorded
		McMurdo Sound†	Ross Sea	—	—	—	—	—	*P. kerguelensis*	1	
		McMurdo Sound	Ross Sea	—	—	—	—	239	*P. kerguelensis*	4	
									Anthometra adriani	3	
		McMurdo Sound	Ross Sea	—	—	—	—	228	*A. adriani*	2	
		McMurdo Sound	Ross Sea	—	—	—	—	239	*A. adriani*	2	
		McMurdo Sound	Ross Sea	—	—	—	—	327	*Florometra mawsoni*	1	
		off Ross Island	Ross Sea	—	—	*TA*	—	917	*Promachocrinus kerguelensis*	1	
									Florometra mawsoni	2	
									Anthometra adriani	6	
		east end of Barrier	Ross Sea	—	—	—	—	183	*Promachocrinus kerguelensis*	1	mud, stones and rocks

* Evidently the Germans here were using man-hauled dredges or dredges operated by hand-driven winches, through holes in the ice. I have not, however, been able to find details.

† In McMurdo Sound the British were also, for at least part of the time, working through holes in the ice. Again, however, I have been unable to find details.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Table C (*cont.*)

station	date	position	locality	sea temperature (° C) surface	sea temperature (° C) bottom	gear	estimated time on bottom (min)	depth (m)	species recorded	no. of speci-mens	nature of bottom
					'*Scotia*' (Scottish)						
—	7 iii 04	74° 01′ S, 22° 00′ W	off Coats Land	—	—	—	—	295	*Anthometra adriani*	1	not recorded
					'*Terra Nova*' (British)						
194	22 ii 11	69° 43′ S, 163° 24′ E	off Oates Land	—	—	*TA*	—	329–366	*Promachocrinus kerguelensis*	2	not recorded
									Anthometra adriani	1	
294	15 i 13	74° 25′ S, 179° 03′ E	Ross Sea	—	—	*TA*	—	289	*Promachocrinus kerguelensis*	3	not recorded
295	27 i 13	73° 51′ S, 172° 57′ E	Ross Sea	—	—	*TA*	—	348	*Notocrinus virilis*	2	not recorded
314	23 i 11	McMurdo Sound	Ross Sea	—	—	*TA*	—	406–441	*Promachocrinus kerguelensis*	1	mud
									Anthometra adriani	3	
									Florometra mawsoni	4	
									Notocrinus virilis	parts	
316	9 ii 11	McMurdo Sound	Ross Sea	—	—	*TA*	—	348–457	*Promachocrinus kerguelensis*	1	mud
									Florometra mawsoni	5	
									Anthometra adriani	1	
317	—	McMurdo Sound	Ross Sea	—	—	*	—	175	*Promachocrinus kerguelensis*	2	not recorded
339	24 i 12	77° 05′ S, 164° 17′ E	Ross Sea	—	—	*TA*	—	256	*P. kerguelensis*	5	mud
340	25 i 12	76° 56′ S, 164° 12′ E	Ross Sea	—	—	*TA*	—	293	*P. kerguelensis*	4	mud
									Notocrinus virilis	1	
349	15 ii 12	McMurdo Sound	Ross Sea	—	—	*TA*	—	146	*Promachocrinus kerguelensis*	9	mud
355	20 i 13	77° 46′ S, 166° 08′ E	Ross Sea	—	—	*TA*	—	547	*P. kerguelensis*	6	not recorded
356	22 i 13	off Granite Harbour	Ross Sea	—	—	*TA*	—	92	*P. kerguelensis*	1	mud
—	—	McMurdo Sound	Ross Sea	—	—	—	—	—	*Anthometra adriani*	1	not recorded
					'*Aurora*' (Australasian)						
1	22 xii 13	66° 50′ S, 142° 06′ E	off Adélie Land	—	−1·85	*TML*	30	649	*Promachocrinus kerguelensis*	36	muddy green diatomaceous ooze
									Solanometra antarctica	1	
									Anthometra adriani	23	
									Notocrinus virilis	3	
2	28 xii 13	66° 57′ S, 145° 20′ E	off Adélie Land	−1·03	−1·79	*TML*	60	583	*Promachocrinus kerguelensis*	7	grey sandy mud
									Anthometra adriani	4	
									Florometra mawsoni	2	
3	31 xii 13	66° 32′ S, 141° 37′ E	off Adélie Land	−0·79	−1·59	*TML*	60	288	*Promachocrinus kerguelensis*	3	green terrigenous mud
									Solanometra antarctica	5	
									Anthometra adriani	3	
									Notocrinus virilis	4	
8	27 i 14	66° 08′ S, 94° 20′ E	off Queen Mary Land	—	−1·42	*DLH*	—	266	*Promachocrinus kerguelensis*	2	green mud
									Anthometra adriani	1	
									Florometra mawsoni	6	
9	28 i 14	65° 20′ S, 95° 27′ E	off Queen Mary Land	—	−1·63	*TML*	—	440	*Promachocrinus kerguelensis*	5	pale green terrigenous sandy mud
									Anthometra adriani	2	
									Florometra mawsoni	2	
10	29 i 14	65° 05′ S, 96° 00′ E	off Queen Mary Land	—	−1·66	*TML*	—	624	*Promachocrinus kerguelensis*	3	green mud
									Florometra mawsoni	4	
12	31 i 14	64° 32′ S, 97° 20′ E	off Queen Mary Land	−0·68	−1·73	*TML*	—	189	*Promachocrinus kerguelensis*	8	grey terrigenous mud
									Anthometra adriani	15	
									Florometra mawsoni	11	

* A townet which touched bottom some time between 7 June and 14 October during the winter of 1911.

TABLE C (*cont.*)

station	date	position	locality	sea temperature (° C) surface	sea temperature (° C) bottom	gear	estimated time on bottom (min)	depth (m)	species recorded	no. of speci-mens	nature of bottom
'*Discovery*' (British, Australian, New Zealand)											
30	27 xii 29	66° 48′ S, 71° 24′ E	Princess Elizabeth Land	−0·67	−0·97	*TML*	20	456	*Anthometra adriani*	11	greyish sandy mud
									Notocrinus mortenseni	8	
34	7 i 30	66° 21′ S, 58° 50′ E	Kemp Land	−0·64	—	*DLH*	20	603	*Anthometra adriani*	1	dark grey mud with some gravel
									Notocrinus virilis	9	
									N. mortenseni	2	
39	17 i 30	66° 10′ S, 49° 41′ E	Enderby Land	−1·30	—	*TML*	13	300	*Anthometra adriani*	1	grey muddy sand
									Notocrinus virilis	1	
40	17 i 30	66° 12′ S, 49° 37′ E	Enderby Land	—	—	*TML*	5	300	*Promachocrinus kerguelensis*	4	brown sandy mud
									Anthometra adriani	34	
									Florometra mawsoni	3	
									Isometra graminea	5	
									Notocrinus virilis	2	
									N. mortenseni	6	
41	24 i 30	65° 48′ S, 53° 16′ E	Enderby Land	−0·70	−1·77	*OTL*	5	209–180	*Promachocrinus kerguelensis*	6	brownish grey shelly mud
									Anthometra adriani	2	
									Florometra mawsoni	3	
									Isometra graminea	1	
									Notocrinus virilis	7	
									N. mortenseni	2	
41	24 i 30	65° 48′ S, 53° 16′ E	Enderby Land	−0·70	−1·77	*TML*	5	193	*Anthometra adriani*	2	brownish grey shelly mud
									Eumorphometra aurora	1	
									Notocrinus virilis	1	
42	26 i 30	65° 50′ S, 54° 23′ E	Enderby Land	−0·24	—	*TML*	5	220	*Promachocrinus kerguelensis*	1	brownish green sandy mud
									Florometra mawsoni	11	
									Anthometra adriani	2	
									Eumorphometra aurora	1	
90	7 i 31	66° 21′ S, 138° 28′ E	Adélie Land	−1·09	—	*DLH*	15	640	*Promachocrinus kerguelensis*	5	fine terrigenous mud
									Anthometra adriani	3	
97	26 i 31	65° 10′ S, 108° 12′ E	Knox Land	—	—	*DLH*	5	474	*Florometra mawsoni*	1	grey sandy mud
98	27 i 31	65° 07′ S, 107° 29′ E	Knox Land	−1·03	—	*DLH*	15	502	*F. mawsoni*	1	not recorded
103	10 ii 31	67° 03′ S, 74° 29′ E	Princess Elizabeth Land	−0·83	—	*DLH*	8	437	*Anthometra adriani*	1	grey sandy mud
105	13 ii 31	67° 46′ S, 67° 03′ E	MacRobertson Land	−0·70	—	*DLH*	15	163	*Promachocrinus kerguelensis*	12	not recorded
									Florometra mawsoni	7	
									Notocrinus virilis	11	
107	16 ii 31	66° 45′ S, 62° 03′ E	MacRobertson Land	−0·21	−1·19	*OTL*	60	219	*Promachocrinus kerguelensis*	150	fine grained quartz sand with almandine garnets
									Florometra mawsoni	23	
									Anthometra adriani	117	
									Notocrinus virilis	45	
									N. mortenseni	7	
107	16 ii 31	66° 45′ S, 62° 03′ E	MacRobertson Land	−0·21	−1·19	*DLH*	10	219	*Promachocrinus kerguelensis*	5	
									Anthometra adriani	2	
									Anisometra frigida	1	
									Isometra graminea	4	
									Notocrinus virilis	2	

TABLE C (*cont.*)

station	date	position	locality	sea temperature (° C) surface	bottom	gear	estimated time on bottom (min)	depth (m)	species recorded	no. of speci-mens	nature of bottom
'Discovery' Investigations (British)											
170	23 ii 27	61° 25′ S, 53° 46′ W	off Clarence Island	0·65	−0·42	*DLH*	5	342	*Promachocrinus kerguelensis*	6	rock
									Isometra hordea	3	
									Notocrinus virilis	17	
									N. mortenseni	2	
172	26 ii 27	62° 59′ S, 60° 28′ W	Bransfield Strait	0·75	0·25	*DLH*	6	525	*Promachocrinus kerguelensis*	2	rock
175	2 iii 27	63° 17′ S, 59° 48′ W	Bransfield Strait	0·35	−0·48	*DLH*	7	200	*P. kerguelensis*	3	mud, stones and gravel
									Phrixometra nutrix	1	
									Isometra vivipara	1	
									Notocrinus virilis	7	
177	5 iii 27	63° 17′ S, 61° 17′ W	Bransfield Strait	0·35	—	*DLH*	6	1080	*Promachocrinus kerguelensis*	8	mud, coarse sand and stones
180	11 iii 27	64° 20′ S, 63° 00′ W	Palmer Archipelago	−0·02	0·00	*OTL*	30	160–330	*P. kerguelensis*	5	mud and stones
									Florometra mawsoni	3	
181	12 iii 27	64° 20′ S, 63° 01′ W	Palmer Archipelago	−0·05	0·40	*OTL*	13	160–335	*Promachocrinus kerguelensis*	3	mud
									Florometra mawsoni	2	
182	14 iii 27	64° 21′ S, 62° 50′ W	Palmer Archipelago	−0·21	0·12	*OTL*	20	278–500	*Promachocrinus kerguelensis*	6	mud
187	18 iii 27	64° 48′ S, 63° 31′ W	Palmer Archipelago	−0·05	0·18	*OTL*	16	259–354	*Notocrinus mortenseni*	1	mud
190	24 iii 27	64° 56′ S, 65° 35′ W	Palmer Archipelago	−0·32	0·55	*DLH*	5	315	*Florometra mawsoni*	1	mud, stones and rock
									Anthometra adriani	2	
									Isometra graminea	5	
									Notocrinus mortenseni	6	
599	17 i 31	67° 08′ S, 69° 06′ W	off Adelaide Island	−0·71	−0·01	*DLH*	1	203	*Promachocrinus kerguelensis*	1	not recorded
									Florometra mawsoni	5	
1644	16 i 36	78° 25′ S, 164° 10′ W	Ross Sea	−0·48	−1·85	*BNR*	55	626	*Promachocrinus kerguelensis*	1	soft mud with rocks
1652	23 i 36	75° 56′ S, 178° 35′ W	Ross Sea	−0·61	−1·90	*DRR*	30	567	*P. kerguelensis*	19	soft mud
									Florometra mawsoni	1	
									Isometra graminea	4	
1658	26 i 36	76° 09′ S, 168° 40′ E	Ross Sea	—	—	*DRR*	55	520	*Promachocrinus kerguelensis*	4	not recorded
									Notocrinus virilis	1	
1660	27 i 36	74° 46′ S, 178° 23′ E	Ross Sea	−0·09	−0·56	*OTL*	20	351	*Florometra mawsoni*	1	soft mud
									Anthometra adriani	1	
1872	12 xi 36	63° 29′ S, 54° 03′ W	off Joinville Island	−1·29	−1·66	*BNR*	30	247	*Isometra graminea*	1	soft mud
1873	13 xi 36	61° 21′ S, 54° 04′ W	off Clarence Island	−0·87	−0·43	*DRR*	15	117	*I. hordea*	1	rock and stones
1948	4 i 37	60° 49′ S, 52° 40′ W	off Clarence Island	0·88	—	*DRR*	20	490–610	*Promachocrinus kerguelensis*	1	not recorded*
									Eumorphometra marri	2	
									Phrixometra longipinna var. *antarctica*	4	
									Isometra hordea	4	
									Notocrinus virilis	1	
									N. mortenseni	1	
1952	11 i 37	62° 05′ S, 58° 05′ W	Bransfield Strait	—	—	*DRR*	20	367–383	*Promachocrinus kerguelensis*	43	soft mud with many large stones
									Anthometra adriani	9	
1955	29 i 37	61° 35′ S, 57° 23′ W	South Shetlands	—	—	*DRR*	10	440–410	*Promachocrinus kerguelensis*	2	not recorded
									Eumorphometra fraseri	1	
									Isometra hordea	4	
1957	3 ii 37	61° 20′ S, 53° 40′ W	off Clarence Island	—	—	*DRR*	30	785–767	*Promachocrinus kerguelensis*	1	stones
		61° 20′ S, 53° 40′ W	off Clarence Island	—	—	*DRR*	30	830	*P. kerguelensis*	1	rough, stony
									Kempometra grisea	2	

* But I recall it as exceedingly stony (cf. Stations 1873, 1957).

Table D. Comatulids of the outlying shelves

station	date	position	locality	sea temperature (° C) surface	sea temperature (° C) bottom	gear	estimated time on bottom (min)	depth (m)	species recorded	no. of speci-mens	nature of bottom
(1) *The Patagonian region including Burdwood Bank*											
'*Antarctic*' (Swedish)											
1	—	33° 00′ S, 51° 10′ W	north of the Plate	—	—	—	—	80	*Isometra vivipara*	1	not recorded
2	23 xii 01	37° 50′ S, 56° 11′ W	off the Plate	—	—	—	—	100	*I. vivipara*	1	gravel and sand
58	11 ix 02	52° 29′ S, 60° 36′ W	Burdwood Bank	—	4·10	—	—	197	*I. vivipara*	1	sand and gravel
59	12 ix 02	53° 41′ S, 61° 10′ W	Burdwood Bank	—	—	—	—	137–150	*Phrixometra nutrix*	1	stony with shell fragments
									Isometra vivipara	9	
'*Discovery*' Investigations (British)											
652	14 iii 31	54° 04′ S, 61° 40′ W	Burdwood Bank	7·62	6·10	*OTL*	17	171–169	*I. vivipara*	18	very rough
WS 81	19 iii 27	51° 30′ S, 61° 15′ W	off Falkland Islands	8·90	8·22	*OTC*	57	81–82	*I. vivipara*	3	sand
WS 83	24 iii 27	52° 28′ S, 60° 06′ W	off Falkland Islands	8·43	7·60	*N7-T*	60	137–129	*I. vivipara*	12	fine green sand and shell
WS 85	25 iii 27	52° 09′ S, 58° 14′ W	off Falkland Islands	8·38	8·30	*OTC*	60	79	*I. vivipara*	4	sand and shell
WS 212	30 v 28	49° 22′ S, 60° 10′ W	Patagonian Shelf	6·42	5·76	*N7-T*	60	242–249	*I. vivipara*	1	green sand, mud and pebbles
WS 228	30 vi 28	50° 50′ S, 56° 58′ W	Patagonian Shelf	5·35	5·22	*OTC*	60	229–236	*I. vivipara*	1	coarse white sand
WS 248	20 vii 28	52° 40′ S, 58° 30′ W	Patagonian Shelf	5·16	5·24	*OTC*	60	210–242	*I. vivipara*	4	fine green sand, pebbles and shells
WS 824	19 i 32	52° 29′ S, 58° 27′ W	Patagonian Shelf	8·30	5·45	*OTC*	65	146–137	*I. vivipara*	2	green speckled sand and shells
WS 877	4 iv 32	52° 35′ S, 61° 04′ W	Patagonian Shelf	5·58	4·86	*BNR*	50	349	*I. vivipara*	11	not recorded
(2) *The South Georgia area* (*with Shag Rocks*) *and the South Sandwich Islands*											
'*Antarctic*' (Swedish)											
20	6 v 02	54° 12′ S, 36° 50′ W	West Cumberland Bay	—	—	—	—	250	*Promachocrinus kerguelensis*	1	small stones
22	14 v 02	54° 17′ S, 36° 18′ W	East Cumberland Bay	—	1·50	—	—	75	*P. kerguelensis*	2	clay and algae
34	5 vi 02	54° 11′ S, 36° 18′ W	off Cumberland Bay	—	1·45	—	—	252–310	*P. kerguelensis*	1	clay with stones
'*Discovery*' Investigations (British)											
MS 14	17 ii 25	—	East Cumberland Bay	—	—	*DRS*	10	190–110	*P. kerguelensis*	2	not recorded
MS 71	9 iii 26	—	East Cumberland Bay	—	—	*BTS*	20	110–60	*P. kerguelensis*	28	
MS 74	17 iii 26	—	East Cumberland Bay	—	2·75	*NCS-T*	20	22–40	*P. kerguelensis*	parts	
27	15 iii 26	—	West Cumberland Bay	—	—	*DL*	15	110	*P. kerguelensis*	1	mud and rock
39	25 iii 26	—	East Cumberland Bay	2·85	1·02	*OTL*	60	179–235	*P. kerguelensis*	1	grey mud
42	1 iv 26	—	off mouth of Cumberland Bay	—	2·08	*OTL*	60	120–204	*P. kerguelensis*	8	mud
123	15 xii 26	—	off mouth of Cumberland Bay	1·60	0·47	*OTL*	90	230–250	*P. kerguelensis*	1	grey mud
144	5 i 27	54° 04′ S, 36° 27′ W	off mouth of Stromness Harbour	2·00	−0·15	*OTL*	60	155–178	*P. kerguelensis*	6	green mud and sand
148	9 i 27	54° 03′ S, 36° 39′ W	off Cape Saunders	3·56	0·22	*OTL*	30	132–148	*P. kerguelensis*	4	grey mud and stones
149	10 i 27	—	mouth of East Cumberland Bay	3·55	0·10	*OTL*	60	200–234	*P. kerguelensis*	5	mud
152	17 i 27	53° 51′ S, 36° 18′ W	off South Georgia	—	0·68	*DLH*	10	245	*P. kerguelensis*	2	rock
156	20 i 27	53° 51′ S, 36° 21′ W	off South Georgia	—	—	*DLH*	10	200–236	*P. kerguelensis*	8	rock
									Phrixometra longipinna var. *antarctica*	1	
160	7 ii 27	53° 44′ S, 40° 57′ W	near Shag Rocks	3·00	1·42	*DLH*	4	177	*Eumorphometra aurora*	1	grey mud, stones and rock
									Phrixometra rayneri	1	
									Isometra flavescens	12	
345	8 ii 30	55° 20′ S, 34° 47′ W	off South Georgia	2·88	1·11	*N7OV*	5	180	*Promachocrinus kerguelensis*	1	small stones, shells
363	26 ii 30	56° 20′ S, 27° 30′ W	South Sandwich Islands	0·90	0·43	*DLH*	3	329–278	*P. kerguelensis*	3	scoria
366	6 iii 30	59° 30′ S, 27° 15′ W	South Sandwich Islands	0·20	−0·02	*OTL*	50	77–152	*P. kerguelensis*	6	black sand
371	14 iii 30	58° 30′ S, 26° 05′ W	South Sandwich Islands	0·00	−0·49	*OTL*	24	99–161	*P. kerguelensis*	5	not recorded

TABLE D (*cont.*)

station	date	position	locality	sea temperature (° C) surface	sea temperature (° C) bottom	gear	estimated time on bottom (min)	depth (m)	species recorded	no. of specimens	nature of bottom
			(3) *Prince Edward, Marion, Crozets, Kerguelen and Heard Island*								
			'*Challenger*' (British)								
144A	26 xii 73	46° 48′ S, 37° 49′ E	off Marion Island	5·00	—	*DRC*	—	92	*Hathometra exigua*	1	volcanic sand
145	27 xii 73	46° 43′ S, 38° 05′ E	off Prince Edward Island	5·28	—	*DRC*	—	257	*H. exigua*	2	volcanic sand
									Eumorphometra hirsuta	1	
—			at Kerguelen	—	—	*DRC*	—	18–183	*Promachocrinus kerguelensis*	1	volcanic mud
149C	from 9 i 74 to 29 i 74	49° 28′ S, 70° 13′ E (approx.)	Balfour Bay, Kerguelen	—	—	*DRC*	—	37–110	*P. kerguelensis*	2	
149D			Royal Sound, Kerguelen	—	—	*DRC*	—	51	*P. kerguelensis*	1	
149E			off Greenland Harbour, Kerguelen	—	—	*DRC*	—	55	*P. kerguelensis*	1	
149H			off Cumberland Bay, Kerguelen	—	—	*DRC*	—	233	*P. kerguelensis*	2	
150	2 ii 74	52° 04′ S, 71° 22′ E	between Kerguelen and Heard I.	3·06	1·78	*DRC*	—	275	*Solanometra antarctica*	8	coarse gravel
151	7 ii 74	52° 59′ S, 73° 33′ E	off Heard Island	2·33	—	*DRC*	—	137	*Promachocrinus kerguelensis*	1	volcanic sand
									Solanometra antarctica	3	
			'*Discovery*' (British, Australian, New Zealand)								
5	16 xi 29	49° 33′ S, 69° 50′ E	Royal Sound, Kerguelen	—	—	*DRS*	3	20	*Promachocrinus kerguelensis*	1	dark coloured muds of volcanic origin
15	23 xi 29	49° 27′ S, 70° 02′ E	Royal Sound, Kerguelen	—	—	*DRS*	15	55	*P. kerguelensis*	4	
47	7 ii 30	49° 50′ S, 69° 33′ E	off Kerguelen	3·78	—	*DLH*	5	150	*P. kerguelensis*	3	
58	22 ii 30	49° 30′ S, 70° 04′ E	Royal Sound, Kerguelen	6·05	—	*DLH*	5	50	*P. kerguelensis*	1	not recorded
64	2 iii 30	49° 28′ S, 70° 33′ E	off Kerguelen	—	—	*OTL*	60	91	*P. kerguelensis*	10	dark volcanic mud
			(4) *Tristan and Gough*								
—	24 iv 04	—	off Gough Island	—	—	*TML*	—	183	*Florometra goughi*	2	not recorded

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

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Table E. Crinoids of the abyssal sea south of 35° S

date	position	bottom temp. (° C)	gear	depth (m)	species recorded	no. of specimens	nature of bottom
18 iii 04	71° 22′ S, 16° 34′ W	—	*TML*	2587	undescribed comatulid	1	mud, with sand, pebbles and small stones
14 iii 99	70° 40′ S, 102° 15′ W	0·50	trawl*	2800	—	—	not recorded
21 iii 04	69° 33′ S, 15° 19′ W	—	*TML*	4807	—	—	blue mud, with big stones
7 iii 03	67° 33′ S, 36° 35′ W	—	*TML*	4589	*Ptilocrinus brucei*	1	not recorded
9 iii 03	66° 40′ S, 40° 35′ W	—	*TML*	4449	—	—	mud
25 xii 29	66° 28′ S, 72° 41′ E	—	*TML*	1266	*Florometra spinulifera*	1	grey mud, with gravel
14 ii 74	65° 42′ S, 79° 49′ E	0·55	*DRC*	3073	—	—	blue mud, many rocks and pebbles
1 iii 03	65° 35′ S, 85° 20′ E	—	—	2450	*Thaumatocrinus renovatus*	2	glacial marine ooze
23 ii 03	65° 30′ S, 85° 40′ E	−0·30	—	2725	*Psathyrometra antarctica*	1	glacial marine ooze
13 iii 03	64° 48′ S, 44° 26′ W	—	*TML*	4559	*Ptilocrinus brucei*	1	blue mud
6 i 14	64° 34′ S, 127° 08′ E	−0·30	*TML*	3110	—	—	glacial mud and stones
21 i 31	64° 28′ S, 114° 59′ E	—	*DLH*	1718	—	—	not recorded
18 i 31	64° 21′ S, 116° 02′ E	—	*TML*	2267	—	—	ooze
17 xii 98	63° 16′ S, 57° 51′ E	−0·50	*TML*	4636	*Ilycrinus australis*	?	blue mud
					Hyocrinus bethellianus	2	
14 i 14	63° 13′ S, 101° 42′ E	−0·22	*TML*	1591	—	—	large rocks
26 ii 74	62° 26′ S, 95° 44′ E	−0·39	*BTC*	3624	—	—	diatom ooze
18 iii 03	62° 10′ S, 41° 20′ W	—	*TML*	3257	*Eometra weddelli*	8	not recorded
					Tonrometra remota	2	
11 ii 74	60° 52′ S, 80° 20′ E	—	*BTC*	2312	—	—	diatom ooze, granite and sandstone pebbles
3 iii 74	53° 55′ S, 108° 35′ E	0·11	*BTC*	3578	—	—	diatom ooze
9 iv 04	51° 07′ S, 09° 31′ W	—	*TML*	3859	—	—	diatom ooze
7 iii 74	50° 01′ S, 123° 04′ E	0·83	*BTC*	3303	*Thaumatocrinus renovatus*	2	globigerina ooze
13 iv 04	48° 06′ S, 10° 05′ W	—	*TML*	3196	—	—	rocky, small stones
12 iv 04	48° 00′ S, 09° 50′ W	—	*TML*	2444	—	—	rocky
5 iii 30	47° 05′ S, 79° 16′ E	—	*TML*	3112	—	—	not recorded
29 xii 73	46° 46′ S, 45° 31′ E	2·00	*BTC*	2514	*Ilycrinus australis*	1	globigerina ooze
30 xii 73	46° 16′ S, 48° 27′ E	1·22	*BTC*	2926	*I. australis*	1	diatom ooze
					Hyocrinus bethellianus	3	
					Thalassometra bispinosa	1	
					Trichometra remota	5	
					Thaumatometra abyssorum	11	
					Thaumatocrinus renovatus	3	
13 xii 12	42° 48′ S, 148° 41′ E	—	*TML*	2330	—	—	ooze
13 iii 74	42° 42′ S, 134° 10′ E	1·06	*BTC*	4771	*Bathymetra carpenteri*	1	red clay
11 ii 76	42° 32′ S, 56° 29′ W	0·94	*BTC*	3743	—	—	globigerina ooze
29 iv 04	39° 48′ S, 02° 33′ E	—	*TML*	4853	—	—	red clay
23 x 75	39° 41′ S, 131° 23′ W	1·55	*BTC*	4679	—	—	red clay
27 x 75	39° 13′ S, 118° 49′ W	1·44	*BTC*	4130	—	—	red clay
10 iii 76	37° 29′ S, 27° 31′ W	1·11	*BTC*	4037	—	—	globigerina ooze
18 x 73	37° 21′ S, 12° 23′ W	—	*DRC*	1832	—	—	hard ground, shells and gravel
14 ii 76	37° 17′ S, 53° 52′ W	2·89	*BTC*	1097	*Phrixometra longipinna*	3	blue mud
					Isometra lineata	1	
					I. angustipinna	1	
18 x 73	37° 15′ S, 12° 20′ W	—	*DRC*	2018	—	—	hard ground
18 x 73	37° 11′ S, 12° 18′ W	2·89	*DRC*	1005	*Thalassometra setosa*	1	hard ground
2 iii 76	36° 44′ S, 46° 16′ W	0·39	*BTC*	4862	—	—	blue mud
14 x 73	36° 12′ S, 12° 16′ W	2·22	*DRC*	3715	—	—	globigerina ooze
23 x 73	35° 59′ S, 01° 34′ E	1·39	*DRC*	4769	—	—	globigerina ooze
24 ii 14	35° 55′ S, 134° 18′ E	—	*TML*	3303	—	—	globigerina ooze
11 x 73	35° 41′ S, 20° 55′ W	1·89	*BTC*	3486	—	—	globigerina ooze
28 ii 76	35° 39′ S, 50° 47′ W	0·61	*BTC*	3486	*Rhizocrinus lofotensis*	1	blue mud
13 iii 76	35° 36′ S, 21° 12′ W	1·89	*BTC*	3716	—	—	globigerina ooze

* Type not specified. Recorded as *chalut*.

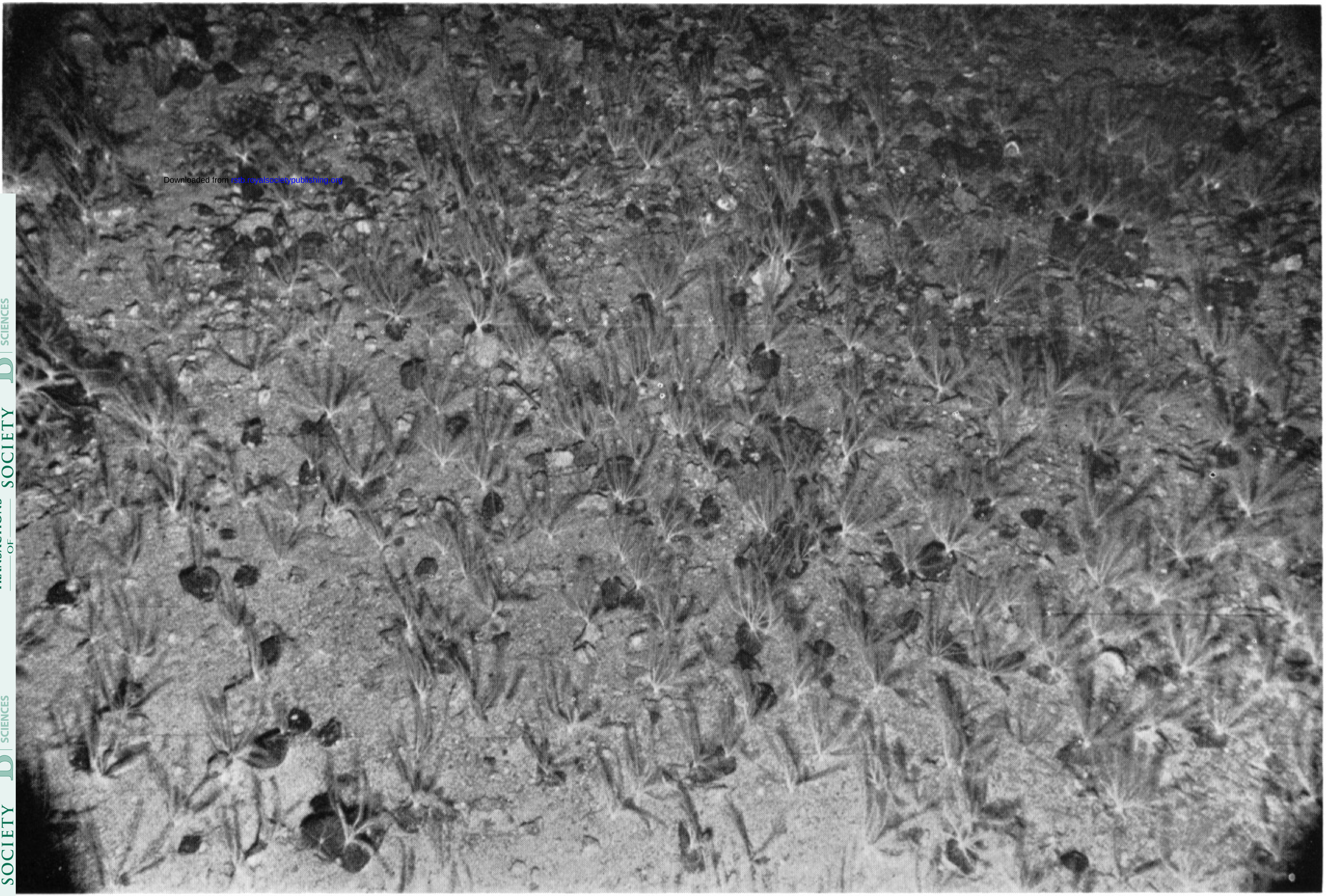

FIGURE 12. A photograph by Dr A. S. Laughton taken on the Galicia Bank in 651 m, 42° 40′ N, 11° 35′ W on 19 June 1958, showing part of a great field of comatulids evidently all belonging to the same, perhaps gregarious, species. Area of picture $1\frac{1}{2} \times 2\frac{1}{2}$ m.