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The terrestrial invertebrate fauna of the Maritime Antarctic

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(Pull-out table, Appendix 3)

INTRODUCTION

During the period from 18 January to 31 March 1964 the author was able to visit certain islands on the Scotia Ridge and parts of the Antarctic Peninsula. Apart from South Georgia, all the areas lie within the Maritime Antarctic region (Holdgate 1964). At each locality an attempt was made to ascertain the composition of the meiofauna from as many terrestrial habitats as possible and, when time permitted, quantitative sampling was carried out. During the previous two years a similar but more detailed study was carried out at Signy Island, South Orkney Islands, but the bulk of these data will be presented elsewhere. Figure 32 shows all the areas visited with the month and number of quantitative samples taken. It was only possible to spend a few hours at certain localities.

The Maritime Antarctic is, by definition (Holdgate 1964), a region bounded by isotherms and supporting a limited but typical vegetation. The types of plant communities have already been discussed (Longton, this Discussion, p. 213) and it is clear that whilst a considerable amount of species and community variation exists there is a basic similarity throughout the region. This general uniformity of climate and vegetation would together appear to offer a similar set of terrestrial habitat conditions. If dispersal were not a limiting factor, one would also expect the invertebrate fauna of such habitats to exhibit a uniform pattern. In fact it does not.

This paper presents the distributional and ecological information obtained on the fauna from each area visited and any species or numerical diversity is discussed in relation to biocoenotic factors. Whilst not able to visit Bouvetøya personally the author has examined the invertebrates collected from that island by Dr M. W. Holdgate in March 1964. Although South Georgia lies outside the Maritime Antarctic region the information obtained on the mite, Collembola and nematode faunas of this island is included for comparative purposes. Some of the figures in this paper, and parts of the text, are based on numerical data presented in another paper which will appear in an American monograph on Antarctic arthropods.

METHODS

At each locality, all areas free of snow were examined, to ascertain their arthropod fauna. Where the substrate consisted of rock *in situ*, boulders, or stony ground, collecting was carried out by means of an aspirator but this method is biased toward the larger more conspicuous forms and may not give a true picture of the species present. Where the mineral fragment was small or vegetation occurred, samples were taken and the arthropod fauna extracted later in a large funnel 'Tullgren type' apparatus. Certain vegetation types were

selected for more detailed quantitative analysis and from these a series of cores of known volume (approximately 10 cm² in surface area and 6 cm deep) were taken. These were divided into upper and lower halves, each then being treated separately. The main extractor used at Signy Island for removal of the arthropods was a modification of the small canister apparatus of Macfadyen (1961) which relies on steep temperature and humidity gradients. A similar but more portable machine was designed in order to carry out

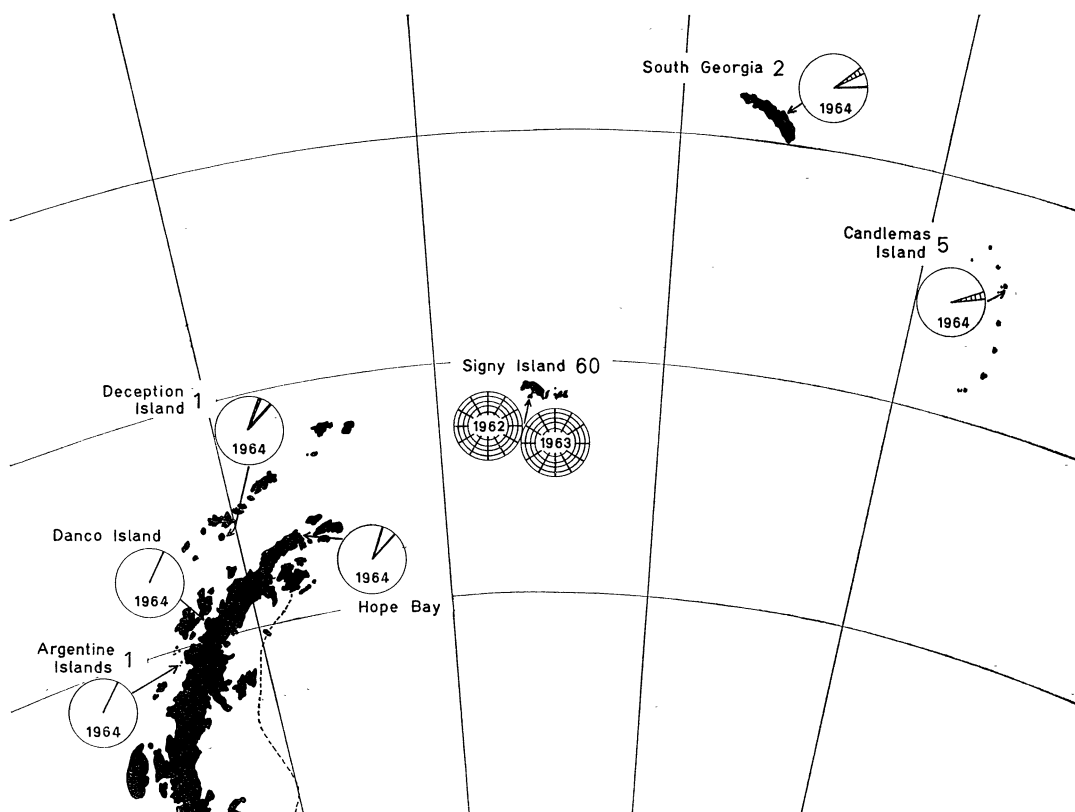


FIGURE 32. The areas visited during the present study. By dividing the circles into twelve sectors, the time of year and length of visit is shown. The figures after the place names indicate the number of quantitative samples taken at those localities.

quantitative work in other areas, and this was mounted in gimbals for use aboard ship. In both extractors electric lamps were the heat source, but the portable machine used air and not water as a coolant beneath the samples. In the portable extractor, small steep-sided glass funnels were used since they permitted smaller and more manageable specimen tubes to be utilized for catching the extracted arthropods. Some cores were teased apart on a wire mesh tray and subjected to 'wet' funnel extraction to ascertain their nematode content.

TOTAL INVERTEBRATE FAUNA

Several collections have been made of free-living invertebrates from terrestrial habitats in the Antarctic, but much of their taxonomy is still imperfectly known. Many of the

groups typically represented in soils of temperate regions are present in the Antarctic. Gressitt (1965) lists the following (parasitic groups excluded):

Protozoa	Tardigrada
Platyhelminthes	Insecta—Collembola
Rotifera	Diptera
Nematoda	Arachnida—Acari

Members of all these groups were found in the Maritime Antarctic region during the present study, but only the mites, Collembola and to a lesser extent the nematodes, were studied in any detail. Presumably because of their more conspicuous size, it is the mites and Collembola which have received most attention in the past, so it is perhaps indicative of the taxonomic state of the Antarctic terrestrial fauna that six new species and two new subspecies of mite were found by the author in this region alone (excluding South Georgia).

Annelid worms belonging to the Enchytraeidae were also found throughout the region, but these were always confined to the shore line and may not be classed as entirely terrestrial. Also, six specimens belonging to two species of Coleoptera were collected (Balfour-Browne & Tilbrook 1966) but one of these is known to be synanthropic and, until further records are obtained, the native status of the other must be treated as doubtful. Two Diptera are known to occur in the Maritime Antarctic region and both are midges (Chironomidae). The winged *Parochlus steineni* has been reported from the South Shetland Islands but was not found at Deception Island during the present study. The other fly is the apterous *Belgica antarctica* which is the southernmost pterygote insect. This was common at the Argentine Islands locality.

GEOGRAPHICAL DISTRIBUTION

The interrelationships of the total free-living mite and collembolan faunas are shown in figure 33. These maps have been compiled from the species distribution list shown as Appendix A. It should be remembered that only the areas visited and the fauna collected during the present study are considered here. No attempt is made to integrate data from other sources or to discuss the affinities of this fauna with other areas of the Antarctic or with the important source areas of South America and the Falkland Islands. The Sub-Antarctic island of South Georgia supports a much larger and more varied land fauna than areas farther south and, indeed, because of the brief and restricted survey of this island, the figures quoted are probably not an accurate indication of its total mite and Collembola fauna. It can be seen that there is a decrease in numbers of species eastwards and southwards from South Georgia reflecting the more harsh climatic conditions and similar decrease in vegetational diversity. Only one collembolan and one mite are found in all the areas. These are *Cryptopygus antarcticus* and *Nanorchestes antarcticus*, both of which are circumpolar in distribution. Apart from these, and a few other widespread forms, there is clearly no uniform distribution of mite and collembolan species throughout the region. This seems to indicate either that dispersal mechanisms are not efficient in all directions or that certain areas offer more favourable environments to certain species.

In the case of the mites, there is clearly a closer affinity between the faunas of certain areas. The South Sandwich Islands, for example, have seven species in common with

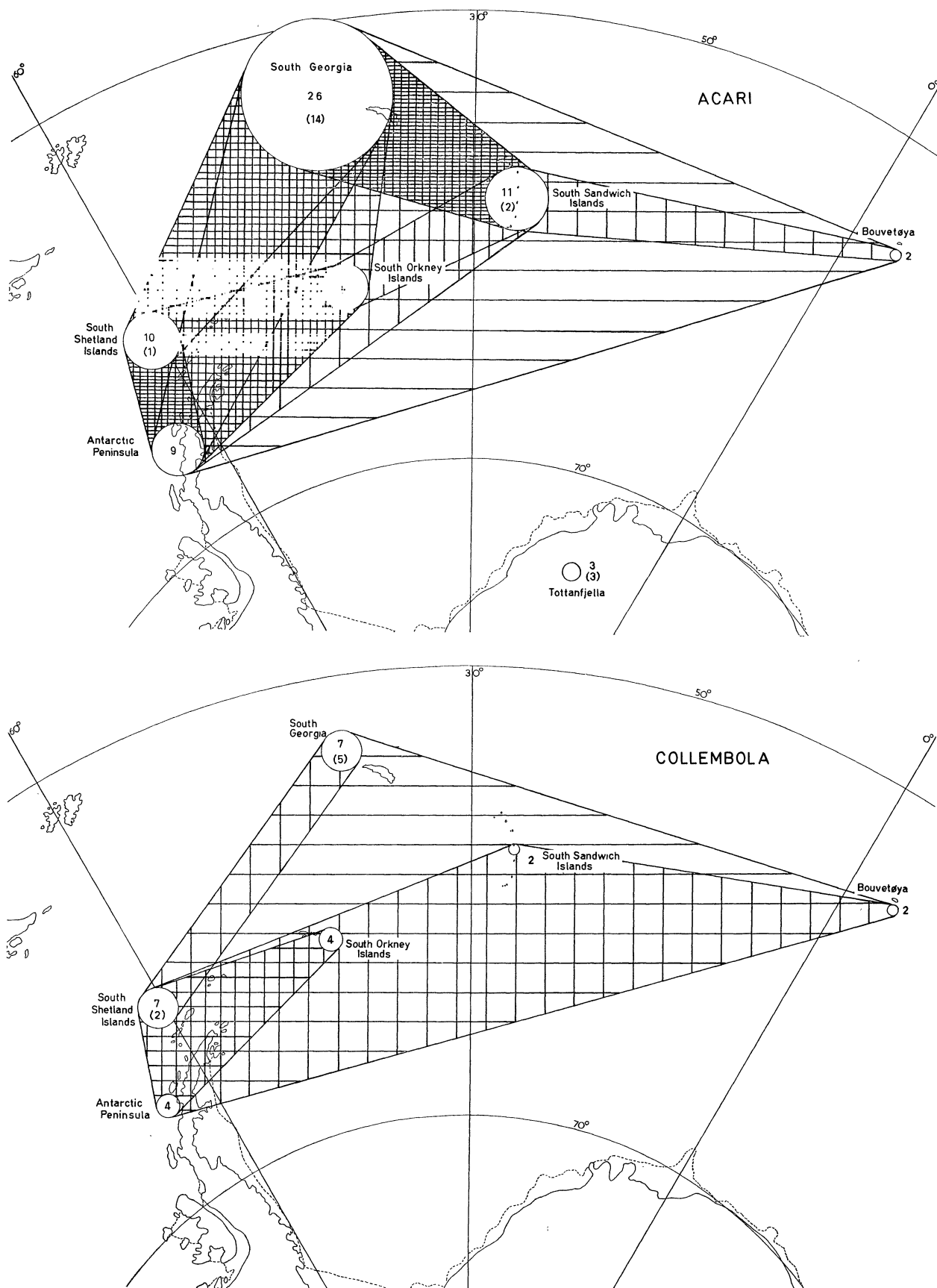


FIGURE 33. The interrelationships of the mite (above) and Collembola (below) species of the areas visited. The size of the circles is proportional to the number of species found in each area. Those species restricted to one area within this region, are indicated by the numbers in brackets. The number of species in common between different areas is shown by the degree of cross-hatching. (Subsequent to the printing of these maps further distribution records have emerged from the collections and these are included in Appendix A.)

South Georgia, five of which are not found elsewhere in this region. The Antarctic Peninsula and the South Shetland Islands also have seven species in common but only one of these is restricted to the two areas. In this latter case the proximity of the two areas could account for the similarity between their faunas. Holdgate (1960) has suggested that air currents have been responsible for conveying to certain mid-Atlantic islands much of their terrestrial fauna. Trapping experiments by aeroplanes, on ships and on land have indicated that air currents also act as an important agent of arthropod dispersal in the Antarctic (Gressitt 1965). Bearing in mind the prevailing westerly airstream, South Georgia would be a logical source area for immigration to the South Sandwich Islands. Three of the South Sandwich mites are oribatids all common at South Georgia. With their highly sclerotized cuticle, these are particularly resistant to desiccation and in this respect lend themselves to airborne dispersal. All the specimens of these three oribatid species were restricted to the more favourable environments surrounding fumaroles. This would suggest that the availability of suitable habitats is a further factor limiting distribution. The effect of these heated areas on the fauna will be dealt with in more detail later. The intermittent nature of many of the fumaroles may explain why more South Georgia mites are not present or it may be that many species are unable to survive the journey of some 600 km. The same similarity between the South Sandwich Islands and South Georgia faunas does not exist in the case of the Collembola and these insects seem particularly susceptible to desiccation. Two other oribatids occur on the South Sandwich Islands and both are subspecific forms of species very common in the maritime localities farther south but not found at South Georgia. This together with the general disparity between the South Orkney and South Sandwich Island faunas suggests a more sporadic dispersal mechanism such as birds. This is consistent with the fact that the westerly winds which blow over the South Orkney Islands rarely have a strong southerly component and would therefore usually pass to the south of the South Sandwich Islands.

It is of interest to note that the first collection of vegetation from the Tottan Mountains revealed three prostigmatid mites none of which have been found in any Maritime Antarctic locality (Bowra, Holdgate & Tilbrook 1966).

HABITAT DISTRIBUTION

As has been mentioned earlier, an attempt was made, at each of the areas visited, to examine the arthropod fauna of all possible terrestrial habitats. The habitats can be grouped under more or less clearly defined headings. First, there are those where macroscopic vegetation is completely or almost completely lacking, the localities consisting of rock fragments or mineral soil. Then there are the vegetated habitats. These may be divided into typical subformations (Longton, this Discussion, p. 213) which reflect certain physical factors of the environment such as drainage, exposure and biotic influence. Using such a classification the seventy non-quantitative samples taken from Signy Island have been divided up and a measure of the frequency of each species shown by the percentage occurrence in each habitat (figure 34). As can be seen, very few arthropods show any clear habitat specificity. This suggests that most of the species mentioned are tolerant of a wide range of habitat conditions. It may be, however, that any preference

has been obscured by the composite nature of some of the samples, or indeed that the habitat divisions adopted are too broad to be relevant to such small organisms. Nevertheless, various features emerge from figure 34 and combined with field observations and information from other Maritime Antarctic localities, permit certain observations on the habitat distribution of the arthropods. *Cryptopygus antarcticus* was found in all the terrestrial habitats examined at Signy Island and indeed has a similar widespread distribution at all the other Maritime Antarctic areas visited. The *Archisotoma* species is very restricted in

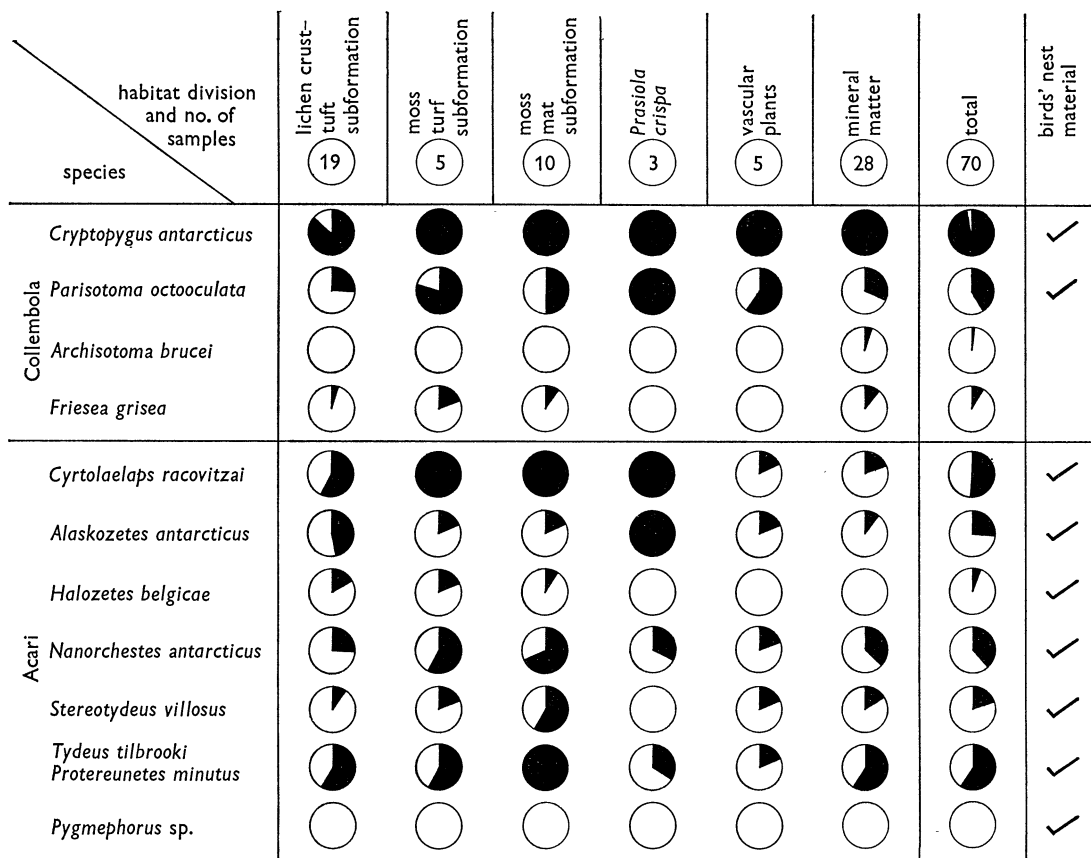


FIGURE 34. Frequency of occurrence, in different habitats, of the free-living arthropods at Signy Island. The shading in each circle is a measure of the percentage number of samples from each habitat in which each species occurred.

distribution and was found in only two samples, both of which were of mineral matter taken from the upper shore zone. It also occurred amongst beach material in other areas and in fact members of this genus are normally confined to such sea-shore habitats (Gisin 1960). It is interesting to note therefore, that in three samples from different islands in the South Sandwich groups, *Archisotoma brucei* was found in bryophyte mats surrounding fumaroles. *Friesea grisea* appears to prefer vegetated habitats but is quite rare at Signy Island where it is small and lightly coloured. This species occurs more frequently and in greater numbers at localities on the Antarctic Peninsula and at Deception Island, where the adults are larger and possess a more typical deep blue pigment. *Hypogastrura viatica*, *Cryptopygus caecus* and *Tullbergia mixta* were the three Collembola found only at Deception

Island in the Maritime Antarctic region. The former two were confined to habitats on the flat ash plain just above sea level and the latter is more common in vegetated areas.

As far as the mites are concerned, figure 34 only serves to emphasize that most of those at Signy Island exhibit little habitat specificity. *Cyrtolaelaps racovitzai*, *Nanorchestes antarcticus* and *Tydeus tilbrooki*/*Prottereunetes minutus* (these are two minute members of the Prostigmata which have so far not been separated during counting) are, in fact, the most frequent species in a wide range of habitats. Although it is not evident in figure 34, the large oribatid *Alaskozetes antarcticus* shows a marked preference for drier habitats and seldom occurs in large numbers within bryophyte mats. *Pygmephorus* sp. although apparently free living, was only found in birds' nests or their vicinity. The nests were often not inhabited but this species was still very abundant. The only astigmatid mite so far found in the Antarctic, *Calvolia antarctica* (Hughes & Tilbrook 1966) was restricted to coastal rocks on Candlemas Island. The vesicular nature of these volcanic rocks provided innumerable protective depressions and in such situations were also found the greatest densities of *Nanorchestes antarcticus*, as well as large numbers of *Alaskozetes antarcticus* and other arthropods. Localized 'pockets' of certain species were very common in most areas throughout the region. They appeared to occur frequently on the undersides of rocks though it may be that this is a false impression gained because in the field they are more conspicuous there than in vegetation. *Cryptopygus antarcticus* and *Alaskozetes antarcticus* are the commonest species to exhibit such aggregations. As well as adults and immature animals, sloughed cuticles and eggs are also often present in large numbers. In localities where macroscopic vegetation is absent, microscopic fungi (Gressitt 1965), algae and perhaps bacteria probably form the food of these arthropods. *Belgica antarctica* was found around the coastal zone in the Argentine Islands, and adults were numerous on the surface of small freshwater pools. The larvae and some adults were, however, also fairly common in bryophyte mats well away from marine influence. Details of all the non-quantitative and semi-quantitative collections made at Antarctic Peninsula and South Shetland Islands localities are given as Appendix B.

QUANTITATIVE DISTRIBUTION

Certain vegetation types were chosen in order that a quantitative comparison of the arthropod and nematode faunas could be made between different areas. These are the *Pohlia* type, the *Polytrichum-Dicranum* type and the lichen encrusted *Polytrichum-Dicranum* type. These were chosen initially for the Signy Island study because they differ in basic mechanical structure and also characterize areas of different environmental conditions. They are called vegetation 'types' because the species of bryophyte was not the same in all areas. Where alternatives had to be sampled, however, they always possessed a similar growth-form and had identical environmental requirements. The *Pohlia* type has a very closely compact structure and represents the moss-mat subformation of wet ground. The *Polytrichum-Dicranum* type falls within the moss turf subformation of well-drained slopes and has a far looser texture with the stiff erect stems presenting larger and regular air spaces. Where this latter type is more exposed it is often encrusted with lichens, and the mechanical structure of the vegetation is very irregular, producing occasional large air spaces. It was not possible to sample from all vegetation types at each area visited.

Figure 35 shows certain physical properties of the types in each area. It is seen that the temperature at 3 cm depth is fairly constant at this time of the year in all the Maritime Antarctic localities (between 1 and 4 °C). In the milder conditions at South Georgia, the temperature at the same depth in these moss types is several degrees higher. Although not demonstrated in figure 35, readings taken over a long period at Signy Island have shown that, because of its looser structure and drier habitat, the *Polytrichum–Dicranum* type is more

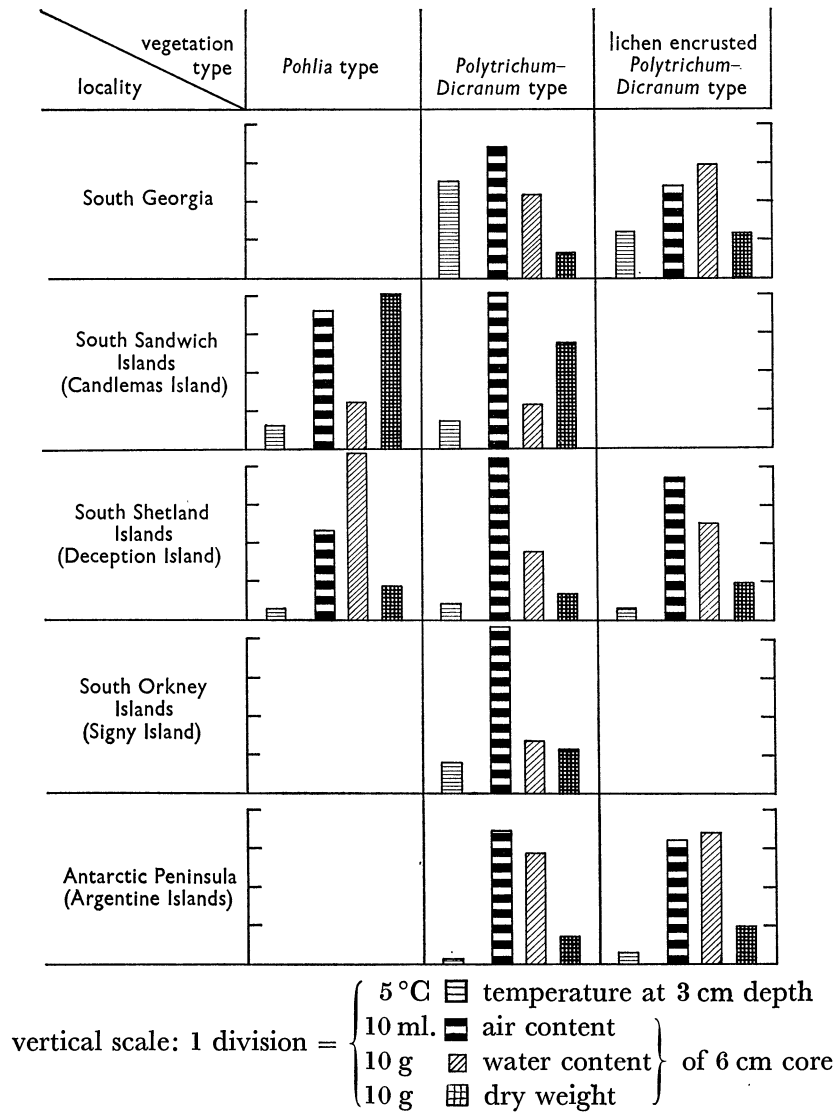


FIGURE 35. Measurements of certain physical factors of different vegetation types at each area.

rapidly warmed by direct radiation and is consistently a few degrees warmer than the *Pohlia* type in summer. As would be expected, the highest air content figures are shown by the *Polytrichum–Dicranum* type and the highest water content by the *Pohlia* type. The South Sandwich figures are somewhat anomalous, with the *Pohlia* type having a relatively high air content and low water content. This is probably due to the porous nature of the underlying volcanic rock in this region which would permit rapid percolation of surface water. The high dry-weight figure is a reflexion of the large quantities of wind-blown ash. The pH values in all cases were between 3.5 and 5.1.

Figure 36 shows the number of mites, Collembola and nematodes extracted, and demonstrates that much variation exists between the same vegetation types in different areas. It must be remembered, however, that the numbers shown are means of very few cores taken at only one time of the year. The Signy Island study has indicated that the fauna there has a very patchy distribution and that considerable variation in numbers exists both spatially and temporally (Tilbrook, in preparation). The figures are presented

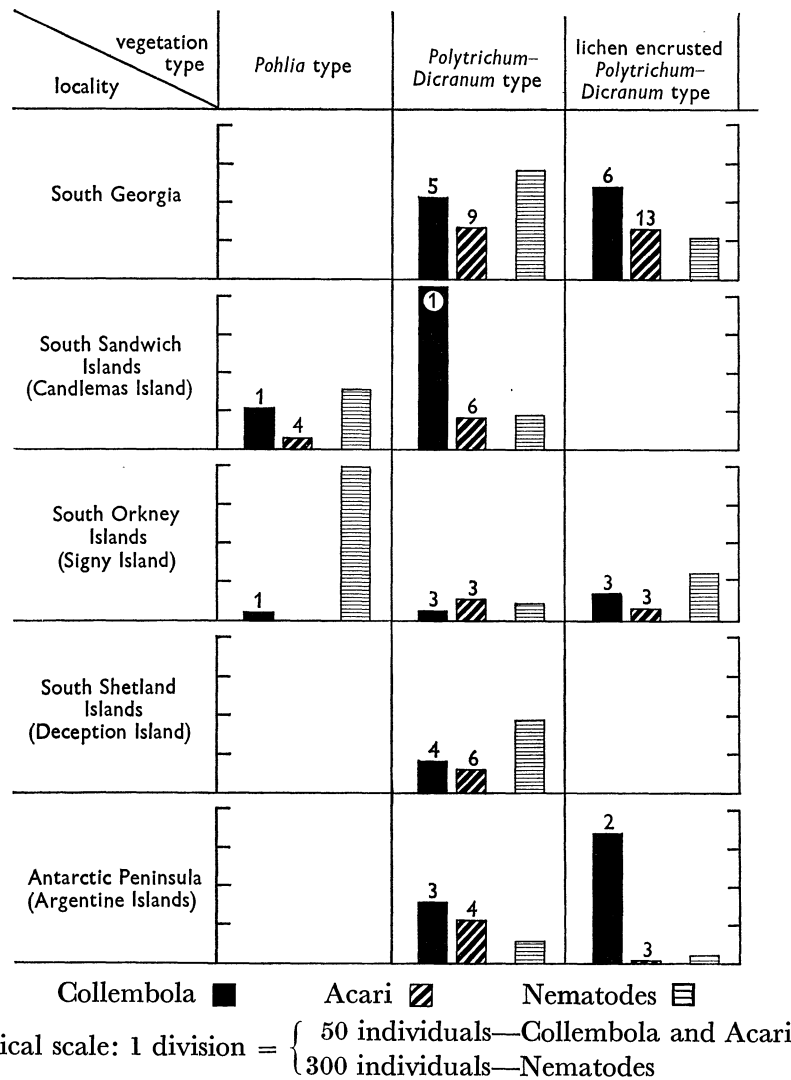


FIGURE 36. The abundance of mites (▨), Collembola (■) and nematodes (▤) in different vegetation types at each area. The columns represent the numbers of individuals in cores approximately 10 cm² in surface area and 6 cm deep. The figures above the mite and Collembola columns indicate the number of species represented. These results are given in greater detail as Appendix C.

here since no other quantitative work has been carried out in the region but they can only be taken as an approximation of abundance. One feature is that, whilst in nearly all cases the numbers of Collembola exceed those of the mites, fewer species are represented. Amongst the Collembola, the dominance of *Cryptopygus antarcticus* is striking. At Deception Island it represented approximately 65% of the total Collembola and at all other Maritime Antarctic localities the figure is above 85%. The greatest density of Collembola occurred

at Candlemas Island where *Cryptopygus antarcticus* was the only species present. In the *Polytrichum–Dicranum* type sampled on this island, a mean figure of 214 individuals was obtained from eight 10 cm² cores ($21.4 \times 10^4/m^2$). At South Georgia this species forms roughly 50% of the total Collembola in the two vegetation types examined and the body size appears smaller than at the other localities.

No such consistent single species dominance occurs in the case of the mites though the prostigmatid species, *Tydeus tilbrooki* and *Protereunetes minutus* are often the most abundant. In the *Polytrichum–Dicranum* type at the Argentine Islands, for example, the mean figure from eight 10 cm² cores was 55 mites ($5.5 \times 10^4/m^2$) and the above two species represented approximately 90% of these. Haarløv (1960), Weis-Fogh (1948) and others have shown that a correlation exists between the distribution of arthropods and soil structure. This may be a purely mechanical relationship, the size of non-burrowing animals inhabiting the soil clearly being influenced by the size of the interstices. Such a factor could apply equally in the case of the vegetation types under study though the bryophytes are likely to provide a more flexible system of passages. Direct observation showed that certain of the larger arthropods often had difficulty in penetrating into the *Pohlia* type of vegetation. The arthropods from these terrestrial habitats need to be surrounded by an air medium so the air/water content of the moss must be considered together with the mechanical structure. It is seen that greater numbers are found in the *Polytrichum–Dicranum* and lichen encrusted types which, compared with the typical *Pohlia* type, have a looser structure and generally a lower water content, so making available more open passages.

As yet no taxonomic work has been carried out on the nematodes collected so they are here treated as a group. These small organisms require a water medium for development and activity, and indeed Banage (1963) states that the chief factor affecting the distribution and abundance of free-living nematodes is the water content of the soil. It might therefore be expected that the largest numbers would be found in the consistently wet *Pohlia* type of vegetation. Such is the case at Signy Island where the density is almost 1200 individuals/10 cm² ($1.2 \times 10^6/m^2$). Observations over a long period at Signy Island confirm that this preference exists. The drop in numbers in the *Pohlia* type from Candlemas Island may be due to the comparatively low water content. Like the nematodes, the tardigrades and rotifers live in moss and soil water and so were often driven out of the samples during 'wet' extractions. It is not known, however, how efficient the extraction method is for these animals. Both groups were represented in the vegetation from all areas and the *Pohlia* type generally supported larger numbers. The highest density of tardigrades occurred in the South Sandwich Islands where the mean figure from three cores was approximately 800 individuals ($8 \times 10^5/m^2$). Some 95% of these were in the upper 3 cm.

VERTICAL DISTRIBUTION

By dividing each 6 cm core in half an indication of the vertical distribution of the fauna has been obtained. Figure 37 shows that the greater proportion of the meiofauna (approximately 84% of the arthropods and 88% of the nematodes) is concentrated in the upper 3 cm layer of the vegetation. As would be expected, the depth penetration of the arthropods can be correlated with the mechanical structure of the moss type. The loose-textured

Polytrichum-Dicranum type and, to a lesser extent, the lichen-encrusted type, support a greater proportion of mites and Collembola in the 3 to 6 cm layer.

The only species to exhibit a preference for the lower layer was the collembolan *Tullbergia mixta* at Deception Island where, out of a total of 103 individuals from twelve cores, 75% inhabited the 3 to 6 cm layer. The samples at this locality were taken from a mat of *Polytrichum alpinum* which has a particularly loose open structure. *Tullbergia mixta* has a white coloration, a feature common to inhabitants of the deeper layers.

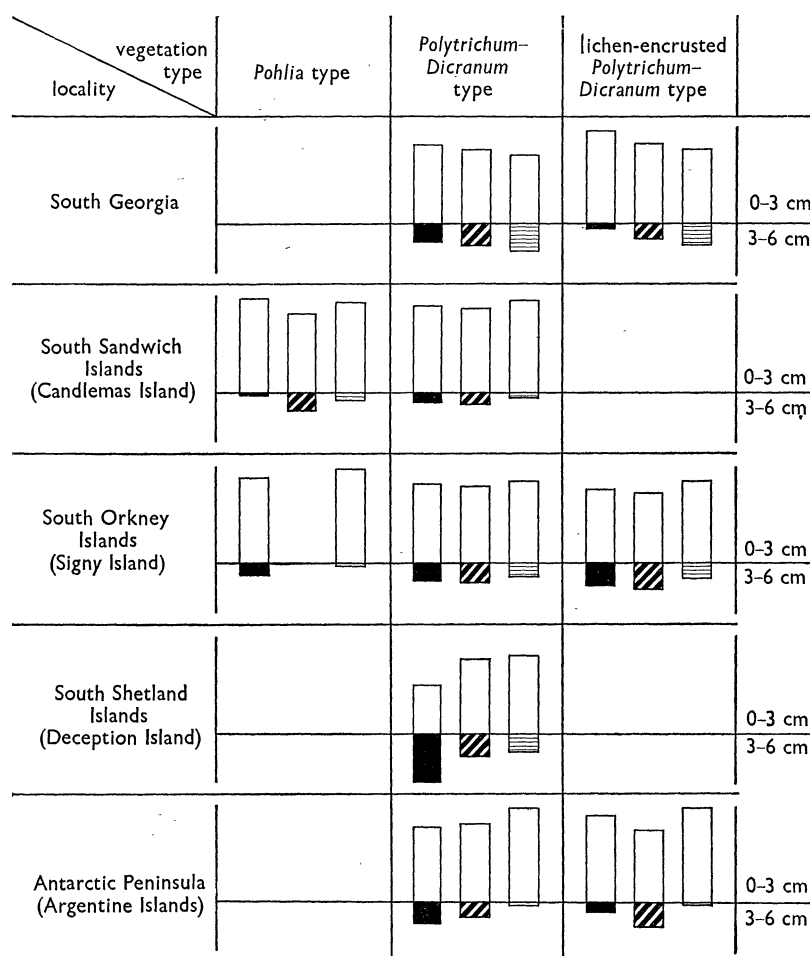


FIGURE 37. The vertical distribution of the mite (▨), Collembola (■) and nematode (▤) faunas of different vegetation types at each area. The proportion in the 3 to 6 cm layer is shown as a percentage of the numbers in the whole core (0 to 6 cm).

EFFECTS OF FUMAROLIC HEAT ON THE FAUNA

The climatic conditions experienced by the South Sandwich Islands are typical of the Maritime Antarctic region and the ice-free areas of these small islands are generally barren. The emission of steam from fumaroles on certain islands has, however, resulted in localized more favourable conditions, with a higher temperature and a consistently high humidity. The effect on the vegetation is striking, with lush mixed mats of bryophytes and hepatics surrounding the vents of these fumaroles. It might be expected that the composition of the

fauna would also be affected in these localized areas. As far as the species content is concerned it has already been stated that three oribatid mites not reported elsewhere in the Maritime Antarctic region were found in this fumarolic vegetation. Various other arthropods were also recorded, namely the collembolan *Isotoma georgiana* and the mite *Eobrachychthonius* sp., both South Georgian species, and the two oribatids, *Edwardzetes dentifer* and a

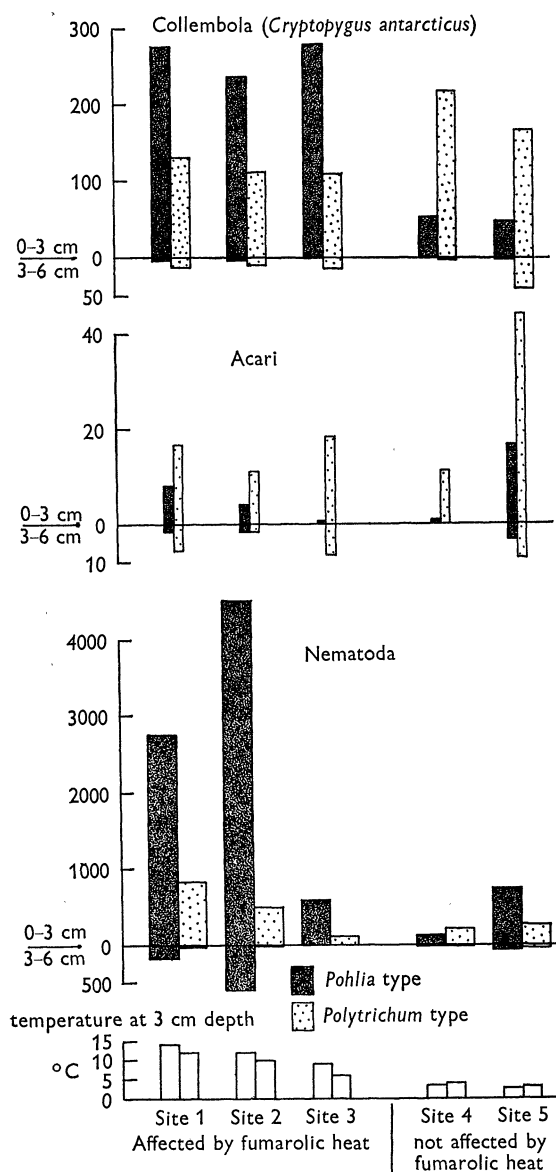


FIGURE 38. The effect of fumarolic heat on the numbers of mites, Collembola and nematodes. Two vegetation types were sampled at five sites on Candlemas Island. The columns represent the numbers of individuals in cores approximately 10 cm² in surface area and 6 cm deep. Variation in width of the columns indicates the use of different vertical scales.

species of Carabodidae, which were not found in South Georgia and probably have a South American source. These records must be treated with caution since only isolated individuals were found and the possibility of contamination during extraction cannot be ruled out. It appears, however, that these heated localities do possess a more varied fauna. The effect on the numbers of invertebrates present is shown in figure 38.

Pohlia and *Polytrichum* types of vegetation were sampled quantitatively at five sites on Candlemas Island. Three of these were around fumaroles and so experienced a higher temperature within the moss mat. It is seen that the density of Collembola is higher at the heated sites compared with unheated sites both on Candlemas Island and elsewhere in the region. At the two unheated localities greater numbers of *Cryptopygus antarcticus* occur in the *Polytrichum* type but the samples taken from similar vegetation types surrounding fumaroles show a reversal in abundance. In these localities it is the *Pohlia* type which supports the greater numbers of *Cryptopygus antarcticus*. It is difficult to account for this phenomenon since there is little difference in the water content or air content of the moss types at the heated and unheated sites. The effect on the mite fauna is not so marked and no similar reversal of abundance takes place. The high number of mites in the *Polytrichum*–*Dicranum* type at site 5 is due to the occurrence of forty-four individuals (mean of six cores) of *Cyrtolaelaps rykei*. This is one species which was never found in localities affected by heat. As far as the arthropods as a whole are concerned it is seen that the greater depth penetration still occurs in the *Polytrichum*–*Dicranum* type. The numbers of nematodes at sites 1 and 2 are very high ($5.1 \times 10^6/\text{m}^2$), compared with the figures for other areas. This suggests that these heated localities are very favourable environments for nematodes. Site 3, however, then proves anomalous with the numbers at a level of abundance similar to the unheated sites. Their preference for the *Pohlia* type is still apparent. It would appear that these heated localities do have some effect on the fauna but whether it is a direct temperature response seems doubtful. Other factors such as food may be involved. More detailed microhabitat data are required.

DISCUSSION

In spite of the harsh climatic conditions and sparse vegetation, terrestrial habitats in the Maritime Antarctic support quite a varied fauna. Many of the larger invertebrates common in temperate localities are absent, however, and it is the arthropods which have the greatest body size. The largest collembolan, *Cryptopygus antarcticus*, is up to 2000 μm long and 300 μm wide and the dimensions of *Alaskozetes antarcticus*, the largest mite, are approximately 1070 and 750 μm . Throughout the Maritime Antarctic region dealt with in this paper there are twenty species and two subspecies of Acari and seven species of Collembola. The arthropod fauna is therefore very impoverished. This is illustrated in figure 39 which compares the fauna of a Signy Island moss mat with that of similar terrestrial habitats in South Georgia and temperate latitudes. The examples from temperate localities whilst not directly comparable, do typify the diversity of the fauna from these regions. The number of mites and collembolans found in a moss mat on South Georgia show an intermediate position typical of the Sub-Antarctic zone. Although it has ten species of mites and two of Collembola in common with South Georgia, the arthropod fauna of the Maritime Antarctic is fairly distinct, reflecting the severe conditions (lack of suitable habitats) and isolation. The decrease in numbers of species continues into Continental Antarctica where the available habitats are very restricted and the environment generally unfavourable. It also appears to possess a discrete arthropod fauna.

In spite of the ostensibly similar terrestrial habitats which are available throughout the Maritime Antarctic region, a considerable amount of variation in the faunal composition

exists between different areas. This is almost certainly due to the oceanic isolation of many of the islands, the faunas of such areas being typically disharmonic. It is suggested that air currents are largely responsible for the existing arthropod distribution. There is probably little competition for available niches and many of the species which have colonized this region are extremely abundant. The density of the fauna from vegetation at Signy Island, for example, is of a similar order of magnitude to that at temperate localities (figure 40). This implies that they are well adapted to the prevailing conditions. Pryor (1962) experimenting on a collembolan from Continental Antarctica found that it was able to withstand

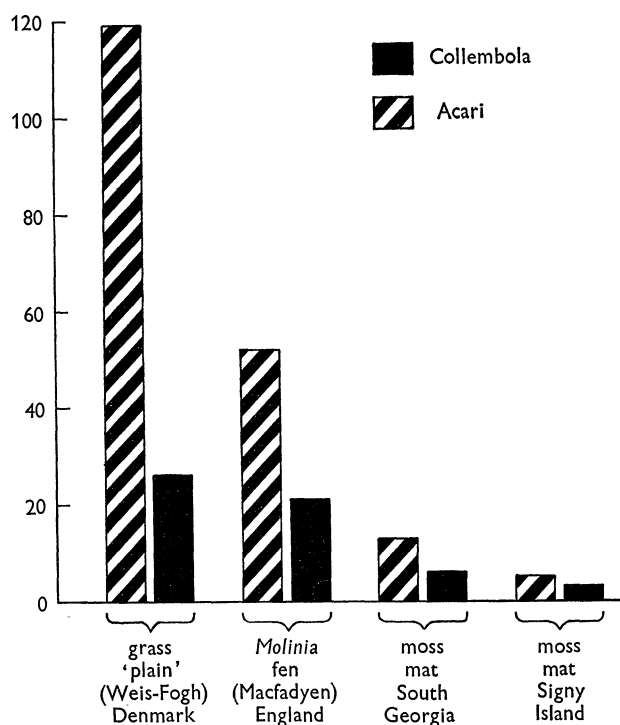


FIGURE 39. Comparison of the number of species of mites and Collembola found in vegetation from temperate (Macfadyen 1952), sub-Antarctic and Maritime Antarctic localities.

temperatures as low as -50°C and a similar tolerance is claimed for an oribatid mite from Dronning Maud Land (Dalenius & Wilson 1958). Another common Continental Antarctic collembolan, however, whilst able to survive at -20°C showed a preference for temperatures around $+11^{\circ}\text{C}$ (Janetschek 1963). It was found during the Signy Island work that direct radiation on rocks or vegetation may raise the temperature at their surface up to 10°C or more above the air temperature. At a depth of 2.5 cm in a *Polytrichum-Dicranum* mat, the highest temperature recorded between May 1962 and December 1963 was 19.14°C (Chambers, personal communication). This was at midday on 15 December 1963, when the air temperature was 2.3°C . The insulating effect of the winter snow cover can also maintain the ground temperature up to 10°C above that of the air. (Tilbrook, in preparation). It is clear, therefore, that environmental conditions are not always as severe as superficial observations and readings would suggest. Although activity usually ceases around freezing point, Mani (1962) states that normal development of nival zone arthropods can take place down to -1.5°C . Dalenius & Wilson (1958) also found that egg development

the oribatid *Maudheimia wilsoni* continues at temperatures below freezing. It appears, then, that microhabitat conditions in the Antarctic may permit arthropod development at times when the external ambient temperatures would seem to preclude it. Little is known of the phenology of the Maritime Antarctic arthropods but it is probable that development takes place throughout the year, whenever conditions allow. The collembolan *Isotoma lovstadi*, from Continental Antarctica, is known to overwinter in both egg and adult stages (Pryor 1962). Also, adult, nymphal and larval stages of many Signy Island arthropods were collected throughout the winter.

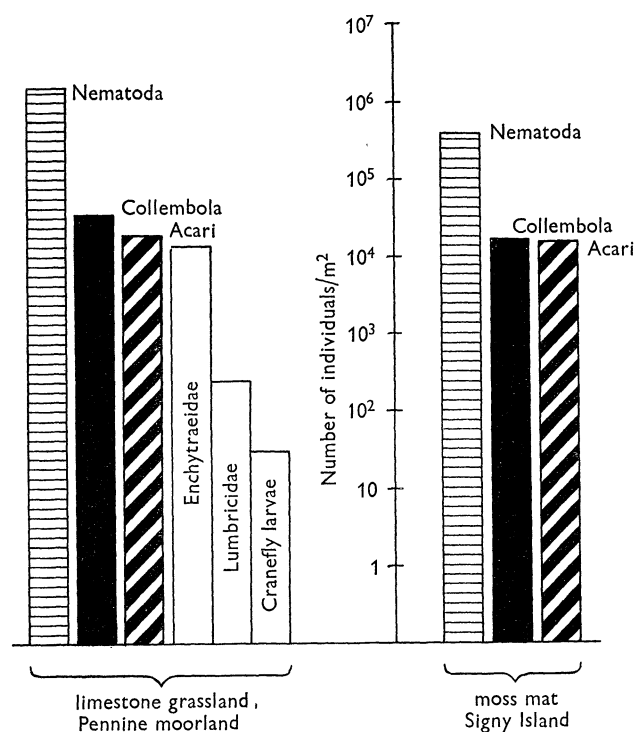


FIGURE 40. Comparison of the number of individuals in the meiofauna between temperate (Cragg 1961) and Maritime Antarctic vegetation.

It has already been stated that the arthropods and nematodes are the largest terrestrial invertebrates in the Maritime Antarctic, and are present in large numbers. Consequently, they are probably responsible for a high proportion of the total animal biomass and respiration. In spite of this numerical abundance and relative importance in the mosses and soils of this region, however, the contribution to the energy cycle of the mites, Collembola and nematodes is small when compared with temperate localities. Yet at the limestone grassland site in the English Pennines, for example, these three groups contribute only about 0.9% of the biomass and 5.3% of the respiration of the total meiofauna (Cragg 1961). In the moorland vegetation it is the less abundant enchytraeids, lumbricids and crane-fly larvae (figure 40) which are the important organisms both in respect to biomass and respiration. The actual annual contribution of the Maritime Antarctic fauna would be expressed by their longer periods of inactivity.

The distribution and abundance of arthropods in the Maritime Antarctic is affected by such habitat factors as air and water content, temperature and structure of the air spaces. The relative humidity of the environment is an important limiting factor especially in the

case of the Collembola which rely on cutaneous respiration. It seems more usual for a complex of factors to operate, however, and the feeding habits of most species, although clearly an important limiting factor, are little known. Bunt (1954) working on the nematodes of Macquarie Island suggests that the food supply is probably the most important factor controlling the numbers. There was no direct evidence of predation amongst the fauna collected although a mesostigmatid mite, *Cyrtolaelaps racovitzai*, was observed devouring a dead collembolan. Gressitt (1965) states that many of the long-legged and fast-moving prostigmatid mites are predacious. Certainly the food chain is attenuated and probably goes no further than the first carnivore level.

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[*Note added in proof 13 April 1967.*] Some names used in this paper refer to new species, the descriptions of which, although in press, may not appear before this volume is published.

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APPENDIX A. DISTRIBUTION OF THE FREE LIVING TERRESTRIAL ARTHROPODS COLLECTED DURING THE PRESENT STUDY

species	locality									
	South Georgia	South Sandwich Islands	Bouvetøya	South Orkney Islands (Signy Island)	South Shetland Islands (Deception Island)	Hope Bay	Danco Island	Antarctic Peninsula	Argentine Islands	
Acari										
Mesostigmata										
<i>Cyrtolaelaps racovitzai</i> (Trouessart)	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
<i>Cyrtolaelaps rijketi</i> Hunter	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
<i>Ayersacarus tilbrooki</i> Hunter	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
<i>Parasitus tarsispinosus</i> Hunter	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
<i>Hydrogamasus antarcticus</i> Trägårdh	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
<i>Daneacarus</i> sp.	✓*	✓	✓	✓	✓	✓	✓	✓	✓	✓
Veigaiaidae gen. et sp.	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
<i>Uropoda</i> sp.	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
Uropodidae gen. (near <i>Uroobouella</i>) et sp.	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
Cryptostigmata										
<i>Platynothrus scoottsbergii</i> Trägårdh ssp. <i>expansus</i> Wallwork	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
<i>Oppia crozetensis</i> (Richters)	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
<i>Oppia losolimeata</i> Wallwork	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
<i>Globophia intermedia</i> Hammer	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
<i>Liochthonius mollis</i> (Hammer)	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
<i>Liochthonius</i> sp.	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
<i>Eobrachychthonius oudemansi</i> Hammer	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
<i>Podacarus auberti</i> Grandjean ssp. <i>occidentalis</i> Wallwork	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
<i>Alaskozetes antarcticus</i> (Michael)	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
<i>Alaskozetes antarcticus</i> (Michael) ssp. <i>intermedius</i> Wallwork	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
<i>Halozetes belgicae</i> (Michael)	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
<i>Halozetes belgicae</i> (Michael) ssp. <i>longiseta</i> Wallwork	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
<i>Magellozetes antarcticus</i> (Michael)	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
<i>Edwardzetes elongatus</i> Wallwork	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
<i>Edwardzetes denisifer</i> Hammer	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
<i>Porozetes polygonalis</i> Hammer ssp. <i>quadrilobatus</i> Wallwork	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
<i>Scotiazetes bidens</i> Wallwork	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
<i>Sandania georgiae</i> Oudemans	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
Carabodidae gen. et sp.	✓*	✓	✓	✓	✓	✓	✓	✓	✓	✓
Astigmata										
<i>Cabolia antarctica</i> Hughes	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
<i>Schwiebia talpa</i> Oudemans	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
Collembola										
Arthropleona										
<i>Tullbergia bisetosa</i> Börner	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
<i>Tullbergia mixta</i> Wahlgren	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
<i>Hylogastrura viatica</i> (Tullberg)	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
<i>Friesea grisea</i> (Schaeffer)	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
' <i>Friesea</i> ' sp.	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
<i>Cryptophygus antarcticus</i> Willem	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
<i>Cryptophygus caesus</i> Wahlgren	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
<i>Isotoma georgiana</i> Schaeffer	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
' <i>Isotoma</i> ' sp.	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
<i>Archisotoma brucei</i> (Carpenter)	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
<i>Parisotoma octo-oculata</i> (Willem)	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
Symphyleona										
Sminthuridae gen. et sp.	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
Diptera										
Chironomidae										
<i>Belgica antarctica</i> Jacobs	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
Coleoptera										
Lathridiidae										
<i>Cartodere apicalis</i> (Blackburn)	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
<i>Lathridius minutus</i> L. †	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓

* Only single specimens found. † Species commonly synanthropic. ‡ Provisional name pending description.

APPENDIX C. RESULTS OF THE QUANTITATIVE EXTRACTION OF ARTHROPODS AND NEMATODES FROM VEGETATION FROM SOUTH GEORGIA AND MARITIME ANTARCTIC LOCALITIES

All figures represent the mean number of individuals from cores approximately 10 cm² in surface area and 6 cm deep.

locality	date of sampling	vegetation type	Collembola											Acari												nematodes																				
			<i>Tullbergia mixta</i>	<i>Tullbergia bisetosa</i>	<i>Friesea grisea</i>	<i>Friesea</i> sp.	<i>Cyphophygus antarcticus</i>	<i>Parisotoma octo-oculata</i>	<i>Isotoma georgiana</i>	<i>'Isotoma'</i> sp.	<i>Sminthuridae</i> sp.	<i>Cyrtolaelaps racovitzai</i>	<i>Cyrtolaelaps nykeri</i>	<i>Ayersacarus tilbrookii</i>	<i>Hydrogamasus antarcticus</i>	<i>Uropoda</i> sp.	<i>Uropoda</i> sp.	<i>Opfia loxolimeata</i>	<i>Opfia crozetensis</i>	<i>Globoppia intermedia</i>	<i>Taochthonus mollis</i>	<i>Alaskozetes antarcticus</i>	<i>Halozetes belgicae</i>	<i>Halozetes longiseta</i>	<i>Magellanozetes antarcticus</i>	<i>Edwardszetes elongatus</i>	<i>Porozetes polygonalis</i>	<i>quadrilobatus</i>	<i>Cryptosigmata</i> sp.-nymph	<i>Nanorchestes antarcticus</i>	<i>Stereohydus villosus</i>	<i>Stereohydus reticulatus</i>	<i>Rhagidia leechi</i>	<i>Tydeus tilbrookii</i> and <i>Proteremetes minutus</i>	total arthropods	number of cores	total number of individuals									
South Georgia	25. ii. 64	<i>Polytrichum strichum</i>	6	1		✓	79	1	56				2	3	1	✓	4	24							✓	4									✓	39	212	3	1096							
		<i>Dicranum aciphyllum</i>	4				27	2	43				✓	3	2				30																	12	131	3	583							
South Sandwich Islands (Candlemas Island)	1. iii. 64	lichen encrusted																																												
		<i>Polytrichum-Dicranum</i>	6	✓	✓	✓	53	8	55	2	✓	✓	✓	3	✓	✓		7	2																			33	182	3	317					
		<i>Pohlia nutans</i>	6				51																																6	78	3	802				
South Shetland Islands (Deception Island)	15. iii. 64	<i>Polytrichum alpinum</i>	6				207						✓																										8	273	3	298				
		<i>Ceratodon</i> sp.	3				54																														✓	55	2	123						
		<i>Polytrichum alpinum</i>	3				220																														4	234	2	225						
South Orkney Islands (Signy Island)	10. ii. 64	<i>Polytrichum alpinum</i>	6	8	2		10	3																																	21	56	3	41		
		<i>Polytrichum alpinum</i> (moribund)	6	10	3		41	3													✓																	19	82	3	1068					
Antarctic Peninsula (Argentine Islands)	8. ii. 63	<i>Pohlia nutans</i>	4				9																																					9	2	1193
		<i>Polytrichum strichum</i> and <i>Dicranum aciphyllum</i>	4		✓		10	1						1																											17	37	2	126		
		lichen encrusted	4				1	30	4																																	10	50	2	371	
Antarctic Peninsula (Argentine Islands)	24. i. 64	<i>Polytrichum strichum</i>	4				8	32	2				2																														3	60	2	64
		lichen encrusted	4				2	168																																		1	174	2	75	
		<i>Polytrichum</i>	4				4	113	1					1																												88	211	2	275	

✓ indicates that only single specimens were collected.

METHODS FOR AND ROUGH EXTRACTION AT SOUTH SHETLAND ISLANDS AND ANTARCTIC PENINSULA LOCALITY

large funnel extraction, from samples approximately 75 cm² in surface area and 3 to 6 cm deep. They are very selective and tend to be biased against the smaller forms. Nevertheless, symbols are used to denote the types of substrate surface.

= < 10, f = 10-100, a = > 100

	Hope Bay				Danco Island				Argentine Islands											
	rocks under snow				mineral material from beach				amongst rocks with moss											
<i>Drepanocladus</i> mat near skua nest	2	15	77		1	20	4	✓	under rock near high water	under rocks—coastal slope	under rocks near shag colony—coastal slope	amongst rocks with moss	<i>Deschampsia antarctica</i>	<i>Deschampsia</i> with little <i>Drepanocladus</i> and <i>Pollia</i>	<i>Deschampsia</i> with little <i>Drepanocladus</i> and <i>Bryum</i>	<i>Drepanocladus</i>	mostly <i>Drepanocladus</i> with <i>Brachythecium</i>	<i>Brachythecium</i>		
<i>Polytrichum alpinum</i> turf	18	34			4	737		✓	under rock near high water	under rocks—coastal slope	under rocks near shag colony—coastal slope	amongst rocks and moss mostly <i>Drepanocladus</i>								
	1				1	1389		✓	under rock near high water	under rocks—coastal slope	under rocks near shag colony—coastal slope	amongst rocks and moss mostly <i>Drepanocladus</i>	<i>Deschampsia antarctica</i>	<i>Deschampsia</i> with little <i>Drepanocladus</i> and <i>Pollia</i>	<i>Deschampsia</i> with little <i>Drepanocladus</i> and <i>Bryum</i>	<i>Drepanocladus</i>	mostly <i>Drepanocladus</i> with <i>Brachythecium</i>	<i>Brachythecium</i>		
	26	10			26			9	under rock near high water	under rocks—coastal slope	under rocks near shag colony—coastal slope	amongst rocks and moss mostly <i>Drepanocladus</i>								
	2	17	12	3					under rock near high water	under rocks—coastal slope	under rocks near shag colony—coastal slope	amongst rocks and moss mostly <i>Drepanocladus</i>	<i>Deschampsia antarctica</i>	<i>Deschampsia</i> with little <i>Drepanocladus</i> and <i>Pollia</i>	<i>Deschampsia</i> with little <i>Drepanocladus</i> and <i>Bryum</i>	<i>Drepanocladus</i>	mostly <i>Drepanocladus</i> with <i>Brachythecium</i>	<i>Brachythecium</i>		
		48	7						under rock near high water	under rocks—coastal slope	under rocks near shag colony—coastal slope	amongst rocks and moss mostly <i>Drepanocladus</i>	<i>Deschampsia antarctica</i>	<i>Deschampsia</i> with little <i>Drepanocladus</i> and <i>Pollia</i>	<i>Deschampsia</i> with little <i>Drepanocladus</i> and <i>Bryum</i>	<i>Drepanocladus</i>	mostly <i>Drepanocladus</i> with <i>Brachythecium</i>	<i>Brachythecium</i>		
	1	20	11	15		8	79	f	under rock near high water	under rocks—coastal slope	under rocks near shag colony—coastal slope	amongst rocks and moss mostly <i>Drepanocladus</i>	<i>Deschampsia antarctica</i>	<i>Deschampsia</i> with little <i>Drepanocladus</i> and <i>Pollia</i>	<i>Deschampsia</i> with little <i>Drepanocladus</i> and <i>Bryum</i>	<i>Drepanocladus</i>	mostly <i>Drepanocladus</i> with <i>Brachythecium</i>	<i>Brachythecium</i>		
	37	1		31	274	6	574	776	a	f	a	a	✓	✓	✓	✓	✓	✓		
	4								f	✓		f	a							
									f	✓		f	✓	✓	✓	✓	✓	✓		
45	133	74		320	34	108	274	6	574	786	2262	232		140	112	166	286	156	2695	10

<i>L. rigyensis</i>						
<i>Brachythemium</i>						
<i>Polytrichum strictum</i> with <i>Barbilophozia</i>						species
						Acari
						<i>Cyrtolaelaps racovitzai</i>
						<i>Parasitus tarsispinosus</i>
		8				<i>Oppia loxolineata</i>
						<i>Liochthonius mollis</i>
						<i>Alaskozetes antarcticus</i>
						<i>Halozetes belgicae</i>
						<i>Magellozetes antarcticus</i>
						<i>Nanorchestes antarcticus</i>
						<i>Rhagidia gerlachei</i>
						<i>Rhagidia leechi</i>
						<i>Stereotydeus villosus</i>
						<i>Pygmephorus</i> sp.
						<i>Tydeus tilbrooki</i> and
						<i>Prottereunetes minutus</i>
						Collembola
						<i>Tullbergia mixta</i>
						<i>Hypogastrura antarctica</i>
	54					<i>Friesea grisea</i>
1 146 54						<i>Cryptopygus antarcticus</i>
						<i>Cryptopygus caecus</i>
						<i>Archisotoma brucei</i>
	20					<i>Parisotoma octo-oculata</i>
						Diptera
	1					<i>Belgica antarctica</i> { larvae adults
2 146 137						total

