ECOLOGICAL STUDIES ON ANTARCTIC TARDIGRADES AND ROTIFERS

by

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CONTENTS

SECTION 1: INTRODUCTION

The inaccessibility of the Antarctic continent and its surrounding waters from the maritime nations of the northern hemisphere has meant that exploration of this vast area has been restricted to the past 100 years or so. The more accessible waters of the Southern Ocean, however, have been investigated since the pioneering voyages of Captain Cook, some 200 years ago. Biological investigations in this area were for many years concentrated on marine animals, and considerable commercial interest has been seen in the once rich stocks of marine mammals, seals and whales.

In the past 30 years the whole character and scale of Antarctic exploration and scientific investigation has changed. Now 10 nations permanently occupy over 30 stations, with many more stations occupied on a temporary basis, both on the Antarctic continent and the surrounding islands of the Southern Ocean. All territorial claims have been suspended by the twelve signatories of the Antarctic treaty in the interests of scientific endeavour. The rewards of this international cooperation were apparent after the 1957-58 International Geophysical Year prior to the signing of the treaty in 1959.

The isolation, freedom from human interference, and the relatively simple terrestrial ecosystem, in terms of component species, make the Antarctic environment of especial interest to biologists and offer considerable advantages for a total functional analysis. Professor J.B. Cragg had visited Signy Island in the South Orkney Islands in 1957 to examine its suitability for biological studies. His favourable report led to the construction in 1963-64 of a permanently manned biological laboratory on the island. Between

1961 and 1970 biological research was carried out which provided essential preliminary information on the composition and ecology of the terrestrial flora and fauna. However, the broad and isolated approach to each project precluded integration of the results. For this reason two contrasting moss communities were selected in 1970 at which future terrestrial studies would be concentrated (Tilbrook, 1973).

The work reported in this thesis was undertaken while I was under contract to the British Antarctic Survey to carry out research on the terrestrial Tardigrada and Rotifera of the land south of lat. 60°S. and bounded by long. 20°W. and 80°W. The primary aim of this research was to undertake intensive studies on the population ecology of both the rotifers and tardigrades in the two moss sites on Signy Island. This investigation will form part of an extensive appraisal of the functional relationships of the various components of these sites, eventually leading to a total ecosystem analysis. Other research completed to date on one or both of these sites include an assessment of one autotrophic group (Broady, 1975) and all of the major heterotrophic groups represented, Protozoa (Smith, 1973a & b), Nematoda (Spaull, 1973a & b), Acari (Goddard, in press a & b) and Collembola (Tilbrook, in press).

Despite a considerable volume of literature relating to the Tardigrada, comparatively little is known about the ecology of individual species. For this reason I took the opportunity to survey the tardigrade fauna of Signy Island generally; the survey was subsequently extended to other islands in the South Orkney group and to other areas of the Antarctic. During 1972 an opportunity arose to use a Cartesian Diver micro-respirometer on Signy Island and the rate of oxygen uptake of an Antarctic tardigrade species was investigated.

Section two of this thesis gives a background to the Antarctic region. Section three presents an introduction to the Tardigrada, especially those which are discussed in detail in later sections. All identifications have been accomplished with the keys presented by Ramazzotti (1972a). Type material of tardigrade species is largely non-existent and the available material is widely distributed. None of the four other tardigradologists in this country was willing or able to examine my identifications, and the reference collection of tardigrades at the British Museum (Natural History) numbered only twenty slides, most of which were unnamed. In order to check my identifications I contacted a number of workers in Europe and T.E. Hallas of Denmark has kindly viewed all my diagrams to this end. The material in sections four, five and six has been accepted for publication as a series of four papers in the British Antarctic Survey Bulletin and three of these are now in press.

It was initially intended to give equal weight to the study of both tardigrades and rotifers; however, the major rotiferan group encountered in mosses (the Bdelloidea) is so poorly known that it was decided to concentrate on the Tardigrada. Less detailed information was obtained on the Rotifera and this is reported in section seven.

The raw data, field notes and preserved material on which this thesis is based are at present held in the library of the British Antarctic Survey (Life Sciences Division). A representative collection of slides is lodged in the British Museum (Natural History) and with the Smithsonian Institution, Washington, U.S.A.

SECTION 2: THE ANTARCTIC REGION

2.1 Description of the collection localities

To a marine biologist the Antarctic region is recognised as the total area to the south of the Antarctic convergence, a circumpolar line at which the cold surface waters of the Southern Ocean meet the warmer waters of the South Atlantic, Pacific and Indian Oceans (Fig. 1). There is, however, no such convenient boundary to the Antarctic terrestrial environment. Several attempts have been made to divide the land areas of this southern circumpolar region into meaningful units, but any sub-division is necessarily arbitrary as conditions are continuously variable. The system adopted in this thesis is the widely used one of Holdgate (1964, 1970), based on climate and vegetation, which is summarized in Table I.

The studies reported in this thesis were made on material collected from the following areas:-

South Georgia	54^{o}S	sub-Antarctic
South Sandwich Islands	57^{o}S	maritime Antarctic
South Orkney Islands	$60-61^{o}$S	maritime Antarctic
South Shetland Islands	$61-62^{o}$S	maritime Antarctic
Northern part of Antarctic Peninsula	$63-66^{o}$S	maritime Antarctic
Islands in Marguarite Bay	$67-69^{o}$S	maritime Antarctic
Alexander Island	70^{o}S	continental Antarctic

2.11 The maritime Antarctic

i) Geology and topography: Geomorphologically these islands are a continuation of the Andean cordillera. The Antarctic Peninsula forms the Antarctandean Ridge (Harrington, 1965) which is linked to South America by the Scotia Ridge, from which rises South Georgia and the

Fig. 1 The Antarctic region, showing the positions of the surrounding continents and of the Antarctic Convergence.

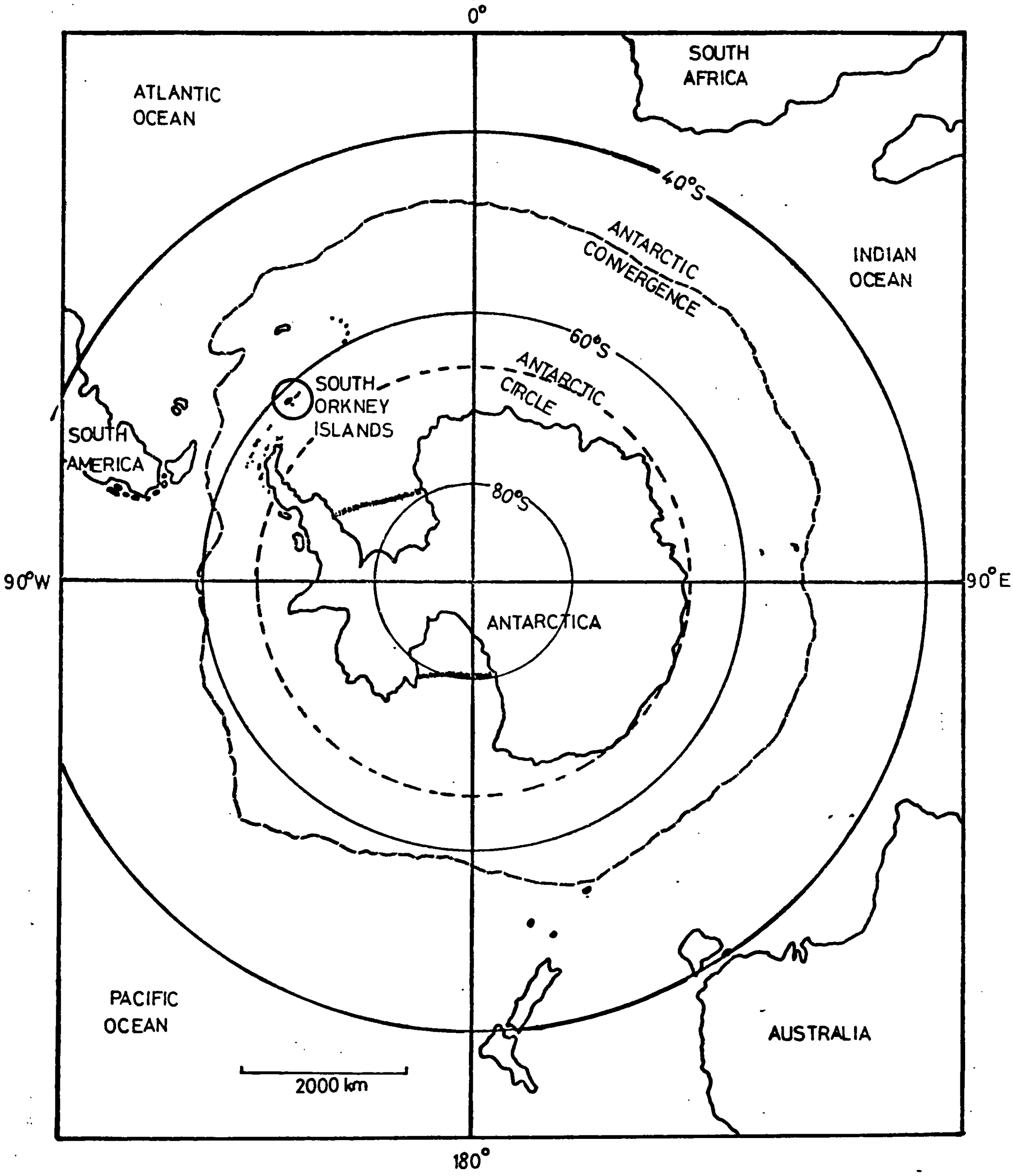

0°
SOUTH AFRICA
ATLANTIC OCEAN
40°S
ANTARCTIC CONVERGENCE
INDIAN OCEAN
60°S
ANTARCTIC CIRCLE
SOUTH ORKNEY ISLANDS
SOUTH AMERICA
80°S
90°W
90°E
ANTARCTICA
PACIFIC OCEAN
AUSTRALIA
2000 km
180°

Table I. Definition of the terrestrial Antarctic zones (after Holdgate, 1970).

Zone	Mean maximum and minimum air temperatures for warmest and coldest months (°C) maximum	minimum	Botanical features	Examples investigated during this research
sub-Antarctic	+8.5	0	Extensive closed phanerogamic vegetation.	S. Georgia
maritime Antarctic	+1.5	-10.0	Rich closed cryptogamic (especially bryophyte) communities.	S. Sandwich, S. Shetland, S. Orkney Islands and islands of Marguarite Bay
continental Antarctic	0	-20.0	Open lichen (and rarely isolated bryophyte) communities.	Alexander Island

South Sandwich, South Orkney and the South Shetland Islands. The geology of the Antarctic Peninsula and associated islands is dominated by igneous rocks of the Andean Granite-Gabbro Intrusive Suite. The South Orkney and eastern South Shetland Islands are dominated by a petrographically distinct sequence of quartz-mica schists (Thomson, 1968).

All the islands, except the smallest islets, are mountainous with indented coastlines. High ground is extensively covered by ice and snow which extends to the coasts as glaciers. The cover of permanent snow is interrupted in many places by rocky peninsulas and cliffs around the coast, and by nunataks inland, which are snow free for at least two months each summer. In some areas there are extensive coastal lowlands with inland valleys bounded by scree slopes which are also clear of snow in summer.

ii) Climate: Islands in the maritime Antarctic experience an oceanic regime dominated by the prevailing westerly airflow and with relatively little annual variation in temperature compared with the continent. At least one month of each summer has a mean air temperature greater than $0^{\circ}C$, while summer ground temperatures may rise to $+28^{\circ}C$ or more. The seas are usually ice free in summer, but are choked in some years by heavy pack-ice and ice-bergs. Most precipitation throughout the year is in the form of snow although there is some rain in the summer. The coldest months of the year are June to September, when mean monthly air temperatures around $-10^{\circ}C$ are usual (Pepper, 1954). Sea ice is often present between May and October, but it may be broken and dispersed by gales. A summary of meteorological observations from the region is given in Fig. 2 (D. Limbert, pers. comm.).

iii) Habitats of the terrestrial invertebrate fauna: Despite severe

Fig. 2 Summary of the meteorological observations at selected locations for the period 1963-72. Locations are from left to right:-

South Georgia

Signy Island

Deception Island (five years data only, 1963-67)

Argentine Islands

Adelaide Island

Fossil Bluff (based on limited data)

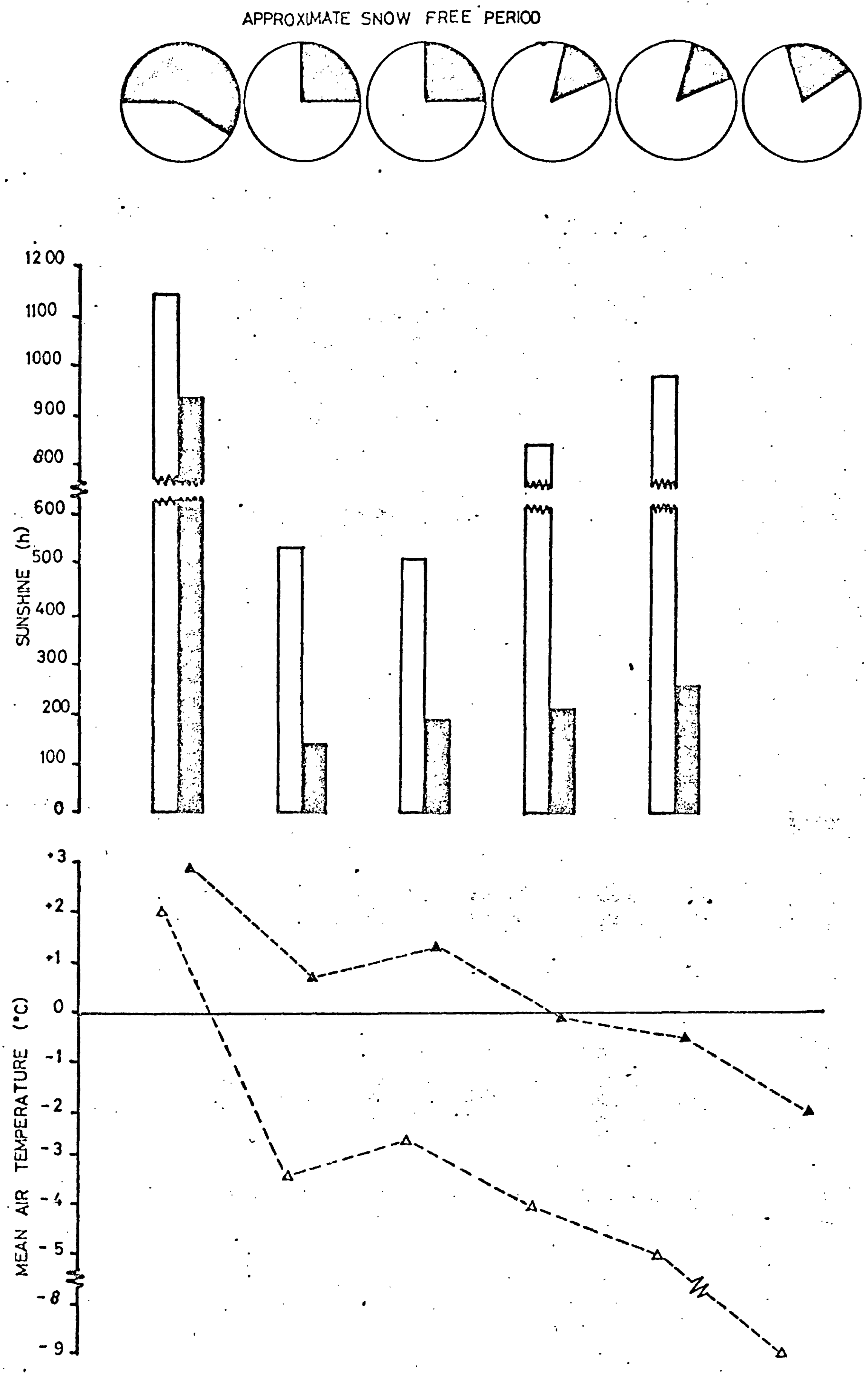
□ Annual sunshine

■ Sunshine in snow free period

△ Mean annual air temperature

▲ Mean air temperature in snow free period

Shading of snow free period is divided in the same fashion as a clock, Signy Island, for example, is snow free in the period 1st January - 31st March.



APPROXIMATE SNOW FREE PERIOD
1200
1100
1000
900
800
600
500
400
300
200
100
0
SUNSHINE (h)
+3
+2
+1
0
-1
-2
-3
-4
-5
-8
-9
MEAN AIR TEMPERATURE (°C)

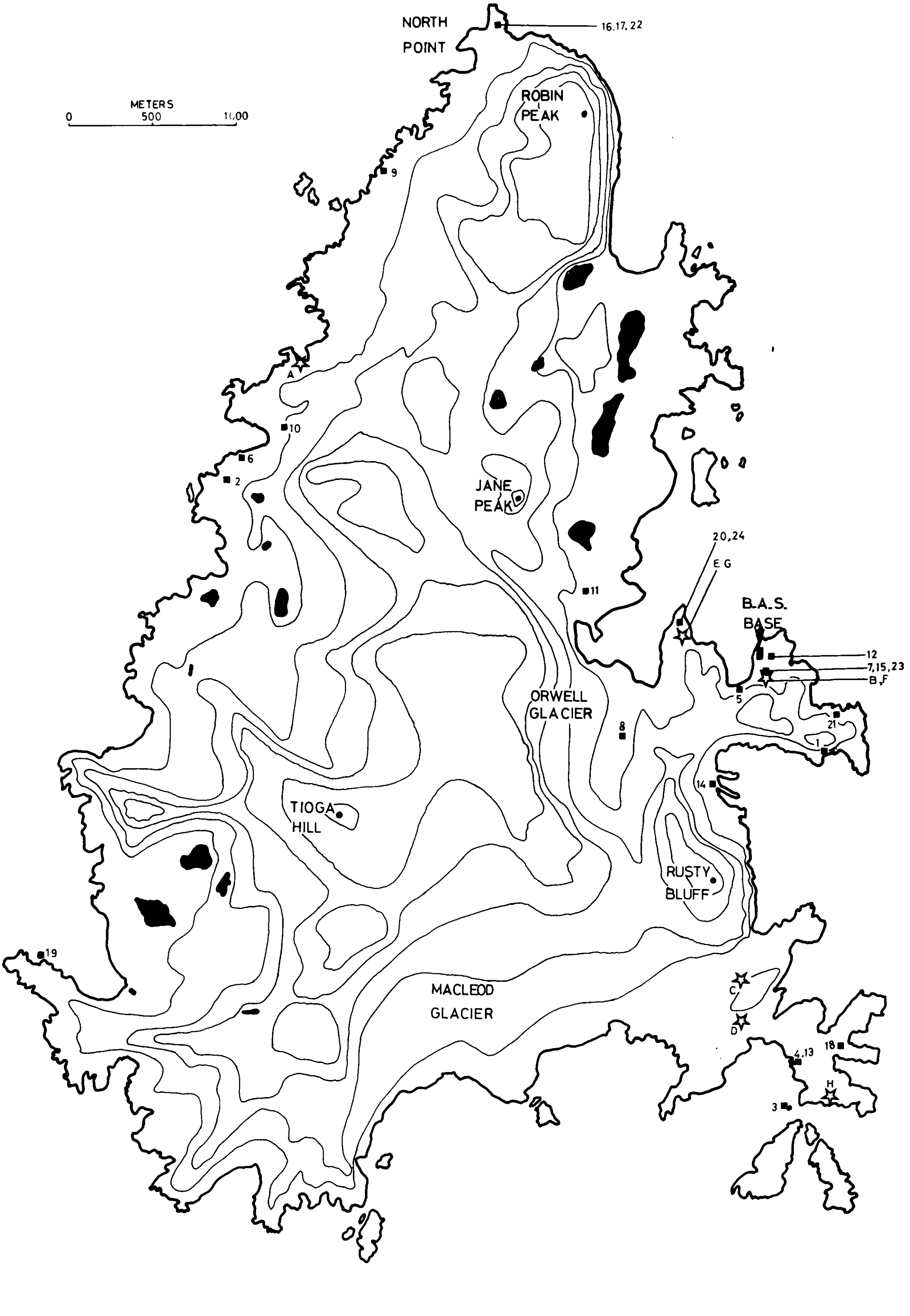
climatic conditions, a considerable diversity of terrestrial habitats exists in the region studied. These habitats support an abundant micro-flora of algae, bacteria, yeasts and fungi and a fauna of Protozoa, Rotifera, Tardigrada, Nematoda, Collembola and Acari (Tilbrook, 1967). Enchytraeidae worms (Oligochaeta) are present but rare (Holdgate et al., 1967). This abundance of life is favoured by a supply of mineral nutrients from the base rich parent rocks, from sea spray carried inland and from the activities of both birds and seals. Furthermore, direct radiant heating of the ground produces micro-climates more favourable to living organisms than ambient air temperatures would suggest. Signy Island has all of the more important habitat types found in the region and will serve as a model for discussion of their features.

2.12 Signy Island

i) Location: Signy Island (lat. 60°43'S., long. 45°38'W.) is one of the smaller members of the South Orkney Islands, which lie in the South Atlantic Ocean on the southern arm of the Scotia Ridge. It has a total surface area of about 20 km^2, a length (from north to south) of 8 km and a maximum height of 280 m. The north point of the island is only 1.5 km from Coronation Island, the largest of the South Orkney Islands group.

ii) Topography: In outline Signy Island is roughly triangular (Fig. 3) but the coastline, which is mostly cliffed, is indented by bays and projects in numerous narrow headlands. Along the western coast there is a strip of lowland which shows prominent terraces, probably of marine origin. On the north-east and south-west there are other low-land areas. The uplands of the island are roughly cruciform in plan, the main axis running NNE-SSW. All the summits are flat topped and the topography as a whole reflects the combined influences of rock

Fig. 3 Signy Island topography with contour lines at 50 m intervals. Also shown are the sampling sites used in this study (designated as in section 4.11).



NORTH
POINT
16.17,22
METERS
0
500
1000
ROBIN
PEAK
9
A
10
6
2
JANE
PEAK
20,24
E G
11
B.A.S.
BASE
12
7,15,23
B,F
5
21
1
ORWELL
GLACIER
8
14
TIOGA
HILL
RUSTY
BLUFF
19
MACLEOD
GLACIER
C
D
18
4,13
H
3

structure, marine erosion and glaciation, the latter being dominant.

There is an ice-cap and a number of permanent snow fields but more than 60% of the island's surface is snow free in summer. These areas are mainly confined to the east and west coasts. The Macleod Glacier is the only remaining large glacier and drains the central plateau to the south, terminating in coastal ice cliffs. A smaller glacier, the Orwell, flows into a shallow bay on the east coast. In the lowland areas there are a number of fresh-water bodies, 16 of which can be described as lakes (Heywood, 1967). These vary greatly in size and duration of ice free period in summer.

iii) Geology: Signy Island is composed of regionally metamorphosed sediments, mainly quartz-mica schists with subordinate amphibolites and marbles (Mathews & Maling, 1967). There has been considerable faulting. The geological division between marble and schist is reflected in the soils, and although the marble bands are thin and localized, fragments of this rock are widely distributed. Solifluction has played an important role in producing the present surface condition.

iv) Soils: Much work has been carried out in recent years on the soils of Signy Island and detailed accounts of the types, their chemical composition and the physical factors influencing their development are available (Holdgate et al., 1967; Allen et al., 1967; Allen & Northover, 1967; Northover & Allen, 1967; Chambers, 1966a & b, 1967; Allen & Heal, 1970).

Allen & Heal (1970) divided the soil types at Signy Island into four groups:-

a. Mineral soils: These range from lithosols to fine glacial debris. They are frequently unstable owing to solifluction phenomena. They have little or no organic content and lichens and mosses colonize only the more stable areas.

b. Organic soils: These are of two types. (1) Moss peat: A peat layer up to 2 m thick is found under some bryophyte communities, particularly the semi-ombrogenous Polytrichum and Chorisodontium species. Loosely packed moss remains overlie a more fibrous peat, but even at the base of the banks, moss shoots are easily identifiable. The pH and nutrient content are higher than in arctic and temperate peats. (2) Protoranker: These are thinner layers of organic material which form under many mosses permeated by drainage water. The mineral content is usually higher and they are less acid than the deeper moss peats.

c. Brown earths: These loamy soils are the most mature of those at Signy Island, since oligochaetes and myriapods - the animals chiefly responsible for soil mixing in temperate regions - are absent, and mature soils do not generally develop. The soils are very restricted in their cover, only being found beneath two phanerogams Deschampsia antarctica Desv. and Colobanthus quitensis (Kunth) Bartl. The relatively low C/N ratio of 11 to 13 and the lack of accumulated organic matter indicate greater decomposition here than in other soils.

d. Ornithogenic soils: These are formed from excretory products which accumulate over the breeding areas of birds and seals. They consist largely of black reducing mud, with a pH of 7-8 and are particularly rich in organic matter, nitrogen compounds, calcium and phosphate.

v) Vegetation: The first detailed survey and analysis of the plant communities on Signy Island was undertaken by Holdgate in 1961-62. Subsequently much attention has been devoted to this subject and the most recent phytosociological classification is that of Smith (1972). Only the broader categories will be summarized here and these are based on physiognomic criteria rather than floristic composition. Since such a division reflects the relationship between vegetational organisation and environment, it is particularly relevant to a study of the components of the mesofauna.

The vegetation of the maritime Antarctic is composed of a large number of recurrent units which are easily recognised and defined. Each vegetational stand is relatively small and homogenous, and a high degree of similarity exists between stands of the same vegetation type. The classification of Smith (Table II) is based chiefly on the frequent recurrence of species groups which result from the repetition of particular habitat and environmental regimes. The criteria for the units of classification may be summarized as follows:-

a. Formations: Units based largely on life form and these fall into two types. The first, and major, tundra formation consists of a wide range of cryptogams in which bryophytes, lichens and algae predominate. The second is a considerably less diverse formation in which two herbaceous phanerogams occur.

b. Sub-formations: Units based on the growth form of the predominant components of respective stands. Growth forms giving rise to cushions, turves and carpets predominate in the ecologically important bryophytes, while fruticose and crustose habits predominate among the lichen flora. The algal communities have been insufficiently studied as yet to recognise sub-formations. The various forms are a response to particular habitat characteristics.

c. Associations: Units based on the floristic similarity between component stands comprising the sub-formations.

Table II. Classification of the terrestrial plant communities of the South Orkney Islands (after Smith, 1972).

A. ANTARCTIC NON-VASCULAR CRYPTOGAM TUNDRA FORMATION

1 Fruticose lichen and moss cushion sub-formation.
  a) Andreaea-Usnea association.
  b) Bryophyte and lichen assemblages of rock micro-habitats.
  c) Tortula-Grimmia antarctici association.
  d) Pottia austrogeorgica association.

2 Crustose lichen sub-formation.
  a) Caloplaca-Xanthoria association.
  b) Buellia-Lecanora-Lecidia association.
  c) Placopsis contortuplicata association.

3 Moss turf sub-formation.
  a) Polytrichum alpestre-Chorisodontium aciphyllum association.
  b) Polytrichum alpinum association.

4 Moss carpet sub-formation.
  a) Calliergidium austro-stramineum-Calliergon sarmentosum-Drepanocladus uncinatus association.

5 Moss hummock sub-formation.
  a) Bryum algens-Drepanocladus uncinatus association.
  b) Brachythecium austro-salebrosum association.

6 Encrusted moss sub-formation.
  a) Lichen encrusted Bryum-Ceratodon cf. grossiretis-Pohlia nutans association.

7 Alga sub-formation.
  a) Prasiola crispa association.
  b) Nostoc association.

8 Snow alga sub-formation.
  a) Chlamydomonas nivalis-Raphidonema nivale-Ochromonas association.

9 Miscellaneous cryptogam assemblages.
  a) Marchantia berteroana community.
  b) Pioneer communities on moraines.

B. ANTARCTIC HERB TUNDRA FORMATION

1 Grass and cushion chamaephyte sub-formation.
  a) Deschampsia antarctica-Colobanthus quitensis association.

SECTION 3: THE TARDIGRADA

Since their discovery by Goeze in 1773 the Tardigrada have been given numerous phylogenetic positions. They have at various times been placed with the Gastrotricha, Rotifera, Nematoda, Arachnida, Onychophora and as larvae of insects. The belief today is that they merit a separate phylum and are most closely related to the Onychophora (Puglia, 1959).

3.1 Scheme of classification

For over half a century it has been realised that the tardigrades could be divided into two distinct taxa. The existing scheme of classification is largely founded on the divisions implied by Murray (1911), although Murray did not assign exact names to his groups. The work of Richters (1926) was the foundation on which the present classification had its beginning. In an important series of papers, Marcus (1929, 1930, 1936) and Thulin (1928) have elaborated and refined the scheme proposed by Richters. This refinement has been continued more redently by Puglia (1959) and Ramazzotti (1962, 1972a, 1974). The scheme of classification (Table III) and keys for the identification of species used throughout this thesis are those given by Ramazzotti (1972a). The modifications proposed by Ramazzotti (1974) have not, as yet, been generally accepted and the only change which may affect nomenclature in the present work is the elevation of Diphascon from sub-generic to generic status.

3.2 Taxonomic criteria and terminology

An understanding of the taxonomic terms applicable to any group is essential for the discussion of animals within that group,

Table III. Systematics of the Tardigrada (after Ramazzotti, 1972a).

Order: HETEROTARDIGRADA Marcus, 1927

Sub-order: Arthrotardigrada Marcus, 1927

Family: Halechiniscidae Puglia, 1959

Genera: Halechiniscus, Pleocola, Actinarctus, Echinursellus, Tetrakentron, Styraconyx, Bathyechiniscus, Florarctus and Tanarctus.

Family: Batillipididae Ramazzotti, 1962

Genera: Batillipes and Orzeliscus.

Family: Stygarctidae Schulz, 1951

Genera: Stygarctus and Parastygarctus.

Sub-order: Echiniscoidea Marcus, 1927

Family: Oreellidae Puglia, 1959

Genera: Oreella, Echiniscoides and Archechiniscus.

Family: Echiniscidae Thulin, 1928

Genera: Echiniscus (Sub-genera: Echiniscus, Bryochoerus, Bryodelphax and Hypechiniscus), Parechiniscus, Pseudechiniscus and Mopsechiniscus.

Order: MESOTARDIGRADA Rahm, 1937

Family: Thermozodiidae Rahm, 1937

Genus: Thermozodium.

Order: EUTARDIGRADA Marcus, 1927

Family: Macrobiotidae Thulin, 1928

Genera: Macrobiotus, Haplomacrobiotus, Hypsibius (Sub-genera: Hypsibius, Calohypsibius, Isohypsibius and Diphascon), Itaquascon and Hexapodibius.

Family: Milnesiidae Ramazzotti, 1962

Genus: Milnesium.

and for this reason the characteristics relevant to the Antarctic Tardigrada are briefly outlined. Extensive reviews of the morphology are given by Marcus (1929), Cuenot (1932) and Ramazzotti (1962, 1972a).

3.21 Cuticle

The studies of Greven (1972) and Bussars & Jenniaux (1973) have recently added much to the chemical and anatomical knowledge of the tardigrade cuticle. In this section, only the morphology of the cuticle as used in taxonomy will be discussed.

In the order Heterotardigrada, cephalic appendages are characteristic. A single Eutardigrade, Milnesium, possesses oral and cephalic papillae. The family Echiniscidae is characterised by clearly defined armour plates which are variously sculptured, as well as carrying a number of spines(whose positions are designated in descriptions by letters). In many species of Hypsibius, Macrobiotus and Milnesium the cuticle is thin and smooth, although pores of various sizes and distribution may be present, along with well defined cuticular folds. The remainder of the species in the genera Hypsibius and Macrobiotus display a variety of sculpture ranging from small wart like granulation, to large irregularly shaped lumps.

3.22 Claws

The number, size and shape of the claws are used in generic and specific identifications. In the genus Echiniscus, four separate claws on each leg are present, except in the immature stages where there are only two. A single short ventral spur may be present on some of these claws, usually the two inner or medial claws. The Eutardigrada usually possess two double claws on each leg. The claws consist of a long primary branch, often with accessory spines at its

Fig. 4 Detail of the processes on the egg of
Macrobiotus furciger, each process is approximately 7 µm long.

Photograph by courtesy of R M Crawford and the Department of Botany, University of Bristol.

tip, and a shorter secondary branch. Two genera are separated on whether the double claws are similar and symmetrical (Macrobiotus) or dissimilar and assymetrical (Hypsibius). The genus Milnesium is easily recognised by the separation of the primary and secondary branches, the secondary being robust with short hooks.

3.23 Buccal apparatus

The buccal apparatus includes the mouth, stylet mechanism, buccal tube and sucking pharynx. Three major forms of buccal apparatus are found:-

i) In the order Heterotardigrada the muscular pharynx has unbroken lines of muscular supports known as placoids, and the stylet mechanism often lacks a stylet support.

ii) In the order Mesotardigrada and in the family Macrobiotidae of the order Eutardigrada (except for Itaquascon) the placoids are not in the form of continuous rods. Here the various fragments have been named. The largest fragments are referred to as the macroplacoids and the smallest, when present, as the microplacoid or comma. The stylet support is generally present.

iii) In the family Milnesiidae and the genus Itaquascon of the family Macrobiotidae, the sucking pharynx lacks any trace of the supporting placoid row.

3.24 Eggs

The eggs take one of two forms:-

i) The eggs are smooth and usually deposited in the cast-off cuticle at the moult. The majority of tardigrade species have eggs of this type, and they are of little taxonomic significance.

ii) The eggs are laid singly or in packets but not in the shed cuticle. These eggs have processes (Fig. 4) and adhere to any available substrate. Most species of the genus *Macrobiotus* have eggs of this type. It is often essential to link egg with adult of any particular species before a positive identification can be made.

3.3 Species recovered in the present investigation

Order: Heterotardigrada Marcus, 1927.

Sub-order: Echiniscoidea Marcus, 1927.

Family: Oreellidae Puglia, 1959.

Oreella mollis J. Murr., 1910. (Fig. 5)

Length 84 µm. Eyes absent. Cuticle dorsally and laterally covered by rounded papillae which become fine granules anteriorly. Very fine granulation ventrally. Buccal aperture sub-terminal. Internal buccal cirri fine, 3 µm long. Cephalic papillae fleshy and conical. External cephalic cirri fine, 6 µm long. Lateral cirrus A long (35 µm) and filiform. Clava shorter (10 µm) but thicker (1 µm), arising from a common bulbous base as the cirrus. Bifid conical protruberance on the medial line at the caudal extremity. Legs long (15 µm at the IV pair). Four large claws without spurs.

This species has previously only been recorded from Australia (Murray, 1910b) and very dubiously from Switzerland (Rahm, 1936).

Family: Echiniscidae Thulin, 1928.

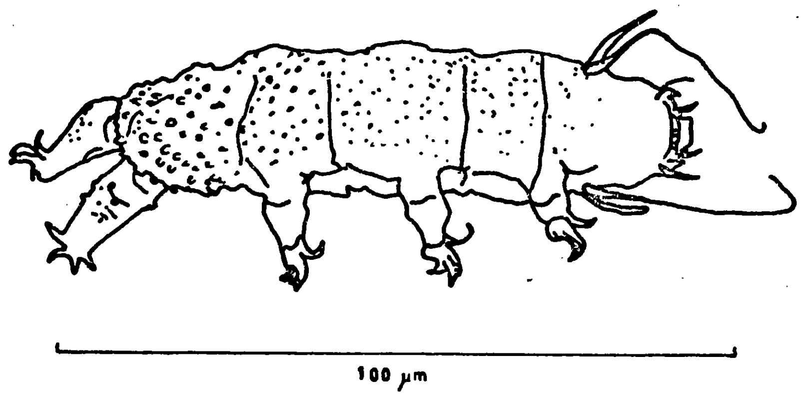
Echiniscus (*Echiniscus*) *meridionalis* J. Murr., 1906. (Fig. 6)

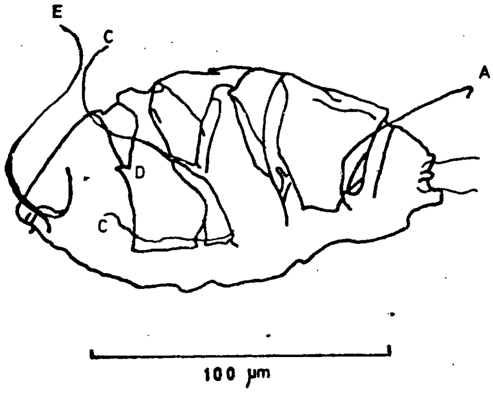
Length 109–163 µm. Sculpture fine depressions. For 109 µm specimen, cirrus A 43 µm long, with papilla at its base. Medial plate 3 present. Terminal plate with notches. Filament C 35 µm lomg.

Fig. 5 General body plan of *Oreella mollis.*

Fig. 6 General body plan of

Echiniscus (*Echiniscus*) *meridionalis*.


100 μm


E
C
A
D
C
100 μm

Filament C^d 45 µm. Short spine D 4 µm, and a trace of spine D^d. Filament E long (87 µm). Indented collar on IV pair of legs. Internal claws 8 µm, with a spur curved towards the base.

This species was originally described from the South Orkney Islands (Murray, 1906) and has not been reported outside the Antarctic.

Echiniscus (Echiniscus) capillatus Ramazzotti, 1956. (Fig. 7)

Length 172-244 µm. Robust with reddish coloration. Cirrus A very long, with a mean length 90% of the body length. Sculpture is a diffused granulation all over the dorsal surface (Fig. 7b). Indented collar on IV pair of legs consisting of 5-8 teeth, their size and distribution irregular. Claw length 18-23 µm, with a sharp backward pointing spur on the interior pair.

This species has been reported only from Italy (Ramazzotti, 1956), where it was found at an altitude of 2400 m. The original specimens were larger in size (300-325 µm) than the material from Signy Island, and had larger claws, reported as 31 µm long. The toothed collar is also reported as having 9-10 teeth, some of which may have been obscured in the present specimens.

Order: Eutardigrada Marcus, 1927.

Family: Macrobiotidae Thulin, 1928.

Macrobiotus ambiguus J. Murr., 1907. (Fig. 8)

Up to 751 µm in length. Small eyespots. Cuticle completely smooth. Buccal aperture terminal. Buccal tube up to 76 µm long, with 8 µm internal diameter. Oval bulb with two macroplacoids, the first 27 µm long and partially divided, the second 14 µm long. Microplacoid absent. Claws large, primary branch of IV pair 34 µm long and joined

Fig. 7 *Echiniscus (Echiniscus) capillatus*.

a) General body plan

b) Detail of plate sculpture

c) Detail of posterior claw

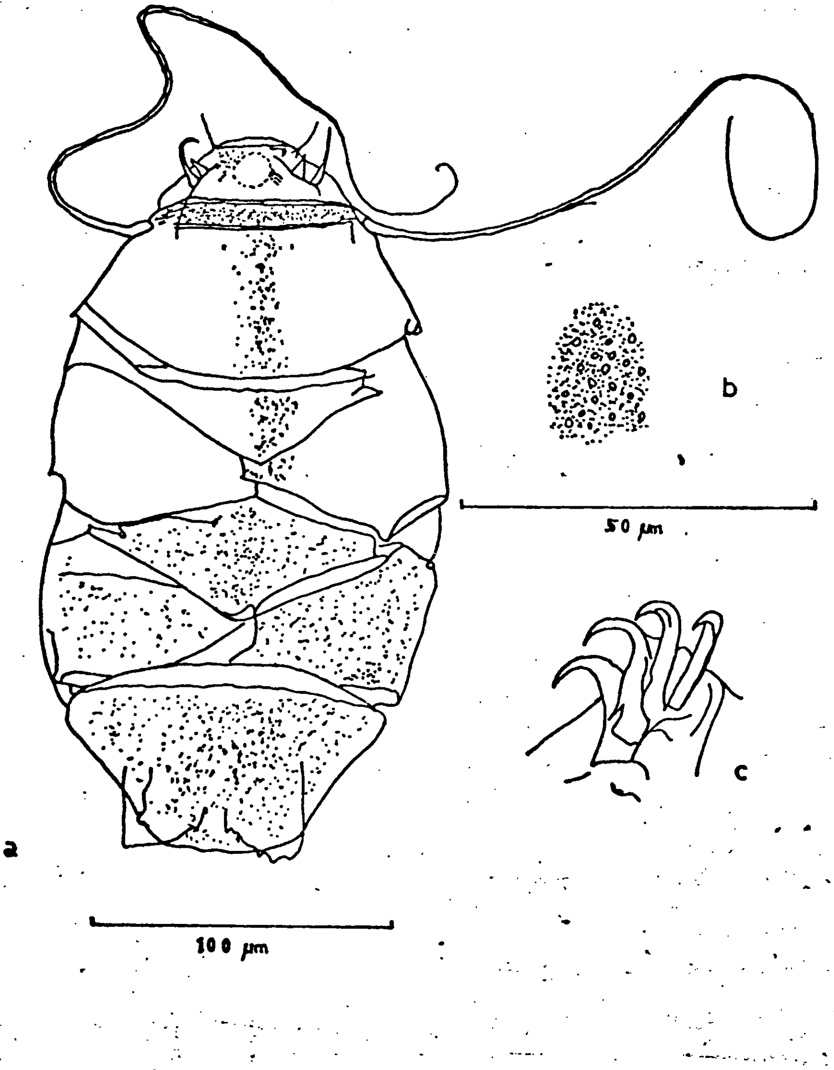
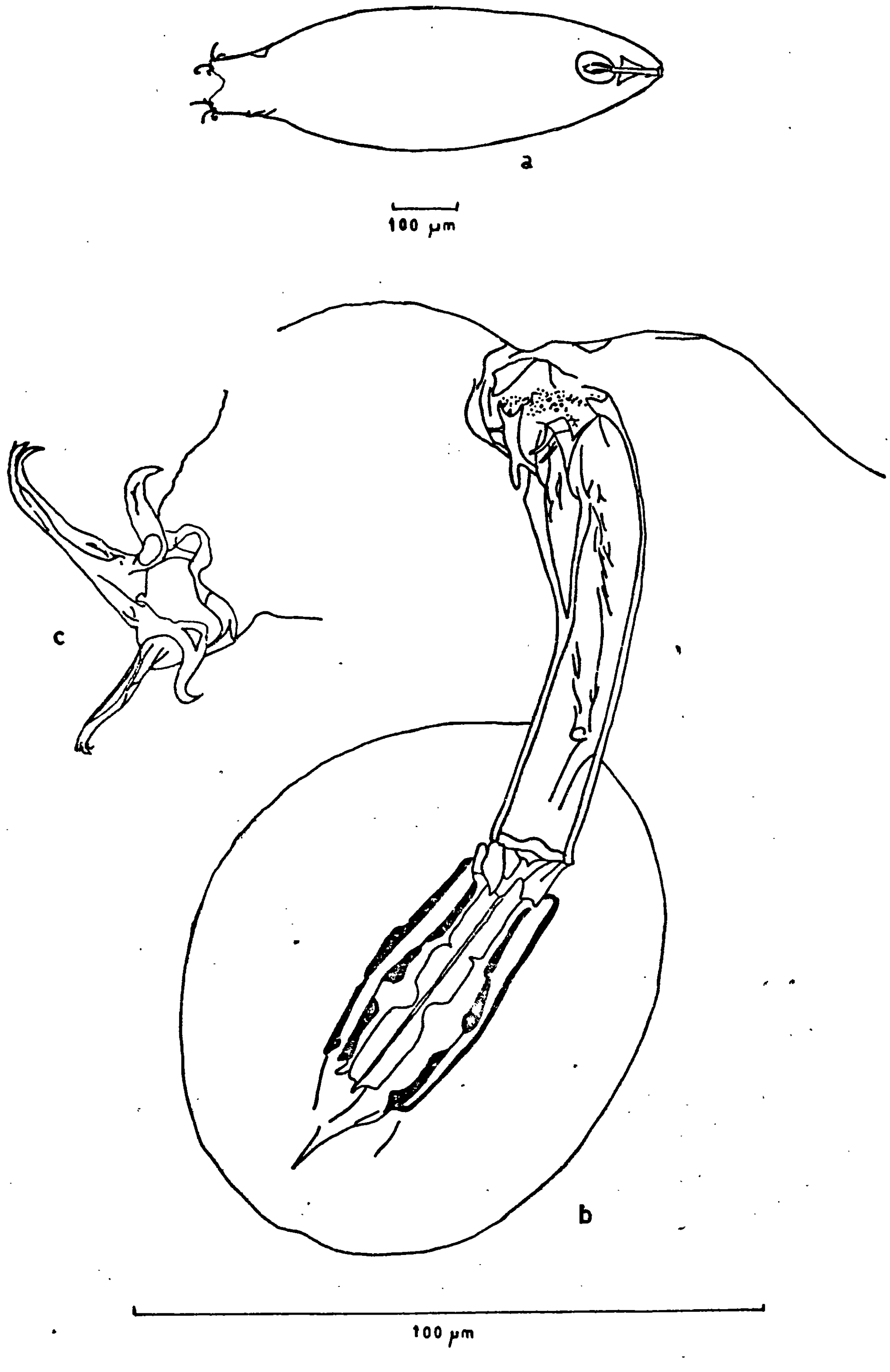

a
b
50 µm
c
100 µm

Fig. 8 *Macrobiotus ambiguus*.

a) General body plan

b) Detail of buccal apparatus - placoids appeared hollow in section and shaded portions represent interior and exterior edges

c) Detail of claw



a
100 µm
c
b
100 µm

to the secondary branch (18 µm long) at the base. Cuticular fold bridges the claws.

This is a cosmopolitan species which has only been recovered from aquatic habitats.

Macrobiotus furciger J. Murr., 1907. (Fig. 9)

Length 174-696 µm, typically 450 µm. Cuticle smooth. Eye-spots large and set forward. Animal brown in transmitted light. Buccal aperture terminal. A crown of triangular teeth evident in the caudal portion of buccal cavity, a feature of the "Macrobiotus areolatus type" (Pilato, 1972). Bulb oval (45 µm by 35 µm) with three granular macroplacoids (7, 6 and 6 µm); tear shaped microplacoids. Claws small (12 µm). Primary and secondary branches of equal length and fused to half their length. Diameter of the egg 96 µm, or with ornamentation 110 µm.

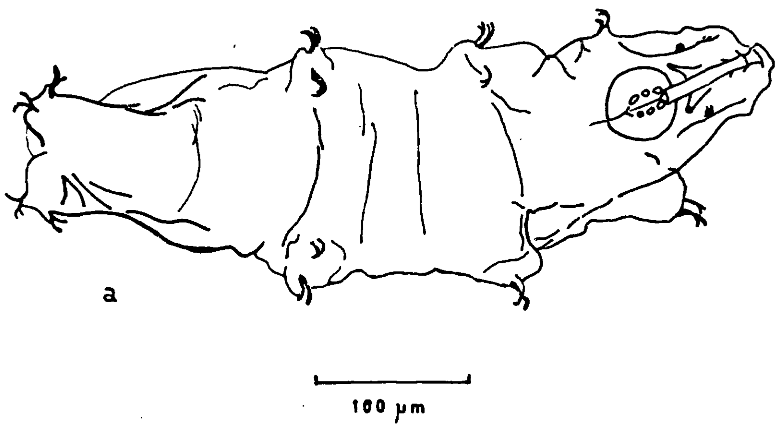
This description of the adult agrees with that of Murray (1906), who recorded this species as the most numerous found in his samples from the South Orkney Islands. However, the eggs of this species were laid free, and it has not been possible in this study to relate egg and adult categorically. All the free Macrobiotus eggs found in the terrestrial sites had conical ornamentation with bifid processes (Fig. 4). These are not the same as the eggs of M. furciger as described by Murray, which have multi-branched processes, but they do correspond to one of his Macrobiotus sp. While identification relies on relating adults with particular egg types, confusion in this group is inevitable.

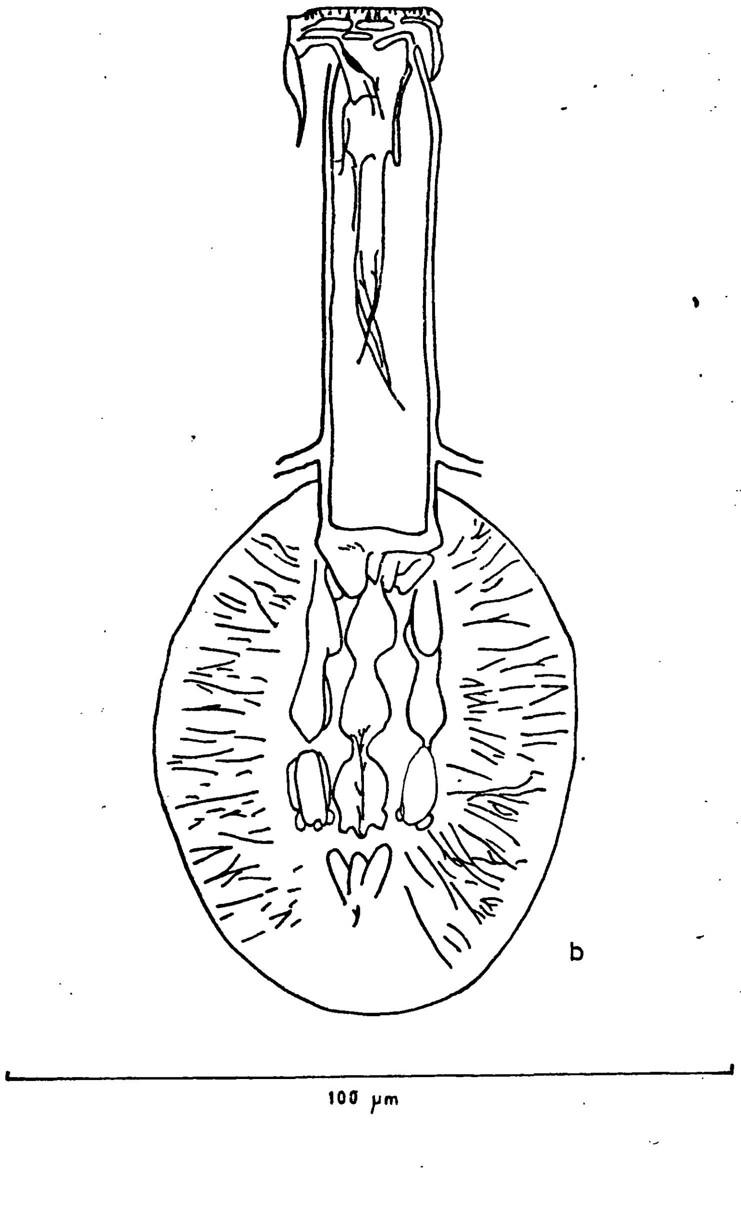
This species was frequently observed attacking Nematoda and inactive bdelloid rotifers in culture at Signy Island. Its gut contents, however, were almost invariably green in colour. Since

Fig. 9 *Macrobiotus furciger.*

a) General body plan

b) Detail of buccal apparatus


a
100 µm


b
100 µm

neither the rotifers nor the nematodes had any green coloration evident, this would suggest that M. furciger is not exclusively carnivorous.

Originally described from the South Orkney Islands (Murray, 1906) this species is cosmopolitan.

Hypsibius (Hypsibius) dujardini (Doy., 1840). (Fig. 10)

Length 115–428 µm, typically 249 µm. Cuticle smooth. Eyespots present. Bulb oval (28 µm by 23 µm) with two macroplacoids, the first usually with a marked constriction and slightly longer (5 µm) than the second (4 µm). Microplacoid absent from all but one specimen. Primary branch of claw with accessory points and longer than secondary. Eggs laid in the moulted cuticle.

An algal feeder (Baumann, 1961) which is a cosmopolitan species. Two specimens which were identified as Hypsibius (Hypsibius) antarcticus (Richters) were recovered from South Georgia. However, it has been suggested by Dastych (1973) that this species is synonymous with H. (H.) dujardini in the simplex stage (see section 5.14).

Hypsibius (Hypsibius) oberhauseri (Doy., 1840). (Fig. 11)

Length 221–497 µm, typically 370 µm. Cuticle with diffuse granulation. Eyespots absent. Colour dull red, but not in stripes. Bulb oval with two macroplacoids; microplacoid absent. Placoid line 11 µm long. Primary branch of claw very long (48 µm) and curved.

The species is cosmopolitan.

Hypsibius (Isohypsibius) asper (J. Murr., 1906). (Fig. 12)

Length 141–565 µm, typically 325 µm. Cuticle dorsally covered with tubercles increasing in size from anterior to posterior. Eyespots present. Buccal aperture sub-terminal. Buccal tube 44 µm

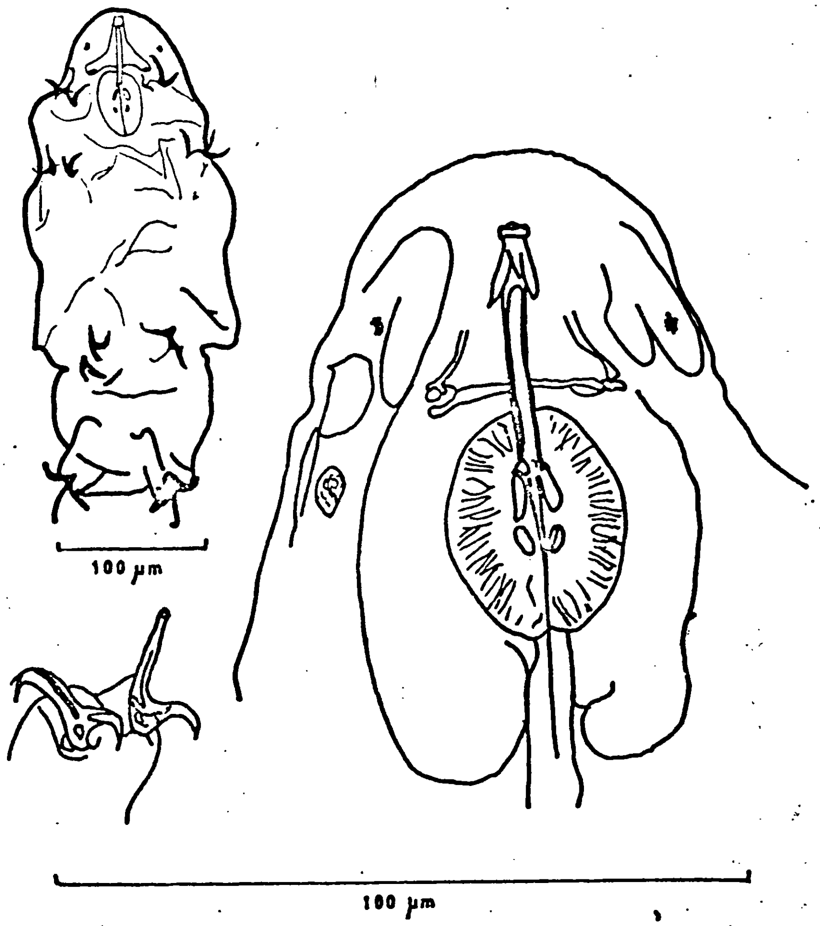
Fig. 10 *Hypsibius* (*Hypsibius*) *dujardini*.

a) General body plan

b) Detail of anterior region

c) Detail of claw

Fig. 11 General body plan of *Hypsibius* (*Hypsibius*) *oberhaeuseri*.


100 μm
100 μm


100 μm

Fig. 12 *Hypsibius* (*Isohypsibius*) *asper*.

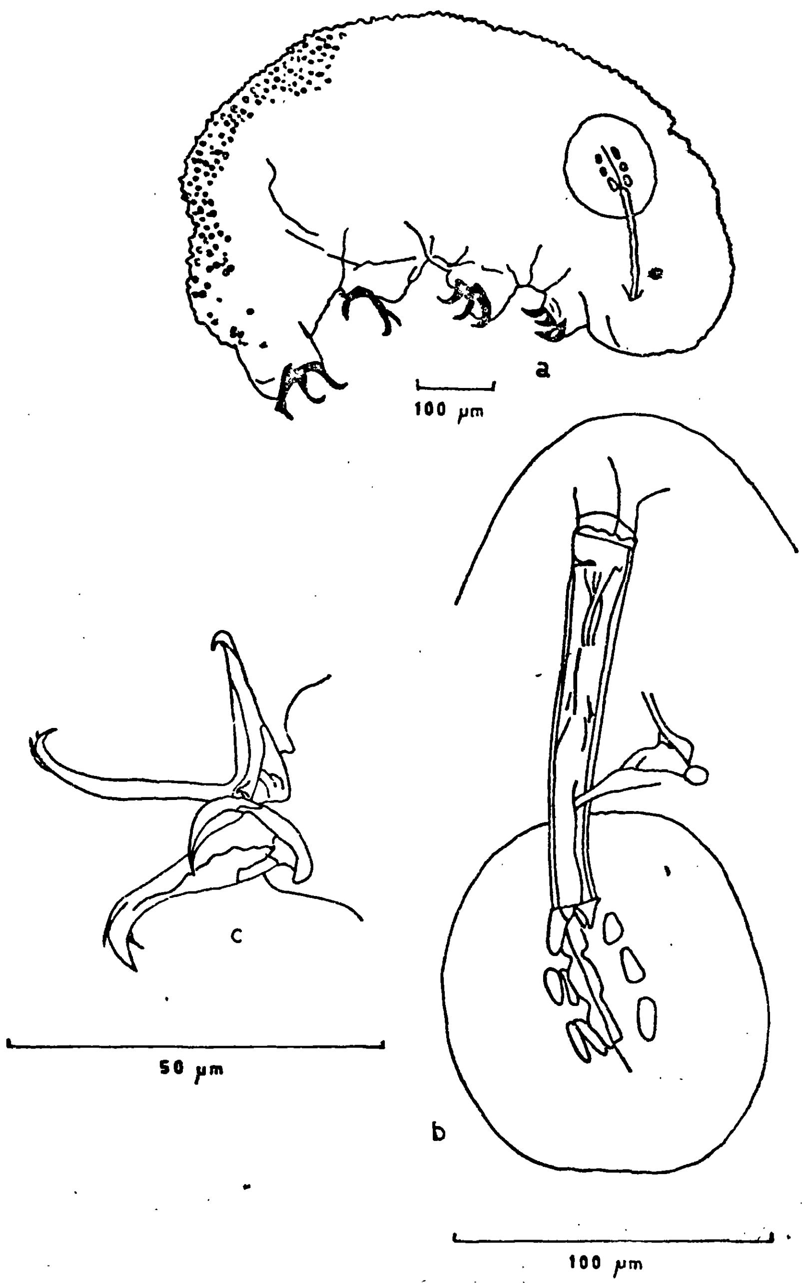
a) General body plan

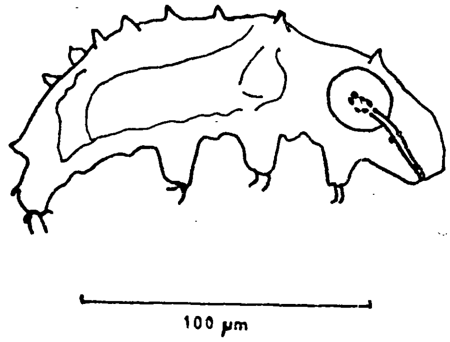
b) Detail of buccal apparatus

c) Detail of claw

Fig. 13 General body plan of

Hypsibius (*Isohypsibius*) *papillifer*.


a
100 µm
c
50 µm
b
100 µm


100 µm

long, 2 µm internal diameter. Bulb almost round (45 µm by 44 µm), containing three granular macroplacoids. Placoid line 21 µm long. Microplacoid absent. Claws large, primary branch 42 µm long. Up to 17 eggs found in the moulted cuticle.

Originally described from the South Orkney Islands (Murray, 1906) it has been found at only two sites outside Antarctica, both in Europe (Ramazzotti, 1972a).

Hypsibius (Isohypsibius) papillifer (J. Murr., 1905). (Fig. 13)

Length 147 µm. Cuticle with 9 transverse lines of small conical projections, interspersed with confused irregular granulation. Bulb with three granular macroplacoids, the third being largest; microplacoid absent.

Only a single specimen was found but the species has a wide-spread distribution elsewhere (Ramazzotti, 1972a).

Hypsibius (Isohypsibius) renaudi Ramazzotti, 1972. (Fig. 14)

Length 144-473 µm, typically 309 µm. Cuticle smooth. Eye-spots present. Buccal aperture sub-terminal. Buccal tube 40 µm long, 2-4 µm wide. Bulb with two macroplacoids, the first 7 µm long and having a medial constriction; the second (4 µm) with or without a constriction. Principle branch of external double claw always very long (up to 40 µm), fine and very curved. The secondary branch, and internal double claws, robust. Accessory points on primary branches of both internal and external claws. Eggs laid in the cuticle.

This description differs from the original (Ramazzotti, 1972b) in the possession of accessory points on the claws. The species was originally described from Kerguelen Island which is the only other locality from which it has been recorded.

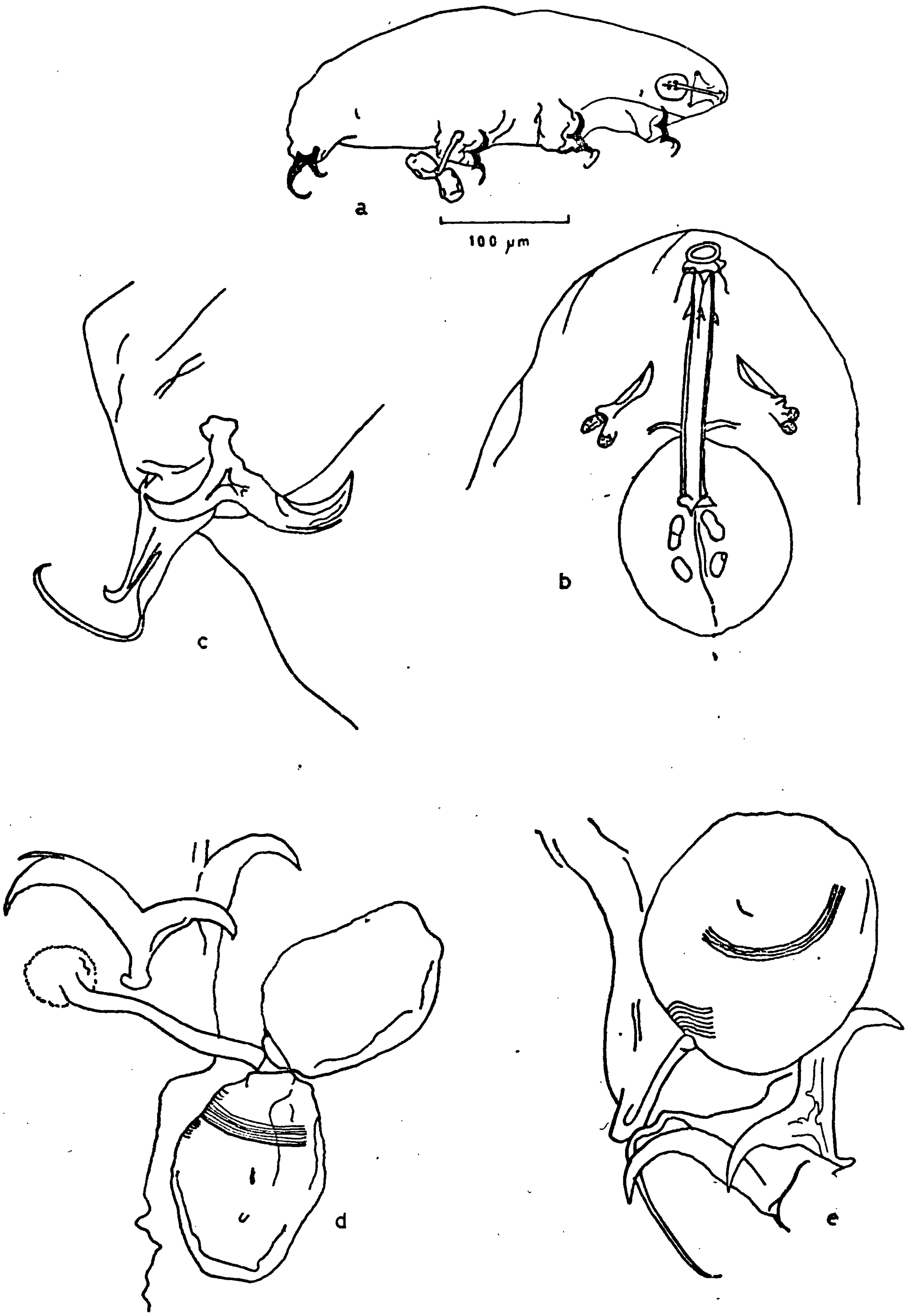
Fig. 14 *Hypsibius* (*Isohypsibius*) *renaudi*.

a) General body plan

b) Detail of anterior region

c) Detail of claw

d) Detail of colonial protozoan
)
e) *Epistylis* sp.



a
100 µm
b
c
d
e
50 µm

Some animals carried up to 14 epizoic peritrichs of the genus Epistylis. Previous accounts of an association between a protozoan (Pyxidium tardigradum Van der Land) and a tardigrade are limited to those of Van der Land (1964) and Iharos (1966).

Hypsibius (Diphascon) alpinus (J. Murr., 1906). (Fig. 15a)

Length 126–285 µm, typically 191 µm. Cuticle smooth. Eyespots absent. Buccal aperture sub-terminal. Buccal tube 0.5–1.5 µm in diameter, with ring markings. Bulb an elongated oval (19 µm by 13 µm). Three macroplacoids, short rods increasing in length from the first to the third (4 µm). Placoid line 14 µm long. Microplacoids and septulum present. Eggs found in the discarded cuticle.

This species is cosmopolitan.

Taxonomic difficulties experienced in distinguishing this species from other members of the sub-genus Diphascon have been discussed by Petersen (1951). In the routine population census counts no separation was made between this species and H. (D.) pinguis Marcus, and it was also found difficult to separate these two species from H. (D.) chilenensis (Plate). Three characters have been used to distinguish between the three species in this study, these being diameter of the buccal tube, length of the placoid line and length of the third macroplacoid. These discriminatory characters are presented in Table IV. Even using those characters which may be quantified along with others which are not as easily measured (e.g. shape of the claw), confusion in identification is inevitable.

Hypsibius (Diphascon) chilenensis (Plate, 1888). (Fig. 15b)

Length 160–251 µm. Cuticle smooth. Eyespots absent. Buccal aperture sub-terminal. Buccal tube 1 µm diameter, with ring

Table IV. Characters used to distinguish between members of the sub-genus *Diphascon* encountered in this study.

Character	*Hypsibius* (*D.*) *alpinus*	*Hypsibius* (*D.*) *chilenensis*	*Hypsibius* (*D.*) *pinguis*	*Hypsibius* (*D.*) *puniceus*	*Hypsibius* (*D.*) *scoticus*
colour	hyaline	hyaline	hyaline	pink	hyaline
cuticular sculpture	none	none	none	caudal granulation	none
body length (µm)	126-285	160-251	129-235	142-176	138-488
diameter of buccal tube (µm)	0.5-1.5	1.0	1.0-2.0	1.0	1.5-3.0
Pharynx length (µm)	19	22	29	11	50
pharynx width (µm)	13	19	18	6	26
length macroplacoid 1 (µm)	2	3	3	2	9
length macroplacoid 2 (µm)	3	3	4	1	7
length macroplacoid 3 (µm)	4	3	6	1	12
length placoid row (µm)	14	10	18	10	35

markings. Bulb almost round (22 µm by 19 µm for 160 µm specimen). Three macroplacoids, granules all of about equal length (3 µm). Placoid line 10 µm long. Microplacoid present, septulum absent.

The species is cosmopolitan.

Hypsibius (Diphascon) pinguis Marcus, 1936. (Fig. 15c)

Length 129–235 µm, typically 182 µm. Cuticle smooth. Eyespots absent. Buccal aperture sub-terminal. Buccal tube 1.0–2.0 µm diameter, with ring markings. Bulb an elongated oval (29 µm by 18 µm). Three macroplacoids, rods increasing in length from the first to the third (6 µm). Placoid line 18 µm long. Microplacoids and septulum present. Eggs seen in the discarded cuticle.

The species is cosmopolitan.

Hypsibius (Diphascon) puniceus Jennings. (Fig. 16)

Length 142–176 µm. Caudal extremity of dorsal surface with numerous granules, elsewhere the cuticle smooth. Eyespots absent. Animal pink in colour. Stylets fine and almost straight. Buccal aperture sub-terminal. Buccal tube narrow (1 µm diameter), with ring markings. Bulb oval, 11 µm by 6 µm (for 142 µm specimen), with small apophyses and three granular macroplacoids, decreasing in size from the first to the third. Microplacoids present. Septulum absent. Placoid line 10 µm long. Claws of the normal Hypsibius type bearing accessory points on the principle branches. Eggs were not found.

This new species has been recovered only from Signy Island.

Hypsibius (Diphascon) scoticus (J. Murr., 1905). (Fig. 17)

Length 138–488 µm, typically 322 µm. Cuticle smooth. Eye-

Fig. 15 Detail of anterior region

a) Hypsibius (Diphascon) alpinus.

b) Hypsibius (Diphascon) chilenensis.

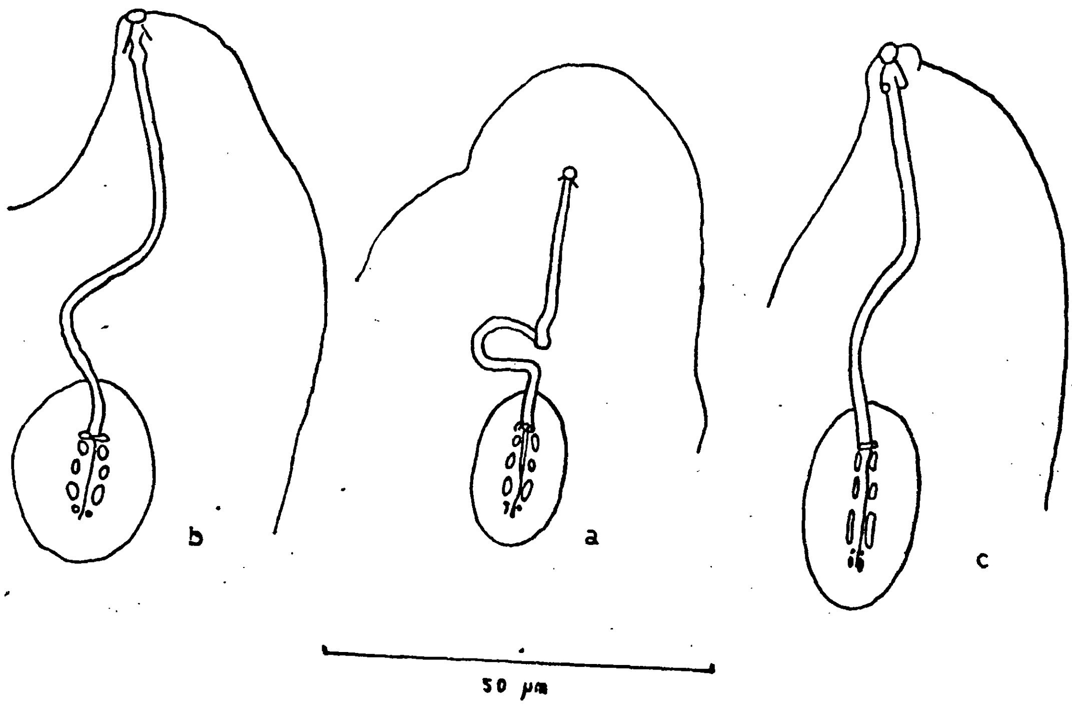
c) Hypsibius (Diphascon) pinguis.

Fig. 16 Hypsibius (Diphascon) puniceus.

a) General body plan

b) Detail of anterior region

c) Detail of posterior region


b
a
c
50 µm

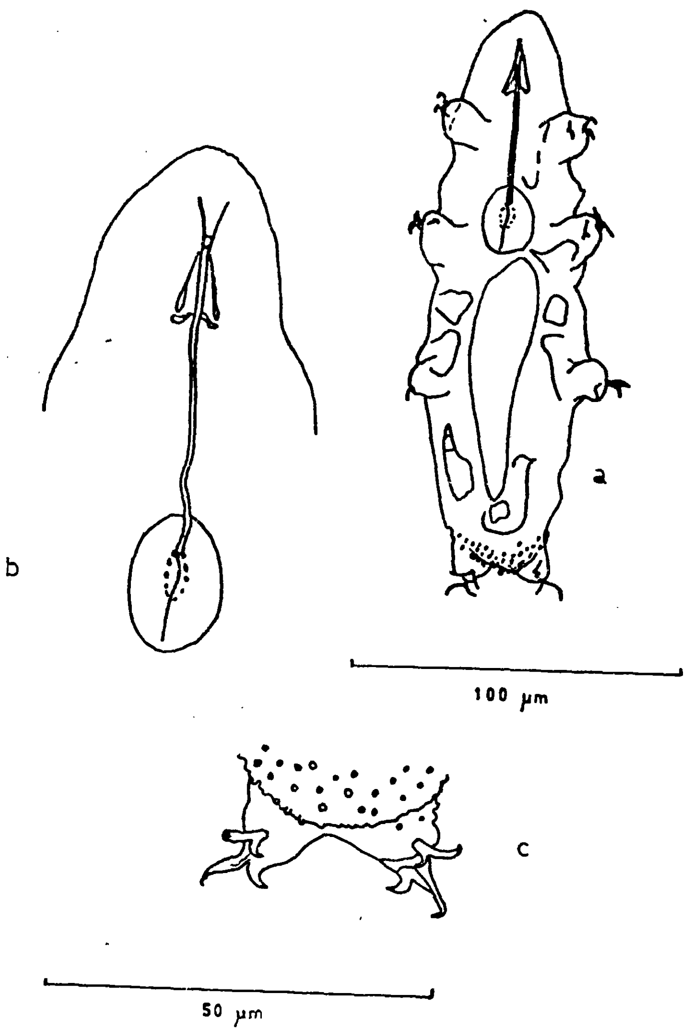

b
a
100 µm
c
50 µm

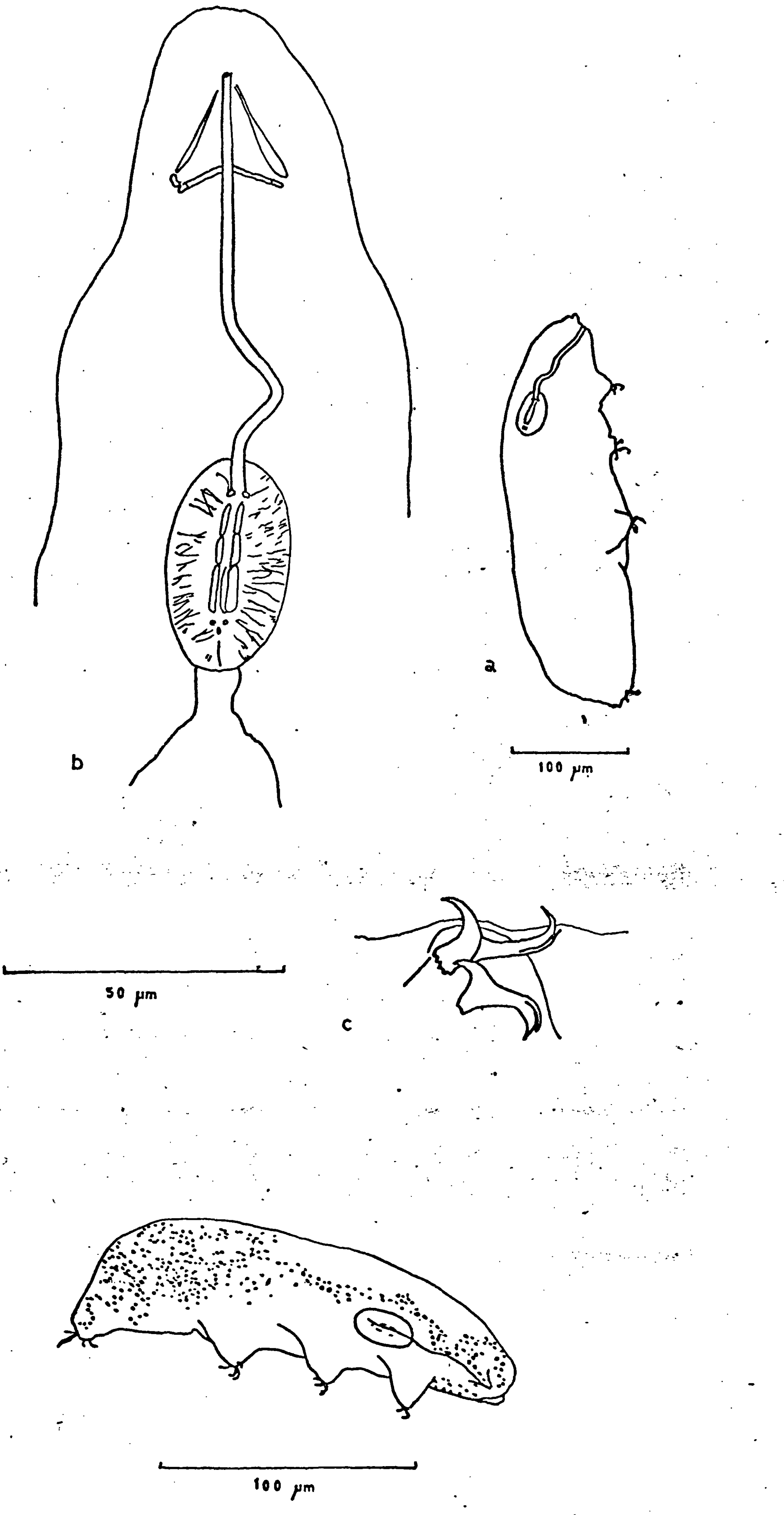
Fig. 17 Hypsibius (Diphascon) scoticus.

a) General body plan

b) Detail of anterior region

c) Detail of claw

Fig. 18 General body plan of Hypsibius (Diphascon) sp.


a
100 µm
b
50 µm
c
100 µm

spots absent. Buccal aperture sub-terminal. Buccal tube 1.5–3.0 µm diameter, with very clear ring markings. Bulb an elongated oval, up to 50 µm by 26 µm. Three macroplacoids 9, 7 and 12 µm. Placoid line 60% of the bulb length. Microplacoids and septulum present.

The species is cosmopolitan.

Hypsibius (Diphascon) sp. (Fig. 18)

Three specimens were recovered from a collection made by P.J. Tilbrook in 1964 from Signy Island. A complete description cannot be given as details of the bulb and its contents are not clear. The most notable feature about the animal is the extensive, diffused, granulation over both dorsal and ventral surfaces. The animals are black in colour, but this may have been caused by the preservative.

Family: Milnesiidae Ramazzotti, 1962.

Milnesium tardigradum Doy., 1840. (Fig. 19)

Length 547–947 µm. Cuticle smooth. Eyespots present. Animal orange-red in colour. Buccal apparatus large and terminal, surrounded by fleshy papillae. Muscular pharynx without macroplacoids. Claws distinctive, with two very long branches and two short three hooked members on each leg. The species is carnivorous and several complete ramate trophi from bdelloid rotifers were found in the gut of several specimens (Fig. 19d). Eggs laid in the moulted cuticle.

This large, easily identified, terrestrial species is cosmopolitan.

Fig. 19 *Milnesium tardigradum*.

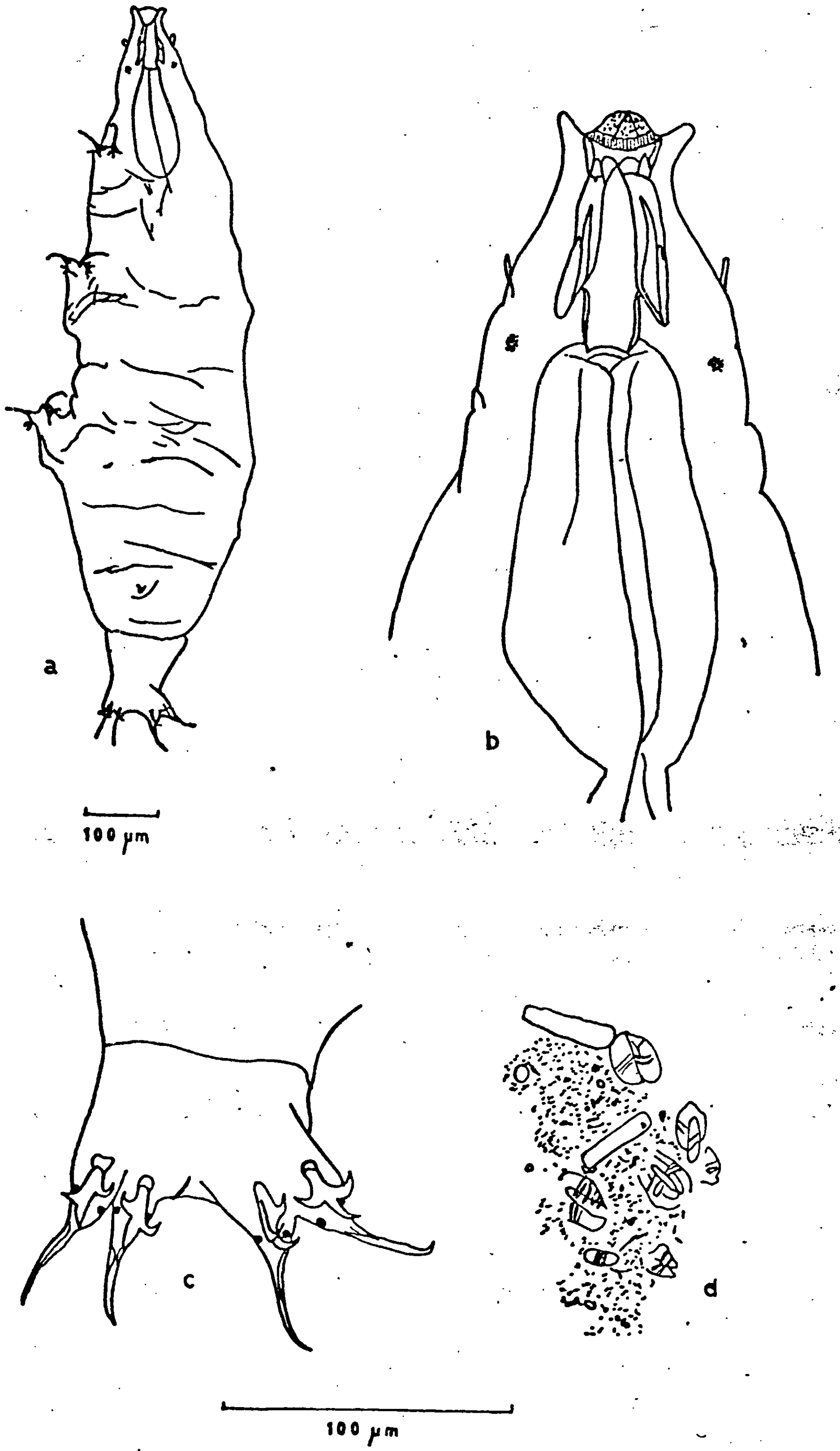
a) General body plan

b) Detail of anterior region

c) Detail of posterior region

d) Detail of gut contents.

Six ramate trophi are clearly visible.


a
b
100 µm
c
d
100 µm

3.4 Survey of the Antarctic tardigrade fauna

Information on the tardigrade fauna of the Antarctic has been given by Richters (1904, 1908, 1909), Murray (1906, 1910b), Sudzuki (1964), Morikawa (1962) and Jennings (1975, in press a, b and c). Ignoring those species which have not been sufficiently described, the number of tardigrade species now recognised from the Antarctic stands at 23 (Table V). Only 11 of these species have been found by two or more investigators, and only *E.* (*E.*) *meridionalis*, *M.* *furciger*, *H.* (*I.*) *asper*, *H.* (*D.*) *alpinus*, *H.* (*D.*) *chilenensis* and *Miln.* *tardigradum* have been recognised by three or more investigators. In section 3.3, the difficulty in separating the small members of the sub-genus *Diphascon* is discussed, and this may have some bearing on the lack of species confirmation by different authors. Some or all of the species in the group *H.* (*D.*) *alpinus*, *H.* (*D.*) *chilenensis*, *H.* (*D.*) *ongulensis*, *H.* (*D.*) *pinguis* and *H.* (*D.*) *puniceus* may have been confused in this and other investigations.

Three studies have now been completed on the Antarctic Peninsula and Scotia Ridge region (Richters, 1908; Murray, 1906; Jennings, 1975, in press a, b, c). The total recorded tardigrade fauna numbers 17 species, 8 of which have been found by more than one investigator. Thirteen species have not been recorded from the Antarctic outside localities in the Antarctic Peninsula and Scotia Ridge region, but this could reflect the intensity of the investigations and the taxonomic progress made in this group in recent years.

3.5 Tardigrade biogeography

Very few of the tardigrade species encountered in this investigation are restricted to the Antarctic region, or even to the

Table V. Comparison of faunistic lists of continental and maritime Antarctic Tardigrada from various authors. Synonyms are given where these have appeared in previous Antarctic literature.
- Not found. 0 Found in the Antarctic. þ Found in the Antarctic Peninsula. * Variety found [Sudzuki (1964) lists H. (D.) chilenensis langhovdensis Sudzuki, which differs slightly from H. (D.) chilenensis].

Species and authority	Richters 1904	Richters 1908	Richters 1909	Murray 1906	Murray 1910	Sudzuki 1964	Morikawa 1962	Jennings in press b	Synonym
Oreella mollis J. Murr., 1910	-	-	-	-	-	-	-	þ	
Echiniscus (Echiniscus) arctomys Ehrbg., 1853	-	þ	-	-	-	-	-	-	
capillatus Ramazzotti, 1956	-	-	-	-	-	-	-	þ	
meridionalis J. Murr., 1906	-	þ	-	þ	-	-	-	þ	
wendti Richters, 1903	-	þ	-	-	-	-	-	-	
Macrobiotus furciger J. Murr., 1907	-	þ	-	þ	-	-	-	þ	M. furcatus
meridionalis Richters, 1909	-	-	0	-	-	-	-	-	
polaris J. Murr., 1910	-	-	-	-	0	-	-	-	
Hypsibius (Hypsibius) antarcticus (Richters, 1904)	0	-	-	-	-	0	-	-	
arcticus (J. Murr., 1907)	-	-	-	-	0	-	0	-	
dujardini (Doy., 1840)	-	þ	-	-	-	-	-	þ	M. murrayi
mertoni simoizumi Sudzuki, 1964	-	-	-	-	-	0	-	-	
oberhaeuseri (Doy., 1840)	-	-	-	-	0	-	-	þ	
(Isohypsibius) asper (J. Murr., 1906)	-	þ	-	þ	-	-	-	þ	M. asperus
papillifer (J. Murr., 1905)	-	-	-	-	-	-	-	þ	
renaudi Ramazzotti, 1972	-	-	-	-	-	-	-	þ	
(Diphascon) alpinus (J. Murr., 1906)	-	þ	-	þ	0	-	-	þ	D. alpinum
chilenensis (Plate, 1888)	-	þ	-	þ	-	*	-	þ	
ongulensis Morikawa, 1962	-	-	-	-	-	-	0	-	
pinguis Marcus, 1936	-	-	-	-	-	-	-	þ	
puniceus Jennings	-	-	-	-	-	-	-	þ	
scoticus (J. Murr., 1905)	-	þ	-	-	-	-	-	þ	
Milnesium tardigradum Doy., 1840	-	þ	-	-	-	0	-	þ	

southern hemisphere. Only the four species O. mollis, E. (E.) meridionalis, H. (I.) renaudi and H. (D.) puniceus have not been recovered from the northern hemisphere, and the last two of these are only recently known to science. It is probable then, that a given tardigrade species may exist wherever suitable environmental conditions are to be found, and the species composition of similar mosses worldwide are not seen to be different (Sudzuki, 1964). The ability of most species to withstand desiccation in the anabiotic state leads to ease of dispersal on wind currents (Sudzuki, 1972), or by accidental transport in the dried mud on birds legs (Spaull, 1973c). However, the Tardigrada are still incompletely studied throughout the world, and their taxonomy is not in a sufficiently ordered state to facilitate such study. To quote one example, the species described in this work as H. (D.) pinguis has a number of variant characters from the same species as described by Mitchell (1973), which is in turn different from the H. (D.) pinguis of Argue (1972). All of these bear some similarity to the original description of Marcus (1936), but without a detailed knowledge of intra-specific variation it cannot be stated that these three groups of individuals are either variants, sub-species or new species in their own right. It has been stressed that the problem of identification in Diphascon is intense, but the problem is not restricted to the Diphascon group alone, it runs throughout the Tardigrada as a whole and is common in the animal kingdom wherever reproduction is predominantly by parthenogenesis.

SECTION 4: SITES AND METHODS

4.1 Selection of Sites

4.11 Signy Island

Samples were collected from 43 sites on Signy Island (Fig. 3). Eight of these were taken as representative of the range of terrestrial habitats on the island and are described in detail in this section. Population density estimates were made for these sites from either cores or quadrats as indicated. Where two samples are mentioned these refer to the end of winter (October 1972) and the end of summer (March 1973) periods. If only a single sample was taken then this would be at the end of the summer period. The remainder of the sites sampled are described in Table VI and these include both terrestrial and aquatic habitats. Physical characteristics for all of the terrestrial sites sampled on Signy Island are presented in Table VII.

A) *Andreaea*-*Usnea* association of the fruticose lichen and moss cushion sub-formation.

This is the most common and widespread association on Signy Island and throughout much of the maritime Antarctic (Gimmingham & Smith, 1970). The site was located on a north facing slope, overlooking a cove on the western coast of the island, at an altitude of about 20 m. It consisted of a fairly extensive mixed community of *Andreaea* sp. and *Usnea* sp. overlying a mineral soil, but approximately 25% of the site was vegetation free owing to the disruptive effects of frost heaving. The moss had a maximum depth of 3 cm, although the fruticose lichen reached a height of 3–4 cm above the general

Table VI. Description of sampling sites on Signy Island, with sampling dates, used for qualitative examination.

No	Site	Date	Location	Notes
1	Andreaea sp and Usnea sp	Apr 1971	Observation Bluff	Exposed southerly slope on scree
2	" " " " "	Oct 1972	Thulla Point	Isolated on large rock, slight easterly slope
3	Unidentified crustose lichens	Aug 1972	Islets off Gourlay Peninsula	On overhanging rocks
4	Caloplaca regalis	Sep 1971	Gourlay Peninsula	Southerly cliff face, on ledges
5	Polytrichum alpestre	May 1971	Factory Cove	Small area affected by elephant seals
6	Chorisodontium aciphyllum	Oct 1972	Foca Point	Eroded moribund near giant petrel nests
7	Brachythecium subplicatum	Oct 1972	Factory Bluffs	On ledges, affected by cape pigeons
8	Calliergidium antarcticum	Feb 1973	Moraine Valley	Bordering melt stream
9	Drepanocladus uncinatus and Brachythecium sp	Mar 1964	North-west Coast	Slight north-westerly slope
10	Drepanocladus uncinatus	Mar 1971	Foca Cove	Extensive stand
11	" "	Feb 1973	Marble Knolls	Extensive discoloured stand
12	Prasiola crispa	Apr 1971	Factory Cove	In dry melt-stream channel
13	" " and unidentified lichens	Sep 1971	Gourlay Peninsula	On cliffs

Table VI. Continued.

14	Prasiola crispa	Feb 1972	Paal Harbour	Around pools (Goodman, 1969)
15	" "	Feb 1972	Factory Cove	On scree
16	" " and Drepanocladus uncinatus	Oct 1972	North Point	On rock in penguin rookery
17	Prasiola crispa and unidentified lichens	Oct 1972	North Point	As in 16
18	Prasiola crispa	Oct 1972	Gourlay Peninsula	Outside field hut
19	" "	Oct 1972	Jebsen Point	Underside of overhanging cliff
20	" "	Jan 1973	Cemetery Flats	Over moulted elephant seal hair
21	Deschampsia antarctica	Apr 1971	Observation Bluff	
22	Organic material	Feb 1972	North Point	From area around penguin rookery
23	" "	Apr 1971	Factory Cove	Disused dam built by whalers, now flooding in summer and heavily drifted in winter
24	" "	Feb 1973	Cemetery Flats	Disused wallow
25	Pool	Mar 1973	SIRS 2	Permanent standing water
26-28	Pools	Feb 1972	Paal Harbour	Fully described by Goodman (1969)
29-35	Lakes			Fully described by Heywood (1967, 1968)

Table VII. Physical parameters of the terrestrial sites on Signy Island (see text).

No	Site	Date	Wet weight (g)	Dry weight (g)	Loss on ignition (%)	Index of humidity	Moisture (%)	pH
A	<u>Andreaea/Usnea</u>	Mar 1973	17.86	5.75	52.33	2.61	-	4.5
2	" "	Oct 1972	28.02	6.45	-	3.34	-	4.5
B	<u>Caloplaca</u>	Mar 1973	8.93	3.10	-	2.32	-	-
C	SIRS 1	Mar 1973	17.13	3.34	96.64	4.22	47.79	-
6	<u>Chorisodontium</u>	Oct 1972	24.42	4.00	94.49	5.11	-	3.6
7	<u>Brachythesium</u>	Oct 1972	9.88	2.74	-	2.60	-	4.5
8	<u>Calliergidium</u>	Feb 1973	21.39	1.33	69.91	15.04	69.49	6.0
H	<u>Drepanocladus</u>	Mar 1973	21,51	3.06	-	6.80	63.91	-
11	"	Feb 1973	11.80	1.62	87.88	6.26	35.25	6.1
16	"	Oct 1973	28.83	3.99	79.34	6.23	-	4.4
D	SIRS 2	Mar 1973	23.57	1.24	93.46	19.67	77.37	5.0
E	<u>Prasiola</u>	Mar 1973	21.77	4.55	89.16	5.04	59.65	5.1
17	" and lichen	Oct 1972	6.05	4.40	66.01	0.37	-	-
18	"	Oct 1972	4.07	1.06	-	2.84	-	4.4
19	"	Oct 1972	1.05	0.66	94.70	1.27	-	-
20	"	Jan 1973	8.96	6.74	57.51	0.57	7.68	7.3
F	<u>Deschampsia</u>	Mar 1973	27.44	9.58	46.33	2.49	61.88	4.4
G	Organic material	Mar 1973	28.98	12.20	41.40	1.76	58.14	6.6
24	" "	Feb 1973	29.56	18.25	24.82	0.63	39.26	7.3

vegetation level. In summer the sub-soil was locally waterlogged from melt-water originating in snow patches higher up the slope. Two samples of twenty units were taken from this site by the quadrat method.

B) Caloplaca-Xanthoria association of the crustose lichen sub-formation.

This lichen community is common on nitrogen enriched rock faces and in large rock crevices, particularly near bird colonies. The site chosen was on Factory Bluffs. Drainage water flushed over the lichens carrying with it organic nutrients from the nests of cape pigeons (Daption capensis Linn.) at a higher altitude on the cliffs. Owing to the difficulty in sampling this habitat only five quadrat sample units were taken.

C) Polytrichum alpestre-Chorisodontium aciphyllum association of the moss turf sub-formation.

Banks of this association constitute one of the most prominant features of the vegetation on the island, and the site chosen (Figs. 20 and 21a) was one being used for a long term study of this moss community - Signy Island Reference Site (SIRS 1), (Tilbrook, 1973). The site is at a mean altitude of 53 m on the north-west slope of the knoll about 500 m south-west of Rethval Point on the Gourlay Peninsula. The two moss types occur in varying proportions ranging from pure stands to areas of co-dominance. Much of the moss surface has been colonized by epiphytic fruticose or crustose lichen, particularly on the steeper and more exposed parts of the site. An acid peat has developed beneath the mosses and this is fairly homogenous throughout its 13-32 cm depth. No permafrost layer is

Fig. 20 A small part of SIRS 1 showing areas of moss turf broken up by rock outcrops. Some residual snow patches and some examples of the strata are also shown.

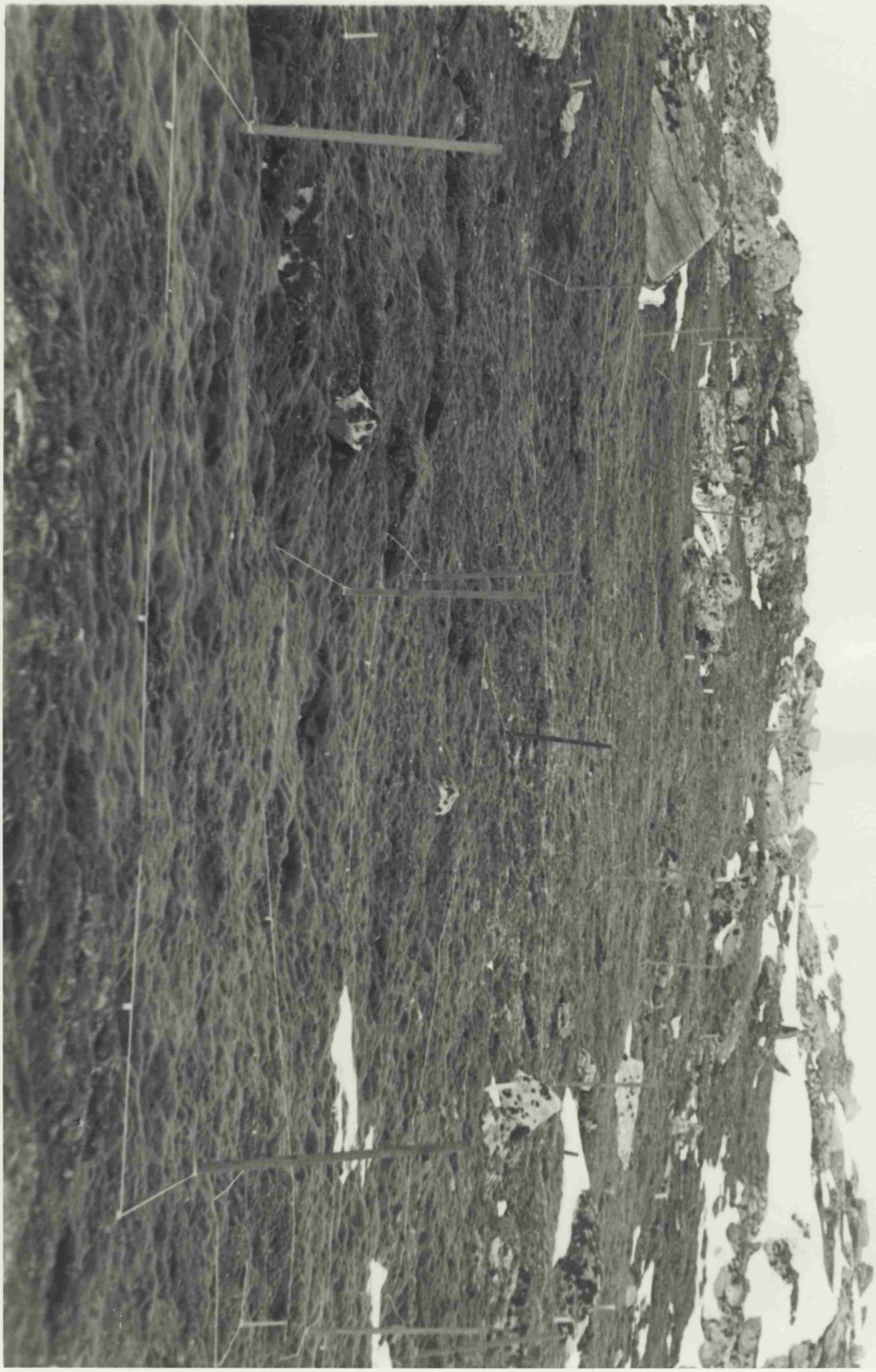


Fig. 21 Maps of the SIRS (modified from Tilbrook, 1973).

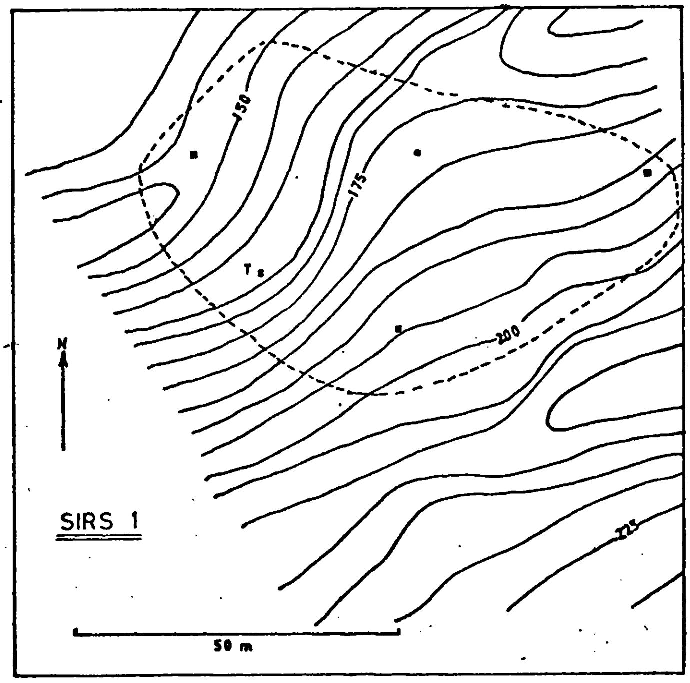
■ Location of snow depth markers

T Location of thermister probes

- - Boundary of site

Contours shown at 5 ft intervals

The portion shaded on SIRS 2 is the area used for sampling throughout this investigation.


150
175
Ts
200
225
N
SIRS 1
50 m

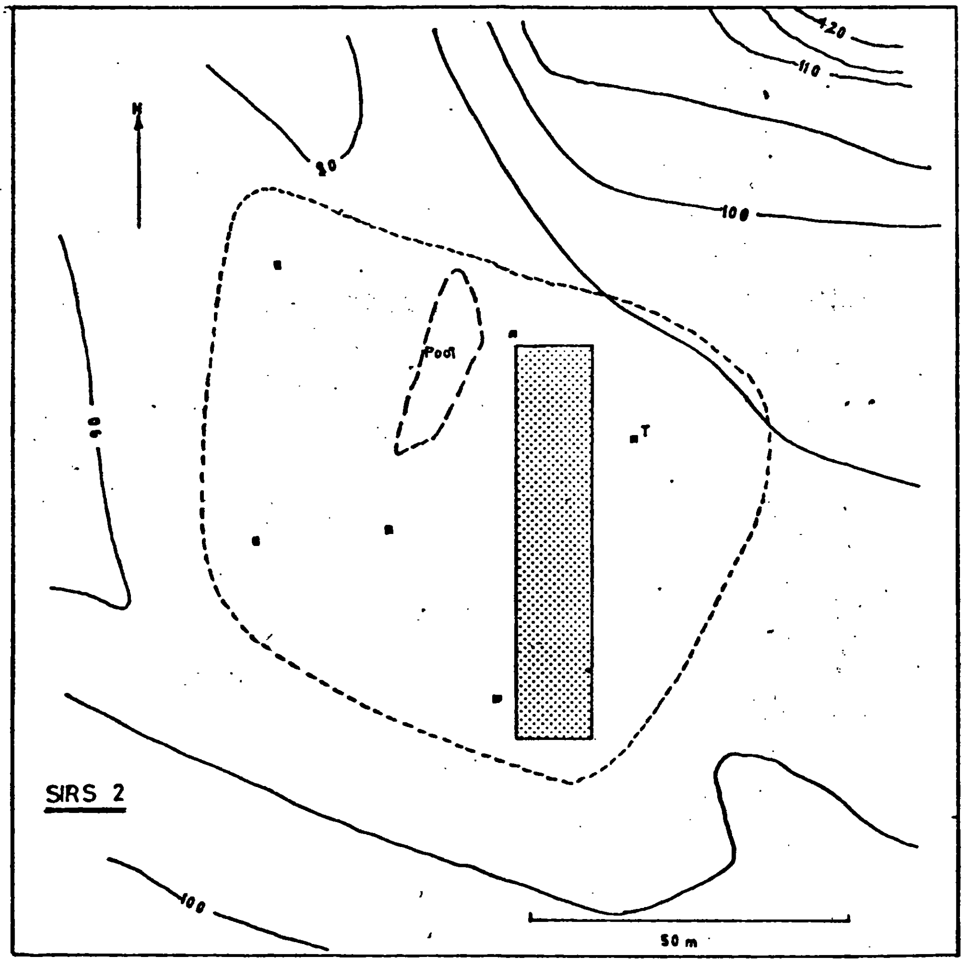

120
110
N
90
100
Pool
T
90
SIRS 2
100
50 m

Table VIII. Mean values for SIRS 1 physical characteristics (see text).

Date	Wet weight (g)	Dry weight (g)	Loss on ignition (%)	Index of humidity	Moisture (%)	pH
05-08-71	49.2	5.5	95.9	8.2	43.7	4.6
05-10-71	43.4	4.9	95.2	7.9	38.5	5.1
04-12-71	31.6	5.6	96.4	4.6	26.0	-
02-02-72	26.5	5.3	97.6	4.0	22.1	-
04-04-72	33.9	6.0	96.9	4.6	27.9	-
04-06-72	47.2	5.6	95.9	7.5	41.5	-
01-08-72	47.4	5.5	96.3	7.8	41.9	-
02-10-72	53.5	5.9	95.8	8.3	47.6	-
30-11-72	40.6	5.7	96.9	6.2	34.9	-
28-01-73	30.7	6.0	96.6	4.1	24.8	-
26-03-73	35.2	6.0	-	4.8	29.1	-

found within the peat. The upper part of the peat consists of erect stems and is usually very cohesive owing to the intertwining of a tomentum of rhizoids which is developed to within 1–2 cm of the apex of Polytrichum alpestre Hoppe stems. Below 7–10 cm the peat is less firm and consists of partially decomposed stems lying at various angles. Although well drained, the mosses and peat have a relatively high water content and this varies with depth and season (Table VIII). Twenty cores were taken at 60 day intervals from this site, giving 11 samples over the period August 1971 to March 1973 for tardigrade analysis.

D) Calliergidium–Calliergon–Drepanocladus association of the moss-carpet sub-formation.

Many permanently wet or moist habitats at low altitudes are vegetated with this mixed moss community. The site selected (Figs. 22 and 21b), SIRS 2 (Tilbrook, 1973), was situated in a shallow basin at an altitude of about 28 m on a fairly flat area inland from Lenton Point and 360 m south-west of SIRS 1. The vegetation consists of a fairly uniform carpet of Calliergon sarmentosum (Wahlenb.) Kindb. and Drepanocladus uncinatus (Hedw.) Warnst. either in small pure stands or mixed together. The leafy liverwort Cephaloziella varians (Gottsche) Steph. was found amongst the mosses and occasionally as a dense mat on the surface, which gave the site a black and moribund appearance. Around the edges of the basin there was a well defined junction between the moss carpet and a turf formed by P. alpestre and C. aciphyllum (Hook.f. et Wils.) Broth., which also locally colonize the site where the underlying rocks were near the surface. Peat had developed to a variable depth on the site, from 1 to over 30 cm, although the depth of the peat was over 6 cm on 80% of the site. The

Fig. 22 The major part of SIRS 2 showing the shallow basin with its cover of carpet-forming mosses bordered by more rocky ground interspersed with turf-forming species. A strip in the foreground between the rocks and the pools was the area used throughout this study.

site was always very wet and occasionally waterlogged (Table IX), with a semi-permanent pool present. The site was frequently crossed by groups of penguins and up to 25 non-breeding brown skuas (Catharacta lönnbergi (Mathews)) were commonly present during the summer months. Twenty cores were taken from this site at thirty day intervals, giving 22 samples over the period July 1971 to March 1973.

E) Prasiola crispa association of the alga sub-formation.

The site was situated in a shallow depression behind a beach to the south of Drying Point and consisted of a dense mat of the green foliose alga Prasiola crispa Meneghini overlying moribund moss and its associated peat. This alga is usually associated with areas contaminated by excreta from bird and seal concentrations and in this instance an elephant seal wallow was situated nearby. The peat was thin with bedrock lying only 3-4 cm below the algal layer and, locally, pools formed on the surface. Twenty cores were taken from this site.

F) Deschampsia antarctica association of the grass and cushion chamaephyte sub-formation.

Locally abundant patches of the grass Deschampsia antarctica Desv. were restricted to certain areas of the island and generally occured on north facing slopes (Edwards, 1972). The site was on a north-west facing ledge of Factory Bluffs. Grass covered an area of approximately 1 m^2, with a root depth of about 3 cm. Two samples of twenty cores were taken from this site.

G) Seal wallow material.

In an attempt to assess the effect on the tardigrade fauna

Table IX. Mean values for SIRS 2 physical characteristics (see text).

Date	Wet weight (g)	Dry weight (g)	Loss on ignition (%)	Index of humidity	Moisture (%)	pH
12-07-71	53.5	3.6	90.2	15.2	49.9	5.2
10-08-71	46.4	2.9	92.2	17.0	43.5	5.1
09-09-71	51.7	3.5	93.1	14.7	48.2	4.8
10-10-71	47.6	3.4	92.8	14.1	44.1	4.6
07-11-71	49.6	3.7	91.1	14.4	45.8	5.4
08-12-71	50.8	3.4	92.7	15.8	47.3	6.7
07-01-72	47.2	4.1	92.5	12.6	43.1	4.2
05-02-72	50.4	4.2	90.5	12.7	46.2	4.1
04-03-72	52.6	4.4	92.3	13.3	48.1	-
04-04-72	48.8	4.2	93.8	11.7	44.6	4.2
04-05-72	51.4	3.8	92.7	14.0	47.7	4.4
02-06-72	57.2	4.9	94.0	11.9	52.3	4.4
04-07-72	58.7	4.5	92.5	12.9	54.2	4.5
01-08-72	52.4	4.5	92.9	12.1	48.0	4.3
04-09-72	51.6	4.9	90.1	10.3	46.8	4.3
02-10-72	50.1	4.0	91.4	12.6	46.2	4.7
31-10-72	51.0	4.4	92.2	11.7	46.6	4.5
30-11-72	66.8	4.4	92.7	15.6	62.4	4.3
30-12-72	50.7	4.8	93.4	10.3	45.9	4.6
28-01-73	62.0	7.7	93.4	11.5	54.3	4.5
28-02-73	56.9	4.3	92.5	13.5	52.6	5.0
26-03-73	48.2	3.4	-	14.3	44.8	-

of high concentrations of nitrogen and phosphorus waste from seals (Allen et al., 1967), an area of fine water-borne mud on the beach just to the south of Drying Point was sampled. The site was intermittently flooded and recieved large amounts of run-off from a nearby elephant seal wallow. Also present on the site was a large number of decomposing oak barrel staves discarded by whalers who worked on the island before pelagic whaling became widely adopted in 1930 (Marr, 1935). A sample of twenty cores was taken from this site.

H) Moss affected by penguins.

Stands of various species of mosses were present above the rookery area on the Gourlay Peninsula. An extensive area of pure D. uncinatus was chosen, on which, at the time of coring, several chinstrap penguins (Pygoscelis antarctica (Forster)) were found. The whole area was heavily marked with droppings and covered with a layer of moulted feathers, although no evidence was found of the disruptive effects of trampling. The site was on a slope with an easterly aspect and at an altitude of approximately 20 m. A sample of twenty cores was taken from this site.

4.12 Sites in other areas

During the austral summer of 1973 the opportunity arose to sample at locations on the Antarctic Peninsula and the islands in Marguarite Bay. The sites chosen were representative of the area and as far as possible were similar in composition to the sample sites previously selected from Signy Island. Owing to circumstances beyond my control all of these samples were lost and arrangements for collection of replacement material were made for the following summer season. This material was transported frozen to the United Kingdom for analysis. Wherever six cores had been taken, a population density estimate was made. However, much of the material was not cored and only qualitative examination was possible. In addition to this collection, material was available from previous studies on the micro-organisms, nematodes and micro-arthropods of the region, but here again only qualitative analysis was possible. In all 70 sites were investigated, the descriptions of which are summarized in Table X, and physical characteristics of the sites are tabulated in Table XI; sites may be located on maps 1 and 2 in the back cover.

4.2 Measurement of environmental factors

During the period of this study a number of environmental parameters were recorded:-

i) pH measurements were made in the laboratory, using a portable meter, on fresh material only.

ii) Wet weight, to the nearest mg, was measured on all quantitative sampling units.

iii) Dry weight, to the nearest mg, was measured after drying to constant weight at 105°C.

iv) Loss on ignition was measured from a sub-sample ashed to constant weight at 550°C.

v) Moisture content, from wet and dry weights, was expressed in two ways:

(a) An index of humidity was given by: $I.H. = \frac{\text{water content}}{\text{dry weight}}$

(b) % by volume where the initial sample volume was known, given by:

$$V = \frac{\text{water content}}{\text{sample volume}} \times 100$$

vi) Floristic composition was recorded for each sample unit.

Climatic data for the areas involved in this study were obtained in a number of ways. Air temperatures outside the British

Table X. Location, vegetation and notes on the tardigrade sampling sites of the Antarctic Peninsula and Scotia Ridge region. Sample collection was made by I.B. Collinge unless otherwise indicated.

Details	No	Vegetation	Notes
South Georgia (King Edward Point)	1	*Juncus scheuchzerioides*	South slope, very wet
54°17'S., 36°30'W.		*Tortula robusta*	
April 1974	2	*Poa flabellata*	Steep slope
	3	*Poa flabellata*	Small knolls affected by seals
	4	*Festuca erecta*	Well drained area
		Polytrichum alpestre	
		Chorisodontium aciphyllum	
	5	*Polytrichum alpestre*	Large stand on level ground
		Chorisodontium aciphyllum	
	6	*Polytrichum alpestre*	Understorey to *Rostkovia magellanica*. Very wet
		Cladonia rangiferina	
		Barbilophozia sp.	
	7	*Tortula robusta*	Understorey to *Acaena decumbens*. Dry
Candlemas Island	8	*Polytrichum* sp.	Away from fumeroles
57°03'S., 26°40'W.	9	*Polytrichum* sp.	Influenced by fumerolic heat
March 1964	10	*Pohlia* sp.	Away from fumeroles
Collected by P.J. Tilbrook	11	*Pohlia* sp	Influenced by fumerolic heat
Munroe Island 60°36'S., 46°03'W.	12	*Drepanocladus* sp.	
Lynch Island 60°39'S., 45°36'W.	13	*Brachythecium* sp.	
	14	*Prasiola crispa*	
Gosling Island 60°39'S., 45°55'W.	15	*Drepanocladus* sp.	
Laurie Island 60°44'S., 44°37'W.	16	*Drepanocladus* sp.	
February 1971			
Collected by H.G. Smith			

Table X. Continued.

Elephant Island	17	*Deschampsia antarctica*	Soil from level ground
61°10'S., 55°14'W.	18	*Deschampsia antarctica*	North slope on moraine
March 1971	19	*Deschampsia antarctica*	Easterly slope
Collected for V.W. Spaull	20	*Deschampsia antarctica*	Level ground
	21	*Drepanocladus uncinatus*	
King George Island (Fildes Peninsula)	I	*Drepanocladus uncinatus*	Level ground
62°12'S., 58°58'W.	22	*Polytrichum alpinum*	West slope
April 1974	23	*Prasiola crispa*	Near Giant petrel nest
Deception Island	24	*Prasiola crispa*	On boulder
62°57'S., 60°38'W. April 1974			
Intercurrence Island	25	*Brachythecium austro-salebrosum*	North slope
63°55'S., 61°24'W. January 1969		*Bryum algens*	
Collected for V.W. Spaull		*Drepanocladus uncinatus*	
Torgersen Island	J	*Deschampsia antarctica*	North slope. Penguin rookery nearby
64°46'S., 64°05'W. March 1974			
Litchfield Island	K	*Chorisodontium aciphyllum*	North slope
64°46'S., 64°06'W. March 1974	L	*Calliergidium* cf *austro-stramineum*	Level ground
Galindez Island	26	*Deschampsia antarctica*	Level ground
65°15'S., 64°15'W.	M	*Polytrichum alpestre*	North-west slope
April 1974	27	*Drepanocladus uncinatus*	In slight hollow. North facing slope
		Pohlia nutans	
	N	*Calliergidium* cf *austro-stramineum*	North slope
Blaiklock Island	28	*Deschampsia antarctica*	West to north-west slope
67°33'S., 67°04'W.	29	*Polytrichum alpinum*	Near melt stream
March 1974		*Pohlia nutans*	
		Cephaloziella sp.	
	30	*Polytrichum alpinum*	Under old dog spans on level ground
	31	*Bryum* sp.	West to north-west slope
		Drepanocladus uncinatus	

Table X. Continued.

Adelaide Island (Rothera Point) 67°34'S., 68°08'W. April 1974	32	Drepanocladus uncinatus	North facing rock clefts
Lagoon Island 67°35'S., 68°16'W. April 1974	33	Deschampsia antarctica	North slope
	34	Andreaea depressinervis	South slope
Limpet Island 67°38'S., 68°18'W. February 1969 Collected for V.W. Spaull	35	Brachythecium austro-salebrosum	South-east rock terrace
	36	Drepanocladus uncinatus	South-east rock terrace
Avian Island 67°46'S., 68°54'W. April 1974	37	Drepanocladus uncinatus Bryum algens	North-east slope
	O	Drepanocladus uncinatus	North facing crevices. Penguin rookery nearby
	P	Drepanocladus uncinatus	Level ground near pond
	38	Brachythecium sp.	
	39	Prasiola crispa	As in O
	40	Lecania brialmontii	As in O
Horseshoe Island 67°51'S.67°12'W. March 1974	41		Site not known
	42	Bare soil	From lake side
	43	Usnea sp.	North rock faces
	44	Lecania brilmontii	North rock faces
Consort Islands 67°52'S.68°42'W.	45		Site not known
Emperor Island 67°52'S., 68°43'W. February 1969 Collected for V.W. Spaull	46	Drepanocladus uncinatus Bryum algens	Exposed rock ledge
Barbara Island 68°08'S., 67°06'W. March 1974	47	Ceratodon sp.	North-west slope of rock outcrop
	48	Prasiola crispa	As in 47
	49	Alectoria miniscula	As in 47
	50	Physcia sp.	As in 47

Table X. Continued.

Stonington Island 68°11'S., 67°00'W. March 1974	51	*Prasiola crispa*	Rock crevices in base area
Neny Island 68°12'S., 67°03'W. March 1974	52	*Colobunthus quitensis*	North-west slope of knoll, dominican gull nest nearby
	53	*Deschampsia antarctica*	As in 52
	54	*Grimmia* sp.	
	55	*Ceratodon* sp.	As in 52
	56	*Prasiola crispa*	As in 52
	57	*Usnea* sp.	As in 52
Terra Firma Islands 68°42'S., 67°32'W. February 1969 Collected for V.W. Spaull	58	*Cephaloziella* sp. *Pohlia nutans*	On bare granite, west slope
Alexander Island (Ablation Point) 70°48'S., 68°22'W. February 1974 Collected by R.B. Heywood	Q	*Bryum* sp., *Campylium* sp.	Wet. North slope
	59	*Bryum* sp., *Campylium* sp.	Wet. North slope
	60	*Bryum* sp., *Lepraria neglecta*	Wet. North slope. Moribund appearence
	61	*Bryum* sp. *Didymodon gelidus* *Encalypta procera* *Distichium capillaceum*	Wet. Level ground. Near skua nest

Table XI. Physical parameters of sites on the Antarctic Peninsula and Scotia Ridge.

No	Location	Wet weight (g)	Dry weight (g)	Index of humidity	Moisture (%)
1	South Georgia	12.62	1.27	8.92	39
2	" "	11.12	3.48	5.12	26
3	" "	25.87	6.50	3.02	67
4	" "	19.99	7.90	2.63	41
5	" "	11.87	2.45	3.92	33
6	" "	6.58	1.45	3.53	17
7	" "	18.11	3.01	5.24	53
22	King George Island	9.64	3.06	2.15	23
I	" " "	12.55	1.74	6.24	38
23	" " "	13.99	8.66	0.75	-
24	Deception Island	4.75	3.90	0.22	-
J	Torgersen Island	12.61	2.84	3.59	34
K	Litchfield Island	10.53	3.16	2.32	25
L	" "	16.86	0.81	21.01	58
26	Galindez Island	14.93	3.93	2.80	-
M	" "	18.06	5.43	2.40	44
N	" "	14.61	1.58	8.35	47
28	Blaiklock Island	30.82	20.05	0.54	-
30	" "	14.82	11.67	0.27	-
31	" "	32.31	15.39	1.10	-
32	Adelaide Island	15.76	2.06	6.65	-
33	Lagoon Island	34.16	8.00	3.27	-
34	" "	7.70	2.00	2.82	-
O	Avian Island	10.33	1.03	8.17	33
P	" "	13.59	1.55	7.86	44
39	" "	2.68	1.16	1.31	-
40	" "	5.97	4.23	0.41	-
42	Horseshoe Island	30.13	27.58	0.09	-
43	" "	2.55	2.29	0.12	-
44	" "	7.38	5.43	0.37	-
47	Barbara Island	11.87	9.12	0.30	-
48	" "	6.32	2.33	1.71	-
49	" "	0.87	0.86	0.01	-
50	" "	2.50	2.27	0.10	-
52	Neny Island	16.06	10.55	0.52	-
53	" "	9.09	5.34	0.70	-
55	" "	62.75	41.91	0.50	-
56	" "	23.67	19.25	0.32	-
57	" "	8.89	7.97	0.11	-
59	Alexander Island	32.60	5.17	5.33	95
60	" "	20.87	12.62	0.64	28
61	" "	26.93	4.88	4.51	76
Q	" "	24.80	6.00	3.77	65

Antarctic Survey's biological laboratory on Signy Island were recorded continuously, as was the duration of bright sunshine, over the whole of the study period. From January 1972, air temperature, moss surface temperature and moss temperatures at 1.5, 4.5, 7.5 and 10.5 cm depth were recorded at two sample sites on Signy Island together with incident solar radiation. Snow depth at these two sites was also monitored throughout the study. Data from other areas has been obtained by the British Antarctic Survey since 1947, and a summary of this information in the period 1963-72 is given in Fig. 2.+ 2.8

4.3 Sampling methods

It was known at the outset of this study that two different methods of field sampling would be required, one for the summer and one for the winter season. Using experiance gained in previous studies (Baker, Smith, Spaull & Tilbrook, pers. comm.) two corers were produced, each having a cross-sectional area of 1/1,000 m^2 (approx. 3.5 cm circular diameter). One of these corers, however, proved inadequate for some of the wetter substrates. For this reason, all coring during the summer (thaw period) was accomplished using a dual corer/canister as used by Capstick (1959).

4.31 Summer sampling

The corer/canisters were simple open ended aluminium tubes, which had been sharpened at one end to give a cutting edge for coring. By inserting a rubber bung at one end and replacing a water-tight cap at the other, these corers were easily transformed into transportation canisters. Most cores were taken to a depth of 6 cm (see section 6) and these were divided into 3 cm deep horizons for extraction. To avoid water loss it was found necessary to take the cores in two halves (Fig. 23). The equipment used for summer sampling is illustrated in Fig. 24.

4.32 Winter sampling

Between April and December–January all moss in the study areas was frozen and, clearly, different sampling equipment was required (Fig. 25). Up to 0.5 m of snow and ice was sometimes present on the sample sites, and this had to be excavated using an ice-axe, pick-axe or shovel. Care was needed to prevent any damage to the moss surface, and after coring as much snow as possible was returned to the hole, but considerable disruption was inevitable particularly when collecting the samples immediately preceding the melt. The corer consisted of a steel tube bearing a number of hardened teeth at one end. Between July 1971 and December 1971 this corer was driven by a conventional hand brace with a modified chuck. From April 1972 to January 1973 an electric drill was available for use, powered by a portable generator. Cores were taken in one 6 cm piece, and were sub-divided later in the laboratory while still frozen.

4.33 Sampling at other times

Although autumn and spring are not usually recognised in the Antarctic, some rapid changes in climatic conditions were evident at the major freeze toward the end of summer and thaw at the end of winter. During these periods the moss was often frozen in layers, which led to great difficulty in coring. During the melt, a large quantity of free water was often trapped in the snow; on one sampling occasion coring had to be accomplished through 30 cm of water which filled the snow hole as fast as the snow was excavated. A variety

Fig. 23 Summer coring method:-

a) Corer pressed 3 cm into the moss.

b) Small hole excavated to one side of the corer and a knife slid across the base, cutting through the peat.

c) Process repeated for 3-6 cm horizon using a longer corer.

d) Corer acting as transport canister for upper 3 cm core.

e) Corer acting as transport canister for lower 3 cm core.

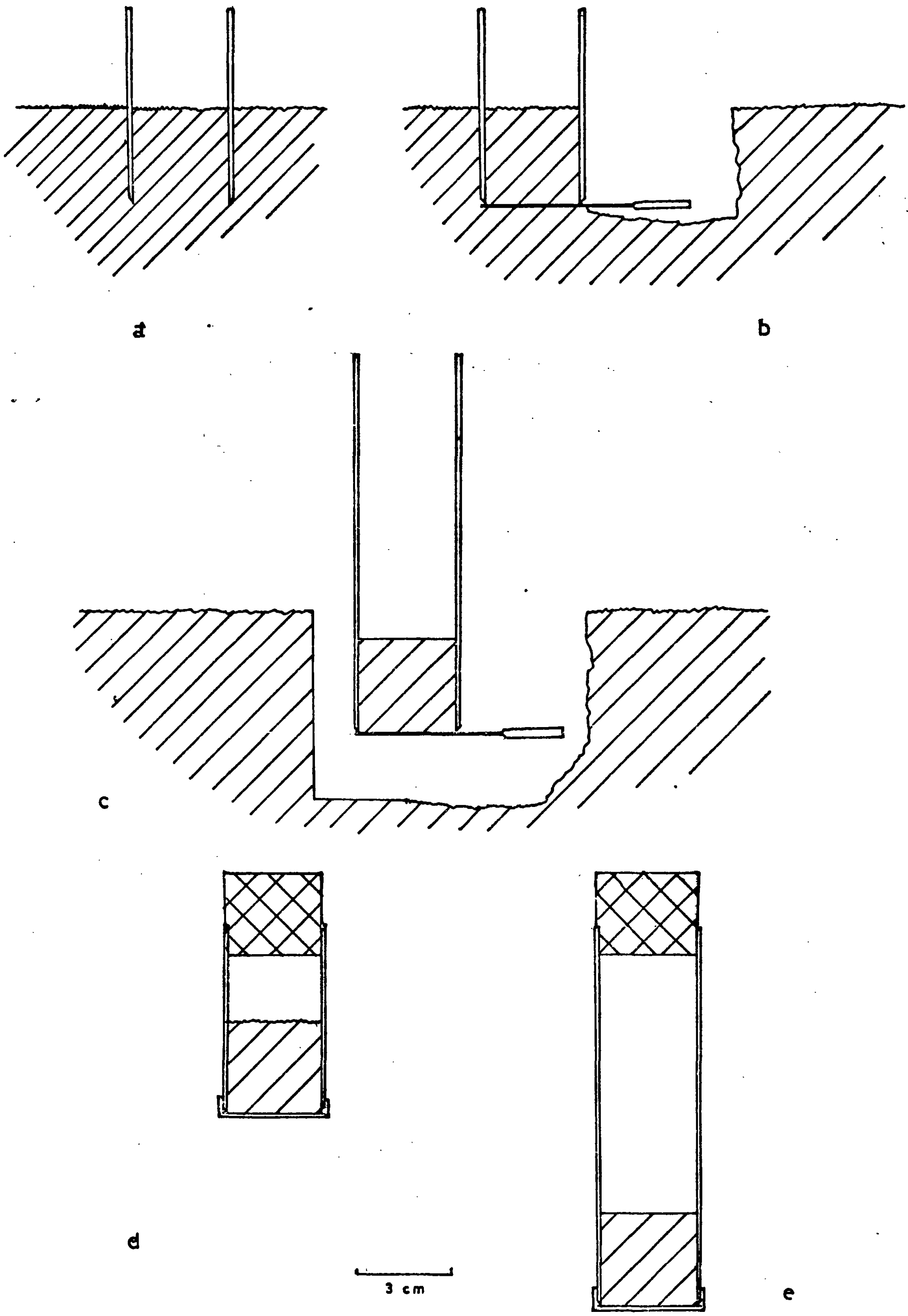

a
b
c
d
3 cm
e

Fig. 24 Summer sampling equipment.

a) Conventional corer

b) 0–3 and 3–6 cm horizon corers

c) Corers converted to transportation canisters

d) Polythene core hole markers (see section 6.31)

e) Plunger for recovery of core from corer

f) Knife for cutting peat and sliding across base of corer

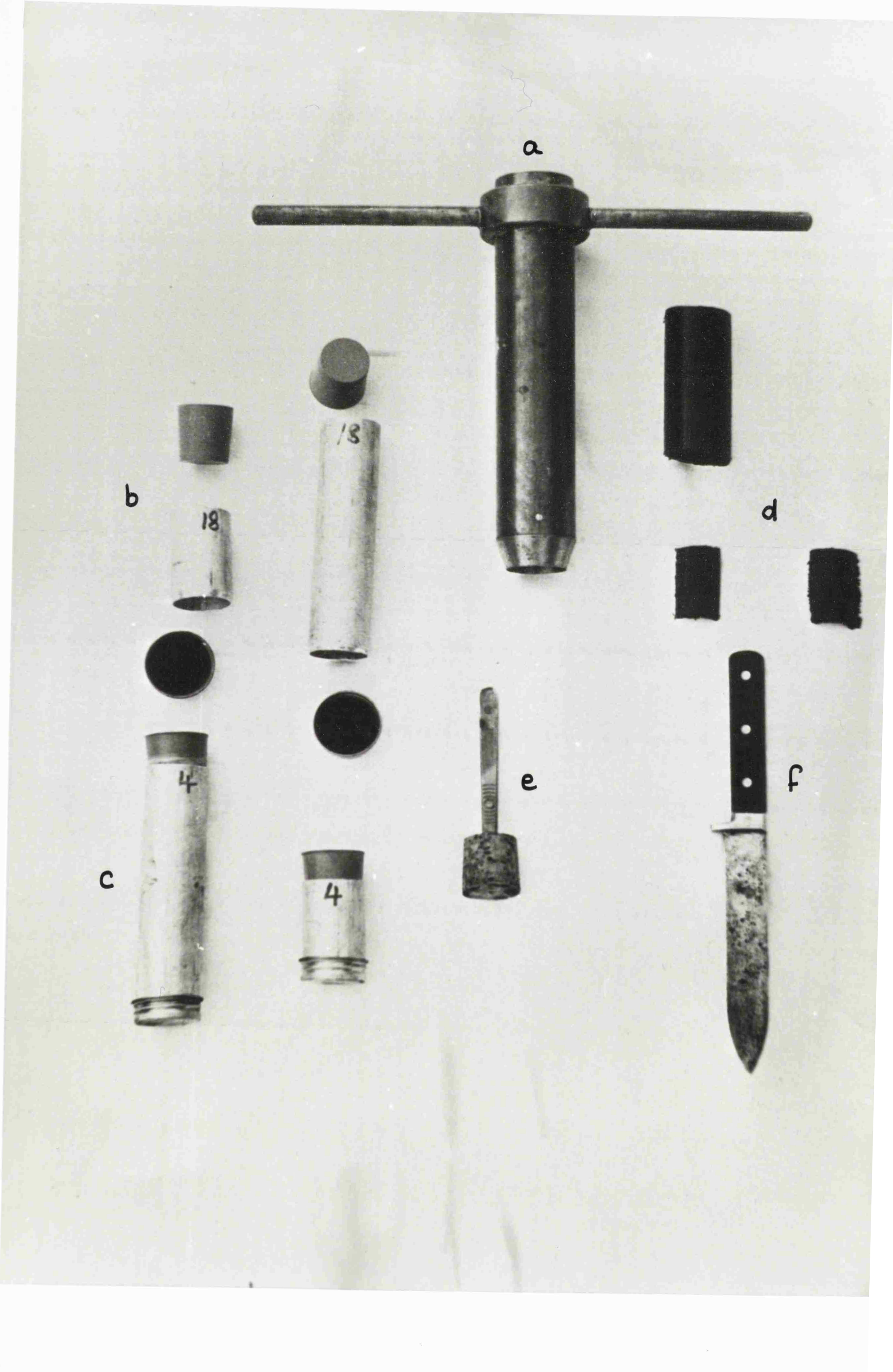

a
b
18
18
d
c
4
4
e
f

Fig. 25 Winter sampling equipment.

a) Power drill for driving corer in 1972 winter

b) Chuck key for power drill

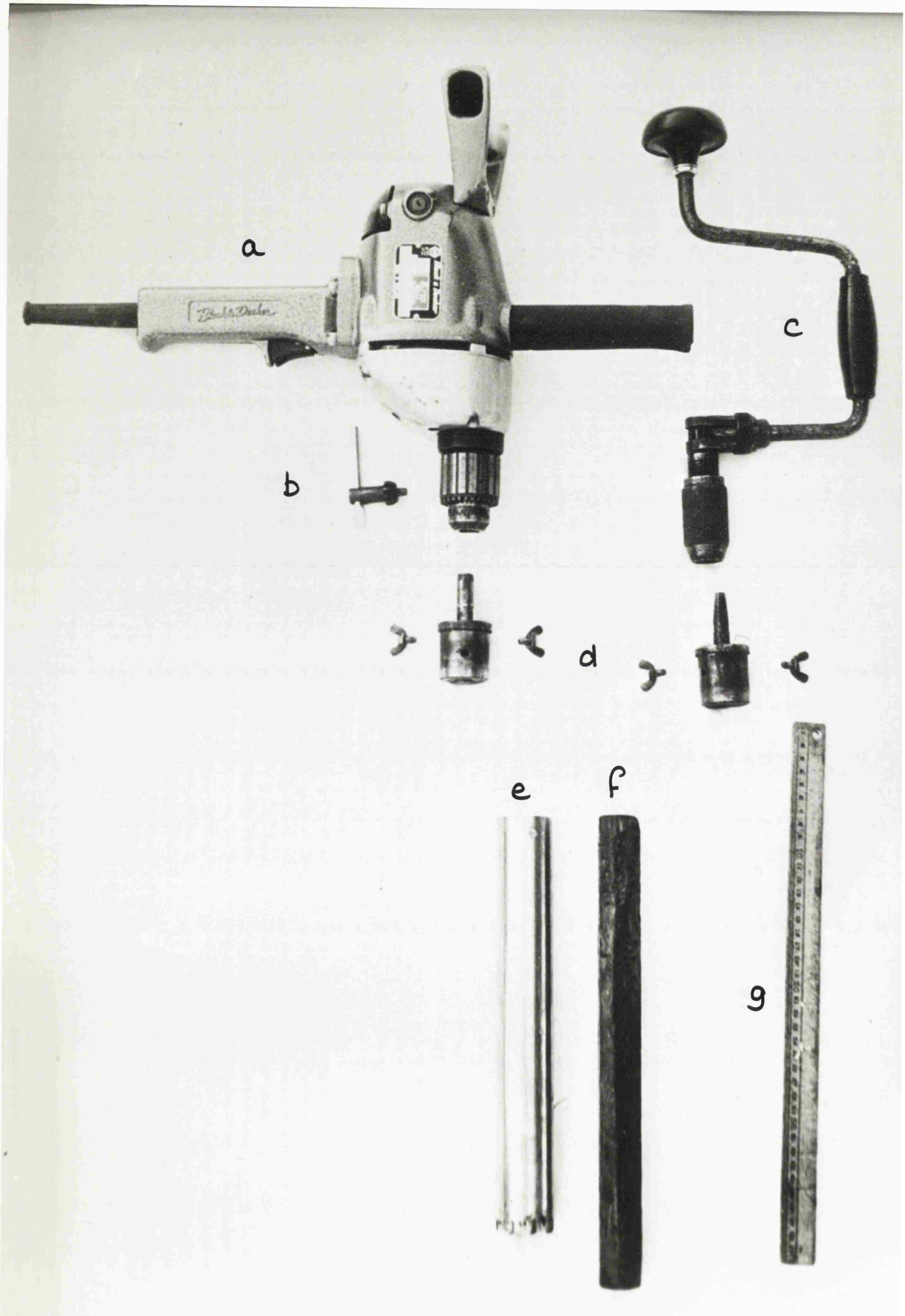
c) Hand brace for driving corer in 1971 winter

d) Modified chucks for power drill and hand brace

e) Winter corer with hardened teeth

f) Plunger for recovering core from corer

g) Rule


a
b
c
d
e
f
g

of equipment was required at these times of the year, none of which were ever entirely successful.

4.34 Qualitative and quadrat sampling

For certain habitats coring was not an acceptable method of sampling (e.g. where the substrate was less than 3 cm deep) and on these occasions a quadrat was used, having sides of 5 cm length. All vegetation within this quadrat was collected by hand and formed the sampling unit. When quantitative samples were not required, a piece of substrate was simply scooped-up by hand and transported to the laboratory for analysis.

4.4 Quantitative examination

4.41 Extraction

At the onset of this study no generally acceptable method of extraction was available for the Tardigrada. Consequently, a test was carried out on three methods known to be efficient for the extraction of a closely related group, the Nematoda, to determine the most appropriate method for the faunal components under study. These three methods were:-

i) Wet funnel (Baermann, 1917).

ii) Seinhorst mistifier (Seinhorst, 1950).

iii) The tray method, a modified Baermann funnel (Whitehead & Hemming, 1965).

For each method, two cores from a D. uncinatus moss carpet were extracted simultaneously for 12 h. The total number of Tardigrada extracted from the two cores by the wet funnel was only 19 (8 and 11). It had been claimed previously that this method was not efficient for the extraction of Tardigrada (Overgaard, 1948). The Seinhorst method yielded higher numbers (135 and 481), but by far the greatest numbers were recovered by the modified Baermann funnel (750 and 1320). It may be that with certain substrates, a combination of the latter two methods may provide a more efficient extraction process, but the fine mineral and peat fragments common to most Signy Island substrates would have been washed into the final extract in unacceptable quantities, so making sorting and counting extremely difficult. Despite the low replication, on the basis of these findings, the tray method was used thereafter. Hallas (in press) has developed a mechanical extraction process as an alternative to the tray method. The method appears to work at least as efficiently as the tray method, and it has the added advantage of recovering the moulted tardigrade cuticles, some of which may contain eggs. The eggs of Macrobiotus are not extracted because their processes adhere very efficiently to the substrate.

The tray method was originally employed for the extraction of active Nematoda and has been fully described by Whitehead & Hemming (1965). It also appears to work successfully for the Tardigrada and Rotifera, and has been used in a slightly modified form for a quantitative study of the Tardigrada in forest soils by Hallas & Yeates (1972). In the present study, 22 by 36 cm plastic seed trays, each of which contained a flat nylon mesh sheet ("Netlon" - 5 mm mesh) supporting a double ply tissue ("Kleenex Mansize"), were used. The substrate sample unit was teased onto the tissue and distilled water added (approximately 250 ml) until it just covered the mesh. After extraction the water in each tray was rinsed into stoppered bottles and stored at 7^{o}C until the contents were either analysed or preserved. The substrate and tissue were retained to obtain dry and ashed weights.

In order to determine a suitable extraction period, six cores were left for four days and counts were made of the Tardigrada extracted at 12 h intervals. The number of animals extracted after 96 h did not represent the total population at the onset of the experiment. This was because the extractor relies on the activity of the animals and only after an infinite time will they all have moved 'down' out of the moss. It was therefore necessary to derive a figure for the total population to assess extraction efficiency. One estimate of the initial population was based on maximum likelihood (Moran, 1951) originally developed for estimating total population levels of a finite population from trapping data. This method involved the following assumptions concerning the population:-

i) That the probability of any animal being extracted remained constant throughout the experiment.

ii) That the population was static (i.e. with no mortality or natality).

iii) That the chance of extraction was equal for each individual.

An alternative approach was the empirical method of Skellam (1962), where the data were transformed ($y = \log_{10}$ number extracted, $x = b/(b + \text{time})$, where b was arbitrary) so that estimates of the initial population were read directly from the intercept. These two approaches have been used to estimate the total population for each faunal component in this study (Table XII) and there is close agreement between them. Using both estimates the percentage extracted after 12, 48 and 96 h have been calculated. Although a greater number were extracted after 96 h, more water had to be added after two days to replace evaporative losses, and this inevitably washed detritus into the extractant. It was decided, therefore, to use an extraction period of 48 h for all subsequent work.

Table XII. Comparison of the total extractable populations of Tardigrada predicted by the maximum likelihood estimate (M.L.E.) of Moran (1951), and the empirical method of Skellam (1962). Percentage extraction after 24, 48 and 96 h. has been calculated for each method.

	Total numbers			% extracted from predicted population					
	observed	predicted		M.L.E.			empirical		
	after 96 h	M.L.E.	empirical	24 h	48 h	96 h	24 h	48 h	96 h
Hypsibius sp.	2011	2216	2780	47	69	91	37	55	72
Macrobiotus sp.	316	356	398	39	70	89	35	63	79
Echiniscus sp.	21	24	22	38	67	88	41	73	95

Hallas & Yeates (1972) tested their extraction efficiency by introducing a known number of Tardigrada into autoclaved soil. They recovered 87% in 24 h. This is much higher than the figure found in the present study, although their result is not directly comparable since they used a different substrate which had been homogenised prior to extraction. It may also be significant that they used only 69 tardigrades in their experiments, in a substrate which bears little resemblance to natural conditions, whereas over 2,000 tardigrades were extracted from fresh substrate in the present study.

It was considered that the three assumptions required by the maximum likelihood estimate held true for the Tardigrada. Therefore, all tardigrade densities reported in this study have been increased by 30%, since this method predicts about a 70% extraction in 48 h for the three genera of Tardigrada investigated.

It was noted during counting that at laboratory temperatures above 15°C the tardigrades became less active and often formed tuns (reducing their surface area by assuming a short barrel shape), although during the summer months the temperature at which this occurred was often exceeded in the mosses of Signy Island. Ambient temperatures during extraction, however, never exceeded this level.

4.42 Identification and counting

It was possible to identify most of the tardigrade species found in this study during counting. Two species groups were not resolved,however, because of the difficulty of separation at low magnification; these were E. (E.) capillatus + E. (E.) meridionalis and H. (D.) alpinus + H. (D.) pinguis.

Counting was started immediately after extraction (taking an average of two weeks to complete), or the sample was preserved in 10%

formalin for analysis at a later date. There was no evidence that the tardigrade composition changed appreciably during any period of storage. Four eggs of H. (D.) pinguis which were isolated from a freshly extracted sample unit into a hanging drop took just over one month to hatch at the storage temperature of $7^{o}C$. All dead animals were counted in the extracts.

Aliquots of 5 ml were pipetted into a counting cell made from a plastic disposable petri-dish (Fig. 26) - a modification of the Sedgwick-Rafter cell as used by Pennak (1940) and Arora (1966). Counts were made at low magnification with a compound microscope (x45, or for difficult specimens, x150).

Population estimates for sites A, F and G were obtained by counting five successive 5 ml aliquots from a bulked sample of five extracted sample units. The estimate of sampling variance obtained in this way was comparable with that obtained by counting each unit individually, but the mean was calculated from only four independent estimates (in a sample of 20 sampling units) and much information on the spatial dispersion of the population was lost. For all other sites, therefore, either a single 5 ml aliquot of each sample unit, or the entire sample unit, was counted.

The counting procedure relied on a number of assumptions which may or may not hold true for each of the components under study:-

i) That the animals in each sample unit prior to sub-sampling conform to a Poisson distribution. This was tested by taking successive sub-samples from each unit, calculating the variance to mean ratio, and applying a χ^2 test. Results were well within the 5% confidence limits for the faunal components in this study.

ii) That the organisms are immobile in the counting tray. This held true for the Tardigrada when separated from their normal substrate.

Fig. 26 Dish used for rotifer and tardigrade counts (modified Sedgwick-Rafter cell).

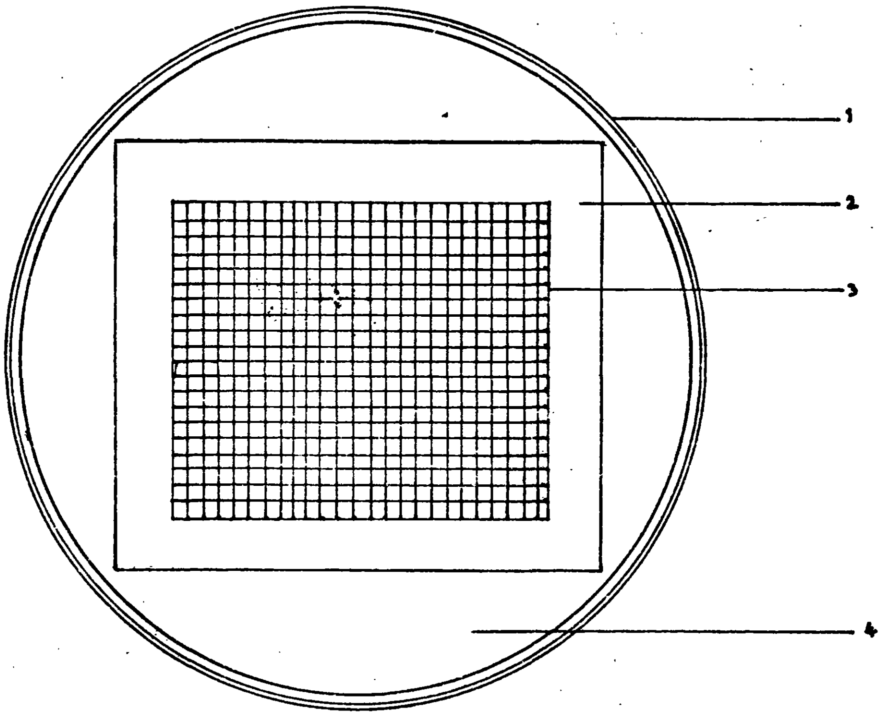
1 Base of cell made from lid of petri-dish

2 Plastic spacer (2.5 mm thick) cemented to the base

3 Base scored into squares having an area less than the field of view at x10

4 Cover slip made from base of petri dish

Actual size shown


1
2
3
4

iii) That the animals extracted have been recorded regardless of size, shape or colour. Although an attempt was made to reduce detritus to a minimum in the extracted samples, a few were so contaminated that some smaller individuals may have been overlooked. Animals in the genus Echiniscus posed their own problems in that their coloration, shape and sluggish movements always made them difficult to distinguish from microscopic particles of plant material.

4.43 Biomass estimation (see also section 6.42)

Biomass was estimated by the method used by Hallas & Yeates (1972). All Tardigrada were taken to have a density of 1.04, and except for Echiniscus were assumed to be cylindrical. A weight for each specimen was obtained by:-

$$\text{Weight} = \text{Length} \times \pi \times \left(\frac{\text{Length}}{2 \times R}\right)^2 \times 1.04 \times 10^{-6}\ \mu g$$

where R was the ratio of length to width.

The shape of Echiniscus was assumed to be half a prolate spheroid. The weight was given by:-

$$\text{Weight} = \frac{1}{12} \times \text{Length} \times \pi \times \left(\frac{\text{Length}}{R}\right)^2 \times 1.04 \times 10^{-6}\ \mu g$$

The ratios measured and mean weight calculated for each species are given in Table XIII.

4.5 Qualitative examination

Many sites were investigated where coring techniques were not applicable, or where too few cores were taken to permit statistical analysis, and thus no population density estimates are available. Here the samples were either extracted and counted in the normal way, or were washed from the moss into a counting tray. The extracted animals were later removed with a fine capillary under a dissecting microscope (x12) for permanent mounting. Two mountants

Table XIII. Mean ratio length:width, and mean animal weights used in the estimation of tardigrade biomass.

Species	L:W ratio	weight (ug)
Oreella mollis	3.7	0.034
Echiniscus (Echiniscus) capillatus -		
Echiniscus (Echiniscus) meridionalis	1.9	0.727
Macrobiotus furciger	4.3	4.301
Hypsibius (Hypsibius) dujardini	3.0	1.400
Hypsibius (Hypsibius) oberhaeuseri	3.6	1.145
Hypsibius (Isohypsibius) asper	2.4	5.750
Hypsibius (Isohypsibius) renaudi	2.9	3.072
Hypsibius (Diphascon) alpinus -		
Hypsibius (Diphascon) pinguis	2.5	1.076
Hypsibius (Diphascon) chilenensis	3.3	0.721
Hypsibius (Diphascon) puniceus	2.5	1.193
Hypsibius (Diphascon) scoticus	3.6	2.515
Milnesium tardigradum	3.4	26.604

polyvinyl lactophenol with 1% cotton blue and Hoyers medium, were used throughout this study. Results with the lactophenol were initially good for the more robust specimens, which maintained much of their internal structure for some time, although eyespots disappeared immediately. Later, however, the specimens tended to deform, becoming almost completely clear during this process. With Hoyers medium the tardigrades cleared almost immediately but retained their eyespots. Shrinkage also occured, but the animals then regained some of their original shape as the mountant dried. Both these methods had the advantage of requiring no pre-treatment of either living or preserved material before mounting. The relative abundance of each faunal component was then estimated from the slides.

SECTION 5: DISTRIBUTION AND POPULATION STUDIES

5.1 Distribution and density of the Antarctic Tardigrada

Forty three sites were investigated from Signy Island and a further 70 from other locations on the Scotia Ridge and Antarctic Peninsula. From these 113 sites, 5 genera and 17 species of Tardigrada were recovered (Tables XIV and XVIII). From all the sites where more than ten specimens were recovered, a figure for the percentage occurrence of each species has been given. Clearly greater confidence can be held in the percentages where the number of specimens exceeds 100, than in those where only a few specimens were recovered.

5.11 The distribution of the Tardigrada on Signy Island

Two species and one species-group stand out as being very widespread on Signy Island, these are M. furciger, H. (H.) dujardini and H. (D.) alpinus + H. (D.) pinguis. All of these occurred in both the terrestrial and aquatic habitats. The habitat preferences of each tardigrade species became more apparent when the data were grouped according to habitat type (e.g. vegetation sub-formation, organic material, pools and lakes) in Table XV. There was some indication that organic waste from seals and birds increased the species diversity and population density of Tardigrada. The foliose alga Prasiola crispa had the most diverse fauna, with ten of the 15 species and species-groups represented. Two components were present in high proportions in all habitat groups of Table XV. These are H. (H.) dujardini and H. (D.) alpinus + H. (D.) pinguis. The next most abundant species was M. furciger which occurred in six of the nine habitat types (E. (E.) capillatus + E. (E.) meridionalis and H. (D.)

Table XIV. The distribution and percentage occurrence of 14 species/species-groups of Tardigrada in 43 samples from Signy Island. Sites may be located in Fig. 3. (þ is given where percent occurrence was less than 1%, or where total tardigrade recovery was less than 10 individuals).

		Date	Oreella mollis	Echiniscus sp.	Macrobiotus ambiguus	Macrobiotus furciger	Hypsibius (H.) dujardini	Hypsibius (I.) asper	Hypsibius (I.) renaudi	Hypsibius (I.) papillifer	Hypsibius (D) alpinus-pinguis	Hypsibius (D.) chilenensis	Hypsibius (D.) sp.	Hypsibius (D.) puniceus	Hypsibius (D.) scoticus	Milnesium tardigradum	Total number of specimens	Number of species per site
A	Andreaea sp./Usnea sp.	Mar 73	1	1	-	þ	54	-	-	-	42	-	-	þ	1	-	4436	7
1	Andreaea sp./Usnea sp.	Apr 71	-	-	-	21	-	-	-	-	74	5	-	-	-	-	21	3
2	Andreaea sp./Usnea sp.	Oct 72	-	-	-	5	-	-	-	-	91	-	-	4	-	-	80	3
3	Crustose lichens	Aug 72	-	-	-	-	-	-	100	-	-	-	-	-	-	-	17	1
B	Caloplaca	Mar 73	-	2	-	-	36	-	-	-	-	-	-	-	-	62	85	3
4	Caloplaca	Sep 71	-	-	-	-	-	-	-	-	100	-	-	-	-	-	25	1
5	Polytrichum	May 71	-	-	-	þ	þ	-	-	-	þ	-	-	-	-	-	8	3
6	Chorisodontium	Oct 72	-	-	-	þ	-	-	-	-	þ	-	-	-	-	-	5	2
C	SIRS 1	Mar 73	-	-	-	64	10	-	-	-	26	-	-	-	-	-	103	3
7	Brachythecium	Oct 72	-	-	-	þ	-	-	-	-	-	-	-	-	-	þ	5	2
8	Brachythecium	Feb 73	-	-	-	-	5	-	-	-	94	-	-	-	1	-	137	3

Table XIV. Continued.

9	*Drepanocladus* and *Brachythecium*	Mar 64	-	-	-	-	-	-	-	-	þ	-	þ	-	-	þ	9	3
H	*Drepanocladus*	Mar 73	-	-	-	4	23	-	-	-	66	-	-	-	7	-	2945	4
10	*Drepanocladus*	Mar 71	-	-	-	þ	-	-	-	-	þ	-	-	-	-	-	2	2
11	*Drepanocladus*	Feb 73	-	þ	-	6	2	-	-	-	92	þ	-	-	-	-	244	5
D	SIRS 2	Mar 73	-	þ	-	22	2	-	-	-	75	-	-	-	þ	-	3770	5
E	*Prasiola*	Mar 73	-	-	-	þ	98	-	-	-	1	-	-	-	þ	-	22592	4
12	*Prasiola*	Apr 71	7	-	-	-	7	57	-	-	7	7	-	-	7	7	14	7
13	*Prasiola* and lichens	Sep 71	-	-	-	-	-	-	100	-	-	-	-	-	-	-	15	1
14	*Prasiola*	Feb 72	-	-	-	69	-	-	-	-	23	8	-	-	-	-	13	3
15	*Prasiola*	Feb 72	-	þ	-	þ	-	-	-	-	-	-	-	-	þ	-	10	3
16	*Prasiola* and *Drepanocladus*	Oct 72	-	-	-	9	-	-	-	-	36	-	-	-	36	19	11	4
17	*Prasiola* and lichens	Oct 72	-	-	-	61	2	-	-	-	2	-	-	-	-	35	128	4
18	*Prasiola*	Oct 72	-	-	-	þ	þ	-	-	-	-	-	-	-	-	-	4	2
19	*Prasiola*	Oct 72	-	-	-	-	-	-	-	-	þ	-	-	-	-	-	5	1
20	*Prasiola*	Jan 73	-	-	-	21	-	-	36	-	43	-	-	-	-	-	19	3
F	*Deschampsia*	Mar 73	-	þ	-	-	70	þ	-	-	28	-	-	þ	1	þ	399	7
21	*Deschampsia*	Apr 71	-	-	-	-	þ	þ	-	-	þ	-	-	-	-	-	4	3
G	Wallow material	Mar 73	-	-	-	1	93	-	-	-	5	þ	-	-	þ	-	16606	5
22	Organic material	Feb 72	-	-	-	-	-	-	100	-	-	-	-	-	-	-	16	1
23	Organic material	Apr 71	-	-	-	2	-	-	-	-	4	-	-	-	94	-	64	3
24	Organic material	Feb 73	-	8	-	-	38	-	-	-	54	-	-	-	-	-	13	3
25	Pool	Mar 71	-	-	-	-	36	-	-	-	64	-	-	-	-	-	16	2

Table XIV. Continued.

26	Pool	Feb 72	-	-	-	-	þ	-	-	-	-	-	-	-	-	-	6	1
27	Pool 2B	Feb 72	-	-	-	-	100	-	-	-	-	-	-	-	-	-	12	1
28	Pool 4	Feb 72	-	-	-	-	100	-	-	-	-	-	-	-	-	-	17	1
29	Lake	Apr 71	-	-	-	-	-	þ	-	-	-	-	-	-	-	-	4	1
30	Lake	May 71	-	-	-	-	-	þ	-	-	þ	-	-	-	þ	-	4	3
31	Lake 1	Jan 64	-	-	-	-	þ	þ	-	þ	-	-	-	-	-	-	8	3
32	Lake 2	Feb 64	-	-	þ	-	þ	-	-	-	-	-	-	-	-	-	2	2
33	Lake 2	Mar 71	-	-	þ	-	-	þ	-	-	þ	-	-	-	-	-	5	3
34	Lake 2 bottom sample	Jan 73	-	-	-	5	-	7	-	-	88	-	-	-	-	-	132	3
35	Lake 3	Sep 64	-	-	þ	-	-	þ	-	-	-	-	-	-	-	-	2	2

Species occurrence in:

43 samples	2	7	3	21	22	9	4	1	29	5	1	3	12	7
32 terrestrial habitats	2	7	0	20	16	3	4	0	25	5	1	3	11	7
11 aquatic habitats	0	0	3	1	6	6	0	1	4	0	0	0	1	0

Table XV. The distribution and mean percentage occurrence of 14 species/species-groups of Tardigrada in nine broad habitat types at Signy Island.

	Crustose lichen	Organic material	*Prasiola*	Lakes	Moss cushion	Moss carpet	*Deschampsia*	Pools	Moss turf
number of sites giving % abundance	3	4	7	1	3	4	1	3	1
Oreella mollis	-	-	1.0	-	0.3	-	-	-	-
Echiniscus sp.	0.6	2.0	þ	-	0.3	þ	þ	-	-
Macrobiotus ambiguus	-	-	-	þ	-	-	-	-	-
Macrobiotus furciger	-	0.7	22.9	5.0	8.6	8.0	-	-	64.0
Hypsibius (H.) dujardini	12.0	32.7	15.3	þ	18.0	8.0	70.0	78.6	10.0
Hypsibius (I.) asper	-	-	8.2	7.0	-	-	þ	-	-
Hypsibius (I.) renaudi	33.3	25.0	19.5	-	-	-	-	-	-
Hypsibius (I.) papillifer	-	-	-	þ	-	-	-	-	-
Hypsibius (D.) alpinus-pinguis	33.3	15.7	16.0	88.0	69.0	81.7	28.0	21.3	26.0
Hypsibius (D.) chilenensis	-	þ	2.2	-	1.6	þ	-	-	-
Hypsibius (D.) puniceus	-	-	-	-	1.3	-	þ	-	-
Hypsibius (D.) scoticus	-	23.5	6.2	þ	0.3	2.0	1.0	-	-
Hypsibius (D.) sp.	-	-	-	-	-	þ	-	-	-
Milnesium tardigradum	20.6	-	8.7	-	-	þ	þ	-	-
number of species	5	7	10	8	8	8	7	2	3
Accumulate percentage of: *M. furciger*, *H. alpinus-pinguis* and *H. dujardini*	45.3	49.1	54.2	93.0	95.6	97.7	98.0	99.9	100.0

scoticus also occurred in six types but not with as high proportions as *M. furciger*). These four species alone accounted for over 90% of the tardigrade fauna in six of the habitat types in Table XV. The three habitat types in which the proportion fell below 90% occurrence were all influenced by vertebrates. In these habitat types, other components became proportionally more important than elsewhere and *H.* (*I.*) *renaudi*, for example, was completely absent from all other sites. *H.* (*D.*) *scoticus*, although fairly widespread, showed particular preference for the rich organic soils of elephant seal wallows, alluvial deposits and under *Prasiola*. On the other hand, *Milnesium tardigradum* reached a high proportion in only two of the habitat types, and here enrichment was probably not the only causal factor. Whereas most habitats on Signy Island were to some extent sheltered from the most severe conditions by snow cover, both crustose lichens and *Prasiola*, although usually benefitting from enrichment from some source, colonized extremely exposed positions on scree, cliff faces and bluffs. The index of humidity for *Caloplaca* (a crustose lichen) was 2.32, and for *Prasiola* it was 2.01. Both these were considerably less than the mean value (5.90) from all other sites (Table IX). Mihelčič (1954) has placed *Milnesium tardigradum* in a division which he terms the Eurytope, that is, a habitat subject to a wide range of ambient humidities, while Cuenot (1932) noted an apparent association between this species and *Xanthoria* (another crustose lichen which is present on Signy Island). The distribution of *Milnesium tardigradum* found in this study (Table XIV) supports these observations. Of the remaining species, only those of the genus *Echiniscus* were widespread, but never abundant. They were never observed in an aquatic environment. It is difficult to comment on the distribution of the remainder of the species as their occurrence was so limited.

5.12 The density of Signy Island Tardigrada

The distribution and abundance of ten species and species-groups in the eight sites used for quantitative examinations are shown in Table XVI. In the surface 3 cm, total numbers varied from 0.011 x 10^6 m^{-2} in the Polytrichum-Chorisodontium moss turf (C), to 14.130 x 10^6 m^{-2} in a mat of Prasiola crispa (E) situated near a large elephant seal wallow. There was no apparent correlation between total tardigrade density and either pH or moisture content (Table IX). The presence of vertebrate enrichment appears to be the most important single factor governing tardigrade population densities between sites. The very low population density in the Polytrichum-Chorisodontium moss turf has been noted at other localities (Ramazzotti, 1958) and was attributed to either the absence of suitable food organisms in the moss type, or the mechanical difficulties of piercing the thick cell walls by tardigrade stylets. While interpreting the data presented in Table XVI, it must be remembered that the sites showing the highest densities are those which are very restricted in their cover. Tilbrook (1970) estimated that less than 5% of the snow free surface of Signy Island consists of 'ornithogenic' soils, and this point was further discussed by Collins et al. (1975).

Using the mean tardigrade weight (from Table XIII) and the number of each species in Table XVI, an estimate of biomass for each species on the eight sites used in the quantitative study has been made (Table XVII). The lowest total weight of tardigrades was found on the Polytrichum-Chorisodontium moss turf (C) at 26.1 mg m^{-2}, while all those sites affected by vertebrates (B, E, G and H) have a total tardigrade biomass in excess of 1 g m^{-2} (1.2 - 19.8 g m^{-2}). The

Table XVI. The distribution and mean density m^{-2} of tardigrade species/species-groups in eight sites on Signy Island. Site descriptions are given in section 4.11. Confidence limits at the 95% level are underlined.

Site	Date	Oreella mollis	Echiniscus sp.	Macrobiotus furciger	Hypsibius (H.) dujardini	Hypsibius (I.) asper	Hypsibius (D.) alpinus-pinguis	Hypsibius (D.) chilenensis	Hypsibius (D.) puniceus	Hypsibius (D.) scoticus	Milnesium tardigradum	Total tardigrades
A	Oct 72	-	2 000	4 290	8 570	-	123 430	-	1 290	16 570	-	153 430
			1 170	1 170	10 090		97 890		454	20 250		69 900
	Mar 73	4 450	5 600	114	297 260	-	198 740	-	690	110	-	506 970
		2 200	2 560	240	103 950		53 530		700	240		110 270
B	Mar 73	-	1 370	-	25 370	-	-	-	-	-	43 430	70 170
			3 810		43 340						69 490	69 660
C	Mar 73	-	-	5 240	860	-	2 190	-	-	-	-	11 100
				5 130	1 800		1 420					7 060
D	Oct 72	-	1 260	57 690	13 730	-	316 640	-	-	-	-	394 370
			1 550	32 530	19 290		137 150					158 060
	Mar 73	-	370	86 860	70	-	173 650	-	-	-	-	272 760
			380	32 180	150		59 680					75 580
E	Mar 73	-	-	5 200	14 017 070	1 480	103 940	-	-	2 970	-	14 130 660
				4 650	3 307 460	3 100	207 500			4 830		3 242 230
F	Oct 72	-	2 600	1 480	20 040	740	84 260	-	370	15 580	-	115 070
			2 260	1 930	38 040	2 360	14 730		1 180	50 710		48 780
	Mar 73	-	1 480	-	81 670	300	32 070	-	300	1 480	890	118 190
			1 530		53 050	620	10 440		620	1 530	1 070	60 480
G	Mar 73	-	-	44 540	4 626 720	14 110	254 370	740	-	370	-	4 931 480
				46 420	2 566 830	17 720	214 600	2 360		1 180		2 607 170
H	Mar 73	-	-	36 230	201 050	-	573 740	-	-	63 550	-	874 560
				67 930	94 832		355 360			48 090		392 280

Table XVII. Estimate of tardigrade biomass m^{-2} in eight sites on Signy Island (in mg).

Site	Date	*Oreella mollis*	*Echiniscus* sp.	*Macrobiotus furciger*	*Hypsibius (H.) dujardini*	*Hypsibius (I.) asper*	*Hypsibius (D.) alpinus-pinguis*	*Hypsibius (D.) chilenensis*	*Hypsibius (D.) puniceus*	*Hypsibius (D.) scoticus*	*Milnesium tardigradum*	Total tardigrades
A	Oct 72	-	1.5	18.4	12.0	-	132.9	-	1.5	41.7	-	208.0
	Mar 73	0.2	4.1	0.5	416.1	-	213.9	-	0.8	0.3	-	635.9
B	Mar 73	-	1.0	-	35.5	-	-	-	-	-	1 155.4	1 191.9
C	Mar 73	-	-	22.5	1.2	-	2.4	-	-	-	-	26.1
D	Oct 72	-	0.9	248.1	19.2	-	340.9	-	-	-	-	609.1
	Mar 73	-	0.3	373.6	0.1	-	186.9	-	-	-	-	560.9
E	Mar 73	-	-	22.4	19 621.1	8.5	111.9	-	-	7.5	-	19 771.4
F	Oct 72	-	1.9	6.4	28.1	4.3	90.7	-	0.4	39.2	-	171.0
	Mar 73	-	1.1	-	114.3	1.7	34.5	-	0.4	3.7	23.7	179.4
G	Mar 73	-	-	191.6	6 476.5	81.1	264.1	0.5	-	0.9	-	7 014.7
H	Mar 73	-	-	155.8	281.4	-	617.6	-	-	159.8	-	1 214.6
Percent of total biomass over all sites		$\ll$0.1	$\ll$0.1	3.3	85.5	0.3	6.3	$\ll$0.1	$\ll$0.1	0.8	3.7	

remainder of the sites (A,D and F) had a total tardigrade biomass of 171 to 636 mg m^{-2}. The four species previously recorded as being widespread and abundant, M. furciger, H. (H.) dujardini and H. (D.) alpinus + H. (D.) pinguis, account for 95.1% of the total biomass recorded in Table XVII.

No seasonal trend was apparent on the three sites (A, D and F) which were sampled in October and March, however, seasonal variation in population density is discussed in greater detail in section 6.

5.13 The distribution of the Tardigrada in the maritime Antarctic

Here the same two species and one species-group, M. furciger, H. (H.) dujardini and H. (D.) alpinus + H. (D.) pinguis, were very widespread (Table XVIII). The distribution patterns of H. (H.) dujardini and H. (D.) alpinus + H. (D.) pinguis were similar to those observed on Signy Island. These two components were found in all eight vegetation sub-formations (Table XIX). M. furciger, however, did not follow this pattern, and in the wider investigation it was found in only half the habitat types. The accumulate percentage of these three components was similar to that found on Signy Island for each of the habitat types, and accounted for 95.3% of the estimated biomass for these areas, as opposed to the 95.1% estimated for Signy Island sites. H. (I.) renaudi, however, had a more widespread distribution than would have been expected from comparison with the Signy Island data, although in all areas, the percentage occurrence of this species is only high on the Prasiola crispa sites, which invariably benefit from nutrient enrichment. It was noted on Signy Island that H. (D.) scoticus showed some preference for the relatively rich organic soils rather than moss and peat substrates. This was true not only for Signy Island, since in the maritime Antarctic this species was recorded in high proportions in the nutrient rich brown

Table XVIII. The distribution and percentage occurrence of 11 species/species-groups of Tardigrada in 70 samples from the Scotia Ridge and Antarctic Peninsula region. Site descriptions are given in Table X. (þ is given where percent occurrence was less than 1%, or where total tardigrade recovery was less than 10 individuals).

		Echiniscus sp.	*Macrobiotus furciger*	*Hypsibius* (*H.*) *antarcticus*	*Hypsibius* (*H.*) *dujardini*	*Hypsibius* (*H.*) *oberhaeuseri*	*Hypsibius* (*I.*) *asper*	*Hypsibius* (*I.*) *renaudi*	*Hypsibius* (*D.*) *alpinus-pinguis*	*Hypsibius* (*D.*) *chilenensis*	*Hypsibius* (*D.*) *scoticus*	*Milnesium tardigradum*	Total number of specimens	Number of replicates
1	King Edward Point	-	-	-	-	-	þ	-	þ	-	-	-	2	2
2	" " "	-	-	-	-	-	-	-	þ	-	þ	-	2	2
3	" " "	-	-	þ	-	-	-	-	-	-	-	-	1	2
4	" " "	-	þ	-	-	-	-	-	þ	-	-	-	5	2
5	" " "	-	70	-	-	-	-	-	30	-	-	-	17	2
6	" " "	-	þ	-	-	-	-	-	-	-	-	-	7	2
7	" " "	-	99	1	-	-	-	-	-	-	-	-	158	6
8	Candlemas Island	-	-	-	81	-	-	19	-	-	-	-	16	2
9	" "	-	-	-	-	-	-	-	-	-	-	-	0	1
10	" "	-	-	-	100	-	-	þ	-	-	-	-	117	2
11	" "	-	-	-	-	-	-	-	-	-	-	-	0	2

Table XVIII. Continued

12	Monroe Island	-	54	-	-	-	-	5	36	-	5	-	22	1
13	Lynch Island	-	-	-	23	-	-	-	67	-	-	-	16	1
14	" "	-	-	-	92	-	4	-	4	-	-	-	27	1
15	Gosling Island	-	100	-	-	-	-	-	-	-	-	-	30	1
16	Laurie Island	-	92	-	-	-	-	-	8	-	-	-	25	1
17	Elephant Island	-	100	-	-	-	-	-	-	-	-	-	17	1
18	" "	-	5	-	-	-	-	-	40	2	53	-	55	1
19	" "	-	2	-	-	-	-	-	34	-	64	-	103	1
20	" "	-	8	-	1	-	-	-	18	-	73	-	115	1
21	" "	-	99	-	-	-	-	-	1	p	p	-	316	1
22	King George Island	-	-	-	-	-	-	-	-	-	-	-	0	1
I	" " "	-	p	-	-	-	-	-	100	-	-	-	1 922	6
23	" " "	-	-	-	-	-	-	97	3	-	-	-	69	2
24	Deception Island	-	-	-	-	-	-	100	-	-	-	-	300	2
25	Intercurrence Island	-	5	-	-	-	-	-	95	-	-	-	19	1
J	Torgersen Island	6	-	-	82	-	-	6	6	-	-	-	17	6
K	Litchfield Island	-	-	-	-	-	-	-	100	-	-	-	2	6
L	" "	-	78	-	-	-	-	-	22	-	-	-	65	6
26	Galindez Island	-	-	-	p	-	-	-	-	-	-	-	1	1
M	" "	-	-	-	-	-	-	-	-	-	-	-	0	6
27	" "	-	100	-	-	-	-	-	-	-	-	-	40	1

Table XVIII. Continued.

N	Galindez Island	-	32	-	-	-	-	-	68	-	-	-	25	6
28	Blaiklock Island	-	-	-	-	-	-	-	100	-	-	-	14	1
29	" "	-	-	-	100	-	-	-	-	-	-	-	14	1
30	- " "	-	-	-	þ	-	-	-	-	-	-	-	9	1
31	" "	-	-	-	þ	-	-	-	-	-	-	-	4	1
32	Adelaide Island	2	91	-	-	-	-	-	7	-	-	-	33	1
33	Lagoon Island	-	19	-	81	-	-	-	-	-	-	-	21	2
34	" "	-	þ	-	-	-	-	-	-	-	-	-	3	1
35	Limpet Island	-	67	-	-	-	-	-	33	-	-	-	69	1
36	" "	-	94	-	4	-	-	-	2	-	-	-	103	1
37	Avian Island	-	68	-	32	-	-	-	-	-	-	-	28	1
O	- " "	-	72	-	1	-	-	-	27	-	-	-	181	6
P	" "	-	93	-	-	-	-	-	6	-	1	-	264	6
38	" "	-	72	-	28	-	-	-	-	-	-	-	65	1
39	" "	-	-	-	-	-	-	þ	-	-	-	-	2	1
40	" "	-	-	-	-	-	-	-	þ	-	þ	-	9	1
41	Horseshoe Island	-	-	-	100	-	-	-	-	-	-	-	24	1
42	" "	-	-	-	þ	-	-	-	-	-	-	-	7	1
43	" "	-	-	-	þ	-	-	þ	-	-	-	-	2	2
44	" "	þ	-	-	þ	-	-	-	-	-	-	-	7	2
45	Consort Island	-	-	-	-	-	-	þ	-	-	-	-	9	1
46	Emperor Island	-	85	-	14	-	-	-	1	-	-	-	87	1

Table XVIII. Continued.

47	Barbara Island	-	-	-	-	-	-	-	-	-	-	-	0	1
48	" "	-	-	-	55	-	-	45	-	-	-	-	168	1
49	" "	þ	-	-	-	-	-	þ	-	-	-	-	2	2
50	" "	-	-	-	þ	-	-	-	-	-	-	-	1	1
51	Stonington Island	-	-	-	þ	-	-	þ	-	-	-	-	6	2
52	Neny Island	-	-	-	89	-	-	-	11	-	-	-	53	1
53	" "	-	-	-	þ	-	-	-	þ	-	-	-	9	1
54	" "	-	-	-	38	-	-	-	62	-	-	-	13	1
55	" "	-	-	-	þ	-	-	-	þ	-	-	-	2	1
56	" "	-	-	-	98	-	-	-	2	-	-	-	81	1
57	" "	-	-	-	17	-	-	-	83	-	-	-	12	1
58	Terra Firma Island	-	-	-	-	-	-	-	þ	-	-	-	2	1
Q	Ablation Point	1	40	-	33	1	-	2	20	-	-	3	228	6
59	" "	-	14	-	11	-	24	-	49	-	-	2	71	2
60	" "	-	-	-	-	-	-	-	þ	-	þ	-	2	2
61	" "	10	13	-	13	-	5	-	58	-	-	1	39	2
	Species occurrence in 70 sites	6	30	2	31	1	4	13	38	2	9	3		

Table XIX. The distribution and mean percentage occurrence of eight species/species-groups of Tardigrada in eight broad habitat types in the maritime Antarctic (excluding South Georgia and Alexander Island).

	Crustose lichen	Alga	Moss cushion	Moss carpet	Antarctic herbs	Moss turf	Moss Hummock	Encrusted moss
number of sites giving % abundance	0	5	1	14	8	3	4	1
Echiniscus sp.	þ	-	-	þ	1	-	-	-
Macrobiotus furciger	-	-	þ	70	17	-	56	-
Hypsibius (H.) dujardini	þ	49	17	4	32	60	12	100
Hypsibius (I.) asper	-	1	-	-	-	-	-	-
Hypsibius (I.) renaudi	þ	48	þ	þ	1	7	-	þ
Hypsibius (D.) alpinus-pinguis	þ	2	83	25	25	33	32	þ
Hypsibius (D.) scoticus	þ	-	-	þ	24	-	-	-
Hypsibius (D.) chilenensis	-	-	-	þ	þ	-	-	-
Number of species	5	4	4	7	7	3	3	3
Number of species on Signy Island	5	10	8	8	7	3	-	-
Accumulate percentage of: M. furciger H. alpinus-pinguis and H. dujardini	-	51	100	99	74	93	100	100
Accumulate percentage of these three species/species-groups on Signy Island	45	54	96	98	98	100	-	-

earth soils under the Antarctic phanerogams. Other tardigrade species were not found in sufficient numbers to determine any such distribution trends.

5.14 Density of the Tardigrada in the maritime Antarctic

Few of the 70 sites investigated were directly affected by vertebrates. Sites J and O which were likely to be enriched, did not support the view that enrichment leads to higher tardigrade densities (Table XX). However, the present results support the earlier data for the moss turves of Signy Island, where the tardigrade population densities were relatively low. A Chorisodontium moss turf (K) from Litchfield Island yielded only 0.002 x 10^6 tardigrades m^{-2}, while no Tardigrada were extracted from six cores of a Polytrichum moss turf from Galindez Island. The range of population densities found at other sites was from 0.025 x 10^6 m^{-2} in a Calliergidium moss carpet on Galindez Island to 1.922 x 10^6 m^{-2} in a Drepanocladus moss carpet on King George Island.

As at Signy Island, no clear correlation existed between tardigrade population density and moisture content of the moss (Table XI). Although, subjective grouping of the sites into "wet" and "dry" sites (where this was possible) indicated that higher numbers of tardigrades (Table XVIII) were extracted from the "wet" substrates ($t = 2.02$ with $df = 32$). However, this analysis cannot be accepted as completely reliable since it does not take the varying sample size into account. Also, many of the samples classified as "dry" consist of Polytrichum and/or Chorisodontium, a substrate which supported few tardigrades regardless of its overall moisture content.

Little pattern emerges when densities are considered in relation to climate. A number of climatic factors for the geographical range studied are illustrated in Fig. 2, while tardigrade population

Table XX. The distribution and mean density m^{-2} of tardigrade species/species-groups in nine sites from the Antarctic and maritime Antarctic region. Site descriptions are given in Table X. Confidence limits at the 95% level are underlined. * Sites affected by vertebrates.

Site	*Echiniscus* sp.	*Macrobiotus furciger*	*Hypsibius* (*H.*) *dujardini*	*Hypsibius* (*H.*) *oberhaeuseri*	*Hypsibius* (*H.*) *renaudi*	*Hypsibius* (*D.*) *alpinus-pinguis*	*Hypsibius* (*D.*) *scoticus*	*Milnesium tardigradum*	Total tardigrades
I	-	1 800 5 730	-	-	-	1 920 500 1 292 440	-	-	1 922 300 1 296 820
J *	900 2 870	-	14 410 11 460	-	900 2 870	900 2 870	-	-	17 110 11 820
K	-	-	-	-	-	1 800 0	-	-	1 800 0
L	-	51 340 137 610	-	-	-	13 510 42 990	-	-	64 860 180 600
M	No tardigrades recovered								
N	-	8 110 20 060	-	-	-	17 110 37 260	-	-	25 220 57 330
O *	-	129 710 63 190	1 800 5 730	-	-	49 540 34 510	-	-	204 030 148 340
P	-	245 020 367 760	-	-	-	15 310 22 020	3 600 4 050	-	264 830 386 370
Q	1 800 4 050	90 980 144 200	75 670 21 830	900 2 870	5 400 17 200	45 940 45 950	-	7 210 5 730	227 900 211 200

density and biomass are given in Tables XX and XXI respectively. For a single moss type (Drepanocladus, sites H, I, O and P) both population density and biomass decreased markedly southward from the South Shetland Islands, then increased again further south along the Antarctic Peninsula at Marguarite Bay. Even when a variety of moss types are considered from Table XX, this pattern persists. This apparent paradox may relate to micro-environmental factors, which although not measured in this region, may be deduced from Fig. 2. Tardigrades are only active when the moss is not frozen and free water is available. This active period can only occur during the brief Antarctic summer when the insulating snow cover melts or ablates. Temperatures at plant level in the maritime Antarctic often show little correlation with those measured in Stevenson screens. The characteristic summer pattern is one of wide diurnal fluctuations (Greene & Longton, 1970). Daytime surface temperatures in the moss communities are closely linked to site aspect and radiation reciept and can exceed air temperature by up to 20^{o}C (Longton, 1972). On Signy Island temperatures in the upper 3 cm of a moss carpet have reached 20^{o}C, whilst 28^{o}C has been recorded in a moss turf (E.P. Wright, pers. comm.). The high tardigrade densities of the South Orkney Islands and the South Shetland Islands with a higher air temperature but fairly low radiation reciept contrast with the low densities of the colder, cloudier north Antarctic Peninsula. The direct microclimate effect of increased solar energy might be expected to reverse this trend (Marguarite Bay and Alexander Island) even though the latitude is higher and the mean air temperature lower. Further, the longer day length experienced at these high latitudes during the summer months presumably would tend to reduce the diurnal fluctuations in moss temperature. The effect of a favourable micro-environment appears also to affect the species diversity (Table XXII).

Table XXI. Estimate of tardigrade biomass m^{-2} in nine sites in the Antarctic and maritime Antarctic region (in mg).

	Echiniscus sp.	*Macrobiotus furciger*	*Hypsibius* (*H.*) *dujardini*	*Hypsibius* (*H.*) *oberhaeuseri*	*Hypsibius* (*I.*) *renaudi*	*Hypsibius* (*D.*) *alpinus-pinguis*	*Hypsibius* (*D.*) *scoticus*	*Milnesium tardigradum*	Total tardigrades
I	-	7.7	-	-	-	2 066.4	-	-	2 074.2
J	0.6	-	20.2	-	2.8	1.0	-	-	24.6
K	-	-	-	-	-	1.9	-	-	1.9
L	-	220.8	-	-	-	14.5	-	-	235.4
M	-	-	-	-	-	-	-	-	-
N	-	34.9	-	-	-	18.4	-	-	53.3
O	-	557.9	2.5	-	-	53.3	-	-	613.7
P	-	1 053.8	-	-	-	16.5	9.1	-	1 079.3
Q	1.3	391.3	105.9	1.0	16.6	49.4	-	191.7	757.3
Percent of total biomass over all sites	$\leq$0.1	46.8	2.6	$\ll$0.1	0.4	45.9	0.2	4.0	

Table XXII. Relative abundance (%) of tardigrade species/species-groups by latitude zones. * Includes data from Signy Island. þ less than 1% occurence.

	Sites	Latitude South	Oreella mollis	Echiniscus sp.	Macrobiotus furciger	H. (H.) antarcticus	H. (H.) dujardini	H. (H.) oberhaeuseri	H. (I.) asper	H. (I.) renaudi	H. (D.) alpinus-pinguis	H. (D.) chilenensis	H. (D.) scoticus	H. (D.) puniceus	H. (D.) sp.	Milnesium tardigradum	Mean No species/site
South Georgia	1-7	54°	-	-	84	þ	-	-	þ	-	15	-	þ	-	-	-	1.7
S. Sandwich Islands	8-11	57°	-	-	-	-	90	-	-	10	-	-	-	-	-	-	1.0
S. Orkney Islands	12-16,*	60-61°	þ	þ	18	-	20	-	3	9	38	þ	6	þ	þ	4	3.5
S. Shetland Islands	17-24,I	61-62°	-	-	32	-	þ	-	-	23	23	þ	22	-	-	-	2.3
Northern part of Antarctic Peninsula	25-27,J-N	63-66°	-	1	36	-	13	-	-	1	48	-	-	-	-	-	1.6
Marguarite Bay	28-58,O-P	67-69°	-	þ	39	-	39	-	-	3	20	-	þ	-	-	-	1.8
Alexander Island	59-61,Q	70°	-	3	22	-	19	þ	9	þþ	42	-	þ	-	-	2	5.0

Although the pattern is complicated by the results from South Georgia (where competition with other organisms not present in habitats at higher latitudes may account for the low species diversity) and the South Sandwich Islands (where sample replication was very low) a trend of decreasing species diversity to Marguarite Bay followed by a large increase at Alexander Island is apparent.

Only two specimens of H. (H.) antarcticus were recovered from South Georgia, and it has been suggested by Dastych (1973) that this species represents specimens of H. (H.) dujardini in the simplex stage (i,e. that period before the moult when the entire buccal apparatus has been lost and before it has fully reformed). However, in this instance, no specimens of H. (H.) dujardini were recovered from South Georgia, but with such a small sample this suggestion can be neither refuted nor confirmed. Table XXII shows that M. furciger, H. (I.) asper, H. (D.) alpinus + H. (D.) pinguis and H. (D.) scoticus were present in a wide geographical range of habitats, from the sub-Antarctic (South Georgia) to the truly continental Antarctic (Alexander Island). Comments on the zoogeoraphical distribution of individual tardigrade species are at present of limited value, since the samples used here are too few and too small to support more general conclusions for this large area.

SECTION 6: STUDIES ON THE SIGNY ISLAND REFERENCE SITES

6.1 The sites and sampling procedure

6.11 Introduction

Between June 1971 and April 1973 a sampling programme was undertaken to determine the temporal distribution of tardigrades and rotifers at the two Signy Island reference sites (SIRS 1 and 2). This investigation will form part of an extensive appraisal of the functional relationships of the various biological components, eventually leading to a total ecosystem analysis of these two moss communities. Both sites have been described in detail by Tilbrook (1973), and in section 4.51.

6.12 Sampling procedure

Between June 1971 and January 1972 the entire area of SIRS 1 was used for random sampling. However, after January 1972 samples were taken at random from within 150 meter squares so arranged that none had to be entered to collect the sample (Fig. 20), thus eliminating any trampling effect.

Preliminary sampling of SIRS 2 showed that extreme aggregation of the tardigrade fauna existed. In an attempt to minimize the variance a stratified random sampling procedure was adopted. An area 720 m^2 was chosen, which at the time of selection was considerably less waterlogged than the remainder of the site but was otherwise representative of SIRS 2. The selected area was long and narrow (60 m x 12m) and the long axis ran north-south. The area was divided for sampling into ten consecutive strips, each 12 m x 6 m.

Samples were taken from SIRS 1 once in every 60 days. These samples were extracted and preserved in 10% formalin for analysis in the United Kingdom. SIRS 2 was sampled at 30 day intervals and here the samples were extracted and counted at the Signy Island biological laboratory. In each case 20 sampling units were taken to a depth of 6 cm.

6.2 Microclimate data

As part of a long term study an autographic recorder was established midway between the two sites in January 1972. To house this instrument a strengthened shed (the walls of which were insulated with expanded polystyrene) was erected. This hut also acted as a convenient store for sampling equipment and articles of field clothing which were required.

Two Grant type D 20 channel recorders were used, one of which monitored temperature and incoming radiation at hourly intervals, the other acting as a standby instrument. Five Grant type C thermister probes were positioned at various depths in one area of typical vegetation on each site, and a Kipp and Zonen CM5 solarimeter was mounted on the roof of the hut used to house the autographic recorder. Both aspect and slope will affect any measured incoming radiation and data supplied by this instrument must be interpreted with this reservation. Much of the incoming long wave radiation is also not recorded since the instrument dome is glass covered. Occasionally in winter this dome became covered with rime, and on one occasion the dome was blown completely off, but the effect of these factors on the recorded level was believed to be of little significance as the radiation at this time of year was extremely low and all the mosses were snow covered.

The channel numbering for the recorders was as follows:-

1	SIRS 1 surface		6	SIRS 2 surface	
2	" "	- 1.5 cm	7	" "	-1.5 cm
3	" "	-4.5 cm	8	" "	-4.5 cm
4	" "	-7.5 cm	9	" "	-7.5 cm
5	" "	-10.5 cm	10	" "	-10.5 cm

11 Inside hut air temperature next to the recorder

12 Outside the hut at 120 cm for air temperature

14
Resistors to monitor the instrument calibration
17

20 Kipp and Zonen solarimeter

It was expected that very low air temperatures inside the hut would adversely affect the recorder and a paraffin heater was installed in the hut. At temperatures below -20°C the recorded cycles were incomplete and innaccurate and the heater had to be in operation before the temperature in the hut reached this level. This often required considerable foresight and inevitably some data were lost. During one particularly cold period in 1972, when the air temperature dropped to -39°C, the heater failed to keep the hut above -20°C and some data were lost on this occasion also. However, considering the working conditions under which this instrument operated, it proved relatively trouble free. The causes for data loss are given below:-

13.1.72 - 15.1.72	Gearbox failure
24.1.72	Skuas uprooted probes at SIRS 2
13.2.72 - 15.2.72	Miscalculation of chart length
25.2.72 - 3.3.72	Gearbox slipping (data unreliable)
20.5.72 - 23.5.72	Untraced fault
2.6.72	Low temperatures
6.6.72	" "

15.6.72 - 21.6.72	Gearbox slipping
26.6.72 - 30.6.72	" "
3.7.72	Low temperatures
9.8.72	" "
18.9.72 - 23.9.72	Solarimeter dome blown off
29.9.72	Low temperatures
28.10.72	" "

From this date the recorder was free of fault until March 1973.

All charts from this instrument were read by eye on Signy Island, the data being transferred later to punch cards for computer correction and recalibration.

6.3 Density and distribution of the Tardigrada on SIRS

Despite a considerable volume of literature relating to the Tardigrada, comparatively little is known about the ecology of individual species. Several authors have dealt with population densities in the soil and litter (Franz, 1941, 1950; Nef, 1957; Ramazzotti, 1959; Hallas & Yeates, 1972), however, only the studies of Higgins (1959), Franceschi *et al*. (1962-63), Morgan (1973) and the present work have given figures for tardigrade density in mosses. Only the last two authors have provided area related population density estimates for the mosses, so little data are available for comparison with the present work.

6.31 Population studies

Of a total of 14 species and species-groups found on Signy Island (section 5.11), four were recovered regularly from the SIRS (Appendix I). The species and species-groups found were *E*. (*E*.) *capillatus* + *E*. (*E*.) *meridionalis*, *H*. (*H*.) *dujardini*,

H. (D.) alpinus + H. (D.) pinguis and M. furciger. Three other species, H. (D.) scoticus, H. (I.) asper and H. (I.) renaudi, were recovered during the sampling period but in each case the number of individuals did not exceed ten, so they are not considered further here.

It is generally recognised that for many groups tundra habitats lack the species diversity found in temperate or tropical regions. The Tardigrada do not follow this pattern. In this study four species/species-groups were found on the two SIRS, while Morgan (1973) found four species in mosses at Swansea and Franceschi et al. (1962-63) only report on two species from mosses in Italy. Although Hallas & Yeates (1972) list ten species from forest soil and litter this number is comparable with the most species rich sites on Signy Island (section 5.11).

In terms of the maximum recorded density (maxima being 309,030 and 712,620 tardigrades m^{-2} for SIRS 1 and 2 respectively), this study is intermediate between that of Morgan (1973) with 2,287,000 animals m^{-2} and that of Hallas & Yeates (1972) with 12,096 animals m^{-2}. However, up to 14,000,000 animals m^{-2} have been found at other sites on Signy Island (section 5.12). Morgan (1973) comments on the similarity between his increase in density from the minimum to the maximum recorded, and that of Hallas & Yeates (1972) both of whose increases are between 10 to 20 fold. In the present work the maximum increase for all Tardigrada was only three to fourfold, although, for Echiniscus on SIRS 2 this increase was in excess of 100 fold.

Most of the authors mentioned earlier have linked population density changes to a variety of environmental factors. These include moisture (Franceschi et al., 1962-63; Morgan, 1973), temperature (Franceschi et al., 1962-63) and availability of food organisms

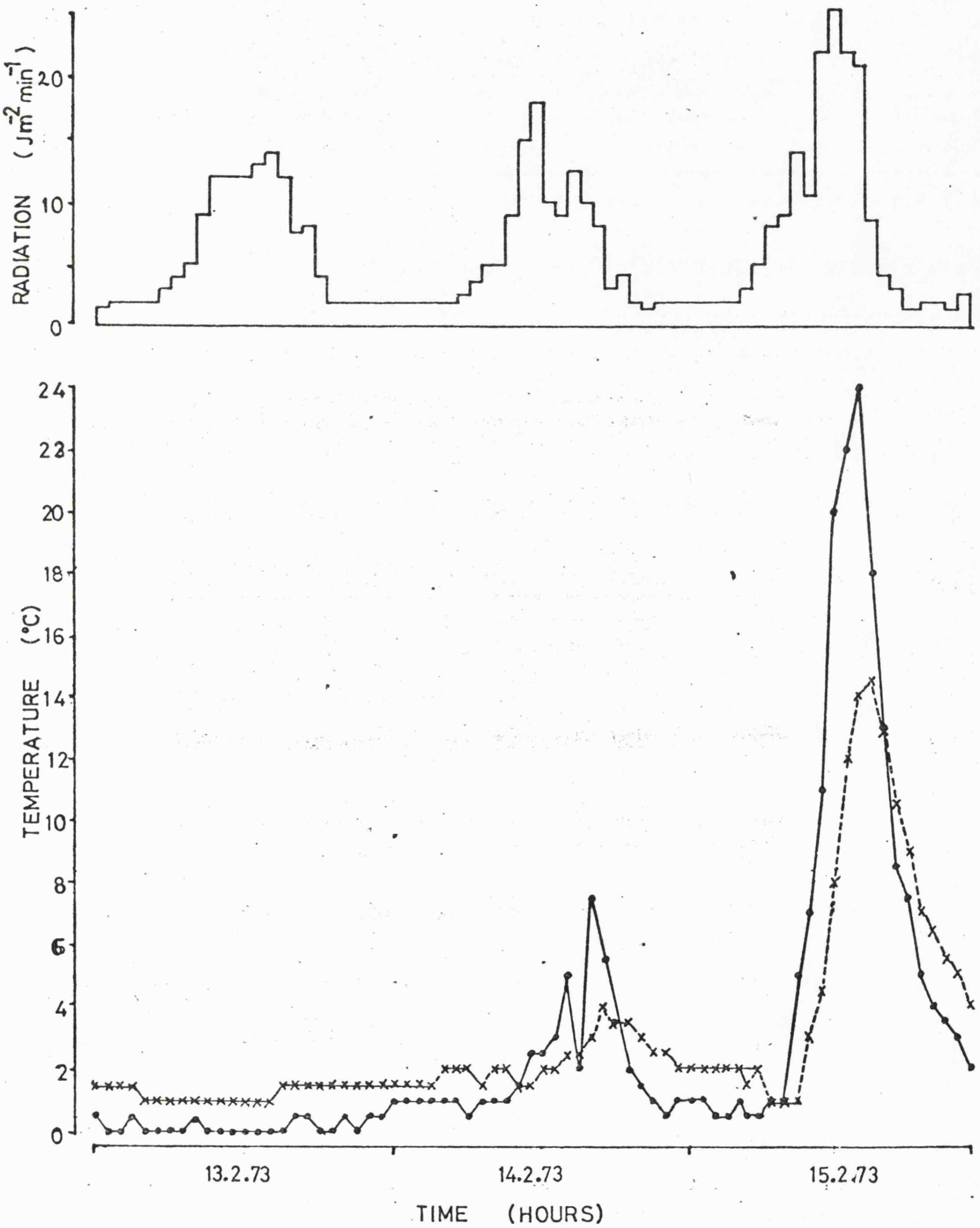
(Hallas & Yeates, 1972). The present study differs considerably from all previous work in that the mosses of Signy Island are buffered from extreme air temperature fluctuations by snow cover in excess of 13 cm (Wright, 1975). Summer conditions are similar to temperate winter conditions with wide diurnal fluctuations in temperature (Fig. 27) and the mosses never dry out completely. The period in which Tardigrada on Signy Island can be active is relatively short, only an average of four months each year, and this is followed by eight months of moss temperatures consistently below freezing point (Fig. 28).

Only the genus Echiniscus at SIRS 2 showed a clear annual cycle (Fig. 29). Quite a high number overwintered in the moss in 1972, presumably leading to the very high numbers recovered during the following early summer months. This pattern was not as clear at SIRS 1, although it was strongly suggested. The relatively high density of SIRS 2 Echiniscus during the winter of 1972 appeared to be mirrored by M. furciger and H. (D.) alpinus + H. (D.) pinguis. A general decline in numbers until October 1971 was recorded for both of these components, followed by a fairly sharp increase at the thaw. This higher level was maintained throughout the following winter but no further increase took place at the subsequent thaw and the population of H. (D.) alpinus + H. (D.) pinguis declined quite substantially. Both H. (D.) alpinus + H. (D.) pinguis and M. furciger on SIRS 1 followed a similar trend of slight increase at the melt and decrease over winter, but showed an overall increase during the study period. Fluctuations in the population densities of H. (H.) dujardini on both sites tended to be far more extreme and erratic. On SIRS 2 this may have been partially caused by the presence of a semi-permanent pool spanning two strata, both of which were very rich in this species (Fig. 30). Again no cyclic pattern was evident on either site (Fig. 29)

Fig. 27 Hourly temperature record (^{o}C) and incident solar radiation ($J\ m^{-2}\ min^{-1}$) measured at SIRS 1 on three consecutive days. During day 1 the moss was snow covered; this snow dispersed during day 2 and day 3 illustrates the rapid response of moss temperature to radiation input.

●———● Moss surface temperature

×- - -× Temperature at -1.5 cm in the moss



RADIATION ($Jm^{-2}min^{-1}$)
0
10
20
TEMPERATURE (°C)
0
2
4
6
8
10
12
14
16
18
20
22
24
13.2.73
14.2.73
15.2.73
TIME (HOURS)

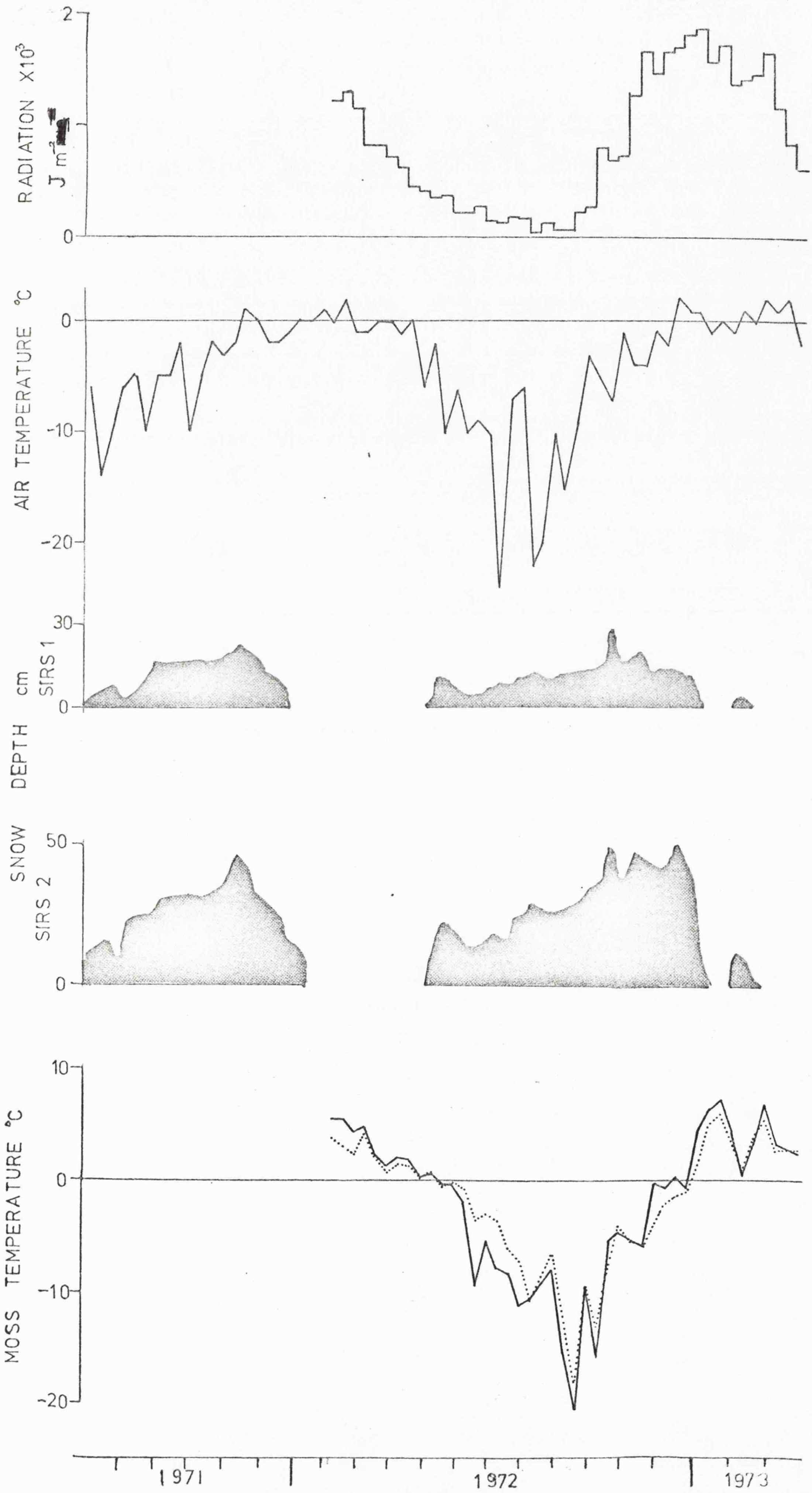
Fig. 28 Meteorological data for the SIRS.

Total radiation receipt (J m^{-2}) over ten day intervals.

Ten day mean air temperature outside the British Antarctic Survey biological laboratory.

Snow depth (cm).

Ten day mean moss temperature (^{o}C) in the upper 6 cm of SIRS 1 (continuous line) and SIRS 2 (broken line).



RADIATION X10³
J m⁻²
2
1
0
AIR TEMPERATURE °C
0
-10
-20
SNOW DEPTH cm
SIRS 1
30
0
SIRS 2
50
0
MOSS TEMPERATURE °C
10
0
-10
-20
1971
1972
1973

Fig. 29 Three month running means of density m^{-2} for each faunal component of SIRS 1 and 2 over the study period 12-07-71 to 26-03-73.

■ *E.* (*E.*) *capillatus* + *E.* (*E.*) *meridionalis*

▲ *M.* *furciger*

○ *H.* (*H.*) *dujardini*

● *H.* (*D.*) *alpinus* + *H.* (*D.*) *pinguis*

x Total Rotifera

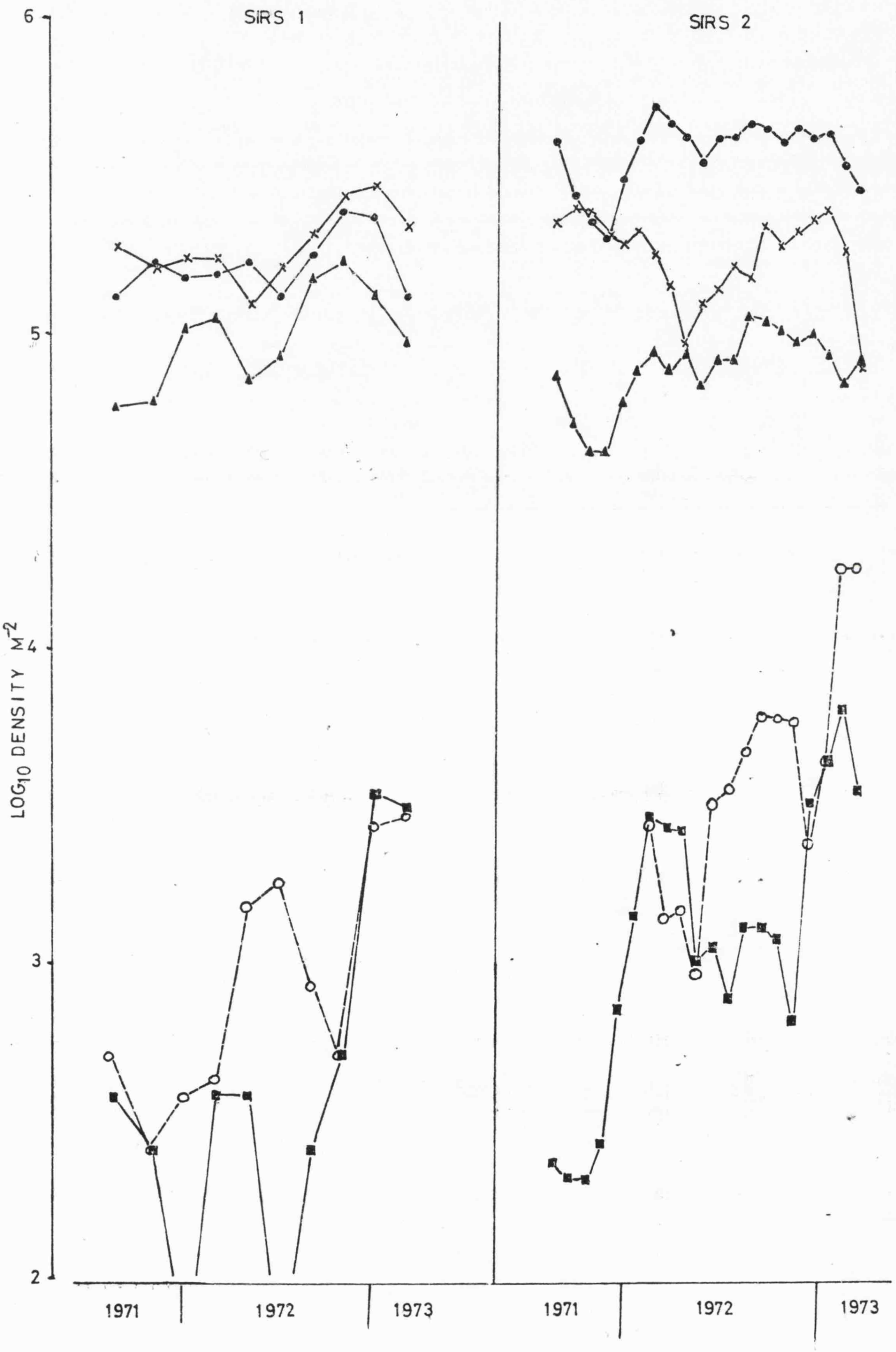
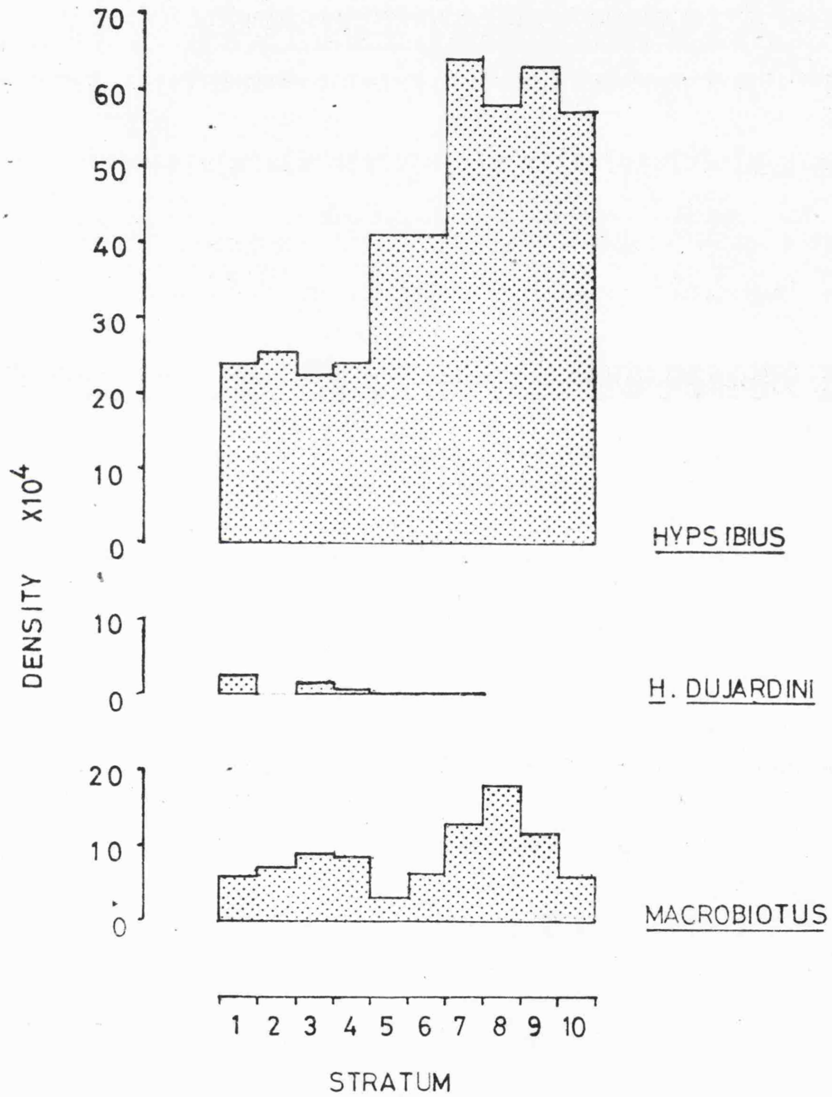

SIRS 1
SIRS 2
6
5
4
3
2
LOG10 DENSITY M-2
1971
1972
1973
1971
1972
1973

Fig. 30 Mean density m^{-2} in each stratum of SIRS 2 for three components over the entire study period 12-07-71 to 26-03-73.

(The high density predicted in stratum 1 for *H.* (*H.*) *dujardini* results from a single core containing 750 individuals. This species was not recovered from the stratum at any other time).



DENSITY X10^4
70
60
50
40
30
20
10
0
HYPSIBIUS
10
0
H. DUJARDINI
20
10
0
MACROBIOTUS
1 2 3 4 5 6 7 8 9 10
STRATUM

but a general increase in density over the period was detected.

In order to establish in greater detail the spatial distribution and habitat preferences of each of the faunal components studied, an attempt was made at mapping the actual core distribution on SIRS 2. To this end, a labelled marker was inserted into each core hole on each sampling occasion. Originally these markers were 6 cm lengths of polythene tubing, however, these proved to be much too conspicuous during the snow free period and attracted the interest of numerous non-breeding skuas present at the site. After the summer of 1972, therefore, these markers were considerably reduced in size (see Fig. 24). Even these, however, were sought by the inquisitive skuas and when an attempt was made to map the site, only half the markers inserted were recovered from the two strata mapped. Shortly after this mapping was begun, inclement weather forced the abandonment of the project.

In the absence of a map, habitat preferences of each faunal component were investigated by combining the results from individual cores into groups, on some factor such as moisture content or vegetation composition. Little was gained from this analysis since the differences which appeared were not consistent and therefore could not be taken as definitive indicators of habitat preference. Clearly variations in micro-habitat do have substantial effects on the faunal populations as Fig. 30 indicates, although no correlation is evident between numbers of animals and any other measured factor.

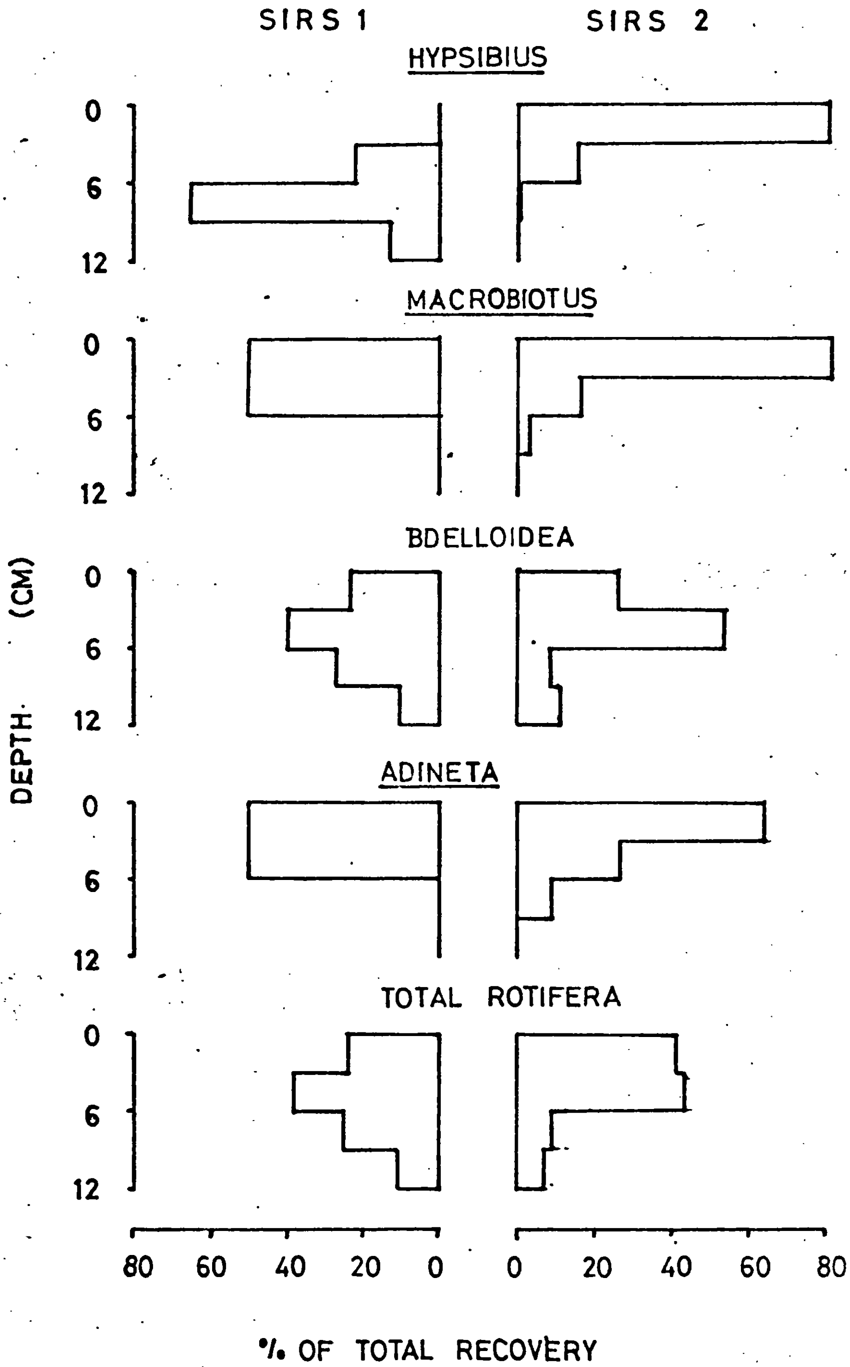
6.32 Vertical distribution

It was assumed initially that most of the tardigrade fauna was restricted to the upper 6 cm of the moss. In order to test this assumption, ten 12 cm deep cores were taken from each site in March

1973 and transported at $-20^{\circ}C$ for extraction in the United Kingdom. The results of this experiment (Fig. 31) may not be completely reliable, since the relative density in the top 0–3 cm of SIRS 1 differed markedly from the values obtained during the previous two years (Appendix I). More confidence can be placed in the results from SIRS 2, and here the population recovered from the upper 6 cm of the moss accounted for over 80% of the total in the 12 cm cores. A further point which should be considered is that the peat on SIRS 1 and 2 are not uniform in depth over each site. SIRS 1 has a depth between 12 cm and 32 cm (Tilbrook, 1973) whereas Fig. 32 shows the frequency distribution of depth at the centre of 231 meter squares which were mapped to determine the spatial distribution of the tardigrades (see section 6.31). Only 21% of these were less than 6 cm deep and 63% were less than 12 cm deep. Thus the proportion of the total population which was not accessible during the monthly coring to 6 cm was quite small.

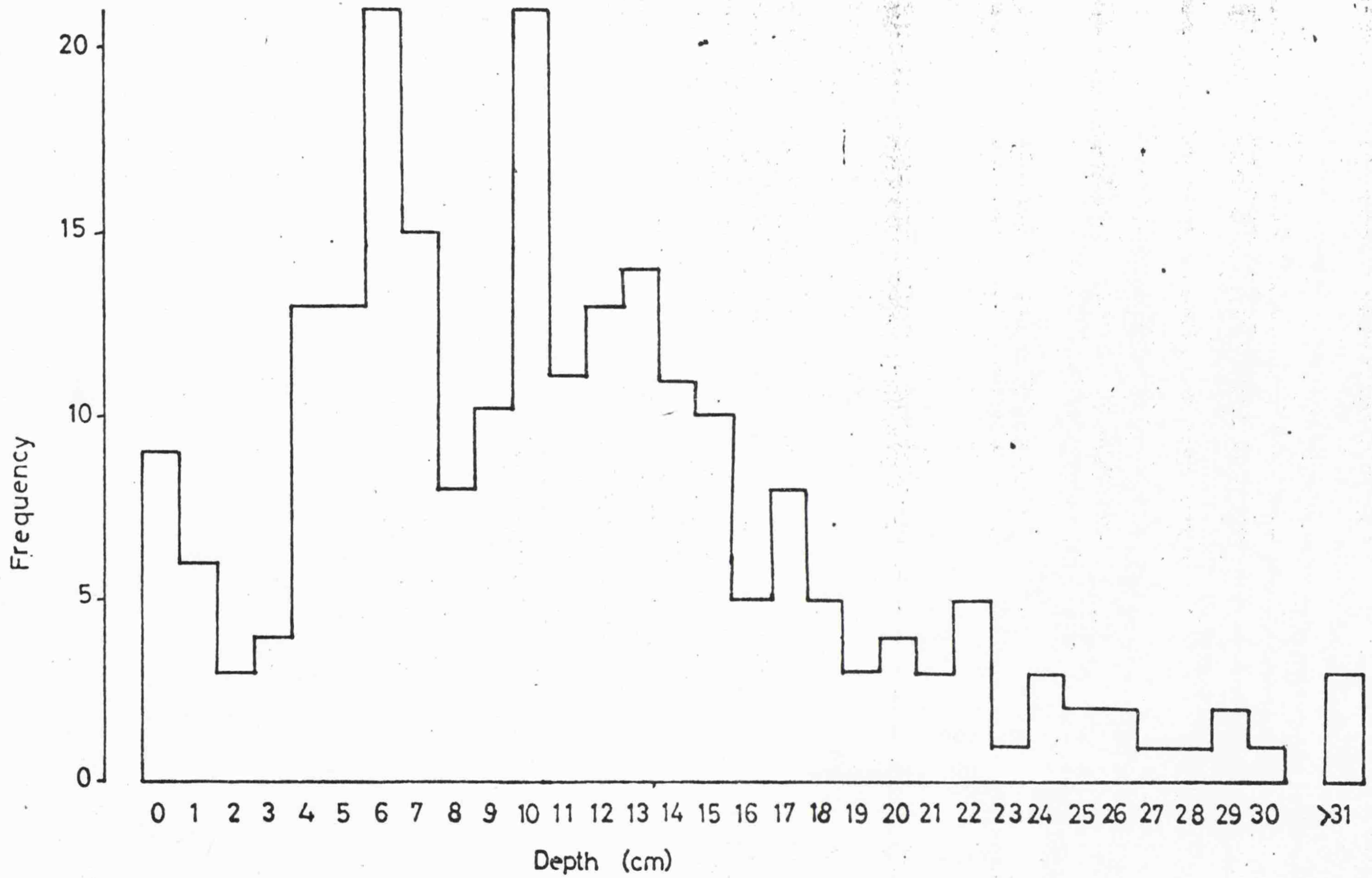
Whereas Spaull (1973a) found that at various times vertical migration of the nematode fauna on Signy Island was significant, no similar movement was apparent for the tardigrades. In general over 70% of the individual components in both sites were found in the top 3 cm of the moss (Appendix I). Although the depth of moss at SIRS 2 was in places over 30 cm (Fig. 32), a silver plate inserted in the moss indicated that only the top 7–8 cm were aerobic, and this finding was further confirmed by two silver wires at other locations on the site. This, with the lower temperatures (Longton, 1972) and the decline of the microflora with depth (Broady, 1975) could explain the very rapid decline of faunal populations with depth. In a pure stand of <u>Chorisodontium</u> the anaerobic layer was not found by Baker (pers. comm.), and on SIRS 1 the decline of the fauna was not as rapid.

Fig. 31 Percentage occurrence of each faunal component at 3 cm depths in ten 12 cm cores from each of SIRS 1 and SIRS 2.



SIRS 1
SIRS 2
HYPSIBIUS
MACROBIOTUS
BDELLOIDEA
ADINETA
TOTAL ROTIFERA
DEPTH (CM)
0
6
12
80 60 40 20 0
0 20 40 60 80
% OF TOTAL RECOVERY

Fig. 32 Frequency distribution of the depth of moss and peat at the centre of 231 meter areas on SIRS 2.


Frequency
0
5
10
15
20
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 >31
Depth (cm)

6.4 Oxygen uptake of *Macrobiotus furciger*

Of the four species or species-groups present on the SIRS, only one was sufficiently large and robust enough to enable relatively easy handling, and this was *M. furciger*. In addition to being an important component of both SIRS it was also widespread at other sites on Signy Island and throughout the maritime Antarctic (see section 5.1).

6.41 Respirometry

The animals used for the measurement of oxygen uptake were extracted from the moss of SIRS 2 using the modified Baermann funnel technique (section 4.41). The animals were extracted at room temperature which, depending on time of year, ranged from 3°C to 15°C. They were then stored at 7°C until required for the experiments.

Measurements of oxygen uptake were made using a Cartesian Diver micro-respirometer (Linderstrøm-Lang, 1943; Holter, 1943) in a constant temperature room at Signy Island. Stoppered divers were used having a gas volume of 0.75–6.68 µl and the animals were introduced into the divers by the sedimentation method described by Klekowski (1971) for aquatic animals. The animals were equilibrated in the respirometer at the experimental temperature for at least 1 h before readings at 30 minute intervals were undertaken.

Initially oxygen uptake of individual animals was measured, but for the size of divers in use the change in gas volume during each experiment was very small. Therefore, on all subsequent occasions measurements were made on several animals, usually five, in each diver (Appendix II). Unfortunately this required considerable pre-sorting of the material under a binocular microscope in order to reduce size variation within the group. The day before they were required for respirometry the specimens were sorted into five arbitrary body length groups. These were as follows:-

1	$\leqslant$250 µm
2	251 - 350 µm
3	351 - 450 µm
4	451 - 550 µm
5	$\geqslant$551 µm

The respiration experiments were continued for at least 4 h. Even with five animals in the diver, the total change in gas volume was less than 2%. After each experiment the animals were removed from the divers and mounted on slides in polyvinyl-lactophenol. Unfortunately, some specimens, particularly in the smaller size groups, were lost during this procedure. The two experimental temperatures used in this study, 5^{o}C and 10^{o}C, were chosen as being representative of summer conditions in Signy Island moss (cf. Fig. 28), but lack of time limited the number of measurements made at 10^{o}C.

6.42 Length and weight derivation

During the mounting process some animals expanded in size, thus giving an overestimate of body length, and the cuticle ruptured in a few of these causing a decrease in overall length. Furthermore, all specimens shrank progressively with time. For these reasons direct measurement of body length was unreliable, and it was necessary to find another parameter to which this could be related but which was unaffected by the mounting technique. A linear correlation exists between the muscular pharynx length and body length in M. islandicus Richters (Higgins, 1959) and M. hufelandii Schultze (Franceschi & Lattes, 1969), but the muscular pharynx is a soft structure, which in some cases distorted during mounting. The buccal tube and placoids are both hard parts, unaffected by the mountant, and are shed and replaced before each moult. These structures were used in this study.

The relationship between body length of *M. furciger* and the length of the buccal tube (A) and the length of the placoids (B) were derived using preserved material from a single sampling unit, all mounted at the same time and measured on the same occasion (Fig. 33). From the resulting regression equations two estimates of body length were derived for each of the experimental animals and for sub-samples from selected months from preserved material of SIRS 2. The mean of the two lengths estimated from lengths A and B was then used in all subsequent calculations. As both the measured structures are lost before the moult, no body length estimates were available for animals in the simplex stage. The weight of each animal was then obtained in the manner given in section 4.43.

6.43 Results

A total of 55 oxygen uptake rates was obtained, 44 at 5°C and 11 at 10°C (Appendix II). The relationship between $\log_{10}$ live weight and $\log_{10}$ oxygen uptake individual^{-1} is shown in Fig. 34. This includes both individual and group means and both these have been used to calculate the two regression lines

$$R = 0.31W^{0.51} \text{ (n = 44, r = 0.67) at } 5^{\circ}C$$

$$\text{and } R = 0.57W^{0.51} \text{ (n = 11, r = 0.89) at } 10^{\circ}C$$

where R = oxygen uptake and W = live weight.

The variability in these results may partially reflect the inaccuracies inherent in the estimation of both length and weight. Another source of error could arise from the use of groups containing animals of differing sizes, where the length of one or more animals is not included in the mean for the group owing to loss during recovery from

Fig. 33 Relationship of characters lengths A and B to body length. The equations for the linear regressions are:-

A: $y = 0.08x + 13.96$, $r = +0.95$.

B: $y = 0.05x + 5.39$, $r = +0.93$.

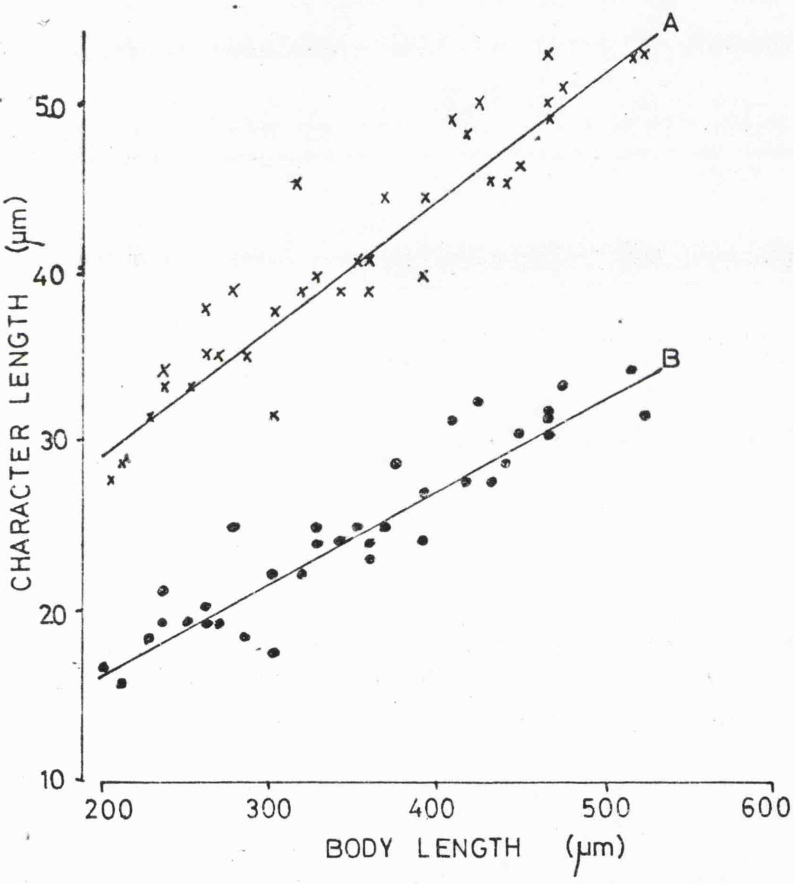

A
B
CHARACTER LENGTH (μm)
50
40
30
20
10
200
300
400
500
600
BODY LENGTH (μm)

Fig. 34 Relationship between oxygen uptake per individual and live weight of *M. furciger* at 5° and 10°C plotted on a double $\log_{10}$ scale.

▲ Rates for individuals at 5°C

● Rates for individuals at 10°C

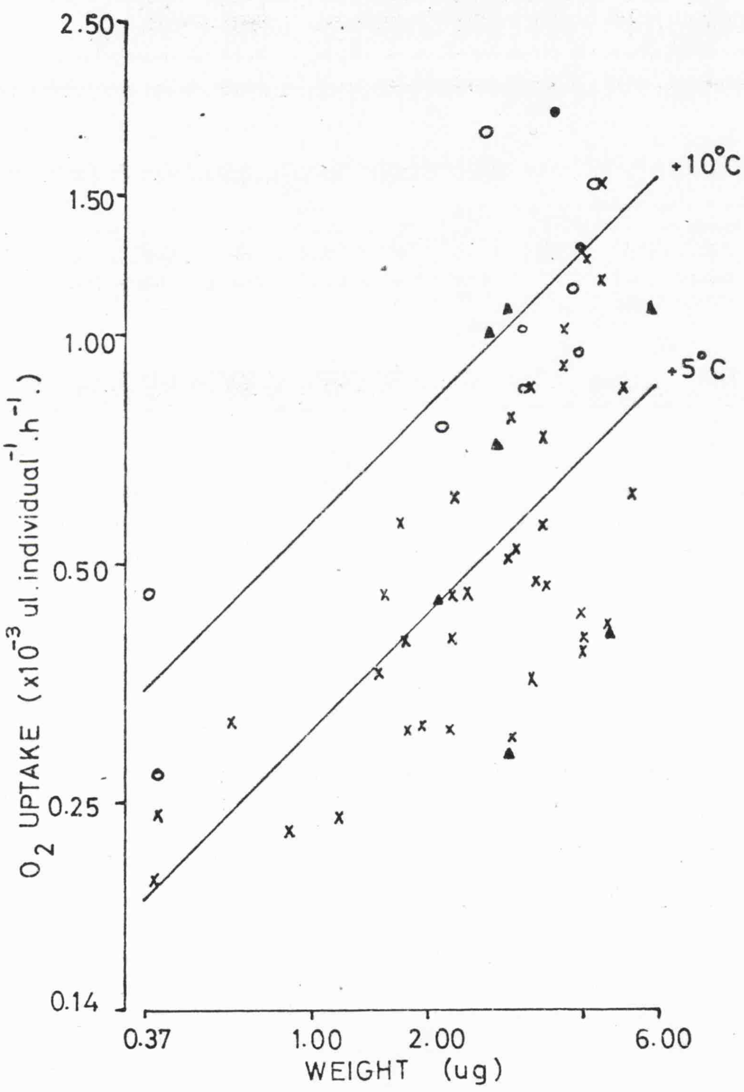
× Rates for group means at 5°C

○ Rates for group means at 10°C

The equations for the linear regressions are:-

5°C: $\log_{10}y = 0.51 \log_{10}x - 0.31$, $r = +0.67$

10°C: $\log_{10}y = 0.51 \log_{10}x - 0.57$, $r = +0.89$



2.50
1.50
1.00
0.50
0.25
0.14
O_2 UPTAKE ($x10^{-3}$ ul. individual^{-1}.h^{-1}.)
+10°C
+5°C
0.37
1.00
2.00
6.00
WEIGHT (ug)

the diver, or the absence of values for animals in the simplex stage. The parallel nature of the two regression lines in Fig. 34 ($t = 0.06$ with $df = 51$) indicates that the relationship between metabolic rates at the two temperatures was constant over the whole weight range. The calculated Q_{10} for the temperature range $5^{\circ}C$ to $10^{\circ}C$ is 3.46.

To determine the oxygen uptake of a given population, it is essential to know the age structure of the population. Various authors have reported estimates of the number of moults through which each species may pass, and these have been reviewed by Ramazzotti (1972a). The number of moults for Macrobiotus is reported as being from 6 to 12. Using body length-frequency analysis (Higgins, 1959; Franceschi & Lattes, 1969; Morgan, 1973) no pattern was distinguished in the present study, possibly because of the small sample size. Even with a large sample the problems involved in interpreting the data are numerous, and the method has been criticized by Baumann (1961) and Hallas (1972). However, it is desirable to express the respiration data in a form which can be applied easily to field populations. Five equal but arbitrary size groups were selected covering the body length range of the experimental animals (although it was known that some Signy Island specimens exceed 650 µm). Using the mid-point of each size group a body weight has been calculated and oxygen uptake rates per individual have been taken from Fig. 34 (Table XXIII). Weight specific oxygen uptake rates are also shown and they show the expected decrease with increasing body weight.

6.5 Metabolism of Antarctic Tardigrada

Of respiratory studies completed on small metazoan poikilotherms, few relate to the terrestrial fauna. Of those which do, the majority have been undertaken at temperatures well above those used in

Table XXIII. Live weight and oxygen uptake at 5° and 10°C for the mid-size of each size class of *Macrobiotus furciger*.

Size class	Body length (µm)	Live weight (µg)	Oxygen uptake: µl O_2 $g^{-1}h^{-1}$		Oxygen uptake: µl O_2x10^{-3} $individual^{-1}h^{-1}$	
			5°C	10°C	5°C	10°C
1	151-250	0.35	519.1	965.1	0.18	0.34
2	251-350	1.19	285.0	529.8	0.34	0.63
3	351-450	2.83	186.4	346.5	0.53	0.98
4	451-550	5.52	134.4	249.8	0.74	1.38
5	551-650	9.54	102.8	191.1	0.98	1.82

the present investigation. Thus a comparison of this study with other results is difficult. No other weight related metabolic data are available for the Tardigrada, but figures are presented in Table XXIV for representatives of other mesofaunal groups which are found at the SIRS. The value for the exponent b (in the equation $R = aW^b$) for Rotifera (b = 0.39) and Tardigrada (b = 0.51) are lower than those usually found for small poikilotherms: 0.6 to 1.0 (Hemmingsen, 1950; Zeuthen, 1953). Doohan (1973) suggested that the low value for the Rotifera examined resulted from the progressively higher proportion of total body weight contributed by metabolically inactive yolk and lorica as body size increases. The low value for Tardigrada may also, in part, be attributed to an increase in yolk in the larger size groups, but it is unlikely that any proportional increase in skeletal structures takes place.

The only other measurements on the respiration rates of Tardigrada are those of Pigon & Weglarska (1953, 1955a and b, 1957) in Poland. As part of a study comparing respiration rates of tardigrades in different physiological states, they examined active animals of <u>M. hufelandii</u> and <u>M. dispar</u> J. Murr. using a Cartesian Diver micro-respirometer. Groups of 10 individuals were used and all measurements were made at 20°C. The rate for <u>M. hufelandii</u> was 9.8×10^{-4} µl individual^{-1} h^{-1}, but as no body size measurements were given a comparison with the present study is not possible. The specimens of <u>M. dispar</u>, however, were between 500 - 700 µm in length and gave a mean rate of oxygen uptake of 1.0×10^{-3} µl individual^{-1} h^{-1}. This rate is much less than that calculated for the largest size group of <u>M. furciger</u> at 10°C (Table XXIII). The regression line at 10°C (Fig. 34) is based on only 11 points but nevertheless the comparison suggests some physiological adaptation of <u>M. furciger</u> to the low

Table XXIV. Values for the exponent b in the equation $R = aW^b$ for five groups of small invertebrate poikilotherms.

Group	b	Author	Notes
Rotifera	0.39	Doohan (1973)	6 aquatic species
Nematoda	0.67	Klekowski *et al.* (1972)	22 soil species
Tardigrada	0.51	Jennings (1975)	1 Antarctic species
Acari	0.70	Berthet (1964)	16 litter species
Collembola	0.75	Block & Tilbrook (1975)	1 Antarctic species

temperatures of the maritime Antarctic.

6.51 *Macrobiotus furciger* size class analysis

As indicated previously a size-frequency histogram of the SIRS *M. furciger* population did not show the pattern found by Higgins (1959), Franceschi & Lattes (1969) and Morgan (1973) for other species of *Macrobiotus*. Consequently, estimates of size distribution for selected months at SIRS 2 were made by sub-sampling from preserved material and grouping individuals into five equal size classes based on body length estimates (Table XXV). The similar size distribution throughout the year, particularly the consistently high proportion of individuals in size classes three and four, makes interpretation very difficult. A similar pattern has been noted for an Antarctic micro-arthropod (Tilbrook, in press) and also a temperate tardigrade (Morgan, 1973). Both authors point out that this may be caused by some short-comings in technique, leading to a loss of many of the smaller sized animals. Since all three techniques were widely different, however, and all three results so similar, an alternative explanation should be sought. It has been suggested by Hallas (1972) that newly hatched Eutardigrades are invariably no longer than three times the egg diameter, and that the egg size is controlled by environmental factors. The mean egg diameter of *M. furciger* found on Signy Island was 96 µm, and using the three times rule of Hallas, a newly hatched specimen would be 288 µm. The low proportion of specimens falling into size class one is not, therefore, as unexpected as it may at first appear. An alternative explanation has been advanced by Tilbrook (in press) for an Antarctic collembolan. If development after hatching was rapid compared with subsequent growth, a build up of the medium sized groups would result. Neither of these two suggestions can be accepted at the present time without a more detailed study of the life history of

Table XXV. Size class distribution of *Macrobiotus furciger* on SIRS 2.

Date	Number measured	% in size class (µm) 1	2	3	4	5
		250	251-350	351-450	451-550	551
07-01-72	56	3.6	17.9	30.5	35.7	12.4
05-02-72	85	10.6	20.0	28.2	30.6	10.6
04-05-72	61	4.9	31.1	36.1	21.3	6.6
02-07-72	38	7.9	21.0	28.9	34.2	7.9
04-09-72	100	4.0	15.0	38.0	37.0	6.0
02-10-72	42	4.8	7.1	40.5	42.9	4.8
30-12-72	85	10.6	27.1	37.6	17.6	7.1
28-01-73	105	14.3	29.5	34.3	16.2	5.7
28-02-73	100	7.0	17.0	23.0	35.0	18.0

M. furciger. The similar proportion in all size classes throughout the year would suggest a continuous recruitment period, with eggs hatching as conditions allow. It seems likely that generations span more than one year and that growth is sporadic, probably due to the environmental conditions.

6.52 Macrobiotus furciger population metabolism on the SIRS

From the respiration data presented in section 6.43, population densities discussed in section 6.31 and the size class structure of section 6.51 it is possible to make an estimate of the total population metabolism of this species. It was assumed in this analysis that tardigrade respiration below $0^{o}C$ is negligible. The physiological state adopted during the winter months by Signy Island tardigrades is not known but Pigon & Weglarska (1953) state that the respiration rate of cysts of M. dispar was 4 times slower than the respiration of the active animals at $20^{o}C$ and that dried specimens of M. hufelandii respired 600 times slower than the active specimens. The population metabolism for 30 day periods between January 1972 and March 1973 on SIRS 2 has been calculated (Fig. 35). These estimates range from 36.831 ml O_2 m^{-2} to a negligible amount during the winter months. The mean monthly rate over the period February 1972 to January 1973 was 10.551 ml O_2 m^{-2}, or an annual uptake of 126.610 ml O_2 m^{-2}.

In the absence of published information on tardigrade energetics the present data were used to extrapolate population metabolism for M. furciger at SIRS 1, and total metabolism for all species of Tardigrada at both sites. It was assumed that the age class structure on SIRS 1 was identical to that found for SIRS 2. Thus the estimated range of population metabolism at SIRS 1 (Fig. 36)

Fig. 35 Mean 30 day moss temperature (0–6 cm in ^{o}C), fluctuations in mean population density ($\times 10^{3}$ m^{-2}), mean biomass (mg m^{-2}) from Table XIII (broken line) and Tables XXIII + XXV (continuous line) and total population respiration (ml m^{-2}) of _M. furciger_ on SIRS 2.

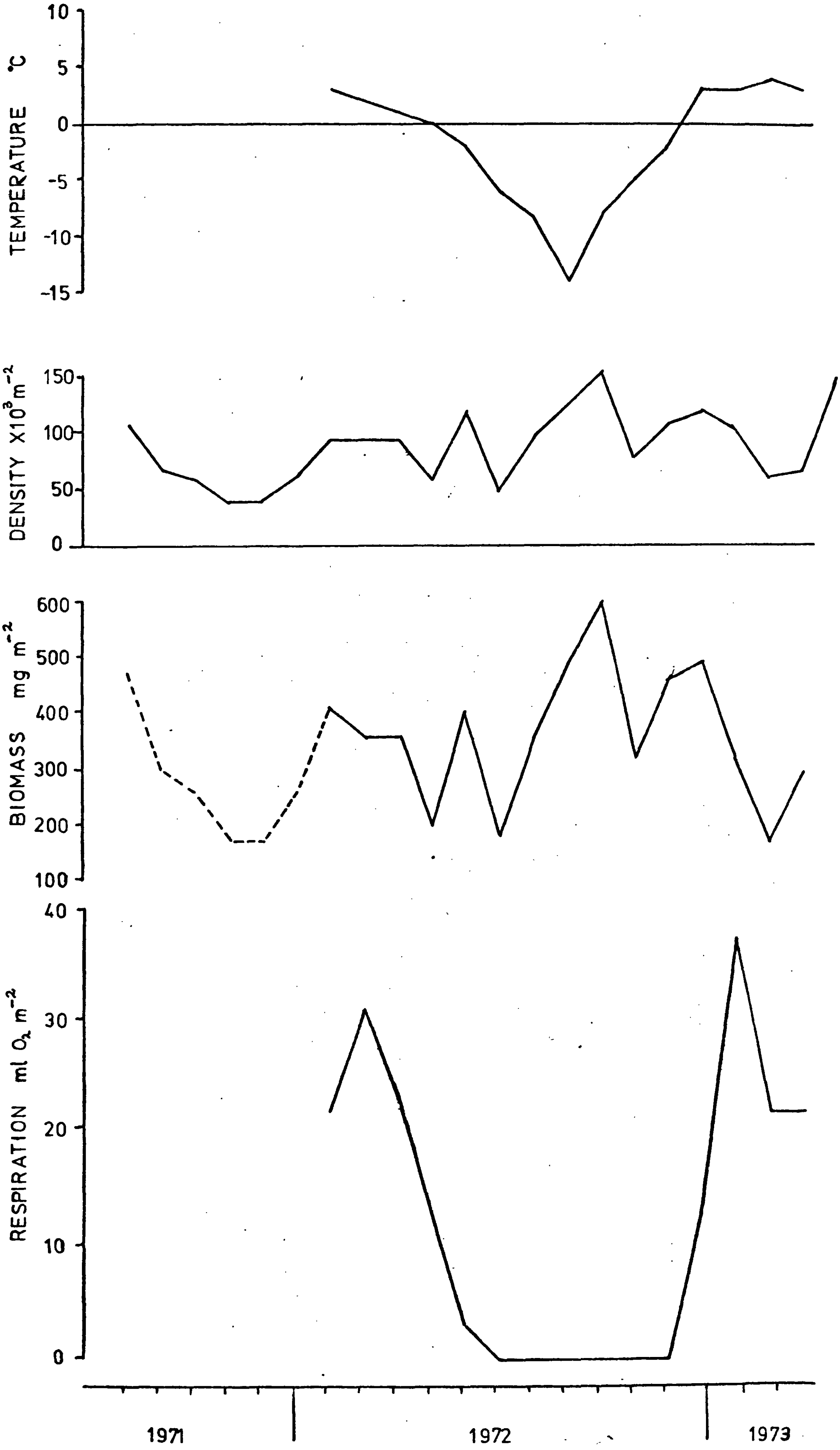
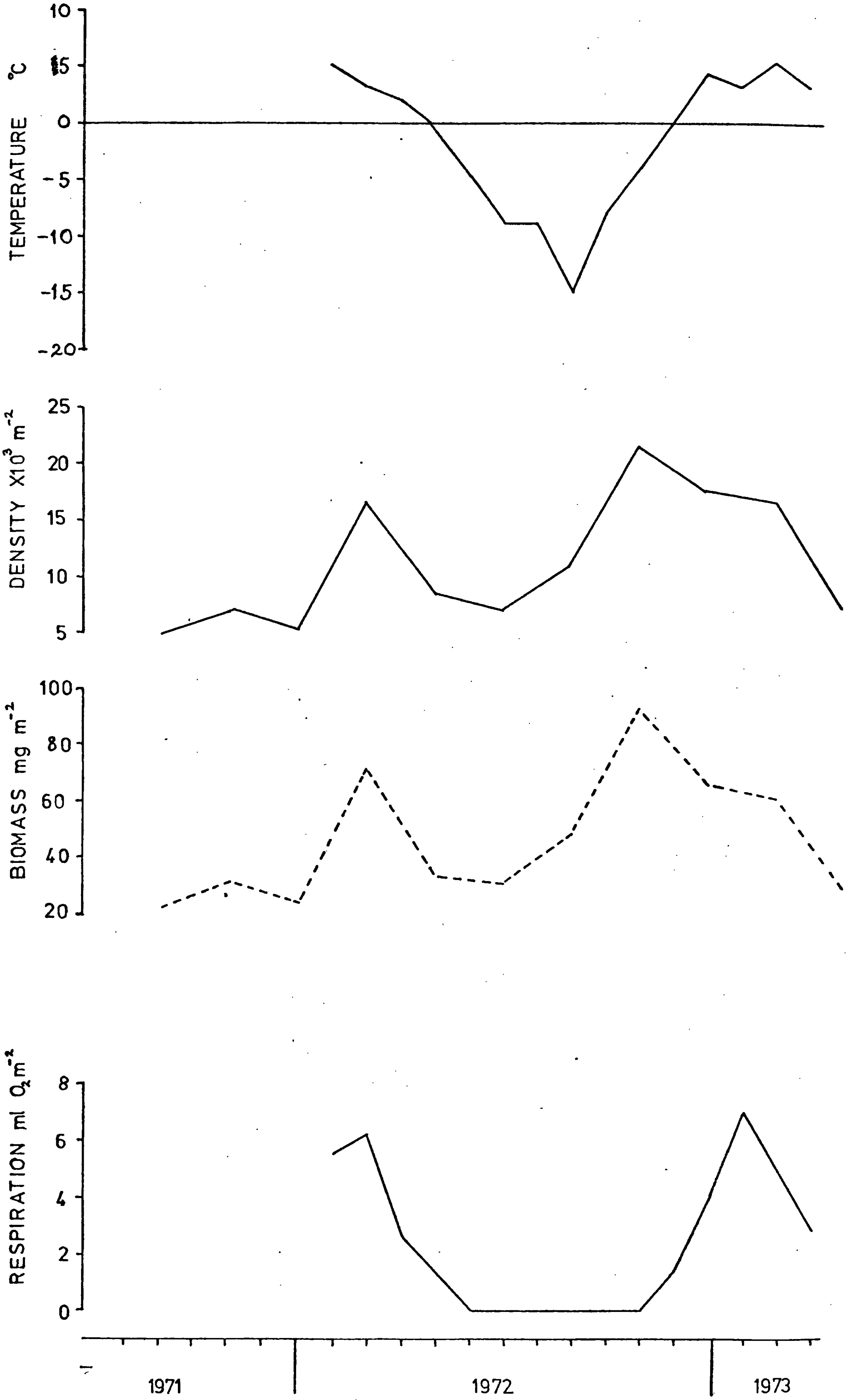

TEMPERATURE °C
10
5
0
-5
-10
-15
DENSITY X10^3 m^{-2}
150
100
50
0
BIOMASS mg m^{-2}
600
500
400
300
200
100
RESPIRATION ml O$_2$ m^{-2}
40
30
20
10
0
1971
1972
1973

Fig. 36 Mean 30 day moss temperature (0–6 cm in ^{o}C), fluctuations in mean population density ($x10^{3}$ m^{-2}), mean biomass (mg m^{-2}), assuming mean animal weight from Table XIII, and total population respiration (ml O_2 m^{-2}) of M. furciger on SIRS 1.



TEMPERATURE °C
10
5
0
-5
-10
-15
-20
DENSITY X10³ m⁻²
25
20
15
10
5
BIOMASS mg m⁻²
100
80
60
40
20
RESPIRATION ml O₂ m⁻²
8
6
4
2
0
1971
1972
1973

was 7.153 ml O_2 m^{-2} to a negligible amount in the period May to October with a monthly mean of 1.890 ml O_2 m^{-2}, or six times less than that found on SIRS 2. Since the mean monthly density of M. furciger on SIRS 1 (13 x 10^3 animals m^{-2}) was eight times less than that of SIRS 2 (102 x 10^3 animals m^{-2}) then the inference is that SIRS 1 was the more favourable habitat in terms of tardigrade activity. This conclusion, however, should be treated with care. The observation that M. furciger activity decreased at temperatures above 15°C (section 5.41) warrants further investigation in this context, since temperatures in the upper 3 cm of SIRS 1 moss often exceeded 15°C during the summer months of both 1972 and 1973, whereas SIRS 2 moss temperatures only rarely rose to this level.

6.53 Total tardigrade metabolism at the SIRS

Activity, food source and basal metabolic rate are likely to vary from species to species, and this would in turn affect the rate of oxygen uptake of individuals. However, to give an indication of the total tardigrade metabolism at the two sites, the mean weights of Echiniscus sp., H. (H.) dujardini and H. (D.) alpinus + H. (D.) pinguis (from Table XIII) have been used to estimate their rates of oxygen uptake from the curves obtained for M. furciger. The resulting annual rates (Table XXVI) for all species are 210.817 ml O_2 m^{-2} and 507.230 ml O_2 m^{-2} on SIRS 1 and 2 respectively, giving a mean monthly rate of 17.568 ml O_2 m^{-2} on SIRS 1 and 42.269 ml O_2 m^{-2} on SIRS 2. The difference between these two estimates is therefore only a factor of 2.4.

Unfortunately, no information is available on the numbers of eggs of any tardigrade species, nor were any experiments undertaken on the oxygen uptake of the eggs, and so this component is not included in the above estimates.

Table XXVI. Total population respiration (ml O_2 m^{-2}) over 30 day intervals on the SIRS for each tardigrade species and species-group. Respiration assumed to be negligible at moss temperatures below $0^{\circ}C$ (May 1972 to October 1972 on SIRS 1, June 1972 to November 1972 on SIRS 2).

	SIRS 1					SIRS 2				
	Echiniscus sp.	Macrobiotus furciger	Hypsibius (H.) dujardini	Hypsibius (D.) alpinus-pinguis	Total tardigrades	Echiniscus sp.	Macrobiotus furciger	Hypsibius (H.) dujardini	Hypsibius (D.) alpinus-pinguis	Total tardigrades
Jan 72	0	5.54	0.11	30.33	35.99	0.14	22.44	0.73	62.05	85.36
Feb 72	0	6.16	0.13	33.66	39.95	0.35	31.18	0.28	112.95	144.77
Mar 72	0.06	2.57	0.11	22.45	25.20	0.62	23.98	0.14	83.91	108.92
Apr 72	0.07	1.36	0.10	17.96	19.49	0.08	13.00	0.11	36.05	49.24
May 72						0.02	2.63	0.02	6.62	9.29
Nov 72	0.02	1.38	0.03	10.69	12.11					
Dec 72	0.06	4.05	0.09	33.30	37.51	0.02	18.98	0.35	48.70	68.06
Jan 73	0.67	7.15	0.80	67.91	76.53	0.41	36.83	1.69	88.00	126.94
Feb 73	1.35	5.00	1.56	67.88	75.78	0.82	20.66	2.36	103.49	127.33
Mar 73	0	2.56	0.14	0.39	3.09	0.87	20.78	9.55	48.92	80.12

SECTION 7: THE TERRESTRIAL ROTIFERA OF THE ANTARCTIC REGION

The moss inhabiting Rotifera have been very poorly studied anywhere in the world, and this lack of study is particularly evident for the Antarctic region. Those papers which have been published have been predominantly concerned with descriptive taxonomy, rather than ecological aspects of the Rotifera (Richters, 1907; Murray, 1910a; Sudzuki, 1964). Even in this aspect, the difficulties encountered are formidable, leading Sudzuki (1964) to comment "The moss-dwelling rotifers are generally deemed too difficult to be classified up to the level of the species". This is because the moss rotifers (predominantly Bdelloidea) belong to the illoricate group and are liable to contract into a ball very rapidly under the slightest stimulation, making determination even to the category of family impossible. Generic characteristics often depend on details of the foot, and specific identification is only possible when the animals are actively feeding.

However, the Rotifera are a conspicuous component of the Antarctic moss fauna, and an understanding of their ecology (no matter how incomplete) is an essential precursor to the total ecosystem analysis which is envisaged for the two SIRS.

7.1 Methods

The methods used to recover and count the Rotifera were identical to those used for the Tardigrada (section 4), and the information on both groups was obtained simultaneously from the same samples. Because of the difficulties of identification previously mentioned only four categories were recognised:-

(1) _Adineta_ - here the rostrum is not retractile and the wheel organ (from whence the name Rotifera is derived) is not of the normal

bdelloid type. Instead a terminal ciliated area is present on which the animals glide over their substrate.

(2) Bdelloidea (other than _Adineta_) - similar in general appearance to the _Adineta_ but with well developed wheel organs. The animals either creep in a leech like fashion or (rarely) swim freely.

(3) Monogononta - body of various forms but all lack the rostrum, they glide or swim but never proceed like a leech.

Before the onset of the field study some attempt was made to identify the species present on the SIRS, with the help of Dr J Donner, A/2801 Katzelsdorf, Austria. He kindly identified a number of species from SIRS 1, and these were:-

Adineta gracilis	_Habrotrocha pulchra_	_Philodina plena_
A. steineri	_H. constricta_	_Philodina_ sp.
A. vaga	_H. crenata_	
Macrotrachela concinna	_Mniobia ostensa_	
M. kallosoma	_M. vicina_	

The extraction technique was not as efficient for the rotifers as it was for tardigrades (Table XXVII). The densities reported for the Rotifera, therefore, has not been increased as there is some evidence that the population changed during the extraction. Isolated Rotifera were kept in a hanging drop under the conditions of an extraction and were observed daily for a period of 21 days. Nine of the ten Rotifera studied produced eggs within the first six days, three within the first four days. Of those which produced eggs the mean duration between successive eggs was three days, and each egg took between six and seven days to hatch. The favourable environment during extraction may therefore hasten the development of eggs already in the moss core, since a control group kept at $0^{o}C$ did not produce any eggs.

Table XXVII. Comparison of the total extractable populations of Rotifera predicted by the maximum likelihood estimate (M.L.E.) of Moran(1951), and the empirical method of Skellam (1962). Percentage extraction after 24,48 and 96 h has been calculated for each method.

	Total numbers			% extracted from predicted population					
	observed	predicted		M.L.E.			empirical		
	96 h	M.L.E.	empirical	24 h	48 h	96 h	24 h	48 h	96 h
Bdelloidea	5093	5280	6803	59	78	96	46	61	75
<u>Adineta</u>	1304	14243	3163	2	5	9	10	21	41

The very low efficiency predicted by both the maximum likelihood estimate and by Skellam's empirical method for the extraction of Adineta may be accounted for by its feeding habits. Adineta does not possess the trochal discs of other bdelloid Rotifera. Instead it glides over the substrate on its ciliated rostral area cropping the overlying film. It is thus possible that this dependence on contact with the substrate makes it less likely for the animals to move down into the extraction tray.

With respect to the three assumptions on which the counting procedure relies (section 4.42) only the second assumption needs further comment. In the counting tray (Fig. 26) the Rotifera remain highly mobile. The Bdelloidea, for example, although rarely swimming freely, were still capable of moving rapidly into and out of the microscope field of view. Consequently the Rotifera numbers reported are only approximate densities within each site.

7.2 Distribution and population studies of the Rotifera

7.21 Signy Island

The distribution and abundance of the four broad taxonomic groupings of Rotifera in eight sites is represented in Table XXVIII. Little pattern emerges from these data, although it is noteworthy that the two highest population densities were recorded for sites which are known to be directly influenced by vertebrates, Prasiola crispa and Drepanocladus uncinatus (E and H). However, this group also attains moderately high densities (0.500×10^6 m^{-2}) in the Deschampsia antarctica site (F). Nematoda were found to reach their highest densities on Signy Island in soils under vascular plants (Spaull, 1973a), with 7.470×10^6 m^{-2} from a Deschampsia site. In a penguin

Table XXVIII. The distribution and mean density m^{-2} of rotifer groups in eight sites on Signy Island. Site descriptions are given in section 4.11. Confidence limits at the 95% level are underlined.

Site	Date	Adineta	Bdelloidea (other than Adineta)	Monogononta	Unidentified	Total Rotifera
A	Oct 72	6 720	8 960	13 840	4 320	33 760
		7 489	5 948	6 223	4 709	12 327
	Mar 73	10 320	61 040	2 800	32 320	106 480
		4 282	21 907	1 830	8 548	27 795
B	Mar 73	1 920	169 040	-	195 520	366 480
		4 321	308 142		437 979	749 633
C	Mar 73	11 433	69 037	-	28 391	108 861
		20 575	33 667		20 174	54 196
D	Oct 72	43 342	51 709	1 611	11 329	107 992
		22 733	44 388	1 184	10 601	69 889
	Mar 73	14 291	6 756	-	7 068	28 115
		18 368	9 452		7 531	25 961
E	Mar 73	55 815	677 571	48 747	205 589	931 388
		15 503	335 997	27 127	69 399	403 022
F	Oct 72	7 276	424 690	11 641	57 789	497 239
		8 794	333 316	4 947	58 716	352 920
	Mar 73	22 659	299 549	79 201	83 566	484 974
		8 904	100 509	61 090	45 987	159 480
G	Mar 73	119 113	136 574	6 653	43 030	305 370
		153 006	95 767	10 795	42 546	256 699
H	Mar 73	129 507	261 924	10 186	218 685	618 223
		36 153	116 376	6 505	124 896	205 871

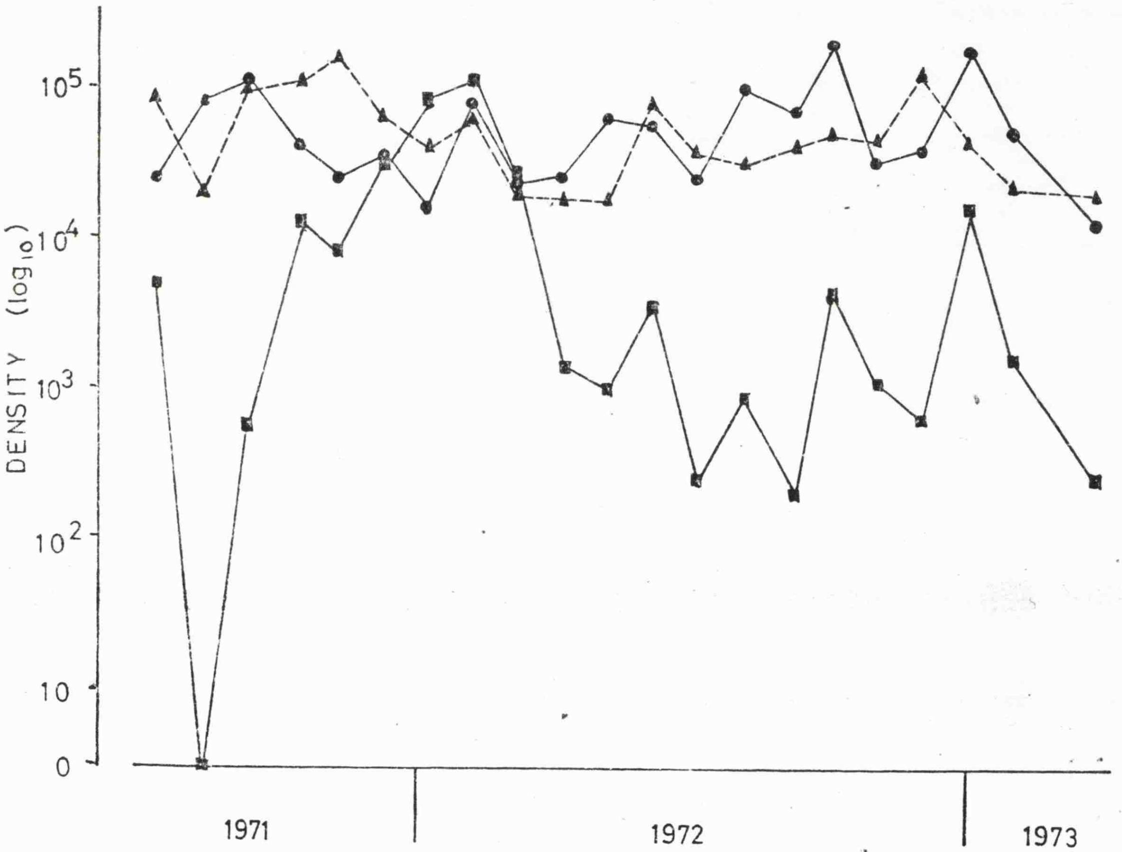
Fig. 37 Three month running means of density m^{-2} for each of the rotifer groups on SIRS 2.

▲ Adineta

● Bdelloidea other than Adineta

■ Monogononta

(Total Rotifera are shown on Fig. 29).



10^5
10^4
10^3
10^2
10
0
DENSITY ($\log_{10}$)
1971
1972
1973

rookery the population density was estimated at $4.040 \times 10^6\ m^{-2}$, much higher than in most of the moss communities and in this respect similar to the distribution of the rotiferan and tardigrade populations. Smith (1973c) however, did not report a similar pattern for the Protozoa of Signy Island.

7.22 The maritime Antarctic

Rotifera were found in all samples collected in the austral summer of 1974. Adinetids were present in 84% of the samples, while other bdelloid rotifers were recovered from 98% of the samples. Although Monogononta were never abundant, they were found in 30% of the samples. Total rotifer densities ranged from $0.005 \times 10^6\ m^{-2}$ in a mat of Drepanocladus on level ground, to $0.223 \times 10^6\ m^{-2}$ in a mat of Drepanocladus near a penguin rookery. Both these samples were taken from Avian Island (M and N).

7.23 The SIRS

Because the samples from SIRS 1 were preserved by 10% formalin only the total Rotifera recovered were counted (Appendix I). On SIRS 2, however, each of the four components recognised were counted (Appendix I). The rotifer density of SIRS 1 and 2 were maintained at a level similar to that recorded for the Tardigrada, and here again there are no marked cyclical trends. Only the monogonont Rotifera of SIRS 2 showed any consistent pattern, with a maximum density reached during February 1972 and December 1972 (Fig. 37).

As was seen for the Tardigrada on the SIRS (section 6.31), core densities could not be linked with any other measured factor.

SECTION 8: DISCUSSION

8.1 Comments on the tardigrade fauna in the Antarctic region

There is evidence that Signy Island was overridden by the South Orkney Islands ice sheet about one million years ago, and similar glaciations were likely to have occured throughout the maritime Antarctic at this time. Substantial retreat of these ice sheets has only taken place in the past few thousand years (Holdgate, 1967). Much of the present terrestrial fauna has, therefore, resulted from immigration in the fairly recent past, since the climate during this glacial advance was too severe for the survival of relic populations (Gressitt, 1965).

The arrival of nematodes from other areas, and presumably many other microscopic invertebrates, probably occurs continuously, but, due to direct unfavourable biotic and abiotic factors, a great number do not survive (Dao, 1970). The most important single factor for species survival in the Antarctic region is an ability to withstand the long winter freeze. This lasts for seven to eight months on Signy Island, longer elsewhere (Fig. 2), with subzero temperatures followed and preceded by freeze-thaw cycles (Chambers, 1966b).

The mechanisms for winter survival of the Antarctic terrestrial fauna are not known, although whole animal freezing experiments, particularly of the insects, are providing clues to this problem. There are two common natural means by which living organisms may avoid frost injury (Asahina, 1966) and these are supercooling and frost resistance. The former avoid freezing injury while the latter can withstand the formation of small ice crystals within their tissues. Sayre (1964) has shown that Antarctic winter soil temperatures fall well below the level to which nematodes usually supercool and so it seems likely that the nematodes at least fall within the frost resistant groups. The eggs of nematodes, however, may supercool to much lower temperatures (Sayre, 1964) and are therefore a potential means for surviving the winter freeze. This seems unlikely to apply to the Tardigrada, however, since high numbers of adults were found throughout the winter on the SIRS (Fig. 29).

Having survived the winter freeze, if they are to maintain viable populations, the fauna must be able to adequately reproduce to compensate for winter mortality. The rate of development of small metazoan poikilotherms depends largely on the temperature of their environment, and although the period when development is possible in the Antarctic is only four to five months at the maximum, summer temperatures in the upper layers of the moss are more favourable than the macro-climatic data would suggest (Fig. 28). Respiration studies on an Antarctic collembole (Tilbrook and Block, 1972; Block and Tilbrook, 1975) and mites (Goddard, in press a and b; Block, in press) suggest that some degree of metabolic adaptation to low temperatures exists in these groups. The data presented for an Antarctic tardigrade (section 6.43) also indicate some adaptation to a colder environment, suggesting that this may play a significant role in Antarctic faunal development generally. The higher metabolic rates of these cold adapted animals at low temperatures, when compared with similar temperate species, mean that they are better able to utilise the cooler temperatures of the brief Antarctic summer.

8.2 Food requirements of the SIRS Tardigrada

Hallas & Yeates (1972) have suggested that the feeding habits of the Tardigrada may be deduced from the structure of the buccal apparatus, and their suggestions would fit the observations made in the present study. The sturdy apparatus and terminal mouth of M. furciger suggests a carnivorous diet, and this species has often been observed attacking active Nematoda and inactive Rotifera. It was also once observed investigating a moribund specimen of its own species. However, the green gut contents of this species suggests an omnivorous diet since none of the animals on which it has been seen to feed have any green coloration in their gut or elsewhere. The weak stylets and sub-terminally positioned mouth of H. (D.) alpinus and H. (D.) pinguis suggests that these are detritus feeders, while H. (H.) dujardini is known to feed on algae (Baumann, 1961).

8.3 Energetics

Although it has been suggested by Collins et al. (1975) that the Tardigrada are of little significance in the energy flow of the terrestrial Antarctic ecosystem when compared with other groups, this does seem to be the case. Table XXIX shows the density and biomass of the mesofaunal groups represented on the SIRS. Even though some of these estimates lack the precision desirable, they do indicate that the biomass of the tardigrades is second only to that of the collembola on SIRS 1, and that they are the most important single group on SIRS 2. Naturally the micro-organisms of both sites are likely to be of far greater importance in terms of their biomass and energy throughput than any of the groups studied to date, and Holdgate (1967) has pointed out that the biomass of plant material vastly exceeds that of the fauna dependant upon it.

Several studies along the lines envisaged for the SIRS have now been completed in tundra areas under the auspices of the International Biological Programme (Rosswall & Heal, 1975). It is perhaps significant that discounting the report by Collins et al. (1975), which deals with Signy Island, the Tardigrada are only once mentioned (Bliss, 1975) and no mention whatsoever is made of any rotiferan fauna, although both groups probably occur on many of the sites considered.

Table XXIX. Mean density (d) of animals m^{-2} and biomass (b) in mg ww m^{-2} of each mesofaunal group represented on the SIRS. Density and biomass are also given for a mossy ridge at Tareya, USSR, (Chernov et al., 1975) and a spruce forest in Finland (Huhta & Koskenniemi, 1975).

	Rotifera		Tardigrada		Nematoda		Enchetraeidae		Lumbricidae		Acarina		Collembola		Others	Total
	d	b	d	b	d	b	d	b	d	b	d	b	d	b	b	b
SIRS 1	207,000	35[a]	192,000	235[e]	1,002,000[f]	156[f]	-	-	-	-	12,000[g]	39[g]	63,000[h]	807[h]	-	1,272
SIRS 2	180,000	31[a]	531,000	816[e]	21,000[f]	11[f]	-	-	-	-	-	-	10,000[g]	362[g]	-	1,220
USSR	-	-	-	-	1,700,000	1,020	800	1,660	5	1,990	7,600	210	44,000	1,860	400	7,140
Finland	31,800	5[c]	48,200	105[e]	1,125,000	200	4,000	956	0.3	20	73,100	1,223	25,400	105	613	3,227

a Mean weight of Rotifera derived assuming inactive specimens to be spheres of a radius 34 μm and density 1.04. Then ; weight $= 4/3 \pi (r)^3 \times 1.04 \times 10^{-6}$ μg.

c Biomass figures are not given in the original. Rotifer weights calculated as above, mean tardigrade weight assumed to be 2.19 μg (from Table XIII).

e Present study.

f Spaull (1973b).

g Goddard (pers. comm.).

h Tilbrook (in press).

This, perhaps, is a reflection of the assumed relative insignificance of these two groups in the tundra biome, where other mesofaunal and larger herbivores are present. However, as Table XXIX indicates, the Tardigrada are a significant faunal component in the Signy Island sites, and although these sites support only 1/6 of the total invertebrate biomass found in Tareya (Chernov et al., 1975) and 1/3 of that reported for a finnish spruce forest (Huhta + KOSKENNIEMA, 1975), they may warrant further investigation in other sites. For example, the tardigrade densities of 100 tardigrades m^{-2} in a pasture soil of Devon Island, Canada, reported by Ryan (1972), were derived from cores extracted by the Baermann funnel. In the present study this extraction procedure recovered only 19 animals, whereas the tray method recovered 2,070 tardigrades (section 4.41). Since the tray method was only 70% efficient for the Tardigrada, Ryan could be dealing with population densities up to 130 times as high as his data would suggest.

8.4 Future studies

The neccessity of obtaining a firm taxonomic understanding of the Tardigrada has been emphasized. This work is now likely to be undertaken by American workers using material in the Smithsonian Institution, where a worldwide reference collection is now being created, and the results of this work should be available within the next few years. The majority of the works on Tardigrada are of a descriptive nature, but certain aspects of their physiology have also attracted much interest, such as the animal in anabiosis. Studies on the structure of the tardigrade cuticle are also very popular at the present time. However, very little sound ecological work has been undertaken, and this is probably not due to taxonomic difficulties alone, although these are formidable, but may also in part be caused by the lack of a standard extraction procedure. Until recently, the

classical method of recovery was to soak air dried mosses in tap water, and subsequently rinsing the samples until no further tardigrades were recovered. This process was laborious (estimated by Ramazzotti, 1972a, to take four days to analyse a 5 cm^3 sample) restricting the number of units which could be dealt with, and was likely to alter in efficiency between workers and locations. Morgan (1973) has used a refinement of this technique, but reverted to the washing previously described in order to obtain eggs. The modified Baermann or tray method has been adopted independantly by both Hallas & Yeates (1972) and in this study. Its main advantage is that it is inexpensive and simple, and it therefore allows the handling of large numbers of sampling units.
Although it is relatively efficient, it still does not extract the eggs. Recently, however, Hallas (in press) has developed an extraction procedure based on flotation and filtration principles which will extract moulted cuticles containing eggs, although with an unknown efficiency. It is not capable of recovering many of the Macrobiotus eggs which adhere to the substrate with their processes. The drawback to this method is that it is intended for the extraction of tardigrades alone, whereas the tray method was developed for nematodes and works well with both tardigrades and rotifers, thus making it more attractive to workers having a broadly based interest in several groups.

Only two reports of tardigrade respiratory studies have been made, and only the present work was intended for use in an ecological investigation. The studies of Pigon & Weglarska (1953, 1955a and b, 1957) formed part of an investigation of the animal in anabiosis. Clearly, these studies must be continued, particularly for the smaller but more numerous Hypsibius component, which are invariably present in the mosses worldwide, and are usually numerically dominant.

Knowledge of the food requirements of most species is unknown. Although their culture is reported to be simple (Dougherty, 1964; Sayre, 1969), attempts made during the present investigation were fruitless. Without information on the food intake of this group it is not possible to assess the true role of individual species within a given ecosystem and this aspect therefore warrants a much fuller investigation.

8.5 The Rotifera

Many of the comments made above are equally applicable to the Rotifera. Perhaps the most significant obstacle in any investigation involving the bdelloid rotifers is their identification. Of over 100 workers reported by Gilbert (1973), only four have any declared interest in the Bdelloidea, by far the majority specialising in the truly aquatic rotiferan fauna. There is a complete lack of any type material for the Bdelloidea, and only recently (Robotti & Lovisolo, 1972) has a method been developed for obtaining such material. Only Dr J Donner has the knowledge and experience in this group, which many possess for other animal groups. Little progress can be expected in studies of this group until the taxonomic difficulties have been overcome, but few wish to tackle this aspect.

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SUMMARY

1 The general development of Antarctic research and the reasons for the research presented in this thesis were outlined.

2 The Antarctic region was divided into continental, maritime and sub-Antarctic areas on climatic and floral characteristics. Physical and biotic features of the maritime Antarctic were then described, particularly those on Signy Island.

3 Features of taxonomic significance in the phylum Tardigrada were discussed, with particular reference to those of the Antarctic tardigrades.

4 The tardigrade species recovered from the Antarctic in this study were described and illustrated. These were *Echiniscus* (*E.*) *meridionalis*, *E.* (*E.*) *capillatus*, *Oreella mollis*, *Macrobiotus ambiguus*, *M. furciger*, *Hypsibius* (*H.*) *dujardini*, *H.* (*H.*) *oberhaeuseri*, *H.* (*Isohypsibius*) *asper*, *H.* (*I.*) *papillifer*, *H.* (*I.*) *renaudi*, *H.* (*Diphascon*) *alpinus*, *H.* (*D.*) *chilenensis*, *H.* (*D.*) *pinguis*, *H.* (*D.*) *puniceus*, *H.* (*D.*) *scoticus*, *H.* (*D.*) sp. and *Milnesium tardigradum*.

5 Small members of the sub-genus *Diphascon* were difficult to distinguish, separation in this work was made on the diameter of the buccal tube, length of the placoid line and length of the third macroplacoid.

6 The recoveries in this investigation are compared with those of previous workers in the Antarctic region. The total Antarctic tardigrade fauna was found to number 23 species, only 11 of which had been found by two or more investigators. It was suggested that the lack of species confirmation may relate to the difficulties in identification of the *Diphascon* group.

7 Only four species had not been recorded in other regions of the world, and two of these were only recently known to science.

8 The taxonomic difficulties encountered with the Rotifera meant that only four categories were recognised: *Adineta*, Bdelloidea (other than *Adineta*), Monogononta and inactive rotifers.

9 A total of 43 sampling sites on Signy Island were described, eight in detail since they were considered to be representative of the most common vegetation types of the Antarctic and these were used to determine tardigrade and rotifer population densities.

10 The sampling techniques used were described.

11 The efficiency of the wet funnel, Seinhorst mistifier and modified Baermann funnel were compared for the extraction of tardigrades. The numbers extracted were 19, 616 and 2070 respectively. Therefore the modified Baermann or tray method was used thereafter.

12 A test was performed to determine a suitable extraction period. The time chosen was 48 h, yielding 70% of the tardigrades present.

13 Most tardigrade species were identified during the counting procedure, however, *E.* (*E.*) *capillatus* + *E.* (*E.*) *meridionalis* and *H.* (*D.*) *alpinus* + *H.* (*D.*) *pinguis* were not resolved.

14 The counting procedure and its disadvantages were discussed.

15 The method used to determine biomass for each tardigrade species was given. Tardigrades were assumed to be cylindrical with the exception of *Echiniscus* which was assumed to be half a prolate spheroid.

16 The distribution of Tardigrada on Signy Island was discussed. *M. furciger*, *H.* (*H.*) *dujardini* and *H.* (*D.*) *alpinus* + *H.* (*D.*) *pinguis* were recorded from most habitats. *H.* (*D.*) *scoticus* and *H.* (*I.*)

renaudi were found in the richer substrates, usually affected by vertebrate waste. *Milnesium tardigradum* was found in habitats where moisture content was variable. Other species were recovered from too few habitats to draw any general conclusions.

17 The distribution and abundance of ten tardigrade species and species-groups on Signy Island was discussed. A *Polytrichum-Chorisodontium* moss turf supported the lowest tardigrade population (11×10^3 animals m^{-2}) and a *Prasiola* site supported the greatest (14×10^6 animals m^{-2}).

18 Biomass estimates were made for the eight sites and those affected by vertebrates had a total tardigrade biomass between 1.2–19.8 g m^{-2}. Sites unaffected supported less than this weight.

19 All sites affected by vertebrates, particularly the *Prasiola* sites, were found to support the most diverse tardigrade fauna. This was considered to be the most important single factor governing tardigrade density and distribution on Signy Island.

20 The distribution pattern of rotifers on Signy Island was similar to that of the tardigrades and nematodes.

21 Samples of mosses and lichens were collected from 70 sites in the Antarctic Peninsula and Scotia Ridge region. These were briefly described.

22 *H.* (*H.*) *dujardini* and *H.* (*D.*) *alpinus* + *H.* (*D.*) *pinguis* were found in most habitats from this region. *M. furciger* was more restricted in its distribution than on Signy Island, while *H.* (*I.*) *renaudi* had a more widespread distribution. Other species had a similar distribution to that found on Signy Island.

23 The microclimate at locations along the Antarctic Peninsula and Scotia Ridge region was deduced for macro-climatic data, it was then used to account for tardigrade densities and species diversity

in the region.

24 M. furciger, H. (I.) asper, H. (D.) alpinus + H. (D.) pinguis and H. (D.) scoticus were recovered throughout the geographical range investigated (South Georgia to Alexander Island).

25 Rotifera were recovered from all samples taken in the region.

26 Two sites on Signy Island were chosen as being representative of two moss communities which are common throughout the maritime Antarctic. These sites were the Signy Island terrestrial reference Sites (SIRS 1 and 2). Between June 1971 and April 1973 the temporal distribution of Tardigrada and Rotifera was examined on these two sites.

27 Four species of Tardigrada were found to occur regularly on the SIRS, Echiniscus sp., H. (D.) alpinus +H. (D.) pinguis, H. (H.) dujardini and M. furciger.

28 The population density estimates of each of the four species/ species-groups showed little consistent pattern over the period of study on either site. Only Echiniscus showed any suggestion of mortality over the winter months.

29 There was no apparent correlation between tardigrade densities in individual cores and any other measured factor.

30 Up to 80% of the tardigrades were found in the upper 6 cm of the moss cores. The reasons for this were discussed.

31 Oxygen uptake of M. furciger was investigated using a Cartesian Diver micro-respirometer. This species was chosen because it was relatively large and robust, was numerically important on the SIRS and had a widespread distribution on Signy Island and elsewhere in the maritime Antarctic.

32 Direct body length measurements of M. furciger were unreliable. The length of the buccal tube and placoid line, therefore, were used to derive body lengths for each experimental animal. The

body weight of each animal was estimated from the body length.

33 A total of 55 oxygen uptake rates were obtained, 44 at 5°C and 11 at 10°C. From these rates two regression lines were derived:

O_2 uptake = 0.31(body weight)$^{0.51}$ at 5°C and

O_2 uptake = 0.57(body weight)$^{0.51}$ at 10°C.

34 Q_{10} for the temperature range 5°–10°C was 3.46.

35 The rate of oxygen uptake of a 600 µm individual of *M. furciger* at 10°C was compared with that of an individual of *M. dispar* at 20°C from a temperate climate (*M. furciger* = 1.82 x 10^{-3} µl O_2 h, *M. dispar* = 1.0 x 10^{-3} µl O_2 h^{-1}). The higher rate for the Antarctic species was advanced as evidence of physiological adaptation to low temperatures.

36 Size-frequency analysis of *M. furciger* populations did not show the discontinuities usually associated with the moult. It was impossible, therefore, to divide the population into instar size classes. Reasons for this finding were discussed.

37 In order to apply respiratory data to field populations, five equal size classes were chosen at 100 µm intervals between 151 to 651 µm. The proportion of individuals in each class was then determined for selected months on SIRS 2.

36 Using respiration data, population densities, size class structure and field temperatures on SIRS 2, total population metabolism of *M. furciger* was calculated. Assuming the resipiration was negligible at field temperatures below 0°C, the annual population metabolism of this species was 127 ml O_2 m^{-2}.

37 The calculation was repeated for SIRS*1 assuming that the population size structure was similar to that on SIRS 2. Annual metabolism of *M. furciger* on SIRS 1 was 23 ml O_2 m^{-2}.

38 The respiration data for *M. furciger* were extrapolated for

all species of Tardigrada present on the SIRS. Total annual metabolism was 211 ml O_2 m^{-2} on SIRS 1 and 507 ml O_2 m^{-2} on SIRS 2.

39 The presence and survival of the Antarctic terrestrial mesofauna, with particular emphasis on the tardigrades, was discussed.

40 Some observations were made on the food requirements of the SIRS Tardigrada.

41 The research presented in this thesis was compared with that on other groups at the SIRS and with other works of a similar nature elsewhere. It was suggested that the Tardigrada were not as insignificant as was previously believed.

APPENDIX I. Population density m^{-2} on the SIRS (95% confidence limits underlined). % occurence in the upper 3 cm of the moss is also given. Sample dates bracketed are for SIRS 1, when this differed from SIRS 2.

1 *Hypsibius* (*H.*) *dujardini*

Date	SIRS 1 0–6 cm	% 0–3 cm	SIRS 2 0–6 cm	% 0–3 cm
(05-08-71)	810 1 350	100		
(05-10-71)	270 600	100		
(04-12-71)	270 600	100		
07-01-72			5 130 4 530	94
05-02-72 (02-02-72)	540 850	100	1 350 1 470	100
04-03-72			2 500 3 590	81
04-04-72	810 600	100	740 750	100
04-05-72			1 620 1 600	62
02-06-72 (04-06-72)	2 430 5 420	100	740 1 250	91
04-07-72			8 240 11 140	100
01-08-72	1 350 1 980	80	2 770 3 270	78
04-09-72			4 460 6 700	91
02-10-72	540 1 200	0	12 630 9 740	99
31-10-72			2 570 1 200	95
30-11-72	540 1 200	100	3 720 2 810	62
30-12-72			1 620 2 190	100
28-01-73	5 400 4 960	100	8 980 10 820	96
28-02-73			50 200 111 390	100
26-03-73	740 1 290	73	1 490 3 160	4

APPENDIX I.

2 Echiniscus sp.

Date	SIRS 1 0-6 cm	SIRS 1 % 0-3 cm	SIRS 2 0-6 cm	SIRS 2 % 0-3 cm
12-07-71			78	70
			150	
10-08-71	540	100	200	67
(05-08-71)	563		260	
09-09-71			470	100
			340	
10-10-71	540	100	0	
(05-10-71)	775			
07-11-71			200	100
			260	
08-12-71	0		670	90
(04-12-71)			850	
07-01-72			1 420	100
			1 050	
05-02-72	0		2 360	99
(02-02-72)			2 120	
04-03-72			5 540	98
			4 290	
04-04-72	810	69	810	100
	920		480	
04-05-72			2 230	91
			1 720	
04-06-72	0		270	100
(02-06-72)			370	
04 -07-72			1 080	94
			1 380	
01-08-72	0		1 150	100
			1 470	
04-09-72			2 030	100
			1 810	
02-10-72	540	100	1 150	100
	770		1 560	
31-10-72			670	100
			600	
30-11-72	540	100	270	100
	770		370	
30-12-72			9 660	99
			2 550	
28-01-72	6 750	96	4 520	97
	6 000		1 630	
28-02-73			6 620	88
			5 880	
26-03-73	0		340	100
			400	

APPENDIX I.

3 Macrobiotus furciger

Date	SIRS 1 0-6 cm	SIRS 1 % 0-3 cm	SIRS 2 0-6 cm	SIRS 2 %0-3 cm
12-07-71			110 690	70
			42 010	
10-08-71	5 130	60	70 500	40
(05-08-71)	2 890		36 220	
09-09-71			61 720	71
			25 840	
10-10-71	7 290	71	39 440	74
(05-10-71)	4 920		14 920	
07-11-71			40 720	80
			15 310	
08-12-71	5 680	100	61 180	56
(04-12-71)	3 510		30 740	
07-01-72			96 030	70
			32 300	
05-02-72	16 750	81	96 000	82
(02-02-72)	10 470		38 690	
04-03-72			96 370	84
			39 220	
04-04-72	7 830	83	61 450	62
	4 210		20 630	
04-05-72			124 060	58
			48 920	
02-06-72	7 290	96	48 220	69
(04-06-72)	5 680		16 710	
04-07-72			96 710	70
			25 590	
01-08-72	11 070	62	127 100	73
	4 940		81 680	
04-09-72			155 390	84
			56 290	
02-10-72	21 610	88	79 080	67
	11 180		37 200	
31-10-72			112 100	56
			56 750	
30-11-72	15 130	63	120 140	68
	6 570		63 980	
30-12-72			105 080	92
			77 040	
28-01-73	14 050	94	60 040	91
	11 070		25 580	
28-02-73			64 760	78
			23 580	
26-03-73	6 540	75	148 370	65
	5 600		38 590	

APPENDIX I.

4 Hypsibius (D.) alpinus + H. (D.) pinguis

Date	SIRS 1 0–6 cm	SIRS 1 %0–3 cm	SIRS 2 0–6 cm	SIRS 2 %0–3 cm
12-07-71			604 750	61
			204 870	
10-08-71	70 230	59	429 840	59
(05-08-71)	28 200		113 860	
09-09-71			319 430	75
			156 950	
10-10-71	202 600	72	165 390	74
(05-10-71)	95 340		50 500	
07-11-71			277 900	76
			98 720	
08-12-71	155 590	72	234 200	71
(04-12-71)	83 870		98 720	
07-01-72			507 030	72
			142 670	
05-02-72	161 270	97	612 900	82
(02-02-72)	84 070		158 410	
04-03-72			594 350	84
			125 230	
04-04-72	170 720	98	280 870	81
	83 790		110 150	
04-05-72			514 660	74
			213 440	
02-06-72	185 040	94	357 000	79
(04-06-72)	113 530		94 960	
04-07-72			521 750	72
			211 740	
01-08-72	100 490	90	542 760	63
	32 690		235 430	
04-09-72			454 360	84
			102 130	
02-10-72	286 340	92	485 960	60
	97 160		122 740	
31-10-72			403 840	52
			129 890	
30-11-72	237 170	73	588 140	64
	93 170		189 310	
30-12-72			399 790	94
			115 620	
28-01-73	271 210	96	455 570	94
	97 870		202 550	
28-02-73			296 870	90
			31 300	
26-03-73	2 340	86	185 510	85
	1 380		63 300	

APPENDIX I.

5 Total Rotifera

Date	SIRS 1 0-6 cm	SIRS 1 % 0-3 cm	SIRS 2 0-6 cm	SIRS 2 % 0-3 cm
12-07-71			144 510	68
			23 280	
10-08-71	194 910	66	285 370	72
(05-08-71)	92 750		264 420	
09-09-71			294 420	82
			147 300	
10-10-71	194 910	58	232 340	64
(05-10-71)	63 380		83 470	
07-11-71			250 110	79
			79 870	
08-12-71	142 540	72	182 880	90
(04-12-71)	30 530		56 560	
07-01-72			189 980	83
			130 620	
02-02-72	226 490	52	280 510	87
(05-02-72)	69 150		185 830	
04-03-72			99 990	88
			54 000	
04-04-72	137 140	65	68 440	84
	37 920		30 920	
04-05-72			124 170	81
			45 240	
02-06-72	119 900	67	212 410	92
(04-06-72)	35 750		84 470	
04-07-72			106 200	91
			59 010	
01-08-72	214 650	46	206 530	62
	55 300		89 160	
04-09-72			164 030	89
			81 900	
02-10-72	230 650	49	344 350	45
	65 110		465 170	
31-10-72			107 080	63
			44 430	
30-11-72	347 640	50	245 040	59
	93 170		153 680	
30-12-72			393 800	71
			546 200	
28-01-73	281 770	36	129 040	63
	97 870		70 090	
28-02-73			80 590	72
			90 140	
26-03-73	173 180	53	55 130	81
	73 380		59 310	

APPENDIX II. Details of the respirometry experiments on M. furciger includind estimated length (µm), estimated weight (µg), air volume of the diver = Vg (µl), change in gas pressure = P (mm h^{-1}) and oxygen uptake for individuals (µl O_2 x 10^{-3} h^{-1}) and a weight related basis (µl g^{-1} h^{-1}).

B animals in simplex stage, – animals lost.

5^oC

Length	Weight	Mean Weight	Vg	ΔP	animal O_2 uptake	g^{-1}
399	2.82	–	1.357	9.17	1.003	356
414	3.14	–	1.075	11.55	1.087	346
417	3.22	–	0.750	4.47	0.289	90
362	2.10	–	1.292	2.89	0.455	217
549	7.32	–	1.458	7.59	1.090	149
508	5.81	–	1.517	2.79	0.415	80
405	2.93	–	2.633	2.80	0.723	247
528	6.54					
495	5.38	5.41	1.517	31.42	1.170	216
482	4.97					
475	4.75					
312	1.35					
306	1.28					
273	0.91	1.18	1.292	9.44	0.239	203
B	–					
B	–					
297	1.17					
266	0.83					
244	0.64	0.88	2.117	5.55	0.231	263
B	–					
B	–					
390	2.62					
349	1.89					
B	–	2.26	2.633	6.01	0.311	138
B	–					
B	–					
471	4.63					
427	3.44					
401	2.85	3.64	3.975	11.06	0.863	238
B	–					
B	–					

APPENDIX II. 5°C

445	3.91					
432	3.58					
425	3.40	3.32	1.292	20.77	0.527	159
406	2.97					
395	2.74					
480	4.91					
445	3.91					
438	3.72	3.99	1.517	16.09	0.479	120
425	3.40					
-	-					
493	5.32					
477	4.80					
464	4.42	4.41	1.767	26.34	0.914	207
412	3.10					
-	-					
525	6.33					
490	5.20					
479	4.86	5.30	2.117	37.85	1.574	297
477	4.80					
-	-					
342	1.77					
329	1.58					
312	1.35	1.47	1.292	14.49	0.368	250
299	1.19					
-	-					
482	4.97					
453	4.11					
393	2.70	3.29	2.633	5.82	0.301	91
388	2.59					
362	2.10					
488	5.14					
484	5.03					
408	3.02	4.40	2.117	24.49	1.018	231
-	-					
-	-					
508	5.81					
497	5.44					
477	4.80	4.97	2.633	7.53	0.389	78
471	4.63					
454	4.16					
490	5.20					
486	5.08					
417	3.22	3.88	1.517	19.18	0.571	147
414	3.14					
397	2.78					

APPENDIX II. 5^{o}C

416	3.18					
362	2.10					
358	2.04	2.29	2.117	11.13	0.462	202
345	1.83					
B	-					
558	7.70					
532	6.67					
528	6.45	6.65	2.633	12.02	0.622	94
523	6.33					
514	6.00					
427	3.44					
421	3.31					
419	3.27	3.18	1.975	13.26	0.515	162
393	2.70					
-	-					
419	3.27					
393	2.70					
379	2.41	2.48	2.117	11.15	0.464	187
377	2.37					
332	1.63					
519	6.20					
510	5.88					
491	5.26	5.78	2.633	8.23	0.425	74
B	-					
B	-					
299	1.19					
247	0.67					
192	0.31	0.62	1.075	15.00	0.317	511
190	0.31					
-	-					
355	1.98					
329	1.58	1.78	1.517	10.36	0.309	174
-	-					
-	-					
495	5.38					
480	4.91					
469	4.58	4.91	2.633	8.42	0.435	89
464	4.42					
462	4.37					
388	2.59					
375	2.34					
356	2.10	2.31	2.117	14.82	0.616	267
B	-					
B	-					
471	4.63					
453	4.11					
438	3.72	3.89	3.975	9.49	0.741	190
438	3.72					
419	3.27					

APPENDIX II. 5°C

536	6.82					
460	4.31					
416	3.18	3.79	1.075	22.90	0.484	128
406	2.97					
336	1.68					
355	1.98					
323	1.50					
B	-	1.74	1.300	15.77	0.403	232
-	-					
-	-					
458	4.26					
430	3.53					
401	2.85	3.22	1.517	26.38	0.786	244
369	2.24					
B	-					
527	6.47					
488	5.14					
482	4.97	5.01	2.117	30.26	1.258	251
427	3.44					
B	-					
449	4.01					
445	3.91					
427	3.44	3.67	1.725	10.66	0.361	98
421	3.31					
-	-					
356	2.01					
331	1.60					
331	1.60	1.53	1.517	15.50	0.462	302
325	1.52					
273	0.91					
386	2.55					
345	1.83					
338	1.71	1.92	1.300	12.35	0.315	164
331	1.60					
-	-					
558	7.70					
536	6.82					
527	6.47	6.24	2.117	20.68	0.860	138
514	6.00					
456	4.21					

APPENDIX II. $5^{o}C$

421	3.31					
380	2.44					
343	1.80	2.29	1.725	11.94	0.405	177
331	1.60					
-	-					
197	0.34					
216	0.45					
199	0.35	0.40	0.900	6.64	0.117	293
216	0.45					
-	-					
218	0.46					
218	0.46					
199	0.35	0.40	1.300	7.70	0.197	493
192	0.31					
B	-					
343	1.80					
343	1.80					
319	1.45	1.68	2.242	13.05	0.574	342
B	-					
-	-					
515	6.07					
510	5.88	4.94	2.492	17.89	1.094	221
469	4.58					
417	3.22					

APPENDIX II. 10°C

477	4.80	–	2.52	5.31	1.292	269
453	4.11	–	6.68	3.00	0.989	471
242	0.63					
210	0.41					
192	0.31	0.37	0.900	26.72	0.464	1254
186	0.29					
171	0.22					
453	4.11					
425	3.40					
419	3.27	3.38	1.517	34.84	1.020	302
417	3.22					
403	2.89					
521	6.27					
488	5.14					
466	4.47	4.52	2.492	23.93	1.151	255
412	3.10					
434	3.63					
242	0.63					
155	0.17					
–	–	0.40	0.900	12.51	0.272	680
–	–					
–	–					
355	1.98					
373	2.30	2.14	2.492	12.76	0.767	358
–	–					
–	–					
414	3.14					
401	2.85					
368	2.20	2.73	1.517	36.43	1.066	390
–	–					
–	–					
464	4.42					
440	3.77					
362	2.10	3.43	2.633	16.74	0.850	248
–	–					
–	–					
497	5.44					
488	5.14					
480	4.91	4.76	2.733	17.98	0.948	199
458	4.26					
451	4.06					
508	5.81					
491	5.26					
490	5.20	5.28	2.992	27.07	1.563	296
486	5.08					
484	5.03					

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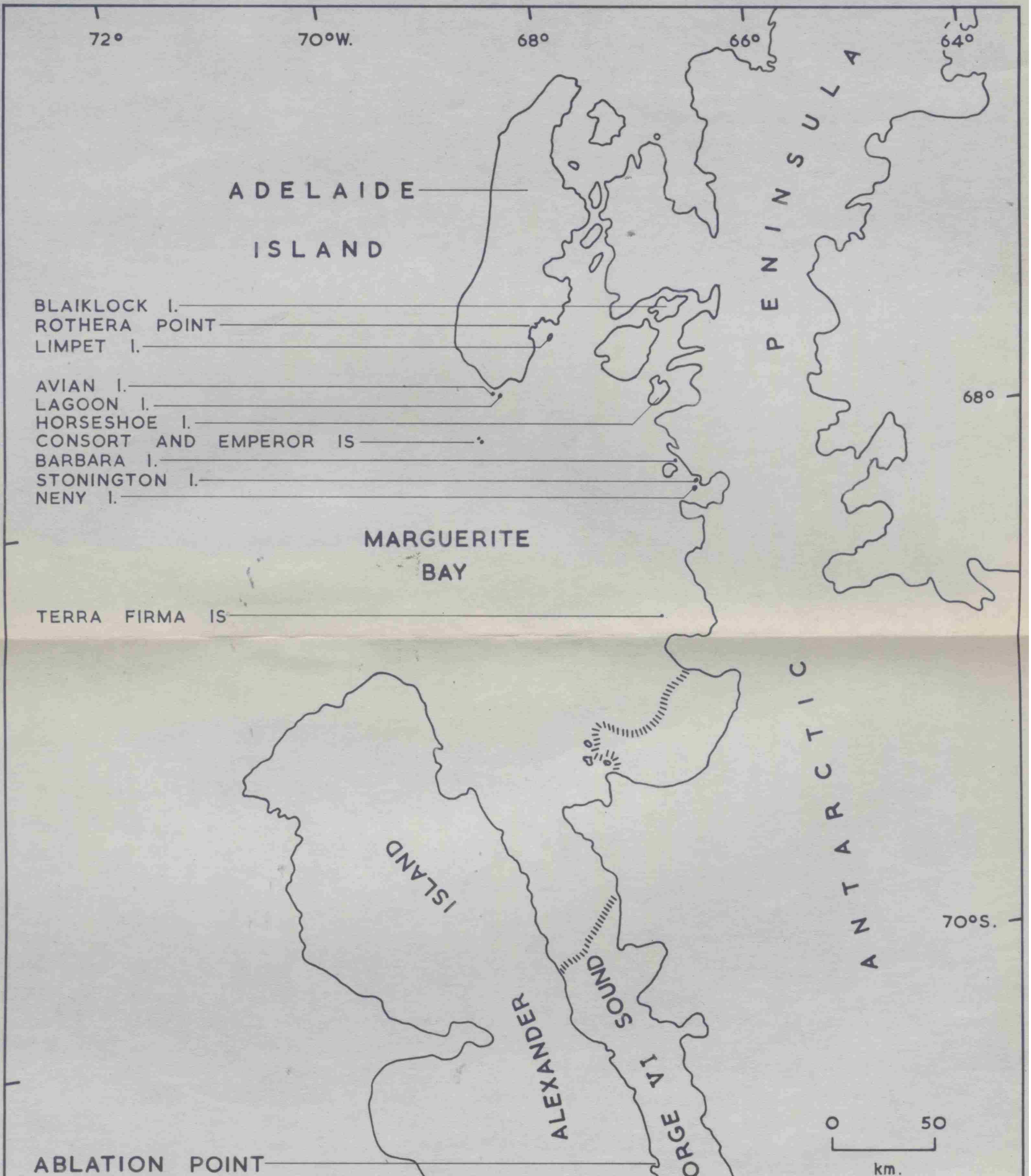

72°
70°W.
68°
66°
64°
68°
70°S.
ADELAIDE
ISLAND
BLAIKLOCK I.
ROTHERA POINT
LIMPET I.
AVIAN I.
LAGOON I.
HORSESHOE I.
CONSORT AND EMPEROR IS
BARBARA I.
STONINGTON I.
NENY I.
MARGUERITE
BAY
TERRA FIRMA IS
PENINSULA
ANTARCTIC
ALEXANDER
ISLAND
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P.G. JENNINGS. Ph.D. Thesis. 1976.

SUMMARY

1 The general development of Antarctic research and the reasons for the research presented in this thesis were outlined.

2 The Antarctic region was divided into continental, maritime and sub-Antarctic areas on climatic and floral characteristics. Physical and biotic features of the maritime Antarctic were then described, particularly those on Signy Island.

3 Features of taxonomic significance in the phylum Tardigrada were discussed, with particular reference to those of the Antarctic tardigrades.

4 The tardigrade species recovered from the Antarctic in this study were described and illustrated. These were Echiniscus (E.) meridionalis, E. (E.) capillatus, Oreella mollis, Macrobiotus ambiguus, M. furciger, Hypsibius (H.) dujardini, H. (H.) oberhaeuseri, H. (Isohypsibius) asper, H. (I.) papillifer, H. (I.) renaudi, H. (Diphascon) alpinus, H. (D.) chilenensis, H. (D.) pinguis, H. (D.) puniceus, H. (D.) scoticus, H. (D.) sp. and Milnesium tardigradum.

5 Small members of the sub-genus Diphascon were difficult to distinguish, separation in this work was made on the diameter of the buccal tube, length of the placoid line and length of the third macroplacoid.

6 The recoveries in this investigation are compared with those of previous workers in the Antarctic region. The total Antarctic tardigrade fauna was found to number 23 species, only 11 of which had been found by two or more investigators. It was suggested that the lack of species confirmation may relate to the difficulties in identification of the Diphascon group.

7 Only four species had not been recorded in other regions of the world, and two of these were only recently known to science.

8 The taxonomic difficulties encountered with the Rotifera meant that only four categories were recognised: Adineta, Bdelloidea (other than Adineta), Monogononta and inactive rotifers.

9 A total of 43 sampling sites on Signy Island were described, eight in detail since they were considered to be representative of the most common vegetation types of the Antarctic, and these were used to determine tardigrade and rotifer population densities.

10 The sampling techniques used were described.

11 The efficiency of the wet funnel, Seinhorst mistifier and modified Baermann funnel were compared for the extraction of tardigrades. The numbers extracted were 19, 616 and 2070 respectively. Therefore the modified Baermann or tray method was used thereafter.

12 A test was performed to determine a suitable extraction period. The time chosen was 48 h, yielding 70% of the tardigrades present.

13 Most tardigrade species were identified during the counting procedure, however, E. (E.) capillatus + E. (E.) meridionalis and H. (D.) alpinus + H. (D.) pinguis were not resolved.

14 The counting procedure and its disadvantages were discussed.

15 The method used to determine biomass for each tardigrade species was given. Tardigrades were assumed to be cylindrical with the exception of Echiniscus which was assumed to be half a prolate spheroid.

16 The distribution of Tardigrada on Signy Island was discussed. M. furciger, H. (H.) dujardini and H. (D.) alpinus + H. (D.) pinguis were recorded from most habitats. H. (D.) scoticus and H. (I.)

renaudi were found in the richer substrates, usually affected by vertebrate waste. *Milnesium tardigradum* was found in habitats where moisture content was variable. Other species were recovered from too few habitats to draw any general conclusions.

17 The distribution and abundance of ten tardigrade species and species-groups on Signy Island was discussed. A *Polytrichum-Chorisodontium* moss turf supported the lowest tardigrade population (11×10^3 animals m^{-2}) and a *Prasiola* site supported the greatest (14×10^6 animals m^{-2}).

18 Biomass estimates were made for the eight sites and those affected by vertebrates had a total tardigrade biomass between 1.2–19.8 g m^{-2}. Sites unaffected supported less than this weight.

19 All sites affected by vertebrates, particularly the *Prasiola* sites, were found to support the most diverse tardigrade fauna. This was considered to be the most important single factor governing tardigrade density and distribution on Signy Island.

20 The distribution pattern of rotifers on Signy Island was similar to that of the tardigrades and nematodes.

21 Samples of mosses and lichens were collected from 70 sites in the Antarctic Peninsula and Scotia Ridge region. These were briefly described.

22 *H.* (*H.*) *dujardini* and *H.* (*D.*) *alpinus* + *H.* (*D.*) *pinguis* were found in most habitats from this region. *M. furciger* was more restricted in its distribution than on Signy Island, while *H.* (*I.*) *renaudi* had a more widespread distribution. Other species had a similar distribution to that found on Signy Island.

23 The microclimate at locations along the Antarctic Peninsula and Scotia Ridge region was deduced for macro-climatic data, it was then used to account for tardigrade densities and species diversity

in the region.

24 *M. furciger*, *H.* (*I.*) *asper*, *H.* (*D.*) *alpinus* + *H.* (*D.*) *pinguis* and *H.* (*D.*) *scoticus* were recovered throughout the geographical range investigated (South Georgia to Alexander Island).

25 Rotifera were recovered from all samples taken in the region.

26 Two sites on Signy Island were chosen as being representative of two moss communities which are common throughout the maritime Antarctic. These sites were the Signy Island terrestrial reference Sites (SIRS 1 and 2). Between June 1971 and April 1973 the temporal distribution of Tardigrada and Rotifera was examined on these two sites.

27 Four species of Tardigrada were found to occur regularly on the SIRS, *Echiniscus* sp., *H.* (*D.*) *alpinus* +*H.* (*D.*) *pinguis*, *H.* (*H.*) *dujardini* and *M. furciger*.

28 The population density estimates of each of the four species/species-groups showed little consistent pattern over the period of study on either site. Only *Echiniscus* showed any suggestion of mortality over the winter months.

29 There was no apparent correlation between tardigrade densities in individual cores and any other measured factor.

30 Up to 80% of the tardigrades were found in the upper 6 cm of the moss cores. The reasons for this were discussed.

31 Oxygen uptake of *M. furciger* was investigated using a Cartesian Diver micro-respirometer. This species was chosen because it was relatively large and robust, was numerically important on the SIRS and had a widespread distribution on Signy Island and elsewhere in the maritime Antarctic.

32 Direct body length measurements of *M. furciger* were unreliable. The length of the buccal tube and placoid line, therefore, were used to derive body lengths for each experimental animal. The

body weight of each animal was estimated from the body length.

33 A total of 55 oxygen uptake rates were obtained, 44 at $5^{\circ}C$ and 11 at $10^{\circ}C$. From these rates two regression lines were derived:

O_2 uptake = 0.31(body weight)$^{0.51}$ at $5^{\circ}C$ and

O_2 uptake = 0.57(body weight)$^{0.51}$ at $10^{\circ}C$.

34 Q_{10} for the temperature range 5°–$10^{\circ}C$ was 3.46.

35 The rate of oxygen uptake of a 600 µm individual of *M. furciger* at $10^{\circ}C$ was compared with that of an individual of *M. dispar* at $20^{\circ}C$ from a temperate climate (*M. furciger* = 1.82×10^{-3} µl O_2 h, *M. dispar* = 1.0×10^{-3} µl O_2 h^{-1}). The higher rate for the Antarctic species was advanced as evidence of physiological adaptation to low temperatures.

36 Size-frequency analysis of *M. furciger* populations did not show the discontinuities usually associated with the moult. It was impossible, therefore, to divide the population into instar size classes. Reasons for this finding were discussed.

37 In order to apply respiratory data to field populations, five equal size classes were chosen at 100 µm intervals between 151 to 651 µm. The proportion of individuals in each class was then determined for selected months on SIRS 2.

36 Using respiration data, population densities, size class structure and field temperatures on SIRS 2, total population metabolism of *M. furciger* was calculated. Assuming the respiration was negligible at field temperatures below $0^{\circ}C$, the annual population metabolism of this species was 127 ml O_2 m^{-2}.

37 The calculation was repeated for SIRS*1 assuming that the population size structure was similar to that on SIRS 2. Annual metabolism of *M. furciger* on SIRS 1 was 23 ml O_2 m^{-2}.

38 The respiration data for *M. furciger* were extrapolated for

all species of Tardigrada present on the SIRS. Total annual metabolism was 211 ml O_2 m^{-2} on SIRS 1 and 507 ml O_2 m^{-2} on SIRS 2.

39 The presence and survival of the Antarctic terrestrial mesofauna, with particular emphasis on the tardigrades, was discussed.

40 Some observations were made on the food requirements of the SIRS Tardigrada.

41 The research presented in this thesis was compared with that on other groups at the SIRS and with other works of a similar nature elsewhere. It was suggested that the Tardigrada were not as insignificant as was previously believed.