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## VEGETATION OF THE SOUTH ORKNEY ISLANDS WITH PARTICULAR REFERENCE TO SIGNY ISLAND

Ву

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(Manuscript received 30th October, 1970)

## **ABSTRACT**

A DETAILED account of the terrestrial vegetation of Signy Island, South Orkney Islands, is presented, based on an analysis of floristic and edaphic data.

The general features of Signy Island, including its topography, soils and climate are considered briefly, and these are related to conditions on the remaining South Orkney Islands. An historical review is given of the botanical work carried out in these islands since the first report of vegetation by Weddell in 1823. It was not until the early 1960s that any systematic study of their vegetation was begun.

The classification of the vegetation presented here comprises four hierarchical categories, namely formation, sub-formation, association and sociation. The two major formations are based on life form, and named the Antarctic non-vascular cryptogam tundra formation and Antarctic herb tundra formation. Within the first formation eight sub-formations have been described on the basis of the growth form of the predominant species or genera. One further sub-formation is described in the second formation. A total of 16 associations has been recognized, each differentiated according to the degree of constancy of one or more species in physiognomically similar groups of communities. An association may possess several floristically similar sociations, the smallest units of the classification, which are determined according to the dominance or co-dominance of particular species. The change in dominance from one sociation to another can generally be attributed to minor variations in the habitat. There are 48 sociations described, and for most of these details are provided of the habitat occupied, and of certain edaphic features. Species lists, giving percentage cover and percentage frequency or semi-quantitative assessments of frequency, are presented for most sociations. A few assemblages have not been classified in detail due to their rarity or lack of uniformity, and consequently a further four community types have been recognized which do not comply with the general features of the classification.

The development and distribution of the plant communities of Signy Island are considered with regard

The development and distribution of the plant communities of Signy Island are considered with regard to the availability of habitats, the ecesis of propagules and the ensuing success and competition exhibted by the ecologically more important species. Several climatic, edaphic and biotic agents of erosion are discussed in relation to the degeneration or destruction of various community types. While certain erosion processes may prevent establishment of vegetation in some habitats, new habitats are occasionally created which are suitable for colonization.

Various examples of environmental pattern are described and illustrated for the five most widespread associations on the island. Morphological pattern is restricted to a single group of mosses. In a few instances, small-scale successional and cyclical changes have been recognized in certain community types or groups of communities. Several sociations within some associations are arranged in distinct zones related to certain habitat factors. The floristic similarity of many sociations when correlated with environmental gradients suggests a rather indistinct multi-directional continuum of variation.

Particular reference is made to the bryophyte and lichen assemblages which constitute the most important units of the vegetation of Signy Island and elsewhere in the maritime Antarctic. These have been studied in relation to the principal environmental factors and gradients which influence the physiognomy and spatial arrangement of individual species and the composition, distribution and extent of the communities which they develop. The relatively rich and varied bryophyte and lichen flora of Signy Island is compared with that of other southern polar regions, and is attributed mainly to a regular and generally non-limiting supply of moisture, and to a wide range of environmental factors, of which stability and texture of the substratum, origin and base status of the soil, degree of shelter, insolation and protection by snow lie in winter, exposure to high evaporation stresses, micro-topography, micro-climate and aspect are all important.

The description of the vegetation of the South Orkney Islands is concluded with a brief account of the principal associations observed at a number of localities on Coronation and Powell Islands and on Fredriksen, Matthews and Lynch Islands.

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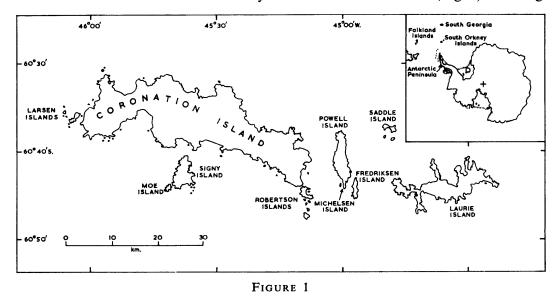
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## I. INTRODUCTION

THE South Orkney Islands, lying close to lat. 60°S. and long. 45°W., comprise two main and several small islands occupying a position on the Scotia Ridge about 1,440 km. south-east of Tierra del Fuego and 640 km. north-east of the northern extremity of the Antarctic Peninsula (Fig. 1). The largest island



The South Orkney Islands, showing the position of Signy Island with reference to the other islands of the group. The inset shows the position of the South Orkney Islands in relation to the rest of the Antarctic.

of the group, Coronation Island, is about 48 km. from east to west; to the south of its central part lies Signy Island (lat. 60°43'S., long. 45°38'W.), where the British Antarctic Survey's station is situated.

The South Orkney Islands thus lie in the maritime Antarctic zone of southern polar lands (Holdgate, 1964, 1970), a zone confined mainly to the western coastal area of the Antarctic Peninsula but including offshore islands, together with the island groups comprising the southern part of the Scotia Ridge, i.e. the South Sandwich, South Orkney and South Shetland Islands, and also Bouvetøya and Peter I Øy. Within this region the modified Antarctic climate permits the existence of a relatively rich and varied flora. The macroscopic terrestrial vegetation is almost entirely cryptogamic in composition (Longton, 1967; Gimingham and Smith, 1970), consisting of a large number of lichens and mosses, and a very much smaller number of species of hepatics, algae and fungi. Two phanerogams, *Deschampsia antarctica* Desv. and *Colobanthus quitensis* Bartl. (= C. crassifolius (D'Urv.) Hook. f.) also occur, although their distribution is considerably more restricted (Greene and Holtom, 1971).

The aim of the present work is to provide a detailed description of the terrestrial plant communities in one locality in the maritime Antarctic, namely Signy Island in the South Orkney Islands. Aspects of the dynamic ecology of the island's vegetation are also discussed, and the relationship of the Signy Island plant communities to those in other parts of the maritime Antarctic and other tundra regions at the world level is briefly considered.

## II. GENERAL FEATURES OF THE SOUTH ORKNEY ISLANDS

## 1. Topography and soils of Signy Island

Signy Island (Fig. 2) is roughly triangular in outline, measuring 8 km. by 5 km. and its "mountainous" interior rises to a maximum of 281 m. a.s.l. The island has a small permanent ice cap but in summer much of the ground is snow- and ice-free, particularly in the low-lying east and west coastal areas.

Matthews and Maling (1967) described the island as being composed of regionally metamorphosed sedimentary rocks, mainly quartz-mica-schists and amphibolites, with local marble outcrops which

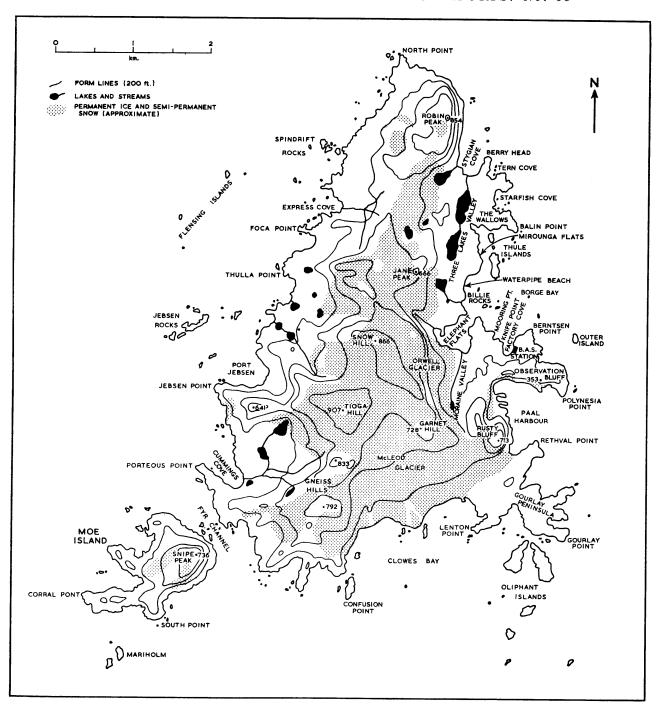


FIGURE 2
Signy Island, indicating localities referred to in the text.

occur either as thin bands in the schists or as prominent knolls in coastal areas. There is ample evidence of glacial erosion in the landforms (Plate Ia). Much of the lower terrain is mantled by a substantial heterogeneous layer of unconsolidated glacial drift and fluvio-glacial outwash which include frequent marble fragments. The texture, structure and depth of these colluvial deposits vary considerably but they generally consist of coarse inorganic material with local pockets of fine clay and organic debris, with no development of mature soils. These mineral soils are alkaline to mildly acid in reaction with a fairly high base status. They are considerably disturbed by drainage and cryoturbation phenomena. Where there are deep accumulations of such soils, permafrost develops at about 1 m. below the surface,

although only the upper 40-60 cm. are considered as "active" (Chambers, 1967). Frost action and freeze-thaw cycles result in various forms of patterned ground including stone polygons, circles and stripes. Chambers (1966a) has shown that, although frost heaving is responsible for the general uplifting of the surface and the formation of these features, it is a solifluction and slumping mechanism which causes the differential sorting of the debris. At the other extreme are extensive stone- and boulder-strewn slopes forming various types of scree or talus.

The soils of Signy Island have been discussed by Holdgate and others (1967). Depending on the type and abundance of vegetation, organic debris may accumulate and become incorporated with the mineral soil, or build up deep deposits of almost pure moss peat. The deepest peats are formed beneath the semi-ombrogenous banks of *Polytrichim alpestre* and *Chorisodontium aciphyllum*, while extensive shallow deposits occur beneath the soligenous carpets of *Brachythecium* cf. antarcticum, *Drepanocladus uncinatus* and *Calliergon* cf. sarmentosum. In situations where the vegetation is of a more open nature, only small patches of organic matter accumulate among the coarser mineral material. Beneath the larger stands of *Deschampsia antarctica* a somewhat loamy soil develops, and is the only soil type approaching a brown earth, having a relatively active micro-flora and micro-fauna.

Mechanical weathering by frost action is the main factor in the derivation of the soils of Signy Island, particularly through the shattering of the schist. However, marble and biotite are susceptible to chemical break-down (Holdgate and others, 1967).

Because of the oceanic conditions prevailing, the frequent precipitation and sea spray, the proximity of large bird and seal colonies, together with the continual break-down of the schist and widespread distribution of marble and hornblende fragments by glacial action and solifluction, there is an adequate supply of all the principal nutrients even where intense leaching occurs. The source and availability of nutrients with regard to their retention by plants has been discussed by Allen and others (1967). However, nitrogen in a form extractable by plants may be very locally distributed (Holdgate and others, 1967). Many of the soil nutrients follow a seasonal fluctuation, reaching a maximum concentration in the soil in late winter immediately prior to the spring melt. The greatest peaks have been found in the levels of extractable ammonia-nitrogen and phosphorus, and to a lesser extent of sodium and potassium, while calcium and magnesium showed very little seasonal change (Allen and Northover, 1967; Northover and Allen, 1967; Northover and Grimshaw, 1967). This late winter peak is attributed to the build-up of the fauna before the spring melt occurs, as well as to the release in the melt of the mineral nutrients which accumulated during the previous season. The author has found that the concentration of marine salts in bryophytes and lichens decreases during the winter when the marine influence is at a minimum.

Since a large area of Signy Island is snow-free for at least 3 months of the year, and because of the wide range of topographical and geological variations, a considerable number of habitat types occur which are suitable for bryophyte and lichen establishment. However, as water availability, exposure and stability of the substratum are the principal factors affecting the distribution of most species, the more extensive stands of vegetation are restricted to low altitudes, particularly in coastal regions. Thus bryophyte communities predominate in the moist areas around lakesides, drainage channels, depressions, etc., and decrease in abundance and extent at higher altitudes, while the drier, more exposed habitats, although supporting several small cushion-forming mosses, are normally characterized by a large number of lichens, especially epipetric species.

## 2. Climate of Signy Island

As a result of the ameliorating effects of the surrounding ocean, Signy Island experiences relatively high air temperatures, with a small seasonal range which, together with the consequent availability of rain and melt water, is largely responsible for the comparatively rich and varied flora. In common with other regions within the maritime Antarctic, at least one of the summer months has a mean sea-level air temperature above freezing point, while in winter the mean for the coldest month is seldom below  $-12^{\circ}$  C. Mean monthly meteorological data for a 20 yr. period for Signy Island and a 46 yr. period for Laurie Island are summarized in Table I. Table II compares some of the data for Signy and Laurie Islands with comparable data for Galindez Island, Argentine Islands, the latter being thought to be one of the richest botanical regions south of the South Orkney Islands. Although slightly colder and more arid, the Argentine Islands experience less strong wind and more sunshine than the South Orkney Islands. The prevailing winds on Signy Island are from south-west to north-west, while in addition, there are

TABLE I
MEAN MONTHLY CLIMATIC DATA FOR SIGNY AND LAURIE ISLANDS

Month		nperature °C)		velocity (sec.)	Relative (per			sunshine ir.)	Precipitation (mm.)
Monin	Signy Island (1948– 67)	Laurie Island (1904– 50)	Signy Island (1948– 65)	Laurie Island (1904– 50)	Signy Island (1948– 61)	Laurie Island (1904– 50)	Signy Island (1948– 66)	Laurie Island (1904– 50)	Laurie Island (1904– 50)
January	0·78	0.11	6.0	4.1	85	85	2.3	1.5	35 · 2
February	0.87	0.23	7.3	4.8	85	86	1 · 7	1 · 4	39·1
March	0.29	-0.57	7.7	5.0	87	<b>8</b> 6	1 · 2	1 · 1	47.9
April	$-2 \cdot 27$	-3.32	7.9	5.4	86	<b>8</b> 6	1.0	0.8	41 · 4
May	-6.22	<b>−7·12</b>	6.7	5.3	85 · 5	85	0.7	0.55	31.6
June	<b>−7·96</b>	-10.37	6.7	4 · 8	86	85	0.4	0.3	26.0
July	-10.28	-10.87	6.6	5 · 1	84	83	0.9	0.6	31.7
August	9.38	-10.22	7.0	5.3	85	84	1.6	1 · 4	31 · 8
September	-5.34	-6.92	8.8	5.5	86	84	1.9	2.2	28.7
October	-2.75	-3.93	9.1	7.7	86	86	2.1	2.2	29.0
November	-1.38	$-2 \cdot 30$	7.8	4.8	86	86	2.2	1.8	32.2
December	-0.18	-0.77	6.2	4.0	87	85	2.0	2.0	26.5
Annual mean	-3.65	-4·67	7.3	5.0	85.5	86	1.55	1.3	398 · 4

Signy Island data have been taken from Pepper (1954) for the years 1948-50, from the Falkland Islands Dependencies annual meteorological tables for the years 1951-59, from the British Antarctic meteorological annual tables for the years 1960-61, and from the meteorological records maintained at the station for the years 1962-67.

Laurie Island data have been taken from Direccion General del Servicio Meteorologico Nacional (1951).

frequent, warm northerly winds resulting from föhn effects created by the 1,000–1,200 m. mountain barrier of central Coronation Island. Frequent, heavy cloud cover and lack of sunshine are typical features of the climate, and give the high frequency of precipitation which maintains a high relative humidity throughout the year.

From early December to late March, air temperatures frequently rise above  $0^{\circ}$  C, and mean temperatures may be above freezing point for 1 to 3 months during summer. On calm sunny days, ground temperatures may briefly exceed  $30^{\circ}$  C as rocks, soil and plant surfaces are warmed by incident radiation, and in summer considerable areas of the lowlands become clear of snow. Even in winter, katabatic wind may cause an increase in temperature of  $20^{\circ}$  C in a few hours, bringing temporary thaws. Most of the vegetation is covered by varying depths of snow throughout much of the winter and, although the air temperature may fall below  $-30^{\circ}$  C, the corresponding temperature on the moss surface rarely drops below  $-15^{\circ}$  C, except where snow protection is absent in exposed habitats (Plate Ib). Longton (1972) has given an account of the temperature regime at plant level in various *Polytrichum alpestre* communities.

The extent to which winter snow disappears in the summer depends principally on the length of time temperatures are above freezing, and on the amount and frequency of rainfall. For example, the most extensive retreat of the snow line on Signy Island in recent years was in the summer of 1964–65, following mean monthly air temperatures of  $0.5^{\circ}$ ,  $2.2^{\circ}$ ,  $2.8^{\circ}$  and  $1.8^{\circ}$  C (mean  $1.8^{\circ}$  C) for the months December to March, respectively. During the summer of 1965–66 the mean temperature for the same 4 months was  $0.4^{\circ}$  C, when there was a very gradual and much less extensive disappearance of snow, and a number of lakes remained frozen throughout the year.

TABLE II

MEAN ANNUAL CLIMATIC DATA FOR SIGNY, LAURIE AND GALINDEZ ISLANDS

	Air	Wind	C	Relative	Number	Number	Number		Number of	days with		Total equivalent
Station	tempera- ture (°C)	velocity (m./sec.)	Sunshine (hr.)	humidity (per cent)	of gales	of cloudy days	of clear days	Snow	Sleet	Rain	Drizzle	rainfall (mm.)
Signy Island	-3·65 (20)	7·3 (20)	555 (20)	85·5 (14)	63 (14)	258 (14)	7·5 (14)	259 (11)	57 (11)	76 (11)	1 <b>00</b> (11)	Data not available
Laurie Island	-4·7 (47)	5·0 (46)	483 (46)	86 (45)	Data not available	288 (46)	4 (46)	262 (42)	Data	not availal	ole	398 (44)
Galindez Island	-5·2 (20)	3·9 (18)	777 (14)	86 (14)	14 (15)	236 (15)	15 (15)	229 (11)	40 (11)	47 (11)	41 (11)	330 (4)

Figures in parentheses give the number of years from which mean values were determined.

Signy and Galindez Islands' data have been taken from Pepper (1954) for the years 1948-50, from the Falkland Islands Dependencies annual meteorological tables for the years 1951-59, from the British Antarctic meteorological annual tables for the years 1960-61, and from the meteorological records maintained at the stations for the years 1962-67. Laurie Island data have been taken from Direction General del Servicio Meteorologico Nacional (1951).

Cloudy days on Signy and Galindez Islands are those on which the sum of cloud cover for the 12.00, 18.00 and 24.00 hr. G.M.T. observations  $\geq$  20 oktas. For Laurie Island they are those days on which the mean for the 24 hourly observations  $\geq$  8/10 cover.

Clear days on Signy and Galindez Islands are those on which the sum of the cloud cover for the 12.00, 18.00 and 24.00 hr. G.M.T. observations  $\leq$  4 oktas. For Laurie Island they are those days on which the mean for 24 hourly observations  $\leq$  2/10 cover.

The meteorological station on Laurie Island is approximately 40 km. east of the meteorological station on Signy Island.

#### 3. Other islands

The three principal islands of the South Orkney Islands, Coronation, Powell and Laurie Islands (Fig. 1) are heavily glacierized and possess few extensive areas of snow-free terrain. The largest, Coronation Island (Fig. 3) is about 48 km. east—west and rises to a maximum altitude of 1,288 m. at Mount Nivea while a number of other mountains in the centre and at the eastern end exceed 1,000 m. There are several large glaciers reaching sea-level and much of the island is covered by small hanging glaciers and permanent ice caps. Most of the low-lying headlands and offshore islands on the south side of Coronation Island become snow-free in summer and, in the absence of penguin (*Pygoscelis* spp.) colonies, vegetation is fairly well developed. The few exposed areas on the north coast are mainly precipitous and no habitats for vegetation have been reported. Inland, inaccessible ice-free cliffs and nunataks occur to about 1,000 m.

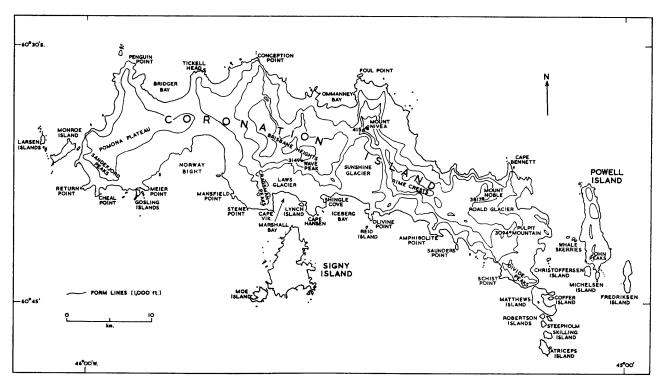


FIGURE 3

Coronation Island and related smaller islands, showing the main localities referred to in the text.

The easternmost of the South Orkney Islands, Laurie Island (c. 24 km. east—west) is irregularly mountainous and also largely glacierized but many of the coastal lowland areas are free of snow and ice in summer. In these areas locally extensive stands of vegetation have been reported.

Powell Island (c. 13 km. north-south), between Coronation and Laurie Islands, is heavily glacierized with an extensive ice piedmont on the eastern side. Only a few areas, mainly on the west coast, are snow-free and support most of the island's vegetation. Michelsen Island, joined to Powell Island by a narrow isthmus which is submerged at high tide, is entirely snow-free in summer but is occupied by very large colonies of penguins and other sea birds and consequently supports little vegetation.

Fredriksen Island, between Powell and Laurie Islands, is the least ice-covered island of the larger islands of the group, being narrow and rather precipitous with very little surface water. Many sites otherwise apparently suitable for plant growth are occupied by penguin colonies, but vegetation covers much of the rookery-free ground on the northernmost part of the island.

Of the smaller islands several have small glaciers or ice caps, although there is proportionately more snow-free ground than on most of the larger islands. The largest of these lesser islands include the Larsen Islands and Monroe Island off the west end of Coronation Island and the Robertson Islands off its south-eastern tip, Moe Island off the south-west of Signy Island, Christoffersen Island close to Michelsen

Island, and Saddle and Weddell Islands in Washington Strait. Most of these islands are high and steep with many of the headlands or screes occupied by colonies of penguins thus reducing the extent of available habitats for plant colonization.

Geologically, most of Coronation Island is composed of the same metamorphic complex which forms Signy Island (Matthews and Maling, 1967), although there is a far wider range of rock types on the latter (Thomson, 1968). Thus the greater part of Coronation Island appears to be quartz-mica-schist, with occasional amphibolites, while marbles such as those frequently occurring on Signy Island are known only from Penguin Point in the north-west. The extreme eastern end and the Robertson Islands, together with most of Powell Island, consist of much younger conglomerates with local shale beds. Laurie and Fredriksen Islands and parts of Powell Island consist mainly of a greywacke-shale succession.

A comparison of meteorological data recorded on Laurie Island at the Argentine station "Orcadas del Sur" and at the British Antarctic Survey station on Signy Island (Table I) shows that there is little climatic difference between the eastern and western areas of the South Orkney Islands. On account of the extensive snow and ice cover and the high altitude of Coronation Island, it can be expected that the climate of that island may be more severe than elsewhere in the South Orkney Islands, especially in inland areas. Temperature data from Laurie Island are slightly lower than those of the much smaller and less mountainous Signy Island, while the former is also more cloudy but apparently less windy.

## III. HISTORY OF BOTANICAL INVESTIGATION

## 1. Earliest reports

Several accounts have been given in recent years of the historical background of botanical observations and collections in the Antarctic (Llano, 1956; Greene, 1964a, b, 1967; Rudolph, 1966), but no detailed account has yet been provided for the South Orkney Islands.

The South Orkney Islands were discovered as recently as 1821 by George Powell in the sloop *Dove*, accompanied by the American Nathaniel Palmer in *James Monroe*, while searching for new fur and elephant seal colonies (Marr, 1935). However, no biological observations resulted from this visit. In 1823, James Weddell (1825) landed at Cape Dundas, Laurie Island, at the eastern end of the group, and reported "a patch of short grass", the earliest record of vegetation in the islands. When the French Antarctic Expedition called at Laurie Island in 1838, its leader, Dumont D'Urville (1842, p. 131), observed what was probably the same vegetation as that reported by Weddell on the rocky coast near Cape Dundas. These considerable patches he described as "doit appartenir à la famille des lichens, peut-être à l'*Usnea melanoxantha*", but he made no mention of Weddell's reputed grass; he believed that the grass was, in fact, the lichen *Usnea*. During the next 65 yr. only three sealing expeditions are known to have visited the South Orkney Islands, the sole outcome of which seems to have been the extermination of the fur, elephant and Weddell seal populations (Marr, 1935).

## 2. Between 1902 and 1947

The first scientific work carried out in the South Orkney Islands was undertaken by the Scottish National Antarctic Expedition, 1902–04, when a party spent the winter of 1903 at Scotia Bay, Laurie Island (Rudmose Brown and others, 1906). Botanical collections, including bryophytes, lichens and a large number of marine algae, were made by Rudmose Brown (1905, 1906, 1912a, b). It is, perhaps, unfortunate that the scientific work was restricted to Laurie Island and, although very few specimens of the plants forming the terrestrial vegetation were brought back, these observations represented a starting point for future botanical studies. Ten moss species were identified and described by Wright (1905). These were later checked and re-named Cardot (1911, 1912), together with another four species collected by La Valette, an Argentine from the meteorological observatory on Laurie Island. Only 11 species of lichen were collected, and these were identified by Darbishire (1905, 1912).

Rudmose Brown mentioned the rich and extensive lichen cover on the rock faces, where the orange and olive-green coloration provided by species of *Placodium* (now referred to *Caloplaca* and *Xanthoria*) and *Usnea melaxantha* (probably *U. antarctica* and *U. fasciata*) respectively was a prominent feature, especially during the winter when most of the other vegetation was covered by snow. He found no grass or hepatics, although both were already known as far south as lat. 65° S. on the Antarctic Peninsula.

Like D'Urville, he believed that Weddell's grass was the lichen *Usnea*. Of the mosses collected, only *Polytrichum subpiliferum* (= *P. juniperinum*; Longton, 1972) possessed "many and well-developed fruits" (Rudmose Brown, 1912a). Although at least 15 species have now been found fruiting on Signy Island, the only known fertile representative of the Polytrichaceae is *Polytrichum alpinum* in which sporophytes have been seen rarely in only three localities (Longton, 1972). *Prasiola crispa* was the only terrestrial alga collected.

The next expedition to the South Orkney Islands was an intensive biological and hydrographic survey carried out from R.R.S. Discovery II in 1932-33 (Marr, 1935), when collections and observations were made of the flora, at places other than Laurie Island. Marr reported that "the richest and largest patches of vegetation occur on the south side of the group, for there suitable ice-free sites are more numerous than elsewhere", and "it is on Signy, the southernmost yet least glaciated island of the group, especially on the gentle slopes behind the old whaling station, that the most luxuriant moss growth of all is found". Despite this, Marr went on to say that "so far as is known at present the flora is poorer in individual species than that of the South Shetlands and north-western coast of Graham Land, both of them localities which lie nearer the Pole than the South Orkneys". Of the nine moss species recorded, eight had already been collected by Rudmose Brown in 1903. The label bearing the collecting data of the remaining species, Racomitrium lanuginosum, has been lost, but it is considered more likely to have been collected on South Georgia than in the South Orkney Islands, as this species, together with several other bryophytes mixed in the specimen, have never been recorded south of South Georgia (personal communication from S. W. Greene). The mosses collected from Signy Island and some others from Michelsen Island, Fredriksen Island and Sandefjord Bay at the west end of Coronation Island, were identified by Dixon (1935). This then is the first reference to vegetation on Signy Island, and the earliest published list containing eight species of moss. However, there exists in the British Museum (Nat. Hist.) some mosses and lichens collected by A. G. Bennett between 1912 and 1915 on Signy Island. Both Lamb (1964) and Greene and others (1970) have referred to specimens from this collection.

Even after a second expedition to the South Orkney Islands by R.R.S. *Discovery II*, no hepatics had been reported. However, from the specimens examined by Dixon, several additional bryophytes have since been isolated, including at least three mosses and three liverworts. Included in this collection from Borge Bay, Signy Island, were the first specimens of *Deschampsia antarctica* and *Colobanthus quitensis* from the South Orkney Islands (Skottsberg, 1954).

## 3. Post-1947

In the year prior to the establishment of the British Antarctic Survey station on Signy Island, a temporary base was maintained at Cape Geddes, Laurie Island, not far from the Argentine station "Orcadas del Sur". During the 1946-47 season, approximately 12 mosses and three hepatics were collected from the Cape Geddes area, while recent examination of these specimens has revealed small plants of both the grass and the pearlwort (Greene and Holtom, 1971). A permanent station has been in existence on Signy Island since 1947 (Holdgate, 1965), and various collections of bryophytes and lichens have been made by personnel of the Falkland Islands Dependencies Survey and the British Antarctic Survey. Collections made prior to 1962 were collated by Greene (1964a) and later collections by Greene and others (1970). At least 25 species of moss and several liverworts were identified. A number of lichens have been described by Lamb (1948, 1964, 1968) and Lindsay (1969a, b, 1971a, b, c, d, 1972). In 1961-62 and 1963-64, M. W. Holdgate made a comprehensive collection of the species forming the island's vegetation. This and subsequent collections by R. E. Longton, D. C. Lindsay and the author are at present being evaluated and are increasing substantially the number of species previously known from Signy Island (personal communication from S. W. Greene and D. C. Lindsay).

The first primary ecological survey of the terrestrial vegetation of Signy Island was carried out by Holdgate (1964a) between 1961 and 1964. He classified the vegetation into three broad groupings according to the relationship of the principal bryophytes and lichens to habitat types. The three formations which he recognized were characterized by the dominance of species of:

- i. Andreaea and Usnea.
- ii. Polytrichum and Dicranum (= Chorisodontium).
- iii. Acrocladium (= Calliergon), Brachythecium and Drepanocladus.

Within each of these groups several variants were listed. In a more detailed, unpublished account in the manuscript collection of the British Antarctic Survey's Botanical Section, Holdgate described 15 community types which were distinguished both by structure and composition, and related to differences in habitat. Descriptions of these were supplemented by semi-quantititive analyses and by lists of species which were as comprehensive as taxonomic knowledge at the time of the survey permitted. In addition, Holdgate mapped the distribution of the island's principal vegetation types.

Subsequent field work led to a modification in the terminology of certain of the vegetation categories, in particular, the restriction of the word "formation" to categories defined in terms of physiogonomy rather than floristics. An extension of this system, incorporating the views and findings of C. H. Gimingham, M. W. Holdgate, D. C. Lindsay, R. E. Longton and the author was outlined by Longton (1967) and later considerably amplified by Gimingham and Smith (1970).

As a result of the collections made by the above workers and other British Antarctic Survey personnel, the number of bryophyte species believed to exist on Signy Island has risen from the eight mosses recorded by Dixon (1935) to about 75 species of mosses and 12 species of hepatics. The number of lichen species may be as high as 250 (personal communication from D. C. Lindsay), but the nomenclature for many bryophytes and lichens remains largely provisional.

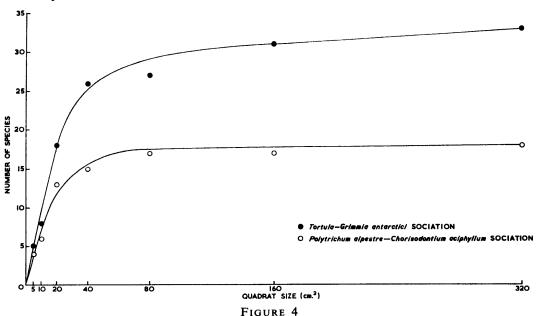
Thus, the structure and composition of the main categories of the vegetation having been established, the foundation was laid for a more detailed ecological survey.

## IV. METHODS AND LOCALITIES VISITED

## 1. Analysis of communities

The majority of the plant communities on Signy Island, as elsewhere in the maritime Antarctic, are remarkably homogeneous. Generally, most stands cover small areas, often as little as 15 m.<sup>2</sup>, and several widely differing communities may be represented in an area of, say 50 m. by 50 m. Thus the species recorded in quadrats of a comparatively small size can provide a sufficiently accurate indication of community composition.

As an empirical guide to the appropriate size of sample area for the analysis of stands, the "minimal area" technique of Braun-Blanquet (1932) and Poore (1955a, b, c) was used. Fig. 4 shows how the increase in the number of species recorded is related to the size of the sample area as the latter is successively doubled, in two widely differing sociations on Signy Island. The graphs change in slope between quadrat sizes of 20 cm. by 20 cm. and 40 cm. by 40 cm., beyond which few additional species were encountered



Species-area curves showing the relation between the number of species and the size of the sample area in two widely differing sociations on Signy Island.

as sample size was further increased. Although it has been shown by Greig-Smith (1957) that the concept of "minimal area" has no meaning as a property of the community, for an analysis of the present type it may serve as a rapid guide to the selection of a sample size above which increase in area would yield little additional information. In view of the time taken by a single worker to record data in cryptogamic vegetation in quadrats larger than 20 cm. by 20 cm., this was adopted as the standard quadrat size.

For each of five well-separated sites representing a particular sociation, the total number of species, together with the percentage cover afforded by each, was recorded in ten randomly placed quadrats, usually within an area of 25 m.<sup>2</sup>. However, certain species lists are likely to be incomplete with regard to the crustose lichens since determinations in the field of these plants were only occasionally possible. The quantitative data from the 50 quadrats for each of some 31 sociations, together with semi-quantitative data from a number of others, have been collated to give the species lists in the following account. In all, more than 1,500 lists of quadrat data were obtained.

Floristic trends which follow environmental gradients were examined by analysis of 20 cm. by 20 cm. quadrats placed at regular intervals along transects. In each quadrat, cover abundance of all species was recorded and in some the moisture content, loss on ignition, pH and occasionally base status of the soil was determined on the fresh material. The profile of most transects was obtained and snow-depth measurements taken during September when accumulation was greatest.

The use of a narrow belt transect has been employed to study the transition from one community type to another in situations where there are abrupt changes in the habitat. In some other cases the distribution of colonies of species in relation to aspects of the habitat has been mapped. The cover data of the ecologically important species were plotted graphically in relation to the transect profile. Snow-depth and soil data have been superimposed where they are available.

## 2. Analysis of soils

Soil from a large number of stands was collected from 2-5 cm. below the vegetation, or to about 10 cm. in the case of the peat-forming communities where there is no clear demarcation between living and dead moss.

Hydrogen ion concentration (pH) was determined by reducing the soil samples to a thick paste with de-ionized water and using a glass electrode and pH meter. Moisture content was obtained by the total extraction of water at 105° C, the results being expressed as a percentage of the oven-dry weight to give the field capacity. These samples were then ground and the fraction comprising particles of less than 2 mm. diameter was ignited in a muffle furnace at 550° C till constant in weight, thus indicating the organic content by loss on ignition (L.O.I.). The values for base saturation given in some of the illustrations were determined by the method of Brown (1943).

## 3. Localities visited

Almost all the quantitative data provided in the following account were recorded on Signy Island between December 1964 and February 1967. Stand analyses were carried out in all parts of the island except the south-west corner and some of the higher ground. However, the areas which received the most intensive study were on the east coast between Rusty Bluff and Stygian Cove, and the Gourlay Peninsula area, and on the west coast from Thulla Point to North Point (Fig. 2). The only additional quantitative data obtained were from stands of *Deschampsia antarctica* and *Colobanthus quitensis* on the north side of Lynch Island (Fig. 3).

A number of other localities on the western islands of the South Orkney Islands were visited during 1964-65 and 1965-66, when collections of species and observations on the plant communities were made. Landings of varying duration were made on Fredriksen, Powell and Michelsen Islands, on Matthews Island, at Saunders Point, Olivine Point, Reid Island, Shingle Cove and the moraines and buttress to its north, Cape Hansen, Cape Vik, Mansfield Point and Meier Point, all on or close to Coronation Island (Fig. 3). Most of the islands around Signy Island were examined, although only Moe Island, the Oliphant Islands and the largest of the Thule Islands (Fig. 2) supported extensive vegetation. The data recorded during these surveys are entirely qualitative, but they provide adequate evidence to suggest that no further community types exist in the western part of the South Orkney Islands which are unrepresented on Signy Island.

## V. PLANT COMMUNITIES ON SIGNY ISLAND

#### A. CLASSIFICATION

ONE purpose for creating a classification of Antartcic terrestrial vegetation is to provide a basis for further investigation of the organization and ecology of its plant communities both to establish a uniform treatment of the vegetation throughout the region and to allow comparison with other regions of the world. However, plant communities seldom show clear-cut discontinuities in structure or composition, and variation between them may be more or less continuous and multi-directional. This is certainly true of the vegetation of the sub-Antarctic island of South Georgia where the application of ordination techniques by the author has revealed a clear continuum of variation. Nevertheless, the vegetation of Signy Island, and other regions of the maritime Antarctic, comprises a large number of recurrent units which may be readily recognized and defined. An important feature of these assemblages is their relatively small size combined with a high degree of homogeneity within each and a uniformity of composition and structure between similar stands. Although many of these units are discrete entities with clearly marked boundaries, two or more adjacent stands of different communities may intergrade along their common margin to produce a narrow band of heterogeneous vegetation composed of species belonging to both stands. However, it has proved feasible to erect a workable system of classification based chiefly on the frequent recurrence of certain assemblages of species which result from the repetition of particular habitat regimes.

Classification of vegetation is a controversial subject, and various approaches are open to the ecologist, who can choose in the first place between attempting a more or less objective procedure based on statistical methods, or a subjective method relying on his own informed judgement supported by detailed investigation. When a large area with appreciable vegetational diversity is under review, the former may be exceedingly time-consuming, and in order to achieve a workable system within the time available, the latter approach was adopted for Signy Island (Gimingham and Smith, 1970). However, detailed quantitative data have been obtained from limited study areas and subjected to the normal association analysis treatment of Williams and Lambert (1959, 1960). The resulting assemblages compare favourably with those recognized by the more subjective method (Gimingham, 1967). Further analyses by the ordination techniques of Bray and Curtis (1957) and others are being assessed.

The heirarchical system of classification used in this report is founded on the concepts of Braun-Blanquet (1932) but it incorporates the modifications of several other phytosociologists including Du Rietz (1930), Gams (1932), Tansley (1939) and Poore (1962). The present classification (Table III, overleaf) has proved compatible with, but considerably more detailed than, the two most recent world-wide systems of vegetation classification which have been outlined by Ellenberg and Mueller-Dombois (1966) and Fosberg (1967).

The criteria for the units of classification, which were discussed in some detail by Gimingham and Smith (1970), may be summarized as follows:

- i. Formations. Units based on major physiognomic criteria of which life form is the most important. The vegetation of the maritime Antarctic may be separated into two major tundra formations, one comprising a wide range of cryptogams in which bryophytes, lichens and algae predominate (Antarctic non-vascular cryptogam tundra formation), and a considerably less diverse formation in which the two herbaceous phanerogams occur (Antarctic herb tundra formation).
- ii. Sub-formations. Units based on the growth form of the predominant components of respective stands. Of the ecologically important bryophytes, several growth forms are used to distinguish a number of sub-formations, e.g. large and small cushions, turves and carpets. Similarly, the crustose and fruticose habits predominate among the lichen flora, but the algal communities have not been studied in sufficient detail to permit satisfactory recognition of sub-formations. The various forms of community structure are a reflection of particular habitat characteristics.
- iii. Associations. Units based on floristic similarity between component stands and differentiated according to the high constancy of a small group of species. Thus within a sub-formation there may be several physiognomically identical associations each typical of a specific habitat regime and, where a particular combination of environmental complexes exists, communities of similar structure and species composition may be expected.

#### TABLE III

## CLASSIFICATION OF TERRESTRIAL PLANT COMMUNITIES OF THE SOUTH ORKNEY ISLANDS

#### A. ANTARCTIC NON-VASCULAR CRYPTOGAM TUNDRA FORMATION

- 1. Fruticose lichen and moss cushion sub-formation
  - Andreaea-Usnea association
    - i. Andreaea-lichen sociation
    - ii. Andreaea sociation
    - iii. Andreaea-foliose hepatic sociation
    - iv. Andreaea-Racomitrium cf. crispulum sociation
    - v. Andreaea-Dicranoweisia grimmiacea sociation
    - vi. Andreaea-Dicranoweisia grimmiacea-Usnea-Omphalodiscus sociation
    - vii. Andreaea-Himantormia lugubris sociation
    - viii. Usnea-Himantormia lugubris sociation
    - ix. Usnea-Omphalodiscus-Himantormia lugubris sociation
    - x. Usnea antarctica sociation
  - b. Bryophyte and lichen assemblages of rock micro-habitats
    - i. In siliceous rock crevices
    - ii. In calcareous and base-rich rock crevices
  - c. Tortula-Grimmia antarctici association
    - i. Tortula sociation
    - ii. Grimmia antarctici sociation
    - iii. Tortula-Grimmia antarctici sociation iv. Tortula conferta-Bryum sociation
  - d. Pottia austrogeorgica association
    - i. Pottia austrogeorgica sociation
- 2. Crustose lichen sub-formation
  - a. Caloplaca-Xanthoria association
    - i. Verrucaria sociation
    - ii. Caloplaca sociation
    - iii. Xanthoria elegans sociation
    - iv. Xanthoria elegans-Ramalina terebrata sociation v. Caloplaca regalis sociation

    - vi. Caloplaca-Xanthoria elegans-Pertusaria sociation
  - b. Buellia-Lecanora-Lecidea association
    - i. Buellia-Lecanora-Lecidea sociation
  - c. Placopsis contortuplicata association
    - i. Placopsis contortuplicata sociation
- 3. Moss turf sub-formation
  - a. Polytrichum alpestre-Chorisodontium aciphyllum association
    - i. Polytrichum alpestre sociation
    - ii. Polytrichum alpestre-lichen sociation
    - iii. Chorisodontium aciphyllum sociation iv. Chorisodontium aciphyllum-lichen sociation
    - v. Polytrichum alpestre-Chorisodontium aciphyllum sociation

    - vi. Polytrichum alpestre-Chorisodontium aciphyllum-lichen sociation vii. Polytrichum alpestre-Chorisodontium aciphyllum banks heavily colonized by epiphytic lichens
  - b. Polytrichum alpinum association
    - i. Polytrichum alpinum sociation
    - ii. Polytrichum alpinum-Drepanocladus uncinatus sociation
- 4. Moss carpet sub-formation
  - a. Brachythecium cf. antarcticum-Calliergon cf. sarmentosum-Drepanocladus uncinatus association
    - i. Brachythecium cf. antarcticum sociation
    - ii. Calliergon cf. sarmentosum sociation
    - iii. Drepanocladus uncinatus sociation
    - iv. Brachythecium cf. antarcticum-Calliergon cf. sarmentosum sociation
    - Calliergon cf. sarmentosum-Drepanocladus uncinatus sociation
    - vi. Brachythecium cf. antarcticum-Calliergon cf. sarmentosum-Drepanocladus uncinatus sociation
- 5. Moss hummock sub-formation
  - a. Bryum algens-Drepanocladus uncinatus association
    - i. Bryum algens-Drepanocladus uncinatus-Tortula excelsa sociation
    - ii. Bryum algens sociation
  - b. Brachythecium austro-salebrosum association
    - i. Brachythecium austro-salebrosum sociation

#### TABLE III—continued

- 6. Encrusted moss sub-formation
  - a. Lichen encrusted Bryum-Ceratodon cf. grossiretis-Pohlia nutans association
    - i. Lichen encrusted Ceratodon cf. grossiretis-Pohlia nutans-Cephaloziella varians sociation
- 7. Alga sub-formation
  - a. Prasiola crispa association
    - i. Prasiola crispa sociation
  - b. Nostoc association
  - i. Nostoc sociation
- 8. Snow alga sub-formation
  - a. Chlamydomonas nivalis-Raphidonema nivale-Ochromonas association
    - i. Chlamydomonas nivalis-Raphidonema nivale-Ochromonas sociation
- 9. Miscellaneous cryptogam assemblages
  - a. Marchantia berteroana community
  - b. Pioneer communities of moraines
- B. ANTARCTIC HERB TUNDRA FORMATION
  - 1. Grass and cushion chamaephyte sub-formation
    - a. Deschampsia antarctica-Colobanthus quitensis association
      - i. Deschampsia antarctica sociation
      - ii. Colobanthus quitensis sociation
      - iii. Deschampsia antarctica-Colobanthus quitensis sociation

Where only the generic name is given, either the species is unknown or two or more species are involved.

iv. Sociations. Units based on the dominance of one or more species within the stands of an association. An association may therefore comprise several sociations exhibiting little variation in species composition and general habitat requirements, but the abundance of the principal species varies and in each instance a different species assumes dominance. This change in dominance from one stand to another, producing a number of ecological variants within a particular association, appears to be a response to minor variations in the habitat.

## B. ANTARCTIC NON-VASCULAR CRYPTOGAM TUNDRA FORMATION

## 1. Fruticose lichen and moss cushion sub-formation

Most of the cryptogam communities occupying the drier, rockier and more exposed habitats are composed largely of physiognomically similar assemblages in which short cushion mosses and bushy fruticose lichens predominate. Thus, wind-swept screes, plateaux, ridges, knolls and rock faces from near sea-level to the highest rock exposures on Signy Island (c. 280 m.), and to over 500 m. on Coronation Island, support a wide variety of communities belonging to this sub-formation. Certain of these communities cover extensive areas while others with more restricted habitat preferences may be only a few square metres in extent.

Associated growth forms usually include a rich understorey of epipetric crustose lichens, while those habitats in which there is some soil may support several short turf-forming mosses. Bryophytes usually predominate in the more stable habitats, particularly where there is some accumulation of soil or organic matter which retains moisture. Such situations often occur in hollows, desposits of glacial detritus and sheltered, gentle sloping hillsides, which, unlike the drier, more exposed habitats, receive protection and moisture from winter snow accumulation.

a. Andreaea-Usnea association (Table IV). This association comprises a large number of sociations, several of which are similar in species composition, and most of these communities may be considered as facies in a small-scale continuum. It is the most common and widespread association on Signy Island and probably throughout the maritime Antarctic. Since the exposed, stony or rocky substrata favoured by these communities cover much of the snow- and ice-free ground, several of the sociations provide some of the most extensive stands of vegetation on the island.

TABLE IV

PERCENTAGE COVER AND PERCENTAGE FREQUENCY OF SPECIES IN SOCIATIONS

OF THE Andreaea-Usnea ASSOCIATION

		Sociations s	howing percentag	ge cover; percentag	ge frequency or fi	requency assessm	nent of species	
Species	Andreaea– lichen	Andreaea	Andreaea– foliose hepatic	Andreaea– Dicranoweisia grimmiacea– Usnea– Omphalodiscus	Andreaea– Himantormia lugubris	Usnea– Himantormia lugubris	Usnea– Omphalodiscus– Himantormia lugubris	Usnea antarctica
	Sites 1–5	Sites 6-10	Sites 11–15	Sites 16-18	Sites 19-23	Sites 24–28	Sites 29-32	Sites 33-37
Mosses								
Andreaea depressinervis	69; 100	_	4; 36	o	7; 92	2; 40	_	3; 60
Andreaea gainii		49; 72	2; 18	f-a	_	1; 26	<1; 18	-
Andreaea regularis	_	41; 58	31; 96	o	7; 48	<1; 22	3; 36	<1; 4
Total Andreaea spp.	69; 100	90; 100	37; 98	f–a	14; 96	4; 70	3; 54	3; 64
Bartramia cf. patens	-	-	_	o	-	-	<1; 9	<1; 2
Bartramia spp.	-	-	_	r-o	_	-	-	_
Calliergon cf. sarmentosum	_	<1; 36	4; 48	_	_	-	_	-
Ceratodon cf. grossiretis	-	-		o-f	_	_	_	2; 30
Chorisodontium aciphyllum	<1; 20	<1; 34	<1; 18	О	<1; 18	<1; 2	_	_
Conostomum pentastichum	-	_	4; 30	-	_	_	-	_
Conostomum perangulatum	-	_	<1; 20	-	-	_	-	_
Dicranoweisia grimmiacea	-	_	_	f–la	-	+; 2	<1; 9	-
Dicranoweisia sp.	<1; 4	<1; 12	6; 78	o	<1; 10	<1; 8		2; 44
Dicranum oleodictyon	_		_	vr	_	-	-	_
Distichium cf. capillaceum	_	-	_	_	-	<1; 2	_	-
Drepanocladus uncinatus	<1; 6	1; 54	2; 48	o–la	<1; 10	<1; 2	-	<1; 8
Grimmia antarctici	_	<1; 4	_	o	_	-	-	_
Plagiothecium sp.	<b>–</b>	_	_	r-o	_	-	_	-

		Sociations sh	nowing percentag	ge cover; percentag	ge frequency or f	requency assessm	ent of species	
Species	Andreaea– lichen	Andreaea	Andreaea– foliose hepatic	Andreaea– Dicranoweisia grimmiacea– Usnea– Omphalodiscus	Andreaea– Himantormia lugubris	Usnea– Himantormia lugubris	Usnea– Omphalodiscus– Himantormia lugubris	Usnea antarctica
	Sites 1–5	Sites 6-10	Sites 11–15	Sites 16-18	Sites 19-23	Sites 24-28	Sites 29-32	Sites 33-37
Mosses—continued			:					
Pohlia cruda var. imbricata	-	<1; 2	<u> </u>	-	_	_	_	_
Pohlia nutans	<1; 2	<1; 16	1; 40	: <b>O</b>	<1; 6	-	_	2; 38
Polytrichum alpestre	_	_	3; 22	0	-	_	_	
Polytrichum alpinum	<1; 6	<1; 8	5; 68	o	<1; 16	<1; 8	_	<1; 10
Psilopilum antarcticum	_	- -	<1; 4	_	_		_	_
Racomitrium cf. crispulum	-	_	2; 16	-	_	_	-	_
Tortula conferta	-	_	-	r	_	_	<1; 4	-
Tortula fuscoviridis	-		. <del>-</del>	r	_	<del>-</del>	-	_
Hepatics								
Anthelia sp.		_	<1; 8	r	_	_	_	-
Barbilophozia hatcheri	_	<1; 10	2; 48	f	<1; 4	_	_	<1; 16
Cephaloziella varians	<1; 2	<1; 6	16; 100	o-f	2; 44	<1; 6	-	1; 34
Herzogobryum teres	-	4; 36	8; 36	o	4; 36	2; 24	-	<1; 8
Hygrolembidium isophyllum	_	_	14; 56	_	_	<1; 6	_	-
Metzgeria sp.	-	_	-	o	_	_	-	_
Pachyglossa dissitifolia	-	<1; 12	9; 84	f-la	<1; 6	<1; 6	-	<1; 6
Lichens					TO THE PROPERTY OF THE PROPERT	The state of the s		
Acarospora macrocyclos	-	_	_	-	<u> </u>	_	<1; 4	_

TABLE IV—continued

		Sociations sh	howing percentag	e cover; percentag	ge frequency or fi	requency assessm	ent of species	
Species	Andreaea- lichen	Andreaea	Andreaea– foliose hepatic	Andreaea– Dicranoweisia grimmiacea– Usnea– Omphalodiscus	Andreaea– Himantormia lugubris	Usnea– Himantormia lugubris	Usnea– Omphalodiscus– Himantormia lugubris	Usnea antarctica
	Sites 1-5	Sites 6–10	Sites 11-15	Sites 16–18	Sites 19-23	Sites 24-28	Sites 29-32	Sites 33-37
Lichens—continued								
Alectoria chalybeiformis	<1; 2	_	_	_	_	<1; 20	<1; 18	<1; 22
Alectoria nigricans	<1; 10	_	_	r	-	<1; 6	-	<1; 20
Alectoria pubescens	<1; 22	-	_	_	-	<1; 4	1; 27	<1; 14
Biatorella antarctica	-	-	_	_	~	_	<1; 4	-
Buellia coniops + B. russa	<1; 4	<1; 2	<1; 2	o–f	<1; 6	<1; 2	<1; 14	-
Buellia subpedicellata+B. granulosa	1; 24	<1; 14	<1; 4	ola	3; 68	6; 68	5; 22	<1; 12
Caloplaca cf. holocarpa	<1; 2	_		o	1; 8	<1; 4	<1; 18	_
Caloplaca sublobulata		_	_	r	_	<1; 6	_	<1; 4
Caloplaca regalis	-	-	_	-	-	_	+; 4	-
Candelariella vitellina	-	_	-	-	_	_	<1; 4	_
Catillaria corymbosa	-	_	_	o	<1; 4	<1; 16	1; 14	<1; 10
Cladonia carneola+C. metacorallifera	<1; 12	<1; 8	<1; 16	o	<1; 2	<1; 6	-	<1; 6
Cladonia chlorophaea	5; 84	<1; 12	1; 36	o-lf	<1; 2	<1; 10	-	1; 28
Cladonia spp. (probably including C. furcata, C. gracilis, C. phyllophora, C. squamosa var. allosquamosa)	2; 26	<1; 8	<1; 12	-	<1; 2	<1; 4	<1; 14	<1; 12
Collema sp.	-	_	_	f	<1; 2	-	_	_
Cornicularia aculeata	2; 56	<1; 4	_	r	<1; 10	3; 72	_	2; 52
? Cypheliopsis spp.	<1; 4	<1; 6	<1; 16	<del>-</del>	-	<1; 6	_	<1; 2
Cystocoleus niger	_	_	_	o	<1; 6	<1; 6	_	<1; 12

[-				4.1				
Species	Andreaea– lichen	Andreaea	Andreaea– foliose hepatic	Andreaea– Dicranoweisia grimmiacea– Usnea– Omphalodiscus	Andreaea– Himantormia lugubris	Usnea– Himantormia lugubris	Usnea– Omphalodiscus– Himantormia lugubris	Usnea antarctica
	Sites 1-5	Sites 6-10	Sites 11–15	Sites 16–18	Sites 19–23	Sites 24–28	Sites 29–32	Sites 33-37
Lichens—continued								
Dermatocarpon sp.	-	-	_	-	-	_	<1; 14	-
Haematomma erythromma	-	_	_	-	_	_	<1; 18	-
Himantormia lugubris	<1; 10	<1; 10	_	o	68; 100	34; 100	7; 58	<1; 2
Lecanora aspidophora	<1; 12	<1; 4	_	o	<1; 2	<1; 2	2; 58	<1; 10
Lecanora spp. (incl. L. atra)	<1; 26	<1; 10	<1; 2	o-lf	<1; 2	_	<1; 18	<1; 26
Lecidea spp. (incl. L. dick-sonii)	<1; 18	3; 60	<1; 6	o-la	1; 34	<1; 2	8; 95	1; 70
Lepraria sp.	-	_	-	_	-	_	<1; 4	-
Leptogium puberulum	-	<1; 4	-	0	_	_	-	_
Omphalodiscus antarcticus	-	_	_	f-la	_	_	12; 95	+; 2
Omphalodiscus decussatus	-	_	_		_	_	2; 27	_
Parmelia saxatilis	-	<1; 12	_	o-la	_	<1; 2	3; 22	_
Parmelia sp.	-	_	_	-	_	_	<1; 4	-
Pertusaria corallophora	_	_	_	0	_	_	<1; 22	-
Pertusaria spp.	_	-	_	0	<1; 2	3; 42	2; 50	-
Physcia caesia	_	_	_	o o	_	-	<1; 4	_
Ochrolechia antarctica	-	_	_	o	_	_	<1; 9	_
Ochrolechia frigida	4; 98	<1; 22	1; 28	f	3; 80	5; 90	<1; 32	3; 86
Rhizocarpon geographicum + R. superficiale	<1; 6	-	<1; 2	o–lf	1; 40	3; 70	5; 76	<1; 10
Rinodina petermannii	_		-	_	_	_	<1; 27	-
Sphaerophorus globosus	9; 92	-	<1; 4	· o	<1; 4	3; 74	<1; 9	2; 62

		Sociations sh	nowing percentag	re cover; percentag	ge frequency or fi	requency assessm	ent of species	
Species	Andreaea– lichen	Andreaea	Andreaea– foliose hepatic	Andreaea– Dicranoweisia grimmiacea– Usnea– Omphalodiscus	Andreaea– Himantormia lugubris	Usnea– Himantormia lugubris	Usnea- Omphalodiscus- Himantormia lugubris	Usnea antarctica
	Sites 1-5	Sites 6-10	Sites 11–15	Sites 16–18	Sites 19-23	Sites 24-28	Sites 29-32	Sites 33-37
Lichens—continued								
Stereocaulon alpinum (possibly includes S. botryosum)	<1; 8	<1; 6	2; 40	· ·	_	_	_	<1; 2
Usnea antarctica	12; 94	_	_	f–la	<1; 18	4; 58	17; 95	57; 100
Usnea fasciata	2; 12	_	<1; 4	r	<1; 16	34; 100	4; 45	4; 40
Xanthoria candelaria	-	_	-	r	_	_	2; 14	_
Unidentified crustose lichens	<1; 20	<1; 4	: : —	o	<1; 16	<1; 18	<1; 14	<1; 14
Alga								
Prasiola crispa	-	_	<1; 2	o-la	-	_	<1; 18	<1; 18
Substratum								
Bare rock, soil, etc.	4; 70	7; 56	4; 54	o-f	9; 94	13; 98	14; 100	24; 100
Summary					!			
Moss percentage cover, approx.	70	94	66	-	16	5	4	8
Hepatic percentage cover, approx.	<1	5	49	_	6	2	0	2
Lichen percentage cover, approx.	38	6	6	-	80	93	83	78
Bare ground, percentage cover	4	7	4	- -	9	13	14	24

Details of sites are given in the Appendix.

The fact that the sum of the cover values in each column may exceed 100 per cent is due to the overlap of numerous species, particularly between bryophytes and lichens. Percentage cover, the figure before the semi-colon, and percentage frequency, the figure after the semi-colon, is normally based on 50 quadrats, i.e. ten from each of five sites. +, Species present in close vicinity but absent from quadrats. Frequency assessment according to the scale: a, abundant; f, frequent; o, occasional; r, rare; vr. very rare: with the prefix 1 locally e.g. la = locally abundant

All the community types recognized possess one or more species of Andreaea or Usnea or of both genera. The more sheltered, moister ground and rock face habitats tend to support sociations dominated by bryophytes, particularly species of Andreaea and locally of Racomitrium and a variety of foliose hepatics. Small circular encrustations of species of Buellia, Caloplaca, Lecanora, Lecidea and Ochrolechia frequently occur as epiphytes on the moss cushions. Sometimes the cushions of Andreaea coalesce to form a closed undulating stand overlying a shallow accumulation of moss peat from which the living shoots arise, thus resembling the moss carpet growth form. Closed stands of short Andreaea spp. intermixed with other mosses and hepatics occasionally develop on sheltered, damp rock faces.

The more arid, wind-swept habitats are occupied chiefly by communities of various fruticose lichens on rock and stony ground, with numerous crustose species associated. Species of *Usnea* and *Himantormia lugubris* dominate the driest and most exposed situations, while those which receive some degree of shelter and often moisture support species of *Alectoria*, *Omphalodiscus* and *Usnea antarctica*, together with small cushion mosses such as *Andreaea*, *Dicranoweisia* and *Grimmia*.

i. Andreaea-lichen sociation (Gimingham and Smith, 1970, pl. 1, p. 778). Predominant species: Andreaea depressinervis, Cladonia spp., Ochrolechia frigida, Sphaerophorus globosus and Usnea antarctica. Habitat: dry, fairly exposed soils, gravels and stones on level or gently sloping ground. Usually well covered by snow in winter. Frequently affected by frost heaving and solifluction. Soil data: (mean of 39 samples), pH 5·1, moisture content 29 per cent, L.O.I. 11·5 per cent. Altitudinal range: 5-200 (-270) m.

This is the most widespread community type in the association and is typically dominated by Andreaea depressinervis although other species of Andreaea may be present. The principal bryophyte associates include a species of Dicranoweisia, Chorisodontium aciphyllum and Polytrichum alpinum, the two latter species occasionally forming quite large patches. Of the lichens, Usnea antarctica usually predominates but species of Cladonia, Ochrolechia frigida (epiphytic on Andreaea), Sphaerophorus globosus and sometimes Usnea fasciata may be quite abundant. Epipetric crustose lichens vary in quantity according to the amount of rock surface in the habitat.

Very often the habitat is considerably influenced by frost heaving and solifluction, giving the community an overall open appearance. On level ground the continuity of the vegetation is broken by soil and stone polygons, clay puddles and frost boils. These features are seldom more than 1 m. in diameter and are usually fringed by Usnea fasciata on the coarser material around the periphery. The resulting colour pattern is one of dark brown Andreaea, greenish yellow Usnea and grey soil and stone polygons. On the steeper slopes where solifluction action causes numerous parallel soil and stone stripes, the Andreaea-lichen sociation is reduced to a series of narrow strips on the more stable, coarser material, separated by mobile clay and gravel. Here too the coarser material is pushed to the edge and, depending upon the wetness of the ground, may be colonized by bryophytes such as Calliergon cf. sarmentosum, Drepanocladus uncinatus, Anthelia sp. and Cephaloziella varians, with Andreaea spp., Polytrichum alpinum, Bartramia cf. patens and other short acrocarpous species on the drier soil.

Depending on the situation, this sociation frequently merges into the *Polytrichum alpestre-Chorisodontium aciphyllum* association, with increasing invasion by small hummocks of *Chorisodontium* towards the peat communities. As the habitat becomes wetter, *Drepanocladus uncinatus* and occasionally *Calliergon* cf. sarmentosum encroach into the *Andreaea*-lichen sociation.

ii. Andreaea sociation (Plate IIIa). Predominant species: Andreaea gainii, A. regularis and Herzogobryum teres. Habitat: moderately sheltered area where there is an accumulation of sandy, gravelly soil, particularly in depressions or on level or gently sloping ground where the soil is stable. Well-covered by snow in winter and often in summer. Soil data: moist hollows (mean of 16 samples), pH 5·1, moisture content 136 per cent, L.O.I. 4·9 per cent. Dry gravelly soils (mean of 37 samples), pH 5·7, moisture content 18 per cent, L.O.I. 4·6 per cent. Altitudinal range: 15-135 m.

The most extensive stands of a more or less pure, frequently closed Andreaea community occur in moist sheltered hollows and on level deposits of glacial detritus. Unlike the Andreaea-lichen sociation, in which the dominant moss is almost entirely A. depressinervis, the almost pure Andreaea sociations are dominated by A. gainii and A. regularis. The former has a slight preference for the moister habitats, being particularly abundant on wet vertical rock faces. Of the associated species,

Drepanocladus uncinatus and the hepatic Herzogobryum teres are the most frequent bryophytes, with local patches of Polytrichum alpinum and, where wetter, Calliergon cf. sarmentosum. Lichens are generally scarce in this sociation, but epiphytic species of Buellia, Lecidea and Ochrolechia frigida occur on the drier coalesced cushions of species of Andreaea. As the ground becomes drier and more broken by frost action the community becomes more open and lichens tend to form a more mixed Andreaea—lichen sociation.

iii. Andreaea-foliose hepatic sociation. Predominant species: Andreaea regularis, Cephaloziella varians, Hygrolembidium isophyllum, Herzogobryum teres and Pachyglossa dissitifolia. Habitat: permanently moist, gravelly soil on sloping ground. Altitudinal range: 15-100 m.

This sociation is very local, and is usually adjacent to Andreaea-lichen sociations or the pure Andreaea sociations of the moister soils. All three species of Andreaea, A. depressinervis, A. gainii and A. regularis, occur although A. regularis is usually dominant. Quite large expanses of coalesced cushions are typical, producing almost a turf or carpet type of growth form of the three species intermixed. A species of Dicranoweisia and Polytrichum alpinum are frequent associates on the drier soils, while Calliergon cf. sarmentosum and Drepanocladus uncinatus may be locally abundant where the habitat is wetter. The five commonest foliose hepatics on Signy Island also occur here, i.e. Barbilophozia hatcheri, Cephaloziella varians, Herzogobryum teres, Hygrolembidium isophyllum and Pachyglossa dissitifolia, often forming mixed colonies of up to 0.5 m. in diameter. The hepatics give a greater cover in this sociation than in any other, and it is the only one in which Hygrolembidium isophyllum is at all frequent. The rare Conostomum pentastichum, C. perangulatum and Psilopilum antarcticum are locally abundant in some stands. Lichens are usually occasional, with species of Cladonia, Ochrolechia frigida and Stereocaulon alpinum being the most frequent on or amongst the species of Andreaea.

iv. Andreaea-Racomitrium cf. crispulum sociation. This, like the next community type, is rare and has been recorded in only a very few localities on Signy Island. Both are closely related to other sociations within the Andreaea-Usnea association, and may be considered as variants of these in which one of the community components achieves the role of dominant. No species lists or soil data are available for either sociation.

Small, almost pure stands of coalesced cushions of Racomitrium cf. crispulum are occasionally encountered on dry stony slopes and fine scree on sheltered hillsides, usually at fairly low altitudes. This community type resembles most closely the Andreaea-foliose hepatic sociation, in which Racomitrium cf. crispulum is usually found, and the associated species are largely those of that assemblage. The Racomitrium does not often form stands larger than 4 m.², although open Racomitrium-dominant communities of considerably larger area have been seen. The commonest associates are Andreaea spp., Dicranoweisia sp., Drepanocladus uncinatus, Hygrolembidium isophyllum, Polytrichum alpinum and Pachyglossa dissitifolia, while species of Cladonia, Stereocaulon alpinum, and occasionally Usnea fasciata and Himantormia lugubris on the stones, are the chief lichens. Andreaea-Racomitrium communities are not infrequent on dry rock habitats in the Argentine Islands.

- v. Andreaea-Dicranoweisia grimmiacea sociation. Like the last community type, this is a very uncommon assemblage and has been seen in two localities only, with Dicranoweisia grimmiacea dominant on dry gravelly soil. D. grimmiacea is a common and typical cushion moss of rock surfaces where it produces sporophytes in profusion. However, the small, dark green cushions of Dicranoweisia in this community type are invariably infertile. The moss does not form a closed stand, but small numbers of the cushions may coalesce to form a unit of up to 250 cm.². The community in both cases lies adjacent to stands of the Andreaea-lichen sociation. The principal associates are Andreaea depressinervis, Drepanocladus uncinatus, Pohlia nutans and Polytrichum alpinum, with small quantities of species of Cladonia and crusts of several lecanoroid lichens on the stones.
- vi. Andreaea-Dicranoweisia grimmiacea-Usnea-Omphalodiscus sociation. Predominant species: Andreaea gainii, Dicranoweisia grimmiacea, Pachyglossa dissitifolia, Omphalodiscus antarcticus and Usnea antarctica. Habitat: sheltered rock faces supplied with trickling melt water. May be covered by ice in winter. Altitudinal range: 2-155 m.

A comparatively rich flora exists on moist rock faces, and bryophytes are often abundant,

forming closed cover over the wetter parts. Lichens usually predominate on the drier surfaces. The greatest cover is provided by Andreaea gainii, although A. depressinervis and A. regularis may sometimes be present also. Dicranoweisia grimmiacea, Ceratodon cf. grossiretis and Drepanocladus uncinatus are frequent. Foliose hepatics are often abundant, growing over and among the short, coalesced mat-like Andreaea cushions, with Barbilophozia hatcheri, Cephaloziella varians and Pachyglossa dissitifolia being the most widespread species. Occasionally Grimmia antarctici and Tortula fuscoviridis occur in small quantities, indicating a slight degree of flushing from bands of marble or amphibolite higher up the cliff face.

The moister, more sheltered situations are ideal for luxuriant growth of *Omphalodiscus* antarcticus, which in places festoons the rock faces with brownish grey thalli up to 25 cm. in diameter. Usnea antarctica is a frequent associate, and it too may grow to very large proportions, i.e. up to 15 cm. tall. Small thalli of Usnea are not uncommon growing as epiphytes on the *Omphalodiscus*. Parmelia saxatilis may be locally abundant and frequently spreads over moss cushions, as do several other species of Parmelia and Physcia.

No quantitative analyses of this sociation have been made, but the species of five sites have been listed in Table IV together with semi-quantitative data.

vii. Andreaea-Himantormia lugubris sociation. Predominant species: Andreaea depressinervis, A. regularis and Himantormia lugubris. Habitat: dry, exposed stony plateaux, ridges, etc. Usually covered with snow in winter. Altitudinal range: 100-170 m.

This local community type is conspicuous as a dark stand of vegetation, seldom extensive, in which the black fruticose lichen Himantormia lugubris has a cover value of 60-75 per cent. The lichen is most frequent on stones and rock surfaces, but a more slender, wiry form sometimes occurs amongst the associated Andreaea. Species of this genus, principally A. depressinervis and A. regularis, grow on the small pockets of soil and gravel amongst the loose stones, with smaller, isolated cushions on the stones. The only other frequent bryophyte is the foliose hepatic Herzogobryum teres, which seems to tolerate relatively dry conditions. As in most habitats where species of Andreaea occur, Ochrolechia frigida and other epiphytic lichens form circular encrustations on the moss. Species of Usnea are generally scarce. The most noticeable difference in habitat between this community type and the Usnea-Himantormia lugubris sociation is that in winter, due to local topographical features, there is a significant accumulation of snow in the former, whereas in the latter the ground is blown free of snow, although a thin layer of ice may persist. viii. Usnea-Himantormia lugubris sociation (Plate IIa, b and c; Gimingham and Smith, 1970, pl. 2, p. 778). Predominant species: Himantormia lugubris, Usnea antarctica and U. fasciata. Habitat: stony hillsides, exposed knolls, ridges, plateaux, etc. Largely snow-free in winter. Soil data: (mean of six samples), pH 5·2, moisture content 22 per cent, L.O.I. 7·4 per cent. Altitudinal range: 3-280 m. This is a widespread community type on almost all exposed stony ground. Since the substratum

is somewhat stonier with less soil accumulation than the Andreaea-Himantormia lugubris sociation, bryophytes account for only 5-10 per cent of the cover, the predominant species being Andreaea depressinervis, A. gainii, A. regularis and Herzogobryum teres. The co-dominant lichens, Usnea fasciata and Himantormia lugubris, constitute about 70 per cent of the cover, although H. lugubris tends to have a rather irregular distribution. Usnea antarctica is usually present but affords little cover. Species of Cladonia, Cornicularia aculeata and Sphaerophorus globosus are frequent associates amongst the smaller stones and two dominant lichens, while many crustose species cover most of the exposed rock surfaces. Species of Buellia, Lecidea, Lecanora, Ochrolechia, Pertusaria and Rhizocarpon are often abundant. In a very few localities, on scree composed of small fragments of rock, Usnea fasciata alone predominates and Himantormia is virtually absent. ix. Usnea-Omphalodiscus-Himantormia lugubris sociation (Plate IId). Predominant species: Buellia spp., Lecidea spp., Himantormia lugubris, Rhizocarpon spp., Omphalodiscus antarcticus and Usnea antarctica. Habitat: dry, exposed, quartz-mica-schist rock faces. Altitudinal range: 3-280 m. (-620 m. on Coronation Island).

Most dry rock faces are colonized by a large variety of fruticose and crustose lichens, and sparse cushions of moss. This sociation is most typical of rock surfaces at higher altitudes, and because of the lack of moisture, and the high saturation deficits experienced in this type of habitat, bryophytes are very scarce and often found only in small crevices or overhangs where the atmos-

phere remains slightly more humid. Andreaea gainii and A. regularis give the greatest bryophyte cover, and where the habitat becomes moister there is an abrupt change to an Andreaea-Dicranoweisia grimmiacea-Usnea-Omphalodiscus sociation in which the Andreaea is dominant.

This sociation is almost identical to the *Usnea-Himantormia lugubris* sociation described above. However, the present community occurs almost entirely on rock faces and outcrops rather than on the loose, gravelly soil and stones occupied by the latter sociation. Also, species of *Omphalodiscus* are important additional associates seldom found on the ground habitats.

The most prominent species are the tall, fruticose Usnea antarctica and to a lesser extent U. fasciata, Himantormia lugubris, and the foliose Omphalodiscus antarcticus. Himantormia lugubris appears to be most abundant in the more exposed situations such as the crests of precipices and rocky summits of several of the higher mountains. This is rather contrary to its habitat preference on stony level ground where it occupies sites with some degree of shelter, at least in winter. In very wind-swept localities H. lugubris is frequently accompanied by small scattered thalli of Omphalodiscus decussatus, a species more prominent farther south, but on Signy Island it is locally abundant on dry, exposed rock surfaces (Lindsay, 1969b). Usnea antarctica may also be abundant in the most exposed situations, while U. fasciata seems to be less tolerant of strong winds, but it is usually present in varying quantities within the sociation. Alectoria pubescens and Parmelia saxatilis may be locally abundant.

Numerous crustose lichens often give extensive understorey cover, both on the rock, on the scattered moss cushions and on holdfasts of the larger lichens. Species of *Buellia*, *Lecidea*, *Lecanora*, *Ochrolechia*, *Pertusaria* and *Rhizocarpon* may all be frequent associates.

x. Usnea antarctica sociation. Predominant species: Usnea antarctica. Habitat: dry deposits of fine gravel and sandy soil on exceptionally exposed, wind-swept ridges, crests of knolls, etc. No snow accumulation in winter. Soil data: (mean of six samples), pH 5·2, moisture content 16 per cent, L.O.I. 6·0 per cent. Altitudinal range: 8-235 m.

Unlike the two previous sociations, the *Usnea antarctica* sociation appears to avoid stony ground and shows a preference for a finer and looser substratum. Where larger material prevails *U. fasciata* and *Himantormia lugubris* are usually present, although extensive stands of *U. antarctica* are found on volcanic rock and screes in the South Shetland Islands. The poverty of bryophytes is probably due to the considerable exposure resulting in high saturation deficits, and the lack of snow cover during winter. *Andreaea depressinervis* and a little *A. regularis* account for about one-third of the approximately 10 per cent cover contributed by bryophytes, while small colonies of *Ceratodon* cf. *grossiretis*, *Dicranoweisia* sp., *Distichium* cf. *capillaceum*, *Pohlia nutans* and *Polytrichum alpinum* occur very sparsely. A few shoots of hepatics are found in the moister lee of some of the larger stones. Although about a quarter of the substratum is open, there are large numbers of lichens present, but none, other than *Usnea antarctica*, contribute much cover. *Cornicularia aculeata* and *Sphaerophorus globosus* may be locally frequent amongst *Usnea*, while several crustose lichens, e.g. species of *Buellia*, *Lecidea* and *Ochrolechia*, occur on the soil and small stones. The dominant *Usnea* varies considerably in its abundance, ranging from 45 to 80 per cent cover.

b. Bryophyte and lichen assemblages of rock micro-habitats (Tables V and VI). Almost any large rock surface possesses crevices, fissures, overhangs and narrow ledges, and in many of these small deposits of soil accumulate and provide a growing surface for a wide variety of bryophytes and lichens. The majority of the bryophyte species which occur on Signy Island may be encountered in such habitats, while a few appear to be restricted to damp and shaded crevices (e.g. Amblystegiella cf. densissima and species of Metzgeria and Plagiothecium). The growth form of the species occurring in these micro-habitats is largely of a short cushion structure, e.g. species of Andreaea, Bartramia, Barbula, Bryum, Dicranoweisia, Grimmia, Pohlia and Tortula, but a few species assume a prostrate, creeping system of interwoven shoots, e.g. species of Campylium, Drepanocladus, Metzgeria and Plagiothecium. Thread-like forms are represented by species of Amblystegiella, Isopterygium and Cephaloziella varians. The only species with a growth form resembling a weft is a species of Pseudoleskea.

Because of the considerable diversity within these micro-habitats, it has not been possible to distinguish separate sociations. However, depending upon the rock type, two distinct groups may be recognized, one occurring on base-rich rocks and the other on the more acid schist. The species composition of the

TABLE V
FREQUENCY ASSESSMENT OF SPECIES IN SILICEOUS ROCK CREVICES

Species	Dry or slig habit	htly damp tats	Wet h	abitats	Damp crevice	
	Sites 38-41	Site 42	Site 43	Site 44	Site 45	
Mosses						
Amblystegiella cf. densissima	o	-	_	-	_	
Andreaea depressinervis	_	-	a	-	_	
Andreaea gainii	a	f-a	-	a	p	
Andreaea regularis	-	f	_	_	-	
Barbula sp.	r	-	_	_	_	
Bartramia cf. patens	o	r	f	-	_	
Bartramia spp.	o	-	f	o	р	
Brachythecium austro-salebrosum	r	_	-	-	-	
Bryum algens (short form)	r	_	О	-	p	
Ceratodon cf. grossiretis	o	f–a	_	_	-	
Chorisodontium aciphyllum	-	_	o	-	-	
Conostomum pentastichum	-	_	_	r	_	
Conostomum perangulatum	r	_	_	_	_	
Dicranoweisia grimmiacea	О	f	f	o	_	
Dicranoweisia sp.	lf	-	-	-	_	
Distichium cf. capillaceum	r	-	r	_	-	
Drepanocladus uncinatus	0	f	la	r	p	
Encalpyta sp.	vr	-	_	-	_	
Grimmia antarctici	О	o	o	_	_	
Isopterygium sp.	vr	_	_	_	_	
Plagiothecium sp.	r	o	r	_	p	
Pohlia cruda var. imbricata	o	-	o		_	
Pohlia nutans	_	o	0	_	_	
Polytrichum alpestre	_	_	lf	_	_	
Polytrichum alpinum	_	-	1f	_	_	
Pottia austrogeorgica	r	-	_	-	_	
Pseudoleskea sp.	o	_	_	_	_	
Tortula conferta	r	-	_	-	_	
Tortula fuscoviridis	r	_	_	_	_	

TABLE V—continued

Species	Dry or slig habit	htly damp tats	Wet h	abitats	Damp crevice
	Sites 38-41	Site 42	Site 43	Site 44	Site 4:
Hepatics					
Anthelia sp.	r	-	_	-	_
Barbilophozia hatcheri	o	f	f	-	р
Cephaloziella varians	О	f	f	-	р
Metzgeria sp.	o	lf	-	-	р
Pachyglossa dissitifolia	o	lf	_	f	р
Unidentified foliose hepatics	o	-	_	f	_
Lichens					
Alectoria nigricans	_	_	r	_	_
Buellia anisomera	r	-	_	<del>-</del>	р
Buellia punctata	_	o	f	-	_
Buellia subpedicellata $+$ $B$ . granulosa	lf	f	o	r	_
Caloplaca cf. holocarpa	o	-	o	-	_
Caloplaca sp.	r	-	_	_	-
Cladonia carneola	_	-	f	o	_
Cladonia spp.	o	o	f	r	р
Collema sp.	f	o	o	-	-
Cystocoleus niger	_	$\mathbf{f}$	_	-	_
Himantormia lugubris	o	_	<del>-</del>	-	_
Lecanora aspidophora	o	_	o	-	_
Lecanora spp.	1f	o	o	o	-
Lecidea spp.	a	o	o	o	_
Leptogium puberulum	o	-	_	-	_
Ochrolechia antarctica	_	o	_	-	_
Ochrolechia frigida	f	f	f–a	o	_
Parmelia saxatilis	_	lf	_	o	p
Pertusaria corallophora	_	lf	lf	-	_
Pertusaria spp.	o–lf	o	_	-	р
Physcia caesia	_	f	_	-	p
Placopsis contortuplicata	la	o	_	-	_
Psoroma hypnorum	_		f	_	

TABLE V-continued

Species	Dry or sligi habit	htly damp ats	Wet h	Damp crevice	
	Sites 38-41	Site 42	Site 43	Site 44	Site 45
Lichens—continued					
Psoroma sp.	r	_	_	_	-
Rhizocarpon geographicum $+$ $R$ . superficiale	lf	o	_	r	-
Sphaerophorus globosus	-	o	f	-	-
Omphalodiscus antarcticus	r	o	f	lf	_
Usnea antarctica	o	o	f	r	-
Usnea fasciata	r	-	_	-	-
Xanthoria candelaria	-	r	_	-	-
Alga					
Prasiola crispa	_	o	f	r	_

Details of sites are given in the Appendix. Frequency assessment according to the scale used in Table IV. p Present.

more calcareous micro-habitats is similar in many respects to that of the calcicolous *Tortula-Grimmia* antarctici communities, while the assemblages occupying the more siliceous rocks are predominantly those of certain sociations of the *Andreaea-Usnea* association.

i. In siliceous rock crevices. The moister crevices may possess a wide range of species, although lichens are generally infrequent. The list in Table V differs little from that of the Andreaea-Dicranoweisia grimmiacea-Usnea-Omphalodiscus sociation, but the bryophytes seldom provide much cover. The drier crevices are much more sparsely colonized, and the species list resembles that of the Usnea-Omphalodiscus-Himantormia lugubris sociation of dry rock faces.

Foliose hepatics are typical and often abundant in the moist crevices, particularly Barbilophozia hatcheri, Cephaloziella varians and Pachyglossa dissitifolia, while short cushion mosses such as Andreaea spp., Bartramia spp., Ceratodon cf. grossiretis, Dicranoweisia spp., Pohlia nutans, etc., are usually present. Where soil accumulation is greater, Chorisodontium aciphyllum, Dicranoweisia sp., Drepanocladus uncinatus and Polytrichum alpinum are not uncommon. Although generally rare, a species of Plagiothecium and Metzgeria may occasionally be well represented, and they are usually found together. Other rare species, which appear to be confined to this habitat, are a tall long-leaved species of Bartramia and a species of Barbula, Isopterygium and several foliose hepatics.

Lichens vary in abundance according to the dampness and nitrogen content of the habitat, and are represented chiefly by crustose species of such genera as Acarospora, Biatorella, Buellia, Lecanora, Lecidea, Lepraria, Pertusaria, Rhizocarpon, etc., although a few larger forms may be present, including Bacidia stipata, Cystocoleus niger, Lecania brialmontii, Pertusaria corallophora, Usnea antarctica and species of Cladonia, Parmelia and Physcia. The analyses of some of these assemblages given in Table V also include a list of 14 species recorded in a very small rock crevice.

ii. In calcareous and base-rich rock crevices. On Signy Island, marble usually crops out in the form of low knolls, although there are places where quite extensive marble banding occurs in the quartz-mica-schist cliffs, particularly at the north end of the island. Amphibolite generally occurs as large outcrops and occasionally as bands in the schist. In the crevices and moister surfaces of these base-rich rocks various calcicolous species occur (Table VI) but seldom give much cover. Most

TABLE VI
FREQUENCY ASSESSMENT OF SPECIES OF CALCAREOUS AND BASE-RICH ROCK CREVICES

Species	Site 46	Site 47
Mosses		
Amblystegiella cf. densissima	o	_
Barbula sp.	r	_
Bartramia cf. patens	r	_
Brachythecium austro-salebrosum	o	o
Bryum algens (short form)	o	О
Bryum algens (short, robust form)	r	r
Bryum argenteum	_	r
Didymodon gelidus	o	o
Distichium cf. capillaceum	r	_
Drepanocladus cf. plicatus	o	_
Drepanocladus uncinatus	o	o
Encalypta spp.	o	o
Grimmia antarctici	la	lf
Pohlia cruda var. imbricata	r	_
Pottia austrogeorgica	o	o
Pseudoleskea sp.	la	o
Sarconeurum glaciale	_	r
Stegonia latifolia	r	r
Tortula conferta	r	o
Tortula excelsa	o	o
Tortula fuscoviridis	o	o
Tortula cf. grossiretis	r	o
Hepatics		
Marchantia berteroana	o	o
Lichens		
Buellia spp.	f	o
Caloplaca cf. citrina	lf	lf
Caloplaca regalis	lf	lf
Catillaria corymbosa	lf	_

TABLE VI-continued

Species	Site 46	Site 47
Lichens—continued		
Cladonia pocillum	o	r
Dermatocarpon intestiniforme	lf	o
Dermatocarpon lachneum	o	О
Haematomma erythromma	o	lf
Himantormia lugubris (on schist)	o	-
Lecania brialmontii	lf	_
Lecanora atra	f	-
Lecanora spp.	f	o
Lecidea cf. crustulata	o	o
Leptogium puberulum	О	o
Mastodia tesselata	f	o
Ochrolechia frigida	o	o
Omphalodiscus antarcticus (on schist)	lf	o
Parmelia sp.	o	_
Pertusaria sp.	f	f
Physcia caesia	f	o
Physcia muscigena	o	_
Ramalina terebrata	la	la
Rhizocarpon geographicum (on schist)	f	_
Usnea antarctica (on schist)	la	o
Verrucaria cf. elaeoplaca	lf	_
Xanthoria elegans	О	lf
Algae		
Nostoc sp.	r	o
Prasiola crispa	_	r

As both sites, details of which are given in the Appendix, consist of quartz-mica-schist with numerous bands of marble, several non-calcicole species also occur in this habitat.

Frequency assessment according to scale used in Table IV.

3.

of these are found in the Tortula-Grimmia antarctici association typical of calcareous ground habitats.

The principal bryophytes are small cushion- or short turf-forming species such as Bryum algens, Encalypta spp., Grimmia antarctici, Pohlia cruda var. imbricata, Pottia austrogeorgica, Stegonia latifolia and Tortula spp., while Ambylstegiella cf. densissima and Pseudoleskea sp. are locally frequent. The short compact turves of Barbula sp., Didymodon gelidus and Sarconeurum glaciale are rare, particularly the latter, the occurrence of which on Signy Island marks the northernmost extremity of its range (Greene and others, 1970). Marchantia berteroana is the only hepatic which is at all frequent in the damper crevices accompanied at times by a species of Campylium and Drepanocladus uncinatus.

Lichens are scarce and usually restricted to species of Buellia, Caloplaca, Lecanora, Lecidea, Pertusaria and Xanthoria, with occasional fruticose species such as Bacidia stipata, Catillaria corymbosa and Ramalina terebrata as well as the foliose Leptogium puberulum and Physcia caesia. From two basic rock crevices Dermatocarpon intestiniforme has been recorded.

c. Tortula-Grimmia antarctici association (Table VII). The local outcrops and knolls of marble on Signy Island provide an extremely base-rich substratum on which Grimmia antarctici, Tortula fuscoviridis and Tortula cf. grossiretis form either pure or mixed stands. These co-dominant species are accompanied by a number of short acrocarpous mosses rarely found in other habitats. Within this association there are frequent local concentrations of a large number of species, giving rise to small complex stands which show little or no uniformity. Fig. 5 illustrates such a unit of calcicolous vegetation in which 14 species of bryophytes, six species of lichens and one alga were present in an area 12 cm. by 8 cm. Some of the species were revealed only when the larger moss shoots were pulled apart, e.g. Amblystegiella cf. densissima, Cephaloziella varians and a species of Pseudoleskea. The communities are developed on the grey, sandy or clayey soils derived from the eroded marble and, mixed with the less calcareous quartz-mica-schist, give a soil with a pH ranging from about 7.0 to 8.5. The pure, nodular, marble soils derived directly from weathered marble have a pH range from 8.0 to over 9.0 but are virtually devoid of vegetation due to the exceptionally high concentrations of certain mineral ions, particularly calcium. Some chemical analyses for these soils have been provided by Holdgate and others (1967). Like this soil type, the weathered surface of the marble is rarely colonized by bryophytes, although Grimmia antarctici and Tortula fuscoviridis may occasionally occur.

In areas of morainic detritus, a heterogeneous substratum of boulders and soils from quartz-mica-schist, amphibolite and marble gives a soil with a relatively high base status but such areas are locally unstable and the vegetation cover, in which *Grimmia* is usually predominant, is broken up by frost boils and polygons. On the basic soils, in which boulders of quartz-mica-schist also occur, there is a contrasting pattern of communities, with calcareous species of the *Tortula-Grimmia antarctici* association on the richer soil and weathered marble erratics, and dimunitive patches of an *Andreaea*-lichen sociation on the more acid soil and stones. Thus several calcifuge species, such as *Andreaea depressinervis*, *Chorisodontium aciphyllum*, *Polytrichum alpinum*, *Himantormia lugubris*, *Sphaerophorus globosus* and *Usnea antarctica* may occur within the *Tortula-Grimmia antarctici* association, but are seldom frequent, occurring only where the substratum is locally suitable.

As with the Andreaea-Usnea association, the principal bryophytes, i.e. species of Bryum, Grimmia and Tortula possess a cushion growth form, while several small species form short open turves in which the individual shoots are scattered at some distance from one another, e.g. Encalypta spp., Pohlia cruda var. imbricata, Pottia austrogeorgica, Stegonia latifolia, and a species of Distichium. Species of Brachythecium and Drepanocladus uncinatus are common mosses with a creeping, prostrate growth form.

The sociations discussed below are seldom extensive, particularly the pure Grimmia and Tortula stands, and are rarely found above 80 m., due mainly to the restriction of suitable habitats to low altitudes.

i. Tortula sociation. Predominant species: Bryum algens and Tortula fuscoviridis. Habitat: slightly sheltered, fairly dry, sandy and gravelly soils on gently sloping ground mildly influenced by solifluction. Usually covered by snow in winter. Soil data: T. excelsa dominant (mean of two samples, eight for pH), pH 7·7, moisture content 100 per cent, L.O.I. 13·4 per cent; T. fuscoviridis dominant (mean of 17 samples, 21 for pH), pH 8·2, moisture content 53 per cent, L.O.I. 14·4 per cent; T. cf. grossiretis dominant (mean of six samples, nine for pH), pH 7·8, moisture content 15 per cent, L.O.I. 3·3 per cent. Altitudinal range: 8-85 m.

Although Tortula fuscoviridis and T. cf. grossiretis are often intermixed, occasionally either may occur alone as a more or less pure stand. However, T. fuscoviridis is considerably more abundant than T. cf. grossiretis. T. excelsa, a species characteristic of the moss hummock sub-formation of wetter habitats, is only rarely present in this sociation. T. cf. grossiretis would appear to have the

TABLE VII

PERCENTAGE COVER AND PERCENTAGE FREQUENCY OF SPECIES IN SOCIATIONS
OF THE Tortula-Grimmia antarctici ASSOCIATION

Species	Sociations showing percentage cover; percentage frequency of species		
	Tortula	Grimmia antarctici	Tortula–Grimmia antarctici
	Sites 48-52	Sites 53-57	Sites 58-62
Mosses			
Amblystegiella cf. densissima	<1; 12	<1; 2	<1; 16
Bartramia cf. patens	-	<1; 2	<1; 4
Brachythecium austro-salebrosum	4; 90	<1; 16	1; 48
Bryum algens (short form)	14; 98	<1; 14	11; 92
Campylium sp.	-	<1; 2	2; 24
Ceratodon cf. grossiretis	-	<1; 8	<1; 4
Distichium sp.	<1; 26	<1; 2	<1; 10
Drepanocladus cf. plicatus	2; 48	3; 16	<1; 24
Drepanocladus uncinatus	3; 82	7; 92	4; 98
Encalypta spp.	2; 40	1; 30	1; 28
Grimmia antarctici	<1; 6	73; 100	46; 100
Pohlia cruda var. imbricata	<1; 18	_	<1; 2
Pottia austrogeorgica	<1; 4	1; 26	<1; 8
Pseudoleskea sp.	_	<1; 4	<1; 16
Stegonia latifolia	_	<1; 8	<1; 4
Tortula excelsa	<1; 14	_	_
Tortula fuscoviridis	63; 100	2; 48	29; 100
Tortula cf. grossiretis	4; 62	<1; 12	2; 24
Hepatics			
Cephaloziella varians	<1; 6	<1; 4	<1; 6
Marchantia berteroana	4; 58	<1; 8	1; 16
Lichens			
Buellia subpedicellata + B. granulosa	<1; 28	<1; 22	<1; 12
Caloplaca cf. cerina	_	<1; 2	-
Caloplaca cf. citrina + Xanthoria elegans	<1; 28	<1; 14	<1; 22
Cladonia carneola	_	_	+; 2
Cladonia pyxidata $+C$ . pocillum	<1; 2	<1; 10	1; 30

TABLE VII-continued

Species	Sociations perce	Sociations showing percentage cover; percentage frequency of species		
	Tortula	Grimmia antarctici	Tortula–Grimmia antarctici	
	Sites 48-52	Sites 53-57	Sites 58-62	
Lichens—continued				
Cornicularia aculeata	-	_	<1; 2	
? Cypheliopsis sp.	1; 40	2; 54	2; 70	
Dermatocarpon lachneum	<1; 6	3; 22	<1; 14	
Lecanora aspidophora (on schist)	<1; 2	<1; 4	<1; 2	
Lecanora subfusca	<1; 4	<1; 12	<1; 4	
Lecidea cf. crustulata	<1; 6	<1; 2	<1; 10	
Leptogium puberulum	3; 60	2; 60	3; 78	
Ochrolechia frigida	<1; 4	1; 36	<1; 24	
Peltigera rufescens	<1; 2	-	<1; 4	
Peltigera spuria	_	<1; 4	<1; 2	
Physcia muscigena	<1; 10	<1; 2	<1; 8	
Placopsis contortuplicata	_	<1; 2	<1; 4	
Psoroma hypnorum	_	<1; 20	_	
Stereocaulon alpinum	_	<1; 2	_	
Usnea antarctica (on schist)	<1; 6	<1; 4	<1; 4	
Other groups				
Basidiomycete	<1; 6	_	<1; 2	
Nostoc sp.	5; 50	2; 48	3; 70	
Substratum				
Bare ground	5; 82	9; 54	6; 74	

Details of sites are given in the Appendix. Percentage cover and percentage frequency were estimated as in Table IV.

greatest ecological amplitude of the three species, occupying damp flushed situations as well as extremely dry, gravelly, basic soils. The species list for this sociation given in Table VII is almost identical to that of the *Grimmia antarctici* sociation, but *Bryum algens* becomes the leading associate, while *Brachythecium austro-salebrosum*, *Drepanocladus uncinatus* and occasionally *Drepanocladus* of. *plicatus* are frequent. As the habitat becomes moister, *T. excelsa* increases in abundance and may locally form quite extensive deep cushions.

The epiphytic lichens? Cypheliopsis sp. and Ochrolechia frigida are much less frequent on the tall, more loose Tortulas than on Grimmia. Leptogium puberulum is also an important constituent of the flora.

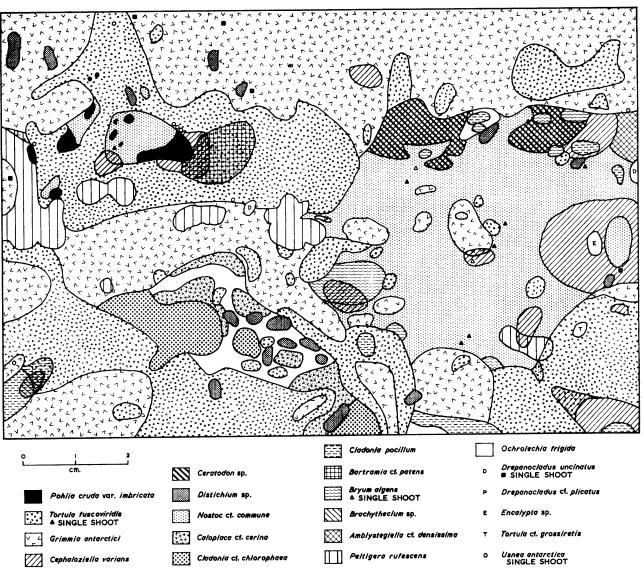


FIGURE 5

Distribution of species in a stand, 12 cm. by 8 cm., of the Tortula-Grimmia antarctici sociation at an altitude of c. 100 m. below an outcrop of marble between North Point and Robin Peak.

ii. Grimmia antarctici sociation. Predominant species: Drepanocladus uncinatus and Grimmia antarctici. Habitat: dry, base-rich, sandy and gravelly soil and morainic debris, which is frequently disturbed by frost action, forming clay puddles, frost boils and polygons. Little snow cover in winter. Soil data: slightly moist, Drepanocladus frequent (mean of six samples), pH 6·1, moisture content 52 per cent, L.O.I. 19 per cent; dry, pure Grimmia (mean of 12 samples), pH 8·0, moisture content 21 per cent, L.O.I. 6·7 per cent. Altitudinal range: 8-85 m.

This sociation is very similar to the Andreaea and Andreaea—lichen sociations in general appearance and structure. The loose cushions of Grimmia antarctici coalesce to form large mats, but frequently these are broken by frost action, leaving unstable clay puddles and stone polygons. Grimmia antarctici appears to be less calcicolous than Tortula fuscoviridis and T. cf. grossiretis, and the sociation extends on to soils of lower base status with pH values as low as 6·0. The community, like the Andreaea sociation, occurs in almost pure, closed stands where the soil is deeper, in the moister sheltered hollows. Drepanocladus uncinatus and occasionally the plumose Drepanocladus cf. plicatus are the most frequent associates. Several short cushion- or turf-forming

species occur sparsely, e.g. Bartramia cf. patens, Bryum algens, Ceratodon cf. grossiretis, Distichium sp., Encalypta spp., Pottia austrogeorgica and Stegonia latifolia. Where the soil is moister Marchantia berteroana is frequently present. Tortula fuscoviridis and Tortula cf. grossiretis are seldom absent, but rarely contribute more than 1-2 per cent cover, and occur merely as isolated groups of shoots.

The lichens are largely crustose forms with species of Caloplaca and Xanthoria elegans growing on the stones and rock surfaces, and Ochrolechia frigida and? Cypheliopsis sp. occurring as epiphytes on Grimmia antarctici. Leptogium puberulum is usually a frequent associate, being a useful indicator of flushed or base-rich soils. Several large lichens such as Peltigera rufescens, Cladonia spp. and Physcia muscigena are locally common. The almost encrusting Dermatocarpon lachneum is occasionally important as a colonizer of bare soil.

iii. Tortula-Grimmia antarctici sociation (Gimingham and Smith, 1970, pl. 4, p. 779). Predominant species: Bryum algens, Grimmia antarctici and Tortula fuscoviridis. Habitat: dry, sandy and gravelly soil on level or gently sloping ground, locally disturbed by frost action. Usually has some snow cover in winter. Soil data: (mean of 31 samples, 35 for pH), pH 7.9, moisture content 30 per cent, L.O.I. 8.9 per cent. Altitudinal range: 5-85 m.

There is no noticeable difference in habitat between this and the two previous sociations, and it is best regarded as a combination of the two with *T. fuscoviridis* and *G. antarctici* occurring together. This mixed community is considerably commoner than the pure sociations of either of the co-dominants. *T.* cf. grossiretis is also usually present in small quantities. Bryum algens and Drepanocladus uncinatus are again the principal associates. Sparse turves and cushions of short calcicolous acrocarps are typical amongst the taller mosses.

Species of Ochrolechia and ? Cypheliopsis occur on Grimmia antarctici as small white circular patches while species of Cladonia and Leptogium puberulum are regular associates among the moss shoots. As in all moist base-rich habitats, small, globular gelatinous growths of the bluegreen alga Nostoc are occasionally numerous on the fine clayey soil.

iv. Tortula conferta-Bryum sociation. Predominant species: Bryum algens, Ceratodon cf. grossiretis, Drepanocladus uncinatus and Tortula conferta. Habitat: pockets of soil on rock ledges which are commonly used as bird perches, nesting sites, etc., near the shore. Also on accumulations of limpet shells (Patinigera polaris) deposited by Dominican gulls (Larus dominicanus). Soil data: (mean of nine samples), pH 7·3. Altitudinal range: 2-65 m.

Coastal cliff ledges at low altitudes frequently support small open stands of short cushion-forming mosses. Such habitats are frequently influenced by birds which use the ledges as nesting sites and perches, hence enriching the soil. In other situations, bryophytes and occasionally lichens, colonize accumulations of limpet shells deposited by gulls, particularly around the breeding colonies of these birds. The chief components of this diminutive sociation are generally Bryum algens (rarely B. argenteum) and Tortula conferta, with Ceratodon cf. grossiretis. Drepanocladus uncinatus, Pottia austrogeorgica and other species of Tortula associated. Lichens include various nitrophilous forms such as a species of Caloplaca especially on limpet shells, Parmelia sp., Physcia sp., Lecania brialmontii, Xanthoria candelaria and X. elegans. The pockets of soil often have small feathers and pieces of shell incorporated in them.

No quantitative data or species lists have been recorded for this community type.

- d. Pottia austrogeorgica association (Table VIII). Habitats with unstable substrata seldom support vegetation except for scattered, small colonies of lichens or bryophytes. However, small patches of stable ground subjected to frost heaving and solifluction, or disturbed and enriched by gulls, terns (Sterna vittata) or elephant seals (Mirounga leonina) may be temporarily colonized by scattered bryophytes of small cushion or turf growth form, particularly by Pottia austrogeorgica. Occasionally their establishment may lead to permanent communities, although these are seldom extensive, the largest being about 20 m.<sup>2</sup> on fine clay soil littered with fragments of amphibolite. More often such stands are only about 1 m.<sup>2</sup> in extent.
  - i. Pottia austrogeorgica sociation. Predominant species: Bryum algens, Marchantia berteroana and Pottia austrogeorgica. Habitat: fine, moist, clayey and gravelly soil, usually base-rich and unstable due to frost action. Soil data: (mean of four samples), pH 7·9, moisture content 19 per cent, L.O.I. 4·1 per cent. Altitudinal range: 2-50 m.

TABLE VIII

PERCENTAGE COVER AND PERCENTAGE FREQUENCY OF SPECIES
IN THE Pottia austrogeorgica SOCIATION

Species	Sites 63-67	Species	Sites 63-67
Mosses		Lichens	
Andreaea gainii	<1; 2	Acarospora macrocyclos	<1; 2
Bartramia cf. patens	<1; 12	Buellia subpedicellata+B. granulosa	2; 42
Brachythecium spp.	2; 48	Caloplaca cf. citrina	<1; 26
Bryum algens (short, slender form)	4; 52	Candelariella vitellina	<1; 10
Bryum algens (short, robust form)	+; 2	Cladonia chlorophaea	<1; 16
Bryum argenteum	<1; 4	? Cypheliopsis sp.	3; 76
Calliergon cf. sarmentosum	<1; 2	Dermatocarpon lachneum	<1; 14
Campylium sp.	<1; 20	Lecanora aspidophora	1; 48
Ceratodon cf. grossiretis	1; 30	Lecanora subfusca	<1; 22
Distichium sp.	<1; 4	Leptogium puberulum	2; 50
Drepanocladus uncinatus	2; 82	Ochrolechia frigida	<1; 2
Encalypta spp.	<1; 10	Parmelia saxatilis	<1; 4
Grimmia antarctici	<1; 14	Placopsis contortuplicata	<1; 2
Polytrichum alpinum	<1; 4	Psoroma hypnorum	<1; 16
Pottia austrogeorgica	18; 100	Usnea antarctica	<1; 12
Stegonia latifolia	<1; 4	Other service	
Tortula excelsa	+; 2	Other groups	<1; 2
Tortula fuscoviridis	<1; 8	Basidiomycete	4; 58
Tortula cf. grossiretis	<1; 12	Nostoc sp.	7, 56
Hepatics		Substratum  Bare ground	57; 100
Anthelia sp.	<1; 12	Dai o ground	2,,100
Cephaloziella varians	3; 40		
Marchantia berteroana	7; 52		

Details of sites are given in the Appendix. Percentage cover and percentage frequency were estimated as in Table IV.

The principal species of this sociation is *Pottia austrogeorgica* which may reach a cover value as high as 25 per cent but this may be considered exceptional, with 10-15 per cent being more usual. The success of this species in rapidly colonizing bare, semi-stable soils is probably due to its prolific production of sporophytes and spores. That the spores were viable was shown by the behaviour of a sample of vegetation-free soil, with *Pottia austrogeorgica* growing about 0.5 m. away, which was taken from an area of fine clay as soon as the winter snow cover had melted. The soil was kept moist in a petri dish at  $18^{\circ}$  C in the laboratory, and within 10 days it was covered with shoots of P. austrogeorgica, the protonemata appearing on the fourth day.

Few other species contribute much cover and most of the associated bryophytes are those of the marble and other basic soils in the *Tortula-Grimmia antarctici* association. *Brachythecium austro-salebrosum*, *Bryum algens*, *Ceratodon* cf. *grossiretis* and *Drepanocladus uncinatus* are the commonest associates, while *Cephaloziella varians* and *Marchantia berteroana* may be locally abundant. The rare *Stegonia latifolia* has also been found in this sociation.

Most of the lichens observed were very young thalli of crustose species on fragments of stone, with occasional species such as Candelariella vitellina, ? Cypheliopsis sp., Leptogium puberulum, Ochrolechia frigida, Dermatocarpon lachneum and Psoroma hypnorum growing directly on the soil. A species of the blue-green alga Nostoc was also regularly found on the moister soils.

## 2. Crustose lichen sub-formation

A number of epipetric lichen assemblages have been recognized in which bryophytes are absent or at the most very sparsely represented. Communities in which *Himantormia lugubris* and species of *Omphalodiscus* and *Usnea*, etc., are abundant have been classified in the fruticose lichen and moss cushion sub-formation because of the prominence of the fruticose growth form and the frequent occurrence of small cushion mosses. Similarly, bryophyte stands heavily encrusted by epiphytic lichens are included in the encrusted moss sub-formation or, in the case of the lichen-encrusted peat banks, in the moss turf sub-formation.

The majority of these predominantly crustose lichen communities\* on Signy Island appear to be either halophilous or ornithocoprophilous, and are consequently seldom found far from the influence of the sea or cliff-breeding sea birds. A large number of crustose genera are represented, in particular, Acarospora, Biatorella, Buellia, Caloplaca, Haematomma, Lecidea, Lecanora, Rinodona and Verrucaria, while the placodioid Xanthoria elegans is also an important species. Several nitrophilous fruticose species may be locally frequent with Bacidia stipata, Caloplaca regalis, Catillaria corymbosa, Lecania brialmontii, Ramalina terebrata and Xanthoria candelaria being typically, although not strictly, coastal in their distribution while nitrophobous species of Omphalodiscus and Usnea extend into these communities from the more montane habitats. Foliose genera are few and represented chiefly by Mastodia tesselata and species of Parmelia and Physcia.

Farther inland and at higher altitudes, communities of crustose lichens occur locally on dry rock surfaces, although most frequently they exist as an understorey below fruticose species or associated with bryophytes in the fruticose lichen and moss cushion sub-formation. However, occasional colonies of species of *Buellia*, *Lecanora*, *Lecidea*, *Ochrolechia*, *Pertusaria*, *Placopsis* and *Rhizocarpon* occur in the absence of other growth forms.

a. Caloplaca-Xanthoria association (Table IX). This association was originally designated as the Caloplaca association by Gimingham and Smith (1970). However, the transference of Caloplaca elegans to Xanthoria as X. elegans requires the renaming of the association and some of the sociations.

Due to enrichment by sea-bird excrement, communities of this association are most typical of coastal rocks and, with the exception of one sociation which occurs on marble outcrops several hundred metres inland, they seldom extend far from the shore. There is little variation in the species composition of coastal communities, with species of *Caloplaca* or *Xanthoria* being present throughout, although each sociation is dominated by a different species. The communities are very colourful, particularly with orange, yellow and greenish species, and are among the most characteristic features of the vegetation of Signy Island in winter.

Several of the sociations are distinctly zoned in relation to nitrogen availability and to the height above the high-water mark. Brownish and blackish species of *Verrucaria* appear to be the most salt tolerant lichens and occur above or occasionally within the filamentous green alga (possibly a species of *Enteromorpha*) zone on the intertidal rocks. The *Verrucaria* zone gives way to one or more orange *Caloplaca* zones, which in turn merge into areas dominated by the orange *Xanthoria elegans* or *Caloplaca regalis*, the yellow *Haematomma erythromma* or *Ramalina terebrata*, or even the greenish *Usnea antarctica*. Several of these sociations are very similar to the *Ramalinetum terebratae* association (p. 110) described by Follmann (1965) from the west coast of the Antarctic Peninsula.

<sup>\*</sup> Many of the data and observations on the crustose lichen sub-formation were provided by D. C. Lindsay.

OF THE Catoptaca-Xunthorta ASSOCIATION

		Sociations showing percentage cover; percentage frequency of species						
		Cale	oplaca					
Species	Verrucaria	With Caloplaca cirrochrooides dominant	With Caloplaca sp. dominant	Xanthoria elegans	Xanthoria elegans- Ramalina terebrata	Caloplaca regalis		
	Sites 68-71 (using 11 quadrats)	Sites 72-74 (using 7 quadrats)	Sites 75-77 (using 4 quadrats)	Sites 78–80 (using 10 quadrats)	Sites 81–83 (using 6 quadrats)	Sites 84–85 (using 6 quadrats)		
Lichens								
Acarospora convoluta	_	-	<del>-</del> I	<1; 20	_	_		
Acarospora macrocyclos	_	_	_	2; 30	1; 17	_		
Bacidia stipata	_	_	_	<1; 20	<1; 17	_		
Biatorella sp.	_	-	<u> </u>	_	_	<1; 17		
Buellia spp.*	<1; 9	2; 29	10; 100	5; 80	10; 51	1; 17		
Caloplaca cirrochrooides	2; 36	27; 100	8; 50	<1; 10	_	_		
Caloplaca regalis	_	_	1; 25	2; 20	9; 84	43; 100		
Caloplaca sublobulata	_	2; 29	5; 25	-	_	<1; 17		
Caloplaca sp.	5; 54	1; 29	20; 75	-	-	_		
Candelariella vitellina	_	_	-	<1; 30	<1; 17	_		
Catillaria corymbosa	_	_	-	1; 20	1; 17	<1; 17		
Cladonia sp.	-	-	_	<1; 10	_	_		
Haematomma erythromma	_	_	<1; 25	8; 90	6; 84	<1; 17		
Lecania brialmontii	<1; 9	<1; 14	2; 50	1; 50	<1; 33	<1; 33		
Lecanora aspidophora	-	_	_	<1; 20	<1; 17	_		
Lecanora atra	-	-	_	2; 50	1; 33	-		
Lecanora spp.	-	3; 29	2; 50	2; 50	2; 33	4; 51		
Lecidea spp.	<1; 9	3; 56	9; 75	9; 90	12; 100	3; 33		
Lepraria sp.	-	_	_	+; 20	-	_		
Mastodia tesselata	<1; 9	1; 14	1; 25	3; 60	<1; 17	<1; 17		
Microglaena antarctica	-	_	+; 25	_	_	-		
Pannaria sp.	-	_	_	_	<1; 17	-		
Parmelia sp.	_	_	_	_	-	2; 17		
Pertusaria sp.	_	1; 29	_	_	<1; 17			

		Sociations sh	owing percentage cov	er; percentage frequen	ncy of species	
		Cal	oplaca			,
Species	Verrucaria	With Caloplaca cirrochrooides dominant	With Caloplaca sp. dominant	Xanthoria elegans	Xanthoria elegans– Ramalina terebrata	Caloplaca regalis
	Sites 68-71 (using 11 quadrats)	Sites 72-74 (using 7 quadrats)	Sites 75-77 (using 4 quadrats)	Sites 78-80 (using 10 quadrats)	Sites 81–83 (using 6 quadrats)	Sites 84-85 (using 6 quadrats)
Lichens—continued						
Physcia caesia	-	-	<1; 25	<1; 10	<1; 17	3; 67
Physcia cf. grisea	_	-	_	_	<1; 17	-
Physcia sp.	_	-	_	_	<1; 17	1; 17
? Placynthium sp.	_	-	_	<1; 10	+; 17	-
Ramalina terebrata	-	-	<u> -</u>	<1; 10	19; 100	2; 17
Rinodina petermannii	_	-	-	1; 10	-	_
Usnea antarctica	_	-	1; 50	<1; 30	5; 51	2; 17
Verrucaria ceuthocarpa	22; 81	2; 43	4; 50	_	_	-
Verrucaria elaeoplaca	_	-	<del>-</del>	<1; 10	-	_
Verrucaria maura	1; 9	-	_	_	-	-
Verrucaria psychrophila	5; 36	-	-	_	-	-
Verrucaria tesselatula	35; 90	1; 29	4; 50	. –	-	_
Xanthoria candelaria	-		_	2; 50	2; 67	5; 67
Xanthoria elegans	<1; 18	1; 43	3; 50	23; 100	21; 100	<1; 17
Mosses						
Andreaea regularis	_	-	- -	1; 30	_	_
Grimmia antarctici	_	_	_	_	_	<1; 33
Tortula excelsa	_	- -	_	_	_	<1; 17
Algae						
? Enteromorpha sp.	3; 9	_	<del>-</del>	_	_	_
Prasiola crispa	_	<u>-</u>	- -	<1; 20	+; 17	<1; 33
Substratum						
Dana mosts	20, 100	55 100	20 100	40.400	10.100	

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i. Verrucaria sociation. Predominant species: Verrucaria ceuthocarpa and Verrucaria tesselatula. Habitat: intertidal zone and dry or moist rock within the spray zone of the shore. Altitudinal range: (-2) 0-5 m.

The coastal rocks immediately above, or even occasionally slightly below, the high-water mark are typically colonized by several brownish or black species of *Verrucaria*. Clearly these lichens must be tolerant of high concentrations of marine salts, and in some instances must be able to with-stand periods of submergence by sea-water, particularly *Verrucaria psychrophila*. The two principal components of the sociation, *V. ceuthocarpa* and *V. tesselatula*, may form extensive aereolated patches on the rock surface, with the former species usually predominating in the more exposed situations. Species of *Caloplaca* are occasional, but increase towards the upper limit of the *Verrucaria* zone, and finally become dominant to form the *Caloplaca* sociation. Other species are generally very sparse or absent. It is probable that more *Verrucaria*-dominant sociations may be recognized.

ii. Caloplaca sociation. Predominant species: Caloplaca cirrochrooides, Caloplaca sp., Buellia spp., Lecidea spp., and locally Orthotrichum crassifolium. Habitat: dry or moist nitrogen-rich coastal rocks within the spray zone but above the Verrucaria zone. Altitudinal range: 2-10 m.

Within the Caloplaca zone three groupings may be recognized, namely, a Caloplaca cirrochrooides dominant community, a Caloplaca sp. dominant community and a Caloplaca-Verrucaria-Orthotrichum crassifolium assemblage.

Stands of *C. cirrochrooides* are usually adjacent to and intergrade with the lower *Verrucaria* zone, while an unidentified species of *Caloplaca* generally occupies the upper region of the *Caloplaca* zone. However, both species, together with *Caloplaca sublobulata* and *Xanthoria elegans*, may all be closely associated, although the latter are sparse. *Xanthoria elegans* increases in abundance as the sociation merges with the *Xanthoria elegans* and *Xanthoria elegans*–Ramalina terebrata sociations at a slightly higher altitude. Species of *Verrucaria* may be locally frequent, especially in the lower reaches of the habitat where the influence of salt water is greater. *Acarospora convoluta* and a species of *Biatorella* may also be frequent on damp nitrogen-enriched rocks. Several nitrophilous species of *Buellia*, *Lecanora* and *Lecidea* are usually present, and locally produce stands of sufficient size to merit the status of an independent association (p. 43).

Occasionally stands of *Verrucaria* and *Caloplaca* possess *Orthotrichum crassifolium* as an important associate. This moss appears to be restricted in its distribution to rocks near the shore and seldom occurs above 8 m. Its dark, often fertile, blackish green cushions rarely give much cover on the rock. The habitat occupied is usually wet or moist rock surfaces with some degree of soil accumulation in small fissures and crevices. *O. crassifolium* appears to be one of the few bryophytes able to tolerate the high salt concentration of such a situation, and extends to within 1 m. of highwater mark. *Pottia austrogeorgica* occurs in crevices at about 2 m., while *Andreaea* spp., *Ceratodon* cf. grossiretis and *Drepanocladus uncinatus* may be associated at altitudes over 2 m.

No quantitative data were obtained, but Table X (overleaf) gives the species recorded, with their relative abundance, in four separate localities.

iii. Xanthoria elegans sociation. Predominant species: Buellia spp., Lecidea spp., Haematomma erythromma and Xanthoria elegans. Habitat: dry nitrogen-enriched coastal rocks and cliffs above the Verrucaria and Caloplaca zones and close to bird or seal colonies. Altitudinal range: 5-75 (-155) m.

This is one of three principal community types occurring above the Caloplaca zone on coastal cliffs and rock faces a little inland, particularly below ledges occupied by breeding colonies of birds. Occasionally it may lie immediately above the Verrucaria zone. Usually only Xanthoria elegans is at all abundant, although nitrophilous species of Buellia and Lecidea as well as Haematomma erythromma may locally provide considerable cover. Lecanora spp., Caloplaca regalis, Rinodina petermannii and Xanthoria candelaria are also frequent associates. Mastodia tesselata is generally restricted to the lower areas of the habitat, occupying the niche formed by fissures in the rock, particularly on horizontal surfaces.

iv. Xanthoria elegans-Ramalina terebrata sociation. Predominant species: Buellia spp., Lecidea spp., Ramalina terebrata and Xanthoria elegans. Habitat: dry, slightly basic nitrogen-enriched rocks and cliffs close to the shore, usually near bird colonies. Altitudinal range: 5-35 (-125) m.

TABLE X FREQUENCY ASSESSMENT OF SPECIES IN THE Caloplaca-Verrucaria-Orthotrichum crassifolium ASSEMBLAGES OF THE Caloplaca SOCIATION

Species	Site 86	Site 87	Site 88	Site 89
Mosses				
Andreaea gainii	О	О	_	_
Brachythecium austro-salebrosum	О	_	_	_
Bryum algens	o	_	-	_
Ceratodon cf. grossiretis	_	О	_	_
Dicranoweisia grimmiacea	_	О	_	_
Drepanocladus uncinatus	О	f	r	o
Orthotrichum crassifolium	f–la	f–a	la	la
Pohlia nutans	_	О	_	_
Pottia austrogeorgica	О	О	r	_
Tortula conferta	o	_	_	_
Tortula excelsa	-	r	_	_
Hepatics				
Cephaloziella varians	О	f	-	_
Lichens				
Acarospora convoluta	1f	la	О	_
Acarospora macrocyclos	О	la	_	f
Bacidia stipata	o	_	_	_
Caloplaca regalis	lf	-	_	_
Caloplaca spp. (incl. C. cirrochrooides)	la	1f	a	la
Catillaria corymbosa	o	o	o	_
Collema sp.	o	f	o	o
Lecania brialmontii	lf	_	_	o
Leptogium puberulum	lf	lf	О	-
Mastodia tesselata	lf	_	o	lf
Parmelia saxatilis	0	_	_	_
Physcia caesia+Physcia cf. grisea	f	О	o	f
Physcia muscigena	О	_	О	_
Psoroma hypnorum	_	О	_	_
Ramalina terebrata	0	_	_	_
Verrucaria spp.	f	la	la	o
Unidentified crustose lichens	lf	О	f	lf
Alga				
Prasiola crispa	f	_	_	_

Details of sites are given in the Appendix.
Frequency assessment according to the scale used in Table IV.
The lists include species from wet and dry rock surfaces and crevices at each site.

This second community type occurring above the Caloplaca zone is frequently locally adjacent to Usnea-dominated stands. As with the previous sociation, this one is particularly frequent near colonies of cliff-breeding birds. Ramalina terebrata appears to favour slightly basic rocks, such as marble- and amphibolite-banded quartz-mica-schist, and is present usually on north-facing rocks. There are usually varying quantities of Xanthoria elegans associated with the Ramalina, together with Buellia spp., Caloplaca regalis, Haematomma erythromma, Lecidea spp., and Usnea antarctica, all of which may provide extensive cover locally. Thus, basically, this sociation is almost identical to the previous one except that Ramalina terebrata is co-dominant with X. elegans.

v. Caloplaca regalis sociation. Predominant species: Caloplaca regalis and Xanthoria candelaria. Habitat: coastal nitrogen-enriched rock faces and large crevices, above the spray zone and near bird colonies. Altitudinal range: 3-50 (-75) m.

The brilliant orange frutico-crustose lichen Caloplaca regalis is a characteristic coastal rock species which locally gives a high cover value. In species composition this third ornithocoprophilous sociation is very similar to the two previous sociations and usually intergrades with them. The principal associates include Physcia caesia, Xanthoria candelaria, X. elegans and numerous unidentified species of Buellia, Lecanora and Lecidea, together with occasional colonies of Usnea antarctica and less commonly Ramalina terebrata.

vi. Caloplaca-Xanthoria elegans-Pertusaria sociation. Predominant species: Caloplaca cf. citrina, Lecidea spp., Pertusaria sp., Verrucaria sp. and Xanthoria elegans. Habitat: dry marble outcrops and bands, both coastal and inland. Altitudinal range: 3-155 m.

The coarse surface of marble may be colonized by an open community of crustose lichens, of which Caloplaca cf. citrina and Xanthoria elegans are the most prominent components. Locally, a white crustose species of Pertusaria is dominant, while a black species of Verrucaria and white and grey species of Lecidea, and to a lesser extent of Lecanora, form small patches on the rock. Usnea antarctica, although a strict calcifuge, occasionally colonizes the surface of calcicolous crustose species, usually of the genus Pertusaria, in which the thick encrusting thallus provides a fine layer of organic material on which the Usnea can become established.

No species lists are available for this community.

b. Buellia-Lecanora-Lecidea association. Many of the species of this second association of epipetric crustose lichens have a wider ecological amplitude than those of the Caloplaca-Xanthoria association. The Buellia-Lecanora-Lecidea association has not been studied in great detail, and for this reason only one sociation has so far been recognized, but several nitrophilous and nitrophobous assemblages could be given sociation status. Most of the stands occur on coastal rocks or cliffs, but in more sheltered situations which receive less sea spray than the former association. The principial species may form large colonies adjacent to communities dominated by species of Caloplaca or Xanthoria, or as an understorey beneath fruticose lichens in more montane habitats. In the latter instance the crustose species are considered as components of other saxicolous communities, particularly in the fruticose lichen and moss cushion subformation.

No species lists or quantitative data are available for communities of this association.

i. Buellia-Lecanora-Lecidea sociation. Predominant species: Buellia spp. (including B. cladocarpiza, B. coniops, B. granulosa, B. isabellina, B. latemarginata, B. russa and B. subpedicellata), Lecanora spp. and Lecidea spp. Habitat: dry, schistose rock faces near the shore, but above the spray zone, or inland to higher altitudes. Altitudinal range: shore communities 3-20 m.; inland communities to about 270 m.

Nitrophilous species of Buellia, Lecanora and Lecidea are usually represented in the less hygrohaline communities of the Caloplaca-Xanthoria association. In these coastal habitats they frequently form fairly large colonies of assorted grey, white or blackish thalli, but generally in the absence of either Caloplaca or Xanthoria. This would suggest some degree of shelter from wind and spray. Inland, nitrophobous species of Lecanora and Lecidea, together with Ochrolechia antarctica, and species of Pertusaria and Rhizocarpon often associate to form extensive stands on dry rock surfaces, although usually occurring as a partial understorey below certain fruticose lichens or in association with various cushion mosses. It would appear that through these genera there is a continuous

range of communities from the crustose lichen sub-formation to the fruticose lichen and moss cushion sub-formation.

c. Placopsis contortuplicata association. This is a relatively infrequent and usually very fragmentary association, and is more common in the South Shetland Islands (Collins, 1969; Lindsay, 1971e). In the South Orkney Islands, however, the pinkish thalli of Placopsis contortuplicata, together with occasional other crustose lichens, form small colonies on loose debris, boulders and rock faces. It is typically a montane community type.

No species lists or quantitative data are available for this association.

i. Placopsis contortuplicata sociation. Predominant species: Placopsis contortuplicata. Habitat: solifluction fragments at the margins of stone stripes and on stone "rivers"; occasionally on dry, shaded rock faces. Altitudinal range: 30-220 m. (-620 m. on Coronation Island).

Placopsis contortuplicata occasionally forms small open stands on stones and gravel on gently sloping stone "rivers" and the margins of stone stripes, usually on exposed hillsides at fairly high altitudes. From what often appears to have been a central colony of the lichen, solifluction and frost heaving generally disrupt the encrusted stones, dispersing them in a radiating fashion downhill from the supposed point of origin. This creates a very open stand covering 1 m.<sup>2</sup> or more, and each small thallus develops as a tiny individual colony. Other plants are seldom present, although scattered species of Pannaria, Lecidea and short cushion- and turf-forming mosses may occur.

On dry rock faces *P. contortuplicata* forms large, almost circular colonies which may intergrade with each other. The largest single colony measured by the author on Signy Island was 78 cm. in diameter, but large thalli at about 620 m. have been observed on Coronation Island by D. C. Lindsay (personal communication). Species of *Buellia*, *Lecanora*, *Lecidea* and *Rhizocarpon* may be associated.

## 3. Moss turf sub-formation

The community types which belong to this sub-formation are largely dominated by two turf-forming species, *Polytrichum alpestre* and *Chorisodontium aciphyllum* both of which have a tall turf growth form and a rhizoid system of varying density. In both species the main stem has the ability to continue growth year after year and as a result can build up banks of peat over 1 m. deep. However, *Polytrichum alpinum*, the principal component in the *P. alpinum* association, also has the turf growth form typical of the genus, but it may not be very tall and seldom builds up a peat of more than 10–20 cm. in depth. Instead, due to its well-developed underground shoot or "rhizome" system, it tends to develop radially and commonly forms circular colonies up to 1 m. in diameter.

The two associations of this sub-formation are usually restricted to well-drained slopes or gravelly porous ground, although once a peat is developed a permanent reservoir of water is maintained and in the case of the deeper banks, a permafrost layer forms about 20–30 cm. below the surface.

a. Polytrichum alpestre-Chorisodontium aciphyllum association (Table XI). In suitable situations Chorisodontium aciphyllum, with or without Polytrichum alpestre and epiphytic lichens, forms extensive banks of semi-ombrogenous peat which constitute one of the most prominent features of the vegetation of Signy and Moe Islands. Stands of these species range from shallow undulating turves, 20-30 cm. in depth, to isolated banks up to almost 2 m. deep. They occur on level or gently sloping, well-drained ground, usually overlying stabilized scree, from near sea-level to about 155 m., with considerably smaller stands extending to about 235 m. P. alpestre and C. aciphyllum are generally found together forming closed stands of a deep mixed turf, but occur in varying proportions and locally either species may form pure stands, although those of Polytrichum alpestre are seldom extensive in the South Orkney Islands. Wherever the substratum becomes wetter, as at the edge of a peat bank where snow accumulates, or where melt water often issues immediately below a protruding rock, Chorisodontium aciphyllum becomes the prominent species, particularly on more level ground. As the gradient increases and drainage improves, Polytrichum alpestre takes the leading role. On steep slopes peat accumulation is seldom more than 50 cm. deep and, because of solifluction within the bank, a series of steps or terraces often develops. The stability of the moss banks on these slopes, the angle of which sometimes exceeds 40°, locally up

TABLE XI

PERCENTAGE COVER AND PERCENTAGE FREQUENCY OF SPECIES IN SOCIATIONS OF THE Polytrichum alpestre-Chorisodontium aciphyllum ASSOCIATION

	Sociation	is showing percen	ntage cover; perce	ntage frequency	
Species	Chorisodontium aciphyllum	Chorisodontium aciphyllum- lichen	Polytrichum alpestre– Chorisodontium aciphyllum	Polytrichum alpestre- Chorisodontium aciphyllum- lichen	aciphyllum heavily colonized by epiphytic
	Sites 90-94	Sites 95–99	Sites 100-104	Sites 105–109	lichens Sites 110–111
losses					
Andreaea depressinervis	_	_	_	<1; 2	<1; 5
Andreaea regularis	<1; 10	<1; 2	-	_	-
Brachythecium cf. antarcticum	<1; 10	<1; 2	<1; 16	<1; 6	-
Calliergon cf. sarmentosum	<1; 6	_	<1; 18	_	_
Chorisodontium aciphyllum	100; 100	74; 100	59; 100	32; 100	11; 85
Drepanocladus uncinatus	<1; 6	_	<1; 16	<1; 4	_
Pohlia nutans	3; 76	2; 58	2; 60	1; 36	4; 60
Polytrichum alpestre	<1; 2	-	41; 100	47; 98	7; 70
Iepatics					
Barbilophozia hatcheri	_	-	2; 44	1; 20	-
Cephaloziella varians	3; 100	4; 100	3; 100	4; 100	4; 65
Lichens					
Alectoria chalybeiformis	-	2; 42	<1; 2	2; 46	<1; 10
Alectoria nigricans	<1; 4	<1; 14	_	2; 38	_
Alectoria pubescens	_	_	_	<1; 2	_
Buellia punctata	<1; 8	15; 100	<1; 14	7; 74	32; 100
Cladonia carneola	_	2; 80	<1; 2	1; 30	3; 50
Cladonia vicaria	_	_	_	<1; 16	_
Cladonia spp.*	<1; 2	4; 84	<1; 4	4; 96	1; 30
Cornicularia aculeata	_	1; 28	-	2; 62	-
Cornicularia epiphorella	_	_	_	<1; 4	_
Ochrolechia frigida	<1; 12	8; 100	<1; 20	5; 94	26; 100
Psoroma hypnorum	_	<1; 4	<1; 4	<1; 2	_
Sphaerophorus globosus	<1; 4	5; 82	<1; 2	12; 100	2; 25

TABLE XI-continued

	Sociation	is showing percen	tage cover; perce	entage frequency	of species
Species	Chorisodontium aciphyllum	Chorisodontium aciphyllum- lichen	Polytrichum alpestre- Chorisodontium aciphyllum	Polytrichum alpestre– Chorisodontium aciphyllum– lichen	Polytrichum alpestre— Chorisodontium aciphyllum heavily colonized by epiphytic lichens
	Sites 90-94	Sites 95-99	Sites 100-104	Sites 105-109	Sites 110-111
Lichens—continued					
Usnea antarctica	<1; 2	6; 96	<1; 6	16; 98	<1; 15
Unidentified crustose lichens	-	_			12; 100
Algae					
Blue-green alga	_	2; 44	_	3; 56	2; 30
Prasiola crispa	<1; 14	<1; 12	<1; 6	<1; 14	<1; 40

Details of sites are given in the Appendix.

Percentage cover and percentage frequency were estimated as in Table IV.

to 70°, depends upon the proportion of the dominant species. *Polytrichum*-dominant banks are generally the most stable due to the binding ability of the dense tomentum of the interwoven stems which form a compact firm turf. *Chorisodontium*-dominant banks, on the other hand, are usually moister and much less compact since the shoots are very slender and have a sparser rhizoid system. Consequently, the turf is easily broken or cracked by trampling and wind erosion.

A feature of this association is the build-up on gently sloping ground, of oval dome-shaped "islands" of peat formed principally by *Chorisodontium aciphyllum* which resemble the palsen of the Scandinavian tundra (Mårtensson, 1956). Many of these *Chorisodontium* banks cease abruptly in an almost vertical face, occasionally almost 2 m. deep, particularly on the down-hill side (Plate IVa; Gimingham and Smith, 1970, pl. 5, p. 780).

The surfaces of the peat banks undergo a succession of changes commencing with pure C. aciphyllum or mixed Chorisodontium aciphyllum and Polytrichum alpestre (Plate IVb), but they become increasingly colonized by fruticose and crustose lichens as the micro-topography becomes more exposed to wind. The less wind-swept parts of the banks support, in varying abundance, such epiphytic lichens as species of Alectoria and Cladonia, Cornicularia aculeata, Sphaerophorus globosus and Usnea antarctica (Plate IVc), but as the exposure increases species of Buellia and Ochrolechia as well as species of blue-green algae may replace the living moss to form an almost complete encrusting community growing epiphytically on the surface of the dead or dying moss (Plates IVd and Va).

The recognition of several sociations within this association is based solely on the dominance or codominance of *Polytrichum alpestre* and *Chorisodontium aciphyllum* and whether or not lichens are important associates. Indeed species lists and habitats are often identical in what are regarded as different sociations, to such an extent that two or more sociations may exist in the same bank and intergrade with each other.

Stands of pure *Polytrichum alpestre*, or *P. alpestre* with lichens, are not generally extensive on Signy Island, and frequently contain small quantities of *Chorisodontium aciphyllum*. However, *P. alpestre* is known to form large stands in other parts of the maritime Antarctic, notably in the Argentine Islands (Gimingham and Smith, 1970).

<sup>\*</sup> Includes Cladonia chlorophaea, C. furcata, C. gracilis, C. phyllophora and C. squamosa var. allosquamosa.

i. Polytrichum alpestre sociation. Predominant species: Polytrichum alpestre. Habitat: level or gently to steeply sloping, well-drained ground, usually overlying rocks. Slight to considerable snow cover in winter depending on incline of ground and exposure. Altitudinal range: 15-80 m.

Stands of lichen-free Polytrichum alpestre without Chorisodontium aciphyllum are seldom extensive in the South Orkney Islands, and generally occur within larger mixed stands of the two turf-forming species. P. alpestre tends to develop shallow banks of compact peat on level or sloping ground, overlying boulders so that the substratum is well drained. Cephaloziella varians, Barbilophozia hatcheri and Pohlia nutans are the most frequent associates, although there are usually scattered shoots of Chorisodontium aciphyllum also present. Because of the infrequency of these Polytrichum alpestre stands on Signy Island, no quantitative data have been obtained.

ii. Polytrichum alpestre-lichen sociation. Predominant species: Polytrichum alpestre, Buellia punctata, Cladonia spp., Ochrolechia frigida, Sphaerophorus globosus and Usnea antarctica. Habitat: level or gently to steeply sloping, well-drained rocky ground. Generally fairly exposed and receiving little snow cover in winter. Altitudinal range: 15-80 m.

This community variant occurs in almost identical situations to the previous sociation, but where exposure to wind has increased lichens tend to colonize the moss surface. The compact Polytrichum alpestre turf, which generally has a small quantity of Chorisodontium aciphyllum present, is colonized chiefly by crustose lichens, expecially Buellia punctata and Ochrolechia frigida, and to a lesser extent by the usual fruticose epiphytes, e.g. species of Alectoria, Cladonia, Sphaerophorus globosus and Usnea antarctica. However, these stands are infrequent on Signy Island and no quantitative data have been obtained.

iii. Chorisodontium aciphyllum sociation (Plate IVa). Predominant species: Chroisodontium aciphyllum. Habitat: level to steeply sloping ground usually supplied with small quantities of melt water. Covered by snow in winter. Soil data: (peat, mean of 14 samples), pH 4·4, moisture content 548 per cent, L.O.I. 95·3 per cent. Altitudinal range: 2-80 m.

Stands of pure Chorisodontium aciphyllum are seldom extensive and usually merge into the more common Chorisodontium aciphyllum-lichen sociation of slightly more exposed situations. This community type is typical of the somewhat sheltered marginal areas of deep peat banks where moisture is more readily available because of snow accumulation in winter and occasionally during summer. It is also found along the margins of small melt streams, where C. aciphyllum develops as tall coalesced hummocks, which frequently intergrade with stands dominated by Drepanocladus uncinatus.

The filamentous foliose hepatic Cephaloziella varians is always present among the shoots of Chorisodontium aciphyllum and occasionally grows over the surface of the moss where it has become moribund. Barbilophozia hatcheri may be frequent while a species of Lepidozia is a rare associate. Pohlia nutans is the only other species of importance, occurring either as isolated shoots or as small clumps amongst the C. aciphyllum, particularly in the hollows of the hummocky surface which is a typical feature of the moss banks. Where the substratum is moist, Calliergon cf. sarmentosum, Drepanocladus uncinatus and a procumbent short form of Brachythecium cf. antarcticum may be present in small quantities, amongst Chorosidontium aciphyllum.

iv. Chorisodontium aciphyllum-lichen sociation (Plate IVc and d). Predominant species: Chorisodontium aciphyllum, Buellia punctata, Ochrolechia frigida, Cladonia spp., Sphaerophorus globosus and Usnea antarctica. Habitat: level or sloping ground accumulating little snow in winter. Soil data: (peat, mean of 14 samples), pH 4·3, moisture content 464 per cent, L.O.I. 94·5 per cent. Altitudinal range: 2-95 (-185) m.

This sociation occupies virtually the same habitats as those of the previous community. However, while it may be lacking from the moister situations, it develops on the more exposed parts of the banks. Consequently, snow cover is usually only slight, the increase in exposure resulting in the preponderance of lichens which are more tolerant to strong wind than Chorisodontium aciphyllum. Cephaloziella varians and Pohlia nutans are again the main bryophyte associates. Several lichens are locally abundant, notably Alectoria chalybeiformis, various species of Cladonia, Sphaerophorus globosus, Usnea antarctica, the encrusting species Buellia punctata and Ochrolechia frigida and blue-green algae.

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v. Polytrichum alpestre-Chorisodontium aciphyllum sociation (Plate IVb). Predominant species: Chorisodontium aciphyllum and Polytrichum alpestre. Habitat: gently to steeply sloping stony ground, usually fairly well drained, with variable snow cover in winter. Soil data: (peat, mean of ten samples), pH 4·3, moisture content 487 per cent, L.O.I. 96·4 per cent. Altitudinal range: 3-185 (-235) m.

Banks formed by *P. alpestre* and *C. aciphyllum* are generally shallower than those in which *C. aciphyllum* is the sole peat producer. On the drier substrata *Polytrichum alpestre* usually assumes dominance as does *Chorisodontium aciphyllum* in moister parts of the habitat. Apart from the drainage factor on the steeper slopes, *P. alpestre* is probably dominant because of its tolerance to slumping from solifluction, which could lead to serious erosion in banks on such gradients dominated by *Chorisodontium aciphyllum*.

Cephaloziella varians and Pohlia nutans may be frequent in small amounts and Barbilophozia hatcheri is also a regular associate, especially among the less dense shoots of Polytrichum alpestre. vi. Polytrichum alpestre-Chorisodontium aciphyllum-lichen sociation. Predominant species: Chorisodontium aciphyllum, Polytrichum alpestre, Buellia punctata, Ochrolechia frigida, Cladonia spp., Sphaerophorus globosus and Usnea antarctica. Habitat: gently to steeply sloping stony ground, usually fairly well drained. Winter snow cover slight or none. Soil data: (peat, mean of 41 samples from 5 cm. deep), pH 4·4, moisture content 456 per cent, L.O.I. 94·3 per cent; (peat, mean of 20 samples from 20 cm. deep), pH 4·4, moisture content 424 per cent, L.O.I. 85·7 per cent. Altitudinal range: 3-185 (-235) m.

The habitat occupied by this assemblage is the same as that of the foregoing sociation, but appears to be more wind-swept, and hence derives little protection from snow cover in winter. The same two species of Polytrichum and Chorisodontium are again more or less co-dominant and a large number of lichens are present in varying proportions. Barbilophozia hatcheri and Pohlia nutans seem less frequent than in the previous sociation, but Cephaloziella varians is well represented. Of the fruticose lichens, Alectoria chalybeiformis, A. nigricans, several species of Cladonia including C. chlorophaea, C. furcata, C. gracilis, C. phyllophora and C. squamosa var. allosquamosa, Cornicularia aculeata, Sphaerophorus globosus and Usnea antarctica are locally abundant, while the less common Cladonia pleurota, Cladonia vicaria and Cornicularia epiphorella are occasional. The usual combination of Buellia punctata, Ochrolechia frigida and blue-green algae are often abundant or even locally dominant on the surface of the banks.

vii. Polytrichum alpestre-Chorisodontium aciphyllum banks heavily colonized by epiphytic lichens (Plate Va). Predominant species: Buellia punctata, Ochrolechia frigida, Cladonia spp., Sphaerophorus globosus and Usnea antarctica as epiphytes on living or dead Chorisodontium aciphyllum or Polytrichum alpestre. Habitat: exposed areas of Polytrichum-Chorisodontium banks. Snow cover is absent in winter, but the bank may be covered by a thin layer of ice. Altitudinal range: 3-155 m.

Although most *Polytrichum-Chorisodontium* banks are superficially colonized to some degree by epiphytic lichens, separate recognition has been given to those stands in an advanced stage of colonization. At this stage the moss surface is almost totally covered by crustose and fruticose species, as occurs especially on the crests and windward slopes of many of the dome-shaped peat banks. Where some degree of shelter is afforded, particularly in winter by drifted snow, fruticose species may dominate the surface of the mosses, while the crustose lichens generally colonize dead moss and eroded peat in more exposed situations. The fruticose species usually become established on or amongst the shoots of living moss, and may gradually kill it. The compact stable surface provided by *Polytrichum alpestre* appears to be more frequently encrusted than that of *Chorisodontium aciphyllum*. Where encrustation of the peat is advanced, the entire surface may be covered by black, white, grey and yellowish sterile crustose species as well as *Buellia punctata* and *Ochrolechia frigida*, while yellow, grey and brown species of *Cladonia* are frequent associates. Several species of blue-green algae also frequently occur.

Certain parts of some Polytrichum-Chorisodontium banks have almost 100 per cent cover of bushy fruticose lichens, the principal species being Usnea antarctica which is very extensive on some banks on the west coast of the island. Its growth form tends to be much denser and bushier than on rock habitats, and it is often considerably yellower in colour. Sphaerophorus globosus may be locally co-dominant, and Alectoria chalybeiformis, A. nigricans, several species

of Cladonia, Cornicularia aculeata and occasionally Psoroma hypnorum are usually present in varying amounts. Unlike the encrusted peat surfaces, those dominated by fruticose lichens have frequent patches of living moss between the lichen colonies and there is generally a living understorey of moss.

No quantitative data have been recorded for assemblages with heavy fruticose lichen cover.

b. Polytrichum alpinum association (Table XII). The only common uniform assemblage on Signy Island in which Polytrichum alpinum is the dominant species is the Polytrichum alpinum—Drepanocladus uncinatus sociation found in low-lying coastal areas.

Circular stands of *P. alpinum* are a common feature in this association, and as already mentioned, the largest measured about 1 m. in diameter. These latter show a distinct cycle of change in which the central area dies out and becomes re-colonized by other bryophytes and crustose lichens (p. 73). *P. alpinum* has a wide ecological amplitude and occurs as an associate in many different communities. It is seldom abundant, except in the present association, although it may form dense colonies locally amongst species of *Andreaea* and some of the taller lichens, and at the margin of shallow *Polytrichum alpestre-Chorisodontium aciphyllum* banks.

TABLE XII

PERCENTAGE COVER AND PERCENTAGE FREQUENCY OF SPECIES IN THE

Polytrichum alpinum-Drepanocladus uncinatus SOCIATION

Species	Sites 112-116	Species	Sites 112-	-116
Mosses		Lichens		
Andreaea depressinervis	2; 58	Acarospora macrocyclos	<1;	8
Ceratodon cf. grossiretis	2; 12	Buellia punctata	2; 4	12
Chorisodontium aciphyllum	<1; 16	Buellia subpedicellata + B. granulosa	<1; 1	6
Distichium cf. capillaceum	<1; 6	Cladonia carneola	<1; 2	22
Drepanocladus uncinatus	20; 100	Cladonia chlorophaea, C. furcata, C. phyllophora	2; 3	36
Pohlia nutans	16; 84	Lecanora aspidophora	<1;	6
Polytrichum alpestre	<1; 10	Lecanora subfusca	3; 3	32
Polytrichum alpinum	30; 94	Ochrolechia frigida	<1; 1	
lepatics		Rinodina turfacea	<1; 2	22
Barbilophozia hatcheri	<1; 12	Sphaerophorus globosus	<1;	2
Cephaloziella varians	13; 78	Stereocaulon alpinum	<1;	6
		Usnea antarctica	<1;	2
		Unidentified crustose lichen	10; 9	2
		Alga		
		Prasiola crispa	1; 4	10
		Substratum		
		Bare ground	9; 6	54

Details of sites are given in the Appendix. Percentage cover and percentage frequency were estimated as in Table IV. i. Polytrichum alpinum sociation. Predominant species: Polytrichum alpinum. Habitat: moist peaty substrata usually near biotically disturbed areas. Soil data: (mean of four samples), pH 4·8, moisture content 176 per cent, L.O.I. 68·2 per cent. Altitudinal range: 3-50 m.

This sociation is poorly represented in the South Orkney Islands and is more typical of moist ash soils on certain of the South Sandwich and South Shetland Islands where *Polytrichum alpinum* locally forms extensive almost pure stands. However, small, almost pure stands of *Polytrichum alpinum* occur on Signy Island, usually at low altitudes and close to areas disturbed by elephant seals and giant petrels (*Macronectes giganteus*). The most extensive closed stands measured only about 10 m.<sup>2</sup>. Associated bryophytes are few and usually include *Drepanocladus uncinatus*, *Ceratodon* cf. grossiretis, Cephaloziella varians and occasionally *Pohlia nutans*, but on more mineral soils, where the former moss is abundant, the community may be considered as the *Polytrichum alpinum-Drepanocladus uncinatus* sociation.

No quantitative data are available on account of the infrequency and small size of stands of this sociation.

ii. Polytrichum alpinum- Drepanocladus uncinatus sociation. Predominant species: Drepanocladus uncinatus, Pohlia nutans, Polytrichum alpinum, Cephaloziella varians, and a sterile species of yellowish crustose lichen. Habitat: fairly moist organic soil at margins of biotically disturbed coastal areas, such as below cliff-breeding bird colonies on moist but well-drained slopes. Well covered by winter snow which often persists into summer. Soil data: (mean of four samples), pH 5·8, moisture content 35 per cent, L.O.I. 15·3 per cent. Altitudinal range: 2-30 m.

This sociation developes around the margins of areas disturbed by wallowing elephant seals, breeding colonies of giant petrels, at the foot of cliffs or on ledges where snow petrels (*Pagodroma nivea*) and cape pigeons (*Daption capensis*) nest, and to a lesser extent around the margins of penguin colonies. The larger stands usually occur at the base of slopes where winter snow lies late into spring, providing a fairly wet but well-drained soil.

Because of the dampness of the substratum, *Drepanocladus uncinatus* is frequently co-dominant with *Polytrichum alpinum*, but in the wetter conditions the former may form small pure stands; on the drier stonier areas *P. alpinum* may develop small, pure coalesced circular colonies. The principal bryophyte associates are *Cephaloziella varians* and *Pohlia nutans*, either of which may be locally dominant. *Andreaea depressinervis* and *Ceratodon* cf. *grossiretis* are sometimes frequent as isolated cushions. *Deschampsia antarctica* may be an occasional associate, and is locally frequent in some stands, particularly near the shore. Lichens vary in abundance, but a yellowish green sterile crustose species and several other sterile lichens, probably species of *Buellia* and *Lecidea*, sometimes give quite a high cover value, usually growing epiphytically on the dead *Polytrichum alpinum* and associated bryophytes.

The more disturbed and eroded areas of this sociation, where the bryophyte cover has largely been killed, may be almost entirely encrusted by white, grey and yellowish lichens. In addition to species of *Buellia* and *Lecidea*, there are frequently varying quantities of *Ochrolechia frigida*, *Psoroma hypnorum*, several fruticose species of *Cladonia* and occasionally sparse tufts of *Usnea antarctica*.

### 4. Moss carpet sub-formation

Many permanently moist or wet habitats on level or gently sloping ground at low altitudes are vegetated by closed soligenous or topogenous communities dominated by species of *Brachythecium*, *Calliergon* and *Drepanocladus*. The growth habit of these species is rather variable but in the wetter situations, where the most extensive stands occur, they develop a turf-like growth form, whereas in drier habitats they form a thin mat of more or less procumbent shoots. The reasons for designating the turf-like growth form of these Antarctic pleurocarps as carpets, i.e. with close-packed, almost parallel ascending shoots arising from a connecting, more horizontal-lying basal layer, have been discussed by Gimingham (1967). But some species such as *C. cf. sarmentosum* and particularly *D. uncinatus* possess a wide range of growth forms which are probably correlated with their wide ecological amplitude. These communities produce a shallow soligenous peat up to 10–15 cm. in depth. As the annual growth increment of these swamp mosses is relatively high (personal communication from N. J. Collins), the decomposition rate must also be high, at least by comparison with the *Polytrichum-Chorisodontium* peat.

a. Brachythecium cf. antarcticum—Calliergon cf. sarmentosum—Drepanocladus uncinatus association (Table XIII; Plate VIa). Because of the wide range of wet habitats available, communities of this association form the largest expanses of closed vegetation so far recorded in the Antarctic. Some small stands of Calliergon cf. sarmentosum and Drepanocladus uncinatus occur over 235 m., but all the large stands are restricted to low-lying areas, particularly around the coast. As with the Polytrichum alpestre—Chorisodontium aciphyllum association, the communities within the Brachythecium cf. antarcticum—Calliergon cf. sarmentosum—Drepanocladus uncinatus association are very similar to one another, and any combination of the four principal species may occur, so that local pure stands of each are quite common. However, they appear to have slightly different habitat preferences and in some situations there is a distinct zonation (p. 99). In the wettest parts, where water sometimes lies on the surface for short periods, a tall robust form of B. cf. antarcticum predominates, frequently with a tall loose form of Calliergon cf. sarmentosum, although the latter is usually just outside the wettest areas. A short, slender form of B. cf. antarcticum occurs in damp hollows on some hillsides. C. cf. sarmentosum and D. uncinatas are most abundant on drier, better-drained ground and at the margins of the wetter areas, where they tend to produce a more typical mat growth form.

The surface of the *Brachythecium* carpet, as with that formed by *Calliergon* and *Drepanocladus*, is frequently parasitized by an ascomycetous fungus, *Thyronectria antarctica* var. *hyperantarctica*, with hyphae producing small white circular patches on the moss which eventually kill the shoot apices. Outbreaks of this miniature "fairy ring" fungus occur after prolonged periods of snow cover, as in early spring and following longer spells of summer snow.

Six sociations have been recognized, based on the dominance of various species, and quantitative data for each are given in Table XIII. The Brachythecium cf. antarcticum, Calliergon cf. sarmentosum and Drepanocladus uncinatus sociations are separated solely because locally these species form large pure stands, although mixed stands are often formed adjacent to pure stands. Associated species are very few and usually appear where the substratum is drier, as among shoots of the dominant species overlying a raised frost-heaved group of stones. The most abundant associate is Cephaloziella varians which occasionally forms patches almost 1 m. in diameter over the surface of the Brachythecium or Calliergon. Pohlia nutans is sometimes present, and Polytrichum alpinum and Ceratodon cf. grossiretis may occur at the edge of the community where the soil is considerably drier. As the effects of flushing increase, e.g. in the vicinity of basic rocks, Bryum algens, Tortula excelsa and several other mildly calcicolous bryophytes become prominent. Lichens are rare, the only important species tolerating wet conditions being Leptogium puberulum and Psoroma hypnorum, the former occurring where the soil has a higher base status. Crustose species of Acarospora and Lecanora, together with Buellia russa, Staurothele gelida and Verrucaria elaeoplaca colonize wet stones in these habitats. Of the macroscopic algae, Prasiola crispa and a morphologically similar species of Nostoc may be frequent on the wet moss or soil surface, while a reddish brown felt of algae is locally common in runnels, lake margins and saturated, biotically disturbed soil.

i. Brachythecium cf. antarcticum sociation. Predominant species: Brachythecium cf. antarcticum. Habitat: of tall, robust form, swamps on level ground usually traversed by melt runnels and on wet lakeside flats; of short, slender form, wet or moist hollows where snow lies late into spring. Soil data: (mean of three samples), pH 5·0, moisture content 893 per cent, L.O.I. 77·0 per cent. Altitudinal range: 5-80 m.

Pure stands of *Brachythecium* cf. antarcticum are quite common in the wettest areas of the island and develop wherever the species is not in danger of being permanently submerged. These stands may comprise either the tall, somewhat loose form of *B*. cf. antarcticum, or the much more compact, slender form, although both may be found together. The spongy carpet formed by this moss may exceed 15 cm. in depth. Occasional shoots of *Calliergon* cf. sarmentosum and *Drepanocladus uncinatus* may be present.

ii. Calliergon cf. sarmentosum sociation. Predominant species: Calliergon cf. sarmentosum. Habitat: swamps, runnel margins and wet, gravelly ground. Altitudinal range: 8-80 m.

Stands of Calliergon cf. sarmentosum are locally common, but may occur either as a community in habitats similar to those occupied by Brachythecium cf. antarcticum, or on wet, gravelly sloping ground and along the margins of small or temporary melt runnels. In the wetter, more level habitats the Calliergon is tall and ascending, whereas in the better-drained stonier habitats it assumes a more prostrate mat growth form. Drepanocladus uncinatus and Cephaloziella varians are the most frequent associates.

TABLE XIII

PERCENTAGE COVER AND PERCENTAGE FREQUENCY OF SPECIES IN SOCIATIONS OF THE Brachythecium cf. antarcticum-Calliergon cf. sarmentosum-Drepanocladus uncinatus ASSOCIATION

		Sociations showing percentage cover; percentage frequency of species						
Species	Brachythecium cf. antarcticum		sarmentosum uncinatus c		Brachythecium cf. antarcticum -Calliergon cf. sarmentosum	Calliergon cf. sarmentosum– Drepanocladus uncinatus	Brachythecium cf. antarcticum -Calliergon cf. sarmentosum- Drepanocladus uncinatus	
	Sites 117-120	Sites 121–122	Sites 123-127	Sites 128-133	Sites 134–138	Sites 139–143	Sites 144-148	
Mosses								
Brachythecium cf. antarcticum (short, slender form)	98; 100	-	_	_	11; 20	1; 10	17; 60	
Brachythecium cf. antarcticum (tall, robust form)	_	99; 100	_	_	42; 76	<1; 6	12; 42	
Brachythecium austro-salebrosum	_	-	_	<1; 2	_	<1; 8	_	
Calliergon cf. sarmentosum	2; 45	<1; 5	100; 100	<1; 8	46; 96	59; 98	32; 94	
Conostomum perangulatum	_	_	<1; 8	_	-	_	-	
Drepanocladus uncinatus	1; 38	<1; 5	<1; 26	100; 100	1; 22	41; 94	42; 98	
Pohlia nutans	<1; 20	-	<1; 12	_	<1; 2	<1; 4	, <del>-</del>	
Polytrichum alpinum	-	_	_	_	-	<1; 4	-	
Tortula excelsa	_	-	<del>-</del>	_	-	<1; 2	_	
Hepatics							TOTAL COMPANY OF THE PARTY OF T	
Barbilophozia hatcheri	<1; 5	-	_	_	_	_	_	
Cephaloziella varians	<1; 13	-	2; 22	<1; 4	<1; 2	<1; 10	_	
Lichens								
Lecanora subfusca	<1; 8	_	_	_	_	_	<u>-</u>	
Psoroma hypnorum	_	-	_	<1; 6	-	-	_	
Alga								
Prasiola crispa	<1; 13	<1; 10	_	<1; 10	2; 32	<1; 4	_	

iii. Drepanocladus uncinatus sociation. Predominant species: Drepanocladus uncinatus. Habitat: drier margins of swampy areas, usually on fairly well-drained or porous stony ground. Soil data: (mean of three samples), pH 4·9, moisture content 196 per cent, L.O.I. 54·0 per cent. Altitudinal range: 2-155 (-200) m.

Although extensive stands of pure *Drepanocladus uncinatus* are found only at low altitudes, small mats occur in moist hollows over most of the higher areas of the island. Where this species grows in wet habitats, its growth form is tall and of a carpet structure, but on the drier stonier ground it becomes more prostrate and forms a mat of interwoven branching shoots easily detached from the substratum.

iv. Brachythecium cf. antarcticum-Calliergon cf. sarmentosum sociation. Predominant species: Brachythecium cf. antarcticum and Calliergon cf. sarmentosum. Habitat: swamps on level ground, usually traversed by melt runnels and on wet lakeside flats. Soil data: (mean of three samples), pH 5·4, moisture content, 1,125 per cent, L.O.I. 83·9 per cent. Altidutinal range: 5-80 m.

Brachythecium cf. antarcticum and Calliergon cf. sarmentosum form mixed stands in some of the wettest habitats, representing a community type transitional between the pure Brachythecium cf. antarcticum and pure Calliergon sociations. Both species contribute towards the development of a shallow peat below the carpet.

v. Calliergon cf. sarmentosum-Drepanocladus uncinatus sociation. Predominant species: Calliergon cf. sarmentosum and Drepanocladus uncinatus. Habitat: drier marginal areas of swamps with improved drainage and along margins of melt runnels and on wet stony ground. Soil data: (mean of 20 samples), pH 5·3, moisture content 321 per cent, L.O.I. 40·5 per cent. Altitudinal range: 5-80 (-200) m.

Stands of Calliergon cf. sarmentosum and Drepanocladus uncinatus occur in less wet habitats than those occupied by the Brachythecium cf. antarcticum—Calliergon cf. sarmentosum sociation, generally on stony or gravelly substrata, where a relatively shallow peat develops.

vi. Brachythecium cf. antarcticum-Calliergon cf. sarmentosum-Drepanocladus uncinatus sociation (Gimingham and Smith, 1970, pl. 6, p. 780). Predominant species: Brachythecium cf. antarcticum, Calliergon cf. sarmentosum and Drepanocladus uncinatus. Habitat: swampy areas, usually traversed by melt runnels and on wet lakeside flats. Soil data: (mean of 26 samples), pH 5·4, moisture content 528 per cent, L.O.I. 60·1 per cent. Altitudinal range: 5-80 m.

This assemblage represents the intermixing of the previous five sociations in which all three mosses are co-dominant, or at least present in varying proportions with each becoming dominant locally.

# 5. Moss hummock sub-formation

Whereas the moss carpet communities develop chiefly in situations with a permanent supply of standing water, the moss hummock sub-formation occurs where there is moving water, usually enriched by cations derived from nearby basic rocks or soils, so approaching an eutrophic bog. These flushed habitats generally occur below marble or amphibolite outcrops which provide the soil with a realtively high base status and the water with a high conductivity. Like the moss carpet communities, this sub-formation develops a shallow peat beneath the living moss, the principal species being Brachythecium austro-salebrosum, Bryum algens, Drepanocladus uncinatus and Tortula excelsa. The growth form of these species varies from that of either a tall compact cushion (B. algens), a tall loose cushion (Brachythecium austro-salebrosum and Tortula excelsa), or a deep undulating carpet (Drepanocladus uncinatus). The Bryum is very variable in its morphology, ranging from a low 0.5-3 cm. cushion with small, rounded ovate leaf apices, to a high 5-20 cm. cushion with bands of dense rhizoids and large, acuminate or lanceolate leaves with recurved margins; there is also a tall form with no rhizoids and large, rounded concave leaves. The large cushions of the various species usually coalesce to form a closed hummocky surface.

a. Bryum algens-Drepanocladus uncinatus association (Table XIV). Only the Bryum algens-Drepanocladus uncinatus-Tortula excelsa sociation is well-represented on Signy Island, although stands of the Bryum algens sociation may be locally prominent. As in other wet habitat communities, lichens are scarce, with the mildly calcicolous Leptogium puberulum being the most prominent associate. Prasiola crispa and a species of Nostoc may be frequent.

i. Bryum algens-Drepanocladus uncinatus-Tortula excelsa sociation (Gimingham and Smith, 1970, pl. 7, 781). Predominant species: Brachythecium austro-salebrosum, Bryum algens, Drepanocladus uncinatus and Tortula excelsa. Habitat: flushed soils below marble outcrops and along base-rich

TABLE XIV

PERCENTAGE COVER AND FREQUENCY OF SPECIES IN SOCIATIONS
OF THE Bryum algens-Drepanocladus uncinatus ASSOCIATION

	Sociations showing perc percentage frequency	
Species	Bryum algens-Drepanocladi uncinatus-Tortula excelsa	Bryum algens
	Sites 149–154	Sites 155-156
Mosses		
Brachythecium austro-salebrosum	8; 69	9; 80
Bryum algens (short form)	8; 58	12; 100
Bryum algens (tall form)	18; 58	83; 100
Total Bryum algens	26; 97	95; 100
Calliergon cf. sarmentosum	2; 18	-
Ceratodon cf. grossiretis	<1; 5	_
Drepanocladus cf. plicatus	1; 13	-
Drepanocladus uncinatus	37; 93	2; 35
Pottia austrogeorgica	<1; 2	-
Tortula excelsa	26; 81	<1; 5
Tortula fuscoviridis	<1; 2	_
Tortula cf. grossiretis	<1; 7	_
Hepatics		
Cephaloziella varians	<1; 7	_
Marchantia berteroana	<1; 2	_
Lichens		
Leptogium puberulum	<1; 15	<1; 15
Ochrolechia frigida	<1; 3	-
Alga		
Nostoc sp.	<1; 3	_
Substratum		
Bare ground	4; 38	3; 20

Details of sites are given in the Appendix. Percentage cover and percentage frequency were estimated as in Table IV. melt runnels. Soil data: (mean of three samples), pH 7·7, moisture content 193 per cent, L.O.I. 31·6 per cent. Altitudinal range: 3-50 m.

This sociation, quantitative data for which are given in Table XIV, is characteristic of the wetter base-rich areas on Signy Island below marble outcrops and knolls. The Bryum and Brachythecium austro-salebrosum often line the runnel margins with deep coalesced hummocks, while the Drepanocladus and Tortula appear to prefer the less wet, often stonier ground. Both Bryum algens and Drepanocladus uncinatus frequently form pure stands within this sociation, although neither is extensive. In the wetter situations occupied by T. excelsa, where it may be dominant locally, the moss is usually a reddish brown colour, whereas in the drier localities it becomes bright green.

Brachythecium austro-salebrosum, Campylium sp. and Calliergon cf. sarmentosum are sometimes quite abundant associates, particularly on the drier, more gravelly situations. Leptogium puberulum is the only important lichen. Deschampsia antarctica may occasionally be present.

ii. Bryum algens sociation. Predominant species: Bryum algens. Habitat: gently sloping wet stony ground by the margins of melt runnels, usually close to marble outcrops. Soil data: (mean of 11 samples), pH 6.7, moisture content 246 per cent, L.O.I. 43.5 per cent. Altitudinal range: 3-35 m.

This sociation is locally common along the margins of melt runnels and in flushes enriched by the proximity of marble. The stands are composed mainly of large deep cushions of *Bryum algens* which coalesce to form an undulating surface. Small forms of the same species are also frequent in this sociation, while other associates usually include *Brachythecium austro-salebrosum*, and a closely related species, *Drepanocladus uncinatus* and *Tortula excelsa*. *Leptogium puberulum* is the only frequent lichen. Quantitative data are provided in Table XIV.

The Bryum algens sociation is probably a variant of the Bryum algens-Drepanocladus uncinatus sociation referred to by Gimingham and Smith (1970), which is so frequent in western coastal areas of the Antarctic Peninsula where a shorter form of Bryum algens, associated with D. uncinatus, forms small stands in damp, slightly base-rich habitats. Alternatively, on Signy Island, the peninsula sociation may be incorporated in communities of the Tortula-Grimmia antarctici association of basic soils.

- b. Brachythecium austro-salebrosum association (Table XV; Plate VIb). Brachythecium austro-salebrosum forms prominent golden-green hummocks which coalesce to produce locally extensive undulating stands. As with other communities of this sub-formation, this association may be considered as mildly calcicolous and occupies flushed habitats comparable to the previous association to which it is closely related.
  - i. Brachythecium austro-salebrosum sociation. Predominant species: Brachythecium austro-salebrosum. Habitat: margins of melt runnels running over stony ground and also on wet sloping rocks, in both cases usually with some degree of flushing. Soil data: (mean of four samples), pH 7·2, moisture content 224 per cent, L.O.I. 43·2 per cent. Altitudinal range: 3-85 m.

TABLE XV

PERCENTAGE COVER AND PERCENTAGE FREQUENCY OF SPECIES
IN THE Brachythecium austro-salebrosum SOCIATION

Species	Sites 157–158
Mosses	
Brachythecium austro-salebrosum	96; 100
Bryum algens (tall form)	1; 30
Calliergon cf. sarmentosum	<1; 5
Drepanocladus uncinatus	6; 65

Details of sites are given in the Appendix.

Percentage cover and percentage frequency were estimated as in Table IV.

Stands of *Brachythecium austro-salebrosum* are seldom extensive and are largely restricted to low-lying flushed areas and melt runnel margins, Table XV providing some data for two such stands. The tall, loosely packed shoots are easily disturbed and broken by trampling. On wet rocks a more open community of shorter cushions is formed.

Drepanocladus uncinatus is the principal associate, although close to stands of the Bryum algens-Drepanocladus uncinatus-Tortula excelsa sociation, Bryum algens may be locally frequent where the two sociations intergrade.

# 6. Encrusted moss sub-formation

This sub-formation has been described by Longton (1967) as "a thin crust of small turf- and cushion-forming mosses, largely moribund, and so heavily colonized by crustose lichens that the vegetation as a whole assumes the colour of the most abundant lichen". Such an association of bryophytes and lichens is not common in the South Orkney Islands and nowhere does it form the extensive stands which are locally frequent on the soils of volcanic ash of certain islands in the South Sandwich and South Shetland Islands. On Signy Island, stands of short cushion- and turf-forming mosses, encrusted by various lichens, occur in moist, often biotically disturbed coastal situations but rarely exceed a few square metres in area. The heavily encrusted surface of many peat banks has not been included in this sub-formation as these are considered as a stage in a simple succession within the *Polytrichum alpestre-Chorisodontium aciphyllum* association.

a. Lichen encrusted Bryum-Ceratodon cf. grossiretis-Pohlia nutans association. In the South Orkney Islands this association is represented only by small assemblages, usually comprising Ceratodon cf. grossiretis, Pohlia nutans and Cephaloziella varians, all of which may be variably encrusted with several species of poorly developed white, grey or yellowish sterile lichens. Bryum algens and Psoroma follmannii which are regular associates in communities of this association on soils of volcanic origin elsewhere in the maritime Antarctic, are seldom present. This is probably due to the somewhat acid nature of the more organic substratum.

No quantitative data are available for the sociation recognized on Signy Island.

i. Lichen encrusted Ceratodon cf. grossiretis-Pohlia nutans-Cephaloziella varians sociation. Predominant species: Ceratodon cf. grossiretis, Pohlia nutans, Cephaloziella varians, Buellia spp., Lecidea spp. and Ochrolechia frigida. Habitat: moist, level or gently sloping peaty substrata, generally in or close to biotically disturbed areas. Altitudinal range: 2-20 m.

This sociation generally consists of small mixed stands of Ceratodon cf. grossiretis, Pohlia nutans, Cephaloziella varians and a number of crustose lichens, chiefly of the genera Buellia, Lecidea and Ochrolechia. These stands develop locally near Polytrichum alpinum-Drepanocladus uncinatus communities on level or gently sloping damp soil, often with a fairly high organic content, usually close to the shore, and probably influenced to some extent by birds and seals. On a considerably smaller scale, these species often occur in the central dead area of circular Polytrichum alpinum stands (p. 74) as well as locally outside these colonies.

Associated species usually include *Drepanocladus uncinatus*, *Chorisodontium aciphyllum*, *Polytrichum alpinum* and occasionally *Bryum algens*. Several species of *Cladonia* and *Psoroma hypnorum* may also be abundant.

# 7. Alga sub-formation

On Signy Island this sub-formation is represented chiefly by communities containing two species of macroscopic terrestrial algae. Only the green thallose alga, *Prasiola crispa*, is abundant and in suitable habitats it develops extensive stands forming a crinkly sheet overlying muddy substrata. The gelatinous alga *Nostoc* cf. *commune* forms only very small open colonies, and is more typical as an associate in some of the more calcicolous communities.

No species lists or quantitative data are available for the representative associations.

a. Prasiola crispa association. This widespread green alga is a frequent associate in many wet habitats, particularly those enriched by bird or seal excreta. However, it is most characteristic of permanently wet and heavily contaminated muddy pools near penguin colonies where it often forms pure, closed stands of loose thalli, which are readily detached from the substratum by wind or biotic agents.

i. Prasiola crispa sociation. Predominant species: Prasiola crispa. Habitat: wet, muddy and stony depressions in and near penguin colonies and elephant seal wallows and on wet rock surfaces, crevices and in melt streams usually enriched by bird excreta. Soil data: (from Holdgate and others, 1967, sample No. 53), pH 3.7, L.O.I. 25.3 per cent. Altitudinal range: 2-30 (-100) m.

The depressions in and around penguin colonies and seal wallows usually have temporary pools of stagnant melt water. Such heavily trampled and disturbed areas are typically vegetated by Prasiola crispa, apparently the only macroscopic plant species able to tolerate the biotic disturbance, high acidity and the high concentrations of sodium, phosphorus and nitrogen derived from the excreta of these animals. The alga forms pure, generally open stands of varying dimensions, those on Signy Island being comparatively small reaching only about 100 m.2. Elsewhere on the island Prasiola crispa is not extensive and is usually considered as an associate in other community types. It is locally abundant in shallow melt pools and runnels, and frequently lies on the surface of the chief mosses of the Brachythecium cf. antarcticum-Calliergon cf. sarmentosum-Drepanocladus uncinatus association as well as in wet depressions on Polytrichum-Chorisodontium banks. It is sometimes abundant also on wet rock faces, in crevices and on ledges at low altitudes, particularly near the shore in the vicinity of cliff-nesting birds.

Because of the effects of continual trampling by penguins and the high sodium, phosphorus and nitrogen content of the water and mud, bryophyte species are only found in very sparse colonies on drier ground, usually on the outer margins of the Prasiola zone. These mosses include Brachythecium austro-salebrosum, Bryum algens, Ceratodon cf. grossiretis, Drepanocladus uncinatus, Pohlia nutans and Tortula excelsa. The most frequent lichens are crustose species of Acarospora, Buellia, Caloplaca, Lecanora, Lecidea, Microglaena antarctica, Staurothele gelida and Verrucaria elaeoplaca, together with Leptogium puberulum and Lecania brialmontii, all of which colonize the wet or moist stones.

b. Nostoc association. The blue-green alga Nostoc cf. commune produces small colonies of gelatinous thalli in various mildly base-rich moist habitats, but it does not develop large stands in the South Orkney Islands. Further investigation may reveal other species or genera and groupings which should be treated as separate sociations but which at present have been included in a single sociation.

i. Nostoc sociation. Predominant species: Nostoc cf. commune. Habitat: damp, usually slightly

flushed base-rich gravelly soil. Altitudinal range: 5-50 m.

Nostoc cf. commune is a frequent though sparse associate in several communities occurring on flushed or base-rich substrata, and amongst the heterogeneous bands of bryophytes and lichens along the margins of stone stripes. On Signy Island it rarely forms aggregations larger than 400 cm.2 and consequently must be considered one of the least significant communities in the vegetation of the island.

Pure closed stands of considerable size of a species of Nostoc have been observed by the author on Robert Island in the South Shetland Islands, while Lindsay (1971e) has reported large open

stands of small rosettes of a species of Nostoc also in the South Shetland Islands.

### 8. Snow alga sub-formation

The aggregations of unicellular chionophilous algae which discolour the surface of melting snow and ice are a prominent feature in many coastal areas of the maritime Antarctic, especially from mid to late summer. Although not strictly part of the terrestrial flora, these transient populations of algal cells often develop temporary "stands" several hundred square metres in area. Fogg (1967) considered the sudden appearance of these algal blooms to be due to the mechanical accumulation of cells at the surface, as ablation of the snow proceeds, rather than to excessively rapid reproduction.

a. Chlamydomonas nivalis-Raphidonema nivale-Ochromonas association. This association, although inadequately studied, has been recognized largely from data provided by Fogg (1967). The principal algal species contributing to these colourful cryoplankton communities are Chlamydomonas nivalis, Raphidonema nivale and a species of Ochromonas. Fogg described the characteristic red snow as "occurring on well-drained firn snow, especially at the margins of ice exposures where the snow has been reduced to a thin layer by ablation" and that "gelatinous aggregations of red snow algae were often encountered on bare ground from which the snow had recently disappeared". A pale yellow discoloration by algae occurs in similar situations, while a less frequent green coloration occurs in waterlogged or flushed firn snow where there is a greater availability of liquid water.

During the course of the present work, extensive areas of dense red and green snow algae were observed lining the margins of melt-water channels and in the melt-wash fans on McLeod Glacier and other areas of permanent ice from sea-level to about 230 m. on Signy Island.

The only available quantitative data are those provided by Fogg (1967). He gave cell counts, per mm.<sup>3</sup>, for red, green and yellow snow samples collected on Signy and Coronation Islands.

i. Chlamydomonas nivalis-Raphidonema nivale-Ochromonas sociation. Predominant species: Chlamydomonas nivalis, Hormidium subtile, Ochromonas sp. and Raphidonema nivale. Habitat: well-drained to waterlogged firn snow. Altitudinal range: 0-230 m.

Fogg (1967), in his observations on snow algae on Signy Island, has shown that there is little difference in species composition between red, yellow and green cryoplankton communities. However, too few data are yet available to describe them in detail or to distinguish separate communities.

Green snow is characterized by higher densities than the two other snow colours and by the absence of the red resting spores of *Chlamydomonas nivalis* and *Chlorosphaera antarctica*. Hormidium subtile was found only in green snow. The principal species, which may exceed 4,000 cells per mm.<sup>3</sup>, are *Chlamydomonas nivalis*, Raphidonema nivale and Ochromonas sp., although Fogg stated that none has an absolute association with a particular snow colour.

Red snow is determined by the intense colour of the spores of the two species described above, either of which may be represented by relatively few vegetative cells. R. nivale may be the most abundant alga in either green or yellow snow, although in the latter case the cells are chlorotic due, presumably, to mineral deficiency.

# 9. Miscellaneous cryptogam assemblages

A few assemblages of bryophytes and lichens, which occur only rarely on Signy Island or elsewhere in the maritime Antarctic, do not appear to fit into the classification system given in Table III. In most cases these groups are formed by one of the less important associates of a particular community type becoming dominant. They are seldom extensive in area. Some of the bryophytes which form small, pure or mixed stands are Campylium sp., Ceratodon cf. grossiretis, Cephaloziella varians, Marchantia berteroana, Pohlia cruda var. imbricata and P. nutans. However, most of these stands may be considered merely as variants or components of previously described sociations. Of the ilchens, small stands of Haematomma erythromma, Mastodia tesselata and various species of Acarospora, Buellia, Lecidea, Lecanora, Pannaria, Pertusaria and Rhizocarpon are not infrequent. Most of these lichens colonize dry rock surfaces.

Two of the more extensive bryophyte-dominated community types are described below, since they cannot be conveniently accommodated in any of the sub-formations recognized on Signy Island.

a. Marchantia berteroana community (Plate Vd). Marchantia berteroana possesses a unique growth form with regard to the previously described sub-formations of Signy Island. However, very few stands of this thalloid hepatic have been observed and it has been considered inappropriate to raise these to the status of a separate sub-formation.

The largest stand of almost pure, closed Marchantia berteroana on Signy Island is about 15 m.², the others being considerably smaller and usually broken by Deschampsia antarctica or species of the Pottia austrogeorgica or Tortula-Grimmia antarctici associations. The thalloid hepatic forms dense cover on steep moist slopes, with fine, fairly basic soil or clay derived mainly from marble or amphibolite outcrops. Consequently, it is probably an extreme form of one of the Tortula-Grimmia antarctici sociations in which the associated M. berteroana becomes dominant almost at the expense of all other species. The associated bryophytes include Bartramia cf. patens, Brachythecium austro-salebrosum, Bryum algens, Distichium sp., Drepanocladus uncinatus, Encalypta spp., Grimmia antarctici, Pottia austrogeorgica, Tortula excelsa, T. fuscoviridis, T. cf. grossiretis and a species of Riccardia which has not been found in any other community type. Leptogium puberulum is the only lichen usually present, and Deschampsia antarctica may be locally abundant.

b. Pioneer communities of moraines. There are many small but distinct terminal and lateral moraines on Signy Island, and at least one medial moraine on McLeod Glacier. Although these consist principally of large unsorted boulders and stones, there are frequent pools of muddy clay, which in places may be quite extensive. This soil generally has a high base status and if comparatively stable may be colonized by various calcicoles and certain other species.

The species lists recorded on several inland moraines are often similar. The best developed and most studied moraine is that separating the north-east flank of Orwell Glacier from Moraine Valley (Table XVI).

TABLE XVI

FREQUENCY ASSESSMENT OF SPECIES ON THE OUTER AND INNER MORAINE TERRACES BELOW ORWELL GLACIER, SIGNY ISLAND

Species	Outer terrace	Inner terrace
Aosses		
Andreaea depressinervis	o	_
Andreaea gainii	o	-
Andreaea regularis	o	_
Bartramia cf. patens	О	_
Brachythecium austro-salebrosum	o	r
Bryum algens (short and tall forms)	o-f	o
Bryum argenteum	_	r
Ceratodon cf. grossiretis	o-f	o
Dicranoweisia grimmiacea	o	_
Distichium cf. capillaceum	-	r
Drepanocladus uncinatus	la	r
Encalypta sp.	o	_
Grimmia antarctici	o	r
Pohlia cruda var. imbricata	o	_
Pohlia nutans	o	_
Polytrichum alpinum	o-f	_
Pottia austrogeorgica	o-f	o
Stegonia latifolia	r	o
Tortula conferta	o	r
Tortula excelsa	o	r
Tortula fuscoviridis	o	r
Tortula cf. grossiretis	r	r
Lichens		
Buellia spp.*	o-f	r-o
Caloplaca spp.	o-f	o

TABLE XVI-continued

Species	Outer terrace	Inner terrace
Lichens—continued		
Candelariella vitellina	o	_
Cladonia carneola	r	_
Cladonia spp.	r	_
Haematomma erythromma	o	_
Lecanora spp.	o–f	r–o
Lecidea spp.	o–f	r–o
Ochrolechia frigida	r	
Omphalodiscus antarcticus	r	_
Omphalodiscus decussatus	r	_
Rhizocarpon geographicum $+R$ . superficiale	o–f	_
Usnea antarctica	o–f	r
Usnea fasciata	o	-
Xanthoria elegans	o	_
Other groups		
Deschampsia antarctica	vr	_
Prasiola crispa	o	-

Frequency assessment according to the scale used in Table IV.

This moraine is terraced in its lower region, the inner terrace of recent debris adjacent to the ice being separated by a narrow ditch from the outer and lower terrace. The inner terrace is almost wholly bare, much of it being fine muddy clay with a pH exceeding 9.0, and susceptible to frequent solifluction. A few of the larger boulders bear crusts of certain lichens, mainly species of Buellia, Caloplaca, Lecanora, Lecidea and Rhizocarpon, and occasional small colonies of Usnea antarctica. The pioneer bryophyte colonists are widely scattered on the more stable pockets of soil and are chiefly small turves or cushions of Bryum algens, B. argenteum, Ceratodon cf. grossiretis, Pottia austrogeorgica and Stegonia latifolia. In contrast, the lower terrace is evidently less disturbed by freeze-thaw cycles and has a fairly extensive although scattered flora, particularly at the seaward end where the difference between the old and new deposits is most marked. The soil here is considerably less alkaline, with a pH value of about 6.5. Small closed stands of moss occur locally on level areas or in the hollows where moisture is retained. Drepanocladus uncinatus is usually dominant, while Tortula excelsa, T. fuscoviridis, Grimmia antarctici, Polytrichum alpinum, Pohlia cruda var. imbricata and Bryum algens are generally associated and form a mixed community. Apart from the usual epipetric lichens, Cladonia chlorophaea, Leptogium puberulum and several epiphytic crustose species are sometimes present. A single tuft of Deschampsia antarctica has also become established on the north-facing slope, close to the shore. In several areas on some of the moraines, as well as on some coastal cliff ledges, accumulations of limpet shells deposited by gulls around their nests locally increase the alkalinity of the soils. Species of Tortula are frequent, particularly T. conferta.

<sup>\*</sup> Includes Buellia anisomera, B. granulosa, B. isabellina and B. subpedicellata.

#### C. ANTARCTIC HERB TUNDRA FORMATION

### 1. Grass and cushion chamaephyte sub-formation

The two native phanerogams which occur in the maritime Antarctic are very locally distributed but frequently found together (Greene and Holtom, 1971). In only a few situations do they form a closed community; more typically they occur as scattered tufts or cushions associated with various non-vascular cryptogams. The characteristic growth form of the grass, *Deschampsia antarctica*, varies from isolated, small, yellowish, almost prostrate tufts up to 10–20 cm. in diameter on dry, gravelly well-drained soils, to tall, luxuriant, rich green tufts up to 20 cm. high and coalesced to form a continuous, hummocky "sward" of several square metres, where the soil is deeper, richer and permanently moist.

Colobanthus quitensis is very much more restricted in its distribution with approximately ten sites known on Signy Island compared with about 70 for Deschampsia antarctica. It forms compact low cushions up to 25 cm. in diameter and only occasionally do these coalesce. Its most characteristic habitat is a fine clay mixed with coarser material, to give a highly inorganic, moist soil, usually on fairly steep, north-facing slopes near sea-level.

An account of the behaviour and performance of these flowering plants on Signy Island has been provided by Edwards (1972).

- a. Deschampsia antarctica-Colobanthus quitensis association (Table XVII, overleaf). Both Deschampsia antarctica and Colobanthus quitensis occupy well-drained, north-facing sheltered habitats, usually on sloping ground at low altitudes in coastal areas. Isolated tufts of Deschampsia antarctica are quite frequent amongst bryophyte and lichen communities both on the ground and on rock ledges, or to a lesser extent on almost barren, frost-disturbed stony ground. Although most abundant close to the shore, both species have been found as single plants at a distance of about 300 m. inland, D. antarctica in several localities and one small cushion of C. quitensis near the shore of the lake to the south of Stygian Cove. The highest site for the grass on Signy Island is at about 140 m. above Paal Harbour on Rusty Bluff, while the pearlwort has been recorded at about 90 m. on the south side of Port Jebsen. Both species must be tolerant of fairly high concentrations of marine salts (from sea spray) and of nitrogen and phosphorus (from bird excreta) in the soil, Deschampsia antarctica in particular being extremely luxuriant immediately below nests of snow petrels and cape pigeons and also at the margins of areas disturbed by elephant seals. Colobanthus quitensis appears to be intolerant of organic soils, yet although it has not been observed colonizing moss, as has Deschampsia antarctica, it is capable of growing amongst the grass. It seems most suited to fine clays and gravels on deep, often mobile slopes, and certainly its seeds appear to germinate most readily on this type of soil.
  - i. Deschampsia antarctica sociation (Plate VIc). Predominant species: Deschampsia antarctica and Drepanocladus uncinatus. Habitat: generally moist, fine soils on north-facing slopes not extending far inland and on rock ledges below breeding sea-bird colonies and the margins of seal-wallow areas. Stands are best developed where flushing occurs. Soil data: (base-rich wet soil, mean of seven samples), pH 7·1, moisture content 456 per cent, L.O.I. 61·2 per cent; (base-rich dry soil, mean of five samples), pH 7·0, moisture content 49 per cent, L.O.I. 9·3 per cent; (acid moist soil, mean of 15 samples), pH 5·1, moisture content 148 per cent, L.O.I. 30·9 per cent. Altitudinal range: (1-) 3-30 (-140) m.

On Signy Island only small pure stands of coalesced grass tufts occur, seldom exceeding 1 m.<sup>2</sup> in area. However, extensive, continuous, pure and mixed swards of *Deschampsia antarctica* exist on Lynch Island (formerly named "Grass Island"), about 1.6 km. north of North Point, Signy Island, in Marshall Bay on the south side of Coronation Island. Elsewhere, stands of *Deschampsia antarctica* are usually open and the grass is growing amongst a variety of bryophytes and lichens, but isolated tufts of grass in distinctly cryptogamic communities do not warrant classification in this sociation.

The only constant associates are *Drepanocladus uncinatus* and *Cephaloziella varians*, but *Brachythecium austro-salebrosum*, *Bryum algens*, *Polytrichum alpinum* and occasionally *Barbilo-phozia hatcheri*, *Marchantia berteroana*, *Tortula excelsa* and *T. fuscoviridis* may be locally abundant. Few lichens occur, although species of *Cladonia* and *Leptogium puberulum* are often present. The principal associate, *Drepanocladus uncinatus*, varies considerably in abundance, and in some stands

TABLE XVII

PERCENTAGE COVER AND PERCENTAGE FREQUENCY OF SPECIES IN SOCIATIONS

OF THE Deschampsia antarctica-Colobanthus quitensis ASSOCIATION

Species			entage frequency of species		
	With low Drepanocladus uncinatus cover Sites 159-165	With high Drepanocladus uncinatus cover Site 166	tica With high Andreaea and lichen cover Sites 167–168	Colobanthus quitensis Sites 169–170	Deschampsic antarctica— Colobanthus quitensis Sites 171–17
Colobanthus quitensis	+; 1	2; 30	1; 30	31; 100	7; 70
Deschampsia antarctica	57; 100	54; 100	26; 100	1; 30	71; 100
Mosses					
Andreaea depressinervis	<1; 1	_	34; 80		_
Andreaea regularis	<1; 3		-	-	_
Bartramia cf. patens	<1; 14	-	<1; 10	<1; 15	<1; 17
Brachythecium austro-salebrosum	7; 61	-		14; 100	7; 84
Bryum algens (short form)	6; 43	-	_	8; 90	<1; 17
Bryum argenteum	_	_	-	-	<1; 3
Calliergon cf. sarmentosum	<1; 7	_	-	_	_
Campylium sp.	3; 24	_	_	<1; 20	3; 37
Ceratodon cf. grossiretis	<1; 23	_	_	<1; 5	<1; 17
Ceratodon sp.	_	-	_	1; 15	_
Chorisodontium aciphyllum	<1; 3	<1; 10	2; 35	-	-
Dicranoweisia grimmiacea	_	-	<1; 5	-	-
Distichium cf. capillaceum	_	-	<1; 15	_	-
Distichium sp.	<1; 3	_	_	<1; 10	-
Drepanocladus cf. plicatus	1; 14	-	<del>-</del>	-	_
Drepanocladus uncinatus	15; 94	51; 100	16; 100	4; 55	4; 70
Encalypta sp.	_	_	-	<1; 10	-
Pohlia cruda var. imbricata	<1; 10	-	-	-	
Pohlia nutans	<1; 9	-	<1; 15	-	-
Polytrichum alpinum	5; 33	<1; 10	6; 50	-	2; 17
Pottia austrogeorgica	<1; 1	_	-	1; 30	<1; 3
Tortula excelsa	2; 29	-	-	5; 75	4; 50
Tortula fuscoviridis	3; 34	-	_	1; 30	_
Tortula cf. grossiretis	<1; 7	-	-	<1; 15	1; 13
Hepatics					
Barbilophozia hatcheri	1; 24	~	3; 40	-	1; 10
Cephaloziella varians	5; 61	2; 40	5; 100	8; 45	2; 37
Marchantia berteroana	<1; 19	-	_	11; 60	2; 30

TABLE XVII-continued

Species	Sociations showing percentage cover; percentage frequency of species						
	Deschampsia antarctica				Deschampsia		
	With low Drepanocladus uncinatus cover Sites 159–165	With high Drepanocladus uncinatus cover Site 166	With high Andreaea and lichen cover Sites 167–168	Colobanthus quitensis Sites 169–170	Deschampsia antarctica- Colobanthus quitensis Sites 171-173		
						Lichens	
Acarospora macrocyclos	<1; 3		_	_	_		
Buellia subpedicellata $+$ B. granulosa	<1; 1			3; 35	_		
Caloplaca sp.		-	-	<1; 20	<1; 10		
Cladonia carneola		<1; 20	2; 45	_	_		
Cladonia phyllophora	<1; 3		-	_	_		
Cladonia pocillum	<1; 1	-	·	_	_		
Cladonia spp.	2; 36	2; 30	9; 90	2; 45	2; 40		
Collema sp.	-	_	2; 40	_	_		
Cornicularia aculeata	_	_	3; 55	_	_		
? Cypheliopsis sp.		_	_	2; 25	_		
Dermatocarpon lachneum	<1; 1	_	_	_	_		
Lecania brialmontii	<1; 1	_		-	_ `		
Lecanora aspidophora	<1; 9		_	<1; 5	_		
Lecidea sp.	<1; 1	-	-	-	_		
Leptogium puberulum	<1; 26	_		7; 90	1; 37		
Ochrolechia frigida	<1; 3		2; 25	_	<1; 3		
Peltigera spuria	2; 13	_	_	_	_		
Physcia muscigena	<1; 1	-	-	_	<1; 3		
Placopsis contortuplicata	_	_	<1; 5	_	_		
Psoroma hypnorum	<1; 3	1; 20	2; 45	3; 45	<1; 3		
Sphaerophorus globosus	_	-	11; 75	_	<1; 3		
Stereocaulon alpinum	<1; 4	<1; 10	9; 100	_	<1; 6		
Usnea antarctica	_	-	4; 40	_	_		
Unidentified crustose lichens	<1; 19	_	-	_	1; 30		
Algae							
Nostoc sp.	<1; 6	-	-	<1; 15	_		
Prasiola crispa	2; 53	-	-	<1; 10	1; 47		
Substratum							
Bare ground	2; 23	_	2; 50	18; 85	2; 23		

Details of sites are given in the Appendix. Percentage cover and percentage frequency were estimated as in Table IV. it may attain a cover value of over 50 per cent when it becomes co-dominant with *Deschampsia* antarctica.

ii. Colobanthus quitensis sociation (Plate VId). Predominant species: Colobanthus quitensis. Habitat: fine, slightly base-rich mineral soils, generally on north-facing slopes. Soil data: (mean of ten samples), pH 7·1, moisture content 36 per cent, L.O.I. 6·0 per cent. Altitudinal range: 3-30 (-90) m.

There appear to be very few localities in the South Orkney Islands where *C. quitensis* grows in the absence of *D. antarctica*, and in such situations it is never abundant. The cushions occasionally coalesce but the stands are always of an open nature. The highly mineral soil amongst the *Colobanthus* plants often supports several mildly calcicolous bryophytes and lichens of which *Brachythecium austro-salebrosum*, *Bryum algens*, *Ceratodon* cf. *grossiretis*, *Drepanocladus uncinatus*, *Marchantia berteroana* and *Tortula excelsa* are usually the most frequent associates.

iii. Deschampsia antarctica-Colobanthus quitensis sociation. Predominant species: Colobanthus quitensis, Deschampsia antarctica and Drepanocladus uncinatus. Habitat: moist fine soils on north-facing slopes not extending far inland with C. quitensis most frequent on fine, base-rich mineral soils. Soil data: (mean of 15 samples), pH 5·4, moisture content 81 per cent, L.O.I. 28·5 per cent. Altitudinal range: 3-30 (-90) m.

Most stands of this community are almost identical to those of the *Deschampsia antarctica* sociation, with the exception that *Colobanthus quitensis* is associated with the grass, occasionally reaching the status of co-dominant. *C. quitensis* is most widespread and abundant on Lynch Island where both flowering plants are locally important associates in the *Andreaea*-lichen sociation as well as in communities of the *Brachythecium* cf. antarcticum-Calliergon cf. sarmentosum-Drepanocladus uncinatus association and rock ledge and crevice assemblages. The grass occurs occasionally amongst the *Polytrichum alpestre-Chorisodontium aciphyllum* communities.

The commonest associates are almost the same as those of the *Deschampsia antarctica* sociation, namely *Brachythecium austro-salebrosum*, *Bryum algens*, *Drepanocladus uncinatus* and *Cephaloziella varians*, with *Polytrichum alpinum*, *Tortula excelsa*, *Marchantia berteroana*, and species of *Cladonia* being occasionally frequent.

## VI. DEVELOPMENT OF PLANT COMMUNITIES

# 1. Availability of habitats

With more than half of Signy Island free of snow and ice during the summer months, i.e. from early December to late March, extensive areas displaying much topographic and edaphic variation are available for the development of bryophyte and lichen communities. Favourable habitats occur most commonly on headlands, raised beaches, valley floors and lakeside flats. However, in lowland areas which are disturbed by penguins or seals, or unstable due to the effects of solifluction and frost heaving, vegetation is often sparse or absent, stands of the green alga *Prasiola crispa* being an exception in the former type of habitat. Dry, wind-swept, rocky or scree habitats are generally occupied by open stands of moss cushions and various lichens, with the latter frequently predominating.

There is much evidence that the present glacierization was formerly more extensive, and even at the moment the margins of the existing ice cap fluctuate from year to year according to the severity of the season. This is illustrated by a comparatively extensive but shallow *Polytrichum alpestre-Chorisodontium aciphyllum* bank on level stony ground adjacent to the south-eastern flank of McLeod Glacier, close to Gourlay Peninsula. This bank is completely dead and blackened except for occasional re-colonizing species, and it appears that the glacier has advanced laterally and gradually killed the living moss, probably by bulk accumulation of snow and ice rather than by actual movement as there is little surface erosion, over the previously developed peat bank. When the snow line receded, the dead *P. alpestre* and *C. aciphyllum* turf became exposed and is now being slowly and sparsely re-colonized (p. 71). Further evidence of a receding snow line is seen in several hollows at higher altitudes, e.g. on Rusty Bluff, Snow Hill and Gneiss Hills where the stable substratum of small angular stones shows no patterned arrangements, and no bryophytes or lichens have become established. Vegetation is also absent on recently exposed rock surfaces adjacent to permanent ice. However, a rock outcrop or erratic which recently

appeared at an altitude of about 85 m. in McLeod Glacier between Garnet Hill and Clowes Bay possesses several species of crustose lichens as well as small moribund mats of *Drepanocladus uncinatus* in soil-filled cracks. This would suggest that the rock was colonized by vegetation before being covered by the glacier, which is now both receding and thinning.

Presumably the earliest habitats to become available for ecesis were exposed cliff faces, ledges and crevices, and various lichens were the initial colonizers. Once ground habitats became snow-free, the development of plant communities would depend principally on the stability of the substratum, assuming that moisture is in adequate supply. The various forms of freeze-thaw activity described by Holdgate and others (1967) and Chambers (1966b) which prevail in immature and unstable soils would prevent any long-term development of communities and most likely favour only a few taxa capable of rapid establishment either by spores or vegetative propagules (e.g. species of Andreaea, Bryum, Ceratodon, Pohlia, Pottia and Stegonia). Such bryophytes, and occasionally lichens, on unstable ground rarely form large stands and many may be considered as transient populations, except on the coarser, more stable material. This frequently results in the patterned ground typical of valley slopes or hillsides having sparse bryophyte and lichen growth on the larger material which flanks the barren, usually mobile clay and soil fines. Similar patterns exist where frost heaves, polygons and clay puddles are formed on level ground and these will be discussed later (p. 79).

It has been suggested above that the relative richness and variety of the flora of Signy Island should be attributed to the availability of water, particularly during the growing season, i.e. from early December to late March. But other factors also play an important role in determining the suitability for plant establishment in such a wide range of habitat types. Of these, stability of the substratum, drainage patterns, distribution of the various rock and soil types, the degree of shelter and aspect, and the proximity of bird and seal colonies, etc., all influence plant colonization and establishment. Maximum development of bryophyte and lichen stands occurs where several of these conditions are optimal.

Moisture availability depends mainly upon the regularity of precipitation and the drainage pattern of the habitats concerned. Rainfall, which is often frequent on Signy Island and the more northerly regions of the maritime Antarctic during summer, provides the vegetation and substratum with a direct supply of moisture. Similarly, snow may melt on contact with these warmer surfaces or remain in a frozen state and release moisture over a long period as melting proceeds, thus acting as a reservoir of water. The high humidity and low cloud which prevail on Signy Island are also important sources of moisture, particularly to bryophytes (Gimingham and Smith, 1971). The availability of ground water to plants is largely dependent on the drainage pattern of the substratum and is itself controlled by the topography and soil texture. Hence, depressions, valley floors, glacial outwash fans, and lake and stream margins usually receive a seasonal supply of moisture which also aids in the accumulation of fine soil in such situations. Here, as long as the habitat is relatively stable, vegetation often achieves its greatest development. Where the substratum is composed of coarse material, drainage is rapid and water is lost to the open communities of short cryptogamic vegetation which lack any form of deeply penetrating underground organs. The semi-ombrogenous peat banks formed by Polytrichum alpestre and Chorisodontium aciphyllum appear to derive much of their water during the growing season by capillary action through the tomentum of the former, from the water released by the thawing permafrost about 20-30 cm. below the moss surface (Gimingham and Smith, 1971).

Stability of the substratum is an important criterion in determining the development of communities. On Signy Island many snow-free slopes are rendered unsuitable for plant colonization due to solifluction and the formation of mobile stone and soil stripes. Habitats in level situations such as plateaux, broad valley floors and glacial outwash fans are frequently disrupted by various frost-heaving phenomena resulting in an open patchwork of vegetation. Similarly, rock surfaces may be subject to frequent frost shattering so that moss and lichen colonization may not be possible.

The distribution of the various rock and soil types also plays an important role in the composition, distribution and extent of many community types. The most striking example on Signy Island is the restriction of certain communities, comprising chiefly calcicole species, to the scattered outcrops of marble (Plate Ia) and, to a lesser extent, to those of amphibolite. Soils derived from these rocks have a high base status and support similar assemblages. Although the general mantle of detritus on the island is derived from the predominant quartz-mica-schists, glacial activity has locally produced soils of a more heterogeneous nature, composed of both schist and marble fragments and a high proportion of clay material.

Within these areas are pockets of base-rich or more acid mineral soil which is responsible for the development of a mosaic of several community types within a relatively small area. Where organic matter has been incorporated into the soil, the pH decreases and provides a more suitable substratum for certain communities with more calcifuge requirements.

The more favourable habitats for extensive plant growth derive some degree of shelter from strong winds which can cause serious damage to the surface of the vegetation as well as excessive evaporation from the plants themselves and the substratum. Studies by Gimingham and Smith (1971) on the relationship between the water balance of certain mosses of various growth forms and their habitat have shown that small cushion-forming species, although they lose their moisture slowly, are capable of retaining a relatively high proportion during periods of high saturation deficit and are consequently able to tolerate the conditions prevailing in the most exposed situations. Conversely, species with a carpet or a large, loose cushion growth form, characteristic of permanently wet areas, do not possess this property and are thus confined to the more sheltered, wetter habitats. In the former type of habitat, small cushion mosses and numerous lichens are predominant and because of their tolerance of more severe conditions, do not rely on much protection by snow cover in winter, and in fact, many such communities remain uncovered throughout the coldest months. The more extensive, bryophyte-dominated assemblages in the more sheltered situations tend to receive considerable protection in winter by snow accumulation and this also provides the vegetation with a supply of moisture early in the growing season, even before the disappearance of the snow over the plants. Most well-developed stands are situated on north-facing slopes or inland basins which receive maximum insolation and radiation absorption. In these situations the micro-climate in which the vegetation exists is considerably more favourable for growth than the ambient conditions suggest, while conditions in habitats with a more southerly aspect are likely to resemble more closely those of the surrounding air (Longton and Holdgate, 1967). Although vegetation is by no means restricted to habitats with a northerly aspect, certain communities including those formed by Polytrichum alpestre and Chorisodontium aciphyllum, many of the larger moss carpet stands and the two phanerogams are generally found only in such situations.

The influence of biotic agents is a locally important factor in restricting the distribution of vegetation and Rudmose Brown (1912a, 1928) suggested that this is one of the principal reasons for the impoverished flora of the South Orkney Islands. Although only a small proportion of the coastline or inland cliffs of Signy Island is affected by breeding colonies of sea birds or wallowing elephant seals, it is probable that the strong winds together with the sea spray and melt streams distribute certain ornithogenic salts over the entire island (Holdgate and others, 1967). Stands of vegetation close to beaches and flats occupied by large groups of moulting and wallowing seals are frequently partially destroyed by these animals or growth is prevented by their presence. Several low-lying rocky headlands are almost devoid of vegetation due to the intensive trampling and excessive enrichment of the habitat by dense populations of penguins. Only on rocks out of reach of these birds are a few species of ornithocoprophilous lichens able to exist, while in the muddy pools in and near to the colonies the green alga *Prasiola crispa* may succeed in forming quite large stands. Colonies of other sea birds on cliffs or on the ground have a more localized and less severe influence on the habitat and vegetation, which is similarly eliminated from the immediate vicinity of the nesting areas.

# 2. Availability of propagules

Observations on the means of reproduction of bryophytes and lichens on Signy Island suggest that the dissemination and subsequent establishment of many species is by vegetative propagules rather than by the production of spores. Slightly fewer than 25 per cent of the island's moss species have been found with sporophytes, and of these only Andreaea gainii, A. regularis, Grimmia antarctici, Dicranoweisia spp., Bartramia spp., Encalypta spp., Pottia austrogeorgica and Stegonia latifolia produce fruit frequently and in abundance. The performance of certain sporophyte-producing mosses has been discussed by Longton (1966), Longton and Greene (1967), and Longton (1972).

It is not yet known how viable moss spores are and to what extent the spread of fertile species depends upon them. Certainly *Pottia austrogeorgica* and *Stegonia latifolia* can colonize open clayey soil quite rapidly and effectively by means of spores. Stands of these short acrocarps, observed over a period of 18 months, increased quite considerably both in area occupied and in percentage cover when spores from the nearby parent plants germinated shortly after the ground became free of snow in spring. The

two species of *Encalypta* produce sporophytes in profusion and there can be no doubt that spore production is their principal mode of spread. However, neither form extensive closed stands but only small units of short turf.

The remaining common sporophyte-producing mosses are all widespread, short cushion-forming species typical of rock habitats belonging to the genera Andreaea, Dicranoweisia and Grimmia and, although there is no evidence that their spores are capable of germinating, it would be surprising if they were not. An attempt to germinate spores of Dicranoweisia grimmiacea, Grimmia antarctici and Pottia austrogeorgica on moist filter paper in the laboratory, proved successful only with the latter moss. Pottia austrogeorgica was readily grown from spores in samples of barren calcareous soil taken from close to stands of the parent plants (p. 37) as was Stegonia latifolia. Polytrichum alpinum is known to be fertile in only two localities on Signy Island (Longton, 1972), but on Lynch Island, P. alpinum sporophytes were seen by the author in abundance during 1965–66 when the viability of their spores was proved by successfully germinating some on moist peaty soil as reported by Longton (1972).

Bryum algens is very rarely fertile on Signy Island but in many other localities from the South Shetland Islands to Marguerite Bay it develops capsules prolifically. Similarly, several other species not fertile on Signy Island have been recorded with sporophytes from more southerly regions, e.g. Drepanocladus uncinatus, Pohlia cruda var. imbricata, Pohlia nutans and Polytrichum alpestre. Both Tortula fuscoviridis and T. cf. grossiretis produce sporophytes on Signy Island but only very rarely. Orthotrichum crassifolium is sometimes abundantly fertile on sheltered, north-facing coastal rocks.

The viability of lichen spores and the extent to which they are liberated is not known. Many encrusting genera produce large numbers of apothecia or other reproductive structures (e.g. species of Acarospora, Buellia, Caloplaca, Lecanora, Lecidea, Ochrolechia, Placopsis, Rhizocarpon, Rinodina and Verrucaria) as do species of several foliose genera (e.g. Leptogium, Parmelia and Xanthoria) and of fruticose genera (e.g. Cladonia, Himantormia and Usnea fasciata). However, many species of the above genera have been found to lack ascospores despite the production of the appropriate reproductive structures (personal communication from D. C. Lindsay).

Vegetative propagation is a common feature in Antarctic bryophytes and certain lichens, and may take several forms, although the production of specialized propagules is less frequent. Little experimental work has been carried out to study the extent of colonization by vegetative means, but it is clear that most species, and the communities they develop, arise from these rather than from spores (Steere, 1965; Rudolph, 1970).

Undoubtedly the most common form of vegetative propagation is by simple fragmentation, which in bryophytes is often the shedding of the shoot apices. In many species the actively growing apex is readily deciduous and these may be blown some distance from the parent plants. Detached shoot apices of Bryum algens, B. argenteum, Chorisodontium aciphyllum, Pohlia nutans and Polytrichum alpestre, placed on moist filter paper at room temperature, all produced abundant rhizoids within a week. In the two species of Bryum and in Pohlia nutans rhizoids were developed after only four days, and new shoots by the tenth day. These five species, and those of several other genera, e.g. Andreaea, Ceratodon, Grimmia and Tortula, frequently lose their apices as a result of trampling by birds, strong winds and snow and ice abrasion. The tiny turf-forming Bryum argenteum produces both deciduous lateral and terminal buds which may be seen scattered around the parent plants. In certain fruticose lichens fragmentation is also the principal means of dispersal, e.g. in species of Alectoria and Cladonia.

Another typical and important mode of vegetative reproduction in mosses is regeneration from old shoots. This is particularly common in *Chorisodontium aciphyllum*, *Drepanocladus uncinatus*, *Polytrichum alpestre* and *Polytrichum alpinum*, as well as in the tall forms of *Pohlia nutans* and *Bryum algens*. This revival of moribund species is the principal means of re-establishment in certain communities susceptible to frequent erosion by wind, soil movement or biotic factors, especially the sociations of the moss turf sub-formation.

No gemmiferous mosses are known from Signy Island but at least two hepatics produce abundant gemmae, namely, *Barbilophozia hatcheri* and *Marchantia berteroana*. In early spring, gemmae are often abundant on the soil where *Marchantia* is present, and these propagules have proved readily viable when germinated on moist filter paper.

Several unusual modes of vegetative propagation have been observed in other mosses. In *Didymodon gelidus* small multicellular globular bulbils occur at the base of the short shoot, where the dense mass of

rhizoids originates. These structures correspond closely to those found on a form of Barbula recurvirostra from Central Europe described by Moenkemeyer (Dixon, 1954) as B. botelligera. In Sarconeurum glaciale, which is extremely rare on Signy Island, the leaf apices are deciduous and have been observed by the author to produce both leaves and rhizoids. This has also been noted by Savicz-Ljubitzkaja and Smirnova (1961). In Stegonia latifolia the production of long club-shaped bulbils from the base of the stem is another type of structure, probably concerned with vegetative propagation. A fourth means of vegetative propagation which has been observed is the formation of leaf filaments in the fine form of Brachythecium cf. antarcticum. In this moss, from one to several marginal cells near the leaf apex develop protuberances which increase in length and become chains of cells with oblique end walls several times the length of the leaf. These leaf "protonemata" are frequently branched and have chloroplasts. Very rarely they develop a knot of cells which eventually produce buds comprising rudimentary leaves and stem. In each leaf axil on the main shoot, there is also a very short filament of one to three cells, together with a small axillary bud. These may be deciduous but rarely develop into branches. Similar, but shorter, leaf filaments are not uncommon in the temperate moss Amblystegium serpens.

Specialized vegetative structures are also common in several genera of lichens, e.g. soredia in species of Cladonia, Physcia and Usnea antarctica, and isidia in Cornicularia epiphorella and Parmelia saxatilis. On Signy Island both Deschampsia antarctica and Colobanthus quitensis produce abundant flowers, although only the latter species appears to form seed each year; the grass produces mature seed only in favourable seasons. Seedlings of C. quitensis are quite common around the parent plants, while those of D. antarctica have only occasionally been observed. However, seedlings of both plants have been seen

in profusion on Lynch Island.

#### 3. Colonization and establishment

The more stable substrata are often extensively vegetated by a wide variety of community types, depending on the nature of the habitats and the degree of exposure. Where optimum conditions prevail the establishment of mixed stands probably proceeds fairly rapidly, lichens predominating on rock surfaces and bryophytes on soil where moisture is more freely available. These communities form a characteristic patchwork of adjacent and marginally intergrading stands, uniform within themselves and frequently linked to each other by certain species common to several community types but varying considerably in their abundance from one to another. Unlike the vegetation of the less stable, stonier and frequently more exposed habitats, such communities may form extensive closed units comprising many species or even pure stands of a single bryophyte species.

The majority of plant communities on Signy Island, once established, appear to be climax units of vegetation and only occasionally is there some evidence of successional stages. There seldom appears to be effective competition for available habitats and, generally speaking, each habitat type is occupied by a specific group of bryophyte and lichen species which constitute distinct and easily recognizable communities. Thus, when a particular habitat becomes available for plant establishment it is colonized only by the species typical of a sociation favouring the conditions provided by that habitat. In most cases, one or a few species are more successful than the rest and will form the basis of the community, usually as the dominant or co-dominant components. Various sociations which lie adjacent to one another show little evidence of serious competition or the displacement of one by the other, but merely form a heterogeneous zone where the stands merge. However, the peripheral drier areas of swamp communities, dominated principally by species of Calliergon and Drepanocladus, may be invaded by cushions or turves of mosses such as Andreaea depressinervis, Chorisodontium aciphyllum and Polytrichum alpinum, which may in time produce a mixed bryophyte community. Chorisodontium aciphyllum may also invade stands of mixed Andreaea-lichen sociations in the form of tall turf-like cushions. Elsewhere, there are areas of intermixed communities where the substratum is very variable and numerous habitat types occur. The north-facing slope behind the British Antarctic Survey station in Borge Bay supports about ten sociations in a heterogeneous, closed bryophyte-dominated expanse of vegetation, while localities with bands of marble traversing the terrain may also give rise to several markedly different, intermixed sociations.

## 4. Distribution of communities

A large number of plant communities has been described from Signy Island but of these only four associations are extensive and widespread. These are the *Andreaea-Usnea* association, *Caloplaca-*

Xanthoria association, Polytrichum alpestre-Chorisodontium aciphyllum association and Brachythecium cf. antarcticum-Calliergon cf. sarmentosum-Drepanocladus uncinatus association. The first association accounts for approximately two-thirds of the island's vegetation, ranging from near sea-level to about 280 m. and favouring dry, rocky exposed situations. Bryophytes in most of these communities are predominant only in moist sheltered habitats where there is some soil. At higher altitudes, snow-free ground is colonized almost entirely by open stands of lichen-dominated communities in which bryophytes are generally sparse. The openness of these stands is due to absence of soil and a coarse substratum together with the freeze-thaw action, long periods of snow cover and strong winds. Rock outcrops, boulder fields, cliff faces, etc., are vegetated principally by lichens, although bryophytes dominate wet rock surfaces at low altitudes. Several sociations occur within this association and all may be considered as components of a continuum of variation ranging from pure mats of coalesced cushions of species of Andreaea in sheltered moist hollows, to communities of fruticose lichens on dry exposed rock and gravel surfaces. However, mixed stands of species of Andreaea and various lichens are most common on fairly low-lying ground, while at higher altitudes species of Usnea and Himantormia are predominant. The structurally similar Tortula-Grimmia antarctici association is restricted to base-rich soils in the vicinity of marble and amphibolite outcrops, usually at low altitudes.

Banks of Polytrichum alpestre and Chorisodontium aciphyllum show distinct preference for north-facing slopes, with the Polytrichum usually predominant on the steeper and better drained areas and the Chorisodontium in the moister habitats. The larger banks are generally below about 80 m., although smaller ones extend considerably higher. In several localities on Signy Island extensive banks of peat have developed on steep, well-drained rocky slopes, e.g. above Paal Harbour, Factory Cove, Observation Bluff, and North Point. Similar but shallower banks are formed locally over level or gently sloping ground, particularly in the area between Lenton Point and Gourlay Peninsula. However, the most extensive banks are the isolated peat "islands" on the north-west coast of the island, and on Moe Island, where deposits of loose fibrous peat up to almost 2 m. in depth cover large areas on gentle slopes separated by swampy ground with moss carpet communities. Many of these banks are formed solely by Chorisodontium aciphyllum, but most become superficially colonized by fruticose and crustose lichens.

Extensive swamp habitats are largely restricted to coastal lowlands, lakeside flats and occasionally valley floors. Such permanently wet areas, frequently flooded by melt water, are dominated by species of carpet-forming mosses of the genera *Brachythecium*, *Calliergon* and *Drepanocladus* which locally form very large stands. Where the ground slopes and is dissected by melt streams, these moss-carpet communities are limited in extent to the wet marginal areas which receive a continuous supply of water. Such situations, particularly where there is some degree of flushing, often support deep hummocks of species of *Brachythecium*, *Bryum* and *Tortula* with a large cushion growth form. A shallow waterlogged, and hence reducing, peat is frequently formed by dead horizontally lying moss shoots. Lichens are seldom present, except at the margins of the swamps where the habitat becomes drier. At higher altitudes the extent of the wet areas decreases considerably, and these are usually restricted to local hollows where accumulated soil may hold melt water for short periods and support small stands of *Drepanocladus uncinatus* and *Calliergon* cf. sarmentosum.

The final major association is that in which species of Caloplaca and Xanthoria prevail. The several sociations included here may be considered as units in a small-scale continuum of variation. The association is essentially one of low-lying coastal rocks in which crustose lichens predominate and bryophytes are scarce or absent. With increase in altitude, fruticose lichens become more abundant and there may be a gradation into communities dominated by species of Usnea and Himantormia lugubris with associated bryophytes. This association is typical of low altitudes but large patches of orange and yellow species of Caloplaca and Xanthoria extend to about 155 m. or higher in some localities. There are often numerous associated species, many of which belong to the genera Buellia and Lecidea.

The two angiosperms, although restricted in ecological amplitude, are by no means uncommon on Signy Island. Colobanthus quitensis is very locally distributed on suitably sheltered, north-facing slopes with a fine clay or gravel soil, seldom far inland. Deschampsia antarctica, on the other hand, is considerably more frequent, occurring in a large number of localities around the coast, but also requiring some degree of shelter, moisture and a northerly aspect. It occupies a wider range of habitats than C. quitensis, growing on organic or inorganic, wet or relatively dry soils and not infrequently occupying rock ledges on which sea birds nest. The grass rarely forms extensive swards of coalesced tufts, although on Lynch Island

there are large almost pure stands. Both plants usually occur as components of bryophyte communities, in which *Drepanocladus uncinatus* is predominant.

#### 5. Influence of erosion

Erosion affects most plant associations on Signy Island to varying degrees, and several environmental factors may be responsible.

a. Frost action. The effects of solifluction and frost heaving are regarded as the principal causal factor of pattern in several community types, especially in the Andreaea-Usnea and Tortula-Grimmia antarctici associations. On level stony ground, closed stands of Andreaea spp., Grimmia antarctici or mixed Andreaea-lichen communities are frequently disrupted by frost heaves which usually produce circular or polygonal puddles of muddy clay with coarse material towards the periphery (Plates IIa and IIIc). Such features exist for very long periods, and being unstable, are seldom colonized, so that only the marginal vegetation is affected, although occasional newly-formed frost boils will break up the living plant cover. Frost heaving may also cause stones or boulders to disrupt the shallower banks of Polytrichum alpestre and Chorisodontium aciphyllum and the resulting exposed stones or soil may become sparsely colonized by species of Andreaea and Dicranoweisia.

Solifluction causes considerably more damage to stands of vegetation on sloping ground, but as with frost heaving, the fine clay "rivers" between stone stripes are not colonized, and only marginal vegetation may be affected. Such stone-stripe assemblages are usually of the Andreaea-Usnea association (Plate IIIb). Stands of Calliergon cf. sarmentosum. Drepanocladus uncinatus and occasionally a species of Campylium on wet, gravelly or muddy slopes may be buckled and puckered into a rippled carpet due to the movement of the underlying substratum to which the moss is only loosely attached. These species, and also carpets and cushions of Bryum algens, Brachythecium cf. antarcticum, B. austro-salebrosum, and sometimes species of Andreaea may become covered by mud and debris washed down by melt water during the spring thaw or by infrequent heavy summer rain. The extent of damage to vegetation depends on the volume of mobile material, and in extreme cases large carpets of moss may be torn up and washed down-hill, while less severe conditions may only bury the moss under mud, through which new shoots can readily penetrate, if the alluvium is not too deep. The banks of runnels are sometimes eroded and marginal bands of vegetation may again be torn up or buried.

Polytrichum alpestre-Chorisodontium aciphyllum banks on steep slopes, inclined at 30-40° and locally at over 70°, undergo slumping, probably due to solifluction of the upper unfrozen peat layers over the permafrost, resulting in a series of broad steps and rises. The crests of these ramps usually become encrusted with lichens and are the sites of local cracking of the moss surface. In places the moss turf is opened up so much to wind and water erosion that substantial areas are removed.

b. Wind. Wind erosion is the principal agent in the destruction of large parts of the deeper peat banks, particularly on the west coasts of Signy and Moe Islands and also in the Robertson Islands off the south-east corner of Coronation Island. This erosion is initiated by the break-up and ultimate removal of the lichen-encrusted surface which develops on the more exposed parts of the banks (Plate Va). These areas receive little or no protective snow cover in winter, and wind and frost action lead to puckering of the bare peat (Plate Vb). The eroded faces of the deeper banks result to some extent from wind action, but are probably caused largely by melting snow and ice in spring (Plate IVa). Here and there vertical faces are cut back into alcoves, the floors of which accumulate the eroded peat debris.

Erosion on a smaller scale is seen on the ripple systems formed on the surface of Chorisodontium aciphyllum banks (Plate IVd). It is suggested that, because of air turbulance over such an undulating surface, the abrasive action of wind-blown snow and ice tends to kill the living moss on the leeward side of these ridges, by preventing the accumulation of a protective layer of snow in winter. Once the surface is killed and becomes encrusted with lichens, erosion appears to set in, while the windward side of the ripples remain healthy, since it receives a slight covering of snow. However, the converse has been observed on deep mats composed of species of Andreaea and Drepanocladus uncinatus. In stands of these species, where the surface is only slightly undulating, representing the coalescence of cushions or hummocks, the windward side tends to be killed by wind and drifting snow. The result is similar to that in Racomitrium lanuginosum heath in the Scottish Highlands, although less pronounced. In the

case of stands of species of *Andreaea* and other cushion- and turf-forming mosses, the dead moss surface frequently becomes colonized by species of crustose lichens belonging to *Buellia*, *Caloplaca*, *Lecidea*, *Ochrolechia* and *Pannaria*.

c. Snow and ice. The most outstanding example of this kind of erosion on Signy Island has already been mentioned, i.e. the large expanse of a shallow Polytrichum alpestre-Chorisodontium aciphyllum bank, on gently sloping stony ground by McLeod Glacier, which has been killed by prolonged snow and ice cover, during a period of glacial advance (p. 64). Following the recent retreat of the ice, the dead surface of the peat is locally being re-colonized by Brachythecium cf. antarcticum, Calliergon cf. sarmentosum, Chorisodontium aciphyllum, Drepanocladus uncinatus, Pohlia nutans and Polytrichum alpestre. It is not known how long snow cover must persist to kill vegetation, but it has been shown that samples of Chorisodontium aciphyllum, Drepanocladus uncinatus, Pohlia nutans and a species of Cephaloziella survived deep frozen in the dark, at -15° C for 3 yr. and recommenced growth on thawing (Longton and Holdgate, 1967). The vegetation on certain slopes and hollows remains covered by deep snowdrifts, following a severe winter or where snow accumulation has been excessive, but such patches do not often persist more than one or two years and most bryophytes and lichens appear to survive these short periods of burial.

Considerable damage is done to rock face and ledge flora by wind-blown ice particles (Lamb, 1968) as well as melting snow and ice in early spring. Slabs of falling snow and ice or running water dislodge from rock surfaces large numbers of moss cushions composed of species of Andreaea, Ceratodon, Dicranoweisia, Grimmia, Pohlia, and species of fruticose lichens of the genera Himantormia, Omphalodiscus and Usnea. Large turves of Chorisodontium aciphyllum, Polytrichum alpestre and P. alpinum, with associated species of lichens such as Cladonia spp. and Sphaerophorus globosus, may also be torn away. Similarly, slabs of rock on which vegetation is growing may break away from cliffs by frost shattering. Following a day of high temperatures or brilliant sunshine, the ground below a cliff may be littered with bryophytes and lichens, and during periods of spring thaw accompanied by high winds, such fragments of moss and lichen may be transported considerable distances. The author has found detached entire plants of Usnea antarctica and U. fasciata on Powell Island up to 1.6 km. from the nearest exposed rock, but fragments can probably be blown much farther. Below many well-vegetated cliffs there is frequently a rather heterogeneous assemblage of plants comprising species derived in this way from the rock above.

The tall robust form of *Bryum algens*, occurring in basic flushes as deep cushions, is sometimes locally killed at its surface. This appears to be caused by ice forming during the summer, and because of the structure of the moss shoots, which are erect with large spreading leaves, small pools of water are able to lie on the surface without soaking away. These large globules may freeze, and this is thought to kill the embedded shoot apices which later break off and leave a patch of brown moribund moss. If the dead area is not extensive, the moss usually regenerates within a short time, but in more extreme cases further erosion may take place. *Brachythecium austro-salebrosum* and *Drepanocladus uncinatus* are occasionally affected in this way also.

Parts of Colobanthus quitensis cushions are frequently dead, and it has been noticed that these moribund patches are exposed during periods of summer snowfall when temperatures may be well below 0° C. These parts receive no protection from ice and wind, and it is suggested that while the plants are actively growing during the summer months, the shoots cannot tolerate long periods of freezing temperatures. The dead parts usually become detached from the cushion and may eventually be replaced by new shoots or even seedlings of C. quitensis, or less commonly by one or more species of moss, e.g. of Bryum, Ceratodon or Pohlia.

d. Biotic agents. Of the wildlife on Signy Island, elephant seals cause the greatest damage to vegetation. During the summer months they haul out in large numbers on beaches and low-lying coastal areas to moult and wallow in damp muddy areas. Some of these areas are vegetated to varying extents, usually by stands of moss carpet, turf or hummock communities. Damage by elephant seals is particularly evident in the coastal area between Elephant Flats and Stygian Cove on the east side of the island where the surface of the vegetation has been broken and the underlying peaty layer has become mingled with faeces, urine, drainage water and hair to produce a highly organic, nitrogenous anaerobic mud. Wallowing seals frequently scoop out hollows 50 cm. deep amongst stands of moss, which later become filled with

melt water and may result in a series of small oval pools of muddy stagnant water (Plate VIa). In this way, large areas of *Drepanocladus uncinatus*, *Calliergon* cf. sarmentosum, Brachythecium spp. and Polytrichum alpinum are broken up and commonly killed.

Several extensive coastal areas are occupied by large dense colonies of penguins and other sea birds. In such localities the biotic influence is again deleterious to all but a few species of plants, much of these areas being devoid of any vegetation. However, horizontal rock surfaces which are not usually trampled by birds may support communities of the *Caloplaca-Xanthoria* association, while wet muddy depressions are often colonized by *Prasiola crispa*. This alga seems to tolerate excessive trampling and temporary submergence in pools of highly nitrogeneous water which also contains high concentrations of marine salts. Bryophytes are usually restricted to local cushions or small stands in situations inaccessible to the penguins.

Rocky knolls occupied by giant petrels are frequently fringed by a partially eroded zone of crustose lichens colonizing Ceratodon cf. grossiretis, Drepanocladus uncinatus, Pohlia nutans and Polytrichum alpinum. This community often merges with a Polytrichum alpestre-Chorisodontium aciphyllum bank. The breeding area on the crest of the knolls is almost barren because of the accumulation of pebbles used as nesting material, and the trampling and excreta. Since the birds usually need to run a considerable distance before becoming airborne, there are places where tracts of moss and lichen-encrusted peat are used as "runways", and the excessive trampling tends to kill the vegetation which in time undergoes erosion.

Skuas (Catharacta skua lonbergii) usually nest on Polytrichum-Chorisodontium banks and pluck tufts of moss around their nests. Their nests consist of depressions scooped out of the moss surface, and sometimes several of these are made by a single pair of birds in one breeding season, although only one nest is occupied. Sheathbills (Chionis alba) have also been observed to pull up tufts of moss during territorial display. These moss banks, particularly on steep slopes, are the preferred nesting sites for colonies of dove prions (Pachyptila desolata), and locally the intensive tunnelling by these birds may accelerate slumping and lead to break-away and erosion of the peat.

In recent years on Signy Island the human element has become an increasingly destructive agent of erosion to vegetation. Some erosion around the British Antarctic Survey station is inevitable, and has been responsible for the removal of a fairly large area of vegetation. Trampling can be extremely destructive to deep, loose turves and carpets of moss, particularly to species of *Bryum*, *Brachythecium*, *Chorisodontium*, *Tortula*, etc., and footmarks may persist in the moss for over a year. The cracks and slumping caused by human activities may lead to further erosion by wind and frost action.

# VII. PATTERN WITHIN PLANT COMMUNITIES

The widespread non-random arrangement of plants in bryophyte and lichen communities on Signy Island, and elsewhere in the maritime Antarctic, is often more marked and more easily accounted for than that exhibited by complex stands of flowering plants in most other parts of the world. These cryptogamic communities seldom appear to be affected by competition from adjacent communities or the occurrence and performance of colonies of different ages of many individual species. This tends to produce various forms of small-scale pattern similar to those discussed by Kershaw (1964), which can be correlated with several interacting habitat factors such as moisture availability, base status and micro-topography. However, other critical environmental factors such as nutrient concentrations or the carbon/nitrogen ratio of the substratum have little apparent effect on community composition in this type of vegetation.

Pattern may result, in some rare instances, from intrinsic features of particular species. On Signy Island such morphological pattern is virtually restricted to one group of mosses, namely the Polytrichaceae. In some members of this family an underground stem system is well developed and colonies of these mosses tend to form circular stands of aerial shoots, due to the underground stems radiating outwards from a common centre. However, these circular colonies are infrequent on Signy Island and are best developed on the fairly dry, porous gravelly or ashy soils of the South Shetland and South Sandwich Islands (Longton, 1967). Invasion of stands by one or more species characteristic of another stand is rare on Signy Island, but examples of this type of sociological pattern are demonstrated in certain com-

munities, e.g. where hummocks of turf-forming mosses require the presence of carpet- or cushion-forming species on which to become established.

In certain situations the distribution of species or communities may be arranged in zones, although these do not always have distinct boundaries. Such zones result from gradients in environmental factors, particularly exposure, and the moisture regime of the substratum. In a few instances the zoned pattern of communities appears to be other than static and may represent seral phases in a succession. There is also evidence of occasional small-scale cyclical processes occurring in certain stands of vegetation or more frequently in individual species.

In almost all other examples, pattern within cryptogamic communities develops in response to gradients in one or more environmental factors and results in contagious or random variation in the density and spatial arrangement of the species concerned.

On Signy Island, environmental pattern is a common feature of the vegetation, being caused by a number of interacting factors, notably availability of moisture and drainage patterns, soil pH and base status, stability, cryopedogenic processes, texture of the substratum, exposure to wind and the degree of winter snow accumulation. Each of these is controlled to varying degrees by changes in microtopography.

Thus the vegatation of Signy Island exhibits four prominent types of pattern, namely, morphological, sociological, zonal and environmental pattern, although only the latter is well represented. Because of the wide ecological amplitude and abundance of several species, and the physiognomic and floristic similarity of many communities, much of the vegetation of this island constitutes a number of small-scale continua incorporating a mosaic of community types which exhibit various forms of pattern related to environmental fluctuations.

## 1. Individual species

On Signy Island morphological pattern, i.e. that due to the growth form of a species, is commonly only exhibited by members of the Polytrichaceae. The best examples are given by *Polytrichum alpinum*, but some form of pattern may be shown by *Polytrichum alpestre*, *P. juniperinum* and *Psilopilum antarcticum*.

In the *Polytrichum alpinum-Drepanocladus uncinatus* sociation, typical of coastal lowland areas disturbed locally by biotic influences, *P. alpinum* frequently produces circular stands up to 1 m. in diameter. The periphery of several of these stands was marked in March 1966 and re-examined exactly one year later; it was found that new aerial shoots had appeared in many places up to 1 cm. outside the former marked margin of the colony, indicating a fairly rapid rate of spread. Some idea of the density of these colonies may be judged from the following observations made on two colonies of this species, which were excavated from dry ashy soil on Deception Island in the South Shetland Islands. One colony measured 27.5 cm. by 26.5 cm. and comprised a total of 80 leafy aerial shoots and at least 56 immature shoots still below the surface, all 136 shoots arising from a single subterranean system of radiating stems. Another colony 12 cm. by 15 cm., again consisting of a single plant, had 44 aerial and 30 underground shoots.

Many of the older larger *P. alpinum* circles give rise to cyclical changes. In situations where other species are infrequent, *Polytrichum alpinum* develops pure, tall circular stands, occasionally exceeding 5 cm. in height. As the colony expands, the stems in the central oldest portion become brownish, and gradually turn a blackish colour before disappearing and leaving the central area bare. However, by this stage, as the moss becomes moribund, other species begin to colonize the peaty soil amongst the *Polytrichum* shoots, *Ceratodon* cf. *grossiretis*, *Drepanocladus uncinatus*, *Pohlia nutans* and *Cephaloziella varians* being frequent associates. As the stand becomes more open and more soil is revealed, various yellowish, grey and white sterile crustose lichens colonize the decaying *Polytrichum* turf and debris. Some of the more advanced circles may eventually be re-colonized by shoots of *P. alpinum*, which slowly displace the encrusting lichens and the associated bryophytes.

Many of the larger *Polytrichum alpinum* circles appear to remain static once the central part is dead, consisting of only a ring of tall, living shoots with shorter brown or black dead shoots immediately inside. Fig. 6 illustrates a typical mature *P. alpinum* circle.

Polytrichum alpestre has a mode of growth rather different from that of P. alpinum, in that it does not have a well-developed underground stem system radiating from a central point. Instead it is capable of indeterminate vertical growth, which leads to the formation of deep peat banks. Nevertheless,

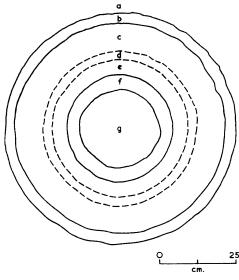


FIGURE 6

Diagram of a circular colony of *Polytrichum alpinum* exhibiting several stages in a cyclical morphological pattern, at an altitude of 5 m. above the east shore of Factory Cove.

- (a) Area outside the *Polytrichum* colony, usually with *Ceratodon* cf. grossiretis, Cephaloziella varians, Drepanocladus uncinatus, Pohlia nutans and numerous species of crustose lichens.
- (b) Scattered young shoots of the Polytrichum arising from the underground stem system.
- (c) Tall (1-5 cm.), living Polytrichum.
- (d) Dying, brown Polytrichum.
- (e) Moribund, black Polytrichum.
- (f) Thin layer of decaying *Polytrichum* peat, usually colonized by *Ceratodon* cf. grossiretis, *Cephaloziella varians*, *Drepanocladus uncinatus*, *Pohlia nutans* and several species of crustose lichens.
- (g) Peaty soil often heavily encrusted with lichens, but also with occasional shoots of Cephaloziella varians, Pohlia nutans and regenerating Polytrichum.

P. alpestre occasionally forms circular stands amongst Chorisodontium aciphyllum on shallow peat banks. It is not certain if these circular stands are derived entirely from a single plant, as with P. alpinum circles. in the few examples seen, the stems were short and had up to 20 per cent associated Chorisodontium aciphyllum. These stands do not show any cyclical change and the central parts do not appear to die out, although the more mature central areas may sometimes have a few thalli of fruticose lichens growing as epiphytes on their surface. On dry stony ground P. alpestre tends to produce tall dome-shaped hummocks showing little outward spread.

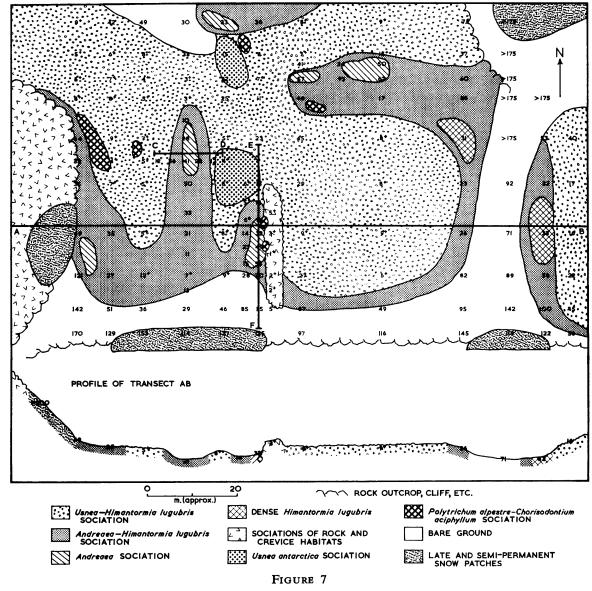
Polytrichum juniperinum is comparatively rare on Signy Island, growing on slightly basic, dry gravelly soils and not positively associated with any particular species. However, being similar in growth form to P. alpinum, it also produces small circular colonies of from one to a few plants, but there is no evidence of cyclical change. On the dry, ashy volcanic soils on Deception Island and other islands in the South Shetland Islands, P. juniperinum and P. piliferum, the latter a species so far unknown in the South Orkney Islands, produces short open circles over 1 m. in diameter with a few associated bryophytes and lichens. Psilopilum antarcticum, a rare moss on Signy and Deception Islands, forms small circular stands as a result of a radiating underground stem system. Again, however, there is no evidence of cyclical changes occurring within a colony.

Morphological pattern is not normally evident in lichens, although a form of pattern approaching this occurs in the often circular colonies of certain crustose and foliose species which exhibit a small-scale cyclical process. As the colony increases in diameter its central part dies out, leaving a complete or broken ring representing the periphery of the thallus. This central area may eventually become colonized by species of crustose lichens or less commonly by fruticose lichens or even small cushion mosses on the crust of organic material provided by the original lichen. Species in which such a cyclical pattern is visible include *Parmelia saxatilis*, *Placopsis contortuplicata*, *Xanthoria elegans* and species of *Buellia*, *Caloplaca* and *Lecidea*.

### 2. Andreaea-Usnea association

Many examples of environmental pattern in the Andreaea-Usnea association resulting from gradients in exposure may be seen on Signy Island. These gradients act principally through the accumulation and persistence of winter snow and the degree of moisture availability, both of which can be directly related to micro-topography. Substratum stability and soil accumulation are also important factors and distinct topographic patterns may be observed around areas disturbed by frost heaving.

An example of the type of pattern caused by wind exposure and snow lie on the distribution of several sociations of the Andreaea-Usnea association is given in Fig. 7, which depicts a fairly level area on the exposed plateau west-north-west of Observation Bluff, behind the British Antarctic Survey station, at an altitude of about 100 m. The substratum consisted largely of coarse stony material on which an Usnea-Himantormia lugubris sociation was predominant; it also included pockets of soil where species of Andreaea and occasionally other mosses had become established. The south-west area was relatively sheltered by the bluff south of Factory Cove and supported sociations of rock and crevice habitats,



Distribution of community types on a wind-swept plateau, at an altitude of c. 100 m., c. 250 m. west-north-west of Observation Bluff. Figures give snow depth (cm.) on 9 September 1966; a + denotes ice, usually lying as a thin crust on the surface of the fruticose lichens. Transects C-D and E-F are illustrated in Figs. 8 and 9, respectively.

while in the shallow hollows there was an accumulation of finer material with small almost pure stands of species of Andreaea or mixed stands of Andreaea and lichens in which Polytrichum alpinum and Himantormia lugubris were frequent associates. The cover was locally broken by frost heaving, and near the east side of the plateau was an approximately north to south running, barren wind gap, the flanks of which retain snow well into summer, connecting two permanent or semi-permanent snow banks at the northern and southern ends. A similar strip of vegetation-free ground ran along the south perimeter of the plateau, adjacent to the semi-permanent snow patches and the cornice at the head of the Paal Harbour cliffs.

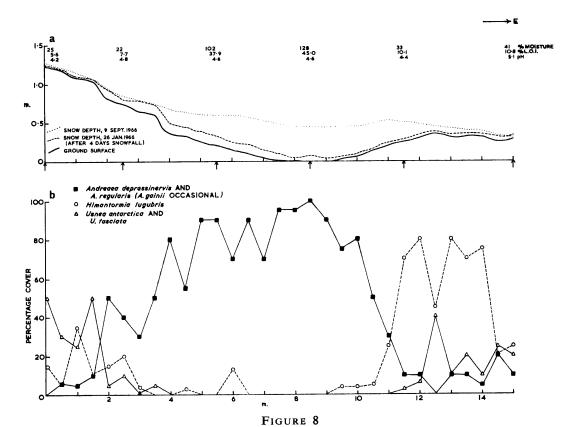
A sequence of stages could be clearly traced from these semi-permanent snow patches, northwards along the unstable and fairly exposed barren zone to an increasingly more stable and mature substratum on which cushions of species of *Andreaea* gave progressively more cover. An exposed, slightly raised region of fine, dry sandy debris susceptible to frost action was dominated by *Usnea antarctica*, while stony areas, very slightly sheltered by the local micro-topography, were dominated almost solely by *Himantormia lugubris*. The highest point on the plateau was a small north to south running schist outcrop, about 1-2 m. above the surrounding terrain, bearing sociations of rock and crevice habitats, mainly of the *Usnea-Omphalodiscus-Himantormia lugubris* sociation. Elsewhere, where there was maximum shelter, small mixed turves of *Polytrichum alpestre* and *Chorisodontium aciphyllum* occurred.

In winter, much of the plateau was blown free of snow although a thin crust of ice, 1–5 cm. thick, sometimes formed over the surface of the lichens and the surrounding stony material. The distribution of ice and snow cover measured late in the winter of 1966 is shown in Fig. 7, and it can be seen that in hollows dominated by species of *Andreaea* snow accumulated to depths of up to 1 m. It was also observed that following summer snowfalls these hollows were lightly covered for short periods. The *Himantormia lugubris* dominant communities also received a fairly deep covering of snow, while the *Usnea antarctica* stands had only a very thin coating of ice. Those areas with little or no snow become exposed very early in spring, in some cases as much as 2 months before the hollows with the Andreaeas were clear.

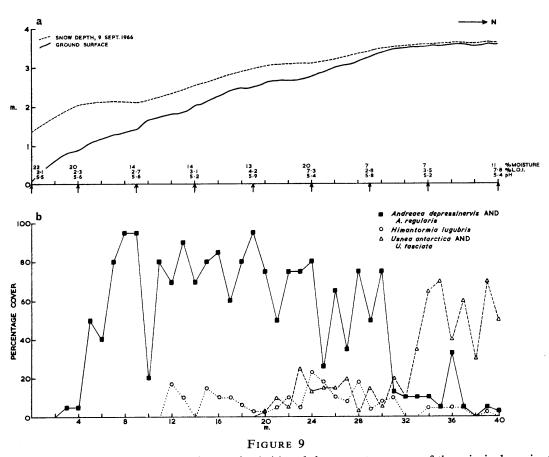
A series of quadrats was laid along a transect indicated by line C-D in Fig. 7, through one of the hollows dominated by species of Andreaea below the rocky slope on the west side of the plateau. The data recorded (Fig. 8) show the transition from the Usnea-Himantormia lugubris sociation on the slightly raised, stony, more exposed ground to the coalesced cushions of Andreaea depressinervis and A. regularis which predominated in the moister, more sheltered hollow where there was an appreciable accumulation of soil. Measurements of snow depth in January, after 4 days of intermittent snow showers, showed that the Andreaeas were readily covered with up to 15 cm. of snow, whereas the Usnea-Himantormia lugubris community had only 1-3 cm. cover. In winter, after 5 months of snow accumulation, the hollow was filled to almost the level of the surrounding raised ground. Snow depth here was about 50 cm., whereas the wind-swept lichen-dominated ground often had only about 1-5 cm. of ice in which the fruticose lichen tufts were embedded. The moisture content of the soil in the depression was considerably higher than that amongst the stones of the higher ground.

A second transect, indicated by line E-F in Fig. 7 was laid from a permanent snow patch on the south side of the plateau, through the adjacent barren stony soil, the colonizing cushions of species of Andreaea, the mature Andreaea and Andreaea-lichen sociations, and into the Usnea antarctica dominated stand on the higher, more exposed ground to the north (Fig. 9). The vertical rise along this 40 m. transect was about 3.5 m. The first colonists of the bare ground, at about 4 m. beyond the limits of the permanent snow patch included a few circular encrustations of lichens on some of the stones, and scattered small cushions of Andreaea regularis. With increasing distance from the snow patch, the Andreaea regularis increased in abundance with A. depressinervis becoming an important associate higher up the slope. As exposure to wind increased Himantormia lugubris became prominent but gradually gave way to a predominance of species of Usnea.

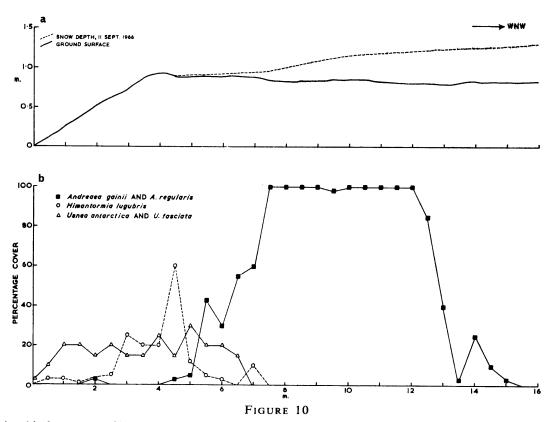
With increasing shelter, soil accumulation and moisture, species of Andreaea may form pure stands of variable size. Fig. 10 illustrates the change in vegetation from close to the crest of a high exposed cliff with a thin stony substratum to the sheltered depression where some soil accumulation had taken place. The exposed cliff top was colonized by an Usnea antarctica sociation on a substratum of fine gravelly material, and by an Usnea-Himantormia lugubris sociation on coarser stones immediately adjacent to it. Beyond the exposed steep slope these sociations merged into an almost pure, closed stand of tall species of Andreaea which occurred on the more or less level floor of the shallow basin which was kept moist



The relationship between profile, soil data and snow depth (a) and the percentage cover of the principal species (b) along the line C-D shown in Fig. 7. The arrows indicate the positions on the profile where soil data were obtained.



The relationship between profile, soil data and snow depth (a) and the percentage cover of the principal species (b) along the line E-F shown in Fig. 7. The arrows indicate the positions on the profile where soil data were obtained.



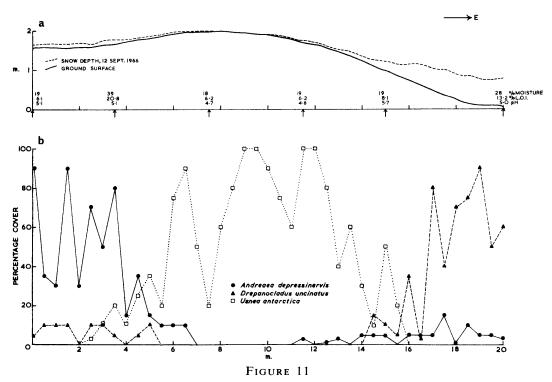
The relationship between profile and winter snow depth (a) and the percentage cover of the principal species (b) along a transcet from the edge of a steep wind-swept slope to a late snow patch, at an altitude of c. 100 m., above the north-west corner of Paal Harbour.

by percolating melt water from a permanent snow patch on the steep stony slope some distance away. The central part of this depression, where the substratum was wettest, was dominated by A. gainii with associated foliose hepatics, and as the habitat became slightly drier towards the margins of the hollow, A. regularis assumed dominance. Both species approached a short turf growth form in which the upper parts of the stems formed a vertical branching system of parallel shoots arising from a more or less horizontal mat of dead material. This closed stand of moss had a fairly abrupt margin on the side farthest from the exposed cliff top corresponding exactly with the limit of the finer material, and consequently of increased moisture. Beyond this was a zone of dry stones with numerous, small scattered pioneer cushions of A. regularis decreasing in number away from the margin of the parent stand (Plate IIIa). Over 3 m. from this margin the stony ground was barren and represented an area which, until late into summer, was covered by a down-hill extension of the neighbouring snow patch. This barren zone may in some years remain covered by snow and hence colonization of such a habitat must proceed very slowly. It is probable that the margins of the snow patch are receding gradually and that the small group of Andreaea cushions adjacent to the main population represents the first area to become exposed and hence available for colonization.

Elsewhere, in exposed situations where the substratum consists of fine gravelly or sandy mineral soil, a similar type of environmental pattern is frequently encountered. In such localities an *Usnea antarctica* sociation often predominates in the most wind-swept habitats and usually intergrades with an *Andreaea*-lichen sociation or stands dominated by other bryophytes where there is some shelter and some degree of winter snow cover.

In many places on Signy Island, particularly near the coast, there are low knolls with a thin mantle of sandy and gravelly acid soil which frequently support dense stands of *Usnea antarctica*. As with most habitats in which members of the Usneaceae occur, snow does not lie for long periods, although a thin crust of ice is quite frequent and may persist for much of the winter. As soon as some shelter is afforded below the summit of these knolls, *U. antarctica* usually intergrades with an *Andreaea*—lichen community.

Parts of the slope, liable to accumulate deep drifts of snow which remain late into spring, as where the ground levels out at the foot of the knoll, may be colonized by species of a *Polytrichum alpinum-Drepanocladus uncinatus* sociation. In these places the soil is likely to be damper than on the slopes and crest of the hillock, and *Chorisodontium aciphyllum* and *Drepanocladus uncinatus* may become prominent. Fig. 11 records the change in the cover of the predominant species from an *Andreaea*—lichen sociation developed on the lee side of such a knoll through an *Usnea antarctica* sociation dominating the crest into a *Polytrichum alpinum—Drepanocladus uncinatus* sociation on the short steep slope on the east-facing windward side. In the former part of this transect winter snow accumulated to a depth of up to 15 cm., and at the other end to over 1 m., while the exposed summit was blown free. The substratum throughout the transect was of a stony nature with abundant pockets of dry sandy soil.

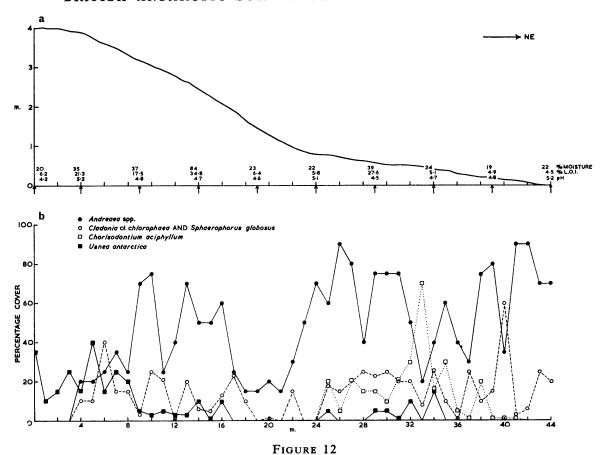


The relationship between profile, soil data and winter snow cover (a) and the percentage cover of the principal species (b) along a transect across a low knoll, at an altitude of c. 7 m., close to Mooring Point. The arrows indicate the positions on the profile where soil data were obtained.

A similar trend is shown by Fig. 12, which illustrates the transition from the crest of an *Usnea antarctica* dominated knoll at a slightly higher altitude, through an *Andreaea*-lichen community, into a prominent north-east-facing zone of *Chorisodontium aciphyllum* colonizing *Andreaea depressinervis* where the slope levels out and becomes moister due to increased snow lie. However, when the soils were examined in mid-summer, they showed little difference in moisture content, although the latter increased significantly where there was a high organic content. Values for pH throughout the transect were fairly low.

One of the most prominent environmental patterns is that associated with instability of the substratum. Several sociations in the *Andreaea-Usnea* association frequently exhibit a characteristic mosaic on exposed flat ground where there is a comparatively deep mantle of detritus and regular disturbance by various forms of frost heaving which produce a series of patterns from stone and soil polygons to fine clay puddles. Where coarser material prevails, the debris is thrown into hummocks and hollows with a vertical range of about 0.3 m. The structure and form of such areas has been investigated in detail by Chambers (1966a, b, 1967, 1970).

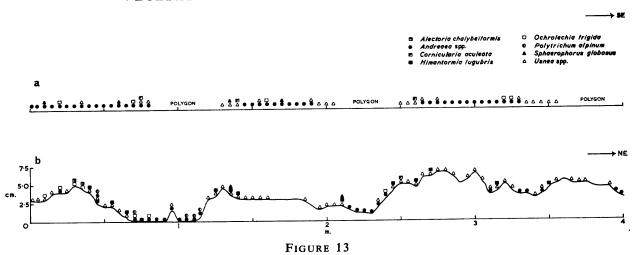
Frost boils and clay puddles are semi-permanent features and because of their superficial instability are only rarely colonized by bryophytes and lichens. Andreaea spp., Bryum argenteum, Pottia austro-



The relationship between profile and soil data (a) and the percentage cover of the principal species (b) along a transect down the leeward slope from the crest of a low hill, at an altitude of c. 25 m., north-north-east of Lenton Point. The arrows indicate the positions on the profile where soil data were obtained.

georgica, Stegonia latifolia and Candelariella vitellina may occasionally occur in such areas but they never become extensive. These frost heaves are themselves often patterned, with the larger stones arranged peripherally and the finer material grading in towards the centre, although smaller stones may be arranged in the form of small polygons throughout the fine clay. Occasionally species of Andreaea, Usnea and some crustose lichens become established on these coarser strips. The substratum between such frost heaves consists mainly of larger stones with interspersed scattered pockets of soil, giving an overall pattern of Usnea spp., and to a lesser extent Himantormia lugubris on the stonier ground, and species of Andreaea on the soil and stones of the open, circular or polygonal frost heaves. In some cases, the pattern may be regular with the unstable soil being devoid of plants, a band of Usnea spp. on the slightly raised fringe of peripheral stones and species of Andreaea plus occasional other mosses and fruticose lichens on the fine but relatively stable debris between the frost heaves. The other associated species are those typical of an Andreaea-lichen sociation, e.g. Chorisodontium aciphyllum, Drepanocladus uncinatus, Alectoria chalybeiformis, A. nigricans, several species of Cladonia, Sphaerophorus globosus, Usnea antarctica and epiphytic encrusting lichens.

Fig. 13a illustrates the species recorded at 5 cm. intervals along a transect through several frost heaves separated by distinct zones of *Andreaea* spp. and *Usnea* spp., while Fig. 13b shows a less regular pattern on considerably more stony ground where frost action produced hummocks rising to about 10 cm. separated by narrow strips of finer material, where bryophytes were locally frequent. Only occasional pockets of clay occurred and, as with the more extensive counterparts in Fig. 13a, these were barren because of their instability. The stony hummocks were dominated by *Himantormia lugubris*, *Usnea antarctica* and *U. fasciata*, and the moister depressions between them by species of *Andreaea* and occasional associated bryophytes and lichens (Plate IIa and b).

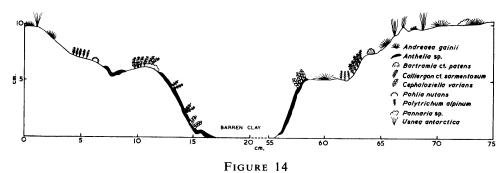


Line transects through two Andreaea-lichen stands on a plateau, at an altitude of c. 120 m., south of Factory Cove. The distribution of species is related to micro-topography on (a) level ground disrupted by three soil and stone polygons and (b) undulating ground subjected to irregular frost heaving.

On stony sloping ground, solifluction is a common phenomenon. The down-hill movement of debris and its re-arrangement into stone stripes and soil "rivers" gives rise to another pattern system. As with frost heaves, the coarser material is separated from the finer sands and clays until a well-developed series of stable stone stripes and mobile clay fines exists. These fines range from short V-shaped strips to continuous muddy "rivers" up to 50 m. long and several metres wide in places. Such areas are characterized by being usually fairly well irrigated by temporary melt runnels which appear for short spells during the summer, either as continuous streams or as springs issuing from below large boulders, representing the emergence of underground water percolating through the porous substratum. Because of the instability of these habitats, bryophyte and lichen colonization is often very sparse and restricted to the larger stones or the more consolidated ramps of soil and gravel at the margins of the mobile fines (Plate IIIb). On the drier stonier stripes, Andreaea gainii, A. regularis, Dicranoweisia grimmiacea, Himantormia lugubris, Usnea antarctica and U. fasciata, as well as numerous epipetric crustose lichens, are all locally abundant. Where small pockets of soil occur and moisture is more plentiful, Andreaea spp., Polytrichum alpinum and occasional cushions of Dicranoweisia grimmiacea and another species of Dicranoweisia form small stands. On the more stable margins of the soil fines a large number of species may occur forming long, heterogeneous stands only 10-20 cm. wide. Here, Andreaea gainii, Bartramia cf. patens, Bryum algens, Calliergon cf. sarmentosum, Ceratodon cf. grossiretis, Drepanocladus uncinatus, Polytrichum alpinum, Anthelia sp., Cephaloziella varians, Hygrolembidium isophyllum and Pachyglossa dissitifolia are all frequent. Several lichens are usually common associates, including species of Lecidea, Leptogium, Pannaria and Placopsis. Fig. 14 illustrates the distribution of species along a short profile transect across a typical stone and soil stripe on a gentle slope in Moraine Valley.

The most extensive area of stone stripes and other solifluction phenomena, which result in large-scale instability of the substratum, was in Moraine Valley. Most of the valley floor and lower slopes of Rusty Bluff were barren, except for occasional sparse colonization by bryophytes and lichens on more stable situations. The margins of the stripes may have a mixed and variable flora similar to that illustrated in Fig. 14. However, at about 100–115 m. there was an abrupt transition above which the gradient increased and rocks and coarse scree supported a variety of Andreaea-Usnea community types and occasional Polytrichum-Chorisodontium banks, all indicative of a more stable substratum. During winter the area below this demarcation accumulated up to 1 m. or more of snow, and the melt water, together with the deep, loose mobile nature of the substratum prevented widespread colonization of the stones and soil. There is much evidence to indicate that tall fruticose lichens are intolerant of habitats which accumulate deep snow, presumably because the weight of the snow breaks the plants, whereas the cushion growth form of many bryophytes in such habitats allows the plants to endure this weight.

Cushions of Andreaea, particularly A. depressinervis, occasionally become established in communities dominated by other moss species, thus giving rise to a modified form of sociological pattern. Such



Distribution of species across the marginal ramps of a narrow soil and gravel stripe, at an altitude of c. 50 m., in Moraine Valley.

invasion from nearby Andreaea-dominated stands occurs most frequently in short Drepanocladus uncinatus communities growing over moist or dry gravelly ground. An example of this is described on p. 93. Further evidence of sociological pattern in this association may be considered by the invasion of stands of the Andreaea-lichen sociation by small dome-shaped turves of Chorisodontium aciphyllum. This situation is described in more detail on p. 92.

## 3. Tortula-Grimmia antarctici association

Environmental pattern in the vegetation of Signy Island resulting from a high pH and high base status of the soil is well shown by the distribution of calcicolous species belonging to the *Tortula-Grimmia antarctici* association. Situations where these patterns are particularly well represented are on and around marble erratics and knolls and at the junction between marble or amphibolite and quartz-mica-schist outcrops.

Small marble stones, i.e. 10–20 cm. across, are frequently encountered up to 1 km. from the nearest marble outcrop where any extensive *Tortula–Grimmia antarctici* sociations exist. Yet very often one or several calcicolous mosses, e.g. *Grimmia antarctici*, *Tortula fuscoviridis*, *T.* cf. *grossiretis* and a species of *Distichium*, or lichens, e.g. species of *Caloplaca*, *Pertusaria* and *Physcia muscigena*, may be found on the stone or weathered base-rich debris immediately around it, while the natural vegetation of the area is generally an *Andreaea*-lichen sociation typical of more acid soil. In passing it may be noted that since few of these calcicole species are fertile they must be capable of spreading and colonizing by means of vegetative propagules.

Fig. 15 illustrates the intricate pattern formed by calcicole and calcifuge species in response to differences in base status around a marble erratic, 35 cm. across, situated in a schist substratum dominated by Andreaea gainii and species of Usnea. The marble erratic lay on a gentle slope, which accounts for the predominance of calcicoles on its down-hill side. Grimmia antarctici was the principal calcicole, with some Tortula fuscoviridis and Physcia muscigena, which is locally common in Tortula-Grimmia antarctici communities. Some schist soil had covered the right-hand side of the stone and cancelled the influence of the marble, so that Andreaea gainii, Cladonia chlorophaea, Sphaerophorus globosus and Usnea spp. had been able to encroach.

A similar form of environmental pattern is illustrated in Fig. 16, where the influence of a larger marble block, again on a quartz-mica-schist slope, is shown by the down-hill distribution of calcicoles within stands of species typical of an *Andreaea*-lichen community. A series of pH measurements made throughout the area showed a close correlation between the alkalinity and the occurrence of calcicolous species. Down-hill from the erratic a number of calcicoles occur, with the greatest cover being given by *Pohlia cruda* var. *imbricata*, which formed a relatively large stand immediately below the marble surrounded by small cushions of *Tortula fuscoviridis*. The associated species were those typical of any *Tortula-Grimmia antarctici* community, but outside the zone affected by the marble, where the pH was less than 6·0, the vegetation consisted mainly of species of *Andreaea* and *Usnea antarctica*.

Some of the greatest contrasts in the vegetation of Signy Island occur at the junction between marble and schist outcrops. In some instances the boundary is very distinct, with the white marble, typically discoloured by orange encrustations of species of *Caloplaca* and *Xanthoria elegans*, giving way abruptly

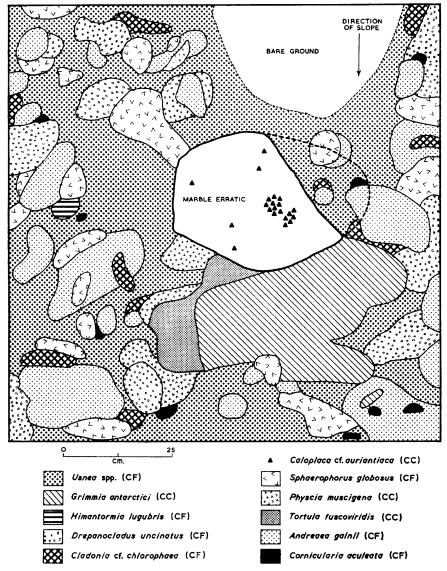


FIGURE 15

Distribution of calcicole (CC) and calcifuge (CF) species around a small marble erratic on a gentle slope of quartz-mica-schist debris, at an altitude of c. 25 m., between Elephants Flats and Mooring Point.

to grey schist which is generally covered with numerous calcifuge crustose lichens, and species of *Usnea* and *Andreaea*. Soils overlying these rock types may vary from a pH of  $8 \cdot 0$  to less than  $5 \cdot 0$  within 1 m., although frequently there has been a certain amount of mixing of the soils resulting in an overall slightly basic reaction. The communities on the two adjacent substrata are structurally similar, with a *Tortula-Grimmia antarctici* sociation on the basic soil and rock, and an *Andreaea*—lichen sociation on the quartz-mica-schist. On the mixed soils, stands of *Grimmia antarctici* alone may occur if they are not too acidic, otherwise species of *Andreaea* usually predominate.

Fig. 17 represents the distribution of the principal species along a narrow belt transect, across a boundary between marble and schist bedrock (Plate IIId). On the soil overlying the marble *Grimmia antarctici*, and to a lesser extent *Tortula fuscoviridis*, provided a discontinuous cover which gave way abruptly to a more closed stand of *Andreaea depressinervis* and *Usnea antarctica* on the schist. The sudden change in base saturation and pH was clearly indicated by the species lists for the two sections, each 3 m. in length, which are given in Table XVIII.

In an area of several low but prominent marble knolls on the east side of Signy Island, north of Elephant Flats, equally abrupt changes are common and produce a similar type of environmental pattern

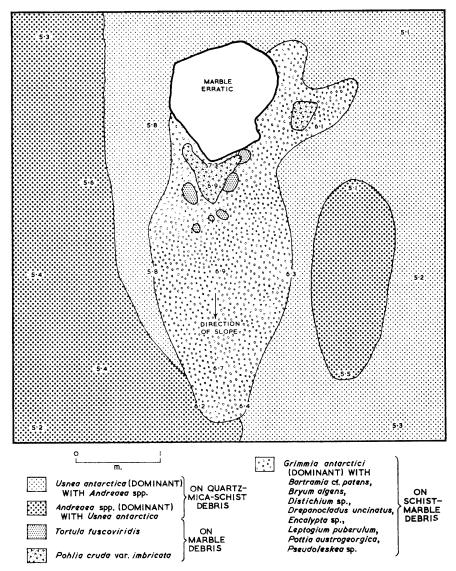


FIGURE 16

Distribution of calcicole species in relation to pH below a marble erratic on a gentle slope of quartz-mica-schist debris, at an altitude of c. 15 m., near Mooring Point.

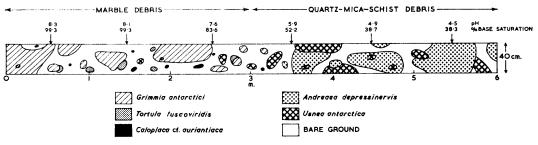


FIGURE 17

Distribution of the principal species along a belt transect across a boundary between marble and quartz-mica-schist and debris on a low hill, at an altitude of c. 40 m., at the north-west corner of Gourlay Peninsula. Re-drawn from Gimingham and Smith (1970). The arrows indicate the positions on the transect where soil data were obtained.

TABLE XVIII

SPECIES RECORDED ALONG A BELT TRANSECT ON MARBLE
OR QUARTZ-MICA-SCHIST AND SOIL

Marble	Quartz-mica-schist
Mosses	Mosses
Drepanocladus uncinatus	Andreaea depressinervis
Encalypta spp.	Drepanocladus uncinatus
Grimmia antarctici	Pohlia nutans
Tortula fuscoviridis	Lichens
Lichens	Alectoria chalybeiformis
Caloplaca cf. auriantiaca	Buellia spp.
Caloplaca cf. citrina	Cladonia carneola
Lecanora sp.	Cladonia chlorophaea
Leptogium puberulum	Cladonia furcata
Ochrolechia frigida	Cornicularia aculeata
Pertusaria sp.	Lecanora spp.
Physcia muscigena	Lecidea dicksonii
Usnea antarctica (on schist pebbles)	Ochrolechia frigida
Xanthoria elegans	Rhizocarpon geographicum
	Sphaerophorus globosus
	Usnea antarctica

in the vegetation. Fig. 18 illustrates the pattern of species distribution on the east-facing slope of one of these knolls where marble and quartz-mica-schist outcrops formed a series of narrow stepped terraces, each about 2 m. wide. It is evident that the type of community which developed is directly related to the type of rock, the nature and depth of its derived soil, and the extent to which the terraces receive melt water from drifted snow. The schist terraces were dominated by *Drepanocladus uncinatus*, with *Bryum algens* and *Ceratodon* cf. grossiretis as associates, while the marble terraces supported *Bryum algens* and smaller mats and cushions of *Drepanocladus uncinatus*, *Brachythecium austro-salebrosum*, *Tortula fuscoviridis* and *T.* cf. grossiretis. The uppermost terrace had the deepest and stoniest soil and was colonized mainly by *Grimmia antarctici* and *Marchantia berteroana*. On the rock surfaces, the schist supported species of *Andreaea*, *Omphalodiscus* and *Usnea*, whereas the marble had cushions of *Tortula fuscoviridis*, *T.* cf. grossiretis and orange encrustations of species of *Caloplaca* and *Xanthoria elegans*. On the lowest terrace, *T. fuscoviridis* and *T.* cf. grossiretis were replaced by *T. excelsa* as the soil became moister.

While the Tortulas are characteristic of base-rich soils, the moisture-holding capacity of the latter determines which species will predominate. *T. excelsa*, for example, has a distinct preference for damper, usually more organic soil than that occupied by the other two species. This type of situation is shown in Fig. 19, which illustrates the transition from a *Bryum algens-Drepanocladus uncinatus-T. excelsa* sociation to one dominated by *T. fuscoviridis* at the junction between the drier fine scree slope of a marble knoll rising from moister almost horizontal ground at its foot. The lower level ground had a deeper accumulation of soil, which contained up to 50 per cent organic debris, and consequently had a higher moisture content

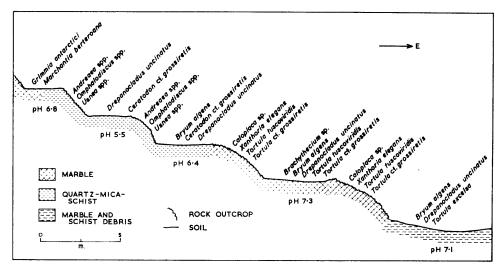
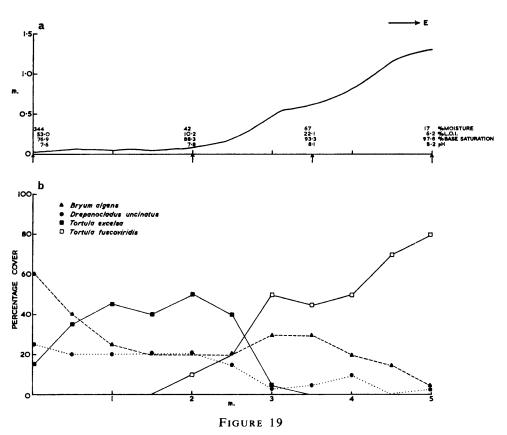


FIGURE 18

Distribution of the predominant species in relation to differences in the substratum, on a series of narrow terraces on a low knoll, at an altitude of c. 16–20 m., west of Waterpipe Beach.



The relationship between profile and soil data (a) and the percentage cover of the principal species (b) along a transect from a base-rich flush on to the dry slope of a low marble knoll, at an altitude of c. 20 m., north of Elephant Flats. The arrows indicate the positions on the profile where soil data were obtained.

than the well-drained inorganic soil on the 18° slope. This, too, was even more alkaline than the wetter soil, although the pH and base status throughout was high. T. excelsa predominated on the moister areas, with Bryum algens and Drepanocladus uncinatus also abundant, but gave way to T. fuscoviridis on the drier sloping ground.

Further instances of environmental pattern produced by abrupt floristic changes within a small area are seen where slightly base-rich soils occur below bands of marble or amphibolite cropping out amongst quartz-mica-schists. Thus local calcicolous communities may arise among an otherwise Andreaea—Usnea association. These flushed soils are frequently colonized by Grimmia antarctici and several other species typical of the Tortula-Grimmia antarctici association, e.g. Pottia austrogeorgica, Leptogium puberulum and Physcia muscigena. Although the substratum is uniform in structure, the local enrichment of the Grimmia-dominated soils is due to melt water trickling over the base-rich strata higher up the slope. The resulting vegetation pattern is one of a clearly defined open band of bright green Grimmia antarctici running longitudinally through an area of dark brown Andreaea comprising one or more species. Fig. 20 records such changes in a Grimmia antarctici flush flanked by A. depressinervis and various lichens near Mooring Point. Where the Andreaea was predominant, the soil pH was about 4·8 but in the Grimmia stand the pH rose to 6·0. This latter value is very low for a Grimmia antarctici sociation which probably accounted for the openness of the community and lack of the more typical small calcicolous species.

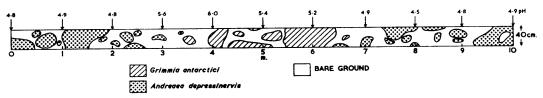


FIGURE 20

Distribution of the calcicole *Grimmia antarctici* and the calcifuge *Andreaea depressinervis* in relation to pH along a belt transect through a narrow damp flush below an outcrop of amphibolite, at an altitude of c. 10 m., near Mooring Point. The arrows indicate the positions on the transect where soil data were obtained.

On glacial debris of relatively high base status, stands of *Grimmia antarctici* with associated species of *Tortula* and other calcicoles, generally replace species of *Andreaea* and fruticose lichens typical of the more acid soils. However, as in several of the sociations of the *Andreaea–Usnea* association, stands of *Grimmia* are often disrupted by frost heaving with consequent polygon formation, but in contrast to the *Andreaea–lichen* communities no zonation is apparent around the polygons. In these calcicolous communities, lichens do not contribute to the pattern which results from the various cryopedogenic processes, although *Leptogium puberulum*, *Peltigera rufescens*, *Physcia muscigena* and several epiphytic crustose species are usually present.

Where glacial debris is composed predominantly of base-rich soil and rock fragments but contains scattered stones of schist or pockets of slightly acid soil, a mosaic of cacilcole and calcifuge species may occur. While the vegetation is usually dominated by *Grimmia antarctici* in association with species of *Tortula* and other calcicolous mosses and lichens, local colonies of calcifuge species such as *Cornicularia aculeata*, *Dicranoweisia grimmiacea*, *Himantormia lugubris* and *Sphaerophorus globosus* together with species of *Andreaea* and *Usnea* provide striking colour contrasts in the rather heterogeneous stands.

On damper sloping ground where solifluction may take place, stone and soil stripe formations are colonized in a manner similar to those in areas of schist-dominated terrain, except that the species are largely calcicoles. Bryophytes, which may be locally abundant at the margins of the mobile soil "rivers" and on the surface of the more stable base-rich outwash fans, include species of Brachythecium, Encalypta, Marchantia berteroana, Pottia austrogeorgica, Pohlia cruda var. imbricata and Tortula excelsa, all of which are typical of flushed soils.

## 4. Caloplaca–Xanthoria association

On Signy Island several of the epipetric lichen communities on coastal rocks, from high-water mark to about 15 m. or higher, exhibit a distinct zoned pattern related chiefly to exposure to wind and sea spray. In these communities the most important habitat factors which the lichens must tolerate are

scouring action of brash ice, the very high concentration of marine salts and at times manuring by birds. Attention has already been drawn to the similarities that exist between the various lichen sociations of maritime rocks and to the fact that they may be considered as variants of a single community type, in which a different species assumes dominance in a series of zoned sociations.

The lowermost zone around high-water mark is frequently colonized by a slender green alga (possibly a species of *Enteromorpha*) typical of the intertidal region of the shore. The first lichen community immediately above this zone, which occasionally extends below high-water mark, is dominated by brown and black species of *Verrucaria*, most of which may receive frequent deluges of spray or waves. Above this band lie one or more sociations dominated by orange species of *Caloplaca*, which in turn merge into one of several community types depending on the height above sea-level and exposure to wind. Frequently the crustose *Caloplaca* zone intergrades with a community dominated by *C. regalis*, although *Buellia* spp., *Haematomma erythromma*, *Lecidea* spp., *Omphalodiscus antarcticus*, *Ramalina terebrata*, *Usnea antarctica* and *Xanthoria elegans* may also be predominant in stands of lichens on these rocks. Those parts of the cliffs with some degree of shelter usually support species of *Omphalodiscus* and *Usnea*, which seem to be intolerant of sea spray.

The zoned patterns which result from the responses of individual species to exposure to sea and wind have been investigated on several coastal cliffs and rocks in the Borge Bay area, on the east coast of Signy Island.

The largest of the Billie Rocks lies about 100 m. from the shore and rises to 9 m., Fig. 21 showing its profile from north-west to south-east and the distribution of the principal species. The pronounced scarp

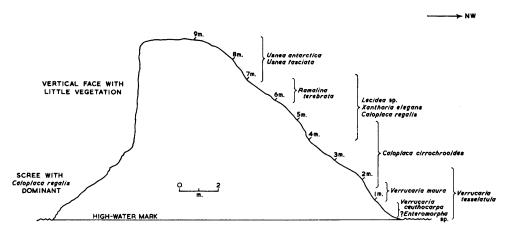


FIGURE 21

The zonation of lichen communities in relation to exposure to sea spray and wind on the largest of Billie Rocks, Borge Bay.

slope facing south-east has vertical and overhanging faces which are almost devoid of vegetation, although Caloplaca regalis formed 10–25 per cent cover over most of the blocks below the main face about 3–4 m. above high-water mark. The north-west facing dip slope was well covered with lichens, and the zonation was quite marked, while species of Buellia, Catillaria corymbosa, Lecania brialmontii, Xanthoria candelaria and the alga Prasiola crispa occupied the moist fissures.

A similar series of lichen communities was examined on the nearby low-lying island of Bare Rock, north-north-east of Berntsen Point, and on Outer Island to the south-east, but on these the larger lichens, e.g. Caloplaca regalis, Ramalina terebrata and Usnea spp. were absent. This was probably due to their intolerance to the considerable deposits of spray, wave action and trampling by penguins and shags (Phalacrocorax atriceps).

Low rocky promontories also show a distinct vegetation zonation in relation to wind and wave action. One such area is Berntsen Point, north-east of the British Antarctic Survey station. The tip of this small headland consists of sloping, rounded wave-worn rock on which little vegetation occurs because of the frequent inundation by waves and the scouring action of ice. The *Verrucaria* zone which occurs on more sheltered rocks was absent, but at 1.5-2 m. above high-water mark, where the rock was less influenced by the sea and the surface fairly rough, there was a broad belt of *Caloplaca cirrochrooides* associated

with another species of Caloplaca. Inland from the crustose Caloplaca zone and at a slightly higher altitude, i.e. 6–12 m., Xanthoria elegans was dominant with Haematomma erythromma a common associate. The wind-swept flat top of the promontory, at about 15–20 m., supported a typical community dominated by Usnea antarctica with occasional Omphalodiscus antarcticus on the vertical faces. On the sheltered east-facing cliff, species of Buellia, Caloplaca, Lecidea and Verrucaria, together with Caloplaca regalis, Mastodia tesselata, Xanthoria candelaria, X. elegans and Prasiola crispa were all frequent. The distribution of the principal species is shown in Fig. 22.

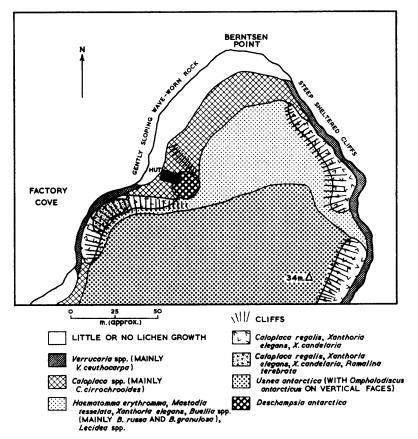


FIGURE 22

The zonation of lichen communities in relation to exposure to wind and wave action at Berntsen Point, Factory Cove.

The influence of spray and wave action on the lichens of maritime rocks may be further illustrated by the performance of species on a small rock promontory at the southern end of the largest of the Thule Islands. This rock (Fig. 23) reached 8 m. high and possessed west and south faces, sloping at about 60–70°; of these, considerably more of the west side was vegetated and had a much larger number of species. The south cliff was facing the open sea in Borge Bay and received a higher amount of spray than the more sheltered west cliff. The lower region of the south face was colonized by species of Caloplaca and Verrucaria, but on the west side only the Caloplacas were present. Besides a large number of unidentified species of Buellia and Lecidea on both faces, about 23 species of lichens were recorded in a series of 100 cm.² quadrats along a transect up the west face, compared with only seven species on the south face. On the upper part of the south cliff there was an absence of fruticose lichens, i.e. species of Omphalodiscus, Ramalina and Usnea which were quite abundant a few metres away, on the west face where there was more shelter.

The summit of this rock promontory was occupied by a small colony of gulls and their influence on the surrounding rocks was obvious from the distribution of the ornithocoprophilous lichens. Bedrock, boulders and large schist fragments were dominated by an extensive growth of *Xanthoria elegans*, with *Haematomma erythromma* and *Mastodia tesselata* as prominent associates. Others commonly occurring

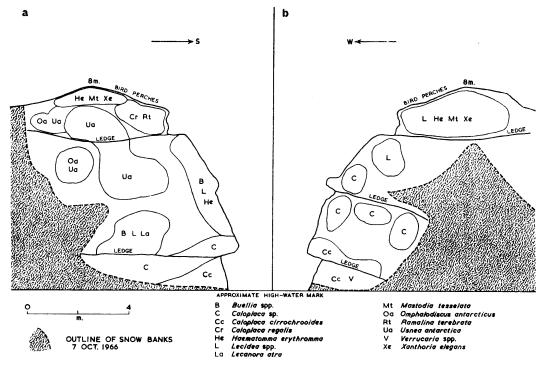


FIGURE 23

The distribution of lichen communities on (a) the sheltered west face and (b) the more exposed south face of a low sea cliff at an altitude of 0-8 m., at the southern end of the largest of the Thule Islands, Borge Bay.

were Bacidia stipata and Lecania brialmontii with, usually in crevices, Acarospora convoluta, Biatorella sp., Buellia spp., Physcia caesia and Xanthoria candelaria. On the small schist fragments, the latter species was dominant, accompanied by numerous species of Buellia and Lecidea together with Haematomma erythromma, Lecanora aspidophora and Prasiola crispa as well as several unidentified black crustose lichens. X. candelaria showed a preference for sloping rock or fissures irrigated by run-off from bird perches. It did not appear to grow on horizontal surfaces, and such areas were usually dominated by X. elegans which tended to avoid heavily dunged situations. Where soil accumulated in perches and nesting sites, several mildly calcicolous bryophytes occurred, including Bryum algens, Ceratodon cf. grossiretis, Drepanocladus uncinatus, Pottia austrogeorgica, Tortula conferta and T. excelsa.

Further observations on the zoned pattern of coastal lichen communities in relation to bird dunging have been made on the cliffs above Factory Cove immediately south of the British Antarctic Survey station. Here, large expanses of the vertical cliff faces were coloured orange and yellow with various crustose species. Numerous ledges were used as nesting sites by cape pigeons and snow petrels, so that locally melt water running down the rock faces was highly nitrogenous. These areas stood out clearly as longitudinal strips of nitrophilous species of Caloplaca. The wet areas which were more or less continuously supplied with melt water were covered with a loose mat of Prasiola crispa and occasional lichens such as species of Acarospora and Biatorella. Where the rock was less frequently soaked, Physcia caesia and Xanthoria candelaria predominated, although on the less steep parts Prasiola crispa was again dominant. The cliff faces which were only moistened slightly supported large expanses of X. elegans and in the more sheltered habitats C. regalis was also, at times, abundant. Both of these species showed variation in colour of thallus from light yellow to a deep reddish orange, apparently correlated with increasing concentration of nitrogenous salts in the melt water. Haematomma erythromma, Microglaena antarctica, Ramalina terebrata and Xanthoria elegans, together with Physcia caesia, X. candelaria and Prasiola crispa occurred on vertical faces at some distance from the nest sites, while those parts of the cliffs unaffected by bird excreta were colonized by the fruticose lichens Alectoria chalybeiformis, A. pubescens, Omphalodiscus spp. and Usnea spp., together with crustose species of such genera as Buellia, Lecanora, Lecidea, Rhizocarpon and Rinodina.

A similar form of zonation occurred on coastal rock faces a little above high-water mark where melt water frequently enriched by bird excreta trickled down the cliff, usually following the path of small cracks and crevices with *Verrucaria elaeoplaca* forming closed brownish encrustations. In minute dry fissures outside this *Verrucaria* zone, *Mastodia tesselata* produced small patches which at times were reduced to "chains" of thalli following the course of the crevice. *Caloplaca cirrochrooides* was often present on drier rock. An example of this pattern is shown in Fig. 24.

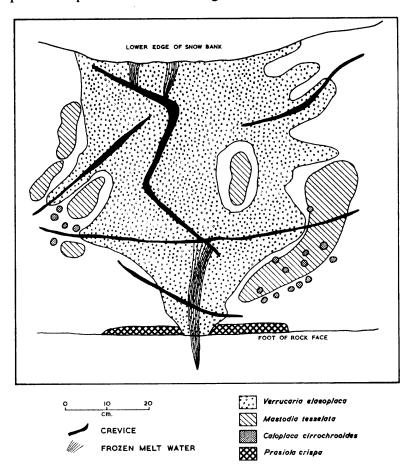


FIGURE 24

The distribution of three lichens and an alga in relation to melt-water courses on a vertical, north-facing sea cliff, at an altitude of c. 1.5 m., south-west of Berntsen Point.

# 5. Polytrichum alpestre-Chorisodontium aciphyllum association

Pattern within the *Polytrichum alpestre-Chorisodontium aciphyllum* association is primarily sociological, although factors such as moisture availability, exposure and biotic influences will determine which species is the most likely to assume dominance in any given situation. The close association of *Polytrichum alpestre* and *Chorisodontium aciphyllum* in the formation of the peat banks of Signy Island has already been mentioned and pattern in the present association largely concerns the development and subsequent changes which take place in these banks.

Although the two species very often grow together, it is apparent that *C. aciphyllum* almost always needs to colonize a moist organic substratum such as an existing moss carpet, mat or stand of coalesced cushions, while *P. alpestre* can develop initially on stony dry ground. In general, on Signy Island, whether or not *P. alpestre* is the first colonizer, *C. aciphyllum* usually becomes dominant. It has been noted earlier that *Chorisodontium aciphyllum* has a preference for those habitats with a higher moisture content than those dominated by *Polytrichum alpestre*. This was most noticeable where extensive banks have developed, as the damp hollows and marginal faces where snow drifts accumulate were dominated by *C. aciphyllum* 

and the drier stonier slopes by *P. alpestre*. The degree to which colonization of the surface of the banks by lichens may take place is related to the dryness of the peat, exposure to wind and the amount of snow which may accumulate in winter.

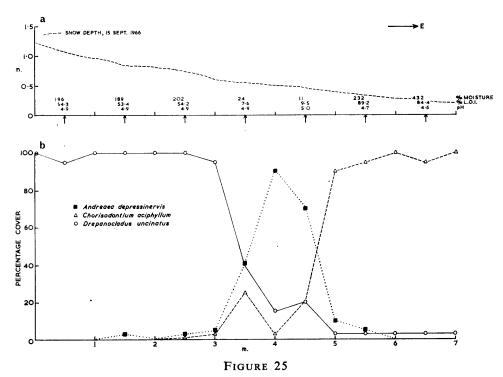
Polytrichum-Chorisodontium communities may develop on wet or dry substrata, but generally hummocky turves of the two species become established within close proximity of a parent stand. Colonization of other community types by P. alpestre is not very common, but there were a few localities where recent establishment had taken place and an estimate of the colonization rate could be determined. These situations were former nesting sites of giant petrels on stony slopes and knolls close to the shore on Berntsen Point, Knife Point and the bluff west of Factory Cove on the east coast of Signy Island. These nesting sites are known to have been occupied when the Falkland Islands Dependencies Survey station was established in 1947, but were deserted by about 1954 following persistent disturbance by man and dogs. In 1967 the nests were still conspicuous and apart from various crustose lichens and occasional small moss cushions, small hummocky turves of P. alpestre were locally prominent. Although the substratum consisted largely of loose small stones and pebbles with pockets of soil, the Polytrichum appeared to be well-adapted to such a habitat. In the 10-12 yr. during which the colonists have become established, some hummocks have reached as much as 15 cm. across and 5 cm. deep, while others have coalesced to form even larger turves. Other colonists such as Andreaea depressinervis, A. regularis, Ceratodon cf. grossiretis, Pohlia nutans and Polytrichum alpinum seldom formed units of more than 5 cm. across. Occasionally in other localities, e.g. on sheltered, gravelly slopes dominated by Usnea antarctica, P. alpestre became established but the colonies were never extensive. Only the small hummocks were of pure Polytrichum alpestre, for as they increased in size, Chorisodontium aciphyllum and Cephaloziella varians became associated, although initially with a low cover value. Eventually the Chorisodontium usually achieved dominance or co-dominance, and lichens may ultimately colonize the surface of the mosses.

It has been pointed out that Chorisodontium aciphyllum can effectively invade stands of other mosses, particularly those dominated by Andreaea depressinervis or Drepanocladus uncinatus. Invasion of one community type by the dominant species of another is not a common phenomenon on Signy Island, but Chorisodontium aciphyllum is one of the few mosses which behaves in this way. Such simplified sociological pattern may be seen on dry gravelly ground, where C. aciphyllum frequently colonizes species of Andreaea, and is a regular, sometimes locally abundant, associate in the Andreaea-lichen sociation typical of fairly level situations which usually receive some protection from the wind, and a moderate cover of snow in winter. In this sociation Chorisodontium aciphyllum forms small hummocks, commencing growth amongst Andreaea, usually A. depressinervis, and gradually overgrowing the surrounding moss so that a profile through a cushion often reveals a thin layer of dead Andreaea below the dome of Chorisodontium. Where an Andreaea-lichen sociation lies adjacent to a Polytrichum-Chorisodontium stand, hummocks of Chorisodontium aciphyllum frequently become established in the Andreaea in the vicinity of the peat bank (Plate IIIc). Polytrichum alpestre and especially Cephaloziella varians may also colonize these Chorisodontium turves in small amounts, while Barbilophozia hatcheri, Drepanocladus uncinatus and Pohlia nutans may become established around the lower region of the hummocks where snow accumulates during summer falls, creating a moister micro-environment.

A similar form of sociological pattern occurs where Chorisodontium aciphyllum turves invade other communities on wet ground. In such instances there is usually a Polytrichum-Chorisodontium bank close to the wet habitat supporting one or several of the Brachythecium cf. antarcticum-Calliergon cf. sarmento-sum-Drepanocladus uncinatus sociations. The stands which are most frequently invaded are generally dominated by Drepanocladus uncinatus with Calliergon cf. sarmentosum often associated peripherally. If the habitat is not too wet, or if there are drier stonier regions caused by frost heaving below the moss, isolated hummocks of Chorisodontium aciphyllum turf frequently become established and may coalesce to form miniature stands up to 1 m. across and 15 cm. above the level of the carpet-forming species (Plate Vc) (Gimingham and Smith, 1970, pl. 8, p. 781). These invading turves are often blackish in colour in contrast to the more typical bright green, and the hummocks can often be detached from the substratum as compact masses tapering towards the base in the form of a peaty cone. A fringe of blackish Cephaloziella varians frequently forms around the Chorisodontium aciphyllum and at the junction of the two sociations, while both Calliergon cf. sarmentosum and Drepanocladus uncinatus may encroach marginally into the Chorisodontium. Since this habitat is considerably wetter than the Andreaea-lichen dominated soils, Polytrichum

alpestre is usually absent from the Chorisodontium hummocks, occurring only in the tallest and largest turves where the influence of the ground water is least. On slopes where mixed peat banks lie close to wet areas around runnels, solifluction may produce strips of raised stony soil crossing the Calliergon-Drepanocladus stands, where Chorisodontium aciphyllum, and to a lesser extent species of Andreaea, Polytrichum alpestre and P. alpinum may become established.

An example of the transition from a *Drepanocladus uncinatus* stand to one dominated by *Chorisodontium aciphvllum* is given in Fig. 25. The site was more or less level but covered by a late-lying snow bank



The relationship between snow depth and soil data (a) and the percentage cover of the principal species (b) along a transect on horizontal ground from a wet, late snow patch to a shallow peat bank on a low hill, at an altitude of c. 30 m., between The Wallows and Starfish Cove. The arrows indicate the positions on the profile where soil data were obtained.

which abutted on its western side against a low rock face. Near to this face there was a pure stand of short Drepanocladus uncinatus which merged with a band of Andreaea depressinervis, the latter intergrading in turn with a shallow bank of Chorisodontium aciphyllum on the more exposed area of dry stony ground (Plate IIIc). Dynamic interactions are suggested, since the hummocks of C. aciphyllum have become established among the Andreaea, while cushions of this species have invaded the Drepanocladus carpet at the drier end of the wet area. In most cases where such invasion takes place, it appears that cushion- or turf-forming species are the most successful in becoming established on or among other mosses. Along this transect, winter snow accumulation was considerably greater at the end with the Drepanocladus than at that with the Chorisodontium, with the deep drift against the rock outcrop persisting over the Drepanocladus for more than a month after the snow had disappeared from the remainder of the transect. The moisture content of the soil from the moist habitat was around 200 per cent compared with only 20 per cent where Andreaea depressinervis was dominant. The humus content was also much higher below the Drepanocladus carpet than below the cushions of Andreaea depressinervis on the drier soil. However, the Chorisodontium peat, although not deep, had a very high organic content and a correspondingly high moisture content.

The deep, often isolated, peat banks (Plate IVa) provide one of the few examples of possible successional stages contributing to sociological pattern in the plant communities of Signy Island. In the *Polytrichum alpestre-Chorisodontium aciphyllum* association, it is suggested that this succession commences with the invasion of stands of species of *Andreaea* (mainly *A. depressinervis*) or *Drepanocladus uncinatus* by small,

isolated turves of Chorisodontium aciphyllum (Plates IIIc and Vc). These dome-shaped turves gradually coalesce and build up a shallow bank over the original mosses. At some point during this later stage, Polytrichum alpestre becomes established amongst the Chorisodontium (Plate IVb), and as the depth of peat increases the Polytrichum may become dominant in the drier habitats. Later an assortment of fruticose lichens may become established on the surface (Plate IVc), to be succeeded by black and white species of crustose lichens which may cover large expanses of the more exposed parts (Plate IVd). Exposure to wind plays an increasingly important role in the development of this succession, and the moss on which the lichens are attached usually becomes moribund and killed by wind and ice action on the broken or raised parts of the turf which have been affected by frost heaving, slumping or other forms of erosion. The crustose species appear to colonize these areas of dead moss (Plate Va), but the surface is by this stage rather loose and puckered, and further wind erosion often removes the entire crust of lichens. This results in the final stage, in which the eroded peat is exposed on the highest parts of the dome-shaped banks, and no living bryophytes or lichens remain (Plate Vb). Occasionally there may be re-colonization by regenerating shoots of Polytrichum alpestre, Chorisodontium aciphyllum and Pohlia nutans, and the establishment of species of Andreaea or other mosses. Some individual peat banks on Signy Island possess all or several of these successional stages, in which pure Chorisodontium aciphyllum gives way to the Chorisodontium with epiphytic fruticose lichens, followed by a mixture of fruticose species and several species of crustose lichens as exposure increases, with finally a fringe of entirely encrusted dead moss, which merges into barren and eroded peat.

Various examples of small-scale environmental pattern on the surface of the peat banks, which are stages in the development of lichen cover, have been observed on many banks on Signy Island. The first stage appears to be the progressive death of the surface layers of moss on slopes which fail to receive adequate protection from winter snow cover. Where conditions are not too severe and winter snow cover is relatively deep, fruticose lichens become established, but on the exposed crests of slopes or the tops of ridges forming part of the surface ripple systems, crustose species predominate.

The bank illustrated in Fig. 26 shows an early stage in the development of a fruticose lichen cover on eroding peat. This bank formed an extensive dome-shaped peat "island" elongated in an east—west direction. The south side ended abruptly in an eroded face up to 1.5 m. high, with a series of alcoves, but the peat on the north side, adjacent to a rock outcrop, was only 30-40 cm. deep. At about 45 m. from the eastern end, near the edge of an area of bare eroded peat, the bank dipped steeply to the west dropping about 8 m. before levelling out again. Most of the higher portion of the bank comprised Chorisodontium aciphyllum with local areas where lichens, and to a lesser extent Polytrichum alpestre,

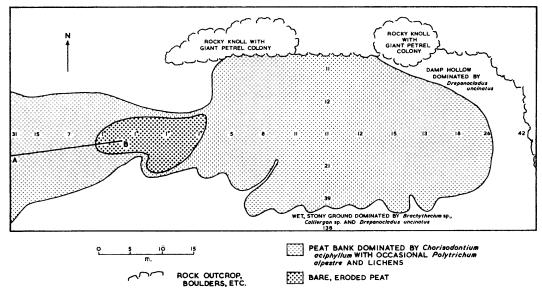


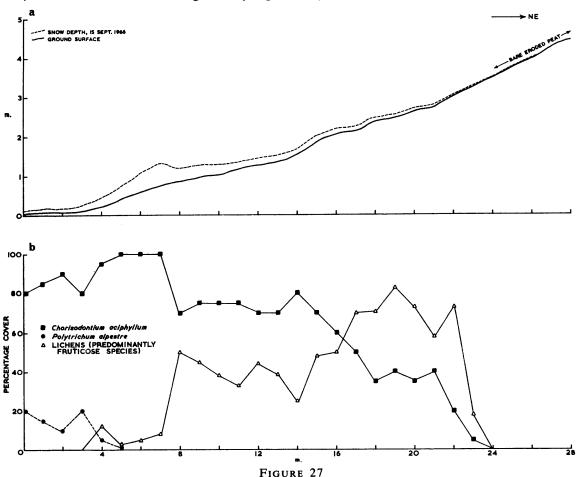
FIGURE 26

The distribution of species in relation to the depth of snow cover (cm.) for 15 September 1966, on an extensive peat bank, at an altitude of c. 55-65 m., inland from Spindrift Rocks. A + denotes ice. Transect A-B is illustrated in Fig. 27.

occurred. The exposed upper part of the slope, which was eroded to bare peat and devoid of living vegetation, covered approximately 70 m.<sup>2</sup> and was surrounded by a zone of crustose lichens on the partially killed fringe of the *Chorisodontium*. Excessive exposure to wind was almost certainly the reason for the bare peat. On the lower less exposed rather stonier ground, the *Polytrichum* increased to become co-dominant with *C. aciphyllum*.

Throughout winter the portion of the bank with bare eroded peat was always blown free of snow except for an occasional thin layer of clear ice on its surface, which was then exposed to frequent spells of low temperature, desiccation and frost action. The rest of the bank was covered by varying depths of snow, depending on the degree of shelter afforded by the topography, and ranged from over 50 cm. at the foot of the slope to as little as 10 cm. on the slope and its higher parts. The south face of the bank rapidly accumulated drift snow and by early winter a gentle ramp formed from the nearby wet hollow to the surface of the *Chorisodontium* bank above the eroded face. Thus the snow depth at this point at times exceeded 1.5 m. and persisted until well into summer.

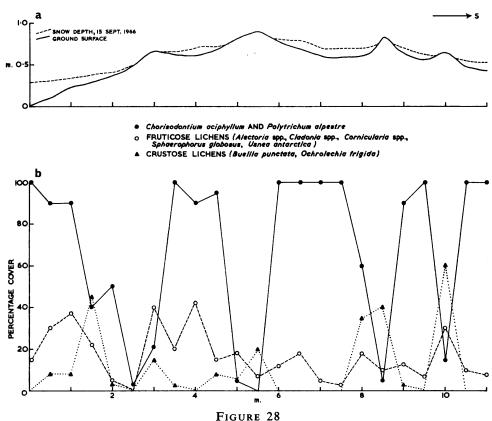
Fig. 27 indicates the change in species, recorded along a transect, indicated by line A-B in Fig. 26, from the gently sloping lower portion of the bank, up the steep slope and into the barren eroded region. The vertical rise was about 3.5 m. The lower part, with a shallower peat and some degree of shelter, was composed of lichen-free *Polytrichum alpestre* and *Chorisodontium aciphyllum*. The relatively moist foot of the slope was of almost pure *C. aciphyllum*, although stems of the hepatic *Cephaloziella varians* were always present among the moss shoots. With an increase in height, and hence in exposure, fruticose lichens, such as species of *Alectoria* and *Cladonia*, *Sphaerophorus globosus* and *Usnea antarctica*, became prominent although they received some protection from winter snow. Thus with increasing exposure, the fruticose lichens were gradually replaced by crustose species which formed a narrow zone



The relationship between profile and winter snow depth (a) and the percentage cover of the principal species (b) along transect A-B shown in Fig. 26.

around the barren eroded peat on the crest of the slope. At this point, as noted above, no snow cover was evident during the winter apart from an occasional coating of thin ice.

The distribution of the principal species on another peat bank studied in some detail, also on the west side of the island, is illustrated in Fig. 28. This fan-shaped bank lay on a moderately steep slope with a westerly aspect, and was flanked by rock outcrops and large boulders (Plate Ic). It increased in depth towards the down-hill face as well as towards the centre. The lower eroded part was at least 1 m. in depth, and showed four prominent ridges running longitudinally down the slope perhaps overlying bands of large stones or former stone stripes. The highest parts of the three principal ridges were wind-eroded



The relationship between profile and winter snow depth (a) and the percentage cover of the principal species (b) along a transect across a locally eroded undulating peat bank, at an altitude of c. 80 m., inland from Spindrift Rocks.

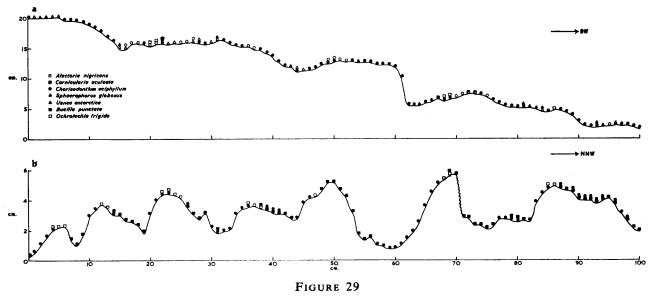
but fringed with lichens, while the hollows between them were dominated by almost pure stands of *Polytrichum alpestre* and *Chorisodontium aciphyllum*. The distribution of species was clearly related to the micro-topography, and also to the cover of winter snow. The bank was composed of both turf-forming mosses, but *Polytrichum alpestre* was dominant towards the foot of the ridges while *Chorisodontium aciphyllum* increased in cover in the depressions. The crests of the ridges, although very low, were partially or entirely encrusted with lichens and received no snow cover in winter. In the hollows, where the living mosses predominated with scattered fruticose lichens, snow depth exceeded 20 cm. (Plate Id).

A repeating micro-topographic pattern caused by wind exposure and the presence of regular undulations on the surface of *Chorisodontium aciphyllum*, and to a lesser extent on *Polytrichum alpestre*, is frequently seen on peat banks on Signy Island. The resulting small-scale environmental pattern shows a similar distribution of living moss, fruticose and crustose lichens as in the larger examples described above. Many of the deeper banks exhibit this rippling feature with ridges and troughs apparently aligned at right-angles to the direction of the local wind. In most cases they lie from north-west to south-east but in places, depending on the influence of local topography and wind direction, the axis is from northeast to south-west. It is not certain how these ripple systems originated, but wind direction and frost action are probably responsible.

Although these ripple systems are very low micro-topographic features, there is considerable variation in exposure between the crests and the hollows. The broad, widely separated crests which receive considerable protection by snow in winter do not occur on strongly wind-swept terrain. The moss in these areas is usually colonized by various fruticose lichens, particularly Alectoria spp., Cladonia spp., Cornicularia aculeata, Sphaerophorus globosus and Usnea antarctica, while on the more exposed peat banks the narrow ripples exhibit a small-scale zoned pattern of living moss and encrusting lichens which repeats itself on each successive ridge and trough (Plate IVd). Generally, while the more wind-swept ridge crests are colonized by white encrustations of Ochrolechia frigida, it is the leeward slope which apparently becomes eroded and colonized by blackish species of blue-green algae and Buellia punctata. The base of the hollow, if it has not accumulated pieces of eroded peat and detached fruticose lichens, is moister and may have varying amounts of Drepanocladus uncinatus and Pohlia nutans amongst the living Chorisodontium aciphyllum. The windward slope consists of pure living Chorisodontium aciphyllum and gives way on the crest to the white lichens, thus repeating the pattern on each ridge and hollow. There is some evidence that these ridges are not static features. A profile cut through one such series indicated that the system was advancing, presumably along the direction of the local wind.

The height of a ridge is seldom more than 15 cm. above its related hollow. Measurements of a series of Chorisodontium aciphyllum ridges on one extensive bank showed that the mean distance apart of a sequence of 22 of these small ripple systems was 10.8 cm. (range 6–15 cm.), although one series of 12 had a mean of 14.4 cm. (range 11-20 cm.). Similar dimensions are also typical of other banks, but another series of 18 ridges, rather higher than the former, averaged 28.7 cm. apart. However, this small-scale pattern does not develop when Polytrichum alpestre is present as an associate. On a gently sloping Polytrichum-Chorisodontium bank overlying stony soil near the north-west coast of Signy Island, the shallow peat was subjected to frost action. Here a series of eight frost-heaved ridges reached 35 cm. above the hollows and they were spaced about 200 cm. apart, although a second series of eight had a mean of only 97.5 cm. from crest to crest. The ridge summits of these were at least 10 cm. broad compared with the sharp crests of the narrowly spaced systems.

Fig. 29a illustrates the pattern found on the windward side of a deep peat bank in the north-west part of the island. In this example the ridges were on a slope of about 10°, so that development took the form of a series of steps, formed possibly by the action of solifluction, rather than crests and hollows. Being near the edge of the bank, below the most exposed part, winter snow lay quite deep over the surface and afforded considerable protection from wind and low temperatures. This permitted the growth of



The distribution of epiphytic lichens in relation to micro-topography across (a) the stepped surface of a deep *Chorisodontium* aciphyllum bank, at an altitude of c. 70 m., inland from Spindrift Rocks, and (b) the undulating surface of a shallow *Chorisodontium* aciphyllum bank moulded into a regular series of low ridges and troughs by wind and frost action, on a low hill, at an altitude of c. 60 m., north-west of Gourlay Peninsula.

fruticose lichens over the moss, while crustose species were almost absent. The tops of the steps were usually colonized by species of *Alectoria*, *Cornicularia*, *Sphaerophorus globosus* and *Usnea antarctica*, with a noticeable absence of *Cladonia* spp. The *Chorisodontium aciphyllum* beneath the larger tufts of lichen had died and it is possible that if these epiphytes become detached from the surface, crustose species may colonize the dead moss, and lead to a pattern similar to that described below.

An example of the repetitive zoned pattern is given in Fig. 29b in which species were recorded at single points 1 cm. apart over a series of Chorisodontium aciphyllum ripples with a mean wave-length of 11·2 cm. Living Chorisodontium occurred on what appeared to be the windward side of these ripples, while the more exposed ridge crests were colonized by white Ochrolechia frigida and the eroding leeward slopes were covered by blackish Buellia punctata and blue-green algae. The ripple system lay on a fairly exposed low hill in the south-east of Signy Island, but the peat it had formed was only 20-30 cm. deep. Using small portable cup anemometers, comparative measurements of air movement were made on the crests and in the hollows of another of these systems. At a time when the wind velocity recorded by the meteorological anemometer at the British Antarctic Survey station was 5·2 m./sec. the wind speed on the crest of a nearby peat-bank ripple system was 1·4 m./sec., and in the hollows about 10 cm. below, only 0·2 m./sec. Temperature and humidity differences were also considerable.

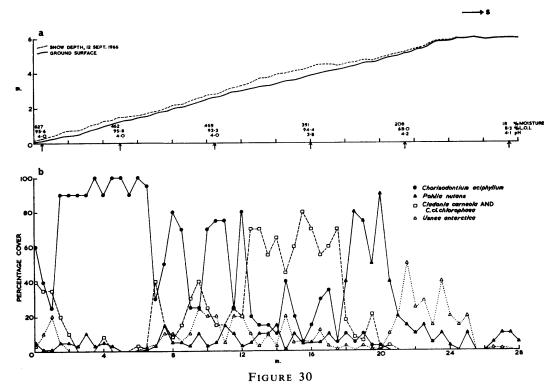
The interaction of environmental and biotic factors may cause a zoned pattern of communities on rocky knolls and ridges in low-lying coastal areas. The slopes of such knolls are frequently vegetated by stands of *Polytrichum alpestre* and *Chorisodontium aciphyllum*, while the exposed rocky crests may be occupied by small colonies of giant petrels. These large sea birds depend on the thermals created by the steeply rising slope for their take off, and when doing so tend to run out from the rocky summit and over the upper region of the peat banks before becoming airborne. The combination of wind exposure and the resulting absence of winter snow cover together with the excessive trampling and manuring of the knoll crests by the birds, precludes the development of vegetation beyond a few scattered moss cushions, crustose lichens and thalli of *Prasiola crispa*. Where the *Polytrichum-Chorisodontium* bank extends to the upper part of the slope it may be killed or replaced by a narrow zone of the *P. alpinum-Drepanocladus uncinatus* sociation. Associated with these two species are often large quantities of *Pohlia nutans* and various sterile crustose lichens. Because of down-washing and scattering by the birds' feet, mineral debris is spread over the surface of the peat and gradually becomes incorporated in it. The proportion of organic material is thus considerably lowered, consequently allowing a variety of fruticose lichens and occasional mosses to become established.

Below the area of influence by the birds, the peat bank is unaffected and *Polytrichum alpestre* and *Chorisodontium aciphyllum* develop typical stands with varying quantities of epiphytic lichens depending on the degree of exposure.

An example of this kind of situation is given in Fig. 30, which shows the change in species composition up a steep C. aciphyllum dominated slope onto a level stony terrace which was a former nesting site of giant petrels. The stony nesting site was nearly barren except for occasional crustose lichens, but immediately below it was a band of lichen-encrusted Pohlia nutans which merged into the Chorisodontium-lichen sociation lower down the slope, while the more sheltered part near the foot of the transect was almost pure Chorisodontium aciphyllum with a little Polytrichum alpestre, Pohlia nutans and Cephaloziella varians. The profile of the transect rose about 5.5 m. and during winter there was up to 50 cm. of snow in the middle region, but the depth decreased rapidly towards the top of the slope, with only 5-10 cm. in the Pohlia-dominated zone, and none on the exposed terrace. The nature of the soil varied considerably from about 95 per cent organic Chorisodontium aciphyllum peat to an almost entirely inorganic soil on the terrace, with a peaty mixture having an organic content of 68 per cent where Pohlia nutans was predominant. The moisture content decreased proportionately, according to the amount of organic matter in the soil. The pH throughout the transect was almost constant but it increased slightly as the mineral content increased.

## 6. Brachythecium cf. antarcticum-Calliergon cf. sarmentosum-Drepanocladus uncinatus association

The most extensive closed stands of vegetation on Signy Island are usually formed by species of the moss carpet sub-formation typical of swampy habitats. The sociations of the *Brachythecium* cf. antarcticum-Calliergon cf. sarmentosum-Drepanocladus uncinatus association exhibit two main types of pattern, namely environmental and sociological pattern.



The relationship between profile, snow depth and soil data, particularly the amount of inorganic material incorporated in the peat (a) and the percentage cover of the principal species (b) along a transect up a peat bank from the edge of a cliff on to a small exposed rocky plateau, at an altitude of c. 10–15 m., at Knife Point. The arrows indicate the positions on the profile where soil data were obtained.

The various sociations in this association are often distributed in a regular zoned pattern related to the wetness of the substratum. In the permanently wet situations, *Brachythecium* cf. antarcticum predominates with Calliergon cf. sarmentosum becoming prominent outside this wet zone, and in turn merging into a Drepanocladus uncinatus dominant zone on the drier, better-drained and stonier substrata where peat accumulation is least. Locally all these species may be found together. Where runnels flow through these habitats, there is often a marginal strip of hummocky Brachythecium austro-salebrosum. The other species, although of carpet growth form, may form a hummocky surface on more gravelly ground where frost action takes place. Wet hollows where snow lies late into spring are frequently dominated by a short slender form of Brachythecium cf. antarcticum, while the tall, more robust form and Calliergon cf. sarmentosum may be present around muddy pools.

Fig. 31 records the change in species composition along a belt transect which passed through a meandering melt stream about 30 cm. wide. In this case, *Calliergon* cf. sarmentosum dominated the marginal area with *Drepanocladus uncinatus* between it and the *Brachythecium* cf. antarcticum zone covering the stream (Gimingham and Smith, 1970, pl. 6, p. 780).

Fig. 32 indicates the distribution of swamp and dry habitat communities in relation to moisture regime and a variable depth of winter snow cover caused by exposure to wind. The swamp lay below the west-facing side of an exposed, dry stony ridge which retained a late snow patch well into summer on its west and north slope. By mid-summer a small portion of this snow patch still remained and provided the swamp with a continual source of water. The two wettest parts of the swamp, apart from a few pools of barren mud, supported closed stands of the fine form of Brachythecium cf. antarcticum, while the slightly drier ground was occupied by a mixed Calliergon cf. sarmentosum-Drepanocladus uncinatus sociation. Beyond the level boggy ground the slope increased slightly and the melt water collected into a system of runnels which were lined by deep coalesced hummocks of Brachythecium austro-salebrosum. Immediately above the swamp on the drier, more porous ground on the slope of the ridge was a narrow zone of dense Dicranoweisia grimmiacea which merged with a narrow stand of the Polytrichum alpinum-Drepanocladus uncinatus sociation. With increasing exposure to wind resulting in shallower snow cover in winter, together

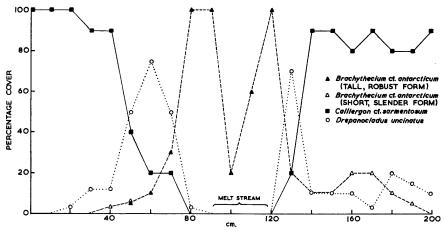


FIGURE 31

Percentage cover of the principal species along a transect across a melt stream meandering through a narrow swamp community, at an altitude of c. 15 m., west of Gourlay Peninsula.

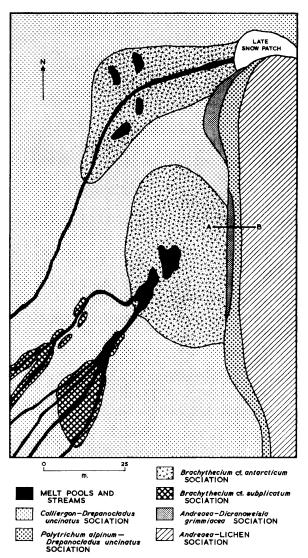
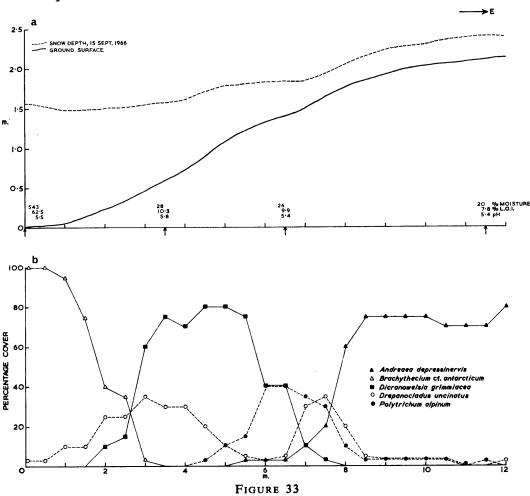


FIGURE 32

Distribution of communities from a permanently wet swamp dominated by species of *Brachythecium*, *Calliergon* and *Drepanocladus* to a low, stony knoll, c. 3 m. high, dominated by species of *Andreaea*, *Dicranoweisia grimmiacea* and lichens, at an altitude of c. 25 m., between Stygian and Starfish Coves. Transect A-B is illustrated in Fig. 33. The *Brachythecium* cf. *subplicatum* has been re-determined as *Brachythecium austro-salebrosum*.

with decreasing soil moisture, an extensive Andreaea-lichen sociation predominated on top of the ridge. Fig. 33 illustrates the environmental pattern produced by the distribution of the various sociations in relation to moisture regime, along line A-B in Fig. 32. The fine form of Brachythecium cf. antarcticum dominated the permanently wet swamp, giving way abruptly to Dicranoweisia grimmiacea on the considerably drier and stonier ground near the foot of the slope below the ridge. With increasing dryness of the soil, the slope became dominated by a Polytrichum alpinum-Drepanocladus uncinatus sociation which near the crest of the exposed ridge intergraded with an Andreaea-lichen sociation. The swamp was covered by deep snow in winter, and this remained until almost mid-summer, particularly along the foot of the slope.



The relationship between the profile, soil data and winter snow cover (a) and the percentage cover of the principal species (b) along transect A-B shown in Fig. 32, from the swamp to near the crest of the dry stony knoll. The arrows indicate the positions on the profile where soil data were obtained.

Certain moss carpet communities occur on gentle slopes of fine, muddy or gravelly soils which are susceptible to solifluction. The resulting micro-topographic pattern occurs particularly in small pure stands of *Calliergon* cf. sarmentosum, which are sometimes affected by movement of the substratum. Eventually the community is pulled into a V-shape, pointing down-hill, with coarser material at the margins. As the closed carpet is forcibly elongated, the upper broader portion begins to tear and the exposed soil may develop into frost boils. In some cases the frontal movement of the vegetation is arrested, although the soil a little up-hill remains mobile, and the carpet becomes buckled into a series of ripples. The carpet is only loosely attached to the substratum and consequently is readily pushed up into undulations. Drepanocladus uncinatus may also form fan-shaped or rippled stands where the substratum is unstable. However, there is no evidence of other species of moss or lichen becoming established on

these ridges such as occurs on the ripple systems seen in the *Polytrichum alpestre-Chorisodontium aciphyllum* association.

Sociological pattern is sometimes prominent in carpet-forming communities and the best examples observed have already been considered in the discussion of the *Polytrichum alpestre-Chorisodontium aciphyllum* association. Where stands of *Calliergon* cf. sarmentosum and *Drepanocladus uncinatus* occur in the less saturated areas of swamps near to shallow peat banks, or even occasionally adjacent to stands dominated by species of *Andreaea*, marginal invasion of the carpet communities may take place by turfor cushion-forming mosses from the neighbouring sociations, as already noted (p. 93, Fig. 25).

## VIII. OTHER MEMBERS OF THE SOUTH ORKNEY ISLANDS

ALTHOUGH the greatest diversity of species and the best-developed communities in the South Orkney Islands are found on Signy Island, many other areas support extensive stands of vegetation.

The greatest expanses of bryophytes and lichens are found on low promontories and islands which become free of snow and ice in summer, provided that they are not used as breeding sites by penguins. However, scattered colonies of bryophytes and lichens have been found at over 465 m., with occasional lichens going as high as over 650 m. The most widespread community types are those belonging to the Andreaea-Usnea, Polytrichum alpestre-Chorisodontium aciphyllum and Brachythecium cf. antarcticum-Calliergon cf. sarmentosum-Drepanocladus uncinatus associations, while the Caloplaca-Xanthoria association is well represented on coastal rocks. No communities have been seen which are not represented on Signy Island, but several of those found on that island have not been encountered elsewhere in the South Orkney Islands, e.g. some of the sociations occurring on calcareous soils and rocks and in flushed situations. The two flowering plants have been seen in several localities towards the western end of Coronation Island and both are known to occur on Laurie Island (Greene and Holtom, 1971). No quantitative studies were undertaken in any areas away from Signy Island.

# A. CORONATION ISLAND

## 1. Meier Point and Gosling Islands

Meier Point is a large promontory rising to about 30 m., the highest point being close to a permanent ice ramp leading to Pomona Plateau, at the western end of Coronation Island. The area is sparsely vegetated, although there are several small fresh-water pools and melt streams which provide suitable habitats for relatively large pure or mixed stands of Brachythecium cf. antarcticum, Calliergon cf. sarmentosum and Drepanocladus uncinatus. Drier ground is frequently colonized by a tall blackish form of Grimmia antarctica, Tortula cf. grossiretis and to a lesser extent by T. fuscoviridis suggesting that the rock and soil is fairly basic. Andreaeaa gainii is very scarce, and likely habitats are usually barren or support small stands of Bryum algens, Drepanocladus uncinatus, Pohlia nutans or Deschampsia antarctica. The grass also occurs around some of the pool margins but the tufts are usually small.

There is a notable absence of several common and widespread mosses including Andreaea depressinervis, A. regularis, Chorisodontium aciphyllum, Polytrichum alpestre and P. alpinum. Although Usnea antarctica is frequent, U. fasciata and Himantormia lugubris were not seen. Because of the relative scarcity of vegetation and the small number of species, together with the similarity of community composition with certain localities off the west coast of the Antarctic Peninsula, it is suggested that Meier Point has been only comparatively recently exposed by the receding ice of the Pomona Plateau ice cliffs.

Of the Gosling Islands, only the largest is well vegetated as the others have large colonies of breeding penguins. The most extensive stands on this island are banks of *Polytrichum alpestre* and *Chorisodontium aciphyllum*. The *Caloplaca-Xanthoria* association is also well represented.

### 2. Mansfield Point

This small promontory rises to about 25 m. and is extensively vegetated. The predominant species are those comprising the *Brachythecium* cf. antarcticum-Calliergon cf. sarmentosum-Drepanocladus uncinatus, the Andreaea-Usnea and the Polytrichum alpestre-Chorisodontium aciphyllum associations. Although only Andreaea regularis was collected, both A. depressinervis and A. gainii were present. The north side of the

point dips to the north and most of the vegetation occurs on this slope. Deschampsia antarctica is locally abundant here.

# 3. Cape Vik

The steep scree slopes and gullies between Laws Glacier and Cape Vik, at the west end of Marshall Bay, are snow-free to about 155 m. Because of the instability of the substratum and the lack of ground water, vegetation is sparse and almost restricted to the broad ledges of the cliff above the scree and to the fine material at the junction between cliff and scree. The rocky slopes of Cape Vik are occupied by large colonies of penguins and consequently are almost devoid of bryophytes and lichens, except for small stands of Brachythecium austro-salebrosum, Ceratodon cf. grossiretis, Drepanocladus uncinatus and Pohlia nutans. The largest turves are formed by Chorisodontium aciphyllum and Polytrichum alpinum on moist rock ledges. A single tuft of Deschampsia antarctica was found midway between Cape Vik and Laws Glacier, at an altitude of about 62 m. Cliffs near the shore support large expanses of Caloplaca-Xanthoria communities, while Usnea spp., Himantormia lugubris and many other lichens occur to around 310 m. on the higher rock faces of Maling Peak.

## 4. Lynch Island

Lying about 1.5 km. to the north of Signy Island in Marshall Bay, this island rises to a height of 33.5 m. and slopes northward. The usual bryophyte and lichen associations are widespread and the island is of particular interest in possessing extensive and well-developed stands of Deschampsia antarctica and Colobanthus quitensis. Certainly the largest stands of D. antarctica in the South Orkney Islands occur on Lynch Island, both on a relatively dry stony terrace at about 6 m. and on the damp north-facing slopes rising from it to around 15 m. Over much of these areas the grass forms a continuous deep sward. Colobanthus quitensis is also more abundant here than in any other locality in the South Orkney Islands. The island is also of interest in that Polytrichum alpinum has been found producing sporophytes in abundance in several localities. At its east end a large colony of gulls and terns creates a fairly baserich habitat supporting a poorly developed Bryum algens-Drepanocladus uncinatus-Tortula excelsa community.

# 5. Cape Hansen

Very little of this extensive area has been examined, but the precipitous slopes here rise to 286 m. and the higher parts form a fairly level plateau. This summit area is largely covered by communities of the Andreaea-Usnea association, particularly Usnea spp., and Himantormia lugubris. The north-west slopes near sea-level, opposite Lynch Island, support the greatest diversity of vegetation and include occasional small Polytrichum alpestre-Chorisodontium aciphyllum banks. The drier rockier ground has communities typical of the Andreaea-Usnea association, while wet rocks, gullies and depressions have Brachythecium austro-salebrosum, B. cf. antarcticum, Drepanocladus uncinatus and Calliergon cf. sarmentosum as well as scattered tufts of Deschampsia antarctica. J. A. Edwards (personal communication) has noted the occurrence of Colobanthus quitensis. The steep scree on the east side of the cape is colonized mainly by lichens but small Polytrichum alpestre-Chorisodontium aciphyllum banks occur on the lower, more stable areas.

## 6. Shingle Cove

The headland which forms the south side of the cove at the west end of Iceberg Bay is a continuation of the Cape Hansen range of hills and rises to 210 m. The eastern area is locally vegetated by bryophytes, although the rocks and cliffs support a rich lichen flora. The most extensive moss stands are formed by Polytrichum alpestre and Chorisodontium aciphyllum, but the wet habitat communities are more frequent. Deschampsia antarctica is abundant in places between the field hut and the east end of the promontory. The lower region of the block scree and parts of the coastal cliffs near the penguin colony are extensively covered by Caloplaca regalis, Xanthoria elegans and other nitrophilous crustose lichens typical of the Caloplaca—Xanthoria association. The easternmost promontory supports the only colony of Ramalina terebrata yet seen on Coronation Island.

Vegetation was also observed on a nunatak and nearby moraines north of Shingle Cove. This nunatak

forms a prominent twin buttress at 450–480 m. and lies a little to the south-west of Beaufoy Ridge. The area is extremely wind-swept and only part of the west-facing cliff has an extensive growth of *Usnea antarctica*, *U. fasciata* and *Himantormia lugubris*. Several crustose lichens are frequent, in particular species of *Buellia*, *Lecidea*, *Placopsis* and *Rhizocarpon*, with *Alectoria minuscula*, *A. pubescens*, *Omphalodiscus decussatus* and *Sphaerophorus globosus* among the less common of the larger species. Several minute thalli of *Umbilicaria cristata* were also seen on sheltered rock (Lindsay, 1969b). Apart from a few small cushions of *Andreaea regularis*, *A. gainii* and some shoots of species of *Pseudoleskea* in soil-filled crevices, bryophytes are rare.

The moraines lying below the nunatuk to the south-east and south-west at altitudes of 301 and 170 m., respectively, were only cursorily examined in late October and much of the rock was still covered by winter snow. The lichen flora is typical of montane regions, with species of *Usnea* predominant and numerous associated crustose species. A species of *Caloplaca* occurs on rocks on the lower moraine. Again the only mosses present were species of *Andreaea* but, as with the outcrops of the nunatak, many suitable bryophyte habitats were covered by snow at the time of observation.

### 7. Olivine Point

This extensive low-lying headland is adjacent to the east end of Sunshine Glacier and to a range of high precipitous cliffs to the north. The promontory rises to 37 m. at the south end, and topographically is very similar to the eastern coastal area of Signy Island. The south and east sides, together with Reid Island a few hundred metres offshore, have high cliffs and are locally covered by lichens typical of the coastal Caloplaca-Xanthoria association, while the west side dips in the form of a basin to a bay facing the glacier. Extensive wet habitat communities occur here, particularly around the small melt streams. The majority of the terrain is rocky and vegetated principally by communities of the Andreaea-Usnea association and less frequently by stands of Polytrichum alpestre and Chorisodontium aciphyllum, these latter species often forming an open association amongst local boulder fields. Rock faces support large quantities of Andreaea spp., Dicranoweisia grimmiacea, Himantormia lugubris and species of Omphalodiscus and Usnea together with an assortment of crustose lichens. The larger boulders and scree slopes are also well covered by these species. Extensive stands of Usnea spp. cover the rock faces at higher altitudes. Locally, areas of quartz-mica-schist stones have been split by frost action to give piles of plate-like slabs colonized only by occasional cushions of Andreaea gainii and Dicranoweisia spp. There are several raised beaches on the south side of the headland, and on their stony surface and the dry slopes rising from them small open stands of Andreaea spp., Dicranoweisia grimmiacea, Polytrichum alpinum and Racomitrium cf. crispulum occur.

An outcrop of amphibolite on the east side supports mixed communities of calcicolous bryophytes such as Bryum algens, Grimmia antarctici, Pohlia cruda var. imbricata, Pottia austrogeorgica, Tortula excelsa and T. fuscoviridis.

### 8. Devils Peak

Devils Peak is a mountain rising to 744 m. between Olivine Point and Rime Crests. The highest accessible rock exposure examined during a visit by D. C. Lindsay was at 698 m., where a lichen with numerous minute black rhizomorphs and light brown areolae, provisionally identified as *Buellia* cf. pycnogonoides, was collected. A minute thallus of *Usnea antarctica* was also found in a sheltered crevice. At a slightly lower altitude, 673 m., *Placopsis contortuplicata* was fairly frequent, producing large almost circular colonies 20–25 cm. in diameter.

### 9. Saunders Point

Separated from a rocky headland on the mainland of Coronation Island by a narrow channel, Saunders Point is the southern tip of a small island rising to 41.5 m. The most extensive vegetation is formed by communities of the Andreaea-Usnea association, with only small stands of Polytrichum alpestre and Chorisodontium aciphyllum and species of the swamp mosses Brachythecium, Calliergon and Drepanocladus. The north end of the island consists of cliffs in which rock crevice communities, with species of Andreaea, Dicranoweisia, Omphalodiscus and Usnea, give considerable cover. Wet rocks support Brachythecium austro-salebrosum, while occasional cushions of Grimmia antarctici and Tortula fuscoviridis occur on some

of the drier cliffs. Rocks near the shore are locally covered by species characteristic of the *Caloplaca-Xanthoria* association.

### 10. Matthews Island

Matthews Island, the largest and northernmost of the Robertson Islands group, rises to an altitude of 357 m. It is separated from the south-eastern extremity of Coronation Island by the narrow channel known as The Divide. Much of the lower snow-free slopes are occupied by large colonies of chinstrap penguins (Pygoscelis antarctica) and the area with the best-developed vegetation is the low promontory at the north-east corner of the island, rising to about 60 m. All the commoner bryophyte and lichen community types occur on this headland, where there are numerous banks of Chorisodontium aciphyllum which in places reach 1.5 m. in depth. As on the west side of Signy Island, the surface of these banks grades from pure, living Chorisodontium aciphyllum to heavily lichen-encrusted dead moss, and to expanses of wind-eroded bare peat. In the vicinity of flat muddy areas and pools close to a penguin colony and seal wallow, Prasiola crispa forms large stands. Small units of vegetation, composed principally of species of Andreaea and lichens, and of Chorisodontium aciphyllum, Drepanocladus uncinatus and Brachythecium austro-salebrosum, occur on broad rock ledges and occasional soil-covered slopes in several localities around the island to quite high altitudes. An extensive area of moraine on the north-west side of the island contains occasional small calcicolous cushion species including Grimmia antarctici, Tortula excelsa and T. fuscvoiridis. Most of the other moraines serve as breeding sites for penguins.

Rock faces are frequently festooned with Himantormia lugubris, Omphalodiscus spp. and Usnea spp. and shore cliffs are locally covered by species of Caloplaca, Xanthoria and other crustose genera. Despite the considerable exposure, several species of mosses and lichens occur on the small flat summit of the highest peak. Andreaea gainii, A. regularis, Dicranoweisia grimmiacea, Chorisodontium aciphyllum, Drepanocladus uncinatus, Polytrichum alpinum and the lichens Cladonia spp., Himantormia lugubris, Omphalodiscus decussatus, Placopsis contortuplicata, Rhizocarpon spp., Sphaerophorus globosus, Usnea antarctica, and U. fasciata, plus numerous unidentified crustose species, were all found at about 350 m.

Coffer Island, off the east side of Matthews Island, is also well-vegetated except where there are penguin colonies.

## B. POWELL AND FREDRIKSEN ISLANDS

# 1. Powell Island

Powell Island is the third largest island in the South Orkney Islands, measuring about 11 by 3 km. and rising to about 620 m. It is heavily glacierized except for the cliffs and summits of a central chain of mountains, as well as occasional snow-free headlands and an extensive low-lying peninsula at the south end, Michelsen Island. This is separated from Powell Island by a narrow isthmus which becomes submerged at high tide. Most localities were visited, except the northern extremity of Powell Island. Michelsen Island and the adjacent areas on Powell Island are occupied by very large colonies of penguins and other sea birds, and also by large numbers of seals. These areas are almost devoid of bryophyte vegetation due to the biotic influence, but species of the *Caloplaca-Xanthoria* association are abundant on the rocks, while the stony muddy pools support extensive stands of *Prasiola crispa*. The largest bryophyte community consists of a small stand of *Polytrichum alpinum*, mixed with *Andreaea depressinervis*, *Ceratodon* cf. grossiretis, *Drepanocladus uncinatus* and *Pohlia nutans*.

Considerable vegetation cover occurs on the promontories on the west coast from Falkland Harbour northwards, including Cape Disappointment which was not examined. The three main promontories rise to about 62 m. and possess extensive Chorisodontium aciphyllum peat banks reaching 1 m. in depth. Polytrichum alpestre is occasionally associated but not abundant. Communities of the Andreaea-Usnea and Brachythecium cf. antarcticum-Calliergon cf. sarmentosum-Drepanocladus uncinatus associations are widespread in all suitable habitats. Racomitrium cf. crispulum is locally frequent on the fine screes with species of Andreaea and various hepatics.

On the east coast three exposures of schist were examined, all about 125-155 m. a.s.l. and lying adjacent to an extensive ice piedmont. These outcrops, boulder fields and cliffs are locally covered by open stands of the Andreaea-lichen and Usnea-Himantormia lugubris sociations, with occasional small patches of Chorisodontium aciphyllum, Drepanocladus uncinatus, Polytrichum alpinum and P. alpestre. The sheltered wet cliffs are locally festooned with species of Omphalodiscus and Usnea. Another outcrop above the

north-west shore at about 280 m. is colonized mainly by small cushions of Andreaea spp., Dicranoweisia grimmiacea, Grimmia antarctici, Pohlia cruda var. imbricata, Tortula fuscoviridis and T. cf. grossiretis, as well as Drepanocladus uncinatus and Polytrichum alpinum. The most abundant plants on the rocks and cliff faces are species of Usnea and Himantormia lugubris.

Inland, conditions are considerably more arid and there is a marked contrast in the vegetation, which is usually very sparse and consists largely of montane lichen species. Most of the mountains rise from the ice piedmont to the east and there are several glaciers to the west. Usnea antarctica, U. fasciata and Himantormia lugubris are locally distributed, with Alectoria pubescens and Omphalodiscus decussatus usually associated. Crustose lichens are often frequent, especially species of Buellia, Lecanora, Lecidea, Ochrolechia, Placopsis and Rhizocarpon. All these genera occur on the numerous rock surfaces examined, to an altitude of about 450 m., while Parmelia saxatilis and Xanthoria candelaria are occasionally found on sheltered cliffs at lower altitudes. Grimmia antarctici and Tortula cf. grossiretis were recorded on a moist rock ledge at about 250 m., while Andreaea spp., Bartramia cf. patens, Dicranoweisia grimmiacea, Drepanocladus uncinatus, Pohlia nutans and Cephaloziella varians occur in crevices and on the more exposed rock surfaces. Of these species, A. depressinervis, A. gainii, Dicranoweisia grimmiacea, Drepanocladus uncinatus and Cephaloziella varians have been collected at the summit of John Peaks, at 422 m. altitude and A. gainii and D. grimmiacea at over 430 m. on an outcrop farther north.

### 2. Fredriksen Island

Despite its rather mountainous topography, Fredriksen Island is almost entirely snow-free in summer. A brief visit was made to below the col about midway along the island, on the east coast. Much of this area is occupied by large colonies of chinstrap penguins while cape pigeons and snow petrels breed on the rock ledges. Consequently the vegetation is restricted to rock faces and occasional ledges where the biotic effect is not too severe.

Prasiola crispa is the most frequent species on soil, but most rock surfaces support large stands of the Caloplaca-Xanthoria association and at higher altitudes species of Usnea and Omphalodiscus antarcticus are prominent. The only bryophytes seen were Drepanocladus uncinatus and Ceratodon cf. grossiretis. However, towards the north end of the island extensive bryophyte cover was observed from a distance and this has since been examined by N. J. Collins (personal communication), who noted large hummocky turves of Polytrichum alpinum not unlike those reported from Deception Island by Longton (1967). Small stands of Drepanocladus uncinatus with Pohlia nutans, Ceratodon cf. grossiretis and an associated species of Tortula occurred in moist situations. Small turves of Chorisodontium aciphyllum and cushions of Andreaea depressinervis were also noted, but no Polytrichum alpestre was seen. The only saxicolous moss noted was Dicranoweisia grimmiacea. The paucity of vegetation appears to be correlated with the extremely dry substratum as well as the extensive bird colonies.

## C. OTHER LOCALITIES

There are numerous localities which have not been visited by the author, but which having been observed from a distance, or from the presence of collections in various herbaria, and are known to possess bryophytes and lichens.

Atriceps, Skilling and Steepholm Islands in the Robertson Islands group and Christoffersen Island to the west of Michelsen Island (Fig. 3) all have large expanses of vegetation, and peat banks occur on the north sides of all these islands. On Steepholm Island there are extensive deep banks of *Chorisodontium aciphyllum*, large areas of which are eroded to barren peat. Amongst the penguin colonies on the two smaller unnamed islands in the Robertson Islands group there are small stands of what appears to be *Drepanocladus uncinatus*.

Extensive peat banks are known to exist between Rayner Point and Fulmar Crags on the north side of Gibbon Bay, north-east Coronation Island (personal communication from D. C. Lindsay). Lindsay has also noted large stands of species of *Usnea* at various altitudes to over 100 m. on Fulmar Crags, on cliffs on the south side of Gibbon Bay and at various altitudes to about 180 m. on several headlands and sea cliffs at the western end of Coronation Island between Penguin Point and Monroe Island.

Vegetation has been observed by the author\* on most snow-free low-lying promontories and offshore islands along the south coast of Coronation Island. Almost all coastal rocks bear communities of species of *Caloplaca* and *Xanthoria* which stand out as vivid orange splashes on the cliffs. At higher altitudes, the greenish colour of species of *Usnea* may also be prominent, and has been seen at about 620 m. on Divide Peaks at the eastern end of Coronation Island, and Beaufoy Ridge to the north of Shingle Cove flanking the western edge of Sunshine Glacier.

Small stands of bryophytes or lichens are also known to occur in the following localities, as well as on various intervening rock outcrops, moraines, etc.; Saddle and Weddell Islands in Washington Strait, Whale Skerries in Lewthwaite Strait, the cliffs at the eastern extremity of Divide Peaks range, the moraine on the north side of The Divide, Schist Point, Tophet Bastion (a high promontory to the east of Saunders Point), the promontory opposite Saunders Point, Amphibolite Point, the promontory opposite Lynch Island, Stene Point, Cleft Point (on the east side of Norway Bight), Cheal Point, Return Point, Monroe Island and Larsen Islands.

Collections were made during the visit of R.R.S. Discovery II in 1933 to Fredriksen and Michelsen Islands, as well as to Sandefjord Bay at the west end of Coronation Island. Other collections from that island include those made by W. J. L. Sladen in 1950 in the vicinity of Amphibolite Point and below Wave Peak, and by H. A. D. Cameron and P. Kennett in 1961 on Coffer Island off the east coast of Matthews Island. British and Argentine personnel have made several collections at various places on Laurie Island, notably Cape Geddes.

From the above evidence, it would appear that any snow-free rock or soil substrata, at least below about 300 m., will support limited stands of cryptogamic vegetation. Unfortunately, no landings or sightings of vegetation have yet been made on the north coast of Coronation Island.

### IX. DISCUSSION

In the Arctic, north of lat. 70° N., and at high altitudes in alpine areas, phanerogams are usually an important component of many plant communities. In the Antarctic, however, only two angiosperms, Deschampsia antarctica and Colobanthus quitensis, penetrate as far south as lat. 68° S. in Marguerite Bay towards the southern end of the Antarctic Peninsula, where some 30-40 species of bryophytes (personal communication from S. W. Greene) and some 200 species of lichens (Lamb, 1970) occur. These figures contrast strikingly with the approximately 500 species of phanerogams and the same number of bryophytes, as well as about 800 species of lichens at the same latitude north in Scandinavia (Mårtensson, 1956). According to Rudmose Brown (1912a, 1928) and Longton and Holdgate (1967), geographical isolation, the severe climate resulting in a shortage of suitable habitats with a regular supply of water, and the short cold summer with frequent sub-zero temperatures, are probably the most critical limiting factors in preventing the establishment of a wider range of phanerogams and cryptogams in the region

\* Since this report was written a brief survey of the vegetation at several additional localities in the South Orkney Islands was made during 1970-71 by M. McManmon (personal communication). On the largest of the Gosling Islands, off Meier Point, he noted stands of the Brachythecium cf. antarcticum-Calliergon cf. sarmentosum-Drepanocladus uncinatus association on wet slopes and around pool margins. Several moss species indicative of base-rich soils were collected in flushes and rock crevices, e.g. Grimmia antarctici and Tortula excelsa. An unnamed island north-east of Meier Point in Norway Bight revealed few species other than a stand of Drepanocladus uncinatus in a sheltered hollow with Usnea-dominated communities on the rocks above the penguin colonies. Similar vegetation occurred on the east side of Return Point at the south-west corner of Coronation Island.

Similar vegetation occurred on the east side of Return Point at the south-west corner of Coronation Island.

The southern half of Monroe Island was observed to be well vegetated to over 100 m., although much of the south-east coast was occupied by penguin rookeries. To the south and west of the permanent ice cap at the northern end of the island several flushes, melt streams and pools contained large stands of the Brachythecium cf. antarcticum—Calliergon cf. sarmentosum—Drepanocladus uncinatus and the Prasiola crispa associations. Elsewhere the less wet areas supported small stands of Polytrichum alpinum with associated Drepanocladus uncinatus and Pohlia nutans. At higher altitudes, species of Andreaea and Usnea were predominant. Occasional small banks of Chorisodontium aciphyllum were observed above the penguin colonies.

Although the two islands comprising Saddle Island are densely populated by penguins, according to McManmon the eastern island possesses eroded peat banks to about 100 m. a.s.l. While no living Chorisodontium aciphyllum was noted, partial re-colonization of the peat by other mosses had taken place. Species typical of the Andreaea-Usnea association were seen on rocks at various altitudes up to about 185 m. On the western island only Prasiola crispa was recorded, although the higher ground above the penguin colonies was not inspected.

On Laurie Island, banks of Chorisodontium aciphyllum with occasional Polytrichum alpestre were noted on the slopes above Points Rae and Davis, and Capes Valavielle, Geddes and Dundas, the best-developed banks being at the latter locality. At these places also there were frequent stands typical of the Andreaea-Usnea, Polytrichum alpinum-Drepanocladus uncinatus and Brachythecium cf. antarcticum-Calliergon cf. sarmentosum-Drepanocladus uncinatus associations. Several species of bryophyte occurred at over 310 m. on Cape Dundas.

south of lat. 60° S., i.e. within the Antarctic botanical zone. The problems relating to geographical distribution of plants within the Antarctic have been reviewed recently by Lamb (1970).

Although the South Orkney Islands experience a cold oceanic climate typical of the maritime Antarctic, considerable differences exist between Coronation Island, the main island of the group, and Signy Island immediately to the south of its central part. The former is high and mountainous with extensive glaciers and ice fields, and little snow- or ice-free ground even during summer. Signy Island is much smaller and of lower altitude but barely half of the island is covered by permanent snow or ice. In addition, it exhibits wide variations in rock and soil types, texture and stability of the substratum, topography, drainage patterns and moisture availability, exposure, and aspect. In contrast to Signy Island, the more continental conditions on Coronation Island reduce the range and availability of habitats, and consequently there is a marked paucity of plant species and of community types, as well as a reduction in the development and extent of stands of vegetation.

As a result of its environmental diversity, Signy Island supports a relatively well-developed vegetation, which, as elsewhere in the maritime Antarctic, must tolerate a wide range of environmental extremes. But, because of the comparatively severe conditions, its flora is restricted almost entirely to non-vascular cryptogams of which bryophytes and lichens are the main life forms. Both *Deschampsia antarctica* and *Colobanthus quitensis* are present, but they occur only in small quantities.

While the vegetation of the maritime Antarctic comprises communities almost entirely composed of cryptogams, such assemblages are not unique in the ecosystems of the world. In most other polar regions, where the environment presents relatively severe conditions for plant growth, purely cryptogamic communities are composed largely of lithophytes and chionophytes. On the basis of the present classification, these are represented in the South Orkney Islands, and elsewhere in the maritime Antarctic, principally by the fruticose lichen and moss cushion sub-formation and by the crustose lichen sub-formation. Indeed many of the sociations of Signy Island compare favourably with the descriptions and lists of species of cryptogamic communities in Arctic-alpine regions, e.g. Watson (1925), Gams (1932), Mårtensson (1956) and McVean (1964). Gams (1932), in his general classification of bryophyte "societies", commented on the preponderance of epipetric bryophyte and lichen communities, which he termed "Epipetria", in Antarctic regions. He also mentioned "Helophytia" or swamp and peat-forming communities of regions around the Antarctic coasts. However, it seems probable that these latter regions incorporate sub-Antarctic and possibly certain southern cold temperate lands.

Outside the Antarctic, pure stands of bryophytes, in which phanerogams are absent, are generally small in extent but are typical of Arctic-alpine late snow beds where many of the species, especially hepatics, are typically chionophilous. On Signy Island similar assemblages are represented by communities dominated by species of Andreaea and Polytrichum alpinum in which foliose hepatics are often abundant. Certain southern cold temperate regions with high rainfall and humidity, e.g. Staten Island, also possess extensive pure bryophyte stands. Elsewhere, bryophytes and lichens may form a closed understorey beneath such phanerogams as dwarf shrubs, forbs and particularly certain forest communities, while the latter may also possess distinct epiphytic assemblages of both bryophytes or lichens.

Several of the communities occurring in the maritime Antarctic bear a close resemblance to certain of those in slightly less severe environments where vascular plants are associated, as in the tundra regions of the sub-Antarctic or the Arctic. For example, many of the terricolous cryptogam communities on Signy Island are found in similar habitats on South Georgia but with the inclusion of occasional phanerogams and various bryophytes and lichens which are not known farther south. Communities of species of Andreaea, fruticose lichens and occasional Racomitrium cf. crispulum and Chorisodontium aciphyllum which occur on Signy Island are replaced in sub-Antarctic, Arctic and alpine regions by physiognomically similar assemblages constituting the typical Racomitrium, Cladonia and dicranoid tundra "heath". The permanently wet communities supporting the moss carpet and moss hummock sub-formations of the maritime Antarctic are replaced in other regions of the world by stands of Sphagnum forming ombrotrophic raised bog or hochmoore, although several of the important associates belong to genera which are well represented on Signy Island and farther south, e.g. Calliergon and Drepanocladus. The deep Polytrichum-Chorisodontium banks of the South Orkney Islands are replicated on South Georgia and have their equivalent formation in certain Arctic regions where deep Sphagnum bogs, often with associated species of Polytrichum and Dicranum, may develop a permafrost and become subjected to frost heaving with the production of raised dome-shaped palsen (Mårtensson, 1956) or thufur (Raup, 1965). Several phytosociologists have produced broad classification systems of the terrestrial vegetation of the world, which are designed to include virtually all categories of plant communities in a great diversity of geographical regions and environmental situations. However, these include little or no consideration of Antarctic or in fact of sub-Antarctic vegetation except for occasional reference to the general type of vegetation which exists in these regions. This situation inevitably results from the fact that the well-documented systematic and quantitative treatments of vegetation which exist for most parts of the world have so far not been provided for Antarctic regions, exceedingly little having been published so far on the synecology of the southern polar regions. Hence the present detailed account of the terrestrial plant communities of one region in the maritime Antarctic should provide a basis from which to rectify this situation.

The quantitative and qualitative investigations of the vegetation of Signy Island reported in this paper have led to the recognition of a large number of more or less discrete floristic units. For this reason it has been possible to erect a hierarchical system of classification based on the method originally proposed by Braun-Blanquet (1932). By contrast, the vegetation of South Georgia, which has also been the subject of a phytosociological analysis by the author, has been found to exhibit a distinct multi-directional continuum of variation.

In addition to establishing a classification of the island's terrestrial vegetation, descriptions and quantitative floristic and edaphic data have been provided for the majority of the vegetation units recognized on Signy Island. Both physiognomic and floristic criteria have been used and the sub-units at the lower level of the hierarchy, although reflecting features of the environment, may be easily distinguished in the field.

The two primary sub-divisions have been based on physiognomic features of the island's flora. As life form was held to be the most important of these features, it resulted in the recognition of an Antarctic non-vascular cryptogam tundra formation and an Antarctic herb tundra formation, both of which could be satisfactorily incorporated in the "moss, lichen and dwarf shrub tundras" formation, a sub-class of the world vegetation classification scheme of Ellenberg and Mueller-Dombois (1966) who, in fact, made no reference to Antarctic vegetation. On the other hand, Fosberg's (1967) system of world vegetation separated closed and open bryophyte and lichen vegetation into distinct formation classes so that the presently constituted non-vascular cryptogam tundra formation would have to be split between his "closed bryoid vegetation" and "bryoid steppe" formations. Under this system the Antarctic herb tundra communities would have to be included in a closed "short grass" formation class or an open "desert herb vegetation" formation class. Although the two Antarctic tundra formations fit most easily into the Ellenberg and Mueller-Dombois scheme, even that will need some modification if the present proposals gain wide acceptance.

Within the cryptogamic formation described for Signy Island, several sub-formations have been identified on the basis of a further physiognomic criterion, namely the growth form of the predominant species. Associations, on the other hand, are differentiated on the basis of floristic similarity of component stands which possess a high degree of constancy in a particular group of species. Within an association there may be several floristically similar assemblages, each of which is distinguished according to its dominant species. These ecological variants, classed as sociations, are attributed to minor variations in the habitat.

Earlier attempts to describe or classify Antarctic vegetation are few and incomplete. Skottsberg (1905, 1912, 1950) provided an account of various communities of certain northern areas of the Antarctic Peninsula and the South Shetland Islands. He described, by the use of species lists, several predominantly lichen assemblages, a wet *Brachythecium* "carpet" community and several *Polytrichum* and *Andreaea* tundra "formations". Lamb (1948, 1964, 1968) has provided ecological notes and habitat descriptions for various groups of Antarctic lichens.

A more systematic descriptive treatment of Antarctic vegetation was provided by Holdgate (1964), who outlined a preliminary classification of the plant assemblages of Signy Island, which provided a basis for subsequent systematic study of Antarctic terrestrial vegetation. Longton (1967) broadened this classification to incorporate other regions of the maritime Antarctic while the present work has explored in depth its detailed application to the vegetation of the South Orkney Islands. Elsewhere it has been shown (Gimingham and Smith, 1970) that this detailed treatment can also be applied to other parts of the Antarctic botanical zone.

The only other critical assessment of Antarctic vegetation that has been published so far is by Follmann (1965), who confined his description and classification to a single prominent lichen "association" frequent on coastal rocks along the western coast of the Antarctic Peninsula. Although he applied the method and nomenclature of Braun-Blanquet (1932), whereby plant assemblages were described according to floristic criteria, chiefly dominance and constancy derived from the inspection of species lists, physiognomic criteria were not considered and very few quantitative data were presented. He recognized a Ramalinetum terebratae association for stands in which Ramalina terebrata predominated, and described two ecological variants, occupying slightly different habitats, in which Polycauliona (= Caloplaca) regalis and Thamnolecania gerlachei (= Lecania brialmontii) were the most important associates. These variants were termed Polycaulionetosum regalis and Thamnolecanietosum gerlachei, respectively. Follmann suggested that this association bears close affinities to coastal Ramalineta in other parts of the world, and implied that it could be included in the lichen classification proposed by Klement (1955) for the epipetric lichen associations of Central Europe, or the more universal system proposed by Mattick (1951). The ecological variants of Follmann's Ramalinetum terebratae association are equivalent to the Xanthoria elegans-Ramalina terebrata sociation of the Caloplaca-Xanthoria association recognized on Signy Island; they may also incorporate the Xanthoria elegans and Caloplaca regalis sociations.

Gimingham (1967) has pointed out that the range of bryophyte growth forms in the maritime Antarctic is considerably less than in temperate regions, being largely restricted to cushion, turf and carpet growth forms, while species exhibiting a pleurocarpous habit are very infrequent. Lichens are predominantly of crustose or fruticose growth form, and representatives of certain genera, which are crustose in other parts of the world, develop a fruticose habit in Antarctic regions (Lamb, 1970).

It has been demonstrated by Gimingham and Birse (1957) that growth form in mosses is correlated with features of the environment, of which the type of substratum, moisture availability and the degree of shading were considered the most important. On Signy Island terrestrial habitats may be grouped into broad categories, namely dry exposed substrata with very irregular moisture availability and those where there is a permanent supply of water, with some degree of shelter and soil accumulation. Species growing in the former situations tend to possess a low cushion, or to a lesser extent a short turf growth form, in which the moisture content must fluctuate almost daily between saturation and near dehydration. Gimingham and Smith (1971) have shown that cushion and turf species from these situations on Signy Island hold only about half the volume of moisture contained by carpet species occupying wet habitats on the same island. However, they also demonstrated that the former group of species lose water considerably more slowly, but take up water more rapidly than those from wet habitats. Similarly, when exposed temporarily to high evaporation stresses mosses from the dry habitats retain a small proportion of moisture, whereas those from wet habitats may become completely dehydrated and fail to recover when water is again available.

The availability of water in the maritime Antarctic is largely dependent upon the climate, and in particular on the temperature regime at ground level. Holdgate (1964) was the first to demonstrate for Signy Island that the environment at this level is considerably more favourable for plant growth than ambient data alone suggest. The degree of exposure to solar radiation, the aspect of a site, particularly in relation to north, and the slope and moistness of the habitat are important factors affecting ground level temperatures and their diurnal amplitude. It has been shown that the growth and reproductive performance of many species can be closely related to the temperature regime of this micro-environment (Longton and Greene, 1967; Longton and Holdgate, 1967; Longton, 1970, 1972).

In the summer months Antarctic vegetation is subjected to a rapidly fluctuating diurnal temperature regime which barely exists in the surrounding air. Thus, during their metabolically active period, the plants must tolerate not only a considerable daily amplitude, but also frequent sub-zero temperatures, especially at night. In addition, they have to contend with great extremes of temperature, with a possible annual range of  $70^{\circ}$  C, e.g. on Signy Island. The vegetation is also subjected to a regular, often daily, freeze-thaw cycle with only short periods when the temperature remains above freezing point. According to Ahmadjian (1970), Antarctic mosses can "photosynthesize and respire at temperatures near  $-4^{\circ}$  C, and below this photosynthesis ceases but respiration continues. Deschampsia does not photosynthesize below  $0^{\circ}$  C but respires at high rates down to  $-10^{\circ}$  C." In the case of certain Antarctic lichens, Gannutz (1969) stated that the most favourable conditions for gas exchange are under a high moisture content, low light values and temperatures between  $-2^{\circ}$  and  $+14^{\circ}$  C. Ahmadjian (1970) quoted Gannutz as

reporting that in Antarctic lichens the optimal temperatures required to maintain a positive metabolic balance were between  $-10^{\circ}$  and  $+10^{\circ}$  C. Kappen and Lange (1970) have shown that the metabolism of several Antarctic lichens was unaffected after being cooled to  $-196^{\circ}$  C in liquid nitrogen. From data provided by Longton (1972) it would appear that during much of the summer ground-level temperatures in favourable habitats on Signy Island remain at least  $5^{\circ}$  C above freezing point for much of the day.

On Signy Island, and elsewhere in the maritime Antarctic, the limited range of life forms and growth forms, together with the relatively small number of species, leads to the formation of simple communities, the most luxuriant and extensive stands only developing where optimum conditions exist. Indeed it is apparent that one of the distinctive features of Antarctic vegetation is the homogeneity of species composition within many of the communities and the consistency with which these floristic units are replicated both on Signy Island and in the maritime Antarctic as a whole. Gams (1932) noted that this feature was characteristic of closed bryophyte communities in general. Furthermore, on Signy Island, many assemblages of bryophytes and lichens may be almost identical in structure and species composition, differing only in their dominant species. Because of this, ecologically important species frequently replace each other in response to environmental gradients, although both may have a relatively wide ecological amplitude and occur in a number of different communities. With further study it may be possible to use the behaviour of some of these species as indicators of fairly precise environmental conditions.

Previous studies of Antarctic terrestrial plants have paid little attention to the spatial arrangement of species or communities in relation to environmental gradients. An exception was Longton (1967), who described various moss and hepatic zones around fumaroles on Candlemas Island, South Sandwich Islands, correlated with temperature and humidity gradients.

Other workers have mapped the large-scale distribution of cryptogamic assemblages in relation to topography or rock types in certain Antarctic regions, e.g. Rudolph (1963) at Cape Hallett, Victoria Land, and Matsuda (1963) for moss communities on East Ongul Island, Dronning Maud Land. But it is thought that the number of small-scale patterns and phytosociological gradients which have been revealed by the many sets of transect data obtained on Signy Island is the first indication of how wide-spread and important these small-scale patterns may be in the interpretation of Antarctic vegetation. Pattern analysis, successional and cyclical processes have been investigated in similar predominantly cryptogamic tundra-type vegetation in other parts of the world, although in such cases phanerogams were generally present as sparse associates, e.g. Watt (1947), Wilson (1952), Sheard (1968) and Billings and Mark (1961). Although these small-scale patterns and processes on Signy Island appear to be caused almost exclusively by a few micro-environmental factors such as micro-topography, micro-climate, cryoturbic disturbances and edaphic variations, they appear to be remarkably similar to situations described in other parts of the world where more diverse factors may operate.

A typical feature of pattern in communities on Signy Island is the abruptness of the transition in floristic composition between adjacent stands; this is closely correlated with habitat gradients which in some cases may be very marked, e.g. along the margins of swamp areas, and boundaries between marble and schist. Where the environmental boundaries are more gradual and communities intergrade, there may be an admixture of species representing both assemblages producing a rather heterogeneous stand along the ecotone. A consistent feature of most communities is that they appear to be stable and in equilibrium with their environment, and go through virtually no successional phases from the time of their establishment. This conclusion is based on the uniformity of composition and the regularity of occurrence of small units of vegetation in their appropriate habitats. Consequently, it is thought that where successional development does occur, the process appears to be rather slow. However, before any precise statements may be adduced, it is essential to initiate long-term studies employing the use of permanent quadrats and marked plants or colonies of plants in order to measure such changes. It is also necessary to acquire more knowledge of the autecology of the species concerned, e.g. their growth rates, environmental tolerances, ecological amplitude and competitive ability, etc.

The most obvious example of possible succession occurs within the *Polytrichum alpestre-Chorisodontium aciphyllum* association, particularly in the establishment and build-up of the deep peat banks and their subsequent degeneration or destruction by frost and wind.

The peat banks in the South Orkney Islands occur in various phases ranging from pure moss without epiphytic lichen associates to complete cover by crustose, and to a lesser extent by fruticose, lichens particularly in the more exposed parts of the banks. Following the encrusting stage, the moss surface

appears to be killed and wind and frost action gradually destroy the lichen cover also. The banks finally enter a degenerative phase when erosion commences and removal of the moribund moss and lichen reveals areas of barren, puckered fibrous peat. Plates IVa-d and Va and b illustrate these successional stages. Subsequent re-colonization appears to be very slow and possibly incomplete.

Samples of moss shoots from the base of these banks are easily identifiable, and carbon dating of one sample, from the base of a bank 180 cm. deep, has shown that the bank commenced development approximately 2,000 yr. ago (Godwin and Switsur, 1966). Since bacterial and fungal activity is retarded by the low temperatures, organic break-down is extremely slow and a decomposition rate of 2 per cent per annum has been calculated from one bank of *Chorisodontium aciphyllum* (personal communication from J. H. Baker). As the permafrost occurs only a short depth below the living moss surface, compression of the peat must be minimal, although banks of moss shoots lying at considerable angles to the vertical are not infrequent, suggesting some degree of movement within the banks. If the oldest moss banks on Signy Island are approximately 2,000 yr. old, a mean growth increment of barely 1 mm. per annum is suggested. However, the author has measured annual increments ranging from 1 to 13 mm. within a single stand of *Polytrichum alpestre*. Discussion with N. J. Collins has led to the suggestion that a series of cyclical phases, possibly correlated with minor climatic variations, may be responsible for the apparently retarded growth of the banks. Hence, once a bank has built up and gone through several phases including surface erosion, development is suspended until re-colonization has taken place.

Although the majority of the Signy Island plant assemblages have been presented as distinct entities, some groups of basically similar communities possess such close affinities, in structure and composition, as to suggest a rather simple, small-scale continuum of variation. This is particularly noticeable in the range of communities in which species of Andreaea and Usnea predominate. The lack of uniformity throughout the stands of Deschampsia antarctica and Colobanthus quitensis also provide evidence of a continuum ranging from a pure grass sward to a community in which Drepanocladus uncinatus or other bryophytes become dominant and the phanerogams are merely isolated associates.

In some instances, notably lichen communities of coastal rocks, the pattern takes the form of a distinct zonation of floristically similar stands but with each zone being dominated by a different species. These zoned lichen assemblages bear a close resemblance to coastal rock communities in many other regions of the world. As with most other aspects of the spatial arrangement of plant assemblages on Signy Island, these are related to environmental factors.

Almost all the examples of pattern and other dynamic aspects of the vegetation are caused by features of the environment such as variations in the moisture regime, base status, pH, micro-topography, exposure, degree of soil or snow accumulation, etc. When several of these factors interact within a small area, certain species or groups of species which respond to minor differences in the habitat combine to produce an overall colourful and rather intricate pattern of very small bryophyte and lichen units, which may be regarded as polyclimax communities controlled by a number of environmental factors. In other parts of the world where the vegetation usually contains numerous phanerogams, many conspicuous forms of pattern result also from sociological and morphological characteristics of the plants themselves. Such causal factors of pattern are rare in the purely cryptogamic communities in the maritime Antarctic.

Perhaps the best example of an autogenic factor resulting in sociological pattern, whereby one group of species modifies a habitat and permits the establishment of other species, is provided by occasional soligenous moss carpets which may be colonized or invaded by turves of *Chorisodontium aciphyllum*. These may ultimately lead to the development of a more ombrogenous peat bank in which *Polytrichum alpestre* and numerous epiphytic lichens become established. One of the few examples of morphological pattern on Signy Island is provided by *Polytrichum alpinum*; other members of the Polytrichaceae behave similarly in other regions of the maritime Antarctic. Due to the radial development of the underground stem system of this moss, individual plants tend to produce small circular stands which may exhibit cyclical changes. As noted earlier, when the central zone of the *Polytrichum alpinum* colony dies, several species of bryophytes and encrusting lichens may become established and eventually may themselves be displaced by newly produced aerial shoots from underground stems of *P. alpinum*. A similar cycle of stages has been observed in tufts of *Deschampsia antarctica*, cushions of *Colobanthus quitensis* and occasionally in large circular colonies of crustose lichens.

It is thought that the diversity and development of plant communities on Signy Island is not entirely representative of the vegetation of the South Orkney Islands. Since Signy Island is considerably less

glacierized than most of the other islands, it provides a wider range of habitats and rock types for colonization and the establishment of assemblages. Hence, it is not surprising that many more bryophyte and lichen species and community types are known from Signy Island. But the comparative richness of this island may simply reflect the fact that few of the many suitable habitats known to occur elsewhere in the group have not yet been examined by botanists, and so inadequacy of survey may be the main reason why no community type has been identified from elsewhere in the group which does not also occur on Signy Island.

Similarly, considerably less attention has so far been paid to localities on or near the west coast of the Antarctic Peninsula, although several distinct community types have been reported by Gimingham and Smith (1970) which are not represented in the South Orkney Islands. It is not yet clear, however, how representative the vegetation of Signy Island is of the maritime Antarctic and extensive phytosociological and ecological survey using the same methods as applied to Signy Island is necessary both within the other South Orkney Islands and elsewhere in the region before this question can be satisfactorily answered.

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APPENDIX DETAILS OF SITES ON SIGNY AND CORONATION ISLANDS REFERRED TO IN THE SOCIATION TABLES

Site number	Locality	Altitude (m.)	Aspect	Slope (degrees)
	Andreaea-lichen sociation			
1	Col between two low hills south-west of Mirounga Flats	30	Level	0
2	Low hill between The Wallows and Balin Point	30	SE	3
3	Low hill between Stygian and Starfish Coves	30	WNW	8–10
4	Slope of low hill north-east of Lenton Point	23	NW	2
5	Lenton Point	20	WNW	3
	Andreaea sociation			
6	Knoll north-east of Moraine Valley	62	WNW	0–4
7	Small plateau north-east of Moraine Valley	75	Level	0
8	Hollow below late or permanent snow patch, north slope of Rusty Bluff	95	NE	3
9	East of lake situated south-west of Stygian Cove	30	WNW	6
10	East of Express Cove	70	NW	0-2
	Andreaea-foliose hepatic sociation			i 1
11	Slope on east side of Factory Cove	65	NNW	16
12	Western slope of Rusty Bluff, Moraine Valley	70	NW	20
13	North-western slope of Rusty Bluff, Moraine Valley	75	NW	24
14	Below late snow patch, north-western slope of Rusty Bluff	70	NW	14
15	North slope of Observation Bluff	60	NNW	12–15
	Andreaea-Dicranoweisia grimmiacea-Usnea-Omphalodiscus sociation			
16	Cliffs on south side of Factory Cove	55	NW-N	80–90
17	Cliffs above Paal Harbour on east side of Rusty Bluff	60	NE-E	80–90
18	Near summit of largest of Thule Islands	20–25	Variable	30–60
	Andreaea-Himantormia lugubris sociation			
19	Ridge between Jane Peak and Foca Point	135	Level	0
20	Ridge between Jane Peak and Express Cove	155	w	2–5
21	Plateau north-west of Jane Peak	130	w	10
22	Plateau west of Observation Bluff	90	NE	1–2
23	Plateau west of Observation Bluff	90	Level	0
	Usnea-Himantormia lugubris sociation			
24	Plateau west of Observation Bluff	90	NNW	7

Site number	Locality	Altitude (m.)	Aspect	Slope (degrees
25	Plateau west of Observation Bluff	90	Level	0
26	Near summit of Snow Hill	265	N-W	1–15
27	North slope of Rusty Bluff	100	NE	11
28	Plateau south of Factory Cove	120	Level	0
:	Usnea–Omphalodiscus–Himantormia lugubris sociation			
29	Outcrop on plateau south-west of Robin Peak summit	200	W-NE	30–90
30	Near summit of largest of Thule Islands	20–25	Variable	30–60
31	Near summit of Observation Bluff	100	NW-NE	70–80
32	Cliffs on south side of Factory Cove	75–95	NW-NE	60–80
	Usnea antarctica sociation			
33	Summit of low hill north-east of Lenton Point	30	E-N-W	0–5
34	Plateau north-west of Jane Peak	130	ENE	11
35	Col between plateau south of Factory Cove and north side of Rusty Bluff	80	WNW	7
36	Knoll near Mooring Point	7	NW-E	0–10
37	Ridge south-west of Factory Cove	40	Level	0
	Assemblages in siliceous rock crevices			
38-41	Cliffs above Paal Harbour on east side of Rusty Bluff	60–90	NE-E	60–90
42	Cliffs south-east of Port Jebsen	125	N	70-90
43	Small cliff on north side of Knife Point	1 · 5 – 3	NE	75
44	Sloping rock face on east side of Moraine Valley below Rusty Bluff	95	WNW	45
45	Crevice 15 cm. long by 5 cm. high by 5 cm. deep, in cliffs above Paal Harbour on east side of Rusty Bluff	90	ENE	0
	Assemblages in calcareous and base-rich rock crevices			
46	Cliffs above south-west corner of Stygian Cove, below Robin Peak	35–40	E-SE	70–90
47	Ridge south-east of North Point, on north-west side of Robin Peak	40	W-N	90
	Tortula sociation			
48	Between North Point and Robin Peak, below marble outcrops	45	WNW	18
49	North-facing slope of ridge between Foca and Thulla Points	20	NNW-N	18
50	Marble knoll between Elephant Flats and Waterpipe Beach	15	w	18

Site number	Locality	Altitude (m.)	Aspect	Slope (degrees)
51	Marble knoll between Elephant Flats and Waterpipe Beach	20	E-ESE	15
52	Marble knoll at south side of Waterpipe Beach	5	N-NNE	14
	Grimmia antarctici sociation			
53	Below amphibolite outcrops on west side of northernmost lake in Three Lakes Valley	28	E	14–22
54	Below marble knoll on east side of southernmost lake in Three Lakes Valley	20	w	4
55	Below marble outcrop on north side of low hill south-west of Mirounga Flats	20	NNE-NE	56
56	Plateau of glacial detritus between southernmost and middle lakes in Three Lakes Valley	30	Level	0
57	Plateau of glacial detritus between southernmost and middle lakes in Three Lakes Valley	30	S	2–5
	Tortula-Grimmia antarctici sociation			
58	Marble knoll between Elephant Flats and Waterpipe Beach	15	E	12
59	Marble knoll between Elephant Flats and Waterpipe Beach	15	ENE	16
60	Slope east of Thulla Point	30	SW-W	7
61	Slope east of Thulla Point	35	wsw	8
62	Marble knoll at south side of Waterpipe Beach	6	ESE	9
	Pottia austrogeorgica sociation			
63	Muddy wallow area on north side of Elephant Flats	10	SSE-S	3
64	Below marble outcrop on east side of southernmost lake in Three Lakes Valley	20	w	4
65	Below marble outcrop on east side of southernmost lake in Three Lakes Valley	20	w	5
66	Above south-west shore of Factory Cove	1.5-2.5	ENE	0–5
67	Below amphibolite outcrop north of The Wallows	25	wsw	6–10
	Verrucaria sociation			
68	North-west side of largest of Billie Rocks	0–2	NW	50–90
69	South-west of Berntsen Point	0–1 · 5	NW	50–90
70	South side of Waterpipe Beach	0-2.5	N-NNE	60–90
71	Southern end of largest of Thule Islands	0–2	NE	25–50
	Caloplaca sociation, with Caloplaca cirrochrooides dominant			
72	North-west side of largest of Billie Rocks	2–3	NW	60–90

Site number	Locality	Altitude (m.)	Aspect	Slope (degrees)
73	Southern end of largest of Thule Islands	1.5	S-W	70–90
74	South side of Waterpipe Beach	1.5	N	85
	Caloplaca sociation, with Caloplaca sp. dominant			
75	South-west of Berntsen Point	1.5	NNW	60–90
76	Southern end of largest of Thule Islands	1.5	S-W	40–50
77	South side of Waterpipe Beach	3	N	85
	Xanthoria elegans sociation			
78	South-west of Bernsten Point	<b>5</b> 7	NW	26
79	Southern end of largest of Thule Islands	5	NNE	40
80	South side of Waterpipe Beach	5	N	60
	Xanthoria elegans–Ramalina terebrata sociation			
81	North-west side of largest of Billie Rocks	6	NW	60-90
82	Southern end of largest of Thule Islands	5–7	w	80–90
83	South side of Waterpipe Beach	6	N	60-90
	Caloplaca regalis sociation			
84	North-west side of largest of Billie Rocks	4–5	NW	50–90
85	Cliffs above south side of Factory Cove	30	N-NNE	90–100
	Caloplaca sociation, Caloplaca-Verrucaria-Orthotrichum crassifolium assemblages			
86	South side of Tern Cove	1 · 5 – 5	NE	20–90
87	Above shore north of Observation Bluff	1 · 5 – 3	N-NE	50-90
88	Above shore north of Observation Bluff	1 · 5 – 3	N-NE	70–90
89	Polynesia Point	8–10	E	0–15
	Chorisodontium aciphyllum sociation			
90	Area east of Spindrift Rocks	65	w	5–7
91	Area east of Spindrift Rocks	65	w	6
92	Area east of Spindrift Rocks	50	WNW	7
93	Area east or Spindrift Rocks	40	w	6
94	Crest of ridge between Thulla and Foca Points	55	SSE-S	10–20

Site number	Locality	Altitude (m.)	Aspect	Slope (degrees)
	Chorisodontium aciphyllum-lichen association			
95	Area east of Spindrift Rocks	55	W-WNW	18-20
96	Area east of Spindrift Rocks	65	W-WNW	4
97	Area north-east of Spindrift Rocks	65	W-WNW	5
98	Area north-east of Spindrift Rocks	80	WNW	8
99	Between Lenton Point and Gourlay Peninsula	23	Level	0
	Polytrichum alpestre-Chorisodontium aciphyllum sociation			
100	South side of Factory Cove	20	N-NE	32
101	North side of Observation Bluff	40	N	26–30
102	Area east of Spindrift Rocks	65	WNW	11
103	West side of hill south-east of McLeod Glacier, near Gourlay Peninsula	50	w	3
104	Between Lenton Point and Gourlay Peninsula	23	Е	2
i	Polytrichum alpestre-Chorisodontium aciphyllum-lichen sociation			
105	Area east of Spindrift Rocks	50	W	11
106	Area east of Spindrift Rocks	65	W	15
107	Area north-east of Spindrift Rocks	90	WNW	20
108	Knife Point	15	NNW-N	17
109	Slope on east side of Factory Cove	65	N	24
	Polytrichum alpestre-Chorisodontium aciphyllum banks heavily colonized by epiphytic lichens			
110	Area east of Spindrift Rocks	50	WNW	7
111	South-south-west of Knife Point	25	N-NE	5–10
	Polytrichum alpinum-Drepanocladus uncinatus sociation			
112	Between Elephant Flats and Mooring Point	7	WNW	9
113	East side of Factory Cove	6	WNW	8
114	Knife Point	16	ENE	8
115	Mooring Point	3-5	ESE	14
116	East side of ridge in The Wallows	16	ENE	20
	Brachythecium cf. antarcticum sociation with short, slender form of B. cf. antarcticum			
117	Late snow patch hollow on slope east of Factory Cove	30	NW	5

Site number	Locality	Altitude (m.)	Aspect	Slope (degrees)
118	North-east side of Factory Cove	12	Level	0
119	Between Lenton Point and Gourlay Peninsula	20	SE	4
120	South-east of Stygian Cove	25	NW	3
	Brachythecium cf. antarcticum sociation with tall, robust form of B. cf. antarcticum			
121	Between Express Cove and North Point	50	W	5–7
122	Between Express Cove and North Point	45	W	2–5
	Calliergon cf. sarmentosum sociation			
123	North end of Moraine Valley	45	WNW	5
124	Near stream issuing from southernmost lake in Three Lakes Valley	18	SSE	3
125	Between Express Cove and North Point	55	NW	5
126	Between Express Cove and North Point	50	W	5–7
127	Between Express Cove and North Point	50	W	2
	Drepanocladus uncinatus sociation			
128	Between Lenton Point and Gourlay Peninsula	12	E-ESE	2–3
129	Between southernmost lake in Three Lakes Valley and Waterpipe Beach	20	ESE	10
130	North end of middle lake in Three Lakes Valley	16	SSE	4
131	Slope west of Mirounga Flats	12	ESE	11
132	North-east of The Wallows	23	SE	15
133	Between Express Cove and North Point	55	Level	0
	Brachythecium cf. antarcticum-Calliergon cf. sarmentosum socia-			
134	Late snow patch hollow on slope east of Factory Cove	30	NW	8
135	Slope above south-east shore of Elephant Flats	3–7	w	9
136	Between Express Cove and North Point	50	w	7
137	Between Express Cove and North Point	50	w	5
138	South-east of Foca Point	4–7	wsw	7
	Calliergon cf. sarmentosum-Drepanocladus uncinatus sociation			
139	South end of middle lake in Three Lakes Valley	18	N	5
140	North end of middle lake in Three Lakes Valley	16	ESE	5
141	South-east of Stygian Cove	20	NW	4

Site number	Locality	Altitude (m.)	Aspect	Slope (degrees)
142	North end of Moraine Valley	40	WNW	5
143	Slope on east side of Factory Cove	30	NW	14
	Brachythecium cf. antarcticum–Calliergon cf. sarmentosum– Drepanocladus uncinatus sociation			
144	South-east of Stygian Cove	15	NW	5
145	Between Lenton Point and Gourlay Peninsula	20	SE	2
146	Slope west of Mirounga Flats	8	E	6
147	South-east of Foca Point	7	wsw-w	7
148	Between The Wallows and south side of Starfish Cove	20	SE	15
	Bryum algens-Drepanocladus uncinatus-Tortula excelsa sociation			
149	North-east of soutehrmost lake in Three Lakes Valley	15	wsw	5
150	Among marble knolls between Elephant Flats and Waterpipe Beach	15	ENE	3–4
151	Wallow area north of Elephant Flats	12	wsw-w	3
152	Wallow area north of Elephant Flats	15	SSE	2
153	Slope north-west of Waterpipe Beach	5–8	SE	10
154	Between Elephant Flats and Waterpipe Beach	15	wsw-w	10-14
	Bryum algens sociation			
155	South of North Point	40	WNW	8
156	North slope of ridge between Foca and Thulla Points	15	NW-NNW	14
	Brachythecium austro-salebrosum sociation			
157	South-east of Stygian Cove	15	NW	7
158	Slope west of Mirounga Flats	7	E	5–6
	Deschampsia antarctica sociation with low Drepanocladus uncinatus cover			
159	Between Factory Clove and Berntsen Point	4	N	0–20
160	West side of cove north of Observation Bluff	30–35	E	30-40
161	North side of Observation Bluff	30	N	12–18
162	North-facing slope of ridge between Foca and Thulla Points	30	NW	5–10
163	North-facing slope of ridge between Foca and Thulla Points	30	NW	5–10
164	Between The Wallows and Starfish Cove	40	N	5–30
165	South-east side of Factory Cove	3–5	N	15–37

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Site number	Locality	Altitude (m.)	Aspect	Slope (degrees)
	Deschampsia antarctica sociation with high Drepanocladus uncinatus cover			
166	North side of Lynch Island, Marshall Bay, Coronation Island	8	N	2-8
	Deschampsia antarctica sociation with high Andreaea and lichen cover			
167	North side of Lynch Island, Marshall Bay, Coronation Island	8	N	0-5
168	North side of Lynch Island, Marshall Bay, Coronation Island	8	N	0-3
	Colobanthus quitensis sociation			
169	North-facing slope of ridge between Foca and Thulla Points	3	NNW	20
170	North-east of Spindrift Rocks	6–7	W	40–50
	Deschampsia antarctica–Colobanthus quitensis sociation			
171	North-east of Spindrift Rocks	3–5	W	30–45
172	North side of Observation Bluff	25	N	30–38
173	North side of Lynch Island, Marshall Bay, Coronation Island	7	N	0–10

#### PLATE I

- a. A general view of part of the east coast of Signy Island looking south-east over the inlet of Elephant Flats to Factory Cove with the British Antarctic Survey station on its distant shore to the right of Berntsen Point. The light-coloured low marble knolls in the foreground rising to c. 25 m. and the intervening base-rich soils support stands of the Tortula-Grimmia antarctici association. These are surrounded by grey-coloured stands of the moss carpet and moss hummock sub-formations on moist to wet glacial outwash debris dissected by small melt streams and pools. In the middle distance, beyond Elephant Flats, the grey-coloured schist outcrops and dry stony ground rising to c. 135 m. support stands of the Andreaea-Usnea association and occasional Polytrichum alpestre-Chorisodontium aciphyllum banks on north-facing slopes, with moss carpet communities on the dark-coloured wet ground. February 1966.
- b. Winter conditions on knolls and a ridge at altitudes of 50-100 m. above the south-south-west side of Factory Cove. The dark-coloured snow-free ground on the wind-swept ridge to the right is dominated by species of *Usnea* and *Himantormia lugubris* while the deep snow filling the depressions and on the more sheltered slopes to the left covers stands of *Andreaea* spp. and associated lichens. Coronation Island, rising to 1,288 m. in Mount Nivea at the left is visible in the background. August 1966,
- c. A relatively deep Polytrichum alpestre-Chorisodontium aciphyllum bank at an altitude of c. 80 m. inland from Spindrift Rocks. The wind-swept ridges of the bank have been croded by wind and frost action, and lack plant cover. The slopes of the ridges are colonized by epiphytic lichens which are absent on the moss surface in the more sheltered depressions. The ski stick is c. 130 cm. in length. January 1967.
- d. The Polytrichum alpestre-Chorisodontium aciphyllum bank in Plate Ic showing winter snow accumulation. The wind-swept eroded peat on the ridge crests lack snow cover, while the upper slopes of the low ridges bear a thin crust of ice. The depressions and lower parts of the bank are covered by up to 40 cm. of snow. The ski sticks are c. 130 cm. in length. Early September 1966.

PLATE I

#### PLATE II

- a. Usnea-Himantormia lugubris sociation on an exposed, wind-swept plateau at c. 125 m. above the north side of Paal Harbour. Lichens occupy the raised stony frost heaves, while species of Andreaea dominate the moist soil in the depressions. The distance between the stakes is 5 m. December 1966.
- b. As Plate IIa, following a light summer snowfall. The depressions dominated by Andreaea depressinervis are filled with snow while the more exposed lichen-dominated frost heaves are generally snow-free. December 1966.
- c. Usnea-Himantormia lugubris sociation on an exposed ridge at an altitude of c. 140 m. on the north side of Rusty Bluff. The light-coloured lichens are mostly Usnea fasciata with some U. antarctica. The black fruticose lichen is Himantormia lugubris. A few scattered cushions of Andreaea regularis occur at the top right. The lens cap is 5 cm, in diameter. February 1966.
- d. Usnea-Omphalodiscus-Himantormia lugubris sociation on a rock outcrop at c. 100 m. on Observation Bluff. The greyish fruticose lichen is U. antarctica, the foliose thalli are of O. antarcticus (smooth) and O. decussatus (crinkly). Crustose species of Buellia and Rhizocarpon occur at the bottom right. The lens cap is 5 cm. in diameter. January 1966.

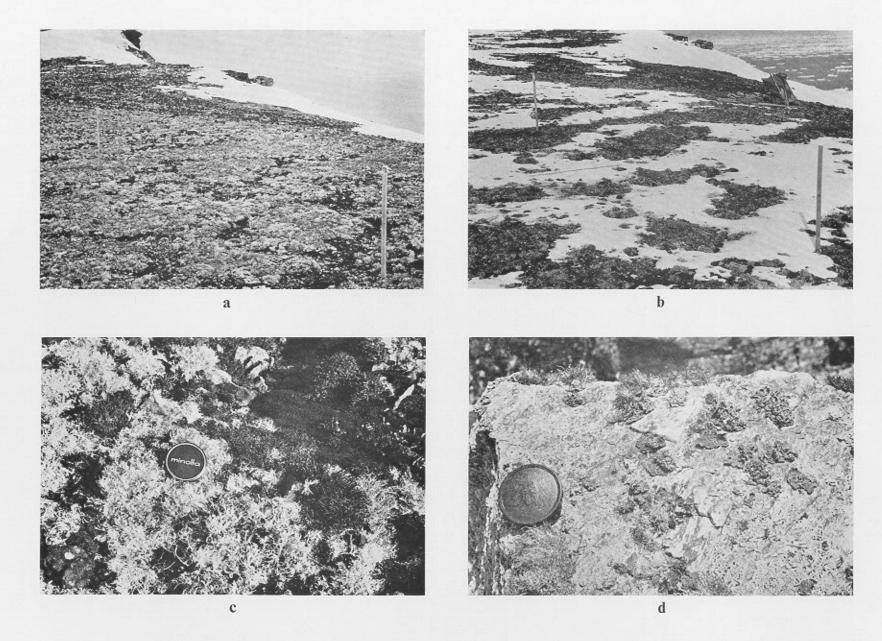


PLATE II

#### PLATE III

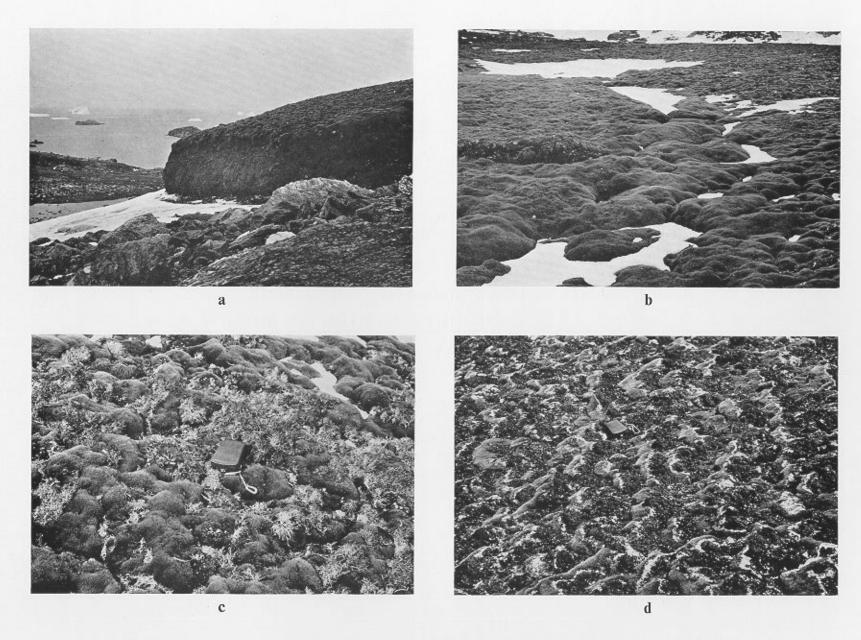
- a. Margin of a stand of Andreaea gainii and A. regularis on moist stony ground at an altitude of c. 100 m. above the north-west corner of Paal Harbour. The dry stony foreground is being colonized by small pioneer cushions of A. regularis. The scale object is 1 m. in length. January 1966.
- b. Distribution of vegetation around a stone stripe at an altitude of c. 35 m. in Moraine Valley. The mobility of the bare central part of the stripe is indicated by the down-hill displacement of the line of white stones during a period of 4 yr. The larger stones along the margins of the stripe are colonized by *Usnea* spp. and crustose lichens while the more stable ground beyond this is dominated by *Andreaea* spp. with other bryophytes and occasional lichens associated. The distance between the large stakes is c. 3 m. January 1965.
- c. Transition from a closed stand of *Drepanocladus uncinatus* (right), through a narrow open stand of *Andreaea depressinervis* (centre) to a shallow bank of *Chorisodontium aciphyllum* (left), at an altitude of c. 30 m. between The Wallows and Starfish Cove. The *Drepanocladus* occupies damp ground below a rock outcrop. The drier frost-heaved ground beyond the limits of the moss carpet supports coalesced cushions of *Andreaea depressinervis*, while the relatively sheltered ground farthest from the late snow is colonized by the moss turf community. Small cushions of the *Andreaea* can be seen invading the drier margin of the *Drepanocladus* carpet, while cushion-like turves of *Chorisodontium aciphyllum* are becoming established amongst the *Andreaea*. February 1966.
- d. Boundary between marble (white, on left) and lichen-covered quartz-mica-schist (grey, on right) on a low hill at an altitude of c. 40 m. north of Gourlay Peninsula. Dark moss cushions on the marble are Grimmia antarctici and Tortula fuscoviridis, those on the schist are Andreaea depressinervis. The grey fruticose lichen covering most of the schist is mainly Usnea antarctica. The ski stick is c. 130 cm. in length, February 1966.

PLATE III

### PLATE IV

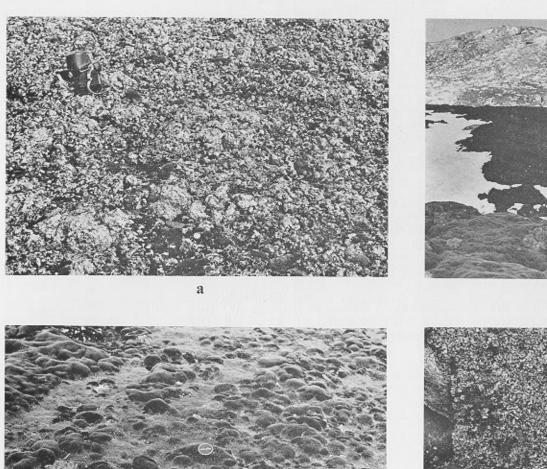
- Eroding face of a deep Chorisodontium aciphyllum bank, at an altitude of c. 65 m. north-cast of Thulla Point. The edge of the bank is c. 1.5m. in depth. February 1965.
- b. The undulating surface of a Chorisodontium aciphyllum bank with Polytrichum alpestre associated locally. The bank is at an altitude of c. 70 m. inland from Spindrift Rocks, January 1967.
- c. The undulating surface of a Chorisondontium aciphyllum bank being colonized by Usnea antarctica. The bank is at an altitude of c. 70 m. inland from Spindrift Rocks. The exposure meter is 7.5 cm. in length. January 1967.
- d. Rippled surface of a wind-swept shallow bank of Chorisodontium aciphyllum on a low hill at an altitude of c. 65 m. north-west of Gourlay Peninsula. Living C. aciphyllum occurs on the windward side of the ridges, while the ridge crests are encrusted with white Ochrolechia frigida and the croding leeward side and troughs encrusted with black Buellia punctata and blue-green algae. The exposure meter is 7.5 cm. in length. December 1966.





### PLATE V

- a. The heavily encrusted surface of a Polytrichum alpestre-Chorisodontium aciphyllum bank at an altitude of c. 30 m. near Knife Point. The moss surface is colonized by Buellia punctata, Ochrolechia frigida and species of Cladonia. The camera is 10 cm high. December 1966.
- b. The bare eroded surface of a Chorisodontium aciphyllum bank at an altitude of c. 70 m. inland from Spindrift Rocks, with living C. aciphyllum in the foreground. The ski stick is c. 130 cm. in length. Late November 1966.
- c. Small cushion-like turves of Chorisodontium aciphyllum invading a carpet of Drepanocladus uncinatus, at an altitude of c. 30 m. west of Starfish Cove. The shallow parent bank of Chorisodontium is situated at the top left. The lens cap is 5 cm. in diameter. December 1965.
- d. Dense stand of Marchantia berteroana with associated Bryum algens and Brachythecium austro-salebrosum, at an altitude of c. 50 m. south-east of North Point. The lens cap is 5 cm. in diameter. January 1967.





c

## PLATE VI

- a. An extensive stand of *Drepanocladus uncinatus* with *Brachythecium* cf. antarcticum and *Calliergon* cf. sarmentosum locally associated. The site is at an altitude of c. 15 m. south-east of Stygian Cove. The area is susceptible to trampling and erosion by clephant seals as the wallow in the foreground illustrates. The ski stick is c. 130 cm. in length. February 1966.
- b. Brachythecium austro-salebrosum lining a melt-water channel at an altitude of c. 25 m. above the cove to the south-south-east of Foca Point. Beyond the margins of the stream the Brachythecium merges into a Bryum algens and Drepanocladus uncinatus sociation. February 1966.
- Deschampsia antarctica on a moist base-rich slope below an outcrop of marble, at an altitude of c. 20 m. above the cove south-south-east of Foca Point. February 1965.
- d. Cushions of Colobanthus quitensis with associated Bryum algens, Brachythecium austrosalebrosum and Marchantia berteroana. The site is at an altitude of c. 6 m. on the west coast of Signy Island north of Spindrift Rocks. January 1967.

PLATE VI