PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

# Vegetation in the Maritime Antarctic

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# PLANT AND INVERTEBRATE ECOLOGY

## Vegetation in the Maritime Antarctic

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[Plates 17 to 19]

### Introduction

The pioneer studies of Skottsberg (1912), supported by the observations of Bertram (1938) and Bryant (1945), showed that a range of bryophyte and lichen communities are developed in many localities along the west coast of the Antarctic Peninsula and on its offshore islands. In contrast, the terrestrial vegetation over much of the Antarctic continent is apparently restricted to sparse, widely scattered communities of lichens, with mosses playing only a subordinate role, particularly in inland areas (Siple 1938; Rudolph 1963; Greene 1964). Holdgate (1964) thus proposed a division of the Antarctic botanical zone into Maritime and Continental areas, the former having an oceanic rather than a continental climate, and supporting liverworts and two species of vascular plants in addition to well-developed moss and lichen communities. The Maritime area, which can thus be characterized in vegetational and floristic terms, has yet to be clearly defined geographically, but extends over much of the Scotia Ridge–Antarctic Peninsula sector.

The present paper aims at giving a preliminary account of the vegetation in this area, based on observations made in a variety of localities from Candlemas Island south to Neny Island. The distribution of these sites is indicated in figure 17, and the extent of observations at each locality has been described elsewhere (Longton 1966*a*). Because of taxonomic difficulties a detailed analysis of the vegetation in each area was impracticable, since many of the taxa can at present be named only to the generic level (Greene 1964). The major divisions of the vegetation have been defined, however, and their distribution is discussed in relation to climatic, edaphic and biotic factors, enabling an attempt to be made at outlining the geographical boundaries of the Maritime Antarctic.

### General features of the area

#### *Topography, geology and soils*

The area under consideration consists in the north of isolated oceanic archipelagoes, and in the south of islands off the west coast of a long slender peninsula extending northwards from the Antarctic continent, only Hope Bay, near the north-east tip of the Antarctic peninsula, lying on the mainland (figure 17). It is characteristically mountainous terrain, and permanent snow and ice covers much of the higher ground, extending to the coast as glaciers and piedmonts. Intervening rocky capes, headlands and coastal cliffs, together with isolated inland nunataks, are exposed during part of the year, and in some localities extensive coastal lowlands, as well as inland cliffs and screes, also become clear of snow during the summer. However, evidence of ice scouring, moraine deposition and other glacial action indicates that much of the ground now exposed was formerly covered by ice sheets, while widespread raised beaches and wave cut platforms provide evidence that many of the lowland habitats have only become available for colonization comparatively recently in geological time (Nichols 1964).

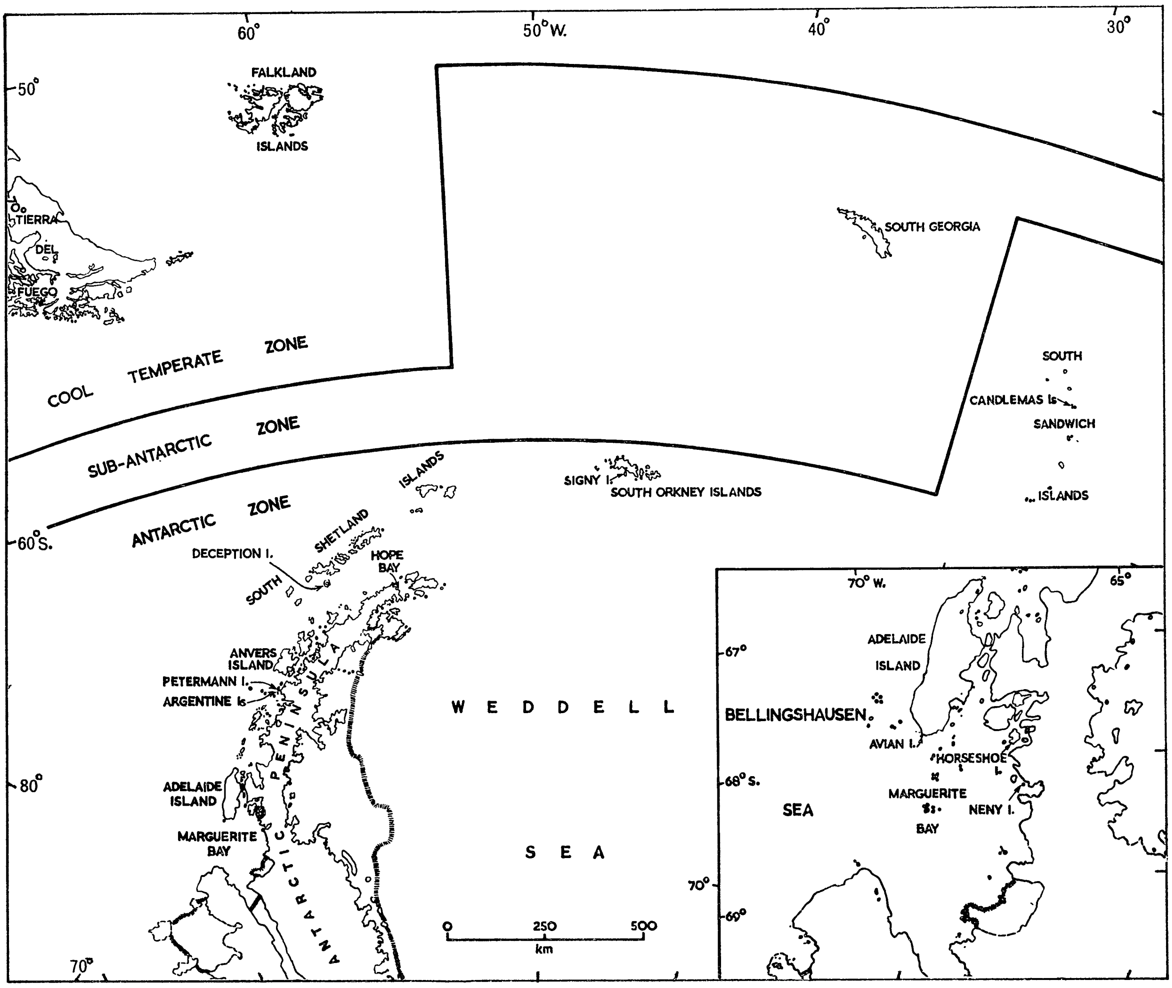


Figure 17. The Scotia Ridge–Antarctic Peninsula sector of Antarctica showing localities covered by vegetation survey. Stonington Island and Trepassey Islets are respectively about 1·5 km NNE and 1·5 km ENE from Neny Island. Laggard Island is approximately 1·5 km off the south coast of Anvers Island. Localities between Anvers Island and the Argentine Islands are referred to collectively in the text as 'islands off the Graham Coast'. Reproduced from Longton (1966*a*) by courtesy of British Antarctic Survey.

In a recent review of the geological history of Antarctica, Adie (1964) included the Scotia Ridge and Antarctic Peninsula in the Andean Province of West Antarctica, and pointed to the stratigraphical correlation between this area and the Andes of South America. The surface rocks include a variety of igneous and metamorphic types which weather to give predominantly acid mineral soils, though basic rocks outcrop locally. Candlemas Island and Deception Island, however, show evidence of recent volcanic activity, and are largely covered by plains and slopes of volcanic ash with outcrops of consolidated lava and agglomerates. These substrata are likely to be less acid, and indeed pH determinations on ash from two parts of Deception Island gave values of 6·6 and 6·8.

Allen & Northover (1967, this Discussion, p. 179) have provided a more detailed account of the soils on Signy Island, noting the high pH of those on the local marble outcrops compared with the generally acid soils derived from the predominating quartz-mica-schists, and drawing attention to the effects of enormous sea-bird colonies and blown sea spray in increasing the concentrations of ammonium, phosphate, potassium and other ions. Little detailed knowledge of edaphic conditions in other localities is available, but immature soils under a comparable maritime influence are a feature of most of the area under discussion.

### *Climate*

The climatic conditions prevailing in the Scotia Ridge–Antarctic Peninsula sector are undoubtedly of utmost importance in determining the nature of the vegetation. The general features of the climate have been summarized by Pepper (1954), while some aspects of the meteorological data shown in table 11 indicate the principal features of the Maritime Antarctic climate. However, it should be noted that the microclimate experienced by the vegetation may differ markedly from that indicated by the standard meteorological data, particularly with regard to temperature (Longton & Holdgate 1967, this Discussion, p. 237). There are no records for Candlemas Island comparable to those in table 11, but observa-

Table 11. Summary of meteorological data recorded at stations in the Scotia Ridge–Antarctic Peninsula sector

| | | temperature (°C) | | | | |
|---|---|---|---|---|---|---|
| | number of years records | mean annual | mean for warmest month of year | mean daily maximum for warmest month of year | mean daily minimum for warmest month of year | mean for coldest month of year |
| Signy I. | 14 | −3·9 | +1·2 | +3·3 | −0·5 | −12·0 |
| Deception I. | 15 | −3·2 | +1·6 | +3·8 | −0·1 | −9·4 |
| Argentine Is. | 15 | −5·4 | +0·5 | +2·7 | −1·3 | −13·8 |
| Horseshoe I. | 4 | −6·9 | +1·1 | +3·2 | −0·8 | −15·6 |
| Stonington I. | 3 | −7·6 | +0·7 | +3·1 | −1·7 | −16·4 |
| Hope Bay | 10 | −6·0 | +0·1 | +3·0 | −2·5 | −13·6 |

| | | | mean number of days per year | | | |
|---|---|---|---|---|---|---|
| | mean daily duration sunshine (h) November to February | mean annual relative humidity | cloudy | rain/drizzle | sleet/snow | gales |
| Signy I. | 3·0 | 86 | 258 | 77 | 203 | 63 |
| Deception I. | 2·0 | 87 | 244 | 70 | 213 | 33 |
| Argentine Is. | 3·8 | 86 | 236 | 54 | 193 | 14 |
| Horseshoe I. | 5·5 | 76 | 217 | — | — | 30 |
| Stonington I. | — | 80 | 189 | 10 | 138 | 33 |
| Hope Bay | 4·6 | 79 | 178 | 28 | 174 | 81 |

Data taken from Pepper (1954) for the years 1944 to 1950 and from the *Annual Meteorological Tables* published by the British Antarctic Survey Meteorological Service for the years 1951 to 1961. Precipitation data are from Pepper only.

The coldest and warmest months of the year varied at each base from (May) June to August (September) and from (November) December to February (March) respectively. Cloudy days were those when total cloud amounts at three observations was 20 oktas or more.

tions made during a survey of the South Sandwich Islands in March 1964 (Baker *et al.* 1964) suggest that its climate may be at least as severe as that of the South Orkney Islands and South Shetland Islands.

The Antarctic Peninsula lies in the path of a predominantly westerly air flow, and so experiences frequent cloud cover and precipitation, particularly in the north and west. Summer daylength is long, ranging from approximately 19 h at Signy Island to 24 h in the Marguerite Bay area, and this, combined with the distribution of cloud cover, results in the greatest duration of sunshine being recorded in the summer at Horseshoe Island in the south and Hope Bay in the north-east. The isotherms lie in a south-west to north-east direction, with mean air temperatures slightly higher at Deception Island and Signy Island than elsewhere. Mean monthly air temperatures only marginally exceed 0 °C during high summer at each station, but seldom fall below −15 °C in winter. Strong winds with frequent gales are prevalent, though wind direction and strength are influenced by local topography, and strong winds are much less frequent at the Argentine Islands than at other stations. The high plateau of the Antarctic Peninsula acts as a barrier to the oceanic influence of the westerly winds, and in consequence conditions on the east coast of the Peninsula are cooler and drier than at comparable latitudes on the west.

## Classification of the vegetation

One of the first serious attempts to classify Antarctic vegetation was that of Holdgate (1964) who recognized three intergrading series of bryophyte and lichen communities on Signy Island, each series characterized by habitat and by the growth form of the most abundant species. This system has been extended following more recent studies (table 12), but each division is again based on growth form and habitat, while subformations 1, 2 and 3 of the Antarctic Cryptogam Formation correspond respectively with the *Andreaea–Usnea*, *Polytrichum–Dicranum* and *Drepanocladus–Acrocladium–Brachythecium* formations of the previous scheme. However, the remaining subformations are recognized for the first time, as is the presence of vascular plant communities within the Antarctic botanical zone.

Table 12. A Classification of vegetation in the Maritime Antarctic

*Polar-Alpine tundra formation type*

A. Antarctic cryptogam formation
1. Lichen and moss cushion subformation
2. Moss turf subformation
3. Moss carpet subformation
4. Moss hummock subformation
5. Encrusted moss subformation
6. Thallose alga subformation

B. Antarctic phanerogam formation
1. Grass and cushion plant subformation

Most stands of vegetation can clearly be assigned to one or other of the categories indicated in table 12, though some intergradation takes place. For example, scattered individuals of the flowering plants may occur in bryophyte vegetation, while cryptogamic communities in different subformations tend to merge along their margins. In general, however, the major divisions are so distinctive that future amalgamation should be unnecessary: indeed it seems more likely that further study may suggest additional subdivision such as the recognition of several subformations for the lichen and moss cushion communities on the basis of lichen growth form and the abundance of bryophytes. A series of intergrading communities can certainly be recognized within each subformation, and although no attempt is made to define them formally at present their more important characteristics are described.

## Antarctic cryptogam formation

### *Lichen and moss cushion subformation*

The most varied and extensive plant communities in many localities are those in the lichen and moss cushion subformation. This type of vegetation is characteristically open, and comprises a greater range of growth forms than usually present in the other subformations, with crustose, fruticose and foliose lichens in places growing in association with small turf, mat and more frequently cushion-forming bryophytes. These communities occupy two principal habitats, first cliffs, where the almost vertical substratum and frequently dry conditions combine to prevent the formation of closed bryophyte cover, and second, flatter stony ground and scree slopes where solifluxion disturbances or exposure to desiccating and eroding winds have the same effect.

On the cliffs four principal types of community can be recognized, ranging from associations of crustose lichens in the most exposed sites to open bryophyte vegetation in moist, sheltered rock crevices. The crustose lichen communities, particularly those on coastal rocks, are made conspicuous by bright yellow and orange species of *Caloplaca*, *Xanthoria* and other genera. With increase in shelter fruticose species become important, forming a characteristic grouping with crustose lichens, while foliose species such as *Umbilicaria antarctica* and cushion forming mosses in the genera *Andreaea*, *Bartramia*, *Dicranoweissia* and *Grimmia* are also locally frequent. Increase in moisture, in sheltered gullies and flushed situations, leads to a reduction in the prominence of most lichens. *Umbilicaria antarctica* is an exception, however, becoming more abundant in mixed communities with species of *Andreaea* and other cushion forming mosses. The mosses characteristic of these cliff face communities also extend into sheltered rock crevices, where they combine with a variety of other species to form open vegetation. Small cushions and turfs of *Bryum algens*, *Pohlia cruda*, *P. nutans*, *Tortula conferta* and a species of *Distichium* are characteristic components of these communities, as are mats formed by species of *Brachythecium*, *Drepanocladus* and of the hepatic genera *Barbilophozia*, *Cephaloziella* and *Pachyglossa*. Species of *Hygroamblystegium*, *Plagiothecium* and *Metzgeria*, which are among the rarer plants of the Scotia Ridge–Antarctic Peninsula sector, also occur locally in this habitat.

A comparable trend towards greater abundance of bryophytes with increasing shelter and moisture is seen in communities developed on stony ground and scree slopes. Fruticose lichens generally predominate on the most exposed hill tops and ridge crests, where *Usnea antarctica* gives up to 75% cover in places, being replaced locally on boulders by *U. fasciata* and in particularly exposed situations by *Himantormia lugubris*. These species are associated with a variety of crustose lichens and occasional small cushions of *Andreaea*, but the richest communities in the present subformation occupy stony ground enjoying some degree of shelter. Under these conditions crustose and fruticose lichens grow together with abundant cushions of *Andreaea*, while small turfs and cushions of several other mosses are frequent associates (figure 18, plate 17), the principal species including *Polytrichum alpinum*, *P. alpestre*, *Dicranum aciphyllum* and species of *Ceratodon*, *Dicranoweissia* and *Grimmia*. Hepatics occur more locally, being represented by *Barbilophozia hatcheri* and species of *Cephaloziella* and *Gymnomitrium*.

The present series of communities may be developed further on moist, finely divided mineral material in sheltered montane hollows, and on stone stripes running down moist hillsides in areas subject to solifluxion and otherwise supporting little vegetation. Species of *Andreaea* become even more abundant in these habitats, forming extensive stands with a high cover value. Cushions of *Polytrichum alpinum* and mats of *Gymnomitrium* are locally frequent, while with increasing abundance of species of *Acrocladium* and *Drepanaocladus* the *Andreaea* communities may merge into moss carpets typical of wet slopes.

The floristic composition of lichen and moss cushion communities, both on cliffs and relatively flat ground, is altered dramatically on base rich substrata. Distinctive communities comprising turfs formed by species of *Grimmia* (subgen. *Schistidium*) and *Tortula* are developed locally on flat stony ground around marble outcrops, for example, replacing the *Andreaea* communities of acid ground. Moreover, several other bryophytes, such as species of *Encalypta* and *Pottia*, also show preference for the marble outcrops and for new moraines where the soil is again basic. A comparable community dominated by cushions of *Grimmia*, with a species of *Tortula* as the most frequent associate, occurs on moist, inclined outcrops of tuff, in situations where on older rocks associations of *Andreaea* and *Umbilicaria* would be expected. In addition, the same species of *Tortula*, its leaves having long hyaline hair points, is largely confined in some localities to broken stony ground on broad coastal rock ledges and cliff tops, where it is locally abundant with *Bryum algens* and other mosses in an open community developed among limpet shells deposited by Dominican Gulls (*Larus dominicanus*). In contrast, some taxa, including species of *Andreaea*, were seldom recorded in these base rich habitats.

### *Moss turf subformation*

Banks of tall turf forming mosses are a striking feature of the vegetation in several Maritime Antarctic localities. These often extensive communities are built up of densely packed, erect, sparingly branched shoots, and it seems likely that the larger closed stands have developed through the coalescence of a number of originally discrete turfs. The surface of the banks is irregularly undulating, and lichen colonization is extensive in the highest, most exposed parts, species of *Lepraria* and of the fruticose genera *Alectoria*, *Cladonia*, *Sphaerophorus* and *Usnea* being among the most frequently encountered. In many areas the most conspicuous moss turf communities are dominated by *Polytrichum alpestre*, and occupy broad cliff ledges and relatively dry stable slopes under rock outcrops, especially in north- and west-facing sites in coastal areas. *Polytrichum alpinum*, however, predominates in similar topographic situations on ledges on lava cliffs and on relatively steep slopes of volcanic ash.

Although *P. alpestre* is the most abundant species on many relatively dry slopes, scattered stems and small tufts of *Dicranum aciphyllum* are usually present, the two species

FIGURE 18. Lichen and moss cushion subformation. An association of *Usnea antarctica*, a species of *Andreaea* and other taxa on an exposed boulder on Signy Island. Lettering on the disk is 5 mm tall.

FIGURE 19. Moss turf subformation. Edge of a *Polytrichum alpestre* bank on a rocky slope on Signy Island. The stake at bottom left is 30 cm tall.

(*Facing p.* 218)



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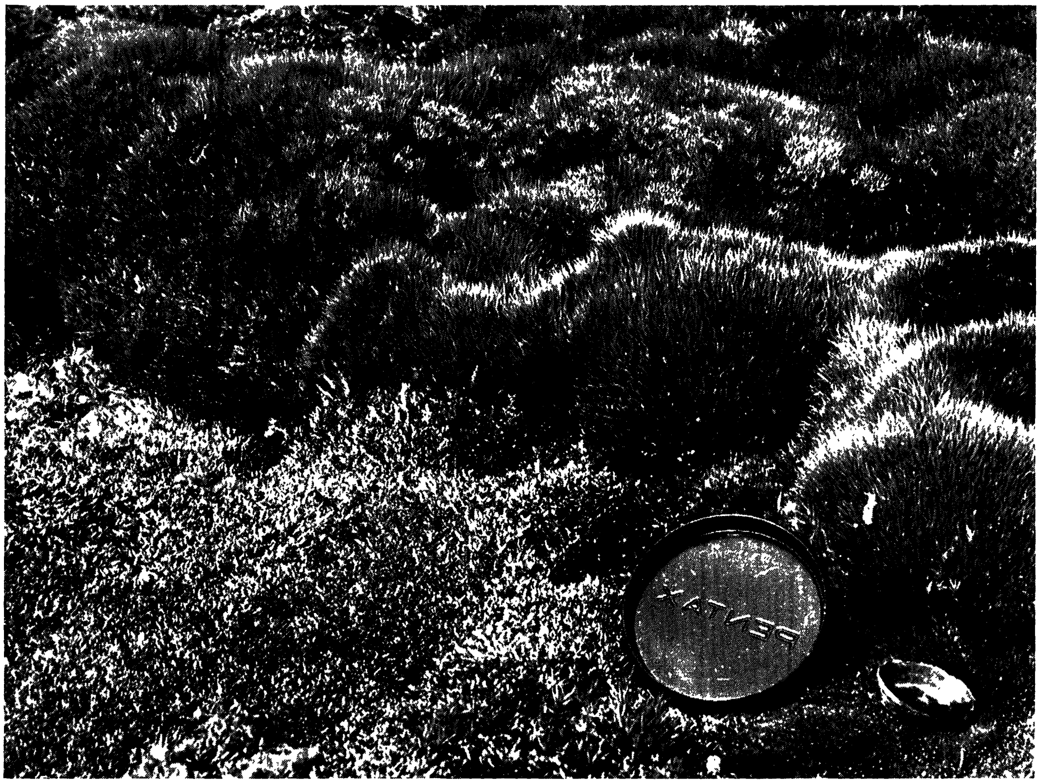

Figure 20. Moss turf and moss carpet subformations. Edge of a *Dicranum aciphyllum* mound by a carpet formed by species of *Acrocladium* and *Drepanocladus* on level, wet ground on Signy Island. The disk is 5 cm in diameter.

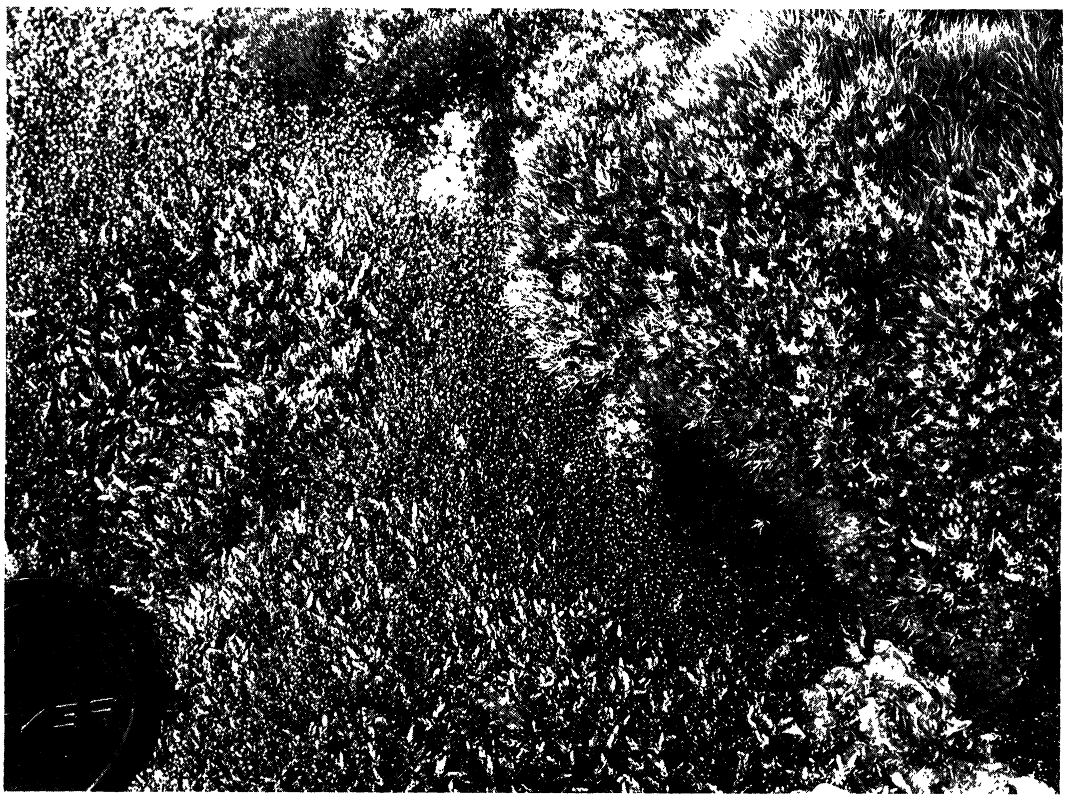

Figure 21. Close up of the communities in figure 20. A narrow belt of *Pohlia nutans* occurs along the margin between the two communities, and scattered stems of *Acrocladium* extend for a short distance among the *Dicranum* turf. Lettering on the disk is 5 mm tall.



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FIGURE 22. Moss hummock subformation. Hummocks formed by a species of *Brachythecium* by a small stream on Signy Island. The disk is 5 cm in diameter.

FIGURE 23. Grass and cushion plant subformation. Part of a large almost pure stand of *Colobanthus crassifolius* on Deception Island. The camera case is 15 cm wide.



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combining to form a deep uneven turf (figure 19, plate 17). *Barbilophozia hatcheri*, *Pohlia nutans* and a species of *Cephaloziella* also occur as scattered stems within the turf, while in damp hollows *Drepanocladus uncinatus* forms small mats on the surface.

The relative abundance of *P. alpestre* and *D. aciphyllum* is variable, and as conditions become wetter the latter frequently replaces *P. alpestre* as the predominant species. *D. aciphyllum* is also characteristic of level ground and gentle slopes with a plentiful water supply, where it may be the most important constituent of extensive mounds raised up to 30 cm or more above the carpets of pleurocarpous mosses developed extensively in such areas (figures 20 and 21, plate 18). *Pohlia nutans* frequently occurs around the basal margin of the mounds, while *Polytrichum alpestre* is normally restricted to the higher drier areas. In some localities, however, the latter species is dominant even on flat wet ground.

*Polytrichum–Dicranum* banks are often extensive, giving continuous cover for up to 50 to 100 m along rocky slopes in several localities. Moreover, they are clearly well developed and long established, and frequently overlie peat deposits up to 50 to 200 cm deep. There is widespread evidence of erosion, however, especially where the uneven surface is dissected by long sinuous fissures resulting from frost heave, and large areas of bare peat devoid of living plant cover are exposed in places. Locally the banks have almost completely eroded, and it is clear that they had developed on slopes strewn with boulders that may be necessary to give stability during early stages in the development of the closed turf.

In some areas *Polytrichum alpinum* communities develop extensively in situations where *P. alpestre* might be expected. Thus *P. alpinum* forms large loose mounds up to 1 m wide and 30 cm deep on Deception Island, frequently coalescing to form larger continuous areas of vegetation. On Candlemas Island a *P. alpinum* community comprises abundant mounds up to 20 cm in diameter, that are not only smaller than those on Deception Island, but are more compact and heavily impregnated with ash. Small mats of *Brachythecium* and *Drepanocladus* occur between the mounds in both localities, and these species also occur as scattered stems in the turf. Acrocarpous mosses grow in similar positions, *Pohlia nutans* being particularly abundant in some areas. Erosion and recolonization appears to be relatively rapid in the *P. alpinum* communities on volcanic ash slopes, particularly on Candlemas Island, preventing the accumulation of deep peat deposits as developed under stands of *P. alpestre*.

*P. alpinum* is also locally abundant on other types of substratum, including rather moist rocky slopes where it forms a discontinuous uneven turf over a shallow deposit of peaty soil. Discrete, almost pure turfs of *P. alpestre* and *Dicranum aciphyllum* are not infrequent associates, while mats of *Drepanocladus uncinatus* are developed abundantly between the taller species. Small cushions of *Pohlia nutans*, with species of *Bartramia*, *Ceratodon* and other acrocarpous mosses are further associates, while a species of *Marchantia* occurs locally in north-facing sites.

### *Moss carpet subformation*

The moss carpet subformation is the typical wet ground vegetation of the Maritime Antarctic, being represented by a further series of widespread communities. The vegetation consists of pleurocarpous mosses forming extensive, closed, spongy carpets, in places covering a thin deposit of peaty soil. This growth form is built up of closely packed, erect, sparingly branched shoots rising from a flattened basal mat, but moss mats lacking the erect shoots are present more locally. Typical habitats include hollows subject to late snow-lie, drainage channels, wet rock ledges, the shores of lakes and meltwater pools, flat pockets on rocky slopes where water tends to accumulate, and gently sloping ground irrigated from above by melt water.

The most abundant constituents of the moss carpets are *Drepanocladus uncinatus*, species of *Brachythecium*, and locally of *Acrocladium*, which either form mixed carpets or stands where one species assumes almost complete dominance. Their distribution appears to be determined largely by the moisture of the habitat, *Drepanocladus uncinatus* in general favouring slightly drier ground than the other species. The associated plants include acrocarpous mosses, liverworts and algae. Turfs of *Pohlia nutans* may become abundant in small stands, for example in late-lying snow beds, while cushions of *Polytrichum alpinum* and species of *Bryum* are also locally frequent. A species of *Cephaloziella* is widespread, both as scattered green stems within the carpet and as small dark red mats on the surface of dead mosses, while the thallose green alga *Prasiola crispa* may also be frequent on the surface of the vegetation.

### *Moss hummock subformation*

Abundant large spongy bryophyte hummocks, formed of robust radiating shoots, locally replace carpet-forming mosses as the dominant growth form in wet habitats (figure 22, plate 19). The presence of running water during much of the growing season appears to be the most important factor leading to their development, and although widely distributed within the Maritime Antarctic, moss-hummock communities are seldom extensive. The most characteristic habitats are rock ledges subject to meltwater flushing and the margins of meltwater streams and seepage areas. Several of the typical hummock forming species exhibit alternative growth forms in different types of community in other habitats.

The most varied communities are established in seepage areas and along the margins of drainage channels on flushed, well-vegetated banks around marble outcrops, where *Bryum algens*, together with other species of *Bryum*, *Tortula excelsa* and a tall form of *Drepanocladus uncinatus*, develop abundant large cushions frequently coalescing to form closed stands of hummocky vegetation. Similar hummocks of a *Bryum* and a large-leaved species of *Brachythecium* are widespread on flushed ledges, while the *Brachythecium* predominates in a moss hummock community along the margins of meltwater streams. Carpet-forming mosses are the most frequent associated species, but both the moss hummock and moss carpet communities differ from most bryophyte vegetation in the Maritime Antarctic in that lichen encrustation rarely develops due to the wet habitats they occupy.

### *Encrusted moss subformation*

Vegetation in the encrusted moss subformation consists of 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 often assumes the colour of the most abundant lichen. However, healthy mosses occur in intervening areas. Communities of this type are developed in large stands on plains and gentle slopes of volcanic ash.

*Pohlia nutans* predominates in the bryophyte crust of the most extensive community on Candlemas Island, forming continuous short turfs. The most frequent bryophyte associates are *Polytrichum alpinum*, *P. juniperinum* and *P. piliferum* which combine with *Pohlia nutans* in circular areas of short mixed turf, while *Bryum argenteum* and a species of *Ceratodon* were recorded more rarely. Numerous small cushions of the *Ceratodon* largely replace *P. nutans* in local areas on the summits of low rounded ash knolls, where species of *Polytrichum* seldom occur. In both communities, however, the mosses are heavily colonized by crustose lichens, of which a species of *Lepraria* is the most abundant, in places giving up to 70 to 80% cover in vegetation which thus appears greenish-white in colour.

Species of *Bryum* and *Ceratodon* are the dominant bryophytes in comparable, widespread communities on Deception Island, forming irregular cushions up to 5 cm wide. The cushions are impregnated with ash, and are often elongated and hollow in the centre, suggesting that they may be subjected to frost heave. Several other acrocarpous mosses, including *Polytrichum alpinum* and species of *Tortula* are widespread associates, together with small mats of *Drepanocladus uncinatus* and species of *Brachythecium*. The moss cushions are again largely colonized by crustose lichens, a species of *Psoroma* normally being the most abundant, and lending an overall reddish brown colour to the vegetation, though *Lepraria* is also conspicuous in places.

A more local community on flat areas of ash on Deception Island comprises short, open turfs of *Polytrichum alpinum*, *P. juniperinum* and *P. piliferum*, which develop extensive underground stem systems enabling them to colonize the unstable substratum. Each species forms almost circular turfs reaching several metres in diameter, which may have developed through radial extension of smaller central colonies as the tallest plants occur towards the centre. Small mats of *Drepanocladus uncinatus* are developed among the *Polytrichum* stems, but the turfs do not appear to act as a focus for general bryophyte colonization, the scattered cushions and turfs of other mosses, including *Psilopilum antarcticum* and species of *Andreaea*, *Bartramia*, *Bryum* and *Ceratodon*, being no more abundant among the *Polytrichum* than on bare ash. Species of *Lepraria* and *Psoroma* are widespread on the surface of the mosses, and although the lichens are seldom abundant this community seems best classified for the present in the encrusted moss subformation, in view of the short turf growth form and the occurrence of similar *Polytrichum* circles within the *Pohlia–Lepraria* community.

### *Thallose alga subformation*

The thallose alga subformation comprises a single community dominated by *Prasiola crispa*, which forms extensive thallose mats around the periphery of bird and Elephant Seal (*Mirounga leonina*) colonies. The largest stands of such vegetation normally surround penguin colonies, smaller areas occurring around the nests of ground breeding birds such as Giant Petrels (*Macronectes giganteus*) and Skuas (*Catharacta skua*), and on cliffs below the breeding colonies of a variety of petrels. The alga is often at its most luxuriant around the margins of pools, and on the cliffs in bird affected areas where manuring by birds is combined with meltwater flushing.

*Prasiola crispa* forms almost pure stands in many localities, being accompanied only by scattered crustose lichens and moss cushions. In places the alga gives up to 70% cover over areas of several hundred square metres, but its abundance is variable and some forms of the community are very sparse, consisting only of scattered thalli among dry scree. *P. crispa* may also occur as an abundant associate in open stands of moss carpet vegetation near penguin colonies, and in *Andreaea–Umbilicaria* communities on the cliffs.

### Antarctic phanerogam formation

#### *Grass and cushion plant subformation*

Scattered individual plants of the grass *Deschampsia antarctica* and the small cushion-forming herb *Colobanthus crassifolius* occur in several of the cryptogamic communities in the Maritime Antarctic, and in places the abundance of both species increases to such an extent that they become the dominant plants in small stands of phanerogamic vegetation. The vascular plant communities are largely confined to slopes with aspects between north-east and north-west. However, they occupy a range of habitats within such situations, differing particularly with regard to water availability. In some cases the vascular plants form almost pure communities in habitats where abundant bryophytes would not be expected, but in other localities *D. antarctica* competes successfully over small areas with a variety of mosses, its cover exceeding 50% in more complex vegetation. *D. antarctica* is the more abundant species, and although it is often accompanied by *C. crassifolius* the latter was seen without the grass at only one site.

In northern areas *D. antarctica* is locally abundant on rather irregular, moist, north-facing slopes, where it forms a series of closed turfs several metres in diameter on a layer of loamy soil. *Drepanocladus uncinatus* and *Polytrichum alpinum* are frequent associates, particularly on the steeper slopes, while *C. crassifolius* may form small cushions among both the grass and the mosses.

Grass communities are normally established in drier habitats in more southerly localities. Thus, on cliff ledges on Laggard Island, the grass gave up to 70% cover in a mixed turf with species of *Brachythecium* and *Tortula* characteristic of relatively dry ground. Open vascular plant communities are developed on Neny Island in an even more arid habitat on a north-north-east facing rock buttress at an altitude of approximately 80 m, where single small colonies of *D. antarctica* and of *C. crassifolius* were growing on a thin layer of sandy soil on gently inclined rocks near the base of the outcrop. Both populations were less than 1 $m^2$ in extent, however, giving only 5 to 10% cover, while extremely scattered crustose lichens and turfs of *Bryum* were the only associates.

Vascular plant communities may also develop on slopes of volcanic ash. *D. antarctica* is locally abundant on flat to gently sloping, south-facing ash on Candlemas Island, where in one site closed grass turfs up to 1 m wide result in approximately 50% cover in an area 7·5 m in diameter, *Pohlia nutans* and *Polytrichum alpinum* occurring frequently between the turfs. The largest vascular plant community seen by the present author, however, was on north-facing ash slopes below a low outcrop of tuff forming the side of a shallow gully on Deception Island. Here, abundant plants of *Colobanthus crassifolius* extended along a strip of ground approximately 30 m × 3 m flanking the base of the outcrop, and in places the cushions had coalesced to form continuous stands up to 1 m or more wide (figure 23, plate 19). *D. antarctica* was not recorded at this site, and, as on Neny Island, only widely scattered crustose lichens and acrocarpous mosses grew among the *Colobanthus*.

In addition to the native species two species of alien vascular plant, *Poa annua* and *P. pratensis*, are known to have survived for periods of several years in a few localities (Corte 1961; Longton 1966*b*), but both have so far formed only very small, possibly transient populations. Nevertheless, as the *P. annua* colony on Deception Island is almost pure, and the individual plants coalesce to form small turfs, it must be classified within the present formation.

## Distribution of plant communities

In view of the variations in climate and geology between the localities under discussion it is hardly surprising that some of the plant communities, for example those in the encrusted moss subformation, do not occur widely throughout the whole area, though others are more generally distributed. The dominant species in most of the communities are widespread, however, suggesting that local differences in ecological factors rather than inefficiency in plant dispersal are responsible for restricting the range of certain vegetation types. When different localities are compared (table 13), it can be seen that Signy Island and islands near the Graham Coast support a broadly similar range of communities that differ in certain respects from those on Candlemas Island and Deception Island on the one hand and those at Hope Bay and near Marguerite Bay on the other.

### *Signy Island and islands near the Graham Coast*

The vegetation at Signy Island and localities near the Graham Coast is varied and often extensive, particularly on rocky knolls, headlands and coastal cliffs. Flat or gently sloping ground around the coasts of Signy Island also supports luxuriant vegetation, but loose mineral debris greatly disturbed by solifluxion covers much of the relatively level ground in inland areas and plant cover is largely confined to boulders and other stable substrata. On Signy Island most types of vegetation are best developed at altitudes below 100 m, although lichen and moss cushion communities may extend considerably higher. Farther south moss carpet and moss turf communities extend to an altitude of *ca.* 170 m near the summit of Petermann Island, the highest ground examined in the Graham Coast region.

Cliff faces in both areas support a wide range of extensive and well-developed communities in the lichen and moss cushion subformation (table 13). Not surprisingly, however, the communities show some differences in floristic composition. For example, species of *Dicranoweissia* are much less frequent in the more southerly localities than on Signy Island, being largely replaced by a species of *Grimmia* (subgen. *Eu-Grimmia*), while the genus *Pachyglossa* was not recorded near the Graham Coast.

Exposed ground and disturbed mineral soil on hill tops and at the crest of ridges support a comparable range of communities to those developed on cliff faces. However, in the southern area a less varied range of communities is present than on Signy Island, as the large stands of vegetation dominated by fruticose and crustose lichens and by species of *Andreaea* are largely replaced by mixed associations of *Usnea antarctica* with other lichens and mosses including species of *Andreaea*, *Ceratodon* and *Polytrichum* (table 13). Scattered plants of *Deschampsia antarctica* may also be present in these mixed communities near the

Graham Coast, rooted among mosses and the more densely tufted lichens and giving up to 10% cover in places, particularly on level and north-facing ground. On cliff tops, and on broad ledges in coastal areas of the Argentine Islands and Laggard Island, these mixed bryophyte and lichen communities frequently give way to open associations of *Bryum algens*, a species of *Tortula* and other mosses, although *Deschampsia antarctica* may remain a frequent associate.

Broad rock ledges and relatively dry stable slopes below the cliffs in both areas are often covered by stands of the moss turf subformation, the extensive deep banks normally being formed largely of *Polytrichum alpestre*. On Signy Island *P. alpinum* may predominate locally on moist rocky slopes but normally an increase in moisture leads to a greater abundance of *Dicranum aciphyllum*, a species which also forms large raised mounds on relatively flat wet ground. *D. aciphyllum* predominates in banks of turf-forming mosses on the sides of a gulley on Litchfield Island (R. W. M. Corner, personal communication), and in a similar habitat on the east coast of Uruguay Island, Argentine Islands, but compared with Signy Island this species is seldom abundant in localities near the Graham Coast. Indeed, in several sites it is replaced by *P. alpestre* even in turfs developed on level ground in moist hollows.

Wet-ground habitats occur extensively on lake shores, gentle slopes irrigated by melt-water and in other situations on Signy Island, and support several communities in the moss carpet subformation (table 13). By contrast, permanently moist substrata are largely confined in the southern localities to smaller areas on rock ledges, in the bottom of gullies and in flat pockets on rocky slopes, although near the summit of Petermann Island melt-water from the ice cap soaks larger tracts of ground. These habitats are occupied by *Brachythecium* and *Drepanocladus* communities similar to those on Signy Island, but no species of *Acrocladium* were recorded near the Graham Coast. Where water flows regularly over rock ledges on Laggard Island and on the Argentine Islands species of *Brachythecium* and *Bryum* develop abundant large hummocks, but vegetation of this type is more widely represented on Signy Island along the margins of meltwater streams and in flushes near marble outcrops.

Finally it can be seen from table 13 that small grass communities are developed in a few north-facing sites in both areas, while *Prasiola crispa* communities occur locally near bird colonies.

The principal differences between the vegetation on Signy Island and localities near the Graham Coast thus lie in the less extensive development of *Dicranum aciphyllum* and moss carpet communities in the latter area, which also supports a less varied range of lichen and moss cushion vegetation on relatively flat exposed ground. As they cover large areas of wet ground near the summit of Petermann Island the generally less extensive development of moss carpet communities on the Argentine Islands and in other localities near the Graham Coast than on Signy Island can clearly be attributed largely to the drier condition of much of the exposed substrata. This may itself result from the decreased frequency of could cover and precipitation, possibly combined with the lower summer air temperatures reducing the flow of melt water (table 11). Similarly, the infrequency of *Dicranum aciphyllum* communities in localities near the Graham Coast may again be related to the shortage of suitable moist habitats. Alternatively, the slightly lower air temperatures compared with Signy Island could be partly responsible, as there is no record of widespread, extensively developed *Dicranum* communities anywhere as far south as the Graham Coast, where such vegetation is locally replaced by stands of *Polytrichum alpestre* even in wet habitats.

Moist finely divided mineral soil provides the principal habitat for *Andreaea* communities on Signy Island, and as such substrata do not occur widely on the Graham Coast islands it is hardly surprising that vegetation of this type was not recorded. The *Usnea*-crustose lichen communities, however, are well developed on particularly exposed ground on Signy Island, and the growth of abundant mosses and scattered grass tufts in association with lichens on exposed rocky knolls on Laggard Island and on the Argentine Islands may be related to the unusually calm conditions (table 11). It is thus of interest that R. W. M. Corner (personal communication) noted lichen communities comparable with those on Signy Island from exposed scree slopes at high altitudes on the Graham Coast mainland.

### *Hope Bay and Marguerite Bay*

From a botanical point of view, the most striking feature of Hope Bay, and localities around Marguerite Bay is the extremely dry, barren condition of much of the terrain. Only widely scattered crustose lichens were seen on Stonington Island, while the low-lying Trepassey Islets appear to be devoid of macroscopic plants. Extensive areas of dry rock and scree on the larger Horseshoe Island and Neny Island also lack plant cover, while lichen communities of the lichen and moss cushion subformation provide the most widespread type of vegetation in other areas, well-developed examples being seen at Hope Bay, at the southern end of Adelaide Island and on Avian Island. In addition, scree slopes on part of Horseshoe Island support a community not seen elsewhere, in which small species of *Alectoria* and *Umbilicaria* are abundant, while *Usnea antarctica* and crustose lichens occur less frequently. The bryophyte component of the lichen communities on coastal rocks around Marguerite Bay is usually sparse and restricted to small cushions of *Andreaea*, but species of *Andreaea*, *Dicranoweissia* and *Grimmia* may be more abundant on cliffs and scree slopes at Hope Bay.

Bryophyte-dominated vegetation is restricted to widely scattered sites in the vicinity of Marguerite Bay. The best developed examples seen were near the summit of Avian Island, where several large meltwater pools and streams provide unusually moist conditions. Moss carpet communities are developed on the margins of these pools, spongy vegetation dominated by *Drepanocladus uncinatus* and species of *Brachythecium* covering areas up to 100 m long by 20 m wide, while along the stream banks hummocks of a *Bryum* become abundant in vegetation approaching a moss hummock community. Moist banks near the centre of the island, as well as damp coastal rock ledges, may also be covered by moss carpet communities, and it may be noted that a dark red form of a *Cephaloziella* is locally frequent on the surface of the mosses.

Flat pockets among rocks on the floor of sheltered gullies on Adelaide Island are a further habitat where water tends to accumulate. Nevertheless, the substratum here is at times very dry, and *Drepanocladus uncinatus*, which predominates in the moss carpet community developed in these areas, forms only scattered mats seldom exceeding 1 m in diameter, associated with several species of small cushion-forming mosses.

TABLE 13. SUMMARY OF THE DISTRIBUTION OF THE

| ›rmation ... | Antarctic cryptogram | | |
|---|---|---|---|
| ›-formation ... | lichen and moss cushion | | moss turf |
| ›ipal habitats ... | dry and exposed or disturbed ground | | |
| | cliffs | boulders and stony ground | relatively dry stable ground |
| ›ny Island | *Caloplaca–Xanthoria* and other crustose lichen communities widespread. *Usnea*–crustose lichen and *Andreaea–Umbilicaria* communities widespread | fruticose–crustose lichen communities, mixed lichen–*Andreaea* communities and *Andreaea* communities widespread. *Tortula* and *Grimmia* communities local | *Polytrichum alpestre* and *Dicranum aciphyllum* communities widespread. *Polytrichum alpinum* community local |
| ›ids near the ›ham Coast | *Caloplaca–Xanthoria* and other crustose lichen communities widespread. *Usnea*–crustose lichen and *Andreaea–Umbilicaria* communities widespread | mixed communities of lichens, mosses and occasional grass tufts widespread | *Polytrichum alpestre* community widespread. *Dicranum acipiyllum* community local |
| ›guerite Bay | *Caloplaca–Xanthoria* and *Usnea*–crustose lichen communities local | *Alectoria–Umbilicaria* community local | *Polytrichum alpestre* community reported locally |
| ›pe Bay | *Caloplaca–Xanthoria* and other crustose lichen communities local. *Usnea*–crustose lichen and *Andreaea–Umbilicaria* communities local | fruticose–crustose lichen communities and mixed lichen–*Andreaea* communities local | *Polytrichum alpestre* community local |
| ›dlemas Island | *Caloplaca–Xanthoria* and *Usnea*–crustose lichen communities widespread | — | *Polytrichum alpinum* community widespread |
| ›eption Island | *Caloplaca–Xanthoria* and *Usnea*–crustose lichen communities widespread | — | *Polytrichum alpinum* community local |

Small areas of a distinctive vegetation type not clearly referable to any of the sub-formations in table 12 were noted on sandy soil at the foot of rocks and in shallow gullies on Horseshoe Island and Neny Island, in situations where water may percolate during at least part of the summer. Here *Bryum algens* and *B. argenteum* form scattered very short turfs partially embedded in the substratum, so that the stem apices barely project above the surrounding soil.

A *Prasiola crispa* community surrounds penguin colonies on Avian Island, while the presence of vascular plants on Neny Island has already been noted, and there are reports of vegetation in several other scattered localities around Marguerite Bay. Thus the unpublished notes and collections of B. J. Taylor indicate the occurrence of vascular plants and a local abundance of bryophytes on Jeny Island, with *Drepanocladus uncinatus* occupying moist ground by melt-water trickles, while specimens collected on Jeny Island by J. Killingbeck show that *Polytrichum alpestre* locally forms turfs at last 10 cm deep. Bryant (1945) reported a local abundance of mosses and flowering plants in a gulley on Lagotellerie Island, in a site exposed to the sun and moistened by melt-water, while Bertram (1938) found deep moss banks on Léonie Island resembling those on the Argentine Islands.

In the Hope Bay area bryophyte-dominated vegetation is again restricted to scattered sites, the best developed community being seen on moist stony ground in a valley on the north side of Mount Flora. Here *Polytrichum alpestre* forms discontinuous turfs up to 10 cm deep, the cover varying from 5 to 20% over an area of approximately 200 m$^2$. Elsewhere around Hope Bay scattered turfs and cushions of *P. alpestre* as well as species of *Andreaea*, *Grimmia* and *Tortula* comprised the only bryophyte vegetation observed on the dry scree slopes and cliffs.

The exposed terrain around Hope Bay and Marguerite Bay is thus largely barren, with


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RINCIPAL COMMUNITY TYPES IN THE MARITIME ANTARCTIC

| Antarctic cryptogram | | | | Antarctic phanerogam |
|---|---|---|---|---|
| moss carpet | moss hummock | encrusted moss | thallose alga | grass and cushion plant |
| wet ground | by running water | plains and gentle slopes of volcanic ash | bird affected areas | north-facing slopes |
| *cladium*, *Brachythecium* and *epanocladus* communities despread and extensive | *Bryum–Tortula–Drepanocladus*, *Brachythecium–Bryum* and *Brachythecium* communities local | — | *Prasiola* community local | *Deschampsia* community local |
| *hythecium* and *Drepano-dus* communities wide-ead in small stands | *Brachythecium–Bryum* community local | — | *Prasiola* community local | *Deschampsia* community local |
| *hythecium* and *Drepano-dus* communities local | — | — | *Prasiola* community local | *Deschampsia* and *Colobanthus* communities local |
| — | — | — | *Prasiola* community widespread | — |
| *hythecium* and *Drepano-dus* communities local | — | *Pohlia–Lepraria* community widespread. *Ceratodon–Lepraria* community local | *Prasiola* community wide-spread | *Deschampsia* community local |
| *anocladus* community despread | *Brachythecium–Bryum* community local | *Bryum–Ceratodon–Psoroma* community widespread. *Polytrichum* community local | *Prasiola* community local | *Colobanthus* community local |

communities in the lichen and moss cushion subformation predominating in much of the scattered vegetation. Turfs of *Polytrichum alpestre* occur locally in both areas, however, and appear to represent the most extensive bryophyte dominated vegetation at Hope Bay, while scattered sites around Marguerite Bay also support communities dominated by vascular plants and carpet-forming mosses. The vegetation thus consists largely of communities comparable with those on Signy Island and islands near the Graham Coast, but existing in an impoverished and restricted form.

Examination of table 11 suggests that low air temperatures are unlikely to be an important factor in markedly restricting the vegetation in these areas—compared, for example, with the Argentine Islands—especially in view of the increased duration of summer sunshine, though an explanation of the dry nature of the ground is provided by the data for humidity and precipitation. The general paucity of the vegetation is almost certainly due more to the lack of available moisture than to any other single factor, a view supported by the local occurrence of luxuriant stands of bryophyte-dominated communities in situations with a particularly favourable water supply.

### *Candlemas Island and Deception Island*

The cliffs of consolidated lava and the plains and slopes of volcanic ash that cover much of Candlemas Island and Deception Island provide substrata that are both unstable and porous, drying out rapidly between the frequent periods of precipitation. There are thus extensive barren areas on both islands, but these are interspersed with large stands of vegetation. A characteristic series of particularly luxuriant communities thrives under conditions of increased temperature and humidity around active fumaroles on Candlemas Island, though fumaroles along the beach on the eastern shore of Port Foster, Deception Island, lack associated vegetation.



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The lichen and moss cushion subformation is widespread at altitudes up to at least 250 m, but bryophyte dominated communities were seldom recorded above 150 m altitude. Lava outcrops and the vertical sides of large boulders on both islands support the usual large stands of communities dominated by crustose and fruticose lichens, and on dry coastal rocks on Deception Island these include an association of *Ramalina terebrata* and *Polycauliana regalis* with other crustose lichens resembling that described by Follmann (1965) as widespread in other localities near the west coast of the Antarctic Peninsula. The lichen communities of Candlemas Island generally have few bryophyte associates except occasional cushions of *Dicranoweissia*, but mosses are more frequent on Deception Island, where a community dominated by cushions of *Grimmia* is established.

Steep ash slopes below rock outcrops on both islands support stands of *Polytrichum alpinum*, but on plains and more gentle ash slopes communities of the encrusted moss subformation provide most of the plant cover. Small grass communities are also established locally, while the largest stand of *Colobanthus crassifolius* yet reported in the Antarctic is developed on more steeply sloping ash between South East Point and Baily Head, Deception Island.

Wet ground habitats are seldom extensive on the porous volcanic substrata, but small carpets of *Drepanocladus uncinatus* occupy drainage channels, with large stands in a few moist hollows in the ash plains, while a *Brachythecium* community is developed locally on ash slopes below the ice cap on Candlemas Island. A community in the moss hummock subformation was recorded on rock ledges by a small waterfall near Collins Point on Deception Island (table 13).

Ash slopes around penguin colonies on Candlemas Island are covered by some of the largest and best developed stands of *Prasiola crispa* so far recorded, particularly on a low-lying isthmus between the two higher parts of the island. On Deception Island the thallose alga subformation was seen in only small areas below colonies of cliff-nesting birds, but by analogy with other localities this type of vegetation may be expected to occur more extensively near penguin colonies on the outer coasts.

The luxuriant vegetation surrounding the fumaroles on Candlemas Island covers areas up to 20 m in diameter, and consists of concentric, intergrading zones occupying a decreasing gradient of temperature and moisture radiating outwards from the centre, where vents emitting steam are often located. The relationships between this vegetation and its unusual environment are considered elsewhere in this Discussion (Longton & Holdgate p. 237).

The innermost zone, developed within the vents, is characteristically open, and comprises shallow mats formed by species of *Cephaloziella* and less frequently of *Lepidozia* and *Riccardia*. The hepatics are associated with *Pohlia nutans*, occurring in sparse groups of prostrate slender stems, and scattered turfs of other mosses more characteristic of the adjacent zone. However, both the bryophytes and the intervening substratum are partially enveloped in a gelatinous growth of an alga in the genus *Mesotaenium*, which is often the most abundant species in the community.

The composition of the remaining zones is more varied, and is determined at least in part by the substratum, the most complex patterns being developed on slopes of volcanic ash. Under these conditions the second zone of vegetation is dominated by varying proportions of tall luxuriant turfs of *Pohlia nutans* and prostrate mats of a large leafy hepatic. Both species frequently overlie partially decayed bryophyte remains which combine with the living plants to form a layer up to 10 cm deep. A range of associated plants include turfs of *Campylopus introflexus*, *Psiloplium antarcticum* and scattered small fruiting bodies of basidiomycete fungi, while extensive thallose mats of a *Marchantia* are developed locally both on the surface of the other plants and on bare ash. The *Pohlia*-hepatic zone may in turn be surrounded by an irregularly undulating turf of *Polytrichum alpinum* up to 15 cm deep with few associates except occasional *P. juniperinum* and *P. piliferum*, while a fourth, outer zone of short *Pohlia nutans* turf encrusted by species of *Lepraria* is also widely developed.

Among lava boulders the vents are frequently surrounded by extensive turfs of *Campylopus introflexus* approximately 10 cm deep and giving 30 to 100 % cover, with *Pohlia nutans* and hepatics as only occasional associates. A shallow mat formed by a small leafy liverwort surrounds the *Campylopus* zone in some cases, but *Polytrichum alpinum* and short *Pohlia nutans–Lepraria* zones were only recorded on ash slopes. The factors controlling the distribution of the dominant species near different fumaroles are not completely clear, however, as a tall turf of *Pohlia nutans* surrounded one series of vents on a slope strewn with lava boulders although *Campylopus introflexus* turfs were developed extensively near neighbouring fumaroles on a similar substratum.

A single example of a third type of fumarole vegetation was located on the main volcanic cone, at a point where steam rises freely from a narrow strip of heated ground at the junction of a bed of scoria capped by impermeable turf. The associated vegetation comprised a single species of dicranoid moss, forming numerous short, sparse turfs up to 1 cm tall over a narrow strip of ground approximately 20 m long and up to 15 cm wide.

When fumarole vegetation is compared with that of unheated ground it is seen that the *Polytrichum alpinum* and *Pohlia nutans–Lepraria* zones on ash slopes resemble closely communities in the moss turf and encrusted moss subformations developed on parts of Candlemas Island and away from the fumaroles. Similarly, the vegetation of the zone immediately surrounding the vents can also be referred to the moss turf subformation in cases where it is dominated by *Campylopus introflexus* or *Pohlia nutans*. However, some of the other characteristic fumarole communities, such as those dominated by the gelatinous alga *Mesotaenium* or the thallose hepatic *Marchantia*, differ physiognomically from other Maritime Antarctic vegetation, and thus lie outside the subformations listed in table 12. The classification of these communities will be discussed more fully in a future detailed account of vegetation in the South Sandwich Islands as a whole.

The vegetation on Candlemas Island and Deception Island thus has several features in common with that in the localities previously considered, but differs in four important respects. First, the encrusted moss subformation, although extensively developed on the volcanic islands, has not yet been recorded elsewhere. Secondly, lichen and moss cushion communities seldom occur on relatively level ground on the volcanic islands, while no species of *Andreaea* were recorded on the cliffs. The third major difference lies in the composition of communities in the moss turf subformation, the stands of *Polytrichum alpinum* on Candlemas Island and Deception Island replacing *P. alpestre* and *Dicranum aciphyllum* communities of other areas. Finally, several of the characteristic communities surrounding the fumaroles on Candlemas Island have not yet been reported elsewhere in the Antarctic.

Comparison of the climatic regime at Deception Island and, for example, Signy Island (table 11) suggests few differences that might account for these modifications in the vegetation. It is therefore considered more likely that the distinctive features of the plant communities away from fumaroles on Candlemas Island and Deception Island are associated with the chemical or physical nature of the unusual volcanic substrata.

## The effect of environmental factors

In previous discussions of Antarctic vegetation low temperatures, shortage of available water and geographic isolation have been regarded as the most important factors controlling the nature and distribution of the plant communities (Rudmose Brown 1906; Siple 1938), and the possible effects of temperature and biogeographical factors have been considered more fully elsewhere in this Discussion (Longton & Holdgate, p. 237). Concerning temperature, it is clear that some plant communities in the Antarctic Peninsula area, especially those dominated by tall turf-forming mosses and vascular plants, have become established most frequently on slopes orientated towards the north, where they receive maximum benefit from warming by absorbed solar radiation. Moreover, the short cool summers in the Maritime Antarctic may well be largely responsible for restricting the vegetation principally to cryptogamic communities.

Low temperatures may thus be important in determining the general character of the vegetation, but availability of water clearly has a greater influence on the distribution of the cryptogamic communities within the Maritime Antarctic. The effects of variation in moistness of the habitat can be seen in controlling both the arrangement of communities within each locality, and the relative abundance of the vegetation in different areas. Within a given area, variation in ground water supply appears to be the most important single factor controlling the distribution of cryptogamic growth form types, and therefore determining the relationship of each series of structurally similar communities to topography and drainage. Thus several of the most widely distributed subformations appear to lie on a gradient leading from moss hummocks by running water to lichen and moss cushion communities on dry stony ground and cliffs (table 13). This conclusion is reinforced by observation on Signy Island that the water-absorbing and water-retaining capacity of bryophyte colonies with different growth forms correlates well with their habitat (Gimingham 1967, this Discussion, p. 251), moss carpets, for example, drying out more rapidly under experimental conditions than moss cushions from exposed situations. Moreover, examples of the distribution of physiognomically similar communities varying in relation to ground water supply can be seen within the moss turf and moss carpet subformations.

Availability of water is clearly not generally limiting for bryophyte growth on Signy Island, as shown by the variety and extent of its vegetation. However, increasing dryness of the exposed substrata southwards along the west coast of the Antarctic Peninsula has resulted in a progressive restriction of the habitats available for many bryophyte communities, until in the Marguerite Bay area, and at Hope Bay in the north-east, closed bryophyte cover is established only in scattered, unusually moist sites. In contrast, however, the vascular plants seem more tolerant with regard to water supply, occurring both on moist ground and in habitats that were extremely dry when examined in the latter part of the summer season, though moisture may have been more readily available during the spring melt. Conditions in Continental Antarctica may be even drier than in the Marguerite Bay area, but further data of an experimental nature will be necessary to establish to what extent lower air temperatures might limit the penetration of the vascular plants and the more luxuriant bryophyte communities of the Maritime Antarctic into continental areas, if water were freely available.

Ground water supply depends both on climate and on the physical nature of the substratum, and the latter has other roles in determining the distribution of Antarctic plant communities. It has been noted that *Polytrichum alpestre* banks are largely confined to relatively stable situations, and the same applies to much of the lichen-dominated vegetation, doubtless because many lichens are firmly anchored to the substratum and have a very slow growth rate. Lichen communities are normally established in habitats that are exposed as well as stable, however, where the risk of erosion is increased, and winter temperatures at plant level may be lower than in sheltered areas due to the poor development of an insulating snow blanket.

In contrast to lichen vegetation, several bryophyte communities, notably those dominated by *Andreaea* or carpet forming mosses, comprise continuous shallow vegetation with little direct connexion with the ground. Consequently they are more tolerant of solifluxion, in places becoming established over finely divided mineral soil. Nevertheless, solifluxion disturbances are undoubtedly responsible for the barren conditions over large areas of such substrata on Signy Island, and probably also on Candlemas Island and Deception Island. Indeed the encrusted moss subformation, characteristic of gentle ash slopes, can clearly withstand conditions that are both unstable and extremely dry at least for short periods. Similarly, *Polytrichum alpinum* communities were recorded most extensively on relatively steep ash slopes on these islands, replacing the stands of *P. alpestre* and *Dicranum aciphyllum* of other areas. Skottsberg (1912), however, reported a *Polytrichum alpinum* tundra on different types of substrata in other parts of the South Shetland Islands, and the factors controlling the relative abundance of the various tall turf communities in different localities remain obscure and intriguing.

Allen & Northover (1967, this Discussion, p. 179) have pointed out that owing to the strong maritime influence the soils on Signy Island have a supply of the basic plant nutrients in concentrations well in excess of those required by the island's vegetation. Nevertheless, the chemical nature of the surface rock may have a dramatic effect on the floristic composition of the communities, particularly those in the lichen and moss cushion subformation. Thus relatively flat stony ground around the basic marble outcrops on Signy Island supports communities comprising species of *Grimmia* and *Tortula*, which replace the stands of *Andreaea* occurring in acid schist areas, and this, and other examples noted earlier, indicate that groups of calcicole and calcifuge species can be recognized in the Antarctic bryophyte flora.

Although birds and seals may indirectly have a beneficial effect on the vegetation through enriching the soil with a variety of nutrients, their densely packed breeding colonies exert





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a serious deleterious effect on the plants in their immediate vicinity. Rudmose Brown (1906), reporting that: 'Almost every spot where plants might gain a hold is covered with these birds (penguins) . . . which would render plant life out of the question', may have exaggerated the extent of the colonies in the Maritime Antarctic as a whole, but not the conditions within them, and areas of moss peat observed beneath trampled sludge around the periphery of penguin colonies on the South Sandwich Islands (Baker *et al.* 1964) gave direct evidence that bryophyte vegetation is destroyed by these birds. The alga *Prasiola crispa* thus thrives in areas where competition from bryophytes is reduced. *P. crispa* is also widespread and often abundant, however, on terrain where well-developed bryophyte communities would not be expected even in the absence of birds, suggesting that it benefits directly from manuring, and the thallose alga subformation has aptly been regarded as a biotic subclimax (M. W. Holdgate, personal communication). The *Caloplaca–Xanthoria* communities also appear to be developed most extensively near sea-bird colonies, and may profit from manuring in a similar way.

Vegetation in the Maritime Antarctic thus reflects the interaction of a comparable range of climatic, edaphic and biotic factors to those moulding the vegetation in lower latitudes, and several parallels may be drawn between the effect of certain of these factors on bryophyte communities in temperature and Antarctic regions. Thus Gimingham & Robertson (1950) found that in Scotland the distribution of bryophyte growth form types is influenced more by the physical nature of the substratum than its chemical composition, though the latter might affect the floristic composition of the communities. Moreover, Birse (1958) found that the distribution of bryophyte growth form types in a Scottish dune slack system varied with ground water supply, as is the case in the Maritime Antarctic.

## Extent of the Maritime Antarctic

The present account of vegetation in the Maritime Antarctic is based on observations in relatively few localities, but there is evidence that Signy Island and islands near the Graham Coast may be representative of at least the more favourable sites on the South Orkney Islands and Graham Coast mainland, in terms both the plant communities represented and of their arrangement in the vegetation as a whole (R. W. M. Corner, personal communication; R. I. L. Smith, personal communication). Similarly, Skottsberg (1912) found *Prasiola crispa* to be conspicuous in many localities in the South Shetland Islands and near the west coast of the Antarctic Peninsula, and described bryophyte and lichen communities apparently resembling those on Signy Island from several localities in this area as well as from Snow Hill Island near the east coast of the Peninsula. Species of *Andreaea* with crustose and fruticose lichens were regarded as characteristic of rocks and stony ground, *Brachythecium* and other hypnoid mosses becoming abundant on wet slopes, while a *Polytrichum alpestre* or *Pogonatum* (= *Polytrichum*) *alpinum* tundra was reported in relatively dry areas.

There appears to be marked contrast between the vegetation at comparable latitudes on the east and west coasts of the Antarctic Peninsula, however, doubtless related to the warmer, moister conditions in the latter area. Skottsberg (1912) reported that lichens formed the most widespread vegetation, with mosses being only sparsely distributed, at several localities near the east coast, and these findings are confirmed by Brading (unpublished) for both inland nunataks and coastal areas south to Larsen Inlet (lat. 64° 30′ S). Similarly, lichens are said to be the most abundant plants in the scattered vegetation of nunataks at higher latitudes near the east coast of the Peninsula as far south as Bingham Glacier (lat. 69° 22′ S). It seems likely that the vegetation in these areas is Continental Antarctic in character, though a relatively rich, if scattered, flora of predominantly acrocarpous mosses occurs locally (M. J. Cousins, personal communication; A. E. Marsh, personal communication).

The Antarctic and Sub-Antarctic botanical zones are separated by an ocean barrier (figure 17) and the latter zone, supporting a range of communities dominated by herbaceous phanerogams, has a sharply defined southern boundary. In view of the continuous land connexion, however, it would not be surprising if Maritime and Continental Antarctic areas were not clearly demarcated, and this indeed seems to be the case. Thus the vegetation at Hope Bay and near the north coast of Marguerite Bay is widely scattered with lichens generally predominating, but vascular plants occur locally in the latter area. Moreover, most of the occasional bryophyte dominated communities are typical of the north and west of the Antarctic Peninsula, exceeding in luxuriance and complexity any reported in Continental Antarctica. It is clear, therefore, that these localities lie near the boundary between the Maritime and Continental Antarctic, their vegetation showing characteristic features of both.

Thus within the Scotia Ridge–Antarctic Peninsula sector the Maritime Antarctic includes the South Sandwich Islands, the South Orkney Islands, the South Shetland Islands and extends along the west coast of the Antarctic Peninsula at least as far south as the Argentine Islands (lat. 65° 15′ S), Snow Hill Island, approximately 120 km south of Hope Bay, possibly being an additional outlying locality. Within these areas *Prasiola crispa* is almost ubiquitous near bird colonies, and bryophyte as well as lichen dominated communities are varied, extensive and well developed in favourable sites, although closed plant cover has yet to become established over much of the ground. The bryophyte component of the vegetation includes a variety of growth form types, while several liverworts and two native species of vascular plant are widely distributed, the latter becoming locally abundant to form small stands of phanerogamic vegetation.

No comparable range of bryophyte communities has been recorded in East Antarctica, where native vascular plants are unknown, and where there are only two records of a hepatic, a species of *Cephaloziella* (Greene 1967). Apart from an abundance of algae, including *Prasiola crispa*, around melt-water pools, the general character of the vegetation in Continental Antarctica appears to resemble that occupying the driest and most exposed habitats in Maritime areas.

It is clear, however, that a more extensive survey of Antarctic vegetation will be necessary to determine whether the Maritime Antarctic type of vegetation is strictly confined to the Antarctic Peninsula–Scotia Ridge sector, while high altitude nunataks near the west coast of the Peninsula require investigation and future studies will assist in assessing more clearly the status of Hope Bay and Marguerite Bay.





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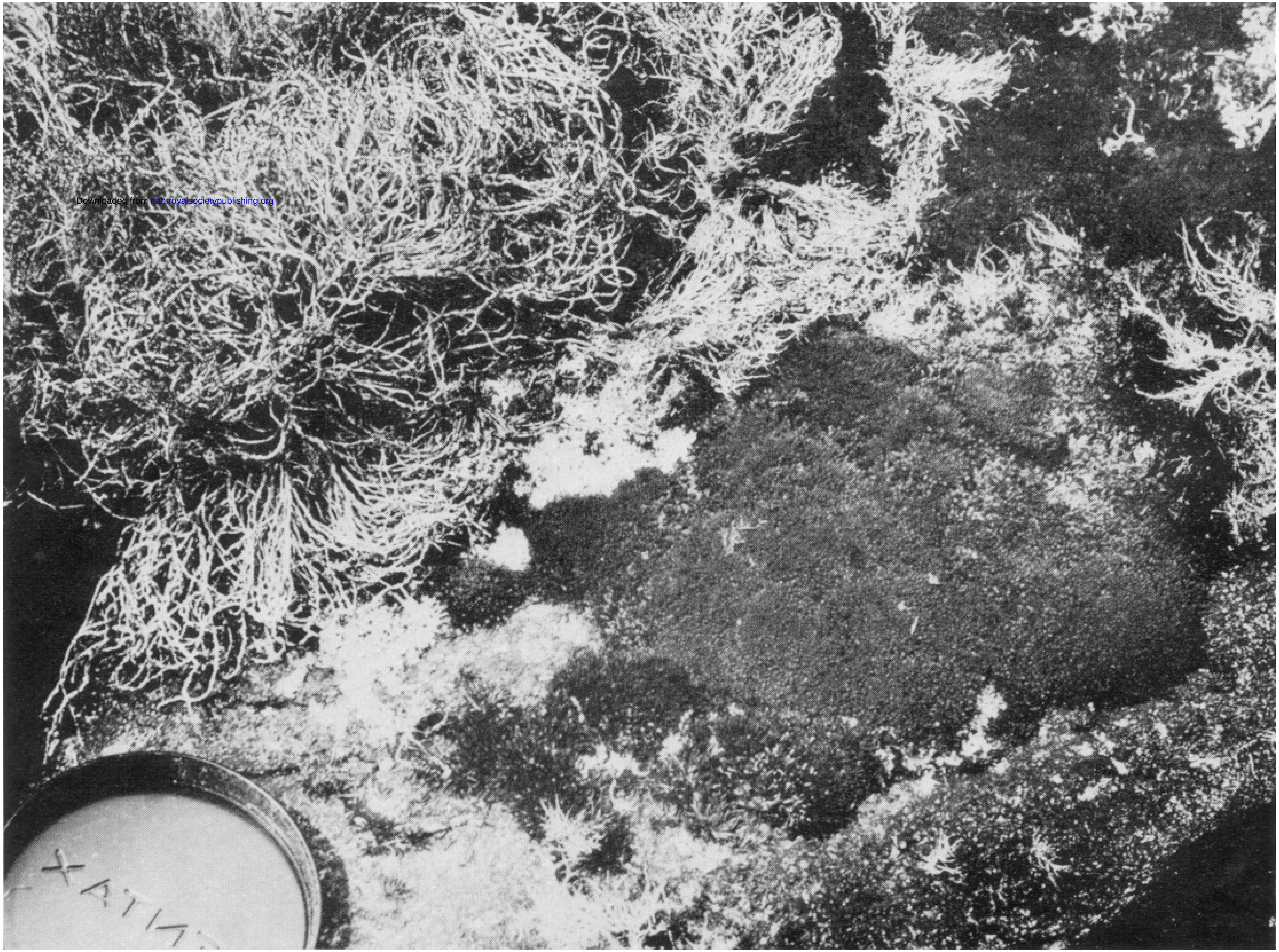

FIGURE 18. Lichen and moss cushion subformation. An association of *Usnea antarctica*, a species of *Andreaea* and other taxa on an exposed boulder on Signy Island. Lettering on the disk is 5 mm tall.



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FIGURE 19. Moss turf subformation. Edge of a *Polytrichum alpestre* bank on a rocky slope on Signy Island. The stake at bottom left is 30 cm tall.


FIGURE 20. Moss turf and moss carpet subformations. Edge of a *Dicranum aciphyllum* mound by a carpet formed by species of *Acrocladium* and *Drepanocladus* on level, wet ground on Signy Island. The disk is 5 cm in diameter.

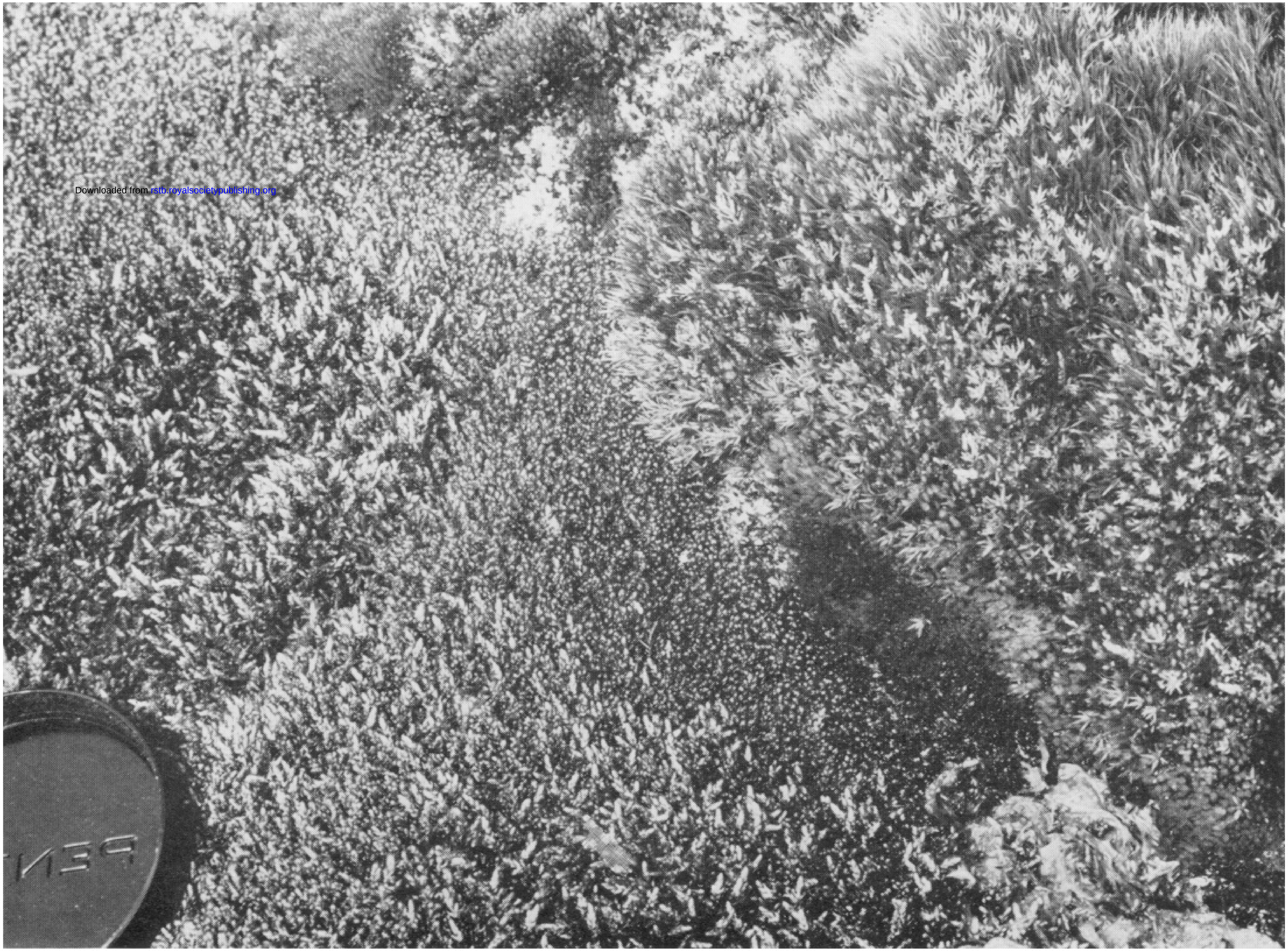

FIGURE 21. Close up of the communities in figure 20. A narrow belt of *Pohlia nutans* occurs along the margin between the two communities, and scattered stems of *Acrocladium* extend for a short distance among the *Dicranum* turf. Lettering on the disk is 5 mm tall.



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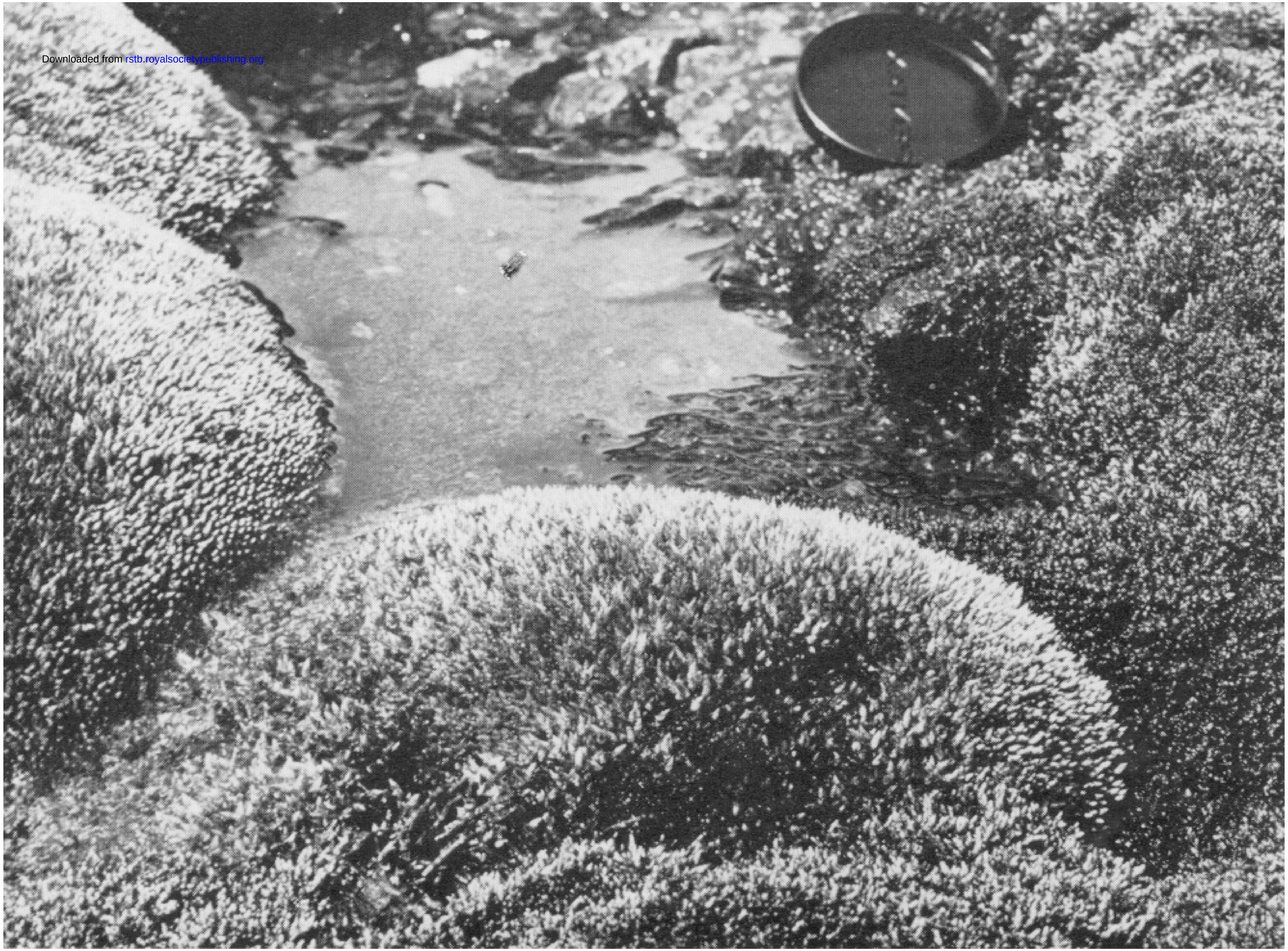

FIGURE 22. Moss hummock subformation. Hummocks formed by a species of *Brachythecium* by a small stream on Signy Island. The disk is 5 cm in diameter.



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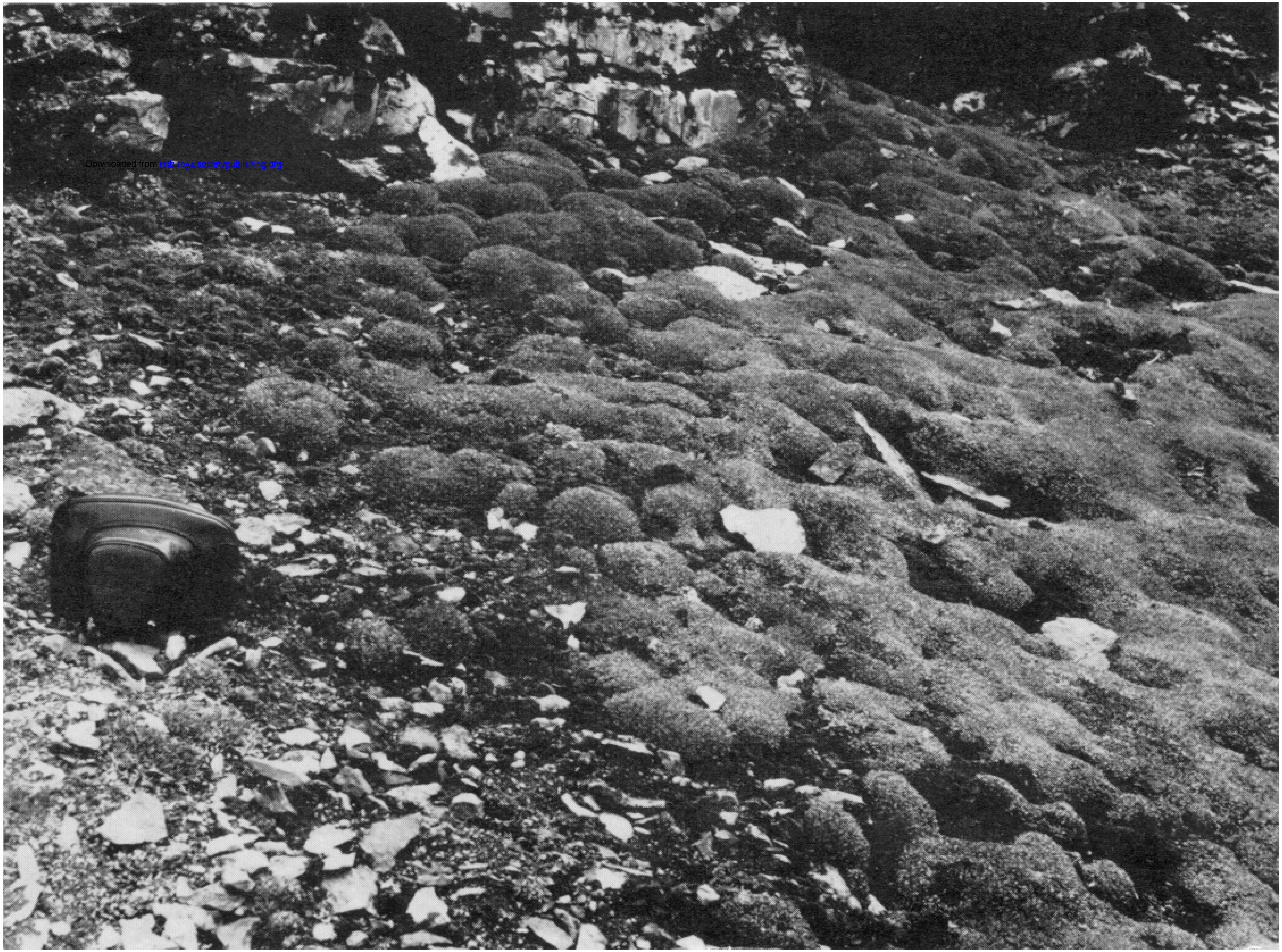

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FIGURE 23. Grass and cushion plant subformation. Part of a large almost pure stand of *Colobanthus crassifolius* on Deception Island. The camera case is 15 cm wide.