

THE DEVELOPMENT OF MOSS-PEAT BANKS IN RELATION TO CHANGING CLIMATE AND ICE COVER ON SIGNY ISLAND IN THE MARITIME ANTARCTIC

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ABSTRACT. Following a consideration of general climatic changes and their consequences during the Pleistocene, evidence is presented of short-term changes in climate on Signy Island, South Orkney Islands, which have resulted in a decrease of persistent snow and ice cover at the present time. A sequence of vegetation development is suggested that has resulted in part from these changes, involving both the colonization of moss carpets by the more slowly decomposing moss turves which leads to the initiation of new moss-peat banks and also to the re-colonization of moss-peat banks that were formerly buried and have been re-exposed by more extensive annual snow melt. Comparisons are made with the development and structure of bryophyte-dominated vegetation in northern Sweden, north-east Greenland and the Canadian Arctic.

VARIOUS authors have agreed that there have been two main periods of glaciation in the Southern Hemisphere (Auer, 1958, 1960; Adie, 1964; Calkin, 1964; John and Sugden, 1971). John and Sugden (1971) pointed out that the earlier, more extensive glaciations may have had more than one maximum, and they also considered that past glaciation of both the South Orkney Islands and South Georgia were less extensive than those of the South Shetland Islands. Holdgate (1967) has suggested that Signy Island (lat. 60° 43' S., long. 43° 38' W.) (Fig. 1) was covered by an ice sheet which extended throughout the South Orkney Islands during the glacial maximum and that snow-free ground has existed only for the last 10,000 years van Zinderen Bakker (1970) similarly supposed that South Georgia and the Antarctic Peninsula lost most of their biota during the maximum glaciation. However, when an ice sheet expands, most of the expansion is in a lateral rather than in a vertical direction, so that an extensive ice sheet over the South Orkney Islands would probably have been relatively shallow and broken by several nunataks.

Isostatic, eustatic and tectonic changes in sea-level may also have affected Signy Island and the rest of the South Orkney Islands, resulting in the group of islands being relatively much lower than at present, and indeed a number of beaches and wave-cut terraces have been recognized at levels of up to 45 m. above sea-level (Adie, 1964). In the South Shetland Islands, John and Sugden (1971) have suggested that the second glaciation was relatively local and that at the onset of deglaciation the sea was up to 54 m. higher relative to the land. If such conditions prevailed in the South Orkney Islands, particularly on Signy Island, much of the land surface free of persistent snow and ice at present affording the more sheltered wet conditions necessary for the development of closed moss- and lichen-dominated communities would have been submerged. At the same time, areas now covered with persistent snow and ice would have been lower lying and, if not covered by a general South Orkney Islands ice sheet, might in part have been snow-free.

Superimposed upon secular climatic changes of large amplitude, as have occurred in the transition from glacial maxima to interglacials, are shorter-term variations in climate. A relatively easily detected symptom of climatic variation is change in the positions of glacier snouts, but such variation will probably have at least as much, if not more, effect on the size and persistence of non-glacial snow beds. It is in regions with prolonged winter snow-lie and much persistent snow and ice that slight variations in climate may be expected to have the greatest effect on the vegetation by varying (a) the area of ground available for plant colonization, (b) the water availability to the plants and (c) the degree of protection afforded to the vegetation by winter snow cover.

Recent descriptions of Antarctic vegetation (Holdgate, 1964; Longton, 1967; Gimingham and Smith, 1970) hint at changes that have taken place and that may still be in progress but these authors seem to take short-term climatic stability as an underlying assumption, since

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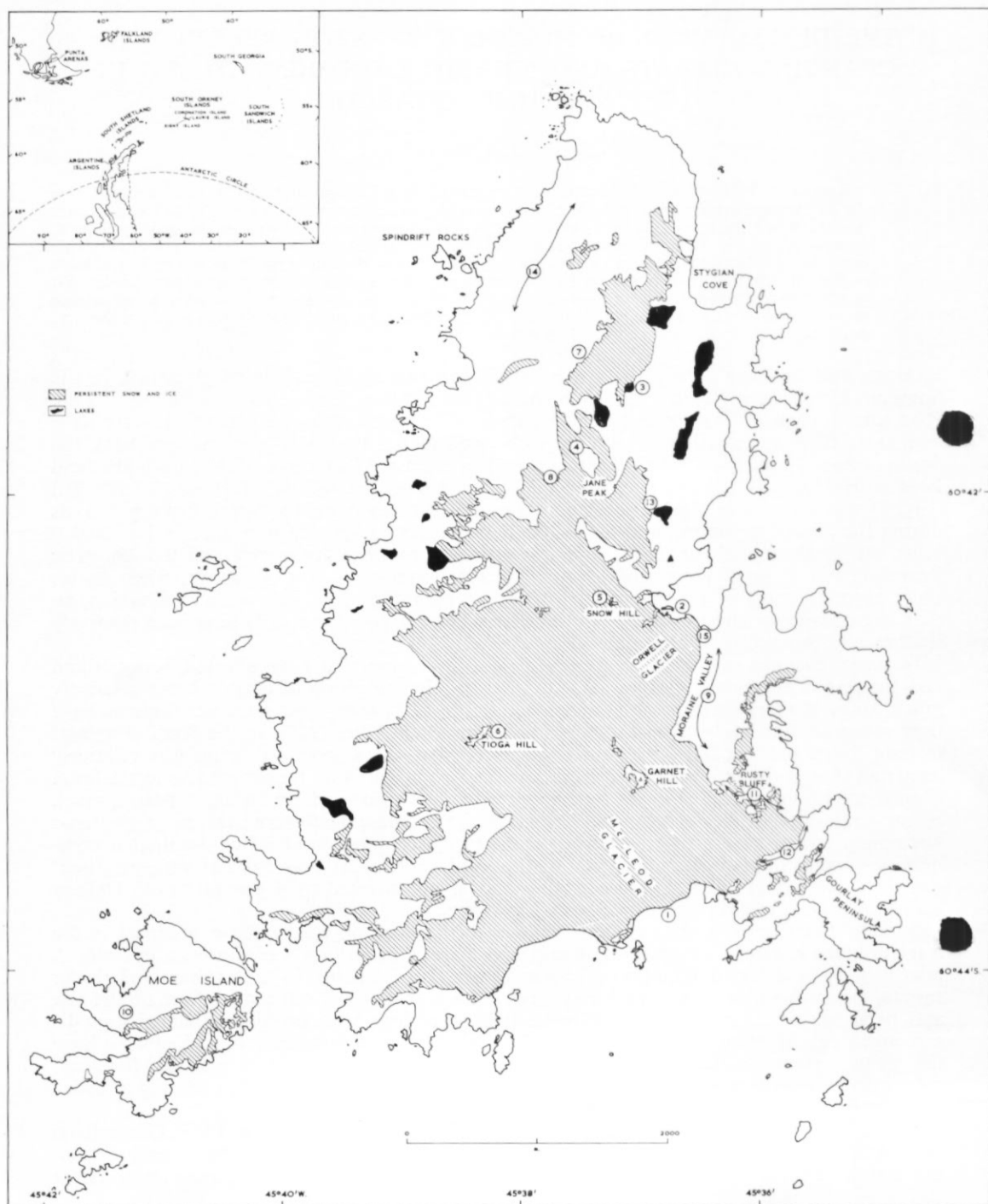


Fig. 1. Signy Island, South Orkney Islands, and its location. The circled numbers refer to sites mentioned in the text.

changes in the vegetation are accorded relatively little importance. Vegetation cannot be regarded as stable without reference to a time-scale; most changes are generally related to Man's life span (Kershaw, 1964) and have been followed as they occur over such a period. Conditions of equilibrium and a "climax" vegetation are unattainable, since climatic variations result in a successional (or cyclical) response in the apparently stable vegetation.

In the following account, evidence of continuous changes in climate and persistent snow and ice cover, particularly on Signy Island, is presented together with evidence from adjacent areas. The vegetation of the island, in particular the status and development of moss-peat banks, is then considered against this background of change, parallels being drawn with moss-dominated vegetation in the Arctic.

CHANGES IN CLIMATE

A tentative outline of climatic changes in the Southern Hemisphere has been given by Lamb (1964), who considered that whilst fluctuations in mean annual temperatures might indicate changes in climate, a more reliable indication was to be found in the changes in the interactions between temperature, wind direction, cloud cover, etc., as is shown in the changing track of depressions.

After the post-glacial optimum there was a climatic deterioration towards the end of the sub-Boreal, according to Lamb (1964), when the track of depressions in both hemispheres shifted towards the Equator. This period culminated between 2,970 and 2,270 yr. B.P. when there was a warming of the climate and the return of depressions to higher latitudes. In the Northern Hemisphere, a second optimum occurred c. 970 yr. B.P., followed by a deterioration in climate 300 yr. later which culminated in the "Little Ice Age" between 1430 and 1850 A.D. In the Southern Hemisphere, this deterioration does not appear to have commenced until 1800–30 A.D. when there was a period of extensive calving of Antarctic ice shelves. At the turn of the last century there were ten successive severe winters, with one mean July temperature of -2°C , recorded at Punta Arenas, Tierra del Fuego. At this time, glaciers on South Georgia were probably advancing (Lamb, 1964; Clapperton, 1971), although Smith (1960), who lacked the benefit of Lamb's results, has suggested that the maximum extension had occurred by 1875.

Of more immediate interest are the meteorological records for Laurie Island, the easternmost of the South Orkney Islands, which have been kept continuously since 1903 (Direccion General del Servicio Meteorológico Nacional, 1951). Fig. 2 shows 5 yr. running means of mean annual temperature for the period 1903–69. Mean annual temperatures for Signy Island, recorded since 1947, follow a pattern similar to those for Laurie Island, both sets of data showing a slightly cooler period in the late 1950's. It seems a reasonable assumption that temperatures on Signy Island approximated to the Laurie Island pattern in the earlier years for which no records are available. There appears to have been a particularly cold decade



Fig. 2. 5 year running mean of annual temperature for Laurie Island and Signy Island, South Orkney Islands.

between 1925 and 1935, Lamb (1964) having reported a similar trend for South Georgia and the Falkland Islands, although this deterioration became progressively less pronounced farther north. It also correlates with a slight advance of the South Georgian glaciers in the 1920's (Clapperton, 1971). There is evidence that continental Antarctica also experienced a climatic deterioration between 1920 and 1930 as it was during this period that the highest precipitation was recorded from snow cores taken at "South Ice" station (lat. 82° S., long. 29° W.) (Lister, 1959).

According to J. H. Mercer (personal communication), there was a maximum advance of the glaciers on the south-west coast of Chile in 1945. Although this does not correlate with the cold decade in the 1920's in regions farther south, this advance might be an example of the time lag that occurs between a period of greater ice accumulation on the surface of a glacier and its subsequent manifestation at the glacier snout (Robin and Adie, 1964).

During the 1950's and 1960's it appears that there was a general decrease in persistent snow and ice over much of the Southern Hemisphere. For example, in 1960, according to Godley (1960, p. 533), the glaciers of the north-west passage of the Beagle Channel in Tierra del Fuego were receding, whilst in the sub-Antarctic Clapperton (1971) noted that after the brief re-advance in the 1920's the glaciers of the Stromness Bay-Cumberland Bay area of South Georgia have been retreating up to and including the present day, with the formation in front of some cirque glaciers of series of terminal moraines which may represent annual deposition. Lamb (1964) also referred to noticeable ice recession on Heard Island (lat. 53° S., long. 73° E.) during "recent years". On the Antarctic continent, precipitation at "South Ice" station had decreased by 1950 to the level determined for the 1890's (Lamb, 1964). In the South Orkney Islands, the mean annual temperatures from the mid-1950's until the present on Laurie Island have been 2° C higher than during the previous 30 yr. and Signy Island seems to have followed a similar pattern (Fig. 2).

It appears, therefore, that whilst an overall decrease in persistent snow and ice has occurred in the Antarctic since the last glacial maximum, relatively short-term fluctuations have been superimposed on this general trend and may have led to short-term increases or decreases in the cover of persistent snow and ice.

CHANGES IN THE COVER OF PERSISTENT SNOW AND ICE

General descriptions of the topography and present distribution of persistent snow and ice cover on Signy Island have been given by Heywood (1967), Holdgate (1967) and Matthews and Maling (1967). Unfortunately, prior to the 1970-71 season no regular records, photographic or otherwise, of variation in cover have been kept and the author, who has examined many photographs taken since the first occupation of the British Antarctic Survey station in 1947, has found none that provides a suitable comparison with present-day conditions because of slightly differing viewpoints. However, during the 1970-71 season a number of stations were established for this purpose and will be re-examined periodically as part of the routine monitoring of changes on the island (personal communication from R. M. Laws).

Although there is neither photographic evidence nor evidence from sustained direct measurements of changes in persistent snow cover, various items of qualitative circumstantial evidence, when considered together, indicate that significant changes have occurred over the last 25 yr. In the following sections detailed evidence from a number of different sites will be considered, each site being referred to by a number, for ease of location on the map of Signy Island (Fig. 1).

Direct evidence

In 1948-49 the ice cliffs of McLeod Glacier (site 1) terminated in Clowes Bay but by 1970-71 they had receded to reveal a beach below parts of the snout (personal communication from R. M. Laws). A very narrow beach was apparent in 1966 (personal communication from R. I. L. Smith). According to R. Stocks (personal communication), the snout of Orwell Glacier (site 2) had retreated considerably between 1961-62 and 1969-70.

Between 1961-62 and 1970-71 there has been considerable change in the position of an abrupt wall of ice on the north-west side of lake 3 (site 3), south-west of Stygian Cove, resulting

in the lake doubling in area in 10 yr. (Light and Heywood, 1973). In 1961–62 the wall of ice was continuous to a depth of c. 5 m. in the lake but by 1970–71 it barely reached the edge of the lake. Furthermore, Heywood (1967) stated that in 1961–62 lakes 4, 3 and 1 were connected mainly by sub-ice streams but during 1969–70 the stream between lakes 4 and 3 was free of snow and ice along most of its length. Heywood (1967) also reported the disappearance of a small ice-dammed lake on the high plateau north-west of Jane Peak (site 4) between 1947–50 and 1961–62.

According to P. J. Rowe (personal communication), M. J. G. Chambers noted that between 1962 and 1968 there had been a decrease in snow thickness of up to 2 m. around the rock outcrop on the summit of Snow Hill (site 5). Chambers (1970) has reported a similar change around Tioga Hill (site 6) and also suggested that there has been some change in the development of solifluction patterns, probably reflecting a change in climate.

The cols south-east of Spindrift Rocks (site 7) and west of Jane Peak (site 8) have had progressively less snow-cover during the decade commencing in 1961 (personal communication from R. B. Heywood and H. G. Smith).

Evidence from "trim lines"

Evidence of a recent decrease in persistent snow- and ice-cover is also provided by "trim lines". These appear as general colour differences between darker weathered rock, well colonized by mosses and lichens, and areas of raw, often pale rock, sparsely colonized by lichens. Areas of uncolonized ground surrounding late snow patches may in fact be uncolonizable, because of the shortness of the growing season, although Matthews and Maling (1967) noted that small nunataks projecting through the ice cap were colonized to the margin of the ice in 1949–50.

Examples on Signy Island include the rock wall to the east of the col between Garnet Hill and Rusty Bluff and lower down in Moraine Valley (site 9), where R. M. Laws (personal communication) noted that there had been a decrease in persistent snow between 1948–49 and 1970–71. On nearby Laurie Island, he also noted that "a particularly strong visual impression of the extent of glacier recession . . . was provided by a belt of differently coloured rock (yellowish as opposed to the grey and weathered surfaces). This was very striking and in places I estimated it to be 30–40 ft. wide." Similar "trim lines" have been noted in the Argentine Islands (Corner and Smith, 1973) and on Elephant Island, South Shetland Islands (Allison and Smith, 1973). The band of uncolonized rock between the "trim line" and the existing ice margin can be as much as 1 m. in many areas in the Argentine Islands and 3 m. on South Georgia (Corner and Smith, 1973).

From the evidence considered so far, it may be concluded that short-term variations in climate have occurred, superimposed upon the secular changes since the last glacial maximum; recent changes in persistent snow and ice cover are likely to be a reflection of such short-term variations. In the following section the development and present status of the vegetation of Signy Island with particular reference to the moss-peat banks is considered against this background.

DEVELOPMENT AND PRESENT STATUS OF MOSS-PEAT BANKS

The development of a vegetation cover dominated by cryptogams may be largely dependent on, but also partly the cause of, substrate stability. The type of plant cover exerts a strong influence on the amount of accumulation of organic matter. In areas permeated by melt water throughout the summer, relatively thin layers between 2 and 10 cm. thick have accumulated beneath the living layer of moss carpets and moss hummocks. Due to the weight of winter snow, partial or complete submergence by melt water in the spring and relatively rapid decomposition, the erect shoots collapse to form the thin organic layer. Disruption may occur as a result of changing melt-flow patterns and solifluction. Typical species of such habitats include *Calliergidium* cf. *austro-stramineum*, *Calliergon sarmentosum* and *Drepanocladus uncinatus*.

Where more stable drier conditions prevail, two turf-forming mosses, *Chorisodontium aciphyllum* and *Polytrichum alpestre*, are able to grow and because decomposition is extremely

slow (Baker, 1972) thick banks of organic matter, up to 2 m. deep, may develop above the general ground level. There is relatively little compaction or compression, although some distortion may occur. Most of the deeper peat banks with eroded edges occur as isolated dome-shaped "islands" on the north-west coast of Signy Island, an area which has probably been free from glacial activity longer than any other part of the island (Heywood, 1967), and it is only in these deeper banks that permafrost exists, 20–30 cm. below the surface.

In areas subject to disturbance by frost shattering or solifluction, more open communities are formed by fruticose lichens, particularly species of *Himantormia* and *Usnea*, and cushion-forming mosses including species of *Andreaea*, *Grimmia* and *Dicranoweisia*. The mosses usually predominate where there is greater stability and a regular water supply. The majority of mosses on Signy Island reproduce and establish vegetatively and only 13 of the 17 species known to produce sporophytes do so regularly; of these only eight are widely distributed (Webb, 1973). Most of these species grow in unstable habitats and, with annual increments of 0.3–0.8 cm. (Table I), it is apparent that there may be rapid turnover amongst such species, since large cushions are rarely found. Such species normally occupy temporarily stable micro-habitats within unstable areas, although cushions sometimes coalesce to form a continuous mat loosely attached to the unstable mineral soil beneath.

During a study of bryophyte productivity on Signy Island, annual length increments of a number of species were measured and an assessment was made of relative decomposition rates and colonization characteristics of the species concerned. From a consideration of the characteristics of the commoner species given in Table I, it appears that changes can occur in the vegetation which involve replacement of one community type (as defined by Gimingham and Smith (1970) and Smith (1972)) by another. Whilst some changes are inevitable when persistent snow cover is in a steady-state, changes in the vegetation may be expected to accelerate if snow-cover is also changing.

It can be seen from Table I that annual length increments are generally higher in carpet-forming mosses (up to 4 cm.) than in turf-forming mosses (0.3–0.7 cm.). Because of a slower rate of break-down and an ability to tolerate drier conditions (Gimingham and Smith, 1971), *Chorisodontium aciphyllum* can invade and colonize the surface of carpets and eventually grow above and displace them. *Polytrichum alpestre* rarely colonizes carpets directly but invades the drier turves of *C. aciphyllum*. Such a sequence is illustrated diagrammatically in Fig. 3a, actual stages being shown in Fig. 4. Fig. 4a and b show early colonization of a carpet with coalescence of turves of *C. aciphyllum* (Fig. 4c), leading ultimately to a continuous cover of this species and *P. alpestre* (Fig. 4d). The latter moss becomes commoner on drier banks and particularly on steeper well-drained slopes (Fig. 3b), where it can colonize sites occupied by cushion-forming mosses. Once the turf has grown above the surrounding ground, with an increasingly thick layer of moss peat below the living turf, it starts to form a minor topographical feature described by the term moss-peat bank.

When there is little change in persistent snow and ice cover from year to year, the actively growing surface layers of the bank will gradually grow to be above the level of winter snow-lie on surrounding ground; this process will occur more rapidly when winter snow-lie is progressively decreasing. As the surface grows higher, it is blown free of snow during winter and becomes exposed to wind and frost erosion, although at the same time suitable habitats are provided for other moss and lichen colonists (Gimingham and Smith, 1970; Smith, 1972). All moss banks with epiphytic lichens present on the surface are probably continuously passing through cyclic changes, the mosaic of *Polytrichum alpestre*, *Chorisodontium aciphyllum* and an assortment of lichens endlessly changing in time and space. On many banks this may have no particular directional trend but under certain conditions a more definite pattern emerges, analogous to the situation described by Watt (1947) for communities dominated by *Racomitrium lanuginosum* or for the dwarf *Callunetum* of high exposed sites in the Cairngorm Mountains of Scotland. The first step is the development of ripples on the surface of some *Chorisodontium aciphyllum* banks, the shoots of the moss growing over the lichen surface. *Buellia* cf. *punctata* and blue-green algae commonly encrust the gentler slopes of these ripples, while *Ochrolechia frigida* occurs on their crests (Smith, 1972).

It might be supposed that such ripple systems develop with a specific orientation to the direction of the prevailing wind, but this is difficult to establish on Signy Island where the

TABLE I. CHARACTERISTICS OF SPECIES BELONGING TO THE MAIN THREE BRYOPHYTE GROWTH FORMS OCCURRING ON SIGNY ISLAND

Growth form and representative species	Habitat and water availability	Colonization	Annual growth		Decomposition and physical removal
			Length increment (cm.)	Production (g. m. ⁻²)	
<p><i>Moss cushions</i> <i>Andreaea</i> spp. <i>Grimmia antarctici</i> <i>Dicranoweisia</i> spp.</p>	Exposed, dry to moist rock faces and stony mineral soils, frequently disrupted by frost heaving and solifluction. Water supply intermittent once spring snow melt has ceased. Winter snow-cover absent or shallow	Rapid, both vegetatively and by spores. Cushion- and short turf-forming species are the only mosses commonly fertile on Signy Island	Up to 0.8	Data not available	Decomposition slow but physical removal fast
<p><i>Moss carpets</i> <i>Calliergon sarmentosum</i> <i>Calliergidium</i> cf. <i>austro-stramineum</i> <i>Drepanocladus uncinatus</i></p>	Relatively sheltered, stable ground, subject to inundation by water and occasionally submerged. Occasionally disrupted by solifluction. Water supply continuous from the onset of the spring melt throughout most of the growing season. Winter snow-cover usually deep	Vegetation spread equal to the annual length increment. Fragments distributed by melt streams and solifluction	Up to 4.0	220-889 300-1,200	Decomposition can be rapid. Some physical disruption or removal as melt streams change course. Carpets may be short-lived and in drier situations may be colonized by other species
<p><i>Moss turves</i> <i>Polytrichum alpestre</i> <i>Chorisodontium aciphyllum</i></p>	Relatively sheltered, dry to moist stable ground. Intolerant of inundation by water. Snow-cover very variable, being deeper over shallow peat banks	<p><i>P. alpestre</i> usually colonizes drier sites where carpet-, turf- or cushion-forming mosses are already present.</p> <p><i>C. aciphyllum</i> colonizes drier carpets and old, re-exposed peat banks both by vegetative propagules and by regeneration</p>	0.3-0.7 but may exceed 1.0 in favourable habitats	430-660 440-510	Very slow decomposition with peat as thick as 2 m. in some localities. Permafrost present in most deeper peat banks. Some physical removal by wind after desiccation and erosion. Intolerant of biotic disturbance

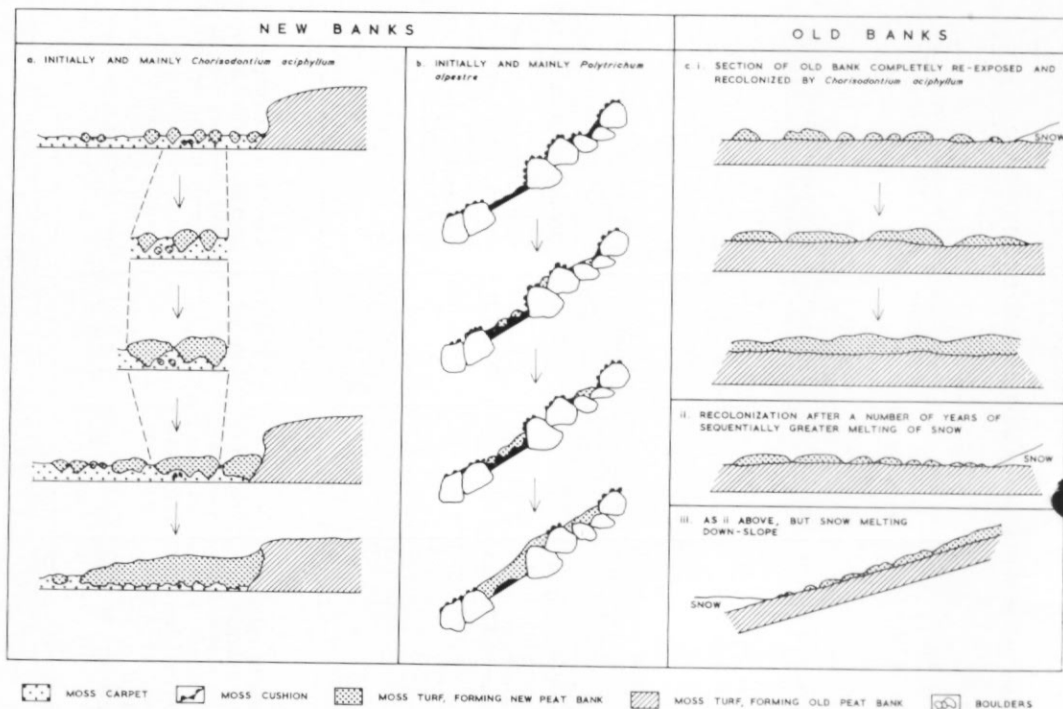


Fig. 3. Diagrammatic sections illustrating the development of moss-peat banks by (a) colonization of a moss carpet adjacent to an older bank, (b) colonization of moss cushions, and (c) re-colonization of or regeneration by old banks, re-exposed after snow retreat.

uneven topography results in complex wind-eddy systems. Above Shingle Cove on Coronation Island, an extensive ripple system has developed on the surface of a moss-peat bank, in which the steeper slopes face south-east, with the most luxuriant growth occurring at the base of the steep slopes. Strong katabatic winds, generated amongst the high mountains of Coronation Island to the north and north-west, frequently blow across this area from Sunshine Glacier and a smaller glacier entering Shingle Cove. Thus the wave crests in this system are at right-angles to the direction of the prevailing winds with distances of *c.* 8 cm. from one crest to the next and *c.* 3 cm. from top of crest to bottom of trough. Each successive wave was at a slightly higher level as illustrated in Fig. 5, with the dip of the lichen-encrusted slope being 18° and the mossy slope 48° . The surface of the bank appeared in places to be quite old with, at its northern edge, re-colonization by a continuous mixed turf of *P. alpestre* and *C. aciphyllum* growing up to and over the old surface from a slightly lower level, although *P. alpestre* was noticeably absent from the ripple system. It is suggested that in this area of the bank new colonies of *C. aciphyllum* grew above the irregularities of the old surface and became moribund and lichen-encrusted on their windward edge, although in other situations this may occur as the entire bank grows out of any shelter from a prevailing wind. Ripple systems then develop with growth of *C. aciphyllum* occurring in the lee of the ridges and along the direction of the wind over the lichen-encrusted surface of the windward slope. These surfaces persist as distinct discontinuities recognizable by differences in coloration and shoot orientation.

If the trend of decreasing persistent snow-cover were to continue until its winter depth and duration were relatively short, erosion will commence. This is not particularly prevalent on Signy Island at the moment probably, in part, because of the irregular topography holding some snow beds until a time when persistent snow-lie increases again. However, at Cape



a



b



c



d

Fig. 4. Stages in the development of moss turves.

- a. Colonization of a carpet of *Calliergon sarmentosum* and *Calliergidium* cf. *austrostramineum* by the turf-forming moss *Chorisodontium aciphyllum*.
- b. Colonization of a carpet of *Drepanocladus uncinatus* by the turf-forming moss *Chorisodontium aciphyllum*.
- c. Coalescing turves of *Chorisodontium aciphyllum* with *Drepanocladus uncinatus* in the moister depressions.
- d. Continuous undulating turf of *Chorisodontium aciphyllum* with scattered colonies of *Polytrichum alpestre*.

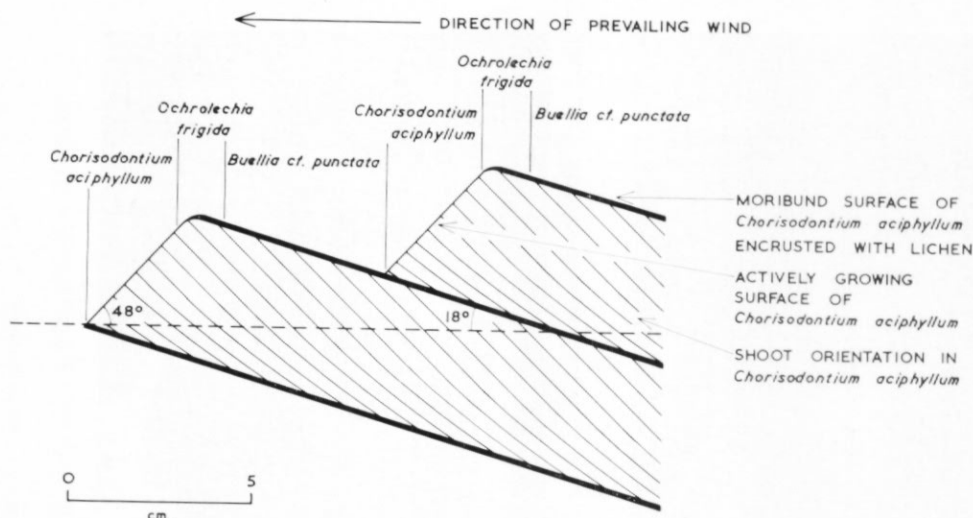


Fig. 5. Diagrammatic section through a ripple system on the surface of a *Chorisodontium aciphyllum* bank above Shingle Cove, Coronation Island.

Dundas, at the east end of Laurie Island, where the entire headland is snow-free in summer, there are eroded remnants of *C. aciphyllum* banks, which must have been formerly more extensive (personal communication from H. G. Smith). It seems probable that the deep isolated banks with eroded edges on the west coast of Signy Island (Fig. 6) and the deep

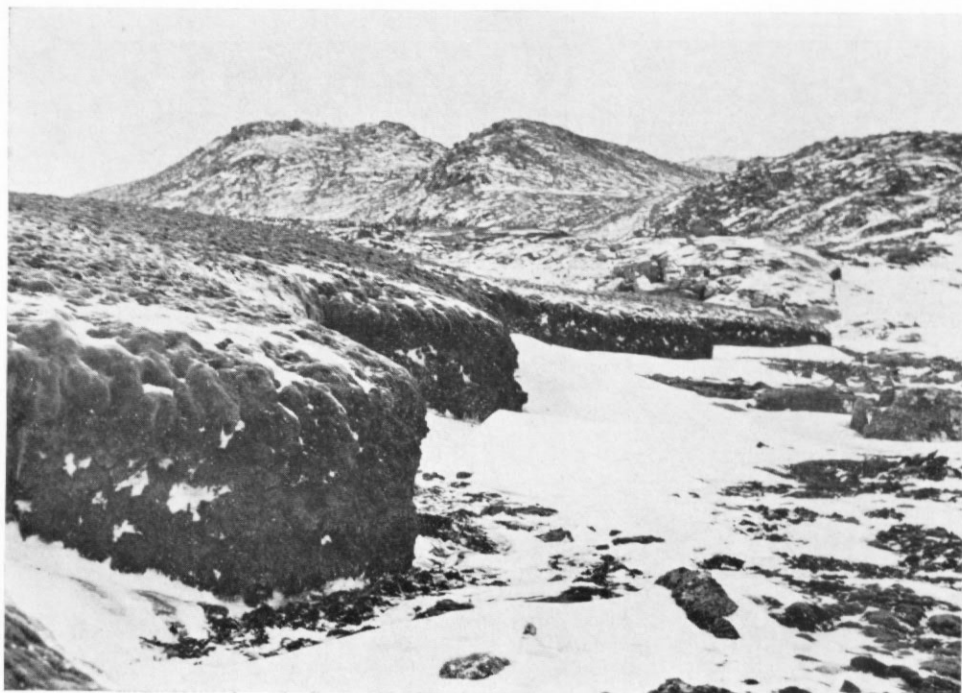


Fig. 6. The eroded edge of an isolated moss-peat bank "island" on the north-west coast of Signy Island. The bank is formed mainly from *Chorisodontium aciphyllum* and is approximately 130 cm. deep.

bank on Elephant Island (illustrated by Allison and Smith (1973, fig. 10)) were also formerly larger in extent. On Moe Island to the south-west of Signy Island, there are some extensive eroded banks (site 10) at present being re-colonized along moist sheltered gullies cut through the fibrous peat. Part of the reason for this erosion probably lies in the relative proximity of a penguin colony which at the present time is increasing in size across an actively growing peat bank. Trampling and the deposition of guano have killed off large areas of moss and there has been rapid colonization of *Prasiola crispa*. Similar disturbance of moss banks has been reported from Elephant Island (Allison and Smith, 1973).

At any stage in the processes outlined above a measure of reversal may occur as a result of oscillations of climate and hence of persistent snow-cover. Innumerable variations are possible and many of the phases have been separately recognized by Gimingham and Smith (1970) and Smith (1972). An increase in persistent snow-cover may lead to the burial of vegetation and indeed, during the recent decrease in snow-cover a number of old moss-peat bank surfaces have been exposed from under snow, having been buried for an unknown number of years. Other banks are still buried and during 1974 a bank 1 m. thick was excavated from under 3-4 m. of snow and ice near the north-eastern margin of McLeod Glacier below Rusty Bluff (site 11) (personal communication from J. H. C. Fenton).

The best examples of re-exposed moss-peat banks occur around the south-east tongue of McLeod Glacier between Rusty Bluff and Gourlay Peninsula (sites 11 and 12, respectively), while a less extensive bank c. 30 cm. deep occurs below Jane Peak (site 13). The surfaces of the moss-peat banks at sites 11 and 12 are covered with a variety of colonizing lichens and bryophytes, as Smith (1972) has described for one site adjacent to McLeod Glacier. At site 12 in particular the diameters of the moss colonies are larger with increased distance from the snow margin. A general view of this site is given in Fig. 7; areas where moribund moss-peat



Fig. 7. The south-east tongue of McLeod Glacier looking towards the western part of Gourlay Peninsula. Site 12 lies on the snow margin; this and a number of other areas of re-exposed moss-peat banks are indicated. Lighter areas of rock, which are mostly unvegetated, are also evident around a number of persistent snow patches.

banks have been exposed are indicated and it can also be seen that there are areas around snow beds where the rocks are lighter in colour. On the other hand, the Jane Peak exposure (site 13) is more recent, being partially inundated by running water from the melting snow bank above, even at the end of season, and has not been colonized by lichens or bryophytes. This bank is formed almost entirely of *Chorisodontium aciphyllum* and the base of the 30 cm. thick layer was ^{14}C -dated at 254 ± 35 yr. B.P. (1696 A.D.). From this evidence, an overall mean annual length increment of less than 2 mm. can be calculated but in this instance it is clear that the bank had not been growing continuously for the entire period.

Chorisodontium aciphyllum is the commonest of the mosses which colonize or regenerate on these re-exposed surfaces, its shoot apices being extremely fragile and when detached serving as vegetative propagules. Once such a propagule has become established and has developed a small cushion-shaped colony (Fig. 8), it spreads laterally and abuts on other developing turves, ultimately coalescing with them. This process is illustrated diagrammatically in Fig. 3c which shows sections through part of a re-exposed peat bank at the edge of a snow-field or glacier.

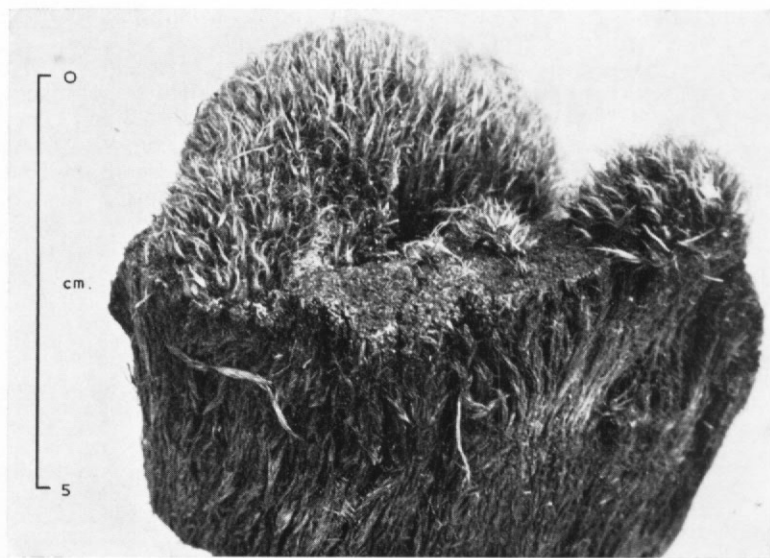


Fig. 8. *Chorisodontium aciphyllum* colonies on the re-exposed surface of a moss-peat bank at site 11.

Above the present snow line on the banks abutting on the south-east tongue of McLeod Glacier (sites 11 and 12) there was in 1969–70 a more or less continuous surface of live *C. aciphyllum*, but the old surface could be traced within the turf with discontinuities in coloration and stem orientation showing as distinct horizons. Fig. 9 shows such horizons in sequential cores taken from a short transect within the peat bank situated 15–20 m. up the slope of the low hill shown in Fig. 7 and above the banks adjacent to the margin of McLeod Glacier (site 12). These horizons are apparent in cores taken from many banks around the island which have a more or less evenly growing surface at the present time. A number of banks on the north-west coast of the island, such as occur inland from Spindrift Rocks (site 14) and which present surfaces similar to those around McLeod Glacier, may all be examples of banks which have been buried by snow for a number of years in the recent past and which are now being re-colonized. It has been virtually impossible to predict where deep snow banks and drifting are most likely to occur except in the very broadest terms.

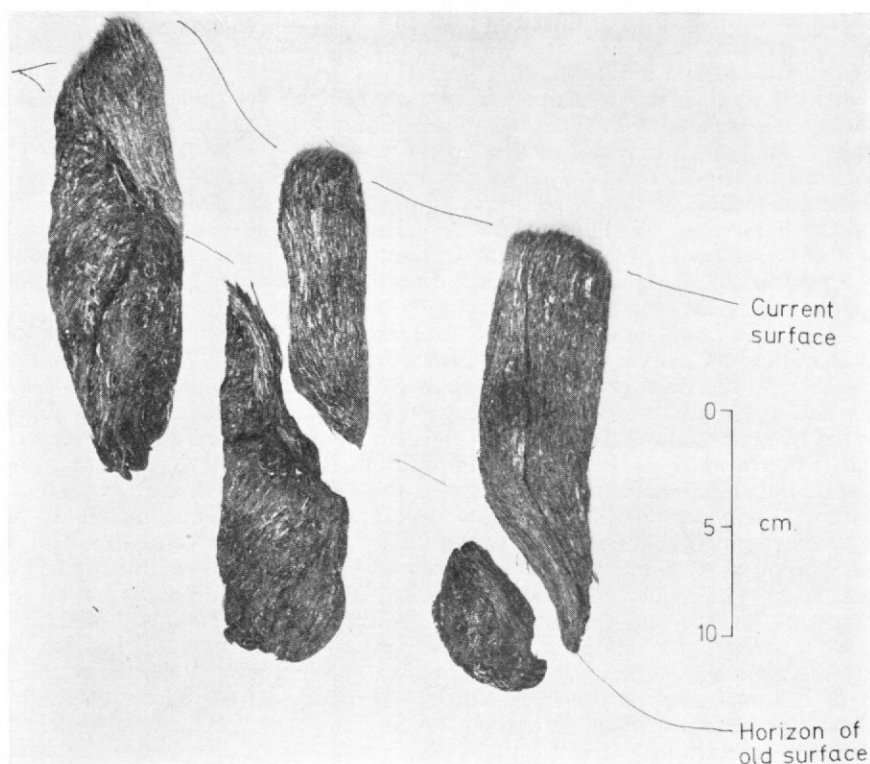


Fig. 9. Sequential cores taken through an evenly sloping bank of *Chorisodontium aciphyllum*. The left-hand core clearly shows a re-colonized surface where the moss shoots have different orientations, whilst the other two cores have more or less split at the surface. The cores were taken from a moss-peat bank on the slopes above McLeod Glacier, shown left of centre in Fig. 7.

DISCUSSION AND SUMMARY

There is evidence that earlier interglacial periods in Antarctic regions were characterized by a much greater abundance of water than at present (Smith, 1960; Cailleux, 1962; Robin and Adie, 1964), whilst John and Sugden (1971) have suggested that during such periods the South Orkney Islands would probably have been largely free of snow and ice. The nature of the vegetation during such periods is unknown, although it is conceivable that remnants of the more slowly decomposing vegetation, such as moss-peat banks, may have survived the subsequent glacial period in areas where they became covered during the extension of snowfields by accumulation rather than by mobile expansion of glaciers with consequent ice scouring. Such conditions would be most likely to prevail on hillsides well above present glacier surfaces, and in this connection it is interesting that Janetschek (1970) recorded peaks of population density and numbers of species of arthropods not in coastal lowland areas of Antarctica but at higher altitudes on coastal mountains and nunataks which he regarded as localities near to or above the highest levels of former glaciations. Similarly, he believed that the pre-glacial flora and fauna had not been completely extinguished.

Secular climatic fluctuations may be of large amplitude, as occurred in the Pleistocene ice age, but other less marked changes have occurred in more recent times. In the Northern Hemisphere, Beschel (1961), from a consideration of lichen growth rates and thallus sizes, has documented glacier fluctuations which occurred over the last 2,000 yr. and obtained consistent results for areas as far apart as Africa and Greenland. On Signy Island, studies of the growth rates of *Usnea antarctica* and *Caloplaca* cf. *cinericola* on introduced substrata,

and the relation of these rates to the size of lichen thalli on the two most recent moraines of Orwell Glacier (site 15), has led Lindsay (1973) to suggest that the deposition of these moraines occurred around 1880 and 1837.

It is evident that, superimposed upon secular changes between glacial maxima and interglacial periods, there have been short-term oscillations in the extent and depth of persistent ice and snow cover which in turn has affected the vegetation.

Evidence has been provided of a recent decrease in the persistent snow and ice cover on Signy Island and probably elsewhere in the South Orkney Islands over the last 25 yr., and certain of the consequent changes in the vegetation have been outlined. Whilst in some instances older peat banks formed by turf-forming mosses have been re-exposed and subsequently re-colonized, there are also examples of new banks which are developing at the expense of the moss-carpet- and moss-cushion-dominated communities.

Baker (1972) has commented on the considerable difference between the limited peat accumulation in moss-carpet communities formed by species of *Calliergidium*, *Calliergon* and *Drepanocladus* and the deep peat banks formed by the turf-forming species *Chorisodontium aciphyllum* and *Polytrichum alpestre*. He suggested that either the rate of decomposition is similar in the two communities with the turf formers having a greater growth rate or, alternatively, that they are more resistant to decomposition. In fact, net annual length increments and productivity can be much greater in carpets than in turves (Table I), but it is suggested by the author that a combination of higher decomposition rates and instability of habitat results in more rapid turnover in moss carpets. Loss in weight per unit length of shoots in the carpet-forming moss *Drepanocladus uncinatus* amounted to 25 per cent by the end of the second year in a wet site and 14 per cent in a dry site (Collins, 1973) compared with 2 per cent per season for the turf-forming moss *Chorisodontium aciphyllum* (Baker, 1972). In addition, with changes in climate the success of carpets will vary, since they are dependent on a fairly constant water supply (Gimingham and Smith, 1971). When the source of water decreases or becomes irregular, carpets will be restricted in their development or may be invaded by more mesic turf-forming species which commence the formation of peat banks. The subsequent development of the peat banks depends on both climatic and habitat conditions and the likely sequences involved have been outlined in Fig. 3.

Cycles of growth and burial, erosion or lichen encrustation probably account for the differences between current annual length increments of 3–7 mm. for the moss turf-forming species and the mean annual length increment of 1 mm., deduced by Holdgate (1967) from a ^{14}C date of $1,843 \pm 96$ yr. B.P. (Godwin and Switsur, 1966) for the base of a bank c. 180 cm. deep and subject to slight slumping (personal communication from M. W. Holdgate). The deepest moss bank so far recorded, on Elephant Island, South Shetland Islands (Allison and Smith, 1973), has a basal radiocarbon age of $1,515 \pm 36$ yr. B.P. (435 A.D.) at a depth of 240 cm.; this indicates a mean annual length increment over the whole period of 1.6 mm. If the annual length increment of shoots of *Chorisodontium aciphyllum* growing at an angle of c. 36° on the rippled surface of the bank near Shingle Cove (mentioned above) was similar to the 3.3 mm. determined for the same species on Signy Island (Baker, 1972), the vertical component of growth will be only about 1.6 mm.

The ^{14}C date of 254 ± 35 yr. B.P. (1696 A.D.) for the shallow peat deposits below Jane Peak (site 13) sheds some further light on the vegetational history of Signy Island. Shoots within the peat, from which the sample was taken, were contiguous and growth may have been more or less continuous from the initial establishment of the turf until burial occurred as the snow bed above and behind it expanded. Assuming a mean growth rate of c. 3 mm. per season, the moribund material present in 1969–70 represented c. 100 yr. growth. Increase in size of the snow bed would then have occurred at the start of the nineteenth century, which correlates well with the inception of the "Little Ice Age" in the Southern Hemisphere (Lamb, 1964) referred to above. Since there had been no re-colonization by 1970, it seems likely that the re-exposure of this bank has occurred quite recently, probably during the period of climatic amelioration throughout the 1950's and 1960's.

Turning to the polar regions of the Northern Hemisphere, a sequence of vegetation development similar to that suggested for Signy Island has been described by Raup (1965) in a discussion of the development of thufur or turf hummocks at Mesters Vig in north-east

Greenland (lat. 72° 30' N.). He considered that the changing pattern of persistent snow-lie was responsible for changes in the distribution of plant communities. Vascular plants add to the complexity of the sequence in Greenland but there was a similar progression with moss mats (equivalent to the carpets of Gimingham and Smith (1970)) being colonized by more mesic mosses and phanerogams. These in turn formed hummocks comparable to the Signy Island peat banks but an ultimate phase of desiccation and erosion resulted from increasing annual melt of snow banks occurring progressively earlier in successive seasons with the eventual cessation of all but a brief water supply in early spring. Finally, only isolated perched plants of *Salix arctica* remained, the entire process from melting snow banks, colonization by moss mats and subsequently by turves, with an ultimate phase of erosion, taking 30 to 40 yr. Similarly, Thorarinsson (1951) has correlated the gradual disappearance of upland bog, patterned ground and also probably of turf hummocks in Iceland with a general decrease in persistent snow-cover.

The correlation between growth form and habitat (Gimingham and Smith, 1970), and between these and the pattern of growth, as summarized in Table I, have also been noted by Kuc (1970) at Fitzwilliam Owen Island (lat. 77° 07' N.) in the western Canadian Arctic. The few vascular plants that occur there are restricted mainly to the coast. Certain moss species on the island were noted to occur as "mats often composed of a single species" and to accrue only a "thin basic peat", whilst other species in the wetter habitats accumulated more and developed peat "hummocks". Although Kuc (1970) did not divide the species according to the growth-form system used by Gimingham and Smith (1970), the parallels are clear and it appears that a similar vegetation and sequence of development may occur in the Canadian Arctic. This also appears true of the Scandinavian Arctic. In a description of the poor mires of Torneträsk, northern Sweden, Sonesson (1970) noted that in some areas only a very shallow peat is formed, whilst in others "hummock structures" form, containing a "thick frozen peat layer".

A number of the common moss species occurring on Signy Island, at Torneträsk (Sonesson, 1970), Mesters Vig (Raup, 1965) and on Fitzwilliam Owen Island (Kuc, 1970) are listed in Table II; this table also relates the different growth forms described by Gimingham and Smith (1970) and Smith (1972) on Signy Island, the habitats given by Sonesson (1970) at Torneträsk and the ecological groups described by Kuc (1970) on Fitzwilliam Owen Island, with the stages of vegetation development suggested by the author for Signy Island in the Antarctic and by Raup (1965) for Mesters Vig in the Arctic. Certain species are common to each locality and indeed a further point of similarity is that some species common to Signy Island, Torneträsk and Fitzwilliam Owen Island occur in both terrestrial and aquatic forms (Mårtensson, 1956; Kuc, 1970; Light and Heywood, 1973), respectively. Few detailed descriptions of Arctic vegetation have been published in which attention has been paid to the bryophyte component but it appears that there are many similarities to the vegetation of the maritime Antarctic. However, it is probably only in the maritime Antarctic, where deep moss-peat banks have developed because of extremely slow rates of decomposition, very limited herbivory or biotic disturbances and a total lack of competition from flowering plants, that such a unique stratigraphical record exists.

It is suggested that an investigation of peat banks involving ^{14}C dating and the location of major horizons representing the re-colonization of earlier surfaces, particularly from hillsides adjacent to the present level of glaciers, should yield valuable information about the biological, geomorphological and glacial history of the Antarctic Peninsula region and the islands of the Scotia Ridge.

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TABLE II. FLORISTIC COMPOSITION OF CLOSELY RELATED BRYOPHYTE-DOMINATED VEGETATION AT FOUR POLAR LOCALITIES

Habitat	Locality			
	Signy Island, South Orkney Islands (lat. 60° 43' S.)	Torneträsk, northern Sweden (lat. 68° 20' N.)	Mesters Vig, north-east Greenland (lat. 72° 30' N.)	Fitzwilliam Owen Island, northern Canada (lat. 77° 07' N.)
Permanently wet habitats, particularly seepage areas and stream margins	Moss carpets and hummocks, often composed of a single species, and producing a thin layer of peat <i>Brachythecium austro-salebrosum</i> <i>Calliergidium</i> cf. <i>austro-stramineum</i> <i>Calliergon sarmentosum</i> <i>Drepanocladus uncinatus</i>	Moss carpets of "poor mire communities" where "peat is shallow" <i>Calliergon sarmentosum</i> <i>Calliergon stramineum</i> <i>Drepanocladus</i> spp.	"Aquatic moss" carpets <i>Calliergon sarmentosum</i> <i>Calliergon stramineum</i> <i>Drepanocladus</i> sp.	Moss "mats, often composed of a single species", producing a thin layer of peat <i>Calliergon giganteum</i> <i>Calliergon sarmentosum</i> <i>Campylium</i> spp. <i>Drepanocladus</i> spp. <i>Tomenthypnum nitens</i>
Intermittently flushed or moist habits	Moss carpets and invading turves in drier areas <i>Chorisodontium aciphyllum</i> <i>Drepanocladus uncinatus</i> <i>Polytrichum alpinum</i>	Moss carpets bordering "hummock structures" (palsas) or "in direct contact with the mineral ground" <i>Drepanocladus schulzei</i> <i>Polytrichum commune</i> <i>Polytrichum affine</i> (= <i>P. juniperinum</i>) <i>Sphagnum</i> spp.	Moss carpets and turves occurring where "small elevations rise above the general level of the water" <i>Dicranum angustum</i> <i>Drepanocladus uncinatus</i> <i>Pogonatum</i> (= <i>Polytrichum</i>) <i>alpinum</i>	Moss carpets and turves of "mesic tundra" <i>Dicranum elongatum</i> <i>Dicranum muehlenbeckii</i> <i>Drepanocladus uncinatus</i> <i>Pogonatum</i> (= <i>Polytrichum</i>) <i>alpinum</i>
Moist, well-drained semi-ombrogenous habitats	Moss turves producing shallow to deep peat accumulations <i>Chorisodontium aciphyllum</i> <i>Polytrichum alpestre</i> (= <i>P. strictum</i>) <i>Polytrichum alpinum</i>	Moss turves of "hummock communities" containing a "thick frozen peat layer" <i>Dicranum elongatum</i> <i>Polytrichum affine</i> (= <i>P. juniperinum</i>) <i>Sphagnum</i> spp.	Moss turves and mats producing peat "hummocks" <i>Bryum pseudotriquetrum</i> <i>Tomenthypnum nitens</i> <i>Pogonatum</i> (= <i>Polytrichum</i>) <i>alpinum</i> <i>Campylium</i> spp.	Moss turves and mats producing "hummock peat" <i>Bryum pseudotriquetrum</i> <i>Polytrichum juniperinum</i> var. <i>gracilis</i> (= <i>P. strictum</i>) <i>Pogonatum</i> (= <i>Polytrichum</i>) <i>alpinum</i> <i>Campylium</i> spp.

Only the commoner species are listed for each locality. Quoted phrases are authors' original terms.

Information for Signy Island from Smith (1972) and the author; for Torneträsk from Sonesson (1970); for Mesters Vig from Raup (1965); for Fitzwilliam Owen Island from Kuc (1970).

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