

REPRODUCTION OF ANTARCTIC MOSSES IN THE GENERA *Polytrichum* AND *Psilopilum* WITH PARTICULAR REFERENCE TO TEMPERATURE

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ABSTRACT. The reproductive capacity of the Polytricha was investigated with relationship to temperature at sites between the Falkland Islands and Marguerite Bay, Antarctic Peninsula. Fruiting was widespread in *Polytrichum alpestre* and *P. piliferum* on the Falkland Islands and in these species and *P. alpinum*, *P. juniperinum* and *Psilopilum antarcticum* in the sheltered north-east coastal lowlands of South Georgia. The frequency of sporophytes may decline in some species, notably *P. alpinum*, at high altitudes and on more exposed coasts of South Georgia, while reproductive success in all five species was drastically reduced in the maritime Antarctic where widely scattered fruiting colonies of only *P. alpestre* and *P. alpinum* were recorded. Moreover, many of the occasional sporophytes at the Antarctic sites were small, aborted, or abnormally shaped and incompletely differentiated, and spores were recorded only in *P. alpinum* on Lynch Island. A sixth species, *Psilopilum tapes*, occurred only rarely at scattered sites on South Georgia; one fruiting specimen was examined.

In the Antarctic, perichaetia of *Polytrichum alpestre* and *P. alpinum* were widespread in most localities but perigonia were less common than on South Georgia, particularly in *P. alpestre*. Sporophyte production in both species often failed even where perigonia were present, and it is suggested that spatial separation of male and female plants, antheridial abortion and failure in fertilization or in the early stages of sporophyte development may all be factors responsible for the rarity of capsules. *Polytrichum juniperinum*, *P. piliferum* and *Psilopilum antarcticum* were less common in the maritime Antarctic than *Polytrichum alpinum* and *P. alpestre*. Both antheridia and archegonia were recorded at least once in each species at the Antarctic sites.

Polytrichum alpestre and *P. alpinum* showed basically similar seasonal patterns of gametangial and sporophyte development in each locality. Overwintering occurred during the development of both gametangia and sporophytes, and reproductive organs of several cycles were present in most specimens. The timing of the gametangial cycle was found to vary by up to several months between localities, and between different years at a given site. Although less detailed information was available, it appears that *P. juniperinum*, *P. piliferum* and *Psilopilum antarcticum* have reproductive cycles similar to *P. alpestre* and *P. alpinum*, at least on South Georgia.

Micro-climate studies were carried out at Signy Island and the Argentine Islands, where ten thermistors were placed near the surface of *Polytrichum* turves, and gave readings every 3 hr. for over a year. The records revealed wide diurnal fluctuations in summer and more stable conditions in winter, the temperatures being intermediate between those experienced by mosses on South Georgia and in continental Antarctica. Rapid freezing to minima below -2°C was infrequent but temperatures varied between sites and in different years.

It was concluded that both the timing and efficiency of the sexual reproductive process in the Polytrichaceae varies widely under climatically different conditions in southern polar regions, and that rapid successful development is apparently related to temperature in the actively growing surface layer of the turf.

STUDIES in northern temperate regions have demonstrated that the gametangia and sporophytes of many mosses show clearly defined seasonal cycles of development, although the timing may differ considerably from species to species (Greene, 1960; van der Wijk, 1960). Several stages of sporophyte reproduction, including gametangial initiation and the rates of development of gametangia and sporophytes, have been shown experimentally to be influenced by such factors as temperature and photoperiod (Hughes, 1962; Benson-Evans, 1964; Monroe, 1965) and it thus seems reasonable to suppose that reproductive cycles in the field are largely under environmental control. Some evidence in support of this view has recently been provided by Benson-Evans and Brough (1966), who have shown that the rate of reproductive development in a number of species at a single locality was influenced by the prevailing climatic conditions. Other work has suggested that the timing of gametangial maturation in *Pleurozium schreberi*, a widespread northern temperate species, may vary considerably between localities in different climatic zones (Longton and Greene, 1969a). The frequency of plants bearing male sex organs was also found to vary dramatically with latitude in Western Europe, thus giving rise to a parallel variation in the frequency of sporophytes. It has been suggested that a comparable situation may also exist in many other dioecious mosses (Longton and Greene, 1969b).

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The Scotia Ridge–Antarctic Peninsula region appeared to offer admirable sites for a more detailed study of variation in bryophyte reproductive behaviour, as it provides localities with increasing climatic severity. An additional feature was that several species are widespread in these regions and also occur in temperate and Arctic regions of the Northern Hemisphere. A comparative field investigation of growth and reproduction was therefore carried out between 1963 and 1965 at the cool-temperate Falkland Islands, on the sub-Antarctic island of South Georgia and at localities in the maritime Antarctic (Fig. 1), detailed attention being focused on

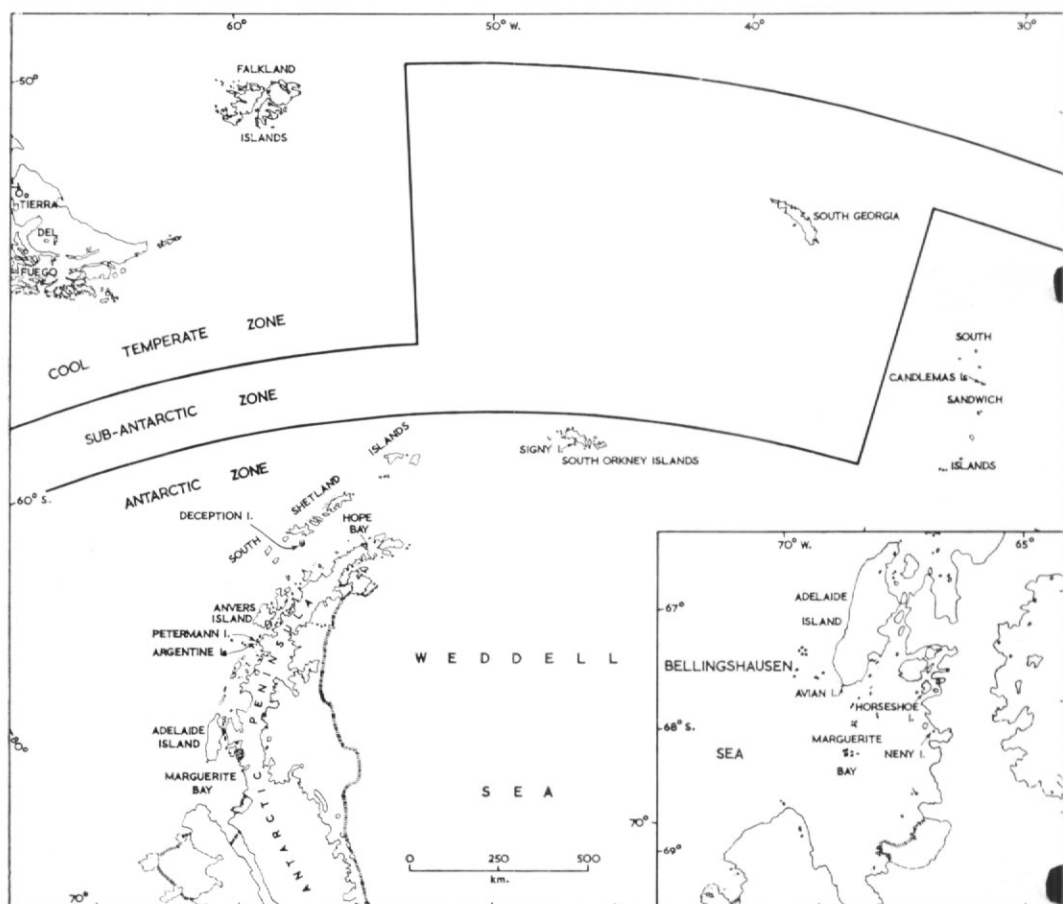


Fig. 1. The Scotia Ridge and Antarctic Peninsula showing botanical zones and the principal localities examined (from Longton, 1966).

bipolar species of the genus *Polytrichum*. Temperature measurements were also undertaken in bryophyte colonies at several sites, as this was considered one of the most important factors limiting plant performance in the relatively oceanic areas studied (Longton and Holdgate, 1967).

An account has already been given of the vegetative growth of one species, *Polytrichum alpestre*, in southern polar regions (Longton, 1970), while the reproductive cycle of *P. alpestre* and the sporophyte cycle of *P. alpinum* on South Georgia have also been described (Longton, 1966; Longton and Greene, 1967).

CLIMATE

The principal features of the climate in the areas studied have been summarized by Moore (1968) for the Falkland Islands, Greene (1964a) for South Georgia and Longton (1967) for the

maritime Antarctic. A detailed treatment, covering all these areas, can be found in Pepper (1954), more recent data being available in the *British Antarctic Meteorological Service annual tables*.

A cool oceanic type of climate prevails throughout the region with relatively little seasonal variation in air temperatures, although conditions generally become cooler with increasing latitude. Thus in summer, mean January air temperatures at Port Stanley (Falkland Islands) are approximately 9° C, compared with 6° C at King Edward Point (South Georgia) and 0° to 3° C at stations in the maritime Antarctic, corresponding figures for the mid-winter month being 2°, -3° and -9° to -15° C, respectively.

Most localities experience generally strong winds with frequent gales, mainly westerlies except near the Antarctic Peninsula, and thus topographic features which modify the air flow can have pronounced effects on the local climate. For example, Richards and Tickell (1968) have recorded considerably more severe conditions at Bird Island, off the extreme north-west of South Georgia, than prevail at King Edward Point which is situated on the north-east coast in the lee of the Allardye Range. They suggest that other sheltered north-east coastal areas may have a milder climate than the rest of the island. In contrast to the other stations, winds at the Argentine Islands are generally light to moderate, with about 20 per cent calms for the year.

All localities receive frequent cloud cover and in consequence sunshine is limited, mean records for mid-summer reaching approximately 7 hr./day at Port Stanley and 4-5 hr./day at Signy and Deception Islands, with intermediate values for sites such as the Argentine Islands which are close to the west coast of the Antarctic Peninsula.

Relative humidity is generally high, mean annual values normally ranging from 70 to 80 per cent at King Edward Point and exceeding 80 per cent at most other stations. Frequent precipitation is characteristic of most areas. Thus at King Edward Point approximately 1,400 mm. rainfall equivalent per year falls mainly as rain in summer and snow in winter. Precipitation is frequent although generally lighter in the maritime Antarctic, where rain or snow falls on over 200 days/yr. at several stations, snow predominating in winter while both are important in summer. At Port Stanley, most of the precipitation is as rain, and an average of 610 mm. falls on about 150 days/yr. Rainfall is greatest in summer and Skottsberg (1913) has suggested that the relatively slight rainfall in spring may impose limitations on plant growth. However, this factor is unlikely to be important in the other areas studied, as an abundant supply of melt water is available at this time of year.

DISTRIBUTION, GROWTH FORM AND HABITAT

The family Polytrichaceae is represented in the area by four species of *Polytrichum*, *P. alpestre* Hoppe, *P. alpinum* Hedw., *P. juniperinum* Hedw. and *P. piliferum* Hedw., and two species of *Psilopilum*, *P. antarcticum* (C. Muell.) Par. and *P. tapes* (C. Muell.) Par. Species of *Dendrologotrichum* and *Polytrichadelphus*, which occur on the Falkland Islands, were excluded from the study as they are unknown farther south.

Only three species, *Polytrichum alpestre*, *P. juniperinum* and *P. piliferum*, were recorded in the field on the Falkland Islands but all six taxa were investigated on South Georgia. All except *Psilopilum tapes* extend southwards into the maritime Antarctic and were examined at many of their known sites. Their distribution in the latter area has been described in detail by Greene and others (1970), who reported the four species of *Polytrichum* from localities as far south as the Fallières Coast and *Psilopilum antarcticum* at scattered sites southwards to the South Shetland Islands. North of the Falkland Islands, all six taxa are known from temperate localities in South America (Cardot, 1908), while the four species of *Polytrichum* are also widespread in temperate and Arctic regions of the Northern Hemisphere.

All the species are robust dioecious turf-forming mosses bearing prominent discoid perigonia or smaller inconspicuous perichaetia at the apices of their erect shoots. In *P. alpestre* the turves range in size from small discrete colonies to large continuous banks of up to 100 m. or more in length overlying 1 or 2 m. of peat. The other species seldom form deep peat deposits and are normally restricted to smaller colonies ranging from a few centimetres to 1 m. in width. *Psilopilum tapes* is a rare species which forms occasional loose turves in wet flushes and along stream banks on South Georgia but the other five species are more widespread and abundant.

Large banks of *Polytrichum alpestre* are a conspicuous feature of the vegetation of well-

drained rocky slopes in many parts of the maritime Antarctic but smaller colonies are widespread on rock ledges and among communities dominated by other mosses. However, this species is surprisingly rare on the South Sandwich Islands and also on many of the South Shetland Islands (personal communication from D. C. Lindsay). On South Georgia, *P. alpestre* is abundant in coastal tussock grassland extending to altitudes of at least 250 m. but it is seldom frequent far from the sea. No extensive banks of *P. alpestre* were observed on the Falkland Islands where the individual colonies, occurring locally in heaths and stony grassland, seldom exceed 2 m. in diameter.

Polytrichum alpinum is also abundant at many stations in the maritime Antarctic. In some areas it tends to occupy moister habitats than *P. alpestre* being common, for example, on damp rocky slopes and ledges, and among *Drepanocladus uncinatus* and other pleurocarpous mosses along the margins of moss-carpet communities of waterlogged ground. It is also one of the most important colonizers of the dry porous volcanic ash plains and slopes on the South Sandwich Islands and Deception Island. In addition, a wide variety of habitats on South Georgia support abundant *P. alpinum*, including rocks, scree slopes, tussock grassland and the more open stands of the grass heath communities. The present species differs from *P. alpestre* in being common several kilometres from the coast, and extends to altitudes of at least 600 m.

Polytrichum piliferum and *P. juniperinum* are, in general, less frequent than the species just discussed, both on South Georgia and farther south. They are characteristic of dry stony habitats on rock ledges, scree and volcanic ash and occur widely on the more open parts of the South Georgian grass heaths, while *P. juniperinum* was also seen locally in moist flushed situations. On the Falkland Islands both species occur in heaths and grassland in habitats similar to those of *P. alpestre*.

Psilopilum antarcticum is less common than the other species in the Antarctic zone but small turves occur locally both in seepage areas and on relatively dry areas of volcanic ash. On South Georgia, it is abundant in a similar range of habitats to *Polytrichum alpinum*, occurring also in flushes and other wet situations.

It may be noted that in many parts of the maritime Antarctic the four species of *Polytrichum*, together with *Psilopilum antarcticum*, are most abundant in situations with a relatively mild micro-climate. Thus, on the South Orkney Islands and on the Argentine Islands, the best developed colonies occupy level or north-facing ground well exposed to solar radiation, while Lindsay (personal communication) has noted that on many of the South Shetland Islands, where strong northerly winds are prevalent, several species of *Polytrichum* are most abundant in well-insolated sites near the more sheltered southern coasts. All five common species were also recorded on the unusually warm moist ground surrounding fumaroles on the South Sandwich Islands (Longton and Holdgate, 1967).

METHODS FOR RECORDING BRYOPHYTE REPRODUCTION

Notes on the abundance and fertility of each of the species under study were made at a wide range of localities between the Falkland Islands and Marguerite Bay, as indicated in Longton (1966). More detailed routine observations were made at 64 small scattered sites in the vicinity of Cumberland and Stromness Bays (South Georgia) and in 18 similar sites on Signy Island, each being selected on the basis that several of the study species were present but without regard to their fertility. Notes were made of the abundance and the habitat of the species at each site. The distribution of the conspicuous male inflorescences was also indicated while sporophyte frequency was recorded by means of fertility indices as used by Longton (1966). Although there is inevitably an element of subjectivity in assigning these indices, their use permits some quantitative comparisons of reproductive success.

The details of the fertility indices are as follows:

Fertility index	Definition
4	Fruiting freely in most tufts
3	Fruiting freely in some tufts
2	Fruiting sparingly in most tufts
1	Fruiting sparingly in some tufts
0	No sporophytes present

Collections of each species from the routine observation sites, as well as from other sites scattered throughout the areas studied, were scored to provide information on the distribution of sex organs and on the seasonal maturation cycles of gametangia and sporophytes. This material was supplemented by herbarium specimens and by collections taken at approximately fortnightly intervals during snow-free conditions from six long-term study colonies of *Polytrichum alpinum* and *P. alpestre* on South Georgia, Signy and Galindez Islands (Table I). Plant-level temperatures were recorded in several of these long-term study colonies for periods of at least 12 months. Most of the specimens examined, including those specified in Appendices A and B, have been deposited in the herbarium of the British Antarctic Survey, at present housed in the Department of Botany, University of Birmingham.

TABLE I. DESCRIPTION OF LONG-TERM STUDY SITES OF *Polytrichum alpestre* AND *P. alpinum* TOGETHER WITH THE DURATION OF SAMPLING

Locality	<i>Polytrichum alpestre</i>	<i>Polytrichum alpinum</i>
South Georgia	Large bank in <i>Poa flabellata</i> grassland on level ground approximately 400 m. north-north-east of the meteorological station, King Edward Point Samples from February 1961 to March 1962 and from December 1963 to January 1965 Site referred to by Longton and Greene (1967)	Several turves in dry level <i>Rostkovia magellanica</i> bog behind Shackleton House, King Edward Point Samples from December 1963 to January 1965 Site referred to by Longton (1966)
Signy Island	Large moderately steep predominantly north-north-east-facing bank approximately 100 m. east-south-east of British Antarctic Survey station Samples from December 1963 to March 1966 Site of probes D, E and F (Table XIII)	Several small turves on a steep north-facing rocky slope at the head of Factory Cove, approximately 100 m. from the British Antarctic Survey station Samples from January 1965 to March 1966 Site of probe A (Table XIII) Several large turves on peaty soil on a gentle north-facing slope in the floor of a small gully approximately 100 m. east-south-east of the British Antarctic Survey station Samples from December 1963 to March 1966 Site of probe B (Table XIII)
Galindez Island	Small moderately steep north-facing bank near Marina Point approximately 85 m. north-east of the British Antarctic Survey station Samples from March 1965 to March 1966 Site of probes J and K (Table XIII)	

Probes C, G and H were not sited in colonies from which regular samples were obtained.

The specimens were scored by the established methods summarized by Longton and Greene (1967). The presence of antheridia could normally be determined by inspection of the surface of the turf, while data for the occurrence of archegonia were obtained by microscopic examination of 20 stems per specimen. Gametangial maturity was normally based on an analysis of five stems of each sex per collection. The number of archegonia at each stage was counted, thus enabling maturity indices to be calculated but, because of their large numbers, the antheridia were normally scored by the majority-state method. Some species of *Polytrichum* are unusual in that the archegonial necks become detached from the venters soon after dehiscing. In the present work archegonia were recorded as *dehiscid* when both brown archegonial bases and detached necks with ruptured cap cells were present in inflorescences. Sporophyte development

was scored by the majority-state method in some species, while in others maturity indices were calculated from counts of the number of sporophytes at each stage, either on the whole specimen or in a sample of at least 20 capsules. However, the sample size was reduced to five fruiting stems per specimen when scoring for young sporophytes in the *swollen venter* and *early calyptra in perichaetium* stages, as dissection of the inflorescences was necessary for examination.

It should be noted that sporophyte cycles are named after the summer in which capsules dehisced, although fertilization and the early stages of sporophyte development occurred during the previous season. The terms "fertile" and "sterile" are used to denote the presence and absence of gametangia respectively, and "fruiting" and "barren" the presence and absence of sporophytes.

FREQUENCY OF SPOROPHYTES

Falkland Islands

The distribution of fruiting colonies was studied by direct observation in the vicinity of Port Stanley, where species of *Polytrichum* were surprisingly infrequent and neither species of *Psilopilum* was seen. *Polytrichum juniperinum*, *P. piliferum* and *P. alpestre* were examined in one, three and six sites, respectively, at altitudes below 70 m., and data for the frequency of sporophytes are summarized in Table II. The single colony of *P. juniperinum* was barren but *P. alpestre* and *P. piliferum* were recorded in fruit at four and two sites, respectively. Apart from a grassy slope on the southern shore of Murrell River, where capsules of *P. alpestre* were abundant in some turves (fertility index 3), indices of 1 were assigned at each fruiting site, indicating that sporophytes had developed only sparsely in a small proportion of individual colonies.

TABLE II. FREQUENCY OF SPOROPHYTES ON THE FALKLAND ISLANDS
IN SPECIES OF *Polytrichum*

Species	Number of sites with fertility indices of:					Total number of sites
	0	1	2	3	4	
<i>Polytrichum alpestre</i>	2	3	0	1	0	6
<i>Polytrichum juniperinum</i>	1	0	0	0	0	1
<i>Polytrichum piliferum</i>	1	2	0	0	0	3

Although seldom freely produced, sporophytes of *P. alpestre* and *P. piliferum* may occur regularly in many of the colonies, as two or three successive annual cycles were represented in most specimens. It may also be noted that fully developed capsules in the *operculum intact*, *operculum fallen* and *empty and fresh* stages were recorded for both species at several sites although in some collections of *P. alpestre* a high proportion of the sporophytes had aborted in the *calyptra in perichaetium* stage.

Little is known of the fertility of the Polytricha elsewhere on the Falkland Islands. Herbarium specimens of *P. alpestre* from several scattered localities were examined but none was fruiting.

South Georgia

In contrast to their scarcity on the Falkland Islands, all the species studied, except *Psilopilum tapes*, are common in the north-east coastal areas of South Georgia. Their known distribution by 5 km. squares of the South Georgian grid,* based on both field and herbarium records (Figs. 2-7), show that the concentrations of fruiting records are in the well-worked areas around Cumberland and Stromness Bays.

* The 5 km. grid is overprinted on the 1 : 200,000 map of South Georgia (D.O.S. (Misc.) 372), a copy of which accompanies Greene (1964b). The place-names used in the present paper will be found on this map.

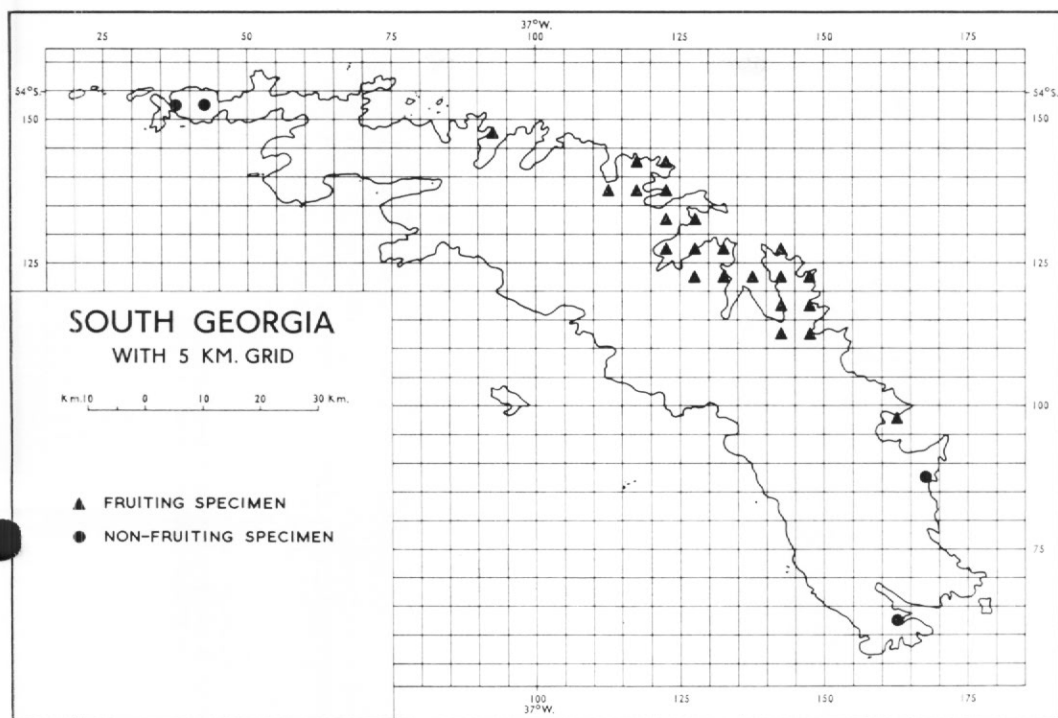


Fig. 2. Known distribution of *Polytrichum alpestre* on South Georgia by 5 km. squares.

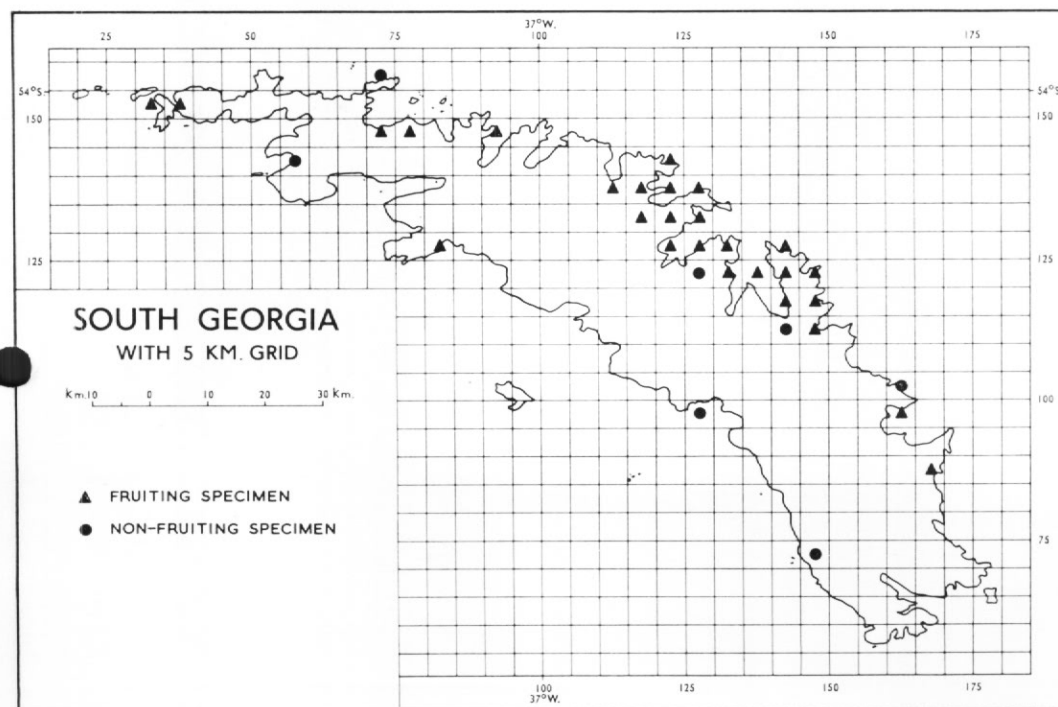


Fig. 3. Known distribution of *Polytrichum alpinum* on South Georgia by 5 km. squares.

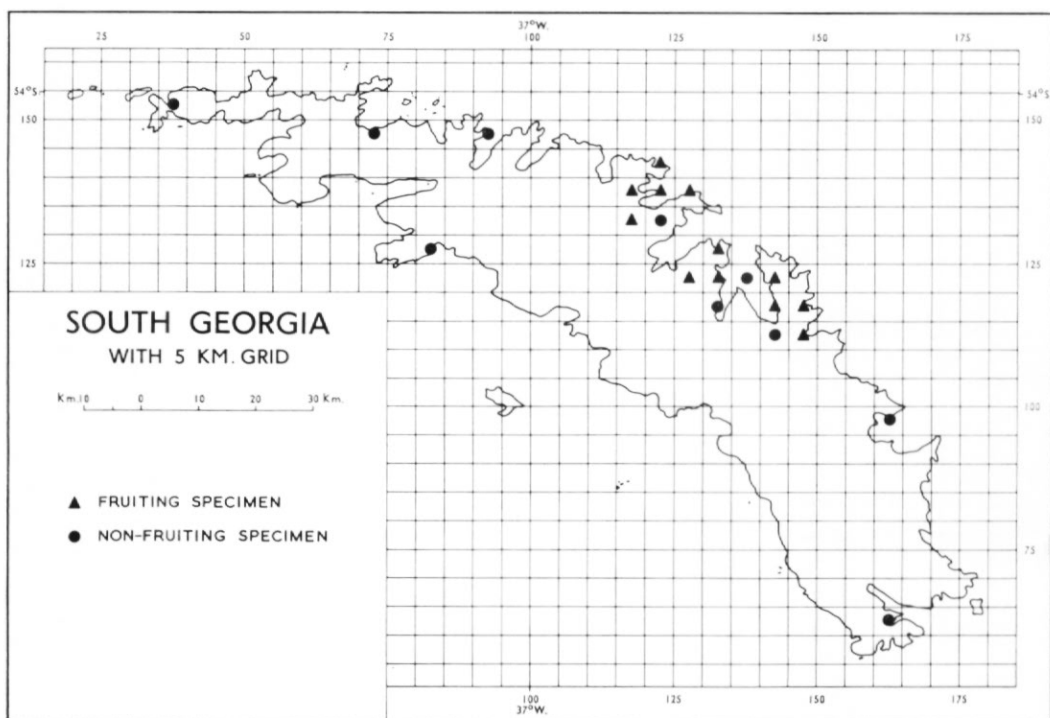


Fig. 4. Known distribution of *Polytrichum juniperinum* on South Georgia by 5 km. squares.

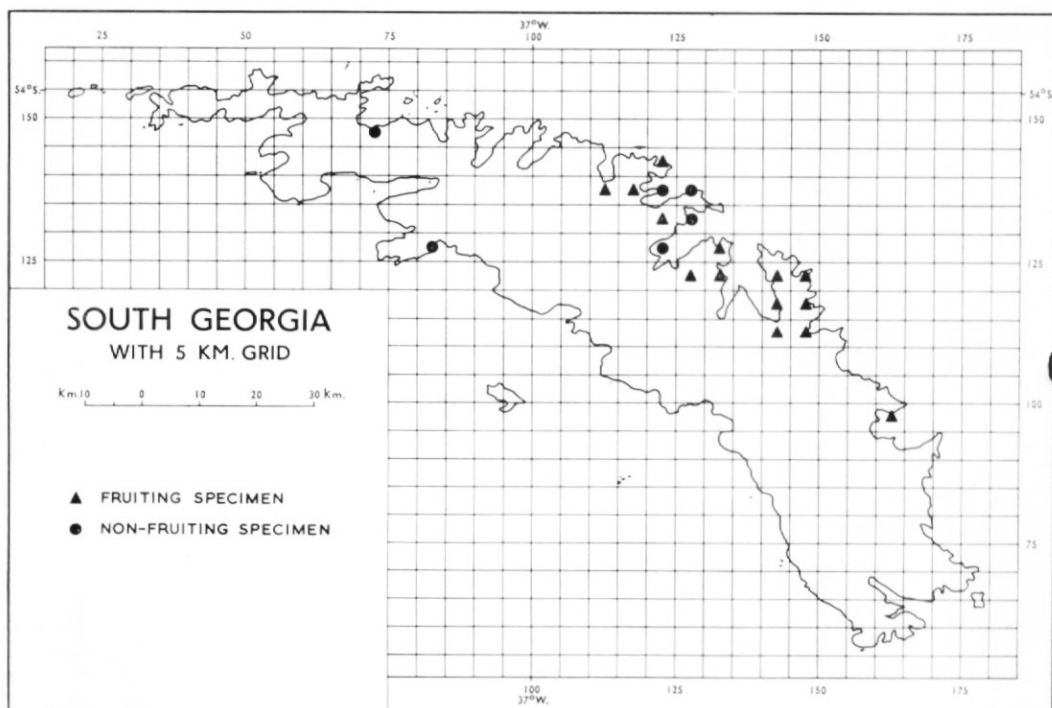


Fig. 5. Known distribution of *Polytrichum piliferum* on South Georgia by 5 km. squares.

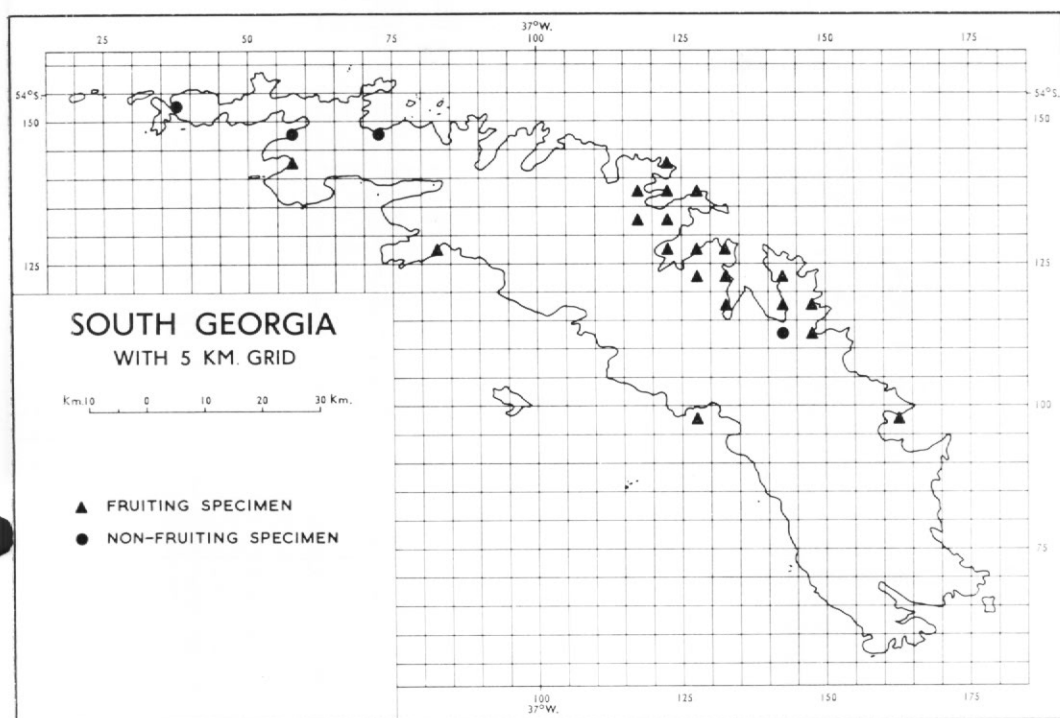


Fig. 6. Known distribution of *Psilopilum antarcticum* on South Georgia by 5 km. squares.

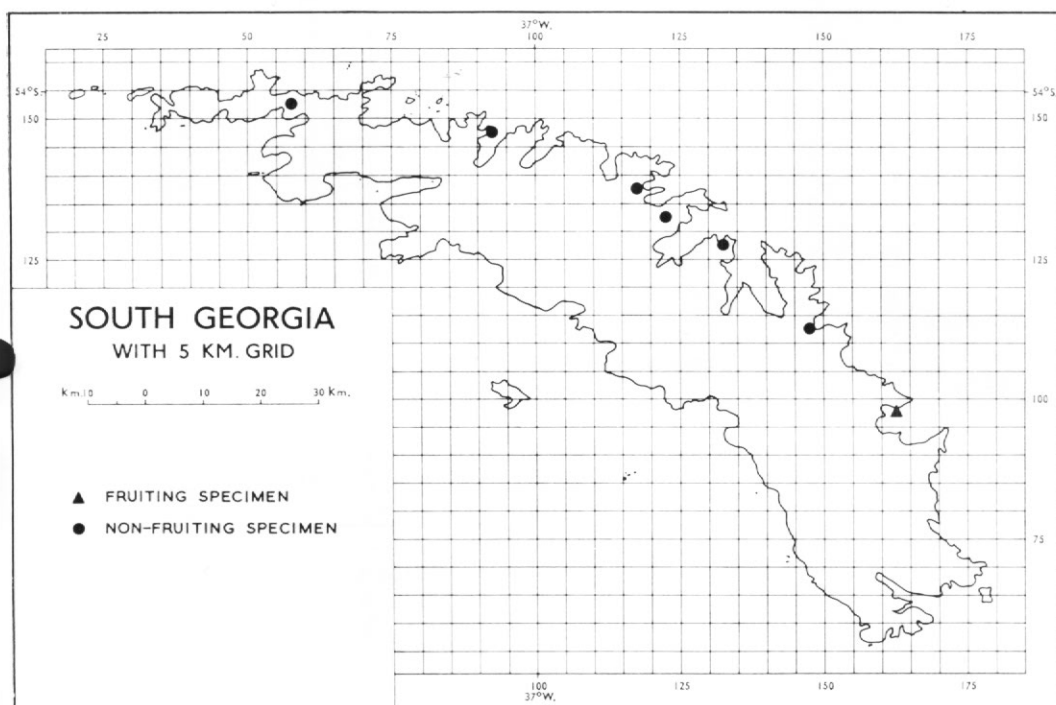


Fig. 7. Known distribution of *Psilopilum tapes* on South Georgia by 5 km. squares.

The data for sporophyte frequency at the 64 routine observation sites are summarized in Table III, the results being arranged on an altitudinal basis. Considering first the lowland sites below 150 m., it is evident that fruiting colonies of *Polytrichum alpestre*, *P. alpinum* and *Psilopilum antarcticum* were recorded at between 92 and 100 per cent of the sites where each species occurred. Moreover, fertility indices of 3 or 4 were assigned to each species at most sites, but some non-fruiting colonies were also recorded while in a few cases fertility indices of only 1 or 2 were given. The results for *Polytrichum juniperinum* and *P. piliferum* suggest that they fruit less commonly than the three previous species as sporophytes were present at a lower percentage of the lowland sites and maturity indices of 1 or 2 were given in a proportionally larger number of cases. *Psilopilum tapes* was present in only three sites and no sporophytes were seen.

TABLE III. FREQUENCY OF SPOROPHYTES AT ROUTINE OBSERVATION SITES AT DIFFERENT ALTITUDES ON SOUTH GEORGIA IN SPECIES OF *Polytrichum* AND *Psilopilum*

Species	Altitude (m.)	Number of sites with fertility indices of:					Total number of sites	Percentage of sites with fruit
		0	1	2	3	4		
<i>Polytrichum alpestre</i>	0-149	0	2	0	13	12	27	100
	150-299	0	0	0	1	1	2	100
	300-600	0	0	0	0	0	0	—
	Total	0	2	0	14	13	29	100
<i>Polytrichum alpinum</i>	0-149	0	1	1	16	20	38	100
	150-299	0	0	2	4	4	10	100
	300-600	3	2	1	0	0	6	50
	Total	3	3	4	20	24	54	94
<i>Polytrichum juniperinum</i>	0-149	4	4	0	2	3	13	69
	150-299	3	2	0	2	0	7	57
	300-600	2	0	0	0	1	3	33
	Total	9	6	0	4	4	23	61
<i>Polytrichum piliferum</i>	0-149	12	4	2	5	4	27	56
	150-299	0	4	1	0	0	5	100
	300-600	1	1	1	0	0	3	67
	Total	13	9	4	5	4	35	63
<i>Psilopilum antarcticum</i>	0-149	2	0	2	11	11	26	92
	150-299	0	1	0	2	1	4	100
	300-600	4	1	1	0	0	6	33
	Total	6	2	3	13	12	36	83
<i>Psilopilum tapes</i>	0-149	3	0	0	0	0	3	0
	150-299	0	0	0	0	0	0	—
	300-600	0	0	0	0	0	0	—
	Total	3	0	0	0	0	3	0
TOTAL	0-149	21	11	5	47	50	134	84
	150-299	3	7	3	9	6	28	89
	300-600	10	4	3	0	1	18	44
	Total	34	22	11	56	57	180	81

The data in Table III for sites between 150 and 299 m. give no indication of a reduction in sporophyte frequency at these altitudes, although it should be noted that most of the sites were situated towards the lower end of the range. The number of upland sites was too few for the effects of altitude on the reproductive capacity of individual species to be analysed satisfactorily but, if the total data for the six species are considered together, it suggests that there may be a serious reduction in the proportion of fruiting colonies at altitudes above 300 m. Thus there were only 44 per cent fruiting records for the high-altitude sites compared with 85 per cent for

sites below 300 m. Moreover, maturity indices of 3 and 4 predominated at sites below 300 m., but indices of 1 and 2 were more commonly assigned above 300 m. *Polytrichum alpinum*, for example, was fruiting in all of its sites below 300 m., with fertility indices of 3 or 4 in 44 out of 48 cases, but sporophytes were seen in only three of the six sites above this level with fertility indices of 1, 1 and 2. Similarly, *Psilopilum antarcticum* was fruiting in only two of six sites above 300 m., with fertility indices of 1 and 2, whereas fruiting plants were present in 28 of its 30 sites below this altitude with indices of 3 or 4 in 25 cases.

Further information on the frequency of sporophytes at different altitudes was obtained from a study of 183 herbarium specimens collected between 1883 and 1969. These specimens were not collected specifically for fertility studies and thus it is not surprising that the results from the herbarium material from the north-east coastal areas gave lower estimates than the field data for the level of fruit in most species (Table IV), since in general collecting by inexperienced

TABLE IV. NUMBERS OF FRUITING AND NON-FRUITING HERBARIUM SPECIMENS FROM SOUTH GEORGIA IN SPECIES OF *Polytrichum* AND *Psilopilum*

Species	North-east coast between Cape Saunders and Cape Harcourt						Other coasts		
	Below 299 m.			Above 300 m.			Below 299 m.		
	Fruiting	Non-fruiting	Percentage fruiting	Fruiting	Non-fruiting	Percentage fruiting	Fruiting	Non-fruiting	Percentage fruiting
<i>Polytrichum alpestre</i>	15	9	63	0	0	0	1	5	17
<i>Polytrichum alpinum</i>	24	18	57	1	6	14	7	20	26
<i>Polytrichum juniperinum</i>	6	9	40	1	3	25	0	7	0
<i>Polytrichum piliferum</i>	3	11	21	1	5	17	0	2	0
<i>Psilopilum antarcticum</i>	10	3	77	1	4	20	3	3	50
<i>Psilopilum tapes</i>	1	2	33	0	—	0	0	2	0
TOTAL	59	52	53	4	18	18	11	39	22

bryologists less emphasis is often placed on obtaining fruiting plants. However, the results agree with the field observations in showing that capsules may occur more widely in *Polytrichum alpestre*, *P. alpinum* and *Psilopilum antarcticum* than in *Polytrichum juniperinum* and *P. piliferum*. There is also support for the suggestion from the field data that a substantial decrease in the reproductive capacity of some species takes place at higher altitudes on the north-east coast. Thus taking the total records for the six species, 53 per cent of the 111 specimens collected below 300 m. were fruiting compared with only 18 per cent of the 22 specimens from above this level; a χ^2 test indicates that this difference is significant at the 1 per cent level.

Polytrichum alpinum and *Psilopilum antarcticum* again gave the most striking results for reduction of fertility with altitude. There are no records for either fruiting or barren plants of *Polytrichum alpestre* or *Psilopilum tapes* from above 300 m. from field or herbarium records. The highest known fruiting colony of any of the six species was at an altitude of just below 600 m. near the summit of Mount Hodges, where a single capsule of *Polytrichum piliferum* was collected by G. C. S. Clarke during 1968. Sporophytes of *P. piliferum* were also collected at an altitude of approximately 550 m. by the author in 1964, but none of the other species has yet been recorded in fruit above 400 m.

The frequency of fruiting in the relatively sheltered area between Stromness Bay and Royal Bay compared with the more exposed coasts of South Georgia is also shown in Table IV. Of the 50 specimens of the six species collected below 300 m. in the latter areas, only 22 per cent had sporophytes compared with 53 per cent among the 111 specimens from the more sheltered

coasts, a difference significant at the 1 per cent level. A χ^2 test shows that a comparable difference in the percentage of fruiting specimens of *Polytrichum alpinum* from sheltered and non-sheltered lowland sites is significant at the 5 per cent level, but the data for the remaining species are inadequate for this test to be safely applied.

It is clear, therefore, that fruiting colonies of five of the six species are widespread in the north-east coastal lowlands of South Georgia. Capsules probably develop regularly year after year, as fruiting over four successive seasons was confirmed in the long-term study colonies of *Polytrichum alpestre* and *P. alpinum* at King Edward Point, while many collections of all the five common species contained sporophytes representing two or three annual cycles. Only one fruiting specimen of *Psilopilum tapes* is known. It was collected by S. W. Greene near the north shore of Royal Bay in February 1961 and it contained ten sporophytes of two cycles.

Occasional cases of abnormal development or abortion were observed at scattered sites in all the species except *Psilopilum tapes*. Nevertheless, it seems clear that the majority of the sporophytes in most lowland colonies develop normally and ultimately liberate spores. It is interesting to note, however, that sporophytes of *Polytrichum alpinum* showed variation in size with changes in altitude or exposure. For example, most of the setae in the four high-altitude fruiting collections and in four of the five specimens from outside the Stromness Bay to Royal Bay area extended only 5–12 mm. above the bracts, whereas around the coasts of Cumberland and Stromness Bays the average seta length exceeded 10 mm. in most colonies and was normally between 15 and 20 mm. It was also noted that the capsules in two of the three high-altitude collections with fully developed sporophytes were little more than 1 mm. in diameter, whereas in the third high-altitude specimen and in most lowland colonies, the capsules were approximately twice this width. However, most of the fruiting specimens from high ground and from southern and western coasts contained sporophytes of at least two annual cycles, again suggesting that some capsules develop regularly in the fruiting colonies.

Maritime Antarctic

The tendency for the frequency of sporophytes to decrease with increasing climatic severity, as noted on South Georgia, became even more pronounced in the maritime Antarctic. This agrees with earlier observations, for Brown (1906), commenting on results obtained on Laurie Island during the Scottish National Antarctic Expedition of 1902–04, noted "among my South Orkney specimens the only species with many and well developed fruits was *Polytrichum subpiliferum* Card.". No fruiting specimens from this collection have been located but six specimens from the South Orkney Islands, originally named *P. subpiliferum*, have been re-determined as *P. alpestre* (personal communication from S. W. Greene) and thus it seems likely that the record refers to this species.

Apart from this, only one fruiting colony of *P. alpestre* and eight of *P. alpinum* have been recorded within the Antarctic botanical zone, although well-developed turves of both species were examined in many areas southwards to the Argentine Islands. *Polytrichum juniperinum*, *P. piliferum* and *Psilopilum antarcticum* were also seen in several localities but no sporophytes were recorded south of South Georgia, while Greene and others (1970) have also reported many non-fruiting specimens of all five species.

The occurrence of a single fruiting colony of *P. alpestre* at Norsel Point (Anvers Island) and of fruiting plants of *P. alpinum* on Candlemas and Deception Islands has already been reported (Longton, 1966) and fruiting records for the latter species have since been added from Lynch Island, from sites on Signy Island and from three areas on Byers Peninsula (Livingston Island) (Greene and others, 1970; personal communication from R. I. L. Smith). Full details of the fruiting records are given in Appendix A and they indicate that sporophytes were sparsely produced within most fruiting turves. Fertility indices of 1 were assigned at the three sites examined in the field, while few sporophytes were present in the other specimens except in one of *P. alpinum* from Lynch Island.

There is also evidence that the frequency of sporophytes in a given colony may vary from year to year. For example, one turf of *P. alpinum* on Deception Island produced sporophytes during the 1963–64 and 1965–66 cycles but not in 1964–65, while in a second fruiting turf only 1963–64 cycle sporophytes were seen. It is also probable that more sporophytes of *P. alpinum* developed on Signy Island during the 1965–66 cycle than in any of the other years between

1964–65 and 1967–68, while the observations from Lynch Island suggest that fruiting occurred in both 1965–66 and 1966–67 but not in the following year. Little is known about the regularity with which capsules occur in the other colonies of *P. alpestre* and *P. alpinum* except that the specimens contained sporophytes of two successive annual cycles.

As in the high-altitude collections from South Georgia, the setae in the fruiting collections of *P. alpinum* from within the Antarctic botanical zone were unusually short, normally less than 10 mm. long, and rarely exceeding 15 mm. Apart from this, the success of sporophyte development varied in different localities. The most successful colonies so far recorded for *P. alpinum* are on Lynch Island, where the majority of sporophytes of the 1965–66 cycle appeared to develop normally. Most capsules in the specimen examined were in the *operculum intact* stage and were only slightly smaller than those typical of the most favourable sites on South Georgia. The capsules examined by the author contained full-size but hyaline spores, although the presence of viable spores in other capsules was confirmed experimentally (personal communication from R. I. L. Smith). A few apparently normal dehiscent capsules of *P. alpinum* were also recorded on Livingston and Deception Islands but most of the latter were unusually small, being little more than 1 mm. in diameter. It is not clear whether these capsules had produced spores. The two 1963–64 cycle sporophytes of *P. alpinum* collected on Candlemas Island were very small and retarded, having reached only the *early calyptra intact* stage by March 1964, and it is considered unlikely that they would subsequently have attained maturity.

A high proportion of the *P. alpinum* sporophytes in the collections from Signy, Deception and Livingston Islands had aborted in the *swollen venter*, *calyptra in perichaetium* or *early calyptra intact* stages, while the majority of the *P. alpestre* sporophytes from Anvers Island had aborted in the *calyptra in perichaetium* stage. The collections also contained many striking cases of abnormal sporophyte development, even where the *early calyptra intact* stage had been successfully passed. Thus the upper parts of some undehiscent *P. alpinum* sporophytes from Signy and Livingston Islands showed no obvious differentiation into capsule and operculum, although they were apparently fully swollen and brown in colour, and in three cases where the capsule was dissected no peristome teeth were present. These capsules contained a columella but no spores and they were often misshapen in various ways (Fig. 8). In particular, it was

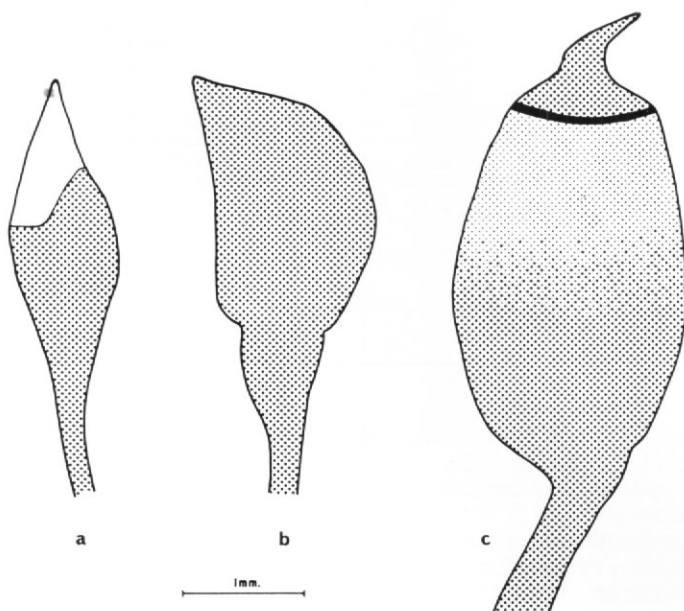


Fig. 8. Two abnormal capsules of *Polytrichum alpinum* from Livingston Island (a and b) and a normal capsule from South Georgia (c). Heavy stippled areas are brown; light stippled areas are greenish brown; unshaded areas are white. The annulus is shown in black.

noted that the operculum beak region was shorter than normal, while in some cases the apophysis was unusually large in relation to the capsule. Many capsules of *P. alpinum* from Livingston Island, and of *P. alpestre* from Anvers Island, were also thin-walled and white in colour, each again containing a columella but no spores. These capsules had opened by regular rupture near the apices but many lacked any evidence of peristome teeth or of the normal darkly coloured cells in the annular region.

It is clear, therefore, that conditions in the maritime Antarctic are often unfavourable for successful sporophyte development in *Polytrichum alpestre* and *P. alpinum* as there is only one confirmed case of viable spore production from within the Antarctic botanical zone. Many sporophytes abort at an early stage of development while in other cases there are irregularities in development during the *calyptra intact* stage, leading to the formation of misshapen, incompletely differentiated capsules. Even where fully developed capsules occur, they are normally small and borne on unusually short setae.

DISTRIBUTION OF PERIGONIA AND PERICHAETIA

Falkland Islands

Field observations in the Falkland Islands demonstrated that male inflorescences were present in the six localities where *P. alpestre* was recorded and in the three sites for *P. piliferum*. Female inflorescences were frequent in the fruiting localities of both species and were also recorded in one of the non-fruiting sites of *P. alpestre*. In the latter site, antheridia and archegonia were collected from separate colonies, and it seems likely that spatial separation of male and female plants was responsible for the absence of sporophytes. The single specimen of *P. juniperinum* bore only female inflorescences. None of the specimens examined, of any of the three species, was completely sterile, although a proportion of sterile stems was usually present. Only one barren bisexual specimen was noted (Table V). Thus it seems that sporophytes normally result when antheridia and archegonia develop in close proximity. The greater proportion of male than female specimens among the non-fruiting material probably arose through a bias in collecting towards plants with the prominent perigonia, and thus the relative frequency of male and female colonies of *P. alpestre* and *P. piliferum* in the field is not clear.

TABLE V. SEX DISTRIBUTION IN SPECIMENS OF THREE SPECIES OF *Polytrichum* FROM THE FALKLAND ISLANDS

Species	Number of fruiting specimens		Number of non-fruiting specimens			
	Female	Bisexual	Male	Female	Bisexual	Sterile
<i>Polytrichum alpestre</i>	1	6	9	2	1	0
<i>Polytrichum juniperinum</i>	0	0	0	1	0	0
<i>Polytrichum piliferum</i>	5	5	2	0	0	0
TOTAL	6	11	11	3	1	0

South Georgia

As on the Falkland Islands, the distribution of perigonia in species of *Polytrichum* and *Psilopilum* on South Georgia was determined by direct observation in the field, while subsequent microscopic examination of specimens gave information on the frequency of perichaetia.

Perigonial distribution in each species at the 64 routine observation sites is summarized in Table VI, which indicates that male inflorescences were recorded at most sites where sporophytes had developed, and it is considered probable that they were present but overlooked at the remainder. As all these taxa, apart from *Psilopilum tapes*, were frequently found in fruit it seems clear that both male and female gametangia of the five common species develop widely in the north-east coastal areas of South Georgia. The regularity of gametangial production in *Psilopilum antarcticum* and the four species of *Polytrichum* is further emphasized by the

TABLE VI. DISTRIBUTION OF PERIGONIA AT ROUTINE OBSERVATION SITES IN SPECIES OF *Polytrichum* AND *Psilopilum* ON SOUTH GEORGIA

Species	Number of fruiting sites		Number of non-fruiting sites	
	With perigonia	Without perigonia	With perigonia	Without perigonia
<i>Polytrichum alpestre</i>	29	0	0	0
<i>Polytrichum alpinum</i>	51	0	1	2
<i>Polytrichum juniperinum</i>	14	0	6	3
<i>Polytrichum piliferum</i>	20	2	5	8
<i>Psilopilum antarcticum</i>	26	4	2	4
<i>Psilopilum tapes</i>	0	0	2	1
TOTAL	140	6	16	18

frequent occurrence of perichaetia and perigonia in specimens from non-fruiting colonies (Table VII), indicating that most such collections were unisexual male or female; a few were bisexual but completely sterile specimens were recorded only for *Psilopilum tapes*.

At the fruiting sites it was noted that the populations of each species commonly comprised both bisexual fruiting turves and other colonies without sporophytes. Some of the latter contained perigonia while in others no inflorescences were seen in the field. However, it seems clear from a microscopic examination of the collections that most of the non-fruiting turves were either unisexual male or unisexual female (Table VII). Thus each species may be represented at the fruiting sites by a series of discrete male, female and bisexual colonies, the latter normally producing sporophytes. In some species fruiting also occurs in female turves where male plants occur nearby. For example, one freely fruiting colony of *Polytrichum juniperinum* near Husvik whaling station had the nearest perigonia approximately 30 cm. distant, while a more sparsely fruiting colony was situated 110 cm. from the nearest male inflorescences.

It has already been noted that *Polytrichum alpestre* commonly forms large banks as well as small discrete turves. A detailed investigation of sex distribution in one of these extensive banks has shown that it comprised a mosaic of male, female and bisexual areas. Bisexual turf was normally fruiting but the fertilization range again appears to be substantial at times, as sporophytes were recorded in female areas up to 75 cm. from the nearest perigonia. The observations on these remarkable bryophyte banks have been reported in detail by Longton and Greene (1967), who suggested that they have developed through the expansion and eventual coalescence of large numbers of discrete turves.

Except for *P. alpestre*, a number of non-fruiting sites was recorded on South Georgia for each species and, as shown in Table VI, perigonia were seen at a proportion of these sites. When specimens from the colonies with perigonia were examined later it was confirmed that the majority were unisexual male, only two collections, one of *Polytrichum juniperinum* and one of *Psilopilum antarcticum*, proving bisexual. Many of the non-fruiting sites with perigonia also supported colonies in which no gametangia were observed in the field. These latter turves were not generally sampled, and thus it is not clear how frequently they contained perichaetia. The presence of unisexual colonies of both sexes was confirmed at one barren high-altitude site for *Polytrichum alpinum* and the presence of only a small number of sterile specimens among the material scored suggests that this arrangement may be more widespread.

The specimens from non-fruiting sites lacking perigonia all proved to be female, with the exception of two sterile collections from a population of *Psilopilum tapes*. The absence of perigonia from the unisexual female sites would, of course, be sufficient to ensure failure of sporophyte production.

TABLE VII. SEX DISTRIBUTION IN NON-FRUITING SPECIMENS OF *Polytrichum* AND *Psilopilum* FROM ROUTINE OBSERVATION SITES ON THE NORTH-EAST COAST OF SOUTH GEORGIA

Species	At fruiting sites				At non-fruiting sites				Total			
	Male	Female	Bisexual	Sterile	Male	Female	Bisexual	Sterile	Male	Female	Bisexual	Sterile
<i>Polytrichum alpestre</i>	7	5	3	0	0	0	0	0	7	5	3	0
<i>Polytrichum alpinum</i>	10	8	2	0	1	4	0	0	11	12	2	0
<i>Polytrichum juniperinum</i>	5	2	0	0	4	3	1	0	9	5	1	0
<i>Polytrichum piliferum</i>	2	3	1	0	3	7	0	0	5	10	1	0
<i>Psilopilum antarcticum</i>	3	4	0	0	1	5	1	0	4	9	1	0
<i>Psilopilum tapes</i>	0	0	0	0	1	1	0	2	1	1	0	2
TOTAL	27	22	6	0	10	20	2	2	37	42	8	2

It is interesting to note that the five specimens of *P. alpinum* from non-fruiting sites, of which four were unisexual female and one unisexual male (Table VII), were collected in three localities above 300 m. Four additional non-fruiting herbarium specimens from similar altitudes were also examined, one proving male and the other three female, and well-developed gametangia were also recorded in high-altitude collections of several of the other species. Thirteen non-fruiting herbarium specimens of *P. alpinum* from low ground outside the north-east coastal area between Stromness Bay and Royal Bay were also scored. Of these, four proved to be sterile, two were unisexual male and seven unisexual female. The occurrence of the sterile specimens contrasts strikingly with the previous data and the present results, combined with the records from the non-fruiting collections from high altitudes, suggest that the conspicuous perigonia of *P. alpinum* may be relatively uncommon in less favourable parts of the island, a factor which must contribute to the reduced frequency of sporophytes.

The results for South Georgia thus indicate a similar pattern of sex distribution in each of the five common species. Both male and female inflorescences develop widely on low-lying ground of the north-east coastal area, leading to sporophyte production in most bisexual colonies. Elsewhere, capsules may occur only sparingly, while in *P. alpinum* even gametangial production appears to fail in some colonies on the exposed south-west coast. There is little information on sex distribution for the sixth species, *Psilopilum tapes*, but male, female and sterile specimens were collected at routine observation sites, while the only fruiting specimen known is bisexual.

Maritime Antarctic

The distribution of gametangia in the five species which occur in the maritime Antarctic, based on both field and herbarium results, is indicated in Table VIII. It can be seen that for some species the production of inflorescences of both sexes takes place over a wide area, and that both perichaetia and perigonia of each species have been recorded at least once. Not surprisingly, most fruiting specimens of *P. alpestre* and *P. alpinum* contained stems of both sexes, although perigonia were not found in two fruiting collections of *P. alpinum* from Livingston Island (Appendix A).

In contrast to the position on the north-eastern coastal areas of South Georgia, a substantial proportion of sterile specimens was recorded for each species, such collections amounting to about 25 per cent of the total (Table IX). In *P. alpestre* and *P. alpinum*, the two most abundant species, colonies with female inflorescences generally outnumbered those with males. The scarcity of perigonia was particularly marked in *P. alpestre* and they were recorded during the field work in only three localities, although perichaetia were collected at a wide range of sites on Signy Island and in places along the west coast of the Antarctic Peninsula and its offshore islands. The highest known station at which inflorescences of *P. alpestre* have been located is near Loubat Point on the Graham Coast, where stems with perichaetia were collected at 300 m., while female inflorescences of *P. alpinum* were present in specimens from southern Adelaide Island from altitudes of approximately 300 m. on Mount Gaudry and 750 m. on Mount Liotard.

Male and female inflorescences of the rarer *Polytrichum juniperinum* and *P. piliferum* have also been recorded from several localities (Tables VIII and IX), but all the fertile specimens proved unisexual with the exception of one bisexual collection of *P. juniperinum* from Deception Island. *P. piliferum* is the only species in which inflorescences (male) have been recorded from the southern part of the cold dry east coast of the Antarctic Peninsula. From the results in Table IX, it appears that male inflorescences may be of more widespread occurrence than female inflorescences in this species. In contrast, female inflorescences of *Psilopilum antarcticum* have been collected on Deception and Signy Islands but perigonia are so far only known from a single site in the vicinity of fumaroles on Bellingshausen Island. However, further data are required to clarify the sex-distribution pattern in the three rarer species.

The most detailed information on the distribution and frequency of inflorescences in the field was obtained on Signy Island during the summers of 1963-64 and 1964-65. *P. alpestre* occurred at 16 of 18 routine observation sites (Table X) and female inflorescences were recorded in seven cases, the specimens from the other nine sites proving sterile. Elsewhere on the island, perichaetia were seen sporadically in continuous banks and in the smaller discrete turves on

TABLE VIII. KNOWN DISTRIBUTION OF GAMETANGIA IN SPECIES OF THE POLYTRICHACEAE IN THE ANTARCTIC BOTANICAL ZONE

Locality	<i>Polytrichum alpestre</i>		<i>Polytrichum alpinum</i>		<i>Polytrichum juniperinum</i>		<i>Polytrichum piliferum</i>		<i>Psilopilum antarcticum</i>	
	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female
<i>South Sandwich Islands</i>										
*Leskov Island	+		+	+						
*Candlemas Island			+	+	+	+				
*Vindication Island				+						
Bellingshausen Island									○	
<i>South Orkney Islands</i>										
Coronation Island,										
Shingle Cove	○	○								
Lynch Island	○	○	○	○						
*Signy Island	○	+	+	+	+					+
<i>South Shetland Islands</i>										
Livingston Island,				*						
Byers Peninsula			○	○				○		
Deception Island,										
*Whalers Bay			+	+	+	+	+	+		+
<i>Antarctic Peninsula (west coast)</i>										
Spring Point		○								
Anvers Island,										
*Norsel Point	+	+		+			○			
*Laggard Island		+		+						
Loubat Point		○								
*Petermann Island	+	+								
Edge Hill							○			
*Uruguay Island			+			+				
*Galindez Island		+	+	+						
*Skua Island		+								
*Corner Islands			+							
Mount Demaria							○			
Cape Tuxen		○								
Berthelot Islands		○					○			
Adelaide Island,										
Mount Mangin				○						
Mount Gaudry				○						
Mount Liotard				○						
Jenny Island	○	○								
<i>Antarctic Peninsula (east coast)</i>										
*Hope Bay		+								
Cabinet Inlet							○			

* Visited during present investigation.

+ Record based on specimen collected by author.

○ Herbarium record.

level ground and north-facing slopes to altitudes of at least 130 m., but none was recorded in the few specimens from south-facing situations.

P. alpinum differed from *P. alpestre* in that perichaetia and perigonia were both widespread within the maritime Antarctic, although the former were normally more frequent at each locality. On Signy Island, perichaetia occurred on plants of *P. alpinum* in a wider range of habitats than in *P. alpestre* and they were recorded in 16 of the 18 routine observation sites (Table X), occurring on both north- and south-facing slopes. Perigonia of *P. alpinum* showed stricter habitat requirements than perichaetia, being characteristic of well-insolated north-facing slopes; they occurred less frequently on level ground and were not observed in south-facing situations. Male and female inflorescences occurred together at seven of the routine

TABLE IX. SEX DISTRIBUTION IN NON-FRUITING SPECIMENS OF POLYTRICHACEAE FROM THE ANTARCTIC BOTANICAL ZONE

Locality	Number of specimens				
	Male	Female	Bisexual	Sterile	Total
<i>Polytrichum alpestre</i>					
South Sandwich Islands	1	0	0	1	2
*South Orkney Islands	4	13	2	12	31
*Antarctic Peninsula and offshore islands	1	16	2	6	25
Total	6	29	4	19	58
<i>Polytrichum alpinum</i>					
South Sandwich Islands	4	10	0	8	22
*South Orkney Islands	4	17	7	1	29
South Shetland Islands	9	1	0	3	13
Antarctic Peninsula and offshore islands	8	9	0	4	21
Total	25	37	7	16	85
<i>Polytrichum juniperinum</i>					
South Sandwich Islands	1	1	0	1	3
South Orkney Islands	3	0	0	0	3
South Shetland Islands	1	7	1	0	9
Antarctic Peninsula and offshore islands	0	1	0	1	2
Total	5	9	1	2	17
<i>Polytrichum piliferum</i>					
South Sandwich Islands	0	0	0	2	2
South Shetland Islands	2	2	0	3	7
Antarctic Peninsula and offshore islands	4	2	0	3	9
Total	6	4	0	8	18
<i>Psilopilum antarcticum</i>					
South Sandwich Islands	2	0	0	2	4
South Orkney Islands	0	1	0	1	2
South Shetland Islands	0	1	0	0	1
Total	2	2	0	3	7
TOTAL	44	81	12	48	185

* Only one specimen from each of the long-term study sites is included.

TABLE X. SEX DISTRIBUTION IN SPECIES OF *Polytrichum* AT ROUTINE OBSERVATION SITES ON SIGNY ISLAND

Species	Number of sites				Total
	Male	Female	Bisexual	Sterile	
<i>Polytrichum alpestre</i>	0	7	0	9	16
<i>Polytrichum alpinum</i>	2	9	7	0	18
<i>Polytrichum juniperinum</i>	1	0	0	0	1
TOTAL	3	16	7	9	35

observation sites (Table X) and subsequent microscopic examination of the specimens indicated that, as on South Georgia, these populations may consist of a series of unisexual male, female and bisexual colonies; indeed the latter may be quite frequent in some localities since bisexual turves were present in 11 of 23 regular samples from a site in Factory Cove (thermistor site A, Table XIII). However, no sporophytes have been reported from this site, although mature antheridia and archegonia, the former liberating motile antherozoids, were observed in a fresh specimen examined in February 1965. A third species, *Polytrichum juniperinum*, was recorded at one of the routine observation sites (Table X), two unisexual male specimens being collected near Foca Point. Perigonia were also recorded in a collection from another site on the west coast of the island.

The analysis of 20 stem samples from the series of regular collections made from the long-term study colonies at Factory Cove (Signy Island) indicated that the frequency of inflorescences in some species may vary from year to year. For example, current-cycle perichaetia were present in a proportion of the shoots of all the 1964-65 and 1965-66 season specimens from one colony of *P. alpestre* (Table XI) but perichaetia of the 1963-64 season were recorded in only one-third

TABLE XI. FREQUENCY OF PERICHAETIA IN SPECIMENS FROM THE LONG-TERM STUDY SITES OF *Polytrichum alpestre* ON SIGNY ISLAND AND GALINDEZ ISLAND

Season	Number of specimens	Number of specimens with current-cycle perichaetia	Mean percentage of shoots with current-cycle perichaetia
<i>Signy Island</i>			
1963-64	6	2	10
1964-65	7	7	31
1965-66	8	8	28
<i>Galindez Island</i>			
1964-65	4	4	67
1965-66	7	7	89

The results are based on a 20 stem sample from each specimen collected between late November and April (Signy Island) and January and May (Galindez Island), i.e. when current-cycle perichaetia are most likely to be present.

of the specimens. Moreover, even the two female specimens from the 1963-64 season contained a lower percentage of fertile stems than those obtained in subsequent years, although it may be noted that several of the earliest samples included perichaetia persisting from the previous cycle. Thus it is clear that, although female inflorescences developed in the colony during four successive seasons, their numbers varied from year to year.

Examination of *P. alpestre* material from the long-term study colony on Galindez Island showed that female inflorescences were again present in all the specimens collected during 1964-65 and 1965-66, in fact occurring on a considerably higher percentage of the shoots than in Signy Island material (Table XI). It may be noted that specimens from female colonies collected at other sites on Signy and Galindez Islands, as well as elsewhere near the Antarctic Peninsula, showed a similar difference, since perichaetia were present on an average of 25 per cent of shoots in 13 Signy Island collections compared with 56 per cent of shoots in 16 specimens from the Antarctic Peninsula region between Hope Bay and the Argentine Islands. A χ^2 test indicated that this difference is not significant. Samples from seven female specimens from South Georgia were also scored and gave similar results to those from the Antarctic Peninsula region, perichaetia being recorded on an average of 50 per cent of the shoots.

Details of the male inflorescences of *P. alpestre* from the Antarctic zone are given in Appendix B. In five of the seven known localities, perigonia were recorded in situations with a northerly aspect, where high levels of insolation can be expected, while on Leskov Island they occurred on ground heated volcanically. Despite these apparently favourable habitats, the majority of the antheridia at several sites had aborted, although a low proportion of normal *dehiscent* antheridia was recorded on Lynch, Anvers and Jenny Islands.

The record for Leskov Island is unusual in that this was the only locality where perichaetia were not also recorded. *P. alpestre* was very rare on this island and only one colony was sampled. Perichaetia were recorded in the other localities with perigonia (Appendix B) but male and female plants were seldom seen mixed in the same turf, an exception being the fruiting colony on Anvers Island. Nevertheless, individual specimens from several other sites contained male and female inflorescences in different pieces of turf, thus indicating that the two sexes occurred in the field within short distances of each other but the female inflorescences examined showed no evidence that fertilization had occurred.

The distribution of male inflorescences at different depths within the turves from Leskov and Anvers Islands indicated that they had been produced regularly over several seasons, but it appeared that the number developing may have varied widely from year to year (Appendix B). The results from Signy Island are particularly striking and it is clear that, while perigonia developed at Factory Cove during the 1959–60, 1965–66, 1967–68 and 1968–69 seasons, they were less common, if present at all during 1963–64, 1964–65 and 1966–67. From this the possibility arises that male plants are more widespread in the maritime Antarctic than the records of perigonia suggest, as they would have been overlooked if they were in the sterile condition. It was noted on South Georgia that male plants in bisexual turves almost invariably had slightly shorter leaves than the females, but it was found that the variation in leaf length between colonies was too great to allow the sex of sterile turves to be determined on this basis.

Perigonia of *P. alpinum* were recorded southwards to the Argentine Islands, being locally common on more or less level areas of volcanic ash on both Candlemas and Deception Islands. Specimens with perichaetia were collected from these localities, and it seems likely that the proportion of female to male colonies was higher than suggested by the data in Table XI, particularly for Deception Island, owing to the preferential collection of specimens with perigonia. It may be noted that the frequency of bisexual colonies in these areas is thought to be low, as all the non-fruiting specimens examined were either unisexual or sterile.

It has been shown, then, that the five species of the Polytrichaceae occurring in the maritime Antarctic are all capable of developing male and female inflorescences, at least in scattered localities, but there appears to be a greater proportion of sterile colonies at the Antarctic sites than on the north-east coast of South Georgia. In particular, male inflorescences of *Polytrichum alpestre* develop only sporadically in the Antarctic region, while in many localities the perigonia of *P. alpinum* are largely confined to particularly favourable habitats.

REPRODUCTIVE CYCLE IN *Polytrichum alpestre* AND *P. alpinum*

Gametangial development

The stages of gametangial and sporophyte development were scored in over 150 specimens each of *Polytrichum alpestre* and *P. alpinum* to investigate the seasonal pattern of maturation. Archegonia were found to develop in groups of one to six in *P. alpestre* or one to eight in *P. alpinum* occupying small terminal perichaetia, while up to 80 or more antheridia occurred in the larger discoid perigonia of each species. There was little obvious difference between localities in the numbers of gametangia per inflorescence within each species, except that under 20 antheridia were noted in many male inflorescences of *P. alpinum* from the maritime Antarctic.

The result of scoring the stages of gametangial development against the dates of collection are given in Figs. 9–12, which compare the cycles for the long-term study colonies on South Georgia, Signy and Galindez Islands with those from single specimens from many other populations.

It is clear from Figs. 9 and 10 that maturation of antheridia in both species followed a similar basic pattern throughout the areas investigated, although the exact timing may vary by several months from locality to locality and from year to year. Development normally began during the late summer and, although some antheridia reached the *immature* stage during March and April, the majority in each population overwintered as *juveniles*. Development was resumed after snow clearance in spring, the antheridia dehiscing during the summer following their initiation. Some results in Fig. 10 appear to suggest that slow antheridial development in *P. alpinum* occurred during the winter of 1964 at the South Georgian study site but this is doubtful, since the late October specimen with a majority of *immature* gametangia was collected

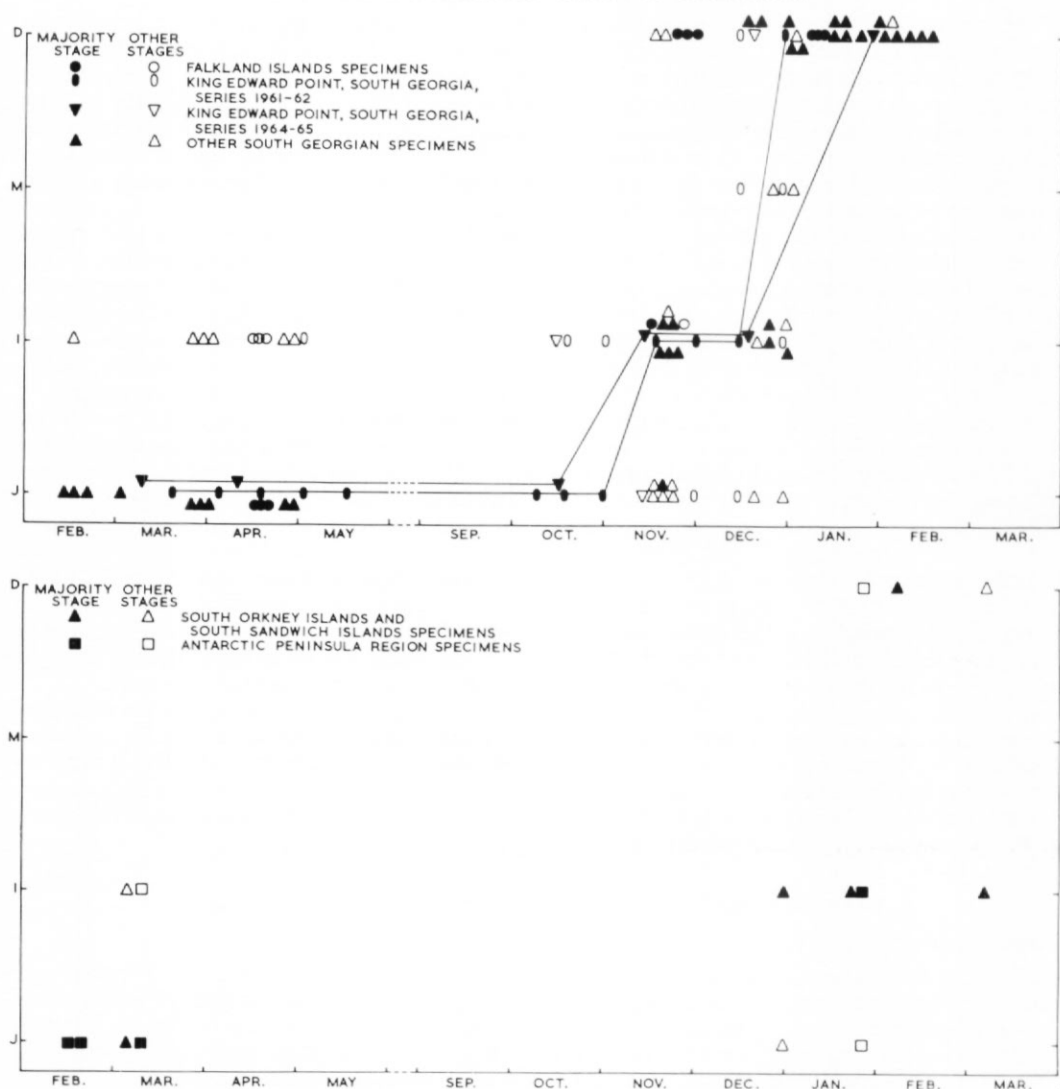


Fig. 9. The maturation cycle for antheridia of *Polytrichum alpestre* from various localities, showing the relationship between the majority stage and other stages present in each specimen, and the date of collection.

at least a week after snow clearance, and an earlier collection from the same season contained no male plants.

Young archegonia were seldom recorded in the autumn collections (Figs. 11 and 12) but they were normally present within a few weeks of snow clearance in spring. Archegonia of *P. alpinum* in the *juvenile* stage were noted at the two study sites on Signy Island during March and April 1965, apparently overwintering in that stage while a single young female inflorescence was also recorded among South Georgian material collected in April 1964. Archegonial development normally continues during spring and summer, so that dehiscence coincides with that of antheridia. During the summer period there was often a considerable spread of development within a specimen, all stages from *juvenile* to *dehiscent* commonly being recorded within a single inflorescence so that dehiscence, particularly in the case of antheridia, could extend over several weeks in each colony.

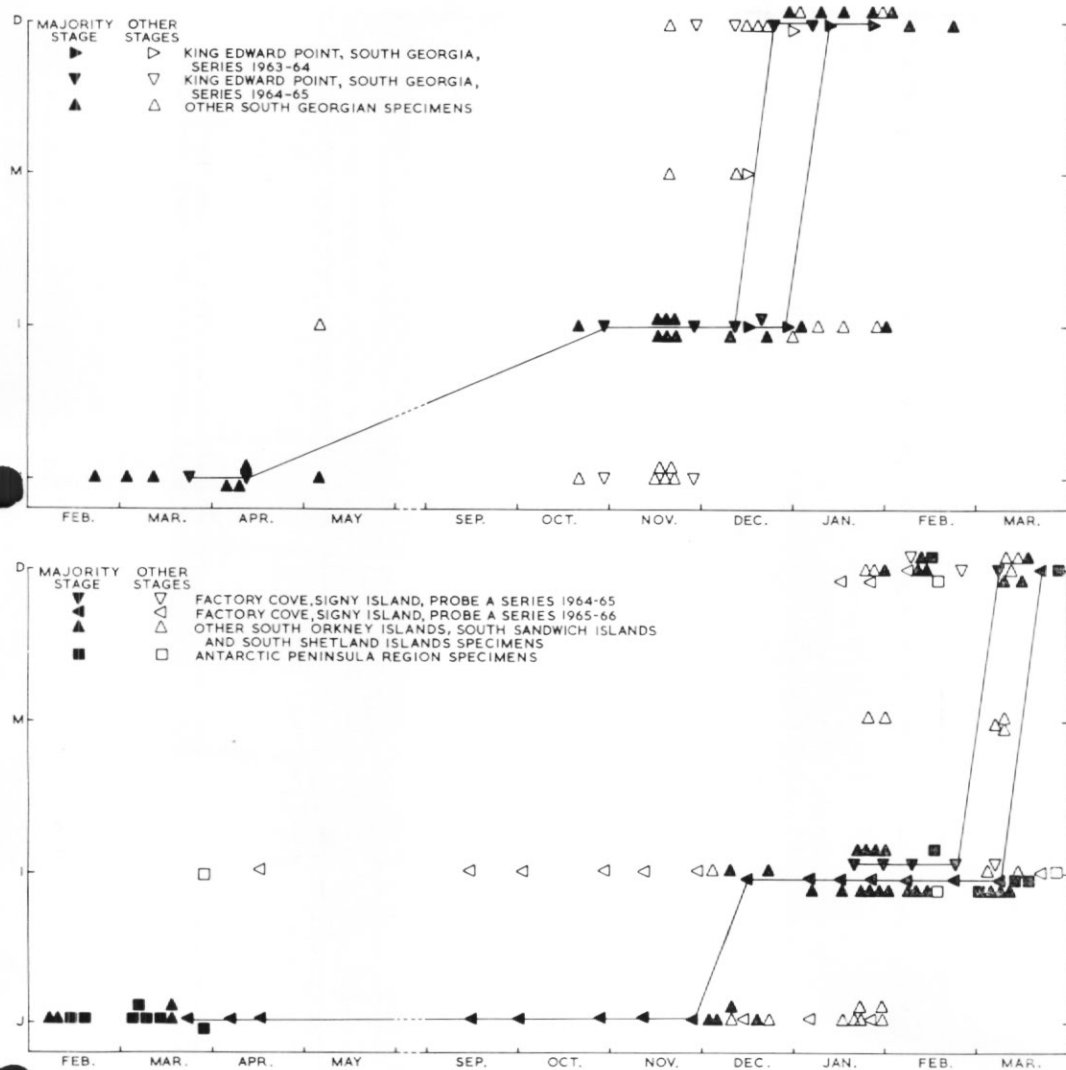


Fig. 10. The maturation cycle of antheridia of *Polytrichum alpinum* from various localities, showing the relationship between the majority stage and other stages present in each specimen, and the date of collection.

Although this basic pattern of development was consistently followed, its timing varied in different localities. Thus the spring phase of gametangial development in both *P. alpestre* and *P. alpinum* was normally under way by late October or November in the north-east coastal lowlands of South Georgia, and maturation was then rapid so that dehiscence was normally completed during December or the first half of January (Figs. 9-12). However, development may be slightly delayed in some populations of *P. alpinum* at high altitudes on South Georgia, or away from the sheltered areas on the island's north-east coast. Maturation of gametangia in both species was clearly retarded in the maritime Antarctic, as dehiscence began later and continued from January to March. The results give little evidence that the cycle differs in cloudy localities on the South Sandwich, South Orkney and South Shetland Islands compared with sunnier areas along the Antarctic Peninsula. In contrast, the few available specimens suggest that archegonial development in *P. alpestre* may be even further advanced on the Falkland

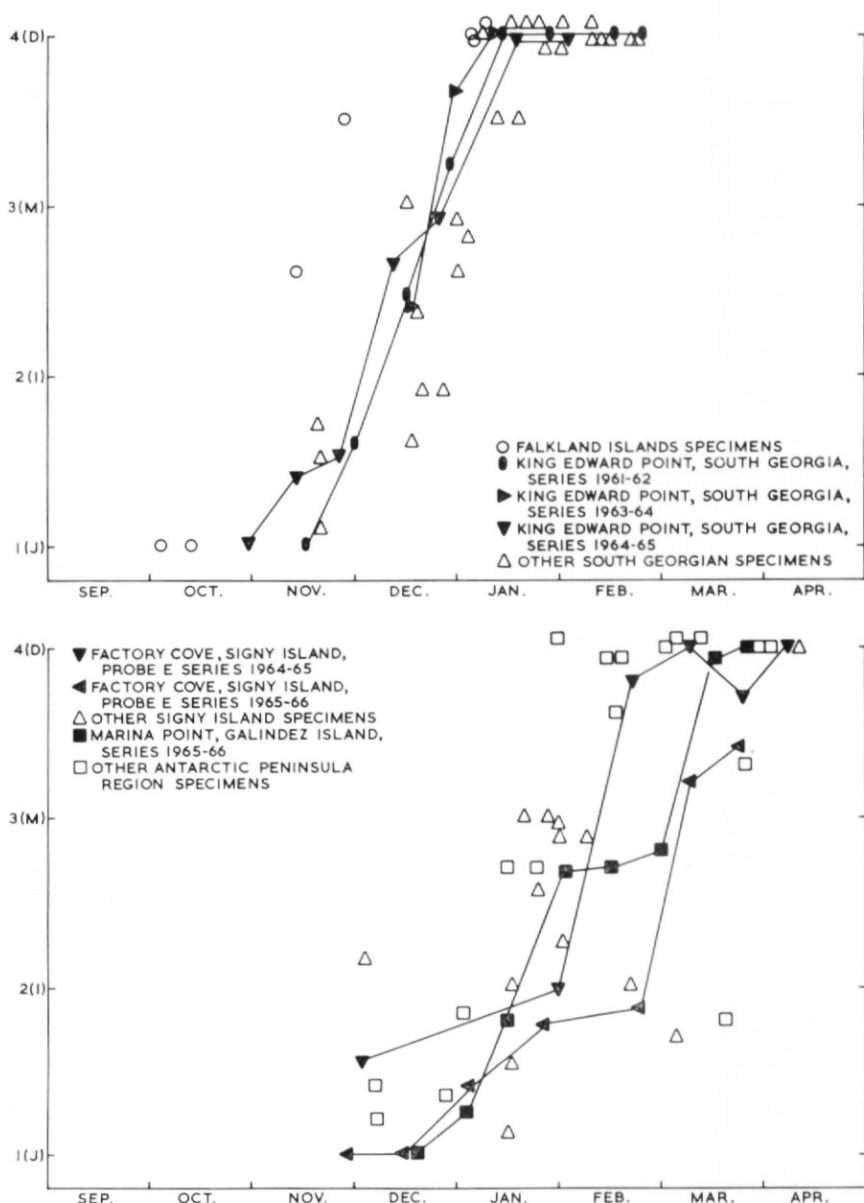


Fig. 11. The maturation cycle for archegonia of *Polytrichum alpestre* showing the relationship between the maturity index of each specimen and the date of collection.

Islands than on South Georgia. Thus the general tendency appears to be for gametangial dehiscence to take place progressively earlier in localities with a more favourable climate.

The present results indicate that gametangial development in *P. alpestre* and *P. alpinum* follows a similar basic pattern in many climatically diverse localities. However, both the onset of development in spring and the rate of maturation during the summer may vary from site to site and from year to year.

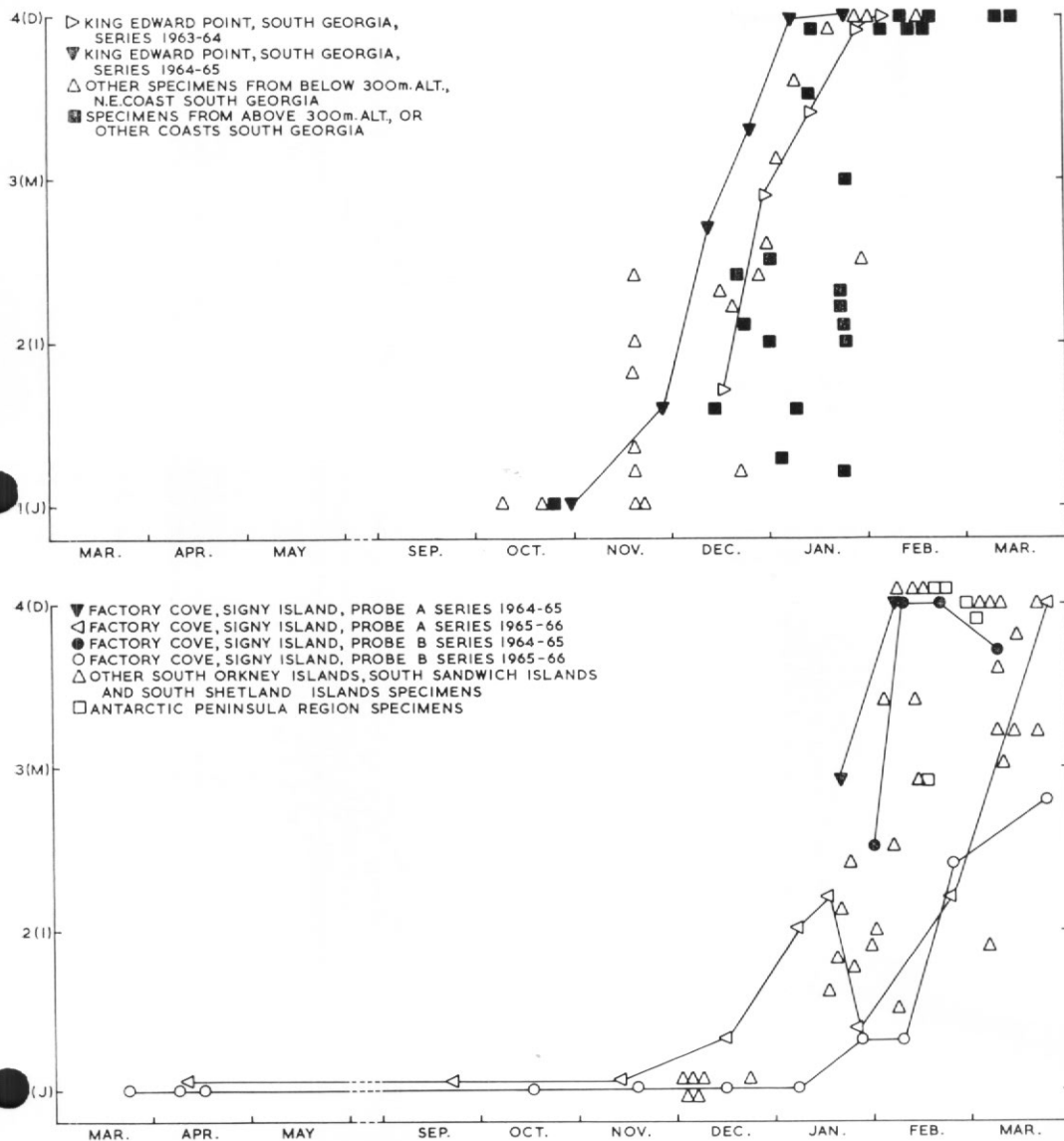


Fig. 12. The maturation cycle for archegonia of *Polytrichum alpinum* showing the relationship between the maturity index of each specimen and the date of collection.

Sporophyte development

The sporophyte maturation cycles of *P. alpinum* and *P. alpestre* on South Georgia, already described in detail by Longton (1966) and Longton and Greene (1967), are summarized in Figs. 13 and 14. It can be seen that young sporophytes in the *swollen venter* stage were first recorded in a specimen of *P. alpinum* collected in mid-November, and that they were present in both species during December. The results for gametangial development indicated that fertilization occurred at about this time and thus it seems clear that the development of the zygote begins almost immediately.

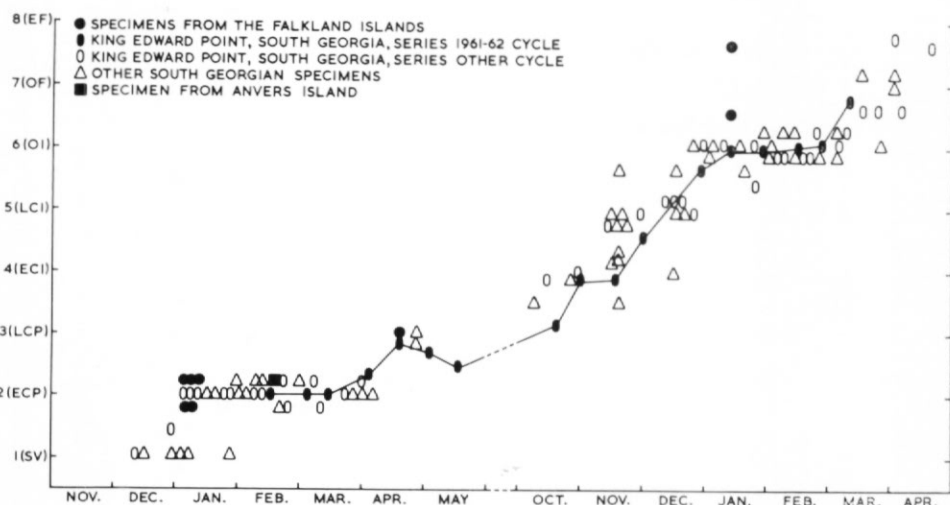


Fig. 13. The maturation cycle for sporophytes of *Polytrichum alpestre* showing the relationship between the maturity index of each specimen and the date of collection.

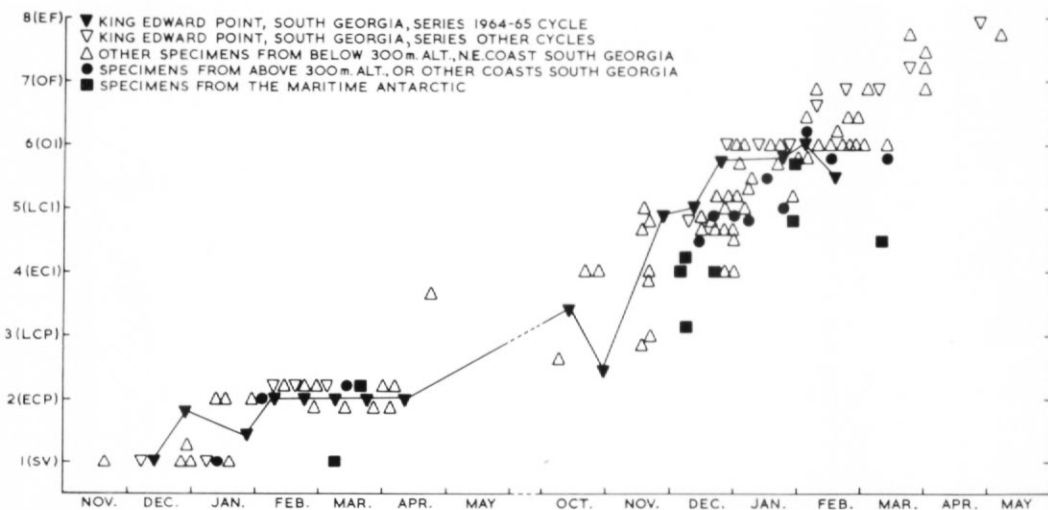


Fig. 14. The maturation cycle for sporophytes of *Polytrichum alpinum* showing the relationship between the maturity index of each specimen and the date of collection.

After reaching the *early calyptra in perichaetium* stage during January and February, the young sporophytes showed little further development until the end of the summer. Some *late calyptra in perichaetium* stages were recorded during April, when a few sporophytes of *P. alpinum* may even reach the *early calyptra intact* stage with the base of the calyptra extending just above the perichaetial bracts.

In the October specimens of both species most sporophytes were in the *late calyptra in perichaetium* or *early calyptra intact* stages with setal elongation still incomplete. It is thus possible that slow development from the *early calyptra in perichaetium* stage occurred under winter snow, but it is considered more probable that much of this slight growth took place between the last autumn collections and the development of snow cover, or between snow clearance and the first spring collection. In mid-November 1964 it was noted in both species

that sporophyte maturity indices in colonies near persisting snow banks were considerably lower than in more exposed populations, suggesting that persistence of snow cover may retard the timing of sporophyte development.

Setal elongation and capsule development in both species were shown to occur between October and December, and by the end of the latter month most capsules had reached the *operculum intact* stage (Figs. 13 and 14). Many remained in this stage during January and February with spore liberation being delayed until March or April. The cycle was thus completed approximately 15 months after fertilization. It will be noted that sporophytes of two cycles were normally present in the fruiting populations from December onwards, often in addition to withered capsules persisting from previous years.

The results provide little evidence of significant variation in the timing of sporophyte development in different localities. The scattered results for *P. alpinum* suggest that the cycle in the maritime Antarctic colonies, as well as at high altitudes and on the more exposed coasts of South Georgia, may be similar to or slightly retarded compared with colonies on the north-east coastal lowlands of South Georgia, although development was clearly delayed in the case of two 1963–64 cycle sporophytes collected on Candlemas Island in March 1964. For *P. alpestre*, the occurrence of sporophytes in the *early calyptra in perichaetium* stage on the Falkland Islands in January and on Anvers Island in February is in accordance with the South Georgian cycle, but the results for two January specimens from the Falkland Islands suggest that dehiscence there may be slightly advanced.

REPRODUCTIVE CYCLE OF REMAINING SPECIES

The reproductive cycles of the other species were studied in less detail. However, the results obtained by scoring sporophyte development by the majority-state method in 75 specimens of *Polytrichum juniperinum*, *P. piliferum* and *Psilopilum antarcticum* suggested that their development on South Georgia may largely coincide with that of the species considered above. Thus sporophytes in the *early calyptra in perichaetium* stage were recorded in the three taxa during late March and early April (Fig. 15) and it seems likely that young sporophytes were present earlier in the season, since, as in *P. alpestre* and *P. alpinum*, *mature* and *dehiscenced* gametangia were recorded during December and January. The remaining data indicate that capsules developed to the *operculum intact* stage during the following spring, dehiscing towards the end of the summer.

REPRODUCTIVE ABNORMALITIES

Abortion of gametangia and sporophytes

Both gametangia and sporophytes in mosses may fail to develop to maturity and many examples of aborted reproductive structures were noted. Aborted gametangia were recognizable by discoloration, some becoming brown, pale straw-coloured or hyaline while in the *juvenile* or *immature* stages. In addition, the necks of archegonia not uncommonly became detached from the venter prior to rupture of the cap cells and gametangia in this condition may also have aborted, as it was not clear whether fertilization could occur.

In *P. alpestre* and *P. alpinum* a few aborted archegonia were commonly present in material collected throughout the areas investigated but most female gametangia appeared healthy except in a few specimens of *P. alpestre*, mostly from sites on Signy Island. It seems likely, however, that a higher proportion of antheridia fail to dehisce in *P. alpestre* due to abortion in the *immature* stage. Aborted antheridia were in the majority in a few specimens from the Falkland Islands and South Georgia, as well as from Antarctic sites, and a proportion of *dehiscenced* antheridia was normally present in specimens collected towards the end of the summer.

Sporophyte abortion may arise through failure in development at the *swollen venter*, *calyptra in perichaetium* or *early calyptra intact* stages, while many cases of abnormal development later in the cycle were recorded for both *P. alpestre* and *P. alpinum*. A low proportion of aborted sporophytes was present in many South Georgian colonies, while occasional white or misshapen capsules were also noted. Moreover, examination of collections from the study colony of *P. alpestre* suggested that most capsules of the 1964–65 cycle became detached from the

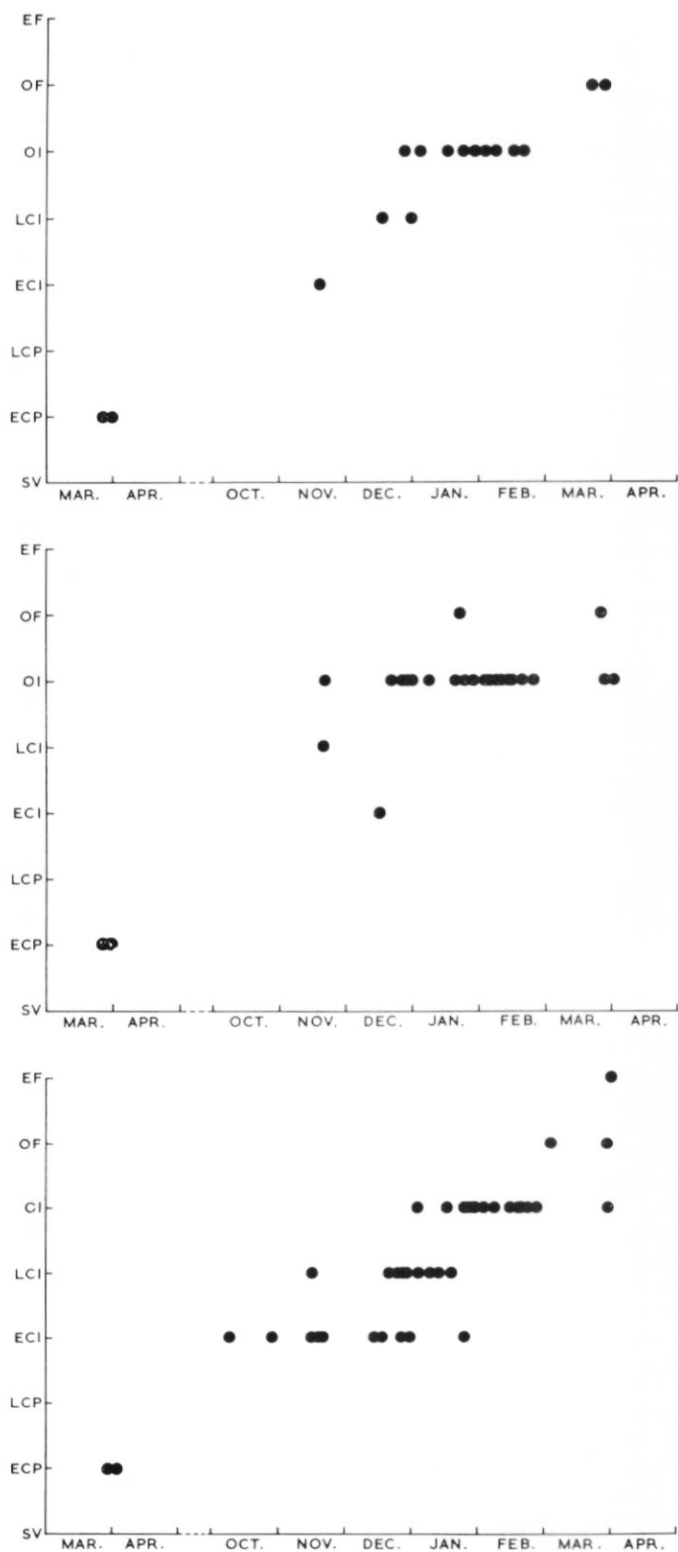


Fig. 15. The maturation cycles for sporophytes of *Polytrichum juniperinum* (upper), *P. piliferum* (middle) and *Psilopilum antarcticum* (lower) showing the relationship between the majority stage of each specimen and the date of collection.

apophyses before dehiscing in January 1965. It has already been noted that a high proportion of sporophytes appears to develop normally in most colonies of both *P. alpestre* and *P. alpinum* on South Georgia, although failure occurs more commonly in the scattered fruiting colonies in the Antarctic botanical zone (Appendix A).

Polysety

The occurrence of polysetous inflorescences provided further examples of sporophyte abnormality. Isolated cases were recorded in *Polytrichum alpestre* from the Falkland Islands and in South Georgian plants of *P. alpinum*, *P. piliferum* and *Psilopilum tapes*, but polysety appears to be most widespread in *Psilopilum antarcticum*, having been recorded in a low proportion of the inflorescences in 21 of the 34 fruiting specimens examined in detail. None of the *P. antarcticum* inflorescences contained more than two sporophytes and the pairs of capsules were often slightly smaller or retarded in development compared with normal sporophytes. These results are similar to data for the Polytrichaceae in Britain, where polysety has been recorded occasionally in several species and occurs in a few inflorescences in most populations of *Atrichum undulatum* (Longton, 1962).

RECORDING OF MICRO-CLIMATE

Equipment

The annual temperature regimes at plant level were recorded for colonies of *Polytrichum alpestre* and *P. alpinum* on Signy and Galindez Islands using methods similar to those described by Chambers (1966) but with modified probes. Stantel F22 thermistors, each housed at one end of a slender glass tube, were sealed into lengths of copper pipe with Araldite resin MY753 and hardener HY951, so that the bead and a 2–3 cm. length of glass tube projected from the pipe. The probes were positioned in the moss turves and were connected by low-resistance cable to recording equipment housed in the station's meteorological offices situated 50–100 m. away. The cables were buried to minimize temperature changes along their length. Each recording instrument comprised a Wheatstone bridge circuit and galvanometer powered by a 1.5 V dry battery which was replaced every 14 days. The resistance of each probe circuit was recorded at 3 hr. intervals by the station's meteorological staff, who also made brief notes on the duration of winter snow cover.

Calibration was carried out over the range -20° to $+40^{\circ}$ C, the resistance ranging from approximately 100 Ω to between 600 and 800 Ω for the different instruments. Each probe was calibrated with its cable intact both before and after use, except for three which were damaged after removal from the field. From the calibration curve obtained for each instrument, temperatures could be read off to the nearest 0.5 Centigrade degree.

Accuracy

There are three main sources of potential error in this type of system:

- i. The resistance/temperature characteristic of the thermistors may vary slightly with time, particularly during the first few months after manufacture (Mortimer and Moore, 1953). The present thermistors were several years old when recording began and in no case was there an appreciable difference between the first and second calibration curves.
- ii. Variation in cable temperature may alter the resistance of the probe plus cable circuit independently of the resistance of the thermistors. The importance of this effect was tested by immersing two probes in a water bath at a constant temperature of 21.5° C and taking successive readings first with the cable at a room temperature of approximately 18° C, secondly after leaving the cable in a deep freeze at -9° C for 21 hr. and thirdly after the cable had been returned to room temperature for a further 9 hr. The maximum difference in resistance for each unit was 1 Ω or the equivalent of approximately 0.1 Centigrade degree.
- iii. The bridge current may heat the thermistor bead thereby reducing its resistance. Mortimer and Moore (1953) have, however, shown that this effect is negligible with a battery voltage as low as 1.5V.

The accuracy of the equipment used at the Argentine Islands was further checked in the field by placing a thermistor beside a dry-bulb mercury thermometer in a Stevenson's screen for a 9 month period. The probe was connected to recording equipment in the meteorological office in the usual way and the resistance was read immediately after the mercury thermometer at each 3 hr. meteorological observation. The difference between the two sets of data for 2 winter and 2 summer months is summarized in Table XII, which indicates that the thermistor tended to give slightly lower readings than the mercury thermometer. However, less than 25 per cent

TABLE XII. COMPARISON OF THERMISTOR AND MERCURY-THERMOMETER READINGS ON GALINDEZ ISLAND

Month	Percentage of thermistor readings higher than mercury by:						Percentage of pairs of readings not differing: 0	Percentage of thermistor readings lower than mercury by:									
	3.0	2.5	2.0	1.5	1.0	0.5° C		0.5	1.0	1.5	2.0	2.5	3.0	3.5	4.0	4.5° C	
July 1965	0.5	—	0.5	0.5	0.5	4.6	23.4	46.2	15.4	4.6	2.8	—	0.5	—	—	0.5	
August 1965	—	—	—	—	2.1	5.9	25.3	43.0	16.7	5.4	1.6	—	—	—	—	—	
January 1966	—	—	—	—	0.8	0.8	17.8	60.0	16.5	2.9	1.2	—	—	—	—	—	
February 1966	0.5	—	—	—	1.5	2.4	23.4	51.2	17.5	2.0	—	0.5	0.5	0.5	—	—	

All readings corrected to nearest 0.5° C.

of the pairs of readings differed by more than 0.5 Centigrade degree, while under 10 per cent during the winter months and below 5 per cent in summer showed discrepancies in excess of 1.0 Centigrade degree. A negligible proportion of the pairs of readings differed by between 2.0 and 4.5 Centigrade degrees but it seems more likely that these larger differences arose through the inevitable human errors in recording rather than deficiencies in the equipment. Similarly, when the final data from the moss turves were examined it was found that isolated results diverged markedly from the normal pattern in ways which could not be explained by reference to the prevailing weather conditions. These anomalies, which accounted for less than 0.5 per cent of the total records, were also ascribed to human error in recording and were omitted from the analysis of the results. The remaining data can thus be considered accurate to within ± 2.0 Centigrade degrees, the level of accuracy in most cases probably being considerably higher.

Sites of probes

Eight probes were placed in bryophyte colonies on Signy Island and two on Galindez Island, as indicated in Table XIII. On Signy Island, data were collected from two colonies of *Polypodium alpestre* approximately 80 m. apart and from three colonies of *P. alpinum* situated up to 170 m. from each other near the British Antarctic Survey station in Factory Cove. The two Galindez Island probes were placed approximately 2 m. apart in a small bank of *P. alpestre* situated approximately 85 m. north-east of the living hut of the British Antarctic Survey station. All the study colonies on the two islands were within 20 m. of sea-level and all faced between north-east and north-west, as this was the typical aspect for well-developed colonies of both species.

Most probes were buried in the turf with the sensitive tips initially placed 2–3 mm. below the surface of the colony and screened by the moss leaves from direct solar radiation. The probes thus recorded near the level of the developing gametangia and the green photosynthetically active leaves at the stem apices. Their readings were influenced by the temperature both of the air among the upper leaves and of the leaf surfaces in contact with the sensitive region. An additional probe was buried at a depth of 2.5 cm. vertically below the surface probe in a *P. alpestre* turf on Signy Island, while another was placed a similar distance above the same colony (Table XIII). The upper probe was shaded by a white painted, hemispherical metal-gauze screen 10 cm. in diameter. It should be noted that the depth of the probes within the turf

TABLE XIII. DETAILS OF THERMISTOR SITES IN *Polytrichum* TURVES ON SIGNY AND GALINDEZ ISLANDS

Probe	Habitat	Distance from surface	Aspect and angle of slope	Recording period
<i>Signy Island</i>				
A	Small turf on moist rocky slope	2-3 mm. below	North; 35°	21.i.1965 to 25.iii.1966
B	Large turf on moist peaty soil in a small gully	2-3 mm. below	North; 10°	19.i.1965 to 25.iii.1966
C	Small turf in <i>Drepanocladus uncinatus</i> carpet on wet stony slope	2-3 mm. below	North-west; 15°	31.i.1965 to 25.iii.1966
D	Large bank on a well-drained rocky slope below cliffs	2.5 cm. below	North-east; 20°	19.i.1965 to 25.iii.1966
E	Within 15 cm. of probe D in same bank	2-3 mm. below	North-east; 20°	19.i.1965 to 25.iii.1966
F	Within 15 cm. of probe D in same bank	2.5 cm. above	North-east; 20°	19.i.1965 to 25.iii.1966
G	Large bank on a well-drained rocky slope below cliffs	2-3 mm. below	North-east; 15°	19.i.1965 to 25.iii.1966
H	Approximately 3 m. from probe G in same bank	2-3 mm. below	North-east; 15°	19.i.1965 to 25.iii.1966
<i>Galindez Island</i>				
J	Bank on dry rocky slope	2-3 mm. below	North-west; 12°	26.iii.1965 to 27.iii.1966
K	Approximately 1 m. from probe J in same bank	2-3 mm. below	North-east; 25°	26.iii.1965 to 27.iii.1966

Probes A-C in *Polytrichum alpinum*.

Probes D-K in *Polytrichum alpestre*.

may have increased slightly during the observations due to upward growth of the plants but this effect is likely to be small, at least in *P. alpestre*, since the annual growth increment in Antarctic colonies of this species is normally only 3-6 mm. (Longton, 1970).

The probes near the surface of the compact colonies of *P. alpestre* were positioned by cutting away part of the turf and drilling a hole, of similar diameter to the probe, into the exposed peat profile and running obliquely upwards to within approximately 2 cm. of the surface. The probe was inserted and the slender glass tube containing the thermistor bead was pushed gently upwards past the end of the hole until the bead was visible from the surface. The probe was then withdrawn slightly and clamped in position, the piece of cut turf being replaced. The surface probes in *P. alpinum* were clamped in a similar position, the loose turf being parted from above to allow the probe to be put in place and then smoothed back into its original form. The probe at a depth of 2.5 cm. in the *P. alpestre* turf was inserted into a horizontal hole drilled at the appropriate level.

The probes were read throughout the southern winter of 1965 and the summer of 1965-66, those on Signy Island also being operative for much of the 1964-65 summer. The 03.00 hr. reading was discontinued at Signy Island from 14 April to 13 September 1965 but, apart from this, approximately 95 per cent of the possible 3 hr. readings were obtained.

PLANT-LEVEL TEMPERATURES ON SIGNY ISLAND

Annual temperature regime

The annual pattern of temperature fluctuations at plant level on Signy Island can conveniently be summarized by comparing the regimes recorded by two probes, A and E, situated respectively in the surface layers of *Polytrichum alpinum* and *P. alpestre* colonies. In Fig. 16 the data for these probes are indicated for three periods each of 2 weeks at different times of the year, and they are related to air temperature and the duration of sunshine. It can be seen from Table XIII that probe A was more favourably orientated to intercept solar radiation. Moreover, during winter, the *P. alpinum* colony was less exposed than the raised bank of *P. alpestre* as

indicated by differences in snow cover, the latter being under a relatively thin layer of snow and ice from early April to mid-October 1965, while the former received deeper snow cover which persisted until early December. It is thus not surprising that higher temperatures were normally recorded by probe A than by probe E throughout much of the year.

During the summer (Fig. 16a) both colonies experienced long periods with regular diurnal fluctuations in temperature ranging from minima of around 0°C at night to maxima of between 10 and 25°C during the day, the daily maxima in the *P. alpinum* colony consistently exceeding those in the *P. alpestre* turf by 5 – 10 Centigrade degrees. Even higher temperatures were recorded at times, and on 11 February 1965 the temperatures recorded by probes A and E reached 36° and 28°C , respectively. The warmest day-time conditions, in general, occurred during sunny weather between mid-December and mid-February when maximum temperatures at plant level often far exceeded maximum air temperatures. However, fluctuating temperatures with peaks of 5 – 15°C also occurred in the moss turf during periods of several weeks with little sunshine. Conversely, there were other periods of cloudy weather during both summers when plant-level temperatures were remarkably stable and seldom rose above 5°C .

The daily minimum temperatures recorded at plant level during summer were, in general, similar to or slightly above the corresponding air temperature. Inversions were infrequent, particularly in the *P. alpinum* colony, although in the *P. alpestre* bank minimum temperatures occasionally fell as far as 3 Centigrade degrees below air temperature. In general, therefore, the daily minimum temperatures in both colonies were within a few Centigrade degrees of freezing point, and at plant level temperatures only rarely dropped below -2°C .

Winter snow cover became established over both colonies early in April 1965 and the difference in snow depth between the two sites resulted in contrasting winter temperature regimes (Fig. 16b). The temperature beneath the relatively deep snow cover over the *P. alpinum* colony showed markedly little fluctuation throughout the winter, remaining stable at *c.* 0°C for long periods and only falling to -3.5°C during the extremely cold weather in mid-August. On the other hand, the temperature near the surface of the less insulated *P. alpestre* colony fluctuated slowly throughout the winter in relation to changes in air temperatures. It was below -10°C for long periods during July and August, reaching a minimum of -16.5°C .

Extreme minimum temperatures reached by gradual cooling are likely to damage plants less than rapid freezing and thawing, and in this respect the winter temperature regime in both colonies was by no means unfavourable. The transitions from autumn to winter and from winter to spring conditions were accompanied by few fluctuations with minima more than a few degrees below freezing, while the low temperatures recorded in the *P. alpestre* colony for a few days in mid-April, and more consistently later in the winter, occurred after considerable periods with plant-level temperatures near or slightly below 0°C . Moreover, even the thin layer of snow over probe E was clearly sufficient to protect the plants from the worst effects of the wide and rapid fluctuations in air temperature from above to below freezing that occurred between July and September as the plant-level temperature on no occasion exceeded 0°C during this period.

Permanent winter snow cover first cleared from the *P. alpestre* site between 15 and 30 October 1965, but it is noteworthy that regular diurnal fluctuations within the range -11.0° to -0.5°C were recorded by probe E during the first half of the month (Fig. 16c). These variations were not directly related to changes in air temperature, suggesting that sufficient radiation was penetrating the remaining thin snow and ice cover during the day to affect plant-level temperatures. Records slightly above 0°C were first given by probe E during the sunny days between 14 and 17 October, and on 18 October a maximum of 9.5°C was achieved. Regular diurnal variation in temperature occurred at the site during the remainder of the month, with maxima up to 9.5°C by day but, in contrast to the results for high summer, minimum temperatures at night commonly remained between 3 and 5 Centigrade degrees above the minimum air temperature. The exact date of snow clearance from this site is unknown and thus it is not clear whether these abnormal results arose through the effect of thin snow cover permitting radiation to warm the turf by day while providing insulation at night, or to the thaw leaving the turf unusually wet and thus reducing the rate of cooling.

During November, the temperature in the *P. alpestre* turf remained close to 0°C for long periods, often coinciding with sunny weather suggesting that further snowfall took place and,

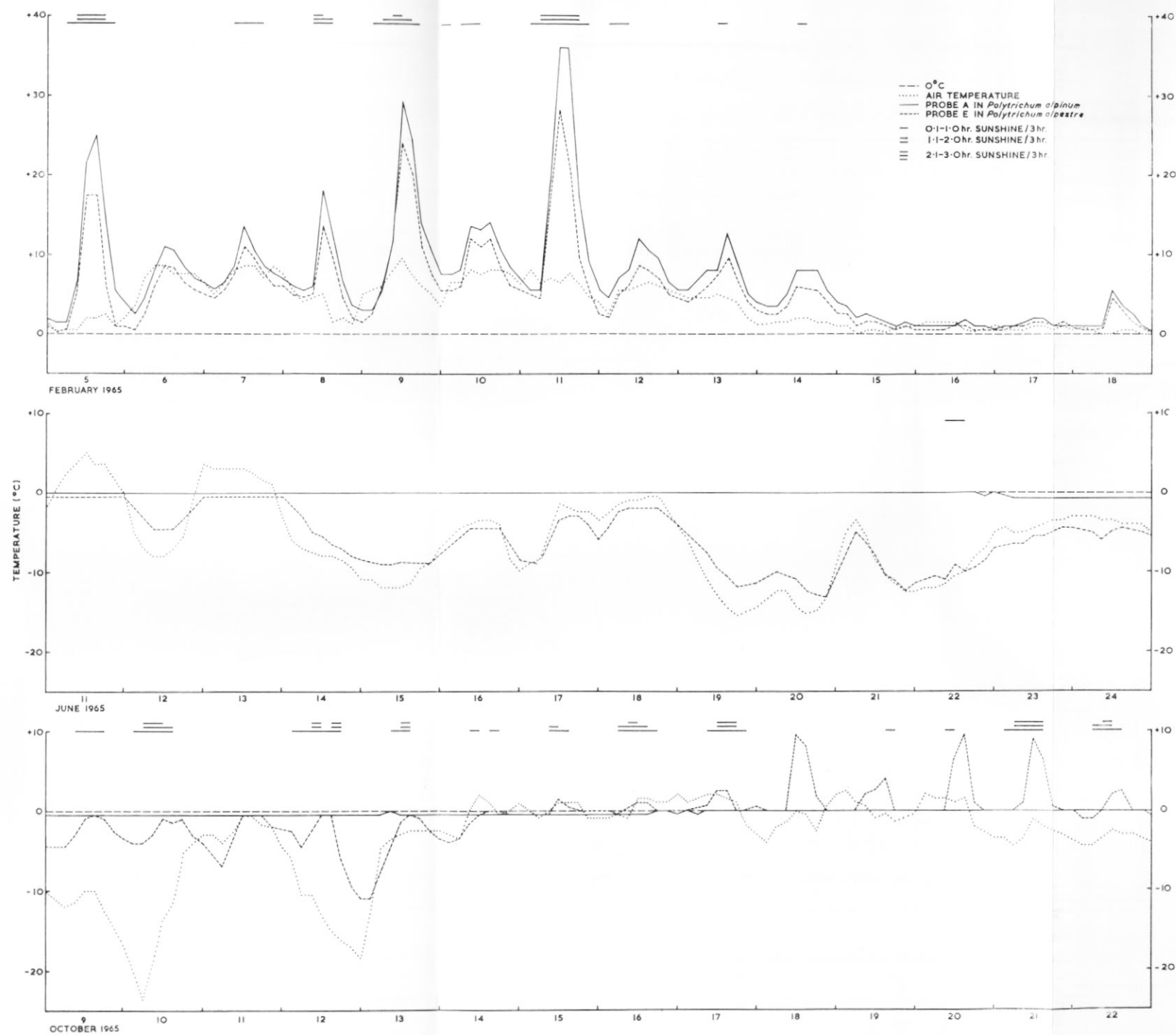


Fig. 16. Temperature regime in *Polytrichum* curves on Signy Island showing 3 hr. readings of probes A and E in relation to air temperature and duration of sunshine.
a. Summer temperatures for 5-18 February 1965.
b. Winter temperatures for 11-24 June 1965.
c. Spring temperatures for 9-22 October 1965.

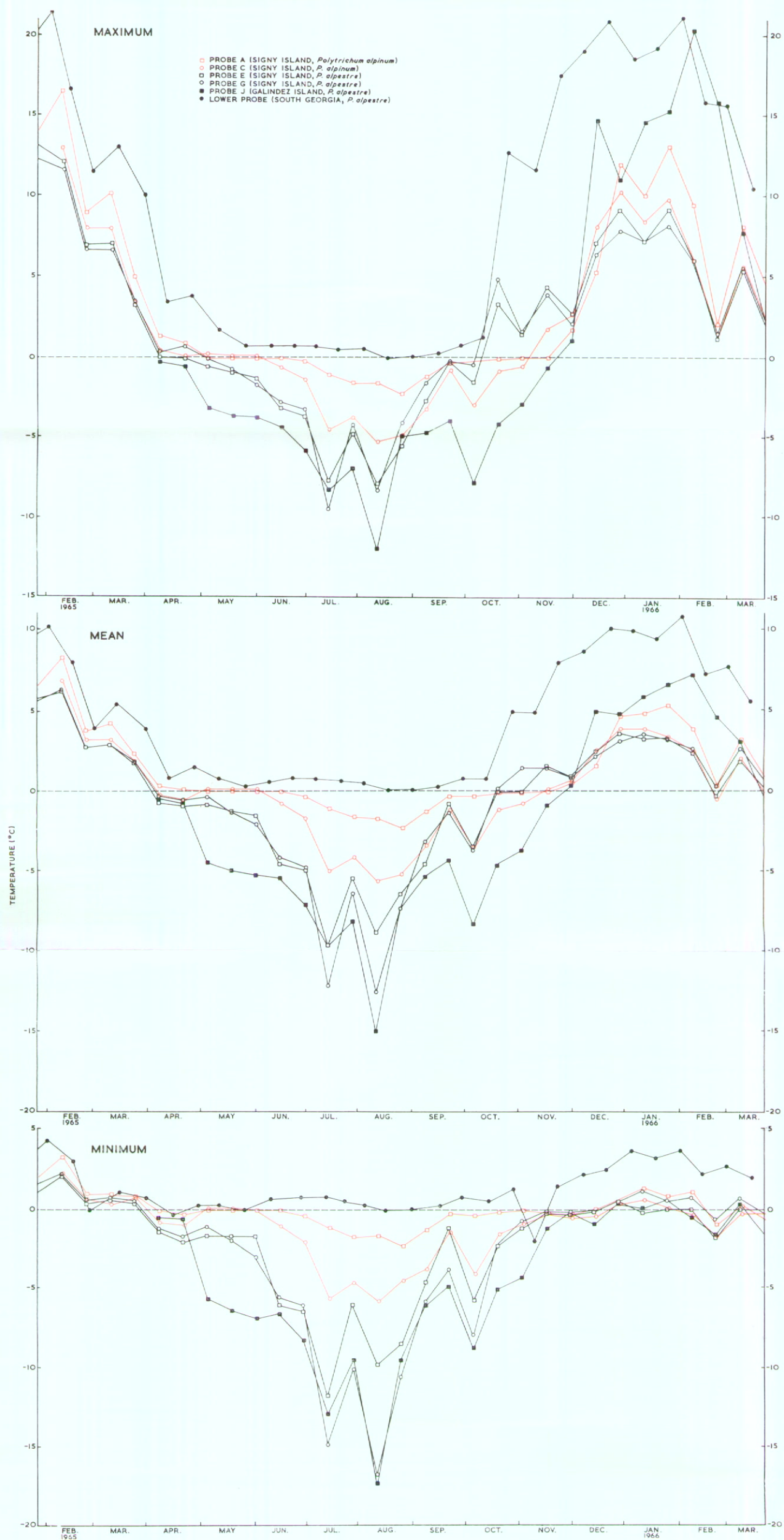


Fig. 18. Mean temperatures for successive 14 day periods near the surface of *Polytrichum* turves on South Georgia (lower probe), Signy (probes A, C, E and G) and Galindez Islands (probe J). South Georgian data are from Longton and Greene (1967).

although both the *P. alpestre* and *P. alpinum* colonies were clear of snow for a few days early in December, it was not until the middle of this month that the typical summer temperature regime was finally established at both sites.

Vertical temperature gradient

While probes A and E recorded conditions at a depth of 2–3 mm. in the colonies, two additional thermistors placed close to probe E at distances of 2.5 cm. below (probe D) and 2.5 cm. above (probe F) the uppermost leaves of the *P. alpestre* turf enabled the vertical temperature gradient near the surface to be investigated. In Fig. 17 the results are compared with air temperature for 4 days in January and February 1965 when the normal 3 hr. readings were supplemented by additional hourly records covering approximately 12 hr./day.

During the day the records from all three probes were consistently well above air temperature. In particular, the temperature indicated by probe E, situated in the surface layer of the turf, rose dramatically each morning to maxima of 15–22° C around noon. At a depth of 2.5 cm. in the turf (probe D), the temperature rose more slowly and the maxima were between 6 and 10 Centigrade degrees lower than those near the surface, occurring 1 or 2 hr. later in the day. Heat was retained longer at the greater depth, however, and at night the minimum temperatures were a few degrees higher than in the surface layer. The maximum temperatures recorded 2.5 cm. above the turf (probe F) were also as much as 10 Centigrade degrees lower than those given by probe E but the temperatures at night were similar. It is possible that the day-time readings of probe F were a little lower than could be expected due to its gauze screen preventing direct solar radiation reaching the turf below and thus reducing the strength of upward currents of warm air.

These results were typical of the summer periods although on cloudy days the differences between the levels were less pronounced. Thus during summer the daily mean temperatures in the surface layer were normally in excess of those recorded both in the air 2.5 cm. above the colony and at a similar depth in the turf. During winter, however, a more regular temperature gradient was maintained as the lowest readings were usually obtained 2.5 cm. above the surface, and the highest at 2.5 cm. below the surface at all times of the day. The gradient was slight as the mean difference between probes D and F seldom exceeded 3–4 Centigrade degrees but the average temperatures at all three levels were consistently above the mean air temperature.

Comparison with other sites

The results from the remaining probes on Signy Island show patterns of temperature fluctuation similar to those recorded by probes A and E. The data from two other probes situated 2–3 mm. deep in the turves are shown as mean daily maximum, mean daily and mean daily minimum temperatures (Fig. 18) at each site during successive 14 day periods, while Table XIV summarizes data from all the probes for four summer periods.

A comparison of the results for probes A, B and C with the remaining Signy Island figures suggests that *P. alpinum* and *P. alpestre* may experience slightly different temperature regimes, especially in winter. The three colonies of the former species all experienced deeper snow cover than the *P. alpestre* banks, and the results for probe B resembled those for probe A in showing little fluctuation during the winter, mean temperatures seldom falling below –2.0° C. In the third *P. alpinum* colony, however, probe C recorded mean temperatures down to –5.6° C during the coldest part of the winter, and the temperature regime was intermediate between those in the first two colonies and in the *P. alpestre* banks. The results given by probe E were clearly typical of the other winter data for *P. alpestre*, the temperature in each colony fluctuating slowly with long-term changes in air temperature. The lowest temperatures were recorded by probe G, which during August gave a mean value of –12.5° C (Fig. 18b), with a mean daily minimum of –16.8° C (Fig. 18c) and a single reading as low as –20.5° C. These figures were only 1 or 2 Centigrade degrees higher than the corresponding results for air temperature.

The *P. alpestre* colonies thus experienced more severe winter conditions than those of *P. alpinum* but their thinner snow cover in each case cleared earlier, resulting in a longer summer period with day-time temperatures above zero (Table XIV). The data suggest that the site of

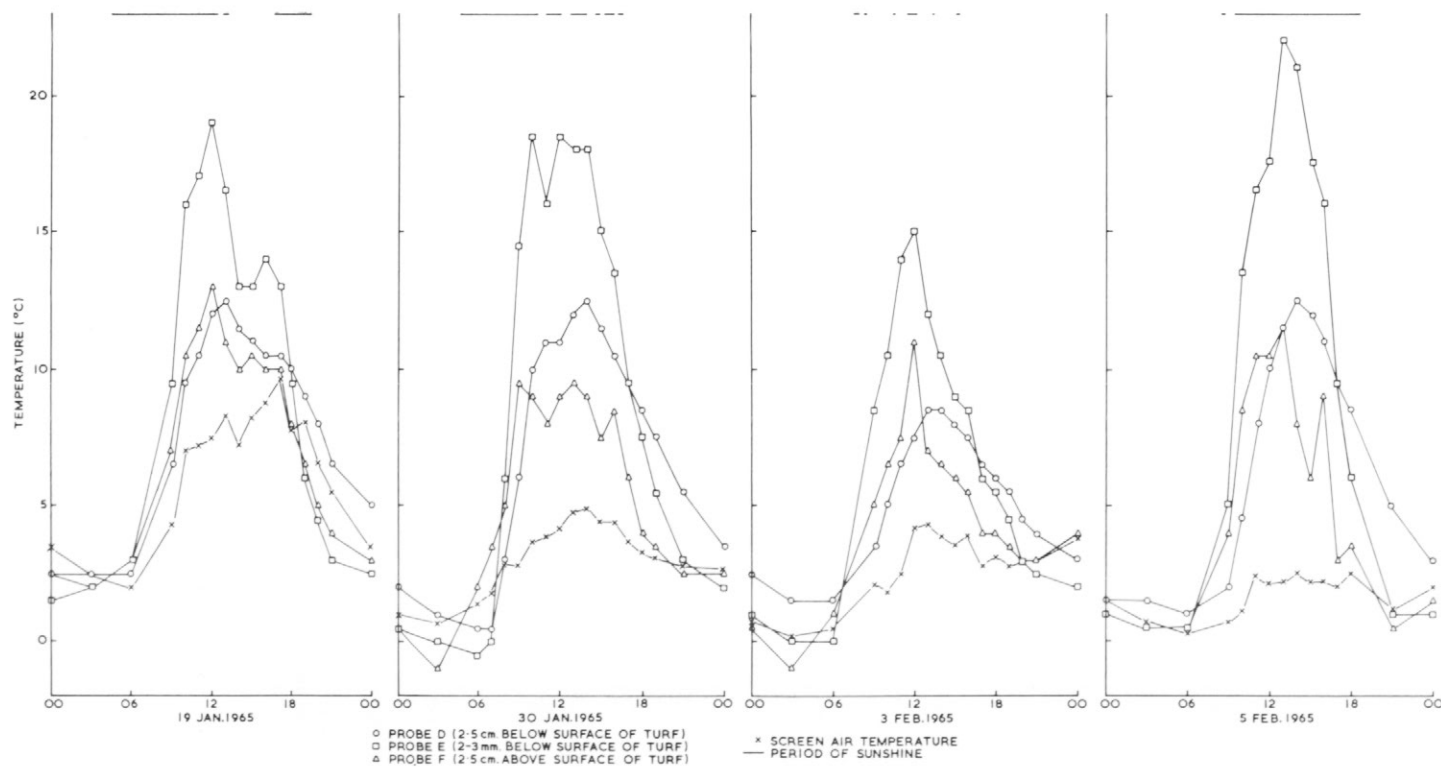


Fig. 17. Temperatures near the surface of a *Polytrichum alpestre* turf on Signy Island, during four sunny summer days, showing hourly readings for probes D, E and F in relation to air temperature and duration of sunshine.

TABLE XIV. MEAN DAILY, MEAN DAILY MAXIMUM AND MEAN DAILY MINIMUM SUMMER TEMPERATURES (°C) IN *Polytrichum* TURVES ON SIGNY AND GALINDEZ ISLANDS TOGETHER WITH AIR TEMPERATURE AND MEAN DURATION OF SUNSHINE

	19.i.-29.iii.1965*			12.x.-6.xii.1965			7.xii.1965-17.i.1966			18.i.-25.iii.1966†		
	Maximum	Minimum	Mean	Maximum	Minimum	Mean	Maximum	Minimum	Mean	Maximum	Minimum	Mean
<i>Signy Island</i>												
Probe A	10.7	1.7	5.0	0.4	-0.2	0.0	9.1	0.7	4.9	7.5	0.1	2.7
Probe B	9.0	1.4	4.3	-0.5	-0.6	-0.5	6.9	0.5	2.8	5.2	0.2	2.0
Probe C	8.1	1.1	3.8	0.7	-0.9	-0.3	8.9	0.2	3.4	4.8	-0.5	1.4
Probe D	5.3	1.7	3.5	1.2	-0.2	0.4	5.1	1.0	2.7	2.7	0.6	1.7
Probe E	8.5	0.8	3.8	2.5	-1.1	0.5	7.7	0.0	3.0	4.7	-0.4	1.4
Probe F	6.2	0.8	3.1	2.0	-2.0	-0.3	5.6	-0.1	2.0	3.1	-0.9	1.0
Probe G	8.0	1.1	3.8	3.1	-0.9	0.9	7.1	0.5	2.9	4.6	0.2	1.8
Probe H	9.1	1.0	4.0	3.1	-1.1	0.4	8.0	0.3	3.1	5.1	-0.2	1.7
Air temperature	3.9	0.8	2.4	0.5	-2.9	-1.2	1.9	-0.7	0.6	1.8	-1.3	0.3
Mean daily duration of sunshine (hr.)	—	—	1.9	—	—	1.5	—	—	1.5	—	—	1.2
<i>Galindez Island</i>												
Probe J	—	—	—	-1.3	-2.3	-1.9	13.7	0.3	5.3	11.4	-0.5	3.7
Probe K	—	—	—	-1.7	-2.8	-2.3	13.4	-0.2	5.1	12.2	-0.6	4.2
Air temperature	—	—	—	-0.5	-5.9	-3.2	1.2	-1.7	-0.2	1.1	-1.5	-0.5
Mean daily duration of sunshine (hr.)	—	—	—	—	—	3.5	—	—	3.9	—	—	4.2

* 22.i.-29.iii.1965 for probe A; 2.ii.-29.iii.1965 for probe C.

† 18.i.-27.iii.1966 for all Galindez Island records.

probe G was the first to become exposed. Temperatures above freezing were recorded sporadically by probe G from 19 September onwards, and it can be seen from Fig. 19 that severe fluctuations were recorded for a short period in mid-October, when maxima of 1.5° and 5.0° C alternated with minima of -14.0° and -13.0° C within 4 days. Such wide and rapid fluctuations from a few degrees above to considerably below zero were exceptional but they may have been more prevalent in some *P. alpestre* banks which were completely exposed throughout much of September.

All three *P. alpinum* colonies became clear of snow during late November or December, and during the subsequent high-summer period the greatest mean daily and mean daily maximum temperatures were recorded consistently by probe A. The comparable results for the other *P. alpinum* colonies, in general, slightly exceeded those for the *P. alpestre* banks but there was little difference between the colonies as regards daily minimum temperatures. The warmest conditions occurred between mid-January and mid-February 1965, and it seems clear that during this period the temperature in the surface layer of all the study colonies often exceeded 5° C for at least 9 hr. each day, commonly being above 10° C for more than 3 hr.

Variation between seasons

Mean plant-level temperatures were considerably higher between mid-January and March in 1965 than during the corresponding period of the following year (Fig. 18b). This point is emphasized in Table XIV, which shows that mean daily temperatures in the surface layers of different colonies ranged from 3.8° to 5.0° C during late summer in the first year compared with only 1.4° to 2.7° C during the second. Moreover, the mean daily temperature indicated by the deeper probe (probe D) at the site where the vertical gradient was investigated was several degrees higher in 1965 than the corresponding record for the shallower probe (probe E) in late summer 1966. This indicates that the difference between years was real and not merely

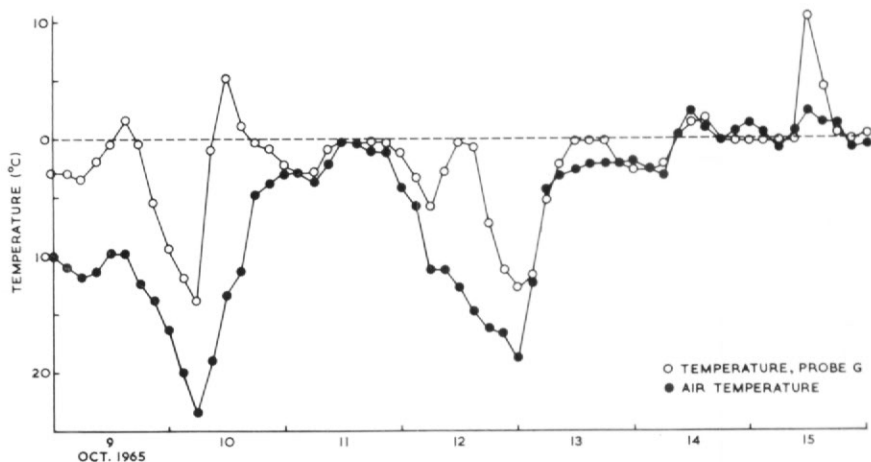


Fig. 19. Temperatures at the surface of a *Polytrichum alpestre* turf on Signy Island (probe G) during a 7 day period in October, in relation to air temperature.

the result of plant growth having left the probes deeper in the turf in 1966 where cooler average conditions can be expected.

The main difference between the seasons was probably due to the greater incidence of sunshine during the late summer of 1965 than in 1966, and the exceptionally high air temperatures prevailing during the former period (Table XIV). A reduction in solar radiation in 1966 may have been largely responsible for the lower daily maxima recorded by the probes, and the effect was particularly marked during a cloudy period in February 1966 (Fig. 18a). However, the differences from 1 to 2 Centigrade degrees at each site between the mean daily minimum temperatures during the two late summer periods probably resulted from the generally high air temperatures in 1965.

PLANT-LEVEL TEMPERATURES ON OTHER ISLANDS

The results for Signy Island are compared in Fig. 18 and Table XIV with data from a *P. alpestre* bank on Galindez Island. The latter colony became snow covered shortly after recording began in late March 1965 and, although the snow was reduced to a thin covering by gales during April, deeper cover became established later in the winter and persisted until early December. During the winter the temperature recorded by the two probes in the surface layer of the bank showed a similar pattern of fluctuation in response to changing air temperature to those on Signy Island. However, the temperatures recorded were generally lower, Galindez Island probe J giving a mean daily temperature as low as -15.6°C during a 2 week period in August with individual readings down to -22.0°C .

Due to the persistent snow cover, mean temperatures remained near or below zero longer in the *P. alpestre* bank on Galindez Island than in the turves of this species on Signy Island. After the thaw, day-time conditions in the colony on Galindez Island were, throughout the summer of 1965–66, consistently warmer than in any of the study colonies of either *P. alpinum* or *P. alpestre* on Signy Island, although daily minimum temperatures on the two islands were similar (Fig. 18c; Table XIV). Thus, during the particularly warm spell in the first 2 weeks of February 1966, a mean daily maximum temperature in excess of 20°C was recorded by Galindez Island probe J with a daily mean temperature for the 14 day period of 7.1°C and a maximum individual reading of 30.5°C . Moreover, the results recorded for both probes on Galindez Island during the 12 week period from December 1965 to February 1966 suggest that plant-level temperatures were often above 10°C for at least 3 hr./day and above 5°C for at least 9 hr. daily, although such favourable day-time conditions were seldom sustained for more than a few weeks on Signy Island.

It is interesting to note that, although the highest mean daily and mean daily maximum

temperatures at plant level were recorded on Galindez Island, the daily mean air temperatures there were slightly lower than on Signy Island (Table XIV). The duration of sunshine was much greater at the former station, and the difference between the plant-level temperature regimes at the two localities probably resulted largely from the different amounts of solar radiation received. However, the low wind speeds and less frequent precipitation at the Argentine Islands could have been contributory factors.

When the results are compared with earlier data from a *P. alpestre* colony on South Georgia (Longton and Greene, 1967), it is clear that plant-level temperatures were considerably higher at the sub-Antarctic station than at either of the present localities in the maritime Antarctic both during the day and night throughout the summer months (Fig. 18). Moreover, the *P. alpestre* turf on South Georgia received deep winter snow cover which stabilized the plant-level temperatures at around or slightly above 0° C, the winter temperature regime resembling more closely that recorded in the Signy Island colonies of *P. alpinum* than in the Antarctic turves of *P. alpestre*.

DISCUSSION

The plant-level temperature regimes recorded in maritime Antarctic bryophyte colonies, characterized by their wide diurnal fluctuations in summer and varying degrees of stabilization by snow cover for 7–8 months in winter, resemble those reported from elsewhere in Antarctic regions (Greene and Longton, 1970). Not surprisingly, the levels of temperature attained were in general intermediate between those recorded in *P. alpestre* turves on South Georgia (Longton and Greene, 1967) and in colonies of other mosses at sites in continental Antarctica (Matsuda, 1964; Rudolph, 1967).

Substantial temperature differences were noted between the two stations on Signy and Galindez Islands as well as between sites within the station on Signy Island in two successive years. During summer, these disparities were often of the order of 1–3 Centigrade degrees for mean daily values but with considerably greater variations in the mean daily maxima, differences which may be expected to have significant effects on the rates of plant metabolic activity at the low temperatures commonly prevailing (Wilson, 1957). In the present work, similar results were generally recorded by each probe in the colonies of a given species at each station. However, one turf of *P. alpinum* received substantially warmer day-time conditions than two of its neighbours, and there are likely to be greater variations between temperatures experienced by different shoots of each species, associated with the micro-topography of individual colonies and with broader differences in aspect, exposure, etc., between colonies (Longton and Holdgate, 1967).

It seems likely that the intensity of solar radiation, air temperature, wind speed and water supply are among the most important factors interacting to control summer temperatures at plant level. In winter, variations in the insulating layer of snow and ice may be of utmost importance, as indicated by the colder less stable conditions prevailing under the thin snow cover on the exposed *P. alpestre* banks on Signy Island compared with the more sheltered colonies of *P. alpinum*. It would be interesting to determine experimentally whether these results reflect contrasting survival capacities for the two species, or whether winter conditions are of secondary importance to habitat differences during summer in determining species-distribution patterns in polar environments. Both species are clearly frost resistant but snow cover at the study sites was in general sufficient to prevent the particularly damaging conditions of rapid freezing and thawing. However, more severe freeze-thaw cycles may well occur during autumn and spring in other colonies of *P. alpestre* lacking snow cover at these periods which, in terms of survival, seem potentially the most dangerous during the year. The minimum nightly temperatures recorded during summer were normally within 1–2 Centigrade degrees of zero, and this may not be low enough to cause frequent freezing within the plant tissues as ice formation is usually preceded by some degree of supercooling (Levitt, 1956).

The continued existence of a species at a given site demands its ability to grow and reproduce during favourable conditions as well as its survival through periods of maximum environmental stress. Although some Antarctic mosses may be able to photosynthesize and respire at temperatures as low as –4° C (Ahmadjian, 1970), stem elongation and leaf production in

P. alpestre appear to take place largely during the snow-free summer period (Longton, 1970), and the same is clearly true of reproductive development in both *P. alpestre* and *P. alpinum*. The regular series of collections from the study sites gave little evidence of activity between the last collections in autumn and the first in spring, even at the *P. alpestre* site on South Georgia in 1961–62 when winter temperatures at plant level remained around or slightly above freezing. It is possible that transmission of radiation through thin snow cover in spring may locally give rise to a “greenhouse” effect resulting in temperatures under the snow rising above freezing during the day, thus allowing the resumption of growth prior to the final snow clearance, but on the present evidence it seems unlikely that such conditions are frequently sustained for long at any given point.

The first visible stage in the reproductive cycle of *P. alpinum* and *P. alpestre* on South Georgia was represented by the appearance of *juvenile* antheridia during February and March. Young perichaetia were seen in occasional colonies of *P. alpinum* at about the same period, but the time of their initiation in *P. alpestre* is uncertain for, although young archegonia were not recorded until spring, they may have overwintered at a stage too small to be detected by the present methods. Some antheridia of both species reached the *immature* stage before winter set in but gametangial development past the *juvenile* stage was largely delayed until spring, beginning at the study sites when the mean daily temperatures in the surface layer of the turves rose above approximately 2° C with daily maxima from 5° to 10° C and minima within a few degrees of zero. Maturation then continued so that gametangial dehiscence was completed during the year following initiation. On South Georgia, gametangia dehiscence mainly during December and early January, but in the Antarctic colonies many antheridia had not dehiscence by mid-March when they were normally becoming discoloured. It is considered unlikely that they could liberate viable antherozoids in this condition.

A close relationship between gametangial development and the environment is suggested from a comparison of the maturation cycles at the study sites (Figs. 9–12) with the dates of snow clearance (Table XV). Thus the snow cleared from the *P. alpestre* colony on South Georgia during mid-October, both in 1961 and 1964, and in both seasons the spring phase of antheridial and archegonial development began during the next few weeks, rapid maturation occurring during the period when mean mid-day temperatures at plant level at one point in the bank ranged from 10° to 20° C, with daily means between 5° and 10° C and daily minima commonly a few degrees above zero.

Development in the *P. alpinum* colonies at King Edward Point also began within a few weeks of snow clearance in 1964 and observations made on other colonies on 18–19 November 1964 again suggest that the date of emergence from snow cover may have an important effect on the timing of archegonial maturation in this species. Thus all the female gametangia recorded in two specimens collected at the edge of persisting snow banks were in the *juvenile* stage, while in five other colonies in more open situations, which had apparently been clear of snow for longer periods, many of the archegonia were further advanced; some were *dehiscence*, while fertilization had even occurred in one specimen, resulting in the presence of at least one sporophyte in the *swollen venter* stage. The antheridial data from the same specimens were less conclusive since one of the collections from the edge of the snow bank lacked antheridia, while *immature* stages were in the majority in the remainder. However, a few dehiscence antheridia were present in two of the collections from the more open sites.

On Signy Island, snow clearance began at the study sites during September and October in 1965 but little reproductive development was recorded in either *P. alpestre* or *P. alpinum* until December. Thus it seems clear that factors other than snow clearance may delay the spring phase of development.

It seems likely that plant-level temperatures were generally low during October and November, as the mean daily temperatures recorded at exposed sites during the latter month were below 1·5° C, whereas during January, February and March, when most development for the cycle occurred, mean daily temperatures in the *P. alpinum* and *P. alpestre* colonies commonly ranged from 3° to 5° C, with mean daily maxima from 7° to 10° C.

These results suggest that the timing of snow clearance may be important in influencing gametangial development only when the plant-level temperature regime in exposed colonies is favourable for development. This would explain why archegonial development in the *P. alpestre*

TABLE XV. DATES OF SNOW CLEARANCE AT LONG-TERM STUDY SITES ON SOUTH GEORGIA, SIGNY ISLAND AND GALINDEZ ISLAND

Species	1961	1964	1965
South Georgia, King Edward Point <i>Polytrichum alpestre</i>	Mid-October	Mid-October	No information
<i>Polytrichum alpinum</i>	No information	Mid-October	No information
Signy Island, Factory Cove <i>Polytrichum alpestre</i> (probe E)	No information	No information	Thermistor site cleared in late October. Early season specimens taken from a nearby part of the bank which was alternately exposed and re-covered from mid-September onwards
<i>Polytrichum alpinum</i> (probe A)	No information	No information	Turf with probe, and most other colonies were covered until early December. Early season specimens were taken from scattered colonies which were alternately exposed and re-covered from mid-September onwards
<i>Polytrichum alpinum</i> (probe B)	No information	No information	Turf with probe was covered until late November. Early season specimens were taken from a colony which was alternately exposed and re-covered from mid-October onwards, but most turves covered until mid-December
Galindez Island, Marina Point <i>Polytrichum alpestre</i> (probes J and K)	No information	No information	Early December

colony on Galindez Island began during 1965–66 at a similar period in late December to that in the colony on Signy Island (Fig. 11) despite a big difference in the date of snow clearance (Table XV). Indeed, dehiscence in the former colony appears to have been completed earlier in the season than at the *P. alpestre* site on Signy Island, and it may be significant that the plant-level temperatures recorded on Galindez Island during the summer were higher than those on Signy Island. It may also be noted that on Signy Island archegonial and antheridial development in *P. alpinum* were completed several weeks earlier in 1964–65 than in the following year. This provides a further correlation between temperature and the rate of gametangial development since conditions at plant level were warmer during the earlier season, at least from mid-January to March.

In the study colonies of both species, the onset of the spring phase of gametangial development and the rate of subsequent maturation thus varied between sites and in different years, accelerated development normally being associated with warmer conditions. In view of the more advanced gametangial development in specimens from other colonies of *P. alpestre* and *P. alpinum* on South Georgia compared with the Antarctic stations, it may be that this temperature effect is widespread. Certainly, gametangial development in spring may be retarded in Scandinavian compared with British colonies of the moss *Pleurozium schreberi* (Longton and Greene, 1969a), and for this species there is experimental evidence that the rate of gametangial development is influenced by temperature independently of photoperiod. Water availability may be another factor affecting gametangial development, as Benson-Evans and Brough (1966) concluded that drought as well as low temperatures can delay their maturation in certain British mosses.

The pattern of sporophyte development between South Georgia and Antarctic stations was strikingly similar in *P. alpestre* and *P. alpinum*, and when healthy capsules occurred in the Antarctic botanical zone they were normally only slightly behind in development. The cycle

seems well suited to polar environments since the slow rate of development during the *early calyptra in perichaetium* stage results in the sporophytes overwintering with their apices situated at most a few millimetres above the turf, and thus less susceptible to frost damage if the snow cover is thin, or mechanical injury from the weight of deeper snow and ice, than if setal elongation had taken place in the autumn. Moreover, almost a full summer is available for the processes of capsule development, meiosis and spore maturation due to the rapidity with which setae elongate following the spring thaw. It is possible that a period of continuously low temperatures followed by warmer conditions is necessary to stimulate extension of setae.

Nevertheless, the success of sporophyte production in the Polytrichaceae varied widely within the areas studied, the pronounced reduction in the numbers maturing in the maritime Antarctic compared with South Georgia being in line with the general decline in the level of fruiting noted among other bryophytes in the two areas (Greene, 1964b; Longton, 1966). Moreover, in some species, notably *P. alpinum*, the proportion of fruiting colonies apparently varied in climatically different areas even within South Georgia.

P. juniperinum, *P. piliferum* and *Psilopilum antarcticum* were seldom abundant in the maritime Antarctic and it is not clear whether sporophytes would develop if the male and female plants occurred together as most of the specimens examined were unisexual. The results for *Polytrichum alpestre* and *P. alpinum* suggest, however, that several factors combine to cause rarity of sporophytes. Female inflorescences of both species were relatively common but perigonia were less frequent, particularly in *P. alpestre*, and this in itself would suffice to prevent sporophyte production at many sites.

A comparable predominance of colonies with female sex organs has been noted in a number of dioecious bryophytes in Europe (Bedford, 1938; Benson-Evans and Hughes, 1955; Longton and Greene, 1969b) but in these cases it was not generally determined whether male plants were rare or of common occurrence but remaining infertile. It is thus of interest that male plants of *P. alpestre* appear to be widespread, at least on Signy Island, but they apparently fail to produce antheridia during some seasons. Where antheridia develop they may, in places, occur too far from archegonia to permit fertilization, and many unisexual male turves of both species have been seen. However, in view of the frequency of plants bearing perichaetia and the relatively long fertilization range noted on South Georgia, it seems likely that additional factors are involved in causing the rarity of sporophytes at sites where antheridia develop. Thus mature antheridia and archegonia, together with motile antherozoids, were noted in a bisexual turf of *P. alpinum* on Signy Island and, although other bisexual turves were common at the site, no sporophytes were seen during the same or the succeeding summer. The existence of aborted antheridia may have a contributory effect but it seems clear that failure in fertilization, or during the early stages of sporophyte development, occurs at times.

Even when sporophyte development begins, conditions in the maritime Antarctic often seem to be too severe for successful maturation, at least in *P. alpinum*. This is indicated by the high rate of abortion prior to capsule swelling, the discoloration, abnormal shape and incomplete differentiation of many of the most advanced capsules, as well as the small size of most of the fully developed sporophytes collected both in the maritime Antarctic and at high altitudes on South Georgia. It seems not unlikely that both the retarded date of fertilization and the climatic conditions prevailing during subsequent maturation may be responsible for the poor performance of the sporophytes. The same may also apply to other mosses, as white thin-walled capsules similar to those in the Polytricha have been seen in maritime Antarctic colonies of several other species, while Greene (1967) has reported aborted capsules of *Bryum antarcticum* from Victoria Land in continental Antarctica. The general low level of fruiting in Antarctic mosses is matched by the position in some parts of the Arctic (Schuster, 1959; Holmen, 1960), while on northern Ellesmere Island, Canada, the populations of *P. alpinum* studied in 1967 resembled those on high ground on South Georgia and in the maritime Antarctic in producing only scattered diminutive capsules (Longton, 1969).

The rarity of mature capsules in Antarctic colonies of *P. alpestre* and *P. alpinum* was thus shown to result from failures at both the gametangial and sporophyte phases of the cycle, and the data suggest that the success as well as the timing of the reproductive processes may be related to temperature. For example, male inflorescences were, in many areas, most common in well-insolated, north-facing or level situations where a warm micro-climate may be expected

and it was noted that the mean daily temperatures recorded during summer on Signy Island by probe A, situated at a site where perigonia of *P. alpinum* were widespread, were commonly up to 1 Centigrade degree higher than those given by probes B and C where the turves contained perichaetia only.

Variation in the reproductive performance between seasons could also be correlated with temperature at plant level. Thus, by analogy with the South Georgian cycle, the antheridia of *P. alpestre* which were widespread on Signy Island during the 1965-66 summer were probably initiated during the autumn of 1964-65 and higher mean temperatures were recorded at the study sites during this period, both during the day and at night, than during the corresponding period of the next summer when it seems that few if any young perigonia were initiated. Similarly, the capsules of *P. alpinum* which were also recorded on Signy Island in 1965-66 clearly resulted from fertilization during the summer of 1964-65 when the gametangial cycle was advanced compared with the following year. Thus it is interesting to note that 1964-65 was also the only summer during 5 years of observations when mature seed of the grass *Deschampsia antarctica* was formed on Signy Island, the reproductive cycle in this species being completed during one season (Holtom and Greene, 1967). The duration of sunshine on Signy Island in 1964-65 was rather less than the average for other years, although greater than in 1965-66, but mean air temperatures were considerably higher than usual. Thus it is not clear whether the day-time temperatures recorded at plant level in 1964-65 were unusually high, but the conditions at night were probably exceptionally warm due to the high ambient temperatures.

Evidence is also accumulating that certain areas of the maritime Antarctic may be more favourable than others for the reproduction of bryophytes and the two native angiosperms. Thus Holtom and Greene (1967) reported particular extensive stands of *Deschampsia antarctica* and *Colobanthus quitensis* on Lynch Island where antheridial development in *Polytrichum alpestre* and the most successful fruiting colonies of *P. alpinum* so far known in the Antarctic botanical zone have been reported. Unfortunately, the favourable characteristics of the environment of Lynch Island remain obscure in the absence of micro-climate data.

In general, however, the relatively sunny conditions prevailing near the west coast of the Antarctic Peninsula appear to be more conducive to successful flowering and seed production in the flowering plants than those on the more cloudy South Orkney and South Shetland Islands (Holtom and Greene, 1967) and several mosses have also been seen fruiting in the former area but not on Signy Island (Longton, 1966). The differences in duration of sunshine suggest that warmer day-time conditions may be expected at plant level during summer at the Antarctic Peninsula stations, and the higher temperatures recorded in *P. alpestre* turf at Galindez Island compared with Signy Island in 1965-66 support this view. It has also been shown that the annual growth increment in shoots of *P. alpestre* is normally greater in colonies near the Antarctic Peninsula than on the South Orkney Islands (Longton, 1970) and the single fruiting colony so far known from the Antarctic botanical zone was discovered in the former area. In contrast, sporophytes of *P. alpinum* within the maritime Antarctic have so far been noted only in the more cloudy northerly island groups, but it should be remembered that the most intensive observations to date have been made in these northern areas.

Considered overall, the present study has shown that *P. alpestre* and *P. alpinum* follow a similar basic reproductive cycle over a wide and diverse sector of their Southern Hemisphere range. However, the timing of development, particularly for gametangia, varies in climatically different regions while sporophyte development in these and many other mosses normally fails in the most climatically severe areas. Thus the Polytricha are not fully adapted to complete their life cycle in the whole range of environmental conditions experienced in Antarctic regions, vegetative propagation being an essential if not the only means of survival in parts of their range. However, conditions in the maritime Antarctic may be only marginally too severe to prevent annual completion of the reproduction cycle since variation in local micro-climate between sites at a given station, and between years at a given site, is such that in some seasons both gametangia and sporophytes are produced and in *P. alpinum* the cycle may be successfully completed. The variation in performance was, at times, parallel to that reported for the native Antarctic flowering plants. The results presented here suggest that enhanced performance may be associated with an increase in summer temperatures at plant level, but the absence of any marked increase in the reproductive success of the Polytricha on warm moist ground near

fumaroles on the South Sandwich Islands underlines the necessity for carefully controlled experiments before firm conclusions can be based on the field data.

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APPENDIX A

DETAILS OF FRUITING SPECIMENS OF *Polytrichum alpestre* AND *P. alpinum*
AND THEIR LOCALITIES IN THE MARITIME ANTARCTIC

South Sandwich Islands

Candlemas Island (Longton 2302)

Polytrichum alpinum was frequent as extensive short turves on a more or less level area of volcanic ash at an altitude of c. 70 m., south of the island's main volcanic crater. There were several fumaroles in the area and *P. alpinum* occurred on both heated and unheated ground.

A single fruiting colony was seen in March 1964 at a distance of c. 20 m. from a fumarole vent but on ground not obviously heated volcanically. Only three sporophytes were recorded, two being in the *early calyptra intact* stage representing the 1963-64 cycle while the third was a young sporophyte in the *swollen venter* stage of the next annual cycle. The two older sporophytes were both very small, extending less than 10 mm. above the perichaetial bracts. Their development was drastically retarded compared with 1963-64 cycle sporophytes on South Georgia, most of which were in the *operculum intact* stage and about to dehisce, and it is considered unlikely that they would have reached maturity.

South Orkney Islands

Lynch Island (R. Smith 514)

Polytrichum alpinum was locally abundant, with other mosses and fruticose lichens, among *Deschampsia antarctica* and *Colobanthus quitensis* on a dry stony slope on the northern side of the island. Sporophytes were first observed by R. I. L. Smith during January 1966 when there were abundant capsules of the 1965-66 cycle in several colonies but no older capsules persisting from 1964-65 or earlier years. In a specimen collected at this time the majority of the capsules were in the *operculum intact* stage. They were borne on setae extending from 6 to 15 mm. above the bracts, the capsules being fully developed and c. 1.5-2.0 mm. wide. Some capsules contained thin-walled, almost colourless spores of normal size, ranging from 16 to 23 μ m. in diameter. A germination test showed that some spores from other capsules were viable (personal communication from R. I. L. Smith), but it was not recorded whether the latter contained chlorophyll. The specimen also contained young *swollen venter* and *early calyptra in perichaetium* stage sporophytes of the 1966-67 cycle, and during the following summer mature capsules of this cycle were recorded in the field (personal communication from R. I. L. Smith). Sporophyte production appears to have failed during the next cycle, as no capsules were recorded at the site during the summer of 1967-68 (personal communication from J. A. Edwards).

Signy Island (R. Smith 464)

Sporophytes of *Polytrichum alpinum* have been recorded at two localities. The first was at an altitude of c. 60 m. on the north side of Observation Bluff where *P. alpinum* was abundant with species of *Andreaea* and

lichens on a moist north-facing slab of rock. R. I. L. Smith (personal communication) reported that 24–36 sporophytes of the 1965–66 cycle had developed in one colony in this area but that no older sporophytes from previous years were observed. It is not clear whether any sporophytes developed during 1966–67, but according to Smith they were certainly less frequent than during the previous year. Only a single withered seta was recorded at the site during 1967–68 (personal communication from J. A. Edwards).

R. I. L. Smith also noted that few sporophytes at the site developed to maturity, a statement supported by the nature of the sporophytes in a specimen collected in February 1966. No capsule had successfully reached the *operculum intact* stage and of 11 sporophytes in the collection at least six had aborted or developed abnormally. For example, one sporophyte had aborted in the *swollen venter* stage while three of the five in the *early calyptra intact* stage were withered at the apices. Four of the remaining sporophytes were in the *late calyptra intact* stage but in each case the capsules were very small and one was white in colour instead of the normal green. The final capsule had swollen to c. 1 mm. in diameter but there was no evidence of differentiation into capsule and operculum; a columella was present but there were no spores. Seta length in the specimen varied from 5–8 mm.

The second fruiting site was at an altitude of 100 m. on the north side of the bluff behind Factory Cove where *P. alpinum* was abundant among species of *Andreaea* and lichens on a moist, gravelly, level sheltered area below a small rock outcrop. Two sporophytes were reported from this area during December 1966 (personal communication from R. I. L. Smith). Both were said to be immature, the capsules not being fully swollen, while the setae were similar in length to those from Observation Bluff. It is not clear whether these capsules represented the 1966–67 cycle or whether they had persisted from 1965–66, having failed to mature.

South Shetland Islands

Livingston Island: Byers Peninsula, December 1965 (Lindsay 133, 159, 436)

The first specimen was taken from a moss bank by scree at the edge of cliffs at an altitude of 60 m., near a flat area south of Clark Nunatak. It contained four normal *early calyptra intact* stage sporophytes of the 1965–66 cycle and c. 12 sporophytes persisting from 1964–65. One of the latter had very short setae and had aborted in the *early calyptra intact* stage while the remainder had setae c. 15 mm. long but no capsules. Apophyses were present at the apex of two of the longer setae but these and the apex of each of the other setae were shrivelled and white in colour. It seems unlikely that normal capsules had developed, as the tips of the setae were quite different in appearance from those where healthy capsules had become detached.

The second fruiting specimen was collected on rocks on a flat area at South Beaches, south-east of Clark Nunatak, also at an altitude of 60 m. Approximately 15 apparently healthy sporophytes of the 1965–66 cycle were recorded, one being in the *early calyptra intact* stage while the remainder were still in the *late calyptra intact* stage. No sporophytes persisting from 1964–65 were observed.

The third fruiting specimen came from the top of a south-west-facing rock outcrop at an altitude of c. 8 m. on the south side of cliffs at the extreme eastern end of South Beaches. It contained three *early calyptra intact* stage sporophytes of the 1965–66 cycle and 18 more advanced 1964–65 cycle sporophytes with setae 10–15 mm. long. The latter included two apparently normal dehiscid capsules with clearly defined rings of dark-coloured cells around the mouth. Short peristome teeth were present but the epiphragms had apparently become detached.

By contrast, five other capsules, ranging from 1 to 2 mm. wide, were undeveloped and were variously misshapen. Two of these are compared with a normal capsule from South Georgia in Fig. 8. The most striking feature of the undeveloped capsules was the absence of the normal ring of reddish cells marking the future line of rupture of the operculum while the operculum beaks were unusually short. Four of the capsules were a normal brown in colour but the fifth was white and thin-walled in its upper parts.

Two other sporophytes had broken setae so that it is not clear whether their capsules had developed, while the remaining nine were dehiscid but were unusual in being either completely white in colour, or brown below and white towards the apex. Dehiscence had occurred by means of a regular circular mouth in most cases but some of the dehiscid capsules lacked peristome teeth and reddish cells in the annular region. A columella was present in most capsules but none contained spores.

Deception Island: near Whalers Bay (Longton 2300, 2303)

P. alpinum formed frequent extensive, often circular, short turves on more or less level volcanic ash in a slight hollow in the plain between Kroner Lake and Ronald Hill, at an altitude of c. 15 m. Two fruiting colonies were observed.

The first was recorded in December 1963 when at least 30 sporophytes of the 1963–64 cycle were present. The majority were in the *early calyptra intact* stage, the setae generally being less than 10 mm. long. The colony was re-examined twice during the summer of 1964–65 but no sporophytes were then recorded except a few withered setae persisting from 1963–64.

The second fruit colony was discovered in December 1964, when it also contained sporophytes of the 1963–64 cycle only. Of these, ten had aborted in the *early calyptra intact* stage but seven small dehiscid capsules were also present. Six of the latter were c. 1 mm. in diameter, while the seventh was approximately twice this width. Seta length rarely exceeded 10 mm. Later in the summer, in March 1965, two sporophytes in the *early calyptra intact* stage of the 1965–66 cycle were collected.

In February 1967 one or two old withered setae were seen in the same area (personal communication from R. I. L. Smith). These setae, which lacked capsules, probably represented the 1965–66 cycle but no developing sporophytes of the 1966–67 cycle were observed.

Thus, sporophytes of the 1963–64 cycle occurred in two colonies and small capsules matured in at least one turf but it was not established whether viable spores were formed. It is also clear that both colonies failed to

produce sporophytes during 1964-65 but young sporophytes of the following cycle were recorded in the second turf. Setal elongation occurred in this part of Deception Island during 1965-66 but it is not clear whether capsules developed.

Palmer Archipelago

Anvers Island: near Norsel Point (Longton 2304)

Polytrichum alpestre was frequent on west-facing rocky slopes at an altitude of c. 15 m., forming turves up to 1 m. wide and 30 cm. deep. In February 1965, one of the larger colonies contained abundant sporophytes of the 1964-65 and 1965-66 cycles. Many of the former had aborted in the *early calyptra intact* stage while the remainder had developed abnormally. The setae were c. 7 mm. long and capsules were c. 1 mm. wide. The capsule walls were unusually thin, being white in colour and partially transparent; most were open at the apex but lacked the normal peristome teeth and epiphragm. Although each contained traces of a columella, there was no evidence that spores had been produced. Most of the young 1965-66 cycle sporophytes were in the *early calyptra in perichaetium* stage and appeared normal.

APPENDIX B

RECORDS OF PERIGONIA FOR *Polytrichum alpestre* FROM THE ANTARCTIC BOTANICAL ZONE WITH NOTES ON THE PRESENCE OF PERICHAETIA

South Sandwich Islands

Leskov Island: March 1963 (Longton 2301)

Perigonia were recorded in a single colony on heated ground near a fumarole on the summit ridge of the island, inflorescences of the 1962-63, 1963-64 and several earlier cycles being present. Most 1962-63 cycle antheridia had aborted and none was confirmed as *dehiscend*. The 1963-64 cycle antheridia were in the *juvenile* stage appropriate to the date of collection.

No perichaetia were recorded.

South Orkney Islands

Coronation Island: Shingle Cove, March 1969 (BAS MISC. 4)

Perigonia were recorded in a *Polytrichum alpestre*-*Chorisodontium aciphyllum* turf on north-east-facing ground (personal communication from E. P. Wright). The specimen had inflorescences of the 1968-69 cycle containing *aborted* antheridia. No perigonia representing the previous two or three annual cycles were seen near the surface of the turf but older perigonia were recorded at a greater depth.

No perichaetia were recorded in the specimen but they were observed elsewhere at the site.

Lynch Island: February 1965 (Longton 2307)

This specimen, collected by N. Bacon from an unspecified part of the island, contained a single perigonium of the 1964-65 cycle. Most antheridia had *aborted* but a few were *dehiscend*.

A single perichaetium was recorded in the specimen.

Lynch Island: January 1966 (R. Smith 513)

Plants with perigonia were abundant along the northern side of the island (personal communication from R. I. L. Smith). The specimen contained over 100 inflorescences of the 1965-66 cycle with *immature* and *aborted* antheridia. Only one perigonium of the 1964-65 cycle was observed.

Plants with perichaetia containing many healthy *dehiscend* archegonia were frequent in turf adjacent to that from which the male specimen was collected.

No perigonia were observed on Lynch Island during the summer of 1966-67 (personal communication from R. I. L. Smith).

Signy Island: Factory Cove, December 1960 (Taylor 398)

Perigonia of the 1959-60 cycle were abundant. The antheridia were mostly in the *immature* stage but a few *juvenile*, *dehiscend* and *aborted* gametangia were also present. No perigonia from previous cycles were seen.

No perichaetia were recorded in the specimen.

Signy Island: December 1963 and November 1964-April 1965

No perigonia were recorded by the author during brief observations at Factory Cove in 1963, or during more intensive studies during the following season at Factory Cove and in other parts of the island.

Perichaetia were widespread.

Signy Island: Factory Cove, March 1966 (R. Smith 465)

Perigonia were common in small turves of *P. alpestre* and *Chorisodontium aciphyllum* on north-facing slopes at Factory Cove as well as in other parts of the island (personal communication from R. I. L. Smith). The specimen had abundant perigonia of the 1965-66 cycle with most of the antheridia *immature*, but a few *dehiscend* and *aborted* gametangia were also recorded. Only four perigonia from previous cycles were noted; one was possibly from 1964-65 while the others were several years old.

No perichaetia were recorded in the specimens containing perigonia.

No perigonia were observed on Signy Island during the summer of 1966-67 (personal communication from R. I. L. Smith).

Signy Island: Factory Cove, March 1969 (BAS MISC. 8)

Perigonia were observed in a large bank of *P. alpestre* and *Chorisodontium aciphyllum* (personal communication from E. P. Wright). The specimen had several perigonia of the 1968-69 cycle containing *immature* and *aborted* antheridia. Several perigonia persisting from a previous year, probably 1967-68, were also present.

No perichaetia were recorded in the specimen.

Palmer Archipelago

Anvers Island: near Norsel Point, February 1965 (Longton 2304, 2305)

Perigonia were present in several turves, each c. 1 m. wide, on a west-facing slope. The two specimens had numerous perigonia of the 1965-66 cycle containing *juvenile* antheridia. Perigonia persisting from previous cycles, including 1964-65, were also present and many antheridia in the latter had dehisced.

Of the two specimens examined, one was bisexual and fruiting, but the other contained no perichaetia.

Graham Coast

Petermann Island: March 1965 (Longton 2306)

Perigonia of the 1965-66 cycle, containing *juvenile* antheridia, were present in the specimen from north-facing rocks on the north-west coast of the island. No perigonia from previous cycles were recorded.

Perichaetia were widespread in the specimen.

Fallières Coast

Jenny Island: January 1962 (Killingbeck 226)

Numerous perigonia of the 1961-62 cycle were present in the specimen from the north side of the island. Most antheridia were *immature* or *aborted* but a few *juvenile* and *dehisced* gametangia were present. Perigonia of the 1960-61 cycle were also recorded but none persisting from previous years was observed.

Perichaetia were present in the specimen.