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ABSTRACT

The flora and vegetation of the South Sandwich Islands are described, and their ecological and phytogeographical significance is discussed. A total of 58 plant species is reported, comprising eight algae, 16 lichens, 11 hepatics, 22 mosses and one angiosperm, but these figures are considered to underestimate substantially the number of cryptogams present. The principal affinities of the flora are with southern South America, South Georgia and the maritime Antarctic. Small southern circum-polar and bi-polar elements, and probably an assemblage of Antarctic endemic lichens, also occur. It is suggested that most species present may have reached the islands via trans-oceanic migration as airborne propagules in the prevailing westerly winds.

The vegetation is essentially Antarctic in character and shows a clear division between that developed on unheated ground and that near fumaroles. On Bristol, Cook, Montagu, Thule and Visokoi Islands and Freezland Rock the cool ground supports principally sparse, widely scattered communities in the crustaceous lichen and alga sub-formations of the Antarctic non-vascular cryptogam tundra formation. A more varied range of plant associations occupies unheated ground on Bellingshausen, Candlemas, Leskov and Vindication Islands: communities in the crustaceous lichen, fruticose and foliose lichen, short moss-turf and cushion, tall moss-turf, bryophyte carpet and mat, alga, and snow-alga sub-formations were recorded, and small stands of the grass *Deschampsia antarctica* occur on Candlemas Island. The distribution of the different growth-form types is correlated with exposure and ground-water supply. Even on the better vegetated islands, the cool-ground communities are interspersed with large areas of virtually barren substratum. The vegetation is everywhere less varied and extensive than at many other maritime Antarctic situations, and in some respects resembles more closely that in continental Antarctica. Aridity, resulting from the porous volcanic substrata, is suggested as a major limiting factor. Analysis of vertical peat profiles from Candlemas Island indicated that all the major bryophyte vegetation types on cool ground may have developed independently of each other, although a succession of species was demonstrated in the most complex community.

Fumaroles were recorded on Bellingshausen, Candlemas, Leskov and Visokoi Islands, and they are surrounded by limited areas of unusually warm moist substrata which support strikingly more luxuriant plant cover than the prevailing cool ground. There is typically a concentric zonation of bryophyte communities associated with a decreasing temperature gradient extending outwards from the vents. Open vegetation of algae with small bryophyte mats and turves frequently occupies the innermost zone. This is

surrounded by a variety of closed communities in the tall moss-turf and the bryophyte carpet and mat sub-formations, in which *Campylopus* spp. and the hepatics *Cryptochila grandiflora* and *Marchantia berteroana* are among the dominant species. These vegetation types are restricted to the fumaroles, but in the outer zones they frequently give way to communities which also occur on cool ground. Temperatures between 5° and 61° C were recorded at a depth of 2·5 cm. in the soil and vegetation in the inner zones of fumarole vegetation and evidence of fluctuations in the intensity of fumarolic activity was obtained. Most of the cool-ground bryophyte species are widespread in other parts of the maritime Antarctic, but many of the taxa restricted to the fumaroles, particularly the liverworts, are more typical of sub-Antarctic and temperate regions. Their occurrence thus suggests that environmental rather than geographical factors may be mainly responsible for the general sparseness of the cryptogamic flora and vegetation in the South Sandwich Islands.

CONTENTS

I. INTRODUCTION

1. *Botanical investigations in the South Sandwich Islands*

The South Sandwich Islands, the only volcanic island arc in Antarctic regions, occupy an isolated position in the South Atlantic Ocean between lat. 58°18′ and 59°28′S. and long. 26°14′ and 28°11′W. Due to their intermediate location between the sub-Antarctic island of South Georgia and the maritime Antarctic region of the South Orkney Islands (Fig. 1), their inaccessibility, and reports of current volcanic activity, there has been speculation as to the nature of their terrestrial flora and vegetation. The first detailed survey of the archipelago, from R.R.S. *Discovery* in 1930 (Kemp and Nelson, 1931), provided little information on these matters. Only one macroscopic land plant, the green alga *Prasiola crispa*, was collected, on Thule Island, and this widespread Antarctic species was assumed to have been responsible for the green patches observed from the sea on several of the other islands. Lichens were reported on Leskov and Vindication Islands, but Kemp and Nelson emphasized the floristic barrenness of the archipelago and the apparent absence of vascular plants, which ran counter to the theories of earlier authors, notably Rudmose Brown (1912).

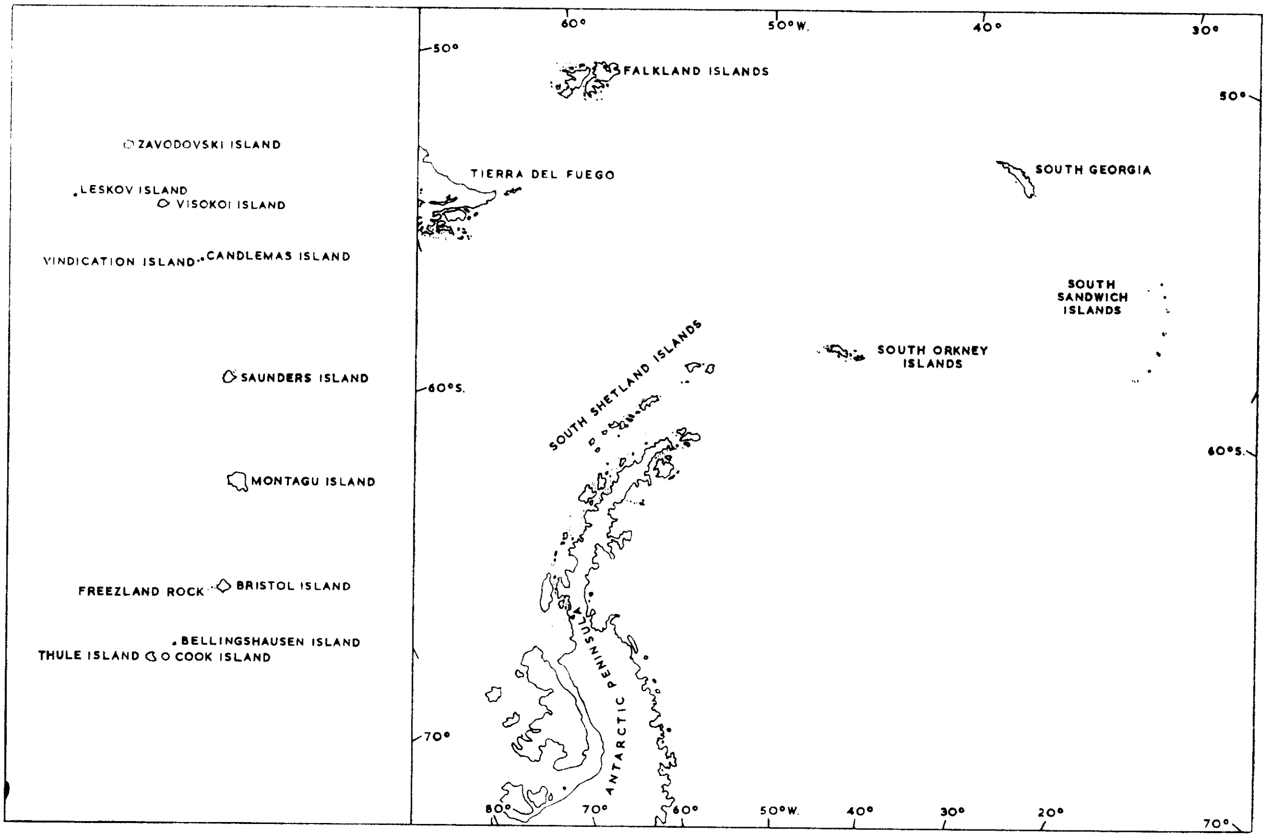

FIGURE 1

The South Sandwich Islands (left) and their position in relation to other land areas in the South Atlantic Ocean (right).

The first extensive landings by scientists on the South Sandwich Islands were made in 1961, when geologists from R.R.S. *Shackleton* visited several locations and collected lichens, mosses, hepatics and the grass *Deschampsia antarctica*. Subsequent observations on Bellingshausen, Candlemas, Saunders, Thule and Vindication Islands, by one of the present authors in 1962, extended the list of land plants and provided the first outline of the vegetation of the group (Holdgate, 1963, 1964). Particularly important was the discovery of extensive, concentrically zoned stands of bryophyte vegetation around fumaroles on Bellingshausen and Candlemas Islands, which supported species otherwise unknown within the Antarctic botanical zone.

The present report arises from field work undertaken as part of a comprehensive survey of the island group undertaken during the period 5–26 March 1964, supplemented by the earlier collections and data. A brief account of the 1964 survey has been given by Baker and others (1964) and an extended description of the topography, volcanic structure and general biological features of the islands by Holdgate and Baker (1979). These authors have also chronicled previous scientific work in the archipelago and published a diary of investigations during the 1964 survey. This shows that observations were made on all the larger islands except Zavodovski Island, but that detailed work was centred on Bellingshausen and Candlemas Islands. The vegetation of Candlemas Island has already been described in broad outline (Longton, 1967), while a preliminary account has been given of the fumarole vegetation throughout the group (Longton and Holdgate, 1967). The aim of the present paper is to describe the flora and vegetation of the islands in as much detail as the brevity of the field studies permits, and to discuss their ecological and phytogeographical significance.

2. *Habitats in the South Sandwich Islands*

Ten of the 11 South Sandwich Islands form a curving chain extending about 386 km. from Zavodovski Island in the north to Thule Island in the south, while the eleventh, Leskov Island, lies to the west of the arc near its northern end (Fig. 1). Other volcanic peaks which fail to break the surface lie north-west from Zavodovski Island and possibly south-west from Cook Island.

The islands are wholly of a volcanic origin and most are still active. In contrast with other island-arc provinces, basalts and basaltic andesites greatly predominate over other rock types. There is a paucity of two-pyroxene andesites and dacites, and an apparent absence of pyroclast-flow deposits. The simple arcuate distribution of the islands, their small size and the obvious youthfulness of many of them, as well as the predominantly basaltic nature of the lavas and the presence of deep water between islands, suggest that the South Sandwich Islands arc is at a relatively early stage of development (Holdgate and Baker, 1979). Magnetic lineations suggest that the islands rise from crust that is at the most 8–10 m. yr. old (Barker and Griffiths, 1972). The latest K-Ar age determinations on rocks from the islands by D. C. Rex of the University of Leeds indicate that most of the exposed area is under 1 m. yr. old. Lava from the foot of the cliffs on Montagu Island was dated at 1·0 m. yr. and on Leskov Island at 0·5 m. yr. The andesite from Freezland Rock (always regarded as the oldest exposed rock in the archipelago) gave an age of 3·1±0·1 m. yr. (personal communication from P. E. Baker).

The dimensions of the 11 major islands are indicated in Table I, which shows that they range from *c.* 1 to 28 km. in length and from *c.* 190 to 1,370 m. in maximum altitude. The more extensive islands, Bristol, Cook, Montagu, Saunders, Thule and Visokoi Islands, are largely covered by ice; glaciers reach the sea on all sides, and rock is exposed mainly on cliffs and in a few projecting lava headlands. Saunders Island has the largest ice-free lowland area of these heavily glacierized islands, with a broad plain of basalt flows at the northern end, and a complex of parasitic cones running out to Nattriss Point in the south-east. Saunders Island, too, is the most active of the larger islands, with continual emission of vapour from its central summit crater, but there has also been considerable recent activity on Bristol Island and there are fumaroles or reports of volcanic activity on Visokoi and Thule Islands.

The smaller islands are virtually ice-free, although permanent snow and ice occur locally in the summit areas of Bellingshausen and Vindication Islands. Mount Curry, one of the most active volcanoes in the arc, forms the summit of Zavodovski Island, while fumarolic activity occurs on Bellingshausen and Leskov Islands. No recent volcanic activity has been recorded, however, on Vindication Island.

Candlemas Island is intermediate in size and character. Its larger, southern section is heavily ice-covered (Fig. 2) and no recent volcanic activity has been reported in this area. In contrast, the northern section is low-lying and virtually ice-free, and is clearly the result of recent eruptions; there are many fumaroles and geysers were active in 1962. It was this diversity of terrain, as well as the central position of the island in the arc (Fig. 1), that led to the choice of Candlemas Island as the area for most detailed study in 1964. An account of its geology has been provided by Tomblin (1979).

The islands are completely surrounded by pack ice between June and November in most years. Typically, the ice clears around the northern islands during December and from the southern islands several weeks

TABLE I

DIMENSIONS AND PRESENCE OF CURRENT VOLCANIC ACTIVITY FOR ISLANDS OF THE SOUTH SANDWICH ISLANDS GROUP

Islands (arranged from north to south)	*Length* (km.)	*Breadth* (km.)	*Maximum altitude* (m.)	*Current volcanic activity*	
				Main centre	*Fumaroles*
Zavodovski	5·5	5·0	551	+	+
Leskov	1·0	0·5	190	–	+
Visokoi	8·5	6·0	1,005	?	+
Candlemas	5·5	3·0	550	+	+
Vindication	3·0	2·5	442	–	–
Saunders	8·0	5·0	990	+	?
Montagu	28·0 (19·0)	18·0 (20·0)	1,370	–	–
Bristol	14·0	12·0	1,100	+	?
Freezland Rock	1·0	0·5			
Bellingshausen	1·5	1·0	253	–	+
Cook	6·0	3·5	1,075	–	–
Thule	8·0 (5·4)	5·0	725	+	–

later. The ice-free period is variable, however, and in some years the southern islands may remain unapproachable throughout the summer. The arc lies well to the south of the Antarctic Convergence, with surface temperatures in the ocean averaging between –2° and +1° C. The limited available climatic data have been summarized by Holdgate and Baker (1979). Mean monthly air temperatures are thought to range between *c.* +3° C in summer and –6° C in winter at the northern end of the arc, and between *c.* –1° and –11° C on the southern islands; the weather is generally cloudy with frequent strong westerly to south-westerly winds. Precipitation, falling mostly as snow, is likely to be higher than in much of the maritime Antarctic. The climate is thus of cold oceanic character, with relatively small seasonal variation in temperature, little sunshine, strong winds and frequent snowfall.

The islands are generally unfavourable as habitats for terrestrial plants. Most of the snow-free ground consists either of lava cliffs or more gently inclined areas of broken lava, scoria and ash. These substrata are highly permeable to water and thus growth may be limited in summer by aridity as well as by low temperatures. Vegetation is further restricted by dunging and trampling in the extensive penguin colonies that occupy many lowland areas. However, the fumaroles on Bellingshausen, Candlemas, Leskov and Visokoi Islands provide an exceptional range of habitats. For here steam may be emitted in quantity, condensing to moisten the ground surface in a continuous rain of tiny droplets, which, combined with the warming of the substratum, create miniature "oases" of damp, frost-free or infrequently frozen habitat in the prevailing cold desert. These "oases" yielded results of particular interest in terms of the biology and geography of the terrestrial plants. The fumarole vegetation appears to be unique within the Antarctic botanical zone and, as it is dependent upon the possibly unstable effects of volcanic activity, the communities associated with specific fumaroles are considered in particular detail in the present account to provide base-line data against which any future changes may be monitored.

II. FLORA

1. *Collections*

Few significant plant collections appear to have been made in the South Sandwich Islands prior to the visit of R.R.S. *Shackleton* in 1961 (Holdgate, 1963). Information on the flora is thus based essentially on material obtained by K. Archibald, H. A. D. Cameron and P. Kennett in 1961, M. W. Holdgate in 1962 and M. W. Holdgate and R. E. Longton in 1964. These collections comprise over 600 specimens, representing all the major islands except Cook Island, but intensive sampling was concentrated on Bellingshausen and Candlemas Islands, and only the alga *Prasiola* cf. *crispa* has been collected on Zavodovski Island. The material covers all the plant groups observed, i.e. algae, basidiomycetes, bryophytes, lichens and flowering plants, but microscopic algae were taken only on Candlemas, Leskov and Visokoi Islands. The specimens have been deposited in the herbarium of the British Antarctic Survey (BAS), currently at Cambridge except for the bryophytes which are on permanent loan to the Institute of Terrestrial Ecology, Penicuik, Midlothian, Scotland.

Identification of the collections has been undertaken by J. H. Belcher and E. M. F. Swale (algae), B. G. Bell and S. W. Greene (mosses), R. F. Grolle (hepatics) and D. C. Lindsay (lichens), supported by specialists in certain groups. Except for the fungi, most specimens have now been determined to the generic level but, due to the well-known taxonomic problems surrounding the Antarctic flora (Greene, 1964), only *c.* 60 per cent of the identifications have been continued to the specific level. Identification of the hepatics has been virtually completed, resulting in a taxonomic and phytogeographical account of the flora (Grolle, 1972), and distribution records of certain algae and lichens have been published (Belcher, 1969; Lindsay, 1969*a*, 1971*a*). Additional plant records have appeared in the preliminary vegetation accounts of Holdgate (1963), Longton (1967), and Longton and Holdgate (1967).

2. *Genera and species recorded*

The taxa identified among collections from the South Sandwich Islands are indicated in Table II. The total number of species stands at 58, comprising eight algae, 16 lichens, 11 hepatics, 22 mosses and one flowering plant. However, it is clear from the number of taxa so far determined only to the generic level (Table II) that complete identification of the present collections may be expected to increase the species list substantially, especially for mosses and lichens. Moreover, further collecting, particularly by specialist lichenologists and phycologists, would undoubtedly result in additional records.

It may be noted that several previously published records from the islands now appear to be erroneous. These include the tentative reports of *Candelariella* sp. and *Ephebe* sp. (Holdgate, 1963) and of *Lecanora aspidophora* (Lindsay, 1971*a*), which were based on misidentifications (personal communications from D. C. Lindsay). The record of *Omphalodiscus antarcticus* (Llano, 1950) is also doubtful; Lindsay (1969*b*) suggested that the material concerned was probably collected on the South Shetland Islands, and no species of *Omphalodiscus* was observed on the South Sandwich Islands during the present study. In addition, the record of *Buellia russa* from Candlemas Island (Lindsay, 1971*a*) is based on material from Vindication Island. Finally, Longton and Holdgate (1967) reported *Campylopus introflexus* in fumarole vegetation on four islands in the group but, following a critical examination of the specimens by J.-P. Frahm, it now appears that *C. introflexus* has been collected only on Candlemas and Leskov Islands, the genus *Campylopus* being represented by related species on Bellingshausen and Visokoi Islands (Table II). In view of the possibility that further identifications may be revised as the taxonomy of Antarctic cryptogams is clarified, a list of the identifications upon which Table II is based is included in the Appendix, as a source of reference to the plant names used throughout this account.

3. *Distribution patterns*

The information in Table II on the known distribution of each taxon within the South Sandwich Islands is of necessity incomplete due to irregularities in the intensity of sampling and other factors, but a number of conclusions may be drawn. It is clear, for example, that several taxa have achieved wide distribution within the archipelago, having been recorded on most of the islands supporting substantial vegetation. These include *Usnea antarctica* among the lichens and the mosses *Dicranoweisia grimmiaceae* and *Drepanocladus* cf. *uncinatus*, all of which have been recorded on at least six of the islands. In contrast, many other species appear to be more restricted in distribution. Thus *Andreaea regularis* and *Racomitrium austrogeorgicum* are examples of relatively distinctive mosses of unheated ground whose known distribution within the archipelago is restricted to Leskov Island, while *Tortula conferta* is the only bryophyte so far collected on Freezland Rock but it is as yet unknown on any of the other islands.

The data in Table II also indicate that many species were restricted to the vicinity of fumaroles. This applies to most of the hepatics, to certain algae such as *Mesotaenium* sp. and to several mosses including

TABLE II
PLANT GENERA AND SPECIES RECORDED FROM THE SOUTH SANDWICH ISLANDS AND THEIR DISTRIBUTION WITHIN THE ARCHIPELAGO

Taxon	*Island*									
	Bellingshausen	Bristol	Candlemas	Freezland Rock	Leskov	Montagu	Saunders	Thule	Vindication	Visokoi
ALGAE										
Calothrix sp.					F					
Chlamydomonas nivalis (Bauer) Wille			C							
Eunotia tenella (Grun.) Hust.			F							
Lyngbya sp.			F							
Mesotaenium sp.			F		F					
Navicula muticopsis Van Heurck			B		F					B
Phormidium sp.					F					
Pinnularia borealis Ehr.			B		F					B
Prasiococcus calcarius (Boye Pet.) Vischer			B		F					C
Prasiola cf. *crispa* (Lightf.) Menegh.†		C	B		F	C				B
Scotiella nivalis (Shuttlew.) Fritsch			C							
Stichococcus bacillaris Naeg.										B
Ulothrix sp.					F					
LICHENES										
Acarospora macrocyclos Vain.		B								
Acarospora sp.		C					C	C	C	
Buellia anisomera Vain.		C							C	
Buellia coniops (Wahlenb. ex Ach.) Th. Fr.									C	
Buellia inordinata (Hue) Darb.		C								
Buellia russa (Hue) Darb. var. *russa*									C	
Buellia sp.		C						C		
Caloplaca sp.						C				
Cladonia sp.										F
Lecania brialmontii (Vain.) Zahlbr.									C	
Lecania racovitzae Vain.							C	C		
Lecania sp.							C	C		
Lecanora polytropa (Hoffm.) Rabenh.			B			C			C	

TABLE II—*continued*

Taxon	*Island*									
	Bellingshausen	Bristol	Candlemas	Freezland Rock	Leskov	Montagu	Saunders	Thule	Vindication	Visokoi
Lecanora sp.	C		C				C	C	C	C
Lecidea sp.			B		C		C		C	
Lepraria sp.			C							
Mastodia tesselata (Hook. f. et Harv.) Hook. f. et Harv.			C						C	
Microglaena antarctica M. Lamb									C	
Ochrolechia frigida (Sw.) Lynge			B							
Pertusaria sp.			C						C	
Psoroma hypnorum (Vahl) Grey									C	
Psoroma sp.									C	
Rinodina petermannii (Hue) Darb.			C							
Stereocaulon antarcticum Vain.			C							F
Usnea antarctica Du Reitz	B		B	C	C	C			C	B
Xanthoria candelaria (L.) Arn.			C							
Xanthoria sp.							C			
MUSCI										
Andreaea gainii Card. var. *gainii*						C			C	
Andreaea gainii Card. var. *parallela* (C. Muell.) S. W. Greene	C								C	
Andreaea regularis C. Muell.					C					
Bartramia patens Brid.					F					
Brachythecium sp.	B		C						C	
Bryum algens Card.	F				F					
Bryum argenteum Hedw.			F‡							
Bryum sp.									C	F
Campylopus canescens (C. Muell.) Schimp.										F
Campylopus flavoviridis Dus.			F		F					
Campylopus introflexus (Hedw.) Brid.			F		F					
Campylopus spiralis Dus.	F									
Campylopus sp.	F		F							

TABLE II—*continued*

Taxon	*Island*									
	Bellingshausen	Bristol	Candlemas	Freezland Rock	Leskov	Montagu	Saunders	Thule	Vindication	Visokoi
Ceratodon sp.	B		C		F		F*		C	B
Dicranoweisia antarctica (C. Muell.) Kindb.										F
Dicranoweisia grimmiaceae (C. Muell.) Broth	B				B	C	F*		C	F
Dicranoweisia sp.	F		B		B					
Distichium capillaceum (Hedw.) B.S.G.			F		F					
Drepanocladus cf. *uncinatus* (Hedw.) Warnst.	B		C		C	C			C	F
Grimmia sp.	F						C			
Pohlia nutans (Hedw.) Lindb.	B		B		B		F*			
Polytrichum alpestre Hoppe	F				F					
Polytrichum alpinum Hedw.	B		B		B				C	
Polytrichum juniperinum Hedw.			F‡							
Polytrichum piliferum Hedw.			F‡							
Pottia austrogeogica Card.									C	
Psilopilum antarcticum (C. Muell.) Par.	B		F							
Racomitrium austrogeorgicum Par.					C					
Racomitrium crispulum (Hook. f. et. Wils.) Hook. f. et Wils. var. *crispulum*	F									
Tortula conferta Bartr.				C						
Tortula sp.	C									
HEPATICAE										
Cephalozia badia (Gottsche) Steph.			F		F					
Cephaloziella varians (Gottsche) Steph.	F		B		F					
Cephaloziella sp.	F		B		F					F
Clasmatacolea koeppensis (Gottsche) Grolle	B						F*			
Cryptochila grandiflora (Lindenb. et Gottsche) Grolle	F		F		F					
Lepidozia cuspidata Steph.			F							
Lophocolea secundifolia (Hook. f. et T.) Gottsche, Lindenb. et Nees					F					
Lophozia propagulifera (Gottsche) Steph.	F		F		F					F

TABLE II—*continued*

Taxon	*Island*									
	Bellingshausen	Bristol	Candlemas	Freezland Rock	Leskov	Montagu	Saunders	Thule	Vindication	Visokoi
Marchantia berteroana Lehm. et Lindenb.	B		F		F					
Pachyglossa dissitifolia Herz. et Grolle					B					
Riccardia georgiensis (Steph.) Hässel			F							F
Triandrophyllum subtrifidum (Hook. f. et T.) Fulf. et Hatch.					F					
ANGIOSPERMAE										
Deschampsia antarctica Desv.			F*							

*Occurrence of volcanic heating uncertain (see p. 23–24).
†*Prasiola crispa* was positively identified in a collection from Leskov Island (Longton 493). There are additional field records of *Prasiola* cf. *crispa* on Bellingshausen, Cook, Freezland Rock, Saunders and Vindication Islands.
‡There are additional field records of these species on unheated ground on Candlemas Island.
F Recorded in fumarole vegetation only.
C Recorded in cool-ground vegetation only.
B Recorded in both fumarole and cool-ground vegetation.

Racomitrium crispulum and *Campylopus* spp. Basidiomycetes, also, were recorded only in fumarole vegetation, but none of the lichens so far identified was restricted to this type of habitat, with the possible exception of a species of *Cladonia*.

Despite the restricted areas of heated ground available for colonization, it is striking that *Lophozia propagulifera* and several of the other fumarole hepatics were recorded on three or four of the four islands where suitable habitats occurred (Table II), although others were more restricted in distribution. *Triandrophyllum subtrifidum*, for example, was abundant in fumarole vegetation on Leskov Island but it was not recorded elsewhere. Of the remaining species, some, e.g. *Andreaea* spp. and many lichens, were confined to unheated ground, but others occurred both on cool ground and in the vicinity of fumaroles, where however they tended to be most abundant in the outer cooler zones of vegetation. The relative floristic richness of Bellingshausen, Candlemas, Leskov and Vindication Islands compared with other members of the group is also emphasized in Table II. This is partly related to the occurrence of fumaroles, but even the cool ground on Candlemas and Leskov Islands appeared to support unusually high numbers of mosses and lichens, and fumaroles are unknown on Vindication Island.

Inadequacy of records from other Southern Hemisphere localities makes it impossible to present a thorough phytogeographical analysis of the South Sandwich Islands flora. With regard to bryophytes, however, it is clear that a close affinity exists between these islands and cool-temperate and sub-Antarctic land areas in the South Atlantic sector. Thus Grolle (1972) noted that the 11 hepatic species recorded in Table II all occur in the region including southern South America and South Georgia. Only three species, *Cryptochila grandiflora*, *Marchantia berteroana* and *Triandrophyllum subtrifidum*, are known to be widespread in other south temperate and sub-Antarctic regions but Grolle pointed out that this could be due to lack of collecting. Similarly, most of the mosses recorded from the South Sandwich Islands have also been recorded in South Georgia and southern South America, while some species, such as *Bartramia patens*, are circum-polar in the southern temperate zone, and an additional bi-polar element is represented by such species as *Polytrichum alpestre* and *P. alpinum*. A few of the mosses, notably *Bryum argenteum*, are cosmopolitan. Most of the cool-ground bryophytes recorded in Table II also extend to localities farther south in the maritime Antarctic and a few, including *Bryum algens*, *B. argenteum* and *Tortula* *conferta*, occur in continental Antarctica. Of these, *T. conferta* is circum-polar within the Antarctic, but is so far unknown north of the South Sandwich Islands (Greene, 1967). It is noteworthy, however, that many of the species which in the South Sandwich Islands are restricted to the vicinity of fumaroles appear to be rare or absent elsewhere in the Antarctic zone, e.g. *Campylopus* spp. and several hepatics. Most of the lichen species listed in Table II have been collected in the maritime Antarctic, and currently available records suggest that several may be Antarctic endemics, e.g. *Lecanora racovitzae* and *Microglaena antarctica*. Many of the other lichens are also known from sub-Antarctic and temperate sites, while some, such as *Mastodia tesselata* and *Ochrolechia frigida*, are bi-polar in distribution and *Lecanora polytropa* is cosmopolitan (personal communication from D. C. Lindsay). The grass *Deschampsia antarctica* is widespread in southern South America, South Georgia and the maritime Antarctic, and also occurs on sub-Antarctic islands in the southern Indian Ocean (Holtom and Greene, 1967). Of the algae, several, including *Prasiola crispa*, appear to be characteristic of Antarctic regions, but *Prasiococcus calcarius* was previously unknown outside Europe (Belcher, 1969).

The flora of the South Sandwich Islands thus appears to represent an impoverished version of that occurring in the South Atlantic sector of the cool-temperate, sub-Antarctic and Antarctic botanical zones. A substantial number of species have distributions extending to more distant localities, but there appear to be few Antarctic endemics, except perhaps among the lichens. Many of the restricted fumarole species are essentially sub-Antarctic or temperate in distribution, being rare or absent at most other Antarctic sites.

III. CLASSIFICATION AND GENERAL FEATURES OF THE VEGETATION

A QUALITATIVE description of the vegetation present on the islands was undertaken during the 1964 survey. Most of the plant communities occurring on unheated ground could be placed without difficulty into sub-formations of the Antarctic non-vascular cryptogam tundra formation or the Antarctic herb tundra formation, as recognized in a classification of Antarctic vegetation proposed by Longton (1967) and modified and extended by Gimingham and Smith (1970), Smith (1972) and Longton (1973). The most extensive vegetation types in non-fumarolic areas were communities in the crustaceous lichen, the alga and less commonly the fruticose and foliose lichen sub-formations. In general, the communities were less extensive, floristically poorer and structurally less complex than comparable vegetation elsewhere in the maritime Antarctic. Many extensive tracts of ground were either devoid of macroscopic plants or supported only scattered colonies of crustose lichens, of the green alga *Prasiola* cf. *crispa*, or of fruticose lichens, principally *Usnea antarctica*. Locally, these plants were abundant, forming areas of more luxuriant vegetation. The cool-ground vegetation on Bellingshausen, Candlemas, Leskov and Vindication Islands was less impoverished than that elsewhere in the archipelago and included small stands of the tall moss-turf, the short moss-turf and cushion, and bryophyte carpet and mat sub-formations, as well as those noted above. In addition, communities in the snow-alga sub-formation were recorded on Candlemas Island, which also supported the only stands of the grass and cushion chamaephyte sub-formation observed in the island group. Snow algae may also be expected on most of the other islands.

The luxuriant, concentrically zoned bryophyte vegetation associated with fumaroles was composed principally of tall turf-forming mosses, mat- and carpet-forming leafy hepatics and the thallose liverwort *Marchantia berteroana*. Several of the communities, notably those dominated by hepatics, have proved difficult to place in the existing classification of Antarctic vegetation (Gimingham and Smith, 1970). In order that they may be incorporated, it is here proposed that the moss-carpet sub-formation of the former scheme be broadened in scope and re-named the bryophyte carpet and mat sub-formation. The classification of fumarole communities is considered more fully in the "Discussion" (p. 46–48). Series of intergrading communities were recognized as associations and sociations within each sub-formation. In Table III these units are listed and their known geographical distribution within the archipelago is indicated. It must be emphasized, however, that the classification below the sub-formation level should at present be regarded as tentative due to taxonomic difficulties which, at the time of the field work, precluded identification of many of the species involved.

TABLE III

CLASSIFICATION AND DISTRIBUTION OF PLANT COMMUNITIES IN THE SOUTH SANDWICH ISLANDS

Vegetation type	*Island*										
	Bellingshausen	Bristol	Candlemas	Cook	Freezland Rock	Leskov	Montagu	Saunders	Thule	Vindication	Visokoi
Antarctic non-vascular cryptogam tundra formation											
Fruticose and foliose lichen sub-formation											
Usnea–Andreaea association*											
Usnea antarctica sociation*	F		C		C	C				C	C
Usnea antarctica–Andreaea regularis sociation						C					
Usnea antarctica–Andreaea gainii sociation	C						C			C	
Usnea antarctica–Polytrichum alpinum sociation	C										
Crustaceous lichen sub-formation											
Caloplaca–Xanthoria association*											
Several unclassified sociations			C					C			
Buellia–Lecanora–Lecidea association*											
Several unclassified sociations			C					C	C	C	
Short moss-turf and cushion sub-formation											
Pohlia nutans association											
Pohlia nutans sociation								F†			
Pohlia nutans–Lepraria sp. sociation			C								
Ceratodon association											
Ceratodon sp. sociation			B								F
Tortula–Grimmia association*											
Tortula conferta sociation					C						
Tall moss-turf sub-formation											
Polytrichum alpestre–Chorisodontium aciphyllum association*											
Polytrichum alpestre sociation*						F					

TABLE III—*continued*

Vegetation type	*Island*										
	Bellingshausen	Bristol	Candlemas	Cook	Freezland Rock	Leskov	Montagu	Saunders	Thule	Vindication	Visokoi
Polytrichum alpinum–Pohlia nutans association											
Polytrichum alpinum sociation*	C		B			F				C	
Polytrichum alpinum–Pohlia nutans sociation			B								
Pohlia nutans sociation			F								
Campylopus association											
Campylopus flavoviridis sociation			F								
Campylopus spiralis sociation	F										
Bryophyte carpet and mat sub-formation											
Brachythecium cf. *antarcticum–Calliergon sarmentosum–Drepanocladus* cf. *uncinatus* association*											
Drepanocladus cf. *uncinatus* sociation*	B		C			C	C			C	
Brachythecium sociation	B		C							C	
Cryptochila grandiflora–Triandrophyllum subtrifidum association											
Cryptochila grandiflora sociation	F		F			F					
Cryptochila grandiflora–Triandrophyllum subtrifidum sociation						F					
Marchantia berteroana association											
Marchantia berteroana sociation			F			F					
Cephalozia badia association											
Cephalozia badia sociation			F								
Alga sub-formation											
Prasiola cf. *crispa* association*											
Prasiola cf. *crispa* sociation*	C	C	C	C			C	C	C	C	C
Unclassified communities of microscopic algae and small bryophytes in fumarole vents	F		F			F					
Snow-alga sub-formation											

TABLE III—*continued*

Vegetation type	*Island*										
	Bellingshausen	Bristol	Candlemas	Cook	Freezland Rock	Leskov	Montagu	Saunders	Thule	Vindication	Visokoi
Chlamydomonas nivalis–Raphidonema nivale–Ochromonas association*											
Chlamydomonas nivalis sociation			C								
Antarctic herb tundra formation											
Grass and cushion chamaephyte sub-formation											
Deschampsia antarctica–Colobanthus quitensis association*											
Deschampsia antarctica sociation*			F†								

*Associations and sociations recorded also in the South Orkney Islands (Smith, 1972).
†Occurrence of volcanic heating uncertain (see p. 23–24).
F Confined to fumaroles.
C Confined to cool ground.
B Recorded both near fumaroles and on cool ground.

IV. CANDLEMAS ISLAND

A. GENERAL OBSERVATIONS

Most of the ice-free ground on Candlemas Island was examined in 1964, with the exception of the south and south-east coasts which proved inaccessible by land; these areas were considered unlikely to support extensive vegetation, and none was seen from the air. A sketch map showing the approximate distribution of fumaroles and of the most significant plant communities on unheated ground is provided in Fig. 2.

The principal habitats for vegetation were ash and scoria deposits, and the cliffs of consolidated lava or tuff on the exposed ridges of the older flows. Plant cover was best developed below the northern and western sides of the ice cap, and on Breakbones Plateau (Fig. 2). A particularly rich bryophyte flora existed around fumaroles on the fringes of Lucifer Hill, and small stands of several bryophyte and lichen communities also occurred on cool ground in this area. All the sub-formations listed in Table III were recorded at the sites considered above.

In contrast, much of the other snow-free ground lacked plant cover. Many areas of flat or gently sloping sand and scoria, for example, Chimaera Flats between the two lagoons of Medusa Pool and Gorgon Pool, supported only a meagre flora including scattered cushions of *Ceratodon* sp. with occasional thalli of *Prasiola* cf. *crispa* and crustose lichens, notably *Lecidea* sp. Similarly, only widely scattered crustose lichens and short turves of *Pohlia nutans* had colonized the young lava flows between Lucifer Hill and Breakbones Plateau. The areas occupied by breeding penguins were also without macroscopic plants, except for crustose lichens and *Prasiola* cf. *crispa* on the larger boulders. Thus vegetation along the south-western shore of the island and on cliffs above the northern shore of Gorgon Pool ceased abruptly at the margin of penguin colonies. Moreover, extensive areas of shallow *Polytrichum alpinum* and *Drepanocladus* cf. *uncinatus* peat occurred beneath a thin layer of sludge comprising trampled soil and excrement around the margin of the colony on Carbon Point. This observation gives direct evidence of the effects of manuring and trampling by birds in eradicating bryophyte vegetation, and suggests that the penguin colony may recently have increased in area.

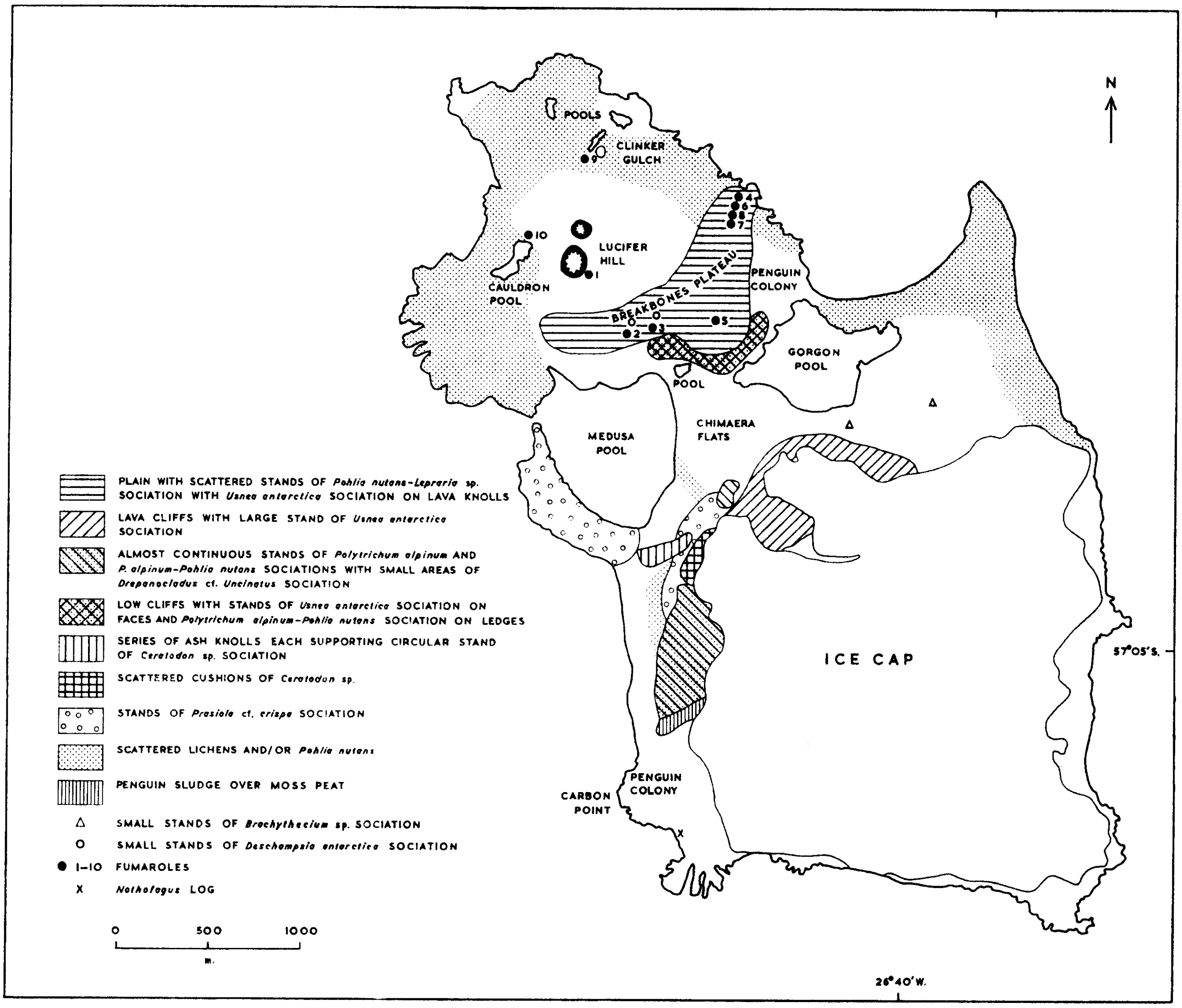

FIGURE 2

Sketch map of Candlemas Island showing the distribution of fumaroles and the principal stands of cool-ground vegetation. The position of a *Nothofagus* log reported by Longton (1977) is also indicated.

B. FUMAROLE VEGETATION

1. *Distribution of fumaroles*

In March 1964 active fumaroles were confined to the northern section of the island. The twin craters of Lucifer Hill were vigorously emitting clouds of steam and sulphurous gases, and extensive deposits of solidified sulphur clothed the upper slopes. This area was virtually barren apart from vegetation around a single fumarole high on the cone. In addition, a series of fumaroles occurred on the lower slopes of Lucifer Hill and on the surrounding terrain, and here luxuriant bryophyte vegetation was developed over areas of up to 20 m. in diameter around most of the vents. The distribution of the ten most important groups of vegetated fumaroles is indicated in Fig. 2. Of these, only fumaroles 1, 3, 4 and 10 were seen actively emitting steam. There were normally several vents in the ground surface, indicating that steam had at one time escaped from most of the fumaroles, and the surrounding substratum was everywhere warm and moist.

2. *Fumaroles near the summit of Lucifer Hill*

Vegetation surrounded a fumarole at an altitude of *c.* 200 m. on the south-eastern lip of the more southerly crater (fumarole 1 in Fig. 2). There were no distinct vents but steam was rising freely from a narrow horizontal strip of ground about 20 m. long and 150 cm. wide at the junction of a bed of scoria and a capping of less permeable tuff. The associated vegetation comprised a single unindentified dicranoid moss, which was sparsely distributed over the strip of steaming ground. Numerous small areas of moss occurred but in each the plants formed only open turf and seldom reached a height of more than 1 cm.

3. *Fumaroles south and east of Lucifer Hill*

Vegetation was more extensively developed around a series of fumaroles occurring at altitudes of approximately 50–80 m. in an arc on Breakbones Plateau (fumaroles 2–8 in Fig. 2). Details of the location and vegetation of five of these fumaroles are given in Tables IV and V, and Figs. 3–5.

TABLE IV

ZONATION OF VEGETATION AT FUMAROLE 3 ON CANDLEMAS ISLAND

Zone	*Approximate distance from vents*	*Dominant species*	*Notes*
1	In vents and up to 10 cm.	Algae	An open community dominated by gelatinous algal growths. Other species, occurring as scattered stems or small turves or mats, included *Campylopus flavoviridis*, *Lophozia propagulifera*, *Cephaloziella* sp. and slender *Pohlia nutans*
2	10–100 cm.	*Cryptochila grandiflora*	Luxuriant, more or less closed carpets and turves of the hepatic *Cryptochila grandiflora*, with less extensive tall turves of *Pohlia nutans*, *Polytrichum alpinum*, *P. juniperinum* and *P. piliferum*. Scattered basidiomycete fruiting bodies were also present and there were abundant crustose lichens on stones. The *Cryptochila* carpet was bright green in colour near the vents, gradually becoming reddish brown further out
3	100–250 cm.	*Polytrichum alpinum*	Tall turves of *P. alpinum* and less frequently *P. juniperinum* and *P. piliferum*. *Usnea antarctica* and crustose lichens, including *Ochrolechia frigida* and *Stereocaulon* sp., occurred on scoria between the *Polytrichum* turves

Fumarole 3 occurred on lava knolls at the head of a small ravine north of the eastern shore of Medusa Pool. Four of the knolls had a series of vents, surrounded by vegetation, in the scoria clothing their southern sides.

TABLE V

ZONATION OF VEGETATION AT FUMAROLE 4 ON CANDLEMAS ISLAND

Zone	*Approximate distance from vents*	*Dominant species*	*Notes*
1	In vents	*Pohlia nutans*, algae	The sides of the vents supported an open growth of slender *Pohlia nutans*, with scattered mats of hepatics including *Cephaloziella varians*, *Cephalozia badia*, *Lophozia propagulifera* and *Riccardia georgiensis*. Both the bryophytes and the intervening ash were partially covered by gelatinous algal growths
2	0–100 cm.	*Cryptochila grandiflora*, *Pohlia nutans*	The vents were surrounded by closed carpets and turves of *Cryptochila grandiflora* and *Pohlia nutans*, the former predominating towards the centre of the zone. *Marchantia berteroana*, *Campylopus* sp., *Polytrichum alpinum* and *Psilopilum antarcticum* were among the associated species
3	100–300 cm.	*Polytrichum alpinum*	An almost pure but discontinuous turf of *Polytrichum alpinum*

Fumarole 4 occupied a north-facing slope of scoria and lava boulders in a small ravine near the east coast of the island. Several vents, each surrounded by concentrically zoned vegetation, occurred between the boulders.

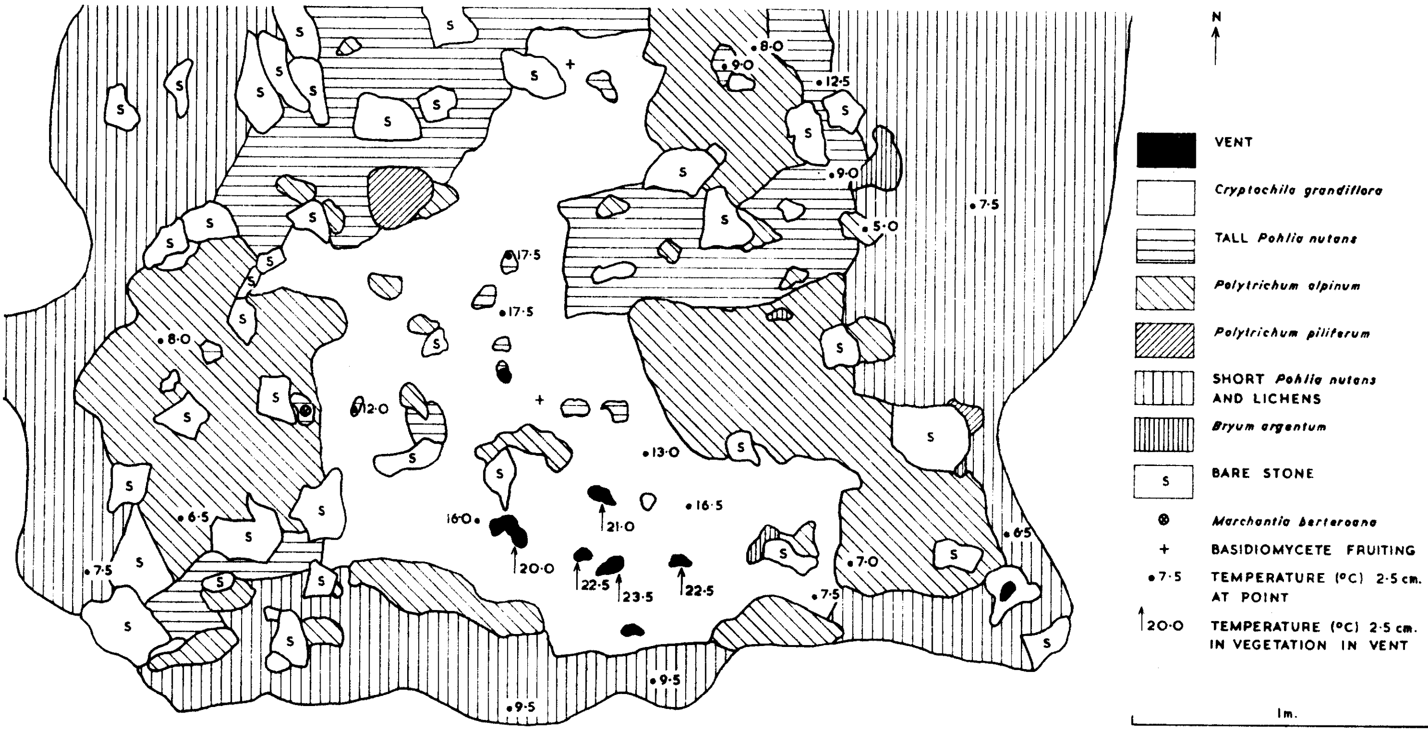

FIGURE 3

Map of the vegetation surrounding one group of vents at fumarole 2 on Candlemas Island. The temperatures (°C) recorded as spot readings 2·5 cm. deep in the soil and vegetation are indicated.

At fumarole 2, situated to the north of Medusa Pool, the vegetation was developed on ash and scoria on the southern side of a low lava knoll. Several groups of small narrow vents, each vent up to 10 cm. long, occurred in the ash and a map of the vegetation surrounding one group of vents is given in Fig. 3. Fumaroles 3 and 5 were also associated with low lava knolls (Table IV; Fig. 4), while fumaroles 6–8 were located on gentle, south-facing ash slopes near the east coast of the island (Fig. 2). Fumaroles 3, 5 and 7 had one or more small but distinct vents resembling those at fumarole 2, but no obvious vents were recorded at fumaroles 6 and 8. Fumarole 4 (Table V) lay on a north-facing slope of ash and lava boulders, and had several vents up to 50 cm. wide between the boulders.

The central zone of vegetation around fumarole 2 (Fig. 3) occurred on the inner sides of the vents, which were partially clothed with *Pohlia nutans* in a form having slender, often prostrate stems and small, distantly spaced leaves. Small, bright green mats of *Cephaloziella* sp. were also present, and the bryophytes and intervening areas of ash were in places covered with a gelatinous growth of microscopic algae. It can been seen from Fig. 4 and Tables IV and V that the vents at fumaroles 3, 4 and 5 also supported slender *Pohlia nutans* associated with gelatinous algae, which included a species of *Mesotaenium* at fumarole 5. The mosses *Distichium capillaceum* and *Campylopus* sp., and the leafy hepatics *Cephalozia badia*, *Cephaloziella varians*, *Lophozia propagulifera* and *Riccardia georgiensis*, were recorded as associates in some cases. Algae and slender *Pohlia nutans* were also present in the single vent at fumarole 7, but the present community was not recorded in the absence of vents at fumaroles 6 and 8.

A second zone, up to 3 m. wide and dominated by *Pohlia nutans* and the hepatic *Cryptochila grandiflora*, was a consistent feature of the vegetation at fumaroles 2–8 (Tables IV and V; Figs. 3–5). Here, *P. nutans* occurred as tall turves of densely packed, bright green erect shoots with crowded leaves, contrasting strongly with the form of the same species occurring in the vents, and *C. grandiflora* formed luxuriant carpets, or less frequently turves, up to 10 cm. deep. In some places the *Cryptochila* carpet gradually changed from a green colour near the vents to reddish brown further out. Zone 2 normally comprised a mosaic of areas occupied by one of the two dominant species, rather than an intimate mixture of the two, and the relative abundance of the two species varied between different fumaroles. Thus *C. grandiflora* predominated at fumarole 3 (Table IV), and in the inner region around the vents at fumarole 2 (Fig. 3). In contrast,

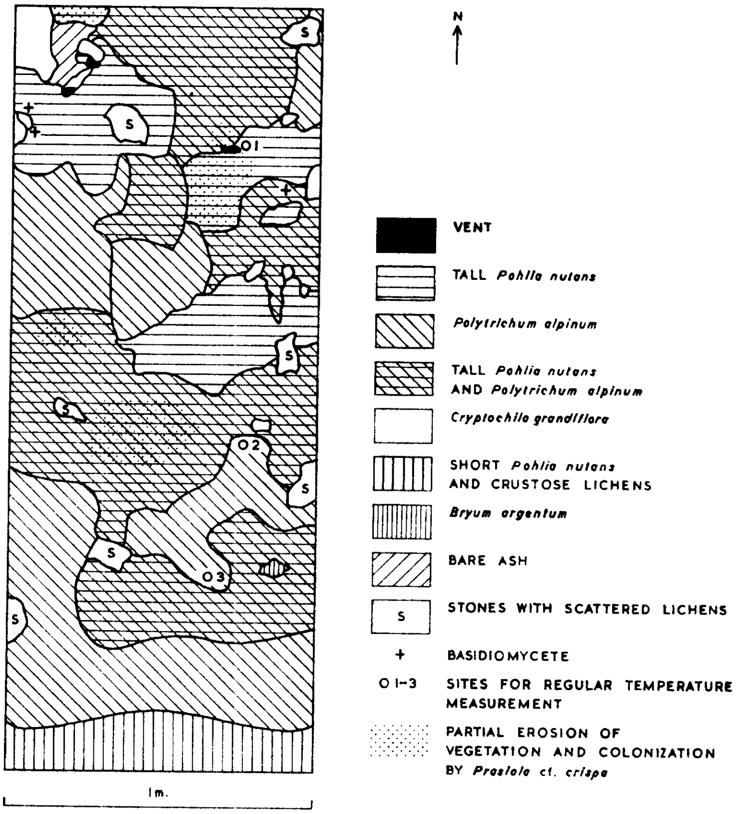

FIGURE 4

Map of a transect across vegetation to the south of a group of vents at fumarole 5 on Candlemas Island. Fumarole 5 comprised several groups of small vents in the scoria around the south side of a lava knoll. Slender *Pohlia nutans*, with *Cephaloziella* sp., *Mesotaenium* sp. and other algae, occurred in the vents.

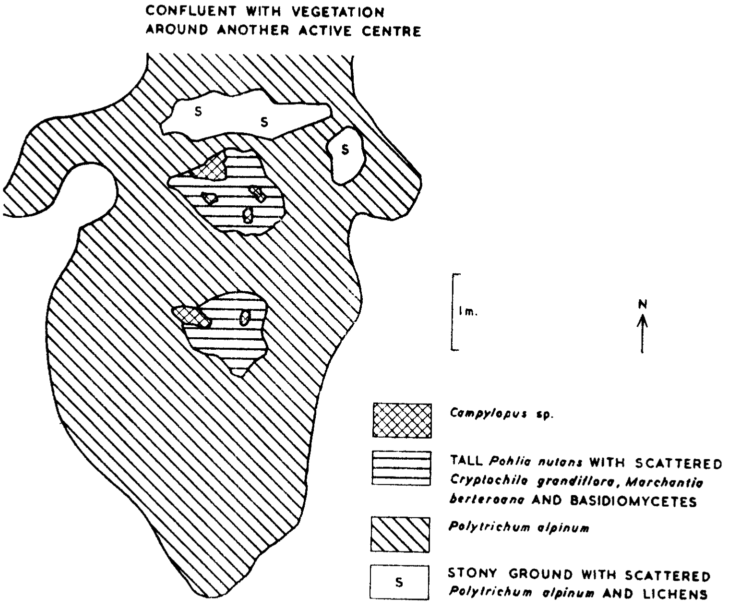

FIGURE 5

Sketch map of part of the vegetation at fumarole 6 on Candlemas Island. Fumarole 6 was located on gentle south-facing ash slopes; there were no distinct vents.

P. nutans was dominant around the *Cryptochila* carpet at fumarole 2, and throughout zone 2 at fumaroles 6–8 (Fig. 5). Small basidiomycete fruiting bodies and a variety of bryophytes, including *Bryum argenteum*, *Campylopus* sp., *Distichium capillaceum*, *Polytrichum alpinum*, *Psilopilum antarcticum* and *Marchantia berteroana*, were recorded as associates in zone 2 for at least one of the fumaroles. *Polytrichum alpinum* was abundant with *Pohlia nutans* throughout zone 2 at fumarole 5 (Fig. 4) and at fumarole 7 *Marchantia berteroana* formed almost pure mats up to 30 cm. wide growing over the surface of other bryophytes.

Tall turf-forming mosses predominated in the third zone of vegetation, which formed a discontinuous belt 1–2 m. wide around the *Pohlia–Cryptochila* community at fumaroles 2–6 (Tables IV and V; Figs. 3–5). *Polytrichum alpinum* was the dominant species, associated locally with *P. juniperinum*, *P. piliferum* and *Bryum argenteum*, while *Usnea antarctica* and crustose lichens were locally abundant on scoria between the moss turves.

A fourth, and outer zone, was recorded only at fumaroles 2 and 5 (Figs. 3 and 4). It extended for distances ranging from 10 cm. to several metres, and comprised a short turf of *Pohlia nutans*, in this case yellow in colour and heavily colonized by a species of *Lepraria* and other crustose lichens. *Usnea antarctica* and the crustose lichens *Acarospora macrocyclos* and *Lecanora polytropa* also occurred on stones projecting through the moss turf.

Fumaroles 2–8 were thus surrounded by up to four concentrically arranged but somewhat intergrading zones of vegetation. The zonation was normally irregular, due to unevenness of the ground surface, the tendency for vegetation surrounding different groups of vents to merge, thus creating complex patterns of plant communities, and other factors. Typical irregularities are illustrated in Fig. 3 for the vegetation around one group of vents at fumarole 2. For example, it can be seen that the *Cryptochila* carpet extended further from the vents to the north than to the south, that the short *Pohlia–Lepraria* turf was interrupted in the north where the inner zones were continuous with the vegetation associated with a second group of vents, and that in the west the *Pohlia–Lepraria* community merged with the outer zone of vegetation surrounding a third series of vents.

Two additional, less characteristic vegetation types were recorded locally. First, at fumarole 3 luxuriant vegetation of crustose and fruticose lichens, including *Ochrolechia frigida* and a species of *Stereocaulon* occurred on the surface of a lava knoll above the vents, and in contact with rising steam. Secondly, the bryophyte vegetation at fumarole 5 was partially eroded (Fig. 4), possibly by a pair of giant petrels (*Macronectes giganteus*) which were nesting on the summit of the lava knoll where it occurred. *Prasiola* cf. *crispa* was colonizing the eroded areas, with smaller quantities of microscopic algae including *Navicula muticopsis* and *Pinnularia borealis*.

4. *Fumaroles north and west of Lucifer Hill*

Two further groups of fumaroles were recorded at altitudes of *c.* 30 m. to the north and west of Lucifer Hill. They were situated on steep slopes of lava boulders partially covered in ash, and the vents occurred as fissures up to 1·5 m. wide between the boulders. A group of 12 fumaroles occurred on the slopes in Clinker Gulch (fumarole 9 in Fig. 2), each with the associated vegetation forming a strip up to 20 m. long and 5 m. wide running down the hillside. A sketch map of the plant communities at one of these fumaroles is given in Fig. 6. Two more fumaroles were recorded on the slopes above Cauldron Pool on the north-west coast of the island (fumarole 10 in Fig. 2), and these were surrounded by stands of vegetation approximately 20 m. wide.

Only two or three zones of vegetation were present in both groups, and in the flora of the inner zone, covering the vertical sides of the boulders forming the vents, these fumaroles resembled those south of Lucifer Hill. Microscopic algae, including *Eunotia tenella*, *Prasiococcus calcarius* and *Mesotaenium* sp., together with *Cephaloziella* sp. and the slender form of *Pohlia nutans*, were the most abundant plants, while a small mat of *Lepidozia cuspidata* was also recorded at fumarole 10. Towards the top of the vents, however, the lava usually supported turves of *Campylopus* spp. extending from zone 2.

The second and most extensive zone comprised dense turves of *Campylopus flavoviridis* and *C. introflexus*, which gave complete cover over large areas except on the steep sides of projecting lava boulders. Occasional turves of *Pohlia nutans* grew among the *Campylopus*, but *Cryptochila grandiflora* and *Polytrichum alpinum* were rare. However, one fumarole in Clinker Gulch differed from its neighbours in that *Pohlia nutans* was dominant in the second zone.

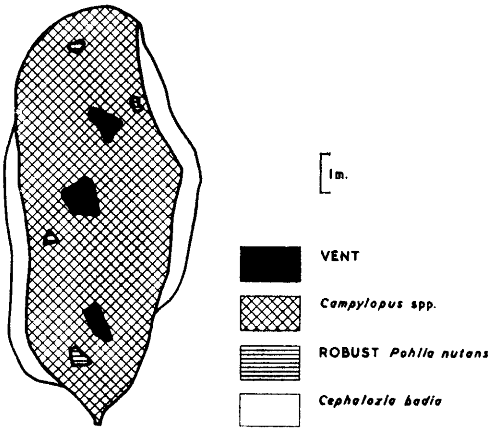

FIGURE 6

Sketch map of the vegetation around one series of vents at fumarole 9 on Candlemas Island (after Longton and Holdgate, 1967).

A third zone was developed around only a few fumaroles in Clinker Gulch, where a shallow, almost pure compact mat of the leafy hepatic *Cephalozia badia* surrounded the *Campylopus* turf; the hepatic had abundant perianths. There were no zones with abundant *Polytrichum alpinum* or short *Pohlia nutans* and lichens, although occasional short turves of *Pohlia nutans* occurred among the surrounding lava boulders. Both the boulders and the *Campylopus* turf supported frequent crustose lichens, including species of *Lecanora* and *Lecidea.*

A striking feature of the present fumaroles was the moribund condition of much of the vegetation, which was yellow-brown in colour and of a slimy texture suggesting bacterial decay. All species in the two outer zones were affected, but *Campylopus* spp. and *Pohlia nutans* were beginning to recover through the production of young green shoots. By contrast, both the *Cephaloziella* and the slender *Pohlia nutans* growing in the vents were bright green and apparently healthy, and moreover, the *Pohlia nutans* surrounding one fumarole in Brimstone Gulch was also unaffected.

5. *Fumaroles: summary*

Three distinct types of vegetation pattern were thus associated with the fumaroles on Candlemas Island. The most complex type occurred on the gentle ash slopes south of Lucifer Hill, where the vegetation often surrounded the southern sides of low lava knolls. Most of these fumaroles had small vents supporting an open community of algae and small bryophytes, which formed the innermost zone of vegetation. The second zone was dominated by luxuriant carpets and turves of *Cryptochila grandiflora* and *Pohlia nutans* in varying proportions, while *Polytrichum alpinum* and short lichen-encrusted turves of *Pohlia nutans* in some cases dominated third and fourth zones respectively around the *Cryptochila–Pohlia* carpet. The second type of fumarole, occurring on the steep boulder-strewn slopes north of the cone, had similar plant communities forming the innermost zone to those further south, although covering greater areas in the larger vents. Unlike the more southerly fumaroles, however, *Campylopus* spp. were dominant in the second, most extensive zone, while the third zone, where present, comprised a shallow mat of the hepatic *Cephalozia badia.* The single example of the third type of vegetated fumarole, recorded high on the volcanic cone, supported only a sparse growth of a single dicranoid moss.

C. VEGETATION OF UNHEATED GROUND

1. *Crustaceous lichen sub-formation*

A wide range of cryptogamic communities was also developed on Candlemas Island in areas away from the influence of volcanic heat and moisture. Crustose lichens and other forms projecting only a few millimetres above the substratum predominated in a variety of habitats. Communities in the crustaceous lichen sub-formation formed the characteristic vegetation on coastal cliffs, where bright yellow and orange species including *Xanthoria candellaria* were locally abundant, with species of *Acarospora* and other crustose forms occurring as associates. Similar species, accompanied by *Mastodia tesselata* and *Rinodina petermannii,* occurred less abundantly on boulders in penguin colonies, where sparse lichen-dominated communities were frequently the only vegetation. The algae *Navicula muticopsis, Prasiococcus calcarius* and *Prasiola* cf. *crispa* were collected from lichen-dominated communities in the penguin colonies. Similar vegetation was also colonizing shingle on a bank separating Gorgon Pool from the sea, the lichens *Acarospora macrocyclos, Lecanora* sp. and *Mastodia tesselata* and the algae *Prasiococcus calcarius* and *Prasiola* cf. *crispa* being represented in the collections. Crustose lichens were also locally abundant on drift-wood spars scattered around Chimaera Flats and other low-lying parts of the island.

2. *Fruticose and foliose lichen sub-formation*

The larger fruticose lichen *Usnea antarctica* became abundant in inland areas, particularly on crags under the north face of the ice cap, on cliffs north-west of Gorgon Pool, and on lava knolls projecting through the ash deposits south and east of Lucifer Hill (Fig. 2). A wide variety of crustose lichens was also present beneath the *Usnea* fronds, including *Acarospora macrocyclos, Buellia anisomera, Rinodina petermannii* and a species of *Lecidea.* Small cushions of *Pohlia nutans* and of *Dicranoweisia* sp. formed the only bryophyte component of this vegetation, but nevertheless, total cover-value in places exceeded 70 per cent.

3. *Short moss-turf and cushion sub-formation*

Communities in the short moss-turf and cushion sub-formation formed the most extensive vegetation on plains and gentle slopes south-east of the cone, where large areas on Breakbones Plateau supported an association of *Pohlia nutans* and crustose lichens. A similar community was recorded on level sand forming the south-eastern shore of a pool in Clinker Gulch on the north coast. The vegetation was built up from a more or less continuous turf of *Pohlia nutans,* which formed a crust approximately 1 cm. deep over the ash. Much of the moss was moribund and colonized by species of *Lepraria* and other crustose lichens. Indeed the lichen growth was so extensive that the vegetation as a whole appeared pale whitish green from a distance. Species of *Polytrichum* were the most frequent associates, *P. alpinum* and more locally *P. juniperinum* and *P. piliferum* forming circular turves up to 1 m. wide among the *Pohlia.* The turves were open, with abundant *Pohlia* growing between the *Polytrichum* stems and, moreover, the latter reached a height of only 1–2 cm., thus contrasting strongly with the luxuriance of *P. alpinum* in communities of the tall moss-turf sub-formation elsewhere on the island. Small scattered cushions of *Bryum argenteum* and of a species of *Ceratodon* were also recorded locally, but the *Pohlia–Lepraria* community was in general species-poor. So too was a second community, which was developed on an ash and scoria bank to the south of Medusa Pool (Fig. 2). The bank was deeply dissected by drainage channels and the slopes between many of the gullies were crowned by a distinct circular umbo. On these summit areas the ground was more stable than that over most of the bank, and each supported circular stands of vegetation from 5 to 20 m. in diameter. *Ceratodon* was dominant, in cushions that had coalesced to give undulating sheets of vegetation from 2 to 3 cm. deep. Crustose lichens including *Lecanora polytropa* were abundant on the surface of the moss, and *Usnea antarctica* was anchored to pieces of scoria projecting through the moss cover. Scattered stems of *Polytrichum alpinum* were also recorded.

Ceratodon was also locally abundant on moraine material washed down on to steep ash slopes below the north-west corner of the ice cap (Fig. 2). Small cushions of *Ceratodon* up to 5 cm. diameter gave 10–20 per cent cover over strips of ground up to 5 m. by 20 m. running down the slope, and these strips extended over approximately 100 m. of hillside. No associated species were recorded in this vegetation and it seems likely that it had only recently colonized the morainic substratum.

4. *Tall moss-turf sub-formation*

The most complex plant association of unheated ground on Candlemas Island was dominated by tall turves of *Polytrichum alpinum* and *Pohlia nutans* which occurred on, and at the base of, steep scoria slopes, and on broad scoria-covered ledges on the lava cliffs. It covered extensive areas of ground sloping down from the western side of the ice cap, and there was a smaller area in a similar situation under lava cliffs north of the ice cap (Fig. 2). The best development of the association in its cliff habitat was seen along the north-west shore of Gorgon Pool.

Polytrichum alpinum was normally the most abundant species on scoria slopes, where it formed tall hummocky turves, but *Pohlia nutans* was always a frequent constituent and on the cliffs ledges it gave up to 70 per cent cover. *Pohlia nutans* grew in turves between the hummocks and as scattered stems among the *Polytrichum*, while *Drepanocladus* cf. *uncinatus* and a species of *Brachythecium* were also widespread, forming small mats up to 25 cm. wide. Thin, dark red mats of a species of *Cephaloziella* had in places colonized the surface of the mosses, particularly *Drepanocladus*.

Crustose lichens, including *Stereocaulon antarcticum*, were frequently invading the surface of the mosses, *Polytrichum alpinum* and *Pohlia nutans* being the worst affected species, while brown moribund areas of *Polytrichum alpinum* were also noted in the absence of lichens. The south-facing sides of the hummocks were normally the first to be damaged. The other bryophyte species seemed less prone to colonization by lichens, although they were by no means totally immune, and in places *Cephaloziella* sp. was seen growing over the surface of the crustose lichens.

5. *Bryophyte carpet and mat sub-formation*

The bryophyte carpet and mat sub-formation is typical of moist habitats irrigated by melt water, and its distribution away from fumaroles on the South Sandwich Islands was severely restricted compared with other maritime Antarctic situations by the dry condition of much of the substratum. On Candlemas Island, however, *Drepanocladus* cf. *uncinatus* and a species of *Brachythecium* occurred locally in small, almost pure stands. *Drepanocladus* was most abundant on the west coast, where it formed pure carpets up to 10 m. wide in damp, slightly depressed pockets of level ground within larger areas dominated by tall turf-forming mosses. Open, less well-developed carpets of *Drepanocladus* were also recorded in hollows in the ash slopes south of Lucifer Hill.

Brachythecium carpets several metres wide, and containing only a few isolated turves of *Pohlia nutans* and *Polytrichum alpinum* as associated species, occurred on two small areas of the north-facing slopes below the ice cap south of Gorgon Pool (Fig. 2). This vegetation was likely to be influenced by melt water from the ice cap throughout the summer.

6. *Alga sub-formation*

The green alga *Prasiola* cf. *crispa* was a conspicuous feature of the central part of Candlemas Island, being particularly abundant on ash banks below the northern side of the ice cap (Fig. 2). Parts of the bank were completely barren, but other extensive and apparently similar areas were covered by a thin sheet of *Prasiola*. From a distance the banks appeared uniformly green, but the alga was in fact arranged in a reticulate pattern over the ash, giving 50–70 per cent cover. There were virtually no associated species. Penguin carcasses were widely distributed over this area and, although the nearest breeding colony was several hundred metres distant, they undoubtedly enhanced the supply of nitrates and other salts.

Prasiola was widespread, though less abundant, elsewhere on ash slopes occasionally frequented by penguins, but within the breeding colonies it was restricted to boulders. It also grew on lava cliffs under the ice cap in places subject to dripping melt water, and was locally frequent on ash knolls around giant petrel nests, both among the tall turf-forming mosses on the west coast and on ash slopes to the east and west of Lucifer Hill.

7. *Snow-alga sub-formation*

Extensive areas of snow coloured red, yellow or green by abundant microscopic algae were noted locally, particularly along the western margin of the ice cap, and less frequently on snow banks on Breakbones Plateau. A specimen from the latter site contained abundant *Chlamydomonas nivalis*, and smaller quantities of *Navicula muticopsis*, *Pinnularia borealis* and *Scotiella nivalis*.

8. *Grass and cushion chamaephyte sub-formation*

The grass *Deschampsia antarctica* was confined to the relatively flat scoria-covered ground on Breakbones Plateau. Scattered plants grew throughout this area and *Deschampsia* was dominant in two larger stands of vegetation near fumaroles 2 and 3 (Fig. 2). Six turves, between 8 and 45 cm. in diameter, were recorded between 1 and 2 m. from a vent at fumarole 3, and a larger stand measuring 7 m. by 8 m. was situated approximately 15 m. north-east of the fumarole. Within this stand, grass cover was approximately 50 per cent and the individual plants had coalesced to give continuous turves up to 1 m. wide. *Pohlia nutans* and *Polytrichum alpinum* were frequent associates. In the second stand, approximately 30 m. north of fumarole 2, *D. antarctica* gave only 25 per cent cover in an area 6 m. by 4 m., the individual turves seldom exceeding 25 cm. in diameter. As noted later (p. 25), it is uncertain whether the *Deschampsia* populations were in areas slightly affected by volcanic heat.

D. TEMPERATURES IN VEGETATION NEAR FUMAROLES AND ON UNHEATED GROUND

1. *Spot readings*

In view of the contrast between the vegetation of heated and unheated ground on Candlemas Island, a series of temperature measurements was made to compare conditions in the fumarolic and other areas, and to determine whether the zonation of the fumarole vegetation was associated with a decreasing temperature gradient outwards from the vents. The readings were taken on several days during March 1964, at times when air temperature 2 m. above ground level was between 0° and 2° C. There was little sunshine during the period of observation. Most readings were made to the nearest 0·5° C using a mercury thermometer with its bulb at a depth of 2·5 cm. in the vegetation, but some data were obtained with a Rototherm and others with a thermistor at similar depths. The data for the fumarolic areas are summarized in Table VI and Fig. 3 shows temperatures at precise points in the vegetation around fumarole 2.

The highest temperatures were recorded at fumarole 1, on the main volcanic cone (Table VI). A single reading at a depth of 2·5 cm. under the moss was 55° C, while only 0·5 cm. below the moss surface five readings ranged from 21° to 37° C with a mean of 28·2° C.

The other fumaroles were markedly cooler, mean temperatures in the vents ranging from approximately 13·5° to 22·0° C. There was clearly a decreasing temperature gradient outwards from the vents, and average temperatures in zones 3 and 4 of the fumaroles south of the cone varied from approximately 4° to 12° C. In only one case was a higher mean temperature recorded in one zone of vegetation than in a more central zone of the same fumarole, the mean temperature in the short *Pohlia nutans*–lichen community surrounding fumarole 2 being approximately 1° higher than the mean for the more central areas dominated by *Polytrichum alpinum*.

Despite the regular temperature gradient surrounding each group of vents, there were marked variations between the temperatures in comparable vegetation around different fumaroles. Thus temperatures among the tall form of *Pohlia nutans* in zone 2 of the vegetation at fumarole 5 were on average 7·6° higher than among similar plants at fumarole 4, while there was a difference of 9·3° between the mean temperatures recorded in moribund *Campylopus* at fumaroles 9 and 10.

The present data do not, however, account for the relative abundance of *Campylopus* spp., *Pohlia nutans* and *Cryptochila grandiflora* in the second vegetation zone around different vents. For example, fumaroles 9 and 10, where *Campylopus* predominated, were respectively among the coolest and warmest fumaroles studied, while of the fumaroles where *P. nutans* was particularly abundant, fumarole 2 was relatively warm but fumaroles 6 and 7 were much cooler (Table VI). The mean temperature recorded among *Cryptochila* was always between 11·2° and 14·9° C, and in the three cases where records were obtained for both erect *P. nutans* and *C. grandiflora* in zone 2 of the same fumarole, higher means were obtained for the latter species. It may thus be significant that the hepatic tended to occupy a more central position than the tall form of *P. nutans* (Fig. 2; Table V), while outside the South Sandwich Islands *P. nutans* extends farther south in Antarctic regions than does *C. grandiflora*. At fumarole 3, it was noted that *C. grandiflora* was bright green when growing near the vents but gradually tended to a reddish brown colour towards the outer margin of zone 2. This difference may also be related to temperature, since the green plants apparently experienced warmer conditions, the means of five readings among green plants around two series of vents being 18·9° and 12·1° C, while corresponding data for brown plants were 12·1° and 10·7° C.

The temperature measurements made on the scoria slopes on Breakbones Plateau, but outside the main areas of fumarole vegetation, are summarized in Table VII. Conditions here were clearly cooler than immediately surrounding the vents; thus temperatures in a short *Pohlia nutans*–*Lepraria* community approximately 25 m. south of fumarole 5 ranged from only 0·5° to 1·5° C, although readings up to 6° C were

TABLE VI

TEMPERATURES (°C) IN VEGETATION AROUND FUMAROLES ON CANDLEMAS ISLAND

Zone	Species	Fumarole number																										
		1			2			3			4			5			6			7			9			10		
		Max.	Mean	Min.	Max.	Mean	Min.	Max.	Mean	Min.	Max.	Mean	Min.	Max.	Mean	Min.	Max.	Mean	Min.	Max.	Mean	Min.	Max.	Mean	Min.	Max.	Mean	Min.
	Air temperature in vents							23·0	21·4	20·0	14·5	13·4	12·2											20·0*				
1	*Pohlia nutans* (slender)				23·5	21·9	20·0				19·0	15·7	13·0	17·0	15·6	13·5								9·5*				
	Algae														18·0*											29·5	21·3‡	11·0
	Campylopus sp. (moribund)																									20·0	17·8	15·0
	Dicranaceae	37·0	55·0* 28·0§	21·0																								
2	*Cryptochila grandiflora*				17·5	14·1	7·5	20·5	13·5	8·0	13·5	11·2	8·0	16·0	14·9	14·5				8·5	5·5‡	2·5						
	Pohlia nutans (tall)				17·5	12·0	9·0				6·0	5·2	4·0	17·0	12·8	10·0	12·5	9·7	7·5				2·5	2·5	2·5			
	Pohlia nutans with *Marchantia berteroana*																											
	Campylopus sp.																									19·5	12·8	9·0
	Campylopus sp. (moribund)																						8·5	7·0†	5·5	19·5	16·3	2·0
	Polytrichum alpinum (moribund)																							7·5*				
	Cryptochila grandiflora (moribund)																							5·0*				
3	*Polytrichum alpinum*				8·0	6·9	5·0	9·5	7·8	6·0	5·0	3·9	2·5	14·5	11·6	9·5	6·0	5·3	4·5									
4	*Pohlia nutans* (short with lichens)				9·5	8·1	6·5							8·5	7·9	7·5												

*Single reading.
†Mean based on two readings.
‡Mean based on three readings.
§Mean based on five readings at a depth of 0·5 cm.
Measurements were made at a depth of 2·5 cm. in the vegetation and means are based on 5–20 readings, except where indicated.
Temperatures of gaseous emissions in vent orifices indicated where air temperatures measured.

TABLE VII

TEMPERATURES (°C) IN VEGETATION AWAY FROM FUMAROLES ON CANDLEMAS ISLAND

Site		*Maximum*	*Mean*	*Minimum*
Bare ash 7 m. south of edge of vegetation at fumarole 5		6·0	5·2	4·0
Short *Pohlia nutans* with *Lepraria* sp.	25 m. south of fumarole 5	1·5	1·4	0·5
Short *Polytrichum alpinum*		6·0	3·4	1·0
Bare ash		3·5	1·8	0·5
Short *Pohlia nutans* with *Lepraria* sp.	75 m. west of fumarole 5	4·5	2·8	1·0
Short *Polytrichum alpinum*		5·0	2·9	2·0
Bare ash		5·0	2·9	1·0
Short *Polytrichum alpinum* midway between fumaroles 3 and 5		5·0	3·7*	3·0
Deschampsia antarctica 1·5 m. from fumarole 3		7·0	5·9	5·0
Deschampsia antarctica 15 m. from fumarole 3		6·5	6·0	5·5

*Mean based on ten readings.
Readings were made at a depth of 2·5 cm. and means are based on five readings except where indicated.

obtained among *Polytrichum alpinum* in the same area. The temperatures recorded both in bare ash and in the sparse vegetation were in general a few degrees higher than air temperatures, even in cloudy weather, and in particular it may be noted that the scoria beneath turves of *Deschampsia antarctica* near fumarole 3 was at approximately 6° C at a time when air temperature was only 2° C.

It is difficult in this case to distinguish between the effects of volcanic heat and absorbed solar radiation. On Deception Island, South Shetland Islands, temperatures a few degrees higher than air temperature have been recorded during cloudy weather in volcanic ash overlying a glacier where there could not have been any volcanic influence (Longton, 1966). However, cooler conditions were recorded at distances of 25 and 75 m. from fumarole 5 than at sites occupied by *Deschampsia antarctica* at distances of 1·5 and 15 m. from fumarole 3 (Table VII). The results thus raise the possibility that volcanic warmth extended for at least 15 m. from the vents at fumarole 3 and affected the ground where the grass was growing.

2. *Temperature fluctuations*

Periodic fluctuations in intensity are a normal feature of many volcanic regions, and there is evidence of a similar situation on Candlemas Island. Thus, geysers active on the north-west coast of the island in 1962 (Holdgate, 1963) were inactive when examined several times in 1964. Moreover, the presence of distinct vents in several areas of heated ground from which no steam was rising in 1964 suggests that activity may have been greater in the past.

To investigate short-term changes in volcanic heating, bent-stem mercury thermometers were inserted at a depth of 2·5 cm. in the vegetation at five sites at varying distances from a vent at fumarole 5, as indicated in Fig. 4, and they were read at intervals between 7 and 10 March. The weather was continuously cloudy, with daily maximum air temperatures between 0° and 3° C and slight frost at night. The results are presented in Fig. 7.

These data indicate a general temperature decrease through about 4° during the 24 hr. prior to mid-day on 8 March and, as this change was equally marked both at site 5, about 50 m. away from the fumarole, and near the vents, it seems probable that it resulted from variation in the general climatic conditions. Similarly, all five sites agreed in showing a rise in temperature through several degrees during the afternoon and evening of 10 March. Other data, however, indicate greater fluctuations near the vents than were recorded at the more distant sites, suggesting changes in the intensity of fumarolic activity. The greatest variation was recorded 1 m. from the vent (site 2), where the temperature rose from 9·5° to 18° C between

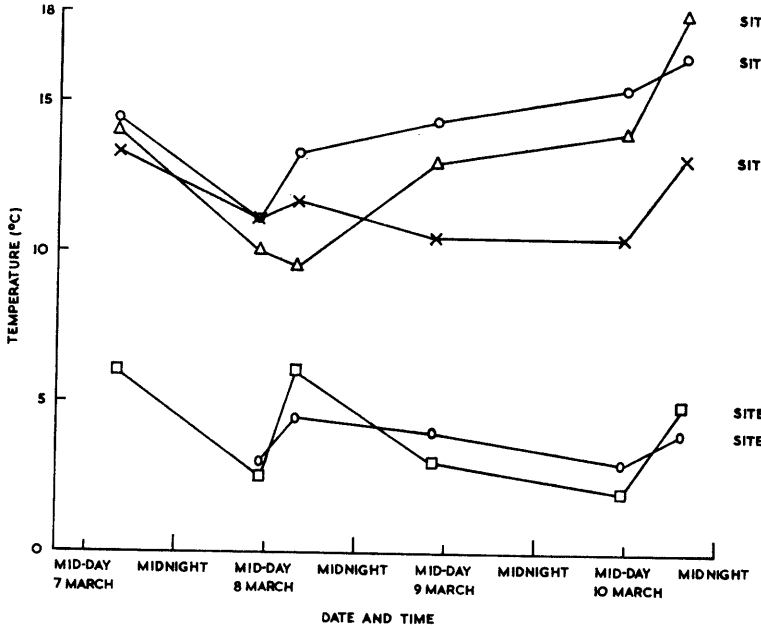

FIGURE 7

Temperature fluctuations during a 4 day period at a depth of 2·5 cm. in vegetation at five sites near fumarole 5 on Candlemas Island. Site 1 was in tall *Pohlia nutans* 1 cm. from a vent; sites 2–5 were in *Polytrichum alpinum* at distances of 1·0 m. (2), 1·5 m. (3), 20 m. (4) and 50 m. (5) from the nearest vent. The positions of sites 1–3 are indicated in Fig. 4.

8 and 10 March. The patterns of fluctuations were by no means identical at the three inner sites, and indeed, on 10 March the temperature 1 cm. from the vent was lower than that recorded 1 m. away. This indicates slight changes in the pattern of activity at the fumarole, although, as previously noted, the extensive series of spot readings at several fumaroles confirmed that a gradually decreasing temperature gradient outwards from the vents is normally maintained.

E. EVIDENCE OF PLANT SUCCESSION FROM PEAT PROFILES

Decay of plant remains is slow under the climatic conditions prevailing on Candlemas Island, at least away from the fumaroles, and thus peat deposits up to 20 cm. deep were present in some places beneath the living vegetation. The peat profiles below different types of community were investigated for evidence of plant succession and the possibility of seral relationships between the communities.

The deepest, most complex organic debris occurred below the tall turf community dominated by *Polytrichum alpinum*. 24 samples collected from two sites were examined, and seven of the profiles are illustrated in Figs. 8 and 9a and b, and Plate I, which show that several species formed discrete layers in the peat. Towards the base of the profile the remains were commonly fragmented and impregnated with ash, but they could normally be identified microscopically, right down to the substratum.

Polytrichum alpinum was the most abundant living species in the community and normally formed the greater part of the peat. However, *Ceratodon* was the species most frequently recorded at the base of the profile (Fig. 8a–c). Its remains normally occurred as small cushions, from which, in several cases, stems of *Polytrichum alpinum* could be seen radiating to give rise to typical *Polytrichum* hummocks (Fig. 8b). In other places, especially where *P. alpinum* had colonized the ash directly, or following an initial growth of *Pohlia nutans*, the *Polytrichum* stems were erect and parallel (Fig. 9a and b).

Ceratodon was rarely abundant in the upper layers of peat, though it was once recorded in a shallow turf over the surface of *P. alpinum*. *Pohlia nutans*, however, was widely distributed throughout the profiles, occurring at the base (Figs. 8d and 9d), as scattered stems among *Polytrichum* (Figs. 8b, d and 9b), and as pure turves on the surface (Fig. 8a). *Brachythecium* and *Drepanocladus* cf. *uncinatus* were recorded in small mats both on bare scoria and on the surface of other mosses (Fig. 8a and c), but they seldom formed pure layers beneath other species. The pleurocarpous mosses lacked abundant rhizoids such as those stabilizing

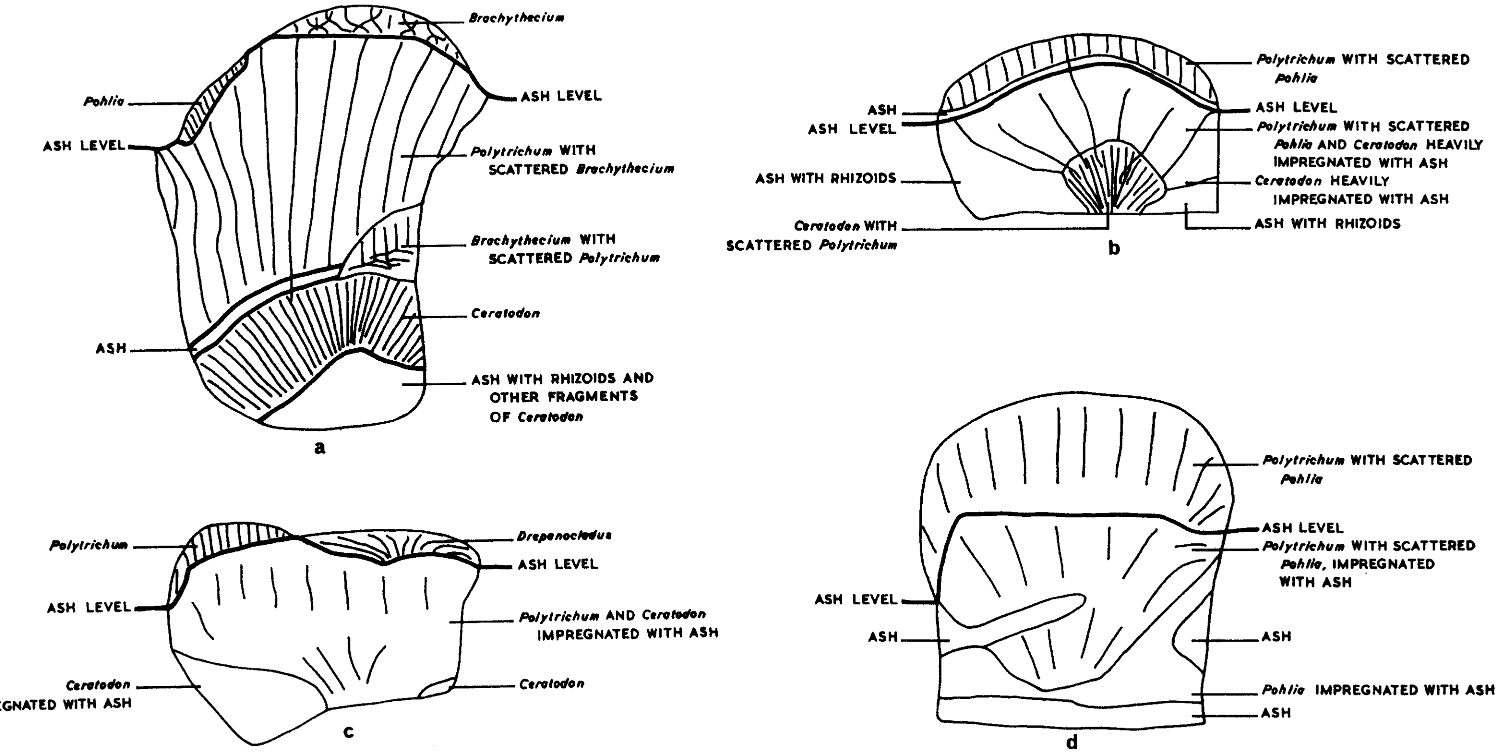

FIGURE 8

Diagrams of peat profiles from a stand of the *Polytrichum alpinum* sociation on Candlemas Island. See Plate I.

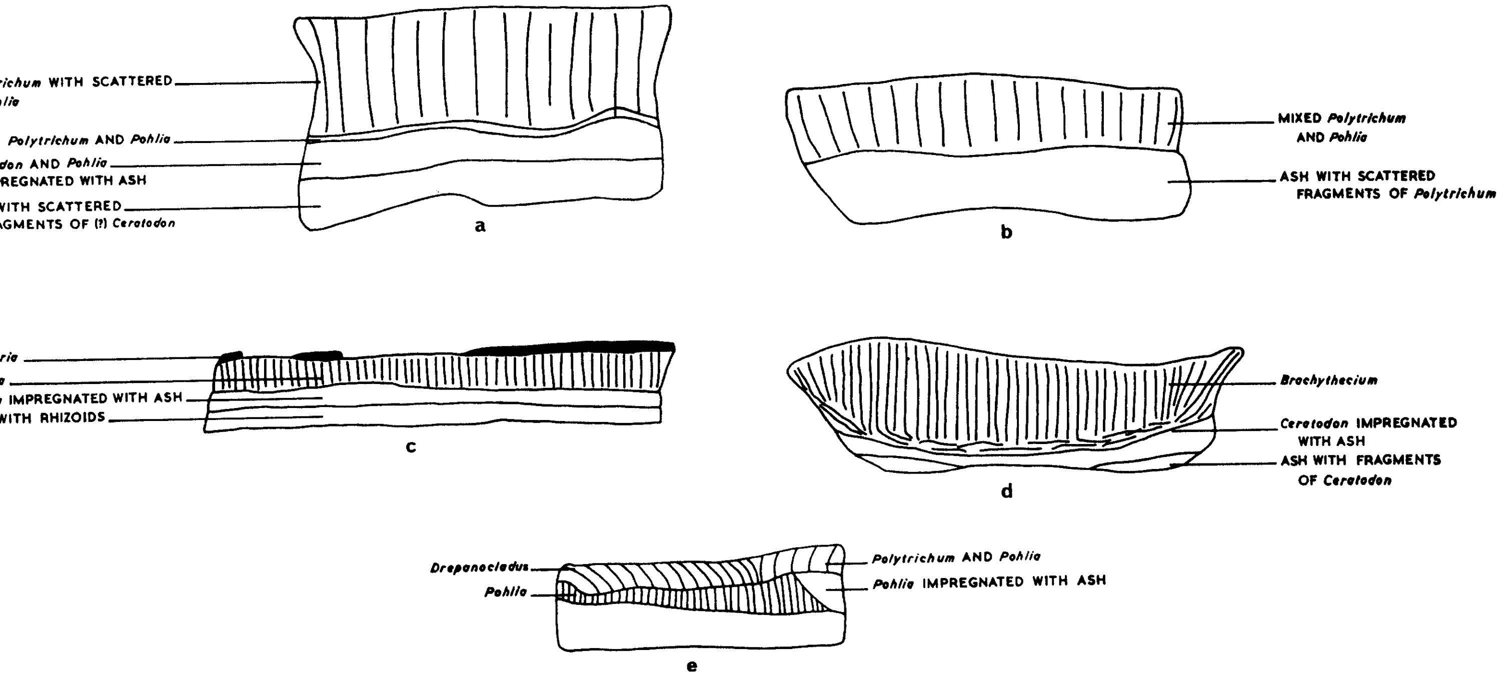

FIGURE 9

Diagrams of peat profiles from stands of the *Polytrichum alpinum* (a and b), the *Pohlia nutans–Lepraria* sp. (c), the *Brachythecium* sp. (d) and the *Drepanocladus* cf. *uncinatus* (e) sociations on Candlemas Island.

the ground beneath the acrocarps and they adhered only loosely to the substratum. Their carpets may thus be too unstable to support a growth of other mosses.

Several profiles had a thin band of more or less pure ash between layers of moss peat (Fig. 8a and b), and in the field it was common to find a similar layer of compact, finely divided ash on the surface of moribund areas of moss. It is considered probable that these deposits resulted from local deposition of wind-blown ash, and that they may frequently be colonized by upward growth of plants from below.

Analysis of the peat profiles thus indicates that, while all the mosses commonly occurring in the *Polytrichum alpinum* tall turf community can at times act as colonizers of bare ground, *Ceratodon* is the most important species in this role. This conclusion was supported by field observations which suggested that a cycle of erosion and re-colonization was in progress. Erosion of the peat and living vegetation was clearly widespread, especially where the mosses were moribund or lichen-encrusted; pieces of peat were commonly seen on the surface of the vegetation, and areas of ash were left bare and surrounded by shallow, recently exposed peat profiles. These areas of exposed ground were frequently being colonized by cushions of *Ceratodon*, in which scattered stems of *Polytrichum* had commonly become established. Wind, combined with instability of the substratum, seemed the most probable cause of erosion, which might be more extensive except for a build-up of the ground level around much of the vegetation (Fig. 8a and b).

Clearly stratified peats were more or less restricted to the *Polytrichum alpinum* tall turf community, the profiles under the other vegetation types being more simple and seldom exceeding a depth of 5 cm. Seven specimens of peat from the *Pohlia–Lepraria* community were examined and each was found to consist of a turf of *Pohlia nutans* extending to the scoria below, and heavily encrusted by lichens above (Fig. 9c). Occasional scattered stems of *Pohlia nutans* and *Ceratodon* occurred on the surface of the lichens, but *Ceratodon* was recorded only as widely scattered fragments in the peat below the living vegetation. In specimens collected from the circular stands of *Polytrichum* spp., which occurred within the *Pohlia–Lepraria* community, the *Polytrichum* stems were embedded in *Pohlia* peat. By contrast, no *Pohlia nutans*, either living or as peat, was recorded in a single specimen from the *Ceratodon–Lepraria* community. The material comprised cushions of *Ceratodon*, colonized by lichens, with the *Ceratodon* stems extending down to the substratum.

Peat profiles below the moss-carpet communities were also relatively simple. In two samples from the *Brachythecium* community the dominant moss formed a carpet of tall erect shoots arising from a narrow layer of prostrate stems below. In places the prostrate stems lay directly on the substratum, but there was normally a thin layer of *Ceratodon* remains between the ground and the *Brachythecium* (Fig. 9d). The *Ceratodon* was partially fragmented, many of the stems were prostrate, and any original cushion structure had disintegrated. Observations on peat profiles beneath the *Drepanocladus* cf. *uncinatus* community were also restricted to two samples. In the first, an extensive carpet of *Drepanocladus* extended downwards to the substratum, while in the second the *Drepanocladus* covered a thin band of *Pohlia nutans* peat with a third lower layer comprising ash mixed with *Pohlia* fragments. Part of a small turf of *Polytrichum* and *Pohlia* can be seen to the side of the specimen (Fig. 9e).

The field observations, combined with an analysis of peat profiles, thus suggest that cushions of *Ceratodon* may be important in the early development of the *Polytrichum alpinum* tall turf community, and possibly of *Brachythecium* carpets. The scattered cushions of *Ceratodon* colonizing the steep slopes below the north-eastern corner of the ice cap (p. 22) may thus be a forerunner of one of these communities, both of which have developed in a similar habitat elsewhere around the ice cap.

It is possible that the same applies to the small circular stands of the *Ceratodon–Lepraria* community on the summits of ash knolls near the north-east corner of the ice cap. Although this community was clearly well established, as indicated by the more or less closed cover and by the abundance of lichens on the surfaces of the *Ceratodon* cushions, other bryophytes contributed little to the vegetation, which thus showed no evidence that it is developing towards a different type of community.

Pohlia nutans clearly colonized the volcanic deposits directly to give rise to many of the thin *Pohlia–Lepraria* crusts, but there is little evidence that this type of vegetation represents a stage in the development of other communities. The local frequency of short turves of *Polytrichum alpinum* in the *Pohlia–Lepraria* vegetation at first suggested development towards the *Polytrichum–Pohlia* tall turf community. This is considered improbable, however, as *Ceratodon* remains were commonly abundant beneath the *Polytrichum*-dominated vegetation but were rare or absent beneath the *Pohlia–Lepraria* crust. The present data also suggest that *Drepanocladus* cf. *uncinatus* can colonize volcanic ash directly and, although it may in places be preceded by *Pohlia nutans*, it is considered unlikely that the moist-ground moss carpets have normally developed through colonization of *Pohlia–Lepraria* communities similar to those now occurring on the dry ash plains. It may also be noted that the pure stands of *Prasiola* cf. *crispa* also occurred directly on the ash substratum. Thus all the principal types of cryptogamic community on the scoria plains and slopes in unheated parts of Candlemas Island appear to have developed independently of each other.

The position regarding the stands of *Deschampsia antarctica* is less clear. Scattered individual grass turves were recorded on otherwise bare scoria, but the continuous stands were normally associated with short turves of *Pohlia nutans* and less frequent *Polytrichum alpinum*. It was not determined, therefore, whether bryophyte cover preceded the development of the few stands of vegetation dominated by vascular plants.

V. BELLINGSHAUSEN ISLAND

A. General Observations

Bellingshausen Island is smaller and lower than Candlemas Island (Table I) and is almost devoid of permanent snow and ice. Much of its surface is covered by scoria, which is strikingly furrowed on the western flanks of the central cone. Lava cliffs occur about the coasts and within the crater, and basalt lava flows only partly covered in scoria are present on the southern lowlands, where there are large penguin colonies.

As on Candlemas Island, the vegetation is sparse on unheated ground, especially over porous unstable scoria and in areas with marked sea-bird influence. However, rich bryophyte vegetation surrounds fumaroles and fissures within the southern lip of the main crater, and on the outer southern flanks. Around many of these fumaroles, several intergrading, concentrically zoned plant communities were recognized. The general distribution of vegetation and of the principal fumaroles is shown in Fig. 10.

B. Fumarole Vegetation

1. *Fumaroles on southern flanks of the cone*

The fumaroles studied in greatest detail were aligned on an evident fissure running at an altitude of *c.* 90 m. along a gently inclined south-facing terrace traversing the southern flanks of the cone. The vegetation surrounding two vents towards the western end of the fissure (1 and 2 in Fig. 10) is summarized in Tables VIII and IX, and in Fig. 11. At fumarole 1 the vent was a round pit about 1 m. deep and 3 m. wide, with smoothly sloping sides and a generally symmetrical, funnel-shaped form. Fumarole 2 had a shallower pit, only 50–60 cm. deep and with very gently sloping sides. Steam emission was also less at fumarole 2 than at fumarole 1, but the zonation of the vegetation was similar.

Plant cover in the innermost zone was generally sparse, the moist gravel around the vents supporting an open community of algae and small acrocarpous mosses, in which a dicranoid species was prominent in places. Outwards, this rapidly gave way to taller closed turves of *Campylopus spiralis* with frequent mats of *Marchantia berteroana* and other bryophyte associates. The *Campylopus* zone was in turn surrounded by extensive carpets and turves of *Cryptochila grandiflora*, which predominated in zones 3–5. The leafy hepatic varied in luxuriance and colour. In zone 3 it formed bright orange closed stands, with *Marchantia berteroana* and *Campylopus spiralis* still prominent, while in zone 5 it occurred as scattered dark reddish brown shoots forming an open community with abundant *Usnea antarctica*. *Racomitrium crispulum* and other mosses were often abundant in zone 4, and small basidiomycete fruiting bodies were scattered throughout much of the hepatic belt. Finally, *Cryptochila grandiflora* died out approximately 6 m. from the vents, leaving open vegetation comprising *Usnea antarctica* and a variety of bryophytes.

Vegetation elsewhere on the terrace showed less distinct zonation, due to the large number of adjacent vents which complicated the environmental gradients. A shallow trough ran along the line of the main fissure between fumaroles 1 and 2, extending eastward along the terrace and, although it was not emitting steam, it was clearly warmer centrally than on the flanks. The central area supported a community dominated by *Marchantia berteroana*, *Brachythecium* sp. and *Psilopilum antarcticum*, with smaller quantities of *Cryptochila grandiflora* and other species. Laterally, *Cryptochila* was dominant, with scattered basidiomycetes and small areas of *Racomitrium crispulum*, *Polytrichum alpinum*, *P. alpestre* and *Psilopilum antarcticum*, while *Usnea antarctica* occurred on stones. The lateral zone thus resembled zones 3–5 around

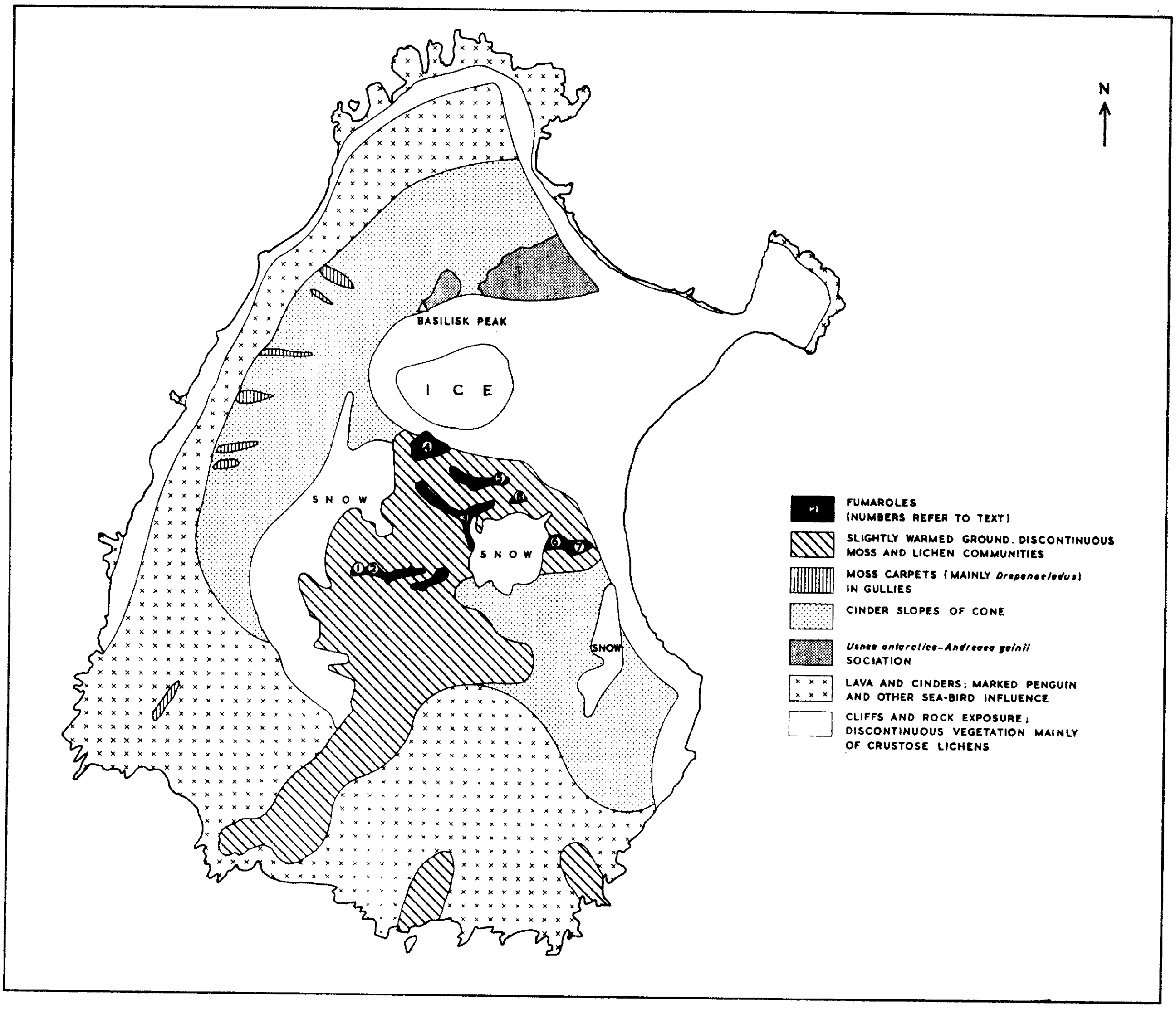

FIGURE 10

Sketch map of Bellingshausen Island showing the distribution of fumaroles and the principal stands of cool-ground vegetation.

the more distinct fumaroles (Tables VIII and IX), but the inner area differed from zones 1 and 2, for example, in the abundance of *Brachythecium*.

2. *Fumaroles on southern cliffs of the crater wall*

Comparable vegetation was developed around a large number of fumaroles occurring along a low cliff within the southern lip of the crater and on a prominent buttress in its south-western corner (4 on Fig. 10). Condensation of the copious steam rising from many minor vents made these areas generally very wet and extensive plant cover had developed. The close proximity of many vents complicated the vegetation patterns, which lacked the concentric series noted about single fumaroles. Zonation was evident in a few cases and fumarole 3, a typical example, was studied in some detail. It is evident from Table X that the inner zones of vegetation at fumarole 3 closely resembled those at fumaroles 1 and 2, but that a community dominated by *Brachythecium* sp. surrounded the *Cryptochila* carpet, thus restricting the open *Usnea antarctica* and mixed bryophyte vegetation to boulders breaking though the closed bryophyte cover. However, in some of these areas, such as the large buttress on the south-west flank of the crater, the outer

TABLE VIII

ZONATION OF VEGETATION AROUND FUMAROLE 1 ON BELLINGSHAUSEN ISLAND

Zone	*Approximate distance from vents*	*Dominant species*	*Notes*
1	0–30 cm.	Algae and a small dicranoid moss	Glistening areas of algae, together with abundant turves of a small dicranoid moss, scattered stems of *Bryum* sp. and taller turves of *Campylopus spiralis*
2	30–150 cm.	*Campylopus spiralis*	Turves of *Campylopus spiralis* dominant. *Cryptochila grandiflora* and *Marchantia berteroana* frequent. *Polytrichum alpinum* and *Pohlia nutans* recorded as associates
3	150–270 cm.	*Cryptochila grandiflora*	*Cryptochila grandiflora* increased in frequency to form a luxuriant, closed, bright orange stand. *Campylopus spiralis* and *Marchantia berteroana* abundant in central areas, dying out further from the vent, where *Psilopilum antarcticum* recorded as an associate. Basidiomycete fruiting bodies scattered throughout
4	270–390 cm.	*Cryptochila grandiflora* and mosses	*Cryptochila grandiflora* became drier and dark reddish brown in colour, being interspersed with large areas of *Racomitrium crispulum* and other mosses including *Drepanocladus* cf. *uncinatus* and *Pohlia nutans*. Basidiomycetes persisted
5	390–570 cm.	*Cryptochila grandiflora* and *Usnea antarctica*	*Cryptochila grandiflora* very dark brown and dry, forming an open community with *Usnea antarctica*. *Psilopilum antarcticum* frequent. *Polytrichum alpinum* and *Racomitrium crispulum* recorded as associates
6	>570 cm.	*Usnea antarctica*	Abundant *Usnea antarctica* on bare stones, with less common cushions and turves of *Dicranoweisia* sp., *Pohlia nutans* and *Polytrichum* as well as small mats of *Lophocolea secundifolia* and *Cephaloziella* sp.

zones contained a greater variety of crustose lichens and macro-lichens than was seen elsewhere on the island.

3. *Fumaroles within the eastern rim of the crater*

The hottest fumaroles on Bellingshausen Island occurred within the rim of the volcanic crater. Much of the ground on the south-eastern part of the crater was generally barren, but vegetation was developed around a series of especially vigorous fumaroles near the rim, on the eastern side (Fig. 10). The steaming vent of one example, fumarole 5 in Fig. 10, was surrounded by a narrow belt of ground completely devoid of vegetation, which extended approximately 15 cm. from the vents. This fumarole differed further from those previously described in the absence of a community dominated by *Cryptochila grandiflora*. Only two vegetated zones were present, the inner extending from *c*. 15 to 30 cm. from the vents, having open vegetation of *Marchantia berteroana* and small acrocarpous mosses, while the outer, which extended from *c*. 30 to 90 cm., supported an almost closed carpet of *Brachythecium* sp. with occasional *Marchantia*.

4. *Sulphur-emitting fumaroles*

Additional, vigorous fumaroles were studied in a minor depression high up on the outer south-eastern slopes of the cone (fumaroles 6 and 7 in Fig. 10), and in the south-eastern rim of the crater (fumarole 8). In these areas the vents were surrounded by sublimed crusts of sulphur and other minerals, while even outside the areas of active sulphur deposition there was a belt of hot barren rock devoid of macroscopic plants. Active sulphur deposition was not seen at vegetated fumaroles elsewhere on the island.

Fumarole 6 may be regarded as typical of those on the south-eastern slopes of the cone, and it can be seen from Table XI and Fig. 12 that the inner vegetated zone supported a community of algae, *Marchantia*

TABLE IX

ZONATION OF VEGETATION AROUND FUMAROLE 2 ON BELLINGSHAUSEN ISLAND

Zone	*Approximate distance from vents*	*Dominant species*	*Notes*
1	0–? cm.	Algae and dicranoid moss	Open vegetation of a small dicranoid moss and algae surrounding a small area of wet, barren reddish gravel at the centre of the pit
2	?–90 cm.	*Campylopus spiralis*	*Campylopus spiralis* dominant. Considerable areas of *Cryptochila grandiflora* also recorded, with large mats of *Marchantia berteroana* covering the floor of the hollow in places
3	90–150 cm.	*Cryptochila grandiflora*	Closed, bright orange stand of *Cryptochila grandiflora*, with a wide variety of associated species including the mosses *Campylopus spiralis*, *Pohlia nutans*, *Polytrichum alpinum*, *Psilopilum antarcticum* and *Racomitrium crispulum*, as well as the hepatics *Cephaloziella varians* and *Clasmatocolea koeppensis*
4	150–330 cm.	*Cryptochila grandiflora* and mosses	*Cryptochila grandiflora* abundant but drier and darker in colour. *Polytrichum alpinum*, *Psilopilum antarcticum* and *Racomitrium crispulum* prominent in places
5	330–600 cm.	*Cryptochila grandiflora* and *Usnea antarctica*	Open vegetation comprising brown and meagre *Cryptochila grandiflora* with scattered turves of *Pohlia nutans*, *Polytrichum alpinum* and *Psilopilum antarcticum*. *Usnea antarctica* frequent on stones and gravel
6	>600 cm.	*Usnea antarctica*	Generally stony ground with sparse vegetation of *Usnea antarctica* and small stands of several unidentified mosses and liverworts

and acrocarpous mosses similar to that developed at other fumaroles. This was surrounded, however, by a dense carpet of *Drepanocladus* cf. *uncinatus*, which was not normally an abundant species on heated ground in other areas. The moss carpet gradually thinned out further from the vent and merged into a final open association of *Drepanocladus* cf. *uncinatus* and *Prasiola* cf. *crispa*. Similar vegetation was recorded at the fumaroles within the south-eastern rim of the crater. Fumarole 8 was of particular interest since a crust of sulphur had been deposited over the dead remains of the vegetation, providing direct evidence of a fluctuation in fumarolic activity.

5. *Fumaroles: summary*

It is clear, therefore, that on Bellingshausen Island, as on Candlemas Island, similar vegetation occurred in the innermost zones around most of the fumaroles, while the pattern in the outer zones was more variable. The innermost vegetation normally comprised algae together with a small dicranoid moss and other acrocarpous bryophytes with *Campylopus spiralis* and *Marchantia berteroana* becoming increasingly frequent further from the vents. These communities were surrounded by more luxuriant bryophyte vegetation dominated either by the hepatic *Cryptochila grandiflora* (e.g. fumaroles 1 and 2) or by the mosses *Drepanocladus* cf. *uncinatus* (fumarole 6) or *Brachythecium* sp. (fumarole 5). At fumarole 3, *Brachythecium* sp. predominated in the bryophyte carpet further from the vents, giving way to *Cryptochila grandiflora* more centrally. Areas dominated by the latter species supported as associates *Campylopus* spp., *Marchantia berteroana*, *Racomitrium crispulum*, *Psilopilum antarcticum*, *Polytrichum* spp., *Pohlia nutans*, dicranoid mosses and basidiomycetes.

In several places, the outer margins of the closed bryophyte carpets gradually merged into open vegetation more typical of unheated areas of the island. At fumaroles 1 and 2, for example, *Cryptochila* was gradually replaced by open vegetation dominated by *Usnea antarctica* and *Polytrichum alpinum*, while at fumarole 6 the closed *Drepanocladus* cf. *uncinatus* carpet merged into a more open *Drepanocladus–Prasiola* community characteristic of cool moist slopes with some biotic influence.

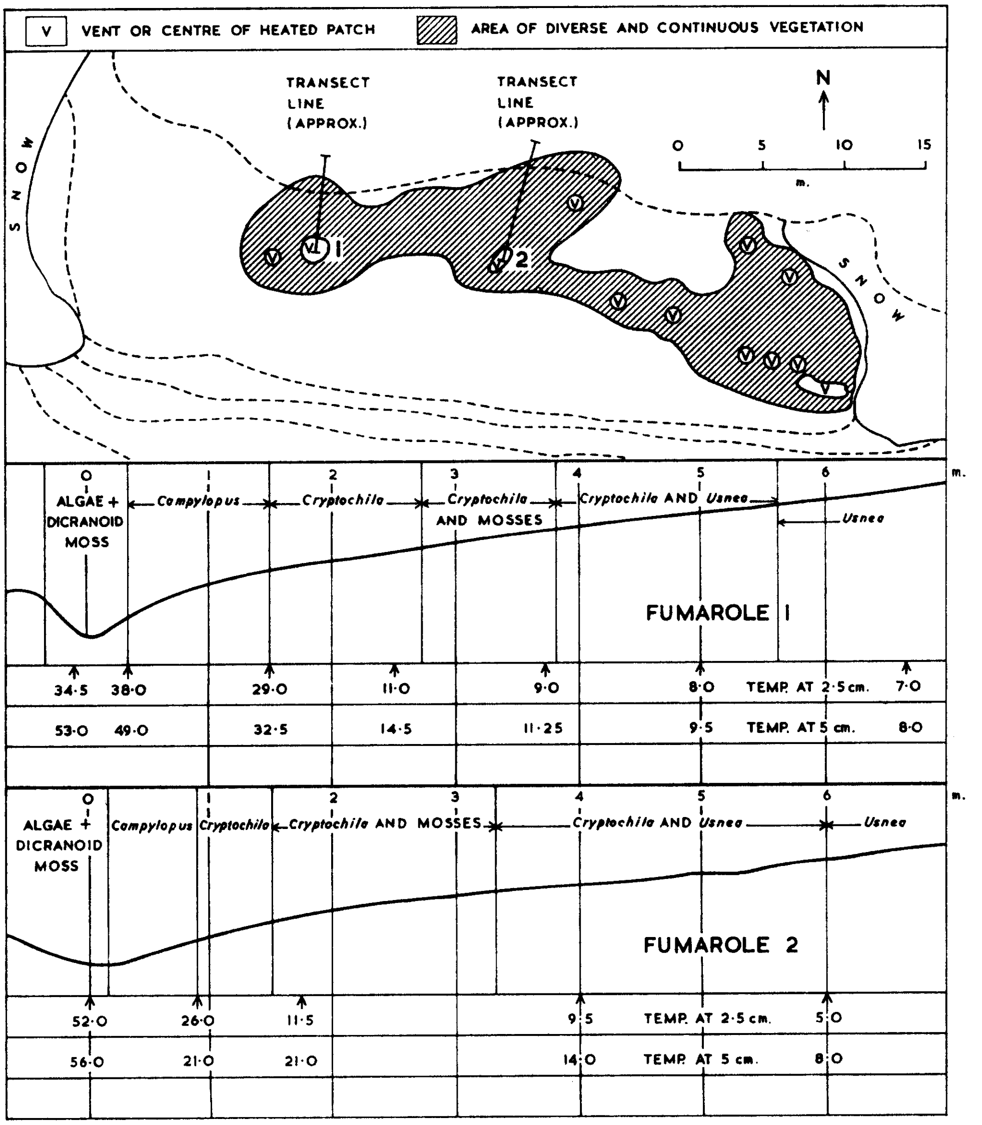

FIGURE 11

Sketch map of a fumarole series on the south flank of the cone, Bellingshausen Island, with transects across the vegetation at fumaroles 1 and 2 showing temperatures (°C) recorded as spot readings at different distances from the vents.

C. TEMPERATURES IN FUMAROLE VEGETATION

1. *Spot readings*

Temperatures in the vegetation around the fumaroles on Bellingshausen Island were recorded with a portable thermistor probe to compare conditions there with those on Candlemas Island. At fumaroles 1, 2 and 6, the readings were made at depths of 2·5 and 5·0 cm. at intervals along transects running outwards from the vents (Figs. 11 and 12), while less complete data were obtained at fumaroles 3 and 5. Most records were based on a single reading at each site. As on Candlemas Island, the measurements at 2·5 cm. depth demonstrated the presence of a decreasing temperature gradient outwards from the vents, while the readings at 5 cm. were higher but showed a similar pattern. Many fumaroles were hotter than most of those on Candlemas Island and greater quantities of steam were issuing from the vents. The high temperatures may account for the absence of vegetation in the zone immediately surrounding some vents on Bellingshausen Island, a situation not encountered on Candlemas Island, where the vents themselves invariably contained plants.

TABLE X

ZONATION OF VEGETATION AROUND FUMAROLE 3 ON BELLINGSHAUSEN ISLAND

Zone	*Approximate distance from vent*	*Dominant species*	*Notes*
1	0–15 cm.	Algae	Hot barren reddish ground surrounded by a fringe of slimy textured algae
2	15–45 cm.	*Campylopus spiralis* and *Marchantia berteroana*	A community comprising *Marchantia berteroana* and *Campylopus spiralis* with other smaller mosses as associates
3	45–135 cm.	*Cryptochila grandiflora*	A broad belt dominated by bright orange *Cryptochila grandiflora*, with small basidiomycete fruiting bodies and a wide range of bryophytes including *Brachythecium* sp., *Ceratodon* sp., *Drepanocladus* cf. *uncinatus*, *Psilopilum antarcticum*, *Racomitrium crispulum*, *Marchantia berteroana* and *Lophozia propagulifera*
4	135–300 cm.	*Cryptochila grandiflora*	A further broad belt of *Cryptochila grandiflora* but darker and reddish brown in colour. The basidiomycetes died out but *Brachythecium* sp. became more abundant, especially in areas of water seepage
5	>300 cm.	*Brachythecium* sp. in low areas, *Usnea antarctica* and *Andreaea gainii* var. *parallela* on rocks	Abundant carpets of *Brachythecium* sp. in a wet area of broken rock. Stones breaking through the carpet supported a different community dominated by *Usnea antarctica* and large cushions of *Andreaea gainii* var. *parallela. Clasmatocolea koeppensis* and *Dicranoweisia* sp. were among the associated species

TABLE XI

ZONATION OF VEGETATION SURROUNDING FUMAROLE 6 ON BELLINGSHAUSEN ISLAND

Zone	*Approximate distance from vent*	*Dominant species*	*Notes*
1	0–75 cm.	—	Hot barren ground with white surface and no macroscopic plants
2	75–330 cm.	Algae and acrocarpous mosses	A sparse growth of algae, small acrocarpous mosses and more rarely *Marchantia berteroana*, the cover gradually increasing with distance from the vent. The mosses included a small dicranoid species, *Pohlia nutans* and species of *Bryum* and *Ceratodon*
3	330–450 cm.	*Drepanocladus* cf. *uncinatus*	Zone 2 gave way abruptly to a carpet of *Drepanocladus* cf. *uncinatus*, with *Usnea antarctica* on stones and other mosses as associates. Cover was high, approaching 90 per cent in places
4	>450 cm.	*Drepanocladus* cf. *uncinatus* and *Prasiola* cf. *crispa*	The *Drepanocladus* carpet thinned out down the outer slopes of the cone. *Prasiola* cf. *crispa* became increasingly abundant and *Usnea antarctica* persisted on the stones

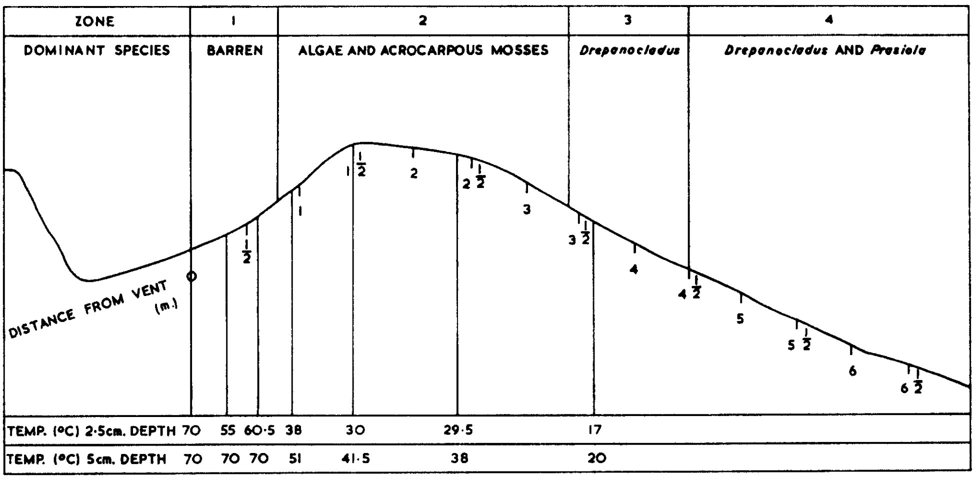

FIGURE 12

Transect across the vegetation at fumarole 6 on Bellingshausen Island, showing temperatures (°C) recorded as spot readings at different distances from the vents.

Records from the transect at fumarole 6 indicated that the innermost open vegetation of algae and acrocarpous mosses began where the temperature at 2·5 cm. was between 38° and 60·5° C and that at 5 cm. was between 51° and 70° C (Fig. 12). Where vegetation had been killed and was encrusted with sulphur, temperatures at 2·5 cm. exceeded 70° C. Comparable conditions were recorded at the inner margin of the vegetation at some other fumaroles, the highest temperature of 61° C being encountered at a depth of 2·5 cm. at fumarole 5. Observations at four sites along the inner margin of plant growth around another fumarole adjoining fumarole 6, in contrast, gave lower values of 30°, 27°, 21·5° and 15° C at 2·5 cm. and 49·5°, 38°, 31° and 20° C at 5 cm. depth.

Temperatures recorded under the closed bryophyte communities farther from the vents also varied, although invariably declining outwards. At fumarole 6, the ground 2·5 cm. below the vegetation at the inner margin of the *Brachythecium* carpet was at 39° C, and 38° C was recorded in the middle of this zone 5·0 cm. from the vent. Temperatures at 2·5 cm. under *Cryptochila grandiflora* vegetation were generally comparable with those under similar communities on Candlemas Island, ranging from 8° C at fumarole 1 (Fig. 11) to 25° C at fumarole 3. At fumarole 6, a temperature of 17° C was encountered 2·5 cm. below a *Drepanocladus uncinatus* carpet. The outer *Usnea–Polytrichum* and *Drepanocladus–Prasiola* communities extended from obviously warmed ground around the fumaroles to areas that were frozen in March 1964.

2. *Fluctuations in fumarolic activity*

It has been reported that the vegetation surrounding fumarole 8 was covered with a crust of sublimed sulphur, indicating that the intensity of the fumarole had increased during the period since the vegetation developed. This conclusion was supported by a general observation that more steam was rising from this and other fumaroles (6 and 7) in the south-eastern corner of the crater in 1964 than in 1962. Conversely, the fumaroles on the lava terrace (fumaroles 1 and 2), those on the prominent fissure traversing the inner southern slopes of the crater, and those on the buttress on the west wall of the crater (fumarole 4) all appeared to be steaming more vigorously in 1962. Changes of this kind may help to explain the variable temperatures recorded at the inner limits of plant growth. It must be borne in mind, however, that the visibility of steam emerging from the vents is influenced by such factors as air temperature and the amount of percolating melt water in the soil, and is thus not a fully reliable guide to fumarolic activity.

Fluctuations in temperature around fumarole 1 were tested over a 3 day period by bent-stem thermometers inserted at a depth of 5 cm. at points 165, 330 and 630 cm. from the vent. The positions of the thermometers are indicated in Fig. 11, and it can be seen from the data in Table XII that only slight fluctuations in temperature were recorded.

Air temperature fell during the period of observation, a cold spell commencing overnight on 8–9 March, with a fresh north-west wind and light snowfall. Rime formed on stones and *Usnea* branches to within 5 m.

TABLE XII

FLUCTUATIONS IN TEMPERATURE NEAR FUMAROLE 1 ON BELLINGSHAUSEN ISLAND

	Date 8 March	 9 March	 10 March
Thermometer 1 (165 cm. from vent)	25	24·5	21·4
Thermometer 2 (330 cm. from vent)	15·5	14·75	13·3
Thermometer 3 (630 cm. from vent)	11·5	8·3	8·3

Temperatures were recorded in °C, 5 cm. below the surface of the vegetation.

of the vent, and snow lay within approximately 8 m. of the centre. Generally cold conditions persisted throughout 9 and 10 March. Melt water probably has an appreciable influence on soil temperature in the upper soil layers in the fumarolic areas, and the slight fall in the temperature recorded by the two inner thermometers on 10 March may have resulted from this rather than from fluctuation in the intensity of volcanic heating from below.

D. VEGETATION OF UNHEATED GROUND

A variety of plant communities was developed on unheated ground on Bellingshausen Island but, in contrast to the fumaroles, cover was normally low and extensive tracts of barren scoria, ash and lava separated the vegetated areas. Plant cover was probably restricted to under 5 per cent of the exposed rock and soil surfaces. The communities were both poor in species and restricted in distribution. In relatively favourable areas, crustose and fruticose lichens, and turf, mat and carpet bryophyte forms occurred side by side in mosaics related to the irregularity of the ground, and probably to variations in water regime. The assignment of these fragmented vegetation types to sub-formations must therefore be regarded as tentative.

1. *Fruticose and foliose lichen sub-formation*

A mosaic of bryophyte and lichen communities occurred locally on slopes of scoria and ash on the southern slopes of the cone. *Usnea antarctica* was abundant on stones and gave up to 30 per cent cover, while crustose lichens, including species of *Lecidia* and *Lecanora*, occurred in rocky areas. Patches of *Polytrichum alpinum* turf with up to 20 per cent cover were the main bryophyte component of the mosaic.

A second mixed bryophyte and lichen community was recorded on loose stones and outcrops of lava on the upper northern slopes of the cone, north-east from Basilisk Peak. Here, *Andreaea gainii* was the dominant bryophyte, associated with *Usnea antarctica*. Crustose lichens and less frequently *Drepanocladus* cf. *uncinatus*, *Tortula* sp. and *Ceratodon* sp. were also recorded.

The slopes of the cone falling from Basilisk Peak, northward and westward to the cliffs between Hardy Peninsula and North Point, contain extensive penguin colonies, and a sparse growth of crustose lichens with scattered *Prasiola* cf. *crispa* was the principal vegetation type.

2. *Tall moss-turf and cushion sub-formation*

Polytrichum alpinum was widespread on the south flanks of Bellingshausen Island, associated with *Pohlia nutans* and *Psilopilum antarcticum* in places; it was often difficult to determine how far the ground was affected by volcanic heat, but in several areas patches of moss turf occurred adjacent to bryophyte carpets and mats containing species typical of fumaroles, e.g. *Cryptochila grandiflora*, *Marchantia berteroana*, *Clasmatocolea koeppensis*, as well as *Brachythecium* sp. and *Drepanocladus* cf. *uncinatus*.

3. *Bryophyte carpet and mat sub-formation*

As on Candlemas Island, moss-carpet communities were restricted to areas where melt water may affect the ground surface in summer. Away from fumaroles, *Drepanocladus* cf. *uncinatus* was the dominant species in such habitats, forming small carpets in hollows and drainage channels, for example, in gullies on the west slopes of Basilisk Peak and in hollows near the south coast. *Prasiola* was associated in the latter areas, in places receiving the run-off from penguin colonies.

4. *Alga sub-formation*

On ash and scoria around the periphery of the penguin colonies, the frequency of *Prasiola* cf. *crispa* increased, and it was often the sole component of the vegetation.

VI. LESKOV ISLAND

A. General Observations

Luxuriant stands of bryophyte vegetation, some over 20 m. in diameter, surrounded a series of active fumaroles along the northern part of the summit ridge of Leskov Island, especially on the eastern side of the ridge and on the upper slopes below its northern extremity. Away from the fumaroles, the richest vegetation was in stable areas among the scree- and scoria-covered northern and western slopes, among rock outcrops on these slopes, and along the summit ridge. Elsewhere, terrain subject to solifluction disturbances was comparatively barren. Much of the ground and vegetation was frozen at the time of the 3 hr. visit in March 1964. The cool-ground vegetation recorded was restricted to communities in the fruticose and foliose lichen sub-formation and the bryophyte carpet and mat sub-formation, but it is considered probable that the crustaceous lichen and the alga sub-formation may also be represented in unvisited parts of the island.

B. Fumarole Vegetation

Many of the fumaroles along the summit ridge were emitting steam in March 1964 and some smelled of sulphur. The ground surface was warm to the touch throughout the luxuriantly vegetated areas. Water squeezed from the bryophyte carpets had a pH of *c.* 5, as determined by colour-indicator paper.

Details of the concentric zonation and floristic composition of the plant communities surrounding a typical fumarole are given in Table XIII. The central zone, extending for up to 1 m. from the vents, comprised an open community of algae with *Marchantia berteroana*, the slender form of *Pohlia nutans* and small mats of other bryophytes. A second zone was dominated by carpets of the hepatics *Cryptochila grandiflora* and *Triandrophyllum subtrifidum*, and a third outer zone was formed principally by tall turves of *Polytrichum alpinum* and *P. alpestre*.

A comparable series of communities occurred at most of the other fumaroles. The width of the zones varied, however, due to differences in terrain and possibly in the vigour of the fumaroles, and the zonation was in places obscured where the vegetation surrounding several series of vents merged to give more complex patterns. There were also differences in the floristic composition of the communities. For example, at some of the fumaroles on the northern slopes of the island zone 1 was restricted to a central belt of algae and slender *Pohlia nutans* less than 10 cm. wide, while pure mats of *Marchantia berteroana* several metres in diameter were interspersed among the tall *Pohlia nutans* and leafy hepatics forming zone 2. *Ceratodon* sp. and *Dicranoweisia* sp. were recorded among the *Polytrichum* turves forming zone 3 of certain fumaroles, in addition to the species indicated in Table XIII.

C. Vegetation of Unheated Ground

1. *Fruticose and foliose lichen sub-formation*

The most widespread vegetation away from the fumaroles comprised communities in the fruticose and foliose lichen sub-formation. The bryophyte component of these communities was noticeably better developed on Leskov Island than on several of the other islands in the group. *Usnea antarctica* dominated

TABLE XIII

ZONATION OF THE VEGETATION AROUND A TYPICAL FUMAROLE ON THE SUMMIT RIDGE OF LESKOV ISLAND

Zone	*Approximate distance from vents*	*Dominant species*	*Notes*
1	0–1 m.	Algae, *Pohlia nutans*	Open bryophyte vegetation clothed the inside of a small group of vents and extended over an area up to 1 m. in diameter around them. The slender form of *Pohlia nutans* was the most abundant species, giving up to 50 per cent cover. *Marchantia berteroana* was locally abundant, while basidiomycetes, *Bartramia patens*, and several of the hepatics characteristic of zone 2 occurred as associates. The bryophytes were partially covered by a gelatinous growth of algae including species of *Calothrix*, *Mesotaenium*, *Phormidium* and *Ulothrix*, while the ground between the algae was in places clothed by a thin felt of blue-green algae including a species of *Lyngbya*
2	1–5 m.	*Cryptochila grandiflora*, *Triandrophyllum subtrifidum*, *Marchantia berteroana*	The second zone comprised a dense carpet of *Cryptochila grandiflora* and *Triandrophyllum subtrifidum* approximately 10 cm. deep. The plants were bright green in the inner part of the zone but gradually became reddish brown with increasing distance from the vents. *Marchantia berteroana* was also abundant, forming mats on the surface of the leafy hepatics. Associated species included basidiomycetes, tall *Pohlia nutans* and *Polytrichum alpinum*, and also the hepatics *Cephalozia badia*, *Cephaloziella varians*, *Lophocolea secundifolia* and *Pachyglossa dissitifolia*
3	5–8 m.	*Polytrichum alpinum*, *Polytrichum alpestre*	The dominant species formed tall turves. *Dicranoweisia grimmiaceae*, *Distichium capillaceum* and *Triandryophyllum subtrifidum* were recorded as associates, and *Usnea antarctica* occurred on stones projecting through the bryophyte cover. The following algae were also collected: *Navicula muticopsis*, *Pinnularia borealis*, *Prasiola* cf. *crispa* and *Prasiococcus calcarius*

a community that was widespread on cliffs and rock ledges. Crustose lichens, including *Lecidea* sp., and the cushion-forming mosses *Andreaea regularis*, *Dicranoweisia grimmiaceae* and *Racomitrium austrogeorgicum*, were common associates, except below bird-breeding ledges where *Prasiola* cf. *crispa* was conspicuous. *Andreaea regularis* was particularly abundant on rocks on the western slopes where it formed cushions up to 15 cm. wide. Small carpets and turves of *Drepanocladus* cf. *uncinatus*, *Pohlia nutans* and *Polytrichum alpinum* also occurred beneath the dominant *Usnea* where soil had accumulated on the rock ledges or among rocky knolls. A similar, though less rich community, was recorded on gently sloping ground along the summit ridge, with *Usnea antarctica* and crustose lichens on the larger stones, small mats of *Drepanocladus* cf. *uncinatus* in the hollows, and small cushions of *Dicranoweisia grimmiaceae* on the fine scree and sandy detritus. In some areas on the northern slopes it was noted that small cushions of *Dicranoweisia grimmiaceae*, *Polytrichum alpinum* and *Racomitrium austrogeorgicum* were partially buried by wind-blown scoria.

2. *Bryophyte carpet and mat sub-formation*

The bryophyte carpet and mat sub-formation was represented by carpets of *Drepanocladus* cf. *uncinatus* several metres wide, which occurred in hollows at around 80 m. altitude on the western scree slopes of the island. Crustose lichens and *Dicranoweisia* sp. were recorded as associates in open areas between the carpets. *Drepanocladus* was also abundant on parts of the summit ridge, especially in hollows on the gently sloping flanks, and on areas of scoria. Here, small carpets of the pleurocarp predominated in an open community with scattered lichens, *Dicranoweisia* sp. and *Prasiola* cf. *crispa*.

VII. VISOKOI ISLAND

A. FUMAROLE VEGETATION

During the 1964 survey detailed botanical studies were undertaken only at Finger Point on the north coast of the island. Here, a penguin colony occupied much of the lower ground by the shore, and behind this, moderately steep ash- and lava-covered slopes rose to high ice-clad cliffs. A ridge of scoria running down the slope contrasted strongly with the surrounding barren ground as it was covered by vegetation over an area *c.* 30 m. long and 5 m. wide. A sketch map of the vegetation is given in Fig. 13. There were two main areas of plant cover, and several small vents in the scoria, each up to 5 cm. in diameter, occurred in the centre of each stand. No steam was visible but the ground around the vents was distinctly warm. The two stands of more or less closed vegetation were separated by a strip of scoria supporting only a sparse growth of *Usnea antarctica*, accompanied by occasional *Cladonia* sp.

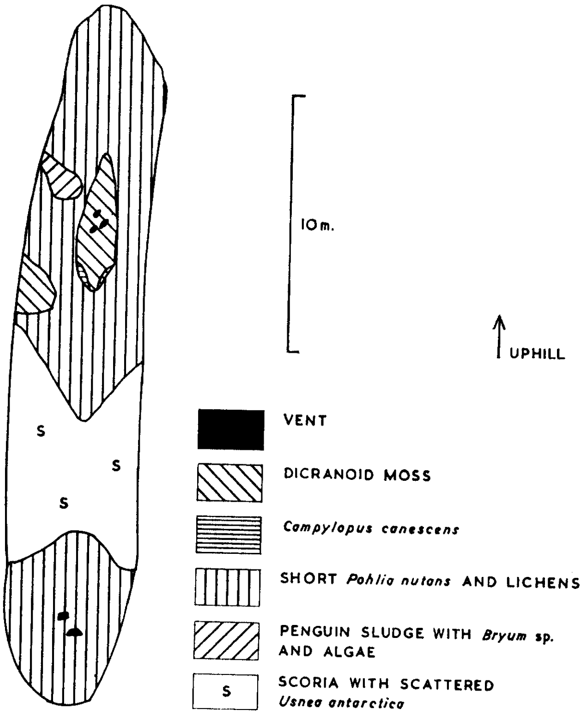

FIGURE 13

Sketch map of the vegetation at a fumarole on Visokoi Island.

Three zones were distinguished in the upper area of plant cover. The small vents had a similar flora to those on Candlemas Island comprising scattered mats of *Cephaloziella* sp., *Lophozia propagulifera*, *Riccardia georgiensis* and slender *Pohlia nutans*. The bryophytes were again partially enveloped in abundant algae, including *Navicula muticopsis*, *Pinnularia borealis*, *Prasiococcus calcarius*, *Prasiola* cf. *crispa* and *Stichococcus bacillaris*. Around the vents followed a second zone, up to 2 m. wide, which was dominated by short yellow turves of an unindentified dicranoid moss, and supported a variety of less frequent bryophytes including *Lophozia propagulifera*, *Campylopus canescens* and species of *Ceratodon* and *Dicranoweisia*. This was surrounded by a more extensive outer zone comprising a short turf of *Pohlia nutans* abundantly colonized by lichens, principally crustose species. *Lophozia propagulifera* and the mosses *Ceratodon* sp., *Dicranoweisia antarctica*, *D. grimmaceae* and *Drepanocladus* cf. *uncinatus* were among the associated bryophytes. The lichen crust was in general sterile and unidentifiable but *Stereocaulon antarcticum* and a species of *Cladonia* were collected from projecting scoria. In one small area the moss turf was covered by a thin layer of penguin sludge partially colonized by a species of *Bryum* and by several of the algae recorded in the vents, i.e. *Prasiola* cf. *crispa*, *Navicula muticopsis*, *Pinnularia borealis* and *Stichococcus bacillaris*. A similar *Pohlia nutans*-lichen community occurred extensively in the lower stand of vegetation, but here the Dicranaceae zone was not represented, and only slender *Pohlia nutans* and *Riccardia georgiensis* were recorded in the vents.

B. VEGETATION OF UNHEATED GROUND

Except around the fumaroles, the cliffs and scoria-covered slopes around Finger Point were in the main conspicuously barren. A sparse growth of *Usnea antarctica*, with scattered *Lecanora* sp. and other crustose lichens, *Prasiola* cf. *crispa* and *Ceratodon* sp., occurred locally on lava boulders, while *Ceratodon* was also recorded on the ash around the base of boulders. In addition, large green areas, probably of *Prasiola* cf. *crispa*, were seen high on the cliffs.

The available evidence suggests that other parts of Visokoi Island may have similar, generally sparse vegetation. Thus, above Irving Point ash slopes were reported as barren, while *Prasiola* cf. *crispa* was abundant on the cliffs (personal communication from R. W. Vaughan). The vegetation on the north-east coast was also reported to be very sparse (personal communication from J. Barr), although *Usnea antarctica*, a dicranoid moss, crustose lichens including a species of *Lecanora* and the five species of algae recorded in the fumarole vents were collected from a lava flow at altitudes of 200–350 m. Thus, away from fumaroles, only widely scattered open communities in the fruticose and foliose lichen and the alga sub-formation have so far been recorded on Visokoi Island.

VIII. SAUNDERS ISLAND

1. *General observations*

Saunders Island appeared conspicuously barren in 1962 and in 1964. Most of the vegetation, which was estimated as covering less than 1 per cent of the ice-free land surface, belonged to the crustaceous lichen sub-formation. The alga sub-formation and two small stands of vegetation in the short moss-turf and cushion sub-formation were also recorded. It was not possible to explore the areas of current volcanicity in the island's summit area.

2. *Crustaceous lichen sub-formation*

Open communities of crustaceous lichens were recorded locally. Rocks in the northern lava desert bore patches of *Lecidia* and a sterile crustose species, and *Lecania* sp. was collected on coastal rocks above Nattriss Point. Around Yellowstone Crags, *Acarospora* sp. was common on boulders, and *Lecania racovitzae*, *Lecanora* sp. and *Xanthoria* sp. also occurred. There were numerous penguins near Yellowstone Crags and in the northern desert area, and their wastes may have facilitated the development of the lichen vegetation.

3. *Short moss-turf and cushion sub-formation*

No active fumaroles were seen on the lowlands of Saunders Island but two points on the northern lava plain, where low vertical cliffs at the margins of basalt flows overhung small caverns, had the superficial aspect of fumaroles. These were located just north of Yellowstone Crags and a little south of Harper Point. *Pohlia nutans* was prominent in both these areas, forming areas of short turf each less than 1 m. across. In one, *Ceratodon* sp. and *Dicranoweisia grimmiaceae* were associates. At the second site *Grimmia* sp. and *Clasamatocolea koeppensis* were present. These were the only areas on Saunders Island where bryophytes were collected, and all the species recorded occur in fumarole vegetation on the more densely vegetated islands. However, *Ceratodon* sp., *Dicranoweisia grimmiaceae* and *Pohlia nutans* are also among the characteristic species of unheated ground elsewhere in the archipelago. Fumarolic activity was not confirmed by temperature measurements as air and moss at Yellowstone Crags were both recorded at 0° C and snow at $-0 \cdot 5°$ C on the afternoon of 13 March 1964. Thus, it is not clear whether the localities were favourable for bryophytes because of intermittent volcanic heat and moisture, because the overhang provided shelter from birds and falling scoria, or because humidity remained high and melt water frequently percolated in situations of this kind.

4. *Alga sub-formation*

Prasiola cf. *crispa* was abundant in moist areas frequented by penguins. Cook (1777) reported seeing from the sea hills in the vicinity of Yellowstone Crags "apparently covered with green turf" and *Prasiola* cf. *crispa* formed substantial stands there in 1964. Kemp and Nelson (1931), who knew of Cook's observation, reported however that this area appeared barren in 1930.

IX. VINDICATION ISLAND

1. *General observations*

Most of the exposed ground on Vindication Island, except the western cliffs and a large rocky bluff above Crosscut Point in the extreme north, was examined in March 1964. The eastern slopes were covered with ash and an accumulation of fine soil, both the slopes and the rock outcrops providing a generally less porous substratum than found on most islands in the group. As a result, the ravines of Leafvein Gulch and Pothole Gulch, and the minor valleys, appeared to have more permanent streams in summer, and showed much more evidence of water erosion than can be seen on the other islands. These factors may account for the widespread vegetation on Vindication Island; there were no fumaroles and relatively little closed plant cover, but substantial areas supported a variety of open bryophyte and lichen communites.

Unstable, barren talus slopes were noted on the high ground below Quadrant Peak, and around Leafvein Gulch and Pothole Gulch, and in some areas erosion of the vegetation was in progress. Wind, combined with instability of the substratum, was thought to account for the disintegration of some moss carpets on the eastern slopes of the island, but biotic factors were clearly important elsewhere. For example, a thin layer of trampled sludge, partially colonized by *Prasiola* cf. *crispa*, was noted on the surface of several *Brachythecium* and *Drepanocladus* carpets near a large chinstrap penguin (*Pygoscelis antarctica*) colony in Pothole Gulch. Farther north, the most extensive closed bryophyte vegetation on the island was developed on a series of rocky knolls above the north-east coast, but even here the mosaic of *Brachythecium* and *Polytrichum alpinum* communities was in places eroding, and the flattened nature of parts of the surrounding vegetation suggested bird trampling, probably by silver-grey fulmars (*Fulmarus glacialoides*), which nest in thousands on the cliffs below. Light manuring by the birds may, however, be partly responsible for the general luxuriance of the vegetation on the knolls.

2. *Crustaceous lichen sub-formation*

Communities dominated by crustose species and other small lichens occurred widely on rocks on Vindication Island, but plant cover was often sparse. Species of *Lecidea* and *Lecanora*, including *Lecanora polytropa*, were encountered most commonly.

3. *Fruticose and foliose lichen sub-formation*

Extensive areas on the more stable rocky knolls and ridges high up on Vindication Island supported communities in the fruticose and foliose lichen sub-formation, interspersed with patches of the crustaceous lichen sub-formation on cliffs and boulders, with areas of tall moss turf on some of the knolls, and with carpet-forming mosses in the hollows. Among the lichens, *Usnea antarctica* was widespread and locally abundant, attaining up to 50 per cent cover on some rocky outcrops above the eastern cliffs, where the cover of associated crustose lichens reached as much as 30 per cent. *Lecidea* spp., *Lecanora polytropa*, *Lecanora* sp., *Lecania brialmontii*, *Pertusaria* sp., *Microglaena antarctica*, *Buellia anisorma*, *B. russa* and *Acarospora* sp. were all found within the areas of fruticose and foliose lichen sub-formation sampled on Vindication Island. The bryophyte flora was also comparatively rich. Scattered cushions of *Dicranoweisia grimmiaceae* were the only mosses present on the eastern cliffs, but a richer association of mosses and lichens occurred extensively, in association with *Usnea antarctica*, on the rocky knolls and boulder-strewn slopes mounting to Quadrant Peak. Here, *Andreaea gainii* and *A. gainii* var. *parallela* were locally abundant in hollows between the rocks and on patches of mineral soil. *Dicranoweisia* cushions were present on rocks and soil, and *Ceratodon* sp. also occurred. In moist hollows, small mats of *Drepanocladus* cf. *uncinatus* and *Brachythecium* sp. were characteristic and there were also patches of *Polytrichum alpinum*. It was noted that in some areas *Usnea antarctica* was normally anchored in clefts and crevices in the boulders, and most of the *Andreaea* cushions were also centred on small clefts.

4. *Bryophyte carpet and mat sub-formation*

Brachythecium sp. and *Drepanocladus* cf. *uncinatus* were normally dominant in the less extensive stands of closed bryophyte vegetation. *Drepanocladus* covered small areas of scree and soil among boulders in several parts of the island, and thin, golden-coloured discontinuous mats and carpets were characteristic of stony slopes and flats in areas above the north-east coast which received drainage from bird colonies. There had apparently been some incorporation of organic material into the soil on these slopes to give an accumulation of fine black mud over the scree. Small mats of *Brachythecium* and of *Prasiola* cf. *crispa* were associated with *Drepanocladus* carpets, while on drier stony ground the latter merged into an association of *Andreaea gainii*, *Usnea antarctica* and crustose lichens.

Larger continuous carpets of *Drepanocladus* cf. *uncinatus* covered moist gentle slopes on the cliff tops, and on the bases of rocky knolls near the northern end of the island. Widespread erosion of the vegetation had taken place, however, exposing ash slopes and flat stones which had been colonized by *Usnea antarctica*. Much of the ash was covered by a layer of dark sandy soil up to 2 cm. deep.

Extensive, almost pure carpets of *Brachythecium* were recorded in several parts of the island, occurring in moist situations both on stable slopes and on level ground. For example, a stand of *Brachythecium* formed a low bank approximately 20 m. long along the side of one ravine, and carpets up to 20 m. in diameter also occurred on rocky knolls and on the cliff tops near the northern end of the island. Smaller stands were noted on steep rocky slopes above the knolls, particularly on ledges where soil had accumulated. Small carpets of *Brachythecium* were widespread in Leafvein Gulch and in Pothole Gulch, being interspersed with crustose lichens and scattered *Prasiola* cf. *crispa* on stony ground and with mats of *Prasiola* in drainage channels. In Pothole Gulch, it was noticeable that *Brachythecium* became increasingly frequent away from a penguin colony at the seaward end. *Ceratodon* sp. and the lichens *Buellia coniops*, *B. russa* and *Mastodia tesselata* were among the associated species collected from one stand of *Brachythecium* carpet.

5. *Tall moss-turf sub-formation*

In addition to *Brachythecium* carpets, the knolls on the northern cliffs also supported numerous turves of *Polytrichum alpinum* up to 10 cm. deep and several metres wide. An unidentified species of *Bryum* was the most conspicuous associated species, giving up to 50 per cent cover in places, especially around the margin of the *Polytrichum* turves, where they merged into stands of *Brachythecium*. Lichens, among them *Psoroma hypnorum* and scattered *Usnea antarctica*, colonized the surface of both the *Brachythecium* and *Polytrichum* communities, while boulders projecting through the mosses supported *Dicranoweisia*, *Usnea antarctica* and crustose lichens including *Lecania brialmontii*.

6. *Alga sub-formation*

Few large pure stands of *Prasiola* cf. *crispa* were recorded on Vindication Island, although small mats of the alga were frequent in drainage channels and in other moist habitats near the penguin colonies. Much of the ground around the bird colonies supported open vegetation, with *Prasiola* on mud and crustose lichens on stones together giving up to 20 per cent cover. Further removed from biotic influence this type of vegetation gradually merged into the open *Bryum*–crustose lichen community or closed moss carpets.

X. BRISTOL, COOK, MONTAGU AND THULE ISLANDS, AND FREEZLAND ROCK

INVESTIGATIONS were made on five other islands in the archipelago, namely Bristol Island, Freezland Rock (a small islet west of Bristol Island), Montagu Island, Cook Island and Thule Island. Nowhere in this series of islands was volcanic heat and moisture thought to influence the development of vegetation. In contrast to Candlemas Island and Bellingshausen Island, these islands were largely barren and only a restricted range of plant communities was encountered.

Bryophytes were, in general, rare. They were collected, together with lichens, on a gently sloping terrace on the southern side of Allen Point on Montagu Island. The slope was boulder-strewn, with rock outcrops and areas of frozen cinder. Penguins were locally numerous and there was no trace of volcanic heat. The available collection and notes (personal communication from R. W. Vaughan) suggest that the area may have supported three main vegetation types: an association of *Usnea antarctica*, crustose lichens (*Caloplaca* sp. and *Lecanora polytropa* were collected) and *Andreaea gainii* on boulders; *Drepanocladus* cf. *uncinatus* on intervening, perhaps wet ground; and *Prasiola* cf. *crispa* (with some *Mastodia* sp.) in areas affected by penguins.

Elsewhere, bryophytes were seen only locally on Freezland Rock, which consists of a mass of volcanic tuff and intrusive dykes surrounded by debris slopes, descending at an angle of about 45° to the boulder-fringed shore. A single moss, *Tortula conferta*, was collected from small scattered turves on stable ledges at the base of the high cliffs, above the areas trampled and manured by the many thousands of penguins moulting below. *Usnea antarctica* and crustaceous lichens were collected on the rocks of this island.

The most widespread vegetation types on all these islands were stands of *Prasiola* cf. *crispa*, communities of crustose lichens, and mixed communities of lichens and algae. Such vegetation was, in places, well developed. Even *Prasiola* and the crustose lichens were, however, only sparsely distributed on several of the islands. There was little ice-free lowland on Bristol Island and the few exposed headlands were much affected by birds. *Prasiola* cf. *crispa* was collected at Harker Point, but inspection from the air revealed no areas on Bristol Island likely to support well-developed plant cover, except perhaps the outcrops at Pryer Point on the northern coast. The area around Hewison Point, on Thule Island, was also strikingly barren. The boulder talus, muddy detritus and local outcrops of lava were much affected by both seals and birds, and the scattered vegetation covered well under 5 per cent of the surface. *Lecanora* sp. was the most commonly collected lichen but species of *Acarospora*, *Buellia*, *Lecanora* and *Lecania*, including *L. racovitzae*, were also present on the boulders of this headland, and *Prasiola* cf. *crispa* was locally abundant. Similarly, it is unlikely that well-developed vegetation occurs on Cook Island, where no plants have yet been collected, although *Prasiola* cf. *crispa* and crustose lichens were reported from lava flows on the small areas of low-lying ground at Reef Point (personal communication from P. E. Baker).

XI. DISCUSSION

A. Origin of the Flora

The South Sandwich Islands are an isolated oceanic archipelago lying about 2,300 km. south-east of South America, 1,400 km. north-east of the Antarctic Peninsula, 1,300 km. north-west of Dronning Maud Land and 4,300 km. south-west of South Africa (Fig. 1). Only a few other islands lie between the present group and the southern continental landmasses, the closest of these being South Georgia, approximately 470 km. to the north-west. Moreover, the South Sandwich Islands arc is young, rising from crust with a probable age of about 8 m. yr. (Barker and Griffiths, 1972) and with no exposed rocks older than 3·1 m. yr. (personal communication from P. E. Baker). One is therefore forced to the conclusion that the South Sandwich Islands biota has arrived exclusively by trans-oceanic migration.

The taxonomy of the flora is at present too confused for a detailed assessment of its geographical affinities to be presented. It is clear, however, that most of the cool-ground bryophytes and lichens are widespread in maritime Antarctic localities to the south-west. The majority are also known from southern South America and South Georgia, while some species have a circum-polar distribution in the Southern Hemisphere, and there are also small bi-polar and cosmopolitan elements. These distribution patterns are compatible with the view that most species may have reached the South Sandwich Islands as airborne spores dispersed in the prevailing west winds. The feasibility of this means of dispersal, at least for micro-organisms, is indicated by the records of viable aerial spores of several fungi, not recorded in Antarctic soils, at sites on the Antarctic Peninsula and the South Orkney Islands (Corte and Daglio, 1964; Heal and others, 1967). South America, the Falkland Islands and South Georgia seem the most likely sources for bryophyte propagules reaching the South Sandwich Islands, in view of the generally low fertility of mosses and liverworts in the maritime Antarctic (Longton, 1972; Webb, 1973) and the large distances of other landmasses to the west. This is particularly so in the case of species, in the South Sandwich Islands, confined to fumaroles, in view of the restricted distribution of these taxa elsewhere in the Antarctic zone. The arrival of propagules from more southerly regions cannot be entirely discounted, however, particularly in the case of Antarctic endemic lichens.

The dispersal of seeds and spores by birds, or in ocean currents, are other possible methods of trans-oceanic migration. The discovery of a *Nothofagus* log, probably of New Zealand origin and apparently washed up on Candlemas Island, has been reported by Longton (1977), who reviewed other data on the long-distance transport of floating objects in the Southern Ocean. In general, animal and water dispersal are considered less likely than the transport of airborne propagules to account for the arrival of the predominantly cryptogamic flora of the South Sandwich Islands.

Bryophyte distribution among the islands within the archipelago appears to have been efficient, as several species are widely dispersed within the group. It is particularly striking that many of the restricted fumarole bryophytes were recorded on several of the islands, where these small and probably transient habitats were examined. *Campylopus introflexus* may be mentioned as an example. This predominantly New World and Southern Hemisphere moss was collected on Candlemas Island and Leskov Island, and it has also demonstrated considerable powers of short-range dispersal through its rapid spread within the British Isles during the past 35 years (Richards, 1963; Richards and Smith, 1975). Richards (1963) suggested that its spread in Britain may have been by spores and he also drew attention to its ability to colonize new habitats rapidly, a factor which may be important in the success of *C. introflexus* and other species in temporary fumarolic areas.

B. Cool-ground Vegetation

The nature of the vegetation on the South Sandwich Islands was for a long time subject to speculation due to the infrequency with which the group was visited and the difficulty of landing. Rudmose Brown (1912), noting the position and the north–south orientation of the archipelago, forecast the discovery on the southern islands of cryptogamic communities comparable with those that he had studied on the South Orkney Islands, and suggested that the northern members of the group might support vegetation resembling more closely that on the sub-Antarctic island of South Georgia. However, the present results, supporting those of Kemp and Nelson (1931) and Holdgate (1963), should dispel the notion that extensive phanerogamic vegetation occurs anywhere within the archipelago. Observations on all the major islands, except Zavodovski Island, have revealed the presence of almost entirely cryptogamic communities. Mosses, lichens and algae predominate, hepatics becoming abundant only near fumaroles, and the vegetation is thus Antarctic rather than sub-Antarctic in character. This is in line with the limited meteorological data, which indicate that the climate may be severe for these latitudes, and comparable with that in the South Orkney Islands to the south-west (Holdgate and Baker, 1979).

The vegetation shows a clear division between its sparse development in volcanically inactive areas, and thus reflecting the interaction of climate and soil conditions with biotic and biogeographical factors, and the more luxuriant communities around fumaroles where the environment is locally modified by volcanic heat and moisture. In terms of cool-ground vegetation the islands fall into two main series. Bristol, Cook, Montagu, Saunders, Thule and Visokoi Islands, and Freezland Rock, form the first group; they are largely devoid of plant cover, while the vegetation that does occur is composed largely of *Prasiola* cf. *crispa* and crustaceous lichens. Macro-lichens are rare, even *Usnea antarctica* being only sparsely distributed, while mosses are largely restricted to small, widely scattered colonies of small turf- and cushion-forming species. The vegetation thus consists largely of communities in the crustaceous lichen and alga sub-formations. The second group of islands, where the unheated ground supports more extensive and varied cryptogamic vegetation, comprises Bellingshausen, Candlemas, Leskov and Vindication Islands. All sub-formations of the Antarctic cryptogam tundra formation, except the moss-hummock sub-formation, are represented on these islands, but even here the moss, lichen and alga communities are generally interspersed with large areas of almost barren ground. Conditions on Zavodovski Island are uncertain but observations from the air suggest that cool ground there may be comparatively poorly vegetated, although the occurrence of *Prasiola* and mosses has been noted (Holdgate, 1963; Holdgate and Baker, 1979).

There is thus considerable variation between the vegetation of different islands but relationships between habitat and growth form, similar to those reported elsewhere in the maritime Antarctic (Holdgate, 1964; Longton, 1967; Smith, 1972), can clearly be seen. Exposed coastal cliffs and boulders commonly support well-developed communities belonging to the crustaceous lichen sub-formation, in which *Acarospora*, *Lecania*, *Lecidea* and *Xanthoria* are among the prominent genera. Inland boulders and lava cliffs on the four better vegetated islands also support an abundance of the fruticose lichen *Usnea antarctica*, which predominates in mixed communities with crustaceous lichens and mosses. *Buellia*, *Lecidea* and *Lecanora* are among the widely distributed lichen genera of these communities of the fruticose and foliose lichen sub-formation. Cushion-forming mosses, including species of *Andreaea* and *Dicranoweisia*, are prominent in rocky areas of Bellingshausen, Leskov and Vindication Islands, but on Candlemas Island the bryophytes locally associated with *Usnea antarctica* are restricted to occasional small turves and cushions of *Pohlia nutans* and *Dicranoweisia* sp.

The tall moss-turf sub-formation, whose deep peaty banks of *Chorisodontium aciphyllum* and *Polytrichum alpestre* are perhaps the most impressive feature of vegetation in the South Orkney Islands, is poorly represented in the South Sandwich Islands group. However, broad ledges on lava cliffs on part of Candlemas Island, as well as some steep ash slopes below the ice cap, support extensive stands of closed hummocky turf dominated by *Polytrichum alpinum* and *Pohlia nutans*. Rocky ledges on Leskov and Vindication Islands support less extensive turves of *Polytrichum alpinum*, which on the latter are locally encrusted by lichens, while on ash slopes on Bellingshausen Island the tall moss-turf sub-formation is represented locally by stands of an open community comprising turves of *P. alpinum* with *Usnea antarctica*, crustose lichens and several small bryophytes occupying the intervening scoria and ash.

The vegetation on more level ground varies from island to island in relation to the nature of the substratum. On Vindication Island the rocks are less porous than elsewhere, resulting in moister soil conditions. Here, level ground and gentle slopes support extensive areas of the bryophyte carpet and mat sub-formation, communities dominated by *Drepanocladus* cf. *uncinatus* and by a species of *Brachythecium* being well represented, while the former species generally predominates on ash and scoria away from fumaroles on Bellingshausen and Leskov Islands. On Candlemas Island, stands of *Drepanocladus* are restricted to relatively small areas in moist hollows in the ash plains, and carpets of *Brachythecium* were seen only locally on slopes where melt water might be expected to percolate throughout much of the summer. These communities are largely replaced on the dry ash plains and gentle slopes of Candlemas Island by extensive thin crusts of moribund, lichen-encrusted acrocarpous mosses, representing the short moss-turf and cushion sub-formation. Small stands of *Deschampsia antarctica* occur locally in a similar habitat and are the only outposts of the Antarctic herb-tundra formation so far recorded in the archipelago.

Large areas of ash plains around the coasts of Candlemas Island are clothed with *Prasiola* cf. *crispa*, while luxuriant growths of this alga were also recorded on cliffs, particularly where dripping melt water occurs near nesting colonies of cape pigeons and other birds. *Prasiola* is also abundant on scoria slopes near penguin colonies on Bellingshausen Island, but the alga sub-formation is less extensive in the areas of Leskov and Vindication Islands covered by the present survey.

The range of growth-form types represented in the cool-ground vegetation of Bellingshausen, Candlemas, Leskov and Vindication Islands is thus comparable with that in other parts of the maritime Antarctic (Longton, 1967), and these islands support several of the specific communities, e.g. the *Drepanocladus* cf. *uncinatus* sociation, reported by Smith (1972) in a detailed study of vegetation on Signy Island, South Orkney Islands (Table III). Nowhere in the South Sandwich Islands, however, does the relative area of plant cover on ice-free ground reach that typical of the other maritime Antarctic areas so far studied, and the cool-ground vegetation on these islands also appears to support a more restricted range of communities within each sub-formation than stations on the South Orkney Islands and near the west coast of the Antarctic Peninsula. For example, *Usnea antarctica* was the only macro-lichen making a significant contribution to the vegetation anywhere in the South Sandwich Islands, and thus communities of the fruticose and foliose lichen sub-formation were considerably less varied than at other maritime Antarctic sites, where *Usnea fasciata*, *Himantormia lugubris* and species of *Alectoria* and *Umbilicaria* may also be prominent. Similarly, in the bryophyte carpet sub-formation no vegetation dominated by species of *Calliergon* was noted on the South Sandwich Islands, while in the grass and cushion chamaephyte sub-formation *Colobanthus quitensis* was not recorded.

It has already been pointed out that the vegetation of Candlemas Island resembles more closely that existing on the geologically similar Deception Island, prior to the 1967 eruptions, than that at most other maritime Antarctic stations (Longton, 1967). This similarity is seen in the abundance of communities in the short moss-turf and cushion sub-formation, in the importance of *Polytrichum alpinum* rather than *Politrichum alpestre* or *Chorisodontium aciphyllum* among the tall turf-forming mosses, in the restricted distribution of carpet-forming mosses, and in the absence or extreme rarity of *Andreaea* spp. (Longton, 1967). The short moss-turf and cushion sub-formation appears to be more widespread on Candlemas Island than on other members of the South Sandwich Islands group, some of which may support a local abundance of *Andreaea*. Otherwise, the comparison with Deception Island appears to hold good for the archipelago as a whole, while *Polytrichum alpinum* may also be dominant in the tall moss-turf communities not only on Deception Island but also on neighbouring islands in the South Shetland Islands group (Lindsay, 1971*b*).

The predominance of short turf- and cushion-forming mosses in the cool-ground bryophyte vegetation of Candlemas Island is thus atypical of the maritime Antarctic in general, but it resembles the situation near McMurdo Station, Victoria Land, and at other sites in continental Antarctica (Rudolph, 1963; Matsuda, 1968; Longton, 1973). Moreover, in terms both of abundance and growth-form representation, the scattered communities of crustaceous lichens and algae recorded on the sparsely vegetated islands in the South Sandwich Islands group also resemble the vegetation reported in coastal areas of continental Antarctica. The same applies to Bouvetøya, situated about 2,150 km. to the east (Holdgate and others, 1968). Together with Bouvetøya, the South Sandwich Islands represent the most northerly land within the Antarctic botanical zone, as understood by Holdgate (1970), Greene (1964) and Skottsberg (1960). Nevertheless, it is clear that in the abundance, structure and diversity of their cool-ground vegetation most of these islands show greater resemblance to continental Antarctica than to the climatically less severe maritime regions of the Antarctic zone, and even in the most favourable localities the vegetation is less well developed than at typical maritime Antarctic locations. Some of the factors that may be responsible for this apparent anomaly are considered later (p. 48).

It is interesting to note that data derived from vertical profiles through stands of vegetation on Candlemas Island indicate the independent development of all the major cool-ground bryophyte communities, no one community appearing to act as a seral stage in the formation of a second. In several cases, the dominant bryophytes appear capable of colonizing the bare ash and scoria directly, for example, in the case of short lichen-encrusted turves of *Pohlia nutans*. The occurrence of simple successional processes was indicated, however, by the abundant lichen encrustation of short turf-forming mosses, and was further demonstrated by samples from the most complex community in unheated parts of the island, where tall turves of *Polytrichum alpinum* and *Pohlia nutans* had frequently become established in cushions formed by a species of *Ceratodon*. Evidence was presented of a cyclical process of erosion followed by re-colonization, first by *Ceratodon* and then by *Polytrichum*, *Pohlia* and other mosses. Even here, however, it is not clear whether an initial growth of *Ceratodon* is essential for the establishment of the turf-forming species. As noted above, *Pohlia nutans* appears to colonize the substratum directly in parts of the island, and *Polytrichum alpinum* is a successful colonizer of bare volcanic substrata on Deception Island. It is considered probable that cyles of erosion and re-colonization may also affect other communities on Candlemas Island, without leaving evidence in the peat profiles, particularly those dominated by carpets of *Brachythecium* sp. or *Drepanocladus* cf. *uncinatus* which have little direct connection with the substratum by means of rhizoids.

These conclusions resemble to some extent the findings of Smith (1972) that on Signy Island most communities "appear to be stable and in equilibrium with their environment and go through virtually no successional phases from the time of their establishment", although lichen encrustation followed by erosion may occur in certain instances, and a succession from carpet- to turf-forming mosses was also recorded. The possibility is thus raised that succession in Antarctic bryophyte vegetation may be predominantly cyclical rather than directional, and long-term observations of marked stands of a variety of community types are desirable to test this hypothesis.

C. FUMAROLE VEGETATION

Fumarole vegetation was recorded on Bellingshausen, Candlemas, Leskov and Visokoi Islands, and may also be expected on Zavodovski Island. The most striking features are firstly its luxuriance and varied floristic composition compared with that on unheated ground, and secondly the zonation of communities along the gradient of decreasing temperature, and probably also water availability, extending outwards from the vents. A similar pattern of communities is apparent at many of the fumaroles. There is typically open vegetation in a relatively narrow innermost zone, occurring within and around the vents, and comprising algae, with small mats and turves of leafy hepatics and acrocarpous mosses. A slender form of *Pohlia nutans* and *Cephaloziella varians* are among the most characteristic bryophytes, while dicranoid mosses are prominent on Bellingshausen Island. The open vegetation is commonly surrounded by deep carpets and turves of the robust leafy liverwort *Cryptochila grandiflora*. Scattered basidiomycetes and a wide variety of other bryophytes occur among the *Cryptochila*, and *Triandrophyllum trifidum* and *Pohlia nutans* in places assume dominance on Leskov Island and on Candlemas Island, respectively.

Turves of *Campylopus* spp. and thallose mats of *Marchantia berteroana* are also widespread and often abundant in the fumarole vegetation. They are the main constituents of a community developed between the alga/acrocarpous moss and the *Cryptochila grandiflora* zone at some fumaroles on Bellingshausen Island, while on Candlemas Island turves of *Campylopus* sp. replace *Cryptochila* at several fumaroles. A further variation from the characteristic zonation pattern was noted on Visokoi Island, where *Cryptochila* is replaced by turves of unidentified dicranoid mosses, while at a single fumarole on Candlemas Island the vegetation comprises merely a short open turf, again formed by a dicranoid moss.

The communities so far considered are all restricted to the fumaroles, but cool-ground vegetation types were also recorded in the volcanic areas, where they normally occur in outer zones surrounding the more restricted communities. Examples include the zone dominated by *Polytrichum alpinum* on Candlemas and Bellingshausen Islands, the extensive carpets of *Brachythecium* sp. and *Drepanocladus* cf. *uncinatus* on Bellingshausen Island, and the short turves of *Pohlia nutans* encrusted by lichens recorded on Candlemas Island.

These latter communities, which occur both in fumarolic areas and on unheated ground, can clearly be included within one of the widely distributed sub-formations of the Antarctic cryptogam formation on the basis of their growth form (Table III). The classification of the more restricted fumarole communities presents greater difficulty, and neither Longton (1967) nor Gimingham and Smith (1970) placed them in any of the sub-formations in their treatment of cryptogamic vegetation within the maritime Antarctic. Following detailed study of samples from these communities, we now propose the following procedure:

i. Communities dominated by *Campylopus* spp. or by tall robust forms of *Pohlia nutans* be placed within the tall moss-turf sub-formation.
ii. The moss-carpet sub-formation be broadened to include both moss and liverwort communities, and also to encompass the mat as well as the carpet growth form. Re-named "the bryophyte carpet and mat sub-formation", this grouping would then accommodate the thallose mats of *Marchantia berteroana*, the compact mats of *Cephalozia badia* recorded on Candlemas Island and the stands of *Cryptochila grandiflora* and *Triandrophyllum subtrifidum* (Table III).

This arrangement is not entirely satisfactory as *Cryptochila grandiflora* shows a gradation from the carpet to the turf growth form, although the former predominates. We believe, however, that the proposed change in the definition of the present sub-formation will provide an adequate framework for the classification of the fumarole communities, and that it may also be of value with regard to cool-ground vegetation elsewhere in the maritime Antarctic. For example, the bryophyte carpet and mat sub-formation as proposed here can readily accommodate the community dominated by mats of *Marchantia berteroana*, recorded locally on Signy Island by Smith (1972), who assigned it to a temporary grouping, the miscellaneous cryptogamic assemblage. The present proposal will also facilitate the classification of communities dominated by *Drepanocladus* cf. *uncinatus*, as this species ranges from the carpet to the mat growth form at some sites.

Fumarole vegetation on the South Sandwich Islands is richer than any reported from other volcanic areas of the Antarctic. Janetscheck (1963) and Ugolini and Starkey (1966) have described a soil micro-flora of fungi, bacteria and blue-green algae from Mount Erebus, Ross Island, but no bryophytes were present. No luxuriant bryophyte vegetation has been reported from fumaroles on the South Shetland Islands, although Collins (1969) has reported the discovery of a species of the Funariaceae, previously unknown in the Antarctic, at a fumarole resulting from recent eruptions on Deception Island. However, cryptogams have been reported among the early colonizers of volcanic substrata surrounding fumaroles in other areas. For example, Griggs (1933) recorded mosses, liverworts and algae around fumaroles in the Katmai district of Alaska, where hepatics were also the most important primary colonizers of undisturbed ash on cool ground. In Mexico, Eggler (1959) noted that mosses were prominent around certain fumaroles on Paricutin, drawing attention also to the importance of mosses, lichens and algae among the initial colonizers of lava flows on Paricutin and to the local abundance of *Campylopus* spp. in similar habitats on Jorullo.

A closer similarity with the present vegetation is seen in the hot-spring floras of Iceland, Greenland and the Siberian peninsula of Kamchatka (Hesselbo, 1918; Lange, 1973; Halliday and others, 1974). The springs differ from fumaroles in emitting a stream of heated water but, like the fumaroles, they may be surrounded by vegetation strikingly more luxuriant than that in surrounding unheated areas and showing zonation in relation to environmental gradients. In Iceland, for example, Hesselbo described an inner stand of leafy hepatics giving way to a broader zone dominated by species of *Sphagnum*, while on cooler ground a wide variety of hypnoid mosses, including species of *Calliergon*, *Drepanocladus* and *Hylocomium*, occurred among *Carex* spp. and other phanerogams. Species of *Riccia* were recorded among the leafy hepatics at springs containing substantial amounts of hydrogen sulphide, but the *Sphagnum* and hypnoid moss zones were poorly developed in these habitats. Sulphurous fumes were a characteristic feature of the South Sandwich Islands fumaroles, and it may be noted that a belt of *Drepanocladus* cf. *uncinatus* surrounding a zone of *Marchantia berteroana* with algae and acrocarpous mosses was recorded at fumaroles on Bellingshausen Island where solidified sulphur had been deposited.

Hesselbo (1918) observed that the Icelandic hot springs supported a wide variety of mosses and hepatics not recorded elsewhere on the island, and Lange (1973) noted that several species of *Sphagnum*, which were characteristically associated with the hot springs, can be considered members of an oceanic element. The Greenland springs also supported several mosses and flowering plants that, on Greenland, were either unrecorded elsewhere, or which reached their northern limits in the hot-spring vegetation. Similarly, on the South Sandwich Islands, no less than seven of the 11 species of liverworts identified on the islands (Grolle, 1972) were confined to the fumaroles, as were several mosses (Table II). The liverwort *Cephaloziella varians* and a wide range of mosses such as *Polytrichum alpinum* and *Pohlia nutans* were recorded both near fumaroles and in unheated areas, and, at least among the bryophytes, it seems clear that most of the cool-ground species are also able to grow in the outer zones of fumarole vegetation.

It is interesting to note that *Campylopus flavoviridis* and several of the hepatics collected near the fumaroles had produced sporophytes, which were particularly abundant in *Cephalozia badia* on Candlemas Island. This contrasts with the position in other hepatics elsewhere in the maritime Antarctic, which are extremely rare in fruit. Large numbers of young, early calyptra intact stage sporophytes were also noted in *Pohlia nutans* near the fumaroles on Candlemas Island. Apart from this, and the occurrence of male gametangia of *Polytrichum alpestre* on Leskov Island, there was little evidence of enhanced reproductive success in cool-ground species extending into the volcanic areas. This is perhaps surprising, as plant-level temperatures appear to be critical in reducing the reproductive success of several mosses in other parts of the maritime Antarctic (Longton, 1972).

D. ENVIRONMENTAL FACTORS

The floristic and vegetational poverty of the South Sandwich Islands may be related both to unfavourable climatic and edaphic conditions, and to geographical isolation. It has been pointed out that the local abundance and diversity of mosses and liverworts under the unusually favourable conditions near fumaroles suggests that environmental rather than biogeographical factors may be mainly responsible for the general sparseness of bryophyte vegetation within the archipelago (Holdgate, 1964; Longton and Holdgate, 1967). Ocean barriers are likely to be more effective in preventing the spread of angiosperms than of light-spored cryptogams. Thus the richness of the fumarole bryophyte flora, combined with the rarity of higher plants, do not, in themselves, provide evidence that environmental conditions in the South Sandwich Islands are too severe for the growth and survival of angiosperms. However, several other reasons have been put forward which suggest that conditions in the maritime Antarctic, including the present islands, may be too harsh to permit the development of extensive phanerogamic vegetation, although some additional species of flowering plants might become established locally if dispersal barriers were removed (Longton and Holdgate, 1967). This conclusion is supported by the generally poor growth and survival of Falkland Islands plants in transplant experiments on Signy Island (Edwards and Greene, 1973).

The cool summer-temperature regime has been regarded as one of the major factors limiting vegetation in the maritime Antarctic mainly to cryptogamic communities, but water availability was considered to be of prime importance in determining the distribution of growth-form types within the region (Longton, 1967). Despite the generally high relative humidity, low water availability appears to be a particularly critical factor in the porous substrata of the South Sandwich Islands, as indicated by the sparse distribution of carpet-forming mosses, and the absence of the moss-hummock sub-formation which occupies wet ground by running water at several maritime Antarctic sites. The restricted distribution of these vegetation types on similar volcanic substrata on Deception Island, as compared with neighbouring and climatically similar islands in the South Shetland Islands group (Longton, 1967; Lindsay, 1971*b*), is also indicative of the local importance of aridity in restricting certain bryophyte communities within the maritime Antarctic. The similarity of some features of the vegetation in the South Sandwich Islands and in parts of continental Antarctica may also be related to aridity, although here the situation is complicated by the low summer temperatures of the latter region. It is thus suggested that aridity may be a major factor limiting the range and distribution of cryptogamic communities in non-fumarolic areas of the South Sandwich Islands, and that certain of the inter-island differences in vegetation, for example, the relative richness of Vindication Island, may also be related to water availability. Until more reliable information on the climate is available, it is impossible to distinguish with certainty between the effects of aridity, cold, high incidence of cloud cover and other climatic factors.

Instability, low organic content and shortage of certain minerals, notably nitrogen compounds, are other factors commonly held responsible for the slow colonization of recent volcanic soils (Griggs, 1933). In view of the prominence of liverworts in the South Sandwich Islands fumarole vegetation, it may be noted that *Cephaloziella byssacea* and *Lophozia bicrenata*, the most abundant plants observed on recent volcanic deposits at Katmai, Alaska, were found to be capable of rapid growth on a medium with a nitrogen concentration below the threshold for detection (Griggs and Ready, 1934). On the South Sandwich Islands, however, it is considered unlikely that these factors are severely limiting for the development of cryptogamic cover on any but the most recent volcanic substrata, although differences in rock chemistry may well account for some of the floristic variation between islands, for example, the distribution of *Andreaea* spp. The soils are almost certainly under a comparably strong marine influence to those on Signy Island, where Allen and Northover (1967) reported that the supply of all the principal nutrients is well in excess of that required by the biota, while the fumarole vegetation confirms that the ash and scoria deposits are capable of supporting a luxuriant growth of bryophytes under favourable conditions of temperature and moisture. Moreover, if soil nitrogen were limiting, one would expect enhanced development of vegetation around the periphery of penguin colonies and in other areas with moderate biotic influence, but no such effect was observed except for the increased abundance of *Prasiola* cf. *crispa*, a species well known to prefer such habitats. Within the penguin colonies, disturbance and concentration of waste products has inhibited all but a sparse growth of *Prasiola* and a few lichens. Evidence of extensive penguin damage to existing bryophyte vegetation was noted locally on Candlemas Island, while erosion on a smaller scale is caused by giant petrels and other birds.

The fumarole vegetation is developed locally in areas where the environment is unusually favourable. It has been suggested elsewhere that the free availability of water may be important in allowing the luxuriant growth of several typical cool-ground species, such as *Brachythecium* sp. and *Pohlia nutans*, near the fumaroles, while the warm conditions are probably vital for the growth of many of the hepatics and other restricted fumarole species (Longton and Holdgate, 1967). As many of the latter taxa are rare or unknown elsewhere in the Antarctic zone, being more typical of sub-Antarctic and temperate regions, their discovery at Antarctic stations may indicate the local incidence of particularly favourable conditions.

Ground temperatures at 2·5 cm. depth in the innermost zones of vegetation varied widely at different fumaroles, from approximately 5° C to a remarkable 61° C. The hottest conditions were noted on Bellingshausen Island, where vegetation was absent from the innermost areas in several cases. Evidence of slight temperature changes due to fluctuations in fumarolic activity was noted during a 3 day period on Candlemas Island, and it is clear that more severe fluctuations have had adverse effects on the vegetation, as sublimed sulphur was noted on the surface of dead mosses near a fumarole on Bellingshausen Island. The moribund condition of *Campylopus* turf near several fumaroles on Candlemas Island may also have been caused by variations in fumarolic activity, although it is not clear whether it had resulted from adverse temperatures or from fume damage, such as Dickson (1965) has described for vegetation on Tristan da Cunha. More extensive data on changes in fumarolic activity, and on the effects of sunshine and of winter conditions, are required before the fumarole environment is fully understood.

The South Sandwich Islands, a recent, isolated oceanic archipelago, thus possess less well-developed and varied cool-ground vegetation than many localities farther south in the maritime Antarctic region, but at the same time their small, and possibly transient fumarolic areas support luxuriant bryophyte vegetation composed of many species more typical of the sub-Antarctic or southern temperate zones. Studies on the future development of the biota may therefore be expected to yield further results of considerable ecological and biogeographical significance.

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APPENDIX

List of Specimens Identified

THE list below cites all specimens from the South Sandwich Islands in the K. Archibald, M. W. Holdgate and R. E. Longton collections that have so far been identified to the generic or specific level. It is upon these records that Table II is based. Collecting data for each specimen are available from the British Antarctic Survey data bank.

Algae

Calothrix sp.	Longton 494
Chlamydomonas nivalis (Bauer) Wille	Longton 582
Eunotia tenella (Grun.) Hust.	Longton 636
Lyngbya sp.	Longton 495
Mesotaenium sp.	Longton 494, 580, 636
Navicula muticopsis Van Heurck	Longton 493, 581, 582, 639, 640, 682, 771, 772
Phormidium sp.	Longton 494
Pinnularia borealis Ehr.	Longton 493, 581, 682, 771, 772
Prasicoccus calcarius (Boye Pet.) Vischer	Longton 493, 598, 636, 639, 640, 641, 682, 772
Prasiola cf. *crispa* (Lightf.) Menegh.	Holdgate 800a, 850a, 807a, 849; Longton 493, 581, 598, 639, 640, 641, 771, 772
Scotiella nivalis (Shuttlew.) Fritsch	Longton 582
Stichococcus bacillaris Naeg.	Longton 771, 772
Ulothrix sp.	Longton 494

Lichenes

Acarospora macrocyclos Vain.	Longton 563, 615, 659b, 660, 669, 690, 691b
Acarospora sp.	Holdgate 435, 454, 463, 465, 468, 470, 831c; Longton 613b
Buellia anisomera Vain.	Longton 668, 743
B. coniops (Wahlenb. ex Ach.) Th. Fr.	Holdgate 856b
B. inordinata (Hue) Darb.	Longton 658
B. russa (Hue) Darb. var. *russa*	Holdgate 856d; Longton 737, 741
Buellia sp.	Holdgate 831f; Longton 619d
Caloplaca sp.	Holdgate 803a, 806
Cladonia sp.	Longton 768
Lecania brialmontii (Vain.) Zahlbr.	Longton 725
L. racovitzae Vain.	Holdgate 459, 467
Lecania sp.	Holdgate 831a, 831e, 850
Lecanora polytropa (Hoffm.) Rabenh.	Holdgate 803a; Longton 545, 547, 565, 616, 618, 659a, 662, 678, 691a, 734
Lecanora sp.	Holdgate 424, 434c, 451, 453, 455, 456, 457, 458, 473, 474, 476, 831b, 831d; Longton 611, 617, 619a, 620a, 647, 740a, 776
Lecidea sp.	Holdgate 452, 469, 471, 845; Longton 537, 546, 564, 566, 619b, 620b, 724, 738, 742, 744a, 744b
Lepraria sp.	Longton 542, 548, 549b
Mastodia tesselata (Hook. f. et Harv.) Hook. f. et Harv.	Holdgate 856c; Longton 607a, 613a
Microglaena antarctica M. Lamb	Longton 740b
Ochrolechia frigida (Sw.) Lynge	Longton 560a, 579b
Pertusaria sp.	Longton 667, 739
Psoroma hypnorum (Vahl) Grey	Longton 727a
Psoroma sp.	Longton 738
Rinodina petermannii (Hue) Darb.	Longton 608, 610, 672
Stereocaulon antarcticum Vain.	Longton 656, 768
Usnea antarctica Du Rietz	Holdgate 423, 427, 432, 436, 475, 801, 809a, 812c, 818a, 823a, 825c, 830c, 837d, 852c; Longton 535, 557b, 559a, 560b, 561, 562, 579c, 602b, 604, 605, 625, 663, 675, 721, 722, 744c, 767, 777
Xanthoria candelaria (L.) Arn.	Longton 674
Xanthoria sp.	Holdgate 464

Musci

Andreaea gainii Card. var. *gainii*	Holdgate 804a; Longton 745
A. gainii Card. var. *parallela* (C. Muell.) S. W. Greene	Holdgate 437, 825a, 852a; Longton 747
A. regularis C. Muell.	Longton 525, 530

Bartramia patens Brid.	Longton 490c, 492
Brachythecium sp.	Archibald 3; Holdgate 420b, 426, 428, 429c, 445b, 815c, 824d, 842, 851b, 853, 855; Longton 540b, 588, 593, 665, 685, 717, 735
Bryum algens Card.	Holdgate 429d; Longton 519
B. argenteum Hedw.	Longton 555, 698
Bryum sp.	Longton 718, 730a, 754, 781
Campylopus canescens (C. Muell.) Schimp.	Longton 757
C. flavoviridis Dus.	Longton 520, 622, 706, 712b
C. introflexus (Hedw.) Brid.	Holdgate 833b; Longton 508b, 513, 514, 518b, 626
C. spiralis Dus.	Holdgate 409b, 415, 821b, 822, 827c, 841b
Campylopus sp.	Holdgate 412b, 810a, 830d; Longton 568
Ceratodon sp.	Archibald 2, 22, 36; Holdgate 430d, 431c, 438, 448a, 448b, 477, 810b, 817b, 818c, 823c, 846a, 856a, 859, 860; Longton 522b, 592, 664, 666, 715, 736, 752, 755, 766
Dicranoweisia antarctica (C. Muell.) Kindb.	Longton 761
D. grimmiaceae (C. Muell). Broth.	Holdgate 430b, 439, 478, 804b, 825d, 836b, 837c, 846b; Longton 488, 521, 522a, 523, 526, 528, 534, 719
Dicranoweisia sp.	Holdgate 406; Longton 510, 556b, 603, 633
Distichium capillaceum (Hedw.) B.S.G.	Longton 509b, 554, 572
Drepanocladus cf. *uncinatus* (Hedw.) Warnst.	Holdgate 421c, 440, 444, 447, 802, 818b, 823b, 852b; Longton 527, 539, 587, 655, 687, 720, 762
Grimmia sp.	Holdgate 430c, 434b
Pohlia nutans (Hedw.) Lindb.	Archibald 5b, 6; Holdgate 407, 421a, 425a, 433, 442a, 446, 812b, 816b, 817a; Longton 538, 540a, 541, 549, 553, 556a, 573, 589, 595, 628, 630, 686, 699, 703, 704, 705, 780, 789
Polytrichum alpestre Hoppe	Holdgate 412a, 820b, 834a; Longton 512
P. alpinum Hedw.	Archibald 5a; Holdgate 404, 417, 429a, 445a, 449, 811a, 820a, 835a, 836a, 838a, 851a; Longton 489, 511, 590, 594, 683, 684, 692, 696, 697a, 700, 712a, 716, 778, 792
P. juniperinum Hedw.	Holdgate 443; Longton 702
P. piliferum Hedw.	Longton 701
Pottia austrogeorgica Card.	Longton 730b
Psilopilum antarcticum (C. Muell.) Par.	Holdgate 405a, 418, 429b, 480, 812a, 814a, 815a, 816a, 824a, 828a, 829a, 840b; Longton 782
Racomitrium austrogeorgicum Par.	Longton 524
R. crispulum (Hook. f. et Wils.) Hook. f. et Wils. var. *crispulum*	Holdgate 410b, 811e, 820d, 824e, 825e, 829b, 839d
Tortula conferta Bartr.	Holdgate 808
Tortula sp.	Holdgate 823d

HEPATICAE

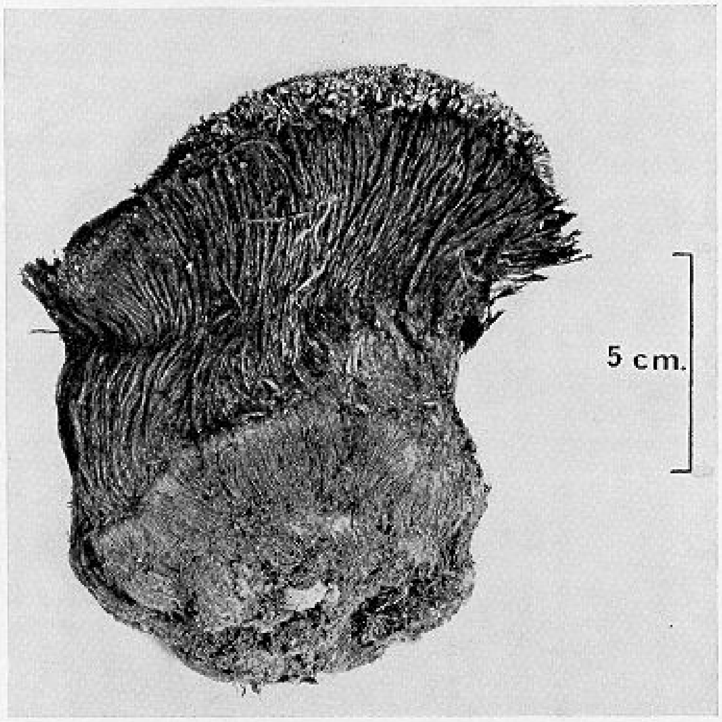
Details of hepatic records may be found in Grolle (1972).

ANGIOSPERMAE

Deschampsia antarctica Desv.	Archibald 38; Longton 600, 601

PLATE I

Photograph of a peat profile from a stand of the *Polytrichum alpinum* sociation on Candlemas Island. See Fig. 8a.



5 cm.