COLONIZATION AND RECOVERY BY CRYPTOGAMS FOLLOWING RECENT VOLCANIC ACTIVITY ON DECEPTION ISLAND, SOUTH SHETLAND ISLANDS

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ABSTRACT. The sparse and floristically impoverished vegetation of Deception Island before the three eruptions of 1967–70 is described. Much of the pre-eruption vegetation was destroyed through burial by ash, mud and other tephra, but recovery by acrocarpous mosses has been possible where burial was only a few centimetres deep or where most of the deposits were quickly removed by wind or down-washing. Pleurocarpous mosses were unable to regenerate unless the deposits were removed completely. New stable soil surfaces are slowly being recolonized locally by bryophytes and lichens. Areas where geothermal activity has persisted provide unusual but favourable habitats, and support several taxa new to the island and some new to the Antarctic biome. The floras associated with such fumaroles and experiments to investigate the propagule bank of barren soils are discussed in relation to the hypothesis that Antarctic regions receive an influx of spores transported long distances by wind from more northerly latitudes. Unless the spores are genetically and physiologically pre-adapted to the prevailing conditions, however, germination and subsequent growth and survival of the progeny cannot proceed. At least some of the apparently exotic taxa that grow on moist soil may thus be considered as native but are unable to grow under normal polar conditions.

INTRODUCTION

The vegetation of Antarctic regions consists almost entirely of cryptogams with lichens predominating in drier more exposed situations and bryophytes prominent in the more sheltered habitats where moisture accumulates or is sporadically available during the short cold summers. The flora is impoverished due both to the harsh environment and to isolation from the other continents of the southern hemisphere by a cold and turbulent ocean barrier. However, a diversity of plant communities exists on a wide range of substrates that become snow free in summer (Longton, 1967, 1979, 1982; Gimingham and Smith, 1970; Smith, in press).

Apart from taxonomy and floristics, botanical research in the Antarctic has concentrated on descriptive and phytosociological accounts of the vegetation. Intensive continuous botanical research, involving both field and laboratory experimental studies has been largely confined to Signy Island, South Orkney Islands. Two of the major questions to be answered in relation to any vegetated habitat in the Antarctic biome are 'what is the potential for plant establishment and what conditions are required for colonization to proceed?' These problems are being studied at Signy Island and the colonization potential, in terms of viable propagules present in barren recently deglaciated soils, is being tested experimentally. It is proposed that much of the Antarctic, particularly the South American sector, receives a 'rain' of wind-transported cryptogamic spores derived from more northerly latitudes. Additional propagules, including viable vegetative fragments and seeds, may reach these regions by adhering to the feet or feathers of birds that migrate to the Antarctic from, for example, Tierra del Fuego. However, it is impossible for these immigrant propagules to germinate or develop under the

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prevailing climatic or edaphic conditions unless they are deposited on a site where exceptionally favourable conditions exist.

Very few sites of volcanic activity occur in the Antarctic. Within the maritime Antarctic only Deception Island, South Shetland Islands, several islands in the South Sandwich Islands and Bouvetøya are volcanically or geothermally active. Sites of recent geothermal activity offer ideal natural, although very unusual, conditions to test the hypothesis proposed above. The investigation described here provides some information on colonization and community development by native and exotic

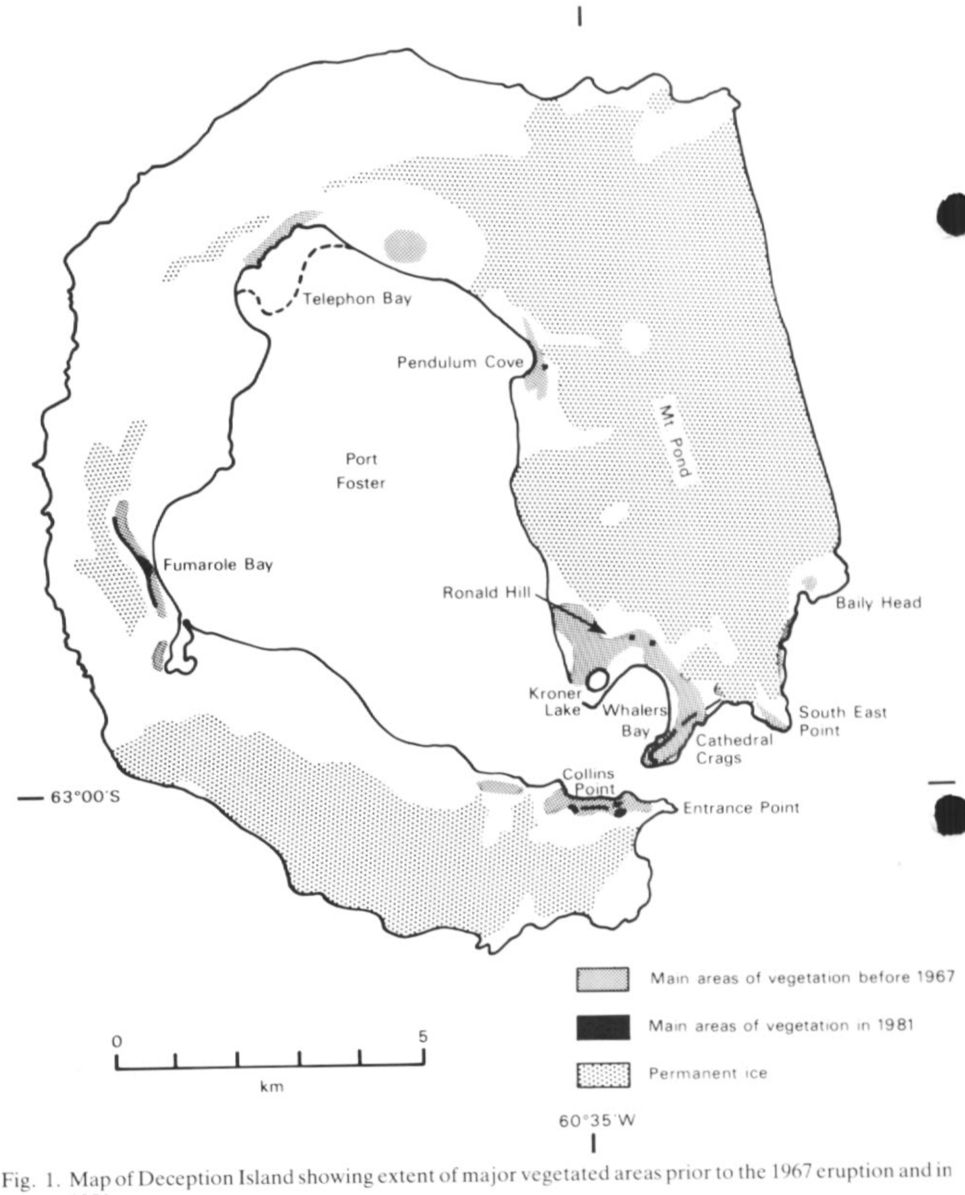

Fig. 1. Map of Deception Island showing extent of major vegetated areas prior to the 1967 eruption and in 1981.

bryophytes on old and recently created soil surfaces on Deception Island, and on the recovery of vegetation buried by recent volcanic eruptions.

Study Area

Deception Island (lat. 63° 00′ S, long. 60° 40′ W) is a horseshoe-shaped island about 14 km across with a flooded caldera open to the sea on its south side through a 0.5 km wide entrance (Fig. 1). The rim of the caldera ranges from about 200 to 550 m in altitude. Freshwater exists in several small shallow lakes in former subsidiary

Fig. 2. Deception Island showing deposition of ash during the 1967, 1969 and 1970 eruptions (isopachs in centimetres).

craters and occasional small melt streams, often of a temporary nature. About half the landmass is covered by glacier ice. The slopes and plains are composed mainly of fine ash and dust and coarser scoriae, broken by outcrops and cliffs of lava and tuff, often of a loose crumbling nature. The ash terrain is extremely porous and dries out rapidly after precipitation. This material is unstable and subjected to frequent redistribution by wind. Heavy rain and melt water readily erode the surface, cutting deep channels and causing considerable downwashing of finer material. Climatically, Deception Island is typical of the northern maritime Antarctic, although it has a relatively high precipitation (mean annual equivalent rainfall about 500 mm with up to 90 mm rain occasionally falling within 24 hours, and with snow or sleet falling on more than half the summer days) and low mean incidence of sunshine (*c.* 565 h yr^{-1} with the sunniest month, December, having a mean of 4.5 h d^{-1}). Mean annual wind speed is high (7.2 m s^{-1}) with gales occurring on 30–70 days per year. The mean annual air temperature is −2.9°C but the annual range of mean monthly temperature is small, from 1.4°C for January, to −8.1°C for July; extreme temperatures range from 11 to −28°C.

Recent Volcanic Activity

Deception Island has a history of volcanic activity (Roobol, 1973, 1980) and several minor eruptions have occurred since its discovery in the early 1800s, the most recent being in 1967, 1969 and 1970. These affected about two-thirds of the terrain either by direct eruptive activity or through coverage by ash or lahars, but there were no lava flows (Baker and others, 1975; Roobol, 1982). The area covered by ash at each eruption is illustrated in Fig. 2.

In December 1967, a major eruption occurred at two centres at the north end of the caldera. At one of these centres the submarine eruption in Telephon Bay created a new island 60 m high (Clapperton, 1969; Roobol and others, 1975). In February 1969 another eruption from several vents occurred to the north-east of Port Foster between Pendulum Cover and Mt Pond. It created massive fissures or chasms up to 200 m deep and 200 m wide along the length of the west side of Mt Pond. The melting of glacier ice caused huge floods of water (jökuhlaups) to rush downslope and engulf large areas in mudflows or lahars extending 6 km from Pendulum Cove to Whalers Bay (Baker and Roobol, 1975). In August 1970 there was a third eruption from at least 13 vents, 12 of which were very close to the 1967 craters and one offshore in Port Foster (Baker and McReath, 1975). The new island in Telephon Bay became attached to the mainland by a low area of deposited ash.

Fumarolic activity along certain beaches around Port Foster has long been a feature of the island, and there are early reports of occasional transient fumaroles and areas of heated ground at inland sites, e.g. near the summit of Mt Pond in 1909 (Gourdon, 1911) and in 1958 (Hawkes, 1961), and above Pendulum Cove (Kendall, 1832; Webster, 1934). The influence of geothermal heat and moisture has been more widespread since the eruptions in 1967–70.

Botanical Investigations on Deception Island

No intensive study of the flora and vegetation of Deception Island has ever been carried out although several small collections of bryophytes and lichens have been made. Perhaps the first 'botanical' observation reported was that of Kendall (1832) who remarked 'There was nothing in the shape of vegetation except a small kind of lichen . . . '. Similarly, Webster (1834) reported 'Vegetation is a word of very limited significance when applied with reference to Deception Island; for it would then include only the growth of a dimunitive moss, and a striped coralloid lichen [*Usnea antarctica*] . . .'. Wilkes (1845) also commented on the sparsity of vegetation: 'The only sign of vegetation was a lichen, growing in small tufts, around the mouth of several small craters, of three or four feet in diameter'. Among the earliest scientists to visit the island were the biologist L. Gain and geologist E. Gourdon of the 2nd French Antarctic Expedition 1908–10. However, they collected

Table I. The pre- and post-eruption bryoflora of Deception Island.

Taxon	*Recorded before 1967 eruption*	*Recorded after 1970 eruption*	*Presence of sporophytes*
Andreaea gainii Card.	r	–	yes
Andreaea regularis C. Muell.	r	–	no
Bartramia patens Brid.	o	o	yes
Brachythecium austro-salebrosum (C. Muell.) Kindb.	la	vla	no
Bryum cf. *algens* Card. (various forms)	f–la	f	yes
Bryum argenteum Hedw.	o	o	no
Bryum sp.* (bulbiferous)	–	lf	no
*Campylopus canescens** (C. Muell.) Schimp. in Jaeg.	–	la	no
Campylopus cf. *introflexus** (Hedw.) Brid.	–	r	no
Ceratodon cf. *purpureus* (Hedw.) Brid.	f–la	o–la	yes
Ceratodon cf. *grossiretis* Card.	f	o	no
Ceratodon sp. (cultured from propagules in soil)	–	r	no
Didymodon gelidus Card.	o–f	o	no
Dicranoweisia grimmiaceae (C. Muell.) Broth.	r–o	–	yes
Drepanocladus uncinatus (Hedw.) Warnst.	la	vla	yes (vr)
Funaria cf. *hygrometrica** Hedw.	–	vlf†	yes
Grimmia antarctici Card.	la	lf	yes
Grimmia cf. *apocarpa* Hedw.	o	o	yes
Grimmia sp. (hair pointed)	?	r	no
Leptobryum cf. *pyriforme** (Hedw.) Wils.	–	vlf	yes
*Philonotis gourdonii** Card.	vr	–	no
Pohlia cruda (Hedw.) Lindb. var. *imbricata* (Card.) Bartr.	?	vlf	no
Pohlia nutans (Hedw.) Lindb.	r	r	no
Polytrichum alpestre Hoppe	dubious record	–	no
Polytrichum alpinum Hedw.	la	la	yes (vr)
Polytrichum juniperinum Hedw.	vla	r	no
Polytrichum piliferum Hedw.	vlf	–	no
Pottia heimii (Hedw.) Hamp. var. *heimii*	o	r	yes
Pseudodistichium austro-georgicum Card.	o	–	yes
Psilopilum trichodon (Hook. f. et Wils.) Mitt.	vlf	–	no
Sarconeurum glaciale (C. Muell.) Card. et Bryhn	vr	–	no
Tortula cf. *conferta* Bartr.	o	r	no
Tortula excelsa Card.	o	r	no
Tortula fusco-viridis Card.	o	o	no
Tortula grossiretis Card.	o–f	o	no
Barbilophozia hatcheri (Evans) Loeske	r	–	no
Cephaloziella cf. *exiliflora* (Tayl.) Steph.‡	f–la	o	no
Lophozia excisa (Dicks.) Dum.	r	r	no
*Marchantia berteroana** Lehm. and Lindenb.	–	vla	no

*Taxa associated only with fumaroles.
† Recorded only between 1967 and 1970 eruptions.
‡ previously reported as *Cephaloziella varians* (Gott.) Steph.
r, rare.
o, occasional.
f, frequent.
a, abundant.
l, locally.
v, very.

only two plant species, *Grimmia antarctici* and a species new to science, *Philonotis gourdonii* (Cardot, 1911). A more impressive collection of eight mosses was made in 1918 or 1919 by J. Robins who described the location rather vaguely as above 'a lagoon about 500 yards in diameter' . . . 'there is a mountain 1500 feet high which has no ice, and it was here in the warmth and shelter I found the green piece of moss' (Dixon, 1920). The collecting site was probably on the west side of Mt Pond overlooking Whalers Bay. The magistrate (A. G. Bennett) of the whaling station at Deception Island made a significant collection between 1918 and 1923, while the British Graham Land expedition made a small collection 1935–36, but much of this material remains unidentified in the British Museum (Natural History), London.

Collections by more recent expeditions have increased the known bryoflora to about 35 moss and four liverwort taxa (Table I). Of these, 30 taxa were recorded before the 1967–70 eruptions and 29, including seven species new to the island, more recently. The number of lichen species is less accurately known due to the poor state of Antarctic microlichen systematics. The lichen flora probably comprises about 40 taxa, of which less than one-third are macrolichens. Algae, notably *Prasiola crispa*, are frequent only in association with seabird colonies. The two native Antarctic vascular plants were each represented at single sites; *Deschampsia antarctica* no longer exists at its former Ronald Hill crater site but *Colobanthus quitensis* still maintains a foothold between South East Point and Baily Head. Even before the recent eruptions distinctive plant communities were few, nowhere extensive, and composed of relatively few species, due to the porous unstable substrate and consequent scarcity of water.

The first ecological account of the island's vegetation was by Longton (1967), and phytosociological data obtained by the present author were summarized by Collins (1969). All previous accounts of the effects of the eruptions on the vegetation concern the period prior to the third eruption in 1970 (e.g. Collins, 1969; Cameron and Benoit, 1970; Young and Kläy, 1971).

Effect of the 1967–70 Eruptions on the Vegetation and its Localized Recovery

Changes in the existing vegetation

The main vegetated areas on the inner slopes of the caldera prior to the 1967 eruption and as they existed in 1981 are indicated in Fig. 1. Only one area appeared to be unaffected throughout the eruptive phase – that around Fumarole Bay. Despite an active fumarole on the beach close to the vegetated slopes and further fumarolic activity along the beach to the south, the relatively well-developed vegetation and moderately diverse flora remained unchanged with open communities dominated by *Brachythecium austo-salebrosum*, *Bryum algens* and *Polytrichum alpinum* on a moist ash slope, and a variant of the *Tortula–Grimmia* association occurring on large eroding blocks of tuff (Table II).

Collins (1969) described in some detail the processes of regeneration of former stands of moss and lichens following burial by ash. Unfortunately most of the areas he examined and in which he established long-term study quadrats were re-covered by ash or destroyed by volcanic activity, mudflows or erosion during the 1969 and 1970 eruptions. It was clear from his investigations that recovery of existing vegetation and colonization of new surfaces can proceed quickly in situations where the substrate is relatively stable and moist, although the growth form and water relations of the species are critical. Most short acrocarpous mosses (e.g. *Bryum, Ceratodon, Grimmia, Polytrichum, Tortula*), and the hummock-form of *Brachythecium austro-salebrosum*, were capable of regenerative growth through up to 3 cm of

Table II. Species recorded at site unaffected by any recent eruptions above Fumarole Bay.

Moist ash slope		*Dry tuff blocks*	
Brachythecium austro-salebrosum	la	*Didymodon gelidus*	o
Bryum cf. *algens*	f	*Grimmia antarctici*	f
Cephaloziella cf. *exiliflora*	f	*Grimmia* sp. (hair point)	r
Drepanocladus uncinatus	o–f	*Tortula fusco-viridis*	o
Pohlia cruda var. *imbricata*	lf	*Tortula grossiretis*	o
Polytrichum alpinum	la	*Tortula* sp.	o
Tortula excelsa	f		
		Caloplaca cf. *sublobulata*	f
Leptogium puberulum	f	*Lecanora* cf. *deceptionis*	f
Psoroma cf. *cinnamomeum*	f	*Leptogium puberulum*	o
Sterile white crustose lichen	o	*Ochrolechia* cf. *antarctica*	f
		Pertusaria corallophora	o
Prasiola crispa	o	*Physcia caesia*	f
		Physconia muscigena	o
Omphalina antarctica	f	Unidentified crustose lichens	o–f
Tephrocybe atrata	f		

r, rare. a, abundant.
o, occasional. l, locally.
f, frequent.

ash, commencing immediately after burial, while the pleurocarpous hydric species *Drepanocladus uncinatus* was not capable of such recovery.

The ash slopes above the shore between Collins Point and Entrance Point possessed three of the largest closed stands of vegetation on the island before 1967, each dominated by large hemispherical coalesced turves of *Polytrichum alpinum*. Two stands above Collins Point are now very much reduced in extent and exist as discrete turf hummocks with occasional other cryptogams associated on stable ash between the hummocks, especially on the downhill side where there is some protection afforded from frequent burial (see Table III, Site 1). The main *P. alpinum* site (Fig. 3), indeed probably the largest existing stand of moss on the island, lies at about 30–75 m altitude to the north of Entrance Point in a broad north to north-east facing gully, but it too has been reduced to an open community mainly of isolated turf hummocks. Collins (1969) described and illustrated the recovery of these *Polytrichum alpinum* hummocks following shallow burial by ash, but by 1981 the surviving turves were considerably fewer than in the original stands and the number of associated species was less (Fig. 4). Between many of the healthy hummocks, moribund but barely decomposed *Polytrichum* lies buried about 10–20 cm below the present ash surface, the depth having been augmented by redistributed ash. Profiles cut through live hummocks revealed several bands of ash representing aeolian deposition during periods of strong winds. While this must inhibit growth during the same or following growing season, the annual growth increments during a favourable summer appear to be up to 2 cm (Fig. 5). Collins (1969) stated that plants artifically covered by moist ash *in situ* grew up to 1 cm in just over one month.

The more sheltered and wetter ash below the *Polytrichum* community at about 15–25 m altitude is dominated by a physiognomically similar stand of isolated loose *Brachythecium austro-salebrosum* hummocks (Fig. 3). As with the *Polytrichum*, much of the original closed community has disappeared due to burial or erosion. Short turves and cushions of *Bryum* cf. *algens, Tortula excelsa* and *Ceratodon* spp. and occasional large turves of *P. alpinum* and encrusting thalli of *Psoroma* cf. *cinnamomeum* are also associated. A similar stand formerly occurred on the slope south-east of Collins

Table III. Comparison of the cryptogamic species composition of several vegetated sites on Deception Island in 1967 and 1981.

	Site number																							
	*1**		*2*		*3*		*4**		*5*		*6*		*7*		*8*		*9*		*10*		*11**		*12*	
	1967	*1981*	*1967*	*1981*	*1967*	*1981*	*1967*	*1981*	*1967*	*1981*	*1967*	*1981*	*1967*	*1981*	*1967*	*1981*	*1967*	*1981*	*1967*	*1981*	*1967*	*1981*	*1967*	*1981*
Andreaea gainii	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–
Andreaea regularis	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	1	–
Bartramia patens	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	2	–	–	1	–	–	–	2	1
Brachythecium austro-salebrosum	2	2	5	–	2	1	1	–	–	–	1	1	3	2	2	2	–	–	–	–	–	–	–	–
Bryum argenteum	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	2	2	–	–	–	–	–	–	–
Bryum cf. *algens*	3	3	3	–	3	1	2	–	6	1	4	2	3	2	2	2	3	–	3	1	1	–	2	–
Ceratodon cf. *purpureus* (+ *C.* cf. *grossiretis*)	3	2	3	–	2	1	4	–	4	1	3	2	2	2	2	2	3	–	2	–	2	–	2	1
Dicranoweisia grimmiaceae	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–
Didymodon gelidus	–	–	–	–	–	–	–	–	–	–	–	–	2	2	2	1	2	–	3	2	–	–	–	–
Drepanocladus uncinatus	3	2	3	–	6	2–3	4	–	2	1	3	2	2	1	2	1	2	–	2	–	2	–	2	1
Grimmia antarctici (+ *Grimmia* cf. *apocarpa*)	–	–	–	–	–	–	1	–	–	–	–	–	3–4	3	3	3	2	–	4	–	–	–	2	–
Polytrichum alpinum	7	4–5	2	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	4	1
Polytrichum juniperinum	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3	1
Polytrichum piliferum	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	4	–
Pottia heimii var. *heimii*	–	–	–	–	–	–	–	–	–	–	–	–	2	1	2	–	2	–	1	–	–	–	–	–
Pseudodistichium austro-georgicum	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	2	–
Psilopilum trichodon	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–
Sarconeurum glaciale	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–
Tortula cf. *conferta*	–	–	–	–	–	–	–	–	–	–	–	–	2	–	1	1	–	–	–	–	–	–	–	–
Tortula excelsa	2	2	4	–	2	–	1	–	–	–	1	1	–	–	2	2	–	–	–	–	–	–	–	–
Tortula fusco-viridis	–	–	2	–	–	–	1	–	–	–	–	–	2	1	2	–	–	–	–	–	–	–	–	–
Tortula grossiretis	2	–	2	–	–	–	1	–	1	–	2	1	2	2	3	3	2	–	2	–	3	–	2	–
Cephaloziella cf. *exiliflora*	–	–	2	–	1	–	5	–	3	–	4	1	–	–	–	–	–	–	–	–	–	–	2	–
Lophozia excisa	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–
Prasiola crispa	–	–	–	–	1	–	–	–	–	–	–	–	2	2	2	2	–	–	–	–	–	–	–	–
Buellia latemarginata	–	–	–	–	–	–	–	–	–	–	–	–	2	2	2	2	–	–	–	–	–	–	–	–
Caloplaca regalis	–	–	–	–	–	–	–	–	–	–	–	–	3–4	3–4	3–4	3	–	–	–	–	–	–	–	–
Caloplaca sublobulata	–	[illegible]	–	–	–	–	–	–	–	–	–	–	3–4	3–4	[illegible]	3	2	1	1	–	1	–	1	–
Cladonia spp.	1	–	–	–	–	–	1	–	–	–	–	–	1	–	1	–	–	–	2	–	2	–	3	–
Haematomma erythromma	–	–	–	–	–	–	–	–	–	–	–	–	2–3	2	3	2–3	–	–	–	–	1	–	–	–

Lecanora cf. *deceptionis*	–	[illegible]	–	–	–	–	–	–	–	–	–	–	2	2	[illegible]	–	–	–	–	–	–	–	–	–
Lecanora cf. *lavae*	–	[illegible]	–	–	–	–	2	–	–	–	–	–	2	2	[illegible]	2	–	–	–	–	2	–	1	–
Leptogium puberulum	–	–	–	–	–	–	–	–	–	–	–	–	2	1	2	–	3	–	2	–	–	–	–	–
Lepraria sp.	–	–	–	–	–	–	–	–	–	–	2	–	1	–	1	–	–	–	–	–	–	–	–	–
Lecanora aspidophora	–	–	–	–	–	–	2	–	–	–	–	–	2	2	2	2	–	–	–	–	2	–	1	–
Mastodia teselata	–	–	–	–	–	–	–	–	–	–	–	–	2	2	2	2	–	–	–	–	–	–	–	–
Pertusaria sp.	–	–	–	–	–	–	–	–	–	–	–	–	2	2	1	–	–	–	–	–	–	–	–	–
Physcia caesia	–	–	–	–	–	–	–	–	–	–	–	–	2	2	2	2	–	–	–	–	–	–	–	–
Psoroma cf. *cinnamomeum*	3	2	3	–	1	–	4	–	5	–	6	2	2	2	2	–	–	–	2	–	4	–	2	–
Ochrolechia frigida	–	–	2	–	–	–	1	–	–	–	–	–	1	–	1	–	–	–	–	–	4	–	2	–
Ramalina terebrata	–	–	–	–	–	–	–	–	–	–	–	–	3	3	3	2–3	–	–	–	–	–	–	–	–
Rinodina petermannii	–	–	–	–	–	–	–	–	–	–	–	–	2	2	1	–	–	–	–	–	–	–	–	–
Stereocaulon glabrum	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	4	–
Usnea antarctica	–	–	–	–	–	–	–	–	–	–	1	–	3–5	3–4	3–4	2–3	–	–	–	–	5	–	2	–
Xanthoria candelaria	–	–	–	–	–	–	–	–	–	–	–	–	2–3	2–3	2	2	–	–	–	–	–	–	–	–
Xanthoria elegens	–	–	–	–	–	–	–	–	–	–	–	–	2	2	2	–	–	–	–	–	–	–	–	–
Unidentified crustose lichens mainly *Buellia* and *Lecanora* spp.)	–	–	–	–	–	–	2	–	–	–	2	1	2–3	2	2–3	2	2	1	2	–	2–3	–	2	–

* Sites destroyed and still uncolonized in 1981.

Key to site numbers

1. Extensive closed stand of *Polytrichum alpinum* forming deep turf hummocks on moist ash slope to south of Collins Point, Port Foster.
2. *Brachythecium austro-salebrosum–Drepanocladus uncinatus–Tortula excelsa* community on moist ash slope to south-east of Collins Point, Port Foster.
3. Extensive *Drepanocladus uncinatus* dominated area on moist ash plain north-east of BAS station, Whalers Bay.
4. Extensive open *Drepanocladus uncinatus–Ceratodon* cf. *purpureus–Cephaloziella* cf. *exiliflora–Psoroma* cf. *cinnamomeum* community on dry stony substrate to south-west of Kroner Lake, Whalers Bay.
5. *Bryum* cf. *algens–Ceratodon* cf. *purpureus–Psoroma* cf. *cinnamomeum* community on moist ash plain to north of BAS station, Whalers Bay.
6. *Bryum* cf. *algens–Ceratodon* cf. *purpureus–Cephaloziella* cf. *exiliflora* community heavily encrusted by *Psoroma* cf. *cinnamomeum* on dry ash on north-east slope of Cathedral Crags, Whalers Bay.
7. Heterogeneous community dominated by nitrophilous lichens on crumbling cliffs of tuff on north side of Cathedral Crags, Whalers Bay.
8. As 7 on outcrop between Collins Point and Entrance Point, Port Foster.
9. As 7 on dry lava cliffs and rocks on west side of Ronald Hill, Whalers Bay.
10. As 9 but on wetter rock surfaces.
11. Open *Usnea antarctica*–dominant community on crumbling boulders of tuff to the north-east of Kroner Lake, Whalers Bay.
12. Heterogeneous community dominated by Polytrichaceae and fruticose lichens on dry ash and cinder floor to west of Ronald Hill, Whalers Bay.

Key to abundance coding

1 <1% cover (very few individual plants)
2 1–5% cover
3 5–10% cover
4 10–25% cover
5 25–50% cover
6 50–75% cover
7 75–100% cover

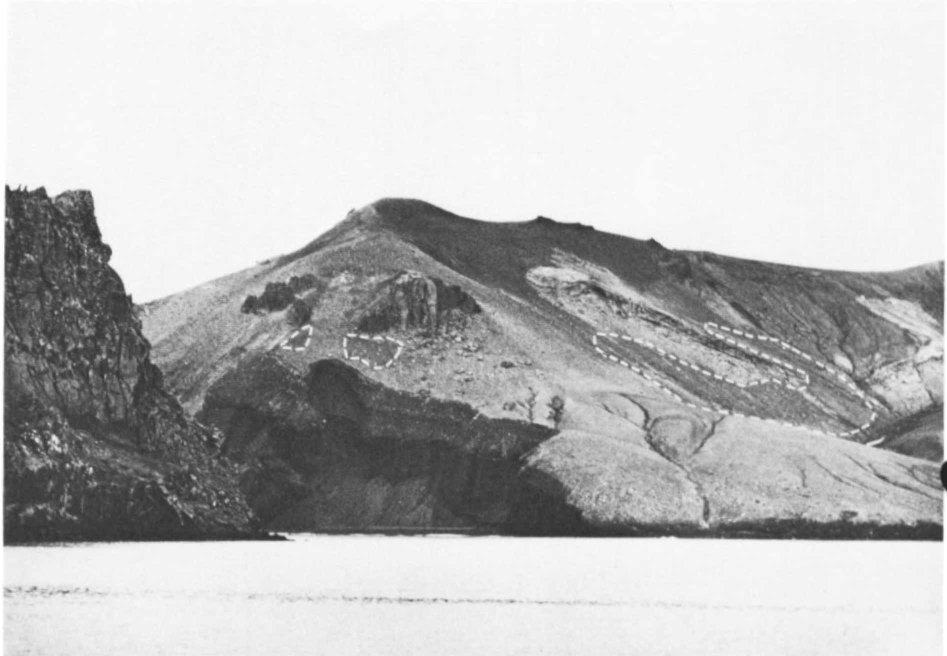

Fig. 3. Ash slopes and lava outcrops between Entrance Point and Collins Point, with Cathedral Crags on the left. Relatively extensive stands of *Polytrichum alpinum* and *Brachythecium austro-salebrosum* are indicated by the dotted line.

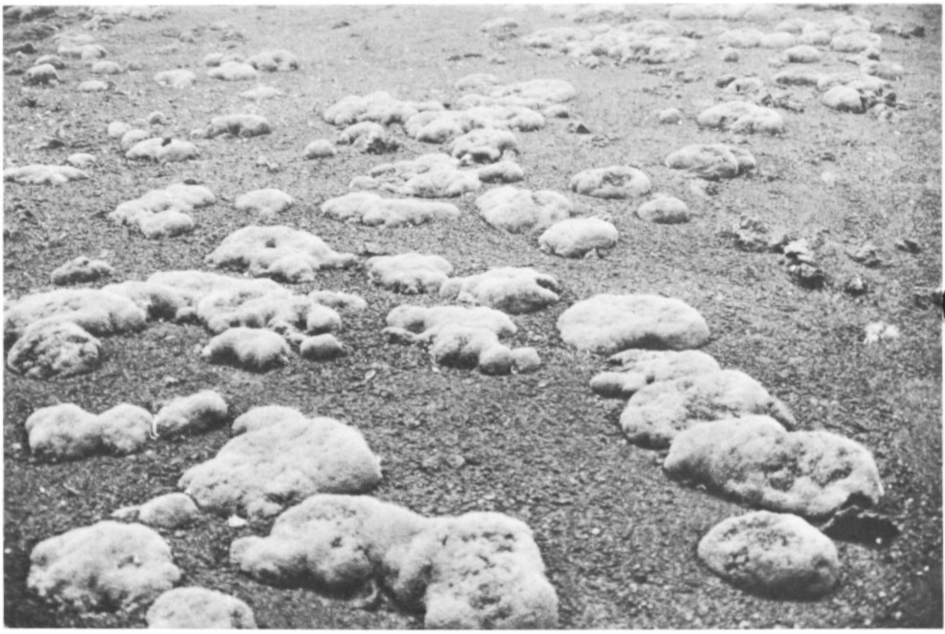

Fig. 4. Isolated turf hummocks of *Polytrichum alpinum* regenerating from a former continuous stand of this moss which was buried by shallow ash in 1967 and 1969. To north of Entrance Point, 25 March 1981

Fig. 5. Profile through *Polytrichum alpinum* turf showing layers of ash recently deposited by wind. Maximum depth of turf is 7 cm.

Point but this no longer exists. Several small stands of a similar *Brachythecium* community along the north-east slopes below Cathedral Crags were similarly affected and survive as more open and less extensive patches.

At the foot of the slopes and on the ash plain along the shore between Collins Point and Entrance Point there were locally extensive stands of *D. uncinatus* and more open stands dominated by *Brachythecium austro-salebrosum, D. uncinatus* and *Tortula excelsa* (Table III, Site 2). This area received a light covering of ash during the 1967 eruption and about 5 cm in 1969, although much of this would have been quickly redistributed by wind and downwashing. No vegetation exists now on the ash beach terrace except for occasional pioneer colonies of the green foliose alga *Prasiola crispa*. This may be largely due to the recent disturbance the area has received from an increasing population of fur seals (about 200 young bulls in 1981), which has re-established on the island, possibly for the first time since their extermination in the South Shetland Islands in the 1820s and 1830s. It is possible that the occurrence of the relatively luxuriant former plant communities in this area may originally have relied on volatilized nutrients, especially nitrogen, from nearby

Fig. 6. Recovery by *Drepanocladus uncinatus* along the moist margin of a temporary melt stream behind the former whaling station, Whalers Bay, 25 March 1981.

chinstrap and gentoo penguin rookeries between Collins Point and Entrance Point (Gain, 1914). However, neither these nor the colonies of several other avifauna have existed here for many decades and probably disappeared during the 1920s or earlier due to disturbance and predation from the whaling station in Whalers Bay.

The area of ash plain between Whalers Bay, Kroner Lake and Ronald Hill was traversed by a network of melt stream channels. This intermittently moist area was extensively covered by a moss carpet community dominated by *Drepanocladus uncinatus*, with *Bryum* cf. *algens*, *Ceratodon* cf. *purpureus* and *Tortula excelsa*, and locally *Brachythecium austro-salebrosum*, as frequent associates (Table III, Site 3). In similar but less wet situations the short acrocarpous mosses and *Psoroma* cf. *cinnamomeum* were locally frequent (Table III, Site 4). In all the wetter bryophyte stands basidiomycete fungi (*Omphalina antarctica* and *Tephrocybe atrata*) were often frequent. In 1969 much of this area was affected by lahar from which regeneration has not been possible. Recovery of *D. uncinatus* along stream margins has occurred in the few sites where the moss had not been deeply buried, but covered by 5–10 cm of ash from each eruption, which was probably subsequently washed away by melt water (Fig. 6). However, an area of recolonizing *Drepanocladus* and *Bryum* observed in 1976 between the whaling station and Kroner Lake had disappeared by 1981, probably due to burial by alluvial material.

Collins (1969) commented on the inability of *D. uncinatus* to recommence growth immediately after being covered by ash more than a few millimetres deep. Where the moss carpet had been re-exposed, sporadic branch innovations or apical extension did eventually occur. However, the moss tended to dry out rapidly and the desiccated carpet was susceptible to cracking and fragmentation. In these stands *Bryum* cf. *algens*, if present, appeared to recover quickly and, in the absence of competition from *Drepanocladus*, became more abundant than before the 1967 eruption at the Kroner Lake site (later destroyed in 1969).

Elsewhere in the Whalers Bay–Cathedral Crags–Baily Head area moist ash slopes formerly supported a distinctive open community described by Longton (1967) and Gimingham and Smith (1970) as the Encrusted Moss sub-formation and restricted almost exclusively to volcanic soils. Here, short cushions and turves of *Bryum* and *Ceratodon*, with intervening mats of *Drepanocladus, Brachythecium* and *Cephaloziella*, were encrusted by the lichens *Psoroma* cf. *cinnamomeum, Ochrolechia frigida* and *Lepraria* sp. The encrusted *Bryum* and *Ceratodon* colonies were hemispherical to almost spherical in shape and surrounded a core of ash. However, they were not detached from the substrate in the same manner as the 'rolling moss balls' reported from other Antarctic and sub-Antarctic locations (Smith, 1983). The intervening soil was stabilized by the lichens and mat-forming bryophytes. Elsewhere a similar but less well-developed community occurred on moister ash and cinder surfaces, but where mosses had a more typical cushion growth-form the stabilizing influence of *Cephaloziella* mats and *Psoroma* crusts was less. The curious basiocarps of *Leptoglossum retirugum* var. *antarcticum* were occasionally frequent but very inconspicuous in this community, growing on the soil, bryophyte or lichen surfaces, in cavities beneath *Bryum* and *Ceratodon* cushions, and on the underside of *Psoroma* thalli (see Horak, 1982). No stands of these distinctive communities were seen in 1981 and it is possible that the thin coverings of ash in 1967 and 1969 were sufficient to kill the lichens and liverwort and render the surface unstable, enhance erosion and allow the moss to become detached and blow or wash away. However, a few scattered moss cushions had survived or had recolonized the site (Table III, Sites 5 and 6).

Also throughout this area, but particularly on the crumbling tuff cliffs of Cathedral Crags and on an outcrop between Collins Point and Entrance Point, communities of the Fruticose Lichen and Cushion Moss subformation were abundant. These cliffs, outcrops and screes are the breeding sites of several species of sea birds, and their enrichment of the environment is evident since the lichen vegetation is dominated by colourful nitrophilous taxa; there is also a relatively rich bryoflora. This habitat has the greatest diversity of cryptogams on the island, with *Grimmia antarctici* and *Bryum* spp. the dominant mosses and several more calcicolous taxa also locally frequent (e.g. *Didymodon gelidus, Pottia heimii, Tortula* spp.). On wetter ledges or rock faces *Brachythecium austro-salebrosum* is occasionally abundant. The lichen component is dominated by *Usnea antarctica, Ramalina terebrata, Caloplaca regalis*, and numerous other nitrophilous species (Table III, Sites 7 and 8). The sites were within the 1–5 cm ash isopachs but being on vertical and steep rock substrata were probably quickly blown or washed free and the vegetation, with the possible exception of fruticose lichens, appears to have suffered little except on ledges and depressions where the ash accumulated further. However, nowhere within the zone of 5 cm or more ash deposition have fruticose lichens been recorded since the eruption, confirming the very slow rate of colonization and subsequent growth by these plants. An area of fine grained lava cliffs on the west side of Ronald Hill formerly supported a relatively diverse cryptogamic assemblage (Table III, Sites 9 and 10), but only a few species were recorded there in 1981. Lava outcrops around Telephon Bay formerly supported *Usnea antarctica, Caloplaca sublobulata* and various other lichens and scattered cushions of *Bartramia patens, Bryum algens, Grimmia antarctici, Tortula grossiretis* and *Ceratodon* spp. These remained largely unaffected after the 1967 eruption, despite the proximity of the underwater centre about 100 m away. However, the site was destroyed by the 1970 eruption and no trace of vegetation could be found in 1981. A similar situation was experienced on the lava outcrops south-east of Pendulum Cove where, in 1981, only few thalli of *C. sublobulata* and *Lecanora* cf. *lavae* and minute cushions of *Grimmia* and *Didymodon* were noted.

A relatively extensive fellfield community formerly existed on a ridge of scoria and cindery soil to the north-east of Kroner Lake, although stands were also frequent on many of the exposed outcrops and ridge crests, e.g. between Cathedral Crags and Baily Head. This community was typical of the Fruticose Lichen and Moss Cushion subformation, being dominated by *Usnea antarctica* but with several other fruticose and crustose lichens and cushion mosses also prominent. However, this site was buried by a deep lahar during the 1969 eruption and the habitat no longer exists (Table III, Site 11).

Of particular interest is the colonization by lichens of timber surfaces associated with the former whaling station, notably the deck of a barge embedded in the ash beach and the south wall of the former explosives hut. The surface of the barge is densely colonized by *Lecanora aspidophora, Physcia caesia, Xanthoria candelaria, Buellia* spp., *Rinodina* spp., *Prasiola crispa* and small thalli of *Usnea antarctica*. A similar assemblage occurs on the hut wall, but with greater abundance of *Usnea* and none of the alga. These surfaces were first examined by the author in 1964 and appear to have changed little in 1981. The barge deck must have been covered by several centimetres of ash in 1967 and 1979 yet the plants have suffered no ill effects, indicating rapid removal of the debris. The only moss observed growing on this alien substrate was *Ceratodon* sp. although it, together with *Bryum* cf. *algens, Pottia heimii, Tortula* cf. *conferta, Cephaloziella* sp. and *Prasiola crispa* were growing on whale vertebrae and skulls on the beach. *Caloplaca sublobulata, Physcia caesia* and *Xanthoria candelaria* were also occasionally present.

Colonization of new surfaces

Following the three eruptions various new surfaces became available for colonization by plants. However, most of these remained dry, porous, unstable and therefore unsuitable for establishment. Most of the area within 1–2 km of the 1967 and 1970 eruptive centres was covered by ash up to 1 m in depth, which, unless it was redistributed quickly, destroyed any existing vegetation and prevented regeneration. Thus large tracts of ash plains and slopes remain devoid of macrophytes. Collins (1969) described how the new island in Telephon Bay appeared to have no suitable sites of colonization a year after its creation and no evidence of any form of migrant propagules was obtained on exposed sticky traps. Cameron and Benoit (1970), however, found that significant microbial colonization had occurred after one year, particularly in moist ash around the shore of crater lakes and in ash associated with a fumarole on the island. Nitrogen-fixing bacteria and algae were found only at the latter site. No protozoan colonizers were isolated after one or two years but three

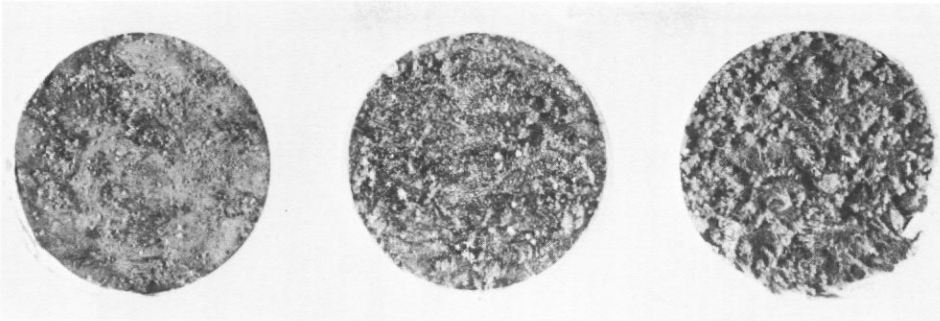

Fig. 7a. Soil from Ronald Hill crater lahar incubated for three months at 5°C (left), 15°C (centre) and 25°C (right). Several scattered short moss shoots (mainly *Bryum* spp.) are visible on the cold plate and almost 100% cover is afforded by tall *Ceratodon* sp. on the warm plate; this moss also dominated the intermediate temperature plate.

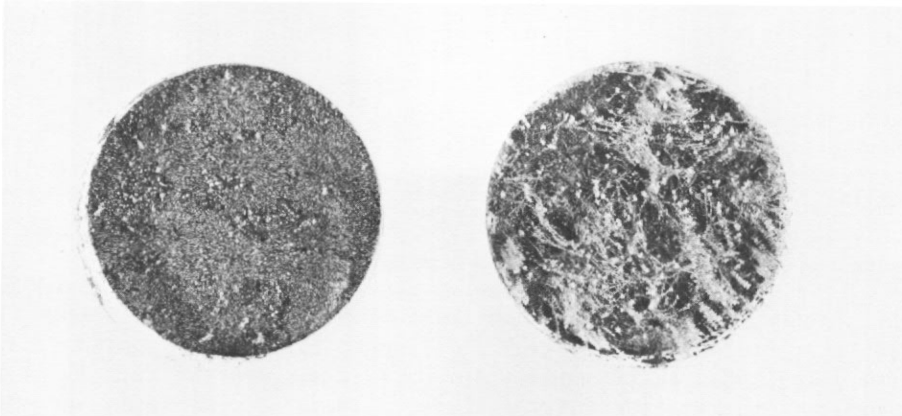

Fig. 7b. Soil from the inland geothermal site above Pendulum Cove, incubated for three months at 8°C (left) and 20°C (right). At the lower temperature gelatinous blue-green algae were frequent and at the higher temperature *Ceratodon* sp. predominated.

species were recorded in 2½-year-old tephra (Smith, 1974). The island suffered catastrophic erosion following the 1970 eruption and is now joined to the mainland; by 1981 there was still no trace of macroscopic vegetation even near to the isthmus lake or around prominent bombs used as bird perches. However, bacteria (up to 10^5 g^{-1} fresh wt), yeasts (rare) and fungi were isolated from the dry ash plain below the southern summit in 1981 (D. D. Wynn-Williams, pers. comm.).

One of the most diversely, though sparsely, vegetated sites on Deception Island used to be the shallow crater between Ronald Hill and Kroner Lake (Table III, Site 12). However, the entire area was obliterated in 1970 by a jökuhlaup with floods of water issuing from fissures, which opened high on Mt Pond and which affected much of the inner east coast of Deception Island, burying the Ronald Hill crater with metres of lahar of fine reddish clay-like dust. When examined in 1981 it was moist and received melt water from nearby semi-permanent snow patches. While the area appeared completely barren, closer inspection revealed several patches of diminutive scattered moss shoots. These included *Ceratodon* cf. *purpureus*, *Bartramia patens*, *Drepanocladus uncinatus* and small radiating colonies of

Table IV. Plants cultivated from propagule bank in lahar from Ronald Hill crater.

Species	*Temperature (°C)* 5	15	25
Bryum cf. *algens*	abundant	frequent	occasional
Bryum sp. (bulbiferous)	occasional	very rare	–
Ceratodon sp.	rare	frequent	abundant, dense
Tortula excelsa	occasional	very rare	–
Botrydiopsis sp.	present	–	–
Desmococcus sp.	present	–	–
Oocystis sp.	present	–	–
Unidentified coccoid green alga	–	present	–
Hantzschia amphioxys	present	present	abundant
Pinnularia sp.	present	–	–
Stauroneis sp.	present	–	–
Navicula sp.	–	present	–

Polytrichum alpinum and *P. juniperium*; no macroalgae or lichens were observed. *Bartramia* was the only fertile species. Samples of the upper 5 mm of soil were collected from a position at least 20 m from the nearest visible moss shoots. The soil was placed in sterile deep Petri dishes and sealed in the field, transported to England at −10°C and subsequently stored at −20°C. Nine months after collection the dishes were cultured in an illuminated thermogradient incubator at 5, 15 and 25°C. The dishes had deionized water added weekly or whenever they showed signs of drying out. After three weeks moss shoots appeared on the soils at the two higher temperatures, and after a further week, also on the 5°C soils. The appearance of the plates after three months is shown in Fig. 7a and the floristic composition given in Table IV. Besides an unidentified species of *Ceratodon* the most frequently occurring mosses, algae and diatoms grew best at the lowest temperature, indicating their adaptation to the prevailing harsh climate; in addition they must have been tolerant of the exceptionally low nutrient concentrations (see below and Table V). The composition of the bryoflora is unusual and the occurrence of a bulbiferous species of *Bryum*, apparently a taxon new to the island and restricted to heated ground elsewhere on the island where gametophytes are prominent (see below), is of interest, suggesting that the apical bulbil clusters are being dispersed by wind, birds and possibly Man.

Colonization of heated ground

The most interesting habitats on Deception Island are the occasional sites above the intertidal zone where fumarolic activity heats the substrate. The endemic *Philonotis gourdonii* is known from a single collection from the summit of Mt Pond where, in December 1909 according to the collecting details, it grew in small mats on the calcareous and sulphureous deposits of warm springs at 450 m. In 1958–59 Hawkes (1961) reported '"warm spots" or patches of snow-free ground, the highest of which is only 50 ft [15 m] below the summit of Mt Pond'. Also there is a narrow area of free ice ranging from 385 to 500 m altitude on a subsidiary summit above Pendulum Cove but there has been no fumarolic activity there in recent times (Hawkes, 1961). Gourdon (1911, 1914) reported an area of hot ground situated at 200 m above Pendulum Cove on the lower slopes of Mt Pond and some snow-free

Table V. Chemical analysis of soil in vegetated sites on Deception Island.

		Extractable (mg per 100 g dry wt)										
Location and vegetation	*LOI (%)*	*Na*	*K*	*Ca*	*Mg*	*Mn*	*Fe*	*Al*	PO_4-*P*	*NO_2 + NO_3-N*	*NH_4-N*	*Total N (%)*
Fumarole Bay (unaffected by recent volcanic activity)												
Unvegetated ash plain (1–3 cm)	0.6	27	14	67	15	1.6	720	–	2.9	0.044	0.3	<0.01
Beneath *Brachythecium* mat (1–3 cm)	1.8	28	11	96	20	1.0	800	–	4.1	0.062	1.7	0.06
Beneath *Polytrichum alpinum* turf (1–3 cm)	2.3	61	11	130	31	3.3	1100	–	1.9	<0.01	3.4	0.10
To north of Entrance Point												
Beneath *Polytrichum alpinum* turf (5–10 cm)	7.6	44	26	150	77	1.9	580	–	4.1	0.027	3.8	0.41
Beneath *Polytrichum alpinum* turf (10–15 cm)	9.1	48	32	100	55	2.7	970	–	4.4	0.027	14.0	0.29
Ronald Hill Crater												
Primary colonists on lahar mud (1–3 cm)	0.5	28	14	67	15	1.6	700	–	2.6	0.045	1.1	<0.01
Pendulum Cove beach fumarole												
Beneath colonizing bulbiferous *Bryum* (1–3 cm)	0.5	240	20	19	34	0.6	720	–	1.6	<0.01	0.09	<0.01
Pendulum Cove inland gully with geothermal areas												
Beneath *Campylopus–Ceratodon–Marchantia* community (1–3 cm)	0.4	11	3	16	5	0.3	400	140	0.15	0.10	0.7	0.03

Na, K, Ca, Mg, Mn and PO_4-P extracted with 2.5% acetic acid; Fe and Al extracted with 3% oxalic acid; NO_2 + NO_3-N and NH_4-N extracted with 6% sodium chloride (see Allen and others, 1974). LOI: loss on ignition at 550°C, expressed as percentage dry wt.

Fig. 8. Fumarolic activity on a recently formed ash slope near the 1967 land centre, a year after the eruption. The heated moist soil was already locally colonized by fruiting *Funaria* sp., a taxon new to the Antarctic. Thermistor probe at lower left recorded temperatures up to 36°C within the vegetation. White areas are sulphurous deposits. (Photo N. J. Collins, December 1968.)

ground still exists at that altitude. Occasional other inland fumarole sites have been reported (e.g. Smiley, in Wilkes, 1845; Ferguson, 1921) but no vegetation was associated with them.

A year after the 1967 eruption extensive fumarolic activity occurred in two areas near the land centre between Telephon Bay and Pendulum Cove (Collins, 1969). Associated with these areas were colonies of a species of *Funaria* (possibly *F. hygrometrica*, personal communication from C. M. Matteri) growing on the warm humid ash and lapilli (Fig. 8). The shoots were only *c.* 5 mm above the ash surface, but there were abundant sporophytes. This moss appeared to be spreading rapidly by means of spores, in a manner typical of ephemerals. Wefts of protonemata were abundant between the colonies and on the decaying lapilli. Under experimental cultivation these produced gametophytes. The taxon was reported as new to the Antarctic and was restricted to areas of heated ground. The moss was dying where fumaroles had ceased to be active suggesting that it was not adapted to the normal environmental conditions of the maritime Antarctic. A fumarolic area on the rim of a crater on the new island yielded an abundance of aerobic bacteria, fungi and algae, with a high proportion of nitrogen fixers, but no macroscopic vegetation (Cameron and Benoit, 1970). However, all these heated areas had ceased to exist by 1981 and no vegetation was seen throughout the area of many square kilometres.

Undoubtedly the most interesting area currently is at Pendulum Cove. Nine months after the 1969 eruption Young and Kläy (1971) reported that bryophyte colonization was well advanced on areas of moist heated ash and cinders along the edges of a fissure at the north end of the Mt Pond glacier. Elsewhere in the rift, material a few centimetres below the surface was incandescent. The vegetation, scattered over an area of *c.* 20 m^2, consisted of a species of *Tortula*, a species of Funariaceae (cf. Collins, 1969), and *Marchantia polymorpha*, although there were only about 20 small thalli of the latter. No specimens were fertile but the shape of the liverwort thalli indicated development from gemmae. During the 1970 eruption, this site received a covering of only about 1 cm of ash, which was probably quickly washed or blown away and did not affect the health of the plants.

This area, or one close to it, was examined in 1981. A shallow broad gully at about 75 m altitude on an ash and cinder-strewn slope supported stands of bryophytes which in places formed closed turves of several square metres, broken only by protruding scoriae (Fig. 9). This site appeared to be the only one on the island where the colonists have been able to maintain a foothold and develop as a simple succession at a considerably faster rate than has been observed elsewhere in the Antarctic biome. Here the heat appears to be diffusing through the entire vegetated area rather than

Fig. 9. Geothermally heated gully inland from Pendulum Cove. Discontinuous bryophyte vegetation extends almost to the foot of the slope. Dominant plants were *Marchantia berteroana*, *Campylopus introflexus*, *Polytrichum juniperinum*, *Ceratodon* cf. *purpureus* and *Leptobryum* cf. *pyriforme*. (Photo D. Hamer, 25 March 1983.)

being restricted to a specific vent; consequently no pattern in the distribution of plant species has developed. Similar heated ground has been reported on Bouvetøya where luxuriant growth on *Brachythecium austro-salebrosum* was noted (Engelskjøn, 1981). However, on neither island is there such advanced development as the zone bryophyted communities associated with fumarole vents on some of the South Sandwich Islands (Longton and Holdgate, 1979) where conditions have presumably been more favourable and stable for a longer period.

A distinctive community had developed dominated by short turf-forming mosses, while *Marchantia berteroana* (probably the same taxon as described by Young and Kläy (1971) as *M. polymorpha*) was locally abundant (Fig. 10). The most prominent moss was *Campylopus* cf. *introflexus*, but *Leptobryum* cf. *pyriforme*, *Ceratodon* cf. *purpureus* and *Polytrichum juniperinum* were also abundant; several other species appeared to be scarce (e.g. *Bryum* cf. *algens*, *B. argenteum*, *Tortula excelsa*), while others are thought to have been overlooked. Both *Campylopus* and *Leptobryum* are new to the island and the latter new to the Antarctic; *C. introflexus* was previously known only from fumarole habitats on Candlemas and Leskov islands in the South Sandwich Islands (Longton and Holdgate, 1979). Basidiocarps of *Ricknella fibula* (= *Gerronema schusteri*) were frequent on the mosses and are also recorded for the first time from Deception Island. Barren ash and cinders from close to a *Marchantia*-dominated stand were placed in Petri dishes *in situ* and sealed, then stored at −20°C until cultured nine months later on a thermogradient incubator at 8 and 20°C. Neither yielded any *Marchantia* but an abundance of an unidentified bulbiferous *Bryum* (see below), *B.* cf. *algens*, *Campylopus* cf. *introflexus* and a few shoots of *Bryum* cf. *argenteum* developed at the lower temperature. On the warmer soil *B.* cf. *argenteum*, *Pohlia* cf. *nutans*, *Ceratodon* sp. and *Campylopus* cf.

Fig. 10. *Marchantia berteroana* and *Leptobryum* cf. *pyriforme* showing moisture droplets condensed onto the moss shoot apices at site illustrated in Fig. 9. (Photos by D. Hamer, 25 March 1983.)

Fig. 11. Pendulum Cove beach. Note the snow-free (black) heated areas along parts of the crests of wave-formed terraces. e.g. by the two figures in the foreground. These areas had a surface temperature of about 20°C and were sparsely colonized by several mosses. Steam can be seen rising from the sea water. (25 March 1983.)

introflexus had sporadic occurrences. *P. nutans* has been recorded only once before on the island, from a single small collection from an unknown site (Greene and others, 1970).

The only other vegetation associated with geothermal activity was on the cindery beach in Pendulum Cove which had been devastated during each of the eruptions. Above the normal high water mark is a series of low wave-formed terraces extending from about 5 to 20 m inland (Fig. 11). In places along some of these the ground was warm and kept free of the snow which was falling heavily at the time of the author's visit. The temperature of the moist surface was 20°C and at 15 cm it was 40°C. The shoreline and the surface of the sea for about 100 m offshore were also about 40°C and clouds of steam drifted across the beach. The temperature of a hot spring within the beach area was over 70°C. Virtually no vegetation was visible but beneath the superficial layer of cinders small colonies of moss shoots were locally abundant within areas of about 100–150 cm^2. The principal plant was a bulbiferous species of *Bryum*, with *Ceratodon* sp. and *Campylopus canescens* less frequent and another unidentified species of *Bryum* was also present. All shoots were very short and seldom more than 5 mm tall. The bulbiferous *Bryum* (Fig. 12) produced masses of apical bulbils which were readily detached when disturbed and were observed scattered amongst the cindery substrate close to the gametophytes.

In the Antarctic biome *Campylopus canescens* was previously known only from around a fumarole on Visokoi Island, South Sandwich Islands (Longton and Holdgate, 1979). Unvegetated ash and cinders placed in Petri dishes in the field at this site and cultivated at 5 and 20°C yielded only the bulbiferous species of *Bryum*

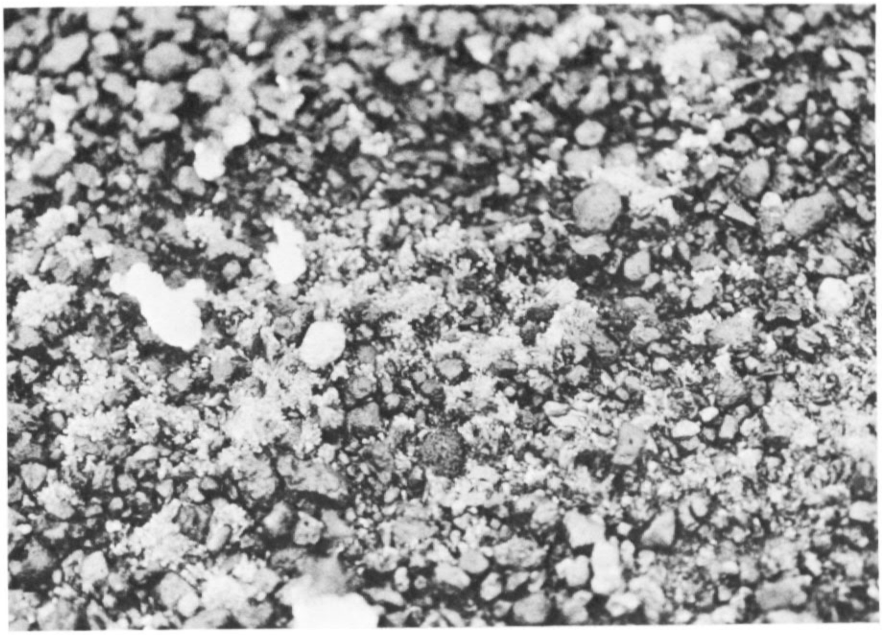

Fig. 12. Dimunitive shoots of *Bryum* sp. producing quantities of deciduous apical bulbils and growing amongst the heated cinders of a beach terrace at Pendulum Cove. (25 March 1981).

and several unidentified unicellular, gelatinous and filamentous green algae, some of which were thought to be blue-green taxa (Fig. 7b). It is interesting to note that moss protonemata have been found in heated moist soil on the crater rim of Mt Erebus (*c.* 400 m) on Ross Island, but they have not developed gametophytes under various experimental conditions (K. Thompson, pers. comm).

A survey of nematophagous fungi at 16 sites on the island yielded nine taxa from soil associated with bryophyte vegetation, five occurring in non-heated soils and the remaining four in the heated soils on the beach and ridge at Pendulum Cove; none was common to both habitat types and none was isolated from eight sites of barren unheated soil. The endoparasitic phycomycete *Myzocytium* sp. was isolated only from the heated beach site and since these fungi have motile spores, low temperatures are probably responsible for their absence elsewhere on the island and in the Antarctic generally (Gray, in press).

Macro-vegetation was observed in freshwater only in Kroner Lake where extensive growths of blue-green, green and red-brown algae covered much of the substrate in water up to 10 cm deep. This vegetation was most evident near to springs from which hot sulphurous water (*c.* 30–40°C) was issuing. The algae became sparser away from these springs as the temperature decreased to 8–10°C.

Factors Affecting Immigration, Establishment and Survival

At the time they are deposited volcanic materials are sterile and lacking in organic nutrients; only inorganic nutrients are available but even these, especially nitrogen, are often deficient. Thus pioneer colonists must be preadapted to tolerate relatively unstable conditions and, in particular, minimal nutrient concentrations. A chemical analysis of several ash soils on Deception Island is given in Table V. In all cases the organic content of the ash is very low, particularly at sites where colonization is proceeding. Both extractable and total N are in exceptionally low concentrations, while most other major nutrients are also present in exceedingly small amounts, especially phosphorus and potassium, increasing slightly beneath closed stands of vegetation. The inland fumarole site above Pendulum Cove has the lowest of all values, yet, because of the favourable microclimate regime, this site has the greatest development of vegetation indicating the low nutrient requirement of bryophytes. It is probable that sufficient nutrients are derived largely from precipitation in the form of rain, snow and wind-blown sea spray. Some of the numerous algae which grew on soil culture plates from propagules in these barren soils were blue-green taxa which may have had the capacity to fix atmospheric nitrogen and therefore increase its availability to bryophytes. Griggs (1933) and Griggs and Ready (1934) showed that liverworts, especially *Cephaloziella*, can be dominant pioneer plants on nitrogen-free ash following major eruptions and may establish conditions suitable for secondary colonists.

Primary colonists of newly created volcanic surfaces rely on invasion of propagules from nearby, if suitable sources still exist, and, for small islands, on immigration by long distance dispersal from overseas. Most accounts of primary colonization of new volcanic soil refer to bryophytes as being among the first macroscopic plants to become established. Colonization by these cryptogams appears to occur after about three to four years on unheated ground (e.g. Eggler, 1959; Johannsson, 1968) but the process may be greatly enhanced on heated ground with steam where bryophyte gametophytes and sporophytes may develop within a year of the creation of a new surface (e.g. Collins, 1969; Young and Kläy, 1971). The development of relatively diverse communities of bryophytes associated with geothermal areas has also been well documented (Eggler, 1959; Yoshioka, 1968; Sjögren, 1974; Longton and Holdgate, 1979; Given, 1980). The majority of the primary colonists are short acrocarpous taxa and, not surprisingly, several are ephemerals (e.g. *Funaria, Physcomitrium* and *Leptobryum*) (Eggler, 1959; Dickson, 1965; Einarsson, 1967; Collins, 1969). The *Funaria* sp. and the bulbiferous *Bryum* reported as colonists of heated ground on Deception Island appear also to behave as ephemerals. Elsewhere on Deception Island colonization of ash soils and lahar mud is mainly by a few taxa of short acrocarps, especially species of *Bryum, Ceratodon* and *Polytrichum*, the latter being particularly effective in binding loose soil and stabilizing the substrate prior to secondary colonization; the importance of Polytricha as stabilizing agents has long been recognized (Leach, 1931).

With regard to the developing community on heated ground above Pendulum Cove on Deception Island, it is interesting to note that one of the dominant colonists is a species of *Campylopus*, a genus which dominates some of the zoned communities around fumaroles in the South Sandwich Islands (Longton and Holdgate, 1979) and abounds in similar habitats in New Zealand (Given, 1980), Mexico (Eggler, 1959) and Hawaii (van Zanten, 1978). *Marchantia* spp. are also sometimes early colonists on heated ground where the thalli serve to stabilize the loose substrate (Young and Kläy, 1971; Magnusson and Fridriksson, 1974; Longton and Holdgate, 1979).

Several methods of colonization of new surfaces may exist. Since few species of Antarctic bryophytes produce sporophytes (Webb, 1973) dissemination and establishment from local sources is largely by vegetative means and numerous modes of vegetative reproduction are known (Rudolph, 1970; Gimingham and Smith, 1970; Smith, 1972). In the colonizing bryoflora of Deception Island, leaf and stem apical fragments (especially in species of *Brachythecium, Bryum, Campylopus*, and *Ceratodon*) are probably the most common form of spread although a relatively high proportion (35%) have been recorded with sporophytes (Table I), but axillary buds (*Bryum argenteum*), shoot base bulbils (*Grimmia antarctici* and *Pottia heimii*), shoot apex bulbils (*Bryum* sp.) deciduous leaf tips (*Sarconeurum glaciale*), and gemmae (*Barbilophozia hatcheri* and *Marchantia berteroana*) are also produced. In favourable habitats such propagules must be an important means of rapid dissemination. In the predominantly dry and windy environment of Deception Island, propagules will be blown or washed to new habitats and, where adequate moisture and stability persist, these vegetative units will develop rhizoids and become established. While establishment by spores of local provenance also undoubtedly occurs (see Table IV) perhaps the greatest input to the gene pool of the bryophyte population of a small island is the addition of plants derived from exotic spores. While spores of species already established on the island are likely to be pre-adapted for survival in such an environment there is also an influx of non-Antarctic taxa as is evidenced by the occurrence of several species unique to the biome which have been found only in association with heated ground on Deception Island and in the South Sandwich Islands, where growing conditions are atypical but favourable for the growth of more temperate taxa. The major source of such species is probably southern South America and it is likely that there is an influx of spores over much of the Antarctic biome derived from more northerly latitudes. This hypothesis is also supported by van Zanten (1978) who stated, 'There is probably a continuous supply of spores being transported by air currents from one area to another within the belt of strong westerly winds in the Southern Hemisphere, and these spores will probably have descended into new areas perpetually over millions of years'. However, this has yet to be tested and quantified by trapping experiments, although the occurrence of exotic pollen at various levels in a deep Signy Island peat deposit provides an indication of the rate of deposition (Churchill, 1973).

Germination and subsequent development and survival are possible by only those species genetically and physiologically pre-adapted to tolerate the prevailing conditions. It is these that form the basis of the present Antarctic bryoflora and vegetation, while those that are not pre-adapted but are fortunate enough to be deposited on areas affected by geothermal activity, although existing sometimes for only a short duration, develop unique and occasionally transient communities of extremely restricted distribution.

The new record of *Marchantia polymorpha* on heated ground on Deception Island was attributed by Young and Kläy (1971) to long distance dispersal from South America, the nearest source of this species. However, this liverwort was probably the very similar *M. berteroana*, which was found at the same site ten years later and, while unknown in the island's flora before the eruptions, it may have been derived from nearby (*c.* 150 km) but scarce populations elsewhere in the South Shetland Islands or on the north-west of the Antarctic Peninsula. Also, its arrival as spores or gemmae at the fumarolic area may have been by human agency (e.g. adhering to boots), as several scientists inspected this area shortly after the 1969 eruption. Other new taxa at heated sites may have also been accidentally introduced by this method. It should not be overlooked that, prior to the Antarctic Treaty, sheep and poultry were kept at the Chilean station at Pendulum Cove during the 1950s and early 1960s, and seeds, spores, etc., were probably introduced in fodder imported for this livestock. Bales of such fodder still exist in a corral used for sheep at the Chilean base Arturo Prat on Greenwich Island, South Shetland Islands. Longton (1966) reported the occurrence of several alien phanerogam seedlings near the Pendulum Cove station and also of more persistent populations of *Poa annua* and *P. pratensis* at the former whaling station in Whalers Bay. The *P. annua* colony was thriving and spreading rapidly at the time of the 1967 eruption but had disappeared by the following year (Collins, 1969) and there was still no evidence of the grass in 1981, the site having been swept by the 1969 mudflow. However, some of the more resistant cryptogam spores may have remained dormant for many years in the ash and germinated as a result of the increased geothermal activity following the eruptions. Van Zanten (1978) showed that spores of many moss species are capable of remaining viable after three years desiccation with or without subsequent wet or dry freezing treatment at −30°C. Van Zanten and Pócs (1981) discussed the longevity of bryophyte spore viability; some acrocarpous moss species are capable of germinating after up to 20 years of desiccated storage. Also, the spores of liverworts have very low survival capacity, possibly correlated with the hydrophytic nature of these plants; they also tend to have larger heavier spores which are less conducive to long distance dispersal than are moss spores. Similarly, spores of pleurocarpous mosses are much less drought resistant than those of acrocarps, which may account for the low incidence of the former growth-form throughout the Antarctic biome.

Thus it is conceivable that the spore rain over the Antarctic creates a bank of propagules in the soil (and probably in the ice), a proportion of which retain their viability for many years. Should some succeed in being deposited in or being redistributed to niches where temperature and moisture are favourable, they may be able to germinate. If the stability, edaphic conditions and microclimate of the substrate remain adequate then a few colonists may survive long enough to establish small colonies, which together with similar colonies of the same or other species, may gradually develop a distinctive community characteristic of the environmental features of the habitat (Smith, 1972).

Deception Island, therefore, offers an ideal situation for studying the dynamics of ecesis and community development in a very basic ecosystem restricted to cryptogamic vegetation in which interactions are minimal and the processes of the propagule immigration–colonization–succession catena are very much simplified. The processes and rates of colonization and development at heated and non-heated sites may be readily compared and the influx of immigrant propagules and the colonization potential of the existing soil propagule bank may be tested and quantified. It is to be hoped that any such research investigations will pay due regard to the vulnerability of such a fragile ecosystem. It is imperative that all visitors (i.e. ships' crews, tourists and scientists alike) to the island observe a sensible code of conservation practice and are aware of the considerable danger of altering the natural environment by their careless but unintentional introduction of alien propagules and disturbance of some of the highly unstable and unique habitats on the island.

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