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Dispersal of the moss *Campylopus pyriformis* on geothermal ground near the summits of Mount Erebus and Mount Melbourne, Victoria Land, Antarctica

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Abstract: Mount Melbourne in northern Victoria Land, Antarctica, is a glaciated 2733 m volcanic cone. The moss *Campylopus pyriformis* occurs on two small areas of steam-warmed snow-free ground near its summit. This moss species also occurs in temperate regions world-wide, but has not been recorded elsewhere in continental Antarctica. RAPD (Random Amplified Polymorphic DNA) studies of 26 samples of *C. pyriformis* from two areas of heated ground on Mount Melbourne showed there was genetic diversity within the population. Genetic evidence for dispersal between the two sites, together with some genetic variation within individual colonies, indicates a single colonisation event has probably occurred at this extremely isolated location followed by multiple mutations. A single sample of moss protonema was collected 25 years ago from steam-warmed ground near the summit of another volcano, Mount Erebus (3794 m), on Ross Island some 300 km south of Mount Melbourne. The moss could not be identified based on morphological and reproductive criteria, as all attempts to differentiate it to a recognisable gametophyte were unsuccessful. The RAPD technique has now shown it to be *C. pyriformis*, and closely related to the population on Mount Melbourne.

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Introduction

Mount Melbourne (74°21'S, 164°42'E), on the west coast of the Ross Sea in northern Victoria Land, East Antarctica, is a 2733 m stratovolcano, the centre of a young (two to three million year old) field of eruptive centres. It is believed to have been most recently active within the last few hundred years. It is covered by permanent snow and ice, which extends to the coast at Edmonson Point some 15 km away. Near its summit, on Cryptogam Ridge, there are a few small areas of steam-warmed ground, fumaroles and ice towers. This heated ground supports a community of plants comprising one species of moss, *Campylopus pyriformis* (Schultz) Brid., one species of liverwort *Cephaloziella varians* (Gott.) Steph., one species of lichenised alga, six chlorophyte species and six cyanobacterial species (Broady *et al.* 1987).

Campylopus pyriformis is widely known from both northern and southern temperate regions of the world, including Australia, New Zealand and South America (Frahm 1994). The genus is not known from elsewhere in continental Antarctica besides Mount Melbourne; other species of *Campylopus* have been found on heated ground on Deception Island, South Shetland Islands, and on the South Sandwich Islands, maritime Antarctica (Smith 1984). On Cryptogam Ridge *C. pyriformis* occurs as small cushions, up to about 4 cm^2, often close together forming populations up to 200 cm^2 with up to 70% ground cover. Growth is most abundant in the vicinity of fumaroles, where the water supply is more plentiful from melting ice and condensing steam. Sporophytes have not been observed there; like most other mosses in Victoria Land, *C. pyriformis* appears to reproduce only asexually, by dispersal of vegetative propagules. Although elsewhere *C. pyriformis* produces distinctively curved brood leaves in the upper leaf axils (Frahm 1994), these have not been observed on specimens from Mount Melbourne. Forms with brood leaves are common in Europe and New Zealand, but rare in Australia.

Southern Hemisphere atmospheric circulation patterns are consistent with the possibility of temperate moss propagules reaching Antarctica (Marshall 1996). Temperature and moisture conditions on heated ground on Mount Melbourne are evidently suitable for the establishment of *C. pyriformis* from vegetative propagules. In order to investigate whether one, several or multiple colonization events had been responsible for the establishment of this extremely remote and isolated population of *C. pyriformis*, we undertook a study of genetic variation within the population.

Close to the summit of another volcano, Mount Erebus on Ross Island (300 km south of Mount Melbourne), an

unidentified moss protonema has been known since a report by Lyon & Giggenbach (1974). Several small areas of steam-warmed ground support very sparse growth of this moss. Only the undifferentiated, filamentous protonemal form has been found (Broady 1984). The summit of Mount Erebus is at 3794 m, the slopes are permanently covered in ice, and no other mosses have been found in the vicinity of the mountain summit or slopes. A single sample of this moss protonema was collected but all attempts failed to differentiate the protonema to a morphologically recognisable gametophyte, using standard methods of moss differentiation on media with altered hormone regimes and environmental conditions (Cove & Broady, personal communication 1997). Thus the identity of the moss specimen has remained unknown.

In Victoria Land two moss species are known from high-altitude geothermal ground – *Campylopus pyriformis* from the summit of Mount Melbourne, and *Pohlia nutans* (Hedw.) Lindb. from the summit of Mount Rittmann (Bargagli *et al.* 1996). From coastal and low-altitude areas on Ross Island and southern Victoria Land the dominant (but generally sparse) moss populations comprise *Bryum argenteum* Hedw., *B. pseudotriquetrum* (Hedw.) Gaertn., Meyer et Scherb., *Sarconeurum glaciale* (Hook.f. et Wils) Card. et Bryhn, *Hennediella heimii* (Hedw.) Zand. and *Ceratodon purpureus* (Hedw.) Brid. (Seppelt & Green 1998). We wished to determine whether the Mount Erebus moss was related to the other known moss populations on geothermal ground, or to other moss species found near sea level on Ross Island and Victoria Land, or to a population from outside the Ross Sea region.

For analysis of genetic diversity within the isolated moss population on Mount Melbourne, and for taxonomic identification of the Mount Erebus moss, we chose the RAPD (Random Amplified Polymorphic DNA) technique. This method has already been used to differentiate between the six dominant moss species found on Ross Island and Victoria Land (Skotnicki *et al.* 1997); subsequently, RAPD primers have been chosen for even greater taxonomic distinction of these species. RAPDs have also proven very useful for comparison of genetic relationships in several species of Antarctic mosses (Selkirk *et al.* 1998, Skotnicki *et al.* 1998a, 1998b, 1999a, 1999b), and the method has distinct advantages over other techniques of genetic analysis for these mosses: no other genetic information is needed, very small samples (such as a single moss shoot) are sufficient, and many samples can be compared rapidly and inexpensively. As mosses are predominantly haploid organisms, the potential problems sometimes encountered with codominance of RAPD bands in diploid organisms are not of concern.

Materials and methods

Collection of moss samples

Samples of a few shoots of *Campylopus pyriformis* were collected from each of the colonies found near the summit of Mount Melbourne. Twenty-three samples were collected from Site A, an elongate area of heated ground *c.* 110 x 15 m, along a 50 m west to east transect. Three samples were collected from Site B, a small (8 x 4 m) area of heated ground, 400 m east of Site A. At Site B, samples were collected along a 5 m north-west to south-east transect. Samples were numbered progressively from west to east; samples 1–23 were from Site A, 24–26 from Site B. They were collected from Mount Melbourne on 21 January 1995, and were air-dried and stored frozen at -20°C. Permits to enter SPA 22 within SSSI 24 (Cryptogram Ridge) and to collect small moss samples were issued by Antarctica New Zealand to K. D. Adam, for use

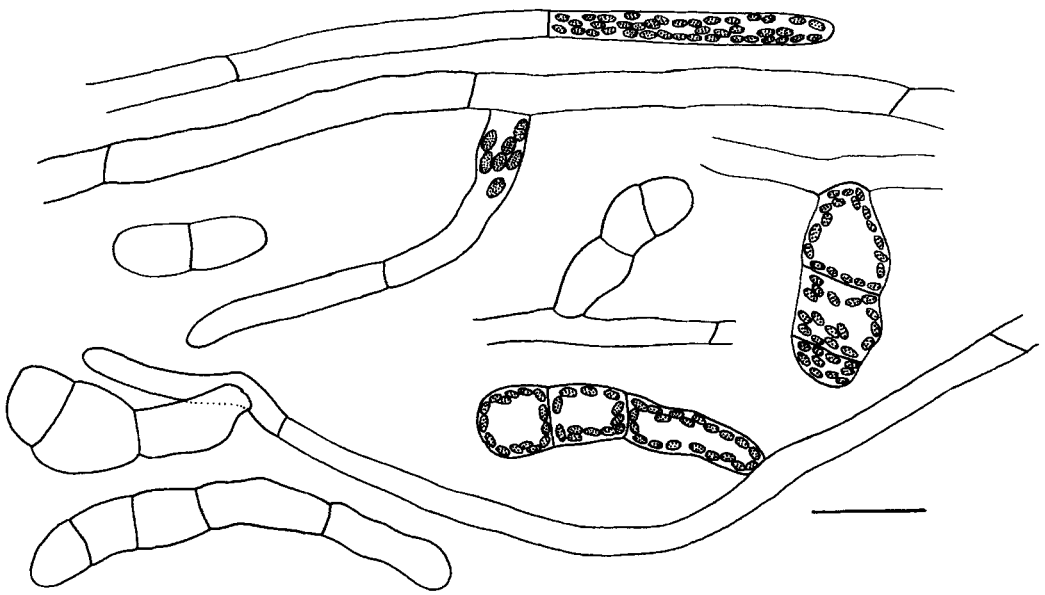

Fig. 1. Mount Erebus moss protonema with associated gemmae of 2–5 cells; from 11 week culture at 20°C. Chloroplasts are shown in some cells. Scale is equivalent to 50 µm.

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by members of Event K022.

Four samples of *C. pyriformis* from two volcanic areas in the North Island of New Zealand (Mount Tarawera, samples T1 and T2; Waimangu Valley, samples W1 and W2) were included in this study for comparison.

Small samples of other moss species found in the region (*Bryum argenteum, B. pseudotriquetrum, Hennediella heimii, Ceratodon purpureus* and *Sarconeurum glaciale*) were collected from several sites in southern Victoria Land and Ross Island (Skotnicki *et al.* 1997). Several small samples of *Pohlia nutans* were also collected near the summit of Mount Rittmann for comparison (Bargagli *et al.* 1996). Moss samples were all collected into paper envelopes and stored frozen until use. Voucher specimens (except for *P. nutans* and the Mount Erebus protonema held at the Australian National University) are held at the University of Waikato herbarium.

On "Tramway Ridge", Mount Erebus, moss protonema was a component of green crusts coating soils, and also occurred in small crevices and depressions, at soil surface temperatures of 10–30°C. It covered a total area of no more than 5 m^2 as scattered patches, and was associated with several coccoid chlorophyte algae and cyanobacteria (Broady 1984). A small sample of this moss protonemal growth was collected in 1990 from steam-warmed ground at site A (*c.* 3400 m altitude) near the summit of Mount Erebus (Broady 1984; a permit was issued by Antarctica New Zealand to enter SSSI 11, "Tramway Ridge", and to collect the small sample described). Cultures were established under sterile conditions in an illuminated growth cabinet at 22°C on Bold's Basal Medium (Bold 1967) with 1.5% agar. In culture the protonema formed gemmae (Fig. 1), but could not be differentiated further.

DNA extraction and RAPD amplification

DNA was extracted from single moss shoots by a method developed previously for Antarctic moss species (Skotnicki *et al.* 1998a). For each sample, a 2–3 mm shoot was ground in CTAB (cetyl trimethyl ammonium bromide) extraction buffer using an electric drill fitted with a sterilised glass bit, extracted with chloroform/isoamyl alcohol, RNase-treated, and precipitated with isopropanol. After rinsing the DNA pellet in ethanol, it was resuspended in 15 µl sterile water and stored at 4°C until used for RAPD amplification.

For the Mount Erebus specimen, a small sample (*c.* 2 mm^3) of the protonemal growth was removed from an axenic culture growing on BBM agar. DNA was extracted in the same manner as for whole moss shoots. The DNA pellet was resuspended in 30 µl sterile water and stored at 4°C until used for analysis. This dilution of the DNA was equivalent to the DNA suspensions from single shoots, and 1 µl gave reproducible RAPD banding patterns, as did the shoot DNA suspensions. It was not found necessary to take additional precautions against microbial contamination, as no RAPD bands were obtained from similar extractions on soil surrounding the Mount Melbourne moss colonies (the protonemal sample was grown under aseptic conditions).

Moss DNA was amplified in RAPD reactions (Rafalski & Tingey 1993) by PCR (Polymerase Chain Reaction, Williams *et al.* 1993) in a microtitre plate (Skotnicki *et al.* 1998a); each standard RAPD reaction contained 1 µl DNA, 0.5 mM primer, 0.25 mM each dATP, dCTP, dGTP and dTTP, PCR reaction buffer (Perkin-Elmer Cetus), 2 mM $MgCl_2$, and 0.5 Units AmpliTaq DNA polymerase (Perkin-Elmer Cetus), in a final reaction volume of 10 µl. Single RAPD primers from the OP-A, OP-B, OP-C and OP-P kits (Operon Technologies) were used for amplification of moss DNA.

PCR reactions were incubated in a Corbett FTS-960 Thermal Cycler, with a program of one cycle of 94°C 3 min, 35°C 2 min, 72°C 3 min, 43 cycles of 94°C 10 sec, 35°C 10 sec, 72°C 50 sec, and one cycle of 72°C 3 min. The reactions were then electophoresed through 1.5% agarose gels, stained in ethidium bromide, and photographed under UV light using standard methods (Sambrook *et al.* 1989).

RAPD bands were scored as present or absent on gels, with PCR reactions being done in duplicate or triplicate to confirm the reproducibility of banding patterns. The Jaccard algorithm in the RAPDistance computer program (Armstrong *et al.* 1995) was used to produce a distance matrix by pairwise comparison of the patterns of DNA fragments. From this matrix a neighbour-joining tree was calculated using the NJTREE and TDRAW programs in the package (Armstrong *et al.* 1995, Ferguson 1990, Jin 1988, Saitou & Nei 1987, Studier & Keppler 1988).

Results

Genetic diversity of Campylopus pyriformis *on Mount Melbourne*

After initial experiments to optimise the RAPD primers for *Campylopus pyriformis*, and controls to ensure reproducibility of RAPD results with this species, we analysed the extent of genetic diversity within the Mount Melbourne population.

DNA from 26 samples of *C. pyriformis* from Mount Melbourne and four from New Zealand was amplified by PCR using five different primers: OP-A1, OP-B6, OP-B12, OP-P1 and OP-P17. A total of 62 bands was scored on gels across all samples. Dendrograms produced by RAPDistance using six different algorithms showed the same groupings of samples: the Mount Melbourne samples clustered separately from the New Zealand samples, and the two Mount Tarawera samples were distinct from those from Waimangu Valley (Fig. 2).

A PTP test on the dendrogram shown in Fig. 2, comparing it with 20 trees produced from randomized sets of the data, gave a result of 35.01. Thus the dendrogram has significantly shorter branch lengths than dendrograms produced from randomised data, strongly suggesting that the tree structure is real.

The dendrogram also showed that not all the *C. pyriformis* samples were genetically identical, i.e. there was some genetic

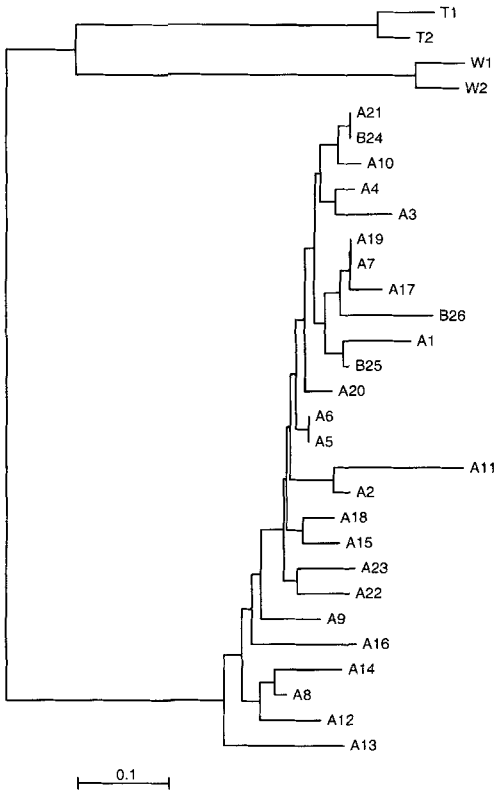

Fig. 2. Dendrogram produced by RAPDistance program, showing relationships between samples of *Campylopus pyriformis*, 26 from Mount Melbourne and four from New Zealand, as shown by similarities of RAPD banding patterns. T = Mount Tarawera, New Zealand, W = Waimangu Valley, New Zealand, A = Mount Melbourne, Antarctica Site A, B = Mount Melbourne, Antarctica Site B, numbers = sample number from each site. A total of 62 RAPD bands was scored, and six other algorithms gave similar dendrograms. A PTP test on this dendrogram gave a value of 35.01, indicating strong support for the tree structure.

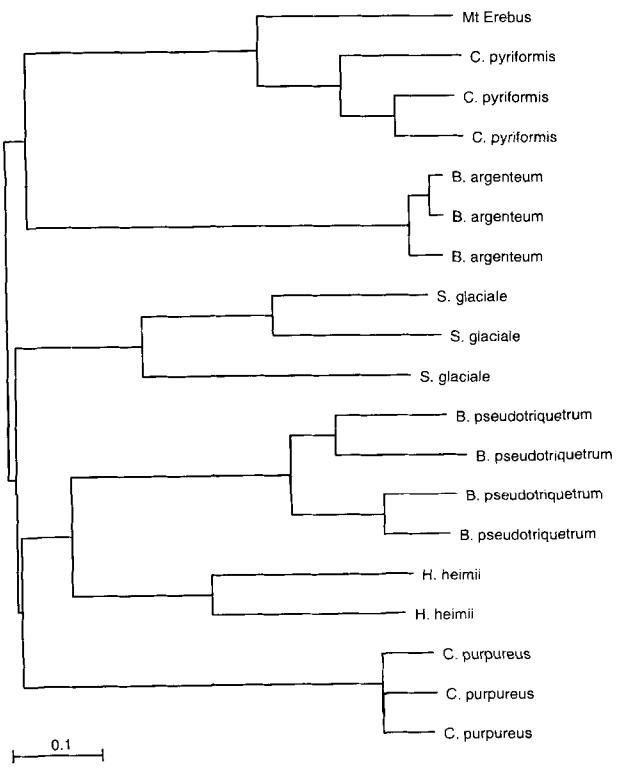

Fig. 3. Neighbour-joining tree obtained from RAPD bands of six moss species (*Campylopus pyriformis, Bryum argenteum, B. pseudotriquetrum, Ceratodon purpureus, Hennediella heimii, Sarconeurum glaciale*) and Mount Erebus protonema, scored after amplification with ten primers (OP-A1, OP-A8, OP-A17, OP-A18, OP-B6, OP-B12, OP-C13, OP-C18, OP-P1 and OP-P17). A total of 125 bands was used, with the Jaccard algorithm of the RAPDistance package; other algorithms of the package gave similar results. The dendrogram clearly shows the similarities between the Mount Erebus sample and *Campylopus pyriformis* from Mount Melbourne.

variation within the population of *C. pyriformis* on Mount Melbourne. The samples from Site A did not group separately from those from Site B: plants from Sites A and B appeared to form a single population. In three pairs of samples, A21 and B24, A19 and A7, and A6 and A5, there was no detectable difference between the pairs (Fig. 2).

In addition to among-colony variation, we also screened multiple shoots from single colonies to analyse genetic variability within colonies. While several pairs of shoots joined at their bases gave identical results within the pairs, separate shoots from the same colonies were not necessarily identical. Six single shoots, separated by 2–5 mm (depending on the size of the sample), were tested from each of three colonies. The RAPD results showed some genetic diversity within each colony, but with shoots being more closely related to others from the same colony than to those from other colonies.

Molecular taxonomy of Mount Erebus moss

Initially, the Mount Erebus protonemal sample was screened with five RAPD primers which have proven useful for distinguishing six Antarctic moss species (OP-A1, OP-A17, OP-A18, OP-B6, and OP-C13; Skotnicki *et al.* 1997, 2000). Three or four samples each of these six mosses (*Bryum argenteum, B. pseudotriquetrum, Ceratodon purpureus, Hennediella heimii* and *Sarconeurum glaciale* from near sea level in southern Victoria Land, and *Campylopus pyriformis* from Mount Melbourne), and of *Pohlia nutans* from Mount Rittmann, were also tested with the same primers. RAPD bands were directly compared on gels between the Mount Erebus protonema and the other specimens.

The results indicated that the Mount Erebus protonema was closely related to the three specimens of *C. pyriformis*, sharing many RAPD bands. It did not show similarities with any other species tested. A neighbour-joining tree of the RAPD results obtained with ten primers demonstrated that the Mount Erebus protonema is *C. pyriformis*, sharing a close relationship with

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the Mount Melbourne specimens (Fig. 3). This dendrogram gave a PTP value of 111.12, demonstrating very strong support for the tree structure.

Subsequently, the Mount Erebus protonema was compared in RAPD analyses with three specimens of *C. pyriformis* using nine primers known to give a good range of RAPD bands for this moss species: OP-A1, OP-A8, OP-A17, OP-B6, OP-B12, OP-C18, OP-P1, OP-P16 and OP-P17. Results clearly demonstrated that it is *C. pyriformis*. Of the sixty bands scored, 34 were identical for all four specimens, 13 were shared between the Mount Erebus sample and some Mount Melbourne *C. pyriformis* colonies, and 13 differed. (In contrast, the Mount Erebus sample shared only two of 125 RAPD bands in common with the *B. argenteum* specimens, one with *S. glaciale* and *C. purpureus*, and none with the other species tested.)

Discussion

Seppelt & Green (1998) describe the bryoflora of southern Victoria Land, Antarctica as including eight species of moss. These all occur on ground heated only by solar energy, subject to ambient soil and climatic conditions. They are relatively widespread, occurring at sites that, for at least part of the year, have available liquid water and are snow-free.

The geothermally heated soils on Mount Melbourne, Mount Erebus and Mount Rittmann differ from cold ground sites in the region not only in their warmer surface soil temperature (0-42°C at Mount Melbourne, Broady *et al.* 1987; up to 60°C at Mount Erebus, Broady 1984; above 0°C for short periods in summer on low altitude cold ground, Campbell *et al.* 1997), but also in the continuous availability of moisture condensing from steam at soil and vegetation surfaces, and in physicochemical characteristics of the soil (Bargagli *et al.* 1996, Broady 1984, Broady *et al.* 1987).

A total of eight species of cyanobacteria, twelve chlorophytes and three bryophytes has been described from the three sites of volcanically heated ground in the Ross Sea region (Broady 1984, Broady *et al.* 1987, Bargagli *et al.* 1996). Of these, two species of cyanobacteria, five species of chlorophytes and one moss (*Campylopus pyriformis*) are known in Antarctica only from one or more of these geothermal sites. We have identified the moss protonema from Mount Erebus to be *C. pyriformis*, and make this addition to the known bryoflora of southern Victoria Land.

Campylopus pyriformis occurs in a range of habitats in temperate regions, including volcanically heated ground in New Zealand (J. Beever, personal communication 1999). It is likely that there is some component (or combination of components) of the volcanic substratum on Mount Melbourne and Mount Erebus that can be tolerated by *C. pyriformis* but not by other moss species that occur in the region. These factors include the relatively acid soils, and the presence of high concentrations of mercuric ions in *C. pyriformis* from Mount Melbourne, perhaps as a result of emissions of gaseous mercury from the fumaroles there (Bargagli *et al.* 1996). Since propagules of *C. pyriformis* have reached and become established on Mount Melbourne and Mount Erebus, it seems likely that propagules of other moss species in the region would also have been deposited there but could not become established.

There is evidence that airborne dispersal has the potential to distribute a wide range of microscopic propagules to many Antarctic sites (Broady *et al.* 1987, Marshall 1996, Smith 1991, Walton 1990, Wynn-Williams 1991). Within Antarctica, genetic studies have provided evidence for dispersal of moss propagules over distances of a few metres (Selkirk *et al.* 1998, Skotnicki *et al.* 1998a, 1999a) to tens of kilometres (Skotnicki *et al.* 1998b, 1999a). We interpret the three pairs of genetically identical samples within the Mount Melbourne population as evidence of local dispersal within and between nearby areas of heated ground. The very close genetic relationship shown here between *C. pyriformis* growth from Mount Erebus (protonemal sample) and Mount Melbourne (three mature gametophyte samples) provides evidence for dispersal between areas of heated ground on mountains some 300 km apart.

Since there is no apparent sexual reproduction occurring within the Mount Melbourne population of *C. pyriformis*, genetic variation within this population indicates one of three possibilities: a single colonization event followed by many mutation events to give the observed variation, or successful establishment by numerous genetically different propagules, or a small number of colonization events followed by some mutation events. In this isolated, high latitude, high altitude environment with high UV-B exposure, post-colonization mutation seems quite likely. Overall, the extent of genetic variation among the isolates of *C. pyriformis* appeared to be similar (as judged by the proportion of polymorphic RAPD bands) to that observed for other discrete, isolated Antarctic moss populations.

In several other Antarctic moss species, *Ceratodon purpureus* (Skotnicki *et al.* 1998a, 2000), *Bryum pseudotriquetrum* (Skotnicki *et al.* 1998b), *Sarconeurum glaciale* (Skotnicki *et al.* 1999a), and *Bryum argenteum* (Skotnicki *et al.* 1999b), we have also detected within-colony variation. This variability was not only due to immigration of propagules from elsewhere, but appeared to be due to mutation within the individual plants. In these species, the fact that multiple shoots from single colonies usually appeared genetically more similar to each other than to shoots from nearby clumps suggests that mutation does occur under the environmental conditions of Antarctica. As similar results were obtained for the Mount Melbourne *C. pyriformis* population, this lends support to the theory that post-colonisation mutation events have indeed taken place.

It is not known whether the occurrence of *C. pyriformis* on Mount Erebus only as protonema reflects unsuitable environmental conditions there for gametophyte (leafy shoot) differentiation, or a mutation that prevents differentiation. Although it seems likely that environmental conditions near

the summit of Mount Erebus could indeed be unsuitable for differentiation, the persistence of the protonemal stage in culture conditions suitable for differentiation suggests that mutation is a distinct possibility. This intriguing possibility will be further investigated.

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