

THE COLONIZATION OF VOLCANIC TEPHRA ON DECEPTION ISLAND BY PROTOZOA: LONG-TERM TRENDS

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ABSTRACT. Samples of volcanic tephra were collected in 1981 and 1984 from sites on Deception Island, South Shetland Islands, which had been studied between 1968 and 1973 following eruptions in 1967, 1969 and 1970. An area unaffected by volcanic activity since before 1829 on Fumarole Bay was also sampled. The protozoa from these sites were determined and the results compared with those of earlier studies. Twenty-three species of Protozoa (5 flagellates, 2 naked rhizopods, 4 testate rhizopods and 12 ciliates) were observed in addition to the 13 species recorded previously. It was concluded that the processes of microbial colonization of sterile tephra had been initiated within 1 year of deposition, with the first protozoan species appearing after 10 months. The rate of increase in numbers of protozoan species in unvegetated tephra was most directly associated with the rate of accumulation of organic matter, though there was also evidence that species numbers showed some increase with the passage of time without any increase in organic content. After 12 years, the protozoan fauna of unvegetated tephra had attained a diversity (5 to 7 species) comparable to that in tephra more than 150 years old. Tephra containing macroscopic bryophyte or thallose alga vegetation had markedly lower pH and higher moisture, organic content and species numbers than unvegetated tephra regardless of age. The fauna of some 12-year-old tephra samples showed a species diversity (9 to 14 species) approaching that of similarly vegetated tephra more than 150 years old (15 to 17 species). The pioneer protozoa of unvegetated tephra (small flagellates) from different sites were similar, but the protozoa from older tephra with vegetation (flagellates, amoebae, ciliates) showed greater heterogeneity between sites. Testate amoebae were recorded only from tephra more than 150 years old with bryophytes except for *Corythion dubium*, which was also observed in 12-year-old tephra with *Drepanocladus*, thus confirming the status of this species as the most ubiquitous and successful testate rhizopod in the maritime Antarctic.

INTRODUCTION

Deception Island, a volcanic island in the South Shetland Islands, is of particular interest for the study of the processes of biological colonization, survival and succession in an ecosystem in which the fauna and flora are impoverished and restricted in abundance even in comparison with other maritime Antarctic locations. Following the three episodes of volcanic activity between 1967 and 1970 (Baker and others, 1975), some detailed observations have been reported on the effects of the eruptions on the cryptogamic flora of the island and on its recovery (Collins, 1969; Young and Klay, 1971; R. I. L. Smith, 1984*a, b*). Observations on the microbiota, however, have been sparse. Cameron and Benoit (1970) noted the presence of bacteria, algae, filamentous fungi and yeasts in bare ash from the new island in Telefon Bay one year after the 1967 eruption. Between 1968 and 1973, observations were made on the protozoan fauna of tephra from the three recent eruptions, varying in age from 0.3 to 4.0 years, collected from up to five sites on four occasions (Smith, 1974). The numbers of species of Protozoa that had colonized the tephra were closely correlated with both the age and the percent loss on ignition of the tephra, the linear regression

line indicating an increase in numbers of species with age at an arithmetic rate of 1.4 species per year between the ages 0.8 and 4.0 years. Samples containing bryophyte vegetation were richer in protozoan species than samples of the same age with no macroscopic vegetation. It was clear, therefore, that colonization of the volcanic tephra by heterotrophic microbes could start within one year after deposition.

In order to assess the longer-term trends in colonization, further samples of tephra were collected in March 1981 and January 1984. Materials were obtained as far as possible from the same sites as previously (1968–73). In addition, samples of both vegetated and unvegetated tephra were collected from the area of Fumarole Bay, an area unaffected by recent eruptions except for a fall of fine ash after the 1969 eruption (Baker and others, 1975) and apparently otherwise unaffected by any activity since before 1829 (Roobol, 1973). It was thus possible to compare the protozoan species of earlier studies with those inhabiting tephra 10–13 years and at least 150 years old.

METHODS

The location of sites sampled is shown in Fig. 1. At each site 500 g samples of the 0–5 cm horizon of both bare and vegetated (if present) tephra were taken from undisturbed ground, using a sterile trowel, and sealed in polythene containers at 4°C during transport to either the UK or the Signy Island station. The species of Protozoa

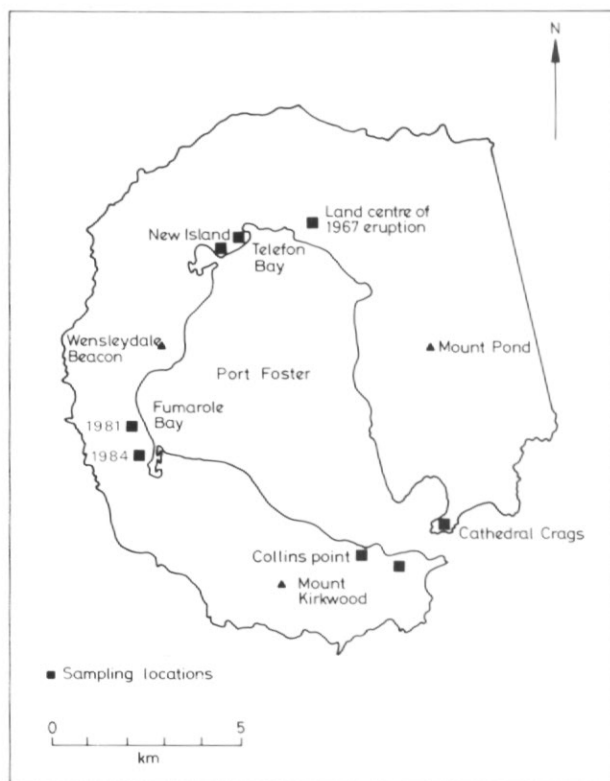


Fig. 1. Sketch map of Deception Island during 1981–4 showing the positions of sampling sites (after R. I. L. Smith and P. G. Copestake).

present and the pH, moisture content and loss on ignition of six replicate subsamples were determined by the same method as those used in previous studies (Smith, 1974).

RESULTS AND DISCUSSION

The full list of samples of volcanic tephra analysed for protozoan fauna, including those collected between 1968 and 1973 as well as those collected in 1981 and 1984, is shown in Table I. The sample code indicates the location and occasion of collection and the nature of the vegetation present, if any.

The new island in Telefon Bay

The area of the new island in Telefon Bay was sampled on all six sampling occasions, so the results for its two sites are the most comprehensive in the study. Created by the 1967 eruption, the area was an actual island only on sampling occasions I and II because much of it was destroyed by the 1970 eruption and the remnant joined to the mainland (Baker and McReath, 1971). Although it is no longer detached from the mainland, the term 'new island' is retained here in order to maintain the identity of this area in conformity with earlier records. Between 1970 and 1973 the topography of the area changed further, apparently owing to wind and water erosion and the slumping of loose ash and scoria. Eye-witness accounts and sketch maps by R. I. L. Smith and D. D. Wynn-Williams in 1981, and by P. G. Copestake in 1984, suggest that there has been no significant further erosion during the last 11 years and that this area has consolidated, with the volcanic ash and lapilli weathering to form pockets of mineral 'soil' resembling the fines that commonly occur in maritime Antarctic fellfields. No macroscopic vegetation has colonized the new island area since 1970 and there is little detectable trend in the monitored physical properties of the tephra, with the pH remaining close to 7.0, the moisture content around 13% dry weight and the loss on ignition 0.5–1.0% dry weight. Nevertheless, there appears to have been a gradual increase in the numbers of protozoan species inhabiting the tephra; these rose slowly from 0 to 5 over 13 years.

This colonization may be consequent upon a gradual increase in the availability of food organisms. In March 1981 (sampling occasion V), D. D. Wynn-Williams determined microflora numbers in the 0–3 cm horizon of tephra from near Site A. This material contained 202 ± 59 total bacteria, 0.08 ± 0.08 total yeasts and 0.003 ± 0.09 total filamentous fungi (colony forming units $\times 10^3$ g⁻¹ dry weight, means of four replicate estimates with standard error). These counts represent increases over those made by Cameron and Benoit (1970) on material from the same area (sample 712) of at least two orders of magnitude. They are also closely comparable to those observed in fellfield fines from other maritime Antarctic and sub-Antarctic locations (Wynn-Williams, 1984). It is clear, therefore, that the microbial community of the new island tephra has been increasing in abundance and diversity over the last 13 years, even though its activity has not had any appreciable influence on the monitored physical properties.

Collins Point

Tephra at Collins Point originated from the 1969 fissure eruptions on the western side of Mount Pond and the 1970 eruption did not affect this area (Baker and others 1975). Material for protozoological analysis was collected from sites 200 m west and 750 m south-east of Collins Point on sampling occasions II to V inclusive and so

Table I. List of samples of volcanic tephra collected on Deception Island between 1968 and 1984 and their characteristics.

Sample code	Date of collection	Age of tephra (yrs)	pH	Moisture (% dry weight)	Loss on ignition (% dry weight)	Numbers of protozoan species recorded
NIA I	10 Dec. 68	1.0	4.8	—	0.09	0
NIB I	10 Dec. 68	1.0	4.7	—	0.14	0
NIA II	11 Dec. 69	2.0	6.2	—	0.19	0
NIB II	11 Dec. 69	2.0	6.0	—	0.23	0
LC II _f	11 Dec. 69	2.0	5.5	—	2.12	6
CC II	27 Nov. 69	0.7	—	—	0.04	0
CP II	11 Dec. 69	0.8	6.4	—	0.53	2
NIA III	18 Dec. 70	0.3	6.8	—	0.31	0
NIB III	18 Dec. 70	0.3	6.5	—	0.28	0
CC III	18 Dec. 70	1.8	6.3	—	0.04	1
CP III	18 Dec. 70	1.8	6.5	—	0.15	2
NIA IV	22 Feb. 73	2.5	7.2	13.1	1.10	3
NIB IV	22 Feb. 73	2.5	7.2	19.4	0.55	2
LC IV	22 Feb. 73	2.5	6.3	10.8	0.57	3
CC IV	23 Feb. 73	4.0	6.3	19.6	1.33	5
CP IV _p	23 Feb. 73	4.0	5.5	56.8	13.7	9
NIA V	4 Mar. 81	10.5	6.9	9.4	0.59	4
NIB V	4 Mar. 81	10.5	7.1	12.4	0.65	3
CP V	25 Mar. 81	12.1	6.7	13.1	0.59	7
CP V _{pr}	25 Mar. 81	12.1	4.2	118.2	1.93	9
CP V _d	25 Mar. 81	12.1	5.7	117.9	19.2	14
FB V	4 Mar. 81	> 152	6.8	8.7	0.85	6
FB V _p	4 Mar. 81	> 152	5.8	59.9	15.8	15
FB V _b	4 Mar. 81	> 152	5.6	69.9	16.5	17
NIA VI	18 Jan. 84	13.4	6.9	12.0	0.70	5
NIB VI	18 Jan. 84	13.4	6.9	12.0	0.73	5
FB VI	18 Jan. 84	> 155	6.9	11.3	2.14	6
FB VI _p	18 Jan. 84	> 155	5.2	37.8	15.0	15

Figures for physical properties are means of reading from six replicate subsamples. Standard errors (omitted for clarity) are: for moisture $\leq 5\%$, for loss on ignition $\leq 10\%$, and for pH $\leq 2\%$ of the mean value.

A key to the sample codes is given below:

Sampling location

- NIA The new island in Telefon Bay, southwest end.
 NIB The new island in Telefon Bay, northeast end.
 LC The site near the land centre of the 1967 eruption.
 CC A site 200 m north of Cathedral Crags.
 CP Sites 200 m west and 750 m southeast of Collins Point.
 FB A site in Fumarole Bay, 2.5 km southwest of Wensleydale Beacon.

Sampling occasions

- I December 1968 (12 months after the 1967 eruption).
 II November–December 1969 (9–10 months after the 1969 eruption).
 III December 1970 (4 months after the 1970 eruption).
 IV February 1973 (1½ years after the 1970 eruption).
 V March 1981 (10½ years after the 1970 eruption).
 VI January 1984 (13½ years after the 1970 eruption).

Vegetation present in the samples

No suffix. Tephra devoid of macroscopic vegetation.

- f* *Funaria hygrometrica* moss
p *Polytrichum alpinum* moss
pr *Prasiola crispa* thallose alga
d *Drepanocladus uncinatus* moss
b *Brachythecium austro-salebrosum* moss

represent a series aged 10 months to 12 years. Like the new island material, no trend with time is apparent over this period in the physical properties of the unvegetated samples, but there was an increase in the numbers of protozoan species recorded, from 2 to 7; so microbial succession in this area may be inferred. Three samples from Collins Point contained macroscopic vegetation: *Polytrichum alpinum* (sampling occasion IV) has presumably regenerated through the 1969 tephra, this acrocarpous moss being the most efficient at growing upwards through an ash covering to reach a new surface (Collins, 1969). *Drepanocladus uncinatus* and *Prasiola crispa* (sampling occasion V) occurred as a result of colonization *de novo* by propagules arriving at the site some time between 1973 and 1981 or regenerated from old surfaces washed free of 1969 ash. All the vegetated samples had markedly greater loss on ignition and moisture content, together with lower pH, than the unvegetated samples, and between 9 and 14 protozoan species were recorded from them. Unidentified species of diatoms, nematodes and Collembola were also observed in the cultures set up to determine protozoan species. Cryptogamic vegetation, then, has been a highly effective agent in promoting the accumulation of organic matter, enhancing water retention and providing habitats for a more diverse microbial and invertebrate community.

Fumarole Bay

The Fumarole Bay area of Deception Island received a dusting of fine ash from a Mount Pond fissure during the last stages of the 1969 eruption (Baker and others, 1975). Apart from this, the area was unaffected by volcanic activity during 1967 to 1970 and, so far as can be deduced from historical observations (Adie, 1957; Roobol, 1973), has been unaffected since before 1829. Unvegetated materials from this area (sampling occasions V and VI) showed close similarities to unvegetated 12- 13-year-old materials from the new island and Collins Point in both physical properties and the diversity of their protozoan fauna recorded. This result suggests that after about 12 years the processes of microbial colonization might have reached the stage where the maximum number of protozoan species (5 to 7) that can coexist in unvegetated tephra is already present.

The vegetated samples from Fumarole Bay show the greatest diversity of protozoan species observed on Deception Island, together with unknown numbers of diatoms, rotifers and nematodes. The numbers of protozoan species were only marginally greater than those observed in *Drepanocladus* from Collins Point, suggesting again that the maximum number of protozoan species that the habitat will support may be attained in about 12 years. These results do not, however, preclude the possibility that successional changes in the species composition of the fauna, without increases in diversity, and also increases in population sizes and therefore in biomass, might continue to occur.

Rates of colonization and changes in tephra properties

Pooling the data from all sites and all sampling occasions (Table I), it is clear by inspection that the numbers of Protozoa increased with the age of unvegetated tephra and that vegetated materials were more species-rich than unvegetated. However, it is not immediately obvious to what extent these phenomena may be regarded as simple functions of the physical properties of the tephra. In order to elucidate the trends indicated by the data in Table I, the triangular matrix of correlation coefficients for all pairs of variables was calculated and is shown in Table II(a). This indicates that the numbers of species are strongly correlated with all other variables

Table II. Correlations between numbers of species of protozoa and the age and physical properties of volcanic tephra on Deception Island.

<i>pH</i>	% moisture	% loss on ignition	Age	
(a) Pooled data all samples				
-0.314 NS <i>n</i> = 27	±0.784*** <i>n</i> = 17	+0.892*** <i>n</i> = 28	+0.663*** <i>n</i> = 23	Numbers of species
	-0.489* <i>n</i> = 17	-0.255 NS <i>n</i> = 27	+0.245 NS <i>n</i> = 22	<i>pH</i>
		+0.915*** <i>n</i> = 17	-0.357 NS <i>n</i> = 12	% moisture
			+0.270 NS <i>n</i> = 23	% loss on ignition
(b) Unvegetated samples				
+0.528* <i>n</i> = 20	-0.298 NS <i>n</i> = 11	+0.728*** <i>n</i> = 21	+0.8.18*** <i>n</i> = 19	Numbers of species
	+0.291 NS <i>n</i> = 11	+0.391 NS <i>n</i> = 20	+0.314 NS <i>n</i> = 18	<i>pH</i>
		+0.061 NS <i>n</i> = 11	-0.501 NS <i>n</i> = 9	% moisture
			+0.561* <i>n</i> = 19	% loss on ignition
(c) Vegetated samples				
+0.369 NS <i>n</i> = 7	+0.448 NS <i>n</i> = 6	+0.818* <i>n</i> = 7	+0.642 NS <i>n</i> = 4	Numbers of species
	-0.526 NS <i>n</i> = 6	+0.664 NS <i>n</i> = 7	-0.455 NS <i>n</i> = 4	<i>pH</i>
		+0.793* <i>n</i> = 6	+0.097 NS <i>n</i> = 3	% moisture
			+0.380 NS <i>n</i> = 4	% loss on ignition

except *pH*; these associations are displayed graphically in Figs. 2 and 3. Also, moisture and loss on ignition are themselves closely correlated. Interpreting the significance of these values is complicated by the fact that those for all the variables in Table I, except age, fall into two discrete clusters; unvegetated samples had high *pH*, low moisture, low loss on ignition and low species numbers, whereas the vegetated samples had relatively low *pH*, high moisture, high loss on ignition and high species numbers (Tables III). In addition the coordinates for vegetated samples in Figs. 2 and 3 are more widely dispersed than those for unvegetated samples, indicating that colonization by vegetation may increase habitat heterogeneity. The correlation matrix was therefore recalculated for the unvegetated and vegetated samples separately with the results shown in Table II(b) and (c). These reveal that the apparently strong correlations with moisture in the combined data (Table II(a)) derived from the bivariate distance between the vegetated and unvegetated clusters rather than from the scatter of coordinates within the clusters. Loss of ignition is the one variable that is strongly correlated with species numbers in both sets of samples. It may thus be inferred that it is the rate of accumulation of organic matter that is an important determinant of the rate at which suitable microhabitats are created within the tephra for colonization by protozoan species. The fact that species numbers are even more strongly correlated with age in unvegetated samples suggests that the simple passage of time may be a secondary determinant of the rate of colonization in the early years,

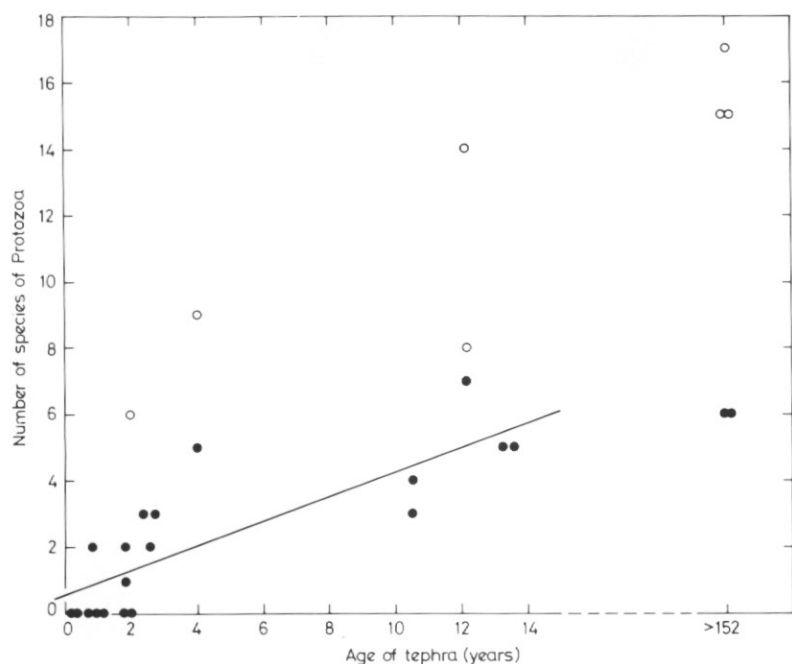


Fig. 2. Relationship between the numbers of species of Protozoa inhabiting volcanic tephra on Deception Island and the age of the tephra. ●, Unvegetated samples; ○, vegetated samples. The linear regression line ($y = 0.374x + 0.572$) is fitted through coordinates for unvegetated samples, omitting those > 150 years old.

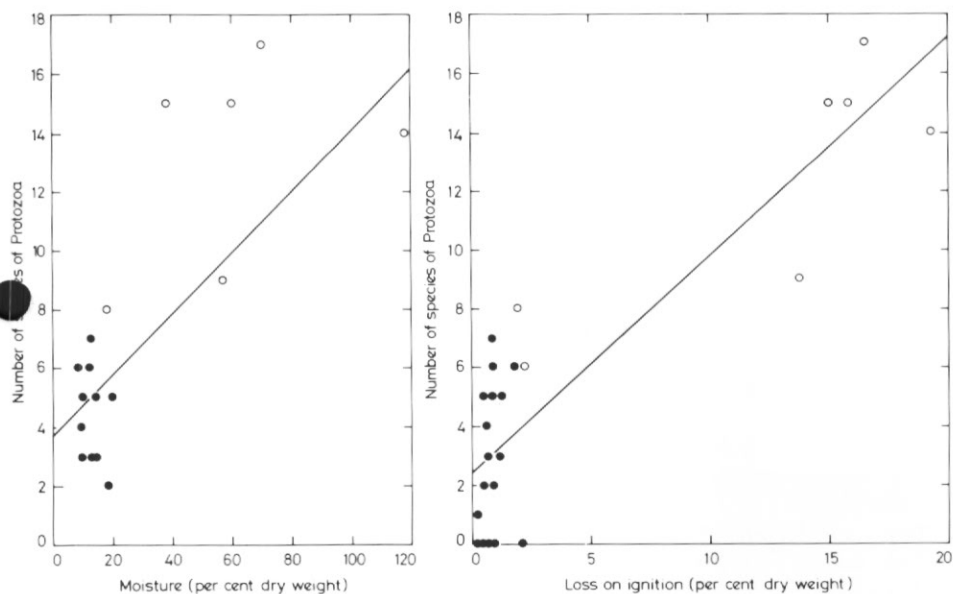


Fig. 3. Relationship between the numbers of species of Protozoa inhabiting volcanic tephra on Deception Island and the moisture content and the loss on ignition of the tephra. ●, Unvegetated samples; ○, vegetated samples. The linear regression lines are fitted through all coordinates:
 with moisture: $y = 0.13x + 3.75$
 with loss on ignition: $y = 0.74x + 2.38$.

Table III. Mean and range values of properties of vegetated and unvegetated samples of volcanic tephra on Deception Island.

	<i>Unvegetated</i>		<i>Vegetated</i>	
	<i>Mean</i>	<i>Range</i>	<i>Mean</i>	<i>Range</i>
Age (yrs)	4.7	0.7-13.4 (+ 2 samples 152 yrs)	7.6	2.0-12.2 (+ 3 samples 152 yrs)
pH	6.5	4.7-7.2	5.4	4.2-5.8
Moisture (% dry weight)	12.9	8.7-19.6	60.1	37.8-117.9
Loss on ignition (% dry weight)	0.56	0.09-2.4	12.0	1.93-19.2
Number of species of Protozoa	2.5	0-7	12.1	6-17

depending on the chance arrival of pioneer propagules. The speed of events on unvegetated tephra, indicated by these data, for the first 13 years are:

Organic matter accumulation at 0.03% dry weight per year; net protozoan species colonization at 0.37 species per year, or 3.46 species per 1% loss on ignition increase.

Once tephra has become vegetated, its age appears to be of little significance, with organic matter accumulation continuing to be the prime determinant of protozoan species colonization at a rate of 0.48 species per 1% loss on ignition increase. Moisture *per se* appears to have little influence on the rates of colonization. However, it is stressed that these data refer to presence or absence of species only; moisture may well be an important determinant of the size of microbial populations and rates of biomass accumulation. Moisture is certainly critical to bryophyte colonization and thus indirectly to the microbial community also.

Composition of the fauna

In addition to the 13 species recorded between 1968 and 1973 (Smith, 1974), a further 23 species of Protozoa were observed in materials collected on sampling occasions V and VI. The cumulative species list for Deception Island derived from 28 samples from six sites on six sampling occasions is shown below; the frequency of occurrence of each species, out of 28, is shown in parenthesis:

MASTIGOPHORA

- Oikomonas mutabilis* Kent (3)
- Oikomonas termo* Ehrenberg (17)
- Polypseudopodius bacterioides*
Puschkarew (2)
- Peranema trichophorum*
(Ehrenberg) Stein (1)
- Petalomonas mediocanellata*
Stein (1)
- Bodo edax* Kelabs (3)
- Bodo saltans* Ehrenberg (13)
- Cercobodo agilis* Martin (9)
- Cercobodo vibrans* Sandon (6)
- Cercomonas longicauda* Stein (10)
- Sainouron mikroteron* Sandon (6)

CILIATA

- Chaenea* sp. Quennerstedt (1)
- Chilophrya* sp. Kahl (2)
- Cryptopharynx* sp. Kahl (1)
- Dileptus* sp. Dujardin (2)
- Enchelys* sp. Hill (6)
- Hemiophrys* sp. Wrzesniowski (1)
- Holophrya* sp. Ehrenberg (1)
- Lacrymaria* sp. Ehrenberg (1)
- Lagynophrya* sp. Kahl (2)
- Litonotus* Wrzesniowski (1)
- Leptopharynx sphagnetorum*
(Levander) Mermod (6)

RHIZOPODA: AMOEBIDA

Mayorella sp. Schaeffer (5)*Vanella* sp. Bovee (3)

RHIZOPODA: TESTACIDA

Assulina muscorum Greef (1)*Corythion dubium* Taranek (4)*Euglypha rotunda* Wailes and Penard (3)*Euglypha strigosa* Ehrenberg Leidy (1)*Cyclidium glaucoma* Muller (1)*Uronema nigricans* (Muller)

Maupas (3)

Vorticella striata Dujardin var. *octava* Stokes (4)*Gonostomum affine* Stein (4)*Oxytricha fallax* Stein (2)*Oxytricha setigera* Stokes (1)*Tachysoma pellionella*

(Muller-Stein) Ehrenberg (8)

Uroleptus sp. Ehrenberg (4)

This species assemblage resembles closely those associated with fellfield and cryptogam-dominated habitats in other parts of the maritime Antarctic (Smith, 1978, 1984). In order to determine if a successional sequence of colonizing species could be detected, the matrix of presence-absence of species in the samples was analysed by the methods of numerical taxonomy, the procedures being those previously used for analysis of data on the protozoan fauna of Signy Island fellfields (Smith, 1984). These involved calculating Sørensen's similarity coefficient for all pairs of samples that contained one or more species to produce a similarity matrix, then ordinating the samples along the matrix axes so as to cluster the highest values of similarity coefficient among the principal diagonal. The sequence of samples so obtained could then be used to list the species in order of their first occurrence in the sequence of samples.

The first attempt to apply this form of analysis to the data produced no coherent pattern owing to the heterogeneity of the fauna in the vegetated samples. This faunal variation however appeared to be related to site; the results suggested that three distinct, though overlapping, faunal successional sequences could be detected, the three being similar in the initial stages of colonization, then diversifying in a site-characteristic manner. Therefore, the similarity analysis was performed separately on the data for: (a) 1967 Land Centre and Cathedral Crag (10 samples), (b) Fumarole Bay (12 samples), (c) Collins Point (11 samples), the data from the new island being incorporated into all three data sets. The three similarity matrices derived by this procedure are shown in Fig. 4. In each case the sequence of samples shows, from left to right, increasing numbers of species, increasing loss on ignition and increasing age of unvegetated materials; the vegetated samples (those with highest species numbers, moisture and loss on ignition) are concentrated at the right-hand end of the sequence. This result is consistent with the hypothesis that the fauna of the new island and other young unvegetated samples represents the pioneer colonizers common to all locations, with the fauna of the older and vegetated samples representing distinctive communities characteristic of the different sites. The species composition of the fauna of each sample is shown in the form of reconstructed presence-absence matrices in Figs. 5, 6 and 7 for the 1967 Land Centre and Cathedral Crag, the Fumarole Bay, and the Collins Point sequences. The vertical sequences of species, listed in order of first occurrence in the horizontal sequences of samples, may be taken as an indication of the succession of protozoan species associated with increasing age of the tephra and its colonization by vegetation. The sequences of species show trends of increasing body size comparable to the one observed for the species inhabiting Signy Island fellfields (Smith, 1984). Plots of log cell volume against position in the sequence show linear trends (Fig. 8) with significant correlation for all three sequences:

1967 Land Centre and Cathedral Crag	$r = 0.637^*$
Fumarole Bay	$r = 0.804^{***}$
Collins Point	$r = 0.790^{**}$

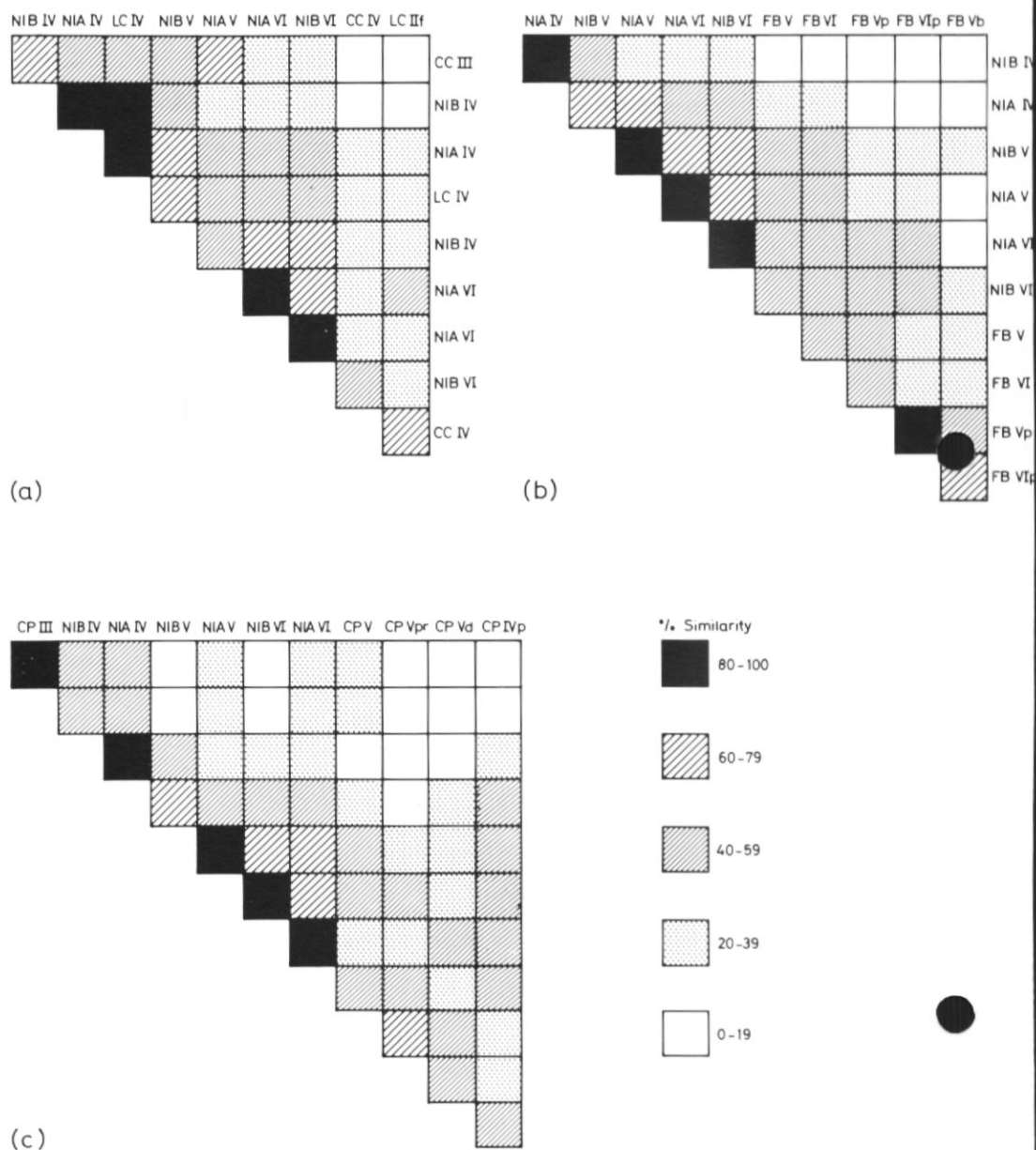


Fig. 4. Similarity coefficient matrices of volcanic tephra samples based on their protozoan fauna. (a) 1967 Land Centre and Cathedral Crags sequence. (b) Fumarole Bay sequence. (c) Collins Point sequence.

These trends are presumably owing to the occurrence of larger water-filled pores associated with cryptogam thalli, shoots or rhizoids, but it is also possible that unvegetated tephra becomes more porous as it ages.

From the reconstructed presence-absence matrices (Figs. 5, 6 and 7) it is possible to identify the common colonizer species and the site-specific faunas. The pioneer

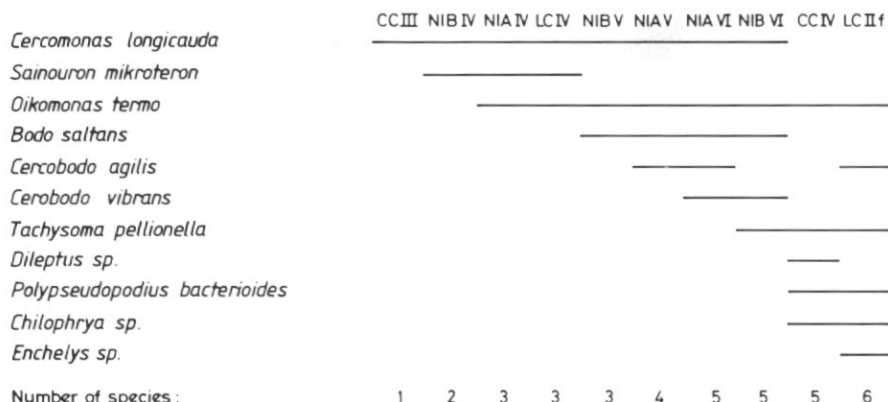


Fig. 5. Reconstructed presence-absence matrix of 11 species of protozoa in the 1967 Land Centre and Cathedral Crags sequence.

colonizers of tephra aged 0.7 to 4.0 years were *Sainouron mikroteron*, *Oikomonas termo*, *Cercobodo agilis* and *Cercomonas longicauda*.

These are all small flagellate species, typically $\leq 10 \mu\text{m}$ long, and apparently able to exist in free-draining materials with less than 1.0% loss on ignition. A second group of widespread colonizer species can be identified; these were also recorded from unvegetated tephra, but most frequently in samples of materials more than 10 years old. This group of species is much more varied, both taxonomically and morphologically. It includes one naked rhizopod (*Mayorella* sp.) and five ciliate species (*Dileptus* sp., *Enchelys* sp., *Leptopharynx sphagnetorum*, *Vorticella striata* and *Tachysoma pellionella*) as well as flagellates (*Bodo saltans* and *Cercobodo vibrans*). All of them are amongst the smallest representatives of their taxa and have non-rigid bodies; they are thus able to utilize small water fields.

Other ciliates that were recorded from more than one site, but only in vegetated samples, were *Lagynophrya* sp. and *Uronema nigricans*.

The rest of the fauna were essentially site-specific species distributed between the 1967 Land Centre and Cathedral Crags (2 species), the Fumarole Bay (10 species) and the Collins Point (10 species) sequences. The low number of species in the 1967 Land Centre and Cathedral Crags sequence may be attributed to no materials older than 4 years having been sampled from these sites, so that the sequence here had progressed little beyond the pioneer colonizer stage.

The similarity in species diversity of the Collins Point and Fumarole Bay sequences might suggest that the passage of 12 years, together with cryptogamic colonization of the tephra, was sufficient to permit fully the establishment of the protozoan community that can be sustained in the prevailing physical conditions. However, it is significant that, of the four testate rhizopod species recorded, three of them occurred only in the Fumarole Bay sequence, suggesting that a longer-term presence of bryophyte vegetation is necessary for a testate rhizopod fauna to become established. This observation is consistent with the known distribution of testates in the maritime Antarctic (Smith, 1978). The exceptional species is *Corythion dubium*, which was recorded from 12-year-old tephra with *Drepanocladus* from Collins Point. This is the most ubiquitous and abundant testate species in maritime Antarctic bryophyte-dominated habitats (Smith, 1973) and is the only one to be recorded from Signy Island fellfields (Smith, 1984). From the evidence reviewed by Cowling (1983) the success

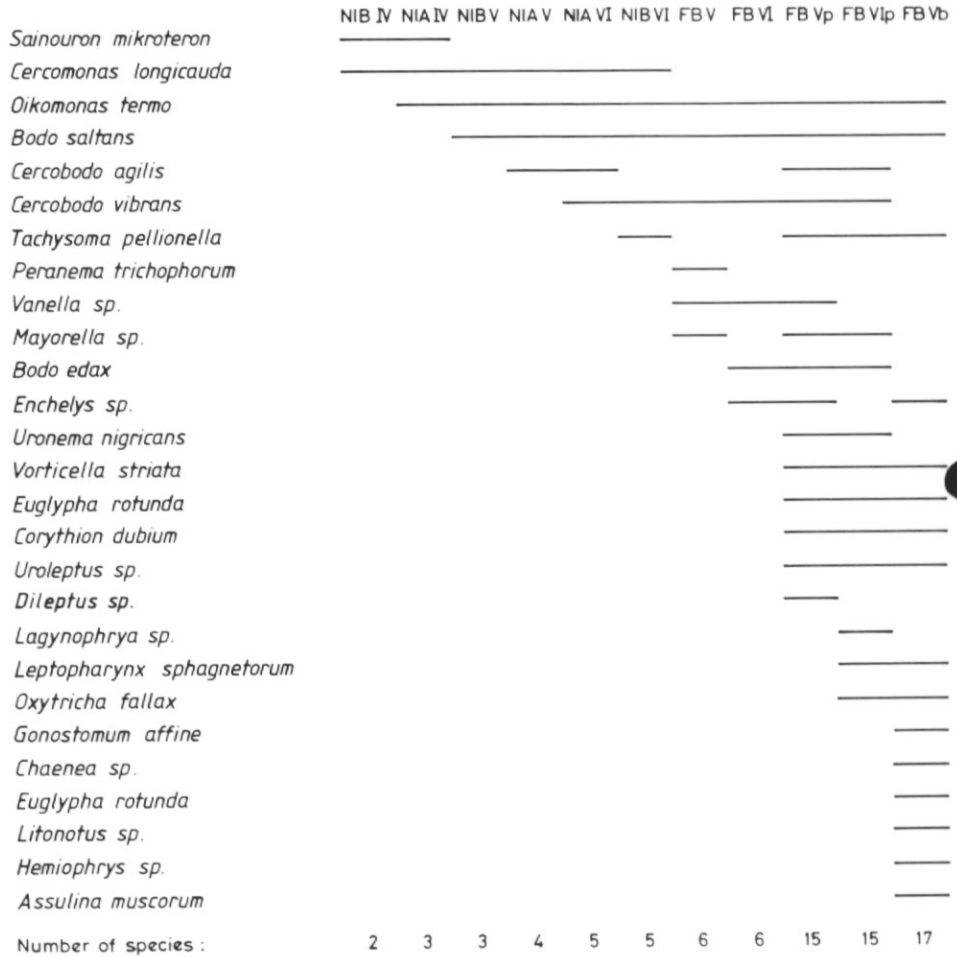


Fig. 6. Reconstructed presence-absence matrix of 27 species of Protozoa in the Fumarole Bay sequence.

of *C. dubium* appears to be due to a combination of physiological efficiency at ambient temperatures and a reproductive strategy whereby it is uniquely adapted to habitats hostile to other testate species.

Whilst the presence of testate rhizopods in the Fumarole Bay sequence can be related to the considerable age of the materials, the available data are insufficient to explain fully the other differences in the site-specific faunas. The chemical nature of the substratum may possibly have some influence since this does show heterogeneity. Evidence assembled by Roobol (1979) is consistent with the hypothesis that eruptive materials on Deception Island originated from several discrete magma pods with varying geochemistry. Analyses of materials from the recent eruptions revealed gradients around the island in certain elements: clockwise from Wensleydale Beacon to the Mount Pond fissures zone, increases in per cent fractions of Fe^{3+} , Mg^{2+} , Ca^{2+} , and decreases of K^+ and P were noted (Roobol, 1979). These observations, however, are not obviously associated with the faunal similarities of the 1967 Land Centre and Cathedral Crags samples, nor with the faunal dissimilarity of the Cathedral Crags and

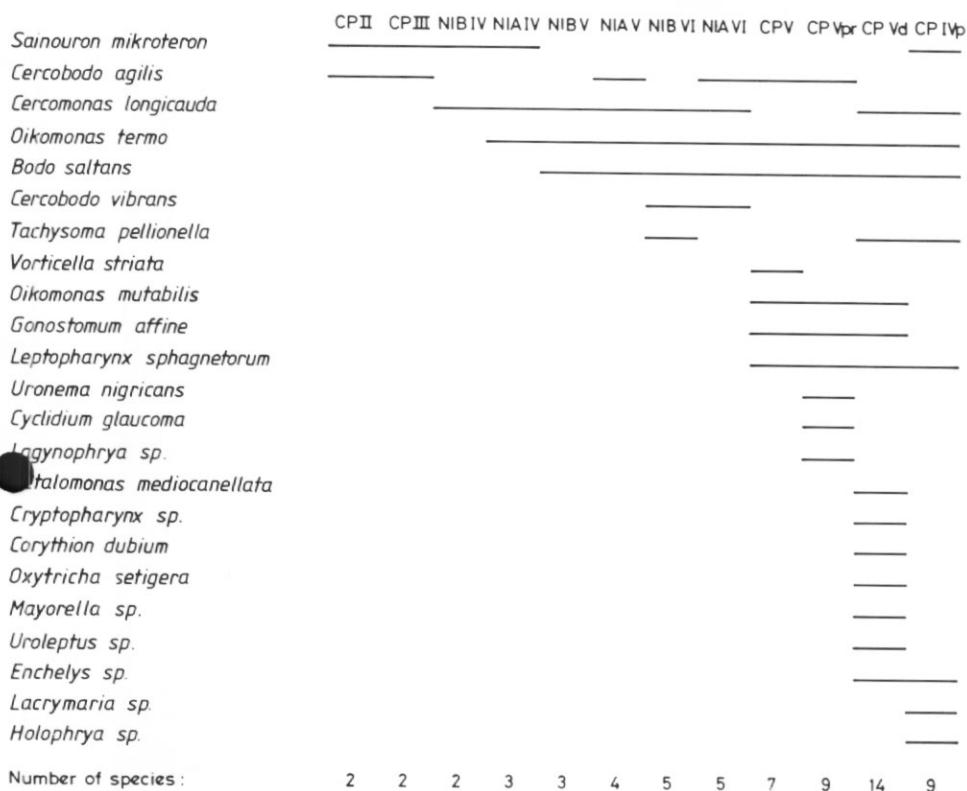


Fig. 7. Reconstructed presence-absence matrix of 23 species of Protozoa in the Collins Point sequence.

Collins Point samples. It would be more plausible to suggest that the differences in the post-eruption fauna were determined by the vegetation, and that regenerating cryptogams act as the inoculum of the colonizers as well as providing environmental conditions for their subsequent establishment. However, further data are needed to support or refute this hypothesis.

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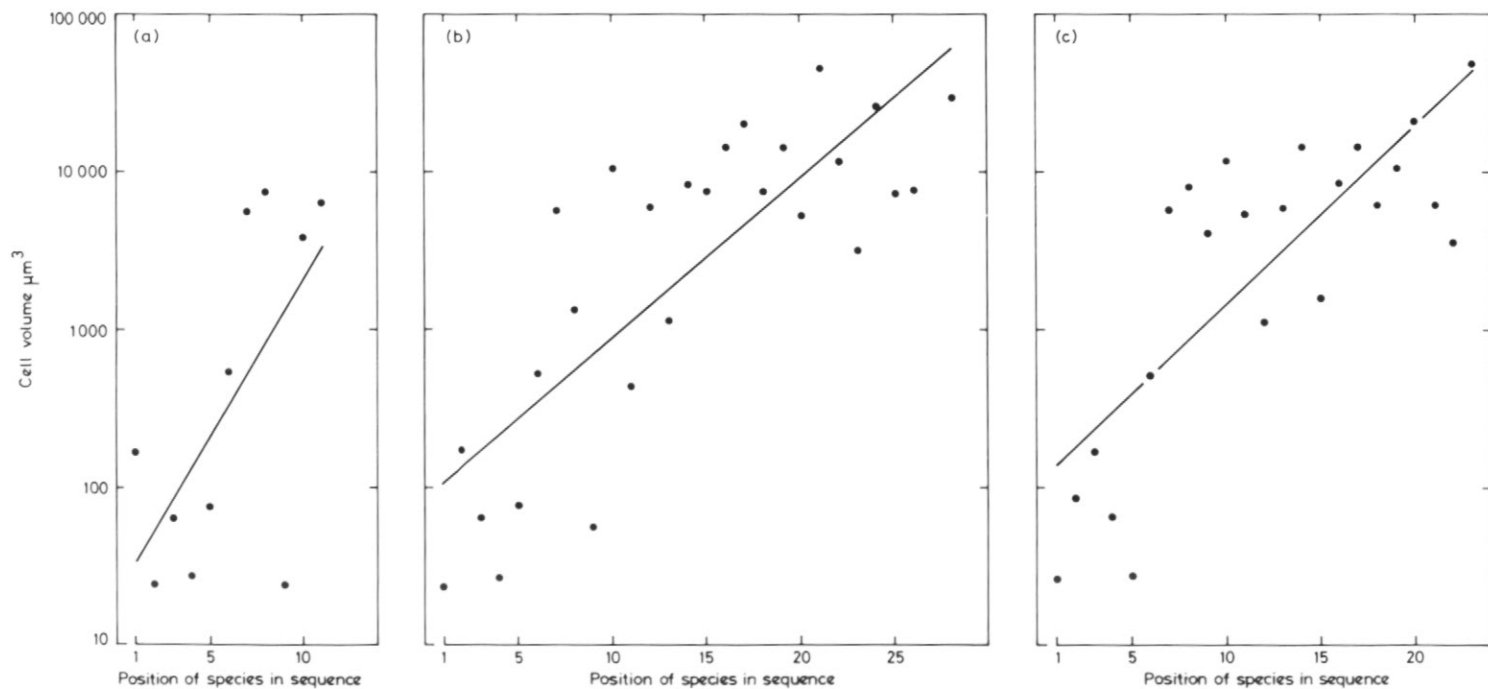


Fig. 8. Relationship between protozoan species' cell volume and their position in vertical sequence derived from the similarity analysis. (a) Land Centre and Cathedral Crags sequence. (b) Fumarole Bay sequence. (c) Collins Point sequence.

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