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Soil testate amoebae from sub-Antarctic Îles Crozet

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Abstract: An ecological study of the soil testate amoebae (Protozoa, Rhizopoda) communities on the sub-Antarctic island of Île de la Possession (Îles Crozet) revealed 65 taxa, belonging to 20 genera. *Trinema lineare* and *Euglypha laevis* were the most dominant species in all types of soils on the island. A Redundancy Analysis revealed three communities that characterize specific habitats: i. fellfield soils, characterized by low moisture values and low organic material content, contained fewer taxa and fewer individuals, ii. peaty valley soils, with lower pH values, showed high abundances and diversity, and iii. soils influenced by sea spray and marine animals had higher nutrient contents, elevated chloride and conductance values, resulting in more tests of *Difflugiella oviformis*, *Nebela dentistoma* and *Edaphonobiotus campascoides*. Special attention was given to the species composition in relation to the soil type and its moisture content. A comparison with aquatic habitats on Île de la Possession was made.

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Key words: bio-diversity, community analysis, ecology, Île de la Possession, moisture, Rhizopoda

Introduction

Unlike their insignificant role in running waters, testate amoebae (Protozoa, Rhizopoda) are a dominant group of protists in soils, contributing to the cycling of nutrients (Schönborn 1992). Testate amoebae occur in many types of terrestrial habitats, but they are particularly abundant in peats and soils with high organic content such as forest soils, moorland and polar tundra (Smith & Headland 1983).

The earliest records of testate amoebae from sub-Antarctic islands (Holdgate 1977) occur in Richters (1907,1908), who examined terrestrial mosses from Îles Kerguelen, Îles Crozet, South Georgia and Heard Island. Specific records of soil testate amoebae in the sub-Antarctic region are rather limited and comprise species lists from Macquarie Island (Penard 1911), South Georgia (Sandon & Cutler 1924, Smith 1982), Marion Island (Grospietsch 1971), and Îles Kerguelen (Bonnet 1981). The only publication on soil testate amoebae from Île de la Possession (Smith 1975), reveals eight species of testate amoebae belonging to the more common genera, such as *Corythion*, *Difflugia*, *Euglypha* and *Trinema*. It is clear that this preliminary study on terrestrial testate amoebae from Île de la Possession is far from complete.

The present paper is the second in a series of papers aiming to enlarge our knowledge of the living testate amoebae communities in soil, moss and freshwater habitats on Île de la Possession. The study in this paper focuses on the different soil types of various parts on the island and tries to link testate amoebae assemblages with their ecological preferences. Special attention will be given to soil moisture, a highly variable parameter in sub-Antarctic soils and an important variable determining the distribution of different types of testate amoebae (Bonnet 1975). The results of this study will later be used in a paleoecological study, where the testate amoebae composition will be examined in a 2500 year old sub-fossil peat core.

Materials and methods

Study site

The Crozet Archipelago (45°48'–46°26'S, 50°14'–52°15'E) (Fig. 1) is composed of a group of several small islands located in the southern Indian Ocean, 2400 km north of the Antarctic Continent and 2400 km south-east from the South African coast. The archipelago, about 300 km north of the Antarctic Convergence, consists of five volcanic islands of which Île de la Possession (156 km^2) is the largest. The islands are mainly composed of plagioclase–basalt (Dreux & Rémy 1963) and their climate is oceanic and cool. Mean air temperature is about 5°C and rainfall usually exceeds 2400 mm per year. Strong winds, prevailing from the west, sweep the island (mean wind speed: 11 m s^{-1} Smith 1978). More information regarding climate, topography and vegetation of the island is given in Van de Vijver *et al.* (1999).

Sampling and physico-chemical analysis

During the summer of 1999–2000 sixty soil samples were collected on Île de la Possession. The physico-chemical results of these samples and detailed information on the laboratory methods have been published in Van de Vijver *et al*. (2002). An additional 29 soil samples were collected during the summer of 2001–02. They were analysed as

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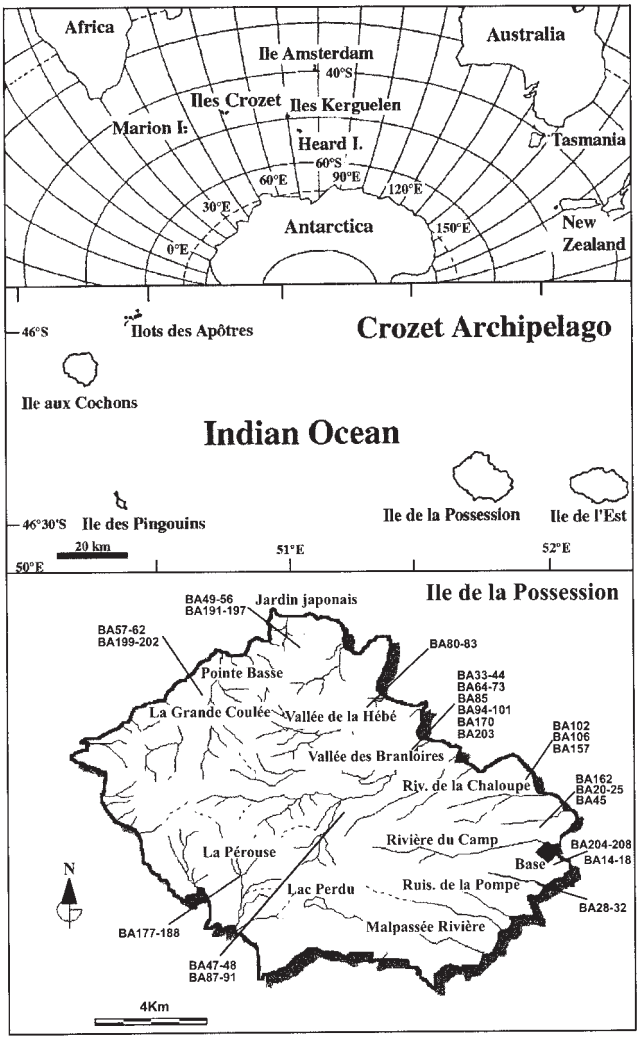


Fig. 1. Sketch map of Antarctica, the Crozet Archipelago and Île de la Possession, showing the locations of the different sampling sites (only first and last sample numbers are shown).

described by Van de Vijver *et al.* (2002). In several of these sampling sites, the soil layer was not thick enough for insertion of the moisture probes (Eijkelkamp TRIME-FM) to measure soil moisture. Table I lists the physico-chemical data of all soil samples used in this study. The additional 29 samples (unpublished) are in italic.

In both sampling programmes, sampling sites and different soil types were randomly chosen from the entire island. Soil samples were taken at a depth varying from 5 to10 cm. The zero level has been determined as being the bare soil after removal of living plant material. The upper 5 cm soil layer has been removed due to the instability of the soil (very high water content) or the unwanted presence of plant roots and/or plant debris. All samples were stored in 50 ml PVC bottles after adding 3% formaldehyde for fixation and kept at the University of Antwerp (UA), Department of Biology, Polar Ecology, Limnology and Paleobiology Unit.

Slide preparation and counting

All 89 soil samples were passed through a sieve with a mesh diameter of 297 µm and concentrated by centrifugation (5 min at 2500 rpm). Afterwards Rose Bengal was added to distinguish dead from living tests (at the moment of sampling). Encysted testate amoebae were considered as being alive. In each soil sample 150 tests were counted using a Leitz Wetzlar® microscope.

Morphological identifications of the testate amoebae are mainly based on works by Deflandre (1928, 1929, 1936), Grospietsch (1964), Decloître (1962, 1978, 1979, 1981), Ogden & Hedley (1980), Ogden (1983) and Hoogenraad & de Groot (1940).

The species *Difflugia globulosa* Dujardin probably includes the species *Phryganella hemisphaerica* Penard, a species commonly reported from soils (Ledeganck *et al.* 2003). These two species can only be distinguished by the shape of the pseudopodia. Since the material was fixed, this observation was not possible.

Data analysis

For pairwise comparison of the testate amoebae fauna of Île de la Possession with other sub-Antarctic islands, the Community Coeffient of Sørensen (1948) was calculated. This index, based on the number of common species of the compared studies, has the following formula: 2C/(A+B+2C), where A and B are the number of species exclusively observed in one site and C is the number of species the two sites have in common.

Diversity analysis [Shannon-Wiener diversity index ($\log_{10}$-based) and evenness number] was performed using the Multivariate Statistical Package (MVSP) (Kovach Computing Services 2002). The Gini evenness was also calculated to obtain a graphical representation of the evenness by means of a Lorenz curve (Nijssen *et al.* 1998). The Gini evenness measure is independent of the number of taxa per sample, allowing a better comparison between the samples.

Prior to the statistical analysis the testate amoebae data set was screened to remove rare taxa. If a taxon was not present in at least one site with a relative abundance of 2%, it was considered a "rare" taxon and removed from further analyses.

Ordination techniques were performed to explore the relationships between modern testate amoebae assemblages and the measured environmental variables. The computer program CANOCO version 4.0 (ter Braak & Smilauer 1998) was used for indirect and direct ordination analyses. A correspondence analysis (CA) revealed that the total gradient length was smaller than 2 SD, indicating a linear relationship between parameters and the species abundance data. Therefore a Redundancy Analysis (RDA) was used to detect patterns of variation in the species data which could

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Table I. Physico-chemical data of all soil samples from Île de la Possession. Additional 29 samples are in italic. Samples removed from further analysis are marked with *.

	pH	Specific conductivity (µS cm^{-1})	PO_4 (mg l^{-1})	NH_4 (mg l^{-1})	Chloride (mg l^{-1})	SO_4 (mg l^{-1})	Hardness (mg l^{-1} $CaCO_3$)	Moisture[a] (%)
BA14	5.5	198	0.56	1.10	0	28	15	28.6
BA15	5.4	795	2.10	1.80	0	0	0	25.6
BA16	6.1	172	0.78	0.79	3.9	3	0	31.2
BA17	6.4	864	7.80	11.60	0	0	0	40.5
BA18	5.8	279	0.86	5.40	0	5	10	44.4
BA19	5.3	296	0.00	3.75	21.6	0	0	89.5
BA20	5.1	346	0.35	5.20	4.6	1	5	87.6
BA21	5.8	58	0.30	0.73	3.6	0	0	33.4
BA22	5.5	211	0.12	4.50	10.8	0	10	69.4
BA23	5	164	1.46	8.10	5	0	0	40.3
BA24	5.1	322	2.30	4.40	0	0	0	81.8
BA25	5.2	137	5.70	5.10	0	0	0	43.2
BA26*	6.6	453	2.70	0.56	2.7	12	15	16.9
BA28	6.7	41	0.09	0.25	27	104	0	19.6
BA29	6.7	41	0.09	0.20	6.6	54	0	19.2
BA30	6.3	208	0.36	1.85	15	0	0	47.8
BA31	6.1	72	0.10	1.25	9.1	10	0	35.4
BA32	5.7	792	3.50	0.20	23	0	15	31.0
BA33	6.1	245	2.90	2.60	17	0	0	69.1
BA34	6.1	750	5.90	1.84	18	0	35	100.0
BA35	6.1	1.22	0.48	1.86	13	29	0	81.7
BA36	4	848	10.00	0.64	100	0	20	25.3
BA37	6.4	141	3.15	0.00	13	0	0	47.0
BA38	7	40	0.54	0.30	12.5	0	0	10.7
BA39	6.2	51	3.50	0.42	29.5	0	0	23.1
BA40	6.4	96	0.65	3.85	6.5	0	0	81.3
BA41	7	1196	0.46	1.05	40	44	5	18.1
BA42	6.4	295	2.05	2.75	13.5	0	0	33.0
BA43	6.1	260	0.87	2.75	20	0	0	30.2
BA44*	6.7	51	0.08	0.40	7.6	0	0	9.2
BA45	6.1	225	0.27	2.25	20.5	14	5	37.0
BA47*	6.7	50	0.48	0.31	22.5	9	10	5.0
BA48*	7.1	46	0.15	0.32	23	9	0	0.0
BA49	5.3	960	4.30	1.10	19.5	13	5	36.7
BA50	4.8	2000	6.75	0.83	680	0	30	41.9
BA51	5.8	977	6.20	1.16	16.5	6	65	45.4
BA52	6.9	8.2	4.12	1.96	15	1	75	31.2
BA53	6.5	775	6.32	11.60	33	16	80	56.1
BA54	5.8	648	4.05	2.04	340	8	20	49.9
BA55	6.2	711	16.00	10.08	37	0	70	59.5
BA56*	7.8	960	2.45	1.16	7.9	96	20	0.0
BA57	5	757	1.20	4.60	295	9	0	33.9
BA60	6.6	100	0.08	0.31	52	0	0	47.6
BA62	5.9	168	1.25	4.32	22.5	0	10	55.0
BA64	6.1	73	0.92	0.86	15	8	5	48.9
BA66	5.8	365	1.80	1.10	14	0	0	100.0
BA69	5.2	1173	6.20	0.82	21.5	0	5	100.0
BA71	5.2	392	1.36	3.08	17	0	0	100.0
BA73	6.2	341	2.56	2.90	40	0	20	59.6
BA80	6.4	242	3.24	2.40	19.5	0	0	54.3
BA83	7.2	141	0.64	1.64	17	0	0	50.6
BA85	5.9	640	3.20	1.26	2.35	0	0	50.3
BA87*	6.6	123	0.00	0.29	21.5	27	35	80.0
BA89	5.4	305	0.88	2.32	32	0	0	65.9
BA91	5.3	72	0.04	0.08	14.5	0	0	81.0
BA94	4.3	1139	7.40	0.38	34	8	30	18.6
BA99*	7.2	368	5.20	5.92	23	14	5	7.0
BA101	5.2	310	5.20	7.04	40	0	0	46.2
BA102	5.9	440	0.52	4.00	18.5	0	0	99.3
BA106	5.8	612	6.20	0.34	36	0	25	65.5
BA157*	*7.7*	*495*	*36.00*	*34.00*	*10*	*68*	*40*	
BA162*	*7.3*	*395*	*13.00*	*49.00*	*0*	*71*	*30*	
BA170	*5.8*	*226*	*2.7*	*0*	*0*	*5.6*	*0*	*16.7*
BA177	*5.9*	*876*	*7*	*6.2*	*0*	*0*	*0*	*73.9*
BA178	*7.1*	*324*	*11*	*0.175*	*0*	*5*	*74*	*51.9*
BA179	*5.4*	*1808*	*19*	*10.1*	*115*	*0*	*0*	*91.4*
BA180	*6.5*	*148*	*0.95*	*0.2*	*7.6*	*4*	*10*	
BA181*	*7.3*	*82*	*0.63*	*0*	*4.1*	*5*	*0*	*30.6*
BA182	*6.8*	*96*	*0.56*	*0.007*	*0*	*3*	*0*	*42.1*
BA183	*4.1*	*601*	*1.25*	*1.8*	*52*	*33*	*10*	*29.9*
BA186	*5.6*	*173*	*0*	*0.004*	*6.1*	*0*	*80*	*97*
BA187	*5.5*	*741*	*1.78*	*0.002*	*0*	*0*	*10*	*45.5*
BA188	*5.8*	*183*	*0.37*	*0.9*	*9.1*	*0*	*0*	*58.2*
BA191*	*5.5*	*785*	*110*	*32*	*42*	*54*	*80*	
BA192	*4.6*	*615*	*0*	*0*	*37*	*0*	*0*	*48*
BA193	*6.1*	*243*	*1.4*	*0*	*26.5*	*20*	*40*	
BA194*	*6.7*	*676*	*104*	*35*	*12*	*54*	*45*	
BA195	*6.4*	*924*	*3.4*	*0.3*	*15*	*17*	*110*	*69.3*
BA197	*7.1*	*100*	*1.1*	*0*	*4.5*	*6*	*0*	
BA199*	*7.5*	*1414*	*7.7*	*0.9*	*20.5*	*0*	*25*	
BA200	*6.5*	*193*	*0*	*0.6*	*14*	*0*	*0*	
BA201	*7.2*	*92*	*0.86*	*0.62*	*9.4*	*0*	*10*	
BA202	*7.1*	*277*	*1.8*	*1.56*	*26*	*0*	*20*	
BA203*	*6.4*	*54*	*0.12*	*0.17*	*4.7*	*0*	*0*	
BA204	*6.6*	*181*	*0.34*	*0.55*	*24*	*7*	*0*	*22.6*
BA205*	*6.8*	*420*	*3.35*	*0.39*	*17*	*4*	*10*	*19.2*
BA206*	*7.1*	*325*	*0.36*	*0.37*	*32*	*27*	*0*	*8.2*
BA207*	*7.1*	*108*	*0.45*	*2*	*8*	*5*	*0*	*9.2*
BA208*	*6.8*	*424*	*0.33*	*0.64*	*50*	*1*	*0*	*10.8*

[a]when measured

be explained by environmental variables (Jongman *et al.* 1987). All environmental variables, except for pH, were log-transformed since they had skewed distributions. Species data were square-root-transformed in order to downweight dominant taxa. Since not all of the eight environmental variables influence the distributions of the testate amoebae independently, forward selection with unrestricted Monte Carlo tests (999 permutations, $P = 0.1$) was carried out. The statistical techniques used are described in detail by Jongman *et al.* (1987).

Results and discussion

Species composition

Eighty-nine samples were analysed, from which 18 were withdrawn from further analysis since they contained little (less than10 tests per slide) or no testate amoebae (see Table I, samples marked with *). An analysis of the samples

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withdrawn showed that they were exclusively taken from either penguin rookeries (seven) or bare ground and fellfield soils (eleven). The same observation has been made by Smith (1972) and Petz (1997), who found no testate amoebae tests in ornithogenic soils and unvegetated mineral moraine clays. Extreme stress conditions (an excess of nutrients in ornithogenic soils and absence of organic material and extreme drought in fellfields) in both habitats are probable explanations for the absence of tests in these soils.

The remaining 71 samples from vegetated soils revealed a total of 65 taxa (including species, varieties and forms) belonging to 20 genera. Forty-two taxa had relative frequencies >1% in at least one sample. An alphabetical list of all observed testate amoebae taxa is given in Appendix A. The list contains several taxa that have only been identified to the generic level (17%). Besides the lack of decent regional morphological studies, two other features must be considered:

i. insular endemism due to the remoteness and isolation of the island,

ii. environmentally induced plasticity within single genotypes (Wanner 1999).

Further morphological analysis of these taxa, using SEM (scanning electron microscopy) is in progress.

A preliminary comparison was made between the testate amoebae fauna of Île de la Possession (aquatic samples: Vincke *et al*. unpublished, soil samples: this paper, moss samples: unpublished data) and two neighbouring sub-Antarctic islands: Îles Kerguelen (Bonnet 1981) and Marion Island (Grospietsch 1971). The Sørensen similarity analysis indicated that the testate amoebae fauna is rather different between the islands, resulting in relatively low similarity values: Île de la Possession – Îles Kerguelen (0.35) and Île de la Possession – Marion Island (0.30). Possible explanations for this relatively low similarity are the differences in sampling intensity (Marion island: 12 samples, Kerguelen: 53 samples, Île de la Possession: 271samples). Secondly, sampling strategy, such as the choice of sampling habitat, may also yield different faunas. Finally, a different taxonomical viewpoint when identifying testate amoebae may cause such results. As mentioned above, the species list of Île de la Possession contains several unidentified taxa. It is possible that the similarity between these islands will increase when the taxonomic study of this island has been completed and more shared taxa will be found.

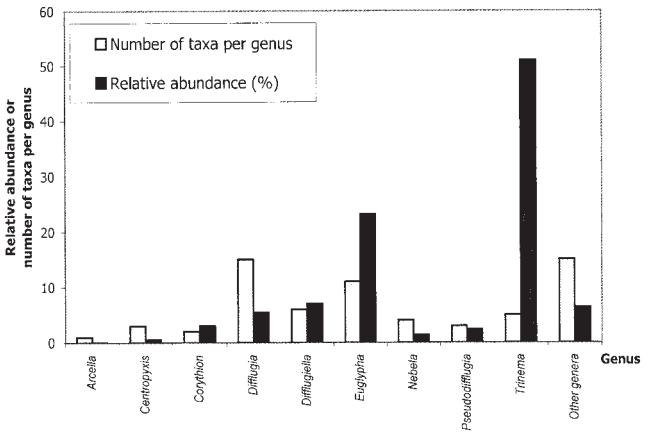


Fig 2. Relative abundance of the main Testacea genera observed in this study (black bars) and the number of taxa occurring in the different genera (white bars)

In the future, a detailed analysis of the moss-inhabiting testate amoebae of (almost) all sub-Antarctic islands will be performed. Only when all results are available can a more complete biogeographical zonation of the testate amoebae fauna in the sub-Antarctic region be given.

The number of taxa per genus and the relative abundance of the different genera are represented in Fig. 2. The most abundant taxa in this study were cosmopolitan and ubiquitous species, and are also found in mosses and aquatic habitats. The overall dominance of the genus *Trinema* is entirely attributed to the presence of *Trinema lineare* Penard. This species, commonly reported from sub-Antarctic and maritime Antarctic vegetated soils (Smith 1978), was found in all samples with a mean relative abundance of 41%. In other words, in a mean sample 61 ± 16 of the 150 counted tests belonged to the species *T. lineare*.

The high frequency of the genus *Euglypha* is mainly due to the occurrence of the taxon *Euglypha laevis* Perty. This eurytopic species was present in all samples with a mean relative abundance of 15% and is known to be ubiquitous in soils (Bonnet & Thomas 1960). As expected, the relative abundance of the genera *Difflugia* and *Arcella* in soils was considerably lower than their relative abundance in aquatic habitats on Île de la Possession (Vincke *et al.* unpublished), which indicates that these two genera are more restricted to the aquatic environment (Beyens *et al.* 1995).

By adding stain to the samples, it was possible to distinguish dead from living testate amoebae. Only 12% of all testate amoebae counted were still alive (including encysted) at the moment of sampling. This percentage was remarkably lower than the number of living tests found in aquatic habitats (36%) on Île de la Possession (Vincke *et al.* unpublished). The explanation for this observation is not clear. Possibly microbial activity in soils on Île de la Possession (fellfields and large peat valleys; see below) is not high enough to stimulate the disappearance of greater number of tests. Also the absence of a frequent freeze-thaw cycle on Île de la Possession during the sampling period may result in a longer persistence of dead tests in the soil (Balik 1994). Higher moisture contents (higher in aquatic habitats) also stimulate the destruction of empty tests

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(Lousier & Parkinson 1981). Corrosion of tests is strongly enhanced by exposure to the air, especially in coarse sediments. Abrasion by wind, vegetation, percolating water, sediment compaction and strong temperature fluctuations will add to this effect (Beyens & Denys 1982). Other explanations seem to be in contrast to the observation made above:

i. Soils on Île de la Possession contain a lot of species with platelets (genera *Trinema*, *Euglypha*, *Corythion,* etc.), tests that normally disappear more easily than tests made of sediment particles (genera *Difflugia*, *Cyclopyxis*, etc.) (Lousier & Parkinson 1981);

ii. Substantially higher numbers of tests are lost in habitats with fluctuating moisture content (Lousier & Parkinson 1981).

Probably the disappearance of empty tests will be a complex combination of both physico-chemical and mechanical features, for which detailed research is necessary.

Diversity analysis

Species diversity in the Antarctic region is usually very low due to the dominance of a single or a few species which are best adapted to the Antarctic terrestrial environment (Smith 1996). The average number of taxa found per sample was 15 ± 4. The lowest number of taxa (eight taxa) was encountered in samples BA17, BA94 and BA204, all from fellfield soils. The highest number of taxa (25) was observed in BA20, a soil sample continuously moistened by drops of water from nearby waterfalls with a rich and diverse vegetation cover mainly composed of *Blechnum penna-marina* (Poir.) Kuhn., *Lycopodium magellanicum* Sw., *Ranunculus biternatus* Smith, *Deschampsia antarctica* Desv. and several bryophytes. Smith (1996) reported high numbers of testate amoebae in soils when the grass

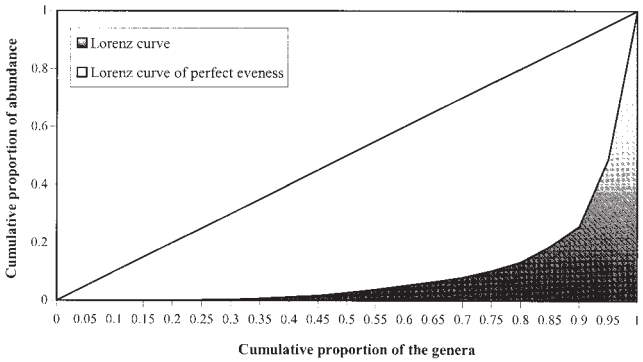


Fig. 3. Graphical representation of the Gini evenness measure by Lorenz curves. The Lorenz curve of perfect evenness (white) compared to the Lorenz curve of the samples (grey). Twice the area of the grey region is equal to the Gini evenness index.

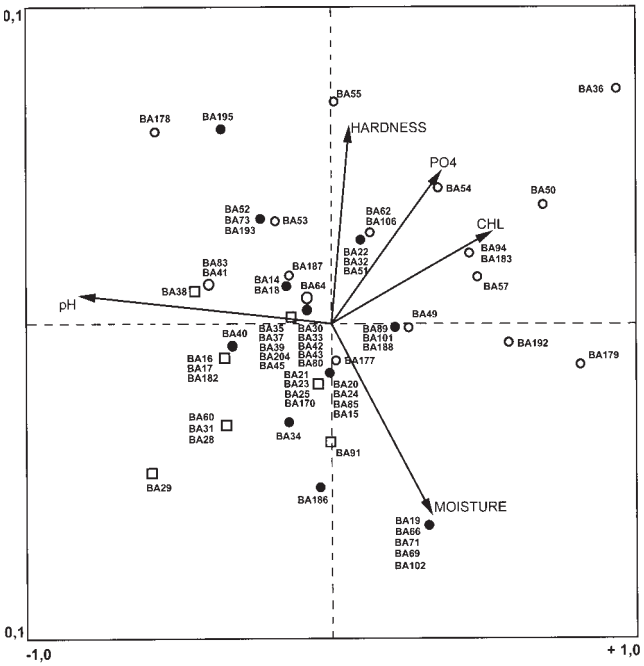


Fig. 4. Redundancy Analysis (RDA) ordination diagram showing the relationship between sites and environmental variables. Arrows indicate environmental variables as detected by forward selection. RDA axes 1 and 2 are shown. Symbols refer to the three different soil types: □ = fellfields, ● = valley soils, ○ = soils influenced by seawater/ marine mammals.

D. antarctica was present and suggested a stimulation of microbial activity in the rhizospheres around flowering plant roots. Since all samples were dominated by the taxon *Trinema lineare*, low diversity indices were to be expected. Diversity analysis of the samples revealed a mean Shannon-Wiener diversity index of 0.81 ± 0.01.

Two measures for evenness, the Shannon-Wiener's evenness number and the Gini evenness index (Nijssen *et al.* 1998), were calculated and compared. Both measures range from 0 to 1, with 1 indicating perfect evenness. The mean Shannon-Wiener's evenness number was 0.69 ± 0.01 and the mean Gini evenness measure was only 0.36 ± 0.01. The Gini measure allows a graphical representation of the evenness by means of a Lorenz curve (Nijssen *et al.* 1998) (Fig. 3). The Gini evenness measure is equal to twice the area under the Lorenz curve. Unlike Shannon-Wiener's evenness value, the Gini evenness measure is independent of the number of species per sample. Knowing that all samples are dominated by a single species, *Trinema lineare*, it is clear that the Shannon-Wiener's evenness number overestimates the equitability of the samples.

Comparison of soil and aquatic samples of Île de la Possession revealed that the number of taxa encountered in soils is clearly inferior (65 vs 85) to that in aquatic habitats (Vincke *et al.* unpublished). There is no significant difference when comparing the number of genera (20 in

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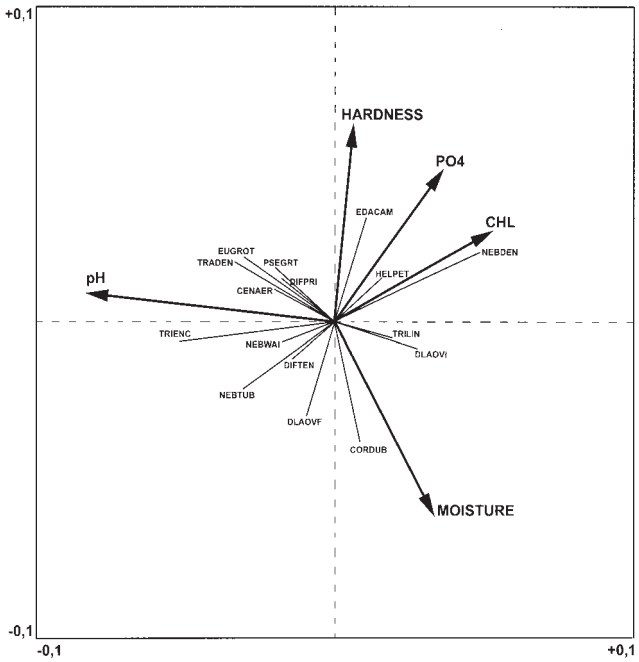


Fig. 5. Redundancy Analysis (RDA) ordination diagram showing the relationship between species and environmental variables. Arrows indicate environmental variables as detected by forward selection. RDA axes 1 and 2 are shown. Codes are explained in Appendix A.

soils vs 21 in aquatic habitats). The same observation has been made by Beyens *et al*. (1995) for South Georgia.

The relatively high number of taxa found on Île de la Possession (65) confirmed the trend of decreasing testate amoebae diversity with increasing southern latitudes (Smith 1982, 1996). Compared to the number of taxa encountered in terrestrial habitats in the maritime Antarctic (Smith 1972: 15 taxa in 23 samples on Elephant Island, Balik 1998: 24 taxa in 43 samples on King George Island, Smith 1992: 26 taxa in 22 samples on the Antarctic continent), it is obvious that species richness decreases towards the South Pole.

Community analysis

A Redundancy Analysis (RDA) was performed to examine the relationship between sites, species composition and the ecological variables. The five ecological variables selected by forward selection were pH, moisture, Total Hardness, chloride and PO_4. Five samples, for which no soil moisture data were measured (Table I), were removed from further analysis. In the RDA-diagram (Figs 4 & 5) arrow length indicates the importance of the variable and its orientation reflects the correlation with the axes. The first axis is relatively strongly related with the pH of the samples (inter-set correlation = -0.59) and the axis 2 is correlated to the hardness (inter-set correlation = 0.40). Monte Carlo unrestricted permutation tests (999 permutations) of axes 1 and 2 indicate that both axes were significant ($P < 0.05$). The first two axes collectively explain 8.5% of the variance in the testate amoebae fauna [$\lambda 1 = 0.057$ (5.7%), $\lambda 2 = 0.028$ (2.8%)]. This low percentage is typical for noisy data sets containing many zero values (Stevenson *et al.* 1991). The species-environment correlation was 0.71 for RDA axis 1 and 0.63 for axis 2, which translates to a total of 63.7% of the testate amoebae-environment being explained by the environmental variables. This high value suggests a strong relationship between the testate amoebae fauna and the selected environmental variables.

The RDA-analysis revealed three groups of soil samples, each characterized by a specific set of physico-chemical parameters (groups are indicated on the diagram: Fig. 4). Within the three groups there were small frequency shifts of different species (Table II). Van de Vijver *et al.* (2002a) found similar groups when investigating the soil diatom communities of Île de la Possession. The three groups, typifying different soil habitats on Île de la Possession, will be discussed in detail below.

Table II. Some characteristics of the different assemblages.

	Fellfield soils	Valley soils	Soils influenced by seawater
Number of samples	18	29	19
Number of taxa	41	59	45
Number of taxa per sample	14.5 ± 0.9	17.1 ± 0.6	13.5 ± 0.8
pH	6.2 ± 0.1	5.8 ± 0.1	5.6 ± 0.2
Conductivity (µS cm^{-1})	149 ± 45	407 ± 53	789 ± 115
PO_4 (mg l^{-1})	1.6 ± 0.5	2.2 ± 0.4	6 ± 1
SO_4 (mg l^{-1})	13 ± 6	3 ± 1	8 ± 3
NH_4 (mg l^{-1})	1.9 ± 0.8	2.5 ± 0.3	3 ± 1
Cl (mg l^{-1})	13 ± 3	15 ± 2	99 ± 39
Hardness ($CaCO_3$ mg l^{-1})	0.28 ± 0.28	16.7 ± 5.5	21 ± 6
Soil moisture (%)	37 ± 5	64 ± 5	47 ± 4
Shannon-Wiener diversity index	0.78 ± 0.02	0.86 ± 0.02	0.76 ± 0.04
Shannon-Wiener eveness number	0.69 ± 0.02	0.70 ± 0.01	0.68 ± 0.03
Gini eveness number	0.37 ± 0.02	0.35 ± 0.01	0.36 ± 0.02
Filosa-Lobosa ratio	-0.68	-0.68	-0.64
% living tests	17	11	9
% dead tests	83	89	91
Present in n% of samples # Mean relative abundance (%) in these samples			
Assulina muscorum	33 # 0.9	55 # 1.1	26 # 1.2
Centropyxis aerophila	44 # 0.9	52 # 1.1	37 # 0.7
Corythion dubium	44 # 1.8	48 # 1.7	26 # 0.1
Difflugia pristis	44 # 0.3	69 # 4	47 # 3
Difflugiella oviformis	77 # 4	86 # 6	90 # 8
Euglypha laevis	100 # 11	100 # 17	100 # 16
Euglypha rotunda	94 # 5	93 # 7	95 # 5
Euglypha tuberculata var. *minor*	50 # 3.3	86 # 4	53 # 3
Edaphonobiotus campascoides	28 # 2	55 # 1	63 # 3
Nebela dentistoma	22 # 2	10 # 0.9	26 # 45
Pseudodifflugia gracilis var. *terricola*	33 # 3.9	59 # 2.9	47 # 3.6
Trinema enchelys	94 # 13	100 # 7	90 # 10
Trinema lineare	100 # 44	100 # 38	100 # 41

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1. Fellfield soils

Fellfields are a widespread ecosystem in the sub-Antarctic region. These are generally in upland areas, are sparsely vegetated and consist mainly of rocky and stony substrates. Their physical environment is characterized by extreme fluctuations of temperature and moisture (Cowling & Smith 1986). Water runs easily through these soils (high porosity and fast percolation), leaving them quite dry between periods of rainfall (Frenot 1986). The lowest values for soil moisture were observed in fellfield soils (Table II). Nutrient conditions are normally very poor in fellfields. The only exception in this study were two samples taken near a nest of skuas (*Catharacta lonnbergi*), whose high mean sulphate content was most likely caused by the remains of prey, broken eggs and guano around the nests (personal observation). The median of sulphate for fellfields however was only 1.5 mg SO_4 l^{-1}, with $Q_1 = 0$ and $Q_3 = 10$ mg SO_4 l^{-1}.

In fellfield soils pH-values are circumneutral or slightly acidic, although the geological substrate is an alkaline basalt. Possible explanations for the moderate acidity are:

i. sample pH-values were measured near plants;

ii. sufficient rainfall causes leaching out of base-forming cations (Ca^{2+}, Mg^{2+}, K^+ and Na^+), leaving the exchange complex dominated by Al^{3+} and H^+ (Brady & Weil 1999).

It is clear that these extreme environmental conditions have their impact on the species composition, resulting in fewer taxa and fewer individuals of testate amoebae observed in fellfields (if observed at all; see Species composition section above). Smith (1975) reported that stony mineral soils on Île de la Possession contained fewer species and also fewer individuals per gram dry weight. Diversity and evenness were low due to the overall dominance of *Trinema lineare* and *Euglypha laevis* in fellfield soils. Additional ubiquitous species of the families *Euglyphidae* and *Trinematidae* were present, but less abundant than in the larger valley soils (see below) (Table II).

2. Valley soils

The soils of the larger valleys of Île de la Possession had lower pH and mineral nutrient values (see Table II). Frenot (1986) reported very low pH values, due to the large amounts of peat in these valleys. Organic material decomposes very slowly under the prevailing climatic conditions (cold and humid) giving these soils a fibrous character.

Valley soils had the most rich species composition and the number of individuals found in these soils was considerably higher than in fellfield soils (Table II). Testate amoebae are usually more numerous in soils with a high organic content (Ogden & Hedley1980) and several studies (reviewed in Smith 1983) stressed the fact that available moisture is an important factor influencing the size and activity of populations. Indeed, soil moisture was relatively high (64%) in the large peaty valleys of Île de la Possession.

Besides the dominant ubiquitous taxa *Trinema lineare* Penard, *Trinema enchelys* Leidy and *Euglypha laevis* Perty, species like *Assulina muscorum* Greeff, *Centropyxis aerophila* Deflandre, *Corythion dubium* Taranek, *Difflugia pristis* Penard, *Euglypha tuberculata* var. *minor* Cash & Wailes and *Pseudodifflugia gracilis* var. *terricola* Bonnet & Thomas were also slightly more abundant in the acidic valley soils.

3. Soils influenced by seawater/marine animals

Soils near the coastline are under the more direct influence of the sea. Direct infiltration of seawater (e.g. in Jardin Japonais; Van de Vijver *et al.* 1999) and indirect sea-spray result in elevated chloride and specific conductance values (Table II). Nutrient conditions are slightly higher in these soils due to the activity of marine birds (penguins, albatrosses and petrels) and mammals (elephant seals and fur seals). Next to a mechanical disturbance of the habitat by these animals, the large amounts of P and N introduce some kind of stress to the testate amoebae community. Foissner (1997) found that testate amoebae were reduced in abundance by at least 50% in agricultural ecosystems enriched by P and N due to the use of fertilisers. In ornithogenic soils no testate amoebae were observed (see Species composition section above).

The number of taxa encountered is considerably lower than in valley soils. Next to the generally dominant species, taxa such as *Difflugiella oviformis* Bonnet & Thomas, *Nebela dentistoma* Penard and *Edaphonobiotus campascoides* Schönborn, Foissner & Meisterfeld were relatively more abundant in soils influenced by the sea. Literature data report that *Difflugiella oviformis* and *Nebela dentistoma* can be found in wet soils, mosses and peat, while the ecological preference of *Edaphonobiotus campascoides* lies in soils and humus (Chardez 1998).

Soils and moisture

Bonnet (1964) observed a vertical distribution of testate amoebae in most soil habitats, which is correlated to some extent with test shape. Larger and more spiny species are found in the upper soil horizons, while flatter, smaller species are observed in the lower horizons. The soil samples on Île de la Possession were taken at a depth varying from 5 to10 cm, which is sometimes rather deep. This may explain the dominance of small testate amoebae of the families *Euglyphidae* and *Trinematidae.* Bonnet (1975) stated that the distribution of types (morphotypical profiles) was closely related to the water availability. Low moisture availability will favour species with reduced test and pseudostome size (reviewed in Foissner 1987). In general, testate amoebae belonging to the morphological types axial, plagiostome with a visor and cryptostome, are typical in

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soils (with a variable moisture content) (Bonnet 1975). The soil samples taken from Île de la Possession contained mostly species with an acrostome (genera Euglypha, Difflugia, *Difflugiella*, *Nebela*) or a plagiostome (genera *Trinema*, *Corythion*, *Centropyxis*). Probably soil samples were taken too deep for species with a cryptostome to be observed and soil moisture had little to do with the absence of genera such as *Plagiopyxis*, *Protoplagiopyxis*, *Trigonopyxis*. Therefore more attention will be given to the relationship between depth and species composition (i.e. morphology) during future campaigns.

The most dominant species in this study inhabit a wide range of environments and may be considered as typical r-strategists (Smith 1992, 1996). The diversity of the testate amoebae fauna of different habitats can be related to the degree of soil development and the successional stage of the associated vegetation (Smith 1982). To characterize the ecological suitability of a biotope, Bonnet (1976) postulated a *Lobosia–Filosa* index (LF-index), varying from -1 to +1. The highest values of the LF-index are typical of the successionally-developed biotopes. The LF-ratios of the different soil habitats in this study (Table II) were all negative due to the dominance of the *Testaceafilosia*, suggesting ecologically less suitable habitats for testate amoebae (Balik 1994). Indeed fellfields and soils near the coast produce some kind of stress (drought or increased nutrients) that effects the species composition (Van de Vijver *et al.* 2002). Even the larger valley soils with more developed vegetation, favour *Filosa* due to the presence of large amounts of undigested organic material. Duchaufour (1970) labelled the acidic peat soils as poor and undeveloped soils.

Conclusion

Despite some differences in species diversity, environmental variables and small changes of the quantitative weight of taxa between the three different groups described, the species composition of testate amoebae in soils on Île de la Possession is rather uniform. The majority of the 65 species found belonged to ubiquitous testate amoebae taxa with a merely cosmopolitan distribution. The number of taxa encountered is considerably higher compared to earlier publications, leaving many opportunities for future research: determination of ecological preferences of testate amoebae, palaeoecological research, biogeographical distribution of testate amoebae in the sub-Antarctic region and the influence of a research station on the island.

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APPENDIX A. List of all observed taxa (codes used in figures are added).

Arcella arenaria Greeff	
Assulina muscorum Greeff	
Assulina seminulum Penard	
Centropyxis aerophila Deflandre	CENAER
Centropyxis aerophila var. *sylvatica* Deflandre	
Centropyxis cassis Deflandre	
Corythion dubium Taranek	CORDUB
Corythionella sp1	
Cryptodifflugia compressa Penard	
Cyclopyxis sp1	
Cyphoderia sp1	
Cyphoderia sp2	
Difflugia ampullula Ehrenberg	
Difflugia bacillifera Penard	
Difflugia bryophila Jung	
Difflugia globulosa Dujardin	
Difflugia globulus Hopkinson	
Difflugia lucida Penard	
Difflugia pristis Penard	DIFPRI
Difflugia pulex Penard	
Difflugia sp3	
Difflugia sp6	
Difflugia sp7	
Difflugia sp8	
Difflugia sp9	
Difflugia sp10	
Difflugia tenuis (Penard) Chardez	DIFTEN
Difflugiella crenulata Playfair	
Difflugiella minuta Playfair	
Difflugiella oviformis (Penard) Bonnet & Thomas	DLAOVI
Difflugiella oviformis var. *fusca* (Penard) Bonnet & Thomas	DLAOVF
Difflugiella pusilla Playfair	
Difflugiella sacculus (Penard) Deflandre	
Edaphonobiotus campascoides Schönborn, Foissner & Meisterfeld	EDACAM
Euglypha acanthophora (Ehrenberg) Perty	
Euglypha bryophila (Penard) Jung	
Euglypha ciliata var. glabra Wailes	
Euglypha compressa Carter	
Euglypha compressa var. *glabra* Cash	
Euglypha cristata Leidy	
Euglypha laevis Perty	
Euglypha polylepis (Bonnet) Bonnet & Thomas	
Euglypha rotunda Wailes	EUGROT
Euglypha tuberculata Dujardin	
Euglypha tuberculata var. *minor Cash & Wailes*	
Heleopera petricola Leidy	HELPET
Heleopera sylvatica Penard	
Hyalosphenia sp 1	
Nebela dentistoma Penard	NEBDEN
Nebela tubulata Brown	NEBTUB
Nebela vas Certes	
Nebela wailesi Deflandre	NEBWAI
Paraquadrula irregularis Deflandre	
Phryganella paradoxa Penard	
Pseudodifflugia fulva Penard	
Pseudodifflugia gracilis Schlumberger	
Pseudodifflugia gracilis var. *terricola* Bonnet & Thomas	PSEGRT
Trachelocorytion pulchellum (Penard) Bonnet	
Tracheleuglypha acolla Bonnet & Thomas	
Tracheleuglypha dentata Vedjowsky	TRADEN
Trinema complanatum Penard	
Trinema complanatum var. *globulosa* Chardez	
Trinema complanatum var. *inflata* Decloitre	
Trinema enchelys Leidy	TRIENC
Trinema lineare Penard	TRILIN

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