

Ciliate biogeography in Antarctic and Arctic freshwater ecosystems: endemism or global distribution of species?

Wolfgang Petz^{1,2}, Alessandro Valbonesi³, Uwe Schiffner², Antonio Quesada⁴ & J. Cynan Ellis-Evans⁵

¹TB UmweltGutachten Petz, Ecological Consulting Office, Hallwanger Landesstrasse, Hallwang, Austria; ²University of Salzburg, FB Organismic Biology, Hellbrunnerstrasse, Salzburg, Austria; ³Università di Camerino, Dipartimento di Scienze Ambientali, via Circonvallazione, Matelica, Italy; ⁴Universidad Autónoma de Madrid, Departamento Biología, Madrid, Spain; and ⁵British Antarctic Survey, Cambridge, UK

Correspondence: Wolfgang Petz, TB UmweltGutachten Petz, Ecological Consulting Office, Hallwanger Landesstrasse 32a, A-5300 Hallwang, Austria.
Tel./fax: +43 0 662 665613;
e-mail: petz@umweltgutachten.at

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Abstract

Ciliate diversity was investigated *in situ* in freshwater ecosystems of the maritime (South Shetland Islands, mainly Livingston Island, 63°S) and continental Antarctic (Victoria Land, 75°S), and the High Arctic (Svalbard, 79°N). In total, 334 species from 117 genera were identified in both polar regions, i.e. 210 spp. (98 genera) in the Arctic, 120 spp. (73 genera) in the maritime and 59 spp. (41 genera) in the continental Antarctic. Forty-four species (13% of all species) were common to both Arctic and Antarctic freshwater bodies and 19 spp. to both Antarctic areas (12% of all species). Many taxa are cosmopolitans but some, e.g. *Stentor* and *Metopus* spp., are not, and over 20% of the taxa found in any one of the three areas are new to science. Cluster analysis revealed that species similarity between different biotopes (soil, moss) within a study area was higher than between similar biotopes in different regions. Distinct differences in the species composition of freshwater and terrestrial communities indicate that most limnetic ciliates are not ubiquitously distributed. These observations and the low congruence in species composition between both polar areas, within Antarctica and between high- and temperate-latitude water bodies, respectively, suggest that long-distance dispersal of limnetic ciliates is restricted and that some species have a limited geographical distribution.

Introduction

There is currently much debate concerning whether all free-living microbial and protist species, and thus also ciliates, have a global distribution, i.e. 'everything is everywhere, the environment selects' (e.g. Finlay *et al.*, 1996; Finlay, 2002) or whether at least some protist species have a limited biogeographical distribution so that these are restricted to a particular region or area, i.e. there is 'local endemism' (e.g. Foissner, 1999, 2004; Mitchell & Meisterfeld, 2005). Briefly summarized, the former proposition refers to the very small body size, the often large population size and the unrestricted ubiquitous dispersal mechanisms of microorganisms, while in contrast to this, large animal and plant species often have geographically limited distributions and fundamentally different modes of dispersal. Opponents of the above hypothesis argue that rare and thus often endemic protist species might be easily overlooked when only small sample volumes are examined (undersampling) and the investigator is taxonomically inexperienced or a nonspecialist. In con-

trast to larger animals and plants, the eukaryotic microbiota is often difficult to identify and may be dormant in the stage of a resting cyst for longer time periods so that species might escape detection. Which of the two biogeographical hypotheses applies to microorganisms has severe implications on many aspects of ecological and ecosystem research (e.g. Wynn-Williams, 1996; McGrady-Steed *et al.*, 1997; Naeem & Li, 1997; Loreau, 2000).

Ciliate diversity (i.e. number of species) is rather limited in freshwater ecosystems of the Antarctic and Arctic because environmental conditions are very harsh. In winter, lakes are usually covered by a thick layer of ice, shallower ponds often freeze completely for extended periods, and rivers and streams dry up or freeze entirely. Light is virtually lacking for up to 6 months and inorganic nutrient availability and primary productivity are often low to very low. In addition to environmental constraints, the Antarctic continent is isolated from all other major land masses by wide expanses of ocean (at least about 1000 km) and has been so for 25–30 million years; Clarke, 2003). In addition, ice-free localities

within the continent can be separated from their closest neighbour by several hundred kilometres. This, therefore, might have favoured the evolution of endemic taxa (Thompson & Croom, 1978; Vincent, 2000; Grémillet & Le Maho, 2003) and might limit the possibilities for (re-) colonization of suitable habitats from more temperate latitudes or from within the continent so that indigenous protist coenoses might have developed. However, it was previously thought that protistan (protozoan) freshwater communities do not exhibit obvious divisions in diversity between the maritime and continental zones (e.g. Heywood, 1984; Ellis-Evans, 1996).

Similar to the Antarctic continent, the High Arctic Svalbard Archipelago is separated from other main land masses by at least several hundred kilometres (Greenland is > 400 km distant, the Norwegian mainland > 600 km). It was previously thought that the Arctic is a much younger system and north polar ecosystems as we know them today evolved only during the last 15 000 years (Grémillet & Le Maho, 2003). However, there are indications that some currently ice-free regions in Antarctica were glaciated during the Last Glacial Maximum and that lakes that are seasonally ice-free now were probably perennially ice covered then while parts of other oases remained free of continental ice (Hodgson *et al.*, 2005). This implies that present-day Antarctic ecosystems might have also evolved quite recently. Despite possible differences in the evolutionary history between northern and southern polar regions, organisms experience more or less the same environmental constraints in these areas (Grémillet & Le Maho, 2003). However, studies on the biodiversity and faunistics of limnetic ciliates from the Antarctic or Arctic are very rare and sometimes dated (e.g. Awerinzew, 1907; Murray, 1910; Sullivan, 1957; Armitage & House, 1962; Hada, 1966; Thompson, 1972; Fenchel, 1975; Dillon & Bierle, 1980; Cathey *et al.*, 1981; Hawthorn & Ellis-Evans, 1984; James *et al.*, 1995; Laybourn-Parry *et al.*, 1997; Petz, 2004; Petz *et al.*, 2005). Thus, it was the aim of this study to investigate selected areas with abundant running and stagnant freshwater bodies with modern methods in both polar regions *in situ* during several expeditions and to assess the results with regard to the above speculations.

Materials and methods

Study sites

Maritime Antarctic

This study site was on Byers Peninsula (Livingston Island, South Shetland Islands, 63°S, 61°W), and comprised eight lakes and pools, and 10 streams. Most streams were located in the coastal lowland on the South Beaches, i.e. in an area of

Table 1. Freshwater bodies sampled in the maritime Antarctic (South Shetland Islands, on Livingston Island unless noted). Most lake and all river names are unofficial

Water body name	<i>n</i>
Lakes:	
Lago Limnopolar	4
Lago Provisional	7
Lago Midge	1
Lago Chester Cone	2
Lago Triangular	1
Lago Turbio	1
Lago Escondido	2
Laguna Refugio	1
Lago Irizar (Decept. Isl.)	1
Laguna de la Bomba (Decept. Isl.)	1
Rivers:	
Rio Petreles	4
Rio Balenas	3
Rio Usnea	1
Rio Tres Cerros	1
Rio Belgica	2
Rio Sumidero	1
Rio Final	1
Rio Refinal	1
Stream 1	1
Stream 2	1
Total	37

Decept. Isl., Deception Island; *n*, number of samples.

raised beaches, and were usually not more than 10–20 cm deep (Table 1). Most samples were collected about 5 m a.s.l.; three samples originated from between or on top of the moraines (40–90 m a.s.l.) bordering the coastal lowland. Most lakes were ultraoligotrophic to oligotrophic and located in the interior of Byers Peninsula (SPA 126) between 60 and 90 m a.s.l. One lake was close to the seashore on the South Beaches (about 2 m a.s.l.) and obviously eutrophic due to fertilization by seals; however, it was apparently not connected to the sea because electrical conductivity was rather low (247 $\mu\text{S cm}^{-1}$). Physicochemical parameters in the water bodies were (ranges): water temperature 2–12 °C, pH 4.9–9.1, electrical conductivity 2–266 $\mu\text{S cm}^{-1}$, dissolved oxygen 8.4–11.7 mg L^{-1} , oxygen concentration 76–97%. Parent rocks were mudstones, sandstones, tuffs, volcanic breccias and conglomerates (López-Martínez *et al.*, 1996).

Additionally, two lakes were sampled once (one fresh, one fixed sample) on Deception Island (South Shetland Islands, 63°S, 61°W), which is about 16 km away, and added to the above data (for further details see Petz *et al.*, 2005); 37 samples in total were taken (Table 1).

The uppermost layer (0–3 cm depth) of fellfield (mineral soil; five samples) and terrestrial moss (with some underlying soil particles; three samples) were collected on the South Beaches and in the interior of Byers Peninsula

Table 2. Freshwater bodies sampled in continental Antarctica (Victoria Land, on Edmonson Point unless noted). Some lake names are unofficial

Water body name	<i>n</i>
Lakes:	
Skua Lake (TNB)	4
Carezza Lake (TNB)	2
Oasi Pond (TNB)	1
Rock pool (TNB)	1
Lake 13	3
Lake 14	1
Lake 14a	1
Lake 15	3
Lake 15a	1
Pond 1	6
Pond 2	3
Pond 3	2
Pond 4	1
Pond 5	1
Rivers:	
Stream 1	1
Stream 2	1
Stream 3	1
Total	33

TNB, Terra Nova Bay area; *n*, number of samples.

(c. 67 m a.s.l.), respectively, for assessing the terrestrial ciliate species composition.

Continental Antarctica

This study area was in the Terra Nova Bay area and on Edmonson Point (Victoria Land, 74–75°S, 164–165°E), and comprised 14 pools and lakes, and three streams, i.e. two lakes and two pools in the area of Terra Nova Bay (40–120 m a.s.l.); and 10 pools and lakes, and three small and shallow meltwater streams on Edmonson Point (3–20 m a.s.l.); 31 samples in total were taken (Table 2). Some of the lakes were completely or partially ice-covered at the time of sampling and at least one pond was possibly ephemeral. Nutrient concentrations in lakes and ponds of this area are generally low (Andreoli *et al.*, 1992). Most stagnant water bodies were ultraoligotrophic to oligotrophic (Andreoli *et al.*, 1992) but some of the smaller ponds investigated were fertilized by birds and seals, and abundant algal growth indicated meso- to eutrophic conditions. One lake was distinctly saline. Physicochemical parameters in the lacustrine water bodies were (ranges): water temperature 0–12 °C, pH 6.7–10.3, electrical conductivity $28 > 25\ 130\ \mu\text{S cm}^{-1}$, dissolved oxygen 1.9–12.6 mg L⁻¹, oxygen concentration 32–92%. Parent rocks were dark volcanic lava and scoria on Edmonson Point and granite in the Terra Nova Bay area (for some additional details see Valbonesi & Petz, 1998).

The uppermost layer of fellfield (0–3 cm depth; 12 samples) and terrestrial moss (0–5 cm depth; three samples)

were collected in the Northern Foothills of Terra Nova Bay and on Edmonson Point for assessing the terrestrial ciliate species composition. One sample from the sea floor (depth about 15 m, substrate mainly gravel and sand) was collected by a scuba diver and two cores from landfast sea ice were drilled with a Siple ice-coring auger in Road Bay (unofficial name), Terra Nova Bay.

The uppermost layer of fellfield (0–3 cm depth; 29 samples) and terrestrial moss (0–3 cm depth; eight samples) were also collected in the environs of Casey Station (Bailey, Clark and Mitchel Peninsulas, Alexander and Haupt Nunataks, Windmill Islands; Budd Coast, 66°S, 110°E; and Davis Islands, Knox Coast, 66°S, 108°E; Wilkes Land), for assessing the terrestrial ciliate species composition (for some additional details see Petz, 1997).

High Arctic

This study area was on Brøgger Peninsula and Ossian Sarsfjellet (Ny-Ålesund, Svalbard, Norway, 79°N, 11°30'–12°30'E), and comprised 21 lakes and pools, and three streams and seeps, i.e. 19 lakes and pools and the running waters on Brøgger Peninsula (about 5–250 m a.s.l.) and one lake and one pool on Ossian Sarsfjellet (80–100 m a.s.l.); 36 samples in total were taken (Table 3). The water bodies were often surrounded by vegetation (mostly mosses). At least one large lake was still ice-covered about 2–3 weeks before the first sampling occasion and another was turbid and coloured red due to a high inorganic particle load. Most lakes and pools were shallower than about 4 m but a few were up to about 28 m deep. Two pools might be ephemeral with maximum depths being less than about 0.3 m. The majority of the stagnant water bodies was ultraoligotrophic to oligotrophic, but some were fertilized by birds (geese) so that abundant algal and plant growth indicated meso- to eutrophic conditions. Some lacustrine sediments were anoxic close beneath the surface and H₂S-rich (for further information on some of these lakes see Ellis-Evans *et al.*, 2001). Physicochemical parameters in the lacustrine water bodies were (ranges): water temperature 5–15 °C, pH > 6–8.9, dissolved oxygen > 9.0 mg L⁻¹, oxygen concentration > 75%. Parent rocks were carbonate rocks and limestone.

The uppermost layer of terrestrial moss (up to 0–7 cm depth, with some underlying soil particles; six samples) was collected from two sites on Brøgger Peninsula 6 and 80 m a.s.l., for assessing the terrestrial ciliate species composition.

Most of the streams investigated in both polar regions were fed by melting snowfields or snowbanks, some by lakes and very few by glaciers. All flow for only the warmest weeks or months each summer and are thus temporary.

For comparison with benthic ciliate populations from temperate latitudes, four mainly beta-mesosaprobic rivers in

Table 3. Freshwater bodies sampled in the High Arctic (Svalbard, on Brøgger Peninsula unless noted). Some lake names are unofficial

Water body name	<i>n</i>
Lakes:	
Tvillingvatnet	2
Solvatnet	2
Groptjørna	1
Storvatnet	2
Kiærdammane	1
Paskavatna	1
Trauvatnet	1
Lake 1	1
Lake 2	1
Lake 3	1
Lake 4	1
Lake 5	1
Pond 1	1
Pond 2	2
Pond 3	3
Pond 4	1
Pond 5	1
Pond 6	1
Pond 7	1
Ny Baikal (OS)	3
Ossian pool (OS)	3
Rivers:	
Stream 1	3
Stream 2	1
Stream 3	1
Total	36

OS, Ossian Sarsfjellet; *n*, number of samples.

Austria (Burgenland) were investigated twice in the course of 2 years (two sites each in the rivers Strem and Lafnitz, and one site each in the rivers Leitha and Wulka, 47°N; 36 samples) and an alpha-mesosaprobic river in Vienna (river Liesing, nine sites, 48°N; 74 samples) was sampled five times over 6 years using the same methods as with the polar samples above. However, only fresh samples were examined.

Sample collection

Lakes, shallow ponds, and small seeps and streams with discharges of only a few to a few tens of litres per second were investigated for their ciliate populations. Samples were collected from various benthic habitats [e.g. cyanobacterial mats, filamentous green algal strands or felts, epilithic periphyton (aufwuchs), aquatic mosses, detritus, uppermost layer of mineral sediments] into wide-mouthed plastic containers (0.5–1 L). Thereby, one sample consisted of several subsamples collected randomly over a distance of up to several tens of metres in the littoral zone of stagnant water bodies or along and across flowing water bodies. Separate habitat samples were usually kept in separate containers. Occasionally, however, integrated samples were

also collected. The proportion of benthic material to water was generally between about 1:2–1:3. H₂S-containing layers were usually not collected to prevent toxic effects on ciliates. Subsequently, the fresh samples were immediately transported to the laboratory at ambient temperatures. Physico-chemical parameters were measured electrometrically at the time of sampling.

Microscopical investigation and statistical analyses

Unpreserved water samples were investigated immediately or as soon as possible, i.e. usually within 24 h after collection, using a compound microscope (magnification up to $\times 1000$). Ciliate morphospecies were identified *in vivo*, often using methyl green-pyronin; selected taxa were impregnated with dry silver nitrate or fixed with Bouin and stained with protargol (silver proteinate) (for detailed descriptions of these methods see Wilbert, 1975; Foissner, 1991). The fresh samples were then stored at ambient temperature (e.g. in a refrigerator) and examined in intervals of a few days for a period of about 4 weeks. No nutrients were added to these raw cultures.

Fresh fellfield and terrestrial moss samples were investigated *in situ* according to the nonflooded petridish method (Foissner, 1987) but usually without initial air-drying; however, some air-dried samples were also examined. These raw cultures were studied in intervals over about 4 weeks and kept at ambient temperatures. Sea floor and sea ice samples were also investigated *in situ*, the latter being treated as described by Petz *et al.* (1995).

Hierarchical cluster analysis was performed using the ciliate species inventory (presence or absence of a species) and dendrograms were constructed using the UPGMA (unweighted pair-group method using averages, i.e. between-groups linkage) and other linkage methods (e.g. nearest-neighbour, furthest-neighbour, average linkage within groups) with the software program SPSS for Windows, version 12.0.1 (SPSS Inc.). Several measures (e.g. Jaccard's Species Identity, Pattern Difference, Sorensen or Dice, Squared Euclidean Distance) were used in generating clusters so that stable groupings could be detected (Mühlenberg, 1993). Stable groups were represented by those calculated with either the Jaccard Species Identity Measure or Pattern Difference and the UPGMA method, which are thus shown. Groups are thereby arranged according to the relative size of the proximity coefficients ('similarity or lowest distance', respectively) at which cases are combined (SPSS Inc.).

Results

In total, 334 ciliate species from 117 genera were identified in stagnant and running waters of the High Arctic and Antarctic (Fig. 1; Petz, 2004). Whereas the High Arctic

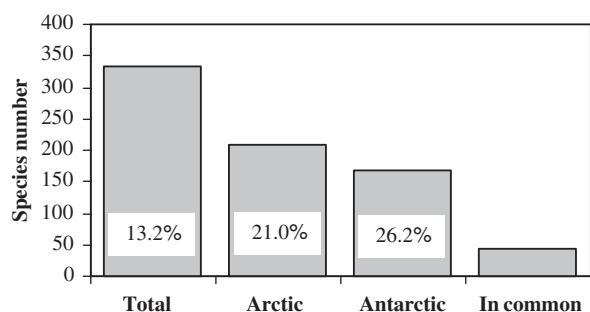


Fig. 1. Ciliate species diversity in High Arctic (Svalbard, 79°N; $n=36$) and maritime and continental Antarctic (Livingston Island, 63°S, and Terra Nova Bay areas, 75°S; $n=68$) freshwater ecosystems and number and percentage of species in common.

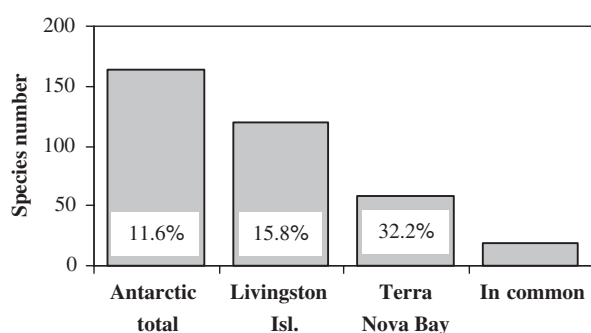


Fig. 2. Ciliate species diversity in maritime (Livingston Island area, 63°S; $n=37$) and continental (Terra Nova Bay area, 75°S; $n=31$) Antarctic freshwater ecosystems and number and percentage of species in common.

freshwater sites harboured 210 species from 98 genera, ciliate diversity was distinctly depauperized in Antarctica, where it further decreased southward (Figs 1 and 2). In the maritime and continental Antarctic locations, 164 ciliate taxa were recorded in total. In the Livingston Island area (maritime Antarctic, 63°S), 120 ciliate taxa from 73 genera were found but only 59 species from 41 genera were identified further south in continental Antarctica (Terra Nova Bay area, 74°S; Fig. 2). Local species richness in the three study localities amounted to 0.7–2.6% of the global ciliate species pool using the high estimate (Table 4).

Although the ranges of many abiotic environmental parameters were quite similar in the summers during our investigations in both polar regions, only 44 species occurred both in High Arctic and in maritime and/or continental Antarctic freshwater ecosystems in this study (Table 5 and Fig. 1). This is equivalent to 13% of the total species number found in both polar regions or, respectively, to 21% of the taxa found in the Arctic or to 26% of those encountered only in the Antarctic (Fig. 1). Thirty-seven of these species were found in maritime and 16 spp. in continental Antarctic water bodies whereas only nine taxa

Table 4. Relative local ciliate species richness expressed as percentage of the global number of species in the study areas High Arctic (Svalbard), maritime Antarctic (Livingston Island area) and continental Antarctica (Terra Nova Bay area)

Study area	A (%)*	B (%)†
High Arctic	2.6	7.0
Maritime Antarctic	1.5	4.0
Continental Antarctica	0.7	2.0

*A, high estimate; percentage based on a global total of 8000 free-living ciliate species (Lynn & Corliss 1991).

†B, low estimate; percentage based on a global total of 3000 taxa (Finlay & Esteban 1998).

of these were found in both Antarctic localities (Table 5). Almost all of these species are widespread and common to freshwater ecosystems in more temperate latitudes and are thus considered to be cosmopolitans (Foissner *et al.*, 1991, 1992, 1994, 1995; Foissner, 1993). Only very few of the taxa in common are rare or new; for example, the colpodid *Rostrophryides* sp. nov., which seems to feed exclusively on filamentous cyanobacteria, has apparently not been found anywhere else previously.

Nineteen ciliate species occurred in both Antarctic localities. In addition to the nine cosmopolitan species shown in Table 5, these are: *Bryophyllum* sp., *Euplotes euryhalinus*, *Fuscheria* sp. nov., *Gastronauta* sp. nov., *Litonotus* sp., *Nassula* sp. (nov.), *Nassulides* sp. nov., *Oxytricha longa*, *Trachelophyllum* sp. and *Vorticella* sp. This equals 12% of the total species number or, respectively, 16% of those found in the maritime or 32% of those recorded in the continental Antarctic (Fig. 2). Among these species are very probably four novel taxa and *Euplotes euryhalinus*, which was described from Antarctica and until now exclusively found there (Valbonesi & Luporini, 1990; Petz, 2005; this study). In contrast to these latter taxa, *Oxytricha longa* was until now reported from Europe, Israel and South Australia (Berger, 1999) and thus might possibly have a cosmopolitan distribution. Although a few other species occurred in abundances too low for a definite species identification, some other frequently occurring species in one of the investigated localities, e.g. *Bursaria truncatella*, *Urostyla grandis* and *Urotricha farcta*, also have or might have a cosmopolitan distribution (Foissner *et al.*, 1991, 1994).

However, some other frequently recorded taxa such as *Acineria uncinata* (encountered on Livingston and Deception Islands here) and possibly many of the more rarely found ciliates such as *Rostrophrya regis* (identified on Livingston Island) were previously observed only on some continent sites or at just a few sites (Foissner, 1993; Foissner *et al.*, 1995; Alekperov, 2005) and thus might have a restricted geographical distribution. A notable example is the genus *Stentor*, several species of which were found in High Arctic freshwater bodies in this study, i.e. *S. igneus*,

Table 5. Ciliate species found in High Arctic as well as in maritime and/or continental Antarctic freshwater ecosystems

Taxon	ARC	mANT	cANT
<i>Aspidisca cicada</i>	+	+	–
<i>Blepharisma hyalinum</i>	+	+	–
<i>Bryometopus pseudochilodon</i>	+	+	–
<i>Chilodonella uncinata</i>	+	+	–
<i>Cinetochilum margaritaceum</i>	+	+	+
<i>Climacostomum virens</i>	+	+	–
<i>Cyloidium glaucoma</i>	+	+	+
<i>Cyrtolophosis mucicola</i>	+	+	–
<i>Dileptus margaritifer</i>	+	+	–
<i>Frontonia acuminata</i>	+	+	–
<i>Frontonia angusta</i>	+	–	+
<i>Furgasonia</i> cf. <i>trichocystis</i>	+	+	–
<i>Fuscheria</i> cf. <i>nodosa</i>	+	–	+
<i>Halteria grandinella</i>	+	+	+
<i>Kreyella minuta</i>	+	+	–
<i>Lacrymaria filiformis</i>	+	+	+
<i>Leptopharynx costatus</i>	+	+	–
<i>Litonotus lamella</i>	+	+	–
<i>Nassulopsis</i> cf. <i>elegans</i>	+	+	–
<i>Odontochlamys alpestris</i>	+	+	–
<i>Opercularia coarctata</i>	+	+	–
<i>Oxytricha balladyna</i>	+	–	+
<i>Oxytricha setigera</i>	+	+	+
<i>Oxytricha similis</i>	+	+	–
<i>Paramecium aurelia</i> complex	+	+	–
<i>Phialina vertens</i>	+	+	–
<i>Platyophrya vorax</i>	+	+	–
<i>Protocyclidium muscicola</i>	+	–	+
<i>Protospathidium</i> sp.	+	+	–
<i>Pseudovorticella monilata</i>	+	+	–
<i>Rimostrombidium</i> sp.	+	–	+
<i>Rostrophryides</i> sp. nov.	+	+	–
<i>Sathrophilus muscorum</i>	+	–	+
<i>Sphaerophrya terricola</i>	+	+	–
<i>Sterkiella histriomuscorum</i>	+	+	+
<i>Stichotricha aculeata</i>	+	+	–
<i>Stylonychia mytilus</i> complex	+	+	–
<i>Tetrahymena rostrata</i>	+	+	+
<i>Trachelophyllum apiculatum</i>	+	+	+
<i>Uroleptus gallina</i>	+	+	–
<i>Urotricha agilis</i>	+	+	–
<i>Urotricha</i> cf. <i>armata</i>	+	–	+
<i>Vorticella aquadulcis</i> complex	+	+	–
<i>Vorticella infusionum</i> complex	+	+	+
Total	44	37	16

ARC, High Arctic (Svalbard); cANT, continental Antarctica (Terra Nova Bay area); mANT, maritime Antarctic (Livingston Island area); +, found; –, not found.

S. muelleri, *S. multiformis*, *S. niger*, *Stentor* cf. *amethystinus* and an unidentified *Stentor* sp. However, members of this very conspicuous taxon have, to our knowledge, not been recorded in Antarctica. This is based on perusal of over 50 publications on taxonomy and/or ecology of ciliates from

south polar lakes, ponds and streams appearing within the last 100 years (W. Petz, unpublished data). Likewise, *Metopus es* (found in Svalbard) has until now been recorded only from the holarctic and the palaeo- and neotropics (Foissner, 1998); no single member of the genus, as with *Stentor*, has been recorded from Antarctica (W. Petz, unpublished data). Some other ciliates were previously reported exclusively from particular biogeographical zones; for example, *Calypotricha lanuginosa*, *Nassula citrea*, *Pseudochilodonopsis polyvacuolata* and *Wallackia bujoreani* were found in the High Arctic here and previously also exclusively in the holarctic (which includes the Arctic) or, additionally, in the palaeotropical zone (Foissner *et al.*, 1994, 2002; Foissner, 1998). *Protospathidium terricola* (observed in continental Antarctica in this study) was previously reported only from the archinotis (Antarctic zone) and the palaeotropics (Foissner, 1998). These and other examples indicate that some ciliate species from limnetic ecosystems might have a limited geographical distribution.

Most of the species in common to both polar regions occurred with frequencies above 10%, while many other species were found less often. For instance, 75 species out of 120 spp. (63%) identified in the maritime Antarctic appeared in less than 10% of the freshwater samples. This shows that many species occurred only rarely or in low abundances. In each of the three polar locations investigated, at least about 10–20% of the species encountered are probably new to science, i.e. c. 13% in the High Arctic, around 21% in the maritime Antarctic and 15% in continental Antarctica. As these novel species have yet to be recognized formally, these percentages are only preliminary. However, these are likely to be minimum numbers because some of the rarer species might also be new, but because only very few specimens were found, this cannot be definitely concluded for these taxa.

Some of the species found in freshwater ecosystems in the present study, e.g. *Gonostomum affine*, *Homalogastra setosa*, *Kahlilembus attenuatus*, *Metopus es*, *Nassula citrea*, *Odontochlamys gouraudi*, *Platyophrya spumacola*, *Protospathidium terricola*, *Pseudochilodonopsis mutabilis*, *Pseudochilodonopsis polyvacuolata*, *Pseudoplatyophrya nana*, *Uroleptus lepisma*, *Uronema nigricans*, *Vorticella similis* and *Wallackia bujoreani*, may also live in moss or soil (cf. Foissner, 1998; this study). Several of these taxa are primarily soil ciliates, which may have actively migrated or were passively washed into some of the freshwater bodies. Usually, however, there was a considerable difference in the ciliate species composition between terrestrial (mineral soil, moss) and limnetic biotopes. This is corroborated by cluster analysis, which revealed distinct differences between the communities found in 21 lakes, three rivers and two wet terrestrial moss sites on Svalbard (High Arctic; Fig. 3). Similar clear separations were also found for the maritime (Fig. 4) and continental

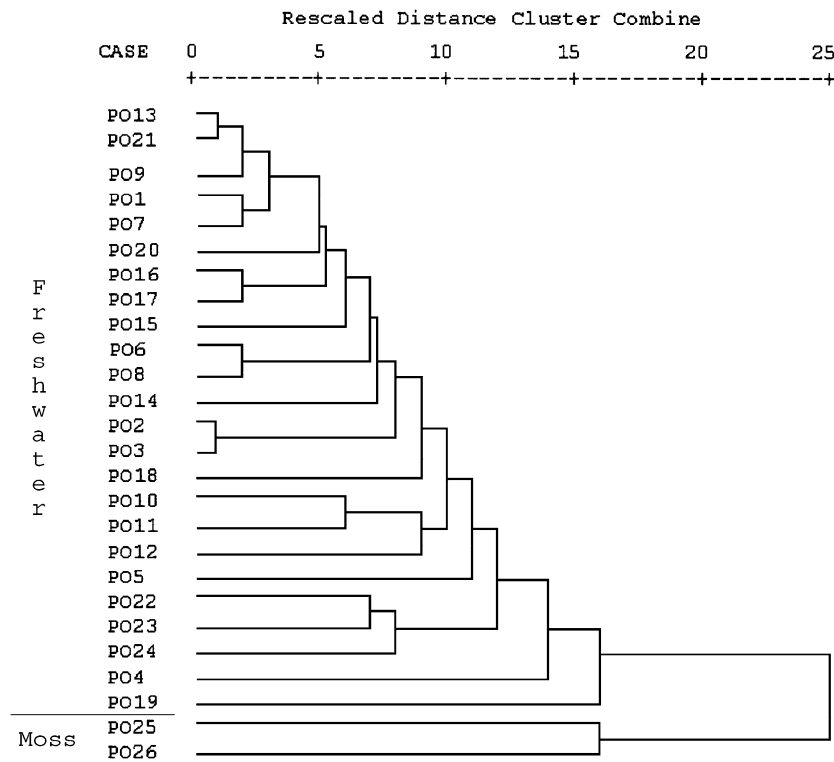


Fig. 3. Hierarchical cluster analysis (Pattern Difference) of 21 freshwater lakes and ponds (PO 1–6, 8, 10–17, 19–24), three rivers (PO 7, 9, 18) and two wet terrestrial moss sites (PO 25, 26) in the High Arctic (Svalbard, 79°N) based on their ciliate assemblages, indicating a distinct difference in the freshwater and terrestrial coenoses. Species of several samples were pooled for a single site where multiple samples were available.

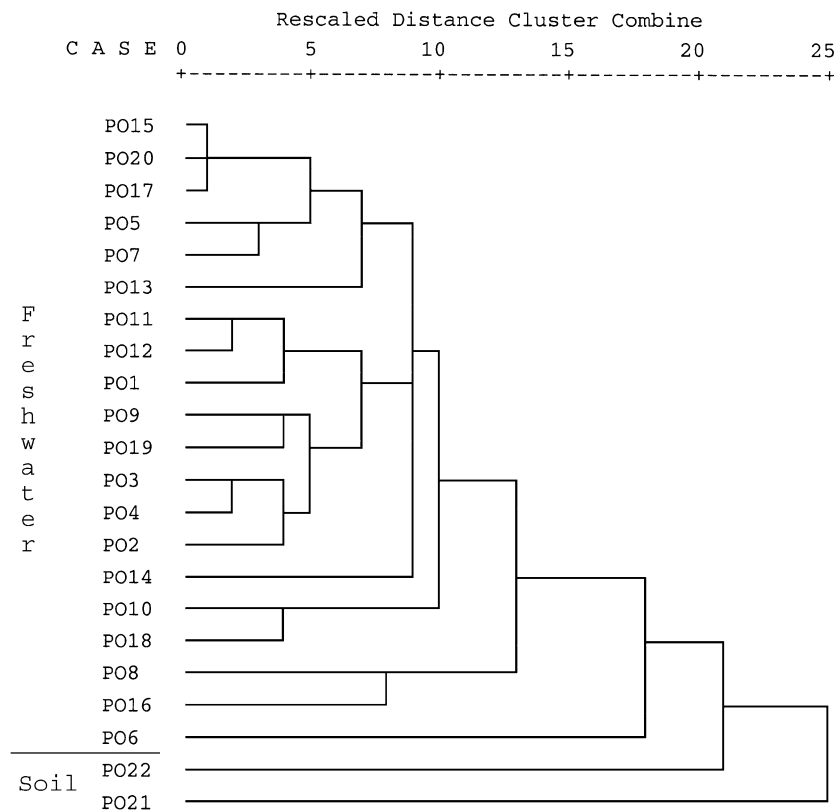


Fig. 4. Hierarchical cluster analysis (Pattern Difference) of 10 freshwater lakes and ponds (PO 11–18, PO 19, 20 from Deception Island), 10 rivers and streams (PO 1–10), one terrestrial moss (PO 21) and one fellfield (PO 22) site in the maritime Antarctic (South Shetland Islands, Livingston Island unless noted, 63°S) based on their ciliate assemblages, indicating a separation of freshwater and terrestrial coenoses. Species of several samples were pooled for a single site where multiple samples were available.

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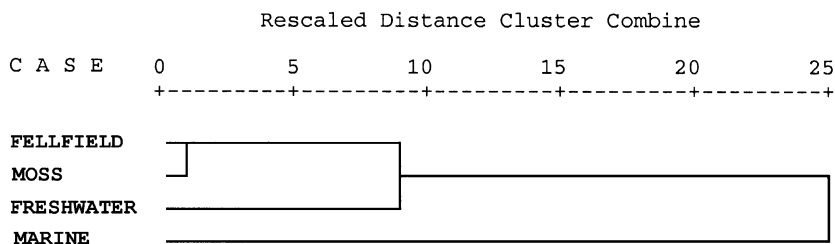


Fig. 5. Hierarchical cluster analysis (Jaccard Measure) of 17 freshwater lakes, ponds and streams, three terrestrial moss and 12 fellfield samples and two marine habitats (two landfast sea ice cores, one sea floor sample) in continental Antarctica (Terra Nova Bay area, 75°S) based on their ciliate assemblages, indicating a distinct separation of marine, freshwater and terrestrial coenoses whereas terrestrial habitats (moss, fellfield) show a high similarity in their species inventory. Species of all samples were pooled for each respective biotope.

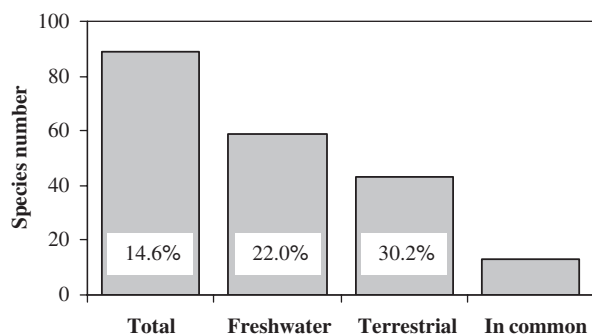


Fig. 6. Ciliate species numbers found in limnetic ($n = 31$) and terrestrial biotopes (fellfield, moss; $n = 15$) of continental Antarctica (Terra Nova Bay area, 75°S) and number and percentage of species in common.

Antarctic localities (Fig. 5). Terrestrial biotopes harboured fewer ciliate species than limnetic biotopes and only some of these taxa were also found in freshwater bodies (e.g. Fig. 6). In continental Antarctica (Terra Nova Bay area), for instance, 13 species (22%) found in freshwater occurred also in fellfield (mineral soil) and/or terrestrial moss (Fig. 6). The ciliate community inhabiting marine biotopes such as the sea floor or brine channels within landfast sea ice differed even more from the coenoses living in nearby freshwater bodies or soil (Fig. 5), indicating that limnetic communities are not recruited from the sea as previously suggested (Kepner *et al.*, 1999).

When comparing the ciliate species composition found in terrestrial and limnetic biotopes of several polar localities, two distinct clusters were revealed: one containing mainly continental Antarctic sites and the other combining the Arctic and most maritime Antarctic biotopes (Fig. 7). However, usually different biotopes of a particular locality grouped together or appeared at least in the same cluster. Only the community recorded in terrestrial moss on Livingston Island (maritime Antarctic) was more similar to terrestrial habitats of the coastal continental Antarctic near Casey Station (66°S, Fig. 7).

Considerable differences were also revealed by cluster analysis between the limnetic ciliate communities of polar

and temperate latitudes, e.g. five rivers in Austria (47–48°N). Although the assemblages from the Austrian rivers are quite similar, there is a distinct separation from the High Arctic (but in the same cluster) and the maritime and continental Antarctic communities (Fig. 8). Of the 218 ciliate species found in the five Austrian rivers, 76 (35%) were recorded in at least one of the polar regions in this study.

Discussion

Knowledge of the species composition, diversity and distribution of ciliates in the Arctic and Antarctic is still limited. The highest species diversity was found in the High Arctic; considerably fewer species were recorded in the Antarctic and these numbers decreased further with increasing southern latitude (Figs 1 and 2). The relative local species richness of ciliates in polar regions is slightly higher than that of some multicellular organism groups in other geographical locations (e.g. nematodes, bivalves) but still in the same range as that of, for example, polychaetes when based on a global total of 8000 ciliate species (Lynn & Corliss, 1991; Hillebrand *et al.*, 2001; Table 4). However, as this proportion depends considerably on the global number of ciliate species, it may differ by over 100% (Table 4). As the latter is currently not known for ciliates (recent estimates lie between 3000 and 8000 or even more; Lynn & Corliss, 1991; Finlay & Esteban, 1998; Foissner *et al.*, 2005) comparisons with multicellular organisms can be only preliminary. However, even a high relative local species richness does not preclude the possibility that at least some ciliate species might have a restricted geographical distribution.

The ciliate coenoses in freshwater were distinctly different from those in mineral soil and/or moss as revealed by cluster analysis, given that only a few species were common to these biotopes (Figs 3 and 4). For instance, only 22% of the species recorded in freshwater in the continental Antarctic Terra Nova Bay area occurred also in fellfield or terrestrial moss there (Fig. 6). Similar findings were made at the other localities, and are in accordance with the data of Foissner

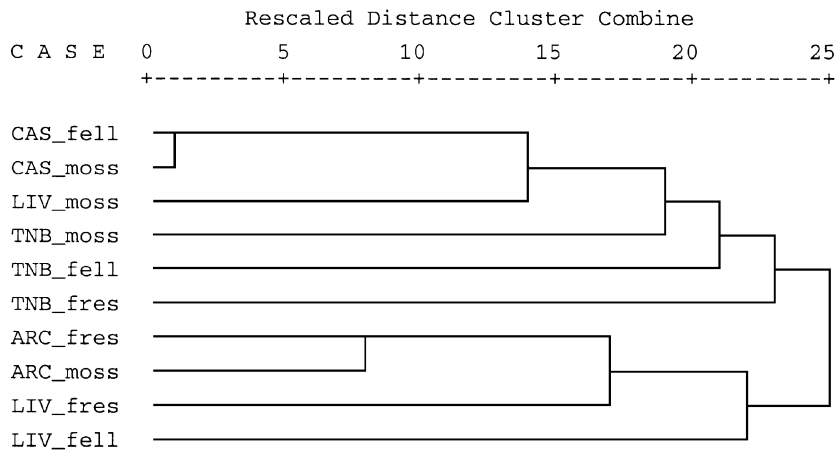


Fig. 7. Hierarchical cluster analysis (Jaccard Measure) based on the ciliate coenoses of freshwater and soil ecosystems of the High Arctic (ARC, Svalbard, 79°N) and the maritime (LIV, Livingston Island area, 63°S) and continental Antarctic (TNB, Terra Nova Bay area, 75°S; CAS, Casey Station area, 66°S), indicating that often different biotopes of a particular locality group together or appear at least in the same cluster. The species of all samples were pooled for each respective biotope: fell, fellfield; fres, freshwater; moss, terrestrial moss.

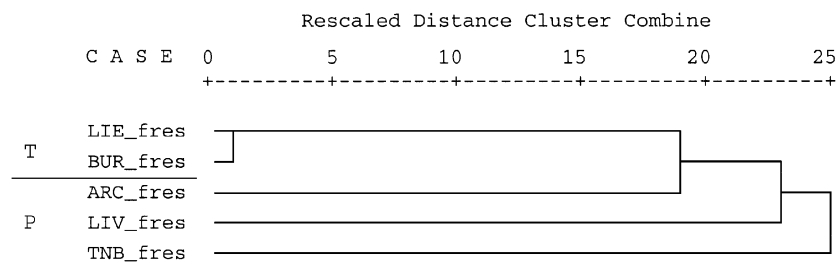


Fig. 8. Hierarchical cluster analysis (Jaccard Measure) based on the ciliate coenoses of freshwater ecosystems of the High Arctic (ARC, Svalbard, 79°N; $n=36$), the maritime (LIV, Livingston Island area, 63°S; $n=37$) and continental Antarctic (TNB, Terra Nova Bay area, 75°S; $n=31$), and temperate latitudes (Austria: BUR, rivers Lafnitz, Strem, Leitha and Wulka pooled, 47°N, $n=36$; LIE, river Liesing, 48°N, $n=74$), indicating distinct differences between the ciliate assemblages of temperate (T) and polar (P) freshwater localities. The species of all freshwater samples were pooled for each respective location.

(1998), who reported that about 25% of the described terrestrial ciliate species have been reliably recorded from both soil and freshwater habitats. This indicates that in polar regions a high proportion of ciliates inhabit mainly or exclusively limnetic environments and another group only soils and/or mosses. However, this is in contrast to the assumption of Finlay *et al.* (2004), who proposed a ubiquitous dispersal for microbial eukaryotes such that the species occur in virtually all types of habitats (e.g. Smith, 1978; Schaefer & Tischler, 1983).

Many ciliate morphospecies found in the course of the present investigation in the Arctic and in Antarctica have a cosmopolitan distribution and are widespread in other regions of the world as well. However, there are exceptions, e.g. *Stentor* and *Metopus* spp. (see above). Likewise, several other species, e.g. *Euplotes euryhalinus*, *Spathidium seppelti*, *Sterkiella thompsoni* and *Urosomoida granulifera*, from brackish water, freshwater and terrestrial environments have not yet been found outside Antarctica (e.g. Thompson, 1972; Valbonesi & Luporini, 1990; Foissner, 1996; Petz & Foissner, 1997) although they were recorded from new localities on this continent in the present study. Further-

more, up to about 20% of the limnetic species found in any of the polar study areas are apparently new to science. Although the discovery of new species is not conclusive evidence *per se* for the existence of endemic ciliate taxa, this shows at least that there is a considerable potential for species having a limited geographical distribution in polar freshwater biotopes. This is corroborated by the fact that survival in inhospitable environments often requires particular physiological adaptations (Grémillet & Le Maho, 2003).

Undersampling, i.e. lack of knowledge on the species inventory of many geographical areas and biotopes and the distribution of species, is certainly a problem when investigating and reviewing the biogeography of ciliates and deciding whether locally endemic species exist. However, the polar regions are far more undersampled compared with elsewhere so that a higher sampling effort in high latitudes might further increase the number of new taxa found there.

Indications for the existence of endemic protist species in polar or other biogeographical regions come also from marine ciliates and terrestrial testate amoebae. Some tintinnids, e.g. *Laackmanniella naviculaefera*, *Codonellopsis balechi*

and *Codonellopsis gaussi* and all members of the genus *Cymatocylis*, are very likely restricted to the Southern Ocean, although sometimes loricae (empty?) are transported slightly north of the Polar Front (Alder, 1999), which forms the boundary to the other oceans. Most of these taxa are frequent and widespread in the plankton of the Southern Ocean but have not been found in other oceans or seas even though there is a long history of marine planktonic surveys worldwide. Likewise, the testate amoebae *Apodera vas* (synonym *Nebela vas*) has not been found in Europe or North America despite numerous studies on these continents (Mitchell & Meisterfeld, 2005), and *Centropyxis gasparella* had thus far been recorded only from the Arctic, i.e. in northern Canada, Greenland and Svalbard (Chardez *et al.*, 1988; Beyens & Chardez, 1997; Petz *et al.*, 2006).

Unhindered random dispersal is proposed as a prerequisite for the cosmopolitan distribution of all microbial species, i.e. also unicellular eukaryotes (Fenchel *et al.*, 1997; Finlay, 2002). Thus, geographical distance should not matter for microbial assemblages, which are able to live under similar environmental conditions, e.g. in similar biotopes. Three main dispersal mechanisms are recognized for microorganisms, which have each played an important role in the recent colonization history of Antarctica: transport by air masses, animal vectors (mainly birds) and humans (Kennedy, 1999). It can be assumed that the same processes may contribute to the colonization of geographically isolated Arctic islands such as the Svalbard Archipelago. Although local airborne dispersal seems to be easily achieved in protists, long-range dispersal to Antarctica and between ice-free localities involves enormous distances (up to several hundred or thousand kilometres) and thus may present problems (Broady, 1996). While wind-driven dispersal of freeze-dried portions of benthic mats from lakes and ponds has been observed within Antarctica (Parker *et al.*, 1982), favourable conditions for immigration from the southernmost tip of South America or other continents may occur only once within several hundred years; Kennedy, 1999). Although transport by wind is widely assumed to be a dispersal mechanism for protists (e.g. Broady, 1996), ciliates (in durable resting cysts) are rare or often absent in aerosol collections (Schlichting, 1961; Sudzuki, 1972; Benninghoff & Benninghoff, 1985; Marshall, 1996; Marshall & Chalmers, 1997; Rogerson & Detwiler, 1999). Likewise, ciliates were not found on Antarctic flying birds, which may act as dispersal agents for algae and other protists (Schlichting *et al.*, 1978). However, the latter might have been a methodological problem because all bird specimens fell into the sea prior to collection and cysts may have been washed off or be inactivated due to the saline water. Another more important reason may be that at least some limnetic ciliate species or even entire genera do not form resting cysts (Foissner, 1987), which are thought to be a prerequisite for long-distance transport.

The low congruence in the ciliate species composition between High Arctic and Antarctic freshwater bodies (i.e. 13% of the species) as well as between both investigated south polar localities (Figs 1 and 2) suggests that there are restricted cosmopolitan dispersal capabilities of limnetic ciliates. This is also indicated by our cluster analysis. In all studied localities, there was generally a clear distinction in the ciliate communities between freshwater and terrestrial biotopes (e.g. Figs 3–5), suggesting that separate assemblages exist in these. This is in accordance with observations of Foissner (1987, 1998). Despite this, however, the species similarity between different, i.e. aquatic and edaphic, biotopes within a given geographical area (e.g. High Arctic freshwater and moss; continental Antarctic freshwater, fellfield and moss; maritime Antarctic freshwater and fellfield) was higher than between similar biotopes of more distant regions (Fig. 7). Likewise, the ciliate assemblages in Austrian rivers are remarkably different from those in the polar regions (Fig. 8). This indicates that geographical distance does matter and the exchange of species between far distant sites is more restricted than between different biotopes within a rather small spatial scale, albeit that the species similarity is generally low between limnetic and terrestrial biotopes (see also Foissner, 1998). This is in accordance with the results of Hillebrand *et al.* (2001), who found a decreasing species similarity with increasing geographical distance in ciliates and benthic diatoms of temperate latitudes. Thus, it can be concluded that some limnetic ciliate species might have a restricted geographical distribution and that many freshwater taxa are not ubiquitous. For these reasons, it is premature to neglect the effect of unicellular eukaryote biodiversity on ecosystem function, in particular in aquatic and terrestrial systems of polar regions, where only very few multicellular organisms occur.

Telford *et al.* (2006) also showed that dispersal limitations occur at least in some microbial species so that the regional species pool of freshwater diatoms is decoupled from the global pool. Likewise, geographical barriers may have led to an evolutionary diversification of picoeukaryotic algae as suggested by Šlapeta *et al.* (2006). Despite studies on the biogeography of prokaryotes being limited, recent evidence indicates that there are also endemic archeal, bacterial and cyanobacterial species both at high and at temperate latitudes (e.g. Ellis-Evans, 1996; Taton *et al.*, 2003; Whitaker *et al.*, 2003). For instance, Taton *et al.* (2003) found endemic cyanobacterial species in the Antarctic based on morphological and molecular methods. Franzmann (1996), Vincent (2000) and Aislabie *et al.* (2006) listed bacterial, fungal and microalgal candidates for microorganismal endemism from various biotopes at high latitudes (e.g. saline lakes, soils, seawater, sea ice) and at least one yeast species seems to occur exclusively in Antarctica (Fogg, 1998). Whitaker *et al.* (2003) showed in more temperate latitudes that

hyperthermophilic archaea are isolated by geographical barriers so that local adaptations have evolved. All this contradicts the notion of Finlay *et al.* (1996) that 'everything microbial is everywhere, but the environment selects'.

The higher similarity in the ciliate species composition of terrestrial moss on Livingston Island and terrestrial habitats of the coastal continental Antarctic (Casey Station, 66°S; Fig. 7) might be explained possibly by 'local' dispersal. This could be achieved by a narrow ring of easterly winds surrounding the continental coast or that, moving in the opposite direction and being associated with high wind speeds, there are cyclonic low-pressure systems, which are known to reach in an eastward path from off the coast of Wilkes Land to the tip of the Antarctic Peninsula (Blüthgen & Weischet, 1980). However, Wilkes Land is about 5000 km distant from Livingston Island. Although the former process might suggest airborne transport from the South Shetland Islands to Wilkes Land, the latter would argue for a dispersal in the opposite direction. As all terrestrial ciliate species produce resting cysts (Foissner, 1987), wind-induced transport is probably more easily achieved in these than in many limnetic ciliates.

Conclusion

Data on community composition, species diversity and distribution of ciliates in the Arctic and Antarctic are still limited. In the present study, highest ciliate species diversity was found in the High Arctic on Svalbard while in the Antarctic distinctly fewer species were recorded and these decreased with increasing southern latitude. The rather high ciliate species diversity indicates that it is premature to neglect the effect of unicellular eukaryote biodiversity on ecosystem function, especially in aquatic and terrestrial systems of polar regions where only very few multicellular organisms occur. In all localities investigated, the ciliate community in freshwater was distinctly different from that in soil or other ecosystems, suggesting that many ciliates are not ubiquitous. Although most of the species identified in the polar freshwater bodies have a cosmopolitan distribution, at least some species might not; for example, members of the genera *Stentor* and *Metopus* have not yet been recorded in Antarctica whereas some other species have been exclusively found there. In addition, up to over 20% of the taxa recorded in any polar locality are probably new to science. This indicates at least the potential for the existence of locally endemic species, which might have evolved particular adaptations to the harsh environments either in Arctic (Laurasian) or Antarctic (Gondwanian) freshwater systems. Long-distance dispersal capabilities of limnetic ciliates, which are a prerequisite for their cosmopolitan distribution, seem to be restricted given that exchange of species between far distant sites is more limited than

between different biotopes within a local area. As at least some freshwater ciliates do not produce a dormant resting cyst, this might further restrict their dispersal. Thus, protists may have similar biogeographical distribution patterns to many larger metazoans and higher plants.

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