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Evidence Supporting the Concept of a Regionalized Distribution of Testate Amoebae in the Arctic

Louis BEYENS[1] **and Anatoly BOBROV**[2]

[1] **University of Antwerp, Department of Biology, ECOBE, Wilrijk, Belgium;** [2] **Moscow State University, Faculty of Soil Science, Moscow, Russia**

Abstract. Forty different sites, represented by 1483 samples, ranging from Alaska eastwards to Siberia, have been studied to assess the circumpolar testate amoebae species diversity. A total of 378 species have been recorded. The most common taxa are cosmopolitan and are widely distributed across various arctic habitats. Statistical analysis of testate amoebae species at sites across the Arctic have yielded geographic clusters of sampling sites that have been matched with climatic regions in the Arctic. We put forward the hypothesis that the differences in testate amoebae diversity across the Arctic hint to the existence of protozoological arctic regions. The problems concerning the question of the origin of the testate amoebae in the Arctic are also discussed, with emphasis on two arctic flagship species.

Key words: Testate amoebae, biogeography, Arctic, climate, flagship species, biodiversity.

INTRODUCTION

For a few decennia the Arctic has been in the spotlights due to the incertitudes and environmental changes related to global warming. This is reflected in the number of papers dealing with arctic topics and the substantial increase in interest showed by many governmental institutions in arctic issues. One big issue is the biodiversity, although in popular terms it is mostly reduced to concerns for iconic organims as the polar bear. Also at the scientific level, it seems that more insights are gained in the more visible biocomponents of the ecosystems (macroorganisms) than in the rather "invisible" microorganisms. Still a lot of questions remain, among other things on the origin of biota in the Arctic. The study of testate amoebae in the Arctic has followed the classic road from accidental sampling done by geographical and exploring expeditions, collecting all they could get, and the subsequent protistological analysis by researchers well skilled in protistology but not in arctic ecology, till the planned and structural sampling and ecological experiments from the last 20 years of the 20th century on. However, the sampling of arctic habitats in perspective of a long-time project was the quest of only a few researchers, i.e. Anatoly Bobrov for the Russian Arctic, Louis Beyens and Didier Chardez and collaborators for the non-Russian Arctic. Their papers represent a huge database, which in part has been explored as a metadaset by Jun Yang *et al.* (2010). None of the previous works has however looked intensely into the question of infra-Arctic testate amoebae diver-

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Address for correspondence: Louis Beyens, Department of Biology, ECOBE, CDE, University of Antwerp, Universiteitsplein 1, BE-2610 Wilrijk, Belgium; E-mail: louis.beyens@uantwerpen.be

sity. The Arctic is indeed not characterized by one main climate type, but exhibits major differences as well in latitudinal as in longitudinal ranges.

Studies on protist biogeography have been blossoming in recent years, with papers of proclaiming cosmopolitan view (e.g. Finlay 2002, Finlay *et al.* 2004) triggering the responses of the advocates of (some) endemism (e.g. Vanormelingen *et al.* 2008, Smith *et al.* 2008, Foissner 2008, Foissner *et al.* 2008). The current idea is that some degree of endemism does occur, something which is more conspicuous in some groups of organisms and, also important, more easily seen in some biomes. We will focus here on the Arctic as a major biome which long has been undersampled for testate amoebae compared to most other biomes.

The aim of this paper is to consider the following main question: is there some biogeographic trend in the Arctic regarding testate amoebae diversity? If so: can this trend be explained by climatic factors or are other factors involved. In addition to this, we will consider the question of the origin of the arctic testate amoebae fauna and the significance of arctic endemic species.

MATERIALS AND METHODS

Data were gathered from the studies featured in Table 1. The data set was compiled by pooling all the data from one site together, regardless the habitat. This method has the advantage that it gives a more global diversity at the site-level. A blurring effect can be expected, but when differences are detected, they can be expected to be meaningful. The PAST software (Hammer *et al.* 2001) was used for the statistical analysis. This was performed based on the presence-absence data of taxa, compiled from the different studies. Species lists in this case were verifiable. The Ward's method has been used for cluster analysis. This method differs from all other methods of clustering because it uses the methods of analysis of variance to evaluate the distances between clusters. The method minimizes the sum of squares (SS) for any two clusters that can be formed at each step. The method is very effective, but it tends to create clusters of small size. A Principal Coordinates Analysis (PCO) was also performed, using the Euclidean similarity index. We followed Aleksandrova (1980) to delineate the arctic biome. This means however that Iceland is not included in this study. No consensus is found in the literature regarding the geographic denomination of the Arctic. We will use the word "Arctic Circumpolar Region" for the entire Arctic, while with "region(s)" we will indicate a certain part of it. To probe the relation between testate amoebae distribution and climatic zones, we plotted the study sites on a map of the Arctic featuring the climatic zones and regions according to Prik (1981).

RESULTS

1. The global arctic picture: general data

The analysis of 1483 samples from 40 different sites in the Arctic revealed the presence of 378 taxa belonging to 51 different genera. The most common taxa present in at least 50% of the study sites are listed in Table 2, with *Trinema lineare, Assulina muscorum* and *Centropyxis aerophila* leading. While *Trinema lineare* occurred in 85% of the study sites, the 10th taxon, being *Phryganella acropodia*, fell to 58%. Only 13 taxa were observed in at least 50% of the regions. Fifty-three taxa, this is only 14.0%, in at least 25%. 228 taxa, this is 60% of the total, were present in less than 10% of the sites.

A ranking of the genera according to their number of taxa is presented in Table 3. The genus *Difflugia* shows most taxa, followed by *Centropyxis* and *Euglypha*. If we examine these data in relation with the (raw estimated) worldwide known number of taxa, it becomes clear that another picture emerges: of some genera all or almost all their taxa occur in the Arctic, while others are not often found. Concerning the mean number of taxa per study site, *Centropyxis, Difflugia* and *Euglypha* are still the prominent members. The position of *Euglypha* is certainly conspicuous, taking into account the lower number of taxa this genus has compared to *Centropyxis* and *Difflugia*. The number of observed taxa varies from study site to study site (Fig. 1), ranging from 2 to 136. The most common taxa are cosmopolitan ones and have an ubiquitous behaviour regarding habitat choice. There are a few arctic endemic ones, which will be discussed in section 5.

2. Regional arctic testate amoebae fauna's?

The Arctic is not a homogeneous biome as far as climatological, geological and geomorphological characteristics and history are concerned. The question thus arises if the testate amoebae fauna is in some way differentiated as a consequence of major geographical and climatic differences in the Arctic. To gain some insight in the possible similarities between study sites based on their geographical location, a Ward's method cluster analysis has been performed (Fig. 2). The performed cluster analysis shows three major groupings and some subgroups. Putting these clusters on a map reveals a geographic setting (Fig. 4), although some outlying group members occur.

Table 1. List of study areas and references used. S = ID-code for the study site.

S	GEOGRAPHIC LOCATIONS	REFERENCES
1	East Greenland, Tasîlaqfjord area	Beyens *et al*. 1986a, 1986b
2	Jan Mayen	Beyens *et al*. 1986a, 1986b
3	Central and North West Spitsbergen	Beyens *et al*. 1986a, 1986b
4	Edgeøya, Svalbard	Beyens and Chardez 1986c, 1995; Chardez and Beyens 1987
5	Barentzsøya, South coast, August 1985	Beyens and Chardez 1995
6	Hopen Island	Beyens and Chardez 1995
7	Bear Island	Beyens and Chardez 1995
8	Devon Island, Nunavut, Canada	Chardez and Beyens 1988; Beyens *et al*. 1990, 1991; Beyens and Chardez 1994
9	Søndre Strømfjord area, West Greenland	Beyens *et al*. 1992
10	South West Spitsbergen	Beyens and Chardez 1995, 1997
11	Cambridge Bay area, Victoria Island, Nunavut, Canada	Beyens and Chardez 1995, 1997
12	Barrow area, Alaska	Beyens and Chardez 1995
13	Nome area, Alaska	Beyens and Chardez 1995
14	Zackenberg, Northeast Greenland	Trappeniers *et al.* 1999, 2002; Van Kerckvoorde *et al.* 2000
15	Qeqertarsuaq, Disko Island, West Greenland	Beyens *et al*. 2009, Mattheeussen *et al.* 2005
16	Richards Island, Canada	Dalllimore 2004
17	Toolik lake area, Alaska	Mitchell 2004
18	Baffin Island, Canada	Collins *et al*. 1990
19	North West Spitsbergen	Bonnet 1965
20	Kangerdlugssuak, East Greenland	Dixon 1939
21	Scoresby Land, East Greenland	Stout 1970
22	West Spitsbergen	Sandon 1924
23	Barentsburg area, West Spitsbergen	Opravilová 1989
24	West Spitsbergen	Balik 1994
25	Bröggerhalvøya, West Spitsbergen	Schönborn 1966
26	Northeast coast Disko Bay, West Greenland	Decloitre 1956
27	Cape Mamontov Klyk, southern coast Laptev Sea, ca 159 km west of the Lena Delta	Müller *et al.* 2009, Bobrov *et al*. 2009
28	Bykovsky Peninsula, Laptev Sea	Bobrov *et al*. 2003
29	Nikolay Lake, Arga Island, Lena Delta region	Schirrmeister *et al.* 2011
30	Taymir Peninsula	Andreev *et al*., 2003, Bobrov and Wetterich 2012
31	Olenyok canal of Lena river (Yakitia)	Bobrov and Wetterich 2012, Bobrov *et al.* 2013
32	Bol'shoy Lyakhovsky Island, Laptev Sea	Andreev *et al*. 2004, Ilyashuk *et al.* 2006
33	October Revolution Island, Severnaya Zemlya Archipelago	Beyens *et al*. 2000, Andreev *et al.* 2008
34	Bol'shevik Island, Severnaya Zemlya Archipelago	Beyens *et al*. 2000, Andreev *et al.* 2008
35	Samoylovsky Island, Lena Delta (Yakitia)	Schirrmeister *et al.* 2011
36	Nagym, northern bank of Olenyeksky branch on Ebe-Basyn-Sise Island, Lena Delta	Bobrov *et al.* 2013
37	Lena Delta (Yakitia)	Schirrmeister *et al.* 2002, 2011
38	New Siberian Islands – Kotel'ny Island, Maly Lyakhovsky Island, Stolbovoy Island, Bel'kovsky Island	Schirrmeister *et al.* 2011, Bobrov and Wetterich 2012
39	Seward Peninsula, Alaska	Meyer *et al.* 2010, Wetterich *et al.* 2012, Bobrov *et al.* 2013, Lenz *et al.* 2015
40	Chokurdakh (Yakitia)	Bobrov *et al.* 2013, Teltewskoi *et al.* 2016

Table 2. Taxa present in at least 50% of sites. Last column gives the percentual presence in the total number of sites.

Taxa present in at least 50% of sites			%
Trinema	*lineare*	Penard	85
Assulina	*muscorum*	Greeff	83
Centropyxis	*aerophila*	Deflandre	80
Corythion	*dubium*	Taranek	73
Euglypha	*laevis*	Perty	70
Trinema	*enchelys*	Leidy	63
Euglypha	*strigosa f. glabra*	Wailes	60
Centropyxis	*sylvatica*	Thomas	58
Euglypha	*rotunda*	Wailes	58
Phryganella	*acropodia*	Hopkinson	58
Centropyxis	*aerophila v. sphagnicola*	Deflandre	55
Difflugia	*globulus*	Hopkinson	53
Nebela	*collaris*	Leidy	50

Table 3. Ranking genera according to their number of taxa.

Ranking of genera according to their total number of taxa recorded in the Arctic and (estimated number worldwide)		Ranking of genera according to the mean number of taxa taken over all study sites	
Difflugia	70 (300)	*Centropyxis*	9.7
Centropyxis	61 (130)	*Difflugia*	6.7
Euglypha	30 (40)	*Euglypha*	5.5
Arcella	28 (50)	*Nebela*	4.3
Nebela	25 (100)	*Arcella*	3.8
Cyclopyxis	14 (30)	*Trinema*	2.9
Trinema	13 (> 24)	*Corythion*	1.8
Cryptodifflugia	12 (20)	*Cyclopyxis*	1.6
Plagiopyxis	10 (22)	*Assulina*	1.3
Corythion	9 (9)	*Plagiopyxis*	1.0
Paraquadrula	8 (8)	*Phryganella*	1.0
Phryganella	8 (8)	*Cryptodifflugia*	0.7
Heleopera	7 (> 12)	*Placocista*	0.5
Pseudodifflugia	6 (20)	*Pseudodifflugia*	0.4
Assulina	5 (5?)	*Difflugiella*	0.2
Placocista	5 (8)	*Cochliopodium*	0.1

3. Which geographic regions are discernible?

The question of possible biogeographical patterns is the next topic. Fig. 4 shows the geographic position of the members of the different clusters. There are no clusters which are strictly limited to one major region, but most clusters show some geographical delination.

This protistological zonation can be translated as follows:

A Siberian region (cluster A + subgroup B1 + subgroup C1). Outliers are two sites in Nunavut, Canada. These can be explained in terms of the relation of the used sieve widths in the sample preparation procedure and the larger measurements of many *Difflugia* taxa. Another outlier is study site 39 from Alaska.

The Svalbard-Greenlandic region (cluster B2 + cluster B3). Here is a distinct subgroup B2, which is an assembly of study sites along the Fram Strait-Greenland Sea – Denmark Strait-Western part Barentzs Sea.

The subgroup C2 unites two study regions from Nunavut (Canadian Arctic) and two from West-Greenland. Outliers are Edgeøya (East Svalbard) and the Zackenberg area in the East-Greenlandic High Arctic. This could point to a Nunavut-West Greenland region, but this is too uncertain. Therefore we will not consider this further.

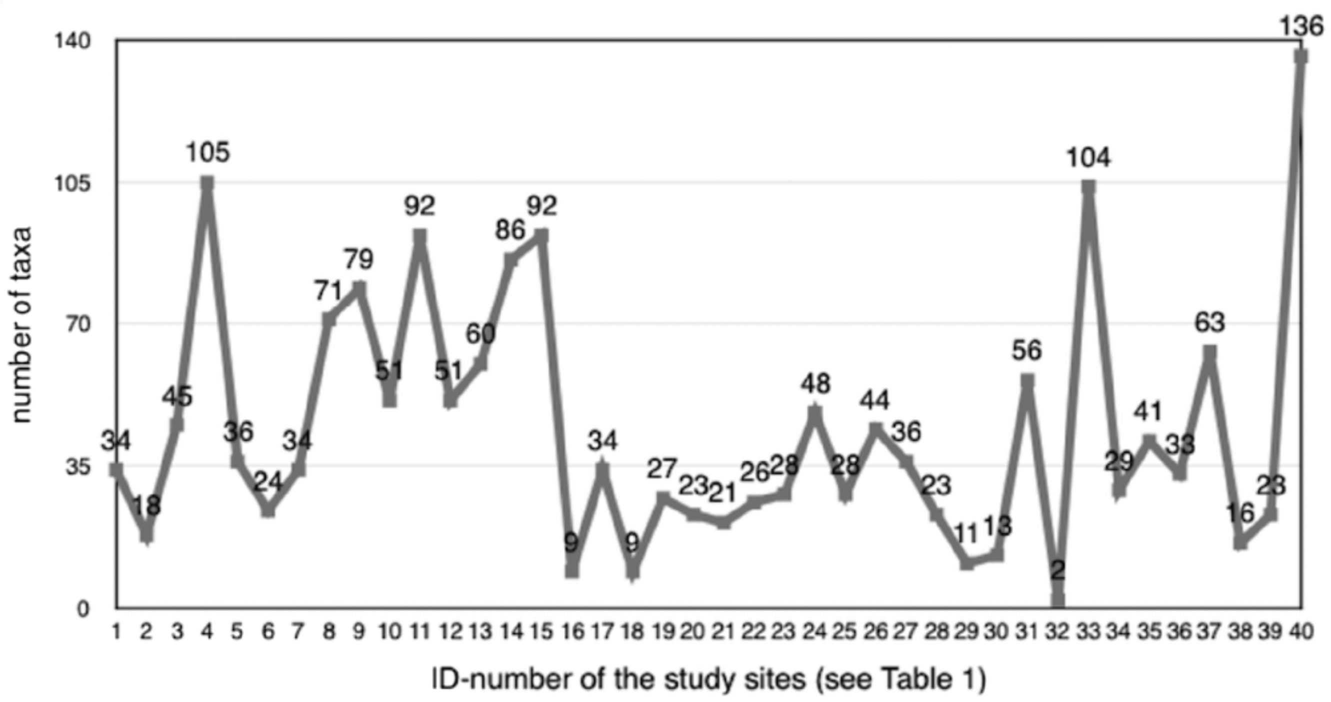

Fig. 1. Number of taxa per study region. X-axis with ID-number of the study site, given in Table 1. Y-axis the number of taxa. Numbers of taxa are also given on the graph.

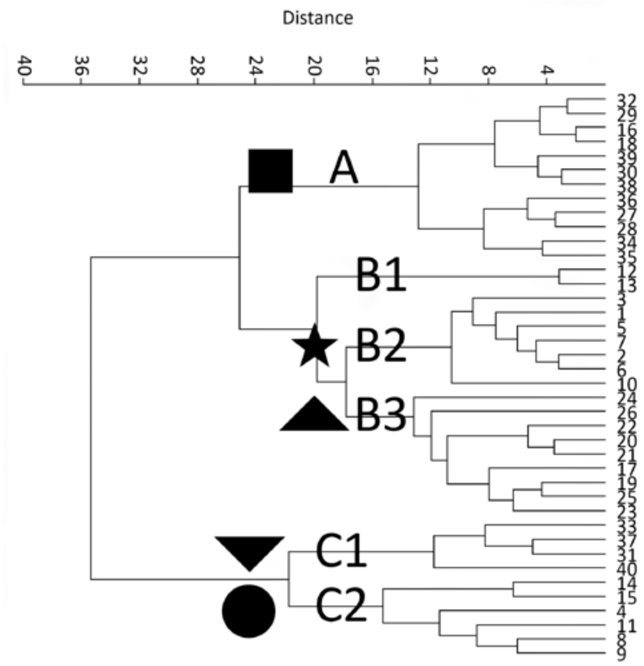

Fig. 2. Cluster diagram (Ward's method). Each cluster is given a symbol which is also used in Fig. 4. Numbers on the right hand represent the site-numbers (see Table 1).

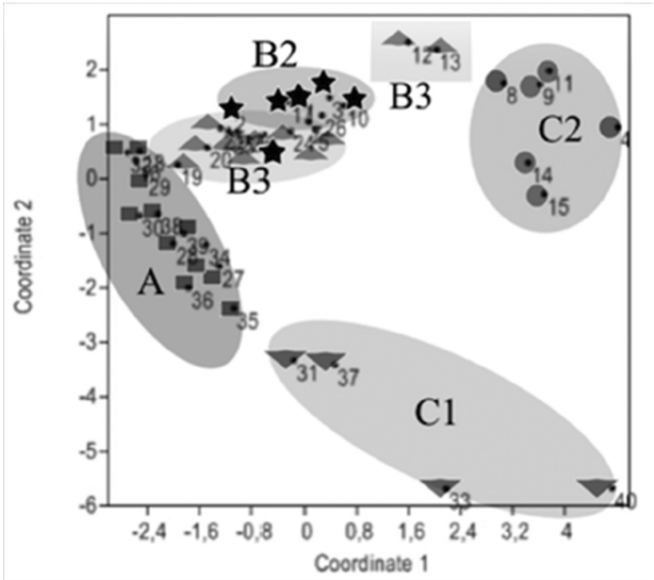

Fig. 3. Ordination diagram. For symbols see Fig.~~1~~2. The numbers in the graph refer to the ID-number of the study site.

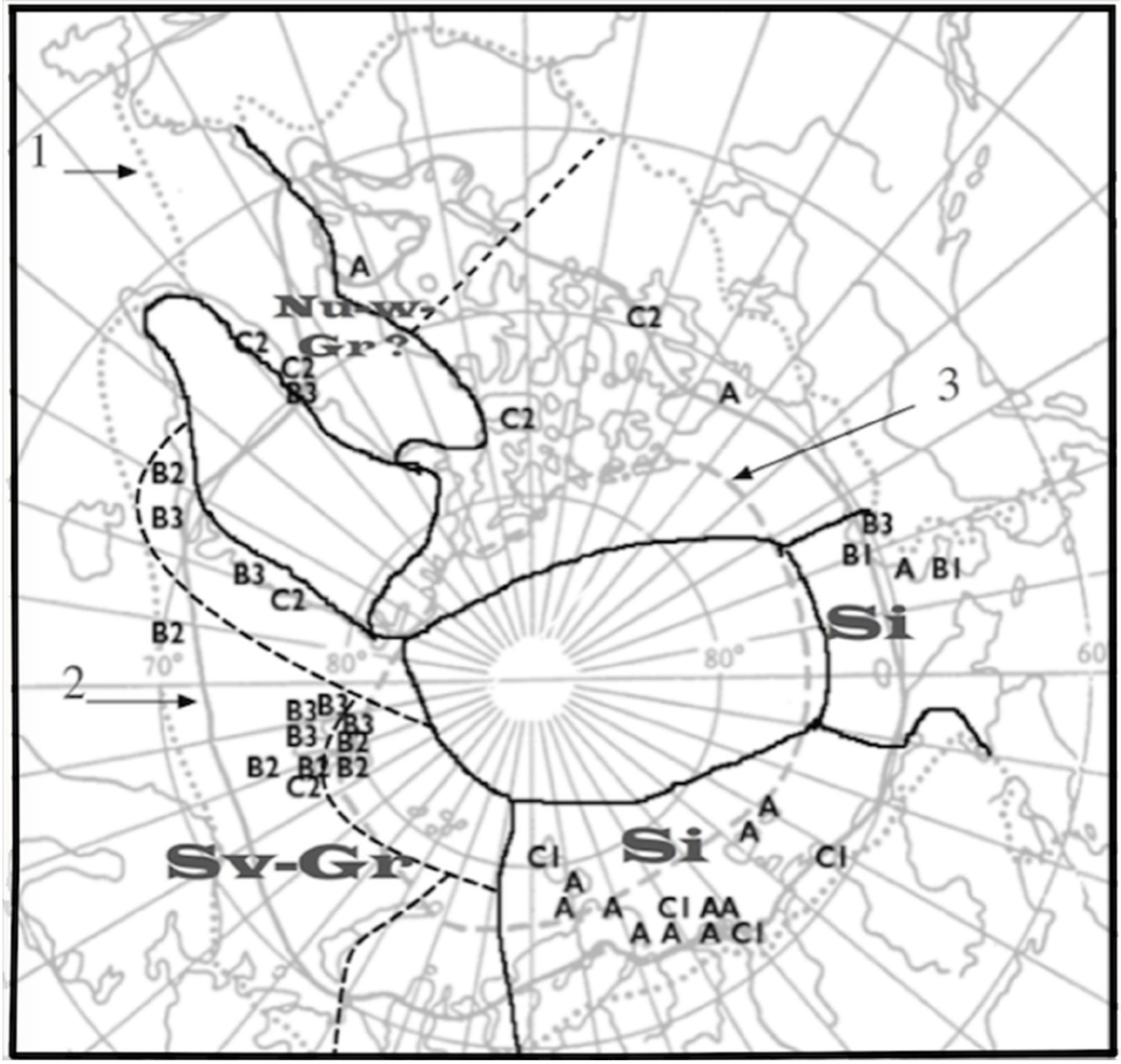

Fig. 4. Map of the Arctic (polar view) with climatic zonations according to Prik (1981) and the location of the different clustergroup members. The delination of the southern limit of the Arctic is given by the arrow with the number 1. The arrow 2 gives the southern limit of the High Arctic, arrow 3 the southern limit of the Polar Desert zone (according to Aleksandrova 1980). Sv-Gr stands for the suggested Svalbard-Greenlandic protozoological region, Si stands for the Siberian.

One feature of a cluster is the mean number of taxa per genus (Table 4). Striking differences between the Siberian and Svalbard-Greenlandic regions are found in the role of *Difflugia* (6.7 mean number of taxa in the Siberian region versus 3.0 in the Svalbard-Greenlandic one) and *Arcella* (4.1 versus 1.3). *Difflugia* and *Arcella* are mainly aquatic genera. Do these differences then reflect major habitat differences between the regions? Or is it merely a methodological difference in the sense that in the Siberian region mostly aquatic habitats were sampled. Given the fact that also for the sites in the Svalbard-Greenlandic region much effort is done to

Table 4. Mean number of taxa per genus in the protistological arctic regions.

SIBERIAN REGION		SVALBARD-GREENLANDIC REGION	
Centropyxis	10.4	*Centropyxis*	5.6
Difflugia	6.7	*Euglypha*	4.8
Euglypha	4.8	*Nebela*	3.6
Arcella	4.1	*Trinema*	3.2
Nebela	3.5	*Difflugia*	3.0
Trinema	2.3	*Corythion*	2.2
Cyclopyxis	1.7	*Assulina*	1.5
Corythion	1.6	*Plagiopyxis*	1.4
Assulina	1.1	*Phryganella*	1.3
Cryptodifflugia	1.1	*Arcella*	1.3
Placocista	1.0	*Cyclopyxis*	0.6
Phrygnella	0.7	*Pseudodifflugia*	0.4
Plagiopyxis	0.5	*Cochliopodium*	0.3
Pseudodifflugia	0.3	*Cryptodifflugia*	0.1
Difflugiella	0.2	*Difflugiella*	0.1
Cochliopodium	0	*Placocista*	0

study also the aquatic sphere, such differences seem to be due to other than sampling strategies. We refer here also to the dissussion on methodological problems.

4. The testate amoebae regions and climatic sectors in the Arctic

The sample groups are found in the ordination (Fig. 3). The first coordinate can be explained by the numbers of samples. Sites with a greater number of samples were mostly more heterogeneous and as such more taxa are found there. The second one (y-axis) is explained by the macro-climate. Along this y-axis the group C1 is clearly separated from the others. It is close to group A, which has some minor overlap with B3 but more similarity in range with C2. B3 is the following one, greatly overlapping with B2. As well B2 and B3 overlap with C2. B1 is to be considered as an outlier since the sample manipulation was greatly aberrant (see Methodological problems). As mentioned above, we will not consider group C2 further because of its geographic heterogeneity.

The Siberian group falls in the Siberian climatic sector, as defined in Prik (1981) (Fig. 5). In winter, this sector is under the influence of a strong anticyclonic circulation with very low temperatures. During summer, there is a predominant anticyclonic circulation in the northern parts of the seas, and a cyclonic one in the northern parts of the continent. That results in the islands of the several archipelagos having another summer regime than the continent. Air temperatures above the (ice covered) seas are around 0° to 2°C. On the coast of the continent, temperatures rise to average values around 10° to 12°C (Prik 1981), which are balmy values for the Arctic and place these areas at the edge of the Arctic. Yet, in the cluster diagram, study sites from the archipelagos are grouped with study sites near the Siberian coast.

The Svalbard-Greenlandic region is situated mainly in the Atlantic climatic sector. The climatic conditions are quite heterogenous due to, amongst other things, different seawater currents. The latitudinal temperature decrease in the southern part is moderated by the warm Gulfstream, which effect reaches northward till the westcoast of Svalbard. Most of the east coast of Greenland is under the influence of the cold current transporting the pack ice from the Arctic Ocean southward.

The cluster groupings of the study sites (according to their testate amoebae fauna) correspond to a high degree with major climatic zones, but the intrazonal climatic heterogeneity is not reflected. This means that at the higher geographic-climatic level, climate is an important driver for testate amoebae biogeographic diversity. More precise, not only a latitudinal gradient is recognized, but also a longitudinal one. The climate of

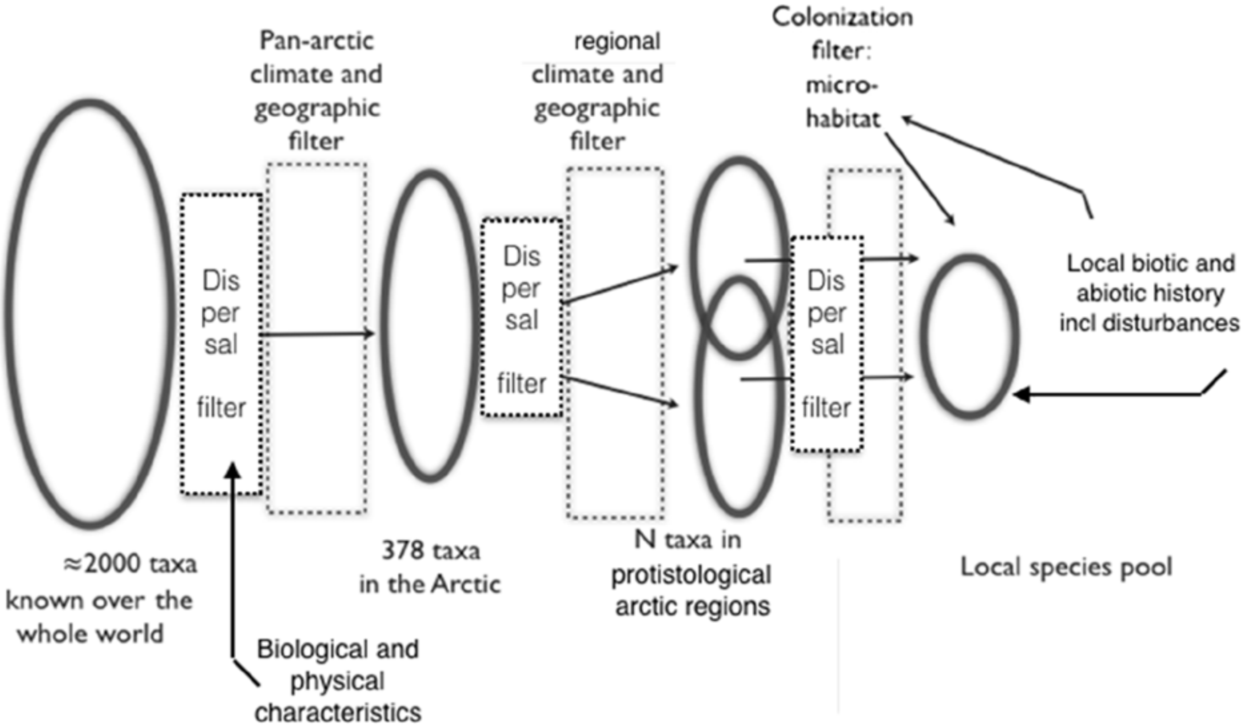

Fig. 5. A hypothetical model for explaining the species diversity in the Arctic.

the Russian Arctic being more severe than this of Svalbard for instance.

We can conclude that within the Arctic, longitudinal differences occur which hint at the overall influence of climatic factors.This should not be a surprise. Longitudinal zonations and gradients are found in higher plants and their communities, and such longitudinal differences formed also the basis for geobotanical division as made by Aleksandrova (1980). Later, molecular analyses for arctic plants also revealed clustering of common elements in regions as Siberia, Atlantic areas, the Canadian Arctic, Beringia (Abbott and Brochmann 2003).

DISCUSSION

1. Methodological problems

When combining protistological data from different studies, there are some methodological problems to deal with. A major problem could be the possibility that different researchers have another view on the taxonomy, resulting in clear differences in species lists. For this study, 42 papers were taken into account, the first author (LB) was involved in 15 of these, the second author (AB) in 16 others. This leaves only 11 papers from other researchers. The fact that the majority of the studies considered are co-authored by the present authors, smooths the problem of taxonomic resolution. There can also be issues on preparation and sampling methods. Differences in mesh width when back sieving samples lead to a selective treatment, with the loss of taxa when mesh width is too big. Only in the study sites 16 and 18 a mesh size was used which was too wide for obtaining a detailed protozoological picture. Bigger taxa as many *Difflugia*'s are thus kept for further analysis, while small taxa are lost. The position of the study sites 16 and 18, both from the Canadian Arctic, in the subgroup A1 can be explained this way. A major concern for the present study is the uneven sampling effort. This can have an impact on the perception of the results depending on the level of interpretation. There are two options: or we could discard all sites which have an outlying sampling effort, or we incorporate all sites in this study. We have opted for the second option because that way we are able to present a more complete survey. A general but important remark should be formulated here. The number of samples is in many cases related to the type of the site: more homogeneous sites are less sampled than more heterogeneous ones. It can indeed be expected, and we also know this from experience: heterogeneous sites harbour more species.

Did differences in sampling size disturb the picture? When the number of samples is noted against the study sites in each cluster group (cluster analysis Ward's method), we see marked differences between the main clusters. But even within this methodological constraint, we had interesting results. If the number of samples should dictate the different clusters, then we should expect that all the sites with the same or a near-same number of samples are grouped. This is not the case. At least 4 sites from the first cluster (16, 39, 27 and 35) should belong then to cluster B. Also, some of cluster B (o.a. 17, 19) would be expected to occur in cluster A. The last main cluster C gives a clue. Sites 33, 37 and 31 would be more fitting in cluster B. This means that these sites have enough protozoological characteristics in common with the others from the group they are placed in. And this can also hold a fortiori for samples which do not have an aberrant number of samples.

Another argument is that Beyens and collaborators sampled as well mosses, waterbodies and soils from their study sites. Yet, there are still subgroups recognizable from their data, meaning that some other factor(s) than habitat and habitat related environmental conditions is (are) playing a role.

2. A model for the establishment of testate amoebae communities

At the more infra-regional to local level, other drivers than climate should be involved. A lot of ecological papers have revealed the importance of habitat availability and other environmental factors (moisture and pH of soils, moss vegetations, waterbodies characteristics with for instance their isolation of each other). We assume that these are responsible for the fine tuning and selecting which communities will occur in this setting.

This leads us to the following hypothetical model: A pan-arctic filter based on climate and geographic characteristics leaves roughly 20% of the known testate amoebae taxa to occur in the Arctic. On a lower hiearchic level (i.e. on the regional scale) further climatic and geographic filters (including the Pleistocene glaciation history and landscape features on a major scale) are responsible for selecting protistological communities. A dispersal filter works on all levels. The final fine tuning is done by colonisation features in combination with (micro)-habitat characteristics, which also include biological phenomena as competitive exclusion (Fig. 5).

3. On the origin of testate amoebae in the Arctic

Biota must be able to reach a region before a selection according to climatic limitations can happen. This is related to the question of the existence of Pleistocene refugia, the degree of glaciation and that of the colonization of the Arctic after the Last Ice Age. The same applies to the origin of the testate amoebae in the Arctic. As for most other biota, there is the possibility of an eventual survival in the Arctic during the Pleistocene. Even with higher plants which are well studied there are large gaps in the knowledge of their arctic history, especially of the founders stocks (Abbott and Brochmann 2003). It seems that some arctic plants are not old species, but that they originate from the Holocene. But, studies of chloroplast DNA have revealed evidence of Quaternary glacial refugia at high latitudes for *Dryas integrifolia* and *Saxifraga oppositifolia* (Abbott and Brochmann 2003). Furthermore, some trends in molecular similarities were detected in *S. oppositifolia* populations from different regions on a mainly east-west transect, which could suggest that at least some populations of the species survived the last glaciation in Beringia and migrated out of this refugium during postglacial times. As the rhizosphere of plants provide, if moisture conditions are suitable, a habitat for testate amoebae, the survival of plants during glacial times in refugia can be an argument to suppose the survival of some testate amoebae in the Arctic as well. We will have to wait for molecular data to detect more patterns and gain more information on this topic.

Endemic species from the Arctic have been described (o.a. Beyens and Chardez 1986c, 1994). Here we will not deal with taxa which have been observed only once, at the place of their discovery (the so-called local endemism). More interesting are the endemic taxa which have a wider distribution in the Arctic. We will discuss here two species which are conspicuous in this regard (Fig. 6). It is improbable that taxa as *Centropyxis pontigulasiformis* (Beyens and Chardez 1986c) or *C. gasparella* (Chardez and Beyens 1988) developed on more than one place, so they had dispersed form their place of origin. When, where and how did the speciation occur? It is possible that they originated during an interglacial, as the Eemian, with temperatures maybe even exceeding the present ones. They could then already have been dispersed during that interglacial and obtained at least a semi-circum-arctic distribution.

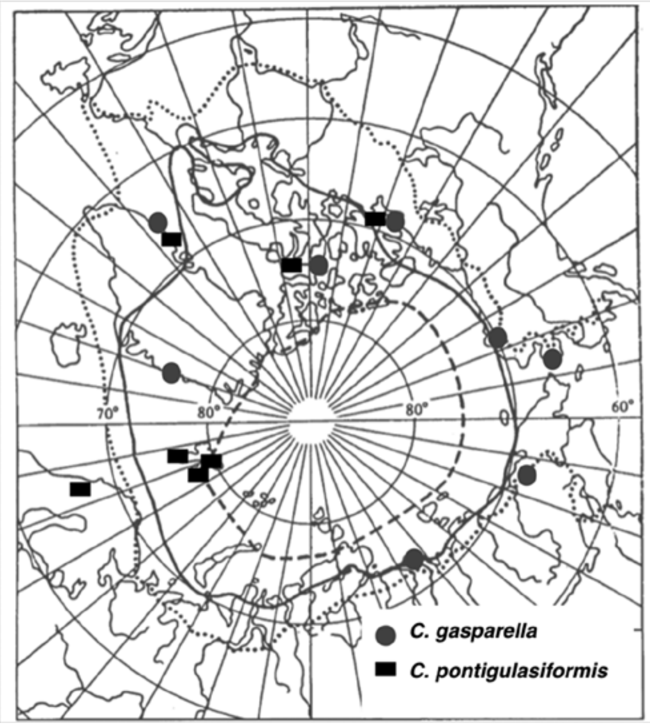

Fig. 6. Distribution map of *Centropyxis pontigulasiformis* and *C. gasparella* in the Arctic and subarctic Norway. Remark that *C. pontigulasiformis* has recently been observed in the Netherlands and in Austria.

To follow this scenario, they became then extincted in areas glaciated during the next glacial stage, surviving in refugia, to spread again during the postglacial. Or did they originate during a glaciation in a refugium, to achieve the present distribution? For plants at least, it is now quite sure that some survived the Quaternary glaciations in arctic refugia. As stated earlier on, there is no reason to exclude testate amoebae from the surviving biota. The higher species richness which we observed in the Siberian region could well be the result of larger areas which were not glaciated while the Svalbard-Greenlandic region had been largely glaciated.

Centropyxis gasparella has been described from Devon Island (Nunavut-Canada) (Chardez and Beyens 1988) and recorded later in other places. Given its wide distribution in the Arctic, its visibility because of size (length of test 100–110 micrometer) and the conspicuous structure of aperture, *Centropyxis gasparella* can be considered as a true arctic flagship species. This is really important, because, according to Foissner (2006): "At the present state of knowledge, micro-organism endemicity can be proved/disproved mainly by flagship species..." Looking at its present known distribution map, we make here a very tentatively suggestion for its origin: a taxon which originated in Beringia, survived the glacial period there, and spread east and west.

4. Arctic flagship species

Centropyxis pontigulasiformis represents another case. It is described from Edgeøya (Svalbard) (Beyens and Chardez 1986c) and observed later in other arctic sites. It is an extremely rare testate amoeba in non-arctic areas. But is has been found in the Netherlands (Ferry Siemensma pers. comm.) and in Austria (Angie Opitz pers. comm.). Although both countries are much more explored regarding their testate amoebae fauna than the whole Arctic, the reports of this taxon are highly exceptional. This taxon is more common in the Arctic. We suspect that this points to a former much wider distribution during Pre-Holocene times, and we suggest that this taxon can be considered as a glacial relict. Glacial relict biota are known from the Netherlands, with plants as *Linnaea borealis*, *Trientalis europaea*, *Cornus suecica*. The present known distribution of *C. pontigulasiformis* reveals that this taxon occurred in more southern latitudes in former times. These southern latitudes have at present a temperate climate, but during glacial times they experienced an arctic climate. Did this taxon then migrate northwards or did it have some strongholds in refugia at higher latitudes during glacial times? Again we are in doubt as has been the case in plant biogeography decennia ago. The distribution of this arctic-alpine taxon suggests the role of the climate during the last glaciation and the postglacial warming, shaping a discontinuous distribution as known from arctic-alpine plants. This leaves us with questions on the modus of dispersal. Dispersal mechanisms found in plants (wind blown seeds, aquatic transport and the involvment of animals, as in bird faeces) have some analogies to the known dispersal mechanisms of testate amoebae (wind blown cysts, cysts in bird faeces, as living cells in the plumage of aquatic birds). It is common knowledge that most bird migration is South-North-South. That can not explain the distribution pattern, as found in *C. gasparella*. But some bird species are recorded to fly along longitudinal gradients in the Arctic (Alerstam *et al.* 2007), enabling an extensive intercontinental Siberian-American migration system. May-be such migration system and its evolution, can be one of the driving forces for the distribution patterns of some testate amoebae taxa in the Arctic.

CONCLUSIONS

Species diversity in the arctic communities is lower than in sub-arctic and more moderate climatic regions. There are no typical testate amoebae communities for the Arctic: they are dominated by species which have a rather cosmopolitan distribution, and which are ubiquistic in their habitat preferences. Distribution of testate amoebae in the Arctic should be viewed as a result of different processes. The data suggest an influence of current climatic regimes, but we suspect that this works on a basic level. Thus, the presence and absence of the taxa reveal regional differences which suggest that we can recognize (at least) two main arctic testate amoebae regions: the Siberian and the Svalbard-Greenlandic. They seem to correspond to major climatic regions in the Arctic.

The number of recognized endemic taxa for the Arctic is extremely low. There is at least one species which can be attritubed the status of arctic flagship species: *Centropyxis gasparella*. Another taxon, *Centropyxis pontigulasiformis*, can be considered to be an arctic-alpine one. The origin of the present arctic communities remains unclear. The importance of the contribution of southern sources and from possible glacial refugia to shape the present testate amoebae communities remains unanswered. More information on the phylogenetic and genetic-molecular status of some species, selected for their importance on the community level, is needed. But also other ecological information, such as encystment and excystment biology together with dispersal biology, could be crucial to understand the historical evolution of the testate amoebae in the present Arctic.

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