

## Habitat Selection of Aquatic Testate Amoebae Communities on Qeqertarsuaq (Disko Island), West Greenland

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**Summary.** The testate amoebae communities living in different substrate types of 31 aquatic sites on Qeqertarsuaq (West-Greenland) were studied. A total of 74 taxa, belonging to 21 genera was observed. While most taxa belonged to the genera *Diffflugia*, *Euglypha* and *Centropyxis*, most counted tests were identified as *Trinema lineare*. The substrate type showed the largest influence on testate amoebae communities, regardless of the habitat type. *Centropyxis aerophila*, *C. aerophila* var. *sphagnicola*, *Diffflugia pristis* and *D. tenuis* showed a clear preference for sediments (sapropelium and rock scraping), both in standing and running water bodies. The differences in site characteristics induced also differences among the epiphytic communities. *Assulina muscorum*, *A. seminulum*, *Diffflugia glans*, *D. tenuis*, *Difflogiella crenulata* var. *globosa* and *Euglypha strigosa* were typical taxa living on macrophytes in standing water bodies. No typical epiphytic taxa were found in running water bodies. Homothermic systems, which are ice-free year-round, accommodate more developed testate amoebae communities. This reflects in a higher ratio of K-strategic lobose testate amoebae as compared to r-strategic *Filosa* (LF-index).

**Key words:** Arctic, Disko Island, ecology, filosa, Greenland, homothermic system, LF-index, lobosa, multivariate community analysis, Qeqertarsuaq, testate amoebae.

### INTRODUCTION

To understand the effects of Global Change on Arctic ecosystems, knowledge of the current biogeography and ecological preferences of the composing organisms is required. A very sensitive group of organisms is formed by the testate amoebae (Protozoa,

Sarcodina, Rhizopoda). Studies on rhizopods in Greenland started with some data from the east coast (Dixon 1939). Later-on, more substantial work was published dealing with rhizopods from the western (Decloître 1954), the eastern (Stout 1970) and the north-eastern Greenlandic coast (Beyens and Chardez 1986; Beyens *et al.* 1986a, b; Trappeniers *et al.* 1999, 2002; Van Kerckvoorde *et al.* 2000). Data from the transition zone between Low and High Arctic however are scarce and the ecological preferences of many species remain unknown. Unfortunately, this transition zone might be one of the first areas affected by Global Change effects.

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Testate amoebae are present in a variety of habitats, ranging from lakes, pools and rivers to wet soils, moss vegetation and peatlands. Their short generation times make them useful indicators of environmental changes. The most important factor in controlling their distribution, activity and population fluctuations is supposed to be the moisture content of their habitat (Smith 1992, Mitchell and Buttler 1999 and references therein). A broad range of other factors are shown to be correlated with the testacean community structure such as pH (Costan and Planas 1986, Beyens and Chardez 1995, Ellison 1995), eutrophication (Schönborn 1962), temperature regime (Medioli and Scott 1988), light, oxygen and food availability (Charman *et al.* 2000).

The aim of this study is to enhance our knowledge of the distribution and ecology of testate amoebae, in particular in the transition zone between Low and High Arctic. Special attention will be given to the ecological differences between homo- and heterothermic systems, an exceptional feature on Qeqertarsuaq. This paper is the first in a series of three describing the testate amoebae communities in different habitats on Qeqertarsuaq.

## MATERIALS AND METHODS

### Study site

Field sampling was carried out between 11 and 31 July 2002 at Qeqertarsuaq (Disko Island), situated on the western coast of Greenland (69°15'N, 53°34'W, Fig. 1). The island is 8578 km<sup>2</sup> large, has a typical arctic maritime climate and is located on the transition zone between Low Arctic and High Arctic (Alexandrova 1980). Mean annual precipitation never reaches 242 mm water equivalent whereas the mean annual air temperature is -4.3°C. Minimum and maximum monthly mean temperatures of -16.2°C and 7.1°C are registered in February and July respectively (Arctic Station meteorological data 1996-2002). The prevailing wind directions are east during winter (cold katabatic air from the Greenlandic ice sheet) and west during summer (warm maritime air from the ocean). Geological and periglacial phenomena, such as glacial valleys and braided rivers, create a broad range of aquatic habitats (Svendsson 1978). The terrestrial vegetation is mainly dominated by dwarf-shrub heaths, with a prominent role for sedges and mosses on wetter areas. Several homothermic systems (Fig. 2) can be found on Qeqertarsuaq having a constant temperature regardless of the season, due to a passage through geothermal or radioactive layers (Heegaard *et al.* 1994). A large number of plants [e.g. *Angelica archangelica* L., *Alchemilla glomerulans* Buser, *Platanthera hyperborea* (L.) Lindley and *Leucorchis albida* (L.) E. Mey] usually limited much farther south, are capable of surviving near these systems, contributing in that way to the botanical diversity of Qeqertarsuaq (more than 50% of all flowering plants of Greenland are present on the island).

### Sampling

Seventy-six water samples were collected from 31 different water bodies ranging from small pools to lakes and rivers (Appendix 1). Sampling sites were randomly chosen in the vicinity of the Arctic Station on the south coast of Qeqertarsuaq (Fig. 1), maximising the differences in site characteristics (e.g. water body type, vegetation, distance to the sea, height, microclimate). Water temperature, pH, oxygen content (% and mg/l) and specific conductance were measured *in situ* using a WTW Multiline P4. Homothermic influence was determined based on the observed vegetation and translated in three classes: 1 - homothermic, 2 - heterothermic with significant homothermic influence and 3 - heterothermic. Samples were taken from three types of substratum: sapropelium, epilithon (rock scraping) and macrophytes (aquatic plants and mosses) and stored in 50 ml polyethylene bottles. Formaldehyde (3%) was added for fixation. Moss vegetation humidity was based on the classification of Jung (1936) with F-value I for completely submerged mosses and F-value II for surfacing/floating mosses. Moss samples were taken by squeezing out water of a considerable part of the sampled moss vegetation. Fresh moss was added to the sample to include also strongly adhered testate amoebae specimens. Sapropelium and rock samples were obtained by scraping the substrate with a bottle.

### Laboratory methods

Water chemistry analysis for SO<sub>4</sub><sup>2-</sup>, Cl<sup>-</sup>, NH<sub>4</sub><sup>+</sup>, NO<sub>3</sub><sup>-</sup>, NO<sub>2</sub><sup>-</sup>, PO<sub>4</sub><sup>3-</sup>, colour and hardness of the site samples was performed using a Palintest interface spectrophotometer. Details of the analytical methods are fully described by MacQuaker (1976).

Samples were passed over a sieve with a mesh diameter of 300 µm and concentrated by centrifugation (5 min at 1250 rpm). To distinguish dead from living tests rose bengal was added. Since the thanatocoenose was a good estimator for the living population ( $F_{1;1053} = 1139.4$  with  $p < 0.001$ ), all further calculations were based on the total of death and living individuals on the moment of sampling.

In each sample a total of 150 tests (including both coloured and uncoloured specimens) were counted using an Olympus BX50 microscope at 400x magnification. Previous research (Warner 1988, Woodland *et al.* 1998) suggested that this number represents the principal taxa in the sample. Identifications were based mainly on Decloître (1962, 1978, 1979, 1981), Deflandre (1928, 1929, 1936), Grospietsch (1964), Hoogenraad and de Groot (1940), Ogden (1983) and Ogden and Hedley (1980). Sixteen samples (on a total of 76) were withdrawn from further analysis since they contained little (less than 5 individuals in 1 slide) or no testate amoebae. Withdrawn samples were taken from glacial melt water streams or contained fine grained clay sediment, preventing any clear microscopical analysis.

### Data analysis

The Shannon-Wiener (Shannon and Weaver 1949) and Gini-evenness (Nijssen *et al.* 1998) indices were calculated respectively for diversity and evenness.

To estimate the developmental stage of a testate amoebae community, the LF-index (Bonnet 1976) was used. Based on the assumption that filose testate amoebae (Filosa) are r-strategic, while Lobosa follow a more K-based strategy, this index is calculated as the ratio between the number of testate amoebae with lobose and filose pseudopodia [ $LF = (Lobosa - Filosa)/(Lobosa + Filosa)$ ] and varies

theoretically from -1 (only Filosa, undeveloped communities) to +1 (only Lobosa, developed, stabilised communities).

All means are given  $\pm 1$  SD.

A hierarchic-agglomerative Cluster Analysis, based on a minimum variance strategy with the Squared Euclidian Distance as a dissimilarity index, was carried out to group the sites (MVSP, Kovach Computing Services 1993). We used Principal Components Analysis (PCA) to determine the main patterns of variation in the chemical variables of the sites. This PCA was based on a standardized correlation matrix of the ln-transformed physical and chemical data, except for pH that is already a logarithmic variable, due to their skewed distributions.

If a taxon didn't show a relative abundance of minimum 2% in at least one sample, it was removed from further community analysis. Since not all the environmental variables influence the distribution of testate amoebae independently, a Canonical Correspondence Analysis (CCA) was used with forward selection and unrestricted Monte Carlo permutation tests (999 permutations,  $p \leq 0.05$ ). The statistical techniques used in this study are described in full detail in Jongman *et al.* (1987). Ordination analyses were performed using the computer program CANOCO 4.0 (ter Braak 1987).

To test whether the distribution pattern of the testacean fauna was determined by either the sampled substrate, the habitat type or a combination of both parameters, a logistic model was used (data did not follow a normal distribution) (SAS version 8). The dependent variable was the abundance of a testate amoeba taxon in a certain sample (with a specific substrate in a certain habitat). The abundance data can be seen as discrete variables since there was always a fixed number of individuals (150) counted per sample. The independent variables were: testate amoebae species, substratum type and habitat type. Two types of substratum were chosen: macrophytes (including submerged plants and mosses) and sediment (combining both scrapings and sapropelium samples), while all 4 categories for habitat were maintained (pool, lake, brook with weak or strong current). Because of the overall dominance of *Trinema lineare* in all samples showing no preference at all, this species was excluded from the analysis. The analysis was performed on the 15 most frequently occurring testate amoebae taxa (PSEFUL, CENAER, TRIENC, DIFGL3, DIFGL2, EUGTUB, DIFOBL, EUGROT, CENPLAT, DIFPRI, PSEGRA, DIFTEN, CENASY, CENASP, DILOVF; abbreviations see Appendix 2). The estimates of the Least Squares Means were used to calculate the proportion of a certain testate amoebae taxon per substrate type and per habitat type.

## RESULTS

### Species Composition

Seventy-four taxa (including species, varieties and forms) belonging to 21 genera were recorded (Appendix 2, Table 1). This number does not include 12 unidentified taxa, of which only a few individuals were found. On average  $18 \pm 5$  taxa per sample were found, with a maximum of 32 taxa in DW042 (submerged moss) and a minimum of 6 taxa in DW043 (rock scraping). The

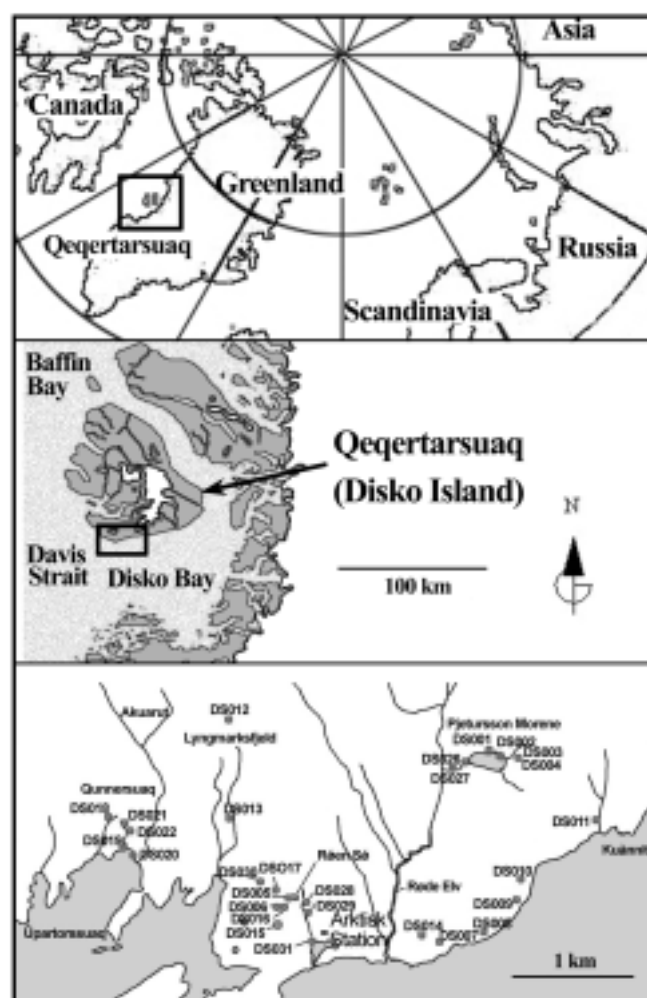


Fig. 1. Sketch maps of Greenland, Qeqertarsuaq (Disko Island) and the sampling area with site numbers.

highest proportion of all counted tests was constituted by *Trinema lineare* (30.7%) present in all samples except DW004. Most taxa belonged to the genera *Diffflugia* (19 taxa), *Euglypha* (11 taxa) and *Centropyxis* (10 taxa). Other important taxa were *Pseudodiffflugia fulva* (6.6%; 74% occurrence), *Centropyxis aerophila* (6.5%; 90% occurrence), *Trinema enchelys* (6.3%; 87% occurrence), *Diffflugia globulus* (6.2%; 75% occurrence) and *D. globulosa* (5.5%; 87% occurrence). Sixty-eight taxa showed mean relative frequencies below 1%.

Based on the currently available literature, only 7 taxa were likely to be recorded for the first time in the Arctic Region (the Arctic being defined as these regions spread-



**Fig. 2.** Examples of heterothermic (top) and homothermic (below) systems, with the typical vegetation of the latter.

ing northwards from the tree limit (Alexandrova 1980), mostly correlated with the 10°C July isotherm).

The mean Shannon-Wiener diversity was  $0.93 \pm 0.16$ . The diversity was significantly higher in sediment samples ( $1.01 \pm 0.16$ ), compared to samples taken from macrophytes ( $0.88 \pm 0.16$ ) ( $t_{2,58} = -2.75$ ;  $p = 0.008$ ). The Gini evenness index did not vary between different groups and reached an overall mean of  $0.43 \pm 0.09$ . The ratio of death to living testate amoebae amounts to 2.35.

### Site characteristics

To summarize the major patterns of variation within the chemistry data, PCA and cluster analysis were used. The results are shown as a cluster dendrogram (Fig. 3) and a PCA-correlation biplot (Fig. 4). The first two PCA-axes accounted for 79.4% of the total cumulative variance ( $\lambda_1 = 0.852$ ,  $\lambda_2 = 0.212$ ). Long arrows represent environmental parameters that explain most of the variation and are therefore more important within the data.



**Fig. 3.** Cluster dendrogram showing all sampled sites. The different clusters based on the physico-chemical LN transformed data, are shown on the right.

Two major groups of variables can be recognized. Total Hardness, oxygen content, pH and water temperature are highly linked to each other while the second group contained all variables related to salinity (specific conductance,  $\text{SO}_4^{2-}$  and chloride).

Cluster analysis divides the sampled sites into two groups, with DS020 set apart as a third separate cluster. Cluster A contained all standing waters, whereas cluster B comprised all running waters. The first cluster was further subdivided into subcluster A1.1 (lakes) and A1.2 (shallow pools); while in cluster B an additional subdivision was made between homothermic (cluster B1) and heterothermic sites (cluster B2). Although total hardness values were very low for all sites, it still seems to be the determining factor separating clusters A1.2 ( $28.0 \pm 8.9$  mg/l) and B ( $2.2 \pm 2.6$  mg/l), with the cluster A1.1 showing intermediate hardness values ( $16.7 \pm 9.0$  mg/l). The separation of DS020 (cluster A2) was based on the elevated salinity variables of this site

**Table 1.** The main observed testate amoebae genera with their relative abundance (%) and the number of present taxa.

|                       | Relative abundance (%) | Number of taxa |
|-----------------------|------------------------|----------------|
| <i>Trinema</i>        | 37.65                  | 3              |
| <i>Diffugia</i>       | 18.92                  | 19             |
| <i>Centropyxis</i>    | 14.44                  | 10             |
| <i>Euglypha</i>       | 11.93                  | 11             |
| <i>Pseudodiffugia</i> | 8.76                   | 3              |
| Other                 | 8.30                   | 40             |
|                       | 100                    | 86             |

**Table 2.** The effect of habitat type, substrate and their interaction on the occurrence of the most important testate amoebae taxa.

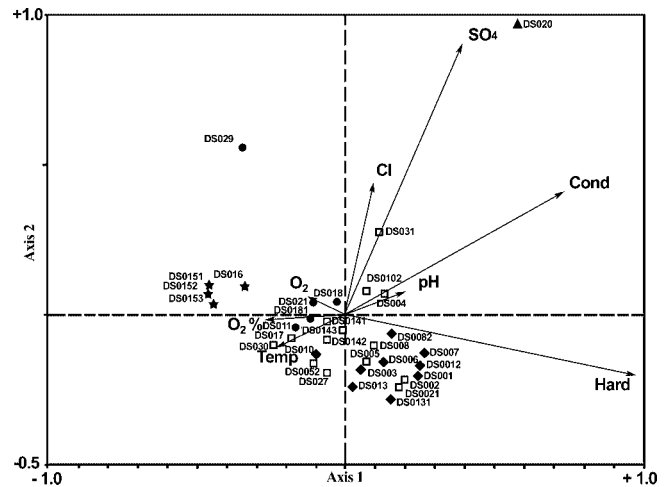
|  | Habitat | Substratum | Habitat × Substratum |
|--|---------|------------|----------------------|
| <i>Centropyxis aerophila</i>                         |         | **         |                      |
| <i>Centropyxis aerophila</i> var. <i>sphagnicola</i> |         | *          |                      |
| <i>Diffugia globulosa</i>                            | **      | *          |                      |
| <i>Diffugia globulus</i>                             | *       | *          | ***                  |
| <i>Diffugia pristis</i>                              |         | *          |                      |
| <i>Diffugia tenuis</i>                               |         | **         |                      |
| <i>Euglypha rotunda</i>                              |         |            | *                    |
| <i>Trinema enchelys</i>                              | *       |            |                      |

\* significant at 0.05 level; \*\* significant at 0.01 level; \*\*\* significant at 0.001 level

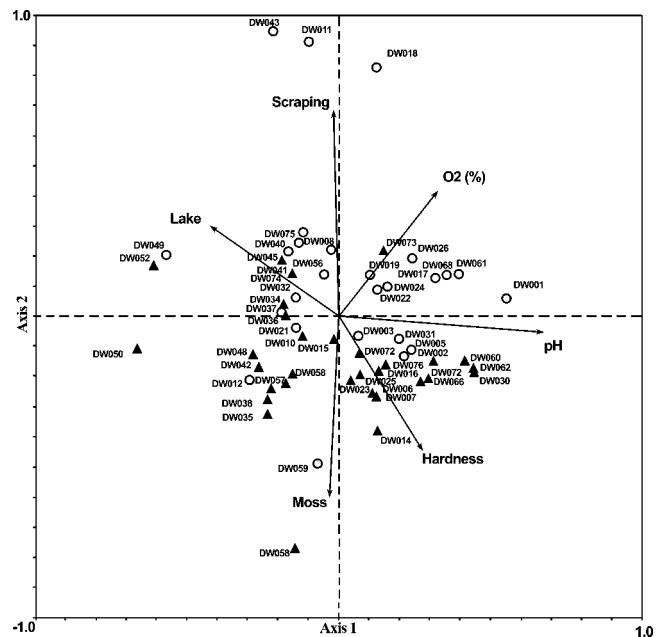
(spec. cond. = 477  $\mu\text{S}/\text{cm}^2$ ), compared to an average  $76.1 \pm 31.02 \mu\text{S}/\text{cm}^2$  for all other sites.

**Community analysis**

The original set of 22 environmental variables was reduced to 6 based on the selection procedures described in the methods section, leaving oxygen content (%), total hardness, pH, habitat type ‘lake’ and substratum type’s ‘scrapings’ and ‘mosses’ as determining variables. When constrained to these 6 environmental variables, the CCA explained only a small proportion of the variance in the species data (Fig. 5). The first two axes account for only 7.3 % of the variance in the testate amoebae data ( $\lambda_1 = 0.139, \lambda_2 = 0.104$ ). This low percentage is typical for noisy datasets containing many zero values (Stevenson *et al.* 1991). In contrast, a rather large proportion of the variance was explained by the



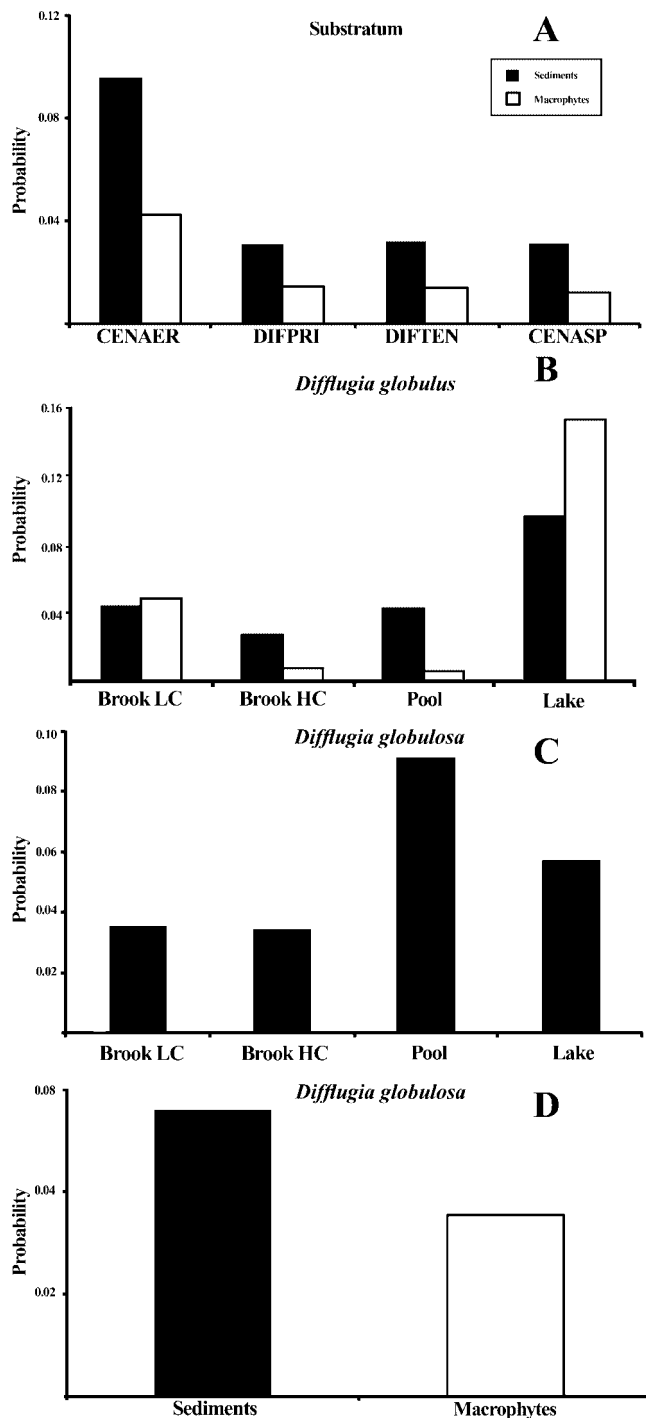
**Fig. 4.** Diagram of the Principal Components Analysis (PCA) showing the different site clusters based on LN transformed dataset (symbols referring to clusters: open square - A 1.1, filled rhomb - A 1.2, filled triangle - A 2, asterisk - B 2).



**Fig. 5.** Canonical Correspondence Analysis (CCA) ordination diagram showing the relation between samples (open circle sediment and filled triangle vegetation samples) and environmental variables. Arrows indicate environmental variables as detected by forward selection.

testate amoebae-environment relationship (75.2 % for the first two axes).

In the CCA diagram axis 1 is strongly related to pH (inter-set correlation 0.55) separating samples with rela-



**Figs 6 A-D.** The significant probabilities of occurrence for (A) *Centropyxis aerophila*, *Diffugia pristis*, *Diffugia tenuis* and *Centropyxis aerophila* v. *sphagnicola* in different substrates and habitat types, (B) *Diffugia globulus* and (C, D) *Diffugia globulosa* in both substrate types and all habitat types. Habitat types Brook HC and Brook LC refer to brooks with high current and low current respectively.

tively high pH on the right side from more acid lakes on the left side. *Diffugia globularis*, *Cyphoderia am-*

*pulla* and *Tracheleuglypha dentata* seem to prefer the more alkaline conditions. *Lesquereusia epistomium* and *Assulina muscorum* on the other hand showed their highest abundances in the acid samples. Axis 2 is related to the sampled substratum (moss and scrape samples; inter-set correlations -0.58 and 0.64). Samples taken from submerged moss vegetations are grouped together and the same applies for the samples from scrapings. *Diffugiella sacculus* and *D. crenulata* seem to be more abundant in scrape samples whereas *Tracheleuglypha acolla*, *Tracheleuglypha dentata* and *Diffugia globularis* tend to prefer bryophyte substrates.

Since habitat type was the determining factor in clustering the samples on the physico-chemical base, while substratum type seemed to classify samples based on the testate amoebae composition, a logarithmic regression was performed to detect effects of habitat, substratum type and their interaction on the distribution of testate amoebae species.

The results showed that for 8 species habitat type, substratum type and the interaction habitat  $\times$  substratum were significant ( $\chi^2$ ) at different levels (Table 2). In general, substratum type seemed to be the most important parameter within all sampled habitats. *Centropyxis aerophila*, *C. aerophila* var. *sphagnicola*, *Diffugia pristis* and *D. tenuis* showed a preference for sediments in all habitat types (Fig. 6A). *Diffugia globulus*, on the other hand, only preferred sediments in small pools and brooks with a strong current. In lakes, *D. globulus* tended to live epiphytic (Fig. 6B). *D. globulosa* seemed to prefer calm aquatic conditions with no or a low streaming velocity (Fig. 6C), and showed a general tendency to prefer sediments (Fig. 6D).

#### Homothermic versus heterothermic systems

The mean LF-index of samples taken in entirely homothermic systems (LF=  $0.279 \pm 0.242$ ) is significantly higher than these of completely heterothermic systems (LF=  $0.066 \pm 0.276$ ) ( $t_{2,41} = 2.577$ ;  $p = 0.014$ ). Samples from the homothermic sites never showed negative LF-values. No differences in species richness between both systems were observed ( $t_{2,41} = -0.893$ ;  $p = 0.377$ ) but the species composition seemed to vary. Taxa with a clear preference for homothermic systems were *Diffugia globulosa*, *D. pyriformis*, *Nebela penardiana* and *Diffugiella minuta*. All cited species belong to the lobose or reticulolobose (*D. minuta*) type. Taxa with a clear preference for the heterothermic

systems comprise among others: *Trinema complanatum*, *Euglypha strigosa*, *Nebela collaris*, *N. dentistoma* and *Corythium dubium*, covering both *Filosa* and *Lobosa*.

## DISCUSSION

### Species composition

The high number of testate amoebae taxa (i.e. 74) found in this study confirms the diversity potential of Qeqertarsuaq. Previous studies on aquatic testate amoebae from Greenland reported only 41 (Beyens *et al.* 1992) and 67 testate amoebae taxa (Trappeniers *et al.* 1999). This high species richness is not surprising since also the phanerogamic diversity of the studied area is remarkably high. Smith (1992) and Ledeganck *et al.* (2002) already demonstrated the close correlation between vegetation and testate amoebae diversity.

*Trinema lineare* dominated all communities, confirming its typical ubiquitous distribution. The species has been reported from all over the arctic region (overview in Beyens and Chardez 1995). Beyens *et al.* (1986b) suggested that, as the number of species diminishes towards the north, *T. lineare*, if present, tends to become the dominant species, a trend also recognised in various alpine studies (Lousier 1976, Todorov 1998). *Diffflugia* comprises the major part of the observed taxa. Taxa of this genus were present in all samples with *D. globulus* and *D. globulosa* as the dominant species. However, the relatively small dimensions of the latter two species protect them against the cold, minimizing the risk of frost fractures (Beyens *et al.* 2000). Therefore, inclusion of a considerable number of empty (=dead) tests might produce this overabundance and this could be an artefact. The process of frost fracture is driven by the expansion of frozen water and diminishes the death/living ratio from 10 in temperate areas to 1 to 3 in arctic conditions (Balik 1994). The highly diverse presence of *Diffflugia* is commonly observed in arctic (Beyens *et al.* 1986b, 1992; Beyens and Chardez 1994; Trappeniers *et al.* 1999) as well as antarctic aquatic habitats (Vincke *et al.* in press).

### Community analysis

#### Habitat specificity

The grouping of the sites into 4 clusters based on total hardness and salinity is explained by the nature of the

sites. Most sampled pools were situated directly on basaltic rocks, where  $\text{Ca}^{2+}$  could easily dissolve into the system. This accumulation of  $\text{Ca}^{2+}$  was slower in larger lakes, while no  $\text{Ca}^{2+}$ -accumulation appeared in running waters. This could explain why the clusters of running waters (B), lakes (A1.1) and shallow pools (A1.2) were ordinated along the hardness gradient. Compared to non-arctic standards, the  $\text{CaCO}_3$  amount and hardness values in all sites were very low, raising the question whether the impact of the amount of  $\text{CaCO}_3$  on the testate amoebae community could be due to  $\text{Ca}^{2+}$ -limitation, rather than hardness levels.

The high salinity values in site DS020 are caused by sea spray since the sampling site was located only a few meters from the shore.

#### Habitat and substratum specificity

Habitat type clearly influences the testate amoebae communities. *D. globulus* is more likely to be found in lakes than in the other habitat types, while *D. globulosa* seems to prefer the more stagnant habitat types (pools and lakes) (Figs 6C, D).

Our results indicate that the composition of the testate amoebae communities is highly influenced by the substratum type. This observation should be carefully taken into account when comparing different studies. Although no species were typical for either the macrophyte samples or the sediment samples, *Centropyxis aerophila*, *C. aerophila* var. *sphagnicola*, *Diffflugia pristis*, *D. tenuis* and *D. globulosa* all preferred the sediment niche within all habitat types (Figs 6A, D). These 4 species are all so-called xenosomic testate amoebae that need exogenous particles for the construction of their test. Idiosomic testate amoebae on the other hand, such as the genus *Trinema*, construct their own building units and are thus not depending on the substrate to provide construction material. This could explain why substratum type did not affect the distribution of these species. *D. globulus*, another xenosomic testate amoeba, preferred both substrates equally, or had a slight preference for sediments. It is unclear why this taxon prefers a more epiphytic substrate in lakes (Fig. 6B). Although no influence on the presence/absence status of the genus *Euglypha* (idiosomic) was found, it was clear that their relative abundance was higher on macrophytes.

#### Thermal properties

Besides habitat type, the testacean communities are also influenced by the thermal properties of their habitat. Homothermic systems are characterized by an annual

positive water temperature, even during the cold arctic winter, keeping them ice-free during periods of lower soil and air temperature (although sometimes free-flowing through a tunnel of snow and ice). During this winter period organisms are still capable of surviving in the homothermic systems, without going into the cyst stadium. Homothermic systems therefore can accommodate more developed, stabilized testate amoebae assemblages, characterized by lobose testate amoebae species.

This is in marked contrast to the heterothermic systems. These systems are completely frozen during wintertime, and the stable communities are usually not preserved, resulting in the formation of pioneer communities with a high proportion of r-strategic filose species. Balik (1994) already reported the correlation between a high LF-index in successively developed habitats, such as peat sediments and wet mosses versus lower LF values in instable habitats such as undeveloped soils. However, the results of our study did not demonstrate higher species richness in the homothermic systems but classified them rather as a totally different habitat, favouring a testate amoebae community characterised by lobose taxa such as *Diffflugia globulosa*, *D. pyriiformis*, *Nebela penardiana* and *Difflogiella minuta*. A possible explanation can be given considering the much lower mean summer temperature. In heterothermic systems, this temperature values over 15°C during sunny days, while it will never exceed 5°C in most homothermic systems.

## Conclusions

Substratum type clearly influences the composition of aquatic testate amoebae communities. In some cases, the distribution of several species is affected by some hydrological characteristics of the habitat type (running vs. standing waters), independently from their choice for a specific substratum type. These two parameters can easily mask the effects of all other physico-chemical variables.

The thermal properties within a specific habitat can have a major influence on the testate amoebae communities that inhabit them. Homothermic systems, year-round ice-free, accommodate more developed communities, dominated by K-strategic lobose testate amoebae. On the other hand, heterothermic systems are dominated by r-strategic filose testate amoebae.

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**Appendix 1.** Physico-chemical site and sample characteristics (S.C.: Specific Conductance)

| Site   | Sample | pH   | T<br>(°C) | S.C.<br>(µS/cm) | O <sub>2</sub><br>(%) | Cl<br>(mg/l) | NO <sub>2</sub><br>(mg/l) | NO <sub>3</sub><br>(mg/l) | PO <sub>4</sub><br>(mg/l) | NH <sub>4</sub><br>(mg/l) | CaCO <sub>3</sub><br>(mg/l) | Habitat  | Substratum  | Thermal<br>class |
|--------|--------|------|-----------|-----------------|-----------------------|--------------|---------------------------|---------------------------|---------------------------|---------------------------|-----------------------------|----------|-------------|------------------|
| DS001  | DW001  | 7.14 | 2.8       | 97              | 95.1                  | 39           | 0.003                     | 0.09                      | 0.37                      | 0.01                      | 40                          | running  | sediment    | 1                |
| DS0012 | DW002  | 6.78 | 3.4       | 97              | 69.5                  | 39           | 0.003                     | 0.09                      | 0.37                      | 0.01                      | 40                          | standing | sediment    | 1                |
| DS002  | DW003  | 7.16 | 11.6      | 90              | 68.6                  | 45           | 0                         | 0                         | 0.2                       | 0.03                      | 35                          | standing | sediment    | 2                |
| DS0021 | DW004  | 8.08 | 14.4      | 68              | 105.6                 | 45           | 0                         | 0                         | 0.2                       | 0.03                      | 35                          | running  | sediment    | 2                |
| DS003  | DW005  | 7.18 | 11.2      | 82              | 63.5                  | 43           | 0                         | 0.013                     | 0.07                      | 0.05                      | 30                          | standing | sediment    | 2                |
| DS004  | DW006  | 7.24 | 9.4       | 77              | 83.8                  | 72           | 0                         | 0.017                     | 0.06                      | 0.03                      | 20                          | running  | macrophytes | 2                |
| DS004  | DW007  | 7.24 | 9.4       | 77              | 83.8                  | 72           | 0                         | 0.017                     | 0.06                      | 0.03                      | 20                          | running  | macrophytes | 2                |
| DS005  | DW008  | 7.98 | 13.8      | 62              | 98.1                  | 56           | 0.001                     | 0.05                      | 0.04                      | 0                         | 15                          | standing | sediment    | 3                |
| DS0052 | DW010  | 7.97 | 14.3      | 63              | 102                   | 56           | 0.001                     | 0.05                      | 0.04                      | 0                         | 15                          | standing | macrophytes | 3                |
| DS005  | DW011  | 7.98 | 13.8      | 62              | 98.1                  | 56           | 0.001                     | 0.05                      | 0.04                      | 0                         | 15                          | standing | sediment    | 3                |
| DS006  | DW012  | 6.71 | 6.3       | 71              | 42.8                  | 80           | 0.004                     | 0.02                      | 0                         | 0                         | 20                          | standing | sediment    | 3                |
| DS003  | DW014  | 7.18 | 14.6      | 82              | 64.9                  | 43           | 0                         | 0.013                     | 0.07                      | 0.05                      | 30                          | running  | macrophytes | 2                |
| DS007  | DW015  | 7.54 | 9         | 197             | 79.9                  | 78           | 0                         | 0.14                      | 0.1                       | 0.25                      | 35                          | standing | sediment    | 3                |
| DS008  | DW016  | 7.57 | 8.9       | 90              | 92.4                  | 64           | 0                         | 0.05                      | 0.33                      | 0.04                      | 20                          | running  | macrophytes | 2                |
| DS008  | DW017  | 7.57 | 8.9       | 90              | 92.4                  | 64           | 0                         | 0.05                      | 0.33                      | 0.04                      | 20                          | running  | sediment    | 2                |
| DS008  | DW018  | 7.57 | 8.9       | 90              | 93.7                  | 64           | 0                         | 0.05                      | 0.33                      | 0.04                      | 20                          | running  | sediment    | 2                |
| DS0082 | DW019  | 7.36 | 3.3       | 136             | 98.9                  | 64           | 0                         | 0.05                      | 0.33                      | 0.04                      | 20                          | standing | sediment    | 2                |
| DS009  | DW021  | 6.79 | 8.4       | 85              | 68                    | 62           | 0.001                     | 0.17                      | 0.29                      | 0.05                      | 20                          | standing | sediment    | 2                |
| DS010  | DW022  | 7.22 | 5.5       | 76              | 84.5                  | 52           | 0                         | 0.01                      | 0.25                      | 0.05                      | 15                          | standing | sediment    | 1                |
| DS010  | DW023  | 7.22 | 5.5       | 76              | 84.5                  | 52           | 0                         | 0.01                      | 0.25                      | 0.05                      | 15                          | standing | macrophytes | 1                |
| DS0102 | DW024  | 7.37 | 8.2       | 73              | 85.3                  | 54           | 0                         | 0.11                      | 0.26                      | 0.05                      | 15                          | running  | sediment    | 1                |
| DS0102 | DW025  | 7.37 | 8.2       | 73              | 85.3                  | 54           | 0                         | 0.11                      | 0.26                      | 0.05                      | 15                          | running  | macrophytes | 1                |
| DS011  | DW026  | 8.61 | 5         | 72              | 94.2                  | 40           | 0                         | 0.04                      | 0.11                      | 0.08                      | 5                           | running  | sediment    | 1                |
| DS013  | DW030  | 7.19 | 1.4       | 60              | 96.5                  | 22           | 0.01                      | 0.06                      | 0.2                       | 0.2                       | 30                          | standing | macrophytes | 3                |
| DS0131 | DW031  | 6.95 | 7.8       | 57              | 65.1                  | 22           | 0.01                      | 0.06                      | 0.2                       | 0.2                       | 30                          | standing | sediment    | 3                |
| DS0141 | DW032  | 7.29 | 13.2      | 112             | 76.2                  | 66           | 0.01                      | 0.02                      | 0.25                      | 0                         | 10                          | running  | sediment    | 3                |
| DS0142 | DW034  | 7.44 | 13.8      | 100             | 69.1                  | 66           | 0.01                      | 0.02                      | 0.25                      | 0                         | 10                          | running  | macrophytes | 3                |
| DS0142 | DW035  | 7.44 | 13.8      | 100             | 69.1                  | 66           | 0.01                      | 0.02                      | 0.25                      | 0                         | 10                          | running  | macrophytes | 3                |
| DS0143 | DW036  | 7.19 | 11.8      | 101             | 67.8                  | 66           | 0.01                      | 0.02                      | 0.25                      | 0                         | 10                          | running  | macrophytes | 3                |
| DS0143 | DW037  | 7.19 | 11.8      | 101             | 67.8                  | 66           | 0.01                      | 0.02                      | 0.25                      | 0                         | 10                          | running  | sediment    | 3                |
| DS0141 | DW038  | 7.29 | 13.2      | 112             | 76.2                  | 66           | 0.01                      | 0.02                      | 0.25                      | 0                         | 10                          | running  | macrophytes | 3                |
| DS0151 | DW040  | 6.53 | 16.2      | 41              | 88.8                  | 45           | 0.001                     | 0.08                      | 0.03                      | 0.03                      | 0                           | running  | sediment    | 3                |
| DS0152 | DW041  | 6.7  | 12.4      | 40              | 95.2                  | 45           | 0.001                     | 0.08                      | 0.03                      | 0.03                      | 0                           | running  | macrophytes | 3                |
| DS0153 | DW042  | 6.28 | 13.7      | 41              | 82.7                  | 45           | 0.001                     | 0.08                      | 0.03                      | 0.03                      | 0                           | running  | macrophytes | 3                |
| DS0153 | DW043  | 6.28 | 13.7      | 41              | 96.5                  | 45           | 0.001                     | 0.08                      | 0.03                      | 0.03                      | 0                           | running  | sediment    | 3                |
| DS016  | DW045  | 6.67 | 13.6      | 44              | 87                    | 45           | 0.001                     | 0.06                      | 0.03                      | 0.1                       | 0                           | running  | macrophytes | 3                |
| DS016  | DW047  | 6.67 | 13.6      | 44              | 87                    | 45           | 0.001                     | 0.06                      | 0.03                      | 0.1                       | 0                           | running  | macrophytes | 3                |
| DS016  | DW048  | 6.67 | 13.6      | 44              | 87                    | 45           | 0.001                     | 0.06                      | 0.03                      | 0.1                       | 0                           | running  | macrophytes | 3                |
| DS017  | DW049  | 5.98 | 15.1      | 41              | 85.2                  | 80           | 0                         | 0.02                      | 0.03                      | 0.09                      | 5                           | standing | macrophytes | 3                |
| DS017  | DW050  | 5.98 | 15.1      | 41              | 85.2                  | 80           | 0                         | 0.02                      | 0.03                      | 0.09                      | 5                           | standing | macrophytes | 3                |
| DS017  | DW052  | 5.98 | 15.1      | 41              | 85.2                  | 80           | 0                         | 0.02                      | 0.03                      | 0.09                      | 5                           | standing | macrophytes | 3                |
| DS018  | DW053  | 7    | 4.5       | 77              | 84.1                  | 80           | 0                         | 0.02                      | 0.03                      | 0.09                      | 5                           | running  | macrophytes | 1                |
| DS018  | DW055  | 7    | 4.5       | 77              | 84.1                  | 80           | 0                         | 0.02                      | 0.03                      | 0.09                      | 5                           | running  | macrophytes | 1                |
| DS018  | DW056  | 7    | 4.5       | 77              | 84.1                  | 80           | 0                         | 0.02                      | 0.03                      | 0.09                      | 5                           | running  | sediment    | 1                |
| DS0181 | DW057  | 7.12 | 3.2       | 80              | 81.8                  | 80           | 0                         | 0.02                      | 0.03                      | 0.09                      | 5                           | running  | macrophytes | 1                |
| DS020  | DW058  | 7.19 | 8.8       | 477             | 68.6                  | 105          | 0                         | 0                         | 0.04                      | 0.05                      | 95                          | running  | macrophytes | 1                |
| DS020  | DW059  | 7.19 | 8.8       | 477             | 68.6                  | 105          | 0                         | 0                         | 0.04                      | 0.05                      | 95                          | running  | sediment    | 1                |
| DS021  | DW060  | 9.78 | 3.5       | 63              | 86.4                  | 54           | 0.001                     | 0.04                      | 0.07                      | 0.06                      | 5                           | running  | macrophytes | 1                |
| DS021  | DW061  | 9.78 | 3.5       | 63              | 86.4                  | 54           | 0.001                     | 0.04                      | 0.07                      | 0.06                      | 5                           | running  | sediment    | 1                |
| DS021  | DW062  | 9.78 | 3.5       | 63              | 86.4                  | 54           | 0.001                     | 0.04                      | 0.07                      | 0.06                      | 5                           | running  | macrophytes | 1                |
| DS026  | DW066  | 7.78 | 11.3      | 63              | 93.3                  | 46           | 0.001                     | 0.04                      | 0.06                      | 0.05                      | 20                          | running  | macrophytes | 2                |
| DS026  | DW067  | 7.78 | 11.3      | 63              | 93.3                  | 46           | 0.001                     | 0.04                      | 0.06                      | 0.05                      | 20                          | running  | macrophytes | 2                |
| DS026  | DW068  | 7.78 | 11.3      | 63              | 93.3                  | 46           | 0.001                     | 0.04                      | 0.06                      | 0.05                      | 20                          | running  | sediment    | 2                |
| DS026  | DW069  | 7.78 | 11.3      | 63              | 93.3                  | 46           | 0.001                     | 0.04                      | 0.06                      | 0.05                      | 20                          | running  | macrophytes | 2                |
| DS027  | DW070  | 7.36 | 10.9      | 64              | 93.5                  | 46           | 0.001                     | 0.04                      | 0.06                      | 0.05                      | 20                          | running  | macrophytes | 2                |
| DS029  | DW072  | 8.18 | 2.6       | 70              | 94.9                  | 56           | 0                         | 0.01                      | 0.08                      | 0.03                      | 0                           | running  | macrophytes | 1                |
| DS029  | DW073  | 8.18 | 2.6       | 70              | 94.9                  | 56           | 0                         | 0.01                      | 0.08                      | 0.03                      | 0                           | running  | macrophytes | 1                |
| DS030  | DW074  | 7.96 | 19.3      | 33              | 94.6                  | 65           | 0                         | 0                         | 0.03                      | 0.05                      | 5                           | standing | macrophytes | 3                |
| DS030  | DW075  | 7.96 | 19.3      | 33              | 94.6                  | 65           | 0                         | 0                         | 0.03                      | 0.05                      | 5                           | standing | sediment    | 3                |
| DS031  | DW076  | 7.89 | 3.7       | 64              | 95.4                  | 55           | 0.001                     | 0.01                      | 0.1                       | 0.14                      | 15                          | running  | macrophytes | 2                |

**Appendix 2.** Taxonomical list of all observed taxa with their corresponding letter codes. New taxa for the Arctic (according to Alexandrova 1980) are marked (\*)

|                 |   |                |  |
|-----------------|---|----------------|--|
| <b>ARCDIS</b>   | <i>Arcella discoides</i> Ehrenberg  | <b>DILOVI</b>  | <i>Diffugiella oviformis</i> (Penard) Bonnet et Thomas                     |
| <b>ASSMUS</b>   | <i>Assulina muscorum</i> Greeff   | <b>DILOVF</b>  | * <i>Diffugiella oviformis</i> var. <i>fusca</i> (Penard) Bonnet et Thomas |
| <b>ASSSEM</b>   | <i>Assulina seminulum</i> Penard  | <b>DILSAC</b>  | * <i>Diffugiella sacculus</i> Penard                                       |
| <b>CAMSP</b>    | <i>Campascus</i> sp1  | <b>EUGACA</b>  | <i>Euglypha acanthophora</i> Perty   |
| <b>CENAER</b>   | <i>Centropyxis aerophila</i> Deflandre                                    | <b>EUGCIL</b>  | <i>Euglypha ciliata</i> Ehrenberg  |
| <b>CENASP</b>   | <i>Centropyxis aerophila</i> var. <i>sphagnicola</i> Deflandre            | <b>EUGCOM</b>  | <i>Euglypha compressa</i> Carter   |
| <b>CENASY</b>   | <i>Centropyxis aerophila</i> var. <i>sylvatica</i> Deflandre              | <b>EUGCRI</b>  | <i>Euglypha cristata</i> Leidy   |
| <b>CENCAS</b>   | <i>Centropyxis cassis</i> Wallich   | <b>EUGFIL</b>  | <i>Euglypha filifera</i> Penard  |
| <b>CENCON</b>   | <i>Centropyxis constricta</i> Deflandre                                   | <b>EUGLAE</b>  | <i>Euglypha laevis</i> (Ehrenberg) Perty                                   |
| <b>CENORB</b>   | <i>Centropyxis orbicularis</i> Deflandre                                  | <b>EUGROT</b>  | <i>Euglypha rotunda</i> Wailes   |
| <b>CENPLAT</b>  | <i>Centropyxis platystoma</i> Penard                                      | <b>EUGSTR</b>  | <i>Euglypha strigosa</i> (Ehrenberg) Leidy                                 |
| <b>CENPLARM</b> | <i>Centropyxis platystoma</i> var. <i>armata</i> Deflandre                | <b>EUGSTG</b>  | <i>Euglypha strigosa</i> f. <i>glabra</i> Wailes                           |
| <b>CENSP1</b>   | <i>Centropyxis</i> sp1  | <b>EUGTUB</b>  | <i>Euglypha tuberculata</i> Dujardin                                       |
| <b>CENSP2</b>   | <i>Centropyxis</i> sp2  | <b>EUGTUM</b>  | <i>Euglypha tuberculata</i> var. <i>minor</i> Taranek                      |
| <b>CORDUB</b>   | <i>Corythion dubium</i> Taranek   | <b>HELSP1</b>  | <i>Heleopera</i> sp1   |
| <b>CRYCOM</b>   | <i>Cryptodiffugia compressa</i> Penard                                    | <b>HELSYL</b>  | <i>Heleopera sylvatica</i> Penard  |
| <b>CYCEUR</b>   | <i>Cyclopyxis eurystoma</i> Deflandre                                     | <b>HYAMIN</b>  | <i>Hyalosphenia minuta</i> Cash  |
| <b>CYCGIG</b>   | <i>Cyclopyxis gigantea</i> Bartos   | <b>HYAPAP</b>  | <i>Hyalosphenia papilio</i> Leidy  |
| <b>CYCSP1</b>   | <i>Cyclopyxis</i> sp1   | <b>HYASUB</b>  | <i>Hyalosphenia subflava</i> Cash  |
| <b>CYPAMP</b>   | <i>Cyphoderia ampulla</i> (Ehrenberg) Leidy                               | <b>LESEPI</b>  | <i>Lesquereusia epistomium</i> Penard                                      |
| <b>CYPPER</b>   | <i>Cyphoderia perlucidus</i> Beyens, Chardez et De Bock                   | <b>LESSPI</b>  | <i>Lesquereusia spiralis</i> Bütschli                                      |
| <b>DIFAMPH</b>  | * <i>Diffugia amphoralis</i> (Leidy) Hopkinson                            | <b>NEBPEN</b>  | <i>Nebela penardiana</i> Deflandre   |
| <b>DIFAMPU</b>  | * <i>Diffugia ampullula</i> Playfair                                      | <b>NEBCOL</b>  | <i>Nebela collaris</i> (Ehrenberg) Leidy                                   |
| <b>DIFBAC</b>   | <i>Diffugia bacillifera</i> Penard  | <b>NEBDEN</b>  | <i>Nebela dentistoma</i> Penard  |
| <b>DIFELE</b>   | <i>Diffugia elegans</i> Penard  | <b>NEBLAG</b>  | <i>Nebela lageniformis</i> Penard  |
| <b>DIFGL1</b>   | <i>Diffugia globularis</i> Wallich  | <b>NEBMIL</b>  | <i>Nebela militaris</i> Penard   |
| <b>DIFGL2</b>   | <i>Diffugia globulosa</i> Dujardin  | <b>NEBTUB</b>  | <i>Nebela tubulata</i> Brown   |
| <b>DIFGL3</b>   | <i>Diffugia globulus</i> (Ehrenberg) Hopkinson                            | <b>NEBWAL</b>  | <i>Nebela wailesi</i> Deflandre  |
| <b>DIFGLA</b>   | <i>Diffugia glans</i> Penard  | <b>PARIRR</b>  | <i>Paraquadrula irregularis</i> (Archer) Deflandre                         |
| <b>DIFMIC</b>   | <i>Diffugia mica</i> Frenzel  | <b>PARMUL</b>  | <i>Parmulina</i> sp1   |
| <b>DIFOBL</b>   | <i>Diffugia oblonga</i> Ehrenberg   | <b>PHRNID</b>  | <i>Phryganella nidulus</i> Penard  |
| <b>DIFPEN</b>   | <i>Diffugia penardi</i> Hopkinson   | <b>PHRPAR</b>  | <i>Phryganella paradoxa</i> Penard   |
| <b>DIFPRI</b>   | <i>Diffugia pristis</i> Penard  | <b>PLACAL</b>  | <i>Plagiopyxis callida</i> Penard  |
| <b>DIFPUL</b>   | <i>Diffugia pulex</i> Penard  | <b>PSEFUL</b>  | <i>Pseudodiffugia fulva</i> (Archer) Penard                                |
| <b>DIFPYR</b>   | <i>Diffugia pyriformis</i> Perty  | <b>PSEGRA</b>  | <i>Pseudodiffugia gracilis</i> Schlumberger                                |
| <b>DIFTEN</b>   | * <i>Diffugia tenuis</i> (Penard) Chardez                                 | <b>PSESP1</b>  | <i>Pseudodiffugia</i> sp1  |
| <b>DIFSP1</b>   | <i>Diffugia</i> sp1   | <b>TRACPU</b>  | <i>Trachelocorythion pulchellum</i> (Penard) Bonnet                        |
| <b>DIFSP2</b>   | <i>Diffugia</i> sp2   | <b>TRACSP1</b> | <i>Trachelocorythion</i> sp1   |
| <b>DIFSP3</b>   | <i>Diffugia</i> sp3   | <b>TRAEAC</b>  | <i>Tracheleuglypha acolla</i> Bonnet et Thomas                             |
| <b>DIFSP4</b>   | <i>Diffugia</i> sp4   | <b>TRAEDE</b>  | <i>Tracheleuglypha dentata</i> Deflandre                                   |
| <b>DILCRE</b>   | <i>Diffugiella crenulata</i> (Playfair) Grospietsch                       | <b>TRICOM</b>  | <i>Trinema complanatum</i> Penard  |
| <b>DILCRG</b>   | * <i>Diffugiella crenulata</i> var. <i>globosa</i> (Playfair) Grospietsch | <b>TRIENC</b>  | <i>Trinema enchelys</i> (Ehrenberg) Leidy                                  |
| <b>DILMIN</b>   | * <i>Diffugiella minuta</i> Playfair                                      | <b>TRILIN</b>  | <i>Trinema lineare</i> Penard  |