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# The Ecology of Testate Amoebae (Protists) in *Sphagnum* in North-western Poland in Relation to Peatland Ecology

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## Abstract

We studied the relationship between testate amoebae (Protozoa) communities and the depth to the water table (DWT), pH, conductivity, and microhabitat type in *Sphagnum* dominated peatlands of north-western Poland and built predictive (transfer function) models for inferring DWT and pH based on the testate amoebae community structure. Such models can be used for peatland monitoring and paleoecology. A total of 52 testate amoebae taxa were recorded. In a redundancy analysis, DWT and pH explained 20.1% of the variation in the species data and allowed us to identify three groups of taxa: species that are associated with (1) high DWT and low pH, (2) low DWT and low pH, and (3) high pH and mid-range DWT. Our transfer function models allow DWT and pH to be estimated with mean errors of 9.89 cm and 0.71 pH units. The prediction error of the DWT model and the tolerance of the species both increase with increasing dryness. This pattern mirrors the ecology of *Sphagnum* mosses: Species growing in wet habitats are more sensitive to change in water table depth than the species growing in drier microhabitats. Our results are consistent with studies of testate amoeba ecology in other regions, and they provide additional support for the use of these organisms in paleoecological and biomonitoring contexts.

## Introduction

Testate amoebae are unicellular organisms living in a variety of habitats including lakes and mires [3, 32, 65]. *Sphagnum* peatlands are characterized by a high diversity of microhabitats in which many testate amoebae species occur. Testate amoebae produce shells (tests) that can be proteinaceous, pseudochitinous, or agglutinated with one or two pseudostome(s) and are diagnostic for identification [70, 77]. Testate amoebae are an important component in the soil microbial food web. Together with other protozoans, testate amoebae are believed to regulate bacterial populations [31] and to play a role in nutrient mineralization and plant growth [29]. Some species are mixotrophic and contain endosymbiotic algae [63].

Many species have well-defined ecological preferences, and this stenotopy makes them very useful bioindicators [30, 47]. Previous studies have shown that the abundance of each taxon and hence the structure of communities are controlled by a set of environmental variables. Water availability (moisture or water table depth) was often identified as being the single most important factor controlling testate amoebae community composition on peatlands, the second most important variable usually being pH [4–6, 10–12, 15, 21, 45, 46, 48, 49, 71, 76]. The correlation between testate amoebae communities and moisture conditions is increasingly used to infer palaeohydrological changes in peatlands and, in the case of ombrotrophic peatlands, these data are ultimately used to infer past climate changes [13, 16–19, 35, 44, 79]. In addition to paleoecology, testate amoebae research can be applied to environmental monitoring of natural ecosystems and those affected by human activities. Examples include the monitoring of lake water pollution [57, 58] and peatland regeneration after peat extraction [14, 34].

Although the body of literature on peatland testate amoebae is growing and similar findings have been ob-
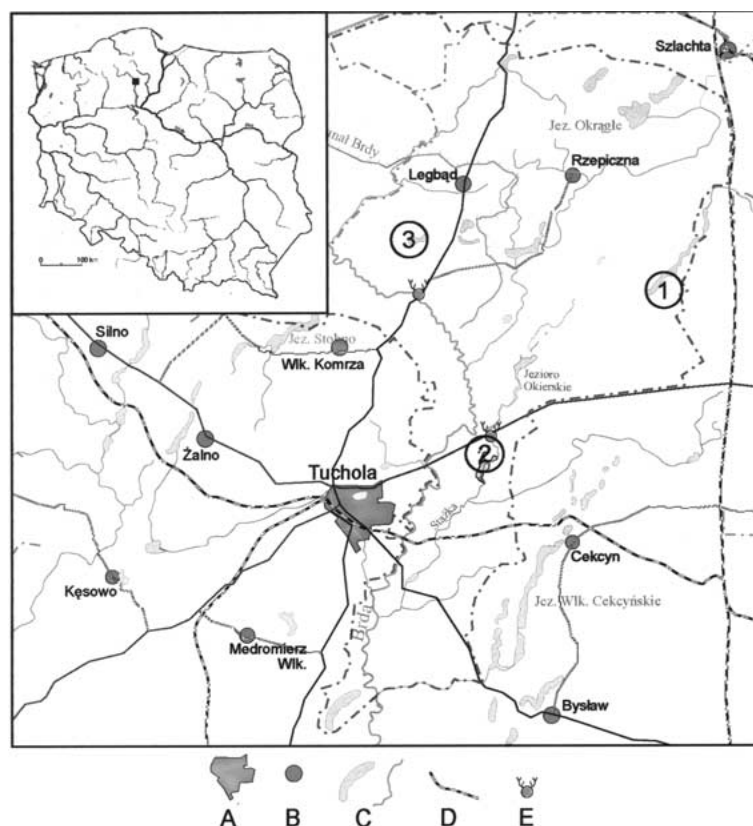
**Figure 1.** Study area and location of the sampling sites. Description of the map, sampling mires: 1—Okoniny (OK), 2—Jeziorka Kozie (KOZ), 3—Jelenia Wyspa (JEL); A—town, B—village, C—surface waters, D—rail, E—forestry managing head office.

tained in most locations, a good understanding of the local ecology of testate amoebae is a prerequisite for their use in paleoecology in any given area.

To date such studies are lacking in peatlands of Poland. Polish peatlands may be different from those of other better-studied regions. In addition, Poland is under the influence of both oceanic and continental climates. This is reflected in the considerable diversity and variation of weather types [81]. Because of this climatic situation, Polish peatlands may be exceptionally sensitive to climatic change. In Poland several earlier studies focused on the ecology and bioindication of lake-dwelling testate amoeba of the Mazury Lakeland area [51, 52, 63, 64]. However, there has been little work on peatland-inhabiting testate amoebae [54, 55].

The peatlands we studied represent the continental type of *Sphagnum*-dominated ecosystems that developed in kettle-hole basins in the range of the last Vistulian glaciation. They are situated in North-western Poland in the Tuchola Forest and include a broad range of mesotrophic to oligotrophic habitats. These peatlands are considered to be peat-accumulating systems, and some of them are still in the early stages of development (i.e., lakes with floating mat entering the water surface—e.g., Jeziorka Kozie). Such mires are common components of the recently glaciated morainic areas or outwash plain in Europe [66, 69].

In this study, we analyzed the structure of communities in relation to three environmental variables (water level depth, pH, and conductivity) in three peatlands of north-western Poland. We hypothesized that these variables could explain the structure of testate amoebae communities in *Sphagnum*-dominated peatlands in the region. The aims of the work were (1) to determine the most important ecological variable controlling the structure of testate amoebae communities in *Sphagnum*-dominated peatlands of north-western Poland and quantify the responses, (2) to develop transfer functions and assess the reliability of testate amoebae for paleoecological reconstruction, (3) to compare our results with existing data on the ecology of testate amoebae from other places, and (4) to put the ecology of testate amoebae in the more general context of peatland ecology.

### Methods

*Study Sites.* Three peatlands were selected in the European Lowland in north-western Poland in the Tuchola Pinewoods region (Fig. 1) [38]. These sites are located within the extent of the last Vistulian glaciation, and as a consequence, the region contains many *Sphagnum*-dominated peatlands and closed basin lakes. The studied peatlands developed on the sandy outwash plain of the Brda River.
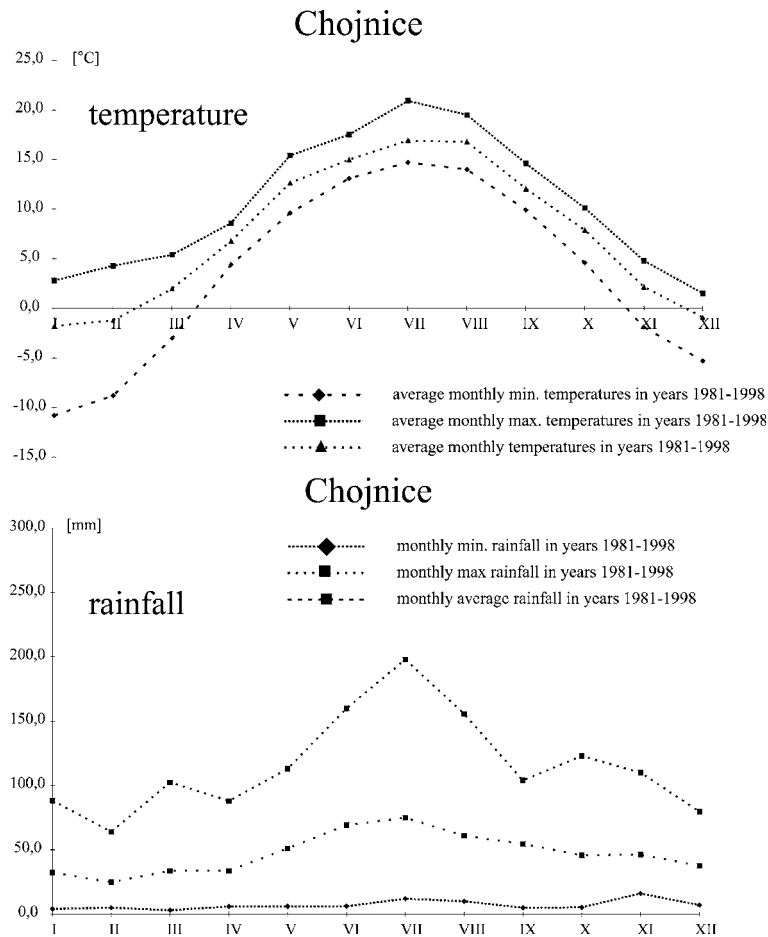
## Chojnice



temperature

- - ◆ - -   average monthly min. temperatures in years 1981-1998
······■······   average monthly max. temperatures in years 1981-1998
···· ▲ ····   average monthly temperatures in years 1981-1998

## Chojnice

rainfall

········◆········   monthly min. rainfall in years 1981-1998
··· ■ ····   monthly max rainfall in years 1981-1998
- - ■ - -   monthly average rainfall in years 1981-1998

**Figure 2.** Rainfall and temperature data of the study area. Chojnice meteorological station is situated 20 km NW of Tuchola.

The average annual total rainfall in the Tuchola Forest area is 600 mm [82]. July is on average (period from 1981 to 1998) the wettest month (approximately 200 mm) and August and September the driest months. The average months temperatures and rainfall are shown in Figure 2 [39]. The average temperatures of January and July are −2°C and +17°C, respectively [23].

The mires selected for this study were considered to be representative of the mires of the region and contained a broad diversity of habitats. The first two peatland sites are kettle-holes at different stages of succession: Okoniny (sample code OK; one mire) and Jeziorka Kozie (sample code KOZ; Kozie Lakes nature reserve, with a peatland complex of four mires). In Okoniny, a floating mat has colonized the entire surface of the kettle–hole, leaving no open water, whereas in Jeziorka Kozie a floating mat is growing from the periphery toward the center, where open water still exists. All of these sites are oligotrophic and are dominated by peat mosses (*Sphagnum* spp.) and vascular plants characteristic of nutrient-poor peatlands (Table 1). Jelenia Wyspa, the third peatland site (sample code JEL), is different from the other sites in that the mires developed in postglacial channels rather than in a kettle-hole. Paleoecological records showed that lakes

occupied these channels during much of the Holocene [40]. At this site, the vegetation is characteristic of mesotrophic to eutrophic conditions in the river valley bottom and of oligotrophic conditions higher up on the sides of the valley. Jelenia Wyspa peatlands are elements of the "Bagna nad Stążką" reserve (Fig. 1).

*Field Sampling and Measurements.* The fieldwork was carried out in July 2003. Sampling methods were based on previous studies [15, 22, 48, 49, 80]. In Jelenia Wyspa mire a transect approach was chosen to span the hydrological and nutrient gradient from fen to *Sphagnum* peatland. In the other sites the sampling plots were selected with the aim of including the highest diversity of habitats. Special attention was paid to the dominant peat mosses (*Sphagnum* spp.) in vegetation occurring in ombrotrophic mires. The rationale for this choice is that ombrotrophic mires dominated by *Sphagnum* mosses are very sensitive to climatic change and hence are likely to provide good palaeoclimatic data [1, 2, 8, 9, 44]. The micro-sites sampled in this study include hummocks, lawns, hollows, laggs, and the edge of floating mats.

A total of 45 samples were taken. A long knife was used to cut around (out) plants from the vegetation. Each

**Table 1.** Location (Coordinates WGS84) and description of the sampling sites and sampling locations

| Sample name | DWT cm | pH | Conductivity | Moss species sampled (other moss species)[a] | Habitat and dominant vascular plant species |
|---|---|---|---|---|---|
| **Okoniny:** (53° 40′ 29.5″ N; 18° 04′ 36.8″ E): Kettle-hole bog with floating mat and wide forested border dominated by *Betula pubescens*, *Pinus sylvestris*, and *Picea abies*. Floating mat include mat include mainly *Sphagnum recurvum*, *Carex rostrata*, and *Eriophorum angustifolium*. | | | | | |
| OK1 | 20 | 3,3 | 0,165 | *S. capillifolium* | Forested peatland, hummock. *Betula pubescens*, *Pinus sylvestris*, and *Ledum palustre* |
| OK2 | 12,5 | 3,5 | 0,047 | *S. magellanicum* | Edge of *Sphagnum* carpet |
| OK3 | 6 | 3,5 | 0,043 | *S. recurvum* | *Sphagnum* carpet. *Rhynchospora alba*, *Carex rostrata*, *Drosera rotundifolia* |
| **Jelenia Wyspa—bog part** (53° 3′27.5″ N; 17° 57′21.7″ E): *Sphagnum* mire with *Sphagnum recurvum* (carpet, hollows, and lagg), *Sphagnum magellanicum* (hummocks and carpet), *S. fuscum* (hummocks), and *S. capillifolium*. Half of the area is covered by *Ledum palustre* and dwarf *Pinus sylvestris* trees. | | | | | |
| JEL1 | 6 | 4,3 | 0,046 | *S. recurvum* | Lagg with *Menyanthes trifoliata* |
| JEL2 | 25 | 4,0 | 0,049 | *S. recurvum* | *Sphagnum* carpet with scatter dwarf *Pinus silvestris* and high cover of *Eriophorum vaginatum* |
| JEL3 | 17 | 4,0 | 0,064 | *S. recurvum* | *Sphagnum* carpet with *Eriophorum vaginatum* and *Oxycoccus palustris* |
| JEL4 | 29 | 3,9 | 0,054 | *S. recurvum* | Hummock covered by *Ledum palustre* |
| JEL5 | 14 | 3,7 | 0,064 | *S. recurvum* | *Sphagnum* carpet with *Eriophorum vaginatum* |
| JEL6 | 33 | 3,9 | 0,068 | *S. magellanicum*, (*P. strictum*) | Hummock with *Ledum palustre* |
| JEL7 | 38 | 3,7 | 0,076 | *Pleurozium schreberi* | Hummock consolidated by *Ledum palustre* |
| JEL8 | 50 | 3,3 | 0,085 | *S. magellanicum* | Hummock, *Andromeda polifolia* and *Empetrum nigrum* |
| JEL9 | 24 | 3,4 | 0,088 | *S. magellanicum* | Hummock |
| JEL10 | 35 | 3,8 | 0,053 | *S. fuscum* | Hummock with *Drosera rotundifolia*, *Vaccinium oxycoccos*, *Ledum* |
| JEL11 | 9 | 3,9 | 0,064 | *S. recurvum* | Hollow |
| JEL12 | −3 | 3,9 | 0,039 | *S. recurvum*, (*S. cuspidatum*) | Hollow |
| JEL13 | 9 | 3,8 | 0,046 | *S. recurvum*, (*S. magellanicum*) | *Sphagnum* carpet with *Scheuzeria palustris* |
| JEL14 | 30 | 4,0 | 0,055 | *S. fuscum* | Hummock with *Andromeda polifolia*, *Ledum palustre*, *Vaccinium* |
| JEL15 | 19 | 3,8 | 0,058 | *S. recurvum* | Wide (1,5 m) hummock with *Andromeda polifolia*, *Drosera rotundifolia* |
| JEL16 | 1 | 3,9 | 0,060 | *S. recurvum* | Hollow |
| JEL17 | 1,5 | 4,1 | 0,046 | *S. recurvum* | Hollow |
| JEL18 | 8 | 4,0 | 0,054 | *S. recurvum* | *Sphagnum* carpet including *Vaccinium oxycoccos*, *Andromeda polifolia*, *Drosera rotundifolia* |
| JEL19 | 21 | 4,1 | 0,061 | *S. fuscum* | Hummock with *Vaccinium oxycoccos* and *Eriophorum vaginatum* |
| JEL20 | 6 | 4,3 | 0,054 | *S. recurvum* | Hollow |
| JEL21 | n.d. | 4,6 | 0,045 | *S. recurvum* | *Sphagnum* carpet with *Menyanthes trifoliata* and *Carex rostrata* |

(Continued)

**Table 1.** Continued

| Sample name | DWT cm | pH | Conductivity | Moss species sampled (other moss species)[a] | Habitat and dominant vascular plant species |
|---|---|---|---|---|---|
| JEL22 | 9 | 4,3 | 0,055 | S. recurvum | Lagg covered by Menyanthes trifoliata and Juncus effusus |
| JEL23 | 40 | 3,8 | 0,052 | S. magellanicum | Hummock embracing Alnus glutinosa stem |
| JEL24 | 0 | 4,2 | 0,032 | S. recurvum | Lagg with Caltha palustris and Menyanthes trifoliata |

**Jelenia Wyspa—fen part:** Open fen and poor fen in the Stazka river valley. Dominated by brown mosses and small sedge species. Bordered by an alder swamp. Peatmosses occur on the edge of the fen.

| Sample name | DWT cm | pH | Conductivity | Moss species sampled | Habitat and dominant vascular plant species |
|---|---|---|---|---|---|
| JEL25 | 25 | 6,4 | 0,179 | S. teres | Limit between a fen and a transitional mire with Theplypteris palustris, Carex rostrata, Eriophorum angustifolium, Epipactis palustris |
| JEL26 | 15 | 6,5 | 0,150 | S. teres | Limit between a fen and a transitional mire with Theplypteris palustris, Carex rostrata, Eriophorum angustifolium, Epipactis palustris |
| JEL27 | 5 | 6,7 | 0,205 | Plagiomnium elliptycum | Fen, vegetation including Theplypteris palustris, Carex rostrata, Calla palustris |

**Jeziorka Kozie** (53° 41′ 09.1″ N; 17° 52′ 57.8″ E): Four kettle-holes with floating Sphagnum mat growing onto water surface. Vegetation include Sphagnum spp. and small Carex species eg. Carex limosa and Carex lasiocarpa. Described as dystrophic. Some parts covered by pine forest.

| Sample name | DWT cm | pH | Conductivity | Moss species sampled | Habitat and dominant vascular plant species |
|---|---|---|---|---|---|
| KOZ1 | 0 | 4,1 | 0,058 | S. cuspidatum, (Calliergon stramineum) | Lagg |
| KOZ2 | 1 | 4,4 | 0,035 | S. cuspidatum, (S. recurvum) | Sphagnum carpet with Rhynchospora alba |
| KOZ3 | 7 | 4,1 | 0,036 | S. recurvum, (S. magellanicum) | Sphagnum carpet with Drosera rotundifolia, Vaccinium oxycoccos |
| KOZ4 | 2 | 4,1 | 0,052 | S. recurvum, S. cuspiadum. Calliergon | Sphagnum carpet with Eriophorum vaginatum and Carex canescens |
| KOZ5 | 20 | 3,9 | 0,064 | S. magellanicum | Hummock with Vaccinium oxycoccos |
| KOZ6 | 25 | 4,1 | 0,047 | S. magellanicum, (P. strictum) | Hummock |
| KOZ7 | 16 | 4,2 | 0,049 | S. recurvum | Hummock with Scheuzeria palustris |
| KOZ8 | 40 | 3,6 | 0,101 | S. magellanicum | Hummock with Ledum palustre and dwarf Pinus sylvestris |
| KOZ9 | 9 | 4,2 | 0,036 | S. recurvum | Sphagnum carpet, edge of floating mat with Peucedanum palustre and Carex lasiocarpa |
| KOZ10 | 0 | 4,3 | 0,014 | S. recurvum | Hollow / edge of floating mat bordered by Carex limosa |
| KOZ11 | 55 | 3,3 | 0,116 | S. magellanicum | Hummock with Vaccinium oxycoccos and Eriophorum vaginatum |
| KOZ12 | 0 | 4,0 | 0,074 | S. cuspidatum | Lagg with Juncus effusus |
| KOZ13 | 0 | 4,3 | 0,027 | S. cuspidatum | Lagg |
| KOZ14 | 6 | 4,0 | 0,024 | S. cuspidatum | Lagg with Eriophorum angustifolium |

DWT: depth of the water table.
S.: Sphagnum; P.: Polytrichum.

sample was packed into a cylindrical plastic container 6 cm in diameter, which was driven into the moss carpet and cut with the knife. The length of the moss samples was 8 cm. Only the living parts of mosses were selected to obtain modern testate amoebae communities. Plant species from the samples as well as from surrounding vegetation were recorded. In all micro-sites pH (accuracy 0.1), water level (accuracy 1 mm), and conductivity (accuracy 0.001 mS) were measured. Depth to water table DWT was measured with a tape gauge, and the zero level was defined as the top of the mosses. Our samples spanned a DWT gradient from −3 (i.e., submerged) to 40 cm, a pH gradient from 3.26 to 6.67 and a conductivity gradient from 0.014 to 0.205 [mS] (at 20°C). Descriptions of sampling sites with coordinates, parameters measured in the field, moss species included in each sample, as well as mosses and vascular plant species of the general habitat are given in Table1.

*Laboratory Procedures.* To extract testate amoebae, the green (approx. 5 cm), living parts of the mosses were boiled in distilled water for 20 min and stirred occasionally. The material was then sieved using a 300-μm-mesh size to separate large constituents. The filtrate was centrifuged at 3000 rpm for 4–6 min. to concentrate the tests. The samples were stored in stoppered vials in glycerol.

Amoebae tests were identified and counted at 200 × and 400 × magnification up to a minimum sum of 150 individuals per sample. Samples for which this number could not be reached were excluded from the data set. Digital photographs were taken with a light microscope in the Geological Institute of the Polish Academy of Sciences (Warsaw) and in the Department of Biogeography and Palaeoecology of Adam Mickiewicz University in Poznań. For some samples, SEM (scanning electron microscope) pictures were also taken to confirm the identification or for photo documentation (taken also in the SEM Laboratory of the Geological Institute). Specimens were identified to the lowest possible taxonomic level. The following literature was used for species/ecophenotypes identification [20, 24, 27, 28, 32, 36, 56], as well as some identification keys that are currently being developed based on these references (Mitchell, unpublished, currently available directly from the author).

*Numerical Analyses.* Relative abundance data of testate amoebae were subjected to a redundancy analysis (RDA) [68]. The species data was transformed prior to the analysis by means of the Hellinger distance [59]. This transformation allows the use of Euclidian-based methods such as RDA rather than Chi-squared distance-based methods such as CCA for the analysis of species data. This option was recently suggested as a way to overcome a problem associated with the Chi-squared metric: that

rare species may have a much larger influence on the analysis than common species [41]. Three quantitative environmental variables measured at the sampling sites (DWT, pH, and conductivity) were used as explanatory variables. One sample with missing DWT value was projected passively in the analysis, and 12 species that occurred in a single sample were removed from the data set prior to the analysis. This left 36 active samples and 41 active species in the analysis. The significance of the environmental variables was tested by means of a Monte Carlo permutation test in the forward selection procedure of environmental variables. The same permutation test was also applied to the canonical axes of the final model. All tests were done using 999 permutations and a significance threshold of $P < 0.05$

The ecological optima and tolerance of species was determined with WACALIB 3.3 [42, 43]. In a second step, the resulting transfer function can then be used for palaeoecological reconstructions in which a modern set of samples is used as a calibration set to build the model and then the transfer function is used to infer past ecological conditions based on the structure of the subfossil communities extracted from the sediment samples [7]. The transfer functions derived here will be used in a parallel paleoecological study (Lamentowicz, Obremska, Mitchell in prep). In WACALIB, several options are available (classical and inverse deshrinking, no transformation of species data, square root, or logarithm transformation). Error estimates are obtained using a bootstrapping procedure, and the performance of the models can be assessed using the root mean square error of the prediction (RMSEP) [43]. Two statistical models were used: simple weighted averaging (WA) and tolerance down-weighted averaging, WA(tol). In addition, the predicted value (weighted average) obtained for each sample was compared with the measured values. To improve the performance of the WA(tol) models, the species with very high tolerance (*Nebela* sp., *Euglypha* sp. *Arcella* sp., and *Arcella discoides*) were excluded, leaving only the best indicator species in the model [7, 42].

### Results

*General Results: Species Richness, Diversity, and Density.* A total of 52 species were found in the 44 samples analyzed. Six samples with low counts were excluded from the analysis, leaving 38 samples with 52 species in the data set. The dominant species were *Amphitrema flavum, Assulina muscorum, Arcella discoides* type, and *Hyalosphenia papilio*, which together represented on average 60.5 % of the total community count. A complete list of species and general statistics are presented in Table 2.

*Correlation of Testate Amoebae Species with Environmental Variables (RDA).* In the RDA of testate amoebae data, two quantitative environmental variables were significant: DWT and pH. Together, these two variables explained 21% of the variation in the species data. Water table depth was correlated positively with the first axis, and pH was correlated positively with the second axis (Fig. 3). Conductivity was not statistically significant as a third variable in the model ($P = 0.179$), although it was significant when tested first ($P = 0.028$).

The RDA ordination shows that the species can be separated into three groups (Fig. 3). The first group includes species that are associated with high DWT values (i.e., dry conditions) and low pH (*Assulina muscorum, Euglypha rotunda, Heleopera sylvatica, Nebela tincta, Corythion*-type, *Euglypha tuberculata*, etc.), The second group includes species associated with low DWT values (wet conditions) and low pH (*Nebela griseola, Hyalosphenia elegans, Amphitrema flavum, A. wrightianum. A. stenostoma, Arcella discoides, Nebela carinata, Difflugia leidyi*, etc.), The third group includes species associated with high pH conditions and mid-range DWT values (*Centropyxis aculeata, C. hirsuta, C. aerophila, C. ecornis, Nebela bohemica*, etc.).

The ordination also separates the sampling habitats and moss species quite well. Hummock sites dominated by *Sphagnum magellanicum, S. fuscum, or S. capillifolium*, mostly have high scores on the first axis. Hollows and lagg sites colonized by *S. cuspidatum* and *S. recurvum* are negatively correlated with the first axis, while the fen site and some lawn sites (mostly *Sphagnum recurvum*) are positively correlated with the second axis.

Despite the general predictable position of species and samples in the ordination space, there were some surprises. For example, three hummock sites (KOZ7, JEL19, and JEL4) had low scores on the first axis, and two of these (JEL19 and JEL4) had high scores on the second axis. KOZ7 and JEL4 represented two of the three hummocks that were colonized by *Sphagnum recurvum*, a rather unusual species for hummocks. KOZ7, was a low hummock with a DWT of 16 cm only. JEL19 was a *Sphagnum fuscum* sample, but the testate amoeba fauna was strongly dominated by *Hyalosphenia papilio*, a species that is usually more common in wetter microhabitats. A few other samples had unusual testate amoebae communities and were thus projected far away from macroscopically similar microsites. KOZ4, a sample categorized as a lawn, contained only two species and was very strongly dominated by *Arcella discoides*-type. This sample was therefore projected close to several lagg samples that had a similar community structure. A few other lawn samples were dominated by species such as *Amphitrema flavum* or *Hyalosphenia elegans*, which, in our samples, were mostly found in samples from hollows. Such patterns may explain the relatively low percentage of variation in the species data that could be explained by the two selected variables (21%). Clearly, other abiotic, or biotic factors have a strong influence on testate amoebae communities.

*Optima and Tolerance of Species.* The water table depth preferences of 52 species that occurred in more than one sample are presented in Table 2. The DWT optima ranged from −0.6 ( ± 2.6) *Amphitrema stenostoma* to 40.9 ( ± 21.92) *Cryptodifflugia oviformis*. Generally, the species indicative of drier conditions (higher DWT value) also had the wider tolerance for DWT, whereas the species indicative of wetter conditions had a lower tolerance (Fig. 4a). Species with a tolerance lower than 7 cm and an optimum lower than 9 cm are: *Arcella gibbosa, A. discoides, Centropyxis aculeata, C. hirsuta, Nebela carinata, Amphitrema wrightianum, Hyalosphenia elegans, Difflugia leidyi, Amphitrema flavum* and *Cyclopyxis arcelloides*. Species indicative of intermediate conditions (optimum range 10–25 cm) are: *Heleopera petricola, Assulina muscorum, Heleopera sphagni*, and *Hyalosphenia papilio*. Species indicative of the driest conditions, with an optimum over 25 cm include: *Heleopera sylvatica, Corythion dubium-type, Euglypha tuberculata, Euglypha rotunda, Bullinularia indica, Trigonopyxis arcula*, and *Euglypha strigosa*. This group has the largest tolerance in the data set, between 10 and 25 cm.

Species preferences for pH are presented in Table 2. The pH optima range from 3.30 for *Euglypha* sp. ( ± 0.7) to 6.65 for *Centropyxis hirsuta* (excluding the species that occurred in a single sample). Testate amoebae can be divided into two groups, representing acidic and near-neutral conditions. Because our samples were taken mostly in oligotrophic mires there are more acidophilic taxa in our data set: e.g., *Nebela collaris* (3.83), *Trigonopyxis arcula* (3.69), *Nebela militaris* (3.56), and *Assulina seminulum* (3.78). At the high end of this group, two species, *Centropyxis platystoma* (4.99) and *Arcella vulgaris* (4.69), may represent a transition toward more neutral conditions. There is then an abrupt shift in pH preferences, with five species having their optimum in near-neutral habitats: *Centropyxis hirsuta* (6.65), *Nebela bohemica* (6.59), *Centropyxis ecornis* (6.39), *C. aerophila* (6.16), and *C. aculeata* (5.7). There are stenotopic taxa (e.g., *Nebela collaris* ± 0.02; *Cryptodifflugia oviformis* ±0.06 and *Arcella gibbosa* ±0.1) and eurytopic taxa (*Arcella vulgaris* ±1.5; *Centropyxis platystoma* ± 1.68; and *Centropyxis aculeata* ± 1.6) in the data set. Unlike the findings for DWT, there was no linear relationship between the optimum and the tolerance of species for pH. Instead, what we observed are lower tolerance values for species at both ends of the gradient and higher values for those near the middle (Fig. 4b)

**Table 2. Frequency of occurrence, relative abundance, and ecological preferences of testate amoebae species for depth of water table (DWT) and pH in *Sphagnum-dominated* peatlands of northwestern Poland**

| Taxon | Relative abundance | | | DWT | | pH | |
|---|---|---|---|---|---|---|---|
| | n | mean | SD | Optimum | Tolerance | Optimum | Tolerance |
| *Amphitrema flavum* | 14 | 17,1 | 34,1 | 5,8 | 5,2 | 4,05 | 0,28 |
| *Amphitrema stenostoma* | 3 | 0,3 | 1,2 | -0,6 | 2,6 | 4,13 | 0,23 |
| *Amphitrema wrightianum* | 7 | 2,5 | 8,4 | 0,4 | 4,0 | 3,98 | 0,27 |
| *Arcella catinus* type | 12 | 4,8 | 14,1 | 24,4 | 13,4 | 4,43 | 1,02 |
| *Arcella discoides* type | 18 | 21,4 | 51,1 | 1,2 | 3,2 | 4,14 | 0,36 |
| *Arcella gibbosa* type | 4 | 1,6 | 5,8 | 3,2 | 3,1 | 4,23 | 0,10 |
| *Arcella* sp. | 2 | 0,1 | 0,7 | 23,5 | 20,5 | 4,02 | 0,33 |
| *Arcella vulgaris* | 8 | 2,9 | 12,2 | 23,2 | 20,7 | 4,69 | 1,52 |
| *Assulina muscorum* | 27 | 19,1 | 31,5 | 31,4 | 15,1 | 3,92 | 0,72 |
| *Assulina seminulum* | 14 | 2,2 | 5,8 | 28,1 | 18,7 | 3,79 | 0,31 |
| *Bullinularia indica* | 5 | 0,3 | 0,7 | 32,9 | 24,3 | 3,73 | 0,47 |
| *Centropyxis aculeata* type | 3 | 0,6 | 3,2 | 4,0 | 3,5 | 5,70 | 1,60 |
| *Centropyxis aerophila* | 4 | 0,5 | 2,5 | 22,0 | 12,8 | 6,16 | 1,11 |
| *Centropyxis ecomis* | 2 | 2,1 | 14,0 | 24,8 | 14,1 | 6,39 | 0,22 |
| *Centropyxis hirsute* | 2 | 1,7 | 10,9 | 5,2 | 7,1 | 6,65 | 0,11 |
| *Centropyxis platystoma* type | 2 | 0,1 | 0,5 | 5,8 | 0,7 | 4,99 | 1,68 |
| *Corythion dubium* | 5 | 2,2 | 7,7 | 29,9 | 17,7 | 3,61 | 0,27 |
| *Corythion-Trinema* type | 4 | 0,1 | 0,4 | 32,8 | 12,8 | 3,48 | 0,28 |
| *Cryptodifflugia oviformis* | 2 | 0,0 | 0,2 | 40,9 | 21,9 | 3,33 | 0,06 |
| *Cyclopyxis arcelloides* type | 11 | 3,8 | 13,9 | 2,2 | 6,5 | 4,21 | 0,18 |
| *Cyphoderia ampulla* | 1 | 0,0 | 0,2 | 5,0 | ** | 6,67 | ** |
| *Cyphoderia trochus* | 1 | 0,0 | 0,3 | 5,0 | ** | 6,67 | ** |
| *Difflugia elegans* | 1 | 0,0 | 0,3 | 1,0 | ** | 4,35 | ** |
| *Difflugia globulosa* | 1 | 0,5 | 3,0 | -3,0 | ** | 3,94 | ** |
| *Difflugia leidyi* | 6 | 0,7 | 2,8 | 0,9 | 5,4 | 4,02 | 0,12 |
| *Difflugia lucida* | 1 | 0,2 | 1,2 | -3,0 | ** | 3,94 | ** |
| *Difflugia* sp. | 1 | 0,0 | 0,3 | 50,0 | ** | 3,26 | ** |
| *Euglypha ciliata* | 1 | 0,1 | 0,6 | 55,0 | ** | 3,29 | ** |
| *Euglypha compressa* | 2 | 0,1 | 0,6 | 7,4 | 0,7 | 4,39 | 0,39 |
| *Euglypha rotunda* type | 8 | 0,8 | 2,1 | 37,6 | 20,3 | 3,75 | 0,92 |
| *Euglypha* sp, | 2 | 0,2 | 0,7 | 39,5 | 24,7 | 3,30 | 0,02 |
| *Euglypha strigosa* | 3 | 0,2 | 1,0 | 34,5 | 25,0 | 3,50 | 0,47 |
| *Euglypha tuberculata* type | 18 | 3,7 | 8,1 | 32,5 | 19,1 | 3,70 | 0,42 |
| *Heleopera petricola* | 16 | 4,7 | 10,8 | 15,1 | 11,9 | 4,02 | 0,61 |
| *Heleopera rosea* | 1 | 0,1 | 0,9 | 25,0 | ** | 6,36 | ** |
| *Heleopera sphagnii* | 11 | 0,5 | 1,4 | 10,6 | 9,6 | 4,07 | 0,70 |
| *Heleopera sylvatica* | 3 | 0,4 | 1,2 | 39,6 | 10,5 | 3,61 | 0,35 |
| *Hyalosphenia elegans* | 13 | 13,3 | 29,4 | 7,8 | 5,4 | 3,95 | 0,29 |
| *Hyalosphenia papilio* | 24 | 35,0 | 53,1 | 13,9 | 8,4 | 4,33 | 0,86 |
| *Nebela bohemica* | 2 | 0,1 | 0,4 | 10,3 | 7,1 | 6,59 | 0,11 |
| *Nebela carinata* | 3 | 0,4 | 2,0 | 1,2 | 4,0 | 4,20 | 0,23 |
| *Nebela collaris* | 2 | 0,2 | 1,0 | 23,9 | 9,9 | 3,83 | 0,02 |
| *Nebela flabellulum* | 1 | 0,0 | 0,2 | 24,0 | ** | 3,38 | ** |
| *Nebela griseola* type | 10 | 1,3 | 3,1 | 8,3 | 8,2 | 3,79 | 0,28 |
| *Nebela langeniformis* | 1 | 0,2 | 1,2 | 5,0 | ** | 6,67 | ** |
| *Nebela militaris* | 7 | 2,5 | 10,3 | 24,9 | 10,6 | 3,57 | 0,30 |
| *Nebela parvula* | 12 | 1,2 | 2,6 | 24,0 | 18,4 | 3,96 | 0,89 |
| *Nebela* sp. | 7 | 0,3 | 0,9 | 15,6 | 17,0 | 4,45 | 1,36 |
| *Nebela tincta* | 14 | 1,3 | 2,9 | 27,2 | 17,3 | 3,78 | 0,63 |
| *Quadrurella symmetrica* | 1 | 0,0 | 0,2 | 5,0 | ** | 6,67 | ** |
| *Sphenoderia lenta* | 1 | 0,0 | 0,3 | 5,0 | ** | 6,67 | ** |
| *Trigonopyxis arcula* | 8 | 1,3 | 4,2 | 30,6 | 15,2 | 3,69 | 0,28 |

**Taxon was present in only one sample, therefore no tolerance could be estimated.

*Transfer Function Models.* The correlation between the observed and predicted values for DWT and pH are presented in Fig. 5. For DWT, the best model was obtained with no data transformation, and with that option, the correlation was higher for the WA(tol) model ($r^2 = 0.91$) than for the WA model ($r^2 = 0.84$). The root mean square error of the prediction (RMSEP) was lower for the WA(tol) model (9.89) than for the WA model
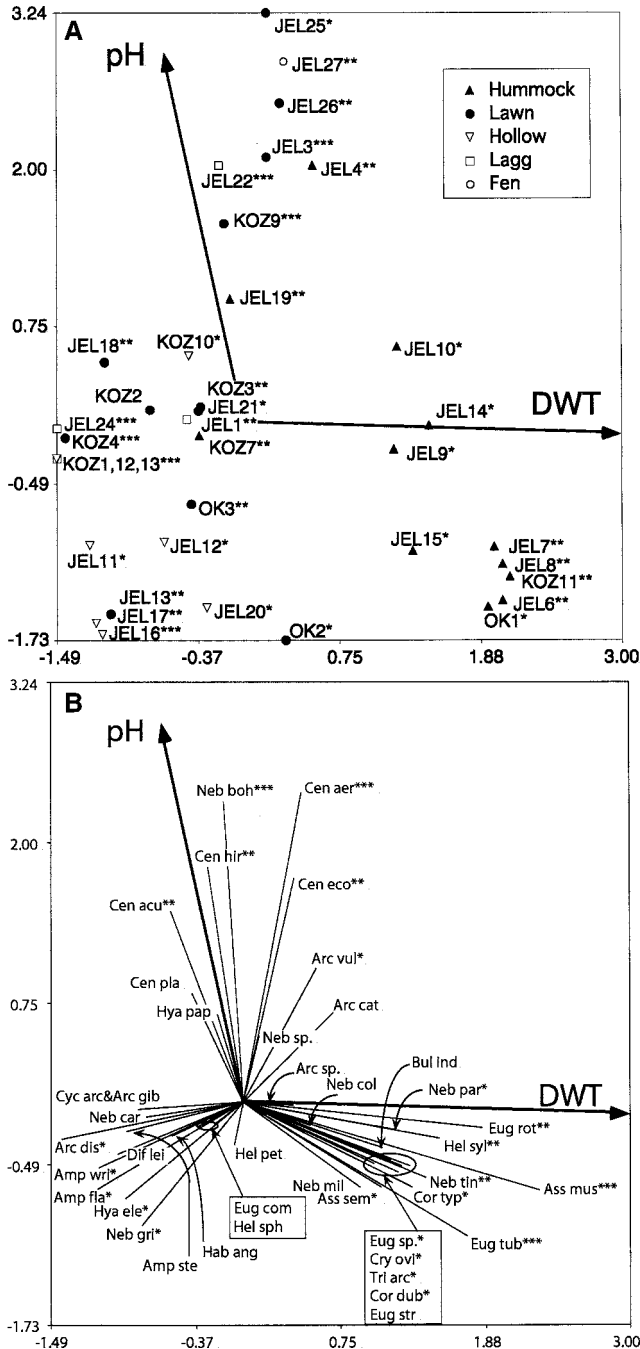
**Figure 3.** Biplots of the RDA analysis of testate amoebae data from Polish *Sphagnum*-dominated peatlands with representation of samples (symbols, in a), species (lines, in b) and environmental variables (arrows, in both biplots). The first two axes are canonical and are constrained by pH and water table depth. Axes 1 and 2 were significant ($P = 0.001$) and explain 15.1% and 5.9% of the species data, respectively. The key to the different symbols used for the samples is given in the inset. The symbols following the species and sample names indicate for the species the percentage of variance of each species explained by the model (no indication: <15%, *: 15–25%, **: 25–45%, ***: 45–60%), and for the samples the percentage fit of the model (no indication: <25%, *: 25–50%, **: 50–75%, ***: 75–100%). For readability, the scores of species and explanatory variables were multiplied by 3.

(10.16). The prediction error increased with increasing water table depth in both models. The prediction error was lowest in the 0-30 cm interval in the $WA_{(tol)}$ model. For DWT values over 30 cm, points are more scattered and the prediction error increases by approximately 10 cm (Fig. 5a).

Contrary to DWT, the best pH model was obtained with a $\ln(x + 1)$ transformation of the species data. Furthermore, the WA model performed better than the WA(tol) model, both in terms of correlation between observed and predicted values and in terms of RMSEP. The correlation between predicted and observed pH values was, however, generally lower than for the DWT models: ($r^2 = 0.69$; RMSEP = 0.72) in the WA model, and ($r^2 = 0.78$; RMSEP = 0.75) in the WA(tol) model.

## Discussion

### General Patterns of Community Structure in Relation to DWT and pH.

This study showed that testate amoebae respond to the same major environmental gradients in Poland as in other parts of the world. The strongest relationship was found between testate amoebae communities and both water table depth and pH. Conductivity, being strongly correlated with pH ($r^2 = 0.96$) was not included in the RDA model, although it was significant if analyzed separately. The position of species in the ordination space of the RDA revealed that most species responded to the water table depth gradient. This observation confirms previous observations where the humidity gradient, usually either water table depth or moisture, emerged as a strong factor determining the composition of testate amoebae communities [10–12, 21, 22, 49, 71, 72, 80].

Our results also illustrate the relationships between testate amoebae and micro-site type. Indeed, in hollows dominated by *Sphagnum cuspidatum*, amoebae species characteristic of wet conditions such as *Nebela carinata*, *Amphitrema wightianum*, and *Difflugia leidyi* were recorded in high numbers, whereas hummocks built by *Sphagnum magellanicum* and *S. fuscum* are colonized mostly by testate amoebae species located at the dry end of the water table gradient, such as *Assulina muscorum*, *Nebela tincta*, *Heleopera sylvatica*, and *Euglypha rotunda*.

Despite the general predictable position of species and samples in the ordination space, there were some surprises (detailed above in the Results). Clearly other abiotic or biotic factors have a strong influence on testate amoeba communities. Nevertheless, despite these limitations, in most cases the patterns were clear and the position of most species and samples in the ordination space is in agreement with previous studies. Our results therefore bring support for the use of testate amoebae in ecological and paleoecological studies of mires. Of special interest to ecologists and paleoecologists is the higher
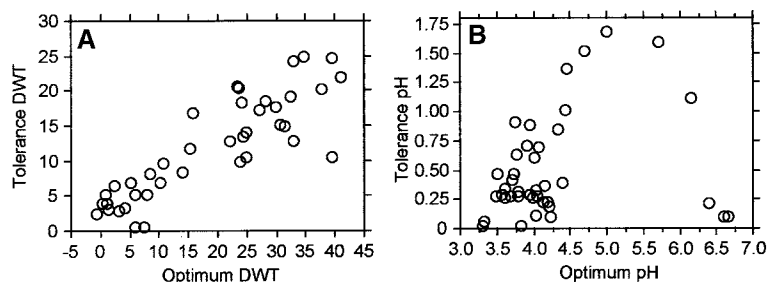
**Figure 4.** Biplot of depth to the water table (DWT) and pH optima of the species versus their tolerance for each variable.

diversity of testate amoebae as compared to bryophytes or plants in *Sphagnum*-dominated peatlands in general and the apparent cosmopolitan distribution of most species [48].

*Optima and Tolerance of Species for DWT and pH.* The analysis of water table depth optima and tolerances revealed that generally xerophylous species are also eurytopic while hygrophilous species are stenotopic (Fig. 4a). A similar pattern of optimum and tolerance has been recorded in New Zealand, Switzerland and France [15, 49]. This suggests that hollow and lagg testate amoebae or *Sphagnum* species appear to be more sensitive than hummock species to changes in water table depth conditions. Such species might therefore be considered more precise indicators of water table change in the sense of climate change than the more ubiquitous xerophylous species. An extreme example of this pattern may be found in laggs, which were characterized by extremely low species diversity and a strong dominance by

a single species, *Arcella discoides*. In some samples only this species occurred and these samples were therefore projected passively in the RDA. Extreme seasonal changes in water table levels and other micro-environmental conditions and the higher ecological sensitivity of testate amoebae characteristic of the wettest conditions may explain the very low testate amoebae diversity found in laggs. Nevertheless, even though taxa indicative of dry conditions may have a higher tolerance for DWT and may not allow as precise a reconstruction in paleoecological studies as pool species, a community shift from hollow to hummock species can still be interpreted as a clear shift in ecological conditions. The question of differential sensitivity to water table depth clearly needs further investigation, preferably with a higher number of samples and a wider range of micro-environmental conditions (e.g., including also permanently submerged situations).

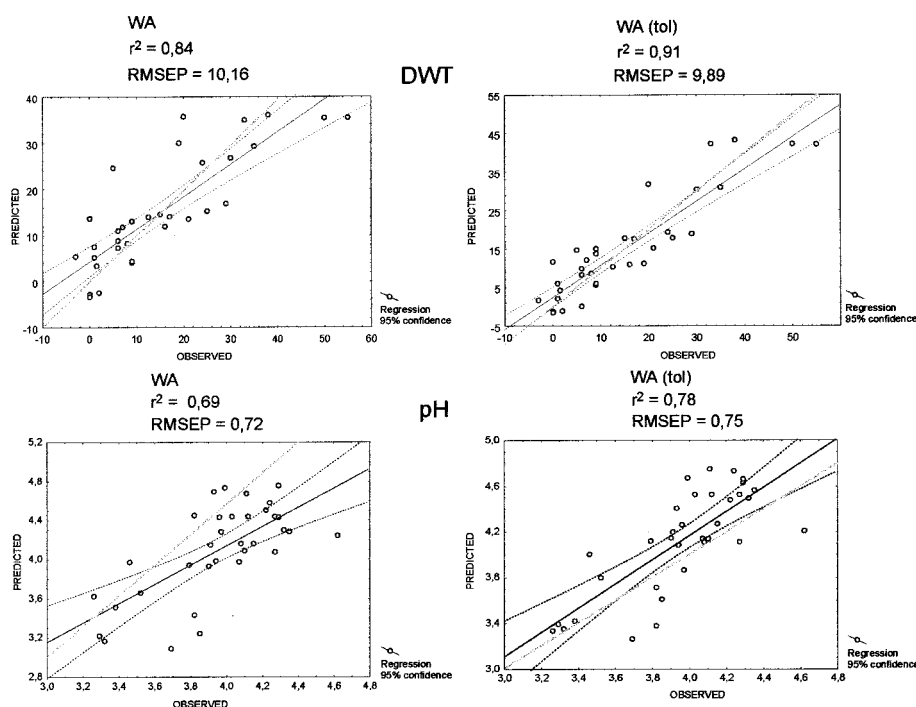Here again, an interesting parallel can be drawn with the ecology of mire bryophytes. In a series of studies



**Figure 5.** Biplot of observed values of depth to the water table (DWT) and pH in the sampling sites versus values predicted based on testate amoebae communities using the weighted averaging transfer function.

Rydin and co-workers observed the vulnerability of species from hollows (e.g., *S. balticum, S. tenellum*) to drying [60–62], whereas the hummock species (e.g., *Sphagnum fuscum*) successfully developed in hollows, and comparable observations were reported by Vitt [75]. Similarly, Grosvernier et al. [33] observed that the growth of *Sphagnum fallax*, a hollow or lawn species, was much more affected than that of *Sphagnum fuscum* by water level. These results show that the effect of moisture on growth is one of the determining factors in *Sphagnum* competition and ultimately leads to mutual exclusion of species along the hollow–hummock gradient. Moisture therefore seems to be a strong factor in shaping the community composition of both bryophytes and testate amoebae in *Sphagnum*-dominated peatlands.

By contrast to the observations made for the species' optima and tolerances for DWT, we did not find a correlation between the species' pH optima and tolerances. Instead species with intermediate pH optimum had the highest tolerance (Fig. 4b). This suggests that the best indicator species for pH are associated with either end of the pH gradient, whereas the species whose optima is in the middle of the gradient are eurytopic. As was the case for DWT, the response of testate amoebae to pH can also be interpreted in the general context of peatland ecology. *Sphagnum* mosses, through several physical and physiological characteristics, have a strong acidifying effect on their environment [25, 26, 73]. As a consequence, once *Sphagnum* becomes established the pH drops sharply. Therefore in *Sphagnum*-dominated peatlands (including bogs and poor fens) most of the surface is characterized by highly acidic conditions, typically between 3.0–4.5 for bogs, and 4.5–5.5 for poor fens, whereas moderately rich and extremely rich fens usually have a pH range between 5.5–7.0 and 7.0–8.0, respectively [66]. Several peatland ecologists have noted the existence of a bimodal frequency distribution of water pH with one mode at values under 5.0 and another at values above 6.0 [78]. The fens with intermediate pH between 5.2 and 5.7 are a rare component of northern landscapes [74, 75]. Interestingly, this is precisely the pH interval at which we find the highest tolerance value for testate amoebae pH preferences. Furthermore, the more acidic bogs show less annual variation in pH than the poor and rich fens [74].

In many parts of Europe the poor and rich fens are rare because of their conversion to agricultural land through drainage, a practice that started long before the extensive harvest of peat for fuel and horticulture [37]. The lack of stenotopic testate amoebae with optimum values in the middle of the pH gradient may simply reflect the general scarcity of such conditions in the environment. From a conservation perspective, it may be under these conditions that rare testate amoebae as well as *Sphagnum* species may be encountered. Being naturally rare in northern landscapes and under higher human pressure, these ecosystems should be considered a top priority for conservation.

*Comparison with Previous Studies.* Out results from Poland correspond very well with those from previous studies. To illustrate this, we used Booth's [12] compilation of DWT optima for 20 common testate amoebae species from previous studies and added the results of this study (Fig. 6). The ecological optima (relative position along the water table depth gradient) of most species correspond relatively well, despite some methodological differences in DWT measurements. Mean annual value of water table depth was used in Great Britain [80], while two methods were used in Finland [71]. In the remaining studies measurements were taken only once during sampling. Although this way of taking DWT measurements would not be sufficient for hydrological studies, the general agreement for DWT optima of testate amoebae species suggests that this method is reliable enough for this purpose.

It is worth noticing that hydrological preferences of stenotopic species restricted to the wettest part of the hydrological gradients are, in most cases, similar among studies, whereas important differences are observed for eurytopic species indicative of drier conditions (lawns to hummocks). This pattern mirrors the above observations on the tolerance of the species along the DWT gradient. All studies agree that three species, *Trigonopyxis arcula*, *Bullinularia indica*, and *Nebela tincta*, are clearly the most xerophylous of the list. Furthermore *Nebela militaris* and *Assulina muscorum* were encountered in all xeric sites. A considerable range in DWT optimum can be seen for *Cyclopyxis arcelloides*. This species was found in very wet habitats in Poland (DWT optimum = 2.2 cm) as well as in Canada, Switzerland, and Great Britain [15, 49, 80]. However it was found in intermediate conditions in the USA and Canada [11, 72] and in very dry conditions in Finland and New Zealand [15, 71]. *Cyclopxis areelloides* is considered by some authors as a species complex [20]. A likely cause for such a wide range of hydrological preferences may therefore be taxonomic uncertainty. By contrast, the three taxa recorded in the wettest microhabitats; *Nebela carinata*, *Arcella discoides*, and *Amphitrema wrightianum*, occur in very similar conditions in most studies.

*Performance of the Models.* The comparison of observed and predicted DWT and pH allows us to assess the potential usefulness of testate amoebae in paleoecological reconstructions of environmental variables. As in some previous studies, the WA(tol) model performed better than the WA model [12, 50]. Using our data from Polish peatlands, water table depth can be inferred from testate amoebae assemblages with a mean estimated error of ±9.89 cm—model WA(tol). The RMSEP values of
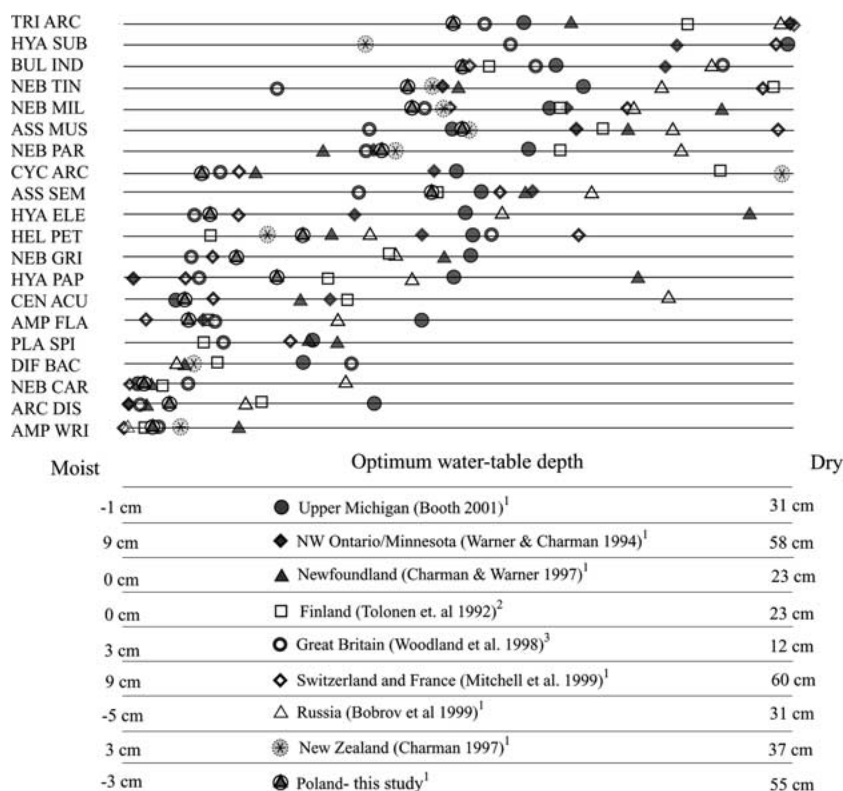
Moist　　　　　Optimum water-table depth　　　　　Dry

| | | |
|---|---|---|
| -1 cm | ● Upper Michigan (Booth 2001)[1] | 31 cm |
| 9 cm | ◆ NW Ontario/Minnesota (Warner & Charman 1994)[1] | 58 cm |
| 0 cm | ▲ Newfoundland (Charman & Warner 1997)[1] | 23 cm |
| 0 cm | □ Finland (Tolonen et. al 1992)[2] | 23 cm |
| 3 cm | ○ Great Britain (Woodland et al. 1998)[3] | 12 cm |
| 9 cm | ◇ Switzerland and France (Mitchell et al. 1999)[1] | 60 cm |
| -5 cm | △ Russia (Bobrov et al 1999)[1] | 31 cm |
| 3 cm | ✳ New Zealand (Charman 1997)[1] | 37 cm |
| -3 cm | ◓ Poland- this study[1] | 55 cm |

**Figure 6.** Comparison of 20 species of common testate amoebae preferences to depth of water level (DWT). Modified from [11] with Polish data added.

previous studies were 6.32 for Canada [21], 8.98 in New Zealand, [15], 5.45 in Russia [10], and 7.67 in the USA [11, 12].

In agreement with previous work, the largest dispersion as well as the highest prediction error were observed in sites with the deepest water level [15, 49]. In Switzerland and France, prediction errors were largest for water table depth situated over 60 cm [49, 50]. The authors interpreted this as being due to the characteristics of the sampling sites, many of which, and especially the sites with extremely high DWT values, were in drained peatlands. By contrast, the sites sampled in the present study were all natural, and low water levels reflected micro-site characteristics related to the autogenic evolution of the micro-topography (hummock formation) and not anthropogenic influence such as drainage. This has important implications for palaeoecological studies. In-

deed, in general, past condition are less likely to have been affected by human activities than in the present. Data from natural peatlands may therefore be especially valuable to build transfer functions for palaeoecological investigations. However, where human impact was important in the past, having only natural peatlands in the modern data set may lead to a situation similar to the classical problem of lack of modern analogues encountered in palynological studies [53].

For pH, the correlation coefficient between observed and predicted pH was low because of data scattering (high RMSEP). Our model performs best for pH values around 3.9, while above and below this value the prediction error increases. To some extent this can be explained by the tendency of predictive models to perform poorly at the ends of the range of values covered. In addition, for high pH values, this can be ex-
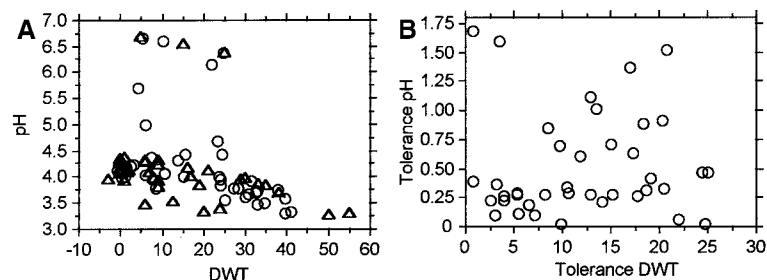


**Figure 7.** Biplot of depth to the water table (DWT) versus pH optima (a) and tolerance (b) of the species. Triangles in (a) indicate the DWT and pH values of samples.
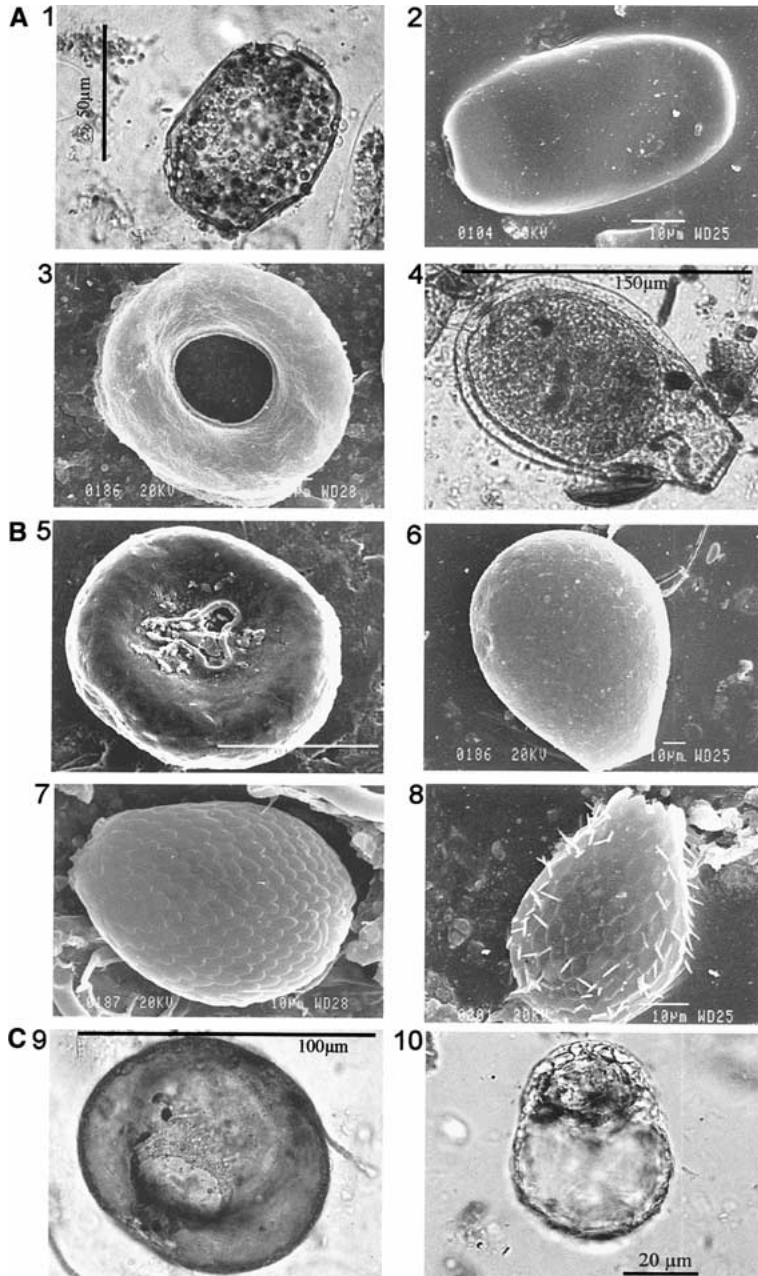
**Figure 8.** Scanning electron micrographs of 10 testate amoebae taxa. Three ecological groups according to pH and DWT preferences are presented. (A) low pH and low DWT value: 1—*Amphitrema wrightianum*, 2—*Amphitrema flavum*, 3—*Arcella discoides*, 4—*Nebela carinata*; (B) Low pH and high DWT value: 5—*Trigonopyxis arcula*, 6—*Nebela tincta*, 7—*Assulina muscorum*, 8—*Euglypha strigosa*; (C) high pH and low DWT: 9—*Centropyxis ecornis*, 10—*Centropyxis aerophila*.

plained by the higher tolerance of species indicative for pH values of 4.5–6.0. Furthermore, the selection of sampling sites was not as well balanced for pH as it was for DWT. A relatively low number of micro-sites had intermediate acidity, but as mentioned above, these situations are naturally rare in northern peatlands. A larger data set and a selective sampling effort in intermediate acidity conditions might help improve the performance of the pH model in the future. By comparison, Bobrov et al. [10] took samples in habitats with relatively high acidity (max pH = 4.26), while Tolonen et al. [71], Booth [12], and Mitchell et al. [49] covered

a wider spectrum of pH (max respectively = 6.3, approximately 6.9, and ranging from 3.8 to 6.4). Finally, some discrepancies in pH range and optima could result from methodological differences of the measurements if different protocols were used [67].

*Comparison of DWT and pH Indicator Value of the Species.* We compared the optimum and tolerance of species for pH versus DWT to determine if good DWT indicators were also good pH indicators and vice-versa (Figure 7). A weak negative correlation is observed for pH versus DWT. Species indicative for high DWT

values (dry habitats) were also indicative for low pH conditions, but species indicative for wetter conditions could either be indicative for low or high pH. This pattern reflects the range of characteristics covered by the sampled sites. Indeed, in Fig. 7a there is a clear correspondence between the position of circles determined by the species optimum for DWT and pH and the triangles that represent the sampling sites. The comparison of tolerances (Fig. 7b) did not reveal any correlation, suggesting that there is no relationship between the tolerance of species for DWT and their tolerance for pH. This means that if species are to be selected for inclusion in a transfer function model based on their tolerance value, the selection of species for the optimal DWT model will not necessarily be the same as for the optimal pH model. SEM illustrations of some good indicators for DWT and/or pH are given in Fig. 8.

## Acknowledgments

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