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Testate amoebae as ecological and palaeohydrological indicators in peatlands – The Polish experience

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ABSTRACT: In this paper we present brief overviews of the ecological study of peatland testate amoebae in northern Poland and applications of testate amoeba analysis in palaeohydrology as well as for the monitoring of natural and human-impacted mires – e.g. Polish Baltic bogs. Testate amoebae are unicellular organisms that produce a test (shell), which protects their cytoplasm. These protists represent a valuable tool in palaeohydrological studies in *Sphagnum* mires. In peatlands, testate amoebae live in mosses and the upper, oxygenated part of the peat. They are very sensitive to water table changes and, to a lesser extend also to pH. Some species occur in moist, slightly acidic hollows and others in dry very acidic *Sphagnum* hummocks. During the vegetation season testate amoebae produce many generations. When conditions become less favourable, (e.g. winter or temporary desiccation in summer), they encyst or die. Empty tests are preserved in peat together with the remains of plants and some other organisms and become part of the peat archive. Peat sediments provide a unique opportunity to reconstruct past hydrological changes in mires on the basis of testate amoebae. To reconstruct water table changes quantitatively a good modern data set is required. For Poland such a data set was recently created from surface samples from Tuchola Pine Forest. We modelled the response of species (optimum and tolerance) to environmental variables. Subsequently, this training set was used for inference of past hydrological conditions from *Sphagnum* mires in northern Poland, Tuchola and Jelenia Wyspa located in the Tuchola sandr area. In addition, plant macrofossils and palynological analyses were used to reconstruct changes in the local and regional vegetation and the history of human impact. In both sites we observed correlations between the testate amoebae inferred hydrology and climate changes as well as human activities (e.g. deforestations or damming).

1 INTRODUCTION

Testate amoebae (*Protista*, also referred to as *Testacea*, testaceans, Arcellaceans,) are characterised by the presence of a shell (called test) that protects the cell and that allows identification. Over 70 taxa have so far been found in mires of Poland (Lamentowicz & Mitchell 2005, unpublished data).

The scientific interest for peatlands dwelling testate amoebae is increasing because they are good indicators of changing environmental conditions. They are thus used in both ecological (Charman & Warner 1992, Booth 2001) as well as palaeoecological studies (Schoning et al. 2005, Charman et al. 2006). A more recent application is their use in applied ecological research on human impacted peatlands and the history of land-use changes (Sjögren & Lamentowicz 2006) or the monitoring of peatland restoration (Davis & Wilkinson 2004). Statistical models commonly used in palaeolimnological research (transfer functions such as weighted averaging) (Birks 1998) are applied on the basis of testate amoebae data (Payne et al. 2006). Testate amoebae are reliable indicators of palaeohydrological conditions in mires. However, can also indicate pH fluctuations (Patterson et al. 2002).

In this paper we present brief overviews of: (a) the ecological study of peatland testate amoebae in northern Poland, (b) applications of testate amoeba analysis in palaeoecological reconstructions.

2 BIOLOGY OF TESTACEA

Testate amoebae are protists with a complex taxonomy. They are regarded as at least biphyletic and are divided into *Cercozoa* (e.g. *Euglypha* – filose taxa) and *Amebozoa* (e.g. *Difflugia* – lobose taxa) (Cavalier-Smith 1997, Foissner 1999, Adl et al. 2005, Nikolaeva et al.

2005). Their shared characteristic is the presence of an external shell, called test from which pseudopods emerge. There are about 1000 to 2000 described taxa.

The morphology of the test is very important for identification. Some species produce autogenous shells, which can be made of pseudo-chitin e.g.: *Archerella (syn. Amphitrema) flavum* or *Arcella vulgaris* or siliceous plates (called idiosomes) (e.g. *Euglypha, Assulina*, etc.). Other taxa use foreign material (referred to as xenosomes) either mineral grains, diatoms, or other organic material such as fungal hyphae to build in the test. Some species also form characteristic horns or other appendices that are useful for identification e.g. *Difflugia leidyi*. These different types of shells may differ also in terms of preservation, a fact that has implications for palaeoecologists. Thus tests made of idiosomes are less durable than those made of xenosomes, which in turn are less durable than the pseudo-chitin type. But there are some exceptions e.g. *Assulina muscorum*, a species that builds shells from idiosomes, but is extremely resistant and even observed in pollen preparations (Charman 2001).

Testate amoebae form cysts to survive unfavourable conditions. This ability, in addition to the presence of a shell allows them to colonize even relatively dry environments. Short generation period allows them to respond fast to environmental changes. For example *Centropyxis aculeata* was observed to have over 60 generations during the year (Schönborn 1981).

Testate amoebae occur in a broad range of habitats: marine sand, soil, sea, the bark of trees, and freshwater environments. They are usually considered to be mostly cosmopolitan organisms because they may disperse easily while encysted in atmospheric dust or carried passively by migratory birds (Charman et al. 2000). Thus the difference in species composition is not large between distant regions e.g. in New Zealand and Great Britain. This situation allows direct comparison of species assemblages and interpretation of differences in terms of ecology. However, some species have restricted Laurasian or Gondwanan distribution, e.g., *Nebela (Apodera) vas* (Foissner 1987).

3 STUDY AREA

In 2002–2004 we carried out a study on the ecology of peatland testate amoebae. Our study was restricted to *Sphagnum* peatlands, mainly three kettle-hole mires (Jelenia Wyspa, Jeziorka Kozie and Okoniny) situated in northern Poland in Tuchola Pinewoods area. We then used this data in two palaeoecological studies of Jelenia Wyspa and Tuchola mire. The study area is presented in Figure 1.

Small lake basins (or mires in this case) are able to record climatic signals (Moore 2002). We therefore hypothesized that Tuchola kettle-hole bog also might have been sensitive to climatic conditions.

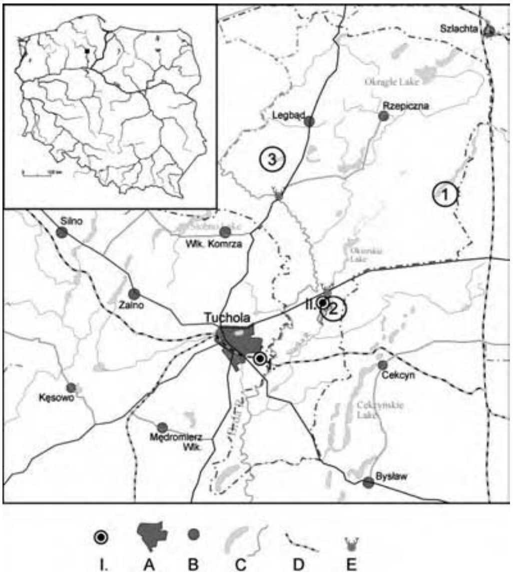

Figure 1. Location of the study sites. Description of the map, surface sampling mires: 1 – Okoniny (OK), 2 – Jeziorka Kozie (KOZ), 3 – Jelenia Wyspa (JEL); coring sites: I – Tuchola mire, II – Jelenia Wyspa mire; A – town, B – village, C – surface waters, D – rail, E – forestry managing head office.

Polish data are exceptionally important because Poland is under several contrasted climatic influences – from oceanic to continental.

Currently we are expanding our focus on Baltic raised bogs (Kartuzy Lakeland) as well as central Poland (Łódz region) to address the possible biogeographic variability of testate amoebae populations and possible response to climatic gradients.

4 METHODS

Surface sampling was conducted on *Sphagnum* mires with the aim describing the ecology of testate amoebae. For each sampling site measurements of pH, depth to water table and conductivity were taken. These parameters were used for description of testate amoeba community structure in relation to the environment Lamentowicz & Mitchell (2005).

Peat cores and monoliths were taken from the two peatlands for palaeoecological analyses with a Russian sampler and subsampled in the laboratory. Pollen, spores and plant macrofossils were also analysed along with testate amoebae. The cores were dated with ^{14}C method and were fit into the calendar time scale.

Species-environment correlations were quantified by means of multivariate statistics. A redundancy analysis (RDA) was used for explaining species relations to environmental parameters (DWT, pH and conductivity) (Lamentowicz & Mitchell 2005).

Transfer functions to be used in palaeecology for quantitative reconstruction of past environmental conditions were produced using either weighted averaging (WA) or weighted averaging partial least squares (WA-PLS) methods (Birks 1995, Birks 1998). The optimisation of the transfer function in an ongoing effort, with new surface samples being added and other improvements to the models (Lamentowicz et al. in prep).

The redundancy analysis was performed using the CANOCO software (ter Braak & Šmilauer 1998) and transfer function inference models were produced using the software C2 (Juggins 2003). The application of these numerical tools allows the integration of ecological and palaeoecological data sets.

5 RESULTS

5.1 *Ecological studies: Species – environment relations and transfer function models*

A total of 52 testate amoebae taxa were recorded during this study. In the redundancy analysis, DWT and pH explained 20.1% of the variation in the species data. This analysis allowed us to identify three groups of taxa: species those are associated with: (1) high DWT and low pH, (2) low DWT and low pH and (3) high pH and mid-range DWT (Fig. 2 A & B).

The next step was to build transfer functions for specific environmental variables. Preliminary analyses revealed that the simplest model – WA (weighted averaging) performed best for DWT parameter, whereas WA-PLS model performed best for pH. The performance of these models was tested using the surface samples. The results are in agreement with data from the other regions of the world (Charman & Warner 1997; Mitchell et al. 1999; Booth 2001).

Despite having gained information on the ecological preferences of most taxa, some species, such as *Difflugia urceolata* and *D. pulex*, are still missing from our training set. This problem exists also in western European data sets. One possible solution to this problem is to sample a broader range of ecological situations in peatland habitats, e.g. rich fens. The effort is now concentrated on improving the transfer functions for palaeoecological reconstructions. Having good data about the ecology of testate amoebae, we can now use them in palaeoecological reconstructions and monitoring practice.

Until now (December 2005), 76 peatland taxa were described for Poland, whereas 68 species were recorded in the modern surface samples and 64 species from the peat material (Lamentowicz, unpubl.). A selection of indicator testate amoebae taxa are presented in Figure 3.

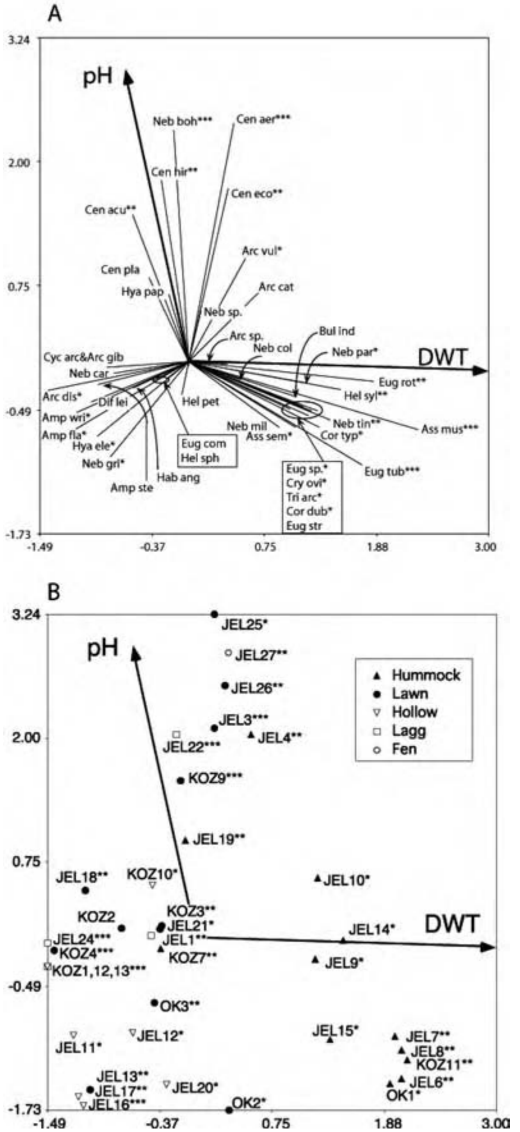

Figure 2. Redundancy analysis biplot for species (A) and samples (B) data. The symbols following the species names indicate the percentage of variance of each species explained by the model (no indication: <15%, *: 15–25%, **: 25–45%, ***: 45–66%). Redrawn from Lamentowicz & Mitchell (2005) with kind permission of Springer Science and Business Media.

5.2 *Palaeoecological studies: Proxies, reconstruction, climate, human impact*

The core from Tuchola mire yielded a 9000 years record of the developmental history. Testate amoebae remains were rare in the early, lake and fen phases of the development.

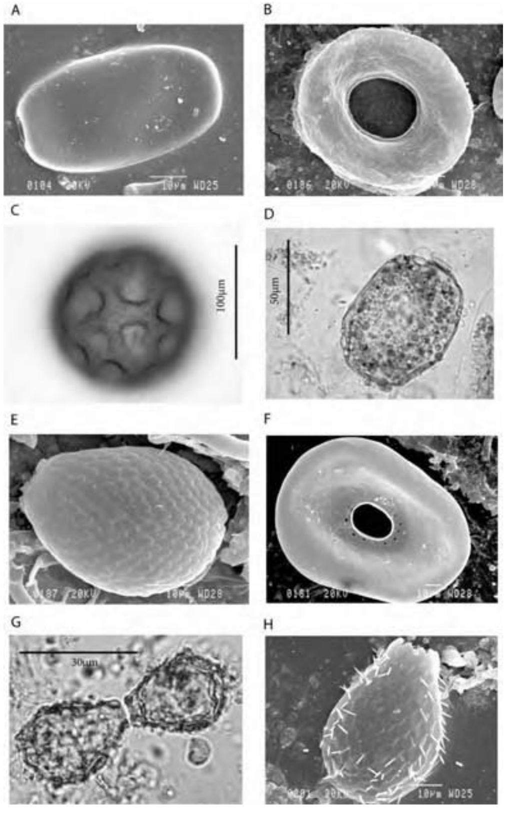

Figure 3. Pictures of testate amoebae species: high water level indicators (A–D), and low water level indicators (E–H); A – *Amphitrema flavum* Carter, 1864; B – *Arcella discoides* Ehrenberg, 1872; C – *Arcella gibbosa* Penard, 1902; D – *Amphitrema wrightianum* Archer, 1869; E – *Assulina muscorum* Greeff, 1888; F – *Arcella catinus* Penard 1890; G – *Difflugia pulex* type Penard; H – *Euglypha strigosa* Ehrenberg 1872.

Palaeoecological reconstruction showed that hydrological conditions were unstable throughout the mire history. Despite local catchment influences this small peatland appears to have responded to regional climatic changes. Palynological studies in this area showed that intensive human impact began in Tuchola Pinewoods in historical time (Miotk-Szpiganowicz 1992, Obremska & Lamentowicz 2002). This mire thus contained a mixture of allogenic (climatic) and anthropogenic (e.g. forest clearance) signals, and the multiproxy approach proved useful to separate these two influences.

One species *Difflugia urceolata* occurred infrequently in the development history of the mire. It was interpreted as an indicator of flooding and eutrophication of mire (Laminger et al. 1979, Schönborn 1981). Today, Tuchola mire is flooded every year mainly during the spring and this situation can be analogous to past conditions where, during moister periods, flooding was more frequent.

Using the water table depth curve wet shifts in the history of the mire were recognized and compared with hydrological events in Poland and across Europe. The results of this study will be presented separately (Lamentowicz et al. in prep.).

Jelenia Wyspa peat archive recorded ca. 2000 years of local environmental changes. The data shows an increasing human impact on the mire. It is very difficult to separate the anthropogenic influences from climatic ones in this mire. Correlation of results from three analyses: testate amoebae, palynological and plant macrofossils show how important the impact of land-use changes was on the mire. The development of *Sphagnum* mire was most likely induced by forest clearance approx. 200 years ago. Implementation of pine monocultures changed considerably the water chemistry of the mire and caused significant water table fluctuations. Jelenia Wyspa is a very good example of a process previously observed also in other parts of Poland (e.g. Wielkopolska region). The results of this study will also be presented separately (Lamentowicz et al. in prep.).

In both of these studies, testate amoebae allowed quantitative reconstruction of hydrological changes that would not have been possible with other palaeoecological methods. The integration of several approaches allowed to reaching an integrated understanding of history of these two sites.

6 CONCLUSIONS

We provided new data on the ecology of testate amoebae in Poland. The data was used to produce a local transfer function (DWT & pH), filling an important geographical gap in central Europe. Testate amoebae were used, for quantitative reconstruction of water table and pH changes in Polish kettle-hole mires. Testate amoeba analyses have been used together with other proxies (pollen and macrofossils). Such multiproxy approach is crucial for reconstructing changes in ecosystems more precisely. Fast-reacting proxies, e.g. stable isotopes, insects, or aquatic organisms can extract climatic signal more directly than long-lived proxies such as vegetation (Lotter 2003). Testate amoebae can be considered as fast-reacting proxies that can track abrupt environmental changes caused by climate or human.

The results show that palaeomoisture data inferred from testate amoebae can be correlated with other signals. In Jelenia Wyspa mire, deforestation around the mire caused a rise and fluctuations of the water table as well as an acidification of the surface. Tuchola mire peat archive covers a longer time period and is most likely influenced primarily by climatic changes during the second half of the Holocene. Currently, further work is carried out on kettle-hole mires and raised bogs of Pomerania and Central Poland.

In view of the ongoing and future change in climate, we need further high-resolution palaeoclimatological studies in order to gain a better understanding of the response of natural ecosystems to past climatic changes. Testate amoebae are very valuable indicators for studying the relationships between peatlands, climate, and human activities (Charman 2001).

In addition to classical palaeoecological studies, testate amoebae can be employed to monitoring mire restoration (Davis & Wilkinson 2004), or spontaneous regeneration (Chapman et al. 2003).

By combining palaeoecological and ecological information we can answer the question – to which conditions we want to restore a site? Knowledge about the past of peatlands provides vital information for managers. We therefore call for including paleoecology in the classical toolbox of peatland management. Having sound knowledge on the developmental history of the peatlands that we restore is not a luxury!

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