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The Variation of Testacean Assemblages (Rhizopoda) Along the Complete Base-Richness Gradient in Fens: A Case Study from the Western Carpathians

Věra OPRAVILOVÁ[1] **and Michal HÁJEK**[1,2]

[1]**Institute of Botany and Zoology, Faculty of Science, Masaryk University, Brno;** [2]**Department of Ecology, Institute of Botany, Academy of Sciences of the Czech Republic, Czech Republic**

Summary. Most recent ecological studies of testate amoebae were conducted in acid *Sphagnum*-dominated mires. Little data exists about the variation in testacean assemblages along the complete gradient from extremely poor acid fens to strongly calcareous spring fens. This so called poor-rich gradient is the most important gradient for the majority of mire biota and can display a time dimension as well. In order to fill this gap we studied modern testacean assemblages in spring fens in the Western Carpathians (Czech Republic and Slovakia). The DCA of all testacean assemblages revealed two major factors controlling species variation, the poor-rich gradient and the microhabitat-type: waterlogged bare sediments versus bryophytes. Sampled sediments of poor acidic fens have species composition similar to that of bryophyte tufts from mineral-richer fens. The ordination of the subset of samples taken from bryophyte tufts shows the clear poor-rich gradient on the first axis and moisture gradient causing variation of "acid" samples along the second axis. Based of DCA results, testacean assemblages were divided into six major types for which the diagnostic species were determined using *phi*-coefficient. Nearly all types are dominated by *Euglyphidae*, *Centropyxidae, Cyclopyxidae* and *Difflugiidae* were characteristic for calcareous habitats. Species richness did not correlate with the poor-rich gradient. The species variation in testate amoebae assemblages is better predicted by both the species composition of the vegetation as a whole and by the composition of bryophyte tuft than by long-term averages of water chemistry variables. The autecology of many species living in acid *Sphagnum* fens corresponds well with published data with several exceptions. On the other hand, the study of the complete poor-rich gradient revealed different species optima reported from higher pH *Sphagnum* fens, and thus it changed our view on the indicative value of some species.

Keywords: bog, calcium, fen, mire, peatlands, pH, *Sphagnum*, spring, testaceans, testate amoebae, vegetation, wetland.

INTRODUCTION

Testate amoebae (Rhizopoda) are often studied in both active *Sphagnum* bogs and Holocene peat deposits. They are used as biondicators of past and present environmental changes because of (i) their high abun-

Address for correspondence: Michal Hájek, Institute of Botany and Zoology, Faculty of Science, Masaryk University, Kotlářská 2, CZ-61137 Brno, Czech Republic; E-mail: hajek@sci.muni.cz

dances in wetland habitats (e.g. Warner 1987, Charman and Warner 1992, Booth 2001), (ii) well-defined ecological preferences (e.g. Tolonen *et al.* 1992, Bobrov *et al.* 1999, Lamentowicz and Mitchell 2005), (iii) rapid response to environmental change (e.g. Jauhiainen 2002, Mitchell 2004) and (iv) possibility of species-level identification even in fossil peat sections (Tolonen 1986). Numerous ecological studies dealing with recent species responses to the water level gradient in *Sphagnum* mires provide a good basis for the usage of testate amoebae as paleoindicators of past hydrological changes

(Hendon *et al.* 2001, Booth 2002, Schnitchen *et al.* 2003, Davis and Wilkinson 2004, Caseldine and Gearey 2005) and also as recent indicators of hydrological changes during restoration or ongoing climate change (Jauhiainen 2002, Kishaba and Mitchell 2005, Schoning *et al.* 2005). However, the responses of testate amoebae species to other environmental factors such as pH and mineral richness are less known in mires. The pH and calcium concentration are the major factors controlling species distribution of mire plants especially at a landscape scale (variation between individual mires) (Waughmann 1980, Vitt 2000, Hájková *et al.* 2004, Nekola 2004, Tahvanainen 2004). The botanical composition, vegetation structure and species richness all change along this base-richness gradient from strongly acid bogs and poor fens to the extremely-rich fens. The high concentrations of calcium and hydrogencarbonates in extremely-rich fens make the occurrence of even calcitolerant *Sphagna* impossible and the so called "brown mosses" (mostly *Amblystegiaceae*) are therefore dominant (Gorham and Janssens 1992, Vitt 2000). The extremely high mineral concentration leads to calcium carbonate (tufa) precipitation (Boyer and Wheeler 1989, Hájek *et al.* 2002) and the occurrence of (sub)halophytic conditions (Cooper 1995, Horsák 2006). This conspicuous species turnover was named poor-rich fen gradient (e.g. Malmer 1986, Økland *et al.* 2001, Hájek *et al.* 2002, Tahvanainen 2004). Changes in species composition along the poor-rich gradient have also been observed in molluscan (Horsák and Hájek 2003), algal (Poulíčková *et al.* 2003) and fungal (Vašutová 2005) communities. Because of this, there is a strong presumption that the same pH/calcium gradient should also influence the variation in testacean assemblages, but current ecological knowledge does not provide sufficient evidence. Most ecological studies of testate amoebae have been conducted in acid, ombrotrophic or only slightly minerotrophic mires (Charman and Warner 1992, Bobrov *et al.* 1999, Mitchell *et al.* 2000). Whenever less acid habitats were included they were either strongly underrepresented (Mitchell *et al.* 1999, Lamentowicz and Mitchell 2005) or represented by the habitats still populated by *Sphagnum* species (Heal 1961, Warner 1987, Charman and Warner 1992, Booth and Zygmunt 2005). Tolonen *et al.* (1992, 1994) included several "brown-moss" rich fens in their study, but these were slightly acid or subneutral and non-calcareous, with the calcium concentration not exceeding 9 mgl^{-1}. Some studies present data on testate amoebae in truly calcareous wetlands, but only this habitat type was studied as opposed to the entire poor-rich fen gradient (Casper and Schönborn 1985, Bonny and Jones 2003, Mattheeussen *et al.* 2005). We therefore hypothetise that the often reported fact, that moisture is the primary and pH only the secondary factor controlling variation in testate amoebae assemblages (Warner 1987, Charman and Warner 1992, Tolonen *et al.* 1994, Charman 1997, Bobrov *et al.* 1999, Mitchell *et al.* 2000), is primarily due to the rather short base-richness gradient studied. The importance of a length of the gradient for appreciating of environmental control of species-data variation is evident from the results of Booth (2001), who found water-table depth to be the most important factor for variation in testacean assemblages from *Sphagnum* substrate, whereas pH turned to be the most important factor when the entire data set including non-*Sphagnum* samples was analysed. Nevertheless, even Booth did not include the complete base-richness gradient in his study as the most "basicole" species had pH optima between pH 5.5 and 6.0. In another study, Booth and Zygmunt (2005) described the species composition of some mineral-rich *Sphagnum*-fens in the Rocky Mountains, which were also rather acid. The lack of recent information about testate amoebae preferences along the poor-rich gradient has important consequences in ecology, i.e. an unprecise interpretation of Holocene environmental change during succession from minerotrophic cyperaceous-rich fens to ombrotrophic bogs and an insufficient partitioning of the effects of pH and water regime in the habitats where these two variables coincide. In order to fill this apparent gap in ecological knowledge, we studied the recent testacean assemblages in spring fens in the Western Carpathian flysh zone (Czech Republic and Slovakia). The study region represents a suitable model area where particular, isolated spring fens vary from calcium-poor acid fens tending to ombrotrophy (about 2 mgl^{-1} of calcium) to extremely calcium-rich petrifying fens (to 300 mg.l^{-1} of calcium). The poor-rich gradient is developed here at the landscape level, independent of the moisture gradient which is displayed only at the within-site scale (Hájková *et al.* 2004). Additionally, the complete poor-rich gradient covered in this study area represents a good opportunity to study the relationships among the botanical composition of the fen, of the moss sample, and the composition of testacean assemblages. The only attempt to test such a relationship was done by Mitchell *et al.* (2000), who found only marginally significant correlations between plant- and testacean species compositions in acidic mires. In the Western Carpathian spring fens, the existing studies showed that the botanical composi-

tion of a fen site or of a moss sample, as expressed by DCA site scores, is a better determinant of variation in the species composition of molluscan, algal and fungal assemblages than the directly measured environmental data including water chemistry and moss water content (Horsák and Hájek 2003, Poulíčková *et al.* 2004, Vašutová 2005). By analogy, vascular plant species composition contributes significantly to water pH when explaining variation in bryophyte assemblages (Hájková and Hájek 2004). In this study, we therefore aimed not only to reveal the species distribution pattern along the poor-rich gradient, but also to test the relative importance of plant species composition and directly measured water-chemistry data for the explanation of variation in testacean assemblages in fens.

MATERIALS AND METHODS

Study area

The Western Carpathians have been chosen due to the variable chemistry of aquifers and, on the other hand, due to similarities in hydrological characteristics and in the origin of spring fens within this area (Rybníèková *et al.* 2005). The study area is located on the western margin of the Western Carpathians and forms part of the flysch belt, in which sandstone and claystone of variable calcium content alternate. Marls, lime-rich claystone, calcareous sandstone and limestone prevail in the south-western part of the study area. Groundwaters are carbonatogenic there and their dominant mineralization process is carbonate dissolution which leads to the calcium-(magnesium)-bicarbonate type of chemistry (Rapant *et al.* 1996). This chemistry type supports cold water travertine (tufa) formation. Not only the extreme values of calcium concentration, but also the high magnesium concentration characterises the springwaters of this geological unit (Hájek *et al.* 2002). Towards the north-east the groundwater is characterised by constantly high concentrations of calcium, but lower contents of magnesium and higher contents of sodium, potassium and iron (Rapant *et al.* 1996, Hájek *et al.* 2002). The northern part of the study area is formed mostly by decalcified, often iron-cemented sandstone which causes that the hydrolythic dissolution of silicates at the interface between water and psammitic-psephitic rocks dominate in a mineralisation process. In this part the calcium concentration is the lowest within the entire study area. Altitude, humidity, temperature, and geographical position correlate with the main chemical gradient, but water chemistry seems to have the most important influence on spring biota (Hájek *et al.* 2002, Horsák and Hájek 2003). Calcium-rich rocks are situated in the south-western part, which is warmer (annual mean temperature is about 8°C) and drier (annual mean precipitation is about 700 mm). The altitudes of the south-western fens are lower though always exceeding 340 m and springs often develops on rather steep slopes. On the contrary, north-eastern fens are located at higher altitudes (max. 911 m) but at more gentle slopes. In addition, the climate of the northeastern part is more humid and cooler. The mean annual precipitation often reaches more than 1400 mm; the mean annual temperature can decrease to *ca* 5°C (Vesecký 1966)

Fourteen sites distributed along the complete water-chemistry and geographical gradients were selected for the research (Fig. 1). In all these sites, monitoring of water chemistry was conducted three times a year during 1999-2003. In order to obtain a balanced set of habitat types, seven localities were selected within calcareous spring fens with different degree of calcium carbonate precipitiation (Hrnčiarky, Hrubý Mechnáč, Valašské Kloubouky, Semetín, Jasenka, Hrubé Brodské and Kelčov) and seven within *Sphagnum*-fens with different share of calcitolerant and calcifobe *Sphagnum* species (Zajacovci 1, Zajacovci 2, Polková, Jančíkovci, Biely Kríž, Obidová 1, and Obidová 2). For the details about vegetation and geographical coordinates see Appendix 1, for further details and information about site selection see Hájek and Hekera (2004) and Poulíčková *et al.* (2005).

Vegetation sampling and analysing

Vegetation was recorded in 16 m² plots (Chytrý and Otýpková 2003) and using the nine-degree Braun-Blanquet cover scale modified by van der Maarel (1979). All vegetation plots used in this paper are the same as those utilized in a more detailed study of vegetation-water chemistry relationships in the study area (Hájek *et al.* 2002). In addition, the bryophyte species composition of the sample for testacean research was recorded using simple four-degree scale (3 - dominance; 2 - sub-dominance or co-dominance; 1 - presence; 0 - absence). Nomenclature follows Kubát *et al.* (2002) for vascular plants and Kučera and Váňa (2003) for bryophytes.

The vegetation plots were subjected to detrended correspondence analysis (DCA) using CANOCO software. The first axis was interpreted clearly as the poor-rich vegetation gradient (Fig. 2). The site scores on the first DCA axis were used as an environmental variable in further analyses. By analogy, the bryophyte composition of 29 samples for testate amoebae research was also subjected to DCA, nine samples from non-bryophyte substrate (sediments) were omitted. The site scores on the first axis, interpreted as a combined gradient of base-richness and moisture, see Fig. 3, were also used as an environmental variable in further analyses to involve moisture variation. The moisture characteristics were not measured directly in this study.

Water chemistry sampling

Water samples were collected from permanent plots (shallow pits), which were located in the surroundings of the major stream or headspring at each locality. The shallow pits were always re-exposed and water was pumped-out of them and allowed to refill before sampling. The contact of sampled springwater with air was short. The groundwater was several centimeters below the surface in many cases. Water conductivity, pH and redox-potential were measured in situ using portable instruments (CM 101 and PH 119, Snail Instruments). The readings were standardized to 20°C (pH, conductivity) and Ag/AgCl reference electrode (redox-potential). Conductivity caused by hydrogen ions was subtracted (Sjörs 1952). Afterwards, water was placed in plastic bottles using a syringe. Preservatives were added to divided samples: for metallic elements, 0.5 ml of 65% HNO_3 per 100 ml of sample; for anions, 3 ml of chloroform per 1000 ml.

Since most water samples were turbid due to colloidal suspensions, filtration or centrifugation (4000 turns per minute, 10 minutes)

was necessary. The concentrations of sulphates, phosphates, nitrates, ammonium ions, and chlorides were determined by DR 2000 spectrophotometry following colour reactions with certificated HACH-reagents Metallic and semimetallic cation (Ca^{2+}, Mg^{2+}, Si^{4+}, K^+, Na^+ and Fe^{3+}) concentrations were determined using a GBC AVANTA atomic absorption spectrometer. All plots were sampled from 1999 to 2003, three times a year (April, July and October). The values of all seasonal measurements were averaged in this study. The calcium concentrations were transformed logarithmically to approximate normal distribution.

Testacean data collecting

Samples for testacean research were taken on the 11th and 12th July 2002. Several samples of moss tufts were taken at each locality. In addition, bottom sediments from small depressions were also sampled. The moss samples were transported in live state to the laboratory and particular bryophyte species were identified (det.: M. Hájek); bottom sediments were preserved in 4% formaldehyde. Mosses were moistened before handling. After extracting the water, 0.1 ml of extract was analysed. Testate amoebae were identified (det.: V. Opravilová) and the total number of individuals was counted. Nomenclature of testate amoebae follows Aescht and Foissner (1989). The complete list of all recorded species is published in Opravilová (2005).

Testacean data processing

The number of testate amoebae individuals was transformed to the scale appropriate for ordination analyses. The highest number of individuals found in the whole species-by-sample matrix was considered as 100%; all other numbers were transformed into the percentage scale. This method was applied in order to avoid over-weighting of species in the samples with low total number of individuals. The resulting percentage scale was logarithmically transformed in ordination analyses. This transformation allowed us to focus primarily on species composition of the testacean assemblage and its changes along environmental gradients. The changes in species abundances were suppressed in this way. Transformed abundance values were subjected to indirect ordination analysis, the detrended correspondence analysis (DCA) with downweighting of rare species, which revealed the main directions of variation in testacean assemblages. The analysis showed, among others, that the substratum type influenced substantially the species composition of the assemblage and impedes an axes interpretation. Therefore, one more ordination was done using only testacean data from bryophytes samples. Both ordination analyses showed that six clear types of assemblages, nearly discontinuously delimited from each other, can be distinguished. The diagnostic species for these six clear types of assemblages were calculated using the *phi*-coefficient. This coefficient shows the concentration of the species in the group of samples - a higher frequency of the species in the group as compared to the species frequency outside the group means a higher *phi*-coefficient (Chytrý *et al.* 2002). In order to calculate *phi*-coefficient properly, all six groups were standardised to equal size whereas the size of target group is always one sixth of the total data set. Zero fidelity was given to the species with the significance of non-random occurrence in target group yielded by Fisher´s exact test lower than 0.01. JUICE software (Tichý 2002) was used for this computation. In addition, the percentage representation of particular testacean families in

samples of six major types was calculated. The total number of individuals found in each sample group was 100% in this case.

All ion concentrations, altitude, slope degrees, DCA site scores of the vegetation and of the bryophyte sample composition and categorical variable indicating character of substratum (bryophytes versus bare sediments) were used as explanatory variables in a canonical correspondence analysis with forward selection of environmental variables. The Monte-Carlo permutation test was used to test the usefulness of each variable to extend the set of explanatory variables used in the ordination model (Lepš and Šmilauer 2003). The goal of this analysis was to find the best set of predictors of species composition of testate amoebae assemblages. The analysis was conducted separately for (i) entire data set and (ii) assemblages from bryophyte samples only.

The correlation between species richness (the number of species found in an assemblage) and environmental factors was assessed using the Pearson´s correlation coefficient.

RESULTS

The DCA of all testacean assemblages revealed two major factors controlling species variation in testacean assemblages. The first axis represented the poor-rich gradient from calcareous spring fens to poor acid spring fens tending to ombrotrophy. The second axis separated samples taken in bare waterlogged sediments, not populated by bryophytes, from the bryophyte samples. The DCA scatter (Fig. 4a) showed an interesting ecological pattern, the shift in species composition of the community from poor-fen sediments towards that of circumneutral *Sphagnum*-fens and, in one case, even towards base-rich "brown-moss" fens. The basicole species forming the left part of the scatter (Fig. 4b, *Difflugia rubescens* Penard, *Difflugia bryophila* Penard, *Difflugia pyriformis* Perty and *Quadrulella symmetrica* (Wallich)) had their optima in calcareous waterlogged bare sediments. *Difflugia bryophila* and *Cyphoderia ampulla* (Ehrenberg) were the best indicators of bare sediments in our study reaching 78% frequency and *phi*-coefficient > 0.5 in samples from sediments. The right part of the scatter plot was composed of acidophilous species that were distributed along the second axis representing a moisture gradient. The ordination of the subset of samples taken from bryophyte tufts showed the clear base-richness gradient from calcareous fens to mineral-poor acid ones. Poor fen samples were divided into drier hummock microhabitats and wetter microhabitats along the second axis. Four separate and ecologically defined sample groups appeared in the scatter plot (Fig. 5a). The position of only one from the 38 samples was unexpected: one assemblage from high-productive calcare-
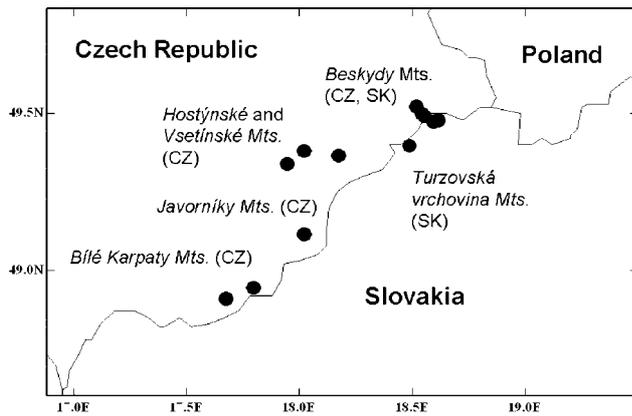
Fig. 1. Distribution of study sites in the Western Carpathians. Coordinates are in WGS 84 system.

Fig. 2. Position of the most important plant species along the first DCA axis. Species with a fit above 50% and weight above 10% were selected. For the full names of the species see Appendix 2.

Fig. 3. Position of the most important species along the first CA axis of the bryophyte sample composition. Species with a fit above 10% were selected into the graph. For the full names of the species see Appendix 2.

ous fen was placed among moderately-rich *Sphagnum* fens.

The species distribution pattern (Fig. 5b) also showed a higher variation in acid habitats, from wet assemblages with *Sphenoderia fissirostris* Penard to *Assulina seminulum* (Ehrenberg) assemblages from drier microhabitats. The species *Arcella catinus* Penard and *Cyclopyxis eurystoma* Deflandre occupied drier microhabitats on the transition between poor- and moderately-rich fens. The species *Difflugia bryophila* Penard, *Difflugia pyriformis* Perty, *Centropyxis constricta* (Ehrenberg), *Centropyxis cassis* Deflandre had their optima in bryophyte tufts of calcareous fens.

The species *Pseudodifflugia gracilis* Schlumberger were the best indicators of calcareous fen sediments (Table 1). Four other species displayed notable fidelity to this microhabitat type. *Cyphoderia ampulla* (Ehrenberg) reached the lowest fidelity as it overlapped into bryophyte tufts of moderately-rich *Sphagnum*-fens. *Arcella hemisphaerica* Perty characterised poor- and moderately-rich fen sediments. Seven species were characteristic for bryophyte tufts of calcareous fens, but only *Paraquadrula irregularis* (Archer) and *Centropyxis discoides* Penard were restricted to bryophyte tufts practically not living in bare sediments. Bryophyte tufts of moderately-rich *Sphagnum*-fens were characterised by *Arcella discoides* Ehrenberg. The poor acid fens had a large group of diagnostic species. The moisture gradient in poor fen assemblages was evident. The species diagnostic of poor fen lawns overlapped to poor-fen sediments and moderately-rich fen bryophytes and displayed therefore lower fidelity values, e.g. *Nebela*

collaris (Ehrenberg) *Phryganella acropodia* (Hertwig and Lesser), *Sphenoderia fissirostris* Penard. The species diagnostic of *Sphagnum* hummocks seemed, on the other hand, not to tolerate mineral-richer habitats and reach high fidelity to this microhabitat (*Nebela militaris* Penard, *Nebela tincta* (Leidy), *Assulina seminulum* (Ehrenberg), *Assulina muscorum* Greeff, *Heleopera petricola* Leidy), with the exception of *Corythion dubium* Taranek and *Nebela bohemica* Taranek that had a wider ecological amplitude.

The analysis of the family level in the six major types of assemblages (Table 2) showed that all types were dominated by *Euglyphidae* with the exception of calcareous bare sediments dominated by *Centropyxidae, Cyclopyxidae* and *Difflugiidae. Euglyphidae* prevailed nearly absolutely in bryophyte tufts of moderately-rich fens. Acid, calcium-poor sediments were also characterised by *Pseudodifflugiidae* and *Arcellidae. Hyalospheniidae* characterised all extremely acid habitats, especially *Sphagnum* hummocks. On the other hand, a high share of *Centropyxidae* was a characteristic of both calcareous habitats.

The species variation of testate amoebae assemblages was best predicted by the species composition of the vegetation as a whole (Table 3). The site score of the vegetation plot on the first DCA axis accounted for more variation in testacean assemblages than did the long-term (i.e. more precise) averages (1999-2003) of water chemistry variables. The composition of bryophyte tuft was the second most important factor and the type of the substratum (bare sediment versus mosses) was the third one.

Table 1. List of species that differentiate six principal types of testacean assemblages presented in Figs 4, 5. The numbers represent the values of standardised *phi*-coefficient of the species concentration in a particular cluster. Zero fidelity is given to the species with significance of non-random occurrence in target group yielded by Fisher´s exact test lower than 0.01.

Group No.	1	2	3	4	5	6
Number of samples	5	4	9	5	6	9
Species differentiating sediments of calcareous fens						
Pseudodifflugia gracilis	80.8	.	.	.	.	.
Difflugia glans	74.9	.	.	.	.	.
Difflugia gramen	74.5	.	.	.	.	.
Cyclopyxis kahli	62.2	.	.	.	.	.
Cyphoderia ampulla	50.6	.	.	.	.	.
Species differentiating sediments of poor and moderately-rich fens						
Arcella hemisphaerica	.	72.5	.	.	.	.
Species differentiating bryophyte tufts of calcareous fens						
Paraquadrula irregularis	.	.	81.1	.	.	.
Centropyxis discoides	.	.	63.2	.	.	.
Centropyxis constricta	.	.	52.3	.	.	.
Centropyxis aculeata oblonga	.	.	51.3	.	.	.
Difflugia pyriformis s.l.	.	.	45.5	.	.	.
Trinema enchelys	.	.	33.2	.	.	.
Centropyris cassis	.	.	32.0	.	.	.
Species differentiating bryophyte tufts of moderately-rich fens						
Arcella discoides	.	.	.	54.4	.	.
Species differentiating bryophyte lawns of poor acid fens						
Trinema complanatum	.	.	.	.	56.9	.
Euglypha cristata	.	.	.	.	53.5	.
Sphenoderia fissirostris	.	.	.	.	47.9	.
Nebela collaris	.	.	.	.	39.9	.
Phryganella acropodia	.	.	.	.	38.5	.
Species differentiating bryophyte hummocks of poor acid fens						
Nebela militaris	.	.	.	.	.	69.7
Nebela tincta	.	.	.	.	.	67.4
Assulina seminulum	.	.	.	.	.	59.5
Heleopera petricola	.	.	.	.	.	61.7
Corythion dubium	.	.	.	.	.	41.9
Nebela bohemica	.	.	.	.	.	34.4
Species differentiating both poor-fen lawn and poor-fen hummocks						
Assulina muscorum	.	.	.	.	48.4	48.4

No environmental variable correlated with the species richness of testate amoebae assemblages, except for a marginally significant and difficult-to-interpret iron concentration. We observed no trends even using non-linear techniques. For these reasons, the correlation coefficients are not shown in this paper.

DISCUSSION

The poor-rich gradient

Our data set from the poor-rich fen gradient was governed by a dominant primary gradient of pH and
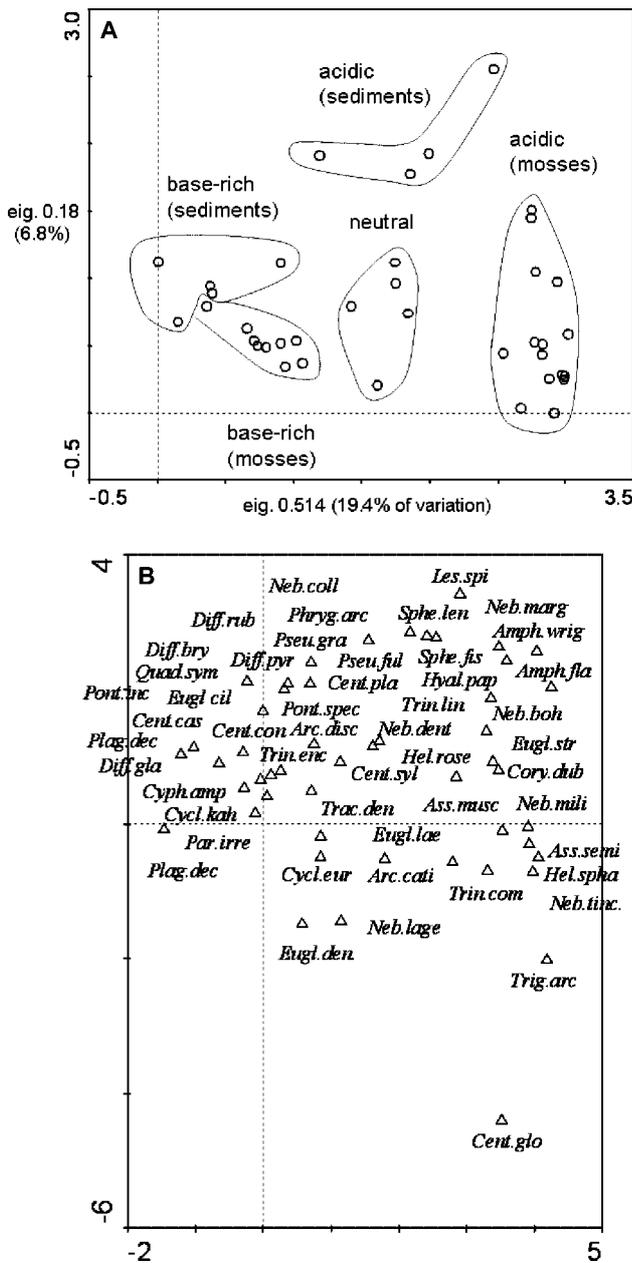
Fig. 4. Detrended correspondence analysis of all testatean assemblages (A) and their species (B). Ecologically interpretable groups of assemblages are indicated, eigenvalues and percentage of explained variance are presented at the axes. For the full names of the species see Appendix 2.

Fig. 5. Detrended correspondence analysis of testatean assemblages from bryophyte tufts (A) and their species (B). Ecologically interpretable groups of assemblages are indicated, eigenvalues and percentage of explained variance are presented at the axes. For the full names of the species see Appendix 2.

calcium, whose influence, according to comparison of DCA eigenvalues, is nearly three times stronger than that of the secondary gradient which has been interpreted as the moisture gradient. Base-richness is only scarcely repo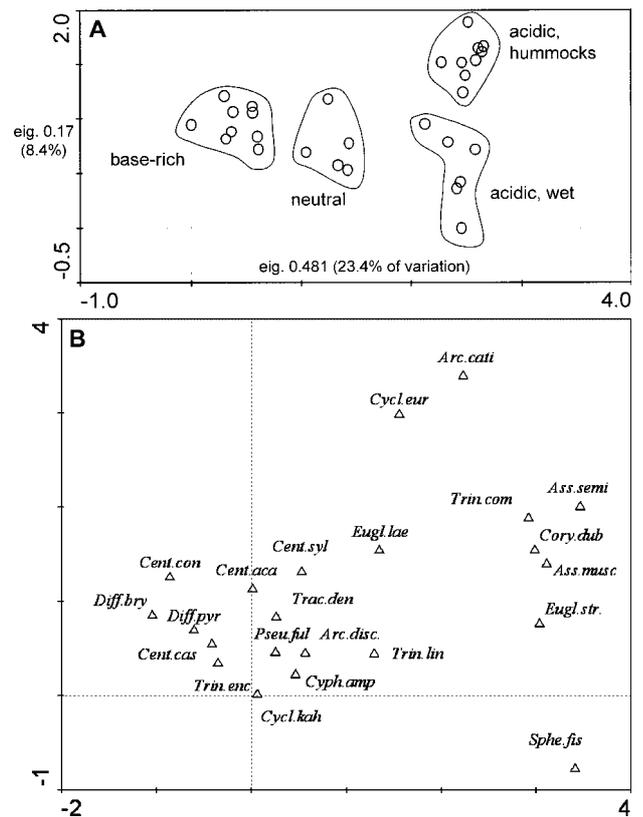rted as the most important environmental control for species variation in testacean assemblages. Mattheeussen *et al.* (2005) found such a result using data from arctic wetlands and Beyens *et al.* (1986), by analogy, from arctic mosses sampled across a wide range of wetland and terrestrial habitats. Booth (2001) found a similar pattern in non-*Sphagnum* wetland microhabitats. Booth and Zygmunt (2005) also suggested mineral richness to be a possible explanation for differences in assemblage composition between two regions of North America. The results of Mitchell *et al.* (1999) suggest that pH may be a major determinant even if the incomplete poor-rich gradient is analysed. On the other hand, Tolonen *et al.* (1994) analysed a longer poor-rich gradient than Mitchell *et al.* (1999) stretching beyond *Sphagnum* fens towards rich brown-moss fens, but the most important variable was still the water regime. The data from the Jura mountains (Mitchell *et al.* 1999) and

Table 2. Percentage representation of particular families in samples of six major types. The highest values for each column and each row are in bold.

Substrata Reaction	sediment base-rich	mosses base-rich	mosses neutral	sediments acid	mosses acid, wet	mosses acid, hummocks
LOBOSEA						
Arcellidae	< 1%	< 1%	< 1%	**10.43%**	< 1%	< 1%
Microchlamyidae	**< 1%**	< 1%	-	-	-	-
Centropyxidae	**41.32%**	11.44%	3.85%	4.26%	< 1%	1.64%
Cyclopyxidae	**13.70%**	4.18%	< 1%	-	< 1%	7.73%
Difflugiidae	**17.81%**	1.56%	< 1%	12.34%	< 1%	< 1%
Heleoperidae	1.83%	1.69%	1.67%	1.06%	1.27%	**2.49%**
Hyalospheniidae	5.71%	7.74%	1.91%	11.28%	23.73%	**36.83%**
Lesquereusiidae	1.37%	< 1%	< 1%	**4.26%**	< 1%	1.09%
Plagiopyxidae	4.11%	< 1%	-	-	-	-
Cryptodifflugiidae	-	-	-	-	< 1%	< 1%
Phryganellidae	1.14%	< 1%	< 1%	**4.26%**	1.10%	< 1%
FILOSEA						
Amphitrematidae	-	-	-	-	< 1%	< 1%
Cyphoderiidae	**2.28%**	< 1%	< 1%	1.70%	-	< 1%
Euglyphidae	10.05%	**71.60%**	**90.47%**	**38.51%**	**73.02%**	**48.07%**
Pseudodifflugiidae	-	< 1%	< 1%	**11.91%**	< 1%	< 1%

Table 3. Results of forward selection in CCA. Only variables significant at the P level 0.01 (Monte-Carlo test) were included to the model.

Entire data set			
Step	Variable	Lambda	Cumulative explained variance
1.	1st DCA axis of vegetation	0.434	16%
2.	1st DCA axis of sample composition	0.226	25%
3.	sediment / mosses	0.159	31%
4.	Ca (log-transformed)	0.085	36%
5.	SO_4^{2-}	0.082	39%
Moss samples only			
Step	Variable	Lambda	Cumulative explained variance
1.	1st DCA axis of vegetation	0.417	20%
2.	1st DCA axis of sample composition	0.160	28%
3.	Si	0.089	33%

from the Western Carpathians (this study) showed one more analogy: in both cases the second ordination axis, interpreted as the axis of moisture, was markedly clearer at the poor, more acid end of the gradient.

Booth (2001) reported a poor-rich gradient very similar to that described in this study. He primarily studied the within-wetland variation and observed a correlation between pH and moisture. Waterlogged depressions in acid wetlands are often not only wetter, but also less acid due to contact with mineral-richer groundwater or due to water aeration caused by water flow (Tahvanainen and Tuomaala 2003). The competition for mineral nutrients between peat mosses and inverte-

brates also plays a significant role. Our assemblages from waterlogged microhabitats of poor acidic fens had species composition corresponding to that of the bryophyte tufts from mineral-richer fens (Fig. 5a). A similar pattern was found in the case of molluscan assemblages (Horsák and Hájek 2003). Booth (2001) found that the testacean species characterising wetter sites also had higher pH optima. This holds not only for testate amoebae, but probably also for other biota in poor fens, diatoms for example (Poulíčková et al. 2004). Our study covered a wider range of pH and calcium concentration and the species turnover extended further, to more alkaline habitats characterised by a high representation

of *Difflugiidae* and *Centropyxidae*. The differentiation among major habitat types distinguished along the poor-rich gradient is therefore less influenced by covariation with moisture.

Our study showed that both the species composition of the vegetation, involving vascular plants and bryophytes, and the species composition of the moss sample characterise testacean assemblages better than even long-term measured water-chemistry data. Mitchell *et al.* (2000) reported rather different results. In their study testate amoebae reflected the chemistry of the groundwater and to a lesser extent the botanical composition of the moss carpet in acid *Sphagnum* mires. In such habitats direct measurements of water chemistry are necessary. On the other hand, our data suggest that the composition of the mire vegetation can substitute for directly measured water chemistry in the research of testate amoebae responses to the poor-rich gradient. The vegetation reflects not only a long-term development of environmental conditions but also possible antagonistic or synergistic influences of environmental factors on the fen biota.

When the species composition of our assemblages is compared with that of bogs and extremely poor fens across Europe (Mitchell *et al.* 2000), the assemblages from the Carpathian poor acid fens correspond rather to subcontinental Fennoscandian bogs than to oceanic bogs of Great Britain and the Netherlands. It is partly inconsistent with the species composition of plants. The studied Carpathian poor fens harbour several suboceanic, but very few boreal higher-plant species (Poulíčková *et al.* 2005). This comparison supports the results of Mitchell *et al.* (2000) that testate amoebae respond to different large-scale environmental factors in acidic mires. On the other hand, the mineral-richer mires studied by Booth and Zygmunt (2005) in North America have some species and groups in common with our rich fens (e.g. *Centropyxis casis, Quadrulella symmetrica, Pseudodifflugiidae*).

The species richness of vascular plants, bryophytes and some invertebrates is extremely low in the most acid poor fens and increases towards circumneutral habitats or further towards calcareous fens (Hájková and Hájek 2003, Chytrý *et al.* 2003, Horsák and Hájek 2003, Poulíčková *et al.* 2003, Tahvanainen 2004). This pattern has been explained by a large calcicole species pool that has resulted from historical and evolutionary processes (for details see Pärtel 2002 and Chytrý *et al.* 2003). The lack of correlation between testacean species richness and pH (this study) as well as between fungal species

richness and pH (Vašutová 2005) suggests that the historical processes considered cannot provide a satisfactory explanation of mire biodiversity patterns or that they are not relevant for some taxonomic groups. Indeed, for both testate amoebae and fungi a set of specialised species populating acidophilous *Sphagnum* plants exists.

Autecology

The autecology of many species living in *Sphagnum* fens corresponds well to published data. *Amphitrema wrightianum* Archer, *A. flavum* (Archer) and *Hyalosphenia papilio* (Leidy) have their optima in wet microhabitats of poor acid fens; the latter species tolerate enhanced mineral supply (Meisterfeld 1979, Charman and Warner 1992, Tolonen *et al.* 1992, Booth 2001, Schnitchen *et al.* 2003, Booth and Zygmunt 2005, Lamentowitz and Mitchell 2005). Nonetheless, these species have a rather wide ecological amplitude and are not significantly a characteristic of any microhabitat type (Table 1). *Assulina muscorum, A. seminulum, Arcella catinus, Nebela militaris, N. bohemica, Trigonopyxis arcula* (Leidy) and *Corythion dubium* characterise rather drier poor-fen microhabitats, the latter species overlap to moderately-rich fens (latter references plus Beyens *et al.* 1986, Tolonen *et al.* 1994, Bobrov *et al.* 1999, Mitchell *et al.* 2000, Opravilová and Zahrádková 2003, Vincke *et al.* 2004). The species *Trinema enchelys* (Ehrenberg), *Tracheleuglypha dentata* (Penard), *Centropyxis cassis* Deflandre, *Cyclopyxis kahli* Deflandre, *Cyphoderia ampulla* (Ehrenberg), *Difflugia glans* Penard and *Quadrulella symmetrica* (Wallich) were often reported either as characteristic for the "higher-pH habitats", i.e. moderately calcium-rich *Sphagnum* fens, or generally as inhabitants of all acid habitats (Heal 1961, Beyens *et al.* 1986, Tolonen *et al.* 1992, Mitchell *et al.* 1999, Mitchell 2004, Vincke *et al.* 2004, Lamentowitz and Mitchell 2005). Having now studied the complete poor-rich gradient, we have found that the majority of these species, namely *Cyclopyxis kahli, Quadrulella symmetrica, Centropyxis cassis, Trinema enchelys, Difflugia glans* and *Cyphoderia ampulla* have their optimum in "brown-moss" calcareous fens (see also Mattheeussen *et al.* 2005).

A disagreement was found in the case of *Pseudodifflugia gracilis* which behaves as an indicator of calcareous fens in our study area, whereas Bobrov *et al.* (1999) reported its occurrence from dry and acid bog hummocks. By analogy, the *Centropyxis aculeata* group reported from acid hummocks by Bobrov *et al.* (1999)

or from moderately-rich *Sphagnum* fens (Tolonen *et al.* 1992, Lamentowitz and Mitchell 2005) is characteristic of calcareous fens in our study. The taxonomical differences or relatively low number of samples used in presented study could be the reason of the differences described above.

The next indicator of calcareous fens, *Paraquadrula irregularis*, is generally not an obligate inhabitant of this habitat type. Nguyen-Viet *et al.* (2004) report its common occurrence in *Tortula muralis* tufts, but exclusively in unpolluted areas.

Lamentowitz and Mitchell (2005) found that assemblages from laggs in north-western Poland, i.e. from moderately-rich and poor fens, are species-poor and strongly dominated by *Arcella discoides*. This species is the best indicator of moderately-rich fens also in our study area.

An interesting analogy between testacean- and plant ecology is drawn by the comparison of the distribution pattern of some testate amoebae with the results of a fertilisation experiment made by Mitchell (2004). The abundance of *Tracheuglypha dentata* and *Phryganella acropodia* increased during fertilisation of wet arctic tundra. In our study area these species are typical for the middle part of the poor-rich gradient. The numerous studies in mire ecology suggest that under extreme pH conditions the availability of major nutrients (N, P, K) is low. Many nutrient-demanding meadow species grow in mires of circumneutral pH in our study area (Hájek and Hekera 2004, Hájková and Hájek 2004). The tendency of some species like *Tracheuglypha dentata* to prefer N- and P-rich habitats is probably the reason why one assemblage from a highly calcareous albeit high-productive fen had a species composition more similar to moderately-rich *Sphagnum* fens than to calcareous fens. Nonetheless, the low number of replications is a certain limitation of this conclusion.

The study of the complete poor-rich gradient improves our view on the indicative value of some species. Species which are often regarded to be ubiquitous such are *Assulina muscorum, Nebella militaris, N. tincta, Heleopera petricola,* and *Corythion dubium* (e.g. Mitchell *et al.* 1999) are among the best indicators of acid environment in our study area.

Knowledge about the responses of testate amoebae species to the poor-rich gradient is still limited as compared to their responses to the moisture gradient. The improvement of understanding the species response to the poor-rich gradient has an important implication for palaeoecology. During the Holocene, not only hydrological regime, but also base-richness can change, as confirmed by macrofossil analyses from central Europe (e.g. Rybníček and Rybníčková 1968), Scandinavia (e.g. Mörnsjö 1969) and northern America (e.g. Kuhry *et al.* 1993). Warner and Charman (1994) compared modern testate amoebae assemblages with fossil ones and found a combined poor-rich and moisture gradient very similar to that presented in this study. Their rich fens were characterised by the genera *Cyclopyxis* and *Centropyxis*, poor fens by the species *Amphitrema flavum, Assulina muscorum* and *Heleopera sphagni* and drier poor-fen hummocks by the species *Nebela militaris* and *Trigonopyxis arcula*.

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Appendix 1. List of localities, their geographical coordinates, altitudes, dominants and long-term averages of physical-chemical characteristics. Cation concentrations are in mgl^{-1}, cond - electrical conductivity of water.

Site name	coordinates	commune	altitude	Ca	Mg	Fe	water pH	cond	Dominants
Biely Kríž	N:49°29'54", E:18°32'47"	Biely Kríž	910	6.72	0.95	4.3	4.63	45	*Sphagnum palustre, S. papillosum, S. fallax, Carex echinata*
Hrnčiarky	N:48°54'30", E:17°40'34"	Strání	440	173.35	16	8.59	7.49	672	*Cratoneuron commutatum, Campylium stellatum, Eriophorum angustifolium, Equisetum telmateia*
Hrubé Brodské	N:49°21'59", E:18°10'30"	Nový Hrozenkov	530	86	11.2	20.67	7.13	431	*Aulacomnium palustre, Homalothecium nitens, Eriophorum latifolium, E. angustifolium*
Hrubý Mechnáč	N:48°56'33", E:17°47'54"	Lopeník	640	79.91	14.68	3.73	7.55	430	*Campylium stellatum, Cratoneuron commutatum, Eriophorum angustifolium, E. latifolium*
Jančíkovci	N:49°29'26", E:18°33'22"	Klokočov	750	3.24	0.74	6.12	4.21	27	*Sphagnum palustre, S. papillosum, S. fallax, Drosera rotundifolia*
Jasenka	N:49°22'41", E:18°01'24"	Vsetín	565	107.48	8.77	81.02	7.19	491	*Cratoneuron commutatum, Fissidens adianthoides, Eriophorum latifolium*
Kelčov	N:49°23'03", E:18°28'47"	Nižný Kelčov	660	63.08	5.29	71.76	7.08	292	*Scorpidium cossonii, Campylium stellatum, Bryum pseudotriquetrum, Eriophorum latifolium*
Obidová 1	N:49°31'03", E:18°31'23"	Visalaje	735	7.34	1.7	11.35	5.43	46	*Sphagnum contortum, S. warnstorfii, Eriophorum angustifolium*
Obidová 2	N:49°31'03", E:18°31'25"	Visalaje	730	10.8	2.53	29.28	5.97	77	*Sphagnum flexuosum, Carex echinata, Viola palustris*
Polková	N:49°28'24", E:18°35'53"	Klokočov - Hlavice	610	6.9	2.36	55.97	5.59	57	*Sphagnum flexuosum, S. subsecundum, Carex nigra*
Semetín	N:49°20'18", E:17°56'51"	Vsetín-Semetín	400	174.42	19.11	11.76	7.23	494	*Tomenthypnum nitens, Bryum pseudotriquetrum, Eriophorum angustifolium, Succisa pratensis*
Valašské Klobouky	N:49°06'47", E:18°01'24"	Valašské Klobouky	370	193.42	5.74	7.84	7.51	463	*Cratoneuron commutatum, Calliergonella cuspidata, Equisetum telmateia, Valeriana simplicifolia*
Zajacovci 1	N:49°28'46", E:18°37'03"	Zajacovci	660	6.64	1.84	2.81	5.23	43	*Sphagnum capillifolium, S. fallax, Carex nigra, Drosera rotundifolia*
Zajacovci 2	N:49°28'40", E:18°37'01"	Zajacovci	640	10.77	2.21	30.57	5.59	71	*Sphagnum subsecundum, S. contortum, Carex nigra, C. lasiocarpa*

Appendix 2. Abbreviations of the names used in ordination diagrams.

Testate amoebae (Figs 4-5)

Arcella catinus	Arc.cati	Pseudodifflugia fulva	Pseu.ful
Arcella discoides	Arc.disc	Pseudodifflugia gracilis	Pseu.gra
Assulina muscorum	Ass.musc	Quadrulella symmetrica	Quad.sym
Assulina seminulum	Ass.semi	Sphenoderia fissirostris	Sphe.fis
Amphitrema flavum	Amph.fla	Sphenoderia lenta	Sphe.len
Amphitrema wrightianum	Amph.wrig	Trigonopyxis arcula	Trig.arc
Centropyxis aculeata	Cent.aca	Tracheleuglypha dentata	Trac.den
Centropyxis cassis	Cent.cas	Trinema complanatum	Trin.com
Centropyxis constricta	Cent.con	Trinema enchelys	Trin.enc
Centropyxis globulosa	Cent.glo	Trinema lineare	Trin.lin
Centropyxis sylvatica	Cent.syl		
Corython dubium	Cory.dub	**Plants (Figs. 2-3)**	
Cyclopyxis eurystoma	Cycl.eur	Agrostis canina	Agro.can
Cyclopyxis kahli	Cycl.kahl	Anthoxanthum odoratum	Anth.odo
Cyphoderia ampulla	Cyph.amp	Calliergonella cuspidata	Call.cus
Difflugia bryophila	Diff. bry	Campylium stellatum	Camp.ste
Difflugia glans	Diff. gla	Carex demissa	Care.dem
Difflugia pyriformis	Diff. pyr	Carex echinata	Care.echi
Difflugia rubescens	Diff.rub	Carex nigra	Care.nig
Euglypha ciliata	Eugl.cil	Cirsium rivulare	Cirs.riv
Euglypha denticulata	Eugl.den	Cratoneuron filicinum	Crat.fil
Euglypha laevis	Eugl.lae	Drosera rotundifolia	Dros.rot
Euglypha strigosa	Eugl.str	Juncus inflexus	Junc.inf
Heleopera rosea	Hel.rose	Nardus stricta	Nard.str
Heleopera sphagni	Hel.spha	Palustriella commutata	Pal.com
Hyalosphenia papilio	Hyal.pap	Philonotis calcarea	Phil.cal
Lesquereusia spiralis	Les.spi	Plagiomnium elatum	Plag.ela
Nebela bohemica	Neb.boh	Polytrichum commune	Poly.com
Nebela collaris	Neb.coll	Prunella vulgaris	Prun.vul
Nebela dentistoma	Neb.dent	Sphagnum denticulatum	Spha.den
Nebela lageniformis	Neb. lage	Sphagnum fallax	Spha.fal
Nebela marginata	Neb.marg	Sphagnum flexuosum	Spha.fle
Nebela militaris	Neb. mili	Sphagnum palustre	Spha.pal
Nebela tincta	Neb. tinc	Sphagnum papillosum	Spha.pap
Paraquadrula irregularis	Par.irre	Sphagnum rubellum	Spha.rub
Phryganella acropodia	Phryg.acr	Sphagnum subsecundum	Spha.sub
Plagiopyxis declivis	Plag.dec	Straminergon stramineum	Stra.str.
Pontigulasia incisa	Pont.inc.	Tomenthypnum nites	Tome.nit
Pontigulasia spectabilis	Pont.spec	Viola palustris	Viol.pal