



# Biogeography and comparative ecology of testate amoebae inhabiting *Sphagnum*-dominated peatlands in the Great Lakes and Rocky Mountain regions of North America

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## ABSTRACT

Testate amoebae (Protozoa: Rhizopoda) are common inhabitants of peatlands. Strong relationships between community composition and substrate moisture in *Sphagnum*-dominated peatlands have made them particularly useful as hydrological proxies in environmental and palaeoenvironmental research. However, stability of these relationships in geographical space is important for widespread applicability. In this study, we compared testate amoeba communities inhabiting *Sphagnum*-dominated peatlands of the Great Lakes and Rocky Mountain regions of North America. Our primary objectives were to describe patterns of community composition in the two regions, develop hypotheses to explain differences, and determine if taxa occupy similar ecological niches with respect to substrate moisture in both places. Our results indicated that testate amoeba communities are relatively different in the two regions, and these differences are probably caused by differences in climate and peatland trophic status, although other factors may also play a role. However, many taxa do occur in both regions and these taxa had comparable moisture preferences in each region, suggesting that the ecological niches of taxa with respect to substrate moisture are similar even within communities of relatively different composition.

## Keywords

Geographical patterns, Great Lakes region, peatlands, Rocky Mountain region, *Sphagnum*, testate amoebae.

## INTRODUCTION

Testate amoebae (Protozoa: Rhizopoda) are amoeboid protozoans that inhabit moist substrates and produce a decay-resistant outer shell, or test. The tests are morphologically distinct, typically allowing species-level identification. Testate amoebae are particularly abundant and well preserved in *Sphagnum*-dominated peats, where they are estimated to represent 5–30% of the total microbial biomass and probably play a major role in the microbial food web (Gilbert *et al.*, 1998; Mitchell *et al.*, 2003). Peatland-inhabiting testate amoebae have been receiving increased attention from palaeoecologists and restoration ecologists because taxa generally occupy discrete ecological niches related to moisture conditions, making them good indicators of past and ongoing hydrological change (Warner & Chmielewski, 1992; Buttler *et al.*, 1996; Mitchell *et al.*, 2000; Charman, 2001; Davis & Wilkinson, 2004).

Palaeoenvironmental work has been focused on developing, refining, and applying transfer functions to infer past surface-

moisture conditions from fossil assemblages. Calibration data sets have now been developed and applied in many regions, including Europe (Woodland *et al.*, 1998; Mitchell *et al.*, 1999; Chiverrell, 2001; Hendon *et al.*, 2001; Langdon *et al.*, 2003), New Zealand (Charman, 1997; Wilmhurst *et al.*, 2003), and North America (Charman & Warner, 1992, 1997; Warner & Charman, 1994; Booth, 2002; Booth & Jackson, 2003; Booth *et al.*, 2004). However, there have been few quantitative studies of geographical patterns of testate amoeba distribution (e.g. Smith & Wilkinson, 1987, 1990; Wilkinson, 1994, 2001; Mitchell *et al.*, 2000), and even fewer direct comparisons of the environmental tolerances of testate amoeba taxa in different regions (Charman & Warner, 1997; Booth, 2001; Lamentowicz & Mitchell, 2004). Because species–environment relationships are the bases of environmental and palaeoenvironmental applications, stability of these relationships in geographical space is important for widespread applicability and reliability (Charman, 2001).

Recent studies in North America have investigated the ecology of testate amoebae inhabiting *Sphagnum*-dominated peatlands

in the western Great Lakes and Rocky Mountain regions (Booth, 2001, 2002; Booth *et al.*, 2005). In this paper, we compare testate amoebae inhabiting *Sphagnum*-dominated peatlands of these two regions, develop hypotheses to explain the differences, and determine if taxa occupy similar ecological niches with respect to substrate moisture in both places.

### STUDY SITES

Samples were collected from 11 peatlands in Michigan and 15 in the Rocky Mountains (Fig. 1). All peatlands sampled were *Sphagnum*-dominated, although a few samples were collected from local areas where *Sphagnum* was absent. Samples collected in Michigan spanned the gradient from ombrotrophic to relatively minerotrophic sites, and included a raised bog, several kettle peatlands, and two coastal peatland complexes adjacent to Lake Superior. *Sphagnum*-dominated peatlands are less common in the Rocky Mountains, although *Sphagnum* is often abundant in 'iron fens' of central and southern Colorado, where the groundwater is highly acidic and rich in dissolved iron and sulphur (Carsey *et al.*, 2003). *Sphagnum* also occurs in relatively isolated basins, particularly on floating peat mats, in a variety of landscape settings in Colorado, western Wyoming, and eastern Idaho. Samples were collected from iron fens, floating mats, and grounded peat mats in the Rocky Mountains. Characteristics of the peatlands in both regions are shown in Table 1. Additional information on the vegetation of the sampled peatlands can be found elsewhere (Booth, 2002; Booth *et al.*, 2005).

### METHODS

#### Field and laboratory methods

The same methods were used to collect and analyse testate amoeba assemblages in the two regions. Multiple samples were collected from within each peatland in an effort to capture the full range of hydrological variability (e.g. hummocks, hollows, pools). At each sampling site, ~10 cm<sup>3</sup> of *Sphagnum* moss was collected from the brown portion of the *Sphagnum* stem directly

below the green, chlorophyllous portion. Samples from this portion of the stem contain higher diversity than the upper portions (Mitchell & Gilbert, 2004), and have often been used for palaeohydrological calibration data sets (e.g. Warner & Charman, 1994; Charman & Warner, 1997; Charman, 1997; Woodland *et al.*, 1998). At sampling sites where *Sphagnum* was absent, we collected ~10 cm<sup>3</sup> of the surface peat for testate amoeba analysis. Various environmental variables (e.g. water-table depth, pH, conductivity) were measured at each sampling site on the day of sample collection, although in this paper we only discuss environmental variables that were found to be the dominant controls on testate amoeba distribution; these include water-table depth, peat percent moisture, and pH (Booth, 2002; Booth *et al.*, 2005). Peatlands of the Great Lakes region were sampled in June and July of 2000, and sampling in the Rocky Mountain region was conducted in June and July of 2002.

Testate amoebae were isolated from moss and substrate samples using standard methods (Hendon & Charman, 1997), by boiling and sieving the samples through nested sieves of 355 µm and 15 µm. The material between 15 and 355 µm in size was mounted in glycerol, and slides were scanned until a total of at least 150 testate amoebae were identified and counted. R.K. Booth performed the analysis on samples from the Great Lakes, and J.R. Zygmunt analysed the samples from the Rocky Mountains. The relative abundance of each taxon was calculated as a percentage of the total counted. The rotifer, *Habrotricha angusticollis*, was included in the analysis because it is commonly found in association with testate amoebae and has been included in other studies (e.g. Charman, 1997; Mitchell *et al.*, 1999).

#### Taxonomy

Biogeographical and ecological research on peatland-inhabiting testate amoebae has been limited by the different taxonomic approaches of various research groups (Charman, 1999). However, comparisons between regions can be made if some taxonomic harmonization, or lumping of similar taxa, is applied. In the present study, taxonomy was based solely on test morphology, as

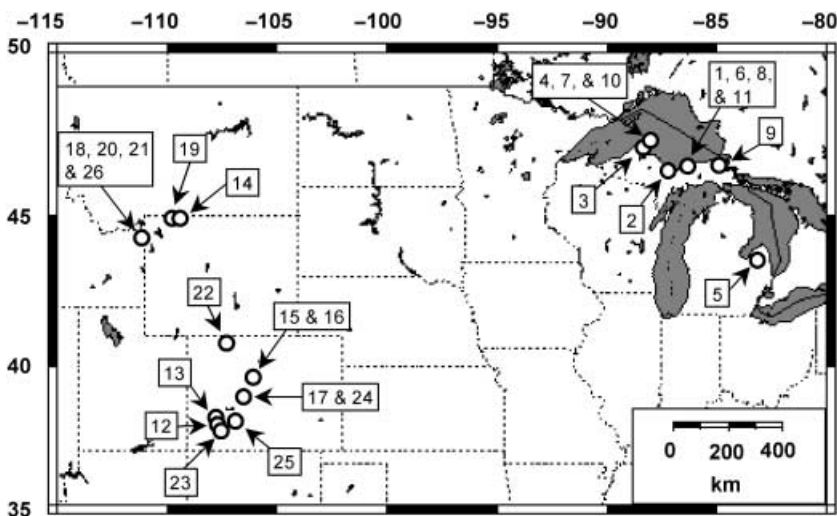


Figure 1 Map showing approximate locations of *Sphagnum*-dominated peatlands that were sampled in the Great Lakes and Rocky Mountain regions. Characteristics of each peatland are listed in Table 1.

**Table 1** Characteristics of the sampled peatlands in the Rocky Mountain (RM) and western Great Lakes (GL) regions, including the range of environmental variables measured, elevation, number of testate amoeba samples collected (n), and *Sphagnum* species. Negative values of water table depth refer to sites with standing water. Conductivity was only measured in the Rocky Mountains. Locations of peatlands are shown in Fig. 1

Site #	Site name and location	Elevation (m)	pH	Percent moisture	Depth to water table (cm)	Conductivity ( $\mu\text{S}/\text{cm}$ )	n	Peatland type and <i>Sphagnum</i> species
1	Adams Trail Peatland (GL) (46°32'52" N, 86°3'32" W)	280	3.7–4.0	72.5–87.8	12 to –2	—	10	Kettle peatland (floating) containing <i>S. papillosum</i> , <i>S. magellanicum</i> , <i>S. capillifolium</i> , <i>S. angustifolium</i> , <i>S. rubellum</i> , <i>S. viridum</i> , and <i>S. isoviitae</i>
2	Au Train Bay Peatlands (GL) (46°25'48" N, 86°51'36" W)	190	3.5–6.4	64.1–86.3	29 to –27	—	22	Coastal ridge-swale peatland (grounded) containing <i>S. papillosum</i> , <i>S. fallax</i> , <i>S. magellanicum</i> , <i>S. majus</i> ssp. <i>norvegicum</i> , <i>S. angustifolium</i> , and <i>S. pulchrum</i>
3	Grand Traverse Bay Peatlands (GL) (47°9'56" N, 88°15'17" W)	180	3.7–5.2	40.0–80.8	45–5	—	8	Coastal ridge-swale peatland (grounded) containing <i>S. pulchrum</i> , <i>S. papillosum</i> , <i>S. fallax</i> , <i>S. angustifolium</i> , and <i>S. majus</i> ssp. <i>majus</i>
4	Independence Peatland (GL) (47°25'9" N, 88°0'37" W)	300	3.7–4.4	56.6–85.9	36 to –14	—	29	Kettle peatland (floating) containing <i>S. viridum</i> , <i>S. majus</i> ssp. <i>norvegicum</i> , <i>S. magellanicum</i> , <i>S. fuscum</i> , <i>S. papillosum</i> , <i>S. angustifolium</i> , and <i>S. majus</i> ssp. <i>majus</i>
5	Minden Bog (GL) (43°36'43" N, 82°50'10" W)	240	3.4–3.6	38.5–78.9	48–12	—	14	Raised bog with <i>S. palustre</i> , <i>S. russowii</i> , <i>S. papillosum</i> , <i>S. isoviitae</i> , <i>S. fallax</i> , <i>S. magellanicum</i> , <i>S. bartlettianum</i> , <i>S. angustifolium</i> , and <i>S. capillifolium</i>
6	North Rhody Peatland (GL) (46°34'57" N, 86°4'20" W)	290	3.8–4.3	60.7–76.3	27–13	—	12	Kettle peatland (grounded) with <i>S. papillosum</i> , <i>S. magellanicum</i> , and <i>S. angustifolium</i>
7	Partridge Lake Peatland (GL) (47°25'11" N, 88°0'27" W)	300	3.5–5.4	63.3–85.0	26 to –10	—	20	Floating mat on edge of lake with <i>S. angustifolium</i> , <i>S. magellanicum</i> , <i>S. fuscum</i> , <i>S. isoviitae</i> , <i>S. russowii</i> , and <i>S. majus</i> ssp. <i>norvegicum</i>
8	South Rhody Peatland (GL) (46°33'57" N, 86°4'30" W)	290	3.7–4.2	76.3–82.0	25–2	—	16	Kettle peatland (grounded) containing <i>S. magellanicum</i> , <i>S. majus</i> ssp. <i>majus</i> , <i>S. cuspidatum</i> , <i>S. viridum</i> , <i>S. fallax</i> , <i>S. angustifolium</i> , <i>S. papillosum</i> , and <i>S. majus</i> ssp. <i>norvegicum</i>
9	Tahquamenon Bay Peatlands (GL) (46°28'31" N, 84°59'41" W)	190	4.2–5.1	67.3–78.7	50–9	—	4	Coastal ridge-swale peatland (grounded) containing <i>S. centrale</i> , <i>S. papillosum</i> , <i>S. magellanicum</i> , <i>S. fallax</i> , and <i>S. russowii</i>
10	Uncle Sam Peatland (GL) (47°25'9" N, 88°0'59" W)	300	3.3–3.7	50.5–62.6	50–48	—	8	Kettle peatland (grounded) containing <i>S. magellanicum</i> , <i>S. angustifolium</i> , <i>S. russowii</i> , and <i>S. girgensohnii</i>
11	West Adams Trail Peatland (GL) (46°33'12" N, 86°6'17" W)	280	3.9–3.9	74.4–80.1	19–19	—	4	Kettle peatland (grounded) containing <i>S. magellanicum</i> , <i>S. fallax</i> , <i>S. papillosum</i> , and <i>S. angustifolium</i>
12	Burro Bridge Iron Fen (RM) (37°50'47" N, 107°43'36" W)	2993	3.0–3.7	44.9–75.1	50–13	880–3400	10	Iron fen containing <i>S. russowii</i> and <i>S. angustifolium</i>
13	Chatanooga Iron Fen (RM) (36°57'41" N, 107°41'33" W)	3109	3.3–4.1	39.7–79.5	50–0	220–3600	15	Iron fen containing <i>S. russowii</i> , <i>S. angustifolium</i> , <i>S. fuscum</i> , and <i>S. balticum</i>
14	East Lily Peatland (RM) (44°57'15" N, 109°41'47" W)	2469	3.9–5.0	49.6–80.6	30–0	50–400	10	Floating mat around lake containing <i>S. russowii</i> , <i>S. angustifolium</i> , <i>S. squarrosus</i> , and <i>S. warnstorffii</i>
15	Henderson Peatland A (RM) (39°22'0" N, 106°34'57" W)	3170	4.4–5.0	61.3–85.4	50 to –1	20–1380	8	Kettle peatland (grounded) with <i>S. platyphyllum</i>
16	Henderson Peatland B (RM) (39°21'15" N, 106°36'9" W)	3200	3.7–4.9	67.1–77.7	33–2	100–330	8	Kettle peatland (grounded) with <i>S. russowii</i> , <i>S. platyphyllum</i> , and <i>S. warnstorffii</i>

Table 1 *Continued*

Site #	Site name and location	Elevation (m)	pH	Percent moisture	Depth to water table (cm)	Conductivity ( $\mu\text{S}/\text{cm}$ )	<i>n</i>	Peatland type and <i>Sphagnum</i> species
17	Keystone Iron Fen (RM) (38°52'1" N, 107°2'23" W)	2865	3.3–3.7	51.6–80.5	40–1	400–2000	11	Iron fen dominated by <i>S. russowii</i> , <i>S. teres</i> , and <i>S. fimbriatum</i>
18	Lilypad Peatland (RM) (44°9'52" N, 111°0'30" W)	1948	3.73–5.60	65.3–85.5	27 to –4	70–290	15	Floating mat around lake with <i>S. squarrosum</i> , <i>S. teres</i> , and <i>S. platyphyllum</i>
19	Little Moose Lake Peatland (RM) (44°58'33" N, 109°45'25" W)	2426	4.3–6.1	65.1–82.9	33–1	110–360	13	Floating mat around lake with <i>S. russowii</i>
20	Lizard Peatland (RM) (44°9'20" N, 111°1'23" W)	1942	4.43–5.76	67.4–75.1	26 to –2	60–230	5	Floating mat around lake with <i>S. squarrosum</i> and <i>S. platyphyllum</i>
21	Robinson Peatland (RM) (44°10'2" N, 111°4'15" W)	1978	3.44–4.47	66.4–83.8	13 to –5	10–250	15	Floating mat within lake containing <i>S. russowii</i> , <i>S. squarrosum</i> , <i>S. platyphyllum</i> , <i>S. fuscum</i> , and <i>S. subsecundum</i>
22	Shafer Lake Peatland (RM) (40°51'56" N, 106°36'18" W)	2739	3.6–5.1	48.2–84.6	41 to –2	40–450	10	Floating mat around lake with <i>S. squarrosum</i> and <i>S. teres</i>
23	South Mineral Iron Fen (RM) (37°48'57" N, 107°43'23" W)	2908	2.9–3.6	40.9–62.0	50–50	940–3260	8	Iron fen with <i>S. russowii</i> , <i>S. angustifolium</i> , and <i>S. fuscum</i>
24	Splains Gulch Lake Peatland (RM) (38°50'3" N, 107°4'32" W)	3164	3.9–4.5	68.1–76.3	24–11	120–500	7	Floating mat around lake with <i>S. russowii</i> , <i>S. squarrosum</i> , <i>S. teres</i> , and <i>S. fimbriatum</i>
25	Wager Gulch Iron Fen (RM) (37°52'41" N, 107°22'7" W)	3365	3.1–3.9	48.4–72.5	50–12	700–2500	10	Iron fen with <i>S. russowii</i>
26	West Robinson Peatland (RM) (44°10'2" N, 111°4'30" W)	1978	3.6–4.3	69.6–84.2	14–0	30–70	5	Floating mat within lake containing <i>S. russowii</i> , <i>S. squarrosum</i> , and <i>S. fuscum</i>

it is in fossil studies, and follows Charman *et al.* (2000), except as noted in Booth (2002). Both live and dead tests were included in the analyses, and samples integrate the accumulation of tests over several years. In a few cases, the taxa defined in this study combine multiple taxa identified in the original studies (Table 2). Given that the complete range of morphological variability in the testate amoebae has not been adequately described, this conservative approach reduces the possibility that differences between the two regions will be inflated because of a few morphologically variable taxa. However, because morphological variability in the testate amoebae is often environmentally forced (e.g. Wanner & Meisterfeld, 1994; Bobrov *et al.*, 1995, 2002; Wanner, 1999; Booth, 2001), our lumping of taxa may obscure some patterns of taxa–environmental relationships between the two regions, particularly for taxa that are extremely variable in morphology.

### Analytical methods

To minimize the influence of extremely rare taxa, only those present in at least 15 samples were included in the analysis. Nine rare taxa were eliminated and the resulting data set contained 49 taxa. Outlier analysis was performed on the combined datasets from the two regions using PC-ORD (McCune & Mefford, 1999) and Sorenson's distance measure, removing samples with species

data more than two standard deviations from the mean. The outlier samples were from both wet and dry habitats, included samples from both regions, and were generally characterized by high relative abundance of only one or two taxa. Three samples from Henderson Peatland A were also removed because of difficulties with accurately measuring the water-table depth, which may have been related to the low porosity of a shallow clay/silt subsurface layer that extended from the upland into the edge of the peatland where those samples were collected. A total of 19 samples were removed, and the resulting data set consisted of 281 samples, with 136 and 145 samples, respectively, from the Rocky Mountain and Great Lakes regions.

To compare testate amoeba assemblages and ecology between the two regions, we used nonmetric multidimensional scaling (NMDS) (Kruskal, 1964; Mather, 1976; McCune & Grace, 2002), which has considerable advantages over other ordination methods because it does not make assumptions regarding underlying species distributions along compositional gradients (Clarke, 1993; McCune & Grace, 2002). We used Sorenson's distance measure in our analyses, along with the automated search feature of PC-ORD (McCune & Mefford, 1999) to identify the best solution and dimensionality. The automated search feature performed 40 runs with real data, each with a random starting configuration and consisting of solutions for one through six

**Table 2** Taxonomic groupings used in this study, which in some cases group together morphologically similar taxa identified from western Great Lakes and Rocky Mountain peatlands. Taxonomy follows Charman *et al.* (2000), except as noted in Booth (2002)

Taxonomic groupings in this study	Taxa included from the original studies in the Great Lakes and Rocky Mountain regions (Booth, 2002; Booth <i>et al.</i> , 2005)
<i>Amphitrema flavum</i>	<i>Amphitrema flavum</i> (Archer) Penard
<i>Amphitrema wrightianum</i>	<i>Amphitrema wrightianum</i> Archer
<i>Arcella artocrea</i> type	<i>Arcella artocrea</i> Leidy type, <i>Arcella catinus</i> Penard type
<i>Arcella discoides</i> type	<i>Arcella discoides</i> Ehrenberg type
<i>Arcella hemisphaerica</i>	<i>Arcella hemisphaerica</i> Perty
<i>Arcella vulgaris</i> type	<i>Arcella vulgaris</i> Ehrenberg, <i>Arcella crenulata</i> Deflandre, <i>Arcella gibbosa</i> Penard type
<i>Assulina muscorum</i>	<i>Assulina muscorum</i> Greeff
<i>Assulina seminulum</i>	<i>Assulina seminulum</i> (Ehrenberg) Leidy
<i>Bullinularia indica</i>	<i>Bullinularia indica</i> Penard
<i>Centropyxis aculeata</i> type	<i>Centropyxis aculeata</i> (Ehrenberg) von Stein type
<i>Centropyxis cassis</i> type	<i>Centropyxis cassis</i> (Wallich) Deflandre type
<i>Centropyxis ecornis</i> Ehrenberg type	<i>Centropyxis ecornis</i> Ehrenberg type
<i>Centropyxis platystoma</i> type	<i>Centropyxis platystoma</i> (Penard) Deflandre type
<i>Corythion-Trinema</i> type	<i>Corythion-Trinema</i> type
<i>Cryptodiffugia oviformis</i>	<i>Cryptodiffugia oviformis</i> Penard
<i>Cyclopyxis arcelloides</i> type	<i>Cyclopyxis arcelloides</i> (Penard) Deflandre type, <i>Phryganella acropodia</i> (Hertwig & Lesser) type <i>Cyclopyxis Kahli</i> Deflandre, <i>Diffugia</i> sp. A
<i>Diffugia acuminata</i> type	<i>Diffugia acuminata</i> Ehrenberg type
<i>Diffugia globulosa</i> type	<i>Diffugia globulosa</i> Dujardin type, <i>Diffugia urceolata</i> Carter
<i>Diffugia leidy</i>	<i>Diffugia leidy</i> Wailes
<i>Diffugi lucida</i> type	<i>Diffugia lucida</i> type
<i>Diffugia oblonga</i> type	<i>Diffugia oblonga</i> Ehrenberg type, <i>Diffugia bacillifera</i> Penard, <i>Diffugia rubescens</i> Penard
<i>Diffugia oviformis</i> type	<i>Diffugia oviformis</i> Cash type
<i>Diffugia pulex</i>	<i>Diffugia pulex</i> Penard
<i>Euglypha rotunda</i> type	<i>Euglypha rotunda</i> Wailes and Penard type
<i>Euglypha strigosa</i> type	<i>Euglypha strigosa</i> (Ehrenberg) Leidy type, <i>Euglypha cristata</i> Leidy
<i>Euglypha tuberculata</i> type	<i>Euglypha tuberculata</i> Dujardin type
<i>Habrotrocha angusticollis</i>	<i>Habrotrocha angusticollis</i> Murray
<i>Heleopera rosea</i> type Leidy	<i>Heleopera Petricola</i> Leidy, <i>Heleopera rosea</i> Penard
<i>Heleopera sphagni</i>	<i>Heleopera sphagni</i> (Leidy) Cash and Hopkinson
<i>Heleopera sylvatica</i>	<i>Heleopera sylvatica</i> Penard
<i>Hyalosphenia elegans</i>	<i>Hyalosphenia elegans</i> Leidy
<i>Hyalosphenia papilio</i>	<i>Hyalosphenia papilio</i> Leidy
<i>Hyalosphenia subflava</i>	<i>Hyalosphenia subflava</i> Cash and Hopkinson
<i>Nebela carinata-marginata</i> type	<i>Nebela carinata</i> (Archer) Leidy, <i>Nebela marginata</i> Penard
<i>Nebela collaris</i> type	<i>Nebela collaris</i> (Ehrenberg) Leidy
<i>Nebela galeata</i>	<i>Nebela galeata</i> Penard
<i>Nebela griseola</i>	<i>Nebela griseola</i> Penard
<i>Nebela militaris</i>	<i>Nebela militaris</i> Penard, <i>Nebela penardiana</i> Deflandre
<i>Nebela tincta-parvula</i> type	<i>Nebela parvula</i> Cash and Hopkinson, <i>Nebela tincta</i> (Leidy) Awerintzew
<i>Nebela tubulosa</i> type	<i>Nebela tubulosa</i> Penard
<i>Nebela vitraea</i> type	<i>Nebela vitraea</i> Penard type
<i>Nebela wailesi</i>	<i>Nebela wailesi</i> Deflandre
<i>Placocista spinosa</i>	<i>Placocista spinosa</i> (Carter) Leidy
<i>Pseudodiffugia fascicularis</i> type	<i>Pseudodiffugia fascicularis</i> Penard type
<i>Pseudodiffugia fulva</i> type	<i>Pseudodiffugia fulva</i> (Archer) Penard type
<i>Quadrulella symmetrica</i>	<i>Quadrulella symmetrica</i> (Wallich) Schulze
<i>Sphenoderia lenta</i>	<i>Sphenoderia lenta</i> Schlumberger
<i>Trigonopyxis arcula</i>	<i>Trigonopyxis arcula</i> (Leidy) Penard
<i>Trigonopyxis minuta</i>	<i>Trigonopyxis minuta</i> Schönborn and Peschke

dimensions. Fifty runs with randomised data were then performed and statistics on the final stress at each dimensionality were accumulated. The best solution for each dimensionality was identified by comparing the final stress values.

To further explore the consistency of relationships between taxa and water-table depth in the two regions, we defined the water-table depth optima for taxa independently in each region using a weighted average model with the software package CALIBRATE (Juggins, 1998). We then compared the water-table depth optima for taxa in the two regions using linear regression.

## RESULTS

A two-dimensional NMDS solution was selected because additional dimensions resulted in only small reductions in stress. We selected the two-dimensional solution with the lowest final stress (final stress = 18.66,  $P < 0.02$ ), and this ordination provided a two-dimensional representation of 78% of the variation in the data set, with 34% loaded on axis 1 and 44% loaded on axis 2. Axis 1 was primarily related to compositional differences between communities in the two regions, with Great Lakes and Rocky Mountain samples clustering on the left and right of the axis, respectively (Fig. 2a). Assemblage variability along axis 2 was strongly related to substrate moisture (water-table depth, percent moisture), and secondarily related to pH (Fig. 2a, Table 3). Relationships among environmental variables and axis 2 sample scores were stronger within each region than they were within the entire data set (Table 3). A total of 37 taxa were encountered in samples from the Rocky Mountain region and 47 from the Great Lakes region, and the relative abundance and frequency of some taxa varied considerably between the two regions (Table 4). The number of taxa encountered in each sample was also higher in the Great Lakes region (Fig. 3).

Taxa that were observed in both regions are generally positioned similarly along axis 2 of the NMDS ordination, suggesting that they occur in similar habitats in the two places, at least with respect to substrate moisture (Fig. 2). Environmental data collected for samples from the two regions were similar, except for the average percent moisture of peat samples which was drier in the Rocky Mountain samples (Fig. 4). Quantitative comparison of water-table depth optima for taxa common to both regions

also suggests that ecological niches with respect to substrate moisture are generally similar in both places, although some small differences do occur (Fig. 5). However, some taxa have a broader tolerance range in one of the regions. For example, *Assulina muscorum* was abundant in habitats of widely varying moisture content in the Great Lakes region, but was more abundant in drier habitats in the Rocky Mountains region (Fig. 2h).

## DISCUSSION

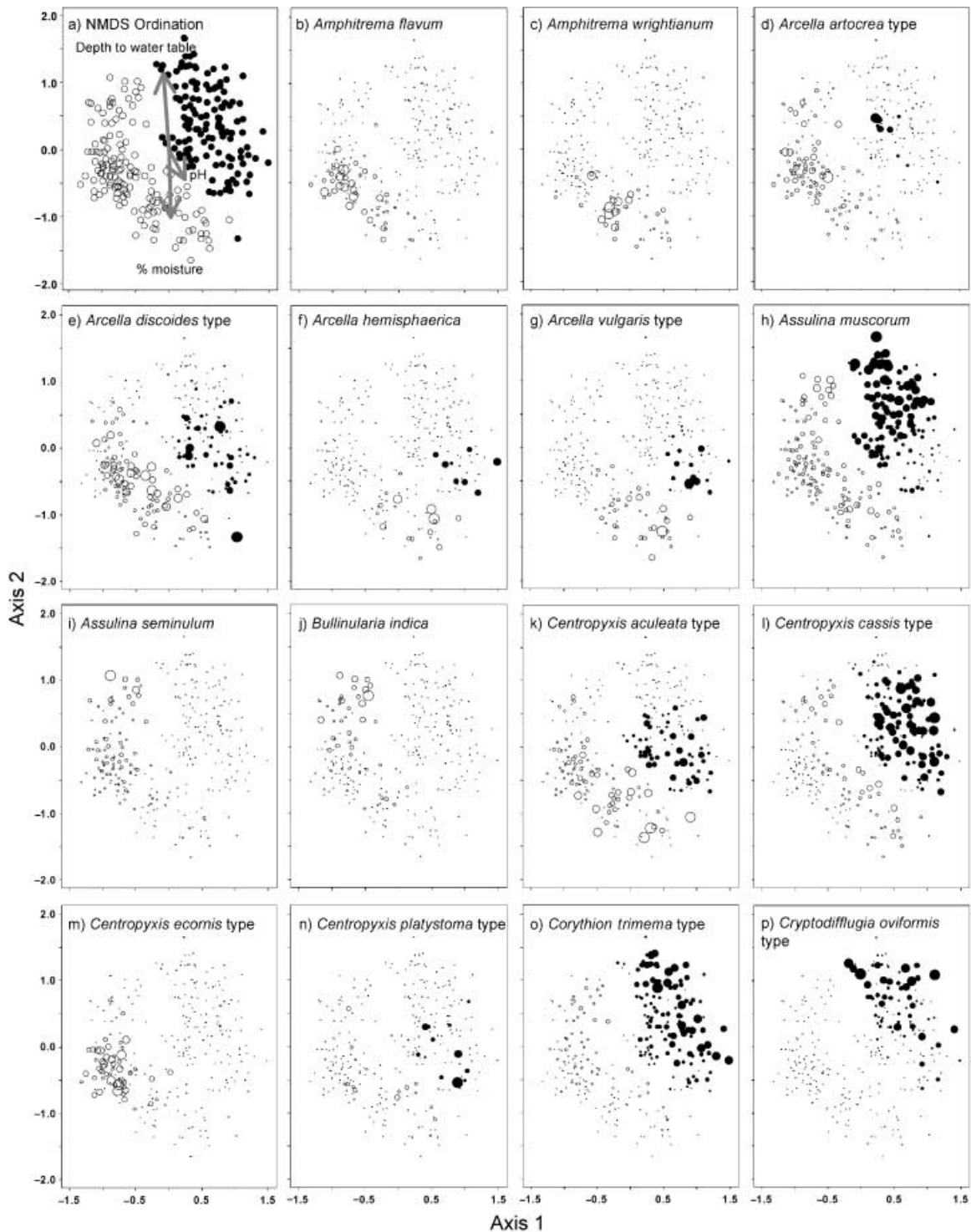
### Biogeographical patterns between regions

Testate amoebae react quickly to environmental change and play an important role in the microbial food web, making them important tools in environmental monitoring and palaeoenvironmental reconstruction (Gilbert *et al.*, 1998; Charman, 2001; Mitchell *et al.*, 2003). Understanding continental and subcontinental patterns of testate amoeba distribution is therefore critical to our environmental interpretation of changes in modern and fossil assemblages. Testate amoebae inhabiting peatlands of the Great Lakes and Rocky Mountain regions have not been very well studied, although more work has been accomplished in the Great Lakes region (Warner & Charman, 1994; Booth, 2001, 2002). In the Rocky Mountains, the most recent research was performed in the late 1800s (Leidy, 1879; Penard, 1891). More data are needed from peatlands throughout North America and elsewhere, before firm conclusions regarding geographical distribution patterns, and their underlying controls, can be reached. However, our results reveal some interesting distribution patterns between the Great Lakes and Rocky Mountain regions, and allow us to develop some preliminary hypotheses to explain these patterns.

The most striking difference between the composition of testate amoeba assemblages in the two regions is the absence or rarity of several taxa in the Rocky Mountain region that are very common in *Sphagnum*-dominated peatlands of the Great Lakes region. The absence in the Rocky Mountain region of several taxa common elsewhere was observed by Penard (1891) in his study of testate amoebae inhabiting high-elevation (3000–3200 m) wetlands in Colorado. He noted the conspicuous absence of several taxa, including *Hyalosphenia papilio*, *Nebela flabulellum*, and *Assulina seminulum*. However, recent studies suggest that *N. flabulellum* may not be as widespread as Penard (1891) suggested (Charman & Warner, 1997; Mitchell *et al.*, 2000). We did not encounter *N. flabulellum* or *A. seminulum* in our Rocky Mountain samples, although we did encounter *H. papilio*, which was restricted to samples collected from floating peat mats in the region. This suggests that the hydrologic stability of floating mats may be particularly important for this taxon to survive in the Rocky Mountain region. Several other taxa that were frequent in peatlands of the Great Lakes were also conspicuously absent in the Rocky Mountains, including *Amphitrema flavum*, *Amphitrema wrightianum*, *Bullinularia indica*, *Heleopera sylvatica*, *Nebela carinata-marginata* type, and *Nebela griseola* (Table 4). Other common taxa in the Great Lakes were extremely rare in the Rocky Mountains, including *Hyalosphenia elegans*, *Diffflugia acuminata*, and *Diffflugia leidy* (Table 4). Taxa that were

**Table 3** Linear correlations among environmental variables and NMDS axes ( $r^2$ )

Samples	Variable	Axis 1	Axis 2
All samples	Water-table depth	0.04	0.57
	Percent moisture	0.01	0.50
	pH	0.12	0.22
Rocky Mountain samples	Water-table depth	0.17	0.64
	Percent moisture	0.14	0.46
	pH	0.28	0.44
Great Lakes samples	Water-table depth	0.29	0.74
	Percent moisture	0.19	0.62
	pH	0.24	0.29



**Figure 2** NMDS ordination of testate amoeba assemblages in the Great Lakes (open circles) and Rocky Mountain (closed circles) regions, and (b–vv) abundance of each taxon within samples of the two regions. Correlations between the ordination space and environmental variables are shown with arrows in (a), with the strength of the correlation corresponding to the length of the arrow. Correlations are also listed in Table 3. In the abundance plots (b–vv), the size of the circle is proportional to the relative abundance of the taxon, and is determined by dividing the total abundance range of each taxon into equal-sized segments. Samples where the taxon was absent are indicated with small dots. Two taxa that were restricted to the Great Lakes region (*Nebela galeata*, *Diffflugia oviformis* type) are not shown.

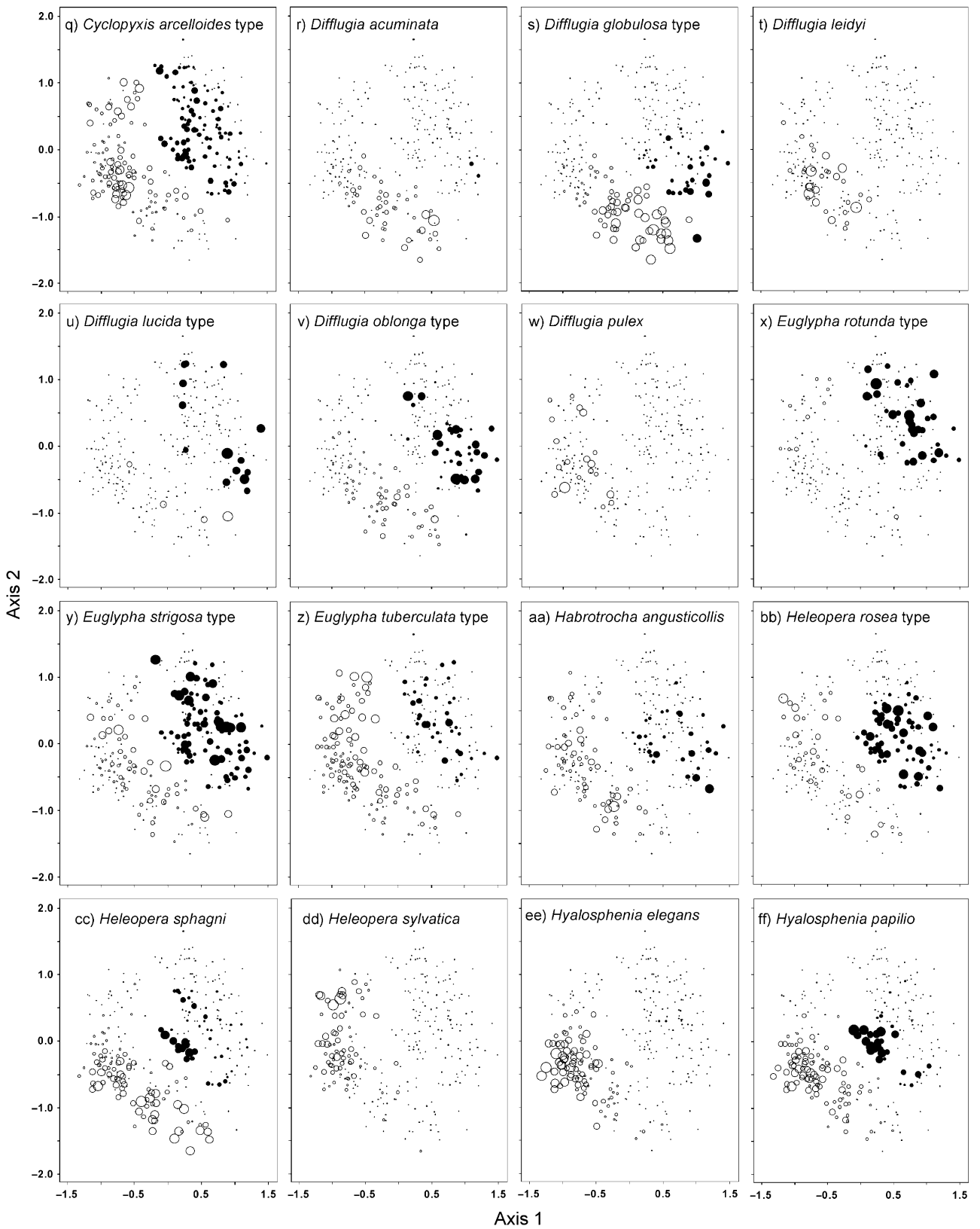


Figure 2 Continued

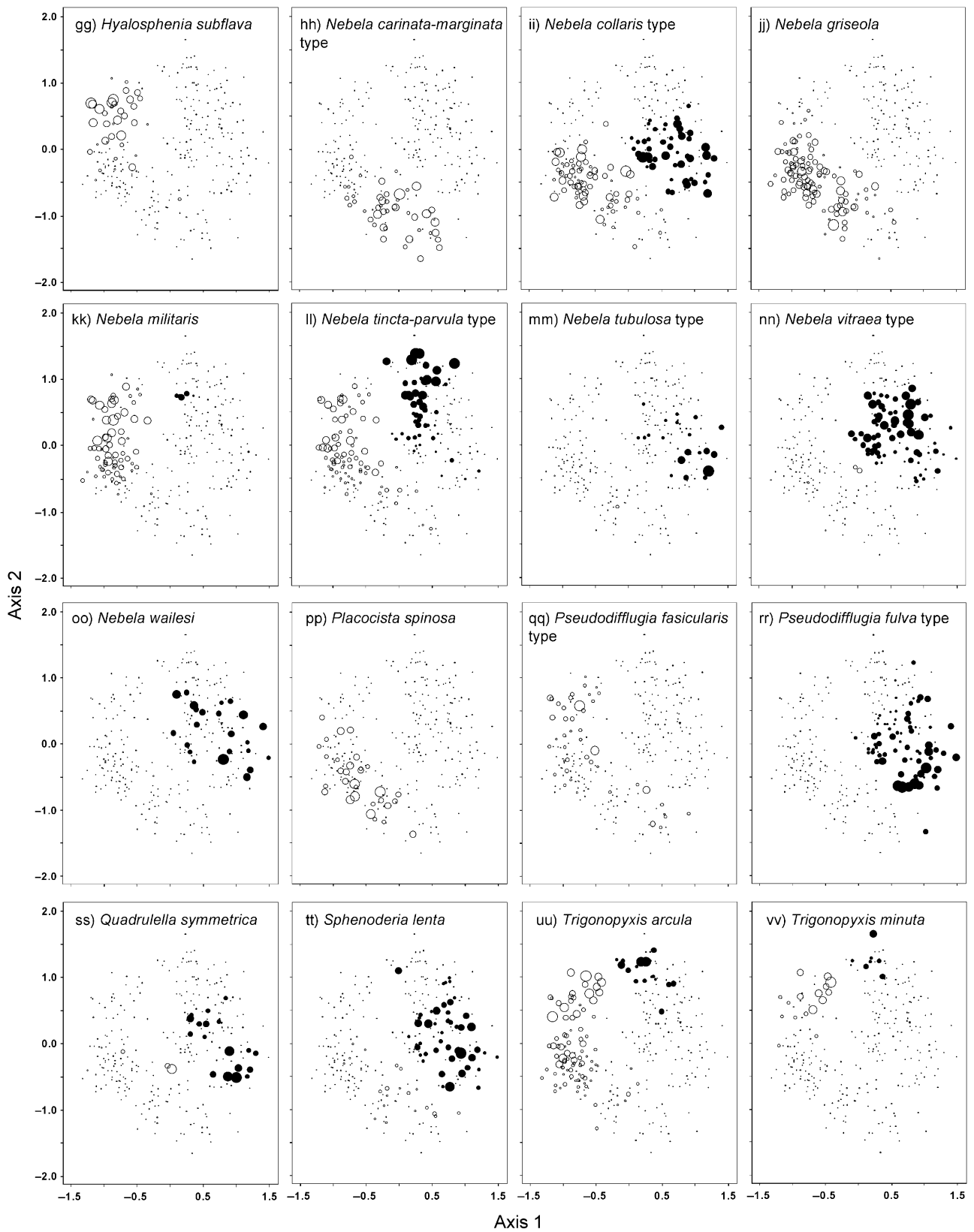
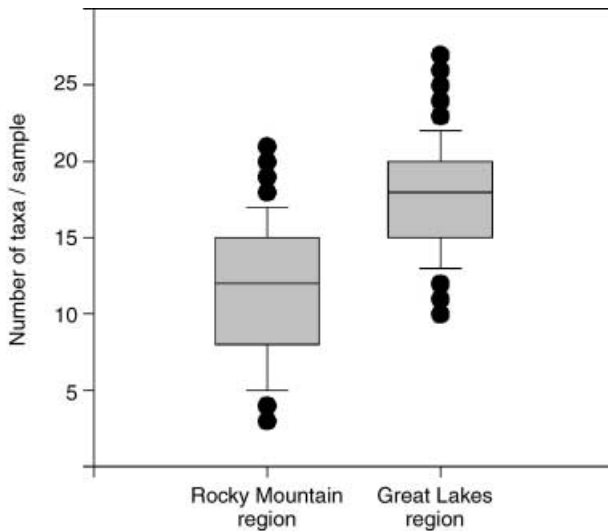


Figure 2 Continued

**Table 4** Taxa that were rare or absent in one of the regions. Rare taxa were defined as those that were present in less than five samples from a region

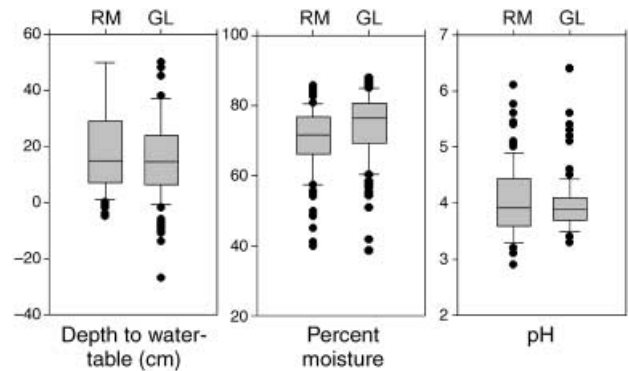
Region	Taxa not encountered	Taxa infrequently encountered
RM	<i>Amphitrema flavum</i> , <i>Amphitrema wrightianum</i> , <i>Assulina seminulum</i> , <i>Bullinularia indica</i> , <i>Centropyxis ecornis</i> type, <i>Heleopera sylvatica</i> , <i>Hyalosphenia subflava</i> , <i>Nebela carinata-marginata</i> type, <i>Nebela galeata</i> , <i>Nebela griseola</i> , <i>Placocista</i> <i>spinosa</i> , <i>Pseudodifflugia fascicularis</i> type,	<i>Difflugia acuminata</i> , <i>Difflugia leidyi</i> , <i>Difflugia</i> <i>oviformis</i> type, <i>Difflugia pulex</i> , <i>Hyalospheniaelegans</i> , <i>Nebela militaris</i>
GL	<i>Pseudodifflugia fulva</i> type, <i>Nebela wailsei</i>	<i>Cryptodifflugia oviformis</i> , <i>Nebela tubulosa</i> type, <i>Nebela</i> <i>vitreae</i> type, <i>Quadrullella symmetrica</i>



**Figure 3** Box plots comparing species richness in samples from the Great Lakes and Rocky Mountain regions. Species richness was significantly higher in samples from the Great Lakes region (*t*-test,  $P < 0.01$ ).

absent or rare in the Rocky Mountains include both those that prefer very wet and those that prefer very dry habitats, indicating that simple moisture differences alone cannot explain the patterns.

Why are so many frequently encountered taxa in the Great Lakes region absent or rare in the Rocky Mountains? Global species distribution patterns have often been attributed to dispersal limitation or lack of suitable habitats, and both of these factors have been suggested as potential causes of testate amoeba distribution patterns (Smith, 1982, 1996; Wilkinson, 1994, 2001). However, dispersal limitation appears to be an unlikely explanation for most biogeographical patterns of testate amoebae because of their small size and ability to encyst for long periods of time. Testate amoebae less than 100  $\mu\text{m}$  in size have been shown to be cosmopolitan in distribution (Wilkinson, 2001), and with the exception of *Nebela carinata-marginata*, all taxa absent in the Rocky Mountains are typically smaller than 100  $\mu\text{m}$ . Also, most of the taxa absent from the Rocky Mountains are not only common in the Great Lakes region, but also in other continents, including Europe, Asia, and New Zealand (e.g. Tolonen *et al.*,

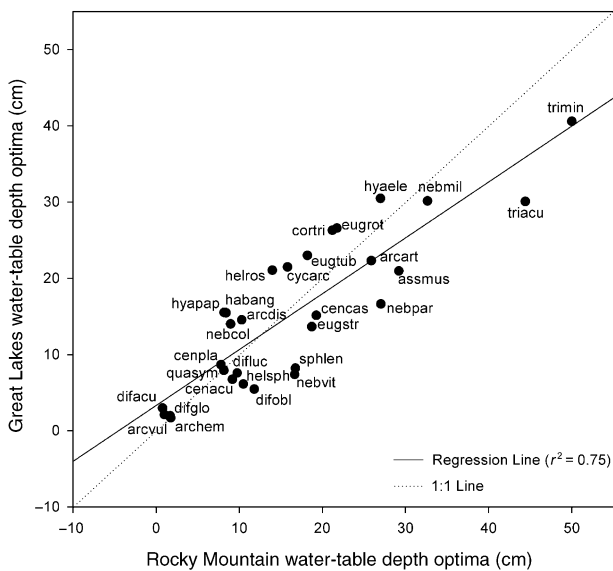


**Figure 4** Box plots comparing environmental data associated with testate amoeba samples collected from *Sphagnum*-dominated peatlands in the Great Lakes (GL) and Rocky Mountain (RM) regions. Only percent moisture was found to be significantly different in samples between the two regions (*t*-test,  $P < 0.01$ ).

1992; Charman, 1997; Woodland *et al.*, 1998; Mitchell *et al.*, 1999, 2000; Bobrov *et al.*, 2002; Wilmhurst *et al.*, 2003).

We hypothesize that absence of suitable habitats in the Rocky Mountains is the most likely reason for the lack of many taxa that are common in *Sphagnum*-dominated peatlands of the Great Lakes region. Differences in the trophic status of peatlands in the two regions may be particularly important, because taxa that are absent or rare in the Rocky Mountains tend to be associated with oligotrophic and ombrotrophic habitats in other regions. For example, *Amphitrema flavum*, *Bullinularia indica*, *Difflugia leidyi*, *Heleopera sylvatica*, *Assulina seminulum*, and *Nebela griseola* are thought to be more common in relatively nutrient-poor habitats, especially truly ombrotrophic peatlands (Tolonen *et al.*, 1992). The few taxa that were more common in the Rocky Mountains than the Great Lakes region (e.g. *Pseudodifflugia fulva* type, *Nebela wailsei*, *Nebela tubulosa* type, *Nebela vitreae* type, *Quadrullella symmetrica*) tend to be associated with relatively nutrient-rich sites in other regions (Tolonen *et al.*, 1992; Charman *et al.*, 2000).

The potential importance of differences in trophic status is also supported by the known characteristics of peatlands in the two regions. Whereas *Sphagnum*-dominated peatlands are quite common in the Great Lakes region, and span the gradient from ombrotrophic to somewhat minerotrophic, they are relatively



**Figure 5** Comparison of the optimum depth to water table for taxa present in both regions, defined by weighted averaging with the CALIBRATE modelling program (Juggins, 1998).

uncommon in the Rocky Mountains where the warm, dry summers only allow peat accumulation in areas of groundwater discharge or surface drainage (Cooper, 1990, 1996; Cooper & Andrus, 1994). *Sphagnum*-dominated peatlands reach their southern limit in the central Rocky Mountains (Halsey *et al.*, 2000), and their occurrence is often associated with acidic geological substrates, particularly in Colorado (Windell *et al.*, 1986; Carsey *et al.*, 2003). Because *Sphagnum*-dominated peatlands in the Rocky Mountains receive relatively large amounts of groundwater, they can all be classified as fens (Windell *et al.*, 1986). In fact, the dominant species of *Sphagnum* in the Rocky Mountains, *Sphagnum warnstorffii*, has relatively minerotrophic requirements (Windell *et al.*, 1986). However, our environmental measurements did not reveal major differences between peatlands of the two regions, with the exception of peat percent moisture (Fig. 4). The importance of differences in peat percent moisture is difficult to assess because it was only measured on the day amoeba samples were collected, which were in different years in the two regions and during a severe drought in the Rocky Mountains. Conductivity values in the iron fens of the Rocky Mountains were quite high (Table 1), consistent with the strong groundwater influence of these peatlands. However, we did not measure conductivity in the Great Lakes region, so we cannot make quantitative comparisons between them. Future comparative studies of testate amoebae should attempt to measure a larger suite of environmental variables, particularly those associated with trophic status (e.g. conductivity, pH, Ca, N).

Indirect consequences of climatic differences are probably the ultimate causes of differences in peatland trophic status in the two regions, because climate restricts *Sphagnum* peatlands to areas of relatively high groundwater influence in the Rocky Mountains. However, climate may also play a more direct role in controlling testate amoeba community composition through its

effect on hydroperiod and summer surface moisture conditions. Low summer humidity and strong evaporative potential in the Rocky Mountains may limit the occurrence of some taxa, as suggested by the restriction of *Hyalosphenia papilio* to the relatively stable moisture conditions provided by floating peat mat environments. One other taxon, *Hyalosphenia elegans*, was also restricted to floating peat mats in the Rocky Mountains although we encountered it only in two samples in the region. Both of these taxa are quite common in both floating and nonfloating *Sphagnum*-dominated habitats of the Great Lakes region. The Great Lakes region has wetter and more humid summers, suggesting that moisture stress may prevent these taxa from being more widely distributed in the Rocky Mountains.

The high altitude of the peatlands we sampled in the Rocky Mountains (~1900–3400 m) may also influence testate amoeba community composition. However, some of the taxa that are conspicuously absent in our Rocky Mountain samples do occur in peatlands of moderately high elevation (~900–1400 m) in other regions (Mitchell *et al.*, 1999; Schnitchen *et al.*, 2003). Increased ultraviolet radiation has been shown to affect testate amoeba density (Searles *et al.*, 2001), and the increased ultraviolet radiation at high altitude might affect community composition. Several of the taxa that are conspicuously absent from our Rocky Mountain samples, including *Amphitrema flavum* and *Amphitrema wrightianum*, contain symbiotic zoochlorellae, and therefore might be particularly sensitive to increased ultraviolet radiation. However, *Heleopera sphagni* also contains symbiotic zoochlorellae and was present in our Rocky Mountain samples, even above 3000 m. More descriptions of testate amoeba communities inhabiting *Sphagnum*-peatlands at high elevation are needed, but it is likely that altitude influences testate amoeba communities primarily through its effect on climatic conditions that affect peatland hydrology (e.g. temperature, evaporative potential). For example, a study of New Zealand peatland-inhabiting testate amoebae found that testate amoeba community composition was correlated with altitude, but this was probably because altitude was highly correlated with climatic variables like annual water deficit (Charman, 1997).

In summary, most *Sphagnum*-inhabiting testate amoebae are cosmopolitan in distribution, although important geographical patterns of distribution do occur. For example, Mitchell *et al.* (2000) described patterns of testate amoeba distribution across Europe, and suggested they may be related to the pollution gradient. Wilkinson (1994) showed the importance of climate and geographical barriers in controlling species richness within the genus *Nebela* in the Southern Hemisphere, and the studies of Smith (1982, 1996) have described latitudinal gradients of diversity related to climate. Because of the widespread dispersal of testate amoebae (at least those smaller than 100  $\mu\text{m}$ ), community composition is primarily controlled by local conditions, and ecological studies clearly show that the local condition of greatest importance in *Sphagnum*-dominated peatlands is substrate moisture (e.g. Jung, 1936; Meisterfeld, 1977; Charman & Warner, 1992; Woodland *et al.*, 1998; Lamentowicz & Mitchell, 2004). However, our present study and previous biogeographical comparisons suggest that environmental factors other than moisture

may be equally or more important in controlling distribution patterns at continental and subcontinental spatial scales. Understanding environmental controls on testate amoeba communities at these broader spatial scales will improve our ability to interpret fossil testate amoeba records, particularly peatland records extending further back in time (e.g. early Holocene and glacial).

### Ecology between regions

Although communities of testate amoebae inhabiting *Sphagnum*-dominated peatlands in the Great Lakes and Rocky Mountain regions are somewhat different, many taxa occur in both places and thus we can compare the ecology in the two. Inter-regional comparisons of testate amoeba ecology are difficult, primarily because different methods have been used for the sampling of testate amoebae and the measuring of environmental variables. For example, with a few exceptions (e.g. Woodland *et al.*, 1998), most investigations of testate amoeba ecology have used instantaneous measures of environmental data (i.e. measured only on the day of sampling), making it difficult to perform direct, quantitative comparisons between studies conducted at different times of year, and in different years. However, semiquantitative comparisons can still be made between regions along environmental gradients, even though the actual values of the environmental variables may not be comparable (Booth, 2001). Although our study suffers from instantaneous measurements of environmental variables, all other sampling methods were identical in the two regions.

Our results lend additional support to the idea that moisture tolerances of testate amoeba taxa are consistent among regions, with taxa common to both the Great Lakes and Rocky Mountain regions having very similar optimum water-table depths in both regions (Fig. 5). These results are consistent with other evidence suggesting that the niche occupied by many taxa, at least with respect to substrate moisture, is relatively similar in widespread regions (Charman *et al.*, 2000; Booth, 2001). Some exceptions may exist (Charman & Warner, 1997), but more comparative studies are needed using annual or seasonal measurements of moisture conditions before these differences are fully understood. The similarity between moisture preferences of taxa in the Rocky Mountain and Great Lakes regions is especially compelling given that testate amoeba communities in the two are often quite different (Fig. 2). Thus, even within communities of different composition, and presumably different population and competitive dynamics, the ecological niches of taxa with respect to substrate moisture appear to be conserved.

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