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## Testate amoebae as indicators of hydroseral change: An 8500 year record from Mer Bleue Bog, eastern Ontario, Canada

Suzanne M. Elliott<sup>a,\*</sup>, Helen M. Roe<sup>a</sup>, R. Timothy Patterson<sup>b</sup><sup>a</sup> School of Geography, Archaeology and Palaeoecology, Queen's University Belfast, Belfast BT7 1NN, United Kingdom<sup>b</sup> Ottawa-Carleton Geoscience Centre and Department of Earth Sciences, Carleton University, Ottawa, Ontario K1S 5B6, Canada

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### ABSTRACT

Testate amoebae have been used widely as a proxy of hydrological change in ombrotrophic peatlands, although their response to abiotic controls in other types of mire and fenland palaeo-environments is less well understood. This paper examines the response of testate amoebae to hydroseral and other environmental changes at Mer Bleue Bog, Ontario, Canada, a large ombrotrophic peatland, which evolved from a brackish-water embayment in the early Holocene. Sediments, plant macrofossils and diatoms examined from a 5.99 m core collected from the dome of the bog record six stages of development: i) a quiet, brackish-water riverine phase (prior to ca. 8500 cal BP); ii) a shallow lake (ca. 8500–8200 cal BP); iii) fen (8200–7600 cal BP); iv) transitional mire (7600–6900 cal BP); v) pioneer raised mire (6900–4450 cal BP); and vi) ombrotrophic bog (4450 cal BP–present).

Testate amoebae, notably small (<25 µm diameter) specimens of *Centropyxis aculeata* type, first appear in low abundances in sediments ascribed to the lacustrine phase. Diatoms from the same horizons record a shallowing in water depth, a decline in salinity and the development of emergent macrophytic vegetation, which may have provided favourable conditions for testate amoeba colonization. The testate amoeba communities of the inferred fen phase are more diverse and include centropyxids, cyclopyxids, Arcellidae and Hyalospheniidae, although the assemblages show some differences to those recently reported in modern European fen environments. The Fen–Bog Transition (FBT) is also dominated by *C. aculeata* type. The change in testate amoeba communities around this key transition is apparent in the results of Detrended Correspondence Analysis (DCA), and appears to reflect a latent nutrient gradient and a secondary moisture gradient. DCA analyses of plant macrofossil remains around the FBT show a similar trend, although the sensitivity of the two proxies to the inferred environmental changes differs. Comparisons with other regional mid-Holocene peatland records confirm the important influence of reduced effective precipitation on the testate amoeba communities during the initiation and development of *Sphagnum*-dominated, raised bog communities.

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### 1. Introduction

Testate amoebae (Protozoa: Rhizopoda) are unicellular organisms that are characterised by enclosed, morphologically distinct tests (Charman, 2001). They are important inhabitants of wetlands, including peatlands, lakes, moist soils and brackish intertidal environments (Medioli and Scott, 1988; Patterson and Kumar, 2002; Booth and Jackson, 2003; Swindles et al., 2010). In peatlands, substrate moisture is the dominant control on species abundance and distribution (Charman and Warner, 1992, 1997; Tolonen et al., 1992; Warner and Charman, 1994; Mitchell et al.,

2008), although pH (Payne et al., 2006; Lamentowicz et al., 2008; Swindles et al., 2009), nutrient status (Tolonen et al., 1994) and water chemistry (Mitchell et al., 2000) have a subsidiary role. Their generally good preservation potential and hydrological sensitivity make them useful proxy indicators of past surface moisture conditions (Charman et al., 2000).

In ombrotrophic peatlands, past water table depth has been commonly inferred via the application of transfer functions developed from the known hydrological tolerances of testate amoeba assemblages (Woodland et al., 1998; Bobrov et al., 1999; Wilmshurst et al., 2003; Charman et al., 2006; Swindles et al., 2007). Testate amoebae have also been used to reconstruct hydrological changes in *Sphagnum*-dominated, moderately minerotrophic mires, however their response to hydrological controls in fenlands is less well understood (Booth, 2001; Booth and Zygmunt,

\* Corresponding author.

E-mail address: [selliott06@qub.ac.uk](mailto:selliott06@qub.ac.uk) (Suzanne M. Elliott).

2005; Payne and Mitchell, 2007). These environments are characterised by minerotrophic, nutrient-rich conditions, which receive both a groundwater and meteoric water supply (Payne and Mitchell, 2007). In such environments, water chemistry, pH and nutrient availability also have an influence on species distribution (Lamentowicz et al., 2009).

The transition between eutrophic fenland and ombrotrophic bog environments represents an important ecological gradient (Wheeler and Proctor, 2000). In modern environments, this transition is largely distinguished by changes in vegetation (Vitt, 1990; Zoltai and Vitt, 1995), but it is also often associated with variations in water chemistry and pH (Glaser et al., 1990; Vitt et al., 1995). Testate amoeba communities show interesting patterns of change along this gradient in response to complex fluctuations in water chemistry, hydrology and vegetation (Heal, 1961, 1964; Tolonen et al., 1992, 1994). Recent contemporary observations at sites in the Swiss Alps and the Western Carpathians have provided important insights into species diversity (Lamentowicz et al., 2009) and the optima and tolerance of species to nutrient richness in such transitional environments (Opravilová and Hájek, 2006). In general, the few studies that have been undertaken in these transitional settings suggest that the diversity of testate amoebae peaks in rich fen environments and is lower in bogs (Heal, 1961, 1964; Lamentowicz et al., 2009).

In the fossil record, transitions within a hydrosere succession occur when one set of ecological or environmental processes are replaced by another (Klinger, 1996). They represent boundaries between distinctive environments, which can occur abruptly or gradually as thresholds are reached (Lamentowicz et al., 2007; Lamentowicz and Obremaska, 2010). The 'Fen–Bog transition' (FBT) is an important successional phase, which is characterised by the replacement of nutrient-rich minerotrophic fen by ombrotrophic bog communities associated with acidic conditions (Granath et al., 2010). This transition has been explored via plant macrofossil analysis at several sites in the UK (Hughes and Dumayne-Peaty, 2002; Hughes and Barber, 2003, 2004; Langdon et al., 2003), northern Minnesota (Janssens, 1992) and southern Québec (Lavoie and Richard, 2000). Transitions via a 'dry-pioneer' and a 'wet-pioneer' route have been identified (Hughes and Barber, 2004). The former is often defined by the presence of *Eriophorum spissum* communities associated with deep or highly fluctuating water tables (Hughes, 2000). Such conditions promote an increase in the depth between mire surface and sub-surface moisture, which can become more acidic under *Sphagnum* coverage. The 'wet-pioneer' transition, in contrast, is associated with near-surface water tables, which promote the development of sedge fen and raised mire communities. These differing transitional modes can be driven by autogenic (Walker, 1970; Tolonen, 1987; Clymo, 1991) and/or allogenic controls, such as changes in effective precipitation (Hughes et al., 2006).

Whilst plant macrofossils are an effective indicator of long-term changes in wetland environments, some studies have highlighted limitations with the proxy, including an insensitivity to minor shifts in mire surface wetness (Hughes et al., 2006), and problems associated with taphonomy (Barber et al., 2004). These can result in poor representation of ecological shifts within the mire succession, which could underestimate the nature of threshold changes. Given the reported sensitivity of testate amoeba communities to hydrological and nutrient-related changes in contemporary FBT environments (e.g. Lamentowicz et al., 2009), and the rapid response shown by testate amoebae to moisture, pH and nutrient enrichment within recent (near surface) and late Holocene mire records (cf. Booth and Jackson, 2003; Mitchell and Gilbert, 2004; Payne and Pates, 2009), it is apparent that the timing and character of shifts is likely to be better constrained when both proxies are used together (Loisel and Garneau, 2010).

This paper presents high-resolution testate amoeba and plant macrofossil data from a 5.99 m core (spanning >8.5 k cal y) from Mer Bleu Bog, eastern Ontario, Canada, and examine the relative utility of the two proxies for assessing periods of ecological and environmental change. This site was chosen because the sequence records several distinct phases of hydrological and hydrosere change, including a mid-Holocene transition from a limnic environment to an ombrotrophic bog via an intermediate fenland phase (Frolking et al., 2010). Each of the main successional stages is considered in terms of hydrosere change and comparisons are made with other regional proxy records of Holocene climate change. Ordination techniques are used to explore the changes in community dynamics during each stage of wetland development and consider the differential responses shown between testate amoebae and plant communities. Finally, the testate amoeba assemblages associated with each environmental transition are examined in detail to provide a greater understanding of the ecology, thresholds and response rates of faunas in relation to inferred changes in vegetation and hydrology. The basal part of the sequence also includes brackish-water minerogenic sediments that have yielded diatoms. These provide additional insights into the factors that controlled the colonization of testate amoebae in the basal, limnic part of the sequence. As testate amoebae also inhabit fresh- and brackish-water lakes (Patterson and Kumar, 2002; Roe and Patterson, 2006; Roe et al., 2010), and brackish coastal environments (Patterson et al., 1985; Charman et al., 1998; Gehrels et al., 2001; Roe et al., 2002; Vázquez-Riveiros et al., 2007) the sequence also provides the opportunity to examine the faunal response to a wider set of environmental controls, particularly to a palaeo-salinity gradient.

## 2. Site description

Mer Bleu Bog (45°24'N; 75°31'W) is an ombrotrophic peatland located 10 km east of Ottawa, Ontario (Fig. 1). It is situated in a post-glacial channel complex that was occupied by the Champlain Sea ca. 13,100 cal BP (Richard and Occhietti, 2005). Marine conditions persisted for 2500 years in the Ottawa–St. Lawrence Valley until ca. 10,600 cal BP, when the sea retreated eastwards (Elson and Elson, 1969; Mott and Camfield, 1969; Fig. 2a). Freshwater conditions then became established in the channel system (Roulet et al., 2007; Fig. 2b). Terrestrialization began 8500 years ago, beginning with the development of fen and later ombrotrophic bog (Fraser et al., 2001; Frolking et al., 2010; Fig. 2c and d).

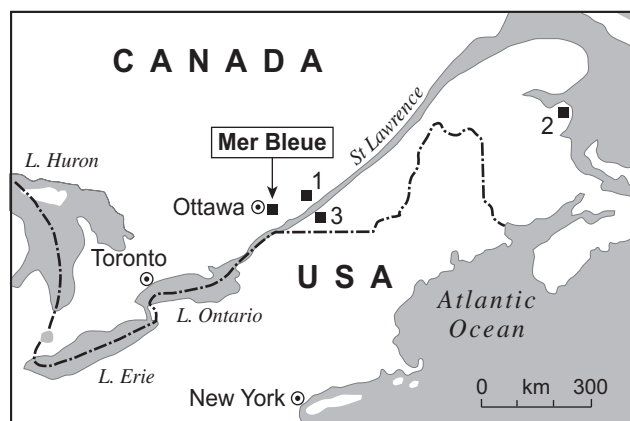


Fig. 1. Map showing the location of Mer Bleu Bog, eastern Ontario. Location of regional peatlands also shown; Mirabel Bog, southern Québec (1); Pointe-Escuminac Peatland, Gulf of St. Lawrence (2); and Frontenac Peatland, southern Québec (3).

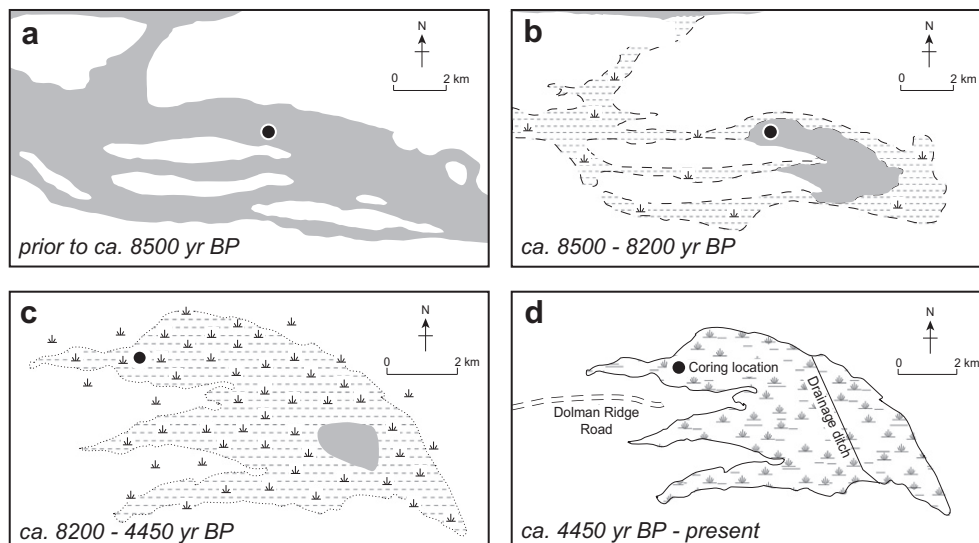


Fig. 2. Schematic representation of wetland succession at Mer Bleu via (a) riverine; (b) lacustrine; (c) fen; and (d) raised bog phases. Black dots denote core (MB1) location.

The peatland currently covers 28 km<sup>2</sup> and is characterized by three drainage 'arms' separated by alluvial sand ridges (Mott and Camfield, 1969; Fig. 2d). The northern arm is domed (Joyal, 1970) with peat depths of 5–6 m, decreasing to 1–2 m around the bog margins. Surface vegetation is dominated by ericaceous shrubs (e.g., *Ledum groenlandicum*, *Chamaedaphne calyculata* and *Kalmia angustifolia*) and *Sphagnum* species (e.g., *S. capillifolium*, *S. fuscum*, *S. magellanicum* and *S. angustifolium*). The bog has a sparse cover of trees (e.g., *Larix laricina* and *Betula populifolia*) and sedges (e.g., *E. spissum*), whilst the fringing woodlands are dominated by *Picea mariana*.

### 3. Methods

A 5.99 m sediment core (MB1) was collected from the dome of Mer Bleu Bog using a Russian corer (Fig. 2d). A monolith was also obtained from the uppermost 60 cm of the sequence using a 80 × 10 × 10 cm box corer to provide compaction-free sediments near the bog surface and permit sampling of the thick *Sphagnum*-dominated acrotelmic peat. The lithostratigraphy of the core was described using the Tröels-Smith (1955) sediment classification scheme. Colour was described using the Munsell classification system. Samples for loss-on-ignition analysis were taken at 4 cm intervals from 0 to 544 cm, below which values fell to 40% and no further readings were taken.

Samples for testate amoeba analysis (2 cm<sup>3</sup>) were taken at 4 cm intervals throughout the core and prepared following the method described by Hendon and Charman (1997). *Lycopodium clavatum* tablets were added to each sample to determine testate amoeba concentrations (Stockmarr, 1971). The size fraction between 10 μm and 300 μm was retained for analysis. Slides were examined under ×200 and ×400 magnification and 150–200 testate amoebae were counted.

The 118 samples quantified were also assessed to determine which ones were statistically significant prior to subsequent statistical analysis. The probable error (pe) for each of the total sample counts was calculated using the following formula:

$$pe = 1.96 \left( \frac{s}{\sqrt{X_i}} \right)$$

where *s* is the standard deviation of the population counts and *X<sub>i</sub>* is the number of counts at the station being investigated. A sample

was judged to have a statistically significant population (SSP) if the total counts obtained for each taxon were greater than the pe (Patterson and Fishbein, 1989). As diversity was low, all samples were deemed to have SSP counts.

Samples below 555 cm were difficult to count because of the high silt and clay content. Thus, in addition to the method described above, a larger sample of sediment (3 cm<sup>3</sup>) from the size fraction 37–300 μm was also examined from the basal, more minerogenic samples (555–599 cm) using a low power binocular microscope. This methodology is commonly employed in lake-based testate amoeba studies (e.g., Patterson and Kumar, 2002) and provides the opportunity to examine larger agglutinating specimens more closely than via the cover-slip based method used in peatland studies. However, no specimens were recorded. The taxonomy employed follows Charman et al. (2000) except, where indicated, Booth (2002). When present, rotifers, cladoceran exoskeletons, chironomid head capsules and foraminifera were also counted to provide supplementary palaeo-environmental information.

Samples for plant macrofossil analysis (3 cm<sup>3</sup>) were taken every 8 cm throughout the core and 4 cm when there was a shift in macrofossil communities. Samples were boiled in 5% KOH to dissolve fulvic and humic acids and then sieved through a 125 μm mesh. The 125 μm size fraction was retained and examined at ×40 magnification. Counts were undertaken using the quadrat and leaf count (QLC) technique (Barber et al., 1994). If present, *Sphagnum* leaves were identified under ×400 magnification. Seeds, fruits, macroscopic charcoal and other macrofossils (e.g., the soil fungus *Cenococcum* spp.) were quantified using a five-point scale of abundance (1 = rare, 2 = occasional, 3 = frequent, 4 = very frequent and 5 = abundant) (cf. Barber, 1974, 1981). Macrofossil identification follows (1992)). Macrofossil identification follows Grosse-Brauckmann (1972, 1974, 1992), Mauquoy and van Geel (2007) and Levesque et al. (1988). The nomenclature used to describe the *Sphagnum* mosses follows Crum and Anderson (1981), whilst the vascular plants are described following Gleason and Cronquist (1991).

Samples from the lower parts of the core (below 556 cm) were also examined for diatoms to provide additional palaeo-ecological information for the basal part of the sequence, particularly around the transition from minerogenic to organic sediments. Samples (1 cm<sup>3</sup>) were prepared following the method of Battarbee et al. (2001). The diatoms were mounted in Naphrax and examined

using light microscopy (x 1000 magnification) and oil immersion. At least 300 diatom valves were counted for each sample. Diatom identifications were made with reference to a range of keys, including Germain (1981), Krammer and Lange-Bertalot (1986, 1988; 1991a; 1991b) and Patrick and Reimer (1975). The diatoms were sub-divided into salinity classes following the classification system of van Dam et al. (1994).

The microfossil and plant macrofossil data were plotted using PSIMPOLL software (Bennett, 2008) and zoned using stratigraphically constrained cluster analysis (CONISS). Shannon Diversity Index (SDI) values were calculated for the testate amoebae (Shannon, 1948) using the equation:

$$S.I. = - \sum_{i=1}^S \left( \frac{X_i}{N_i} \right) \times \ln \left( \frac{X_i}{N_i} \right)$$

where  $X_i$  is the fractional abundance of each taxon in a sample,  $N_i$  is the total abundance of the sample and  $S$  is equal to the species richness of the sample. Stressed environmental conditions are indicated by an SDI between 0.1 and 1.5, intermediate conditions from 1.5 to 2.5 and favourable conditions ranging between 2.5 and 3.5 (Magurran, 1988; Patterson et al., 2002).

Eleven conventional radiocarbon dates were obtained from bulk peat samples. These were calibrated using CALIB v. 5.0.2 (Stuiver and Reimer, 1993; Reimer et al., 2004). An age-depth model based on linear interpolation was produced using 'clam' software (Blaauw, 2010). Detrended Correspondence Analysis (DCA) of the fossil data was carried out using CANOCO version 4.5 (Ter Braak, 1987). The DCA analyses enabled changes in community composition associated with each of the different palaeo-environments represented in the record to be explored. For the plant macrofossil dataset, only the main peat components were included in the ordination; the semi-quantitative counts of seeds, *Sphagnum* leaf counts and 'other macrofossils' were treated passively to avoid introducing bias in the sample scores. Species biplots were constructed using CANODRAW (Smilauer, 1992).

#### 4. Results

The main sedimentary units present in core MB1 are described in Table 1. The lower most section (599–579 cm) is characterized by 'Leda clay' deposits that occur widely in the Ottawa Valley (Aylsworth et al., 2000). There is a gradational colour change between 579 and 571 cm as organics become incorporated into the sediments. A sharp change occurs at 571 cm as the grey 'Leda' clays are abruptly replaced by organic minerogenic peat. Above 530 cm, the sediments comprise highly humified fen peat, which is

gradually replaced at 334 cm by moderately humified *Sphagnum* peat. An age-depth model for core MB1 is presented in Fig. 3 using data summarized in Table 2.

##### 4.1. Diatom assemblages

A total of 55 diatom taxa were recorded in the six samples examined from the basal grey ('Leda') clays (571–591 cm), minerogenic gyttja and the overlying minerogenic peat (555–571 cm) (Fig. 4; Supplementary Online Appendix 1). The assemblages of the grey clays are dominated by *Cymbella ehrenbergii*, *Navicula oblonga* and *Neidium iridis*. Subsidiary frequencies of *Pinnularia viridis* and *Stauroneis phoenicenteron* and *Rhopalodia gibba* also occur. The diatom assemblages undergo a number of distinct changes above 571 cm, as organic sediments replace the grey clays. These include a small decline in the frequency of brackish species and a corresponding rise in freshwater taxa (Fig. 4). Most notably, the principal taxa of the previous phase, *C. ehrenbergii*, *N. oblonga* and *N. iridis* spp., undergo a sharp decline and are replaced by an assemblage dominated by *Sellaphora pupula*, *Nitzschia amphibia* and *Cymbella silesiaca*.

##### 4.2. Testate amoeba assemblages

Preservation of tests was generally good throughout the profile, however, testate amoebae were absent between 362 and 386 cm (Fig. 5). Counts of >150 were achieved throughout the upper 5 m, although counts fell as low as 100 between 516 and 566 cm. Only five small (<25 µm) specimens of *Centropyxis aculeata* type were recorded at 568 cm. Species diversity was highest in the upper 53 cm of the sequence (SDI values: 1.56–2.8) and fluctuates with depth (Fig. 5). The assemblages are sub-divided into six zones prefixed with 'MB'.

###### Zone MB1 (566–524 cm)

This basal zone occurs in highly humified fen peat with occasional sedge remains. The lower most faunas (from 566 to 552 cm) are dominated by a monospecific community of centropyxids, most notably *C. aculeata* type. Other taxa in the overlying sediments include *Arcella discoidea*, *Arcella vulgaris*, *Centropyxis aerophila* and *Centropyxis platystoma* type.

###### Zone MB2 (524–328 cm)

Humified minerogenic peat with *Phragmites* stems forms the sediment of this zone. Above 334 cm, ericaceous rootlets become more abundant. The testate amoeba assemblages include an abundance of *C. aculeata* type. *Amphitrema flavum* and *A. discoidea*

**Table 1**  
Lithostratigraphy of the Mer Bleue core MB1. Sediment classification follows Tröels-Smith (1955) and colour, Munsell (1975).

Depth (cm)	Tröels-Smith	Description	Munsell Colour
0–34	Th2 Dh2	Unhumified, fibrous <i>Sphagnum</i> peat with <i>Chamaedaphne calyculata</i> leaves and <i>polytrichum strictum</i>	7.7 YR 4/2
34–41	Sh1 Th3	Moderately humified <i>Sphagnum</i> peat with <i>Chamaedaphne calyculata</i> stems	5 YR 2/1
41–102	Sh2 Dh1 Th1	Moderately humified <i>Sphagnum</i> peat rich in <i>Chamaedaphne calyculata</i> rootlets	5 YR 2/1
102–132	Sh3 T11 Dh+	Moderately humified <i>Sphagnum</i> peat	10 YR 2/2
132–168	Sh3 T11	Moderately humified <i>Sphagnum</i> peat with unidentifiable wood fragments	10 YR 2/2
168–185	Sh2 T12 Dh+	Moderately decomposed <i>Sphagnum</i> peat	10 YR 2/1
185–210	Sh2 D12 T1+	Moderately decomposed <i>Sphagnum</i> peat	10 YR 2/2
210–334	Sh3 T11	Highly decomposed peat with an abundance of ericaceous rootlets and unidentifiable wood fragments	10 YR 2/2
334–410	Sh3 Dh1	Highly decomposed peat with <i>Phragmites</i> remains	2.5 YR 1.7/1
410–571	Sh3 Dh1	Highly decomposed fen peat	2.5 YR 1.7/1
571–579	Sh1 As2 Ag1	Transitional silty clay with limited organic remains	2.5GY 5/1
579–589	As3 Ag1	Gyttja with silty clay	10GY 5/1
589–599	As4	Silty clay	5B6 6/1

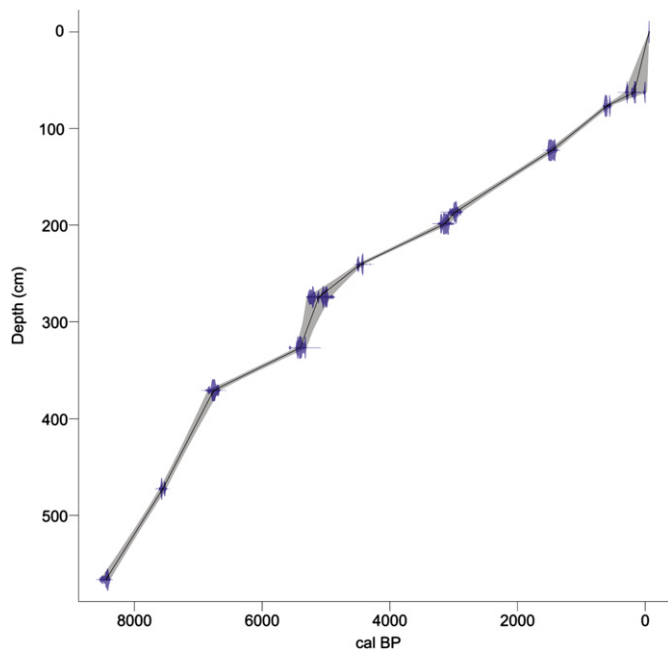


Fig. 3. Age-depth model for Mer Bleu core MB1 based on linear interpolation. Shaded envelopes indicate 95% confidence limits. Radiocarbon dates are given in Table 2.

also peak between 530 and 515 cm. Specimens of *A. muscorum* and *A. seminulum* were degraded between 452 and 430 cm. Between 386 and 362 cm testate amoebae are absent, although acanthamoebae cysts are present. Above 340 cm, *C. aculeata* type increases rapidly, peaking at 328 cm and representing >80% of the total fauna. The dominance of this taxon is registered in the low SDI values (0.75) at 328 cm.

#### Zone MB3 (328–308 cm)

The testate amoebae undergo a sharp transition in this zone as the sediments become rich in ericaceous rootlets and wood fragments. *C. aculeata* type undergoes a rapid transition (80%–7%) and an increase in SDI values from 0.75 to 2.53. *C. platystoma* type and *Nebela tubulosa* type also decline.

#### Zone MB4 (308–128 cm)

This zone occurs in *E. spissum* peat with ericaceous rootlets. This grades into moderately decomposed *Sphagnum* peat at 210 cm. There are oscillations in the frequency of *A. flavum*, with high abundances of *Trigonopyxis arcuata* type (53%) early in the zone. *Trigonopyxis minuta*, *Assulina muscorum* and *Bullinularia indica* peak

at 292 cm. Similarly, *Hyalosphenia subflava* increases from 240 cm. Other taxa present include *Diffflugia pulex* and *Phryganella acropodia*.

#### Zone MB5 (128–24 cm)

The sediments comprise moderately decomposed *Sphagnum* peat with large wood fragments. *A. flavum* dominates between 94 and 86 cm then declines, finally disappearing at 76 cm. Between 50 and 42 cm there is an increase in *Hyalosphenia elegans*, *Hyalosphenia papilio*, *Nebela minor* and a decrease in *H. subflava*, *P. acropodia* and *T. arcuata* type.

#### Zone MB6 (24–0 cm)

The sediments are composed of unhumified, acrotelmic *Sphagnum* peat with remains of *Polytrichum strictum* and stems and leaves of *C. calyculata*. There is a rapid increase in *A. muscorum*, *C. aculeata* type and *T. arcuata* type, which peak between 9 and 4 cm. Idiosomic taxa, including *Euglypha compressa*, *Euglypha rotunda*, *Euglypha strigosa* and *Euglypha tuberculata*, are present in low frequencies in the upper 30 cm.

### 4.3. Plant macrofossil assemblages

Preservation of plant remains and macrofossils was poor in the lower part of the core (554–599 cm) and only a few indeterminate remains were present. The plant macrofossil assemblages above 554 cm are sub-divided into six zones prefixed with 'MPM' (Fig. 6).

#### Zone MPM1 (554–470 cm)

In the basal part of this zone only a few bryozoa statoblasts and unidentifiable organic matter (UOM) were recorded (Fig. 6). In the overlying sediments at 540 cm, sporangia of *Thelypteris* spp. and *Scirpus validus* are present. Seeds of *Lycopus americanus*, *Nymphaea* spp. and *Typha* spp. occur, and *Myrica gale* fruits and leaves also appear. *Sphagnum* section *Acutifolia* represents up to 80% of the *Sphagnum* remains. Subsidiary levels of *Sphagnum magellanicum* occur at 520 cm.

#### Zone MPM2 (470–400 cm)

*Sphagnum papillosum* dominates in this zone, comprising up to 80% of the macrofossil assemblage and replacing *Sphagnum* section *Acutifolia* as the dominant *Sphagnum* species. *Rhynchospora* leaves first appear at 480 cm.

#### Zone MPM3 (400–312 cm)

*Sphagnum papillosum* declines sharply and is replaced by an assemblage dominated by *Rhynchospora alba* leaves and fruits, *Phragmites communis*, *E. spissum* and *Carex limosa*. *Rhynchospora*

Table 2

AMS radiocarbon dates from Mer Bleu core MB1 - analysed at the <sup>14</sup>CHRONO Centre, Queen's University Belfast. The radiocarbon dates were fractionation corrected using the AMS-measured δ<sup>13</sup>C relative to VPDB according to convention (Stuiver and Polach, 1977) and calibrated using the IntCal04 curve.

Depth (cm)	Material dated	Lab number	δ <sup>13</sup> C	<sup>14</sup> C yr BP	Calibrated yr BP <sup>a</sup>
62–63	<i>Sphagnum</i> peat	UBA 11978	–28.3%	204 ± 28	144–216
76–77	Moderately humified <i>Sphagnum</i> peat	UBA 15071	–26.1%	590 ± 24	583–648
122–123	Humified <i>Sphagnum</i> peat	UBA 11979	–29.2%	1566 ± 26	1398–1525
186–187	Humified <i>Sphagnum</i> peat	UBA 11980	–24.4%	2860 ± 22	2922–3067
198–199	Humified <i>Sphagnum</i> peat	UBA 11981	–26.0%	2959 ± 22	3061–3217
240–241	Humified peat	UBA 15072	–27.4%	3971 ± 22	4411–4448
274–275	Humified peat	UBA 11982	–29.4%	4449 ± 32	4959–5087
326–327	Humified <i>Sphagnum</i> peat	UBA 11983	–28.4%	4659 ± 31	5314–5468
370–371	Humified peat	UBA 11984	–26.1%	5934 ± 33	6670–6804
472–473	Humified <i>Sphagnum</i> peat	UBA 13405	–29.2%	6691 ± 28	7507–7610
566–567	Humified peat	UBA 13406	–26.9%	7649 ± 37	8386–8521

<sup>a</sup> Calibrated using CALIB version 5.0.2 (Stuiver and Reimer, 1993).

## Mer Bleu (MB1): Diatoms

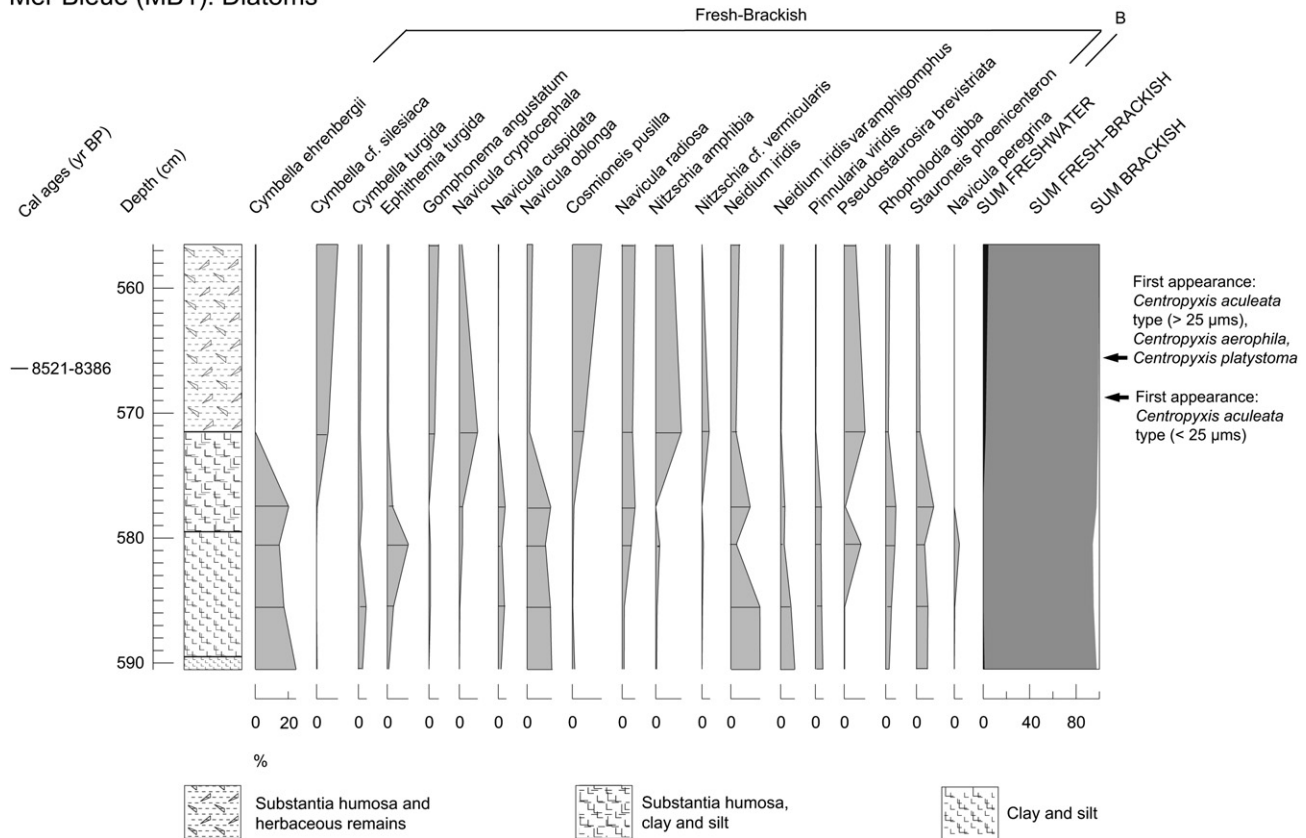


Fig. 4. Diatom percentage diagram (taxa > 3%) for the basal part of the MB1 core (565.5–590.5 cm). Diatom frequencies are expressed as a percentage of total diatom valves (% TDV). Assignment of diatoms to salinity classes follows van Dam et al. (1994). B = Brackish.

spp. decline then disappear towards the end of the zone. *S. magellanicum* undergoes a simultaneous increase, comprising up to 80% of the assemblage.

#### Zone MPM4 (312–240 cm)

*Sphagnum* disappears from the fossil record in this zone except for the remains of unidentifiable degraded leaves in the sample at 268 cm. Instead, ericaceous rootlets dominate, whilst *E. spissum* and unidentifiable wood remains occur throughout. There is an abundance of *Cenococcum* spp. between 284 and 244 cm.

#### Zone MPM5 (240–112 cm)

This zone is characterized by the remains of a rich *Sphagnum* mire community with *S. magellanicum*, *Sphagnum* section *Cuspidata* and *Sphagnum* section *Acutifolia*. Ericaceous rootlets and unidentifiable organic material become less abundant towards the top of the zone.

#### Zone MPM6 (112–0 cm)

The upper part of this zone (0–40 cm) is dominated by unhumified *Sphagnum* remains, particularly *Sphagnum* section *Acutifolia*. Other macrofossils include *C. calyculata*, *Andromeda glaucophylla* and *Eriophorum angustifolium*. *Polytrichum strictum* peaks in abundance at 52 cm and 20 cm. Charcoal is present at 54 cm and 36 cm.

#### 4.4. DCA biplots

In the DCA biplot for testate amoebae (Fig. 7) *Lesquerasia spiralis*, *Centropxyxis cassis* and *Arcella megastoma* are positively correlated

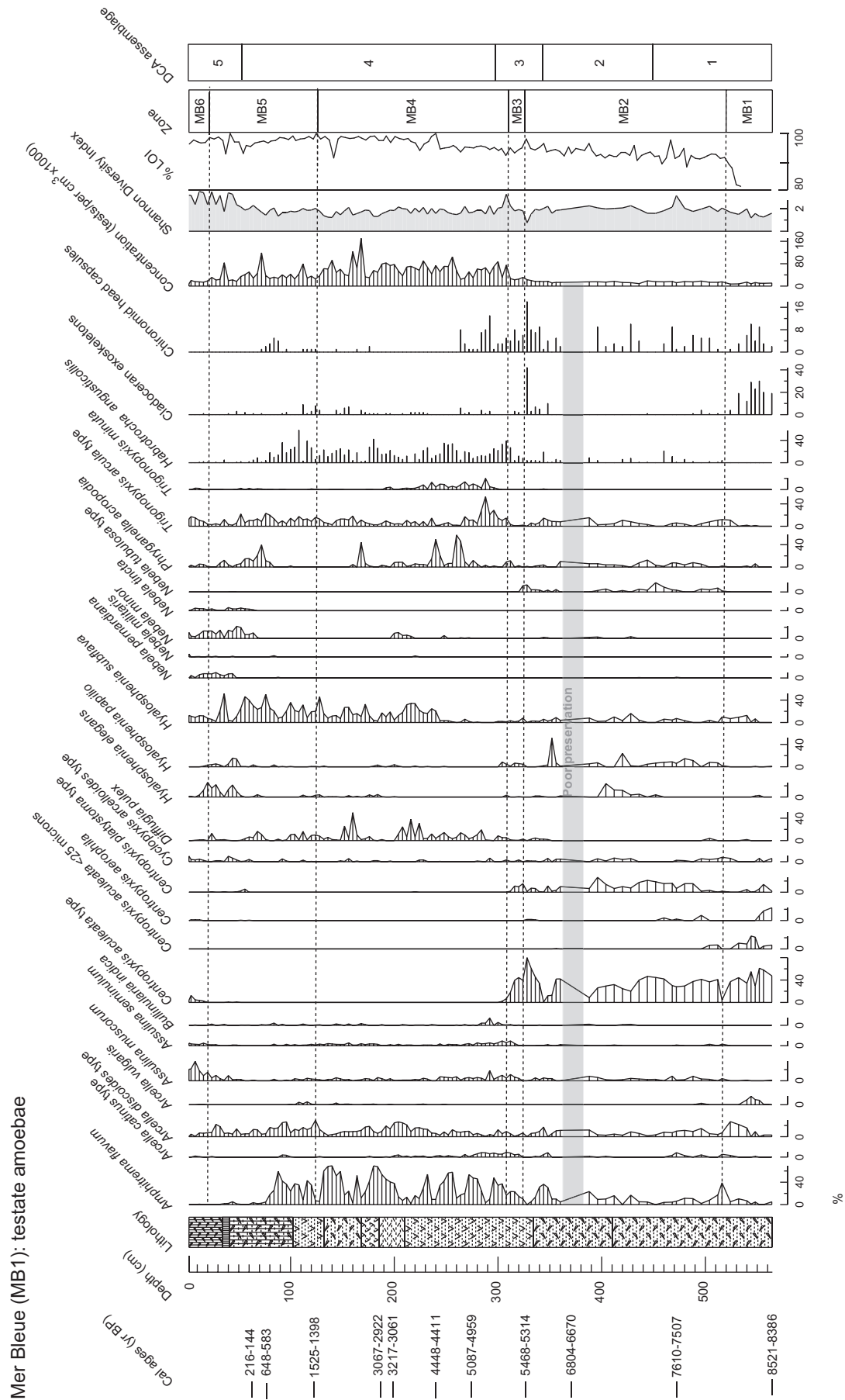
with axis one (Eigenvalue = 0.546), whilst *Diffflugia pristis* and *Diffflugia lanceolata* are negatively correlated. Taxa from the genus *Arcella* appear to be positively correlated with axis two (Eigenvalue = 0.318) and taxa from the genera *Nebela* and *Euglypha* are negatively correlated. Both axes account for 29.2% of the cumulative variance (Table 3).

The DCA biplot for plant macrofossils (Fig. 8) shows that *Equisetum* spp. is positively correlated with axis one (Eigenvalue = 0.696) while *Polytrichum strictum* and *Chamaedaphne* leaves are negatively correlated. Components that are positively correlated with axis two (Eigenvalue = 0.275) include *Cladium mariscus* leaves and *Myrica gale* leaves, whereas *C. limosa* and *Scheuchzeria* are negatively correlated. Both axes account for 35.7% of the cumulative variance (Table 3). Further explanation of the depositional environments associated with the assemblages and the possible gradients influencing species variance is given in Section 5.2.

## 5. Discussion

### 5.1. Phases of hydrosere development

The evolution of Mer Bleu during the Holocene is considered below in terms of the development of a series of distinct wetland environments, beginning as a shallow water body and finally resulting in an ombrotrophic bog. Diatoms, testate amoebae and plant remains are used to define each hydrosere stage. The testate amoeba assemblage response to the transitional phases along this hydrosere gradient is considered in more detail in Section 5.3.



**Fig. 5.** Testate amoebae diagram for Mer Bleue core MB1 (taxa > 5%). Absolute numbers of *Habrotricha angusticollis*, cladoceran exoskeletons and chironomid head capsules are presented as histograms. Lithostratigraphy is described in Table 1. DCA groups correspond to plant macrofossil zones identified in Fig. 5 and communities in Fig. 6.





*Shallow water river (prior to ca. 8500 BP)*

The diatom flora of the lower part of the grey silty clays (below 571 cm) points to the presence of an open water body with a marginal saline influence. Salinities within the fresh-brackish range ( $<0.9\text{‰}$ , *sensu van Dam et al., 1994*) are indicated. Many of the observed species occur in gently moving waters and are consistent with a quiet, shallow water riverine or stream environment. The common occurrence of *N. iridis*, *S. phoenicenteron* and *C. ehrenbergii* in slightly acidic environments, particularly those associated with *Sphagnum* bogs (Germain, 1981), suggests that peatlands were developing in the hinterland.

*Shallow lake (ca. 8500–8200 BP)*

The dominant diatom species above 571 cm point to a quiet water body rich in macrophytic vegetation. A shallow lacustrine environment with emergent aquatic vegetation is further suggested by *Pseudostaurosira brevisstrata*, *Gomphonema angustatum* and *Nitzschia vermicularis*. Slightly acidic conditions are indicated by the diatom *Tabellaria fenestrata*, a common species in peatlands and boggy ponds (Germain, 1981).

The first appearance of centropxyids and *A. vulgaris* during this phase is consistent with a fresh-brackish environment (cf. Patterson et al., 1985; Roe and Patterson, 2006; Vázquez-Riveiros et al., 2007; van Hengstum et al., 2008). Centropxyids (*C. aculeata* type, *C. aerophila* and *C. platystoma* type) are also more tolerant of environments where pH is above 5.5 (Kumar and Patterson, 2000; Patterson and Kumar, 2000a,b; Patterson et al., 2002). They are an opportunistic group, which can withstand relatively low nutrient levels (Schönborn, 1984). In lake-based testate amoeba studies, the occurrence of *C. aculeata* type with *A. vulgaris* can also reflect low oxygen levels within a stressed environment or the presence of fine clastic substrates (cf. Dalby et al., 2000; Roe and Patterson, 2006; Roe et al., 2010). The small size ( $<25\ \mu\text{m}$ ) of the *Centropxyxis aculeata* type specimens in the samples between 568 and 500 cm is noteworthy, suggesting that conditions may have been sub-optimal even during the early stages of deposition for this resilient taxon to survive (Fig. 4). The presence of testate amoebae in this lower part of the profile nevertheless confirms that the peat-based preparation method, which examines the size fraction 10–300  $\mu\text{m}$  and which utilises high power, light microscopy (cf. Hendon and Charman, 1997), is useful when analysing the sedimentary transition from a shallow water environment to fen.

*Fen (ca. 8200–7600 BP)*

The establishment of a fen environment was dominated by *Thelypteris* spp., which is indicative of eutrophic conditions and is a common peat coloniser in the early Holocene (van Geel et al., 1983). *Sphagnum* section *Squarrosa* and *Sphagnum* section *Acutifolia* typically occur early in a fen succession, reflecting a shift towards intermediate trophic conditions and infrequent flooding (Beaulieu-Audy et al., 2009). The disappearance of *Sphagnum* and occurrence of *Carex* spp. seeds, *Lycopus americanus* seeds, *Scirpus validus*, *Nymphaea* as well as *Typha* spp. and roots of *Equisetum* spp., are indicative of an increase in moisture in the early graminoid environment. In the testate amoeba record, the appearance of *A. discoides* corresponds to the initial establishment of *Sphagnum*. It has been suggested that the optima of this taxon is in rich fen bryophyte tufts (Opravilová and Hájek, 2006). However, the peaks in *A. discoides* and *A. flavum* coincide with the early disappearance of *Sphagnum* section *Acutifolia* and *Sphagnum* section *Squarrosa* at ca. 8200 BP, again suggesting an increase in moisture availability (Booth et al., 2004). This could be attributed to a regional cooling event at ca. 8200 BP that has been inferred from peatlands in the Labrador coast (Daley et al., 2009) and in southern Québec (Lavoie and Richard, 2000).

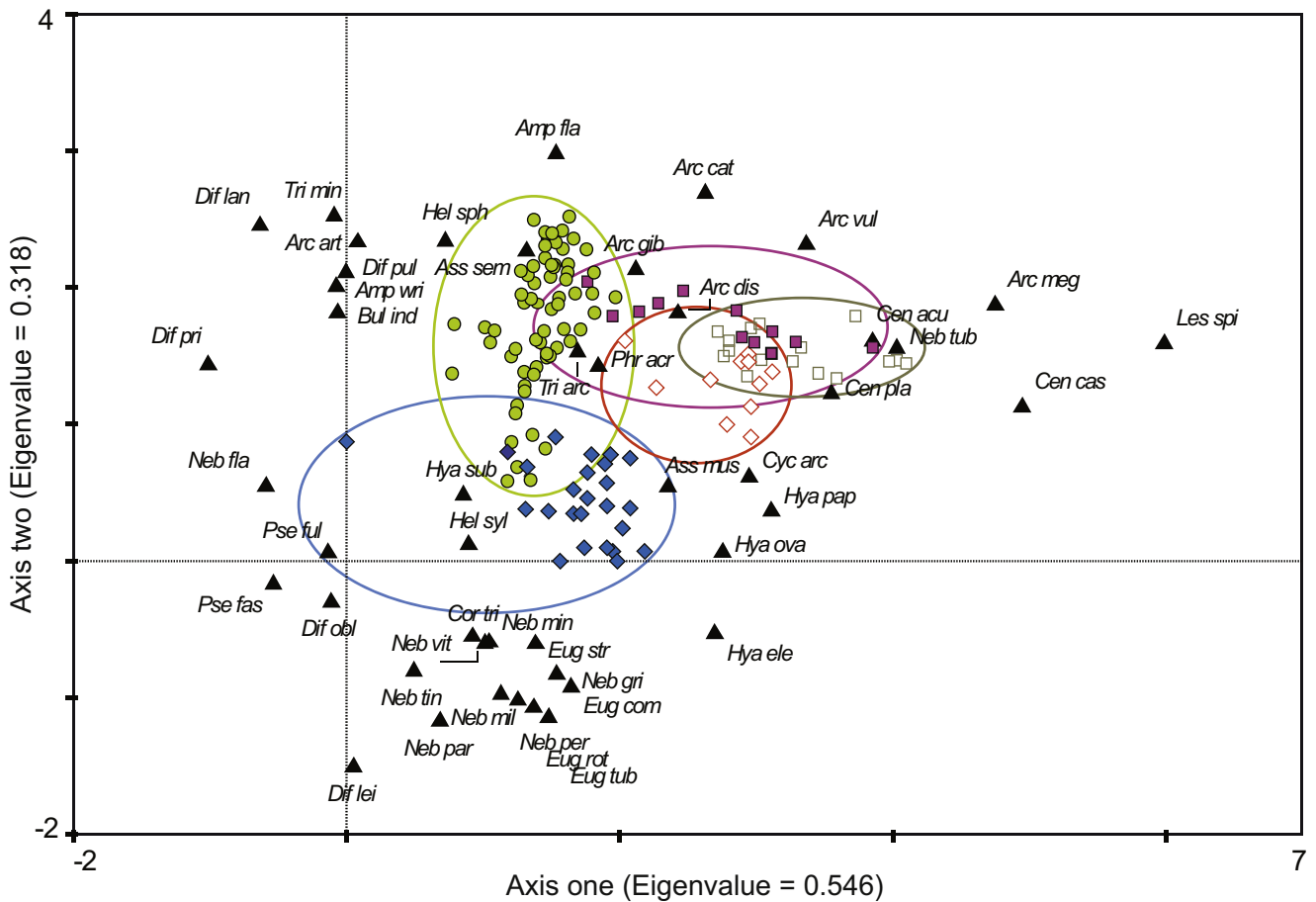
The observed appearance of *Cladium mariscus* at 492–488 cm is indicative of calcium rich or nutrient poor water. Leaves and fruits of *Myrica gale* indicate a mesotrophic fen environment that supported deciduous shrubs (Beaulieu-Audy et al., 2009). The re-appearance of *Sphagnum* section *Acutifolia* and *Sphagnum* section *Squarrosa* suggests that the fen surface stabilized, initiating terrestrialization. In southern Ontario, widespread near-synchronous changes in wetland development have been reported at ca. 8000 BP as open water environments began to terrestrialize (Bunting et al., 1996; Bunting and Warner, 1998). Both this phase and that at 8200 BP are evident from Mer Bleue and thus appear to be influenced by an allogenic forcing factor such as climate. The first at ca. 8200 BP through an increase in precipitation and the second at ca. 8000 BP through a decrease in precipitation, increase in temperature and increase in continentality (Bunting and Warner, 1998).

*Transitional mire (ca. 7600–6900 BP)*

In the plant macrofossil record, the transition from fen to pioneer raised mire is dominated by *S. papillosum* from ca. 7600 BP. This is a mesotrophic, rich fen species tolerant of low lawn positions (Janssens, 1983, 1992). The presence of *Rhynchospora alba*, a pool-edge species, from ca. 7500 BP, is reflective of a near surface mire water table that is stabilizing (Hughes and Barber, 2003). In the testate amoeba record, *H. elegans* and *H. papilio* appear, also suggesting a shift towards wet conditions. These species have a low pH tolerance (Booth and Meyers, 2010). The initial establishment of *S. papillosum* coincides with a marked increase in the testate amoeba SDI values, suggesting that the transition to a *Sphagnum*-rich community represents a more diverse environment. However, the rapid decline and disappearance of *S. papillosum* and replacement by *Rhynchospora* spp. and *Phragmites* spp. coincided with poor testate amoebae preservation. Peatland proxy data (plant macrofossils, testate amoebae and humification analyses) from a plateau bog in eastern Newfoundland have suggested that significant hydrological changes occurred in the region at ca. 7500 BP in (Hughes et al., 2006). Lavoie and Richard (2000) also report a rise in water tables at the same time from a raised bog record from southern Québec. At Mer Bleue, the inferred phase of near surface water tables coincides with this regional cooling period and is thus probably indicative of climate-related allogenic forcing.

*Pioneer raised mire (ca. 6900–4450 BP)*

As an important hummock builder that often precedes ombrotrophy, *E. spissum*, is capable of withstanding a relatively a low or highly fluctuating water table forming a dry oligotrophic mire (Hughes and Dumayne-Peaty, 2002). During the early stages of pioneer raised mire development, the testate amoeba faunas are dominated by *C. aculeata* type, which is indicative of a stressed environment. Studies from surface mire surface sediments have suggested that *C. aculeata* type is more sensitive to relative changes in pH than hydrology, becoming abundant in moderately high pH environments (Lamentowicz and Mitchell, 2005; Booth et al., 2008). The subsequent peak and decline in *C. aculeata* type coincides with a slowing of peat accumulation. From the testate amoeba assemblages, it can be inferred that the terrestrialization phase was associated with a rapid vertical growth of peat resulting in drier surface conditions. A study from Emo Bog, northwestern Ontario (Warner and Charman, 1994) also found a dominance of centropxyids and cyclopyxids in fen peats, which were subsequently replaced by abundances of *T. arcuata* type, indicative of a transitional dry environment. The soil fungus *Cenococcum* spp. is indicative of frequent aeration of mire surfaces (cf. Ferdinandsen and Winge, 1925). During this early raised mire phase, *Sphagnum* is almost entirely absent. Studies from peatlands in south Wales (Hughes and



## Samples

- ◆ Upper ombrotrophic (Assemblage 5)
- Lower ombrotrophic (Assemblage 4)
- Fen - bog transition (Assemblage 3)
- ◇ Transitional mire (Assemblage 2)
- Fen communities (Assemblage 1)

## ▲ Species

## Taxa

*Amp fla*, *Amphitrema flavum*  
*Amp wri*, *Amphitrema wrightianum*  
*Arc art*, *Arcella artocrea*  
*Arc cat*, *Arcella catinus* type  
*Arc dis*, *Arcella discooides* type  
*Arc gib*, *Arcella gibbosa*  
*Arc meg*, *Arcella megastoma*  
*Arc vul*, *Arcella vulgaris*  
*Ass mus*, *Assulina muscorum*  
*Ass sem*, *Assulina seminulum*  
*Bul ind*, *Bulinularia indica*  
*Cen acu*, *Centropyxis aculeata* type  
*Cen aer*, *Centropyxis aerophila*  
*Cen cas*, *Centropyxis cassis* type  
*Cen pla*, *Centropyxis platystoma* type  
*Cor tri*, *Corythion-Trinema* type  
*Cyc arc*, *Cyclopyxis arcelloides* type  
*Dif lan*, *Diffugia laneolata*  
*Dif lei*, *Diffugia leidy*  
*Dif obl*, *Diffugia oblonga* type  
*Dif pul*, *Diffugia pulex*  
*Dif pri*, *Diffugia pristis* type

*Eug com*, *Euglypha compressa* type  
*Eug rot*, *Euglypha rotunda* type  
*Eug str*, *Euglypha strigosa*  
*Eug tub*, *Euglypha tuberculata* type  
*Hel syl*, *Heleopera sylvatica*  
*Hya ele*, *Hyalosphenia elegans*  
*Hya ova*, *Hyalosphenia ovalis*  
*Hya pap*, *Hyalosphenia papilio*  
*Hya sub*, *Hyalosphenia subflava*  
*Les spi*, *Lesquereusia spiralis*  
*Neb fla*, *Nebela flabellulum*  
*Neb gri*, *Nebela griseola*  
*Neb par*, *Nebela parvula*  
*Neb per*, *Nebela pernardiana*\*  
*Neb mil*, *Nebela militaris*  
*Neb min*, *Nebela minor*  
*Neb tin*, *Nebela tincta*  
*Neb tub*, *Nebela tubulosa*  
*Neb vit*, *Nebela vitrea*  
*Phr acr*, *Phryganella acropodia*\*  
*Pse fas*, *Pseudiffugia fascicularis*  
*Pse ful*, *Pseudiffugia fulva*  
*Tri arc*, *Trigonopyxis arcula* type  
*Tri min*, *Trigonopyxis minuta*

Fig. 7. Detrended Correspondence Analysis (DCA) biplot showing species scores for the fossil testate amoebae from Mer Bleue core MB1. Taxonomy follows Charman et al. (2000) except where indicated (\*) by Booth (2002).

**Table 3**  
DCA summary for testate amoebae and plant macrofossils.

Axes	1	2	3	4
DCA summary: testate amoebae				
Eigenvalues	0.546	0.318	0.170	0.108
Length of gradient	3.969	2.493	1.943	2.043
Cumulative % variance of species data	18.5	29.2	34.9	38.6
DCA summary: plant macrofossils				
Eigenvalues	0.696	0.275	0.152	0.120
Length of gradient	3.576	2.366	1.855	1.807
Cumulative % variance of species data	25.6	35.7	41.3	45.7

Dumayne-Peaty, 2002) have also reported an absence of *Sphagnum* in the FBT phase once *E. vaginatum* dominates. The FBT transition is discussed further in Section 5.3.

#### Ombrotrophic bog (ca. 4450 BP–present)

The establishment of a *Sphagnum*-dominated raised bog (*S. magellanicum*, *S.* section *Acutifolia* and *S.* section *Cuspidata*) occurred after ca. 4450 BP. Within the bog succession, increases in *A. flavum* are indicative of increased moisture and the species shows major fluctuations as the surface hydrology of the bog became more sensitive to changes in effective precipitation (cf. Booth and Jackson, 2003; Lamentowicz and Obremaska, 2009). After ca. 650 BP, the bog became much drier, as *A. flavum* almost disappeared and *Sphagnum* section *Acutifolia* increased. Similar droughts have been inferred from peatland records in southeastern Michigan and north-central Minnesota (Booth et al., 2006). Although the impact in eastern Ontario of this dry period is unknown, in southern Ontario it has been related to an increase in fire activity and/or changes in forest vegetation (Booth and Jackson, 2003). The first peak in *Polytrichum strictum* occurs immediately above peat containing macroscopic charcoal, whereas the second occurrence of the moss lags behind a second charcoal deposit. These two charcoal records may correspond to historical fire events reported in the locality at ca. 1820 and the Carleton County fire, 1870 (Talbot et al., 2010). *Polytrichum strictum* colonizes the peat surface and is adapted to drier environments (Quinty and Rochefort, 2003). Interestingly, the dominance of this moss on bare mire surfaces in continental bogs has been associated with post-fire succession (Benscoter, 2006).

The observed absence of idiosomic taxa such as *Euglypha* spp. from the more humified peat below 30 cm could be due to the differential preservation of fossil tests, through platelet dissolution (Payne, 2007; Swindles and Roe, 2007) or a high pH optimum (Lamentowicz and Mitchell, 2005). Similarly, the observed increase in *A. muscorum* in the upper 40 cm could be attributed to taphonomic controls or a preference shown by this species for particular environmental conditions related to temperature and light (Charman et al., 2000). As a robust and siliceous taxon (Swindles and Roe, 2007), it has certainly been widely reported in fossil peats in North America (Booth and Jackson, 2003; Booth et al., 2004).

#### 5.2. Testate amoeba and plant macrofossil assemblages along the hydrosere

The DCA plots for testate amoebae (Fig. 7) and plant macrofossils (Fig. 8) together provide important insights into the key environmental gradients controlling the distribution of communities throughout the sequence. In the testate amoeba DCA ordination, the positive correlation of taxa from the fen, transitional mire and pioneer raised mire samples (Groups 1, 2 and 3) with axis 1 could reflect a nutrient and pH gradient from rich to poor (Lamentowicz

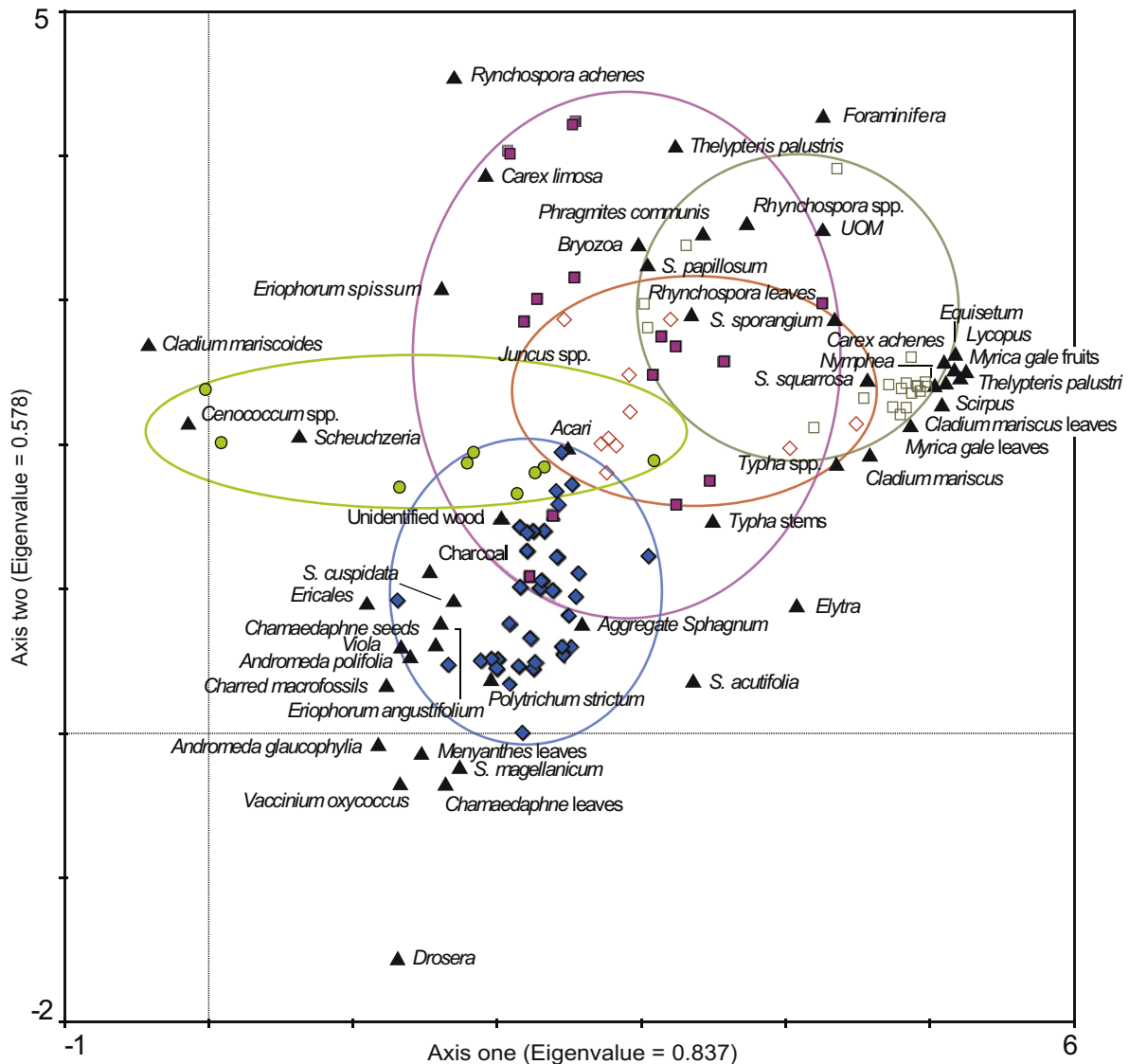
et al., 2007). The occurrence of *L. spiralis* and *C. aculeata* type on the right of the diagram probably reflects the more alkaline environments of the hydro-sequence. The negative correlation of the upper ombrotrophic peat samples (Group 6) with axis 2, in contrast, suggests a moisture gradient from dry to wet (cf. Lamentowicz et al., 2007). Samples from the ombrotrophic sub-groups (Groups 5 and 6) appear to be characterized by moisture, whereas samples from within the lower parts of the sequence (Groups 1, 2, 3 and 4) overlap in ordination space and cannot be divided into well-defined groups. This probably reflects the complex interaction of hydrology, trophic status and biotic factors that control species distribution in minerotrophic environments (Mitchell et al., 2000; Lamentowicz et al., 2009). It also reflects the ability of testate amoebae to tolerate a wide nutrient range from the lower sequence of the core. Interestingly, the transitional mire samples overlap with the ombrotrophic communities and are dominated by taxa such as *T. arcua* and *P. acropodia*, which suggests that these taxa play an important role in the transitional phases between mire environments. Taxa from the genera *Nebela* have been observed to be abundant in surface samples from ombrotrophic peatlands and in acrotelmic *Sphagnum*-dominated peat (Payne and Pates, 2009). However, *N. tubulosa* type is only present in the fen sequence at Mer Bleue, suggesting that it may be more tolerant of eutrophic conditions. Interestingly, surface samples from contemporary minerotrophic fen sites in the Western Carpathians in the Czech Republic and Slovakia have yielded high frequencies of *Euglypha* spp. and *Diffugia* spp. (Opravilová and Hájek, 2006; Payne, 2010). However, in this study the groups are absent from the inferred fen assemblages and instead the former only occurs in frequencies <4% in the upper ombrotrophic peat samples (Group 6). This may imply that the eastern European fenland assemblages are not analogous to those at Mer Bleue, or, as argued above, may reflect taphonomic controls which resulted in loss of the group from the fossil record.

The position of *H. papilio* in the ordination plot suggests that it is trophic status rather than moisture that controls the distribution of this species in ordination space as this species is known to prefer moderately wet sites (Lamentowicz and Mitchell, 2005; Booth and Meyers, 2010) and has a tolerance of high mineral concentrations (Booth, 2001; Booth and Zygmunt, 2005; Opravilová and Hájek, 2006). *Arcella megastoma* is the only taxon that occurs exclusively in the lower fen sequence, which is consistent with it being an indicator of reed-dominated fens (Payne, 2010). In general, the ecology of this species is poorly understood in fens but indications from this study agree that it favours wet, nutrient-rich conditions.

In the plant macrofossil DCA plot (Fig. 8), the positive correlation of the fen and pioneer raised mire assemblages (Groups 1 and 3) with axis one, and the negative correlation of the ombrotrophic sub-groups (5 and 6) with this axis is significant and is suggestive of a nutrient gradient. The groups are not as well defined as the testate amoeba groups, however, suggesting that factors other than nutrients and moisture may be influential, for example changes in pH or taphonomic factors. The passive treatment of the subsidiary peat components (seeds, leaves etc) in the ordination, which was necessary to avoid statistical bias, may also account for some of the overlap shown between the sample groupings. It is interesting to note that similar trends were nevertheless observed in palaeo-mire vegetation records from sites in south Wales, where a transition from nutrient-rich mesotrophic and oligotrophic conditions was also inferred in DCA ordination plots (cf. Hughes and Dumayne-Peaty, 2002).

#### 5.3. Sensitivity of testate amoebae to hydrosereal transitions

This study has demonstrated that testate amoebae show a number of interesting changes along a hydrosereal gradient. Of



## Samples

- ◆ Ombrotrophic communities (Assemblage 5)
- Oligotrophic communities (Assemblage 4)
- Pioneer raised mire communities (Assemblage 3)
- ◇ Transitional mire communities (Assemblage 2)
- Fen communities (Assemblage 1)
- ▲ Species

Fig. 8. Detrended Correspondence Analysis (DCA) biplot showing species scores for plant macrofossils from Mer Bleue core MB1.

particular interest in the Mer Bleue record is the first appearance of the group during the initial stages of hydrosereal evolution from a quiet, open water environment to a fen. The second occurs as the fen evolved into a raised mire. The factors controlling the testate amoeba community response around both of these transitions and the differing sensitivities of the group in comparison to plant communities are considered further below.

### 5.3.1. Open water to fen transition

The diatom assemblages and the sediment stratigraphy provide several insights into the first appearance of testate amoebae in the Mer Bleue record (at 568 cm). For example, the increasing numbers of freshwater and epiphytic diatom species at around this horizon suggests that the colonization of *C. aculeata* type may reflect a slight decrease in salinity or the establishment of emergent vegetation within the water body. Increasing organic inputs, which are

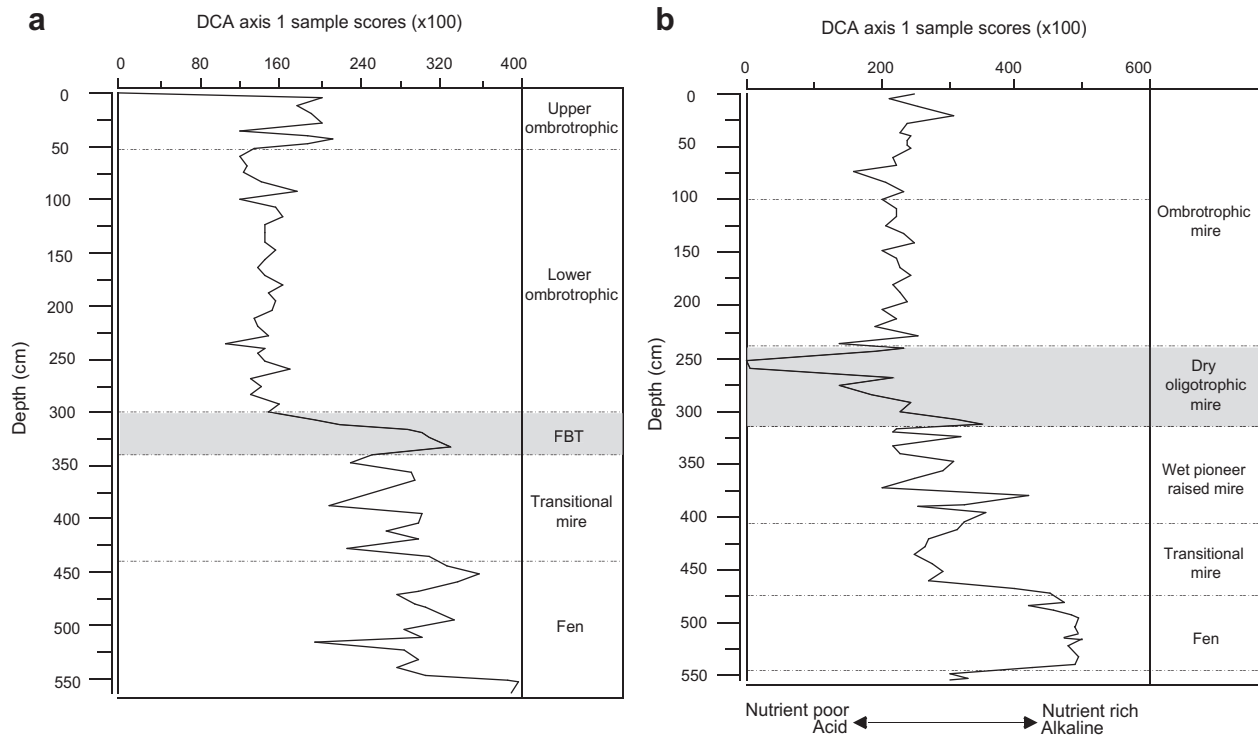


Fig. 9. DCA axis 1 sample scores for a) testate amoebae; and b) plant macrofossil data.

suggested by both the diatoms and the sediments, may also have provided more favourable conditions for testate amoeba colonization, as may changes in pH (cf. Scott and Medioli, 1983; Patterson et al., 1985). A transition from gently flowing to standing water conditions could also have provided more optimal conditions for both the colonization and preservation of testate amoebae (cf. Medioli and Brooks, 2003; Holcová, 2007). Interestingly, the absence of testate amoebae in the basal more minerogenic deposits ('Leda' clay) at Mer Bleue (568–599 cm), is consistent with their absence in early Holocene minerogenic, Lake Agassiz sediments of western Ontario (Warner and Charman, 1994) and is probably related to the requirement of organics for testate amoeba colonization. The small forms of *C. aculeata* type (<25 µm) are composed of an autogenous test with fewer spines than the larger specimens. These are different from those noted in previous lacustrine studies, which generally include more xenogenous material (cf. Patterson and Kumar, 2002; Boudreau et al., 2005). It is interesting to note that 'dwarfed', idiosomic forms of *Centropyxis constricta* "aerophila" have been reported in sink-hole sediments in the Yucatan Peninsula, Mexico, which are considered to be tolerant of slightly brackish conditions (van Hengstum et al., 2008). At Mer Bleue the maximum abundance (23%) of the small forms of *C. aculeata* type appears at the same horizon as two specimens of the foraminiferid *Criboelphidium excavatum* (Terquem, 1875) strain *clavatum*, which might also reflect elevated salinities. Alternatively, these foraminiferids could be re-worked from the underlying 'Leda' clays.

### 5.3.2. The Fen–Bog transition (FBT)

The FBT in core 'MB1' is characterised by a transition between the pioneer mire and ombrotrophic bog. Given the strong apparent influence of nutrient status on plant and testate amoeba distribution, the DCA axis one scores from both ordinations were plotted against depth (Fig. 9) to give a semi-quantitative nutrient status proxy (cf. Hughes and Dumayne-Peaty, 2002). The FBT represents a shift towards a highly sensitive environment, which is able to

record environmental change through testate amoebae, from a poorly stratified zonation of the group in fen and transitional mire communities. The shift from fen to bog occurs rapidly in the testate amoeba record but the response of plant macrofossils is more gradual, possibly reflecting the shorter lifespan of testate amoebae, which can reproduce within a few weeks (cf. Charman et al., 2000). Testate amoebae appear to be more sensitive, suggesting that any sub-surface movement of minerotrophic water to the mire surface had ended by ca. 5200 BP, when *Phragmites* and *Rhynchospora* spp. remains disappeared. In contrast, the decay-resistant remains of *E. vaginatum* persisted for more than 2500 years, declining at ca. 3000 BP. The rapid increase, peak and decrease of *C. aculeata* type is the primary indicator to suggest that this isolation occurred. Taxa diversity is lowest during the transition from minerotrophic to ombrotrophic sediments, where the assemblages are dominated by *C. aculeata* type and is highest immediately after the threshold had been reached. Contemporary surface sample data from Mer Bleue Bog show that *C. aculeata* type peaks in hummock microforms, where the growing surface vegetation is more isolated from the water table (Elliott, unpublished data). The occurrence of *C. aculeata* type with *E. vaginatum* suggests that not only did the water table become deeper during the transition but the vertical accumulation of surface vegetation increased, both reducing the influence of sub-surface moisture. Due to its continental location, the FBT at Mer Bleue may have been more pronounced in the microfossil record due to its reliance upon below surface moisture during summer months (Warner and Charman, 1994).

The DCA axis one scores for the plant remains (Fig. 9b) indicate that the first stage of acidification occurred when *S. papillosum* dominated. A further stage of acidification through a dry 'oligotrophic mire' occurred after the development of pioneer raised mire, yet before the onset of ombrotrophy which occurred by ca. 4450 BP. The sharp boundary between the pioneer mire and oligotrophic stages in the testate amoeba axis one scores plot (Fig. 9a) is defined by the peak in *C. aculeata* type, whereas in the

plant macrofossil plot, *E. vaginatum* persists through both oligotrophic and pioneer stages, resulting in a more muted response of the vegetation communities (Figs. 6 and 9b). The FBT in both proxies is nevertheless characterized by an inferred rapid nutrient shift as water tables became lower and pH decreased with the subsequent establishment of *Sphagnum*.

The inferred drying of the mire surface is consistent with a synchronous warming period which occurred during the Holocene Hypsithermal in eastern North America between ca. 6250–6000 BP (Jetté and Mott, 1995; Bunting and Warner, 1998; Viau et al., 2002; Boudreau et al., 2005). The transition from fen to bog occurred at ca. 6500 BP in peatlands from La Grande Rivière region, Québec (Beaulieu-Audy et al., 2009). At Frontenac peatland, southern Québec, this transition was observed between 6000 and 4400 yrs BP and was correlated with a low water stage in neighbouring Lake Albion (Lavoie and Richard, 2000). The shift from transitional mire to ombrotrophic bog at Mer Bleue appears to have occurred within this period. Testate amoeba and plant macrofossil data both suggest that the FBT at Mer Bleue developed through a 'dry-pioneer' route as opposed to the 'wet-pioneer' route, instigated by climate-driven changes in hydrology (cf. Hughes and Barber, 2004). This suggests that Mer Bleue and the aforementioned sites in Québec synchronously reached a threshold which was influenced by a regional change towards drier and warmer conditions during the climatic optimum. Allogenic influences such as climate can affect mire hydrology through a decrease in precipitation, increase in temperature and an increase in continentality (Bunting and Warner, 1998).

Palaeoecological records from continental bogs in Alberta, Saskatchewan and Manitoba (Yu et al., 2003) suggest that the transition from fen communities occurs because of autogenic vertical accumulation and growth of the bog surface, rather than by climate, which results in long-term drying of the mire surface. Testate amoebae and plant macro-remains from Mirabel Bog and Frontenac Bog in southern Québec indicate a similar dry FBT between 6000 and 5300 BP, which was dominated by *E. spissum* and *C. calyculata* (Lavoie and Richard, 2000; Muller et al., 2003). This was also attributed to the asynchronous response of vegetation (Muller et al., 2003). Given that the FBTs occurred during a period of reduced effective precipitation, this demonstrates the important influence of climate as well as the continued role of autogenic processes at Mer Bleue. Further work is now required to compare species response rates across different types of FBTs at other sites which also record multiple hydrosere stages, and more fully explore the response of testate amoebae to peat initiation.

## 6. Conclusions

1. The ca. 8500 year sequence from Mer Bleue Bog represents one of the longest records with near continuous testate amoeba preservation and includes assemblages associated with three distinct depositional environments (shallow open water, fen and raised bog). The proxy has been shown to have potential for characterizing hydrosere transitions, particularly from i) open water to fen; and ii) pioneer raised mire to ombrotrophic bog. Despite problems associated with the differential preservation of siliceous taxa, testate amoebae should be used alongside plant macrofossils because of their rapid species response and tolerances to changing moisture and nutrient levels. As confirmed by previous studies, the group also have considerable potential for de-limiting changes in salinity, particularly around freshwater to fresh-brackish transitions.
2. DCA analysis of the Mer Bleue data suggests that testate amoebae and plant communities both responded to nutrient and moisture gradients. However, testate amoebae appear to

respond more quickly and show a greater sensitivity to sub-surface moisture and inferred nutrient changes than mire vegetation, especially across the Fen–Bog transition.

3. The FBT, as recorded at Mer Bleue Bog, appears to be similar to that observed at other regional peatland sites, which also record a shift towards ombrotrophy between 6000 and 4400 BP. This highlights the role of an allogenic forcing mechanism such as reduced effective precipitation in controlling plant community dynamics during this successional phase. During the ombrotrophic phase, testate amoeba assemblages show a high degree of variability within the peat sequence as the mire surface responded to fluctuating atmospheric inputs.
4. Further work utilizing testate amoebae alongside plant macrofossils across ecological transitions in lake-fen-bog hydro-sequences would add additional insights into the nature and timing of changes within the hydrosere.

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## Appendix. Supplementary data

Supplementary data related to this article can be found online at doi:10.1016/j.quaint.2011.08.020.

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