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Response of testate amoeba assemblages to environmental and climatic changes during the Lateglacial–Holocene transition at Lake Lautrey (Jura Mountains, eastern France)

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ABSTRACT: We tested the response of lacustrine testate amoebae (thecamoebians) to climate and environmental changes for the Lateglacial–Holocene transition. The palaeoenvironmental history of the study site (Lake Lautrey, Jura Mountains, eastern France) was previously established based on high-resolution multi-proxy studies of the same core. The present study is characterised by a high taxonomic resolution (54 taxa), inclusion of small species (down to 25 μm) and high total counts ($>$500 individuals per sample on average). Changes in the composition of testate amoeba assemblages (dominant species and assemblage structure), as well as in the accumulation rate (tests cm^{-2} a^{-1}), corresponded to major climatic phases (i.e. Oldest Dryas, Bølling–Allerød Interstadial, Younger Dryas, Preboreal) as well as changes in organic matter inputs. Furthermore, decreases in the accumulation rate characterised minor short-lived cooling events, such as Older Dryas event or Gerzensee oscillation. However, the Preboreal oscillation, which was well registered by other proxies at Lake Lautrey, could not be recognised in the testate amoeba record. This work demonstrates that lacustrine testate amoebae can be used for palaeoclimatic and palaeoecological reconstructions. Nevertheless, a better understanding of the relation between climate, organic matter and lacustrine testate amoebae requires further high-resolution studies based on multi-proxy approaches and the development of appropriate modern analogues.

KEYWORDS: testate amoebae; palaeoclimate; Lateglacial; early Holocene; lake sediments.

Introduction

Testate amoebae (or thecamoebians) are common unicellular organisms characterised by a decay-resistant and morphologically distinctive test, or shell, enclosing the cytoplasm (Ogden and Hedley, 1980; Tolonen, 1986; Warner, 1990). They have been used for over a century as palaeoenvironmental indicators owing to their high abundance, diversity, environmental sensitivity and excellent preservation in lakes – even where other freshwater benthic fossil indicators, such as ostracods or molluscs, are poorly preserved due to low pH values (Dallimore *et al.*, 2000) – and wetlands (Asioli *et al.*, 1996; Beyens and Meisterfeld, 2001). There has recently been an increasing interest in the use of testate amoebae in reconstructing Quaternary climate history (Medioli and Scott, 1983; Ellison and Ogden, 1987; Dallimore *et al.*, 2000; Charman, 2001; Boudreau *et al.*, 2005). This renewed interest has been particularly evident in peat-based palaeoclimatic studies, where numerous modern and palaeoecological studies have demonstrated the sensitivity of testate amoebae to hydroclimate variability (Tolonen, 1986; Warner, 1990; Booth, 2001, 2002, 2008; Charman, 2001; Mitchell *et al.*, 2001; Booth and Jackson, 2003; Charman *et al.*, 2007; Lamentowicz *et al.*, 2008). In contrast, the climatic sensitivity of testate amoebae inhabiting lake environments has been less thoroughly investigated, although several studies suggest that testate amoebae in these habitats could be used as climatic proxies (Ruzicka, 1982; Medioli and Scott, 1988; McCarthy *et al.*, 1995; Burbidge and Schröder-Adams, 1998; Boudreau *et al.*, 2005).

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Thanks to their relatively short life cycle (they have a generation time of a few days), testate amoebae should potentially respond rapidly to environmental changes, including climatic ones (McCarthy *et al.*, 1995; Booth, 2001). Palaeolimnological studies have shown that testate amoebae can be used as indicators of trophic status (Scott and Medioli, 1983; Tolonen, 1986; Boudreau *et al.*, 2005), pH and oxygen level (Boudreau *et al.*, 2005), water pollution by heavy metals (Asioli *et al.*, 1996; Patterson *et al.*, 1996), or land use changes in the catchment area (Patterson *et al.*, 2002). However, the response of lake testate amoebae to climate is still a matter of debate (Beyens and Meisterfeld, 2001; Charman, 2001; Andreev *et al.*, 2004). Ruzicka (1982) pointed out a possible relation between even relatively minor climatic fluctuations, such as the Little Ice Age, and a decrease in the number of taxa observed in an Austrian lake. Likewise, in Atlantic Canada, a comparison of testate amoeba and pollen biostratigraphies revealed synchronous changes suggesting common responses to climatic changes (McCarthy *et al.*, 1995). However, Beyens and Meisterfeld (2001) questioned the thermophilous character of some taxa, and Patterson *et al.* (1985) observed few changes in testate amoeba assemblages during known periods of climate change in New Brunswick and Nova Scotia. It is therefore unclear to what extent testate amoebae respond to climate and other environmental changes. The scarcity of available palaeolimnological records as well as of high-resolution multi-proxy studies clearly limits current understanding of possible relations between climate and testate amoeba assemblages in lakes. Two complementary approaches may be used to address this question: (1) modern ecological studies, either correlative or experimental; (2) multi-proxy palaeoecological studies with independent reconstructions of past climatic changes. In this study we follow this second approach.

Magny and co-workers recently produced a high-resolution, multi-proxy palaeoclimate record from Lake Lautrey in eastern France covering the Lateglacial–Holocene (Magny *et al.*, 2006). This detailed record, unique for this region of the Jura Mountains in west-central Europe (combining analyses of pollen, lake level changes, mineralogy, organic matter composition, chironomids, magnetic susceptibility, etc.) provides an ideal opportunity to assess the response of lacustrine testate amoeba assemblages to both millennial and multi-millennial-scale climate changes of the LateglacialHolocene transition, as well as short-term (i.e., sub-millennial)environmental and climatic changes. To understand better thepotential responses of lacustrine testate amoebae to climate variability, we directly compared testate amoeba species richness, species evenness, test accumulation rate and assemblage structure to independently inferred climate and environmental changes at Lake Lautrey, using the same sediment core previously used for detailed multi-proxy analyses (Magny *et al.*, 2006). The results show a clear correlation between testate amoeba and palaeoclimatic and other palaeoenvironmental data. We discuss these correlations and suggest future research priorities to improve the value of lacustrine testate amoebae in palaeolimnological studies.

Regional setting and methods

Site location and sediment core

Lake Lautrey (46° 35′ 14″ N; 5° 51′ 50″ E) is located at 788 m above sea level in the Jura Mountains, eastern France (Fig. 1). It is a small residual lake surrounded by mires that have overgrown most of the former lake surface. Its ~2 km^2 catchment area is hilly, culminating at about 830 m, and covered by *Abies* and *Fagus*-dominated forests. The mean temperature is −1°C in the coldest month and 16°C in the warmest month, with annual precipitation reaching ~1500 mm.

We selected a sediment sequence (core 6) collected close to the northeastern shore of the former lacustrine basin as a good compromise between the various requirements of different proxies (Magny *et al.*, 2006). This sequence was previously used for a high-resolution multi-proxy analysis to document in detail the Lateglacial–Holocene transition. As illustrated in Fig. 2, the chronology was based on an age–depth model resulting from a combination of one tephra (Laacher See Tephra, LST), 12 accelerator mass spectrometry radiocarbon dates from terrestrial plant macrofossils, and oxygen isotope data (Magny *et al.*, 2006). The stratigraphy of the core was composed of four sediment units (Fig. 2). Environmental and

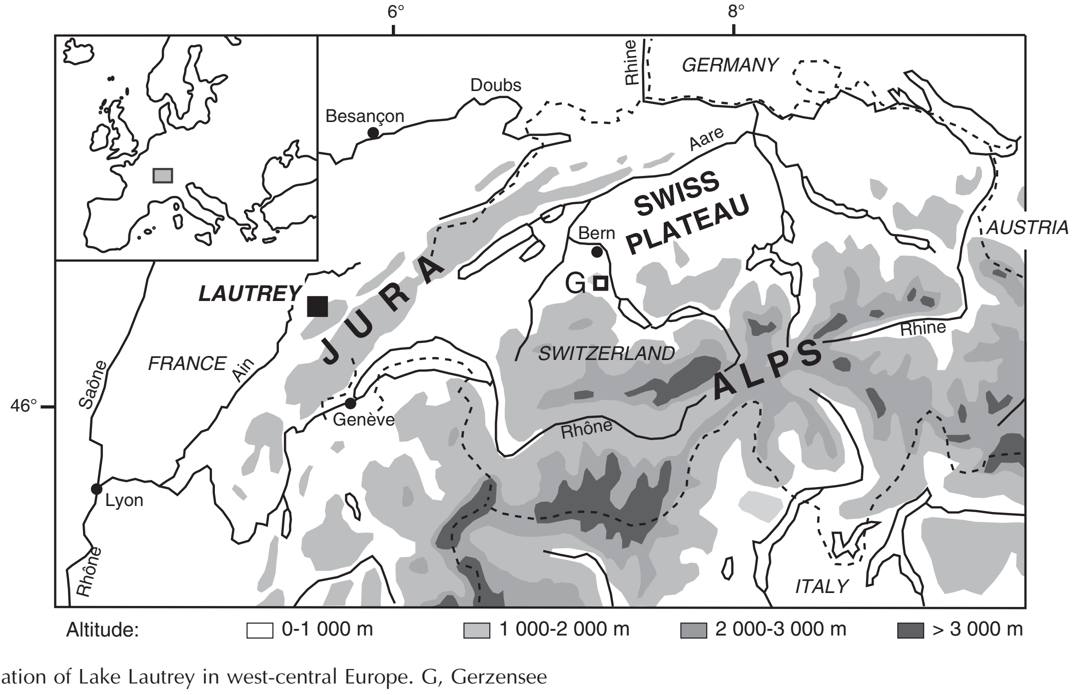

Figure 1 Location of Lake Lautrey in west-central Europe. G, Gerzensee

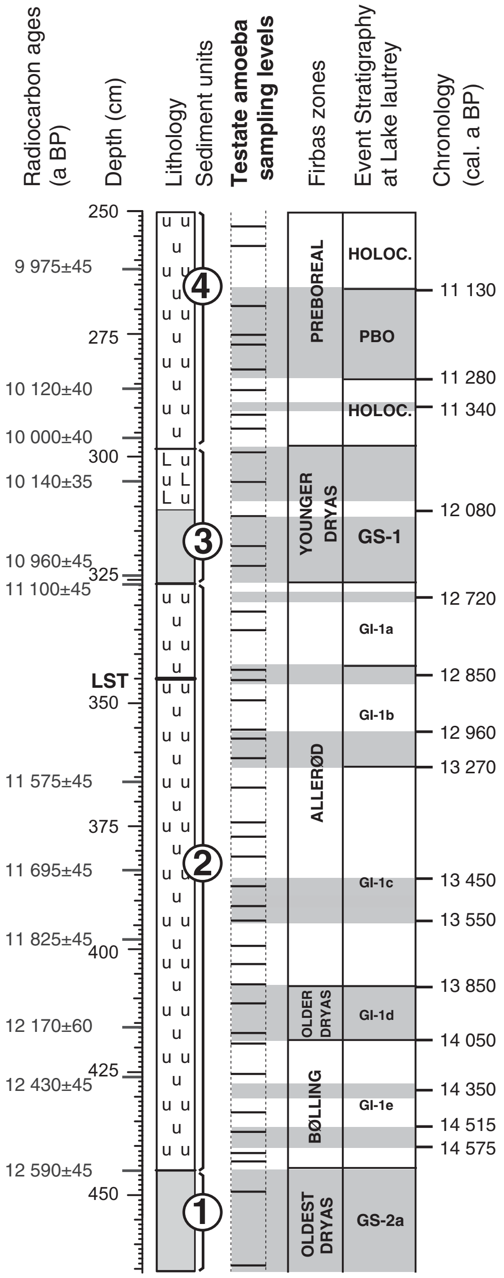

Figure 2 Sediment core 6 from Lake Lautrey with Firbas pollen zones and climatic event stratigraphy for Greenland Interstadial 1, Greenland Stadial 1 and early Holocene as documented by Magny *et al.* (2006). Lithology: grey, clayey silts; U, carbonate lake-marl; LU, clayey silts and carbonate lake-marl; LST, Laacher See Tephra. Grey bands correspond to cooling events documented by several biotic and/or non-biotic indicators. The chronological indications on the right are based on the age–depth model established for core 6 from 12 radiocarbon dates and the LST tephra on the left (Magny *et al.*, 2006). The right-hand column of the lithology indicates levels position for testate amoeba analyses

climatic changes were previously reconstructed for the last Glacial–Holocene transition by using an integrated approach based on a range of biotic and abiotic direct indicators (pollen, chironomids, organic matter, oxygen isotopes, mineralogy, magnetic susceptibility, macroscopic components of lake marl) and some indirect palaeoclimatic records (lake-level reconstructions, as well as pollen–chironomid-based quantitative reconstruction of climatic variables) (Millet *et al.*, 2003; Vannière *et al.*, 2004; Heiri and Millet, 2005; Peyron *et al.*, 2005; Magny *et al.*, 2006). These climatic changes are manifest in the North Atlantic region as an abrupt warming at the start of Lateglacial Interstadial (GI-1), followed by the cold Younger Dryas event (GS-1) and finally a second abrupt warming at the beginning of the Holocene. In addition, short-lived cooling events were identified as the Older Dryas (GI-1d), the Gerzensee oscillation (GI-1b) and the Preboreal oscillation (PBO) (Lowe, 1994; Björck *et al.*, 1998).

Testate amoeba preparation

A total of 42 samples was taken from core 6 for testate amoeba analysis (Fig. 2) corresponding to a mean temporal resolution of ca. 90 a per sample. The samples were 0.5 or 1 cm thick and 0.3 cm^3 in volume. Samples were sieved to retain the 25–250 μm size fractions (Wall *et al.*, 2009). This contrasts with most comparable palaeolimnological studies where only the fraction >63 μm or >45 μm is used (Ruzicka, 1982; Medioli and Scott, 1983, 1988; McCarthy *et al.*, 1995; Asioli *et al.*, 1996; Boudreau *et al.*, 2005). We examined the samples in Hydro-Bios plankton chambers with an inverted microscope (Olympus IX71). Identification to species level whenever possible follows Cash and Hopkinson (1905, 1909), Cash *et al.* (1915, 1919), Chardez (1967), Ogden and Hedley (1980), and Ogden (1983), using the most recent nomenclature (Meisterfeld, 2002a,b). The preservation of tests was good and we counted on average 538 shells per sample (min. 89, max. 3261). A minimum count of 200 tests was reached for all samples except two (level 464 and 381 cm, for which 89 and 191 tests, respectively, were counted in the entire 0.3 cm^3 sample). We calculated the test accumulation rate (in number of tests cm^{-2} a^{-1}) by using the abundance of testate amoebae per sample and the sedimentation rate calculated by Magny *et al.* (2006). Rare occurrences of diatom frustules and few ostracods were also recorded in the samples.

Numerical analyses

A percentage diagram was generated using TILIA and TILIA-Graph (Grimm, 1991). Percentages were based on the total number of tests counted in each sample. Stratigraphic zone limits in the testate amoeba record, defined by major changes in assemblage composition, were determined by using the stratigraphically constrained cluster analysis software Coniss (Grimm, 1991). The statistical significance of these zones were assessed following Bennett's (1996) broken stick model. Bennett's method permits setting up the significance of the zones defined by Coniss by comparison with a model of random distribution of zones within the data. In other words, the number of zones is determined by comparison of the residual variance that results from the structure in dataset to the one due to stochastic processes based on a shuffle of the same data.

We compared the contributions of each species to the assemblage across the samples using rank–frequency curves (Frontier and Pichod-Viale, 1998) to assess whether beyond species richness and density the structure of the assemblage responded to palaeoenvironmental changes. Each curve represents a sample in which the species are arranged in decreasing rank of their relative abundance. Principal component analysis (PCA), rarefaction analysis and box plot of species richness were determined using the PAST software of Palaeontological Statistics version 1.57 (Hammer *et al.*, 2001).

Results

Fifty-four testate amoeba taxa were recorded in the Lateglacial–Holocene transition of core 6 (Fig. 3), mostly belonging to

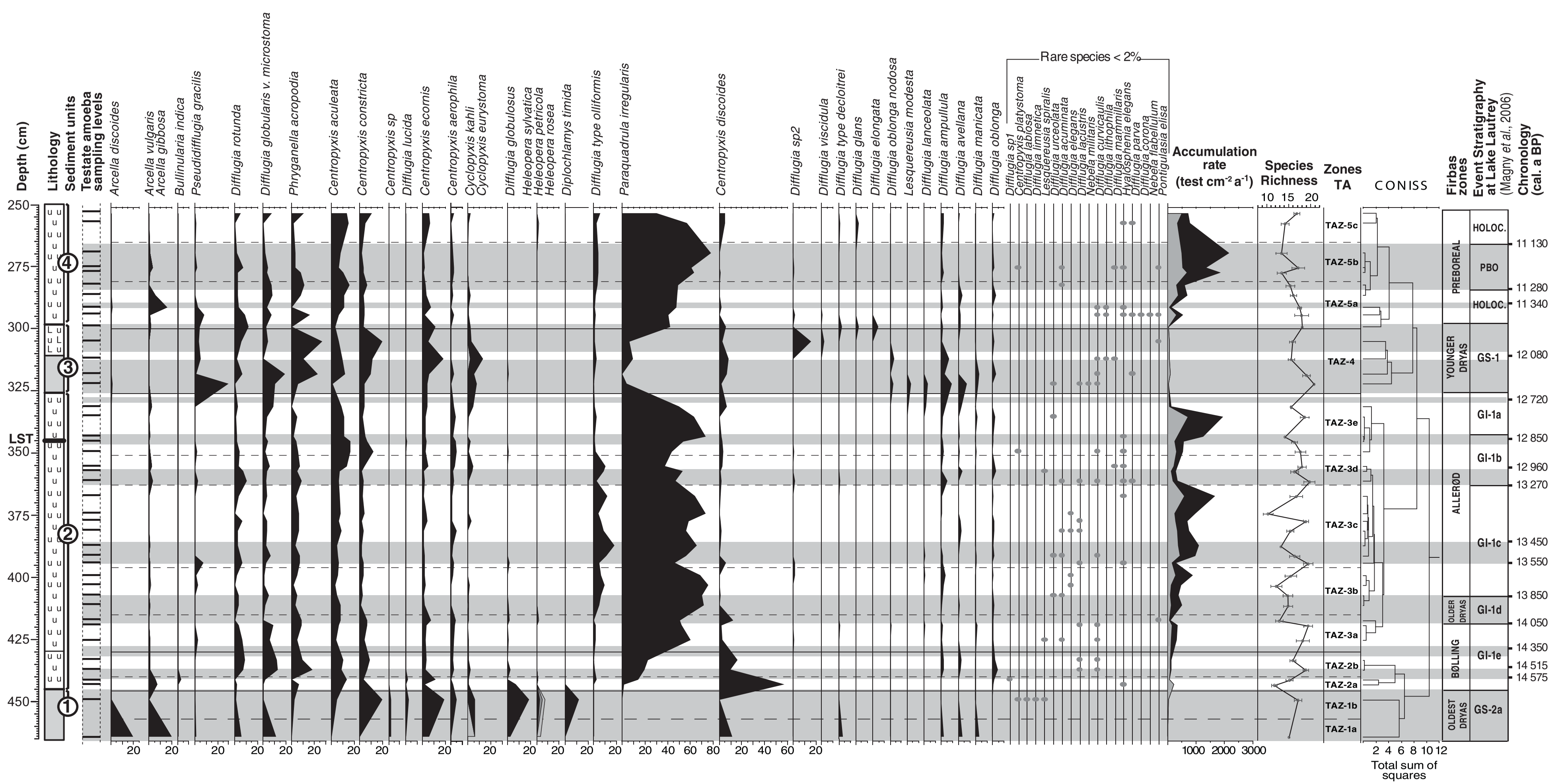

Figure 3 Testate amoeba record of Lake Lautrey core 6. Rare species (<2% of relative abundance) are represented as presence/absence. Testate amoeba accumulation rate and species richness curves are presented at the far right of the diagram; black, total accumulation rate; grey, total accumulation rate without *Paraquadrula irregularis*. Grey bands correspond to cooling events documented by several biotic and/or non-biotic indicators as illustrated in Fig. 2 (Magny *et al*., 2006). The species richness is estimated for a count of 200 tests per sample based on rarefaction analyses, except for samples at levels 464 and 381 cm. TAZ, testate amoeba zones. Results of Coniss analysis are presented as a cluster diagram

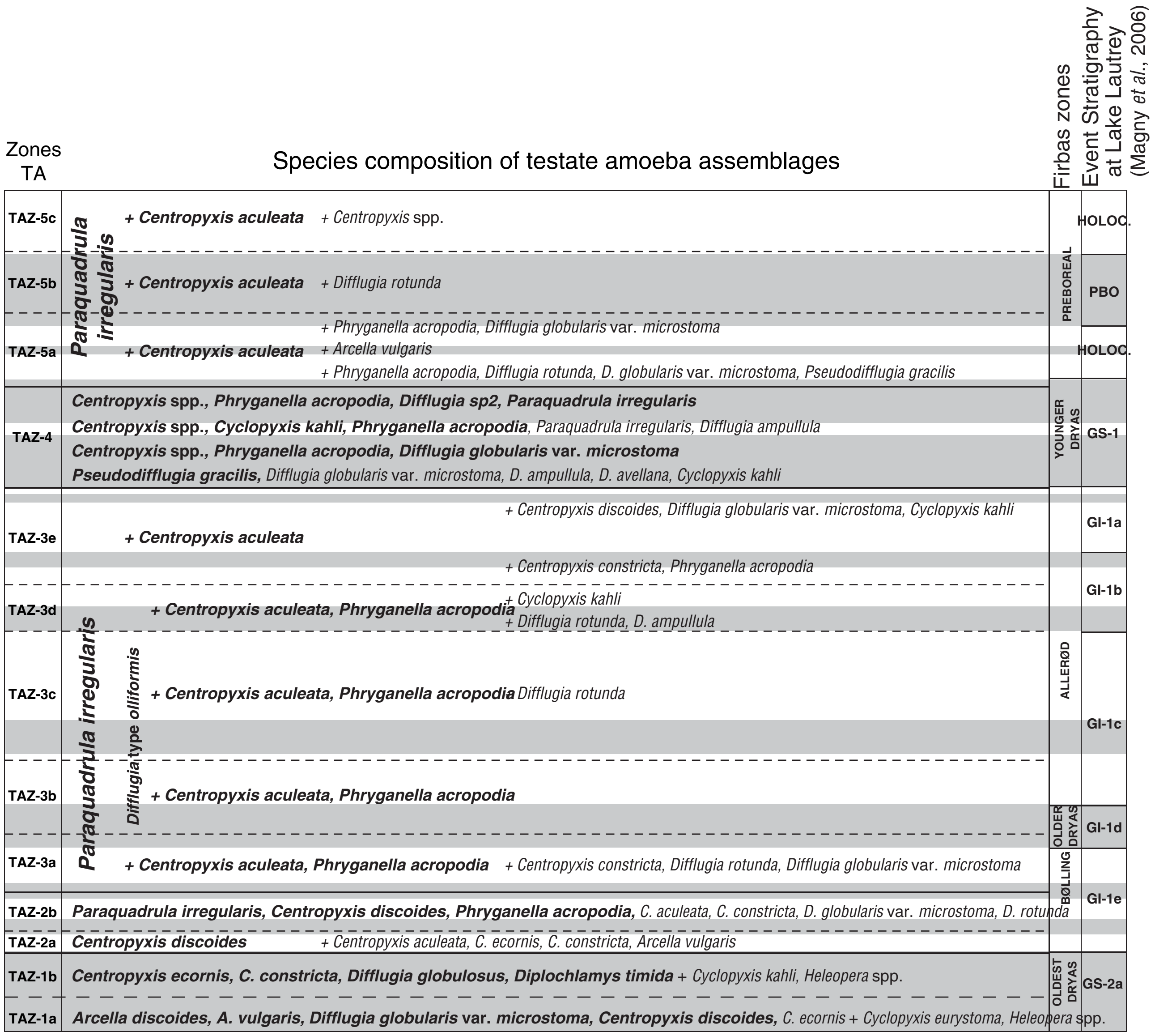

Figure 4 Species composition of testate amoeba assemblages with succession event stratigraphy established at Lake Lautrey

Order Arcellinida Kent, 1880, with one species (*Pseudodifflugia gracilis*) from Class Filosia Leidy, 1879. A Coniss analysis identified five testate amoeba assemblage zones (TAZ) statistically assessed using Bennett's (1996) broken stick model. These zones were further divided into subzones for the description of the diagram (Figs 3 and 4).

TAZ-1 (below 445 cm) corresponds to Lake Lautrey sediment unit 1 (500–445 cm) and is characterised by very low accumulation rate with two successive assemblages. These assemblages can be considered as two separated zones according to Bennett's (1996) broken stick model but, taking into consideration that there are only two samples, they are defined as subzones here. The older subzone (TAZ-1a, 464 cm) is dominated by *Arcella discoides*, *A. vulgaris*, *Difflugia globularis* var. *microstoma* and *Centropyxis discoides*, whereas, in the younger subzone (TAZ-1b, 449 cm), *Centropyxis ecornis*, *C. constricta*, *Difflugia globulosus* and *Diplochlamys timida* prevail. In this zone, some species from the genera *Heleopera* and *Cyclopyxis* are represented in relatively high percentages as compared with other samples from this section of the core.

TAZ-2 (445–430 cm) is also divided into two subzones. In TAZ-2a (445–440 cm), the accumulation rate increases. This subzone is characterised by an abrupt expansion of *Centropyxis discoides*, which dominates the assemblage, and high frequencies of other *Centropyxis* species. *Arcella* spp. and *Difflugia globulosus* show relatively high percentages by comparison with the rest of the analysed samples. TAZ-2b (440–430 cm) shows slight decreases in the accumulation rate and a shift in dominance from *Centropyxis* spp. to *Difflugia* spp., *Paraquadrula irregularis* and *Phryganella acropodia*.

TAZ-3 (430–326 cm), subdivided into five subzones, is dominated by *Paraquadrula irregularis* and continuous but lower frequencies of *Centropyxis aculeata* and *Phryganella acropodia*. TAZ-3a (430–415 cm) marks the beginning of the predominance of *P. irregularis* with an increase in species richness. At level 417 cm *Centropyxis discoides* and to a lesser extent other *Centropyxis* expand in relative abundance. By contrast, frequencies of *P. irregularis* and the accumulation rate decrease. TAZ-3b (415–396 cm) is again dominated by *P. irregularis* accompanied by *Difflugia* type *olliformis* in low percentages. The presence of *D.* type *olliformis* characterises the middle of TAZ-3, from TAZ-3b until TAZ-3d. At level 399 cm, the accumulation rate increases. TAZ-3c (396–363 cm) begins with a sharp fall in accumulation rate and in *P. irregularis* percentages at 394 cm with noteworthy increases in the percentages of *Difflugia rotunda*, *Pseudodifflugia gracilis*, *Phryganella acropodia* and *Centropyxis discoides*. Above 394 cm, the next samples are typified by a high accumulation rate with two peaks at level 387 and 367 cm associated with peaks in *Difflugia* type *olliformis* percentages. This subzone is marked by the predominance of *P. irregularis*. TAZ-3d (363–351 cm) is characterised by a decrease in the accumulation rate associated with a decline in frequencies of *P. irregularis*. By contrast, the percentages of *Difflugia rotunda*, *D. ampullula* and *P. acropodia* rise, followed by those of *Centropyxis* species, *Cyclopyxis kahli* and *D.* type *olliformis*. During TAZ-3e (351–326 cm), the accumulation rate increases progressively to a maximum of 1915.5 tests cm^{-2} a^{-1} at level 335 cm *Difflugia* type *olliformis* disappears. At the beginning of this subzone, *Centropyxis aculeata* and *C. constricta* expand until level 345 cm, when they disappear until level 331 cm. The end of this zone is defined by a sharp fall in accumulation rate (level 331 cm) associated with a relative increase in frequencies of *D. globularis* var. *microstoma*, *Cyclopyxis kahli* and *Centropyxis discoides*.

TAZ-4 (326–300 cm) corresponds globally to sediment unit 3 (i.e. Younger Dryas age) and displays low accumulation rate values with a disappearance of *P. irregularis*. During this period, the most abundant testate amoeba species are *Phryganella acropodia*, *Centropyxis*, *Cyclopyxis* and *Difflugia*. The beginning of this zone (level 322 cm) is characterised by a predominance of *Pseudodifflugia gracilis* associated with *Difflugia globularis* var. *microstoma*, *D. ampullula*, *D. avellana* and *Cyclopyxis kahli*. Then, *Centropyxis* species appear in very low percentages. At level 318 cm, the dominant species is *Phryganella acropodia* together with *D. globularis* var. *microstoma*. At this level, the percentages of *Centropyxis* species increase. In the middle of TAZ-4, the most abundant species is *Centropyxis ecornis*, with a good representation of other *Centropyxis* and *Cyclopyxis* species. Subsequently, *Phryganella acropodia* dominates the assemblage. In the same way, *Centropyxis constricta* and *Difflugia sp.2* show peaks at level 305 cm. This zone ends with a return of *P. irregularis* to high frequencies and a decline in *Centropyxis* species percentages, except for *C. ecornis*.

In TAZ-5 (above 300 cm), the accumulation rate of testate amoebae increases rapidly and reaches a maximum of 2148.4 tests cm^{-2} a^{-1} at level 269 cm. In this zone, *P. irregularis* maintains high percentages, accompanied by *Centropyxis aculeata*. In TAZ-5a (300–281 cm), the accumulation rate reaches 540 tests cm^{-2} a^{-1} at level 294 cm. *Centropyxis* spp. occur in low percentages except for *C. aculeata*. *Paraquadrula irregularis* is well represented in this subzone, and peaks in *Phryganella acropodia*, *Difflugia rotunda*, *D. globularis* var. *microstoma* and *Pseudodifflugia gracilis* proportions are observed. At level 291 cm the testate accumulation rate drops sharply and a peak in *Arcella vulgaris* and a rise in *Centropyxis* spp. percentages occurs. The upper part of this subzone shows an increase in accumulation rate. This part is characterised by an assemblage composed of *P. irregularis*, *Centropyxis* species, *Phryganella acropodia* and *D. globularis* var. *microstoma* and by a decline of *A. vulgaris*. TAZ-5b (281–265 cm) is dominated by *P. irregularis*, which reaches a maximum of 77.5% of relative abundance abundance at level 269 cm (i.e. 1664.6 tests cm^{-2} a^{-1}). *Centropyxis aculeata* percentages remain stable. A peak of *Difflugia rotunda* and a slight increase in *Arcella vulgaris* percentages occur at level 275 cm, where the accumulation rate is minimal for this subzone. The last subzone, TAZ-5c (above 265 cm) records a drop in test accumulation rate associated with a decline in *P. irregularis* percentages in favour of *Centropyxis aculeata* and other *Centropyxis* species.

Figure 3 illustrates how *P. irregularis* amplifies the variations in accumulation rates. However, the signal of this species does not modify the global fluctuation tendency of the whole testate amoeba assemblages, except in the upper part of the diagram (257 cm and 269 cm).

Discussion

Overall testate amoeba assemblage composition

Testate amoeba tests are found in significant numbers in all analysed sediment samples from the Lateglacial–early Holocene sequence from Lake Lautrey core 6. The overall assemblage composition is coherent with the habitat: most testate amoeba species recorded belong to genera *Difflugia* (28 species) and *Centropyxis* (7 species) (Fig. 5), which include mostly aquatic freshwater taxa (Chardez, 1965, 1968; Schönborn, 1967). Yang *et al.* (2005, 2009) found the same dominant genera in nine plateau lakes from China. *Centropyxis* and *Difflugia* species are generally the most abundant taxa in Quaternary lake deposits. Species from other genera, such as *Arcella*, *Hyalosphenia*, *Heleopera* and *Nebela*, mostly belong to littoral or lake surrounding habitats (Schönborn, 1967; Ellison and Ogden, 1987).

The overall composition of testate amoeba assemblages is also in accordance with the position of the core, towards the lake margin (Magny *et al.*, 2006). Identification of the presence of aquatic vegetation in previous work from this site is confirmed by the occurrence in testate amoeba assemblages of genera such as *Arcella*, *Hyalosphenia*, *Paraquadrula* and some *Centropyxis*, which live in the Aufwuchs (periphyton) of water plants (Schönborn, 1967, 1984; Lena, 1982). The occurrence of taxa characteristic of mosses and *Sphagnum* such as *Hyalosphenia elegans* and *Heleopera* species indicates the influence of terrestrial inputs, in agreement with the TeOC and TOC/N data (Fig. 6).

The amount of organic matter available in the lake sediment either originating from *in situ* primary production or from allochthonous sources likely influenced the testate amoeba communities. Indeed, in addition to representing a food source for bacteria and fungi on which the testate amoebae partly feed, this organic matter also serves as building material for the shells. Actually, most of the observed testate amoeba taxa (e.g. genera *Difflugia*, *Centropyxis*, *Cyclopyxis*, *Phryganella*, *Bulli-*

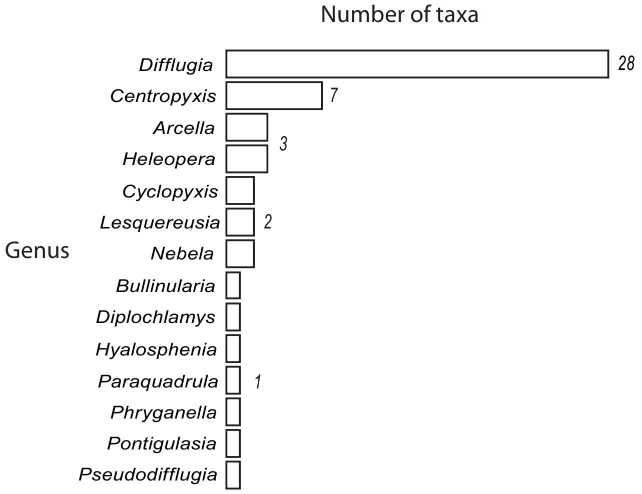

Figure 5 Number of testate amoeba taxa observed in Lake Lautrey core 6 for each genus

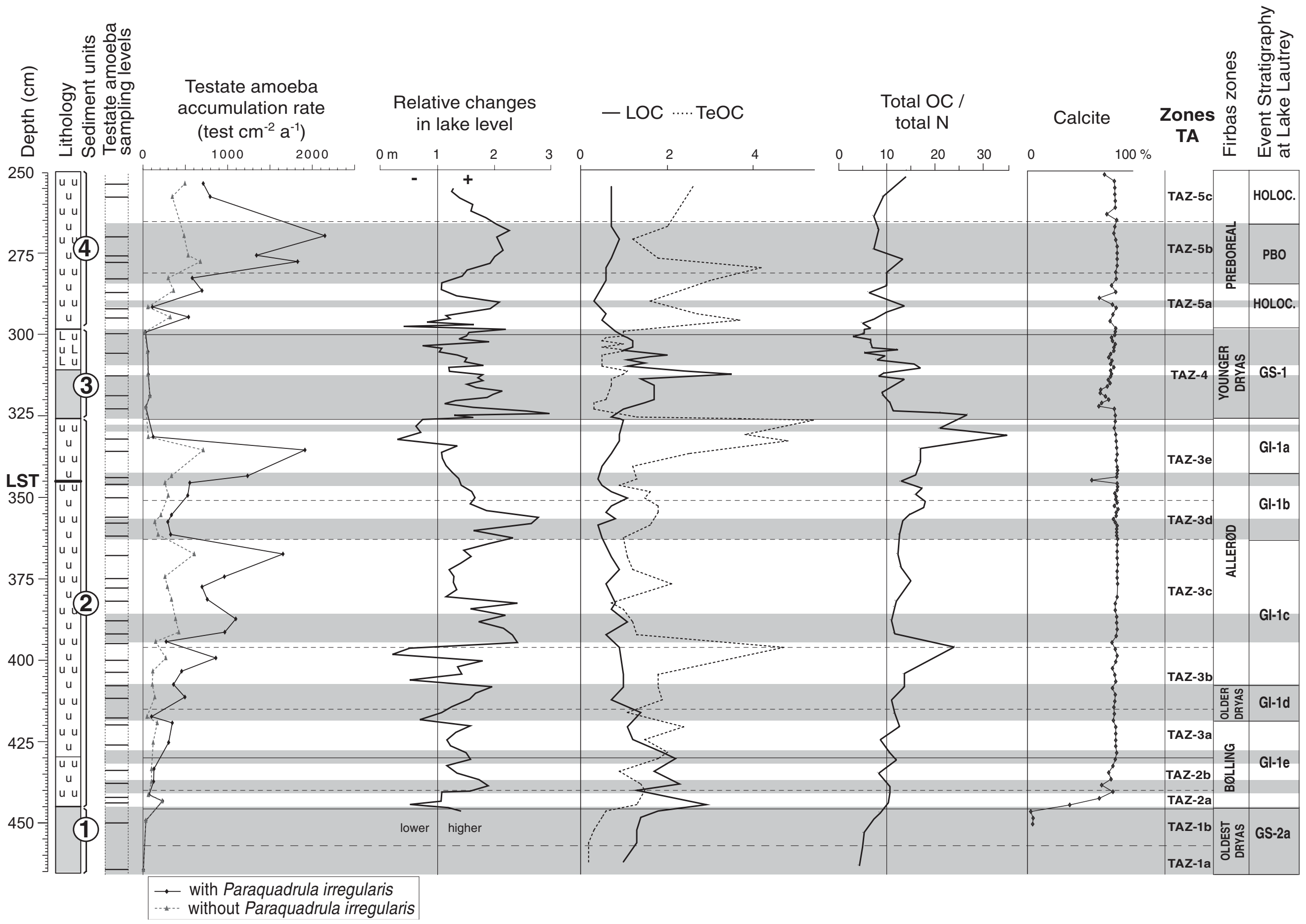

Figure 6 Comparison of testate amoeba accumulation rate in Lake Lautrey with other proxies from Magny *et al.* (2006). Trophic level is reconstructed using chironomid data. LOC, organic carbon of autochthonous origin (as percentage of total organic carbon); TeOC, organic carbon of allochthonous origin (percentage of sediment). Testate amoeba and Firbas zones as well as climatic event stratigraphy are summarised on the left

nularia, *Pseudodifflugia*) build their tests from organic or mineral particles available in their immediate environment (Lena, 1982; Ellison and Ogden, 1987). A notable exception is *Paraquadrula irregularis*, which secretes its shell from calcite in agreement with the calcareous origin of the sediments (Schönborn, 1984).

Testate amoeba accumulation rate and species richness

The abundances of testate amoeba observed in Lake Lautrey core 6 are comparable to those recorded in other studies (Ruzicka, 1982; Andreev *et al.*, 2004). As observed by Andreev *et al.* (2004) in Nikolay Lake in Arctic Russia, the test accumulation rate mirrors climatic oscillations. Thus the major cold periods (Oldest and Younger Dryas) correspond to very low test accumulation rates (Fig. 3), in contrast with higher rates observed during the Bølling–Allerød Interstadial (GI-1) and the Preboreal. However, the increases in test accumulation rate observed at the beginning of the GI-1 and the Preboreal are limited and gradual with maximum values (up to 1500 tests cm^{-2} a^{-1}) being reached only in the middle of GI-1 (ca. 13 350 cal. a BP). Nevertheless, during the early Holocene, the expansion of the testate amoeba assemblage appears to have been quicker insofar as the maximal values (more than 2100 tests cm^{-2} a^{-1}) are attained only ca. 300 a after the beginning of the Holocene (Fig. 3).

Interestingly, even short-lived cooling events, such as GI-1d and GI-1b at ca. 13 550–13 450 cal. a BP (GI-1c2 as defined by Brauer *et al.*, 2000, from the Meerfelder Maar sequence in Germany), also correspond to decreases in test accumulation rate. A notable exception is the PBO, which coincided with a maximal accumulation rate. This PBO anomaly is all the more surprising because a minor 'forerunner' cooling event registered by other proxies at level 291 cm (Magny *et al.*, 2006,

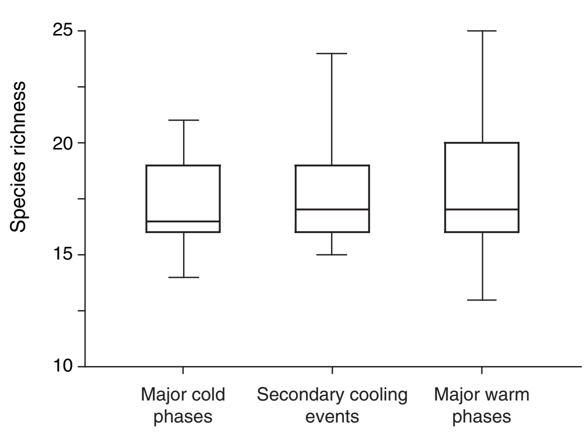

Figure 7 Box plot (box-and-whisker plot) of testate amoeba species richness in the different climatic phases at Lake Lautrey; i.e. major cold phases: Oldest and Younger Dryas; sub-millennial-scale cooling events: Older Dryas, GI-1c2, Gerzensee Oscillation, forerunner of PBO, PBO; major warm phases: Bølling–Allerød Interstadial and Preboreal. The plot depicts the different groups with minimum value, lower quartile, median, upper quartile, and maximum value

2007) is clearly defined in the testate amoeba assemblages by both a decrease in test accumulation rate (Fig. 3) and a peak in *Arcella vulgaris* frequencies. Overall, the response of testate amoebae to climate change seems to be more rapid and marked in assemblage structure and composition (particularly in terms of species dominance), than in the accumulation rate (see below).

The species richness corresponds to that observed in other palaeolimnological studies for the Holocene (Andreev *et al.*, 2004; 57 species). However, in contrast to abundance patterns, the variations in species richness observed at Lake Lautrey are not correlated with climatic oscillations (Figs 3 and 7) as was the case in Nikolay Lake (Arctic Russia).

Testate amoeba assemblages and climate event stratigraphy

The comparison of palaeoenvironmental records from Lake Lautrey suggests a tight link between testate amoeba assemblages and environmental and climatic variations during the Lateglacial–Holocene transition: (1) the major testate amoeba zones agree well with the Firbas pollen zones and the major climatic events, such as, the Oldest Dryas, Bølling–Allerød Interstadial, Younger Dryas and Preboreal; (2) the PCA analysis revealed a clear correlation between the testate amoeba data and other climatic proxies (Fig. 8); (3) changes in composition (Figs 3 and 4) and structure (Fig. 9) of testate amoeba assemblages as well as in accumulation rate (Fig. 3) are associated with major variations in climate.

Variations in dominance patterns

Testate amoeba assemblage dominance patterns revealed two patterns: (1) a clear difference is observed in the dominant species recorded between cold and warm phases (Figs 3 and 4); and (2) several distinct assemblages are observed in cold phase samples. During the Oldest Dryas, two successive assemblages are observed, i.e. TAZ-1a and TAZ-1b. These assemblages differ from that of the Younger Dryas (TAZ-4). By contrast, warm periods, i.e. GI-1 (Bølling–Allerød Interstadial) and the early Holocene, clearly display a more common pattern, with a marked dominance of *Paraquadrula irregularis*. Moreover, just at the beginning of the Bølling zone, a short-lived warm assemblage, TAZ-2a, is characterised by the dominance of *Centropyxis discoides*. This zone can be considered a transitional zone between the Oldest Dryas and the Bølling–Allerød Interstadial, also documented by the chironomid, mineralogy and magnetic susceptibility records (Magny *et al.*, 2006).

Some species observed during specific climatic phases or periods require further study: *Arcella discoides*, *Cyclopyxis kahli*, *C. eurystoma*, *Heleopera* species, *Diplochlamys timida*, *Difflugia sp.2*, *D. globulosus*, *D. viscidula*, *D.* type *decloitrei*, *D. oblonga nodosa*, *D. lanceolata* and *Lesquereusia modesta* were recorded mostly in cold periods (Figs 3 and 4), while *Paraquadrula irregularis* and *Difflugia* type *olliformis* were observed in warm phases. Other taxa were noted only in a specific climatic period, e.g. *Arcella discoides*, *Difflugia globulosus*, *Heleopera* species and *Diplochlamys timida* for the Oldest Dryas; and *Difflugia sp.2*, *D. globulosus*, *D. viscidula*, *D. oblonga nodosa*, *D. lanceolata* and *Lesquereusia modesta* for the Younger Dryas.

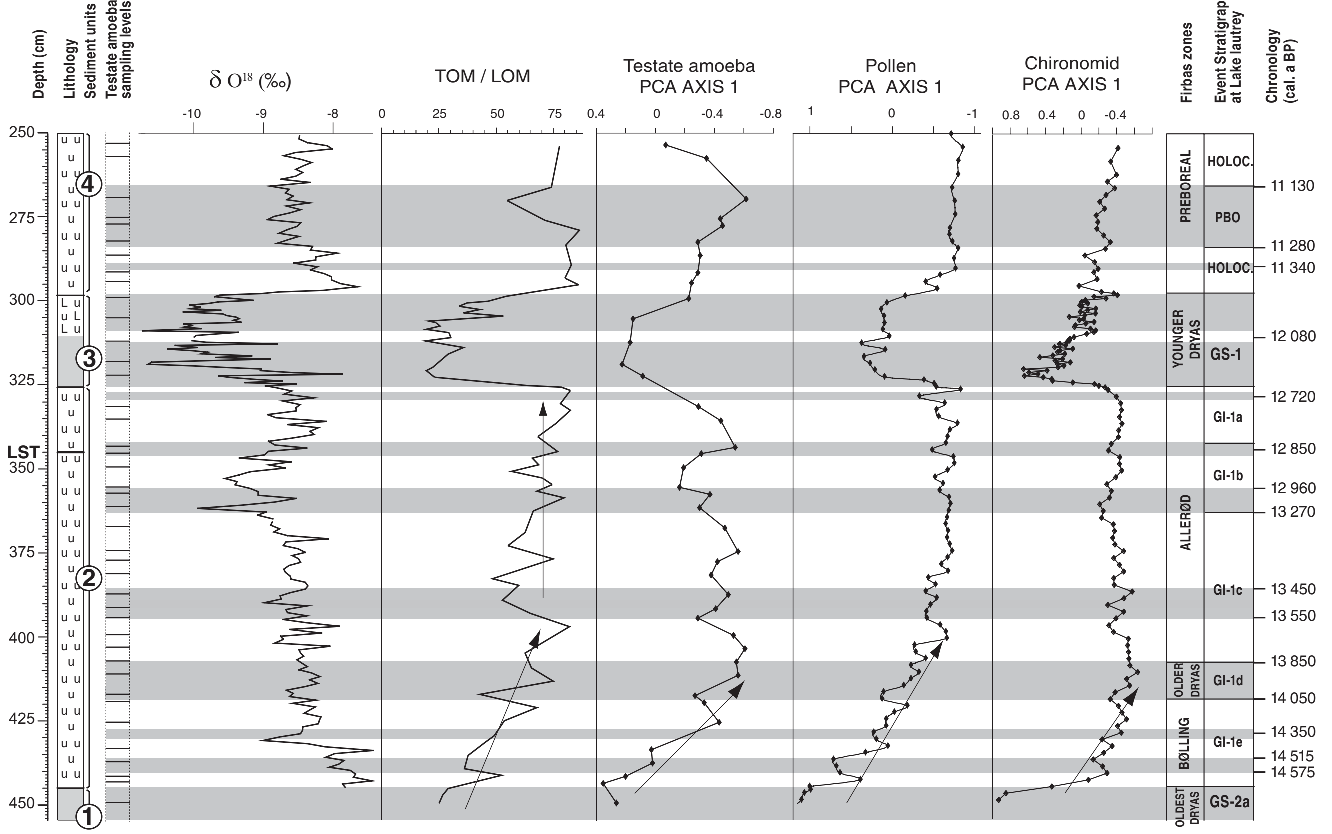

Figure 8 PCA axis 1 representation of testate amoeba, pollen and chironomid data presented in parallel to oxygen isotope record and terrestrial organic matter (TOM)/organic matter of lacustrine autochthonous origin (LOM) ratio from Magny *et al.* (2006). The positions of testate amoeba samples are represented next to the lithology. Grey bands correspond to cooling events documented by several biotic and/or non-biotic indicators

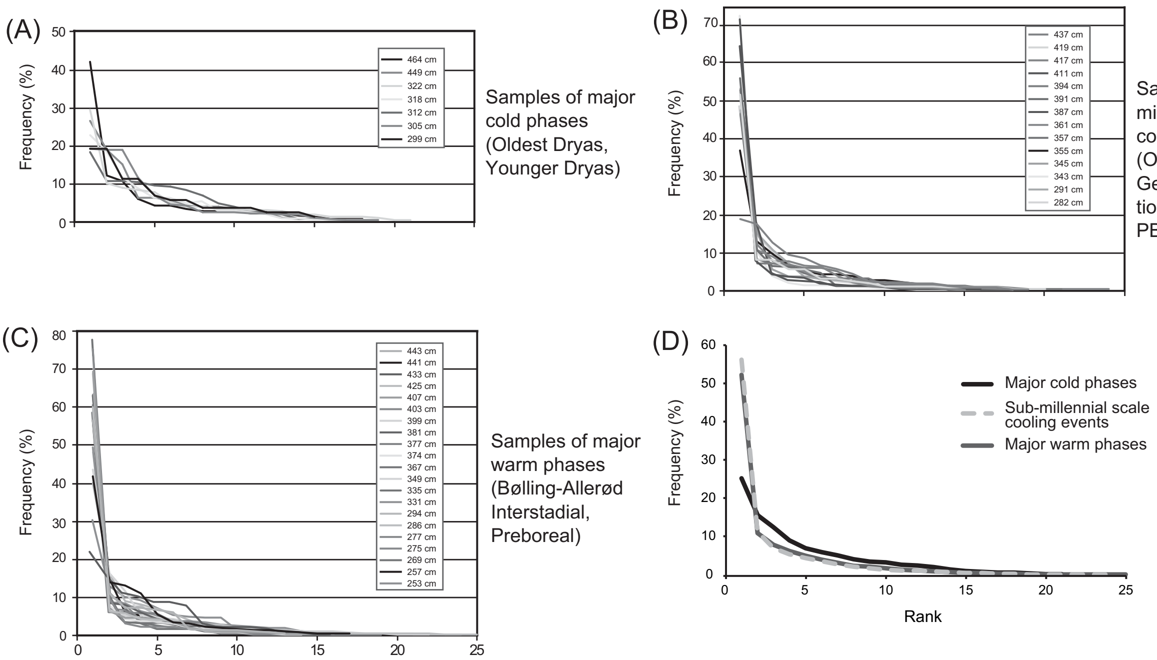

Figure 9 Testate amoeba assemblage structure represented in rank–frequency diagrams established for samples documenting (A) major cold phases, i.e. Oldest Dryas (GS-2a) and Younger Dryas (GS-1), (B) sub-millennial-scale cooling events, i.e. Older Dryas (GI-1d), GI-1c2, Gerzensee Oscillation (GI-1b), forerunner of PBO and PBO, and (C) major warm phases, i.e. Bølling–Allerød Interstadial (GI) and Preboreal (early Holocene). Each curve represents for a given sample the successive relative abundance (as percentage of total assemblage) in the assemblage of the different species ordered in decreasing order (rank). (D) Mean curves for each of three climatic categories

Variations in assemblage structure (rank–frequency)

In addition to changes in taxon dominance, the differences between cold and warm periods are clearly illustrated in rank–frequency diagrams (Fig. 9). During warm phases, the testate amoeba assemblages show an unbalanced structure with a strong dominance of a single taxon, namely *Paraquadrula irregularis*. However, the trend in assemblage structure of sub-millennial-scale cooling events is similar to that of major warm periods. Conversely, the characteristic assemblages for the major cold phases present a more balanced structure, with several species well represented. Finally, the structure of assemblage TAZ-5a (300–281 cm) is intermediate between the balanced assemblage structure in TAZ-4 (Younger Dryas cold event) and the unbalanced pattern observed in TAZ-5b (281–265 cm, Preboreal warmer period).

Size of testate amoebae species and climatic phases

During major cold phases the proportion of large species increased. As illustrated by assemblages TAZ-1 and TAZ-4, the majority of species have a shell longer than 63 μm, i.e. most *Centropyxis*, *Arcella*, *Difflugia* and *Cyclopyxis* species. By contrast, warmer climatic periods are dominated by small species such as *Paraquadrula irregularis*, *Phryganella acropodia* and *Difflugia* type *olliformis*. This is in agreement with Dallimore *et al.* (2000), who observed larger and coarser shells of testate amoeba species in Arctic climatic conditions compared with smaller species that are typical of temperate environments.

Possible environmental controls over testate amoeba assemblage variations

Although a clear correlation was observed between the testate amoeba data and climatic phases in our data, this does not necessarily imply a direct control of climate on testate amoeba density and assemblage structure. Indeed, nutrient resources, oxygen levels, soil moisture and pH are known as important factors that influence the composition of testate amoeba assemblages (Asioli *et al.*, 1996; Burbidge and Schröder-Adams, 1998; Reinhardt *et al.*, 1998; Dallimore *et al.*, 2000; Patterson *et al.*, 2002). In lacustrine basins such as Lake Lautrey, Millet *et al.* (2003) and Heiri and Millet (2005) showed that benthic fauna are particularly affected by the climate as well as other environmental factors such as organic matter inputs. Likewise, Burbidge and Schröder-Adams (1998) and Dallimore *et al.* (2000) highlighted the link between the abundance of testate amoebae and organic matter as a nutrient resource. In the same way, Medioli and Scott (1983) suggested that some testate amoeba species can reflect, among others, variations in organic matter inputs. A comparison with other proxies analysed at Lake Lautrey (Figs 3, 6 and 8) suggests additional possible (direct or indirect) factors that may explain the apparent link between climate and testate amoeba assemblages:

1. In this study, testate amoeba scores following PCA axis 1 broadly mirror the curves of TOM/LOM, chironomid and pollen PCA axis 1 (Fig. 8). The expansion of testate amoeba at the beginning of the Holocene is matched by similar abrupt changes at the beginning of GI-1 and the Holocene for other proxies, such as pollen, chironomid and TOM/LOM ratio (Fig. 8).
2. Most of the observed taxa (e.g. genera *Difflugia*, *Centropyxis*, *Cyclopyxis*, *Phryganella*, *Bullinularia*, *Pseudodifflu-*

gia, etc.) build their tests from organic or mineral particles available in their immediate environment (Lena, 1982; Ellison and Ogden, 1987). Testate amoeba communities are thus likely to be influenced by the amount of organic matter available in the lake as well as its origin (either from *in situ* primary production or from allochthonous sources). A correlation is indeed observed between the TOM/LOM ratio and testate amoeba PCA axis 1 (Fig. 8). Also, at levels 393–398 cm and 325–335 cm, a C/N ratio higher than 20 (resulting from high terrestrial inputs of organic matter) together with very low lake levels, seems to have had a negative influence on testate amoebae, resulting in decreases in testate accumulation rate (Fig. 6). During the Allerød, the other decreases in testate accumulation rate correspond to lower peaks in terrestrial organic inputs as well as C/N ratios >15 (levels 375–379 cm and 347–360 cm), suggesting that the influence of organic matter inputs on testate amoeba assemblages is important during this phase. However, as observed at levels 393–398 cm and 325–335 cm, C/N ratios > 20 and low lake levels can affect the oxygen level in the sediment and cause a decrease in testate amoeba abundances. This hypothesis may explain the early fall in accumulation rate at the end of TAZ-3 (Figs 3 and 6). Throughout the other periods, the relation between testate amoeba assemblages and organic matter inputs is not synchronous, with C/N ratio around 10 (Fig. 6). Thus this observation suggests that C/N ratios higher than 15 have a negative influence on testate amoebae and/or that other factors influence the assemblages.

3. *Centropyxis discoides*, which strongly dominated the testate amoeba assemblage for a short period at the beginning of the Bølling zone (TAZ-2a), appears to be a pioneer species correlated to a peak in autochthonous organic matter, resulting from algal production (Figs 3 and 6). This parallels the pattern of *Chironomus* (Chironomidae) for the aquatic domain and *Juniperus* and *Betula* pollen for the terrestrial vegetation, whose curves increase at the same levels (Magny *et al.*, 2006). Moreover, in this sequence, *C. discoides* is mostly found when lacustrine organic matter inputs are important and when the presence of Characeae oogonia is observed (Magny *et al.*, 2006). This observation is in accordance with the herbivorous dietary pattern of this species, which mostly feeds on microalgae and plant cells (Chardez, 1964). Furthermore, according to Schönborn (1967), *Cyclopyxis kahli* is more abundant in oligotrophic conditions with a C/N ratio below 10. Indeed, in the Lake Lautrey sequence, *Cyclopyxis kahli* and *C. eurystoma* are preferentially observed during cold phases (Oldest and Younger Dryas) where C/N ratios are lower together with oligotrophic or slightly mesotrophic water conditions (Fig. 6).
4. The early expansion of *Paraquadrula irregularis* at the end of Younger Dryas (Fig. 3, level 299 cm) and the increase in the testate amoeba PCA curve (Fig. 8) at the beginning of the Bølling–Allerød Interstadial offer an additional indication for earliness of the response of aquatic organisms to climatic changes, as shown by the chironomid data and PCA axis 1 (Magny *et al.*, 2006) and as illustrated by other multi-proxy records (Ammann *et al.*, 2000; Birks *et al.*, 2000; Yu, 2000). Thus the sample at the beginning of TAZ-5 (level 299 cm), can be considered as defining the transition between the Younger Dryas and the Preboreal, as observed in the chironomid records (Magny *et al.*, 2006).

It might be tempting to attribute the absence of *Paraquadrula irregularis* in the Oldest Dryas to the absence of biogenic calcite precipitation (which is necessary for its shell constitution) in the lake during this period (Figs 3 and 6). However, the strong decline of this species during the Younger Dryas when calcite was available seems to indicate that other factors were at play, such as climatic deterioration and origin of organic matter input. The similarity between the accumulation rate of *Paraquadrula irregularis* and terrestrial organic matter inputs for the same period (Figs 3 and 6) certainly suggests a possible causal link.

Future research priorities

An important question that thus far has received little attention is the taphonomy of testate amoebae in lake sediments. Mitchell *et al.* (2008b) recently addressed this for peat but with the exception of Ruzicka's (1982) work this has not been studied in lakes. Indeed, Ruzicka (1982) observed in the upper part of its sequence on Lake Krotten (from Oldest Dryas to the last century) that testate amoeba abundances increase considerably. Furthermore this increase is more marked towards the present period. This could be explained either by the preservation of the shells or by the influence of other environmental factors.

Additional high-resolution multi-proxy palaeolimnological studies are required to assess whether the strong correlation between testate amoeba data and palaeoclimatic signal we observed also occurred elsewhere. In particular, studies of the same climatic periods but in different regions or geographical setting would be especially useful for comparisons with the Lake Lautrey record.

Finally, as in the case of peatlands, studies on modern lake testate amoeba communities are needed to better interpret the patterns of changes in density, diversity and assemblage composition (Mitchell *et al.*, 2008a). It would be especially interesting to know more about spatial patterns (e.g. lakeshore to lake centre gradient), seasonal and inter-annual patterns and the impact of spatially or temporally defined disturbance (e.g. heat waves, local pollution) on lake testate amoebae. Indeed, the correlation between testate amoeba assemblages and organic matter inputs (Figs 6 and 8) observed in the Lake Lautrey sequence calls for detailed work on the impact of nutrient inputs (in terms of quantity and quality) on testate amoebae. Such work would help in the identification of optimal coring sites for future palaeolimnological work.

Conclusions

A comparison of testate amoeba with high-resolution data obtained from previous multi-proxy studies of a Lateglacial–early Holocene sediment sequence at Lake Lautrey provides an opportunity to test the response of testate amoebae to known climate oscillations. Although the ecological preferences of lake testate amoebae requires further work, the results strongly suggest that there is a correlation between testate amoebae and climatic and other environmental changes as follows:

- Changes in the composition of testate amoeba assemblages (dominant species and assemblage structure), as well as in the test accumulation rate corresponded to major climate events that typify the Lateglacial–Holocene transition (i.e. GS-2a, GI-1, GS-1, Preboreal).
- Decreases in test accumulation rate occur during short-lived cooling events such as GI-1d or GI-1b. A notable and unexplained exception was the PBO cooling event, which,

although well marked by other proxies, could not be recognised in our testate amoeba data.
- This study adds weight to the existence of a cooling event (GI-1c2) between the cool oscillations GI-1d and GI-1b.
- Organic matter inputs (both in quantity and quality) are an important determining factor for the abundance of testate amoeba assemblages until the Preboreal period. Modern ecological studies are needed to understand the mechanisms involved.

The demonstration of the value of lacustrine testate amoebae for palaeoclimatic reconstructions now calls for a major effort to further our understanding of lacustrine testate amoeba ecology. We suggest a dual approach with (1) more detailed multi-proxy high-resolution studies for the same periods at other sites, and (2) the study of present-day ecology of lacustrine testate amoebae and the development of transfer functions that can be applied to fossil sequences.

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