



PERGAMON

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# Biostratigraphic and palaeoenvironmental applications of testate amoebae

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## Abstract

Testate amoebae (also referred to as rhizopods, thecamoebians and arcellaceans) are single-celled organisms in which the cytoplasm is enclosed within an external shell (the test). They live in a wide range of terrestrial and aquatic habitats, including wet soils, lakes and saltmarshes, and fossil tests have been recovered from sediments from all these environments. This paper reviews existing and recently developed applications of testate amoebae analysis to biostratigraphic description of Quaternary sediments and palaeoenvironmental reconstruction. Advances in testate amoebae analysis are discussed for three key areas of Quaternary research and the potential for the further exploration and use of the technique is emphasised. These areas are: (1) *Peatlands and palaeoclimates*: Testate amoebae have been used as a new method of reconstructing palaeoclimates from ombrotrophic peats; (2) *lake sediments*: Testate amoebae respond to acidity levels in lakes but they may also be useful as indicators of pollution and temperature; (3) *saltmarshes and sea-level change*: Testate amoebae can now be added to diatoms and foraminifera as potential indicators of sea-level change. The paper concludes with an examination of future developments in testate amoebae research and highlights the need for further work to explore their full range of occurrence in Quaternary sediments. © 2001 Elsevier Science Ltd. All rights reserved.

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## 1. Introduction

It is now widely acknowledged that multi-proxy approaches to reconstructing Quaternary environments yield a much more complete picture of the past, especially where these integrate biological, lithological and isotopic evidence. Within the ‘biological’ data, it is now usual to study a wide range of fossil groups, either with the aim of obtaining information on a broader range of palaeoenvironmental parameters or to cross-check inferences from particular lines of evidence. Studies on some groups of protozoans (particularly Foraminifera in marine environments) have contributed to Quaternary science for many years but there has recently been renewed interest in freshwater shell-forming taxa—the testate amoebae. The reasons for this are diverse, but they primarily relate to discoveries of testate amoebae in association with other indicators (e.g. Scott et al., 1991), increased understanding of the modern ecology in particular habitats (e.g. Tolonen et al., 1992, 1994) and studies demonstrating that they

may be of use as indicators of a greater range of environmental conditions than was previously known (e.g. Reinhardt et al., 1998). Despite the recent renewed interest in this group of organisms, research still lags considerably behind that of most of the key bioindicators in Quaternary science, many of which have also benefited from a large body of new and existing ecological literature. Although there has been a considerable amount of work on the taxonomy of testate amoebae over the past two hundred years (for example Lamarck (1816) was aware of them), there has been rather little ecological research and the full distribution and occurrence of many taxa is only vaguely known. This paper is a review of the current position of testate amoebae research in Quaternary science. A discussion of the characteristics and taxonomy of testate amoebae focuses on the potential advantages and pitfalls in their use in Quaternary studies. This is followed by an examination of recent developments in their use as indicators in three areas of Quaternary science. In the first two of these areas (peat and lake sediments), applications are relatively well established, although still being extensively developed and refined. In the third (saltmarsh sediments and Holocene sea-level change), relatively little is known, although there may be

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considerable potential. Finally, the limitations of existing knowledge in both the occurrence and value of testate amoebae in Quaternary sediments are examined and future research directions are highlighted.

## 2. Characteristics of testate amoebae: issues for fossil studies

### 2.1. Structure and taxonomy

Unlike the Foraminifera, testate amoebae are not an easily defined taxonomic group (Charman, 1999) and thus have been referred to by a number of other terms including thecamoebians, Arcellaceans and rhizopods. In this paper, the term testate amoebae refers to all shell-forming non-marine taxa of single celled protists. Fig. 1 is a photomicrograph of a live specimen of *Nebela tinctoria*, showing the main characteristics of the organism. The test is the outer shell that encloses the living cell. There are several types of test, referred to as xenosomic or idiosomic tests, depending on the source of the materials used in their construction. Xenosomic tests are composed of particles derived from the environment

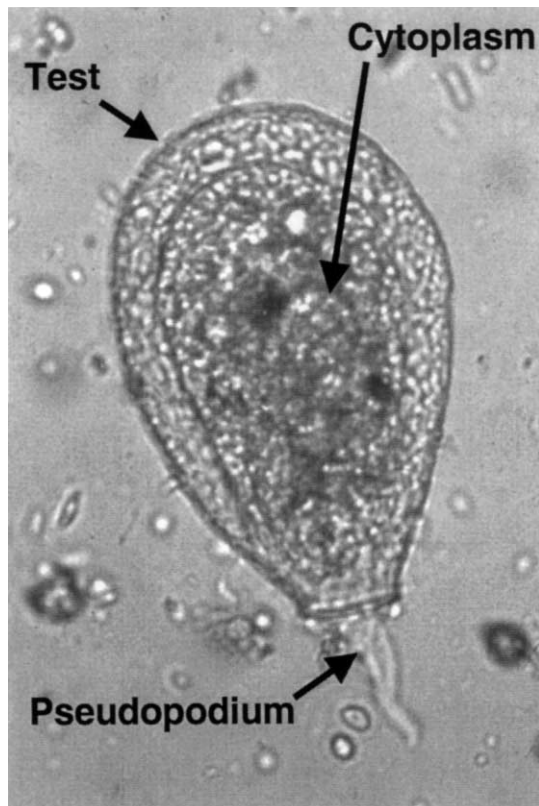


Fig. 1. Living *Nebela parvula* about 145  $\mu\text{m}$  in length. The test is composed of irregularly shaped siliceous plates, some of which are derived from other prey taxa. The pseudopodium protrudes from the mouth of the shell and is used for locomotion, attachment and feeding. From an original photograph by D. Hendon.

such as small grains of silica and sometimes including other detritus such as pollen and diatom frustules. These are fixed together with secreted cement of variable composition. Idiosomic tests are composed of materials produced by the parent amoebae at reproduction, such as pre-formed, regularly shaped overlapping plates that are usually round or oval. Spines may also be formed by this process, although some are also continuous with test walls and are not separate idiosomic structures. Some tests do not have plates but are formed entirely of a smooth proteinaceous secretion. Other tests are intermediate between idiosomic and xenosomic. For example, taxa in the genus *Nebela* often form tests that include plates of other smaller taxa, which they have consumed, as well as secretion and perhaps pre-formed plates. While some taxa appear to be entirely idiosomic, many xenosomic taxa may be capable of producing tests entirely of secretion when deprived of suitable materials (Medioli et al., 1987).

Five principal problems, related to the structure of testate amoebae, have previously been identified with fossil testate amoebae studies (Charman, 1999), of which four are relevant here:

1. Effects of fossilisation on test preservation.
2. Morphological variability within taxa.
3. Identification is based solely on test characteristics, not on the pseudopodia, which is sometimes critical.
4. Visibility of distinguishing features on specimens mounted using standard techniques. Orientation and lack of manoeuvrability under the coverslip may limit taxonomic precision.

The last two of these problems are self-explanatory and simply result in grouping of otherwise separable taxa, a not uncommon approach in palaeoecological studies. The first two are more fundamental and affect the range of applicability of testate amoebae analysis and the environmental indicator value of particular taxa. The effects of fossilisation on tests are largely unknown and although intuitively they should be related to test construction, observations show that this is not necessarily the case. For example, Medioli and Scott (1988) suggest that idiosomic tests will not be preserved as well as xenosomic tests, but some idiosomic tests are precisely those that survive rather harsh preparation treatments based on pollen analysis when other taxa are destroyed (e.g. *Assulina muscorum*—van Geel, 1978; Hendon and Charman, 1997). Differential preservation is therefore difficult to predict and further studies on the relative susceptibility to decay are required, perhaps including studies on the chemical structure of idiosomes and cementing secretions. The issue of morphological variability has been discussed at length before (Medioli and Scott, 1983). Essentially, the problem is that many taxa show gradational morphological change, so divisions between many taxa are arbitrary and therefore

vary considerably between observers (Charman, 1999). This issue is discussed further below in terms of the applications of testate amoebae analysis to specific issues in Quaternary research.

## 2.2. *Reproduction, transport and taphonomy*

The biology and reproductive strategies of testate amoebae are such that they have a profound influence on the use of testate amoebae in Quaternary research. Testate amoebae mostly reproduce by asexual binary fission, but sexual reproduction has also been reported on rare occasions (Schönborn and Peschke, 1990; Mignot and Raikov, 1992). Rates of reproduction are rapid with field observations suggesting 10–27 generations per year (Heal, 1964; Schönborn, 1992a). Even higher rates are recorded in laboratory studies with population doubling times of 2–3 days (Ogden, 1981; Lousier, 1984a, b). Clearly reproduction is a relatively fast process and this has several potential implications for Quaternary studies. Firstly, it should make testate amoebae temporally sensitive indicators of palaeoenvironmental changes. Secondly, given the scope for morphological plasticity within species (Schönborn, 1992b; Wanner and Meisterfeld, 1994) it could result in relatively rapid evolutionary change.

Another aspect of reproduction is that of movement of living tests and colonisation of new sites. Again, rather little is known about the importance of different mechanisms of transport or what proportion of any population is likely to be involved. However, the basic processes involved are known and given the rapid reproduction times, it would not require movement of a large number of tests to colonise barren areas or to introduce new species to existing assemblages. The starting point is the encystment of the living test where the cytoplasm seals itself within the test, presumably as protection against unfavourable conditions. Encysted tests can be transported in the wind or perhaps also adhere to birds' feet to move relatively long distances. This potential for rapid dispersal may be partly responsible for the wide cosmopolitanism of testate amoebae. Closely related taxa are found in many habitats almost throughout the world, giving the potential for comparisons of change on a broad geographic scale. Little is known about taphonomic processes affecting necrocoenoses of testate amoebae but there is some suggestion that in lakes, a significant proportion of the assemblage may be derived from the catchment rather than the lake itself (Ellison, 1995). In terrestrial wetlands such as peatlands and saltmarshes, small spatial scale variability in the composition of living and recently deceased assemblages suggests that this is not occurring to any appreciable extent in these habitats (e.g. Charman and Warner, 1997; Charman et al., 1998).

## 3. Applications in Quaternary biostratigraphy

It will have become apparent from the above discussion that there are many potential advantages but also some not inconsiderable problems in using testate amoebae analysis as a tool in Quaternary science. While some of these issues can be described and discussed in general terms, it is more useful to review the principal applications currently being used or explored for their potential to bring out the strengths and weaknesses in the approach. This section of the paper examines three main areas of testate amoebae analysis applied in Quaternary science and is followed in the next section by summary of where these efforts may be directed in the future.

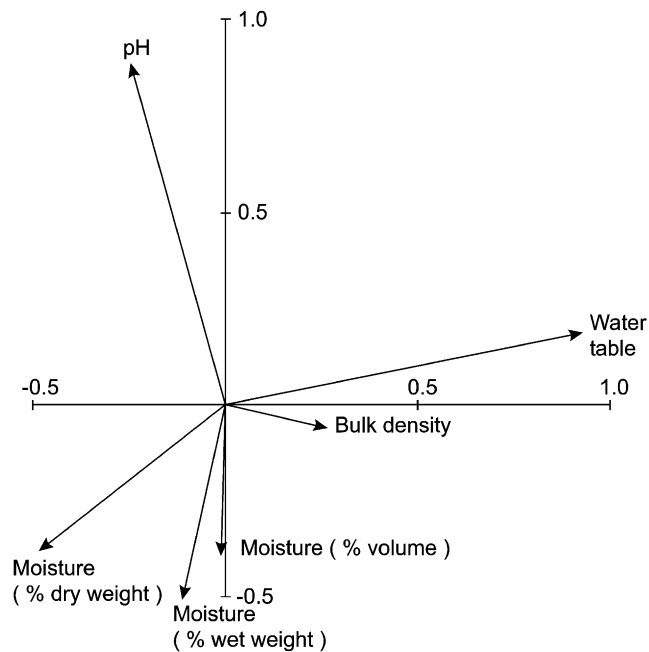
### 3.1. *Peatlands, palaeohydrology and palaeoclimate*

Peat deposits, especially the 'ombrotrophic' raised and blanket mires of the world, are well known as a source of palaeoclimatic information and a variety of techniques has been used to exploit this (Blackford, 1993). All approaches are based upon the reconstruction of the hydrological status of the peatland and the link between this and the prevailing climatic conditions. Testate amoebae analysis has been one of the techniques used in reconstruction of palaeohydrological conditions (Tolonen, 1986) as it has been known for some time that different assemblages are characteristic of different states of surface wetness (Harnisch, 1927).

Testate amoebae occur in the surface mosses and other wet vegetation of peatlands. They are present in all soils but are particularly abundant in the wet peaty soils of both ombrotrophic and minerotrophic mires. Studies of their ecology show that assemblages are principally determined by moisture status but are also influenced by nutrient status and especially by pH levels. Fig. 2 shows the relationship between these main environmental variables and testate amoebae assemblages on peatlands in Newfoundland, Canada (Charman and Warner, 1997). The nature of the relationship is typical of that on mire systems in many places (Tolonen et al., 1992; Charman and Warner, 1992; Charman, 1997; Bobrov et al., 1999) with hydrological variables (% moisture, depth to water table) showing the strongest relationship with species composition whereas pH provides a secondary, though still important, gradient. Where only sites with relatively narrow pH variability have been sampled (such as ombrotrophic and oligotrophic sites), hydrology is the only significant influence on species composition (e.g. Woodland et al., 1998).

Understanding of the nature of the relationship between testate amoebae and hydrology has improved considerably in the last 30–40 years of research. Most of the earlier work was based on qualitative assessments, often based on hydrological data consisting of the

## (a) Newfoundland active variables:



## (b) Newfoundland species:

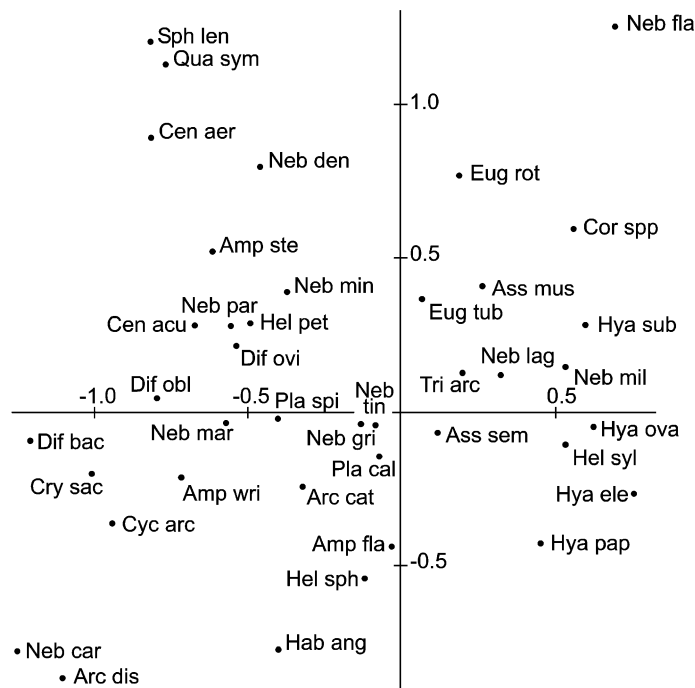


Fig. 2. The results of a canonical correspondence analysis (CCA) shown as an ordination of (a) environmental variables and (b) species. The lengths of the arrows are proportional to the strength of the relationship with the axes. An orientation close to an axis represents a strong relationship with only that axis. Key for (b): Amp fla, *Amphitrema flavum*; Amp ste, *Amphitrema stenostoma*; Amp wri, *Amphitrema wrightianum*; Arc cat, *Arcella catinus*; Arc dis, *Arcella discoïdes*; Ass mus, *Assulina muscorum*; Ass sem, *Assulina seminulum*; Cen acu, *Centropyxis aculeata* type; Cen aer, *Centropyxis aerophila* type; Cor spp, *Corythion* type; Cry sac, *Cryptodiffugia sacculus*; Cyc arc, *Cyclopyxis arcelloïdes*; Dif bac, *Diffugia bacillifera*; Dif obl, *Diffugia oblonga*; Dif ovi, *Diffugia oviformis*; Eug rot, *Euglypha rotunda* type; Eug tub, *Euglypha tuberculata*; Hab ang, *Habrotrocha angusticollis*; Hel pet, *Heleopora petricola*; Hel sph, *Heleopora sphagnicola*; Hel syl, *Heleopora sylvatica*; Hya ele, *Hyalosphenia elegans*; Hyl ova, *Hyalosphenia ovalis*; Hya pap, *Hyalosphenia papilio*; Hya sub, *Hyalosphenia subflava*; Neb car, *Nebela carinata*; Neb den, *Nebela dentistoma*; Neb fla, *Nebela flabulellum*; Neb gri, *Nebela griseola*; Neb lag, *Nebela lageniformis*; Neb mar, *Nebela marginata*; Neb mil, *Nebela militaris*; Neb min, *Nebela minor*; Neb par, *Nebela parvula*; Neb tin, *Nebela tincta*; Pla spi, *Placocista spinosa*; Pla cal, *Plagiopyxis callida*; Qua sym, *Quadrulella symmetrica*; Sph len, *Sphenoderia lenta*; Tri arc, *Trigonopyxis arcula*. Based on Charman and Warner (1997), Fig. 2.

moisture classes described by Jung (1936) from I (wettest) to VIII (driest). Meisterfeld (1977) converted this into a semi-quantitative scale using estimates based on the appearance of the mire surface and the amount of water expressed when moss polsters are squeezed by hand. This was superseded by more rigorous quantitative approaches where the moisture content of surface mosses was measured by weight loss on drying (Tolonen et al., 1985; Warner, 1987) so that species niches could be identified more precisely. Subsequent work has concentrated on this approach but moving to the use of water table data as well as moisture content (Charman and Warner, 1992, 1997; Tolonen et al., 1992, 1994). Seasonal changes in hydrological conditions are also now being taken into account with the use of mean annual water table data (Woodland et al., 1998).

The dominance of hydrology on species composition combined with the availability of quantitative hydrological data have allowed the development of transfer functions for reconstructing past changes in water tables. Warner and Charman (1994) first used this approach in reconstructing water table changes at Emo bog in north west Ontario, Canada, using a simple weighted averaging calculation. Developments in statistical modelling of species-environment relationships (Birks, 1995) and in the software to apply these easily (Line et al., 1994; Juggins and ter Braak, 1999) now allow testing of a variety of regression models for transfer functions (Woodland et al., 1998). While this approach clearly has advantages to subjectively interpreted sequences, adequate analogues for fossil assemblages remain elusive. A recent intensive study using fossil testate amoebae from peatlands in northern England has shown that analogues are rather poor for some of the older assemblages, particularly those dominated by *Hyalosphenia subflava* (Hendon, 1998). These assemblages have been interpreted as representing rather dry conditions on the basis that *H. subflava* is one of the most extreme dry indicators in Britain and elsewhere (Woodland et al., 1998; Tolonen et al., 1992). However, maximum percentages of this taxon in modern samples from Britain are only 20–30%.

Despite these potential difficulties, there is good agreement between surface wetness records based on testate amoebae and those from plant macrofossils (Charman et al., 1999) showing that the approach is robust. A further finding has been that the reconstructed water tables from adjacent but hydrologically independent mires show the same main changes over the past 4000 years (Hendon, 1998), demonstrating the dominant role of climate in determining surface wetness on ombrotrophic mires (Barber, 1981) and the link to testate amoebae assemblages through fluctuations in the water table. Perhaps more important is the agreement between a combined water table record from several sites and independent climate records (Fig. 3). Similar

multi-site water table reconstructions from testate amoebae will provide a new source of palaeoclimate data for temperate oceanic regions with ombrotrophic mires.

### 3.2. Lake sediments

Tolonen (1986) cites two early papers dealing with fossil testate amoebae in lake sediments (Lindberg, 1899; Lagerheim, 1902) but also makes it clear that there was rather little interest in their use in palaeolimnology until the 1970s and 1980s. While this revival began in Europe with the work of Schönborn (1973, 1984) and Ruzicka (1982) and was followed by a few other papers such as Ellison (1995) and Asioli et al. (1996), it has been more vigorously pursued in North America by Scott and Medioli (1983); Patterson et al. (1985, 1996); Patterson (1987); Medioli and Scott (1988); Collins et al. (1990); McCarthy et al. (1995); Reinhardt et al. (1998) and Patterson and Kumar (in press). There has also been considerable debate over the taxonomy of lake-dwelling species especially as applied to fossil studies, with several important papers arguing for greater grouping of many species (Medioli and Scott, 1983; Kumar and Dalby, 1998) but attempting to establish the concept of morphological strains for some stressed environments (Reinhardt et al., 1998). When Tolonen (1986) reviewed the use of testate amoebae, the principal environmental control on species distribution was trophic status, presumably acting through the influence of a combination of oxygen availability, the C:N ratio, grain size of sediments and surrounding vegetation. The recent work that has been done on both fossil and modern testate amoebae suggests that the palaeoenvironmental indicator value of lacustrine species may be rather greater, including response to pollution and temperature change.

Post-European settlement changes appear to have had a significant influence on the testate amoebae assemblages of Lake Erie (Scott and Medioli, 1983; Medioli and Scott, 1988). This was the first study of fossil testate amoebae in North America and effectively combines the use of data from modern and fossil assemblages to reconstruct spatial and temporal differences in the lake sediment record from a large lake. Fig. 4 summarises the main findings from this study. Three locations in the lake were cored, representing three main basin areas. The main changes were related to the period after AD 1850, when numbers of testate amoebae increased rapidly, the assemblages altered composition and the spatial variability in the lake increased. The nature of the changes in each basin is slightly different with increases in *Diffugia tricuspis* in the western basin, *D. oblonga* in the central basin and the appearance of *D. ureolata* in the eastern basin (Fig. 4). The increased concentrations of testate amoebae are likely to be related to the higher nutrient input to the lake following

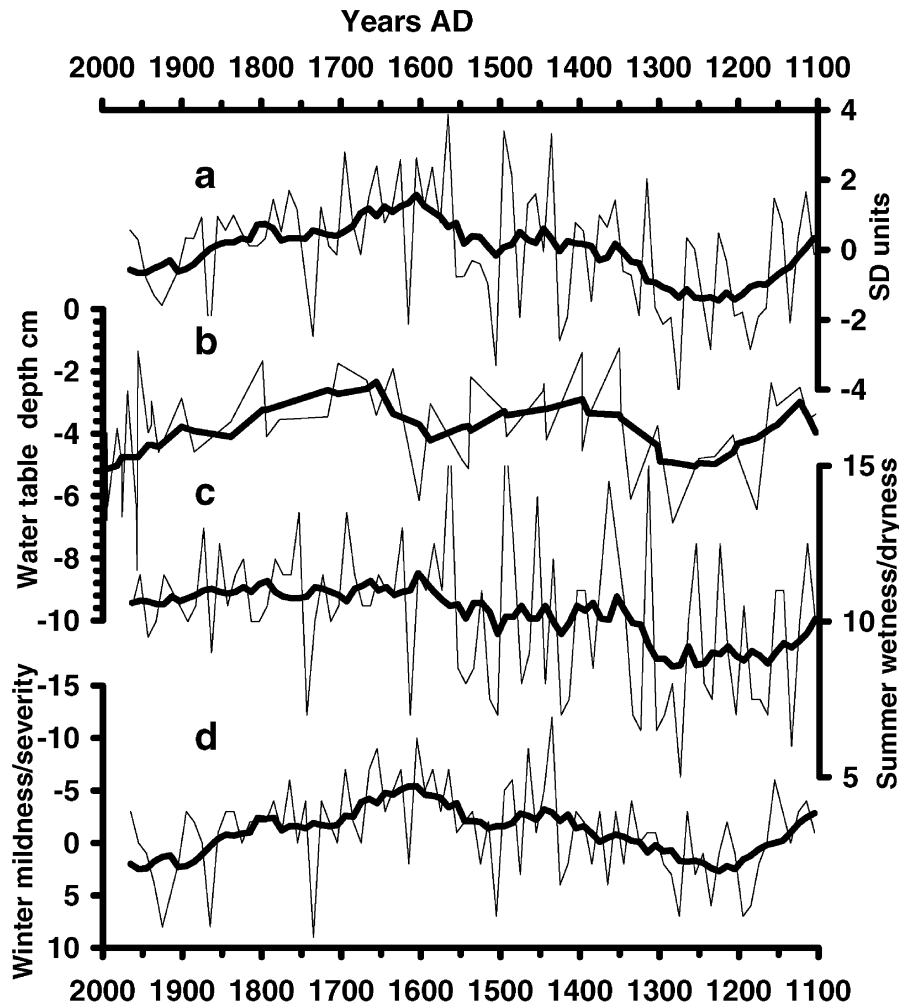


Fig. 3. Reconstructed mean annual water table record from three cores on two sites in northern England compared with instrumental and documentary climate data over the past 900 years (derived from data presented in Charman and Hendon, 2000). The upper curve represents normalised summer wetness plus winter severity indices of Lamb (1977), plotted as standard deviations from the mean. High values indicate wet summers and/or cold winters, low values indicate drier summers and/or warmer winters. The original data from which the normalised curve was derived are shown in the lower two plots as the published indices of summer wetness/dryness and winter mildness/severity (Lamb, 1977). These curves were normalised before combining to produce the index shown in the upper curve. The mean annual water table curve is derived from three cores on two separate ombrotrophic sites with deeper water tables (dry conditions) indicated by high negative figures. Thick lines are 100-year running means, thin lines are raw data. The relatively low temporal resolution of the water table data limits the scope of analysis but shows a good general agreement between water table fluctuations and the combined summer wetness plus winter severity curve on centennial timescales.

human settlement since AD 1850 (Medioli and Scott, 1988). The compositional changes may be the result of more complex factors resulting from the same initial cause, but *D. tricuspis* at least is known to be a eutrophic indicator. Increases in organic matter availability may also have been the proximal factor in changes to the testate amoebae assemblages (Scott and Medioli, 1983).

Responses to temperature change appear to be more variable. Patterson et al. (1985) found relatively little change in Holocene assemblages from eastern Canada. However, McCarthy et al. (1995) demonstrate significant changes, apparently related to temperature, over the Lateglacial and Holocene in Newfoundland and Nova Scotia. In this latter study, three lakes showed a

rather similar sequence of changes that coincided with the main climatic variations as reconstructed from pollen analysis. The testate amoebae record was therefore considered primarily to reflect climate changes as opposed to basin-scale processes. A point of particular interest was that the testate amoebae showed a short-lived Lateglacial climatic reversal which was not reflected in the pollen records. Although the chronology of the cores is rather poor, the most likely explanation for this mismatch is that this is related to the Younger Dryas Lateglacial Stadial period (GS-1, *sensu* Björck et al., 1998). McCarthy et al. (1995) suggest that this reflects the sensitivity of testate amoebae to environmental change as well as a rapid response rate related to

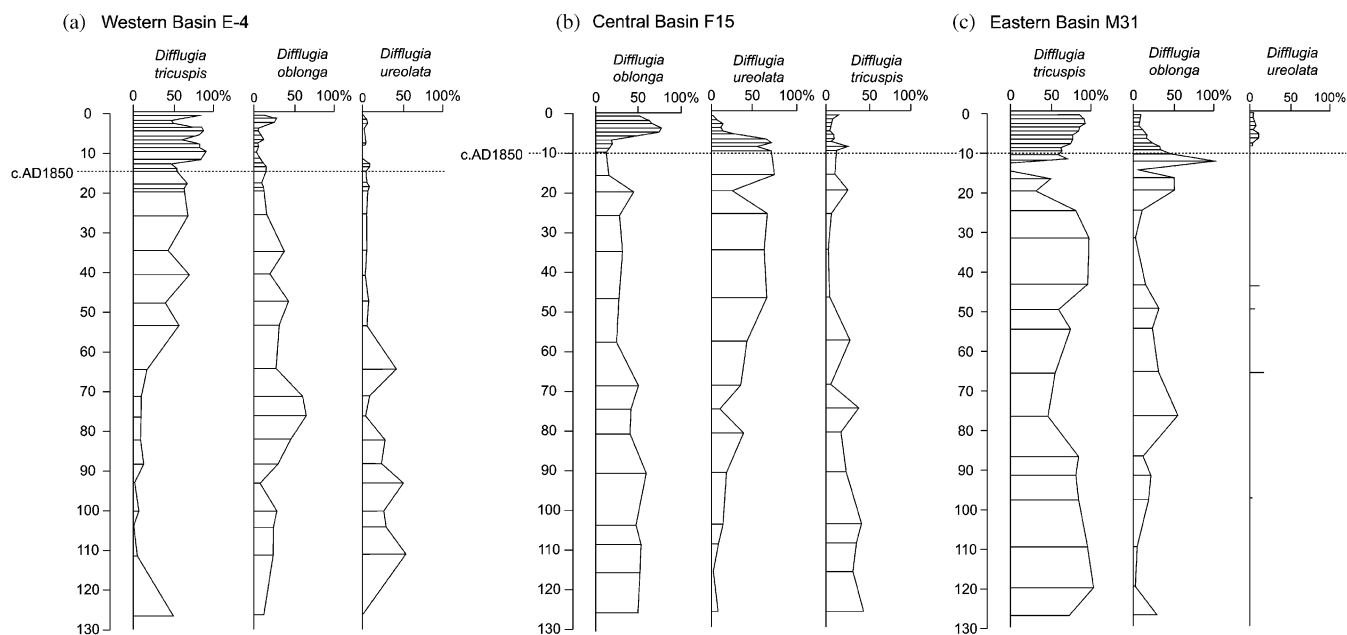


Fig. 4. Summary of changes in main taxa from three cores in Lake Erie, North America. (compiled from Scott and Medioli, 1983).

their short generation times. *Centropyxis aculeata* is a taxon which is apparently tolerant of low temperatures and low organic matter content of sediments. Some taxa (notably *Pontigulasia compressa* and *Diffflugia bacillifera*) may be restricted to higher temperature bottom waters and others only appear after paludification in the catchment, suggesting inwash from surrounding organ-rich soils.

A final area of work which is just beginning to emerge is that of the use of testate amoebae as indicators of heavy metal pollution in lakes (Asioli et al., 1996; Patterson et al., 1996; Reinhardt et al., 1998; Patterson and Kumar, in press). Most of this work has been based entirely on modern assemblages and their distributions in relation to mining activities and concentrations of contaminants such as arsenic and mercury. Work on the fossil record for temporal variability of changes in heavy metal pollution has only just begun (Patterson and Kumar, in press) although it is an area that appears to have much potential for the future.

One area of this work that has wider implications is that of taxonomic treatment of distinctive variants of some taxa. Much of the work on lake assemblages has been heavily influenced by the taxonomic groupings of Medioli and Scott (1983) who argue convincingly that many previously separated 'species' are in fact attributable to a relatively small number of genuine species. On this basis, subsequent studies have usually grouped together taxa into what some would regard as over-large clusters of closely related species (see for example the identification guide to lake taxa of Ellison and Ogden, 1987). Splitting of testate amoebae taxa into closely

related species has been carried out over the past century or so by many different authors, but many of these divisions cannot be easily sustained as true 'species' separations (Medioli and Scott, 1983). However, in palaeoenvironmental studies, it can be argued that without such splitting, useful environmental information related to more minor morphological variations may be lost. However, in the work on heavy metal contamination, Reinhardt et al. (1998) suggest one way of overcoming this dilemma, by the erection of 'infraspecific strains'. These are informal nomenclatural terms for different morphotypes that are regarded as being part of the same species but distinguished on the basis of relatively small variations in morphology. Table 1 summarises different assemblages related to mining pollution in Ontario, Canada. This shows that different strains of the same species may be characteristic of different environments. For example, in Table 1, *Diffflugia oblonga* 'oblonga' reaches its highest abundances in the 'Diatom mud' and 'High diversity' assemblages. In contrast *Diffflugia oblonga* 'glans' is most abundant in the 'Deep water contaminated' and 'Deep water raw tailings' assemblages. Clearly minor morphological variability can be important in characterising environmental conditions in the present and therefore also in the past. Whether it is necessary to define an entirely new set of 'strains' within species in an attempt to use a true biological species concept for testate amoebae is less certain. Perhaps it would be better to use the finest taxonomic splits that are practically applicable in particular environments and sediment types, but to base these on the extensive

Table 1

Testate amoebae assemblages (percentage values) in lakes contaminated by mine tailings, Ontario, Canada (based on Reinhardt et al., 1998). This shows the use of 'intraspecific strains' to differentiate between environments, denoted by the additional names in inverted commas after the species names. See text for discussion. Values >10% shown in bold to emphasise differences between assemblages

|                                   | <i>Cucurbitella</i><br><i>tricuspis</i> | <i>Diffugia</i><br><i>oblonga</i><br>' <i>oblonga</i> ' | <i>Diffugia</i><br><i>protaeiformis</i><br>' <i>amphorella</i> ' | <i>Diffugia</i><br><i>oblonga</i><br>' <i>glans</i> ' | <i>Diffugia</i><br><i>protaeiformis</i><br>' <i>claviformis</i> ' | <i>Centropyxis</i><br><i>aculeata</i><br>' <i>aculeata</i> ' | <i>Centropyxis</i><br><i>aculeata</i><br>' <i>psillata</i> ' | <i>Centropyxis</i><br><i>constricta</i><br>' <i>bassa</i> ' |
|-----------------------------------|---|---|--|---|---|--|--|---|
| Diatom mud                        | <b>49</b>                               | <b>10</b>   | <b>10</b>  | 4   | 3   | 2  | 1  | 1   |
| High diversity                    | <b>18</b>                               | <b>14</b>   | 9  | 4   | 4   | 9  | 2  | 1   |
| Deep water contaminated           | <b>11</b>                               | 8   | 2  | <b>20</b>   | <b>16</b>   | <b>10</b>  | 1  | 3   |
| Deep water raw tailings           | 4                                       | 0   | 0  | <b>14</b>   | <b>58</b>   | 0  | 1  | 1   |
| Shallow contaminated substrate    | 9                                       | 6   | 3  | 4   | 1   | <b>23</b>  | <b>21</b>  | 6   |
| Organic rich shallow contaminated | 9                                       | 2   | 2  | 3   | 2   | <b>37</b>  | 3  | <b>20</b>   |

existing published 'species' definitions in the literature. As long as it is clear what criteria are being used, the actual names used are immaterial! In other areas, splitting of taxa has now also been shown to be important in terms of the environmental indicator values of some taxa (Bobrov et al., 1999).

### 3.3. Saltmarshes and sea-level change

One of the main distinctions between the habitat requirements of the closely related protozoan groups testate amoebae and Foraminifera, is that the former are principally restricted to freshwater and the latter are exclusively marine. Despite this general division several studies over the years have reported testate amoebae in coastal settings, particularly in saltmarshes (Scott and Martini, 1982; Scott et al., 1991, 1995), with the potential for records of sea-level change. However, these were relatively minor occurrences compared to the numbers of Foraminifera found in the same and adjacent samples and in general only a few taxa were reported. More recently it has been shown that the numbers and diversity of the testate amoebae fauna from surface samples on saltmarshes are much greater than has previously been realised (Charman et al., 1998, in press). This is primarily due to the detection of smaller taxa (<63 µm in size) which are missed by conventional preparation treatments for Foraminifera. An additional finding has been that within the upper marsh and supra-tidal areas of a marsh, the zonation in relation to elevation (and therefore to sea level) is distinctive and strong. Presence of testate amoebae in fossil coastal sediments has previously been taken to indicate the transition between saline and freshwater conditions but the new work suggests that the detail of the assemblage composition may yield more specific information than this. For example, Patterson et al. (1985) show that *Centropyxis aculeata* is the first taxon to colonise in periods of regressive sea-level change, also shown by the sequence of change in an isolation basin in western Canada (Hutchinson et al., 2000).

There are two fundamental questions that need to be addressed if testate amoebae are to be used as indicators of past sea-level change for the late Quaternary. First, there is the question of whether the results from the pilot study at the Taf estuary in Wales (Charman et al., 1998) can be replicated elsewhere. Second, the occurrence of fossil tests in coastal sediments needs to be more thoroughly evaluated. Early results suggest that testate amoebae are present in the upper areas of most saltmarshes in southern Britain (Charman, Roe, Gehrels, unpublished data, Fig. 5 Gehrels et al., 2001) but that the detail of the zonation may differ in the lowest parts of the tolerance range. Fossil testate amoebae are present in a variety of sediments but numbers are much lower and further work is needed on techniques to concentrate the fossil tests to provide a workable technique for sea-level studies.

### 4. Future potential and research priorities

This paper has reviewed the current status of testate amoebae research in Quaternary science. It will have become clear that the amount of work that has been done is still relatively small and that much of the existing work has been of an exploratory nature with relatively few studies concentrating on the applications rather than on assessing and developing the technique. The purpose of this section is therefore to make suggestions on the most promising avenues for research over the next decade or two. The central message to Quaternary scientists of all persuasions is that more data are needed on the occurrence of testate amoebae in a variety of settings and sediments. Without these and without more people actually aware of and looking for these organisms, progress is almost certain to be slow.

The work on peatlands is probably the area that is most actively being pursued at the moment, especially in the United Kingdom. At least five separate research groups are now using testate amoebae as indicators of change on ombrotrophic peatlands in the UK with at



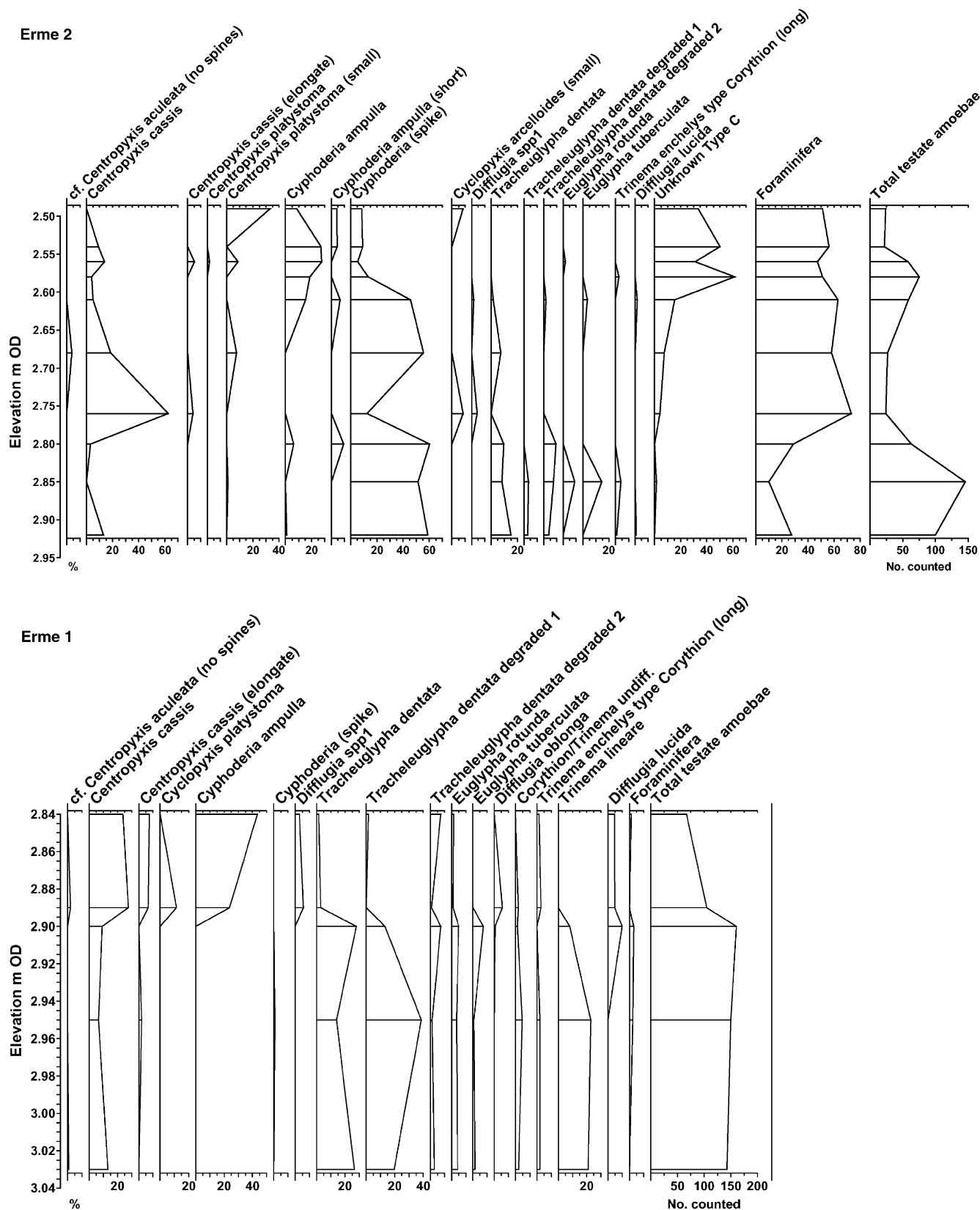


Fig. 5. Percentage testate amoebae in relation to elevation on two transects across a saltmarsh on the River Erme, Devon. The zonation in relation to elevation is strongest on transect Erme 1. In Erme 2, the testate amoebae are restricted to only the very uppermost areas of the marsh, probably due to particularly high salinity levels on this area. Taxa names in these diagrams are working names only and include morphological variants with purely descriptive epithets. These have been separated during analysis in order to investigate their differential response to the tidal gradient. Note that the elevation scale is plotted in reverse with lower elevations at the top.

least two others elsewhere in the world, primarily as a means of assessing past wetness and palaeoclimate. The application across a much greater number of sites by a larger number of researchers will ultimately guide further development work on the technique but already there are indications of the likely needs of the ‘user’ community and the potential applications for the future.

- *Quality of modern analogues.* The general indicator values of the main peatland taxa are now well established. However, the data quality for some taxa can be improved and assemblage analogues are not always good (Hendon, 1998). More and improved modern data will be required.
- *Biogeography and spatial extent of applicability.* Modern data have shown the potential for the use of testate amoebae over many areas of the world. Further work on this is desirable and likely to be profitable, especially in areas such as the Pacific fringes of northern North America and Asia.
- *Use of multi-proxy reconstructions.* Analysis of testate amoebae is one of a number of techniques that can be applied to ombrotrophic peats. Rather little work has been done on combining the results of different approaches, although this has begun (e.g. Charman et al., 1999, Mauquoy and Barber, 1999; McGlone and Wilmschurst, 1999).
- *Range of peat types and environmental indicators.* Virtually all work so far has concentrated on the reconstruction of surface wetness conditions. The development of pH transfer functions and reconstructions is possible and needs to be assessed.
- *Range of peat ages.* At the moment, all data from peats come from Holocene sequences. This may be because preservation in older sediments is poor or it may be that there has not been a systematic search for testate amoebae.

The use of testate amoebae in lake sediments is long-standing but has not yet been exploited in relation to many current issues in Quaternary science. The work undertaken by North American researchers in recent years has demonstrated that there is further potential here but there is still work to be done. The particular issues of highest priority are:

- *Responses to environmental variables.* The suggestions that temperature (McCarthy et al., 1995) and other environmental parameters (e.g. Patterson et al., 1996) are important in determining assemblage composition are intriguing but require work to establish the nature and relative importance of these factors in particular situations. This would add to and perhaps clarify the role of trophic status which has been presumed to be the dominant factor until recently (Tolonen, 1986).

- *Geographical and temporal range of deposits studied.* Lakes are much more widely distributed across the world than peat deposits yet the geographical range of fossil studies is much more restricted. As with peatlands, only a limited temporal range of sediments has been examined for testate amoebae.
- *Multi-proxy studies.* The relative importance of the contributions of the benthic communities as opposed to tests from floating macrophytes and fringing plants and soils has not been properly assessed. Several studies have suggested that both could play a role (Ellison, 1995; Patterson et al., 1996). Comparisons with other proxies that can be more clearly attributed to either autochthonous or allochthonous sources may help to resolve this issue.

The work on coastal environments and deposits has only just begun yet it is possible that testate amoebae may provide a source of data for sea-level reconstructions in addition to those based on Foraminifera or diatoms. Some simple issues need to be resolved before this can be properly assessed including:

- *The replicability of zonation.* The replicability of zonation in response to tidal parameters at different geographical locations and within varied plant communities.
- *The occurrence and detectability of fossil testate amoebae in coastal sediments.* Initial work has suggested that this may be much harder than for terrestrial peats and lake sediments.

This paper has taken a liberal interpretation of the Quaternary biostratigraphy remit of this volume and explored the range of known occurrence and palaeoecological significance of testate amoebae. The limited nature of available data, especially for sediments older than OIS2 means that it is not yet possible to use these organisms as biostratigraphic markers for mid- to late-Quaternary sediments in the traditional sense. Despite this, the range of occurrences and responses discussed here suggests that there is potential for their use in late glacial and Holocene biostratigraphic description and correlation from many areas of the world, including Europe. Increasing numbers of pre-Quaternary occurrences (see Medioli and Scott, 1988) suggest that these organisms could be widely distributed in sediments from various geological periods.

In conclusion, work on testate amoebae in Quaternary science is still in its infancy. This paper has highlighted the successes of existing work but also the problems that have become apparent through gaining a greater understanding of the ecology, taxonomy and occurrence in fossil sediments of this intriguing group of organisms. It remains to be seen whether their potential in all the possible applications can be fulfilled and

whether yet further areas will be identified and pursued in the future.

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