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Holocene palaeohydrology from testate amoebae analysis: developing a model for British peatlands

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HOLOCENE PALAEOHYDROLOGY FROM TESTATE AMOEBAE ANALYSIS: DEVELOPING A MODEL FOR BRITISH PEATLANDS.

by

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"There is a tide in the affairs of men,
Which, taken at the flood, leads on to fortune;
Omitted, all the voyage of their life
Is bound in shallows and in miseries.
On such a full sea are we now afloat,
And we must take the current when it serves,
Or lose our ventures."

William Shakespeare.

To Mum and Dad

ABSTRACT

Testate amoebae (Protozoa: Rhizopoda) are particularly abundant in peatlands. Previous studies have used testate amoebae in palaeoenvironmental studies, but have used qualitative data only, so that results are expressed only in terms of 'wet', 'dry' or 'moist'. This study uses testate amoebae to derive quantitative reconstructions of mire surface wetness for part of the Holocene and is split into two parts.

The first part of this study modelled the responses of individual testate amoebae species to environmental variables on ombrotrophic mires, since the peatland-climate link makes these habitats the one of the most useful in palaeoclimate reconstructions. 163 samples of modern testate amoebae faunas were obtained from 9 ombrotrophic mires across Britain. Environmental variables (mean annual water table, moisture content, dissolved organic carbon, pH, Ca^{2+}, Mg^{2+}, SO_4^{2-}, Cl^-, conductivity and host plant species) were measured. A hydrological monitoring programme on an ombrotrophic mire on Dartmoor provided a detailed record of hydrology and selected water chemistry over a year and identified the season most representative of mean annual environmental conditions. Weighted averaging regression applied to the faunas provided absolute moisture content and mean annual water table optima for 38 common testate amoebae species.

In the second part of the study weighted averaging calibration was used to derive transfer functions from the modern species' optima. From these, mean annual water table and substrate moisture content were reconstructed for the top 100 cm of a selected fossil peat core from Bolton Fell Moss, Cumbria. These reconstructions were compared with those derived from plant macrofossil and peat humification analyses. Testate amoebae provided a further insight into the decline of *Sphagnum imbricatum*, clarified noisy areas of the existing palaeohydrological record and suggested that hydrological changes at Bolton Fell Moss were likely to have been gradual, rather than the sudden event implied by the plant macrofossil record.

This study demonstrates the future potential of testate amoebae as palaeohydrological indicators. Expansion of the modern data set in terms of species composition and geographical extent, further applications of testate amoebae into multi-proxy palaeohydrological reconstructions and taxonomic refinements are suggested to improve the technique further.

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AUTHOR'S DECLARATION

At no time during the registration for the degree of Doctor of Philosophy has the author been registered for any other University award.

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Signed..... W. Woodland .....

Date..... 21. 6. 96. .....

Part One

Introduction to the study

Chapter 1

Introduction

1.0 Testate amoebae and palaeohydrological reconstructions

Testate amoebae (also referred to as rhizopods, thecamoebae or testaceans) are microscopic protozoa (5µm - 250µm in size: Ogden and Hedley, 1980) which are particularly abundant in moist soils and freshwater habitats. In *Sphagnum* peatlands, they are a dominant component of the microfauna, numbering approximately 16 million individuals per square metre of peat (Heal, 1962).

Sphagnum peatlands have been used for palaeoenvironmental reconstructions since the late 19th century (Blytt, 1876; Weber, 1900; Sernander, 1908; von Post and Sernander, 1910). At present, much of this work is concentrating on the reconstruction of palaeohydrological conditions on British ombrotrophic peatlands and the relationship with past climate (Chambers, 1984; Blackford and Chambers, 1991, 1993a and b; Barber *et al.*, 1994a,b,c,d). However, testate amoebae have not been used in many palaeohydrological studies, with rare exceptions (Van der Molen and Hoekstra, 1988; Van Geel and Middledorp, 1988; Warner, 1989; Warner and Charman, 1994). In fact, since the first use of fossil testate amoebae by Harnisch (1927) they have largely been ignored as palaeohydrological indicators. Instead, researchers have inferred palaeohydrological conditions from other peat components such as plant macrofossils and pollen (Walker and Walker, 1961; Barber, 1981; Barber *et al.*, 1994a,b,c,d) or the physical properties of peat, principally the degree of humification (Blackford and Chambers, 1991, 1993a,b; Barber *et al.*, 1994b). This neglect arises partly because palaeoecology generally follows the uniformitarian approach - that the present can be used to interpret the past. This assumes extensive knowledge of the modern ecology of an organism but, while the present-day ecology of most *Sphagnum* species (with the

exception of, for example, *Sphagnum imbricatum* - Stoneman *et al.*, 1993) may be so well understood that interpreting their fossil remains is relatively straightforward, so little is understood about the modern hydrological relationships of peatland testate amoebae that their use in quantitative palaeohydrological reconstructions must be approached with caution. This is despite the demonstration of close links between testate amoebae faunas and the moisture content of their habitat (Harnisch, 1927; Jung, 1936; Schönborn, 1963; Meisterfeld, 1977; Warner, 1987; Charman and Warner 1992; Tolonen *et al.*, 1992; 1994).

Until the late 1980s however, only qualitative hydrological descriptions of testate amoebae existed, based on Jung (1936) and Meisterfeld (1977). Palaeohydrological trends could be expressed only in relative terms of wet, moist and dry (Charman *et al.*, 1996) rather than in terms of precise water table depth and percent moisture content. More recently, however, several studies have sought to quantify the modern relationship between peatland hydrology and testate amoebae in an attempt to improve their use as palaeohydrological indicators (Charman and Warner, 1992; Tolonen *et al.*, 1992; 1994). These studies confirm Jung's (1936) suggestion that many testate amoebae species are sufficiently stenotopic (having a narrow hydrological tolerance range) to have considerable potential as palaeohydrological indicators.

A secondary factor which restricts the palaeoecological use of testate amoebae are taxonomic difficulties. Overall, the taxonomy of fossil testate amoebae is less clear than that of pollen and Heal (1962) conceded that, in the past, more than one species of testate amoebae may have been included in the same taxa. Conversely, one species may have been given several different names in the past. This difficulty also applies to this thesis and where identification problems do exist, detailed taxonomic notes have been made for comparison with other studies and are incorporated into an identification key (presented in the Appendix).

A third problem in the use of testate amoebae data has been preparation techniques, and a number of studies have rejected their use on the basis of inappropriate preparation methods (for example Barber, 1981). Testate amoebae are fragile and, since pollen preparations destroy a large number of testate amoebae shells, special techniques need to be used in their preparation.

The difficulties mentioned above should not detract from the potential of testate amoebae in palaeoecological reconstructions. Testate amoebae preserve well in peat and, with further refinements in their taxonomy and a clearer quantification of individual species' hydrological optima, they could provide a further useful technique for palaeohydrological reconstructions on peatlands.

1.1 Research hypotheses

Given the close links that have been established between peatland testate amoebae and hydrology and their good preservation in peat deposits, two hypotheses are investigated in this study:

1. hydrology (expressed variously as water table depth or percent moisture content of the host substrate) is the most important edaphic influence on modern testate amoebae distribution on British peatlands.

2. this relationship can be used to reconstruct palaeohydrological curves from testate amoebae assemblages for British ombrotrophic mires.

1.2 Study aims

This thesis aims to address the above hypotheses by quantifying the modern relationship between ombrotrophic peatland testate amoebae and hydrological conditions in Britain and, by so doing, to improve the utility of testate amoebae as a palaeoecological tool.

To investigate the first hypothesis, this study will quantify the influence of hydrology on the modern distribution of testate amoebae on ombrotrophic peatlands by investigating two issues that have, to date, been neglected in ecological studies:

i. whether the use of water table data from continuously monitored peatlands can give a more accurate description of the relationship between testate amoebae and moisture than data from "single-shot" sampling on non-monitored sites.

ii. whether such data are more useful in establishing a fully quantitative (rather than the existing qualitative and semi-quantitative) relationship between specific testate amoebae assemblages and the moisture content of their host Sphagna.

A supplementary aim is to extend the investigations of Charman and Warner (1992) and Tolonen *et al.* (1992; 1994) into testate amoebae and water chemistry to explore their potential as palaeochemical indicators.

The modern ecological study will improve interpretation, based on testate amoebae, of hydrological changes on peatlands. If the first hypothesis is corroborated then investigating the second hypothesis provides a further, palaeoecological, theme to the thesis: to apply the modern ecological information to the interpretation of fossil peat cores. This will be achieved by:

i. developing a set of transfer functions for water table depth and percent moisture content for testate amoebae assemblages in Britain.

ii. applying these transfer functions to a fossil testate amoebae assemblage to reconstruct palaeohydrological changes on an ombrotrophic peatland.

iii. comparing the reconstruction from testate amoebae with that derived from peat humification and plant macrofossil analyses to assess the utility of testate amoebae analysis in palaeohydrological studies.

1.3 Thesis structure

This thesis has a four-part, nine-chapter structure (Figure 1.1). Part One (Chapters 1, 2 and 3) defines the problem, develops the hypotheses and comprises essential background information to the study. Since this research is developing a methodology for reconstructing British mire palaeohydrology from testate amoebae, Chapter 2 describes the mire ecosystems that occur in Britain and summarises their development and classification. Particular attention is paid to ombrotrophic mire systems, since it is on these that modern ecological studies of testaceans will be made in this study. Chapter 3 reviews the current knowledge of testacean biology and ecology, and reviews previous work on their relationship with peatland hydrology. Using this information, the final part of Chapter 3 considers the potential of testate amoebae in palaeoecological applications.

Part Two concerns the modern ecology of testate amoebae in Britain. Chapter 4 details the sampling strategies and analytical methods that were devised, implemented and improved upon in a survey of testacean populations on British ombrotrophic peatlands. Chapter 5 presents the results of an intensive study of the hydrology and water chemistry of one ombrotrophic peatland. In Chapter 6, this detailed information is combined with data from

additional sites in Britain to quantify the hydrological relationships of modern peatland testate amoebae.

Part Three comprises the development and application of testate amoebae-based transfer functions for water table depth and percent moisture content. Chapter 7 details the development of the transfer functions based on the ecological relationships established in Chapter 6. In Chapter 8, the transfer functions are applied to a fossil peat core from Bolton Fell Moss in Cumbria. A pair of palaeohydrological curves (one for water table depth and one for moisture content) are derived from the application of the transfer functions to the fossil assemblage. These curves are compared with those derived from peat humification and plant macrofossil analyses on an adjacent core and the usefulness of testate amoebae as palaeohydrological indicators is assessed.

Part Four consists of the concluding chapter (Chapter 9). It is set apart from the previous material by its consideration of the wider implications of this study for palaeoecology. The application of testate amoebae in future palaeoecological studies is considered and suggestions are put forward for the improvement of the technique.

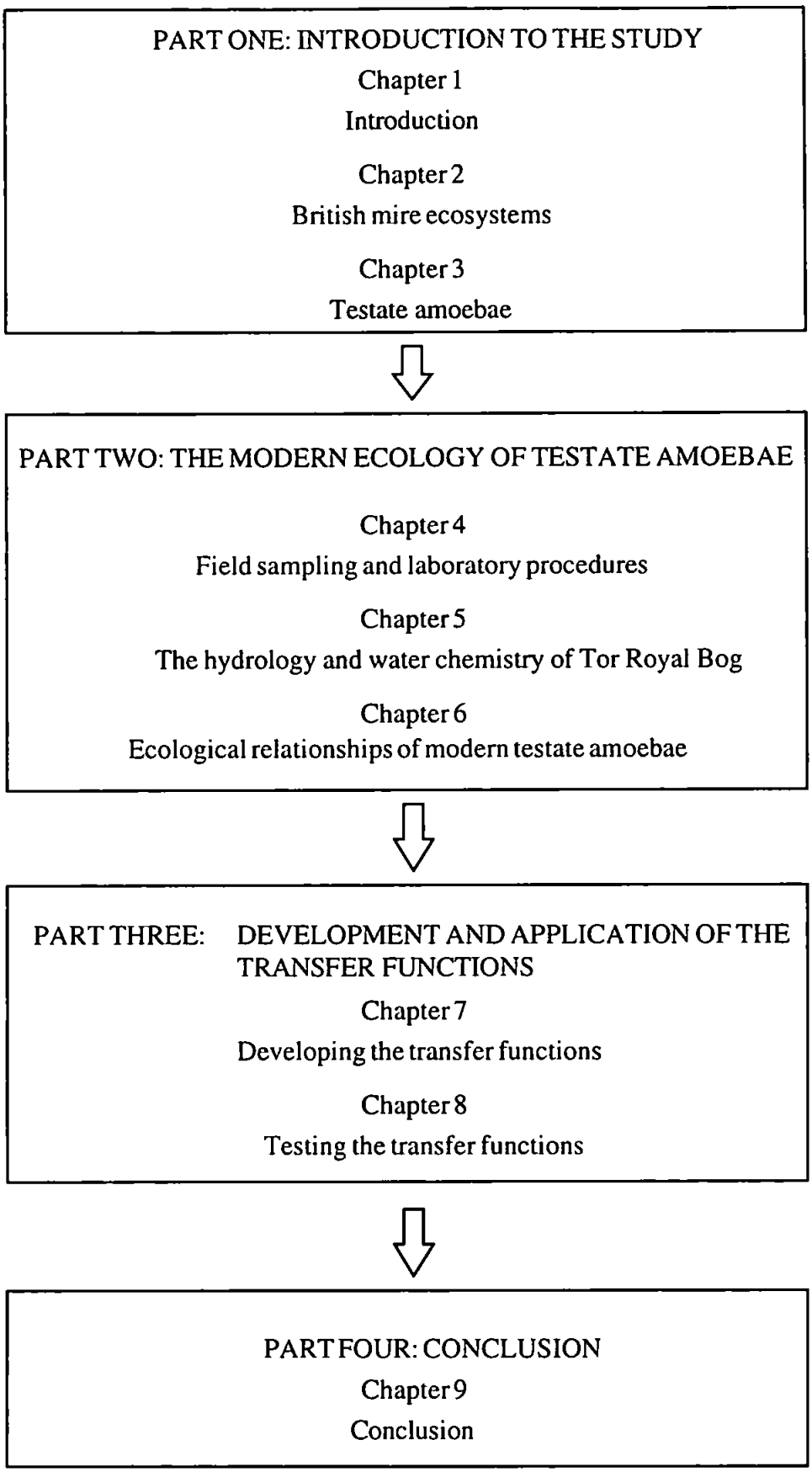


Figure 1.1: Thesis structure

Chapter 2

British mire ecosystems

2.0 Introduction

Peatlands are an extremely broad subject area and the terminology used to describe them can be confusing. This chapter aims to clarify the terms used and considers in detail the peatland type that is directly relevant to this study, British ombrotrophic mires.

2.1 British mires: classification and terminology

Under Scandinavian terminology, all waterlogged areas where peat develops as a consequence of reduced decay rates under anaerobic conditions are termed "mires" (Lindsay *et al.*, 1988) and this term will be used in this context throughout this thesis. There are many mire types in Britain but no single unified system of classification. There are two main reasons for this. Firstly, the prevalence of vernacular terminology and the variable use of terms such as "wetland", "fen", "bog", "swamp", "moss" and "flow". Secondly, different types of classification schemes have been introduced by workers according to their study aims. For example, classifications of mires based on their potential for exploitation are made mainly with peat extraction and forestry in mind (for example Fraser, 1948; Tolonen *et al.*, 1982) and are more concerned with generalities such as peat depth and condition. Ecological classifications are far more detailed and consider both macro- and micro-features, while hydrologists are more interested in the supply of water to the mire, and geomorphologists in the topographical relationship of a mire to the surrounding relief. While this study recognises the diversity of mire classification schemes, the following section will summarise only the criteria that are relevant to this particular research project.

Gore (1983) and Diersson (1982) have reviewed a total of eight criteria which can used be to classify peatland systems (Figure 2.1). They are:- peatland morphology, ontogeny,

Gore (1983) and Diersson (1982) have reviewed a total of eight criteria that can used be to classify peatland systems (Figure 2.1). They are peatland morphology, ontogeny, ecological development and palaeobotanical features, topographic situation, vegetation, chemistry, hydrology, and the potential for physical and chemical exploitation. Of these, the most useful criteria for this project are water chemistry, vegetation, ontogeny, ecological development, morphology and hydrology.

a) Classifications based on hydromorphology

The interrelationship between peatland hydrology and morphology is so strong that these features can be considered as a combined attribute, termed "hydromorphology" (see Lindsay *et al.*, 1988). Hydromorphological classifications are based on several functional hydrological levels. Ivanov (1981) lists these levels as the "macrotope" (where several mires escape their topographical confines to coalesce in a "mire complex"), "mesotope" (a body of peat which is a single hydrological entity), "microtope" (the features, such as pools, ridges and hummocks, which make up the mire surface) and "microform" (a single pool or hummock - Figure 2.2).

While the morphology of a mire ecosystem at the macrotope level is determined by the hydromorphology of the constituent mesotopes, microtopes and microforms, the shape of the mire also affects the overland flow and throughflow of water and, through this, the development and shape of the peat.

Whether the hydrological input is from precipitation or from groundwater, cations and anions will always be present in solution, although the occurrence and concentration of these components will vary according to the hydrological source. Mire form exerts such a strong influence on hydrological (and therefore nutrient) inputs, that one can distinguish between nutrient-poor "ombrotrophic" mires (commonly known as bogs), which are

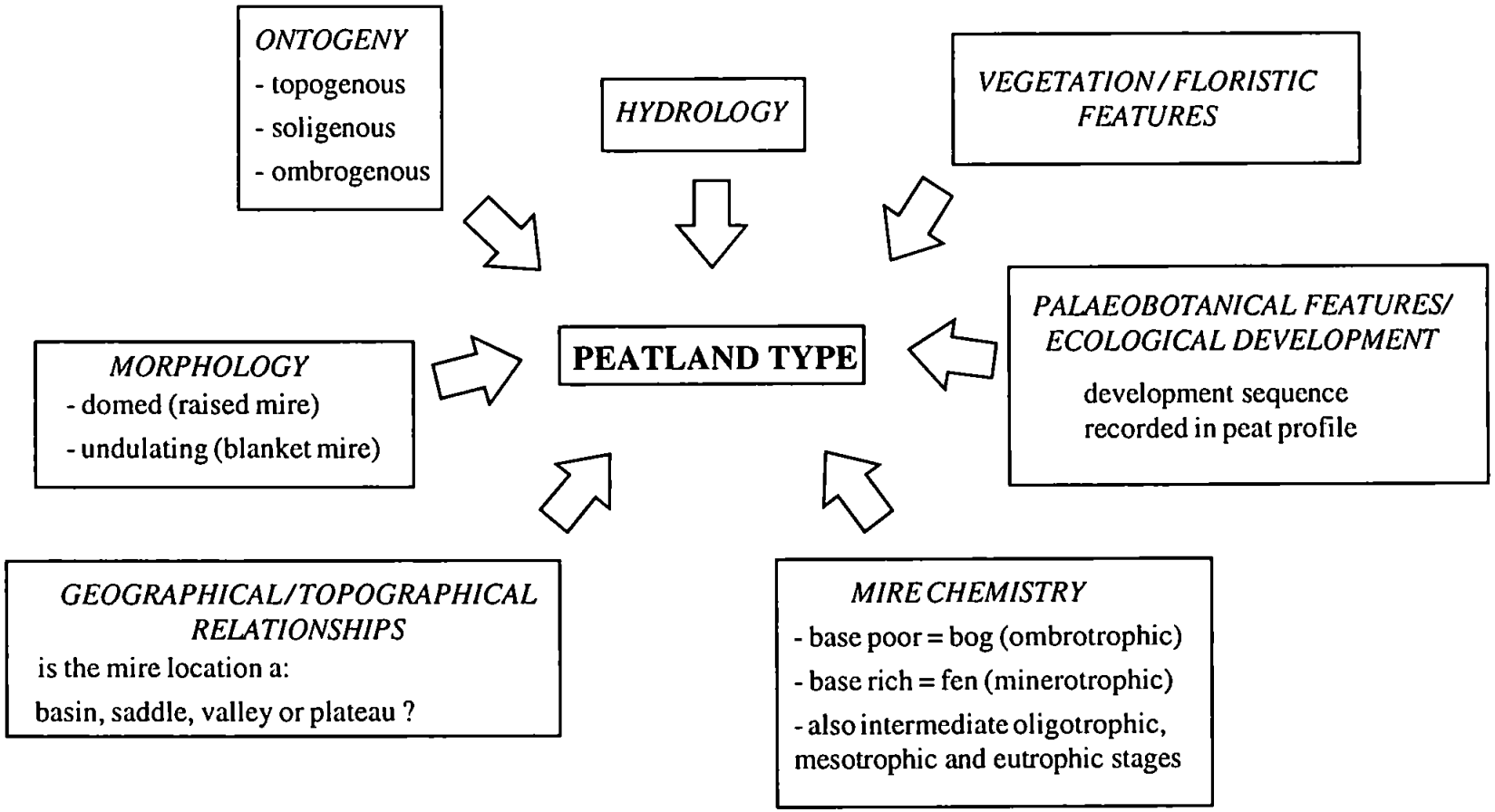
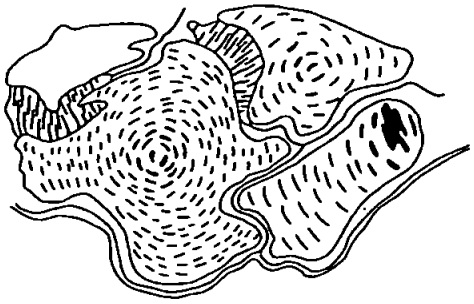
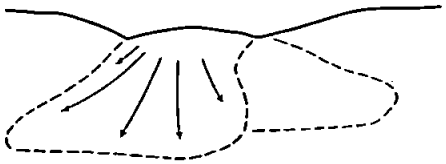


Figure 2.1: Criteria which have been used to classify peatland systems (from Gore, 1983 and Diersson, 1982)

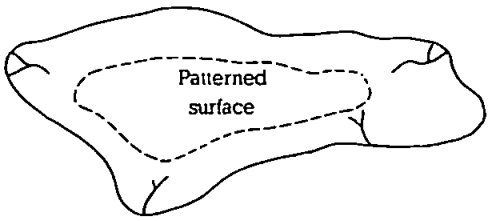
1. MACROTOPE



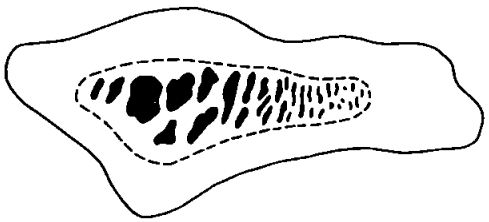
2. MESOTOPE - hydromorphology



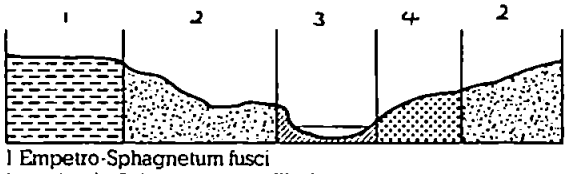
2. MESOTOPE - mire margin/expanse



3. MICROTOPE - surface patterns



4. MICROFORMS - hummock-hollow complex



1 Empetro-Sphagnetum fusci
2 Narthecio-Sphagnetum papillosi
3 Caricetum rostratae
4 Narthecio-Sphagnetum papillosi, phase *Sphagnum tenellum*

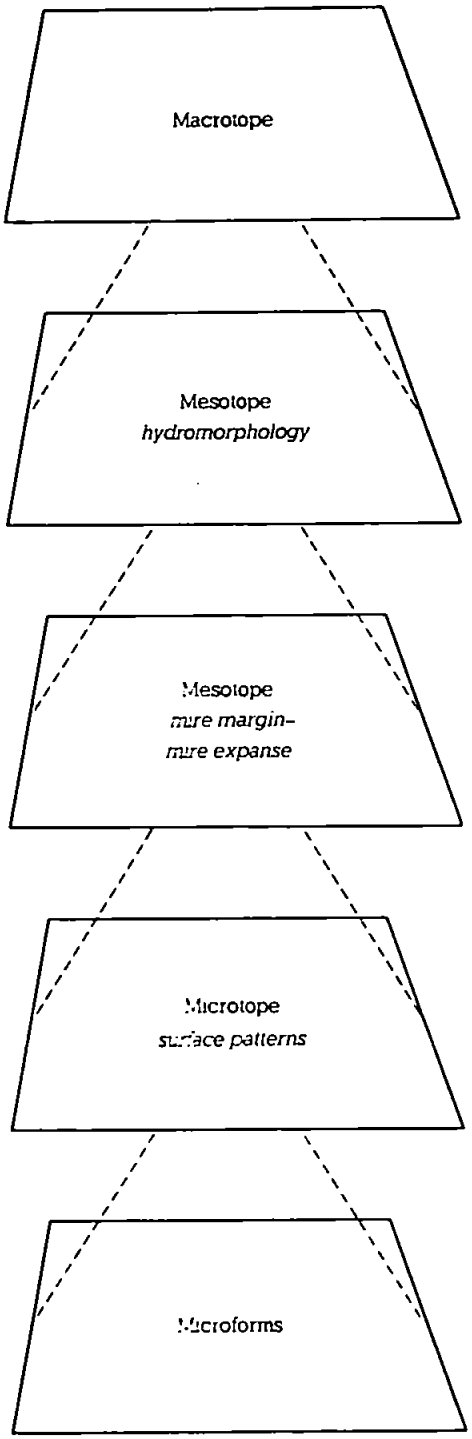


Figure 2.2: The four levels of functional hydrology in a mire system described by Ivanov, 1981 (source: Lindsay *et al.*, 1988, p.25).

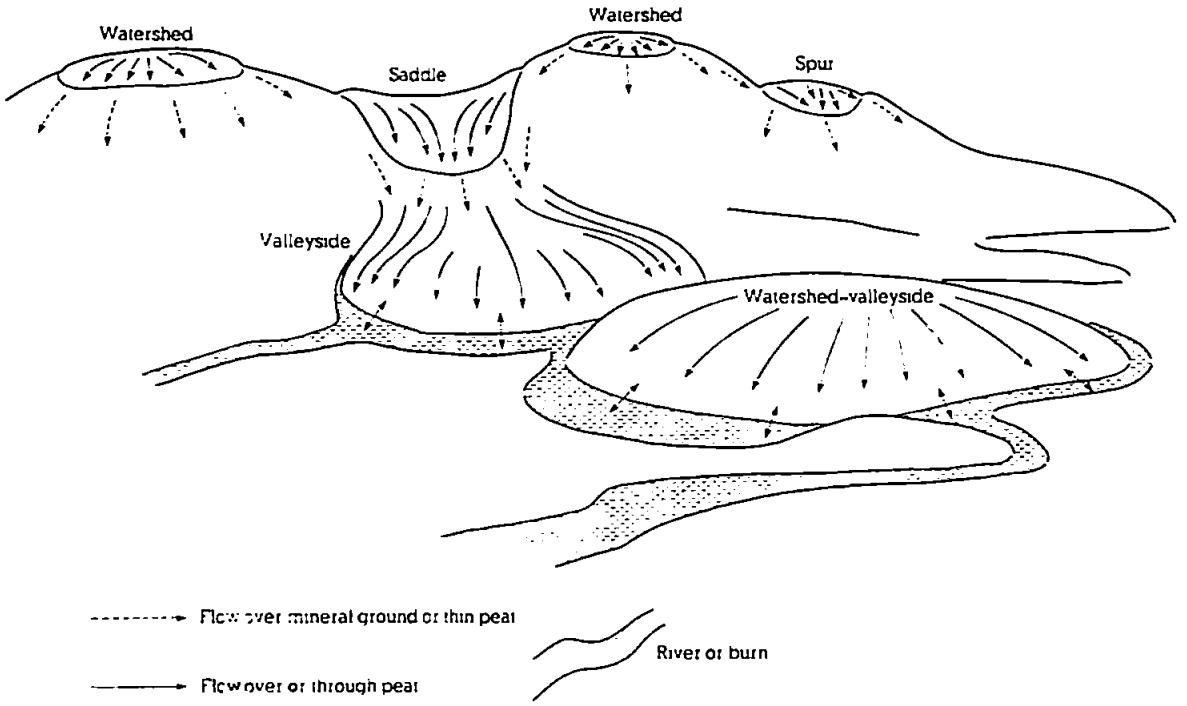
maintained by precipitation only, and nutrient-enriched "minerotrophic" mires (known as fens), which receive nutrient-enhanced water (Gore, 1983). A further subdivision of minerotrophic mires is possible. "Topogenous mires" (Hughes and Heathwaite, 1995) are formed as a result of local topography (for example, a kettle hole, or flood plain). "Soligenous" mires develop in springs, flushes, slope hollows and channels (Hughes and Heathwaite, 1995) and are strongly influenced by flowing water.

Ombrotrophic systems divide into "raised" mires and "blanket" mires (Tansley, 1939). Raised mires are "confined" systems (Hulme, 1980) whose development is restricted to lowland river and estuarine floodplains and lake basins and are entirely independent from groundwater influence (Hughes and Heathwaite, 1995); their development is detailed in section 2.2.1. Blanket bogs correspond to Hulme's (1980) "unconfined" mire system and they develop as a result of paludification (the saturation of once dry land under a wet climate). Blanket mires are particularly widespread in parts of western Britain, where the climate is markedly oceanic and sufficiently cool, and form a mantle across upland areas. Blanket bogs may cloak extremely steep hillslopes, provided the climate is sufficiently cool and wet (as in, for example, the Brecon Beacons, the Pennines and the Scottish Highlands). During a survey of northern Scotland, Lindsay *et al.* (1988) further subdivided blanket bogs into five mire units (mesotopes), according to their hydromorphology and geomorphological location - watershed, valleyside, watershed-valleyside, saddle and spur, each with a unique nutrient status, flow of surface water and arrangement of microtopes (Figure 2.3).

b) Classifications based on vegetation

While hydromorphological features are obviously valuable classification criteria, mires are more commonly distinguished using vegetation, because plants are readily identified and

1. Generalised location within the landform.



2. Surface water flow patterns (aerial view).

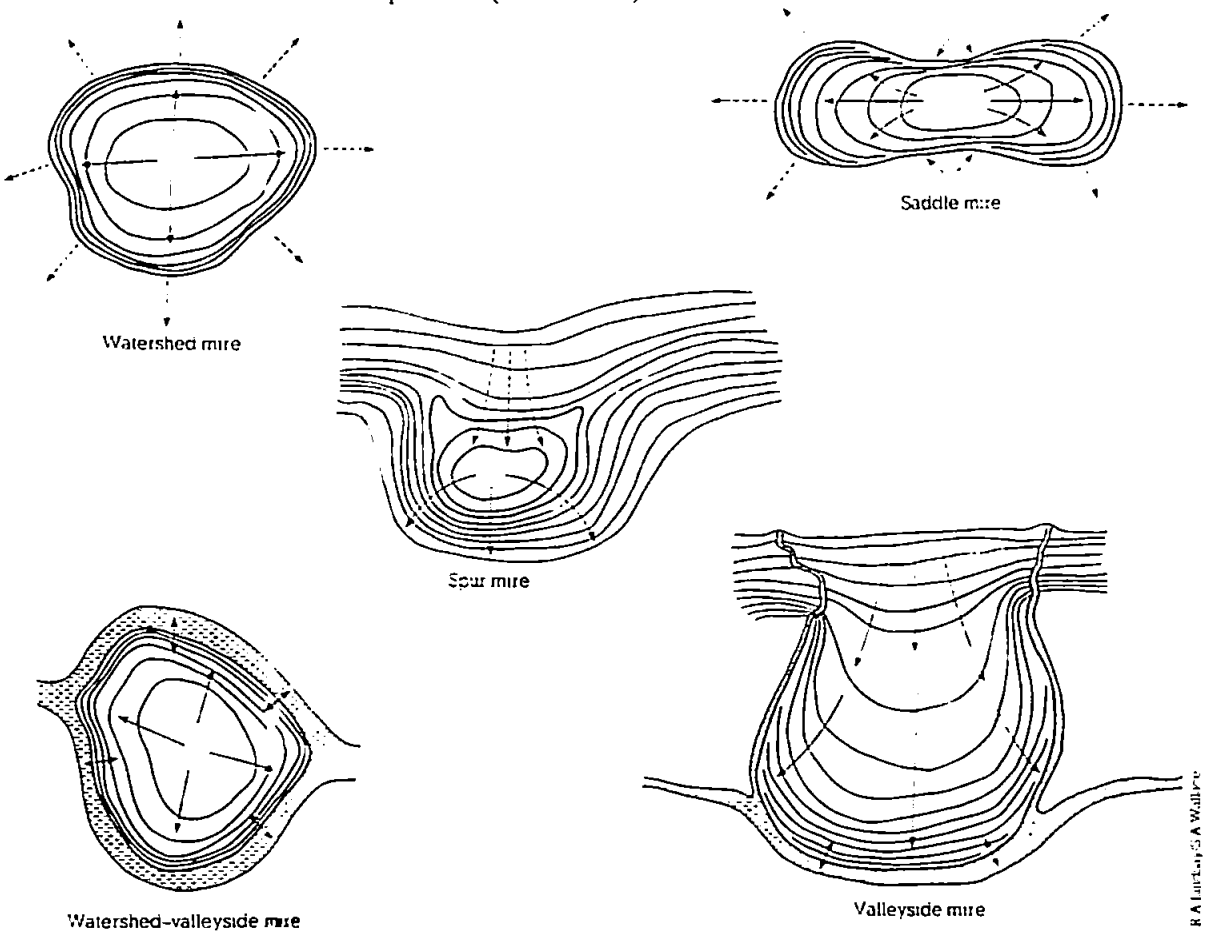


Figure 2.3: Hydromorphological blanket mire types (mesotopes) in northern Scotland (source: Lindsay *et al.*, 1988, p.69).

recorded in the field. Thus, vegetation may highlight differences in mires that (initially) appear morphologically similar.

Prior to the introduction of the National Vegetation Classification (NVC - Rodwell, 1991) different phytosociological approaches to mire vegetation produced three separate classifications (Tansley, 1939; McVean and Ratcliffe, 1962; Daniels, 1978). They related mainly to blanket mire and are summarised in Table 2.1. Although the schemes were in agreement within a small region, discrepancies arose when they were applied to larger areas. The NVC was introduced to provide an overall framework of vegetation classification in Britain (Rodwell, 1991) and it resulted in the description of 38 mire types based on vegetation. Those NVC mire types that are synonymous with previous classifications are listed in Table 2.1.

c) Classification based on water chemistry

Classifications based on the origin and chemistry of water supplies to a peatland may give an immediate and unambiguous distinction between "bog" and "fen" (Gore, 1983), but in practice very few classification schemes based on water chemistry have actually used chemical readings from mire waters. This is because vegetation assemblages (which are more tangible in the field than water chemistry) readily lend themselves for use as proxy chemical indicators and have therefore been used more often than water chemistry measurements.

Several water chemistry measurements for British mires have been published, notably by Boatman and Armstrong (1968), Daniels (1978) and Proctor (1992). Proctor (1992) conducted a nationwide study of ombrogenous mires in Britain, recording regional and local variations in water chemistry. The results show substantial variations, especially in relation

Tansley (1939)	McVean and Ratcliffe (1962)	Daniels (1978)	Rodwell (1991)
Sphagnetum (wide range of sites in the British Isles)	-	-	*Sphagnum auriculatum* bog pool community (NVC code: M1). *S. cuspidatum / recurvum* bog pool community (NVC code: M2).
Rhyncosporetum (western Ireland)	-	-	*Sphagnum auriculatum* bog pool community (NVC code: M1). *S. cuspidatum/recurvum* bog pool community (NVC code: M2).
Schoenetum (western Ireland)	*Tricophoreto-Eriophorum typicum*	-	*Schoenus nigricans-Juncus subnodulosus* mire (NVC code: M13). *Schoenus nigricans-Narthecium ossifragum* mire (NVC code: M14).
Eriophoretum (southern Pennines, England)	*Calluneto-Eriophoretum* (eastern Highlands, Scotland)	*Calluna-Eriophorum vaginatum*; upland *Calluna-Eriophorum vaginatum*	*Calluna vulgaris-Eriophorum vaginatum* blanket mire (NVC code: M19)
Scirpetum (western & northern Scotland)	*Tricophoreto-Eriophoretum typicum (western Highlands, Scotland)*	*Erica tetralix-Scirpus; Calluna-Narthecium*	*Scirpus cespitosus-Erica tetralix* wet heath (NVC code: M15). *Scirpus cespitosus-Eriophorum vaginatum* blanket mire (NVC code: M17).
Molinetum (Scotland & western Ireland)	*Molineto-Callunetum* (western Highlands, Scotland)	*Molinia-Erica tetralix*	NVC code: M15; *Erica tetralix-Sphagnum compactum* wet heath (NVC code M16). *Molinia caerulea-Potentilla erecta* mire (NVC code: M25).
Callunetum ("not to be regarded as part of the bog or moss formation")	-	mixed *Calluna*	*Calluna vulgaris-Deschampsia flexuosa* heath (NVC code: H9).

Table 2.1: Classification of (mainly) blanket mire types in Britain and Ireland based on vegetation. Descriptions by Tansley (1939), McVean and Ratcliffe (1962), Daniels (1978) and Rodwell (1991).

to distance from the sea and are an important complement to vegetation and hydromorphological classification schemes.

More recently, Heathwaite *et al.* (1993) have suggested that peatlands can be classified into four types according to trophic status; eutrophic peatlands have a high nutrient and Ca^{2+} content; mesotrophic systems have medium nutrient and Ca^{2+} contents; oligotrophic peatlands are characterised by a low nutrient and Ca^{2+} content and dystrophic systems have a high humic acid content. However, Heathwaite *et al.* (1993) do not give absolute values for these components.

d) Classifications based on ontogeny and stratigraphy

Stratigraphy can be used very effectively to classify mires. Most peats will remain stratified in their depositional sequence, preserving a record of mire development. This introduces an historical dimension that readily interlinks with the other classification methods mentioned above, because a stratigraphic investigation of a mire can reveal its hydromorphological, chemical and vegetation history.

Moreover, stratigraphy can indicate the relationship of the peatland to surrounding relief during the early stages of peat initiation and growth. This may allow the extension of classification schemes to consider a mire's origin as well as its present status. Moore and Bellamy (1974) provide perhaps the best example of this scheme by grouping peatlands as "primary", "secondary" or "tertiary". Primary peatlands develop in topographical hollows; if the primary peatland acts as a reservoir, it may allow peat growth to spread beyond the confines of the hollow to form a secondary peatland. Tertiary peatlands develop beyond the influence of groundwater.

In conclusion, despite the apparently daunting nature of the task, detailed classifications of mires are possible. Although a standard scheme for Britain has yet to be introduced, the hydromorphological scheme has been adopted by Scottish Natural Heritage and was used in a survey of peatlands in Caithness and Sutherland (Lindsay *et al.*, 1988); it would seem to give the most accurate reflection of variation within mire systems. However, there is still a role for other classifications based on water chemistry, stratigraphy and vegetation and perhaps they are better applied as subsidiaries to the hydromorphological scheme.

2.2 The development of British ombrotrophic mires during the Holocene

During the Holocene, peatlands have developed along two main routes: either from the terrestrialisation of water bodies (particularly lakes) or from the paludification of once dry land. What follows is an account of the development of ombrotrophic bogs through the Holocene, since they relate directly to this study.

a) Blanket mires

Most of the research into the onset of peat development in Britain has concentrated on blanket mire. Chambers (1984; p.1), in a study of the initiation and growth rate of blanket peat in the Brecon Beacons, considered that "the formation of peat begins at that 'point' in time when accumulation of organic material at the ground surface exceeds transport or decomposition". Putting an exact age on this point and identifying the peat initiation factors at individual sites can be a contentious issue and one that requires thorough consideration of all controlling variables. Decay rates are crucial - many peatlands have very low productivity, but decay rates are also low, which favours high accumulation rates. Moore (1975) identified three important factors that were thought to initiate blanket peat development: climatic change, soil maturation, and the influence of human activity.

Dates for the initiation of blanket peat development in Britain are wide-ranging. Birks (1975, in Jones and Keen, 1993) gives a date of 9000 BP in the severe climate of the Scottish Highlands but, further south, initiation was later - between 7500 and 2000 BP. Climatic deterioration towards higher precipitation and lower temperatures (hence reducing evapotranspiration rates) around 5000 BP (Jones and Keen, 1993) is thought to have been responsible for the southward spread of peat development in Britain. Such conditions favoured paludification (thus preparing the ground surface for peat growth) by encouraging localised development of mor humus, and iron pans, which impeded drainage in podsols on base-poor parent material. Paludification can affect large tracts of land and it probably accounts for the origin of most boreal peatlands (Sjors, 1961), but blanket mire can also be an extension of a raised mire where it escapes a topographical constraint.

b) Raised mires

A common sequence of peatland development results from succession along a hydrosere, when lakes silt up and allow encroachment of marginal vegetation into the remaining open water (Walker, 1970). Lakes are lentic systems and do not have a throughflow of water (and dissolved oxygen), so that the benthic layers soon become anaerobic. At the end of the growing season, such a volume of dead aquatic or marginal vegetation may sink to the lake bed that even the benthic anaerobes (organisms that are able to metabolise food in the absence of free oxygen) cannot decompose it quickly enough. As a result, organic matter accumulates and, if repeated on an annual basis, peat deposits will develop.

In the early stages of lake encroachment, climate plays a minor role and the system is topogenous, influenced by the nutrient status of the lake, its depth and area and conditions in its catchment area. However, towards the final stage of the hydrosere, climate becomes increasingly important and ultimately dominant. If the climate is sufficiently wet and the water table begins to fall at the former lake margins, the centre of the peat body may

continue to rise, eventually doming into a raised mire (Ivanov, 1981). At this point, the surface of the raised bog is considered to be rain-fed and is, like blanket bog, classified as ombrotrophic. Throughout this sequence, different peats develop, each characteristic of a specific stage in the succession and with the remains of different vegetation, depending on the stage in the hydrosere. Lowe and Walker (1984) identify three types of peat associated with this sequence: limnic, telmatic and terrestrial.

Raised mires in Britain are most commonly found in lowlands such as Cheshire and Lancashire, and on river flood plains bordering estuaries - for example, Thorne and Hatfield Moors on the Humberhead Levels in South Humberside, Glasson Moss and Wedholme Flow on the Solway Firth in Cumbria, and Borth Bog on the Dyfi Estuary in west Wales.

These two processes of peat formation, terrestrialisation and paludification, are responsible for the bulk of Britain's peat resources, and Robertson and Jowsey (1968, in Lindsay *et. al.*, 1988) calculate that they form more than 1.3 million hectares of commercially viable peat reserves.

2.3 Using ombrotrophic mires in palaeohydrological studies

2.3.1 Theoretical basis

Ombrotrophic mires are used in palaeoenvironmental studies because they receive their moisture and nutrients direct from precipitation and may therefore be more sensitive to environmental fluctuations than surrounding deposits (Foster and Wright, 1990; Barber, 1981). Moreover, the peat contains recognisable fragments of the vegetation from which it is derived. Combined with stratigraphy, this provides an autochthonous lithological and biological record of mire development, which can be used to reconstruct previous Holocene environments.

Peatlands also accumulate local microfossil remains (such as pollen and testate amoebae), which may provide additional evidence of environmental change (Foster and Wright, 1990). Using pollen and plant macrofossils, fossil plant communities can be reconstructed and related to small-scale changes in hydrology, chemistry and productivity during the mire's development. These communities may also reflect hydroseral stages from open water to raised mire and reveal the former nutrient status and levels of productivity with progression along the hydrosere (Lowe and Walker, 1984). Sedimentological evidence can also be used in these studies, since the gradation from limnic deposits through telmatic to terrestrial peats show the gradual terrestrialisation of the open water body.

The successful application of this evidence from ombrotrophic mires assumes uniformitarianism: for biological evidence, that the properties of the fossil organisms are identical to those of modern individuals. While depositional environments are likely to have remained constant over a long period, the reaction of organisms to their environment may well have altered, so that a particular species may no longer be a reliable palaeoenvironmental indicator.

2.3.2 Techniques used in palaeohydrological studies on ombrotrophic mires

Although this study recognises the numerous techniques used in palaeoclimate studies, the following section reviews two techniques used in palaeohydrological studies on ombrotrophic mires that are of direct relevance to this study. They are peat stratigraphy (specifically peat humification) and plant macrofossil analysis.

a) Peat humification

The term "humification" is used in peat stratigraphy studies to express the decompositional status of a peat deposit. A peat comprising decomposed organic material is described as "well-humified", while undecomposed organic matter is described as "poorly-humified". In

palaeoclimate studies, peat humification is most commonly used to infer surface moisture conditions at the time of formation (Aaby and Tauber, 1975; Barber, 1981; Chambers, 1984; Blackford and Chambers, 1991; 1993a; Barber *et al.*, 1994 a,b,c,d).

Four main approaches - visual examination, physical properties, chemical properties and the chemical extraction of soluble materials - have been used to assess the degree of humification in peat (Blackford and Chambers, 1993a). Measurement by chemical properties is directly relevant since it is against a curve derived from this method (Barber *et al.*, 1994c,d) that those derived from testate amoebae analysis in this study will be compared (see Chapter 8).

Complex chemical changes occur within plant matter as decomposition advances (Blackford and Chambers, 1993a) and measurement of chemical properties allows quantification of the extent of humification. Humic acids are produced as plant material decomposes, giving humus a distinctive dark brown colour. As humification continues, the proportion of humic acid in peat increases and the measurement of this as an expression of the degree of humification has been conducted, as for example by Aaby and Tauber (1975) to determine the rate of peat formation on a Danish raised mire. The technique employs colorimetry to determine the absorbtion of an alkaline extract of peat. Generally, higher rates of light transmission through the extract "are indicative of and proportional to, but not an exact measure of, lower degrees of humification" (Blackford and Chambers, 1993a; p.17). Blackford and Chambers (1993b; p.4) also note that "colorimetric data are best reported as 'percentage light transmission' rather than as 'percentage degree of humification' because absolute humification (i.e. values of 100%) have not been demonstrated".

NaOH extraction of continuous samples of peat is the most favourable measure of peat humification, because (unlike other methods) the technique recognises changes in species

composition of peats (Blackford and Chambers, 1993a). This is now the established approach in peat humification studies and has been used in several recent reconstructions of Holocene climate change in Britain (Blackford and Chambers, 1991; Barber *et al.*, 1994a,b,c,d). Using this technique, curves of past surface wetness can be reconstructed for ombrotrophic mires (Blackford and Chambers, 1991; Barber *et al.*,1994c,d).

Although decomposition in peatlands is extremely slow (Johnson and Damman, 1991), the process is not a linear one. The speed of decomposition, and hence the degree of peat humification, is dependent upon the species composition of the dead material and local accumulation rates. This influence is of crucial importance to this study, since it can affect the palaeohydrological curve derived from peat humification analysis.

Johnson and Damman (1991) demonstrated the differences in the decay rates of *Sphagnum cuspidatum* and *Sphagnum fuscum*, common occupants of hollows and hummocks respectively on ombrotrophic mires. *S. cuspidatum* decayed 1.5 times faster than *S. fuscum*, showing that the rapidity of *S. cuspidatum* decay occurred in spite of wetter, anaerobic conditions, while *S. fuscum* decayed slowly even on the drier, aerobic hummock tops in conditions considered favourable for decay. Such differential decay may introduce a potential error into palaeohydrological reconstructions based on peat and/or plant macrofossil analysis. *S. cuspidatum*, a species indicative of wet conditions and therefore one which is expected to remain intact in fossil cores will instead decompose relatively quickly, giving a potentially well-humified peat that might be falsely interpreted as indicative of drier bog surface conditions.

However, Barber (1994) points out that most *Sphagnum* plants retain sufficient structural integrity in lightly-humified peat to allow their identification in sub-fossil form to species or section level. It would appear that in well-humified peat the problem of differential

decay is most acute, since with the more advanced decomposition inherent in such peats, most of the structure of the rapidly decaying Sphagna will have disappeared. Blackford and Chambers (1993a) suggest that palaeohydrological investigations should concentrate on the direction of vegetation changes, citing the example of a "dry" mire assemblage dominated by *Calluna vulgaris* being replaced by a *Sphagnum*-dominated "wetter" assemblage. In this situation, the degree of humification is reduced because *Sphagnum* decays at a slower rate under the same conditions. Such a change in the plant assemblage would be readily identified by colorimetry.

b) Plant macrofossil analysis

In British ombrotrophic peats, most macrofossils are derived from Sphagna, monocotyledons and ericaceous remains (principally *Calluna vulgaris* and *Erica tetralix* twigs). Sphagna leaves preserve well in peat and it is possible to identify some of them to species level with light microscopy (Barber, 1993). This makes them a good complement to peat stratigraphy as a proxy-record of climate change. Hence, a number of recent studies (beginning with Barber in 1981) have combined peat stratigraphy and macrofossil analyses to extend and quantify climatic signals from ombrotrophic mires (see, for example Smith, 1985; Wimble, 1986; Svensson, 1988; Haslam, 1987; Stoneman, 1993; Stoneman *et al.*, 1993; Barber *et al.*, 1994a,b,c,d).

Several of these studies have used the "Quadrat and Leaf Count" (QLC) method, developed by Haslam (1987) to improve on previous methods by providing a more quantitative estimate of species abundance. A grid is placed on a microscope eyepiece to derive random quadrats, which are used to estimate percentage abundances for plant macrofossils. Fifteen quadrats are then "thrown" on a sample of washed macrofossils, at least 100 individual *Sphagnum* leaves are randomly selected, mounted on a microscope slide, identified and counted and the mean percent abundance of the *Sphagnum* species groups can then be

calculated (Barber *et al.*, 1994a). Wetness indices (Dupont, 1986) can then be applied to produce hydroclimatic curves (detailed in Chapter 8).

The most intensive plant macrofossil investigations have been conducted at Southampton University (for example: Barber, 1981, 1993; 1994a,b,c,d; Haslam, 1987; Stoneman, 1993). They have been directed towards the relationship between plant macrofossil remains and moisture conditions on ombrotrophic mires and refining the link from this to climate. Some studies (see, for example, Barber *et al.*, 1994b,c,d) have combined plant macrofossil analysis with peat humification analysis to produce multi-proxy palaeomoisture reconstructions for ombrotrophic mires.

The macrofossil investigations have shown that uniformitarianism cannot be applied to ombrotrophic mires because major changes have occurred in their species composition, especially over the last several hundred years (Barber, 1993). This is illustrated particularly well by the decline of *Sphagnum imbricatum* - once the dominant peat-forming species (Barber, 1993; Green, 1968) - and its replacement by *S. magellanicum* and/or *S. papillosum*, which commonly occurs in the top 100 cm section of cores in Britain (for example: Barber, 1981; Wimble, 1986; Van Geel and Middledorp, 1988; Stoneman, 1993; Barber, 1994; Barber *et al.*, 1994a,b,c,d).

The palaeoecology of *S. imbricatum* has been established by several authors. Green (1968) suggested that in the past *S. imbricatum* was semi-aquatic, growing in lawns underlain by higher water tables than at present. Stoneman *et al.* (1993) noted that other authors also found the palaeoecology of *S. imbricatum* to be typified by very wet conditions and that it frequently dominated unhumified peat. The present ecology of the species contradicts this, however. *S. imbricatum* has declined from a dominant position in the plant community to one of extreme rarity and is thought to be confined to the tops of isolated hummocks in

very wet oceanic mires. Here, its compact growth form can withstand desiccation more successfully than other Sphagna (Green, 1968; Flatburg, 1986). This growth form is in contrast to the lax form which was dominant in wetter conditions of the past and is more characteristic of *S. imbricatum* ssp. *austinii*, whose present-day distribution in the British Isles is restricted to mires of the oceanic west coast. Macrofossil research (Barber, 1981; Stoneman *et al.*, 1993) has shown *S. imbricatum* to be present in both hummocks and lawns, while Haslam (1987) suggested a low-hummock niche for the species.

The reason for the marked decline of *S. imbricatum* is unclear and is reflected in wide-ranging suggestions for its demise. Most investigations have focused on climate as a cause (Barber, 1981) and, more specifically, falling water tables (Green, 1968) leading to out-competing by other Sphagna. Anthropogenic causes such as aerosol deposition (Van Geel and Middledorp, 1988), drainage and burning (Barber, 1993) have also been considered. Water table fluctuations are of the greatest relevance to this study because testate amoebae may help to clarify the relationship between *S. imbricatum* and hydrology.

Green (1968) experimented with *S. imbricatum* growth-forms in relation to water table depth and concluded that:

> "...the great bulk of Post-glacial *S. imbricatum* peat may have been formed under very wet conditions by the aquatic ecad of the species unlike the hummock forms best known in the country today, and that in this case the drying of mire surfaces may well have been a primary factor leading to the species' present day restriction."
>
> (Green, 1968 p.56).

Green (1968) also suggested that water chemistry changes may have further contributed to the decline of *S. imbricatum*. In particular, *S. imbricatum* was shown to out-compete *S. papillosum* under conditions of high Ca^{2+} concentration, suggesting that *S. imbricatum* has high mineral requirements, which are not provided by ombrotrophic mires at present. The

species' restriction to oceanic areas of the British Isles was thought to be a reaction to the higher mineral content of precipitation in oceanic areas.

Extinction by species competition was forwarded by Stoneman *et al.* (1993), who suggested that *S. imbricatum* survives today on hummock tops because this is the only position where it can out-compete other Sphagna. The slower growth-rate of *S. imbricatum* compared to *S. papillosum*, *S. recurvum* and *S. magellanicum*, for example, means that it cannot survive in lawn environments and has therefore retreated to hummock tops where other species cannot thrive.

2.4. Summary: potential contributions from fossil testate amoebae analysis in palaeoclimatic studies on ombrotrophic mires in Britain.

Both peat humification and plant macrofossil techniques have clarified the link between palaeohydrology and climate on ombrotrophic bogs, but the section above has shown how the changing ecological niche of a dominant peat component has limited the application of plant macrofossils. In addition, neither technique yields quantitative data on 'real' variables such as substrate moisture content or water table depth. Given these issues, it is clear that there is great potential for testate amoebae in palaeohydrological reconstructions.

The most exciting prospect for testate amoebae is as a complementary technique for plant macrofossil and peat humification analyses, particularly in cores that are dominated by a restricted macrofossil assemblage comprising five or six taxa (Stoneman, 1993; Barber *et al.*, 1994d). The restriction means that replacement of one plant species by another apparently indicates a sudden hydrological change, but a more likely reason is that gradual hydrological change leads ultimately to a sudden change in species composition at the sample point. As a result, palaeohydrological curves derived from macrofossil analysis are "noisy" (Barber *et al.*, 1994d) and it is difficult to identify a clear trend because the curve

reflects erratic changes in species composition. However, testate amoebae assemblages are rarely so restricted. For example, twenty-five species of fossil testaceans were found by Charman and Warner (1992) on a peatland in Ontario, Canada and with such a diverse fossil testate amoebae assemblage, reactions of several species to moisture fluctuations can be used to derive a smoother transition between hydrological changes.

A natural progression from the above is the use of testate amoebae from sites where *Sphagnum* macrofossils are absent, either on the drier margins of a blanket bog or where *Eriophorum spp.* and/or *Calluna spp.* dominate the surface vegetation. Work is currently in progress to assess the replicability of palaeohydrological curves from testate amoebae between these contrasting locations (D. Hendon, pers. com.).

Before they can be used in palaeohydrological studies, the modern ecology of testate amoebae must be established. By quantifying the relationship between mire hydrology and testacean faunas living on the mire surface, more detailed and hydrologically meaningful interpretations can be made from fossil testacean faunas, and the relationship between peatland hydrology and climate can be further quantified. The following chapter describes previous studies of modern peatland testate amoebae and the attempts made to relate this information to fossil assemblages and hydrological changes on ombrotrophic mires.

Chapter 3

Testate amoebae

3.0 Introduction

Since this study is investigating both modern and fossil testate amoebae, an understanding of the biology and ecology of peatland testaceans is necessary. This chapter reviews previous work on these subjects to provide a context for fieldwork results from this study, while palaeoecological work conducted on testaceans to date is assessed as a background to the investigation of a fossil peat core.

3.1 Modern testate amoebae

Modern peatland testaceans are not noticeably cosmopolitan in their global distribution. Hoogenraad and de Groot (1979) recognised a northern fauna (North America, Europe and Asia) and a southern fauna (South Africa, Australia and New Zealand). However, there is considerable overlap between species' occurrences in these regions (D. Charman, pers. com.). Studies of peatland testaceans have generally concentrated on specific geographical areas, such as the northern temperate zones (Meisterfeld, 1977 and Schönborn, 1962b; 1963; 1965; 1967; 1982 in Germany; Beyens and Chardez, 1982 in Belgium; Heal, 1959; 1961; 1962 in northern England; Beyens and Chardez, 1984 in south-west Ireland; Lousier and Parkinson, 1981; Bonnet, 1973; Warner, 1987; Charman and Warner, 1992 in Canada) and the southern temperate zones of southern Latin America and southern New Zealand (Wilkinson, 1990a). Testacean assemblages in the polar latitudes have also been investigated (Heal, 1965; Wilkinson, 1990a,b in the Antarctic; Beyens *et al.*, 1986a,b; 1990 in the Arctic).

3.1.1 Systematics

Modern testate amoebae are assigned to the taxon Protozoa (Greek "proto" first; "zoion" animal) because, in common with other protozoans, they share the simplest cellular organisation of all animals (most protozoa are unicellular and possess at least one well-defined nucleus).

Protozoa now includes over 65,000 named species, of which half occur only as fossils (Committee on Systematics and Evolution of the Society of Protozoologists, 1980). The Protozoa are not a natural evolutionary group, but have been placed together for convenience and contain seven sub-groups: sarcomastigophora, labyrithomorpha, apicomplexa, microspora, ascetospora, myxospora and ciliophora.

Even at such a high taxonomic level, there is disagreement regarding the status of Protozoa. Under traditional classification schemes (see, for example, Penard, 1902) all living organisms are divided into Kingdom Planta and Kingdom Animalia. These form the highest taxonomic levels and Protozoa are considered as a subkingdom of the Kingdom Animalia. However, modern classification schemes have divided living organisms into five kingdoms, comprising Monera, Protista, Plantae, Fungi and Animalia (Whittaker, 1969; Leedale, 1974). Under this widely-used system, Protozoa are considered as a subkingdom of Kingdom Protista and the seven former major groups of Protozoa become phyla.

Under modern classification schemes, testate amoebae comprise the Subclass Testacealobosia in Superclass Rhizopoda, within the sub-phylum Sarcodina (phylum Sarcomastigophora). They are recognised as a Subclass because they are the only members of Rhizopoda who possess a test (shell), which encloses the body. This is the reason why the term 'testate amoebae' or 'testacean' should be used in preference to the term 'rhizopod' (*cf.* Tolonen, 1986).

The classification of testaceans down to Subclass level is generally accepted and all authors at least recognise Superclass Rhizopoda. But some authors (Luftenegger *et al.*, 1988 and Schönborn and Peschke, 1990) have identified a second Subclass - Testaceafilosia - which may be evolutionarily younger than Testacealobosia.

The division of testate amoebae down to family level and authorities for the orders and superfamilies are shown in Table 3.1. The Committee on Systematics and Evolution of the Society of Protozoologists (1980) recognises two orders in Superclass Testacealobosia. These are order Arcellinida, comprising the superfamilies Arcellacea and Cryptodifflugiacea, and order Gromida, which comprises the superfamilies Gromiacea and Euglyphacea. Two main criteria are used to divide the superclass Rhizopoda: the cytoplasmic form of the pseudopodia and the structure of the test. Division into classes is based on the characters of the pseudopodia, whilst the orders are separated on the presence or absence of a protective covering. Further divisions into superfamilies are based on the detailed structure of the test. The families Cochliopodiidae and Microcoryciidae have no test and are of no use to this study; they are therefore excluded from Table 3.1).

3.1.2 The cell structure of testate amoebae

While testate amoebae belong to the most basic taxonomic group yet discovered, they should not be considered as primitive, since functions performed by organ systems in higher forms are, in testate amoebae, carried out within a single cell. Testaceans have evolved over millions of years, albeit on a different scale from higher organisms.

a) The test

Test composition and ornamentation are fundamental to the identification and taxonomic classification of testate amoebae. Each testate amoeba possesses a test encasing the

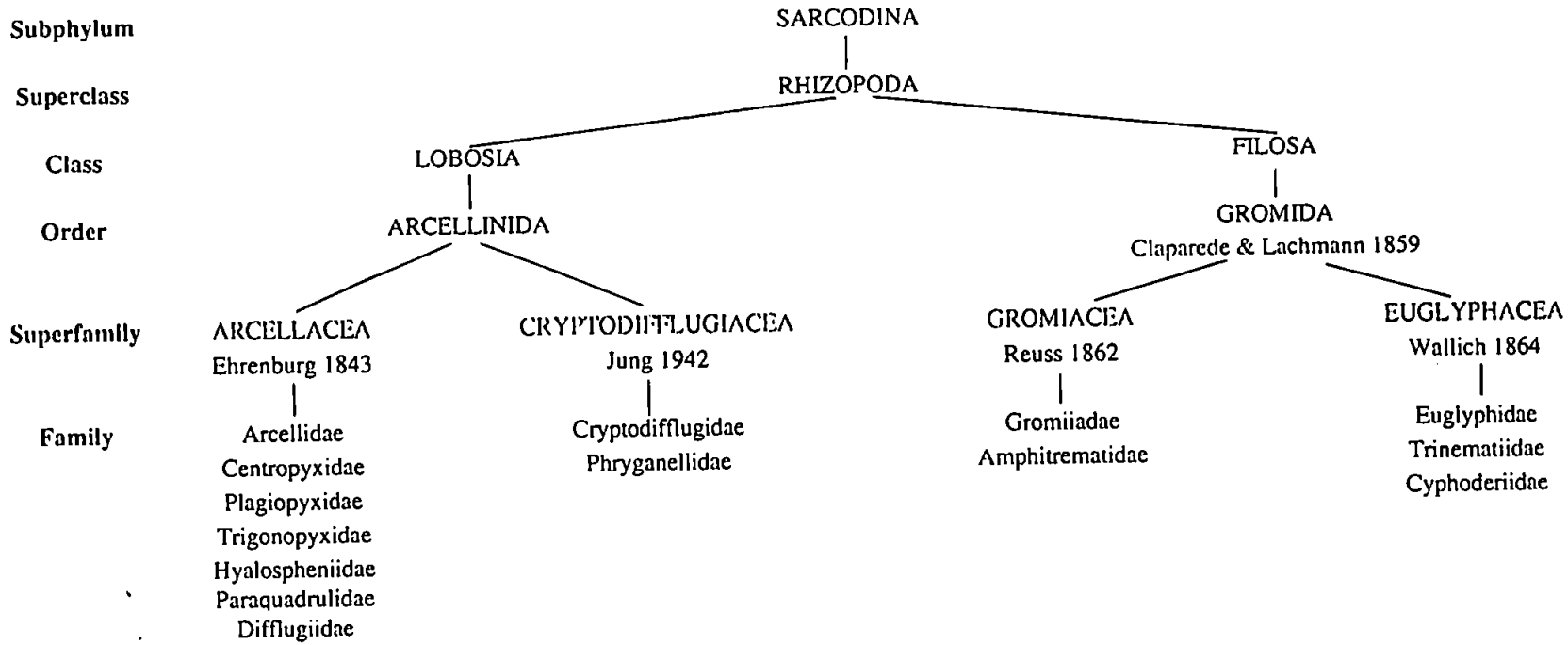


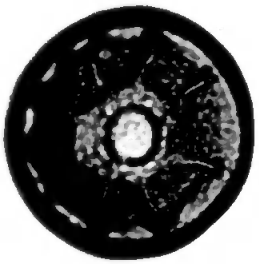
Table 3.1: Classification of testate amoebae down to family level. For genera, see Appendix.

cytoplasm, which is formed by secretions of organic material manufactured within the cytoplasm (Plate 3.1). This material is proteinaceous or mucopolysaccharide secretion (Sleigh, 1989) variously described as "chitin", "pseudochitin" or "tectin". Such material may comprise the entire structure of the cell (for example, *Arcella*- Plate 3.1a) or it may be reinforced by foreign materials such as sand grains derived from airborne dust or diatom frustules brought by inflowing water (Heal, 1962) - such as *Difflugia* (Plate 3.1b). These particles are ingested by the animal and embedded in the matrix (Barnes, 1968). Additional secreted material in the form of siliceous plates may also be incorporated into the test - for example, in *Euglypha* and *Quadrulella* (Plate 3.1c) the plates are pre-formed internally and fitted into precise positions during test formation. Some testaceans may incorporate material from other testate amoebae into their own shell; the plates from *Euglypha* (in addition to diatom frustules) provide the source material from which *Nebela* constructs its test (Corbet, 1973; Chardez, 1984).

Test size varies within species and the phenomenon was investigated in detailed biometric studies by Ogden (1980), who concentrated on the genus *Difflugia*, and later by Luftenegger *et al.* (1988) in a wider study of several genera. Heal (1963) attributed size variation in *Nebela tincta* to the water content of *Sphagnum*, finding that individuals at the top of the *Sphagnum* hummock (which was relatively dry) were smaller than those at the base of the hummock, in the wettest *Sphagnum* (see section 6.9*l*, p.284, for similar observations in the present study). This variation is a function of the tiny physical spaces that testate amoebae occupy within a *Sphagnum* hummock.

Testate amoebae depend on water to live because they possess an unprotected cell membrane for feeding (Warner, 1990). Testaceans inhabit water films around soil particles or plant leaves and roots, and these water bodies can be extremely small; the water film in the concavity of a *Sphagnum* leaf may be only 300µm in diameter (Corbet, 1973), so

a) *Arcella arenaria:* proteinaceous or mucopolysaccharide secretion (Chartley Moss, Staffordshire).



b) *Difflugia bacillifera:* proteinaceous or mucopolysaccharide secretion reinforced by diatom frustules (Penard Collection, British Museum, Natural History).

c) *Quadrulella symmetrica:* preformed siliceous plates (Penard Collection, British Museum, Natural History).

Plate 3.1: Photomicrographs showing test composition and ornamentation of three common testate amoebae.

testaceans must adapt morphologically to survive. Small size and the development of a flat surface allow continued survival should the water film shrink further during periods of desiccation. Schönborn (1992a) noted that the shells of testaceans in the upper, drier, horizons of a spruce forest soil showed the same response to moisture gradients as peatland testaceans, being extremely small, flattened and round. The small size and flattened shape was thought to allow the shell to fit into the small water films between the spruce needles, while roundness reduced evaporative loss.

After the living cell dies, its test may be preserved over a considerable time period, especially in peat (see Chapter 2). Besides substrate type, the length of preservation will also be determined by test composition, creating the potential for variable decay resistance and inconsistent death assemblages. The latter will be considered in section 3.3.2, but the relative resistance of tests is discussed here because it relates directly to test construction and may have implications for fossil studies.

A definitive order of decay for empty tests in peatlands has yet to be established, but Lousier and Parkinson (1981) produced a version for soil testaceans (Table 3.2). Their results showed that species with tests of sediment particles embedded in robust layers of organic cement were more resistant to decay than species with tests of platelets and secretion.

The most resistant tests, however, are chitinous. Species with this test construction, such as *Arcella* and *Amphitrema flavum* (where chitin comprises the entire test) and *Difflugia* (where it is reinforced by sand grain and diatom frustules) tend to be concentrated in ombrotrophic mires, and Tolonen (1986) refers to this group as the "most useful" species of testate amoebae, presumably because they preserve well in peat and are abundant in fossil peat cores. While differential decay is a potential problem for fossil testate amoebae

analysis, one of the benefits of establishing a modern analogue data set is that it allows an assessment of any such effect.

	Species	Test construction
Most resistant	*Arcella* spp.	Chitinous
	Most *Difflugia* spp. *Phryganella acropodia* *Cyclopyxis eurystoma* *Centropyxis aerophila*	Sediment particles embedded in robust layers of organic cement
	Euglypha *Trinema lineare* *Difflugia oviformis*	Platelets
Least resistant	*Hyalosphenia subflava* *Heleopera petricola*	Secretion

Table 3.2: Order of decay for empty testacean shells. Data from Lousier and Parkinson (1981).

b) The nucleus

The nucleus contains the chromosomes whose genetic material (DNA) controls the structure of proteins within the testacean cell. It is vital to the continued life of the cell and if the nucleus is removed, the cell will die immediately (Roberts, 1975).

The nucleus has two functions: the replication of the cell's genetic material and the release of genetic information to the cell organelles. Replication involves the synthesis of new DNA to duplicate the chromosomes and subsequently the separation of chromosomes into daughter nuclei immediately before cell division. Ogden (1981) gives a very detailed account of reproduction and the production of daughter cells by simple division in *Euglypha compressa.*

c) The cytoplasm

That part of the protoplasm not located in the nucleus can be identified as cytoplasm (Hale and Margham 1988). Superficially, the cytoplasm appears structurally homogenous, but closer inspection shows that the cytoplasm contains numerous granules and inclusions. Food materials are stored within the cytoplasm and it is also here that complex chemical reactions take place.

Contractile vacuoles are located within the cytoplasm close to the plasma membrane and appear to have an osmoregulatory function: that is, controlling the osmotic potential in the organism. Water molecules tend to move from an area of low osmotic pressure to an area of high osmotic pressure when separated by a semi-permeable membrane (the plasma membrane in testaceans) in order to equalise the osmotic pressure on each side of the membrane. In a dry or marine environment an organism will lose water to its surroundings; in wet environments and especially freshwater habitats, the organism may have difficulty in losing water and may therefore drown. To overcome this problem, the contractile vacuole swells with water (diastole) before collapsing (systole) and releasing the water to the outside medium. The efficiency of this function is enhanced by coalescing of smaller vacuoles to increase the size of the contractile vacuole, which may also be carried about in the cytoplasm before release at the cell surface. This allows testate amoebae to survive in permanently waterlogged conditions. The food vacuole is also located within the cytoplasm and its function is concerned with the intake and digestion of food.

The pseudopodia flow over and around food particles, eventually closing and sealing the food within the cytoplasm. The organic contents of the vacuole are then digested by enzymes, causing the vacuole to shrink slightly. Subsequent absorption of soluble materials into the cytoplasm leads to a final shrinkage of the vacuole into a bag containing

indigestible residue, which leaves the cell through holes in the test or through the test aperture (Figure 3.1a).

d) Pseudopodia

Testate amoebae move by the use of pseudopodia, which are protoplasmic projections from the main body of the organism (Figure 3.1b). In living testaceans, the pseudopodia are used in classification (see Committee on Systematics and Evolution of the Society of Protozoologists, 1980) but, because the pseudopodia are destroyed during laboratory preparation of living testaceans and decompose rapidly after death, they cannot be used in studies of fossil faunas.

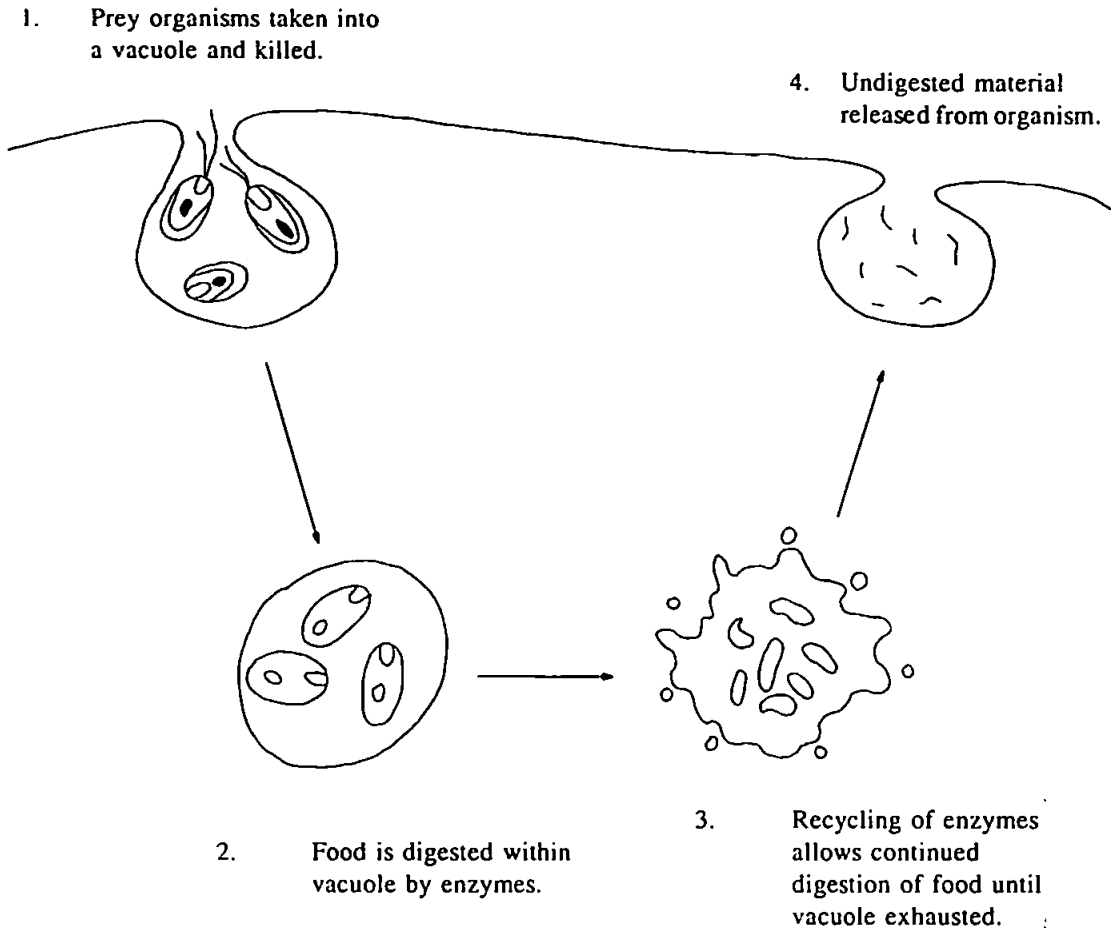
3.2 Previous ecological studies of testate amoebae

Living testaceans were first observed by van Leeuwenhock in Europe in 1674 (Brown, 1909), but the earliest survey of testaceans was not conducted until 1879, when Leidy published his monograph entitled "Freshwater Rhizopods of North America". Much testacean work has been conducted on the European continent and is principally concerned with the hydrological preferences of testate amoebae (see section 3.2.1 below).

In Britain, the first testacean studies were made at the beginning of the 20th century by, amongst others, Cash, Wailes and Hopkinson (1901-1919), Wailes and Penard (1911), and Brown (1909; 1912; 1915). While these monographs provided a comprehensive species list of British testaceans, they were essentially descriptive microscopic investigations with no indication of environmental influences on assemblages.

Between 1928 and 1958, Wang (1928), Lackey (1938), Webb (1956) and Bamforth (1958) conducted several studies on the seasonal succession of testaceans in water bodies and Singh (1955) included testate amoebae in studies of soil Protozoa. The first ecological

(a)



(b)

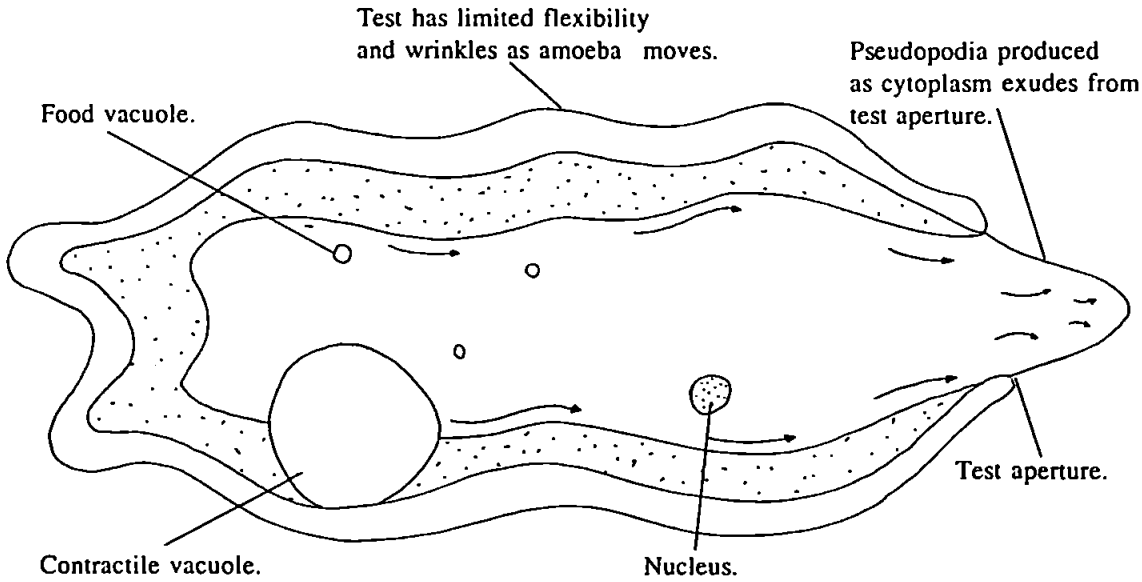


Figure 3.1: (a) feeding and (b) mobility in testate amoebae; (a) redrawn from Sleigh (1989), p.25.

investigation of British peatland testaceans was conducted by Heal (1959) at Moor House National Nature Reserve in Northumbria. He studied three main aspects of peatland testacean ecology: their relation to stages in moss succession, environmental factors influencing this succession, and the relationship between testate amoebae and other organisms. From his Ph.D. research came further papers on the influence of pH (Heal, 1961) and moisture content (Heal, 1962) on testacean faunas, both of which are discussed below.

Of the studies conducted on testate amoebae, water availability (expressed as moisture content of the substrate) has been uppermost, with others considering varied aspects of water chemistry. A detailed account of these investigations is given in the following section.

3.2.1 Testate amoebae and hydrology

Most studies on testaceans and moisture have been conducted in mainland Europe. Following Harnisch (1927), it is possible to identify three phases of research namely qualitative, semi-quantitative and quantitative.

a) Qualitative investigations (1927-1962)

Links between testate amoebae and hydrology were first investigated by Harnisch (1927) and Steinecke (1927; 1929) on the European continent to clarify the development of mires and their response to post-glacial climate change. Steinecke's (1927; 1929) studies were considered too detailed to be useful in palaeoenvironmental interpretations (Frey, 1964) and instead the testate amoebae associations of Harnisch (1927) were preferred. These associations were interpreted as functions of *Sphagnum* bog wetness (Frey, 1964) and could therefore be used to infer past climatic conditions from changes in bog-surface wetness. Four testate amoebae associations were recognised by Harnisch (1927):

"I. Forest moss type. Consisting of various species of *Difflugia, Centropyxis, Arcella, Assulina, Euglypha, Nebela, Corythion* and *Trinema*. This community is typical of non-bog-forming Sphagna in forests, heaths and along lake shores.

II. *Hyalosphenia* type. Containing *Hyalosphenia elegans* and *H. papilio* in addition to the species present in Type I. This community occurs in all Zwischenmoors (middle-aged mires), mature Hochmoors (raised mires) and in marginal areas.

III. *Amphitrema flavum* type. Containing the species of Type II, plus *A. flavum*. It is the most widely distributed in Hochmoors.

IV. *Amphitrema wrightianum* type. Containing *A. wrightianum* in addition to the species in Type III. It is not very common, being restricted to well-developed Hochmoors and is always the most diverse assemblage."

(Harnisch, 1927; pp 348-349).

The *Amphitrema flavum*-type was further thought, incorrectly, to be exclusive to ombrotrophic bogs (Harnisch, 1927 p.348) and the *A. wrightianum*-type to "old, well-developed raised bogs" (Harnisch, 1927 p.349) but the later studies listed above have demonstrated that no species are exclusive to ombrotrophic sites (Tolonen, 1986).

From the beginning of the 20th century, recurrence surfaces in peat profiles had been used for stratigraphical correlation, dating and environmental reconstruction (Barber, 1985), with the 'Grenzhorizont' (c. 2500 BP) being particularly prominent and thought to represent a general change to wetter conditions. Harnisch (1949) used established testacean associations to identify whether this change was caused by climate or a secondary factor. All the cores studied by Harnisch (1949) showed a greater abundance of testacean species in the younger peat overlying the Grenzhorizont, inferring moister, anaerobic conditions. Harnisch interpreted this as indicative of peat accumulation in a rapidly-growing bog under relatively anaerobic conditions in a deteriorating climate.

Bartos (1940) sampled testacean assemblages from 43 sites in the Carpathian Mountains of eastern Europe. He divided testate amoebae into four groups, according to moisture content: hydrophilous, hygrophilous, xerophilous and eurytopic species (Table 3.3).

Several species, although not classed by Bartos as eurytopic, crossed moisture classes - notably *Arcella arenaria*, *Bullinularia indica* and *Centropyxis cassis*. Other species, *Centropyxis aerophila* var. *sphagnicola* and *Nebela collaris*, are recognised as both hygrophilous and eurytopic. Clearly, the qualitative moisture classes did not allow precise moisture ranges to be expressed for individual species.

Hydrophilous	Hygrophilous	Xerophilous	Eurytopic
Arcella discoides	*Arcella rotundata*	*Arcella arenaria*	*Assulina muscorum*
A. vulgaris	*A. arenaria*	*Bullinularia indica*	*Centropyxis eurystoma*
Centropyxis cassis	*A. catinus*	*Centropyxis aerophila*	*C. aerophila sylvatica*
Difflugia acuminata	*Assulina seminulum*	*Phryganella hemispherica*	*Euglypha ciliata*
Nebela vitrea	*Bullinularia indica*	*Trigonopyxis arcula*	*Nebela collaris*
	Centropyxis aculeata		
	C. aerophila sphagnicola		
	C. cassis		
	C. platystoma		
	Corythion dubium		
	Euglypha strigosa		
	Heleopera petricola		
	Hyalosphenia elegans		
	Nebela collaris		
	N. lageniformis		
	N. militaris		
	N. tubulosa		
	Pontigulasia spiralis		
	Quadrulella symmetrica		
	Trinema enchelys		

Table 3.3: Classification of peatland testate amoebae by Bartos (1940) according to qualitative moisture classes.

De Graaf (1956) sought to redefine Bartos' (1940) associations after noting that, within the hygrophilous group in particular, there were differences between the moisture optima of species. For example, de Graaf found that the optima for *Hyalosphenia elegans* lay near to the wet side of the association, while *Nebela collaris* and *N. militaris* lay towards the drier side. He therefore suggested that the hygrophilous group be subdivided into α-hygrophilous and β-hygrophilous associations, the eurytopic group be rejected and the hydrophilous and xerophilous groups of Bartos be retained (Table 3.4). However, absolute moisture values still could not be derived from these groups and palaeohydrological changes on peatlands continued to be described in relative terms.

hydrophilous	α-hygrophilous	β-hygrophilous	xerophilous
Arcella crenulata	*Hyalosphenia elegans*	*Assulina seminulum*	*Assulina muscorum*
Difflugia globulosa	*H. papilio*	*Euglypha strigosa*	*Bullinularia indica*
	N. carinata	*Nebela collaris*	*E. laevis*
	Trinema enchelys	*N. militaris*	*Nebela tincta*

Table 3.4: Classification of testate amoebae associations by de Graaf (1956) based on moisture content.

b) Semi-quantitative investigations (1962-mid 1980s)

Schönborn (1962b) produced a semi-quantitative system by matching groups of testaceans to a I-VIII scale commonly used to estimate the water content of the moss layer on peatlands (Jung, 1936). Figure 3.2 illustrates Schönborn's associations showing that, in the driest zone, the xerophilous species of de Graaf (1956) such as *Trigonopyxis arcula* and *Phryganella hemispherica* were most common. In the wettest areas, hydrophilous species such as *Difflugia globulosa* and α-hygrophilous species such as *Nebela carinata* dominated

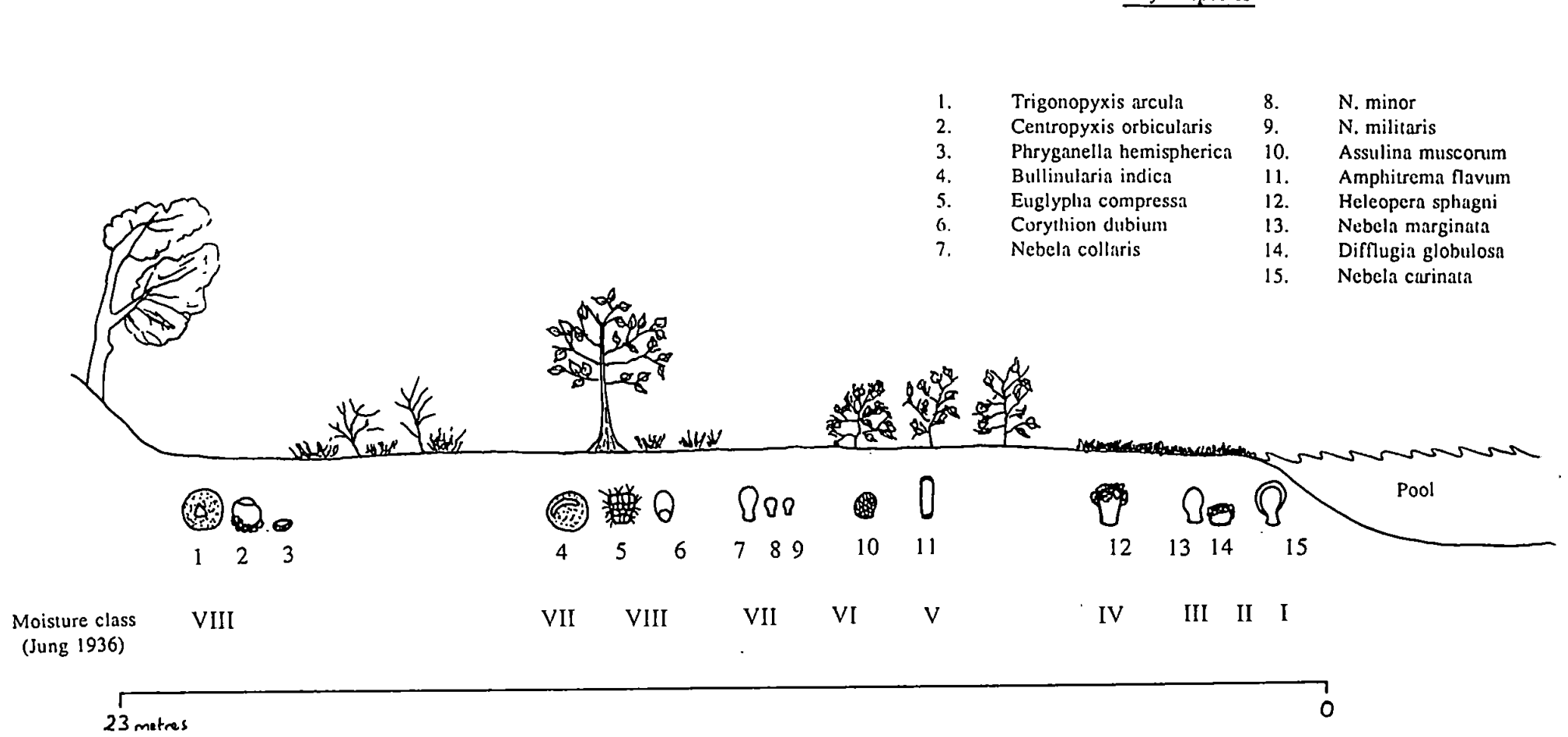


Figure 3.2: Horizontal distribution of testate amoebae within a small forested mire along the moisture gradient corresponding to moisture classes I-VIII, according to Schönborn, 1962 (redrawn from Tolonen, 1986; p.649).

the assemblage. Tolonen (1986) suggests that this detailed type of association is more useful in the interpretation of fossil assemblages than the five broader associations described earlier by Harnisch (1927).

Until 1992, the most quantitative hydrological description of peatland testaceans was provided by Tolonen (1986). This scheme was based on Meisterfeld (1977), who quantified Jung's (1936) moisture classes for Sphagna, according to moisture content. Table 3.5 shows the position of de Graaf's testacean associations with respect to the moisture classes and average moisture content of the host Sphagna. The combination provided the most accurate information available for palaeoenvironmental investigations, but the scheme still had several shortcomings. Firstly, the percent moisture content could be shared by several testacean classes - for example, the α-hygrophilous group includes Jung's moisture class IV (in which Meisterfeld's estimated moisture content is ca. 95%) and also moisture class V (which contains 95-85% moisture). The xerophilous group ranges between 50-80% and there is an interval between 80 and 85% moisture content for which no corresponding testacean group is identified. Differentiating between these groups is complicated by the subjective descriptions of moisture content, such as "half-wet", "moist" and "half-dry" and which refer to water being squeezed from the *Sphagnum* plants by "strong" or "moderate" pressure. Describing moisture optima for associations rather than for individual testate amoebae species means that recognition of the assemblage is dependent on all constituent members - absence of several species would make identification of the association difficult and raise uncertainties regarding the inferred hydrological conditions. Thus, despite the relative improvement in estimations of species' hydrological optima, palaeoenvironmental applications were still limited by subjectivity and the absence of absolute values for individual species.

Testate amoebae group (de Graaf, 1956)	Moisture class (Jung, 1936)	Relative water content (Jung, 1936)	Average water content (Meisterfeld, 1977)
	I	Open water or submerged vegetation.	>95%.
Hydrophilous	II	Floating vegetation, partly submerged, partly at the surface.	>95%.
	III	Emerged vegetation, very wet, water drops out without pressure.	>95%.
α-hygrophilous	IV	Wet, water drops out with moderate pressure.	95-85%.
	V	Half-wet, water drops out with moderate pressure.	95-85%.
β-hydrophilous	VI	Moist, water drops out with strong pressure.	85-90%.
Xerophilous	VII	Half-dry, a few drops with strong pressure.	<80%.
	VIII	Dry, no water drops with strong pressure.	<50%.

Table 3.5: Combination of testate amoebae groups (de Graaf, 1956), *Sphagnum* moisture content classes (Jung, 1936), relative water content (Jung, 1936) and average water content of the substrate (Meisterfeld, 1977) by Tolonen (1986) to provide a semi-quantitative estimate of testate amoebae species' hydrological optima.

c) Quantitative investigations (mid 1980s - present)

Since the mid 1980s, studies have aimed to derive fully quantitative estimates of individual species' hydrological optima. All have been conducted in Canada (Tolonen *et al.*, 1985; Warner, 1987; Warner, 1990; Warner, 1991; Charman and Warner 1992) or Finland (principally Tolonen *et al.*, 1992; 1994).

Tolonen *et al.* (1985) used testate amoebae analysis as part of a multi-proxy investigation into the development of a coastal raised bog in New Brunswick, Canada. This was the first published example of the use of weighted averaging techniques to calculate the peat moisture content optima of twelve modern testate amoebae species whose fossil counterparts dominated the fossil profile (see Table 3.6).

Warner (1987) studied testacean assemblages and hydrology on *Sphagnum* mires in southern Ontario, Canada which experienced great seasonal fluctuations in moisture content, including periodic drying of the mire surface. The sites were chosen because there were likely to be stronger hydrological influences on testaceans in such a stressed environment, allowing more accurate estimations of hydrological optima to be derived. Warner (1987) recognised three main testacean assemblages: *Centropyxis arcelloides*-type, *Hyalosphenia subflava* and *Sphenoderia lenta* were characteristic of moderately dry sites (78-89% water content); *Hyalosphenia papilio, Phryganella acropodia, Heleopera sphagni* and *Nebela collaris* were common on moderately wet sites (90-95% water content) and *Assulina muscorum* was indifferent to moisture content (Warner, 1987).

Warner (1991) later refined the technique and used it to calculate moisture preferences for individual species on four mires from Ontario and New Brunswick. Hydrological optima were calculated as percent wet weight where the species was most abundant (Table 3.6) and were similar to those calculated earlier by Tolonen *et al.* (1985). Warner noted that

Species	Coastal New Brunswick (Tolonen *et al.* 1985)	Southwestern Ontario (Warner, 1987)	Fort Frances-Rainy River, Ontario (Warner, 1989)	Wally Creek, Ontario (Charman and Warner, 1992)
Amphitrema flavum	93.2 (87.9-95.1)	90.1 (85.4-95.4)	86.9 (79.4-97.0)	86.3 (80.0-92.4)
Assulina muscorum	90.5 (70.8-95.1)	85.4 (62.0-96.7)	88.9 (39.9-97.0)	68.7 (64.0-73.0)
A. seminulum	90.5 (70.8-95.1)	62.0 (62.0-96.7)	85.3 (52.8-89.0)	70.4 (65.5-75.3)
Bullinularia indica	70.8 (70.8-88.3)	94.7 (92.3-94.7)	86.5 (-)*	67.5 (57.8-77.2)
Heleopera sphagni	90.2 (70.8-95.1)	90.1 (62.0-95.4)	86.9 (79.3-93.0)	78.0 (67.2-88.9)
H. petricola	90.5 (70.8-95.1)	91.1 (78.4-96.7)	88.9 (52.8-89.0)	70.1 (64.4-75.6)
Hyalosphenia elegans	90.2 (70.8-95.1)	90.1 (85.4-95.4)	86.9 (86.9-95.5)	83.9 (77.1-90.8)
H. ovalis	90.3 (73.0-95.1)	95.1 (-)*	80.2 (80.2-86.3)	77.1 (73.0-81.2)
H. papilio	93.2 (90.2-93.2)	90.1 (85.4-95.4)	93.0 (93.0-97.0)	88.8 (84.5-93.1)
H. subflava	88.3 (88.3-95.1)	88.0 (62.0-95.4)	39.9 (39.9-95.5)	59.7 (53.5-65.9)
Nebela militaris	90.5 (70.8-95.1)	85.7 (62.0-96.7)	52.8 (39.9-95.5)	70.0 (65.4-74.5)
Trigonopyxis arcula	73.0 (71.0-88.4)	93.4 (62.0-96.7)	64.8 (39.9-97.0)	67.4 (63.2-71.7)

Table 3.6: Comparison of moisture optima of selected testate amoebae from mires in New Brunswick (Tolonen *et al.*, 1985) and Ontario (Warner, 1987, 1989; Charman and Warner, 1992); * denotes single occurrence.

Hyalosphenia ovalis was extremely rare in southern Ontario mires, but common on hummocks on ombrotrophic mires in northern Ontario and New Brunswick, while *Arcella artocrea* was almost confined to mire pools in the Atlantic raised bogs (Warner, 1991). This suggested that these species were sensitive to periodic drying, but

> "Only through more intensive and widespread sampling of the faunas across eastern Canada will it be possible to test these rather speculative generalisations."
>
> (Warner, 1991; p.10)

Charman and Warner (1992) and Tolonen *et al.* (1992; 1994) provide the most quantitative estimates of species' hydrological optima published to date, based on separate studies from Canada and Finland respectively. The widespread availability of computer software packages for community ordination (see Chapter 6) means that more detailed investigations of species-environment relationships are possible, while the use of more powerful numerical software allows the processing of more complicated numerical data than hitherto possible. Both Charman and Warner (1992) and Tolonen *et al.* (1992;1994) have employed such techniques to confirm moisture as the dominant control on testate amoebae assemblages on peatlands.

Included in the sampling strategy of Tolonen *et al.* (1992) was one testate amoebae sampling site for which three years of continuously-monitored hydrological data was available, including water table depth. For the remaining sites, the mean water table depths for the sampling period (4 weeks) were used. This is significant in two respects. Firstly, no previous published study had considered recording depth to water table, either on the day of sampling or for a period prior to sampling, using instead substrate moisture content. Secondly, the use of several years of hydrological data meant that representative problems of "single-shot" samples (arising from sampling during an unusually dry or wet year) would be minimised. Charman and Warner (1992) also sampled from a site which was being

monitored as part of an experimental forested peatland, although mean annual water table data were not available. Once hydrology had been confirmed (by ordination) as the strongest influence on testate amoebae assemblages, both studies used weighted averaging (Oksanen *et al.*, 1988) to derive hydrological optima for each species. This method is described fully in Chapters 6 and 7 in terms of the present study.

Because the sampling locations of Tolonen *et al.* (1992) and Charman and Warner (1992) were very different (Tolonen *et al.* sampled from six different mire types in oceanic Finland, while Charman and Warner sampled from a single forest peatland in continental Canada), direct comparisons between the percent moisture content optima for species are questionable. Table 3.7 illustrates this clearly, showing that the Canadian moisture optima are all lower than corresponding Finnish estimates. This reflects perhaps the continental setting of the Canadian site, but it may also be a function of different sampling times (Charman and Warner, 1992). However, a relative comparison can be made between species rankings in the two data sets, which are very similar (Table 3.7).

Existing estimates of hydrological optima for common species on peatlands are summarised in Table 3.8. The table also illustrates the progression from qualitative to quantitative estimates. Clearly, the work of Tolonen *et al.* (1992) and Charman and Warner (1992) epitomise the way forward for modern ecological studies on testaceans, and Warner and Charman (1994) produced optimum water table depths for individual testacean species in North America. All three studies form a sound base for future workers to conduct quantitative investigations, from which the absolute hydrological optima of modern testaceans may be derived.

Species	Charman & Warner (1992) Canada		Tolonen *et al.* (1992) Finland	
	%	Rank	%	Rank
Hyalosphenia papilio	88.8	1	95.1	5
Amphitrema flavum	86.27	2	96.0	1
Hyalosphenia elegans	83.90	3	95.3	4
Centropyxis aculeata	78.54	4	95.6	2
Heleopera sphagni	78.02	5	94.1	8
Hyalosphenia ovalis	77.06	6	94.5	7
Euglypha tuberculata	74.38	7	90	11
E. rotunda	71.03	8	89.6	12
Assulina seminulum	70.40	9	92.2	9
Corythion spp.	70.17	10	87.0	15
Heleopera petricola	70.12	11	95.6	2
Nebela militaris	69.95	12	89.3	13
Assulina muscorum	68.66	13	86.6	17
Euglypha strigosa	68.15	14	94.8	6
Arcella artocrea	67.53	15	87.4	14
Bullinularia indica	67.50	16	80.9	22
Trigonopyxis arcula	67.43	17	85.1	18
Centropyxis arcula	67.29	18	83.6	20
Nebela parvula	64.55	19	86.7	16
N. tincta	64.08	20	83.2	21
Cyclopyxis arcelloides	63.66	21	84.1	19
Arcella catinus	44.18	22	91.7	10

Table 3.7: Moisture optima for selected species from Canadian (Charman and Warner, 1992) and Finnish studies (Tolonen *et al.*, 1992). Source: Charman and Warner (1992).

a) Testate amoebae species indicative of wet mire surfaces.

	Europe		Canada/US	
Species	**Inferred hydrological optima**	**Author**	**Inferred hydrological optima**	**Author**
Amphitrema flavum	wet conditions	Corbet (1973)	moisture content = 93.2%	Tolonen *et al*. (1985)
	wetter parts of hummocks	Tolonen (1966)	moisture content = 90.1%	Warner (1987)
	water table depth = -2.8cm	Tolonen *et al*. (1992)	moisture content = 86.9%	Warner (1989)
	moisture content = 96%	Tolonen *et al*. (1992)	moisture content = 86.2%	Charman & Warner (1992)
			water table depth = -15cm	Warner & Charman (1994)
Amphitrema wrightianum	mire pools	Corbet (1973)	moisture content = >90%	Warner (1989)
	water table depth = 0.8cm	Tolonen *et al*. (1992)		
	moisture content = 95%	Tolonen *et al*. (1992)		
Arcella discoides	floating, submerged or very wet *Sphagnum*	Tolonen (1986)	very wet conditions	Warner (1987)
	water table depth = -4.8cm	Tolonen *et al*. (1992)	water table depth = -9cm	Warner & Charman (1994)
	moisture content = 96.7%	Tolonen *et al*. (1992)		
Centropyxis aculeata	aquatic habitats	de Graaf (1956)	very wet conditions	Warner (1987)
	water table depth = -7.8cm	Tolonen *et al*. (1992)	moisture content = 78.5%	Charman & Warner (1992)
	moisture content = 95.6%	Tolonen *et al*. (1992)	water table depth = -24cm	Warner & Charman (1994)
Difflugia bacillifera	mire pools	Corbet (1973)	very wet	Warner (1987)
	water table depth = -3.3cm	Tolonen *et al*. (1992)		
	moisture content = 96.4%	Tolonen *et al*. (1992)		
Heleopera petricola	moisture content = 95%	Tolonen *et al*. (1992)	moisture content = 90.5%	Tolonen *et al*. (1985)
	water table depth = -3.1cm	Tolonen *et al*. (1992)	moisture content = 91.1%	Warner (1987)
			moisture content = 88.9%	Warner (1989)
			moisture content = 70.1%	Charman & Warner (1992)
			water table depth = -31cm	Warner & Charman (1994)
Heleopera sphagni	water table depth = -9.1cm	Tolonen *et al*. (1992)	moderately wet	Warner (1987)
	moisture content = 94%	Tolonen *et al*. (1992)	moisture content = 78%	Charman & Warner (1992)
			water table depth = -42cm	Warner & Charman (1994)

Table 3.8: Qualitatively and (more recently) quantitatively inferred hydrological optima for modern testate amoebae species on peatlands of the northern European and North American continents.

b) Testate amoebae species indicative of moderately wet mire surfaces.

	Europe		Canada/US	
Species	**Inferred hydrological optima**	**Author**	**Inferred hydrological optima**	**Author**
Hyalosphenia elegans	mire hummocks	Corbet (1973)	moisture content = 90.2%	Tolonen *et al.* (1985)
	moisture content = 95.3%	Tolonen *et al*. (1992)	moisture content = 90.1%	Warner (1987)
	water table depth = -8cm	Tolonen *et al*. (1992)	moisture content = 86.9%	Warner (1989)
			moisture content = 83.9%	Charman & Warner (1992)
			water table depth = -27cm	Warner & Charman (1994)
Hyalosphenia papilio	wet *Sphagnum* in mire hummocks	Heal (1961)	moisture content = 93.2%	Tolonen *et al.* (1985)
	moisture content = 95%	Tolonen *et al*. (1992)	moisture content = 90.1%	Warner (1987)
	water table depth = -7.1cm	Tolonen *et al*. (1992)	moisture content = 93%	Warner (1989)
			moisture content = 90-95%	Warner (1990)
			moisture content = 88.8%	Charman & Warner
			water table depth = -10cm	Warner & Charman (1994)
Nebela collaris	moderately dry	de Graaf (1956)	moisture content = 90-95%	Warner (1987)
N. militaris	wet *Sphagnum* on mire hummocks	Corbet (1973)	moisture content = 90.5%	Tolonen *et al.* (1985)
	moisture content = 89.3%	Tolonen *et al*. (1992)	moisture content = 85.7%	Warner (1987)
	water table depth = -15.1cm	Tolonen *et al*. (1992)	moisture content = 52.8%	Warner (1989)
			water table depth = -42cm	Warner & Charman (1994)
Phryganella acropodia	water table depth = -12.8cm	Tolonen *et al.* (1992)	moisture content = 90-95%	Warner (1987)
	moisture content = 91.6%	Tolonen *et al*. (1992)	water table depth = -53cm	Warner & Charman (1994)

Table 3.8: Qualitatively and (more recently) quantitatively inferred hydrological optima for modern testate amoebae species on peatlands of the northern European and North American continents.

c) Testate amoebae species indicative of drier mire surfaces.

	Europe		Canada/US	
Species	**Inferred hydrological optima**	**Author**	**Inferred hydrological optima**	**Author**
Assulina muscorum	xerophilous conditions	de Graaf (1956)	moisture content = 90.5%	Tolonen *et al.* (1985)
	water table depth = -16.6cm		moisture content = 85.4%	Warner (1987)
	moisture content = 86.6%	Tolonen *et al*. (1992)	moisture content = 88.8%	Warner (1989)
			moisture content = 68.6%	Charman & Warner (1992)
			water table depth = -44cm	Warner & Charman (1994)
A. seminulum	hygrophilous	de Graaf (1956)	moisture content = 90.5%	Tolonen *et al*. (1985)
	mire hummocks	Corbet (1973)	moisture content = 62%	Warner (1987)
	water table depth = -10.9cm	Tolonen *et al.* (1992)	moisture content = 85.3%	Warner (1989)
	moisture content = 92%	Tolonen *et al*. (1992)	moisture content = 70.4%	Charman & Warner (1992)
			water table depth = -40cm	Warner & Charman (1994)
Bullinularia indica	mire hummocks	Heal (1964)	moisture content = 70.8%	Tolonen *et al.* (1985)
	relatively dry conditions	Tolonen (1966)	moisture content = 86.5%	Warner (1989)
	dry hummock Sphagna	Tolonen (1988)	moisture content = 67.5%	Charman & Warner (1992)
	water table depth = -12.7cm	Tolonen *et al*. (1992)	water table depth = -50cm	Warner & Charman (1994)
	moisture content = 80.9%	Tolonen *et al.* (1992)		
Corythion dubium	dry conditions	de Graaf (1956)	moisture content = 70%	Charman & Warner (1992)
	dry conditions	Schonborn (1962)	water table depth = -46cm	Warner & Charman (1994)
	moderately dry conditions	Meisterfeld (1977)		
	water table depth = -14.1cm	Tolonen *et al.* (1992)		
	moisture content = 87%	Tolonen *et al*. (1992)		
Cyclopyxis arcelloides	moisture content = 84.1%	Tolonen *et al.* (1992)	moisture content = 78-89%	Warner (1987)
	water table depth = -20.6cm	Tolonen *et al*. (1992)	moisture content = 63.6%	Charman & Warner (1992)
Hyalosphenia subflava			moisture content = 88.3%	Tolonen *et al.* (1985)
			moisture content = 88%	Warner (1987)
			moisture content = 39.9%	Warner (1989)
			indicative of drained peatlands	Warner (1989)
Nebela parvula	moisture content = 86.7%	Tolonen *et al.* (1992)	very dry conditions	Warner (1987)
	water table depth = -15cm	Tolonen *et al*. (1992)	moisture content = 64.5%	Charman & Warner (1992)
Nebela tincta	xerophilous	de Graaf (1956)	moisture content = 64%	Charman & Warner (1992)
	water table depth = -22.4cm	Tolonen *et al*. (1992)	water table depth = -32cm	Warner & Charman (1994)
	moisture content = 83.2%	Tolonen *et al*. (1992)		

Table 3.8: Qualitatively and (more recently) quantitatively inferred hydrological optima for modern testate amoebae species on peatlands of the northern European and North American continents.

3.2.2 Testate amoebae and other ecological variables

While this thesis emphasises the relationship between testaceans and hydrology, the following section summarises research on testaceans and other environmental variables, chiefly light, food supply and water chemistry. This provides a full summary of testacean ecology by considering other environmental factors that may also influence testacean distribution and abundance. Any study attempting to use testaceans as environmental indicators must be aware of the potential effect of these other factors.

a) Light and food supply

Sphagnum plants are divided into green and brown sections. Beneath the capitulum there is a green section, with well developed leaves and branches, and this grades (at varying depths) into a brown - coloured section where branches are more sparsely distributed (Plate 3.2). Since *Sphagnum* has no roots, the base of the brown fraction grades almost imperceptibly into the underlying peat. Studies by Schönborn (1963) and Meisterfeld (1977) revealed that testacean populations followed this vertical zonation very closely. Most species peaked between 6 - 12 cm below the surface, with no living testaceans found below approximately 15 cm in very wet *Sphagnum* (Meisterfeld, 1977). Those with symbiotic zoochlorellae (which require light to function), such as *Hyalosphenia papilio*, were most abundant above 6 cm (Figure 3.3). This zonation is almost certainly linked to light and food availability. In the uppermost parts of the green fraction, food sources are scarce and only those species that can obtain nourishment from symbiotic zoochlorellae and have transparent tests will survive. This close symbiotic relationship was illustrated by Schönborn (1965), who showed that testaceans with symbiotic zoochlorellae died out when their habitat was artificially darkened.

In drier conditions, where higher rates of microbial decomposition deprive the deeper horizons of detritus, the difference between testacean assemblages in the green and brown

Plate 3.2: Green and brown sections of *Sphagnum cuspidatum* plants

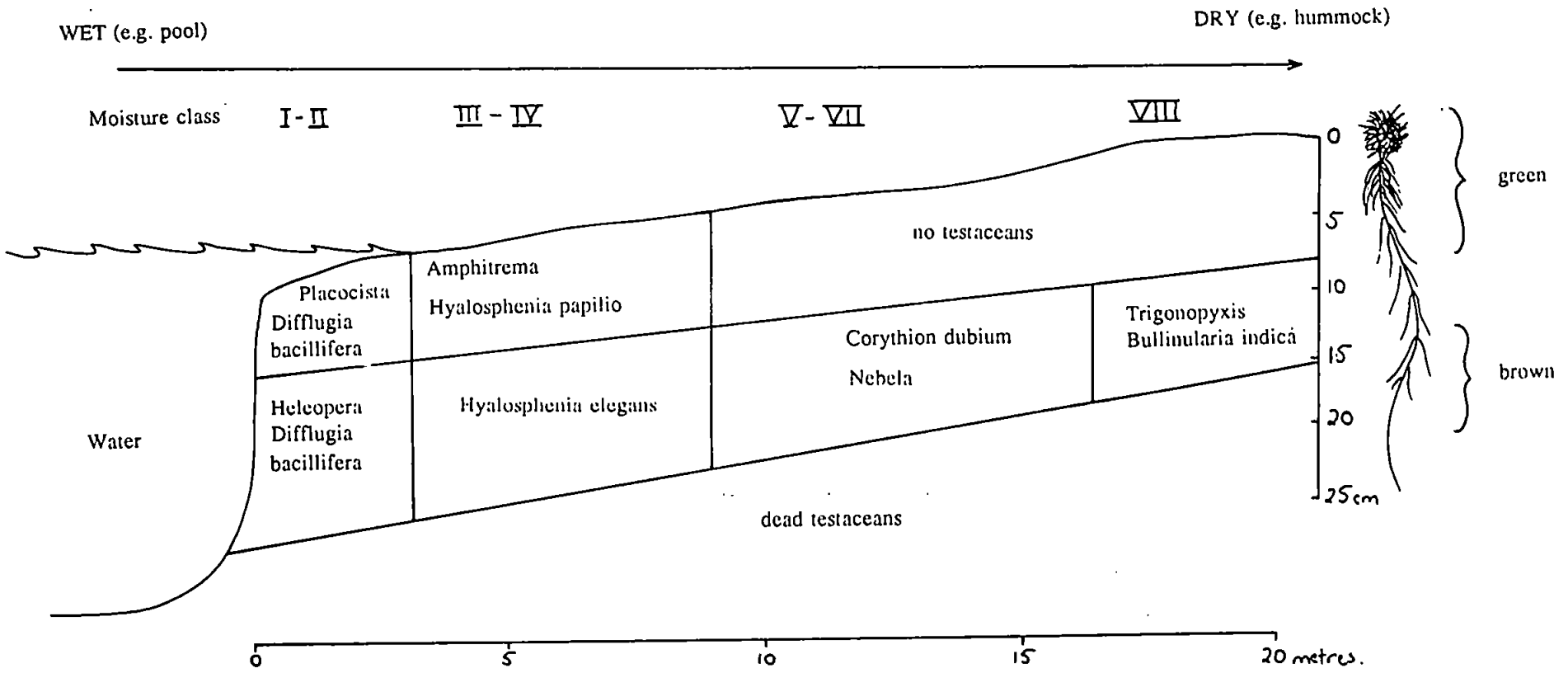


Figure 3.3: Distribution of living testaceans in a *Sphagnum* mire (redrawn from Schönborn (1963) in Corbet, 1973; p.835).

Sphagnum sections is more marked. The very driest areas are without testaceans and this limit moves higher in drier hummocks, thought by Schönborn (1963) to correspond to the thickness of the brown fraction of *Sphagnum*, within which (due to respiration during microbial decomposition) dissolved oxygen is present only in low concentrations (Tolonen, 1986). Most living testaceans are found lower down where microbial decomposition is slower and where decomposing brown *Sphagnum* provides the detrital food source (Schönborn, 1963) and material is available for test construction (Heal, 1963). This horizon also contains the empty tests of all species (which are washed down from the overlying green section) and, therefore, it is this section that is of greatest value in palaeoecological applications, since it contains tests that will eventually be incorporated directly into the peat deposit.

b) Water chemistry

Although the importance of moisture as a basic limiting factor and light and food as secondary influences are accepted, a number of other ecological parameters that affect the growth and distribution of modern testaceans have been investigated by several authors. Chief among these have been pH (Heal, 1961; Corbet, 1973; Costan and Planas, 1986; Beyens *et al.*, 1986b; Charman and Warner, 1992), dissolved oxygen concentration (Beyens *et al.*, 1986a; Tolonen *et al.*, 1992), nutrient status of the substrate (Tolonen, 1986) and the carbon/nitrogen (C/N) ratio of the peat (Tolonen *et al.*, 1992).

In a study of Lake Erie, Scott and Medioli (1983) related testacean communities to organic carbon, observing changes in the predominance of *Difflugia* species with changes in organic carbon concentration. In an autecological study of testaceans in Finnish mires, Tolonen *et al.* (1992) noted a wide distribution of species in relation to peat carbon : nitrogen ratios and dissolved organic carbon in the peat water, suggesting that the carbon and nitrogen are less important limiting factors than moisture content.

Charman and Warner (1992) identified pH as the secondary control on species distribution and abundance, while Corbet (1973) suggested that pH may determine the microdistribution of testaceans when acid hummocks emerge from alkaline flushes. Heal (1961) studied the distribution of testaceans in bog and fen habitats, finding that species had distinct preferences for either bog or fen sites and that fens (pH > 5.0) had a greater species diversity than bog habitats (pH < 5.0). Beyens *et al.* (1986b) found a positive relationship between species diversity and alkalinity and Tolonen *et al.* (1992) calculated pH preferences for individual species. Building on the potential for testaceans as water quality indicators, Costan and Planas (1986) observed the effects of short-term acidification on a testacean community within a lake system. pH is a second variable that is worth investigating for palaeoecological studies and is followed up in this thesis. If pH optima can be derived for individual species, then pH (as well as hydrological) transfer functions from testaceans are a likely prospect. Testaceans could be used alongside diatoms in water chemistry studies and offer the potential to extend these to non-aquatic habitats.

3.3 Fossil testate amoebae

3.3.1 The development of fossil testate amoebae analysis

Almost as soon as living testate amoebae were studied seriously at the end of the nineteenth century, their fossil counterparts were scrutinised as workers tried to link living and fossil testaceans. The first studies (Lindberg, 1899; Lagerheim, 1902) concentrated on subfossil testacean remains in lacustrine deposits, but when testaceans were discovered in other habitats, the studies diversified. Because subfossil testaceans preserved well in peat they were readily incorporated into mire stratigraphical studies, beginning with an investigation on German peatlands by Steinecke (1927) and Harnisch (1927) and continuing with Harnisch (1949), Grospietsch (1951) and de Graaf (1956 - see section 3.2.1 for details of this research).

During this period, Harnisch (1951) postulated that the habitat dependence of peatland testaceans was not likely to have developed until ca. 6000 years BP and that it would therefore be impossible to interpret faunal lists from older periods based on present ecology. Harnisch had recovered ten interglacial species (which he considered to be a diverse assemblage), without the dominance of species typical of present *Sphagnum* bogs (Frey, 1964). The explanation forwarded for this in Tolonen (1986) is that a long-term "natural" development of mire habitats has occurred since the last glaciation and peat-stratigraphical studies support this (Tolonen, 1986). For example, *Amphitrema wrightianum*, which at present in central and western Europe is restricted to pools on raised bogs (Heal, 1959; 1962), was discovered in earlier wet minerotrophic fen stages in central Europe (Meisterfeld, 1977). In Finland, Tolonen (1967, 1968) found *A. wrightianum* as a subfossil in the same conditions from ca. 7000 BP. Harnisch's theory has important implications for fossil testate amoebae analysis, but has never been investigated further.

Two reasons may account for the lack of interest in Harnisch's theory. Firstly, the proposal was based on his final study on testaceans, which comprised a very restricted data set from a single German study site (Harnisch, 1927). Secondly, inappropriate treatment of the peat samples may have damaged the tests - a factor that is ignored in Frey (1964) and Tolonen (1986). Harnisch reported that "the rhizopod tests were often so few and so distorted that they could not be identified to species level" (Harnisch, 1927 p. 228), but earlier states that the peat samples were treated with NaOH (Harnisch, 1927, p.222). This would certainly have destroyed all but the most resistant chitin tests and it is interesting to note that the more fragile tests of *Euglypha* spp., *Hyalosphenia* spp. and *Heleopera* spp. were all absent from the samples, while the more resistant tests of *Amphitrema flavum* and *Difflugia* spp. were dominant. At present, Harnisch's theory is best treated with considerable caution until studies similar to Tolonen (1967; 1968), which investigate the palaeoecology of testaceans beyond 6000BP, have been conducted.

The paucity of published material from other countries suggests that fossil testacean analysis continued principally in Germany and the Netherlands during the forty years after Steinecke's pioneering study (1927). Chief among German workers was Schönborn, who used testate amoebae in stratigraphical analyses of bogs in both Germany (1962a,b; 1963; 1967) and Swedish-Lappland (1966; 1975). In the Netherlands, Hoogenraad (1935; 1936) and Hoogenraad and de Groot (1940) used testate amoebae in similar mire stratigraphical studies. In 1966, Tolonen conducted the first testacean analysis in Finland when he combined the technique with peat stratigraphy to elucidate the history of a raised mire in southern Finland.

In the 1970s, fossil testacean analysis was used for the first time in Denmark (Aaby and Tauber 1975; Aaby 1976) and, in Britain, Barber (1981) attempted to use fossil testaceans as supplementary evidence in his examination of the theory of cyclic peat bog regeneration, albeit without success:

> "The results were disappointing. They added very little to the macrofossil analyses and were not at all consistent in highlighting wet or dry phases in the bog's growth. Over a longer time-span encompassing much more variable stratigraphy, including fen peat, they may add some useful data and, significantly, this is the way in which Tolonen (1966) and Casparie (1972) have made use of them".
>
> Barber (1981) pp. 72-73.

However (in common with many other workers), Barber was searching for testate amoebae in samples that had been prepared for pollen analysis. A large proportion of the testacean shells would be destroyed in this process (see also Chapter 8 of this thesis for a more detailed discussion of this method). Modern preparation treatments for testate amoebae (such as that in Tolonen, 1986) recognise the damage caused by such chemical treatments, and use only water to disaggregate them from *Sphagnum* plants and peat (see Chapter 4 for a full description of preparation techniques).

At present, fossil testacean analysis on peatlands is progressing faster in Canada than in Europe, where studies have diversified to lake sediments (for example, Schönborn, 1984; 1990). Although Tolonen published the first stratigraphic profiles of testaceans in 1966 (from a raised bog in Nova Scotia), testacean analysis remained on the fringes of palaeoecology in Canada until the mid 1980s. Since then, two Holocene palaeohydrological reconstructions have been conducted on peatlands (Warner 1989; Warner and Charman, 1994). In the most recently published study, Warner and Charman (1994) reconstructed the water table depth for Emo Bog on the US/Canadian border from 6500BP. Their study is characteristic of the present objectives in peatland testate amoebae analysis.

3.3.2 Problems encountered in fossil testate amoebae analysis

Although fossil testacean analysis shows immense promise as a palaeoecological technique, there are still several problems that must be resolved before its full potential can be realised. They are: (a) a limited understanding of the hydrological affinities of modern testaceans; a similar lack of information on (b) the production biology of modern species and (c) differential decay rates of tests; (d) inappropriate preparation techniques and (e) taxonomic confusion. Of these, (a) and (e) are probably the most severe limitations to fossil testate amoebae analysis.

a) Limited understanding of the hydrological affinities of testate amoebae

This problem has two aspects, since palaeohydrological investigations with testate amoebae generally use either the semi-quantitative information in Table 3.5 (from Tolonen, 1986), or the quantitative approach of Warner and Charman (1994). Those workers who prefer to use the moisture estimates listed in Table 3.5 encounter the subjective descriptions identified in section 3.2.3.1. There is also further uncertainty regarding the exact derivation of Jung's (1936) moisture classes.

Those who adopt the approach of Warner and Charman (1994) encounter the inaccuracies inherent in "single-shot" sampling strategies, where samples are taken from sites with no long-term hydrological data (see above). Such studies have data for a single time period only which, although comparable within a study, are not necessarily comparable between studies. There is no continuum through raw data from different studies and each data set brings with it a unique set of environmental parameters, making it impossible to produce meaningful estimates of hydrological optima. Indeed, Charman and Warner (1992) stated that until a wider range of data became available it would be impossible to proceed from the statistical analysis of results towards the development of a model of the relationship between hydrology and testaceans that could be used in palaeoecological studies. However, the use of modern optima from Tolonen *et al.* (1992) where three years' hydrological data exist would remove the problems associated with sampling in a year that might be unusually dry or wet. This is the ideal approach on which to base future investigations and upon which this present study is based.

b) Production biology

Relatively few production studies have been conducted on modern testaceans (Schönborn, 1975, 1977, 1978, 1982, 1992a,b; Ogden, 1981; Lousier, 1984a,b; Costan and Planas, 1986) and none of these relate directly to peatland ecosystems. Such studies are crucial to palaeoenvironmental investigations using testate amoebae since the relative contribution of individual species to the living assemblage will partly affect the composition of the fossil fauna.

Existing production studies show a very rapid doubling time for testaceans (the length of time required to double the population). In cultures of *Euglypha*, doubling occurred within 2.3-4.4 days depending on the species, while cultured populations of *Assulina muscorum* took between 2.3 and 2.9 days to double (Ogden, 1981). Additional information on

individual species are rare, but Lousier (1984a,b) provides information for *Euglypha* spp., *Trinema* spp., *Phryganella acropodia* and *Difflugia oviformis* in whole litter, fragmented litter, humus and black mineral layers of aspen woodland soils. The results showed that populations in all except the humus layer experienced seasonal fluctuations, with fastest doubling in spring. Doubling time was generally fastest in the litter layer, presumably reflecting greater availability of detrital food in this horizon (Table 3.9).

The rapid population doubling time makes testate amoebae a potentially good palaeoenvironmental indicator because they may react faster to environmental changes than, for example, plant macrofossils and peat stratigraphy. However, this statement can only remain as a generalisation until the production biology of individual species on peatlands has been quantified.

c) Differential decay rates

Apart from Lousier and Parkinson (1981- see section 3.1.2.1 of this thesis), authors have ignored the possibility of differential decay rates in testacean shells. Differential decay means that a death assemblage may not accurately reflect the living community, since species with less resistant tests will be under-represented relative to those with more resistant tests. There is clearly a need to quantify decay rates for peatland testaceans in the same way that Havinga (1964, 1971) did for pollen and spores, so that adjustments can be made in the interpretation of fossil assemblages. One way of circumventing this problem is to compare modern analogues with fossil testate assemblages to check if there is any significant divergence of composition.

d) Inappropriate preparation techniques

Section 3.3.1 above has already demonstrated the effects of inappropriate preparation techniques on testacean assemblages. Tolonen (1986) details a laboratory preparation

Species	Estimated doubling time (in days) for litter layer (Lousier, 1984a,b)				Estimated doubling time in days (Ogden, 1981).
	Whole litter	Fragmented litter	Humus	Black mineral	
Assulina muscorum	-	-	-	-	2.3 - 2.9
Difflugia oviformis	4.7 +/- 0.58	3.4 +/- 0.31	4.1 +/- 0.70	2.4 +/- 0.42	-
Euglypha acanthophora	-	-	-	-	2.7
E. cashii	-	-	-	-	2.3 - 2.8
E. compressa	-	-	-	-	4.0 - 4.4
E. dickensii	-	-	-	-	2.6 - 3.1
E. laevis	9.6 +/- 1.5	5.5 +/- 0.9	3.1 +/- 0.3	15.9 +/- 4.7	-
E. rotunda	11.4 +/- 1.5	4.9 +/- 0.7	6.7 +/- 1.6	6.1 +/- 1.3	-
E. scutigera	9.7 /- 1.0	4.7 +/- 0.8	6.6 +/- 1.1	7.5 +/- 1.2	-
E. cuspidata	11.4 +/- 3.0	5.7 +/- 1.5	3.6 +/- 0.4	-	-
Phryganella acropodia	11.2 +/- 1.7	10.0 +/- 3.0	4.8 +/- 1.3	6.5 +/- 2.8	-
Trinema lineare	4.8 +/- 0.63	4.8 +/- 0.61	4.3 +/- 0.47	3.8 +/- 0.57	-
T. enchelys	5.2 +/- 0.7	3.3 +/- 0.4	2.5 +/- 0.3	5.0 +/- 0.8	-

Table 3.9: Estimates of population doubling time (in days) for selected testate amoebae species in litter layer of soils (Lousier, 1984a,b) and cultures (Ogden, 1981) "-" denotes comparable data unavailable.

procedure for concentrating tests in both peats and lake sediments that does not damage the tests. Significantly, this is the preparation technique adopted by Warner (1987; 1989), Charman and Warner (1992) and Warner and Charman (1994) with excellent results. There is scope for this to be adopted as the standard technique in modern and fossil testate amoebae analyses, although further refinements are still being developed (D. Hendon, pers. com.)

e) Taxonomy

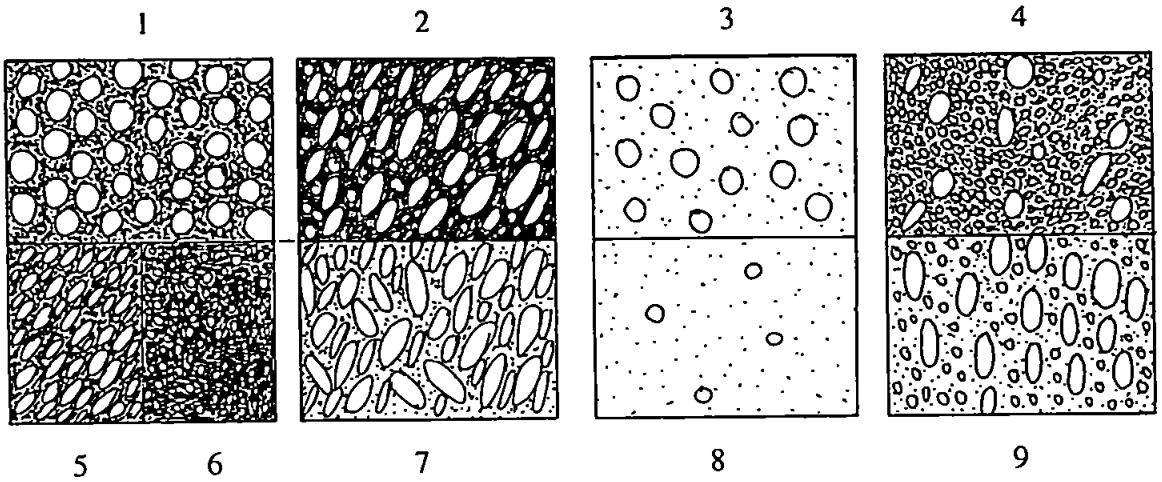
Identification and classification of testaceans to the order and family levels are reasonably straightforward with the use of modern high-powered light microscopy. However, identification down to genus and species level is more difficult. Early studies of testaceans in particular were conducted without the benefit of SEM, meaning that the finer diagnostic features of test ornamentation were often missed. A clear example of this difficulty is given in Heal (1962) who conceded that more than one species may be included under one taxon - for example, *Amphitrema wrightianum* may have included *Amphitrema stenostoma.* In many cases, the indistinction has been such that individuals once assigned to a particular genus are now, with SEM, being recognised as separate taxon in their own right. This is a common problem for a number of testate amoebae species, as Table 3.10 summarises.

Of the diagnostic features, test shape, ornamentation, colour and size are most commonly used (see, for example, Grospietsch, 1958; Corbet, 1973; Tolonen, 1986; Ellison and Ogden, 1987). Test ornamentation can be inconsistent within a species, as clearly identified by Bobrov *et al.* (1995) in *Nebela militaris.* A total of nine different surface patterns were observed in individuals from two samples collected from Ontario and Siberia (Figure 3.4a). Variations in surface patterns can compound confusion between *Nebela* species that have a similar test morphology. For example, *Nebela parvula* and *N. tincta* share similar size ranges (*N. parvula* between 78-90µm and *N. tincta* between 70-120µm - Corbet, 1973) and

Taxa	Indistinct from	Other comments
Assulina muscorum	*A. seminulum.*	Polymorphism in *A. muscorum* affects size and colour of tests (range from russet to colourless - Schönborn & Peschke, 1990). Usually brown, but occasionally colourless (Ogden, 1981).
Arcella artocrea	*A. gibbosa* (Tolonen *et al.* 1992).	
Arcella discoides	*A. megastoma* and *A. polypora* (Warner, 1987).	See below.
Arcella rotunda aplanata	*A. discoides scutelliformis* (Tolonen, 1986); *A. vulgaris* (Warner, 1987).	Systematics of *Arcella* poorly understood. Intermediate forms difficult to identify (Tolonen, 1986).
Centropyxis aculeata	*C. hirsuta* (Tolonen, 1986).	Regarded by Heal (1962) as a species complex.
Corythion dubium	*Trinema lineare* (Tolonen, 1986).	Plates diagnostic, but very small test size (18-35µm - Ogden & Hedley, 1980) makes identification very difficult. Often grouped together as same species.
Centropyxis aerophila-type	*C. cassis; C. constricta; C. ecornis* and *C. platystoma* (Warner, 1987).	Conglomerate group, which may contain a number of separate species with specific niches (Tolonen, 1986; Warner & Chmielewski, 1992).
Cyclopyxis arcelloides-type	*Cyclopyxis arcelloides*	As for *Centropyxis aerophila*-type.
Euglypha strigosa-type	*E. compressa, E. ciliata* (Warner, 1987).	
Heleopera petricola	*H. rosea* (Warner, 1987)	Samples stained with safranine-O invalidates wine-red colour of *H. rosea* as diagnostic feature (Warner, 1987).
Phryganella hemispherica	*Centropyxis eurystoma* Tolonen (1986); *Difflugia globulosa* (Tolonen, 1986); *Cyclopyxis arcelloides* (Meisterfeld, 1979).	Also referred to as *Phryganella acropodia* (Warner, 1987).

Table 3.10: Common peatland testate amoebae with disputed taxonomy.

(a) Common surface patterns in *Nebela militaris.*



(b) Variations in aperture shape in *Trigonopyxis arcula.*

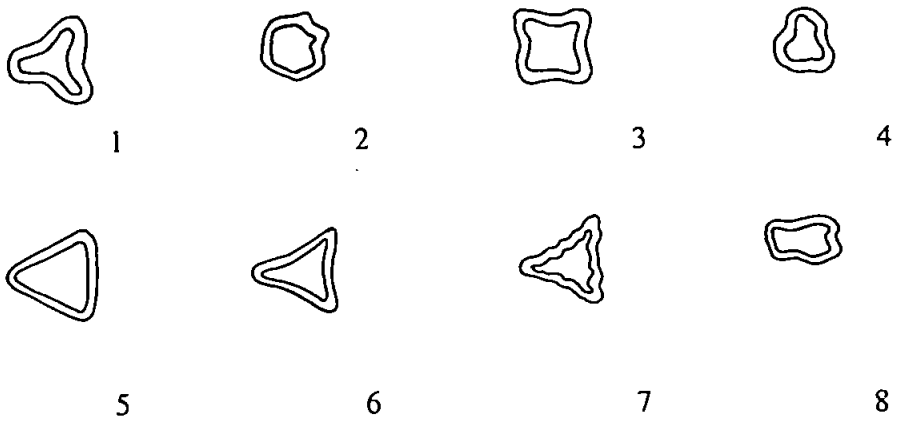


Figure 3.4: Sketches showing (a) common surface patterns of *Nebela militaris* and (b) variations in aperture shape in *Trigonopyxis arcula*, observed by Bobrov *et al.* (1995).

a diagnostic feature is the presence of lateral pores in *Nebela tincta* (Corbet, 1973). However, during preliminary counting, the author had frequent difficulty locating the pores in *Nebela tincta* and, if variations in surface pattern occur in *Nebela militaris*, there is no reason why variations could not occur in *N. parvula* and *N. tincta* to the extent that the two separate species could have very similar surface patterns, so that *N. tincta* is wrongly identified as *N. parvula.* Added to this is polymorphism, which occurs in *N. tincta* in response to the moisture content of their host substrate. Heal (1963) demonstrated that *N. tincta* individuals were smaller in drier sites than in wetter locations in a *Sphagnum* hummock-hollow complex and these smaller individuals could be misidentified as *N. parvula.*

Test colour is frequently used as a diagnostic feature in taxonomic texts (for example, Corbet, 1973; Ogden and Hedley, 1980), which often identify a subjective range of colours for one species. The colour of *Trigonopyxis arcula*, for example, ranges from "yellowish-gold to dark brown, often becoming darker as the shell size increases" (Bobrov *et al.*, 1995, p.120), while Corbet (1973, p.807) describes the colour as "red-brown". *Hyalosphenia papilio* can be described as "almost colourless to light yellow" (Bobrov *et al.*, 1995, p.123) or "delicately coloured" (Corbet, 1973; p.812). Colouring can also be masked by the common use of red safranine-O staining in preparations (which is supposed to improve identification!); the natural wine-red colouring of *Heleopera rosea* is then of limited use for identification if other species of *Heleopera*, such as *H. petricola* and *H. sphagni* have absorbed the staining (Warner, 1987; Tolonen *et al.*, 1992). Schönborn and Peschke (1990) showed how polymorphism occurred in *Assulina muscorum*, normally a straightforward species to identify. In *Sphagnum*, it occurred in two colours - the normal russet colour and colourless - each of which comprised four shapes. Each form was identified as a genotype that could occur for short periods in such habitats. Identification is hampered if a sample at a particular point in time comprises two or more of these genotypes, in which case a

misidentification of *A. seminulum* (a larger, colourless species of *Assulina*) for *A. muscorum* would be the most likely outcome. This may have occurred in samples studied by Ogden (1981, p.148), who describes *A. muscorum* as "usually brown, but occasionally colourless in the wild".

Aside from differences in test ornamentation are variations in the test aperture. These can be considerably diverse within a single species. For example, Bobrov *et al.* (1995) noted eight different aperture shapes in *Trigonopyxis arcula* individuals in two samples collected from Ontario and Siberia (Figure 3.4b). Such variations are also critical to the identification of other species with pronounced apertures, such as *Bullinularia indica*, *Centropyxis* spp. and *Cyclopyxis* spp.

The paucity of identification keys listing all peatland testaceans is a major limitation in taxonomic studies (Tolonen, 1986) and it becomes necessary to refer to several separate monographs in which authors often concede to grouping difficult taxonomic groups together (Table 3.10). Corbet (1973) noted that both of the books written in English and devoted to the systematics of testaceans (Leidy, 1879 and Cash *et al.*, 1905) are out of print and hence unavailable to most workers, because they contain fine colour plates that would be particularly valuable. Grospietsch's textbook (1958) gives keys for, and pictures of, most peatland testaceans and is probably the most widely available, but it is written in German. Ellison and Ogden (1987) argue that the standard taxonomic reference for testate amoebae is provided by Penard (1902), with Hoogenraad and de Groot (1940) making significant contributions to studies.

A further problem is that most identification manuals have been compiled from the physiology of *living* amoebae, using the soft parts (pseudopodia, the cytoplasm and the nucleus) as well as test ornamentation as diagnostic features (see Corbet, 1973; Ellison and

Ogden, 1987, and the references therein). The palaeoecologist studying fossil testacean remains will have only tests to work with, yet it has been noted above that the usefulness of many early monographs is reduced by their limited descriptions of test ornamentation under optical microscopes.

Using SEM, a number of authors have partially addressed this problem, notably Ogden (1980) who attempted to improve the descriptions by Cash *et al.* (1902) of five known species of *Difflugia.* Ellison and Ogden (1987) produced a monograph which was devoted solely to fossil testaceans recovered in Quaternary lake sediments and included scaled outline drawings. This is especially useful because it may allow the positive identification of some species with a wide range of intraspecific variation - *Nebela,* for example. Warner (1990) produced a review of testate amoebae analysis, which included SEM micrographs and line drawings of locomotive and empty tests of representative peatland testaceans. The line drawings are particularly valuable because they assist in making the link from an empty test to living organism.

However, SEM must not be regarded as a panacea for the problems of fossil or modern testacean analysis, since testate amoebae continue to present taxonomical and identification problems. Schönborn and Peschke (1990) conducted an evolutionary study on the *Assulina* - *Valkanovia* complex of testaceans in *Sphagnum* and soil. *Assulina* is polymorphic, presenting at least four growth forms of different shapes and sizes, and the study found that, even with the use of SEM and X-ray analysis of the chemical composition of the shells, it was impossible to distinguish *Assulina muscorum* from *Valkanovia elegans* (a new genus). Corbet (1973) pointed out that the tests of some forms of *Nebela* appeared to be made of secretion rather than of a mosaic of regular plates that are characteristic of the genus, even though they are identical in shape to the typical *Nebela* species.

3.4 Summary

This chapter has detailed current perceptions of testate amoebae and their present uses in palaeoecology. Although the moisture content of the surrounding environment has been identified since the early part of this century (Harnisch, 1927) as a controlling factor on distribution and abundance, their usefulness as palaeohydrological indicators has been hampered by insufficient information on their absolute hydrological optima. The above sections, however, have shown how ecological studies have since progressed from qualitative through semi-quantitative to fully quantitative investigations (Charman and Warner, 1992; Tolonen *et al.*, 1992; Warner and Charman, 1994) whose aim is to derive absolute hydrological optima for species.

This chapter has also identified the considerable problems in both modern and fossil testate amoebae analysis that arise from gaps in our current knowledge of modern testacean ecology and their transition to fossil assemblages. This study aims at least to address the taxonomic problems by producing a standardised identification key for light microscopy, by incorporating the author's own work and identification keys published by other authors (see Appendix).

Clearly, more sites from a greater range of geographical areas for which long runs of hydrological data already exist have to be sampled to improve the accuracy of hydrological optima. This is particularly important in Britain where the use of moisture classes such as those in Table 3.5 would be inappropriate, because a greater precipitation input reduces moisture gradients across mires, rendering moisture classes less clear. Achieving this for Britain is the remit of this project, where data will be collected from a range of mires for which long runs of data already exist, allowing individual species' hydrological optima to be derived.

Part Two

The modern ecology of testate amoebae

Chapter 4

Field sampling and laboratory procedures

4.0 Introduction

Nearly all quantitative palaeoenvironmental reconstructions involve two stages (Birks, 1995). Firstly, the responses of modern taxa to contemporary environmental variables are modelled. Secondly, the modelled responses are used to derive values for environmental variables from fossil assemblages. Chapters 4, 5 6 and 7 are concerned with the first stage, while Chapter 8 details the second stage of the process.

This chapter details the collection of quantitative data on the modern ecology of peatland testate amoebae. Chapter 1 stated that the first objective of this study was to provide a better understanding of the modern relationship between testate amoebae and moisture conditions on mires in Britain. Quantifying this relationship is crucial, since it will form the modern analogue from which transfer functions will be derived.

With this in mind, two data collection programmes were implemented. First, a hydrological monitoring programme was established on a local ombrotrophic mire to record water table levels and chemical ion concentrations over one year. This gave a detailed picture of short term (over several days) and long-term (over one year) hydrological fluctuations on an ombrotrophic mire and was used to describe the moisture optima of testate amoebae sampled from the site. It also removes the problems inherent in single-shot samples by allowing environmental optima to be calculated on the basis of annual means. More importantly, it allows an assessment of the effects of seasonality on sampling, so that if single-shot sampling had to be conducted, a time could be identified when environmental variables are representative of annual means at a site.

The second programme involved sampling modern testaceans from additional ombrotrophic mires across Britain to build up a modern data set that was large enough to be both statistically viable and representative of British ombrotrophic mires. Sampling was restricted to sites that were already the subject of hydrological monitoring programmes, because this would allow inter-site comparisons, providing an accurate description of testacean faunas and hydrology on British ombrotrophic mires from which the transfer functions could be derived.

4.1. The hydrological monitoring programme at Tor Royal Bog, Dartmoor, Devon

4.1.1 Suitability of the site

To establish representative hydrological optima for modern testate amoebae, assemblages had to be studied throughout a wide range of pool, hummock and lawn microhabitats across a mire. Tor Royal Bog possesses a wide variation in microtopography and testacean distribution in all these microhabitats can be studied. Tor Royal Bog is a typical British ombrotrophic mire (English Nature, 1984) and a pilot study revealed a wide range of testaceans in surface moss samples from a variety of microsites.

Security of both the site and the monitoring equipment were additional considerations in site selection. The monitoring programme was planned to operate for one year, requiring assurance that the site would be undisturbed for this period at least. The area is popular with walkers and this could have jeopardised the monitoring programme in three ways: by causing surface compaction; by general disturbance of the monitoring equipment (especially the temperature and conductivity probes) and through body weight, which may have caused artificial fluctuations in water table levels. However, disturbance, tampering and removal of equipment was restricted by the mire's designation as a Site of Special Scientific Interest (SSSI) and lack of public access.

Logistically, Tor Royal was ideally located, being less than 25 km from Plymouth University. This enabled frequent sampling visits and minimised the transit time for water samples from the field to the laboratory. This was an important factor in maintaining the chemical stability of the water samples (Proctor, 1993).

Tor Royal Bog was also of long-term benefit to the strictly palaeoclimatic aspects of the research aims. Reconnaissance cores from the mire revealed a maximum peat depth of over six metres, which implies a rapid accumulation of peat at the site. Such an extensive peat profile might give a full and uninterrupted record of the mire's development up to the present day, and West *et al.* (1996) find no break in pollen and stratigraphical records from the site. This was a further advantage to the investigation because it meant that, in addition to being an excellent site for modern ecological studies of testaceans, Tor Royal Bog was also (potentially) a suitable site upon which transfer functions might be tested at a later date.

4.1.2 Site description

a) Location and surface features

Tor Royal (SX 602728) is a farm approximately 1.3 km south east of Princetown on the granite massif of Dartmoor. Six hundred metres to the south (at 395 m O.D.) lies Tor Royal Bog (Figure 4.1), described by English Nature (1984) as "one of the best examples of blanket mires in Devon and an important representative of such mires in South West Britain" (English Nature, 1984). However, the domed profile of the mire surface, with its steep, convex margins (possibly rands) are more reminiscent of a raised mire and this is further confirmed by morphometric studies of the mire (West *et al.*, 1996), which show that it consists of a single sediment body with an abrupt northern margin and more gradually thinning southern edge. A further notable feature of the mire is the dome apex, which is offset north eastwards from the deepest peat deposit, suggesting that the site as an eccentric

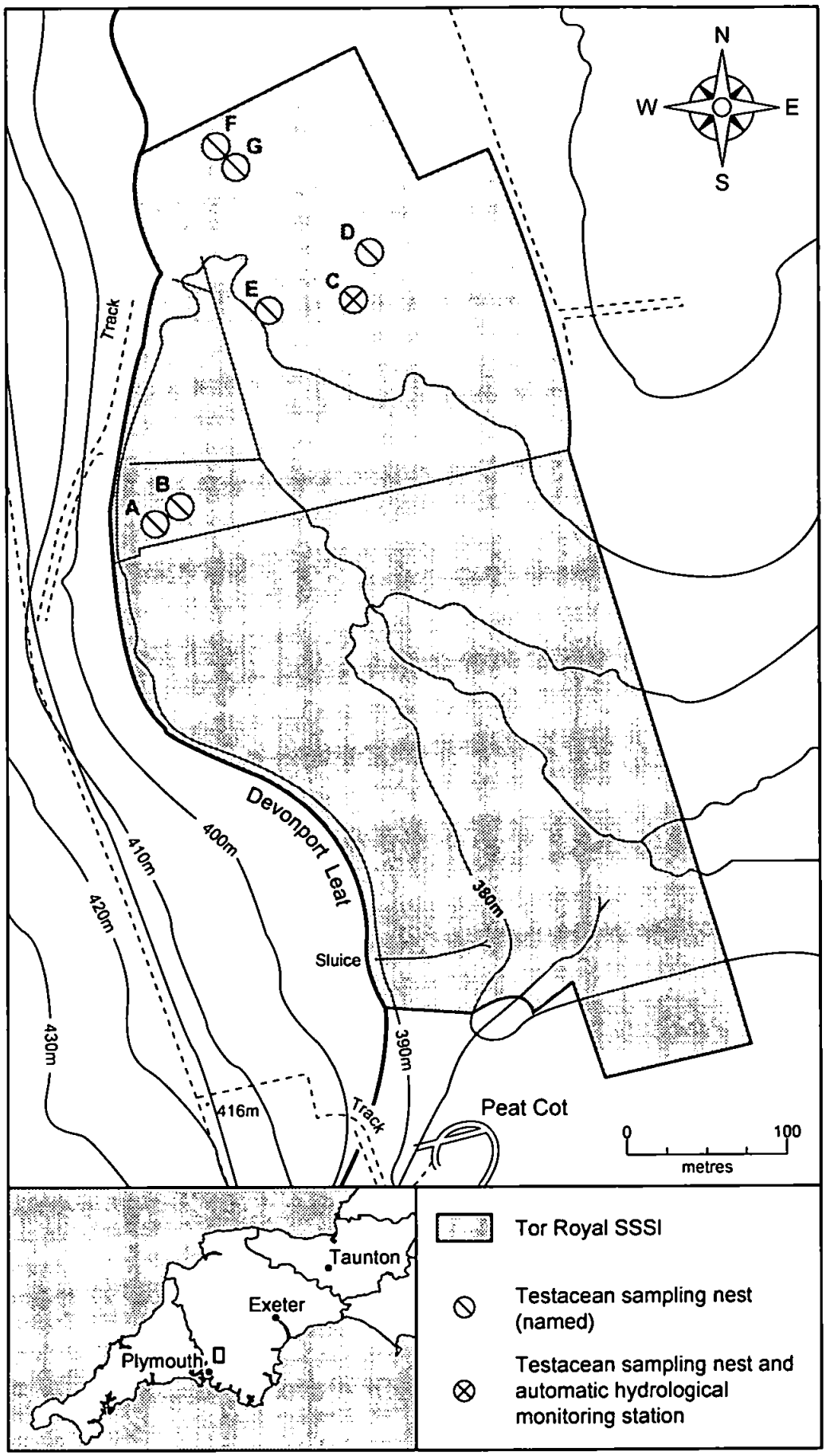


Figure 4.1: Location of Tor Royal bog and testacean / water chemistry sampling nests.

raised mire. Geochemical and pollen analyses by West *et al.* (1996) also confirm its status as a raised mire.

Tor Royal Bog covers 58 ha. The western limit of the mire is marked by Devonport Leat, an artificial watercourse that was originally constructed in 1793 to supply drinking water directly to Devonport in Plymouth. The remaining mire edges correspond to existing field boundaries (Plate 4.1). The southern two-thirds of the mire is shallow peat affected by cutting, drainage and grazing; this study is therefore restricted to the northern third, which is intact.

b) Present vegetation

All plant names in this thesis follow Stace (1991). Tor Royal Bog supports a diverse floristic community of Sphagna, lichens, hypnaceous mosses and vascular plants, and shrubs are represented by *Vaccinium myrtillus*. *Sphagnum papillosum* and *S. cuspidatum* dominate the *Sphagnum* lawn and pool communities and *S. auriculatum* is also present. *Rhyncospora alba* and *Tricophorum cespitosus* are abundant across the mire, and shrubs are represented by *Vaccinium myrtillus*.

Peat hummocks are an extensive feature of the mire surface and, being generally drier than their surroundings, they show a finer scale vertical zonation of vegetation on their surface, from Sphagna at the base to mosses (*Aulacomnium palustre, Racomitrum lanuginosum*), lichens (*Cladonia* spp.), vascular plants (such as *Potentilla erecta, Vaccinium myrtillus*) and grasses (*Festuca ovina, Eriophorum vaginatum*) on the hummock top.

Plate 4.1: View northeast across Tor Royal SSSI, showing the intact third of the mire surface on which testacean sampling and hydrological monitoring were conducted.

4.1.3 Testacean sampling

a) Field sampling

The aim of the testacean sampling programme at Tor Royal was to represent a range of hydrological conditions from xerophilous (on hummock tops) to hygrophilous (in pools) described by previous authors (Harnisch, 1927; de Graaf, 1956; Tolonen, 1986; Charman and Warner, 1992; Tolonen *et al.* 1992; 1994 - see Chapter 3). Individual species would be isolated from the assemblages and, according to their abundance, would be assigned absolute optima for water table depth and percent moisture content.

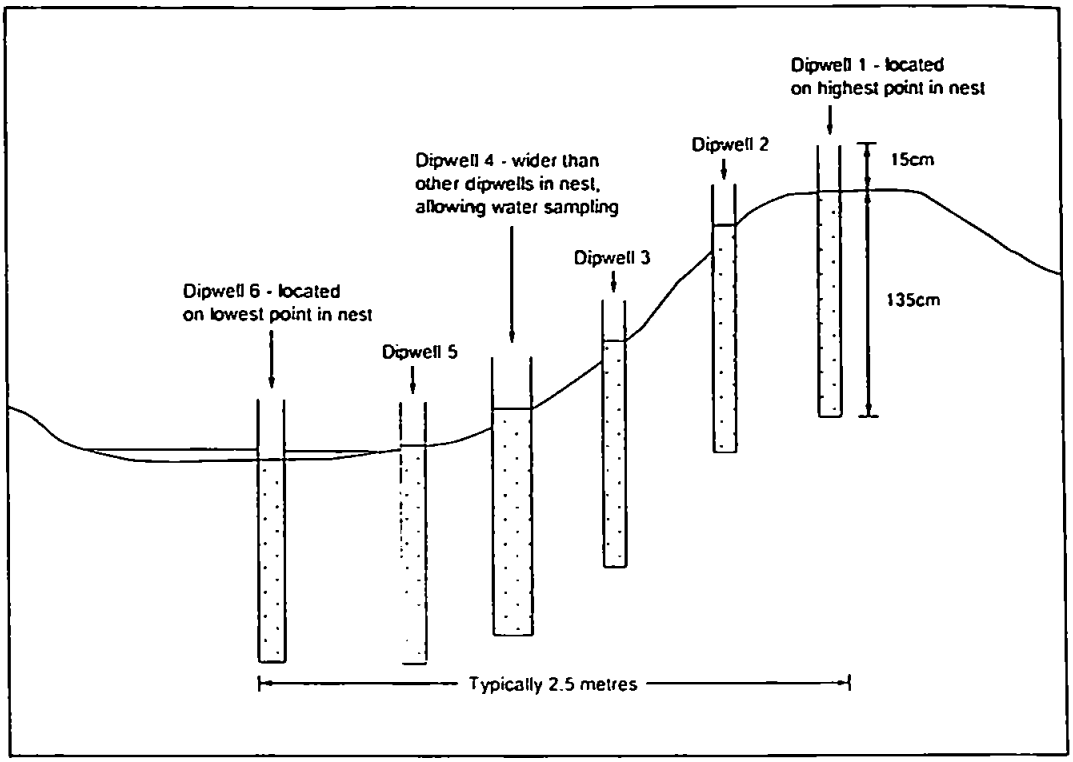
A preliminary survey of the surface vegetation was conducted to identify potential sampling locations across the mire. 42 testacean assemblages were sampled across the mire to reflect its wide topographical and vegetational diversity (Table 4.1). Samples were concentrated in 7 "nests" (labelled A to G) within separate pool-hummock sequences, each nest comprising 6 samples, which were distributed across the range of microtopographical features within the sequence. With the exception of nest E, which was a transect across a hummock-pool-hummock complex, sample 1 was located on the highest point in the sequence (a hummock) and sample 6 was located on the lowest point (a pool), with samples 2, 3, 4 and 5 at intermediate heights between these points (Figure 4.2).

The same retrieval procedure was followed at each sampling point. The sharpened end of an open-ended 11 cm-diameter steel cylinder was pushed through the acrotelm to a depth of 30 cm to ensure that both the green and brown fractions of *Sphagnum* plants were collected. After rotating the cylinder to cut through plant stems, it was removed and the moss sample was held within the steel cylinder. The sample was carefully removed and laid out on a cutting surface, where the green and brown fractions were separated with sharp scissors and individually bagged (Plate 4.2). For later reference, each bag was labelled with

Sample code	Microtopography	Floristic composition
TRA1	Low (8cm) hummock	*Eriophorum vaginatum* (25%); *Rhyncospora alba* (25%); *Molinia caerulea* (25%); Hypnaceous mosses (25%).
TRA2	Very low (4cm) hummock	*Sphagnum auriculatum* (25%); *Carex panicea* (10%); *C. demissa* (65%).
TRA3	Very low (4cm) hummock	*S. auriculatum* (60%); *C. panicea* (20%); *C. demissa* (20%).
TRA4	Flat lawn	*S. papillosum* (25%); *Eriophorum angustifolium* (30%); *M. caerulea* (25%); *C. panicea* (20%).
TRA5	Flat lawn	*S. auriculatum* (60%); *C. demissa* (15%); *C. panicea* (10%); *Juncus bulbosus* (15%).
TRA6	Shallow pool	Bare peat (100%) in shallow (3cm deep) pool.
TRB1	Low (7cm) hummock	*E. vaginatum* (25%); *R. alba* (30%); *M. caerulea* (15%); Hypnaceous mosses (30%).
TRB2	Low (5cm) hummock	*S. papillosum* (50%); *E. vaginatum* (15%); *E. angustifolium* (15%); *R. alba* (20%).
TRB3	Flat lawn	*S. papillosum* (100%).
TRB4	Flat lawn	*S. papillosum* (45%); *E. angustifolium* (30%); *R. alba* (5%); *M. caerulea* (20%).
TRB5	Hollow	*S. auriculatum* (100%).
TRB6	Flat lawn	*S. cuspidatum* (100%).
TRC1	High (35cm) hummock	*S. auriculatum* (25%); *E. angustifolium* (30%); Hypnaceous mosses (30%); *R. alba* (15%).
TRC2	Low (7cm) hummock	*S. auriculatum* (40%); *E. angustifolium* (30%); *R. alba* (30%).
TRC3	Flat lawn	*S. cuspidatum* (80%); *S. auriculatum* (10%); *R. alba* (10%).
TRC4	Hollow	*S. cuspidatum* (80%); *R. alba* (15%); *E. angustifolium* (5%).
TRC5	Hollow	*S. cuspidatum* (95%); *R. alba* (5%).
TRC6	Flat lawn	S. cuspidatum (100%).
TRD1	High (30cm) hummock	*Erica tetralix* (45%); *E. vaginatum* (5%); *Calluna vulgaris* (10%); Hypnaceous mosses (40%).
TRD2	Low (15cm) hummock	*S. auriculatum* (25%); *E. angustifolium* (10%); *R. alba* (55%); Hypnaceous mosses (10%).
TRD3	Very low (4cm) hummock	*E. vaginatum* (100%).
TRD4	Very low (3cm) hummock	*E. vaginatum* (100%).
TRD5	Flat lawn	*S. cuspidatum* (45%); *E. angustifolium* (45%); *R. alba* (10%).
TRD6	Flat lawn	*S. cuspidatum* (75%); *S. auriculatum* (25%).
TRE1	High (40cm) hummock	*E. tetralix* (45%); *E. angustifolium* (30%); *Vaccinium myrtillus* (10%); *Cladonia* spp.(15%).
TRE2	Base of hummock	*E. angustifolium* (40%); *V. myrtillus* (30%); *S. papillosum* (15%); *Polytrichum commune* (5%); *R. alba* (10%).
TRE3	Edge of pool	*S. auriculatum* (65%); *E. angustifolium* (30%); *R. alba* (5%).
TRE4	Centre of pool	Bare peat (85%); E. *vaginatum* (15%).
TRE5	Edge of pool	*S. auriculatum* (70%); *Drosera rotundifolia* (20%); *E. vaginatum* (10%).
TRE6	High (20cm) hummock	*E. angustifolium* (55%); *E. tetralix* (15%); *Cladonia* spp. (25%); Hypnaceous mosses (5%).
TRF1	High (25cm) hummock	*E. vaginatum* (30%); *E. tetralix* (25%); *V. myrtillus* (15%); *Cladonia* spp. (5%); Hypnaceous mosses (25%).
TRF2	Base of high hummock	As for TRF1
TRF3	Flat lawn	*S. cuspidatum* (75%); *E. angustifolium* (25%).
TRF4	Flat lawn	*S. cuspidatum* (100%).
TRF5	Edge of pool	*S. cuspidatum* (100%).
TRF6	Pool	Bare peat (75%); *E. angustifolium* (25%).
TRG1	Low (7cm) hummock	*E. vaginatum* (30%); *E. tetralix* (25%); *V. myrtillus* (15%); *Cladonia* spp. (5%); Hypnaceous mosses (25%).
TRG2	Edge of hummock	*S. auriculatum* (35%); *S. papillosum* (35%); *E. angustifolium* (20%); *R. alba* (10%).
TRG3	Flat lawn	*S. papillosum* (80%); *E. angustifolium* (10%); *D. rotundiflora* (5%); *R. alba* (5%).
TRG4	Edge of pool	*S. cuspidatum* (100%).
TRG5	Pool	*S. cuspidatum* (95%); *E. angustofolium* (5%).
TRG6	Pool	Bare peat (100%).

Table 4.1: Topographic and floristic features of testacean sampling points on Tor Royal.

a) Generalised section, nests A,B,C,D,F,G.



b) Generalised section, nest E.

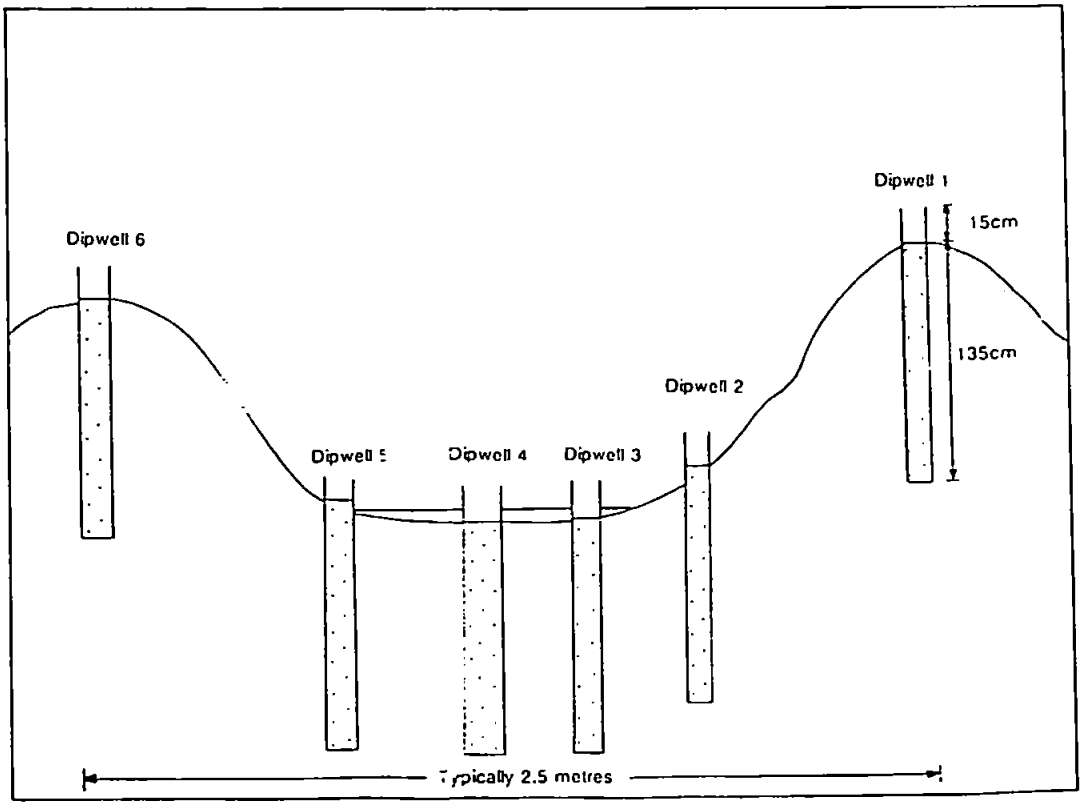


Figure 4.2: Location of dipwells in pool-hummock sequences at Tor Royal. For full explanation, see text.

a) The steel cylinder is driven through the *Sphagnum* into the peat layer.

b) The core is retrieved and supported within the cylinder.

Plate 4.2: Testacean sampling procedures at Tor Royal.

c) The core is carefully removed and placed on a clean cutting surface

d) ...where the green and brown *Sphagnum* sections are separated and individually bagged.

Plate 4.2 (continued)

the location, date of collection and depth of the green and brown *Sphagnum* fractions (for calculations of sample volume). Excess air was expelled from the bags, which were then sealed and returned to the laboratory and refrigerated, pending analysis.

b) Laboratory analysis

In the laboratory, only the brown fraction of the *Sphagnum* plants was processed. This is because tests in the brown fraction will eventually comprise the fossil community and are therefore of direct relevance to the palaeoecological aspect of this study (see, for example, Tolonen, *et al.*, 1992). Hence, data from this fraction would be used to derive the transfer functions. Calculations were made for bulk density and percentage moisture content following the standard procedures described by Tolonen *et al.* (1992) and Charman and Warner (1992). One quarter of each moss sample disc was removed, placed in a previously weighed soil moisture tin, heated for 24 hours at 105°C, removed and reweighed. Using the equation below, the percentage moisture content of each sample was calculated:

$$\% \text{ moisture content} = \frac{\text{wet sample weight - dry sample weight}}{\text{wet sample weight}} \times 100$$

Bulk density was also calculated for the brown fraction, using the equation below, since this would give an additional expression of moisture content.

$$\text{bulk density} = \frac{\text{dry weight of sample}}{\text{sample volume}}$$

Generally, a lower bulk density is indicative of less humified material (and therefore a higher moisture content); more humified material has a higher bulk density (Charman and Warner, 1992).

One half of each moss disc was processed for testacean analysis, following Tolonen (1986). Early in the processing, modifications were made to this technique. It was found that more testaceans could be concentrated from the host Sphagna if the moss disc was soaked in water for 24 hours before processing. Accordingly the disc was weighed, then placed in 250 ml of water and left for 24 hours to allow preliminary disaggregation of testaceans from their host moss. Although percent abundance was preferred to test concentration in this study (see below), an inoculum of 4 *Lycopodium* tablets (University of Lund batch no. 710961) was added to each sample to allow calculation of test concentrations if required (Stockmarr, 1971). The samples were boiled and stirred for 10 minutes to encourage disaggregation (Tolonen, 1986). Tolonen (1986), Warner (1989) and Charman and Warner (1992) recommend that the samples are passed through a 700µm sieve, but this was considered too coarse, since clumps of detritus appeared on the microscope slides and obscured the testacean shells. Eventually, a 300µm mesh sieve was selected; this was the smallest mesh size that could be used without losing testacean shells (the maximum size of testacean shells is 250µm - Ogden and Hedley, 1980), but which would still give a cleaner microscope slide. Samples were then concentrated in a centrifuge for 5 minutes, stained with safranine-O (to enhance contrasts within the test ornamentation and hence aid identification and photography under light microscopy), rinsed until the supernatant was clear, and mounted in glycerine. The remaining quarter of each sample was kept refrigerated to be used as backup material should the original samples be accidentally destroyed during preparation.

c) Identification and counting

Testate amoebae were counted at x400 magnification using an Olympus light microscope. Identifications down to species level were made using de Graaf (1956), Grospietscsh (1958), Corbet (1973), Ogden and Hedley (1980), Beyens *et al.* (1990), Warner (1989), Patterson and Hedley (1992) and reference slides from the Penard Collection in the British

Museum (Natural History). Normally, a minimum of 150 individuals were counted per sample, although this was not always possible; two slides were occasionally necessary to gain a minimum count of 100 individuals. The minimum count size was established by recording the number of individuals and species counted per sample and plotting this cumulatively (Figure 4.3). The plots showed a large increase in species diversity early in the counting, but as the number of individuals counted increased, species diversity eventually stabilised, represented by a plateau on the cumulative plots. Analysis of the graphs showed that this plateau effect began at approximately 150 individuals, suggesting that counts in excess of 150 were unlikely to identify additional species that would be significant members of the assemblage.

Species' occurrences were expressed as percent abundance rather than concentration for two reasons. Firstly, percent abundances are conventionally used in weighted average calculations of species' environmental optima (see Chapter 6). Secondly, percent abundances are less affected than concentrations by differences in mass between surface moss samples and fossil peat (see Chapter 8).

Despite combined use of the identification keys mentioned above, considerable difficulties were encountered in identification and they were generally of the type detailed in Chapter 3 and summarised in Table 3.10 (page 67). Additional problems were caused by many of the keys detailing features of the test aperture to assist in identifying *Difflugia* spp. and *Nebela* spp. However, the space between the microscope slide and coverslip was so small that standing the tests "up on end" to see the aperture more clearly was impossible. The alternative of viewing without a coverslip was also impossible since the sample was no longer contained and dripped off the microscope slide. There was also the risk of damaging the objective lens through direct contact with the sample.

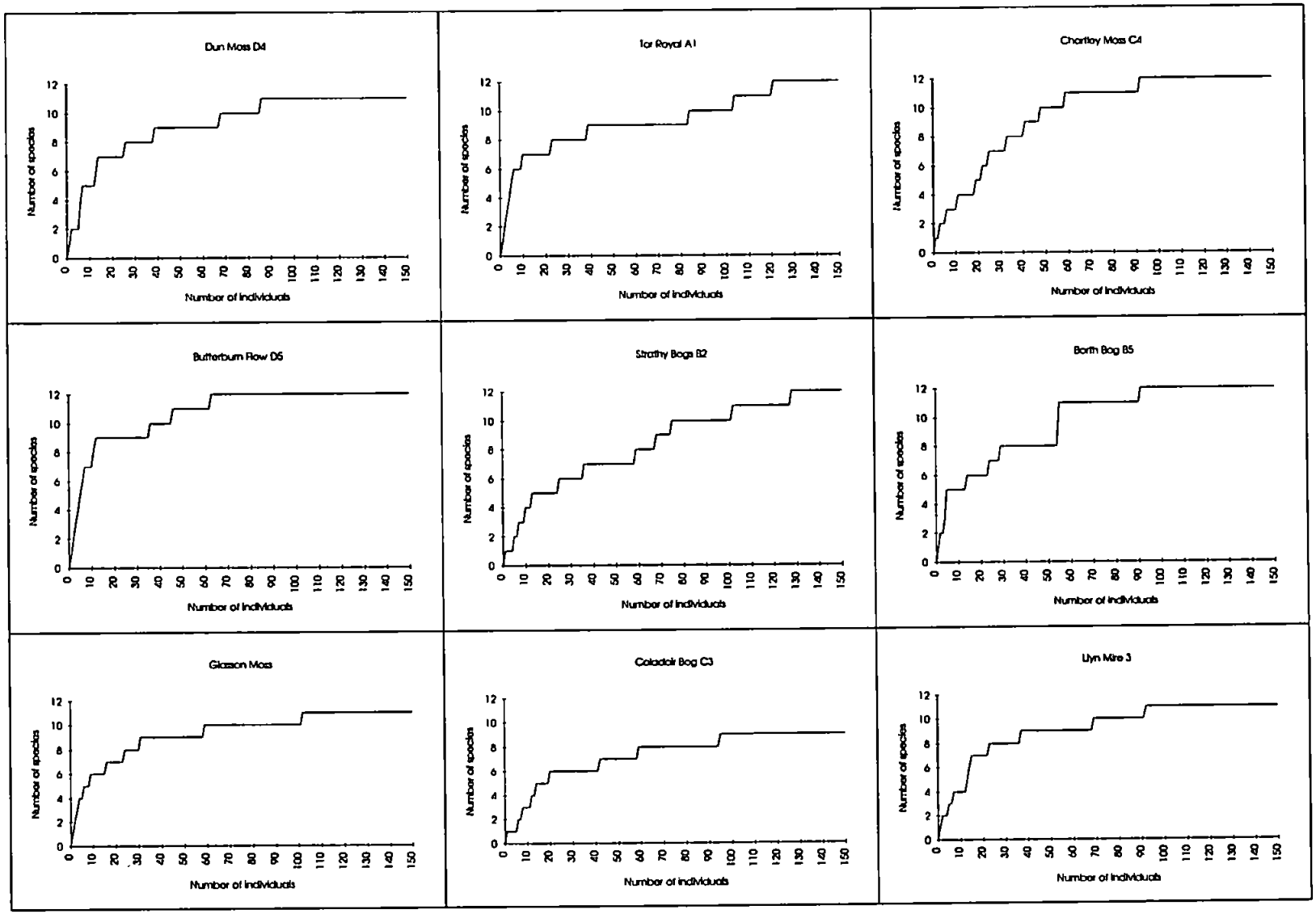


Figure 4.3: Number of individual tests plotted against number of species for selected samples from the British data set. For topographic and floristic details, see Tables 4.1 and 4.2.

To overcome these problems, detailed biometric records (test length, breadth and aperture size, where possible) were made and photomicrographs taken of each species encountered. This was also done for the remaining modern samples from Britain and for the fossil samples (Chapter 8); the full records are presented in the Appendix of this thesis. The Appendix has been written as an identification key, and it combines records from this study with the identification keys mentioned above. It is designed to be used independently from the main thesis and is aimed towards workers who have access to light microscopy only. It is hoped that this key will be of use in future studies of modern and fossil testate amoebae.

4.1.4 Collection of water table and water chemistry data

a) Selection of chemical ions

Section 3.2 (page 58) described how, although Tolonen *et al.* (1992) had identified moisture content as the principal control on Finnish peatland testaceans, they had also calculated optima for testaceans and selected ions in mire waters. These included Ca^{2+}, dissolved organic carbon (DOC) and N, while optima were also derived for pH and electrical conductivity. Charman and Warner (1992) had also considered the influence of water chemistry (expressed as pH) on testate amoebae populations in Canada and, through ordination, showed water pH to have a secondary influence on testacean distribution. A supplementary aim of this thesis is to extend investigations into testaceans and water chemistry to explore their potential as water chemistry indicators and it was therefore necessary to monitor water chemistry in addition to water table fluctuations at Tor Royal. Ca^{2+}, DOC, NO_3^-, pH and electrical conductivity were selected to provide common data with Tolonen *et al.* (1992a) and Charman and Warner (1992). Additionally, Cl^-, Mg^{2+} and SO_4^{2-} concentrations were monitored to assess coastal influences on precipitation reaching the mire.

b) Field sampling

Water table fluctuations were measured using dipwells. Each dipwell was a 1.5 m length of standard plastic plumbing piping and, at each nest, two different diameters of piping were installed (Figure 4.2). Five dipwells, which were used for water table readings only, were 2.5 cm in diameter - wide enough to suspend an electronic-contact well dip-probe inside. A small diameter was essential for maximising the volume of inward and outward water flow and hence recording rapid changes in water table depth (Gilman, 1994). The 2.5 cm diameter was chosen as a compromise between minimising water table disturbance at each site and minimising meniscus effects within each dipwell. The remaining dipwell in each nest (dipwell number 4) was wider (8 cm diameter) to allow simultaneous use of pH and conductivity probes and collection of samples for water chemistry analysis.

Each dipwell was divided into two sections, separated by a line, 15 cm from the top of the pipe. Below the line, the pipe was perforated to allow water to percolate through the perforations and represent the true position of the water table. The hydraulic conductivity of peat is poor (Ivanov, 1981; Gilman, 1994) and, without these perforations, water pressure would have been insufficient to force the water level to the height of the surrounding water table.

The section of pipe above the 15 cm mark was unperforated, sprayed with a fluorescent paint to aid future recognition in the field and labelled. The dipwells were positioned in the mire and spirit-levelled to ensure that each was vertical. Each pipe was pushed in until the 15 cm mark was coincident with the ground surface; this mark was used as a reference point for subsequent levelling and adjustments when the pipes had either sunk or lifted slightly as a result of freezing during the winter, or peat shrinkage during very dry conditions. Every well was stoppered with a rubber bung to prevent entry by insects, vegetative matter and recent rainfall, which would have created unrepresentative readings.

However, these bungs were constantly replaced after being chewed or plucked from the dipwell by sheep and cattle which grazed the site. The livestock also chewed the well tops, so that occasional adjustments and levelling of the pipes was necessary.

Site visits were made to Tor Royal at fortnightly intervals between June 1993 and September 1994. This sampling frequency generated the widest range of representative data which could be achieved within the time constraints of the study. Greater sampling frequency would have required more laboratory analysis, taking up more time than was available.

At each nest, the water level within each dipwell was first measured using a well dip probe manufactured by the University workshops. During the readings, care was taken not to stand too near the dipwell and to distribute weight evenly over the surrounding bog surface to prevent disturbance to the water level by pressure from body weight.

Following the water table readings, water temperature and conductivity (using a Wissenschaflich Technische Werkstatten ("WTW") meter), and pH (using a Whatmans meter) were recorded. The probes were allowed to settle for 5 minutes at each nest before reading. After their removal, a 250 ml water sample was taken from the dipwell using a hand-held suction pump and transferred to a labelled glass bottle (filled to the brim to prevent gaseous exchange). A glass bottle was used for sample collection because tests for DOC were performed on the samples after their return to the laboratory. Had plastic bottles been used, some carbon may have escaped from the plastic and contaminated the water sample. The suction pump and probes were rinsed with distilled water between nests to prevent cross-contamination. Water samples were then returned to the laboratory, where they were refrigerated at 4 °C, pending analysis.

Although time constraints limited the sampling visits to fortnightly intervals, for the sampling programme to be effective, a daily record of water table and water chemistry fluctuations between site visits was essential. Accordingly, an automatic monitoring station was installed at nest C (chosen because it afforded easiest accessibility) to allow continuous recording of air temperature and precipitation, water table fluctuations, and soil water conductivity and temperature (Plate 4.3). Data were recorded at 12-hour intervals and stored on a "Rustrak Ranger" datalogger, which was powered by a 9-cell 4 volt battery. There was also an auxiliary supply from a 12 volt car battery, stepped down to 4 volts, although this was not normally used. Precipitation events were measured by a tipping bucket rain gauge, which consisted of two small buckets (each with 0.196 mm capacity) positioned beneath a collecting funnel. The logger recorded the frequency of tips and, using a simple calibration, converted this frequency into mm of precipitation.

Water table depth was measured independently using both a pressure transducer and a potentiometer (which responded to water level changes and was powered at 3 volts), since concern had been expressed over the reliability of the pressure transducer in such a harsh environment. Soil water conductivity and temperature were measured on a second "WTW" meter. This was powered from the car battery, via voltage step-down circuitry at 9 volts. To protect the monitoring equipment and to minimise disturbance from livestock, an electric fence (powered by a second 12 volt DC car battery) enclosed site C (Plate 4.3).

At the start of the monitoring programme, pH was monitored automatically, but the glass probe proved to be error-prone and pH was instead measured fortnightly using a Whatmans pH field test kit. A connector between the pressure transducer and data logger also proved faulty (probably a result of contact with water) and was replaced within the first 3 weeks of the monitoring programme. Thereafter, frequent breakdowns between the pressure transducer and data logger provided erroneous data and its use was terminated. Manual

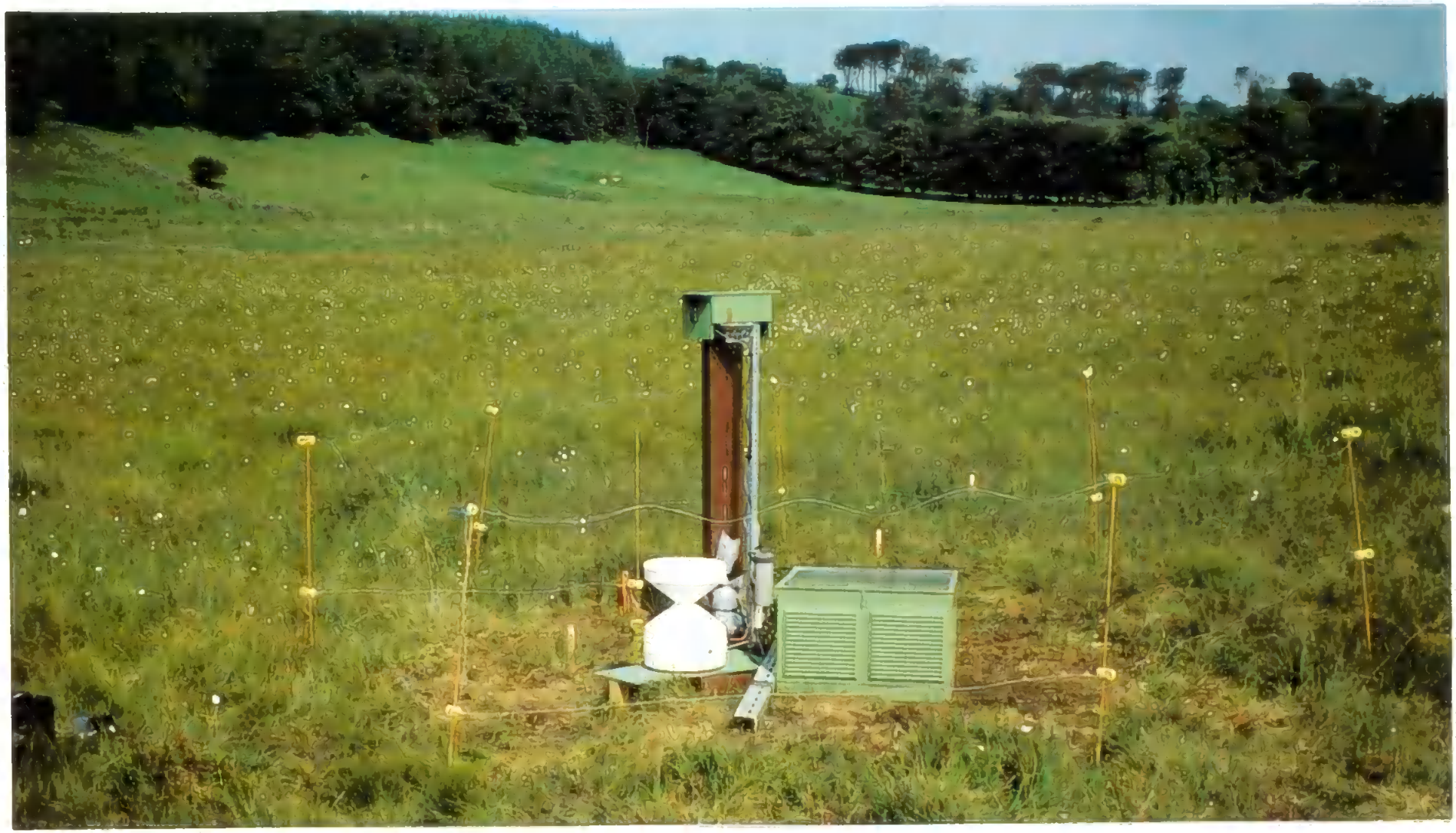


Plate 4.3: The automatic recording station at Tor Royal. The white funnel is the raingauge; the conductivity and temperature probes and batteries are contained in the green box. The potentiometer and float for recording water table movements are housed in the brown pipe. An electric fence surrounds the equipment.

checks showed that the simultaneous water table depth readings from the potentiometer were error-free (see Chapter 5, p. 133) and these were continued for the remainder of the monitoring programme.

c) Laboratory analysis

Within 24 hours of collection, samples were filtered through Whatmans 0.45µm glass microfilter paper, and transferred to a second set of clean glass bottles. At the same time, a subsample was taken and analysed for dissolved organic carbon content via high-temperature (680°C) catalytic oxidation using a non-dispersive infra-red (NDIR) detector.

Within 28 days of collection, refrigerated samples were tested for SO_4^{2-} and Cl^- concentrations. SO_4^{2-} concentration was determined in an autoanalyser using a standard colorimetric test (industrial method no. 226-72W; Lazrus *et al.*, 1965). Cl^- ions were measured using the colorimetric test method 409-89E (O'Bien, 1962). Ca^{2+} and Mg^{2+} ion concentrations were determined using an atomspectrophotometer.

4.2 Other British sampling sites

4.2.1 Site selection

A representative picture of modern testacean ecology in Britain required data collection from as many sites as possible within the time constraints of the project. Although numerous ombrotrophic mires were accessible for sampling, the objectives of this project required that only those where hydrological monitoring had been conducted within the last 10 years could be sampled, which greatly reduced the choice of available sites.

After discussions with Miss S Ross (Uplands Division, Scottish Natural Heritage - SNH), Dr O Bragg (Department of Biological Sciences, Dundee University) and representatives of SNH, English Nature (EN) and the Countryside Council for Wales (CCW), 8 sites in

addition to Tor Royal were eventually chosen for the sampling programme - all are either Sites of Special Scientific Interest or National Nature Reserves (illustrated in Figure 4.4 and listed in Tables 4.2 and 4.3). An additional Scottish site (Silver Flowe in Galloway) was also selected, but was rejected when it was discovered that the proposed sampling point had been recently burned, causing loss of the surface *Sphagnum* communities.

On each site, a hydrological monitoring programme had operated for at least 3 consecutive years throughout the last 10 although, by 1993, the programme had been decommissioned at several sites. Instantaneous water table measurements were also taken at each site to compare with instrumental records. With the exception of Strathy Bogs, which was sampled on 4th August 1993 during a separate visit to the area, the sites were sampled in a 3 week period between 20th August and 7th September 1993.

4.2.2 Site descriptions and location of sampling points

a) Strathy Bogs N.N.R., Sutherland.

Site description

This site lies south of Bettyhill in eastern Sutherland and covers 908.69 ha (Figure 4.5). The blanket mire here is transitional between the more continental systems of Caithness, where dwarf shrubs become more dominant, and the marked oceanic formations of the west coast of Sutherland, where open water becomes a major feature of bog surfaces (SNH, 1984). Strathy Bogs includes valley-side and watershed flows, forming the best examples of this type of blanket mire in Britain (SNH, 1984). Vegetation is rich in *Sphagnum*, including abundant *Sphagnum imbricatum*, now rare in Britain. Dwarf shrubs, including *Betula nana* and *Arcostaphylos uva-ursi* are also present.

Figure 4.4: Location of British ombrotrophic mires sampled in this study.

Site name	National grid reference	Area (ha)	Mire type	Number & type of hydrological monitoring points	Details of hydrological monitoring programmes
Tor Royal	SX 601731	58.00	Eccentric raised mire	42 dipwells arranged in 7 nests	June 1993-September 1994. This study. Water table (recorded every 12 hours) and water chemistry data (collected fortnightly).
Strathy Bogs	NC 790555	908.69	Blanket mire	4 lysimeters	May 1988-September 1990. University of Dundee. Weekly records of water table depth.
Coladoir Bog	NM 550292	52.20	Oceanic blanket mire	6 water recorders	1984-1989. Scottish Natural Heritage. Daily records of water table depth.
Dun Moss	NO 169559	133.30	Upland raised mire	7 lysimeters	December 1989-July 1992. University of Dundee. Weekly records of water table depth.
Butterburn Flow	NY 675761	400.00	Upland raised mire	4 lysimeters	May 1988-May 1991. University of Dundee. Weekly records of water table depth.
Glasson Moss	NY 238604	101.25	Lowland raised mire	2 water recorders	1989-1992. English Nature. Fortnightly records of water table depth.
Chartley Moss	SK 025281	40.00	Schwingmoor	4 dipwells	1989-1992. University of Nottingham. Weekly records of water table depth and water chemistry.
Borth Bog	SN 640995	3339.44	Estuarine raised mire	3 water recorders	1989-1992. Countryside Council for Wales. Daily records of water table depth.
Llyn Mire	SO 016553	35.00	Schwingmoor	6 dipwells	1985-1989. Institute of Hydrology. Daily records of water table depth.

Table 4.2: Geographical and hydrological details of British sites sampled during August and September 1993.

Site	Sample code	Microhabitat	Floristic composition	Mean water table level in each nest on day of collection (cm)	Standard deviation of the mean (cm)	Water table level in instrument on day of collection (cm)	Difference between water table level in instrument and mean level in nest (cm)	Mean annual water table level (cm)
Coladoir Bog	CB A1-A6	20cm high hummock.	*Erica tetralix* (20%); *Polytrichum commune* (5%); *Eriophorum vaginatum* (15%); *Sphagnum capillifolium* (15%); *Scirpus cespitosus* (45%).	-9.80	0.10	-10.10	0.30	-12.19
	CB B1-B6	10cm high hummock	*S. capillifolium* (80%); *E. tetralix* (10%); *Rhyncospora fusca* (10%).	-7.10	0.10	-6.30	0.80	-8.19
	CB C1-C6	5cm high hummock.	*S. capillifolium* (95%); *R. fusca* (5%).	-9.30	0.15	-8.40	0.90	-7.39
	CB D1-D6	Hummock/lawn	Edge of *S. capillifolium* hummock (50%) and *S. cuspidatum* lawn (50%).	-6.80	0.21	-7.50	0.70	-5.07
	CB E1-E6	Lawn	*S. cuspidatum* (80%); *Carex limosa* (10%); *R. fusca* (10%).	1.10	0.09	0.90	0.20	-3.15
	CB F1-F6	Pool	*S. cuspidatum* (85%); *Menyanthes trifoliata* (20%).	2.40	0.10	1.80	0.60	-0.53
Dun Moss	DM A1-A5	Lawn	*S. cuspidatum* (70%); *S. tenellum* (30%).	-6.30	0.23	-5.80	0.50	-1.80
	DM B1-B5	Lagg fen	*S. palustre* (10%).	-8.70	0.45	-9.40	0.70	-7.30
	DM C1-C5	Hollow	*E. angustifolium* (70%); *Cladonia* spp. (30%).	-13.95	0.18	-14.40	0.45	-10.70
	DM D1-D5	15cm high hummock	*S. magellanicum* (100%).	-22.40	1.14	-22.30	0.10	-12.80
	DM E1-E5	Lawn	*E. angustifolium* (10%); *Cladonia* spp. (5%); *S. magellanicum* (85%).	-5.60	0.32	-5.20	0.40	-3.30
	DM F1-F5	15cn high hummock	*S. capillifolium* (100%).	-16.20	0.57	-15.90	0.30	-9.70
	DM G1-G5	Hollow	*Calluna vulgaris* (60%); bare peat (40%).	-26.60	1.14	-23.70	2.90	-15.30
Butterburn Flow	BF A1-A5	Hollow	*S.magellanicum* (50%); *S. cuspidatum* (15%); *S. cespitosus* (5%); *E. angustifolium* (5%); *Ossifragrum* spp. (5%); *C. vulgaris* (10%); *E. tetralix* (10%).	-2.60	0.54	-3.80	1.20	-6.20
	BF B1-B5	Lawn	*S. papillosum* (95%); *Drosera rotundifolia* (<5%); *Andromeda* spp. (<5%); *E. vaginatum* (<5%).	-3.00	1.00	-2.10	0.90	-3.30
	BF C1-C5	10cm high hummock	*S. magellanicum* (50%); *C. vulgaris* (40%); *Polytrichum commune* (<5%); *Carex rostrata* (<5%); *Andromeda* spp. (<5%).	-16.40	0.54	-16.10	0.30	-13.30
	BF D1-D5	Lawn	*S. recurvum* (80%); *Molinea caerulea* (15%); *E. tetralix* (5%).	0.50	0.00	0.00	0.50	-1.70

Table 4.3: Microtopography, vegetation and water table data from British sites sampled during the study ('-' depth below ground surface; '+' height above ground). For details of Tor Royal, see Table 4.1.

Site	Sample code	Microhabitat	Floristic composition	Mean water table level in each nest on day of collection (cm)	Standard deviation of the mean (cm)	Water table level in instrument on day of collection (cm)	Difference between water table level in instrument and mean level in nest (cm)	Mean annual water table level (cm)
Glasson Moss	GM A1-A4	10cm high hummock	S. papillosum (80%); D. rotundifolia (5%); E. tetralix (5%); C. vulgaris (5%); S. cespitosus (5%).	-7.8	0.18	-8.5	0.7	-3.8
Chartley Moss	CM A1-A6	Open lawn	S. recurvum (100%).	0	0	-0.2	0.2	0
	CM B1-B6	Lawn	S. recurvum (90%); Pinus sylvestris (10%).	0	0	0	0	-1.3
	CM C1-C6	8cm high hummock	S. recurvum (80%); Betula pubescens (5%); Sorbus aucuparia (5%); Quercus robur (10%).	-8	0.25	-6	2	-1.3
	CM D1-D6	Open lawn	S. recurvum (95%); B. pubescens (5%).	0	0	0	0	-0.6
Borth Bog	BB A1-A2	10cm high hummock	S. imbricatum (90%); E. vaginatum (10%).	-11.2	1.23	-11	0.2	12.8
	BB B1-B6	Lawn	S. cuspidatum (80%); Myrica gale (5%); E. angustifolium (10%); S. cespitosus (5%).	-0.5	0	-0.5	0	0
	BB C1-C6	Lawn	S. cuspidatum (100%).	0	0	0	0	0
Llyn Mire	LM A1-A6	Lawn	S. recurvum (80%); Juncus bulbosus (15%); P. commune (5%).	0	0	0	0	-5
	LM B1-B6	Lawn	S. recurvum (80%); B. pubescens (10%); E. angustifolium (10%).	-1.5	0	-1	0.5	-7.5
	LM C1-C6	Open lawn	S. recurvum (100%).	0	0	0	0	0
	LM D1-D6	30cm high hummock	S. rubellum (100%); E. tetralix (<1%).	-27	0.04	-28	1	-31
	LM E1-E6	Lawn	S. recurvum (95%); Pinus sylvestris (5%).	0	0	0	0	-2
	LM F1-F6	Hollow	C. vulgaris (30%); E. vaginatum (20%); E. tetralix (45%); Andromeda spp. (5%).	-18	0.03	-15	3	-11
Strathy Bogs	SB A1-A6	25cm high hummock	S. magellanicum (50%); Vaccinium myrtillus (20%); E. tetralix (30%).	-22	1.63	-25	3	-30
	SB B1-B6	15cm high hummock	S. magellanicum (50%); E. tetralix (50%).	-16	1.37	-15.5	0.5	-16
	SB C1-C6	Hollow	Bare peat (100%).	-2	0.47	2.1	4.1	-6.9
	SB D1-D6	Pool	S. cuspidatum (100%).	0	0	0	0	-2.3

Table 4.3 (continued): Microtopography, vegetation and water table data from British sites sampled during the study ('-' depth below ground surface; '+' height above ground). For details of Tor Royal, see Table 4.1.

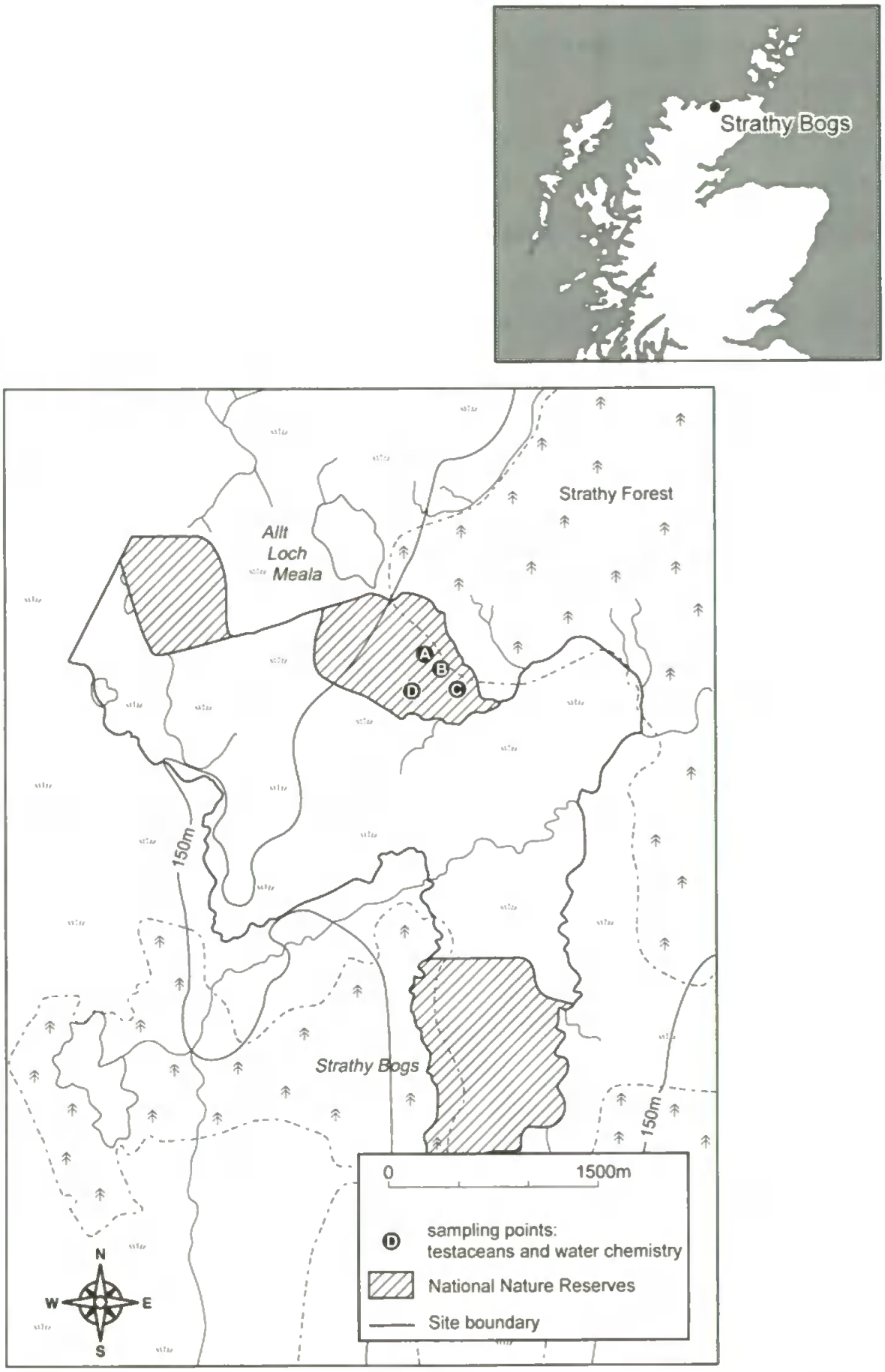


Figure 4.5: Strathy Bogs N.N.R., Sutherland: site location, topography and location of sampling points.

Strathy Bogs was an ideal sampling site since it is remote and access to the site is by permission only. It is located in a sparsely-populated area and only recently have parts of the surrounding area been afforested.

Sampling procedures

Four lysimeters had been installed by the Department of Biological Sciences, Dundee University in a 2500 m^2 area south of Allt Loch Meala (Figure 4.5) and monitoring was conducted between May 1988 and September 1990. Lysimeters 1 and 2 were located on hummocks, lysimeter 4 was located in a pool and lysimeter 3 at an intermediate height on bare peat (see Table 4.3 for details of vegetation in each lysimeter). These lysimeters were identified in the field and the vegetation within each recorded.

To avoid disrupting the recording programme, researchers at Dundee University had requested that no sampling was conducted within a five-metre radius of each lysimeter. To relate the testacean samples and the water table recorded on the day of sampling with the instrumental data, an area of vegetation and microtopography identical to that in each lysimeter was identified on the edge of the exclusion zone and six replicate samples were taken from here. Field recordings were also made of water pH, conductivity and temperature and a water sample recovered, following the procedures in section 4.1.4b (p.90). Water and moss samples were stored at 4°C until analysis; water samples were analysed within 28 days of collection.

b) Coladoir Bog S.S.S.I., Isle of Mull

Site description

Coladoir Bog is an oceanic blanket mire covering 52.2 ha of Glen More on the River Coladoir floodplain in the southwest corner of the Isle of Mull (Figure 4.6 and Plate 4.4).

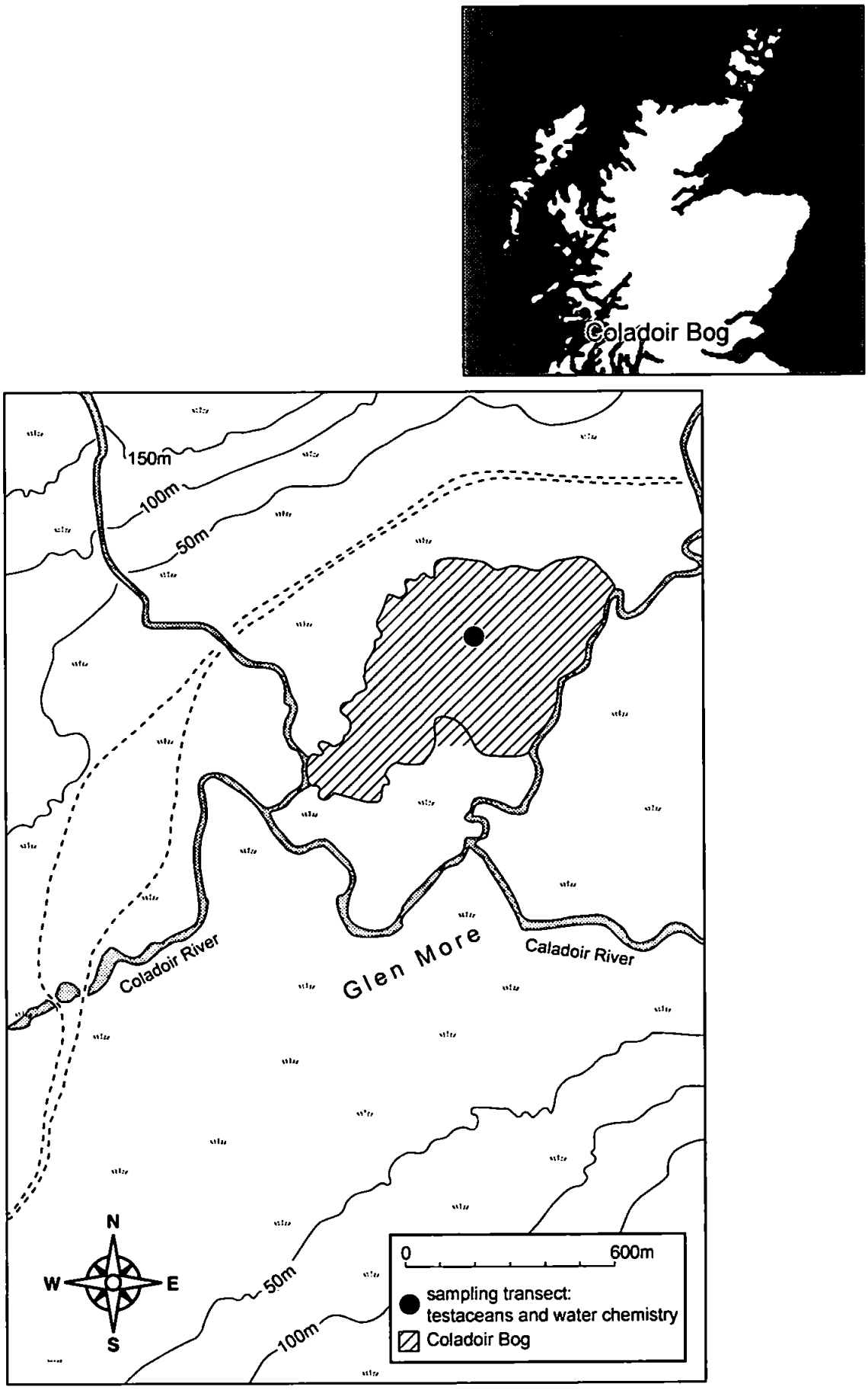


Figure 4.6: Coladoir Bog S.S.S.I., Isle of Mull: site location, topography and location of sampling points.

Plate 4.4: General view across the raised mire surface of Coladoir Bog, Isle of Mull

The mire is bounded on all sides by streams and the site schedule identifies characteristic features of both raised and valley side flows. The mire has characteristic pool and hummock microtopography and the hummocks of *Rhacomitrium lanuginosum*, at up to 80 cm high, are impressively large. A number of oceanic indicator species are present, including *Carex limosa, Utricularia minor, Pleurozia purpurea, Campylopus atrovirens*, and the restricted *Rhyncospora fusca.*

In terms of site attributes, Coladoir Bog was very similar to Strathy Bogs, being located in a remote area, having restricted access and only recent afforestation in the vicinity. Like Strathy Bogs, the afforestation was sufficiently distant (500 m) to be considered of no significance to the hydrology of the sampling points. The absence of major industrial areas also greatly reduced the expected input of pollutants.

Sampling procedures

The hydrological monitoring programme on Coladoir Bog was operated by Scottish Natural Heritage and was different to that at Strathy Bogs. No lysimeters were installed at the site, but six water table depth recorders had been positioned across a four metre long hummock-hollow-pool transect (Plate 4.5) on the raised section of the mire complex. This was ideal since unlike the valley flows, which would probably be nutrient-enriched from groundwater flow, hydrological input was expected to be from precipitation only. A comparable complex was located within two metres of the transect and six microhabitats that were almost identical to the original complex were selected as sampling points. With permission from SNH, the testacean samples were collected within two metres of the monitoring equipment, closer than at Strathy Bogs. It was felt that very little difference in water table depth would occur within this distance and this was confirmed by comparing water table depths between the sampling points and the instruments. All were found to be between 0.5 cm and 1 cm of each other (Table 4.3) - an acceptable margin.

Plate 4.5: Water table recorders installed by SNH across a hummock-hollow complex, Coladoir Bog. The comparable complex is out of the picture, on the right hand side, on a line with the depth recorders.

There was a possibility of the water depth recorders being reinstated, so the number of samples taken from each of the six nests was reduced to three to avoid jeopardising future monitoring, giving a total of 18 samples. Six water samples (one from each testacean sampling nest) were recovered and the water table depth, water pH, temperature and conductivity recorded at each nest.

c) Dun Moss S.S.S.I., Perthshire.

Site description

Dun Moss is a confined upland saddle raised mire, which lies at 350 m O.D. and covers 133.3 ha in the Forest of Alyth (Figure 4.7). The wet heath vegetation on the site is particularly rich in *Cladonia*, and contains a number of Sphagna - notably *Sphagnum magellanicum, S. tenellum, S. cuspidatum* and *S. capillifolium*. Generally, the flatter central area of the dome consists of *Eriophorum, Cladonia and Sphagnum* and the more freely drained rand is dominated by *Calluna vulgaris*. It is surrounded by a poor fen lagg on its eastern side, dominated by *Carex rostrata, Juncus effusus, S. palustre* and *S. recurvum*. The remainder is bounded by a poor fen soak lagg (Ratcliffe, 1977).

Again, the remote location of Dun Moss away from industrial areas minimised site damage from human interference and pollution, so that testacean samples would be representative of normal environmental conditions on the mire complex.

Sampling procedures

Seven lysimeters had been installed in a range of microhabitats by Dundee University (Plate 4.6). From nest A to G, the lysimeters were located in a *Sphagnum cuspidatum/S. tenellum* lawn; a *S. palustre* lagg fen; an *Eriophorum/Cladonia* hollow; an *Eriophorum / Cladonia / S.magellanicum* hummock; an *Eriophorum / Cladonia / S.magellanicum* lawn; a *S. capillifolium* hummock and in a dry patch dominated by *Calluna vulgaris* (Table 4.3).

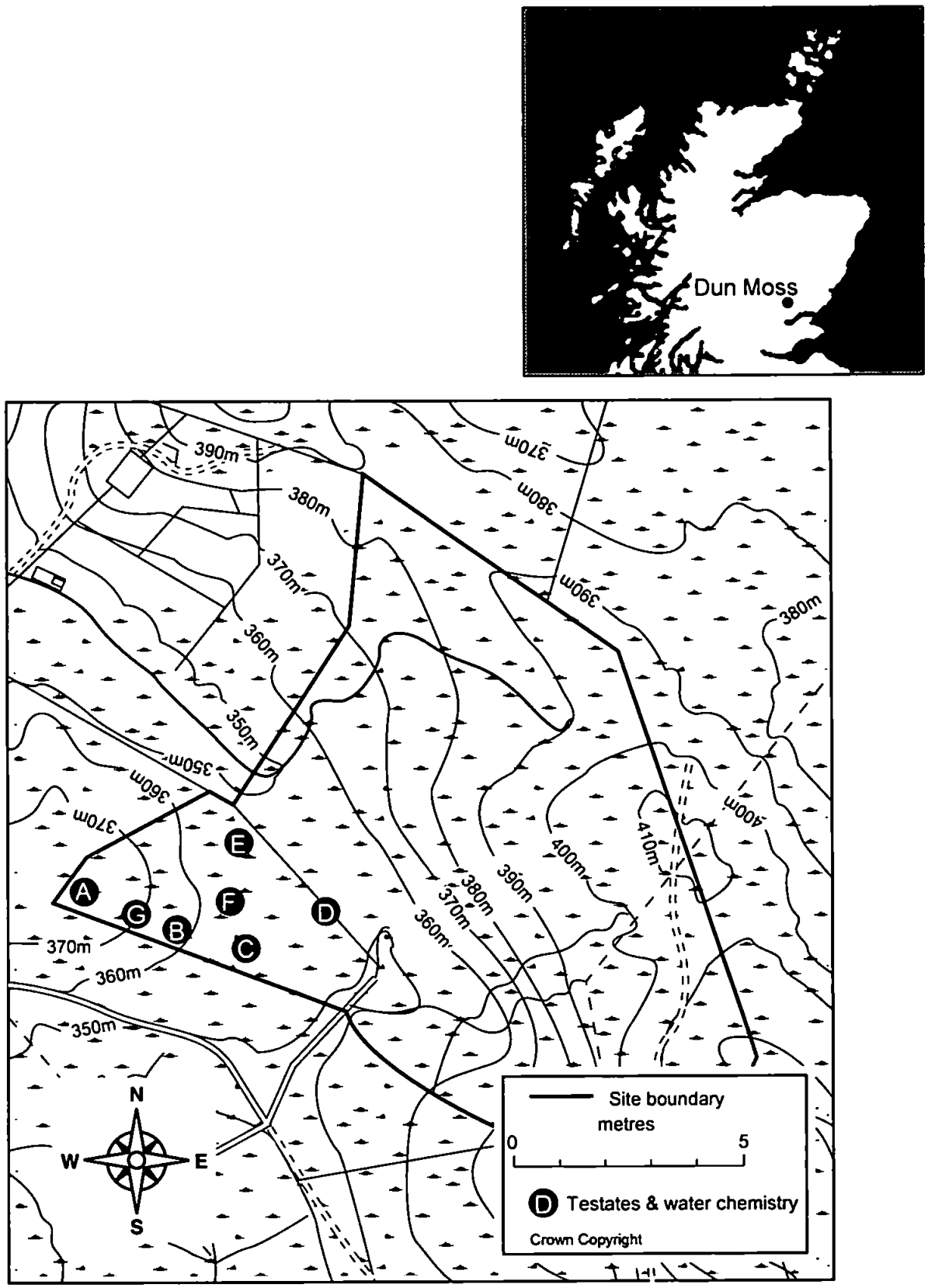


Figure 4.7: Dun Moss S.S.S.I., Perthshire: site location, topography and location of sampling points.

Nest C: *Eriophorum angustifolium* / *Cladonia* spp. hollow.

Nest E: *E. angustifolium* / *Cladonia* spp. / *Sphagnum magellanicum* hollow.

Plate 4.6: Examples of the lysimeters installed by Dundee University at Dun Moss. The lysimeter is the green circular object; within this is a dipwell (grey pipe). To the left of each lysimeter is an anchor to measure peat movement. Diameter of each lysimeter ca. 60 cm. For details of vegetation, see Table 4.3.

Again, a five metre radius was left between each lysimeter and the corresponding sampling site. Five testacean samples were collected from each point, giving a total of 35 samples. Water samples were collected and water pH, conductivity, temperature and water table depth were recorded at each sampling site.

Dun Moss is located in eastern Scotland, in the rainshadow of the South West Highlands. Whereas the two previous sites had received precipitation during the preceding 10 days (15th-25th August, 1993), Perthshire had remained hot and dry. Consequently, with the exception of the sampling point in the lagg fen, the *Sphagnum* plants at all nests on Dun Moss displayed severe desiccation. In general, this affected only the top 2-3 cm of the plants, leaving the underlying green and brown sections fully hydrated. Only the testacean assemblages from the brown fraction are of interest to this study and, given that the average depth of the chlorophyllous section of the *Sphagnum* plants was 8 cm and the average brown depth 12 cm, it is unlikely that desiccation affected the testaceans in the brown fraction.

d) Butterburn Flow N.N.R., Cumbria.

Site description

This is an extensive upland raised mire that covers approximately 4 km^2 at ca. 275 m O.D. on the edge of Wark Forest (Figure 4.8). The mire is the most important *Sphagnum*-rich blanket mire outside Scotland (Ratcliffe, 1977) and is drained west to east by the Lawrence Burn, which drains into the River Irthing and divides Butterburn Flow into two areas. To the south of the burn, the mire surface is extremely hummocky and the vegetation is dominated by *Eriophorum* and *Sphagnum magellanicum*. The northern part of Butterburn Flow is much flatter, dominated by *Eriophorum angustifolium*, with *Sphagnum magellanicum* and *S. papillosum* lawns interrupted by *S. imbricatum* hummocks.

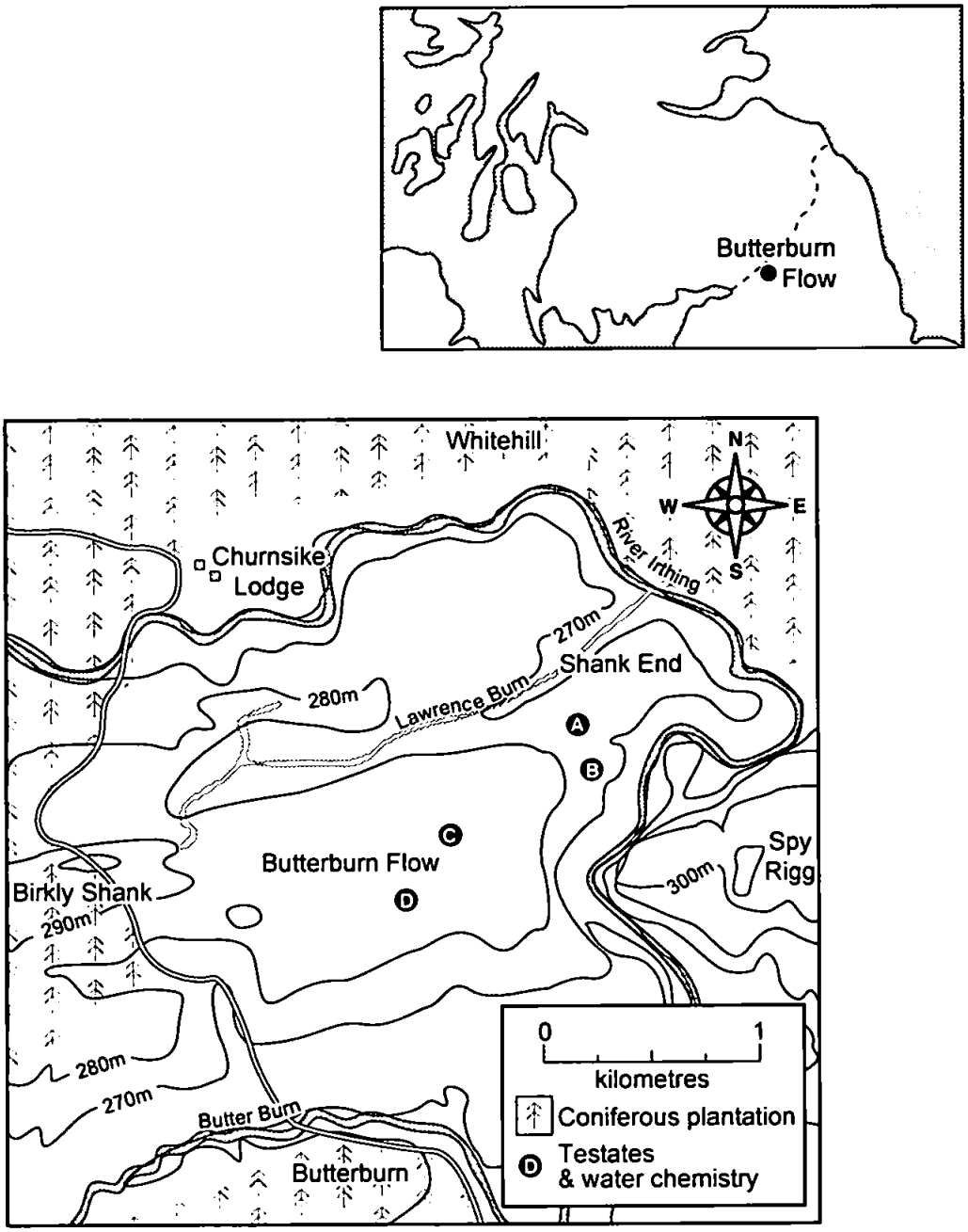


Figure 4.8: Butterburn Flow N.N.R., Cumbria: site location, topography and location of sampling points.

Like the previous sites, Butterburn Flow is remotely situated; it is also located within the Army firing range complexes at Otterburn. As such, access to the area is severely restricted and the general appearance of the site suggests that human interference is minimal. Although closer to sources of industrial pollution from the industrial conurbations of northern England relative to the remaining sites, the distance was still far enough and the direction of the prevailing winds sufficient to reduce the perceived risk of atmospheric pollution at the site.

Sampling procedures

Four lysimeters had been installed and monitored by Dundee University between May 1988 and May 1991 (Plate 4.7). Although the lysimeters were decommissioned, future recommissioning was likely, so the exclusion zone of five metres was established around each lysimeter. The vegetation within each lysimeter was identified and identical microhabitats that fell outside the five metre zone were selected for sampling.

Lysimeter 1 (nest A) was located in a *Sphagnum magellanicum/ S. cuspidatum* hollow; lysimeter 2 (nest B) on a *S. papillosum* lawn; lysimeter 3 (nest C) incorporated a small *S. magellanicum / Calluna vulgaris* hummock and lysimeter 4 (nest D) was situated on a *S. recurvum* lawn (Table 4.3). Five testacean samples were collected from each sampling point, giving a total of 20 samples from Butterburn Flow. One water sample was collected from each nest, and the water table depth, water pH, conductivity and temperature recorded.

e) Glasson Moss N.N.R., Cumbria.

Site description

Glasson Moss is a raised mire, situated at 10 m O.D. on the south side of the Solway Firth. The reserve covers 250 ha and contains the largest surviving undamaged area of a once extensive tract of raised mire (Figure 4.9). The northern part of the mire remains intact and

Nest A: *Sphagnum magellanicum / S. cuspidatum* hollow.

Nest B: *S. papillosum* lawn.

Plate 4.7: Testacean sampling points on Butterburn Flow, Cumbria. The testacean samples were collected from vegetation identical to that in each lysimeter.

Nest C: Small (5cm high) *Sphagnum magellanicum* / *Calluna vulgaris* hummock.

Nest D: *Sphagnum recurvum* lawn.

Plate 4.7: (continued)

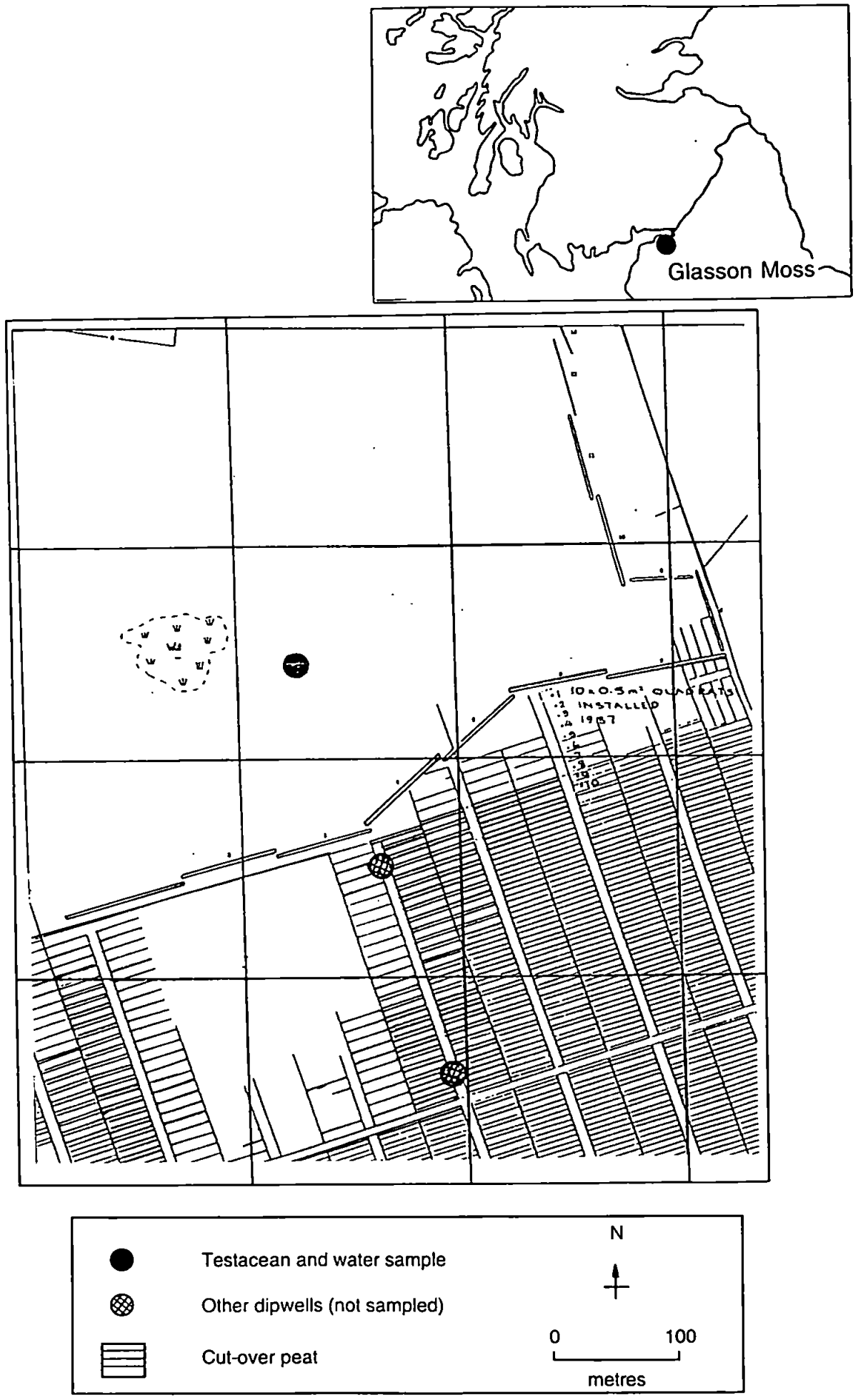


Figure 4.9: Glasson Moss NNR, Cumbria: site location, topography and location of sampling points

gently undulating *Sphagnum* hummocks are separated by low hollows. The hummocks comprise an association of *S. pulchrum* - *Rhyncospora alba* - *Andromeda polifolia*, while *S. cuspidatum* is dominant in the hollows. In the southern area, commercial peat cutting has left a dry surface, colonised by *Calluna vulgaris*. English Nature is currently attempting to restore this area to raised mire. Water table depths at three points on the Moss had been monitored continuously by the site manager for the period 1989-1992 for an M.Sc. dissertation, providing a detailed hydrological record.

Sampling procedures

Only one dipwell on Glasson Moss was of use to this study. This was located in a wetter part of the dome apex and also contained an anchor to monitor the movement of the peat body (Plate 4.8). Although a suitable testacean sampling point was identified, an insect trap was already in place, making sampling difficult. Four testacean samples were collected from adjacent comparable microhabitats together with water table depth, water pH, conductivity and temperature. A water sample was also obtained.

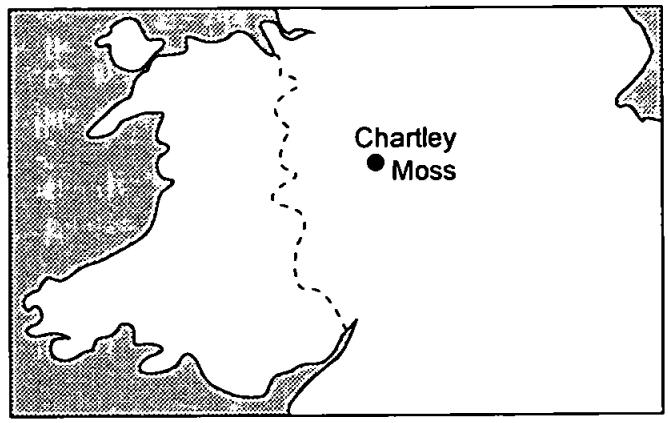
The remaining two dipwells were located in an area of the mire that had previously been milled and that was now being restored. Although the open water between the peat ridges had limited recolonisation of *S. cuspidatum*, the peat ridges were still dry and *Sphagnum* cover here was so sparse (and the peat surface so disturbed) that no further samples were collected for testacean analysis.

f) Chartley Moss N.N.R., Staffordshire

Site description

Chartley Moss is a partially wooded basin mire occupying two depressions in glacial deposits overlying Keuper Marl (Figure 4.10). It is located 9 km south-west of Uttoxeter and 2.5 km north-east of Stowe-by-Chartley. The western basin contains a raft of

Plate 4.8: The testacean sampling point on Glasson Moss, Cumbria.



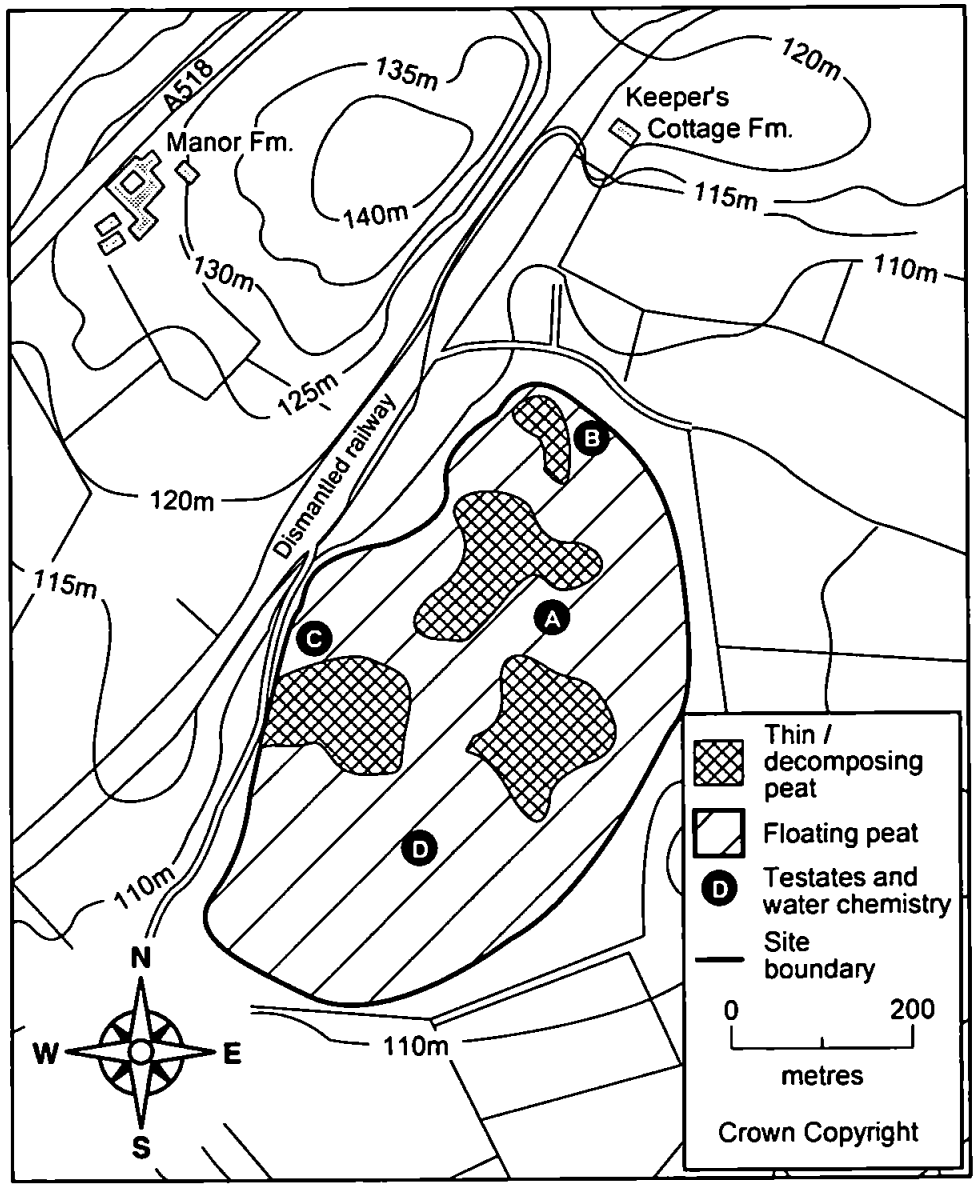


Figure 4.10: Chartley Moss N.N.R., Staffordshire: site location, topography and location of sampling points.

oligotrophic *Sphagnum* peat floating above a deep water body (ca. 16 m - Ricks, 1970), comprising the largest "schwingmoor" in Britain. The site is at an advanced hydroseral stage (drainage by a previous landowner has accelerated this process) and Ahmad-Shah and Rieley (1989) identify five representative vegetation communities. Where the *Sphagnum* raft is wettest and unstable, tree growth is inhibited and an open *Sphagnum recurvum* lawn with hummocks of the same moss dominate. Towards the drier raft margins there is a transition from stunted *Pinus sylvestris* to full pine forest. The solid, drier peat is colonised by mixed woodland (*Betula pubescens, Scorbus aucuparia, Pinus sylvestris* and *Quercus robur*). Open fen woodland (composed mainly of *Alnus glutinosa*) and birch forest (*Betula pubescens*) are found towards the peat margins. Within the floating raft are two pools - Shooter's Pool and Dead Pine Gulch - which are being slowly colonised by *S. recurvum* and *E. angustifolium*.

Chartley Moss was chosen because hydrological monitoring had been conducted at the site for the preceding three years by the University of Nottingham (Ahmad-Shah and Rieley, 1989). However, of all the British sites sampled during the fieldwork programme, Chartley Moss was likely to receive the highest input of atmospheric pollution as a result of both its local and regional location. Chartley Moss lies within 80 km of the West Midlands conurbations and it is likely that aerosols of, for example, nitrogen oxides (NO_x) and sulphur dioxide (SO_2) are carried northward on prevailing winds and deposited over the site in precipitation. Land use in the surrounding area is predominantly agricultural and is split between arable and pastoral. There may be some dust input during ploughing or from fertilizer application at certain times of the year and the possible effects of these inputs are considered in detail in Chapter 6.

Sampling procedures

Sampling at Chartley Moss was considerably hampered by the danger of falling through the unstable *Sphagnum* raft and into underlying deep water. In many places, the raft was too thin to support any weight and, on advice from the Site Manager, most of the sampling was conducted from boardwalks.

Four sampling points were selected from a grid of water table monitoring points installed by Nottingham University (Figure 4.11). The four nests were chosen to reflect both microtopographical and hydroseral variations over Chartley Moss. Nest A was located in open *Sphagnum recurvum* lawn on the edge of Shooter's pool; nest B near Dead Pine Gulch in a clearing in the pine woodland; nest C in *S. recurvum* hummocks in mixed woodland and nest D in open *S. recurvum* lawn in birch woodland (Plate 4.9). The fen areas were not sampled. At each sampling point, six samples were retrieved, the water table depth measured and a water sample collected. Water pH, conductivity and temperature were also recorded.

g) Borth Bog (Cors Fochno) N.N.R., Dyfed

Site description

Borth Bog (Cors Fochno) is an estuarine raised mire, covering 3339 ha on the south side of the Dyfi estuary (Figure 4.12). Although the raised mire surface has now been reduced to one-third of its original extent by agricultural reclamation and peripheral peat cutting, it is still the most extensive tract of undisturbed raised mire in Britain (Ratcliffe, 1977; CCW, 1990). It is efficiently buffered by the surrounding areas of modified raised mire and by a lagg community, comprising *Salix cinerea* carr. Along the western margin, adjacent to the Afon Leri, the mire grades from raised mire to salt marsh.

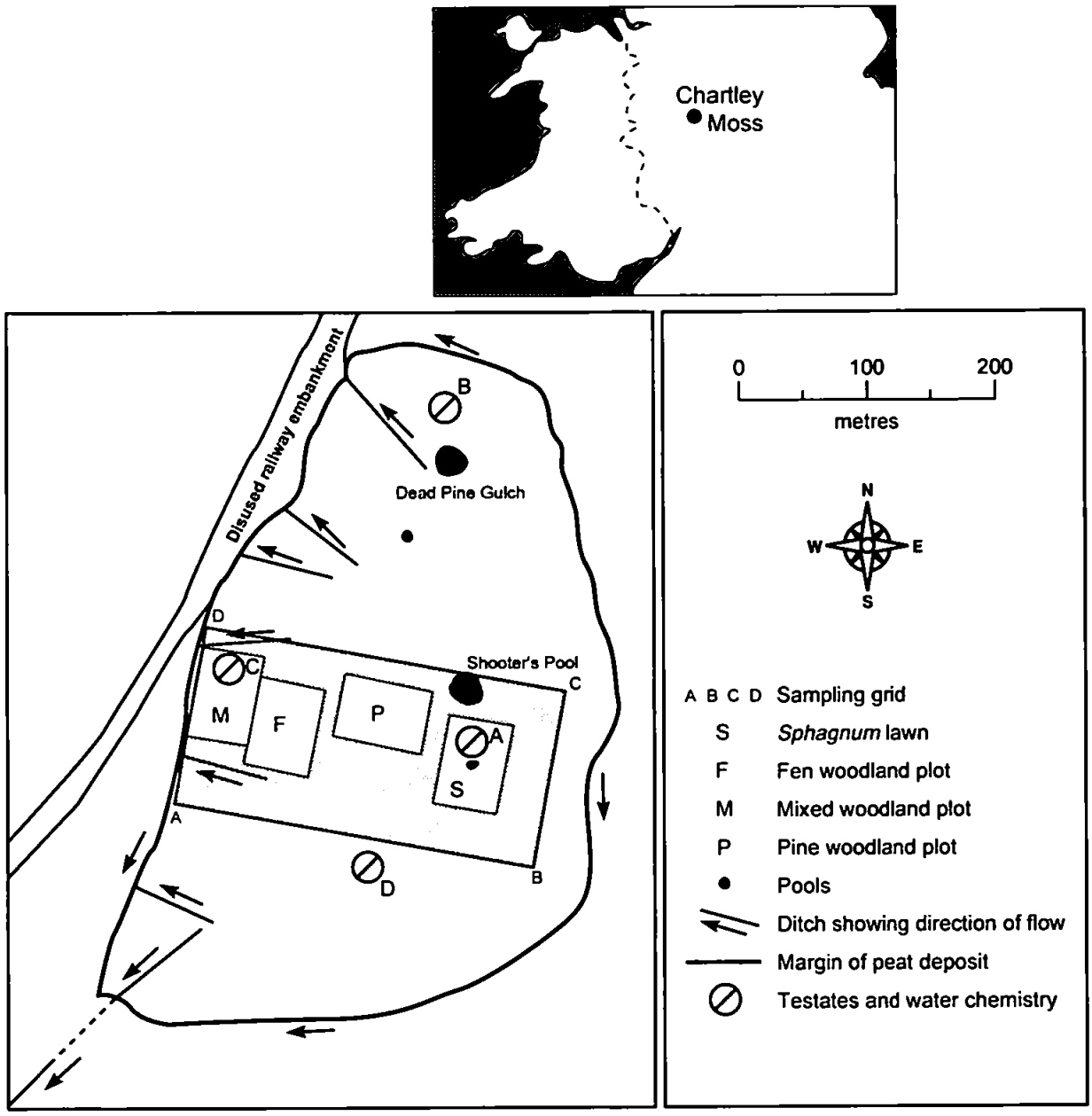
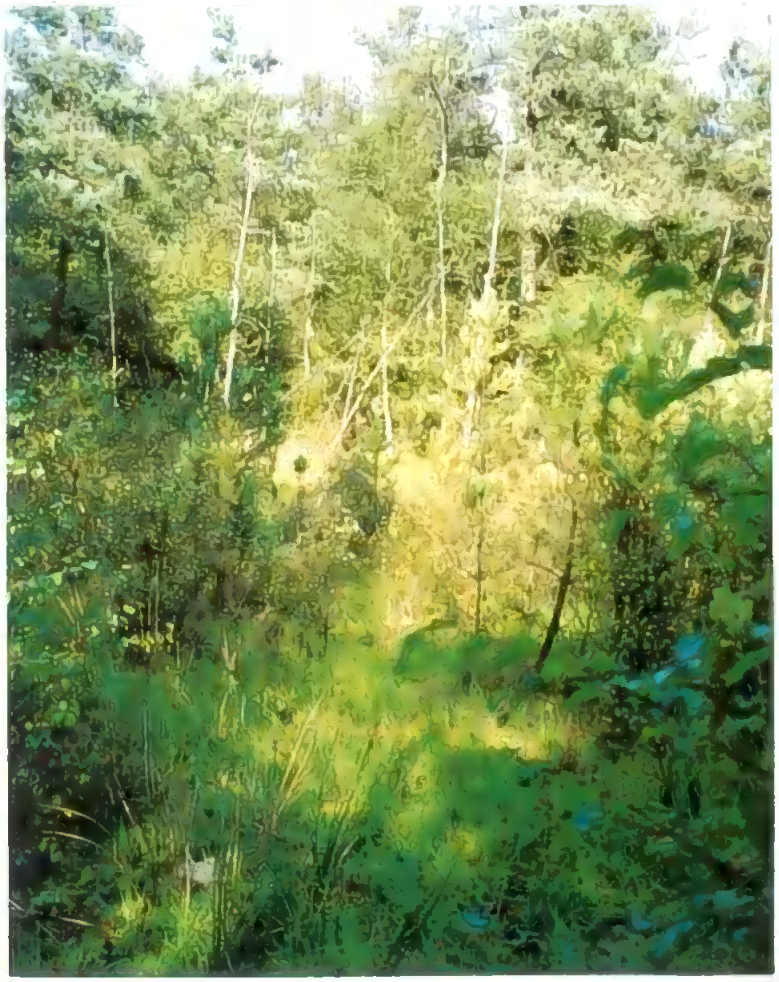


Figure 4.11: Plan of Chartley Moss N.N.R. showing the location of the testacean samples and associated vegetation/water sampling grid installed by the University of Nottingham (source: Ahmad-Shah and Rieley, 1989; p.358).

Nest A: Open *Sphagnum recurvum* lawn on the eastern edge of Shooter's Pool.



Nest B: *S. recurvum* clearing in *Pinus sylvestris* woodland (Dead Pine Gulch).

Plate 4.9: Testacean sampling points on Chartley Moss, Staffordshire

Nest C: *Sphagnum recurvum* hummocks in mixed woodland.

Nest D: Open *S. recurvum* lawn in *Betula pubescens* woodland.

Plate 4.9 (continued)

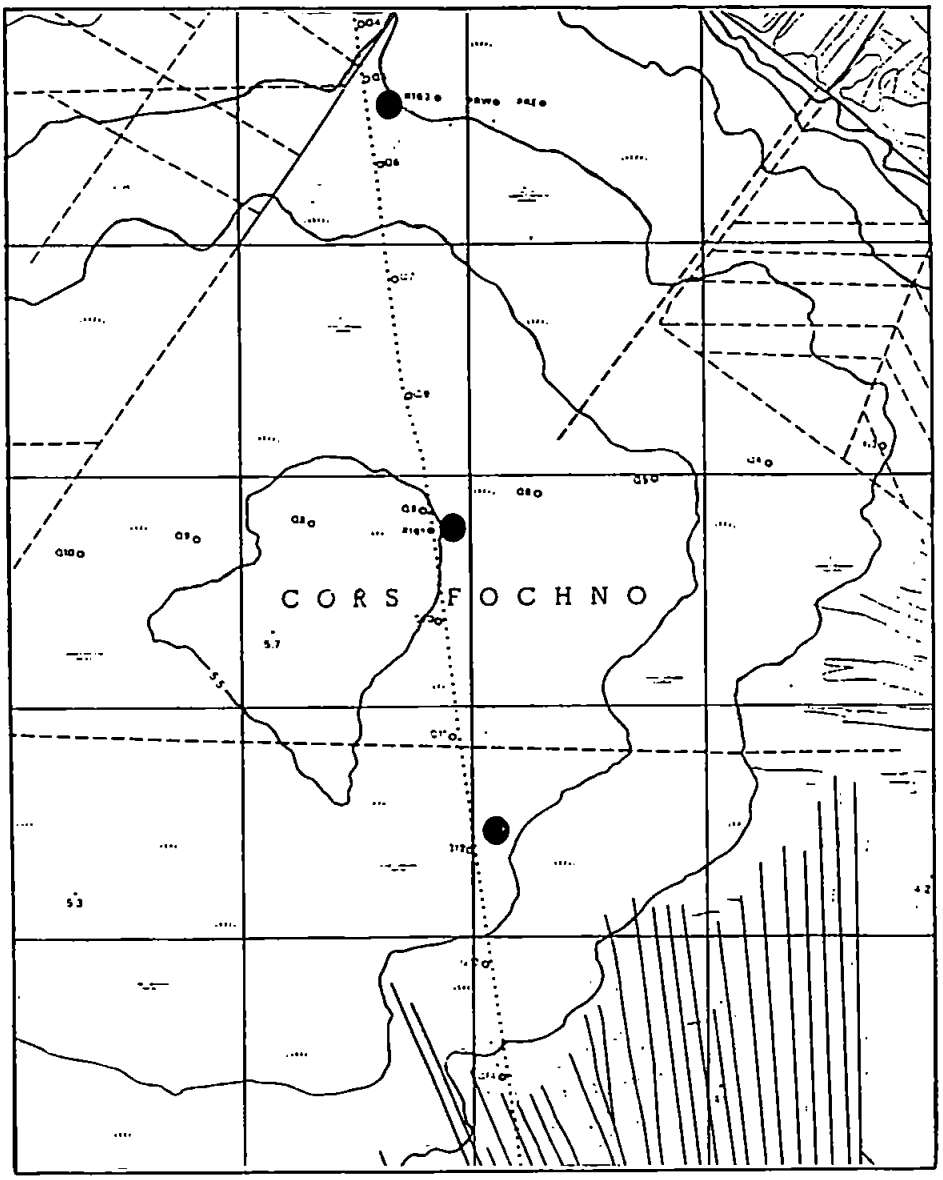


Figure 4.12: Borth Bog NNR, Dyfed: site location, topography and location of sampling points

The central raised mire community on Borth Bog is similar to that on Glasson Moss, comprising a gently undulating hummock - hollow mosaic, over which *Sphagnum* cover is shallow and discontinuous. Hollows have a *Sphagnum pulchrum - Rhyncospora alba - Andromeda polifolia* association, but pools in the larger hollows are dominated by *S. cuspidatum* and *Eriophorum angustifolium*. Additional to the hummock-hollow mosaic are large *S. pulchrum* and *S. tenellum* lawns with *R. alba, Erica tetralix, Eriophorum angustifolium, Narthecium ossifragum, Drosera rotundifolia* and *D. anglica*. The hummock-forming *S. papillosum, S. rubellum* and *S. magellanicum* occur in association with *Calluna vulgaris*. *S. imbricatum* is rare and present only locally.

Borth Bog was chosen as a sampling site because hydrological monitoring had been conducted by CCW between 1987 and 1990. A further important feature of the site was the presence of *Sphagnum imbricatum*. Since the species is rare in Britain it was grossly under-represented in the modern British data set. Collecting *S. imbricatum* samples from Borth Bog meant that all the major Sphagna were represented and also that *S. imbricatum*, a species that features strongly in fossil data, was represented in the modern data set.

Sampling procedures

CCW had installed three water table recorders in the centre of the peat dome, and these were reached via a boardwalk (Figure 4.12). One was located in a *S. imbricatum* hummock (nest A), one on open *S. cuspidatum* lawn with *Scirpus cespitosus* (nest B) and the third on *S. cuspidatum* lawn with *Myrica gale, Eriophorum angustifolium, Myrica gale* and *S. cespitosis* (nest C). At the request of the Site Manager, who was concerned by the restricted distribution of *S. imbricatum* across Borth Bog, sampling was restricted to two samples from one *S. imbricatum* hummock to avoid depleting the existing *S. imbricatum* population.

In total, 14 testacean samples were recovered - two from the *S. imbricatum* hummock and six from comparable microhabitats surrounding the other two recording stations. Water table depth, pH, conductivity and temperature were recorded and a water sample collected.

h) Cors y Llyn (Llyn mire) N.N.R., Powys

Site description

Cors y Llyn is an elliptical basin mire situated on a plateau to the east of the River Wye, 4 km north of Newbridge, Powys. Llyn is a small site and has been subjected to relatively little human interference, preserving a semi-natural vegetation community that progresses along a hydrosere from open *Sphagnum* pools to peripheral *Betula* carr (Figure 4.13).

Old peat cuttings in the northern section of the bog are now colonised by *Eriophorum angustifolium, Sphagnum recurvum* and *Vaccinium oxycoccus*, and the ridges in between support mature *Pinus sylvestris*. In the northern section of the bog, a floating raft of poor fen vegetation, which includes *Eriophorum angustifolium, S. recurvum, Potentilla palustris, Carex rostrata* and *V. oxycoccus* has developed relatively recently over open water, thought to be an area of abandoned peat cuttings (Ratcliffe, 1977).

Like Chartley Moss, the southern part of Llyn Mire is an acidic "schwingmoor", dominated by *S. papillosum, S. recurvum, Rhyncospora alba, Narthecium ossifragum, Vaccinium oxycoccus* and *Erica tetralix*. Hummocks have been colonised by *Calluna vulgaris, Molinia caerulea, Scripus cespitosus, Empetrum nigrum, Eriophorum vaginatum, Cladonia impexa* and *S. rubellum* (Ratcliffe, 1977).

Sampling procedures

A network of 16 dipwells had been installed by the Institute of Hydrology (Figure 4.13) and water table readings were available for the period between 1985 - 1989 (Gilman, 1994),

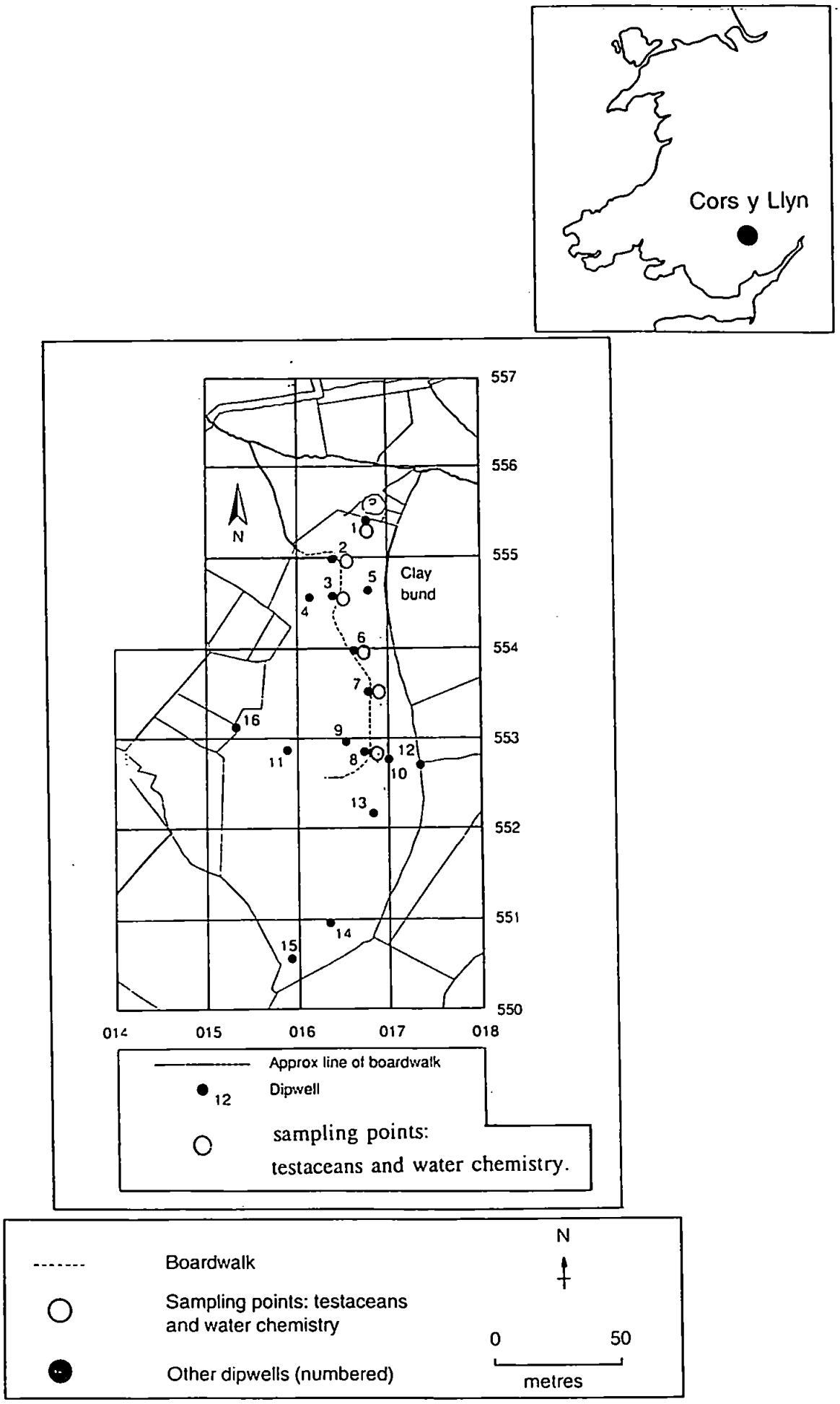


Figure 4.13: Cors y Llyn (Llyn mire) NNR: site location, topography and location of sampling points (map source: Gilman, 1994 p.47).

giving a comprehensive site record to include in the modern British data set.

Llyn Mire is virtually identical to Chartley Moss in that deep water underlies a floating *Sphagnum* raft. Again, the author was advised to keep to the boardwalk, but this presented no problems for sampling as the dipwells are located within easy reach of the boardwalk. Six dipwells were chosen to give a range of microhabitats and, at each site, a nest of six samples were taken from each. Nest 1 was located on *Sphagnum recurvum* lawn with *Juncus* spp. and *Polytrichum commune*; nest 2 on *S. recurvum* lawn with *Betula pubescens* and *Eriophorum angustifolium* nearby; nest 3 was situated in an open *S. recurvum* lawn; nest 4 on an *S. rubellum* hummock (approximately 30 cm high) colonised by *Calluna vulgaris*; nest 5 on *S. recurvum* lawn in *Pinus* woodland, and nest 6 in the driest area of the site, colonised by *Calluna vulgaris, Eriophorum vaginatum, Scirpus cespitosus* and *Andromeda* spp. Water table depth was recorded, a water sample collected, and pH, conductivity and temperature recorded.

4.3 Storage of samples

The green and brown fractions of the *Sphagnum* plants were separated, individually bagged and excess air expelled. The bags were then transferred to sturdy cardboard boxes. Each box contained cardboard dividers so that bags were stacked to a maximum of four high to avoid crushing the samples and squeezing water (and testaceans) from the moss. Water samples were packed in the same way in one box. All samples were stored for transit in cool conditions with the aid of ice blocks, which were regularly refrozen.

Twenty-four days elapsed between the collection of the first water sample and the first analyses. Given the consistently low storage temperatures that were maintained during the fieldwork period, it is extremely unlikely that the chemical composition of the mire water samples changed to any significant degree (Proctor, 1992; 1993).

4.4 Water chemistry analyses and testacean analyses

The same chemical parameters that were analysed in the Tor Royal samples were also analysed for the above sites - see section 4.1.4 (page 94) for a description of the procedures. The laboratory preparation and counting of testate amoebae also follows the procedure detailed in section 4.1.3 (page 85).

4.5 A note on the representativeness of the instrumental hydrological records with respect to the testacean sampling points

Given the exclusion zones imposed by some of the monitoring parties, the usefulness of historical hydrological data to this study may be in doubt. This possibility was uppermost during the field sampling programme and to assess the representativeness of the hydrological records, the water table depth in the recording instruments was measured and compared to that measured in each testacean sampling point. Table 4.3 summarises these data for all British sites and shows that the depth in the testacean sample was generally within 1 cm of instrumental records and that the difference never exceeded 3 cm. This small depth variation confirms that the testacean assemblages can be related with confidence to the historical hydrological records. Future investigations might adjust the mean annual data by these differences.

Further, the generally small standard deviations of mean water table level in each nest demonstrates the coherence of their water table data. Standard deviations were greatest in hummock nests, reflecting the greater microtopographical differences on each hummock compared with the uniform microtopography of lawns and pools, when the standard deviations are smaller.

Chapter 5

The hydrology and water chemistry of Tor Royal Bog

5.0 Introduction

Chapter 3 identified "one-shot" sampling methods as one of the key problems in understanding the modern ecology of testaceans and their relationship with water table depth and substrate moisture content. This results from a lack of information on annual water table fluctuations. It may also be argued that there are likely to be significant fluctuations in mire water quality according to season, principally due to changes in the dilution of surface waters (Proctor, 1992, 1994; Ahmad-Shah and Rieley, 1989). Since recent studies have identified water quality as a secondary control on species distributions (Charman and Warner, 1992; Tolonen *et al.*, 1992, 1994), testaceans could, potentially, be used to reconstruct past changes in water chemistry. It is therefore important to investigate both water table and water quality fluctuations on ombrotrophic mires. Chapter 4 introduced the monitoring programme that was implemented at Tor Royal to provide more specific data on a greater range of hydrological parameters. It also detailed the collection of information from a suite of sites across Britain where long-term water table data were available.

However, there are few sites in many areas of the world where long-term records of water table variations are available and "single-shot" sampling may provide the only possible means of collecting data on modern analogues for fossil communities. It is therefore crucial to assess the accuracy of such an approach so that errors inherent in the method can be included in quantitative reconstructions of past water tables. This study offers an excellent opportunity to address this issue in some detail.

To assess the integrity of "single-shot" sampling methods, it is important to investigate the fluctuations in water table depth and water chemistry occurring within an ombrotrophic bog over a prolonged sampling period. The programme at Tor Royal aimed to monitor water table and water chemistry over one year at a reasonably fine temporal resolution and to identify seasonal trends. The data would be used to assess the accuracy of "single-shot" sampling used in previous studies (Warner, 1987; Charman and Warner, 1992; Tolonen *et al.*, 1992). If fluctuations were limited around an annual mean, a single measurement could be considered an accurate representation of annual conditions, supporting the "single-shot" sampling approach. Alternatively, it might be possible to identify a period in the annual cycle when water tables were most representative of annual means or at least relatively stable for a period of time.

If the water tables regularly deviate markedly from the annual mean, a single sample could not be considered a reasonable representation of average conditions. Given such a result, the only way forward in the quantification of testaceans' response to water table variations is to establish more extensive hydrological monitoring programmes at sampling sites. The development of other techniques for standardising data sets for comparability may also be necessary and this is considered in Chapter 6.

If the usefulness of testaceans as palaeoenvironmental indicators is to be extended beyond water availability (expressed as depth to water table and percent moisture content) and into water quality reconstructions at a later stage, it is essential to obtain quantitative information on their modern relationship with mire water chemistry. This will allow "single-shot" sampling methods for water chemistry to be evaluated. It is for this reason that water chemistry monitoring was implemented to run in tandem with the hydrological programme at Tor Royal.

This chapter presents the results from the monitoring programme at Tor Royal and is divided into sections on precipitation variability, water table activity in response to precipitation and evapotranspiration, and variations in selected chemical ion concentrations. The implications of this work for the development of transfer functions from testate amoebae for mire hydrology and water chemistry are also discussed.

5.1 Reliability of the automatic readings

Table 5.1 summarises the setup for the Rustrak logger throughout the monitoring programme at Tor Royal to record water table depth, water temperature, water conductivity, precipitation and air temperature in dipwell C3 (see Figure 4.1, page 77, for the location of dipwell C3).

Variable	Equipment	Units	Recording interval	Length of record
Water table depth	Pressure transducer	cm	Every 15 mins to 1.6.93. Then 12-hourly.	1.6.93-27.7.93
Water table depth	Potentiometer	cm	As above.	1.6.93-26.11.93
Water temperature	Temperature probe	°C	As above.	1.6.93-29.9.94
Air temperature	Temperature probe	°C	As above.	1.6.93-29.9.94
Water conductivity	Conductivity probe	$\mu S\ cm^{-1}$	As above.	1.6.93-29.9.94
Precipitation	Tipping bucket raingauge	mm	Every 15 mins until 26.11.93. Then 12-hourly.	1.6.93-29.9.94

Table 5.1: Summary of automatic water table depth and water chemistry readings from Tor Royal between June 1993 and September 1994.

For the first fortnight of the programme, readings for all variables were taken at 15-minute intervals, generating over 8000 data points. These readings were analysed and shown to be consistent over 12-hourly intervals (see section 5.3.3 below). Hence, 12-hourly readings (at 00:00 hours and 12:00 hours) were implemented on 1st June 1993 and continued for the remaining monitoring period. 15-minute records of precipitation were maintained, however,

to allow detailed analysis of water table response (measured by the potentiometer) to precipitation events. When the potentiometer recordings were terminated on day 179, due to instrument failure, the logger was reset to record 12-hourly precipitation totals.

The numerous problems experienced with the pressure transducer, potentiometer and pH probe highlight the difficulties inherent in a monitoring programme of this kind. Clearly, the reliability of the instruments in an exposed environment has been challenged by this project. The additional problems presented by a field site that is too far away for daily checks of the recording equipment are also considerable. Given the comments of Ingram (1983), this is a common problem in studies of mire water tables:

> "Modern developments in pneumatic and electronic pressure transduction seem not to have been applied to the study of mire water tables. Expense and lack of robustness in a harsh, wet environment may have been discouraging factors."
>
> (Ingram, 1983; p. 106).

More recently, a non-electronic approach to shallow water table monitoring on mires has been published by Bragg *et al.* (1994). The apparatus records maximum and minimum water table depths between site visits using a simple float mechanism. It is accurate to within 2 mm, does not require electricity and the simple mechanical parts require negligible maintenance. The latter two points would have been advantageous to the study on Tor Royal, dispensing with the need to carry heavy car batteries over rough terrain and to carry out maintenance in inclement weather. Had this design been available when the Tor Royal programme was devised, it might have been used in preference to the electronic water table monitoring attempted at this site. However, it would not have reproduced the temporal resolution that electronic equipment is able to generate.

Given the failure of the pressure transducer, it was important to check the reliability of water table data that had been recorded by the potentiometer, since this was now the only available daily record of water table level. While the potentiometer was functioning, a manual water table depth reading was taken from the same dipwell at the same fortnightly intervals as the remaining dipwells. These manual readings were taken at an identical time (11:00 hours) on each sampling visit and a comparison between this manual depth reading and the potentiometer reading at 12:00 hours could therefore be made to check the reliability and accuracy of the automatic data taken during the period 1.9.93 to 26.11.93. Figure 5.1 is a scatter plot of manual readings taken at 11:00 hours against the automatic reading taken at 12:00 hours on the sampling day. Spearman's rank correlation coefficient (r_s) is 0.996 ($p<0.01$), which confirms that the potentiometer recordings were accurate during the period and that the equipment was operating normally.

After day 179 (26th November, 1993), the potentiometer developed several malfunctions and failed to transmit any sensible data; this was probably a consequence of preceding severe weather conditions. After several unsuccessful attempts to repair and replace it, only potentiometer readings to 26th November 1993 were retained; the potentiometer was dismantled in January 1994 and measuring continued manually at fortnightly intervals thereafter.

5.2 Precipitation

In total, 1874 mm of precipitation fell on Tor Royal during the year 1st June 1993 to 31st May 1994 and 2242 mm fell during the extended monitoring period (1st June 1993 to 29th September 1994). Approximately two-thirds of the precipitation (687 mm) for the year 1st June 1993 to 31st May 1994 fell between 1st September 1993 and 29th February 1994 (Figure 5.2).

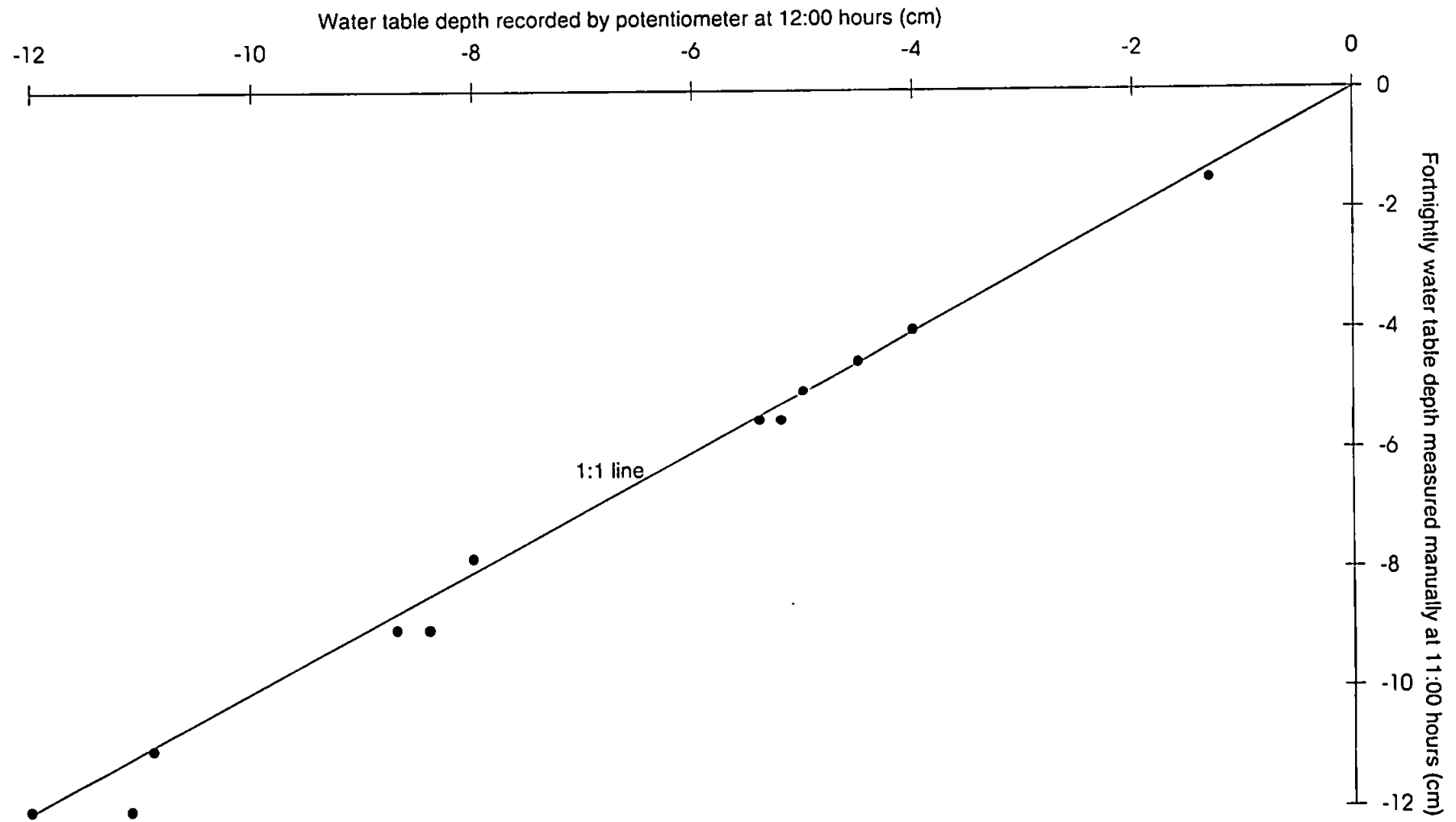


Figure 5.1: Scatterplot showing water table depth recorded manually (at 11:00 hours) and by potentiometer (12:00) at Tor Royal during the 179 days that the potentiometer functioned.

Figure 5.2: Monthly precipitation totals for Tor Royal, 1.6.93-29.9.94.

During the extended monitoring period 1.6.93 to 29.9.94, precipitation fell on 164 days, leaving 323 dry days. The longest continuous period of precipitation occurred during December 1993 and lasted for 13 consecutive days between the 12th and 25th (days 195 and 228 respectively). The longest dry period lasted 20 days from 12th October to 1st November 1993 (days 134 to 154 respectively). The most intensive precipitation occurred between 18th and 26th February 1994 (days 283 to 291 respectively), when 140 mm of precipitation fell in 9 days.

For this study, it was important to confirm that the water table data were collected from Tor Royal during a typical year in terms of climate and that precipitation at the site was characteristic of the Dartmoor region as a whole. It was also important to establish whether the remaining British sites were sampled during a typical year. If the sampling was conducted in unusually wet or dry years then subsequent transfer functions would not reflect typical hydrological conditions.

To establish whether precipitation totals for Tor Royal for 1.6.93 to 31.5.94 were typical for the immediate locality, a comparison was made with a similar locale. The nearest available data came from a meteorological station operated by the University of Plymouth near Burrator Reservoir (SX567692), 3 km southwest of Tor Royal (Figure 5.3). The Burrator Head Weir raingauge is positioned at an altitude of 220 m O.D. in a woodland clearing and has operated since January 1976. For the year 1.6.93 to 31.5.94, precipitation at Tor Royal was lower than at Burrator (1874 mm compared to 2121 mm; Figure 5.4), which is surprising considering the higher altitude (395 m O.D.) of Tor Royal relative to Burrator (220 m O.D., a height difference of 175 m). The rain gauge at Tor Royal was placed in an exposed position, which probably caused under-recording of precipitation by the instrument. In a more sheltered location, lower wind speeds would allow precipitation to drop directly into the raingauge collecting funnel. However, with exposure to strong

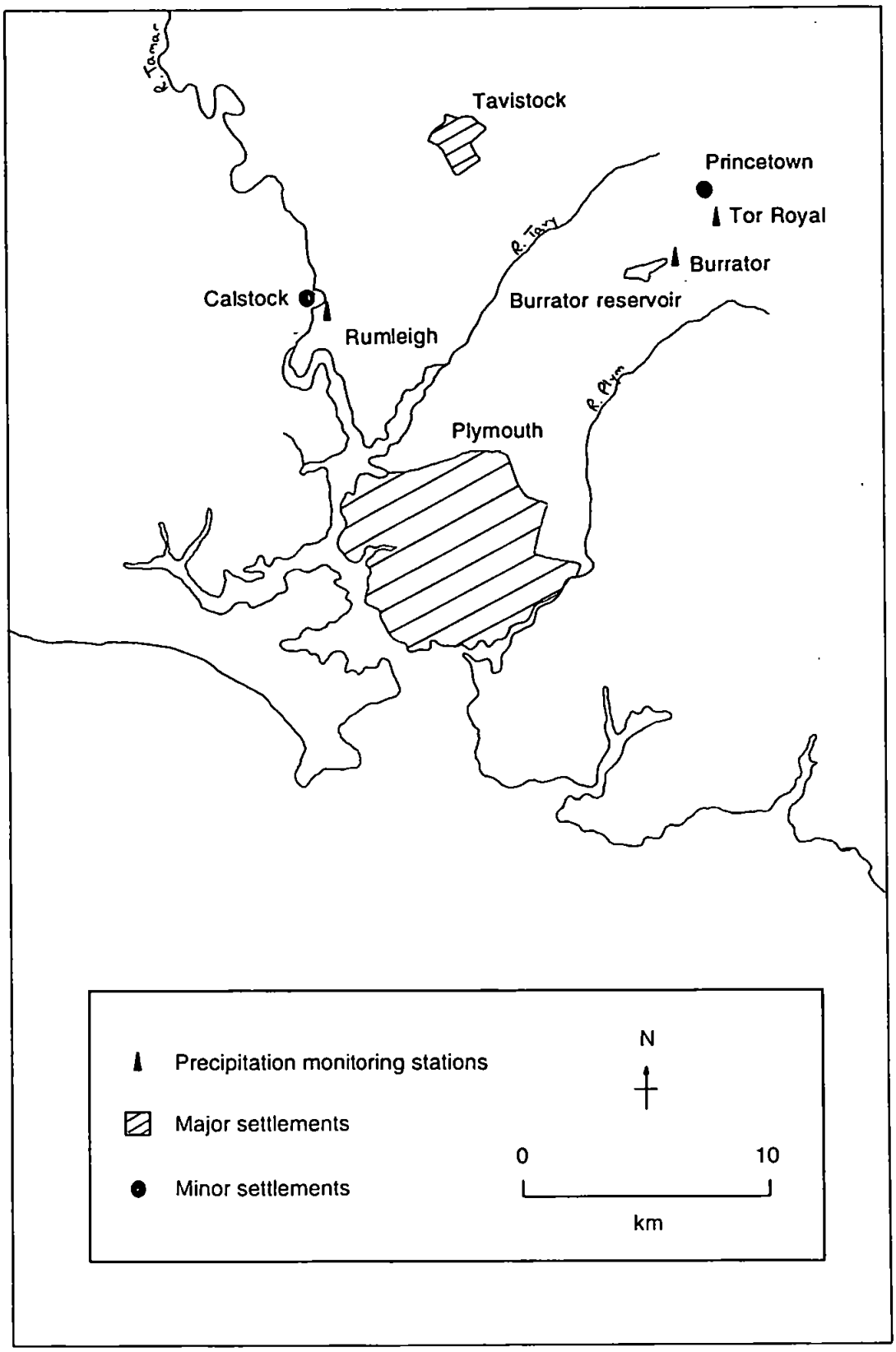


Figure 5.3: Location of precipitation monitoring stations mentioned in the text.

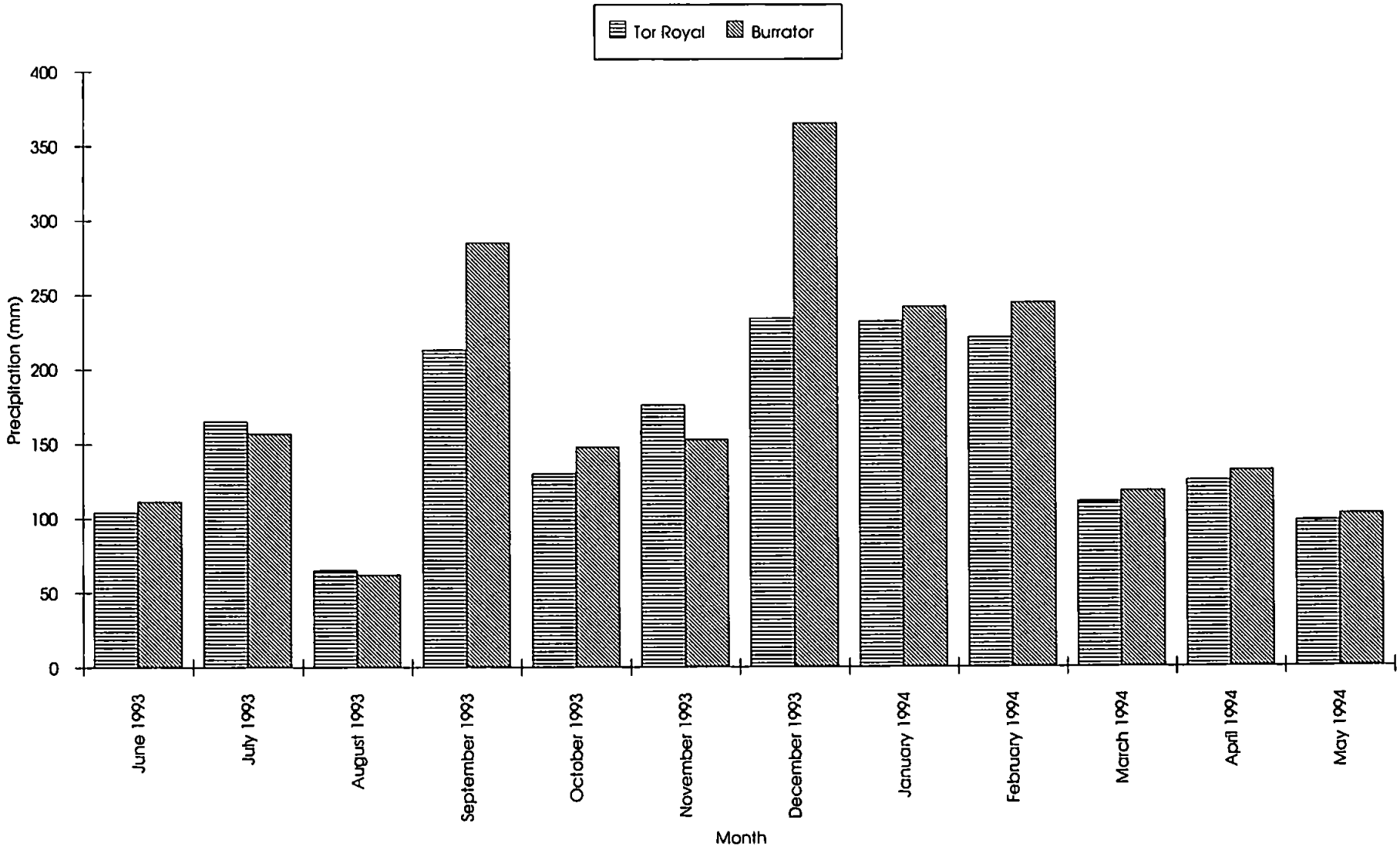


Figure 5.4: Monthly precipitation totals for Tor Royal and Burrator, 1.6.93-31.5.94.

winds, raindrops would be blown across the face of the funnel, causing under-recording of precipitation totals. The vertical aspect of the funnel (positioned perpendicular to the ground surface) may also have contributed to under-recording. Sims (1981) showed that rain gauges facing directly into the prevailing wind (and hence precipitation) caught more rain than vertically-placed rain gauges. However, a Mann-Whitney test to compare the monthly precipitation totals over the first year is not significant at $p<0.05$. There is no statistical difference between the precipitation totals for the two sites and monthly precipitation totals at Tor Royal for 1.6.93 to 31.5.94 are generally characteristic of the immediate locality.

To establish the representativeness of 1993/94 in terms of the temporal distribution and amount of precipitation for the general locality, precipitation data from Tor Royal were compared with longer-term records from other local sites. Burrator has already been identified as the closest equivalent site to Tor Royal in terms of precipitation and, because precipitation records cover 1976 to 1994 inclusive, it could be used to establish the representativeness of the June 1993 - May 1994 precipitation levels. Figure 5.5 gives a general impression of precipitation during 1993/94 relative to previous years at Burrator. By calculating the long-term average of precipitation totals for the years June-May 1976/77-1993/94 (1702 mm), the percentage difference of the 1993/94 totals at Tor Royal from the long-term average can be expressed. During 1993/94, precipitation at Tor Royal was 10% (173 mm) higher than the long-term average and can be viewed as reasonably representative of the previous 18 years at least.

Additional precipitation records from a second University of Plymouth meteorological station at Rumleigh (SX442679) near Calstock in Cornwall, 15 km southwest of Tor Royal (Figure 5.3) may also be used, but with caution. Rumleigh station is located at 30 m O.D. and, consequently, mean monthly precipitation is always lower than for Burrator and Tor

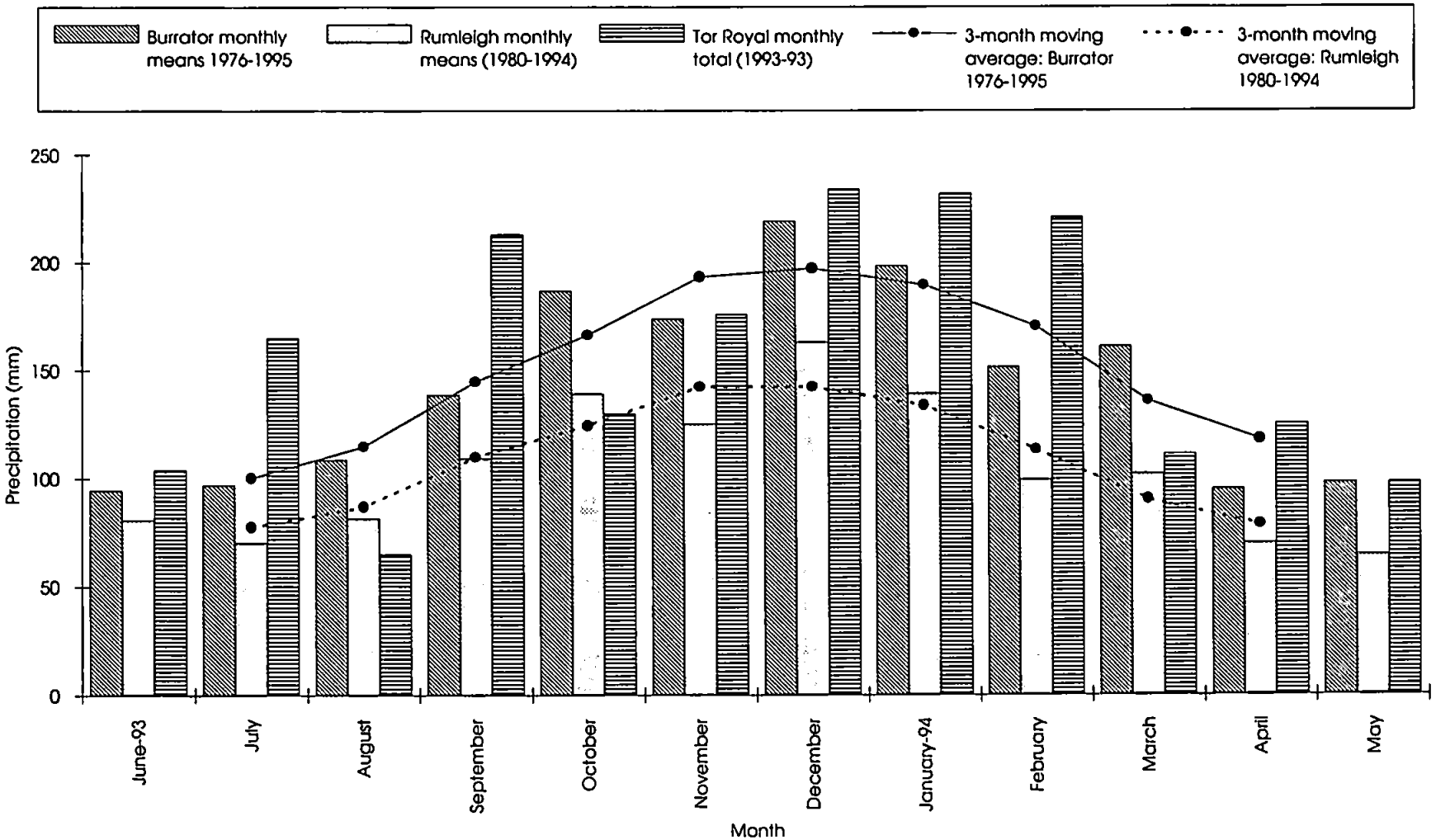


Figure 5.5: Comparison of total monthly precipitation at Tor Royal (1.6.93-31.5.94) with monthly means from Rumleigh and Burrator stations.

Royal (Figure 5.5). Despite this, the smoothed temporal distribution of precipitation (calculated from the three-month moving average) is similar to Burrator (Figure 5.5).

Both investigations detailed above show that the precipitation data derived from the monitoring programme at Tor Royal are reasonably representative of both the Dartmoor region in general during 1993/94 and that 1993/94 was representative of precipitation for Dartmoor from the past 19 years. Water table and water quality records from the mire should therefore represent a typical year at Tor Royal.

Representativeness of the remaining British mires

For the remaining British sites, annual precipitation levels for 1993 were between 96% and 117% of the 1961-1990 mean (Institute of Hydrology, 1994; Table 5.2). For August and September combined, when testate amoebae sampling was conducted, mean precipitation ranged between 48% and 122% of the 1961-1990 monthly means. However, these data

Site	Regional water authority	1993 precipitation as % of 1961-1990 annual means	Mean regional precipitation totals for August and September as % of 1961-1990 monthly means
Strathy Bogs	Highland R.P.B.	96.0	48.5
Coladoir Bog	Clyde R.P.B.	102.0	54.0
Dun Moss	Tay R.P.B.	117.0	83.0
Glasson Moss	North West (N.R.A.)	97.0	75.5
Butterburn Flow	Northumbria (N.R.A.)	113.0	122.0
Chartley Moss	Severn-Trent (N.R.A.)	111.0	107.0
Borth Bog	Welsh (N.R.A.)	104.0	88.5
Llyn Mire	Welsh (N.R.A.)	104.0	88.5

Table 5.2: Annual and mean rainfall during August and September 1993 (shown as percentages of the 1961-1990 means) in selected regions of Britain. For explanation, see text (source: Institute of Hydrology, 1994).

relate to the National Rivers Authority (N.R.A., now the Environment Agency) regions in England and Wales and from the River Purification Boards (R.P.B.) in Scotland. By their nature, these are extremely large geographical areas and the percentages in Table 5.2 represent general conditions across each region. They can be used as a general guide only and no direct connections can be made to individual sites.

5.3 Water tables

5.3.1 Water table fluctuations at each dipwell nest

Figure 5.6 illustrates the water table fluctuations recorded at each dipwell nest at Tor Royal throughout the monitoring programme. The water table depth for a given dipwell has been plotted against the number of days elapsed since the monitoring programme began (with day 1 representing 1st June 1993 and day 457 representing 29th September 1994), rather than a calendar date. This is because there were occasions (particularly during the winter of 1993/94) when more than 14 days elapsed between site visits due to poor weather conditions, although the period between site visits never exceeded 18 days. While this does not affect the water table records, it does affect the water chemistry sampling, which could only be conducted during site visits. Showing days elapsed illustrates clearly when these delays occurred and, since this style is used for the water chemistry graphs (see section 5.4.1), the same scale is also used in the water table graphs to maintain consistency in data presentation.

Table 5.3a details the mean, median and modal water table depths in all dipwells at Tor Royal for the year 1.6.93 - 31.5.94 and extended year 1.6.93 - 29.9.94. Table 5.3b summarises the mean, median and modal water table depths for individual seasons. For the purposes of this study, the seasons are defined as follows: summer 1993 (June - August 1993 inclusive); autumn 1993 (September - November 1993); winter 1993/94 (December 1993 - February 1994 inclusive); spring 1994 (March 1994 - May 1994 inclusive); summer

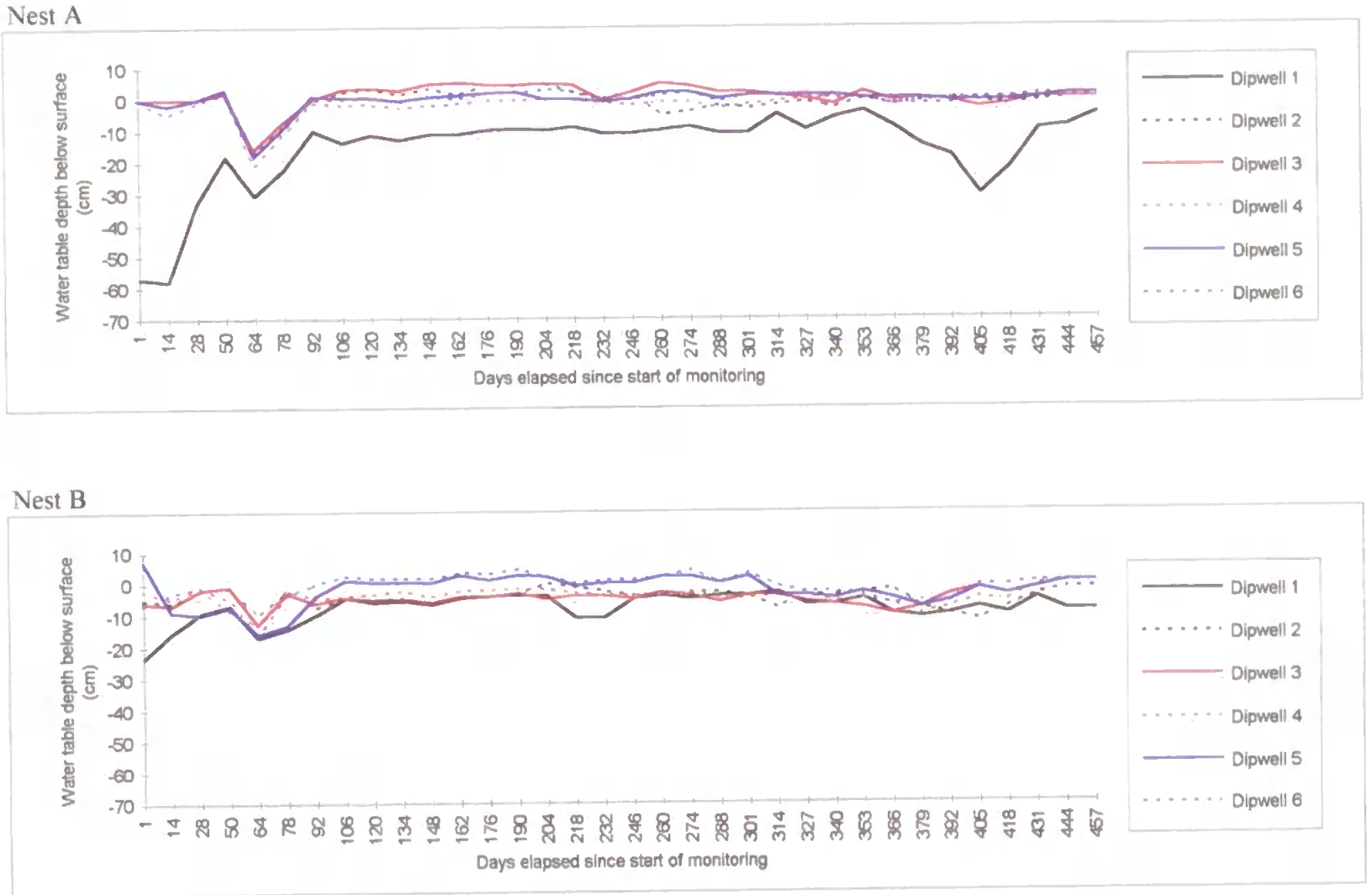
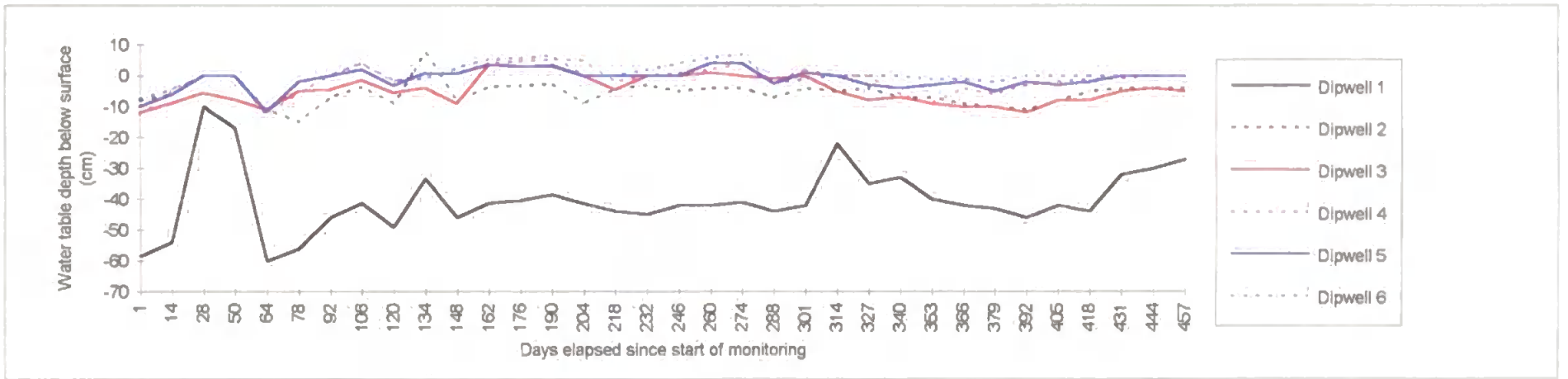


Figure 5.6a: Water table levels for nests A and B at Tor Royal, 1.6.93-31.5.94 (days 1-457).

Nest C



Nest D

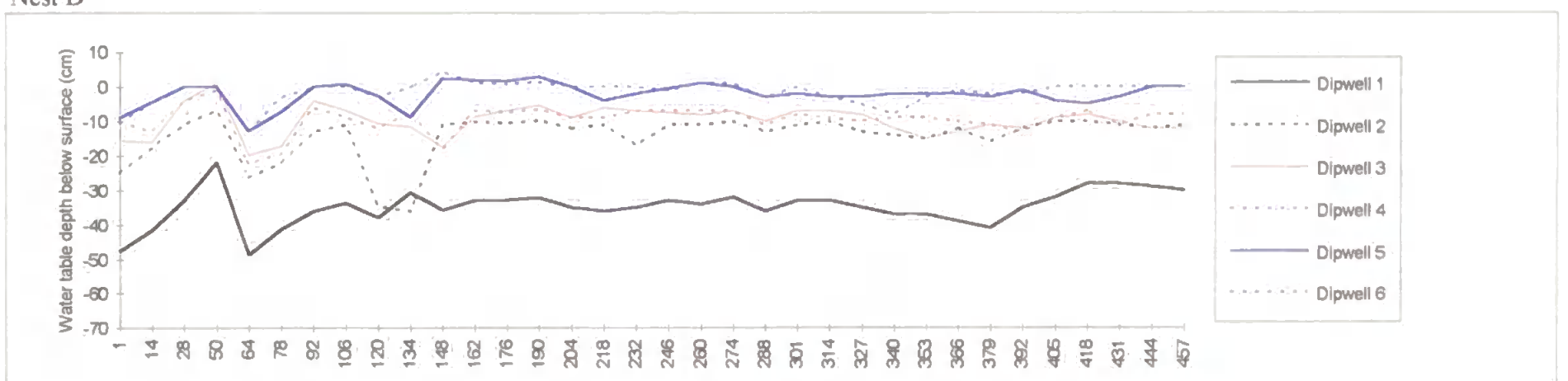


Figure 5.6b: Water table levels in nests C and D at Tor Royal: 1.6.93 - 29.9.94 (days 1 - 457).

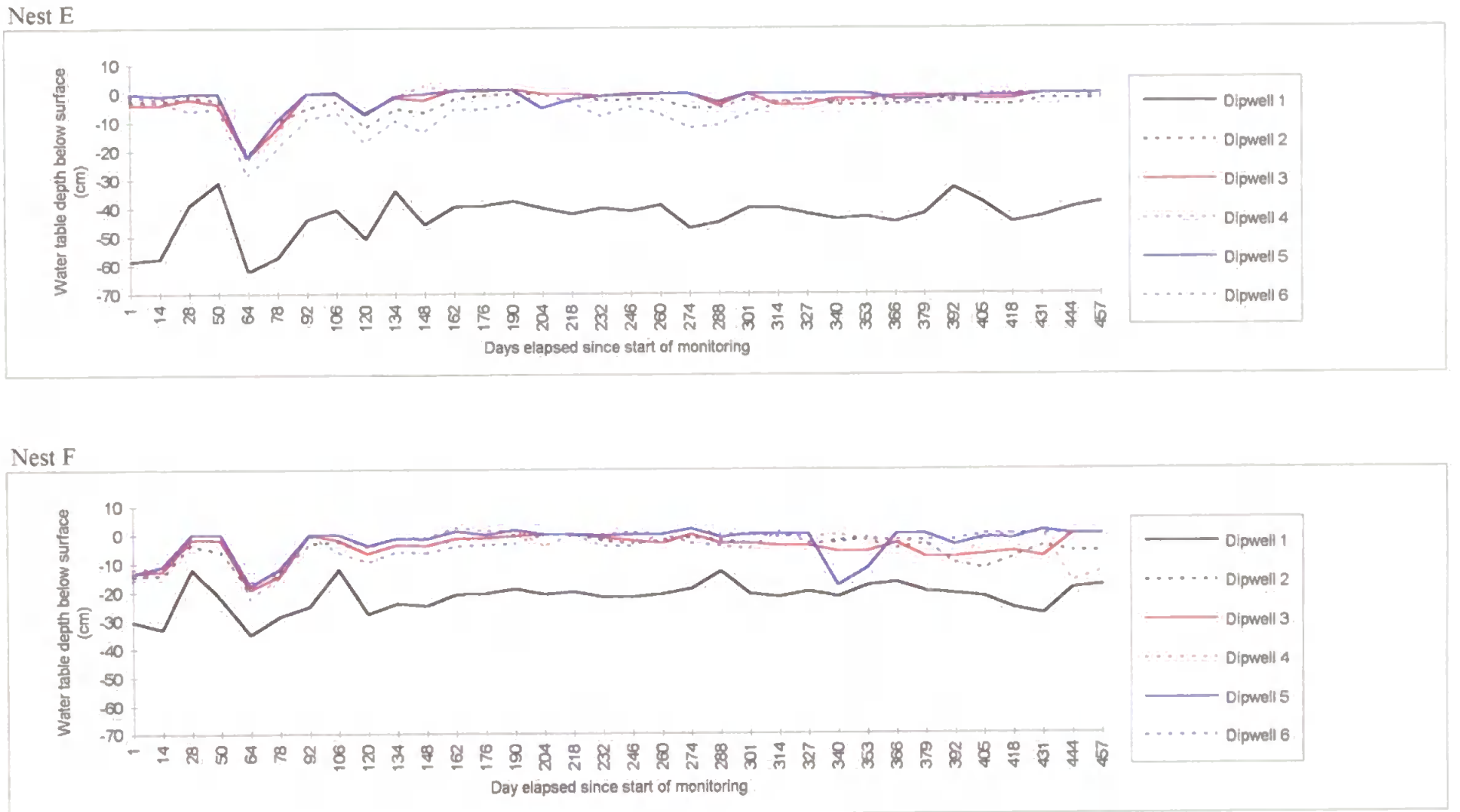


Figure 5.6c: Water table levels in nests E and F at Tor Royal: 1.6.93-29.9.94 (days 1 - 457).

Nest G

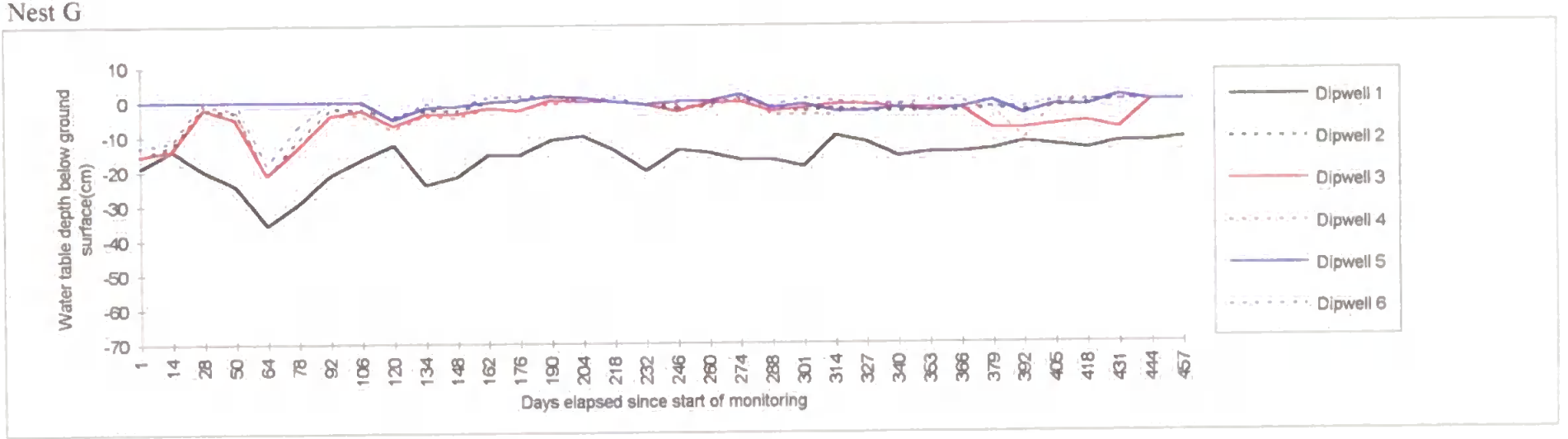


Figure 5.6d: Water table levels in nest G at Tor Royal: 1.6.93-29.9.94 (days 1 - 457).

Dipwell	Mean 1.6.93-31.5.94	Standard deviation	Median 1.6.93-31.5.94	Modal class 1.6.93-31.5.94	Range 1.6.93-31.5.94	min	max	Mean (1.6.93-29.9.94)	Standard deviation	Median (1.6.93-29.9.94)	Modal class (1.6.93-29.9.94)	Range 1.6.93-29.9.94	min	max
A1	-17.0	13.8	-11.0	9-10cm	53.0	-5.0	-58.0	-15.8	12.6	-11.0	10-11cm	53.0	-5.0	-58.0
A2	-0.4	4.6	0.0	0-1cm*	21.7	5.0	-16.7	-0.6	3.9	0.0	0-1cm	5.0	5.0	-21.7
A3	1.3	4.5	2.0	0-1cm*	21.3	5.3	-16.0	0.7	4.0	0.5	0-1cm*	5.3	5.3	-21.3
A4	-2.5	4.5	-1.1	0-1cm	22.5	1.5	-21.0	-1.8	4.0	-1.0	0-1cm	1.5	1.5	-22.5
A5	-0.5	4.3	0.5	0-1cm*	21.0	3.1	-17.9	-0.4	3.6	0.0	0-1cm	3.1	3.1	-21.0
A6	-0.5	4.4	0.2	0-1cm*	21.5	3.0	-18.5	-0.5	3.8	0.0	0-1cm	3.0	3.0	-21.5
B1	-7.9	5.1	-5.8	3-4cm	20.5	-3.0	-23.5	-8.0	4.4	-7.0	4-5cm	20.5	-3.0	-23.5
B2	-4.2	2.2	-4.0	3-4cm	10.0	0.0	-10.0	-4.5	2.7	-4.0	4-5cm	12.0	0.0	-12.0
B3	-4.8	2.2	-4.3	3-4cm	12.0	-1.0	-13.0	-4.7	2.6	-4.2	4-5cm	13.0	0.0	-13.0
B4	-4.0	2.4	-4.0	3-4cm	12.0	-1.0	-13.0	-4.2	2.7	-4.0	5-6cm	13.0	0.0	-13.0
B5	-1.9	5.4	0.1	2-3cm*	23.0	7.0	-16.0	-2.4	4.8	-0.5	0-1cm	23.0	7.0	-16.0
B6	-0.4	4.3	1.0	0-1cm*	20.5	4.5	-16.0	-1.1	4.1	0.0	0-1cm	20.5	4.5	-16.0
C1	-41.3	11.6	-42.0	41-42cm	50.1	-10.0	-60.1	-40.3	10.4	-42.0	42-43cm	50.1	-10.0	-60.1
C2	-4.9	4.2	-4.1	3-4cm	22.4	7.5	-14.9	-5.5	3.9	-5.0	3-4cm	22.4	7.5	-14.9
C3	-3.5	4.4	-4.3	0-1cm	15.5	3.5	-12.0	-4.7	4.4	-5.0	0-1cm	15.5	3.5	-12.0
C4	-0.3	4.7	0.0	0-1cm	18.4	5.4	-13.0	-1.2	4.4	0.0	0-1cm	18.4	5.4	-13.0
C5	-0.7	3.9	0.0	0-1cm	15.7	4.0	-11.7	-1.1	3.4	0.0	0-1cm	15.7	4.0	-11.7
C6	0.5	4.3	0.0	0-1cm*	18.4	7.0	-11.4	0.2	3.7	0.0	0-1cm*	18.4	7.0	-11.4
D1	-35.3	5.3	-34.5	32-33cm	26.8	-21.9	-48.7	-34.8	5.1	-34.5	32-33cm	26.8	-21.9	-48.7
D2	-15.2	7.7	-11.1	10-11cm	29.2	-6.8	-36.0	-14.3	6.7	-11.6	10-11cm	29.2	-6.8	-36.0
D3	-9.1	4.8	-7.8	6-7cm	20.8	1.0	-19.8	-9.8	4.3	-9.0	6-7cm	20.8	1.0	-19.8
D4	-9.4	4.7	-8.4	6-7cm	21.3	-1.0	-22.3	-9.5	4.0	-9.0	6-7cm	21.3	-1.0	-22.3
D5	-2.2	3.9	-1.3	0-1cm	15.6	2.8	-12.8	-2.2	3.4	-2.0	0-1cm	15.6	2.8	-12.8
D6	-1.5	3.7	0.0	0-1cm	17.2	4.4	-12.8	-1.5	3.4	0.0	0-1cm	17.2	4.4	-12.8
E1	-43.8	7.8	-40.7	39-40cm	31.1	-31.0	-62.1	-43.0	6.9	-41.5	39-40cm	31.1	-31.0	-62.1
E2	-4.1	4.6	-2.6	1-2cm	21.0	0.0	-21.0	-3.8	3.9	-2.6	1-2cm	21.0	0.0	-21.0
E3	-2.9	5.0	-1.3	0-1cm	23.8	1.5	-22.3	-2.3	4.3	-1.0	0-1cm	23.8	1.5	-22.3
E4	-2.2	5.6	0.0	0-1cm	26.5	2.7	-23.8	-1.9	4.8	0.0	0-1cm	26.5	2.7	-23.8
E5	-2.0	5.0	0.0	0-1cm	23.8	1.5	-22.3	-1.6	4.2	0.0	0-1cm	23.8	1.5	-22.3
E6	-8.1	6.3	-6.3	2-3cm	28.7	0.0	-28.7	-6.2	6.1	-4.3	2-3cm	28.7	0.0	-28.7
F1	-22.3	5.6	-21.5	20-21cm	22.9	-12.0	-34.9	-22.0	5.1	-21.0	20-21cm	22.9	-12.0	-34.9
F2	-4.8	5.1	-3.0	2-3cm	19.8	0.0	-19.8	-5.1	4.7	-3.5	2-3cm	19.8	0.0	-19.8
F3	-4.2	5.1	-2.5	0-1cm	19.1	0.0	-19.1	-4.5	4.6	-3.0	0-1cm	19.1	0.0	-19.1
F4	-2.4	5.1	0.0	0-1cm	19.2	2.5	-16.7	-3.1	5.5	-0.5	0-1cm	19.2	2.5	-16.7
F5	-2.4	5.2	0.0	0-1cm	19.9	2.0	-17.9	-2.7	5.5	0.0	0-1cm	19.9	2.0	-17.9
F6	-5.2	5.7	-4.0	0-1cm	23.3	1.0	-22.3	-4.0	5.2	-3.0	0-1cm	23.3	1.0	-22.3
G1	-17.8	6.0	-16.8	18-19cm	25.5	-10.0	-35.5	-16.5	5.5	-15.0	13-14cm	25.5	-10.0	-35.5
G2	-3.7	5.4	-2.0	1-2cm	22.8	1.8	-21.0	-3.1	4.7	-2.0	1-2cm	22.8	1.8	-21.0
G3	-4.4	5.5	-2.6	0-1cm	21.4	0.4	-21.0	-4.4	5.0	-2.6	2-3cm	21.4	0.4	-21.0
G4	-4.6	5.5	-3.1	3-4cm	22.0	1.0	-21.0	-3.8	5.0	-2.0	1-2cm	22.0	1.0	-21.0
G5	-0.6	1.6	0.0	0-1cm	7.1	2.0	-5.1	-0.8	1.6	-0.1	0-1cm	7.1	2.0	-5.1
G6	-2.2	5.0	0.0	0-1cm	19.9	2.0	-17.9	-1.7	4.3	0.0	0-1cm	19.9	2.0	-17.9

Table 5.3a: Mean, median, modal and ranges of water table depths for all dipwells at Tor Royal for the annual cycle (1.6.93-31.5.94) and extended annual cycle (1.6.93-29.9.94). All units in cm; * denotes level above ground.

Dipwell	Summer 1993 mean	Standard deviation	Summer 1993 median	Summer 1993 modal class (depth below surface)	Autumn 1993 mean	Standard deviation	Autumn 1993 median	Autumn 1993 modal class (depth below surface)	Winter 1993/94 mean	Standard deviation	Winter 1993/94 median	Winter 1993/94 modal class (depth below surface)	Spring 1994 mean	Standard deviation	Spring 1994 median	Spring 1994 modal class (depth below surface)	Summer 1994 mean	Standard deviation	Summer 1994 median	Summer 1994 modal class (depth below surface)
A1	-39.40	15.60	-33.00	#N/A	-13.65	4.10	-12.20	#N/A	-10.15	0.79	-10.00	9-10cm	-9.57	1.99	-10.00	10-11cm	-15.06	8.86	-15.00	#N/A
A2	-2.94	6.92	0.00	0-1cm*	0.43	4.08	2.00	#N/A	2.83	1.84	3.10	#N/A	-2.14	2.10	-2.00	1-2cm	-1.29	1.03	-1.00	0-1cm
A3	-2.80	6.65	0.00	0-1cm*	1.10	4.06	2.85	#N/A	3.87	1.98	4.50	4-5cm*	2.29	1.58	2.00	2-3cm*	-1.00	1.51	-1.00	2-3cm
A4	-5.10	8.24	-1.00	#N/A	-3.43	3.59	-1.85	#N/A	-0.58	0.54	-0.50	0-1cm*	-1.43	0.90	-1.00	1-2cm	-0.29	0.45	0.00	0-1cm
A5	-3.36	7.45	0.00	0-1cm*	-1.17	3.58	0.50	0-1cm*	0.70	1.12	0.60	0-1cm*	1.00	0.76	1.00	1-2cm*	-0.29	0.70	0.00	0-1cm
A6	-3.50	7.67	0.00	0-1cm*	-1.55	3.68	0.00	0-1cm*	1.50	1.14	1.80	0-1cm*	0.71	0.88	1.00	1-2cm*	-0.86	0.99	0.00	0-1cm
B1	-14.44	5.88	-15.50	#N/A	-7.82	3.33	-6.40	#N/A	-6.42	3.26	-4.45	10-11cm	-4.57	1.18	-4.00	4-5cm	-8.71	1.98	-10.00	10-11cm
B2	-4.80	3.19	-5.00	#N/A	-5.02	1.68	-4.90	#N/A	-2.58	1.52	-2.95	#N/A	-4.29	1.58	-4.00	4-5cm	-6.71	3.49	-8.00	8-9cm
B3	-5.80	4.26	-6.00	#N/A	-4.93	1.07	-5.00	#N/A	-4.08	0.52	-4.05	3-4cm	-4.57	1.05	-4.00	4-5cm	-6.14	2.64	-7.00	8-9cm
B4	-5.94	4.43	-5.00	#N/A	-3.47	1.01	-3.70	#N/A	-2.55	0.76	-2.30	2-3cm	-4.14	0.64	-4.00	4-5cm	-6.71	1.67	-6.00	5-6cm
B5	-7.06	7.60	-9.00	#N/A	-2.53	5.08	0.25	#N/A	1.18	1.33	1.50	#N/A	-0.29	2.49	0.00	2-3cm*	-4.71	1.83	-5.00	4-5cm
B6	-6.40	5.20	-5.00	#N/A	0.53	2.06	1.50	1-2cm*	2.30	1.49	2.50	#N/A	0.86	2.23	1.00	#N/A	-4.00	2.27	-4.00	6-7cm
C1	-39.92	21.78	-54.00	#N/A	-45.35	6.96	-46.00	45-46cm	-41.82	2.13	-41.40	#N/A	-38.29	7.15	-42.00	41-42cm	-41.43	3.85	-42.00	41-42cm
C2	-5.00	4.38	-6.00	0-1cm*	-5.83	6.84	-7.50	#N/A	-4.27	2.17	-3.40	#N/A	-4.71	1.03	-4.00	4-5cm	-8.14	1.88	-8.00	6-7cm
C3	-9.06	2.31	-9.00	#N/A	-4.92	2.23	-4.75	#N/A	0.82	2.81	1.50	2-3cm*	-1.86	3.09	0.00	0-1cm*	-9.14	1.55	-9.00	9-10cm
C4	-6.06	5.82	-4.50	0-1cm*	-0.33	3.04	0.30	#N/A	2.87	2.82	4.40	#N/A	1.00	1.77	1.00	2-3cm*	-4.43	2.56	-4.00	6-7cm
C5	-5.54	4.89	-6.00	0-1cm*	-0.28	1.77	0.35	#N/A	1.63	1.65	1.40	0-1cm*	0.50	2.58	0.00	0-1cm*	-3.00	1.07	-3.00	2-3cm
C6	-4.68	4.40	-4.50	0-1cm*	0.38	2.19	-0.50	#N/A	3.30	2.74	3.75	0-1cm*	1.93	3.43	0.00	0-1cm*	-0.57	0.73	0.00	0-1cm
D1	-38.52	10.00	-41.50	#N/A	-35.87	3.28	-35.85	#N/A	-34.00	1.40	-34.00	34-35cm	-33.71	1.28	-33.00	32-33cm	-35.57	4.07	-37.00	36-37cm
D2	-17.28	7.57	-17.50	#N/A	-21.28	10.57	-17.55	#N/A	-11.75	2.45	-10.80	#N/A	-11.29	1.16	-11.00	10-11cm	-12.71	2.19	-12.00	12-13cm
D3	-10.86	7.94	-15.50	#N/A	-11.28	4.95	-11.10	#N/A	-7.13	1.29	-6.90	#N/A	-7.79	0.99	-7.50	6-7cm	-11.43	2.19	-12.00	12-13cm
D4	-10.06	7.45	-10.00	#N/A	-11.95	5.11	-10.40	#N/A	-7.62	1.01	-7.15	6-7cm	-8.43	1.50	-8.00	6-7cm	-9.71	1.75	-9.00	9-10cm
D5	-5.26	5.03	-4.50	0-1cm*	-2.60	4.16	-1.35	#N/A	0.07	2.39	0.80	#N/A	-1.50	1.54	-2.00	3-4cm	-2.71	1.28	-2.00	2-3cm
D6	-5.56	5.29	-4.50	0-1cm*	-0.32	2.48	-0.15	0-1cm*	0.57	0.59	0.40	0-1cm*	-1.43	2.13	-1.00	1-2cm*	-2.29	2.55	-2.00	2-3cm
E1	-49.62	12.30	-57.50	#N/A	-45.33	7.35	-44.85	#N/A	-39.68	1.34	-39.75	39-40cm	-42.00	2.73	-41.00	39-40cm	-41.43	4.10	-43.00	45-46cm
E2	-6.10	7.49	-3.00	2-3cm	-6.93	3.15	-5.95	#N/A	-0.87	1.01	-0.35	0-1cm*	-3.00	1.31	-2.00	2-3cm	-3.43	0.90	-4.00	4-5cm
E3	-7.20	7.59	-4.00	3-4cm	-3.77	4.45	-1.90	#N/A	0.43	0.86	0.40	0-1cm*	-1.80	1.94	-0.50	0-1cm*	-1.57	0.49	-2.00	2-3cm
E4	-5.56	9.14	-1.00	0-1cm	-3.13	5.71	-0.60	#N/A	0.52	0.92	0.65	1-2cm*	-1.21	1.46	0.00	0-1cm*	-2.00	1.41	-2.00	3-4cm
E5	-4.66	8.83	0.00	0-1cm*	-2.85	3.92	-0.50	0-1cm*	-0.70	2.31	0.00	#N/A	-0.43	1.05	0.00	0-1cm*	-1.00	0.76	-1.00	1-2cm
E6	-9.00	9.96	-5.30	#N/A	-12.47	4.55	-11.45	#N/A	-4.32	2.49	-4.65	#N/A	-6.79	3.40	-7.00	6-7cm	-2.14	1.25	-2.00	3-4cm
F1	-26.54	8.45	-30.50	#N/A	-23.67	5.46	-24.90	#N/A	-20.58	0.93	-20.75	20-21cm	-19.71	2.91	-21.00	21-22cm	-20.86	2.75	-21.00	22-23cm
F2	-11.58	5.95	-14.00	#N/A	-5.38	3.76	-3.60	#N/A	-0.80	0.83	-0.60	0-1cm	-2.71	1.03	-3.00	3-4cm	-6.00	3.74	-5.00	2-3cm
F3	-9.70	6.91	-12.50	#N/A	-5.03	4.64	-3.65	#N/A	-0.63	0.51	-0.75	1-2cm	-2.71	1.28	-3.00	3-4cm	-6.29	1.58	-6.00	6-7cm
F4	-7.94	6.76	-11.00	0-1cm*	-3.23	4.58	-1.00	0-1cm*	0.25	2.10	0.65	0-1cm*	0.14	0.99	0.00	0-1cm*	-2.57	3.54	-2.00	2-3cm
F5	-8.48	7.27	-11.00	0-1cm*	-3.08	4.14	-1.40	0-1cm*	0.38	0.78	0.00	0-1cm*	0.14	0.83	0.00	0-1cm*	-5.20	6.45	-1.60	0-1cm
F6	-9.86	8.81	-11.00	0-1cm*	-7.07	4.43	-6.15	#N/A	-2.42	1.74	-3.25	3-4cm	-2.57	2.06	-3.00	3-4cm	-1.57	1.18	-2.00	3-4cm
G1	-22.56	7.25	-20.00	#N/A	-20.83	5.33	-21.35	#N/A	-14.33	3.25	-14.75	#N/A	-14.86	2.90	-15.00	16-17cm	-14.14	1.25	-14.00	15-16cm
G2	-10.80	7.31	-12.50	#N/A	-4.08	3.17	-2.55	#N/A	0.13	0.83	0.00	0-1cm*	-1.71	1.28	-2.00	2-3cm	-2.43	0.73	-3.00	3-4cm
G3	-11.48	7.02	-14.00	#N/A	-5.58	3.61	-3.80	#N/A	-0.83	1.08	-0.50	0-1cm*	-1.50	1.10	-1.00	3-4cm	-5.00	2.67	-6.00	2-3cm
G4	-10.66	7.77	-13.50	#N/A	-6.20	3.29	-4.30	3-4cm	-1.00	0.95	-0.75	0-1cm*	-2.14	1.81	-2.00	4-5cm	-2.71	3.45	-2.00	2-3cm
G5	0.00	0.00	0.00	0-1cm*	-1.32	1.84	-0.65	0-1cm*	0.30	0.82	0.25	#N/A	-1.00	1.69	-1.00	0-1cm*	-1.94	1.13	-2.00	2-3cm
G6	-8.48	7.24	-11.50	0-1cm*	-2.42	2.73	-1.00	#N/A	0.77	0.95	1.25	#N/A	0.07	1.08	0.00	0-1cm*	-0.71	0.88	0.00	0-1cm

Table 5.3b: Seasonal mean, median and modal water table depths for Tor Royal, 1.6.93-31.5.94. All units in cm (* denotes level above ground; #NA denotes no modal class).

Dipwell	Summer 1993 range	Minimum depth (summer 1993)	Maximum depth (summer 1993)	Autumn 1993 range	Minimum depth (autumn 1993)	Maximum depth (autumn 1993)	Winter 1993/94 range	Minimum depth (winter 1993/94)	Maximum depth (winter 1993/94)	Spring 1994 range	Minimum depth (spring 1994)	Maximum depth (spring 1994)	Summer 1994 range	Minimum depth (summer 1994)	Maximum depth (summer 1994)
A1	39.7	-18.3	-58	12.4	-10	-22.4	2.3	-9	-11.3	6	-5	-11	26.7	-4	-30.7
A2	18.7	2	-16.7	11.8	3.5	-8.3	5	5	0	7	2	-5	3	0	-3
A3	18	2	-16	12.2	4.8	-7.4	5.8	5.3	-0.5	5	5	0	5	2	-3
A4	22.5	1.5	-21	10.2	-1.2	-11.4	1.5	0	-1.5	3	0	-3	1	0	-1
A5	21	3.1	-17.9	10.1	1	-9.1	3.2	2.2	-1	2	2	0	2	1	-1
A6	21.5	3	-18.5	10.5	0.8	-9.7	3	3	0	3	2	-1	2	0	-2
B1	16.6	-6.9	-23.5	9.8	-4.5	-14.3	7.4	-3.6	-11	4	-3	-7	6	-5	-11
B2	9	-1	-10	5.5	-2	-7.5	4.3	0	-4.3	5	-3	-8	10	-2	-12
B3	12	-1	-13	3.2	-3	-6.2	1.8	-3.2	-5	3	-3	-6	8	-2	-10
B4	12	-1	-13	2.8	-2	-4.8	2.3	-1.7	-4	2	-3	-5	5	-5	-10
B5	23	7	-16	14.3	1	-13.3	3.6	2.6	-1	6	2	-4	6	-2	-8
B6	15	-1	-16	6.2	2.4	-3.8	4.5	4.5	0	7	4	-3	6	-1	-7
C1	50.1	-10	-60.1	22.8	-33.4	-56.2	6.4	-38.6	-45	22	-22	-44	13	-33	-46
C2	11	0	-11	22.4	7.5	-14.9	6.4	-2.6	-9	3	-4	-7	6	-5	-11
C3	6.5	-5.5	-12	7.5	-1.5	-9	8.1	3.5	-4.6	9	1	-8	5	-7	-12
C4	13	0	-13	10	4.3	-5.7	7.4	5.4	-2	6	4	-2	8	-1	-9
C5	11.7	0	-11.7	5.2	2	-3.2	3.6	3.6	0	7	4	-3	3	-2	-5
C6	11.4	0	-11.4	5.9	4.1	-1.8	6.7	6.7	0	9.5	7	-2.5	2	0	-2
D1	26.8	-21.9	-48.7	10.6	-30.7	-41.3	3.8	-32.2	-36	4	-32	-36	13	-28	-41
D2	19.3	-6.8	-26.1	25	-11	-36	7.3	-9.7	-17	3	-10	-13	6	-10	-16
D3	20.8	1	-19.8	13.5	-4	-17.5	3.6	-5.4	-9	3	-7	-10	7	-8	-15
D4	21.3	-1	-22.3	13.3	-6	-19.3	2.6	-6.4	-9	4	-7	-11	6	-7	-13
D5	12.8	0	-12.8	11.2	2.4	-8.8	6.8	2.8	-4	4	1	-3	4	-1	-5
D6	12.8	0	-12.8	7.6	4.4	-3.2	1.4	1.4	0	6	1	-5	8	0	-8
E1	31.1	-31	-62.1	23.2	-34	-57.2	4.5	-37.5	-42	8	-39	-47	12	-33	-45
E2	20	-1	-21	9.3	-2.7	-12	2.5	0	-2.5	3	-2	-5	2	-2	-4
E3	20.3	-2	-22.3	12.5	0.2	-12.3	2.5	1.5	-1	4.1	0	-4.1	1	-1	-2
E4	23.8	0	-23.8	16.7	2.7	-14	2.5	1.5	-1	3.5	0	-3.5	4	0	-4
E5	22.3	0	-22.3	9.8	0.5	-9.3	6.5	1.5	-5	3	0	-3	2	0	-2
E6	26.7	-2	-28.7	12.7	-6.6	-19.3	8	0	-8	10	-2	-12	4	0	-4
F1	22.9	-12	-34.9	16.6	-12	-28.6	3	-19	-22	9	-13	-22	9	-17	-26
F2	16.3	-3.5	-19.8	10.9	-2.4	-13.3	2	0	-2	3	-1	-4	10	-2	-12
F3	17.6	-1.5	-19.1	14.4	0	-14.4	1.3	0	-1.3	4	0	-4	5	-3	-8
F4	16.7	0	-16.7	12.9	0	-12.9	6.5	2.5	-4	3	2	-1	11	0	-11
F5	17.9	0	-17.9	11.9	0	-11.9	2.1	1.6	-0.5	3	2	-1	17.9	0	-17.9
F6	22.3	0	-22.3	14.7	0	-14.7	4	0	-4	6	1	-5	3	0	-3
G1	21.5	-14	-35.5	16.8	-12.5	-29.3	10	-10	-20	9	-10	-19	4	-12	-16
G2	19	-2	-21	9	-2	-11	2.8	1.8	-1	4	1	-3	2	-1	-3
G3	19	-2	-21	10.6	-2.5	-13.1	3	0.4	-2.6	3	0	-3	6	-2	-8
G4	20	-1	-21	9	-3.8	-12.8	2.4	0	-2.4	5	1	-4	11	0	-11
G5	0	0	0	5.3	0.2	-5.1	2.5	1.5	-1	5	2	-3	3.8	0	-3.8
G6	17.9	0	-17.9	7.3	0	-7.3	2.6	1.6	-1	3.5	2	-1.5	2	0	-2

Table 5.4: Seasonal water table ranges for all dipwells at Tor Royal, 1.6.93-29.9.94. All units in cm.

1994 (June 1994 - August 1994 inclusive). The water table ranges at Tor Royal for the same monitoring periods are summarised in Table 5.4. A great deal of data is presented in these tables but, for the purposes of this study, the following discussion will consider in detail only data which identifies periods when the water table depth was most representative of annual means or at least was relatively stable.

Calculating the sum of the differences between the mean annual (1.6.93-31.5.94) and mean seasonal water table depths and dividing this by the number of dipwells (42) indicates the factor difference between the seasonal and annual mean and median water table depth (Table 5.5). In terms of this study, water tables most representative of the June 1993/May 1994 means occurred during autumn 1993 (when water table depths differed by a factor of 0.03) and were slightly less representative during spring 1994 (difference = 0.04) and summer 1994 (difference = 0.04). By far the least representative season was summer 1993 (difference = 0.1) and reasons for this discrepancy are discussed in section 5.4.2 below.

Ranked representativeness relative to mean annual water table depth		**Ranked representativeness relative to median annual water table depth**	
Season	factor difference	Season	factor difference
Autumn 1993	0.03	Spring 1994	0.01
Spring 1994	0.04	Winter 1993/4	0.03
Summer 1994	0.04	Autumn 1993	0.04
Winter 1993/4	0.06	Summer 1994	0.05
Summer 1993	0.10	Summer 1993	0.14

Table 5.5: Representativeness of seasonal mean and median water table depths (1.6.93-29.9.94) relative to annual mean and median water table depths for Tor Royal (1.6.93-31.5.94) based on the factor difference. Seasons are ranked from most to least representative of the 1.6.93-31.5.94 mean and median water table depths. Data from all dipwells.

Dipwell	Summer 1993 range	Minimum depth (summer 1993)	Maximum depth (summer 1993)	Dipwell	Autumn 1993 range	Minimum depth (autumn 1993)	Maximum depth (autumn 1993)	Dipwell	Winter 1993/94 range	Minimum depth (winter 1993/94)	Maximum depth (winter 1993/94)	Dipwell	Spring 1994 range	Minimum depth (spring 1994)	Maximum depth (spring 1994)	Dipwell	Summer 1994 range	Minimum depth (summer 1994)	Maximum depth (summer 1994)
G5	0	0	0	B4	2.8	-2	-4.8	F3	1.3	0	-1.3	A5	2	2	0	A4	1	0	-1
C3	6.5	-5.5	-12	B3	3.2	-3	-6.2	D6	1.4	1.4	0	B4	2	-3	-5	E3	1	-1	-2
B2	9	-1	-10	C5	5.2	2	-3.2	A4	1.5	0	-1.5	A4	3	0	-3	A5	2	1	-1
C2	11	0	-11	G5	5.3	0.2	-5.1	B3	1.8	-3.2	-5	A6	3	2	-1	A6	2	0	-2
C6	11.4	0	-11.4	B2	5.5	-2	-7.5	F2	2	0	-2	B3	3	-3	-6	C6	2	0	-2
C5	11.7	0	-11.7	C6	5.9	4.1	-1.8	F5	2.1	1.6	-0.5	C2	3	-4	-7	E2	2	-2	-4
B3	12	-1	-13	B6	6.2	2.4	-3.8	A1	2.3	-9	-11.3	D2	3	-10	-13	E5	2	0	-2
B4	12	-1	-13	G6	7.3	0	-7.3	B4	2.3	-1.7	-4	D3	3	-7	-10	G2	2	-1	-3
D5	12.8	0	-12.8	C3	7.5	-1.5	-9	G4	2.4	0	-2.4	E2	3	-2	-5	G6	2	0	-2
D6	12.8	0	-12.8	D6	7.6	4.4	-3.2	E2	2.5	0	-2.5	E5	3	0	-3	A2	3	0	-3
C4	13	0	-13	G2	9	-2	-11	E3	2.5	1.5	-1	F2	3	-1	-4	C5	3	-2	-5
B6	15	-1	-16	G4	9	-3.8	-12.8	E4	2.5	1.5	-1	F4	3	2	-1	F6	3	0	-3
F2	16.3	-3.5	-19.8	E2	9.3	-2.7	-12	G5	2.5	1.5	-1	F5	3	2	-1	G5	3.8	0	-3.8
B1	16.6	-6.9	-23.5	B1	9.8	-4.5	-14.3	D4	2.6	-6.4	-9	G3	3	0	-3	D5	4	-1	-5
F4	16.7	0	-16.7	E5	9.8	0.5	-9.3	G6	2.6	1.6	-1	E4	3.5	0	-3.5	B4	4	0	-4
F3	17.6	-1.5	-19.1	C4	10	4.3	-5.7	G2	2.8	1.8	-1	G6	3.5	2	-1.5	E6	4	0	-4
F5	17.9	0	-17.9	A5	10.1	1	-9.1	A6	3	3	0	B1	4	-3	-7	G1	4	-12	-16
G6	17.9	0	-17.9	A4	10.2	-1.2	-11.4	F1	3	-19	-22	D1	4	-32	-36	A3	5	2	-3
A3	18	2	-16	A6	10.5	0.8	-9.7	G3	3	0.4	-2.6	D4	4	-7	-11	B4	5	-5	-10
A2	18.7	2	-16.7	D1	10.6	-30.7	-41.3	A5	3.2	2.2	-1	D5	4	1	-3	C3	5	-7	-12
G2	19	-2	-21	G3	10.6	-2.5	-13.1	B5	3.6	2.6	-1	F3	4	0	-4	F3	5	-3	-8
G3	19	-2	-21	F2	10.9	-2.4	-13.3	C5	3.6	3.6	0	G2	4	1	-3	B1	6	-5	-11
D2	19.3	-6.8	-26.1	D5	11.2	2.4	-8.8	D3	3.6	-5.4	-9	E3	4.1	0	-4.1	B5	6	-2	-8
E2	20	-1	-21	A2	11.8	3.5	-8.3	D1	3.8	-32.2	-36	A3	5	5	0	B6	6	-1	-7
G4	20	-1	-21	F5	11.9	0	-11.9	F6	4	0	-4	B2	5	-3	-8	C2	6	-5	-11
E3	20.3	-2	-22.3	A3	12.2	4.8	-7.4	B2	4.3	0	-4.3	G4	5	1	-4	D2	6	-10	-16
D3	20.8	1	-19.8	A1	12.4	-10	-22.4	B6	4.5	4.5	0	G5	5	2	-3	D4	6	-7	-13
A5	21	3.1	-17.9	E3	12.5	0.2	-12.3	E1	4.5	-37.5	-42	A1	6	-5	-11	G3	6	-2	-8
D4	21.3	-1	-22.3	E6	12.7	-6.6	-19.3	A2	5	5	0	B5	6	2	-4	D3	7	-8	-15
A6	21.5	3	-18.5	F4	12.9	0	-12.9	A3	5.8	5.3	-0.5	C4	6	4	-2	B3	8	-2	-10
G1	21.5	-14	-35.5	D4	13.3	-6	-19.3	C1	6.4	-38.6	-45	D6	6	1	-5	C4	8	-1	-9
E5	22.3	0	-22.3	D3	13.5	-4	-17.5	C2	6.4	-2.6	-9	F6	6	1	-5	D6	8	0	-8
F6	22.3	0	-22.3	B5	14.3	1	-13.3	E5	6.5	1.5	-5	A2	7	2	-5	F1	9	-17	-26
A4	22.5	1.5	-21	F3	14.4	0	-14.4	F4	6.5	2.5	-4	B6	7	4	-3	B2	10	-2	-12
F1	22.9	-12	-34.9	F6	14.7	0	-14.7	C6	6.7	6.7	0	C5	7	4	-3	F2	10	-2	-12
B5	23	7	-16	F1	16.6	-12	-28.6	D5	6.8	2.8	-4	E1	8	-39	-47	F4	11	0	-11
E4	23.8	0	-23.8	E4	16.7	2.7	-14	D2	7.3	-9.7	-17	C3	9	1	-8	G4	11	0	-11
E6	26.7	-2	-28.7	G1	16.8	-12.5	-29.3	B1	7.4	-3.6	-11	F1	9	-13	-22	B1	12	-33	-45
D1	26.8	-21.9	-48.7	C2	22.4	7.5	-14.9	C4	7.4	5.4	-2	G1	9	-10	-19	C1	13	-33	-46
E1	31.1	-31	-62.1	C1	22.8	-33.4	-56.2	E6	8	0	-8	C6	9.5	7	-2.5	D1	13	-28	-41
A1	39.7	-18.3	-58	E1	23.2	-34	-57.2	C3	8.1	3.5	-4.6	E6	10	-2	-12	F5	17.9	0	-17.9
C1	50.1	-10	-60.1	D2	25	-11	-36	G1	10	-10	-20	C1	22	-22	-44	A1	26.7	-4	-30.7

Table 5.6: Ranked water table ranges measured in dipwells at Tor Royal during summer 1993. Those with the smallest range are at the top of each list. All units in cm.

If water table data could not be collected during the autumn, then an alternative would be to sample when water tables are at least relatively stable, to avoid the influence of extreme values in the calculation of transfer functions. This relative stability can be derived from the range between the maximum and minimum seasonal water table depths recorded during the year 1.6.93-31.5.94 (Table 5.6). The overall seasonal range can be calculated from the difference between the largest and smallest dipwell range (Table 5.7).

At Tor Royal, water table levels were most stable during winter 1993/94, when the minimum water table depth range was 1.3 cm (dipwell F3) and the maximum range was 10 cm (dipwell G1), giving a seasonal range of 8.7 cm. During the remaining seasons, water tables were far less stable, with ranges of 20 cm (spring 1994); 22.2 cm (autumn 1993); 25.7 cm (summer 1994) and 50 cm (summer 1993). Again, summer 1993 presents as an extreme season; this is related to climate conditions during the period, which are discussed in section 5.3.3 below. From the ranges in Table 5.7 one can conclude that, if sampling was not possible during the autumn, then the next best season to sample would have been winter (preferably early, to benefit from representativeness during the autumn) when water tables were at least stable.

Season	Maximum water table depth range recorded by dipwells (cm)	Minimum water table depth range recorded by dipwells (cm)	Overall seasonal range (cm)
Winter 1993/94	10.0	1.3	8.7
Spring 1994	22.0	2.0	20.0
Autumn 1993	25.0	2.8	22.2
Summer 1994	26.7	1.0	25.7
Summer 1993	50.0	0.0	50.0

Table 5.7: Range of water table depths recorded by all dipwells at Tor Royal (1.6.93-29.9.94). Seasons are ranked from least to greatest water table depth range.

The isolated ranking of the summer 1993 mean water tables in Tables 5.6 and 5.7 emphasises the hazards of using the mean as a measure of central tendency. Extreme values (in this study, extraordinarily high or low water tables) can give rise to a misleading mean and Matthews (1981) suggests that of mean, median and modal measures, the mean is the most sensitive to extreme cases. Given this and the evidence of extreme water table levels (Figure 5.6), the median and mode would be more representative of normal water table depths throughout the year since they are less affected by extreme values. This was recognised by Tolonen *et al.* (1992), who used the averages of median water table depths for the three-year hydrological record at one of their study sites.

However, the nature of the monitoring programme rejects the use of modal values because, although the same water table depth in an individual dipwell may have been repeated occasionally during the monitoring programme, it was seldom repeated within a season; for several seasons, a modal value cannot be calculated (Table 5.3b).

Median values for water table depths recorded during the monitoring programme can be calculated to assess the relative stability and representativeness of the seasonal water tables, as for the mean figures (Table 5.3b), to give the same indication of optimum sampling seasons (Table 5.5). Based on median values, water table depths during spring 1994 were most representative of the 1993/94 annual median (difference = 0.01), followed by winter 1993/94 (difference = 0.03); autumn 1993 (difference = 0.04); summer 1994 (difference = 0.05) and summer 1993 (difference = 0.14). Again, summer 1993 is an extreme season.

Within each nest, the water table recorded in dipwell 1 (which was always located on the highest point in the nest) is conspicuously lower than the remaining 5 water tables (Figure 5.6). This is because water table levels were measured in terms of depth from the ground

surface. In nests C, D, E and F the difference between dipwell 1 and the remaining dipwells clearly reflects the height of the hummock in which dipwell 1 was located; the higher the hummock, the greater the difference in water table height between dipwell 1 and the remaining water tables. For example, the water tables for TRC1 and TRE1 (located on 35 cm and 40 cm-high hummocks respectively) consistently reach depths in excess of 50 cm and have an annual mean depth of -42.46 cm and -44.30 cm respectively. This gives a difference between dipwell 1 and dipwell 2 (located on the next highest point in the nest) of 37.43 cm and 40.05 cm respectively. Where the difference is less clear, it is a product of the lower hummocks in which dipwell 1 was placed; for example in nests A, B and G (8 cm, 7 cm and 7 cm high respectively - see Table 4.1, page 81), the differences in the water table depth between dipwells 1 and 2 is 18 cm, 4.38 cm and 16.42 cm respectively.

In terms of fluctuations, all water tables within a nest show the same general pattern - a fall in the level of one water table in a dipwell is generally replicated throughout the nest. Excluding the water table depth in dipwell 1 at each nest (see above), the remaining water tables in each nest all lie within 15-20 cm of the ground surface for most of the monitoring period (marked deviations from this pattern are discussed in section 5.3.3 below), suggesting that the water table is shallow across the areas of Tor Royal that were included in this study.

5.3.2 Water table fluctuations and the representativeness of fortnightly readings at Tor Royal Bog

Figure 5.7 shows daily precipitation and corresponding water table depth measured at the automatic monitoring station on Tor Royal up to day 179, when automatic recording was terminated (see section 5.1 above). Given the failure of the automatic water table recording programme, it is important to assess the representativeness of fortnightly water table readings as a measure of mean water table over the previous fortnight as a substitute.

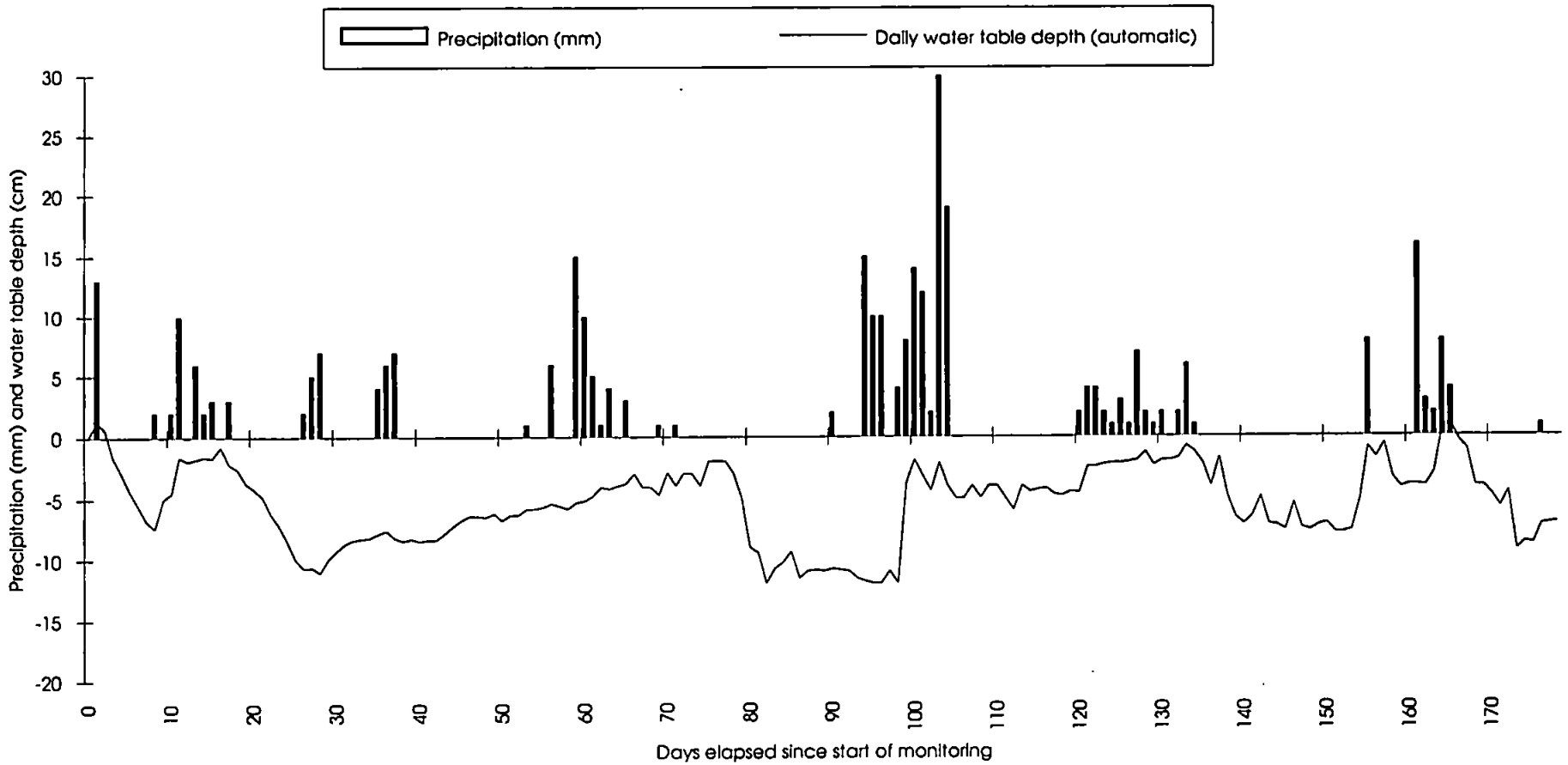


Figure 5.7: Automatically recorded daily water table depths and precipitation totals for dipwell C3, Tor Royal: days 1 to 179 inclusive.

Figure 5.8 compares daily water table readings with fortnightly measures between days 1 to 179 to illustrate how daily water table fluctuations are missed by fortnightly sampling. For example, between the sampling visits on day 0 and day 14, the daily records show that the water table rose from 0 cm to 0.6 cm above ground level, then deepened to a maximum depth of 7.4 cm, before recovering to 1.6 cm depth on day 14. In contrast, the fortnightly readings imply that the water table has dropped only 1.6 cm during the fortnight and the detailed movements remain undetected.

However, the transfer functions ultimately derived from this study will never be used to reconstruct fossil water tables over such a fine time-scale; the finest temporal resolution at which they could be applied would be for one to two-year reconstructions and even this resolution would require extremely thin slices of a fast-accumulating peat. In this respect, it is more important to establish the usefulness of daily and fortnightly water table measurements to calculate seasonal and annual means. Without a full year of daily recordings, this study cannot comment in terms of annual cycles but, at the seasonal level, data does exist for summer and autumn 1993 (Table 5.8).

	Summer 1993	Autumn 1993
Fortnightly mean water table depth (cm)	-9.06 (2s.e.=0.34)	-4.92 (2s.e.=0.72)
Daily mean water table depth (cm)	-7.71 (2s.e.=0.48)	-4.93 (2s.e.=0.78)

Table 5.8: Comparison of seasonal means calculated from daily and fortnightly water table records at dipwell C3, Tor Royal: days 1 to 179 inclusive (2s.e. = two standard errors).

The greatest difference between the daily and fortnightly means occurs during the summer 1993 season, reflecting water table response to evapotranspiration and sporadic precipitation events during this period. Short-term fluctuations detected by daily readings were missed

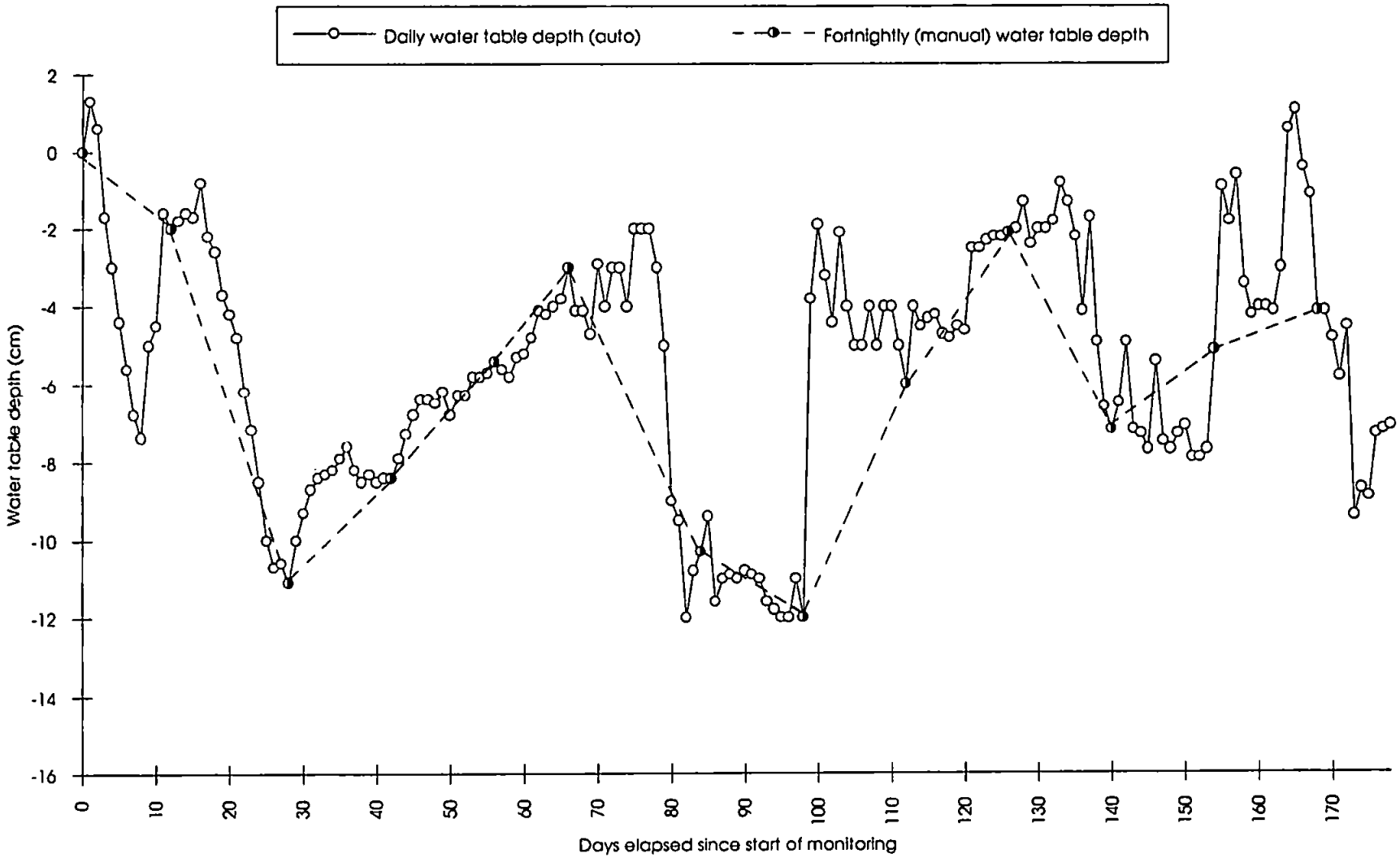


Figure 5.8: Comparison of water table table depths measured daily and fortnightly, days 1 to 179 inclusive.

by fortnightly sampling confirming that, during the summer season at least, daily water table records are more representative of hydrological conditions than are fortnightly readings. During the autumn season, when precipitation is less sporadic and evapotranspiration is less influential, the difference between daily and fortnightly records is minimal (Table 5.8) and the two recording intervals are equally representative (to 0.1 cm) of hydrological conditions at Tor Royal. This suggests that fortnightly readings are acceptable for water table reconstructions down to seasonal level. Further daily monitoring would be required to establish differences between daily and fortnightly means for the remaining seasons and for the annual cycle and also to establish whether the water table fluctuations on ombrotrophic bogs are sufficiently large to justify weekly, or more frequent, water table sampling.

5.3.3 Water table response to precipitation

For the first two weeks of monitoring, water table depth and precipitation events were measured at 15-minute intervals. These recordings showed steady changes within the 12 hour period, during which fluctuations were limited to mm of change, attaining a maximum range of 9 mm but generally lying within a 6 mm range. The effect of precipitation on the water table within the fortnight was limited, reflecting the relatively small amount (33 mm) of precipitation falling during the period. The events during the first two days of the monitoring programme clearly illustrate this. Precipitation began falling at Tor Royal at 14:30 on 1st June 1993 and stopped at 16:30. A total of 7.3 mm fell in this two-hour period and there was no detectable response in the water table during this time (Figure 5.9). At 18:45, 2¼ hours after the rainfall had stopped, the water table rose slightly (0.02 cm). A second precipitation event was recorded between 22:00 and 23:30, when 5.7 mm precipitation fell. During this time, the water table rose to 0.6 cm (at 00:15), then dropped to 0.32 cm by 02:45, where it remained for 8¼ hours. It then fell to 1.7 cm below ground between 11:00 and 17:45, remaining there until 00:00 on 3.6.93. Greater variations may

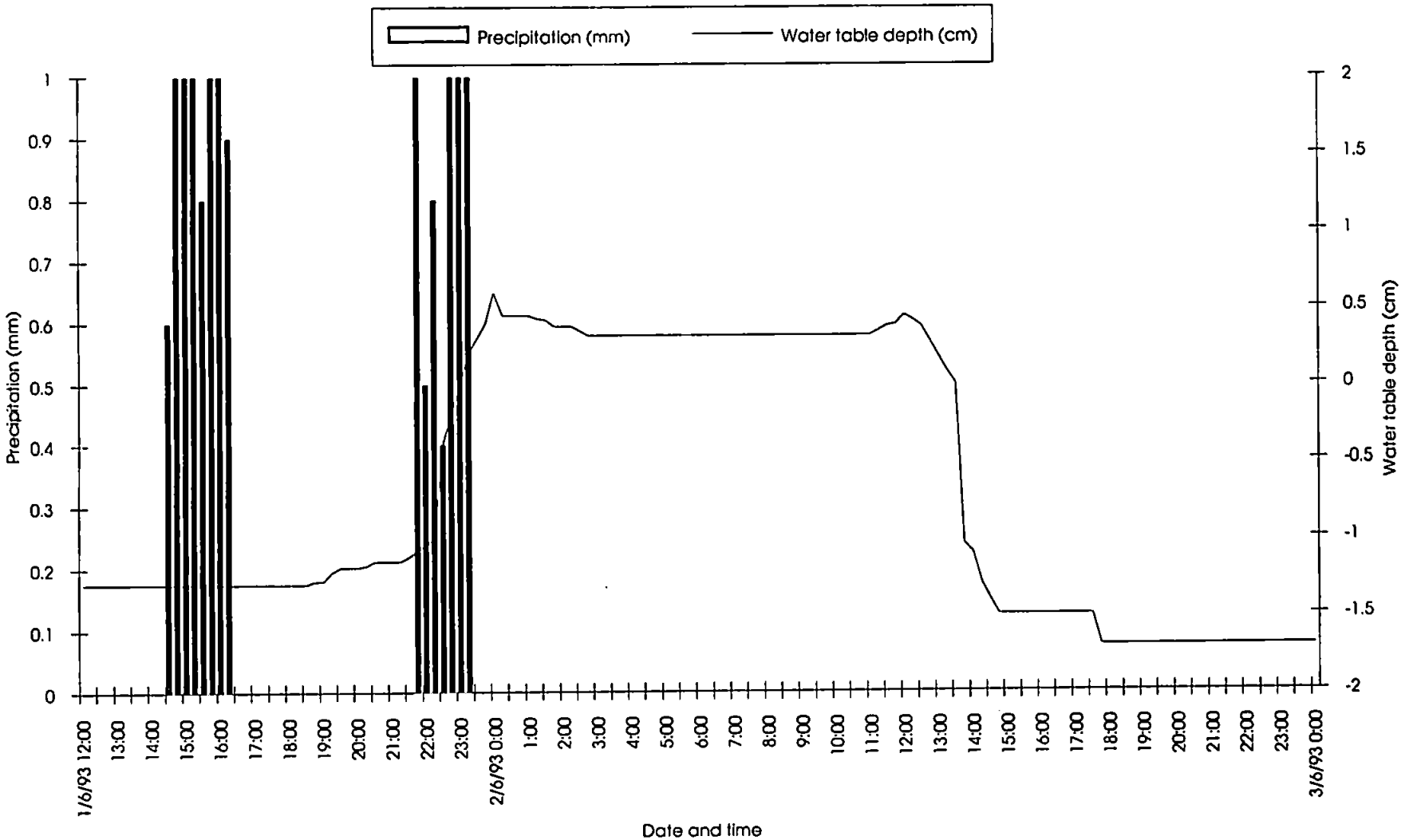


Figure 5.9: Precipitation (measured by raingauge) and water table depth (recorded by potentiometer) at 15 minute intervals, Tor Royal, 1st-2nd June 1993.

have occurred later in the monitoring programme and future work could focus on these short-term fluctuations. However, while this may be hydrologically interesting, it is probably of little relevance to the testate amoebae populations.

The delayed response of the water table to precipitation at Tor Royal between 1.6.93 and 2.6.93 may result from the relatively small amount of precipitation falling during that period, which may have been insufficient to have a significant effect on the water table depths. A second reason may be the structure of the peat, which has very small pore spaces and restricts infiltration of surface water. A third reason may be that surface water infiltrates slowly because the underlying peat is already saturated.

Such limited water table fluctuations at such a fine temporal scale result in 12-hourly readings which are very close to the mean of the 15 minute readings during the preceding 12 hours, and always within 1.5 cm of the calculated 24 hour mean (Table 5.9). Thus, 12-hourly readings are representative of the water table at Tor Royal and the large quantities of data generated by 96 15-minute readings in 24 hours can be reduced to a more manageable size.

Day	Mean of 15 minute readings to 12:00hrs (cm)	12:00 hrs reading (cm)	Mean of 15 minute readings to 00:00 hrs (cm)	00:00 hrs reading (cm)	Daily mean depth (cm)
1	*	*	-1.2	-1.3	-1.2
2	0.4	0.6	0.3	0.5	0.6
3	-1.9	-1.7	-1.4	-1.7	-1.7
4	-3.3	-3.3	-2.8	-3.0	-3.0
5	-5.6	-5.3	-3.0	-3.5	-4.4
6	-4.0	-3.8	-6.9	-7.4	-5.6
7	-6.9	-7.2	-6.2	-6.4	-6.8
8	-7.0	-7.4	-7.1	-7.4	-7.4
9	-3.6	-4.0	-5.7	-6.0	-5.0
10	-4.3	-4.8	-3.8	-4.2	-4.5
11	-1.0	-1.4	-2.1	-1.8	-1.6
12	-2.0	-1.9	-2.4	-2.1	-2.0
13	-1.8	-1.6	-1.7	-2.0	-1.8
14	-1.9	-1.6	-1.8	-1.6	-1.6

Table 5.9: Comparison of the means of 15-minute readings with the 12-hour reading collected on days 1-14 inclusive of the monitoring programme at Tor Royal.

On a daily time-scale (with two 12-hourly recordings), the water table does not always rise in response to precipitation input and fall when precipitation is absent (Figure 5.10). Between days 39 to 43, the water table actually rises 6.5 cm, despite 14 days without precipitation. In this respect, the lag time displayed by the water table in response to precipitation inputs is clearly affected by antecedent conditions. It is difficult to comment on the relationship beyond day 179 because only fortnightly readings are available, which do not give a sufficiently detailed resolution to assess daily lag times.

A Spearman's rank correlation on the daily water table depth and precipitation totals returns a very poor value of $r_s = 0.035$ ($p < 0.10$). For daily precipitation totals and water table depth on the following day, the correlation is slightly stronger at $r_s = 0.048$ ($p < 0.10$). This suggests that rainfall was not the primary control on water table depth at Tor Royal up to day 179 and that evapotranspiration was also influential.

A notable feature of both the daily and fortnightly water table levels at Tor Royal is the deepening of the water table between precipitation events, which is especially marked during the spring and summer months. It is highly probable that evaporative losses from standing surface water (especially from the large pool at nests F and G) and transpiration losses from the vegetation cover were significant controls on water table depths during the monitoring period. To derive an accurate value for evapotranspiration losses at Tor Royal would have required measurements of evapotranspiration rates, but this was not conducted. However there are a number of studies (Bavina, 1967; Neuhäusl, 1975 and Clymo, 1964) that have addressed specifically the derivation of absolute values for evapotranspirative losses from mires. An absolute comparison of these values between sites will always be difficult because an exact match between the species composition, relative abundance within the communities and between climatic conditions at two sites will not exist. The values expressed in the above studies, however, have been derived from similar

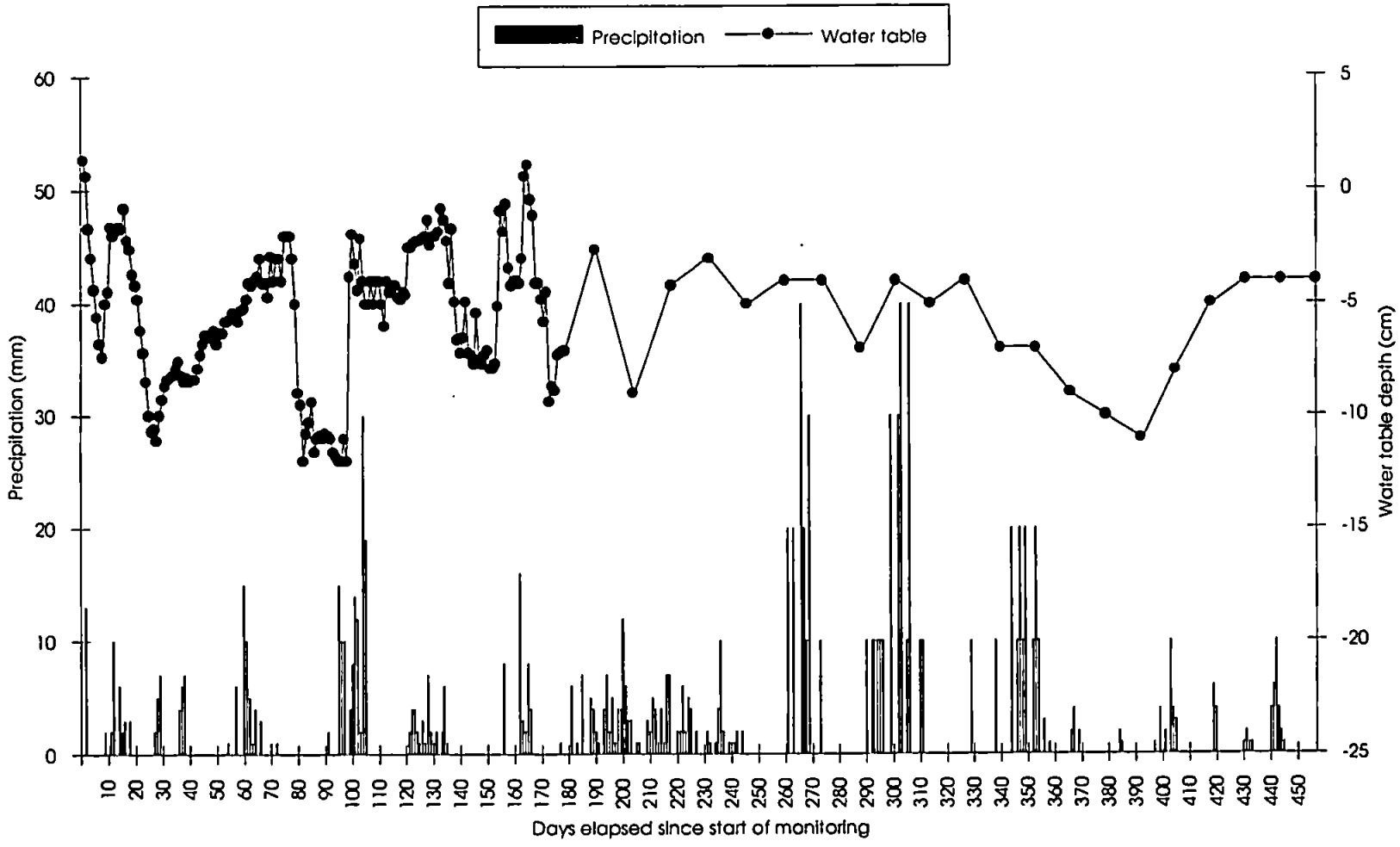


Figure 5.10: Precipitation and water table depth at Tor Royal, 1.6.93-29.9.94. Water table recorded automatically to day 179 and manually thereafter.

communities to those at Tor Royal and they may be tentatively applied to this work, with the above limitations.

Neuhäusl (1975) produced a set of estimates of daily stand transpiration rates associated with mire vegetation during the summer months which can be used to approximate transpiration losses at Tor Royal (Table 5.10).

	Moisture loss day^{-1}	Floristic community
Negligible transpiration but high evaporation from open water surfaces (E=Eo)	<1 mm	*S. cuspidatum* and *S. recurvum* stages of secondary succession in old peat cuttings.
Low evapotranspiration ($E<E_o$)	< 2 mm	*Eriophorum vaginatum*-*Sphagnum recurvum* stage of secondary succession in old peat cuttings: *S. magellanici* on primary, open mire expanse.
Moderate transpiration ($E=>E_o$)	2-4 mm	*Carex rostrata* stage of secondary succession.
High transpiration ($E>>E_o$)	>4 mm	Degraded successional stage following drainage of the mire expanse. *Vaccinium myrtillus* in *Picea abies* plantations on the mire expanse.

E is the evapotranspiration of the stand, E_o the evaporation from an extensive open water surface.

Table 5.10 : Estimates of daily evapotranspiration rates from vegetation stands. After Neuhäusl (1975).

Stands with negligible transpiration (up to 1 mm day^{-1}) are associated with *Sphagnum cuspidatum* and most of the moisture loss is from evaporation from open water surfaces; this accords well with nests C, F and G at Tor Royal. Of the 12 dipwells in nests F and G, 9 were located in an open pool and they give a clear indication of water table fluctuations at the nest (Figure 5.6). Both nests record a rapid drop in water table level between day 50 and day 64 (17th - 31st August), when the average temperature was 17°C. Boatman *et al.* (1975) found that, in dry periods, the water level in a pool on Brishie Bog in Galloway dropped by 0.6 cm day^{-1} and this was attributed to evaporation. During a

summer month when there were 15 dry days, a total of 9 cm of water was lost by evaporation. Belotserkovskaya *et al.* (1969, in Gore 1983) working on a raised mire near Leningrad found that evapotranspiration from pools exceeded that from ridges by up to 33% under average mid-summer conditions.

Water loss of the same magnitude was observed at Tor Royal in nests F and G between days 50 and 64, when the pool dried up completely, leaving a hardened crust on the bare peat surface. At this time, the average water table depth beneath this crust was 19 cm. When precipitation fell again, two days before sampling, the water table had shown little sign of recovery. This was probably due to the impermeability of the surface crust, which slowed infiltration rates into the peat, or there may have been insufficient precipitation during the event to make an impression on the water table depth.

Low transpiration rates (up to 2 mm day^{-1}) are characteristic of *Eriophorum vaginatum-Sphagnum recurvum* stands (Neuhäusl, 1975), equating with the *Eriophorum vaginatum* - dominated community at nests A, B, D and E.

During the summer months, water table deepening was particularly marked. Between days 3 and 9 and between days 17 and 26, the water table at nest C dropped 7.5 cm in 6 days and 10.5 cm in 8 days respectively probably as a result of evapotranspiration.

The rising water table between days 43 and 53 (in Figure 5.10) in the absence of precipitation is important because it may be a manifestation of the reaction of bog vegetation to deepening water tables in the previous 22 days. Bavina (1967) suggested that *Sphagnum* reacts to deepening water tables in summer by altering its colour as it dries out. This was noted on Tor Royal, where desiccated *Sphagnum cuspidatum* plants were pale green-white in colour compared to a deeper green hue characteristic of fully hydrated

individuals. The effect of a lighter colour is to increase the albedo of *S. cuspidatum* so that it reflects a greater proportion of incident radiation (Bavina, 1967). During the late summer and early autumn, senescence and death reduces transpiration. With less moisture being released from the system, the water table level may at least be maintained.

5.3.4 Implications for modern analogues and palaeoenvironmental reconstruction

Modern analogues

1. Testate amoebae sampling and hydrological monitoring were conducted at Tor Royal during a typical year in terms of climate conditions in the locality and across the Dartmoor region as a whole. The data are therefore free of complications introduced, for example, by unusually wet winters or unusually dry summers.

2. Data supplied to the author by researchers at the remaining British fields sites are for mean annual water table depths, so mean annual values from Tor Royal will be used for the remainder of this study to maintain a consistent data set. However, the use of median values as better representatives of annual conditions is recognised and their use as an alternative to mean values (e.g. Tolonen *et al.*, 1992) should be investigated in any future hydrological monitoring on ombrotrophic mires. This is because the latter may be less susceptible than the mean to extraordinary values.

3. Autumn is the most representative period of the year in which to sample using 'one-shot' techniques.

Palaeoecological reconstructions

1. Deriving annual mean water table depths from fortnightly readings means that seasonal conditions could potentially be derived in palaeoenvironmental

reconstructions. At present, however, the finest resolutions are likely to be for one to two-year periods.

2. Testate amoebae can be used with great confidence to derive transfer functions for mean annual water tables if the relationship between mean annual water table and species assemblages can be successfully modelled (see Chapters 6 and 7).

5.4 Water chemistry

The seasonal relationships between water chemistry and precipitation, and the effects on ombrotrophic mires, have been investigated by several authors (such as Malmer, 1962; Braekke, 1981; Gorham *et al.*,1985; Proctor, 1992; 1994). This is particularly relevant to this study's secondary objective of assessing the potential of testaceans as water chemistry indicators. As this study is restricted to ombrotrophic mires, an insufficient range of chemistry was sampled for definitive assessments to be made for other habitats (Chapter 6 and 7), but the seasonal fluctuations on an individual site (Tor Royal) are still relevant to the development of the technique in the future.

Following Sjors (1950), who suggested that in very acid waters (typical of ombrotrophic mires) most electrical conductivity is produced by H^+ ions, electrical conductivity readings were adjusted to compensate for the disproportionate contribution of H^+ ions. Removing this contribution gives a more accurate representation for the remaining salts, which is particularly important at Tor Royal where generally low concentrations of Ca^{2+}, Mg^{2+}, Cl^- and SO_4^{2-} are common. Conductivity readings were thus taken in the field, but later corrected for H^+ concentrations using the values given in Sjors (1950).

5.4.1 Results

The mean, median, mode and range of selected chemical ions at Tor Royal during the monitoring programme are presented in Tables 5.11 and 5.12. To allow a full evaluation of seasonal fluctuations in water chemistry at Tor Royal, the main concentration trends for each ion are identified separately in the section below in the following order: Ca^{2+}, Mg^{2+}, H^{+}, Cl^{-} No^{3-}, SO_4^{2-}, pH and electrical conductivity. From this, the trends can be evaluated within the wider context of mire water chemistry - particularly in relation to seasonal changes in precipitation and water table depth.

a) Calcium (Ca^{2+})

Over the extended monitoring period (29th June 1993 - 29th September 1994), Ca^{2+} concentrations at Tor Royal ranged from 0 mg l^{-1} (on days 64, 120 and 134 at nest F) to 1.88 mg l^{-1} (on day 260 at nest C). The mean annual concentration (29th June 1993-31st May 1994) for all seven nests was 0.56 mg l^{-1} Ca^{2+}, but there were three main phases of activity during the monitoring period (Figure 5.11). For the first 162 days, Ca^{2+} concentrations fluctuated markedly between a minimum of 0 mg l^{-1} and maximum of 1.02 mg l^{-} at all sampling nests. During the second phase, from day 176 to day 392, the fluctuations lay within a 0.5 mg l^{-1} range (approximately half those of the previous phase) and the mean Ca^{2+} concentration during this phase was approximately 0.5 mg l^{-1} higher (Ca^{2+} concentrations range from 0.5 mg l^{-1} to 1 mg l^{-1}). The anomaly in this pattern occurred on day 260, when Ca^{2+} concentrations rose markedly at nests A, B, C, D and E, while the rise was lower at nest G and concentrations fell at nest F. During the third phase, between day 392 and the end of the monitoring period on day 457, Ca^{2+} concentrations showed a similar magnitude of fluctuation to the first phase as values shifted between a maximum of 1.48 mg l^{-1} and a minimum of 0.6 mg l^{-1} (a range of 0.88 mg l^{-1}).

a) Ca^{2+}

	Mean (mg l^{-1}) 1.6.93-31.5.94	Standard deviation (mg l^{-1})	Median (mg l^{-1}) 1.6.93-31.5.94	Mode (mg l^{-1}) 1.6.93-31.5.94	Range (mg l^{-1}) 1.6.93-31.5.94	Maximum (mg l^{-1})	Minimum (mg l^{-1})	Mean (mg l^{-1}) 1.6.93-29.9.94	Standard deviation (mg l^{-1})	Median (mg l^{-1}) 1.6.93-29.9.94	Mode (mg l^{-1}) 1.6.93-29.9.94	Range (mg l^{-1}) 1.6.94-29.9.94	Maximum (mg l^{-1})	Minimum (mg l^{-1})
Nest A	0.64	0.39	0.58	0.29	1.66	1.66	0.00	0.72	0.40	0.72	0.29	1.66	0.00	1.66
Nest B	0.58	0.35	0.53	0.47	1.70	1.82	0.12	0.65	0.35	0.65	0.65	1.70	0.12	1.82
Nest C	0.56	0.37	0.48	0.45	1.75	1.88	0.13	0.64	0.35	0.59	0.45	1.75	0.13	1.88
Nest D	0.57	0.33	0.58	0.66	1.34	1.35	0.01	0.65	0.32	0.66	0.54	1.34	0.01	1.35
Nest E	0.54	0.36	0.55	0.76	1.27	1.29	0.02	0.57	0.33	0.61	0.76	1.27	0.02	1.29
Nest F	0.47	0.23	0.51	0.57	0.87	0.87	0.00	0.54	0.27	0.54	0.54	1.30	0.00	1.30
Nest G	0.48	0.26	0.43	0.16	0.89	1.00	0.11	0.55	0.27	0.55	0.42	1.01	0.11	1.12

b) Cl^-

	Mean (mg l^{-1}) 1.6.93-31.5.94	Standard deviation (mg l^{-1})	Median (mg l^{-1}) 1.6.93-31.5.94	Mode (mg l^{-1}) 1.6.93-31.5.94	Range (mg l^{-1}) 1.6.93-31.5.94	Maximum (mg l^{-1})	Minimum (mg l^{-1})	Mean (mg l^{-1}) 1.6.93-29.9.94	Standard deviation (mg l^{-1})	Median (mg l^{-1}) 1.6.93-29.9.94	Mode (mg l^{-1}) 1.6.93-29.9.94	Range (mg l^{-1}) 1.6.94-29.9.94	Maximum (mg l^{-1})	Minimum (mg l^{-1})
Nest A	10.33	3.51	10.73	11.00	14.35	15.80	1.45	11	3	10.73	15	14.35	1.45	15.80
Nest B	11.39	3.70	11.45	#N/A	18.41	20.00	1.59	11	3	10.60	10.6	18.41	1.59	20.00
Nest C	10.12	3.51	10.09	10.20	14.18	15.60	1.42	10	3	10.15	10.2	14.18	1.42	15.60
Nest D	11.14	3.85	10.55	10.00	15.87	17.30	1.43	11	3	11.00	10	15.87	1.43	17.30
Nest E	11.26	3.68	11.55	14.60	15.78	17.20	1.42	11	4	11.25	14.6	16.26	0.94	17.20
Nest F	10.68	3.69	11.15	#N/A	15.13	16.60	1.47	11	4	10.94	13.1	15.78	0.82	16.60
Nest G	10.91	3.99	11.35	16.50	15.46	16.90	1.44	11	4	11.14	16.5	16.03	0.87	16.90

c) Mg^{2+}

	Mean (mg l^{-1}) 1.6.93-31.5.94	Standard deviation (mg l^{-1})	Median (mg l^{-1}) 1.6.93-31.5.94	Mode (mg l^{-1}) 1.6.93-31.5.94	Range (mg l^{-1}) 1.6.93-31.5.94	Maximum (mg l^{-1})	Minimum (mg l^{-1})	Mean (mg l^{-1}) 1.6.93-29.9.94	Standard deviation (mg l^{-1})	Median (mg l^{-1}) 1.6.93-29.9.94	Mode (mg l^{-1}) 1.6.93-29.9.94	Range (mg l^{-1}) 1.6.94-29.9.94	Maximum (mg l^{-1})	Minimum (mg l^{-1})
Nest A	0.10	0.03	0.10	0.14	0.12	0.15	0.03	0.11	0.03	0.11	0.14	0.12	0.03	0.16
Nest B	0.08	0.04	0.07	0.07	0.14	0.16	0.02	0.09	0.04	0.09	0.14	0.14	0.02	0.16
Nest C	0.08	0.04	0.07	0.02	0.14	0.16	0.02	0.09	0.04	0.08	0.02	0.14	0.02	0.16
Nest D	0.07	0.03	0.07	0.07	0.15	0.15	0.00	0.07	0.03	0.08	0.08	0.15	0.00	0.15
Nest E	0.08	0.04	0.08	0.07	0.17	0.17	0.00	0.08	0.03	0.08	0.07	0.17	0.00	0.17
Nest F	0.09	0.04	0.08	0.06	0.14	0.17	0.02	0.09	0.03	0.08	0.09	0.14	0.02	0.17
Nest G	0.08	0.04	0.07	0.07	0.16	0.17	0.01	0.08	0.04	0.07	0.08	0.16	0.01	0.17

Table 5.11a-c: Mean, median, mode and ranges of selected chemical ion concentrations at Tor Royal for the annual cycle (1.6.93-31.5.94) and extended annual cycle (1.6.93-29.9.94).

d) SO_4^{2-}

	Mean (mg l^{-1}) 1.6.93-31.5.94	Standard deviation (mg l^{-1})	Median (mg l^{-1}) 1.6.93-31.5.94	Mode (mg l^{-1}) 1.6.93-31.5.94	Range (mg l^{-1}) 1.6.93-31.5.94	Maximum (mg l^{-1})	Minimum (mg l^{-1})	Mean (mg l^{-1}) 1.6.93-29.9.94	Standard deviation (mg l^{-1})	Median (mg l^{-1}) 1.6.93-29.9.94	Mode (mg l^{-1}) 1.6.93-29.9.94	Range (mg l^{-1}) 1.6.94-29.9.94	Maximum (mg l^{-1})	Minimum (mg l^{-1})
Nest A	4.39	2.36	3.88	3.75	12.25	13.40	1.15	5.00	2.41	4.34	3.75	12.25	13.40	1.15
Nest B	4.03	2.34	3.52	3.50	12.08	13.40	1.32	4.60	2.34	4.21	3.50	12.08	13.40	1.32
Nest C	3.71	2.36	3.43	#N/A	12.25	13.50	1.25	4.11	2.20	3.76	4.00	12.25	13.50	1.25
Nest D	4.09	1.98	3.77	4.00	10.18	11.50	1.32	4.48	1.95	3.94	4.00	10.18	11.50	1.32
Nest E	3.74	1.07	3.80	3.80	5.22	6.65	1.43	4.01	1.39	3.80	3.80	6.97	8.40	1.43
Nest F	3.87	1.73	3.55	4.30	8.46	9.73	1.27	4.17	1.73	3.71	4.30	8.46	9.73	1.27
Nest G	3.38	1.44	3.40	1.94	6.17	7.48	1.31	3.62	1.58	3.34	1.94	6.41	7.72	1.31

e) pH

	Mean 1.6.93-31.5.94	Standard deviation	Median 1.6.93-31.5.94	Mode 1.6.93-31.5.94	Range 1.6.93-31.5.94	Maximum	Minimum	Mean 1.6.93-29.9.94	Standard deviation	Median 1.6.93-29.9.94	Mode 1.6.93-29.9.94	Range 1.6.94-29.9.94	Maximum	Minimum
Nest A	4.71	0.17	4.76	4.80	0.70	5.00	4.30	4.58	0.25	4.60	4.80	0.80	4.20	5.00
Nest B	4.63	0.19	4.65	4.70	0.94	5.04	4.10	4.51	0.25	4.60	4.70	0.94	4.10	5.04
Nest C	4.48	0.23	4.48	4.40	0.90	4.90	4.00	4.43	0.22	4.40	4.40	0.90	4.00	4.90
Nest D	4.50	0.28	4.50	4.40	1.03	4.93	3.90	4.45	0.26	4.40	4.40	1.03	3.90	4.93
Nest E	4.50	0.28	4.47	4.80	1.00	5.00	4.00	4.45	0.25	4.40	4.40	1.00	4.00	5.00
Nest F	4.40	0.27	4.30	4.20	0.90	4.90	4.00	4.38	0.23	4.30	4.20	0.90	4.00	4.90
Nest G	4.52	0.20	4.50	4.40	0.80	4.80	4.00	4.47	0.19	4.45	4.40	0.80	4.00	4.80

f) Conductivity (μScm^{-1})

	Mean (μScm^{-1}) 1.6.93-31.5.94	Standard deviation (μScm^{-1})	Median (μScm^{-1}) 1.6.93-31.5.94	Mode (μScm^{-1}) 1.6.93-31.5.94	Range (μScm^{-1}) 1.6.93-31.5.94	Maximum (μScm^{-1})	Minimum (μScm^{-1})	Mean (μScm^{-1}) 1.6.93-29.9.94	Standard deviation (μScm^{-1})	Median (μScm^{-1}) 1.6.93-29.9.94	Mode (μScm^{-1}) 1.6.93-29.9.94	Range (μScm^{-1}) 1.6.94-29.9.94	Maximum (μScm^{-1})	Minimum (μScm^{-1})
Nest A	41.53	12.85	41.95	#N/A	57.40	67.50	10.10	41.43	11.05	41.95	#N/A	57.40	10.10	67.50
Nest B	43.92	11.58	44.30	#N/A	46.60	66.20	19.60	44.37	10.25	44.60	44.20	46.60	19.60	66.20
Nest C	39.78	11.51	39.10	#N/A	39.30	61.50	22.20	39.89	10.31	39.45	#N/A	39.30	22.20	61.50
Nest D	46.75	19.33	44.95	#N/A	83.20	92.60	9.40	47.26	16.33	47.25	#N/A	83.20	9.40	92.60
Nest E	49.28	11.19	50.65	#N/A	47.90	70.20	22.30	48.65	9.50	48.70	48.40	47.90	22.30	70.20
Nest F	41.65	14.74	40.50	40.50	61.20	77.20	16.00	44.55	13.38	43.60	40.50	61.20	16.00	77.20
Nest G	45.99	16.42	39.75	34.30	72.10	85.50	13.40	49.39	14.89	53.20	34.30	72.10	13.40	85.50

Table 5.11d-f: Mean, median, mode and ranges of selected chemical ion concentrations at Tor Royal for the annual cycle (1.6.93-31.5.94) and extended annual cycle (1.6.93-29.9.94).

a) Ca^{2+}

	Summer 1993 mean ($mg\ l^{-1}$)	Standard deviation ($mg\ l^{-1}$)	Summer 1993 median ($mg\ l^{-1}$)	Summer 1993 mode ($mg\ l^{-1}$)	Autumn 1993 mean ($mg\ l^{-1}$)	Standard deviation ($mg\ l^{-1}$)	Autumn 1993 median ($mg\ l^{-1}$)	Autumn 1993 mode ($mg\ l^{-1}$)	Winter 1993/94 mean ($mg\ l^{-1}$)	Standard deviation ($mg\ l^{-1}$)	Winter 1993/94 median ($mg\ l^{-1}$)	Winter 1993/94 mode ($mg\ l^{-1}$)	Spring 1994 mean ($mg\ l^{-1}$)	Standard deviation ($mg\ l^{-1}$)	Spring 1994 median ($mg\ l^{-1}$)	Spring 1994 mode ($mg\ l^{-1}$)	Summer 1994 mean ($mg\ l^{-1}$)	Standard deviation ($mg\ l^{-1}$)	Summer 1994 median ($mg\ l^{-1}$)	Summer 1994 mode ($mg\ l^{-1}$)
Nest A	0.35	0.10	0.34	#N/A	0.36	0.29	0.29	0.29	0.60	0.18	0.62	#N/A	1.13	0.24	1.04	#N/A	0.87	0.30	0.88	#N/A
Nest B	0.50	0.18	0.47	0.71	0.37	0.31	0.25	#N/A	0.52	0.13	0.49	#N/A	0.89	0.41	0.67	0.65	0.80	0.21	0.77	#N/A
Nest C	0.37	0.16	0.45	0.53	0.38	0.27	0.30	#N/A	0.46	0.12	0.47	#N/A	0.93	0.42	0.87	#N/A	0.78	0.22	0.76	#N/A
Nest D	0.47	0.39	0.24	#N/A	0.31	0.24	0.33	#N/A	0.59	0.15	0.57	#N/A	0.84	0.25	0.78	0.66	0.83	0.14	0.87	0.98
Nest E	0.29	0.25	0.28	#N/A	0.21	0.15	0.20	0.06	0.62	0.13	0.61	#N/A	0.95	0.22	0.97	0.76	0.65	0.14	0.65	0.54
Nest F	0.41	0.25	0.47	#N/A	0.41	0.29	0.45	#N/A	0.49	0.18	0.42	0.42	0.55	0.12	0.57	#N/A	0.64	0.21	0.54	0.54
Nest G	0.40	0.24	0.38	#N/A	0.31	0.23	0.18	#N/A	0.44	0.12	0.42	#N/A	0.71	0.21	0.72	#N/A	0.69	0.20	0.63	#N/A

b) Mg^{2+}

	Summer 1993 mean ($mg\ l^{-1}$)	Standard deviation ($mg\ l^{-1}$)	Summer 1993 median ($mg\ l^{-1}$)	Summer 1993 mode ($mg\ l^{-1}$)	Autumn 1993 mean ($mg\ l^{-1}$)	Standard deviation ($mg\ l^{-1}$)	Autumn 1993 median ($mg\ l^{-1}$)	Autumn 1993 mode ($mg\ l^{-1}$)	Winter 1993/94 mean ($mg\ l^{-1}$)	Standard deviation ($mg\ l^{-1}$)	Winter 1993/94 median ($mg\ l^{-1}$)	Winter 1993/94 mode ($mg\ l^{-1}$)	Spring 1994 mean ($mg\ l^{-1}$)	Standard deviation ($mg\ l^{-1}$)	Spring 1994 median ($mg\ l^{-1}$)	Spring 1994 mode ($mg\ l^{-1}$)	Summer 1994 mean ($mg\ l^{-1}$)	Standard deviation ($mg\ l^{-1}$)	Summer 1994 median ($mg\ l^{-1}$)	Summer 1994 mode ($mg\ l^{-1}$)
Nest A	0.12	0.02	0.11	#N/A	0.09	0.02	0.10	#N/A	0.06	0.02	0.06	#N/A	0.13	0.02	0.13	#N/A	0.11	0.03	0.11	#N/A
Nest B	0.07	0.04	0.06	#N/A	0.06	0.02	0.07	#N/A	0.05	0.01	0.05	#N/A	0.12	0.03	0.13	#N/A	0.12	0.01	0.11	0.11
Nest C	0.05	0.02	0.05	#N/A	0.06	0.03	0.07	#N/A	0.06	0.01	0.06	#N/A	0.14	0.02	0.14	#N/A	0.11	0.03	0.11	#N/A
Nest D	0.05	0.02	0.04	#N/A	0.07	0.03	0.08	#N/A	0.05	0.02	0.05	0.04	0.11	0.03	0.11	#N/A	0.07	0.02	0.07	0.08
Nest E	0.08	0.01	0.08	#N/A	0.08	0.04	0.09	0.08	0.05	0.02	0.05	#N/A	0.12	0.04	0.12	#N/A	0.09	0.01	0.08	#N/A
Nest F	0.09	0.01	0.09	#N/A	0.07	0.03	0.07	#N/A	0.05	0.02	0.06	#N/A	0.13	0.03	0.13	#N/A	0.09	0.03	0.08	0.08
Nest G	0.11	0.04	0.11	#N/A	0.07	0.02	0.07	#N/A	0.03	0.02	0.02	#N/A	0.10	0.03	0.10	#N/A	0.08	0.01	0.07	#N/A

c) Cl^{-}

	Summer 1993 mean ($mg\ l^{-1}$)	Standard deviation ($mg\ l^{-1}$)	Summer 1993 median ($mg\ l^{-1}$)	Summer 1993 mode ($mg\ l^{-1}$)	Autumn 1993 mean ($mg\ l^{-1}$)	Standard deviation ($mg\ l^{-1}$)	Autumn 1993 median ($mg\ l^{-1}$)	Autumn 1993 mode ($mg\ l^{-1}$)	Winter 1993/94 mean ($mg\ l^{-1}$)	Standard deviation ($mg\ l^{-1}$)	Winter 1993/94 median ($mg\ l^{-1}$)	Winter 1993/94 mode ($mg\ l^{-1}$)	Spring 1994 mean ($mg\ l^{-1}$)	Standard deviation ($mg\ l^{-1}$)	Spring 1994 median ($mg\ l^{-1}$)	Spring 1994 mode ($mg\ l^{-1}$)	Summer 1994 mean ($mg\ l^{-1}$)	Standard deviation ($mg\ l^{-1}$)	Summer 1994 median ($mg\ l^{-1}$)	Summer 1994 mode ($mg\ l^{-1}$)
Nest A	10.66	3.16	9.05	#N/A	8.10	3.26	9.00	#N/A	11.79	4.75	13.60	#N/A	10.74	0.70	10.65	#N/A	11.45	2.00	10.20	#N/A
Nest B	12.18	4.62	9.30	#N/A	7.60	3.26	9.12	#N/A	14.32	0.79	14.30	#N/A	11.57	1.42	11.80	#N/A	11.04	1.58	10.40	10.60
Nest C	9.58	2.20	9.85	#N/A	6.43	3.13	6.25	#N/A	14.47	0.95	14.40	15.60	9.95	1.22	9.70	#N/A	10.77	1.82	10.10	#N/A
Nest D	9.65	1.81	9.40	#N/A	7.06	3.06	8.07	#N/A	15.50	1.43	15.75	#N/A	11.98	2.39	12.20	#N/A	11.88	1.46	11.70	#N/A
Nest E	10.17	3.43	8.95	#N/A	7.89	3.64	9.90	#N/A	15.33	1.26	15.05	14.60	11.44	0.62	11.60	11.00	12.09	1.73	10.80	#N/A
Nest F	10.39	3.26	9.58	#N/A	6.31	3.38	7.51	#N/A	13.90	1.15	13.60	#N/A	11.89	1.20	11.50	#N/A	12.03	2.09	10.88	#N/A
Nest G	13.24	2.62	14.42	#N/A	6.00	3.72	5.58	#N/A	14.07	1.96	13.45	#N/A	10.75	1.17	10.65	#N/A	11.52	1.51	10.98	#N/A

Table 5.12a-c: Seasonal mean, median, mode and ranges of selected chemical ion concentrations at Tor Royal for the annual cycle (1.6.93-31.5.94) and extended annual cycle (1.6.93-29.9.94).

d) SO_4^{2-}

	Summer 1993 mean ($mg\ l^{-1}$)	Standard deviation ($mg\ l^{-1}$)	Summer 1993 median ($mg\ l^{-1}$)	Summer 1993 mode ($mg\ l^{-1}$)	Autumn 1993 mean ($mg\ l^{-1}$)	Standard deviation ($mg\ l^{-1}$)	Autumn 1993 median ($mg\ l^{-1}$)	Autumn 1993 mode ($mg\ l^{-1}$)	Winter 1993/94 mean ($mg\ l^{-1}$)	Standard deviation ($mg\ l^{-1}$)	Winter 1993/94 median ($mg\ l^{-1}$)	Winter 1993/94 mode ($mg\ l^{-1}$)	Spring 1994 mean ($mg\ l^{-1}$)	Standard deviation ($mg\ l^{-1}$)	Spring 1994 median ($mg\ l^{-1}$)	Spring 1994 mode ($mg\ l^{-1}$)	Summer 1994 mean ($mg\ l^{-1}$)	Standard deviation ($mg\ l^{-1}$)	Summer 1994 median ($mg\ l^{-1}$)	Summer 1994 mode ($mg\ l^{-1}$)
Nest A	3.98	0.21	3.95	#N/A	3.71	0.65	3.73	#N/A	2.77	1.01	3.04	#N/A	6.65	3.14	4.80	#N/A	7.32	1.45	7.50	#N/A
Nest B	3.61	0.37	3.50	#N/A	3.75	0.36	3.61	3.50	2.12	0.54	2.31	#N/A	6.22	3.18	4.98	#N/A	6.35	1.76	7.20	#N/A
Nest C	3.30	0.29	3.30	#N/A	3.45	0.60	3.60	#N/A	2.00	0.52	2.33	#N/A	5.69	3.45	4.00	#N/A	5.14	1.56	4.50	#N/A
Nest D	3.70	0.23	3.76	#N/A	4.15	0.79	3.88	#N/A	2.41	0.77	2.82	#N/A	5.75	2.65	4.60	4.05	5.64	1.72	6.20	#N/A
Nest E	3.87	0.29	3.80	#N/A	3.98	0.39	3.83	#N/A	2.36	0.67	2.68	#N/A	4.63	0.93	4.71	4.71	5.18	1.92	4.10	#N/A
Nest F	3.68	0.38	3.47	#N/A	4.43	0.98	4.23	#N/A	2.18	0.60	2.41	#N/A	4.98	2.24	3.76	#N/A	5.31	1.47	6.30	6.30
Nest G	3.72	0.33	3.78	#N/A	4.06	1.61	3.78	#N/A	1.61	0.25	1.57	1.94	4.05	1.08	3.63	#N/A	4.74	1.84	4.80	#N/A

e) pH

	Summer 1993 mean	Standard deviation	Summer 1993 median	Summer 1993 mode	Autumn 1993 mean	Standard deviation	Autumn 1993 median	Autumn 1993 mode	Winter 1993/94 mean	Standard deviation	Winter 1993/94 median	Winter 1993/94 mode	Spring 1994 mean	Standard deviation	Spring 1994 median	Spring 1994 mode	Summer 1994 mean	Standard deviation	Summer 1994 median	Summer 1994 mode
Nest A	4.78	0.04	4.80	4.80	4.88	0.07	4.90	4.90	4.72	0.11	4.71	4.60	4.50	0.11	4.51	4.60	4.24	0.05	4.20	4.20
Nest B	4.72	0.04	4.70	4.70	4.63	0.05	4.60	4.60	4.80	0.14	4.78	#N/A	4.41	0.17	4.50	4.60	4.21	0.10	4.20	4.20
Nest C	4.48	0.07	4.50	4.40	4.35	0.22	4.35	#N/A	4.56	0.24	4.53	#N/A	4.53	0.25	4.60	4.80	4.26	0.09	4.30	4.30
Nest D	4.48	0.07	4.50	4.40	4.30	0.33	4.30	4.40	4.73	0.17	4.71	4.70	4.50	0.26	4.60	4.70	4.27	0.07	4.30	4.30
Nest E	4.42	0.04	4.40	4.40	4.27	0.26	4.20	4.00	4.77	0.17	4.80	4.80	4.51	0.25	4.70	4.70	4.30	0.09	4.30	4.20
Nest F	4.42	0.10	4.50	4.50	4.35	0.29	4.40	4.60	4.67	0.25	4.75	4.90	4.20	0.09	4.20	4.20	4.30	0.08	4.30	4.30
Nest G	4.42	0.12	4.40	4.30	4.50	0.20	4.45	4.40	4.69	0.13	4.75	4.80	4.46	0.21	4.50	4.60	4.30	0.08	4.30	4.30

f) Conductivity

	Summer 1993 mean (μScm^{-1})	Standard deviation (μScm^{-1})	Summer 1993 median (μScm^{-1})	Summer 1993 mode (μScm^{-1})	Autumn 1993 mean (μScm^{-1})	Standard deviation (μScm^{-1})	Autumn 1993 median (μScm^{-1})	Autumn 1993 mode (μScm^{-1})	Winter 1993/94 mean (μScm^{-1})	Standard deviation (μScm^{-1})	Winter 1993/94 median (μScm^{-1})	Winter 1993/94 mode (μScm^{-1})	Spring 1994 mean (μScm^{-1})	Standard deviation (μScm^{-1})	Spring 1994 median (μScm^{-1})	Spring 1994 mode (μScm^{-1})	Summer 1994 mean (μScm^{-1})	Standard deviation (μScm^{-1})	Summer 1994 median (μScm^{-1})	Summer 1994 mode (μScm^{-1})
Nest A	44.73	18.35	46.40	#N/A	35.35	11.48	40.10	#N/A	39.88	6.00	40.95	#N/A	45.96	10.95	46.10	#N/A	40.00	4.64	38.50	#N/A
Nest B	47.86	15.59	53.90	#N/A	35.73	7.48	35.25	#N/A	44.47	5.68	43.50	#N/A	47.66	11.28	44.40	#N/A	48.20	3.38	49.30	#N/A
Nest C	39.74	13.24	38.30	#N/A	32.48	6.59	30.45	#N/A	36.58	7.08	36.00	#N/A	48.80	10.65	50.20	#N/A	40.83	7.08	43.30	#N/A
Nest D	55.04	27.40	52.60	#N/A	31.98	11.26	32.50	#N/A	46.22	7.14	47.60	#N/A	53.96	17.45	53.60	#N/A	48.94	2.82	49.30	#N/A
Nest E	54.04	9.14	51.10	#N/A	41.70	11.45	43.95	#N/A	52.58	4.41	53.85	#N/A	49.56	12.87	50.40	#N/A	47.09	1.74	47.50	48.90
Nest F	48.72	18.65	42.70	#N/A	35.02	8.76	37.45	#N/A	46.88	12.99	42.50	#N/A	37.79	13.21	34.50	34.50	52.99	4.28	54.80	#N/A
Nest G	52.02	18.47	55.80	#N/A	41.13	12.59	34.90	#N/A	41.90	6.56	39.50	#N/A	49.34	20.87	53.70	#N/A	57.14	3.75	56.50	#N/A

Table 5.12d-f: Seasonal mean, median, mode and ranges of selected chemical ion concentrations at Tor Royal for the annual cycle (1.6.93-31.5.94) and extended annual cycle (1.6.93-29.9.94).

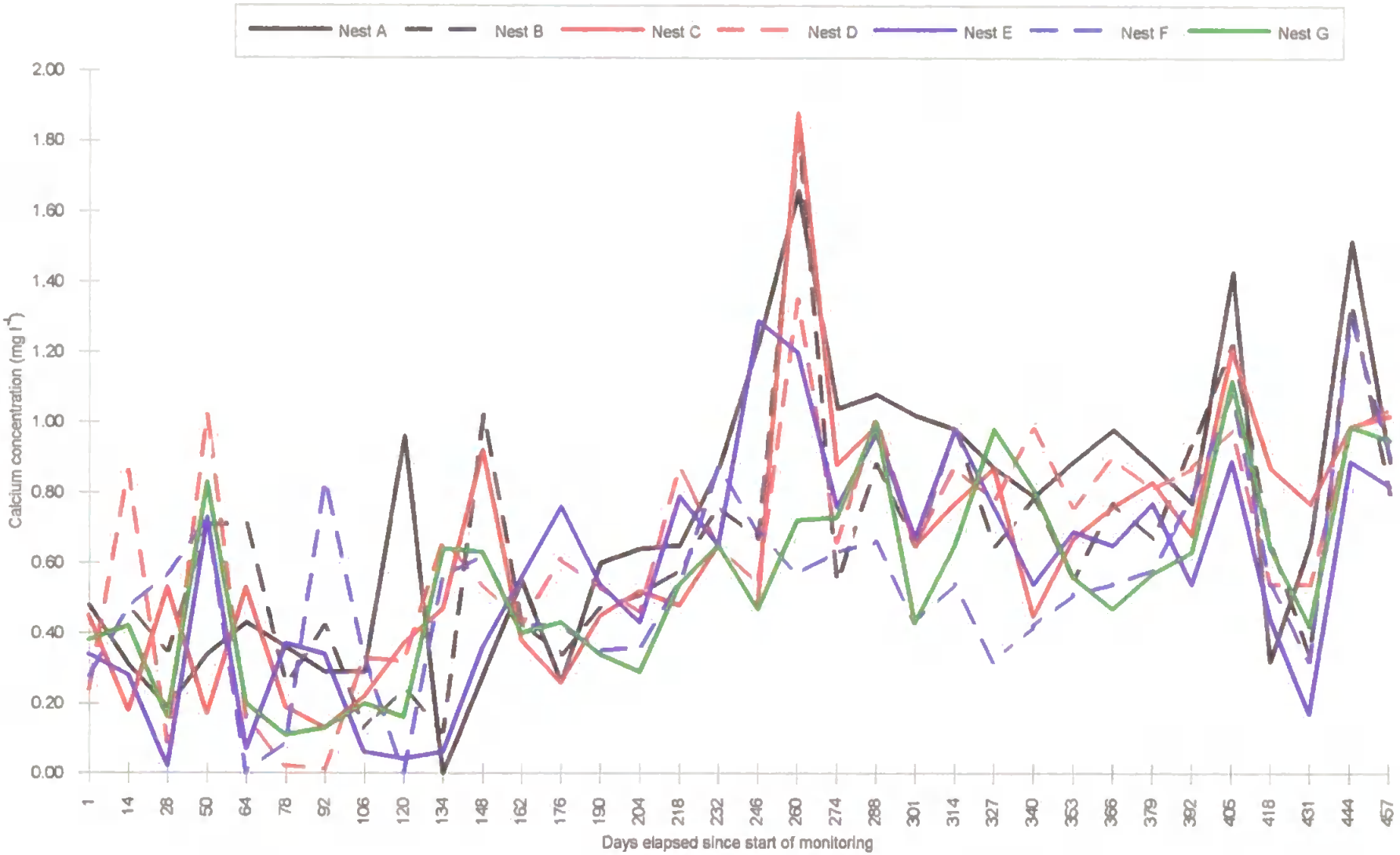


Figure 5.11: Calcium concentrations for all nests at Tor Royal, 1st June 1993-29th September 1994.

In terms of optimum sampling seasons for water chemistry, the same calculations that were made for the seasonal representativeness of water table depth in section 5.3.1 can be made for water chemistry. For Ca^{2+}, seasonal concentrations were most representative of the annual concentration during winter 1994/94 and least representative during spring 1994 (Table 5.13). For the median concentration, the relative performances were identical (Table 5.14). The relative stability of Ca^{2+} concentrations is linked to this, with the most stable concentrations occurring during winter 1993/94 and the most unstable concentrations occurring during spring 1994 (Table 5.15).

A comparison between the summer months of June to August 1993 and 1994 shows that mean Ca^{2+} concentrations during summer 1994 at all nests were higher than in summer 1993 by a factor of two. The possible causes for this increase are considered in section 5.4.2 below.

b) Magnesium (Mg^{2+})

Mg^{2+} concentrations ranged from 0 mg l^{-1} to 2.44 mg l^{-1} in the seven nests on Tor Royal bog during the monitoring programme, giving a mean annual concentration of 1.11 mg l^{-1}. Figure 5.12 shows two different phases of Mg^{2+} activity which are separated by a steady increase in Mg^{2+} concentrations at all nests on Tor Royal between days 232 and 260. Before day 232, Mg^{2+} concentrations ranged from 0 mg l^{-1} to 2 mg l^{-1} and the average concentration for all seven sites was 0 mg l^{-1}. Over a period of 14 days, all sampling nests on Tor Royal bog recorded appreciable increases in Mg^{2+} concentrations and at day 246, all peaked between 1.64 mg l^{-1} and 2.10 mg l^{-1}. From this point, nests A, B, C and D continued to experience high Mg^{2+} levels, while concentrations became slightly diluted at nests E, F and G. The dilution of Mg^{2+} in nests B,C, and D was far more rapid than for nest A, B and G, while nest F showed a delayed dilution effect over 27 days after day 274. After the peak in concentration at day 246, only nest D approached previous trends. The

Ion	Season	Factor difference
Ca^{2+}	Winter 1993/94	0.02
	Summer 1993	0.15
	Summer 1994	0.20
	Autumn 1993	0.21
	Spring 1994	0.31
Mg^{2+}	Summer 1993	0.00
	Summer 1994	0.01
	Autumn 1993	0.01
	Winter 1993/94	0.03
	Spring 1994	0.04
Cl^-	Summer 1993	0.00
	Spring 1994	0.35
	Winter 1993/94	0.36
	Summer 1994	0.71
	Autumn 1994	0.78
SO_4^{2-}	Autumn 1993	0.05
	Summer 1993	0.19
	Spring 1994	0.54
	Winter 1993/94	0.68
	Summer 1994	0.78
pH	Summer 1993	0.00
	Autumn 1993	0.00
	Spring 1994	0.09
	Winter 1993/94	0.17
	Summer 1994	0.26
Conductivity (μScm^{-1})	Winter 1993/94	0.06
	Spring 1994	0.45
	Summer 1994	0.75
	Summer 1993	0.75
	Autumn 1993	0.93

Table 5.13: Representativeness of mean seasonal water chemistry parameters with respect to annual means.

Ion	Season	Factor difference
Ca^{2+}	Winter 1993/94	0.01
	Summer 1993	0.14
	Summer 1994	0.21
	Autumn 1993	0.24
	Spring 1994	0.28
Mg^{2+}	Autmn 1993	0.00
	Summer 1993	0.00
	Summer 1994	0.01
	Winter 1993/94	0.03
	Spring 1994	0.05
Cl^-	Spring 1994	0.18
	Summer 1994	0.26
	Summer 1993	0.90
	Autumn 1993	0.30
	Winter 1993/94	0.30
SO_4^{2-}	Summer 1993	0.03
	Autumn 1993	0.19
	Spring 1994	0.74
	Winter 1993/94	0.10
	Summer 1994	0.20
pH	Spring 1994	0.01
	Summer 1993	0.02
	Autumn 1993	0.06
	Winter 1993/94	0.20
	Summer 1994	0.25
Conductivity (μScm^{-1})	Winter 1993/94	0.39
	Spring 1994	0.50
	Summer 1994	0.50
	Summer 1993	0.50
	Autumn 1993	0.60

Table 5.14: Representativeness of median seaonal water chemistry parameters with respect to annual means.

a. Ca^{2+}

Season	Maximum range recorded by dipwells (mgl^{-1})	Minimum range recorded by dipwells (mgl^{-1})	Overall seasonal range (mgl^{-1})
Winter 1993/94	0.61	0.36	0.25
Autumn 1993	0.96	0.33	0.63
Summer 1993	0.93	0.29	0.64
Summer 1994	1.11	0.44	0.67
Spring 1994	1.41	0.31	1.10

b. Mg^{2+}

Season	Maximum range recorded by dipwells (mgl^{-1})	Minimum range recorded by dipwells (mgl^{-1})	Overall seasonal range (mgl^{-1})
Winter 1993/94	0.06	0.03	0.03
Summer 1994	0.08	0.04	0.04
Spring 1994	0.11	0.06	0.05
Autumn 1993	0.11	0.05	0.06
Summer 1993	0.11	0.04	0.07

c. Cl^-

Season	Maximum range recorded by dipwells (mgl^{-1})	Minimum range recorded by dipwells (mgl^{-1})	Overall seasonal range (mgl^{-1})
Summer 1994	5.90	4.52	1.38
Autumn 1993	10.08	8.57	1.51
Spring 1994	8.07	1.80	6.27
Summer 1993	12.24	5.10	7.14
Winter 1993/94	14.35	2.30	12.05

Table 5.15a-c: Range of water chemistry components recorded in all nests at Tor Royal (1.6.93-29.9.94). Seasons are ranked from least to greatest range.

d. SO_4^{2-}

Season	Maximum range recorded by dipwells (mgl^{-1})	Minimum range recorded by dipwells (mgl^{-1})	Overall seasonal range (mgl^{-1})
Summer 1993	1.04	0.60	0.44
Summer 1994	4.96	3.46	1.50
Winter 1993/94	3.17	0.63	2.54
Autumn 1993	5.06	1.00	4.06
Spring 1994	10.05	3.05	7.00

e. pH

Season	Maximum range recorded by dipwells	Minimum range recorded by dipwells	Overall seasonal range
Summer 1993	0.30	0.10	0.20
Summer 1994	0.30	0.10	0.20
Winter 1993/94	0.70	0.30	0.40
Spring 1994	0.80	0.30	0.50
Autumn 1993	1.00	0.10	0.90

f. Conductivity (μScm^{-1})

Season	Maximum range recorded by dipwells (μScm^{-1})	Minimum range recorded by dipwells (μScm^{-1})	Overall seasonal range (μScm^{-1})
Summer 1994	21.80	4.60	17.20
Autumn 1993	35.67	16.40	19.27
Winter 1993/94	40.90	12.50	28.40
Spring 1994	72.10	34.10	38.00
Summer 1993	74.20	27.10	47.10

Table 5.15d-f: Range of water chemistry components recorded in all nests at Tor Royal (1.6.93-29.9.94). Seasons are ranked from least to greatest range.

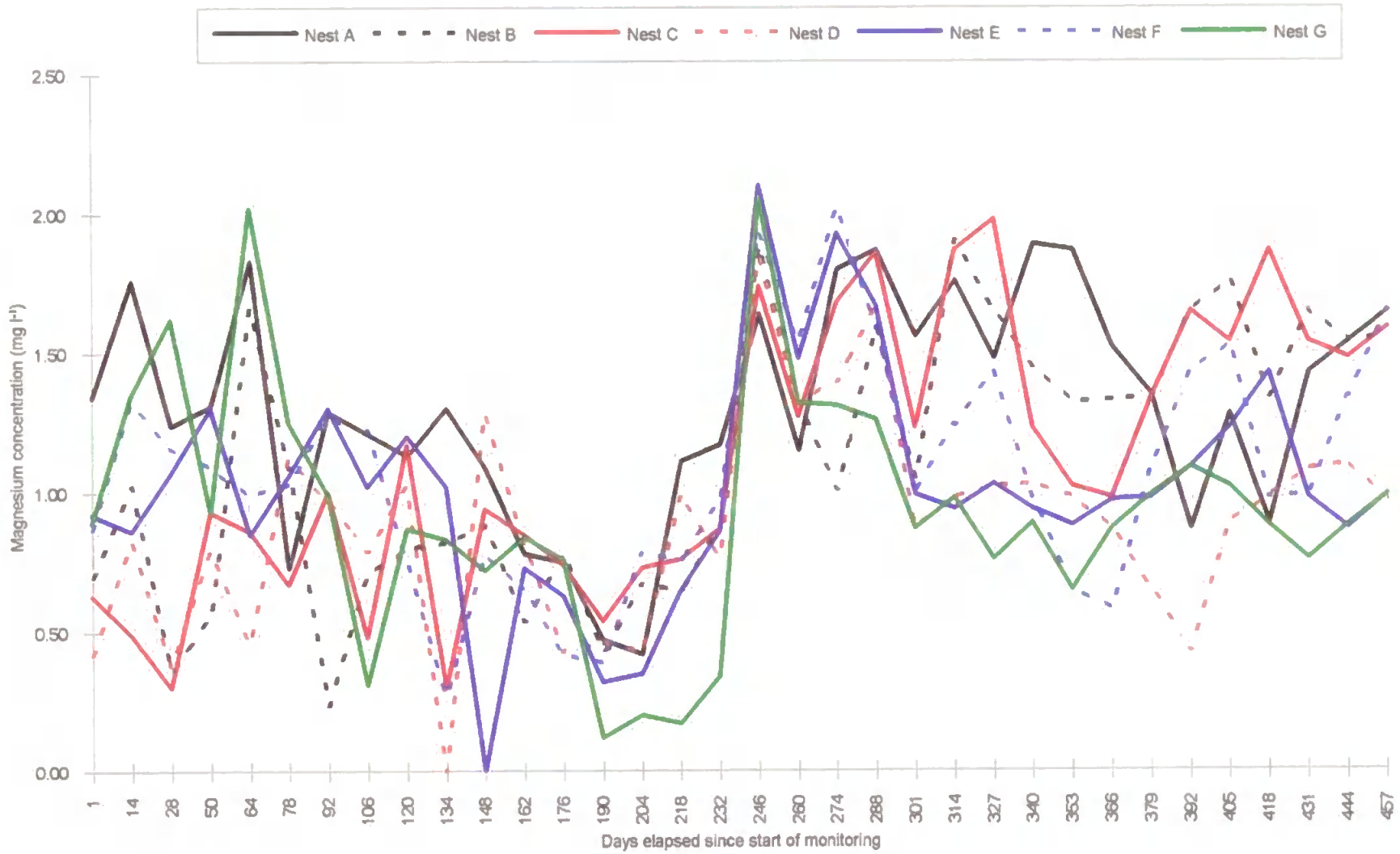


Figure 5.12: Magnesium concentrations at Tor Royal, 1st June 1993-29th September 1994.

remaining nests all showed higher average Mg^{2+} concentrations, reflected in the average for this phase (1.26 mg l^{-1}).

Like the Ca^{2+} concentrations at Tor Royal, Mg^{2+} concentrations exhibited a degree of seasonality. Of the seven nests, five showed a mean increase of between 0.116 mg l^{-1} and 0.506 mg l^{-1} in the spring and summer of 1994 compared with the mean levels during the preceding autumn and winter months. Mean concentrations at the remaining two nests (D and E) were 0.187 mg l^{-1} and 0.269 mg l^{-1} lower during the spring/summer season than in the previous autumn/winter season.

The mean concentration for Mg^{2+} between 1st June 1993 and 31st May 1994 was 0.08 mg l^{-1}. In terms of developing modern analogues for water chemistry transfer functions, the season most representative of this annual mean concentration was summer 1993, while spring 1994 was the least representative (Table 5.13). The season most representative of the annual median concentration was autumn 1993 and the least representative was spring 1994 (Table 5.14). Mg^{2+} concentrations were most stable during winter 1993 and least stable during summer 1993 (Table 5.15), although the difference between the largest and smallest seasonal range is only 0.04 mg l^{-1}.

c) Nitrate (NO_3^-)

NO_3^- concentrations were sampled up to November 31st 1993, but thereafter sampling ceased because NO_3^- concentrations were consistently below 0.001 mg l^{-1} and practically undetectable by the autoanalyser. On several occasions erroneous negative values for NO_3^- were recorded. Proctor (1994), working on an ombrotrophic mire at Plym Head, approximately 4 km south of Tor Royal, had also noted very small amounts of NO_3^- in water samples. During a 14-month sampling period, only one sample had just exceeded 0.1 mg l^{-1} NO_3^-. Proctor suggested that *Sphagnum* peat was a highly efficient sink for NO_3^-,

while Urban *et al.* (1988) have identified uptake by *Sphagnum* and other plants, microbial activity and nitrification as being responsible for low NO_3^- concentrations in mid-continental mires in the United States.

Given the unacceptable error factor that was inherent in the analytical technique and the lack of more sensitive equipment, the findings by Proctor (1994) and Urban *et al.* (1988) and the poor chance of major seasonal NO_3^- trends being identified, NO_3^- recording at Tor Royal was terminated.

d) pH (H^+ concentration)

The mean annual pH value recorded at Tor Royal during the monitoring programme was pH 4.5. Throughout the monitoring, the pH values fluctuated around the mean, reaching a minimum of pH 3.9 (nest D on day 120) and a maximum of pH 5.0 (nest B on day 176).

Overall, there was a smooth change from higher pH values in the autumn and winter months to lower pH values during the spring and summer (Figure 5.13). During the autumn/winter season, mean pH was 4.6, and this lowered during the spring and summer to pH 4.3 - a seasonal trend which reflects the activities of the chemical ions that were analysed at Tor Royal. This relationship is discussed in section 5.4.2 below.

In terms of sampling for modern water quality analogues, the seasons most representative of the annual mean pH were summer and autumn 1993 (Table 5.13), while spring 1994 was most representative of the annual median (Table 5.14). The least representative season for both measurements was summer 1994. Summer 1993 was the most stable season, while the widest range of pH values occurred in autumn 1993 (Table 5.15).

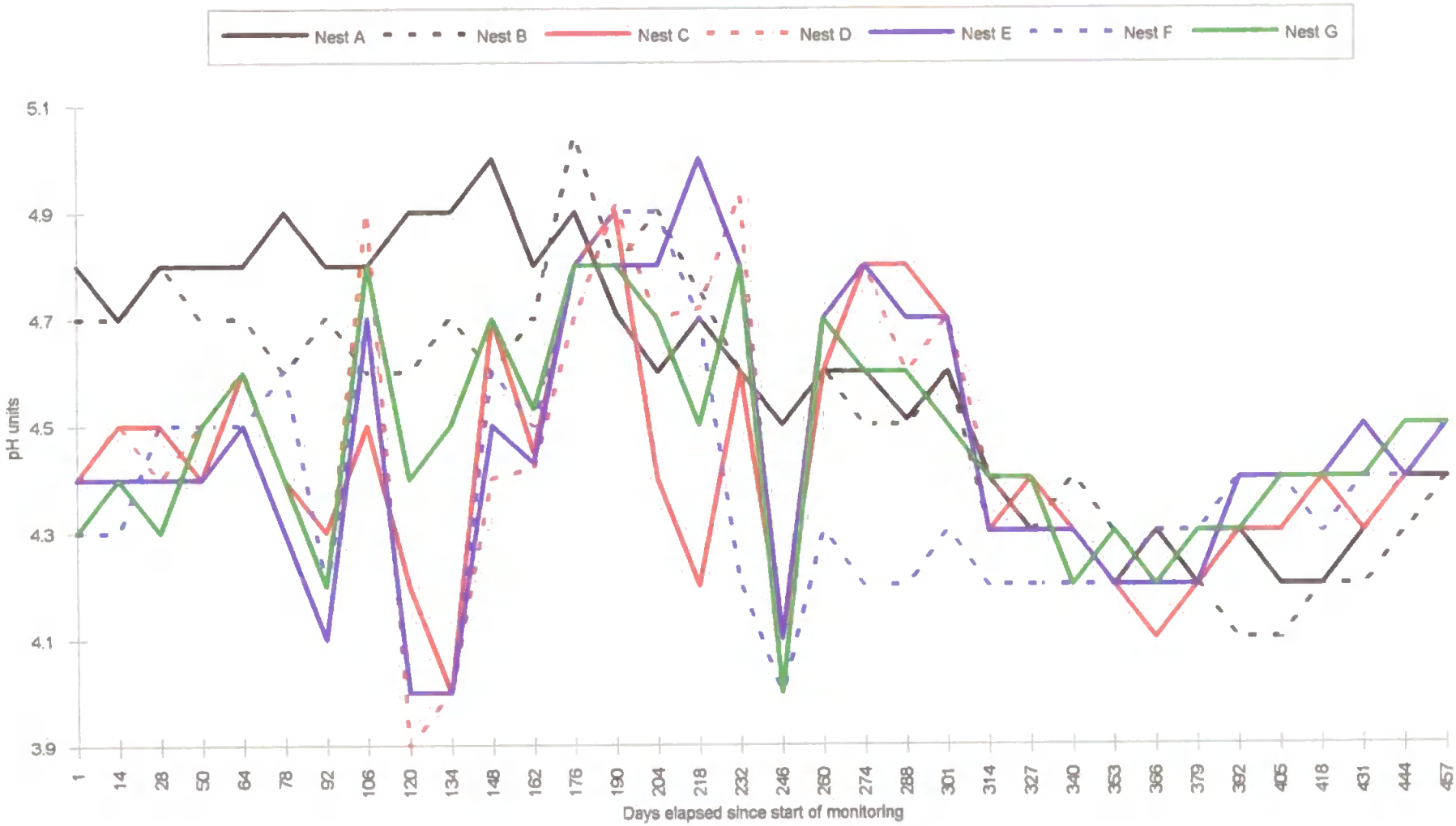


Figure 5.13: pH fluctuations in all nests at Tor Royal, 1st June 1993-29th September 1994.

e) Chloride (Cl^-)

Cl^- ion concentrations ranged from 0.82 mg l^{-1} to 20 mg l^{-1}, fluctuating markedly around an annual mean of 10.89 mg l^{-1} (Figure 5.14). The larger-magnitude fluctuations occurred between days 1 and 162, after which the fluctuations were of a smaller magnitude. These fluctuations are in fact strong expressions of precipitation events at Tor Royal and this relationship is discussed fully below.

There was an appreciable seasonal pattern in Cl^- concentration on Tor Royal. During the autumn/winter 1993/94 season, mean Cl^- concentration was 11.53 mg l^{-1}, compared to 10.83 mg l^{-1} during the summer months of 1993. There is also an apparent anomaly between the mean Cl^- concentrations for the 1994 and 1993 summer seasons which are 12.05 mg l^{-1} and 11.53 mg l^{-1} respectively. Six of the seven nests have higher mean Cl^- concentrations in the 1993 summer season than in summer 1994. Only nest G has a lower value for summer 1993. Cl^- concentrations during summer 1993 were raised by a combination of larger precipitation events and greater evaporation effects, both of which are discussed below.

For modern water quality analogues, the season most representative of the annual mean was summer 1993 and the least representative was autumn 1993 (Table 5.13). Summer 1993 was closest to the median annual concentration (Table 5.14), while summer 1994 the most stable season (Table 5.15).

f) Sulphate (SO_4^{2-})

SO_4^{2-} concentrations generally stabilised around an annual mean concentration of 3.90 mg l^{-1} SO_4^{2-} up to day 120, after which there were four events where SO_4^{2-} concentration increased sharply (Figure 5.15).

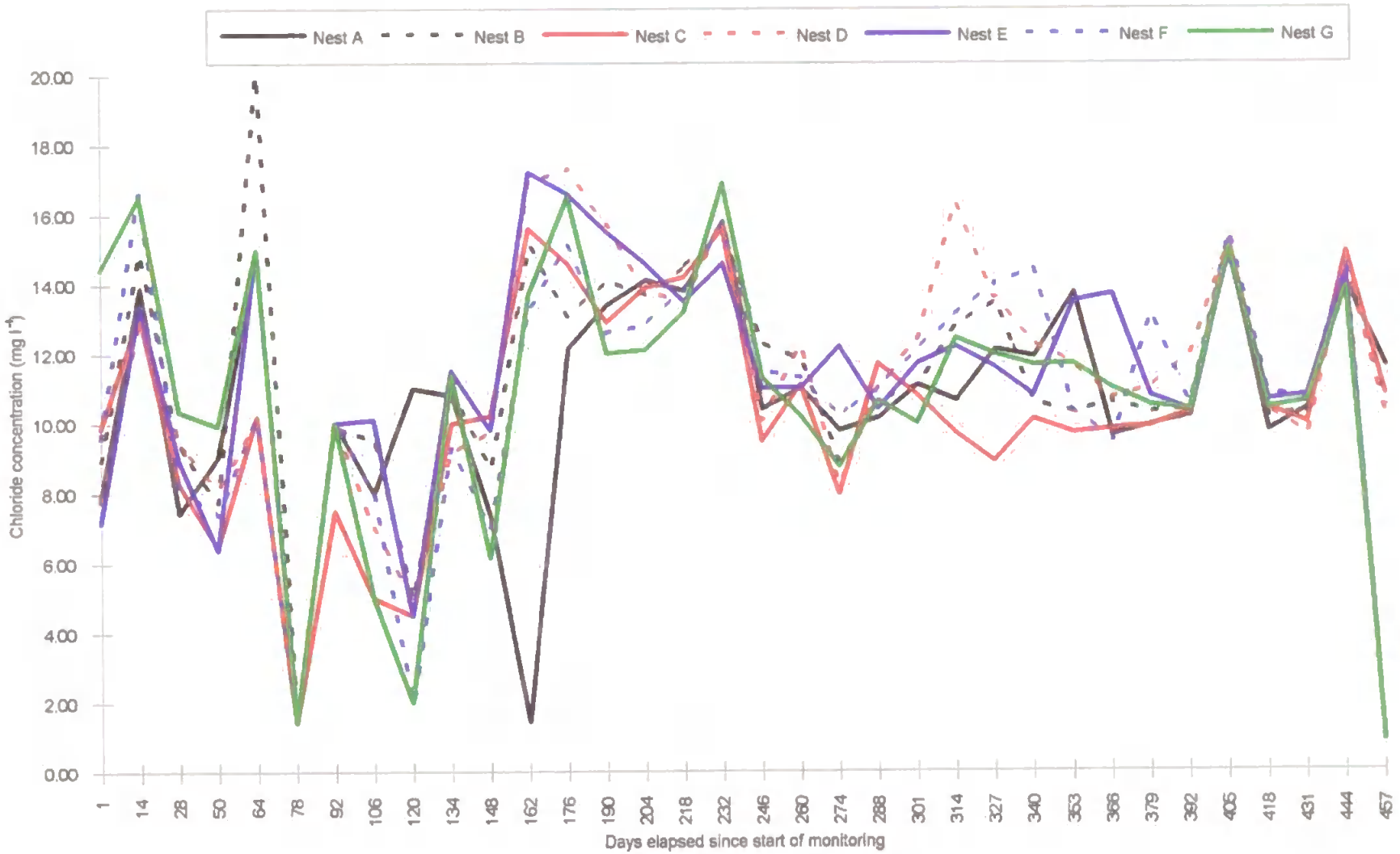


Figure 5.14: Chloride concentrations in all nests at Tor Royal, 1st June 1993-29th September 1994.

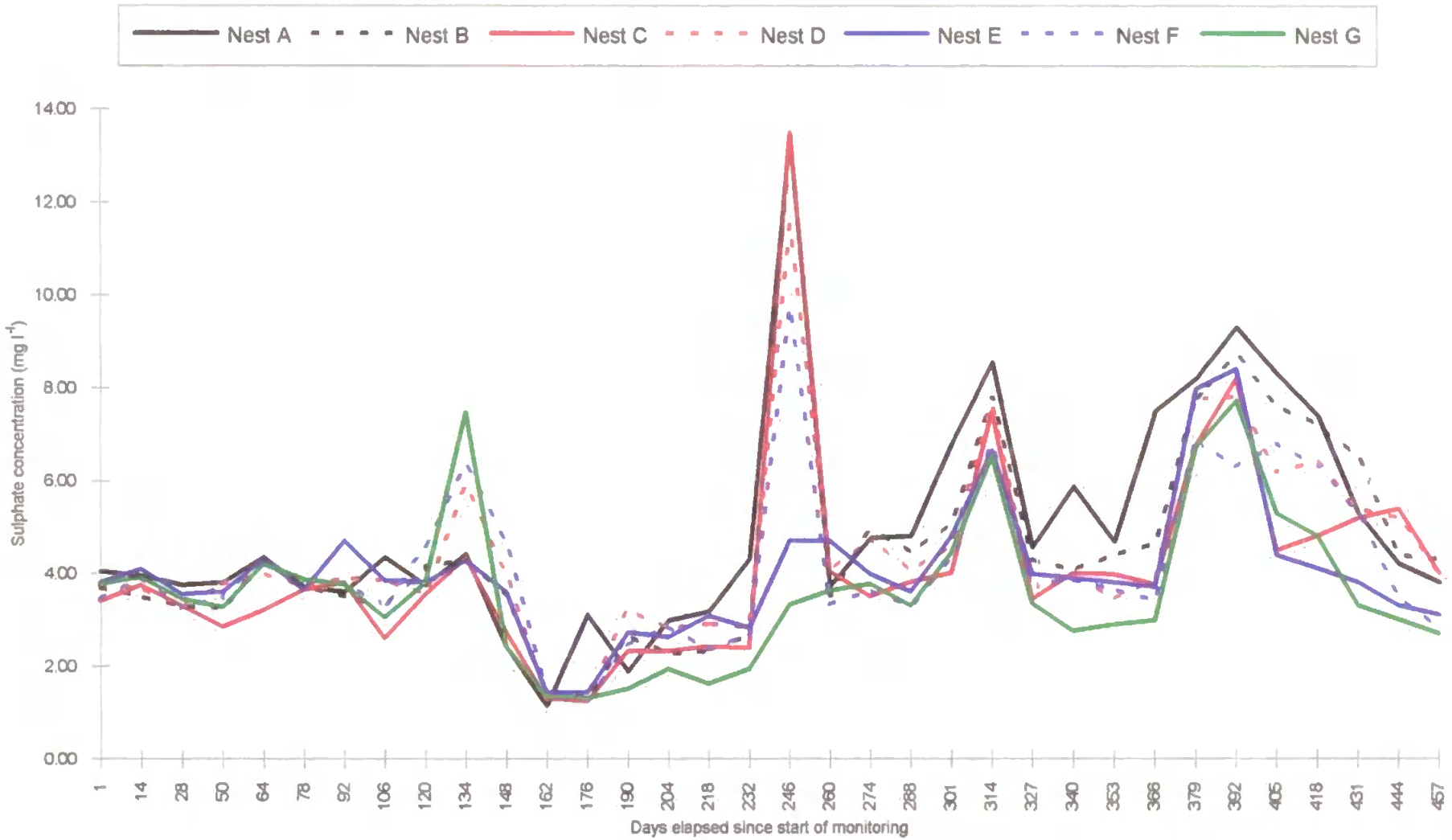


Figure 5.15: Sulphate concentrations in all nests at Tor Royal, 1st June 1993-29th September 1994.

The first event, which affected nests F, G and D to the greatest extent, occurred on day 134. At nest G, SO_4^{2-} concentration peaked at 7.48 mg l^{-1}, an increase of 3.68 mg l^{-1} on the previous recording. Nest D returned an increase in SO_4^{2-} of 2.35 mg l^{-1} compared to the previous recording, while SO_4^{2-} levels at nest F were 6.35 mg l^{-1}, giving an increase of 1.75 mg l^{-1} in the same 14 days. The remaining nests showed only a slight increase in SO_4^{2-} concentrations over the same time period.

The second event, centred on day 246, dominates Figure 5.15. Five nests showed a marked increase in SO_4^{2-} levels and the effect was greatest at nest C, where SO_4^{2-} rose from 2.42 mg l^{-1} to 13.50 mg l^{-1} in 14 days. Nests A, B, D and F followed suit, while nests G and E recorded far more subtle increases in SO_4^{2-} concentration. The cause of this rapid increase is discussed below.

The third event, on day 314, is marked by a peak in SO_4^{2-} concentrations after a steady rise over 14 days and is most clearly expressed at site A. Here, SO_4^{2-} rose from 4.8 mg l^{-1} on day 288 to 8.14 mg l^{-1} on day 314, a near-doubling in concentration. A similar increase was recorded by the remaining sites.

The fourth event is notable because it shows a steady rising limb that originates on day 366, climbs to a peak SO_4^{2-} concentration on day 392 and falls equally steadily towards day 444. Throughout this event, the highest SO_4^{2-} levels were recorded at nest A and the lowest at nests C and E.

There was a strong seasonal element underlying the mean SO_4^{2-} levels (3.89 mg l^{-1}) at Tor Royal which, similar to the ions described in the sections above, has important consequences for the development of transfer functions from modern analogues. The SO_4^{2-} content of the water in every nest was higher in the summer season of 1994 (average

concentration from the seven nests = 5.66 mg l^{-1} SO_4^{2-}) than in the preceding winter season (average concentration = 2.21 mg l^{-1} SO_4^{2-}). Autumn 1993 was the most representative of annual mean concentrations (Table 5.13), while summer 1993 was most representative of the annual median (Table 5.14) and also the most stable in terms of SO_4^{2-} concentrations (Table 5.15).

Of further interest is the difference in SO_4^{2-} between summer 1993 and summer 1994. The mean content for all seven nests during summer 1993 was 3.69 mg l^{-1} SO_4^{2-}; in summer 1994, this mean rose to 5.66 mg l^{-1} SO_4^{2-}. An explanation is provided by the final peak in SO_4^{2-} concentrations (running from day 366 to day 444) which was described above. This event coincides with the summer 1994 season and the high SO_4^{2-} levels that were sustained during this event would raise the mean SO_4^{2-} value for this season.

g) Electrical conductivity (μScm^{-1})

The mean annual corrected electrical conductivity reading for Tor Royal over the monitoring period was 44.54 μScm^{-1}. Fluctuations were greater during the first 288 days of the monitoring programme, after which electrical conductivity values stabilised around the mean (Figure 5.16).

Being a measure of the total ions in a solution, the conductivity readings reflect seasonal patterns of ion concentrations. During winter 1993/94, the mean conductivity reading at Tor Royal was 44.07 μScm^{-1}. In the following summer months, the value increased to 47.88 μScm^{-1}, reflecting an overall increase in the ionic concentration of water in the peat body. Mean electrical conductivity decreased insignificantly by 1.00 μScm^{-1} from 48.88 μScm^{-1} in summer 1993 to 47.88 μScm^{-1} in summer 1994. For both mean and median electrical conductivity values, winter 1993/94 was the most representative of annual patterns (Tables 5.13 and 5.14), while summer 1994 was the most stable period (Table 5.15).

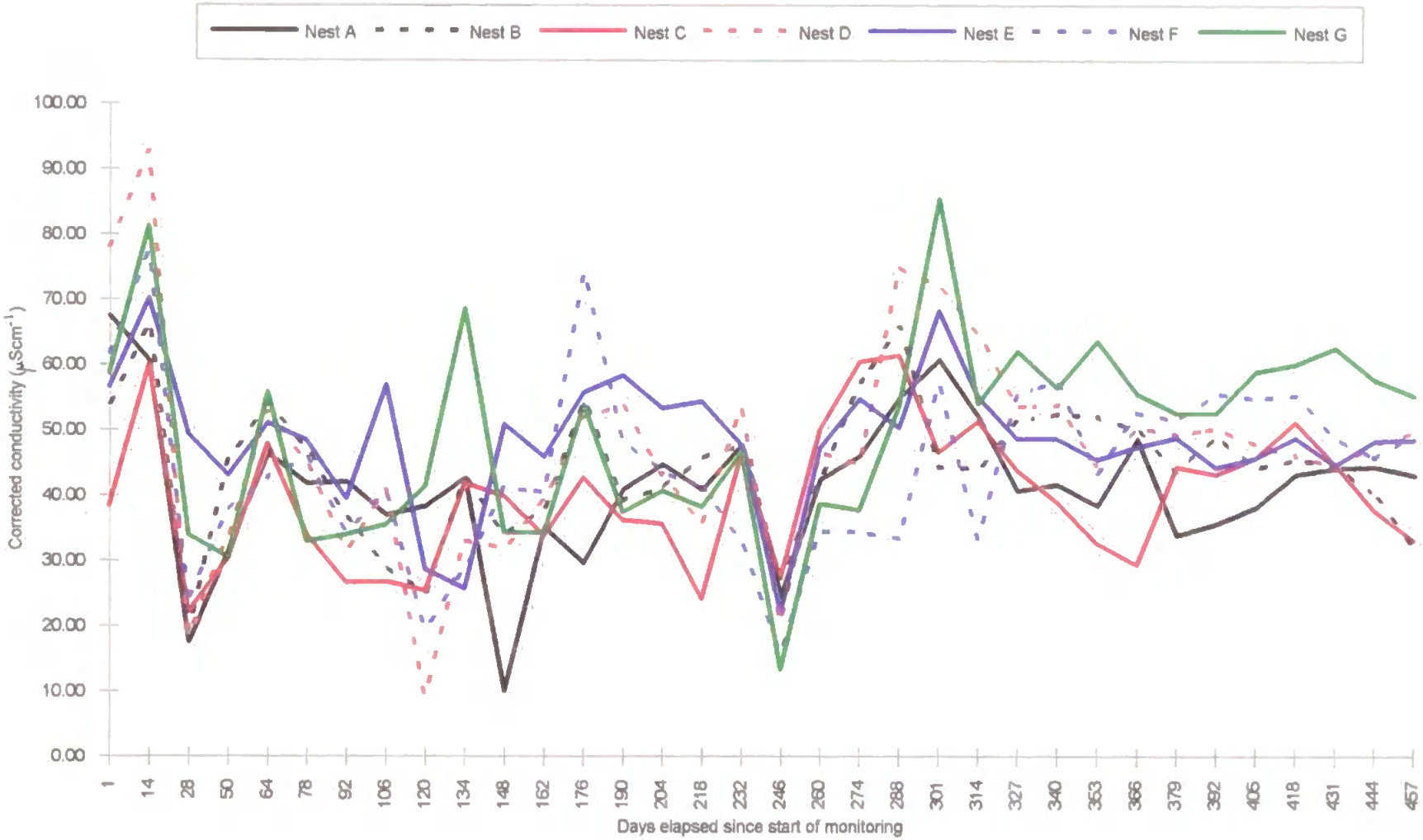


Figure 5.16: Corrected elecetrical conductivity for all nests at Tor Royal, 1st June 1993-29th September 1994.

5.4.2 Discussion

The results described above have revealed a series of detailed changes in water chemistry during the 15-month monitoring programme. These changes can be explained in terms of precipitation inputs and processes operating within the peat body. In particular, the fluctuations of chemical ions at the site reveal a complex interdependence between several variables. The following discussion is a detailed appraisal of these relationships, which focuses on the provenance of the individual chemical ions, their relationships with each other, and with water table and precipitation variations at Tor Royal.

A significant finding from the study on Tor Royal was the strong seasonal variation in ionic concentration. Ca^{2+}, Mg^{2+}, H^{+} (expressed as pH) and SO_4^{2-} tended to reach maximum concentrations in the summer months after which they declined during the winter.

The exception to this pattern was Cl^{-}, which showed more frequent variations (often on a fortnightly basis) in response to rainfall events. The link was particularly strong during the autumn and winter months (Figure 5.17) when south-westerly winds carried salt-laden precipitation from the Atlantic Ocean to be deposited on Dartmoor. This pattern was also noted by Sutcliffe and Carrick (1983), whose study sites in the Lake District were also in a south-westerly airstream that had crossed a marine area (albeit the Irish Sea, which has a smaller fetch than the Atlantic Ocean). The Spearman's rank correlation coefficient of r_s= 0.821 between mean fortnightly rainfall and mean fortnightly Cl^{-} concentration is significant at $p < 0.01$.

A seasonal comparison of Cl^{-} concentrations at Tor Royal is difficult because the magnitude and frequency of the individual precipitation events will tend to inflate seasonal averages. Similarly, a comparison of Cl^{-} concentrations between summer 1993 and summer 1994 is difficult because the weather during the two summer seasons was not identical. However,

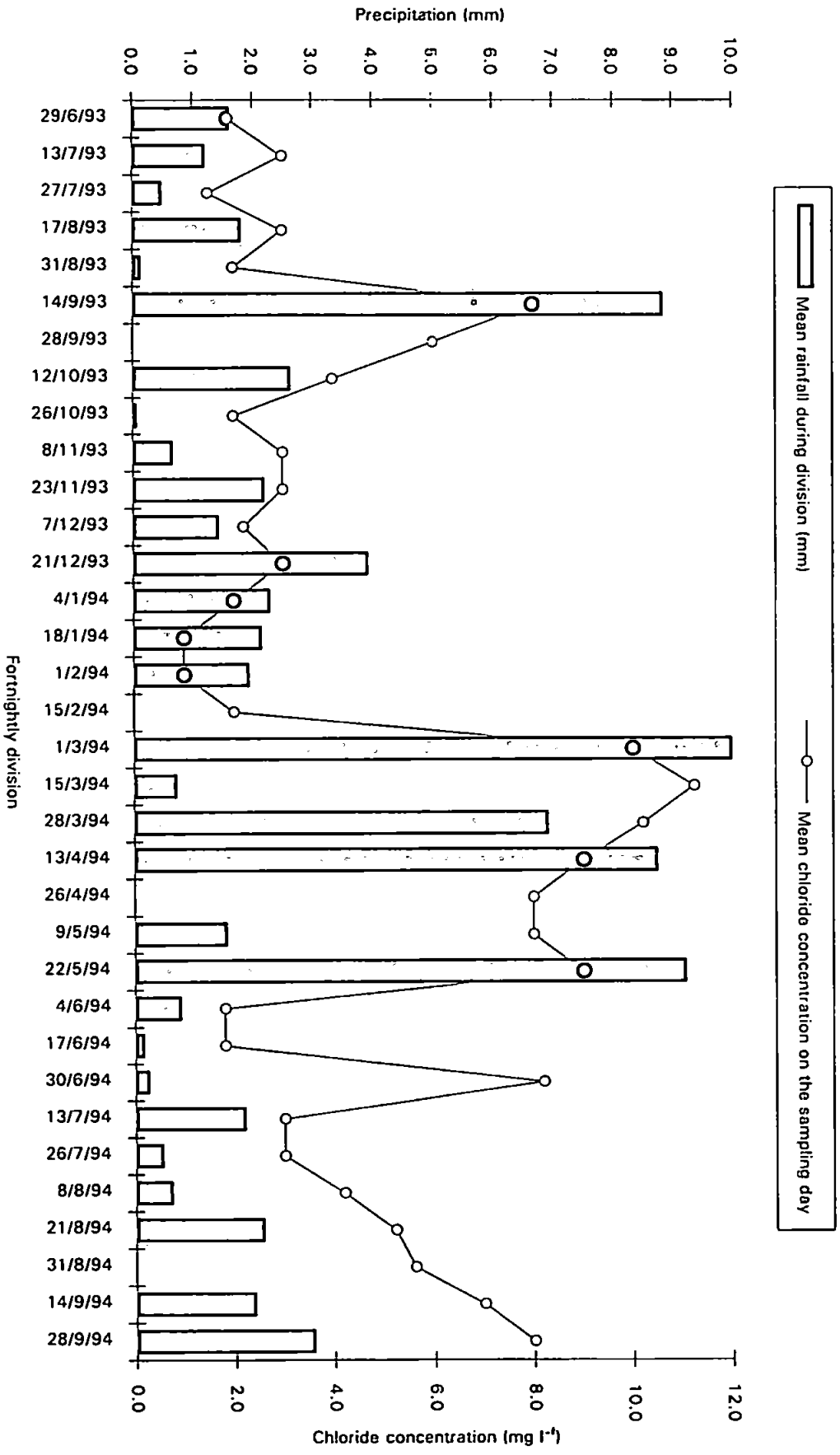


Figure 5.17: Chloride concentration on sampling day and precipitation totals (mm) for the preceding fortnight, Tor Royal: 29.6.93-28.9.94

it is possible to focus on short-term changes in Cl^- concentration during the summer months (June - August inclusive), where the effects of evaporation on Cl^- were marked.

During dry summer months, evaporative losses from pools can be considerable; Boatman *et al.* (1975) recorded a reduction in pool depth of 0.6 cm day^{-1} on Brishie Bog in Galloway and this was attributed to evaporation. Over 15 dry days, a total of 9 cm of water was lost by evaporation alone, which increased the concentration of ions in the pools by a factor of at least x1.5. This is also apparent at Tor Royal where, during a dry period of 14 days in August 1994, Cl^- concentrations rose to between 14.87 mg l^{-1} and 15.4 mg l^{-1} from a previous reading of between 10.2 mg l^{-1} and 12 mg l^{-1} Cl^-. As expected, the rise was greatest in the large pool at Tor Royal (nests F and G) where there was an increase of 4.86 mg l^{-1} and 4.62 mg l^{-1} Cl^- respectively at nests F and G.

Similarly, 9 mm of precipitation in 45 days was sufficient to raise Cl^- concentrations to the highest recorded during the monitoring programme, on 31st August 1993 (Figure 5.17). It is unlikely that 1 mm of precipitation on the previous day was solely responsible for the inflated Cl^- levels. Rather, in the previous 43 dry days when temperatures reached 25°C, evaporation raised the concentration of Cl^- ions in solution. Hence, input from precipitation and evaporative concentration during dry periods are the most important controls on Cl^- levels at Tor Royal.

Ca^{2+} concentrations at Tor Royal peaked during the spring/summer months and reached a minimum during the autumn/winter season. This is consistent with findings by Boatman *et al.* (1975) working on the Silver Flowe in Galloway, Sutcliffe & Carrick (1983) working in the Lake Windermere catchment in the Lake District and by Proctor (1994) working on nearby Plym Head. At Tor Royal, the most striking feature of Figure 5.11 is the Ca^{2+} peak on day 260 (15th March 1994), after which the average concentration rises to 0.79 mg l^{-1}

Ca^{2+} compared with 0.42 mg l^{-1} Ca^{2+} before 15th March. However, the magnitude of fluctuations after day 260 are still very low.

Ca^{2+} ions in ombrotrophic mires originate mainly from terrestrial dust (Sutcliffe & Carrick, 1983; Proctor, 1994) and there are two principal sources from which an increased input of Ca^{2+} ions may have been derived at Tor Royal. A small amount may have come from decaying plant litter (Boatman *et al.*, 1975). Since Ca^{2+} ions are released slowly over time from decaying matter (Sutcliffe & Carrick, 1983) they would account for the higher mean Ca^{2+} concentrations in the second half of Figure 5.11, but not for the sudden peak in Ca^{2+} at day 260. This increase was probably progressive over the preceding fortnight and not detected by the fortnightly sampling programme.

A second origin may be linked to agriculture or agroforestry. Boatman *et al.* (1975) recorded very high concentrations of Ca^{2+} (up to 9.53 kg ha^{-1}) at Silver Flowe which were traced to airborne spraying of calcium phosphate on nearby forestry plantations. A similar origin - from improved agricultural land which lies to the southwest of Tor Royal - may be responsible for the peak at the site. Calcium phosphate (for liming) used on this land may have been taken up into the airflow and deposited in precipitation at Tor Royal (albeit in smaller concentrations than the Silver Flowe example). This is feasible, since most lime is spread on agricultural land in the spring and day 260 is February 15th, 1994. Favourable weather conditions in the locality may have encouraged the early application of lime on agricultural land.

Mg^{2+} is principally marine in origin (Boatman *et al.*, 1975; Sutcliffe & Carrick, 1983; Gorham *et al.*, 1985; Proctor, 1994). At Tor Royal, there was a strong match between the Mg^{2+} and Cl^- trends at Tor Royal (see Figures 5.12 and 5.14), suggesting that large amounts

of Mg^{2+} are, like Cl^-, deposited at Tor Royal from precipitation derived from oceanic sources.

Uptake of Mg^{2+} by *Sphagnum* was observed by Boatman *et al.* (1975) and this may have caused the extremely low Mg^{2+} concentrations (despite inputs via precipitation) which were recorded during the monitoring programme (Figure 5.12). This is particularly evident at nests D and E (both located in *Sphagnum* lawns) where, on two occasions during the late summer season, Mg^{2+} concentrations registered 0 mg l^{-1}. However, further research would be required to confirm this hypothesis.

The strongest seasonal trend at Tor Royal was displayed by SO_4^{2-}. The results section above demonstrated how mean spring/summer SO_4^{2-} levels were higher than autumn/winter levels This matches observations by Boatman *et al.* (1975), Gosling & Baker (1980) and Proctor (1992; 1994), where rising SO_4^{2-} was linked to a falling water table. As the graphs for water table depth and sulphate concentrations show, the same relationship exists at Tor Royal (Figure 5.18).

At the level of the water table and below it, H_2S (hydrogen sulphide) is produced. In the anaerobic conditions of waterlogged peat, H_2S is stable in its reduced form, but as the water table falls, air replaces water in the peat pores and H_2S is oxidised, releasing SO_4^{2-}. This process was summarised for peaty soils containing iron pyrites by Gosling & Baker (1980) as

$$FeS_2 \xrightarrow[H_2O]{O_2} Fe^{2+} + SO_4^{2-}$$

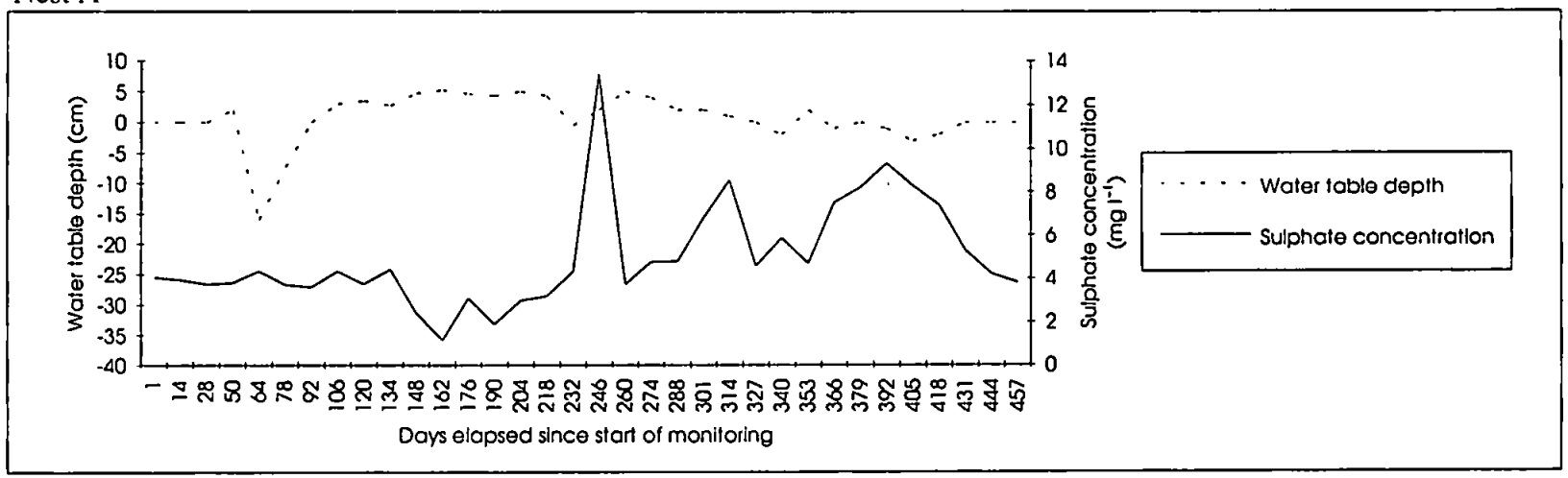
and it is likely that the same or similar process occurs at Tor Royal.

This effect was especially marked at nest A, where mean summer SO_4^{2-} concentrations were 1.69 mg l^{-1} higher during summer 1994 than the previous winter in response to a consistently deep water table (between 10 and 15 cm below the ground surface). Throughout the previous autumn and winter months, the water table was higher, creating reducing conditions in which the peat acted as an efficient sink for sulphate (Brown & Macqueen, 1985; Brown, 1986; Proctor, 1994) and SO_4^{2-} was readily incorporated into the organic matter or into organic sulphides (mainly FeS_2 - Gosling and Baker, 1980). As the water table dropped, the peat became aerated and FeS_2 oxidised to form Fe^{2+} and SO_4^{2-}. This is supported by a reduction in pH values at nest A from pH 4.7 to pH 4.2 from day 305 onwards.

The effect of this oxidation can be rapid; Gosling and Baker (1980) reported a drop in pH in sulphidic soils on a broadland site in Norfolk from near-neutrality to pH 3 over three weeks, following drainage improvement in surrounding farmland. This is supported by Hemond (1980) who reported that the oxidation of SO_4^{2-} during the summer season caused pH to fall well below that expected from precipitation and evaporative concentration alone. The lag time at Tor Royal was two weeks, but undetected increases in SO_4^{2-} concentrations could have occurred at any point within the fortnight between sampling visits. The change is probably rapid because the ombrotrophic peat at Tor Royal is already base-poor and receives minimal base input. A more accurate assessment of the speed of changes on SO_4^{2-} concentrations would have required daily recording of sulphate levels, but time and equipment limitations prevented this.

Peaks in SO_4^{2-} concentration also occurred at Tor Royal during the winter months (Figure 5.18) and such peaks are often attributed to atmospheric pollution. For example, Gorham *et al.* (1985, p.356) cite "excess sulphate owing to air pollution at Featherbed Moss, Axe Edge Moss and Ringinglow Moss". Despite outputs from the city of Plymouth, 18 km

Nest A



Nest B

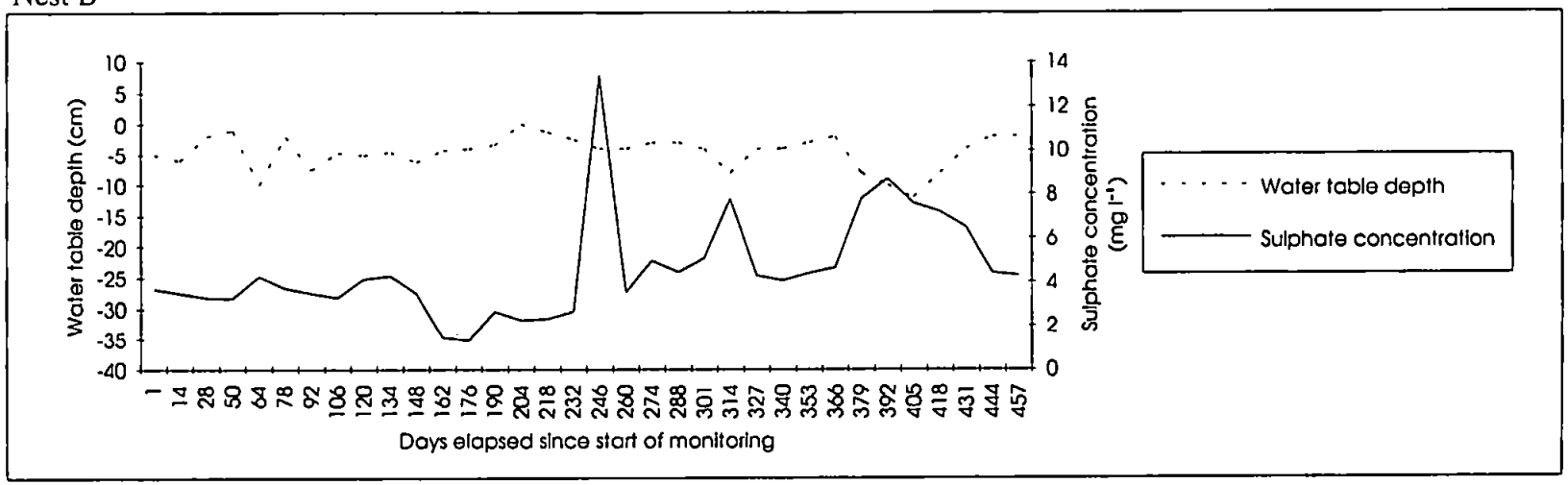
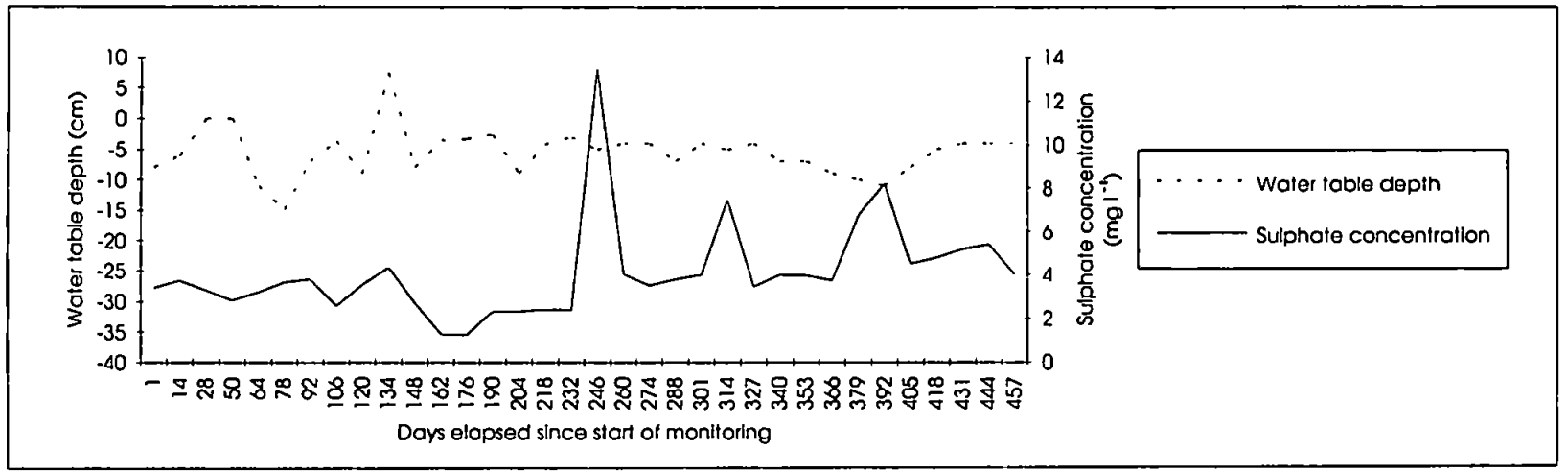


Figure 5.18a: Water table depth and sulphate concentrations in dipwells sampled for water chemistry, nests A and B, at Tor Royal: 1.6.93-29.9.94.

Nest C



Nest D

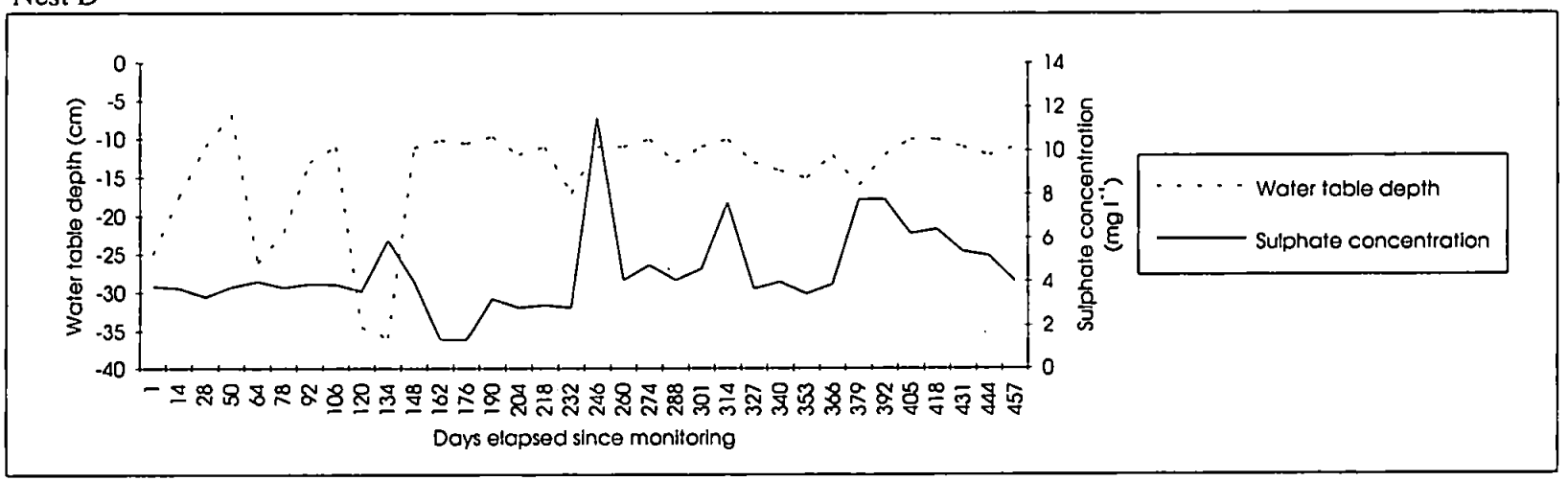
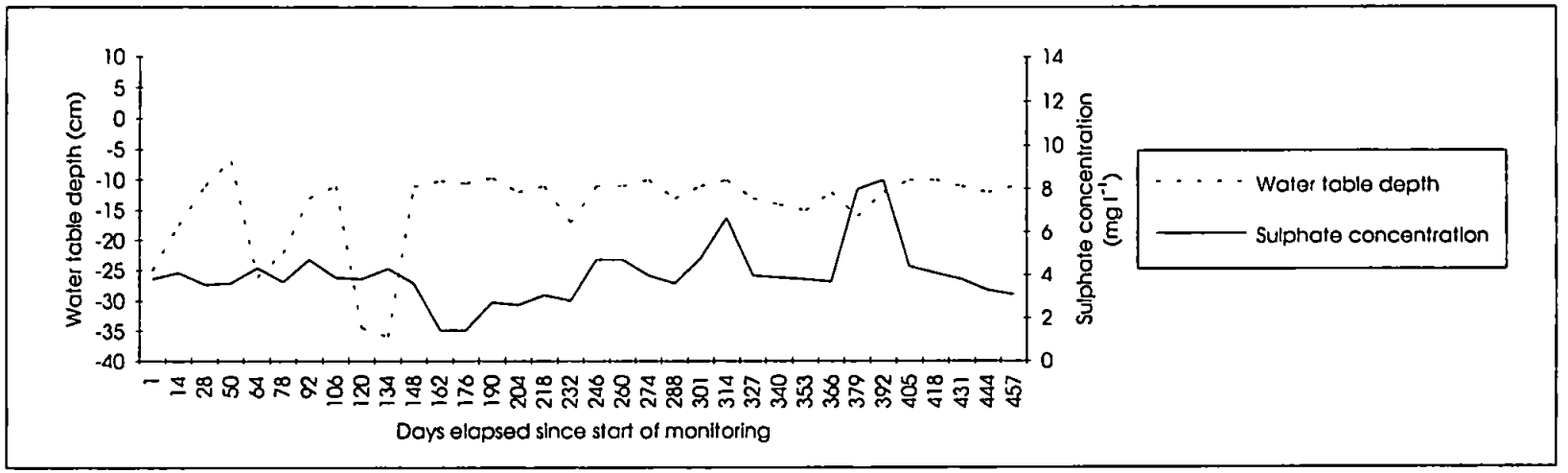


Figure 5.18b: Water table depth and sulphate concentrations in dipwells sampled for water chemistry, nests C and D, Tor Royal: 1.6.93-29.9.94.

Nest E



Nest F

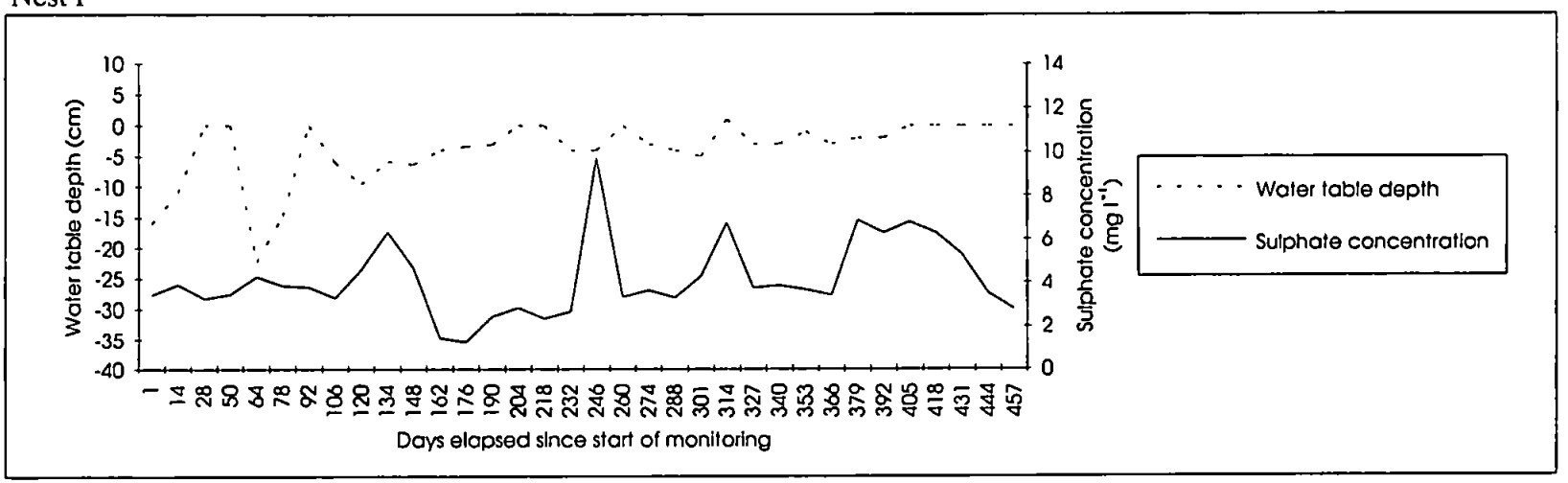


Figure 5.18c: Water table depth and sulphate concentrations in dipwells sampled for water chemistry, nests E and F: 1.6.93-29.9.94.

Nest G

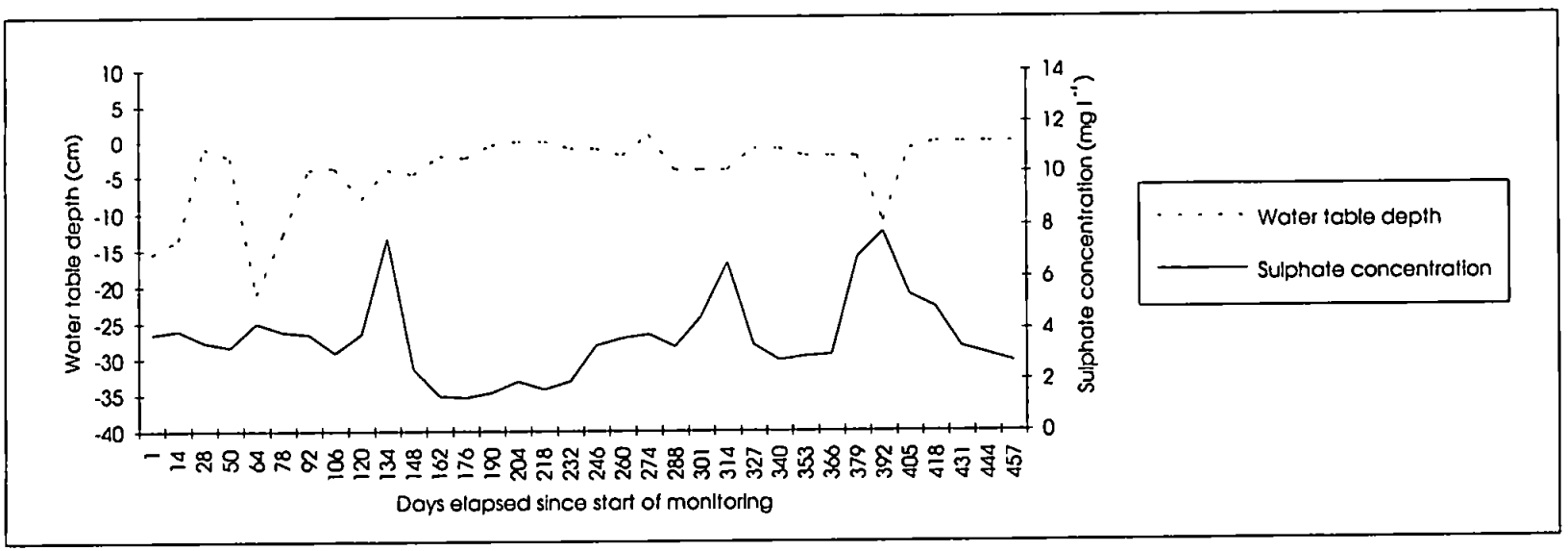


Figure 5.18d: Water table depth and sulphate concentration in the dipwell sampled for water chemistry, nest G, at Tor Royal: 1.6.93-29.9.94.

southwest of Tor Royal, air pollution is unlikely to be the cause of sulphate peaks at the site, because non-marine SO_4^{2-} deposited on Dartmoor rarely exceeds 0.2 mg l^{-1} day^{-1} (United Kingdom Group on Acid Rain, 1990). Rather, the winter peaks are likely to be a result of an influx of marine-derived SO_4^{2-} in precipitation (Table 5.15), since this is the third largest component of seawater behind Cl^- and Na^+. In southwest Britain, more than 60% of detected SO_4^{2-} is marine-derived (United Kingdom Review Group on Acid Rain, 1990) and it is likely that winter peaks in SO_4^{2-} are attributable to this source.

The altitude of Tor Royal may cause a further increase in SO_4^{2-} through orographic effects, principally the seeder-feeder process (Browning *et al.* 1974; United Kingdom Review Group on Acid Rain, 1990). In areas of high relief, most precipitation results from the scavenging of cap cloud by orographic cloud (Figure 5.19). In this process, air containing aerosols (including SO_4^{2-} and H^+) is lifted by higher ground and incorporated into cap cloud (the feeder) composed of droplets within the size range 3-15μm (United Kingdom Review Group on Acid Rain, 1990). These cloud droplets are efficiently scavenged by precipitation falling from higher altitude (the seeder cloud) and are therefore incorporated into the precipitation falling on areas of high relief. Chemical ion concentrations can be raised considerably by this process; Hill *et al.* (1981, in United Kingdom Group on Acid Rain, 1990) recorded between a two and three-fold increase in the concentrations of the major ions in precipitation over an altitude range of 200 m to 850 m O.D. Given the altitude of Tor Royal (395 m O.D.), it is likely that the process operates here, albeit at a smaller magnitude.

Both pH and electrical conductivity trends at Tor Royal provide an expression of the general water chemistry at Tor Royal, in a fortnightly and seasonal context. Overall, pH changed smoothly from an average of pH 4.6 during the autumn/winter months to pH 4.4 during the spring/summer months. This pattern accords well with the trend at nearby Plym

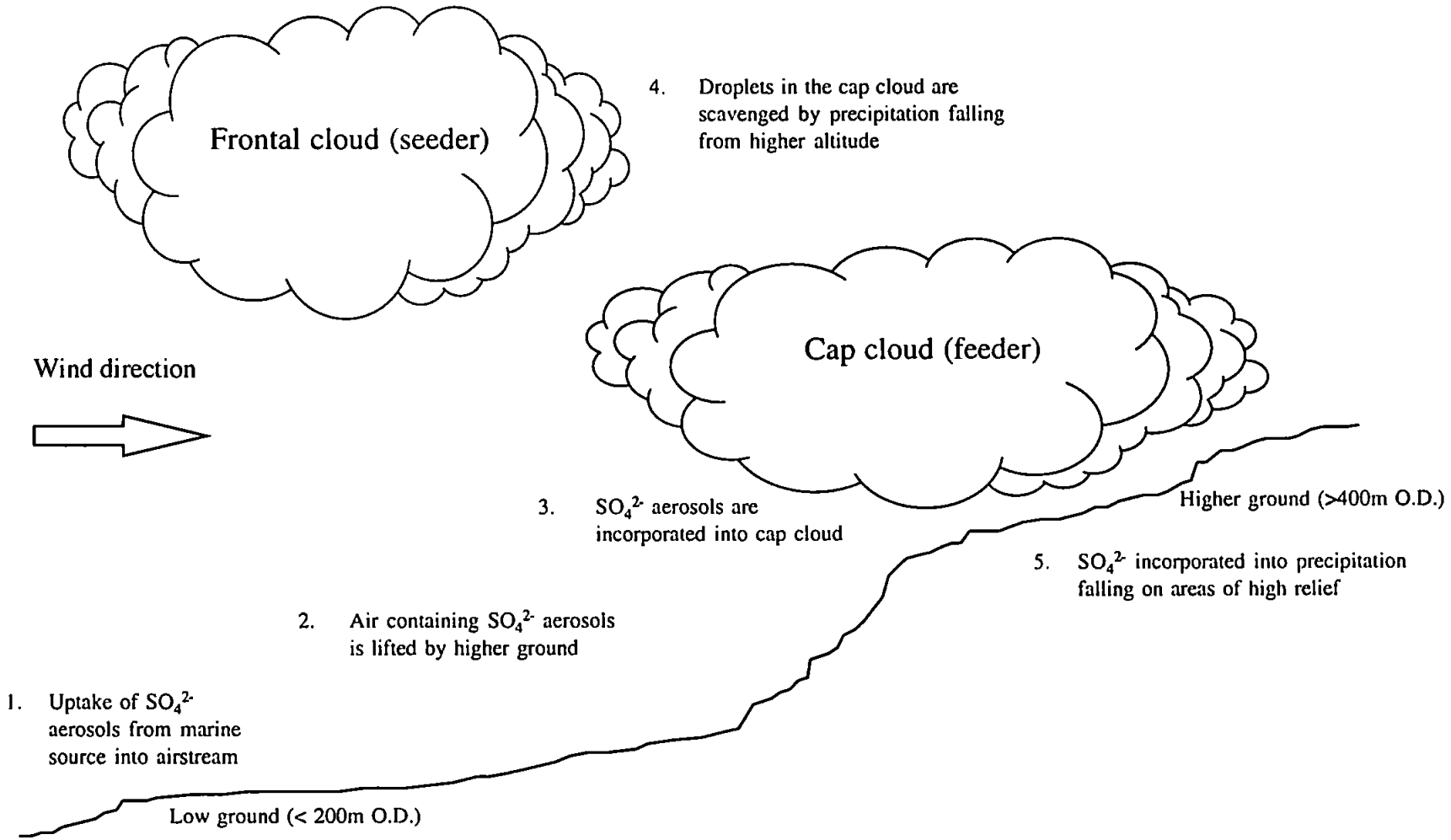


Figure 5.19: The seeder-feeder mechanism for enhanced concentrations of SO_4^{2-} in precipitation at higher altitude (after United Kingdom Review Group on Acid Rain, 1990).

Head where Proctor (1994) noted an equally smooth change from pH 4.4 during the winter to pH 4.2 during the summer.

This pattern is a result of the relative anion (SO_4^{2-}) and cation (Mg^{2+}, Ca^{2+}) composition of the peat water at Tor Royal. Where the SO_4^{2-} concentration is high, a concomitant drop in Ca^{2+} and Mg^{2+} concentrations leaves insufficient cations to balance the acidity of SO_4^{2-}. Conversely, when Ca^{2+} and Mg^{2+} levels are high and SO_4^{2-} concentrations are low, the dominance of bases raises pH. This relationship is clearly illustrated by the readings taken on days 246 and 260 (see Figure 5.7). On day 246, pH at six of the seven sites fell to between 4.0 and 4.1; the exception was site A, with pH 4.5. SO_4^{2-} concentrations on this day were the highest of the monitoring period - up to 13.50 mg l^{-1} at nest C. Conversely, the highest levels for Ca^{2+} and Mg^{2+} at this point were 1.29 mg l^{-1} and 2.10 mg l^{-1}. Clearly, increased SO_4^{2-} concentrations were responsible for depressing pH values. On the next sampling visit (day 260), pH had increased to between 4.3 and 4.7; SO_4^{2-} had dropped to between 3.33 mg l^{-1} and 4.05 mg l^{-1}; Ca^{2+} concentrations rose to between 0.57 mg l^{-1} and 1.88 mg l^{-1} and Mg^{2+} peaked between 1.7 5mg l^{-1} and 2.44 mg l^{-1}. On this occasion Ca^{2+} and Mg^{2+} concentrations were sufficient to raise the pH of sampled water.

Obviously important to the pH readings taken at Tor Royal is the seasonal influx of H^+ ions. H^+ fluctuations on mires were linked to cation exchange by Clymo (1964; 1984), who showed that uptake of selected cations (such as Na^+, K^+, Ca^{2+} and Mg^{2+}) was via cation exchange with H^+ at cation-exchange sites within the *Sphagnum* cell walls.

Clymo (1984) demonstrated the influence of *Sphagnum* on the acidity of local waters. Rainwater at pH 5.6 trickling over a *Sphagnum* plant initially became more acid (typically pH 3.0 to 3.2), but reversed towards neutrality as the H^+ ions were consumed by cation exchange. An important requirement to maintaining consistently low pH is constant growth

of the *Sphagnum* plant to provide fresh cation-exchange sites and Clymo (1984) showed that, with the regeneration of cation-exchange sites, a value of pH 4.0 could be maintained.

This corresponds well with the seasonal pattern at Tor Royal, where lower pH values during the spring and summer match the *Sphagnum* growing season from April to September. Cation exchange within the cell walls of *Sphagnum* had clearly combined with the increased production of SO_4^{2-} during periods when the water table fell, to create more acid conditions on Tor Royal during the spring and summer seasons.

Several of the nests displayed differences in pH between a hummock, a *Sphagnum* lawn and an open pool microhabitat (see Figure 5.6). Generally, pH increased from the hummock (where pH values were relatively low), through the *Sphagnum* lawn to the open pool (where pH was highest). The contrasting pH values may reflect vegetation characteristics at each microsite and, in particular, differences in the cation exchange capacity of *Sphagnum* species. Clymo (1984) identified more cation-exchange sites in the cell walls of *Sphagnum capillifolium* than in *S. cuspidatum* and it may be that the *Sphagnum papillosum* and surrounding plants are releasing more H^+ ions into the surface water than *S. cuspidatum*. This is supported by the pH readings from the pools during periods when evaporation was minimal (evaporation would raise SO_4^{2-} concentrations particularly and lower pH), but where pH is higher because there are no *Sphagnum* plants nearby to release H^+ ions.

In Figure 5.13, a consistently higher pH value is recorded at nests A and B relative to the remaining nests at Tor Royal. This is evident in the mean annual values of pH 4.7 for nest A and pH 4.6 for nest B, while the mean values for the remaining nests are pH 4.4 and 4.5. These two nests were both situated in wet heath dominated by *Carex panicea, Carex demissa, Eriophorum vaginatum, Molinia caerulea* and *Sphagnum auriculatum*. The higher

pH values may therefore relate to the vegetation composition of these sampling nests: *Sphagnum auriculatum* may release fewer H^+ ions during cation exchange. Further, livestock grazing was more intense on the wet heath than on the main mire surface and defecation products may have raised the pH of the surrounding area. Equally, the higher pH values could reflect an additional water input into the two nests, since they were not located on the main raised mire surface (Figure 4.1, page 77).

As a measure of total ionic concentration, electrical conductivity is related to the sums of cationic and anionic concentrations (Sutcliffe *et al.*, 1982). The higher the ionic content of a solution, the lower its resistivity and hence the higher its conductivity. This pattern is not particularly clear at Tor Royal because an event cannot be isolated where all ionic concentrations are minimal. The concentration of other ions that were not measured during monitoring (such as Na^+, K^+, PO_4^{2-}) may have also affected the total conductivity readings so a dip in concentrations of, for example, SO_4^{2-}, Ca^{2+} or Mg^{2+} might be counterbalanced by higher levels of Na^+, K^+ and PO_4^{2-}.

5.4.3 Implications for reconstructions of past mire water chemistry

The detailed study of water chemistry on Tor Royal has identified behaviour similar to that of water tables. While mean concentrations can be calculated, a marked seasonality in concentrations can also be identified that is common to all the ions studied and it creates a "noisy" water chemistry data set.

Water chemistry from Tor Royal for previous years is not available and it may be assumed that, because climate conditions during 1993/94 were typical of preceding years, then the water chemistry measured at the site may also be typical. But longer-term studies - of the type incorporated into the water table data for this thesis - are essential before sufficient data has been amassed to produce representative transfer functions. However, this is

unlikely in practice and, given the likelihood of data being based on 'one-shot' samples for water chemistry and the noise in this data set, it is difficult to identify a suitable season for sampling. Additionally, time limited this study to a very restricted range of ions. Monitoring of additional ions would be required to derive a more complete data set for water chemistry.

The study on Tor Royal also demonstrated the wide variability of sources for ions, even within such a restricted chemistry. In terms of palaeochemical studies on mires, reconstructions based on testate amoebae alone would be limited to reconstructing water chemistry during the mire's development. It would be impossible to extend the interpretation to infer the provenance of individual ions given the potentially large source of origin. For example, a high Cl^- concentration may be due to increased deposition at the site in precipitation, or from evaporation in pools; high SO_4^{2-} levels may result from marine sources in precipitation, or from a change to aerobic conditions after the water table falls. Simultaneous pollen, macrofossil and stratigraphical studies would be required to give a more complete palaeoenvironmental reconstruction.

5.5 Conclusions

The monitoring programme at Tor Royal Bog has provided detailed information on hydrological and water chemistry changes on an ombrotrophic bog over a period of 15 months. With the exception of Tolonen *et al.* (1992; 1994) this is the most detailed study of hydrology and water chemistry in relation to testate amoebae and is certainly the first of its type in Britain.

The study has illustrated the variability of the water table and water chemistry on an ombrotrophic mire and has identified a range of factors that influence this activity. The implications for testate amoebae studies, both in terms of modern analogues and developing

transfer functions, have also been emphasised. In particular, the seasonality of both water table movements and water chemistry means that, if single-shot samples are to be used, they must be timed to give the best representation of mean annual conditions, or at least during a period when the water table is most stable at a site. This is necessary to allow for seasonal effects on environmental data during a typical year, so that unusual climatic conditions are excluded from transfer functions. If this requirement is met then, based on the study from Tor Royal, there is no reason why a testate amoebae assemblage cannot be interpreted as reflecting typical modern conditions at the site.

The hydrological and water chemistry data collected from Tor Royal and the remaining British field sites were selected to include those factors that previous authors had linked to testacean assemblages. The data set is therefore composed of "environmental controls" which may, or may not, influence the composition and distribution of such assemblages. It is therefore essential to quantify the relative influence of each environmental control on testacean populations and this is described in Chapter 6. The chapter will assess which of the environmental parameters measured above has the strongest influence on modern testate amoebae populations and transfer functions will be derived for this variable in Chapter 7.

Chapter 6

Ecological relationships of modern testate amoebae

6.0 Introduction

The preceding chapter described the temporal variability in hydrology and selected water chemistry at Tor Royal and used this to investigate the usefulness of one-shot sampling techniques in hydroecological studies of modern testate amoebae. The chapter demonstrated that, although mean annual water table depths and chemical ion concentrations could be derived, there were considerable seasonal fluctuations about this mean. This emphasised the importance of a well-planned sampling strategy in which sampling for environmental variables takes place when water table depths are most representative of typical annual conditions on an ombrotrophic mire.

Given the main hydrological and water chemistry features that have been identified, an examination is now required of their relative influence on modern testate amoebae assemblages. This chapter will use the hydrological and water chemistry data collected from all of the British sites in an attempt to explain the modern distribution of testate amoebae. A variety of techniques will be used to assess relationships and to identify those hydrological and water chemistry parameters that have the strongest control on testate amoebae assemblages. The chapter will end by using the information to calculate optima and tolerance ranges for testate amoebae taking into account the most influential environmental parameters.

6.1 Species-environment relationships

In quantitative palaeoenvironmental reconstructions, modelling the response of modern taxa to contemporary environmental variables is a regression problem (ter Braak and Prentice, 1988; Birks, 1995). In ecology, the relationship between species abundance and associated

environmental variables (commonly termed 'environmental gradients') is explored using gradient analysis (Table 6.1). The technique is based on the concept of individual species being abundant around their particular environmental optimum (ter Braak and Prentice, 1988).

Within the broad field of gradient analysis, a number of regression analyses may be used to assess the influence of environmental controls on species distribution and to interpret species response to environmental gradients. Such analyses can be based on linear response models, unimodal response models or weighted averaging. Linear response models have a limited ecological application since a linear relationship between species and environmental factors rarely exists. Unimodal response models are extensions of the linear techniques and they incorporate Gaussian response models (ter Braak and Prentice, 1988). In this study, weighted averaging regression is used to model modern species-environment relationships because the technique has several advantages over other regression methods (see section 6.1.1).

6.1.1 Weighted averaging regression

Weighted averaging regression is based on the Gaussian model, which interprets species distribution as a unimodal response to a selected environmental factor; that is, a species will attain maximum abundance and thrive when the environmental variable reaches a particular value (the 'optimum'). Surrounding this optimum are a range of values (the 'tolerance' limits) within which the species can survive but will not thrive (Figure 6.1). The species cannot exist beyond the tolerance range. Weighted averaging techniques fit this unimodal response rather than the linear model, and allow the weighting of individual species' responses along the environmental gradient. Each method in the weighted averaging group therefore has a Gaussian counterpart (Table 6.1). Weighted averaging of site scores is the unimodal-based equivalent of multiple linear regression, weighted

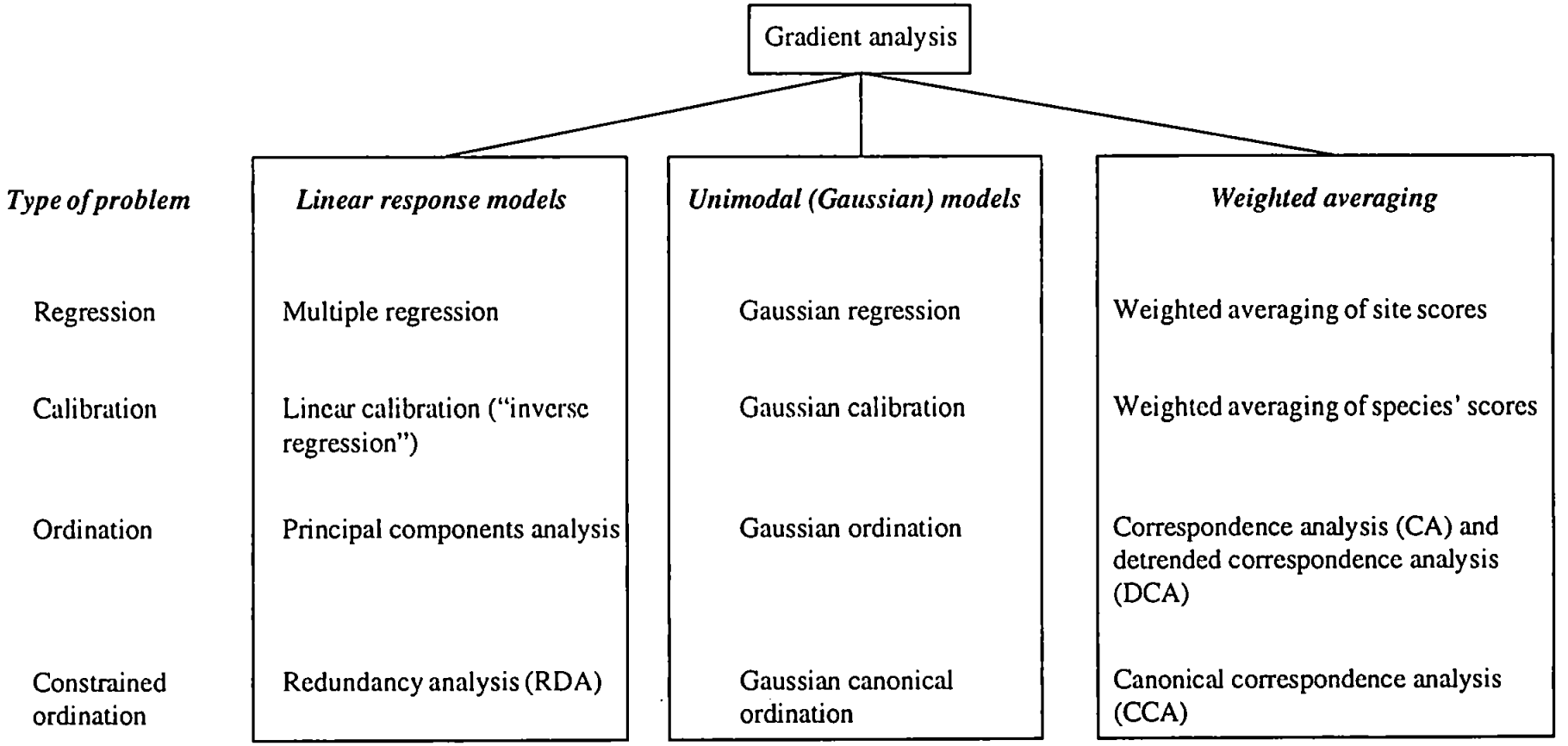


Table 6.1: Classification of gradient analysis techniques relevant to this study by type of problem, response model and method of estimation (after ter Braak and Prentice 1988, p.276). For explanation, see text.

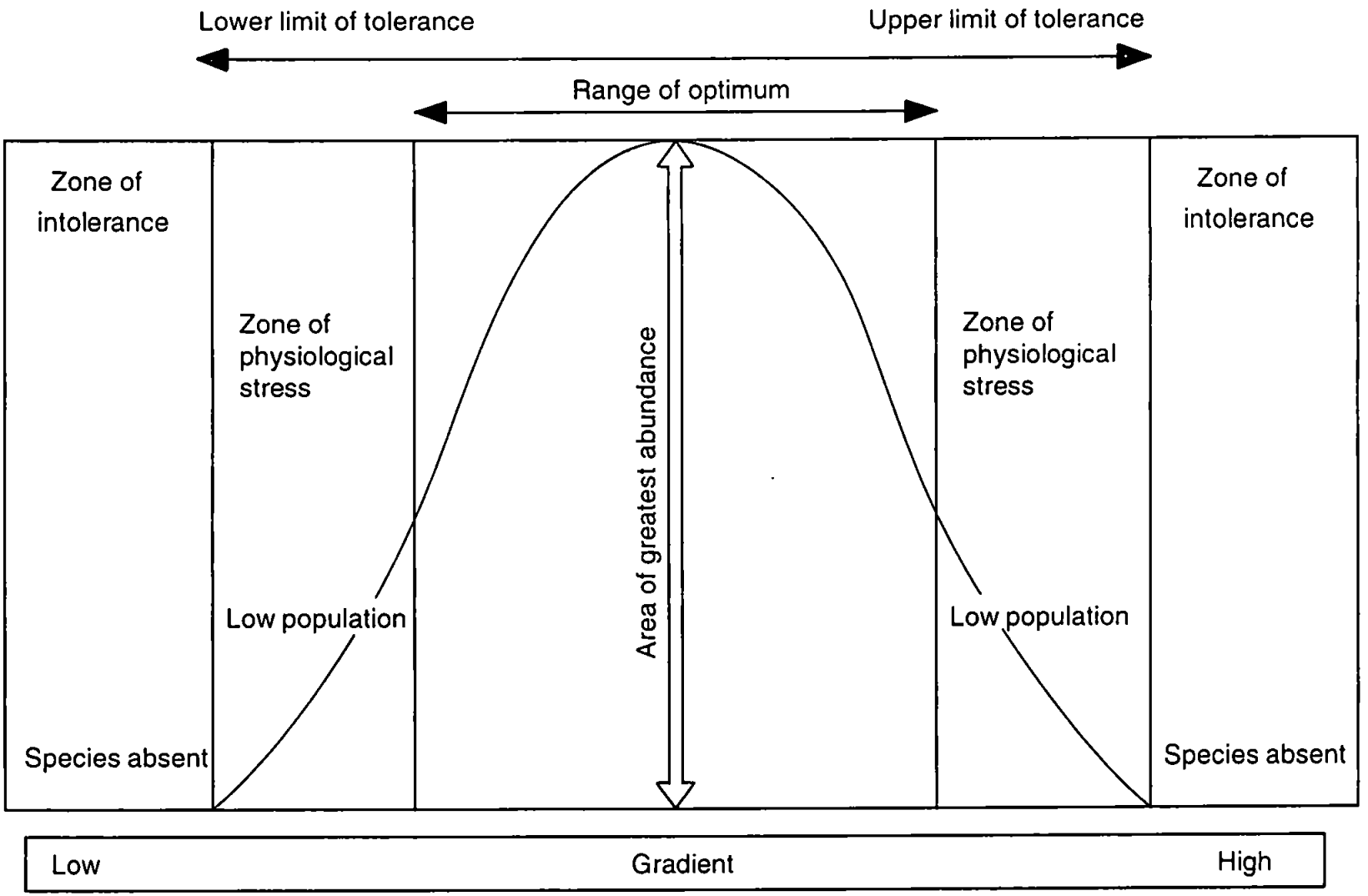


Figure 6.1: The Gaussian model of species distribution, shown as the response to a single environmental factor (redrawn from Kent and Coker, 1992).

averaging of taxa scores is the unimodal-based equivalent of inverse linear regression, while correspondence analysis and canonical correspondence analysis are the unimodal-based equivalents of principal components analysis and redundancy analysis respectively.

Since weighted averaging regression accommodates the Gaussian model, it is readily applicable to this study. On an ombrotrophic bog surface with a particular water table depth, testate amoebae species with optima close to that depth will be most abundant. Further, a species with a small water table depth tolerance range will be a better environmental indicator and therefore of more use in a palaeoecological reconstruction than one with a large range (ter Braak and van Dam, 1989). Consequently, the species with a small tolerance range can be given more weight in the weighted average regression. Indifferent taxa are of little reconstructive use and can be given a zero weighting (ter Braak and van Dam, 1989). The reconstructed water table or moisture content is generated from a testate amoebae assemblage by calculating the weighted average of the optima of the taxa present in that sample.

For this study, weighted averaging regression has the advantage that it works best with species-rich data, but where species may be absent in many of the samples (ter Braak and Juggins, 1993). Conversely, weighted averaging regression also has several shortcomings: it is sensitive to the distribution of the environmental variable in the training set; it considers each environmental variable separately and it disregards correlations that remain after fitting the environmental variable to species distributions. These residuals are often caused by environmental variables that are not taken into account in the regression (ter Braak and Juggins, 1993), but which may affect the species assemblage. As a solution, weighted averaging-partial least squares regression was introduced by ter Braak and Juggins (1993), in which the partial least squares component also considered the residuals in the regression cycle (see Chapter 7).

Of the three model groups (Table 6.1), only weighted averaging is of direct relevance to this study and, from that group in order of application, ordination, constrained ordination, regression and calibration will each be applied to the data in this study. Each method will be described in the appropriate section of this chapter and Chapter 7. The following section considers ordination methods and their application to this study.

6.1.2 Ordination methods

Ordination methods are widely used in plant ecology to provide a simplified graphical ordering of species and samples on two or three axes of variation to aid the exploration of similarities and differences between samples. More sophisticated ordination techniques allow environmental variables to be entered in the analysis to assess relationships between species, environment and axes of variation.

Ordination methods are essentially descriptive and they allow the formulation of possible causal relationships between variations in species assemblages and the environment (Kent and Coker, 1992). In this case, the testate amoebae data are the species and ordination is used to summarise variation in the testate amoebae data and to define related environmental gradients.

The methods are conveniently grouped into "indirect" or "unconstrained" ordination (correspondence analysis (CA) and detrended correspondence analysis (DCA), for example) and "direct" or "constrained" ordination (such as canonical correspondence analysis - CCA). There are several texts that discuss these techniques (see Digby and Kempton, 1987; ter Braak, 1987a,b, 1988; ter Braak and Prentice, 1988; Kent and Coker, 1992) and there is no consensus over which method gives the "best" ordination with the least distortion of data (Kent and Coker 1992, p. 233). In Britain and North America, the most popular methods of ordination are DCA and CCA (Kent and Coker, 1992).

The methods used for this study are CA and CCA. Although first introduced as an ordination technique in the social sciences, CA is now widely used in ecology (Roux and Roux, 1967; Hill, 1974; Gauch *et al.*, 1977; Digby and Kempton, 1987; Kent and Coker, 1992). Detailed mathematical and computational accounts of CA are given in ter Braak (1988), while more readable versions of its application are given in ter Braak and Prentice (1988) and Kent and Coker (1992). The following is a general account of CA in relation to this study.

As an indirect ordination technique, CA uses only the species compositional data of the samples to produce a species ordination and a corresponding sample ordination (Digby and Kempton, 1987). Weighted averaging is applied to a data set "so that quadrat scores are derived from species scores and weightings and conversely, species scores can similarly be derived from quadrat scores and weightings" (Kent and Coker, 1992 p. 215). Thus, axes of variation may suggest environmental trends, but no environmental data are used in their construction.

Although simple to compute (with the use of the CANOCO computer programme - ter Braak, 1988) and comparatively straightforward to interpret, Kent and Coker (1992) identify two problems inherent in CA - an arch effect and compression of the axes. The arch effect occurs because, in CA ordination plots, the second axis may be a quadratic distortion of the first axis (Kent and Coker 1992, p. 221). This was shown by Hill (1979) to result in a characteristic arch in an ordination plot derived from artificial data which should have formed a straight line. If this effect is transferred to subsequent axes, it becomes difficult to identify clear ecological trends. Kent and Coker (1992) suggest that when the arch effect occurs, the ordination may be interpreted by studying the distribution of points along the length of the arch, since this will clarify the environmental gradient of the first axis.

The second problem, axes compression, results from the absence of clear definitions for axes scalings (Kent and Coker, 1992). This means that points at the end of the ordination axis are plotted closer together than they should be, whereas points in the middle of the axis remain unaffected and are plotted in their true positions (see Kent and Coker, 1992 for examples of these effects).

DCA (Hill, 1974) has frequently been used to overcome the interpretation problems presented by the arch effect and axis compression, but the technique has been criticised by ter Braak (1987b) on mathematical grounds. However, it is generally accepted as an improvement on CA and is incorporated in the CANOCO computer programme used in this study.

As a direct ordination technique, CCA differs from CA and DCA because it uses additional environmental data to "constrain" the axes. In this way, axes can be more clearly associated with particular environmental variables. Computational details for CCA are given in ter Braak (1988) and the following is a general summary of the method.

CCA incorporates correlation and regression between species data and environmental factors within the ordination analysis. Using multivariate analysis and multiple regression, an ordination of plot of species and associated environmental variables is produced (Kent and Coker, 1992). Like CA, iterations continue until the scores eventually stabilise.

To facilitate environmental interpretation, species-environment or site-environment biplots derived by CCA can easily be constructed using CANODRAW Lite (Smilauer, 1992). Since species are assumed to have unimodal responses to environmental factors, reaching maximum abundance at their ecological optimum, the CCA ordination plot represents this by points that correspond to this optimum in two dimensions (ter Braak and Prentice,

1988). Environmental variables are represented in the plot by arrows - the longest arrows are most important in influencing community variation (Kent and Coker, 1992). The perpendicular position of the species points relative to the arrow indicates the strength of the relationship between the species and the environmental variable; species close to the arrow tip are strongly correlated with the environmental variable (Kent and Coker, 1992). The position of the arrow relative to the axis is also important, since it shows how closely correlated the axis is with that environmental factor (Kent and Coker, 1992).

6.2 Choice of ordination methods

CA and CCA were chosen with clear data interpretation aims in mind. CA was run first on the data set to identify the main pattern of variation in testate amoebae species composition. This technique had the advantage that no prior hypothesis was needed on the relative importance of the environmental variables on testate amoebae species distribution and it could therefore be used as an independent test of the relative importance of each environmental variable on testate amoebae assemblages. It would also indicate whether the hypotheses forwarded in Chapter 1 could be examined further by CCA.

6.3 Pilot ordination studies using the Tor Royal data set

Conducting a pilot study at the beginning of the ordination exercise had three main benefits for the research project. Firstly, it allowed different analysis techniques to be tested quickly and effectively with a minimal input of computing time. Secondly, it gave an indication of the main hydrological and water chemistry gradients affecting testate amoebae distribution within a coherent data set, without the attendant problems of measurements by different methods over different timescales. Finally, it allowed comparisons of the ordination results from a site with tight measurement controls (Tor Royal) with the British data set to assess the spatial variability in data at a larger scale.

6.3.1 Correspondence analysis of the Tor Royal data: all nests

Both CA and CCA of the Tor Royal data set were run on the CANOCO computer programme (ter Braak, 1988). For the environmental data file, the mean annual and seasonal water table depths were entered (the definitions of "mean annual" and "seasonal" are identical to those in Chapter 5), but only mean annual water chemistry values from each dipwell were used. Values for percent moisture content and bulk density (calculated for each surface moss sample from which the testate amoebae assemblages were obtained) were also entered.

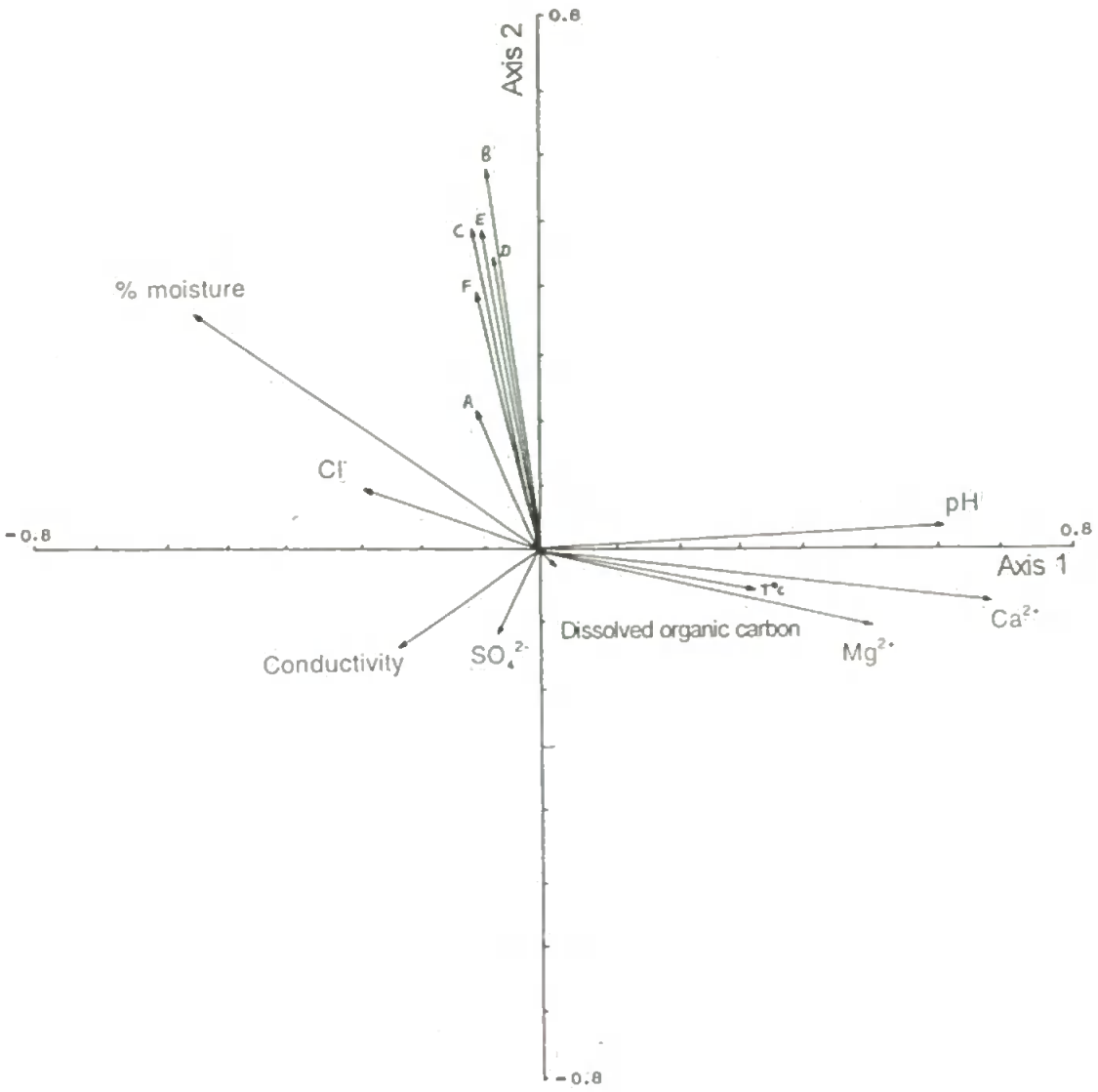
Of the 42 sampling points at Tor Royal, 28 were located in one vegetation community and only 14 were sited in a different vegetation type (wet heath). The variability of vegetation in the data set was considered too restricted to allow meaningful relationships to be established between testate amoebae assemblages and vegetation types. Therefore, vegetation data from Tor Royal were not included in the preliminary ordination work.

a) Environmental variables

In Figure 6.2, axis one (eigenvalue = 0.424; Table 6.2) is a water chemistry axis, most strongly correlated with Ca^{2+} (r= 0.7600), pH (r= 0.7112) and Mg^{2+} (r= 0.6353). These correlations are all significant at $p< 0.05$. The remaining hydrological variables are most strongly correlated with axis two (Table 6.2).

b) Site ordination

In Figure 6.2 (overlay), there is a conspicuous grouping of sites, with most of the outlying samples belonging to sampling nest A and scoring highly on axis one. Their position relative to the environmental arrows suggests that these sites are very strongly correlated with pH and Ca^{2+}. Nest A is apparently less acidic and has a higher Ca^{2+} concentration



A	Mean water table depth: summer 1993
B	Mean water table depth: autumn 1993
C	Mean water table depth: winter 1993/94
D	Mean water table depth: spring 1994
E	Mean water table depth: summer 1994
F	Mean annual water table depth (1.6.93-31.5.94)
T°C	Mean annual temperature (1.6.93-31.5.94)
A1	Sampling site

Figure 6.2: Ordination of environmental variables and sites (overlay) in the Tor Royal data set following correspondence analysis.

Variable	Axis 1	Axis 2
Eigenvalue	0.4240	0.3720
% variance explained	16.5000	10.6000
Ca^{2+}	0.7600**	-0.0977
pH	0.7112**	0.0452
Mg^{2+}	0.6353**	-0.1625
% moisture content	-0.5652**	0.4502*
Temperature	0.3514	-0.0570
Cl^-	-0.2815	0.1238
Conductivity	-0.2353	-0.1762
Mean water table depth (summer 1993)	-0.1381	0.2715
Dissolved organic carbon	-0.1038	0.2937
Mean water table depth (summer 1994)	-0.0899	0.5286**
SO_4^{2-}	-0.0787	-0.1708
Mean annual water table depth	-0.0765	0.5296**
Mean water table depth (winter 1993/4)	-0.0710	0.5592**
Mean water table depth (spring 1994)	-0.0470	-0.0140
Mean water table depth (autumn 1993)	-0.0318	0.5793**

Table 6.2 : Correlation coefficients between environmental variables and axes one and two in the Tor Royal data set, following correspondence analysis (** $p<0.05$; * $p<0.10$).

than the remaining sampling points on Tor Royal and this is confirmed by the mean annual Ca^{2+} and pH values for the nests for the site (Table 6.3).

	Mean annual value (1.6.93-31.5.94)						
Nest	A	B	C	D	E	F	G
Ca^{2+}(mg l^{-1})	0.64	0.58	0.56	0.57	0.54	0.47	0.48
pH	4.71	4.63	4.48	4.50	4.50	4.40	4.52

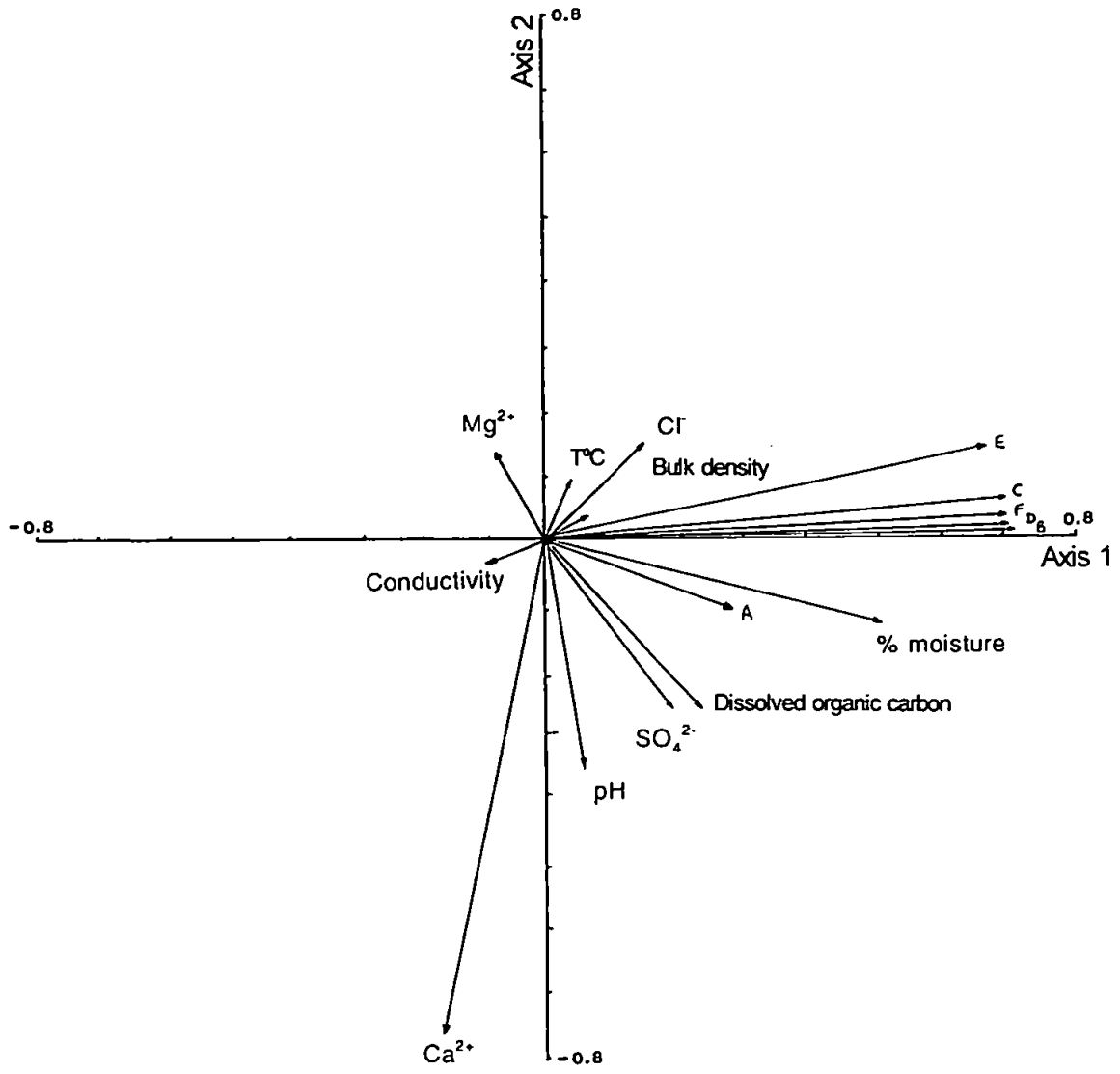
Table 6.3: Mean annual Ca^{2+} and pH values for nests at Tor Royal (1.6.93-31.5.94).

Nest B was located 10 m closer to the mire expanse than nest A and it does not form such extreme outliers as nest A along the water chemistry gradient. Within this short distance, water chemistry may have changed slightly in comparison with nest A, but this change had a strong influence on the ordination results. This is a consequence of a small data set in which a slight change in a parameter has more influence than it would in a larger data set. Experimental error is not a convincing explanation for the difference; while errors might account for the occasional rogue chemistry reading, it is highly unlikely that they would be maintained over the entire monitoring period and be confined to one nest.

6.3.2 Correspondence analysis of the Tor Royal data: nest A excluded

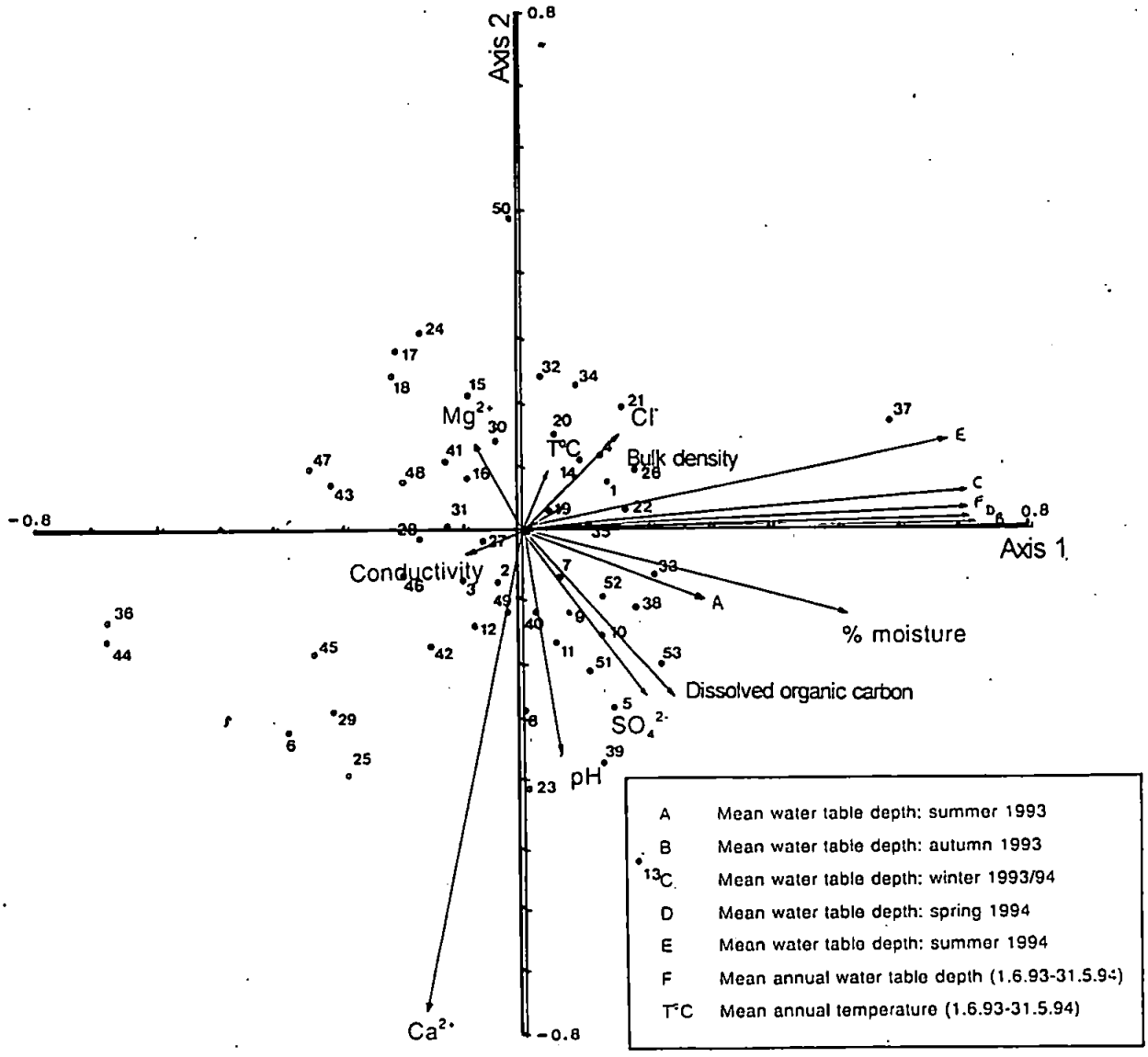
The higher pH readings at nest A lend excess weighting to the pH gradient, making it appear artificially more influential. To limit the suspected bias introduced by data from nest A, a second correspondence analysis was applied the Tor Royal data set, from which nest A had been excluded.

Ordination plots from the second CA on the Tor Royal data are shown in Figures 6.3 and 6.4. The difference between these and Figure 6.2 are striking. Removing station A has altered the overall position of the environmental gradients along the two axes by reducing



A	Mean water table depth: summer 1993
B	Mean water table depth: autumn 1993
C	Mean water table depth: winter 1993/94
D	Mean water table depth: spring 1994
E	Mean water table depth: summer 1994
F	Mean annual water table depth (1.6.93-31.5.94)
T°C	Mean annual temperature (1.6.93-31.5.94)
A1	Sampling site

Figure 6.3: Ordination of environmental variables and sites (overlay) in the Tor Royal data set following correspondence analysis. Nest A removed.



1.	Amphitrema flavum	14.	Cyclopyxis arcelloides	27.	Euglypha ciliata	40.	N. flabellulum
2.	Assulina muscorum	15.	C. eurystoma	28.	E. rotunda	41.	N. griseola
3.	A. seminulum	16.	Difflugia angulostoma	29.	E. strigosa	42.	N. marginata
4.	Arcella discoides	17.	D. bacillifera	30.	E. tuberculata	43.	N. militaris
5.	A. vulgaris	18.	D. bacillarianum	31.	Heleopera petricola	44.	N. minor
6.	Bullinularia indica	19.	D. elongata	32.	H. rosea	45.	N. parvula
7.	Corythion-Trinema type	20.	D. leidyii	33.	H. sphagni	46.	N. tincta
8.	Centropyxis aculeata	21.	D. globulosa	34.	Hyalosphenia elegans	47.	N. vitrea
9.	C. aerophila	22.	D. longicollis	35.	H. papilio	48.	Placocista spinosa
10.	C. aplanata	23.	D. oblonga	36.	H. subflava	49.	Pontigulasia spp.
11.	C. cassis	24.	D. penardi	37.	Nebela barbata	50.	Pseudodifflugia fulva
12.	Cryptodifflugia oviformis	25.	D. rubescens	38.	N. carinata	51.	Phryganella acropodia
13.	C. sacculus	26.	D. tuberculata	39.	N. collaris	52.	Trigonopyxis arcula
						53.	Trinema lineare

Figure 6.4: Ordination of environmental variables and testate amoebae species (overlay) in the Tor Royal data set following correspondence analysis. Nest A removed.

Variable	Axis 1	Axis 2
Eigenvalue	0.3620	0.3470
% variance explained	12.1000	9.6000
Mean water table depth (autumn 1993)	0.7224**	0.0501
Mean water table depth (spring 1994)	0.7146**	0.0882
Mean annual water table depth	0.7047**	0.0349
Mean water table depth (winter 1993/4)	0.7022**	0.0592
Mean water table depth (summer 1994)	0.6990**	-0.1688
% moisture content	0.5232**	-0.1330
Mean water table depth (summer 1993)	0.2946	-0.1243
Dissolved organic carbon	0.2396	-0.2685
SO_4^{2-}	0.1876	-0.2689
Cl^-	0.1639	0.1534
Ca^{2+}	-0.1546	-0.7477**
Conductivity	-0.0958	-0.0167
Mg^{2+}	-0.0776	0.1611
pH	0.0449	-0.3376
Temperature	0.0353	0.1031

Table 6.4: Correlation coefficients between environmental variables and axes one and two in the Tor Royal data set, following correspondence analysis. Nest A removed (** $p<0.05$; * $p<0.10$).

Dipwells D1, D2, D3, D5 and E1 are apparently influenced by Ca^{2+} concentrations, possibly a result of the vegetation communities at each dipwell in which Sphagna were absent (Table 4.1). Cation exchange in the walls of *Sphagnum* plants is responsible for the release of H^+ ions into the surrounding water body (Clymo, 1964). If *Sphagnum* plants are absent, this will reduce the release of H^+ ions to levels that are insufficient to equal or exceed the input of bases (such as Ca^{2+}), and the surrounding water will be less acid.

c) Testate amoebae species ordination

In Figure 6.4, the greatest variation in species occurs along the water table depth gradients of axis one. Most species cluster around the centre of the plot, but *Nebela barbata* is an outlier, attaining a high score on axis one. The lowest values for axis one are held by *Hyalosphenia subflava* and *Nebela minor*. For axis two, *Pseudodifflugia fulva* scores highly, while *Cryptodifflugia sacculus* has a low value.

From the CA it was possible to test further the hypothesis that testate amoebae species at Tor Royal are influenced primarily by the availability of water, with nutrient content (expressed as Ca^{2+} and pH) as a secondary influence. Testing this hypothesis, however, required the species' ordination to be constrained by the environmental variables. This was achieved by direct ordination, using CCA.

6.3.3 Canonical correspondence analysis (CCA) on the modified data set

CCA was chosen to examine the data sets for two reasons. Firstly, it incorporates the correlation and regression between testate amoebae data and environmental data within the analysis. Secondly, the resulting ordination axes are constrained to be linear combinations of environmental variables.

a) Environmental variables

The effect of CCA is to create an ordination plot (Figure 6.5) that is almost a mirror image of the CA plot presented in Figure 6.3. Axis one (eigenvalue = 0.290, Table 6.5), is correlated strongly with depth to water table for autumn 1993 ($r = -0.7840$, $p<0.01$); spring 1994 ($r = -0.7623$, $p<0.05$), winter 1993/94 ($r = -0.7547$ $p<0.05$), the mean annual water table depth ($r = -0.7542$ $p<0.05$) and summer 1994 ($r = -0.7178$ $p<0.05$). The correlation coefficient for moisture content ($r = -0.5158$) is significant at $p<0.10$. Summer 1993 is again identified as an unusual season, for which the correlation coefficient with axis one ($r = -0.3908$) is not significant at $p<0.10$. Hence, the rank order for seasonal water table correlations is similar to that for the seasonal representativeness of the mean annual depth to water table listed in Table 5.4. Ca^{2+} is most strongly correlated with axis 2 ($r = -0.6880$; $p<0.05$).

b) Site ordination

Although absolute values cannot be extracted from the ordination plot for environmental variables (Figure 6.5), relative values can be interpreted. At low values on axis one, the water table is close to the surface and moisture content of the surface peat is high. At high values on axis one, water table depth is greater and moisture content of the surface peat is lower. Given that dipwell 1 was located on the highest point in the nest and dipwell 6 in the lowest, it is no surprise to find that sampling points 4, 5 and 6 all cluster around the area where the depth to water table is relatively low and the moisture content high (Figure 6.5). Conversely, those sampling points suffixed 1, 2 and 3, which were located on the higher points in the sampling nest, are found where the moisture levels are low and depth to water table is greater. Points E1 and C1 illustrate this point precisely. Hummock C1 was 35 cm high and E1 was 45 cm high and, throughout the monitoring programme, the water table was always at least 35 cm and 45 cm below the hummock top at C1 and E1

Variable	Axis 1	Axis 2
Eigenvalue	0.2900	0.2660
% variance explained	15.1000	13.9000
Mean water table depth (autumn 1993)	-0.7840***	0.1850
Mean water table depth (spring 1994)	-0.7623**	0.2609
Mean water table depth (winter 1993/4)	-0.7547**	0.2581
Mean annual water table depth	-0.7542	0.2274
Mean water table depth (summer 1994)	-0.7178**	0.3562
% moisture content	-0.5156*	0.0948
Mean water table depth (summer 1993)	-0.3908	0.2884
Dissolved organic carbon	-0.2471	-0.4283
SO_4^{2-}	-0.2208	-0.3615
Conductivity	0.1699	0.2064
Mg^{2+}	0.1527	0.2682
pH	-0.1227	-0.4223
Cl^-	-0.0795	0.1193
Ca^{2+}	0.0573	0.6880**
Temperature	0.0205	0.2391

Table 6.5: Correlation coefficients between environmental variables and axes one and two in the Tor Royal data set, following canonical correspondence analysis. Nest A removed (*** $p<0.01$; ** $p<0.05$; * $p<0.10$).

respectively. Hence, C1 and E1 are found at extreme positions along the water table depth gradient.

c) Testate amoebae ordination in relation to environmental variables

The plot in Figure 6.6 presents the ordination of testate amoebae species in relation to environmental variables at Tor Royal. The species correlate more closely with depth to water table and moisture content, a relationship that is consistent with previous work on peatlands (Heal, 1962; Schönborn, 1962a,b, 1963; Charman and Warner, 1992; Tolonen *et al.*, 1992). Full consideration of individual species' responses to peatland hydrology will be given in the interpretation of the CCA on the British data set in section 6.4 below, but some features of Figure 6.6 deserve attention in this section.

Nebela barbata, a species characteristic of wetter microhabitats, which displayed an extreme position with respect to the depth to water table and moisture gradients in Figure 6.4, has been constrained by CCA and scores a low value on axis one. It is a member of a cluster of species (*Centropyxis aerophila*, *Nebela carinata*, *N. marginata*, *Heleopera sphagni* and *Centropyxis aculeata*) that are strongly positively correlated with water table depth and can be interpreted as species that are characteristic of wetter conditions.

Hyalosphenia subflava and *Nebela minor* are found at the extreme "dry" limits of the moisture gradient where depth to water table is greatest. This reflects the microhabitat of dry bog hummocks in which these two species occurred most frequently. *Bullinularia indica* and *Nebela parvula* were also more abundant in bog hummocks and are found in the same area of the ordination plot.

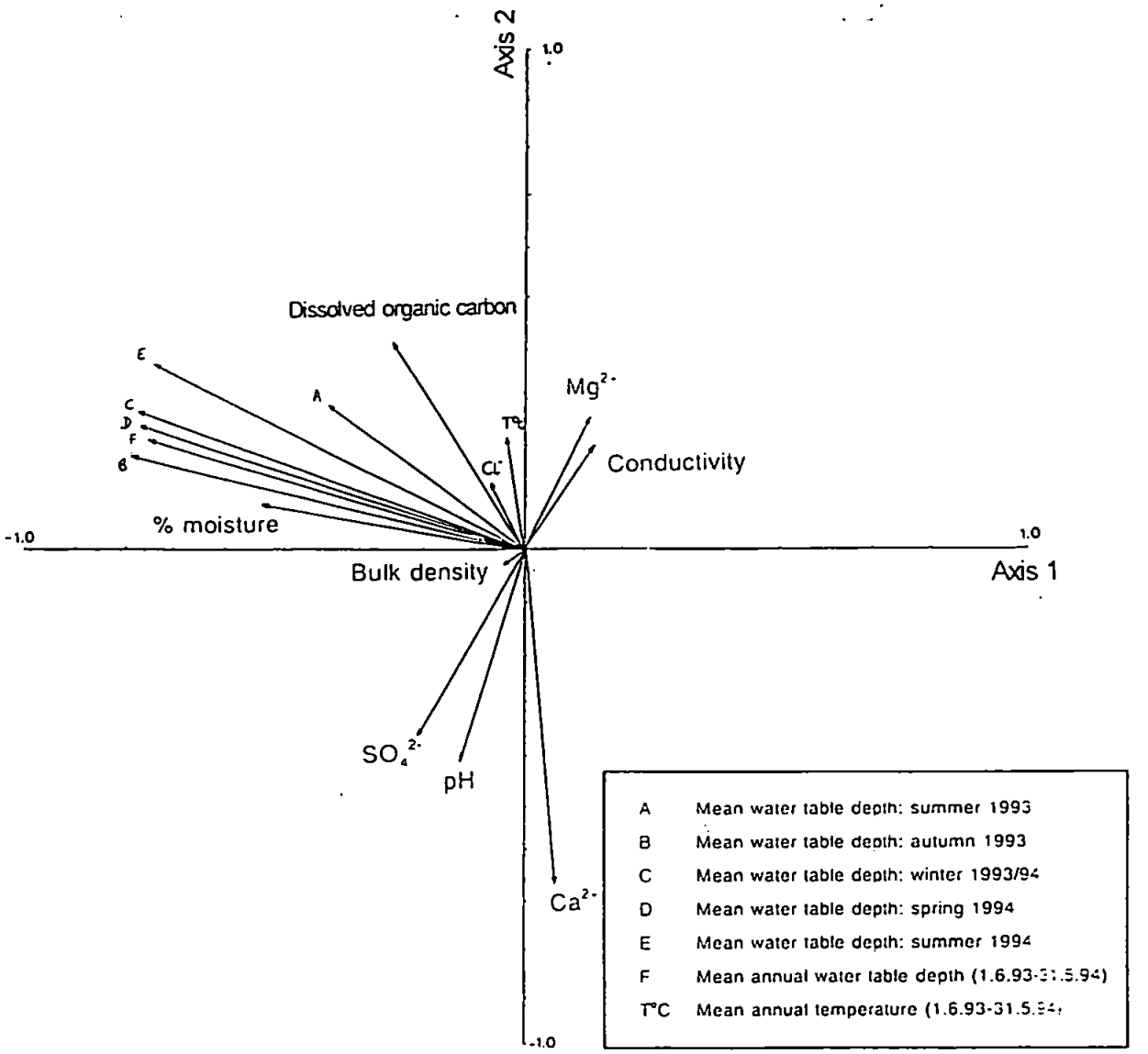


Figure 6.6: Ordination of environmental variables and testate amoebae species (overlay) in the Tor Royal data set following canonical correspondence analysis. Nest A removed.

6.3.4 Conclusions from the pilot study

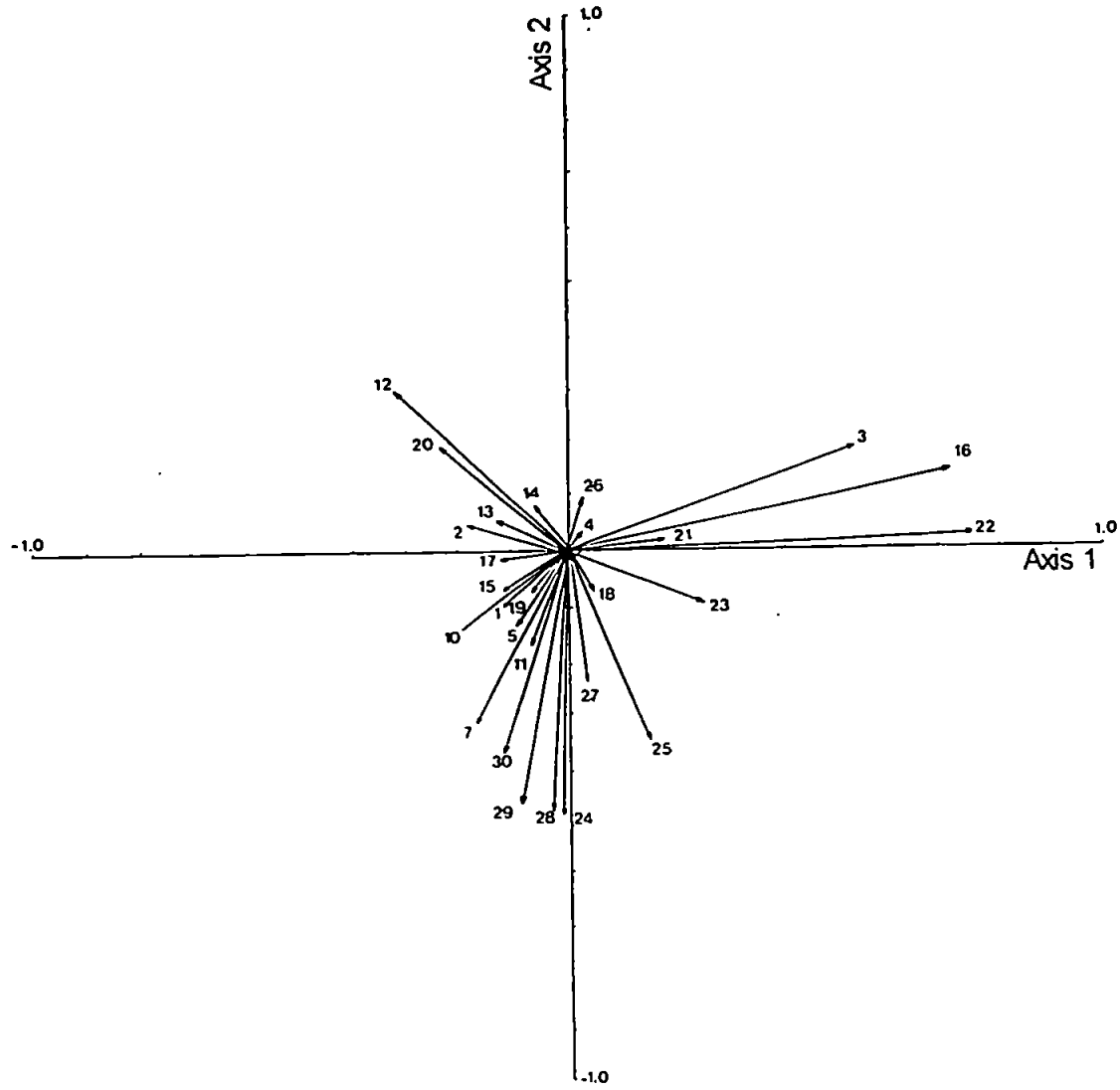
CA and CCA identified water availability (expressed as water table depth and percent moisture content) and, to a lesser extent, the nutrient status of the water as having the most important relationship with testate amoebae populations at Tor Royal. The ordination scores also indicated that seasonal water tables are related to testate amoebae assemblages at Tor Royal. The exception was summer 1993, which had already been identified as an unusual season in Chapter 5. However, the mean annual water table depth would seem to be the most meaningful measure to use and, given that water table data from the remaining sites are expressed as annual means only, this measure will be carried forward from Tor Royal into the full British data set.

Given the identification of these relationships, the next step is to confirm these for the full British data set. CA on the British data was considered unnecessary, since the principal environmental controls had been established by CA and CCA on the Tor Royal data set. CCA was therefore performed on the British data (which included the modified Tor Royal data) and the results are presented in the following section.

6.4 CCA on the British data set

a) Environmental and vegetation variables

Vegetation data were included in the British environmental data set, as a greater range of species was present than at Tor Royal. In Figure 6.7, axis one (eigenvalue = 0.304) is most strongly correlated with percent moisture content of the substrate ($r = 0.7508$; $p<0.01$: Table 6.6). This is followed by *Menyanthes trifoliata* ($r = 0.7294$; $p<0.01$), *Sphagnum cuspidatum* ($r = 0.5570$; $p<0.05$) and *Erica tetralix* ($r = 0.3231$; $p<0.10$). Axis one is clearly a hydrological gradient; percent moisture content is a direct expression of water availability and *M. trifoliata*, *S. cuspidatum*, *E. tetralix* and bulk density are all related to water table



1.	Sphagnum auriculatum	16.	Menyanthes trifoliata
2.	S. capillifolium	17.	Molinia caerulea
3.	S. cuspidatum	18.	Myrica gale
4.	S. imbricatum	19.	Polytrichum commune
5.	S. magellanicum	20.	Bulk density
6.	S. palustre	21.	Open water
7.	S. papillosum	22.	% moisture
8.	S. pulchrum	23.	Water table depth
9.	S. recurvum	24.	Conductivity
10.	Calluna vulgaris	25.	Temperature
11.	Carex species	26.	pH
12.	Erica tetralix	27.	Cl^-
13.	Eriophorum spp.	28.	SO_4^{2-}
14.	Hypnaceous mosses	29.	Ca^{2+}
15.	Juncus spp.	30.	Mg^{2+}

Figure 6.7: Ordination of environmental variables in the British data set following canonical correspondence analysis.

Variable	Axis 1	Axis 2
Eigenvalue	0.3040	0.2370
% variance explained	13.9000	10.9000
% moisture content	0.7508***	0.0220
Menyanthes trifoliata	0.7294***	0.1521
Sphagnum cuspidatum	0.5570**	0.1874
Erica tetralix	-0.3231*	0.2714
Mean annual water table depth	0.2554	-0.1139
Bulk density	-0.2416	0.1935
Calluna vulgaris	-0.2172	-0.1559
Sphagnum capillifolium	-0.2020	0.0597
Eriophorum spp.	-0.1909	0.0660
Open water	0.1855	0.0589
Sphagnum papillosum	-0.1728	0.3285*
Temperature	0.1530	-0.3603*
Sphagnum magellanicum	-0.1403	-0.1027
S. auriculatum	-0.1252	-0.0999
Molinia caerulea	-0.1186	-0.0288
Juncus spp.	-0.1018	-0.0868
Ca^{2+}	-0.0918	-0.4852**
Carex spp.	-0.0885	-0.1426
Mg^{2+}	-0.0687	-0.4916**
Polytrichum commune	-0.0531	-0.0350
Myrica gale	0.0425	-0.0824
Hypnum cupresseforme	-0.0407	0.0106
Cl^-	0.0303	-0.2518
SO_4^{2-}	-0.0262	-0.4913**
pH	0.0220	0.0814
Conductivity	-0.0178	-0.3742**
Sphagnum imbricatum	0.0170	0.0170
S. pulchrum	-0.0074	-0.0650
S. recurvum	-0.0073	-0.4716**

Table 6.6: Correlation coefficients between environmental variables and axes one and two in the British data set, following canonical correspondence analysis (*** p <0.01; ** p<0.05; * p<0.10).

depth. *M. trifoliata* and *S. cuspidatum* thrive in very wet conditions, particularly bog pools, while *E. tetralix* usually occupies drier habitats. The remaining vegetation species have negligible influence in the ordination. A partial CCA performed on the water table data alone gave r= -0.7079 ($p<0.01$; eigenvalue = 0.133) and explained 49% of the variance along axis one, confirming the influence of water table depth and suggesting that the co-correlation of the vegetation and hydrological variables was masking the real influence of water table on testate amoebae in the British data set.

Axis two is strongly associated with water chemistry, although the correlation is less than for hydrology. Of the chemical ions, Mg^{2+} is most strongly correlated with axis two (r= -0.4916), followed by SO_4^{2-} (r= -0.4913) and Ca^{2+} (r= -0.4852); all are significant at $p<0.05$. The presence of *S. recurvum* which, at r= -0.4716 ($p<0.05$) is equally significantly correlated with axis two, reflects the species' distribution in the British data set. This species was most abundant in the schwingmoors of Chartley Moss and Llyn Mire (Table 4.2) whose water chemistry differed from the remaining British field sites (see below).

The position of sites and samples relative to axis one in Figures 6.8 and 6.9 can be interpreted primarily in terms of hydrology (water table depth and percent moisture content), with water chemistry as a secondary control.

b) Site ordination

In Figure 6.8, most of the sites cluster around the intersection of axes one and two, but there are notable outliers from Coladoir Bog around the *S. cuspidatum* and *M. trifoliata* gradient. These samples all come from nests B, C and D, which were all situated within, or on the edge of, bog pools. In all cases, the hydrophilous species *Sphagnum cuspidatum* and *Menyanthes trifoliata* were dominant and thus it is not surprising to find a strong correlation between site and vegetation type here.

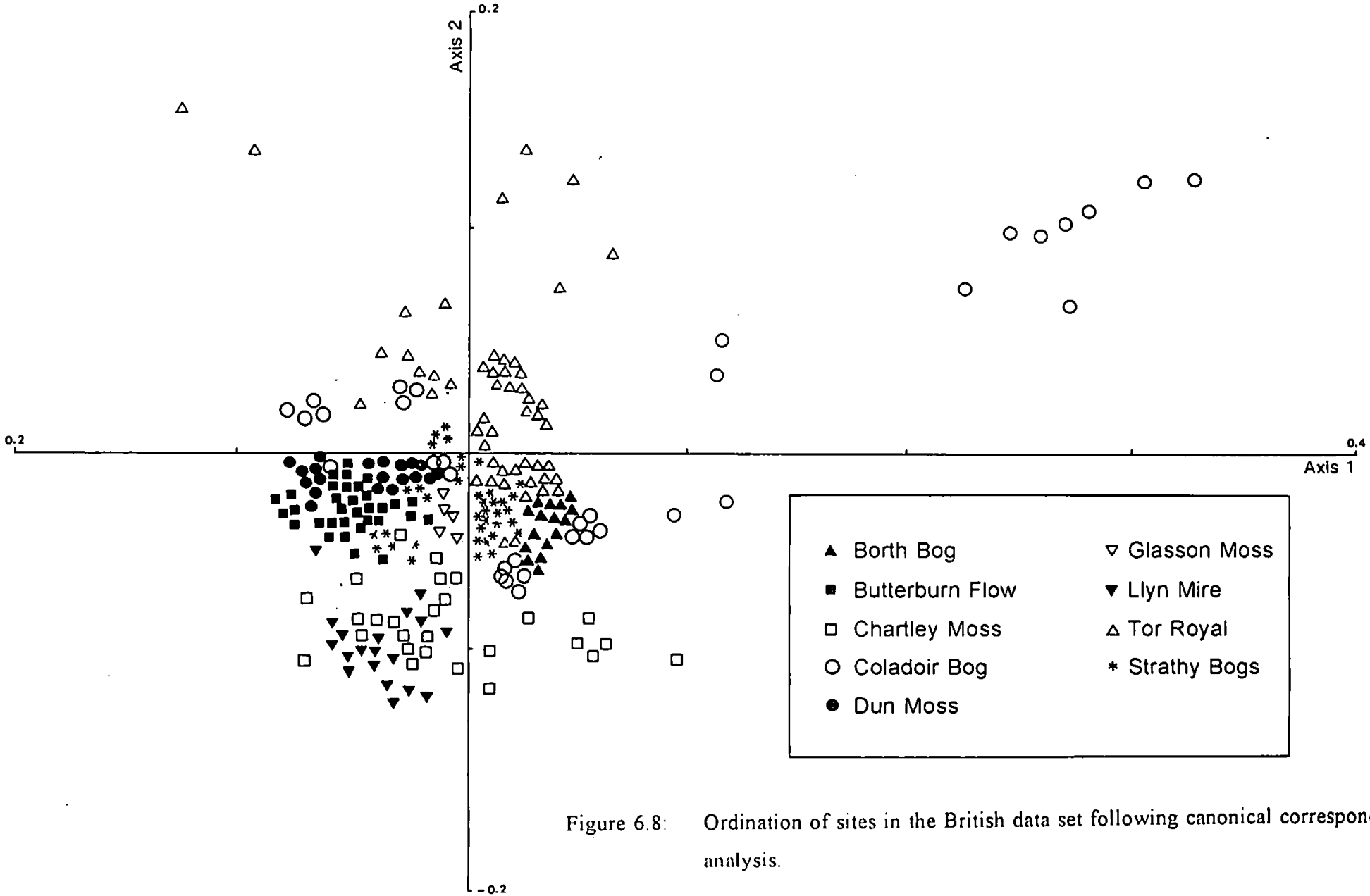


Figure 6.8: Ordination of sites in the British data set following canonical correspondence analysis.

The tight clustering of the British sites around the axes origins reflects the restricted variability of water chemistry conditions. The research project required that only oligotrophic sites were sampled; their substrate is rain-fed and hence they maintain low nutrient status. The variation that does exist comes from the inclusion of Chartley Moss and Llyn Mire. Both are "schwingmoors" (a raft of peat floating above a deep water body) and although the middle of the raft comprises oligotrophic *Sphagnum* peat, the nutrient status improves with transition to the drier margins. In the fieldwork programme, samples were taken from the drier margins of both sites as well as from the central *Sphagnum* raft and it is these samples (such as sample nests C and D at Chartley Moss) which contribute the small amount of variation in the water chemistry data. The nutrient status at Chartley Moss is further enhanced by a previous cover of *Pinus sylvestris* woodland, cleared in 1990. The influence of tree canopies on the chemistry of rain water reaching the surface of Chartley Moss has been reported by Ahmad-Shah and Rieley (1989). They showed a supplementation of Ca^{2+}, SO_4^{2-}, NO^{3-} and Cl^- ions in precipitation falling through the tree canopies and that this was greatest under the *Pinus sylvestris* canopy. Additional inputs were thought to originate primarily from dust raised by ploughing of nearby fields, with a contribution to higher nitrate levels from rook colonies in older *Pinus sylvestris*. This would certainly account for the higher nutrient levels at sample nest D (which was located on the site of a recently-cleared *Pinus sylvestris* canopy) which are shown in Table 6.7.

	Nest A	Nest B	Nest C	Nest D
pH	4.4	4.4	3.8	5.1
Ca^{2+}(mg l^{-1})	6.52	7.83	4.60	9.82
SO_4^{2-}(mg l^{-1})	30.84	28.90	14.34	32.72
Cl^- (mg l^{-1})	21.74	20.65	13.54	23.84

Table 6.7: Mean pH and concentrations of selected chemical ions from sampling nests at Chartley Moss. For vegetation details at each nest, see Table 4.2).

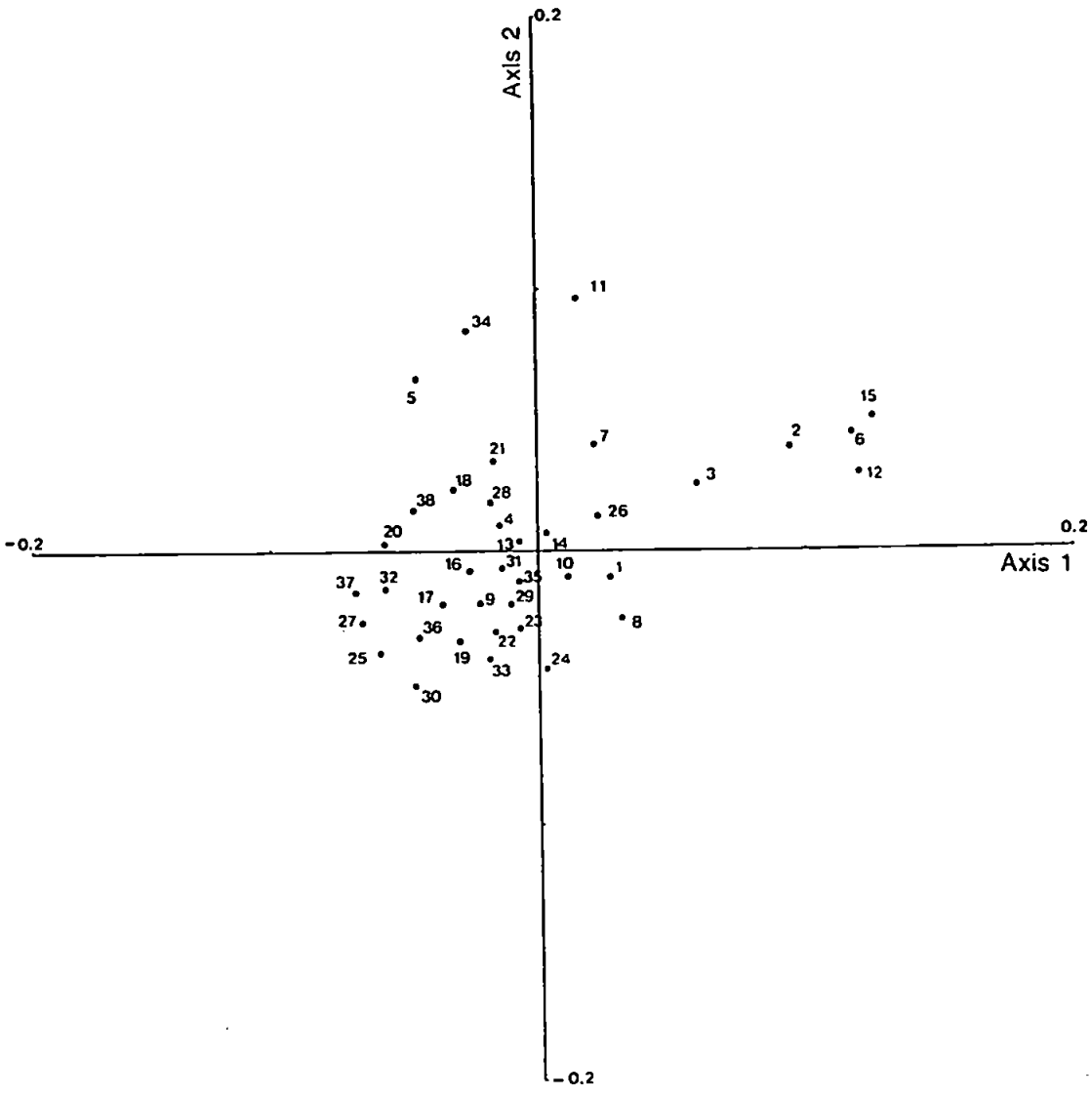
c) Testate amoebae species ordination in response to environmental and vegetation variables

Figure 6.9 presents the ordination plot for testate amoebae; only species with greater than 16 occurrences (an arbitrary 10% of the total) are shown on the plot. This filtering was conducted as one cannot be confident that an appearance in less than 16 samples accurately represents the species' environmental optimum and the species is therefore of limited value for deriving transfer functions. Accordingly, from the 78 testate amoebae species encountered in the British data set, 38 were selected for further analysis.

Testate amoebae ecology

A full account of testate amoebae ecology is given with respect to other published work in section 6.8, since this is where optima and tolerances for individual species for selected environmental variables are calculated. For the purposes of this present section, a brief interpretation of the species ordination derived from CCA (Figure 6.9) is given in the following paragraphs.

Species that are found at the highest moisture levels are *Difflugia rubescens, Arcella discoides, Centropyxis aerophila, D. bacillifera, Assulina muscorum, Centropyxis aculeata* and *Nebela carinata. Amphitrema flavum* and *Cyclopyxis eurystoma* are found where water tables are closest to the ground surface. This accords very well with the CCA ordination plot from Tor Royal (Figure 6.6) where, for example, *Nebela carinata* and *Centropyxis aculeata* occur in "wetter" areas. Likewise, the xerophilous species in Figure 6.6 such as *Bullinularia indica* and *Nebela vitrea* are also xerophilous species in Figure 6.9. It is also possible to identify species with a less extreme position along the hydrological gradient, since these are clustered around the axes origins. *Difflugia leidyi, Nebela minor*



1.	Amphitrema flavum	20.	Heleopera petricola
2.	Arcella discoides	21.	H. rosea
3.	Assulina muscorum	22.	H. sphagni
4.	A. seminulum	23.	Hyalosphenia subflava
5.	Bullinularia indica	24.	H. papilio
6.	Centropyxis aerophila	25.	H. subflava
7.	C. aculeata	26.	Nebela carinata
8.	Corythion-Trinema type	27.	N. collaris
9.	Cyclopyxis arcelloides	28.	N. flabellulum
10.	C. eurystoma	29.	N. griseola
11.	Difflugia angulostoma	30.	N. militaris
12.	D. bacillifera	31.	N. minor
13.	D. leidyi	32.	N. parvula
14.	D. penardi	33.	N. tincta
15.	D. rubescens	34.	N. vitrea
16.	Euglypha ciliata	35.	Phryganella acropodia
17.	E. rotunda	36.	Placocista spinosa
18.	E. strigosa	37.	Trigonopyxis arcula
19.	E. tuberculata	38.	Trinema lineare

Figure 6.9: Ordination of testate amoebae species in the British data set following canonical correspondence analysis.

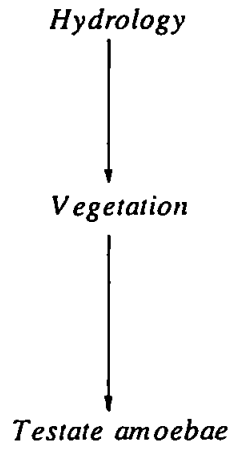
and *Euglypha ciliata* are found in relatively wetter conditions than *Euglypha rotunda, Nebela militaris* and *N. parvula.*

Testate amoebae: hydrology- or vegetation-controlled ?

Given the strong correlations between axis one and plant species (for example, *Menyanthes trifoliata* and *Sphagnum cuspidatum*) in addition to the expected hydrological parameters, it is important to investigate the role of vegetation in the modern distribution of testate amoebae. From the evidence presented in Figure 6.7, it could be argued that vegetation equals hydrology as a control on modern testate amoebae distribution. Evidence is required to establish whether (a) vegetation independently influences testate amoebae distribution or whether (b) the inferred importance of vegetation from the CCA ordination plot is a result of the co-dependence on hydrology of vegetation and testate amoebae (Figure 6.10).

This issue can be resolved by investigating several sampling points where vegetation characteristics are variable, but where water availability and testate amoebae assemblages remain constant. Nest F at Coladoir Bog was located in a pool colonised by *Menyanthes trifoliata* (20% covering) and *S. cuspidatum* (80%). Dipwell E4 on Tor Royal was situated in a pool with only a 15% covering of *Eriophorum vaginatum* over bare peat. In Figure 6.7, *M. trifoliata* and *S. cuspidatum* - in addition to moisture content - were shown to have a strong influence on testate amoebae assemblages. In Figure 6.9, four testate amoebae species are strongly correlated with this vegetation - *Difflugia rubescens, Centropyxis aerophila, Nebela carinata* and *D. bacillifera.* As expected, the same four species dominate the testate amoebae assemblage in nest F at Coladoir Bog. However, the same four species also dominate the testate amoebae assemblage at point E4 at Tor Royal, even though *S. cuspidatum* and *M. trifoliata* are absent. Common to both sampling points, however, is a high moisture content and high water table (both are in pools) and it is likely that the distribution of these four species is governed by hydrology rather than vegetation.

a) Hydrology controls vegetation assemblages, which then influence testate amoebae. A direct link between testate amoebae and hydrology cannot be made.



b) Vegetation and testate amoebae assemblages are independently influenced by hydrology. A direct link between testate amoebae and hydrology exists.

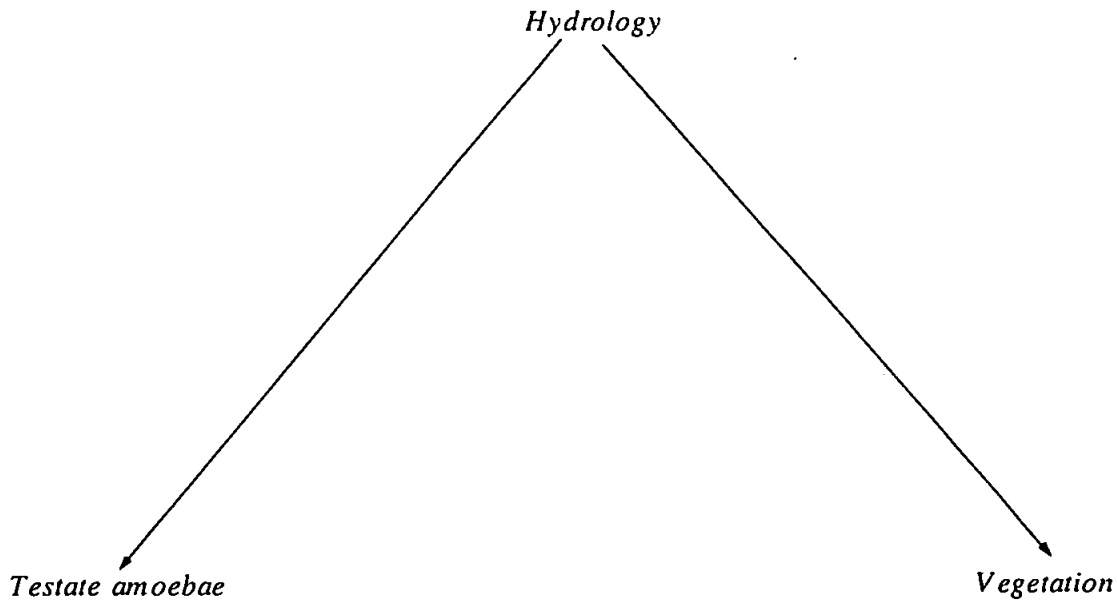


Figure 6.10: Possible environmental controls on testate amoebae assemblages.

There is a similar trend in more xerophilous conditions. In Figure 6.9, *Bullinularia indica, Cryptodifflugia sacculus* and *Nebela vitrea* occur in dry conditions and are associated with *Erica tetralix* (characteristic of drier ground). However, *E. tetralix* is not always a dominant component of vegetation assemblages in the dry areas sampled. For example, for hummocks of 20-40 cm height, where the water table is commonly greater than 10 cm deep, *Erica tetralix* ranges from an important component (> 30% surface cover) at nest A at Strathy Bogs and dipwells F1 and E1 at Tor Royal, to absent or very rare (< 1% surface cover) at nest A at Borth Bog, nest D at Llyn Mire and dipwell C1 at Tor Royal. At all these nests, however, *B. indica, C. sacculus* and *N. vitrea* are all important components (> 10%) of the testate amoebae assemblage.

Given this variable relationship between testate amoebae assemblages and plant species with a strong correlation with axis one (Table 6.6), the remaining vegetation variables probably exert negligible influence over testate amoebae distributions. Rather, hydrological conditions simultaneously, but independently, influence testate amoebae species and vegetation. One possible influence that plant species may exert on testate amoebae is a morphological one. Bryophytes, and especially *Sphagnum*, have a more suitable structure for the retention of water films than most higher plants. They may therefore raise the moisture level of the substrate under otherwise similar hydrological conditions.

b) Species response to water chemistry

There is no clear relationship between testate amoebae species and water chemistry in the British data set. This probably reflects the restricted water chemistry data that were collected in this study. The other ions that were not measured may have a stronger influence on testate amoebae distribution. For example, Tolonen *et al.* (1994) found that the C/N ratio of the peat was an important control on species distribution in Finland.

The restricted range of water pH in this study makes it impossible to differentiate between species assemblages on the basis of pH. This contrasts with Heal (1961) who, with a broader range of water chemistry samples from mire and fen habitats, was able to differentiate between assemblages in the two habitat types on the basis of this determinand (see section 3.2). Charman and Warner (1992) identified pH as a secondary control on testate amoebae species distribution and abundance in a study on a Canadian site, but there is insufficient evidence from the present study to identify the same role for pH in British ombrotrophic mires. More information, on a wider range of water chemistry and peatland sites, is required before the potential of testate amoebae as water chemistry indicators in mires can be assessed.

6.5 Conclusions from the ordination results

CA on the full and modified Tor Royal data set tested the hypothesis that water availability (expressed as moisture content and depth to water table) was the most important control on modern distributions and abundances of testate amoebae, with water chemistry as a secondary influence. Corroborating evidence for this hypothesis was also supplied by CCA on the Tor Royal data set. However, while a CCA applied to the full British data set confirmed the importance of water availability on testate amoebae populations, it failed to identify water chemistry as a significant secondary control. This was probably a consequence of the restricted range of water chemistry which was sampled.

This study, in common with previous quantitative investigations (Warner, 1989; Tolonen *et al.* 1992, 1994; Charman and Warner, 1992; Warner and Charman, 1994) has expressed water availability as depth to water table and the moisture content of the substrate. Given that these two variables have been identified as the most important controls on modern testate amoebae, weighted averages for testate amoebae optima and tolerances of these two variables may be calculated. This is described in the following section.

6.6 Determining individual species' responses to hydrology

For this study, mean annual water table depth is a logical water table parameter to consider, given its close relationship with testate amoebae species and the paucity of data regarding average seasonal water table depths from all British sites. In addition, analysis of the Tor Royal data showed that this parameter is a reasonable summary of water table characteristics. Hence, percent moisture content and mean annual water table depth will be the subject of all subsequent analyses.

6.6.1 Calculation of species' optima and tolerances

Weighted averages for each species' optimum water table depth and moisture content were calculated using the regression equation of Oksanen *et al.* (1988):

$$w_i = \frac{\Sigma y_{ij}\, x_j}{\Sigma y_{ij}}$$

where w_i is the weighted average of percent moisture or depth to water table for species *i*, which occurs at *y*% abundance at site *j*, which has the moisture content or depth to water table x_j. This means that the weighted average for each species is measured in the units of *x* and the values of *x* are weighted by species abundance (Oksanen *et al.*, 1988). Oksanen *et al.* (1988) make the important observation that if the species abundances are unimodal then the weighted average is an "unbiased estimate of the true optimum" Oksanen *et al.*, 1988; p.41). Tolerance limits were produced for this study by calculating the standard deviation of the weighted average from the expression:

$$s_i = ((\Sigma y_{ij}\ x^2 - (\Sigma y_{ij}\ x_j)^2/\Sigma y_{ij})/\Sigma y_{ij})^{1/2}$$

(Oksanen *et al.*, 1988)

These were expressed as 95% confidence limits by calculating ± two standard errors from

$$\frac{2.\ s_i}{\sqrt{n}}$$

where n = the numbers of samples in which the species occurs.

6.7 Discussion of the weighted averages

Species' optima for percent moisture and water table depth are shown in Figures 6.11 and 6.12 respectively for Tor Royal and in Figures 6.13 and 6.14 for the full British data set. These are the first quantitative plots of their kind produced in Britain. The following discussion is divided into three sections which compare (i) species' hydrological optima from the Tor Royal and British data sets; (ii) hydrological optima for species in the British data set; (iii) this study with previous studies conducted in Canada, Finland and continental Europe.

6.7.1 Comparison of the Tor Royal and British data sets

For the separate parameters of water table depth and moisture content of host substrate, two weighted averaging exercises were conducted. Firstly, weighted averaging was applied to the Tor Royal data set in isolation from the remaining British data (in the same way that the Tor Royal data set had been isolated from the remaining British data in preliminary ordination exercises). Secondly, the Tor Royal data was included in the full British data set and identical weighted averaging was applied to the data. The two data sets were separated to investigate the influence of data set size upon the weighted averages and to assess local versus regional variability in species-environment relationships.

Fewer species appear in the Tor Royal plots (Figures 6.11 and 6.12) than in the plots for the full British data set (Figures 6.13 and 6.14) because "rare" taxa (those with less than 4 occurrences; equivalent to appearances in less than 10% of the samples) were excluded from the Tor Royal data set, in the same way that rare taxa had been excluded from the British data set above. Accordingly, 28 species are shown in each plot for Tor Royal and 38 are shown in the British plots.

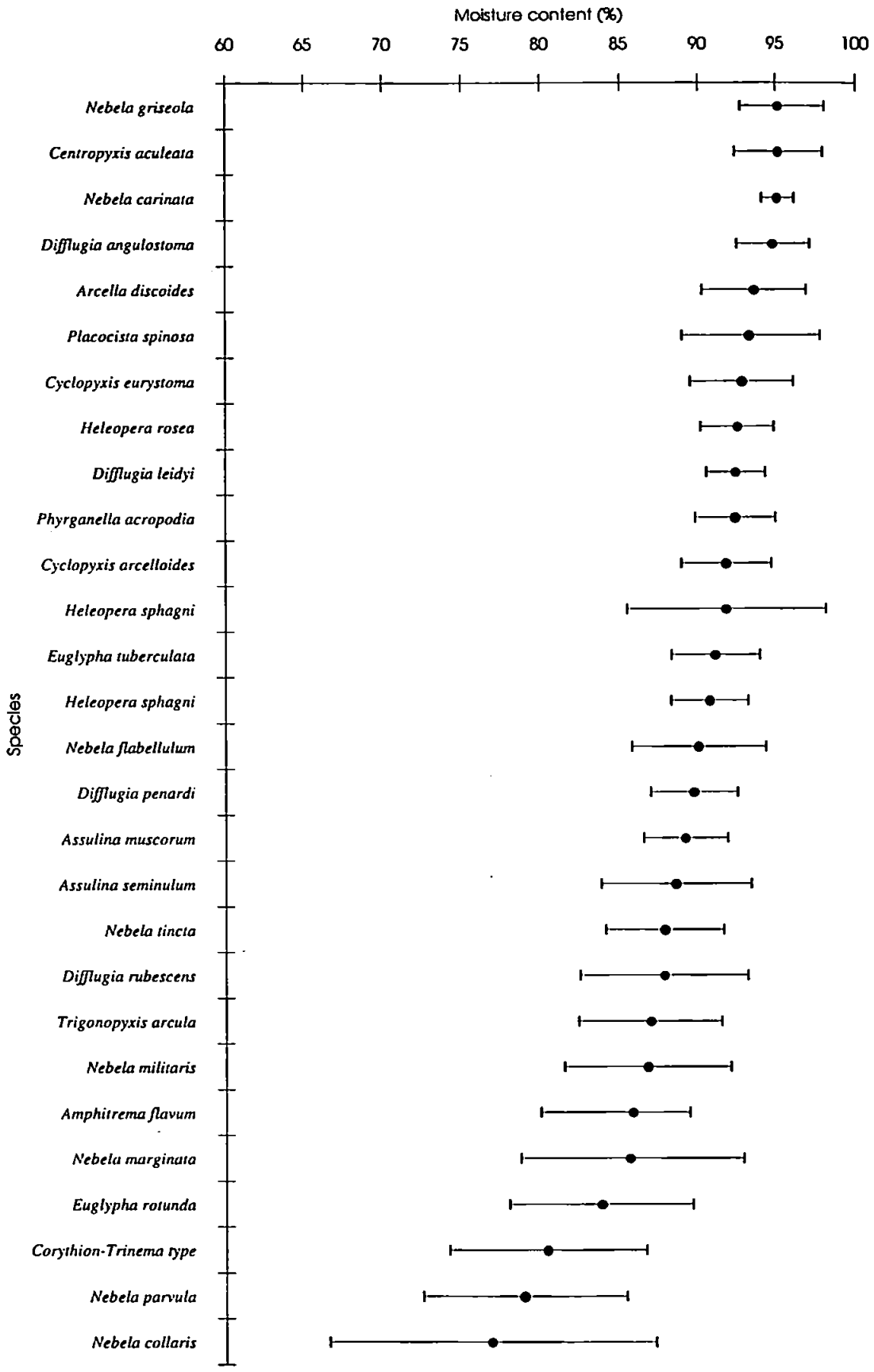


Figure 6.11: Species' optima (filled circles) and tolerances (error bars) for moisture content at Tor Royal shown as the weighted average ± two standard errors. Only those species with > 4 occurrences (10% of samples) are shown.

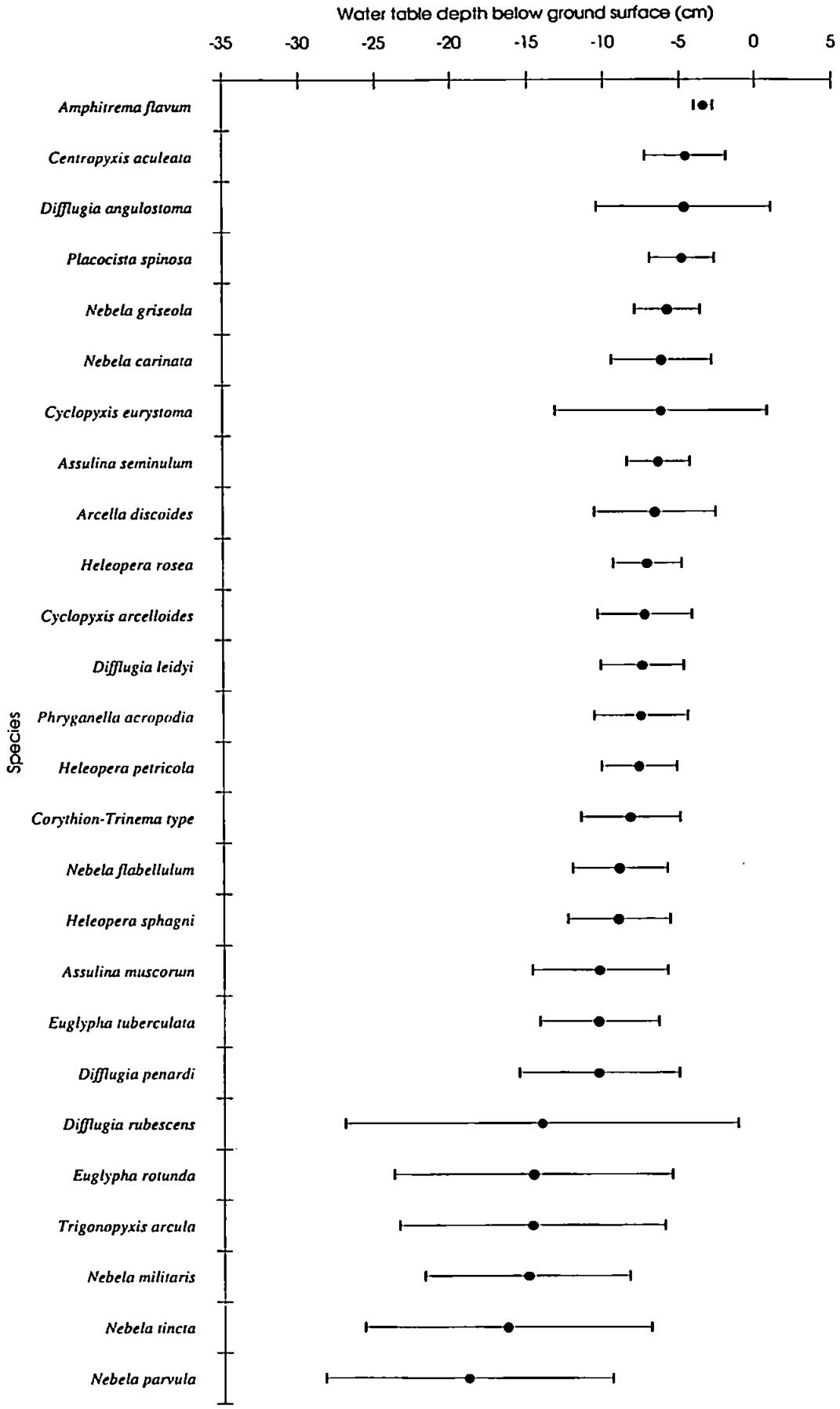


Figure 6.12: Species' optima (filled circles) and tolerances (error bars) for water table depth at Tor Royal shown as the weighted average ± two standard errors. Only those species with > 4 occurrences (10% of samples) are shown.

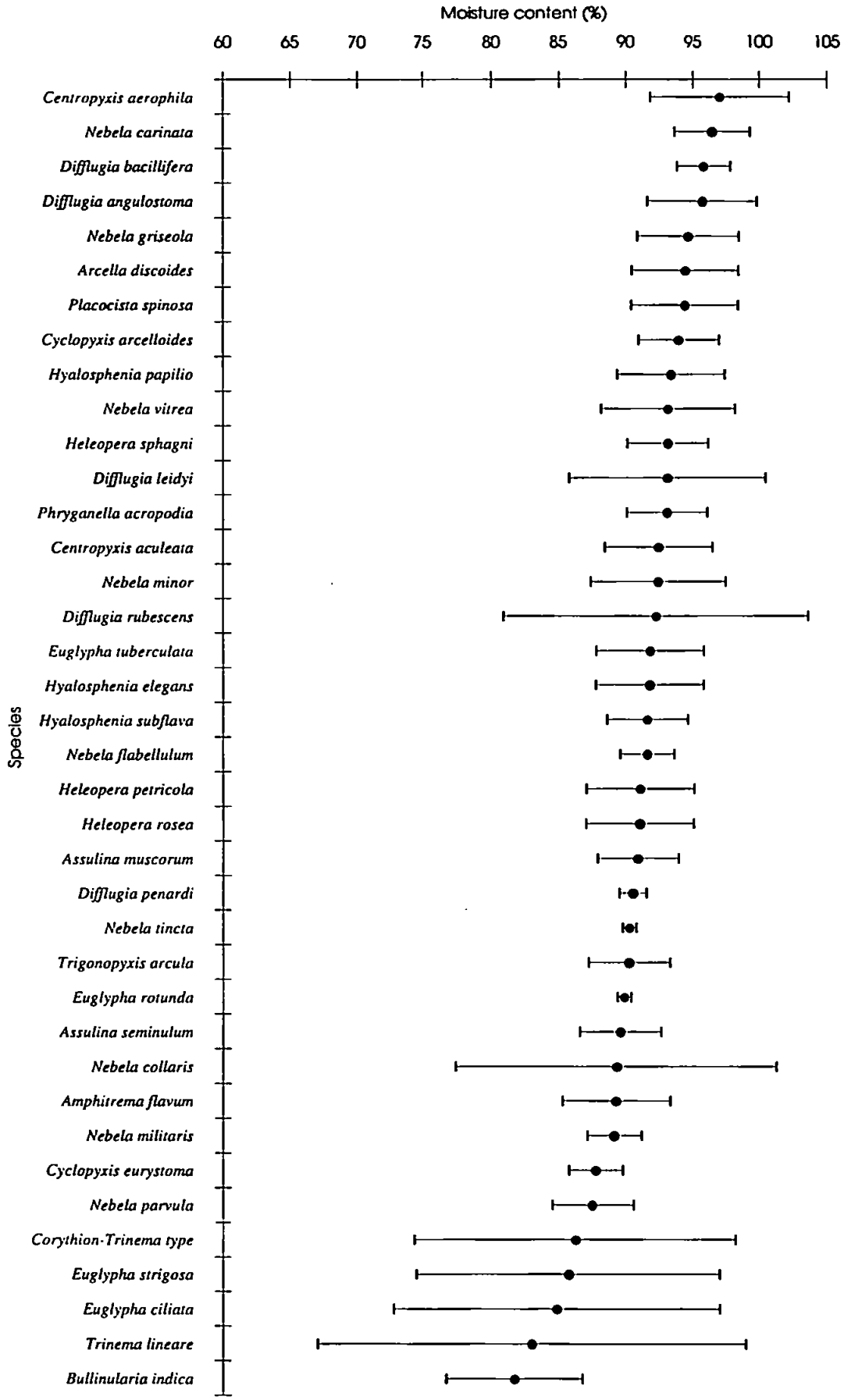


Figure 6.13: Species' optima (filled circles) and tolerances (error bars) for moisture content in Britain shown as the weighted average ± two standard errors. Only those species with > 16 occurrences (10% of samples) are shown.

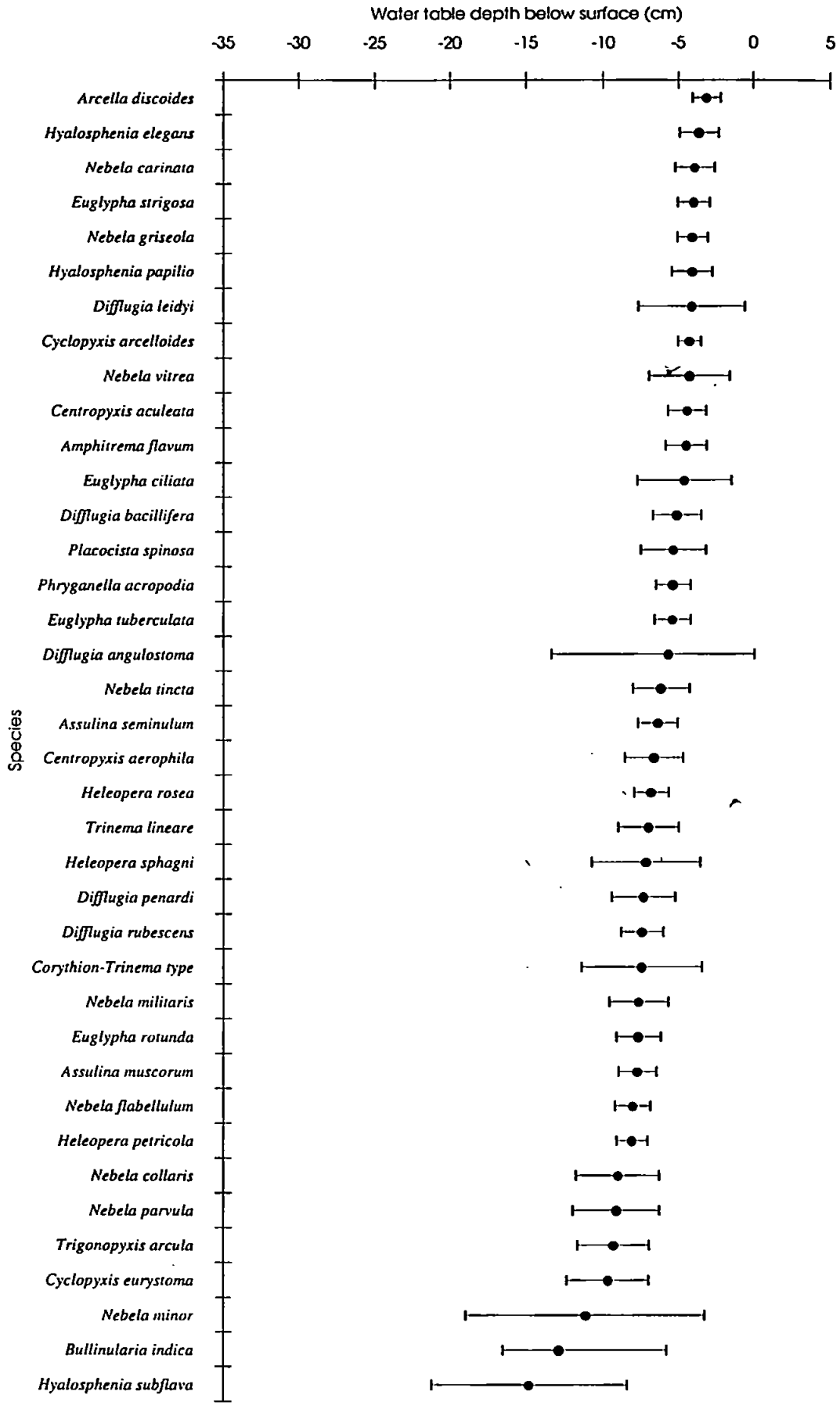


Figure 6.14: Species' optima (filled circles) and tolerances (error bars) for water table depth in Britain shown as the weighted average ± two standard errors. Only those species with > 16 occurrences (10% of samples) are shown.

Taxa	Water table ranking Tor Royal	Water table ranking Britain	Moisture content ranking Tor Royal	Moisture content ranking Britain
Amphitrema flavum	1	7	23	22
Centropyxis aculeata	2	6	2	10
Difflugia angulostoma	3	11	4	2
Placocista spinosa	4	8	6	5
Nebela griseola	5	3	1	3
Nebela carinata	6	2	3	1
Cyclopyxis eurystoma	7	26	25	24
Assulina seminulum	8	13	17	21
Arcella discoides	9	1	5	4
Heleopera rosea	10	14	8	15
Cyclopyxis arcelloides	11	5	7	6
Difflugia leidyi	12	4	9	8
Phryganella acropodia	13	9	10	9
Heleopera petricola	14	23	16	14
Corythion-Trinema type	15	18	22	26
Nebela flabellulum	16	22	13	13
Heleopera sphagni	17	15	12	7
Assulina muscorum	18	21	15	16
Euglypha tuberculata	19	10	11	12
Difflugia penardi	20	16	14	17
Difflugia rubescens	21	17	19	11
Euglypha rotunda	22	20	24	20
Trigonopyxis arcula	23	25	20	19
Nebela militaris	24	19	21	23
Nebela tincta	25	12	18	18
Nebela parvula	26	24	26	25

Table 6.8: Comparison of ranked species' hydrological optima derived from the Tor Royal and British data sets. Only species common to both data sets are shown (1 = hydrophilous; 26 = xerophilous).

a) Water table depth

Ranking the species according to the water table depth provides both a useful comparison between the two data sets and a basis for comparisons with previous studies (section 6.8). Table 6.8 shows the ranking of the 26 species common to both data sets according to water table depth. Using Spearman's rank correlation coefficient (r_s) to measure the strength of the relationship between the ranked Tor Royal and British data sets gives a value of r_s = 0.592 ($p<0.05$; Table 6.9) indicating that the two data sets are related, although the relationship is not perhaps as strong as might have been expected.

	Water table ranking (Tor Royal)	Water table ranking (Britain)	Moisture ranking (Tor Royal)
Water table ranking (Britain)	0.592**		
Moisture ranking (Tor Royal)	0.575**	0.756**	
Moisture ranking (Britain)	0.465*	0.702**	0.901***

Table 6.9 : Spearman's rank correlation coefficients for the Tor Royal and British data sets. ***p<0.01; **p<0.05; *p<0.10.

The differences in individual species' ranking are not of a large magnitude. Of the 26 species in the British data set, 24 are ranked to within 10 places of the Tor Royal data set. The exceptions are *Cyclopyxis eurystoma* and *Nebela tincta*, which are both ranked lower (and hence towards the xerophilous end of the hydrological gradient).

The variation in rankings suggests a difference in the species' optima and tolerances between the two data sets which is visible in Figures 6.11 - 6.14. This underlines the importance of using the largest data set possible to derive transfer functions and shows the degree of error that can be introduced by using one site rather than a large regional data

set. The difference is clear in the scatterplot in Figure 6.15, where the calculated optima for water table depth are generally lower for Tor Royal than for the British data set. An explanation may arise from the range of water table depths that were recorded at Tor Royal during the monitoring programme. Chapter 5 reported that a large hummock had been incorporated into nests C, D and E at Tor Royal. The hummocks measured 30 cm, 35 cm and 50 cm high respectively and, consequently, the water table depth during the monitoring period never rose above 10 cm, 22 cm and 31 cm depth within the respective dipwells; occasionally it reached depths in excess of 60 cm during dry summer months, giving average annual depths of -40.15 cm, -38.2 cm and -45.8 cm respectively (see Figure 5.7 in Chapter 5). At the remaining British sites, however, the average depth recorded was between 0 and -9 cm depth. The three deepest water tables at Tor Royal lowered the calculated species' optima and tolerances for the site, while the larger number of sites sampled in the British data set gave a more moderate range of species' optima and tolerances.

b) Moisture content

For optimum moisture content, the species' rankings are similar to that for water table (Figures 6.11 and 6.13; Table 6.8). *Amphitrema flavum*, however, is indicative of a high water table in this study, but in terms of moisture content the species is xerophilous and is ranked 23rd at Tor Royal and 22nd in the British data set. This may reflect the microhabitat in which *Amphitrema flavum* is most abundant or the weather conditions both in the days preceding the sampling and on the sampling day itself.

The use of long-term hydrological data means that "one-shot" sampling is not a problem with the water table values used in this study. However, it might still be a problem for moisture content calculations that are derived from "one-shot" samples and are therefore

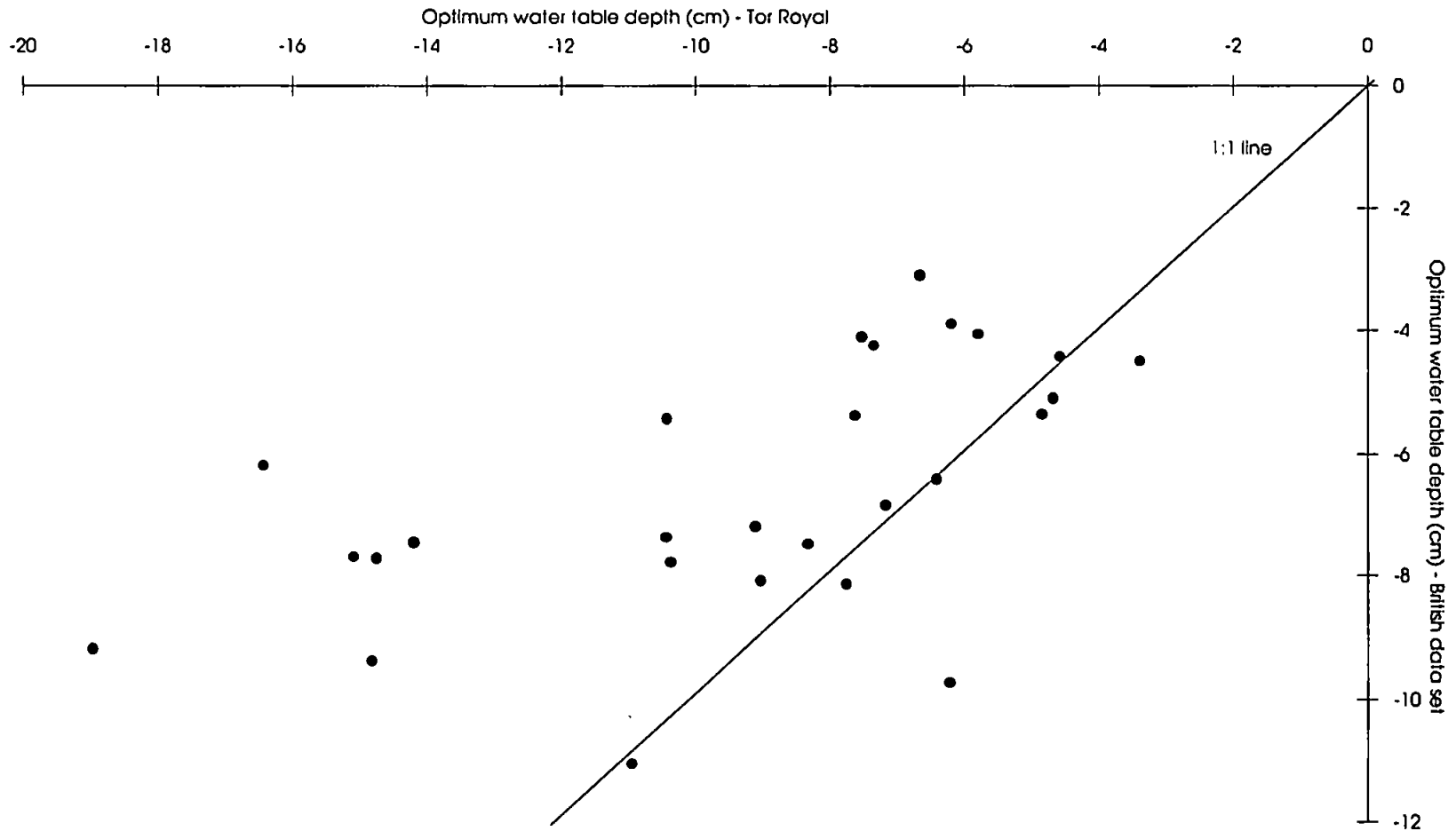


Figure 6.15: Scatterplot of species' water table depth optima derived from weighted averaging regression on the Tor Royal and British data sets. Only species common to both data sets are shown.

prone to short-term changes, particularly desiccation. On the sampling days for the British sites, many of the samples with abundant *A. flavum* were taken from *Sphagnum* that had desiccated owing to high daytime temperatures (although the underlying plant was still fully hydrated), giving a relatively low moisture content (between 75-80%), even though the water table was shallow on the sampling day. Figure 6.16 illustrates this clearly, where several sites with a relatively shallow water table (less than 15 cm deep) have a low moisture content (less than 80%). Clearly, the moisture optima and tolerances should be treated with caution and cannot be interpreted with the same confidence as those for water table depth. This further supports the need for seasonal water table depths to be included in data sets.

For moisture content, there is a closer correlation between the two data sets than for water table depth; $r_s = 0.901$ ($p<0.01$ - Table 6.9). The strength of the relationship is also evident in the scatterplot in Figure 6.17. The lowest moisture content values were recorded in the Tor Royal data (Figure 6.17) and these lowered species' moisture optima at Tor Royal. When incorporated into the British data set, the low moisture readings are compensated for by the large number of high moisture readings. Hence the consistently higher moisture optima evident in the British data.

The above section clearly emphasises the importance of using a large regional data set to moderate extreme values occurring in data from single sites. In terms of palaeoecological investigations, extreme hydrological optima derived from single sites will be carried forward into transfer functions and will, potentially, generate large errors. Accordingly, the remainder of this chapter considers only the hydrological optima derived from the full British data set.

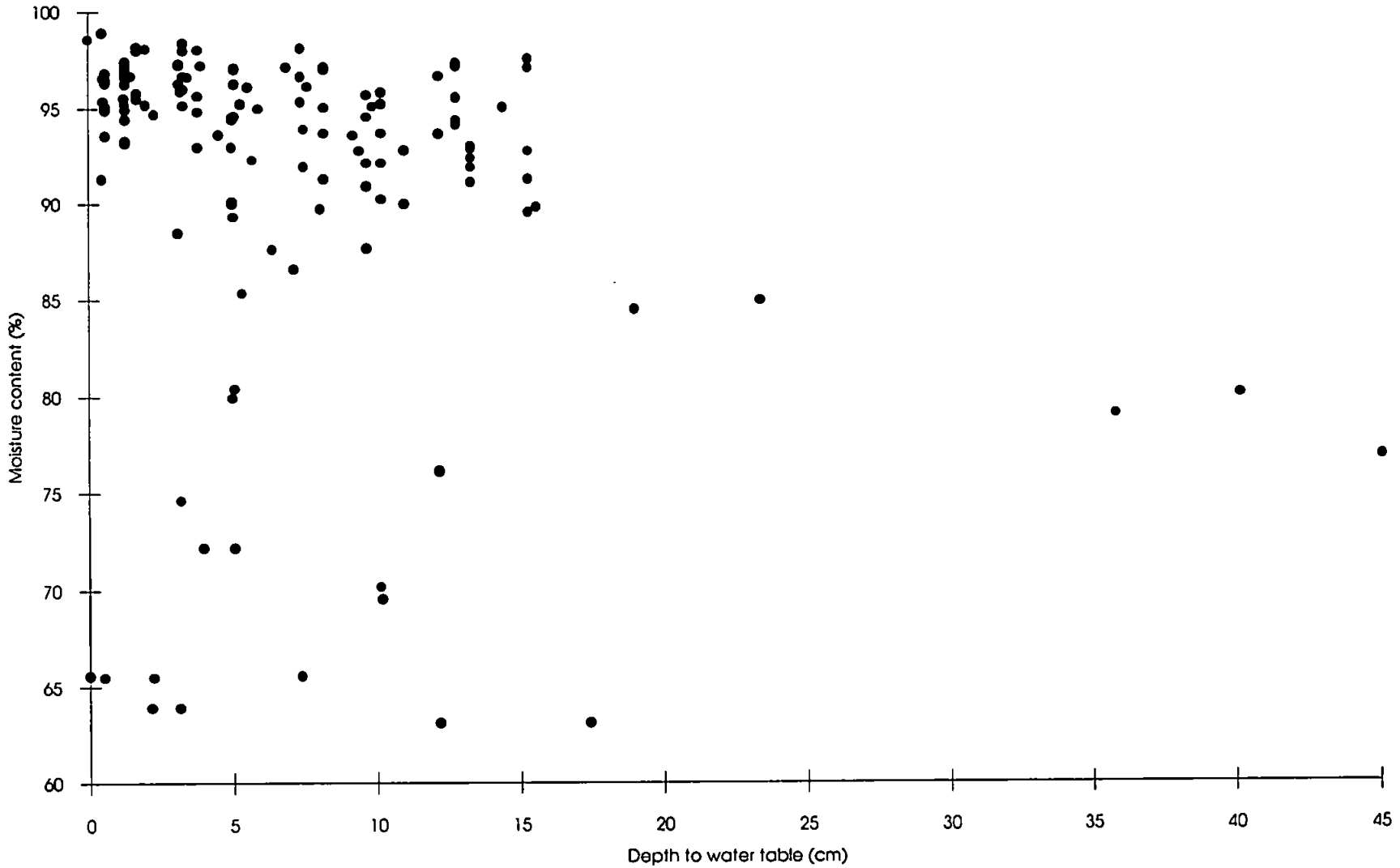


Figure 6.16: Depth to water table plotted against % moisture content for all British sites.

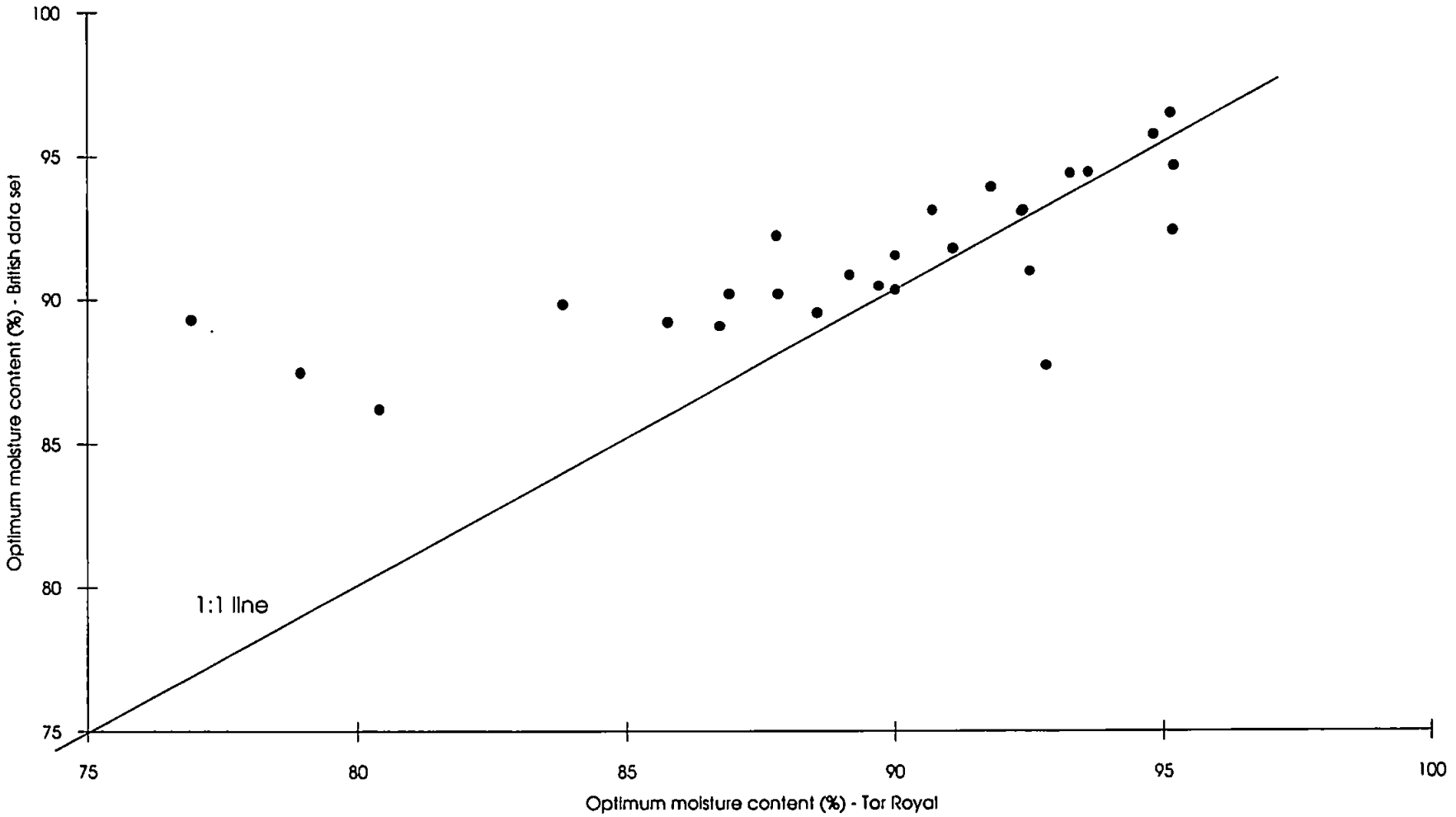


Figure 6.17: Scatterplot of species' moisture optima derived from weighted averaging regression on the Tor Royal and British data sets. Only species common to both data sets are shown.

6.8 Comparison of the optima and tolerances for moisture content and depth to water table in the British data set

a) Optima

Species' ranked optima for percent moisture content and water table depth are not identical in the British data set (Figures 6.13 and 6.14; Table 6.10). This is clarified by the Spearman's rank correlation coefficient, r_s= 0.480 ($p<0.10$ - Table 6.9), which is not particularly strong.

Species which have high percent moisture optima (in excess of 92%), such as *Arcella discoides, Hyalosphenia papilio, Nebela carinata* and *N. griseola*, also have a water table optima of less than 5 cm below the ground surface. Conversely, those species that prefer relatively drier conditions (less than 90% moisture), such as *Nebela collaris* and *Nebela parvula*, occur where the water table depth is 9 cm or greater. *Phryganella acropodia, Centropyxis aculeata, Euglypha tuberculata,* and *Heleopera rosea*, which are indifferent to ranked moisture content, occupy similar positions in the ranked water table preferences.

There are notable anomalies in this pattern, however (Figure 6.18). In terms of water table depth, *Hyalosphenia subflava* prefers the driest conditions (where water table depth is 14.86 cm), but is ranked within the top third for moisture content, with an optimum of 91.57%. This is also the pattern for *Nebela minor* and other species (such as *N. flabellulum* and *Euglypha tuberculata*) found in hummocks where lichens and Sphagna dominate the vegetation. Although the water table was deep beneath these hummocks, moisture retention by Sphagna probably maintained optimum hydrological conditions for these testate amoebae. A good example is provided by microsite A3 on Dun Moss. This was an 8 cm-high hummock, colonised by *Calluna vulgaris* and *Sphagnum capillifolium*; on the sampling day, the water table was 9.5 cm below ground, giving a total depth of 17.5 cm below the hummock top. Over the previous five years the average annual water table depth had been

Species	Ranking (% moisture optima)	Ranking (depth to water table optima)
Centropyxis aerophila	1	20
Nebela carinata	2	3
Difflugia bacillifera	3	13
Difflugia angulostoma	4	17
Nebela griseola	5	5
Arcella discoides	6	1
Placocista spinosa	7	14
Cyclopyxis arcelloides	8	8
Hyalosphenia papilio	9	6
Nebela vitrea	10	9
Heleopera sphagni	11	23
Difflugia leidyi	12	7
Phryganella acropodia	13	15
Centropyxis aculeata	14	10
Nebela minor	15	36
Difflugia rubescens	16	25
Euglypha tuberculata	17	16
Hyalosphenia elegans	18	2
Hyalosphenia subflava	19	38
Nebela flabellulum	20	30
Heleopera petricola	21	31
Heleopera rosea	22	21
Assulina muscorum	23	29
Difflugia penardi	24	24
Nebela tincta	25	18
Trigonopyxis arcula	26	34
Euglypha rotunda	27	28
Assulina seminulum	28	19
Nebela collaris	29	32
Amphitrema flavum	30	11
Nebela militaris	31	27
Cyclopyxis eurystoma	32	33
Nebela parvula	33	33
Corythion-Trinema type	34	26
Euglypha strigosa	35	4
Euglypha ciliata	36	12
Trinema lineare	37	22
Bullinularia indica	38	37

Table 6.10: Comparison of common species' rankings in the British data set according to moisture content and water table depth. 1 = hydrophilous, 38 = xerophilous; only species with > 16 occurrences are shown.

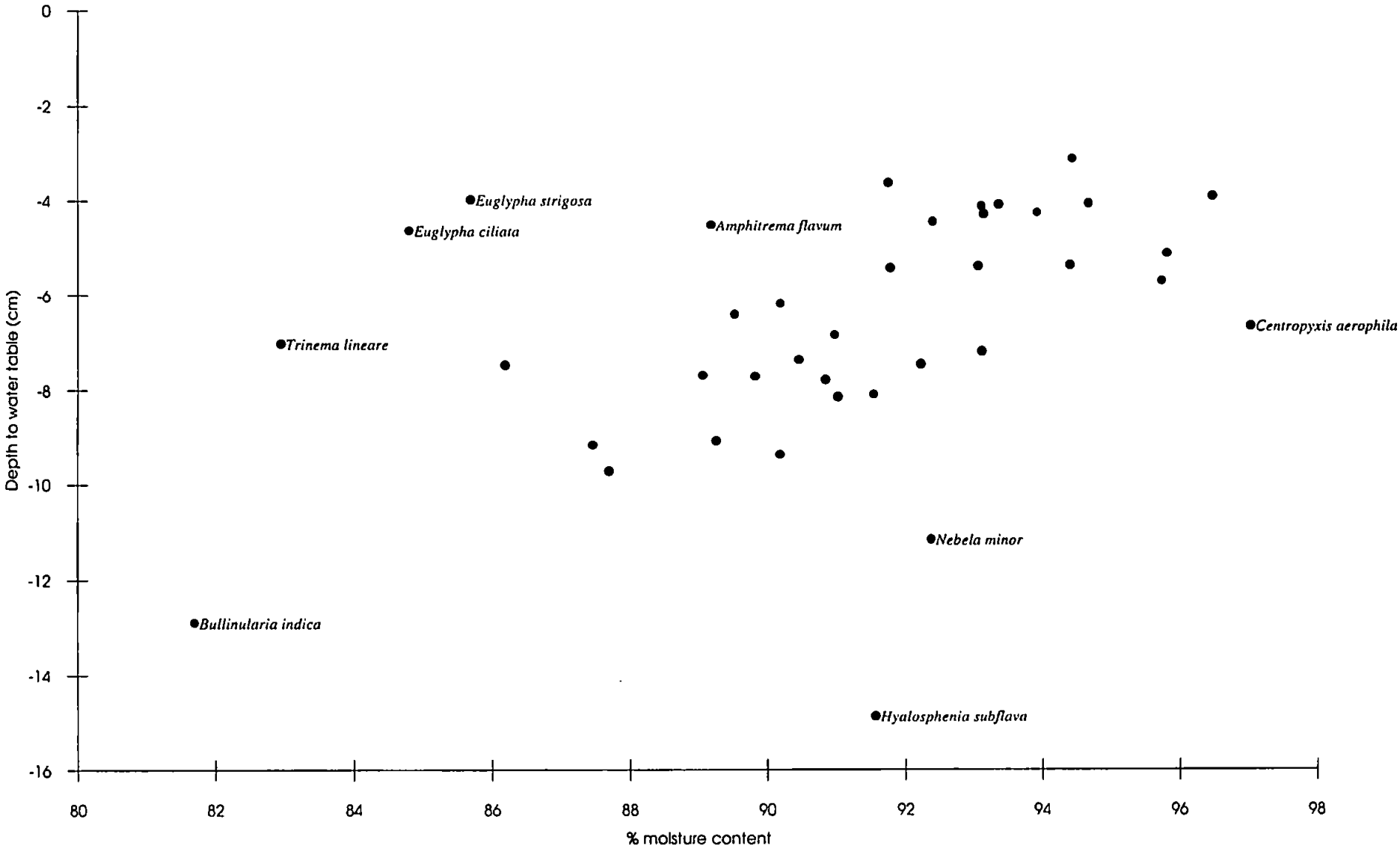


Figure 6.18: Hydrological optima for common species (> 16 occurrences) in the British data set. Outlier species are identified.

15.3 cm (Bragg, pers. com.). The moisture content of the microsite on the sampling day, however, was 92.76%. This suggests that the *Sphagnum capillifolium* plants retain sufficient moisture during precipitation events to maintain optimum moisture conditions for certain testate amoebae species.

The same anomaly occurs in species that are xerophilous in terms of moisture content, but hydrophilous in terms of water table. A good example is *Euglypha strigosa* which is ranked 35th with respect to optimum moisture content, but 4th on the basis of depth to water table. *Euglypha ciliata* (ranked 36th and 12th respectively) and *Amphitrema flavum* (ranked 30th and 11th respectively) are less extreme examples. Again, this can be explained in terms of the composition of the host vegetation community. Tolonen *et al.* (1992) encountered this in *Bullinularia indica* and suggested that the species prefers surfaces colonised by lichens rather than Sphagna. Lichens (unlike Sphagna) cannot retain large quantities of moisture and desiccate quickly as the water table drops beneath the ground surface. Hence this group of testaceans may be characterised by their ability to survive more extreme fluctuations in moisture than in water table depth. These are all small, relatively flat testaceans that would need only a thin water film to survive (see section 3.1.2; p.35).

b) Tolerance ranges

At first glance, the species' tolerance ranges for moisture (Figure 6.13) appear wider than for water table depth (Figure 6.14), but this is an effect of comparing tolerance ranges for two different parameters that are measured in different units. It is difficult to quantify the percent moisture change that accompanies a 1 cm change in water table depth - it may be 1%, 5%, 10% or greater. Thus, species with a narrow tolerance range for water table depth have a wider range for percent moisture content (for example, *Difflugia rubescens*, *E. ciliata*) and vice versa (*Hyalosphenia subflava* and *Nebela minor*, for example).

Further, the range of moisture content (65%-102%) is narrow but for clarity, moisture ranges are expanded on paper in Figure 6.13 by restricting the y-axis to this range. Thus, with the exception of *Difflugia leidyi, D. rubescens, Nebela collaris, Corythion-Trinema* type, *Euglypha strigosa, Euglypha ciliata* and *Trinema lineare*, all tolerance ranges for percent moisture are within 5% of the optimum.

6.9 Comparison of this study with previous studies

a) Moisture content

In Table 6.11, species' moisture optima from Figure 6.13 are compared to studies conducted by Schönborn (1963; based on Jung, 1936); Meisterfeld (1977), Tolonen *et al.* (1985), Warner (1987; 1989) Charman and Warner (1992) and Tolonen *et al.* (1992). With the exception of Schönborn (1963) and Meisterfeld (1977) which are, respectively, qualitative and semi-quantitative, the same weighted averaging technique has been applied to the species data, so the results between this study and the remaining studies are directly comparable. The studies by Schönborn (1963) and Meisterfeld (1977) are still useful because they show the progression from qualitative to quantitative studies and because Meisterfeld attempted to quantify Jung's original moisture classes. Besides Tolonen *et al.* (1992), they are also the only other source of European data.

Some species in the British data set have no comparable moisture optima in the other studies (*Cyclopyxis eurystoma, Difflugia angulostoma, D. penardi, D. rubescens, Euglypha ciliata, Nebela vitrea* and *N. flabellulum*), while other species are common to all studies (*Amphitrema flavum, Assulina muscorum, Hyalosphenia elegans, H. papilio* and *Nebela militaris*) and a number of direct comparisons are possible.

Generally, moisture content optima from the studies listed in Table 6.11 are within 10% of those calculated in this study. For nine species, optima from other studies are within 1%

Species	Schonborn (1963) after Jung (1936)	Meisterfeld (1977)	Tolonen *et al.* (1985)	Warner (1987)	Warner (1989)	Charman and Warner (1992)	Tolonen *et al.* (1992)	This work
Centropyxis aerophila	*	*	*	*	*	67.29	*	97.03
Nebela carinata	II	>95(I)	*	*	*	*	96.6	96.48
Difflugia bacillifera	II	>95(I)	*	*	*	*	96.4	95.81
Difflugia angulostoma	*	*	*	*	*	*	*	95.74
Nebela griseola	*	*	*	*	*	*	*	94.68
Arcella discoides	*	*	*	*	*	*	96.7	94.44
Placocista spinosa	I	*	*	*	*	*	97.8	94.41
Cyclopyxis arcelloides	*	>95(III)	*	*	*	63.66	83.2	93.93
Hyalosphenia papilio	III	95(IV)	88.3	90.1	93	88.80	95.1	93.37
Nebela vitrea	*	*	*	*	*	*	*	93.15
Heleopera sphagni	*	*	90.2	90.1	86.9	78.02	94.1	93.12
Difflugia leidyi	*	*	*	*	*	*	96.3	93.11
Phryganella acropodia	*	*	*	*	*	*	91.6	93.06
Centropyxis aculeata	II	*	*	*	*	78.54	95.6	92.41
Nebela minor	*	*	*	*	*	*	*	92.38
Difflugia rubescens	*	*	*	*	*	*	*	92.23
Euglypha tuberculata	*	*	*	*	*	74.38	90.0	91.80
Hyalosphenia elegans	IV	95(IV)	90.3	90.1	86.9	83.90	95.3	91.77
Hyalosphenia subflava	*	*	73	88	39.9	59.70	*	91.57
Nebela flabellulum	*	*	*	*	*	*	*	91.55
Heleopera petricola	II	*	90.5	91.1	88.9	70.12	95.6	91.04
Heleopera rosea	*	*	*	*	*	60.62	*	90.99
Assulina muscorum	IV	80-50(VII)	90.5	85.4	88.9	68.66	86.6	90.85
Difflugia penardi	*	*	*	*	*	*	*	90.47
Nebela tincta	V-VII	95-85(V)	*	*	*	64.08	*	90.20
Trigonopyxis arcula	*	*	73	93.4	64.8	67.43	84.1	90.19
Euglypha rotunda	*	*	*	*	*	71.03	89.6	89.83
Assulina seminulum	IV	*	90.5	62	85.3	70.40	92.2	89.53
Nebela collaris	V-VII	95-85(V)	*	*	*	*	*	89.27
Amphitrema flavum	III	>95(III)	93.2	90.1	86.9	86.27	96.0	89.20
Nebela militaris	V-VII	80-5-(VII)	90.5	85.7	52.8	69.50	89.3	89.07
Cyclopyxis eurystoma	*	*	*	*	*	*	*	87.70
Nebela parvula	*	*	*	*	*	64.55	86.7	87.47
Corythion-Trinema type	V-VII	85-80(VI)	*	*	*	70.17	87.0	86.20
Euglypha strigosa	*	*	*	*	*	68.15	94.8	85.70
Euglypha ciliata	*	*	*	*	*	*	*	84.81
Trinema lineare	*	*	*	*	*	66.85	*	82.95
Bullinularia indica	*	*	70.8	84.7	86.5	67.50	*	81.70

Table 6.11: Comparisons between the weighted average moisture content calculated for testate amoebae in this work and those derived by other authors. * denotes species absent.

Species	Schonborn (1963) after Jung (1936)	Meisterfeld (1977)	Tolonen *et al.* (1985)	Warner (1987)	Warner (1989)	Charman and Warner (1992)	Tolonen *et al.* (1992)	This work
Centropyxis aerophila	*	*	*	*	*	16	*	1
Nebela carinata	2	1	*	*	*	*	3	2
Difflugia bacillifera	2	1	*	*	*	*	4	3
Difflugia angulostoma	*	*	*	*	*	*	*	4
Nebela griseola	*	*	*	*	*	*	13	5
Arcella discoides	*	*	*	*	*	*	2	6
Placocista spinosa	1	*	*	*	*	*	1	7
Cyclopyxis arcelloides	*	3	*	*	*	20	23	8
Hyalosphenia papilio	6	6	8	3	1	1	10	9
Nebela vitrea	*	*	*	*	*	*	*	10
Heleopera sphagni	*	*	7	3	4	5	12	11
Difflugia leidyi	*	*	*	*	*	*	5	12
Phryganella acropodia	*	*	*	*	*	*	15	13
Centropyxis aculeata	2	*	*	*	*	4	7	14
Nebela minor	*	*	*	*	*	*	*	15
Difflugia rubescens	*	*	*	*	*	*	*	16
Euglypha tuberculata	*	*	*	*	*	6	16	17
Hyalosphenia elegans	8	6	6	3	4	3	9	18
Hyalosphenia subflava	*	*	9	7	10	22	*	19
Nebela flabellulum	*	*	*	*	*	*	*	20
Heleopera petricola	2	*	2	2	2	10	8	21
Heleopera rosea	*	*	*	*	*	21	*	22
Assulina muscorum	8	10	2	9	2	12	21	23
Difflugia penardi	*	*	*	*	*	*	*	24
Nebela tincta	11	5	*	*	*	19	24	25
Trigonopyxis arcula	*	*	9	1	8	15	22	26
Euglypha rotunda	*	*	*	*	*	7	17	27
Assulina seminulum	8	*	2	10	7	8	14	28
Nebela collaris	11	8	*	*	*	*	*	29
Amphitrema flavum	7	3	1	3	4	2	6	30
Nebela militaris	11	11	2	8	9	11	18	31
Cyclopyxis eurystoma	*	*	*	*	*	*	*	32
Nebela parvula	*	*	*	*	*	18	20	33
Corythion-Trinema type	11	7	*	*	*	9	19	34
Euglypha strigosa	*	*	*	*	*	13	11	35
Euglypha ciliata	*	*	*	*	*	*	*	36
Trinema lineare	*	*	*	*	*	19	*	37
Bullinularia indica	*	*	11	11	6	14	25	38

Table 6.12: Comparisons between the ranked weighted moisture content calculated for 38 common species in this study and those derived by other authors. * denotes species absent; 1 = hydrophilous.

of this study; two-thirds of these species are in the Finnish data set (Tolonen *et al.* (1992) and the remaining third are in the Canadian data sets of Tolonen *et al.* (1985) and Warner (1987). *Hyalosphenia subflava* and *Nebela militaris* are notable for their extremely low moisture optima in the Canadian studies (Warner, 1989; Charman and Warner, 1992) relative to this study. The moisture optimum for *Hyalosphenia subflava* in the British data set is 91.57%; in the Canadian data sets its optimum is 39.9% (Warner, 1989) and 59.70% (Charman and Warner, 1992). For *Nebela militaris*, the moisture optimum in Britain is 89.07% and 52.8% in Canada (Warner, 1989). The lower moisture optima from the Canadian individuals are a consequence of single-shot sampling under the dry conditions experienced in these continental peatlands during the summer months.

In Table 6.12, the same species are ranked according to their moisture optima to indicate their relative position within each study. The Spearman's rank correlation coefficients for this study compared to previous authors are summarised in Table 6.13.

The correlation is stronger between this study and other European investigations than for North American and Canadian studies. But the poor agreement North American and Canadian studies cannot be entirely due to continentality since this would not necessarily affect the rank ordering of species.

	Schönborn (1963)	Meisterfeld (1977)	Tolonen *et al.* (1985)	Warner (1987)	Warner (1989)	Tolonen *et al.* (1992)	Charman & Warner (1992)
This work	0.821***	0.716**	-0.224	0.335	0.412	0.572**	0.170

Table 6.13: Spearman's rank correlation coefficients for comparisons of species' rankings for optimum moisture content between this study and previous investigations (***$p<0.01$; **$p<0.05$).

A second explanation may be seasonality and the effects of single-shot samples. Long-term hydrological data of the type used in this study and by Tolonen *et al.* (1992) were unavailable for the North American studies. The potential for data distortion from unusually dry or wet seasons is therefore considerable and was partially recognised by Charman and Warner (1992) when they compared their data with that of Tolonen *et al.* (1992) and suggested that differences were due to sampling at different times of the year (June-July for Charman and Warner (1992) and October-November for Tolonen *et al.*,1992). This emphasises the potentially misleading data that can be generated from single-shot samples and reaffirms the need to establish the representativeness of mean seasonal hydrological parameters.

Alternatively, there may be real geographical differences between the North American and European testate amoebae populations, although this would require further investigation by future studies.

b) Depth to water table

In Table 6.14 species' optima for water table depth in Britain are compared to Tolonen *et al.* (1992), the only other quantitative water table optima to be produced for testate amoebae. Generally, the optima from Tolonen *et al.* (1992) are lower (implying tolerance of a deeper water table) than for the British data set. This may reflect the less intense oceanic climate of Finland compared to Britain or variations between the sampling methods for the two data sets.

Of the three sites studied by Tolonen *et al.* (1992), hydrological records for the preceding three years were available for only one site. Water table records for just one year were used for the remaining two sites. The three-year record represents only levels during "snow free periods" (Tolonen *et al.*, 1992; p.130) and is, therefore, likely to be more representative of

Species	This study	Tolonen *et al.* (1992)
Arcella discoides	-3.11	-4.8
Hyalosphenia elegans	-3.61	-8.0
Nebela carinata	-3.90	-1.4
Euglypha strigosa	-3.98	-8.1
Nebela griseola	-4.06	-9.3
Hyalosphenia papilio	-4.08	-7.1
Difflugia leidyi	-4.11	-2.3
Cyclopyxis arcelloides	-4.25	-20.6
Centropyxis aculeata	-4.44	-7.8
Amphitrema flavum	-4.51	-2.8
Difflugia bacillifera	-5.12	-3.3
Placocista spinosa	-5.36	-2.8
Phryganella acropodia	-5.38	-12.8
Euglypha tuberculata	-5.43	-14.6
Nebela tincta	-6.18	-22.4
Assulina seminulum	-6.41	-10.9
Heleopera sphagni	-7.19	-9.1
Corythion-Trinema type	-7.48	-14.1
Nebela militaris	-7.68	-15.1
Euglypha rotunda	-7.71	-15.4
Assulina muscorum	-7.77	-16.6
Heleopera petricola	-8.14	-3.1
Nebela parvula	-9.17	-15.1
Trigonopyxis arcula	-9.37	-19.5
Bullinularia indica	-12.90	-12.7

Table 6.14: Species' optima for water table depth (cm below ground surface) from this study and from Tolonen *et al.* (1992). Only species common to both studies are listed.

mean seasonal rather than mean annual water table depths across the mire. A further complication is the exact duration of the snow-free period, which may encroach upon specified seasonal boundaries. Hence, a direct comparison between the water table optima from the British and Finnish sites is difficult.

A more meaningful comparison can be made between the relative species rankings in the British and Finnish data sets (Table 6.15), for which $r_s = 0.540$ ($p<0.01$). Most species are ranked within 10 placings, but there are anomalies; for example, *Cyclopyxis arcelloides* is ranked 8th in the British data set, but 24th in the Finnish study; *Heleopera petricola* is a relatively dry species at 22nd place in the British data set, but in the Finnish study it is ranked 5th. Despite these anomalies, the rankings show good agreement between this study and that of Tolonen *et al.* (1992).

The overall trend shown in Table 6.15 is for hydrophilous species in this study to be ranked as more xerophilous in the Finnish study; for example, *Arcella discoides* (ranked 1st in the British data set and 7th in the Finnish study), *Hyalosphenia elegans* (ranked 2nd and 10th respectively), *Euglypha strigosa* (ranked 4th and 11th respectively), *Nebela griseola* (ranked 5th and 13th respectively) and *Cyclopyxis arcelloides* (ranked 8th and 24th respectively). Differences between the species rankings in the middle and lower half of the table tend to be less.

The differences in the top half of the table may be attributed to the water table data used in the Finnish study. Given that two of the three Finnish water table records covered only one year and all were seasonally selective, the weighted averages calculated for water table optima may have been influenced by extreme water table depths, especially if the monitored year was particularly dry, or if the snow-free period was dry. The latter is very

Species	This study	Tolonen *et al.* (1992)
Arcella discoides	1	7
Hyalosphenia elegans	2	10
Nebela carinata	3	1
Euglypha strigosa	4	11
Nebela griseola	5	13
Hyalosphenia papilio	6	8
Difflugia leidyi	7	2
Cyclopyxis arcelloides	8	24
Centropyxis aculeata	9	9
Amphitrema flavum	10	3
Difflugia bacillifera	11	6
Placocista spinosa	12	4
Phryganella acropodia	13	16
Euglypha tuberculata	14	18
Nebela tincta	15	25
Assulina seminulum	16	14
Heleopera sphagni	17	12
Corythion dubium	18	17
Nebela militaris	19	19
Euglypha rotunda	20	21
Assulina muscorum	21	22
Heleopera petricola	22	5
Nebela parvula	23	20
Trigonopyxis arcula	24	23
Bullinularia indica	25	15

Table 6.15: Ranked water table depth optima for species in this study and in Tolonen *et al.* (1992). 1 = hydrophilous, 25 = xerophilous. Only species common to both studies are shown.

likely, since these would be the non-winter months. Again, this emphasises the disadvantages of single-shot samples and short hydrological records at sampling sites.

6.10 Individual species' optima

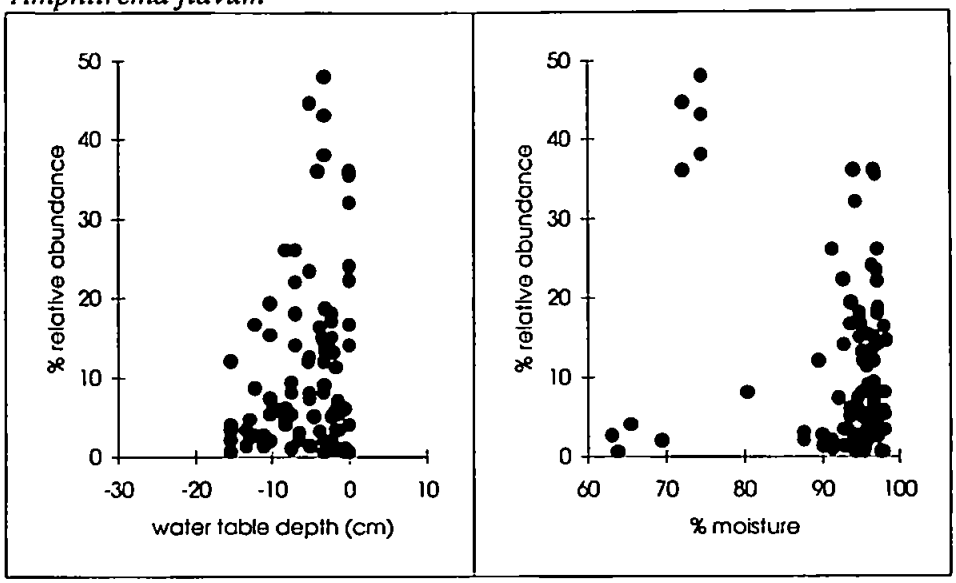
This section interprets the hydrological optima of individual testate amoebae species in terms of percent moisture content and depth to water table; where possible, previous work is reviewed. Since some species have no comparable data, the following discussion is generically arranged.

a) *Amphitrema*

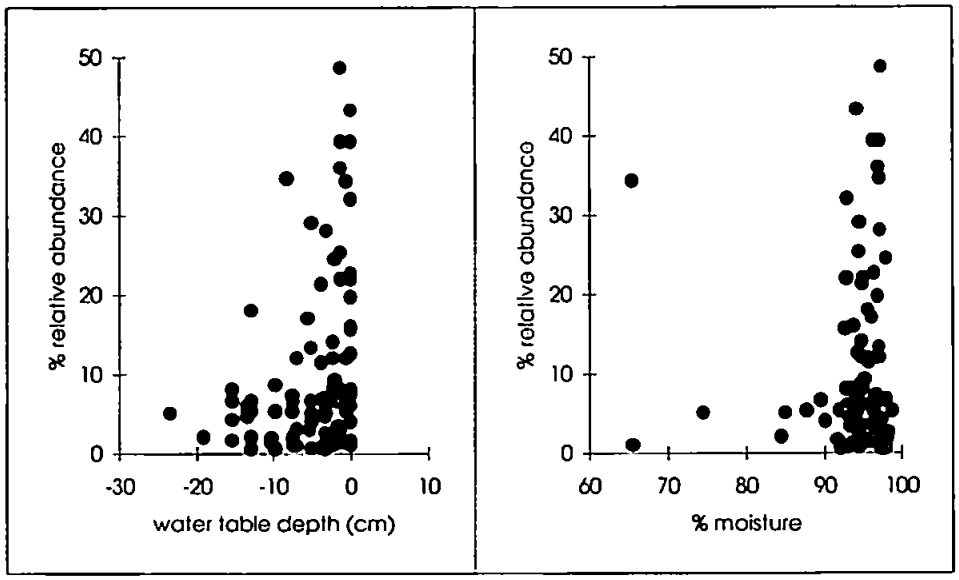
Warner and Charman (1994) considered *A. flavum* an important palaeohydrological indicator because the species' moisture optimum was consistent between Canadian and Finnish studies (Table 6.11). In all previous studies *A. flavum* is hydrophilous in terms of moisture but, in this study, the species is relatively xerophilous. Conversely, if species are ordered according to optimum water table depth, *A. flavum* becomes hydrophilous, with an optimum of 5 cm; only 2 cm deeper than the wettest species (*Arcella discoides*). This affinity is clear in plots of the species' abundance against water table depth and moisture content (Figure 6.19). *A. flavum* is most common where water table depths are 0-5 cm, but the species can exist where moisture is less than 70%.

Given the restricted moisture range recorded in this study, the water table optima plot in Figure 6.14 is probably a better indication of species' hydrological preferences. Hence, *A. flavum* can be considered hydrophilous, although not as extreme as suggested by Heal (1962), Tolonen (1986), Charman and Warner (1992) and Tolonen *et al.* (1992). Corbet's (1973) description of *A. flavum* as a common species in the wetter parts of hummocks would be in agreement with this study.

Amphitrema flavum



Arcella discoides



Bullinularia indica

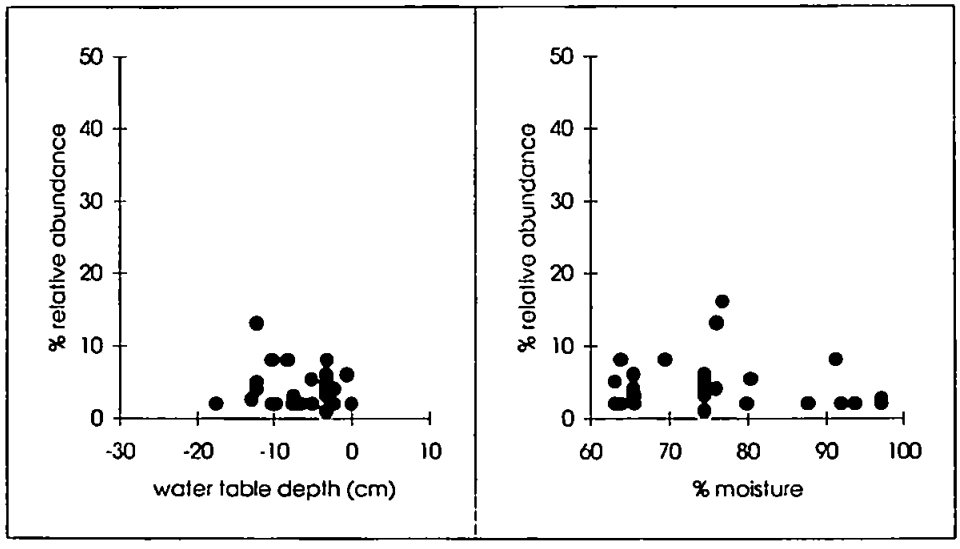


Figure 6.19: Abundances for *Amphitrema flavum*, *Arcella discoides* and *Bullinularia indica* in response to hydrology in the British data set.

b) *Arcella*

Only Tolonen *et al.* (1992) have published hydrological optima for *Arcella discoides*. They calculate a moisture optima of 96.7% and a water table depth optima of 4.8 cm, compared to 94.44% and 3.11 cm respectively in this study. *A. discoides* was distributed across a wide hydrological gradient in this study (between water table depths of 0-25 cm and moisture conditions of 65-98%; Figure 6.19) and the species' flattened test probably enables it to exist across an extended hydrological range, although it is clearly more abundant in wetter locations.

c) *Bullinularia*

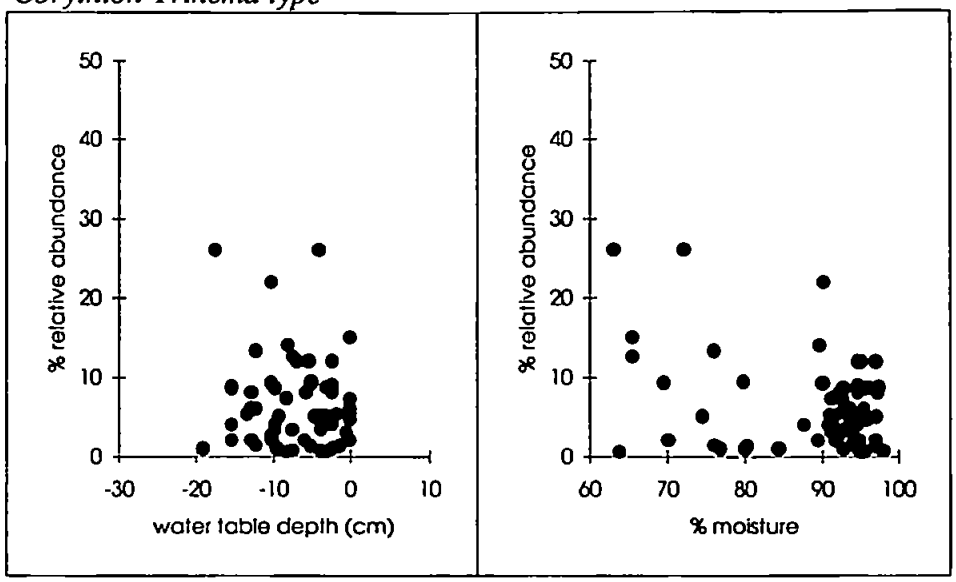
For both moisture content and water table depth in Britain, *Bullinularia indica* is a xerophilous species (Figures 6.13 and 6.14). This is consistent with the species' moisture optima in both northern Europe and North America (Table 6.11).

In a qualitative description, de Graaf (1956; p. 191) describes *B. indica* as "a typical xerophilous species, whose optimum distribution lies in dry *Sphagnum* and other mosses, especially those growing in woods. It may be found in open water habitats occasionally, but always in smaller populations and generally in single individuals only". This is supported by plots of the species' abundance against moisture (Figure 6.19) which shows that relatively few individuals exist where the moisture content is greater than 90%. *B. indica* can therefore be considered as a good indicator species of xerophilous conditions on ombrotrophic peatlands.

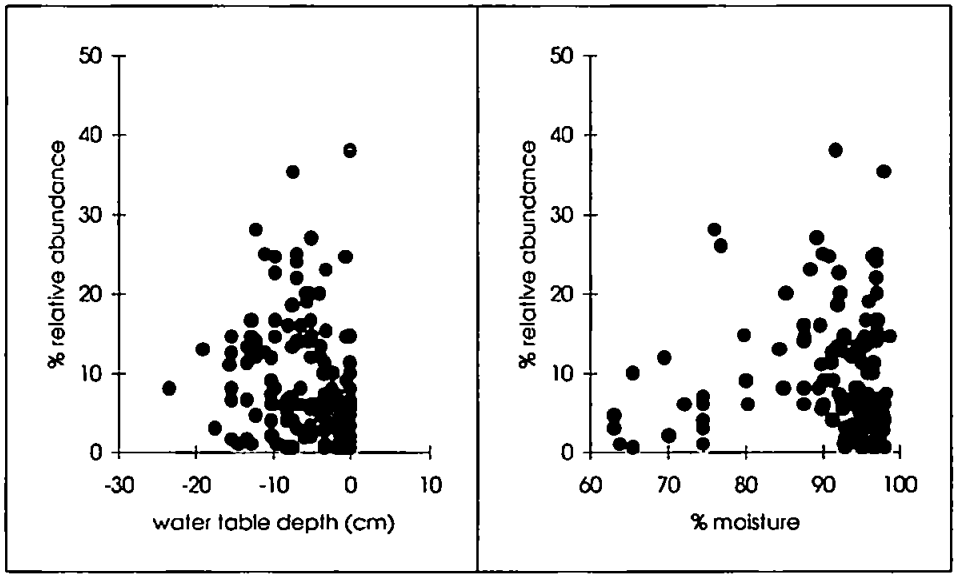
d) *Corythion-Trinema* type

In terms of moisture, *Corythion-Trinema* type is xerophilous, with a wide tolerance range (Figures 6.13 and 6.20), although the tendency is less pronounced in relation to water table depth (Figures 6.14 and 6.20). In previous studies *Corythion-Trinema* type has also

Corythion-Trinema type



Assulina muscorum



Assulina seminulum

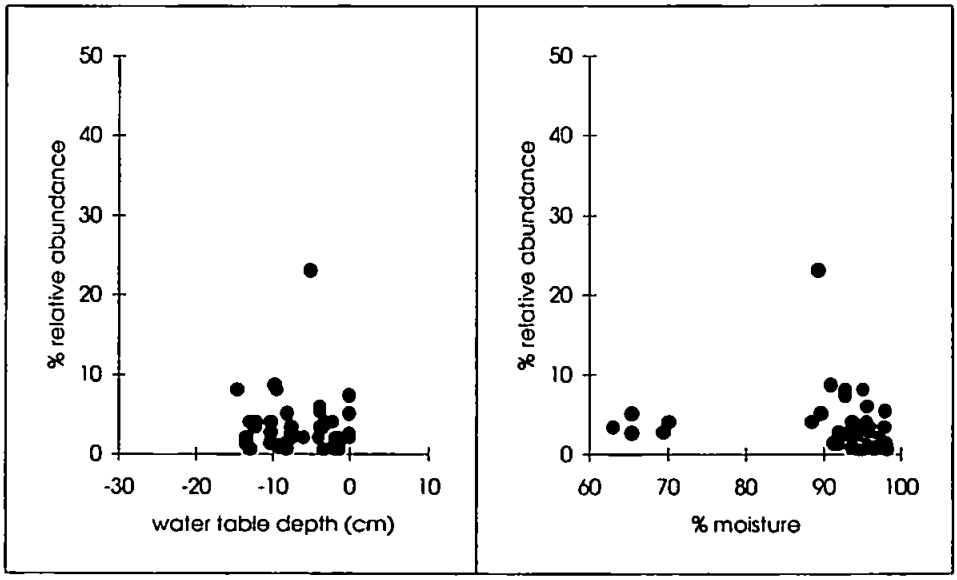


Figure 6.20: Abundances for *Corythion-Trinema* type, *Assulina muscorum* and *A. seminulum* in response to hydrology in the British data set.

occupied a range of moderately xerophilous to xerophilous positions with respect to moisture (Table 6.11). It is likely that the small test (30-60μm; Corbet, 1973; Ogden and Hedley, 1980) allows this species type to survive in small water films.

e) *Assulina*

In this study, *Assulina muscorum* and *A. seminulum* were particularly abundant in moderately dry samples collected from bog hummocks and mire margins (Figure 6.20). Consequently, the calculated optima for moisture and water table depth are moderately xerophilous. Among published work, *Assulina* is generally regarded as a xerophilous genus (Brown, 1912; Schönborn, 1962a,b; Laminger, 1972; Corbet, 1973; Meisterfeld, 1977; Bonnet, 1981; Tolonen, 1986; Beyens *et al.*, 1986a,b; 1990; Tolonen *et al.*, 1992; 1994), although Charman and Warner (1992, p.2479) observed that *A. muscorum* "showed no preference for a particular range of moisture conditions". On South Georgia, Smith (1982) found *A. muscorum* as an abundant component of wet mosses. This led Beyens *et al.* (1990) to state that:

> "It is thus obvious that species ecology is not a fact, established once and for all, but a rather variable parameter which must be constantly reviewed in relation to the specific ecology of the region studied, at least as far as some (cosmopolitic) species are concerned".
>
> Beyens *et al.* (1990), p.436.

This highlights the inherent problems in inter-site comparisons of species optima in which data are derived from sites without long-term hydrological records. Consequently, it reaffirms the need for such long-term data and for investigations into the representativeness of seasonal average hydrological parameters to remove the problems associated with single-shot sampling techniques and to stabilise this "rather variable parameter". It is, therefore, interesting to note further comments by Beyens *et al.* (1990, p.346):

> "The observations of *A. muscorum*...in a few wet mosses...can probably be ascribed to the changing moisture content of these habitats: from rather wet in early summer to dry later on".

f) *Centropyxis*

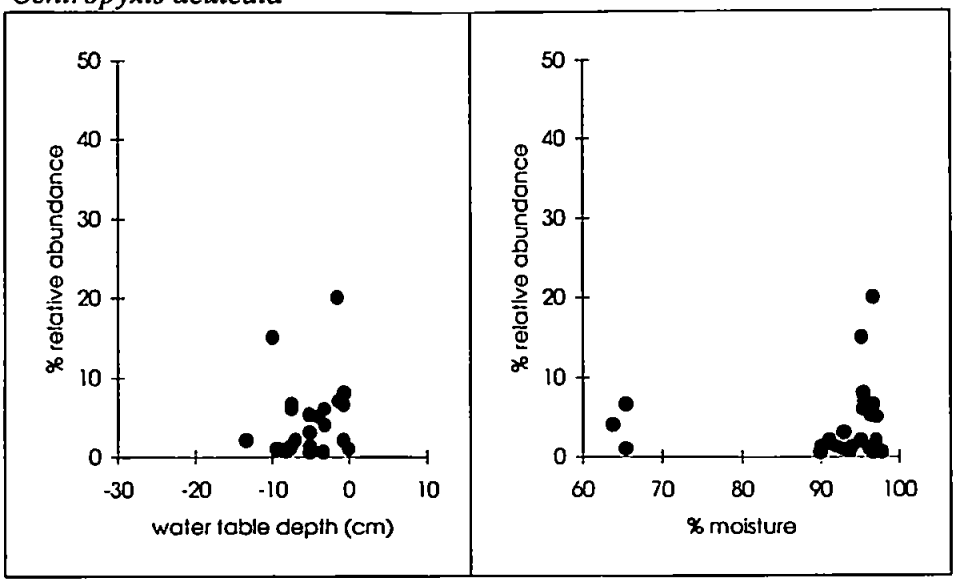
In this study, *C. aerophila* is hydrophilous in terms of moisture; at 97.03%, its optima is the highest in the British data set (Figure 6.13). For water table depth, however, the species is indifferent (Figure 6.14) and, for both parameters, the species has a relatively wide tolerance range (Figure 6.21). In the British samples, *C. aerophila* was occasionally present where water table depths exceeded 10 cm and moisture content was less than 70%. The hydrophilous position of *C. aerophila* in Britain is consistent with estimations in other countries (Schönborn, 1963; Tolonen, 1986; Warner, 1987; Charman and Warner, 1992; Tolonen *et al.*, 1992 - Table 6.11).

Warner and Charman (1994) suggest that *Centropyxis aerophila* is part of a larger taxonomic group that may include *C. aculeata* and is characteristic of ponds, shallow peatland pools and very wet to dry *Sphagnum* soils. In this study, *C. aculeata* is hydrophilous in terms of water table, with an optimum of less than 5 cm depth, although the species is only moderately hydrophilous in terms of moisture content (Figure 6.13). The evidence presented in the British data set supports Warner and Charman (1994) and further suggests that members of *Centropyxis* can withstand periods of desiccation.

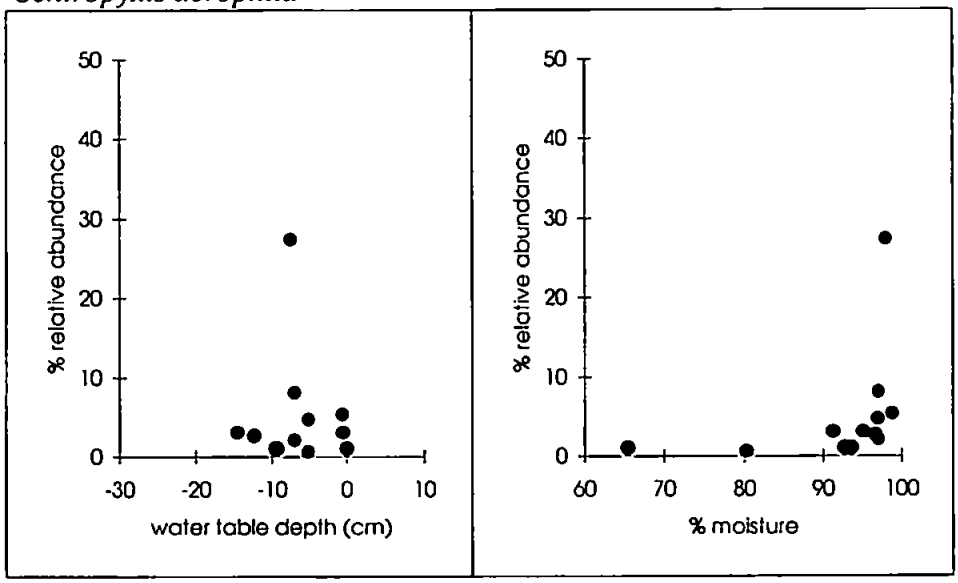
g) *Cyclopyxis*

Cyclopyxis arcelloides occupies a range of hydrological conditions in peatlands (Table 6.11). In this study, it is hydrophilous (Figures 6.13 and 6.14), although the abundance plots (Figures 6.21 and 6.22) demonstrate the species' ability to exist in conditions far beyond its hydrological optimum. This may explain its position in other data sets: Meisterfeld (1977) included *C. arcelloides* in moisture class III (>95% moisture content) indicating a moderately hydrophilous species, but in Tolonen *et al.* (1992) and Charman and Warner (1992), the species is xerophilous (Table 6.11).

Centropyxis aculeata



Centropyxis aerophila



Cyclopyxis arcelloides

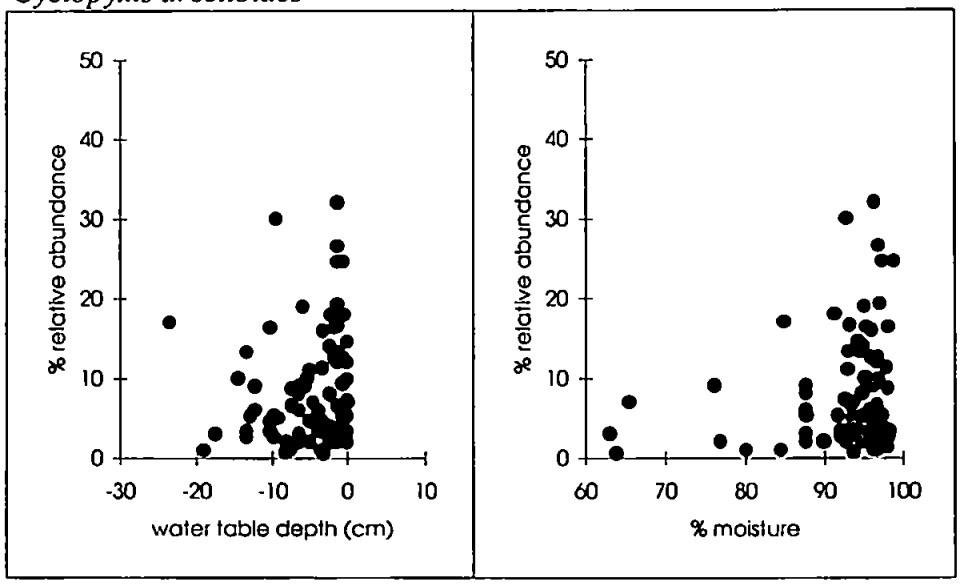
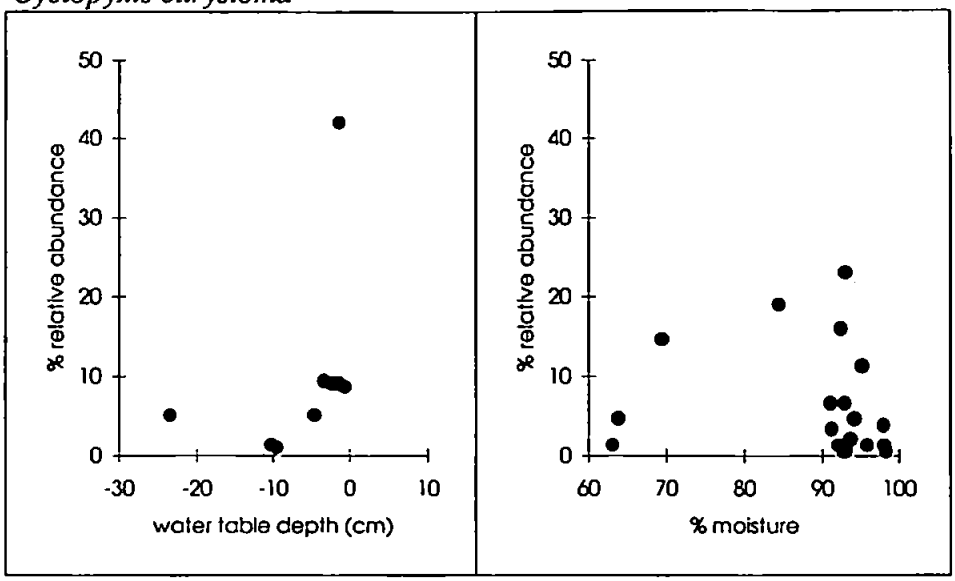
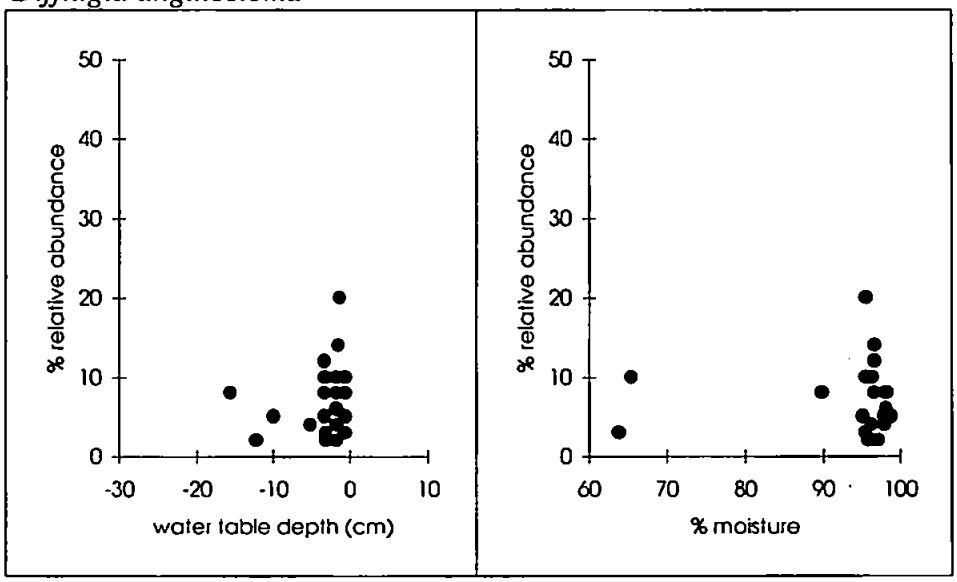


Figure 6.21: Abundances for *Centropyxis aculeata*, *C. aerophila* and *Cyclopyxis arcelloides* in response to hydrology in the British data set.

Cyclopyxis eurystoma



Difflugia angulostoma



Difflugia bacillifera

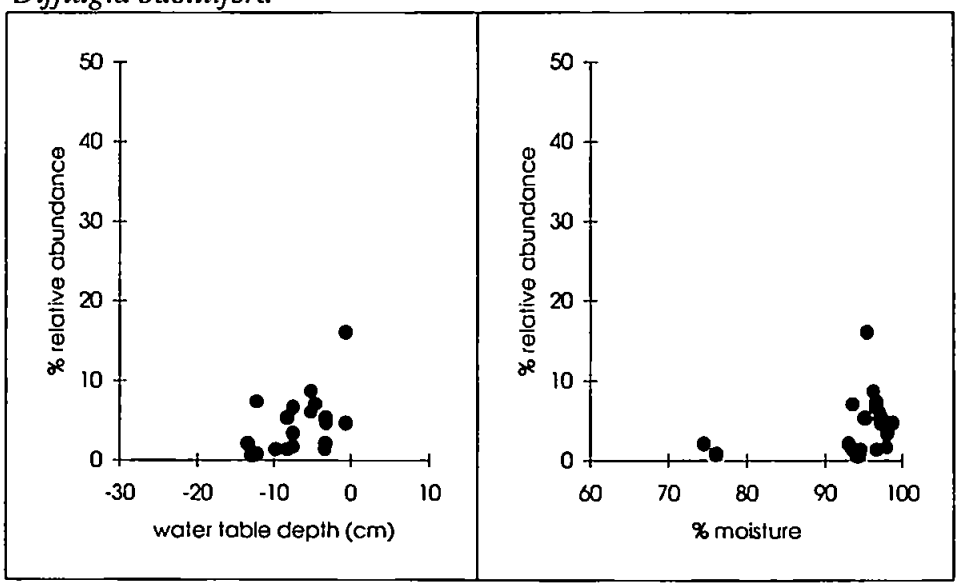


Figure 6.22: Abundances for *Cyclopyxis eurystoma*, *Difflugia angulostoma* and *D. bacillifera* in response to hydrology in the British data set.

C. arcelloides and *C. eurystoma* occupy contrasting positions along the hydrological gradient in this study; whereas *C. arcelloides* is clearly hydrophilous, *C. eurystoma* is xerophilous (Figures 6.13 and 6.14). Since additional hydrological data and ecological descriptions for *C. eurystoma* do not exist, it is impossible to explain the species' relationship. However, such a wide variation in hydrological optima within genera is not unusual in this study. For example *Difflugia, Euglypha, Hyalosphenia* and *Nebela* all display similar divergences and, where possible, these are examined in the context of each genera below.

h) *Difflugia*

There are no comparable hydrological studies of *Difflugia angulostoma* and no published information on the species' ecology. In the British data set, *D. angulostoma* is hydrophilous, (moisture optimum = 95.74%; water table depth optimum = 5.7 cm), although individuals occur occasionally in drier conditions (Figure 6.22). This is reflected in the relatively wide hydrological tolerance range of *D. angulostoma* (Figures 6.13 and 6.14).

D. bacillifera's optima of 95.81% for moisture and 5.12 cm for water table depth reflects the species' abundance in pool microsites sampled for this study. This distribution was also noted by Corbet (1973) and it is probably dictated by the species' shell construction. *D. bacillifera* has an agglutinate shell composed of diatom frustules (Ogden and Hedley, 1980). Under light microscopy it was difficult to identify the species derivation of the diatom frustules but Ogden and Hedley (1980), using SEM, identified frustules from the genera *Tabellaria, Frustulia, Pinnularia* and *Eunotia*. These are freshwater diatoms (Barnes, 1968) and it is likely that their presence in the mire pools encouraged the presence of *D. bacillifera*.

The water table depth optimum for *D. bacillifera* implies an ability to survive in areas where, although the water table is below ground, Sphagna are dominant and retain sufficient moisture for the species. This is reflected in the species' abundance plots in Figure 6.22 and is further supported by Schönborn (1966; 1992b) who suggests that *Difflugia* are incapable of encysting. Thus, it is essential for *D. bacillifera* to remain in microsites of high water content to prevent desiccation of the cytoplasm.

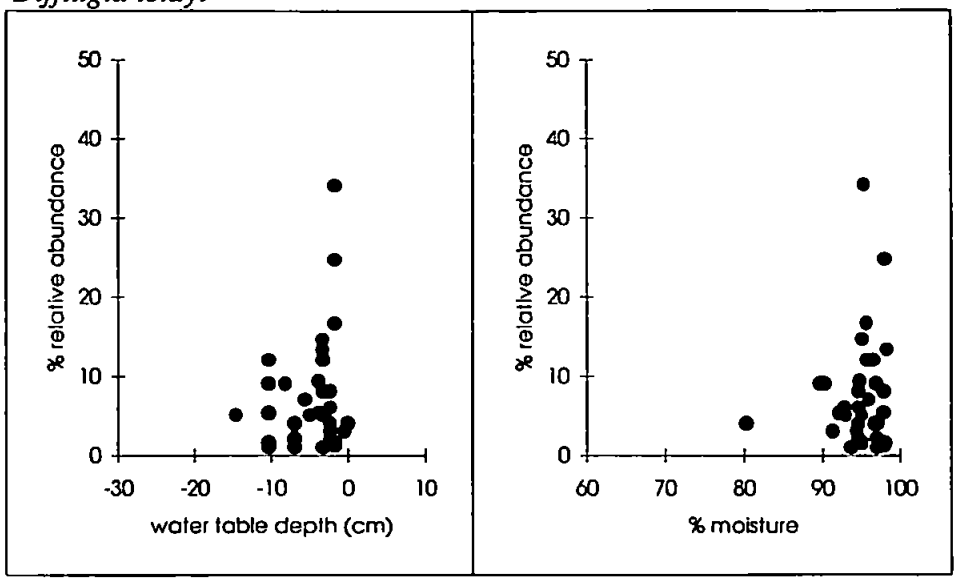
Conversely, *D. penardi* is moderately xerophilous (moisture optimum = 90.47%; water table depth optimum = 7.37 cm). The species' abundance plots (Figure 6.23) illustrate its presence in drier samples, although below 70% moisture content, the species is restricted to isolated occurrences. Again, the small size of *D. penardi* (60-65µm in this study) probably allows it to survive in thin water films as the host substrate desiccates, where larger species of *Difflugia* (such as *D. bacillifera* and *D. leidyi*) would not survive.

In this study, *D. leidyi* is hydrophilous (Figures 6.13 and 6.14), although the species' abundance plots (Figure 6.23) demonstrate a wider distribution with respect to moisture than water table depth to include relatively drier conditions (80% moisture content and 15 cm water table depth). For *D. leidyi*, comparable hydrological data exists only in Tolonen *et al.* (1992), where, for both moisture and water table depth, the species thrives in slightly wetter conditions (96.3% moisture and 2.3 cm water table depth).

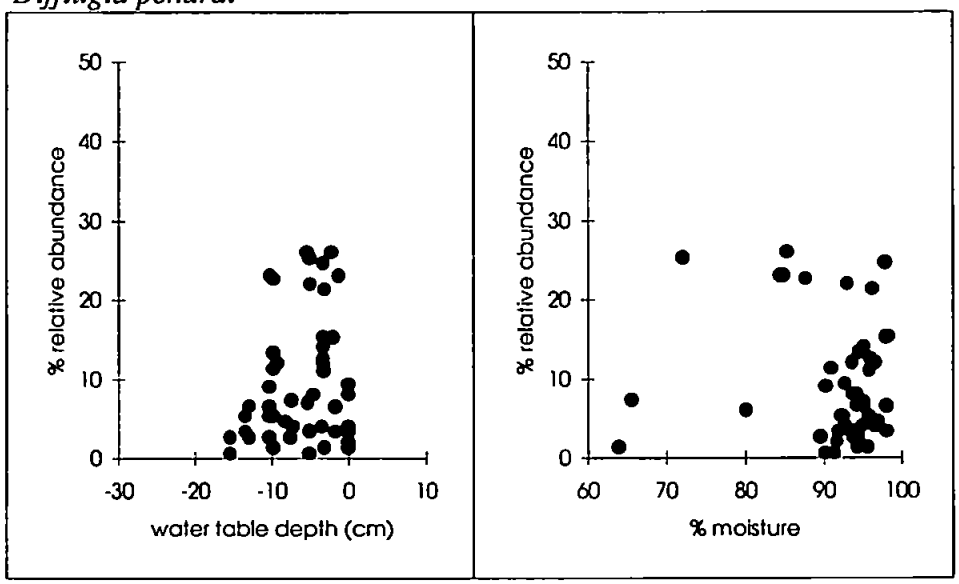
i) ***Euglypha***

Members of *Euglypha* use mineral particles to seal off the test aperture to prevent desiccation of the cytoplasm (Foissner, 1987; Schönborn, 1992a). This enables individuals to survive temporary desiccation (Foissner, 1987), a feature that is illustrated clearly in plots of abundance versus soil moisture and water table depth for the genus (Figures 6.24 and 6.25). *E. ciliata*, *E. rotunda* and *E. strigosa* appear particularly well adapted to

Difflugia leidyi



Difflugia penardi



Difflugia rubescens

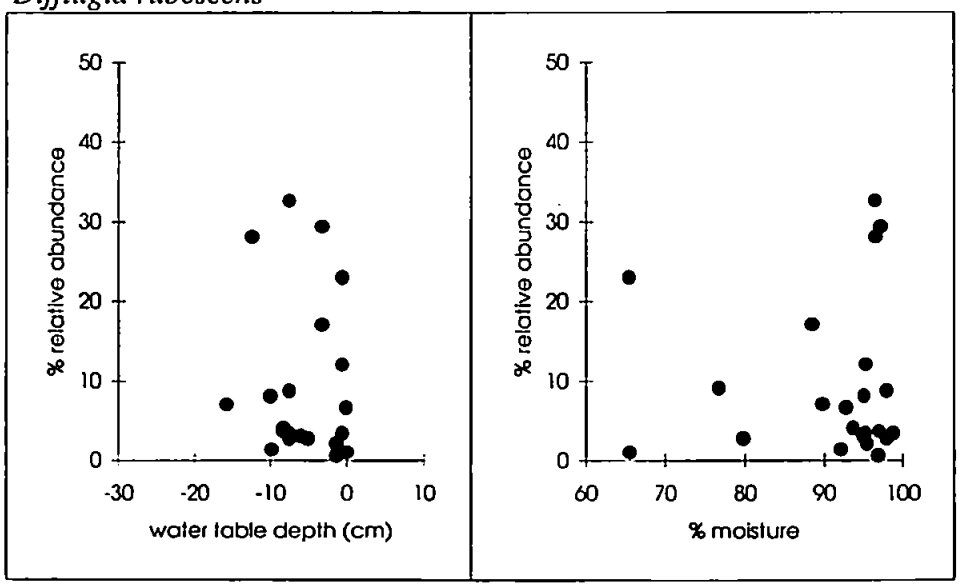
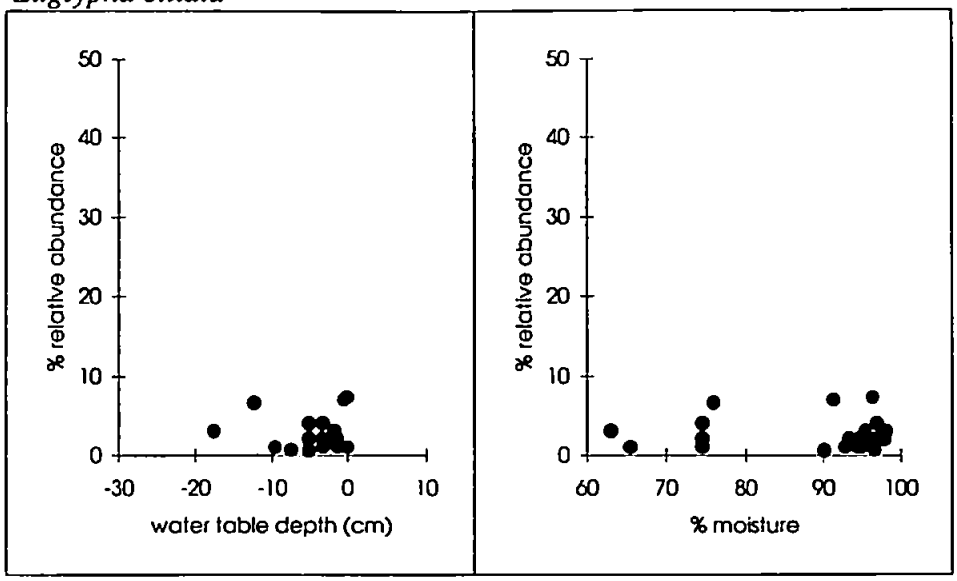
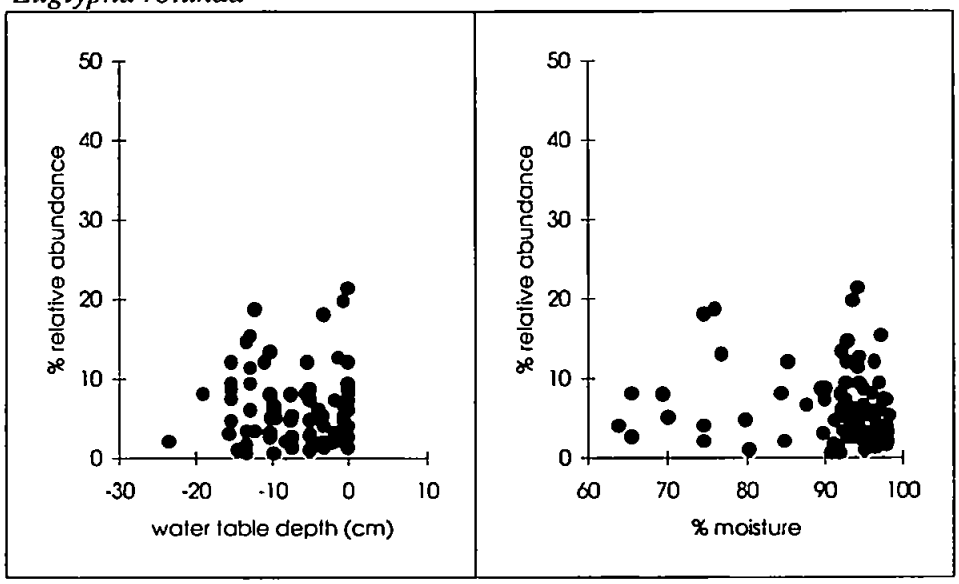


Figure 6.23: Abundances for *Difflugia leidyi*, *D. penardi* and *D. rubescens* in response to hydrology in the British data set.

Euglypha ciliata



Euglypha rotunda



Euglypha strigosa

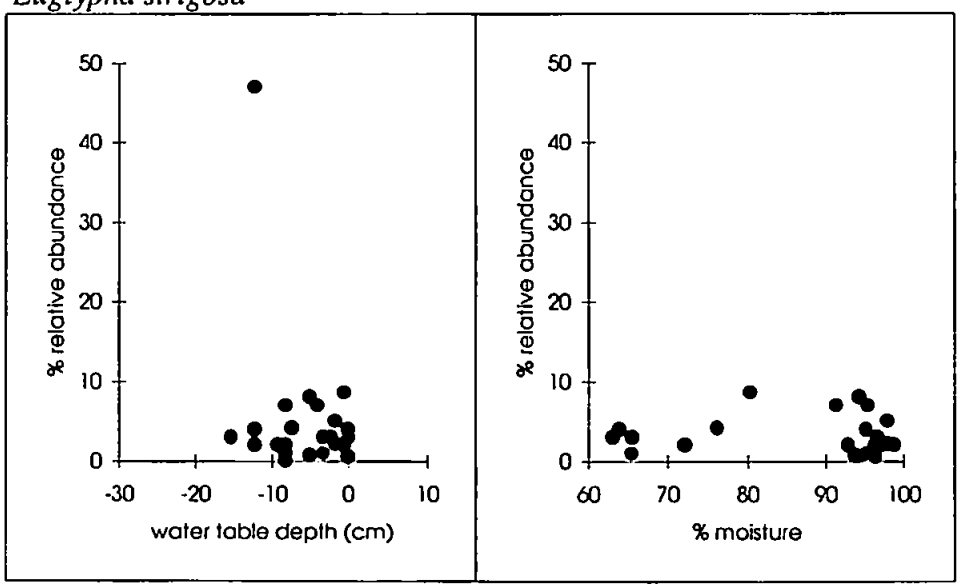
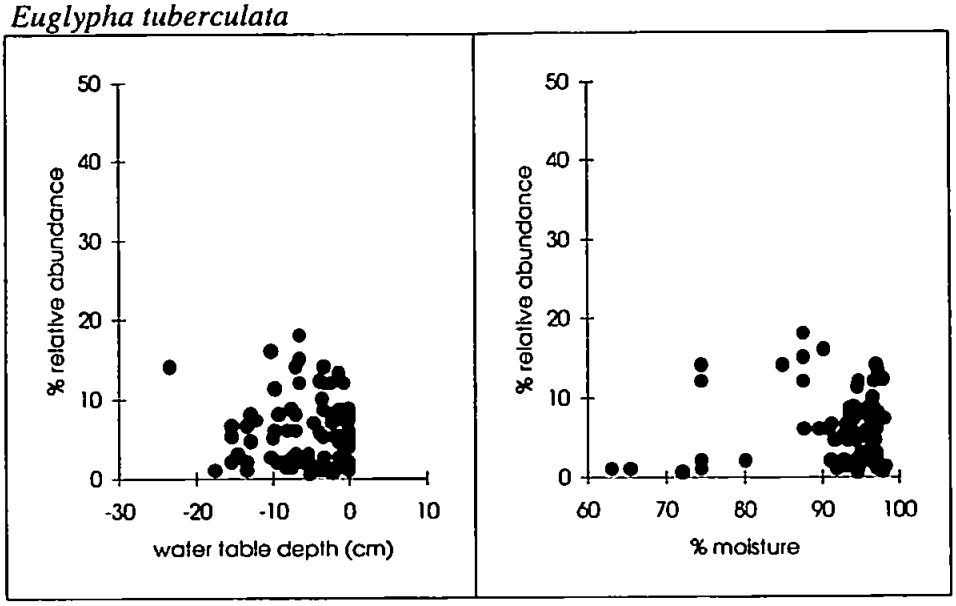
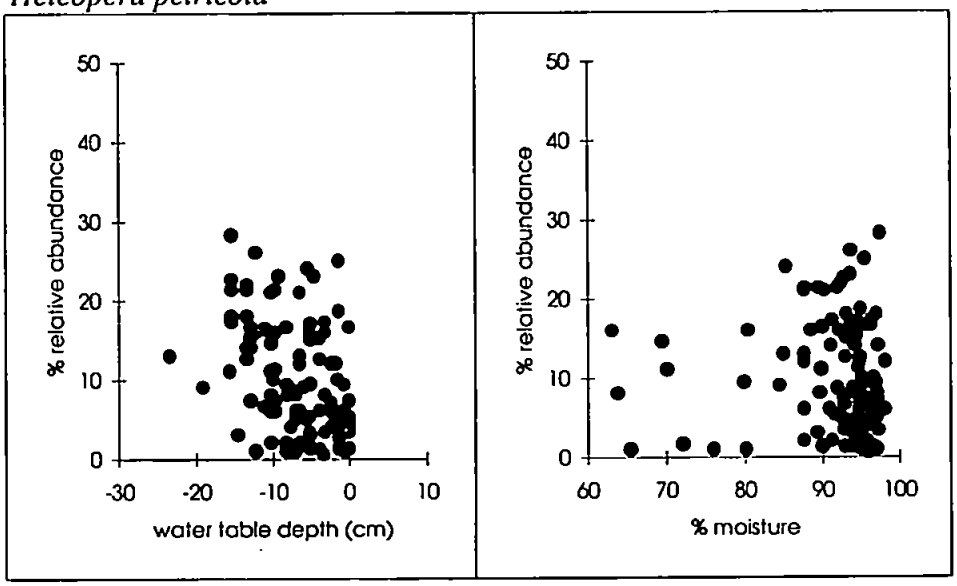


Figure 6.24: Abundances for *Euglypha ciliata*, *E. rotunda* and *E. strigosa* in response to hydrology in the British data set.

Euglypha tuberculata



Heleopera petricola



Heleopera rosea

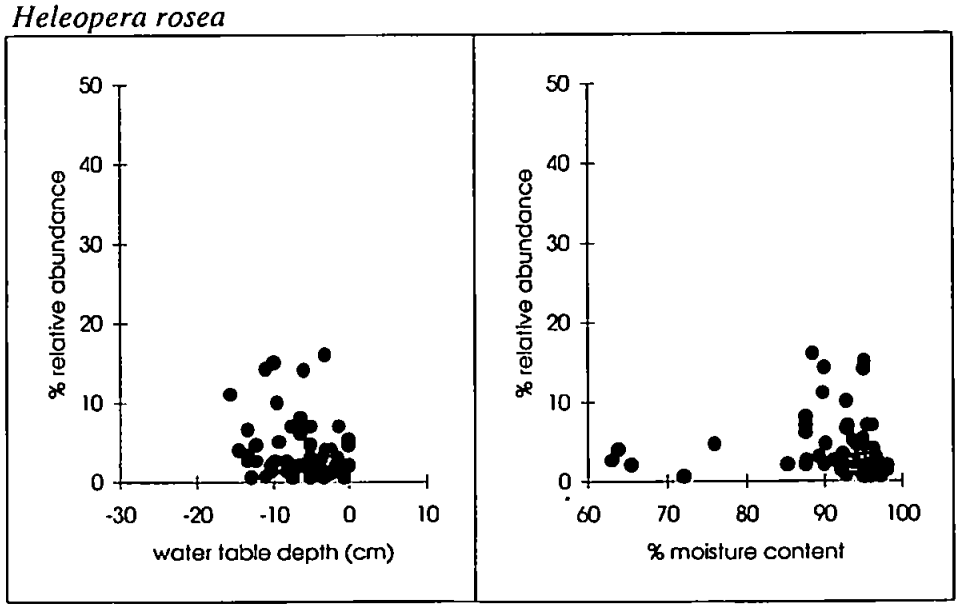


Figure 6.25: Abundances for *Euglypha tuberculata, Heleopera petricola* and *H. rosea* in response to hydrology in the British data set.

xerophilous conditions, displaying little reduction in abundance as moisture falls below 70%. For water table, there is a similar pattern, although no species were found in samples where water table depth exceeded 25 cm. This suggests that, even with a sealed aperture, *Euglypha* cannot survive in extreme xerophilous conditions.

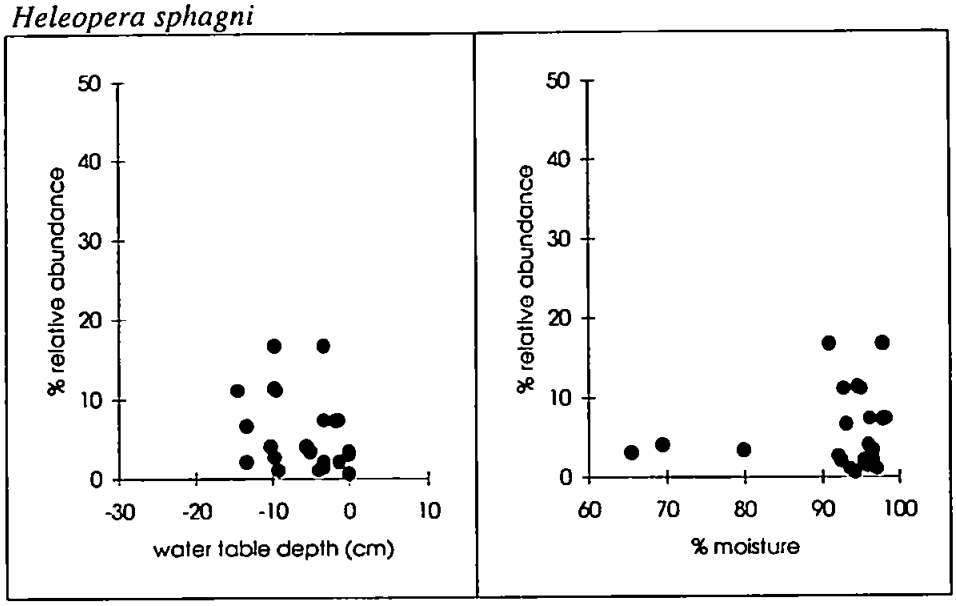
E. tuberculata shows no preference for moisture availability in the British data set (Figures 6.13 and 6.14). Tolonen *et al.* (1992) described this species as xerophilous, while Charman and Warner (1992) found *E. tuberculata* in wetter conditions. The effect of the aperture may be to reduce the hydrological dependence of *E. tuberculata*, so rendering the species indifferent to hydrological conditions.

j) ***Heleopera***

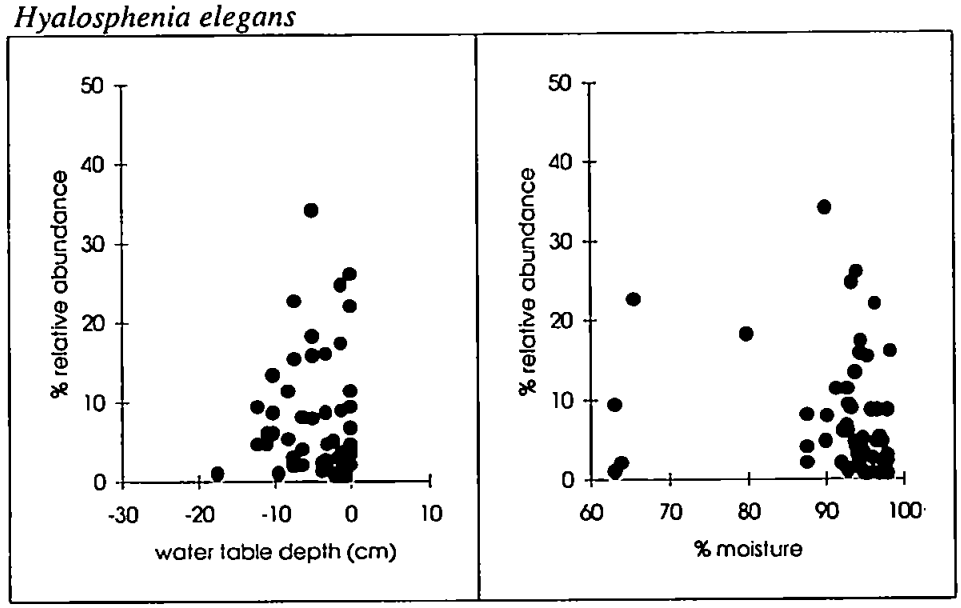
Members of *Heleopera* have an optimum water table depth in excess of 5 cm in the British data set (Figure 6.14), but are relatively widely distributed between depths of 0 and 20 cm (Figures 6.25 and 6.26). For *H. sphagni* the calculated optimum of 7.19 cm is close to an optimum of 9.1 cm in the Finnish data set (Tolonen *et al.*,1992), but for *H. petricola* the British optimum is 5 cm deeper than the Finnish optimum (Table 6.14). There are no comparable water table data from Canadian studies.

For moisture content, *H. petricola* and *H. rosea* are mid-range species with very similar optima of 91.04% and 90.99%; *H. sphagni* has a slightly higher optima of 93.12%. Given the moderately xerophilous water table depth optimum for these species (Figure 6.14), *Heleopera* probably use their compressed tests (see Appendix) to survive in thin water films when water table levels deepen.

Heleopera sphagni



Hyalosphenia elegans



Hyalosphenia papilio

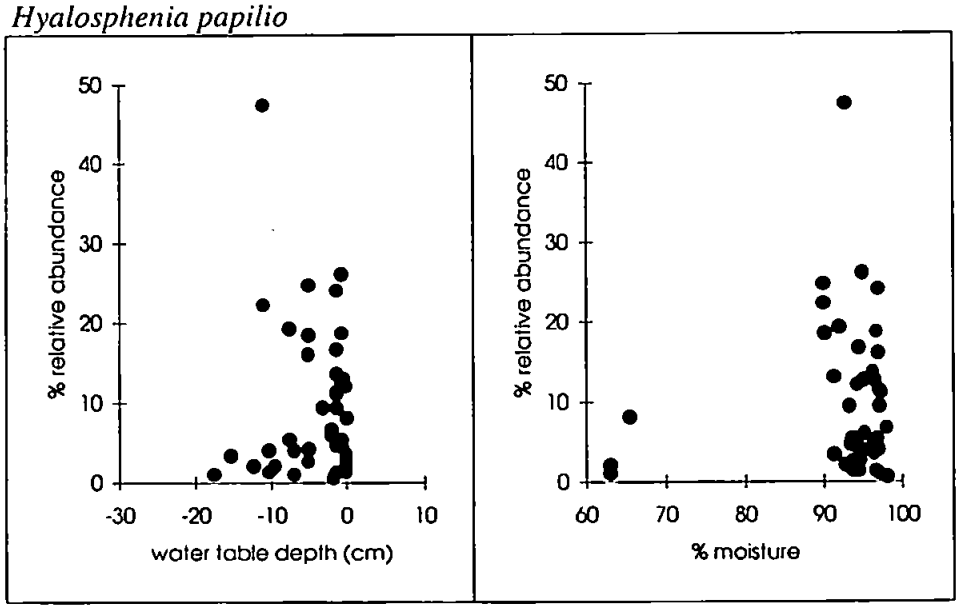


Figure 6.26: Abundances for *Heleopera sphagni, Hyalosphenia elegans* and *H. papilio* in response to hydrology in the British data set.

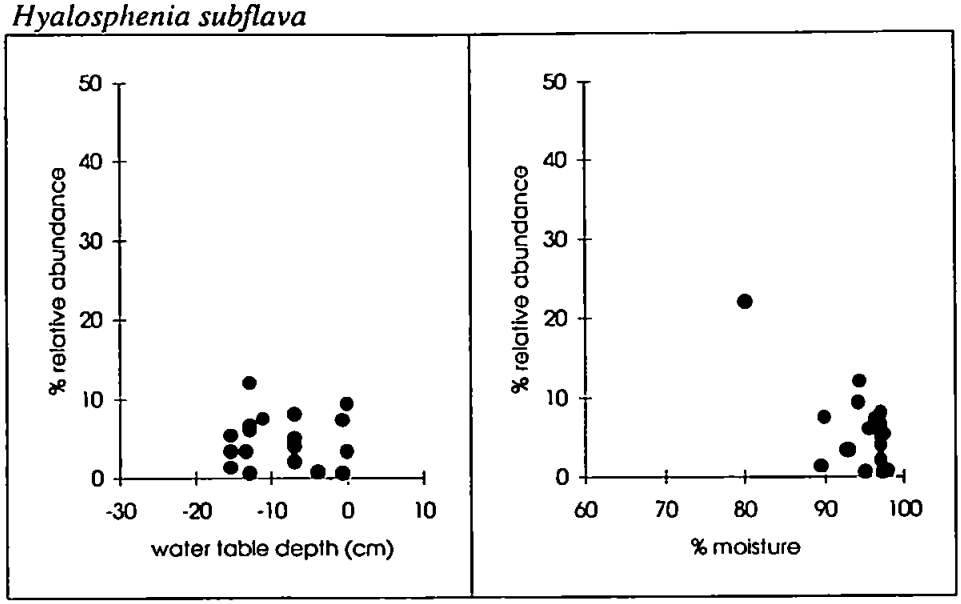
k) *Hyalosphenia*

De Graaf (1956; p.197) described *H. papilio* as a common species in "very wet and wet *Sphagnum*". In this study the species is hydrophilous, with optimum of 93.37% for soil moisture and 4.08 cm for water table depth. Hydrological data from previous studies corroborates this; with the exception of Tolonen *et al.* (1985) and Charman and Warner (1992), working on continental peatlands, the species' moisture optima always exceeds 90%. For water table, Tolonen *et al.* (1992) calculated a deeper optimum of 7.1 cm in Finland, but the species' abundance plots (Figures 6.26 and 6.27) indicate its ability to exist in more xerophilous conditions in Britain.

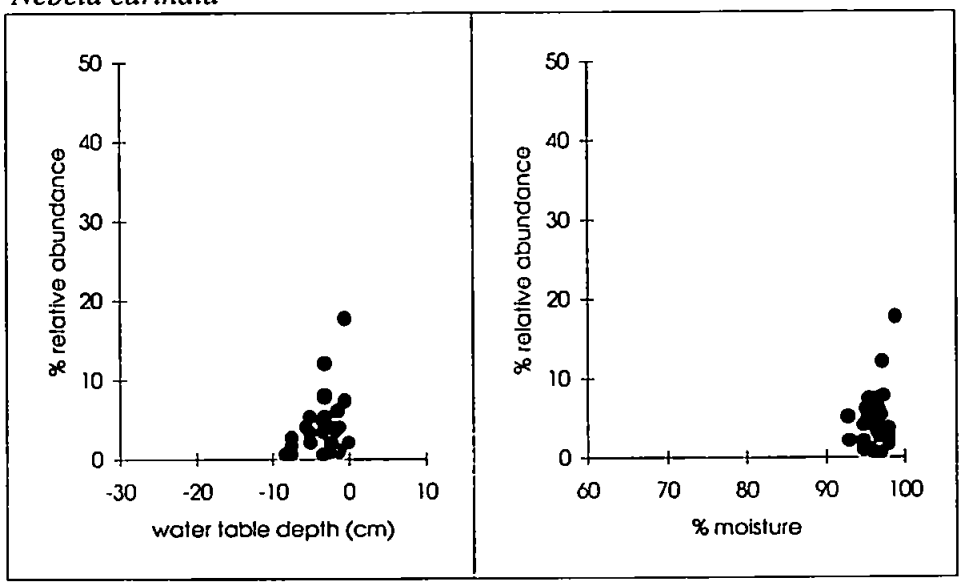
Expressed in terms of water table depth, *H. elegans* is hydrophilous (Figure 6.14), although the species is indifferent towards moisture (Figure 6.13). The water table ranking agrees with the moisture rankings of *H. elegans* in previous studies (Table 6.12), where, with the exception of Tolonen *et al.* (1992), the species is always within the top 5 wettest species. The high water table and low moisture content may reflect the species' colonisation of surfaces that desiccate quickly.

In this study, *Hyalosphenia subflava* is indifferent to moisture content (Figure 6.13), but xerophilous in terms of water table depth, where it tolerates the deepest water table of all species in the British data set (Figure 6.14). Grospietsch (1954), Tolonen (1986) and Warner (1987; 1990) also recognise *H. subflava* as xerophilous and suggest that it is characteristic of drained and marginal areas of peatlands. The morphological adaptation of *H. subflava* to existence in small water films between Sphagna leaves is well-documented (Heal, 1962; Foissner, 1987) and, although there is no information concerning encystment of individuals, it may combine with the flat test to enable survival in extreme xerophilous conditions.

Hyalosphenia subflava



Nebela carinata



Nebela collaris

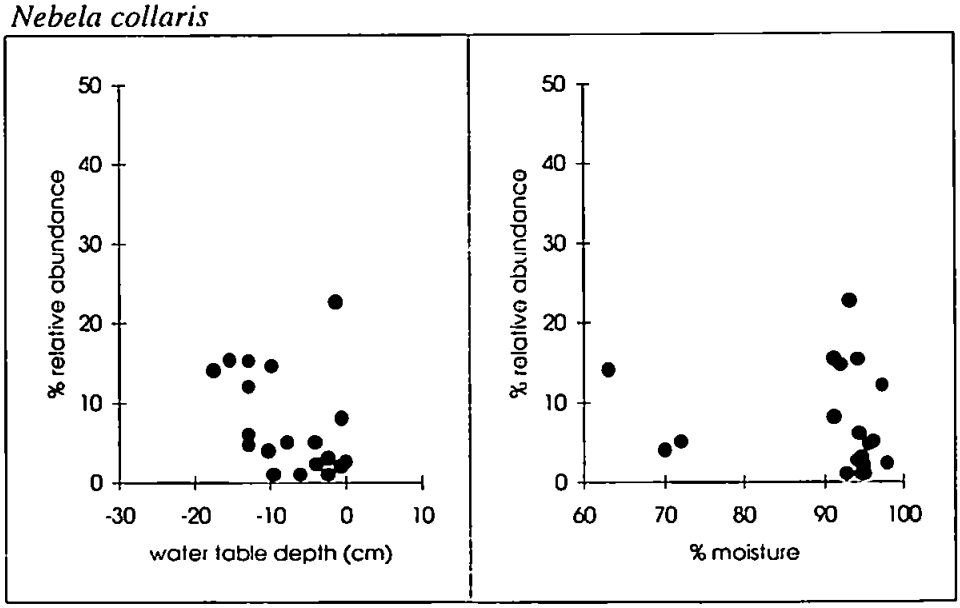


Figure 6.27: Abundances for *Hyalosphenia subflava, Nebela carinata* and *N. collaris* in response to hydrology in the British data set.

l) *Nebela*

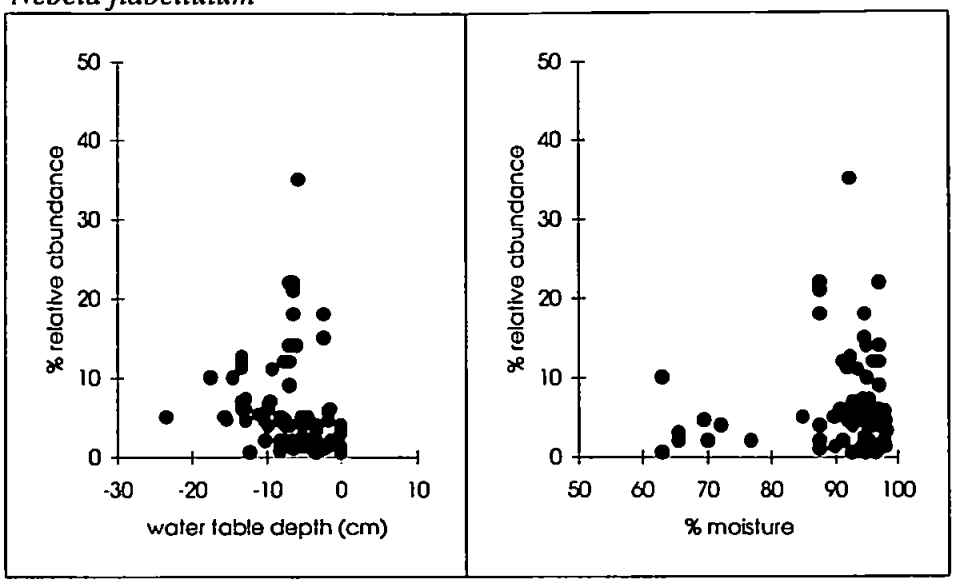
In the British data set, *N. carinata* has optima of 96.48% for moisture and 3.9 cm for water table depth, rendering it hydrophilous. Figures 6.13 and 6.14 show the small tolerance range of *N. carinata* and this is further supported by the species' abundance plots in Figure 6.27, where it is restricted to water table depths of 0-10 cm and moisture values of 90-100%. These plots imply a poor tolerance of unstable hydrological conditions.

Sparse historical information is available on the ecology of *Nebela carinata*. Brown (1912, p.231), noted that the taxa "appeared to be restricted to *Sphagnum* rather than the drier mosses". Schönborn (1963) and Meisterfeld (1977) both identify *N. carinata* as a hydrophilous species, where it is ranked 2nd and 1st respectively. In Tolonen *et al.* (1992) the species occupies a slightly lower ranking (6th). These data indicate that *N. carinata* is a species that is indicative of wet conditions (>95% moisture content - see Table 6.10) on ombrotrophic mires and they corroborate the results of this study.

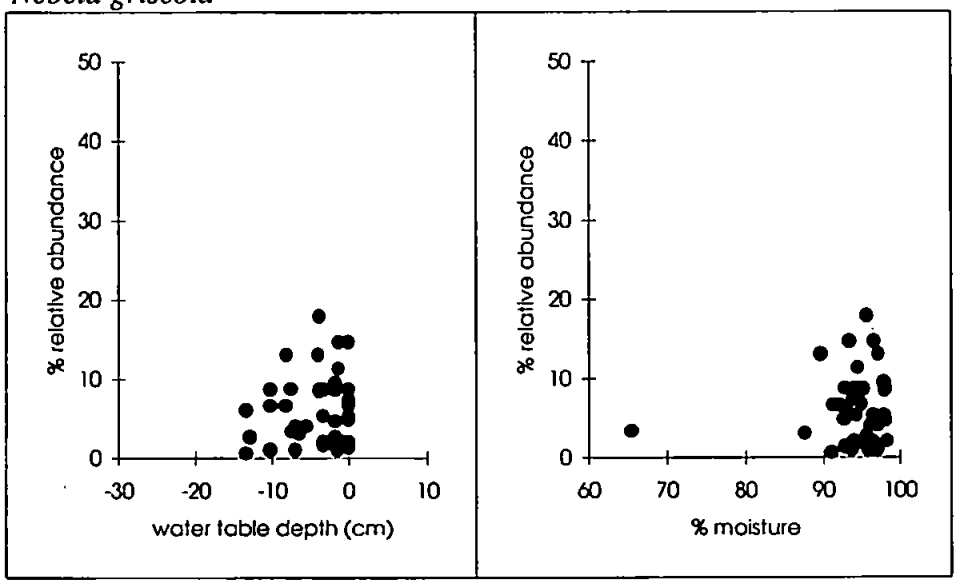
In this study, *Nebela griseola* was found on wetter sites, but was not abundant in open water. This is consistent with the species' hydrological distribution (Figure 6.28) and with its hydrological optima (94.68% for moisture and 4.06 cm for water table depth). There are no comparable hydrological data for *N. griseola*; although Corbet (1973) found *Nebela griseola* as a common species in bog hummocks, she does not mention whether they were wet or dry hummocks.

In the British data set, *Nebela militaris* is xerophilous (Figures 6.13, 6.14, 6.28). The species was found in similar conditions by Meisterfeld (1977), Warner (1987; 1989) and Tolonen *et al.* (1994), although Corbet (1973) found *N. militaris* in the wet *Sphagnum* of bog hummocks. In Charman and Warner (1992), the species shows no hydrological preference.

Nebela flabellulum



Nebela griseola



Nebela militaris

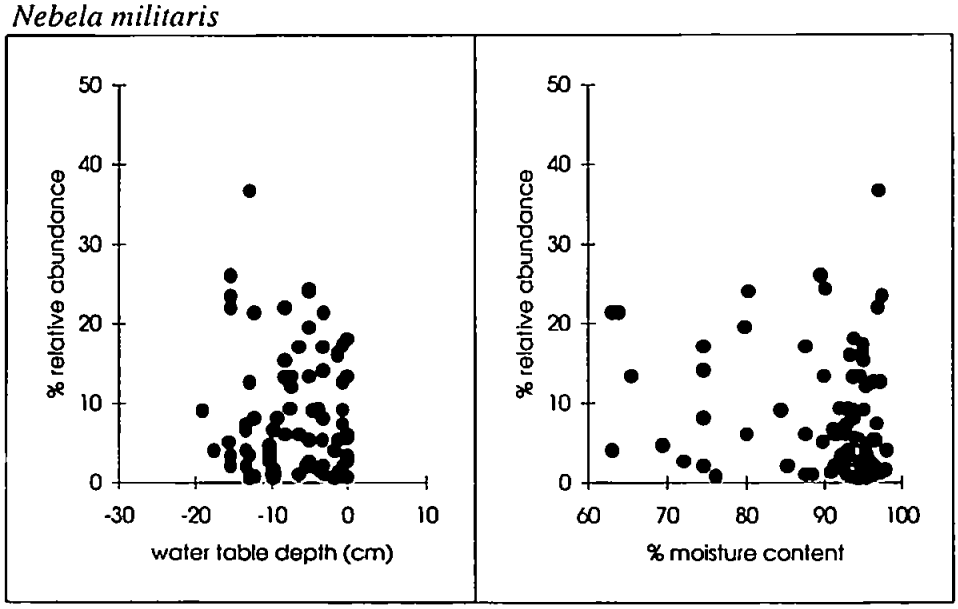


Figure 6.28: Abundances for *Nebela flabellulum*, *N. griseola* and *N. militaris* in response to hydrology in the British data set.

Nebela parvula and *N. tincta* tolerate a wide hydrological range (Figure 6.29). An interesting feature in this study was a morphological adaptation of *Nebela tincta*, apparently in response to surrounding moisture conditions. At the top of hummocks, under drier conditions, the average shell area of *N. tincta* individuals was smaller than those collected from the damper hummock bases. Figure 6.30 illustrates this relationship and a coefficient of $r = 0.72$ ($p<0.01$) identifies a strong correlation between test area and moisture content. In the same way that other species have flattened tests (for example, *Placocista spinosa, Hyalosphenia subflava*), the dwarfing of *N. tincta* in dry habitats enables it to move in thin water films (Heal, 1962).

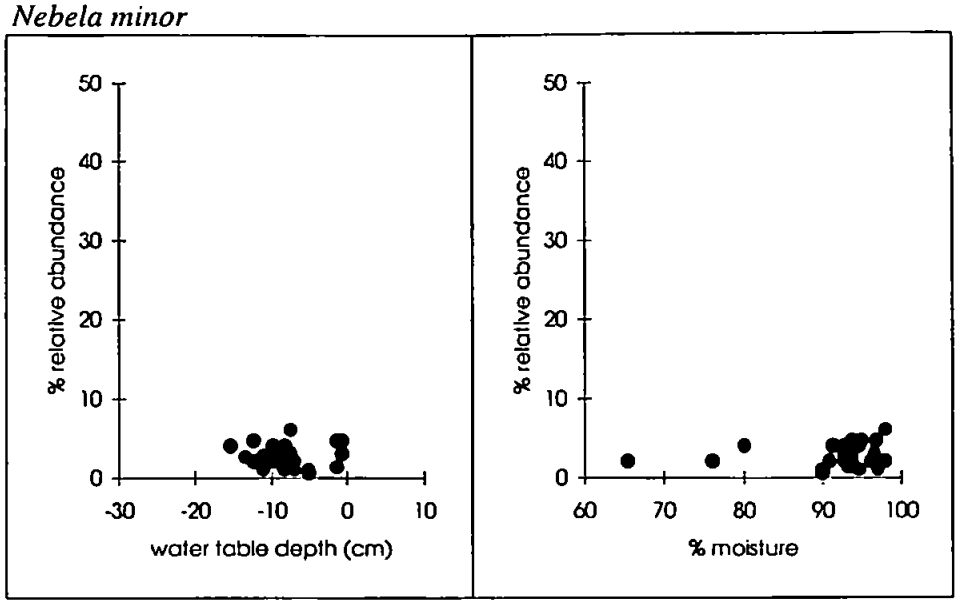
There are no comparable hydrological descriptions of *Nebela vitrea.* In this study, the species is hydrophilous (moisture optimum = 93.15%; water table depth = 4.28 cm; Figures 6.13 and 6.14), although individuals were counted in more xerophilous samples (Figure 6.31).

m) *Phryganella*

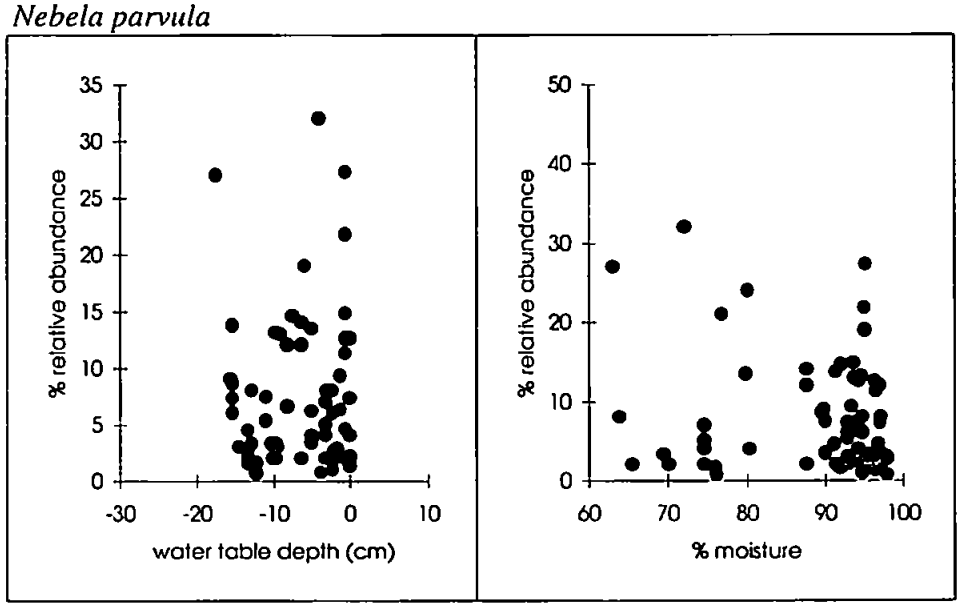
In this study, *Phryganella acropodia* was positioned within the top third of the species rankings for both moisture and water table depth (Figures 6.13 and 6.14). The species' optimum water table depth (5 cm) in this study is supported by Smith (1982) and Beyens *et al.* (1990). who observed *P. acropodia* in wet mosses in the Canadian Arctic. In Tolonen *et al.* (1992; 1994), *P. acropodia* shows no hydrological preference and is generally abundant in moist to wet microsites.

Other references to *P. acropodia* are sparse and this probably arises from its difficult identification under light microscopy (Hoogenraad, 1935; Meisterfeld, 1977; Tolonen, 1986) and the use of an alternative species name by certain authors; *Phryganella acropodia* is

Nebela minor



Nebela parvula



Nebela tincta

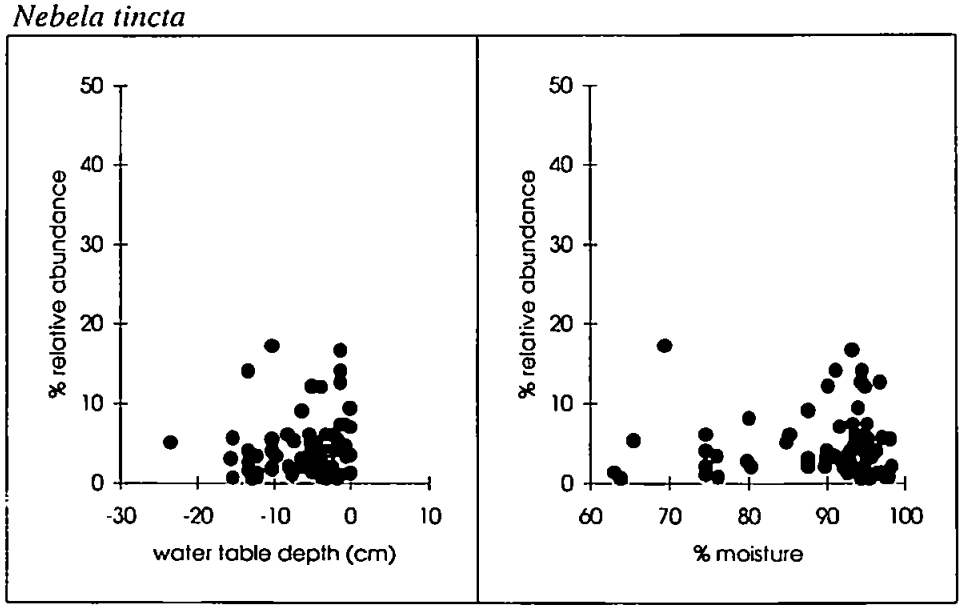


Figure 6.29: Abundances for *Nebela minor*, *N. parvula* and *N. tincta* in response to hydrology in the British data set.

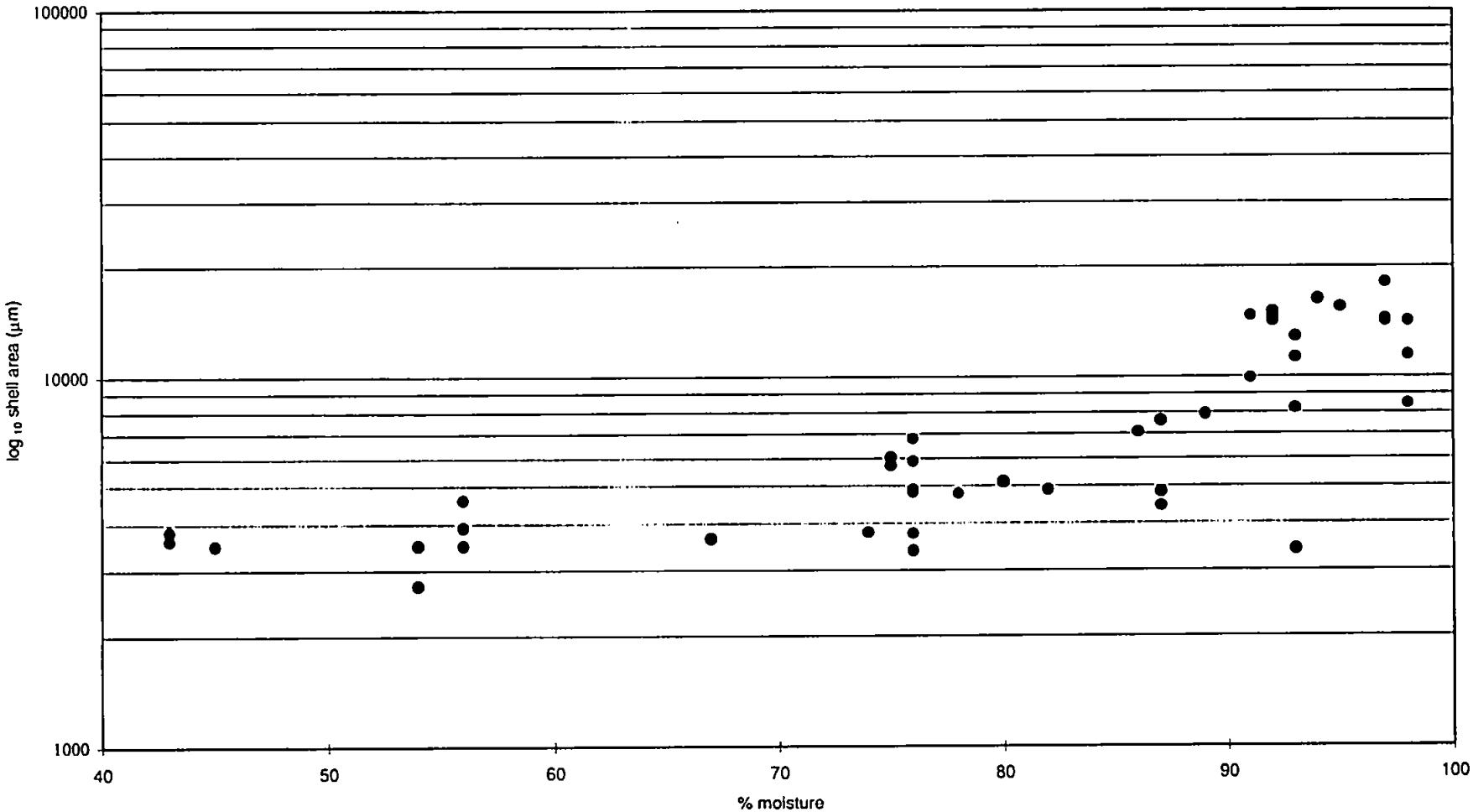
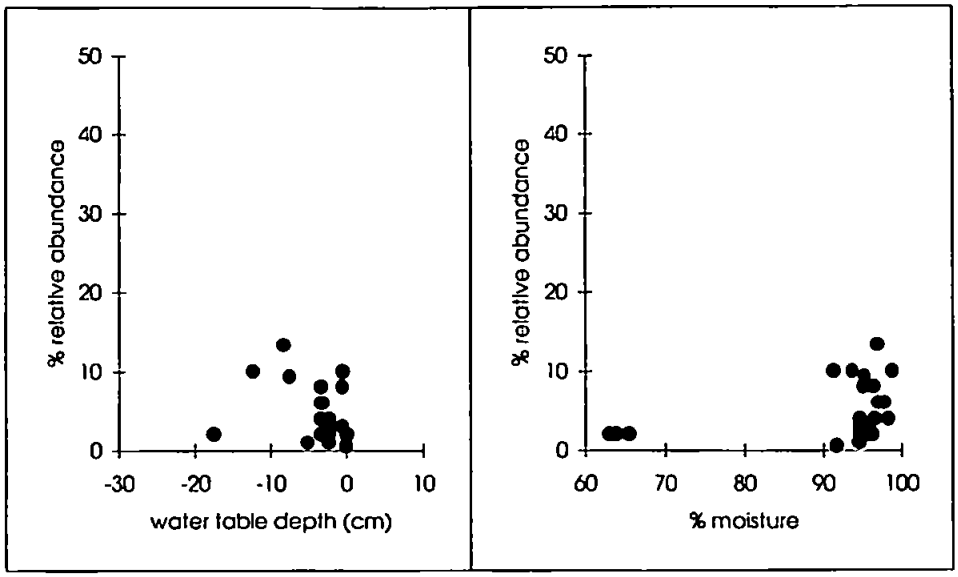
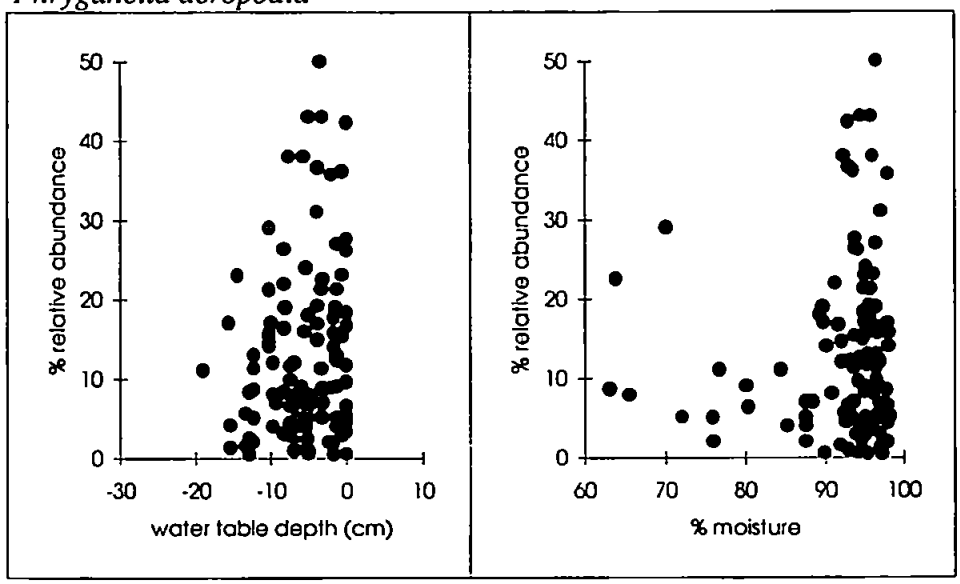


Figure 6.30: Scatterplot showing the relationship between the shell area of *Nebela tincta* and substrate moisture content.

Nebela vitrea



Phryganella acropodia



Placocista spinosa

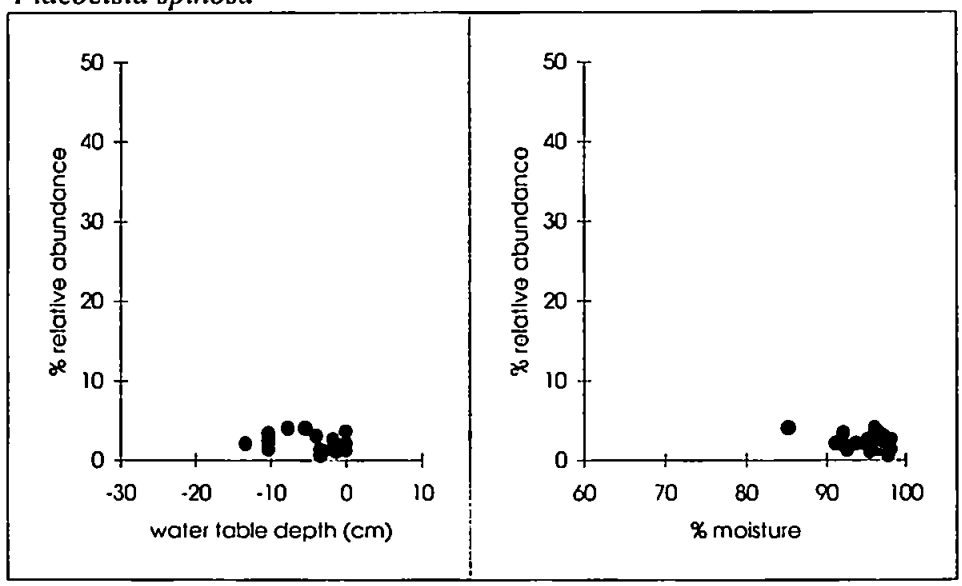


Figure 6.31: Abundances for *Nebela vitrea*, *Phryganella acropodia* and *Placocista spinosa* in response to hydrology in the British data set.

often named as *P. hemispherica* (Warner, 1987). However, *P. acropodia* and *P. hemispherica* are generally considered synonymous (Tolonen, 1986). In this study, it was impossible to distinguish between the two and the more commonly used *P. acropodia* was therefore adopted (see Appendix).

n) ***Placocista***

Corbet (1973) found *Placocista spinosa* in the *Sphagnum* of bog pools; the hydrological data from this study and Tolonen *et al.* (1992) support this observation. For moisture, the respective optima are 94.41% and 97.8%, while water table depth optima are 5.36 cm and 2.8 cm. These data are consistent with Schönborn's (1963) location of the species in Jung's (1936) moisture class I (the wettest class). Individuals in this study were present in relatively deep water table conditions (up to 15 cm depth; see Figure 6.30) suggesting that the compressed test of *P. spinosa* probably enables it to survive in thin water films when the water table drops below the species' optimum of 5 cm.

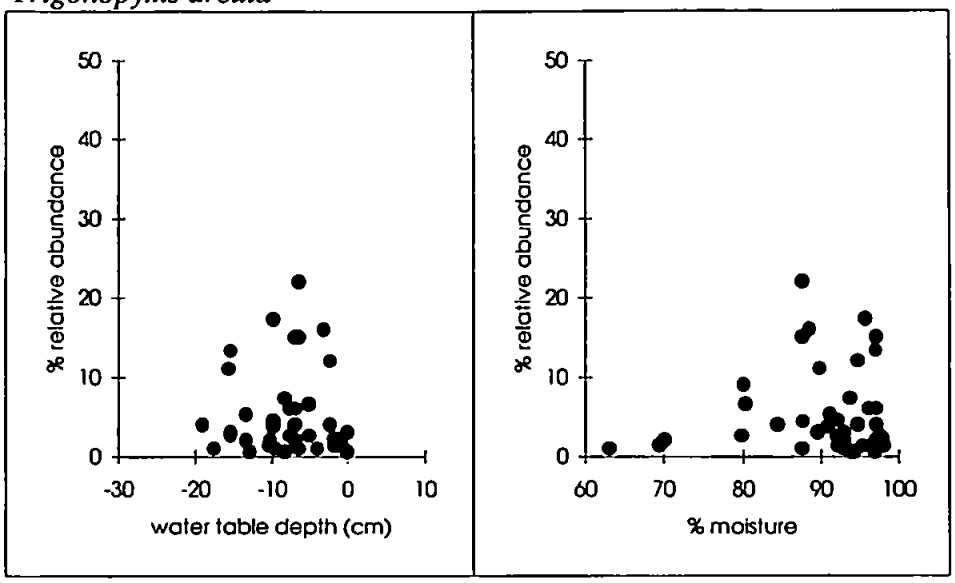
o) ***Trigonopyxis***

In this study, *Trigonopyxis arcula* is identified as relatively xerophilous (Figure 6.32), preferring a moisture content of 90% (Figure 6.13) and depth to water table of 9 cm (Figure 6.14). This is consistent with Tolonen *et al.* (1992; 1994) and Charman and Warner (1992), showing that the species is a universal indicator of relatively xerophilous conditions. De Graaf (1956) considered it to be an indicator of the final dry stages of degenerating raised bogs.

6.11 Summary

This chapter has confirmed the hypothesis that water availability is the most important influence on testate amoebae in Britain. Furthermore, it has revealed the strength of this

Trigonopyxis arcula



Trinema lineare

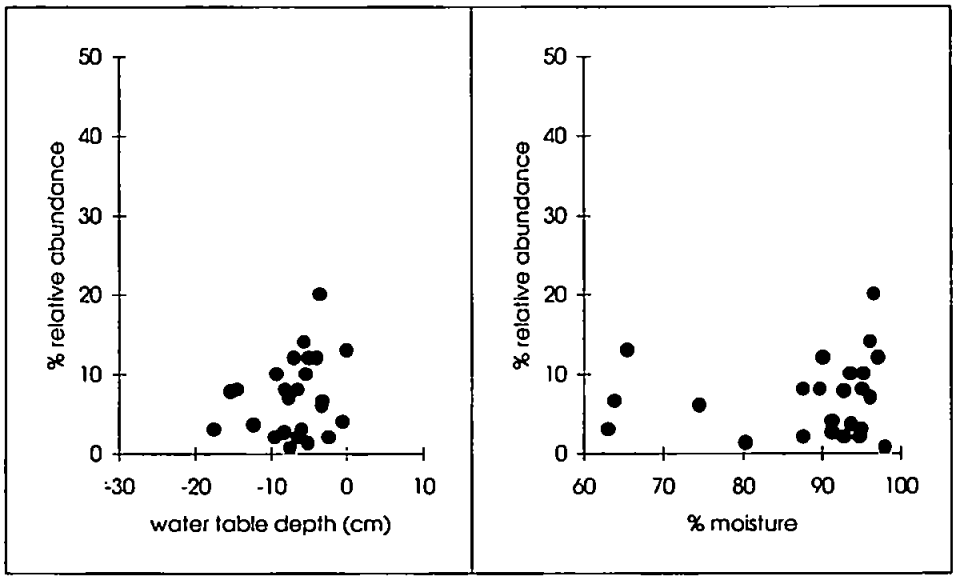


Figure 6.32: Abundances for *Trigonopyxis arcula* and *Trinema lineare* in response to hydrology in the British data set.

relationship when water availability is expressed in terms of water table depth and the percentage moisture content of the host substrate. When a single site is considered, water chemistry is apparently a secondary influence on species' distributions and abundances, but within a large data set, this influence is less significant. This emphasises the need for ecological interpretations to be based on the largest data set possible.

The British data compare well with those derived from Finland. For studies based in continental areas of North America, Canada and Germany, the correlation is less strong and can be at least partly ascribed to the unfavourable effects of single-shot sampling used in these investigations. Clearly, additional studies are required on ombrotrophic sites for which long runs of hydrological data exist, so that more meaningful comparisons can be made.

The correlation of species' hydrological optima between this study and those in Finland is extremely encouraging for palaeoecological applications in northwest Europe. The collection of data from a wide geographical area and wide range of microtopographical positions on British ombrotrophic peatlands has provided a data set upon which a quantitative model can be based. The following chapter is concerned with the development of this model.

Part Three

Development and application of the transfer functions

Chapter 7

Developing the transfer functions

7.0 Introduction

Chapter 6 presented new data collected from Tor Royal and other British ombrotrophic mires and related modern testate amoebae assemblages to contemporary water table depth, substrate moisture content and water chemistry. CCA, applied to both data sets, identified moisture content and water table depth as the environmental variables that were most strongly related to testate amoebae abundance and distribution.

The strength of these relationships, which are supported by results from studies in Canada (Tolonen *et al.*, 1985; Warner, 1987; 1988; 1989; Charman and Warner, 1992) and Finland (Tolonen *et al.*, 1992; 1994), confirm that testate amoebae can be exploited for quantitative palaeohydrological reconstructions on ombrotrophic mires. From the hydrological optima calculated by weighted averaging regression in Chapter 6, a quantitative reconstruction of palaeohydrological conditions on British ombrotrophic mires is possible.

Before transfer functions can be applied to palaeoenvironmental data, they must be validated in some way. Without validation, any distortions or bias in the transfer functions will remain undetected and could be incorporated into palaeoenvironmental data. In this study, two types of validation are applied. Firstly, in this chapter, a range of models will be tested using cross-validation techniques. Secondly, the model that performs best will be applied to a fossil data set and the results compared with those from other palaeoecological techniques (Chapter 8).

The aim of this chapter is to assess the performance of four regression models for generating palaeoecological transfer functions. These models are: weighted averaging (WA);

tolerance downweighted weighted averaging (WA-Tol); partial least squares regression (PLS) and weighted averaging-partial least squares regression (WA-PLS). The robustness of each model will be evaluated by comparing the models' predicted water table depth and percent moisture values (inferred from testate amoebae) against observed water table depth and moisture content for each sample site in the modern data sets. The model that produces predictions corresponding most closely with the observed data will be used as a transfer function to reconstruct water table depth and moisture content in a fossil peat core using testate amoebae assemblages (Chapter 8).

7.1 Transfer functions

In palaeoecology, a quantifiable relationship between a selected environmental parameter and a species' distribution is termed a "transfer function" because the value of an environmental variable is a function of biological data (Jones *et al.*, 1993; Birks, 1995). In this study, percent moisture content and water table depth are functions of the testate amoebae assemblage. The first transfer functions were derived by Imbrie and Kipp (1971), who applied least-squares regression to foraminifera assemblages to reconstruct sea-surface temperatures and salinity. These were later improved by Gasse and Tekaia (1983) and Gasse (1987) in palaeoecological estimations of pH in tropical semi-arid lakes from diatom assemblages. They had suggested that valuable species-environment information was being lost by using principal components regression and introduced the use of direct gradient analysis, which used all components of a single predictive environmental variable.

The regression methods applied in the above studies, however, gave all species the same weighting regardless of their abundance. To resolve this, weighted averaging regression was introduced into palaeoecological reconstructions; this method has been described and was used in Chapter 6 to derive the hydrological optima of modern testate amoebae.

7.2 Suitability of the data for generating transfer functions

Certain ecological assumptions must be made when establishing the relationship between species and environmental variables for regression and calibration purposes (Birks *et al.*, 1990; Korsman and Birks, 1996).

The first assumption is that the taxa that are to be used to model the response of testate amoebae to contemporary water table depth and moisture content are systematically related to the physical environment in which they live. This has been demonstrated by the ordination exercises that were conducted in Chapter 6 and also from previous studies, notably Heal (1962); Schönborn (1966); Charman and Warner (1992); Tolonen *et al.* (1992; 1994). All show a clear relationship between testate amoebae assemblages and hydrology, expressed variously as water table depth and/or substrate moisture content.

Secondly, and at the heart of all palaeoecological reconstructions, one assumes that the taxa in the fossil core are identical to the modern data set in their ecological requirements. Further, those requirements must not have altered in the time-span represented by the fossil peat core. If the requirements are identical then the testate amoebae can be used to reconstruct water table depth and moisture changes through time. In Chapter 3, it was noted that Harnisch (1951) had postulated that the habitat dependence of testate amoebae was not likely to have developed until ca. 6000 years BP and that it would therefore be impossible to interpret faunal assemblages from older periods based on present ecology. However, several shortfalls were identified in Chapter 3 which suggest that this theory cannot be substantiated. Until future work proves otherwise, this study will assume that the environmental optima of fossil testate amoebae are identical to modern taxa.

Thirdly, the mathematical model used in the regression and calibration exercises must "adequately model the biological responses to the environmental variable of interest"

(Imbrie and Kipp 1981, in Birks *et al.* 1990). Before the introduction of weighted averaging regression and calibration, the most popular expression of species response to environmental parameters was provided by the Gaussian model (Gauch, 1982), which was considered as a meaningful expression of species response (see Chapter 6). The integrity of the Gaussian model has been considered in depth by Oksanen *et al.* (1988) and ter Braak and van Dam (1989), who consider the technique as "ecologically realistic" (ter Braak and van Dam, 1989) and it is upon this approach that the regression and calibration models used in this study are based.

The fourth assumption is that "environmental variables other than the one of interest...have negligible influence, or their joint distribution with the variable of interest in the fossil set is the same as in the training set" (Birks *et al.*, 1990; Birks, 1995). In this study, ordination by CA and CCA (see Chapter 6) showed that, in the full British data set, other parameters were less influential than water table depth and moisture content in the distribution of testate amoebae taxa in the modern data sets. The restriction of the modern data to oligotrophic mires means that the transfer functions derived from them are only applicable to fossil samples from oligotrophic peat.

7.3 Regression techniques as generators of palaeoecological transfer functions

The performance of four regression techniques to derive transfer functions are evaluated in this study. In addition to weighted averaging regression (WA), they are tolerance downweighted weighted averaging (WA-Tol), partial least squares regression (PLS) and weighted averaging-partial least squares regression (WA-PLS).

7.3.1 Weighted averaging (WA)

Chapter 6 demonstrated how WA regression has become widespread in ecology. The method has also become popular in palaeoecology because it is a simple, powerful

computational technique for environmental reconstruction (ter Braak and Juggins, 1993) that does not assume a linear relationship between species and environmental variables.

In Chapter 6, weighted averaging regression was used to quantify the optima of testate amoebae species along water table depth and percent moisture gradients. Weighted averaging calibration assumes that, given a range of species with optima distributed along an environmental gradient, a particular site along the gradient will tend to be dominated by species with an optimum close to the environmental value of that site. An estimate of the environmental value at the site is given by averaging the optima of the species present (Juggins, 1992).

WA calibration was introduced into palaeoecology by Ellenberg (1948) as a technique for inferring pH and other environmental variables from vascular plants (ter Braak and van Dam, 1989). Later, Pantle and Buck (1955) used weighted averages of algae and bacteria abundances to estimate organic pollution levels in freshwater. In limnology, the technique has been applied to diatom assemblages to predict lake acidity (Oksanen *et al.*, 1988) and to characterise lake water chemistry (Jones *et al.*, 1993).

In palaeoecology, WA calibration has been used in several forms in a number of applications. This reflects the advantages of WA over previous methods, which were summarised by Birks, *et al.* (1990; p.274): "WA is ecologically more realistic, statistically more robust, and numerically more accurate than other methods". To reconstruct palaeotemperatures from fossil foraminifera assemblages, Lynts and Judd (1971) and Hutson (1977) used simple WA calibration, while Berger and Gardner (1975) used a tolerance weighted version (Table 7.1). Ter Braak (1987a) introduced WA calibration into palaeolimnology as an improvement on the reconstruction techniques that had been used to date (Line and Birks, 1990) and it has since had widespread use in palaeolimnology

Model type	Problem	Authors
WA calibration	Inferring pH and other environmental variables from vascular plants.	Ellenburg (1948)
WA calibration	Estimation of organic pollution in freshwaters using abundances of algae and bacteria.	Pantle and Buck (1955)
WA calibration	Reconstruction of palaeotemperatures from fossil foraminifera assemblages.	Lynts and Judd (1971)
Tolerance-weighted WA calibration	Reconstruction of palaeotemperatures from fossil foramnifera assemblages.	Hutson (1977)
WA calibration (CA)	Reconstruction of pH in east African lakes from diatoms.	Gasse and Tekaia (1983)
WA ordination	Reconstruction of Holocene temperature and rainfall based on palaeoecology and isotope geology. The Netherlands.	Dupont (1986)
WA calibration	Reconstruction of palaeohydrology of Nigerian lakes.	Gasse (1987)
WA calibration	Improvement on previous reconstruction techniques used in limnology.	ter Braak (1987)
WA calibration	Prediction of lake acidity from diatom assemblages.	Oksanen *et al*. (1988)
WA calibration	Reconstruction of pH in selected Scottish lakes from diatoms.	Birks *et al*. (1990)
WA calibration (CCA)	Reconstruction of 20th-century salinity and water levels in Devils Lake, North Dakota.	Fritz (1990)
WA calibration (CA)	Climatic transfer function from Quaternary molluscs in European loess deposits.	Rousseau (1991)
WA calibration	Reconstruction of lake-water temperatures from chironomid assemblages.	Walker *et al.* (1991)
WA calibration (CA)	Inferring phosphorus concentrations in lakes from diatoms in British Columbia.	Hall and Smol (1992)
WA calibration	Salinity transfer function derived for Thames estuary from diatoms.	Juggins (1992)
WA calibration (CCA)	Reconstruction of changes in salinity and climate in lakes of the northern Great Plains, U.S.	Fritz *et al*. (1991; 1993)
WA calibration	Characterisation of lake water chemistry.	Jones *et al*. (1993)
WA-PLS	Reconstruction of water chemistry in lakes from Norway, Sweden and UK.	ter Braak and Juggins (1993)
WA ordination	Reconstruction of Holocene palaeohydrology from plant macrofossils, Bolton Fell Moss, England.	Barber *et al*. (1994b)
WA calibration	Reconstruction of peatland palaeohydrology from testate amoebae, Canada.	Warner and Charman (1994)
WA calibration, WA-Tol, WA-PLS.	Salinity transfer functions from diatom assemblages in lakes of the Great Northern Plains, U.S.	Juggins *et al*. (1994)

Table 7.1: Chronological listing of some weighted averaging applications in palaeoecology.

(Birks *et al.*, 1990; Fritz *et al.*, 1991, 1993; Hall and Smol, 1992; Juggins *et al.*, 1994). Juggins (1992) also makes the important point that the pH transfer function produced for East African lakes by Gasse and Tekaia (1983) using correspondence analysis is also underlain by WA (see Table 6.1). More recently, and directly relevant to this study, Warner and Charman (1994) used weighted averaging regression and calibration to reconstruct surface moisture on a Canadian peatland from testate amoebae assemblages. In the present study, weighted averaging calibration will be used to reconstruct water table depth and moisture content from a fossil testate amoebae assemblage (Chapter 8).

7.3.2 Tolerance downweighted weighted averaging (WA-Tol)

Species with narrow tolerance ranges are generally of more value in palaeoecological reconstructions. A modified version of WA calibration can be used to give these species more weight in the calibration exercise; this technique is known as tolerance downweighted weighted averaging (WA-Tol). WA-Tol also allows the downweighting of individual species that, for example, are allochthonous (Juggins, 1992). Opinion is divided over the degree of improvement in the accuracy of transfer functions derived from WA-Tol. Ter Braak and van Dam (1989) and Birks *et al.* (1990) found no improvement in performance using WA-Tol. Juggins (1992), however, noted that WA-Tol generated smaller prediction errors, which supports earlier successes by Berger and Gardner (1975) and Oksanen *et al.* (1988).

7.3.3 Partial least squares regression (PLS)

Partial least squares regression (PLS), which assumes a linear response, is most widely used in chemometrics and, in particular, spectroscopy (Helland, 1988), where it is often used to predict chemical composition from near infra-red spectra (Helland, 1988; ter Braak and Juggins, 1993). Helland (1988) and ter Braak and Juggins (1993) note that PLS is closely related to principal component regression (known as PCR - Helland, 1988 or PCAR - ter

Braak and Juggins, 1993). Both PLS and PCAR are favoured in spectroscopy investigations because they are not affected by co-linearity, a problem that arises from the generation of vast numbers of wavelengths. This proves problematical in studies that consider each wavelength as an explanatory variable, when the number of wavelengths commonly exceeds the number of chemical samples (Helland, 1988). Ter Braak and Juggins (1993) note that PLS gives a smaller prediction error than PCAR and have therefore combined the method with WA to produce WA-PLS.

7.3.4 Weighted averaging partial least squares regression (WA-PLS)

Weighted averaging partial least squares regression (WA-PLS) was presented as a refinement of WA regression by ter Braak and Juggins (1993). The method combines the non-linear method of WA with the linear method of partial least squares regression in an attempt to maximise the predictive power of transfer functions, particularly in terms of improving the accuracy of predicted species' optima. Several components are obtained in WA-PLS. The first PLS component of the transformed data is generally equivalent to WA. Additional components are obtained by using the residuals of the regression as new site scores in subsequent regressions. The final prediction equation is therefore a WA of the updated optima, but in contrast to WA, the optima are updated by considering the residual correlations in the biological data (Birks, 1995). The overall effect is to improve the species' optima in the final prediction output. WA-PLS may also remove edge effects, which give nonlinear distortions in WA regression and calibration. The improvement achieved with this method has been shown by ter Braak and Juggins (1993) to depend on the level of noise in the data set - significantly higher reductions in prediction errors can be achieved in datasets with low noise than in noisy datasets. WA-PLS model performance can also be influenced by the number of components which are retained. If only the first component is retained, WA-PLS has a similar performance to WA (Birks, 1995). If two or three components are used, up to a 60% improvement in model performance over WA may

be achieved in some data sets (Birks, 1995). The computer program used in this study allows the retention of up to six components to optimise model performance (section 7.4).

7.4 Model performance assessment: the CALIBRATE computer program.

The regression techniques were evaluated in this study using the computer program CALIBRATE (Juggins, unpublished), which was developed by Juggins and ter Braak (1992) for species-environment calibration. The program comprises the models for weighted averaging regression and calibration (WA); tolerance-downweighted weighted averaging regression (WA-Tol); partial least squares regression (PLS), and weighted averaging partial least squares regression (WA-PLS). In addition, it allows principal components analysis (PCA) to be performed on the data set, but this was not used here.

In terms of this study, CALIBRATE had the advantage that it provided a very quick and simple way to generate transfer functions using several models and to evaluate individual model performance. Generating these transfer functions on a spreadsheet alone would have been time-consuming and complicated, thus introducing the risk of calculation errors. Reading the original FORTRAN data files that had been used for the CANOCO ordination work maintained an important consistency in the data processing.

7.4.1 Assessment criteria: root mean squared error (RMSE) and maximum bias

The performance of each model was assessed using similar techniques to those of Juggins *et al.* (1994). For each regression model, CALIBRATE uses two criteria to test model performance - the root mean square of the errors (RMSE) and maximum bias along particular sections of the environmental gradient (Juggins *et al.*, 1994). RMSE is a measurement of random differences in the model predictions, while maximum bias expresses systematic differences in the predictions (Birks, 1995).

In this study, maximum bias is calculated by dividing the sampling range of water table depth and percent moisture content into equal intervals (usually 10; Birks, 1995). The mean bias for each interval is calculated and the largest value for an interval is used as a measure of maximum bias (Birks, 1995). Maximum bias is therefore a measure of sample distribution along the environmental gradient. The lower the maximum bias, the more evenly distributed are the samples along the environmental gradient.

One "apparent" and two "predicted" RMSE and maximum bias values are produced. The "apparent" values are based on a comparison of predicted and observed values when all samples are included in the analysis. The "predicted" values refer to a comparison of observed and predicted values when either a block of samples or a single sample at a time are excluded from the analysis (see section 7.4.2, below).

If based on the training set alone, the apparent RMSE and maximum bias values will always produce an over-optimistic performance assessment because the same data that were used to generate the transfer function are also used to evaluate the prediction (ter Braak and van Dam 1989; Oksanen *et al.*, 1988). Hence, the prediction model should always provide a good match of the observed data (Oksanen *et al.*, 1988).

7.4.2 Cross-validation and jackknifing

To gain a more reliable indication of model performance, assessments by "cross-validation" and "jackknifing" are performed. Cross-validation has been widely used in palaeoecological studies to check the reliability of RMSE values in WA transfer functions (e.g. Birks *et al.*, 1990; Fritz *et al.*, 1991; Juggins *et al.*, 1994) and in CALIBRATE the process operates by excluding blocks of samples or individual samples from the regression. For example, the British data set - which had 163 samples - was split by default into six components (that is, five blocks of 27 samples and one block of 28) and the regression run six times through

the data set, each time leaving out one component. By excluding one component per cycle, a second data set is generated from the original (complete) data set, which then creates sufficient variation on which to test the regression model. CALIBRATE allows the user to set the number of components depending on the degree of robustness required.

The jackknifing or "leave-one-out" method (Juggins *et al.*, 1994) is a more computer-intensive method of cross-validation. This method operates by running a series of regression cycles, but excluding one sample from the cycle each time and then applying the derived transfer function to that sample.

7.5 Comparison of model performances based on RMSE and maximum bias values

Both the Tor Royal and British data sets were run through CALIBRATE to generate transfer functions. Four sequential modelling exercises were conducted as the models WA, WA-Tol, PLS and WA-PLS were applied to the data.

This section evaluates the performance of each model's predictive powers. The evaluations were made in two ways: firstly, by comparing the summary statistics of RMSE and maximum bias for each model and secondly, by using scatterplots to graphically examine the correlation between model prediction and the observed water table depth/moisture content.

In Table 7.2, one "apparent" and two "predicted" RMSE and maximum bias values are listed for each CALIBRATE regression model for both the Tor Royal and British data sets. The "apparent" RMSE is based on the error when every sample is included in the analysis. The "predicted" RMSEs refer to the error when either a block of samples are excluded from the analysis under cross-validation or one sample is excluded via jackknifing (Juggins, pers. comm. - see section 7.4.2 above). The RMSE gives an overall indication of the accuracy

a) Ranked model performances for moisture content

1. Apparent errors

Britain			Tor Royal		
Method	RMSE	Max bias	Method	RMSE	Max bias
PLS	4.7694	9.1438	PLS	9.3812	14.3200
WA-PLS	4.9522	9.9676	WA-Tol	10.1032	14.3400
WA	8.0411	19.8200	WA	11.4822	14.8300
WA-Tol	8.7136	24.6900	WA-PLS	12.1842	15.4100

2. Prediction errors (cross-validated)

Britain			Tor Royal		
WA-PLS	8.0419	19.8063	PLS	10.1240	15.0100
WA-Tol	8.4538	23.7900	WA-Tol	10.3281	15.0900
WA	8.9604	19.8600	WA	12.3183	15.2500
PLS	13.3831	14.2189	WA-PLS	13.0412	16.8600

3. Prediction errors (jackknifed)

Britain			Tor Royal		
WA	7.7926	20.4600	WA-Tol	9.8413	13.9800
WA-PLS	7.7946	20.4580	PLS	10.0310	14.0300
WA-Tol	8.2722	22.9700	WA	11.5160	15.0300
PLS	9.2450	10.9638	WA-PLS	12.0100	14.3200

b) Ranked model performances for water table

1. Apparent errors

Britain			Tor Royal		
Method	RMSE	Max bias	Method	RMSE	Max bias
PLS	4.5349	9.3009	PLS	5.2565	4.6152
WA-PLS	4.6273	9.6043	WA-PLS	5.3668	4.6813
WA	6.3627	12.9600	WA-Tol	9.1135	10.8000
WA-Tol	6.9917	14.8700	WA	9.1280	9.0130

2. Prediction errors (cross-validated)

Britain			Tor Royal		
WA-PLS	6.3619	12.9594	WA-PLS	4.9122	4.6427
PLS	7.0724	12.8350	WA	10.5869	12.4487
WA	7.1648	12.3143	PLS	10.6680	10.3483
WA-Tol	7.8935	14.8900	WA-Tol	11.8795	13.7694

3. Prediction errors (jackknifed)

Britain			Tor Royal		
WA	5.6242	12.2200	WA-PLS	9.5722	11.4982
WA-PLS	5.6243	12.2185	WA	9.5734	11.5000
WA-Tol	5.7235	13.0800	WA-Tol	10.0890	13.0800
PLS	6.1105	11.9186	PLS	11.3105	12.8441

Table 7.2: Ranked performances of the regression models used in this study, based on the root mean squared error (RMSE). Results are in % for moisture content and cm for water table depth.

of the model's prediction in comparison with the observed data. The lower the RMSE, the closer the model's predicted values are to the observed data and, as such, the predicted RMSE is very useful in comparing model performances.

For apparent RMSE error, the PLS model gives the best performance in both the Tor Royal and British training sets for water table depth and moisture content (Table 7.2). However, an apparent error does not give a reliable indication of a model's performance, since the regression cycle is applied to the same data set which was used to generate the transfer function. A more reliable estimation of the model performances is given by the predicted errors obtained by cross-validation, while the most robust evaluation is obtained by jackknifed cross-validation. The differences between the calculated RMSEs using different validation procedures highlights the potential for different interpretations of model performance. Hence, the following discussion is based on jackknifed prediction errors alone.

For water table depth predictions based on jackknifing using the British training set, Table 7.2 shows that when ranked in ascending order of RMSE size, the simple WA model produced the smallest RMSE of 5.6242 cm, with a maximum bias of 12.2200 cm. This performance was only marginally better than from the WA-PLS model, which had a RMSE of 5.6243 cm, with a maximum bias of 12.2185 cm. The WA-Tol gave a slightly less satisfactory performance (RMSE 5.7235 cm; maximum bias 13.0800 cm), while the poorest performance was given by the PLS model (RMSE 6.1105 cm; maximum bias 11.9186 cm).

The results for Tor Royal were similar, although the best performance was from the WA-PLS model (RMSE 9.5722 cm; maximum bias 11.4982 cm); followed by WA (RMSE 9.5734 cm; maximum bias 11.5000 cm). WA-Tol gave a less satisfactory performance

(RMSE 10.0890 cm; maximum bias 13.0800 cm) and PLS again gave the poorest performance (RMSE 11.3105 cm; maximum bias 12.8441 cm).

For moisture content, ranked model performances were identical in the British data set but, for Tor Royal, the best performance was from the WA-Tol model (Table 7.2).

The slightly poorer performance of WA-PLS compared to WA for both parameters in the British data set occurred despite the use of six regression components. Table 7.3 shows that RMSE and maximum bias improved only slightly beyond three components, confirming that using any more than six components would not have significantly improved the WA-PLS performance and would have been computationally inefficient.

	Water table depth (cm)		Moisture content (%)	
Component	RMSE	Max bias	RMSE	Max bias
1	6.8920	13.1018	8.4593	21.7810
2	6.2817	12.6309	8.2813	21.7538
3	5.8143	12.4187	8.0137	21.3890
4	5.7328	12.2872	7.7993	20.7851
5	5.6827	12.2413	7.7951	20.8314
6	5.6243	12.2185	7.7946	20.4580

Table 7.3: Predicted RMSE and maximum bias values for water table depth and moisture content in the British data set derived from each of six components used in the WA-PLS model.

The RMSE results confirm that WA is marginally more reliable than WA-PLS for use with the British data set. WA can therefore be used to derive a transfer function for predicting water table depth with a prediction error of 5.6242 cm. For moisture content, the WA model gives a prediction error of 7.7926%. This performance parallels Juggins *et al.* (1994), who compared the performance of various transfer function methods and concluded that WA was the most reliable method for use with their diatom data set. Birks *et al.* (1990) and Oksanen *et al.* (1988) had also found WA to be the most reliable model for diatoms and pH reconstruction.

An important factor to consider in the interpretation of the RMSE values is the possibility of "rogue" values in the training set, as highlighted by the scattergraphs for the British data set in Figures 7.1 and 7.2. For both moisture content and water table depth, a number of outliers existed. For moisture content (Figure 7.1), the outlier samples all resulted from consistent over-optimistic predictions of moisture content by CALIBRATE. For water table depth (Figure 7.2) they were confined to both ends of the water table depth range. Where observed water tables were deep, the model tended to predict shallower depths. Conversely, where water table levels were high, CALIBRATE predicted deeper levels. This was reflected in the correlation coefficients for observed versus predicted moisture content ($r=0.747$; $p<0.01$) and observed versus predicted water table depth ($r=0.605$; $p<0.01$). For this exercise, the original data sets had been used and the rogue samples that had been identified in the ordination exercises (Chapter 6) were probably responsible for the outliers in Figures 7.1 and 7.2.

Birks *et al.* (1990), in their analysis of a diatom training set, also identified the presence of outliers:

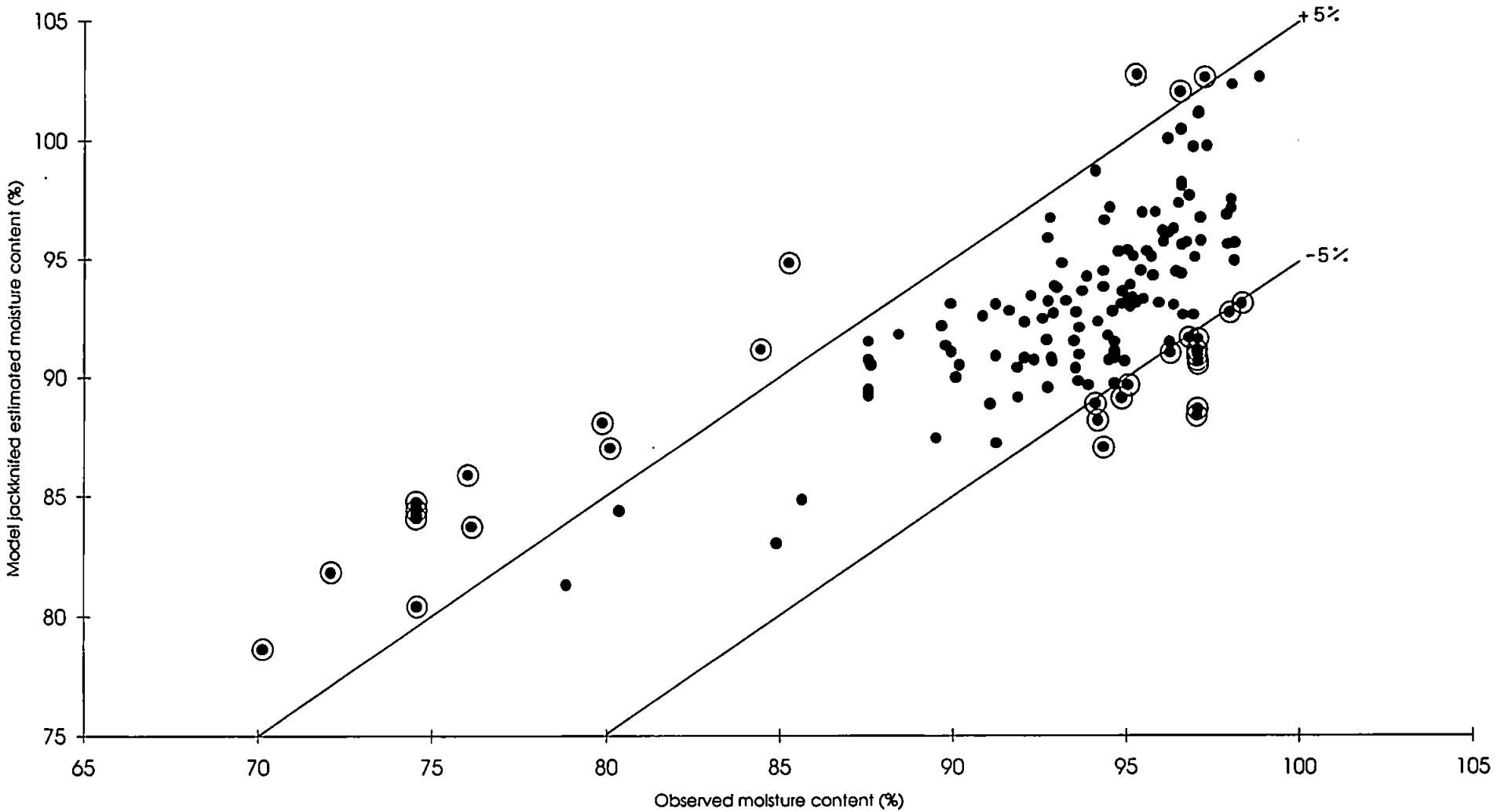


Figure 7.1: Scatter graph showing observed against model predicted moisture content for the British data set (◉ outlier samples: ± 5% difference between observed and predicted values).

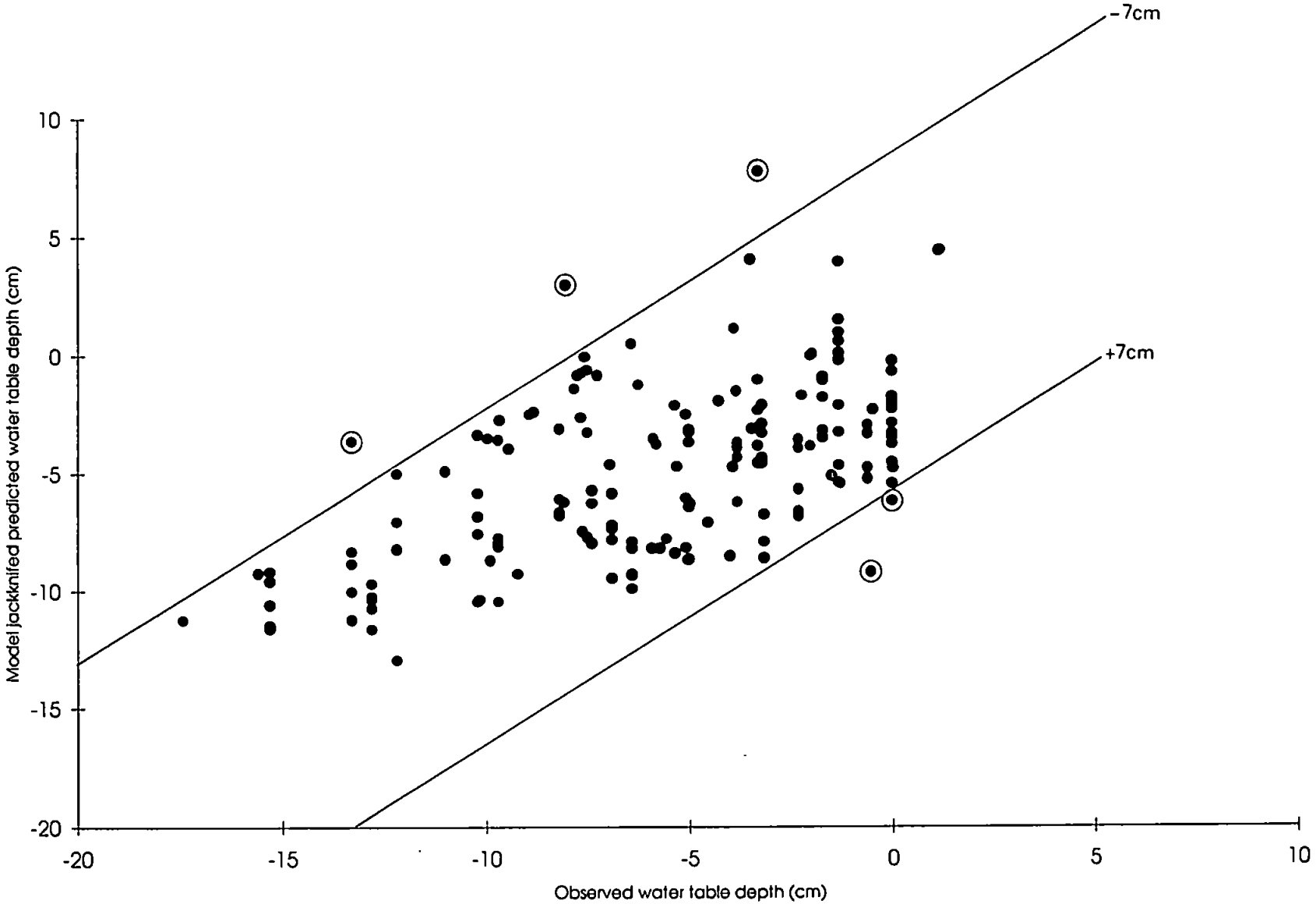


Figure 7.2: Scatter graph showing observed against model predicted water table depth for the British data set (◉ outlier samples: ± 7 cm difference between observed and predicted values).

> "In such a large, heterogeneous data set such as the 178-lake training set, it is possible that some samples are "rogues" or atypical observations, for example with unusual diatom assemblages weakly related to pH, with poor or unreliable pH data, or with environmental variables other than pH having a major influence on the diatom composition".
>
> Birks *et al.* (1990).

Birks *et al.* (1990) performed a "data-screening exercise" to identify and exclude rogue values from their training set and, as a result, gained considerable improvements in their RMSE values. In the light of the ordination exercises in Chapter 6 which had identified a number of outliers, especially at Tor Royal, a similar decision was taken in this study. The objective of performing a screening exercise in this study was two-fold. Firstly, the WA model had performed only marginally better than the WA-PLS model; by removing outlier values, a clearer indication of model performance could be achieved. Secondly, the removal of outliers would encourage a better model performance, hence reducing the RMSE values and increasing the predictive power of the transfer function. Further regression models were restricted to the British data set.

The following exclusion criteria (which parallel Birks *et al.*, 1990) were established. Depth to water table and percent moisture content are different parameters and therefore separate exclusion criteria were applied to both parameters:

i. For percent moisture content, a sample was deleted if it exceeded 5% difference between observed and predicted moisture content (Figure 7.1). This was considered an acceptable margin, given the restricted range of the percent moisture data.

ii. For depth to water table, a sample was deleted from the training set if it exceeded ±7 cm difference between observed and predicted water table depth (Figure 7.2). This value was chosen because it excluded minimal data points, while retaining an

acceptable error margin, given the range of water table depths in the British data set (0 to -43 cm).

iii. Samples that formed an extreme outlier in the ordination analyses (see Chapter 6) were also deleted.

In total, 29 of the 163 British samples met one or all of the above exclusion criteria and were deleted from the training set before the second regression exercise, leaving a British data set of 134 samples. Table 7.4 summarises the revised RMSEs resulting from the exclusion of the rogue values and it shows that WA out-performed the other models by a larger margin than in the first regression exercise.

	Ranked model performance for water table depth		Ranked model performance for moisture content	
Model	**RMSE**	**Maximum bias**	**RMSE**	**Maximum bias**
WA	3.4870 (5.6252)	5.4870 (12.2200)	3.9839 (7.7926)	8.2970 (20.4600)
WA-PLS	3.7334 (5.6243)	5.7146 (12.2185)	4.8542 (7.7946)	9.8258 (20.4580)
WA-Tol	6.4398 (5.7235)	8.4434 (13.0800)	7.4769 (8.2722)	10.5487 (22.9700)
PLS	7.7662 (6.1105)	9.2538 (11.9186)	8.4529 (9.2450)	12.7834 (10.9638)

Table 7.4: Revised jackknifed prediction RMSE scores for the British data set derived from various regression models, following the exclusion of rogue samples. Prediction RMSEs from the first regression exercise are shown in brackets. Units are cm for water table and % for moisture content. For explanation, see text.

For water table depth predictions, the relative ranking remained unchanged after the second regression exercise. WA again returned the best performance with an RMSE of 3.4870 cm; WA-PLS again performed less well, recording a RMSE value of 3.7334 cm. WA(Tol) was ranked third (RMSE = 6.4398 cm) and the worst performance was from PLS (RMSE = 7.7662 cm). The same rankings applied to the moisture content predictions.

The figures show that, although the relative model ranking remained unchanged, considerable reductions in the predicted RMSEs meant that model performance had been greatly enhanced by the exclusion of rogue samples and the WA and WA-PLS models in particular benefited from data screening.

The above sections emphasised the two main advantages of using the RMSE values generated by each model for evaluation purposes. Firstly, they assisted in the identification of rogue samples to be excluded and therefore enhanced the model performances. Secondly, they allowed the selection of the most robust model - WA - for the generation of transfer functions. The actual transfer functions (the testate amoebae species' optima and tolerances) generated by WA for water table depth and moisture content could now be assessed, based on the correlation of the model predictions with observed values for both parameters.

7.6 Performance assessment of WA regression based on correlations of observed versus model predicted water table depth/moisture content

A further graphical impression of model performance was obtained by producing scatter plots of observed versus model estimates of both water table depth and moisture. The observed versus model predictions were plotted for moisture content and water table depth for the British data set, using the more robust jackknifed optima, and these are presented in Figures 7.3 and 7.4 respectively. This improvement is clearly evident in the scattergraphs

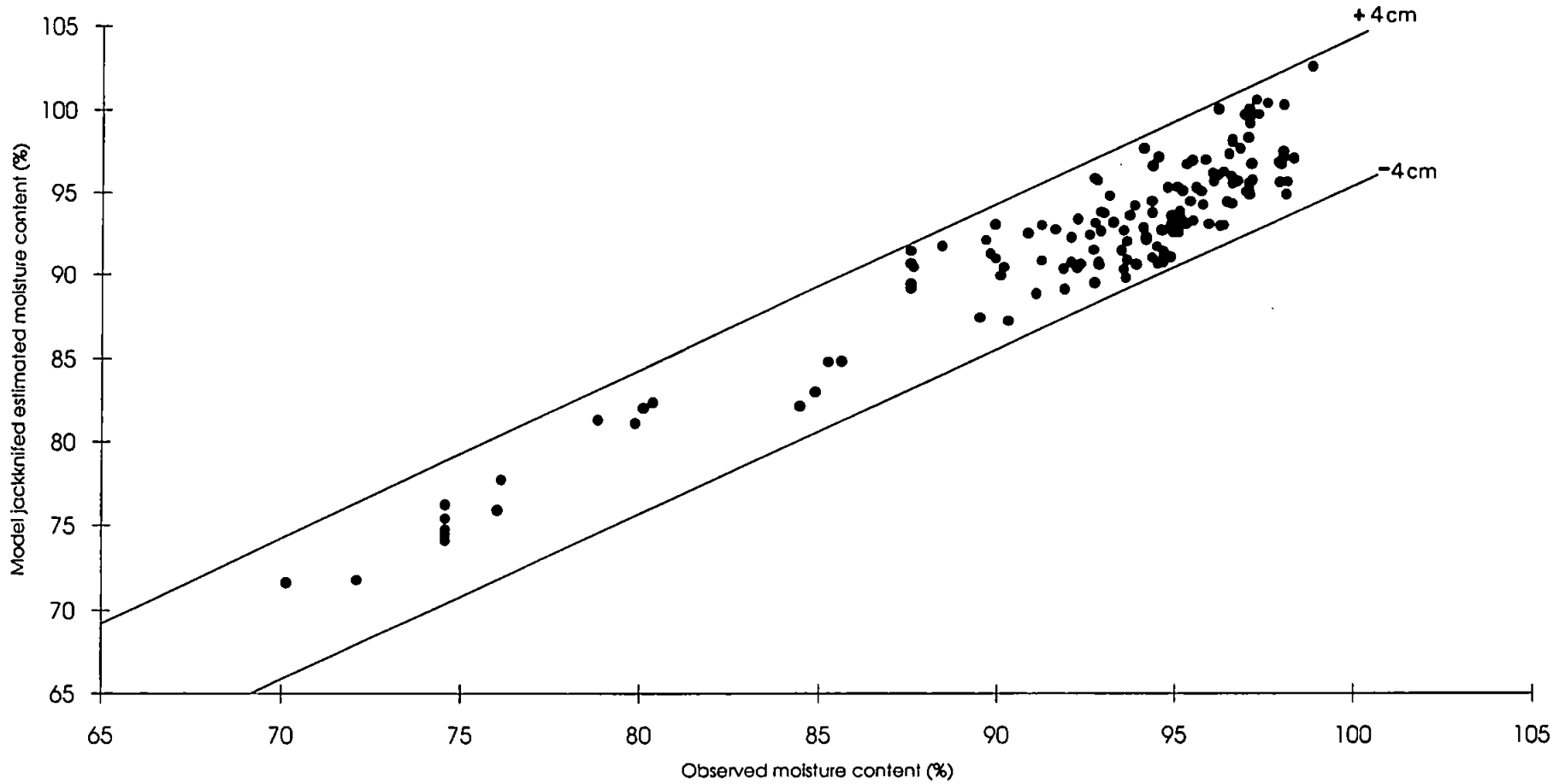


Figure 7.3: Scattergraph showing observed against model predicted moisture content after removal of outliers.

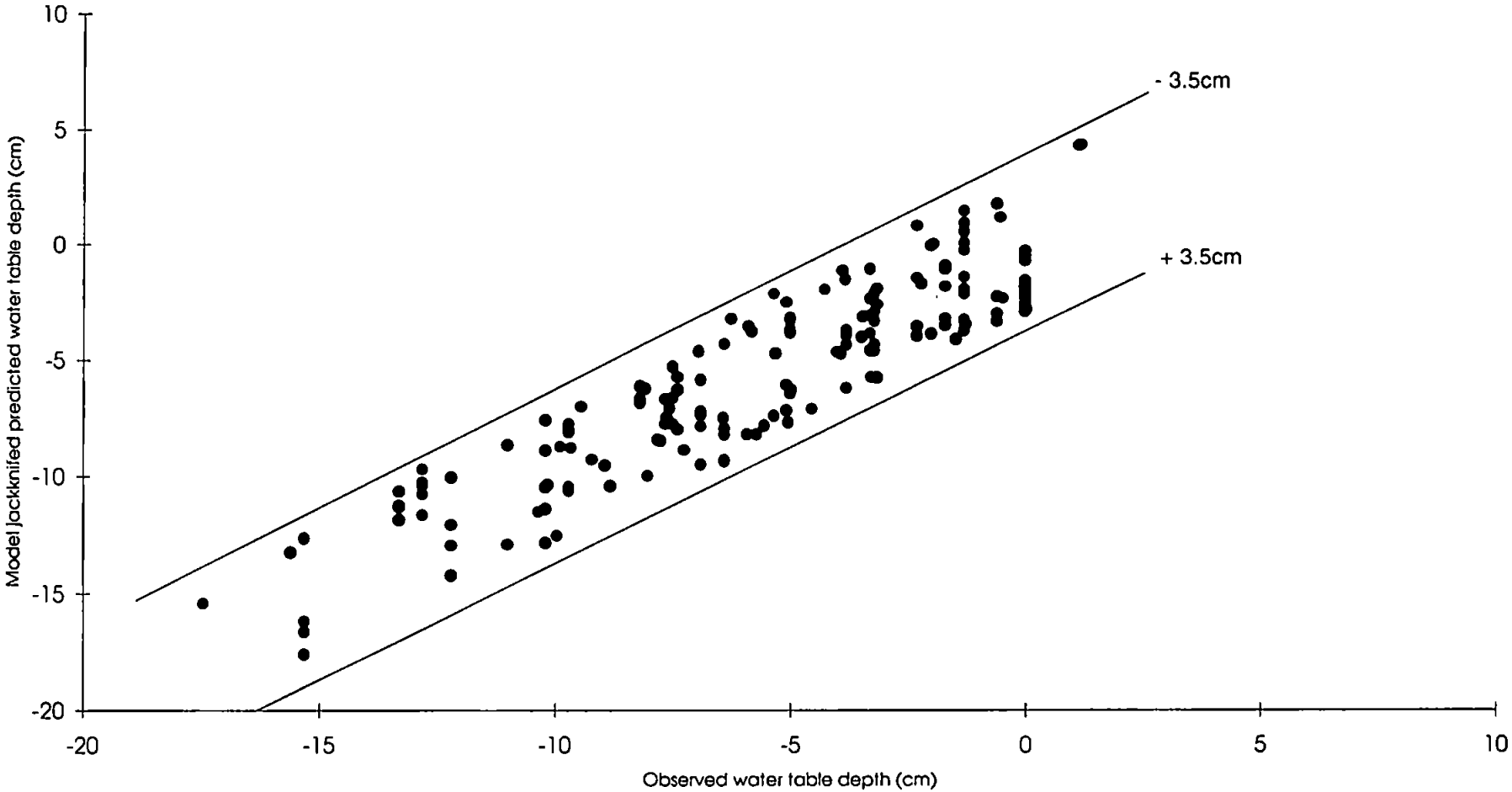


Figure 7.4: Scattergraph showing observed against predicted water table depth for the British data set, after removal of outliers.

where the margins between observed and predicted values are within 3.5 cm for water table depth and 4% for moisture content. Accordingly, correlation coefficients between observed and predicted values for the two variables are greatly improved. For water table depth, r= 0.899 ($p<0.01$); for moisture content r= 0.923 ($p<0.01$).

The reduction of the RMSEs therefore improves the predicted values for water table depth and moisture content. For depth to water table, the revised prediction RMSE is 3.49 cm (an improvement of 2.14 cm); for moisture content, the RMSE is reduced by 3.817% to 3.98%. The implication of this is that moisture and water table values can be reconstructed for a species assemblage at any point in space or time to within ±4% and ±3.5 cm respectively if the overlap between modern and fossil testate amoebae species is at a maximum.

7.7 Summary

This chapter concludes the first stage in the construction of transfer functions for testate amoebae on ombrotrophic peatlands. A variety of regression techniques have been used to model the relationship between modern testate amoebae and contemporary substrate moisture content and water table depth.

Two main conclusions can be drawn from the information presented in this chapter. Firstly, the chapter has shown how regression and calibration by WA is the most robust method for deriving testate amoebae transfer functions. This finding has been supported by other workers in similar palaeoecological fields, who have reported that either simple WA or variants of the technique (such as WA-PLS) were the best methods for generating transfer functions.

Secondly, this chapter has also emphasised the importance of using a large training set for the derivation of transfer functions. By using data filtering exercises to eliminate outlier

samples, a model can be further enhanced to derive the most accurate species' optima and tolerances.

The transfer functions developed in this chapter can now be applied to a fossil peat core. This forms the second stage of the quantitative palaeoenvironmental reconstruction and is a calibration problem (ter Braak and Prentice, 1988; Birks, 1995). In Chapter 8, the transfer functions will be applied to a fossil testate amoebae assemblage from a core for which data on plant macrofossils and humification analyses already exist. These data, and the palaeohydrological curves derived from them, will be used in a provisional comparison with palaeohydrological curves from the testate amoebae transfer functions.

Chapter 8

Testing the transfer functions

8.0 Introduction

This chapter addresses the second stage of palaeoenvironmental reconstructions, in which the modelled responses of modern testaceans to contemporary hydrology are used to infer hydrological values from a fossil assemblage. This is a calibration problem (ter Braak and Prentice, 1988; Birks, 1995) that will be solved by the application of weighted averaging to the fossil assemblage, since this was the most reliable regression technique for use with the modern British data set (Chapter 7).

8.1 Objectives for comparing testate amoebae against plant macrofossils and peat humification as palaeohydrological indicators

The need for clarification of palaeohydrological signals derived from plant macrofossil and peat humification analyses (see section 2.4, page 27) presents an opportunity where the usefulness of testate amoebae can be assessed. Hence, two palaeohydrological curves (one for moisture and one for water table depth) derived from testate amoebae analysis will be compared with humification and plant macrofossil curves from the same site. Since these curves all represent the same peatland system, a further comparison will be made for the time period covered by the core with independent records for precipitation, provided by dendroclimatology (Briffa *et al.*, 1990), estimated rainfall (Lamb, 1977a), summer wetness / winter severity indices (Lamb, 1977b) and with palaeohydrological curves produced for other ombrotrophic mires (Barber *et al.*, 1994d). Given that this is the first application of its type in Britain and applies to a single core, this exercise will provide a provisional assessment of the usefulness of testate amoebae in palaeohydrological reconstructions.

If the humification, plant macrofossil and testate amoebae curves correlate well, this will suggest increased confidence in any one of the three techniques. If the curves do not match, then reasons for the disagreements will have to be investigated.

8.2 The case study: a palaeohydrological curve produced from peat humification and plant macrofossil analysis for Bolton Fell Moss, Cumbria

Validating the palaeohydrological curves derived from testate amoebae required their comparison with a set of robust curves obtained from peat humification and plant macrofossil analysis. A series of such curves has been produced for Bolton Fell Moss in Cumbria after almost 30 years' research (Table 8.1), providing an ideal testing ground for the testate amoebae transfer functions. In addition, sufficient peat material was still available (courtesy of Dr K. E. Barber, University of Southampton) for comparative palaeohydrological studies using testate amoebae analysis on an intensively studied profile.

Site description

Bolton Fell Moss is an ombrotrophic raised mire situated at 150 m O.D., approximately 15 km northeast of Carlisle in Cumbria. The Moss covers almost 400 hectares and, with neighbouring Walton Moss (2 km south-east of Bolton Fell Moss), it comprises one of the more extensive raised mires found below 150 m O.D. in lowland Cumbria (Figure 8.1). A detailed description of Bolton Fell Moss is given in Barber (1981). The following section summarises the development and present-day surface features of Bolton Fell Moss based on Barber (1981) and Barber *et al.* (1994a, b).

Stratigraphical and pollen analyses suggest that Bolton Fell Moss originated as standing water in shallow depressions on a late-Devensian till surface. Hydroseral development during the Holocene culminated in a raised mire, in common with most other mires in the

DATE	AUTHOR	TYPE OF INVESTIGATION
1966	Walker	A study of the late Quaternary history of the Cumberland lowland (PhD).
1981	Barber	Testing the relationship between peat stratigraphy and climatic change - a formal test of Sernander and Osvald's cyclic regeneration theory. Peat stratigraphy, pollen analysis, plant macrofossil analysis, exploration of the usefulness of other techniques such as iodine, silica, fungal hyphae and testate amoebae analysis. Data were used to falsify the cyclic regeneration theory. This study also demonstrated the sensitivity of ombrotrophic bogs to climate. Establishment of the phasic theory of bog growth, where raised bog growth occurs in climatically-forced phases.
1987	Haslam	Characterisation of a major humification change using "quadrat and leaf count" (QLC) method to analyse plant macrofossils. Bolton Fell Moss was one of a suite of 18 bogs sampled across Europe, from the oceanic west (Ireland) to the continental east (Poland).
1993	Stoneman	Extending and refining the model of Holocene palaeoclimate derived from peat stratigraphy using the QLC method. Bolton Fell Moss was one of 10 bogs studied across the Anglo-Scottish border.
1992 1994	Dumayne Dumayne & Barber	Assessing human impact on the vegetation of northern Cumbria during the Late Holocene with especial reference to the Iron Age and Roman periods.
1994a-d	Barber *et al.*	NERC Palaeoclimate Special Topic grant: "Spatial and temporal variability of Late Holocene palaeoclimates derived from peat stratigraphy". Macrofossil and humification analyses production of palaeoclimate curve derived from peat stratigraphy and plant macrofossil analyses.
1996	This study	Comparison of palaeohydrological curve derived from testate amoebae analysis with that from plant macrofossil and peat humification analyses.

Table 8.1: Palaeoecological studies on Bolton Fell Moss, 1966 to present.

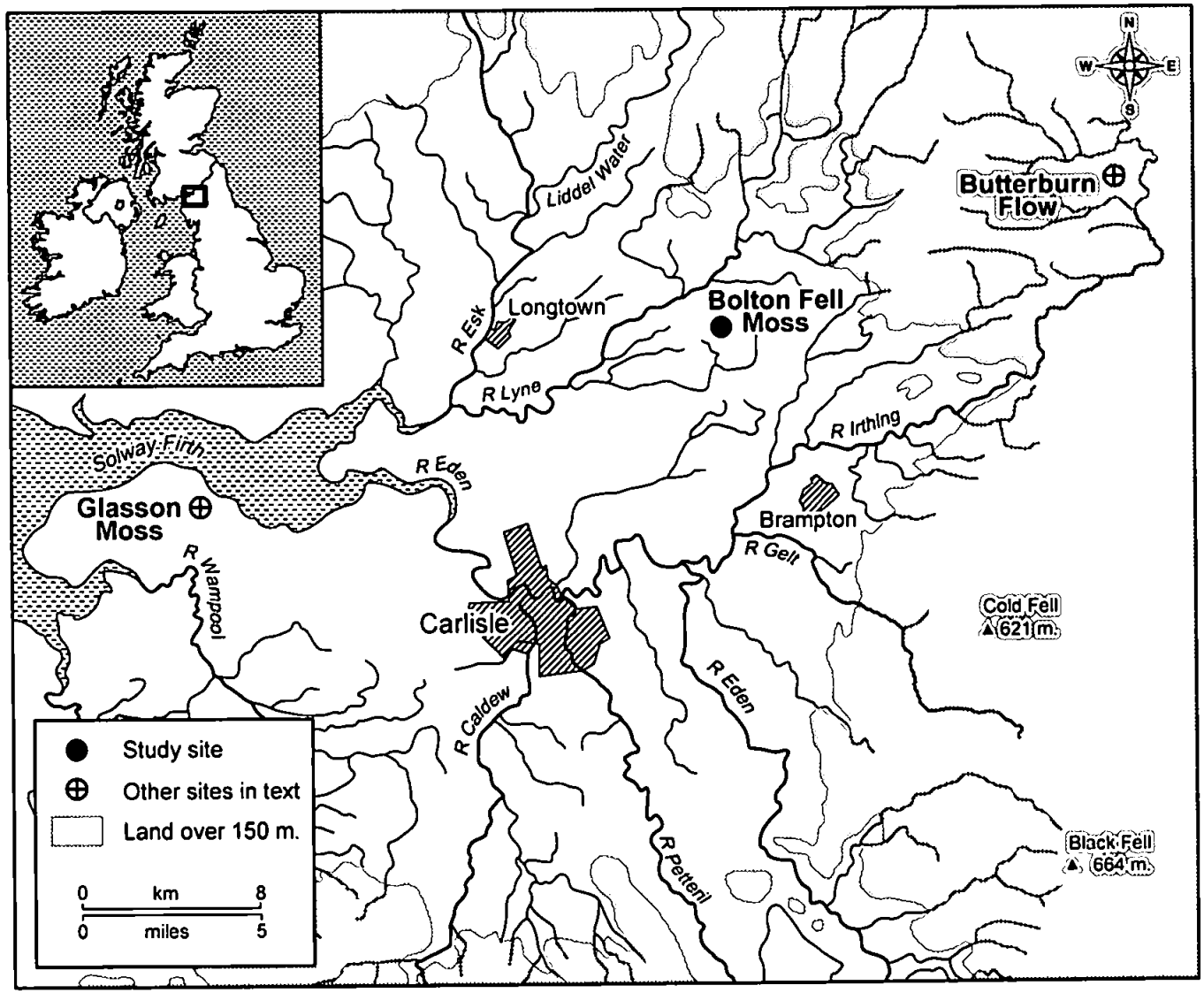


Figure 8.1: Location of Bolton Fell Moss and other sites mentioned in the text. Redrawn from Barber *et al.* (1994b), page 21.

locality (Barber, 1981 and see page 19 of this thesis). Once an extensive tract of peatland covering 4 km^2, Bolton Fell Moss has been reduced to its present size by peat-cutting activities, either through direct removal of peat or indirectly via drainage programmes, which have caused a loss in peat volume through shrinkage. Only the southwestern quarter of the mire, on common land, remains uncut and intact. The uncut area is dominated by an *Eriophorum angustifolium* sward, which is underlain by an undulating *Sphagnum* layer. *Calluna vulgaris* and *Eriophorum vaginatum* interrupt this sward, growing on *S. magellanicum* and *S. rubellum* mounds, while the *S.cuspidatum* hollows are richer in *Erica tetralix*, *Narthecium ossifragum* and *Rhyncospora alba.*

In relating peat deposits to climatic changes, three important prerequisites should ideally be satisfied. Firstly, one must locate an ombrotrophic mire that has developed under climatic influence alone up to the present day. Secondly, the peat deposit must be deep enough to allow a long time scale to be studied. Thirdly, the peat should have accumulated rapidly enough to give a detailed resolution of events within this temporal range (Barber, 1981).

Bolton Fell Moss satisfies all three criteria. While assessing the potential of Bolton Fell Moss for palaeoenvironmental studies, Barber (1981) found peat deposits at the site which had accumulated rapidly and attained in excess of 10 m depth towards the centre of the bog. At that time, manual peat cutting was still practised which left underlying peat undisturbed, thus preserving sections that extended to the modern surface and were likely to have developed over a long period of time.

8.3 The palaeohydrological curves derived from peat humification and plant macrofossils

8.3.1 Origins: sample location

Five series of peat sampling have been conducted by the University of Southampton at Bolton Fell Moss - in 1968, 1987, 1990, 1991 and 1993. The monolith subsampled for this study was obtained during the N.E.R.C. Palaeoclimate Special Topic "Spatial and temporal variability of late Holocene palaeoclimates derived from peat stratigraphy". This project started in April 1991 and was conducted jointly with the University of Keele. Its aim was to quantify further the palaeohydrological curves that had been produced by earlier research at Bolton Fell Moss (see Table 8.1) and to investigate palaeoclimate signals from other ombrotrophic mires.

To maintain continuity, a new sampling site - point J - was located in one of the drainage ditches in the uncut area of Bolton Fell Moss which exhibited identical stratigraphy to that recorded in the 1960's by Barber (Figure 8.2). At this sampling point, two 100 cm-deep monoliths (J1 and J2) "adjacent to each other and correlating depth for depth" (Barber *et al.*, 1994, p.39) were taken from the edge of the intact part of Bolton Fell Moss and immediately behind these a 5 m core was also taken. A total of 12 radiocarbon date estimates were obtained for monolith J1; the base section (493-500 cm depth) was dated at 5315 +/-35BP and, using a simple linear model, the peat accumulation rate was calculated at 12.4yr cm^{-1} (Barber *et al.*, 1994a).

8.3.2 Production of the palaeohydrological curves

Macrofossil analyses, using the quadrat and leaf count method (Barber *et al.*, 1994b) were conducted on monolith J1 at the University of Southampton; detailed methods are given in Barber *et al.* (1994a,b). The top 100 cm of the resulting plant macrofossil diagram has been included later in this chapter (Figure 8.10, page 347) to allow detailed interpretation of the

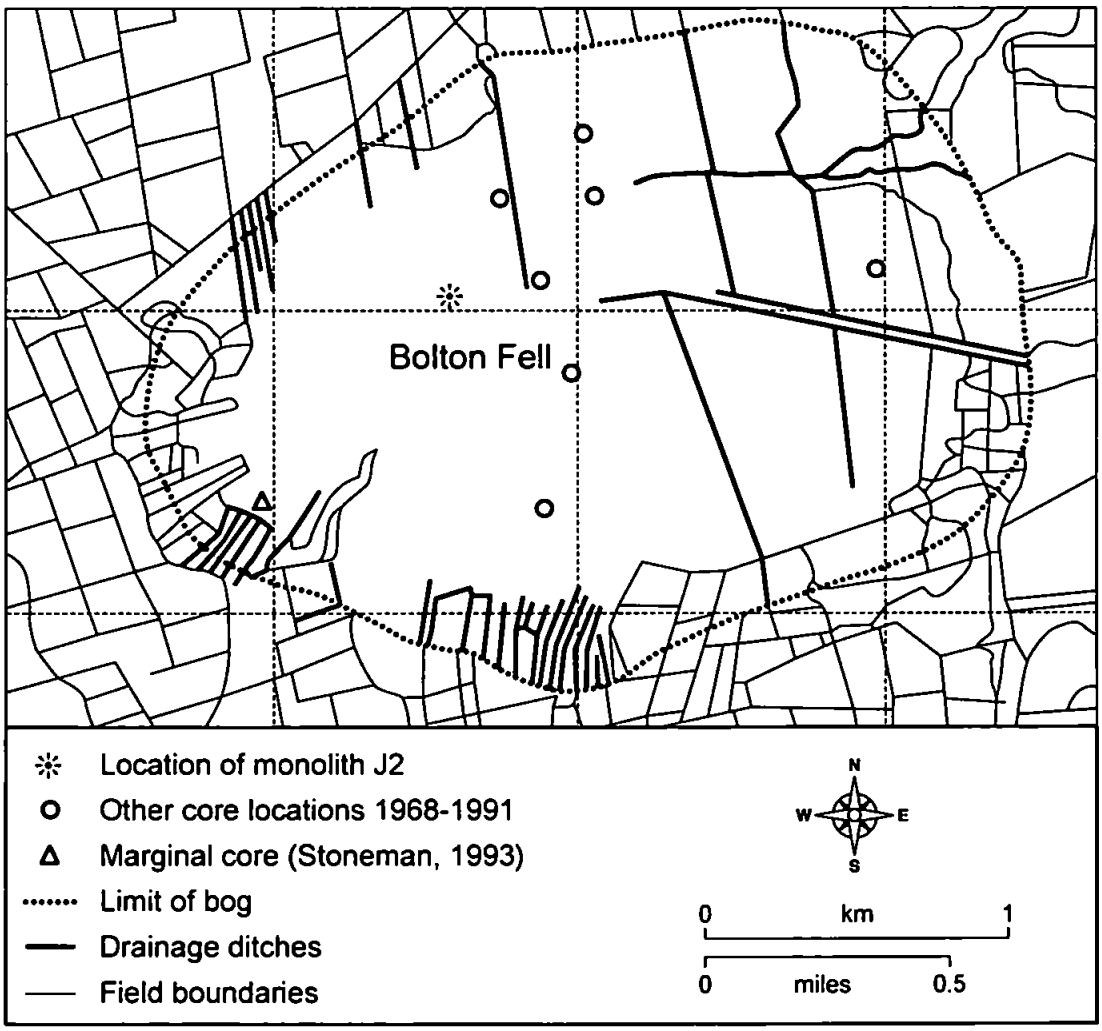


Figure 8.2: Location of sampling sites on Bolton Fell Moss (1968-1993). Redrawn from Barber *et al.* (1994b), page 23.

resulting palaeohydrological curves. A full palaeoecological interpretation of the diagram is not appropriate here. However, the major ecological change at 42 cm (Barber *et al.*, 1994a), from a *S. imbricatum*-dominated assemblage to one dominated by *S. magellanicum*, is a feature of the diagram which may be clarified by testate amoebae analysis and this is considered later in section 8.6.6.

Peat humification for monolith J2 was assessed at the University of Keele (Barber *et al.*, 1994b), using colorimetry (see Blackford and Chambers, 1993 for full details of this method). This produced a proxy-record of climate change at Bolton Fell Moss (Figure 8.3a) in which a lower degree of humification indicated wetter conditions and higher degrees reflected a drier mire surface at the time of deposition (see Blackford and Chambers, 1993).

Following the indicator values of Dupont (1986), a similar palaeohydrological curve was derived from the plant macrofossil data (Figure 8.3a). Detrended correspondence analysis (DCA) applied to the macrofossil data identified water table depth as the major control on taxa variability. On the assumption that mire water table depths are mainly climatically controlled, Barber *et al.* (1994a) compared the macrofossil assemblages from the top 44 cm of the Bolton Fell Moss core (extending to 1100AD) to Lamb's (1977b) record of climatic variation. A close match was achieved by a climate response model, confirming the influence of climate (via water table levels) on species assemblages (Barber *et al.*, 1994a). This allowed the interpretation of the axis 1 scores from the DCA plot as a proxy-record of changing climatic conditions (Barber *et al.*, 1994a), in addition to the record provided by peat humification. The DCA scores were plotted against peat age and the resulting palaeohydrological curve is shown in Figure 8.3b.

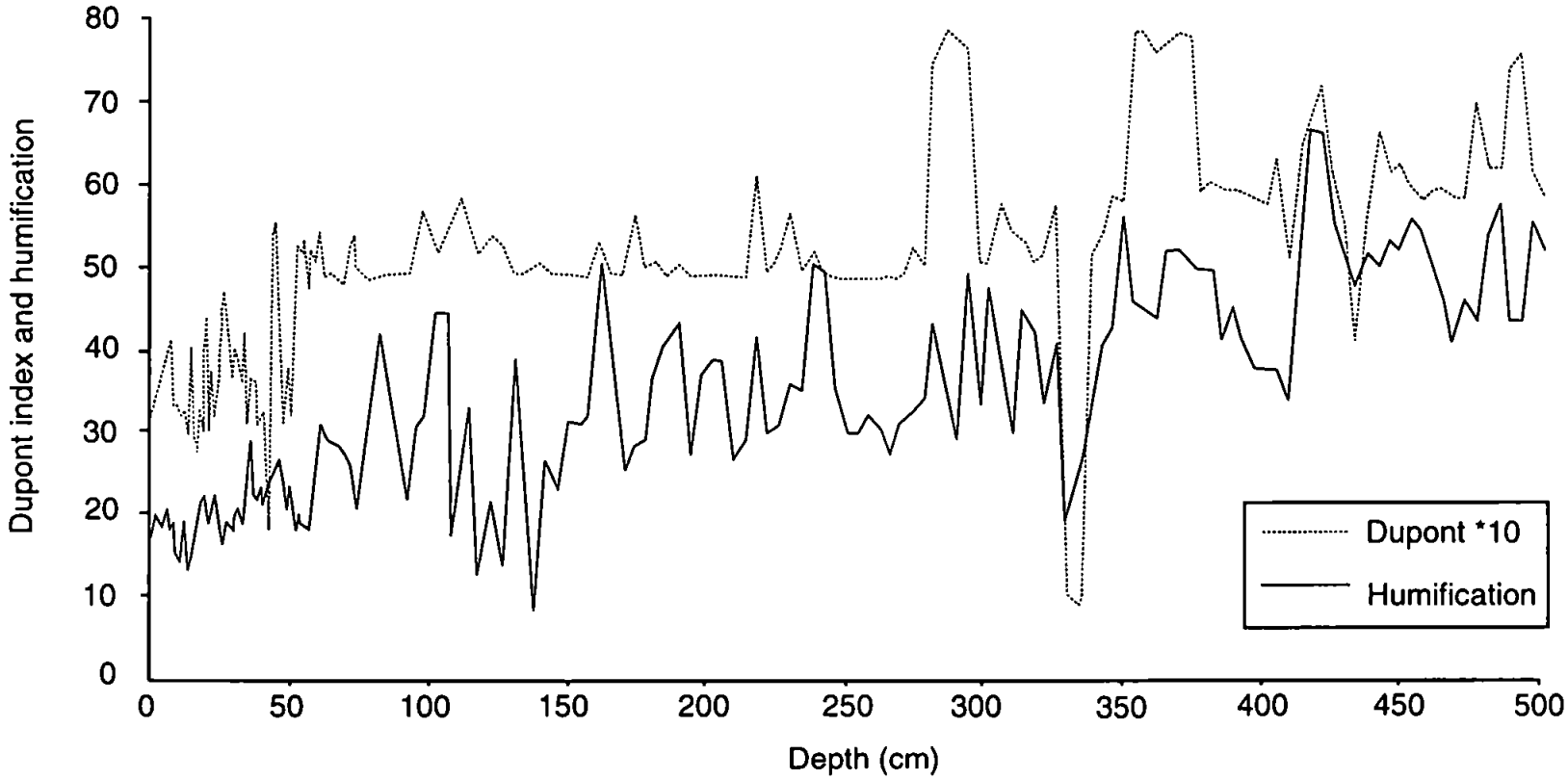


Figure 8.3a: Reconstructed palaeohydrological curves for Bolton Fell Moss derived from peat humification analysis and Dupont indices. Redrawn from Barber *et al.* (1994b) page 42.

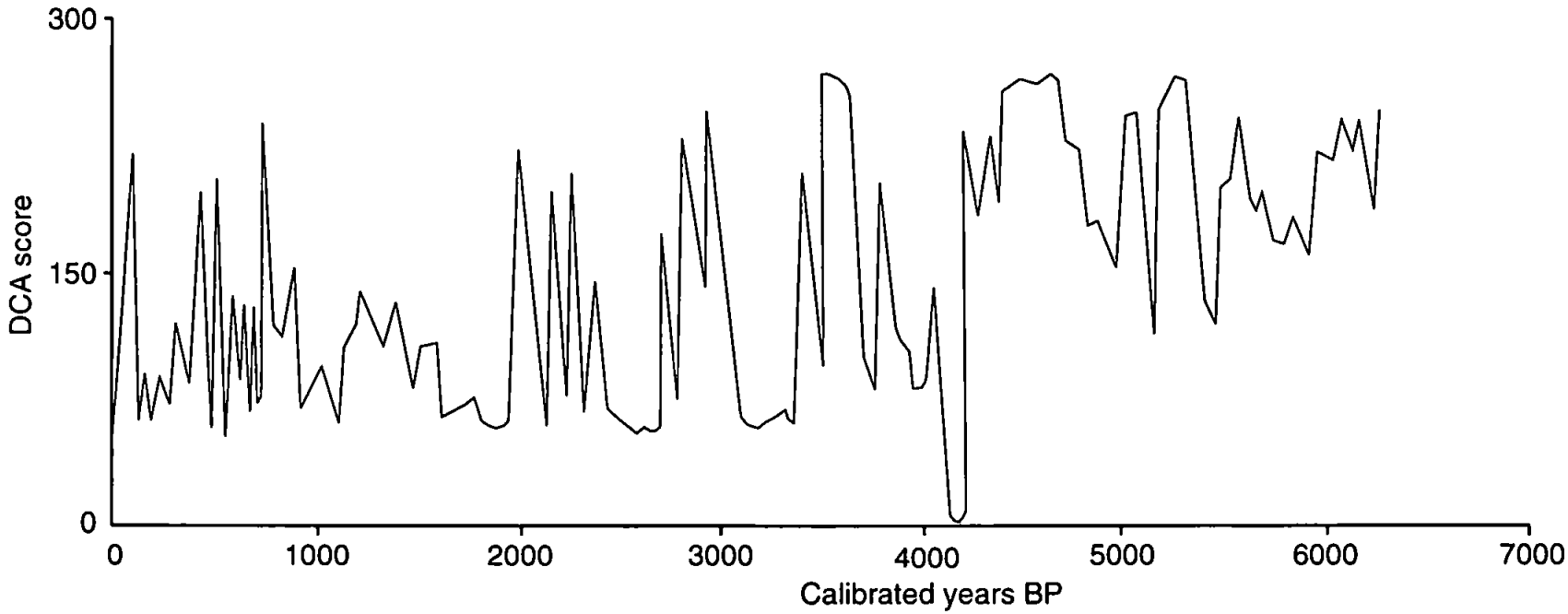


Figure 8.4b: Reconstructed palaeohydrological curve for Bolton Fell Moss derived from DCA scores for plant macrofossils. Redrawn from Barber *et al.* (1994c) pp. 58-59.

8.3.3 The palaeohydrological curves for Bolton Fell Moss

Figures 8.3a and b are the most refined quantitative palaeohydrological curves that have been produced for Bolton Fell Moss thus far. This is particularly pertinent to the DCA scores plotted in Figure 8.3a and b. D. Maddy (pers. comm.) is of the opinion that the DCA curve is a more appropriate representation of changes in surface hydrology at Bolton Fell Moss than the Dupont indices. Additionally, Barber *et al.* (1994a) have already demonstrated the close relationship between water table depth and taxa variability through DCA. Hence, the remainder of this chapter will not consider the Dupont curve and will concentrate instead on the DCA and humification curves only.

The curves in Figure 8.3 reproduce similar general palaeohydrological trends throughout the core, but discrepancies exist at a finer resolution where the signals diverge. Of these, divergences within the top 100 cm of the curves are of most relevance to this study because they can be directly compared to contemporary curves derived from testate amoebae.

One divergence between the plant macrofossil and humification curves occurs between 70 and 66 cm. The plant macrofossil curve suggests a change from dry - wet - dry conditions, while the humification curve implies opposite conditions. A similar divergence is evident between 30 and 20 cm. The reason for these discrepancies is unclear and has not been interpreted by Barber *et al.* (1994a,b,c,d). A possible explanation may be the differences in the species composition of the peat between the two monoliths. This would introduce variations in the decompositional properties of the peat (Blackford and Chambers (1993), so that the peat humification evidence conflicts with that from the plant macrofossils. Alternatively, noise in both data sets may be responsible for the divergence.

Additionally, the plant macrofossil curve is erratic and this is almost certainly a result of noise in a species-poor data set. Only 8 species or species groups are present in the core

(Figure 8.10, page 347), four of which dominate the assemblage (the monocotyledon group, *S.s. Acutifolia, S.imbricatum* and *S. magellanicum*). Rapid changes in relative abundance are evident in all the dominant species and, although the changes may be gradual (the demise of *S. imbricatum* from 80 cm to 45 cm, for example), the eventual disappearance of one species and its replacement by another (*S. magellanicum*, in this example) is interpreted as evidence of a sudden hydrological change. The plant macrofossil curves therefore reflect the erratic abundances of these major species components.

The divergence and erratic nature of the palaeohydrological curves and the dominance of individual species in a low-diversity assemblage provide an ideal testing ground for testate amoebae analysis in five areas:

1. To give greater resolution in relatively "insensitive" parts of the macrofossil record where monocotyledons or *Sphagnum imbricatum* are dominant. In a palaeoclimatological sense, these zones can be considered "insensitive" as they fail to yield detailed palaeohydrological information. Testaceans, however, may exhibit more subtle changes in species composition from which a more detailed hydrological curve can be produced.

2. To clarify signals from "noisy" areas of the macrofossil record where the palaeohydrological curve fluctuates rapidly and frequently. This "spiky" profile may reflect edge effects (which include drainage and burning) and also a naturally more variable water table (Barber *et al.*, 1994b). A more likely cause, however, is the poor species diversity of plant macrofossil records. The greater species diversity of the testate amoebae fauna compared to macrofossils may overcome this problem and allow the construction of smoother transitions between extreme palaeohydrological peaks.

3. Investigating further the sudden replacement of *Sphagnum imbricatum* by *Sphagnum magellanicum* and/or *S. papillosum*. Section 2.3.2 (page 26) discussed the broadly-held view among ecologists that *S. imbricatum* has the same moisture tolerances as *S. magellanicum* but that the slower growth-rate of *S. imbricatum* resulted in out-competing by *S. magellanicum* and other Sphagna. Testate amoebae analysis offers an independent means of assessing the moisture optimum of *S. imbricatum* during the Holocene and the existence of moisture changes associated with its decline.

4. Most importantly, to give a meaningful quantitative environmental scale to changes recorded in peat stratigraphy in terms of changes in water tables or percent moisture content.

8.4 Testate amoebae analysis

Plant macrofossil analysis had consumed all of monolith J1, so the adjacent monolith (J2) was sampled for testacean analysis.

8.4.1 Preparation and counting

A slice, measuring 100 x 2 x 2 cm, was cut from the monolith and then divided into 100 contiguous 1 cm subsamples measuring 4 cm^3 each. Each 4 cm^3 cube of peat was divided into two equal halves (2 cm^3 each), one being prepared for testate amoebae analysis and one kept as spare material.

The procedure for identification and counting of the tests follows section 4.1.3 (page 86). Cumulative plots of species diversity and number of individual tests counted (Figures 8.4a - 8.4f) showed a similar pattern to that of the modern species samples, where a rapid increase in species diversity occurred early in the counts, but eventually stabilised and plateaued -

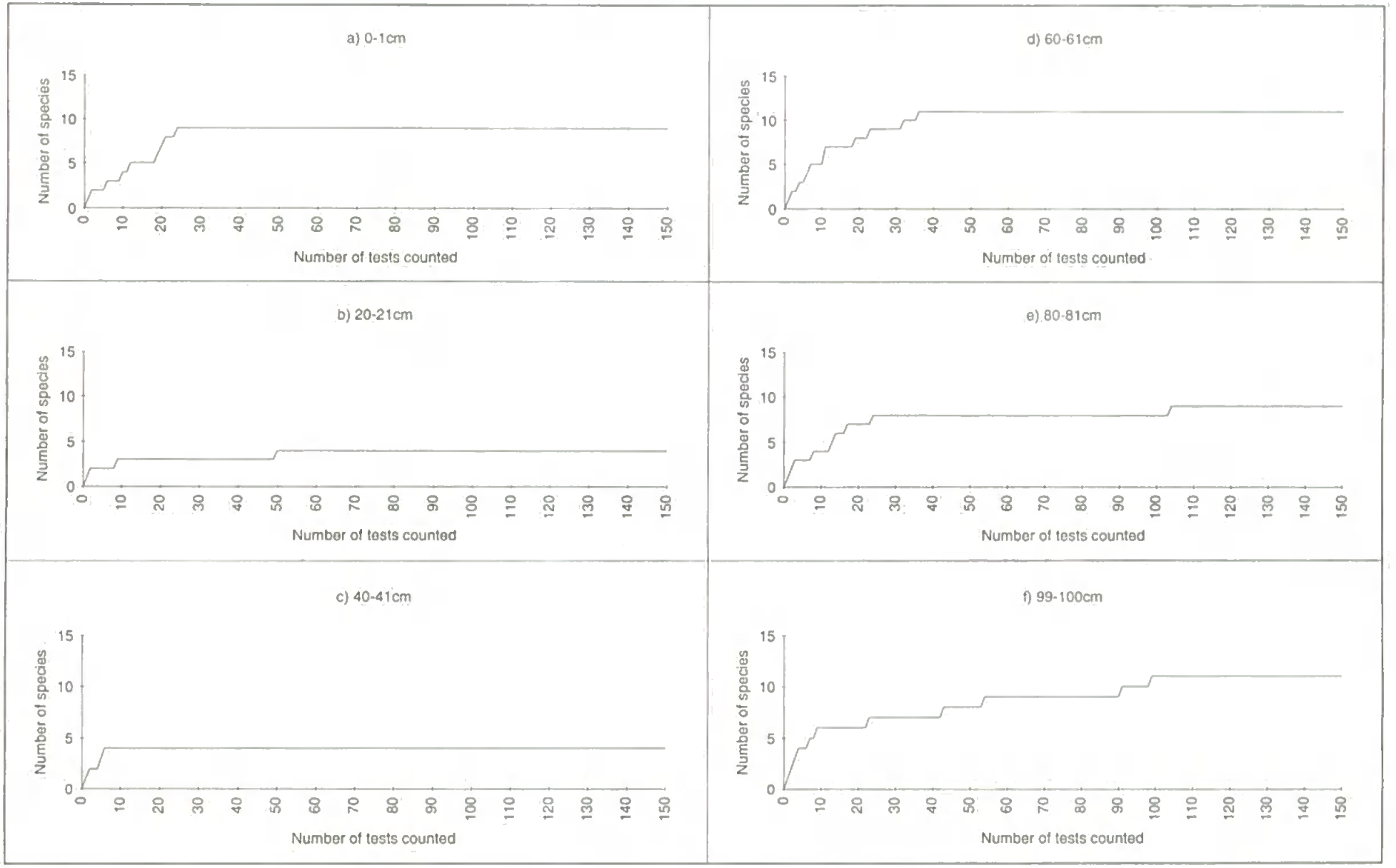


Figure 8.4: Cumulative testate amoebae species diversity plotted against tests counted for selected sample depths, Bolton Fell Moss.

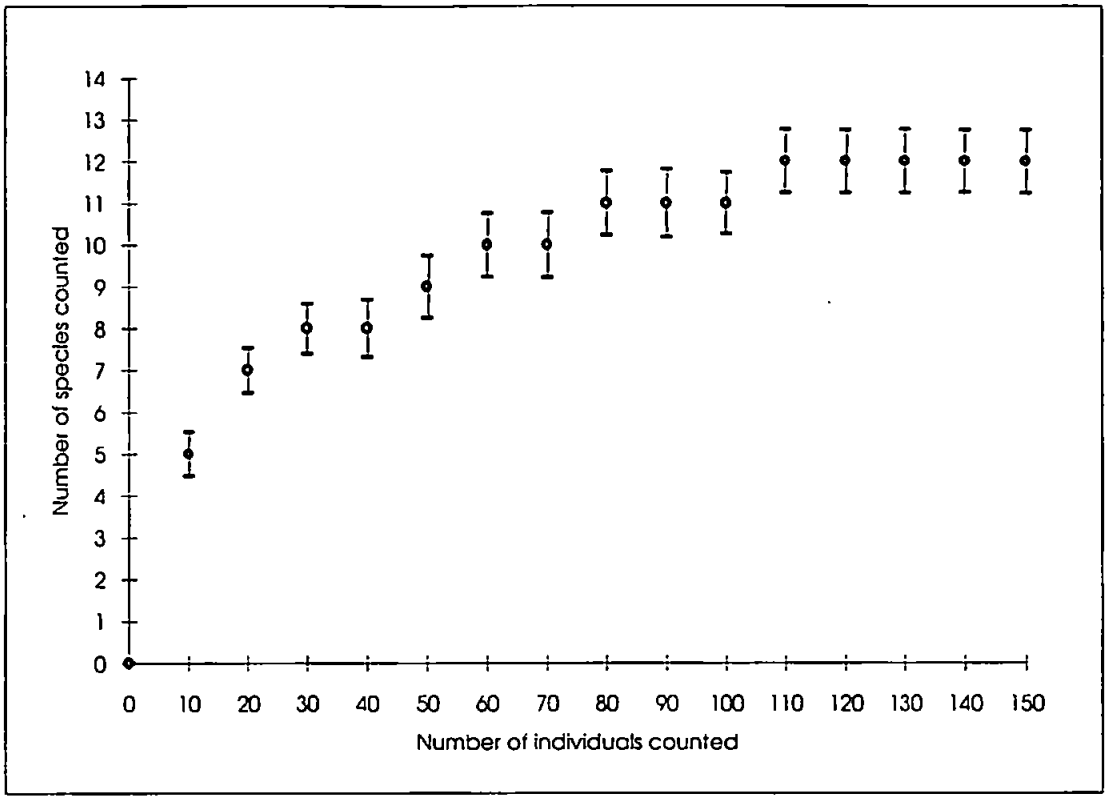
usually by a count of 100 and almost always by a count of 150 tests. Only very rare species were detected beyond counts of 150 and these would be of negligible value in the subsequent palaeohydrological reconstruction. A minimum of 100 and maximum of 150 tests were therefore considered sufficient to give an accurate reflection of the testacean assemblage at each depth.

8.4.2 Comparison of species diversity between modern and fossil data sets in this study

Species diversity was lower in the Bolton Fell Moss fossil samples (mean species abundance = 8) than in the modern British samples (mean species abundance = 12). Figure 8.5 illustrates species diversity in the respective data sets and shows how this increased more rapidly in the modern data set before reaching a plateau at 110 individuals, while the increase was slower in the fossil data set. Here, species diversity also plateaued slightly earlier, at 100 individuals. Since the preparation techniques were identical for both the modern and fossil testate samples, the difference may be attributable to the effects of differential decay rates for individual species. Alternatively, it could represent a real difference between modern and fossil faunas from Bolton Fell Moss.

In a study of the decay of empty tests in the litter and mineral horizons of *Populus tremula* woodland soils, Lousier and Parkinson (1981) found that test disappearance was much quicker than had previously been thought, spanning weeks rather than years. Testate amoebae species with tests composed of platelets (such as *Euglypha* spp. and *Trinema* spp.) decayed exponentially and almost 98% of the species disappeared from the soil after two weeks. Those species with tests composed of mineral particles (such as *Phryganella acropodia, Centropyxis* spp. and *Cyclopyxis* spp.) decayed linearly, with 83% of tests disappearing in the same time period. The high rates of decay may reflect the moist, aerobic conditions soils under *Populus tremula*, where microbial activity is intense. No

a) Modern data set (n=163)



b) Fossil data set (Bolton Fell Moss; n=50).

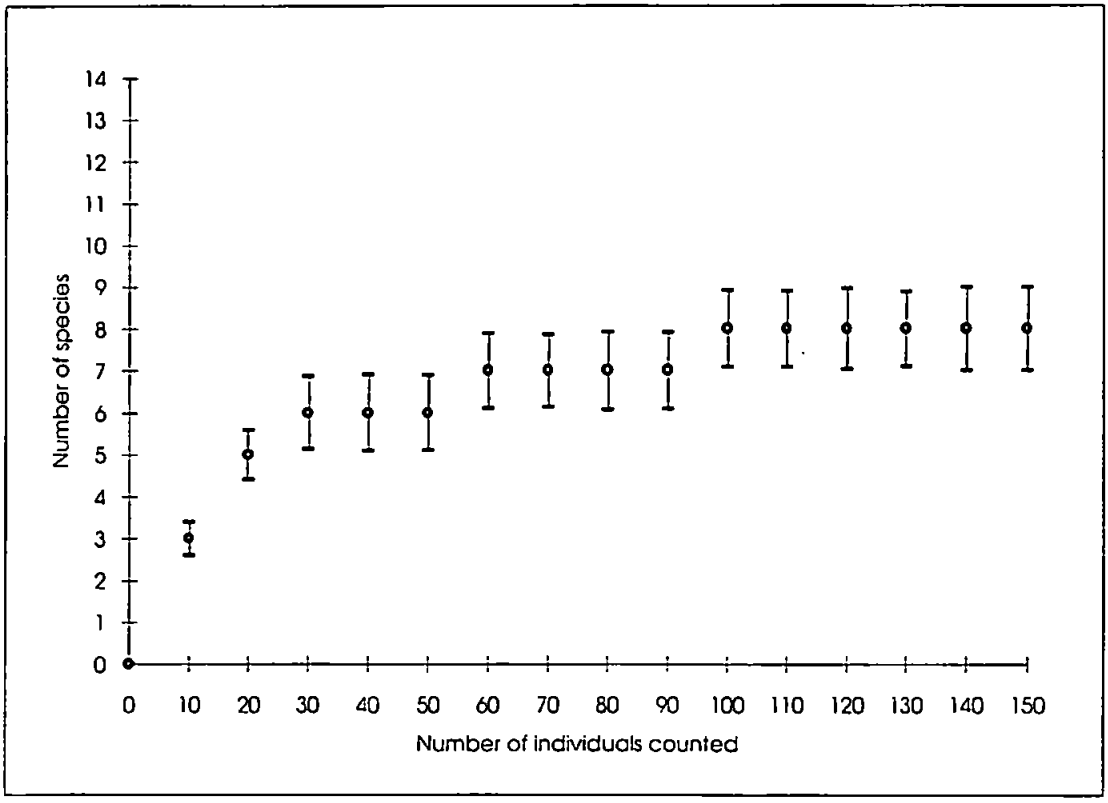


Figure 8.5: Species diversity in the modern and fossil testate amoebae assemblages investigated in this study, shown as the mean, ± 2 standard errors.

investigations have been made into the rates of decay in *Sphagnum* and peat, but it is likely that rates would be lower in *Sphagnum* and peat environments where anaerobic conditions prevail. If the same hierarchy of decay rates existed in this environment, then it may explain the absence of *Trinema* and all species of *Euglypha* except *E. rotunda* in the fossil assemblage at Bolton Fell Moss (see Figure 8.10, page 347). Clearly, further investigations are required to establish a suite of decay rates for testate amoebae in *Sphagnum* and peat environments to improve the palaeoenvironmental interpretation of fossil assemblages.

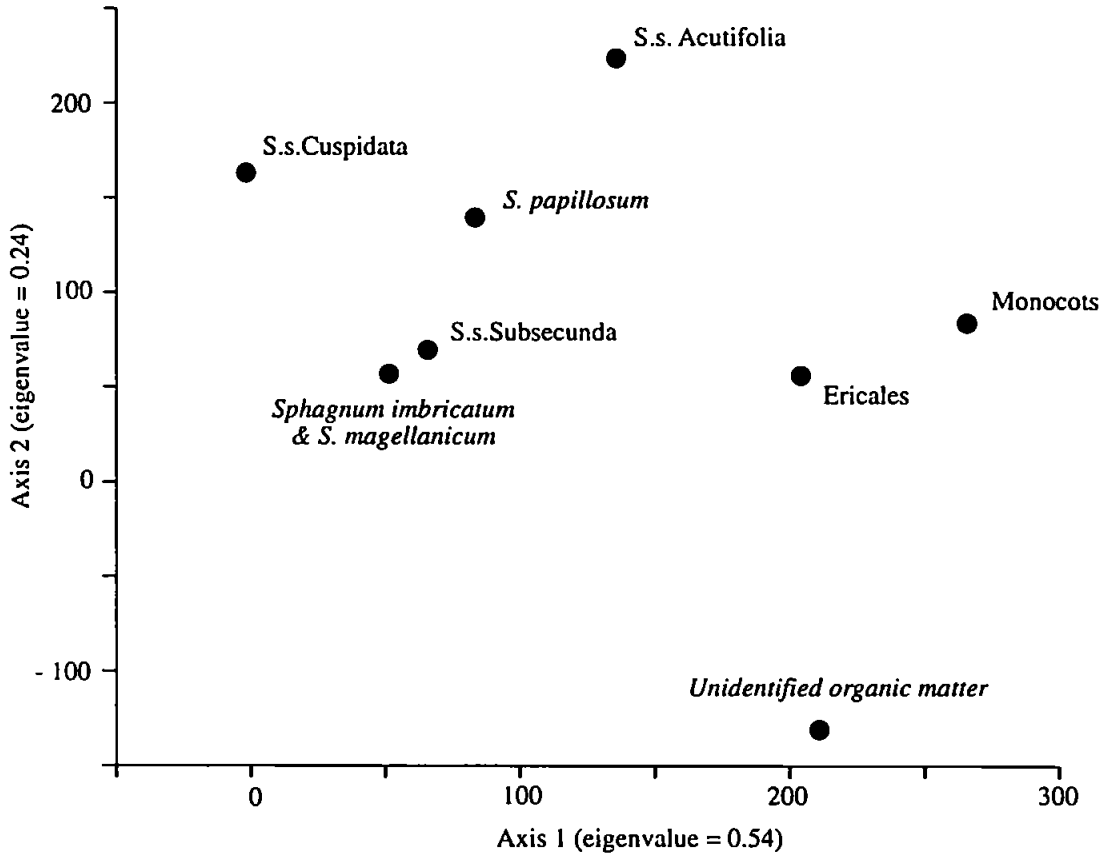
8.4.3 Comparison of ordination plots for modern and fossil samples

To assess the quality of the modern analogues, ordination plots were constructed for both the modern and fossil testate amoebae assemblages and the modern and fossil vegetation data.

DCA of the Bolton Fell Moss macrofossil data had identified water level as the strongest control on species distribution (eigenvalue = 0.54; Barber *et al.*, 1994c) and the resulting ordination plot is shown in Figure 8.6a. DCA on the vegetation in the modern British data showed that the most important influence on taxa variability in the modern British data set was also hydrological (axis 1 eigenvalue = 0.914; Figure 8.6b), where wetter species (such as *Sphagnum papillosum* and *S. cuspidatum*) attained low axis 1 scores and drier species (*Erica tetralix* and *Calluna vulgaris*) were found at the opposite end of the scale. The vegetation assemblages from the modern and fossil data sets show very similar relationships between vegetation and hydrology, confirming the possibilities for comparing the two data sets.

Fossil testate amoebae data were expressed as percent relative abundance of each secies, in common with the modern data set (page 87). There are two reasons why, in this study, abundances were preferred to test concentrations.

a) Bolton Fell Moss (fossil data set): redrawn from Barber *et al.* (1994; p.59).



b) Modern British data set

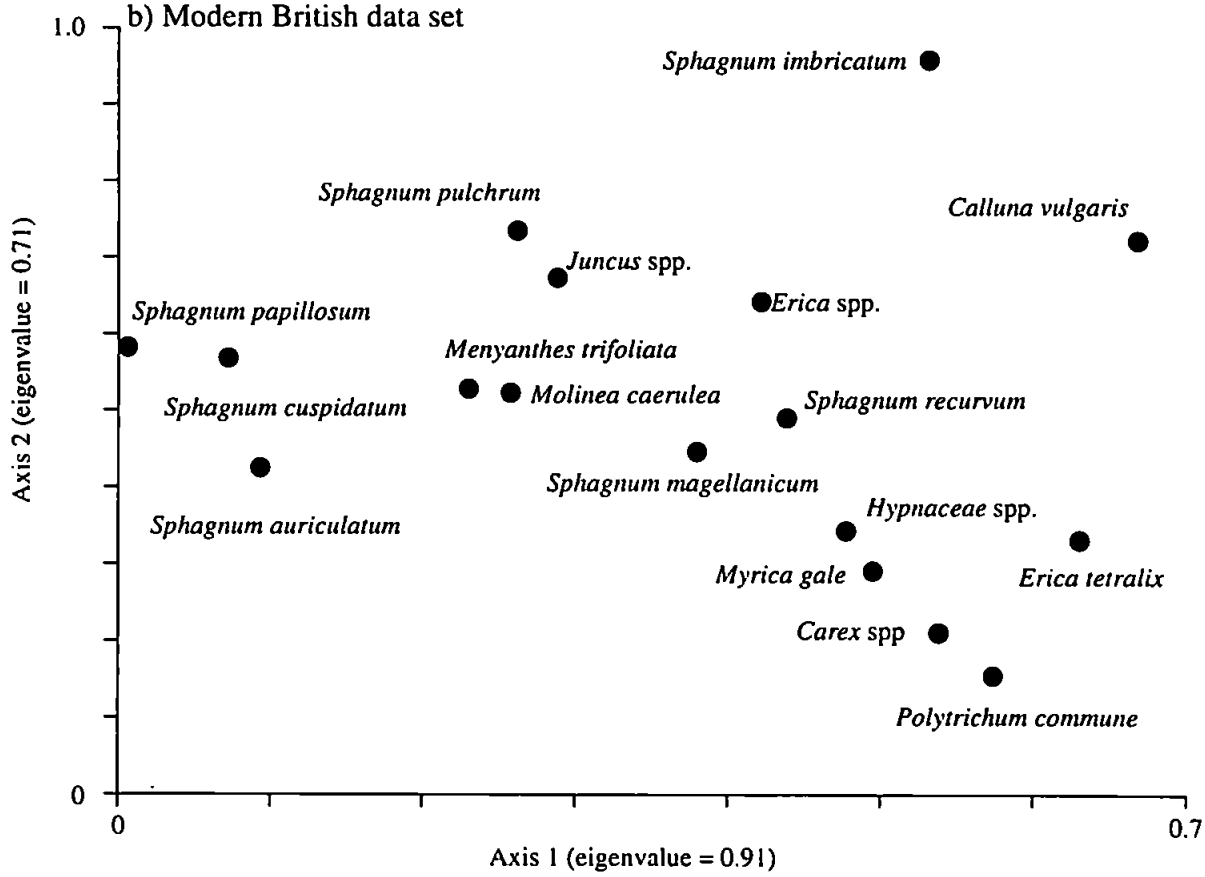


Figure 8.6: Comparison of DCA ordination scores for (a) the plant macrofossil assemblage from Bolton Fell Moss and (b) the vegetation assemblages from the modern data set.

Firstly, fossil test concentrations are dependent upon peat accumulation rates and it therefore becomes difficult to make sensible comparative studies, not only between different sites and sediments (soil and peat, for example), but also between different depths within a peat core. Accumulation rates are controlled by several factors, including species composition, differing microhabitats and prevailing climatic conditions (Stoneman, in Barber *et al.*, 1994a). Percentage counts of tests, however, are calculated on the basis of the total number of tests counted on a slide (usually 150 in this study) and are less affected by differential rates of test decay and peat accumulation, thus allowing intersite comparisons.

Secondly, and most importantly in transfer function applications, the mass of the modern moss sample differs from the mass of fossil peat. This is because decay processes remove much of the vegetative material that is present in modern samples. Therefore, modern and fossil test concentrations are not directly comparable.

To assess the usefulness of percent abundance and concentration data for the palaeohydrological reconstructions, data generated by the two techniques were compared to the modern British samples. Two rounds of correspondence analysis were applied to the data - first comparing fossil and modern concentration data, then comparing fossil and modern percent abundance data - to identify overlap between the data sets. The resulting ordination scores are shown in Figures 8.7 and 8.8. There is very little overlap between the fossil and modern concentration samples (Figure 8.7), confirming that transfer functions from these data would be inaccurate.

Using percent abundance to generate transfer functions is more valid. In Figure 8.8, all 50 Bolton Fell Moss samples overlap closely with the modern data set. As might be expected in a fossil core from an oligotrophic ombrotrophic mire, most of the Bolton Fell Moss

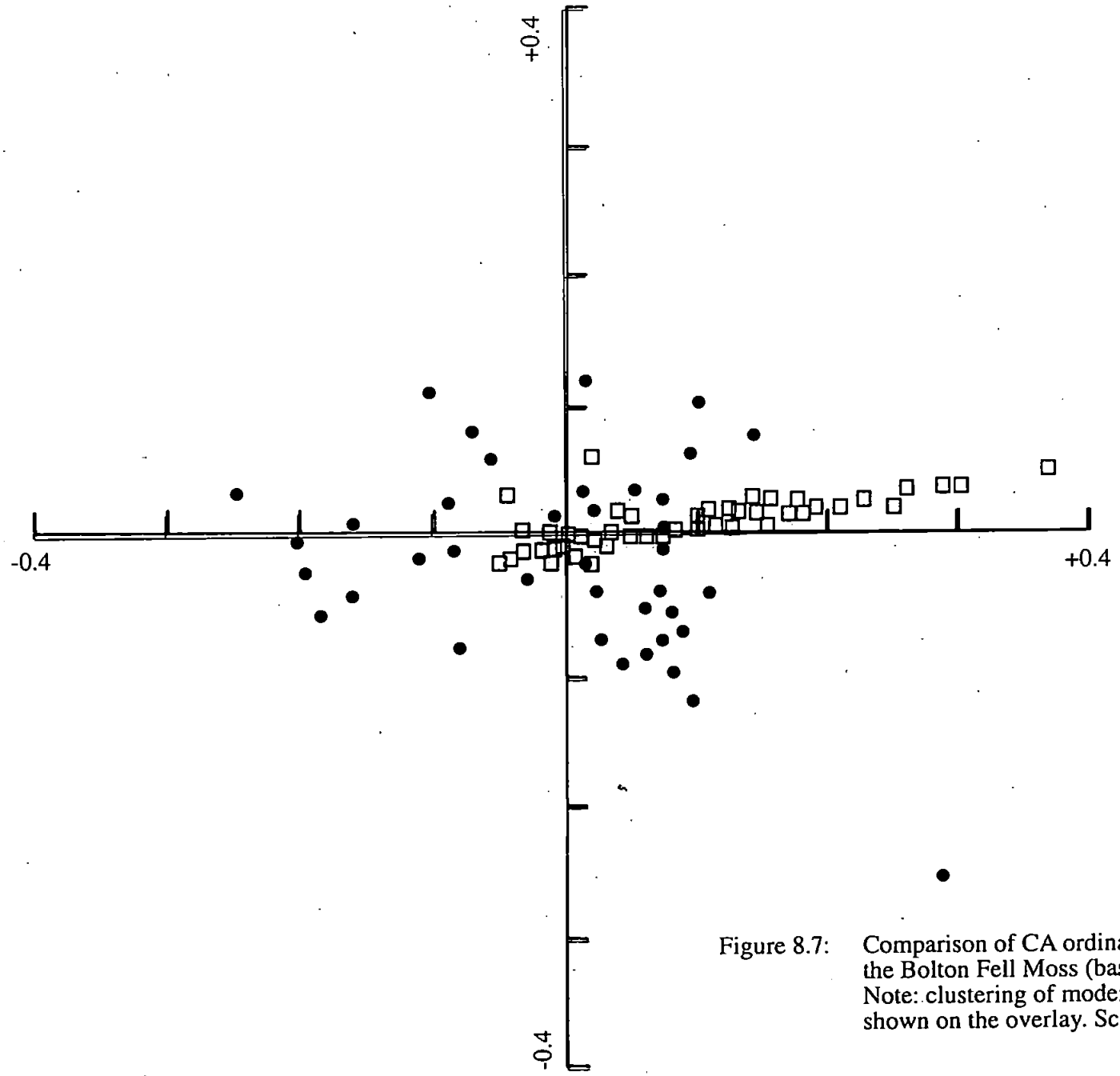


Figure 8.7: Comparison of CA ordination scores derived from test concentrations in the Bolton Fell Moss (base diagram) and modern British samples (overlay). Note: clustering of modern British samples is so great that not all are shown on the overlay. Scales on both diagrams are identical.

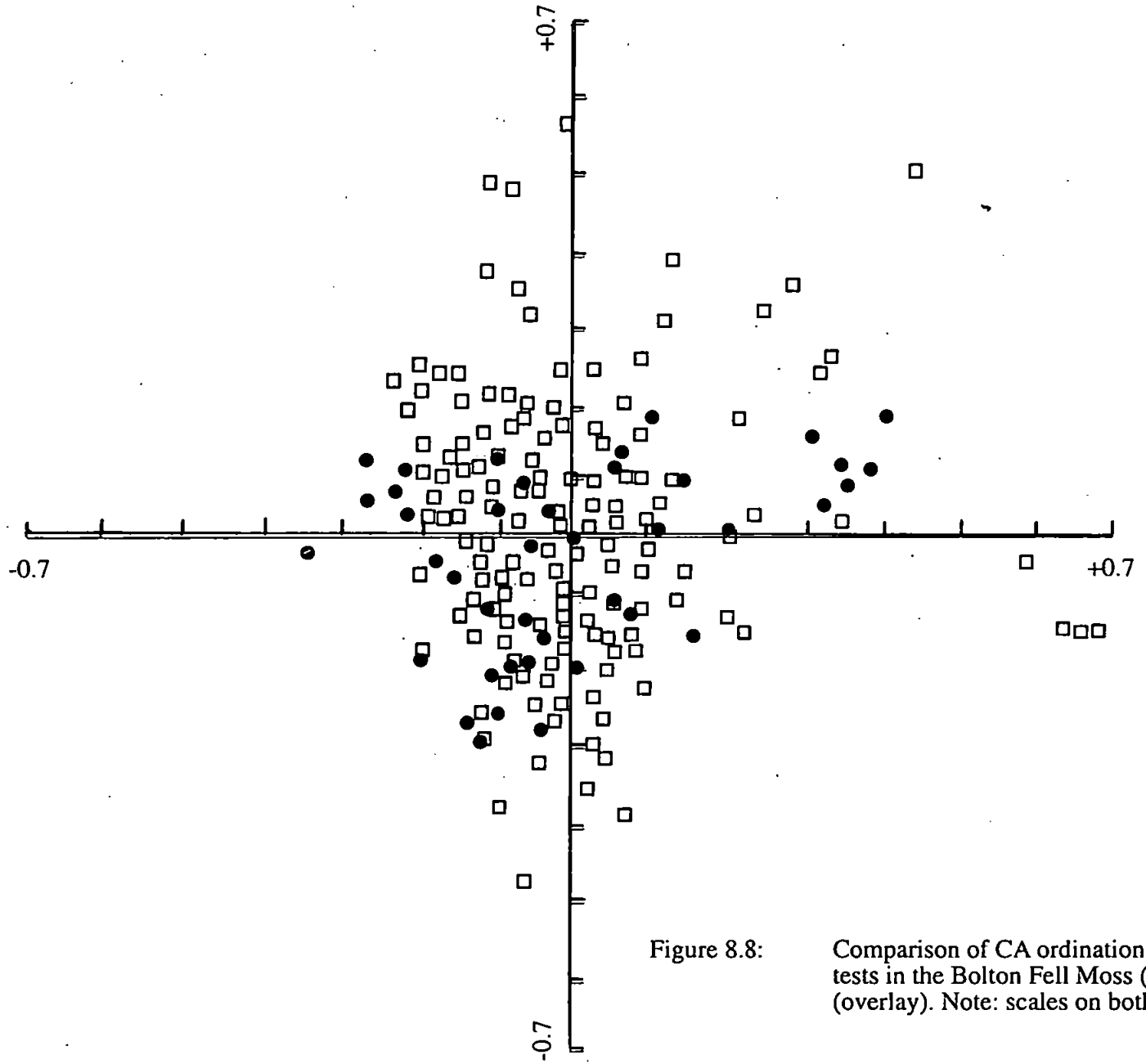


Figure 8.8: Comparison of CA ordination score derived from percentage abundance of tests in the Bolton Fell Moss (base diagram) and modern British samples (overlay). Note: scales on both diagrams are identical.

samples show greatest similarity with those from modern mires of similar nutrient status and have less in common with some assemblages on the slightly nutrient-enriched schwingmoors of Chartley Moss and Llyn Mire. The ordination plots nevertheless show that, on the whole, the modern and fossil testate amoebae assemblages based on percent abundance bear very close resemblance. Although the modern data set reflects only a small selection of the peat types in Britain, the ordination scores confirm that the modern British analogues can be used in palaeohydrological interpretations of the fossil assemblage at Bolton Fell Moss. This also suggests that the lower diversity of the fossil samples does not significantly affect their similarity to modern analogues.

8.4.4 Reconstruction of water table and percent moisture curves for Bolton Fell Moss

After conversion of the percent testate amoebae abundance counts for Bolton Fell Moss into FORTRAN format, weighted averaging calibration was applied using the CALIBRATE computer programme (Juggins, 1992) to derive values for both water table depth and percent moisture content. CALIBRATE gave a reconstructed value (shown as a solid line in Figure 8.9) and a tolerance range (broken line) for both parameters for each sample depth. The tolerance range was calculated from the mean tolerance of all species in the fossil assemblage at that depth. The resulting data were plotted as palaeohydrological curves, with prediction errors.

8.4.5 The testate amoebae diagram for Bolton Fell Moss

Raw counts for testate amoebae were converted into percentage abundance and graphed using the TILIA and TILIAGRAPH computer programmes (Grimm, 1991). The fossil testate amoebae diagram for Bolton Fell Moss is presented in Figure 8.9 and is arranged along a hydrological gradient, moving left to right from a high to a low water table, following the species' hydrological rankings derived in Chapter 7. The reconstructed curves

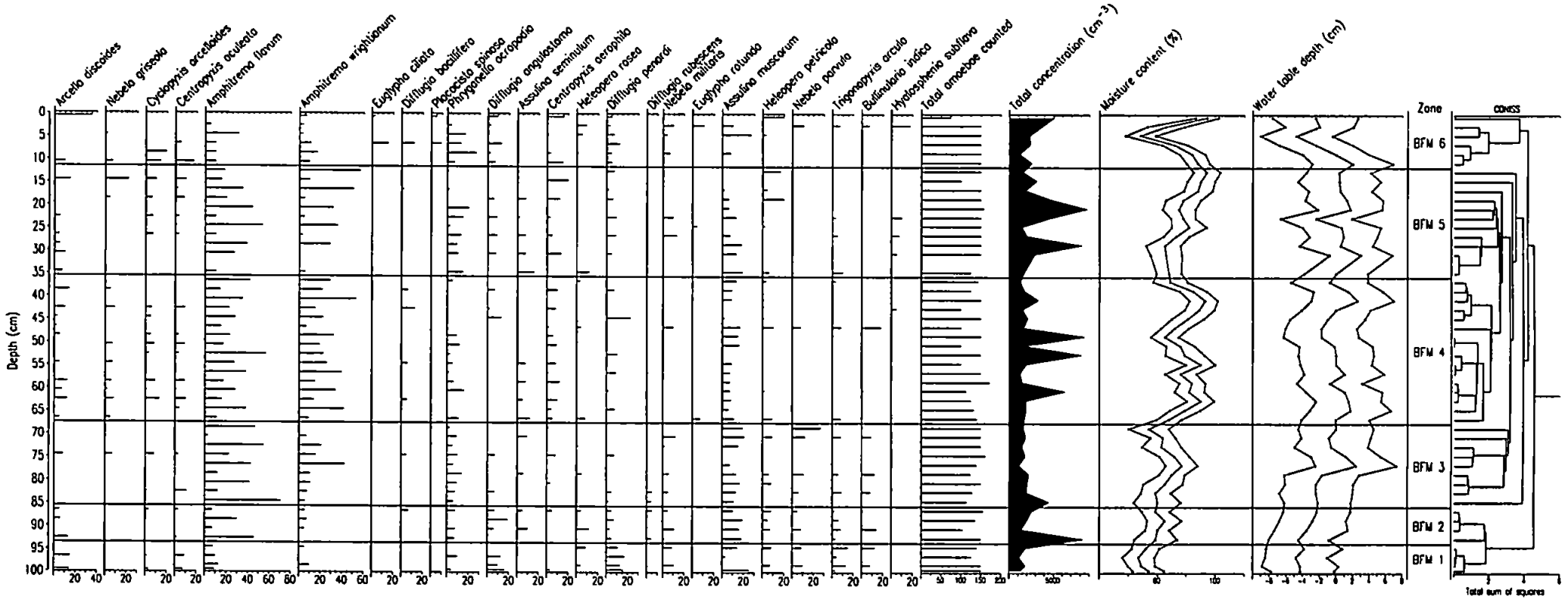


Figure 8.9: Testate amoebae assemblages and reconstructed palaeohydrological curves for the top 100 cm of monolith J2, Bolton Fell Moss.

for percent moisture content and water table depth derived from the testate amoebae species assemblages are also shown. These curves are discussed fully below.

A total of 24 testate amoebae species were identified, giving a far more diverse assemblage than that found by Barber (1981), who found six species only. This may reflect the preparation techniques adopted by Barber (1981). Barber did not use hydrofluoric acid (HF) digestion on the pollen samples from Bolton Fell Moss and counted the testate amoebae tests along with the pollen grains on the assumption that, by omitting the extremely corrosive HF stage, the testate amoebae would be robust enough to survive KOH digestion and acetolysis.

Acetolysis is used in pollen preparations to remove cellulose (a polysaccharide; Moore *et al.*, 1991). Although some species of *Difflugia* and all members of Euglyphacea have siliceous plates and particles incorporated in their tests (which are resistant to acetolysis), all species have organic cement composed of mucopolysaccharide secretion (Ogden and Hedley, 1980; Sleigh, 1989;) which would be dissolved by acetolysis, thus destroying the test structure. Further, if treatment with 10% HCl preceded the acetolysis and KOH stages, the calcareous tests of species such as *Paraquadrula irregularis* and *Cryptodifflugia oviformis* (Ogden and Hedley, 1980) would certainly de destroyed. More detailed work on the effects of pollen preparations shows a reduction in the abundance and diversity of faunas that are subjected to acid digestion (D. Hendon, pers. comm.). The preparation technique for testate amoebae described in section 4.1.3 (page 85), which uses no chemicals, should therefore be used in preference to the pollen preparations described above. The improved testate amoebae preservation in samples would considerably outweigh the inconvenience of applying separate preparation techniques for pollen and testate amoebae analysis.

A notable feature of the diagram in Figure 8.9 is the presence of *Amphitrema wrightianum* which, although abundant throughout the fossil assemblage, was not present in any of the surface moss assemblages from Britain. Of further interest is the species' decline from a peak abundance of 60% at 12.5 cm to less than 10% at 0.5 cm and its replacement in the assemblage by species from both the hydrophilous (e.g. *Arcella discoides)* and xerophilous *(Heleopera petricola, Assulina muscorum, Nebela parvula, Trigonopyxis arcula, Bullinularia indica*) limits of the hydrological gradient between 12.5 cm and 4.5 cm. *A. wrightianum* is absent from the modern British data set and recent work on fossil peat cores from other Cumbrian sites (Coom Rigg Moss, The Wou and Butterburn Flow) all show a similar *A. wrightianum* decline towards the peat surface (D. Hendon, pers. comm.).

The reason for the *A. wrightianum* decline is uncertain. The species is absent from other published palaeoecological studies (for example, Tolonen *et al.,* 1985; Warner and Charman, 1994). Charman and Warner (1992) did not find the species in their modern study on a forested peatland in northeastern Ontario, but Tolonen *et al.* (1992) found *A. wrightianum* in the wettest parts of southern Finnish mires (where depth to water table was 0.8 cm, with a standard deviation of 1.56 cm and moisture content 97.6%, standard deviation 1.06%). Although the Canadian peatland may have been too dry for *A. wrightianum*, the moisture status of the Finnish raised mires is close to that of raised mires in Britain, as the comparison between weighted averages for water table and moisture content between this study and Tolonen *et al.* (1992) in Chapter 7 confirmed. The *A. wrightianum* and *A. flavum* abundances in Figure 8.9 suggest competition between the two species. Both thrive in similar hydrological conditions (Heal, 1962; Tolonen *et al.,* 1992) and *A. flavum* may be out-competing *A. wrightianum* in Britain. Increased atmospheric pollution during the last 200 years may be a further contributary factor. *A. wrightianum* declines occurred within the top 15 cm of peat cores from Cumbrian sites (this study and D. Hendon, pers. com.), which may post-date the Industrial Revolution in Britain. The

species' demise may result from the deposition of pollutants and, if so, *A. wrightianum* is potentially a sensitive chemical indicator on ombrotrophic mires. Further work, into the exact timing of the *A. wrightianum* decline, the replacement of *A. wrightianum* by *A. flavum* in fossil assemblages and into the present-day spatial distribution of *A. wrightianum* with respect to industrial areas in Britain, is required to investigate this hypothesis.

The absence of *A. wrightianum* from the modern British data set introduces the problem of a fossil testate amoeba that has no modern analogue. Two issues arise from this in the calibration exercise. Since there are no hydrological data for *A. wrightianum* in the modern data set, the species has no influence on reconstructed hydrological curves. Secondly, the relative abundances of remaining species in the assemblage (for which hydrological optima have been derived) are suppressed and their influence in the hydrological reconstructions is reduced. Section 8.4.6 details procedures that were adopted to address this issue.

For ease of interpretation, the testate amoebae diagram in Figure 8.9 has been zoned using the numerical zonation programme CONISS (Grimm, 1987). It recognises six major faunal assemblage zones which have been used to structure the interpretations below and are given the codes BFM 1 (oldest) to BFM 6 (youngest). The main features of each division are summarised in Table 8.2 and interpretations follow the hydrological optima and ranges for each testacean species presented in Chapter 7.

BFM 1 (100 - 94 cm): characterised by a diverse testate amoebae assemblage, this zone covers a shorter accumulation period relative to other BFM zones. There is a wide spread of species across the hydrological gradient (see Table 8.2 for species' percentages) although the wettest species are either absent from the zone (*Nebela griseola*) or are erratic and disappear at the top of the zone (*A rcella discoides*). 16 of the 24 species recorded at Bolton Fell Moss are present in BFM 1 and the reconstructed water table curve suggests that the

Zone	Depth (cm)	Description
BFM 6	11 - 0	Disappearance of *N. griseola, C. arcelloides, C. aculeata* towards middle of zone, reappearance of dry species at 4.5cm (*E. rotunda, A. muscorum, N. parvula, T. arcula, B. indica*) to dominate assemblage. Steady decline of *A. wrightianum* to <10%, disappearance of *A. flavum* at top of zone. Maximum abundance of *H. petricola* (20%) and A. discoides (35%) at top of zone, slight recovery of *A. wrightianum* at 2.5cm. Water table falling from peak at base of zone to reach a minimum at 4.5cm depth, thereafter rapid recovery.
BFM 5	35 - 11	Low *A. flavum* (10% at base of zone), recovery to peak mid zone (58%), followed by decline to 20%. Erratic rise in *A. wrightianum* (<10% at base to 58% at top of zone). Disappearance from mid-zone upwards of *D. angulostoma, Phryganella acropodia, Assulina seminulum, H. subflava, N. militaris, A. muscorum, T. arcula.* Greater species diversity in bottom half of zone, assemblage then dominated by wetter species only (*A. wrightianum, A. atrocrea, N. griseola, Cyclopyxis arcelloides, C. aculeata*). Suggests steadily rising water table, interrupted by brief fall in middle of zone.
BFM 4	66 - 35	Erratic behaviour of *A. flavum* and *A. wrightianum* - but general decline of both taxa towards middle of zone, followed by recovery throughout remainder. Dry species (*B. indica, T. arcula, N. parvula, A. muscorum*) show concomitant recovery. Appearance of rare mid-range species (*Nebela militaris, H. suflava, Difflugia rubescens, Heleopera rosea, D. bacillifera*) at peak abundances. Suggests hydrological conditions mid-zone which are within the tolerance range of many species, encouraging a diverse assemblage. Return to wetter conditions thereafter.
BFM 3	86 - 66	*A. flavum* dominates assemblage (peak abundance at 75%), although abundances are erratic. Recovery to maximum abundances *of A. wrightianum* (48%), *Phryganella acropodia* (15%) mid-zone. Rare appearances of wetter species (*Arcella disoides, N. griseola, C. arcelloides, C. aculeata*) in mid-zone; synchronous demise of xerophilous species (*B. indica, T. arcula, N. parvula, A. muscorum*). Thereafter, xerophilous species recover and hydrophilous species decline. Infers an increase in surface wetness to a maximum in mid-zone, followed immediately by a dry phase which continues to top of zone.
BFM 2	94 - 86	Recovery of *Amphitrema flavum* (reaching peak abundance at 46%) at base of zone before decline, consistent presence of *Assulina muscorum* (ca. 15-28%), declining abundance of dry species (*T. arcula* <5%; *Bullinularia indica*<5%; *Nebela parvula* 6%). Appearance of wetter species (*Arcella discoides, Cyclopyxis arcelloides, Centropyxis aculeata* at top of zone. Suggests gradual progression to wetter conditions than BFM 1 towards top of zone.
BFM 1	100 - 94	Spread of species across hydrological gradient, but drier species more abundant. *Assulina muscorum* dominates assemblage (maximum abundance=26%), with *Difflugia penardi* (18%), *D. angulostoma* (16%), *Arcella discoides* (17%) and *Trigonopyxis arcula* (15%) less abundant. Suggests moderately wet conditions within the tolerance range of most species.

Table 8.2: Testate amoebae assemblage zones for the Bolton Fell Moss monolith J2, summarising the main characteristics and qualitatively inferred moisture conditions.

mean depth was between 4 and 5 cm below the ground surface, within the tolerance ranges of all but the most hydrophilous species.

Within BFM 1, the mire surface attains a dryness that is not repeated again in the core until the middle of BFM 6. Mean water table depth increases from -4 cm to -4.8 cm between 99 cm and 97.5 cm depth and a synchronous fall occurs in moisture content from 77% to 74%. This change to drier conditions is precipitated by the demise of *Amphitrema flavum*.

BFM 2 (94 - 85.5 cm): A changing testate amoebae assemblage (Table 8.2) results in a reversal to wetter conditions through the base of BFM 2. The consistent presence of *Assulina muscorum* probably reflects its non-preference for the species type of its host substrate, which enables it to thrive on both *S.s.A cutifolia* and *S. imbricatum* hummocks (Heal, 1959). Mean water table depth decreases from -4.6 cm at the base of the zone to -2.2 cm at the top, while the moisture curve shows a lower-magnitude recovery. Moisture content remains stable at ca.80% throughout the zone.

BFM 3 (85.5 - 67 cm): The assemblage in BFM 3 is dominated by both species of *Amphitrema* (Table 8.2) and the reconstructed hydrological curves respond to this. The dominance of *A. flavum* causes a marked rise in the reconstructed water table and % moisture to reach one of the wettest events at Bolton Fell Moss. Mean water table depth rises from -2.2 cm to +2.4 cm above the ground surface, indicating standing water and % moisture reaches 89%. Despite the fluctuations in *A. flavum* and *A. wrightianum*, the percent moisture and water table depth curves do not show dramatic fluctuations with these changes. This suggests that *A. wrightianum* may have similar hydrological preferences to *A. flavum* and that the lack of a modern analogue is compensated for by the robustness of the record derived from the other species alone.

From the middle of BFM 3, the assemblage becomes increasingly species-poor, so that only eight species are present at the top of the zone. Of these, four are xerophilous (*H. subflava, B. indica, T. arcula* and *N. parvula*) and this indicates a drying episode, where the water table drops from +2.4 cm to -0.2 cm below ground and percent moisture content falls to 84%.

BFM 4 (67 - 35.5 cm): The rising water table continues into this zone, reaching one of its higher positions within the core. BFM 4 is characterised by a rise and decline of *Amphitrema flavum*, sporadic appearances by the wetter species and long absences of several xerophilous species. The hydrological curves show a wet opening to the zone, followed by an overall decline to dry conditions, with a brief wet event at the top of the zone.

After a period of generally drying conditions, the major drying episode in BFM 4 begins at 50 cm and peaks at 48 - 46 cm, where xerophilous species (*H. subflava, B. indica, Trigonopyxis arcula, N. parvula* and *A. muscorum*) become an important component of the assemblage, resulting in minima for water table depth and moisture content.

Following this, *Amphitrema spp.* increase, expressed in the reconstructed curves as a reversal towards wet conditions. This begins at 48 cm in the % moisture curve and 46 cm in the water table curve and it continues until 40 cm, where the water table depth (2 cm above ground) and % moisture content (96%) indicate a wet event, with standing water present. From the species' optima produced in Figures 6.13 and 6.14 (pages 244 and 245), the presence of a wider range of hydrophilous species from the British data set would be expected in the assemblage. Such species might reasonably include *A. discoides, Nebela carinata, Euglypha strigosa, N. griseola, Hyalosphenia papilio, Difflugia leidyi, Cyclopyxis arcelloides, N. vitrea, Centropyxis aculeata, A. flavum, Euglypha ciliata* and *D. bacillifera,*

since these species' optima are all less than 5 cm water table depth and greater than 90% moisture content. Of these, however, only *A. flavum* is present and, with *A. wrightianum*, it dominates the assemblage. Given this, the above species may have been out-competed by *Amphitrema* spp.

BFM 5 (35.5 - 11 cm): The strong position of *Amphitrema* spp. in this habitat is again evident in BFM 5. The response of the reconstructed curves is towards generally wetter conditions throughout BFM 5, as mean moisture content increases from 84% (at the base of BFM 5) to 95% (at the top) and mean water table depth decreases from 0 cm to 0.9 cm above ground, although the curves are erratic. The wettest phase in the water table curve begins at the base of BFM 5 and peaks at 30 cm, with 3 cm of standing water and results from the appearance of *A. discoides, C. arcelloides* and *C. aculeata* in the assemblage in addition to *Amphitrema* spp. The moisture curve trends slightly drier at this point, however.

In the top 5 cm of the zone, the reconstructed curves diverge as mean water table falls slightly from +0.5 cm to +0.2 cm above ground surface, but mean moisture content increases from 94% to 98%. This situation is possible because, although the water table may have been falling slightly, moisture content could have been maintained through daily condensation and through generally lower evapotranspiration rates from a dense sward of *Sphagnum*, where the bulk of the plant body would be protected from incoming solar radiation.

BFM 6 (11 - 0 cm): *N. griseola, C. arcelloides, C. aculeata, A. flavum, A. wrightianum* and *D. bacillifera* all disappear from the assemblage within the top 7 cm of BFM 6, while indifferent species (*Heleopera rosea, N. militaris*) and xerophilous species (*Bullinularia indica, T. arcula, N. parvula, A. muscorum*) recover. This indicates a marked drying event, which is the most extreme since that recorded in BFM 1, as mean moisture content and

water table depth reach their respective minima (73%) and maxima (-5 cm) at 4 cm peat depth.

Above 4 cm, a gradual increase in surface wetness is recorded by a rise in *A. discoides* (which reaches a maximum abundance of 35%) and by the disappearance of *A. muscorum, N. parvula, T. arcula, B. indica and H. subflava.* The % moisture content curve rises to 97%, the maximum moisture content which was recorded in the reconstruction. The water table depth also begins to rise, but falls from 4 cm upwards, reaching a depth of -2.5 cm at the modern mire surface.

BFM 6 probably encompasses the living testate amoebae assemblage, where the reconstructed curves would be affected by modern processes operating in the acrotelm. These may include down-washing of tests and migration of species in response to environmental changes, so that the curves within in this zone are not strictly fossil and should therefore be viewed with caution.

8.5 Comparison of the plant macrofossil and testate amoebae assemblages

Figure 8.10 shows the plant macrofossil diagram for the top 100 cm of the monolith, upon which the testate amoebae zones have been superimposed. Sphagna in the macrofossil diagram have been arranged in a hydrological sequence; species on the left are characteristic of a drier environment, those on the right indicate wetter conditions. The following section is a qualitative comparison of the plant macrofossil and testate amoebae assemblages for the top section of the monolith, which is structured according to the testate amoebae zones BFM 1 to BFM 6. This will assist with the quantitative comparisons of the curves later in this chapter, particularly instances where the curves may diverge, since it

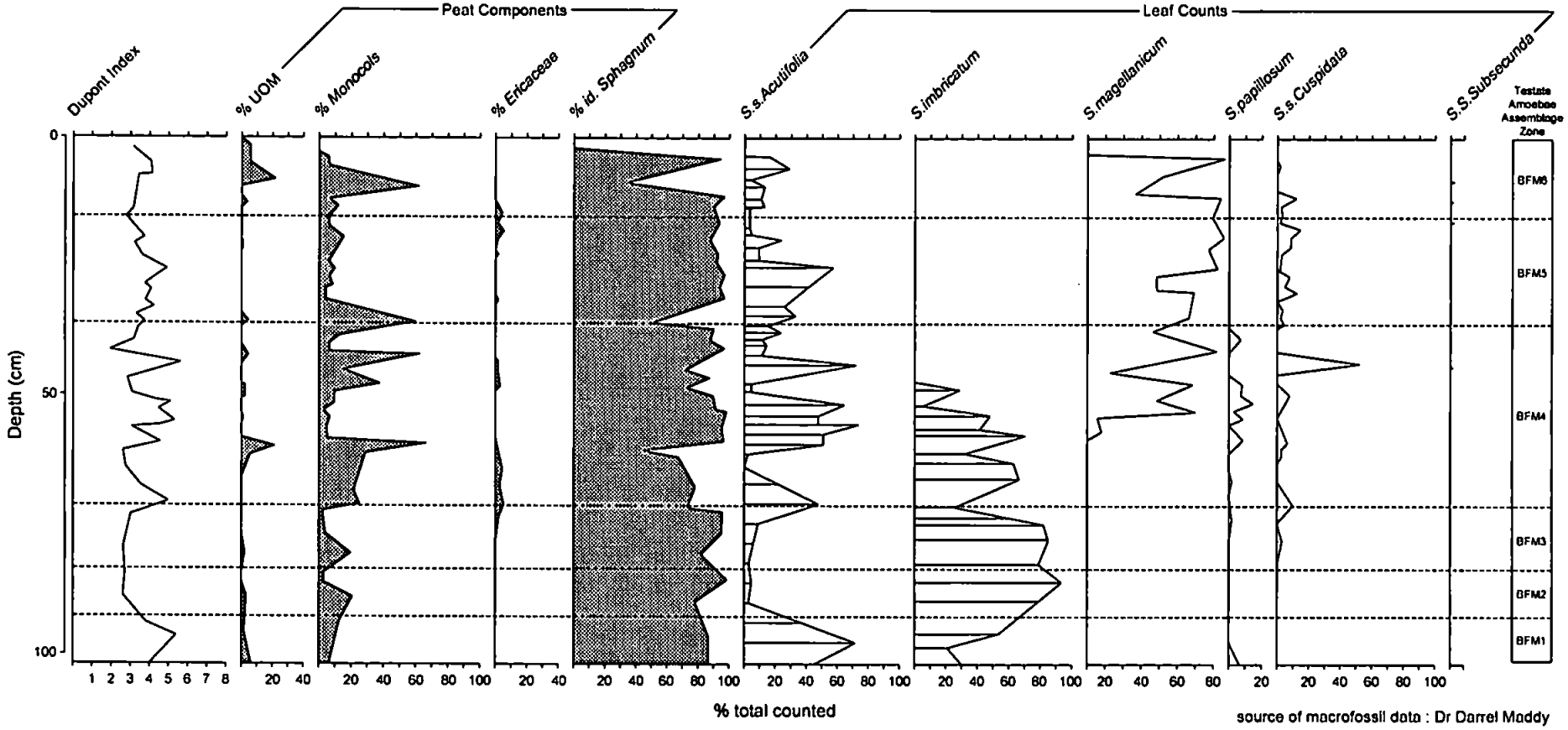


Figure 8.10: Plant macrofossil diagram for the top 100 cm of monolith J1, Bolton Fell Moss. Redrawn from Barber *et al.* (1994d)

is from these assemblages that the DCA, water table and moisture curves have been derived.

BFM 1 (100-94 cm): The drier environment reconstructed from the testate amoebae assemblage is supported by the plant macrofossil diagram. Both *S. imbricatum* and *S. papillosum* are generally interpreted as characteristic of moderately dry mire surfaces, while Sphagnum section Acutifolia is predominantly made up of hummock-top species, such as *S. capillifolium* and *S. capillifolium* var. *rubellum* (Daniels and Eddy, 1985; Barber *et al.*, 1993; 1994b). This accords well with the diverse testate amoebae for the same zone, which was interpreted as representative of a moderately dry environment in which hydrological conditions were still within the tolerance range of many species.

BFM 2 (94 - 85.5 cm): The regression to wetter conditions indicated by the testate amoebae assemblages in this zone is supported in the plant macrofossil record by the recovery of *S. imbricatum*, a wet lawn species in the fossil state (Green, 1968; Stoneman *et al.*, 1993), and the demise of *S. acutifolia.* Hydrophilous Sphagna such as S.s.Cuspidata and S.s.Subsecunda are still absent, however, suggesting that the recent timing of the reversal to wetter conditions may have given insufficient time for these species to colonise the mire surface.

BFM 3 (85.5 - 67 cm): Continued surface wetness in the bottom half of BFM 3 reflects a dominance of *S. imbricatum* and rare appearances by *S. papillosum* and Sphagnum section Cuspidata. In the middle of BFM 3, where the testate amoebae assemblages precipitated a marked rise in water table and moisture, the plant macrofossil record is also in accordance; this is the first appearance in the monolith extract by S.s.Cuspidata. The immediate reversal to a slightly drier testate amoebae assemblage is reflected in the plant macrofossil assemblage by disappearance of S.s.Cuspidata and a slight *S. imbricatum*

decline. The slight reversal to wetter conditions, derived from testate amoebae, in the top 4 cm of BFM 3 also occurs in the plant macrofossil record where S.s. Cuspidata and *S. papillosum* recover, implying a rising water table.

BFM 4 (67 - 35.5 cm): Within this zone, species abundances for monocotyledons, S. s. Acutifolia and *S. magellanicum* are erratic. The first appearance in the profile of *S. magellanicum*, a hydrophilous species (Daniels and Eddy, 1985), coincides with the local extinction of *S. imbricatum*. Replacement of one hydrophilous species by another in the assemblage maintains the trend towards wetter conditions throughout the zone.

The major ecological change in the plant assemblage at ca. 45 cm, which heralds wetter conditions (Barber *et al.*, 1994c) is preceded by the testate amoebae at 48 cm and results from high abundances for *Amphitrema* and a demise of hydrophilous species (*H. subflava, B. indica, T. arcula, N. parvula, H. petricola*). At 41 cm, there is an excellent match between the very high water table inferred from the testate amoebae assemblage and the associated Sphagna at 41 cm. The inferred water table from testate amoebae analysis is 2 cm above the ground surface (i.e. a pool). At the same point, there is a marked rise in S.s. Cuspidata (to 55% abundance), species which are the dominant component of extremely wet locations (Daniels and Eddy, 1985).

Between 55 cm and 45 cm, the plant macrofossil record, particularly that from S.s.Acutifolia, *S. magellanicum*, and unidentifiable organic matter is erratic, implying an unstable hydrological environment, with rapid shifts between wet and dry conditions. In contrast, the testate amoebae assemblages and derived water table / moisture curves are less erratic. This is a reflection of a diverse testate amoebae assemblage (compared to the restricted plant macrofossil assemblage), which moderates the resulting palaeohydrological signals.

BFM 5 (35.5 - 11 cm): The general pattern of greater surface wetness throughout this zone results from a greater proportion of hydrophilous species in both the plant macrofossil and testate amoebae assemblages. S.s.Cuspidata and *S. magellanicum* increase in abundance, while the relatively xerophilous species of S.s.Acutifolia decline through BFM 5. This is synchronous with high abundances of hydrophilous species, such as *A. discoides, N. griseola, Cyclopyxis arcelloides, Centropyxis aculeata, A. flavum* and *A. wrightianum*. Again, the presence of a pool on the mire surface is inferred from a water table of 3 cm above the ground surface.

BFM 6 (11 - 0 cm): From the base to the middle of BFM 6, the plant macrofossil and testate amoebae diagrams both attest to increased desiccation of the mire surface, and the peat humification curve shows relatively stable, dry conditions. Identifiable *Sphagnum* declines, as monocotyledons increase in abundance. Aerobic conditions are suggested by the increase in unidentifiable matter and by the peat humification curve. Several xerophilous testate amoebae approach maximum abundances at this stage (for example, *A. muscorum, N. parvula, T. arcula and B. indica*).

From ca. 5 cm, a gradual increase in mire surface wetness is indicated by the testate amoebae and plant macrofossils as hydrophilous species increase at the expense of xerophilous species. This is manifested in the plant macrofossil diagram as a rise in identifiable *Sphagnum* (principally *S. magellanicum*) and in the testate amoebae assemblages as an increase in *A. discoides* and the local extinction of *A. muscorum, N. parvula, T. arcula* and *B. indica*. However, as before, caution is needed in interpreting the testate amoebae records for the surface of the acrotelm.

Summary: plant macrofossils and testacean assemblages at Bolton Fell Moss

There is an encouraging match between the plant macrofossil and testate amoebae assemblages. There are differences in the relative timing and magnitude of fluctuations between the assemblages and, where possible, explanations have been forwarded in the above section. The analysis is taken one step further in the following section by comparing the reconstructed hydrological curves derived from testate amoebae with those from plant macrofossil and peat humification analysis.

8.6 Comparison of the palaeohydrological curves derived from plant macrofossils, humification and testate amoebae analyses

This section assesses the testate amoebae curves for Bolton Fell Moss by comparing them to the reconstructed palaeohydrological curves derived from plant macrofossils (via DCA) and peat humification (section 8.3.3 and Figures 8.3a and b). Assessment was made in two ways. Firstly, by a straightforward visual comparison of the respective curves. Secondly, given that the hydrological data reconstructed from the plant macrofossils, peat humification and testate amoebae all approximate to a normal distribution, Pearson's correlation coefficient was used to compare the match between the water table / moisture curves and those derived from humification and plant macrofossils.

Two issues are important, however. Firstly, all correlations in this chapter relate to the topmost 100 cm of the core from Bolton Fell Moss and, therefore, appraisals of the relative performance of each reconstruction are restricted to this extract. The information cannot be extrapolated to support comments on, for example, the performance of the plant macrofossil and peat humification analysis throughout the complete 500 cm core. Secondly, calculating correlation coefficients may not be the most appropriate method of assessing the "accuracy" of the various reconstructions in this study, since correlation measures similarities in the proportion of change between two variables (Hammond and McCullagh, 1978). Given that

the plant macrofossil, peat humification and testate amoebae curves are all expressed in different units and that only the testate amoebae curves are expressed in real units (% and cm), magnitudes of change are unlikely to be directly comparable and the correlation will never be perfect. Further, perfect correlations might not be expected in environmental systems. The best solution would be to quantify the plant macrofossil and peat humification curves in terms of real environmental variables such as water table depth and moisture content and this is clearly an issue for future research in these interpretations. Another alternative is to compare each proxy curve with independent records, and this is conducted later in this chapter. However, in the absence of more appropriate measures, correlation is used to compare the reconstructed curves, but with the above caveats in mind.

Following an initial comparison (see Run 1, below), three filtering exercises were performed on the testate amoebae data in an attempt to improve the reconstructed curves from testate amoebae analysis. The filtering was performed not simply to obtain a convenient match with the plant macrofossil and peat humification curves, but in order to improve the testate amoebae curves by using the best indicator species for palaeoenvironmental reconstructions. Gradual modifications were therefore made with the aim of producing a final data set which would contain the best indicator species without significant loss of information from excluded species. After each filtering, the fossil testate amoebae data set was run through CALIBRATE to produce a new pair of hydrological curves.

This section describes the filtering procedures adopted in each of the runs and the resulting comparisons between the reconstructed curves. The curves are illustrated in Figures 8.11 - 8.18 and for ease of interpretation the testate amoebae zones BFM 1 - BFM 6 are superimposed onto each one. Detailed comparisons are made only between the testate amoebae, plant macrofossil and humification curves from Run 1, since these show the best

fit (see later). It was felt that detailed comparisons from the other runs would be superfluous to the study objectives and instead the main trends are summarised in Tables 8.5, 8.6 and 8.7.

8.6.1 Run 1

Initially, all fossil testate amoebae species present in the profile were used to reconstruct the palaeohydrological curves. These curves were shown in Figure 8.9 alongside the testate amoebae assemblages and they are reproduced for detailed comparison with the plant macrofossil and peat humification curves in Figures 8.11 and 8.12. The major trends in the palaeohydrological curves are summarised in Table 8.3.

Table 8.4a gives the Pearson's correlation coefficient for the curves and shows that there is a better relationship between the testate amoebae curves and humification ($r = 0.380$ for water table depth and humification; $r = -0.520$, $p<0.01$ for moisture content and humification) than between testate amoebae and plant macrofossils ($r = -0.240$ for water table depth and DCA; $r = -0.200$ for moisture content and DCA). Interestingly, despite the poorer correlation between the plant macrofossil and testate amoebae curves, the correlation is still stronger than that between the DCA and peat humification curves ($r = 0.196$). These correlations were achieved despite the inclusion in the calibration of *A. wrightianum*, a no-analogue species. The influence of no-analogue palaeoenvironmental reconstructions has been considered by several authors in sea temperature reconstructions from foraminifera (Imbrie *et al.*, 1973; Hutson, 1976, 1977; Berger and Gardner, 1975; Kipp, 1976). Of particular interest to this project was the observation by Hutson (1977, p.366) that for reconstructions based on foraminifera, errors in temperature reconstructions could be reduced by the use of weighted averaging regression and calibration because, unlike other techniques, weighted averaging does not extrapolate under no-analogue conditions. But

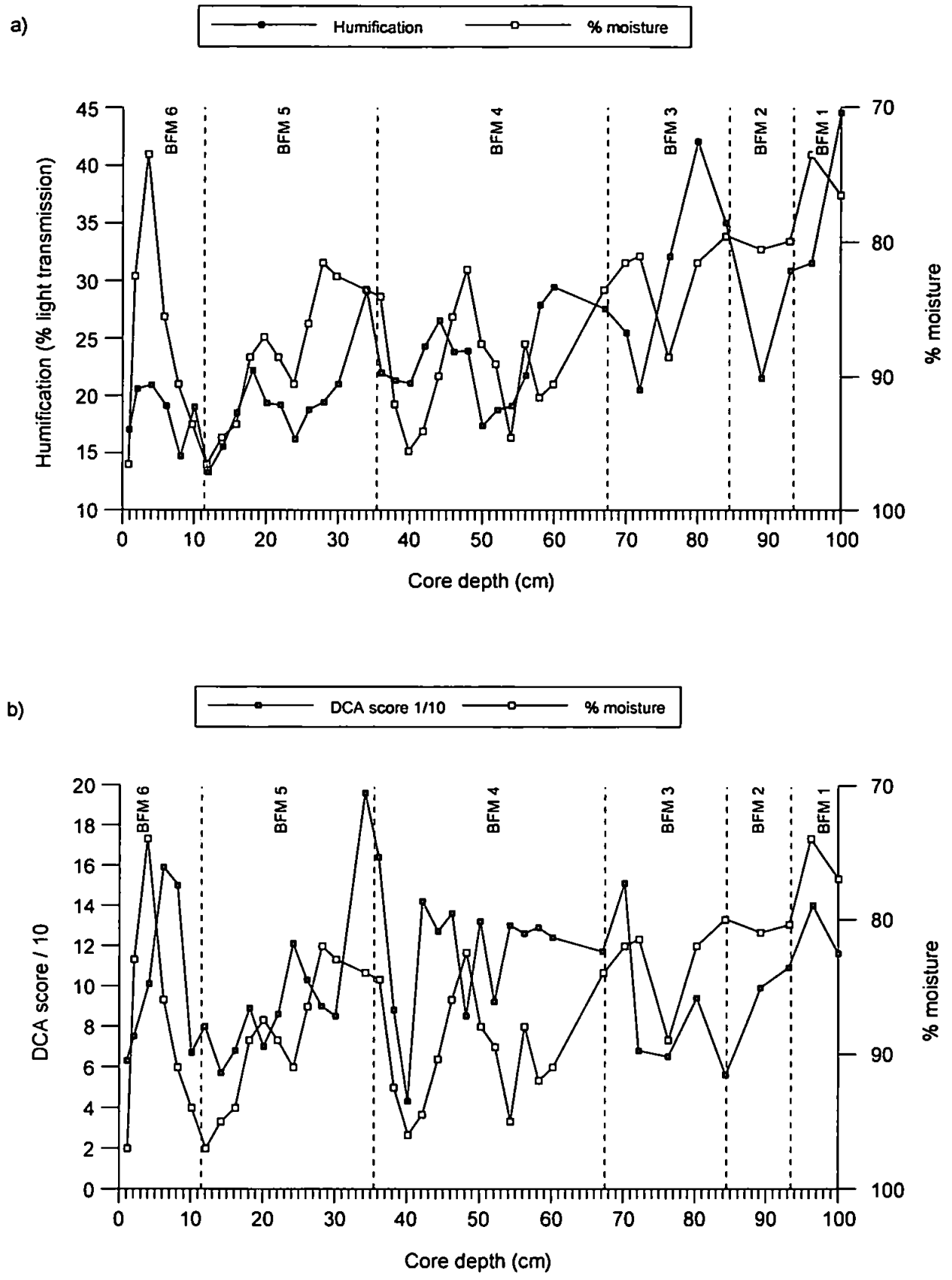


Figure 8.11 : Comparison of testate amoebae moisture curves with a) humification and b) DCA curves, Run 1.

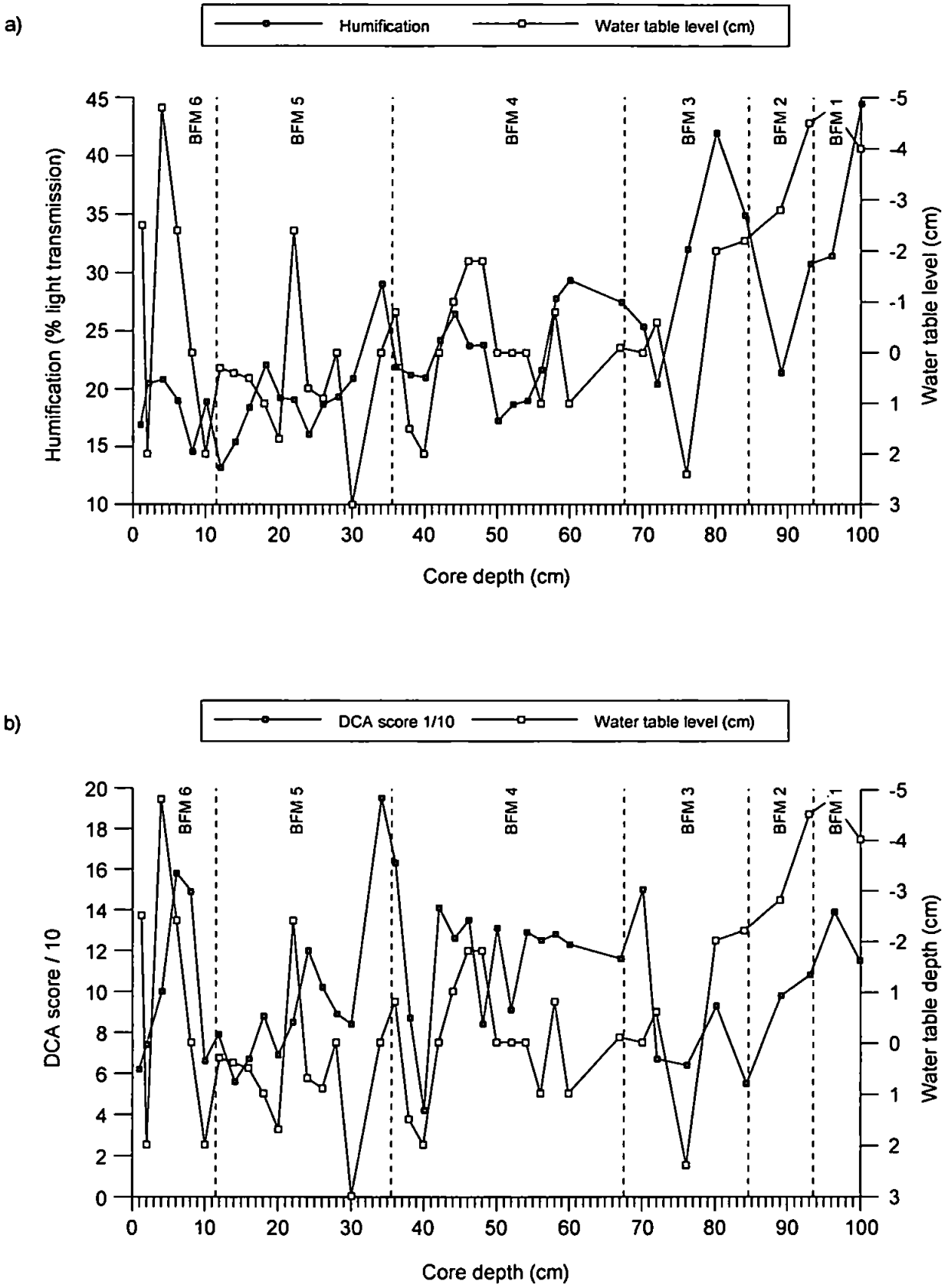


Figure 8.12 : Comparison of testate amoebae water table curves with a) humification and b) DCA curves, Run 1. For water table level, '0' indicates ground surface.

Zone	Testate amoebae curves	Peat humification curve	DCA axis 1 score.
BFM 6	Major swings in both curves. Water table curve shows continued wet conditions, then strong swing to dry at 10cm to mid-zone. Thereafter, slight recovery, followed by fall in water table. % moisture falls in lower half of zone, then reverses at 4cm.	Change to slightly drier conditions in bottom third of zone, then lesser shift than plant macrofossil diagram to wetter conditions in top 6cm of zone.	Marked reversal to dry surface conditions in mid-zone. Swing to wetter conditions follows, sustained to top of core.
BFM 5	Water table curve trending slightly wetter, but very erratic. Wettest event at 30cm, when water table +3cm above surface. Moisture curve shows stronger wetter trend.	Short, drier event at base of BFM5, then gradual progression to wetter conditions. Curve is erratic, but less so than for the plant macrofossil curve.	Begins dry, but sustained progression to wetter conditions, with less erratic curve than in preceding zones.
BFM 4	Similar erratic behaviour to other curves. Overall trend to slightly drier conditions in water table, but interrupted by major wet episode between 48 and 36cm (where reaches +2cm above ground at 40cm). Coincides with CANOCO wet shift.	High-magnitude fluctuation in plant macrofossil curve not evident in peat humification curve. Wet events between 60-50cm and 44-40cm. Thereafter, trending slightly drier.	Wet event begins at 42 cm and peaks at 40 cm. Preceded by peat humification and testate amoebae curves.
mid-BFM 3 to top of BFM 3	Marked reversal as water table falls to - 0.6cm. Top 3cm show ca. 1cm rise in water table. Moisture content falls slightly then more stable in top 2cm of zone.	Reversal to drier conditions, but this episode timed 4cm later than other curves.	Timing of wetter episode in general agreement with peat humification curve.
BFM 2 to mid-BFM 3	Continuation of BFM 1 for water table, which rises to +2.4cm above surface. 11% increase in moisture content to 89%. One ot the wettest events in profile mid - BFM 3.	Humification curve infers progressively wetter conditions to mid-BFM 2. Thereafter, swing to drier conditions to bottom third of BFM 3, then reversal to wetter conditions to mid - BFM 3.	Erratic fluctuations, but overall increase in wetness.
BFM 1	Slight lowering of water table (from -4.0 to -4.8cm), then rise to -4.6 at top of zone Falling moisture content, then rise from 74% to 80% to top of zone. Suggests moderately wet conditions.	Humification curve infers a rapid transition to wetter surface conditions in lower two-thirds of zone. Top third of zone more stable.	Slight reduction in surface wetness. Top half of BFM 1 wetter.

Table 8.3: Comparison between the palaeohydrological trends shown in the testate amoebae, peat humification and plant macrofossil curves, Run 1.

a) Run 1: full data set.

	CANOCO DCA	Peat humification	Water table depth
Peat humification	0.196		
Water table depth	-0.240	-0.380	
% moisture content	-0.200	-0.520*	0.561*

b) Run 2: *Amphitrema wrightianum* only removed from data set.

	CANOCO DCA	Peat humification	Water table depth
Water table depth	-0.057	-0.160	
% moisture content	-0.070	-0.440	0.06

c) Run 3: *Amphitrema wrightianum* and less sensitive species removed from data set (see text for details).

	CANOCO DCA	Peat humification	Water table depth
Water table depth	-0.196	-0.182	
% moisture content	-0.179	-0.300	0.050

d) Run 4: All but the 10 most hydrologically sensitive species removed from the data set (see text for details).

	CANOCO DCA	Peat humification	Water table depth
Water table depth	-0.060	-0.221	
% moisture content	-0.090	-0.206	0.350

Table 8.4: Pearson's correlation coefficients for the reconstructed hydrological curves, Run 1 - Run 4.

Hutson (1977, p.366) also added the caveat that "researchers should be suspicious, however, of estimates under non-analogue conditions unless a modern analogue can be found".

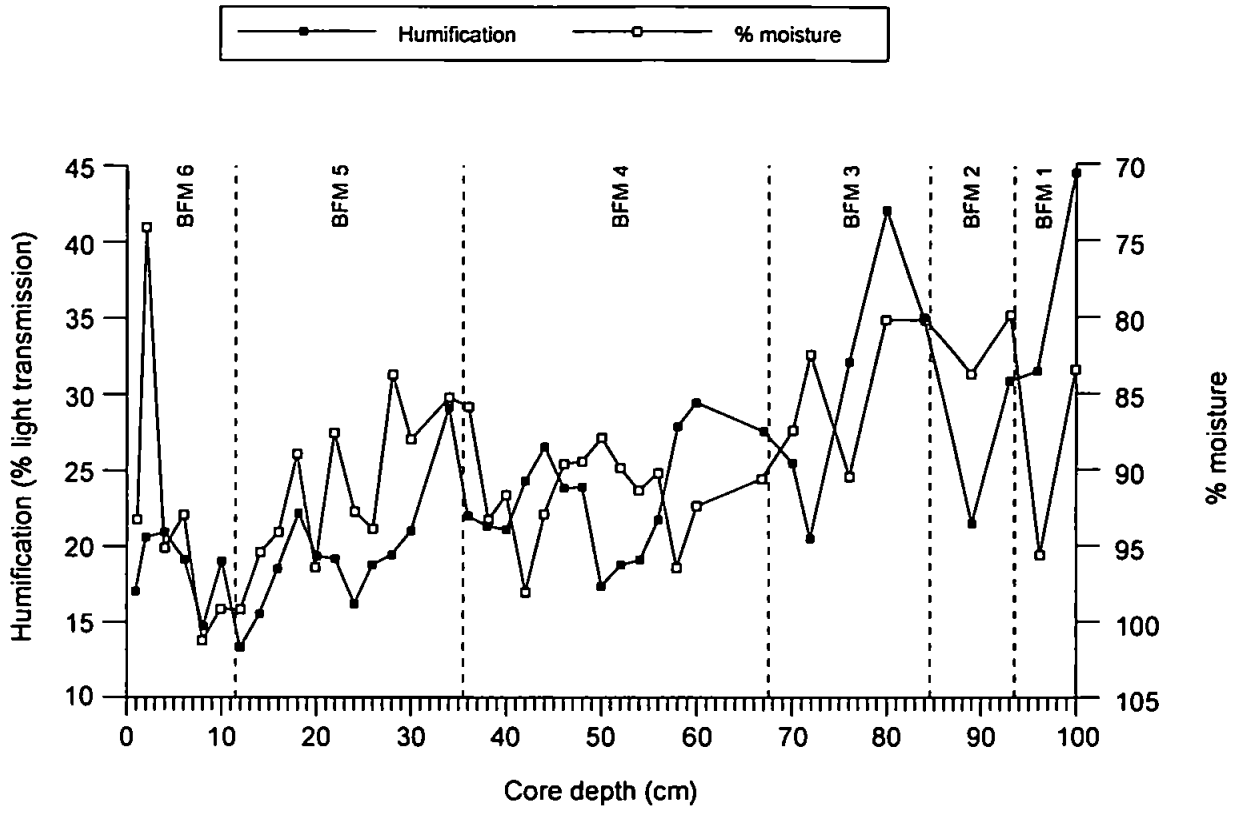
In terms of this study, better correlations between the curves might have been achieved by adding *A. wrightianum* to the modern data set, using the hydrological optima for the species from Tolonen *et al.* (1992), and inferring modern percent abundances from the fossil assemblage. However, insufficient information was available regarding the relationship of *A. wrightianum* with other species (particularly whether *A. wrightianum* occurs in similar abundances to *A. flavum* as the fossil assemblages suggest, for example) for sensible extrapolation of modern abundances. An alternative was to exclude *A. wrightianum* from the fossil calibration set and this was implemented for the second run. Remaining species' abundances were recalculated for Run 2 following the removal of *A. wrightianum* to remove likely dampening effects from the species' dominance in the fossil data set.

8.6.2 Run 2

The resulting palaeohydrological curves from Run 2 are shown in Figures 8.13 and 8.14, and the major palaeohydrological trends are summarised in Table 8.5. The correlation coefficients (Table 8.4b) show that, rather than improve the curves, the exclusion of *A. wrightianum* from the calibration set reduced the match between the curves. The best correlation was again achieved between the humification and moisture curves, although the correlation is not significant at $p<0.01$. For the remaining curves, the correlation was markedly reduced.

The greatest difference between Run 1 and Run 2 is that the curves are more erratic in Run 2 and there may be two reasons for this. Firstly, in Run 1, *A. wrightianum* indirectly moderates the curves via dampening of other species' abundances. Secondly, species with

a)



b)

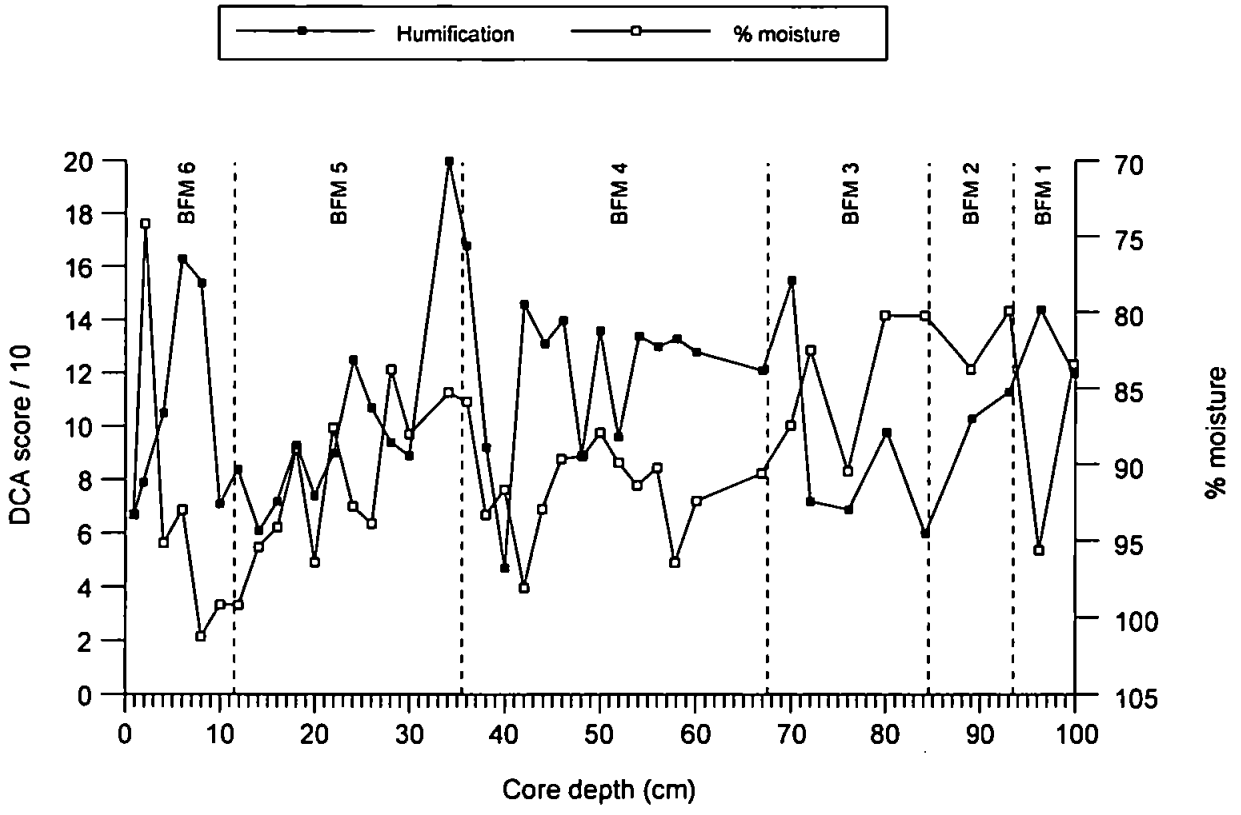


Figure 8.13 : Comparison of testate amoebae moisture curves with a) humification and b) DCA curves, Run 2.

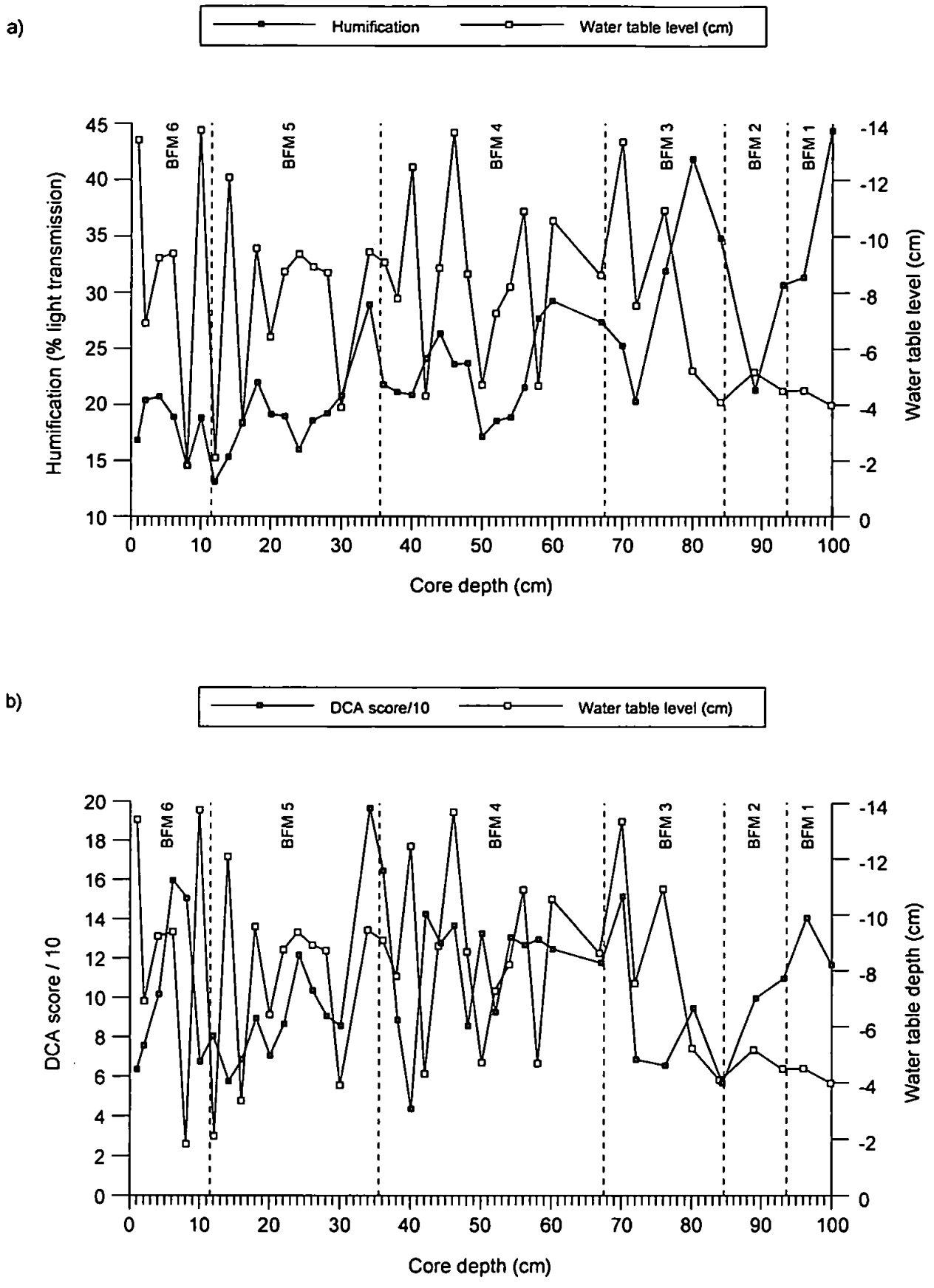


Figure 8.14 : Comparison of testate amoebae water table curves with a) humification and b) DCA curves, Run 2. For water table level, '0' indicates ground surface.

Zone	Testate amoebae curves	Peat humification curve	DCA axis 1 score.
BFM 6	Major swings in both curves. At top of BFM 6, water table is ca. 0.5cm higher than at base. For % moisture, content is ca. 7% lower at top of BFM 6 than at base. Suggests slight drying of bog surface.	Change to slightly drier conditions in bottom third of zone, then lesser shift than plant macrofossil diagram to wetter conditions in top 6cm of zone.	Marked reversal to dry surface conditions in mid-zone. Swing to wetter conditions follows, sustained to top of core.
BFM 5	Curves erratic. Moisture curve trending wetter. Again difficult to identify trend in water table curve.	Short, drier event at base of BFM5, then gradual progression to wetter conditions. Curve is erratic, but less so than for the plant macrofossil curve.	Begins dry, but sustained progression to wetter conditions, with less erratic curve than in preceding zones.
BFM 4	Water table curve increasingly erratic; moisture curve less so. Overall trend difficult to identify, but moisture curve shows slight reduction in wetness.	High-magnitude fluctuation in plant macrofossil curve not evident in peat humification curve. Wet events between 60-50cm and 44-40cm. Thereafter, trending slightly drier.	Wet event begins at 42 cm and peaks at 40 cm. Preceded by peat humification and testate amoebae curves.
mid-BFM 3 to top of BFM 3	Erratic curves but overall 1cm fall in water table and 1% fall in % moisture. Suggests unstable, but drying conditions.	Reversal to drier conditions at 72cm agress with water table curve but contradicts moisture curve.	Timing of wetter episode in general agreement with peat humification curve.
BFM 2 to mid-BFM 3	Erratic and conflicting curves. Continuation of BFM 1 for water table, which falls to -11cm depth. Overall increase (10%) in moisture content.	Humification curve infers progressively wetter conditions to mid-BFM 2. Thereafter, swing to drier conditions to bottom third of BFM 3, then reversal to wetter conditions to mid BFM 3.	Erratic fluctuations, but overall increase in wetness.
BFM 1	Slight lowering of water table (from -4 to -4.6cm). Rising moisture content, then reversal from 96% to 79.5% to top of zone. Suggests moderately wet conditions.	Humification curve infers a rapid transition to wetter surface conditions in lower two-thirds of zone. Top third of zone more stable.	Slight reduction in surface wetness. Top half of BFM 1 wetter.

Table 8.5: Comparison between the palaeohydrological trends shown in the testate amoebae, peat humification and plant macrofossil curves, Run 2.

a large tolerance range have been included in the data set for Run 2. Such species are normally considered to be poor palaeohydrological indicators because they cannot be used to derive precise water table depths and moisture content, and hence an accurate palaeohydrological reconstruction.

8.6.3 Run 3

For the third run, only species with a narrow tolerance range were used in the data set to reconstruct the palaeohydrological curves. Tolerance ranges were established for species beyond which they were considered too broad to be useful as palaeohydrological indicators. On the basis of the species' optima ranges for the modern British data set (Figures 6.13 and 6.14, pages 244 and 245), species with noticeably large tolerance ranges were excluded from the new data set. This resulted in the exclusion of six species in addition to *A. wrightianum*: *Hyalosphenia subflava, Nebela parvula, Difflugia angulostoma, Euglypha ciliata, D. rubescens,* and *B. indica*, leaving 17 species in the calibration data set.

The resulting palaeohydrological curves are shown in Figures 8.15 and 8.16 and are summarised in Table 8.6. Pearson's correlation coefficient demonstrates the variable effects of the filtering exercises on the reconstructed curves. While the fit between the DCA and the water table / moisture curves and between the humification / water table depth curves improved, the match between humification / moisture and between the water table depth / moisture curves was reduced.

The generally poor match between the curves, despite the removal of hydrologically less sensitive species, is unexpected and the reason is unclear. One explanation may be the different tolerance ranges for water table and moisture of individual species. Of the six excluded species, only three (*H. subflava, N. parvula* and *D. angulostoma*) had a wider tolerance range for moisture than water table. While excluding these species would have

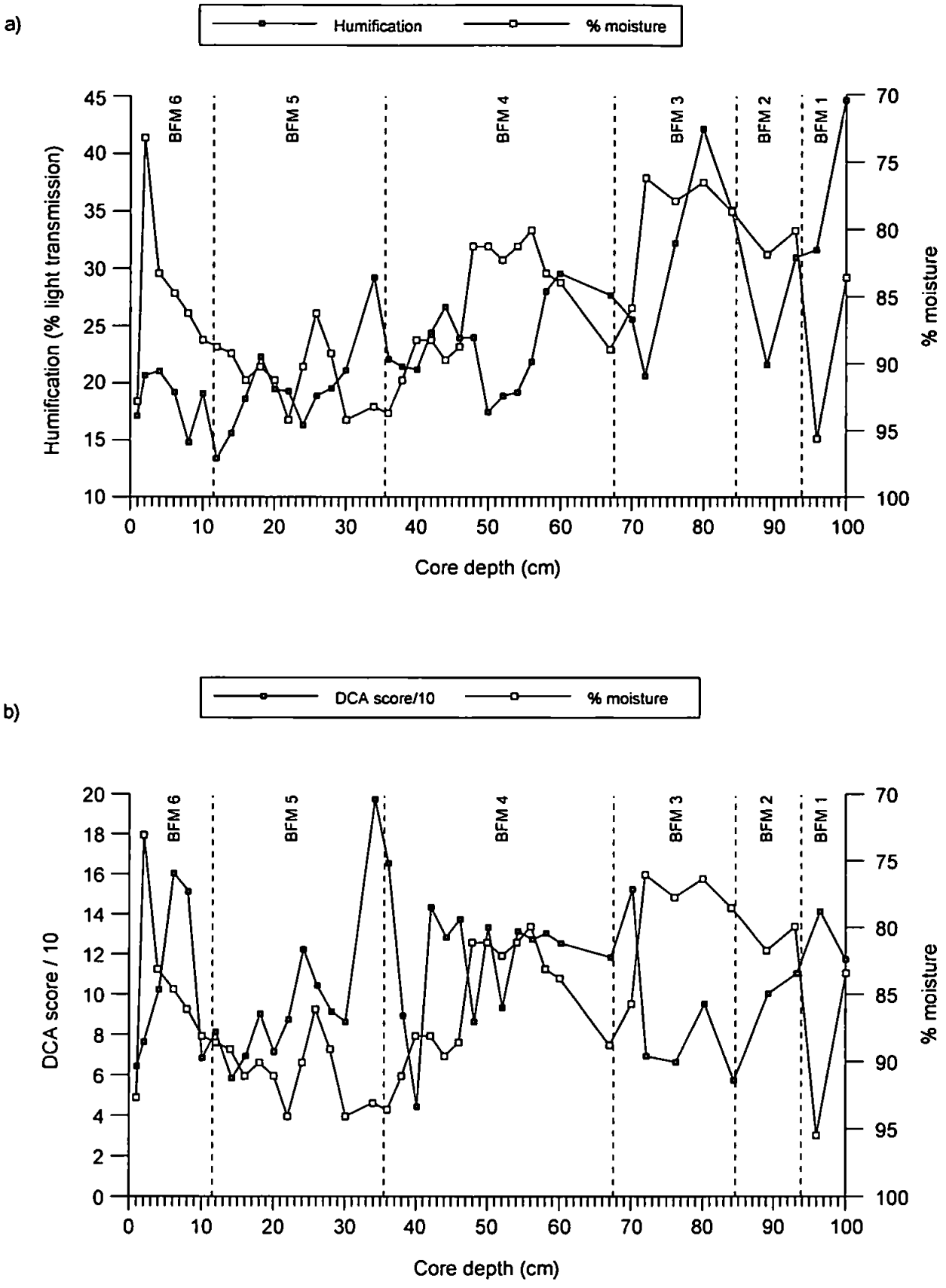


Figure 8.15 : Comparison of testate amoebae moisture curves with a) humification and b) DCA curves, Run 3.

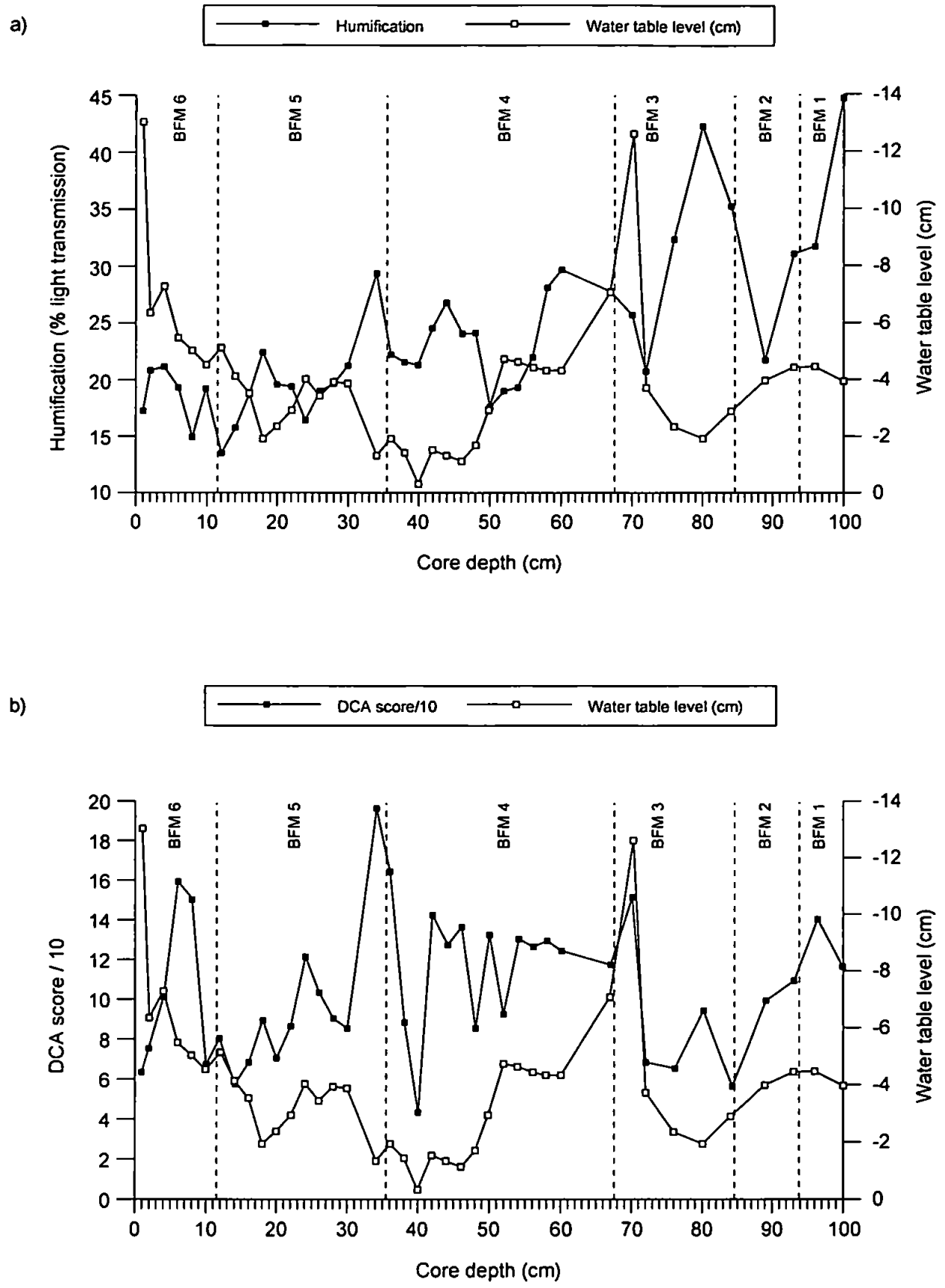


Figure 8.16 : Comparison of testate amoebae water table curves with a) humification and b) DCA curves, Run 3. For water table level, '0' indicates ground surface.

Zone	Testate amoebae curves	Peat humification curve	DCA axis 1 score.
B F M 6	Both curves show progressive dryness throughout zone. But conflicting curves in top 2cm. Water table drops, but moisture content rises.	Change to slightly drier conditions in bottom third of zone, then lesser shift than plant macrofossil diagram to wetter conditions in top 6cm of zone. Agrees with percent moisture curve.	Marked reversal to dry surface conditions in mid-zone. Swing to wetter conditions follows, sustained to top of core and agrees with percent moisture curve.
BFM 5	Water table curve trending drier. Moisture curve matches this. Drying episode at 26cm in moisture curve; more gradual and prolonged in water table curve.	Short, drier event at base of BFM5, then gradual progression to wetter conditions. Curve is erratic, but less so than for the plant macrofossil curve.	Begins dry, but sustained progression to wetter conditions, with less erratic curve than in preceding zones. Matches drying episode at 26cm.
BFM 4	Water table rises from -7 to -2cm, indicating progressively wet mire surface. Wetter conditions between 42-38cm. Moisture curve erratic; rises to 93% at top of zone.	High-magnitude fluctuation in plant macrofossil curve not evident in peat humification curve. Wet events between 60- 50cm and 44-40cm. Thereafter, trending slightly drier.	Wet event begins at 42 cm and peaks at 40 cm. Preceded by peat humification and testate amoebae curves.
mid-BFM 3 to top of BFM 3	Marked lowering of water table (from -4cm to -13cm) for most of zone. Top 2cm show 5cm rise in water table. Moisture content rises to 88% at top of zone.	Reversal to drier conditions at 72cm matches water table and DCA curves	Timing of drier reversal in general agreement with peat humification and water table curves.
BFM 2 to mid-BFM 3	Continuation of BFM 1. 2cm rise in water table to -2cm. Slight loss (3%) in moisture content continues to mid zone. Suggests moderately wet mire surface.	Humification curve infers progressively wetter conditions to mid-BFM 2. Thereafter, swing to drier conditions to bottom third of BFM 3, then reversal to wetter conditions to mid BFM 3.	Erratic fluctuations, but overall increase in wetness.
BFM 1	Slight lowering of water table (from -4 to -4.5cm), moisture content rises from 84% to 95%, then falls to top of zone. Suggests moderately wet conditions.	Humification curve infers a rapid transition to wetter surface conditions in lower two-thirds of zone. Top third of zone more stable.	Slight reduction in surface wetness. Top half of BFM 1 wetter.

Table 8.6: Comparison between the palaeohydrological trends shown in the testate amoebae, peat humification and plant macrofossil curves, Run 3.

removed noise in the moisture data set, removing the other three (*E. ciliata, D. rubescens* and *B. indica*) with smaller tolerance ranges for moisture than water table may have removed a valuable contribution to the moisture signal although, given these species' small contribution to the fossil assemblage, this is unlikely.

A second reason may be that the removal of *H. subflava*, which is a good indicator of dry conditions (Charman and Warner, 1992; Tolonen *et al.*, 1992) and reasonably abundant, has affected this reconstruction.

8.6.4 Run 4

For Run 4 (Figures 8.17, 8.18 and Table 8.7), only the 10 most hydrologically sensitive species (those with the smallest tolerance ranges for water table depth and percent moisture) were used. It was hoped that retaining 10 species would allow the most accurate hydrological indicators to be included in the data set without compromising its diversity. This filtering exercise resulted in the same mixed success as Run 3. While the correlation between the water table and moisture curves improved markedly and a better fit was achieved between the peat humification and water table depth curves compared to Runs 2 and 3 (Table 8.4), the match between the DCA and water table depth / moisture curves was little better than for Run 2 and none improved on the performance for Run 1.

Again, an explanation of these patterns is difficult, but Run 4 confirms that the reconstructions benefit from using the largest possible species assemblage. Restricting the testate amoebae assemblage to 10 species may have created noise in the data set, resulting in a particularly erratic water table curve, which matches very poorly with the plant macrofossils and peat humification curves.

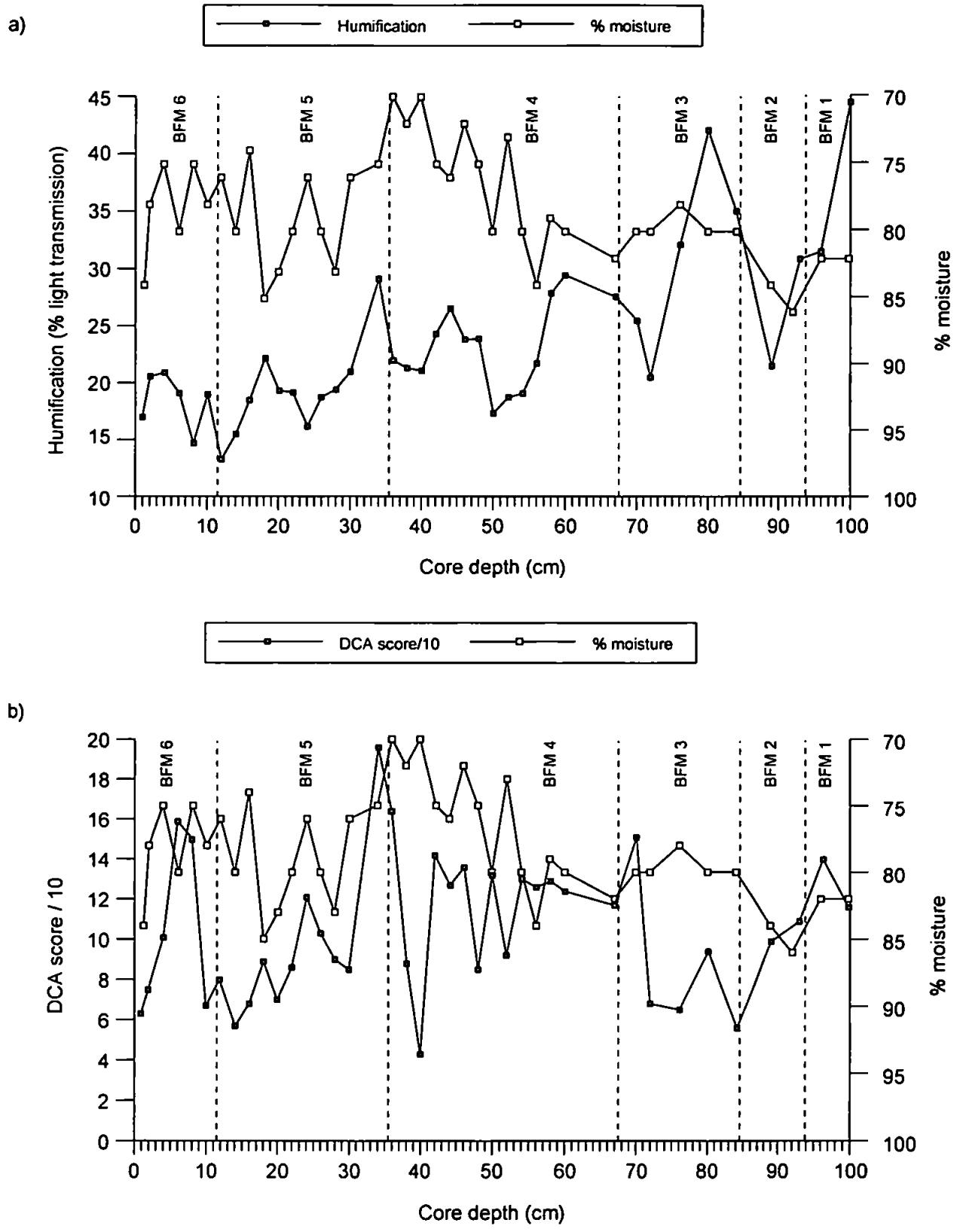


Figure 8.17 : Comparison of testate amoebae moisture curves with a) humification and b) DCA curves, Run 4.

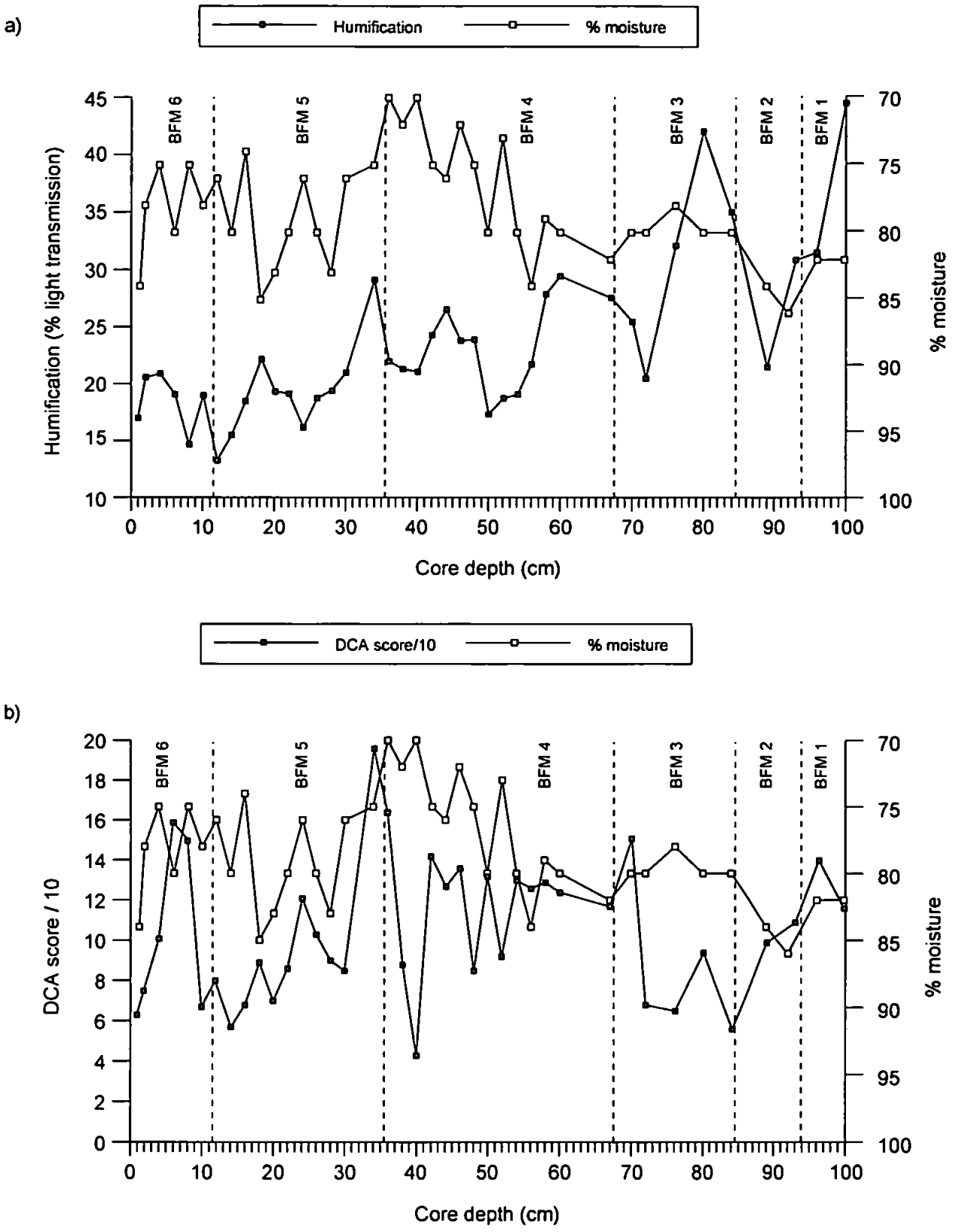


Figure 8.18 : Comparison of testate amoebae moisture curves with a) humification and b) DCA curves, Run 4.

Zone	Testate amoebae curves	Peat humification curve	DCA axis 1 score.
BFM 6	Major swings in both curves. At top of BFM 6, water table is ca. 9.5cm lower than at base. For % moisture, content is ca. 15% higher at top of BFM 6 than at base. Conflicting curves in top 2cm. Mosture infers wetter conditions, water table drier.	Change to slightly drier conditions in bottom third of zone. Lesser shift than plant macrofossil diagram to wetter conditions in top 6cm of zone, which agrees with moisture curve.	Marked reversal to dry surface conditions in mid-zone. Swing to wetter conditions follows, sustained to top of core and agrees with moisture curve.
BFM 5	Very erratic curves, but % moisture less erratic than water table curve. Difficult to identify overall trends.	Short, drier event at base of BFM5, then gradual progression to wetter conditions. Curve is erratic, but less so than for the plant macrofossil curve.	Begins dry, but sustained progression to wetter conditions, with less erratic curve than in preceding zones.
BFM 4	Erratic testate amoebae curves. Overall trend to drier conditions. No major wet shifts recorded.	High-magnitude fluctuation in plant macrofossil curve not evident in peat humification curve. Wet events between 60- 50cm and 44-40cm. Thereafter, trending slightly drier.	Wet event begins at 42 cm and peaks at 40 cm. Preceded by peat humification and testate amoebae curves.
mid-BFM 3 to top of BFM 3	Overall reversal to wetter conditions as water table rises to -4cm from -8cm and moisture content rises 5% to 82%.	Reversal to drier conditions at 72cm disagrees with testate moebae curves.	Timing of wetter episode in general agreement with peat humification curve.
BFM 2 to mid-BFM 3	ca. 4% drop in moisture and 5cm drop in water table. Overall reduction in surface wetness, matches peat humification curve better than DCA curve.	Humification curve infers progressively wetter conditions to mid-BFM 2. Thereafter, swing to drier conditions to bottom third of BFM 3, then reversal to wetter conditions to mid BFM 3.	Erratic fluctuations, but overall increase in wetness.
BFM 1	Slight raising of water table (from -6 to -4cm). Rising moisture content from 82% to 84% to top of zone. Suggests deterioration to wet conditions.	Humification curve infers a rapid transition to wetter surface conditions in lower two-thirds of zone. Top third of zone more stable.	Slight reduction in surface wetness. Top half of BFM 1 wetter.

Table 8.7: Comparison between the palaeohydrological trends shown in the testate amoebae, peat humification and plant macrofossil curves, Run 4.

8.6.5 Overview of all filtering exercises

A better match was consistently achieved between the testate amoebae and humification curves compared to the DCA curve in all four filtering exercises (Table 8.4). Given the caveats detailed above and the fact that this is the first comparison of testate amoebae reconstructions with those from other surface wetness records, definitive statements on the accuracy of the testate amoebae, peat humification and plant macrofossil curves cannot be made. However, the consistently poor match between the plant macrofossil and testate amoebae curves is a significant issue that requires further investigation.

A possible explanation for the poor performance is that the testate amoebae curves are actually giving a more accurate reflection of palaeohydrological changes than the plant macrofossils and that this reflects the restricted plant macrofossil assemblage. This is supported by the correlation coefficients for the peat humification and testate amoebae curves which, with the exception of water table depth in Runs 2 and 3, are consistently higher than between the DCA and peat humification curves. This underlines the importance of multi-proxy palaeoclimate reconstructions, where the use of a third source of evidence may clarify conflicting signals between two records. However, to accept such a statement would require far more exhaustive individual tests of the performance of plant macrofossil and testate amoebae reconstructions based on comparisons with instrumental records than are possible in the present study.

Given the match that was achieved by Barber *et al.* (1994d) with the climate response model, plant macrofossils are unlikely to be inaccurate, but it is equally unlikely that both the testate amoebae and peat humification are giving an inaccurate signal. Further work is clearly needed to resolve this issue.

8.6.6 Detailed analysis of the palaeohydrological curves derived from testate amoebae in Run 1

Figures 8.11, 8.12 and Table 8.3 all describe the palaeohydrological trends at Bolton Fell Moss derived from testate amoebae in Run 1. To give a detailed description in this section would unnecessarily duplicate this information. Instead, this section uses the palaeohydrological curves derived from testate amoebae to interpret unclear aspects of the plant macrofossil and humification curves which were identified in section 8.3.3. It will investigate:

a. "noisy" areas of the plant macrofossil record

b. differences in relative timings of events in the palaeohydrological curves and the reversal to wetter conditions at 42 cm

c. the local extinction of *S. imbricatum*

d. areas of the core where discrepancies exist between the palaeohydrological curves

e. conflicting signals between the testate amoebae curves.

a) Noisy areas of the plant macrofossil record

Section 8.3.3 suggested that rapid and frequent fluctuations of the palaeohydrological curve derived from DCA analysis of the plant macrofossils may result from the replacement of one species by another in a species-poor assemblage. A gradual (rather than sudden) hydrological change that led ultimately to a sudden change in species composition was suggested as a possible mechanism. Between 48 cm and 36 cm, the testate amoebae curves for both water table depth and moisture support this interpretation. The plant macrofossil curve mirrors the marked fluctuations in the relative abundances of monocots, S.s.Acutifolia and *S. magellanicum*, which all dominate the assemblage in this extract. The water table and moisture curves, although agreeing with the general trend in the plant macrofossil curve, indicate less dramatic fluctuations in mire surface wetness. This suggests that the water table depth and moisture reconstructions have benefited from a more diverse testate

amoebae species assemblage. But because the plant macrofossil curve cannot be expressed in the same units as the testate amoebae curve, definitive statements regarding the advantages of the diverse testate amoebae assemblages cannot be made.

b) Differences in relative timings and the reversal to wetter conditions at 42 cm depth

Section 8.4.5 described how the major ecological change in the plant macrofossil assemblage at 42 cm was preceded by the testate amoebae assemblage at 48 cm. Furthermore, the peat humification curve places this reversal at 44 cm (Figures 8.11 and 8.12). This timing difference was translated into the palaeohydrological curves (Figures 8.11 and 8.12) and may again be explained by relative species diversity, since the water table depth, moisture and humification curves all indicate a more gradual progression to wetter conditions than suggested by the plant macrofossil curve. It is likely, therefore, that a gradual change to a wetter mire surface caused a sudden change in the plant macrofossil assemblage and that subtle, earlier signals indicating a more gradual change to wetter conditions which might have been provided by a more diverse plant macrofossil assemblage were absent.

In Figure 8.11, although the humification curve shows a generally similar trend to the moisture curve, it appears to lag behind the moisture curve by approximately 2-4 cm for most of the profile. This pattern is less clear in the erratic water table curve. The lag suggests that testate amoebae respond to surface moisture changes more rapidly than humification. Since peat comprises vegetation matter, the delay may be caused by the naturally longer life span of plants compared to testate amoebae, so that turnover is much slower and vegetation matter takes longer to be incorporated into the peat deposit than empty testate amoebae tests. The rapid population doubling time of testate amoebae has already been highlighted (Lousier, 1984a,b and see page 65 of this thesis) and it is therefore probable that population turnover is equally rapid.

c) The local extinction of S. imbricatum (ca. 45 cm)

At 45 cm *S. imbricatum*, formerly the dominant component of the plant macrofossil assemblage at Bolton Fell Moss, becomes extinct and is replaced in the assemblage by *S. magellanicum* and, to a lesser extent, S.s. Cuspidata. At this time, the testate amoebae indicate an increasingly wetter mire surface, which is reflected in the moisture and water table curves. Although the testate amoebae curves reverse to drier conditions at 40 cm, the mire surface is, if anything, slightly wetter than during the pre-*S. imbricatum* decline. On the evidence of testate amoebae at least, the local extinction of *S. imbricatum* at Bolton Fell Moss cannot be attributed to falling water tables, as suggested by Green (1968; section 2.3.2, page 25, of this thesis). A more likely explanation at this site would be that *S. imbricatum* has been out-competed by *S. magellanicum*, perhaps encouraged by a rise in water tables. This would support the theory forwarded by Stoneman *et al.* (1993; page 25 of this thesis).

d) Discrepancies between the palaeohydrological curves

Although encouraging matches were achieved between the reconstructed curves in Run 1, none attained a perfect correlation. This, in part, reflects disagreements between the curves over the direction of palaeohydrological changes. It may also reflect differences in the magnitude of changes, but without a common scale for all curves, it is difficult to comment further on this.

For the water table depth, moisture and humification curves, there are clear directional differences. Where the humification curve implies a reversal to drier conditions, the water table curve suggests that the change is to wetter conditions (Figure 8.12). This occurs across the BFM 3 - BFM 4 boundary (72 - 58 cm) and across the BFM 5 - BFM 6 boundary (20 - 8 cm). The peat humification curve is probably giving a more representative record of mire surface conditions than the testate amoebae curves, given the agreement

between the humification and plant macrofossil curves at these depths (Figure 8.3). The misleading information from the testate amoebae may be a function of different test morphologies within the assemblage. *Amphitrema flavum* is an important component of the testate amoebae assemblage at these depths. The species is relatively small (50-75µm: Grospietsch, 1958; 45-77µm: Corbet, 1973; 45-70µm: this study) and would easily fit into the shrinking water films surrounding *Sphagnum* leaves as the mire surface began to desiccate. Thus, it is possible to juxtapose a testate amoebae assemblage dominated by a hydrophilous species with a gradually drying humification curve and one must be cautious of making over-simplified interpretations from the testate amoebae curves.

The directional differences between the moisture and humification curves are likely to be a result of the lag created by the slower incorporation of hydrological information into the stratigraphic record relative to testate amoebae (see section b, above). However, these differences should not be overstated since they are generally only minor disagreements and often occur over a very small number of samples. Hence, they may also be accounted for by errors inherent in either or both methodologies.

e) Conflicting signals between the testate amoebae curves

Aside from differences between the plant macrofossil, peat humification and testate amoebae curves, are discrepancies between the water table and moisture curves derived from testate amoebae. These are most obvious within BFM 5 (Figure 8.9) and are expressed as differences in the direction and magnitude of change. The erratic nature of the water table curve (which may reflect a naturally more variable water table) creates difficulties in identifying an overall trend for this variable, but the moisture curve suggests a gradual increase in surface wetness throughout the zone.

Peaks of surface wetness in the water table curve (for example, at 32 cm and 22 cm) are expressed by the moisture curve as continued decreases in surface wetness. This may reflect differences in species' optima for water table depth and moisture. For example, at 30 cm the assemblage is dominated by *A. flavum*, with *A. discoides* as an important component. Table 6.10 (page 254) ranked *A. flavum* 11th in terms of water table depth, but 30th for moisture content (which further suggests that this species can survive in restricted water films); *A. discoides* was ranked 1st and 6th respectively. One might, therefore, reasonably expect a reconstructed moisture value derived from an assemblage of this composition to be 'drier' than a water table value and this has probably occurred at 32 and 22 cm depth.

At the top of BFM 6, the reconstructed curves again diverge (Figure 8.12). This time, the falling water table is simultaneous with rising moisture, contrasting with BFM 5. There may be two reasons for this. Firstly, the top of BFM 6 probably comprises the living testate amoebae assemblage and may be affected by downwashing of empty tests, so that the resulting curves are not strictly fossil (see section 8.4.4.). Secondly, approximately 60% of the assemblage at 2 cm depth, where the signals diverge, are species with a low water table ranking and high moisture ranking, such as *Heleopera petricola, Difflugia penardi, D. angulostoma, Centropyxis aerophila and Placocista spinosa* (Table 6.10, page 254). Derived reconstructions from this assemblage are therefore expected to be wetter for moisture than water table depth.

8.6.7 Summary of the detailed analysis

The palaeohydrological reconstructions from testate amoebae at Bolton Fell Moss clearly benefited from a diverse species assemblage and very little improvement was gained by restricting the assemblage to species that were perceived as better hydrological indicators.

Although testate amoebae were able to clarify directional differences between the plant macrofossil and peat humification curves, the absence of a standard unit of measurement for the curves presented problems in identifying and interpreting differences in the magnitude of these changes.

The curves derived from testate amoebae provided additional information on environmental conditions surrounding the local extinction of *S. imbricatum* at Bolton Fell Moss. The reconstructions suggest that a falling water table was probably not responsible for the species' demise. If anything, the water table rose during this period. The alternative theory (which cannot be investigated by testate amoebae analysis) of the species being out-competed by the faster-growing *S. magellanicum* may be more appropriate at this site.

The differences in relative timings of hydrological changes in the core extract can be attributed to two possible causes. Firstly, there is the faster turnover of testate amoebae compared with plant macrofossils and peat humification. Corroborating this theory would require comparisons of the relative palaeohydrological changes derived from testate amoebae and plant macrofossils with instrumental records. Secondly, the sudden reversal to wet conditions at 42 cm in the plant macrofossil curve was shown to post-date a more gradual change to wetter conditions in the testate amoebae curves. The poor diversity of the plant macrofossil assemblage gave the impression of a sudden hydrological change. In reality, the change was probably gradual, as expressed in the testate amoebae curves.

Differences in individual species' water table depth and moisture rankings were responsible for conflicting curves in the testate amoebae reconstructions. This could prove problematical for palaeoenvironmental reconstructions, but could be overcome if testate amoebae are used in multi-proxy palaeoclimate reconstructions and if the assemblages are carefully interpreted using full information on species' modern ecology. This type of data

may have the potential to indicate variation in oceanicity of climate since high water tables and relatively low moisture content could be considered as indicating strongly seasonal climates, while high water tables and high moisture content would be more indicative of an oceanic climate. This idea would require further sampling and analysis of a greater range of samples covering the continental-oceanic climate gradient.

8.7 Using independent palaeohydrological records to validate the curves

The reconstructed curves from testate amoebae, plant macrofossils and peat humification analysis all originate from the same peat profile. While this provides a good comparison of the methods themselves, it does not assess the climatic relationships of any of the curves. Although the climate response model of Barber *et al.* (1994a) demonstrated a good fit between climate and the DCA curve, the testate amoebae curves attained a better match with the peat humification curve. An independent palaeoclimatic record is therefore required to provide an additional comparison for testate amoebae curves. Such a record may confirm the magnitude and direction of palaeohydrological changes for which the reconstructed curves disagree at present. However, such an interpretation depends on the direct peatland-climate link being accepted.

The closest meteorological station to Bolton Fell Moss with a long run of data is located at Carlisle, Cumbria. Continuous rainfall records extend only to 1864 (University of East Anglia, 1992), so alternative records must be sought to cover at least the section of the profile studied. There are three other potential sources of information that can be used as independent checks on the curves: from dendroclimatological records (Briffa *et al.*, 1988), estimated rainfall trends (Lamb, 1977a), winter severity/summer wetness indices (Lamb, 1977b), and from palaeohydrological curves produced for other raised mires (Barber *et al.*, 1994d).

Numerous attempts were made to obtain precipitation records from dendroclimatological sources. But, after consultation with dendroclimatological researchers who stated that there are no precipitation records from dendroclimatology for Britain from 1500BP (M. Bridges; K. Briffa; V. Hall; J. Pilcher, pers. comm.), this was abandoned. This absence is probably due to insufficient precipitation stresses on trees in Britain (R. Newnham, pers. com.); attempts by researchers at the Queen's University of Belfast to obtain precipitation signals from Irish oaks have yielded poor results (J. Spain; V. Hall, pers. com.).

Dendroclimatological records of summer temperatures (April - August) in Fennoscandia have been produced by Briffa *et al.* (1990) which extend back to ca AD 400 (1480BP) and are based on tree ring widths. Summer temperatures would be of most use to this comparative exercise since April to August is the main growing season for mire vegetation in Britain (Barber, 1981), when vegetation might reasonably be expected to be more sensitive to climate fluctuations. However, Briffa *et al.* (1993, p.86) suggest that, for tree ring widths, "warm season temperatures are the most atypical of seasonal averages" and that "inferring annual climate change on the basis of summer responsive data is therefore highly questionable regardless of spatial scale". In view of these reservations, the Fennoscandian records cannot be applied with great confidence to this study.

Variations in latewood density have been shown to produce clearer palaeoclimate data than tree ring widths (Schweingruber, 1976; Conkey, 1979). A set of summer temperature reconstructions exists for Europe based on maximum latewood density indices of conifers (Briffa *et al.*, 1988) and these will be used as an alternative to those derived from tree ring widths. But, for two reasons, these records must be used with great caution in this study. Firstly, the reconstructions are for temperature only and direct links cannot be presumed between temperature and mire surface wetness. Secondly, the temperature reconstructions apply to the whole of Europe. Only four sites from Britain were used by Briffa *et al.* (1988)

and all are located in central and northern Scotland. Again, this excludes their use as a definitive test of the palaeohydrological reconstructions for Bolton Fell Moss. The temperature reconstructions can, however, be used as a general comparison and it is in this context that they will be used in this study.

Barber (1981) compared the stratigraphical record from Bolton Fell Moss with independent climatic records from Lamb (1977a,b) and the data which he used are also of value to this study. The 100 cm profile from which the testate amoebae palaeohydrological curves are derived represents approximately 1500 years' accumulation (Barber *et al.*, 1994a) and since Lamb (1977a,b) has produced estimates of average rainfall over England and Wales since AD 1100 (850BP) and summer wetness/winter severity indices for Europe from AD 800 (1150BP) to AD 1960, detailed comparisons can be made for the top 60 cm of the core.

Palaeohydrological curves derived from DCA of plant macrofossils have also been produced under the NERC palaeoclimate special topic for Mongan Bog, Co. Offaly and Abbeyknockmoy Bog, Co. Galway (Barber *et al.*, 1994d) and they cover the accumulation period represented at Bolton Fell Moss. They have the advantage of being derived from the same numerical treatment of plant macrofossil data as Bolton Fell Moss and can therefore be used for direct comparison with the plant macrofossil record from Bolton Fell Moss.

Table 8.8 summarises the main climate trends for the last 1500 years derived from the sources listed above. These records can help to clarify and assess the importance of three main features of the reconstructed palaeohydrological curves for Bolton Fell Moss - the major change to wetter conditions timed by the plant macrofossil curve at 42 cm, but preceded by the testate amoebae curves; the erratic behaviour of the water table curve in BFM 5; and the disagreements in the direction of hydrological change in the water table / moisture curves in the top 2 cm of BFM 6.

Depth/date	Testate amoebae/ plant macrofossils/ peat humification curves.	Winter severity/summer wetness indices (Lamb, 1977)	Estimated annual rainfall (Lamb, 1977).	Dendroclimatology records from Fennoscandia (Briffa *et al.* 1990).	Palaeohydrological curves from other ombrotrophic bogs (Barber *et al.* 1994d)
BFM 6 (230-0BP; AD1720-present)	Drying in water table curve. Increased wetness in other curves.	Excess of wet summers and colder temperatures to AD1850. Thereafter no unusual climate identified.	Increasing rainfall from AD1780 onwards.	Warm periods AD1750-1780; 1840-1860. Cool periods 1800-1820.	Mongan Bog: dry, but deteriorating to wetter conditions. Abbeyknockmoy Bog: wet, but rapidly drying bog surface.
BFM 5 (690-230BP; AD1260-1720).	Continued reduction in surface wetness. Erratic testate amoebae water table curve.	Excess of wet summers AD 1320-1500 & 1560 - 1850. These periods also colder in winter & summer.	Wet at beginning (105% of anuual 1916-1950 means); from AD 1270 rainfall decreases.	Cool periods AD1330-1360; 1570-1620. Warm periods AD1400-1440; 1540-1570.	After reversal to wetter conditions, drier conditions resume. Erratic curves.
BFM 4 (ca. 950 - 690BP; ca. AD1000-1260).	Major phase-shift to wetter conditions in plant macrofossils at 880BP (AD 1100). Thereafter reversal to drier conditions.	No unusual climate identified.	Deterioration in climate as rainfall totals ca. 100% of 1916-1950 mean).	Cyclic changes. Cooling to ca.AD1140, rapid warming to ca. AD1160, return to rapid cooling AD 1160-1210. No evidence for Medieval warm epoch.	Mongan Bog: slightly drier; Abbeyknockmoy Bog: one of driest phases.
mid-top BFM 3 (ca. AD1000; 950BP).	Reversal to drier conditions, then second reversal to wetter conditions.	Excess of wet summers.	Slightly wetter than preceding phase.	Warm temperatures AD 960-1000.	Mongan Bog: one of wettest events. Abbeyknockmoy Bog: turning drier after one of wettests periods in record.
BFM 1-mid BFM 3 (AD 800-ca.1000; 1150-ca.950BP).	Moisture curve shows progression to drier conditions. Other curves show progression to wetter conditions.	Excess of wet summers. No severe winters.	Moderately wet (92% of 1916-1950 mean), becoming slightly wetter.	Cool conditions AD 780-830; 850-870. Warming to 1000AD.	Erratic curves, but overall wet. Slight decrease in surface wetness in BFM 2 at Mongan Bog.

Table 8.8: Comparison of the main palaeohydrological trends shown by reconstructed palaeohydrological curves for Bolton Fell Moss and independent palaeohydrological records.

a) Reversal to wetter conditions at approximately 42 cm

From the age-depth model for Bolton Fell Moss (Barber *et al.*, 1994a), 42 cm depth is estimated to be AD 1200 (750 BP). The DCA curve from Abbeyknockmoy Bog (Barber *et al.* (1994d) shows a reversal to wetter surface conditions at AD 750 which is as dramatic as that at Bolton Fell Moss (Figure 8.19a). The equivalent curve for Mongan Bog (Figure 8.19b), however, contradicts this and implies a rapid shift to a drier mire surface. These two records are obviously of little use in confirming contemporary events at Bolton Fell Moss.

Lamb's indices (1977b), however, fail to identify any sudden climate changes. Further, estimated rainfall (Lamb, 1977a) rose gradually from 85% to 102% of the 1916-50 means in England and Wales between AD 1050-1200 (900-750BP). This pattern supports the gradual deterioration presented by the testate amoebae, which started at 48 cm (ca. AD 1050), and suggests that the sudden change in the DCA curve for Bolton Fell Moss (and Abbeyknockmoy Bog) is a product of restricted species diversity.

This behaviour supports the use of multi-proxy techniques in palaeohydrological reconstructions. The delay between the reversals shown in the testate amoebae and plant macrofossil curves is a reflection of the real world, where a gradual deterioration of climate over a number of years - perhaps decades - would have occurred, rather than within the short time-scale implied by the DCA curve.

b) Erratic water table curve in BFM 5.

BFM 5 (35 -11 cm) covers approximately 450 years accumulation from ca. AD 1270 to 1720 (ca. 680-230BP). The erratic water table curve in BFM 5 is also evident in the contemporary DCA curve from Mongan Bog (Figure 8.19a) but absent from Abbeyknockmoy Bog (Figure 8.19b). The summer wetness/winter severity indices,

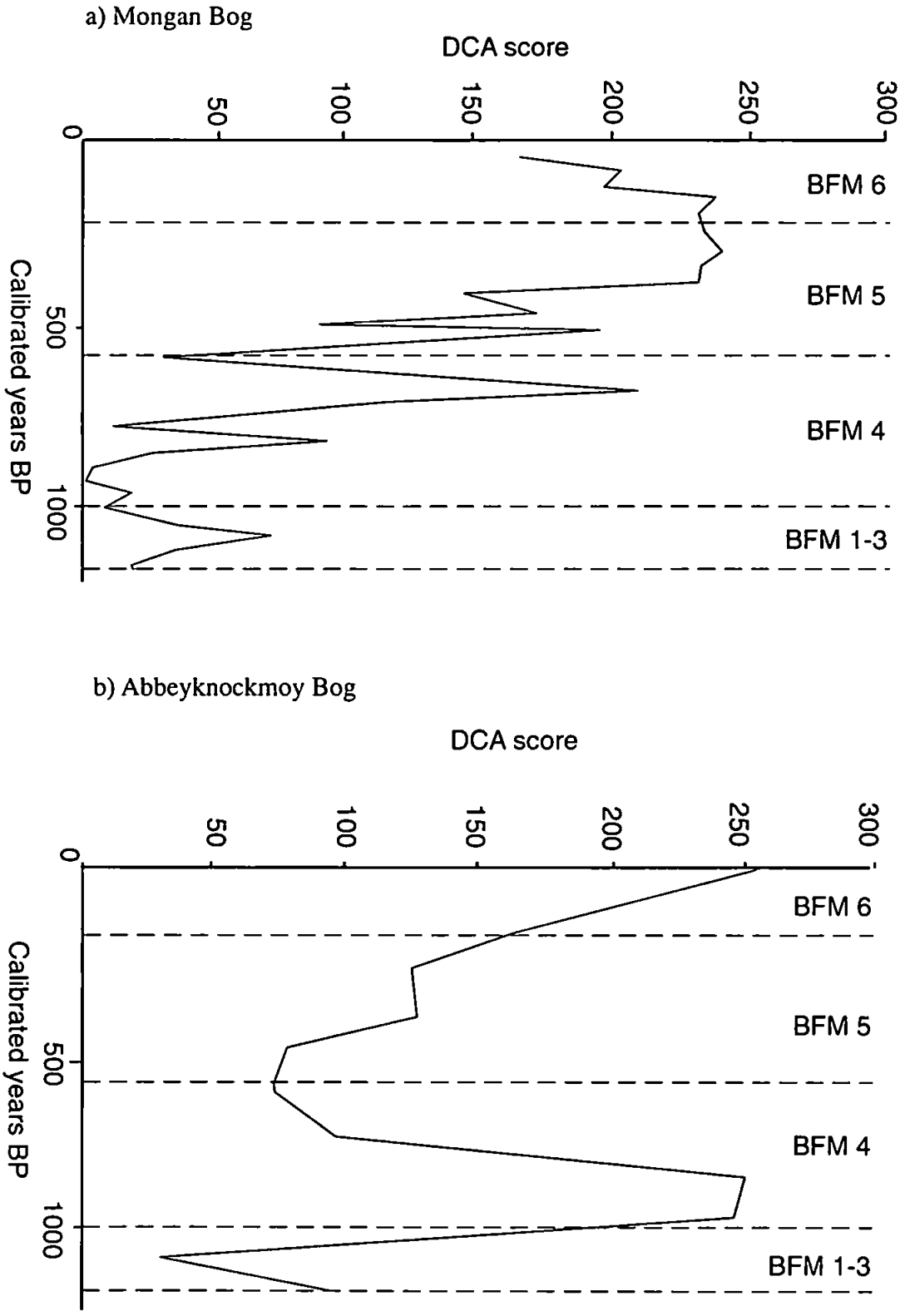


Figure 8.19: Palaeohydrological curve derived from DCA of plant macrofossils for (a) Mongan Bog and (b) Abbeyknockmoy Bog, Ireland. Redrawn from Barber *et al.* (1994d). Testate amoebae zones (BFM1-BFM6) based on accumulation rates of Barber *et al.* (1994a) for Bolton Fell Moss.

estimated rainfall and estimated temperatures from Lamb (1977a,b) also show fluctuations in climatic behaviour during BFM 5 of a similar magnitude to the water table curve.

The major events in the water table curve within BFM 5 - extreme surface wetness at 30 cm and dryness at 22 cm - have variable agreement between the other palaeohydrological records. The age-depth model of Barber *et al.* (1994a), places 30 cm at approximately AD 1350 (600BP). The contemporary DCA curves from both Abbeyknockmoy and Mongan Bogs concur with the peak in surface wetness for Bolton Fell Moss derived from testate amoebae. The estimated temperatures from Lamb (1977a), which fall from approximately 10°C at AD 1280 to approximately 9°C at AD 1420, indirectly support this increased wetness. Lower air temperatures would have reduced evapotranspiration rates, so contributing to a wetter mire surface. Estimated rainfall totals for the period, however, are 95% of the 1916-50 average (Lamb, 1977a), although a lower temperature may have lowered evapotranspiration rates and therefore have offset the effects of reduced rainfall to maintain surface wetness.

The dry event in the testate amoebae water table curve at 22 cm can be placed at AD 1450 (500 BP; Barber *et al.*, 1994a). There is less agreement in the other palaeoclimate records for this event than for the preceding wet peak. At Mongan and Abbeyknockmoy Bogs, the DCA curves show a moderately wet mire surface. Estimated rainfall is only 1% lower and temperatures less than one degree centigrade lower than during the wet peak at AD 1350 (600 BP). It is likely, therefore, that the moisture curve is more representative than the water table curve of conditions on the mire surface at this time.

c) Conflicting palaeohydrological signals in the top 2 cm of the profile.

The final discrepancy - the conflicting palaeohydrological trends which occur in the top 2 cm of the profile - is resolved by collating the independent climate records. Table 8.8

shows that the deterioration to wetter conditions shown by the plant macrofossil, humification and moisture curves is supported by the independent palaeoclimate data. The winter severity/summer wetness indices imply wet summers and colder temperatures up to 1850 AD, whereafter no extraordinary climate events are identified. The estimated rainfall further supports this, showing an increase in annual totals from 1750 AD onwards. The palaeohydrological curve from Mongan Bog is also in agreement with the general trend, beginning dry, but showing a general deterioration to wetter surface conditions.

The record from Abbeyknockmoy Bog, however, is in agreement with the deepening water table derived from testate amoebae analysis at Bolton Fell Moss, showing a continuation of drier conditions to the present bog surface (Barber, 1994d). This trend is against the known climate and that inferred by the other palaeohydrological curves. This drying may arise from human activity, particularly drainage for agricultural improvement in the mire's vicinity, but the causes are not forwarded in Barber (1994d). For the testate amoebae water table curve, the direction may be a result of the transition from fossil to modern faunal assemblages, it was noted above that the present bog surface had desiccated and a migration of hydrophilous testate amoebae species to lower parts of the *Sphagnum* plant may have occurred, leaving an assemblage dominated by xerophilous species. This desiccation is supported in part by the moisture curve which, although showing an increase in moisture content in the upper 2 cm of the profile, is still indicative of only mediocre wetness in comparison with the much wetter events shown by the moisture curve for deeper parts of the core.

8.8 Conclusions

In the light of the material presented above, the following conclusions can be drawn with reference to the four objectives that were set out in section 8.3.3:

a) Testate amoebae may give greater resolution in relatively insensitive parts of the plant macrofossil record

Testate amoebae have provided more detailed resolutions in parts of the profile where other techniques failed to yield detailed palaeohydrological information. This was particularly evident in areas of the plant macrofossil record that were characterised by a species-poor assemblage, in which monocotyledons or *S. imbricatum* / *Sphagnum* s. Cuspidata were dominant.

b) Testate amoebae may clarify signals from noisy areas of the plant macrofossil record

Where the plant macrofossil and peat humification curves were noisy, testate amoebae were able to present a smoother reconstruction of surface wetness. This was believed to be the result of greater diversity in the testate amoebae assemblage and was most effective in investigating the sudden reversal to wetter conditions in the plant macrofossil record. Here, an ecologically more realistic gradual change to wetter conditions (which is supported by independent palaeoclimate evidence) was derived from testate amoebae.

c) Testate amoebae can be used to investigate further the sudden replacement of S. imbricatum by S. magellanicum

The water table and moisture curves derived from testate amoebae suggest that increased mire surface dryness was not responsible for the local extinction of *S. imbricatum*. If anything, the mire surface was wetter during the species' demise. Rather, out-competing by a faster-growing species such as *S. magellanicum*, encouraged by a rising water table, was probably responsible for the demise of *S. imbricatum*.

d) Testate amoebae can give a meaningful, quantitative scale to changes recorded in peat stratigraphy in terms of water table depth and moisture content.

Using testate amoebae, it was possible to express changes in mire surface wetness in terms of water table depth and moisture content. Direct comparisons between these curves and those derived from humification and plant macrofossils were hampered, however, by the absence of real values for the latter. While the direction of changes could be easily compared, their magnitude could not and this prevented a full analysis of palaeoclimatic information from the respective curves.

In wider terms, and even at this preliminary stage, the application of testate amoebae analysis to the core from Bolton Fell Moss has further emphasised the need for multi-proxy palaeoclimate investigations. This was illustrated particularly well by conflicting signals between the water table and moisture curves in the upper sections of the core which could only be unravelled by reference to other palaeoclimate records. The conflicting signals serve as a warning against making over-simplified interpretations from testate amoebae - a warning that applies equally well to any line of palaeoenvironmental evidence.

Part Four

Conclusion

Chapter 9

Conclusion

9.0 Introduction

This concluding chapter aims to synthesise the information presented in this thesis and has been divided into three main sections. The first section summarises and evaluates the main findings of the research in terms of the original hypotheses set out in section 1.1. Following this is a discussion of the main problems that were encountered in the study and the implications for testate amoebae analysis as a palaeoecological technique. Finally, there is a consideration of the potential for .future research into testate amoebae analysis and its contribution to multi-proxy palaeohydrological research on peatlands.

9.1 Testate amoebae and peatland hydrology

Section 1.1 presented two hypotheses, which were subsequently explored in this study:

1. hydrology (expressed variously as depth to water table or percent moisture content) is the most important influence on modern testate amoebae distribution.

2. this relationship can be used to reconstruct palaeohydrological curves from testate amoebae for British ombrotrophic mires.

9.1.1 Modern testate amoebae and peatland hydrology

a) The hypothesis

The study aimed to address the first hypothesis by quantifying the modern relationship between peatland testate amoebae and hydrological conditions in Britain. This has been achieved at two scales. Firstly, detailed mire hydrology and water chemistry data were related to testate amoebae populations at a single site (Tor Royal, Dartmoor). Ordination

by CCA demonstrated a clear relationship between species composition and hydrological parameters and showed that mean annual water table and percent moisture content are representative measures of these influences. Secondly, testate amoebae and hydrological data collected from a total of 163 samples from nine British mire sites were used to calculate hydrological optima (expressed as water table depth and % moisture content) using weighted averaging regression (WA) for 38 common testate amoebae species. The ordination and weighted averaging results both provided strong corroborating evidence for water availability as the most important influence on modern testate amoebae distribution on peatlands in Britain.

Further, this study has confirmed previous suggestions (Tolonen *et al.* 1992; Charman and Warner, 1992) that modern testate amoebae have hydrological optima and tolerances that can be clearly quantified. From these optima it is possible to rank the species and identify those that are indicative of drier or wetter conditions on the surface of ombrotrophic mires in Britain. The quantification of these optima is the crucial first step in the use of testate amoebae as palaeohydrological indicators. This study has provided this quantitative information.

The optima in Chapter 7 accord very well with similar work conducted in Finland (Tolonen *et al.*, 1992) and Canada (Tolonen *et al.*, 1985; Warner, 1987; 1988; 1989; Charman and Warner, 1992), although Chapter 7 suggested that differences between hydrological rankings for species in the Canadian and British data sets may be attributed to the continental setting of the mires used in the Canadian studies.

Although an important influence at a single site (Tor Royal), water chemistry did not significantly influence testate amoebae distribution in the modern British data set. This may reflect the restricted range of chemical ions that were sampled and may have ignored ions

that have a stronger influence on testate amoebae distribution. It is suggested, therefore, that more detailed work should be carried out on the relationship between testate amoebae and a wider range of chemical ions. This is discussed further in section 9.3 with regard to future work in testate amoebae analysis.

b) The representativeness of single-shot samples

An important issue to be addressed in the quantification of the species' optima was the representativeness of single samples of (principally) mean water table depth, percent moisture content and, as an important first step in the examination of the future potential of testate amoebae as palaeochemical indicators, mean chemical ion concentration. The hydrological monitoring programme at Tor Royal showed that individual seasons could be identified as most representative of annual hydrological conditions at an individual site. For Tor Royal, a single sample taken in autumn/winter would be most representative of that year's mean hydrological conditions. Although all measures (with the exception of summer 1993) were shown by ordination to have a similar influence on testate amoebae assemblages, the influence of unusual seasonal hydrological conditions in studies where hydrological data for one year only are used was illustrated clearly by the comparatively dry summer of 1993. Thus, sampling in exceptionally dry summers, such as 1976 and 1995 might give spurious results. Although mean annual water table depth is the most logical measurement to use and is directly comparable with other studies, sampling from sites where a long run of hydrological data exist is crucial to minimise the distorting influence of unusual climate events on calculated species optima.

c) Performance of field and laboratory techniques

No previous study of this type into the relationship between testate amoebae and hydrology has been conducted on oceanic mires in Britain. To this degree, many of the field and laboratory techniques were under test.

Field techniques

In general, the field procedures worked very well, although some future modifications of the sampling equipment are necessary to minimise disturbance during moss / testate amoebae sampling. The steel cylinder that had been manufactured specifically for collection of surface moss samples performed very well, causing little disturbance of the acrotelm and maintaining the coherence of the surface moss samples. Although one end of the steel cylinder had been sharpened, improved sharpness would have allowed a cleaner cut, further minimising disturbance to the acrotelm during sampling. The use of a sharp blade which could be pushed transversely through the cylinder to cut the moss sample free from the underlying peat would have improved the collection method enormously, dispensing with the awkward removal of the moss sample from the ground by hand. This would also minimise the risk of contamination of the upper parts of the brown fraction and of the green fraction with material from the underlying peat that can occur when the moss samples are separated from the peat by hand. The blade might also improve collection from waterlogged microsites, especially from pools where only bare algal mud and sparse *Sphagnum* plants exist. A lot of material was lost in such situations as saturated mud flowed from the open base of the cylinder.

Laboratory techniques

Two modifications were made to the preparation procedures described by Tolonen (1986) and Charman and Warner (1992). Samples processed for testate amoebae analysis were first placed in a 250 ml beaker of water and left for 24 hours to allow preliminary disaggregation of the testaceans from their host Sphagna. The use of a finer sieve size (300µm, instead of the 700µm used in the above studies) meant that when the samples were placed on microscope slides for identification and counting, less detritus was present on the slide and the testate amoebae shells were far less obscured, so improving this stage of the analysis.

Modelling

The use of CALIBRATE to generate the transfer functions allowed rapid and accurate calculations, provided an independent test of the calculations that had been conducted on a spreadsheet and allowed a rapid evaluation of several models based on performance statistics.

9.1.2 Testate amoebae as palaeohydrological indicators

Evaluation of regression techniques using the computer programme CALIBRATE (Juggins and ter Braak, 1992) and comparisons of observed species hydrological optima with model predicted values showed that the most robust model prediction of species' optima with respect to water table depth and percent moisture content was provided by weighted averaging (WA) regression, a slightly better performance than that of weighted averaging partial least squares (WA-PLS) regression (see Table 7.3, page 305).

Following the evaluation, WA calibration was applied to testate amoebae from a fossil peat core from Bolton Fell Moss, Cumbria to reconstruct palaeohydrological curves. These were compared to similar curves derived from plant macrofossil and peat humification analyses.

a) The hypothesis

The second hypothesis, that "the relationship between testate amoebae and water availability could be used to reconstruct palaeohydrological curves from testate amoebae for British ombrotrophic mires" has been only partially corroborated by comparing the range of palaeohydrological curves for Bolton Fell Moss. A palaeohydrological reconstruction for one core does not provide sufficient grounds for a whole-hearted acceptance of testate amoebae as palaeohydrological indicators. The comparison, however, has given clear indications of the potential and problems of testate amoebae analysis in palaeoecology.

b) The potential of testate amoebae in palaeohydrological reconstructions

The Bolton Fell Moss case study identified four advantages of testate amoebae over more established palaeohydrological indicators.

Firstly, testate amoebae gave meaningful environmental measures from qualitative data. This provided absolute water table depths and moisture content, which could not be generated by plant macrofossil and peat humification data.

Secondly, the testate amoebae assemblage was more diverse (with 24 species) and contained a wider spread of species across a hydrological gradient than the plant macrofossils (7 species). Consequently, the palaeohydrological curves derived from testate amoebae analysis were markedly less affected by sudden changes in abundances of dominant species than those from plant macrofossil analysis. Testate amoebae were able to clarify sudden hydrological changes and to moderate erratic curves.

Thirdly, testate amoebae introduced a new perspective on the hydrological events surrounding the demise of *Sphagnum imbricatum*. Falling water tables at Bolton Fell Moss did not appear to have caused the decline of the species. Rather, *S. imbricatum* was probably out-competed by *S. magellanicum* at the site. Before greater credence can be placed on this interpretation, the credibility of testate amoebae analysis must be fully proven by comparisons with other proxy or instrumental climate records by analyses on replicate cores from Bolton Fell Moss and other sites.

Fourthly, the extremely quick and simple laboratory preparation techniques involved in testate amoebae analysis (with the exception of counting) makes this an attractive palaeoecological technique to use. This should go some way to encourage its use alongside the established methods of palynology, plant macrofossil and peat humification analyses.

c) Performance of laboratory and modelling techniques

Taxonomy was again problematical in the identification and counting of both modern and fossil testate amoebae samples in this study. Decay of tests rendered identification of fossil tests especially difficult. It is highly likely that, although an improved identification key may enhance studies of modern testate amoebae, owing to decompositional effects, its transfer into fossil studies would be hampered.

Using CALIBRATE to reconstruct the palaeohydrological curves for Bolton Fell Moss presented only minor problems and these were generally overcome after communication with the programme author.

9.2 Problem areas in testate amoebae analysis

Although the palaeohydrological curves produced in this study are an encouraging first step for testate amoebae analysis, the technique is not without shortcomings and these could not be resolved in this study. The problems concern both modern and fossil testate amoebae and they centre on five principal areas: for modern testate amoebae, the unresolved relationship with water chemistry; for fossil testate amoebae, the possibility of differential decay rates for empty tests, the absence of modern analogues for certain species and the lack of a robust independent assessment of testate amoebae curves (although this reflects the nature of the peatland palaeoenvironmental records in general rather than shortfalls in previous studies). Taxonomy still remains a serious issue for both modern and fossil testate amoebae.

a) Testate amoebae and water chemistry

In this study, water chemistry failed to present as an important controlling factor on testate amoebae assemblages in the modern British data set, although it was significant at a single site (Tor Royal). The weak influence of pH was particularly unexpected and was shown to

d) Absence of robust, independent palaeohydrological records of suitable duration

Besides the replication of palaeohydrological curves from testate amoebae analysis for other ombrotrophic mires in Britain, validation by comparison with other proxy climate records (principally precipitation) are essential to assess the performance of testate amoebae as palaeohydrological indicators. Comparisons with other signals derived from identical material at a site will always give an over-optimistic impression of performance. At present, there are no fully quantitative precipitation reconstructions available for Britain. There are, however, two opportunities for future independent assessment and these are discussed in section 9.3.

e) Taxonomy

This remains a serious problem in testate amoebae analysis and one which has, arguably, suffered from previous *ad hoc* approaches to its solution. The species that have been identified as taxonomically difficult by previous authors also proved problematical in this study. Particularly difficult were the *Cyclopyxis arcelloides*-type and the *Nebela tincta-collaris-parvula* groups (Heal, 1963), while *Difflugia penardii* and *D. angulostoma* were very difficult to separate under light microscopy. All problems are addressed in the identification key in the Appendix to this thesis. Such groups may contain individual species with specific hydrological optima, which may be even better palaeohydrological indicators than the species identified in this study.

9.3 Developing testate amoebae as a palaeoenvironmental tool

This study is the first to produce a set of palaeohydrological transfer functions for testate amoebae on British ombrotrophic mires. By deriving hydrological optima for testate amoebae from a range of sites throughout Britain, it has also extended the hydrological optima of species beyond single sites to regional settings and, as such, is the most extensive study in this context. This research has provided a foundation upon which to extend the

d) Absence of robust, independent palaeohydrological records of suitable duration

Besides the replication of palaeohydrological curves from testate amoebae analysis for other ombrotrophic mires in Britain, validation by comparison with other proxy climate records (principally precipitation) are essential to assess the performance of testate amoebae as palaeohydrological indicators. Comparisons with other signals derived from identical material at a site will always give an over-optimistic impression of performance. At present, there are no fully quantitative precipitation reconstructions available for Britain. There are, however, two opportunities for future independent assessment and these are discussed in section 9.3.

e) Taxonomy

This remains a serious problem in testate amoebae analysis and one which has, arguably, suffered from previous *ad hoc* approaches to its solution. The species which have been identified as taxonomically difficult by previous authors also proved problematical in this study. Particularly difficult were the *Cyclopyxis arcelloides*-type and the *Nebela tincta-collaris-parvula* groups (Heal, 1963), while *Difflugia penardii* and *D. angulostoma* were very difficult to separate under light microscopy. All problems are addressed in the identification key in the Appendix to this thesis. Such groups may contain individual species with specific hydrological optima which may be even better palaeohydrological indicators than the species identified in this study.

9.3 Developing testate amoebae as a palaeoenvironmental tool

This study is the first to produce a set of palaeohydrological transfer functions for testate amoebae on British ombrotrophic mires. By deriving hydrological optima for testate amoebae from a range of sites throughout Britain, it has also extended the hydrological optima of species beyond single sites to regional settings and, as such, is the most extensive study in this context. This research has provided a foundation upon which to extend the

quantification of hydrological optima for modern testate amoebae. Although a wide range of sample sites were included, the study has been confined in terms of mire type to extreme oceanic mires. This was the chosen approach because ombrotrophic peatlands hold the best record of palaeoclimate in Britain and are a relatively simple habitat. As such, they constitute a manageable first step in the development of testate amoebae as a palaeoecological tool.

Arising from this study are four major avenues along which future research into testate amoebae as palaeohydrological indicators should proceed and these are illustrated in Figure 9.1.

a) Increasing the scale of investigation

In Britain, there is a need to extend the study of testate amoebae into other mire types, especially minerotrophic peatlands, to establish whether testate amoebae are subject to similar environmental controls. A natural progression into lacustrine environments would indicate the usefulness of testate amoebae as water chemistry indicators in palaeolimnology, where they could be used with other proxy records such as varves and diatom analysis to augment multi-proxy palaeolimnological reconstructions.

Beyond Britain, two issues must be investigated if regional data sets for testate amoebae are to be compiled. Studies must establish whether species' responses to hydrological parameters are consistent across Europe and whether this can be applied to the Northern Hemisphere and in a global context. For Europe, an obvious first step would be to extend the investigation by Tolonen *et al.* (1992) to a greater number of mires for which long-term hydrological records exist. If this were to be conducted simultaneously with an extended programme in Britain, there exists the possibility of correlating the two to compare species' hydrological optima in two similar oceanic areas.

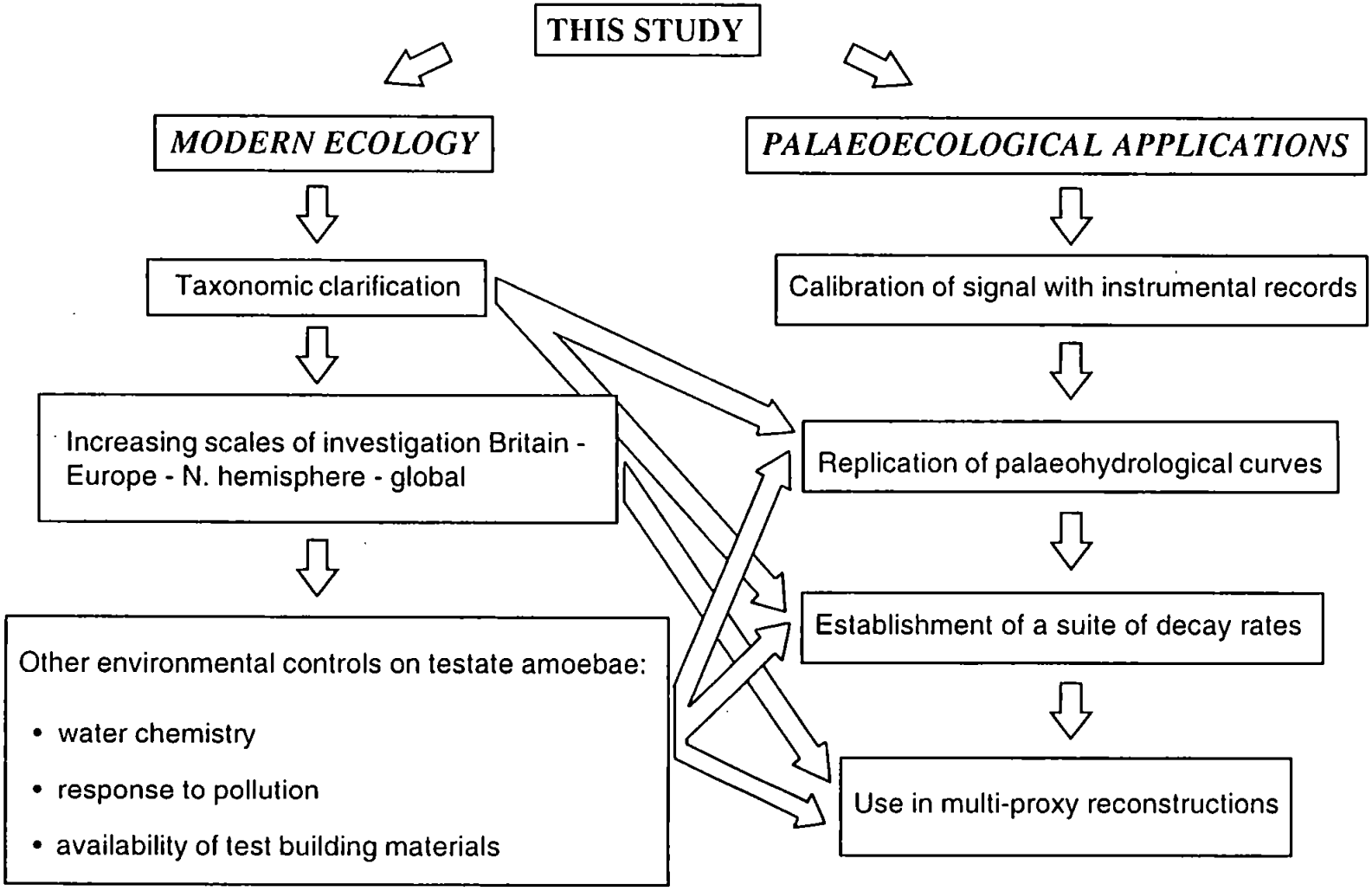


Figure 9.1: Future pathways for testate amoebae analysis.

A study of mires across a hydrological gradient from the extreme oceanic mires of western Britain to the continental mires of Germany would improve our understanding of the effects of changes in surface hydrological conditions on peatland testacean assemblages. This exercise would also generate a European data set on which to base future palaeohydrological reconstructions on peatlands. If this were to be extended to the Northern Hemisphere, for example, then information would be required on regions that are presently under-represented. Currently, work is being undertaken in Arctic Canada and Russia to address this shortfall.

From this, there exists the opportunity to further extend the modern data set into a global context by compiling data sets for the Southern Hemisphere. Work is currently in progress on establishing hydrological optima for species on New Zealand mires that are ombrotrophic but which lack abundant *Sphagnum* (D. Charman, pers. com.)

b) Other environmental controls on testate amoebae

The second avenue of investigation concerns other environmental controls that might be important influences on testate amoebae distribution and abundance. In this study, pH failed to present as an important controlling factor on testate amoebae distributions in the British data set, although it was significant at a single site (Tor Royal). This contrasts with studies by Tolonen *et al.* (1992; 1994) and Charman and Warner (1992) and this was thought to be due to the restricted chemistry of sites included in this study. Widening the investigation to include minerotrophic sites and to more extensive water chemistry, for example, may clarify water quality influences on testate amoebae.

Given the degree of dependence of testate amoebae on their surrounding environment to provide material for shell construction, which has been observed by other authors (Heal,

1963; Corbet, 1973; Foissner, 1987), the influence of the availability of the major test-forming materials - particularly dissolved organic carbon and silica - must be established.

If testate amoebae are found to be sensitive to other environmental controls, there exists the possibility for their use as pollution indicators. Some species are already used for pollution monitoring: for example, *Arcella vulgaris, Centropyxis aculeata* and *Euglypha ciliata* (Curds, 1992), but others may be equally sensitive. This study has already suggested that the decline of *Amphitrema wrightianum* may be pollution-induced and this must be thoroughly investigated.

c) Taxonomic clarification

If precise, quantified hydrological ranges for individual testate amoebae species are to be derived then future work must focus on the taxonomy of conglomerate groups (such as *Cyclopyxis arcelloides*-type and the *Nebela collaris-tincta-parvula* group) in particular. As such, they need to be identified and clearly described and photographed, preferably for identification under light microscopy since this is the medium used for routine counts. Of particular importance is whether apparently separate species that are distinguished by only slight variations in test morphology (such as *Nebela tincta* and *Nebela collaris*) are actually different species or whether the difference is due to slight modifications in growth form in the same species (Heal, 1963). The identification key presented in the Appendix of this thesis is the most recent available in Britain for identification using light microscopy and it is recommended that subsequent keys adopt a similar approach. The problem up to now has been the use of many *ad hoc* identification keys, each based on different taxonomic features. There exists a need for one amalgamated key for modern testate amoebae, although it is accepted that this may not always be easily applicable to fossil testate amoebae.

d) The use of short cores against which instrumental climate records can be compared

A considerable obstacle that prevented independent evaluation of the palaeohydrological curves derived from testate amoebae analysis was the lack of palaeoclimate information covering the same time period as the cores. This will continue to be a problem for cores that extend beyond the coverage of instrumental records. A solution lies in the use of short cores that cover accumulation over the last several hundred years, for which instrumental meteorological records do exist. These records would provide a rigorous independent data source against which palaeohydrological reconstructions from testate amoebae analysis could be compared for accuracy. If the testate amoebae accord well with the instrumental records, it will increase confidence in the use of testate amoebae in older deposits where they comprise the proxy climate record. Any such test is a test of the peatland system itself as much as the testate amoebae record. There is still argument over the degree to which surface wetness is directly linked to climate.

e) Establishing an order of decay for empty tests

If fossil testate amoebae assemblages are to be meaningfully interpreted, then the relative decay rate for every species must be established, in the same way that rates of pollen decay have been investigated. This is critical to all future palaeoecological investigations that incorporate testate amoebae analysis. At present, there are no means for comparing death assemblages with life assemblages; relative test concentrations and percentages cannot be considered sufficiently accurate. However, the ordination of modern and fossil samples, with fossil samples as 'passive' in the analysis does provide a degree of assessment of the overlap between modern and fossil communities (Warner and Charman, 1994).

9.4 The future for multi-proxy palaeohydrological reconstructions on peatlands

Multi-proxy methods of climate reconstruction are already accepted as the preferred approach in palaeoenvironmental studies. Testate amoebae analysis offers an additional

technique, that has the potential to augment existing hydrological data from peatlands for palaeoclimate studies. With the use of short cores to assess the palaeoenvironmental accuracy of testate amoebae and the possibility of additional precipitation reconstructions from European dendroclimatological records in the future (K. Briffa, pers. comm.), there exists the greatest opportunity to date to generate accurate multi-proxy climate reconstructions for peatlands.

9.5 Final conclusions

It is hoped that this study has improved the status of testate amoebae as palaeohydrological indicators on British mires. Although there are still issues to be resolved, there is no reason why their application should not be consolidated in palaeoecological studies on mires and be extended into other areas of palaeoecology. The potential benefits of testate amoebae analysis far outweigh the problems that have been highlighted in this study. The more frequently the technique is applied in palaeoenvironmental reconstructions, the greater will be the opportunities to refine the method and improve its performance. Testate amoebae provide the greatest opportunity to date to augment and refine multi-proxy palaeohydrological records from peatlands. The opportunity exists to raise testate amoebae analysis to the same status as pollen, diatoms, plant macrofossils and peat humification analyses in multi-proxy palaeoenvironmental studies.

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Appendix

1.Introduction

Previous studies of testate amoebae have used separate identification keys, such as Grospietsch (1958), Corbet (1973), Ogden and Hedley (1980) and Ellison and Ogden (1987). However, this presents the problems of taxonomic grouping, the inconsistent use of diagnostic features, and the use of modern cell physiology as determinands.

This Appendix presents a dichotomous key produced by amalgamating previous work with biometric data recorded in this study. The key and species descriptions will enable other workers to compare their data with this study. This key is directly relevant to modern testate amoebae species, but its use in palaeoenvironmental studies is also encouraged as a basis for further taxonomical improvements in fossil testate amoebae analysis.

Scanning electron microscopy (SEM) is impractical for routine counts of testate amoebae and therefore this key is illustrated by photomicrographs. Researchers using SEM are advised to consult Ogden and Hedley (1980) for the most comprehensive atlas of SEM micrographs of the common species of testate amoebae. Where possible, photomicrographs are of species found in this study. Occasionally, species obscured by debris could not be photographed; these are replaced by type slides from the Penard Collection held by the British Museum (Natural History).

2.Use of the key

This key extends the species list described by Corbet (1973) to include additional members of *Difflugia* and it also separates members of the *Centropyxis aculeata* and *C. cassis* groups of Corbet (1973). It has been compiled for use by researchers with no background in testate amoebae identification. In section 3, unusual terminology is defined, improving on existing testate amoebae keys.

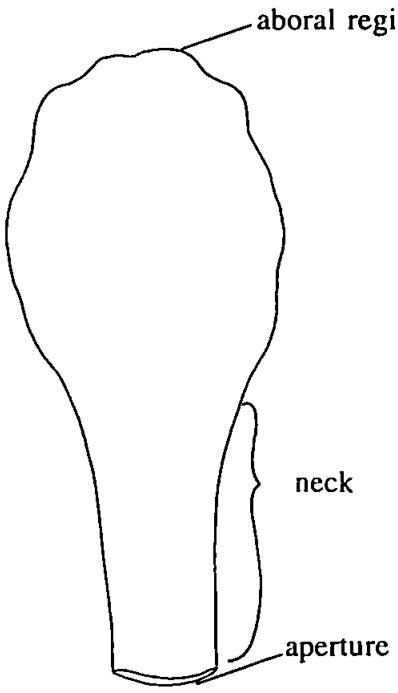
The photomicrographs are intended for simultaneous use with the dichotomous key to confirm identifications. For each species' photograph, details of other keys in which the species is illustrated are included. By cross-referencing these photomicrographs and descriptions with those in Grospietsch (1958); Corbet (1973); Ogden and Hedley (1980) and Ellison and Ogden (1987), any taxonomic details not clear from the photomicrographs may be clarified. This is particularly pertinent to the clarification of test ornamentation in some species of *Nebela, Difflugia* and *Centropyxis* where the use of the SEM micrographs in Ogden and Hedley (1980) are particularly useful.

Section 4 lists the species identified in this study. Species have been arranged in family order following Ogden and Hedley (1980). The authority for each species is also noted.

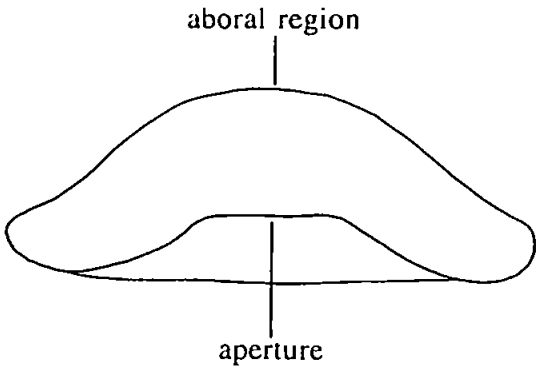
3.Terminology

Existing identification keys for testate amoebae rarely include definitions of terminology. It is particularly important to define elongate, spherical, ovoid and pyriform as descriptors of test shape and to define collars and necks with respect to test extensions, since all are fundamental to testate amoebae classification. Definitions of the terms used here are listed below and illustrated in Figures 1 to 3.

i.	elongate:	test length >1.5x test breadth.
ii.	spherical:	test is close to, or perfectly, circular.
iii.	ovoid:	test is oval-shaped.
iv.	pyriform:	test is pear-shaped, usually wider at the posterior end than the anterior.
v.	aperture:	the mouth of the test through which pseudopodia extend (see chapter 3). Also referred to as the 'pseudostrome'.
vi.	apertural:	in broad lateral view, the region of the test surrounding the aperture. Also referred to as the anterior region (Figure 1).
vii.	aboral:	in broad lateral view, the region of the test farthest from the aperture. Also referred to as the posterior region (Figure 1).
viii:	collar:	short (<10µm) extension surrounding the test aperture.
ix.	neck:	extension from test, terminated by an aperture (Figure 1).
x.	lateral pores:	pores at the test margins in broad lateral view (Figure 2).
xi.	broad lateral view:	see Figure 3(a)
xii.	narrow lateral view:	see Figure 3(b)
xiii.	pole:	situated at both ends of the long axis of the test
xiv.	terminal aperture:	situated right at the end of the test, at right angles to the long axis of the test (as in *Nebela* - Corbet, 1973).
xv.	subterminal aperture:	aperture at or near one end of the test but not symmetrically at right angles to the long axis (as in *Trinema* and *Corythion* - Corbet, 1973).

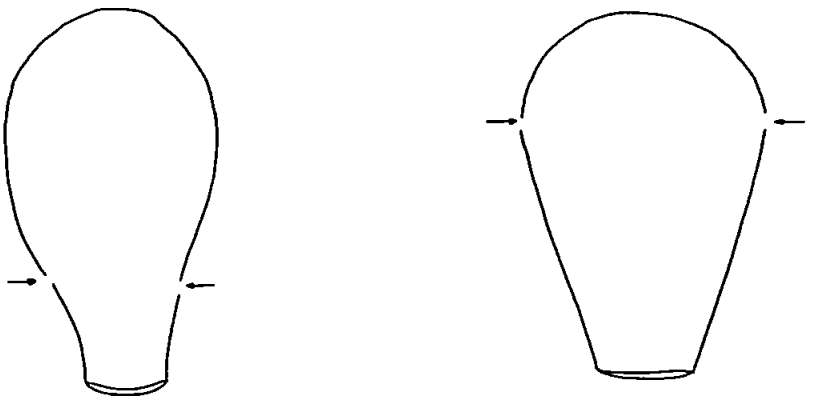


Hyalosphenia elegans



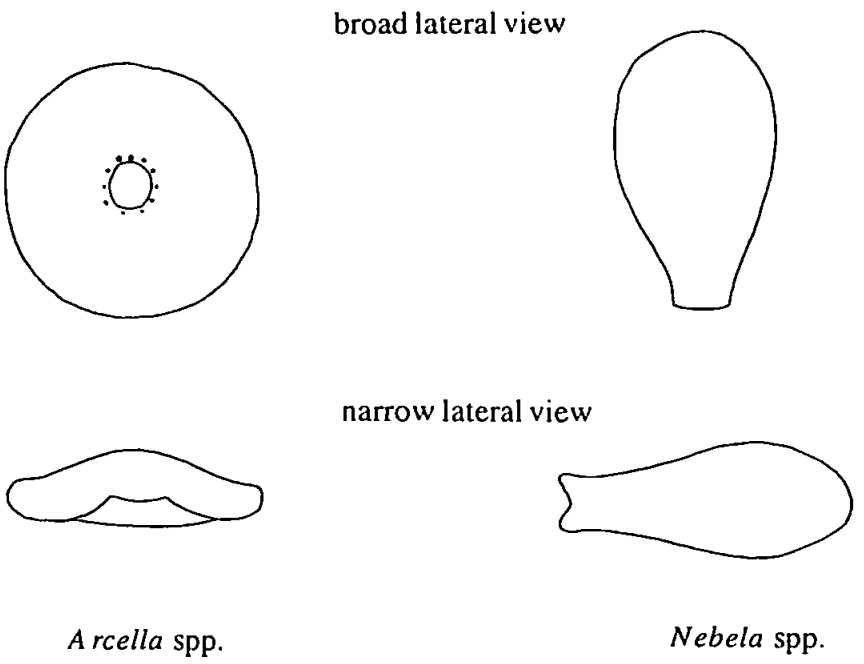
Arcella spp.

Figure 1: test regions



Nebela militaris *Hyalosphenia subflava*

Figure 2: location of lateral pores



Arcella spp. *Nebela* spp.

Figure 3: broad and narrow lateral views

Dichotomous key to be used with photomicrographs

1.	Test of secretion, without visible plates or particles.	2
	Test with plates or particles.	3
2.	Test is disc-shaped, colour ranges from pale yellow to dark brown; aperture central.	4
	Test a different shape; aperture not central.	10
3.	Test with plates or plate-like ornamentation.	17
	Test with particles.	25
4.	Disc not quite circular, dark brown; aperture always ringed with 35-50 pores. Some additional pores visible across test surface. Test diameter 73-123µm; aperture diameter 22-33µm.	*Arcella catinus*
	Disc usually circular; aperture with or without pores.	5
5.	Disc usually circular; often delicate, transparent/pale brown in appearance. Aperture surrounded by shallow lip; usually without pores. Test diameter 38-168µm; aperture diameter 20-31µm.	*A. discoides*
	Test is bowl-shaped or deeper.	6
6.	Convex surface puffy with irregular bulges and hollows. Test diameter 70-125µm; aperture diameter 19-25µm. Aperture without pores.	*A. gibbosa*
	Convex surface an evenly-curved dome.	7
7.	Diameter > 60µm; hemisphere or deeper.	8
	Diameter > 60µm; shallower than hemisphere.	9
8.	Test surface smooth with small pores. Test diameter 60-78µm; aperture diameter 11-14µm.	*A. hemispherica*
	Test surface smooth, diameter 64-86µm. Aperture diameter 10-20µm, may be surrounded by small pores.	*A. rotunda* var. *aplanata*
9.	Test is brown, may have 8-24 apertural pores, sometimes blocked. Test diameter 70-130µm; aperture diameter 20-28µm.	*A. arenaria*
	Test yellow/brown. Test diameter 100-183µm; aperture diameter 22-35µm. Pores sometimes visible across test surface, but no apertural pores.	*A. vulgaris*
	Test brown, diameter 180-200µm; aperture diameter 33-36µm, with approximately 30 pores.	*A. artrocrea*
10.	Test with 2 apertures.	11
	Test with 1 aperture.	12
11.	Test oblong, amber-brown, without particles. Test length 45-77µm.	*Amphitrema flavum*
	Test colourless, spherical often obscured by mineral particles. Apertures have short collars. Test length 50-95µm.	*A. wrightianum*

	Test elongate, colourless. Apertures without collars. Test length 45-97µm.	*A. stenostoma*
12.	Aperture sub-terminal.	13
	Aperture terminal.	14
13.	Test length 40-55µm; shape of plates impossible to distinguish.	*Trinema/Corythion* type
	Test length 18-35µm; aperture circular and serrated.	*Trinema lineare*
14.	Test colourless, circular or ovoid; smooth surface. Circular aperture surrounded by small collar. Length 14-22µm; breadth 12-18µm.	*Cryptodifflugia oviformis*
	Test strongly flattened; mouth at right-angles to long axis. Pinkish, yellowish or clear.	15
15.	Test flask-shaped; narrow necked with surface undulations. Test length 80-110µm. Green zoochlorellae sometimes visible in widest part of living tests.	*Hyalosphenia elegans*
	Test smooth; narrowing gradually towards aperture.	16
16.	Aperture at right angle to test. Test length 90-150µm; breadth 60-91µm. Aperture diameter 31-40µm. Pores always present at widest part of test. Green zoochlorellae often visible in living individuals.	*H. papilio*
	Aperture at right angle to test. Test length 34-49µm, breadth 23-28µm. Aperture diameter 10-12µm. Test colourless or pale yellow. Test more spherical than *H. papilio* and curves smoothly towards aperture. Green zoochlorellae often visible in living individuals.	*H. ovalis*
	Test colourless or yellow and shoulders slope more gently to aperture than *H. papilio*. Aperture oval and 14µm diameter. Test length 47-103µm; test breadth 35-38µm.	*H. subflava*
17.	Test a neat mosaic of plates set in cement.	59
	Test a patterned arrangement of regular plates. No cement visible.	18
18.	Test russet-brown or pale brown (but see *Assulina seminulum* below).	19
	Test clear.	20
19.	Test russet-brown; length 35-60µm, breadth 32-48µm, aperture diameter 12-20µm.	*Assulina muscorum*
	Test russet-brown or pale brown, or occasionally clear; length 65-105µm, breadth 58-74µm, diameter of aperture 21-23µm.	*A. seminulum*
20.	Test with few stout spines, each a modified plate, pointing backwards at posterior end.	*Euglypha acanthophora* (not present in this study)
	Test with scattered thin articulated spines or without spines.	21

21.	Test not compressed; without spines. Hexagonal plates. Aperture bordered by 8-12 thickened plates. Test length 45-100µm.	*E. tuberculata*
	Test compressed; with or without spines.	22
22.	Aperture plates thickened; usually numbering 10-13. Test usually with slender spines scattered across surface. Test length 45-100µm.	*E. strigosa*
	Aperture plates not thickened.	23
23.	Circular aperture; test without spines. Test length 20-50µm. 8-14 apertural plates.	*E. rotunda*
	Oval aperture; test usually with spines.	24
24.	Spines robust, always at test margin; test strongly compressed with sharply-angled margins. Test length 70-132µm. Aperture with 11-12 plates.	*E. compressa*
	Spines less robust, usually marginal, sometimes scattered in pairs over broad face of test; marginal angles less sharp. Test length 40-100µm.	*E. ciliata*
	Test bordered with flattened spines. Wide, concave aperture. Test length 100-174µm, breadth 87-110µm. Oval plates.	*Placocista spinosa*
25.	Test asymmetrical, composed of siliceous rods. Test length 89-150µm, breadth 85-110µm.	*Lesquereusia spiralis*
	Not like this.	26
26.	Test elongate or spherical with small aperture at each end.	11
	One aperture only.	27
27.	Test neat, additional particles coating posterior end.	28
	Particles similar throughout test.	32
28.	Test wine-red/rose-red, with orange apertural margin. Aperture at blunt angle to test. Test length 82-135µm; breadth 63-110µm.	*Heleopera rosea*
	Test violet, greyish, yellow or colourless.	29
29.	Test clear violet/amethyst colour. Test length 80-125µm.	*H. petricola var. amethysta* (not in this study)
	Test grey/yellow/colourless.	30
30.	Test transparent. Shorter (length= 50-75µm) and narrower than other *Heleopera.*	*H. sylvatica*
	Test > 75µm long.	31
31.	Test colourless, untidy with numerous mineral particles. Aperture margins thickened, strongly convex, meeting side walls in a rounded, but definite angle. Length 56-135µm; breadth 39-70µm.	*H. petricola*
	Test golden yellow or brown colour, ovoid (sometimes almost circular) and compressed. Aperture margins not thickened. Aboral region rough and composed of larger (sand) grains than remaining test. Test length 80-130µm; breadth 70-75µm.	*H. sphagni*

32.	Test spherical/elongate with terminal aperture.	33
	Test oval/flattened with aperture on one side.	46
33.	Test spherical.	34
	Test elongate.	38
34.	Aperture with flared rim or blistered test surface.	35
	None of these.	36
35.	Aperture bordered by conspicuous flared rim.	*Difflugia urceolata* (not in this study)
	Test surface blistered.	*D. tuberculata* (not in this study)
36.	Test length <30µm, brown with short collar and untidy test composed of mineral particles and diatom frustules.	*D. pulex*
	Test without collar or collar unclear.	37
37.	Test length <30µm, breadth <30µm, brown with irregular outline produced by covering of additional particles; terminal circular aperture.	*Pseudodifflugia fulva*
	Test length 30-60µm. Slight apertural extension may be a collar, but unclear under light microscopy. Terminal circular aperture.	*D. angulostoma*
	Test diameter 80-160µm, brown, composed of large quartz particles. Terminal circular aperture.	*D. globulosa*
38.	Test with neck or collar and 2 horns of diatom frustules in aboral region. Length 90-115µm, breadth 73-90µm.	*D. leidyi*
	Test with neck or collar, but no horns.	39
39.	Test <65µm long.	40
	Test >65µm long.	41
40.	Test <40 µm long, with short neck and agglutinated particles.	*Cryptodifflugia sacculus*
	Test 60-94µm long, breadth 36-54µm; brown or colourless, composed of quartz particles. Test tapers into wide neck. Smaller particles surrounding aperture.	*D. penardi*
41.	Test with pointed aboral region.	42
	Test with rounded aboral region.	43
42.	Test 3-4 times long as broad, cylindrical, with pointed aboral region. Surface rough with quartz particles.	*D. acuminata* (not in this study)
	Test broader than long; colourless and coated with diatom frustules. Test length 67-140µm;breadth 37-49µm.	*D. bacillariarum*

43.	Aperture margin inturned and crenulated. Test is pyriform, delicate, yellow or brown containing brick-red cytoplasmic granules. Test length 60-105µm, breadth 38-60µm.	*D. rubescens*
	Aperture margin straight.	44
44.	Test colourless or brown with diatom frustules. Length 117-200µm, breadth 54-91µm.	*D. bacillifera*
	Test with mineral particles.	45
45.	Test brown, composed of sand grains. Length 100-300µm, breadth 90-70µm. Aperture is circular and surrounded by regular arrangement of small particles.	*D. oblonga*
	Test brown, composed of sand grains. Length 90-110µm, breadth 45-55µm. Aperture is circular and surrounded by regular arrangement of small particles.	*D. longicollis*
	Test brown, composed of sand grains. Length 110-290µm, breadth 165-225µm.	*Pontigulasia compressa*
46.	Aperture a curved slit.	47
	Aperture not a curved slit.	48
47.	Aperture wide and sickle-shaped. Test dark brown; sand grains give test a rough texture. Test diameter 120-220µm; aperture diameter 65-69µm.	*Bullinularia indica*
	Aperture narrow and sickle-shaped.	*Plagiopyxis callida*
48.	Aperture 3-4 sided. Test is brown with rough surface. Test diameter 54-185µm.	*Trigonopyxis arcula*
	Aperture circular or oval.	49
49.	Aperture central; test hemispherical.	50
	Test bilaterally symmetrical; aperture not central.	52
50.	Test size 35-65µm diameter, almost spherical in cross-section. Usually colourless and coated with quartz particles. Proportionately large aperture (25-30µm diameter).	*Phryganella acropodia*
	Test size >65µm diameter.	51
51.	Test diameter 65-107µm; large circular or oval invaginated aperture. Test colourless or brown, incorporating some large mineral particles.	*Cyclopyxis arcelloides*
	Test diameter 66-79µm; test height 49-52µm. Test almost spherical, but apertural region more blunt than *Phryganella acropodia*. Brown colour produced by mineral grains incorporated into test.	*C. eurystoma*
52.	Test with spines.	53
	Test without spines.	54

53.	Test length 92-178µm, breadth 48-137µm, with 4-5 spines. Test is brown and rough (produced by sand particles).	*C. aculeata*
	Test length 67-150µm, breadth 39-54µm, with 6-9 spines. Test is colourless or brown.	*C. hirsuta*
54.	Test approximately spherical or slightly oval.	55
	Test approximately twice as long as broad, tapers towards apertural region.	58
55.	Test spherical, aperture slightly oval.	56
	Test slightly oval, tapers towards aperture; oval aperture.	57
56.	Test is spherical; brown or colourless; length 42-68µm; breadth 25-37µm. Surface is covered by quartz particles. Spherical/oval aperture surrounded by larger particles.	*Centropyxis aerophila var. sphagnicola*
	Test length 100-145µm; breadth 96-113µm. Distinguished from *Centropyxis aerophila var. sphagnicola* by larger size and more oval aperture.	*C. orbicularis*
57.	Test yellow or brown, flattened in apertural region. Test rough, smoother in apertural region. Test pyriform: length 53-72µm; breadth 44-62µm; depth 32-47µm; aperture diameter 24-34µm.	*C. aerophila*
	Shell colourless, larger particles in aboral region, smooth apertural region. Test length 62-102µm; breadth 37-85µm; aperture diameter 18-40µm.	*C. aerophila var. sylvatica*
58.	Test brown with untidy particles; blunt aboral region. Aperture semi-circular, rimmed by untidy particles; shell length 58-117µm; breadth 48-90µm, constant throughout test. Shoulders more blunt than *Centropyxis platystoma.*	*C. cassis*
	Test brown with untidy particles, rounded aboral region, circular aperture rimmed by untidy particles. Test pyriform, oval or elongate; length 59-95µm; breadth 29-64µm.	*C. platystoma*
59.	Aperture subterminal/oblique.	13
	Aperture terminal.	60
60.	Plates four-sided.	*Quadrulella symmetrica*
	Plates circular, elongate or irregular.	61
61.	Edge of aperture composed of particles and recurved, forming a prominent lip. Test colourless or yellow, composed of siliceous material and plates. Test length 60-88µm; breadth 59-69µm.	*Nebela griseola*
	Edge of aperture not recurved.	62
62.	Aperture edged with plates.	63
	Aperture with smooth edges of secretion.	65

63.	Test colourless, flask-shaped with a distinct neck; usually with siliceous whiskers scattered over test surface. Mixture of spherical, elongate and oval plates. Oval aperture with teeth, although difficult to see under light microscopy. Test length 95-160μm; breadth 38-62 μm.	*N. barbata*
	Test narrowing gradually towards the aperture.	64
64.	Plates oval and elongate, not touching one another; cement between often studded with small holes. Test is colourless; length 81-96μm, breadth 58-80μm.	*N. dentistoma* (not in this study)
	Plates touching one another; shell colourless and ovoid. Aperture bordered by plates. Test length 120-151μm, breadth 104-138μm.	*N. vitraea*
65.	Test flask-shaped, with a distinct, approximately parallel sided neck. Test colourless or tinted yellow. Aperture slightly curved with thin lip of secretion. Test length 95-258μm, breadth 102-145μm.	*N. lageniformis*
	Test narrowing steadily towards the aperture.	66
66.	Aboral region of test edged with a flat keel or entire test margin strongly compressed.	67
	Aboral region of test without a keel or ridge.	69
67.	Test margin strongly compressed, clearly seen in broad lateral view by focusingup and down. Aperture lined with smooth secretion. Test length 180-200μm; breadth 113-153μm, pyriform.	*N. galeata* (not in this study)
	Aboral region edged with a sharp keel.	68
68.	Keel narrow, extending less than halfway to the aperture. Test pyriform, yellow or grey; length 140-170μm.	*N. marginata*
	Keel broad, extending more than halfway to the aperture. Test pyriform, colourless, composed of oval or circular plates. Test length 126-170μm, breadth 89-110μm.	*N. carinata*
69.	A pair of large, conspicuous pores on the broad face of the test. Test pyriform, yellow. Length 153-171μm; breadth 95-115μm.	*N. bigibossa* (not in this study)
	Without pores on the broad face of the test.	70
70.	Test as broad as long, or broader; narrowing abruptly to a straight aperture. Test length 72-120μm; breadth 80-155μm.	*N. flabellulum*
	Breadth of test less than distance from aperture to aboral region.	71
71.	Test usually less than twice as long as broad; aperture length less than one-third maximum width of test.	72
	Test more than twice as long as broad; aperture more than one-third maximum width of test.	73

72.	With a pair of lateral pores, faintly visible as breaks in the side walls, near the mouth. Test yellow, ovoid with small neck at aperture. Test length 70-120μm; breadth 51-83μm.	*N. tincta*
	Usually without lateral pores; test length 78-90μm.	*N. parvula*
73.	Without lateral pores.	74
	With a pair of lateral pores, faintly visible as breaks in the side walls, near the aperture.	75
74.	Test pyriform, tapering gently to wide, curved aperture. Distinguished from *N. collaris* by smaller size (70-100μm long) and broader aperture. Lateral pores sometimes visible.	*N. minor*
	Test ovoid or pyriform, colourless. Distinguished from *N. minor* by larger size (93-184μm long) and strongly curved aperture.	*N. collaris*
75.	Test is pyriform.	76
	Test not pyriform, pores difficult to see.	77
76.	Test is colourless, ovoid or pyriform and small (length 29-72μm, breadth 15-28μm). Concave aperture with thickened margins. Oval, circular and rectangular plates.	*N. militaris*
	Test pyriform and elongate with small compressed margins. Length 140-175μm, breadth 65-80μm.	*N. penardiana*
77.	Test colourless or yellow-brown, flask-shaped with slender neck. Fragile, composed of oval or circular plates. Length 190-264μm; breadth 31-34μm.	*N. tubulosa*
	Colourless; aperture bordered by a collar composed of secretion.	*Sphenoderia lenta*

List of species identified in modern British and fossil samples

1. AMPHITREMIDAE

PLATE 1.1	*Amphitrema flavum*	Archer 1877
PLATE 1.2	*A. wrightianum*	Archer 1869
PLATE 1.3	*A. stenostoma*	Neusslim 1884

2. ARCELLIDAE

PLATE 2.1	*Arcella arenaria*	Greeff 1866
PLATE 2.2	*A. artrocrea*	Leidy 1876
PLATE 2.3	*A. catinus*	Penard 1890
PLATE 2.4	*A. discoides*	Ehrenburg 1843
PLATE 2.5	*A. gibbosa*	Penard 1890
PLATE 2.6	*A. hemispherica*	Perty 1852
PLATE 2.7	*A. rotunda var. aplanata*	Deflandre 1928
PLATE 2.8	*A. vulgaris*	Ehrenburg 1830

3. CENTROPYXIDAE

PLATE 3.1	*Centropyxis aculeata*	Ehrenburg 1830
PLATE 3.2	*C. aerophila*	Deflandre 1929
PLATE 3.3	*C. aerophila var. sphagnicola*	Deflandre 1928
PLATE 3.4	*C. aerophila var. sylvatica*	Deflandre 1928
PLATE 3.5	*C. cassis*	Wallich 1864
PLATE 3.6	*C. hirsuta*	Deflandre 1929
PLATE 3.7	*C. orbicularis*	Deflandre 1929
PLATE 3.8	*C. platystoma*	Penard 1890

4. CRYPTODIFFLUGIIDAE

PLATE 4.1	*Cryptodifflugia oviformis*	Penard 1890
PLATE 4.2	*C. sacculus*	Penard 1902

5. DIFFLUGIIDAE

PLATE 5.1	*Difflugia angulostoma*	Authority unknown
PLATE 5.2	*D. bacillariarum*	Perty 1849
PLATE 5.3	*D. bacillifera*	Penard 1890
PLATE 5.4	*D. globulosa*	Dujardin 1837
PLATE 5.5	*D. leidyi*	Wailes 1911
PLATE 5.6	*D. longicollis*	Gassowsky 1936
PLATE 5.7	*D. oblonga*	Ehrenburg 1838
PLATE 5.8	*D. penardi*	Hopkinson 1909
PLATE 5.9	*D. pulex*	Penard 1902
PLATE 5.10	*D. rubescens*	Penard 1891
PLATE 5.11	*Pontigulasia compressa*	Carter 1864

6. EUGLYPHIDAE

PLATE 6.1	*Assulina muscorum*	Greeff 1888
PLATE 6.2	*A. seminulum*	Ehrenburg 1848
PLATE 6.3	*Euglypha ciliata*	Ehrenburg 1848
PLATE 6.4	*E. compressa*	Carter 1864
PLATE 6.5	*E. rotunda*	Wailes 1911
PLATE 6.6	*E. strigosa*	Ehrenburg 1872
PLATE 6.7	*E. tuberculata*	Dujardin 1841
PLATE 6.8	*Placocista spinosa*	Carter 1865
PLATE 6.9	*Sphenoderia lenta*	Schlumberger 1845

7. GROMIIDAE

PLATE 7.1	*Pseudodifflugia fulva*	Archer 1870

8. HYALOSPHENIIDAE

PLATE 8.1	*Heleopera petricola*	Leidy 1879
PLATE 8.2	*H. rosea*	Penard 1890
PLATE 8.3	*H. sphagni*	Leidy 1874
PLATE 8.4	*H. sylvatica*	Penard 1890

PLATE 8.5	*Hyalosphenia elegans*	Leidy 1874
PLATE 8.6	*H. ovalis*	Wailes 1912
PLATE 8.7	*H. papilio*	Leidy 1875
PLATE 8.8	*H. subflava*	Cash and Hopkinson 1909
PLATE 8.9	*Lesquereusia spiralis*	Ehrenburg 1840
PLATE 8.10	*Nebela barbata*	Leidy 1874
PLATE 8.11	*N. carinata*	Archer 1867
PLATE 8.12	*N. collaris*	Ehrenburg 1848
PLATE 8.13	*N. flabellulum*	Leidy 1874
PLATE 8.14	*N. griseola*	Penard 1911
PLATE 8.15	*N. lageniformis*	Penard 1890
PLATE 8.16	*N. marginata*	Penard 1902
PLATE 8.17	*N. militaris*	Penard 1890
PLATE 8.18	*N. minor*	Penard 1902
PLATE 8.19	*N. parvula*	Cash 1909
PLATE 8.20	*N. tincta*	Leidy 1879
PLATE 8.21	*N. tubulosa*	Penard 1890
PLATE 8.22	*N. vitraea*	Penard 1899
PLATE 8.23	*Quadrulella symmetrica*	Wallich 1863

9. PLAGIOPYXIDAE

PLATE 9.1	*Bullinularia indica*	Penard 1907

10. PHRYGANELLIDAE

PLATE 10.1	*Phryganella acropodia*	Hertwig and Lesser 1874

11. TRIGONOPYXIDAE

PLATE 11.1	*Cyclopyxis arcelloides*	Leidy 1879
PLATE 11.2	*C. eurystoma*	Deflandre 1929
PLATE 11.3	*Trigonopyxis arcula*	Leidy 1879

12. TRINEMATIIDAE

PLATE 12.1 *Corythion-Trinema* type Taranek 1881; Penard 1890

1. AMPHITREMIDAE

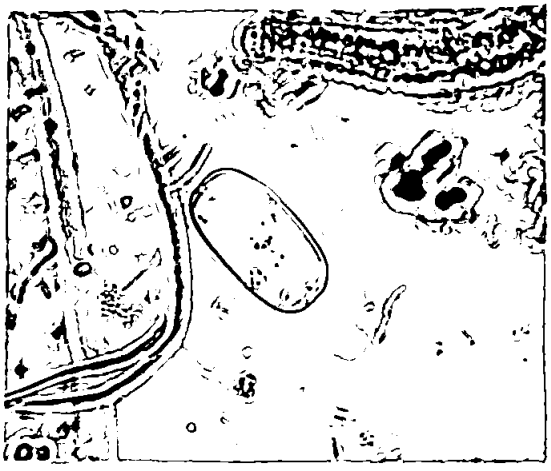
Test is ovoid or elongate and composed of proteinaceous material, sometimes with agglutinated particles; apertures at both poles of test (Ogden and Hedley, 1980; Ellison and Ogden, 1987). Comprises one genus - *Amphitrema*. Distinctive test characteristics (lozenge-shaped, smooth, brown, with one aperture at each pole) render *A. flavum* easy to identify. *A. wrightianum* and *A. stenostoma* can be separated by test shape - in *A. wrightianum* it is spherical, in *A. stenostoma* it is ovoid or elongate. *A. stenostoma* also has a denser covering of particles covering the test surface.

PLATE 1.1:	***Amphitrema flavum* (Archer 1877)**
Dimensions:	45-70µm long (this study); 50-75µm (Grospietsch, 1958); 45-77µm (Corbet, 1973).
Test outline:	elongate in broad lateral view.
Colour:	amber-brown.
Test material:	proteinaceous, without agglutinated particles.
Aperture:	one circular aperture at both poles.
Other features:	modern individuals have zoochlorellae in their cytoplasm; in fossil species this is absent.
References:	Grospietsch (1958); Corbet (1973); Ogden and Hedley (1980); Ellison and Ogden (1987).

PLATE 1.2:	***A. wrightianum* (Archer 1869)**
Dimensions:	50-90µm long (this study); 60-70µm (Grospietsch, 1958); 50-95µm (Corbet, 1973).
Test outline:	spherical in broad lateral view.
Colour:	colourless.
Test material:	proteinaceous test always obscured by mineral particles and diatom frustules.
Aperture:	two; with short, but distinct, collars.
Other features:	Corbet (1973), noted that the agglutinated particles led to confusion between *A. wrightianum* and *A. stenostoma* but, in the Bolton Fell Moss core, *A. wrightianum* was easily distinguished by a more spherical test.
References:	Grospietsch (1958); Corbet (1973); Ogden and Hedley (1980); Ellison and Ogden (1987).

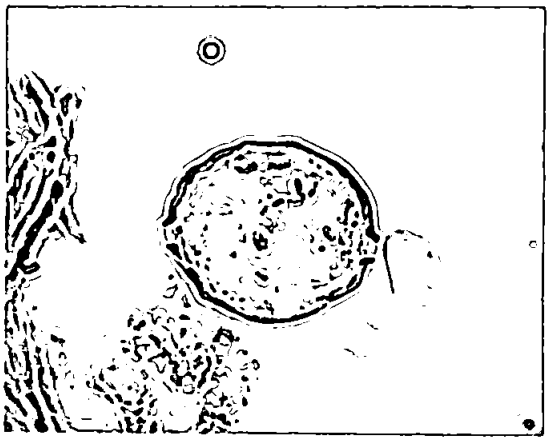
PLATE 1.3:	***A. stenostoma* (Neusslim 1884)**
Dimensions:	45-90µm long (this study); 45-65µm (Grospietsch, 1958); 45-97µm (Corbet, 1973).
Test outline:	elongate in broad lateral view.
Colour:	colourless.
Test material:	proteinaceous, coated with mineral particles.
Aperture:	one at both poles, often obscured by mineral particles (Corbet, 1973).
Other features:	separated from *A. wrightianum* in this study by more elongated test.
References:	Grospietsch (1958); Corbet (1973); Ogden and Hedley (1980); Ellison and Ogden (1987).

PLATE 1.1 *Amphitrema flavum* (modern)



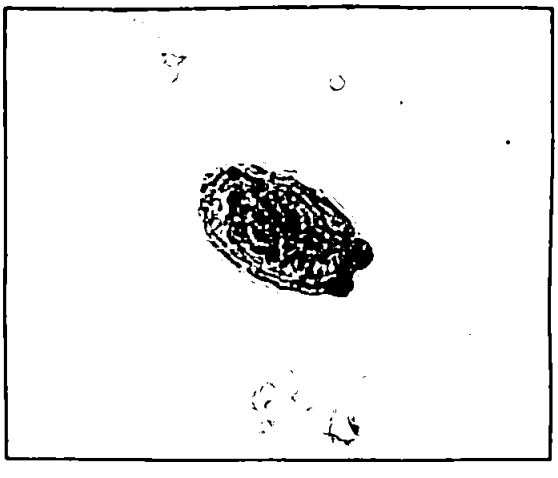
0 30µm

PLATE 1.2 *A. wrightianum* (fossil)



0 30µm

PLATE 1.3 *A. stenostoma* (Penard Collection, British Museum)



0 30µm

2. ARCELLIDAE

Generally smooth, circular test composed of proteinaceous material (Ogden and Hedley, 1980). Central circular aperture sometimes surrounded by pores. One genus - *Arcella*. Test colourless, yellow or brown, smooth. Central aperture sometimes surrounded by pores. In this study species were separated by diameter of test (Ogden and Hedley, 1980; Ellison and Ogden, 1987) and aperture (Ogden and Hedley, 1980) and number of pores surrounding the aperture (Ogden and Hedley, 1980). Ogden and Hedley (1980) suggest that encysted individuals can be identified by the closure of the central aperture by a cyst plug.

PLATE 2.1:	***Arcella arenaria* (Greef 1866)**
Dimensions:	70-130µm diameter (this study); 70-91µm (Grospietsch, 1958); 79-130µm (Ogden and Hedley, 1980).
Test outline:	circular in broad lateral view.
Colour:	brown.
Test material:	proteinaceous material produces a smooth surface.
Aperture:	circular and surrounded by 8-24 pores, sometimes blocked. Diameter 20-30µm (this study); 22-28µm (Ogden and Hedley, 1980).
Other features:	Ogden and Hedley (1980), using SEM, describe a conical aboral region which is divided into segments but large size makes manipulation of specimens impossible under coverslip. Thus, aboral region is not a useful taxonomic feature.
References:	Ogden and Hedley (1980).

PLATE 2.2:	***A. artrocrea* (Leidy 1876)**
Dimensions:	185-190µm diameter (this study); 180-200µm (Grospietsch, 1958); 184-216µm (Ogden and Hedley, 1980).
Test outline:	circular in broad lateral view.
Colour:	brown.
Test material:	proteinaceous material produces a smooth surface; studded by pores across test surface.
Aperture:	33µm (this study); 36µm diameter (Ogden and Hedley, 1980), surrounded by 30 pores of assorted sizes.
Other features:	Ogden and Hedley (1980) noted a conical aboral region which is dented, but the species is too large to rotate into aboral view under a coverslip.
References:	Ogden and Hedley (1980).

PLATE 2.3:	***A. catinus* (Penard 1890)**
Dimensions:	73-114µm diameter (this study); 110-123µm (de Graaf, 1956); 77-116µm (Grospietsch, 1958; Corbet, 1973); 73-114µm (Ogden and Hedley, 1980).
Test outline:	Usually circular in broad lateral view, although many individuals in this study had crumpled edges.
Colour:	dark brown.
Test material:	proteinaceous material produces a smooth surface.
Aperture:	circular aperture; 22-33µm diameter (this study); 23-27µm (de Graaf, 1956); 23-37µm (Ogden and Hedley, 1980). Surrounded by 39-44 pores (this study); 8-18 pores (de Graaf, 1956); 35-50 pores (Ogden and Hedley, 1980).
Other features:	Ogden and Hedley (1980) describe a shallow aboral region; this appears folded when flattened under a coverslip (Corbet, 1973).
References:	de Graaf (1956); Grospietsch (1958); Ogden and Hedley (1980).

PLATE 2.4: *A. discoides* (Ehrenburg 1843)

Dimensions: 80-105µm (this study); 38-73µm (de Graaf, 1956); 53-168µm (Corbet, 1973); 83-104µm (Ogden and Hedley, 1980); 105-110µm (Ellison and Ogden, 1987).

Test outline: circular in broad lateral view.

Colour: pale yellow or transparent. Yellow or brown (Ogden and Hedley, 1980).

Test material: proteinaceous material produces a smooth surface.

Aperture: circular; bordered by a shallow lip (Ogden and Hedley, 1980). Diameter 21-31µm.

Other features: small pores on the test surface are described by Ogden and Hedley (1980) but these may not be visible under light microscopy.

References: de Graaf (1956); Corbet (1973); Ogden and Hedley (1980); Ellison and Ogden (1987).

PLATE 2.5: *A. gibbosa* (Penard 1890)

Dimensions: 87-90µm diameter (this study); 92-100µm (de Graaf, 1956); 70-125µm (Grospietsch, 1958; Corbet, 1973); 90µm (Ogden and Hedley, 1980).

Test outline: circular in broad lateral view.

Colour: yellow or brown.

Test material: proteinaceous.

Aperture: circular, with a distinct rim. Diameter 20µm (this study); 25µm (de Graaf, 1956); 19µm (Ogden and Hedley, 1980). Pores absent.

Other features: Test is characterised by distinctive undulations on the aboral surface. Where these were unclear, *A. gibbosa* was separated from other members of *Arcella*, particularly *A. discoides*, by test diameter, aperture diameter, colour and the absence of apertural pores, following Corbet (1973).

PLATE 2.6: *A. hemispherica* (Perty 1852)

Dimensions: 55-65µm diameter (this study); 46-78µm (de Graaf, 1956); 45-56µm (Grospietsch, 1958; Corbet, 1973); 50µm (Ellison and Ogden, 1987); 55-63µm (Ogden and Hedley, 1980).

Test outline: circular in broad lateral view, but edges may be dented.

Colour: yellow or brown.

Test material: proteinaceous.

Aperture: circular and bordered by a small lip. No pores. Diameter 11-13µm (this study); 11-14µm (Ogden and Hedley, 1980).

Other features: test is covered by small pores which may be difficult to observe under light microscopy. Grospietsch (1958), Corbet (1973), Ogden and Hedley (1980), Ellison and Ogden (1987) describe the test as hemispherical in lateral view but, in common with other species of *Arcella*, individulas may be difficult to rotate and observe under a coverslip. In this study, *A. hemispherica* is separated from *A. gibbosa* by its smaller size.

PLATE 2.7:	*A. rotunda* var. *aplanata*
Dimensions:	diameter 78-84µm (this study) diameter 64-86µm (Grospietsch, 1958).
Test outline:	circular, but may be slightly dented, in broad lateral view.
Colour:	brown.
Test material:	proteinaceous. No pores visible.
Aperture:	central; surrounded by a thickened border.
Other features:	none.
References:	Grospietsch (1958); Tolonen *et al.* (1992).

PLATE 2.8:	*A. vulgaris* (Ehrenburg 1830)
Dimensions:	150-183µm diameter (this study); 100-145µm (Grospietsch, 1958; Corbet, 1973); 104-136µm (Ogden and Hedley, 1980).
Test outline:	not perfectly circular in broad lateral view.
Colour:	amber-brown or brown.
Test material:	proteinaceous, with numerous pores over the test surface.
Aperture:	not perfectly circular; may be invaginated. No pores. Diameter 35µm (this study); 22-32µm (Ogden and Hedley, 1980).
References:	Grospietsch (1958); Corbet (1973); Ogden and Hedley (1980).

3. CENTROPYXIDAE

One genus - *Centropyxis*. Test is yellow or brown, circular or ovoid. Rounded posteriorly and compressed at the apertural end in narrow lateral view. Composed of proteinaceous material with agglutinated mineral particles. Spines sometimes present on posterior margins. Species were separated in this study using Ogden and Hedley (1980) and Ellison and Ogden (1987).

PLATE 3.1:	*Centropyxis aculeata* (Ehrenburg 1830)
Dimensions:	length 116-148µm, breadth 48-60µm (this study); length 120-150µm, breadth 48-60µm (Grospietsch, 1958; Corbet, 1973); length 92-178µm, breadth 77-137µm (Ogden and Hedley, 1980).
Test outline:	ovoid or circular in narrow lateral view. In broad lateral view, test tapers towards aperture.
Colour:	amber-brown (this study); translucent grey-green to dark brown (Corbet, 1973); yellow or brown (Ogden and Hedley, 1980).
Test material:	proteinaceous and covered with quartz particles to produce a rough surface.
Aperture:	sub-terminal, oval and 32-64µm in diameter; 35-70µm diameter (Ogden and Hedley, 1980).
Other features:	*C. aculeata* usually has 4-5 spines.
References:	Grospietsch (1958); Corbet (1973) as part of *Centropyxis aculeata* group; Ogden and Hedley (1980).

PLATE 3.2:	*C. aerophila* **(Deflandre 1929)**
Dimensions:	length 53-72µm, breadth 44-62µm (this study); length 53-85µm, breadth 42-66µm (Grospietsch, 1958); length 53-72µm, breadth 44-62µm (Ogden and Hedley, 1980); length 50-75µm (Ellison and Ogden, 1987).
Test outline:	ovoid in broad lateral view, although some species in this study were pyriform.
Colour:	yellow or brown.
Test material:	proteinaceous; test surface is rough and covered with quartz particles and diatom frustules; smoother in the apertural region.
Aperture:	oval and sub-terminal; diameter 24-34µm (Ogden and Hedley, 1980).
Other features:	*C. aerophila* has no spines.
References:	Grospietsch (1958); Ogden and Hedley (1980); Ellison and Ogden (1987).

PLATE 3.3:	*C. aerophila* **var.** *sphagnicola* **(Deflandre 1928)**
Dimensions:	length 42-68µm, breadth 25-32µm (this study); length 49-66µm, breadth 25-37µm (Grospietsch, 1958).
Test outline:	spherical in narrow lateral section. In broad lateral view, test tapers towards apertural end.
Colour:	brown or colourless.
Test material:	proteinaceous; test surface covered with quartz particles. Larger particles surround the aperture.
Aperture:	oval and sub-terminal; diameter 15-18µm.
Other features:	none.
References:	Grospietsch (1958).

PLATE 3.4:	*C. aerophila* **var.** *sylvatica* **(Deflandre 1928)**
Dimensions:	length 62-98, breadth 37-72µm (this study); length 68-102µm, breadth 43-85µm (Grospietsch, 1958).
Test outline:	slightly oval in narrow lateral view. In broad lateral view tapers towards apertural end.
Colour:	colourless and transparent.
Test material:	proteinaceous; transparency often obscured by agglutinated quartz particles, which produce a rough test surface. Smooth apertural region, larger particles in aboral region.
Aperture:	sub-terminal; oval, diameter 18-40µm.
Other features:	separated from *C. aerophila* var. *sphagnicola* in this study by larger size and oval test outline.
References:	Grospietsch (1958).

PLATE 3.5:	***C. cassis* (Wallich 1864)**
Dimensions:	length 62-82µm, breadth 48-67µm (this study); length 58-67µm, breadth 48-53µm (de Graaf, 1956); length 60-86µm, breadth 50-73µm (Grospietsch, 1958); length 60-85µm (Corbet, 1973); length 79-117µm, breadth 57-90µm (Ogden and Hedley, 1980); length 50-125µm (Ellison and Ogden (1987).
Test outline:	In broad lateral view, sides are parallel and become semi-circular at both poles. In narrow lateral view, test tapers towards apertural region.
Colour:	brown.
Test material:	proteinaceous, covered by quartz grains to produce a rough surface.
Aperture:	sub-terminal; semi-circular and surrounded by untidy particles.
Other features:	separated from *C. platystoma* by blunt appearance of shoulders. No spines. Corbet (1973) recognised a *C. cassis* group, which included *C. aerophila*, *C. orbicularis*, *C. constricta*, *C. platystoma* as well as *C. cassis*.
References:	de Graaf (1956); Grospietsch (1958); Corbet (1973); Ogden and Hedley (1980); Ellison and Ogden (1987).

PLATE 3.6:	***C. hirsuta* (Deflandre 1929)**
Dimensions:	length 67-81µm, breadth 39-48µm (this study); length 72-88µm, breadth 42-54µm (Deflandre, 1929; Grospietsch, 1958); length 120-150µm (Corbet, 1973 as part of the *C aculeata* group).
Test outline:	usually circular in narrow lateral view. Tapers towards aperture in broad lateral view.
Colour:	colourless or brown.
Test material:	proteinaceous, with no visible agglutinated particles.
Aperture:	sub-terminal, invaginated and oval. Diameter 33-50µm (Ogden and Hedley (1980).
Other features:	*C. hirsuta* has 6-9 spines. Corbet (1973) included *C. hirsuta* as a variation in the *C. aculeata* group.
References:	Deflandre (1929); Grospietsch (1958); Corbet (1973); Ogden and Hedley (1980); Ellison and Ogden (1987).

PLATE 3.7:	***C. orbicularis* (Deflandre 1929)**
Dimensions:	length 105-145µm; breadth 96-113µm (this study); length 100-140µm (Grospietsch, 1958); length >100µm (Ellison and Ogden, 1987).
Test outline:	spherical in narrow lateral view. Tapers slightly to give a blunt apertural profile in broad lateral view.
Colour:	colourless or brown.
Test material:	proteinaceous, covered by quartz particles to produce a rough surface.
Aperture:	sub-terminal; oval.
Other features:	in this study, distinguished from *C. aerophila* var. *sphagnicola* by larger size and consistently oval aperture.
References:	Grospietsch (1958).

PLATE 3.8:	*C. platystoma* **(Penard 1890)**
Dimensions:	length 57-74µm, breadth 29-56µm (this study); length 63-95µm, breadth 36-64µm (Grospietsch, 1958); length 60-86µm (Corbet, 1973); length 62-81µm, breadth 34-48µm (Ogden and Hedley, 1980); length <100µm (Ellison and Ogden, 1987).
Test outline:	test pyriform, elongate or ovoid in broad lateral view and tapers markedly in narrow lateral view.
Colour:	brown.
Test material:	proteinaceous and coated by quartz particles.
Aperture:	sub-terminal and circular; 19-27µm diameter (Ogden and Hedley, 1980). Apertural region smoother than remainder of test.
Other features:	Included as part of the *C. cassis* group by Corbet (1973). Ogden and Hedley (1980) note three main areas of variation in the species: the degree of invagination of the aperture; the constriction of the neck; the shape of the test.
References:	Grospietsch (1958); Corbet (1973); Ogden and Hedley (1980); Ellison and Ogden (1987).

4. CRYPTODIFFLUGIIDAE

Ovoid test, composed of proteinaceous material sometimes with an inner calcareous lining. Aperture terminal or sub-terminal, circular (Ogden and Hedley, 1980). Three genera: *Cryptodifflugia, Difflugiella* and *Wailesella*; only *Cryptodifflugia* recorded in this study.

PLATE 4.1	*Cryptodifflugia oviformis* **(Penard 1890)**
Dimensions:	length 15-20µm, breadth 12-17µm (this study); length 14.5-22.2µm, breadth 12.8-17.6µm (Ogden and Hedley, 1980).
Test outline:	circular or ovoid in broad lateral view.
Colour:	colourless.
Test material:	proteinaceous.
Aperture:	terminal; circular and terminal; diameter 3.2-6.4µm (Ogden and Hedley, 1980); bordered by a small collar.
Other features:	none.
References:	Ogden and Hedley (1980).

PLATE 4.2:	*C. sacculus* **(Penard 1902)**
Dimensions:	length 18-25µm, breadth 15-20µm (this study); length 25µm, breath 13µm (type-slide from Penard Collection, British Museum, Natural History).
Test outline:	elongate in lateral view, with short neck.
Colour:	brown.
Test material:	proteinaceous, with agglutinated mineral particles.
Aperture:	terminal; circular and surrounded by mineral particles.
Other features:	none.
References:	Type slide in Penard Collection held by British Museum (Natural History)

5. DIFFLUGIIDAE

Circular, ovoid or pyriform test, composed of agglutinated mineral particles and, occasionally, diatom frustules. Terminal aperture, circular (Ogden and Hedley, 1980; Ellison and Ogden, 1987). Species in this study were identified using Grospietsch (1958); Corbet (1973); Meisterfeld (1979); Ogden (1980); Ogden and Hedley (1980); Ellison and Ogden (1987). Four genera: *Difflugia, Pontigulasia, Curcubitella, Sexangularia* (latter two not recorded in this study).

PLATE 5.1:	***Difflugia angulostoma* (authority unknown)**
Dimensions:	length 30-50µm, breadth 15-50µm (this study); length 35-60µm (Ellison and Ogden, 1987).
Test outline:	spherical in broad lateral view.
Colour:	brown.
Test material:	composed mainly of diatom frustules
Aperture:	terminal; spherical, 7-10µm diameter; apertural rim irregular.
Other features:	slight apertural extension may be a collar, but unclear under light microscopy.
References:	Ellison and Ogden (1987).

PLATE 5.2:	***D. bacillariarum* (Perty 1849)**
Dimensions:	length 67-98µm, breadth 38-49µm (this study); length 100-133µm, breadth 37-43µm (Hoogenraad and de Groot, 1952); length 90-130µm (Grospietsch, 1958; Corbet, 1973); length 67-69µm, breadth 40-44µm (Ogden and Hedley, 1980); length 70-140µm (Ellison and Ogden, 1987); length 73-103µm (Ogden, 1980).
Test outline:	ovoid or circular in narrow lateral view; ovoid in broad lateral view.
Colour:	transparent, colourless or amber.
Test material:	organic cement, with thin siliceous plates overlaid by diatom frustules (Ogden, 1980; Ogden and Hedley, 1980; Ellison and Ogden, 1987).
Aperture:	terminal; size and shape dependent on size and arrangement of diatom frustules which surround it (Ogden, 1980). Diameter 17-24µm (Ogden, 1980); 22-24µm (Ogden and Hedley, 1980).
Other features:	presence or absence of aboral horn as a diagnostic feature is questionable (Ogden, 1980; Ogden and Hedley, 1980). Considerable confusion between *D. bacillariarum* and *D. elegans* (not found in this study) - see Ogden and Hedley (1980) for resolution of this.
References:	Grospietsch (1958); Corbet (1973); Ogden (1980); Ogden and Hedley (1980); Ellison and Ogden (1987).

PLATE 5.3:	***D. bacillifera* (Penard 1890)**
Dimensions:	length 130-200µm, breadth 60-90µm (this study); length 150-160µm, breadth 73-83µm (Hoogenraad and de Groot, 1952); length 120-180µm (Grospietsch, 1958; Corbet, 1973); length 118-168µm, breadth 60-79µm (Meisterfeld, 1979); length 117-176µm, breadth 54-80µm (Ogden, 1980); length 130-194µm, breadth 59-91µm (Ogden and Hedley, 1980); length 125-200µm (Ellison and Ogden. 1987).
Test outline:	ovoid or elongate in broad lateral view, with a distinct long, cylindrical neck.
Colour:	colourless or brown.
Test material:	siliceous: diatom frustules, which often conceal test outline. Small quantities of siliceous cysts of chrysomonad flagellates (Ogden, 1980).
Aperture:	terminal; circular and surrounded by small quartz particles (Ogden and Hedley, 1980). Diameter 24-38µm (Meisterfeld, 1979); 17-27µm (Ogden, 1980); 25-36µm (Ogden and Hedley, 1980).
Other features:	none.
References:	Grospietsch (1958); Corbet (1979); Meisterfeld (1979); Ogden (1980); Ogden and Hedley (1980); Ellison and Ogden (1987).

PLATE 5.4:	*D. globulosa* (Dujardin 1837)
Dimensions:	diameter 88-90µm (this study); diameter 120-150µm (Grospietsch, 1958); diameter 91-119µm (Ogden and Hedley, 1980); diameter 90-160µm (Ellison and Ogden, 1987).
Test outline:	spherical in broad lateral view; hemispherical in narrow lateral view.
Colour:	brown.
Test material:	large quartz particles, but may also include diatom particles.
Aperture:	terminal; circular; smooth margin produced by smaller quartz particles overlaid by cement.
Other features:	Ogden and Hedley (1980) note prolific variation in this species in terms of test composition and ratio of aperture diameter : test diameter.
References:	Grospietsch (1958); Ogden and Hedley (1980); Ellison and Ogden (1987).

PLATE 5.5:	*D. leidyi* (Wailes 1911)
Dimensions:	length 80-115µm, breadth 60-90µm (this study); length 95µm, breadth 73µm (Hoogenraad and de Groot (1952); length 90-110µm (Grospietsch, 1958).
Test outline:	ovoid or pyriform in broad lateral view with two horns at posterior.
Colour:	colourless or brown.
Test material:	siliceous mineral particles (quartz) and diatom frustules.
Aperture:	terminal; spherical with irregular margin produced by quartz particles. Diameter 35-40µm.
Other features:	none.
References:	Hoogenraad and de Groot (1952); Grospietsch (1958).

PLATE 5.6:	*D. longicollis* (Gassowsky 1936)
Dimensions:	length 90-110µm, breadth 45-55µm (this study); length 91-109µm, breadth 47-55µm (Ogden and Hedley, 1980).
Test outline:	pyriform, with a distinct neck which tapers evenly to the aperture in broad lateral view.
Colour:	brown.
Test material:	quartz grains of assorted sizes.
Aperture:	terminal; spherical and bordered by smaller quartz grains.
Other features:	considered by Gassowsky (1936) to be a variety of *D. oblonga*, but Ogden and Hedley (1980) found both species in the same moss sample and were able to separate the two according to size:- *D. longicollis* is smaller than *D. oblonga*.
References:	Ogden and Hedley (1980).

PLATE 5.7: *D. oblonga* (Ehrenburg 1838)

Dimensions: length 170-240µm, breadth 90-146µm (this study); length 245-270µm, breadth 170µm (Hoogenraad and de Groot, 1952); length 100-400µm (Grospietsch, 1958; Corbet, 1973); length 190-237µm, breadth 92-146µm (Ogden and Hedley, 1980); length 100-300µm (Ellison and Ogden, 1987).

Test outline: pyriform, with a distinct neck in broad lateral view.

Colour: brown.

Test material: angular quartz grains.

Aperture: terminal; circular, surrounded by small quartz grains; apertural rim smooth. Diameter 28-38µm (this study); 32-42µm (Ogden and Hedley, 1980).

Other features: Ogden and Hedley (1980) note considerable variation displayed by species and use measurements from Penard (1890) to separate the species from *D. longicollis*.

References: Grospietsch (1958); Corbet (1973); Ogden and Hedley (1980); Ellison and Ogden (1987).

PLATE 5.8: *D. penardi* (Hopkinson 1909)

Dimensions: length 60-65µm, breadth 36-42µm (this study); length 75-94µm, breadth 47-54µm (Ogden and Hedley, 1980); length 60-90µm (Ellison and Ogden, 1987).

Test outline: ovoid and circular in narrow lateral view; pyriform in broad lateral view.

Colour: transparent or yellow.

Test material: small quartz grains, flat diatom frustules (from *Cocconeis* and *Achnanthes*) and spherical siliceous cysts of chrysomonad flagellates arranged on organic cement (Ogden and Hedley, 1980) which produces smooth test surface.

Aperture: terminal and circular, with a smooth rim.

Other features: none.

References: Ogden and Hedley (1980); Ellison and Ogden (1987).

PLATE 5.9: *D. pulex* (Penard 1902)

Dimensions: length <30µm (this study); length 20-40µm (Ellison and Ogden, 1987)

Test outline: pyriform with a short collar in broad lateral view. Spherical in narrow lateral view.

Colour: brown.

Test material: mineral grains and diatom frustules arranged to give an untidy test surface.

Aperture: terminal; diameter is slightly narrower than broadest part of test.

Other features: appears similar to *D. angulostoma*, but separated in this study by the presence of a short, but distinct neck and an untidy test, following Ellison and Ogden (1987).

References: Ellison and Ogden (1987).

PLATE 5.10:	*D. rubescens* (Penard 1891)
Dimensions:	length 70-90µm, breadth 38-54µm (this study); length 80-93µm, breadth 43-60µm (Hoogenraad and de Groot (1952); length 71-78µm, breadth 42-46µm (de Graaf, 1956); length 65-100µm (Grospietsch, 1958); length 65-105µm (Corbet, 1973); length 70-91µm, breadth 38-54µm (Ogden and Hedley, 1980); length 60-105µm (Ellison and Ogden, 1987).
Test outline:	pyriform in broad lateral view; circular in narrow lateral view.
Colour:	yellow or light brown. Brick-red cytoplasmic granules sometimes visible through test in living individuals; not visible in fossil specimens.
Test material:	thin coating of quartz particles and diatom frustules.
Aperture:	terminal, circular and crenulated to produce tooth-like structures (Ogden and Hedley, 1980). Diameter 14-20µm (Ogden and Hedley, 1980).
Other features:	Ogden and Hedley note that the covering varies from a few particles to a thick covering, which may disguise the pyriform outline.
References:	Hoogenraad and de Groot (1952); de Graaf (1956); Grospietsch (1958); Corbet (1973); Ogden and Hedley (1980); Ellison and Ogden (1987).

PLATE 5.11:	*Pontigulasia compressa* (Carter 1864)
Dimensions:	length 195-290µm, breadth 165-225µm (this study); length 110-140µm (Grospietsch, 1958); length 196-289µm, breadth 166-222µm (Ogden and Hedley, 1980).
Test outline:	ovoid or pyriform in broad lateral view, with a short neck; compressed in narrow lateral view.
Colour:	brown.
Test material:	quartz grains arranged on an organic matrix (Ogden and Hedley, 1980).
Aperture:	terminal; circular or ovoid; diameter 45-75µm (Ogden and Hedley, 1980).
Other features:	neck joins the body in a V-shaped wedge which can be seen under light microscopy by moving the stage up and down.
References:	Grospietsch (1958); Ogden and Hedley (1980).

6. EUGLYPHIDAE

Test is ovoid or circular and composed of regularly arranged siliceous plates. Siliceous spines sometimes present. Aperture terminal, circular, oval, or lenticular, surrounded either by plates or organic cement (Ogden and Hedley, 1980). Comprises five genera: *Euglypha, Assulina, Placocista, Sphenoderia* (all present in this study) and *Tracheleuglypha* (not present).

PLATE 6.1:	*Assulina muscorum* (Greeff 1888)
Dimensions:	length 46-58µm, breadth 34-44µm (this study); length 35-60µm (Grospietsch, 1958); length 28-58µm (Corbet, 1973); length 45-53µm, breadth 32-48µm (Ogden and Hedley, 1980); length 50µm (Ellison and Ogden, 1987).
Test outline:	ovoid in broad lateral view and flattened in narrow lateral view.
Colour:	russet-brown.
Test material:	siliceous oval plates, arranged in neat rows; organic cement at collar.
Aperture:	terminal; oval, diameter 16-20µm (this study); 12-18µm (Ogden and Hedley, 1980).
Other features:	Corbet (1973) and Ogden and Hedley (1980) note that, although test plates are normally neatly arranged, irregularities may appear.
References:	Grospietsch (1958); Corbet (1973); Ogden and Hedley (1980); Ellison and Ogden (1987).

PLATE 6.2:	***A seminulum* (Ehrenburg 1848)**
Dimensions:	length 60-68µm, breadth 58-71µm (this study); length 65-105µm (Grospietsch, 1958); 60-90µm (Corbet, 1973); length 72-82µm, breadth 62-74µm (Ogden and Hedley, 1980).
Test outline:	ovoid in broad lateral view; compressed in narrow lateral view.
Colour:	yellowish-brown or colourless.
Test material:	siliceous, oval plates; organic cement at collar.
Aperture:	terminal; oval; surrounded by organic cement; diameter 21-23µm (Ogden and Hedley, 1980).
Other features:	separated from *A. muscorum* by larger size, relative sphericity of test outline and pale/colourless test.
References:	Grospietsch (1958); Corbet (1973); Ogden and Hedley (1980).

PLATE 6.3:	***Euglypha ciliata* (Ehrenburg 1848)**
Dimensions:	length 40-90µm (this study); length 60-100µm (Grospietsch, 1958); length 40-90µm (Corbet, 1973).
Test outline:	ovoid in broad lateral view; compressed in narrow lateral view with short, slender spines.
Colour:	colourless.
Test material:	regularly-arranged siliceous plates. At higher magnification, it is sometimes possible to see the hexagonal shape of these plates.
Aperture:	terminal; oval and compressed; bordered by plates to produce a toothed margin
Other features:	Corbet (1973) notes that *E. ciliata* is separated from *E. tuberculata* by its compressed test and from *E. strigosa* by its unthickened apertural plates. Occasionally, rare spineless forms of *E. ciliata* occur; these are distinguished from *E. rotunda* by their larger size and more elaborately-toothed aperture plates.
References:	Grospietsch (1958); Corbet (1973).

PLATE 6.4:	***E. compressa* (Carter 1864)**
Dimensions:	length 70-132µm (this study; Corbet 1973); 70-130µm (Grospietsch, 1958); length 74-112µm, breadth 38-69µm (Ogden and Hedley, 1980); length 105µm (Ellison and Ogden (1987).
Test outline:	ovoid in broad lateral view; compressed in narrow lateral view; spines visible at margins and across test surface.
Colour:	colourless.
Test material:	approximately 200 oval siliceous plates; siliceous spines.
Aperture:	terminal; oval and surrounded by 11-12 apertural plates (Ogden and Hedley, 1980).
Other features:	may be up to 40 spines scattered across test; these are stout compared to those of *E. strigosa*. Ogden (1980) noted that spines alternate in lateral view along the test margin, one pointing downwards and one upwards.

PLATE 2.1 *Arcella arenaria* (modern)
(a) apertural view (b) aboral view

PLATE 2.2 *A. artrocrea* (modern)

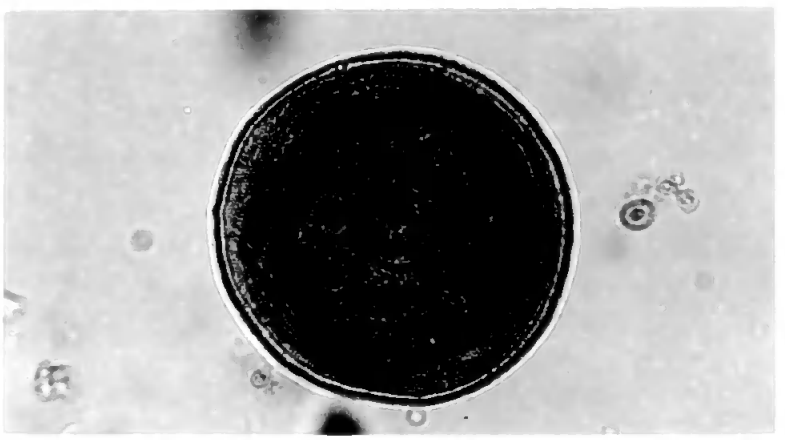


PLATE 2.3 *A. catinus* (Penard Collection, British Museum)

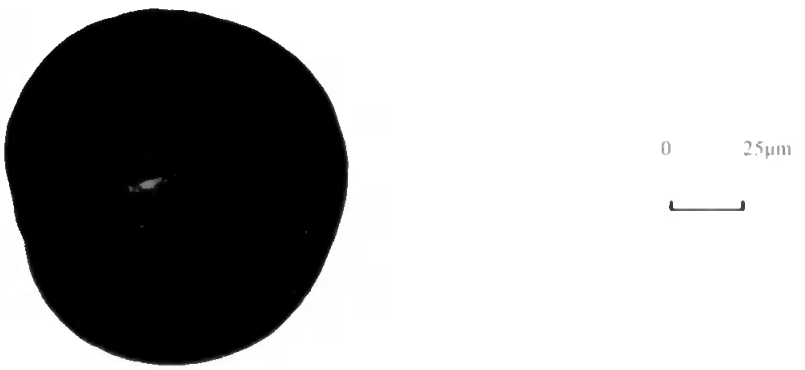
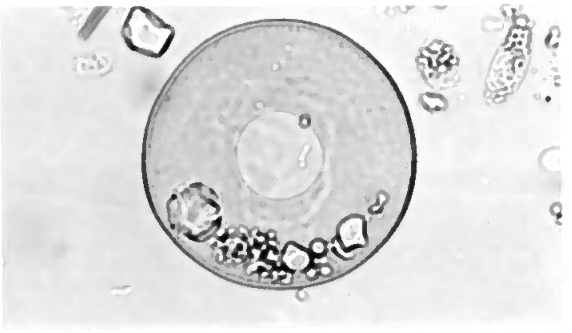
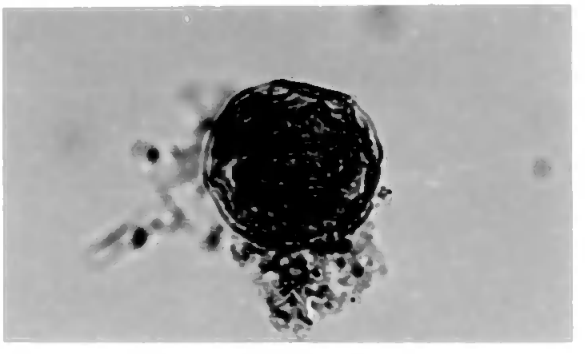


PLATE 2.4 *A. discoides* (modern)



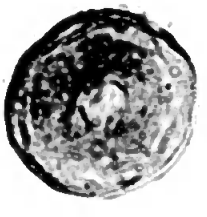
0 25µm

PLATE 2.5 *A. gibbosa* (modern)



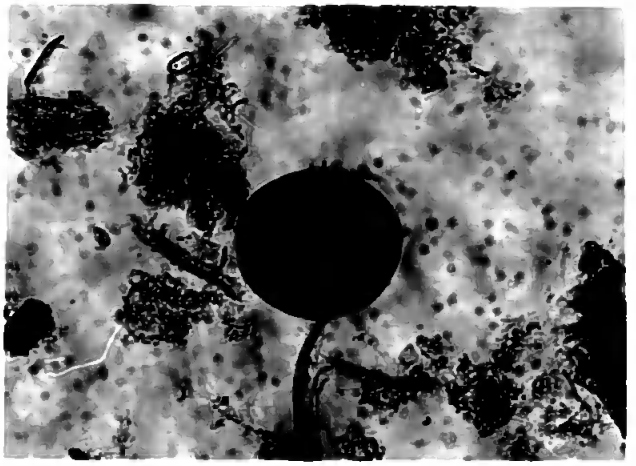
0 40µm

PLATE 2.6 *A. hemispherica* (modern)



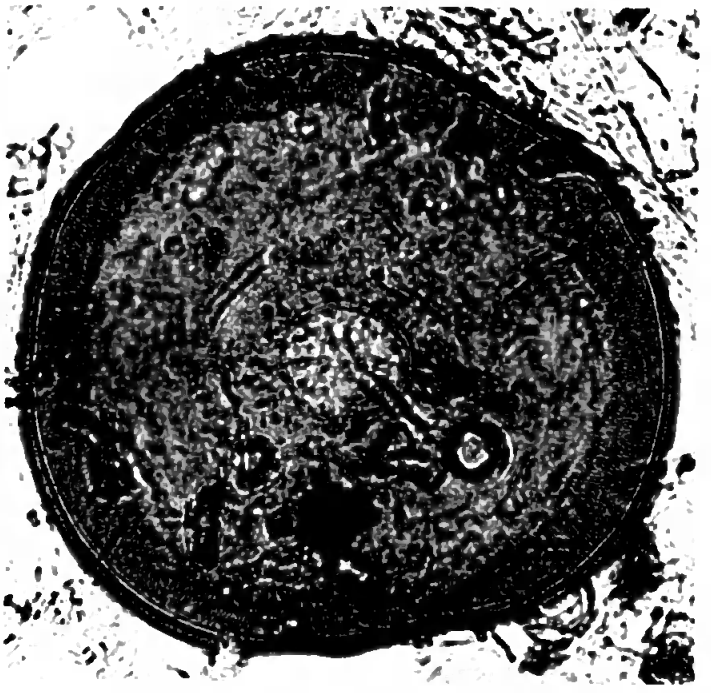
0 25µm

PLATE 2.7 *A. rotunda* var. *aplanata* (modern)



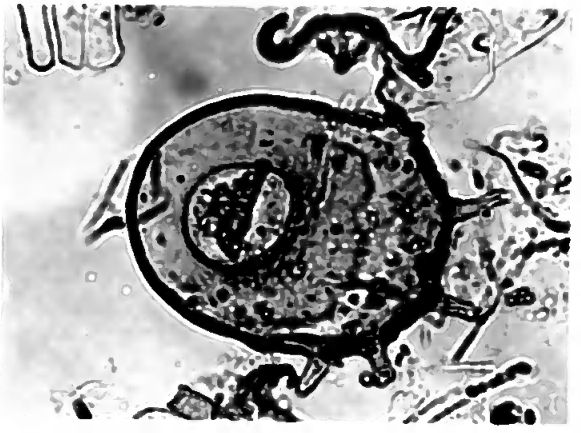
0 30µm

PLATE 2.8 *A. vulgaris* (modern)



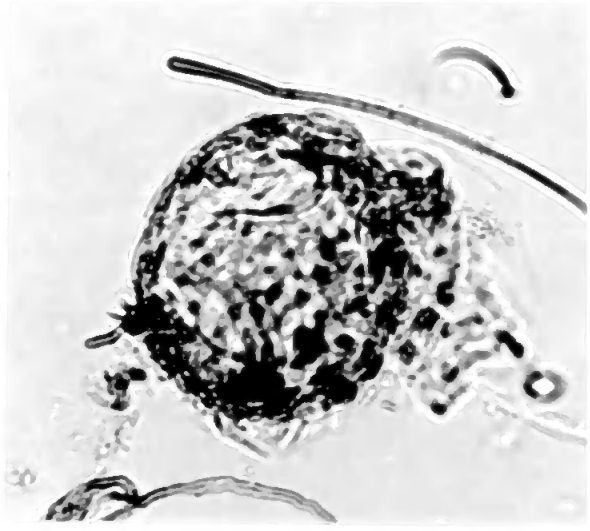
0 20µm

PLATE 3.1 *Centropyxis aculeata* (modern)



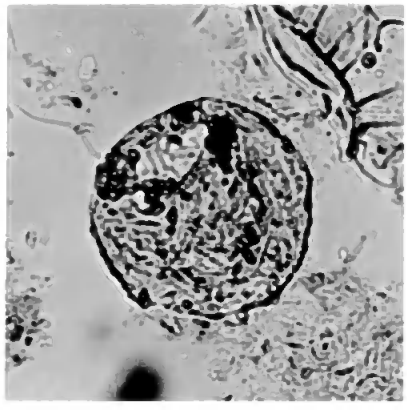
0 20µm

PLATE 3.2 *C. aerophila* (modern)



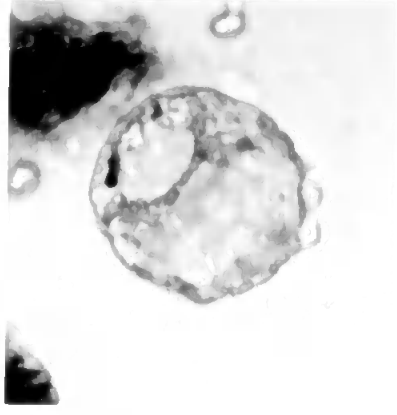
0 15µm

PLATE 3.3 *C. aerophila* var. *sphagnicola* (modern)



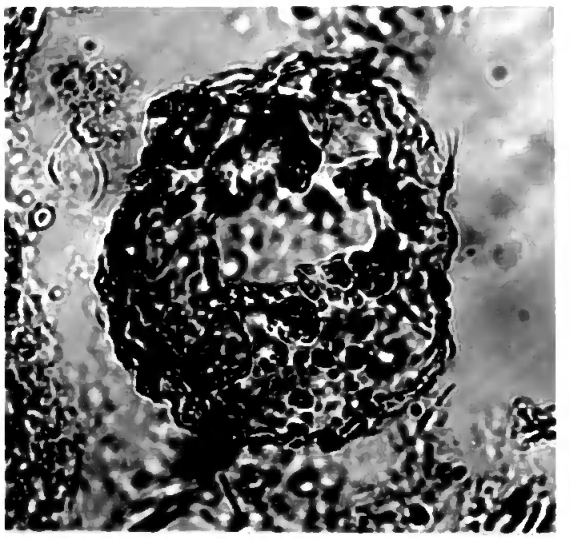
0 20µm

PLATE 3.4 *C. aerophila* var. *sylvatica* (modern)



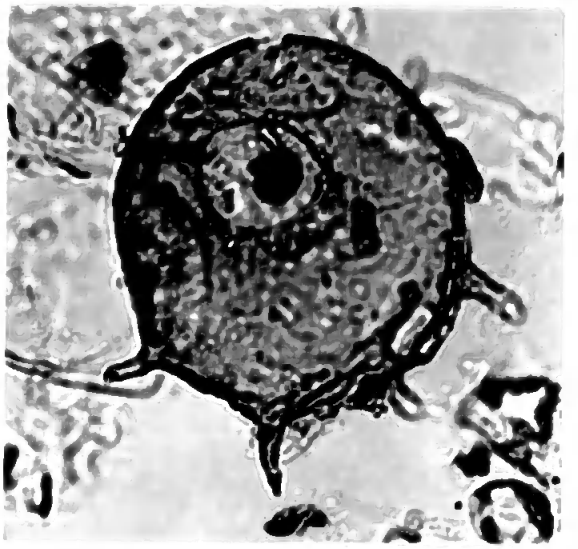
0 25µm

PLATE 3.5 *C. cassis* (modern)



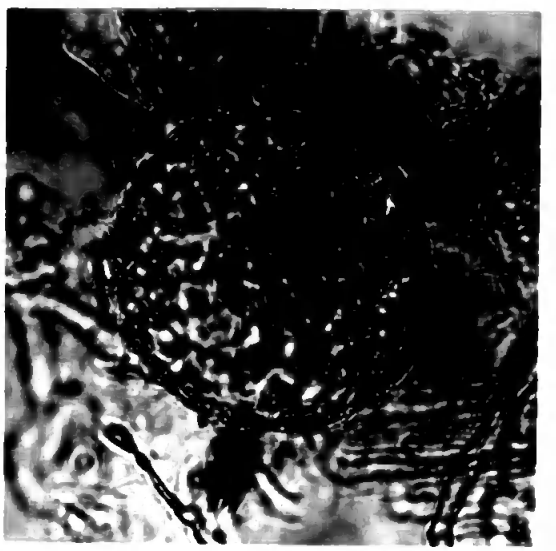
0 15µm

PLATE 3.6 *C. hirsuta* (modern)



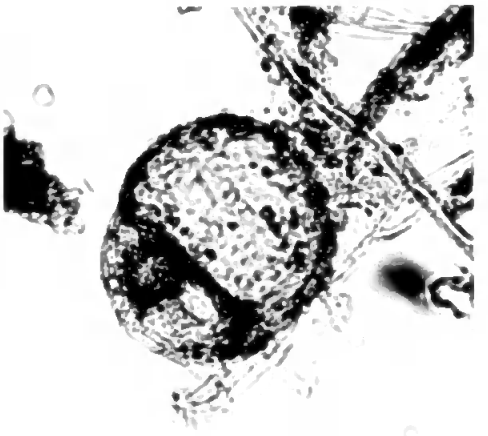
0 15µm

PLATE 3.7 *C orbicularis* (modern)



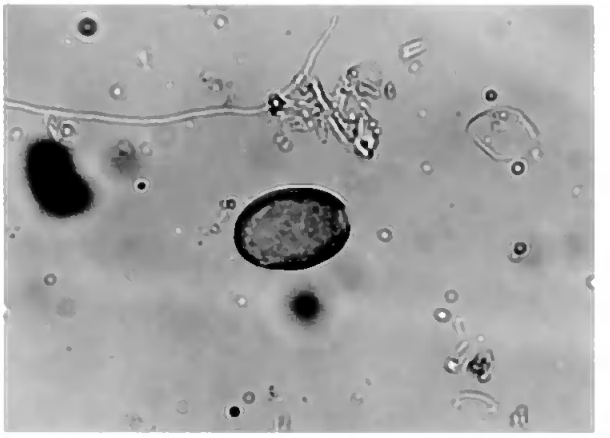
0 25µm

PLATE 3.8 *C. platystoma* (modern)



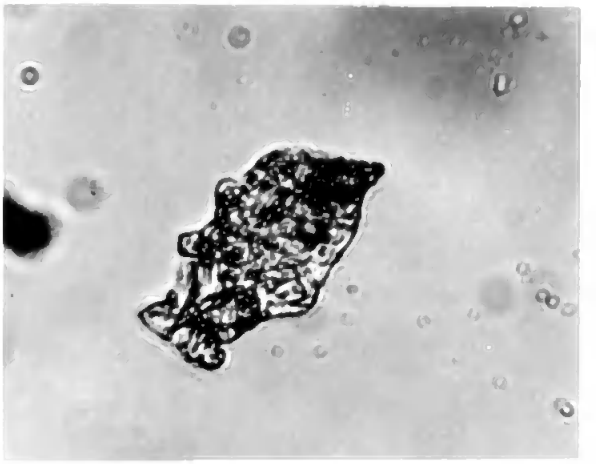
0 20μm

PLATE 4.1 *Cryptodifflugia oviformis* (modern)



0 10μm

PLATE 4.2 *C. sacculus* (modern)



0 5μm

PLATE 5.1 *Difflugia angulostoma* (modern)

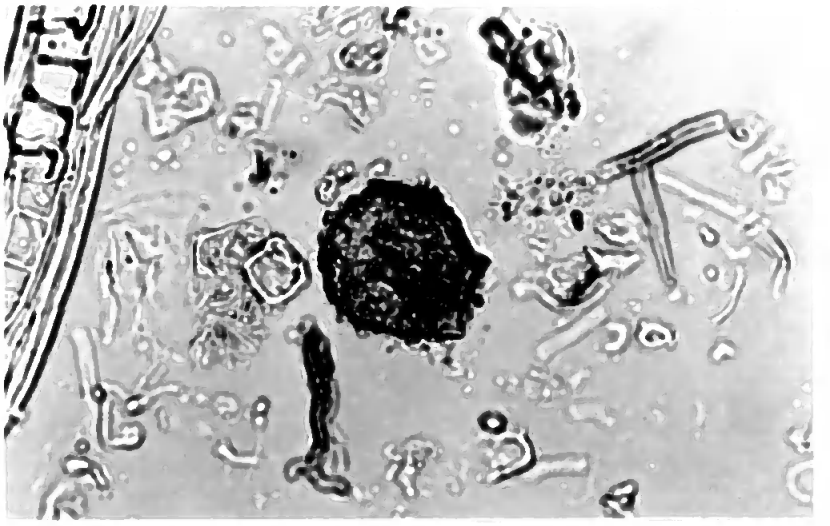
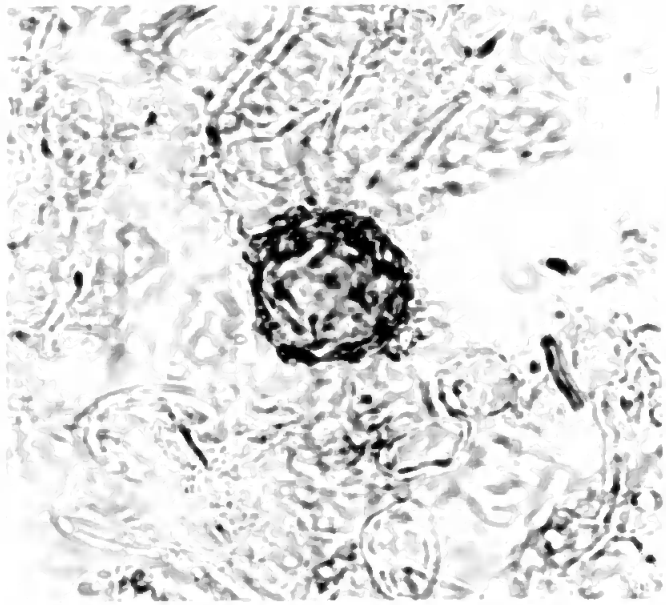


PLATE 5.2 *D. bacillarianum* (Penard Collection, British Museum)

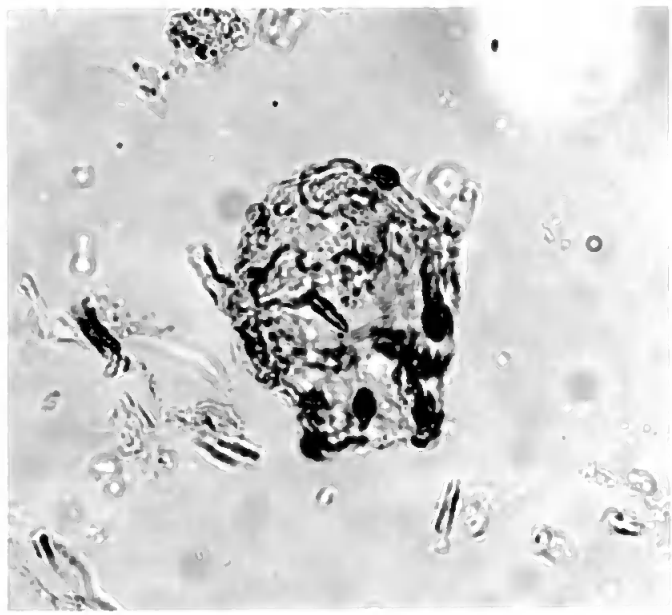
PLATE 5.3 *D. bacillifera* (modern)

PLATE 5.4 *D. globulosa* (modern)



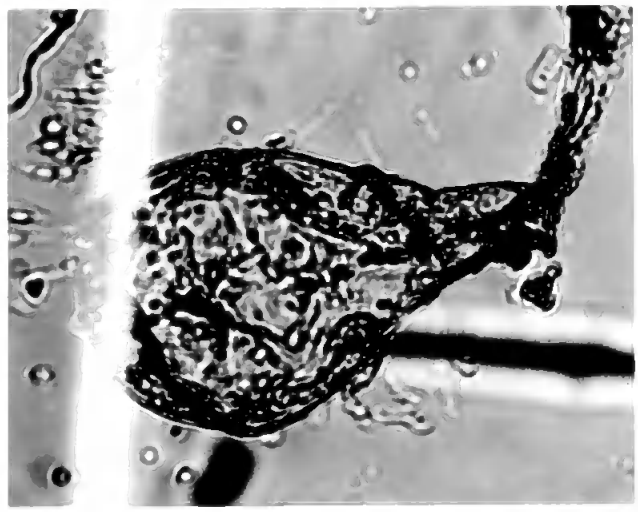
0 40µm

PLATE 5.5 *D. leidyi* (modern)



0 20µm

PLATE 5.6 *D. longicollis* (modern)



0 15µm

PLATE 5.7 *D. oblonga* (modern)

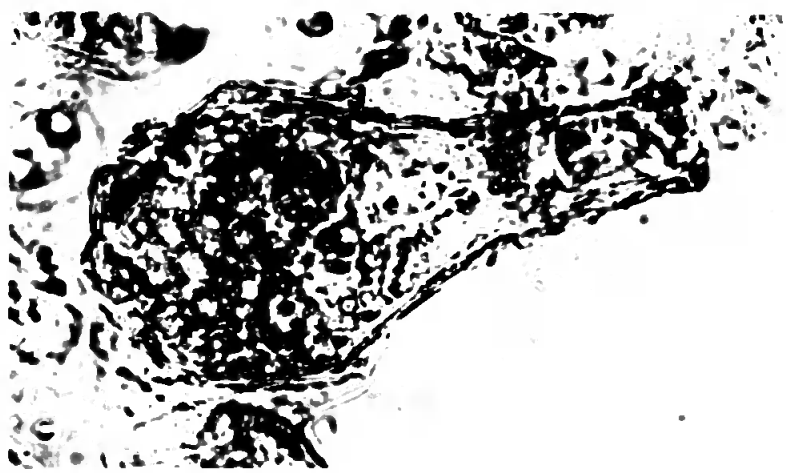


PLATE 5.8 *D. penardi* (modern)

PLATE 5.9 *D. pulex* (modern)

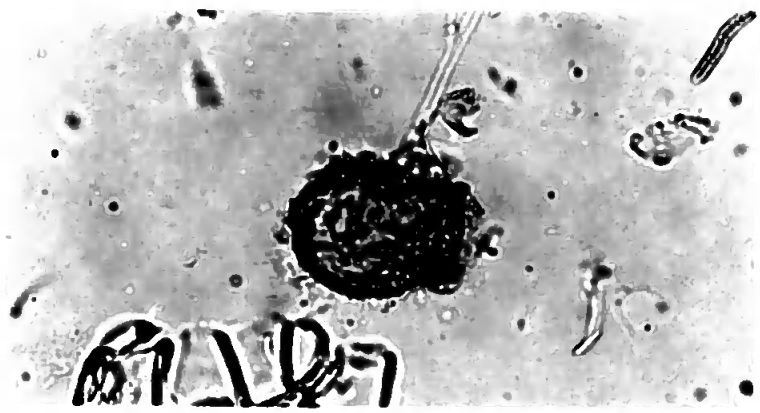


PLATE 5.10 *D. rubescens* (modern)

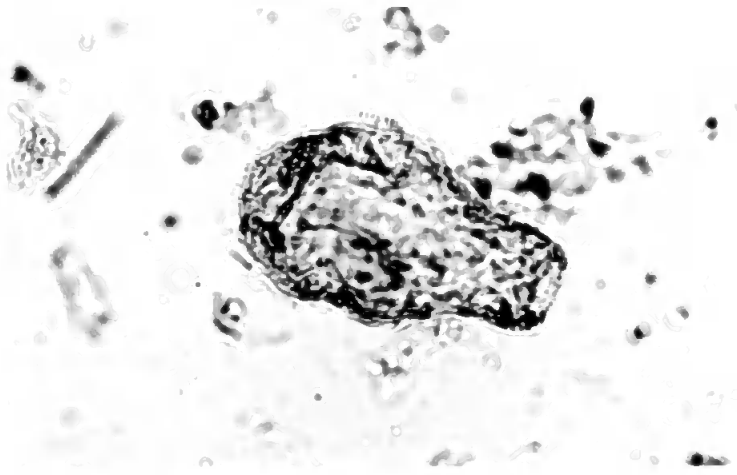


PLATE 5.11 *Pontigulasia compressa* (Penard Collection, British Museum)

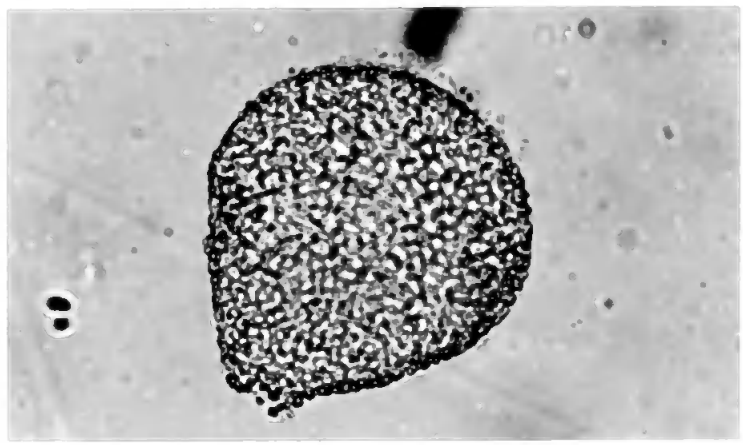


PLATE 6.1 *Assulina muscorum* (modern)

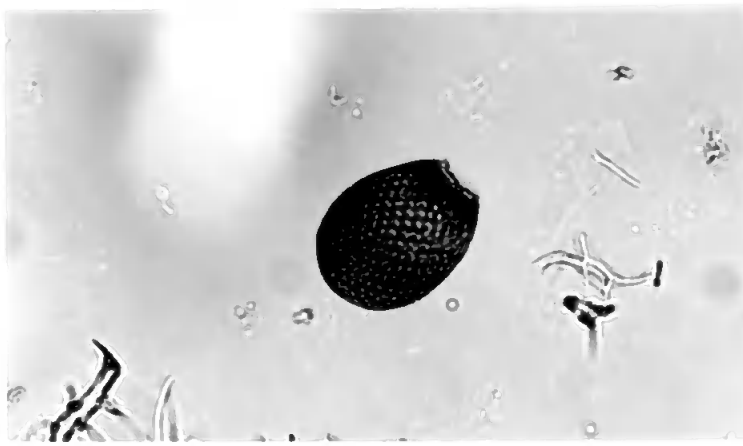
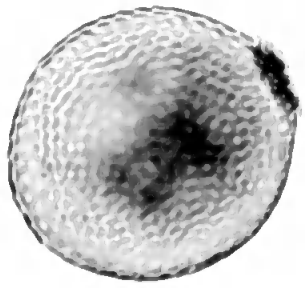
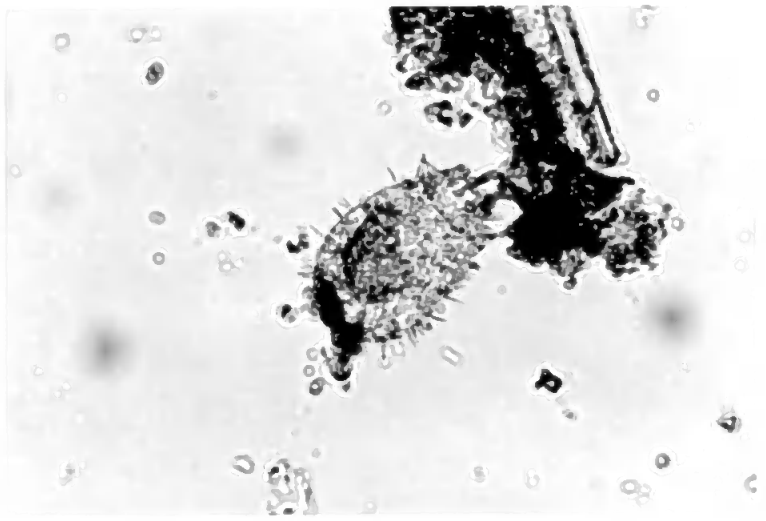


PLATE 6.2 *A. seminulum* (Penard Collection, British Museum)



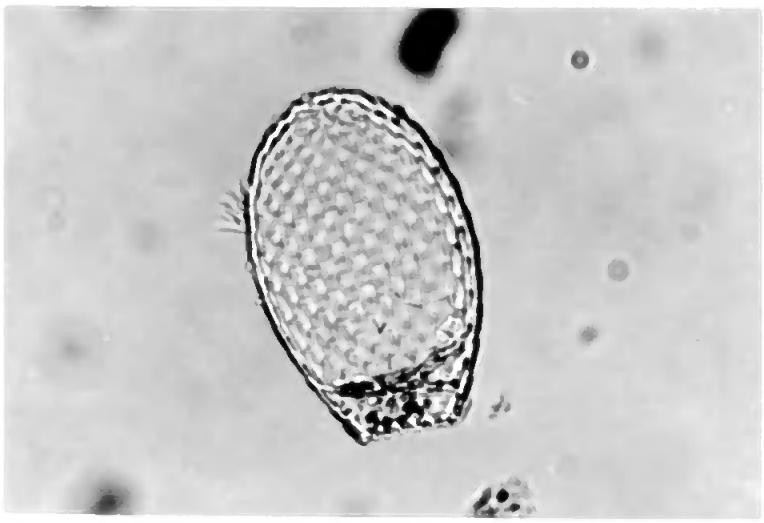
0 15μm

PLATE 6.3 *Euglypha ciliata* (modern)



0 15μm

PLATE 6.4 *E. compressa* (modern)



0 20μm

PLATE 6.5:	***E. rotunda* (Wailes 1911)**
Dimensions:	length 20-50µm (this study); length 22-52µm (Grospietsch, 1958; Corbet 1973); length 34-54µm, breadth 14-24µm (Ogden and Hedley, 1980); length 35µm (Ellison and Ogden, 1987); length 28-57µm (Luftnegger *et al.*, 1988).
Test outline:	ovoid in broad lateral view; circular in narrow lateral view. No spines.
Colour:	colourless.
Test material:	approximately 120 oval, siliceous plates.
Aperture:	terminal; circular and surrounded by 8-14 thickened plates. Diameter 6-10µm (Ogden and Hedley, 1980).
Other features:	none.
References:	Grospietsch (1958); Corbet (1973); Ogden and Hedley (1980); Ellison and Ogden (1987).

PLATE 6.6:	***E. strigosa* (Ehrenburg 1872)**
Dimensions:	length 45-100µm (this study; Corbet, 1973); length 50-85µm (Grospietsch, 1958); length 73-89µm, breadth 32-52µm Ogden and Hedley (1980); length 75µm (Ellison and Ogden, 1987); 72-80µm (Luftnegger *et al.*, 1988).
Test outline:	ovoid in broad lateral view; compressed in narrow lateral view; spines present
Colour:	colourless.
Test material:	approximately 300 oval siliceous plates (Ogden and Hedley, 1980).
Aperture:	terminal; oval and surrounded by 10-14 thickened plates.14-17µm diameter.
Other features:	test covered by slender spines, which project from plate junctions either singly or in pairs. Ogden and Hedley (1980) note that the spines are easily dislodged during preparation for SEM work.
References:	Grospietsch, (1958); Corbet (1973); Ogden and Hedley (1980); Ellison and Ogden (1987); Luftnegger *et al.* (1988).

PLATE 6.7:	***E. tuberculata* (Dujardin 1841)**
Dimensions:	length 45-100µm (this study; Grospietsch, 1958; Corbet, 1973); length 74-95µm (Ogden and Hedley, 1980).
Test outline:	ovoid in broad lateral view; circular in narrow lateral view.
Colour:	colourless.
Test material:	approximately 100 siliceous plates.
Aperture:	terminal; circular; bordered by 8-12 finely-toothed plates. Diameter 18-21µm.
Other features:	in this study, plates of some individuals were more angular hexagonals than those described by Corbet (1973) and Ogden and Hedley (1980), producing an appearance more akin to *E. rotunda*. However, *E. tuberculata* individuals identified by larger test size.
References:	Grospietsch (1958); Corbet (1973); Ogden and Hedley (1980).

PLATE 6.5 *E. rotunda* (modern)
(a) broad lateral view (b) apertural view

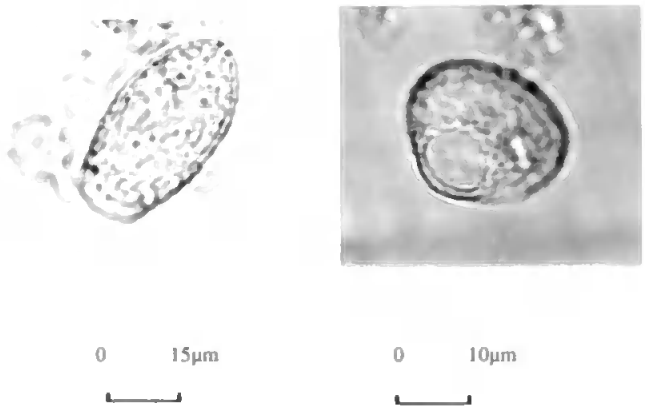


PLATE 6.6 *E. strigosa* (Penard Collection, British Museum)

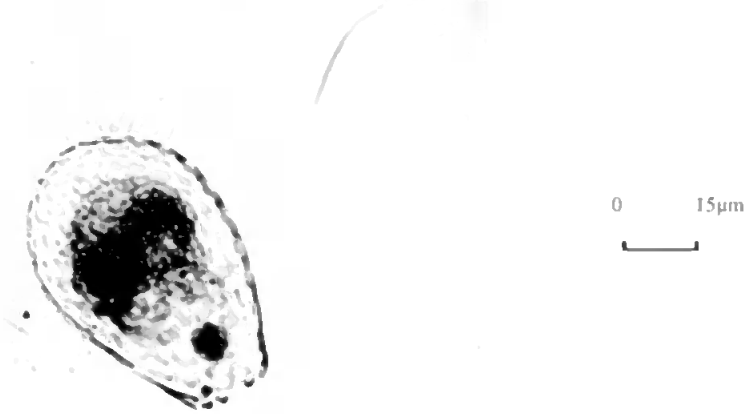


PLATE 6.7 *E. tuberculata* (modern)

PLATE 6.8:	***Placocista spinosa* (Carter 1865)**
Dimensions:	length 143-160µm, breadth 87-110µm (this study; Ogden and Hedley, 1980); length 100-155µm (Grospietsch, 1958); length 116-174µm (Corbet, 1973).
Test outline:	ovoid in broad lateral view, with semi-circular aboral region and blunt, but concave apertural region. Pairs of spines present at test margins.
Colour:	colourless.
Test material:	approximately 400 oval, siliceous plates (Ogden and Hedley, 1980); overlapping and arranged in regular rows. Aperture has thin collar of organic cement.
Aperture:	terminal; wide, concave; 58-79µm diameter.
Other features:	none.
References:	Grospietsch (1958); Corbet (1973); Ogden and Hedley (1980).

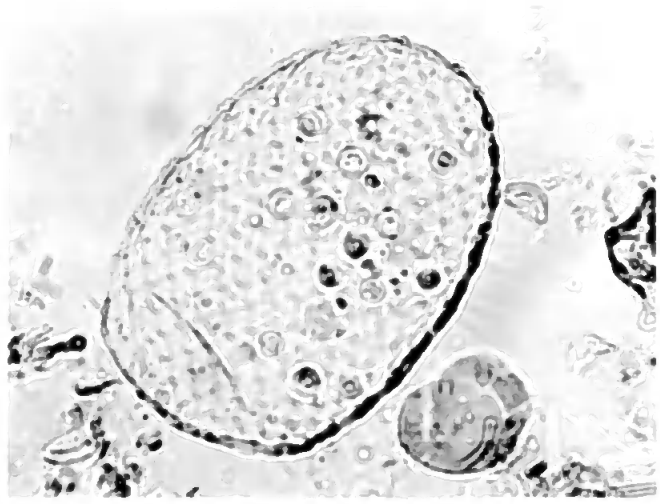
PLATE 6.9:	***Sphenoderia lenta* (Schlumberger 1845)**
Dimensions:	length 49-51µm, breadth 30-33µm (this study); length 30-64µm (Corbet, 1973); length 47-55µm, breadth 35-40µm (Ogden and Hedley, 1980).
Test outline:	circular, with a flared collar in broad lateral view.
Colour:	colourless.
Test material:	approximately 60 circular siliceous plates (Ogden and Hedley, 1980). Smaller plates cover the collar.
Aperture:	terminal, linear (Ogden and Hedley, 1980); 16-19µm diameter.
Other features:	similar to *A. muscorum* in size, but can be distinguished by shape (ovoid) and colourless test.
References:	Corbet (1973); Ogden and Hedley (1980).

7. GROMIIDAE

Test is proteinaceous, sometimes with agglutinated particles. Single aperture. One genus: *Pseudodifflugia.*

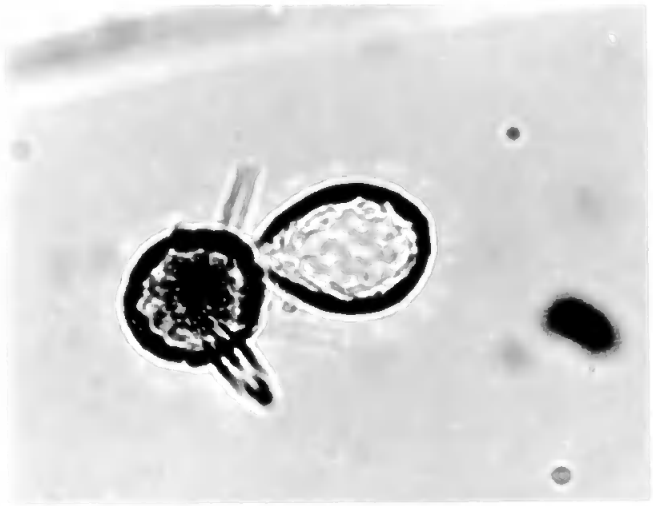
PLATE 7.1:	***Pseudodifflugia fulva* (Archer 1870)**
Dimensions:	length 28-30µm, breadth 24-27µm (this study); length 36µm, breadth 30µm (Ogden and Hedley 1980).
Test outline:	ovoid in broad lateral view, circular in narrow lateral view. Untidy outline produced by agglutinated particles.
Colour:	brown; yellow or brown (Ogden and Hedley, 1980).
Test material:	proteinaceous and thickly coated with agglutinated mineral particles and diatom frustules.
Aperture:	terminal and approximately circular (Ogden and Hedley, 1980).
Other features:	none.
References:	Ogden and Hedley (1980).

PLATE 6.8 *Placocista spinosa* (modern)



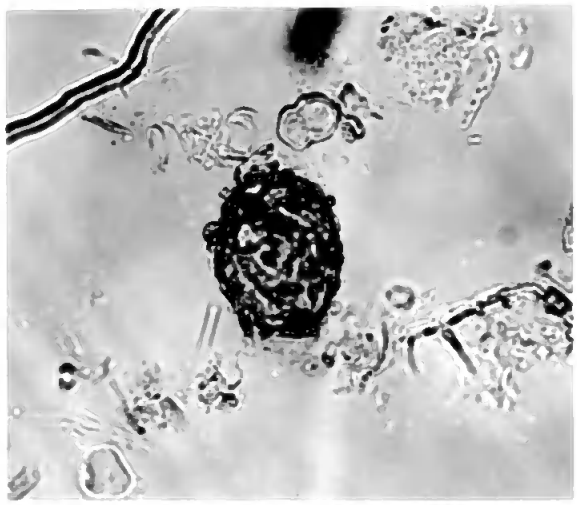
0 25μm

PLATE 6.9 *Sphenoderia lenta* (Penard Collection, British Museum)



0 20μm

PLATE 7.1 *Pseudodifflugia fulva* (modern)



0 15μm

8. HYALOSPHENIIDAE

Ovoid or pyriform test which is laterally compressed; composed of either proteinaceous material or siliceous plates, sometimes with agglutinated mineral particles (Ogden and Hedley, 1980). Terminal aperture; oval, circular or linear. Five genera: *Hyalosphenia; Heleopera; Nebela; Quadrulella; Lesquereusia.*

PLATE 8.1:	*Heleopera petricola* (Leidy 1879)
Dimensions:	length 75-85µm, breadth 50-60µm (this study); length 60-73µm, breadth 40-57µm (Hoogenraad and de Groot (1952); length 56-65µm, breadth 39-46µm and length 90-106µm, breadth 52-70µm (de Graaf, 1956); length 70-135µm (Grospietsch, 1958); length 80-125µm (Corbet, 1973); length 76-84µm, breadth 51-57µm; length 75-95µm (Ellison and Ogden, 1987).
Test outline:	ovoid in broad lateral view; flattened in narrow lateral view.
Colour:	colourless in this study; brown, purple or violet (Ogden and Hedley, 1980).
Test material:	siliceous plates with quartz particles in aboral region.
Aperture:	terminal; 31-34µm diameter; aperture margins thickened, slightly convex; elliptical opening bordered by a thin collar or organic cement (Ogden and Hedley, 1980).
Other features:	Corbet (1973) notes that *H. petricola* varies in size and colour, but that the aperture features separate *H. petricola* from the other species of *Heleopera*, except *H. rosea*, which can be distinguished by its colour (see below).
References:	Hoogenraad and de Groot (1952); de Graaf (1956); Grospietsch (1958); Corbet (1973); Ogden and Hedley (1980); Ellison and Ogden (1987).

PLATE 8.2:	*H. rosea* (Penard 1890)
Dimensions:	length 110-130µm, breadth 95-110µm (this study); length 82-115µm, breadth 63-95µm (Hoogenraad and de Groot (1956); length 95-130µm (Grospietsch, 1958); length 120-135µm (Corbet, 1973); length 117-128µm, breadth 94-107µm (Ogden and Hedley, 1980); length 110-125µm (Ellison and Ogden, 1987).
Test outline:	ovoid in broad lateral view; flattened in narrow lateral view.
Colour:	wine-red in this study; rose-red (Corbet, 1973); red (Ogden and Hedley, 1980).
Test material:	siliceous plates with some quartz particles in aboral region.
Aperture:	terminal; thin linear slit (Ogden and Hedley, 1980); 47-73µm diameter.
Other features:	distinguished from other members of Heleopera by colour.
References:	Hoogenraad and de Groot (1956); Grospietsch (1958); Corbet (1973); Ogden and Hedley (1980); Ellison and Ogden (1987).

PLATE 8.3:	*H. sphagni* (Leidy 1874)
Dimensions:	length 90-120µm, breadth 70-75µm (this study); length 80-130µm (Grospietsch, 1958); length 100-145µm (Corbet, 1973); length 94-108µm, breadth 70-73µm (Ogden and Hedley, 1980); length 90-140µm (Ellison and Ogden, 1987).
Test outline:	ovoid in broad lateral view; compressed in narrow lateral view.
Colour:	golden yellow or brown.
Test material:	siliceous plates at the apertural region; sand grains coating the aboral region.
Aperture:	terminal; slightly convex in lateral view. Narrow and bordered by a thin collar of organic cement (Ogden and Hedley, 1980).
Other features:	in living individuals, the cytoplasm contains zoochlorellae; this is absent in fossil specimens.
References:	Grospietsch (1958); Corbet (1973); Ogden and Hedley (1980); Ellison and Ogden (1987).

PLATE 8.1 *Heleopera petricola* (modern)

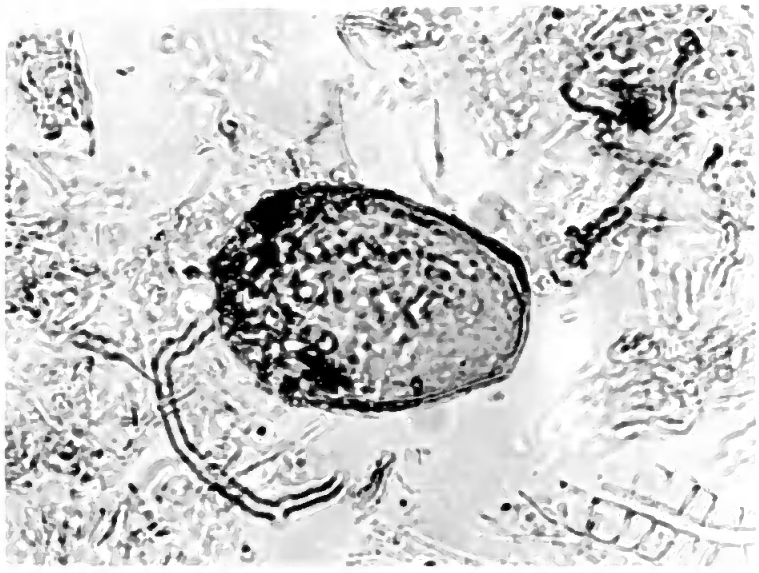


PLATE 8.2 *H. rosea* (modern)

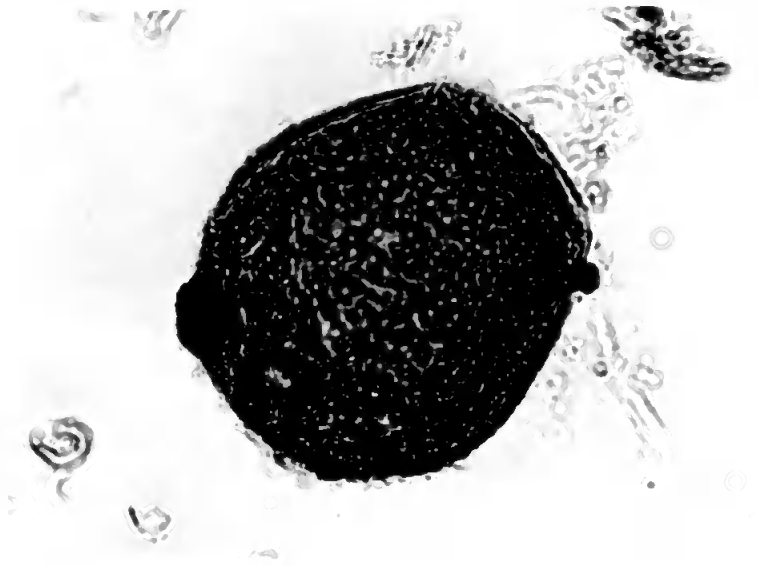


PLATE 8.3 *H. sphagni* (modern)

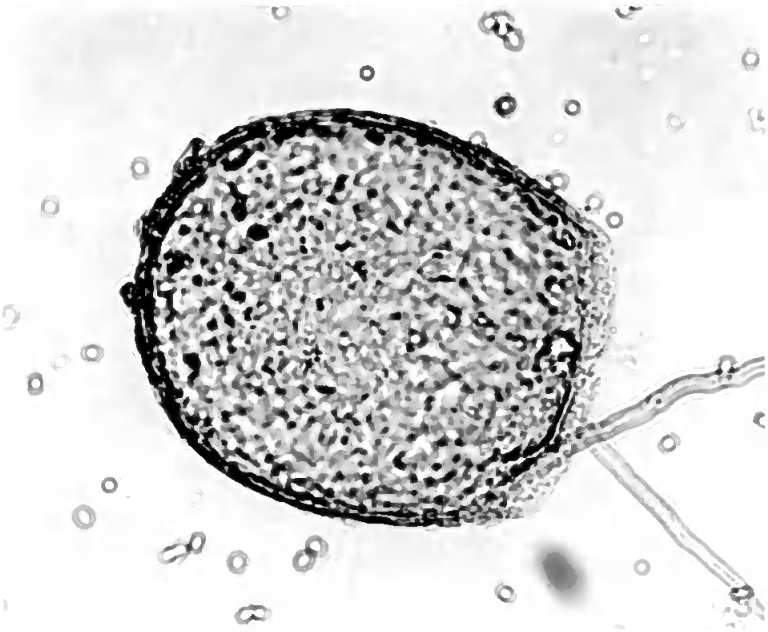
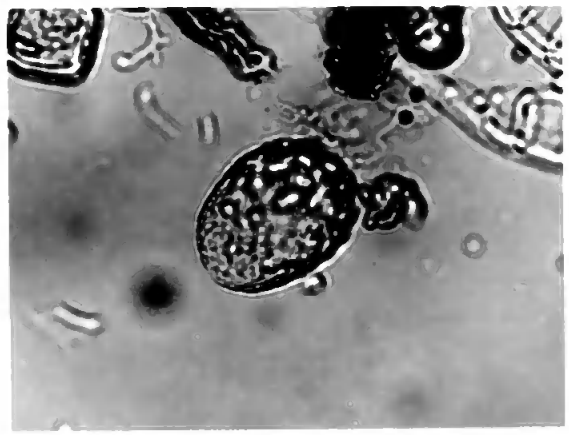


PLATE 8.4:	*H. sylvatica* (Penard 1890)
Dimensions:	length 58-67μm (this study); length 50-75μm (Grospietsch, 1958; Corbet, 1973).
Test outline:	narrower than other members of *Heleopera*, with markedly convex apertural region.
Colour:	colourless; transparent.
Test material:	small quartz particles? or plates?
Aperture:	terminal; strongly convex, curves smoothly round to side walls.
Other features:	none.
References:	Grospietsch (1958); Corbet (1973).

PLATE 8.5:	*Hyalosphenia elegans* (Leidy 1874)
Dimensions:	length 81-96μm (this study); length 90-100μm Grospietsch (1958; Corbet, 1973); length 80μm (Ellison and Ogden, 1987).
Test outline:	flask-shaped in broad lateral view, with distinct neck and surface undulations; compressed in narrow lateral view.
Colour:	colourless; transparent.
Test material:	proteinaceous.
Aperture:	terminal, compressed.
Other features:	a very distinctive species; living individuals contain zoochlorellae in their cytoplasm; this is absent in fossil specimens.
References:	Grospietsch (1958); Corbet (1973); Ellison and Ogden (1987).

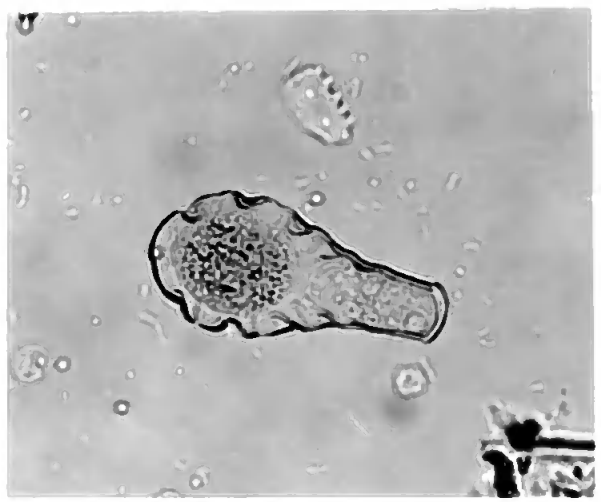
PLATE 8.6:	*H. ovalis* (Wailes 1912)
Dimensions:	length 34-41μm, breadth 25-32μm (this study); length 39μm, breadth 27μm (Warner, 1990).
Test outline:	ovoid in broad lateral view; semi-circular aboral region; walls curve towards aperture.
Colour:	colourless; transparent.
Test material:	proteinaceous.
Aperture:	terminal; straight, with smooth margins; diameter 12μm (this study), 10μm (Warner, 1990).
Other features:	green zoochlorellae are easily seen through the test of living individuals, but are absent in fossil specimens.
References:	Warner (1990).

PLATE 8.4 *H. sylvatica* (modern)



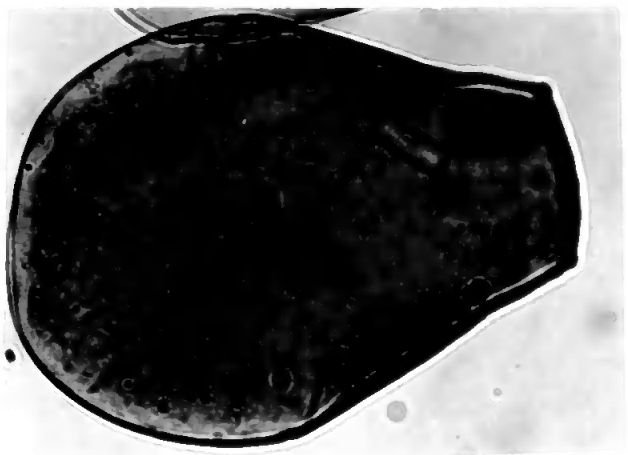
0 **20**µm

PLATE 8.5 *Hyalosphenia elegans* (modern)



0 20µm

PLATE 8.6 *H. ovalis* (modern)



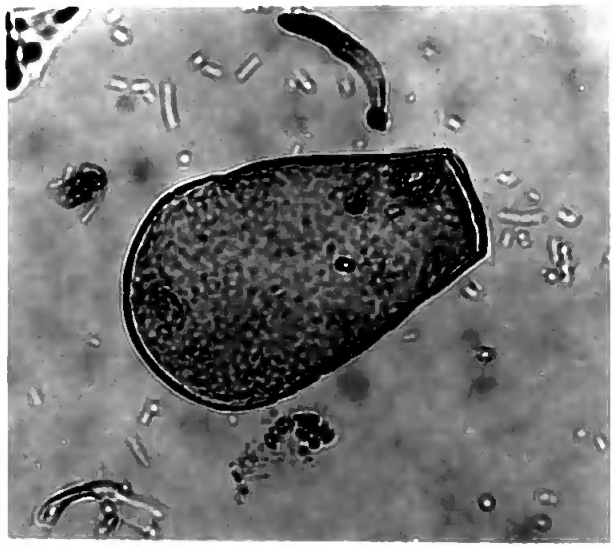
0 5µm

PLATE 8.7:	***H. papilio* (Leidy 1875)**
Dimensions:	length 110-133µm, breadth 80-90µm (this study); length 120µm, breadth 70µm (Hoogenraad and de Groot, 1952); length 90-123µm, breadth 60-81µm (de Graaf, 1956); length 90-130µm (Grospietsch, 1958; Corbet, 1973); length 111-113µm, breadth 81-91µm (Ogden and Hedley, 1980); length 150µm (Ellison and Ogden, 1980).
Test outline:	ovoid or pyriform in broad lateral view and strongly compressed in narrow lateral view.
Colour:	colourless, transparent.
Test material:	completely proteinaceous.
Aperture:	terminal and surrounded by a small collar (Ogden and Hedley, 1980); diameter 31-34µm (this study); 32-40µm (Ogden and Hedley, 1980).
Other features:	one lateral pore present on each side at the widest part of the test. Ogden and Hedley (1980, after Grospietsch, 1965) note a second form of this species which has a concave aperture and several lateral pores, but this was not present in this study.
References:	Hoogenraad and de Groot (1952); de Graaf (1956); Grospietsch (1958); Corbet (1973); Ogden and Hedley (1980); Ellison and Ogden (1987); Boborov *et al.* (1995).

PLATE 8.8:	***H. subflava* (Cash and Hopkinson 1909)**
Dimensions:	length 50-60µm, breadth 35-38µm (this study); length 47-103µm, breadth 53-60µm (Hoogenraad and de Groot, 1952); length 57-70µm (Grospietsch, 1958); length 56-62µm, breadth 37-38µm (Ogden and Hedley, 1980).
Test outline:	ovoid and smooth in broad lateral view; elliptical in narrow lateral view.
Colour:	colourless or yellow; transparent.
Test material:	proteinaceous.
Aperture:	terminal, oval; circular (Ogden and Hedley, 1980).
Other features:	none.
References:	Hoogenraad and de Groot (1952); Grospietsch (1958); Ogden and Hedley (1980).

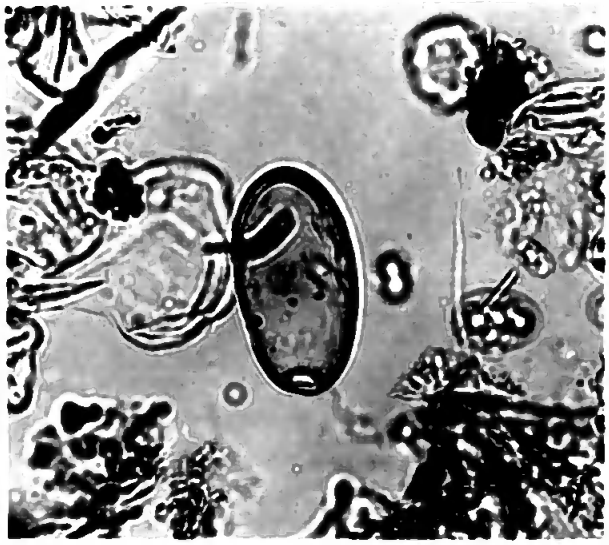
PLATE 8.9:	***Lesquereusia spiralis* (Ehrenburg 1840)**
Dimensions:	length 90-120µm, breadth 85-110µm (this study); length 100-150µm (Grospietsch, 1958); length 89-117µm, breadth 86-109µm (Ogden and Hedley, 1980); length 90-120µm (Ellison and Ogden (1987).
Test outline:	circular or ovoid in broad lateral view, with unsymmetrical neck. Compressed in narrow lateral view.
Colour:	colourless.
Test material:	siliceous rods interspersed with organic cement (Ogden and Hedley, 1980).
Aperture:	terminal, circular and bordered by siliceous rods.
Other features:	none; the curved siliceous rods render this a very distinctive species.
References:	Grospietsch (1958); Ogden and Hedley (1980); Ellison and Ogden (1987).

PLATE 8.7 *H. papilio* (modern)



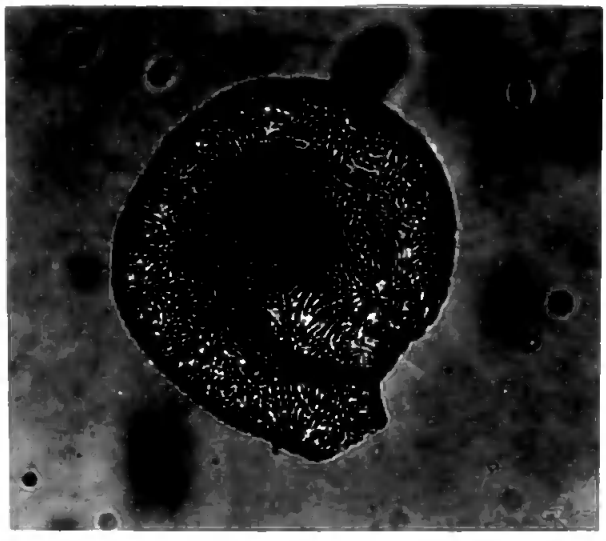
0 25µm

PLATE 8.8 *H. subflava* (modern)



0 20µm

PLATE 8.9 *Lesquereusia spiralis* (Penard Collection, British Museum)



0 20µm

PLATE 8.10:	*Nebela barbata* (Leidy 1874)
Dimensions:	length 96-106µm, breadth 38-44µm (this study); length 95-108µm, breadth 38µm (Hoogenraad and de Groot, 1952); length 120-148µm, breadth 40-62µm (de Graaf, 1956); length 80-160µm (Corbet, 1973); length 96-106µm, breadth 38-44µm (Ogden and Hedley (1980); length 120-150 (Ellison and Ogden, 1987).
Test outline:	pyriform, with an elongated neck in broad lateral view.
Colour:	colourless.
Test material:	a mixture of oval, circular and elongate plates, with fine spines projecting from junctions of shell plates (Ogden and Hedley, 1980).
Aperture:	terminal; oval and surrounded by a collar of organic cement. Ogden and Hedley (1980), using SEM, describe 8 tooth-like protrusions on the inner rim, but these are very difficult to see under light microscopy.
Other features:	spines often flattened against the broad test surface and difficult to see. Ogden and Hedley (1980) suggest that the spines are fragile and may be lost in handling; they also suggest that the tooth-like protrusions lining the aperture may be variable features.
References:	Hoogenraad and de Groot (1952); de Graaf (1956); Corbet (1973); Ogden and Hedley (1980); Ellison and Ogden (1987).

PLATE 8.11:	*N. carinata* (Archer 1867)
Dimensions:	length 140-200µm, breadth 110-152µm (this study); length 197-240µm, breadth 150-173µm (Hoogenraad and de Groot, 1952); length 170-22µm, breadth 125-140µm (de Graaf, 1956); length 167-230µm (Grospietsch, 1958); length 140-180µm (Corbet, 1973); length 155-202µm, breadth 110-152µm (Ogden and Hedley, 1980); length 160µm (Ellison and Ogden, 1987).
Test outline:	oval or pyriform, with a compressed lateral margin which forms a broad keel extending to the aperture in broad lateral view. Flattened with compressed margins in narrow lateral view.
Colour:	colourless.
Test material:	composed of oval or circular siliceous plates. Ogden and Hedley (1980) report that small beads of organic cement are often interspersed with the plates, but these are difficult to see under light microscopy.
Aperture:	terminal; oval and surrounded by a thin collar of organic cement.
Other features:	Ogden and Hedley (1980) note a small lateral pore at each margin, just behind the aperture, but these was not seen during this study.
References:	Hoogenraad and de Groot (1952); de Graaf (1956); Grospietsch (1958); Corbet (1973); Ogden and Hedley (1980); Ellison and Ogden (1987).

PLATE 8.12:	*N. collaris* (Ehrenburg 1848)
Dimensions:	length 107-184µm (this study); length 93-128µm, breadth 62-100µm (de Graaf, 1956); length 94-184µm (Grospietsch, 1958); length 107-184µm (Corbet, 1973); length 98-153µm, breadth 72-91µm (Ogden and Hedley, 1980); length 100-150µm (Ellison and Ogden, 1987).
Test outline:	ovoid in broad lateral view; compressed in narrow lateral view.
Colour:	colourless.
Test material:	oval or circular siliceous plates arranged in regular rows, which do not overlap.
Aperture:	terminal; ovoid; smooth thin collar of organic cement.
Other features:	none.
References:	de Graaf (1956); Grospietsch (1958); Corbet (1973); Ogden and Hedley (1980); Ellison and Ogden (1987).

PLATE 8.10 *Nebela barbata* (Penard Collection, British Museum)

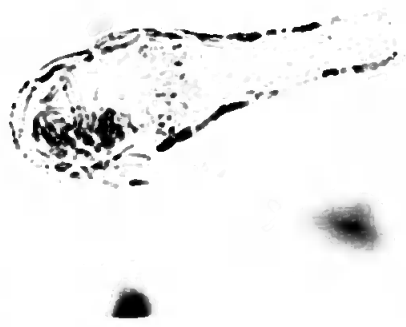


PLATE 8.11 *N. carinata* (modern)

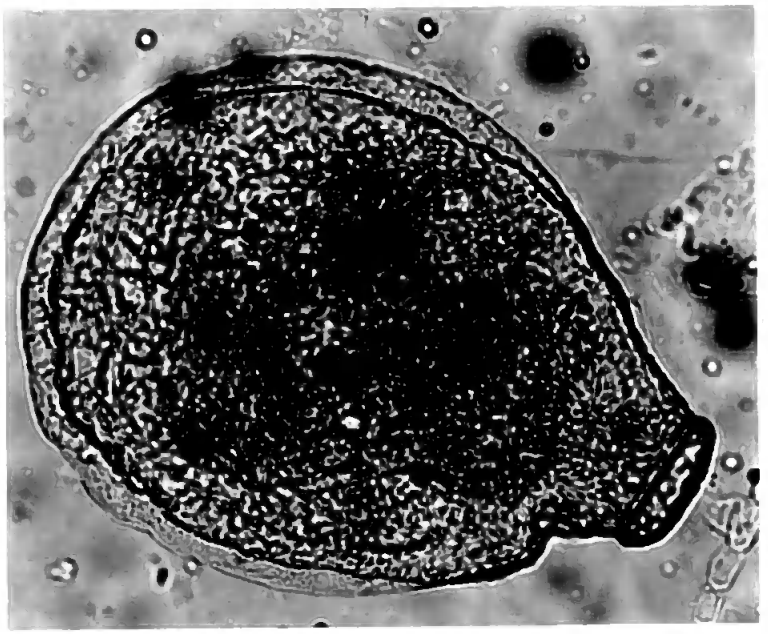


PLATE 8.12 *N. collaris* (modern)

PLATE 8.13: *N. flabellulum* (Leidy 1874)

Dimensions: length 76-150µm, breadth 86-160µm (this study); length 73-100µm, breadth 80-113µm (Hoogenraad and de Groot, 1952); length 72-96µm (Corbet, 1973); length 76-88µm, breadth 86-95µm (Ogden and Hedley, 1980); length 100µm (Ellison and Ogden, 1987).

Test outline: circular or ovoid in broad lateral view; compressed in narrow lateral view.

Colour: colourless.

Test material: siliceous plates of assorted shapes and sizes. The plate edges are sometimes unclear, Ogden and Hedley (1980) ascribe this to a thin covering of organic cement.

Aperture: terminal; straight; oval; surrounded by a collar of organic cement. Diameter 18-25µm (Ogden and Hedley, 1980).

Other features: Ogden and Hedley (1980) note the similarity between this species and *N. tincta* and *N. collaris*, suggesting that it can be separated by being wider in size than long.

References: Hoogenraad and de Groot (1952); Corbet (1973); Ogden and Hedley (1980); Ellison and Ogden (1987).

PLATE 8.14: *N. griseola* (Penard 1911)

Dimensions: length 81-86µm, breadth 63-80µm (this study); length 67-97µm (Grospietsch, 1958); length 70-85µm (Corbet, 1973); length 82-88µm, breadth 62-69µm (Ogden and Hedley, 1980); length 60-100µm (Ellison and Ogden, 1987).

Test outline: pyriform in broad lateral view; in narrow lateral view, slightly compressed.

Colour: yellow or brown.

Test material: siliceous plates and quartz particles.

Aperture: terminal; circular and bordered by a prominent collar of plates. Diameter 20-21µm (Ogden and Hedley, 1980).

Other features: none.

References: Grospietsch (1958); Corbet (1973); Ogden and Hedley (1980); Ellison and Ogden (1987).

PLATE 8.15: *N. lageniformis* (Penard 1890)

Dimensions: length 120-130µm (this study; Corbet 1973); length 53-67µm, breadth 27-33µm (Hoogenraad and de Groot (1952); length 119-131µm (de Graaf (1956); length 119-131µm, breadth 68-85µm (Meisterfeld, 1979); length 120µm (Ellison and Ogden, 1987).

Test outline: flask-shaped in broad lateral view; compressed in narrow lateral view.

Colour: colourless, transparent. Yellow-tinted (Corbet, 1973).

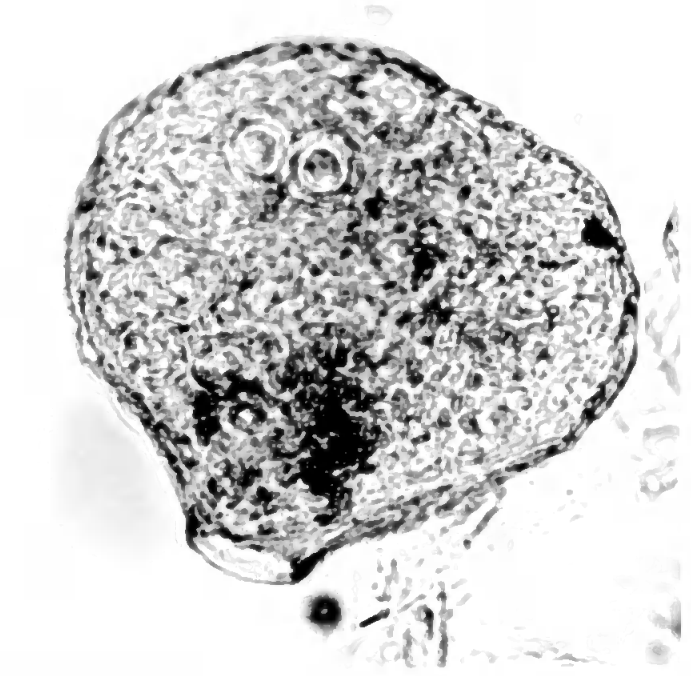
Test material: rounded siliceous plates cemented into neat rows.

Aperture: slightly convex with a thin border of secretion to produce a smooth rim.

Other features: smaller forms have been described as another species, *N. wailesi* (Corbet, 1973; Meisterfeld, 1979).

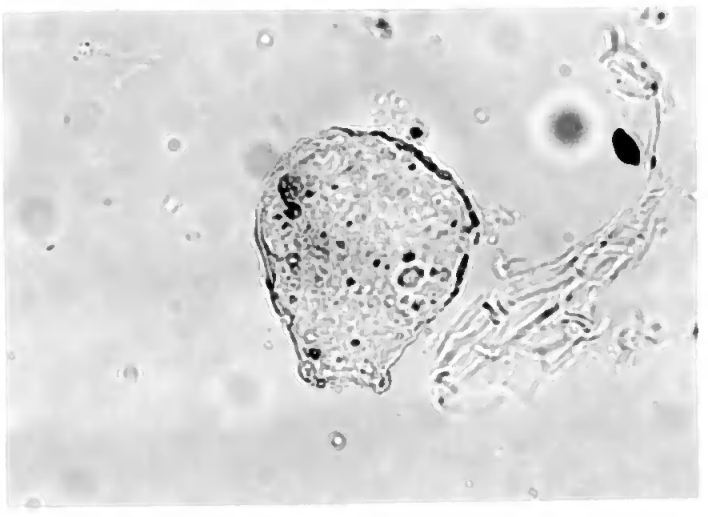
References: Hoogenraad and de Groot (1952); Grospietsch (1958); Corbet (1973); Meisterfeld (1979); Ellison and Ogden (1987).

PLATE 8.13 *N. flabellulum* (modern)



0 20µm

PLATE 8.14 *N. griseola* (modern)



0 25µm

PLATE 8.15 *N. lageniformis* (Penard Collection, British Museum)

0 25µm

PLATE 8.16:	*N. marginata* (Penard 1902)
Dimensions:	length 143-168µm (this study); length 126-150µm, breadth 89-110µm (de Graaf, 1956); length 140-170µm (Grospietsch, 1958; Corbet, 1973; Ellison and Ogden, 1987).
Test outline:	pyriform in broad lateral view with thin compression at margins to produce a narrow keel; compressed in narrow lateral view.
Colour:	tinted yellow-grey; brown (Corbet, 1973).
Test material:	siliceous plates, bound by organic cement. Neatly arranged without touching each other.
Aperture:	terminal; slightly concave, with a thin rim of secretion.
Other features:	this species closely resembles *N. carinata* but can be distinguished by a narrower and shorter keel, which extends for half-distance along the test margins.
References:	de Graaf (1956); Grospietsch (1958); Corbet (1973); Ellison and Ogden (1987).

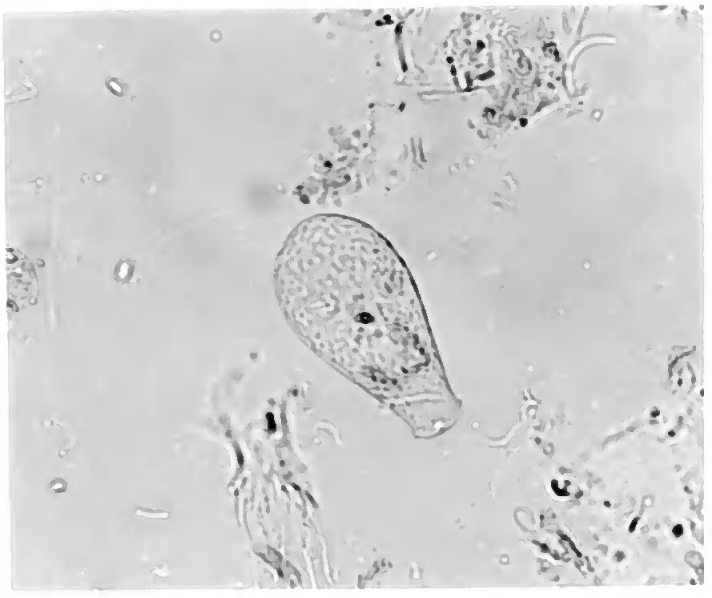
PLATE 8.17:	*N. militaris* (Penard 1890)
Dimensions:	length 47-68µm, breadth 22-26µm (this study); length 50-72µm (Grospietsch, 1958; Corbet, 1973); length 59-70µm, breadth 33-41µm (Ogden and Hedley, 1980); length 45-75µm (Ellison and Ogden, 1987); length 29µm, breadth 15µm (Warner, 1990); length 42-46µm, breadth 24-28µm (Bobrov *et al.*, 1995).
Test outline:	pyriform or ovoid in broad lateral view; compressed in narrow lateral view. Lateral pores positioned near the aperture.
Colour:	colourless.
Test material:	mixture of circular, oval and circular siliceous plates.
Aperture:	terminal; convex in broad lateral view; diameter 10µm (this study); 15-18 (Ogden and Hedley, 1980); 12µm (Bobrov *et al.*, 1995). Narrow slit in transverse section. Surrounded by a thick organic collar.
Other features:	none.
References:	Grospietsch (1958); Corbet (1973); Ogden and Hedley (1980); Ellison and Ogden (1987); Warner (1990); Bobrov *et al.* (1995).

PLATE 8.18:	*N. minor* (Penard 1902)
Dimensions:	length 83-89µm (this study); length 70-84µm, breadth 45-53µm (de Graaf, 1956); length 80-100µm (Corbet (1973).
Test outline:	pyriform; tapers to a wide aperture in broad lateral view.
Colour:	colourless; transparent.
Test material:	elongate siliceous plates neatly cemented together.
Aperture:	terminal; wide (23-27µm), with a thin border of organic cement.
Other features:	a pair of lateral pores (Corbet, 1973); in the specimen illustrated, they are located just behind the aperture.
References:	de Graaf (1956); Corbet (1973).

PLATE 8.16 *N. marginata* (Penard Collection, British Museum)

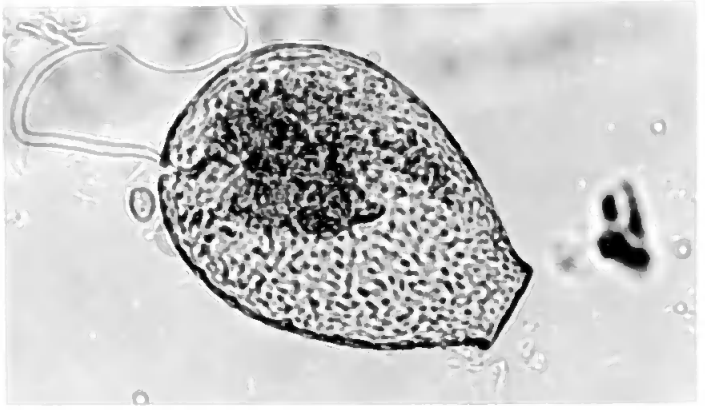
0 25µm

PLATE 8.17 *N. militaris* (Modern)



0 15µm

PLATE 8.18 *N. minor* (Modern)



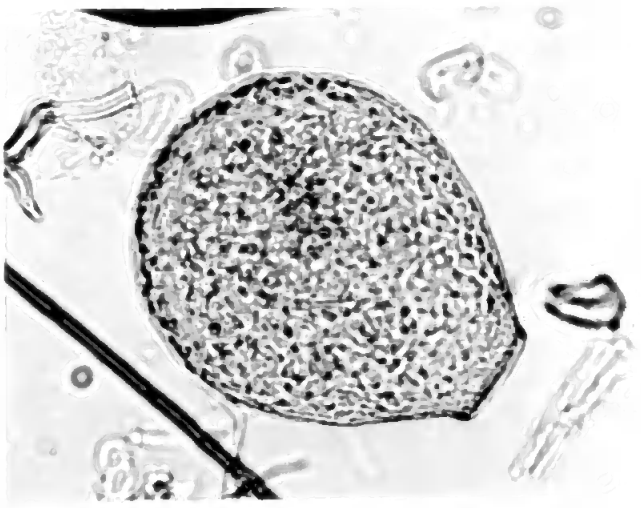
0 30µm

PLATE 8.19:	*N. parvula* (Cash 1909)
Dimensions:	length 82-88µm (this study); length 78-90µm (Grospietsch, 1958; Corbet, 1973)
Test outline:	ovoid in broad lateral view, tapering to a straight aperture; compressed in narrow lateral view.
Colour:	colourless and slightly transparent.
Test material:	polygonal siliceous plates, irregularly cemented together.
Aperture:	terminal; straight, with thin border of secretion.
Other features:	very similar to *N. collaris*, but separated by absence of lateral pores, more transparent test and less pyriform outline (Corbet, 1973).
References:	Grospietsch (1958); Corbet (1973).

PLATE 8.20:	*N. tincta* (Leidy 1879)
Dimensions:	length 78-89µm, breadth 54-67µm (this study); length 80-110µm, breadth 54-83µm (de Graaf, 1956); length 76-92µm (Grospietsch, 1958); length 70-120µm (Corbet, 1973); length 76-94µm, breadth 51-71µm (Ogden and Hedley, 1980).
Test outline:	ovoid, with a small neck at the aperture in broad lateral view; compressed in narrow lateral view.
Colour:	colourless and transparent; yellow (Ogden and Hedley, 1980).
Test material:	oval or circular siliceous plates, obscured by a thin layer of organic cement (Ogden and Hedley, 1980).
Aperture:	terminal; oval and surrounded by a thin collar.
Other features:	a pair of small lateral pores located behind the aperture.
References:	de Graaf (1956); Grospietsch (1958); Corbet (1973); Ogden and Hedley (1980).

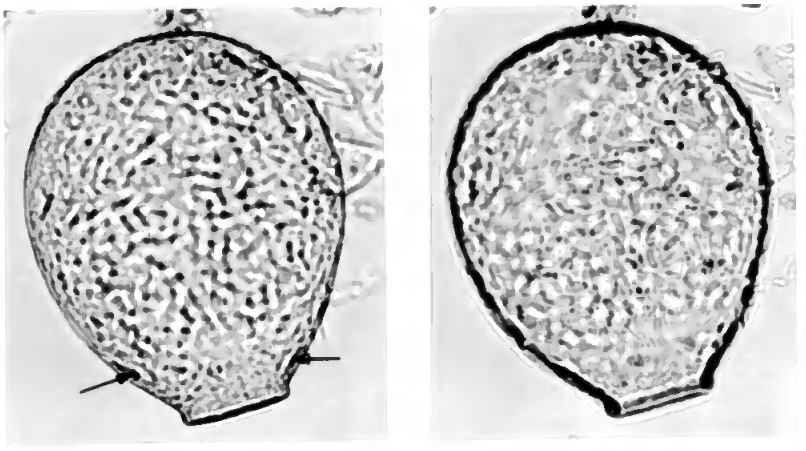
PLATE 8.21:	*N. tubulosa* (Penard 1890)
Dimensions:	length 190-198µm, breadth 134-139µm (this study); length 190-215µm (Grospietsch, 1958; Corbet, 1973); length 213-264µm, breadth 120-155µm (Ogden and Hedley, 1980); length 200-250µm (Ellison and Ogden, 1987).
Test outline:	elongate, pyriform or ovoid with a distinct neck in broad lateral view; compressed in narrow lateral view. Lateral margin extends from base of neck and surrounds test.
Colour:	yellow or brown.
Test material:	oval and circular plates, untidily arranged and overlapping.
Aperture:	terminal, oval; bordered by thin collar of organic cement (Ogden and Hedley, 1980). Diameter 42-54µm.
Other features:	Ogden and Hedley (1980) report a pair of small lateral pores which are difficult to see.
References:	Grospietsch (1958); Corbet (1973); Ogden and Hedley (1980); Ellison and Ogden (1987).

PLATE 8.19 *N. parvula* (modern)



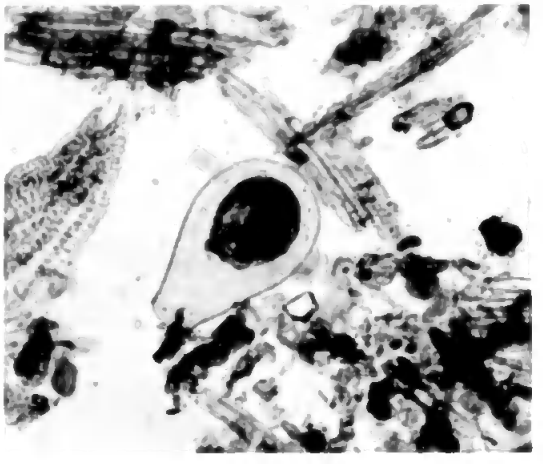
0 15µm

PLATE 8.20 *N tincta* (modern)
(a) location of pores (b) plate details



0 15µm

PLATE 8.21 *N. tubulosa* (modern)



0 80µm

PLATE 8.22:	***N. vitraea* (Penard 1899)**
Dimensions:	length 120-151µm, breadth 104-138µm (this study); length 155-258µm, breadth 120-140µm (Grospietsch, 1958); length 95-231µm (Corbet, 1973); length 117-160µm, breadth 102-145µm (Ogden and Hedley, 1980); length 115-160µm (Ellison and Ogden, 1987).
Test outline:	ovoid in broad lateral view; compressed in narrow lateral view.
Colour:	colourless; glassy, clear yellow (Corbet, 1973).
Test material:	mixture of oval and circular siliceous plates which overlap.
Aperture:	terminal; surrounded by a border of plates; diameter 28-37µm (Ogden and Hedley, 1980).
Other features:	can be difficult to separate from *N. dentistoma* (not found in this study), but Ogden and Hedley (1980) note that separation is possible on the basis of colour and detailed patterning of plates.
References:	Grospietsch (1958); Corbet (1973); Ogden and Hedley (1980); Ellison and Ogden (1987).

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PLATE 8.23:	***Quadrulella symmetrica* (Wallich 1863)**
Dimensions:	length 80µm, breadth 41µm (this study); length 68-120µm (Grospietsch, 1958; Corbet, 1973); length 72-103µm, breadth 36-62µm (Ogden and Hedley, 1980); length 70-110µm (Ellison and Ogden (1987).
Test outline:	ovoid or pyriform in broad lateral view; compressed in narrow lateral view.
Colour:	colourless.
Test material:	four-sided siliceous plates, arranged in regular rows; smaller plates closer to the aperture (Ogden and Hedley, 1980).
Aperture:	terminal; oval; convex in broad lateral view; surrounded by a thin layer of organic cement (Ogden and Hedley, 1980).
Other features:	none.
References:	Grospietsch (1958); Corbet (1973); Ogden and Hedley (1980); Ellison and Ogden (1987).

9. PLAGIOPYXIDAE

Test circular or ovoid; bilaterally symmetrical. Composed of mineral particles. Subterminal aperture usually elongate. Two genera: *Plagiopyxis* and *Bullinularia*; only *Bullinularia* recorded in this study.

PLATE 9.1:	***Bullinularia indica* (Penard 1907)**
Dimensions:	diameter 140-150µm (this study); diameter 160-170µm (de Graaf (1956); diameter 150-220µm (Grospietsch, 1958; Corbet, 1973); diameter 138-148µm (Ogden and Hedley, 1980); diameter 120-200µm (Ellison and Ogden, 1987).
Test outline:	oval or circular in broad lateral view; hemispherical or spherical in narrow lateral view.
Colour:	dark brown.
Test material:	mineral particles cemented together to produce a rough surface.
Aperture:	sub-terminal; narrow, elongate slit; inner lip depressed, outer lip incurved (Ogden and Hedley, 1980). Diameter 66-69µm (this study); 65-69µm (Ogden and Hedley, 1980).
Other features:	none.
References:	de Graaf (1956); Grospietsch (1958); Corbet (1973); Ogden and Hedley (1980); Ellison and Ogden (1987).

PLATE 8.22 *N. vitraea* (Penard Collection, British Museum)

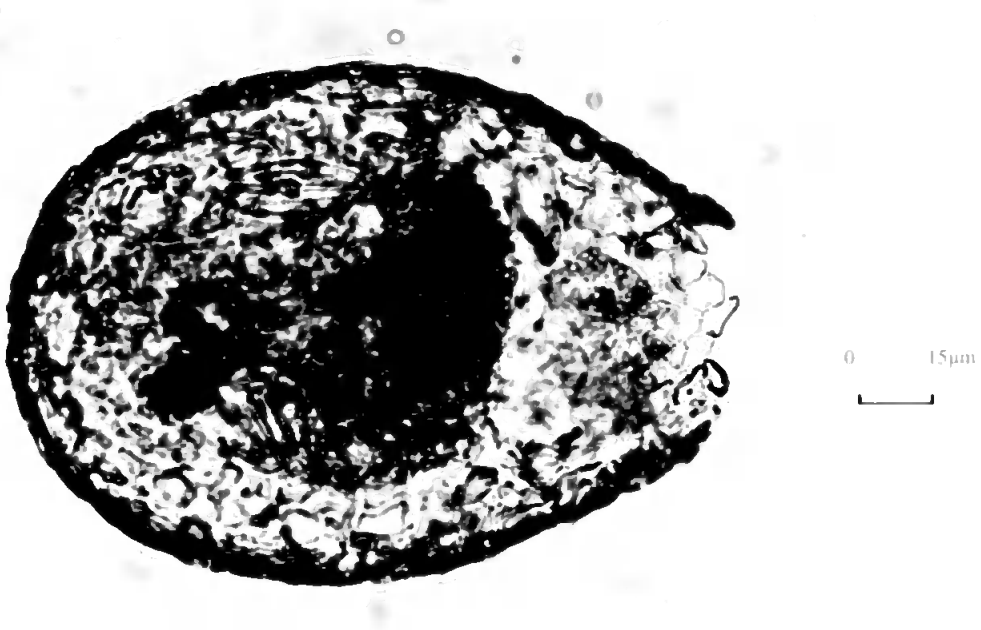
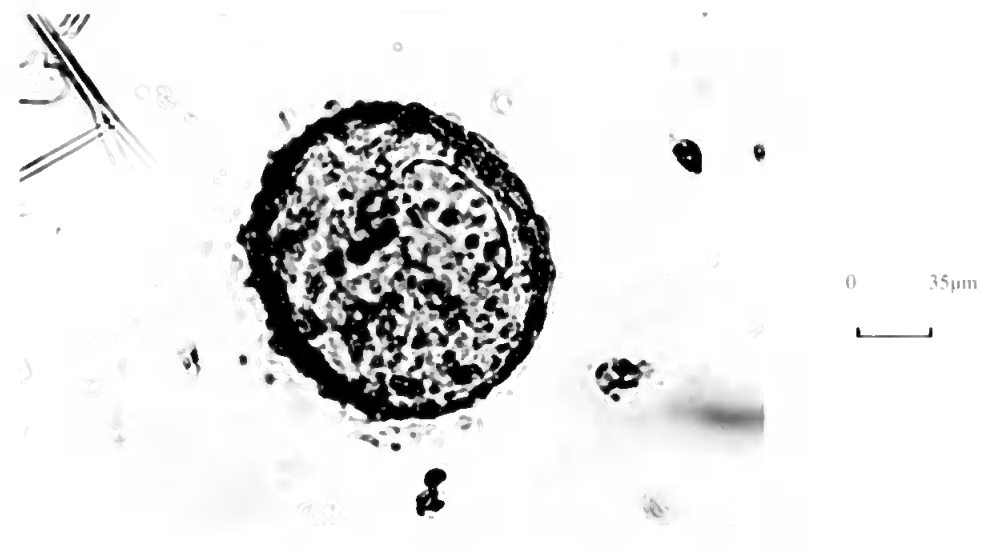


PLATE 8.23 *Quadrulella symmetrica* (Penard Collection, British Museum)

PLATE 9.1 *Bullinularia indica* (modern)



10. PHRYGANELLIDAE

Hemispherical or ovoid test, composed of agglutinated mineral particles; terminal aperture, circular (Ogden and Hedley, 1980).

PLATE 10.1:	***Phryganella acropodia* (Hertwig and Lesser 1874)**
Dimensions:	diameter 35-50μm (this study); diameter 35-65μm (Ellison and Ogden (1987).
Test outline:	circular in broad lateral view; almost spherical in narrow lateral view.
Colour:	colourless or pale brown
Test material:	agglutinated mineral (? quartz) particles
Aperture:	central, circular; composed of mineral particles, producing slightly invaginated margin.
Other features:	sometimes confused with *Centropyxis arcelloides*. In this study, however, *P. acropodia* was always smaller than *C. arcelloides*, with a larger aperture in proportion to test diameter.
References:	Ellison and Ogden (1987).

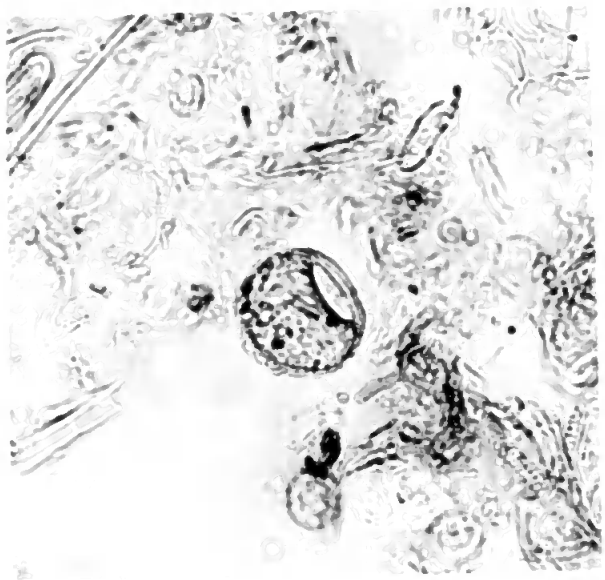
11. TRIGONOPYXIDAE

Circular or hemispherical test, composed of agglutinated particles; central aperture (Ogden and Hedley, 1980). Two genera: *Trigonopyxis* and *Cyclopyxis*. There is some confusion in the literature regarding the definitive genus of *Cyclopyxis arcelloides*, since *Cyclopyxis arcelloides* and *Centropyxis arcelloides* are used interchangeably to describe the same species. For example, Corbet (1973) refers to *Centropyxis (Cyclopyxis) arcelloides* and this is apparently due to *Cyclopyxis* being regarded as a subgenus of *Centropyxis* (Corbet 1973). This study, however, follows the taxonomic conventions of the Committee of Systematics and Evolution of the Society of Protozoology (1980) and recognises *Centropyxis* as a genus of *Centropyxidae* and *Cyclopyxis* as a genus of Trigonopyxidae (Ogden and Hedley, 1980).

PLATE 11.1:	***Cyclopyxis arcelloides* (Leidy 1879)**
Dimensions:	diameter 74-107μm (this study); 80-100μm (Grospietsch, 1958; Corbet, 1973); diameter 65-100μm (Meisterfeld, 1979).
Test outline:	circular in broad lateral view; hemispherical in narrow lateral view.
Colour:	colourless.
Test material:	mineral (?quartz) particles; siliceous particles (Tolonen *et al.*, 1992).
Aperture:	central; large; diameter 30-45μm (this study); 33-56μm (Meisterfeld, 1979); invaginated.
Other features:	see notes under Trigonopyxidae for taxonomic problems.
References:	Grospietsch (1958); Corbet (1973); Meisterfeld (1979); Warner (1990); Tolonen *et al.* (1992).

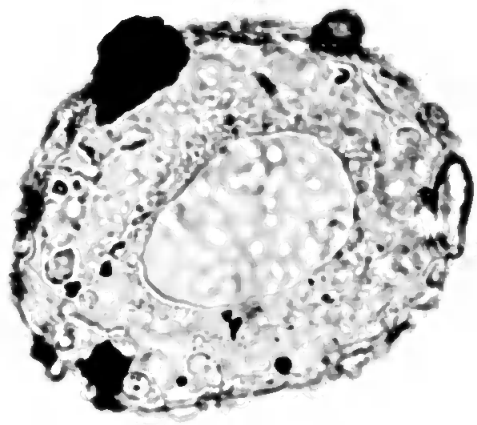
PLATE 11.2:	***C. eurystoma* (Deflandre 1929)**
Dimensions:	diameter 67-70μm (this study); diameter 66μm (Grospietsch, 1958); diameter 69-80μm (Ogden and Hedley, 1980); diameter 40-65μm (Ellison and Ogden, 1987).
Test outline:	circular in broad lateral view, hemispherical in narrow lateral view.
Colour:	brown; yellow or brown (Ogden and Hedley, 1980).
Test material:	mineral particles and siliceous plates bounded by an organic cement.
Aperture:	central; circular; bordered by smooth band of organic cement (Ogden and Hedley, 1980). Diameter 33-39μm (this study); 34-46μm (Ogden and Hedley, 1980).
References:	Grospietsch (1958); Ogden and Hedley (1980); Ellison and Ogden (1987).

PLATE 10.1 *Phryganella acropodia* (modern)



0 20μm

PLATE 11.1 *Cyclopyxis arcelloides* (modern)



0 15μm

PLATE 11.2 *C. eurystoma* (modern)

0 15μm

PLATE 11.3:	***Trigonopyxis arcula* (Leidy 1879)**
Dimensions:	diameter (123-134µm (this study); diameter 85-109µm (Hoogenraad and de Groot, 1952); diameter 100-150µm (Grospietsch, 1958; Corbet, 1973); diameter 95-168µm (Ogden and Hedley, 1980); diameter 100-170µm (Ellison and Ogden, 1987); diameter 85-120µm (Luftnegger *et al.*, 1988); diameter 54-185µm (Bobrov *et al.*, 1995).
Test outline:	circular in broad lateral view; hemispherical in narrow lateral view.
Colour:	dark brown.
Test material:	mineral particles bound by an organic cement.
Aperture:	central; surrounded by a collar of organic cement; shape varies and may be triangular, square or an invaginated circle (Bobrov *et al.*, 1995). Diameter 21-42µm (Ogden and Hedley, 1980).
Other features:	none.
References:	Hoogenraad and de Groot (1952); Grospietsch (1958); Corbet (1973); Ogden and Hedley (1980); Ellison and Ogden (1987); Luftnegger *et al.* (1988); Bobrov *et al.* (1995).

12. TRINEMATIIDAE

Ovoid test with sub-terminal aperture. Test composed of circular siliceous plates. Aperture circular or ovoid and surrounded by plates. Comprises two genera: *Trinema* and *Corythion*, which are separated according to whether the plates touch each other (*Trinema*) or are interspersed by organic cement (*Corythion*). It possible to separate Trinema lineare by its smaller size, but under light microscopy, it is impossible to separate *Corythion dubium* and *Trinema enchelys* due to the small size of the test and transparent plates. The two species are treated together here, following Corbet (1973).

PLATE 12.1:	***Corythion-Trinema* type (Taranek 1881; Penard 1890)**
Dimensions:	*Trinema enchelys*: length 40-60µm (Corbet, 1973); 47-78µm (Ogden and Hedley (1980). *Corythion dubium*: length 30-45µm (Corbet, 1973); length 33-55µm (Ogden and Hedley, 1980).
Test outline:	elongate, ovoid test in broad lateral view; compressed in narrow lateral view
Test material:	both species have siliceous plates. In *C. dubium* the plates are oval and irregularly arranged; in *T. enchelys* they are circular and regularly arranged.
Aperture:	sub-terminal and circular or ovoid; invaginated; <1µm diameter (Ogden and Hedley, 1980).
Other features:	see taxonomic problems above.
References:	Corbet (1973); Ogden and Hedley, 1980).

PLATE 12.2:	***Trinema lineare* (Penard 1890)**
Dimensions:	length 18-35µm (Corbet, 1973); 25-35µm (Ogden and Hedley, 1980).
Test outline:	elongate, ovoid test in broad lateral view; compressed in narrow lateral view.
Colour:	colourless; appears transparent.
Test material:	oval or circular siliceous plates, often difficult to see under light microscopy.
Aperture:	sub-terminal; circular; invaginated. Diameter 1.2-1.5µm (Ogden and Hedley, 1980).
Other features:	small size and transparent test renders this species difficult to see under light microscopy.
References:	Corbet (1973); Ogden and Hedley (1980).

PLATE 11.3 *Trigonopyxis arcula* (modern)

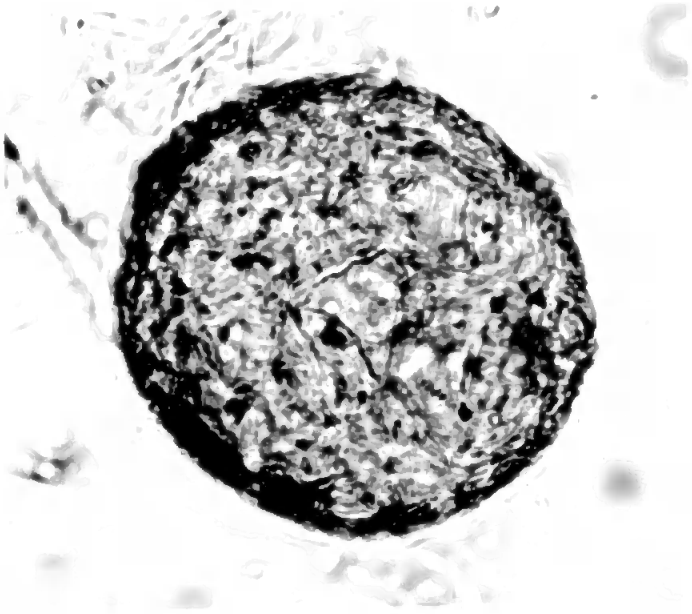


PLATE 12.1 *Corythion-Trinema* type (Penard Collection, British Museum)

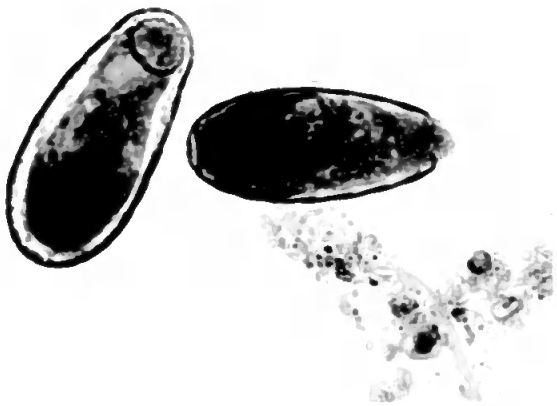


PLATE 12.2 *Trinema lineare* (modern)