

1998

Robustness and precision of Holocene palaeoclimatic records from peatlands using testate amoebae

Hendon, Dawn

<http://hdl.handle.net/10026.1/756>

<http://dx.doi.org/10.24382/3753>

University of Plymouth

All content in PEARL is protected by copyright law. Author manuscripts are made available in accordance with publisher policies. Please cite only the published version using the details provided on the item record or document. In the absence of an open licence (e.g. Creative Commons), permissions for further reuse of content should be sought from the publisher or author.

COPYRIGHT STATEMENT

This copy of the thesis has been supplied on condition that anyone who consults it is understood to recognise that its copyright rests with its author and that no quotation from the thesis and no information derived from it may be published without the author's prior consent.

**ROBUSTNESS AND PRECISION OF HOLOCENE PALAEOCLIMATIC
RECORDS FROM PEATLANDS USING TESTATE AMOEBAE**

by

DAWN HENDON

A thesis submitted to the University of Plymouth
in partial fulfilment for the degree of

DOCTOR OF PHILOSOPHY

Department of Geographical Sciences
Faculty of Science

February 1998

ABSTRACT

ROBUSTNESS AND PRECISION OF HOLOCENE PALAEOCLIMATIC RECORDS FROM PEATLANDS USING TESTATE AMOEBAE

DAWN HENDON

This thesis represents the first attempt to use quantitative testate amoebae (Protozoa: Rhizopoda) analysis to measure hydrological fluctuations in British peatbogs over the Holocene. Changes in the fossil species assemblage are used to reconstruct the mean annual water table records at different locations on mire surfaces using a transfer function designed for application on oligotrophic peatlands. The transfer function was found to provide more precise reconstructions for depth to water table than percentage soil moisture. Multiple cores were extracted from three of the Border Mires; Coom Rigg Moss and Butterburn Flow (both intermediate ombrotrophic bogs) and The Wou (a minerogenic valley mire). Testate amoebae analysis of these cores was used to assess the variability of hydrological change at three spatial scales, in an attempt to separate autogenic and allogenic influences on site hydrology. The morphology of each mire ensured a strong link between water and prevailing climate (precipitation-evaporation balance).

At the micro-scale (1-10m), within the centre of a mire, microtopography explains differences between the hydrological record for two cores. This is inferred because one of the cores appears to have been the location of an insensitive hummock over much of the period of accumulation. At the meso-scale (100-1000m), between the central mire expanse and the mire margins, synchronous changes can be identified, but the edges generally have lower water tables than the central portions of the mires. However, this may be attributable to autogenic factors acting over the whole site, as well as to climate. Between sites, at the macro-scale (1-10km), climatic influences can be clearly identified. The climatic signal is strongest in the centre of the mire and is more consistent between locations in the upper peats. If a hydrological shift is replicated in at least three cores from at least two sites, a climatic signal can be inferred.

The testate amoebae preparation technique was also modified as part of this research to provide cleaner slides for more efficient counting. Testate amoebae analysis provides a new quantitative technique for reconstructing the palaeohydrology and from this, inferred palaeoclimatic conditions of ombrotrophic peatlands.

Contents

Copyright Statement	i
Title Page	ii
Abstract	iii
List of Contents	iv
List of Figures	x
List of Tables	xiv
List of Plates	xvi
Acknowledgements	xvii
Author's Declaration	xviii

PART ONE INTRODUCTION AND BACKGROUND

Chapter One Preface to the thesis

1.0	Introduction	1
1.1	Aims	2
1.2	Hydrological forcing and peatland development	4
1.3	Philosophy and palaeoecology	5
1.4	Thesis structure	8

Chapter Two Testate amoebae and their peatland environments

2.0	Introduction	12
2.1	Peatland-climate relationships and response	12
2.1.1	Peatland distribution	12
2.1.2	The role of <i>Sphagnum</i> in the peatland environment	13
2.1.3	Peat formation	16
2.1.4	Internal mire morphology	18
2.1.5	Peat hydrology	19
2.1.6	Mire classifications	20
2.1.7	The history of peat stratigraphical studies	28
2.2	Testate amoebae as palaeohydrological indicators	33

2.2.1	The systematics of testate amoebae	33
2.2.2	The history of fossil testate amoebae studies	34
2.2.3	The range of testate amoebae research	35
2.2.4	Taxonomy	37
2.2.5	Biology and ecology	39
2.2.6	Environmental factors affecting testate amoebae	44
2.3	Testate amoebae and palaeoecology	57
2.4	Transfer functions for palaeoclimatic reconstructions	59
2.5	Testate amoebae transfer function	61
2.6	Other proxy-climatic indicators	64
2.6.1	<i>Sphagnum</i> macrofossils	64
2.6.2	Other plant indicators	66
2.6.3	Isotopic fractionation	66
2.6.4	Humification	68
2.7	Conclusions	71

PART TWO RESEARCH APPROACH AND METHODOLOGY

***Chapter Three* Site selection and coring locations**

3.0	Introduction	73
3.1	Scales of study	73
3.2	Rationale for field sampling	76
3.3	The Irthinghead Mires	78
3.4	Surveying	82
3.5	Coom Rigg Moss	83
3.6	Butterburn Flow	89
3.7	The Wou	94
3.8	Site synthesis	99

***Chapter Four* Laboratory methods and data analysis**

4.0	Introduction	100
4.1	Laboratory methods	100
4.1.1	Rationale for subsampling	101

4.1.2	Testate amoebae preparation procedure	102
4.1.3	Pollen preparation procedure	115
4.1.4	Taxonomic problems	115
4.1.5	Radiocarbon dating	123
4.2	Data analysis and presentation	128
4.2.1	Introduction	128
4.2.2	Testate amoebae data	128
4.2.3	Pollen data	135
4.3	Conclusions	135

PART THREE CORING SITE RESULTS

Chapter Five Coom Rigg Moss - Testate amoebae and palaeohydrology

5.0	Introduction	137
5.1	CRM I	137
5.1.1	Stratigraphy	137
5.1.2	Testate amoebae	138
5.1.3	Ordination	143
5.1.4	Hydrological reconstructions	149
5.2	CRM II	153
5.2.1	Stratigraphy	153
5.2.2	Testate amoebae	154
5.2.3	Ordination	157
5.2.4	Hydrological reconstructions	159
5.3	CRM III	165
5.3.1	Stratigraphy	166
5.3.2	Testate amoebae	166
5.3.3	Ordination	168
5.3.4	Hydrological reconstructions	171
5.4	CRM IV	175
5.4.1	Stratigraphy	175
5.4.2	Testate amoebae	175
5.4.3	Ordination	179
5.4.4	Hydrological reconstructions	183

5.5	Chronology	187
5.5.1	Pollen data	187
5.5.2	Radiocarbon ages	190
5.6	Conclusions	195

Chapter Six Butterburn Flow - Testate amoebae and palaeohydrology

6.0	Introduction	201
6.1	BBF I	201
6.1.1	Stratigraphy	201
6.1.2	Testate amoebae	203
6.1.3	Ordination	207
6.1.4	Hydrological reconstructions	210
6.2	BBF II	216
6.2.1	Stratigraphy	216
6.2.2	Testate amoebae	216
6.2.3	Ordination	220
6.2.4	Hydrological reconstructions	223
6.3	BBF III	227
6.3.1	Stratigraphy	227
6.3.2	Testate amoebae	227
6.3.3	Ordination	230
6.3.4	Hydrological reconstructions	232
6.4	Chronology	238
6.4.1	Pollen data	238
6.4.2	Radiocarbon ages	243
6.5	Conclusions	244

Chapter Seven The Wou - Testate amoebae and palaeohydrology

7.0	Introduction	248
7.1	TW I	248
7.1.1	Stratigraphy	248
7.2	TW II	250
7.2.1	Stratigraphy	250

7.2.2	Testate amoebae	250
7.2.3	Ordination	253
7.2.4	Hydrological reconstructions	255
7.2.5	Other microfossils	258
7.3	TW III	261
7.3.1	Stratigraphy	261
7.4	Chronology	262
7.4.1	Pollen data	262
7.4.2	Radiocarbon ages	262
7.5	Conclusions	

PART FOUR DISCUSSION AND CONCLUSIONS

***Chapter Eight* Reconstruction and robustness**

8.0	Introduction	267
8.1	Sample preparation	267
8.2	The transfer functions	269
8.3	No-analogue taxa	270
8.3.1	<i>Diffflugia pulex</i> Penard 1902	271
8.3.2	<i>Pseudodiffflugia fascicularis</i> Penard 1902	276
8.4	Poor-analogue taxa	280
8.4.1	<i>Hyalosphenia subflava</i> Cash and Hopkinson 1909	282
8.5	Taxonomic issues	288
8.6	Conclusions	289

***Chapter Nine* Replicability of palaeohydrological reconstructions**

9.0	Introduction	292
9.1	Error estimation in chronology and water table reconstructions	293
9.2	Micro-scale comparison	296
9.3	Meso-scale comparisons	306
9.3.1	Coom Rigg Moss	306
9.3.2	Butterburn Flow	312
9.4	Within-site variability	318

9.5	Macro-scale comparisons	323
9.6	Between-site variability	330
9.7	Climate and peatland surface wetness	332
9.7.1	Mire surface wetness before 500AD	332
9.7.2	Dark Age deterioration	334
9.7.3	Medieval Warm Period	337
9.7.4	Little Ice Age	337
9.8	Testate amoebae and palaeohydrological reconstructions on peatlands	339
9.9	Implications for palaeoclimatic studies on peatlands	342
9.10	Conclusions	343

***Chapter Ten* Conclusions and future work**

10.0	Introduction	345
10.1	Original aims	345
10.2	Methodological issues	345
10.3	Peatland hydrology and climate reconstruction	347
10.4	Future work	348

References	350
-------------------	------------

Glossary	371
-----------------	------------

List of Figures

***Chapter One* Preface to the Thesis**

- | | | |
|-----|---|---|
| 1.1 | Simplified model of the hydrological regime of ombrotrophic mires | 6 |
| 1.2 | Flow diagram of thesis structure | 9 |

***Chapter Two* Testate amoebae and their peatland environments**

- | | | |
|-----|--|----|
| 2.1 | Map of peatland distribution in the British Isles | 14 |
| 2.2 | Functional hydrology, Ivanov, 1981 | 22 |
| 2.3 | Topographic locations of peat bogs | 25 |
| 2.4 | The cyclic regeneration model | 30 |
| 2.5 | Figures of <i>Arcella</i> redrawn from Deflandre (1928) | 39 |
| 2.6 | Population processes affecting test turnover | 42 |
| 2.7 | Horizontal distribution of testate amoebae | 49 |
| 2.8 | Possible environmental controls on testate amoebae assemblages | 53 |

***Chapter Three* Site selection and coring locations**

- | | | |
|------|---------------------------------------|----|
| 3.1 | Scales of study | 75 |
| 3.2 | Location map of field sites | 79 |
| 3.3 | Map of Coom Rigg Moss, Northumberland | 84 |
| 3.4 | South-north transect, Coom Rigg Moss | 87 |
| 3.5 | East-west transect, Coom Rigg Moss | 87 |
| 3.6 | Surface features at Coom Rigg Moss | 88 |
| 3.7 | Map of Butterburn Flow, Cumbria | 91 |
| 3.8 | South-north transect, Butterburn Flow | 93 |
| 3.9 | West-east transect, Butterburn Flow | 93 |
| 3.10 | Map of The Wou, Northumberland | 95 |
| 3.11 | South-north transect I, The Wou | 97 |
| 3.12 | South-north transect II, The Wou | 97 |
| 3.13 | West-east transect I, The Wou | 98 |
| 3.14 | West-east transect II, The Wou | 98 |

***Chapter Four* Laboratory methods and data analysis**

- | | | |
|-----|---|-----|
| 4.1 | Percentage testate amoebae diagrams from preparations A-E | 109 |
| 4.2 | Optima and tolerance values for taxa in the water table transfer function | 133 |

4.3	Optima and tolerance values for taxa in the moisture transfer function	134
-----	--	-----

Chapter Five Coom Rigg Moss (CRM)

5.1	CRM I percentage testate amoebae diagram	139
5.2	Modern and fossil DCA ordination for CRM I	144
5.3	Sample ordination for CRM I	147
5.4	Species ordination for CRM I	148
5.5	CRM I water table reconstruction with 2σ bootstrapped error estimates	150
5.6	CRM I moisture reconstructions with 2σ bootstrapped error estimates	152
5.7	CRM II percentage testate amoebae diagram	155
5.8	Modern and fossil DCA ordination for CRM II	158
5.9	Sample ordination for CRM II	160
5.10	Species ordination for CRM II	161
5.11	CRM II water table reconstruction with 2σ bootstrapped error estimates	163
5.12	CRM II moisture reconstructions with 2σ bootstrapped error estimates	164
5.13	CRM III percentage testate amoebae diagram	167
5.14	Modern and fossil DCA ordination for CRM III	169
5.15	Sample ordination for CRM III	170
5.16	Species ordination for CRM III	172
5.17	CRM III water table reconstruction with 2σ bootstrapped error estimates	173
5.18	CRM III moisture reconstructions with 2σ bootstrapped error estimates	174
5.19	CRM IV percentage testate amoebae diagram	176
5.20	Modern and fossil DCA ordination for CRM IV	180
5.21	Sample ordination for CRM IV	181
5.22	Species ordination for CRM IV	182
5.23	CRM IV water table reconstruction with 2σ bootstrapped error estimates	184
5.24	CRM IV moisture reconstructions with 2σ bootstrapped error estimates	186
5.25	CRM I percentage pollen diagram	188
5.26	CRM II percentage pollen diagram	189
5.27	CRM III percentage pollen diagram	191
5.28	CRM IV percentage pollen diagram	192
5.29	CRM I linear interpolation of calibrated sample ages	193
5.30	CRM II linear interpolation of calibrated sample ages	193
5.31	CRM IV linear interpolation of calibrated sample ages	194
5.32	Percentage testate amoebae chronology for CRM I	196

5.33	Percentage testate amoebae chronology for CRM II	197
5.34	Percentage testate amoebae chronology for CRM III	198
5.35	Percentage testate amoebae chronology for CRM IV	199

Chapter Six Butterburn Flow (BBF)

6.1	BBF I percentage testate amoebae diagram	204
6.2	Modern and fossil DCA ordination for BBF I	208
6.3	Sample ordination for BBF I	209
6.4	Species ordination for BBF I	211
6.5	BBF I water table reconstruction with 2σ bootstrapped error estimates	213
6.6	BBF I moisture reconstructions with 2σ bootstrapped error estimates	215
6.7	BBF II percentage testate amoebae diagram	218
6.8	Modern and fossil DCA ordination for BBF II	221
6.9	Sample ordination for BBF II	222
6.10	Species ordination for BBF II	224
6.11	BBF II water table reconstruction with 2σ bootstrapped error estimates	225
6.12	BBF II moisture reconstructions with 2σ bootstrapped error estimates	226
6.13	BBF III percentage testate amoebae diagram	229
6.14	Modern and fossil DCA ordination for BBF III	231
6.15	Sample ordination for BBF III	233
6.16	Species ordination for BBF III	234
6.17	BBF III water table reconstruction with 2σ bootstrapped error estimates	236
6.18	BBF III moisture reconstructions with 2σ bootstrapped error estimates	237
6.19	BBF I percentage pollen diagram	239
6.20	BBF II percentage pollen diagram	240
6.21	BBF III percentage pollen diagram	241
6.22	BBF I linear interpolation of calibrated sample ages	242
6.23	BBF II linear interpolation of calibrated sample ages	242
6.24	BBF III linear interpolation of calibrated sample ages	243
6.25	Percentage testate amoebae chronology for BBF I	245
6.26	Percentage testate amoebae chronology for BBF II	246
6.27	Percentage testate amoebae chronology for BBF III	247

Chapter Seven The Wou (TW)

7.1	TW II percentage testate amoebae diagram	251
7.2	Modern and fossil DCA ordination for TW II	254
7.3	Sample ordination for TW II	256
7.4	Species ordination for TW II	257
7.5	TW II water table reconstruction with 2σ bootstrapped error estimates	259
7.6	TW II moisture reconstructions with 2σ bootstrapped error estimates	260
7.7	TW II percentage pollen diagram	263
7.8	TW II linear interpolation of calibrated sample ages	264
7.9	Percentage testate amoebae chronology for TW II	265

Chapter Eight Reconstruction and robustness

8.1	<i>Diffugia pulex</i> response to hydrology from individual cores	274
8.2	<i>Diffugia pulex</i> response to hydrology, all cores combined	276
8.3	Distribution of 2cm inferred water table classes for all samples	279
8.4	Gaussian responses of taxa to hydrology	281
8.5	<i>Hyalosphenia subflava</i> response to hydrology from published studies	286

Chapter Nine Replicability of palaeohydrological reconstructions

9.1	Micro-scale ordination plot	298
9.2	Micro-scale water tables 4000BC to present	300
9.3	Micro-scale water table comparisons 500AD to present	302
9.4	Meso-scale ordination plot for Coom Rigg Moss	307
9.5	Meso-scale water tables for Coom Rigg Moss, 500BC to present	309
9.6	Meso-scale ordination plot for Butterburn Flow	313
9.7	Meso-scale water tables for Butterburn Flow, 6500BC to present	315
9.8	Meso-scale water tables for Butterburn Flow, 0AD to present	317
9.9	Macro-scale ordination plot	324
9.10	Macro-scale water tables 3500BC to present	326
9.11	Macro-scale water tables 500AD to present	328
9.12	Humification curve from Talla Moss	335
9.13	<i>Sphagnum</i> macrofossil surface wetness curve from Bolton Fell Moss	336
9.14	Composite summer temperature records for Central England and Europe	340

List of Tables

***Chapter Two* Testate amoebae and their peatland environments**

2.1	Mire microforms in British peatlands	22
2.2	The Bylitt-Sernander scheme	29
2.3	Systematics of higher taxonomy of testate amoebae	34
2.4	The range of ecological and palaeoecological testate amoebae studies	36
2.5	Moisture classes of testate amoebae	47
2.6	Hydrological requirements of taxa from published studies	51

***Chapter Three* Site selection and coring locations**

3.1	Conservation history and status of field sites	80
3.2	Core combinations and scales of study	99

***Chapter Four* Laboratory methods and data analysis**

4.1	Summary of treatments for sample preparations	107
4.2	Raw data from preparation experiments	108
4.3	Summary of taxa recorded in preparation experiments	111
4.4	Taxa found in this study compared to reclassified taxonomy	120
4.5	Radiocarbon dates from CRM, BBF and TW cores	127

***Chapter Five* Coom Rigg Moss (CRM)**

5.1	Stratigraphic description of CRM I	138
5.2	Zone descriptions for CRM I based on testate amoebae assemblages	141
5.3	Species codes for taxa included in DCA ordination analyses	145
5.4	Stratigraphic description of CRM II	146
5.5	Zone descriptions for CRM II based on testate amoebae assemblages	156
5.6	Stratigraphic description of CRM III	165
5.7	Zone descriptions for CRM III based on testate amoebae assemblages	166
5.8	Stratigraphic description of CRM IV	177
5.9	Zone descriptions for CRM IV based on testate amoebae assemblages	178
5.10	Changes in pollen spectra and depths for the four CRM cores	187
5.11	Accumulation rates for CRM I	194
5.12	Accumulation rates for CRM IV	195

Chapter Six Butterburn Flow (BBF)

6.1	Stratigraphic description of BBF I	202
6.2	Zone descriptions for BBF I based on testate amoebae assemblages	205
6.3	Stratigraphic description of BBF II	217
6.4	Zone descriptions for BBF II based on testate amoebae assemblages	219
6.5	Stratigraphic description of BBF III	228
6.6	Zone descriptions for BBF III based on testate amoebae assemblages	228
6.7	Changes in pollen spectra and depths for the three BBF cores	238
6.8	Accumulation rates for BBF I	244

Chapter Seven The Wou (TW)

7.1	Stratigraphic description of TW I	249
7.2	Stratigraphic description of TW II	250
7.3	Zone descriptions for TW II based on testate amoebae assemblages	252
7.4	Stratigraphic description of TW III	261

Chapter Eight Reconstruction and robustness

8.1	Weighted averages for <i>Diffflugia pulex</i> depth to water table (cm) for each core	275
8.2	Published estimates of <i>Hyalosphenia subflava</i> optima and tolerances	285

Chapter Nine Replicability of palaeohydrological reconstructions

9.1	Reconstructed mean water table at CRM core locations prior to and since the planting of the Kielder Forest	311
9.2	Reconstructed mean water table at BBF core locations prior to and since the planting of the Kielder Forest	318
9.3	Wet and dry shifts in the meso-scale core comparisons	319
9.4	Wet and dry shifts in the macro-scale core comparisons	330

List of Plates

Chapter Two Testate amoebae and their peatland environments

- | | | |
|-----|---|----|
| 2.1 | Photomicrograph of a modern <i>Nebela</i> sp. with pseudopodia extended | 43 |
| 2.2 | Photomicrograph of <i>Placocista spinosa</i> consuming <i>Amphitrema flavum</i> | 56 |

Chapter Four Laboratory methods and data analysis

- | | | |
|-----|---|-----|
| 4.1 | Photomicrograph of <i>Amphitrema flavum</i> | 106 |
| 4.2 | Photomicrograph of <i>Assulina muscorum</i> | 106 |
| 4.3 | Photomicrograph of <i>Assulina seminulum</i> | 106 |
| 4.4 | Photomicrograph of <i>Diffugia pristis</i> type a | 117 |
| 4.5 | Photomicrograph of <i>Diffugia pristis</i> type b | 117 |

Chapter Eight Reconstruction and robustness

- | | | |
|-----|---|-----|
| 8.1 | Photomicrograph of <i>Diffugia pulex</i> | 278 |
| 8.2 | Photomicrograph of <i>Pseudodiffugia fascicularis</i> | 278 |
| 8.3 | Photomicrograph of <i>Hyalosphenia subflava</i> | 278 |

Acknowledgements

This research project was completed under the tenure of a research training award from the Natural Environment Research Council. NERC are also thanked for providing 29 radiocarbon assays which were fundamental to this project.

With thanks to all who assisted me with field work, especially Dan, Martin and Charlie, without whom, coring at Butterburn Flow would have been impossible. Thanks to Forest Enterprise, Bellingham for access permission to Coom Rigg Moss and Butterburn Flow, and The Northumberland Wildlife Trust and Mr Oxley the grazier, for access permission to The Wou. English Nature (Cumbria and Northumberland Districts) are thanked for permission to extract cores from Coom Rigg Moss and Butterburn Flow, the Northumberland Wildlife Trust for permission to core at The Wou.

Dr Alan Warren, Department of Zoology, The British Museum (Natural History) is thanked for the loan of slides from The Penard Collection, and for general encouragement with test taxonomy.

Thanks are due to Dr Anatoloy Bobrov (Moscow), Dr David Scott (Nova Scotia), Professor Barry Warner (Ontario), Dr Kimmo Tolonen (Finland), Professor Louis Beyens (Antwerp), Dr Humphry Smith (Coventry), and Professor Golemansky (Sofia), for help in identifying Bob (aka *Diffflugia pristis* type).

At the University of Plymouth:

My supervisors, Dan Charman and Martin Kent are thanked for general encouragement and from stopping me straying off at a tangent. Technicians, Ann Kelly and Pat Bloomfield are thanked especially, for stopping me from going mad in the microscope room. Tim Absolom, Brian Rogers, Ian Stokes and Matthew Chambers are thanked for cartographic support. Computer technicians Adrian Holmes, Andy Collins, Pauline Framingham and David Antwis and Marcus Burrows are thanked for their patience with programs such as TILIA and the hours of pleasure derived from its use!

The postgraduate community, past and present, are thanked for hours of wholesome lunchtime conversations - especially Martin, Steve, Ben and Jon and, for tea and sympathy with Phil and Juliette.

At home over the past year Caroline, Guy and Jock the Toad Slayer cannot be thanked enough for tolerance and tea and Katie who bravely undertook proof reading the beast.

Lu for whisking me off to Florence for art, culture, fine wine and the absolutely no peat! And Zoë for being a supportive sister. Finally, thanks to Mum and Phil for being brilliant parents and for putting up with me and my quest for knowledge!

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.

This study was financed by a studentship awarded by the Natural Environment Research Council (GT4/94/401/G).

The following conferences were attended:

April 1995	Postgraduate Palaeoecology Conference, Plymouth University
July 1995	International Peatlands Convention, Edinburgh
April 1996	Postgraduate Palaeoecology Conference, Cambridge University
April 1996	Quaternary Research Association Annual Field Meeting, Devon
December 1996	British Ecological Society Winter Meeting, Durham University
July 1997	10 th International Congress of Protozoology, University of Sydney, Australia
December 1997	British Ecological Society Winter Meeting, Warwick University

Presentations were made at the following conferences:

April 1995	Postgraduate Palaeoecology Conference, Plymouth University
April 1996	Postgraduate Palaeoecology Conference, Cambridge University
December 1996	British Ecological Society Winter Meeting, Durham University
July 1997	10 th International Congress of Protozoology, University of Sydney, Australia
December 1997	British Ecological Society Winter Meeting, Warwick University

Publications:

Charman, D.J., Hendon, D. and Woodland, W.A. (1996) Quantitative palaeohydrological reconstructions from testate amoebae in peatlands. In: Lüttig, G. (ed.) *10th International Peat Congress - Peatlands past, present and future: Volume 2*. Scheizerbart, Stuttgart, Germany, 339-348

Hendon, D. and Charman, D.J. (1997) The preparation of testate amoebae (Protozoa: Rhizopoda) samples from peat. *The Holocene*, **7** 199-205

Charman, D.J., Hendon, D. and Woodland, W.A. (in prep.) The identification of testate amoebae (Protozoa:Rhizopoda) from British oligotrophic peats.

Charman, D.J., Hendon, D. and Packman, S. (in prep.) Multi-proxy surface wetness records from replicate cores on an ombrotrophic mire: implications for palaeoclimatic records.

Signed Dawn Hendon
Date 24 February 1998

PART ONE

Introduction and background

CHAPTER ONE

Preface to the thesis

1.0 Introduction

Work carried out in Canada (*e.g.* Warner, 1987, 1990; Charman and Warner, 1992, 1997; Warner and Charman, 1994), Finland (*e.g.* Tolonen, 1966, 1986; Tolonen *et al.*, 1985) and more recently Britain (Woodland, 1996; Woodland *et al.*, 1998) and New Zealand (Charman, 1997), has recognised the potential use of testate amoebae (Protozoa: Rhizopoda) in reconstructing the hydrological conditions of peatlands. This thesis is the first attempt to use quantitative analysis of subfossil testate amoebae to measure hydrological fluctuations in British peatlands over the Holocene. A particular focus of this work is to examine the reliability and replicability of the palaeo-hydrological record derived from testate amoebae analysis.

Recent research established the relationship between faunal assemblages and peatland hydrology, as expressed by the depth to water table and percentage soil moisture (Charman and Warner, 1992; Tolonen *et al.*, 1992, 1994; Woodland, 1996; Woodland *et al.*, 1998). The relationship between climate and testate amoebae is not direct, however, there is an indirect link through mire hydrology. If the hydrological record derived from testate amoebae analysis is replicable across a number of sites within a region, a climatic signal may be inferred. Therefore, the quality of the palaeoclimatic record depends upon the reliability of the climate-hydrology relationship, as well as the robustness of the transfer function for hydrological reconstructions.

The use of testate amoebae analysis as a proxy palaeoclimatic record is based upon the assumption of a direct coupling between peatland and climate for ombrotrophic mires shown, for example, by Barber (1981). Due to the fact that ombrotrophic mires receive moisture and nutrient inputs solely from precipitation, a direct relationship may be assumed between climate and mire surface wetness. This assumption does not take into account any possibilities of mire hydrology being influenced by internal dynamics such as drainage or microtopography. In order for a palaeoclimatic signal to be inferred, the influence of autogenic factors on mire surface wetness must be evaluated.

There are three steps to gaining palaeoclimatic information from fossil testate amoebae from ombrotrophic mires:

- a) characterisation of the species composition of a particular assemblage;
- b) consideration of past hydrology by the study of autecology, by the application of a modern analogue transfer function so that the palaeohydrological conditions can be modelled;
- c) assessment of whether hydrological shifts are replicated between sites, therefore indicating that they may be climatic in origin.

Calibration (see Birks, 1995) of the fossil faunal assemblages using the modern analogue transfer function developed by Woodland (1996) and Woodland *et al.* (1998), provides quantification of the depth to water table and moisture conditions in which the subfossil testate amoebae assemblages existed. This is a valuable new addition to other methods of palaeohydrological reconstruction, the usefulness of which will be determined by the level of precision with which bog wetness can be reconstructed from different testate amoebae assemblages. This principally depends on the match or mismatch between modern and fossil assemblages.

The terms testate amoebae, testaceans (*e.g.* Medioli and Scott, 1988), thecamoebians, (*e.g.* Medioli and Scott, 1983), arcellaceans (*e.g.* Patterson *et al.*, 1985) and rhizopods (*e.g.* Tolonen, 1986) are often used synonymously. However, the term testate amoebae is used predominantly in this text, as it best describes the organisms and, is the term used most frequently in recent literature.

1.1 Aims

This study has three main aims from which to assess the use of testate amoebae analysis as a palaeoclimatic reconstruction tool:

- 1) assessment of the replicability of the subfossil testate amoebae record from within and between mires;
- 2) testing the robustness and precision of percentage moisture and depth to water table reconstructions produced from testate amoebae analysis of Holocene ombrotrophic peatlands;
- 3) separation of autogenically and allogically forced hydrological signals, in order to assess the technique as a proxy measure of palaeoclimatic change on peatlands.

Intensive investigation of the spatial and temporal variability of the faunal record must be reliable. There must be confidence in the data and the results should be concordant when repeated. Many recent palaeoecological studies have assumed that one core from a particular mire is representative of that mire as a whole (*e.g.* Chambers *et al.*, 1997). This assumption has not been rigorously tested in palaeoclimatic studies, and is examined here using multiple testate amoebae records from three field sites.

The aim of the transfer function is to express the value of the environmental variable, (*e.g.* depth to water table and percentage moisture), as a function of the biological data, in this case, the testate amoebae assemblage. Modern relationships between species optima, tolerance and hydrological parameters for testate amoebae were modelled statistically by Woodland (1996) and Woodland *et al.* (1998). The resulting transfer function may be used to calculate quantitative estimates of past hydrological conditions from fossil data. Depth to water table and percentage moisture at the time of biocoenosis can therefore be established. This is preferable to a qualitative assessment of surface hydrology based on the presence or absence of taxa and relating that to the literature on faunal ecological requirements.

Critically testing testate amoebae analysis is essential to establish its validity as a proxy hydrological indicator. This depends not only upon the quality of the fossil data, but also upon the transfer function that is used to calibrate the fossil assemblages. Analysis of the data in this research involves testing the transfer function by looking at a wider range of fossil conditions than in previous work. The moisture transfer function was based on single-shot data, taken when the surface moss polsters used to construct the calibration data set were collected. The water table transfer function was based on long-term hydrological monitoring data and the sites used were therefore restricted to those with established monitoring programmes. This causes a bias in the data set, since sites with such programmes tend to be wet sites that are being managed for long term conservation. The water table transfer function developed by Woodland (1996) and Woodland *et al.* (1998) is potentially more useful than other transfer functions developed for Canadian palaeohydrological reconstructions (*e.g.* Warner and Charman, 1994; Charman and Warner, 1997), as the reconstructions are based on mean annual water tables rather than single-shot sampling.

The application of the transfer function adopts a uniformitarian approach as it utilises modern analogues to reconstruct palaeoenvironmental data. The accuracy of the identification of the fossil assemblage will also influence the precision of the water table models derived from the transfer functions. The use of a transfer function (Imbrie and Kipp, 1971; Imbrie and Webb, 1981; Birks *et al.*, 1990a) assumes that:

- a) modern analogues exist for fossil taxa and that their response has not changed significantly over the time of the fossil record;
- b) the reference data set is not limited;
- c) there is a homogenous modern data set, based on the same taxonomic criteria.

If these assumptions are not met, reconstructing past hydrological conditions using testate amoebae, or any other proxy indicator, will not be robust.

1.2 Hydrological forcing and peatland development

Lindsay *et al.* (1988) describe hydromorphology as the shape of a mire system that will affect the area and surface flow of water. Mires can be divided into two broad groups, minerotrophic and ombrotrophic. The former are influenced by telluric nutrient enrichment from the surrounding area. The latter are nutrient poor, as water supply is limited to precipitation alone. The terms fen and bog were coined by Tansley (1939) to refer to minerotrophic and ombrotrophic mires respectively, in Britain. In this study, the term mire is used to refer to any peatland, regardless of nutrient status. Ombrotrophic mires can be divided into raised bogs and blanket bogs. Raised bogs are unique because the water table is virtually independent of groundwater and depends solely on atmospheric inputs for nourishment (*e.g.* Ingram, 1982). Blanket mires have a more complex hydrological regime, as they may be composed of a combination of ombrotrophic and minerotrophic peat, but receive most of their inputs from precipitation. Intermediate mires are ombrotrophic peatlands with characteristics of both raised and blanket mires. Minerotrophic mires, such as valley mires, receive inputs from precipitation and also from the surrounding area in the form of runoff and throughflow. Due to the topographic location of valley mires, it may be expected that an exceptionally dry period will be required to significantly reduce mire surface wetness. Since raised bogs have the simplest hydrological regimes, with bog surface wetness independent of groundwater, the surface wetness should relate to prevailing climatic conditions. Figure 1.1 is a simplified model of the hydrological factors affecting ombrotrophic peat bog development. Allogenic factors are external, mainly

climatic factors. For example, precipitation is the main source of input to ombrotrophic bogs. Conversely, autogenic hydrological factors are self-produced or internal elements, such as drainage, ground water flow, vegetation succession and the accumulation of peat, which modify the hydrological regime. The relative importance of autogenic and allogenic controls on peatland development is a debatable issue (*e.g.* Hu and Davis, 1995) and they are discussed in detail in Chapter Two.

Assessments of the subfossil testate amoebae assemblage at different levels within the peat profiles can give an indication of changes in surface wetness at specific locations. Local reconstructions of peat-surface wetness can be combined to reconstruct regional changes in peat hydrology and by inference, changes in climate. The central parts of ombrotrophic mires are the most useful in this context, as these are the locations where surface wetness is likely to be closely linked to precipitation and evaporation, rather than other site characteristics.

1.3 Philosophy and palaeoecology

Considering the various sub-disciplines of physical geography as a whole, in recent years according to Haines-Young and Petch (1986:201), “there have been very few advances in theories about, or understanding of, the natural world”. There is a requirement therefore, to develop a more critical approach to physical geography, since, “the theoretical framework seems not to have developed as in other disciplines” (Haines-Young and Petch, 1986:201). In order to achieve this and for progress to be achieved, a tradition of theorising, experimentation and the ability to recognise problems needs to be developed.

Quaternary palaeoecology can be considered to be a descriptive historical science, the results of which may be ambiguous or open to interpretation (Edwards, 1983), although Huntley (1996) considers there to have been advances in both methodology and the interpretation of Quaternary palaeoecological data in the past three decades. Quaternary palaeoecology has developed from a long period of inductive activity (see for example, an assessment of this in Edwards, 1983) and has recently acquired more vigorous and deductive frameworks.

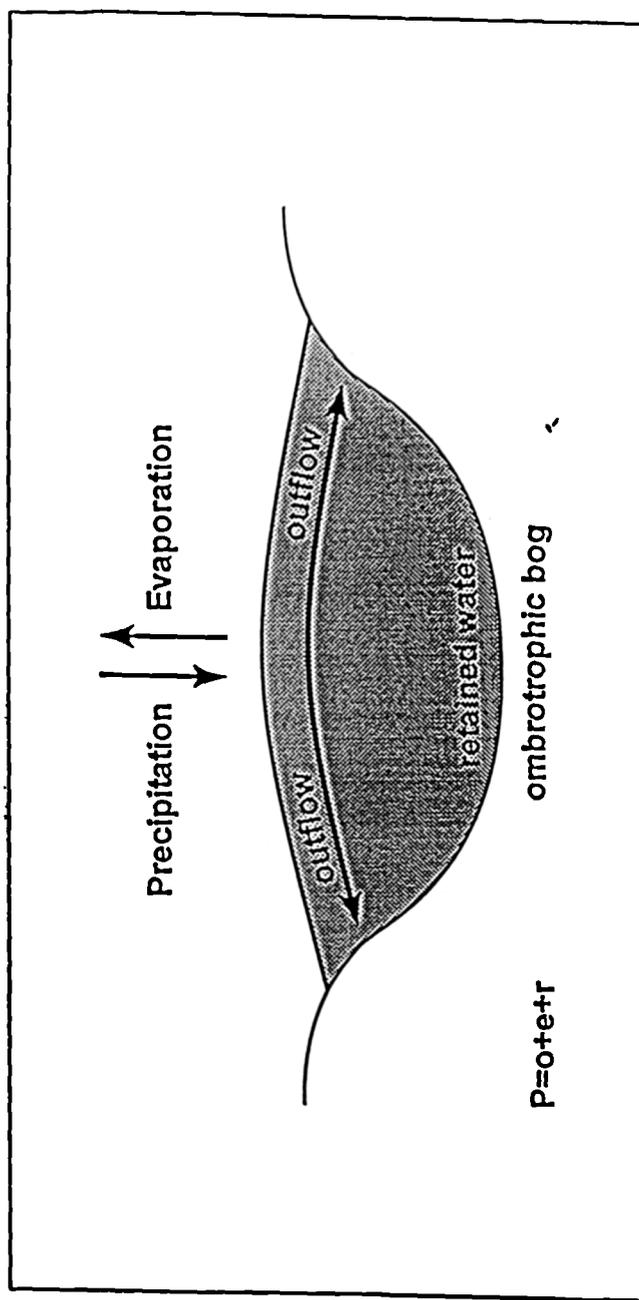


Figure 1.1 Simplified model of the hydrological regime of ombrotrophic mires
P = precipitation, **o** = outflow, **e** = evaporation, **r** = retained water

Inductive studies begin not with hypothesis development and testing but by identification of areas of ignorance by groups or individuals (Oldfield, 1993). Since the 1970s and the popularisation of Popper's (1972) theories, there has been a more deductive approach. This requires identification of a conjunction of environmental contexts, techniques and conceptual models that enable retrospective hypothesis testing. However, the deductive framework is no guarantee against misinterpretation (Oldfield, 1993), indeed explanations can only be as strong as their weakest inferential link (Edwards, 1983).

According to Haines-Young and Petch (1986), a scientific explanation should be presented as a structured argument derived from a logical consequence. This is the view of the *rationalist* who considers science to be ordered, logical and with judgements based upon reasoning (deductive). *Critical rationalism* (Popper, 1972) has three main principles:

- a) of falsifiability, that a theory can only be refuted or corroborated,
- b) of criticism, progress by examination,
- c) demarcation, testing the theory in practice.

Hypothesis testing leads to three possible outcomes:

- a) reject the theory,
- b) reject the refuting evidence or
- c) develop or modify the theory.

The data collection and interpretation in this thesis employ the three stages of the approach of a rationalist, in that

- 1) working hypotheses were developed,
- 2) models generated and
- 3) realistic interpretation of those models were undertaken.

Testing the validity of testate amoebae analysis as a palaeoecological technique involves critically testing and evaluating its utility. As such, this research addresses the concerns of Haines-Young and Petch (1986), as it is an experimental exercise that is critical of the technique used itself and of other similar techniques.

1.4 Thesis structure

Figure 1.2 sets out the thesis structure in the form of a flow diagram. The thesis is divided into four sections. Part One, the introduction and background, contains this preface to the thesis and a review of literature. The literature review is spilt into four sections:

- a) 'Peatland-climate relationships and response', which examines the nature of the peat environment, peat formation and the coupled nature of climate and ombrotrophic mires.
- b) literature concerning testate amoebae in the context of palaeoecological studies is reviewed. This includes an introduction to the modern biology and ecology of testate amoebae and their preservation and taxonomy. An understanding of these issues is essential for interpreting the palaeoecological record.
- c) the transfer function developed by Woodland (1996) is assessed as a tool for reconstructing the surface wetness of mires from testate amoebae analysis.
- d) descriptions of other palaeoecological techniques relating to this mode of study *e.g.* plant macrofossils, humification and isotopic analysis.

Part Two, the research approach and methodology, contains two chapters focussing on the field and laboratory methods. Chapter Three, 'Site selection and coring locations', sets out the rationale for choosing each field site and the coring locations within each site. Surveying data and depth profiles for each site are presented and discussed. The sites are described in terms of conservation status, management practice, surface vegetation, geology and hydrological status.

Chapter Four, 'Laboratory methods and data analysis' sets out the framework of the laboratory-based experimental design. The methods used for testate amoebae and pollen preparations and the rationale for sampling for radiocarbon dating are presented. To date, there has been no standard technique for preparing testate samples, with each worker adopting a different technique for extracting tests from peat. These techniques are diverse, some based on pollen preparation techniques and others using a simpler water-based preparation. Chapter Four (and Hendon and Charman, 1997) presents the results of a series of experiments carried out in order to assess the suitability of the variety of methods utilised in the literature in order to find the least damaging preparation and to improve upon it. Taxonomic problems encountered during the course of intensive testate amoebae analysis are discussed, as are possible solutions to those problems. The lack of clear descriptions of species based on a large sample of

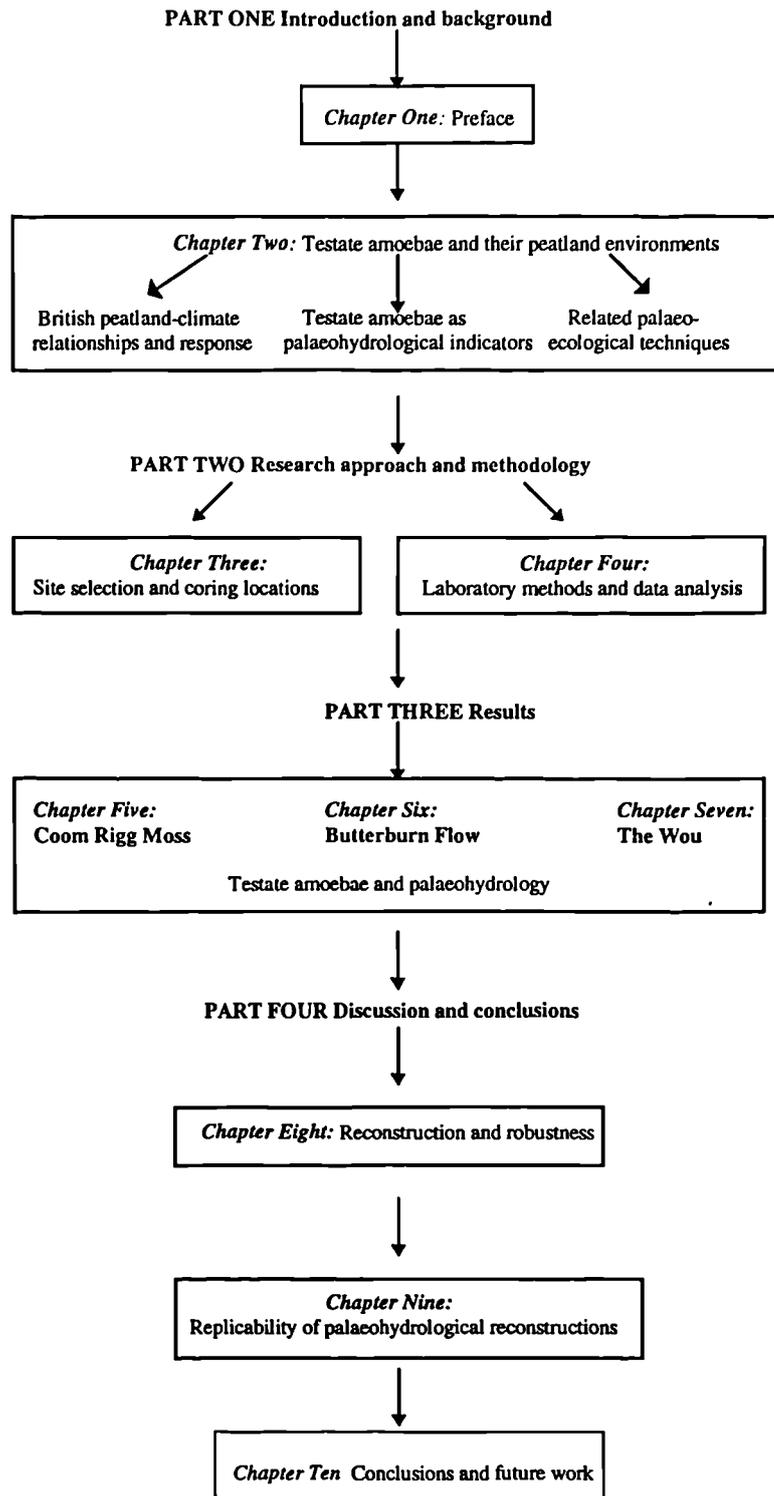


Figure 1.2 Flow diagram of thesis structure

individuals, in conjunction with adequate illustrations, on occasions made identification of taxa difficult. This problem is currently being addressed by the development of an identification guide to British peatland testate amoebae by Charman, Hendon and Woodland (in prep.).

The computer packages used to manipulate, transform and display the data derived from the testate amoebae analysis are also discussed in Chapter Four. TILIA and TILIA GRAPH (Grimm, 1982) were used to calculate the percentages and concentrations of the testate amoebae and pollen data and CONISS (Grimm, 1987), was used to construct the dendrograms for zonation of the testate amoebae diagrams. A Multivariate Statistics Package (MVSP) (Kovach, 1991) was used to transform the data into Cornell condensed format for multivariate analysis. The CANOCO package (ter Braak, 1987-1992) was used for Detrended Correspondence Analysis (DCA) of the fossil testate data and for comparison of the match or mis-match between the fossil and the modern analogue data set. WA CALIB 3.3c (Line and Birks, 1990; Line *et al.*, 1994) was used to calibrate the fossil data with the modern analogue transfer function developed by Woodland (1996) and to construct the bootstrapped error estimates. Radiocarbon dates were calibrated using CALIB 3.0 (Stuiver and Reimer, 1993a,b).

Part Three presents the results of laboratory analyses of the cores from each site. Results include stratigraphical analyses of individual cores and zoned percentage testate amoebae diagrams. Ordination plots for individual cores show the relationships of taxa and samples within each core. Water table and moisture curves from the calibrated testate amoebae data are presented and the relative merits of each are discussed. Pollen diagrams for use as biostratigraphical correlation tools are presented and marker horizons in the pollen profiles are used in conjunction with the radiocarbon dates for the linear interpolation of sample ages.

Part Four contains the discussion and conclusion chapters. Chapter Eight consists of a discussion of the methodological issues raised in this thesis, such as preparation techniques, taxonomy and the robustness of the transfer function. Chapter Nine is the main discussion chapter and includes assessment of the replicability of the testate amoebae record within the mires and across a region at the three scales of study. Using the multiple records of water table reconstructed from the fossil testate amoebae data, an attempt is made to separate the allogenic and autogenic hydrological signals and shifts

in mire surface wetness are related to other proxy climatic records. Conclusions and recommendations for future work are made in Chapter Ten.

CHAPTER TWO

Testate amoebae and their peatland environments

2.0 Introduction

This chapter investigates the nature of the peatland as a physical and hydrological environment, the interaction of mires with climate and the response to and record of climate change from proxy indicators. The mire types used in this study are discussed in detail, regarding their specific relationships with hydrology and their response to allogenic and autogenic factors. The modern ecology, biology and taxonomy of testate amoebae are discussed, in order that their fossils may be interpreted as palaeohydrological indicators. The transfer function for hydrology from testate amoebae in British mires, developed by Woodland (1996), is reviewed. The relationships between climate, peat bogs, hydrology and testate amoebae assemblages are considered. Other relevant proxy climatic indicators; humification, *Sphagnum* macrofossils and isotopes, are also discussed.

2.1 Peatland-climate relationships and response

2.1.1 Peatland distribution

Approximately 5.8% of land in Britain is covered in peat, with the majority concentrated in the uplands of northern and western regions. Peatland distribution within the British Isles is shown in a map compiled by Taylor (1983), (Figure 2.1). The spatial distribution of peatlands is greatly influenced by the presence of the North Atlantic Ocean which creates a relatively cool, temperate and maritime climate. This results in high humidities, cloud cover and precipitation, all of which increase with altitude, to produce a distinct type of upland climate in the north and west of Britain (Taylor, 1983). Conditions are so oceanic in Britain that mire development is possible anywhere in the country (Lindsay, 1995). These conditions are ideal for peat formation. As a high percentage of these sites are ombrotrophic, the potential for palaeoclimatic studies is great and a large number of sites are suitable for palaeoecological studies. The distribution and development of fens and bogs are frequently presumed to be strongly influenced by the interplay of regional climate, site geomorphology and history (Almquist-Jacobson and Foster, 1995).

Peat stratigraphy is claimed to yield a continuous climatic record (Barber, 1981) and is potentially a global source of proxy climatic data (Chambers, 1993), due to the global distribution of peat bogs. Maps in Gore (1983) and Chambers (1993) show that the distribution of mires on a world scale is concentrated predominantly in the northern hemisphere, in the Arctic, Boreal and Northern Temperate zones. In addition, there are large areas of peatlands in the tropics, especially south east Asia, where raised mires also occur. In the southern hemisphere there is little land in latitudes suitable for mire formation and Gore (1983) concentrates on those found in Chile and Australasia. Bog distribution in Western Europe is illustrated by Lindsay (1995) and shows that the area of peatlands found in Britain is relatively small.

2.1.2 The role of *Sphagnum* in the peatland environment

The genus *Sphagnum* (bog-moss) forms part of the bryophyte group along with other mosses (Musci) and the liverworts (Hepaticae). The class *Sphagnopsida* contains a single order, the *Sphagnales*, within which there is one monogeneric family, the *Sphagnaceae* (Smith, 1978; Daniels and Eddy, 1985). There are 40 species of bog-moss in Europe, although most individual bogs contain less than ten species in varying proportions (Barber, 1993). The *Sphagnopsida* are divided into six sections, Sections *Sphagnum*, *Acutifolium*, *Rigida*, *Squarrosa*, *Cuspidata* and *Subsecunda* (Smith, 1978). Section *Sphagnum* includes *S. papillosum*, *S. imbricatum*, *S. magellanicum* and *S. palustre*. Section *Acutifolia* contains *S. fuscum* and *S. rubellum*, which are hummock forming species. Section *Cuspidata* includes *S. tenellum*, *S. cuspidatum* and *S. recurvum*, which are hollow forming species (Daniels and Eddy, 1985). Different species of *Sphagnum* colonise different microhabitats in a hummock-hollow complex and the variety of taxa and ecological niches on a bog is fundamental to the record of climatic change found in peat. Bogs dominated by a single eurytypic taxon would not show the sensitivity of other bogs where several species of *Sphagnum* interact as surface wetness changes. Where several species interact and take over from one another as the wetness of the bog surface fluctuates, the peat profiles are theoretically much more sensitive records of climate change. For example, Bolton Fell Moss, Cumbria (Barber, 1981; Barber *et al.*, 1994a,b).

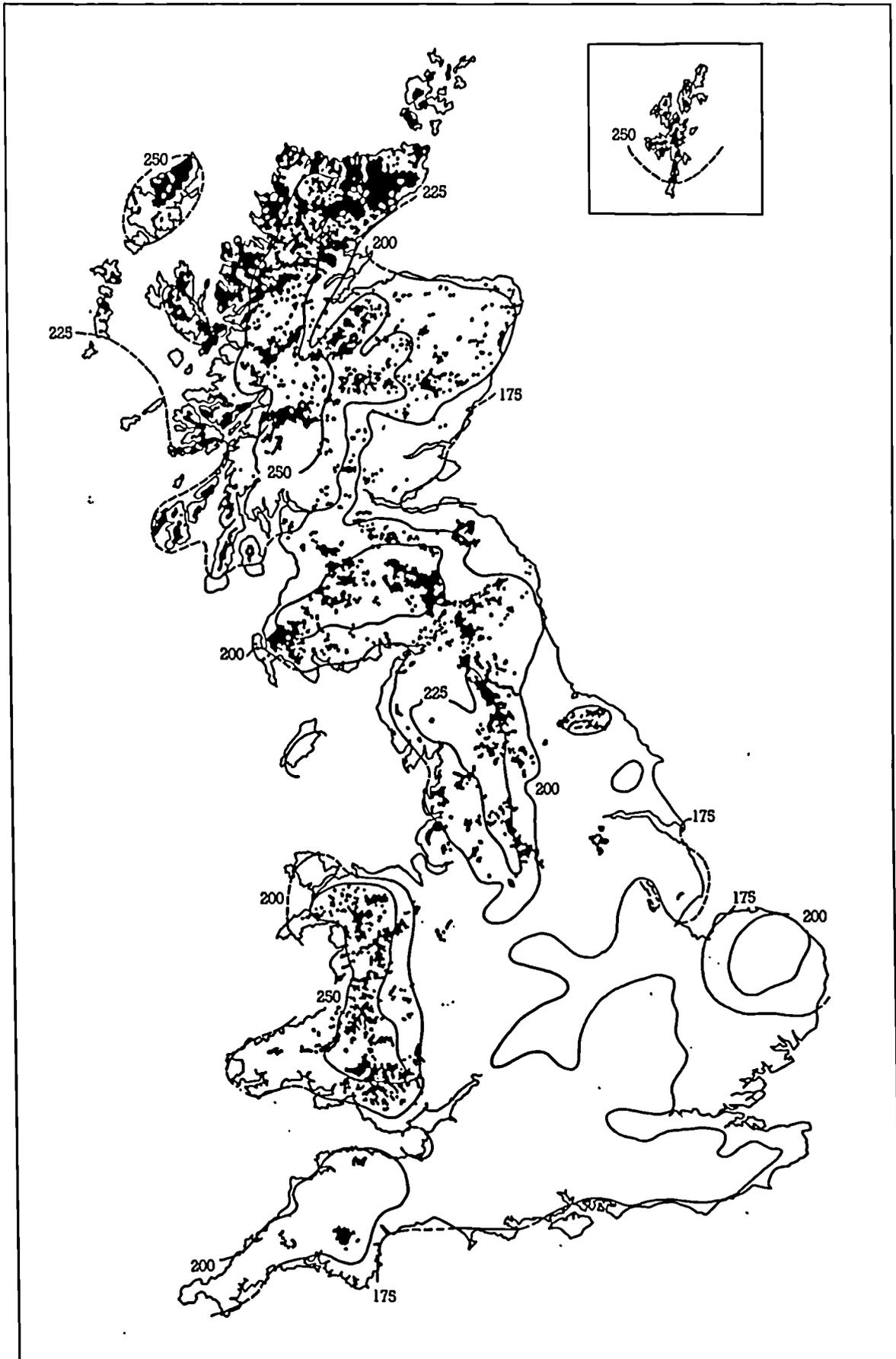


Figure 2.1 Map of peatland distribution in the British Isles
 (after Taylor, 1983; major deep peat deposits in Britain. Isopleths for average number of 'rain days' 1901-1930 are shown)

Sphagna are important plants in the formation of peat bogs. Peatlands are a unique environment, where the *Sphagnum* community deposits a detailed record of its own history in the form of plant macrofossils, *in situ*, as the lower part of each plant dies, but remains preserved in the catotelm (Barber, 1985, 1993). Peat bogs exhibit a special relationship with climatic variability owing to the reliance of *Sphagnum* on moisture for growth. *Sphagnum* mosses grow apically from the capitulum, typically 2-3cm per season and have no roots, so can survive on oligotrophic, nutrient-poor rainwater (Hobbs, 1986). Mosses lack stomata and therefore cannot control evapotranspiration by closing the stomata in the manner of vascular plants.

The maintenance of a high moisture content is achieved by the structure of the *Sphagna*, since they possess empty (hyaline) cells, which are capable of absorbing water many times greater than the dry weight of the plant. *Sphagna* grow above the ground water table, making ombrotrophic bogs dependent on the effective precipitation in order to sustain growth. Bog mosses also have a high Cation Exchange Capacity (CEC), enabling the moss to extract nutrients such as potassium, calcium and magnesium from the surrounding water and return hydrogen ions in exchange (Clymo, 1983). This acidifies the water, which in turn contributes to the preservation of the plants and other organic remains.

Excessive drying results in the bleaching of *Sphagnum*, which reflects more solar energy and results in further moisture losses to evapotranspiration (Clymo and Hayward, 1982). Backéus (1991) has shown that the moisture conditions in August of the previous year represent the most important single factor controlling the growth of *Sphagnum* and that temperature is not significant. In hummock-forming species of drier habitats, the hyaline cells are larger than those in species occupying wetter habitats (Daniels and Eddy, 1985). These factors all have important implications for the existence of testate amoebae assemblages, as discussed in Section 2.2.5.

Raised bogs have been favoured for *Sphagnum* macrofossil studies because of their ombrotrophic status resulting from the direct relationship between the mean water table and effective precipitation. The plants lose mass as a function of the decay process, but if the leaf-size, shape and diagnostic cellular details are still discernible the major parts of the original community can be reconstructed (Barber, 1993). The relationship

between testate amoebae and bog moss is discussed in Section 2.2.6 and the use of *Sphagnum* macrofossils as palaeoclimatic indicators is discussed in Section 2.6.1.

2.1.3 Peat formation

Peat is normally autochthonous and is formed *in situ*, as a consequence of the incomplete decomposition of organic matter, usually as a result of waterlogging. Peat formation is a diagenetic process, involving the transformation of a living vegetation assemblage to a death assemblage and then to a subfossil assemblage (Barber, 1981; Clymo, 1983, 1984, 1991). Decay continues in deeper peats but is very slow (Clymo, 1984). In ombrotrophic systems, as long as there is a positive water balance, peat will remain waterlogged and anaerobic, which inhibits the decay of organic matter. Ivanov (1981) considers water supply to be the most important exogenic factor in determining the development, maintenance and form of a mire and its relationship with the water table.

Hydrology, topography and the permeability of the substrate are important factors affecting peat development. The conditions under which peat begins to accumulate are determined primarily by climate and topography (Hobbs, 1986). Peat initiation may occur as a result of terrestrialisation (Hobbs, 1986; Lindsay *et al.*, 1988; Lindsay, 1995). This occurs due to the sedimentation of water bodies, which develop anoxic layers in the bottom sediments and eventually become filled with peat, forming for example, raised mires. Conversely, peat accumulation may take place as the result of the paludification (swamping) of dry ground. Ground that was once dry becomes wet, often due to increased precipitation and peat formation may be initiated. The deepest peats tend to occur at the wettest sites with more permanent waterlogging and less humification, which encourages more rapid peat formation (Ratcliffe, 1977a).

Allogenic and autogenic factors in mire formation

Mire development as a result of endogenous and exogenous influences has important implications, as the separation of these hydrological signals is fundamental to the aims of this study. There is a limited body of literature dealing specifically with autogenic and allogenic inputs to the mire hydrological system (*e.g.* Winkler, 1988; Foster and Wright, 1990; Hu and Davis, 1995). Wheeler (1992) and Belyea and Warner (1996) discuss some autogenic and allogenic influences on the mire system, but these are not

necessarily hydrological factors. The relative roles of autogenic and allogenic controls in peatlands remains a debatable issue (Hu and Davis, 1995) and the arguments are complex and often contradictory.

Autogenic factors are those that result from internal bog dynamics and include vegetation, microclimate, mire expansion, human impact and site drainage. Autogenic processes affecting mire surface wetness occur as portions of the mire pass through critical stages of bog development, which may be controlled by morphology, hydrology or peat depth (*c.f.* Foster and Wright, 1990) and are responsible for changes in vertical accretion, lateral expansion and the consequent shape of the peatland (Ingram, 1982; Winston, 1994; Almquist-Jacobson and Foster, 1995). The upward growth of peat due to autogenic factors usually takes place where there are only small vertical fluctuations in the water table. The theoretical model developed by Almquist-Jacobson and Foster (1995) combines internal bog dynamics with the external factors of local substrate, regional temperature and moisture conditions. The model suggests that the geometry of raised bogs will adjust to climate change regardless of the stage of bog development or direction of climate change. Almquist-Jacobson and Foster (1995) conclude that all aspects of mire development appear to be closely related to climate.

Conversely, it has been argued that in a suitable climate, autogenic processes are the dominant factors controlling mire development (Walker and Walker, 1961; Tolonen *et al.*, 1985; Foster and Wright, 1990). Autogenic mechanisms may result in drier conditions at mire margins as cooling and wetting (allogenic factors) will raise the water table in central, flatter parts of the bog, due to a lower gradient in hydraulic potential and will raise the water table later in marginal zones (Kilian *et al.*, 1995) (see Section 2.1.7). According to Stoneman (1993), in raised bogs, autogenic forcing affecting bog surface wetness only comes into effect once allogenic factors (principally climate), have upset the equilibrium between bog hydrology and prevailing climate. Furthermore, processes involved in returning the mire back to a state of equilibrium (principally vegetation) are rather slow to operate, as surface wetness constantly changes and may be further over-run by climate change.

Ombrotrophic mires also develop as a result of allogenic inputs, principally climate, as raised mires and the shedding parts of blanket mires are locations where the peat profile is most closely linked to the balance between precipitation and evaporation, rather than

other site characteristics. The topography of a mire will affect the nature and strength of vegetation and testate amoebae response to hydrological change, as it affects the retention of impacting water. It is possible to distinguish between water-shedding and water collecting sites, situated in convex or concave regions of the blanket mire system respectively (Tallis, 1994, 1995). Barber (1981) hypothesised that climate played a major role in peat formation due to the strength of allogenic forcing, but does not take into account autogenic factors such as drainage. The study of multiple cores from a single site is needed to evaluate this. Barber (1981) falsified earlier concepts of autogenic cyclic changes in peatlands by showing that from macrofossil studies, surface wetness patterns occur over entire strata. The layered stratigraphy of moderate relief of many Atlantic bogs or 'flat' stratigraphy is considered by Barber (1994) and Barber *et al.* (1994b) to be more useful and sensitive for climatic reconstruction than would be a stratigraphy dominated by climatically-insensitive hummocks. Hummocks are shifting features, so it is possible that the mid point between hummock and hollow may provide the best record of climate, as shifts in the expansion and contraction of the hummocks are likely to register there.

There is little agreement in the literature about the relative importance of these mechanisms in the peat hydrological record. Broadly, an allogenic hydrological signal would result in a shift in water table simultaneously across the bog in response to broad scale climate change. Autogenic influences would result in more localised hydrological changes in response to crossing critical thresholds of mire growth and expansion. The separation of these signals is central to this study.

2.1.4 Internal mire morphology

Peat bogs are diplotelmic and are composed of two layers: the 'acrotelm' and the 'catotelm' (Ivanov, 1981; Ingram, 1982; Clymo, 1984; Lindsay *et al.*, 1988). The acrotelm is the active, aerobic, upper peat forming layer (the top 10-50cm). In this zone there is intensive exchange of heat and moisture between the peat and the atmosphere, with frequent flux in the level of the water table resulting in fluctuations in the moisture and heat content. The vertical stem structure of plant material near the surface encourages rapid lateral flow and the acrotelm is a zone of water exchange (Lindsay, 1995). There is a high hydraulic conductivity and water yield and a rapid decline of

both with depth. The transition from the acrotelm to the catotelm is gradual and may take place over ten or so years (Clymo, 1991). In the catotelm, the inert layer, there is a constant or little changing water content and a slow exchange of water to the surrounding area. There is a low hydraulic conductivity in this zone. The catotelm is anaerobic due to waterlogging, resulting in low decomposition rates. Bog growth is limited by the balance between rates of peat input into and decay within the catotelm (Clymo, 1984). This has important implications for the net rate of peat accumulation, because, where input exceeds decay, peat accumulates.

Lindholm and Markkula (1984) found clear differences in the depth of the aerobic layer between the hummock and hollows, as the aerobic layer closely follows the level of the water table. If water levels in a pool-hummock system are lowered, then an open water pool that partially dries out may be invaded by *Sphagnum* at the same time as *Sphagnum* is being lost from the drying hummocks (Tallis, 1995).

2.1.5 Peat hydrology

Ingram (1983) and Streefkerke and Casparie (1989) provide excellent overviews of peat bog hydrology. According to Ivanov (1981), peat typically contains 88-97% water, 2-10% dry matter and 1-7% gas by volume. The rate of peat accumulation depends upon two factors: the wetness of the peat (Figure 1.1) and the quantity of heat that it receives. The hydrology of ombrotrophic peat can be summarised as follows:

$$\textit{Precipitation} = \textit{outflow} + \textit{evaporation} + \textit{retention}$$

Retained water is important for creating an anaerobic environment suitable for peat accumulation (Moore and Bellamy, 1974; Clymo, 1984, 1991). Water can be held in the peat matrix: as intracellular water held in the organic matter, as interparticle water that is tightly bound, or as interstitial water that is loosely bound, interparticle (mobile) water (Lindsay *et al.*, 1988). Evaporation may also occur in three ways; as interception, with loss of moisture directly from the plant surfaces, leaves and stems; as transpiration - loss from within the plants; and direct evaporation from the substrate, in this instance from the peat (Ingram, 1983).

The source of water is a useful criterion for the classification of mire types. Mire development in all climatic regions is connected with the relationship between the water budget components; precipitation, evaporation, seepage and their influence on the mean position of the water table (Ivanov, 1981). The high rainfall that contributes to ombrotrophic bog growth can create contrasting effects. High rainfall may result in waterlogging that encourages peat accumulation by creating an anaerobic environment. It can also induce 'flushing' in the acrotelm dome, which washes water rapidly through the peat profile, thereby increasing the breakdown of organic matter (Lindsay *et al.*, 1988). The wettest part of a bog, other than the marginal lagg fen is found on the highest part of the dome, the cupola.

2.1.6 Mire classifications

The classification of British peatlands is complex. Mires are often classified according to the aim of the study, for example, Clymo (1983) distinguishes between:

- a) the classification of the peat substance, *i.e.* age, colour, chemistry, botanical composition, state of decomposition, cation exchange capacity and
- b) the peat forming system, *i.e.* topography, hydrology of the area and bog morphology.

Dierssen (1982) developed the criteria of mire classification according to both the peat substance and the peat-forming system, following the work of Grosse-Braukmann (1962, in Lindsay *et al.*, 1988; Heathwaite *et al.*, 1993). However, Moore (1984) argues that the problem of classification is aggravated by the fact that most of the available criteria, such as floristics, chemistry, peat and morphology are not discontinuous, but are continuous variables and that the definition of discrete units is not possible. Because of the interactions between these variables, only broad distinctions are made here.

Mire morphology

Morphology is the shape of the mire resulting from the accumulation of peat and is influenced by topography, hydrology, climate, plant productivity and decomposition rates and can result in, for example, a domed raised mire or undulating blanket bog.

Winston (1994) has a rather more simplistic view, stating that because peat accumulates beneath the water table, the shape of the peat body should reflect the shape of its water table and thus the hydrology of the bog. The overall shape of the mire surface and the small scale surface patterns of hummocks and hollows can show two very different levels of morphological variation. Aario (1932, in Goode, 1973) called them 'Grossform' and 'Kleinform' respectively. Four levels of the functional hydrology of mires have been listed by Ivanov (1981). They are defined as "active features which both control and are controlled by the underlying hydrology" (Lindsay *et al.*, 1988:20). Ivanov's (1981) division on the basis of functional hydrology, into macrotopes and mesotopes correspond with Aario's (1932) Grossformen and the microtopes and microforms of Ivanov correspond with the Kleinformen of Aario (1932). Figure 2.2 shows the hierarchy of the four levels of functional hydrology described by Ivanov (1981).

Mire macrotopes

Macrotopes are considered to form where mires coalesce, therefore escaping the immediate hydrological confines of each individual bog, *e.g.*, two raised mire units joined together. Most macrotopes are hydrologically complex, combining the hydrological elements of the component mesotopes and microtopes. Each level of hydrological interaction is dependent upon the other levels for stability.

Mire mesotopes

Mesotopes are mire units; bodies of peat that have developed into single, complete, hydrological entities. Goode and Ratcliffe (1977) classify mesotopes according to the topographic and hydrological (hydromorphological) features. *e.g.*, a single raised bog, a saddle mire or a valley mire.

Mire microtopes

Microtopes are an arrangement or combination of several surface features which characterise ombrotrophic mires, *e.g.*, hummocks and pools on a mire surface. The surface patterns of boreal peatlands are examined in detail by Sjörs (1961).

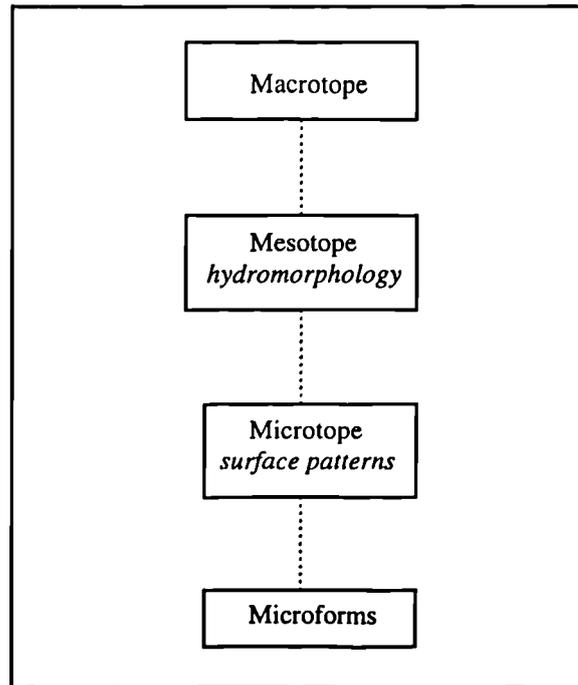


Figure 2.2 Functional hydrology (modified from Lindsay *et al.*, 1988, originally from Ivanov, 1981)

Microform	Characteristics
1 Hummock	mounds of <i>Sphagnum</i> < 1m high, 1-2m diameter, vegetation lies 30-75cm above mean water table
2 High ridge	10-20cm above water table, dominated by dwarf shrubs
3 Low ridge	(lawn) <i>Sphagnum</i> -rich fringe to expanses of high ridge and hummock. 1-10cm above mean water table
4 <i>Sphagnum</i> hollows	(carpet) aquatic zone, composed of <i>S. cuspidatum</i> on an aqueous matrix. 0-10cm below mean water table
5 Mud-bottomed hollows	4-20cm below the water table, little vegetation, dry in summer
6 Drought-sensitive pools	climatically sensitive, distinct from permanent pools, flooded for most of the time, but will dry up in drought conditions. 20-50cm below mean water table
7 Permanent pools	pools several metres deep found only in watersheds, devoid of vegetation
8 Erosion channels	gullies exposed as dry peat for most of the year
9 Erosion hags	surface microtopography becomes accentuated due to erosion, blocks of uneroded peat within a zone of severe erosion
10 Peat mounds	uncertain status - >1m high hummocks in north and west only

Table 2.1 Mire microforms on British peatlands
from Dierrsen (1982), Lindsay *et al.* (1985) and Lindsay *et al.* (1988)

Lindsay *et al.* (1985) demonstrated a link between the range, nature, extent and intensity of surface patterning on bogs and climate, because the most extreme forms of patterning within a region display greater amounts of open water, with increased wetness of climate. Microtope patterning is most pronounced in the areas of the mire expanse and simplest at the margins, this may be a result of autogenic peat development (Section 2.1.3). At Alport Moor, a blanket mire in the southern Pennines, Tallis and Livett (1994) found that microtopographic differentiation of the mire surface into hollows, pools and hummocks resulted from varying rates of peat accumulation locally.

Mire microforms

Microforms are individual surface features, *e.g.*, a single hummock. Lindsay *et al.* (1985) and Lindsay *et al.* (1988) identified ten categories of microform within a patterned microtope (Table 2.1). Few sites exhibit all of the microform features, most have no more than three (Lindsay, 1995).

Ontogeny (ecological development)

The peat contains the record of the site's development- *i.e.*, primary, secondary or tertiary peat (Moore and Bellamy, 1974). *Ontogeny* also deals with the concepts of topogeneous, soligenous and ombrogenous mires (Ratcliffe, 1977a) and du Rietz's (1954) division of ombrotrophy and minerotrophy, into rain and ground water-fed bogs. It is important to distinguish between the ombrotrophy concept of du Rietz (1954) and the contemporary ombrotrophic status of mires. Ombrotrophy relates to the genesis and conditions which gave rise to the mire's development whilst the ombrotrophic status of a mire is derived from being a meteorically-fed system from which it develops its poor nutrient status. Ratcliffe (1977a) adopts a classification system based on major topographic or structural mire types. Ombrogenous mires are subdivided into blanket bogs and raised bogs. Topogeneous mires are divided into three main types: open water transition and floodplain mires, basin mires and valley bogs. Soligenous mires or flush bogs can occur in association with some of the other main types. The division into ombrotrophic and minerotrophic mires is of great importance in this study.

Geographic or topographic relationships

These are used to classify minerotrophic (fen) systems or to separate units within blanket mire, *e.g.*, saddle, plateau, raised bog, valley bog. The topographical location of a mire is very important as it may influence mire initiation, for example, paludification initiating a valley mire. Figure 2.3 shows some examples of topographic locations found in western Europe.

Vegetation characteristics

The structure of vegetation influences the microclimate of the bog surface. Mires are often classified according to the floristics of the bog. However, the floral elements need to have clearly defined optima and limits to growth and many mire plant species have relatively broad limits of tolerance that may hamper this method of classification. The role of *Sphagnum* as a peat-forming species is discussed in Section 2.1.2. The vegetation communities found in mires are discussed in detail by Rodwell (1991).

Palaeobotanical / palaeoecological features

Peat profiles contain multi-proxy records that can be used to reconstruct the developmental sequence of the mire from its stratigraphy and microfossil content, *e.g.* pollen, testate amoebae, coleoptera, isotopes and plant macrofossils. Heathwaite *et al.* (1993) consider the palaeoecological record to be limited for assessing past climate change, as it is almost impossible to isolate climatic influences on mire formation from autogenic changes in mire hydrology, chemistry and biota, as the mire develops. The application of testate amoebae analysis from multiple peat cores will address this concern.

Soil chemistry and water relations

According to Lindsay *et al.* (1988), water chemistry is often used to reinforce classifications based on floristic studies, rather than for classification on a primary basis, for example, nutrient status - base poor = bog, base rich = fen. Goode and Ratcliffe (1977) divided British mires into three broad trophic groups; oligotrophic (nutrient-poor); mesotrophic (medium nutrient status) and eutrophic (nutrient-rich).

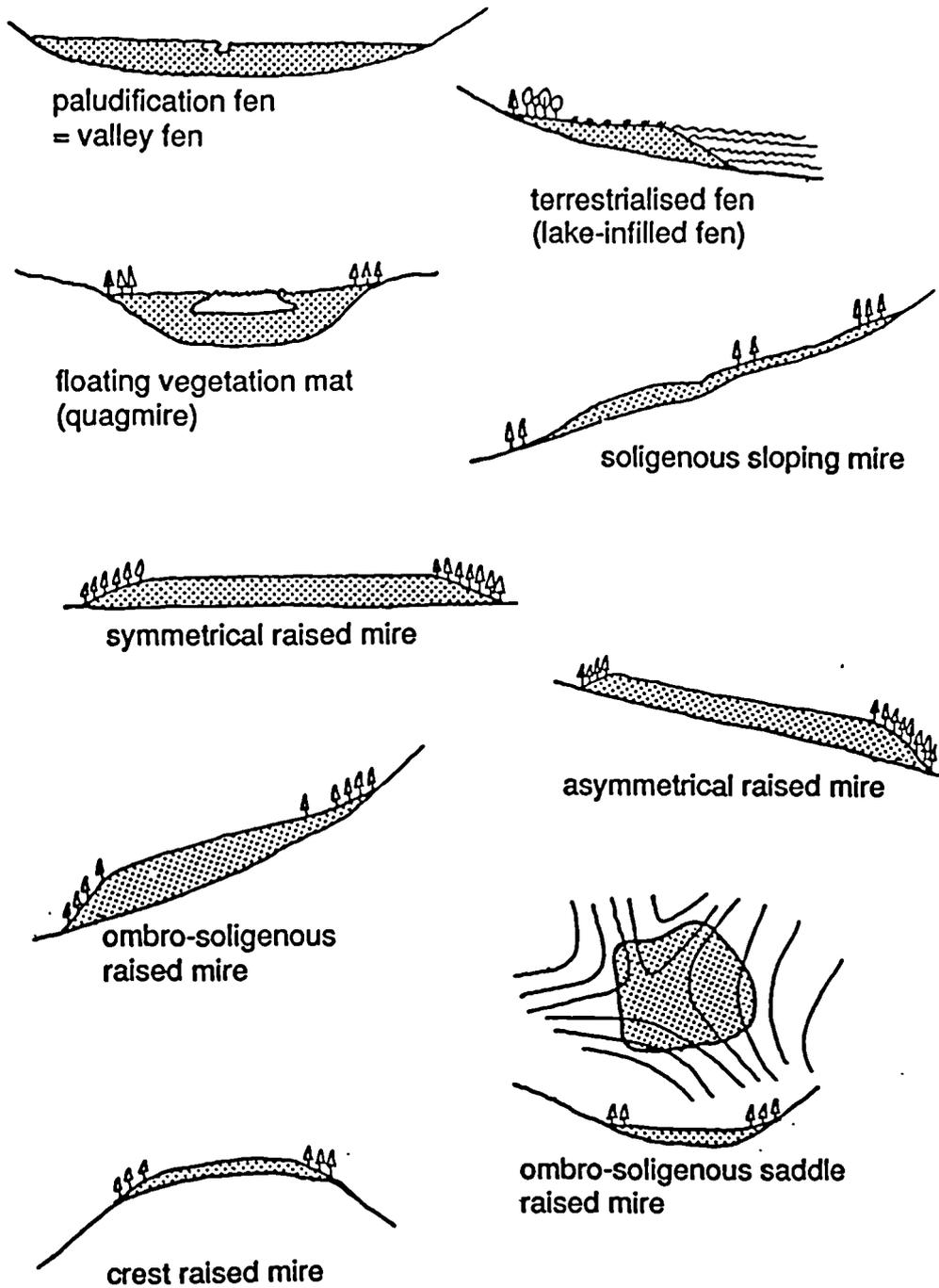


Figure 2.3 Topographic locations of peat bogs (Heathwaite *et al.*, 1993)

These classifications are widely used. In this study, all three sites were oligotrophic. Only three mesotope types are considered below in detail; this is only a small proportion of the peatland variation found in Britain. A range of morphological peat types is examined in detail by Ratcliffe (1977a), Taylor (1983), Wheeler (1984), Hobbs (1986), Lindsay *et al.* (1988) and Lindsay (1995). Only those that are of importance to this study are discussed below, namely, raised bog, blanket bog and valley mire.

Raised bogs

Raised bogs are often formed as a result of terrestriation (Lindsay, 1995). Raised bogs are ombrotrophic; their only source of water is precipitation as the mire surface is isolated from the regional ground water table (Moore and Bellamy, 1974). Raised bogs are usually limited in extent and definable by easily recognisable boundaries, such as a drier, steeply sloping rand at the outer margin and an adjacent stream course or lagg at the transition between the bog and the mineral soil (Gore, 1983; Heathwaite *et al.*, 1993). In an undisturbed state, the surface of a raised bog is domed, often rising in the centre several metres above the underlying mineral soil. The coupling between climate and raised bogs is a direct result of the peat cupola being raised above surrounding ground water and adjacent land. Goode (1973) suggests that raised bogs develop over approximately level terrain and that there is a graduation from the plateau type that has a flat cupola to a convex raised mire. Concentric raised bogs often have a lagg at the edge of the bog, accumulate convex masses of peat, can develop in both open and closed basins and have a distinct surface pattern of concentric ridges and hollows. Eccentric raised bogs have the apex of the cupola displaced from the centre of the mire and the surface pattern consists of a regular alternation of ridges and hollows aligned parallel to the contours of the bog surface (Moore and Bellamy, 1974). Because run-off rates are low, raised bogs do not depend on such a high precipitation/evaporation ratio as blanket mires (Ratcliffe, 1977a). Raised bogs are oligotrophic (nutrient-poor), as they are isolated from the ground water and receive nutrients only from precipitation (Hughes and Heathwaite, 1995; Lindsay, 1995).

Blanket bogs

Blanket bogs are the most extensive mire type in Britain (Hobbs, 1986). Blanket mires require an extreme oceanic climate, with relatively low temperatures and high cloudiness controlling effective humidity. They develop where there is both a high rainfall and a high number of rain days, together with minimum evaporation (*i.e.* cold temperatures). They usually develop over impermeable soil or bedrock in the north and west of Britain, where conditions are suitable for paludification (Moore and Bellamy, 1974; Lindsay *et al.*, 1988; Charman, 1992). Blanket bogs have a more complex hydrological regime than raised mires and may cover diverse topography, resulting in a range of nutrient, hydrological and micro-climatic conditions (Moore, 1984; Hughes and Heathwaite, 1995; Lindsay, 1995). Blanket bogs may be influenced both by meteoric and telluric water supplies, but receive most of their input from direct precipitation. According to Lindsay (1995), the thickness of blanket peats can vary from a few cm to 7-8m, but they are generally shallower than raised bogs. Blanket peats may grow over quite deep basins effectively obscuring them from the surface (Charman, 1994). Where topography is gentle, a hummock-hollow microtope similar to that of a raised mire may develop. Blanket peats were thought to be relatively insensitive to climatic change and too well humified to yield a climatic signal. This was because blanket peats develop in areas with supra-optimal climate for peat growth, where relatively small changes in climate are not registered sufficiently to produce a vegetation response (Tallis, 1995). However, Blackford and Chambers (1991, 1993, 1995) found that the blanket peats previously thought to be too humified could yield a good climatic signal.

In northern England, where morphological features may not be clear, the distinction between raised and blanket mire may be tenuous. An ombrogenous continuum may develop, the components of which vary according to the relative importance of climate and topography at any one point (Ratcliffe, 1977a). Lindsay (1995) discusses the possibility of finding mires where climate and terrain are in a transitional state between blanket and raised mires. These ridge-raised mires or intermediate mires have characteristics common to both raised and blanket bogs. This continuum from lowland raised bog to blanket bog is not sufficiently distinct to categorise in its own right, but instead is classified according to the dominance of features typical to either raised or blanket bog. According to Lindsay (1995), in Britain, this type of mire is uncommon, is hardly found at all in England and Wales and is of only localised distribution in

Scotland. However, it is a largely unrecognised status and is likely that more ombrotrophic mires than is currently thought fall into this category, as they can not clearly be divided into either raised or blanket mires.

Valley mires

Valley mires are elongate mires which develop in topographically restricted areas, such as small, shallow valleys or channels that are not enclosed, but which have impeded drainage. This means that movement of water along the main drainage axis is possible, even though ground slope in that direction may be slight (Ratcliffe, 1977a; Wheeler, 1984). Topogenous mires such as valley mires, owe their origin, if not their maintenance, to drainage water rather than direct precipitation (Walker, 1970). Wetness is maintained by mineral groundwater flowing from above, or seeping laterally at the sides. The origin of valley mires is often paludification (Taylor, 1983). Topogeneous mires develop where local relief results in permanently high water tables (Ratcliffe, 1977a). Hobbs (1986) suggests that the morphology of valley mires may be varied and complex. Moore and Bellamy (1974) and Wheeler (1984) point out that valley mires have a wide base status range and can support a range of vegetation communities, from *Sphagnum* to carr.

2.1.7 The history of peat stratigraphical studies

Peat stratigraphy

Peat bogs have been used as sources of proxy climatic data since the nineteenth century, mainly using stratigraphical analysis (Blackford, 1993). Peat stratigraphic units were regarded as directly resulting from and therefore indicative of, different climatic periods. Blytt (1876) and later Sernander (1906) divided the Holocene into five climatically distinct periods, on the basis of marked changes in peat bog stratigraphy (Table 2.2). This classification is now regarded as too simplistic, as it does not adequately describe long term climatic changes over the whole of north-west Europe.

Approx. Age	Period	Climate	Evidence
2,500 BP	Sub-Atlantic	cold & wet	poorly humified <i>Sphagnum</i> peat
5,000 BP	Sub-Boreal	warm & dry	pine stumps and humified peat
7,000 BP	Atlantic	warm & wet	poorly humified <i>Sphagnum</i> peat
9,000 BP	Boreal	warm & dry	pine stumps and humified peat
	Pre-Boreal	subarctic	macrofossils of subarctic plants

Table 2.2 The Blytt-Sernander Scheme (After Lowe and Walker, 1997)

The cyclic regeneration model

Several theories of peat bog formation have been developed over the past century. Perhaps the most prominent of these has been the ‘cyclic regeneration model’ of von Post and Sernander (1910), refined by Osvald (1923) and popularised by Tansley (1939). Backéus (1991) described this as ‘a hypothesis that became an established truth’. The theory was developed to explain the apparent lenticular features of humified and unhumified peat observed in sections of raised mires. The hypothesis was that peat bogs form self-perpetuating, autogenic systems and that the vegetation and microtopographical mosaic of hummocks and hollows would alternate as peat accumulation took place (Figure 2.4). Plant communities in hollows were thought to deposit vegetation at a greater rate than dry hummock tops, which would eventually become moribund. The hollows gradually fill and rise above the former hummocks, thus reversing the original relationship, the hummocks becoming hollows (Barber, 1982). Osvald (1923) called the central areas of mire growth the ‘Regeneration Complex’ and outlined possible vegetational successions and retrogressions.

This theory was disproved by a number of workers, including Walker and Walker (1961) and Barber (1981), who argued that the alternation of hummocks and hollows was not the typical sequence in most raised mires, but that hummocks maintain themselves. Moore (1991) and others, now believe that the approximate positions of the hummocks and hollows are maintained for long periods of time, with occasional increases in pool abundance as a result of changing hydrological conditions at the mire surface.

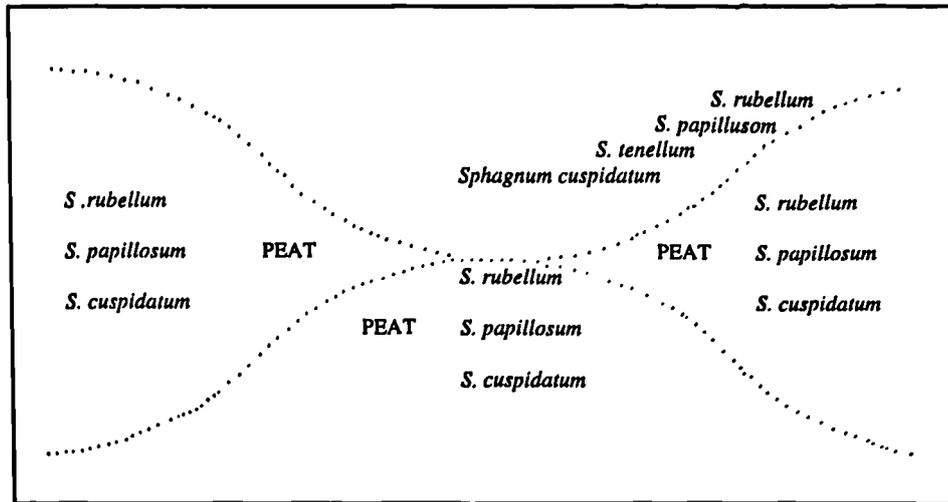


Figure 2.4 The cyclic regeneration model The succession of *Sphagnum* species forming the peat in a typical 'hollow-hummock' cycle (modified from Tansley, 1939).

According to Johnson and Damman (1991), the species of *Sphagnum* bog mosses that occupy the hummocks are more resistant to decay than those species that grow in wet hollows and so their relative position is maintained. Aaby (1976) suggests that hollow peat is likely to show a more detailed record of climatic change than hummocks, where smaller variations in humidity are not registered. If mire water table is a critical factor in determining species composition [of vegetation], then an undulating mire surface, which is not a fixed distance from the water table, can provide a much wider range of niches for groups of species to inhabit (Lindsay *et al.*, 1985). Barber's (1994) theory that small impermanent pools are more sensitive to climatic change than large permanent pools, may have important implications for the study of subfossil testate amoebae in determining the palaeohydrological conditions of bogs, because the location of the core extraction site will influence the assemblage of testate amoebae recovered from the peat. Barber (1994) suggested that hollows with a diameter of 5-200cm may become small pools at times of higher water levels. Such pools are shown by stratigraphic analysis to be short-lived and are readily colonised by bog-mosses. Larger pools act as buffers to a changing climate and there is no clear climatic signal shown in the peat stratigraphy. Therefore, peat cores extracted from sites of small, impermanent pools are likely to reflect climatic variations in greater detail in the testate amoebae assemblage than those from either permanently wet or permanently dry locations.

Recurrence surfaces

Historically, the view prevailed that the only climatic signal obtainable from peat stratigraphy was from the recurrence surfaces, from the gross changes in peat appearance. Recurrence surfaces were first identified by Granlund (1932) as distinct horizons that separate dark, well humified peat from overlying less humified, light *Sphagnum* peat, reflecting a change from warm/dry conditions to cold/wet conditions. He attributed the change in humification to climatic change. Granlund (1932) distinguished five such 'Rekurrensytör' (RY), in the bogs of southern Sweden, at *ca.* 4300BP (RY V); *ca.* 3200BP (RY IV); *ca.* 2600BP (RY III); *ca.* 1600BP (RY II) and *ca.* 800BP (RY I). The most prominent of these being RY III, the Grenzhorizont. They were called recurrence surfaces, since they were thought by Granlund (1932) and von Post (1946) to represent a sequence of similar events, believed to be contemporaneous at a number of different sites. Gore (1983) suggests that Godwin (1946; 1952) assumed that Granlund's hypothesis that climate both controls and limits the height of raised bogs must imply greater climatic wetness, although this was not the case. Barber (1981) demonstrated from plant macrofossil analysis that different parts of mire surfaces respond approximately synchronously to major shifts to wetter and/or cooler climate and that these wet shifts correspond with climate change. The gross changes in stratigraphy could also be due to the threshold in the mires's hydrological regime being breached, while the climate slowly changed to a cooler and/or wetter state. Alternatively, there may have been sudden climatic changes (Barber, 1985). Blackford (1993) does not consider the study of recurrence surfaces from humification analyses to have provided either precise or accurate proxy climatic data. Instead, the data obtained were of an inaccurate age, with unspecific meteorological implications.

The Phasic Theory

Barber (1981:206-7) developed the Phasic Theory as a palaeoecological test of the theory of cyclic regeneration:

"This theory states that raised bog growth is controlled overall by climate even down to the level of relative areas of hummock and pool and that phase-shifts in peat growth are a result of climatic shifts. Threshold factors may cause the operation of the theory to differ from region to region and, to a lesser extent, from bog to bog, but the factors of hydrology and drainage, life cycle of plants, size of pool *etc.* are all subordinate to climate."

Barber (1981) related the changing stratigraphy and *Sphagnum* macrofossil record to known climatic variations in the last 800 years by comparing the peat-based records to Lamb's (1977) summer wetness indices. Barber (1981) and Barber *et al.* (1994b) argue that this theory also unifies the theories of recurrence surfaces and regeneration complexes, the latter being a consequence of the former, so that by the process of pool infill and hummock spread, the bog tends towards a drier state, until the next phase shift.

The Ground Water Mound Theory

The ground water mound theory was developed by Ingram (1982) following work by Childs (1969) and Ivanov (1981). The hypothesis is that the shape and size of raised mires are controlled by soil physics and hydrology. Low hydraulic conductivity in the catotelm is sufficient to account for the ground water mound as water-logged peat is raised above the level of the local water table. During wet periods there is lateral seepage from the acrotelm, but during dry periods the water table is lower in the catotelm, which may cause irreversible changes in the catotelm peat (Clymo, 1991). Soil physics and hydrology determine the shape of the raised bog in vertical section. The model states that under a given climatic regime, a hemi-ellipse is the upper limit for the acrotelm cupola to remain stable. This is a function of bog diameter and the volume of precipitation the bog receives. The critical water balance of a mire is the driest period through which the mire survives without irreversible desiccation, as the longest dry conditions during mire development are major determinants of the final stable shape and maximum height of the dome. The shape may alter to reflect climatic shifts (Lindsay, 1995). An individual raised mire may react to climate change with a time lag. Climatic cooling/wetting will raise the water table in the central, flatter part of the bog first (due to the lower gradient in hydraulic potential, Ingram, 1982) and later in the marginal zones (Kilinan *et al.*, 1995). Therefore, the palaeohydrological record derived from testate amoebae should reflect drier conditions at the margins of raised bogs.

Armstrong (1995) suggests that Ingram's (1982) approach is limited, since he assumes a uniform hydraulic conductivity throughout the profile. From field observation, Armstrong (1995) suggested that peat bogs generally have a decreased hydraulic conductivity with depth and that although the predicted mire shape, using a varying conductivity model, is similar to that used by Ingram (1982), the mire centres are higher and less strongly convex. Baird and Gaffney (1996) disagreed with the premise that

hydraulic conductivity shows an exponential decline with depth and instead hypothesise that trapped methane gas bubbles block pores within the peat and cause a reduction of hydraulic conductivity. Armstrong (1996) advocated the need for more field data describing the internal structure of mires to measure the hydraulic conductivity both horizontally and vertically.

2.2 Testate amoebae as palaeohydrological indicators

Moisture is generally accepted as the most important limiting factor to the distribution of testate amoebae (*e.g.*, Beyens, 1984; Charman and Warner, 1992). This is because they possess unprotected cell membranes which are at risk of desiccation during dry periods. The tests of these fauna are well preserved in peat and are easily identified. Deflandre (1953) considered testate amoebae to be cosmopolitan, but not ubiquitous and this assertion still holds today. Testate amoebae can only be useful palaeohydrological indicators if their modern distributions are known and understood. Most palaeoecological work has used testate amoebae for the qualitative reconstruction of past moisture conditions on bogs. This study adopts a quantitative approach and follows the recent work of Charman and Warner (1992, 1997), Warner and Charman (1994), Woodland (1996) and Woodland *et al.* (1998). In the following section, the modern biology, ecology and taxonomy of testate amoebae are discussed, to put the fossil studies into context.

2.2.1 The systematics of testate amoebae

Testate amoebae are microscopic (20-200 μ m) unicellular organisms in which the cytoplasm is enclosed within a discrete shell or test. The tests can be preserved in peat, lake and soil deposits. Testate amoebae are abundant in peat with Heal (1962) estimating 16,000,000 live tests in *Sphagnum* swards and approximately 20,000,000 dead individuals (empty tests) per m², to a depth of 12cm.. This estimation would however, depend upon the depth of peat sampled. Testate amoebae are an 'informal polyphyletic group' (Medioli *et al.*, 1990), one of the group of amoeboid protozoa and fall within the classes Lobosea and Filosea in the Superclass Rhizopoda, within the Subphyllum Sarcodina (Committee on Systematics and Evolution of the Society of Protozoologists, CSESP, 1980) (Table 2.3). Protozoa are now regarded as a subkingdom within the kingdom Protista, although previous classification schemes

considered Protozoa to be a subkingdom within kingdom Animalia. This classification updates that of Loeblich and Tappan (1964).

Phylum	Sarcomastigophora	Honiberg & Balamuth, 1963
Subphylum	Sarcodina	Schmarda, 1871
Superclass	Rhizopoda	von Siebold, 1845
Class	<i>Lobosea</i>	Carpenter, 1861
Subclass	Testacealobosia	de Saedeleer, 1934
Order	Arcellinida	Kent, 1880
Family	e.g. <i>Arcellidae</i> , <i>Diffflugidae</i>	
Class	<i>Filosea</i>	Leidy, 1879
Order	Gromiida	Claparède & Lachmann, 1859
Family	e.g. <i>Euglyphidae</i>	

Table 2.3 Systematics of the higher taxonomy of testate amoebae (following CSESP, 1980)

2.2.2 The history of fossil testate amoebae studies

Tolonen (1986) outlines the history of testate amoebae analysis as indicators of palaeohydrological change in peatlands and lakes. The first studies of fossil testate amoebae were of those recovered from lacustrine sediments in Finland and Sweden (Lindberg, 1899; Lagerheim, 1902, cited in Tolonen, 1986 and Warner, 1990). There is also quite a large body of German lake work, for example Schönborn (1962; 1965; 1967).

In Scandinavian peat stratigraphical studies, testate amoebae analysis has been used since 1927 to attempt to show the moisture changes of bogs (Harnisch, 1927; Steinecke, 1927). Steinecke (1927) claimed that tests composed of agglutinated particles or siliceous plates disintegrate soon after death, because he found diatom frustules at the surface and not at depth and from this inferred that they, along with the tests gradually dissolve, with the exception of *Amphitrema wrightianum* which was thought to have some mechanism for protecting itself. Harnisch (1927) proposed four communities of tests that appeared to be related to the wetness of the site and hence would be useful in interpreting past conditions. Granlund (1932) attempted to relate test abundance to the humification level of the peat, inferring that the same factors destroyed

tests as decomposed the peat. This has however, been shown to be incorrect, as in this study, highly humified peat often yields a good concentration of tests. Tolonen (1966) conducted a detailed study of bog development on an old raised bog in Southern Finland, using stratigraphical description and testate amoebae analysis. Aaby and Tauber (1975) and Aaby (1976) studied the testate amoebae recovered from Draved Mose, Denmark. They attempted to relate the degree of peat humification to the testate amoebae assemblage, but had rather limited results, possibly due to the method of sample preparation (see Chapter 4, Section 4.1.2). More recently, Barber (1981) counted testate amoebae in conjunction with pollen during his study of the stratigraphy of Bolton Fell Moss. “ The results were disappointing and were not consistent in highlighting wet or dry phases in the bog’s growth” (Barber, 1981:72). However, when a preparation procedure is adopted that is designed specifically for testate amoebae analysis (Section 4.1.2), the diversity and concentration of taxa recovered is much greater and makes it easier to relate the assemblage qualitatively to wet and dry phases in the palaeohydrological record.

2.2.3 The range of testate amoebae research

Given the extent of research into various aspects of testate amoebae analysis from a range of environments, there is a surprising paucity of information on subfossil testates from peatlands, especially from Britain. Work undertaken in the past three decades from a variety of depositional environments and from both modern and fossil studies, is summarised in Table 2.4.

Most other subfossil research from peat bogs appears to be undertaken *post hoc* to other aspects of palaeoecological research, in that tests are found on pollen slides and considered interesting and are counted, even though it was not the aim of the project to do so (*e.g.* Barber, 1981; Dwyer and Mitchell, 1997). This approach can lead to problems, as will be discussed in the preparation procedure (Section 4.1.2).

AIM OF STUDY	STATE	AUTHORS
Faunal distribution, south-west Ireland	modern	Beyens & Chardez, 1984
Biogeography, Arctic	modern	Beyens & Chardez, 1995
Arctic moss and lichens	modern	Beyens <i>et al.</i> , 1986
Aquatic ecology, Canadian High Arctic	modern	Beyens <i>et al.</i> , 1991
Aquatic subantarctic faunas	modern	Beyens <i>et al.</i> , 1995
monitoring peat bog regeneration, Switzerland	modern	Buttler <i>et al.</i> , 1996
Modelling hydrological relationships New Zealand	modern	Charman, 1997
Micro-environmental influences on faunas, Ontario, Canada	modern	Charman & Warner, 1992
Developing a hydrological transfer function, peatlands, Canada	modern	Charman & Warner, 1997
Testate amoebae and foraminifera from estuarine samples, South Wales	modern	Charman <i>et al.</i> , 1998, in press
Biogeography, eastern North American coast	modern	Collins <i>et al.</i> , 1990
Interstitial fauna from supralittoral zone, Aegean Sea, Greece	modern	Golemansky, 1982
Atlantic sublittoral psammal (5-45m), Roscoff, France	modern	Golemansky, 1991
Interstitial fauna from supralittoral zone, Roscoff, France	modern	Golemansky, 1992
Seasonal and spatial distribution in <i>Sphagnum</i>	modern	Heal, 1964
Clonal cultures from soil samples, South Orkney Islands, Antarctic	modern	Heal, 1965
Distribution of fauna in <i>Sphagnum</i> moss	modern	Meisterfeld, 1977
Systematics of fauna from <i>Sphagnum</i> moss	modern	Meisterfeld, 1979
Marine fauna from littoral sands, east coast of England	modern	Ogden & Coûteaux, 1989
Morphology and ecology of soil inhabiting faunas	modern	Schönborn <i>et al.</i> , 1987
Fauna in <i>Drepanocladus</i> moss, Antarctic	modern	Smith, 1974
Fauna in <i>Drepanocladus</i> moss, Antarctic	modern	Smith, 1986
Biogeography, Brabant Island, Antarctic	modern	Smith, 1987
Distribution and ecology of fauna in continental Antarctica	modern	Smith, 1992
Biogeography southern temperate and Antarctic zones	modern	Smith & Wilkinson, 1986
Raised bog regeneration, Eastern North America	modern	Tolonen <i>et al.</i> , 1985
Peat mire fauna autecology, Southern Finland	modern	Tolonen <i>et al.</i> , 1992
Ecology and multivariate analysis, Southern Finland	modern	Tolonen <i>et al.</i> , 1994
Abundance and diversity of faunas	modern	Warner, 1987
Biogeography of <i>Nebela</i> in southern temperate and Antarctic zones	modern	Wilkinson, 1994
Developing a hydrological transfer function for British peatlands	modern	Woodland 1996
Subboreal peatlands, Belgium	fossil	Woodland <i>et al.</i> , 1998
Hydrological reconstructions, peatlands, Svalbard	fossil	Beyens, 1985
Testates as bioindicators Britain	fossil	Beyens & Chardez, 1987
Lacustrine sediments	fossil	Charman & Hendon unpub
Lacustrine palaeoclimatic reconstruction	fossil	Ellison & Ogden, 1987
Palaeolimnological studies	fossil	McCarthy <i>et al.</i> , 1995
Overview of taxonomy, palaeoecology	fossil	Medioli & Scott, 1988
Lacustrine studies, changing trophic status, Poland	fossil	Medioli <i>et al.</i> , 1990
Lacustrine studies, trophic status, Germany	fossil	Schönborn, 1984
Hydrological history of an ombrotrophic bog, Canada	fossil	Schönborn, 1990a
Peatland palaeohydrological changes, Ontario, Canada	fossil	Warner, 1991
Lacustrine sediments, Eastern Canada	modern & fossil	Warner & Charman, 1994
Lacustrine and palaeolimnological studies, Canada	modern & fossil	Medioli & Scott, 1983
Palaeolimnological research, Canada and North America	modern & fossil	Patterson <i>et al.</i> , 1985
Over view of testate amoebae analysis	modern & fossil	Scott & Medioli, 1983
		Tolonen, 1986

Table 2.4 A range ecological and palaeoecological testate amoebae studies under taken in the past three decades

2.2.4 Taxonomy

Following the argument of Finlay *et al.* (1996) regarding the biodiversity of ciliates (Protozoa), the biological species concept is neither appropriate or practical for testate amoebae. The higher taxonomic levels of testate amoebae (Table 2.3) are defined by the morphology of the pseudopodia and the lower taxonomic levels can be recognised by their test characteristics (Charman, 1998 in press). On the assumption that sexual reproduction is rare (Schönborn and Peschke, 1990), if a biological species concept is adopted, then the logical conclusion is one of two extremes. Either all individuals are separate species, or all are one species with a very wide morphological variability (Medioli and Scott, 1983). The 'morphospecies' concept is therefore adopted here as has been done for ciliates (Finlay *et al.* 1996). Morphospecies is considered by Finlay *et al.* (1996) to be a pragmatic definition of 'species', a collection of forms that all fit into a defined range of morphological variation in forms that so far as is possible to tell, all occupy the same ecological niche.

Medioli and Scott (1983, 1985, 1988) and Medioli *et al.* (1987) have considered the state of the taxonomy of testate amoebae from palaeolimnological studies in detail. Although many of the taxa recovered are not the same as those found in British peatlands, the main tenets of their argument remain valid. The main taxonomic difficulties in subfossil studies arise from the absence of some basic diagnostic features, such as the pseudopodia and nuclei of specimens. These are soft parts and are lost during the fossilisation process. Because these fauna are considered to be uniparental (see Section 2.2.5 reproduction), they defy all concepts applicable to other organisms with regular sexuality, since there is no way of objectively demonstrating the validity of specific groupings (Medioli and Scott, 1988). Testate amoebae can only be considered in terms of morphospecies, *i.e.*, organisms which have a similar shape, as they can not be considered to be species in the true sense, because most are formed from uniparental reproduction. Other problems arise as a result of over-splitting (*e.g.* Deflandre, 1953) or over-grouping of taxa.

The taxonomy of this group of organisms has long lacked uniform criteria, particularly for the establishment of species and lower ranking taxa (Medioli and Scott, 1985). Article 62 of the International Code of Zoological Nomenclature (ICZN) has only been in place since 1901, post-dating most of the original publications. In part, the problems arise because the original descriptions and figures are old and not always easily

accessible, resulting in modern identifications being made without comparison to the original texts.

Also, some new taxa were designated on the basis of a simple description without any illustrations, which were published years later, often without further comment, for example, the designation of *Arcella globulus* Ehrenburg, 1848, 1856, (Medioli and Scott, 1985).

Testate amoebae from the Canadian palaeolimnological work have presented many cases of morphological intergradation between main phenetic clusters, with rare morphotypes being designated as distinct taxa. Where a continuum develops there is no definite point to split the group and thus the division may take place on arbitrary grounds (Medioli and Scott, 1983; Medioli *et al.*, 1987). Figure 2.5 illustrates this with an example from Deflandre (1928), showing the continuum of change for various species of *Arcella*. Bobrov *et al.* (1995) call this 'shell polymorphism'. In a study of three taxonomically remote taxa from isolated populations, Bobrov *et al.* (1995) found that although testate amoebae are cosmopolitan in distribution, morphological differences may exist in some taxa, in geographically isolated parts of their geographic range.

Because the sites selected for this study are from a restricted geographical range, problems relating to morphological variations of tests are unlikely to occur. Schönborn (1992a) related shell polymorphism of clonal cultures of *Trinema* and *Euglypha* to different ecological factors. He commented that the size of tests may be ecologically determined.

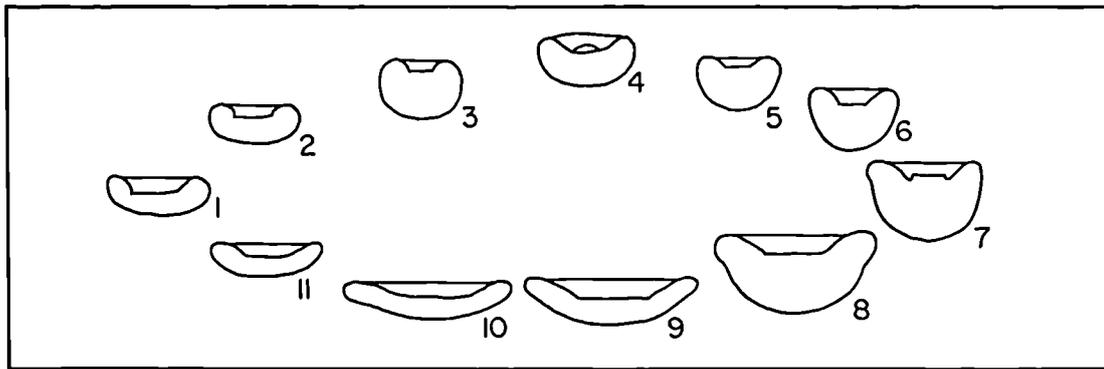


Figure 2.5 Figures of *Arcella* redrawn from Defandre (1928) in Medioli and Scott (1983)

1- *A. rotundata* var. *aplanata*; 2- *A. rotundata*; 3 - *A. rotundata* var. *alta*; 4 - *A. atava*; 5 - *A. hemispherica*; 6 - *A. hemispherica* var. *intermedia*; 7- *A. gibbosa* var. *levis*; 8 - *A. vulgaris*; 9 - *A. discoides* var. *pseudovulgaris*; 10 - *A. discoides*; 11 - *A. discoides* var. *scutelliformis*

2.2.5 Biology and ecology

It is important to understand something of the biology and ecology of modern testate amoebae so that the palaeoecological study of fossil samples can be interpreted accurately.

The test

There are two basic mechanisms for test building, (e.g. Ogden and Hedley, 1980),

- 1) *Autogenous* or *idiosomic* test construction, where the organism secretes pre-formed siliceous plates or a smooth proteinaceous secretion. Calcareous tests are sometimes secreted too (e.g., *Cryptodifflugia oviformis*, Ogden and Hedley, 1980), although this is rarer. Tests with idiosomic shell structure include *Assulina muscorum*, *Euglypha rotunda* and *Quadrullella symmetrica*.
- 2) *Xenogenous* or *agglutinated* tests incorporate particles from the surrounding substrate to construct the tests. Detritus may include mineral grains, diatom frustules, fungal hyphae and even other testate amoebae. The nature of the agglutinated particles were thought for a long time to be a valid diagnostic characteristic of some species, for example, *Difflugia bacillifera* composed of diatom frustules and *D. oblonga* from mineral particles. Heal (1964) thought that the absence of suitable detritus for test construction would prohibit certain taxa from inhabiting hydrologically suitable sites. However, Medioli and Scott (1983) and Medioli *et al.* (1987) found from laboratory

clonal cultures of the *Diffflugia tricuspis* group, that when this supposedly xenogenous taxon were deprived of particles, they produced daughter cells that were autogenous. If this daughter test was supplied with particles, it would in turn produce a xenogenous daughter. In a similar set of laboratory experiments, Medioli *et al.* (1990) found that carborundum powder could be used by the parent to make the shells in the absence of more usual material. From these experiments, it may be assumed that wild assemblages are no different and will also use the available material, be it other testates, *Sphagnum* leaves and in modern populations, wood shavings and glass fragments for test construction, if the site is hydrologically suitable. Therefore, taxonomy based upon the nature of agglutinated particles is dubious, as it appears that the testates will utilise whatever is available. However, very few studies of this nature have been undertaken and the test construction does indicate something about the environment in which the testate amoebae lived (Section 2.2.6), as the material available for test construction may be limited by environmental factors.

Cytoplasm

The cytoplasm is part of the protoplasm that is not located in the nucleus. It is composed of the ectoplasm and the endoplasm, with the test enclosing the cytoplasm. The plasma membrane separates areas of high and low osmotic pressure and water molecules move through this semi-permeable membrane in order to equalise pressure. In dry conditions, the organism loses water to its surroundings and in very wet conditions the organism may drown, as it is unable to lose water. To overcome the possibility of drowning, testate amoebae have contractile vacuoles that swell up with water (diastole) before collapsing to release the water (systole), (Sleigh, 1989).

Pseudopodia

Pseudopodia are flowing prolongations of cytoplasm extending through the pseudostome which are used for locomotion and feeding. The structure of the pseudopodia is often a main diagnostic feature for organising the macro-taxonomy of testaceans (Medioli *et al.*, 1990). Taxonomy based on the appearance of the pseudopodia is not useful for microfossil studies, where soft parts have been lost. For testate amoebae the pseudopodia are either filose, thin, pointed and often branching, or lobose, finger-like, with rounded distal ends. The nature of the pseudopodia forms the

distinction between the Filosea and Lobosea classes of testate amoebae, see Section 2.2.1. Plate 2.1 shows a *Nebela* sp. with pseudopodia extended.

Reproduction

Testate amoebae mostly reproduce by asexual binary fission, although sexual reproduction has also been reported. Schönborn and Peschke (1990) observed what appeared to be sexual reproduction in clonal cultures of *Assulina*. In the ninth month of a 15 month study, one occurrence of copulation was observed, the two parental organisms uniting with their pseudostomes and forming a third test, into which the cytoplasm of both parents flowed. The nuclei fused and the cytoplasm secreted a cyst wall. Schönborn and Peschke (1990) point out that this occurs only occasionally. Mignot and Raikov (1992) observed meiosis from electron microscopy studies of *Arcella vulgaris*. They conclude that testate amoebae can no longer be considered to be entirely asexual. Reproduction predominantly by uniparental means has implications for species definition and taxonomy (Section 2.2.4). From laboratory and field observations, Heal (1964) suggested that there are less than ten generations of testate amoebae per annum, depending on the species. Schönborn (1992c) recorded between 9-27 generations per annum in mosses, but was not able to conclude whether this was representative or not. Small species such as *Assulina muscorum* have a higher turnover than larger tests such as *Nebela collaris*. Tests are therefore unable to respond to ephemeral hydrological conditions, but instead leave a record of general annual trends. This does not pose a problem for palaeoecological work, since the practicalities of subsampling a peat core would prohibit a finer resolution study. The relationships between reproduction, active tests, encystment, dying and the decomposition of tests is shown in Figure 2.6. In mosses, testate amoebae appear to have a low turnover of biomass, but a high production of individuals (Schönborn, 1992b,c).

Cysts

Encystment is a survival mechanism for inhospitable environments, whereby the organism seals the aperture with a plug and the volume of the cytoplasm contracts by dehydration. The cyst is capable of withstanding desiccation, freezing and the lack of food. According to Medioli *et al.* (1990) this makes the faunas useful as palaeoecological tools. However, the fact that the organisms can survive unfavourable conditions means that they are not always as sensitive to environmental change as they may be - the necrocoenoses community may have survived a range of conditions.

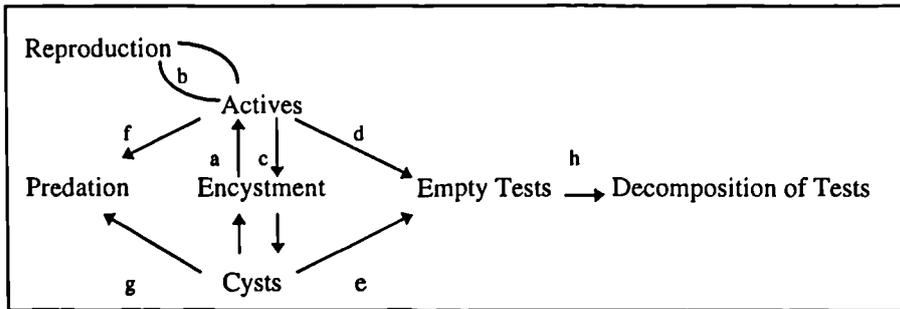


Figure 2.6 Population processes affecting test turnover

(Source: Lousier and Parkinson, 1981) a- encystment, b- reproduction, c- encystment, d- dying of active testacea, e- dying of encysted testacea, f- predation on active testacea, g- predation on encysted tests, h- decomposition of empty tests

It is therefore theoretically possible for a fossil assemblage to be composed of species from two assemblages at the same stratigraphic level, *i.e.* those that were ideally suited to the prevailing environmental conditions and those that had encysted due to unsuitable conditions for their requirements. In practice however, once the peat has undergone humification and compaction, any problems of this nature are likely to be negligible due to the vertical zonation of tests in the acrotelm (Meisterfeld, 1977).

Mortality

In order to assess whether the fossil assemblage represents the life assemblage, the possibilities of predation on active and encysted forms and the decomposition of empty tests should be considered. Lousier and Parkinson (1981) found that an aerobic forest soil environment resulted in greater loss of tests through decomposition than is probable in an anaerobic peatland, although very little work has been done to quantify this. The degree of decomposition of the peat may have a direct influence on the rhizopod assemblage, as greater decomposition will result in increased amounts of organic detritus which is thought to affect assemblages, especially for test construction (Tolonen, 1986). However, since humification takes place in the transition between the acrotelm and catotelm, below the limit which most species can inhabit, it is unlikely in most situations.



Plate 2.1 Photomicrograph of a live *Nebela* with pseudopodia extended.
Test length 145 μ m

Dispersal

Tests can be transported on the feet and in the faeces of birds. During dry periods when tests have encysted, it is also possible that they may be transported by the wind (Medioli *et al.*, 1990). This may be a taphonomic problem that is encountered when the water table of bogs is extremely low and the wind is strong enough to extricate the tests from between the hyaline cells of the *Sphagnum*. However, it is unlikely that this would cause major redistributions of the fauna on British peatlands where it is rare for bogs to be dry enough for this to occur. Also, it is unlikely that any transported tests would account for a significant fraction of the total tests in a single sample.

2.2.6 Environmental factors affecting testate amoebae

Test morphology, the length and breadth of the test and pseudostome diameter, is affected by temperature, food supply and trophic level (Wanner and Meisterfeld, 1994). Morphological features controlled by environmental conditions may be valid criteria for separation, since taxa such as *Diffugia oblonga* and *D. bacillifera*, composed of mineral grains and diatom frustules respectively, look similar but for their composition. This may be due solely to environmental factors controlling the availability of test building materials.

Since the definition of a species is based only on morphological terms, any feature which can clearly and consistently be identified is valid to separate taxa. Medioli *et al.* (1987) highlight eight criteria that are traditionally used for the discrimination of testate amoebae. Each of these is discussed as to why these criteria are questionable or unacceptable taxonomic characteristics.

- The collar* - Schönborn (1962) found that the collars on a test may appear and disappear cyclically. It may be that the presence or absence of collars is environmentally controlled, that for example, the parent test with collars produces a daughter test without collars due to a particular environmental factor. Thus, distinguishing taxa on the basis of collars is valid ecologically.

- Shape* - most species are described as being either ovoid, spherical or pyriform, with a range of shapes for each species. The morphotype continuum, as discussed above, should also be considered here. Ogden (1983) observed that some *Diffugia* spp. could

be difficult to identify due to their irregular shape and the basic outline may be altered by natural variations or by extraneous particles.

- *Nature of test* - Medioli and Scott (1983) and Medioli *et al.* (1987) demonstrated that clonal cultures can change from xenogenous to autogenous depending on the circumstances. There is no reason to believe that this may not also be the case for wild populations in peatlands.

- *Number of apertural lobes* - the number of lobes a species has may vary within a population.

- *Size* - there may be a wide overlap in size between species, leading to an arbitrary dividing point. Heal (1963) found this with the *Nebela tincta-collaris-bohemica* complex. *Assulina* spp. are often not separated (*e.g.* Aaby, 1976), as *A. muscorum* ranges from 28-58 μ m and *A. seminulum* ranges from 60-90 μ m (size according to Corbet, 1973). If all the *Assulina* spp. tests in a particular assemblage are of a size close to that of the divide, then it is difficult to separate them. Similarly, there may also be difficulties in separating *Amphitrema stenostoma* from *A. wrightianum*, as these taxa are of a similar size range (45-97 μ m and 50-95 μ m respectively, size ranges from Charman, Hendon and Woodland, in prep.), but are differentiated by the pseudostome that each taxon has at both ends of the tests. The pseudostomes of *A. wrightianum* have distinct collars, but these may sometimes be obscured by mineral particles, in which case it is difficult to distinguish from the collarless *A. stenostoma* (Corbet, 1973). Bobrov *et al.* (1995:126) noted that "caution should be exercised in establishing taxa which are based on statistically significant differences in size". The dimensions of a test, its length and aperture diameter are not usually sufficient to distinguish species. Thus, it may be valid for a proportion of the genus, but not for all.

- *Colour* - colour may depend upon the nature of the test composition, especially the agglutinate particles incorporated, which is a function of environmental conditions. Some taxa have colour as one of the main diagnostic characteristics, *e.g.*, *Heleopera rosea* (red) and *H. amethysta* (purple).

- *Presence/absence of zoochlorellae* - not applicable in subfossil studies as the zoochlorellae are lost in the fossilisation process.

- *Number of nuclei* - not applicable in subfossil studies as the nuclei are lost during the fossilisation process.

Despite these limitations, with careful examination testate amoebae can nevertheless be accurately identified. Consistent criteria for identification may result in taxa being grouped according to 'synonyms', 'species included' or 'aggregate species', the term preferred by Finlay (1997) for a practical and workable identification system. Charman, Hendon and Woodland are currently preparing a monograph specifically concerned with the identification of the species of testate amoebae commonly found in British peatlands. This aims to clarify the taxonomy, especially in a subfossil context, where tests may be more degraded than modern specimens, rather than add to the confusion by adding another complicated taxonomic paper to the literature. A combination of photomicrographs and SEM images should provide better illustrative material than has been available for accurate identifications to date. The taxonomic classification adopted in this study follows that of Charman, Hendon and Woodland (in prep.).

Moisture

Moisture is considered by many workers as the most important limiting factor to the distribution of testate amoebae (Tolonen, 1966, 1986; Tolonen *et al.*, 1985; Warner, 1987; Charman and Warner, 1992, 1997; Warner and Charman, 1994; Woodland, 1996). The moisture conditions prevailing at the time of peat accumulation should be reflected in the species of testate amoebae recovered from the peat and thus they may be useful palaeohydrological indicators. The distinction between the moisture content of peat and the depth to water table in peat is an important one, although the two are likely to be correlated in practice. The water table is the top of the saturated zone in a soil or peat in which fluid pressure in the voids is equal to atmospheric pressure. Moisture reconstructions are a measure of the percentage of water contained within the sample of peat. The moisture requirements of testate amoebae species may be associated with the diminishing content of algae suitable as food within, for example, the pool to hummock succession, as well as the thickness of the water film. In ombrotrophic sites, fluctuations in moisture can be extreme (Lindholm and Markkula, 1984). Hummock taxa must be more tolerant of such changes than hollow species, which are not subject to such drastic changes. Heal (1961) derived a five-point scale for recording water content, from submerged to dry. In practice this would lead to a certain amount of subjectivity as it is open to interpretation as to what constitutes 'firm' or 'strong' pressure required to squeeze the moss. Moisture may exhibit both a horizontal gradient from pool to hummock and a vertical distribution within the moss (Meisterfeld, 1977;

Beyens, 1984). The horizontal distribution from a pool to a hummock top is considered to be a hydrophilous gradient to which Jung (1936) attributed semi-quantitative moisture classes from I - VIII, to estimate the water content of the moss layers. The corresponding rhizopod groups of de Graaf (1956) from hydrophilous to xerophilous and the average water content of the substrate according to Meisterfeld (1977), classes I-III, IV-VI, VII and VIII (as percentage wet weight), are also shown in Table 2.5.

Rhizopod Group de Graaf, 1956	Class Jung, 1936	Average Water Content Meisterfeld, 1977
Hygrophilous	I	open water or submerged vegetation average water content >95%
	II	floating vegetation, partly submerged partly at the surface; average water content >95%
	III	emerged vegetation, very wet, water drops without pressure >95% average water content
α -Hydrophilous	IV	wet, water drops with weak pressure, - 95% average water content
	V	half - wet, water drops out with moderate pressure, 95-85% water content
β -Hydrophilous	VI	moist, water drops out with strong pressure average water content 80%
Xerophilous	VII	half - dry, a few drops with strong pressure <80% water content
	VIII	dry, no water drops at strong pressure, <50% average water content.

Table 2.5 Moisture classes of testate amoebae (after Jung, 1936; de Graaf, 1956; and Meisterfeld, 1977, cited in Tolonen, 1986; Heathwaite *et al.*, 1993)

Corbet (1973) defined xerophiles, hygrophiles and hydrophiles as follows:

Xerophiles - testate amoebae living in relatively dry habitats and able to withstand desiccation. They are usually small species that can survive in the thin film of water in drying moss. Xerophilous species (*Trigonopyxis arcuata*, *Bullinularia indica*, *Hyalosphenia subflava*) are often considered to be tyrophoxene, in that they inhabit the dry margins, drained areas and disturbed regions of bogs (Tolonen, 1986; Warner 1987). The present subfossil study and Woodland (1996) have shown this to be incorrect, as they also inhabit the dry zones of virgin bogs,

Hygrophiles - testate amoebae living in moist plants, that are subject to desiccation less frequently than xerophiles and normally inhabit an ample film of water in which the tests can be spiky and can be carried upright without disturbing the meniscus,

Hydrophiles - inhabiting submerged mosses. These testate amoebae species are not limited to the water film in *Sphagnum*. The largest species are usually found in very wet habitats.

The classification of testate amoebae as xerophilous, hygrophilous, hydrophilous, or wet and dry indicator taxa may be misleading. By definition, all testate amoebae require water to survive and in inhospitable conditions they encyst. It is assumed that as with other organisms, testate amoebae have a particular optimal value of a particular environmental variable (with testate amoebae the environmental variable is moisture) and cannot survive where the balance of moisture is too high or too low (*sensu ter Braak*, 1987). All taxa tend to occur over characteristic, but limited ranges and are most abundant at or near their environmental optimum (Birks, 1995). The Gaussian curve (Gauch and Whittaker, 1981) is a simple model for unimodal relationships in ecology. Perhaps a more realistic model is the over-lapping Gaussian curves, where the curves are not perfectly Gaussian, but are skewed, bimodal *etc.* (Kent and Coker, 1992). The statistical modelling applied to the testate amoebae data assumes this Gaussian unimodal relationship and the relationship of taxa to an environmental gradient. Whilst it may be considered to be a question of semantics, it may be more appropriate to discuss testate amoebae in terms of a relative wetness scale. All peatland sites are wet by normal standards, but there are degrees of wetness within this. However, the body of literature divides them into 'wet' and 'dry' and it may add to the confusion by developing a new relative wetness scale for test comparisons and descriptions.

Figure 2.7 shows the horizontal distribution of testate amoebae within a small forested bog. The distribution of testate amoebae within a moss is a function of the availability of food, detritus for test building and moisture, light and oxygen. The few centimetres of difference in depth to water table that separate a bog pool and hummock may separate micro-habitats that differ markedly in the degree of wetness of the *Sphagnum* and may contain different rhizopod associations. The micro-topographic features of the bog surface can therefore be examined by the use of testate amoebae analysis at raised bog sites. If the water table goes up or down on a mire, it will also go up or down in all microhabitats. Although a peat core taken from a hummock may show different absolute ranges (*i.e.* drier) than a core taken from a hollow, the direction and magnitude of change should be similar. Some species are restricted to either dry or wet conditions while other taxa exhibit a greater tolerance range. The stenotypic taxa are more useful in palaeoecological studies than the eurytypic taxa, as they are more useful indicator species for particular conditions.

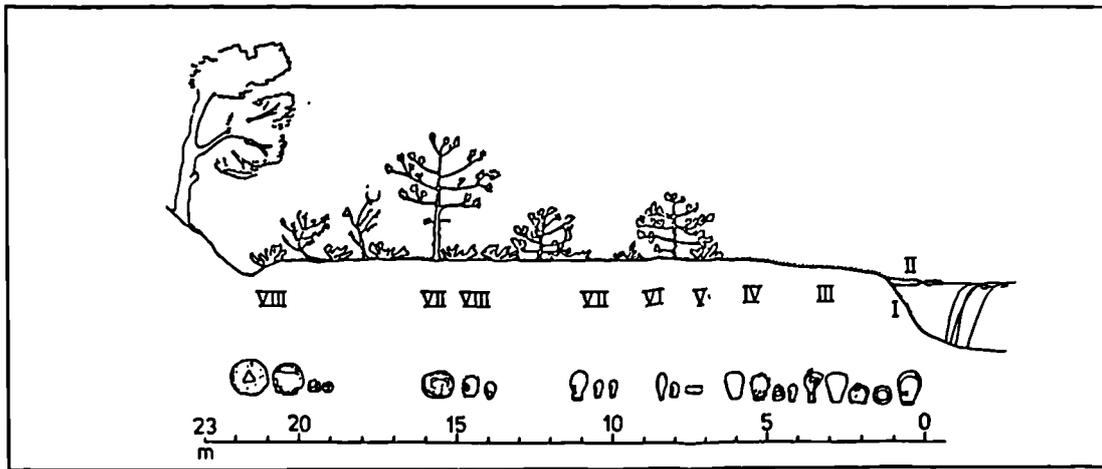


Figure 2.7 Horizontal distribution of testate amoebae

The moisture gradient corresponds to moisture classes I-VIII (Table 2.5). The species on the extreme left is *Trigonopyxis arcuata* and on the far right, *Nebela carinata* (after Schönborn, 1962).

Warner (1987) found that the concentration of tests was greatest at dry sites. Species diversity was found to increase in proportion to moisture and community evenness was found to be greatest in moderately dry sites.

Table 2.6 shows the hydrological parameters of species of testate amoebae derived from the literature. The list is constrained by the documentation of the previous work, since some taxa are defined on the basis of different criteria, for example, the qualitative classification of wet, moderately wet and dry and the more quantitative classification on the basis of the percentage water content of moss samples. Because this information is derived from studies from various parts of the northern hemisphere, it is important to have a modern analogue transfer function derived specifically from Britain to overcome any problems that may result from other regions having slightly different ecological tolerances, affinities or assemblages. For example, the *Sphagnum* peatlands of southern Ontario typically contain faunas adapted to minerotrophic mires which have seasonal and periodic drying and moisture fluctuations. The climate is humid and continental (Warner, 1987). This differs greatly from mires in this study which are oligotrophic, ombrotrophic and oceanic and illustrates the need for a transfer function created to reflect the conditions found specifically in Britain. The data in this table will be used in conjunction with the transfer function created by Woodland (1996).

Relationship with vegetation

The testate amoebae occupy the hyaline cells between the *Sphagnum* leaves.

“The relationship between the bryophyte species and testate assemblage does not necessarily imply a direct ecological link between these two types of organisms, but it is explained by the fact that moisture conditions primarily define the niches of different bryophytes, especially *Sphagnum*” (Charman and Warner, 1992:2479).

However, very little work has been done to assess the relationships between testate amoebae species and the host species of *Sphagna* and it was unfortunately outside the scope of this project.

The feedback mechanisms of *Sphagnum* mosses have important implications for the assemblages of testate amoebae, since the CEC of the moss acidifies the surrounding water, thus affecting the pH (Charman and Warner, 1992), which has an important ecological effect. *Sphagnum* moss as a peat forming material is discussed in Section 2.1.2.

Woodland (1996) discussed the relationship between hydrology, vegetation and testate amoebae. She considered whether vegetation independently influences the distribution of testate amoebae, or whether the inferred importance of vegetation is a result of a co-dependence on hydrology and vegetation.

Figure 2.8A shows that where hydrology controls the vegetation assemblage which influences testate amoebae, a direct link between testate amoebae and hydrology cannot be made. Figure 2.8B shows that where vegetation and testate amoebae are independently influenced by hydrology, a direct link between testate amoebae and hydrology can exist. Woodland (1996) concluded that hydrology simultaneously, but independently, influences testate amoebae and the host vegetation and that vegetation probably exerts a negligible influence on testate amoebae distributions. It is likely however that *Sphagnum* does exert some influence by its ability to retain moisture and raise the water table level above the ground water table.

Taxa	Hydrological parameters	Author
<i>Amphitrema flavum</i>	wet conditions 87.9-95.1% water content >95% water content bog pools - wet water table optimum water table optimum 10.27cm	Tolonen 1966 Tolonen <i>et al.</i> 1985 Tolonen <i>et al.</i> 1992 Warner 1987 Warner & Charman, 1994 Charman & Warner, 1997
<i>Amphitrema stenostoma</i>	bog pools water table optimum 6.5cm	Heal 1961 Charman & Warner, 1997
<i>Amphitrema wrightianum</i>	bog pools - wet bog pools 95 % water content 90% water content, hydric taxa water table optimum 4.07cm	Corbet 1973 Heal 1961 Tolonen <i>et al.</i> 1992 Warner 1989 Charman & Warner, 1997
<i>Arcella artrocrea</i>	88.3-93.2% water content hygrophilous taxa	Tolonen <i>et al.</i> 1985 Tolonen 1986
<i>Arcella catinus</i>	85-90% water content uncertain status dry hummocks 90-95% water content water table optimum 9.06 water table optimum 9.81cm	Tolonen <i>et al.</i> 1992 de Graaf 1956 Heal 1961 Tolonen <i>et al.</i> 1992 Warner & Charman 1994 Charman & Warner 1997
<i>Arcella discoides</i> type	floating, submerged or very wet <i>Sphagnum</i> >95% water content very wet water table optimum 8.98cm water table optimum 0.91 cm submerged <i>Sphagnum</i>	Tolonen 1986 Tolonen <i>et al.</i> 1992 Warner 1987 Warner & Charman 1994 Charman & Warner 1997
<i>Arcella gibbosa</i> <i>Arcella rotunda</i> var <i>aplanata</i>	hydrophilous taxa	de Graaf 1956 de Graaf 1956
<i>Assulina muscorum</i>	dry hummocks - xerophile xerophilous tendency 85-90% moisture content hydro-xerophilous taxa Cosmopolitan water table optimum 42.53cm water table optimum 17.44 cm	Heal 1961 de Graaf 1956 Tolonen <i>et al.</i> 1992 Warner 1987 Warner 1990 Warner & Charman 1994 Charman & Warner 1997
<i>Assulina seminulum</i>	bog hummocks 70.8-95.1% water content water table optimum 39.29cm water table optimum 13.95cm	Corbet 1973 Tolonen <i>et al.</i> 1985 Warner & Charman 1994 Charman & Warner 1997
<i>Bullinularia indica</i>	dry hummocks, xerophile bog hummocks relatively dry conditions 70.8-88.3% water content xerophilous taxa, optimum in dry hummock <i>Sphagnum</i> xerophilous taxa, <85% water content	Heal 1961 Heal 1964 Tolonen 1966 Tolonen <i>et al.</i> 1985 Tolonen 1986 Tolonen <i>et al.</i> 1992
<i>Centropyxis aculeata</i> type	aquatic habitats aquatic habitats hydrophilous taxa very wet conditions water table optimum 24.35cm water table optimum 6.18cm	de Graaf 1956 Schönborn 1962 Tolonen 1986 Warner 1987 Warner & Charman 1994 Charman & Warner 1997
<i>Centropyxis aerophila</i> type	water table optimum 20.53cm water table optimum 5.16cm	Warner & Charman 1994 Charman & Warner 1997
<i>Centropyxis arcelloides</i> type	moderately dry sites, 78-89% water content ponds, shallow peatland pools and very wet <i>Sphagnum</i> soils	Charman & Warner 1997 Warner 1990
<i>Centropyxis cassis</i>	hydrophilous, submerged, wet and moist mosses	Warner & Charman 1994 de Graaf 1956
<i>Corythion dubium</i> type	dry mosses moderately dry conditions dry mosses water table optimum 47.51cm water table optimum 23.51cm	de Graaf 1956 Meisterfeld 1977 Schönborn 1962 Warner & Charman 1994 Charman & Warner 1997
<i>Cyclopyxis arcelloides</i> type	moderately dry, 78-89% water content <80% water content water table optimum 32.01cm water table optimum 4.69cm	Warner 1987 Warner 1989 Warner & Charman 1994 Charman & Warner 1997
<i>Cryptodiffugia oviformis</i>	saturated - submerged to wet <i>Sphagnum</i> top of dry bog hummocks damp and wet mosses, standing water, aquatic plants i.e., cosmopolitan	Heal 1964 Tolonen 1967
<i>Cryptodiffugia sacculus</i>	water table optimum 1.42cm	Hedley, Ogden & Mordan 1977 Charman & Warner 1997
<i>Diffugia acuminata</i>	bog pools hydrophilous	Cash & Hopkinson 1909 de Graaf 1956
<i>Diffugia angulostoma</i>	aquatic	Cash & Hopkinson 1909

<i>Diffugia bacillariarum</i> <i>Diffugia bacillifera</i> <i>Diffugia brevicolla</i> <i>Diffugia globulosa</i> <i>Diffugia leidy</i> <i>Diffugia oblonga</i> <i>Diffugia oviformis</i> <i>Diffugia rubescens</i>	bog pools bog pools bog pools hydrophilous bog pools very wet water table optimum 2.19cm bog pools aquatic habitats >95 % water content a hydrophilous taxa water table optimum 11.00cm water table optimum 5.25 cm water table optimum 7.47cm hydrophilous taxa	Corbet 1973 Heal 1961 Corbet 1973 de Graaf 1956 Heal 1961 Warner 1987 Charman & Warner 1997 Heal 1961 de Graaf 1956 Tolonen <i>et al.</i> 1992 de Graaf 1956 Warner & Charman 1994 Charman & Warner 1997 Charman & Warner 1997 de Graaf 1956
<i>Euglypha rotunda</i> type <i>Euglypha strigosa</i> <i>Euglypha tuberculata</i>	damp & wet mosses, standing water water table optimum 38.91cm water table optimum 18.41cm bog hummocks - drier water table optimum 36.55cm water table optimum 14.43cm	Hedley & Ogden 1973 Warner & Charman 1994 Charman & Warner 1997 Heal 1961 Warner & Charman 1994 Charman & Warner 1997
<i>Heleopera petricola</i> <i>Heleopera sphagni</i> <i>Heleopera sylvatica</i>	70.8-95.1% water content 95% water content ecology variable and disputed water table optimum 31.08cm water table optimum 7.27cm β -hydrophilous taxa, moderately wet 70.8-95.1% water content 90-95% water content moderately wet, 90-95% water content drier mosses water table optimum 23.37cm water table optimum 23.22cm	Tolonen <i>et al.</i> 1985 Tolonen <i>et al.</i> 1992 Warner 1987 Warner & Charman 1994 Charman & Warner 1997 de Graaf 1956 Tolonen <i>et al.</i> 1985 Tolonen <i>et al.</i> 1992 Warner 1987/1990 Tolonen 1986 Warner & Charman 1994 Charman & Warner 1997
<i>Hyalosphenia elegans</i> <i>Hyalosphenia ovalis</i> <i>Hyalosphenia papilio</i>	bog hummocks very wet-wet <i>Sphagnum</i> , α -hydrophilous 73.0-95.1% water content 95% water content moderately wet, 90-95% water content water table optimum 26.26cm water table optimum 21.59cm water table optimum 42.94cm water table optimum 19.96 cm very wet <i>Sphagnum</i> wet <i>Sphagnum</i> in bog hummocks 88.3-95.1% water content 95% water content moderately wet, 90-95% water content >90% water content moderately wet 90-95% water content water table optimum 9.87cm water table optimum 17.74cm	Corbet 1973 de Graaf 1956 Tolonen <i>et al.</i> 1985 Tolonen <i>et al.</i> 1992 Warner 1987 Warner & Charman 1994 Charman & Warner 1997 Warner & Charman 1994 Charman & Warner 1997 de Graaf 1956 Heal 1961 Tolonen <i>et al.</i> 1985 Tolonen <i>et al.</i> 1992 Warner 1987 Warner 1989 Warner 1990 Warner & Charman 1994 Charman & Warner 1997
<i>Hyalosphenia subflava</i>	71-93.2% water content moderately dry, xerophilous, 78-89% water content <80% water content - characteristic of drained peatlands water table optimum 49.92cm water table optimum 22.81cm	Tolonen <i>et al.</i> 1985 Warner 1987 Warner 1989 Warner & Charman 1994 Charman & Warner 1997
<i>Lesquereusia spiralis</i>	>95% water content	Tolonen <i>et al.</i> 1992
<i>Nebela barbata</i> <i>Nebela collaris</i> <i>Nebela carinata</i> <i>Nebela dentistoma</i> <i>Nebela flabellulum</i> <i>Nebela griseola</i> <i>Nebela lageniformis</i> <i>Nebela marginata</i>	hydrophilous taxa β -hydrophilous taxa; moderately dry conditions moderately wet, 90-95% water content very wet <i>Sphagnum</i> bog pools >95% water content water table optimum 1.09cm water table optimum 9.07cm <i>Sphagnum</i> in bog hummocks water table optimum 30.04cm <i>Sphagnum</i> of drier hummocks water table optimum 11.14cm water table optimum 18.01cm α -hydrophilous taxa water table optimum 6.89cm	de Graaf 1956 de Graaf 1956 Warner 1987 de Graaf 1956 Heal 1961 Tolonen <i>et al.</i> 1992 Charman & Warner 1997 Charman & Warner 1997 Corbet 1973 Charman & Warner 1997 Corbet 1973 Charman & Warner 1997 Charman & Warner 1997 de Graaf 1956 Charman & Warner 1997

<i>Nebela militaris</i>	wet <i>Sphagnum</i> of bog hummocks drier mosses dry hummocks, xerophilous 70.8-95.1% water content 85-90% water content water table optimum 41.85cm water table optimum 20.66cm	Corbet 1973 de Graaf 1956 Heal 1961 Tolonen <i>et al.</i> 1985 Tolonen <i>et al.</i> 1992 Warner & Charman 1994 Charman & Warner 1997
<i>Nebela minor</i> <i>Nebela parvula</i>	water table optimum 9.33cm very dry conditions water table optimum 27.58cm water table optimum 6.98cm	Charman & Warner 1997 Warner 1987 Warner & Charman 1994 Charman & Warner 1997
<i>Nebela tinctoria</i>	dry hummocks xerophilous, <85% moisture content very wet water table optimum 32.63cm water table optimum 11.67cm	Heal 1961 Tolonen <i>et al.</i> 1992 Warner 1987 Warner & Charman 1994 Charman & Warner 1997
<i>Phryganella acropodia</i>	moderately wet, 90-95% water content	Warner 1987 Warner 1990
<i>Pseudodiffugia fascicularis</i>	aquatic	Cash & Hopkinson 1909
<i>Placocista spinosa</i>	bog pools, very wet bog pools >95% water content water table optimum 7.44cm	Corbet 1973 Heal 1961 Tolonen <i>et al.</i> 1992 Charman & Warner 1997
<i>Plagiopyxis callida</i>	water table optimum 9.40cm	Charman & Warner 1997
<i>Quadrullella symmetrica</i>	>95% water content water table optimum 22.38 water table optimum 6.00cm	Tolonen <i>et al.</i> 1992 Warner & Charman 1994 Charman & Warner 1997
<i>Sphenoderia lenta</i>	85-90% moisture content moderately dry, 78-89% water content water table optimum 5.86cm	Tolonen <i>et al.</i> 1992 Warner 1987/1990 Charman & Warner 1997
<i>Trinema lineare</i>	hygrophilous taxa	de Graaf 1956
<i>Trigonopyxis arcuata</i>	xerophilous taxa dry hummocks, xerophilous 71-88.4% water content 85-90% water content water table optimum 57.68cm water table optimum 15.58cm	de Graaf 1956 Heal 1961 Tolonen <i>et al.</i> 1985 Tolonen <i>et al.</i> 1992 Warner & Charman 1994 Charman & Warner 1997
Rotifer: Bdelloidea <i>Habrotricha angusticollis</i>	very wet to wet <i>Sphagnum</i> , a hygrophilous taxa open water 95% water content, bog hollows, wet 56-97% moisture content for ombrotrophic sites 82-97% moisture content for minerogenic sites water table optimum 36.76cm water table optimum 3.66cm	de Graaf 1956 Tolonen 1966 Tolonen <i>et al.</i> 1992 Warner & Chengalath 1991 Warner & Charman 1994 Charman & Warner 1997

Table 2.6 Hydrological requirements of taxa from published studies

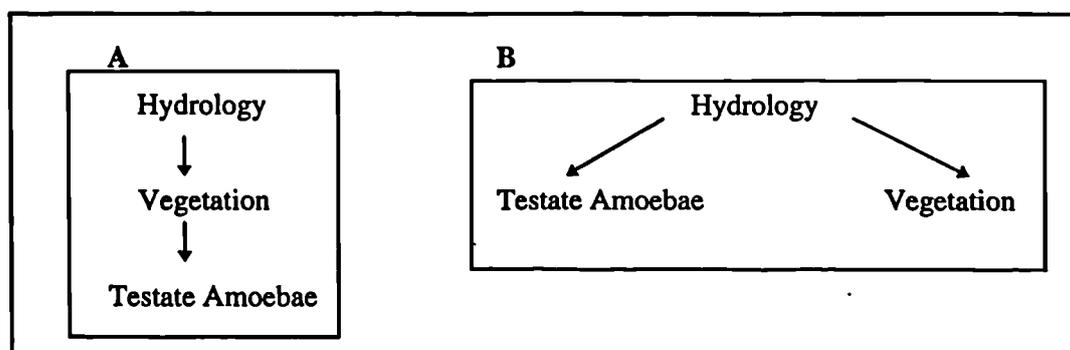


Figure 2.8 Possible environmental controls on testate amoebae assemblages (source: Woodland, 1996)

Size

According to Medioli *et al.* (1990), the size of the organisms is controlled by the volume of cytoplasm available in the parent test at the time of division and this is probably controlled by the availability of food. Therefore, there is no growth after fission. According to Corbet (1973), size is a function of the moisture conditions of the *Sphagnum* moss held within the leaves, this implies that growth is possible after fission. Heal (1963) observed that larger testates were associated with the wetter moss, probably due to the larger space available in the thicker water film. In a palaeoecological study, it is possible to test this theory by assessing whether periods with low reconstructed water tables were composed of small fraction taxa and conversely whether larger taxa dominate the assemblage at the points where the water table was high.

Food

There are limits to the size of food which thecamoebians can consume as most taxa are limited to prey that is smaller in diameter than their pseudostome. The pseudopodia withdraw inside the test carrying bacteria, fungi, algae and even other protozoa. Heal (1964) observed a *Diffflugia tuberculata* that was capable of consuming a desmid *Closterium* too large to be taken in through the pseudostome. Using the pseudopodia, the testate snapped the desmid in half and inserted the pseudopodia inside the cell to remove the algae. The frequency of division was observed by Schönborn (1992c) to increase with greater abundance of food, but that if a certain threshold of food concentration was exceeded, the frequency of division decreased again. Therefore, the abundance and quality of food can be seen to affect reproduction. Heal (1964) also observed that clonal cultures are capable of consuming their own volume in food per day. Plate 2.2 shows an example of *Placocista spinosa* consuming an *Amphitrema flavum*, from the Penard Collection, British Museum (Natural History). Testates are important primary and secondary consumers. Some taxa have zoochloellae (*e.g.* *Amphitrema wrightianum*), which they use for photosynthesis and these species may not consume other organisms, (see section on Light, below). The availability of the food source may be related to moisture conditions, as algae decrease in abundance across a pool to hummock succession, as conditions get drier. Different temperatures and food were shown to cause significant changes in shell and pseudostome diameter of clonal cultures of *Trinema lineare* and *Cyclopyxis kahli* (Wanner and Meisterfeld, 1994). However, they also stated the proviso that the broad variability of shape caused, for

example, by climatic factors, makes taxonomical separation of closely related taxa difficult.

Temperature

The surface temperature of a mire fluctuates during a 24-hour period, with heat lost from the surface by evaporation from the moss as they lack stomata and cannot regulate evapotranspiration (Section 2.1.2). *Sphagnum* are poor conductors of heat to the lower layers, so at depth there is less temperature variation with a more constant low temperature. Low temperatures have been seen to lengthen and higher temperatures shorten, the generation times of testate amoebae (Schönborn, 1992c).

Light

The capitula of the moss are closely packed together and so intercept the light. The region for photosynthesis is therefore only a few centimetres from the surface. Some taxa have symbiotic zoochlorellae, these include *Hyalosphenia papilio*, *Placocista spinosa*, *Amphitrema flavum* and *A. wrightianum*. These are only capable of inhabiting the surface layers of the *Sphagnum* as they are restricted by their light requirements (Meisterfeld, 1977). Light may be a factor affecting generation times, but Schönborn (1992c) is not clear exactly how.

Oxygen

At the mire surface oxygen is in equilibrium with the air. At a depth of 20cm there may be very little free oxygen and so living testates may be absent and empty tests abundant (Corbet, 1973).

Water chemistry

The water chemistry of bogs includes the trophic status, DOC, C:N ratio, N in peat and Ca of water. pH is probably the most important aspect of water chemistry affecting the distribution of testate amoebae on bogs. Ogden and Hedley (1980) thought that the distribution of testate amoebae may be limited by pH, as different groups of species occur on acid moors and alkaline soils, with only a few taxa common to both. Woodland (1996) found no clear relationship between testate amoebae and water chemistry because of the very restricted range of pH values she measured in oligotrophic bogs.

Amphitrema flavum



Plate 2.2 *Placocista spinosa* (Carter 1865) typically 87-110µm long consuming
Amphitrema flavum (Archer 1877) (Penard Collection, British Museum)

Several studies have found pH to be an important factor affecting the distribution of tests (Tolonen *et al.*, 1992; Charman and Warner, 1992, 1997; Warner and Charman, 1994). pH is considered to be the second most important factor affecting the distribution of testate amoebae after hydrology. In this study, all three sites are oligotrophic, as this is a prerequisite for the application of the transfer function developed by Woodland (1996).

Testate amoebae analysis is thought to be generally more successful in studies from ombrotrophic bogs, as the tests tend to be 'pseudo-chitinous' and are relatively resistant to humification and mineralisation (Tolonen, 1986; Heathwaite *et al.*, 1993). The genera of testate amoebae that inhabit minerotrophic bogs are mainly composed of siliceous plates and mineral particles that are prone to dissolving in the decomposition process. Tolonen *et al.* (1992) did not find *Lesquereusia spiralis* on any ombrotrophic sites, suggesting that it prefers wetter and more minerogenic sites.

2.3 Testate amoebae and palaeoecology

Testate amoebae are good hydrological indicators as individual species respond to different hydrological conditions. Whether hydrology is strongly related to climate and whether the fossil testate amoebae assemblages are good matches with modern analogue assemblages is the main focus of this study. It is possible to calculate the levels of effective precipitation received by a site by reconstructing the depth to water table level. Modelled responses of modern testate amoebae to contemporary hydrology are used to infer hydrological values for fossil assemblages. This uniformitarian approach utilises regression and calibration to construct a transfer function. If it is possible to separate the hydrological conditions resulting from climate change from those occurring due to autogenic mire development, then testate amoebae will be considered to be extremely sensitive palaeohydrological indicators. However, using testate amoebae as proxy hydrological and hence proxy climatic indicators, may lead to errors at two stages of analysis: firstly, in the reconstruction of the former test community - a taxonomic problem and secondly, from inferring hydrological conditions based on the reconstruction from transfer functions derived from modern assemblages.

There are several assumptions that Lowe and Walker (1997) cite as being important in order to derive meaningful information about past environments from fossil assemblages:

- a) environmental parameters governing present-day distributions of testate amoebae are understood. Autecology was addressed by Woodland (1996).
- b) present distributions are in equilibrium with their environmental controls, in this case, primarily moisture and depth to water table.
- c) former distributions were in equilibrium with environmental controls.
- d) former distributions have analogues in the modern fauna. This will be established by comparing the taxa found in this study to those found in the modern analogue study by Woodland (1996).
- e) the ecological affinities of the fauna have not changed through time.
- f) the fossil assemblage is representative of the death assemblage and has not been biased by differential decay. Tolonen (1986) equates the degree of correspondence of the necrocoenosis to biocoenoses to the resistance of the tests against decomposition and the down-washing of empty tests within the peat profile.
- g) the taphonomy of the fossil assemblage can be established. Only on very rare occasions are testate amoebae transported from their original location.
- h) fossil remains can be identified to a sufficiently low taxonomic level to enable uniformitarian principles to be applied.

Shell decay

According to Hoogenraad (1935), no change is expected from the transition from biocoenoses to necrocoenoses, but the composition may change later as a function of the disintegration of the test. Lousier and Parkinson (1981) found two patterns of test decay from a forest soil. A linear pattern was found for taxa composed of agglutinated particles and exponential decay for taxa composed of plates. Lousier and Parkinson (1981) found that the aerobic nature of the forest litter encourages test decomposition. Temperature had a negligible effect on test disappearance, but it was impossible to distinguish between the effects of moisture content and biological activity. However, the anaerobic nature of the peatland probably does not advance the decay of tests. No studies have been undertaken looking specifically at test decay from peatlands, but degraded, broken or fragments of tests have not been recorded in any of the published

studies, or in this study. Consequently, test decay is not considered to be a serious problem in fossil work on oligotrophic, saturated peats.

Further possibilities for test destruction occur during preparation. However, the preparation of testate amoebae samples extracted from peat has been assessed and modified by Hendon and Charman (1997) to minimise the loss of assemblage components and retain a complete a fossil assemblage as is possible (Section 4.1.2).

2.4 Transfer functions for palaeoclimatic reconstructions

A transfer function deals with a quantifiable relationship between a selected environmental parameter and the distribution of taxa. The value of the environmental variable is a function of the biological data (Birks, 1995). The quantitative reconstruction of environmental variables from fossil assemblages involves two stages of calculation, a) regression, where the response of the modern taxa to the environmental variable are modelled and b) calibration, where the modelled responses are used to infer the environmental variable value from fossil assemblages (ter Braak and Barendregt, 1986; ter Braak and Prentice, 1988; Birks *et al.*, 1990a; Line and Birks, 1990).

There are five ecological assumptions that need to be taken into account in quantitative palaeoenvironmental reconstructions (Imbrie and Webb, 1981). These are that:

- a) the taxa in the training set are systematically related to the physical environment in which they live
- b) the ecological variable to be reconstructed is, or is linearly related to, an ecologically important variable in the system
- c) taxa in the training set are the same as in the fossil set and their ecological responses have not changed significantly over the time span represented by the fossil data
- d) the mathematical models of regression and calibration adequately model the biological responses to the environmental variable of interest
- e) environmental variables other than the one of interest, or their joint distribution with the variable of interest, in the fossil set are the same as in the training set

Four statistical techniques used in creating regression and calibration transfer functions were tested by Woodland (1996), each of which is discussed in detail by Birks (1995). Weighted Averaging (WA) provides robust regression and calibration where the response variables (testate amoebae), exhibit a unimodal response to the environmental variable (Line and Birks, 1990). Partial Least Squares regression (PLS) assumes a linear response of species to environment (ter Braak, 1985). Weighted Averaging Partial Least Squares (WA-PLS) is a combination of WA and PLS (ter Braak and Juggins, 1993) that can give up to 70% reduction in prediction error from data sets with low noise, but only a small reduction from noisy data sets. Tolerance downweighted weighted averaging (WA-Tol) can be used to give more weight to taxa that have narrow tolerance ranges and that are considered to be more valuable in palaeoecological reconstructions (Juggins, 1992).

Transfer functions have been used extensively in palaeolimnological studies. Different statistical models have been shown to best model different environmental variables. Diatom valves (Bacillariophyta) have most frequently been used to reconstruct lake-water pH (*e.g.* Birks *et al.*, 1990a,b; Korsman and Birks, 1996). WA was found to be ecologically more robust, realistic and numerically accurate than other methods for the reconstruction of pH from the Round Loch of Glenhead, south west Scotland (Birks *et al.*, 1990a). Korsman and Birks (1996) found that WA-PLS out-performed other techniques for lakes with a high relative abundance of the most dominant diatom taxa and a low sample heterogeneity. Diatoms have also been used as a direct record of salinity and an indirect measure of water-level and climate change in the semi-arid regions of North America. The chemistry of closed basins responds directly to changes in the hydrological budget through evaporation and dilution of concentrated dissolved salts (Juggins *et al.*, 1994). WA was found to be the best method for this modelling this data set.

Other fauna used to develop transfer functions include scaled chrysophytes (Pterygota: Neuroptera) which are planktonic algae that are covered with taxon specific siliceous scales. The distribution of scales has primarily been used to reconstruct lake-water pH and also temperature, conductivity, phosphorous, metal concentrations and nutrient levels in the Adirondack drainage lakes of New York (Cumming *et al.*, 1992). WA-Tol was found to produce better models than WA for chrysophyte taxa. The potential has been recognised to develop a European transfer function using chironomid (Insecta:

Diptera) distributions to reconstruct summer surface temperatures at a broad geographic scale for the Late Glacial (Brooks *et al.*, 1997). A WA transfer function derived from modern chironomid data for the quantitative reconstruction of Late Glacial temperatures has been developed for several sites in North America, but at present, climatic inference from British data can only be discussed in relative terms.

Therefore, the potential use of transfer functions using microfossils is broad, but a range of regression and calibration techniques must be evaluated to see which gives the best Root Mean Square Error (RMSE). Depth to water table and percentage moisture modelling from the testate amoebae data, need to have the model assessed for correctness by validation. Good performance at model estimation and calibration does not guarantee correct predictions (Power, 1993). If accurate and meaningful results are to be obtained and used, it is necessary to know how much confidence can be placed in the model results. The model is validated if it corresponds with the actual system. Cross-validation involves dividing the data into two data sets, an estimation set and a prediction data set. The estimation data set is used to estimate model parameters and to assess the replicative validity of the resulting models. The predictive set is used exclusively for predictive validation (Power, 1993). A good model will produce small, uncorrelated predictive errors. The simplest cross-validation approach is jack-knifing (Birks, 1995) and was used by Woodland (1996) and Woodland *et al.* (1998).

2.5 Testate amoebae transfer functions

Transfer functions have been developed by Charman and Warner (1997) and Warner and Charman (1994) for testate amoebae analysis from mires in Canada. Warner and Charman (1994) in a study from Northwestern Ontario, used single-shot hydrological data to create a transfer function. WA calibration was used to reconstruct water table depth from the fossil testate amoebae assemblage. The transfer function developed from data from Newfoundland, Canada was based on single-shot hydrological data (Charman and Warner, 1997). WA-Tol was found to be the best of the four models tested, which is probably related to the high tolerance values of some taxa that have less influence on reconstructed values. Charman and Warner (1997) comment that in order to avoid problems with poor modern analogues, reconstructions should be based on larger, more comprehensive data sets of modern fauna from a wider region.

Woodland (1996) chose nine oligotrophic peatland sites from across the British Isles for her study, constrained by the availability of sites with long-term mean annual water table data. The restriction of the modern data set to oligotrophic mires means that the transfer function derived is only applicable to fossil samples from oligotrophic peat. In total, 207 surface moss polsters were taken from these sites. Of these, 163 samples with good test concentrations were used to construct the transfer functions. The moss polsters were divided into the green growing fraction of the *Sphagnum* moss and any vascular plants and, the brown fraction containing the decomposing mosses and root material above the compacted catotelm peat. This was done in order to obtain a sample from the brown fraction which is representative of the 'death assemblage' and which will ultimately form the fossil assemblage in the peat. The nature of the sites with long term hydrological monitoring programs were towards the wetter end of the range of hydrological variation found on British mires. This was because only wetter sites are monitored for mire conservation purposes and this causes an inherent bias in the transfer function.

Moisture was recorded at a single time when moss polsters for testate amoebae analysis were collected. Water table levels on the sites selected by Woodland were monitored over a long period, generally with at least three years data, as this removes the bias created by single-shot sampling, allowing a more representative assessment of mean annual water table levels and of other environmental optima. This approach also allowed assessment of the most representative time of year should long-term monitoring not be possible in the future. Separate water table and soil moisture transfer functions were derived from the original data set because the relationship with mean annual water table was considered to be a more reliable parameter on which to base palaeohydrological reconstructions than one based on single-shot sampling of moisture data.

Four regression techniques were evaluated by Woodland (1996) to construct the transfer function. These were WA, WA-Tol, PLS and WA-PLS. The model that produced predictions corresponding most closely with observed data was used as the transfer function. In 'jack-knifed' validation, WA produced the lowest prediction errors for water table, but was out-performed by WA-Tol for percentage moisture (Woodland *et al.*, 1998). RMSEP of predicted values using 'jack-knifing' showed that water tables can be predicted to within $\pm 3.9\text{cm}$ and soil moisture to within $\pm 3.4\%$, assuming a good

match between modern and fossil samples. Birks *et al.* (1990:274) considered WA to be “ecologically more realistic, statistically more robust and numerically more accurate than other methods”.

Woodland *et al.* (1998) filtered out samples where the difference between observed and predicted values exceeded 9cm and 5% for water table and soil moisture respectively. This was done on the basis of RMSEP values and identification of outliers with unusual values. For both transfer functions this amounts to one-fifth of the measured range in the data set. Three samples were removed from the water table set and 29 from the soil moisture data set. These outliers may be attributable to 1) samples from exceptionally low water tables compared to the rest of the samples, 2) different water chemistry, altered species composition or 3) assemblages related to unusual vegetation types rather than hydrology.

Woodland (1996) pointed out that a large training set is required for derivation of transfer functions - one limitation of her study is the limited number of samples taken from a small number of sites, so that not all possible microtopographical variability across these oligotrophic sites are represented. 38 taxa were used to develop the transfer function, this is a small number in comparison to total assemblage it is possible to find. Woodland tested the transfer function in a fossil context on a core from Bolton Fell Moss. She found a wide species diversity (24 taxa) and found that very little improvement was made by restricting the assemblage used in the transfer function to those that are perceived to be better hydrological indicators.

Woodland (1996) recognised that sampling from sites where a long run of data exists is crucial to minimise the distorting influence of unusual climatic events on calculated species optima. Because the species moisture optima are calculated from single-shot samples taken in the autumn, there is the possibility of samples being taken under such unusual climatic events. The moisture reconstruction transfer function is therefore less robust than the water table transfer function developed from long-term hydrological data.

2.6 Other proxy-climatic indicators

Other proxy palaeohydrological indicators are discussed here. They all provide semi-quantitative, or relative estimates of past mire surface wetness and as such are not as robust as the palaeoclimatic signal derived from testate amoebae analysis. All are potentially useful for multi-proxy studies in conjunction with testate amoebae analysis, to compare nature of the palaeohydrological record and assess whether all proxies produce the same hydrological signal.

2.6.1 *Sphagnum* macrofossils

The role of *Sphagnum* in the peatland environment is discussed in Section 2.1.2. Barber (1981; Barber *et al.*, 1994c) demonstrated that macrofossil assemblages from different parts of the bog responded more or less synchronously to shifts to wetter and/or drier climates and that these shifts could be correlated with records of climate change from independent and documentary records. On this basis, the record of change in bog vegetation contained in the peat profile is used to reconstruct changes in bog surface wetness. This can be done because of the coupling of ombrotrophic bogs with climate and it can be viewed as a proxy-climatic record. Bolton Fell Moss, Cumbria, is the main site that Barber has studied for palaeoclimatic reconstructions using plant macrofossils (Barber, 1981,1985,1994; Barber *et al.*, 1994a,b,c). The proximity of Bolton Fell Moss to the field sites in this study should enable a crude comparison of reconstructed surface wetness curves from the curves derived from *Sphagnum* macrofossils and testate amoebae. Bolton Fell Moss was also used by Woodland (1996) as a site for the study of fossil testate amoebae as the transfer function derived was applied and tested on a core from Bolton Fell Moss.

The Quadrat Leaf Count (QLC) method for *Sphagnum* macrofossil analysis (Haslam, 1987), used by Stoneman (1993), Barber (1994), Barber *et al.* (1994a,b,c) is a compromise between the 5-point scale approach of Walker and Walker (1961) and Barber (1981) and a more detailed method of Janssens (1983), (Barber *et al.*, 1994a). A comprehensive account of the methodology is presented in Barber *et al.* (1994a). The species assemblage is reconstructed by firstly estimating the main components of washed peat samples, then identifying the *Sphagna* to as low a taxonomic level possible. Results are normally plotted in a hydrophilous sequence from relatively dry (Unidentified Organic Material, UOM) to very wet, *e.g.* *Sphagnum* section *Cuspidata*.

For recent periods, the macrofossil record has been compared with Lamb's High Summer Wetness indices. Lamb (1977) used a diverse array of historical records to reconstruct summer wetness/dryness and winter mildness/severity trends for Central England from AD 1100 to 1850 (Barber *et al.*, 1994c). This reflects only general trends in climate change and can only be used with the caveat that there are inherent problems with this type of documentary reconstruction.

The macrofossil data have been subject to various multivariate analyses which are explained in depth in Barber *et al.* (1994b). Barber and co-workers concluded that all the techniques used confirmed that the data possess a coherent and robust structure and that variations in the data were related to bog water table and through that to climate. The data presented in all of the aforementioned publications are only quantified in relative terms, of dry, wet and very wet. No indication is given of how dry the xerophilous *Sphagnum* communities actually are, or how wet the hydrophilous communities are. The shifts in the reconstructed hydroclimatic diagram (for example Bolton Fell Moss, Barber *et al.*, 1994b) using Dupont's (1986) weight averaged ordination is limited. Each taxon is given an 'indicator value' along a wet-dry axis and, although this may allow comparisons between sites as to the response of taxa to climatic forcing, it would be difficult to compare this type of data to another proxy climatic indicator, for example, the reconstructed water table curves derived from the fossil testate amoebae. This is because the comparison would be between a curve of relative wetness to percentage moisture content or depth to water table.

Stoneman (1993) and Stoneman *et al.* (1993) attempted to quantify the *Sphagnum* macrofossil record by constructing a calibration or training set. However, it was found that one of the major taxa which once formed the bulk of Holocene peat was now virtually extinct over a large extent of its former range, thus making a calibration set unworkable. It is difficult to assume a uniformitarian approach to palaeoecological reconstructions if the niche of a taxon has changed and the other taxa in the assemblage have had to readjust their ecological niches to adapt to this change. The palaeoecological evidence suggests that *Sphagnum imbricatum* ssp. *austinii* once had a wide niche with respect to water table. The high hummocks on which *S. imbricatum* ssp. *austinii* are found today are the only places where it can effectively out-compete other *Sphagna* and can only survive if conditions are oceanic enough to prevent desiccation. *S. magellanicum* appears to have out-competed the lax form of *S.*

imbricatum and today occupies the position that *S. imbricatum* once did. Relating present ecology to past ecology in this context is therefore difficult.

2.6.2 Other plant indicators

The woolly hair moss *Racomitrium lanuginosum* may be a useful proxy climatic indicator on blanket bogs. *Racomitrium* has distinctive leaves which are well preserved in blanket peats. Its occurrence in the peat profile may represent a clear signal relating to the water balance of the mire system as a whole (Tallis, 1994, 1995). Where *Racomitrium* is present, it delimits a zone of climatic change, marking shifts from a dry to a wet climate. It requires an unusual set of circumstances, a wet climate, producing high atmospheric humidity and a dry bog surface with low overall water tables. The combination of these circumstances may often be of short duration as a result of a change to a wetter climate after a prolonged period of drier climate, which allows the temporary spread of *Racomitrium* before being replaced by *Sphagnum*.

Tallis (1997) has also used *Empetrum nigrum* (crowberry) pollen as a proxy indicator of lower summer water table levels on blanket peats in the southern Pennines. *Empetrum* favours well drained situations such as hummock tops and is a good indicator, as it has only very locally dispersed pollen.

2.6.3 Isotopic fractionation

Isotopic studies are used in many areas of palaeoclimatic research, but have only been used in limited ways on peats (*e.g.* Aucour *et al.*, 1996), being more commonly used in ice core studies. Ombrotrophic raised bogs are useful for reconstructing variations in temperature and precipitation over the Holocene, as the main source of input to the mire hydrological regime is precipitation. Peat is a useful medium for this type of isotopic study as it contains so many other proxy climatic indicators against which to compare the isotopic data. Those that complement testate amoebae analysis in palaeohydrological studies are outlined below.

The stable isotopes of oxygen, $^{18}\text{O}/^{16}\text{O}$ and hydrogen isotopes $^2\text{H}/^1\text{H}$ (^2H = deuterium, ^1H = hydrogen), can be used in palaeoclimatic research (Bell and Walker, 1992). These isotopes are fundamental constituents of water, but the ratios of $^{18}\text{O}/^{16}\text{O}$ and $^2\text{H}/^1\text{H}$ vary

over time as changes in the water state occur. This is controlled primarily by temperature, because, on evaporation the water vapour becomes deficient in the heavier isotopes ^{18}O and ^2H relative to the water source (precipitation) and these are recorded in the peat. Palaeoclimatic inferences are based on the relationship between ^{18}O and ^2H , the composition of plant cellulose and the isotopic composition of the plant, its water sources and relative humidity (Aravena and Warner, 1992).

Fractionation is a complex function of climate and plant-physiological parameters (van Geel and Middelorp, 1988), because the isotopic ratio is taxa-dependent, as different species have inherently different isotopic compositions (Brenninkmeijer *et al.*, 1982; Dupont, 1986; Dupont and Mook, 1987; Price *et al.*, 1997). Vascular plants have a greater isotopic enrichment of leaf water (^{18}O and ^2H) compared to the water adhering to the apical growth tips of *Sphagnum* (Brenninkmeijer *et al.*, 1982; van Geel and Middelorp, 1988). Furthermore, the plant cellulose which contains the isotopic record may be difficult to extract, especially from highly humified peat.

In addition to the problems posed by species with different isotopic compositions, an added complication is caused by an indirect effect of temperature fluctuations. During warm periods, the vegetation on ombrotrophic bogs tends to be dominated by taxa favouring dry conditions, for example the Ericales, which, when independent of climatic influences, has a relatively high $^2\text{H}/^1\text{H}$ ratio. During periods of oceanicity, where relative humidity is high and temperature low, bog plants flourish which favour relatively wet conditions, for example, *Sphagnum imbricatum* and *S. papillosum* which have relatively low $^2\text{H}/^1\text{H}$ ratios. Thus ^2H is influenced by climate and also by the vegetation assemblage, which is an indirect function of climate. Variations in the $^2\text{H}/^1\text{H}$ ratio from the influence of plant species changes, may be larger than direct temperature induced variations (van Geel and Middelorp, 1988). Other complications may result from varying lengths of growing season in different climatic periods which may affect the $^2\text{H}/^1\text{H}$ ratio. Dupont (1986), also points out that the isotope record is latitude dependent. During climatic change, temperature differences at higher latitudes are greater than those at lower latitudes. Study site location has to take this into account when isolating temperature as a palaeoclimatic variable.

Hummock-top species of *Sphagnum* may yield lighter isotopic values than hummock-margin species, which is consistent with hummock-top species photosynthesising under

a lower water content and with a lower external diffusion resistance . A large range of ^{13}C values were recorded in hollow samples which may lead to inaccurate climatic interpretations (Price *et al.*, 1997). Conversely for ^{18}O , the heavier oxygen isotope enriched values are found in hummock *Sphagnum* indicating that photosynthesis in hummock taxa is more affected by evapotranspiration than adjacent taxa in hollows (Aravena and Warner, 1992).

Dupont (1986) and Dupont and Mook (1987) attempted to account for these problems by calculating the relative abundance of each taxon in every sample. The $^2\text{H}/^1\text{H}$ ratio can then be corrected for taxa-dependence ^2H variations and a temperature record derived. Van Geel and Middelorp (1988) advocated the selection of one or two taxa to measure the ^2H ratios in order to provide a more useful and less complicated palaeoclimatic record. However, the practicalities of selecting sufficient material for analysis are probably too great, especially in humified peats.

White *et al.* (1994) attempted to reconstruct past variations in atmospheric carbon dioxide by using $^{13}\text{C}/^{12}\text{C}$ ratios in mosses and sedges in peat. Unlike sedges, mosses do not possess stomata and are therefore unable to regulate their uptake of CO_2 and H_2O . The $\delta^{13}\text{C}$ of mosses depends on the atmospheric CO_2 concentration and available water. The $\delta^{13}\text{C}$ of sedges from the same peat sample can be used to remove the water signal, leaving a proxy record of past variations in CO_2 . This type of study is therefore only suitable when the peat is composed of readily separable moss and sedge, which may not always be the case and may be difficult to separate when it does exist, if the peat is highly humified.

Both of these applications of isotopic studies are potentially useful, but their precision in calculating palaeoclimatic conditions is complicated by species assemblages of the peat composition in both cases. In studies where isotopes are used to reconstruct variations in temperature and precipitation, it can be difficult to isolate temperature from other variables because of these taxa-related complications.

2.6.4 Humification

Humification analysis is the study of the degree of decomposition of peat and provides a link between peat stratigraphy and past climate change. According to Aaby and Tauber

(1975), the degree of humification depends upon the surface humidity of the mire at the time of deposition. Poorly humified peat forms when the water table of a mire is high, creating anaerobic conditions which do not favour the breakdown of organic matter. Peat will become humified if the dry season is longer or drier and the water table is low, producing aerobic conditions. If this trend is prolonged, the peat stratigraphic record should contain a transition to more humified peat.

Humic acids are produced by the decomposition of vegetative matter. As the peat decomposes, the proportion of humic acid increases. Blackford and Chambers (1993) identified four categories of techniques for establishing the degree of humification of peat:

- a) *visual examination and classification*, stratigraphic analysis, for example, von Post (1924) scale, Troels-Smith (1955) classification and the Blytt-Sernander scheme. These are visually subjective assessments. The von Post scale is more detailed than the Troel-Smith five point scale, from 1, yellow-light brown peat, often with undamaged *Sphagnum* leaves, to 10, blackish-brown peat, with totally destroyed organic matter. One limitation of the von Post scale is its reliance on the presence of *Sphagna*. The assessment is limited in peats where *Sphagnum* is absent.
- b) *measurement of physical properties*, for example, bulk density and fibre content. As decomposition takes place, large fibres are broken down and the bulk density and proportion of mineral material increases.
- c) *measurement of chemical properties*. This is a complex area. Humified material has a higher CEC, a higher nitrogen content and greater calorific content than undecomposed plant matter (Mathur and Farnham, 1985, in Blackford and Chambers, 1993). The processes involved are as yet not fully understood.
- d) *chemical extraction of soluble material*, using sodium hydroxide to extract the humic acids which are produced by the decomposition of organic material.

Charman (1992, 1994) used a form of visual determination to estimate relative humification values. This involved sieving peat and measuring the depth of water required to obscure a black cross on a white background. Humification was expressed as a reciprocal (per cm) of water depth, where high values represent high humification. This is an imprecise method and Blackford and Chambers (1993) found that analysis of fibre content and NaOH extraction show greater variability in humification than is possible by visual assessment of the stratigraphy or by the sieving method. The NaOH

method adopted by Blackford (1990), Blackford and Chambers (1991, 1993, 1995) and Chambers *et al.* (1997), was developed by Overbeck (1947) and modified by Bahnson (1968). It is a colorimetric determination of an alkali extract of the peat, since the light absorbed is proportional to the amount of humic matter dissolved. Colorimetric measurements of continuous samples can, according to Blackford and Chambers (1993) provide a robust and replicable record. Well humified peats yield a low percentage transmission as there is a high content of humic acids. Poorly humified peats have a high percentage transmission due to the lower humic acid content of the peat. This provides a semi-quantitative estimate of past climate, with higher transmission values being indicative of and proportional to, but not an exact measure of, lower humification (Blackford and Chambers, 1993).

The alkali-extraction of humic acids is more suitable than analysis of the fibre content of a peat, because of the differential response of plants in an assemblage with a changing species composition. In addition to this, Coulson and Butterfield (1978) pointed out that the nature of the original plant material is of great importance in determining the rate of decomposition, as species such as *Eriophorum vaginatum* and most *Sphagnum* spp. have particularly low decay rates. Woody material is likely to take longer to breakdown than soft, fleshy plant matter.

Local reconstruction of peat-surface wetness can be combined to reconstruct regional changes in peat hydrology and by inference, changes in climate. These curves can be supported by other microfossil evidence from the peat, for example, testate amoebae analysis. Blanket bogs were originally thought to be of little or no use in proxy climatic reconstructions, but at least one synchronous change has been shown in humification records across broad regions of the British Isles (Blackford and Chambers, 1991). The application of humification techniques to well humified blanket peats may show marked variations in stratigraphy. Aaby and Tauber (1975) do not recommend comparing ombrotrophic peats with minerogenic peats, since suspended particles from the latter may disturb the light transmission making comparisons impossible.

The semi-quantitative estimate of humification from which past climatic conditions can be inferred does have a number of limitations. Not being able to apply it to minerogenic sites is a limitation in the context of this study, since it precludes comparisons between the ombrotrophic and minerogenic sites. Most of all, the semi-quantitative nature of it

is limiting as it is only a relative measure of past mire surface wetness, (*i.e.*, wet, dry, moderately wet), expressed as percentage transmission. It is not possible to determine from humification analyses exactly how wet 'wet' is and so it may be considered to be imprecise. There are no confidence intervals generated on the data which makes it more difficult to compare humification data from several profiles. Also, it is not clear whether the wet/dry shifts are of uniform size on the percentage humification scale and exactly what these are in terms of percentage moisture content/depth to water table or some other scale. However, it may be interesting to compare results from humification analysis to the quantitative mire surface wetness reconstructions from the testate amoebae analysis, this work is currently in progress (Charman, Hendon and Packman, unpublished data).

Charman, Hendon and Packman are using the testate amoebae data from the micro-scale analysis, cores CRM I and CRM IV, to compare to humification data and *Sphagnum* macrofossil analyses from the same cores. One of the main limitations of this study is that the samples taken for humification analysis were of a larger size than those used for testate amoebae analysis and hence the humification data provides an estimate over a longer period of peat accumulation than the testate data. Humification and *Sphagnum* macrofossil analyses are also not contiguous, as sampling was undertaken subsequent to peat being sent for radiocarbon dating. However, initial results show a good relationship between testate amoebae and humification and a good degree of synchronicity between two methods. This kind of multi-proxy approach may help to alleviate the problems of unquantified relative estimates of surface wetness, but the approach must be further refined so that samples are more comparable.

2.7 Conclusions

This chapter has dealt with a wide range of topics, from the peatland system and its response to climate and internal dynamics, testate amoebae as palaeohydrological indicators and the ecological and biological context of testate amoebae. Other proxy palaeohydrological indicators have also been discussed and their relative merits compared to those of testate amoebae analysis. Biological transfer functions used in palaeoecological studies in general have been discussed and in particular, the transfer functions developed by Woodland (1996) for reconstructing mire hydrological

conditions from testate amoebae data have been evaluated, as this is of prime importance to this study.

Relationships between climate, peat, *Sphagnum*, hydrology and testate amoebae are important. Peatlands are an ideal environment for the colonisation and preservation of testate amoebae. Bogs that are dominated by *Sphagnum* moss are readily colonised by testate amoebae and hydrology in particular will affect the testate amoebae assemblages recovered from peat profiles. Once the relationship between testate amoebae and hydrology has been established, it may be possible to infer a climatic signal from the analysis of multiple cores from across a region.

Both isotopic fractionation and humification analysis are to a certain extent tax-dependent. Different species have differing isotopic compositions and different taxa have varying decomposition rates. Both humification and plant macrofossil analysis link palaeohydrology and climate on ombrotrophic bogs. Neither give true quantitative values in terms of ecologically or climatically meaningful variables. Testate amoebae are potentially useful in combination with humification and/or plant macrofossils to give a more sensitive and quantifiable record, especially where there is a macrofossil record of a limited number of taxa.

Part Two, the research approach and methodology is divided into two chapters. Chapter Three sets out the rationale for choosing field sites and coring locations. Site morphology is an important criterion for field site selection and multiple coring at each site is essential in order to test the replicability of the testate amoebae record. Chapter Four sets out the laboratory and data analysis methods adopted in this study. The transfer function developed by Woodland (1996) will be applied to cores extracted from these sites in Part Three.

PART TWO

Research approach and methodology

CHAPTER THREE

Site selection and coring locations

3.0 Introduction

This chapter sets out the rationale for field site selection and coring locations. Three sites with distinct morphologies and separate hydrological systems were selected for study. This was in order to assess the replicability of the long term hydrological record derived from the testate amoebae analysis from multiple peat cores, compared within and between sites. From this it should be possible to assess the influence of climate on the testate amoebae record, by separating the allogenic hydrological signal that is found synchronously in the testate record both within a bog and across the region, from more localised autogenic hydrological signals. Field sites are examined separately and are described in terms of conservation status, mire morphology and peat type. Survey data are presented for each site and the coring locations at each site are discussed.

3.1 Scales of study

Barber (1981) considered there to be three prerequisites for site requirements in order to relate peat deposits to climate change. These are a) that ombrotrophic mires have developed under climatic influence alone, b) the peat deposit should be deep enough for long time scales to be studied and, c) for peat accumulation to have been rapid enough to give a detailed resolution of events within this temporal range. The first assumption is one that has never been fully tested. It has been assumed that allogenic factors alone influence the growth and expansion of ombrotrophic mires. However, it is likely that autogenic processes generated by internal bog dynamics also influence the development of mires, the theories behind which were discussed in Section 2.1.3. Field sites were required that fulfilled the second and third criteria and allowed the testing of the first.

One of the main aims of the project was to explore the spatial and temporal variability of the palaeohydrological record from several morphologically distinct peatland sites in one region of Britain. The variety of mire morphologies and their relationships with hydrology and response to climate change were discussed in Chapter Two. Two

ombrotrophic sites and a minerogenic valley mire were required within the same climatic district and therefore within a restricted geographical area. Two ombrotrophic mires were required to enable testing of the replicability of the hydrological record within and between the sites. An extensive series of mires with a variety of morphologies occurs in northern England on the Cumbria/Northumberland border and are known as the 'Border Mires'. These were chosen to ensure that as far as possible, the sites have been influenced by the same climatic regime throughout the Holocene.

The variability of the palaeohydrological record was considered at three spatial scales, shown in Figure 3.1. The macro-scale considers variability between sites from cores extracted from the mire centres at a distance of between 1-10km. At a macro-scale, climate is one of the most important factors in controlling mire surface wetness, as a result of the relationship between precipitation and evaporation. Autogenic factors derived from regional groundwater systems may also influence mire development at the macro-scale and the record of climatically determined mire surface wetness may be confused by meso- and micro-scale processes.

At the meso-scale, between 10-1000m, mire expansion and development are key factors as cores were extracted from the centre and edges of the mires. The distance the meso-scale is studied at will depend on the size of the mire. As the central area increases in size and height relative to the rest of the bog it has two effects on the fossil record. Firstly, the bog becomes more ombrotrophic; the central domed area is less likely to be influenced by surface runoff and ground water. Secondly, there are less likely to be major spatial differences in the record of the upper peats, as the area is larger and hydrologically more stable. For these reasons, the palaeohydrological record is more likely to be strongly related to climate in the upper peats than at depth down the cores. Vegetation succession, microclimate and human impact may also affect mire development at the meso-scale. Meso-scale studies allow comparisons to be made within each site, between the centre and edges of the bog and enable attempts to be made to separate the climatic signal within the testate amoebae record from that caused by autogenic mire development.

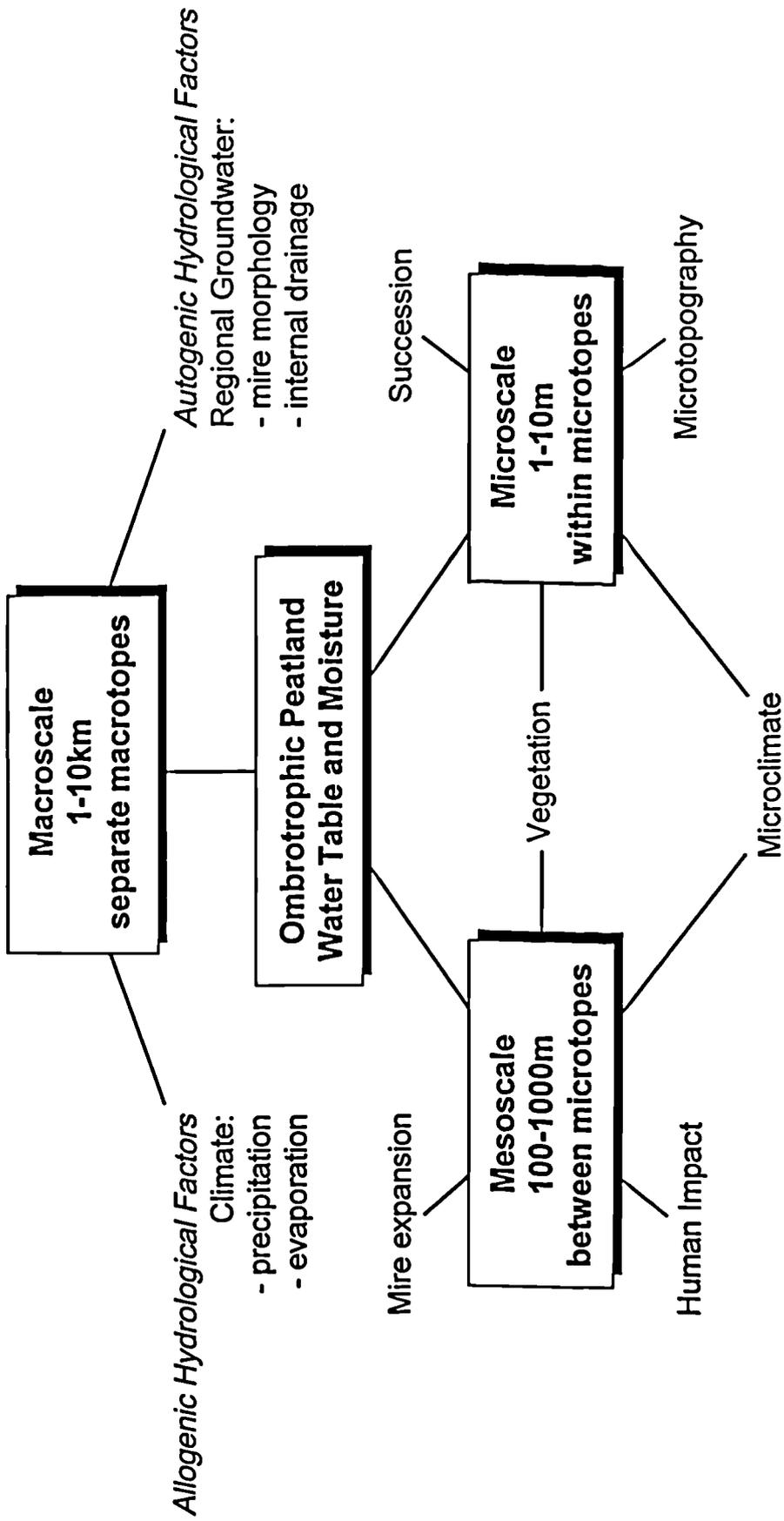


Figure 3.1 Scales of study

Vegetation is also likely to be an important influence at the micro-scale (1-10m). Microclimate, management, succession and competition may result in local differences in vegetation. Vegetation differences may affect evapotranspiration and therefore, surface wetness, as well as being a product of it. Microtopographical features (Lindsay *et al.*, 1988) are also a feature of many ombrotrophic mires. Cores extracted from up to 10m apart from the central portion of the same site allow high precision studies of the replicability of the hydrological record derived from testate amoebae analysis, so that any errors obtained at a broader (macro) scale can be quantified and evaluated and taken into account in the reconstructions of surface wetness. The theories surrounding allogenic and autogenic mire development were discussed in Section 2.1.3.

From the chosen sites, it should be possible to separate hydrological changes that are climatically-forced or allogenic, from those that result from autogenic factors relating to mire morphology, such as internal drainage. If the overall pattern of change in the direction, rate and magnitude of the water table and moisture level fluctuations shown in the surface wetness reconstructions is the same at each site, then it is likely that climatic forcing is the major influence on hydrological change. If however, the hydrological record is different at each site, or within each site, then autogenic factors such as site development and morphology are likely to be the major contributors to surface wetness.

3.2 Rationale for field sampling

A number of cores were extracted from each site, to enable testing of the temporal and spatial variability of the palaeohydrological records of the peatlands. This is not something that has routinely been carried out in palaeoecological studies. For example, the use of *Sphagnum* macrofossils to reconstruct past surface water conditions on bogs has never properly been verified as a palaeoecological technique by multiple core studies. Barber (1981) analysed 20 profiles from Bolton Fell Moss and by comparing that with the work of Smith (1985) and Wimble (1986), Barber *et al.* (1994a) concluded that extracting a single core from a site is representative of that site as a whole. This was a rather *ad hoc* assessment, lacking in verifiable experimental design. Whilst multiple coring from one site is an option, Barber (1994) regards it as time consuming and thus has relied on the replicability of the data collected by Moore (1977) and Smart (1982) which he considers to have shown a good degree of synchronicity. Since neither of these studies has a ^{14}C chronology, temporal comparisons are weak, but show only

similar gross directional changes. As Smart (1982) points out, mire surface features are three dimensional, which does result in stratigraphic profiles which are not identical. Smart (1982) also adds a note of caution, suggesting that apparently synchronous levels in the profiles do not necessarily represent contemporary surfaces because of differential decay and compression of peat. While some degree of replicability between cores can be shown at a broad scale (*e.g.* Svensson, 1988), for higher precision studies, it is necessary to know exactly what the differences are so that this source of error can be quantified and included in surface wetness reconstructions. Tallis (1994) recommends the use of closely spaced multiple cores to compensate for chance variation in the abundance of *Sphagnum* macrofossils over short distances so that the general patterns of change can be determined. The location of core extraction must be 'climatically sensitive'. Therefore it is recommended that the core is not taken from a complacent microtopo such as persistent hummock or from an area subject to drainage at the bog margin, since subtle climatic fluctuations would not register. Heathwaite *et al.* (1993) consider it essential to examine a large number of profiles from the same mire in order to exclude local influences, especially around the marginal area.

In this study, cores were extracted from the centre of each site, since this area is likely to be the most strongly related to climate. Two closely spaced cores were extracted from the centre of Coom Rigg Moss to enable a micro-scale comparison of the hydrological record. Cores were extracted from the centre of the mires to minimise complications from marginal drainage changes resulting from natural bog bursts or human cutting activity (*c.f.* Barber *et al.*, 1994a). The central core and two marginally located cores from each mire will also be used to gauge the influence of meso-scale processes on site hydrology. At a macro-scale, inter-site analysis is possible, as the sites are located within 10km of each other. Macro-scale comparisons will be made by comparing the centrally located cores from all three sites. These cores should provide sufficient evidence of spatial variability across each site at the three spatial scales.

3.3 The Irthinghead Mires

There are over 60 border mires in Northumberland and Cumbria defined by English Nature as the Border Upland Natural Area (Merricks, 1995). The Irthinghead Mires (part of the Border Mire complex), of the Kielder Forest were selected for study, as there is a remarkable range of morphological mire types within a relatively small area, in an undamaged state:

“it is an outstanding complex, not only because of the high intrinsic scientific value of the mires, but also because of the potential which the area has for research into the relationship between vegetation, hydrology and mire dynamics” (Ratcliffe, 1977a:225).

The Irthinghead Mires are composed of eight mires forming an aggregate Site of Special Scientific Interest (SSSI) and an internationally important wetland under the Ramsar Convention (1996 amendments). The Ramsar Convention on Wetlands of International Importance Especially as Waterfowl Habitat (1971) was the first international convention dealing solely with habitat (Ball and Bell, 1994). All sites have to be designated SSSIs before becoming RAMSAR sites. Five sites were originally designated as the Irthinghead Mire complex by Ratcliffe (1977b), these were; Butterburn Flow, Coom Rigg Moss, Felicia Moss, Haining Head Moss and Hummel Knowe Moss. Three other sites were designated post-publication of the Nature Conservation Review (Ratcliffe, 1977b). These were The Wou, Falstone Moss and Gowany Knowe Moss (Burlton, 1996). Of these, three mires were chosen for detailed study, namely, Coom Rigg Moss (CRM) and Butterburn Flow (BBF) which are ombrotrophic macrotope complexes, consisting of raised mire and blanket mire areas which coalesce. The third site is The Wou (TW) a minerogenic valley mire, (Figure 3.2). Table 3.1 sets out details of the conservation history and status of each site and the sites are described in detail below.

Several previous studies have been carried out in the Kielder Forest area (Chapman, 1961, 1964a,b, 1965; Smith and Charman, 1988; Charman and Smith, 1992). These have primarily been concerned with present day ecology and surface vegetation (Chapman and Rose, 1991) and the effect of the surrounding conifer plantations on the hydrology of the bogs (Smith and Charman, 1988). Planting began in 1926, although most plantations were established between 1945-1960, creating an “island of bogs in a sea of forest” (Smith and Charman, 1988; Charman and Smith 1992). A total of 38,388

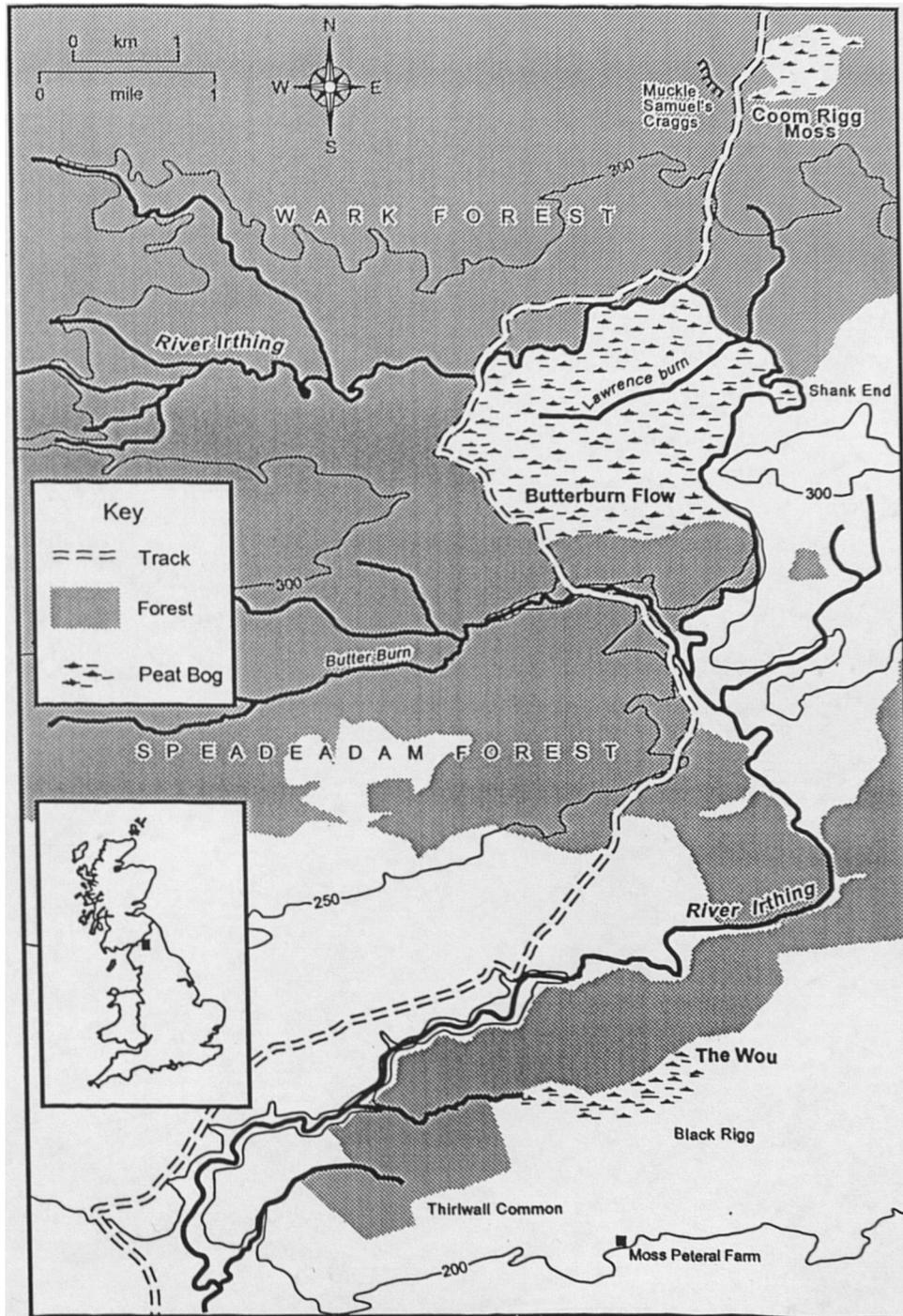


Figure 3.2 Location map of the field sites. Only peatlands sampled in this study are shown

COOM RIGG MOSS <i>OMBROTROPHIC</i>	BUTTERBURN FLOW <i>OMBROTROPHIC</i>	THE WOU <i>MINEROGENIC</i>
First notified a Special Site of Scientific Interest 1959 (National Parks Act, 1949) National Nature Reserve 1960	First notified a Special Site of Scientific Interest 1959 (National Parks Act, 1949)	
Constituent of Irthinghead Mires Complex in A <i>Nature Conservation Review</i> (Ratcliffe, 1977b)	Constituent of Irthinghead Mires Complex in A <i>Nature Conservation Review</i> (Ratcliffe, 1977b)	National Nature Reserve 1968
Renotified SSSI 1983 (Wildlife and Countryside Act, 1981)	Renotified SSSI 1984 (Wildlife and Countryside Act, 1981)	First notified a Special Site of Scientific Interest, 1984
Designated an internationally important wetland site under the RAMSAR convention 1986	Designated an internationally important wetland site under the RAMSAR convention 1986	Designated an internationally important wetland site under the RAMSAR convention 1986
Renotified SSSI 1995 and incorporated into Kielder Mires SSSI composite		Renotified SSSI 1995 and incorporated into Kielder Mires SSSI composite
Proposed as a constituent "Border Mires: Kielder to Butterburn" Special Area of Conservation (SAC) 1995	Proposed as a constituent "Border Mires: Kielder to Butterburn" Special Area of Conservation, (SAC) 1995	Proposed as a constituent "Border Mires: Kielder to Butterburn" Special Area of Conservation, (SAC) 1995
Managed by English Nature (Northumberland), owned by Forest Enterprise, Kielder District.	Managed by English Nature (Cumbria), owned by Forest Enterprise, Kielder District.	Managed by The Northumberland Wildlife Trust.

Table 3.1 Conservation history and status of the field sites

hectares of the Kielder Forest were planted with 69% sitka spruce (*Picea sitchensis*), 15% Norway spruce (*Picea abies*), 9% lodgepole pine (*Pinus contorta*), 3% Scots pine (*Pinus sylvestris*) and 4% other species (Smith and Charman, 1988; Burlton, 1997). The remaining 11,090 hectares, mostly the upland blanket mires that were too wet to afforest, were left unplanted. The area was ploughed and cross-drained prior to planting. Trees were planted in straight lines with no deciduous trees at the edges to break the visual impact of the conifers and very few gaps were left between stands (Burlton, 1995). Crops are felled on a 45-year cycle, so felling has recently commenced in many areas. Clear-felling has been undertaken to harvest the crop of trees but the management plan also includes 'restructuring' measures to clear relatively small blocks of trees to reduce wind-throw and increase habitat diversity for better silvicultural practice (Burlton, 1996). Broad-leaved trees are being planted along water courses and the overall practice should improve conditions for bog conservation.

In the 1980s, the Forestry Commission became a multi-purpose agency, with conservation and recreation becoming an integral part of forest management (Burlton, 1997). Since 1987 there has been an inter-agency approach to bog and forest management. The Border Mires Committee was formed, comprised of English Nature (North East and North West), The Northumberland Wildlife Trust, Forest Enterprise, Newcastle University and the Northumberland National Park. A number of 'first aid' measures has been instigated in an attempt to improve the conditions for the bogs. These include ditch-blocking to raise the water table level and spruce removal from the mires surfaces.

Lowe (1993) redefined the hydrological boundaries of 48 bogs in the Border Mire Complex in Northumberland. This excluded Butterburn Flow, as it lies just within the Cumbria border. The maps presented by Lowe (1993) show the current open area and former mire extent and the area that is presently forested. The maps also show the input/catchment slopes that may have an impact on the edge and lagg area of sites and which may indirectly be affected by the forested area. Peat depths of less than 1m were considered to be outside of the mire boundary. According to Burlton (1995), these definitions of the hydrological boundaries of the mires under the remit of Forest Enterprise will contribute to those sites being preserved in perpetuity.

Geology and hydrology

The underlying bedrock geology of the area is the Scremerstone series of the Lower Carboniferous period. There is a succession of shales, sandstones, thin bands of limestone and many small coal seams overlain by glacial drift (Chapman and Rose, 1991; Merricks, 1995; Burlton, 1997). The impermeable nature of these strata makes them ideal for peat formation. The average annual rainfall in this area is 1270mm and the average monthly evapotranspiration (Pet) never exceeds precipitation (Newson and White, 1993). The high precipitation and relatively undamaged bog surfaces are important factors in maintaining the water table at or very near the surface throughout the year (Merricks, 1995).

3.4 Surveying

Levelling is necessary for determining sub-peat topography and is not used for depth correlation between cores. Levelling mires can be difficult since the surface can be prone to compaction. Since surveying data is primarily used for determining substrate topography within each site, a relative depth scale was used, rather than absolute values relative to Ordnance Datum, since there was no benchmark height visible from the sites. The sites were surveyed at 30m intervals across transects using a hand operated Kern Level to record the surface topography of the bogs (Aaby, 1986). The underlying sediments were probed to give an approximate indication of sediment depth. In several places, the clay beneath the peat was reached, so the diagrams of the bog profiles are sediment depth probes, not peat depth probes. The actual peat depth is known only at coring locations from stratigraphic analyses. These diagrams (Figures 3.4, 3.5, 3.8, 3.9, 3.11-3.14) give an indication of bog morphology and were used in the selection of locations for coring, typically at the deepest points for central cores, so that the longest possible record could be obtained.

The diagrams of the bog profiles are all plotted relative to a zero point at a known location. This means that the relative, not actual, ground surface and profile depths are shown. Point zero was the starting point of each survey, so that the longest possible distance could be surveyed without moving the level.

3.5 Coom Rigg Moss (CRM)

Grid Reference: NY 690 795 Northumberland.

Coom Rigg Moss lies 40 km north-east of Carlisle, within the Northumberland National Park. It is an area of 39.6 hectares and Lowe (1993) classified it as a watershed saddle mire. Chapman (1961, 1964a,b) and Ratcliffe (1977b) consider the site to consist of several raised bog units united by blanket bog and it can therefore be considered a mire macrotope. This study concentrates on the raised bog at the eastern edge of the site. Coom Rigg Moss has sediments from oligotrophic fen peats through to ombrotrophic *Sphagnum* peat at the surface. The watershed lies between the River Irthing to the south and Chirdon Burn to the north. Figure 3.3 shows the surveying transects and coring locations. The site maps for all three locations show forest areas as in 1993, but these will now be altered, due to clear-felling of the forestry plantation.

Conservation status

The site was scheduled as a SSSI in 1959 under the National Parks Act, 1949 (Table 3.1). The site was the first notified of the Border Mires in 1959, was made a National Nature Reserve (NNR) in 1960 and was renotified as a SSSI in 1983, under the 1981 Wildlife and Countryside Act. Coom Rigg Moss is proposed as a constituent part of the 'Border Mires: Kielder to Butterburn' Special Area of Conservation (SAC), (Merricks, 1995). Coom Rigg Moss was incorporated into the composite Kielder mires SSSI in 1995 (Burlton, 1996). The bog is managed by English Nature (North East Region), but is owned by Forest Enterprise, Kielder District.

Vegetation

The bog was almost entirely surrounded by conifer plantations, until felling began in the early 1990s. Between 1954-1957, the land surrounding Coom Rigg Moss was planted with sitka spruce and lodgepole pine. According to Smith and Charman (1988), the land to the north of Coom Rigg Moss was planted in the 1950s and the area to the south in the 1970s. In 1974, the land to the south of the bog was planted with lodgepole pine (Merricks, 1995). The surface is undamaged by burning, peat cutting or drainage and is one of the small number of unplanted areas within the Wark Forest. The surface vegetation is as near to a natural climax vegetation type as is found in the British Isles

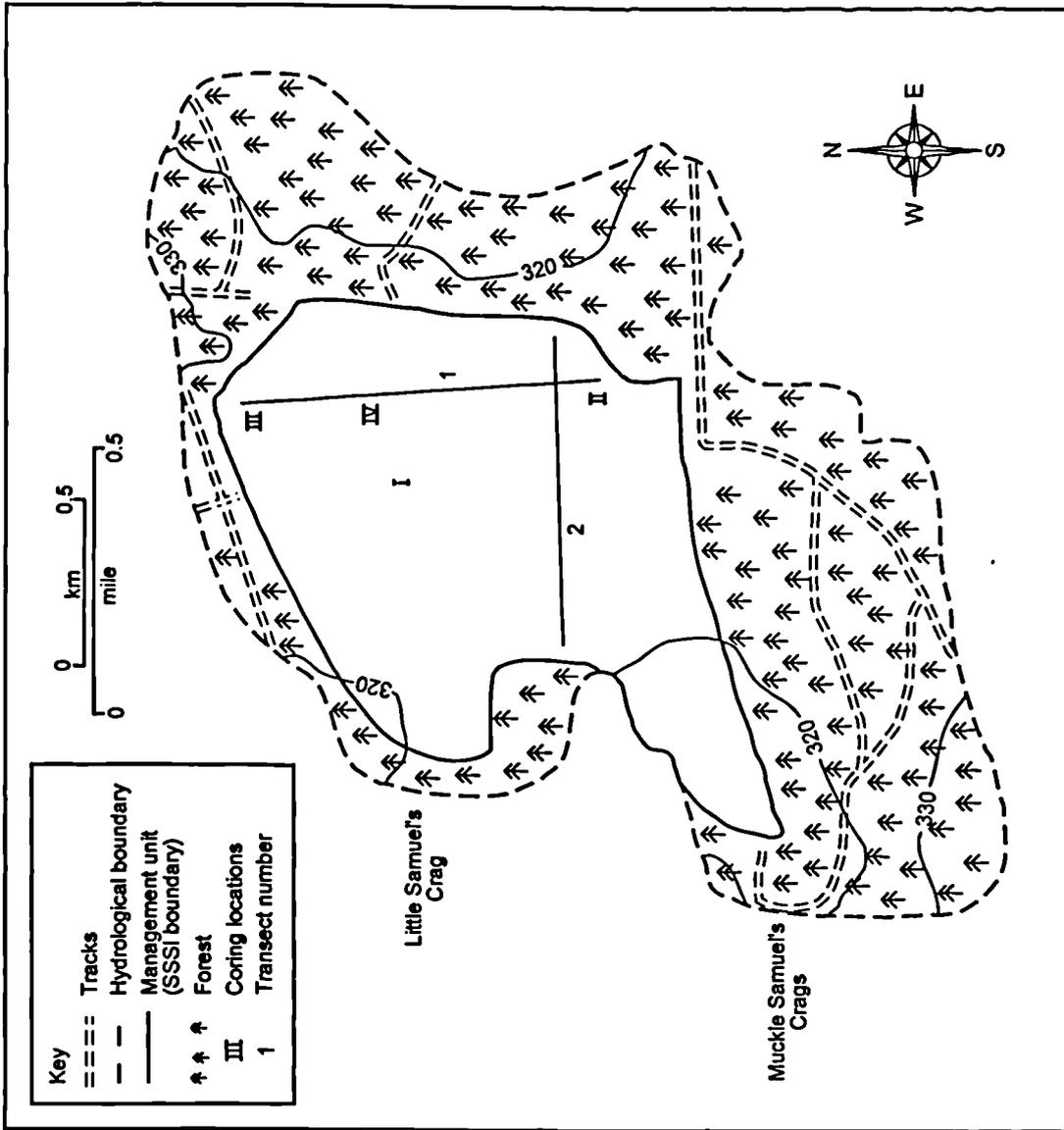


Figure 3.3 Map of Coom Rigg Moss

(Merricks, 1995), formed as a result of *Sphagnum* peat accumulation under climatic conditions where precipitation exceeds evaporation. The vegetation is dominated by *Calluna-Sphagnum-Erica tetralix* communities (Ratcliffe, 1977a). However, Chapman and Rose (1991) and Charman and Smith (1992) state that there has been a change in both the structure and the composition of vegetation in the mire since the area was planted with conifers. Chapman and Rose (1991) found that over a 28 year period (1958-1986) there was an increase in moorland species at Coom Rigg Moss, noticeably *Deschampsia flexuosa* (wavy hair-grass), *Mylia anomola*, *Pleurozium schreberi* and *Polytrichum commune*. There was an associated decline in ombrotrophic species such as the bog-mosses *Sphagnum magellanicum* and *S. papillosum* and *Drosera rotundifolia* (round-leaved sundew), *Narthecium ossifragum* (bog asphodel) and *Andromeda polifolia* (bog rosemary). Another possible factor in the changing composition of vegetation at Coom Rigg Moss is that this site was grazed at low levels by sheep until the 1950s. However, according to Merricks (1995) deer grazing on the site has almost certainly increased since the forest was planted.

Hydrology

Coom Rigg Moss has only a small surrounding catchment area, with soil water now affecting only marginal areas of bog, the greater part of the surface being ombrotrophic (Chapman, 1965). The recent vegetation changes at Coom Rigg Moss are possibly a direct result of afforestation on bog hydrology, since there will have been increased interception and evapotranspiration in the forest adjacent to the bog, reducing the water supply to the bog edges (Chapman and Rose, 1991). The area surrounding the mire that was afforested was ploughed and cross-drained prior to planting. The central area of the bog is a shedding system that is dependent on rainfall, so afforestation should only affect marginal areas. One open pool and several moss-filled hollows are present to the south west of the site.

Past management

Until 1994, the only management practice was the hand-weeding of self-sown conifers from the mire surface. In 1994, approximately 20 plywood dams were installed on the northern edge of the bog to encourage higher water table levels by impeding drainage as a conservation measure. Removal of failed or poor crops from the northern edge began

in 1994 and continued in 1995 (Merricks, 1995). Parts of the western edge of the bog were clear-felled in 1996.

Coring at Coom Rigg Moss

The ombrotrophic section on the eastern side of this bog identified by Chapman (1964a) is of most interest to this study and it is there that the field work was conducted. Figure 3.6 shows the map from Chapman (1964a) that presents the bog surface as a dotted line. This agrees with the Nature Reserve boundary designated by Ratcliffe (1977b) and Lowe's (1993) management unit for Coom Rigg Moss. The solid line represents the former extent of the mire and is similar to the boundaries presented by Lowe (1993) for the input/catchment zone of the mire. The grid lines coincide with the 100m lines of the National Grid, with eastings labelled from A-O and northings from 1-12. Chapman (1964a) found two distinct peat types, the first above hollows in the drift and the second above ridges running beneath the bog. This study concentrates on the former, with a sequence of fen peat, overlain by brushwood peat and above that a *Sphagnum-Eriophorum* peat. The raised bog is composed of a succession from initially minerotrophic basin conditions to ombrotrophic conditions. Work concentrated on the upper, ombrotrophic peat. Transect 1, the south-north transect, lies between eastings H and I of Chapman (1964a) and as can be seen from his diagram, constitutes one of the deepest areas of the site. Transect 2, the east-west transect, lies just to the north of Chapman's transect 8 and the basic morphology is similar. Stratigraphical, ecological, chemical and hydrological studies of the site's development have been carried out on the site by Chapman (1964a,b, 1965). Figures 3.4 and 3.5 show the depth profiles of the sediments at Coom Rigg Moss. The east-west transect was perpendicular to the south-north transect.

The diagrams showing profile depth relative to ground surface and coring locations have a large vertical exaggeration. In reality, the slope angle would be very small. The line showing profile depth is roughly equivalent to the interface between the peat and the underlying late-glacial clay. This slope may have influenced the initial formation of the peat bog by encouraging runoff. However, because of the cohesive characteristics of

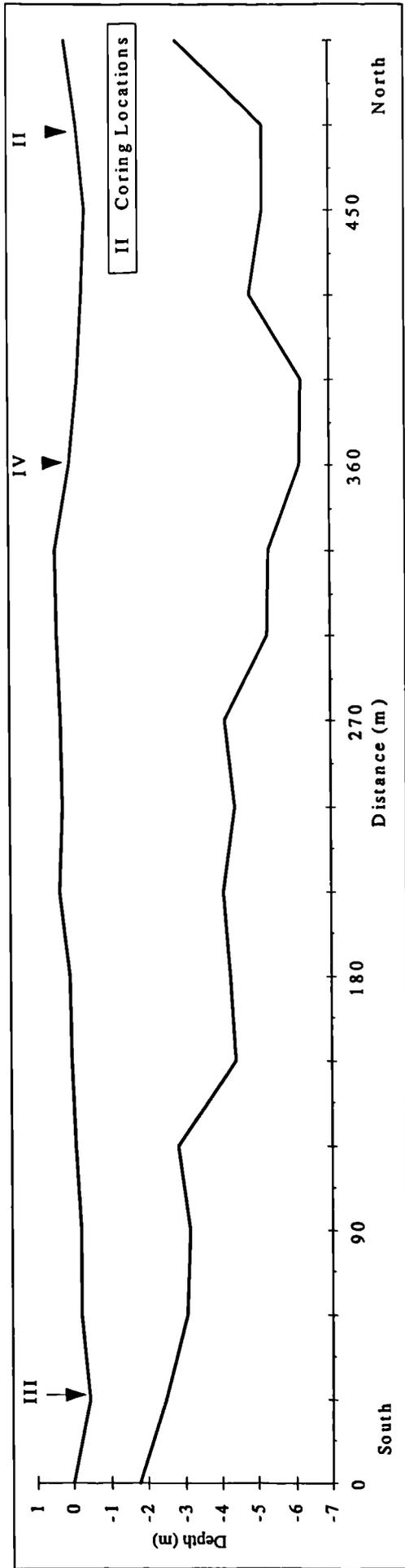


Figure 3.4 South-north transect, Coom Rigg Moss

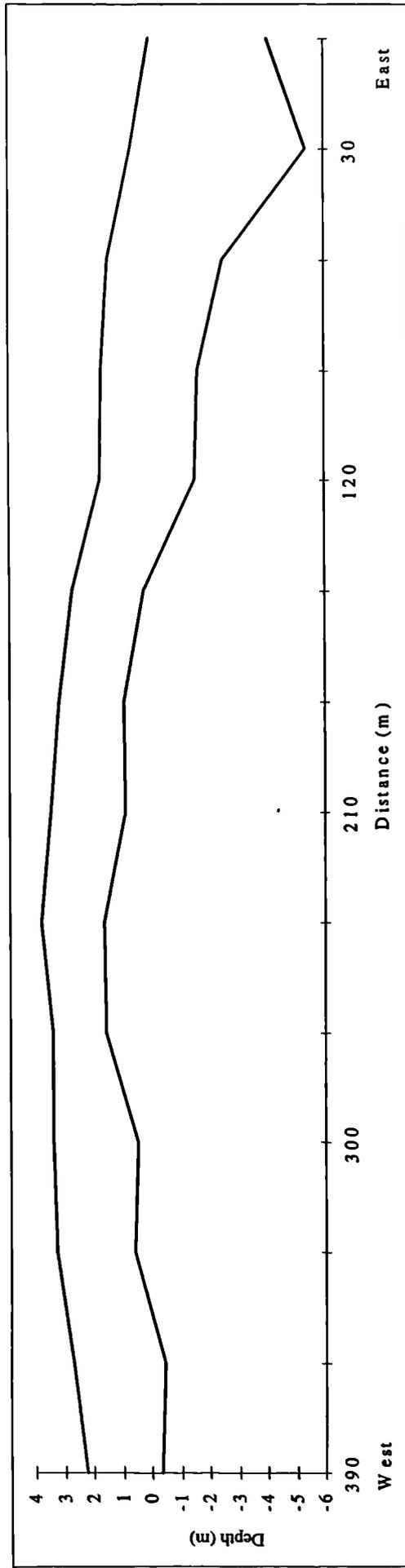


Figure 3.5 East-west transect, Coom Rigg Moss

clay, mineral inputs from the clay to the peat from the runoff may have been slight. Hydrogen bonding between the clay particle surfaces and water causes cohesion and the tendency for clay particles to stick together (Brady, 1990). Initial runoff may have had an autogenic influence on primary fen peat development but will have been less significant, once ombrotrophic peat development was initiated.

At Coom Rigg Moss, the initial plan was to extract five cores; two from the edges of the bog and cores from three points within a hummock-hollow complex, *i.e.* a core from the hummock top, one from the centre of the hollow and a core at a mid-point between. The rationale for this was that the horizontal and vertical distribution of the testate amoebae assemblage within a single micro-topographical feature could be examined, as suggested by Beyens (1984). However, this was not possible, as the hummock-hollow topography was not pronounced enough for this to be practical. Instead, two cores were extracted within 10m of each other from the centre of the raised section of the bog, to enable the replicability of these cores to be studied in a micro-scale comparison.

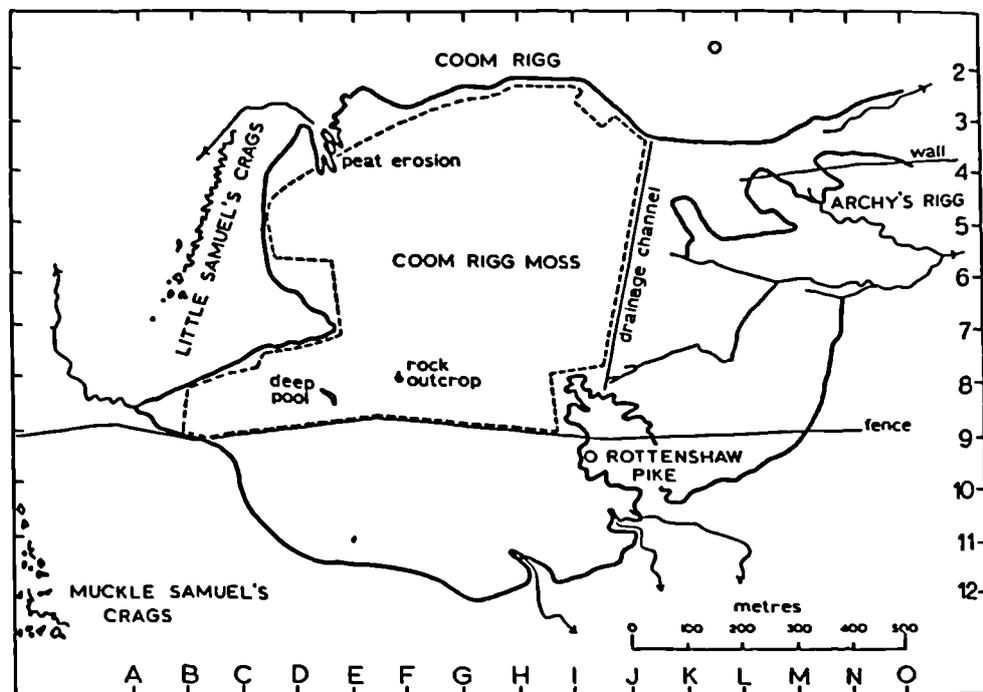


Figure 3.6 Map of surface features at Coom Rigg Moss. (Source: Chapman, 1964a)

The first core from Coom Rigg Moss (CRM I) was extracted in November 1994 from the centre of the bog. The top metre of peat was extracted with a Wardenaar sampler (Wardenaar, 1987), giving a substantial monolith, 10x10x100cm. A wide bore Russian corer was used to extract the rest of the profile contiguously, as described by Barber (1984). The three other cores from Coom Rigg Moss, cores CRM II-IV, were extracted in April 1995 using the Russian corer only. These cores were extracted using parallel holes, so that each core has a five centimetre overlap with the adjacent cores. This was done to ensure that the nose of the corer did not compact the underlying peat, to guarantee a complete stratigraphic record and so that there was a large volume of peat from which to take samples for radiometric radiocarbon dating. Core CRM I was not extracted from the transect, but approximately 10 metres to the west of it. Core CRM II was located 480m along the transect, CRM III 30m along the transect and CRM IV was extracted from 360m along the transect.

When extracted, core CRM I was wrapped in foil, sealed in cling film, placed in lengths of wide diameter guttering and sealed in plastic bags. Subsequent cores were wrapped in non-PVC clingfilm, placed in guttering and sealed in 'Layflat' to prevent desiccation. Dry peat samples tends to make tests brittle and prone to fracture (Warner, 1990). The cores were wrapped in this manner to reduce any possibility of this. All samples were returned to the laboratory, refrigerated at 6°C and were subsequently frozen for long term storage.

3.6 Butterburn Flow (BBF)

Grid Reference: NY 678 771 Cumbria

Butterburn Flow is located in East Cumbria and is considered to be the most important *Sphagnum*-rich blanket mire outside Scotland. "The Flow contains one of the most extensive undamaged Sphagneta in Britain, of a type once widespread in the Scottish Borders and the Pennines, but now rare and still diminishing" (Ratcliffe, 1977b:225). It is the largest of the Irthinghead Mires. The current open conservation area is 365 hectares, the conservation unit afforested area is 91 hectares. Only 7.6% of the conservation unit provides 'input', as the catchment area of the mire is only 34 hectares, (White, 1994). Figure 3.7 is a site map of Butterburn Flow and shows transect and

coring locations. Butterburn Flow is not included in the evaluation of the hydrological boundaries of the Border Mires by Lowe (1993). The hydrological boundary for Butterburn Flow is taken from White (1994).

Conservation status

Butterburn Flow was originally notified as a SSSI in 1959 and renotified in 1982/4. Butterburn Flow was included as a constituent "Border mires: Kielder to Butterburn Special Area of Conservation" (SAC) in 1995. Butterburn Flow is managed by English Nature, North West Region, but is located within the Kielder Forest, owned by Forest Enterprise, Bellingham (Table 3.1).

Vegetation

The surface is dominated by *Sphagnum*-rich facies. *Drosera anglica* (great sundew), *D. rotundifolia* (round-leafed sundew) and *Andromeda polifolia* (bog rosemary) are abundant (Ratcliffe, 1977b). The bog asphodel *Narthecium ossifragum* is also found at this site. Near Butterburn Road on the western edge of the site, the vegetation is dominated by *Molinia caerulea*, but it is still wet under foot (White, 1994). Barber (1981:51) notes that there are two fairly distinct areas of vegetation which both seem undamaged by drainage or peat cutting. South of the Lawrence Burn, which flows west-east into the River Irthing, the bog is dominated by closely spaced hummocks. The water table is high and the upper peat has a tendency to be sloppy in both the hummocks and channels, which may pose a problem when coring in this area. To the north of the Lawrence Burn there is a slightly undulating *Sphagnum* lawn which proved to be the most useful for testate amoebae analysis. Microtopographic surface patterns are not well developed at Butterburn Flow (Lindsay *et al.*, 1988), although there are small linear hollows scattered across the deepest parts of the site.

The bog is grazed and there is some damage to surface vegetation. The peat has been compressed by the All Terrain Vehicle (ATV) used by the grazier to round up stock. Grazing exclosures were set up in September 1988 by Charman and Smith (1992) in conjunction with Forest Enterprise in order to monitor the long term effects of grazing,

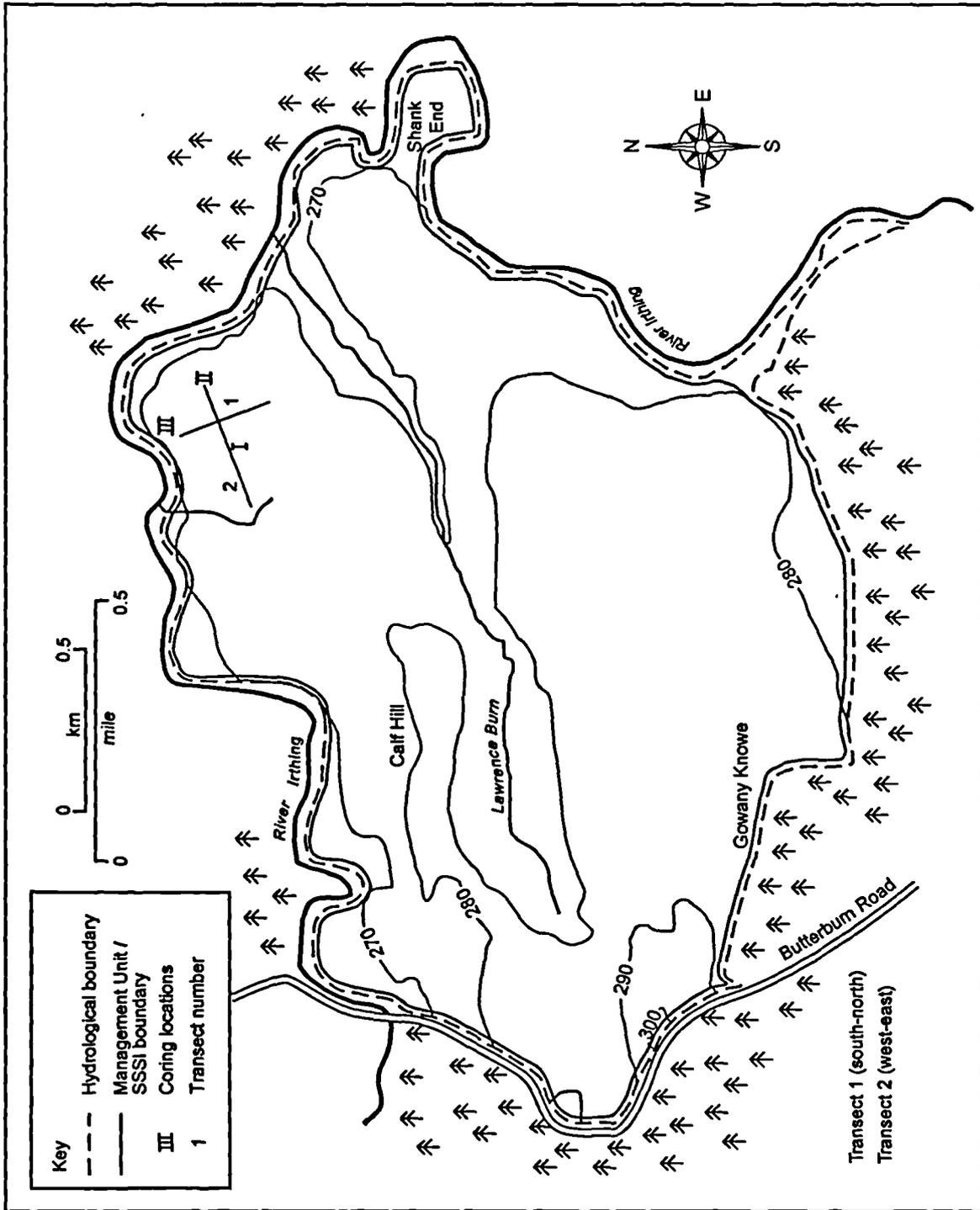


Figure 3.7 Map of Butterburn Flow

as this is the only mire in the area still grazed by sheep. The Garron tracked vehicle used to transport the enclosure posts caused considerable damage to the bog surface. Robinson (1993) notes that the enclosures were constructed in 1988 and the tracks caused by the Garron were still clearly visible in aerial photographs taken in 1991. Transportation in such a manner across a bog has been recognised as a mistake and is unlikely to be repeated.

Hydrology

Butterburn Flow is bounded by the River Irthing to the north and east. To the south, the Butterburn Flow SSSI is bounded by plantations of the Spadeadam Forest, but the hydrological boundary extends considerably further south (Burlton, 1996). The Lawrence Burn drains into the River Irthing at the northern end of the sites. Wreay Sike and Black Sike flow into Stour Cleugh to the south (White, 1994).

Coring at Butterburn Flow

Figures 3.8 and 3.9 show the depth profiles for Butterburn Flow. There is another section of ombrotrophic peat in the south of the bog (GR. NY 684 766), that may also have been suitable for study, but due to time limitations, it was not possible to probe this site and compare it to the area that was cored. Three cores were extracted from the *Sphagnum* lawn to the north of the Lawrence Burn in September 1995, using the parallel hole method. As at Coom Rigg Moss, two cores were extracted from the edges of the mire and one from the centre. Extraction of a core from point zero on south-north transect (Figure 3.8) was not possible due to a ridge to the south that may have introduced surface run-off to the peat, making the ombrotrophic nature of the peat doubtful. Also, the profile was not very deep at this point, making the potential record short. The west-east transect (Figure 3.9) shows that although the profile depth at 120m west was greater than 7.50m (the depth here could not be measured accurately due to lack of probing poles), the surface peat at this point was severely eroded due to a tributary of the Lawrence Burn forming in the area and so could not be sampled. BBF I was extracted from 180m on the south-north transect, where the west-east transect crosses it. BBF II was extracted from 180m on the west-east transect. BBF III was extracted from 390m on the south-north transect.

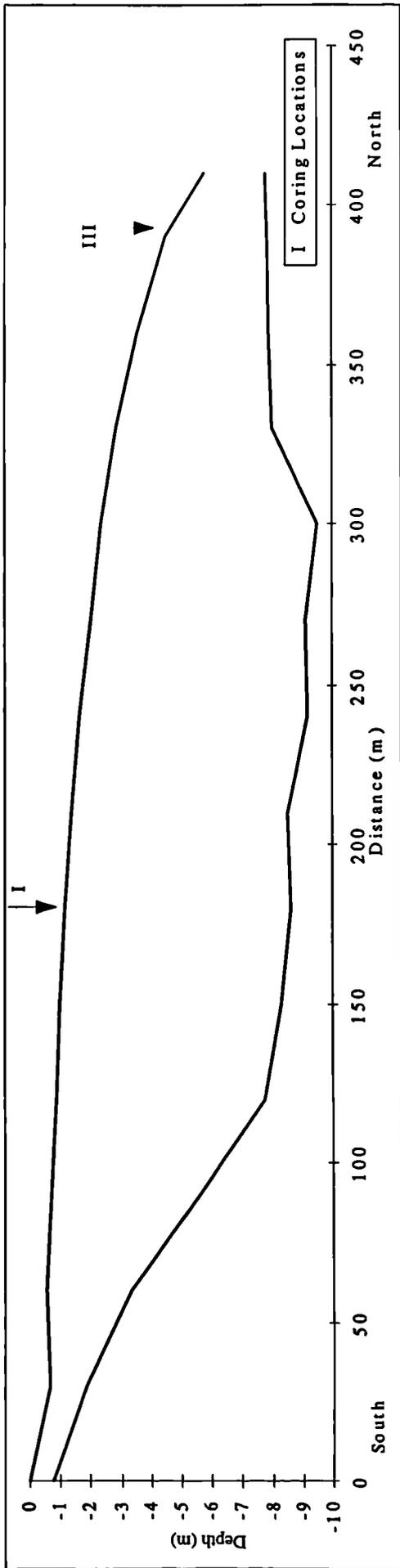


Figure 3.8 South-north transect, Butterburn Flow

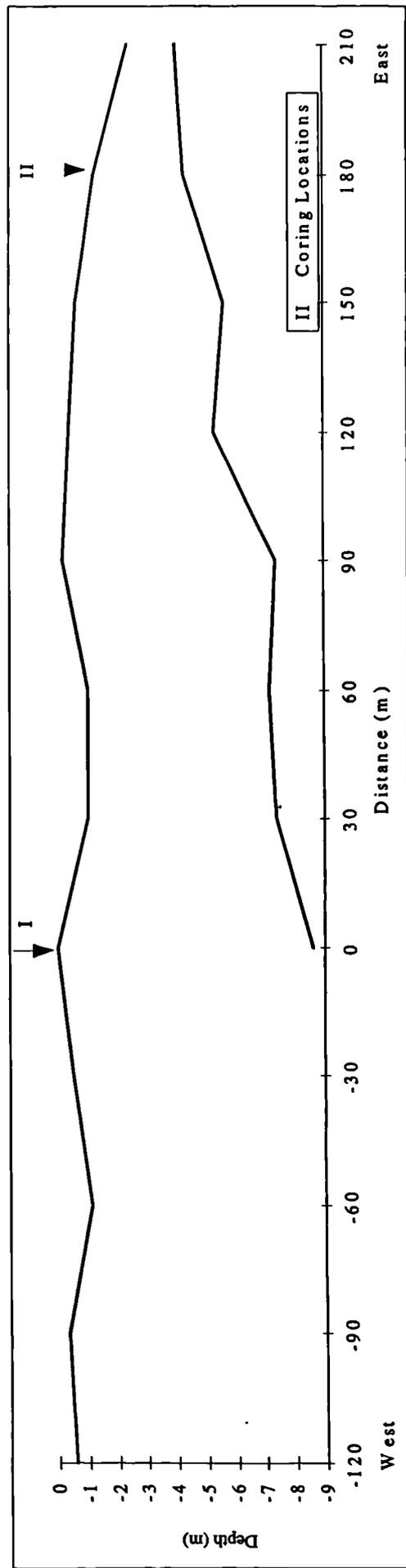


Figure 3.9 West-east transect, Butterburn Flow

3.7 The Wou (TW)

Grid Reference: NY 675 700 Northumberland

The Wou is located three miles north of Greenhead near the River Irthing within the Northumberland National Park, Northumberland. In contrast to the majority of peatlands in the Irthinghead Mire catchment, which are blanket bogs, The Wou is an oligotrophic valley mire. The site has as an area of 178 hectares (439 acres) of which 136 acres cover the slope and floor of a long east-west basin. Figure 3.10 is a site map and shows coring locations and transect sites. The SSSI boundary shows the mire management unit, the hydrological boundary shows the input/catchment zone of the mire (after Lowe, 1993).

Conservation status

This site was designated a Nature Reserve in 1968 and a SSSI in 1984 (Table 3.1). The Wou was incorporated into the composite Kielder Mires SSSI in 1995 and was accepted as an addition to the Irthinghead Mire composite post-publication of the Nature Conservation Review and is thus not referenced in Ratcliffe (1977b). This site is also on the RAMSAR list as a wetland of international importance. The Nature Reserve consists of a large area of grazed acid grassland; valley mire and associated open water and ombrotrophic bog. Two small raised mires are located at the south west end of the site between The Wou and Ealan's Drain. The undisturbed poor-fen, raised mire and open water structure are unique in Northumberland (Northumberland Wildlife Trust, 1993). The Wou is managed by the Northumberland Wildlife Trust (NWT).

Vegetation

The dominant surface vegetation of the bog is a carpet of bog-moss, mainly *Sphagnum recurvum*. In bog pools and wet hollows *Eriophorum angustifolium* (common cotton grass) is frequent and there are flushes of *Carex rostrata* (bottle sedge), *Juncus effusus* (soft rush) and *Menyanthes trifoliata* (bog bean) (Nature Conservancy Council, NCC, 1984). The Wou also has rare sedges such as *Carex curta* (white sedge), *C. limosa* (mud sedge) and *C. magellanica* (bog sedge), (NWT, 1993). The area is too wet to support conifers and the site has never been drained or planted.

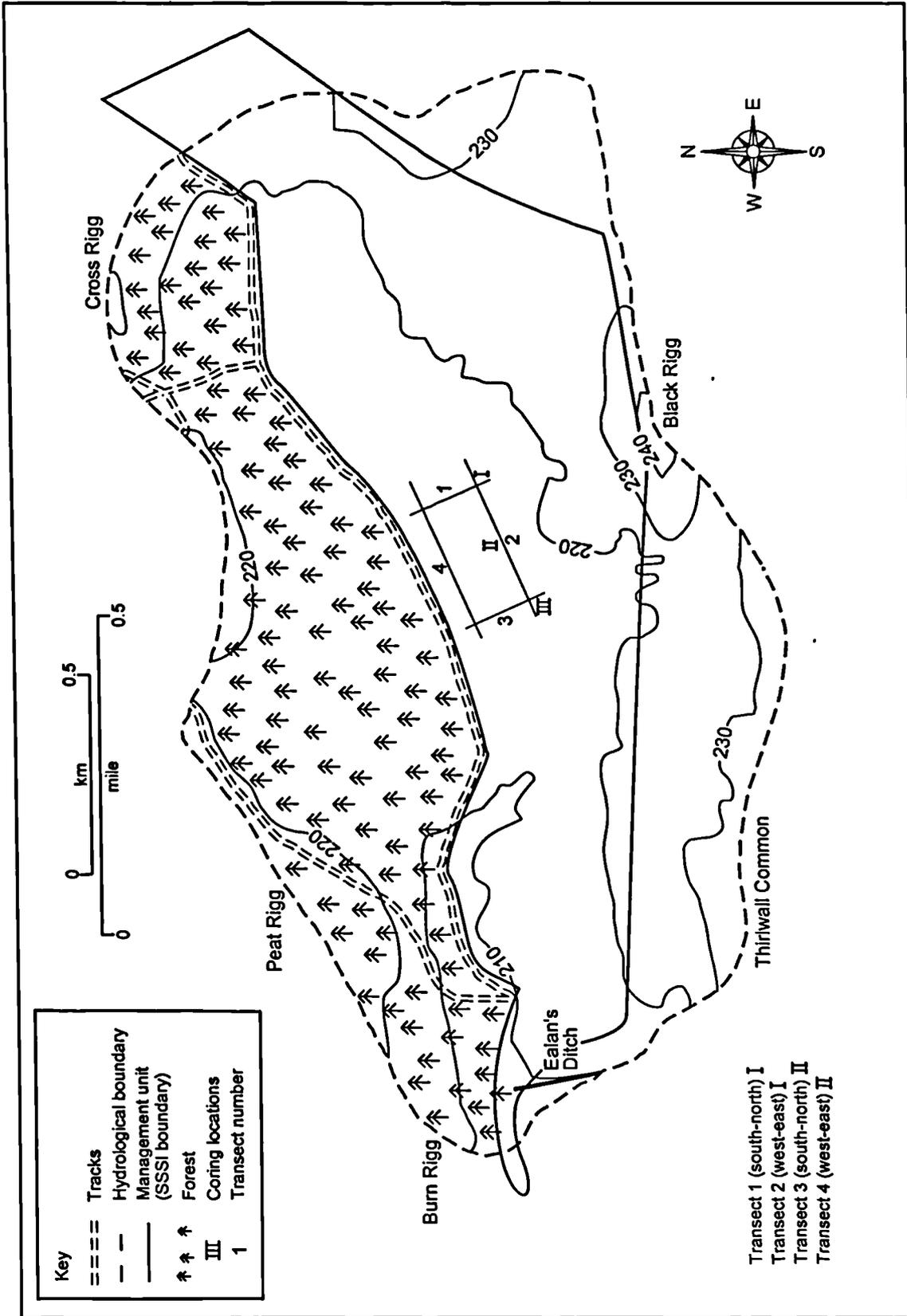


Figure 3.10 Map of The Wou

The adjacent forestry may be affecting the water table but since there are no trees close to the mire, the effect is likely to be insignificant (NWT, 1993).

Hydrology

The Wou poor-fen lies between and is related to in-flowing streams on the eastern and south-eastern edges of the site and the out flowing Crammel Burn, a tributary of the River Irthing at the west end.

Coring at The Wou

Four transects were taken across the widest part of The Wou (Figures 3.11-3.14), at the base of Black Rigg. Figure 3.10 shows the location of these transects on the bog surface. Cores from The Wou were extracted in September 1995. Cores TW I and III were extracted at the bottom of the slope from Black Rigg, Thurwell Common, from 0m on south-north transect I (Figure 3.11) and 15m on south-north transect II (Figure 3.12) respectively. This was to enable examination of slope processes such as run-off that might affect the minerotrophic nature of the test assemblages. Core TW II was extracted from the centre of the site, from 60m along west-east transect I (Figure 3.13). It was not possible to extract the top 30-90cm of this core, since due to the extreme wetness of the peat, no material was retained in the coring chamber. The dotted lines on the west-east transect II (Figure 3.14) represent hypothesised depths as coring poles were unavailable to probe to a greater depth.

Peat development in cores TW I and III was probably affected by runoff from Black Rigg to the south of the mire. Peat formation in TW II may have been more influenced by throughflow along the valley bottom along the east-west axis towards what is now Ealan's Drain. The Wou will have been more affected by autogenic influences than either Butterburn Flow or Coom Rigg Moss due to its hydro-geomorphology, from runoff and through flow from the valley catchment. This is also reflected in the stratigraphy of core extracted from The Wou (Chapter 7).

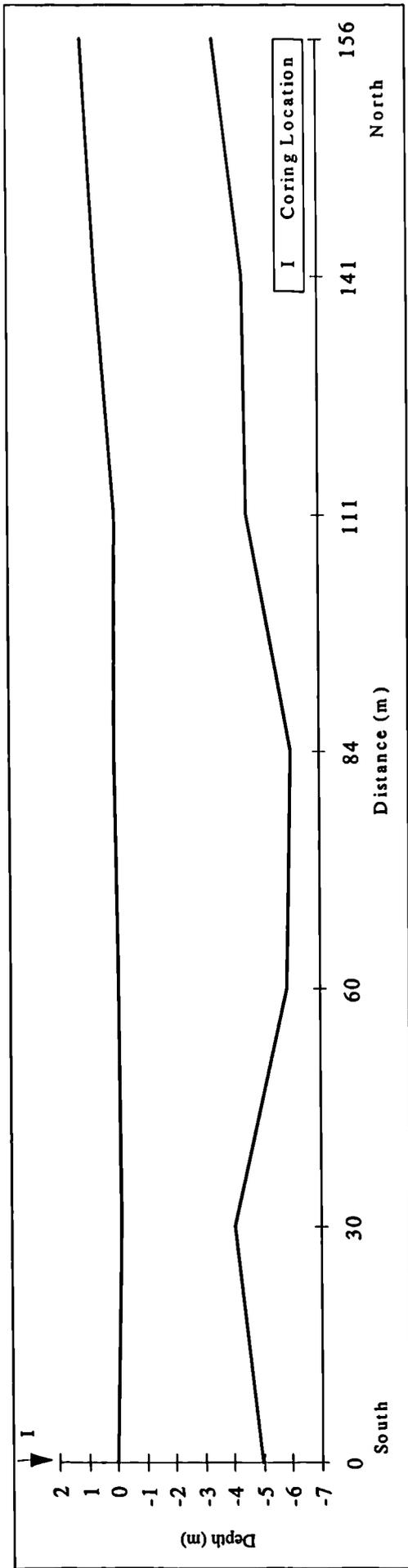


Figure 3.11 South-north transect I, The Wou

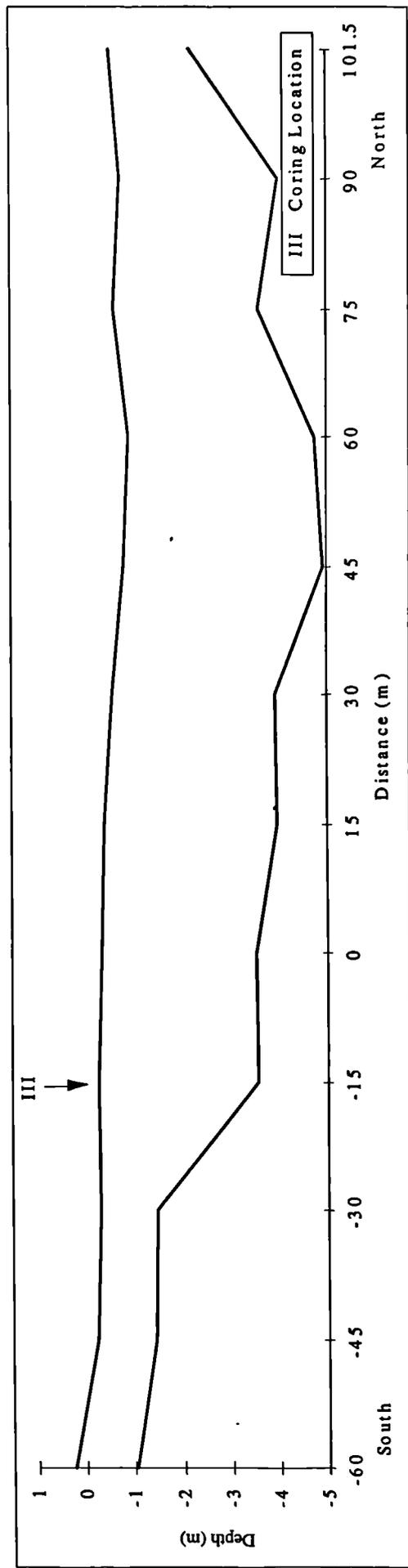


Figure 3.12 South-north transect II, The Wou

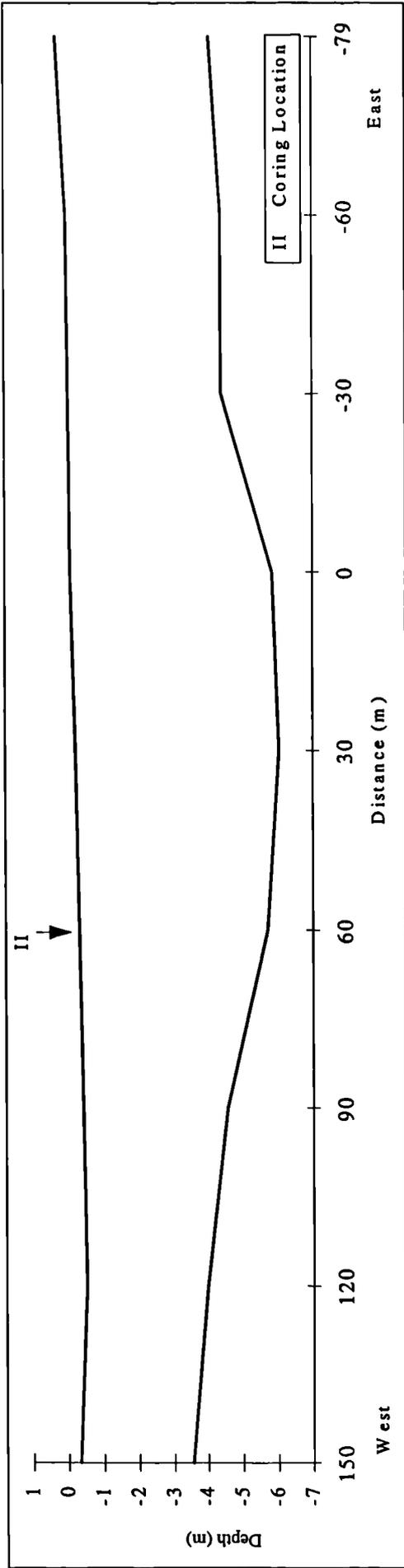


Figure 3.13 West-east transect I, The Wou

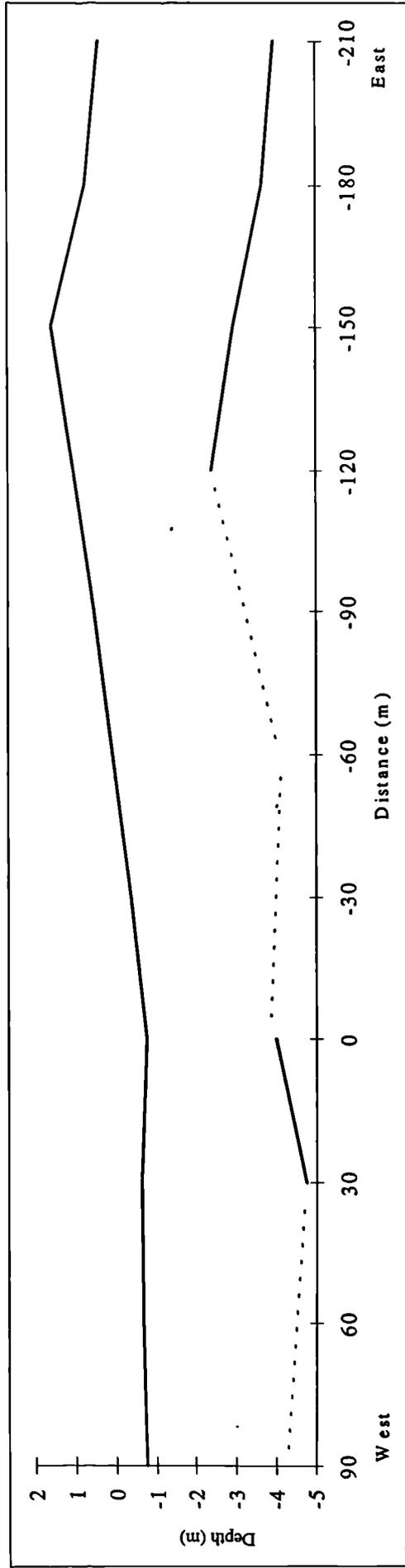


Figure 3.14 West-east transect II, The Wou, where dotted line is hypothesised depth (see text for details)

3.8 Site synthesis

The three sites selected have distinct morphological characteristics. Butterburn Flow and Coom Rigg Moss are both intermediate ombrotrophic sites, between raised and blanket mires and The Wou is a minerogenic valley mire. Testate amoebae analysis from the multiple cores extracted from these sites enabled an assessment of the replicability of the hydrological record both within individual sites and across a wide area. The testate amoebae records from these sites have been evaluated at three spatial scales (Table 3.2). At the micro-scale, a high precision study of the replicability of the testate amoebae record has been undertaken over a short distance. At the meso-scale, cores extracted from the centre and edges of the mires, have been used to attempt to separate the autogenic and allogenic hydrological signals influencing mire development. At the macro-scale, the hydrological records have been compared to assess whether major hydrological fluctuations occur on a regional basis. All of the sites are oligotrophic and so the transfer function developed by Woodland (1996) is applicable to all of the cores.

Scales of Study	Core Combinations
MICRO-	CRM I & CRM IV
MESO-	CRM I CRM II CRM III & CRM IV BBF I BBF II BBF & III
MACRO-	CRM I CRM IV BBF I & TW II

Table 3.2 Core combinations and scales of study

The following chapter sets out the various laboratory procedures applied to the peat cores and the subsequent data analysis used in order that the hydrological record of the peat bogs derived from testate amoebae analysis can be established.

CHAPTER FOUR

Laboratory methods and data analysis

4.0 Introduction

This chapter is divided into two sections. Part one discusses the palaeoecological techniques adopted in this study, the justification for using each of them and their usefulness and application. The procedures for stratigraphical description, subsampling, testate amoebae preparation and analysis, pollen preparation and analysis and radiometric radiocarbon dating are set out. The results of a set of experiments undertaken in an attempt to improve upon existing testate amoebae preparation techniques are presented. The taxonomic problems encountered in testate amoebae analysis are illustrated and discussed. Part two sets out the rationale for using each method of data analysis and presentation.

4.1 Laboratory methods

Cores from Coom Rigg Moss and Butterburn Flow were held in cold storage (6°C) until initial laboratory processing and were subsequently frozen. Cores from The Wou were frozen and thawed before subsampling. Dried samples tend to make tests brittle and prone to fracture and samples should be stored wet and refrigerated, or frozen (Warner, 1990). Frozen storage is preferable for test preservation (Tolonen, 1986). However, freezing may distort the stratigraphy if the peat is water-saturated and the cores are rigidly held (Aaby, 1986). Cores were held in wide diameter guttering so that there was room for expansion and contraction of the cores on freezing and thawing. The peat water content decreased by draining on removal from the mire which reduced the possibility of the stratigraphy being distorted by freezing. Peat cores were cleaned and the stratigraphy of each was recorded, following the sediment description system of Troels Smith. The stratigraphical descriptions for each core are presented in Chapter 5 (Coom Rigg Moss), Chapter 6 (Butterburn Flow) and Chapter 7 (The Wou).

4.1.1 Rationale for subsampling

The cleaned, uncontaminated cores were subsampled at 5cm intervals in the top metre of each profile and at 10cm intervals throughout the rest of the cores. More closely spaced sampling was undertaken in the top metre of each core, since on ombrotrophic bogs, the sites should become more dependent upon precipitation over time. As the central cupola becomes less influenced by runoff and groundwater, the surface rises above and independent of, the water table and becomes more strongly influenced by climate (Section 2.1.3). The climatic record should thus be more evident in the upper peats than at depth down the cores, where the climatic signal is more likely to be masked by autogenic factors. Closely spaced samples, at 5cm intervals, were also later taken around the samples that were radiocarbon dated. These coincided with the major fluctuations in the species assemblages and the reconstructed water table curves. Each sample was 1cm thick. Subsamples of this size were taken to ensure enough material for and the accuracy of, replicate samples for the testate amoebae and pollen analysis. Whilst closely spaced sampling would have been desirable throughout each core, it was not possible to process the large number of samples that this would have generated. This resolution of sampling provides data of a quality high enough to both assess the replicability of the testate amoebae record and separate the hydrological signals indicated by the reconstructed water table and moisture curves. Assuming an accumulation rate of 1cm per 10 years, sampling yields a resolution of 100 years for lower samples (between two samples) and 50 years for upper samples back to *circa* 1000AD. There are better instrumental and independent climatic data for the last 1000 years against which to compare the testate amoebae data, for example, Lamb's climatic indices (Lamb, 1977).

Horizons where the concentration of tests was too low to count are left blank. For individual cores, testate amoebae diagrams are plotted relative to depth (cm). The diagram of fossil testate amoebae shows changes in fauna composition as peat accumulated.

At present there is no single key for the identification of testate amoebae. Instead, several sources were used in conjunction, with careful cross-referencing. The main texts include Grospietsch (1958), Corbet (1973), Ogden and Hedley (1980), Ogden (1983) and Ellison and Ogden (1987). Ogden (1980, 1983, 1984) and Ogden and

Hedley (1980) use SEM photographs to illustrate the tests but often comparison of the image to that seen under the microscope is difficult. For routine counting with light microscopy, the photomicrographs give a better representation of the test. Fine structure characteristics observed under SEM are not seen during routine counting and are therefore less useful. Microscope slides borrowed from the Penard Collection held at the British Museum (Natural History) have been invaluable to confirm identification of several species and have been used to develop a photographic reference collection of testate amoebae.

4.1.2 Testate amoebae preparation procedure

The method used to process peat for testate amoebae analysis is a new, modified technique, based on that of Warner (1990), who developed the method of Tolonen (1986) for laboratory processing, to produce samples suitable for quantitative analysis. Evaluations of the variety of preparation procedures for testate amoebae samples extracted from peat are set out in Hendon and Charman (1997) and below.

Preparation experiments

The aim of the following experiments was to attempt to quantify the impact of different procedures on the concentration and species composition of the faunas. Improvements to the testate amoebae preparation procedure that is currently used were also sought, in order to make the microscope slides cleaner and therefore make counting more efficient.

Descriptions of methods for preparation and counting of testate amoebae are varied, although Tolonen (1966, 1986) provides the closest to a standard procedure. Techniques which have been used are divisible into two groups; those based on pollen preparation and those which are chemically less intensive and specifically for testate amoebae analysis. Studies based on pollen preparations offer time savings, in that pollen grains and testate amoebae can be counted simultaneously, but they may not provide the most reliable data. Also, many such studies only include testate amoebae analysis because tests happen to occur on pollen slides and testate amoebae analysis is included in studies in a *post hoc* way. Separate preparations specifically for testate samples have been generally recommended because of the suspicion of differential damage from chemical techniques (Tolonen, 1986). However, no attempt has been

made to assess the level of damage from each chemical preparation or to adapt preparation procedures for more humified peats where large amounts of fine organic material can make counting difficult by obscuring smaller tests. This section describes the results of previous work and reports results of experimental preparations based on different treatments.

Previous work

Tolonen (1966, 1986) modified the method of Grospietsch (1955, 1958) and variants of this procedure have been widely used in the preparation of modern samples (Tolonen *et al.*, 1992, 1994; Warner, 1987, 1990; Woodland, 1996). The technique is simple, with disaggregation of the sample in boiling water followed by sieving through a mesh. The main difference in previous preparation techniques has been the size of the mesh used to sieve samples. Warner (1987, 1990) and Tolonen *et al.* (1992) used a coarse sieve; a 'kitchen tea strainer', with a mesh size of 750 μ m. This is rather large, as most peatland tests are not greater than 200 μ m. Some species of *Diffflugia* (*e.g.* *D. oblonga* and *D. claviformis*) do exceed 200 μ m (Ogden and Hedley, 1980), but Woodland (1996) found that sieving with a 300 μ m mesh provided far cleaner microscope slides without the loss of tests.

Although a number of palaeoecological studies have used this kind of preparation technique (Tolonen, 1966; Van der Molen and Hoekstra, 1988; Warner, 1990, 1991; Warner and Charman, 1994) most studies have based analysis on slides prepared for pollen analysis (*e.g.* Aaby and Tauber, 1975; Aaby, 1976; Barber, 1981; Smith, 1985; Wimble, 1986; Van Geel and Middelorp, 1988; Van der Molen *et al.*, 1995; Dwyer and Mitchell, 1997). Most of these studies are undertaken because testates are found on pollen slides and look interesting, rather than their analysis being integral to the initial aims of the study. Results from these studies have been viewed with varying degrees of enthusiasm.

Tolonen (1986:652) stated that "a rather common practice is to count rhizopod frequencies as a percentage of some basic pollen sum in connection with pollen analysis". This approach is of limited value; firstly, there is selective destruction of the tests in the chemical treatment necessary for pollen preparations, although he did not

quantify this destruction. Secondly, the process of accumulation of pollen grains is quite different from the 'local' moss-inhabiting testate amoebae. The main taphonomic difference is that testate amoebae are found *in situ*, only on rare occasions their presence may be the result of being blown by the wind during exceptionally dry periods (Medioli *et al.*, 1990).

Aaby and Tauber (1975) and Aaby (1976) used testate amoebae in conjunction with humification analysis on peat extracted from Draved Mose, Denmark. Tests were counted "routinely, together with pollen and spores, leaving only two species intact after chemical treatment" (Aaby and Tauber, 1975:3). According to Aaby (1976:281) "Population frequencies (of testate amoebae) reinforce indications of past changes in the water regime of the bog, as reflected in the humification curve". Barber (1981:72) was less enthusiastic, suggesting that in a macrofossil-based study, little information could be gathered from testate amoebae counted on pollen slides. Only two taxa were recovered from his samples from Bolton Fell Moss, Cumbria.

Wimble (1986) counted testate amoebae along with pollen to "save time". Although no HF treatment was used, only a few species were recovered. The results were not straight forward and he recommended more detailed analyses. Wimble (1986) expressed the results as absolute concentrations of tests per cm³ of peat and calculated this from the exotic pollen data.

Van Geel and Middelorp (1988) counted testate amoebae along with any other recognisable palynomorphs found in pollen preparations. Three species of testate amoebae were found, along with spermatophores of Copepoda and various fungal spores. Van der Molen and Hoekstra (1988) used a combination of pollen preparation and water based preparation in their study. Eleven species were recovered from the peat treated with the testate amoebae preparation, whilst only two species were recovered from the pollen preparation. In the light of this they recommend separate rhizopod analysis if reliable results were required (Van der Molen and Hoekstra, 1988). However, Van der Molen *et al.* (1995) did not use separate testate amoebae analysis for their work on the hummock-hollow complexes on raised bogs in the Irish Midlands and only six species were counted from pollen slides.

The two taxa most commonly found in pollen preparations are *Amphitrema flavum* and *Assulina* spp. This may be either due to their resistance to chemical treatment or the fact that these taxa are easy to identify. Plate 4.1 illustrates *Amphitrema flavum*, Plate 4.2 illustrates *Assulina muscorum* and Plate 4.3 *Assulina seminulum*. These species are also illustrated in van Geel (1978); *A. flavum* (Type 31A), *Assulina muscorum* (Type 32A) and *A. seminulum* (Type 32B). The only other testate species identified by van Geel (1978) is *Hyalosphenia subflava* (Type 46). Since this is a text which is used to identify unknown microfossils, it would seem that these are readily identifiable from it, whereas other testates that may be in these pollen samples are more likely to be overlooked. The recovery of these taxa is likely to cause significant bias in the interpretation of peat bog hydrology. *A. flavum* is an indicator of wet conditions, with >95% peat water content (Corbet, 1973; Tolonen, 1966; Tolonen *et al.*, 1992; Warner, 1987). *A. muscorum* is regarded as a cosmopolitan species (Warner, 1990), while *A. seminulum* indicates relatively dry conditions, with a peat water content of between 78-89% (Tolonen *et al.*, 1992; Warner, 1987) (Table 2.6). In addition, despite the assertion of Aaby (1976, above), it is possible that the entire complement of these taxa does not survive the pollen preparation process and that fluctuations in the resultant curves merely represent minor differences in preparation timing and peat type.

Methods

A peat core from 70-100cm depth was extracted with a wide-bore Russian corer from Coom Rigg Moss in November 1994, close to the location for core CRM I. This depth was used in order to be below the acrotelm-catotelm boundary and within the well preserved ombrotrophic peats. Five replicates of each of six subsamples were taken at five centimetre intervals. Each set of replicates was subjected to a different preparation procedure (Table 4.1). The peat was of uniform stratigraphy between 70-100cm consisting of partially decomposed *Sphagnum* peat with stems preserved and some *Eriophorum* remains [Troels-Smith description - nig 4; strf 4; elas 2; sicc 1; humo 2; Tb³ (Sphag); Th¹ *Eriophorum angustifolium*].



Plate 4.1 Photomicrograph of *Amphitrema flavum* Archer 1877
Typically 45-70 μ m long



Plate 4.2 Photomicrograph of *Assulina muscorum* Greef 1888
Typically 46-58 μ m long

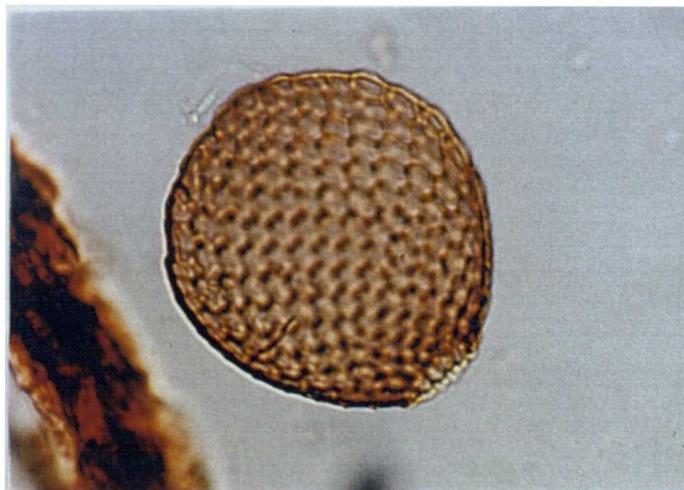


Plate 4.3 Photomicrograph of *Assulina seminulum* Ehrenburg 1848
Typically 60-68 μ m long

The methods used in these experiments were chosen to reflect the range of preparation techniques used in published work and as potential methods which would exploit some of the advantages of pollen preparation, while avoiding some of the more damaging procedures. All samples were prepared with 1cm³ peat and one *Lycopodium* tablet (Stockmarr, 1971), to calculate concentrations, mounted in glycerol and counted at x400 magnification. For each sample, 200 *Lycopodium* spores were counted. Raw count data are presented in Table 4.2. Percentage data are shown in Figure 4.1. Raw count data are equivalent to concentration data as the same number of *Lycopodium* spores were counted in each sample. The rotifer *Habrotrocha angusticollis* was included in the count.

Preparation A is a modification of Tolonen (1986), with the smaller sieve size (300µm), discussed above plus a micro-sieve (15µm) to remove fine detritus and improve slide clarity. Preparations B, C and D are standard pollen preparations (Moore *et al.*, 1991), with variations in alkali treatment and acetylation periods. Preparation B includes a 300µm sieve rather than the standard 180µm sieve used in pollen preparation, to see if additional testates were recovered. Preparation E is a simple KOH digestion. KOH alone can produce reasonable pollen slides from certain peats (Moore *et al.*, 1991), although the quality of pollen grains and spores may not always be as good as when the samples are acetolysed. This technique may therefore be suitable for pollen and testate amoebae analysis.

Treatment	A	B	C	D	E
Boiling water (10 mins)	+	-	-	-	-
10% NaOH (10 mins)	-	+	-	+	-
10% KOH (10 mins)	-	-	+	-	+
Acetylation (10 mins)	-	+	-	-	-
Acetylation (3 mins)	-	-	+	+	-
Sieve (300µm)	+	-	+	-	+
Sieve (180µm)	-	+	-	+	-
Micro-sieve (15µm)	+	-	-	-	-

Table 4.1 Summary of treatments for sample preparation, + indicates treatment carried out

Species	Preparation A						Preparation B						Preparation C						Preparation D						Preparation E																				
	1	2	3	4	5	6	1	2	3	4	5	6	1	2	3	4	5	6	1	2	3	4	5	6	1	2	3	4	5	6	1	2	3	4	5	6									
<i>Amphitrema flavum</i>	23	40	29	20	13	5	4	10	5	2	3	2	2	5	10	5	4	3	5	7	6	1	76	70	41	31	5	2	32	14	2														
<i>Amphitrema wrighianum</i>	44	35	3	4	2							1																																	
<i>Arcella discoides</i> type	2	1	2	2	1	1	5	2	13	1	12	4	10	1	7	2	1	1	1						1																				
<i>Arcella gibbosa</i>	8	61	18	13	4	13	18	10	19	6	3	26	23	5	17	4	13	26	11	16	11	6	10	146	67	21	2																		
<i>Assulina muscorum</i>	3	7				1										4	2	2	2	1	6	14	4																						
<i>Assulina semimilium</i>	1	3	116	82	86	41	1	1	3	1	1	3	1	1	2	1	2	1	1	2	537	295	86	29																					
<i>Diffugia pulex</i>	5	12	25	13	9	7						1	2	1					24	11	4																								
<i>Cyclopyxis arcelloides</i> type	6	13	17	15	9	1													4	39	70	69	24	28																					
<i>Diffugia prisnis</i> type	1																																												
<i>Euglypha rotundata</i> type	3	2																		10	3	1																							
<i>Heleopera petricola</i>	2	1																		29	10	10	2																						
<i>Hyalasphenia subflava</i>	2	1																																											
<i>Nebela flabellatum</i>	29	1																																											
* <i>Habrotrocha angusticollis</i>																				59	7	1	1	1	1																				
<i>Amphitrema stenostoma</i>																				6	27	3																							
<i>Bullimularia indica</i>																				8																									
<i>Centropyxis aculeata</i> type																				1																									
<i>Trigonopyxis arcuata</i>																																													
Total	124	172	240	160	131	62	21	32	21	24	22	3	32	30	23	36	22	6	33	41	28	28	19	11	189	322	794	462	140	68															

Table 4.2 Raw data from preparation experiments. **Habrotrocha angusticollis* is a rotifer

Results

Table 4.2 presents raw count data. Table 4.3 summarises the counts from each of the five treatments in terms of the taxa represented and Figure 4.1 presents percentage diagrams. The taxonomy presented here varies slightly from that in Hendon and Charman (1997) as the taxonomy has been modified in line with Charman, Hendon and Woodland (in prep.). The percentage diagrams are a useful representation of the sorts of differences which would occur in conventional presentation of results from different procedures. However, this can be misleading, as for example, *Hyalosphenia subflava* comprised less than ten percent of sample 3 in preparation A, although 22 tests were counted. However, in preparation C, on the same sample only four tests of this species were counted, but this comprised almost 20% of the total count. For this reason, the raw counts are better for comparing the different types of preparation procedure.

Pollen preparations B-D

In all three pollen preparation experiments with acetylation, only approximately one fifth of the potential tests were recovered, when compared to the testate amoebae preparation (A). An acetylation time of ten minutes may be slightly more destructive than a three minute acetylation, but a significant number of tests and half the potential diversity of species are still destroyed even with this less harsh treatment. Whether NaOH or KOH is used for the deflocculation of peat prior to acetylation does not appear to affect the outcome, as preparations C and D have very similar results at the same length of acetylation. In these samples the mesh size does not appear to make any significant difference because none of the larger species of testate amoebae are present; with other peat samples it is likely to do so. A 300 μ m mesh is recommended over 180 μ m where the loss of tests is more likely.

All three of these treatments show a loss or large reduction in the species *Arcella gibbosa*, *Diffugia pristis* type, *Euglypha rotunda*, *Heleopera petricola*, *Nebela flabulellum* and *Cyclopyxis arcelloides* type. Of these, the loss of *D. pristis* type is especially severe as it is present consistently and in high concentrations in preparations A and E. The contrast between preparations E and B-D confirms that acetylation is the most damaging treatment and may particularly affect agglutinated taxa such as *D. pristis* type.

Taxa	Treatment				
	A	B	C	D	E
<i>Amphitrema flavum</i>	+	+	+	+	+
<i>Amphitrema wrightianum</i>	+	-	+	+	+
<i>Arcella discoides</i> type	+	+	+	+	+
<i>Arcella gibbosa</i>	+	-	-	-	+
<i>Assulina muscorum</i>	+	+	+	+	+
<i>Assulina seminulum</i>	+	+	-	+	+
<i>Diffugia pulex</i>	+	+	+	+	+
<i>Cyclopyxis arcelloides</i> type	+	-	+	-	+
<i>Diffugia pristis</i> type	+	-	-	-	+
<i>Euglypha rotunda</i> type	+	-	-	-	-
<i>Heleopora petricola</i>	+	-	-	-	+
<i>Hyalosphenia subflava</i>	+	+	+	+	+
<i>Nebela flabulellum</i>	+	-	-	-	-
* <i>Habrotrocha angusticollis</i>	+	-	+	+	+
<i>Amphitrema stenostoma</i>	-	-	-	-	+
<i>Bullinularia indica</i>	-	-	-	-	+
<i>Centropyxis aculeata</i> type	-	-	-	-	+
<i>Trigonopyxis arcula</i>	-	-	-	-	+
Total no. counted in 6 samples	835	123	146	150	1744
Total no. taxa	14	6	8	8	16

Table 4.3 Summary of taxa recorded in six samples from the five preparation treatments. The taxa are identified to species level except where named as a 'type', when more than one species may be represented. Taxonomy follows Charman, Hendon and Woodland (in prep.). **Habrotrocha angusticollis* is a rotifer.

The loss of some taxa is not a problem, as long as their absence is not used in reconstructions of water tables and moisture content. However, for those species present in moderately high concentrations, it is evident that concentrations are reduced (e.g., *Amphitrema flavum*). Moreover, when percentage diagrams are compared (Figure 4.1), preparations B-D give very different results to those in preparations A and E. Surviving taxa are over-represented (*Arcella discoides* type, *Amphitrema flavum* and *Assulina muscorum*) and some trends in the diagram are changed. For example, an increasing curve in *A. flavum* (Preparation A) appears as a reducing curve in preparations B-D. Although counted totals are low, this suggests that testate amoebae counts from such preparation procedures are unlikely to be reliable.

Preparations A and E

The results from preparations A and E are comparable based on the concentrations and total number of taxa recorded and are clearly superior in terms of the quality of the record.

However, there are a number of important and surprising differences between the results of the two procedures. The species assemblage of both sets of preparations are similar, although four species present in preparation E are absent from preparation A and two species present in preparation A are absent from preparation E. However, these are all taxa which have very low counts (<3% of total) and these differences are probably an artefact of the count totals used. Normally counts of 150 tests are achieved, as this has been shown to represent the fauna adequately (Woodland, 1996). Using 200 *Lycopodium* as a count total means that some counts fall below this criteria. The patterns of change in the percentage diagrams are almost identical, with the exception of a larger count of *D. pristis* type in the basal sample of preparation E. This appears anomalous and could be due to a real difference in the samples, as biostratigraphic change may not be exactly horizontal in the core. Homogenisation of the samples prior to splitting into replicates would have avoided this problem.

The most striking difference between the preparations is that concentrations in E are almost twice those of A. This is perplexing, as preparation A is theoretically the least damaging of the procedures. The most likely explanation is that KOH treatment disperses the sediment more effectively than disaggregation in boiling water. As a result, a significant amount of tests are retained on the 300µm sieve reducing the overall concentration counted in preparation A. From comparison with the KOH treatment, this does not appear to affect taxa differentially. Both procedures appear to yield good quality data but the counting of treatment E was hampered by poor test preservation. Tests appeared damaged and many features were altered or removed. This did not result in a total impediment to identification but problems could occur in some species assemblages where identification is more difficult. In addition, where original preservation is poor, further damage may make identification impossible.

Conclusion

These preparation experiments demonstrated clearly that both the concentration and number of testate amoebae taxa recorded in samples subjected to conventional pollen analysis will be severely reduced. Whether expressed as concentration or percentage diagrams, the data are unlikely to represent real changes in the fossil record. Large changes in species assemblages may be detected, but it seems unlikely that relatively subtle fluctuations in abundance will be found. To avoid the selective destruction of

testate amoebae species and the destruction of as much as 80% of the potential assemblage, it is recommended that tests are never counted in conjunction with pollen analysis. Of the species found in every type of preparation, it is interesting to see that *A. flavum* and *A. muscorum* are present in each type of pollen preparation, albeit under-represented when compared to the water based preparation. There is no correspondence between the nature of test construction and the level of test destruction from chemical treatments.

The remaining treatments both give good results for these particular samples. However, the KOH treatment may produce unacceptable damage in some cases and makes identification of tests more difficult. The introduction of back-sieving with a 15µm mesh, after sieving with a 300µm mesh, to remove fine fraction detritus, humic acids, salts and other colloids greatly improves the clarity of the microscope slides. In this study, it has been especially useful in highly humified peats, which tend to produce slides with a large proportion of fine detritus. Although it is not possible to quantify the level of improvement, small tests such as *D. pulex* that are often masked by detritus are far easier to count after micro-sieving. Generally, the counting is more efficient without any addition to the length of the preparation procedure. The time taken to micro-sieve is compensated for by the reduced length of time taken to centrifuge the samples in order to be left with the concentrate. The procedure below, modified from Tolonen (1986), Warner (1990) and Woodland (1996) is therefore recommended as being the most efficient and accurate for work with subfossil testate amoebae. This method was adopted in the research described in this thesis.

Preparation procedure

- 1** Subsample peat core and place a known weight (*e.g.*, 2g) in a 250ml beaker.
- 2** Add three tablets of the inoculum *Lycopodium clavatum* L. (Stockmarr, 1971) as an exotic marker to give quantitative rhizopod analysis.
- 3** Boil the samples in 150ml distilled water for 10 minutes and stir occasionally to disaggregate the peat.
- 4** Wash each sample through a coarse sieve (300µm mesh) to remove the coarse detritus and back-sieve through 15µm mesh to remove the fine fraction detritus with distilled water. Retain material between 15µm and 300µm.

- 5 Wash the remains of each sample into centrifuge tubes and centrifuge at 3000rpm for five minutes.
- 6 Pour off supernatant and stain the concentrate of tests with two drops of safranin-O, wash twice with distilled water.
- 7 Store the concentrate in glycerol, in stoppered vials.
- 8 Smear a small drop of concentrate onto a microscope slide and cover with a 50mm coverslip, seal with clear nail varnish. A new pipette is required for each sample to avoid contamination (Tolonen, 1986).

Mounts are made with microscope slides rather than counting from a petri-dish (*e.g.* Medioli and Scott, 1983; McCarthy *et al.*, 1995), as all of the smaller species are unlikely to be picked out from a petri-dish. The method recommended by Scott (pers comm.) involves wet sieving through a 45 μ m sieve (63 μ m sieve, Medioli and Scott, 1983) to remove organic detritus and picking from an open petri-dish. This is a suitable technique for lacustrine samples with large tests, but most peatland taxa are too small (<63 μ m) to be identified under a low-power microscope. Recent work on saltmarsh faunas shows a large increase in diversity and concentration of tests when the <63 μ m fraction is analysed and compared to the >63 μ m fraction (Charman *et al.*, 1998, in press).

The counting of the tests was undertaken along systematic transects on an Olympus Microscope at x400 magnification, under plain transmitted light and at x1000 under oil immersion for difficult tests. Warner (1990) recommended a minimum count of 200 tests per level and no less than 100 to achieve a reasonable representation of the diversity of species in the fossil fauna assemblage. However, Woodland (1996) found that counts of 150 tests were sufficient to gain a representative sample of the fauna. This number was achieved by recording the number of individual tests and taxa counted per sample and plotting these data cumulatively. The plots show a large increase in species diversity early in counting, but as the number of individuals counted increases, the species diversity stabilises. Counts in excess of 150 tests are unlikely to identify additional species that would be significant to the assemblage. In this study, 150 tests per level were counted, or one thousand *Lycopodium* innoculum, where the concentration was too low to make the former possible. The rotifer *Habrotrocha*

angusticollis was included in addition to the testate amoebae counted, as this is considered to be an indicator of extreme wetness (de Graaf, 1956; Tolonen, 1966). However, *H. angusticollis* was left out of all data processing, as there is no modern analogue value for it.

4.1.3 Pollen preparation procedure

Skeleton pollen analysis was undertaken on all cores to enable biostratigraphical correlation of the radiocarbon dates within the sites. Correlation is based on assemblage biozones characterised by particular pollen taxa. The temporal dimension involves the study of the biostratigraphy of each core, the spatial correlation involves comparing the cores within and between the sites. Pollen samples were taken every 20cm and at higher resolution (every 5cm) at the anthropogenic *Pinus* rise (APR) at the top of each profile. Assuming an accumulation rate of 10 years per centimetre, there is *ca.* 200 years between pollen samples, which is a low resolution but provides an indication of the major changes in vegetation history. One hundred and fifty land pollen (TLP) were counted at each level along with aquatics and spores. Preparation followed Moore *et al.* (1991) and taxonomy followed that of Stace (1995).

4.1.4 Taxonomic problems

The taxonomy of testate amoebae is not straightforward (Meisterfeld, 1979). There has been a lack of clear, recent guides to identification, with publications based on modern specimens not fossil material. The identification guides that have been published are often not ideal for routine counting, with the line drawings of Ellison and Ogden (1987) often lacking crucial detail and the SEMS used by Ogden and Hedley (1980) and Ogden (1980, 1983, 1984) often difficult to translate for use during light microscopy.

Descriptions of extant taxa are confused and descriptions of the same species by different authors can be contradictory, with similar or identical specimens given different names. This leads to inconsistency. Furthermore, early publications with the original notifications of species are often difficult to come by and can be confusing as they refer to old names for some species which have either changed or transferred to other genera. In addition to this, some notifications of new species are given with scant

notes and without illustrations. This has on occasions led to over-splitting of taxa on the basis of poor descriptions, for example, Decloitre (1962, 1976) and Gauthiere-Lièvre and Thomas (1958).

These problems which arose during the this study have been addressed by the compilation of a practical and comprehensive guide to testate amoebae which should provide a reliable means of identification that can be consistently repeated by several workers (Charman, Hendon and Woodland, in prep.). The main taxonomic issues encountered prior to the preparation of the identification guide are discussed below.

During the course of routine counting of testate amoebae, a species was recovered in large numbers that could not be identified using any of the literature held in the laboratory at that time. The taxon was thought to belong to either the genus *Diffflugia*, *Cryptodiffflugia* or *Pseudodiffflugia*, but no record could be found of it in any texts, or in the Penard slide reference collection held at The British Museum (Natural History). The test is elongate to ovoid, 50-70µm in length and is at least 1.5 times as long as broad with a small, terminal mouth. The test has a curved aboral region, is composed of agglutinated particles and is red or dark brown in colour, with occasional black fragments at the margins. Organic cement fragments and organic matter are visible. Plates of this taxon are shown in Plates 4.4 and 4.5. Plate 4.4 shows an example that has a slightly diffuse mouth. Plate 4.5 shows a specimen with a more pointed aboral region and a slightly constricted aperture. This illustrates the variations within the taxon and raises the question as to whether they are the same species, showing a natural continuum of variations, as discussed in Section 2.2.4 (*sensu* Medioli and Scott, 1983), or whether they are separate taxa.

Photomicrographs and microscope slide samples of this taxon were sent to seven academics who have each published extensively on testate amoebae recovered from peat bogs and lacustrine sediments. Suggested identifications included *Pseudodiffflugia* spp., *Diffflugia oblonga*, *D. bacillifera* *D. pristis* and *Cryptodiffflugia paludosa*. One person could not offer any suggestion as to what the identification of this species was. Two people suggested *Pseudodiffflugia* spp. as a possibility. One researcher suggested that the samples were of both *D. oblonga* and *D. bacillifera* in different communications. Another researcher could only confirm that it was probably a species of *Diffflugia*.

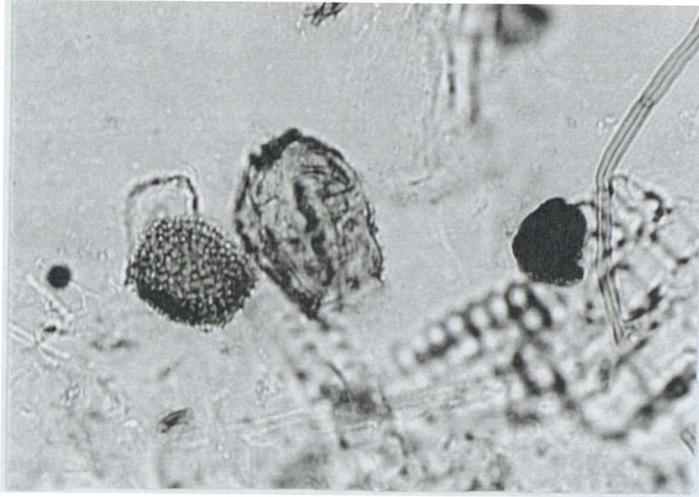


Plate 4.4 *Diffflugia pristis* type a Penard 1902. Typically 51-58 μ m long



Plate 4.5 *Diffflugia pristis* type b Penard 1902. Typically 51-58 μ m long

D. oblonga was discounted as it is generally 100-150µm in length, pyriform, about 2-3 times as long as broad, rounded posteriorly and tapering to the aperture. The test is usually coated with opaque mineral particles (Grospietsch, 1958; Gauthier-Lièvre and Thomas, 1958; Corbet, 1973; Ogden, 1983). From this description it is clear that the specimens recovered are not *D. oblonga*.

D. bacillifera is a pyriform taxon, 120-180µm in length and is coated with diatom frustules (Grospietsch, 1958; Gauthier-Lièvre and Thomas, 1958; Corbet, 1973; Ogden, 1980). Again, the specimens recovered do not fit this description.

The *Pseudodifflugias* (including: *P. fascicularis*, *P. fulva*, *P. gracilis* and *P. horrida*) are a problem to identify to species level, due to poor taxonomic treatment of the group (Warner, pers. comm.). The most likely species is *P. fulva* as it is ovoid, agglutinated and yellow to light brown. However, the length of the shell was considered too small, as it is only 15-30µm (Ogden and Hedley, 1980).

Cryptodifflugia paludosa is not included in the key for the *Cryptodifflugias* (Page, 1966), but since the generic term is applied to taxa with pseudopodia intermediate between lobose and filose, it is unhelpful for fossil studies. The suggestion that the specimens were of *Cryptodifflugia paludosa* Golemansky was discounted when samples were sent to Golemansky, who denied that they were *C. paludosa*, since it is only found in the littoral zone, not in peat or moss (Golemansky, pers. comm.) and who suggested that they were *D. pristis*.

The suggestion that the species is *Difflugia pristis* has been accepted after finding the original authority, Penard 1902 (page 254). Penard (1902) describes the test as ovoid, from 45-65µm length. The xenosomes are composed of quartz fragments and droplets of siliceous material. The mouth is terminal, rounded and relatively small. This species is now regarded as part of the *Difflugia pristis* type by Charman *et al.* a (in prep.) which also contains *D. fallax* and the taxa recorded as *D. angulostoma* and *D. pulex* by Woodland (1996).

This illustrates well one of the major problems with the taxonomy of testate amoebae. The range of possible names that may be attributed to the same species suggests that internationally, the identification of species is not uniform, in some cases the

identification being far removed from the original authority. The application of a transfer function to a species assemblage identified from the range of literature available is therefore likely to contain large variations and inherent errors. It is important that taxa in the fossil data set are identified consistently with the taxa in the training set. If the same taxa are found in both data sets but are named according to different nomenclatures, the reconstructed hydrological models will not accurately reflect mire surface wetness at the time of peat accumulation. This view is supported by Tolonen (pers. comm.) who is concerned about 'serious weaknesses in the taxonomic uncertainties among many genera'. The guide by Charman *et al.* a (in prep.) should greatly assist with solving this problem, at least for oligotrophic peatlands in the British Isles. These problems are not the same for all genera. *Diffflugia* is particularly bad, but the *Amphitrema*s and *Nebela*s are agreed on by almost all workers.

Table 4.4 is included in this chapter, since it puts into context taxa found in this study in relation to the taxonomic classification of Charman, Hendon and Woodland (in prep.). These taxa are found in the cores extracted from Coom Rigg Moss, Butterburn Flow and The Wou, and the data are presented in Chapters Five, Six and Seven respectively. The use of these descriptions of the hydrological requirements of the taxa found in this study must be approached with caution, since the methods adopted in each study vary and the mires are from very different and not necessarily directly comparable locations. The Canadian work (*e.g.* Warner 1987; Warner and Charman 1994; Charman and Warner 1997) is from continental mires, which, from their locations are expected to be drier than the oceanic mire types found in Britain. This may affect the tolerance ranges of the testate amoebae found in these varying sites and this should be remembered when using this information for interpreting the results.

Zones in the testate amoebae diagrams in Chapters Five-Seven can be interpreted qualitatively on the basis of published information. Interpretations on this basis can only be very broad, since the data are derived from studies on both oceanic and continental bog testate amoebae assemblages that may have different ecological requirements, tolerances, or affinities (Section 2.2.5). Taxa have been classified according to varying criteria in Table 2.6 and Table 4.4. Some taxa have been classified as 'wet', 'moderately wet' and 'dry', whilst others have been classified on the basis of the percentage water content of the moss polsters from which they were collected.

Taxonomic Group	Taxa Included *	Peat water content / habitat	Author
<i>Amphitrema flavum</i>		wet conditions 87.9-95.1% water content 95% water content bog pools - wet water table optimum 15.04cm water table optimum 10.27cm found with <i>A. wrightianum</i>	Tolonen 1966 Tolonen <i>et al.</i> 1985 Tolonen <i>et al.</i> 1992 Warner 1987 Warner & Charman 1994 Charman & Warner 1997 Corbet 1973
<i>Amphitrema stenostoma</i>		bog pools water table optimum 6.54cm	Tolonen 1986 Charman & Warner 1997
<i>Amphitrema wrightianum</i>		bog pools - wet 95% water content 90% water content, hydric taxon water table optimum 4.07cm	Corbet 1973 Tolonen <i>et al.</i> 1992 Warner 1989 Charman & Warner 1997
<i>Arcella artrocrea</i>		hydrophilous	Tolonen 1986
<i>Arcella catinus</i> type	<i>A. catinus</i>	uncertain status water table optimum 9.06cm water table optimum 9.81cm	de Graaf 1956 Warner & Charman 1994 Charman & Warner 1997
<i>Arcella discoides</i> type	<i>A. arenaria</i>	xerophilous submerged or very wet <i>Sphagnum</i> >95% water content very wet water table optimum 8.98cm water table optimum 0.91cm	Tolonen 1986 Tolonen <i>et al.</i> 1992 Warner 1987 Warner & Charman 1994 Charman & Warner 1997
<i>Arcella vulgaris</i>	<i>A. rotunda</i> var <i>aplanata</i>	hydrophilous	de Graaf 1956
<i>Assulina muscorum</i>		common - both bog and fen <i>Sphagnum</i> xerophilous tendency 85-90% moisture content hydro-xerophilous taxon cosmopolitan water table optimum 42.53 water table optimum 17.44cm	Corbet 1973 de Graaf 1956 Tolonen <i>et al.</i> 1992 Warner 1987 Warner 1990 Warner & Charman 1994 Charman & Warner 1997
<i>Assulina seminulum</i>		hygrophilous bog hummocks water table optimum 39.29cm water table optimum 13.95cm	de Graaf 1956 Corbet 1973 Warner & Charman 1994 Charman & Warner 1997
<i>Bullinularia indica</i>		xerophilous bog hummocks xerophilous taxa, hummock <i>Sphagna</i> xerophilous taxa, <85% water content	de Graaf 1956 Heal 1964 Tolonen 1966 Tolonen 1986 Tolonen <i>et al.</i> 1992
<i>Centropyxis aculeata</i> type		aquatic habitats aquatic habitats hydrophilous taxa very wet conditions water table optimum 24.35cm water table optimum 6.18cm	de Graaf 1956 Schönborn 1962 Tolonen 1986 Warner 1987 Warner & Charman 1994 Charman & Warner 1997 de Graaf 1956
<i>Centropyxis cassis</i> type	<i>C. cassis</i> <i>C. aerophila</i> type <i>C. aerophila</i> var <i>sphagnicola</i> <i>C. aerophila</i> var <i>sylvatica</i>	hygrophilous, submerged & wet mosses water table optimum 20.53cm water table optimum 5.16cm	Warner & Charman 1994 Charman & Warner 1997
<i>Cyclopyxis arcelloides</i> type	<i>C. arcelloides</i>	moderately dry, 78-89% water content <80% water content moderately dry, 78-89% water content ponds, shallow peatland pools and very wet <i>Sphagnum</i> soils - water table optimum 32.01cm water table optimum 4.69cm	Warner 1987 Warner 1989 Warner 1990 Warner & Charman 1994 Charman & Warner 1997
	<i>Centropyxis eurystoma</i> <i>C. minuta</i> <i>Phryganella acropodia</i>	moderately wet, 90-95% water content moderately wet, 90-95% water content dry mosses moderately dry conditions	Warner 1987 Warner 1990 Schönborn 1962 Meisterfeld 1977

<i>Diffugia acuminata</i> <i>Diffugia bacillifera</i>		bog pools hydrophilous taxon <i>Sphagnum</i> pools hydrophilous taxa bog pools water table optimum 2.19cm aquatic habitats	Cash & Hopkinson 1909 de Graaf 1956 Cash & Hopkinson 1909 de Graaf 1956 Corbet 1973 Charman & Warner 1997 de Graaf 1956 Cash & Hopkinson 1909
<i>Diffugia globulosa</i> <i>Diffugia lanceolata</i> <i>Diffugia leidy</i> <i>Diffugia lucida</i> <i>Diffugia oblonga</i> type	<i>D. oblonga</i>	very wet <i>Sphagnum</i> water table optimum 11.00cm water table optimum 5.25cm	de Graaf 1956 Warner & Charman 1994 Charman & Warner 1997
<i>Diffugia pristis</i> type	<i>D. pristis</i> <i>D. angulostoma</i> <i>Cryptodiffugia paludosa</i> <i>D. fallax</i>	aquatic	Cash & Hopkinson 1909
<i>Diffugia pulex</i> <i>Diffugia rubescens</i>		hydrophilous	de Graaf 1956
<i>Euglypha rotunda</i>		damp & wet mosses water table optimum 38.91cm water table optimum 18.41cm bog hummocks	Hedley & Ogden 1973 Warner & Charman 1994 Charman & Warner 1997 Heal 1961
<i>Euglypha strigosa</i> <i>Euglypha tuberculata</i>		water table optimum 36.55cm water table optimum 14.43cm	Warner & Charman 1994 Charman & Warner 1997
<i>Heleopera petricola</i>		very wet <i>Sphagnum</i> ecology variable and disputed ecology variable and disputed 95% water content water table optimum 31.08cm water table optimum 7.27cm bog hummocks and drier <i>Sphagnum</i>	de Graaf 1956 Tolonen 1986 Warner 1987 Tolonen <i>et al.</i> 1992 Warner & Charman 1994 Charman & Warner 1997 Jung 1936
<i>Heleopera rosea</i> <i>Heleopera sphagni</i> <i>Heleopera sylvatica</i>		β -hydrophilous taxon drier mosses water table optimum 23.37cm water table optimum 23.22cm	de Graaf 1956 Tolonen 1986 Warner & Charman 1994 Charman & Warner 1997
<i>Hyalosphenia elegans</i>		very wet to wet <i>Sphagnum</i> , α - <i>hydrophilous</i> bog hummocks 95% water content moderately wet, 90-95% water content water table optimum 26.26cm water table optimum 21.59cm	de Graaf 1956 Corbet 1973 Tolonen <i>et al.</i> 1992 Warner 1987 Warner & Charman 1994 Charman & Warner 1997
<i>Hyalosphenia papilio</i>		very wet <i>Sphagnum</i> wet <i>Sphagnum</i> in bog hummocks 95% water content moderately wet, 90-95% water content >90% water content moderately wet, 90-95% water content water table optimum 9.87cm water table optimum 17.74cm	de Graaf 1956 Heal 1961 Tolonen <i>et al.</i> 1992 Warner 1987 Warner 1989 Warner 1990 Warner & Charman 1994 Charman & Warner 1997
<i>Hyalosphenia subflava</i>		moderately dry, 78-89% water content, <80% water content water table optimum 49.92cm water table optimum 22.81cm	Warner 1987 Warner 1989 Warner & Charman 1994 Charman & Warner 1997
<i>Lesquereusia</i> spp.		hydrophilous	de Graaf 1956
<i>Nebela barbarata</i> <i>Nebela carinata</i>		hydrophilous taxon wet or very wet <i>Sphagnum</i> bog pools water table optimum 1.09cm	de Graaf 1956 Jung 1936 Heal 1964 Charman & Warner 1997 de Graaf 1956 Warner 1987
<i>Nebela collaris</i>		moderately dry conditions moderately wet, 90-95% water content	de Graaf 1956 Warner 1987
<i>Nebela flabellulum</i> <i>Nebela griseola</i> <i>Nebela marginata</i>		<i>Sphagnum</i> in bog hummocks water table optimum 30.04cm very wet to aquatic <i>Sphagnum</i> water table optimum 11.14cm α -hydrophilous taxon water table optimum 6.89cm	Corbet 1973 Charman & Warner 1997 Heal 1964 Charman & Warner 1997 de Graaf 1956 Charman & Warner 1997

<i>Nebela militaris</i>		drier mosses wet <i>Sphagnum</i> of bog hummocks water table optimum 41.85cm	de Graaf 1956 Corbet 1973 Warner & Charman 1994
<i>Nebela parvula</i>		water table optimum 20.66cm very dry conditions	Charman & Warner 1997 Warner 1987
<i>Nebela tinctoria</i>		water table optimum 27.58cm water table optimum 6.98cm xerophilous, <85% moisture content	Warner & Charman 1994 Charman & Warner 1997 Tolonen <i>et al.</i> 1992
<i>Nebela tubulosa</i>		very wet water table optimum 32.63cm water table optimum 11.67cm	Warner 1987 Warner & Charman 1994 Charman & Warner 1997
<i>Placosista spinosa</i>		bog pools water table optimum 7.44cm	Corbet 1973 Charman & Warner 1997
<i>Pseudodifflugia fascicularis</i>		aquatic	Cash & Hopkinson 1909
<i>Sphenoderia lenta</i>		α -hygrophilous - wet <i>Sphagna</i> 85-90% moisture content moderately dry, 78-89% water content moderately dry, 78-89% water content water table optimum 5.86cm	de Graaf 1956 Tolonen <i>et al.</i> 1992 Warner 1987 Warner 1990 Charman & Warner 1997
<i>Trigonopyxis arcuata</i>		xerophilous taxa water table optimum 57.68cm water table optimum 15.58cm	de Graaf 1956 Warner & Charman 1994 Charman & Warner 1997
<i>Trinema lineare</i>		hygrophilous taxa	de Graaf 1956

Table 4.4 Taxa found in this study compared to taxa classifications in *Charman *et al.* (in prep.) and their hydrological requirements

Some qualitative information about taxa is contradictory or ambiguous. For example, *Nebela militaris* was found to occur in 'drier mosses' (de Graaf, 1956), whilst Corbet (1973) found it in 'wet *Sphagnum* of bog hummocks'.

The classification of Charman, Hendon and Woodland (in prep.) contradicts some qualitative information about certain taxa, but has been classified in this way to create a workable identification system for fossil material from British mires.

Cyclopyxis arcelloides type, including *C. arcelloides*, *Centropyxis eurystoma*, *C. minuta* and *Phryganella acropodia* have been varyingly described as taxa from moderately dry, 78-89% water content (*C. arcelloides*, Warner, 1987; 1990), very wet *Sphagnum* soils (*C. arcelloides*, Warner and Charman, 1994), moderately wet, 90-95% peat water content (*Phryganella acropodia*, Warner, 1987; 1990) and dry (*Phryganella acropodia*, Schönborn, 1962; Meisterfeld, 1977). Bearing these limitations in mind, the testate amoebae diagrams can be loosely described from these qualitative data. Hydrological data from Woodland (1996) are not included in these descriptions since the data are used in the hydrological reconstructions of depth to water table and percentage moisture content.

Taxa with no, or poor, modern analogue values are discussed in Chapter Eight. These include, *Hyalosphenia subflava* and *Diffflugia pulex*. The term 'modern analogue value' is referred to throughout, because where taxa have no modern analogue value in the transfer function, it does not necessarily mean that these species have no modern analogue in contemporary mire surfaces, just that they were not found in the samples used to create the transfer function by Woodland (1996). If a wider range of sites was sampled, it is likely that those taxa currently omitted from the transfer function could be assigned optima and tolerance values.

4.1.5 Radiocarbon dating

Radiocarbon dating was used to date significant changes to the species assemblage of testate amoebae and large fluctuations in the water tables. A total of 29 dates were used to establish a firm chronology both within each site and between the sites. Originally, it was envisaged that eight dates would be required from the central core from each of the three sites. This would be used as a 'master core', with the other cores being correlated using the pollen spectra. The difficulties of radiocarbon dating recent peats may be compensated for by the use of pollen markers, especially the pine rise due to large scale planting on country estates around 1800AD and changes in farming practices (Oldfield, 1963; Barber, 1981). The use of master cores was amended, since the pollen spectra were difficult to correlate clearly apart from at a few depths (see Chapter 5, Section 5.5.1). In addition, since only one core from The Wou, core TW II, was analysed fully due to extremely poor test preservation and concentration in places, it was felt necessary to re-evaluate the dating strategy and concentrate instead on Coom Rigg Moss and Butterburn Flow, with only two dates allocated to The Wou to enable basic correlations.

Radiometric dating was chosen as there was enough material for bulk dating after material had been removed for other analytical procedures. Samples were wrapped in the field as described in Section 3.2. Cores were either kept in cold storage (6°C) or frozen. After sub-sampling for testate amoebae analysis most cores were refrozen. Samples for dating were 5cm thick, with the exception of CRM I 40-42cm which was only 2cm thick due to being extracted from the Wardenaar sampler and TW II 100-115cm which was 15cm long because the core extracted was exceptionally thin. Average weight was *ca.* 150g and it was assumed that with 95% water content and 50%

carbon content, each sample would yield approximately 3.75g carbon. Samples were taken following the guidelines of Pilcher (1991) and were sent to the NERC Radiocarbon Laboratory, East Kilbride, wrapped in foil and sealed in plastic. Pre-treatment of raw samples prior to isotope analyses involved digestion of the raw samples in 2ml HCl at 80°C for 24 hours. Samples were then washed free of acid, filtered and dried to a constant weight in a drying oven (NERC Radiocarbon Laboratory preparation protocol).

Calibration of ¹⁴C dates

The ¹⁴C age may be calibrated to an approximate calendar year using the CALIB 3.0.3c program of the Quaternary Isotope Laboratory, University of Washington (Stuiver and Reimer, 1993a,b). Calibration is undertaken to reduce distortion of chronologies and interpretation due to variations between calendar and radiocarbon ages, which is a result of variable ¹⁴C production through time (Bartlein *et al.*, 1995). The accepted value from the calibration of radiocarbon ages is the median point, which is a way of averaging the data, although the actual age of the sample may fall anywhere within the range. The process of calibration acts to increase the range of possible error within each age while converting the measure of ¹⁴C in a sample to an approximate calendrical age (Shore *et al.*, 1995).). 2σ confidence limits are given in Calibrated Years BP (Table 4.5).

Once dates have been calibrated, the term Calendar Years is not used here. Instead, dates are referred to as Calibrated Age BP (Before Libby's 1950) because Calendar Years implies a level of accuracy which is spurious. Radiocarbon ages tend to be younger than calendar ages over most of the past 20Ka (Bartlein *et al.*, 1995) and there are problems of relating events in a radiocarbon dated profile with events of known calendar age (Dumayne *et al.*, 1995).

Interpolated age per sample

There are two main ways of estimating the age of samples from the radiocarbon dates, these are; a) to interpolate linearly between dates, thereby accepting that the peat accumulation rate can vary throughout the profile and assuming that the radiocarbon dates are correct. This assumes that the location of the dates are points of major change in the rate of peat accumulation. Or, b) to fit a linear or polynomial regression line between the dates. This does not allow for non-systematic variation in accumulation rates, but accepts that the radiocarbon dates are not always accurate by spreading the

error evenly about the points, giving less emphasis to individual dates. Use of a linear regression line also puts too much emphasis on the end dates. For BBF I, the linear regression on median calibrated radiocarbon ages gave an R^2 value of 0.9989, *i.e.*, greater than 95% confidence and therefore better than linear interpolation between adjacent points. Similarly, the R^2 value for linear regression of dates for CRM I was 0.9729 and for CRM IV was $R^2=0.9924$. However, it was decided to use linear interpolation between adjacent dates *c.f.* Bennett (1994), since it was felt necessary to take into account variations in the peat accumulation rate for the hydrological reconstructions to be interpreted more accurately. Accumulation rate estimates are however, crude.

The linear interpolation of median calibrated radiocarbon ages and anthropogenic *Pinus* rise (APR) from which the estimated ages of each sample were calculated are presented for each core, in Chapters, Five, Six and Seven. The calibrated age BP was plotted at the mid-point from which the date was taken, *i.e.*, for date CRM I 40-42cm, the date was plotted at 41cm for linear interpolation of sample ages. This spreads the estimated ages evenly about the radiocarbon dates. The axes cross at zero years BP (1950) with post-1950 dates plotted as minus figures. Sample ages are estimated by calculating the gradient of the line between adjacent pairs of dates and using the equation of the line, set out for each core to calculate the approximate calibrated age per sample. Sample ages for levels below the basal date are extrapolated from the deepest date. Water table reconstructions and TILIA diagrams are plotted against the median calibrated age, converted to approximate calendar years BC/AD.

It is necessary to establish the error in the data to a) establish the reliability of the results; b) enable comparisons of results within sequences or between profiles; and c) help to identify points in the data collection and analysis process that are the main sources of error and attempt to avoid or mitigate these sources (Bennett, 1994). Errors on individual estimates of age are calculated by interpolating between the maximum and minimum calibrated ages. These are plotted as ranges, since the actual sample age may fall anywhere within the maximum and minimum range from the calibrated radiocarbon date. This is, however, approached with caution, since calculating errors on estimated ages involves inherent errors at several stages of the calculation.

Programs such as DEP-AGE (Maher, 1992), are available to create age-depth plots which can calculate sample ages by fitting a variety of exponential, linear and cubic spline regressions and estimate the age of each sample depth by interpolation. This involves extrapolation of ages to the base of the core beyond the last date. Deposition time is calculated from the gradients between adjacent pairs of points and interpolated ages read off for intermediate depths. This technique is superficially crude (Bennett, 1994), but provides a reasonable estimate for both ages and accumulation. However, the method takes no account of errors on radiocarbon ages and is inadequate when confidence intervals on ages are obtained. A linear age-scale can also be generated from inputting ^{14}C ages to the testate or pollen data in TILIA (Grimm, 1982). This was not done since the interpolation carried out is either linear or polynomial, *i.e.*, is equivalent to that described above.

Potential sources of error in radiocarbon dating

Other problems that need to be taken into account are that the size of the peat sample taken for radiocarbon dating will affect the accuracy of the date. The smaller the sample dated, the greater the effect of any contaminant present (Shore *et al.*, 1995). Most samples in this study were 5cm long, with the exception of CRM I 40-42 which was only 2cm long and TW II 100-115 which was 15cm long. CRM I 40-42 will have less potential for error being a shorter sample, but the date for TW II 100-115 will be averaged over a greater size of sample. A 5cm sample, assuming at least 10 years peat accumulation per centimetre spans a minimum period of 50 years, which cannot result in a precise date being obtained. There are also potential errors from carbon contamination, changes in atmospheric carbon composition, decomposition of plant material and the movement of older carbon up the water column, (*e.g.* Methane gas). Carbon may be partially derived from rotting organic matter not from the atmospheric carbon. Inwash of older organic carbon detritus giving the risk of the 'reservoir effect' in dated samples (Olsson, 1986) is unlikely to be a problem on ombrotrophic mires but there is a potential risk of this occurring in runoff and through flow entering a valley mire.

Site	Core	Laboratory Code	Depth (cm)	Conventional Age ¹⁴ C yr BP	δ ¹³ C ‰	Calibrated Age at 2σ confidence			
						max.	median	min.	
BBF	BBF I	SRR-5991	40-45	385 ± 45	-23.9‰	533	479	303	
	BBF I	SRR-5992	100-105	1220 ± 45	-27.4‰	1263	1067	952	
	BBF I	SRR-5993	170-175	2325 ± 40	-27.2‰	2358	2329	2144	
	BBF I	SRR-5994	300-305	3625 ± 45	-27.5‰	4077	3867	3696	
	BBF I	SRR-5995	440-445	5070 ± 45	-27.2‰	5918	5843	5646	
	BBF I	SRR-5996	550-555	6210 ± 45	-27.4‰	7204	7143	6887	
	BBF I	SRR-5997	710-715	8225 ± 45	-27.7‰	9367	9184	8959	
	BBF II	SRR-6108	50-55	540 ± 40	-27.3‰	633	521	471	
	BBF II	SRR-6109	120-125	1875 ± 40	-28.6‰	1872	1719	1570	
	BBF II	SRR-6110	250-255	4560 ± 45	-28.4‰	5317	5250	4876	
	BBF III	SRR-6111	50-55	690 ± 40	-27.8‰	672	644	534	
	BBF III	SRR-6112	130-135	2045 ± 40	-27.7‰	2104	1939	1824	
	BBF III	SRR-6113	280-285	5695 ± 45	-29.6‰	6523	6409	6295	
	CRM	CRM I	SRR-5998	40-42	270 ± 45	-23.7‰	492	306	0
		CRM I	SRR-5999	130-135	1370 ± 40	-26.9‰	1328	1278	1162
CRM I		SRR-6000	200-205	2500 ± 40	-27.8‰	2740	2471	2345	
CRM I		SRR-6001	290-295	3550 ± 40	-27.0‰	3924	3824	3634	
CRM I		SRR-6002	355-360	4585 ± 40	-27.8‰	5442	5285	4988	
CRM II		SRR-6003	45-50	375 ± 45	-25.5‰	517	461	292	
CRM II		SRR-6004	180-185	1340 ± 45	-27.1‰	1309	1263	1068	
CRM II		SRR-6005	270-275	2215 ± 40	-27.8‰	2330	2143	1994	
CRM III		SRR-6006	110-115	1285 ± 40	-28.9‰	1278	1161	981	
CRM IV		SRR-6007	30-35	250 ± 45	-25.4‰	461	291	0	
CRM IV		SRR-6008	160-165	1665 ± 45	-27.0‰	1692	1528	1359	
CRM IV		SRR-6009	220-225	2255 ± 40	-26.3‰	2347	2307	2074	
CRM IV		SRR-6010	330-335	3325 ± 40	-27.0‰	3681	3474	3378	
CRM IV		SRR-6011	385-890	3965 ± 40	-27.0‰	4521	4407	4156	
TW		TW II	SRR-6012	100-115	265 ± 45	-27.4‰	433	286	0
	TW II	SRR-6013	220-225	1340 ± 40	-28.4‰	1296	1235	1064	

Table 4.5 Radiocarbon Dates from Butterburn Flow, Coom Rigg Moss and The Wou. Dates supplied by the NERC Radiocarbon Laboratory, East Kilbride and calibrated using CALIB 3.0.3c (Stuiver & Reimer, 1993a,b)

4.2 Data analysis and presentation

4.2.1 Introduction

Data analysis was undertaken that enabled testing of the technique of testate amoebae analysis in terms of the replicability of the records and error estimation of the modelling. This entailed various stages of data analysis, a) data display; b) ordination; and c) application of the transfer function. Data analysis and display are discussed by Grimm (1988). Robust statistical methods for regression and calibration are required that adequately model the complex relationships between modern taxa and their environment (Birks, 1995). According to Gauch and Whittaker (1981), a robust method is one which gives results that are only mildly affected by sample error or noise *i.e.*, a small perturbation of sample points in random directions, and removal or addition of a small number of samples.

Multivariate numerical techniques permit simultaneous analysis of several levels of data and thus facilitate their simultaneous interpretation (Prentice, 1986; Grimm, 1988; Kent and Coker, 1992; Kovach, 1995). The data processes are split into various categories; classification, ordination and calibration. Classification involves grouping the individual samples into classes on the basis of their attributes in order to look for patterns and order in the data set (Kent and Coker, 1992). The robustness of classification according to Kent and Coker (1992: 280) is that:

“the effectiveness of a method of classification should not be dependent on the properties of a particular data set, the technique should perform well in most applications”.

The best classification is one which enables a clear ecological interpretation to be made. Numerical classification by a variety of algorithms is used to clarify relationships among taxonomic samples.

4.2.2 Testate amoebae data

TILIA (Grimm, 1982) was used to calculate percentages and the concentrations (tests per unit volume of sediment), of individual horizons from the raw count data. Rotifer counts were not included in calculations as there is no modern analogue value for them. These data were displayed using TILIA GRAPH (Grimm, 1982). Percentage diagrams were chosen to display data rather than concentration diagrams, since most counts

achieved the objective of 150 tests per level. Total test concentration curves for each sample are also presented. Where the test concentration was too small to enable counting, the horizons are left blank. TILIA diagrams in the form of histograms are the most appropriate form of graph with which to present the data, as the testate assemblages between sampling intervals are not known. Taxa are presented in alphabetical order.

Zonation

Assemblage zones were added to aid interpretation and discussion of the diagrams. In this context, an assemblage zone is taken to be a body of sediment whose fossil content constitutes a natural assemblage that is distinguishable in biostratigraphic character from adjacent strata (Gordon and Birks, 1972). CONISS, Constrained Incremental Sum of Squares Cluster Analysis, (Grimm, 1987) using percentage testate data only, was used to construct dendrograms to aid zonation. Clusters are constrained so that they only contain stratigraphically adjacent horizons. This is an agglomerative method that is satisfactory for zonation since the clusters are built up locally. Another advantage of this hierarchical method is that relationships among zones are easily examined (Grimm, 1987). The use of numerical methods to subdivide diagrams into zones is favoured by Birks and Birks (1980). This avoids subjective bias and gives consistent and repeatable results. Zonation 'by eye' and by numerical methods often agree, but there may be occasions where zonation by eye makes more sense ecologically than the zonation indicated by the dendrogram.

Dendrograms illustrate the hierarchical relationships defined by analysis (Gauch and Whittaker, 1981). The clusters may be determined by cutting the dendrogram at a given height, but this may be arbitrary. Although the dendrogram construction is objective, zonation and interpretation are still largely subjective and require visual inspection for sensible ecological interpretations.

Confidence limits can be displayed on the testate amoebae diagrams to aid their interpretation, this allows assessment of the precision of the data. Nomograms for calculating the 0.95 confidence limits of the data (Maher, 1972) could have been used. However, there are often problems in evaluating the precision of percentage diagrams, as several factors can result in imprecise data; poor test preservation, inadequate preparation techniques and misidentification. Assuming good preservation, adequate

preparation (Hendon and Charman, 1997) and competent identification, the results depend upon the number of tests in the counts. Confidence intervals make it easier to recognise levels where significant changes take place and ignore minor fluctuations whose confidence intervals overlap. This was not utilised in this study since the water table models have confidence intervals calculated for each sample from bootstrapped error estimates.

Ordination

Ordination can show trends in data and subtle relationships better than cluster analysis (Kovach, 1995), although they are complementary as they show different aspects of the same data. Ordination techniques are commonly used to reduce the variation in community composition to the scatter of samples and species in an ordination diagram (ter Braak, 1988). Detrended Correspondence Analysis (DCA) developed from the FORTRAN program DECORANA (Hill, 1979; Hill and Gauch, 1980) available in CANOCO (Canonical Correspondence Analysis, ter Braak, 1988), is an effective indirect ordination technique that solves the problems of the 'arch effect' and compression of end points at the end of the first axis associated with Correspondence Analysis (CA). (see Peet *et al.*, 1988 for a discussion of this). DCA is used to calculate a) ordination for all the species in a core, b) for individual species, c) for samples in a core and d) for samples from combinations of cores. DCA "is exceptionally robust" (Hill and Gauch, 1980) and is effective at smoothing noise. On a DCA sample plot, the greater the distance between any two points is a reflection of a smaller degree of similarity in the species composition, (Gauch and Whittaker, 1981; Kent and Coker, 1992).

Eigenvalues and percentage cumulative variance explained are presented for each ordination analysis. Eigenvalues represent the relative contribution of each component, or axis, to the explanation of the total variation in the data. The size of the eigenvalue indicates the importance of the axis in explaining the variation in the data set (Kent and Coker, 1992). In a sample ordination, the cumulative percentage variance is a measure of how much variation in the species data is explained along the axes of the ordination.

Ordination plots for modern and fossil samples, plotting fossil samples as 'passive', are included to show the 'match' or 'mis-match' between the two data sets. The reconstructed hydrological curves result in a Root Mean Square Error of Prediction

(RMSEP) for Weighted Averaging (WA) of $\pm 3.9\text{cm}$ for water table and for Tolerance downweighted weighted averaging (WA-Tol) of $\pm 3.4\%$ for moisture reconstructions, only if the overlap between modern and fossil samples is 'good' (Woodland, 1996; Woodland *et al.*, 1998). The degree of match or mis-match will affect the robustness of the hydrological curves. The better the match between modern and fossil samples, the more robust the reconstruction.

Recent discussion of ordination techniques has centred around the order of data entry and that the random rearrangement of data entry was shown by Tausch *et al.* (1995) to change ordination and classification results based on reciprocal averaging. Podani (1997) and Oksanen and Minchin (1997) further discuss this, concluding that much of the instability described by Tausch *et al.* (1995) occurs on axes 3 and 4. For DCA, the main source of instability is an order-dependent bug in the procedure for non-linear rescaling. To correct this bug requires stricter convergence criteria for stable DCA ordinations. To check the ordination plots created using CANOCO (ter Braak, 1987-1992), the programs CEP SHUFL and SOLCOMP (Oksanen and Minchin, 1997) were used and no significant variations were found in the results discussed in this study.

Transfer function

The background to and development of the transfer function used to construct depth to water table and percentage moisture content curves from testate amoebae data is discussed in Chapter Two.

Seven taxa found in the fossil data set are not included in the modern analogue transfer function. These are; *Diffflugia acuminata*, *D. lanceolata*, *D. lucida*, *D. pulex*, *Lesquereusia spiralis*, *Pseudodifflugia fascicularis* and *Sphenoderia lenta*. *D. pulex* is the only taxon that is found in abundance in all cores, so the lack of an analogue may affect the robustness of the transfer function. There is qualitative information about the hydrological requirements of *D. acuminata*, *L. spiralis*, *P. fascicularis* and *S. lenta* (Tables 2.6 and 4.4).

Bootstrapped error estimates (Efron and Gong, 1983; Birks, 1995) on predicted values allow generation of 95% confidence intervals on reconstructed water table and moisture curves using WA CALIB 3.3 (ter Braak and van Dam, 1989; Line and Birks, 1990; Birks *et al.*, 1990a; Line *et al.*, 1994). One thousand bootstrap cycles were performed on each data set. It is important to be able to assess the reliability of individual reconstructed values for each fossil sample. Bootstrapping is also a means of estimating sample specific root mean squared errors of prediction for individual fossil samples (Birks, 1995). Confidence intervals are important for comparison of water table curves within and between sites, to establish the reliability of the results and to identify points in the process of data collection and analysis that are the main sources of error (*c.f.* Bennett, 1994).

The depth to water table and moisture optima and tolerance diagrams for individual taxa in the transfer function occurring in >10% of the total data set from Woodland *et al.* (1998), are presented in Figures 4.2 and 4.3. These show the rank of taxa from the 'wettest' (*Arcella discoides* type) to the 'driest' (*Bullinularia indica*) and illustrates the concept of a 'relative wetness scale' as discussed in Section 2.2.6, as none of the taxa illustrated exist in truly 'dry' conditions, but all have tolerance ranges which are relatively wet.

Problem taxa

Problem taxa are regarded as those with either a poor, or no modern analogue value. These include the seven taxa listed above, that occur in the fossil data set, but not in the modern analogue data set. It also includes *Hyalosphenia subflava*, which has a modern analogue value, but which is probably biased towards the wetter end of the reconstruction, because all of the samples for the transfer function were extracted from very wet sites. This problem is discussed further in Chapter Eight, where more realistic optimal values for the depth to water table and percentage moisture requirements for *H. subflava* are considered and the other no-analogue value taxa discussed.

Poor-analogue taxa, mainly *H. subflava*, but also *Bullinularia indica* and *Nebela collaris*, are regarded as poor because they have broad tolerance ranges (Figure 4.2). This is a result of low abundance of these taxa present in only a small number of samples in the training set. As a result of this, where the percentage occurrence of *H.*

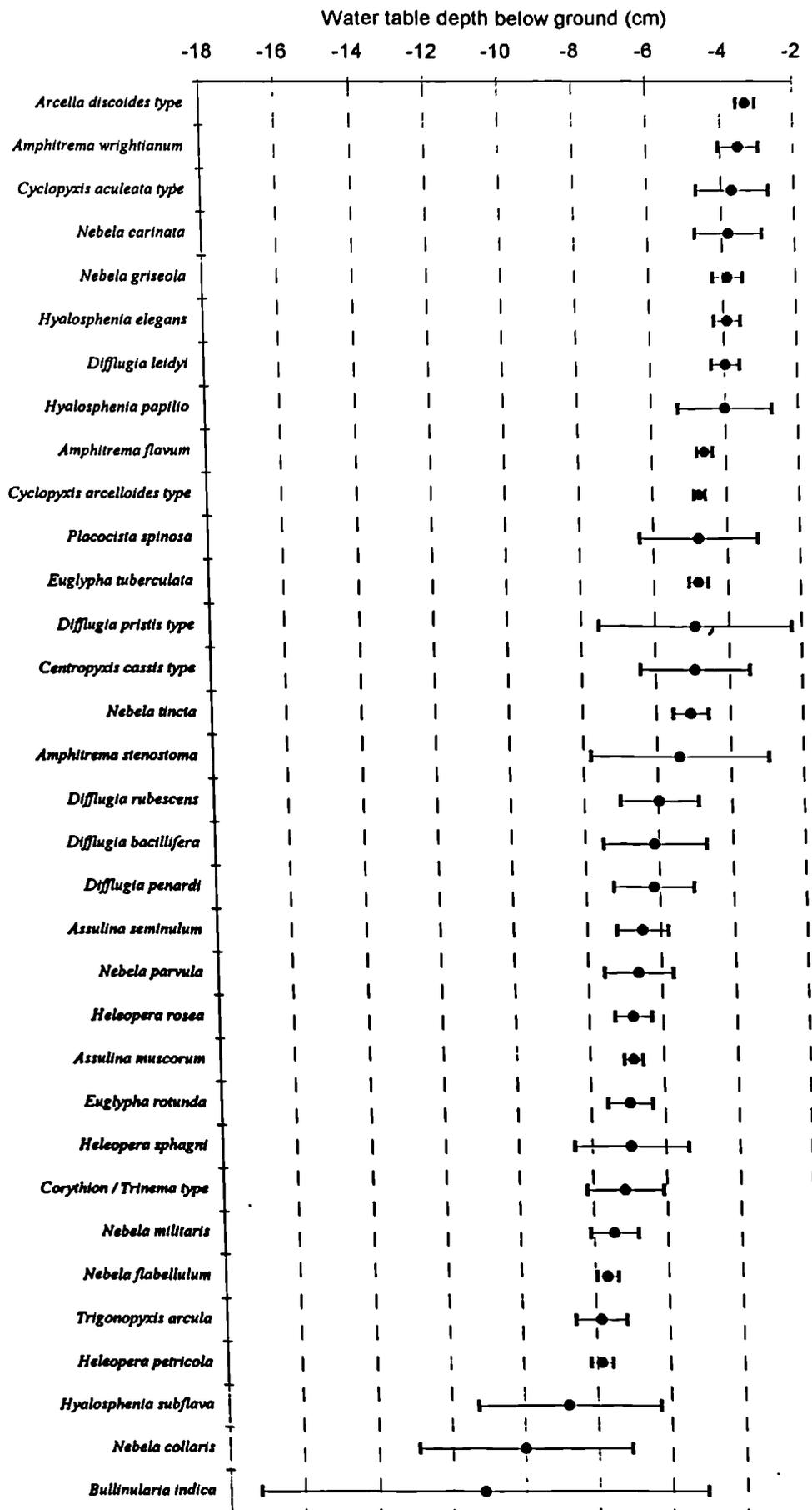


Figure 4.2 Optima and tolerance values for taxa with >10% abundance in the water table transfer function (Woodland *et al.*, 1998)

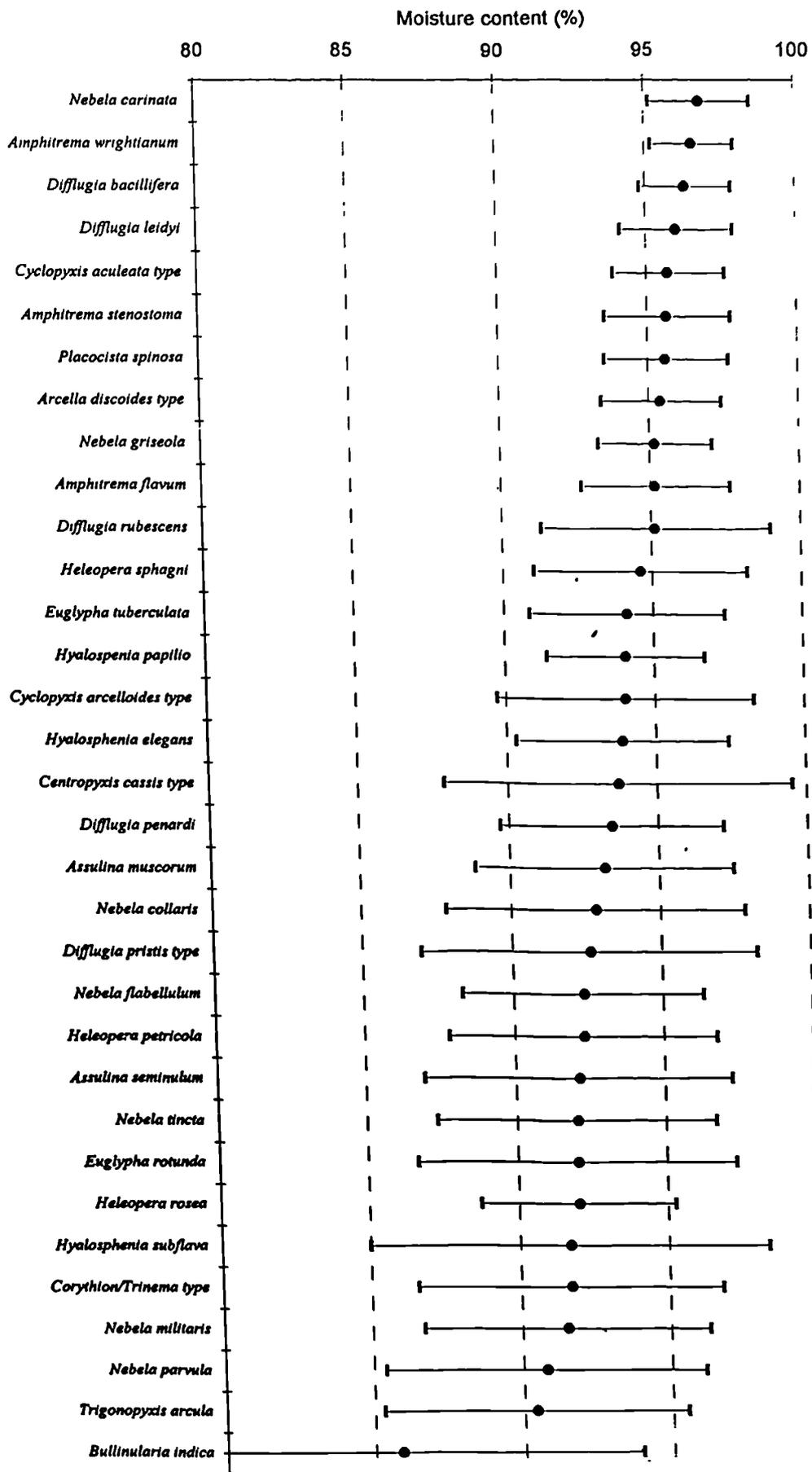


Figure 4.3 Optima and tolerance values for taxa with >10% abundance in the moisture transfer function (Woodland *et al.*, 1998)

subflava is high, the confidence limits on the hydrological reconstructions are wide. Several of the taxa found in the fossil data set were not found in the training set - these are no-analogue value taxa, principally *Diffugia pulex* and also *Pseudodiffugia fascicularis*. These taxa are not used in the hydrological reconstructions. In the computations, if there is 25% *H. subflava*, 25% *Amphitrema flavum* and 50% *D. pulex*, the water table is calculated on the basis of 50% *H. subflava* and 50% *A. flavum*. The confidence intervals are not affected by *D. pulex per se*, since there is no value for it. The reliability of the estimates is doubtful however, because there is no equivalent modern assemblage and the number of individuals used in the calculation is halved.

4.2.3 Pollen Data

Percentage pollen diagrams are presented using TILIA and TILIA GRAPH (Grimm, 1982), as discussed above for testate amoebae data. Aquatics and spores were not included in percentage or concentration calculations. SLOTDEEP (Maher, 1992) could have been used for down core correlation of the taxa to aid biostratigraphic correlation. Constraining the pollen data by the radiocarbon dates would have invalidated its use as an independent biochronological marker. The main use for the pollen is to accurately date the anthropogenic *Pinus* rise (APR), since it is known that conifer planting began in the Kielder Forest in 1926 and continued until 1960. The APR has been set at 1930, as this probably marks the initial rise above background *Pinus* levels. None of the other pollen marker horizons could be accurately correlated or be dated sufficiently to use as biochronological markers.

4.3 Conclusions

This chapter has set out the laboratory procedures used to derive the testate amoebae data and in particular looks at the issues surrounding test preparation and taxonomy. The rationale for choosing the locations of radiocarbon dates in order to obtain a well constrained chronology for each core are discussed in Section 4.1.5 and the problems surrounding radiocarbon dating are also examined. The programs used for data analysis are discussed, the results of which will be presented in Part Three.

Part Three contains the results of the stratigraphic, testate amoebae and DCA analyses. Depth to water table and moisture curves from calibration of the testate amoebae data

using the transfer function developed by Woodland (1996) are presented for each core. The interpolated ^{14}C ages for each sample are shown and the testate amoebae diagrams are presented against age.

PART THREE

Coring site results

CHAPTER FIVE

Coom Rigg Moss -

Testate amoebae and palaeohydrology

5.0 Introduction

This chapter presents the results from the four peat cores extracted from Coom Rigg Moss and is divided into two sections. The first section sets out results from individual cores plotted against depth. These results include: core stratigraphy, the testate amoebae records and ordination analyses of modern and fossil testate data. Ordinations of species assemblages and sample relationships for each core are also presented. Hydrological reconstructions of depth to water table and percentage moisture for each core derived from the testate amoebae data, calibrated using the transfer function developed by Woodland (1996) are presented. The second part of this chapter establishes the chronology for each core, using a combination of pollen marker horizons and radiometric radiocarbon dates. Pollen marker horizons were used as additional chronological markers for events with known dates attributable to them. The chronologies are used for inter-core comparisons in Chapter Nine.

5.1 Coom Rigg Moss Core I (CRM I)

Field techniques and the rationale for extracting cores from particular locations were discussed in Chapter Three. CRM I was extracted from the centre of Coom Rigg Moss in November 1994. In total, four metres of peat were extracted from CRM I. Laboratory preparation and data processing procedures were set out in Chapter Four.

5.1.1 Stratigraphy

The stratigraphy for CRM I is presented in Table 5.1. The stratigraphy for CRM I concurs with the peat description in Chapman (1964a), classified as *Sphagnum-Eriophorum* peat (see Chapter Three). Chapman (1964a) considered this to be a 'raised bog' profile, with *Sphagnum-Eriophorum* peat overlying brushwood and fen peat. This is typical of raised bog development, showing a succession from open water to fen and finally to *Sphagnum* bog and being governed by both climatic and topographic factors. Macro-fossil analyses of CRM I (Charman, Hendon and Packman, in prep.) confirmed this stratigraphic description. Stratigraphic boundaries coincided with zone boundaries

from the testate amoebae assemblages at 55.5cm and 250cm (Section 5.1.2). Below 250cm, the peat contained *Eriophorum vaginatum*, above this level, the peat was composed of very well humified *Sphagnum*. The stratigraphy suggests that the peat is very ombrotrophic from approximately 280cm.

Depth (cm)	Sediment Description
0. - 8.5	nig 1; strf 0; elas 4; sicc 2; humo 0; Tb ⁴ (Sphag). undecomposed <i>Sphagnum papillosum</i>
8.5 - 28	nig 4; strf 0; elas 3; sicc 1; humo 1; Tb ³ (Sphag); Th ¹ . <i>Sphagnum</i> peat, leaves preserved
28 - 31	nig 2; strf 0; elas 4; sicc 1; humo 1; strat 0; Tb ⁴ (Sphag). fresh, undecomposed <i>Sphagnum</i> moss, light green in colour
31 - 34	nig 3; strf 0; elas 2; sicc 1; humo 2; Tb (Sphag) ² ; Th ² <i>Eriophorum angustifolium</i>
34-55.5	nig 3; strf 1; elas 2; sicc 1; humo 2; Tb ³ (Sphag); Th ¹ <i>Eriophorum angustifolium</i>
55.5 - 77.5	nig 3; strf 1; elas 2; sicc 1; humo 1; Th ³ (Sphag); Tb ¹ ; Tl ⁺ ericoid roots and <i>Eriophorum angustifolium</i> dominant
77.5 - 100	nig 4; strf 1; elas 2; sicc 1; humo 2; Tb ¹ (Sphag); Th ³ <i>Eriophorum angustifolium</i>
100 - 140	nig 4; strf 1; elas 2; sicc 1; humo 2. Tb ³ (Sphag); Th ¹ Monocot. fragments throughout, <i>Eriophorum</i> . well humified peat matrix
140 - 190	nig 4; strf 0; elas 3; sicc 1; humo 3; Tb ³ (Sphag); Th ¹ . well humified peat matrix some indistinct monocot. fragments
190 - 212	nig 4; strf 0; elas 2; sicc 1; humo 4; Sh. very well humified <i>Sphagnum</i> peat
212 - 220	nig 4; strf 1; elas 2; sicc 1; humo 3; Tb (Sphag) ^{3/2} ; Th ^{1/2} . well humified <i>Sphagnum</i> peat, with partially decayed monocot fragments
220 - 250	nig 4; strf 0; elas 3; sicc 1; humo 4; (Sh). very well humified peat, plant structure hardly discernible, or completely absent
250 - 268	nig 4; strf 1; elas 1; sicc 1; humo 2. Tb (Sphag) ³ ; Th ¹ ; very wet peat, well humified peat matrix, but with fairly well preserved, large monocot. fragments <i>Eriophorum vaginatum</i> , 'felted' 268 - 280cm
268 - 280	nig 4; strf 1; elas 1; sicc 1; humo 2; Tb (Sphag) ² ; Th ² ; very well humified peat matrix with monocot. fragments - <i>Eriophorum vaginatum</i>
280 - 310	nig 4; strf 0; elas 2; sicc 1; humo 4; (Sh) very well humified peat
310 - 340	nig 3; strf 0; elas 1; sicc 1; humo 3; Tb (Sphag) ³ ; Th ¹ ; (ericoid roots at 340cm)
340 - 400	nig 4; strf 0; elas 1; sicc 1; humo 3; Tb (Sphag) ⁴ ; Th ⁺ . well humified peat, ericoid roots and <i>Betula</i> fragments
400-418	nig 4; strf 0; elas 1; sicc 2; Sh ⁴ + As. silt

Table 5.1 Stratigraphic description of CRM I using the Troels-Smith (1955) sediment description system

5.1.2 Testate amoebae

Of the four metres of peat extracted from CRM I, the top 370cm proved suitable for testate amoebae analysis, (Figure 5.1). From 380-400cm, slides were scanned, but the concentration of tests was poor. This may have been because conditions were

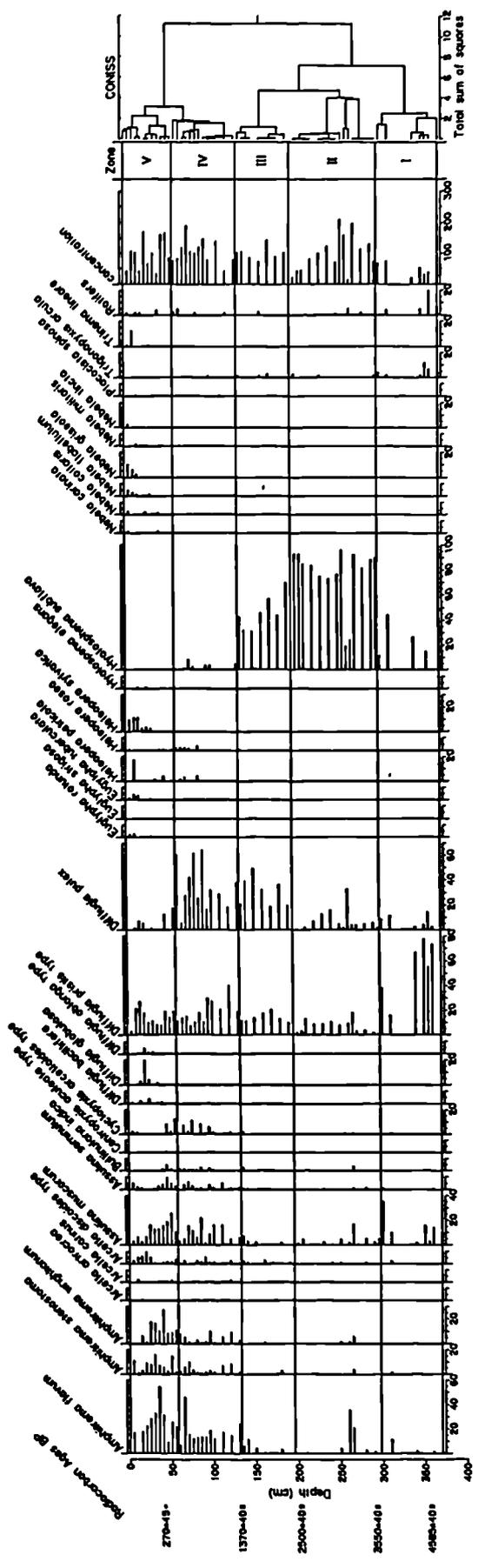


Figure 5.1 CRM I percentage testate amoebae diagram

unsuitable for test colonisation, because tests had been completely destroyed in the humification process or because there was too much material on the slides obscuring them in the woody peat. The rationale for the subsampling strategy was set out in Section 4.1.1.

Testate amoebae preparation procedures followed that set out in Section 4.1.2, with the exception that the samples for CRM I were not micro-sieved with a 15 μ m mesh. This core was analysed prior to the preparation experiments that were undertaken as a direct result of the poor quality of the microscope slides from CRM I.

Data processing and presentation follows that set out in Chapter 4 (Section 4.2). A total of 33 taxa were found in CRM I. CRM I was divided into zones on the basis of the dendrogram constructed using CONISS (Grimm, 1987) (Table 5.2). A division was made between Zones IV and V because there was a greater diversity of taxa in Zone V, including species which only occurred in this zone. It is however, a lower order division than the other zones from this core. The boundary between Zone II and Zone III corresponds with a change to more highly humified peat above 190cm than below. The boundary between Zone IV and Zone V also corresponds with a stratigraphic boundary at 55.5cm. The peat below 55.5cm was less humified and contained wood fragments. Above this level, the peat was more humified. CRM I was cored contiguously, so changes in stratigraphy may have been missed, since changes in lithology are seldom horizontal and may have been found with overlapping cores from adjacent holes. However, from field and laboratory stratigraphy of these peats it was difficult to distinguish clear boundaries without further procedures such as humification analysis. Broadly, less humified peat (humo 0-2), at the top of the core corresponded with the occurrence of taxa that may be interpreted as wet indicator species. In the middle of the core, the highly humified peat contained a limited faunal assemblage dominated by *Hyalosphenia subflava* that may qualitatively be interpreted as a dry indicator species (Table 4.4). At the base of the core, where the peat was less well humified (humo 3-4), *Diffflugia pristis* type dominated.

Zone	Depth (cm)	Major taxa	Zone description
V	0-57.5	<i>Amphitrema</i> spp. <i>Assulina</i> spp. <i>Diffugia pristis</i> type	<i>Nebela</i> spp. and <i>Euglypha</i> spp. appear for the first time in this zone and <i>Heleopera</i> spp. achieve their greatest representation in the profile. There is a greater diversity of <i>Diffugia</i> spp., with <i>D. bacillifera</i> , <i>D. globulosa</i> , <i>D. lucida</i> and <i>D. oblonga</i> type joining <i>D. pristis</i> type and <i>D. pulex</i> . <i>Amphitrema</i> spp. and <i>Assulina</i> spp. decrease to the top.
IV	57.5-132.5	<i>Amphitrema</i> spp. <i>Assulina</i> spp. <i>Diffugia pulex</i> <i>Diffugia pristis</i> type	There is an increase in the number of taxa in this zone. <i>Amphitrema</i> spp. are well represented as are <i>Assulina</i> spp. <i>Cyclopyxis arcelloides</i> type is present in this zone. The zone is dominated by <i>D. pristis</i> type and <i>D. pulex</i> . There is a decrease in the abundance of <i>D. pulex</i> to the top.
III	132.5-195.5	<i>Diffugia pristis</i> type <i>Diffugia pulex</i> <i>Hyalosphenia subflava</i>	This is a transitional zone where <i>H. subflava</i> decreases from 70% at the base to 5% at the top of the zone. At the top, <i>Amphitrema</i> spp. and <i>Assulina muscorum</i> are present, prior to a major rise in Zone IV. <i>D. pristis</i> type and <i>D. pulex</i> are present throughout.
II	195.5-297.5	<i>Hyalosphenia subflava</i> <i>Diffugia pristis</i> type <i>D. pulex</i>	This zone is dominated by <i>H. subflava</i> which increases in abundance to over 90%. <i>D. pristis</i> type is present at circa 10% abundance. Taxa also present throughout this zone are <i>D. pristis</i> type, <i>D. pulex</i> and <i>Assulina muscorum</i> . From 260-265cm, there is a peak in <i>Amphitrema flavum</i> to 35% and <i>D. pulex</i> (32%) and a corresponding drop in <i>H. subflava</i> abundance. Test concentration decreases to the top, possibly related to an increase in humification.
I	297-370	<i>Assulina muscorum</i> <i>Diffugia pristis</i> type <i>Diffugia pulex</i> <i>Hyalosphenia subflava</i>	<i>H. subflava</i> and <i>D. pristis</i> type are abundant. <i>D. pulex</i> and <i>Trigonopyxis arcula</i> are present at the base. At 320cm and 330cm, the concentration of tests was too low to count. Test concentration is low at the base of the zone.

Table 5.2 Zone descriptions for CRM I based on testate amoebae assemblages

Zone I 297.5-370cm This zone may be regarded as moderately dry because of the presence of *Hyalosphenia subflava* (<80% peat water content, Warner, 1987;1991) and *Trigonopyxis arcula*, a xerophilous taxon (de Graaf, 1956) at the base of the zone. *Diffflugia pristis* type and *D. pulex* are found throughout the entire depth of this core and other cores in this study and they may be regarded as cosmopolitan species. The other taxon found in this zone, *Assulina muscorum*, is generally regarded as cosmopolitan (Warner, 1990).

Zone II 195-297.5cm Zone II is dominated by *H. subflava* indicating dry conditions, with a depth to water table optimum recorded by Warner and Charman (1994) and Charman and Warner (1997) from Canadian studies as 49.9cm and 22.8cm. Test concentration decreases towards the top, corresponding with an increase in *H. subflava* and a decrease in *Diffflugia pulex*.

Zone III 195-132.5cm This is a transitional zone ranging from extremely dry at the base, as reflected in the dominance of *H. subflava*, to wetter or cosmopolitan taxa such as *Amphitrema flavum* and *Assulina muscorum* nearer the top. These taxa, along with a high abundance of *Diffflugia pristis* type and *D. pulex* suggest that the top of this zone is moderately wet.

Zone IV 57.5-132.5cm Zone IV is moderately wet, with a much greater diversity of taxa. *Amphitrema* spp. are well represented in this zone, which prefer 90-95% peat water content, bog pools and the wetter parts of hummocks (Tolonen 1966; Tolonen *et al.*, 1992; Warner, 1987, 1991). The presence of *Cyclopyxis arcelloides* type is difficult to interpret, as discussed above. Other major taxa, *D. pristis* type and *D. pulex* may reflect a cosmopolitan assemblage.

Zone V 0-57.5cm Very wet conditions are indicated in the lower part of this zone, although the surface samples (0-10cm) may reflect drier conditions. The presence of *Arcella discoides* type suggests very wet to submerged *Sphagnum*, with a water content greater than 95% (Tolonen, 1986; Tolonen *et al.*, 1992; Warner, 1987). *Amphitrema* spp. are well represented at the base of this zone, but decline towards the top, perhaps reflecting a dry shift towards the surface. The peak in *Diffflugia globulosa* at 25cm may imply aquatic conditions (de Graaf, 1956). There is no information in the literature about the hydrological requirements of *D. lucida*. The increase of *Heleopera*

sylvatica towards the top of this zone may also reflect drier surface conditions, as Tolonen (1986) found it in drier mosses. The xerophilous taxa, *Nebela tinctoria* and *Trigonopyxis arcuata* also increase towards the top of the zone (de Graaf, 1956; Tolonen *et al.*, 1992).

5.1.3 Ordination

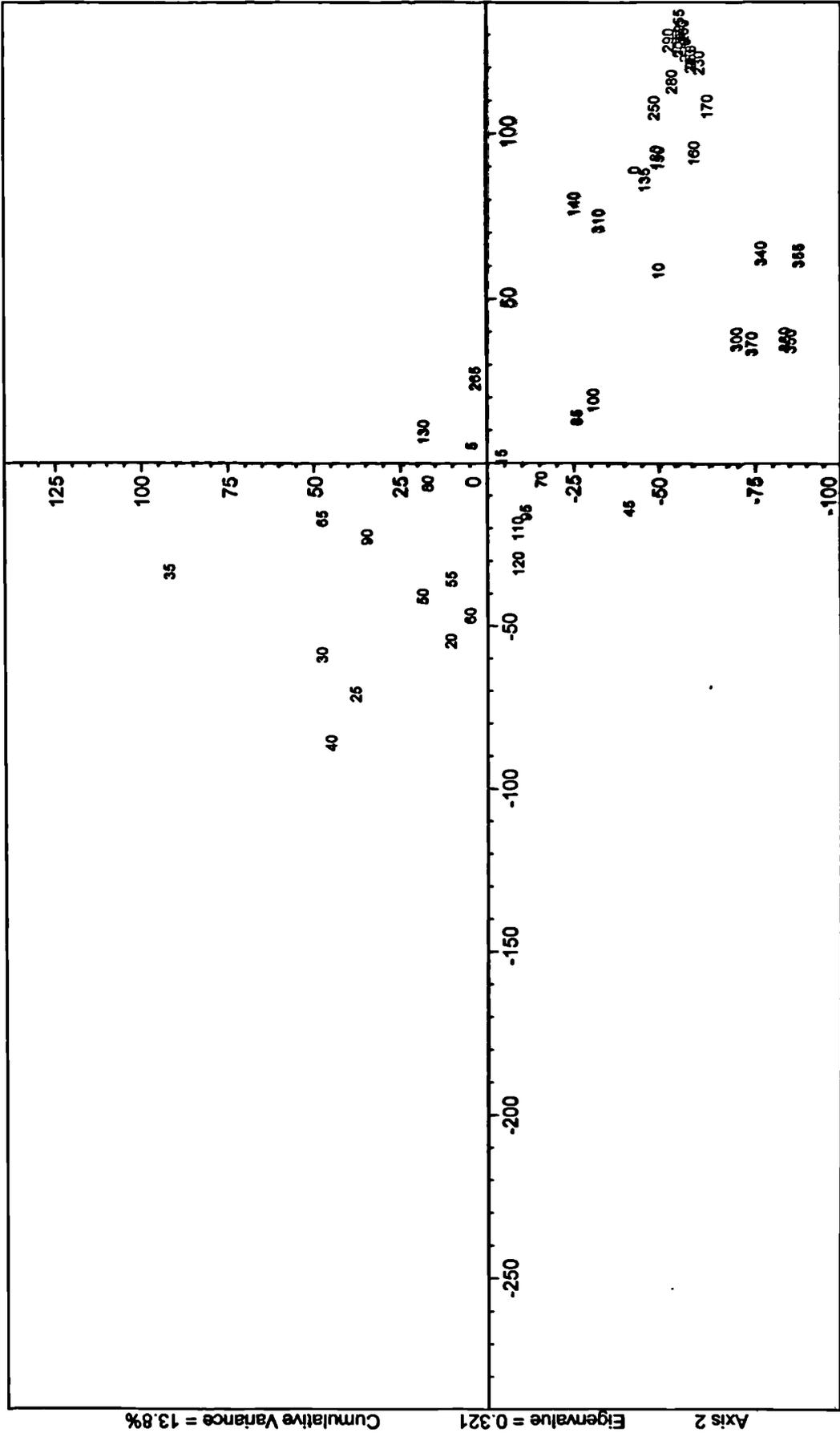
Fossil and modern ordination

Figure 5.2 presents an ordination plot of fossil and modern samples using Detrended Correspondence Analysis (DCA). Fossil samples are plotted as 'passive' *i.e.*, they are not included in the ordination process, but are overlain on the modern ordination.

On the ordination plot, the greater the distance between samples the greater dissimilarities between samples in the species composition. Fossil samples falling outside of the modern sample range will have poor modern analogues. The ordination of modern samples have eigenvalues of axis 1 - .379 and axis 2 - .321. Most of the fossil samples fall within the range of the modern samples. However, in the bottom right-hand corner of the plot, there is a more complex relationship. There is a gradation from samples that match well, those that nearly match, to those that fall outside the modern plot. Samples 160, 170, 300, 340-370cm from CRM I do not overlap modern samples and therefore have poor analogues. These samples have high abundances of *Diffugia pristis* type. There is a clump of fossil samples that overlap each other including 200cm, 230cm, 290cm. These are samples which contain high values of *Hyalosphenia subflava*. Since Figure 5.2 shows that there are fossil samples where the match with modern samples is poor, this will affect the robustness of the hydrological reconstructions, as the quality of the reconstruction is dependent on a good match between modern and fossil samples.

Sample ordination

Sample ordination for CRM I is presented to show the association of fossil samples within the individual core. Figure 5.3 shows a DCA ordination plot of samples from CRM I. Axis 1 has an eigenvalue of .652 and axis 2 has an eigenvalue of .232. The percentage variance for axis 1 is 26.8 and for axis 2 is 9.6. 63.6 percent of the variation is therefore unexplained and may be attributable to other factors.



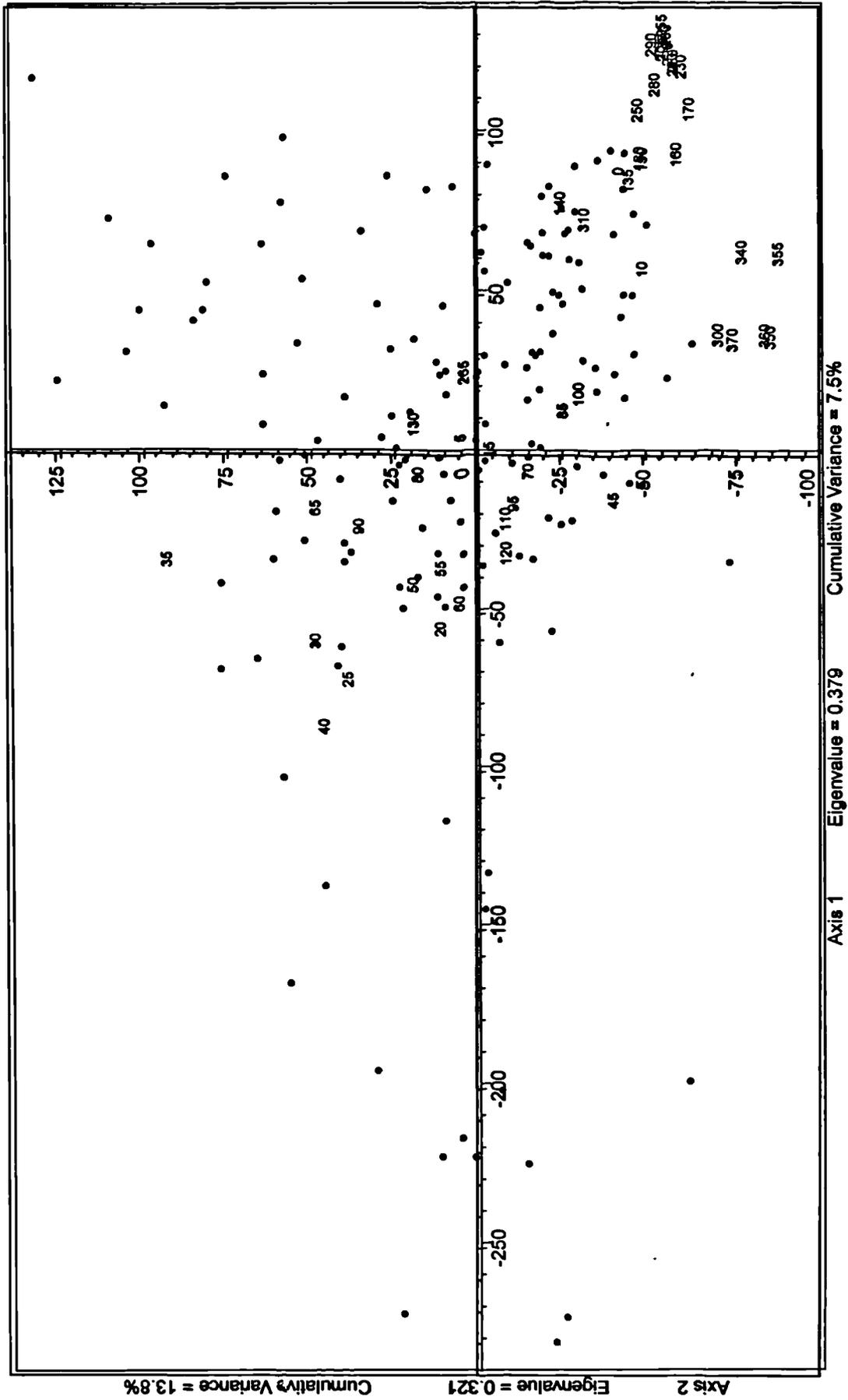


Figure 5.2 Modern and fossil DCA ordination for CRM I. Fossil samples (overlay) plotted as 'passive', modern samples plotted as circles

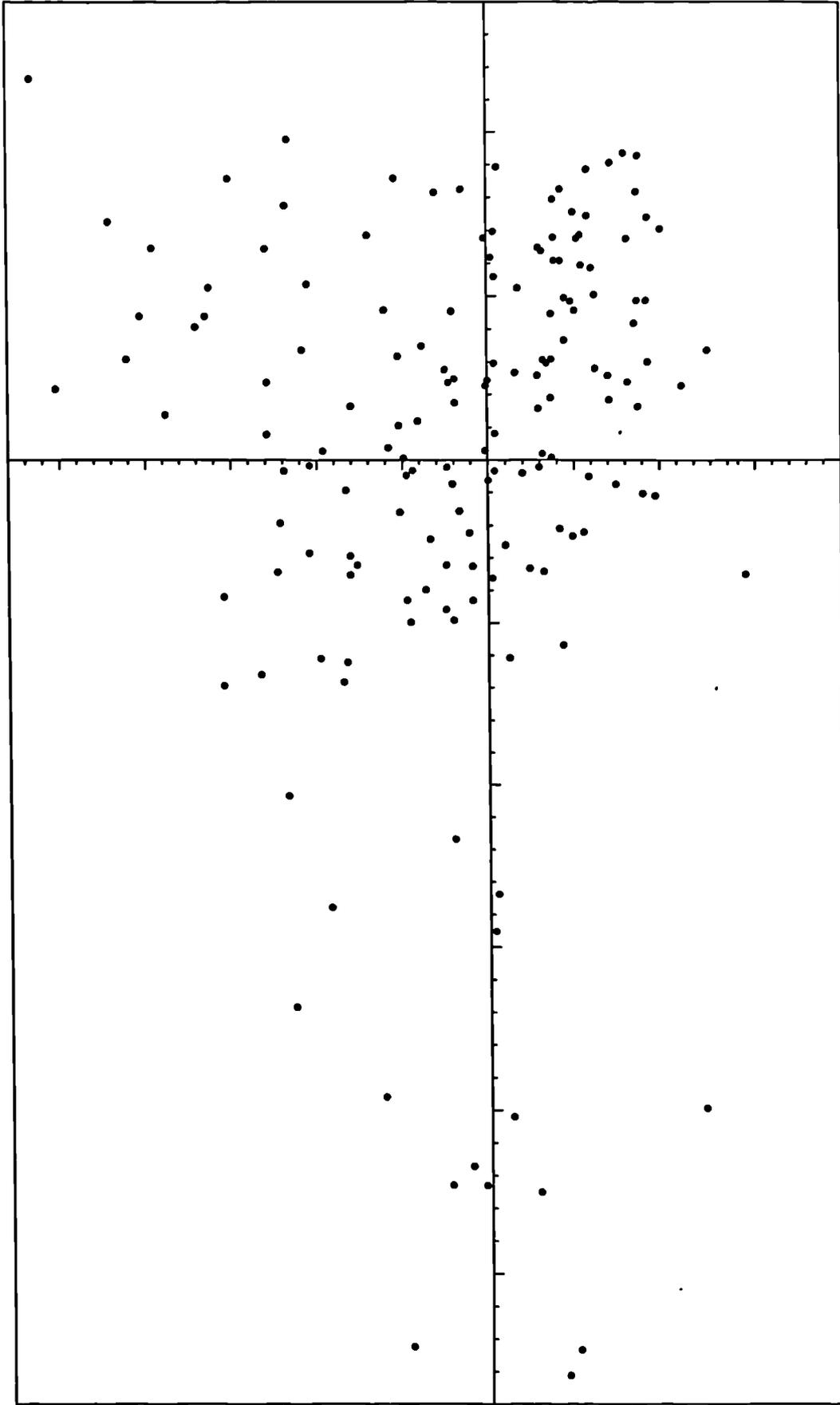


Figure 5.2 Modern and fossil DCA ordination for CRM I. Fossil samples (overlay) plotted as 'passive', modern samples plotted as circles

<i>AMP FLA</i>	<i>Amphitrema flavum</i>	<i>EUG TUB</i>	<i>Euglypha tuberculata</i>
<i>AMP STE</i>	<i>Amphitrema stenostoma</i>	<i>HEL PET</i>	<i>Heleopera petricola</i>
<i>AMP WRI</i>	<i>Amphitrema wrightianum</i>	<i>HEL ROS</i>	<i>Heleopera rosea</i>
<i>ARC ART</i>	<i>Arcella artrocrea</i>	<i>HEL SPH</i>	<i>Heleopera sphagni</i>
<i>ARC CAT</i>	<i>Arcella catinus</i>	<i>HEL SYS</i>	<i>Heleopera sylvatica</i>
<i>ARC DIS</i>	<i>Arcella discoides</i>	<i>HYA ELE</i>	<i>Hyalosphenia elegans</i>
<i>ARC VUL</i>	<i>Arcella vulgaris</i>	<i>HYA PAP</i>	<i>Hyalosphenia papilio</i>
<i>ASS MUS</i>	<i>Assulina muscorum</i>	<i>HYA SUB</i>	<i>Hyalosphenia subflava</i>
<i>ASS SEM</i>	<i>Assulina seminulum</i>	<i>LES SPI</i>	<i>Lesquereusia spiralis</i>
<i>BUL IND</i>	<i>Bullinularia indica</i>	<i>NEB BAR</i>	<i>Nebela barbarata</i>
<i>CEN CAS</i>	<i>Centropyxis cassis</i> type	<i>NEB CAR</i>	<i>Nebela carinata</i>
<i>CYC ACU</i>	<i>Centropyxis aculeata</i> type	<i>NEB COL</i>	<i>Nebela collaris</i>
<i>CYC ARC</i>	<i>Cyclopyxis arcelloides</i> type	<i>NEB FLA</i>	<i>Nebela flabellulum</i>
<i>DIF ACU</i>	<i>Diffugia acuminata</i>	<i>NEB GRI</i>	<i>Nebela griseola</i>
<i>DIF BAF</i>	<i>Diffugia bacillifera</i>	<i>NEB MAR</i>	<i>Nebela marginata</i>
<i>DIF GLO</i>	<i>Diffugia globulosa</i>	<i>NEB MIL</i>	<i>Nebela militaris</i>
<i>DIF LAN</i>	<i>Diffugia lanceolata</i>	<i>NEB PAR</i>	<i>Nebela parvula</i>
<i>DIF LEI</i>	<i>Diffugia leidyi</i>	<i>NEB TIN</i>	<i>Nebela tintca</i>
<i>DIF LUC</i>	<i>Diffugia lucida</i>	<i>NEB TUB</i>	<i>Nebela tubulosa</i>
<i>DIF OBL</i>	<i>Diffugia oblonga</i> type	<i>NEB VIT</i>	<i>Nebela vitraea</i>
<i>DIF PRI</i>	<i>Diffugia pristis</i> type	<i>PSE FAS</i>	<i>Pseudodiffugia fascicularis</i>
<i>DIF PUL</i>	<i>Diffugia pulex</i>	<i>SPH LEN</i>	<i>Sphenoderia lenta</i>
<i>DIF RUB</i>	<i>Diffugia rubescens</i>	<i>PLA SPI</i>	<i>Placosista spinosa</i>
<i>EUG ROT</i>	<i>Euglypha rotunda</i>	<i>TRI ARC</i>	<i>Trigonopyxis arcula</i>
<i>EUG STR</i>	<i>Euglypha strigosa</i>	<i>TRI LIN</i>	<i>Trinema lineare</i>

Table 5.3 Species codes for taxa included in DCA ordination analyses

Sample distribution falls into four clusters which are related to profile depth, with several scattered outliers. Samples from Zone I, the basal zone, which are dominated by *Diffugia pristis* type are located at the top of the plot. Samples from Zone II, which contain high values of *H. subflava* are clustered on the far right side of the plot. Samples from Zone V containing high abundances of *Amphitrema flavum* and *Assulina muscorum* are located on the left side of the plot. Zone IV which is characterised by *Diffugia pristis* type, *D. pulex* and *Hyalosphenia subflava* is clustered in the centre of the plot. Samples from the acrotelm are outliers. These samples contain a richer diversity of taxa, most of which are only found in those samples. They are not, therefore, strongly associated with other samples.

Species ordination

Species ordination plots are presented to determine whether axis 1 is related to a hydrological gradient and to show the distribution of taxa along that gradient (Figure 5.4). Axis 1 (eigenvalue = -.652) appears to be related to the hydrological gradient, with taxa such as *Hyalosphenia subflava*, *Trigonopyxis arcula* and *Bullinularia indica*, which are known to be indicative of low water tables on the right hand side of the diagram. *D. pulex* and *D. pristis* type are plotted in the same region of the ordination plot as the dry indicator species, suggesting that they also tolerate drier conditions.

Clusters at the top and bottom of axis 2 appear to be mixtures of both very wet taxa and taxa from the mid-hydrological range. This would suggest that another, unknown factor is affecting the distribution of species along axis 2.

Fifteen taxa have less than 5% abundance in every sample in which they were found. These species are plotted as crosses to indicate that they are less significant in the ordination than those taxa with greater than 5% abundance in every sample in which they occur. The majority of taxa with <5% abundance in every sample in which they occur are located on the negative side of axis 2.

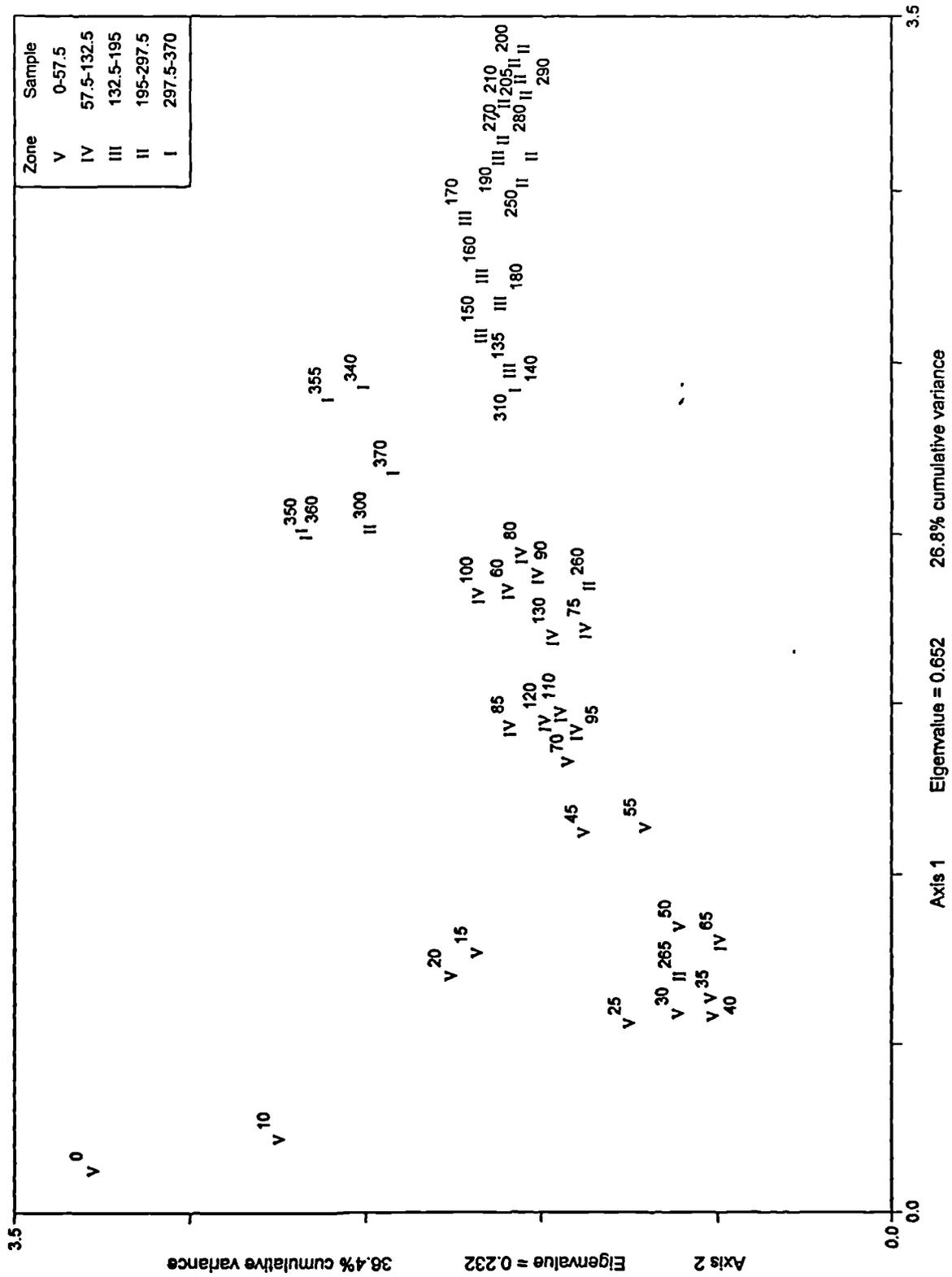


Figure 5.3 Sample ordination for CRM I

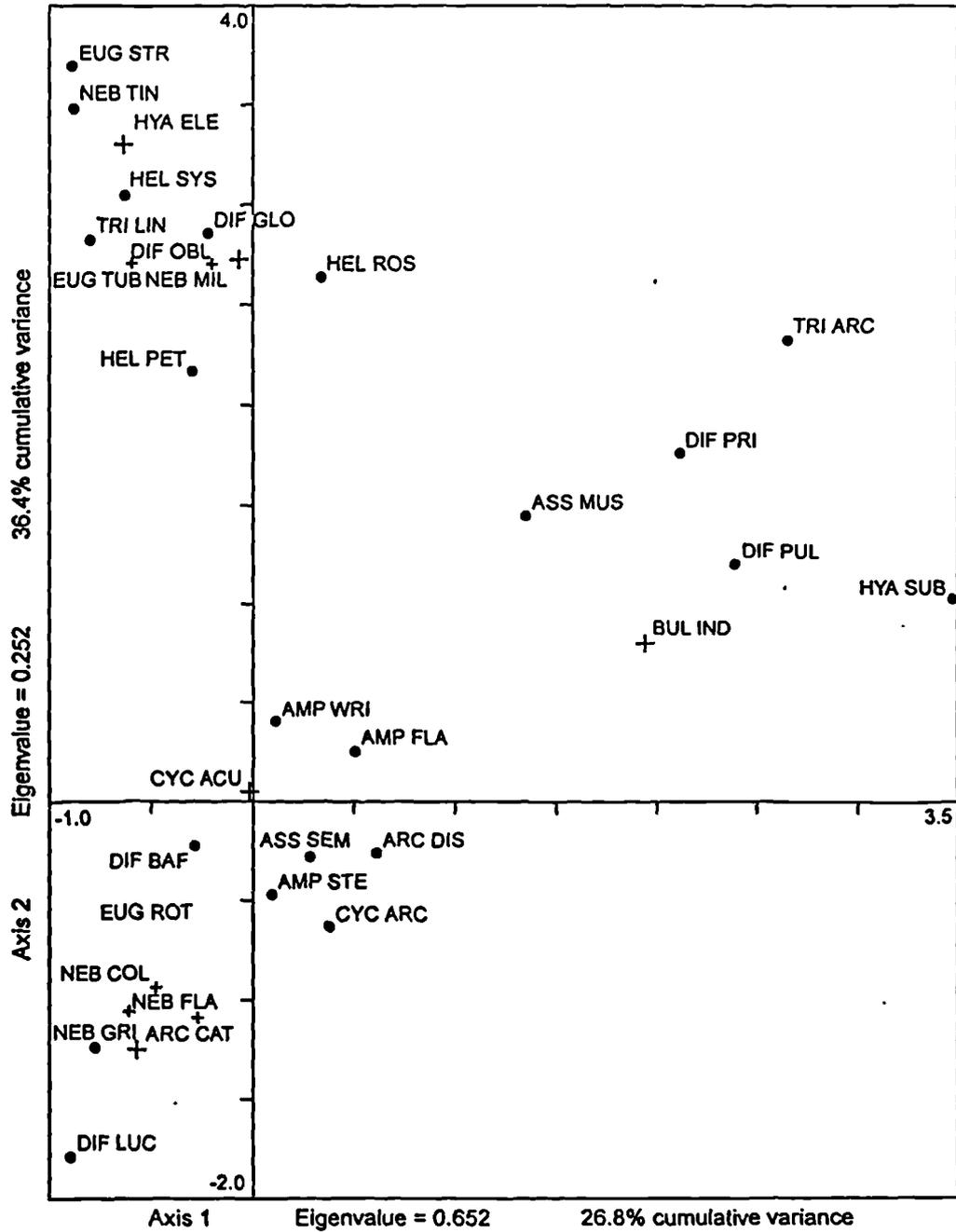


Figure 5.4 Species ordination for CRM I. Taxa with <5% abundance plotted as crosses, refer to Table 5.3 for species codes

5.1.4 Hydrological reconstructions

Water table reconstruction

The transfer functions were discussed in detail in Chapters 2 and 4. Figure 5.5 shows the water table reconstruction for CRM I constructed using the transfer function developed by Woodland *et al.* (1998).

The base of the water table reconstruction at 370cm is -6.5cm below surface. A large part of the assemblage is composed of *Diffflugia pulex* (42%) which accounts for the wide spread of confidence limits at this point. Between 360-340cm, the water table mean fluctuates between -4.9cm to -7.6cm below the surface. Sample 350cm (-4.9cm below surface) is the wettest sample in the lower half of the core. Samples 330cm and 320cm had test concentrations which were too low to count. Between 295-270cm, the water table falls, reaching a mean low of -16.2cm below surface. This corresponds with the testate amoebae assemblage being dominated by *Hyalosphenia subflava*. There is a rise in the water table level between 265-260cm, to -6.6cm. The narrow confidence limits in this area reflect the robustness of the reconstruction when the taxa, dominated by *Amphitrema flavum*, *Assulina muscorum* and *Diffflugia pristis* type, have good modern analogues. Above this, from 255cm to 135cm, is hydrologically stable, without much variation in the depth to water table. This is related to the abundance of *H. subflava* and *D. pulex* which dominate the testate assemblage. At 200cm, the mean water table curve reaches its lowest point of the core at -16.2cm. The curve shows a trend of increasing wetness towards 135cm, which may be attributable to the occurrence of *A. flavum*, but generally, the reconstruction of the water table in this part of the core is not very robust as the assemblage is dominated by *D. pulex* which does not have an analogue value. The quantity of *D. pulex* in a faunal assemblage has the greatest effect on the size of the confidence limits around the mean water table curve. Basing the reconstruction on the low numbers of other taxa that were found here results in a complacent curve with wide confidence limits which probably does not reflect the true nature of the hydrological record at this point.

The section of the reconstruction from 130cm to 0cm shows a greater degree of variation. The reconstruction is more robust, with closer confidence limits, reflecting much wetter conditions. There is a much more diverse faunal assemblage upon which to base the reconstruction and, although most samples are dominated by *Diffflugia pulex*,

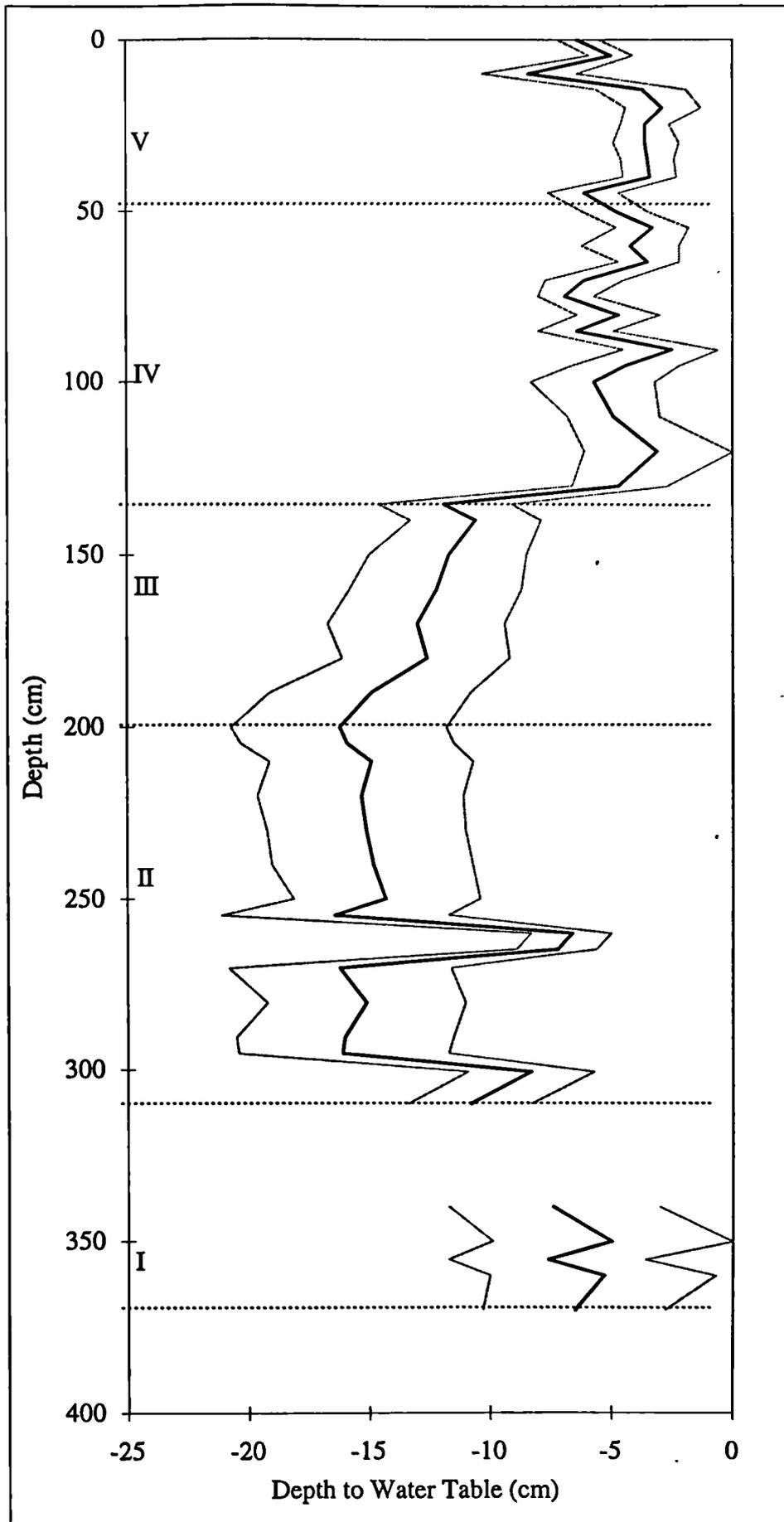


Figure 5.5 Mean water table reconstruction CRM I, with 2σ bootstrapped error estimates shown as thin lines. Assemblage zones marked.

except at the surface, the remainder of the assemblage have good analogues. At 10cm depth there is a dry shift to -8.39cm, which corresponds with peaks in *Heleopera petricola* and *Trinema lineare*, which have water table optimums of -8.06cm and -9.43cm respectively. The 16% abundance of *Diffflugia lucida* at 5cm depth is not included in the reconstruction as it is not in the transfer function. The surface sample shows slightly drier conditions.

Wet areas of the reconstruction curve have smaller confidence limits on the mean curve than drier parts of the curve, because of better analogue values in wetter sections of the curve. Between 255-135cm and 295-270cm, the reconstructions are dominated by *Hyalosphenia subflava* which has a poor analogue because of its large tolerance range and results in wider confidence intervals.

Moisture reconstruction

The moisture reconstruction for CRM I using the WA-Tol transfer function of Woodland *et al.* (1998) is presented in Figure 5.6. From the base of the core at 370cm, mean percentage soil moisture is 91%. The wide confidence limits at the base are associated with the abundance of *Diffflugia pulex*. Mean percent soil moisture declines to 88.8% at 355cm. Between 330cm and 320cm there are no values due to exceptionally low test concentrations. There is an increase in moisture content at 265-260cm to 95% moisture. This is associated with a peak in the abundance of *Amphitrema flavum*. From 240cm to 190cm, the curve is relatively complacent with around 89% moisture, this is associated with the dominance of *Hyalosphenia subflava*, which results in wide confidence limits between these depths. The reconstruction is not particularly robust in this area of the curve because of the taxa included in the transfer function. At 180cm, there is a wetter fluctuation to 92.5% and above this, to 140cm, there is a trend of increasing wetness. At 135cm, there is a sharp decline in the percentage soil moisture which is associated with a peak in *H. subflava* and *D. pulex*, that explains the wide confidence limits around this trough. There is a greater degree of variation in the reconstructed moisture curve from the surface to 130cm. From 35cm (96% moisture) to 0cm (81% moisture) the pattern is one of a trend of increasing dryness to the surface. The surface sample attains the driest mean value of the entire core.

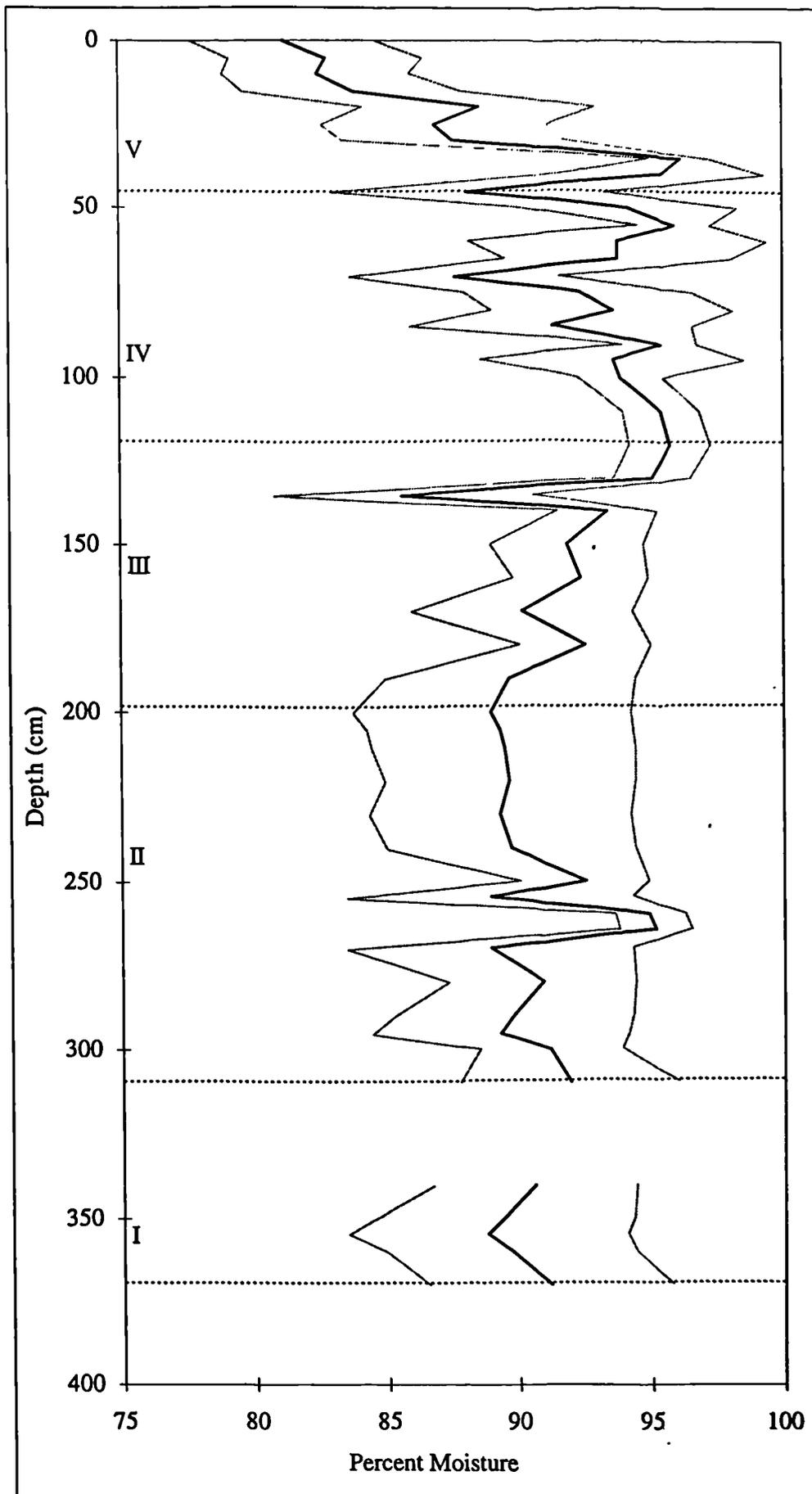


Figure 5.6 Mean moisture reconstruction CRM I, with 2σ bootstrapped error estimates shown as thin lines. Assemblage zones marked.

5.2 Coom Rigg Moss Core II (CRM II)

Core CRM II was extracted so that with CRM III from the northern edge of the mire (Section 5.3) and cores CRM I and CRM IV, it could be used to assess autogenic influences on mire hydrology and thus help to separate the climatic signal from the two central cores. The marginal cores are also used to assess the replicability of the testate amoebae record from different locations on the mire. The rationale for subsampling was similar to that for core CRM I, with closely spaced sampling in the top metre of the core at 5cm intervals and at 10cm intervals for the rest of the core. Closely spaced samples were also taken either side of radiocarbon dates. Testate amoebae preparation procedures followed that set out in Section 4.1.2. Micro-sieving was carried out on all of these samples.

5.2.1 Stratigraphy

Stratigraphical description follows that of Troels-Smith (1955) and is set out in Table 5.4. The stratigraphy of CRM II agrees with that of Chapman (1964a), as the peat is predominantly *Sphagnum-Eriophorum* peat, which suggests that the peat was ombrotrophic throughout its development. CRM II was extracted close to Chapman's (1964a) grid reference I8 (Figure 3.6).

Depth (cm)	Sediment Description
0 - 13	nig 1; strf 0; elas 4; sicc 2; humo 0. Tb ⁴ fresh, undecomposed <i>Sphagnum cuspidatum</i> , <i>Molinia caerulea</i> , <i>Erica tetralix</i> .
13 - 20	nig 2; strf 0; elas 3; sicc 1; humo 1. Tb ³ Th ¹ partially decayed <i>Sphagnum</i>
20 - 50	nig 3; strf 0; elas 2; sicc 1; humo 1. Tb ⁴ Tl ⁺ <i>Sphagnum</i> leaves preserved.
50 - 74	nig 3; strf 1; elas 3; sicc 1; humo 1. Tb ⁴ <i>Sphagnum</i> peat
74 - 120	nig 4; strf 1; elas 3; sicc 1; humo 2. Tb ⁴ <i>Sphagnum</i> peat, mostly leaves preserved.
120 - 155	nig 4; strf 0; elas 1; sicc 1; humo 3. Tb ⁴ well humified <i>Sphagnum</i> peat
155 - 180	nig 4; strf 0; elas 1; sicc 2; humo 2. Tb (Sphag) ⁴ Tl ⁺ ericoid roots
180 - 205	nig 4; strf 0; elas 2; sicc 1; humo 3. Tb ⁴ Tl ⁺
205 - 230	nig 4; strf 0; elas 2; sicc 1; humo 4. Tb ⁴ plant structure hardly discernible.
230 - 280	nig 4; strf 0; elas 1; sicc 1; humo 4. Sh Tl ⁺ Th ⁺ . occasional monocot. fragments, <i>Eriophorum</i> and ericoid roots
280 - 330	nig 4; strf 0; elas 0; sicc 2; humo 4. Sh ³ Th ¹ Monocot. fragments <i>Eriophorum</i>

Table 5.4 Stratigraphic description of CRM II using the Troels-Smith (1955) sediment description system

5.2.2 Testate amoebae

Sample preparation and data presentation follows that of CRM I and was set out in detail in Chapter Four. Core CRM II was 330cm in length, of which the top 280cm was suitable for testate amoebae analysis (Figure 5.7). Slides below 280cm were scanned to determine whether deeper parts of the core had countable concentrations of tests. Samples at 290cm and 300cm had concentrations which were too low to count and from 310-330cm tests were almost completely absent. This reduction in concentration is probably related to the highly humified peat at the base, or may have been because conditions were not suitable for test colonisation when the peat was accumulating. Thirty four taxa were counted in this core and are presented in alphabetical order.

Zone I begins at 280cm, which corresponds with a change in stratigraphy to wetter peat, with a slightly different composition to the overlying material. The top of Zone I, 245cm, does not correspond with changes in stratigraphy. The stratigraphic record changes at 155cm to more humified peat above. This level also marks a change in the assemblage composition, from Zone III to Zone IV. Other zone boundaries are asynchronous with stratigraphic changes.

The testate amoebae assemblage zones (Table 5.5) can be interpreted qualitatively on the basis of hydrological information about them found in the literature (Tables 2.6 and 4.4).

Zone I 245-280cm This zone is dominated by *Hyalosphenia subflava* and *Diffflugia pulex*, with a peak in *Amphitrema flavum* at the top of the zone. These taxa indicate that the conditions were moderately dry when the peat accumulated. *H. subflava* has been found in surface samples with 78-89% water content (Warner, 1987) and *A. flavum* has been found in samples with water contents between 87.9-95%. The overlap in water conditions suggests that these two species occur in the same conditions, although *H. subflava* is regarded as a dry indicator species and *A. flavum* is considered to be a species more indicative of wet conditions.

Zone II 192.5-245cm This zone is dominated by *D. pulex* and *H. subflava* which represent dry conditions. *Trigonopyxis arcuata* is also present in this zone which is also a xerophilous taxon (de Graaf, 1956).

Zone	Depth (cm)	Major Taxa	Zone description
VI	0-27.5	<i>Arcella discoides</i> type, <i>Heleopera</i> spp.	There is a high diversity of taxa in this zone; no one taxon has overall dominance. <i>Arcella discoides</i> type, <i>Nebela</i> spp. and <i>Trigonopyxis arcula</i> achieve their best representation in this zone. <i>Diffflugia pristis</i> type and <i>D. pulex</i> decrease towards the top. <i>Heleopera</i> spp. increase in abundance to the top. The highest concentration of tests in this profile occurs at 20cm.
V	27.5-67.5	<i>Amphitrema</i> spp. <i>Cyclopyxis arcelloides</i> type, <i>Diffflugia pulex</i>	There is greater species diversity in this zone than in the deeper zones. <i>Amphitrema</i> spp. dominate this zone, with <i>A. wrightianum</i> declining sharply to the top. <i>Diffflugia pulex</i> also decreases in abundance to the top. <i>Heleopera</i> spp. are present in significant numbers for the first time in this zone
IV	67.5-155	<i>Amphitrema flavum</i> <i>Diffflugia pulex</i> <i>Hyalosphenia subflava</i>	This zone has a similar faunal assemblage to Zone III. <i>Hyalosphenia subflava</i> increases to the centre of this zone to 64% abundance at 120cm. This trend is curtailed by the peak of <i>Amphitrema flavum</i> at 110cm with 52% abundance. <i>Cyclopyxis arcelloides</i> type increases to the top.
III	155-192.5	<i>Amphitrema flavum</i> <i>Diffflugia pulex</i>	<i>Diffflugia pulex</i> and <i>Amphitrema flavum</i> are the major taxa found in this zone, along with small amounts of <i>Assulina muscorum</i> and <i>Diffflugia pristis</i> type.
II	192.5-245	<i>Diffflugia pulex</i> <i>Hyalosphenia subflava</i>	The only taxa found in large numbers in this zone are <i>Diffflugia pulex</i> and <i>Hyalosphenia subflava</i>
I	245-280	<i>Amphitrema flavum</i> <i>Diffflugia pulex</i> <i>Hyalosphenia subflava</i>	This zone is characterised by high abundances of <i>Diffflugia pulex</i> and <i>Hyalosphenia subflava</i> . <i>Amphitrema flavum</i> is present from 250 to 265cm

Table 5.5 Zone descriptions for CRM II based on testate amoebae

Zone III 155-192.5cm This zone has high values of *Amphitrema flavum* and *A. wrightianum* which are indicative of wet conditions. *Assulina muscorum* has a cosmopolitan distribution.

Zone IV 67.5-155cm Zone IV is also dominated by *D. pulex*. The other taxon with a high abundance in this zone is *H. subflava*, except at 110cm where there is a large peak in the abundance of *A. flavum* and *A. muscorum*. This implies that the general trend in this zone is of dry conditions with a transitory wet phase, followed by drier conditions.

Zone V 27.5-67.5cm The greater species diversity in this zone indicates wetter conditions (Warner, 1987). The presence of all three *Amphitrema* spp. suggests wet conditions as the three indicate 95% water content or bog pools (Tolonen *et al*, 1992;

Warner, 1987, 1991). The abundance of *Cyclopyxis arcelloides* type could either represent moderately dry conditions with 78-89% water content (Warner, 1987, 1991) or shallow peatland pools (Warner and Charman, 1994).

Zone VI 0-27.5cm The bottom of Zone VI is extremely wet, as indicated by the high abundance of *Arcella discoides* type which is found in floating, submerged or very wet *Sphagnum*, with a water content greater than 95% (Tolonen, 1986; Tolonen *et al.*, 1992; Warner, 1987). The surface samples imply fairly dry conditions, although some of the literature regarding the taxa found in these samples is contradictory. *Nebela tinctoria* was found by Tolonen *et al.* (1992) to be a xerophilous taxon with <85% moisture content. Warner (1987) however, found *N. tinctoria* in very wet conditions. Similarly, *N. militaris* has been found in drier mosses (de Graaf, 1956) and the wet mosses of bog hummocks (Warner, 1987). *Heleopera petricola* increases in abundance to the top of Zone I, but its ecology is 'variable and disputed' (Tolonen, 1986; Warner, 1987). The presence of *H. sylvatica* indicates dry mosses (Tolonen, 1986). Interpretation of this zone is therefore complicated, but the presence of *H. subflava* and the decrease in abundance of *A. discoides* type shows that at the base of the zone, conditions were very wet and became much drier towards the surface.

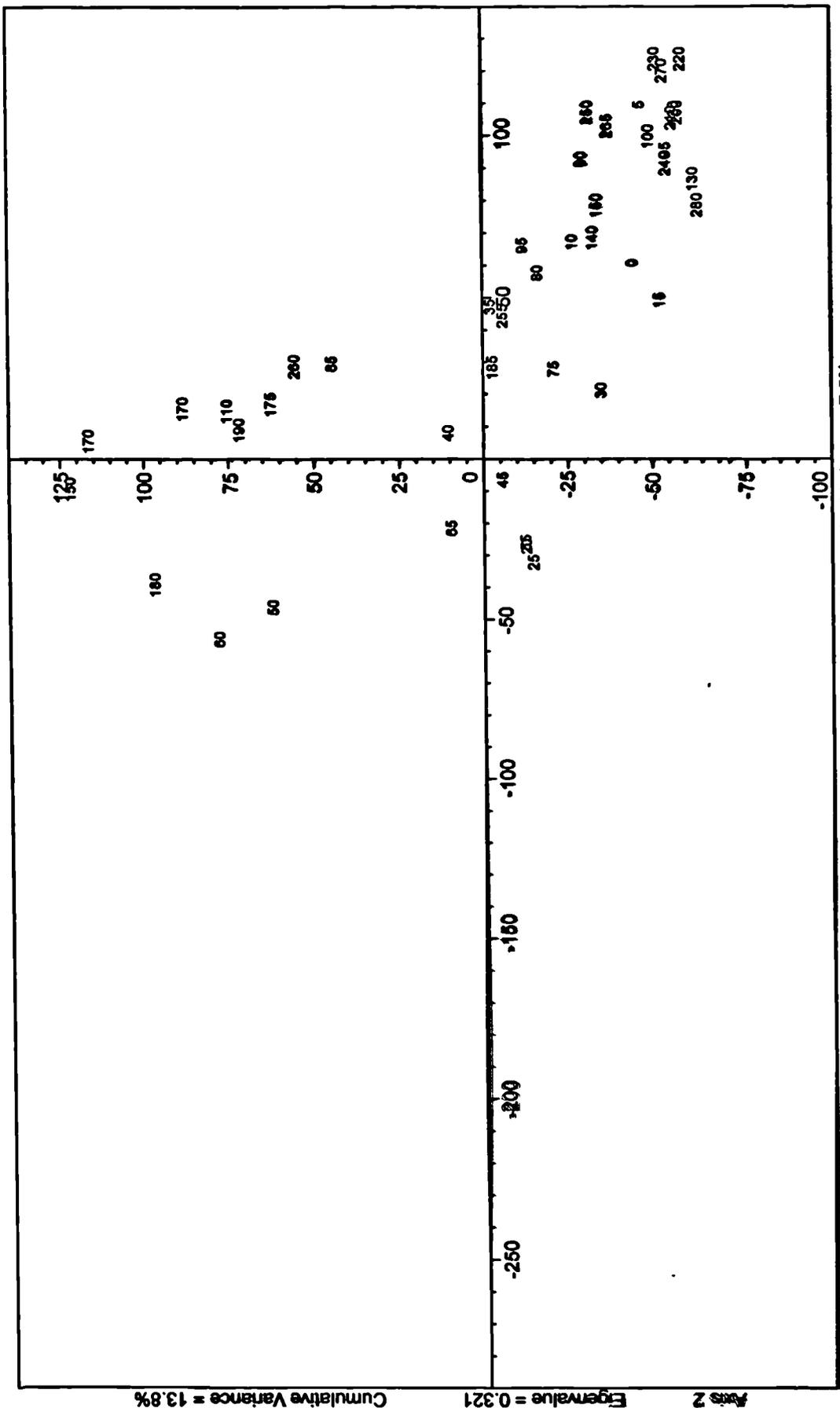
5.2.3 Ordination

Modern and fossil

The modern and fossil ordination plot for CRM II with fossil samples plotted as 'passive' is very similar to that for CRM I and is presented in Figure 5.8. Most of the fossil samples lie within the spread of modern samples although samples dominated by *Diffugia pulex*, such as 170cm, 180cm in the top centre and samples 220cm, 230cm and 270cm in the bottom right hand corner of the plot, are slightly removed from the modern samples. These samples do not have a particularly good match with modern samples and this will affect the robustness of palaeohydrological reconstructions.

Sample ordination

Figure 5.9 shows the sample ordination plot for CRM II. There is a good relationship between sample depth and hydrology, with wetter surface samples plotted closest to axis 2 and the deeper samples whose species composition indicates drier conditions plotted along axis 1. The surface samples (Zone VI) are removed from the main cluster of



Axis 1 Eigenvalue = 0.379 Cumulative Variance = 7.5%

Axis 2 Eigenvalue = 0.321 Cumulative Variance = 13.8%

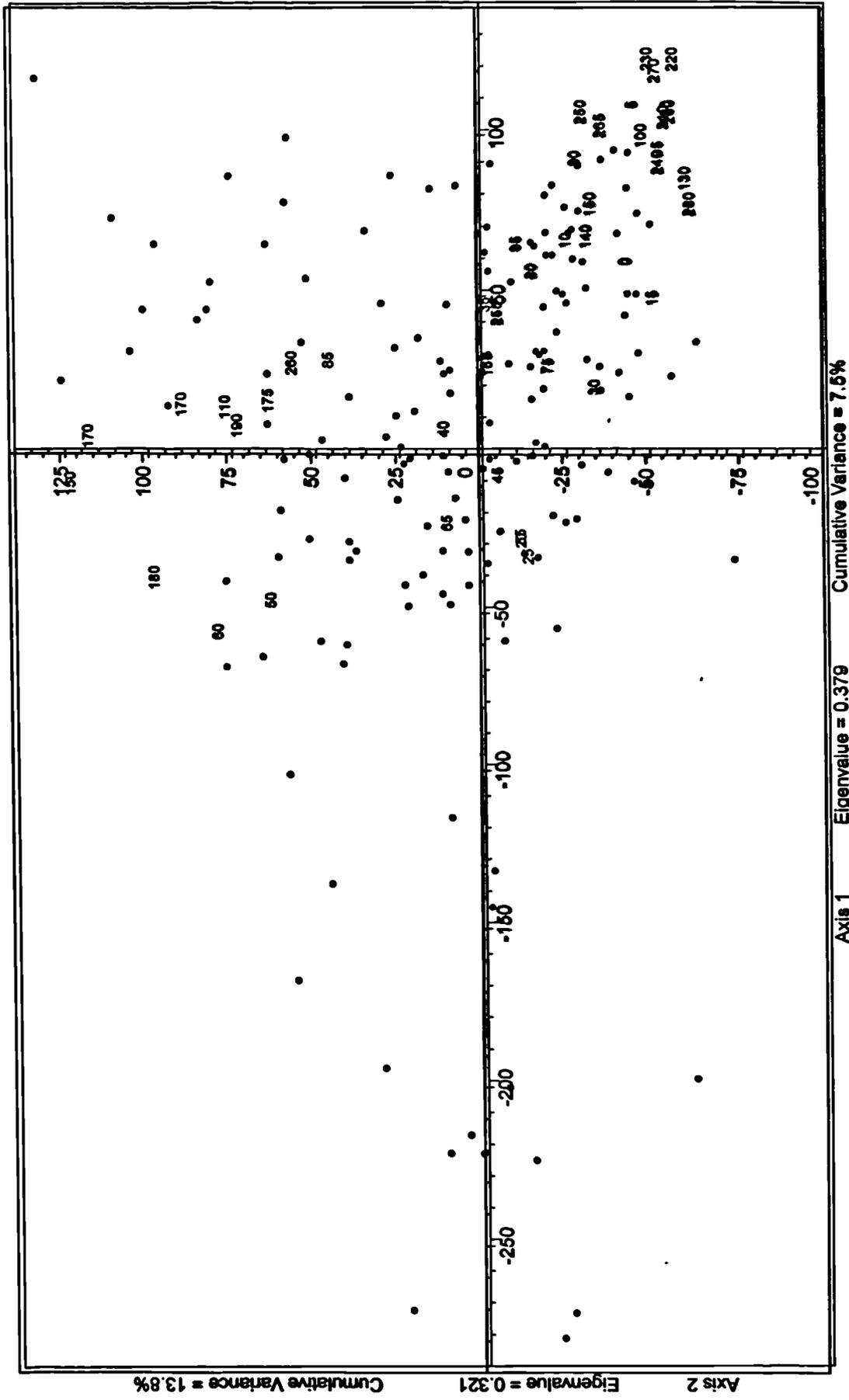


Figure 5.8 Modern and fossil DCA ordination for CRM II. Fossil samples (overlay) plotted as 'passive', modern samples plotted as circles

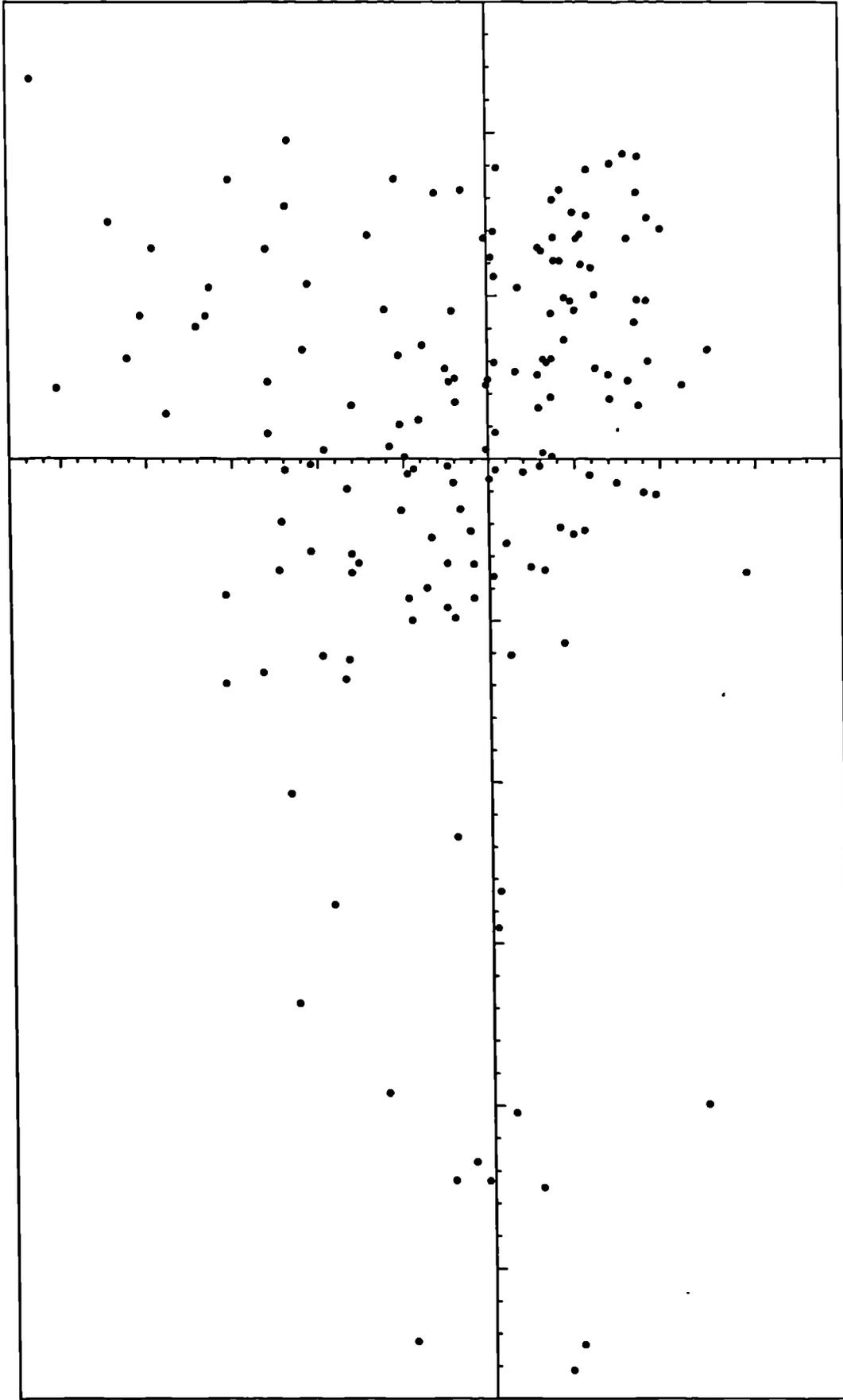


Figure 5.8 Modern and fossil DCA ordination for CRM II. Fossil samples (overlay) plotted as 'passive', modern samples plotted as circles

samples on the far left of the diagram. The mid-core and basal samples are not easily separated but there is a gradual progression of samples from the surface zones on the left side of the plot to basal zones on the right side of the plot.

Species ordination

Figure 5.10 shows the species ordination for CRM II. Taxa found only in the surface samples are grouped to the left of Axis 2. There are three outlier species - *Hyalosphenia subflava*, *H. papilio* and *Diffflugia pulex*. Eighteen taxa occur in less than 5% abundance in every sample in which they occur. These species are less significant in the ordination than those species that have greater abundance. There is no obvious pattern to the distribution of less significant taxa.

5.2.4 Hydrological reconstructions

Water table reconstruction

The water table reconstruction curve for CRM II using WA and with outlier samples removed from the modern analogue data set is presented in Figure 5.11. The base of the curve is -10.5cm below the ground surface. The water table declines to -16cm at 270cm. At 260cm, the water table rises to -6cm below the ground surface and is associated with the peak in *Amphitrema flavum* and a corresponding decline in *Hyalosphenia subflava* in the faunal assemblage. From 250cm to 195cm, the reconstructed water table curve is relatively complacent, with wide confidence limits, greater than 4cm either side of the mean. This is because the dominant taxa in the reconstruction between 250cm-195cm, are *H. subflava* and *Diffflugia pulex*. Between 195cm and 160cm the water table rises to just below the ground surface. The water table fluctuates from -6cm to -2cm below the ground surface. This is one of the wettest areas of this core. The confidence limits between 195-160cm are very narrow, indicating that this part of the reconstruction is robust. Between 150cm to 120cm, there is a slight decline to drier conditions and the water table reaches a low point of -14.8cm at 120cm depth in the peat core. At 110cm there is a dramatic rise in the water table to -4cm below ground surface. This is very wet and is associated with a peak in *A. flavum*. The close confidence limits at this point indicate a good match between the fossil samples and the modern analogues, resulting in a robust reconstruction. At 100cm, the water table level drops back to -14cm below surface.

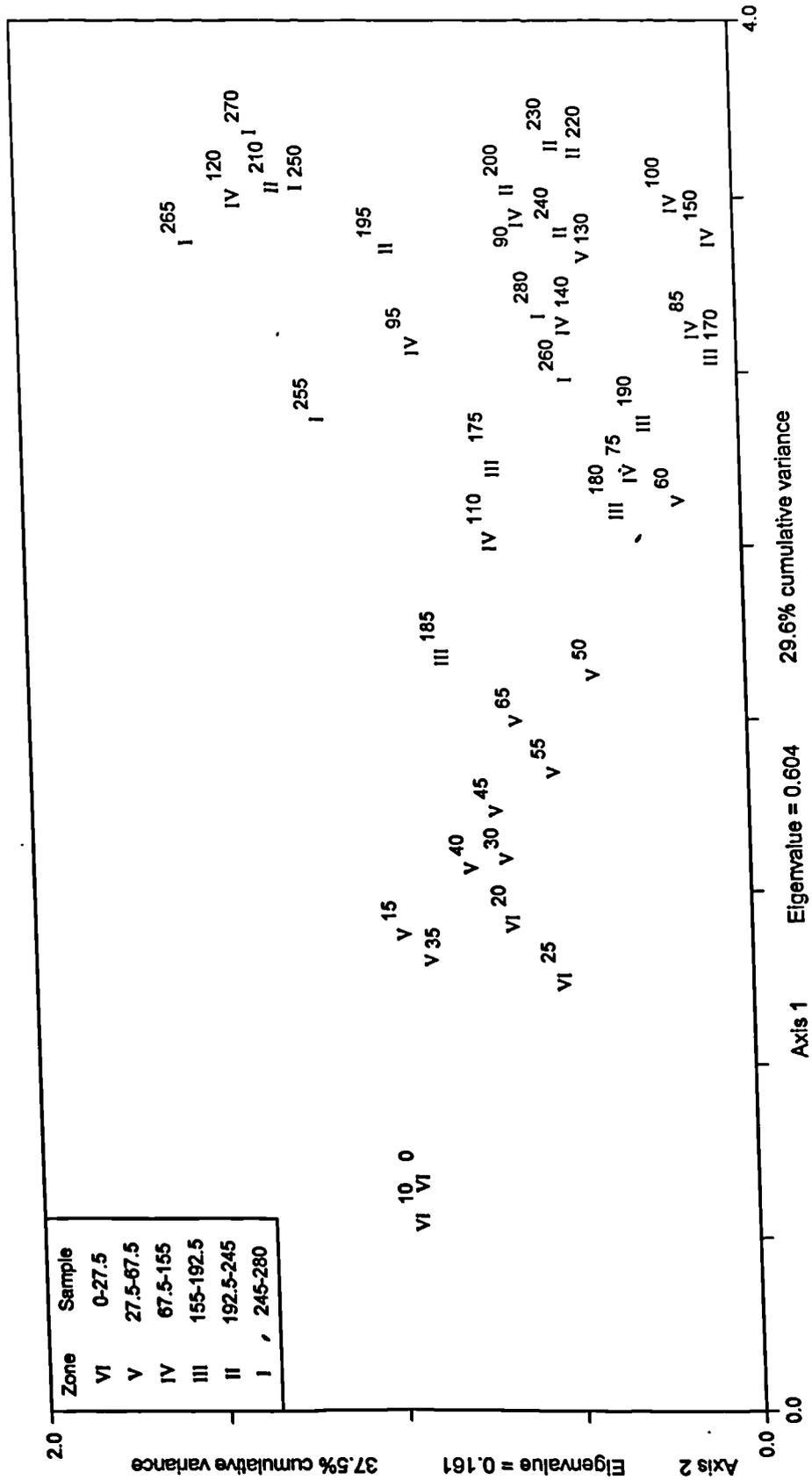


Figure 5.9 Sample ordination for CRM II

Above this to 45cm, there is a trend of increasing wetness, with some fluctuation. The mean water table reaches a high point of -2cm below surface at 25cm peat depth, associated with a peak in *Arcella discoides* type. From 25cm depth to 0cm, the mire surface, there is a trend of deeper water tables and drier conditions. The surface sample has a moderately dry value of -8.8cm, which is reflected in the faunal assemblage.

Moisture reconstruction

The percentage moisture curve is presented in Figure 5.12. The minimum reconstruction curve, on the right side of the mean curve, shows much less variation than the maximum curve.

At the base of the moisture reconstruction for CRM II, 280cm, the mean percent moisture is 92.7%. The moisture value decreases to 90.7% in both samples 270cm and 265cm. The wide confidence limits around these basal samples are associated with the dominance of *Hyalosphenia subflava*. The soil moisture value rises to 94% at 260cm, associated with the high representation of *Amphitrema flavum* and *Assulina muscorum*. Between 195cm and 250cm, the curve is relatively complacent, with a slight trend of decreasing moisture content. The mean moisture content varies from 89.5% to 92.5% moisture content.

Interestingly, the maximum value between the depths shows much greater variation than the minimum value, which is less variable at 94% moisture content. Between 190cm to 185cm there is a dramatic fluctuation from much wetter (95.5%), to drier (91.5%) returning to wetter conditions at 180cm. From 180cm to 120cm, there is a trend of decreasing moisture content, although this part of the reconstruction is dominated by *Diffugia pulex*. From 120cm to 55cm peat depth, the curve fluctuates gently, with a trend of increasing moisture content. Fluctuations are of between 2-3% between each pair of adjacent samples. The maximum confidence limits fluctuate more here than the minimum values. Between 55cm and 15cm there are dramatic fluctuations of between 7-13% between adjacent samples in the reconstructed moisture curve. The lowest point is 82% moisture content at 35cm and the highest value is 97% moisture content at 50cm depth. From 15cm (82%), there is a drop in moisture content to 80.7% at 5cm depth, before it rises to 83% moisture content at the surface (0cm).

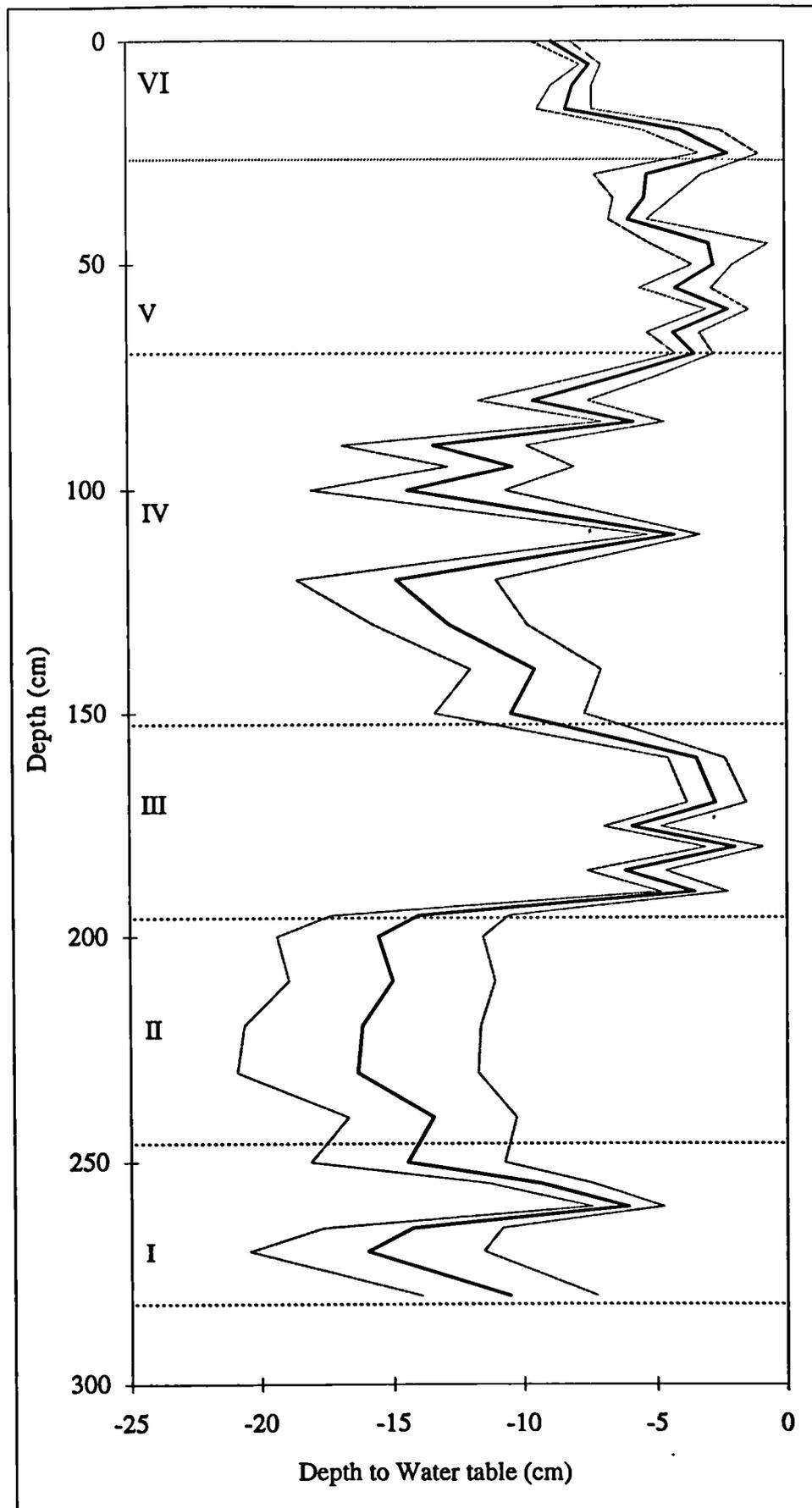


Figure 5.11 Mean water table reconstruction CRM II, with 2σ bootstrapped error estimates shown as thin lines. Assemblage zones marked.

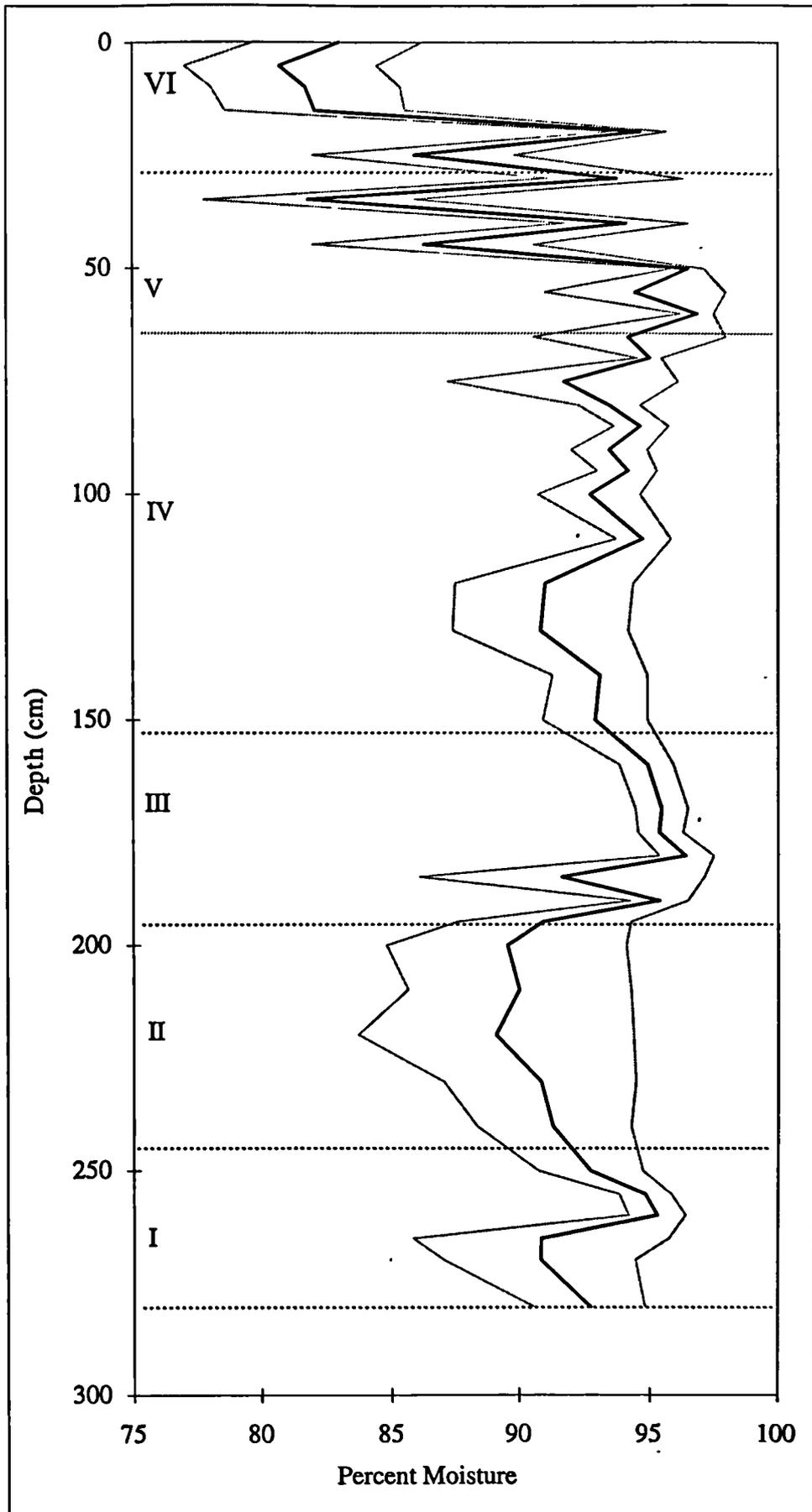


Figure 5.12 Mean moisture reconstruction CRM II, with 2σ bootstrapped error estimates shown as thin lines. Assemblage zones marked.

The 'dry' indicator species *H. subflava* produces a moister reconstruction than the wet indicator taxa at the top of the core where *H. subflava* is scarce. This is probably because there is a greater diversity of taxa at the top of the core, which have better modern analogues than the less diverse assemblages at the base of the core. *H. subflava* also has a higher ranking position with regard to moisture than it has for water table in the optima and tolerance data for the transfer function from Woodland *et al.* (1998), presented in Chapter Four. At the top of the core, there is significantly less *D. pulex* and, since this is one of the taxa that causes most problems in reconstruction due to the absence of a modern analogue, the reconstruction nearer the surface has more confidence and is more robust than the reconstructions at depth. The reconstructions where the curve is dominated by *H. subflava* are more biased to wetter conditions.

5.3 Coom Rigg Moss Core III (CRM III)

Core CRM III was extracted from the northern mire margin in April 1995, using a wide bore Russian corer. The location of core CRM III is shown on Figure 3.3. CRM III, with CRM II are used to analyse the replicability of the testate amoebae record within a mire and to separate the allogenic climatic signal from autogenic hydrological signals resulting from mire development and expansion.

Depth (cm)	Sediment Description
0 - 3.5	nig 2; strf 0; elas 4; sicc 1; humo 0. surface vegetation <i>Sphagnum cuspidatum</i> , <i>S. capitifoilum</i> , <i>Polytricum commune</i> , <i>Vaccinium oxycoccus</i>
3.5 - 8	nig 4; strf 0; elas 1; sicc 1; humo 3. Tb ⁴ <i>Sphagnum</i> peat
8 - 18	nig 3; strf 1; elas 1; sicc 1; humo 2. Tb ³ Th ¹ <i>Eriophorum</i>
18 - 23	nig 2; strf 1; elas 3; sicc 1; humo 1. partially decayed <i>Sphagnum</i> moss
23 - 30	nig 3; strf 1; elas 1; sicc 1; humo 3. Tb ⁴ <i>Sphagnum</i> peat
30 - 55	nig 2; strf 1; elas 1; sicc 1; humo 2. Tb ⁴ partially decayed <i>Sphagnum</i> moss
55 - 65	nig 3; strf 0; elas 1; sicc 1; humo 2. Tb ⁴ TI ⁺
65 - 100	nig 4; strf 0; elas 1; sicc 1; humo 3. Tb ⁴ TI ⁺ ericoid roots present
100 - 130	nig 4; strf 1; elas 0; sicc 1; humo 4. Tb ⁴ Th ⁺ well humified <i>Sphagnum</i> peat
130 - 181	nig 4; strf 0; elas 0; sicc 3; humo 4. Sh ² Th ² TI ⁺ ericoid roots present & <i>Eriophorum</i>
181 - 187	nig 2; strf 0; elas 0; sicc 3; A ⁴ , G ⁺ brown clay, with small sand fraction

Table 5.6 Stratigraphic description of CRM III using the Troels-Smith (1955) sediment description system

Zone	Depth (cm)	Major Taxa	Zone description
II	0-62.5	<i>Amphitrema flavum</i> <i>Cyclopyxis arcelloides</i> type <i>Diffflugia pristis</i> type <i>Hyalosphenia papilio</i>	<i>A. flavum</i> and <i>H. papilio</i> decrease from the base to the top. <i>C. arcelloides</i> type and <i>D. pristis</i> type increase to the top. <i>Pseudodifflugia fascicularis</i> is present for the first time in this profile, from 20cm to 10cm. Test concentration was too low to count at 5cm.
I	62.5-140	<i>Cyclopyxis arcelloides</i> type <i>Diffflugia pulex</i> <i>Hyalosphenia subflava</i>	<i>H. subflava</i> decreases gradually to the top. <i>C. arcelloides</i> type and <i>D. pristis</i> type are both present throughout this zone.

Table 5.7 Zone descriptions for CRM III based on testate amoebae

5.3.1 Stratigraphy

Sediment description for CRM III is shown in Table 5.6. Peat depth is 181cm. The basal 6cm (181-187cm) is composed of brown clay with a small amount of sand. The upper part of this profile is typical of ombrotrophic peat.

5.3.2 Testate amoebae

The top 140cm of the core was suitable for testate amoebae analysis (Table 5.7). Test concentration from 140cm to 160cm was too low to count and in samples 170cm and 180cm tests were almost completely absent. Sampling strategy, preparation and data processing was similar to that for cores CRM I and CRM II (Section 4.1.2). The testate amoebae diagram (Figure 5.13) is divided into two zones. A third zone could be constructed at 112.5cm to reflect the greater abundance of *Hyalosphenia subflava* below 112.5cm. However, this was not justifiable since the species assemblage is so similar to the assemblages to the depth of 62.5cm. The division between Zones I and II corresponds with a change in stratigraphy. At 65cm depth, the peat changes colour from nig 3 above 65cm to nig 4 beneath. The peat below 65cm is more humified (humo 3) than the peat directly above it. The base of Zone I does not correspond directly with a change in stratigraphy. Thirty three taxa were counted in this core.

Zone I 62.5-140cm Zone I is characterised by the abundance of three taxa; *Cyclopyxis arcelloides* type, *D. pulex* and *H. subflava*. These taxa, along with the presence of *Trigonopyxis arcula* and *Nebela militaris* suggest dry conditions with minor wetter phases at 110cm and 85cm indicated by the presence of *A. flavum* and *A. wrightianum*.

Zone II 0-62.5cm Zone II has a very diverse fauna, with 32 taxa present. This leads to a complicated interpretation on the basis of the qualitative information available about the taxa in the literature. The presence of high abundance of the *Amphitrema* spp., *Arcella* spp., *Centropyxis aculeata* type and *Hyalosphenia papilio* indicate very wet or aquatic conditions. Conversely, *Cyclopyxis arcelloides* type and *Nebela collaris* indicate a moderately dry environment. At the base of this zone, the taxa suggest very wet conditions, with a lower water table towards the top of the zone, although the presence of *Pseudodifflugia fascicularis* in the middle may contradict this, as according to Cash and Hopkinson (1909) it is an aquatic taxon. The surface sample (0cm) with an assemblage composed of *Assulina muscorum*, *C. arcelloides* type, *Heleopera sylvatica*, *H. subflava*, *Nebela collaris*, *N. flabellulum*, *N. militaris*, *N. tinctoria* and *Trigonopyxis arcula* overwhelmingly suggests much drier conditions.

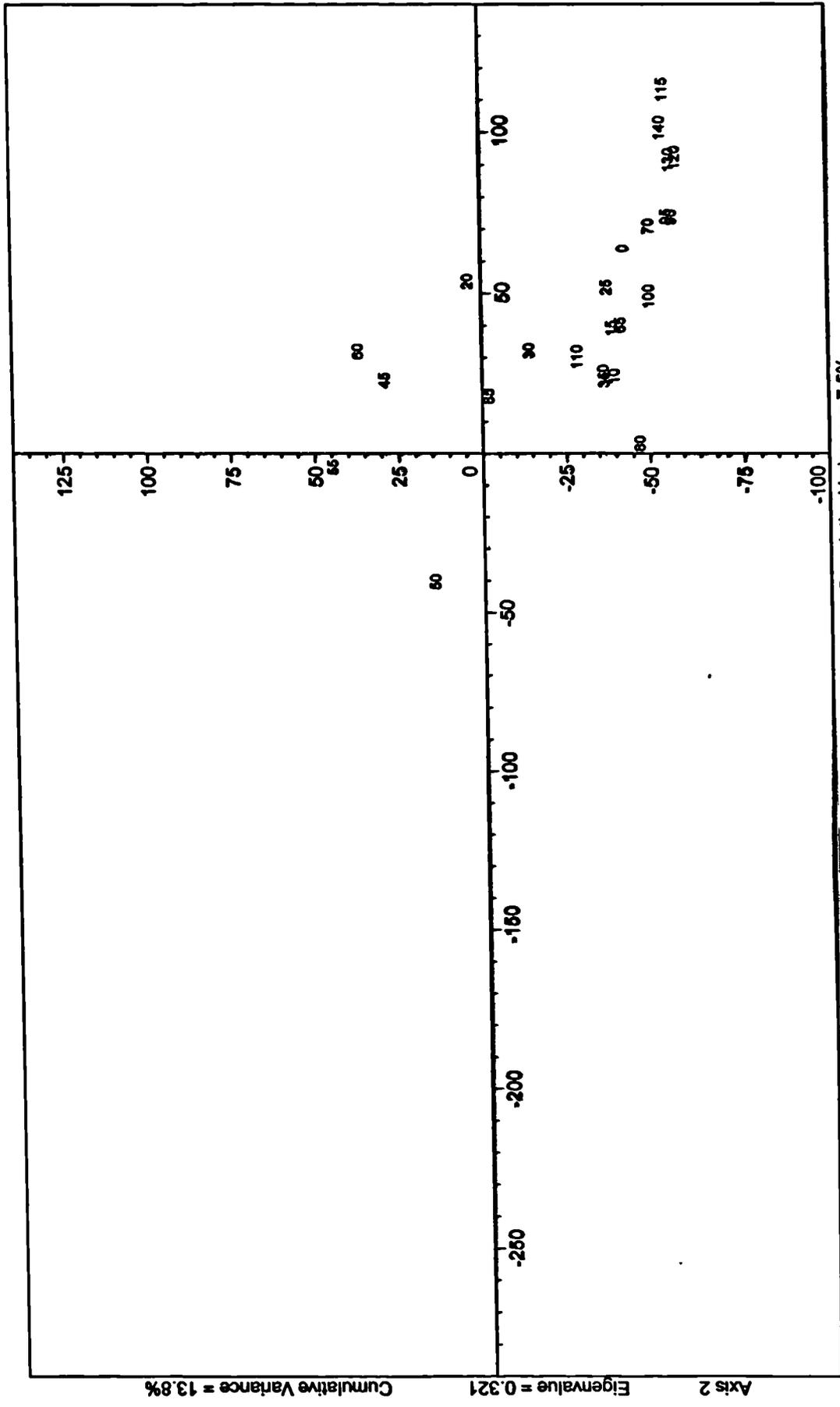
5.3.3 Ordination

Modern and fossil

The ordination plot for modern samples with fossil samples plotted as 'passive' is presented in Figure 5.14. Samples 115, 120, 130 and 140cm from the fossil data set are clustered in the bottom right corner of the plot, removed from the spread of modern samples. These fossil samples contain high abundance of *H. subflava* which do not have a good match with modern samples and therefore will limit the strength of the hydrological reconstructions.

Sample ordination

Samples from Zone I are clustered at the base of the plot, justified to the right (Figure 5.15). Samples from Zone II are clustered to the left side of the plot. Axis 1 appears to be related to depth, with two samples; 0cm and 25cm lying separate from the other samples from Zone II.



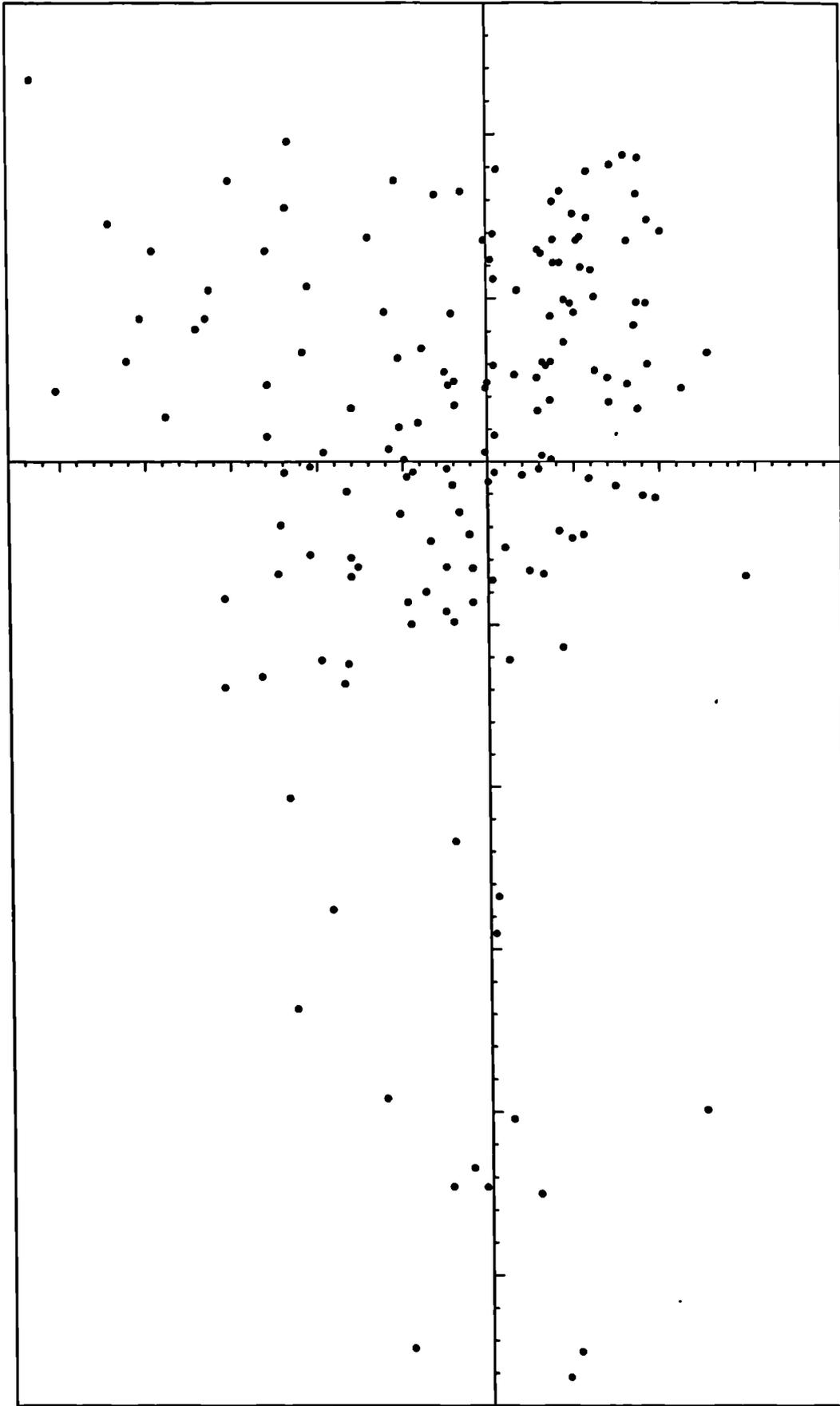


Figure 5.14 Modern and fossil DCA ordination for CRM III. Fossil samples (overlay) plotted as 'passive', modern samples plotted as circles

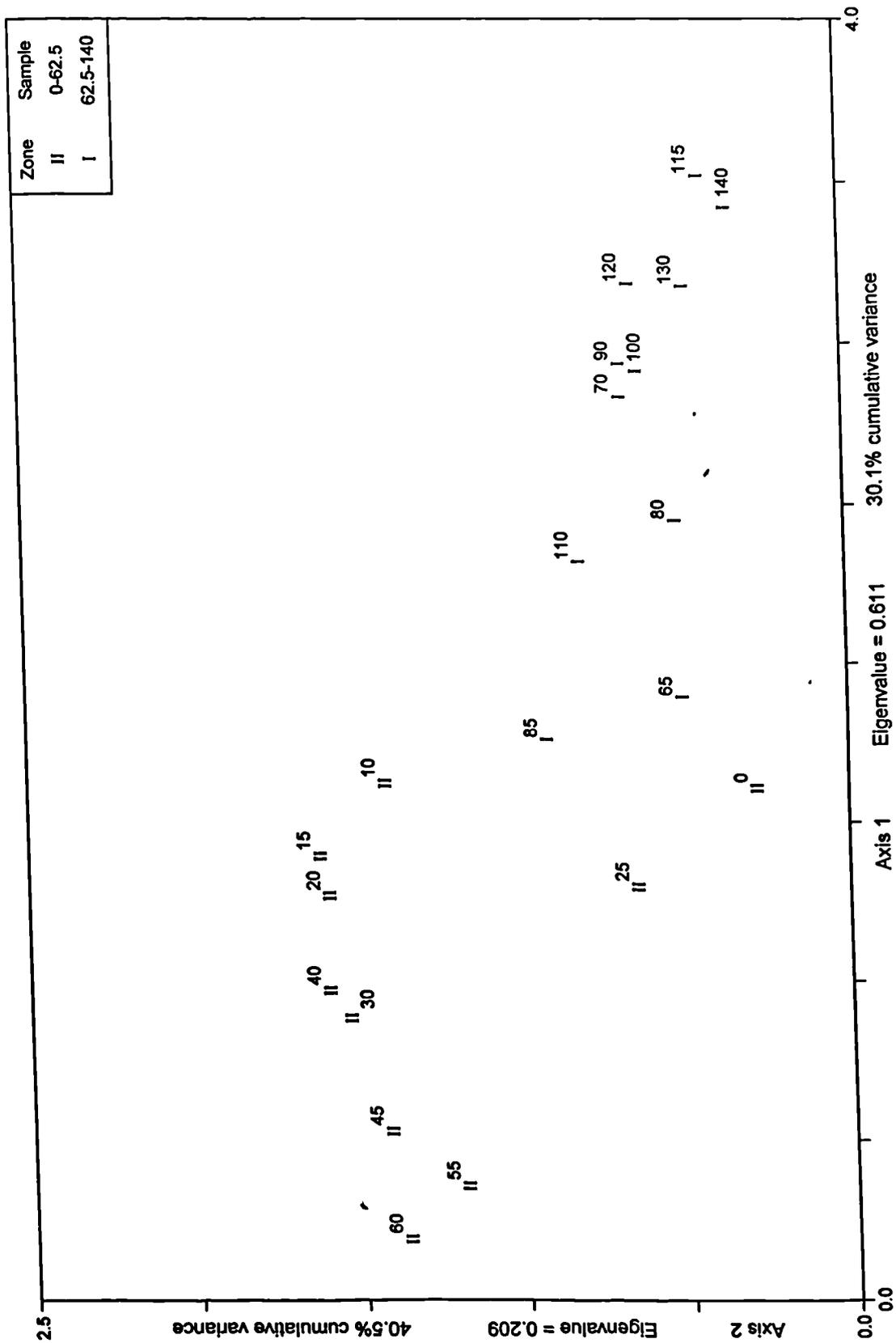


Figure 5.15 Sample ordination for CRM III

Species ordination

Fourteen taxa contain less than 5% abundance in every sample in which they were found (Figure 5.16). There is no distinct pattern to the distribution of less significant samples, with them scattered throughout the plot. *Hyalosphenia subflava* is an outlier, located on the far right of the plot. The most closely associated taxon is *Diffflugia pulex*. *Euglypha rotunda* and *Diffflugia bacillifera* are also outlier taxa.

5.3.4 Hydrological reconstructions

Water table reconstruction

The water table reconstruction for CRM III is presented in Figure 5.17. The basal sample of this core has a mean reconstructed water table value of -14cm. The wide confidence limits at the base of the core are associated with the dominance of *H. subflava* which has a poor modern analogue. There is a trend of increasing wetness to 65cm, with a low water table at 115cm of -15cm, rising to -8cm at 110cm peat depth. Between 85-80cm, there is a high reconstructed water table of -5cm below ground surface. The water table level falls again at 70cm to -10.7cm. From 60-45cm, the reconstructed water table produces a very wet curve of up to -2cm below surface. At 15cm there is a wide spread of confidence limits, with a mean value of -4.7cm, a maximum of -7.5cm and a minimum value of -1.5cm. This is attributable to the peak in *D. pristis* type which has a wide tolerance range. The surface sample (0cm) has a moderately dry reconstructed water table value of -8.8cm.

Moisture reconstruction

The reconstructed moisture curve for CRM III (Figure 5.18), shows wide fluctuations in the percentage moisture for each sample throughout the core. At the base of the core, from 140cm to 115cm, the mean moisture value is *ca.* 90%. At 110cm peat depth, the mean soil moisture value peaks at 95%. From 65cm to the surface of the core, there are dramatic fluctuations in the level of moisture content, with fluctuations of up to 10% between two adjacent points. At 50cm, the highest mean moisture value of 95.5% is achieved. These large fluctuations may be attributable to the presence of *Pseudodifflugia fascicularis* in this part of the core, which is not included in the modern analogue transfer function. The surface sample, 0cm, is the driest, with a mean value of 82%.

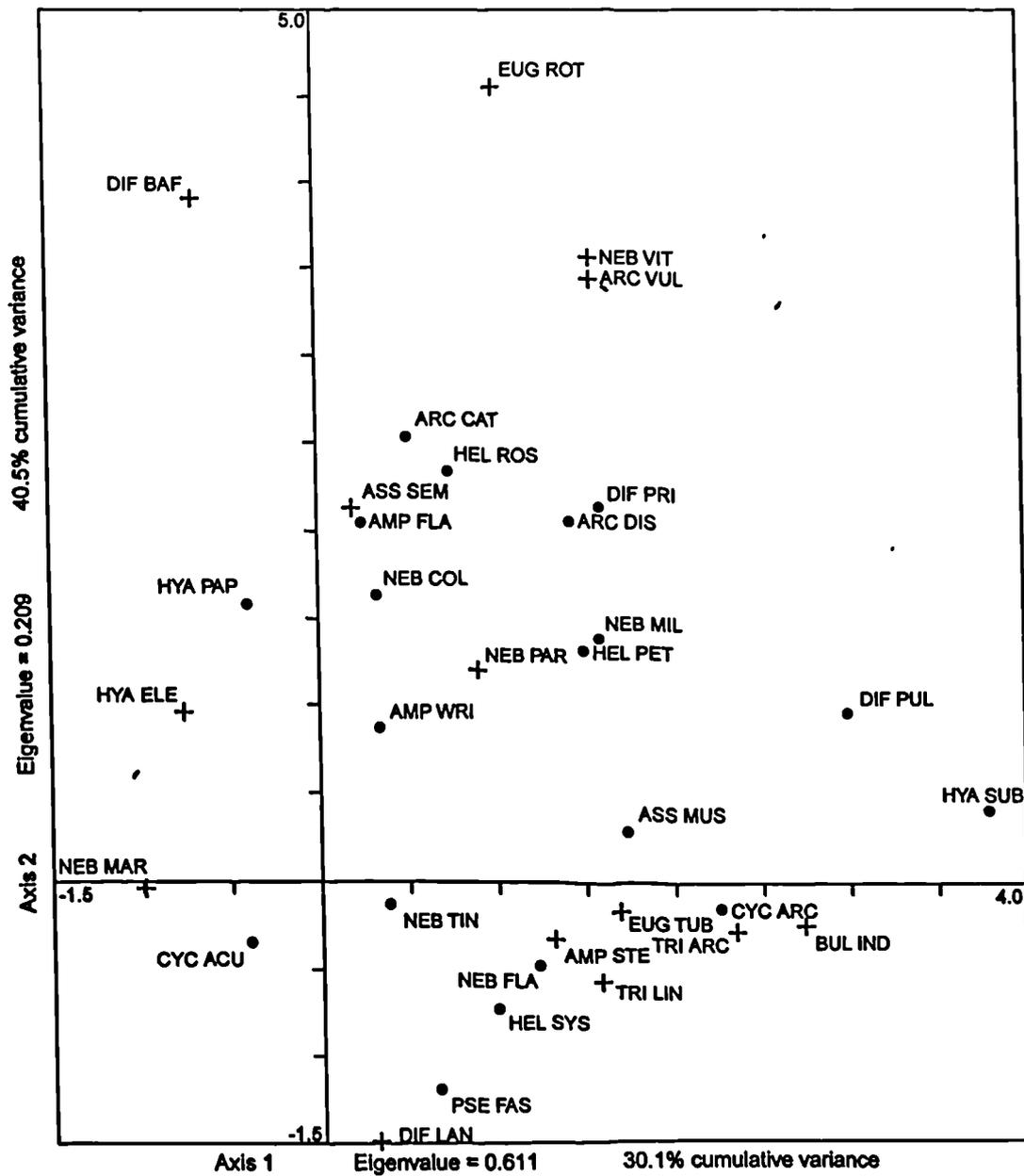


Figure 5.16 Species ordination for CRM III. Taxa with <5% abundance plotted as crosses, refer to Table 5.3 for species codes

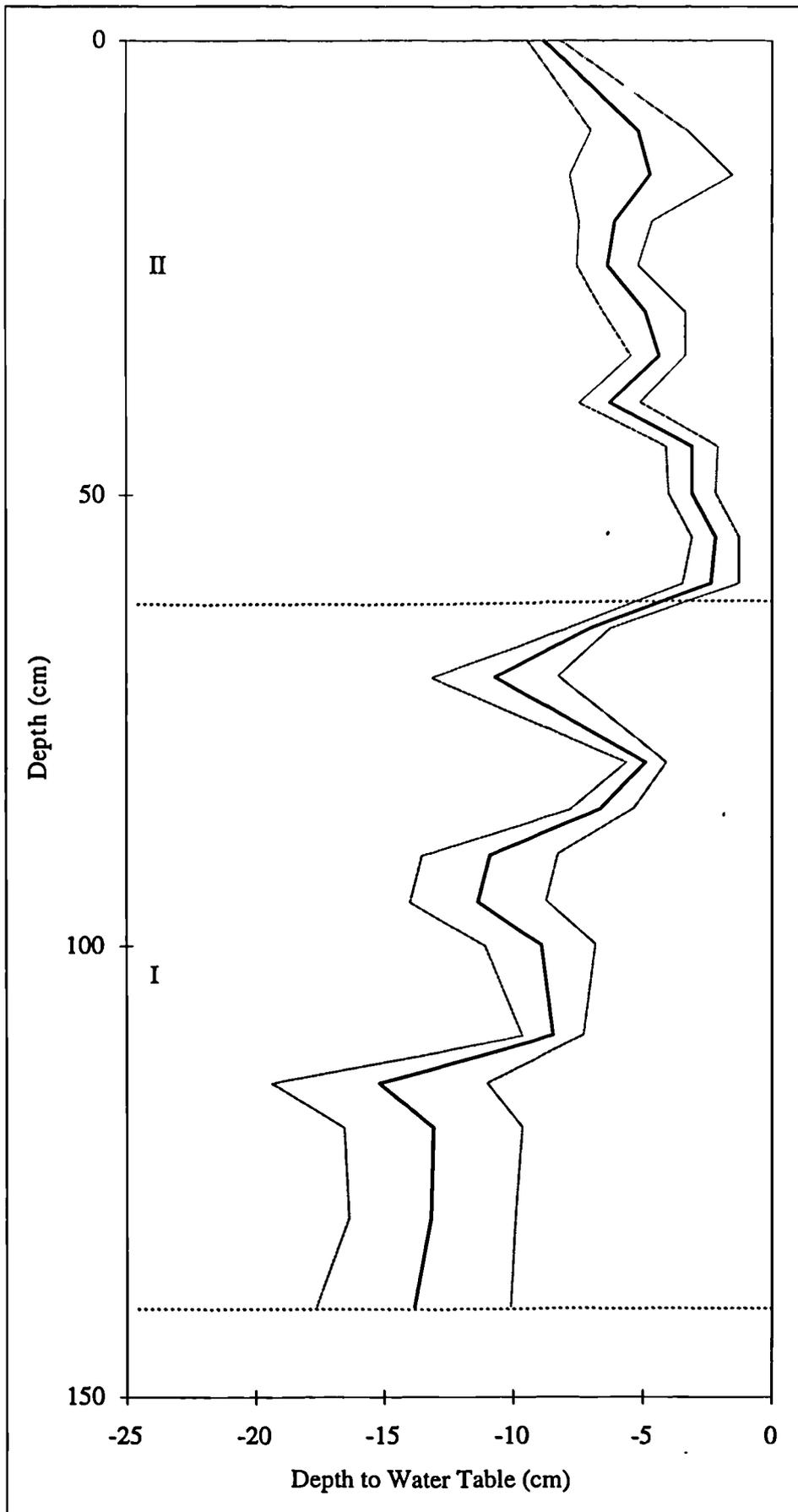


Figure 5.17 Mean water table reconstruction CRM III, with 2σ bootstrapped error estimates shown as thin lines. Assemblage zones marked.

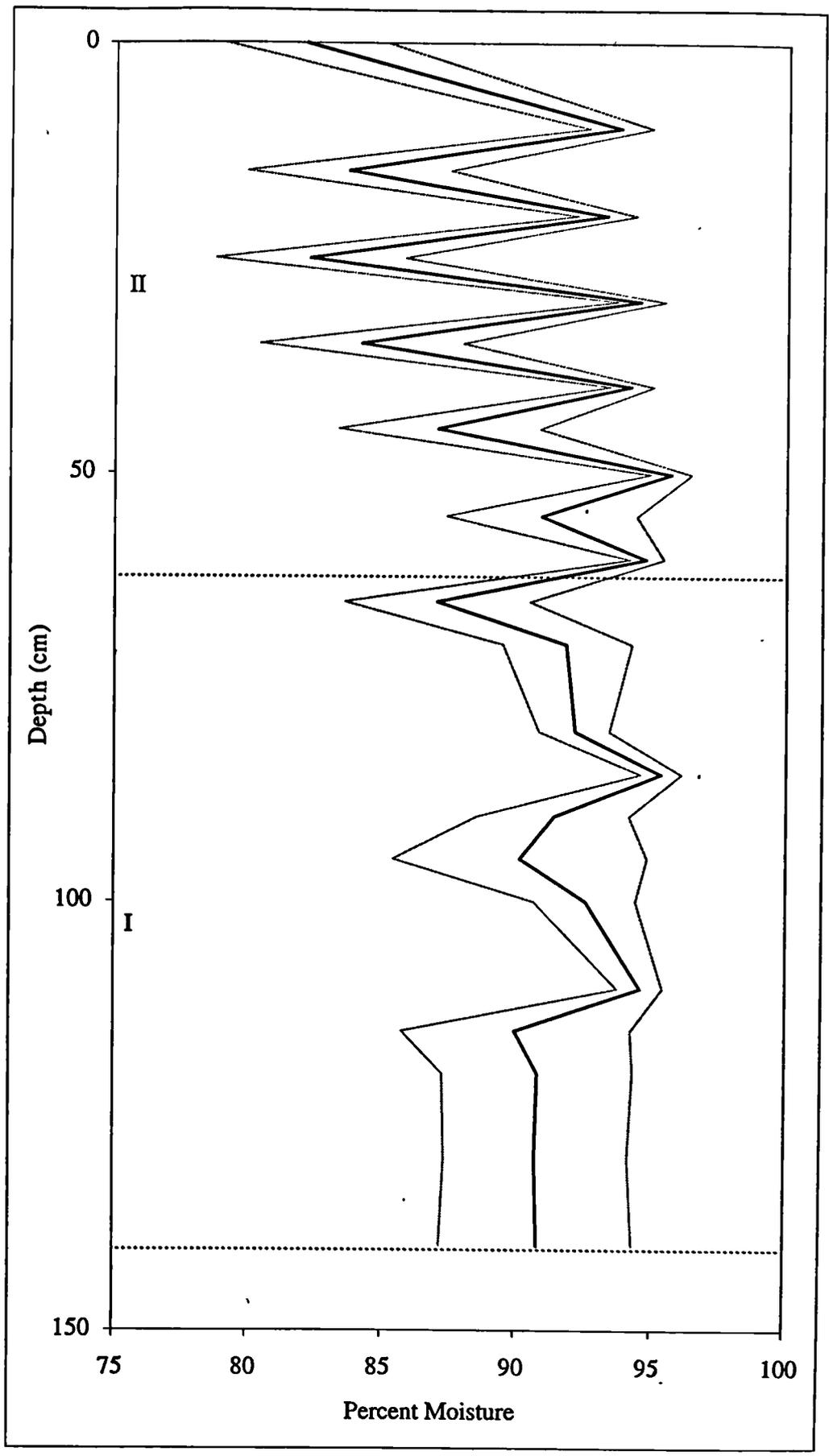


Figure 5.18 Mean moisture reconstruction CRM III, with 2σ bootstrapped error estimates shown as thin lines. Assemblage zones marked.

5.4 Coom Rigg Moss Core IV (CRM IV)

Core CRM IV was extracted from the centre of the mire in April 1995. Core CRM IV is used in conjunction with CRM I for micro-scale analysis of the replicability of the testate amoebae record (Chapter Nine). The location of core CRM IV is shown in Figure 3.3.

5.4.1 Stratigraphy

The stratigraphy of CRM IV is presented in Table 5.8. The stratigraphic description of CRM IV concurs with that of Chapman (1964a) as a *Sphagnum-Eriophorum* peat. Ericoid roots are often associated with more humified peat and macroscopic remains of *Eriophorum* spp. are common. CRM IV was extracted close to Chapmans' (1964a) grid reference I6. The presence of wood fragments below 230cm corresponds to Chapman's (1964) classification of brushwood peat. Above this depth, it is typical of ombrotrophic peat.

5.4.2 Testate amoebae

Subsampling, sample preparation, data processing and presentation follows that adopted for cores CRM I, CRM II and CRM III. Below 400cm, test concentration was poor. Thirty taxa were found in CRM IV (Figure 5.19). The testate amoebae profile has been divided into four assemblage zones (Table 5.9). The base of Zone I does not correspond with a change in stratigraphy. The top of Zone I, at 345cm, is asynchronous with a change in stratigraphy at 355cm. The top of Zone III at 67.5cm, corresponds with a stratigraphic change at 66cm. Above 66cm, the peat was lighter in colour and less humified than below this level.

Zone I 345-400cm This zone is dominated by *Diffugia pulex*. Between 85-90cm, the peak in *Amphitrema flavum* suggests wet conditions of up to 95% water content. The peak in *Habrotrocha angusticollis*, a rotifer, at 85cm, where over 40 individuals were counted also indicates wet conditions as de Graaf (1956), Tolonen (1966) and Tolonen *et al.* (1992) have found *Habrotrocha* to be a wet taxon inhabiting open water or bog hollows.

Zone II 207.5-345cm Zone II is characterised by a high representation of *H. subflava* and *D. pulex*. This probably represents dry conditions, (Table 4.4), except at 320cm and 260cm where the peak in *A. flavum* suggests wetter conditions.

Zone III 67.5-207.5cm This is a transitional zone, representing drier conditions at the base, as indicated by the abundance of *H. subflava*. The taxa at the top of the zone are typical of much wetter conditions reflected by the increased abundance of *A. flavum* and *A. wrightianum*. *D. pulex* decreases in abundance to the top of this zone. *A. muscorum* is well represented in this zone and is regarded as a cosmopolitan taxon (Warner, 1990).

Depth (cm)	Sediment Description
0 - 10	nig 3; strf 0; elas 3; sicc 1; humo 2. Tb ² Th ² surface vegetation, <i>Erica tetralix</i> , <i>Sphagnum tenellum</i> , <i>Juncus effusus</i> , <i>Molina caerulea</i> ,
10 - 14	nig 2; strf 0; elas 3; sicc 1; humo 2. Tb ² Th ² . partially decayed <i>Sphagnum</i> , <i>Eriophorum vaginatum</i>
14 - 36	nig 3; strf 1; elas 2; sicc 1; humo 2. Th ³ Tb ¹ . <i>Eriophorum vaginatum</i> and <i>Sphagnum</i> leaves, ericoid roots
36 - 41	nig 2; strf 1; elas 1; sicc 1; humo 2, Tb ¹ Th ³ <i>Sphagnum</i> stems preserved, <i>Eriophorum angustifolium</i>
41 - 55	nig 3; strf 1; elas 1; sicc 1; humo 2. Th ³ Sh ¹ <i>Eriophorum angustifolium</i>
55 - 66	nig 2; strf 0; elas 3; sicc 1; humo 1. Th ⁴ <i>Eriophorum angustifolium</i>
66 - 70.5	nig 3; strf 1; elas 2; sicc 1; humo 2. Th ³ Tb ¹ <i>Sphagnum</i> stems preserved, <i>Eriophorum angustifolium</i>
70.5 - 81	nig 2; strf 0; elas 1; sicc 1; humo 4. Sh ³ Tb ¹ highly humified peat, <i>Eriophorum angustifolium</i>
81 - 105	nig 3; strf 1; elas 1; sicc 1; humo 3 Tb ³ Th ¹ leaves preserved, <i>Eriophorum angustifolium</i>
105 - 130	nig 4; strf 0; elas 1; sicc 1; humo 3. Tb ² Sh ² Th ⁺ With <i>Eriophorum vaginatum</i>
130 - 140	nig 4; strf 0; elas 0; sicc 1; humo 3. Sh ³ Tb ¹ well humified peat with <i>Eriophorum vaginatum</i>
140 - 150	nig 4; strf 0; elas 0; sicc 1; humo 3. Sh ² Th ² well humified peat with <i>Eriophorum vaginatum</i>
150 - 230	nig 4; strf 0; elas 0; sicc 1; humo 4. Sh ³ Th ¹ ericoid roots in highly humified peat matrix
230 - 255	nig 4; strf 0; elas 0; sicc 1; humo 4. Sh ⁴ Tl ⁺ Th ⁺ roots and woody fragments present in highly humified peat matrix
255 - 280	nig 4; strf 0; elas 0; sicc 1; humo 4. Sh ⁴ Th ⁺ ericoid roots present
280 - 330	nig 4; strf 0; elas 0; sicc 1; humo 4. Sh ⁴ very humified peat, plant structure hardly discernible
330 - 355	nig 4; strf 0; elas 0; sicc 1; humo 4. Sh ⁴ Th ⁺ Tl ⁺ ericoid roots and woody fragments present in highly humified peat matrix
355 - 380	nig 4; strf 0; elas 0; sicc 1; humo 4. Sh very well humified peat, plant structure hardly discernible
380 - 430	nig 4; strf 0; elas 0; sicc 2; humo 4. Sh ⁴ Th ⁺ Tl ⁺ highly humified peat with presence of roots and woody fragments
430 - 455	nig 4; strf 0; elas 0; sicc 2; humo 4. Sh ³ Th ¹ Tl ⁺ ericoid roots and woody fragments present in highly humified peat matrix
455 - 500	nig 4; strf 0; elas 0; sicc 2; humo 4. Sh very humified peat, plant structure hardly discernible
500 - 555	nig 4; strf 0; elas 0; sicc 2; humo 4. Sh ⁴ Tl ⁺ <i>Betula</i> roots

Table 5.8 Stratigraphic description of CRM IV using the Troels-Smith (1955) sediment description system

Zone	Depth (cm)	Major Taxa	Zone description
IV	0-67.5	<i>Amphitrema</i> spp. <i>Assulina muscorum</i> <i>Cyclopyxis arcelloides</i> type <i>Diffugia pristis</i> type	This zone is dominated by <i>Amphitrema</i> spp. at the base which are then replaced by a more diverse assemblage comprised of <i>A. muscorum</i> , <i>C. arcelloides</i> type, <i>Euglypha</i> spp. and <i>Heleopera</i> spp. Test concentration increases to the top
III	67.5-207.5	<i>Amphitrema</i> spp. <i>Diffugia pristis</i> type <i>Diffugia pulex</i> <i>Hyalosphenia subflava</i>	There is a greater diversity of taxa in this zone than in the preceding zones. The zone is dominated by <i>D. pulex</i> . <i>H. subflava</i> values fluctuate in this zone, reaching a maximum abundance of 76% at 165cm but below 25% in the rest of the zone and declines towards the top. At the top there is a rise in the abundance of <i>A. flavum</i> . <i>A. wrightianum</i> , <i>C. arcelloides</i> type which corresponds with the decline in <i>H. subflava</i> .
II	207.5-345	<i>Amphitrema flavum</i> <i>Diffugia pristis</i> type <i>Diffugia pulex</i> <i>Hyalosphenia subflava</i>	This zone is characterised by the high abundance of <i>H. subflava</i> . There are peaks in <i>A. flavum</i> at 320cm and 260cm which correspond with troughs in the abundance of <i>H. subflava</i> . <i>A. wrightianum</i> and <i>A. stenostoma</i> increase towards the top. <i>D. pulex</i> and <i>D. pristis</i> type are present throughout.
I	345-400	<i>Amphitrema flavum</i> <i>Assulina muscorum</i> <i>Diffugia pristis</i> type <i>Diffugia pulex</i>	This zone is dominated by <i>D. pulex</i> throughout, with high abundances of <i>A. muscorum</i> and <i>D. pristis</i> type. <i>A. flavum</i> is abundant in the lower part, the peak of 70% abundance corresponds with a peak in abundance of the rotifer <i>Habrotrocha angusticollis</i> with over 40 rotifer tests counted in sample 385cm.

Table 5.9 Zone descriptions for CRM IV based on testate amoebae

Zone IV 0-67.5cm The faunal assemblage in this zone is complicated to interpret. The overall conditions are wet or moderately wet, with high values of *Amphitrema* spp. The presence of *Assulina seminulum*, *Bullinularia indica* and *Trigonopyxis arcula* suggest very dry conditions, although these taxa are found in relatively small numbers. *D. pristis* type and *D. pulex* are well represented and the absence of information about *D. pulex* hinders interpretation of this zone. The presence of *Arcella discoides* type at the top of the zone suggests very wet conditions (Tolonen, 1986; Tolonen *et al.*, 1992; Warner, 1987).

5.4.3 Ordination

Modern and fossil

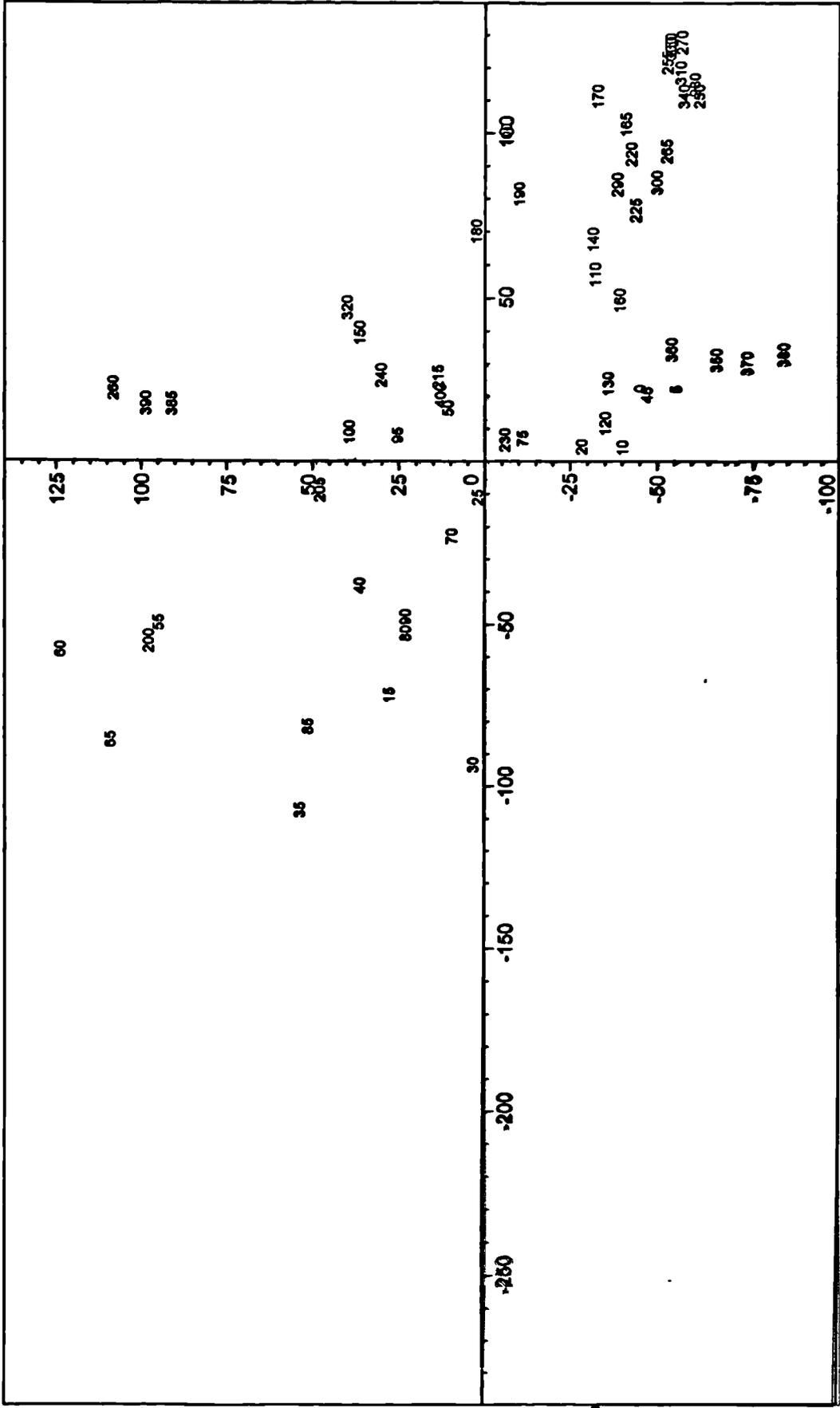
Figure 5.20 shows the ordination plot for CRM IV, with fossil samples plotted as 'passive' over the modern ordination. More fossil samples are peripheral to the modern ordination plot than in the other three cores from Coom Rigg Moss. Samples 65-55cm and 200cm, from the fossil data, are peripheral to the modern data set. These samples are dominated by *A. flavum* and *A. wrightianum*. Samples 260cm, 385cm and 390cm, also dominated by *A. flavum*, form part of the gradation from modern to fossil samples. In the bottom right corner, there is another group of fossil samples that are removed from the spread of modern samples. Samples 165cm, 220cm, 255cm, 265cm, 270cm, 330cm are dominated by *H. subflava*. Samples 350cm, 370cm and 380cm are dominated by *D. pulex* and *D. pristis* type. The samples that lie outside the spread of modern samples are unlikely to have reliable reconstructed values, since they are not 'good matches' with the transfer function data set.

Sample ordination

Samples at 5cm and 10cm are removed from the main cluster of points, indicating that they have different taxon compositions (Figure 5.21). There are no strong relationships between the zones and sample distribution, except that samples from Zones I and II are mostly clustered to the right side of the plot and from Zones III and IV to the left side.

Species ordination

Core CRM IV has an axis 1 eigenvalue of .559 and an axis 2 eigenvalue of .264 (Figure 5.22). There is a broader spread of taxa about Axis 2 in core CRM IV than in other cores from Coom Rigg Moss. *H. subflava* is located on the far right side of the plot in close proximity to *D. pristis* type and *D. pulex*. Sixteen taxa occur with less than 5% abundance in every sample in which they were found. These species are of less significance to the ordination than those taxa that have greater abundance and most are located on the negative side of axis 2.



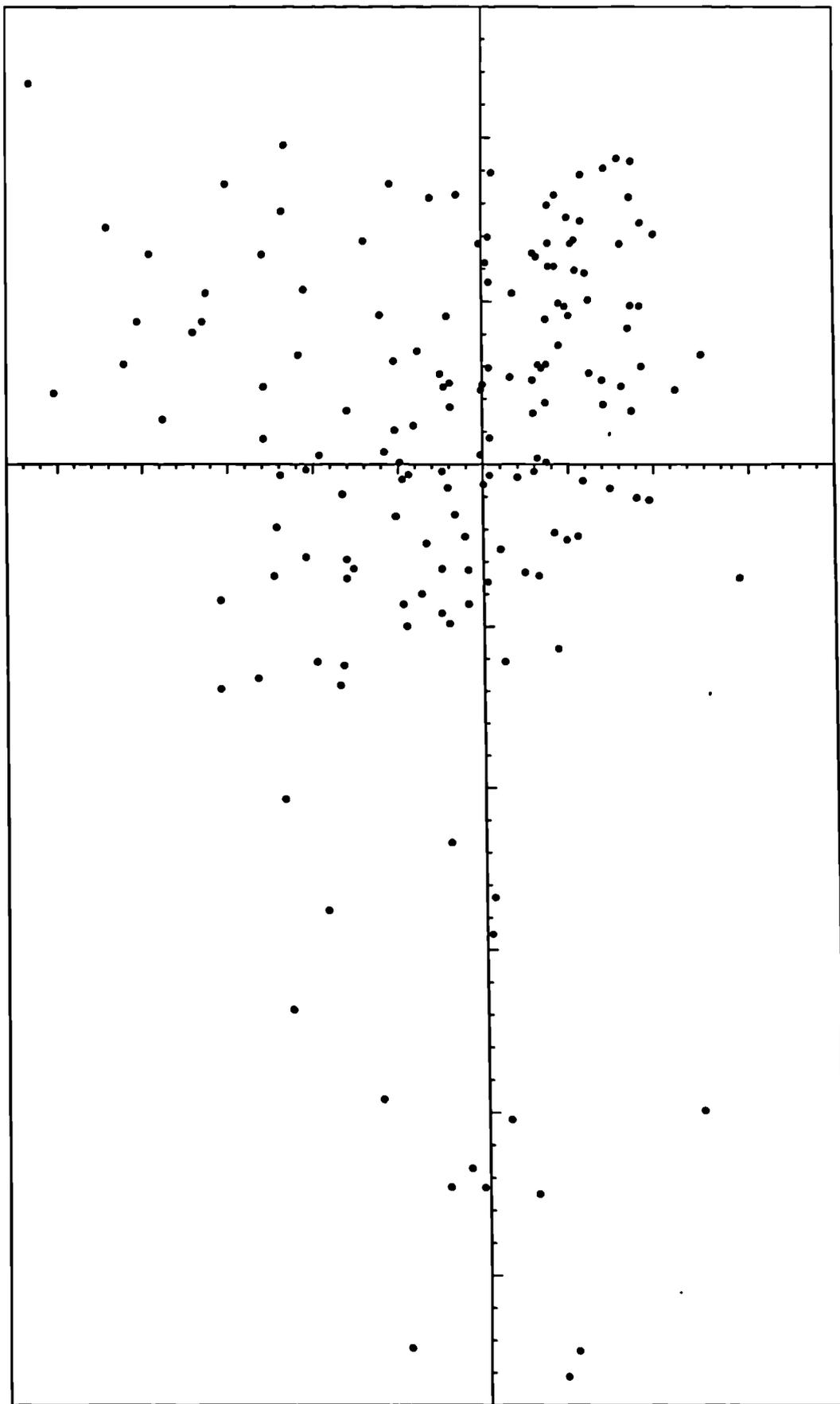


Figure 5.20 Modern and fossil DCA ordination for CRM IV. Fossil samples (overlay) plotted as 'passive', modern samples plotted as circles

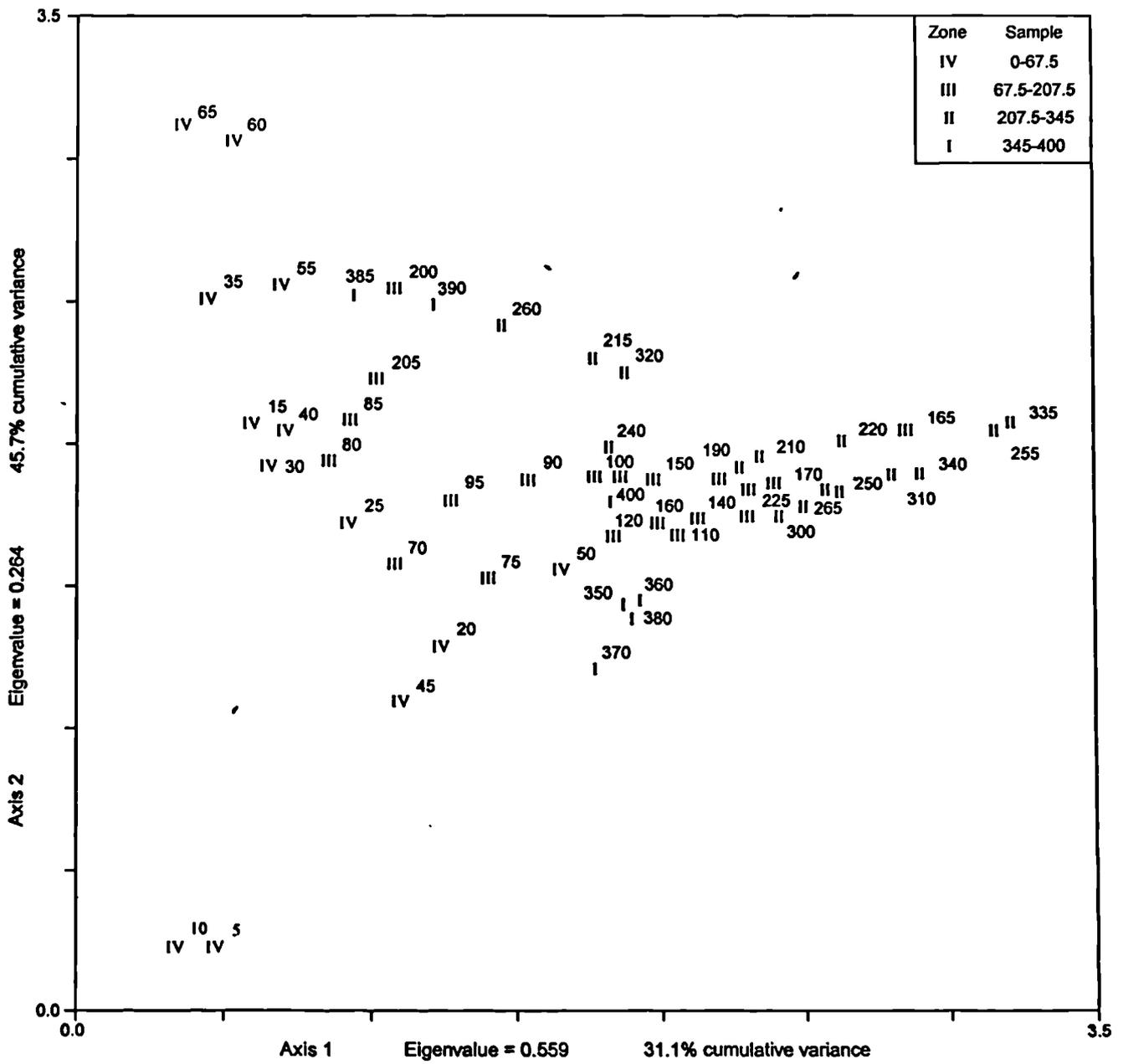


Figure 5.21 Sample ordination for CRM IV

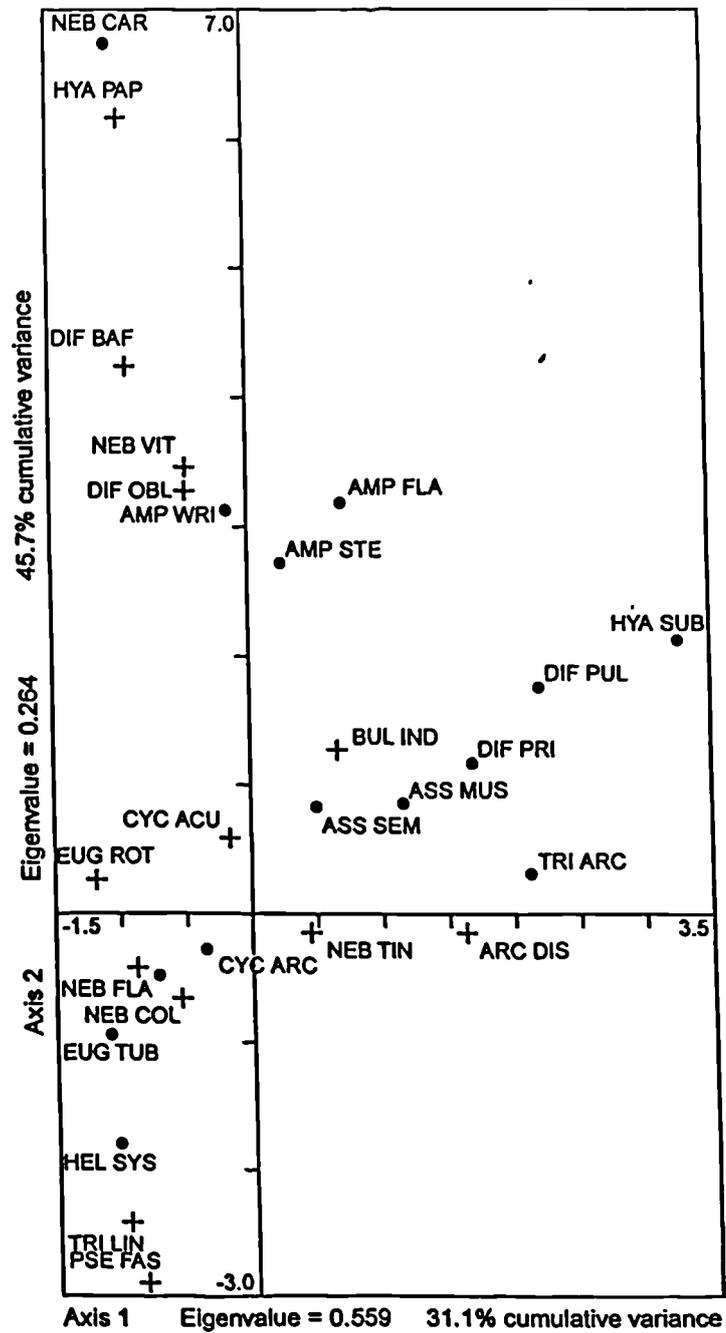


Figure 5.22 Species ordination for CRM IV. Taxa with <5% abundance plotted as crosses, refer to Table 5.3 for species codes

5.4.4 Hydrological reconstructions

Water table reconstructions

Figure 5.23 shows the reconstructed water table for CRM IV using the WA model. CRM IV has a much more sinuous hydrological curve than the others cores from Coom Rigg Moss. The base of the core has a mean value of -4.4cm below ground surface. Between 390-380cm, the water table rises to -2.7cm below ground surface, at 380cm there are wide confidence intervals around the reconstructed mean (max -9.8cm; mean -5cm; min -0.3cm) associated with the abundance of *D. pulex*. Between 340-330cm, there is a low water table reaching an extreme of -16.5cm below surface at 335cm. *H. subflava* dominates the faunal assemblage at this point, which accounts for the wide confidence limits.

Between 265cm and 255cm, there are wide confidence intervals and deep water tables of -13.5cm and -15.5cm respectively. These are associated with the dominance of *H. subflava* in the testate amoebae assemblage. At 260cm there is a high water table of -3.4cm associated with a peak in *A. flavum*. At 200cm, there is a very high reconstructed water table with narrow confidence limits with a maximum of -3cm, mean of -1cm and minimum value of -0.5cm. This is very wet and is associated with high abundances of *Amphitrema* spp. From 200cm to 100cm, the faunal assemblage is dominated by *D. pulex*, which accounts for the wider confidence limits between these depths. At 165cm, there is a peak in *H. subflava* resulting in a drier reconstructed value at this level. However, for the reasons discussed earlier, this is unlikely to be a representative reconstructed value.

The top metre of peat has narrower confidence limits than at depth down the core. This is because there is a greater diversity of taxa in the top metre, where more taxa have analogue values with narrow tolerance ranges. The curve fluctuates markedly in the top metre. Between 35-30cm the water table has a high reconstructed value of -2cm. From 15cm to the surface, there is a trend of lowering water table. At 15cm depth, the water table is -3cm, this drops to -6.7cm at 0cm. As with the other cores at Coom Rigg Moss, CRM IV exhibits drier surface conditions than the immediately underlying samples.

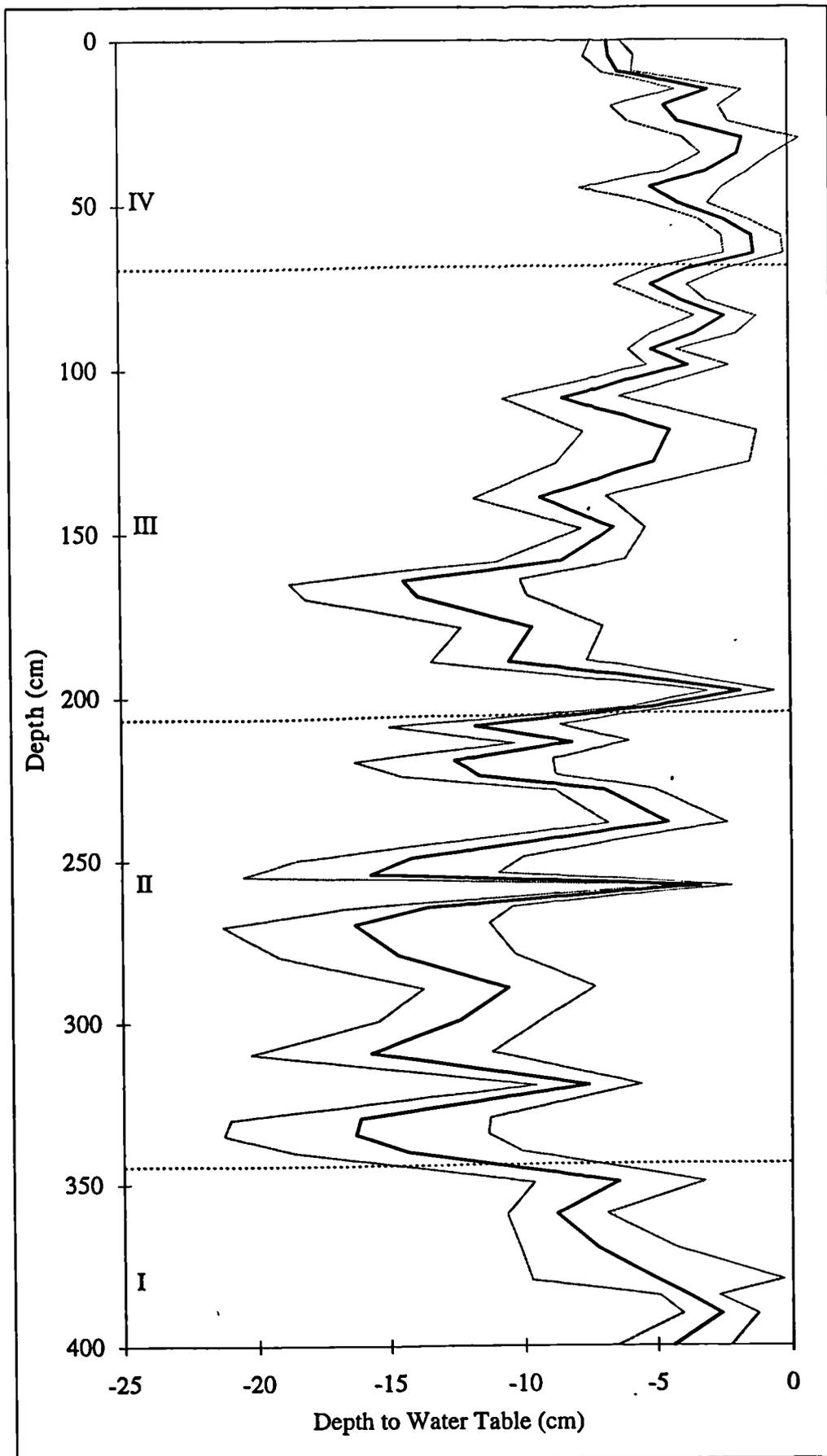


Figure 5.23 Mean water table reconstruction CRM IV, with 2σ bootstrapped error estimates shown as thin lines. Assemblage zones marked.

Moisture reconstructions

The moisture reconstruction for CRM IV is presented in Figure 5.24. The basal sample at 400cm has a mean reconstructed moisture value of 94%. From 385cm to 340cm, the moisture content of the peat drops to 90%. The wide confidence limits between these points are related to the high abundance of *D. pulex*. The moisture content rises at 320cm to 95% associated with a peak in *A. flavum*. The moisture content drops from 310cm to 265cm and rises to 95% again at 260cm. This peak also coincides with a peak in *A. flavum*. From 190cm to 100cm, the curve is relatively complacent, fluctuating between 92-95% moisture content. The top metre of the curve is more sinuous than at depth down the core. Between 65cm to 55cm, the mean reconstruction peaks at 97% with very narrow confidence limits, which is also related to large peaks in *A. flavum*. From 10cm peat depth, with a moisture value of 93%, the moisture level drops at the surface to between 82-83% moisture. This is the driest reconstructed value for the entire core.

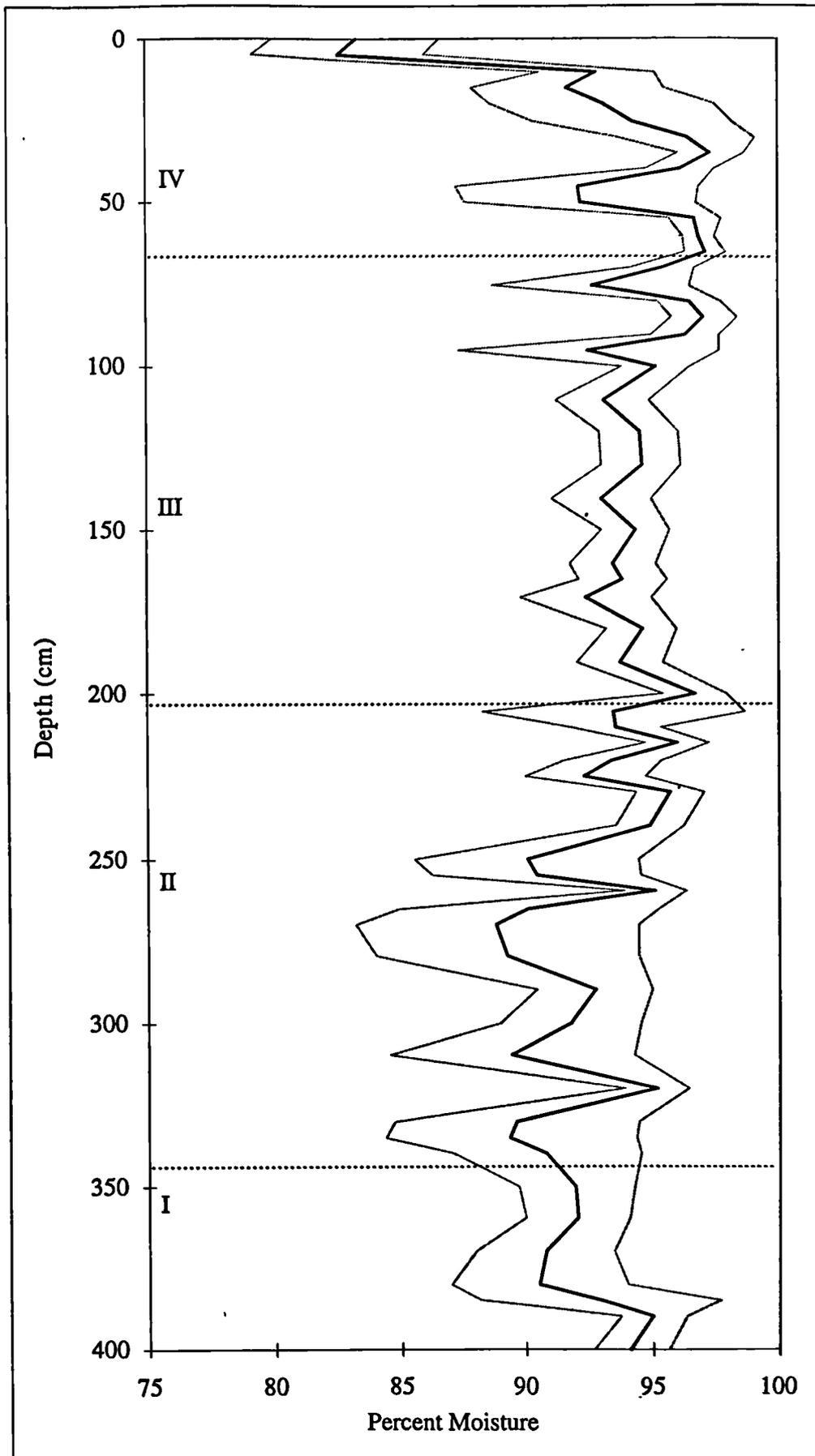


Figure 5.24 Mean moisture reconstruction CRM IV, with 2σ bootstrapped error estimates shown as thin lines. Assemblage zones marked.

5.5 Chronology

5.5.1 Pollen

Pollen sampling rationale and preparation procedure were set out in Chapter Four. The aim of pollen analysis was to provide a biostratigraphic correlation to be used in conjunction with the radiocarbon dates. The initial sampling interval chosen was 20cm to give a general indication of major changes in the pollen spectra. The surface 20cm was counted at closely spaced intervals of 5cm, for a more detailed examination of recent peat accumulation. The pollen spectra are difficult to correlate clearly apart from a few depths. At Coom Rigg Moss, there are three horizons identified as biostratigraphic zones. Table 5.10 sets out these pollen marker horizons, which are also shown on the pollen diagrams, Figures 5.25 - 5.28.

Core	A	B	C
CRM I	17.5	70	310
CRM II	17.5	70	-
CRM III	2.5	70	-
CRM IV	17.5	90	350

Table 5.10 Changes in pollen spectra and depths for the four Coom Rigg Moss cores. A-C represent changes noted on the diagrams and described in the text.

Position A refers to a clearly identifiable rise in *Pinus* pollen which relates to large scale forestry planting of the Kielder Forest. Planting began in 1926 and comprised 69% sitka spruce, 9% lodgepole pine and 3% Scots pine (Section 3.3). Between 1954-1957 the land surrounding Coom Rigg Moss was planted with sitka spruce and lodgepole pine and in 1974, the land to the south of the bog was planted with lodgepole pine (Smith and Charman, 1988; Merricks, 1995). The pollen horizons therefore form a useful chronological maker for this period. Position B relates to the final decline in *Alnus* pollen to below 5% TLP and is clearly identifiable in all profiles. It is also characterised by a rise in *Plantago lanceolata*. Position C marks the point at which a rise in Cyperaceae occurs, together with a decline in *Alnus* and a smaller rise in Poaceae in cores CRM I and CRM IV (Figures 5.25 and 5.28), but is not detected in CRM II and

CRM III (Figures 5.26 and 5.27). These three markers provide a limited comparison between cores, but it is not possible to provide reliable chronologies for all cores on this basis.

The best marker is position A, the anthropogenic *Pinus* rise (APR) which dates from 1926 and was used as an additional chronological marker in conjunction with the radiocarbon dates to calculate the sedimentation rate and age of each sample. Although planting on the land immediately surrounding Coom Rigg Moss did not take place until the 1950s, the APR is assigned the date 1930 (20BP) because it is likely that the initial rise in *Pinus* above background levels took place soon after planting, with a further rise in *Pinus* levels as more of the forest was planted.

5.2.2 Radiocarbon ages

Conventional radiocarbon ages were calibrated using CALIB 3.0.3c (Stuiver and Reimer, 1993a,b). This is set out in Chapter Four, Section 4.1.5. Figures 5.29-5.31 show the location of calibrated ^{14}C ages BP in relation to depth of core, with 2σ confidence intervals for each date, for cores CRM I, CRM II and CRM IV. The APR is also marked on these diagrams. There are no confidence limits for the APR. Linear interpolation for CRM III is not presented, since there was only one radiocarbon date from this core, between 110-115cm (Table 4.5) and there were no samples between the APR (2.5cm) and the next testate amoebae sample. However, estimated ages were calculated on the same basis as the other cores, by extrapolating from the date at 112.5cm to the surface at 1995 and from the date, at the same gradient, to the base of the core. This is rather simple, but for such a short core, of which only the top 140cm contained testate amoebae, it was not justifiable to assign this core more radiocarbon dates which would have improved the accuracy of sample-age estimation.

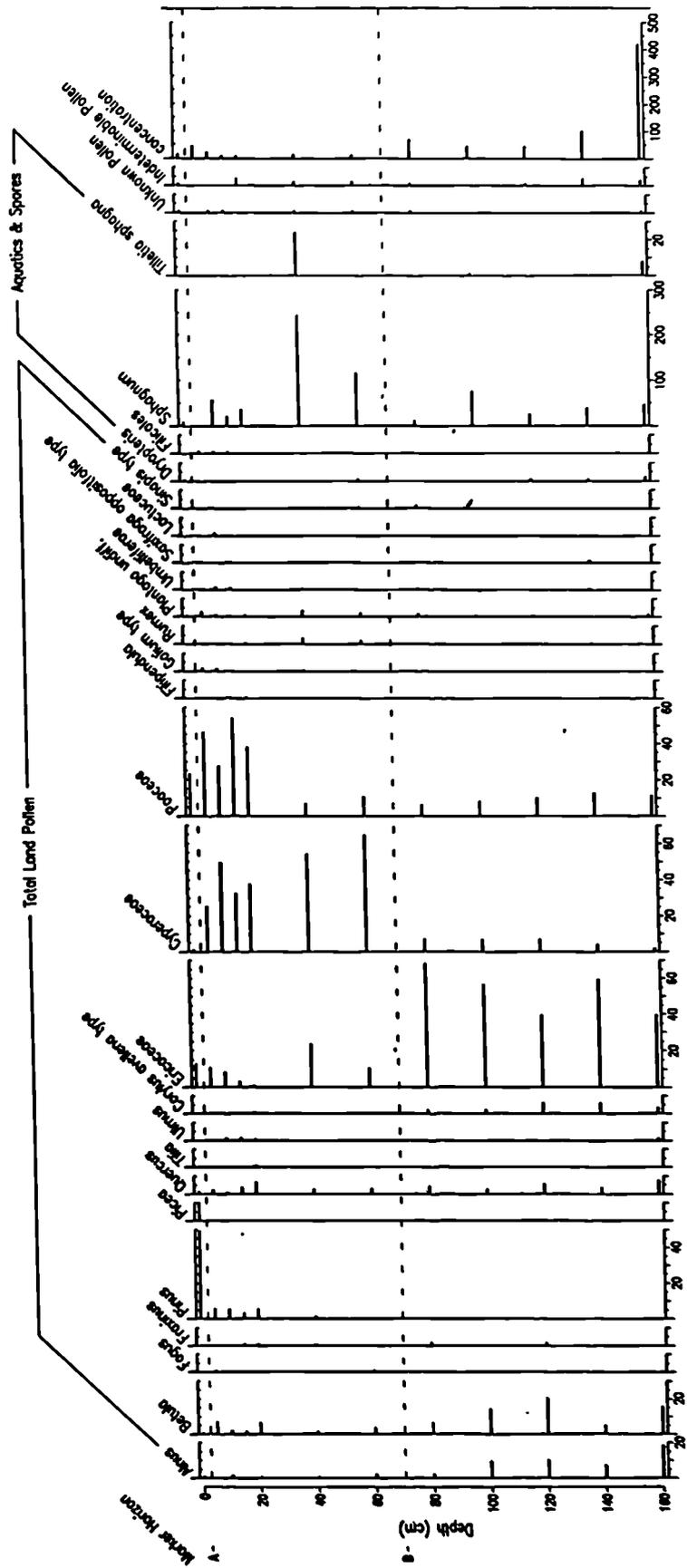


Figure 5.27 CRM III percentage pollen diagram

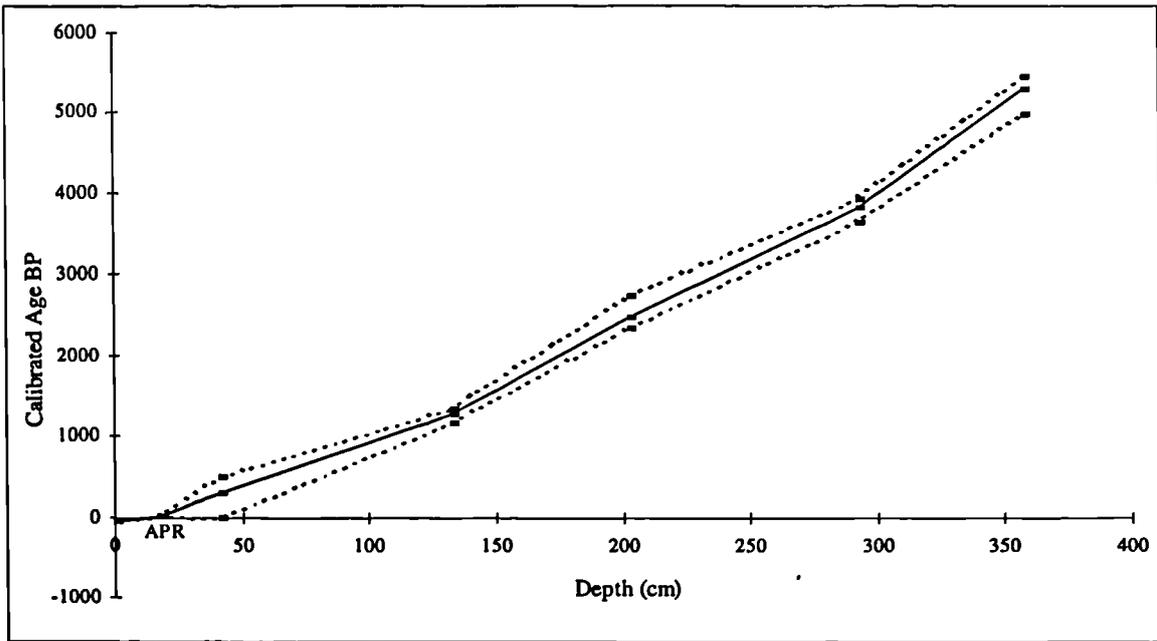


Figure 5.29 Coom Rigg Moss I - linear interpolation of sample ages. Solid line - median linear interpolation from radiocarbon dates and APR, dashed lines - 2σ confidence limits on

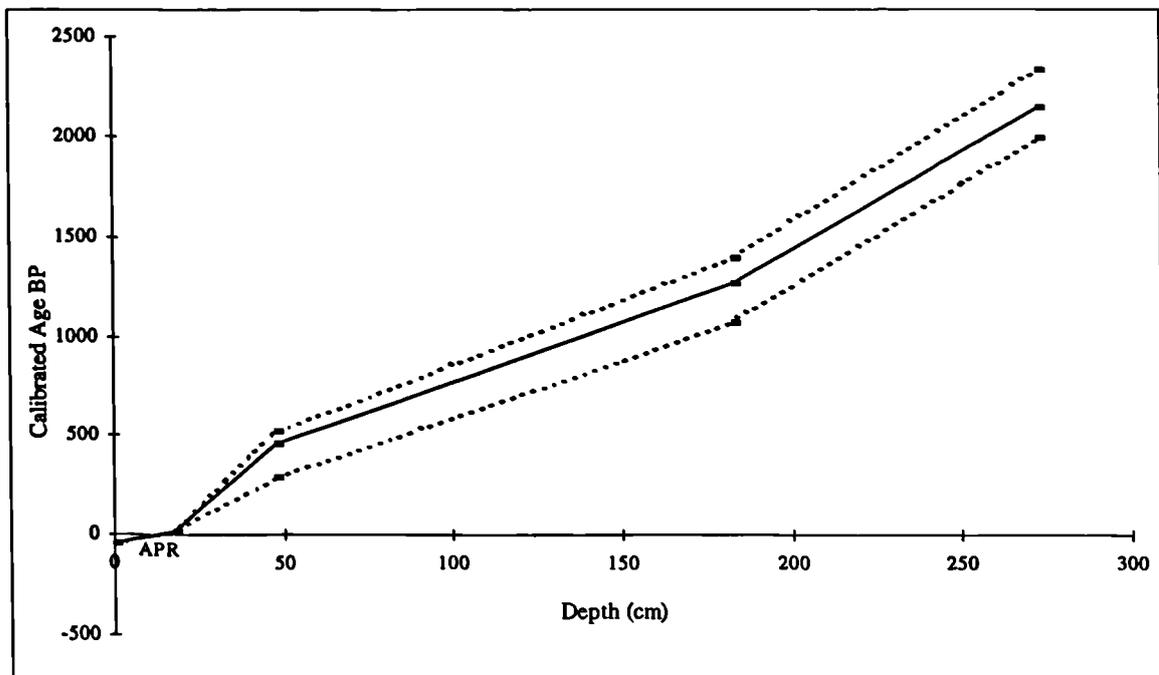


Figure 5.30 Coom Rigg Moss II - linear interpolation of sample ages. Solid line - median linear interpolation from radiocarbon dates and APR, dashed lines - 2σ confidence limits on

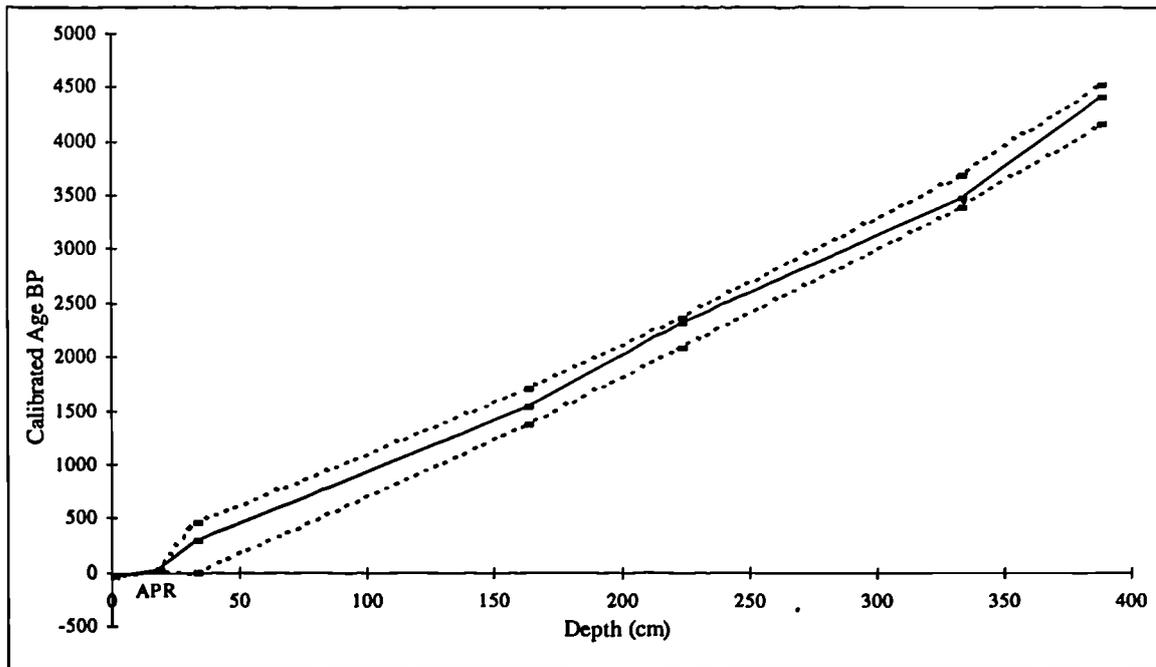


Figure 5.31 Coom Rigg Moss IV - linear interpolation of sample ages. Solid line - median linear interpolation from radiocarbon dates and APR, dashed lines - 2σ confidence limits on

Table 5.11 sets out the estimated accumulation rates for CRM I, calculated by taking the mid-point between radiocarbon dates and dividing by the years from that sample to the surface (1995) at that point. From the base of the peat core to 297AD, the peat accumulation rate is *ca.* 12.5 years per centimetre. At 85cm depth, the accumulation rate is 10 years per centimetre and in the surface layer, the acrotelm, the accumulation rate is approximately 2.5 years per centimetre. This is because the undecomposed *Sphagnum* moss has not undergone compaction. Accumulation rates for CRM II and CRM III are not presented as these cores do not have chronologies which are as well constrained as CRM I and CRM IV.

Depth (cm)	Year BC/AD	year/cm
0-40	1901AD	5
40-130	1177AD	10
130-200	163BC	12.5
200-290	1161BC	12.5
290-355	2505BC	14

Table 5.11 CRM I accumulation rate (yr/cm)

Depth (cm)	Year BC/AD	year/cm
0-30	1939AD	4
30-160	969.5AD	10
160-220	65BC	11
220-330	914BC	11
330-385	1949BC	11

Table 5.12 CRM IV accumulation rate (yr/cm)

Figure 5.31 shows the linear interpolation of sample ages from the radiocarbon dates for CRM IV. The gradient of the line indicates the rate of peat accumulation for this core. This shows that CRM IV, although deeper than CRM I, is younger at the point where the testate amoebae assemblage first occurs. CRM I is shallower where testate amoebae no longer have a countable concentration and the peat is older than CRM IV at that depth. Figures 5.32-5.35 show the percentage testate amoebae chronologies for cores CRM I to CRM IV.

Table 5.12 shows the approximate accumulation rates for CRM IV. At the base of the core, to 65BC, peat accumulation is about 11 years per centimetre. Above this, to 970AD, accumulation is about 10 years per centimetre and in the acrotelm, accumulation is about 4 years per centimetre due to the uncompact *Sphagnum* moss.

5.6 Conclusions

The top 1m to 1.5m of each core from Coom Rigg Moss have better hydrological reconstructions than at depth down the cores. This is because in the upper peats there is a greater diversity of taxa, more of which have good modern analogues. Sampling for the modern analogue transfer function was carried out by Woodland (1996) on sites with conservation status that had long-term hydrological monitoring regimes. These sites are generally wetter which causes the bias in the analogue data set. The wet phases in the palaeohydrological record have better reconstructions than the dry sections. There are three taxa that dominate the testate amoebae assemblage which have either no, or poor modern analogues. Poor modern analogues are regarded as those taxa with large tolerance ranges or inaccurate optima values, when compared to published data.

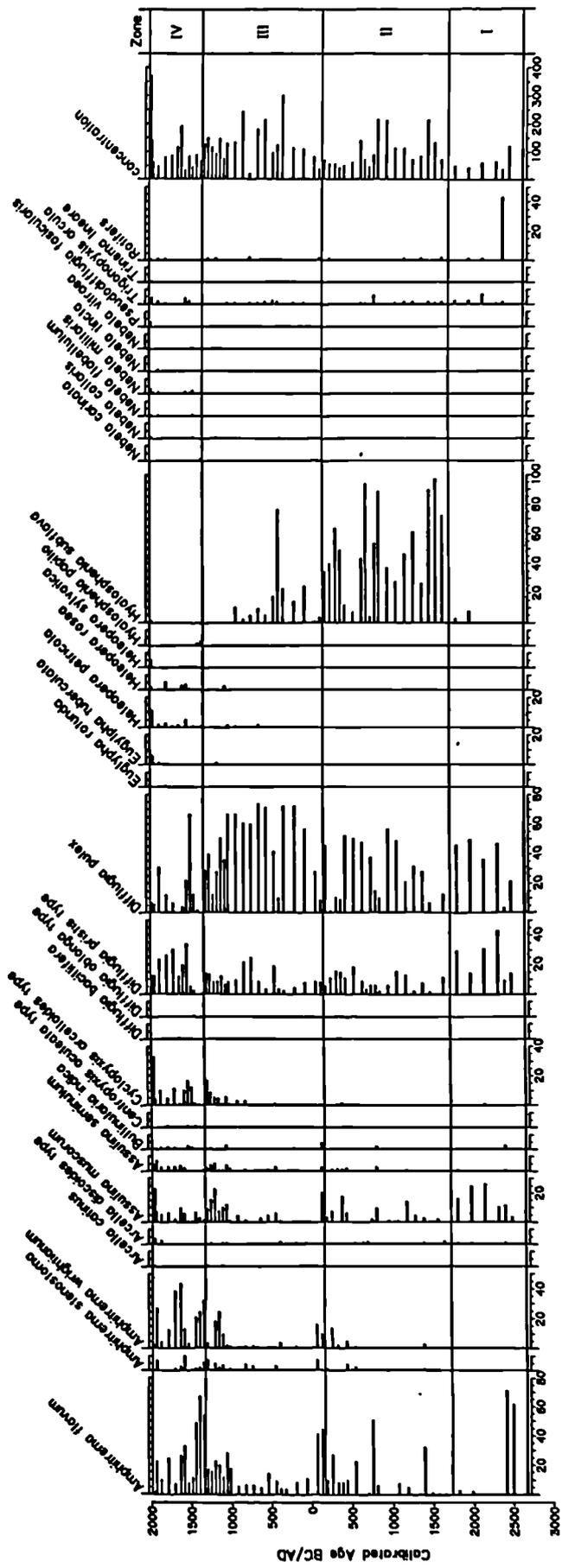


Figure 5.35 Percentage testate amoebae chronology for CRM IV

Their dominance in the testate record affects the robustness of reconstruction at Coom Rigg Moss. Generally the water table reconstructions derived from WA provide better models, with closer confidence intervals than the moisture reconstructions derived from WA-Tol. Due to this, only the water table reconstructions will be used in the chronological assessment of the testate record.

The results from these cores are to be used in Chapter Nine to separate autogenic 'noise' from allogically forced hydrological signals from the water table reconstruction curves. The reliability and replicability of the testate amoebae record will also be considered at three scales of study (see Figure 3.1). At Coom Rigg Moss, micro-scale comparisons are made between the central cores CRM I and CRM IV. This will enable likely 'errors' in the record obtained at the macro-scale from single cores to be quantified. Meso-scale comparisons between all four cores extracted from Coom Rigg Moss will allow separation of hydrological signals resulting from mire expansion and development from the regional climatic signal. This is achieved by comparing the two cores from the mire margins, CRM II and CRM III, with the two central cores. Cores CRM I and CRM IV will also be discussed further in Chapter Nine in a macro-scale comparison with the central cores from Butterburn Flow and The Wou.

Chapter Six

BUTTERBURN FLOW -

Testate amoebae and palaeohydrology

6.0 Introduction

This chapter presents results from the three cores extracted from Butterburn Flow. Presentation of this chapter is similar to Chapter Five, in that the first section presents results from individual cores plotted against depth. Results include; profile stratigraphy, testate amoebae diagrams and ordination analyses of modern and fossil samples to assess the degree of 'match' or 'mis-match' between the modern analogue transfer function and fossil data. Hydrological models using the transfer function are also presented. As with the results from Coom Rigg Moss, the hydrological reconstructions for depth to water table are more robust than those for percentage moisture and these will be the focus for discussion. The second part of this chapter puts the testate amoebae record into chronological context. Sample ages are presented from linear interpolation of pollen marker horizons and radiocarbon dates. Chronologies are used for inter-core comparisons in Chapter Nine.

6.1 Butterburn Flow Core I (BBF I)

730cm of peat was extracted in 32 sections from the centre of the northern end of Butterburn Flow (Figure 3.7 for core location). Cores were extracted in September 1995, from adjacent holes. The rationale for subsampling was similar to that for Coom Rigg Moss. Samples were taken every 5cm in the top metre of peat and at 10cm intervals for the rest of the core. Closely spaced samples were also taken around radiocarbon dates.

6.1.1 Stratigraphy

Stratigraphical description for BBF I is set out in Table 6.1. The presence of *Sphagnum* and *Eriophorum* macrofossils suggests that the mire was ombrotrophic throughout its development.

Depth (cm)	Sediment Description
0 - 3	nig 3; strf 1; elas 3; sicc 1; humo 1; Tb ³ ; Th ¹ . surface vegetation - <i>Molinia caerulea</i> , <i>Eriophorum vaginatum</i> , <i>Calluna vulgaris</i> , <i>Erica tetralix</i> , <i>Drosera rotundifolia</i> , <i>Sphagnum magellanicum</i>
3 - 5	nig 2; strf 0; elas 4; sicc 1; humo 0; Tb ⁴ ; unhumified <i>Sphagnum</i> moss
5 - 23	nig 3; strf 1; elas 4; sicc 1; humo 2; well decomposed peat matrix with stems preserved, <i>Menyanthes</i> seeds
23 - 26.5	nig 1, strf 1; elas 1; sicc 2; humo 1; Tb ⁴ light green matrix with undecomposed fibrous material
26.5 - 30	nig 3; strf 2; elas 2; sicc 1; humo 2; Tb ⁴ <i>Sphagnum</i> moss
30 - 45	nig 2; strf 1; elas 2; sicc 1; humo 2; Tb ⁴ ; good preservation of <i>Sphagnum</i> stems
45 - 48	nig 3; strf 1; elas 1; sicc 1; humo 2; plant structure well decayed
48 - 58	nig 3; strf 3; elas 1; sicc 1; humo 2; Tb ³ ; Th ¹ ; well preserved stems in a humified peat matrix
58 - 70	nig 2; strf 1; elas 0; sicc 1; humo 3; Tb ⁴ ; with <i>Sphagnum</i> stems
70 - 95	nig 4; strf 1; elas 0; sicc 1; humo 4; Tb ⁴ ; with <i>Sphagnum</i> stems
95 - 106	nig 3; strf 2; elas 2; sicc 1; humo 2; Tb ⁴ ; Th ⁺ ; large fragments of <i>Eriophorum</i> 'felted' together
106 - 130	nig 4; strf 1; elas 1; sicc 1; humo 3; Tb ⁴ ; well humified peat matrix with preserved stems
130 - 150	nig 4; strf 1; elas 1; sicc 1; humo 3; Tb ⁴ ; Th ⁺ <i>Sphagnum</i> peat
150 - 180	nig 4; strf 1; elas 1; sicc 1; humo 2; Tb ⁴ ; Th ⁺ <i>Sphagnum</i> peat
180 - 200	nig 4; strf 1; elas 1; sicc 1; humo 3; Tb ⁴ ; Th ⁺ ; woody rootlets and monocots.
200 - 230	nig 4; strf 0; elas 0; sicc 1; humo 4; Tb ⁴ ; + Tl roots
230 - 255	nig 4; strf 0; elas 0; sicc 1; Sh; Th ⁺ plant structure hardly discernible
255 - 268	nig 4; strf 0; elas 0; sicc 1; Sh ⁴ very well humified peat
268 - 330	nig 4; strf 0; elas 0; sicc 1; humo 4; Sh Th ⁺
330 - 375	nig 4; strf 0; elas 0; sicc 1; Sh ⁴ very well humified peat
375 - 405	nig 3; strf 1; elas 1; sicc 1; humo 3; Th ⁴ well humified peat with rootlets
405 - 455	nig 4; strf 1; elas 1; sicc 1; Sh; Th ⁺ <i>Eriophorum</i>
455 - 490	nig 4; strf 0; elas 1; sicc 1; humo 4; Th ⁺ ; Tl ⁺ (rootlets)
490 - 530	nig 4; strf 0; elas 1; sicc 1; Sh ⁴ very well humified peat
530 - 550	nig 3; strf 1; elas 2; sicc 1; Sh ³ ; Tl ¹ well humified peat with wood fragments
550 - 605	nig 4; strf 0; elas 1; sicc 1; Sh ⁴ ; Tl ⁺ well humified peat with occasional wood fragments
605 - 630	nig 4; strf 1; elas 0; sicc 2; Sh ⁴ ; Tl ⁺
630 - 680	nig 4; strf 1; elas 0; sicc 2; humo 4 Sh ³ Tl ⁺ Th ⁺
680 - 730	nig 4; strf 1; elas 0; sicc 2; humo 4; Sh ³ Th ¹ Tl ⁺ (monocots)

Table 6.1 Stratigraphic description of BBF I using the Troels-Smith (1955) sediment description system

6.1.2 Testate amoebae

Sample preparation and data presentation was explained in Chapter Four. Core BBF I was 730cm deep, of which 715cm was suitable for testate amoebae analysis (Figure 6.1). Forty one taxa were found in this profile. Three samples at depths 180cm, 300cm and 700cm had test concentrations too low to count. The testate amoebae record has been divided into six zones, set out in Table 6.2. These zones generally correlate well with changes in stratigraphy.

Above 680cm, the peat contains less sedge peat than below it (Table 6.1). This correlates well with the bottom of Zone II which is related to a large rise in the abundance of *Diffflugia pulex*. The zone change at the top of Zone II, at 565cm, is below the stratigraphic change to a more homogenised sediment at 550cm. The change in the testate amoebae assemblage at the top of Zone III has been placed 10cm below the stratigraphic change, although the dendrogram indicates that the zone may be put at 375cm, the level of stratigraphic change. The zone boundary has been set at 385cm because it matches a sharp decline in *Amphitrema flavum* and an increase in *Assulina muscorum* and *Diffflugia pristis* type at this level. The zone boundary at the top of Zone IV at 252.5cm correlates well with stratigraphic changes at 255cm to peat containing small amounts of highly humified sedge peat.

The boundary for the top of Zone V is 15cm below the stratigraphic change from peat of humo 2 beneath the stratigraphic boundary and of humo 3 above. The dendrogram also indicates that the zone change at this point may be at 155cm, but the testate amoebae assemblage suggests that the zone change should be at 165cm by the sharp decline in the abundance of *Hyalosphenia subflava* and a steep rise in *D. pulex*.

The top of Zone VI at 82.5cm is just below the stratigraphic change at 70cm. This correlates with the decline of both *H. subflava* and *D. pulex* and the increase in *Amphitrema* spp. and *Assulina* spp. The base of Zone VIII (32.5cm) also correlates with stratigraphic changes at 30cm. Above 30cm, the peat is light in colour and unhumified. Below 30cm, the peat is darker in colour and more humified.

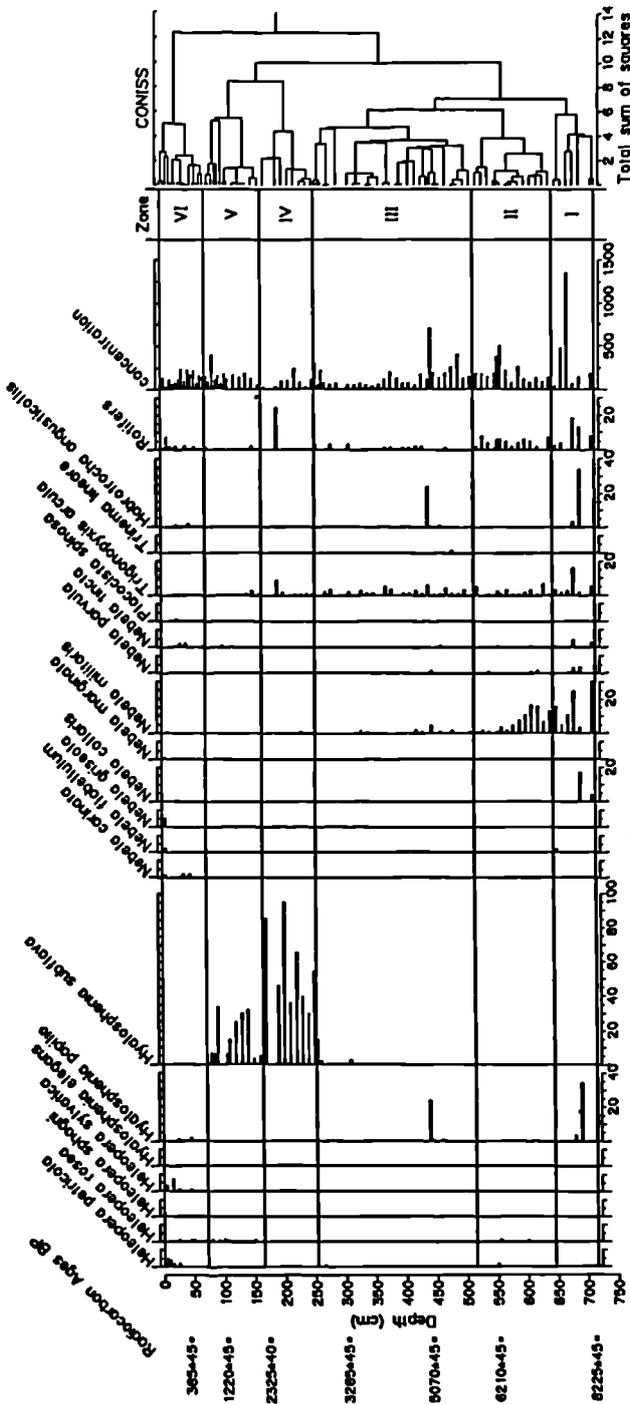
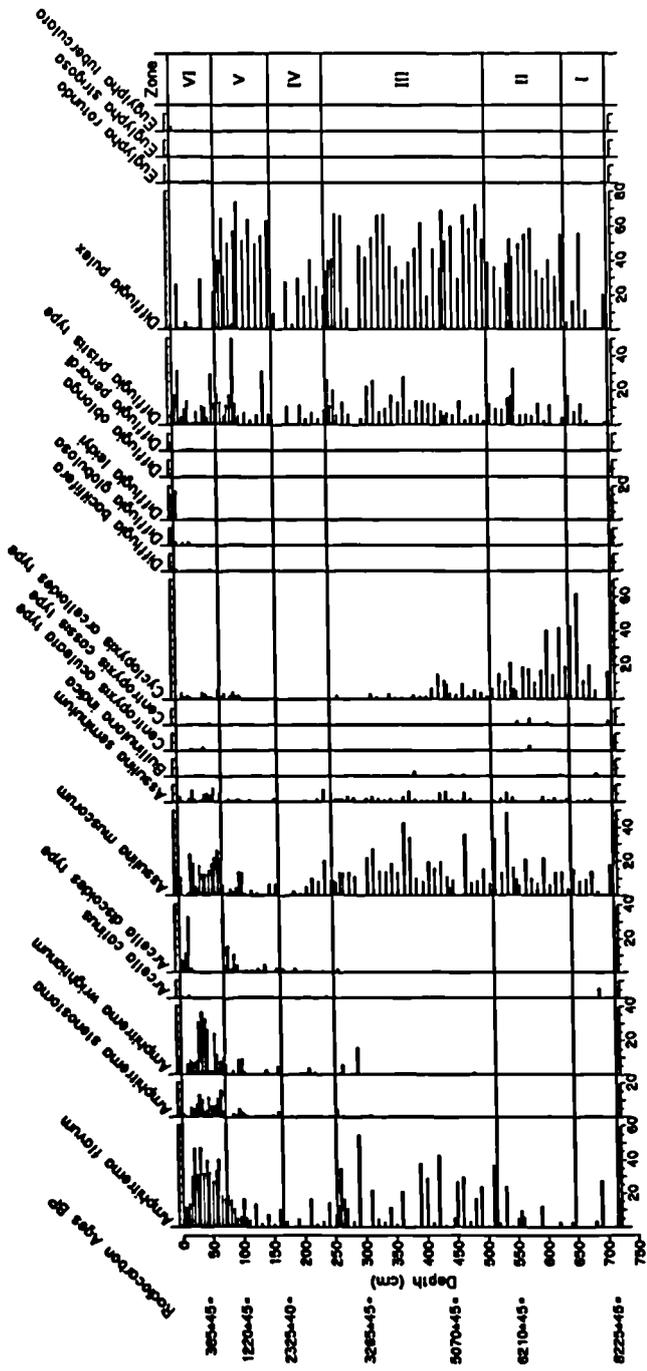


Figure 6.1 BBF I percentage testate amoebae diagram

Zone	Depth (cm)	Major taxa	Zone description
VI	0-72.5	<i>Amphitrema</i> spp., <i>Arcella discoides</i> type, <i>Assulina muscorum</i>	35 taxa were found in this zone. The <i>Amphitrema</i> spp. and <i>A. muscorum</i> dominate, but decrease towards the top. Some taxa, such as <i>Diffugia bacillifera</i> , <i>D. leidyi</i> , <i>D. oblonga</i> , <i>D. penardi</i> and the <i>Nebela</i> spp. are only found in the surface 5cm.
V	72.5-165	<i>Diffugia pristis</i> type, <i>Diffugia pulex</i> , <i>Hyalosphenia subflava</i>	<i>D. pulex</i> dominates this zone. <i>H. subflava</i> is less abundant than in Zone IV and the <i>Amphitrema</i> spp., <i>A. discoides</i> type, <i>Assulina</i> spp. and <i>Cyclopyxis arcelloides</i> type all increase in abundance to the top.
IV	165-252.5	<i>Diffugia pulex</i> , <i>Hyalosphenia subflava</i>	This zone is dominated by <i>H. subflava</i> , which increases in abundance towards the top of this zone. <i>D. pulex</i> decreases to the top, as does <i>A. muscorum</i> . 11 taxa were found.
III	252.5-515	<i>Amphitrema flavum</i> , <i>Assulina muscorum</i> , <i>Diffugia pristis</i> type, <i>Diffugia pulex</i>	<i>Diffugia pulex</i> dominates this zone. <i>Amphitrema flavum</i> and <i>Assulina muscorum</i> have alternately high and low values. There is an isolated peak in <i>Hyalosphenia papilio</i> at 440cm. <i>Assulina seminulum</i> and <i>Trigonopyxis arcula</i> are present in small numbers throughout.
II	515-645	<i>Assulina muscorum</i> , <i>Cyclopyxis arcelloides</i> type, <i>Diffugia pulex</i> , <i>Nebela militaris</i>	<i>C. arcelloides</i> type and <i>N. militaris</i> decrease to the top. <i>A. muscorum</i> increases to the top. <i>Trigonopyxis arcula</i> is present in low values throughout.
I	645-715	<i>Amphitrema flavum</i> , <i>Assulina muscorum</i> , <i>Cyclopyxis arcelloides</i> type, <i>Diffugia pulex</i> , <i>Hyalosphenia papilio</i> , <i>Nebela collaris</i> , <i>Nebela militaris</i> ,	19 taxa were found in this zone. <i>C. arcelloides</i> type and <i>D. pristis</i> type increase in abundance to the top. <i>N. militaris</i> decreases to the top. <i>A. muscorum</i> is present throughout. The rotifer <i>Habrotrocha angusticollis</i> was found in abundance in this zone. Data are absent for 700cm, due to extremely low test concentrations. Concentrations increase to the top.

Table 6.2 Zone descriptions for BBF I based on testate amoebae assemblages

The zone changes for BBF I generally correlate very well with changes in stratigraphy. However, not all changes in stratigraphy are reflected as strongly in the testate amoebae assemblage. These zones are interpreted qualitatively using the data in Table 4.4.

Zone I 645-715cm The species assemblage indicates neither wet nor dry conditions. *A. flavum* and *Hyalosphenia papilio* suggest wet conditions, whilst *Cyclopyxis arcelloides* type, *Nebela militaris* and *Trigonopyxis arcula* indicate dry conditions. However, the rotifer *Habrotrocha angusticollis*, which has up to 20 individuals per sample at the top of this zone corresponds to very wet conditions (de Graaf, 1956; Tolonen, 1966; Tolonen *et al.*, 1992; Charman and Warner, 1997), or alternatively, a depth to water table level of 36.8cm (Warner and Charman, 1994) indicating that it prefers less wet conditions. Wetness and dryness indices are predominantly determined from ombrotrophic bogs, not from minerotrophic systems represented in basal peats and this hampers the interpretation of basal samples.

Zone II 515-645cm This zone is characterised by high values of *D. pulex* throughout. The other taxa in the assemblage, *C. arcelloides* type, *Nebela militaris* and *Trigonopyxis arcula* suggest dry conditions. *A. muscorum* is a cosmopolitan taxon (Warner, 1987).

Zone III 252.5-515cm This zone has a similar species assemblage to Zone II. The drier indicator taxa, such as *C. arcelloides* type decrease in abundance to the top of the zone. The higher abundance of *Amphitrema flavum* in this zone indicates wetter conditions than Zone II, as does the peak in *H. papilio* at 440cm, which prefers very wet *Sphagnum* of between 90-95% water content (de Graaf, 1956; Heal, 1961; Tolonen *et al.*, 1992; Warner, 1987, 1991).

Zone IV 165-252.5cm *H. subflava* dominates this zone indicating dry conditions. The water table optimum for *H. subflava* has been recorded as 22.8cm and 49.9cm (Charman and Warner, 1997; Warner and Charman, 1994). Only 11 taxa were found in this zone, which is the smallest number of taxa of any zone in this profile and, together with the dominance of *H. subflava*, suggests that this is the driest zone.

Zone V 72.5-165cm This is a transitional zone, but is dominated throughout by *D. pulex*. *H. subflava* decreases to the top of the zone, indicating that it is drier at the

bottom of the zone than at the top. The *Amphitrema* spp. and *Arcella discoides* type increase in abundance to the top of the zone implying very much wetter conditions.

Zone VII 32.5-82.5cm The three *Amphitrema* spp. increase in abundance to the top of this zone *A. muscorum* and *A. seminulum* decrease in abundance from the base of the zone to the top, pointing to more hygrophilous conditions at the base and hydrophilous at the top.

Zone VI 0-72.5cm Thirty five taxa were found in this zone. The *Amphitrema* spp. dominate this zone, suggesting very wet conditions with >95% water content, or bog pools (e.g. Tolonen, 1966; Warner, 1991). *Arcella discoides* type is well represented at the top and the presence of a variety of *Diffugia* spp., *Heleopera petricola* and *Nebela griseola* all indicate wet to aquatic conditions. The large number and composition of taxa in this zone, represent very wet conditions.

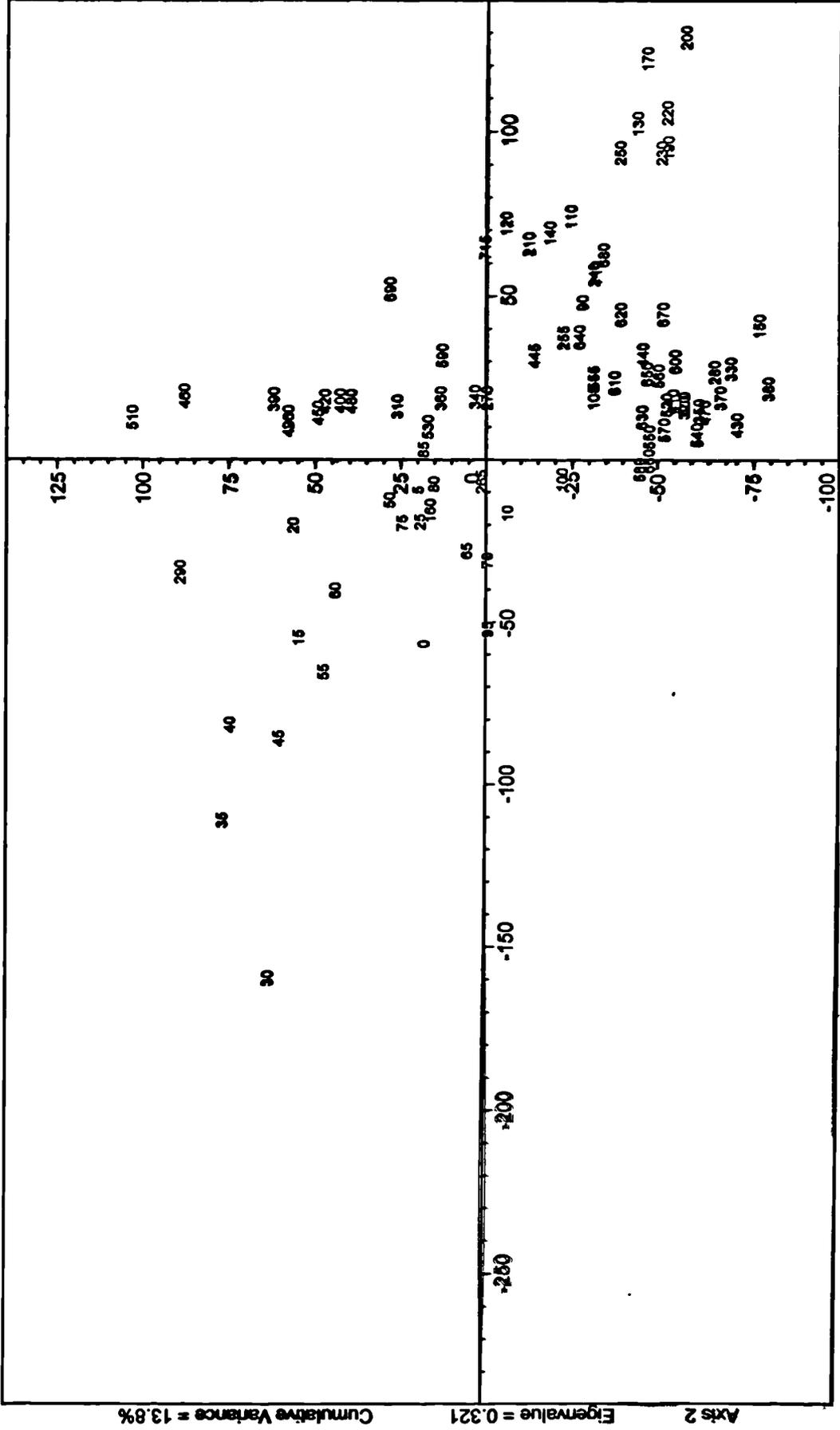
6.1.3 Ordination

Modern and fossil ordination

Figure 6.2 is an ordination plot of the samples from the modern analogue transfer function and the fossil data set for BBF I, plotted as passive samples. Many of the fossil samples are concentrated in the bottom right corner of the plot. There is a gradation of those fossil samples which fall totally outside the modern samples and those which are peripheral to them. The eigenvalue for Axis 1 = .379 and for Axis 2 = .321. Samples 30, 35 and 290cm lie outside the modern plot at the top, these levels are dominated by *Amphitrema flavum* and *A. wrightianum*. In the bottom right corner of the plot, samples 170cm, 200cm, 220cm, 230cm are dominated by *H. subflava* and samples 130cm, 150cm and 430cm are dominated by *D. pulex*. These samples do not have good matches with the modern analogues and therefore will not have robust reconstructed values. Samples such as 265cm and 50cm lay within the spread of modern samples and should therefore have better reconstructed hydrological values.

Sample ordination

The sample ordination plot for BBF I is presented in Figure 6.3. The diagram shows strong bifurcation parallel with the first axis which suggests that the environmental



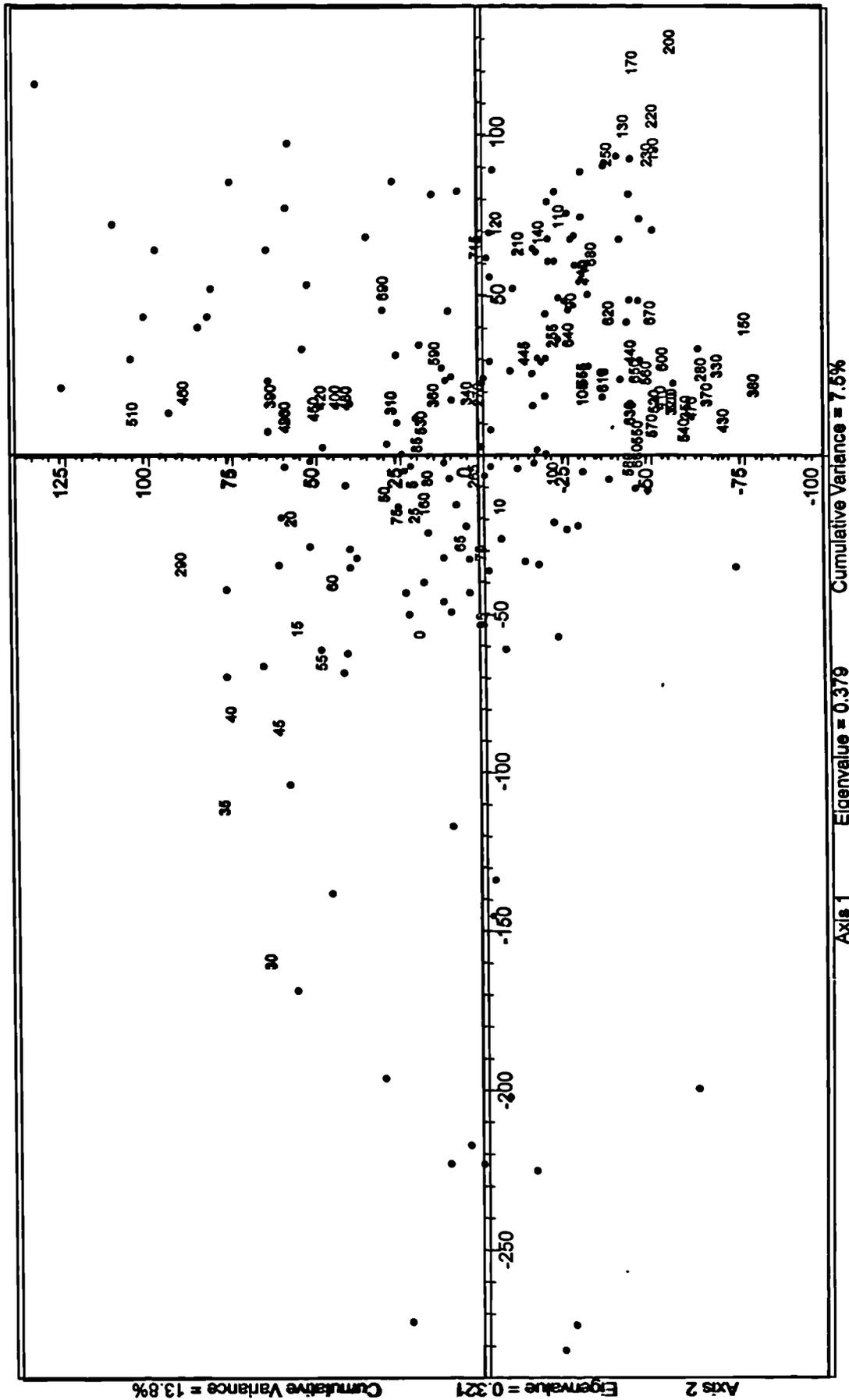


Figure 6.2 Modern and fossil DCA ordination for BBF I. Fossil samples (overlaid) plotted as 'passive', modern samples plotted as circles

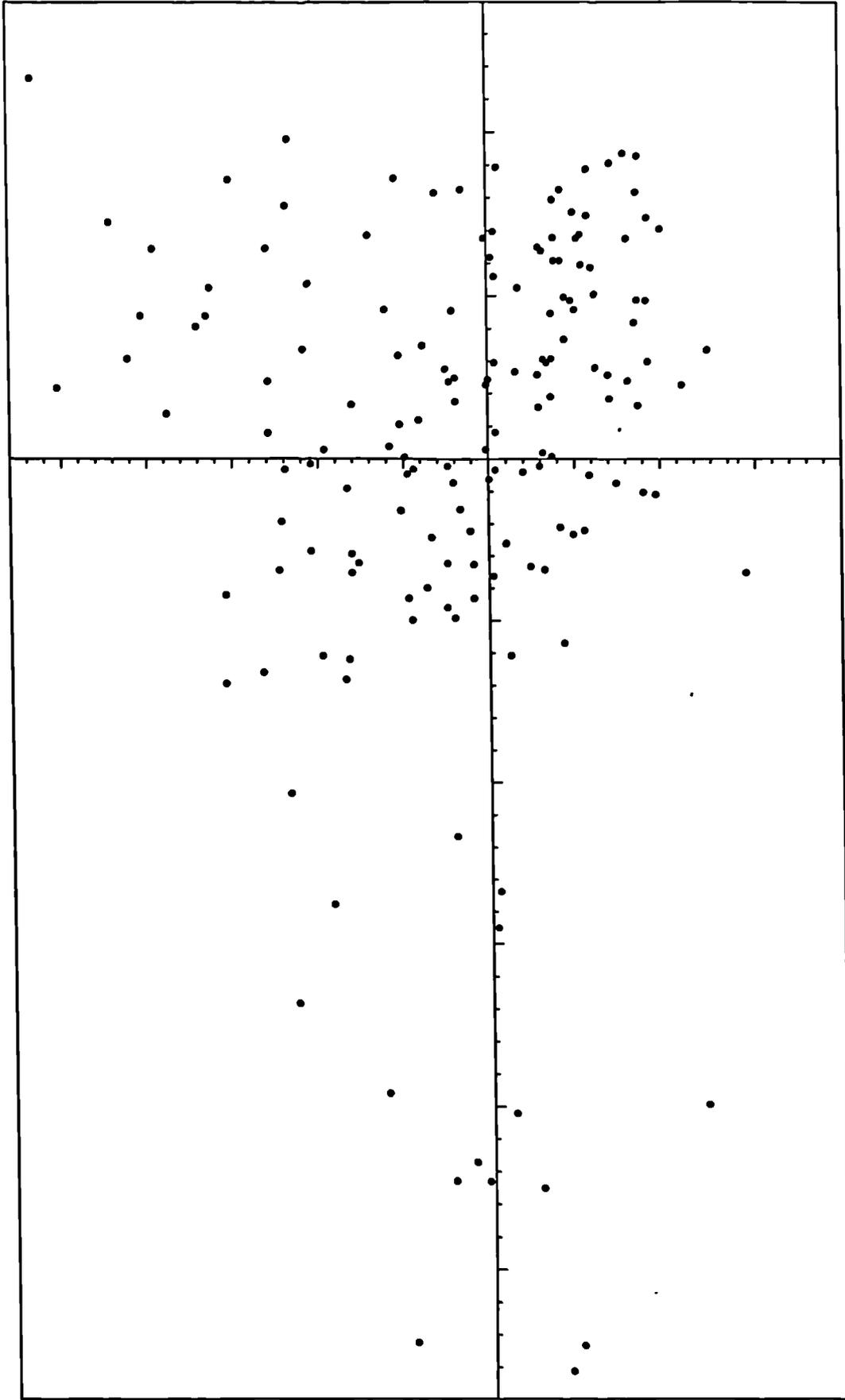


Figure 6.2 Modern and fossil DCA ordination for BBF I. Fossil samples (overlay) plotted as 'passive', modern samples plotted as circles

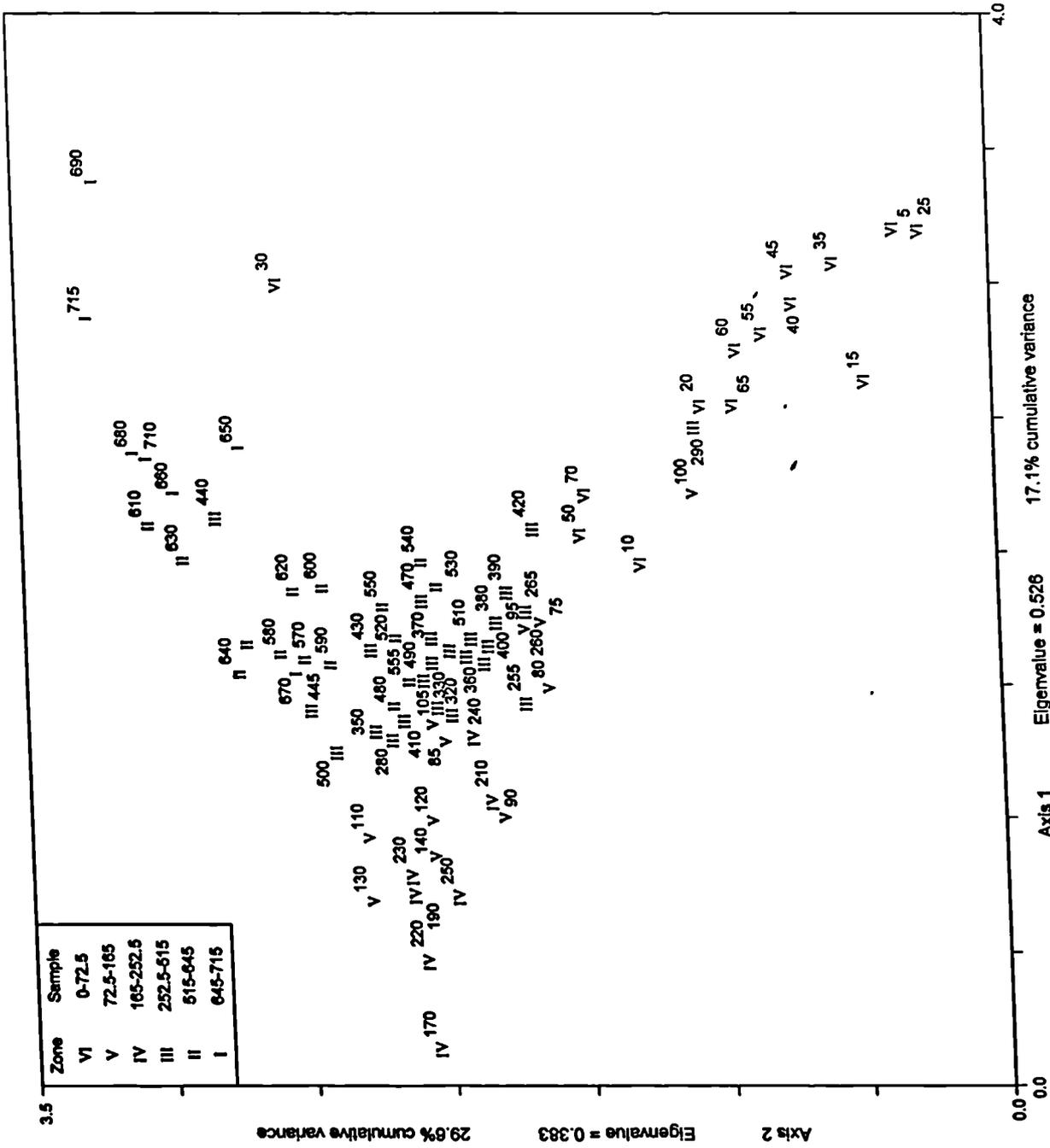


Figure 6.3 Sample ordination for BBF I

factors on both axes influences the distribution of samples. Axis 1 has an eigenvalue of .526 and axis 2 has an eigenvalue of .383. Sample 170cm closest to axis 2, is dominated by *H. subflava*. Other samples close to 170cm, 190cm and 220cm contain dry indicator taxa and are dominated by *H. subflava*. Samples furthest from axis 2, at the top of the plot, such as 690cm are dominated by wet taxa, e.g., *Hyalosphenia papilio* and *A. flavum*. Samples 5cm and 25cm, at the base of the plot, are also dominated by wet taxa. Samples from Zone VI are clustered at the base of the plot and from Zone I at the top of the plot. Zone IV samples are clustered close to Axis 2. Samples from Zones II and III are mixed in the centre of the plot. Axis 1 is therefore a hydrological gradient from dry on the left side, to wet on the right side. Axis 2 also exerts a strong influence on the distribution of species which correlates with depth, separating the very deep Zone I samples from the shallow Zone VI samples.

Species ordination

The ordination plot for taxa (Figure 6.4) follows a similar pattern to the sample ordination plot (Figure 6.3) for BBF I. Twenty species with less than 5% abundance in every sample in which they occur are plotted as crosses. These species are less significant in the ordination than the species indicated by circles. *H. subflava* is an outlier located on the far left of the plot. In the bottom right corner of the plot is a cluster of species that are predominantly found in the top of the core, in Zones V and VI. These are principally wet taxa and most have <5% abundance in every sample in which they occur. The middle of the plot contains taxa such as *Assulina muscorum* and *A. seminulum* which have a more cosmopolitan distribution. Species located at the top of the plot, in a diagonal line, are drier taxa such as *Bullinularia indica* and *Trigonopyxis arcuata*.

6.1.4 Hydrological reconstructions

Water table reconstruction

The transfer function is described in detail in Chapter Four. Figure 6.5 shows the water table reconstruction for BBF I. The water table curve is derived from the WA model (Woodland *et al.*, 1998).

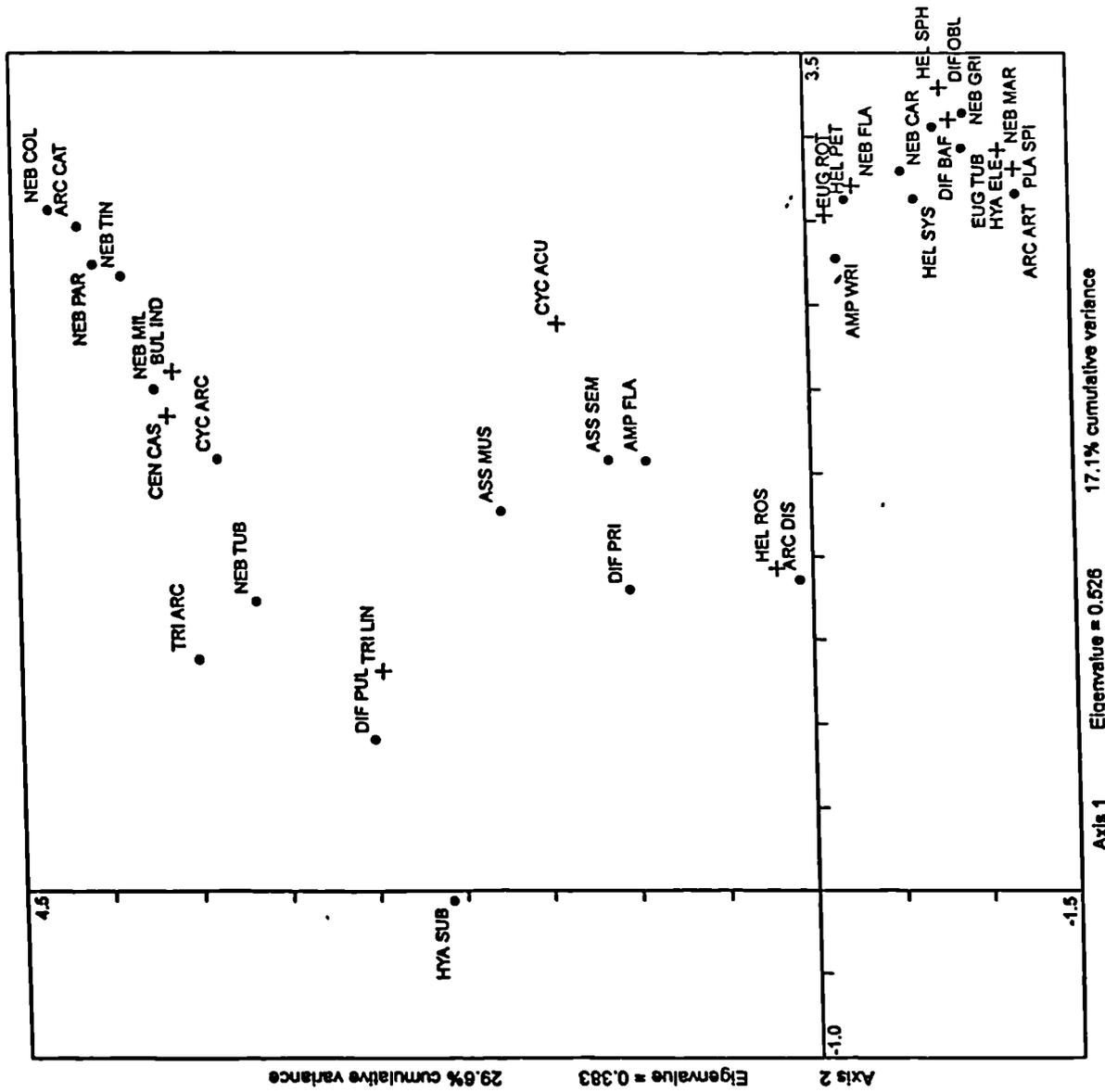


Figure 6.4 Species ordination for BBF I. Taxa with <5% total abundance plotted as crosses

At 715cm peat depth, the reconstructed water table value is -6.3cm below the mire surface. Between 690cm and 680cm, the water table falls from -5.3cm to -8.3cm. At 660cm, there is a relatively high water table of -4cm, associated with the high representation of *Cyclopyxis arcelloides* type. From 650cm to 600cm, the mean reconstructed curve is relatively hydrologically stable, fluctuating between -5cm and -7cm. These samples fall within the modern ordination plot (Figure 6.2) and hence the good match between modern and fossil data sets explains the narrow confidence limits between these samples. At 560cm, there are wide confidence intervals around the mean reconstructed value (-8cm to -0.9cm). Approximately half of this sample is *D. pulex*, which is not included in the transfer function and this accounts for the unreliable reconstruction. From 540cm to 460cm, the mean reconstructed curve is sinuous, fluctuating between -2.7cm and -7.8cm between adjacent points. At 460cm, there is a wet mean reconstructed value of -2.7cm, associated with high values of *A. flavum*. However, the sample contains 59% *D. pulex*, which, since it has no modern analogue value, casts doubt on the accuracy of this reconstruction. There is a trend of slight lowering of the water table from 460cm to 370cm. At 370cm, the water table has a mean value of -8.8cm.

At 330cm, the mean reconstruction has wide confidence intervals, with a maximum value of -9.4cm, a mean value of -6cm and a minimum value of -2.6cm. 290cm has a high water table of -2.5 related to the abundance of *A. flavum*. This sample falls outside the modern ordination plot (Figure 6.2).

From 250cm, there is a trend of lowering of the water table, from -12cm at 250cm peat depth, to -16.5cm at 200cm peat depth. Between these samples are high values of *H. subflava*. At 170cm peat depth, the mean water table is -15cm, rising to -5cm between 150-160cm peat depth. At 140cm, the water table drops back down to -10cm.

There is a trend of increasing wetness towards the top of the core. At 1m peat depth, the reconstructed value is -2.9cm. Between 85cm peat depth and the mire surface, the water table fluctuates between -4.7cm and -1.3cm. These levels have narrower confidence intervals, as most samples have a greater proportion of the species with good modern analogue values. 15cm peat depth has the wettest value of the entire core at -1.3cm, associated with a peak in *Arcella discoides* type and high values of *A. flavum*. The surface sample, 0cm, has a mean water table of -3.9cm.

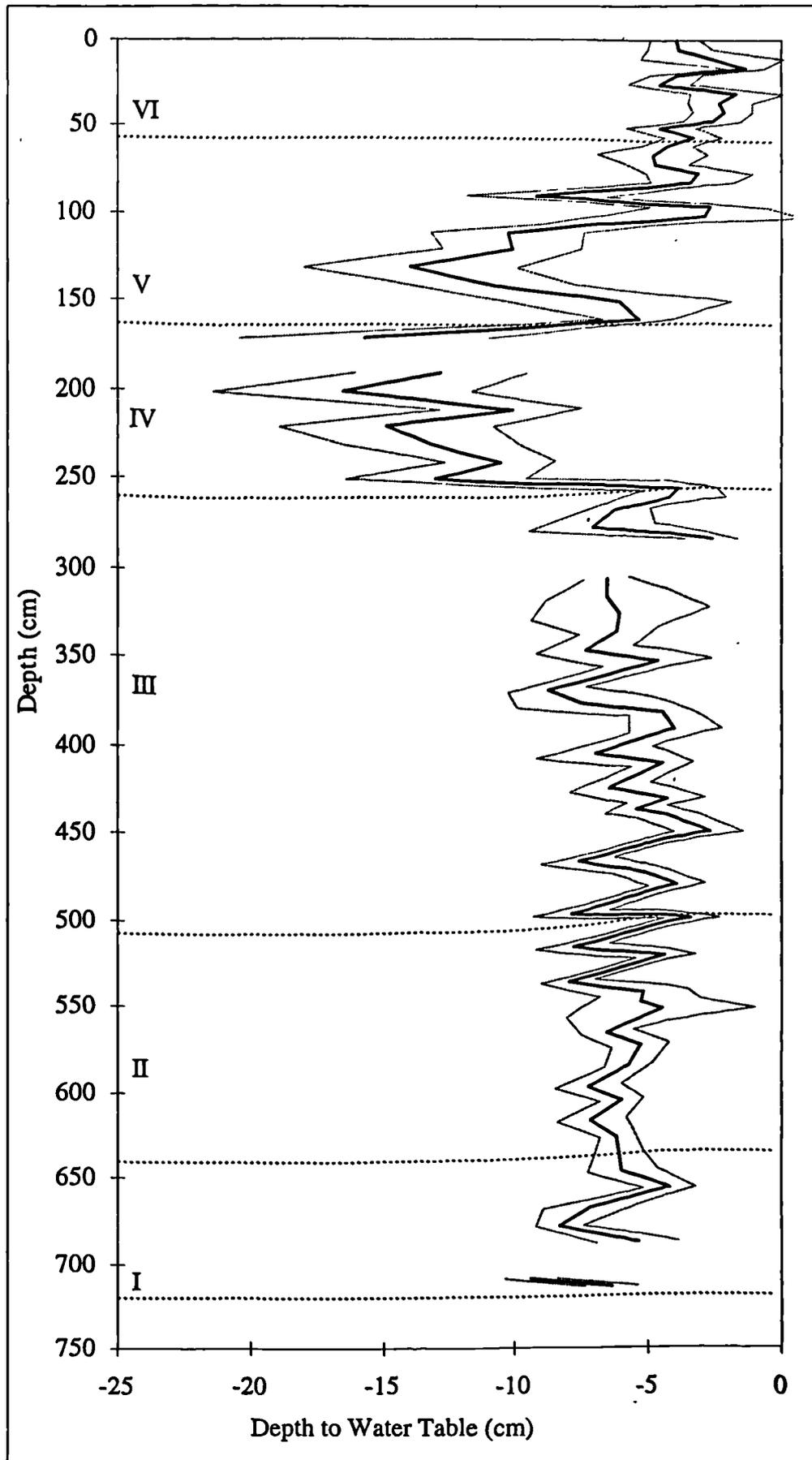


Figure 6.5 Mean water table reconstruction BBF I, with 2σ bootstrapped error estimates shown as thin lines. Assemblage zones marked.

Moisture reconstruction

Figure 6.6 is the moisture reconstruction for core BBF I derived from WA-Tol, with outlier samples removed. The moisture reconstruction is more variable than the water table curve and has wider confidence intervals about the mean, probably due to single-shot sampling of moisture data, rather than the mean annual water table data.

The basal sample at 715cm has a mean moisture value of 92.7%. At 690cm, there are wide confidence intervals, with a minimum moisture content of 89.2%, a mean of 92.6% and a maximum of 96%, this is a deviation of 3.4% from the mean. This sample falls within the spread of modern samples (Figure 6.2). Between 620-600cm the curve is complacent with a mean of *ca.* 91%. From 590-555cm, the mean rises to an average of 93%. Between 540cm and 490cm, the mean curve fluctuates between 91% and 94% between adjacent pairs of points.

At 390cm, there are wide confidence intervals, deviating 5% either side of the mean. This sample is composed largely of *A. flavum* and *D. pulex*. There is a trend of increasing moisture content to 290cm, which has a reconstructed value of 96%. From 290cm to 190cm, there is a trend of decreasing moisture content, reaching a low of 89% at 200cm. This sample contains 94% *H. subflava* and, since this species has a poor analogue value, this moisture value is probably an overestimate of its true moisture content. The wide confidence intervals, deviating 5% from the mean also implies a lack of confidence in the reconstruction at this level.

At 160cm, the moisture content rises to 95.8%. This is a reflection of the presence of the *Amphitrema* spp. and *Assulina* spp., but since the sample also contains 62.6% *D. pulex*, this may also not be an accurate reflection of palaeomoisture content. From 70cm to 55cm, there is a trend of increasing moisture content. Between 60cm and 55cm the palaeomoisture value was 96%. The surface 30cm has wide fluctuations between adjacent pairs of points, with an overall trend of decreasing moisture content. At 30cm, the palaeomoisture value was greatest at 97.5% and at 15cm, lowest at 84.6%.

The pattern of the moisture reconstruction concurs with that for the water table, except for the top metre. The top metre has far greater fluctuations in moisture content and implies a fall which is not seen in the water table reconstruction.

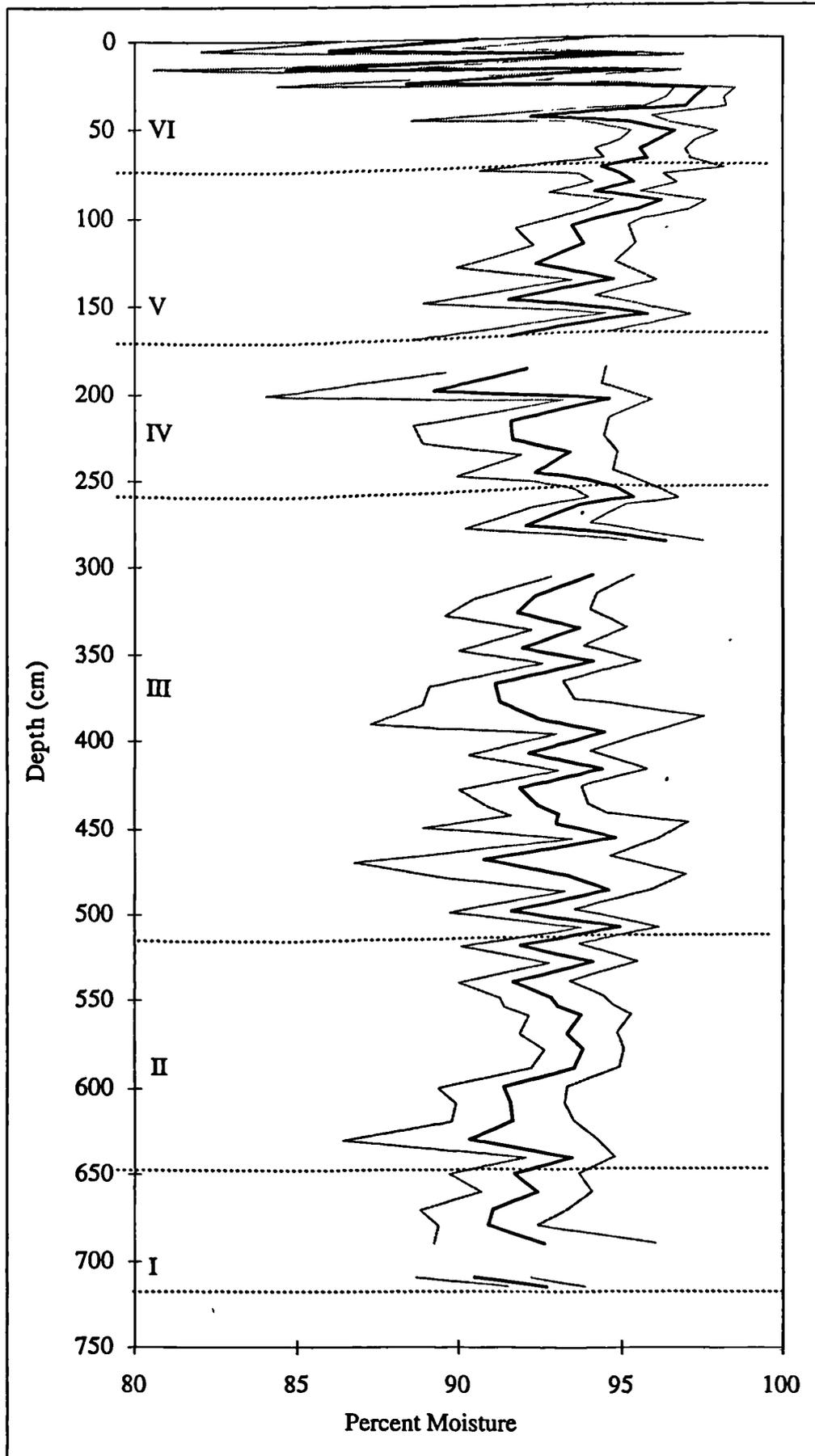


Figure 6.6 Mean moisture reconstruction BBF I, with 2σ bootstrapped error estimates shown as thin lines. Assemblage zones marked.

All of the samples, except for the top metre, are likely to have poor reconstructed values for both moisture content and depth to water table, since samples below 1m are either dominated by *D. pulex* which has no modern analogue value, or *H. subflava* which has a poor modern analogue value. This results in the core having very wet values throughout, with the result that the water table level or moisture content does not drop significantly when the samples contain a large proportion of xerophilous taxa such as *H. subflava*. The top metre therefore has a more accurate reconstructed hydrology than the rest of the core.

6.2 Butterburn Flow Core II (BBF II)

Butterburn Flow Core II was extracted from the eastern edge of the northern part of the mire (Figure 3.7) in September 1995. 2.74m of peat was recovered. Laboratory preparation and data processing procedures are set out in Chapter Four.

6.2.1 Stratigraphy

The stratigraphy for BBF II is set out in Table 6.3. Sediment description follows Troels-Smith (1955). At the base of the core, the peat contains clay and woody material. The peat is ombrotrophic. This is indicated by the presence of *Sphagnum* and *Eriophorum*.

6.2.2 Testate Amoebae

Of the 274cm of peat extracted, tests were counted to 270cm, with the exception of 260cm which had a test concentration which was too low to count (Figure 6.7). A total of 29 taxa were found in this core. This profile has been divided into five species assemblage zones (Table 6.4).

The base of the core was composed of grey clay. The diffuse boundary between clay and peat occurred at 272cm. The boundary between the top of Zone I and base of Zone II does not correspond with a stratigraphic change. At 215cm, the zone boundary, there is a marked fall in *Assulina muscorum*, *Cyclopyxis arcelloides* type, *Diffugia pulex*, *Trigonopyxis arcula* and a rise in the abundance of *Hyalosphenia subflava*. The top of Zone II also does not correspond directly with a change in stratigraphy. The change in species assemblage occurs at 135cm and the stratigraphic change to slightly more

humified peat occurs at 118cm. The species assemblages found in Zones II and III are similar, but a division has been made at 135cm since there is a greater abundance of *H. subflava* in Zone II and a greater abundance of *D. pulex* in Zone III. At 35cm peat depth, the boundary between Zones IV and V, the stratigraphy changes to less humified peat above, corresponding with a change in testate amoebae assemblage to wetter indicator taxa.

The zones for BBF II (Table 6.4) are described qualitatively according to the data set out in Table 4.4.

Zone I 215-270cm The basal sample 270cm is composed of 96% *Pseudodiffugia fascicularis*, which was regarded by Cash and Hopkinson (1909) as an aquatic species, although this may not be a reliable source. This is found just above the boundary with the clay. *P. fascicularis* is composed of minute mineral particles so the location of BBF II on a slight slope (Figure 3.9) probably provides test-building material, as well as suitable hydrological conditions that may not be found in other locations. *Trigonopyxis arcuata* decreases to the base of the core as *H. subflava* increases. These taxa indicate dry conditions, but the presence of the rotifer *Habrotrocha angusticollis* and *A. flavum* implies that conditions were wetter at 250cm.

Depth (cm)	Sediment Description
0 - 2.5	nig 2; strf 1; elas 4; sicc 1; humo 1; Tb ² ; Th ² . <i>Sphagnum magellanicum</i> , <i>Molinia caerulea</i> , <i>Menyanthes</i> seeds
2.5 - 35	nig 3; strf 2; elas 4; sicc 1; humo 1; Tb ³ ; Th ¹ ; unhumified peat, root matrix
35 - 57	nig 3; strf 1; elas 3; sicc 2; humo 2; Tb ³ ; Th ¹ <i>Sphagnum</i> peat with stems
57 - 75	nig 4; strf 1; elas 3; sicc 2; humo 3; Tb ⁴ ; plant structure well preserved
75 - 100	nig 4; strf 1; elas 2; sicc 1; humo 4; Tb ⁴ ; well humified peat matrix with <i>Sphagnum</i> stems
100 - 118	nig 4; strf 1; elas 1; sicc 1; humo 4; very well humified peat matrix
118 - 200	nig 4; strf 0; elas 0; sicc 1; Sh plant structure hardly discernible
200 - 225	nig 4; strf 0; elas 0; sicc 2; Sh very well humified peat
225 - 268	nig 4; strf 0; elas 0; sicc 2; Sh Th ⁺ ; Birch roots and <i>Eriophorum</i> stems
268 - 272	nig 3; strf 0; elas 0; sicc 2; Sh; Ag ⁺ ; well humified material with clay
272 - 274	nig 2; strf 0; elas 0; sicc 3; Ag ⁺ Sh ⁺ confirmed base - peaty clay

Table 6.3 Stratigraphic description of BBF II using the Troels-Smith (1955) sediment description system

Zone	Depth (cm)	Major taxa	Zone description
V	0-35	<i>Amphitrema</i> spp., <i>Cyclopyxis arcelloides</i> type, <i>Diffugia pristis</i> type, <i>Heleopera</i> spp.	Twenty-five taxa were found in this zone. <i>D. pristis</i> type is the most abundant taxon. The <i>Amphitrema</i> spp. decrease in abundance towards the top, as does <i>D. pulex</i> . <i>C. arcelloides</i> type and <i>Heleopera petricola</i> are well represented throughout.
IV	35-62.5	<i>Amphitrema</i> spp <i>Diffugia pulex</i> , <i>Hyalosphenia subflava</i>	This is a transitional zone, similar in species composition to Zone II. <i>H. subflava</i> decreases in abundance to the top, as <i>D. pulex</i> increases in abundance. Between 55-60cm, there is a peak in the abundance of <i>Amphitrema</i> spp.
III	62.5-135	<i>Diffugia pulex</i> , <i>Hyalosphenia subflava</i>	This zone is similar to Zone II. <i>H. subflava</i> decreases to the top. <i>Arcella discooides</i> type is present for the first time in this zone.
II	135-215	<i>Diffugia pulex</i> , <i>Hyalosphenia subflava</i>	This zone is characterised by high values of <i>H. subflava</i> of between 55 - 99% abundance throughout this zone. Eight taxa were found.
I	215-270	<i>Diffugia pulex</i> , <i>Diffugia pristis</i> type <i>Pseudodiffugia</i> <i>fascicularis</i> ,	<i>P. fascicularis</i> dominates the base of the core, attaining nearly 100% representation, but then disappears. There are no data for 260cm due to poor test concentration. <i>Assulina muscorum</i> , <i>D. pristis</i> type and <i>D. pulex</i> increase from 250cm towards the top of the zone. <i>C. arcelloides</i> type and <i>Trigonopyxis arcula</i> decrease in abundance from 250cm to the top.

Table 6.4 Zone descriptions for BBF II based on testate amoebae assemblages

Zone II 135-215cm This zone is dominated by *H. subflava* which suggests dry conditions of less than 80% water content throughout this zone. At 180cm, the assemblage represents slightly wetter conditions, as indicated by the presence of *A. flavum* and *A. wrightianum*.

Zone III 62.5-135cm Zone III is dominated by *H. subflava* and *D. pulex* indicating dry conditions. The top of the zone has increased species diversity, with increasing *Amphitrema* spp and *Arcella discooides* type. This indicates wetter mire surface conditions.

Zone IV 35-62.5cm The *Amphitrema* spp., *Assulina muscorum* and *D. pristis* type dominate the base of the zone, representing very wet to aquatic conditions. The top of the zone is more difficult to interpret, since it is dominated by up to 80% *D. pulex*.

Zone V 0-35cm The major taxa in this zone are *D. pristis* type and *C. arcelloides* type, which, according to Warner and Charman (1994) and Charman and Warner (1997) have a water table optimum that varies between 32.0cm and 4.7cm. The *Amphitrema* spp. indicate that the base of the core has very wet conditions with 95% water content (Tolonen *et al.*, 1992). These are replaced by *A. discoides* type which are also indicative of very wet conditions - of floating, submerged or very wet *Sphagnum* (Tolonen, 1986). *Heleopera petricola* also indicates very wet conditions. The overall species assemblage implies very wet to aquatic conditions. However, the presence of *Bullinularia indica* and *Trigonopyxis arcua*, which are both xerophilous taxa, also suggest drier conditions.

6.2.3 Ordination

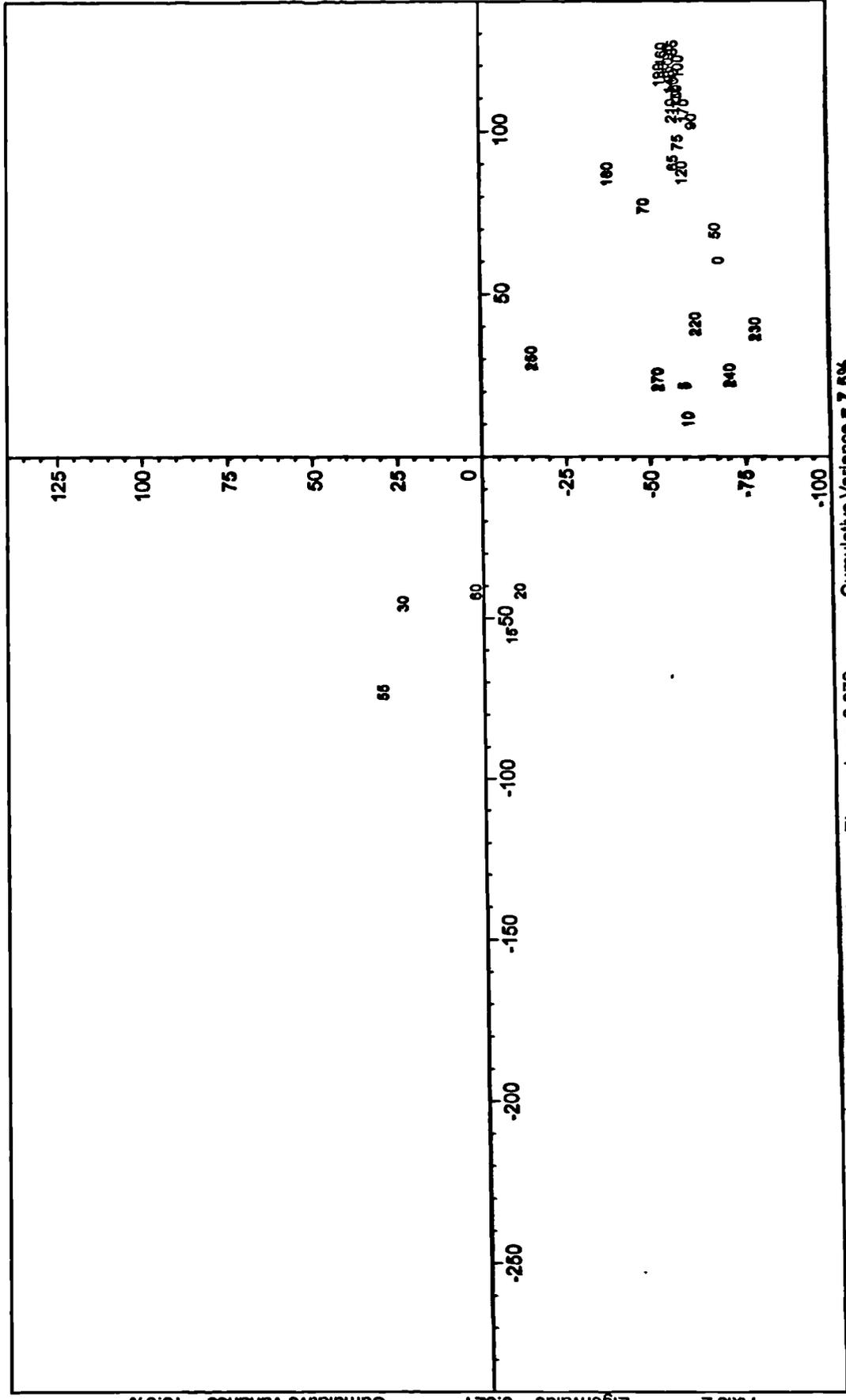
Modern and fossil ordination

There are a large number of samples from BBF II which fall outside the modern samples in the bottom right corner of the plot (Figure 6.8). This mis-match between modern and fossil samples will affect the robustness of the hydrological reconstructions.

The sample at 0cm has an unusual assemblage, with high values of *Heleopera* spp. Samples at 65cm, 75cm, 85cm, 90cm, 100cm, 120cm, 140cm, 160cm, 170cm and 190cm contain high values of *H. subflava* and *D. pulex* which have poor and no modern analogue values respectively. Samples at 50cm, 210m, 230cm and 240cm contain large amounts of *D. pulex* so these levels will also have poor reconstructed values. Sample 270cm will have a very poor reconstructed value, since *Pseudodifflugia fascicularis* has no modern analogue value. Thus, a large number of samples in BBF II will not have accurate hydrological reconstructions and the reconstructed curves are likely to be biased towards wetter reconstructed values.

Sample ordination

Figure 6.9 is presented with sample 270cm removed. This sample was an outlier, containing 95% *P. fascicularis*. Samples containing high values of *D. pulex* and *H. subflava* from Zones II and III, are grouped together on the far right of the plot. Samples from Zone V which contain greater abundances of wetter indicator taxa are located on the left side of the plot, close to axis 2. This suggests that axis 1 is an



Cumulative Variance = 13.8%

Eigenvalue = 0.321

Axis 2

Cumulative Variance = 7.5%

Eigenvalue = 0.379

Axis 1

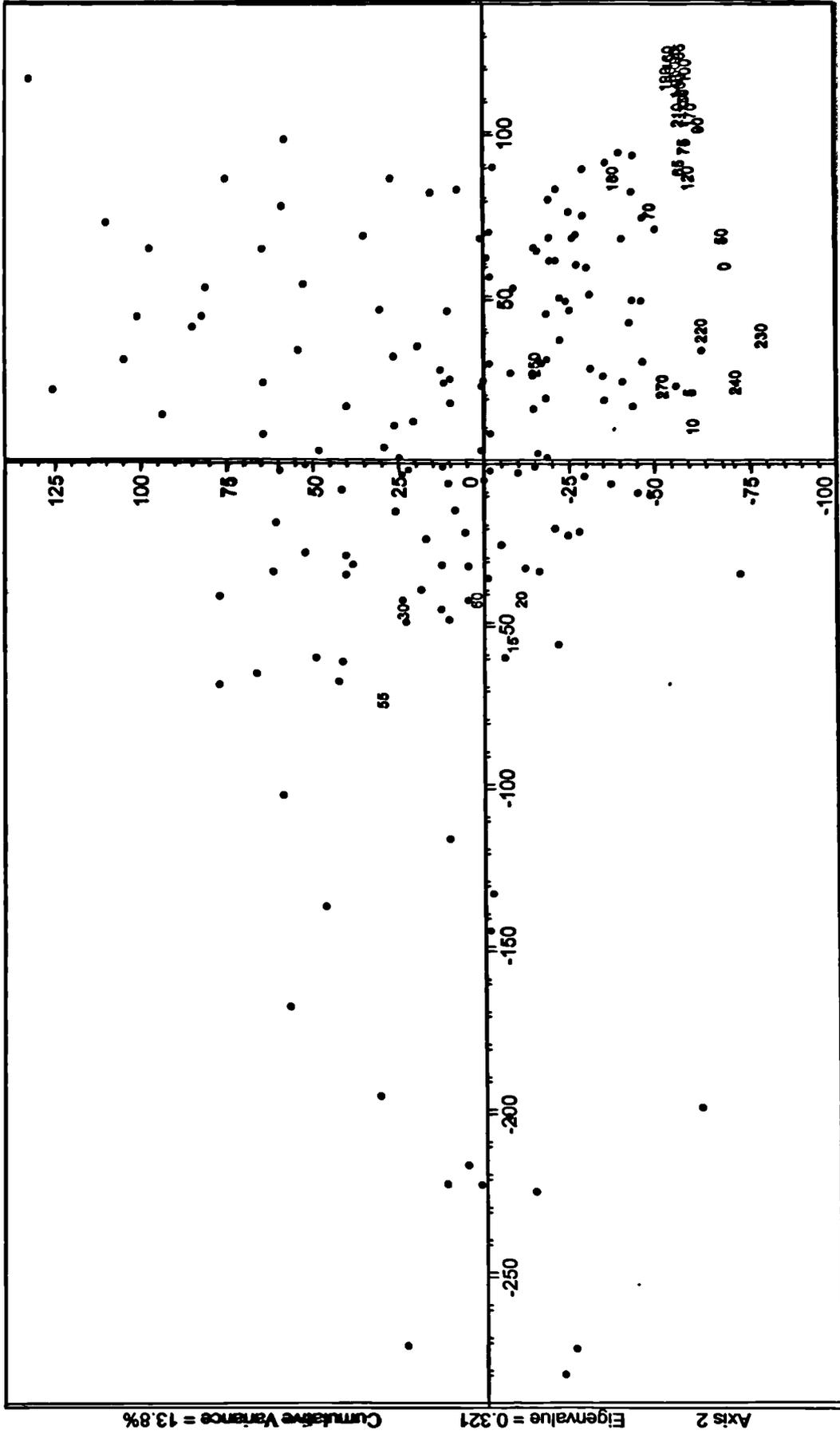


Figure 6.8 Modern and fossil DCA ordination for BBF II. Fossil samples (overlay) plotted as 'passive', modern samples plotted as circles

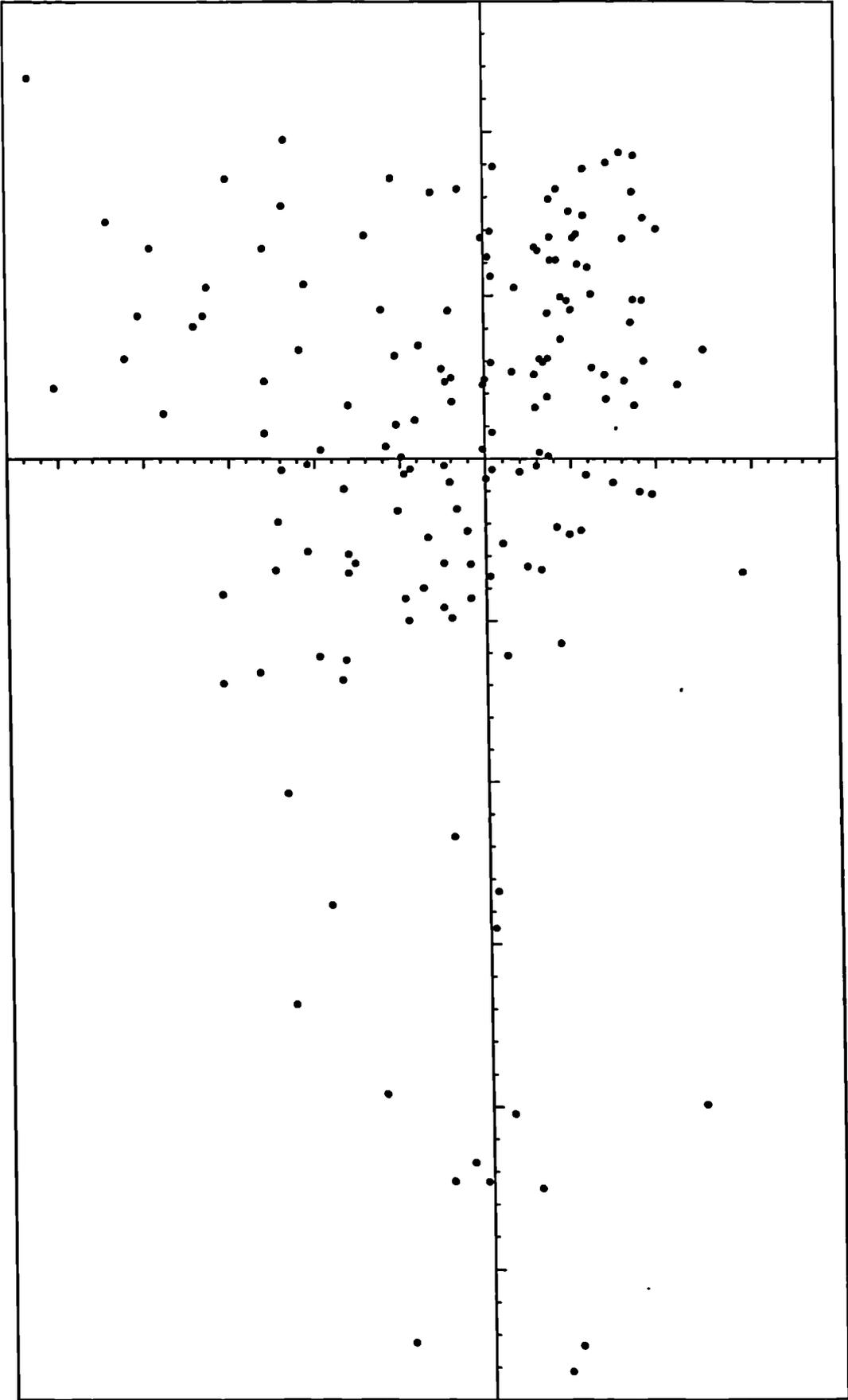


Figure 6.8 Modern and fossil DCA ordination for BBF II. Fossil samples (overlay) plotted as 'passive', modern samples plotted as circles

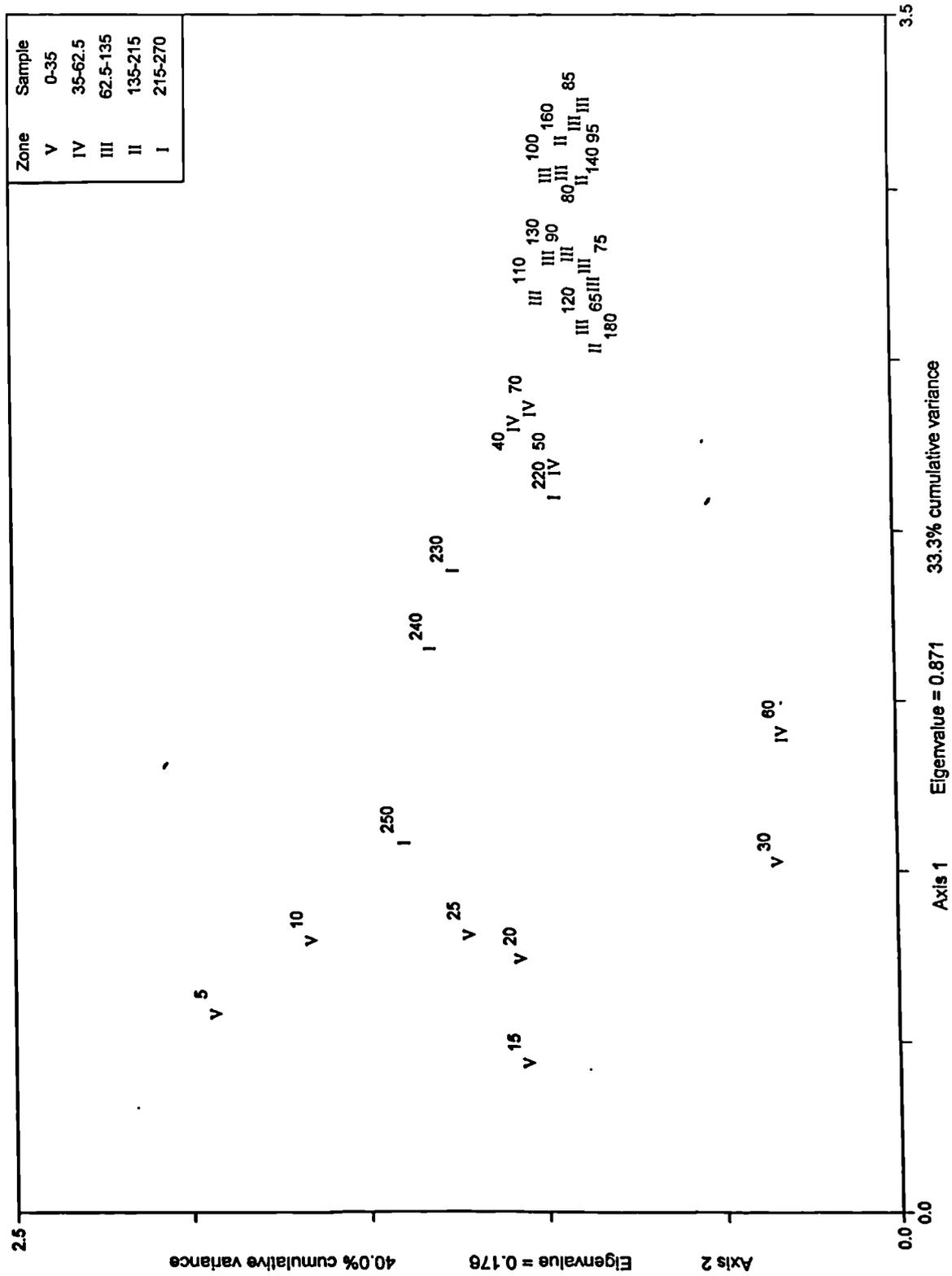


Figure 6.9 Sample ordination for BFF II

hydrological gradient, from very wet on the left side, to drier conditions on the right side of the plot.

Species ordination

Sample 270cm, containing 95% *P. fascicularis*, has been removed from this ordination plot since it was an outlier. No other sample from this core has a similar faunal assemblage (Figure 6.10). *H. subflava* and *D. pulex* are located on the right side of the plot. The eigenvalue for axis 1 is .871 and for axis 2 = .176. Fourteen taxa have been plotted as less significant taxa, indicated by a cross. These species have less than 5% abundance in every sample in which they occur and do not make a significant contribution to the ordination. Most of these low abundance taxa are located on the negative axes. The percentage variance explained by the first axis is 33.3% and 40% is explained by axis 2, which leaves 60% unexplained by the first two axes.

6.2.4 Hydrological reconstructions

Water table reconstruction

The water table reconstruction for BBF II is presented in Figure 6.11. The base of the core at 270cm has a reconstructed value of -4cm, but this is highly unreliable, since it was composed of 95% *P. fascicularis* that has no modern analogue value. From 250cm, the water table drops from -5cm below the surface to -9.5cm below the surface at 220cm peat depth. From 210cm to 65cm peat depth, the mean curve is relatively complacent, fluctuating only slightly between -14 and -16cm below the surface. This is related to the assemblage dominance of *H. subflava*. At 55cm, there is a high reconstructed water table value of -3cm with narrow confidence intervals. This is associated with an increase in species diversity and a greater number of taxa with good modern analogues, such as *A. flavum* and *A. wrightianum*. From 50cm to 15cm, the water table rises from -11cm to -2.5cm. The high water table at 15cm is related to the peak in *Arcella discoidea* type, which has the highest water table value at -3.4cm, of the taxa included in the transfer function by Woodland *et al.* (1998). The water table falls to the surface sample, which has a mean water table value of -7cm.

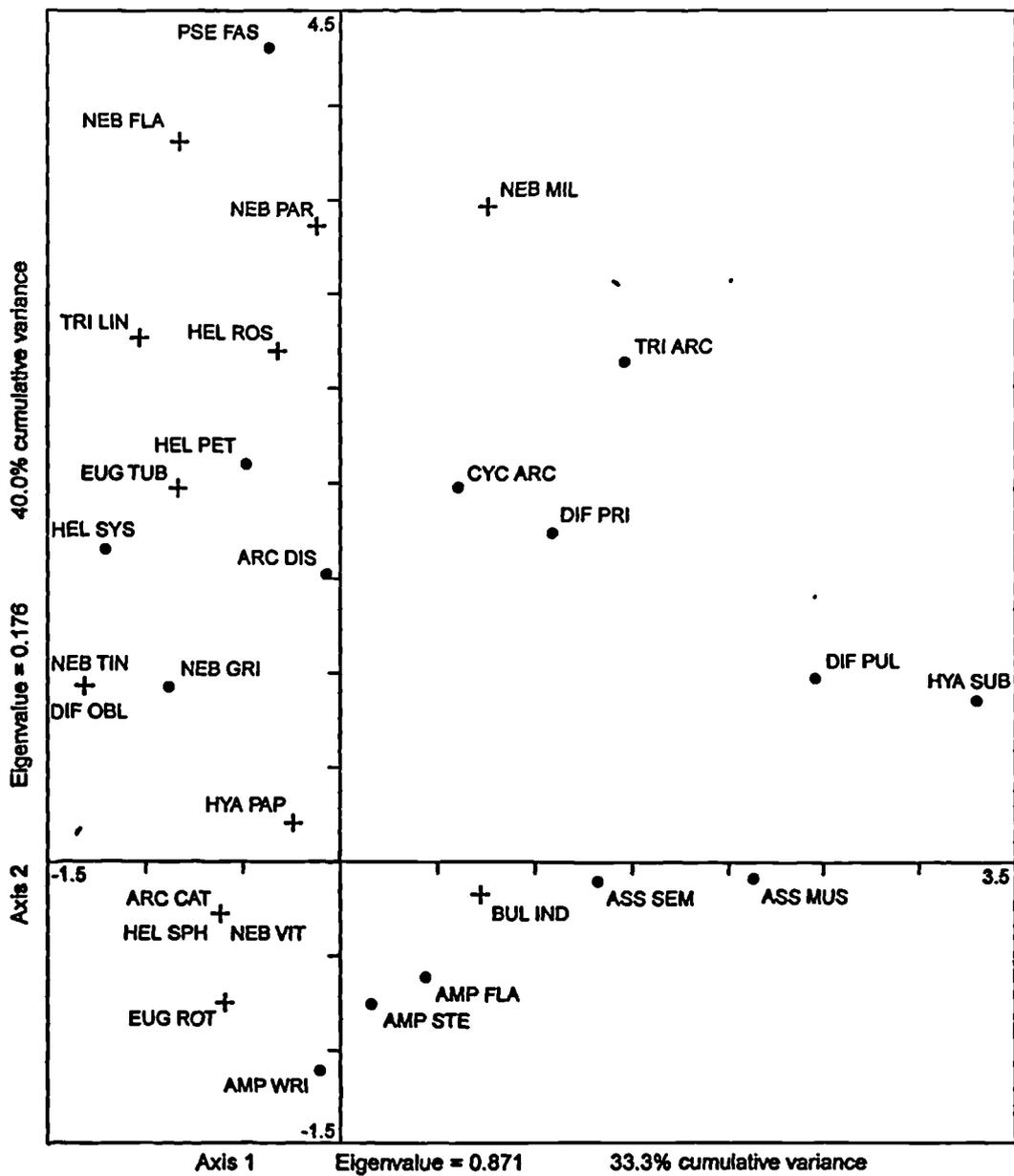


Figure 6.10 Species ordination for BBF II. Taxa with <5% abundance plotted as crosses, refer to Table 5.3 for explanation of species codes

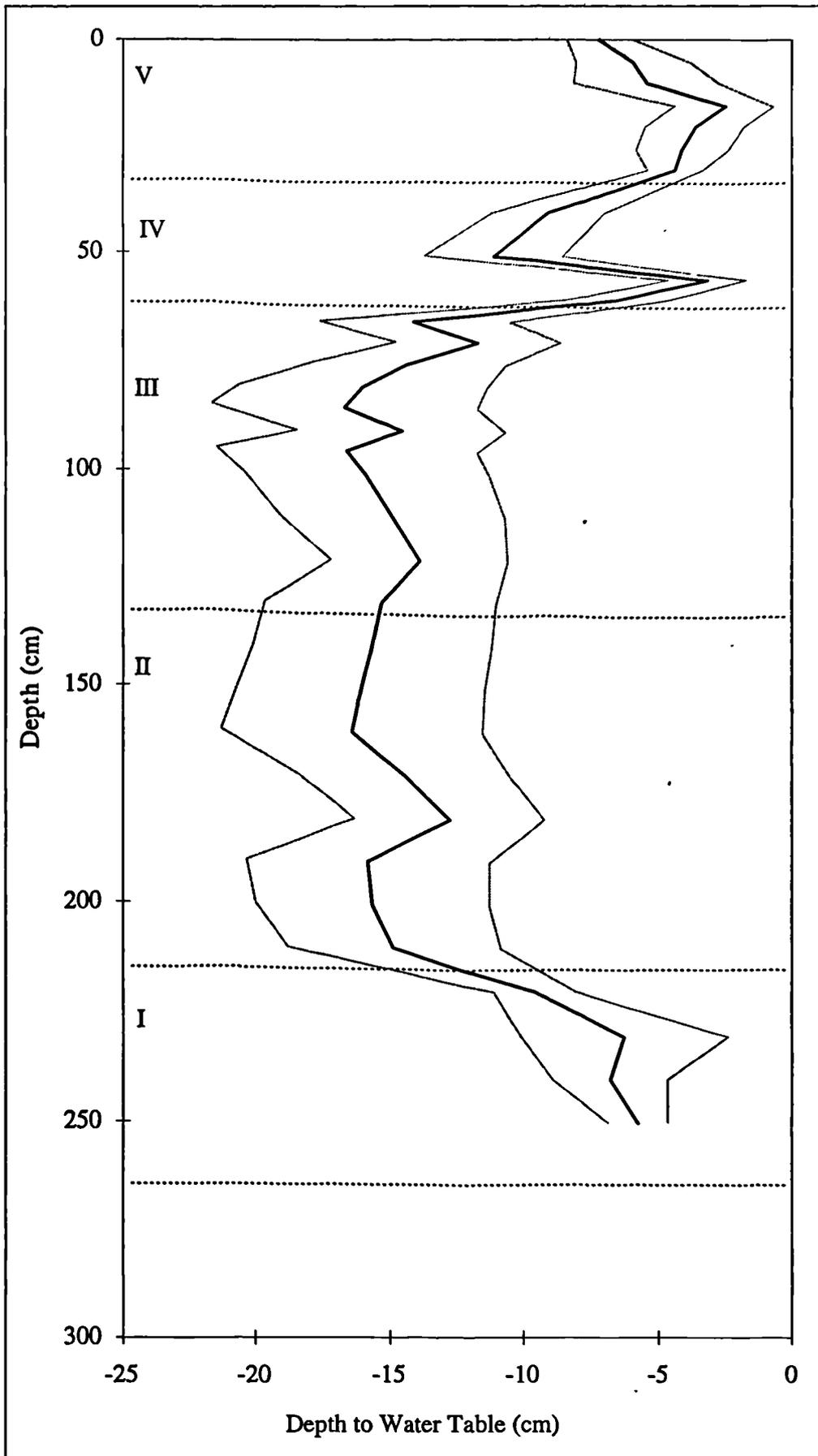


Figure 6.11 Mean water table reconstruction BBF II, with 2σ bootstrapped error estimates shown as thin lines. Assemblage zones marked.

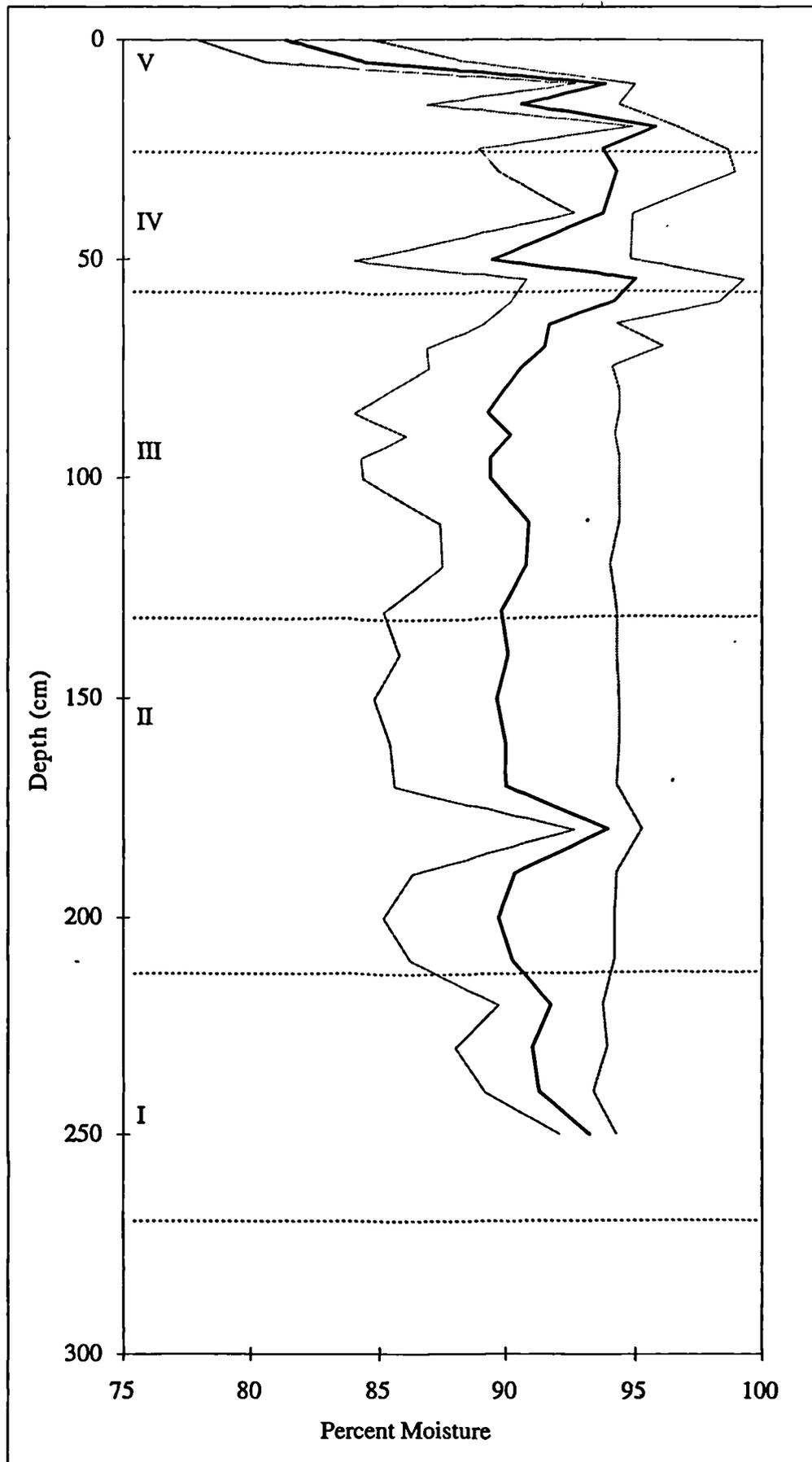


Figure 6.12 Mean moisture reconstruction BBF II, with 2σ bootstrapped error estimates shown as thin lines. Assemblage zones marked.

Moisture reconstruction

Figure 6.12 shows the reconstructed moisture curve for BBF II using WA-Tol with outlier samples removed. As with the water table reconstruction, sample 270cm is not plotted, as it is independent of other data and little confidence can be placed in the mean value of 81% moisture, as there is no analogue value for *Pseudodiffugia fascicularis*. From 250cm, the peat moisture content falls from 93% to 89.7% at 200cm. The wide confidence intervals associated with these levels are related to the broad tolerance range of *H. subflava* (Section 4.2.2). At 180cm, there are narrow confidence intervals and a mean moisture content of 93%. This is associated with the presence of *A. flavum* and *A. wrightianum* which are wet indicator species with good analogues. From 170cm to 65cm peat depth, the mean moisture curve is complacent, between 89-90%. The maximum curve is also complacent, but the minimum curve shows a greater degree of variability. At 55cm peat depth, the maximum value is 99% moisture content, the mean is 95%. From 20cm to the surface, the mean moisture content falls from 95.8% to 81%, associated in the decline in *Amphitrema* spp. and *Arcella discoides* type and a rise in *D. pristis* type.

6.3 Butterburn Flow Core III (BBF III)

Butterburn Flow Core III was extracted from the northern edge of the northern part of the mire in September 1995. Figure 3.7 shows core location. 348cm of peat was extracted. Laboratory preparation and data processing procedures are set out in Chapter Four.

6.3.1 Stratigraphy

Table 6.5 shows the sediment description for BBF III according to Troels-Smith (1955). The presence of *Sphagnum* and *Eriophorum* macrofossils suggests that this is an ombrotrophic peat.

6.3.2 Testate amoebae

The profile was cored to the depth of 348cm, of which 341cm was peat. From 341cm to 348cm, the core was composed of grey clay which was devoid of tests. Tests were counted to 340cm (Figure 6.13).

Depth (cm)	Sediment Description
0 - 2	nig 3; strf 0; elas 4; sicc 1; humo 0; Tb ⁴ ; undecomposed <i>Sphagnum</i> moss, <i>Calluna vulgaris</i>
2 - 6.5	nig 2; strf 0; elas 4; sicc 1; humo 0; Tb ⁴ ; undecomposed <i>Sphagnum</i> moss
6.5 - 26	nig 3; strf 1; elas 1; sicc 1; humo 2; Tb ⁴ ; partially decomposed <i>Sphagnum</i> peat
26 - 37	nig 2; strf 1; elas 2; sicc 1; humo 2; Tb ⁴ ; partially decomposed <i>Sphagnum</i> peat
37 - 51	nig 3; strf 1; elas 2; sicc 1; humo 2; Tb ⁴ partially decomposed <i>Sphagnum</i> peat
51 - 76	nig 4; strf 1; elas 3; sicc 1; humo 3; Tb ⁴ well humified <i>Sphagnum</i> peat
76 - 125	nig 4; strf 0; elas 0; sicc 1; Sh Th ⁺ (Phrag)
125 - 150	nig 4; strf 0; elas 0; sicc 1; Sh Th ⁺ roots and <i>Eriophorum</i>
150 - 200	nig 4; strf 0; elas 0; sicc 2; Sh Th ⁺ well humified peat matrix with roots
200 - 300	nig 4; strf 0; elas 0; sicc 1; Sh Th ⁺ roots and <i>Eriophorum</i>
300 - 341	nig 4; strf 1; elas 0; sicc 2; humo 3 Sh ⁺ Th ¹ birch roots and <i>Eriophorum</i>
341 - 348	nig 3; strf 0; elas 0; sicc 3; As ⁴ Th ⁺ ; grey clay - confirmed base

Table 6.5 Stratigraphic description for BBF III using the Troels-Smith (1955) sediment description system

Zone	Depth (cm)	Major taxa	Zone description
III	0-42.5	<i>Amphitrema</i> spp., <i>Diffugia pristis</i> type	There is a greater diversity of taxa at the top of this zone than at any other point in the core. <i>Diffugia pulex</i> decreases from the bottom to the top. The <i>Heleopera</i> spp. increase to the top, as does <i>Pseudodiffugia fascicularis</i> .
II	42.5-195	<i>Diffugia pulex</i> <i>Hyalosphenia subflava</i>	This zone is characterised by high values of <i>Diffugia pulex</i> and <i>H. subflava</i> . <i>H. subflava</i> decreases to the top. <i>Amphitrema wrightianum</i> occurs for the first time.
I	195-340	<i>Assulina muscorum</i> , <i>Cyclopyxis arcelloides</i> type, <i>Diffugia pristis</i> type, <i>Diffugia pulex</i> , <i>Nebela militaris</i> , <i>Trigonopyxis arcula</i>	The four major taxa found in this zone, <i>A. muscorum</i> , <i>Cyclopyxis arcelloides</i> type, <i>Diffugia pristis</i> type and <i>D. pulex</i> dominate the assemblage. Other taxa found in small numbers throughout the zone include <i>Nebela militaris</i> and <i>Trigonopyxis arcula</i> . The basal sample, 340cm, contains <i>Arcella catinus</i> , <i>Hyalosphenia papilio</i> and <i>N. parvula</i> . The rotifer <i>Habrotrocha angusticollis</i> is also well represented.

Table 6.6 Zone descriptions for BBF III based on testate amoebae assemblages

Thirty five taxa were found in this core, which has been divided into three faunal zones (Table 6.6). The boundary between Zones I and II corresponds with the rise in *Hyalosphenia subflava*. The basal sample from Zone I, 340cm, is very different from the other samples in this zone and may be regarded as an outlier. There are no changes in faunal composition that correspond with major stratigraphic boundaries.

Zone I 195-340cm The species assemblage of xerophilous taxa, for example, *Cyclopyxis arcelloides* type, *Nebela militaris* and *Trigonopyxis arcula* suggests that this zone is dry (Table 4.4). The basal sample contains 25% *Nebela parvula* which, according to Warner (1987), inhabits very dry conditions. 340cm also contains 18.6% *Arcella catinus*, which is the driest indicator species found by Charman and Warner (1992) from sites in northeastern Ontario and 28% *Hyalosphenia papilio*, which prefers very wet conditions. This complicates interpretation. This sample is from the minerogenic transition and, since wetness and dryness indices are predominantly determined from ombrotrophic bogs, not from minerotrophic systems, the assemblages from the basal peats are difficult to interpret.

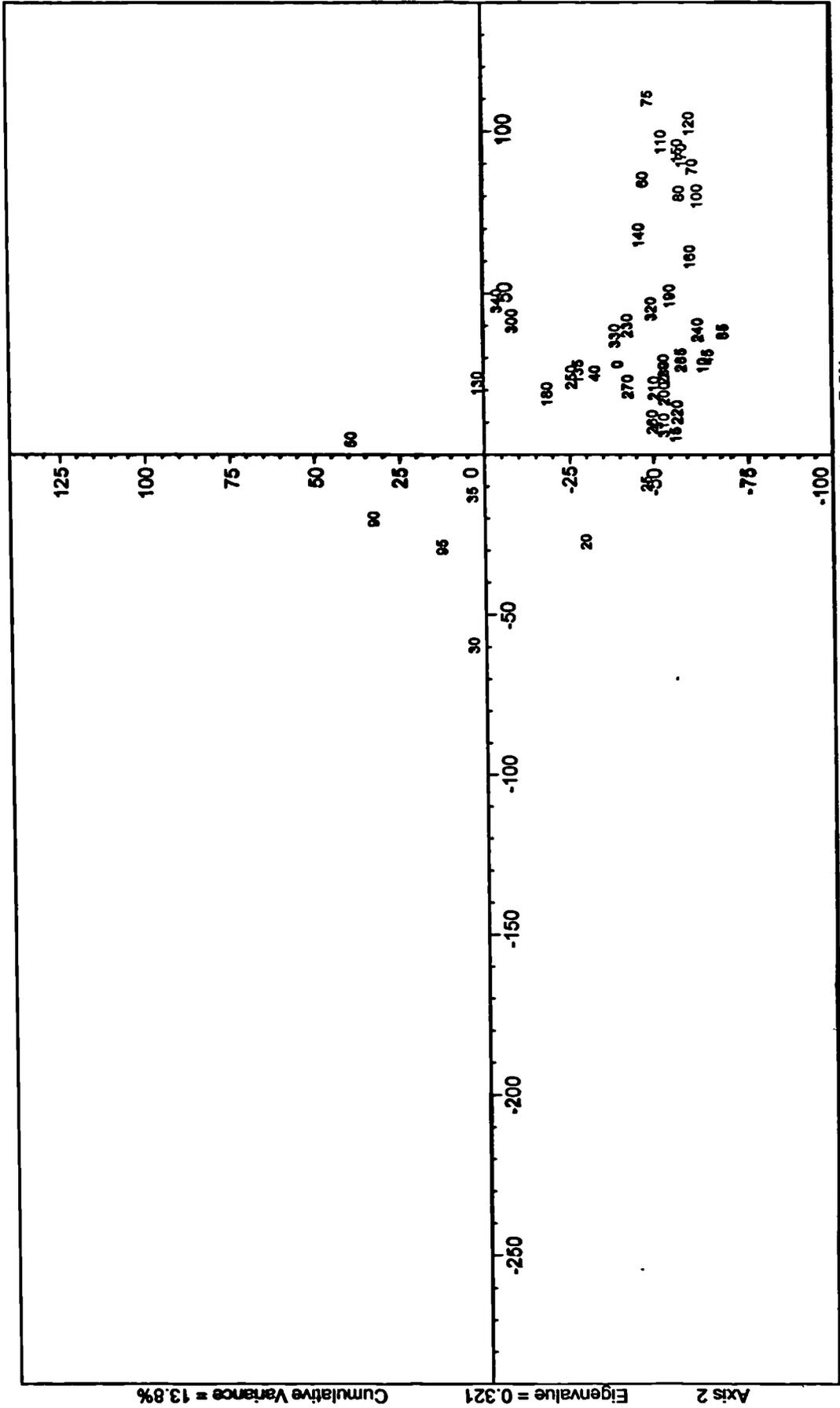
Zone II 42.5-195cm This zone is dominated by *H. subflava* which prefers <80% water content (Warner, 1991), or a water table optimum of up to 49.9cm (Warner and Charman, 1994) and *D. pulex*. There are two wetter parts, at 80-85cm and 130-135cm, where the *Amphitrema* spp increase in abundance and *H. subflava* decreases.

Zone III 0-32.5cm This zone has a greater diversity of species many of which prefer very wet conditions. The *Amphitrema* spp. are abundant at the base and *Arcella discoides* type and *Pseudodifflugia fascicularis* occur as the *Amphitrema* spp. decline. All of these taxa prefer very wet to aquatic conditions. This is the wettest zone of BBF III.

6.3.3 Ordination

Modern and fossil ordination

Figure 6.14 shows that fossil samples are clustered in a similar pattern to BBF II in the bottom right corner of the ordination plot. Outlier samples 70, 75, 80, 100, 110, 120, 150, 160 and 170cm all contain large amounts of *H. subflava* and *D. pulex*. These samples will not have robust hydrological reconstructions as they fall outside of the



Cumulative Variance = 13.8%

Eigenvalue = 0.321

Axis 2

Axis 1 Eigenvalue = 0.379 Cumulative Variance = 7.5%

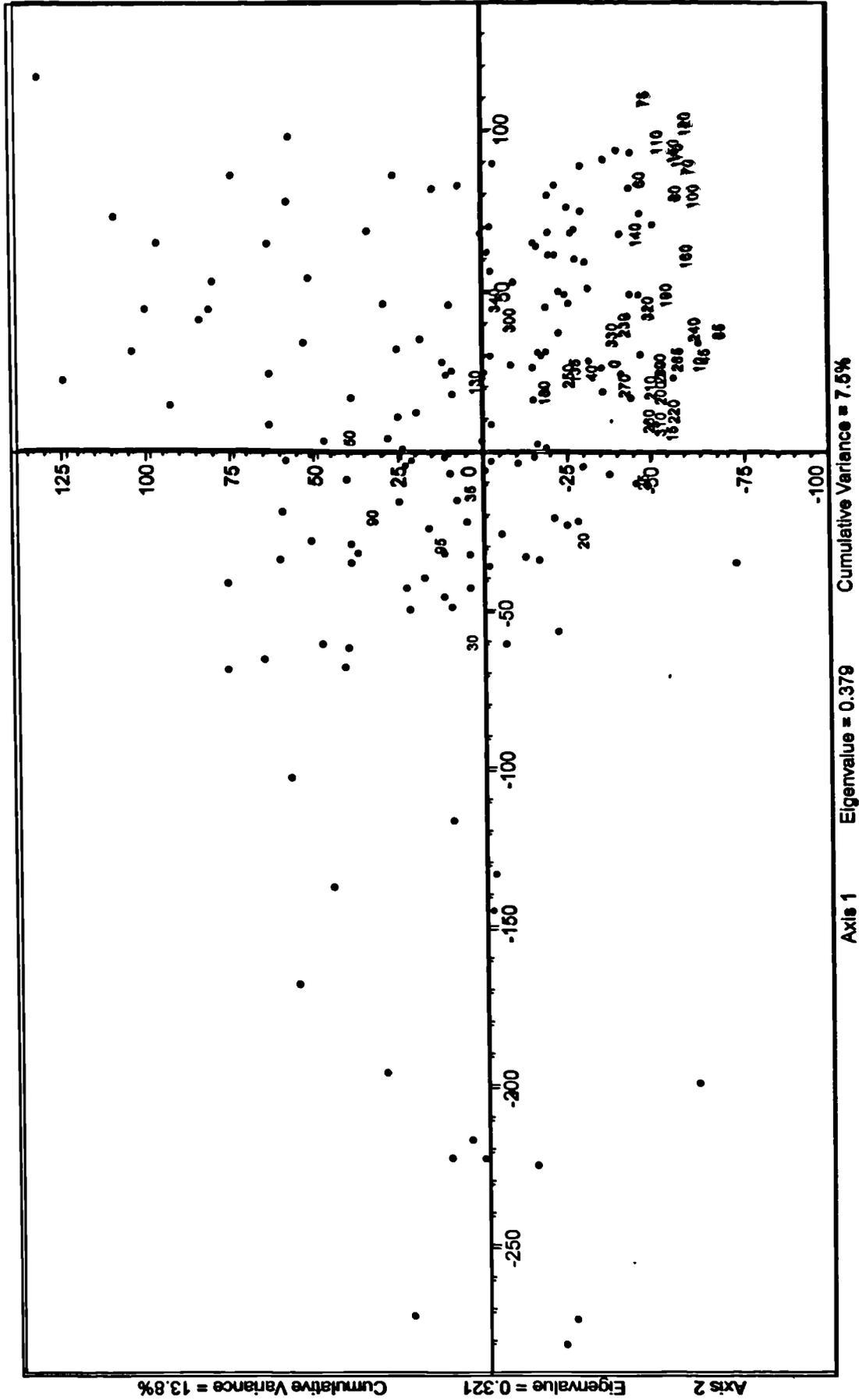


Figure 6.14 Modern and fossil DCA ordination for BBF III. Fossil samples (overlay) plotted as 'passive', modern samples plotted as circles

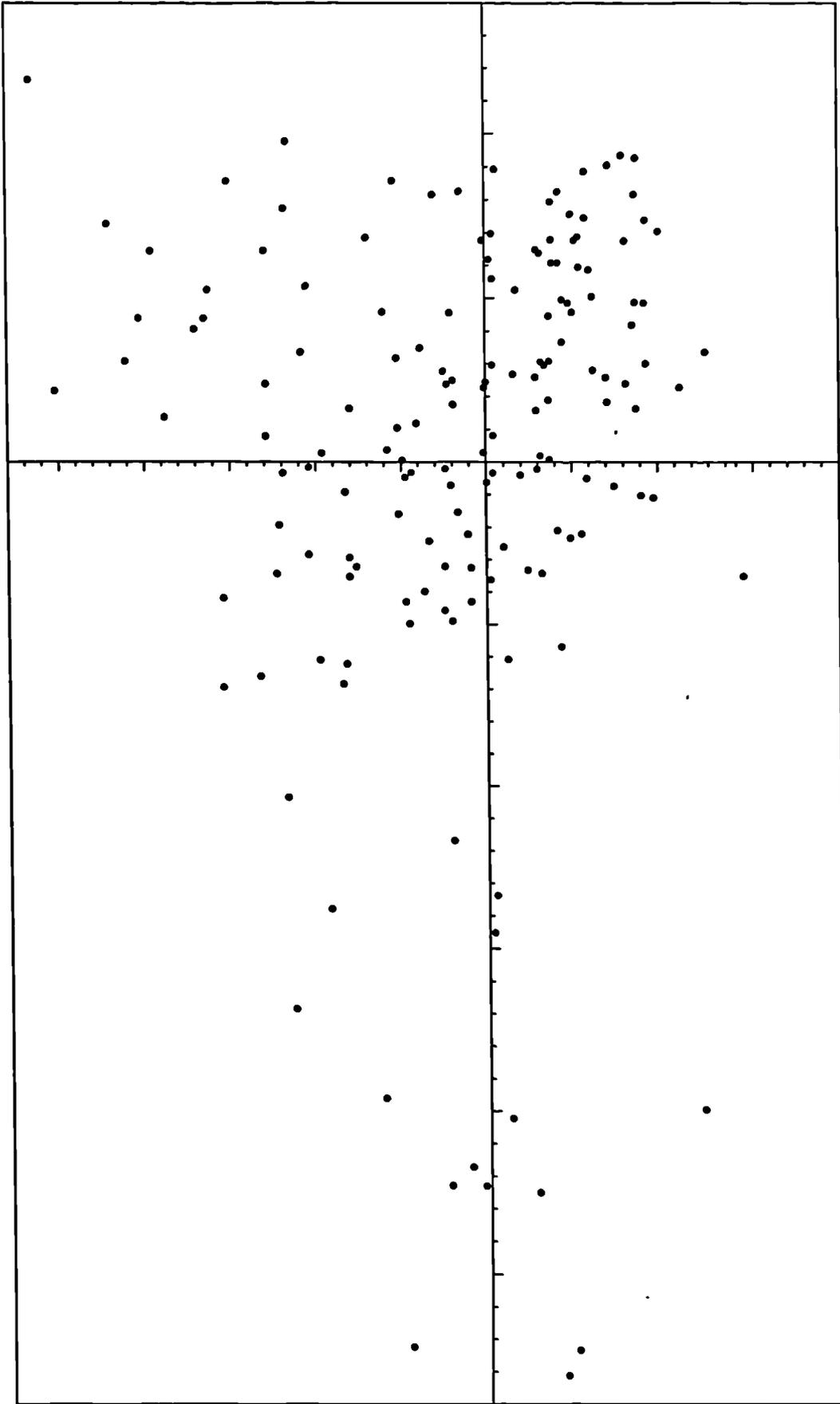


Figure 6.14 Modern and fossil DCA ordination for BBF III. Fossil samples (overlay) plotted as 'passive', modern samples plotted as circles

modern ordination plot. The lack of adequate analogue values for these taxa is discussed in Chapter Eight. Even samples that fall within the spread of modern samples may not have good reconstructions. For example, sample 50cm depth contains 20% *A. flavum*, 57% *D. pulex* and 23% other taxa. Even though 43% of the species assemblage have modern analogue values, the reliability of the reconstruction will be affected because 57% of the assemblage has no analogue value.

Sample ordination

The sample ordination for BBF III is presented in Figure 6.15. This figure is presented to show the relationship between samples within the core. Sample 340cm is an outlier, as it is the only sample that contains high values of *Arcella catinus*, *Hyalosphenia papilio* and *Nebela parvula*. Samples from Zone III are clustered at the bottom of the ordination plot, as axis 2 is related to the depth of samples in the profile. Basal samples are located at the top of the plot and surface samples located at the base of the plot. Samples from Zone II that contain high values of *Hyalosphenia subflava* and *Diffflugia pulex* are clustered on the far left of the plot, while samples from Zone I are clustered along the top. Axis 1 exerts the greatest influence on the distribution of samples with an eigenvalue of .499, Axis 2 has an eigenvalue of .307.

Species ordination

Seventeen species with less than 5% abundance in all samples in which they occur are plotted as crosses, as they have less influence on the ordination than those samples plotted as solid circles (Figure 6.16). Most of the taxa with less significance to the ordination are plotted in the bottom right corner, on the negative side of axis 1. *H. subflava* is plotted in isolation on the far right of the plot.

6.3.4 Hydrological reconstructions

Water table reconstruction

The water table reconstruction for BBF III using WA is presented in Figure 6.17. The base of the core at 340cm has a depth to water table value of -4.5cm. From 340cm to 230cm, the water table fluctuates from -7.7cm to -5cm. The confidence intervals are narrow in this part of the reconstruction because of the high values of *Assulina*

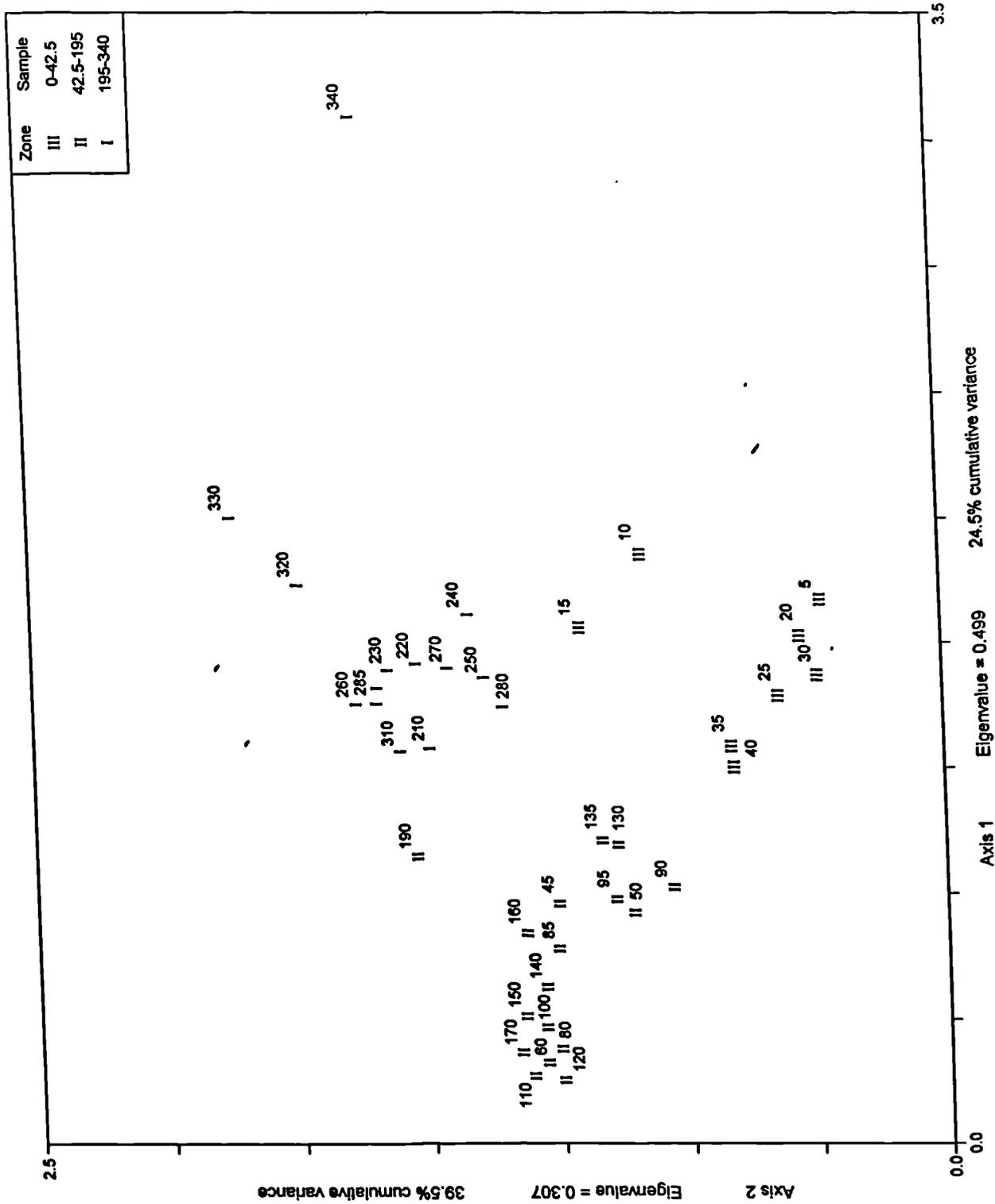


Figure 6.15 Sample ordination for BBF III

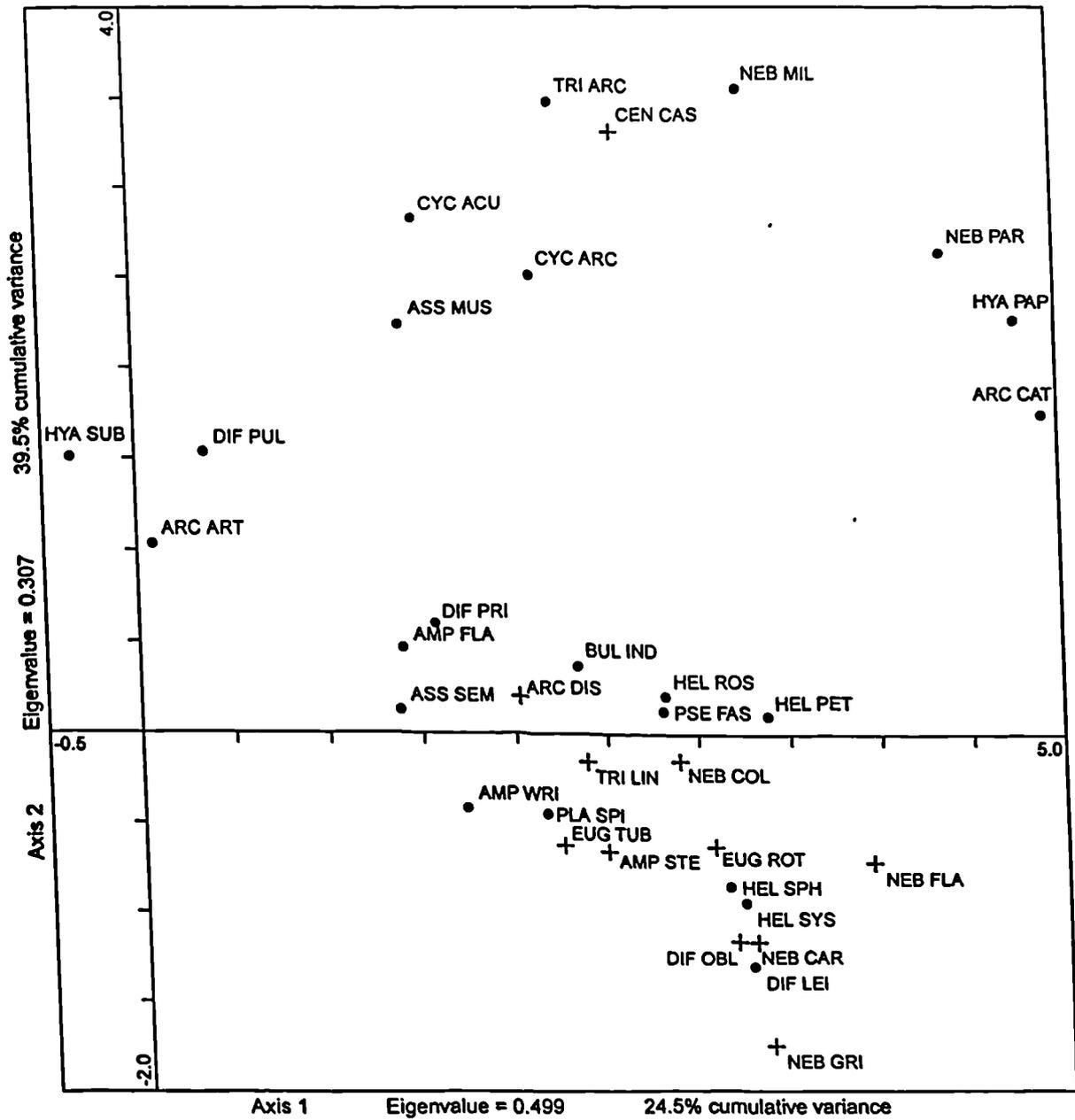


Figure 6.16 Species ordination for BBF III. Taxa with <5% abundance plotted as crosses, refer to Table 5.3 for species codes

muscorum (optimum -7.4cm), *Cyclopyxis arcelloides* type (optimum -5cm), *Diffugia pristis* type (optima -7cm), *Nebela militaris* (optimum -7.9cm) and *Trigonopyxis arcula* (optimum -7.8cm). These taxa have similar optima values and relatively narrow tolerance ranges. From 200cm to 140cm, the water table falls from -5.9cm to -11.2cm. Between 135-130cm, the water rises to -6cm and is associated with peaks in the *Amphitrema* spp. The water table falls between 120-100cm to -13.7cm. This trend of lower water table is interrupted at 90cm, when the water table rises to -3cm. Again, this is associated with a peak in the *Amphitrema* spp. The depth to water table drops back to -15cm at 75cm peat depth. From 40cm, with a water table depth of -4.6cm, the water table level drops gently to -5.7cm at the surface.

Moisture reconstruction

The moisture reconstruction for BBF III using WA-Tol with outlier samples removed is presented in Figure 6.18. The basal sample, 340cm, has a mean reconstructed moisture value of 93.8%. From 330cm to 190cm, the curve is relatively complacent, fluctuating between 90-92% soil moisture content. At 180cm, the moisture level increases to a mean of 97.3%. The minimum reconstructed value is 95.3% and maximum 99.3%. Although the confidence intervals are narrow at this point, the robustness of the reconstruction is questionable since 42% of the species assemblage is *D. pulex* and 20% is *H. subflava* (see Chapter Eight). From 170cm to 40cm, the curve is sinuous, with a maximum moisture value of 95.6% at 90cm peat depth and a minimum value of 88% at 130cm. In the top 35cm, the moisture content of the peat drops dramatically from 94% at 35cm to 85.9% at the surface. This shows a far greater degree of variability than the same depth range in the water table reconstruction.

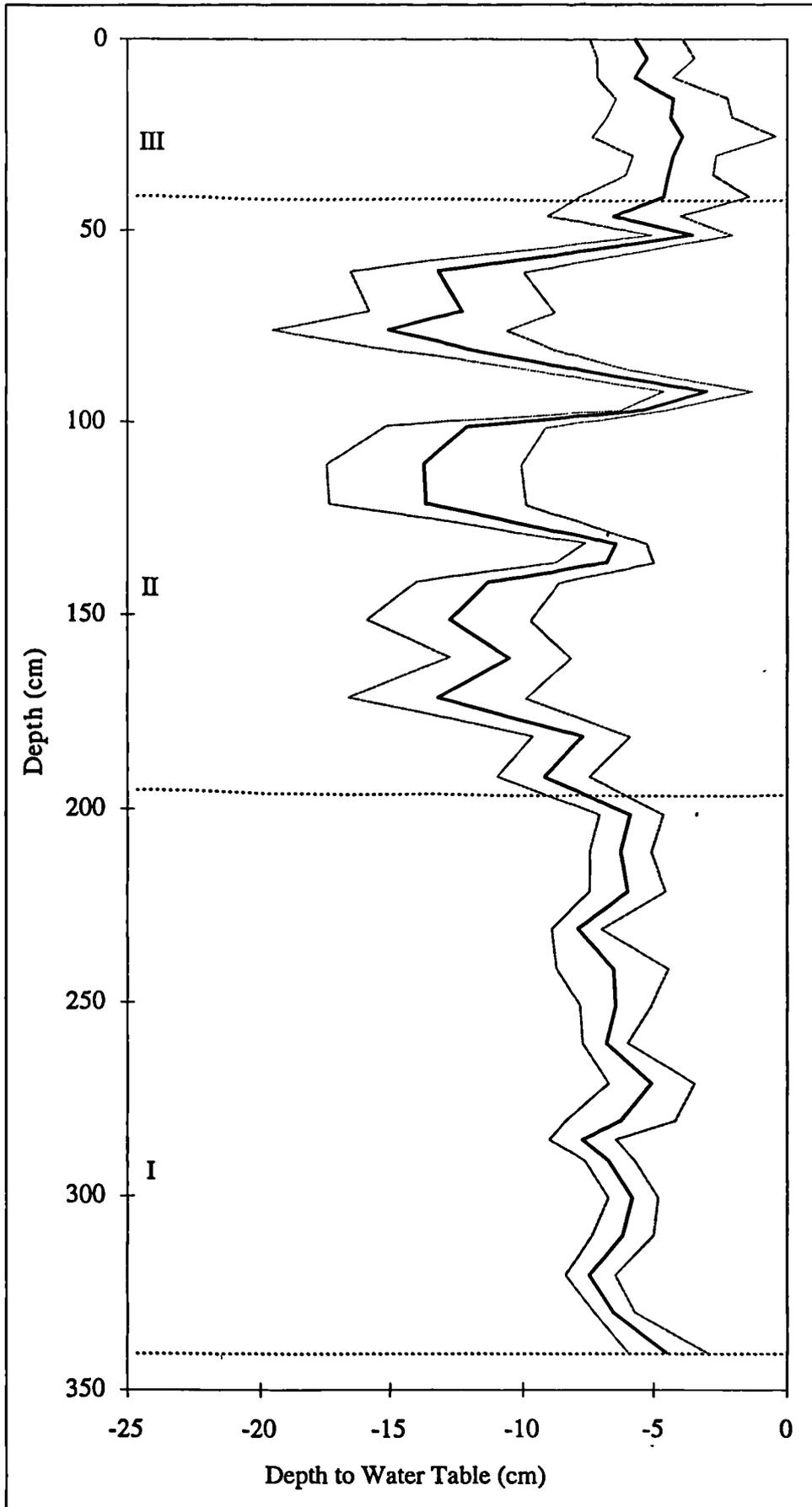


Figure 6.17 Mean water table reconstruction BBF III, with 2σ bootstrapped error estimates shown as thin lines. Assemblage zones marked.

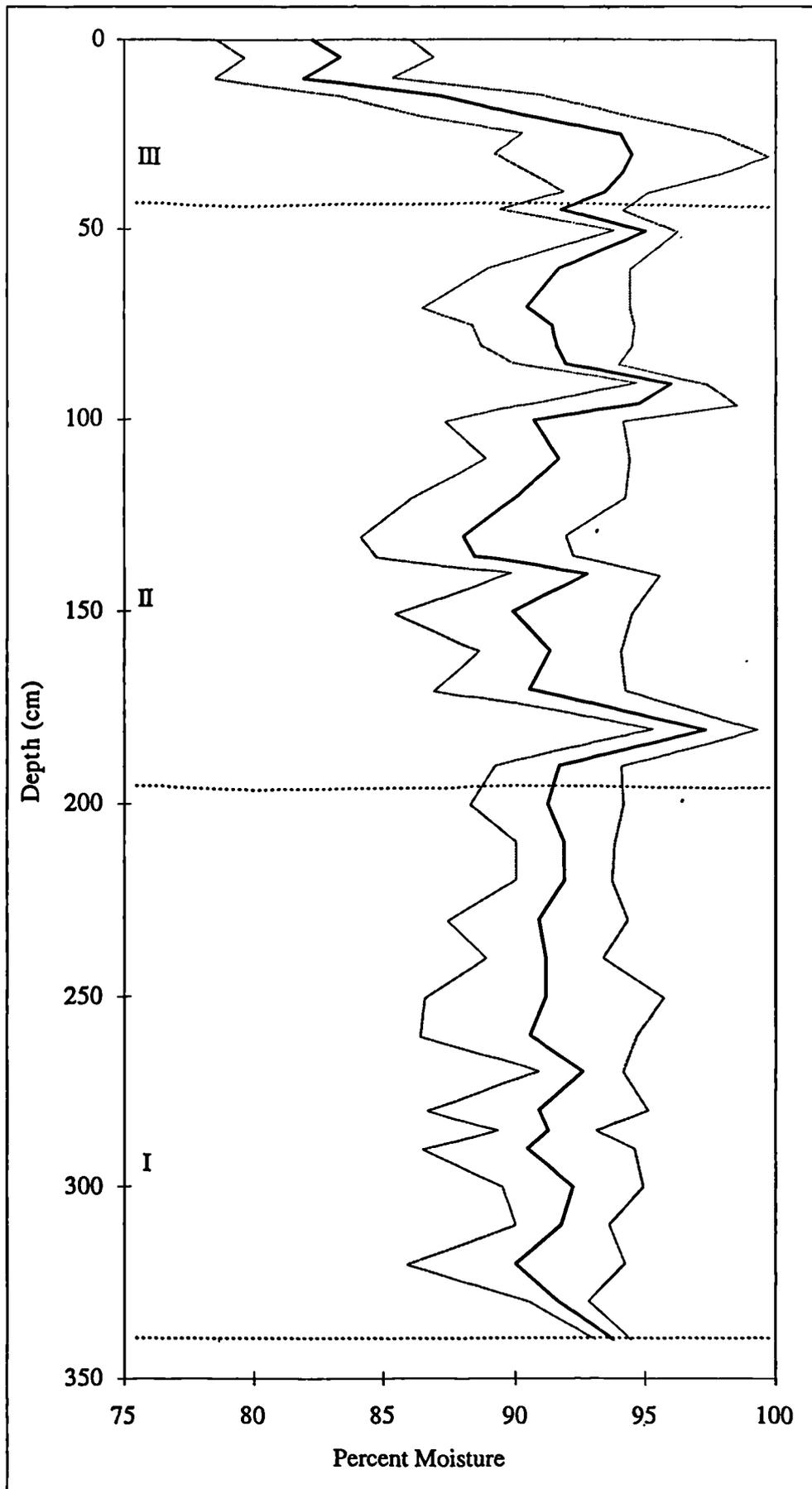


Figure 6.18 Mean moisture reconstruction BBF III, with 2σ bootstrapped error estimates shown as thin lines. Assemblage zones marked.

6.4 Chronology

6.4.1 Pollen data

Pollen sampling rationale and preparation procedures are set out in Chapter Four. As at Coom Rigg Moss, the aim of pollen analysis was to provide a biostratigraphic correlation to be used in conjunction with the radiocarbon dates. The surface 20cm was counted at 5cm intervals to give a detailed record of recent pollen accumulation. The rest of the core was sampled at 20cm intervals, so that major changes in pollen spectra could be identified. Four horizons are identified as marker horizons. These horizons are set out in Table 6.7 and are shown on the pollen diagrams for Butterburn Flow, Figures 6.19-6.21.

Core	A	B	C	D
BBF I	25	70	310	430
BBF II	25	50		
BBF III	25	55		

Table 6.7 Changes in pollen spectra and depths for the three Butterburn Flow cores. A-D represent changes noted on the diagrams and described in the text

These horizons are equivalent to those found at Coom Rigg Moss and therefore, position A relates to the anthropogenic *Pinus* rise (APR) that relates to large scale afforestation of the Kielder Forest which commenced in 1926. Land directly adjacent to the northern end of Butterburn Flow was not forested, but the APR provides a useful chronological marker above background levels. Position B, the decline in *Alnus* pollen to below 5%TLP is clearly identifiable in all three profiles. Position C, which marks the point at which a rise in Cyperaceae and a small rise in Poaceae occurs together with a decline in *Alnus* and is only found in BBF I. The Elm Decline is also found only in BBF I and is shown at horizon D at 430cm (Figure 6.19). The Elm Decline took place between 5300-5000BP in northern Europe (Bell and Walker, 1992) and the pattern and chronological spread of the elm decline does not easily fit any hypothesis such as greater coolness, wetness or continentality (Huntley and Birks, 1983). Since this decline is found only in BBF I, it is not used as a chronostratigraphic marker horizon. Marker horizons A and B provide a limited comparison between the cores from

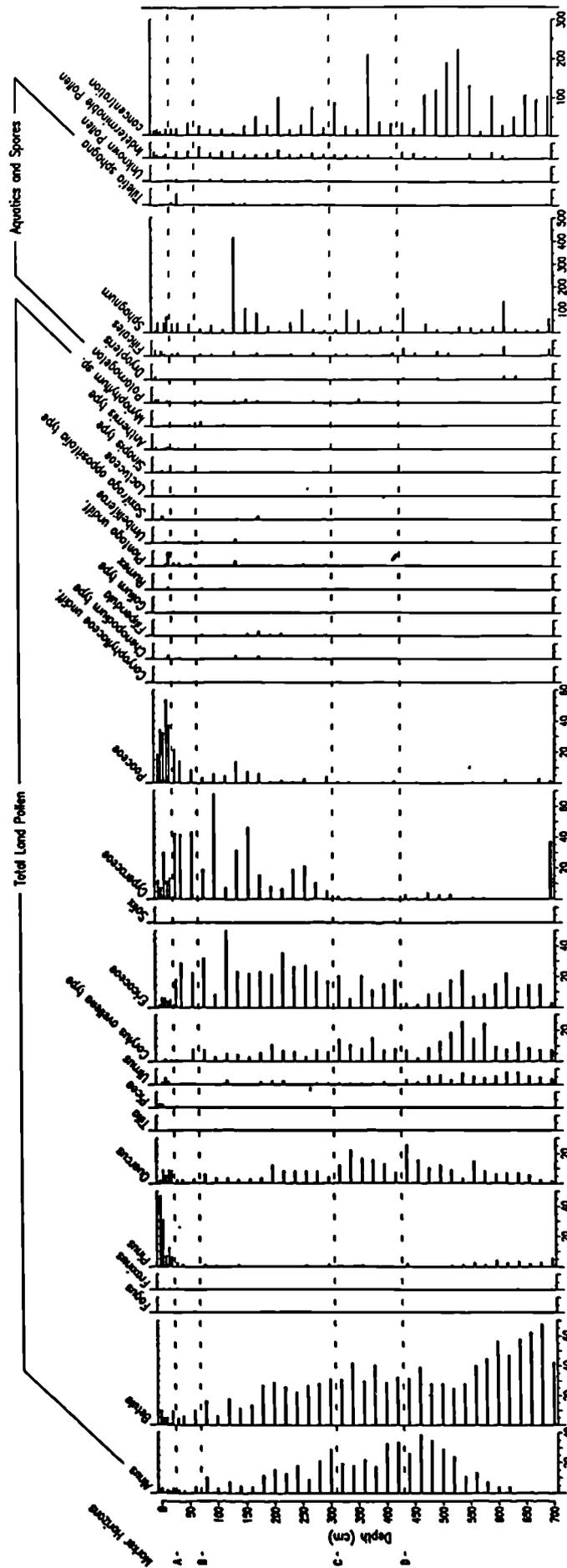


Figure 6.19 BBF I percentage pollen diagram

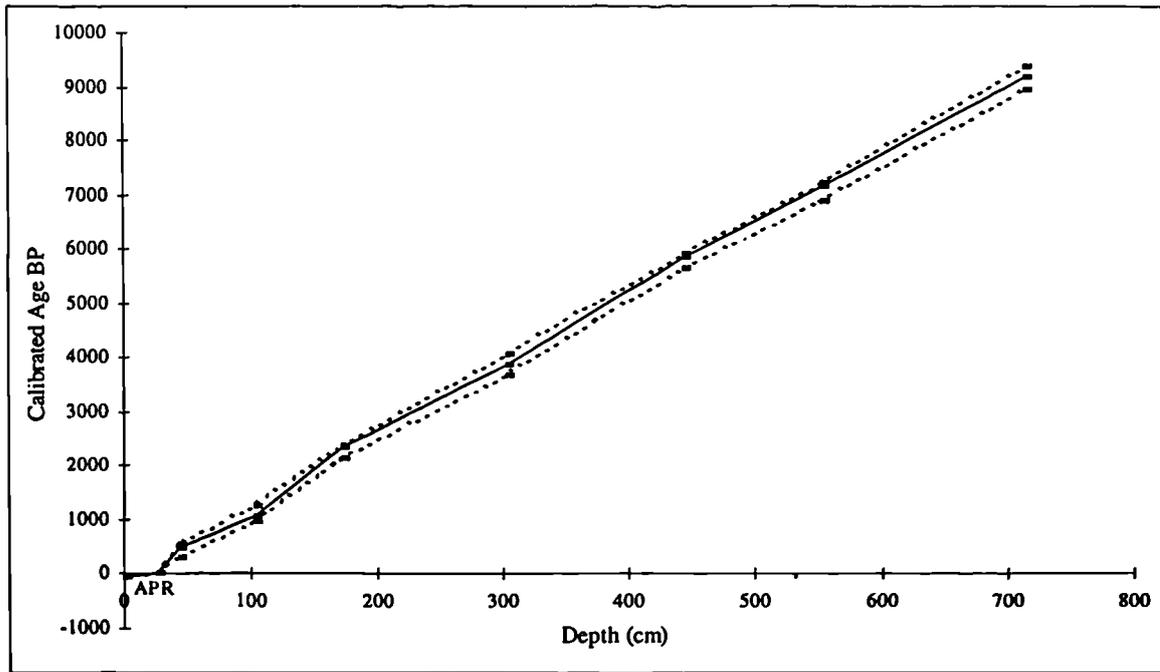


Figure 6.22 Butterburn Flow I - linear interpolation of sample ages. Solid line - median linear interpolation from radiocarbon dates and APR, dashed lines - 2σ confidence limits on

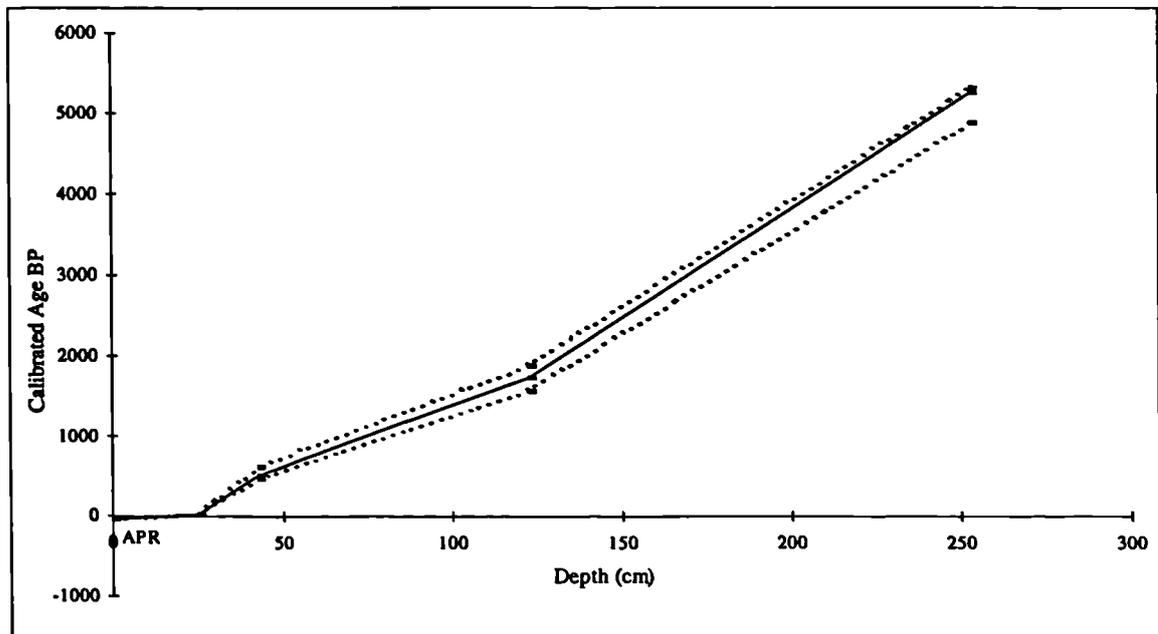


Figure 6.23 Butterburn Flow II - linear interpolation of sample ages. Solid line - median linear interpolation from radiocarbon dates and APR, dashed lines - 2σ confidence limits on

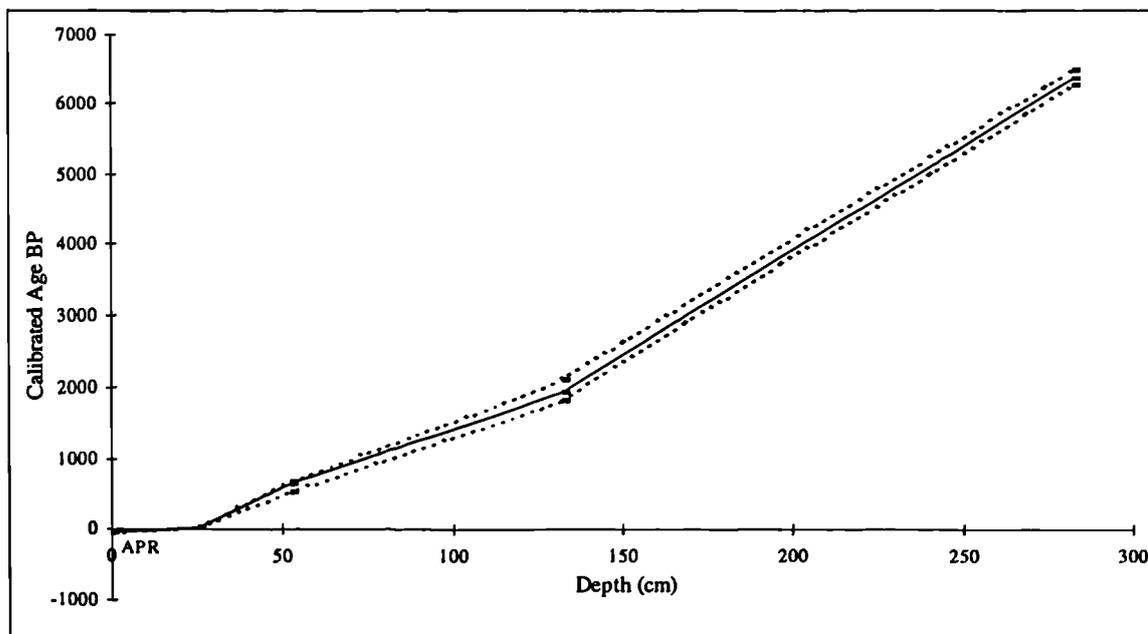


Figure 6.24 Butterburn Flow III - linear interpolation of sample ages. Solid line - median linear interpolation from radiocarbon dates and APR, dashed lines - 2σ confidence limits on

Butterburn Flow. The APR is assigned the date 1930, since it is likely that the initial rise above background *Pinus* levels took place soon after planting.

For BBF I, as for the cores from Coom Rigg Moss, the APR is used as an additional chronological marker in conjunction with the radiocarbon dates to calculate sedimentation rate and the age of each sample. The APR has a date of 20BP (before 1950).

6.4.2 Radiocarbon data

Conventional radiocarbon ages were calibrated using CALIB 3.0.3c (Stuiver and Reimer, 1993a,b), as set out in Chapter Four. Figures 6.22-6.24 shows the location of calibrated ^{14}C ages BP in relation to the depth of core with 2σ confidence intervals for each date from BBF I, BBF II and BBF III. The solid line represents the median linear interpolation of sample ages, the dashed lines represent the maximum and minimum linear interpolation of sample ages (Section 4.1.5). The APR is marked for each core. There are no confidence limits on the APR.

Table 6.8 presents the estimated accumulation rates for BBF I. From the base of the core to 297AD, peat accumulation rate was approximately 12.5 years per cm. Peat

accumulation is approximately 11 years per centimetre between 297AD to 1201AD. The acrotelm peat accumulation is *ca.* 2.5 years per centimetre. Accumulation rates for BBF II and BBF III are not presented as these cores do not have chronologies as well constrained as BBF I, which would result in cruder estimates of peat accumulation. Figures 6.25 to 6.27 show the testate amoebae assemblages for BBF I-BBF III against age.

Depth (cm)	Year BC/AD	year/cm
0-40	1943AD	3
40-100	1201AD	11
100-170	297AD	12.5
170-300	1118.5BC	12.5
300-440	2870BC	12.5
440-550	4513BC	12.5
550-710	6181BC	12.5

Table 6.8 BBF I accumulation rate (yr/cm)

6.5 Conclusions

The top 1m to 1.5m of each core from Butterburn Flow has better hydrological reconstructions than at greater depth down the cores because the upper peats have a greater diversity of taxa in the assemblage and more of these have good modern analogue values. The modern analogue transfer function was developed from samples from wet peat bog conservation sites with long-term monitoring programmes, which biased the hydrological models to better reconstructions for wetter taxa. Most designated conservation sites are wet as these are perceived to be of more conservation value than drier sites, which could have yielded better analogue values for dry taxa. The consequences for the robustness of the reconstructions are discussed in Chapter Eight. Macro-scale comparisons between BBF I and the central cores from Coom Rigg Moss and The Wou are discussed in Chapter Nine, as are the separation of allogenic and autogenic hydrological signals.

Chapter Seven

THE WOU -

Testate amoebae and palaeohydrology

7.0 Introduction

This chapter presents the results from The Wou. TW II from the centre of The Wou was analysed first and, because of the poor test concentrations, extremely poor quality slides and differences between the testate amoebae assemblages from TW II and the cores from Coom Rigg Moss and Butterburn Flow, it was decided not to pursue testate amoebae analysis of the two marginal cores at The Wou any further. Hence, there are no testate data for either TW I or TW III. The first section of this chapter presents the stratigraphy for all three cores and testate amoebae record, ordination analyses and hydrological reconstructions for TW II. The second section of this chapter describes the results for TW II against age. The rationale for coring at The Wou is set out in Chapter Three.

7.1 The Wou Core I (TW I)

TW I was extracted from the bottom of the slope from Black Rigg, from 0m on south-north transect I (Figure 3.10). 405cm of peat was extracted. The stratigraphy of core TW I is set out in Table 7.1. The peat below 175cm is woody, above this the peat contains well humified moss peat.

7.1.1 Stratigraphy

Minerogenic peat is highly variable. The stratigraphy of TW I (Table 7.1) describes a core which contains a higher proportion of woody peat than was found in the ombrotrophic peats (*e.g.* Table 5.1, Table 5.8).

Depth (cm)	Sediment description
0 - 3	nig 1; strf 0; elas 4; sicc 1; humo 0; fresh, undecomposed <i>Sphagnum recurvum</i> moss
3 - 23	nig 1; strf 1; elas 4; sicc 1; humo 1; very well preserved <i>Sphagnum</i> moss
23 - 30	nig 2; strf 1; elas 3; sicc 1; humo 2; Tb ⁴ ; <i>Sphagnum</i> peat with occasional monocots, plant structure partially decayed, though distinct
30 - 50	nig 3; strf 3; elas 3; sicc 2; humo 2; Tb ⁴ Th ⁺ ; fairly well humified <i>Sphagnum</i> matrix with some Ericaceous roots
50 - 100	nig 3; strf 3; elas 3; sicc 1; humo 2; Tb ⁴ Th ⁺ ; moss peat with roots
100 - 125	nig 4; strf 2; elas 3; sicc 1; humo 3; Tb ⁴ well humified moss peat
125 - 175	nig 4; strf 1; elas 2; sicc 1; humo 3; Tb ⁴ Th ⁺ (monoct.) well humified moss peat
175 - 225	nig 4; strf 1; elas 1; sicc 2; humo 4; Tb ³ ; Tl ¹ ; highly humified peat with woody fragments
225 - 243	nig 4; strf 1; elas 1; sicc 2; humo 4; Tb ² ; Tl ¹ ; Th ¹ highly humified moss peat with roots and wood
243 - 250	nig 4; strf 2; elas 3; sicc 2; humo 3; Tb ⁴ well humified moss peat
250 - 294	nig 4; strf 1; elas 2; sicc 2; Tl ³ ; Sh ¹ woody peat with <i>Substantia humosa</i>
294 - 332	nig 4; strf 2; elas 1; sicc 2; Tl ⁴ Sh ⁺ woody peat with <i>Substantia humosa</i>
332 - 338	nig 4; strf 3; elas 1; sicc 2; Tl ³ ; Th ¹ Sh ⁺ woody peat with roots
338 - 350	nig 4; strf 2; elas 0; sicc 2; Tl ⁴ Sh ⁺ woody peat
350 - 405	nig 4; strf 2; elas 1; sicc 3; Th ⁴ Sh ⁺ ; felted monocot. fragments

Table 7.1 Stratigraphic description for TW I using the Troels-Smith (1955) sediment description system

7.2 The Wou Core II (TW II)

Core TW II was extracted from the centre of the site, from 60m along west-east transect I. Sediment to a depth of 497cm was extracted. Sediment from 33-90cm was not retained in the corer as it was too wet to sample.

7.2.1 Stratigraphy

Table 7.2 shows the stratigraphy of TW II. This core contains a high proportion of sedge peat and several layers of silt and sand. This indicates that the peat accumulation has been heavily influenced by groundwater and runoff processes.

Depth (cm)	Sediment description
0 - 6	nig 2; strf 0; elas 4; sicc 3; humo 0; unhumified <i>Juncus effusus</i> , moss
6 - 13	nig 3; strf 1; elas 3; sicc 2; humo 2; Tb ² ; Th ² ; <i>Sphagnum</i> and reeds
13 - 33	nig 3; strf 2; elas 3; sicc 2; humo 1; Th ³ ; Tb ¹ <i>Eriophorum</i> peat
33 - 90	not sampled, material not retained in corer
90 - 126	nig 4; strf 1; elas 3; sicc 1; humo 2; Tb ² ; Th ² ; <i>Sphagnum</i> and <i>Eriophorum</i>
126 - 199	nig 2; strf 1; elas 3; sicc 1; humo 2; Tb ³ ; Th ¹ ; well humified <i>Sphagnum</i> peat with monocot fragments
199 - 209	nig 4; strf 1; elas 1; sicc 1; humo 3; Tb ⁴ Th ⁺ well humified moss peat
209 - 225	nig 4; strf 0; elas 1; sicc 1; humo 4; Sh. highly humified peat
225 - 241	nig 3; strf 1; elas 2; sicc 1; humo 3; Tb ³ ; Th ¹ Tl ⁺ well humified moss peat with roots and wood fragments
241 - 286	nig 3; strf 2; elas 2; sicc 1; humo 2; Tb ² ; Th ² (monocot.) unhumified moss and <i>Eriophorum</i> peat
286 - 300	nig 4; strf 1; elas 1; sicc 1; humo 3; Th ³ ; Tl ¹ Tb ⁺ humified <i>Eriophorum</i> peat with wood
300 - 325	nig 3; strf 2; elas 2; sicc 1; humo 2; Th ⁴ Tb ⁺ unhumified <i>Eriophorum</i> peat
325 - 362.5	nig 4; strf 1; elas 1; sicc 1; humo 3; Tl ⁴ Tb ⁺ Tl ⁺ woody peat
362.5 - 365	nig 3; strf 0; elas 3; sicc 2; Ag ³ Sh ¹ peaty silt
365 - 368	nig 4; strf 1; elas 1; sicc 1; humo 4; Sh highly humified peat
368 - 369.5	nig 2; strf 0; elas 3; sicc 2; Ag ⁴ grey silt
369.5 - 394	nig 4; strf 0; elas 1; sicc 1; Sh ² ; Ag ² silty peat
394 - 424.5	nig 4; strf 1; elas 1; sicc 1; Sh ⁴ Tl ⁺ Ag ⁺ highly humified matrix with silt and roots
424.5 - 448	nig 4; strf 1; elas 1; sicc 2; Sh ⁴ Th ⁺ Ga ⁺ highly humified matrix with sand and wood
448 - 455	nig 4; strf 0; elas 1; sicc 2; Sh ⁴ Tl ⁺ <i>Substantia humosa</i> with wood
455 - 480	nig 4; strf 1; elas 0; sicc 3; Sh ³ ; Th ¹ Gs ⁺ highly humified matrix with sand and roots
480 - 497	nig 4; strf 1; elas 0; sicc 3; humo 3; Tb ² ; Th ² well humified peat, drier

Table 7.2 Stratigraphical description for TW II using the Troels-Smith (1955) sediment description system

7.2.2 Testate amoebae

Of the 497cm of sediment extracted from TW II, the top 270cm was analysed for testate amoebae, (Figure 7.1). Samples were taken at 10cm intervals and slides were scanned to 310cm, but test concentration was negligible below 270cm. The surface sample is missing, as are samples from 33-90cm. The surface sample was composed of *Juncus*

stems and was not suitable for testate analysis. The testate record is missing from 230cm, 250cm and 260cm, due to extremely low test concentrations. The material from which testates were recovered was composed primarily of moss peat. Below 286cm, the peat contains large amounts of *Eriophorum*, from which no tests were recovered. Between 368-369.5cm, there is a band of grey silt and from 424.5cm, the sediment contains sand grains. Zone I, from 270cm to 195cm does not correspond with changes in stratigraphy. Three horizons, at 230cm, 250cm and 260cm are missing from this zone. Zone II spans the depth from 195cm to 125cm. At 125cm, there is a stratigraphic boundary, the peat below 125cm contains sedge, the peat above does not. Zone III, spans the depth from 125cm to 10cm. From 90cm to 33cm, there is a gap in the diagram due to the material not being retained in the corer. Below 13cm, the peat contains a greater proportion of *Eriophorum* than above 13cm. Thirty-eight taxa were found in TW II, of which 32 were found in Zone II. Slides from TW II were difficult to count due to low test concentrations. The inclusion of fine mineral particles which were retained after micro-sieving also obscured tests.

Zone	Depth (cm)	Major taxa	Zone description
III	10-125	<i>Centropyxis cassis</i> type <i>Cyclopyxis arcelloides</i> type <i>Pseudodifflugia fascicularis</i> <i>Trinema lineare</i>	This zone is dominated by, <i>C. cassis</i> type, <i>C. arcelloides</i> type and <i>T. lineare</i> all of which increase in abundance to the top. The <i>Nebela</i> spp. are well represented. No material was retained in the corer between 33-90cm depth.
II	125-195	<i>Amphitrema wrightianum</i> <i>Centropyxis cassis</i> type	32 taxa were found in this zone, which is characterised by the dominance of <i>A. wrightianum</i> and <i>C. cassis</i> type. <i>A. flavum</i> is well represented at the base
I	195-270	<i>Centropyxis cassis</i> type <i>Cyclopyxis aculeata</i> type <i>Cyclopyxis arcelloides</i> type <i>Pseudodifflugia fascicularis</i>	Seven species of <i>Difflugia</i> were found in this zone. <i>Amphitrema</i> spp. increase to the top. <i>P. fascicularis</i> is the dominant taxon, reaching 53% abundance at 210cm. The concentration of tests increases to the top.

Table 7.3 Zone descriptions for core TW II based on testate amoebae

Zone I 195-270cm Zone I contains large amounts of *Pseudodifflugia fascicularis*, which was regarded by Cash and Hopkinson (1909) as an aquatic taxon. The presence of the *Amphitrema* spp. indicate wet conditions, as does *Difflugia rubescens* which was classified by de Graaf (1956) as a hydrophilous taxon and *Hyalosphenia papilio*, which is also found in very wet *Sphagnum* with >95% water content (e.g. Warner, 1987). The species assemblage in this zone indicates wet conditions.

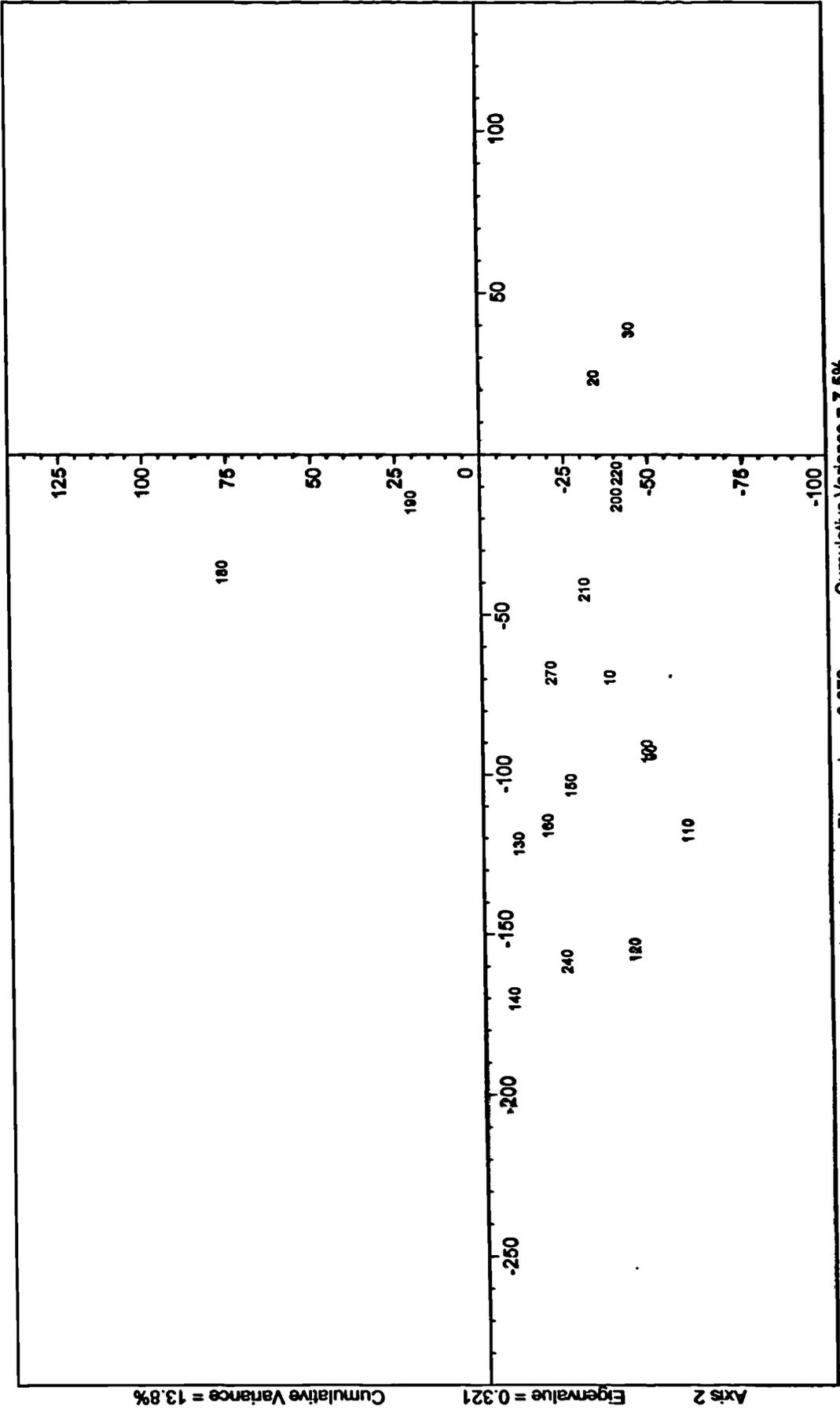
Zone II 125-195cm The dominance of *Amphitrema wrightianum* in this zone suggests wet conditions. *A. wrightianum* was found to have an optimum depth to water table value of -4.07cm from Canadian work (Charman and Warner, 1997). The other species in the assemblage, *A. flavum*, *Centropyxis cassis* type, *C. aculeata* type and *H. papilio* also indicate very wet to aquatic conditions.

Zone III 10-125cm The lack of material between 90-33cm divides the zone, although the species assemblages are very similar. The abundance of *P. fascicularis* at the base of this zone suggests aquatic conditions, which appears to become more hydrophilous towards the surface, as indicated by the abundance of *Trinema lineare* (de Graaf, 1956).

7.2.3 Ordination

Modern and fossil ordination

Figure 7.2 shows the ordination plot of modern samples from the transfer function, with fossil samples from TW II plotted as 'passive'. This is to show the degree of 'match' or 'mis-match' between the two data sets. Four outliers from the modern data set have not been plotted. Most of the fossil samples fall in the middle of the modern ordination plot, between the two groups of modern samples. Samples 100cm, 110cm, 120cm and 270cm, which contain high percentages of *P. fascicularis*, do not have good matches with the modern analogue data set, since this taxon is not in the transfer function. Samples 20cm, 30cm, 180cm and 190cm fall within the spread of modern samples. These samples have good modern analogue values.



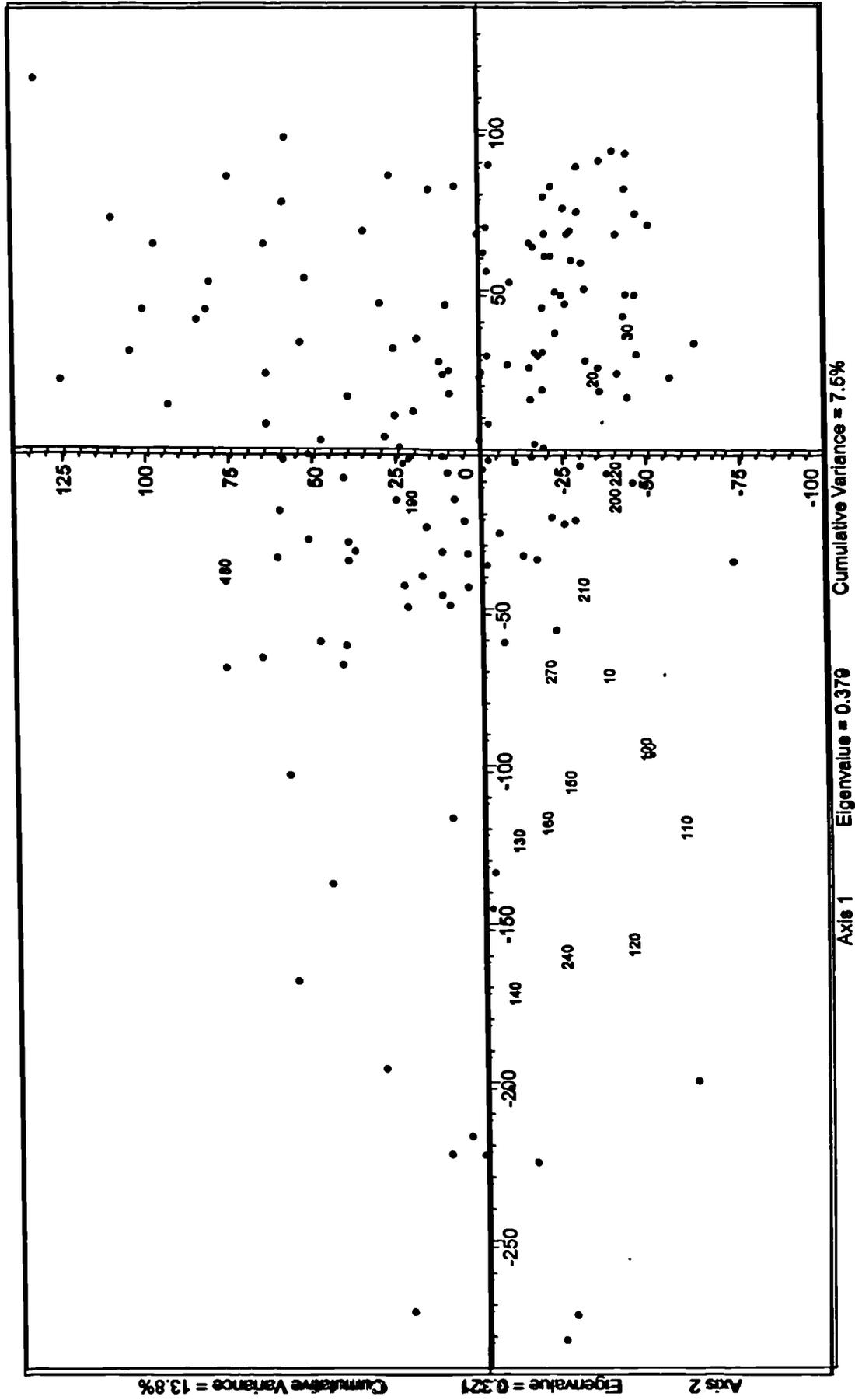


Figure 7.2 Modern and fossil DCA ordination for TW II. Fossil samples (overlay) plotted as 'passive', modern samples plotted as circles

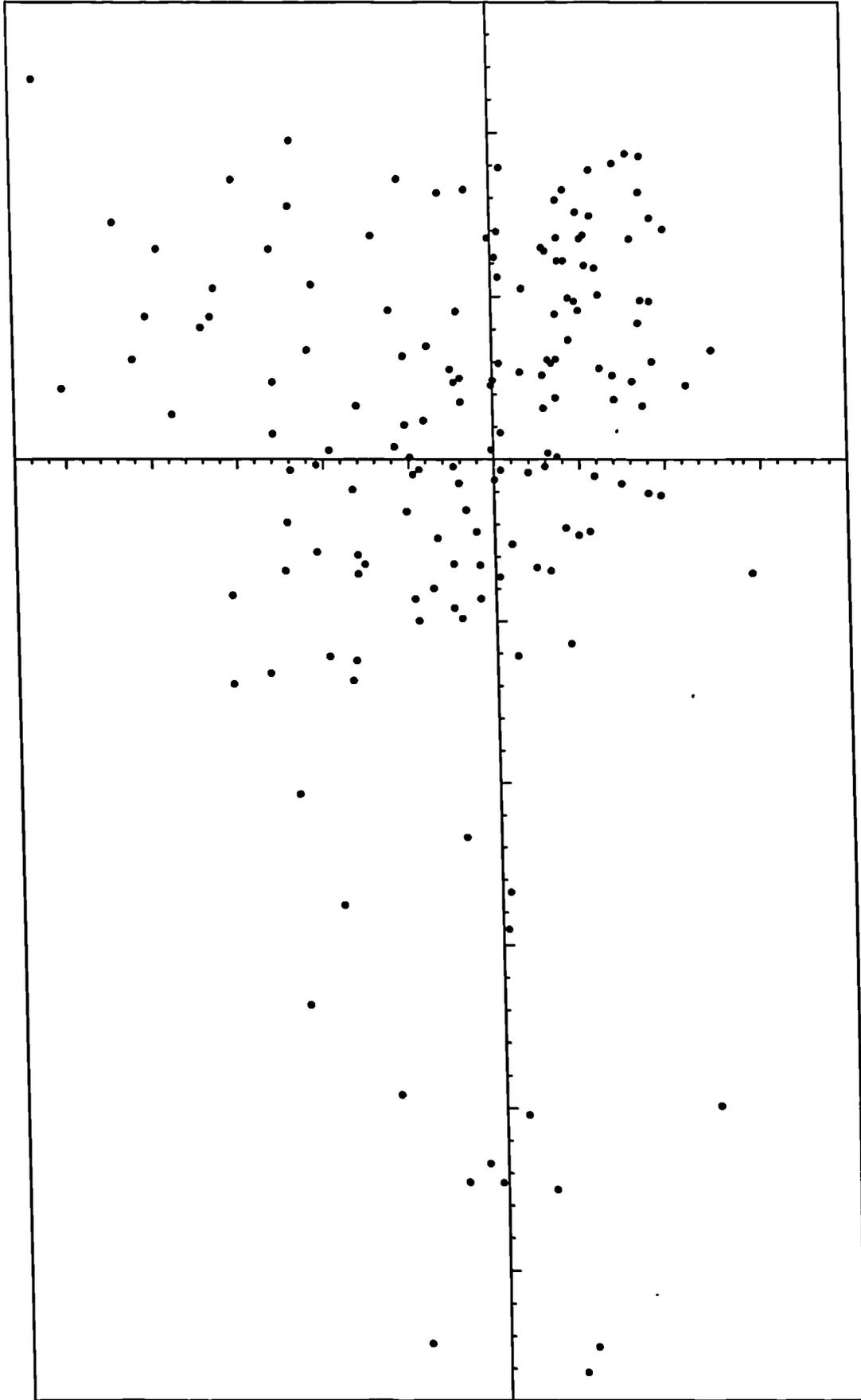


Figure 7.2 Modern and fossil DCA ordination for TW II. Fossil samples (overlay) plotted as 'passive', modern samples plotted as circles

Sample ordination

The ordination plot of samples from TW II is presented in Figure 7.3 to show the association of fossil samples within the core. Samples from Zone I are clustered at the top of the plot, those from Zone II are clustered at the base of the ordination plot. The samples from Zone III are located close on the left side of the diagram. Axis 1 has an eigenvalue of .454 and axis 2 has an eigenvalue of .203.

Species ordination

Figure 7.4 shows the species ordination plot for TW II. Seventeen taxa contain less than 5% abundance in every sample in which they occur. The less significant taxa are scattered throughout the range of more significant taxa. The distribution of taxa about the axes does not show an obvious hydrological gradient since wet, dry and cosmopolitan taxa are adjacent to one another throughout the plot. However, the centre of the plot does contain a greater proportion of wetter taxa such as *Diffugia bacillifera*, *D. globulosa*, *D. oblonga* and *Heleopera petricola*.

7.2.4 Hydrological reconstructions

Water table reconstruction

Figure 7.5 shows the reconstructed water table model for TW II, using WA with outlier samples removed. Samples 270cm and 240cm at the base of the core are not presented since they are isolated data points. Both samples have reconstructed water tables of *ca.* -3.5cm. From 220cm to 90cm, the water table curve varies between -1.6cm at 180cm peat depth and -5.4cm at 200cm peat depth. This is not a large variation in the reconstructed water table value over 130cm. At 30cm peat depth, the reconstructed value is -7.6cm, which falls to -9.4cm at 20cm and then rises to -7.6cm at 10cm. The confidence intervals are close at all points in the reconstruction, with a maximum depth of -2.5cm and a minimum value of -0.8cm at the highest reconstructed point in the water table at 180cm and a maximum value of -12.4cm and a minimum value of -6.3cm at the lowest point in the water table at 20cm.

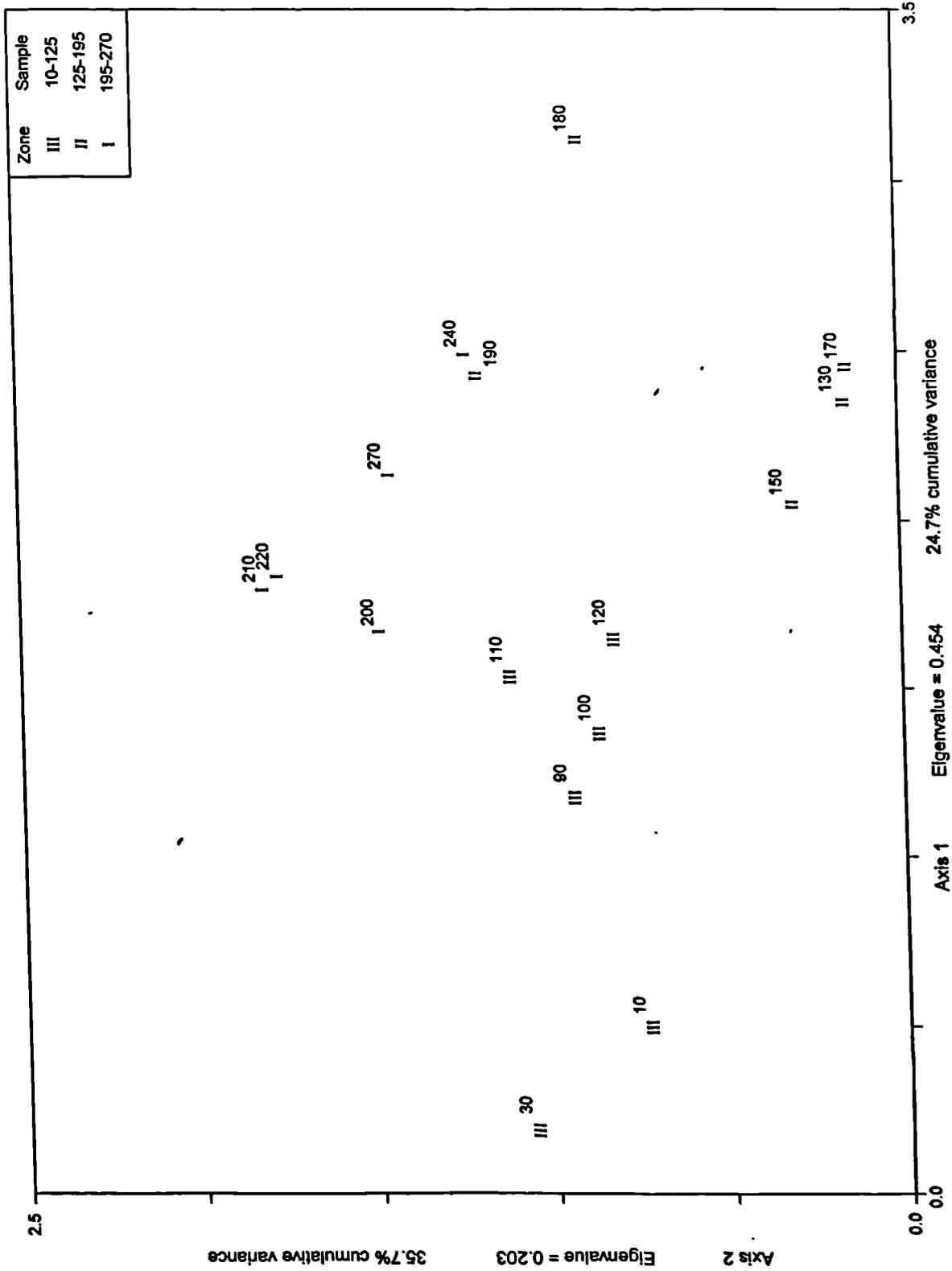


Figure 7.3 Sample ordination for TW II

Moisture reconstruction

The moisture reconstruction for TW II is presented in Figure 7.6. Samples 270cm and 240cm are not presented but both have reconstructed moisture values of 95%. At 220cm, the sample has the lowest reconstructed value of the entire core at 85% soil moisture content. This rises to 95% between 210-200cm peat depth. Between 180cm to 160cm, the mean value is between 96-97% moisture content, this drops to 87.7% at 150cm peat depth. The moisture content of the peat rises from 92.5% at 130cm to 95.9% at 90cm. From 30cm to 10cm, the moisture content rises from 87% to 92%. The confidence intervals on the reconstruction are widest in this part of the core due to the small number of occurrences of *Trinema lineare* in the transfer function. This affects the strength of the reconstruction dominated by this taxon.

7.2.5 Other microfossils

In addition to the testate amoebae found in TW II, many horizons had abundant specimens of desmids. These desmids were not routinely counted, but their presence in samples from The Wou may provide useful insights into the palaeoecological conditions, because, from a qualitative estimate, there was a greater abundance of desmids in horizons with poor test concentrations. Line and Brooks (1980) and Kouwets (1984) were used to identify the desmids as *Euastrum* spp. and which were thought to be the vegetative semi-cells, which indicate pools on the bog surface (Wilmhurst, pers. comm). Desmid vegetative cells have very little resistance to decay and hence there has been very little palaeoecological work carried out on them - the zygospores are thought to be more likely to be recovered from peat, as they are the more resistant form of the life cycle (Andresen, pers. comm.). Work is currently in progress at the University of Wisconsin in Madison, looking at desmids from a palaeolimnological perspective (Winkler, pers. comm.). A multi-proxy approach to reconstructing mire surface wetness reconstructions may be appropriate at some sites using the rotifer *Habrotrocha angusticollis* (*sensu* Warner and Chengalath, 1991), desmids and diatom frustules that are found both included in test construction and free on slides. The rotifers may however, not be found in sufficiently high numbers to be used as an effective palaeoecological tool. These other microfossils may be important hydrological indicators, especially where testate concentrations are poor.

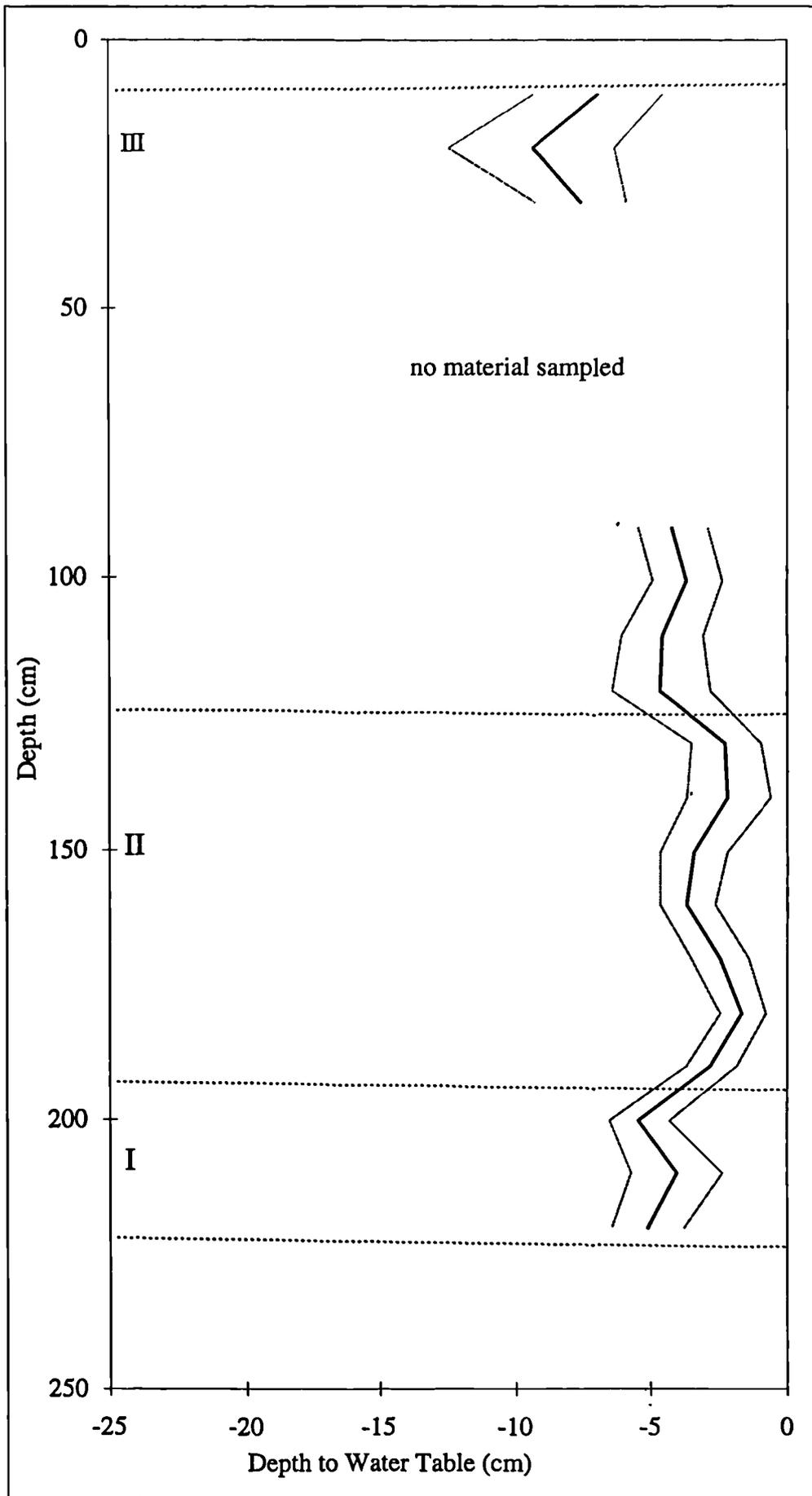


Figure 7.5 Mean water table reconstruction TW II, with 2σ bootstrapped error estimates shown as thin lines. Assemblage zones marked

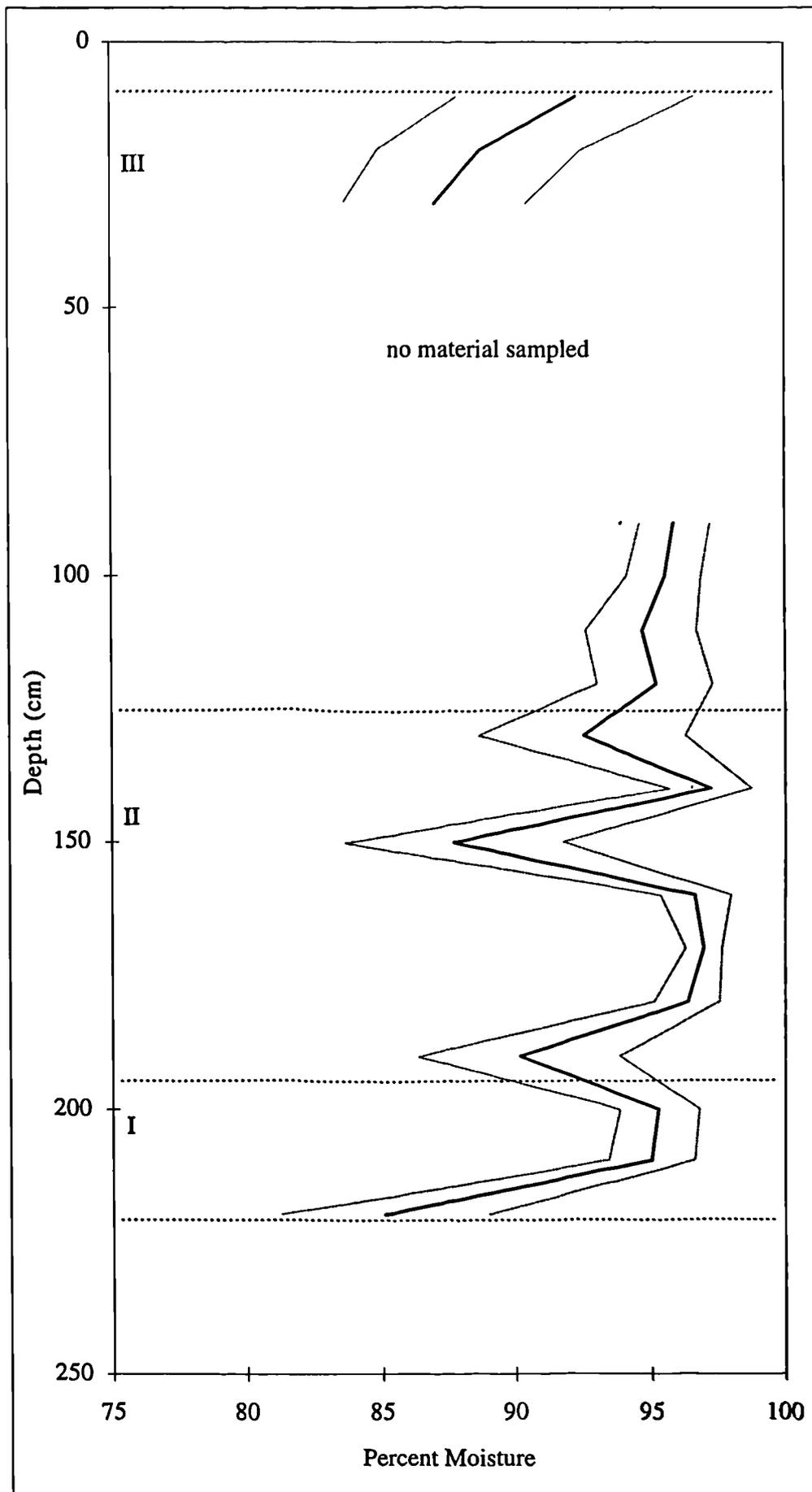


Figure 7.6 Mean moisture reconstruction TW II, with 2σ bootstrapped error estimates shown as thin lines. Assemblage zones marked

7.3 The Wou Core III (TW III)

Core TW III was extracted from the bottom of the slope from Black Rigg, from 15m on south-north transect II. 410cm peat was extracted using a wide-bore Russian corer. The stratigraphy of core TW III is presented in Table 7.4. No further analyses were carried out on TW III due to poor test concentrations from TW II.

7.3.1 Stratigraphy

Depth (cm)	Sediment description
0 - 2.5	nig 2; strf 3; elas 4; sicc 3; humo 0; fresh <i>Sphagnum</i> moss, Polytrichum
2.5 - 8	nig 3; strf 1; elas 3; sicc 3; humo 1; Th ³ (Phrag); Tb ¹
8 - 10.5	nig 4; strf 1; elas 2; sicc 3; humo 2; Tb ⁴ ; Th ⁺ plant structure well preserved
10.5 - 19	nig 3; strf 1; elas 3; sicc 3; humo 1; Tb ⁴ ; unhumified moss peat
19 - 23	nig 4; strf 2; elas 2; sicc 3; humo 2; Tb ² ; Th ² moss and monocot peat
23 - 50	nig 3; strf 2; elas 2; sicc 2; humo 3; Tb ⁴ , well humified peat matrix with stems preserved
50 - 75	nig 4; strf 2; elas 2; sicc 2; humo 3; Tb ⁴ well humified peat, plant structure hardly discernible
75 - 100	nig 4; strf 1; elas 1; sicc 1; humo 3; Tb ⁴ , very well humified peat matrix with some stems preserved
100 - 130	nig 3; strf 1; elas 1; sicc 2; humo 4; Sh Th ⁺ very well humified peat matrix with some stems preserved
130 - 170	nig 4; strf 0; elas 0; sicc 1; Sh no macroscopic structure
170 - 175	nig 4; strf 0; elas 0; sicc 1; Sh Tl ⁺ highly humified peat with roots
175 - 186	nig 4; strf 2; elas 1; sicc 1; Tl Sh ⁺ , birch roots, large wood fragments
186 - 215	nig 4; strf 1; elas 1; sicc 1; Sh Tl ⁺ highly humified peat with roots
215 - 233	nig 3; strf 2; elas 1; sicc 1; humo 3; Th ⁴ Sh ⁺ <i>Eriophorum</i> peat
233 - 281	nig 4; strf 2; elas 1; sicc 1; humo 4; Sh Tl ⁺ very humified peat with woody
281 - 325	nig 3; strf 2; elas 1; sicc 1; humo 3; Th ² ; Sh ² Tl ⁺ Tb ⁺ monocot. leaves and woody roots
325 - 350	nig 3; strf 2; elas 1; sicc 2; humo 3; Th ² ; Tl ² wood and root
350 - 410	nig 4; strf 1; elas 1; sicc 1; humo 4; Sh Tl ⁺ Th ⁺ , birch roots

Table 7.4 Stratigraphic description for TW III using the Troels-Smith (1955) description system

7.4 Chronology

7.4.1 Pollen

Pollen analysis was undertaken on TW II at 20cm intervals. Preparation and subsampling techniques were set out in Chapter Four. The lack of material between 30cm and 90cm means that marker horizon A, the anthropogenic *Pinus* rise (APR) and marker horizon B, the final decline in *Alnus* pollen to below 5%TLP found at Coom Rigg Moss and Butterburn Flow, are not clearly identifiable at The Wou. Therefore biostratigraphic correlations based on the pollen spectra (Figure 7.7) are not possible for core TW II.

7.4.2 Radiocarbon ages

Two radiocarbon dates were assigned to TW II to enable temporal correlation with the Coom Rigg Moss and Butterburn Flow records. Dates were taken at the upper and lower limit of the complete testate record from TW II. The peat sample for the lower date from TW II was 15cm long. This was because the core extracted at this depth was very thin, with a minimal amount of material retained in the corer. The deeper date was 5cm long. Figure 7.8 shows the calibrated radiocarbon dates in relation to the depth of the core, with 2σ confidence intervals. Because of the nature of the pollen data, there is no additional chronological marker for the APR. The linear interpolation was explained in detail in Chapter Four. The actual age of the sample may lie anywhere between the maximum and minimum range of the calibrated dates (as presented in Figure 7.8). The testate amoebae data are presented in Figure 7.9, plotted against age.

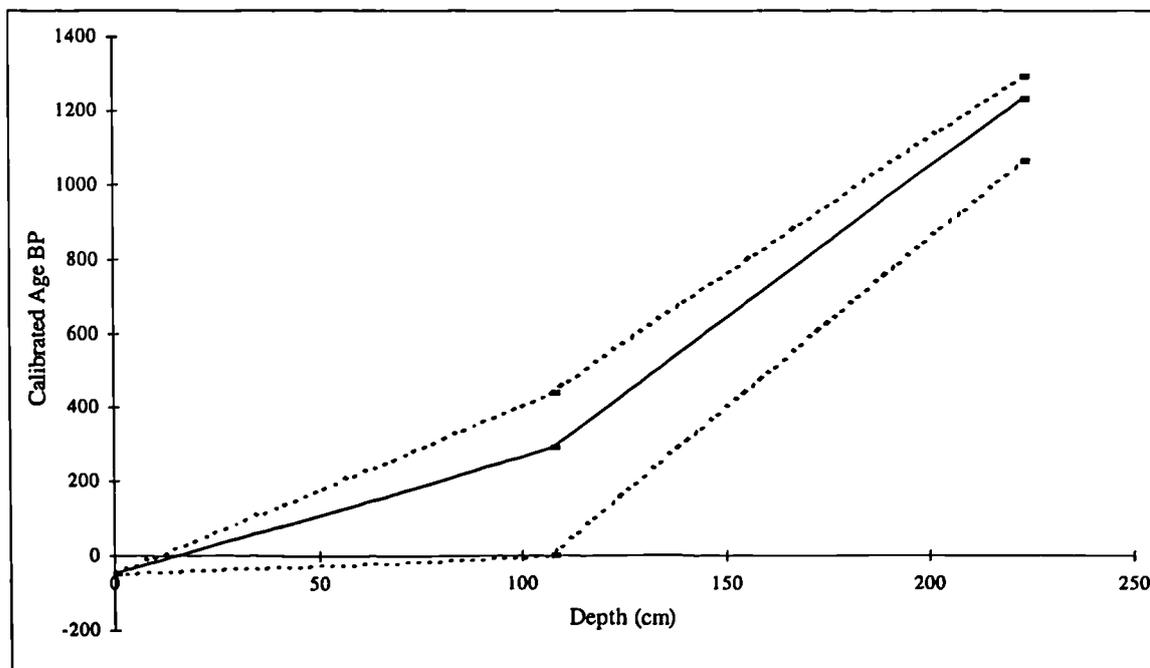


Figure 7.8 The Wou II - linear interpolation of sample ages. Solid line - median linear interpolation from radiocarbon dates, dashed lines - 2σ confidence limits

7.5 Conclusions

Data from The Wou are of limited use due to poor test concentrations from the central core, TW II. Owing to this, it was decided not to carry out further research on the marginal cores TW I and TW III, which were likely to have even lower concentrations due to the location of these cores at the foot of the slope from Black Rigg. The testate amoebae assemblage from The Wou contained a markedly different range of taxa than the cores from the ombrotrophic sites Coom Rigg Moss and Butterburn Flow. Three taxa were found in The Wou that were not recovered from the other sites: *Diffflugia lanceolata*, *D. rubescens* and *Sphenoderia lenta*. *Centropyxis cassis* type, *Pseudodiffflugia fascicularis* and *Trinema lineare* were found in far greater quantities in TW II than in any other core from either Coom Rigg Moss or Butterburn Flow.

Despite the fact that several taxa do not have modern analogue values, because of the poorer representation of taxa such as *Diffflugia pulex* and *Hyalosphenia subflava* and a greater proportion of the assemblage with good modern analogue values, the water table and moisture reconstructions for TW II have close confidence intervals. The poor test concentration and loss of material made the count difficult and not worth further

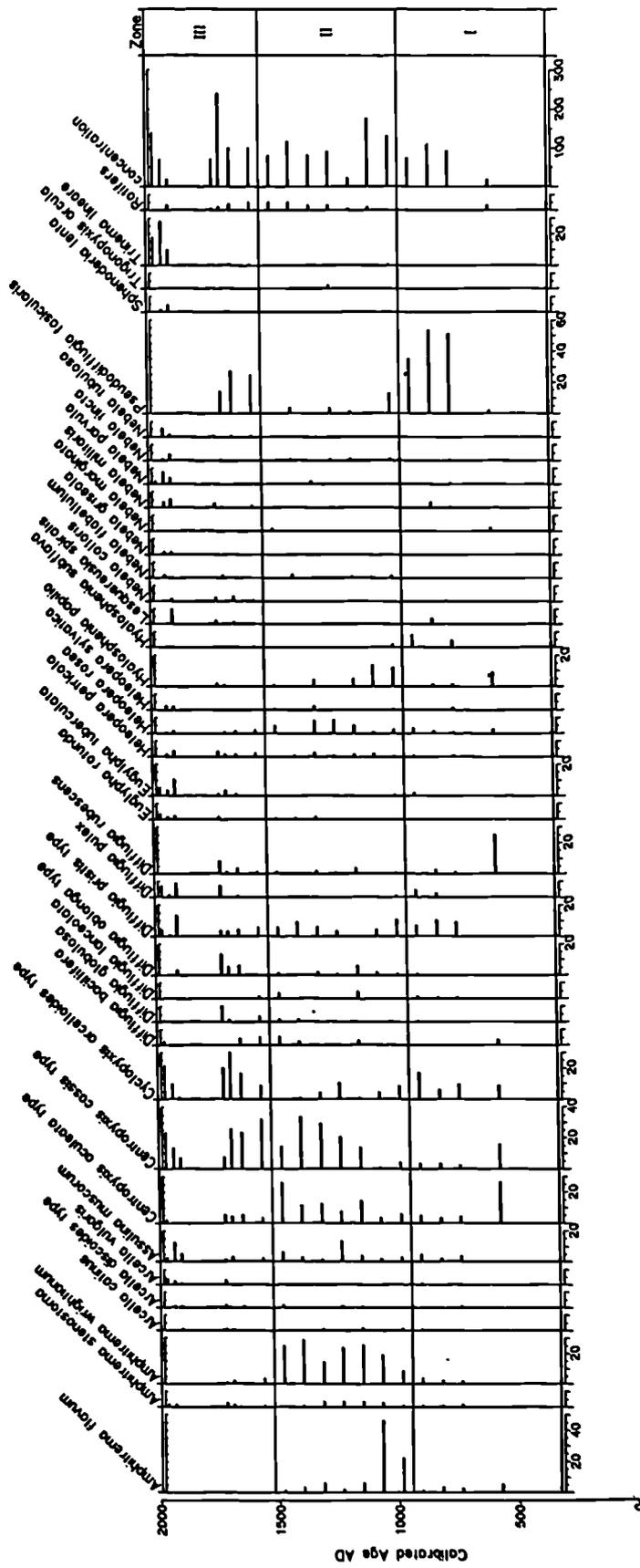


Figure 7.9 Percentage testate amoebae chronology for TW II

pursuing, which is unfortunate, since where there is testate data, the reconstructions are more robust than the those from the two other sites.

Other microfossils, such as desmids and rotifers, may provide additional hydrological information that could be used to interpret sites such as The Wou, which lack a viable testate amoebae record.

PART FOUR

Discussion and conclusions

CHAPTER EIGHT

Reconstruction and Robustness

8.0 Introduction

Chapter Eight consists of a discussion of the methodological issues raised in this thesis. These include a discussion of the preparation procedures for testate amoebae analysis used in this study, compared to those used in similar studies. Possible improvements to the current technique are also suggested. The major part of this chapter deals with the robustness of the transfer function used to reconstruct hydrological models, developed by Woodland (1996). As shown in Chapters Five, Six and Seven, there is not always a good match between fossil taxa and the taxa included in the modern analogue transfer function, which influences the robustness of the hydrological reconstructions derived from calibration of the fossil testate amoebae. Individual species are examined in detail and the possible reasons for poor, or no modern analogue values for 'dry' taxa are discussed. Discussion of the methodological issues raised in this study are presented here to put Chapter Nine, the main theoretical discussion, into context. Issues addressed here influence the nature of the discussion in Chapter Nine, for as long as weaknesses in the hydrological modelling are acknowledged and are consistent in all cores, it can be assumed that the direction and rates of change in the hydrological reconstructions are reliable, but that the magnitudes of change are underestimated for dry shifts.

8.1 Sample preparation

As part of this research, the preparation of testate amoebae samples from peat used in recent publications were evaluated. Whilst the addition of a 15 μ m mesh to micro-sieve samples (Section 4.1.2 and Hendon and Charman, 1997) has improved the quality of slides, further improvements may be possible by refining the upper mesh size used to remove large fraction organic and mineral particles. Woodland (1996) reduced the mesh size from 750 μ m (Warner, 1987) to 300 μ m, which was the mesh size adopted in this study (Chapter Four). However, the size range of taxa recovered were <200 μ m length, with the exception of *Diffflugia oblonga* which can range from 90-240 μ m (maximum recorded dimensions from Charman, Hendon and Woodland, in prep.). Individuals from the upper end of this range are rare and do not form a significant part

of the faunal assemblage. Most larger tests encountered are: *Bullinularia indica* (140-150µm), *Centropyxis aculeata* (116-148µm), *Diffugia bacillifera* (130-200µm), *D. lanceolata* (140-160µm) and *Nebela flabellulum* (76-150µm length, 86-160µm breadth). The mesh size could therefore be reduced to 200µm without significant loss of tests from samples analysed here, which would remove large detritus and significantly improve the quality of the microscope slides. Although tests larger than this have been recorded, they are infrequently encountered and do not appear to make up a significant proportion of the species assemblage from British oligotrophic peats. Smaller tests such as *Diffugia pulex* (15-30µm length) would also be easier to see, as this taxon is often masked by organic detritus and can make up a large proportion of the species assemblage from ombrotrophic peats (Section 8.3.1). The current use of large mesh sieves (e.g. 750µm, Warner, 1987) may be one reason that *D. pulex* has not been recorded in other studies of peatland testate amoebae.

The environment from which the samples were extracted must also be taken into account and a preparation technique suitable for that material adopted. Charman *et al.* (1998, *in press*) have also modified the preparation technique for saltmarsh testates counted in conjunction with foraminifera, by counting the 15-63µm fraction in addition to the >63µm fraction. Previous studies in these environments have only counted the >63µm fraction (e.g. Scott and Medioli, 1983). Charman *et al.* (1998, *in press*) found that the species richness increases from two in the >63µm fraction, to 36 in the <63µm indicating that smaller taxa are far more abundant than previously thought. The concentration also increases from 116 per cm³ counted in the >63µm fraction, to 65,600 per cm³ in the <63µm fraction. This illustrates the need for experimenting with mesh sizes and for not disregarding a particular size fraction, simply because it has not been routinely counted before.

There is also a necessity to strike a balance between the abundance of tests recovered and the ability to count tests on the slides. For example, Preparation E (Chapter Four, section 4.1.2) yielded a greater concentration of tests but these were more degraded and therefore more difficult to identify than those found in Preparation A, the water-based study. It would appear that KOH treatment increases the number of tests in the concentration by up to a half, probably by being more effective at dispersing the sediment than water. However, the tests are far more degraded, with many features

altered or completely removed, which makes counting inefficient and may hamper identification where the original test preservation is poor.

Slides from the minerogenic site, The Wou, frequently contained large amounts of mineral material that masked tests and made counting difficult. The reduction of the mesh size to 200 μ m may help to improve the quality of such slides by removing a greater proportion of detritus, but it should be accepted that samples from certain locations will have tests obscured, because it is impossible to remove all of the mineral particles without destroying tests. These slides are difficult to count and it is impossible with current techniques to improve slide quality from such sites. Testate slides may never be as clean as pollen slides, since the preparation experiments presented in Chapter Four have shown that no chemical preparations are suitable for removing detritus without either affecting test concentration or preservation.

8.2 The transfer functions

The transfer functions for depth to water table and percentage moisture were developed by Woodland (1996) and Woodland *et al.* (1998), using surface moss polsters from nine undamaged peatland sites in the British Isles with long-term hydrological monitoring programmes, to ensure the availability of mean annual water table data. The study used a cross-section of UK ombrotrophic mires, but dry peatlands were not well represented since the wettest sites are of the highest conservation value and dry areas, such as the edges of bogs, have often been cut away, or are not the focus of monitoring programmes. Since the study sites are predominantly wet, drier indicator taxa are not well represented in the modern analogue transfer functions.

The transfer function for moisture from WA-Tol is less robust than the transfer function for water table from WA. This is because the transfer function for moisture was based on single-shot sampling at the time of moss polster extraction for testate analysis. Thirty samples were excluded from the moisture training set which deviated over 5% from predicted values. Only three samples were filtered out of the water table training set, with a >9cm deviation between observed and predicted values. The moisture curves have larger bootstrapped error estimates at 2σ than the water tables, due to the large tolerance ranges of most taxa. These large tolerance ranges are a result of error in the measurement of moisture due to the single-shot sampling and results in less confidence

in the reconstructions. For this reason, moisture reconstructions are not used for comparisons at the three scales of study (Chapter Nine). These are based solely upon the more precise water table transfer function.

One of the five assumptions of quantitative palaeoenvironmental data (Imbrie and Kipp, 1971; Imbrie and Webb, 1981; Birks *et al.*, 1990a), is that the taxa in the training set are the same as in the fossil data set. The degree of match or mis-match between the regression and calibration data sets will affect the robustness of the resultant hydrological curves; the better the match between modern and fossil samples, the more robust the reconstruction. Thus, some samples do not have good reconstructed values. Birks *et al.* (1990a,b) overcame the problem of poor analogue taxa in pH reconstructions using diatoms by using only taxa present in both the modern and fossil data sets in the calibration. This approach has been adopted in this study, but it does cause problems in these data sets, where over 80% of some samples have no, or poor analogue values.

Birks *et al.* (1990b) also recognised the need to improve the modern analogue training set for diatoms used in pH reconstructions. Charman and Warner (1997) recommend that in order to avoid problems of poor analogues, reconstructions should be based on larger, more comprehensive data sets of modern testate amoebae fauna from a wider region. The major limitations of the training set found in this study are discussed below.

8.3 No-analogue taxa

A total of seven taxa found in the fossil data set were not found in the modern training set, these are listed below. However, because certain taxa were not found in the surface samples collected by Woodland (1996), it does not necessarily mean that they do not have modern analogues at other sites not sampled by Woodland as part of her study.

Diffflugia acuminata
Diffflugia lanceolata
Diffflugia lucida
Diffflugia pulex
Lesquereusia spiralis
Pseudodiffflugia fascicularis
Sphenoderia lenta

Lesquereusia spiralis and *Sphenoderia lenta* occurred only in samples from The Wou. *L. spiralis* occurred in five samples, all with less than 10% total abundance and *S. lenta* was found in two samples, with <5% total abundance. *Diffflugia lanceolata* was only found once outside The Wou, with a 1% occurrence at 35cm, CRM III. These taxa therefore occur in the greatest abundance in the minerogenic site and their presence may be attributed to site morphology and geochemical conditions at The Wou. The Wou is an oligotrophic valley mire and, although the transfer function was designed for application on oligotrophic mires, The Wou receives water from the valley catchment in addition to precipitation, which may account for the greater abundance of mineral particles and different faunal assemblage.

Published ecological information for taxa found in this study (Table 4.4), show that *Diffflugia acuminata*, *D. lanceolata*, *L. spiralis* and *Pseudodiffflugia fascicularis* occur in bog pools or aquatic conditions (Cash and Hopkinson, 1909; de Graaf, 1956) and *S. lenta* has been classified as a 'moderately dry' taxon, found in situations with 78-90% water content (de Graaf, 1956; Warner, 1987, 1990; Tolonen *et al.*, 1992). There are few published hydrological data or habitat descriptions for either *D. lucida* or *D. pulex*. Gauthier-Lièvre and Thomas (1958) comment that *D. lucida* is clearly less aquatic than other species of *Diffflugia*, but this is not quantifiable when the relative wetness of other species of *Diffflugia* are not given.

Of the taxa which have no modern analogue values, *D. pulex* and *P. fascicularis* occurred in the greatest abundance and therefore the lack of analogue values for these taxa have the greatest effect on the hydrological reconstructions. Both *D. pulex* and *P. fascicularis* were notified as new species by Penard (1902) and have only rarely been mentioned in the literature since.

8.3.1 *Diffflugia pulex* Penard 1902

There has been some confusion over the taxonomy of *Diffflugia pulex*. The description of *D. pulex* found in Ogden (1983) does not agree with the original description in Penard (1902), as a sharply pyriform test, composed of chitinous material and small siliceous particles. Instead, Ogden (1983) illustrates specimens where the shape of the test is obscured by diatom frustules and is heavily coated with siliceous xenosomes. The length of test identified by Ogden (1983) (28-43µm), is also larger than that

described by Penard (1902) (length 22-25 μ m), or found in this study (Plate 8.1). The small size of *D. pulex* (22-25 μ m length, Cash and Hopkinson, 1909; 15-30 μ m length, this study and Charman, Hendon and Woodland, in prep.), means that samples prepared with a large mesh-sieve may include too much organic or mineral detritus on the microscope slide for it to be easily seen. In studies such as Warner (1987), where a 750 μ m mesh was used to sieve samples, taxa of this size have been hidden, which may account for the lack of data for this species. This may explain the reason why it was found in great abundance in the cores in this study, but has not been documented in previous work. There is however, a decline in the abundance of *D. pulex* towards the top of the cores and since most previous work has concentrated on the modern ecology and distribution of testate amoebae, the presence of this species in the fossil and not the surface samples may also be a function of changing conditions over time. *D. pulex* may no longer have a widespread distribution in contemporary mire surfaces. Also, taxonomic treatments and referencing in most studies have not been as rigorous as they might have been. Most taxa are identified from subsequent taxonomic treatise which may have introduced discrepancies from the original species descriptions, for example, Ogden (1983).

Since there are no hydrological data regarding *D. pulex* in the literature, (Penard, 1902 describes the taxon, but gives no details of habitat requirements) and the taxon was not found in samples used to construct the modern analogue transfer function, the only method of estimating the approximate hydrological requirements of this taxon is to plot the abundance of *D. pulex* against the reconstructed water table depth derived from the analogue taxa in each horizon in which *D. pulex* was found. Figure 8.1 presents these data from individual cores from this study. The data from all of the cores combined are presented in Figure 8.2. This is not an ideal method of assessing the hydrological requirements of this taxon, since it involves plotting the abundance of *D. pulex* for each sample against the mean water table value, constructed with *D. pulex* omitted. There are problems of circularity in this argument, but it is the best method available at present. Any conclusions cannot be used explicitly to reconstruct water tables in these same cores. The modelled water table ranges of all the fossil data are presented in Figure 8.3. The water table estimates for samples containing *D. pulex* are subject to a systematic error and it is not possible to arrive at a reasonable estimate for water table optima for *D. pulex* from this study. The abundance of *D. pulex* and other no/poor analogue taxa in these samples will affect the robustness of the reconstructions since a

large amount of *D. pulex* will result in a poor match between the modern and fossil data sets.

Figure 8.1 shows the relative abundance of *D. pulex* plotted against inferred depth to water table for each sample in which it was found. Abundance ranges from 1% in several samples, to a maximum of 79% in sample 40cm, BBF II. Sample 150cm core CRM II contains 75% *D. pulex*. This sample also contains 13% *Hyalosphenia subflava*, a poor analogue taxon (Section 8.4.1), (optimum -14.95cm). In this extreme example, only 12% of the sample has good modern analogue values, with 4% *Amphitrema flavum* (optimum -4.6cm), 1% *Assulina muscorum* (optimum -7.5cm) and 7% *Diffugia pristis* type (optimum -7.1cm), (optima values from Woodland, 1996), resulting in an unreliable reconstruction. Most cores show that *D. pulex* is associated with a wide range of reconstructed water table depths in varying abundances. There is no pattern of a particular abundance level being associated with a specific water table depth. Cores CRM II, CRM IV, BBF I and BBF II all reach greater than 70% abundance of *D. pulex* in some samples and, for these samples in particular, the reconstructed water tables will be based on a limited fauna only. Core TW II has a much smaller reconstructed water table range and far lower abundances of *D. pulex*. This taxon is far less significant in samples from TW II and will therefore have less effect on the reconstructions.

Figure 8.2 shows the relative abundance of *D. pulex* against water table depth for all cores combined. In total, 90% of the samples with testate amoebae concentrations high enough to count contained this taxon. Samples containing *D. pulex* are not restricted to a small range of water table levels, but instead are spread between -1.3cm to -16.5cm. This cosmopolitan distribution may reflect the true distribution of *D. pulex* but it is more likely to be an artefact of the water table levels calculated from the analogue taxa. Most samples containing *D. pulex* are found in the 4-6cm water table class. *D. pulex* may actually have a lower water table optimum, but since the 'drier taxa' are poorly represented in the transfer function, the distribution of *D. pulex* suggested in the majority of plots may be wetter than their actual value. There is generally a decline in abundance towards the top of the cores which correlates with wetter reconstructions, as seen in the testate amoebae diagrams (e.g. Figure 5.7). However, this is not obvious from the scatter plots presented here. Table 8.1 shows weighted averages (WA) for depth to water table for *D. pulex* for each core. The WA data show that BBF II has the deepest WA value for *D. pulex* at -11.08cm. TW II has the wettest value at -5.77cm.

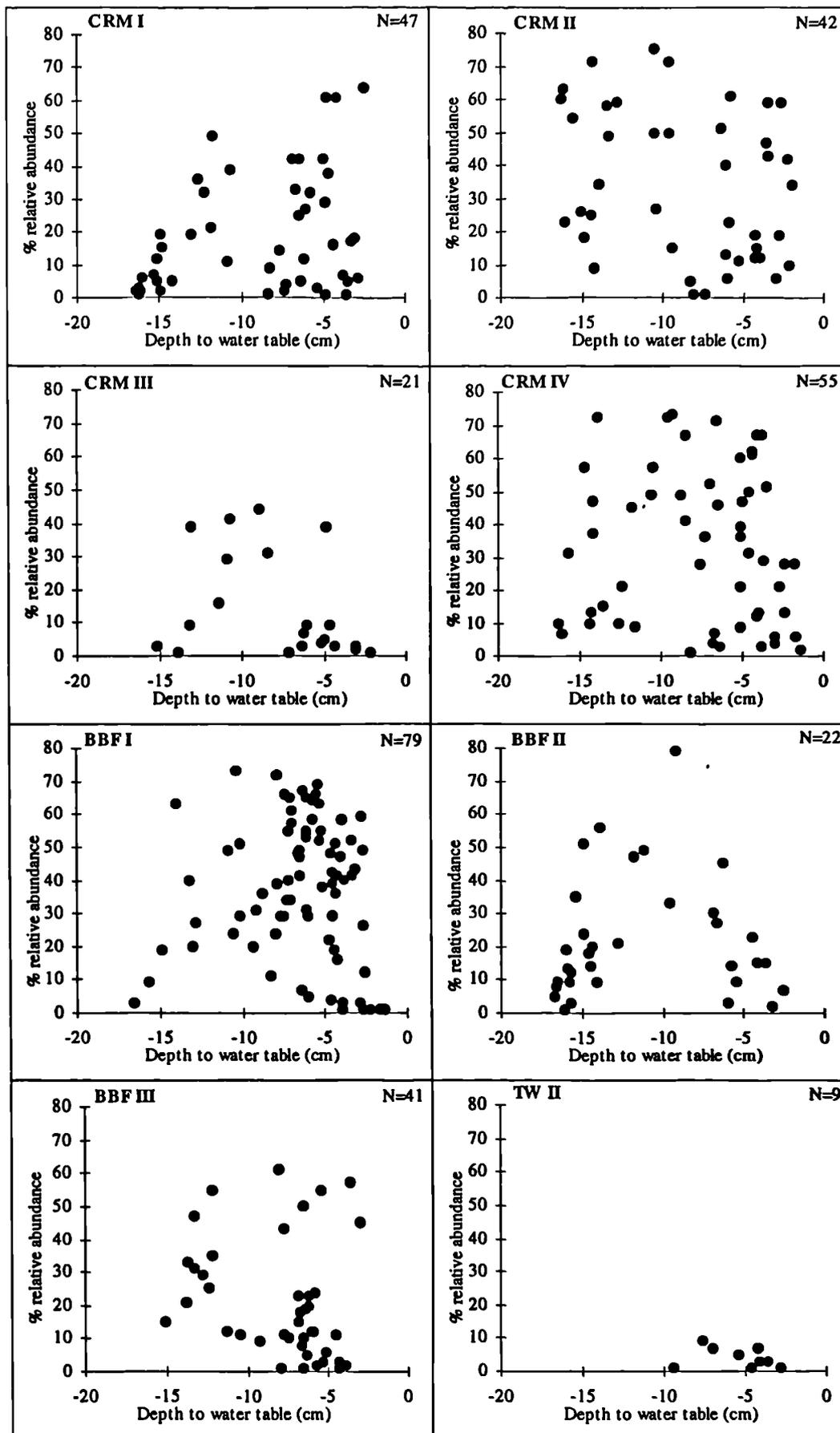


Figure 8.1 *Diffflugia pulex* response to hydrology from individual cores - % abundance of *D. pulex* plotted against the reconstructed water table value for each sample where it occurs. N= number of samples containing *D. pulex*.

The data from The Wou are limited, since the site is wetter overall than Coom Rigg Moss or Butterburn Flow and *D. pulex* occurred in lower abundance levels than was found in all other cores. The WA data for cores from Coom Rigg Moss and Butterburn Flow all have values in the middle range of water table reconstructions, restricted by the limits of the transfer function.

Analyses of the ordination plots presented in Chapters Five - Seven (e.g. Figures 5.4, 5.10, 6.10, 6.16 and 7.4), show those taxa with which *D. pulex* is most closely associated. Taxa that are close to *D. pulex* in the ordination plots are likely to have similar hydrological requirements and therefore offer a subjective assessment of the hydrological tolerances of *D. pulex*. *D. pulex* is closely associated with *Hyalosphenia subflava* in seven of the eight species ordination plots, with the exception of core TW II. Other taxa associated with *D. pulex*, from the cores from Coom Rigg Moss and Butterburn Flow, are *Assulina muscorum*, *Bullinularia indica* and *D. pristis* type. These taxa are all found in the lower half of the range of water table optima from Woodland *et al.* (1998), presented in Figure 4.2. This means that the associates of *D. pulex* are at the 'drier' end of the hydrological scale. Taking the subjective evidence together, *D. pulex* is likely to have a drier analogue value than is suggested by plotting its abundance against the reconstructed water table values.

The taxa from The Wou which are most closely associated with *D. pulex*, are *Lesquereusia spiralis* and *Nebela militaris*. However, since abundance was far less from this site and it is not ideal for application of the transfer function for reasons discussed in Section 8.2, these results are not particularly informative.

Core	WA
CRM I	-7.51
CRM II	-9.38
CRM III	-9.07
CRM IV	-7.79
BBF I	-6.55
BBF II	-11.08
BBF III	-8.48
TW II	-5.77

Table 8.1 Weighted averages for *Diffflugia pulex* depth to water table (cm) for each core

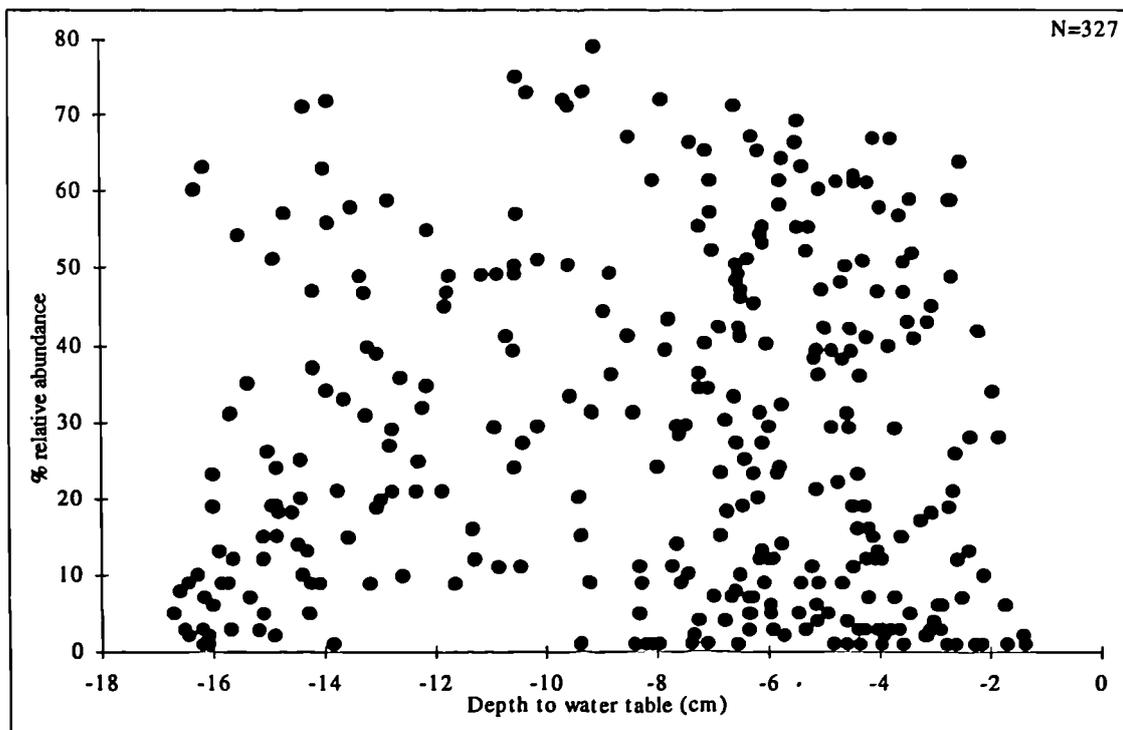


Figure 8.2 *Diffflugia pulex* response to hydrology, all sites combined - percentage abundance against reconstructed water table depth, N equals the total number of samples containing *D. pulex*.

Since the water table plots from which the weighted average values are derived are constructed from assemblages from which *D. pulex* is omitted, conclusions cannot be drawn with any degree of certainty. However, with the data currently available, *D. pulex* appears to be fairly cosmopolitan, but occurs in the greatest abundance with 'drier' taxa such as *H. subflava*, *B. indica* and *Trigonopyxis arcuata*.

8.3.2 *Pseudodiffflugia fascicularis* Penard 1902

Pseudodiffflugia fascicularis also has no modern analogue value. *P. fascicularis* is a small taxon <35µm length and 25µm breadth. The test outline is pyriform, with a short neck and a collar around the terminal aperture composed of mineral particles. The test is transparent or colourless and is composed of mineral xenosomes. Plate 8.2 is a photomicrograph of this taxon. There is no mention of the habitat requirements of *P. fascicularis* in the literature, except for Cash and Hopkinson (1909), who say only that it is an aquatic taxon. Penard (1902) describes this taxon, but does not give details of its habitat requirements.

P. fascicularis was found in five of the eight cores in this study: CRM III, CRM IV, BBF I, BBF II, BBF III and TW II. The maximum occurrence was 95% abundance in sample 270cm from BBF II, although this was highly unusual. The sediment at this level contains small amounts of clay, which is probably the source of mineral material for test construction (Table 6.3, BBF II stratigraphic description). Cores containing *P. fascicularis*, with the exception of TW II, have most occurrences in samples in the surface 50cm. In CRM III, most specimens were found in samples 15cm, 25cm and 35cm, which may be because this core was located at the base of the slope at the northern edge of the mire, representing a source for the minerogenic material used for xenosomes. TW II has the greatest number of samples containing *P. fascicularis*, attaining >50% in samples 210cm and 220cm. As a minerogenic valley mire, The Wou is likely to have mineral particles flowing along the long axis of the mire, thus providing suitable material for test construction.

The species ordination plots as listed above, show that the *Heleopera* spp. are closely associated with *P. fascicularis*. In CRM III (Figure 5.16), *P. fascicularis* is close to *Diffugia lanceolata* and *Heleopera sylvatica*. *D. lanceolata* is also a no-analogue value taxa and the only hydrological information for it is from Cash and Hopkinson (1909), who regarded it to be an aquatic taxon. *H. sylvatica* is found in 'drier mosses' (Tolonen, 1986), (Table 4.4). The ordination plot for species from CRM IV (Figure 5.22), shows that *P. fascicularis* is closely associated with *H. sylvatica* and *Trinema lineare*, which de Graaf (1956) classified as a hygrophilous taxon. The species ordination plot for BBF II (Figure 6.10) is presented with sample 270cm, containing 95% *P. fascicularis* removed, since it was an outlier sample with no other horizon containing a similar faunal assemblage. The species ordination plot for BBF III (Figure 6.16), demonstrates that *H. rosea* and *H. petricola* are closely associated with *P. fascicularis*. Table 4.4 shows that *H. petricola* requires very wet conditions (de Graaf, 1956; Tolonen *et al.*, 1992), but other workers consider its ecology to be variable and disputed. *H. rosea* was recorded by Jung (1936) in bog hummocks and drier *Sphagnum*. This results in a complicated picture of the conditions required by *P. fascicularis* as the hydrological requirements of the associated species are variable and sometimes disputed. Until a transfer function is constructed that samples a suite of mires with a wider range of hydrological conditions and faunal assemblages, it will not be possible to assign this taxon optimum and tolerance values.



Plate 8.1 Photomicrograph of *Diffugia pulex* Penard 1902, taken at x1000 magnification under oil immersion. Typically 22-25 μ m long



Plate 8.2 Photomicrograph of *Pseudodiffugia fascicularis* Penard 1902, taken at x1000 magnification under oil immersion. Typically <30 μ m long



Plate 8.3 Photomicrograph of *Hyalosphenia subflava* Cash and Hopkinson 1909, taken at x400 magnification. Typically 50-60 μ m long

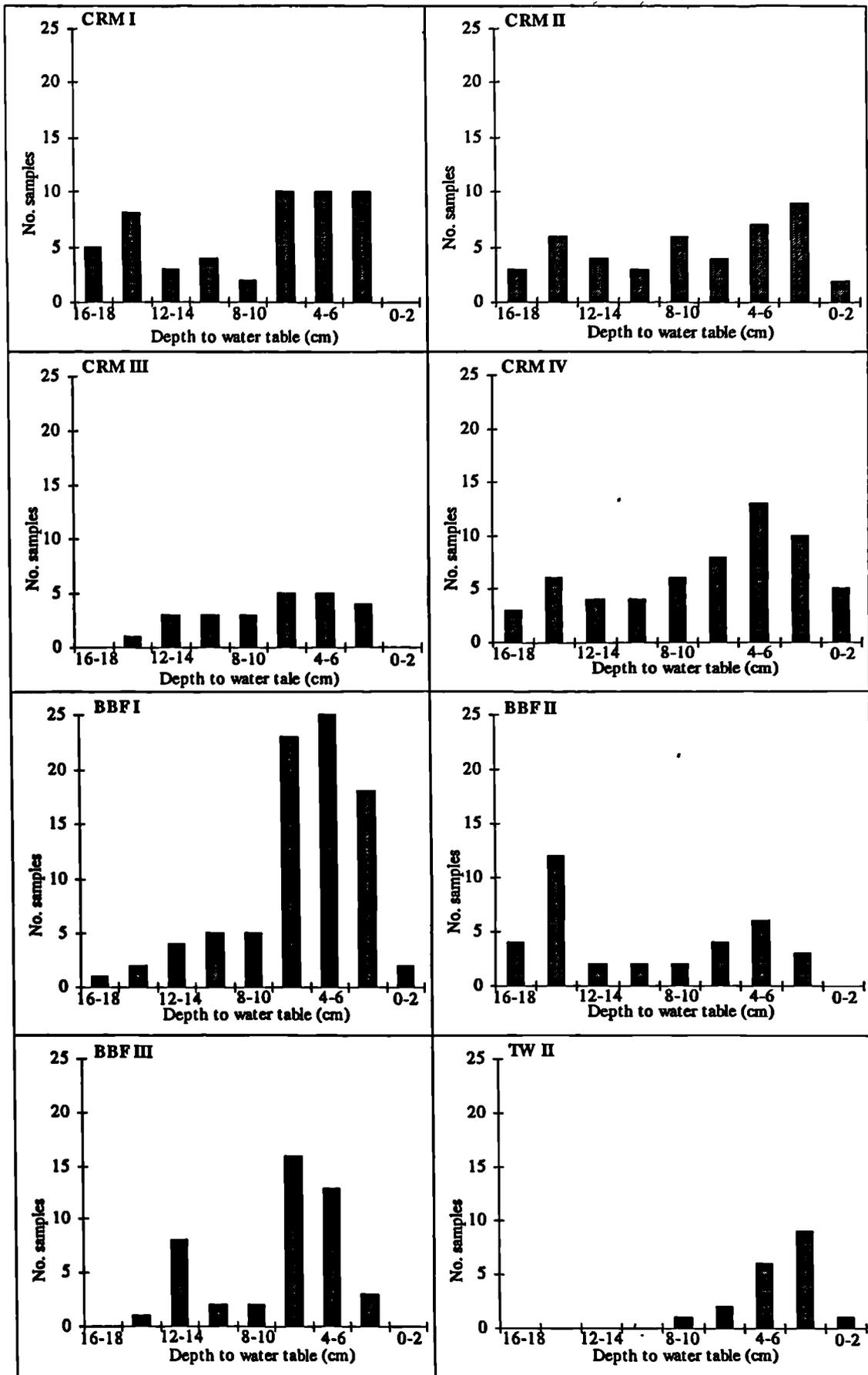


Figure 8.3 Distribution of 2cm inferred water table classes for all samples from each core.

It may be that the primary response of *P. fascicularis* is not to hydrology, but that it requires specific mineralogic, nutrient or some other common factor to thrive. More work is needed to establish this.

8.4 Poor-analogue taxa

Section 8.2 discussed the general problems with the development of the transfer function by Woodland (1996). Because undamaged, wet sites were sampled to construct the transfer function, taxa that tolerate wetter conditions have better modern analogue values than those taxa such as *Bullinularia indica*, *Nebela collaris* and *Hyalosphenia subflava* at the drier end of the range (Figures 4.2 and 4.3). The nature of the sites sampled for the transfer function means that only part of the environmental gradient in which testate amoebae can survive has been sampled. It is probable that the optima and tolerance ranges for some of these taxa extend further along the environmental gradient. The calculated optima for these taxa are therefore probably biased to the wetter end of their range of tolerance as the transfer function gives the optimum value derived from the sites sampled, not the optimum value that may be derived from a suite of sites covering the full hydrological range of any taxon. There are two possible reasons for poor modern analogues; a) that there were only a few occurrences of a particular taxon in the modern data set, or b) that they occurred at low abundances in the modern data set. As a result, their lack of a modern analogue value has been referred to throughout this thesis. The optima and tolerance ranges of the main taxa (>10% abundance) from the modern analogue transfer function, from Woodland *et al.* (1998) were presented in Figures 4.2 and 4.3.

The weighted averaging calibration used to construct the water table models depends upon a unimodal response of taxa to an environmental variable (ter Braak and Prentice, 1988; Birks 1995) (Section 2.4). Figure 8.4 shows a Gaussian species response curve, where in this example, the environmental gradient is hydrology. On ombrotrophic bogs, testate amoebae with an optimum close to that of the depth of the water table will be most abundant. Therefore species with small tolerance ranges are better ecological indicators, as they can be used to model the palaeohydrological conditions more precisely. Figure 8.4a shows the theoretical distribution of a species if the whole of the hydrological gradient is sampled, with the WA optimum corresponding to the greatest

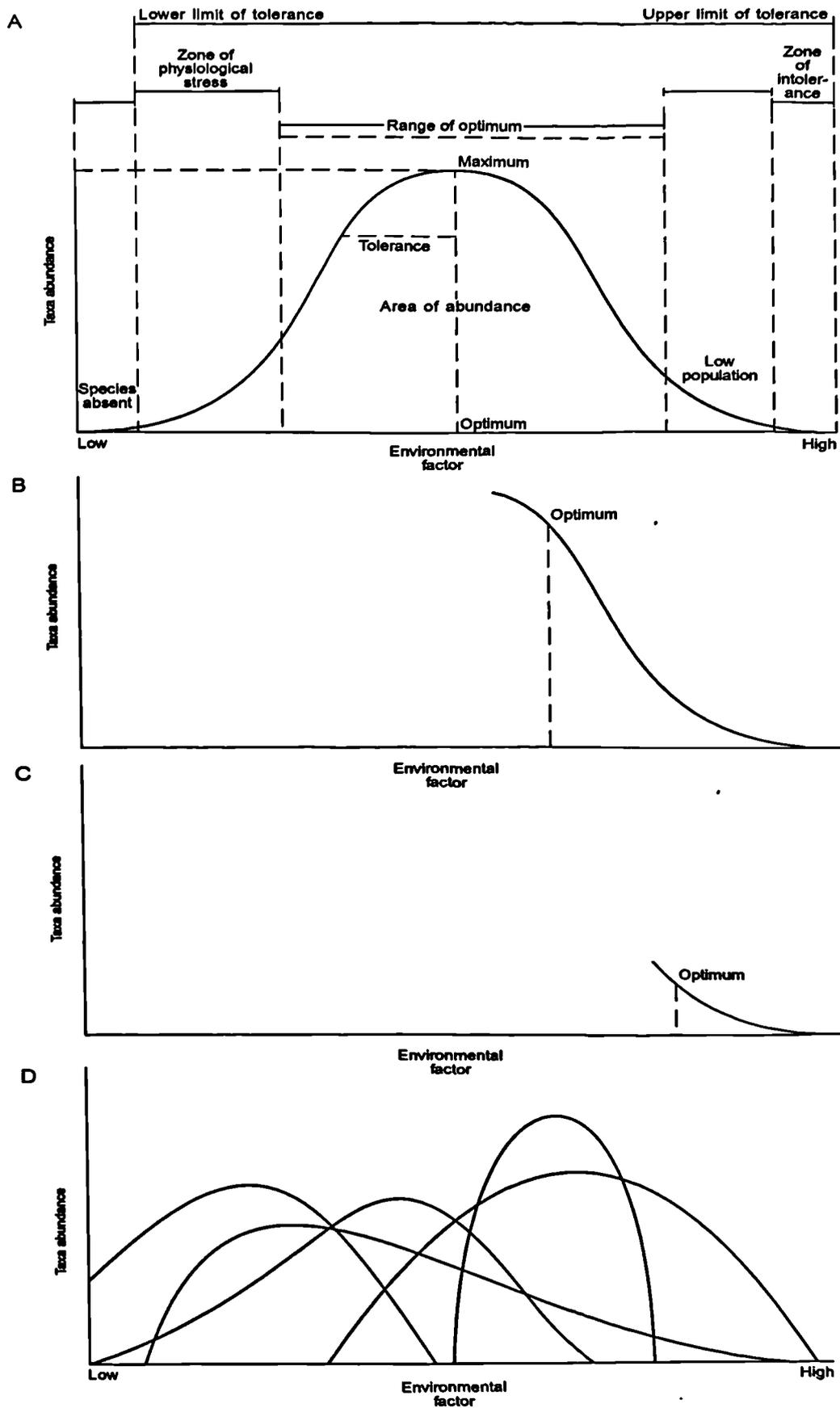


Figure 8.4 Gaussian species response to hydrology: A - Gaussian curve of species response to a single environmental factor, B and C - Species response to a small part of the potential range, where the optimum predicted is part of the tolerance range and D - Overlapping Gaussian curves of species response to an environmental factor (modified from Kent and Coker, 1992)

abundance of that species. If only part of the actual hydrological range is sampled, the optimum derived will be biased in that direction (Figure 8.4b). Plot 8.4c shows an even more extreme example of this. The response of testate amoebae to hydrology shown in Figures 8.4b and 8.4c is more likely to model the species response in the transfer function as only part of the potential hydrological range has been sampled. Plot 8.4d shows a more realistic response of species to hydrology, where each species has different requirements for growth and responds individually to the environmental conditions. Kent *et al.* (1997) point out the limitations of showing the response of multiple species to a single environmental gradient. In reality, multiple species respond to multiple environmental gradients. Thus, for testate amoebae, the major environmental factor affecting species distribution is hydrology, but other factors such as pH may also be influential. Also, the range of research on this distribution of vegetation reviewed by Kent *et al.* (1997) suggest that a skewed, bimodal or 'plateau' shaped response is probably more realistic than the classic bell-shaped Gaussian response. For example, Austin (1990) predicts that there will be a greater degree of skewness as plant species curves move towards either end of the environmental gradient. This means that for testate amoebae in response to hydrology, 'very wet' or 'very dry' taxa at the extremities of the hydrological gradient will be more skewed than moderately wet species distributed in the middle of the hydrological range. However, this theory requires further validation and is subject to debate (Kent *et al.*, 1997).

8.4.1 *Hyalosphenia subflava* Cash & Hopkinson 1909

The main taxon likely to be affected by the problems outlined above is *Hyalosphenia subflava* (Plate 8.3), which has a relatively broad tolerance range in the training set. It occurs in a small number of samples with low abundance in the training set (Woodland, 1996), but is present in a large number of samples, sometimes with high abundance in the fossil data set. Of the 363 samples counted for testate amoebae analyses in this study, 52% contained *H. subflava*. Samples containing large abundances of this taxon are likely to have unrepresentative reconstructed water table depth when calibrated with the modern training set. This assertion is supported by comparison of these data to other studies. *H. subflava* has been found in most studies of modern faunas on ombrotrophic peatlands from Canada (*e.g.*, Tolonen *et al.*, 1985; Charman and Warner, 1992, 1997; Warner and Charman, 1994) and from New Zealand (Charman, 1997).

This section uses data from some of these studies in an attempt to establish a more accurate estimate of water table optima.

Cores CRM I, CRM III, CRM IV, BBF I and BBF II all have samples which contain between 80-100% abundance. The range of water table classes which samples from this study fall into are more restricted than from published studies. This is a restriction imposed by the constraints of the transfer function bias to wetter analogue taxa and to the circular argument around the abundance and optimum of this taxon. There is greatest abundance in the lowest water table samples and a decreasing abundance in wetter samples, suggesting that the preference of this taxon is to dry locations.

In an objective assessment of the taxa most closely related to *H. subflava* in the species ordination plots presented in Chapters Five-Seven, it can be seen that it is closely related to *Diffugia pulex* in seven of the eight cores studied, with the exception of TW II. In all of the species ordination analyses from Coom Rigg Moss and Butterburn Flow, *H. subflava* is located at an extreme of axis 1, as an outlier. From the position of this taxon on the extremity of axis 1, it is possible to say that there are no other taxa with exactly the same hydrological requirements. The most closely associated taxon is *D. pulex* for which there are no published hydrological data (Section 8.3.1).

Figure 8.5 shows the hydrological response of *H. subflava* derived from several studies. The raw data are not published, but have been obtained from the authors and analysed as part of this research. *H. subflava* plots 1a and 1b present hydrological data from British oligotrophic mires. Woodland *et al.* (1998) filtered out samples from the transfer function where the difference between observed and predicted values exceeded 9cm and 5% for water table and soil moisture respectively. This resulted in three samples being removed from the water table transfer function and 30 samples from the moisture transfer function. The three samples removed from the water table data set have the deepest water tables of the entire range. They were removed as they represented a discontinuity in the hydrological gradient. The deepest sample in the regression data set is -19cm depth to water table, whilst the outlier samples had values of -23.4cm, -40.2cm and -45.8cm. Only one outlier, the sample with depth to water table value of -40.2cm contained *H. subflava* (22%). All of the other occurrences of *H. subflava* in 1a have less than 12% abundance and a water table depth of >16cm. However, not all samples from dry sites will contain similar faunas. Three of the 30 outliers from the moisture data set

contained *H. subflava* with values of 94.9%, 97.1% and 97.1%, which are within the range of the samples plotted in Figure 8.5 2b. The range of the entire moisture calibration data set goes down to 63% moisture content. This is 17% lower than the driest sample containing *H. subflava*.

The water table optima and tolerance ranges for *H. subflava* from northeastern Ontario (Figure 8.5, 2a and 2b) were derived from mean annual hydrological data (Charman and Warner, 1992). Single-shot sampling was used to calculate optima and tolerance ranges from northwestern Ontario (Figure 8.5, 3a and 3b) and Newfoundland (4a and 4b), (Warner and Charman, 1994; Charman and Warner, 1997).

Seven samples were removed from Figure 8.5, 2a (Charman and Warner, 1992), where the depth to the mineral substrate was less than the potential range of the water table fluctuation. Figure 8.5 2a contains 29 samples with a depth to water table of -41cm. The dominance of samples with a water table depth of -41cm is difficult to explain, the depth probe used to collect the hydrological data must have been greater than this, since two samples had depths of -43cm and -44cm. Two samples from the moisture data set for 2b had missing values. The hydrological data in this study were collected by Forestry Canada and it has not been possible to establish the exact details.

Plots 3a and 3b show the hydrological response of *H. subflava* from northwest Ontario (Warner and Charman, 1994), with one outlier sample removed from each plot which had an abundance of 53%, a depth to water table value of -54cm and a moisture content of 79.4%. This sample was removed from the plot so that the data from all of the plots could be drawn at the greatest scale possible, with the exclusion of the least number of samples. This data point remains an integral part of the data set. All of the other samples from this study contain <10% abundance and water table values of between -15cm to -40cm.

Figure 8.5 4a, the data from Newfoundland (Charman and Warner, 1997) have a majority of samples containing <5% abundance, with a depth to water table range of +1cm to -46cm. One sample contains 13% abundance and has a water table value of -40cm. This plot may suggest that *H. subflava* can tolerate the conditions of extreme wetness found in a bog pool and conditions found in very low water table locations. These extremes could also be due to inwash of tests from pool margins.

The moisture plots for *H. subflava* (Figure 8.5, 1b-4b) show that the British data set has a moisture range of between 80-100%, with the majority of samples found between the range 90-100% (Woodland, 1996). The moisture range of samples from northeastern Ontario (Charman and Warner, 1992) (Figure 8.5, 2b), is from 15% to 93%. This is a large range, but the majority of the samples contain between 60% to 90% soil moisture content. Plot 3b has one sample that has a moisture value of 40%, the other six samples are between the range of 77-91% peat moisture content. The samples from Newfoundland (Charman and Warner, 1997) had one anomalous sample, with a moisture value of 68%, the other samples contained between 80-95% moisture content. These plots show that 57% of samples containing *H. subflava* contained between 80-100% soil moisture content and 68% of samples contained 75-100% moisture content. These plots indicate that *H. subflava* inhabits moister conditions in the UK than in other areas. Again, this suggests that the full range of moisture optima conditions have not been sampled in the UK.

The range of sampled values for each data set must be considered in order to ascertain to what extent the distributional differences are a result of sampling bias or to what extent they are real. If the differences are due to sampling bias, the use of non-UK data may be considered in the interpretation of fossil data from the UK. If the differences are real, then consideration must be given to why there might be differences in optima between the regions. The data collection from Warner and Charman (1994) and Charman and Warner (1997) were single-shot and had low abundances of *H. subflava*.

Location		Water table optimum	Tolerance (cm)	No. samples	Author
British oligotrophic mires	oceanic	-14.95cm	13.95	20	Woodland, 1996
North-eastern Ontario, Canada	continental	-39.21 cm	1.26	52	Charman & Warner, 1992
North-western Ontario & Minnesota, Canada	continental	-49.92cm	15.91	7	Warner & Charman, 1994
Newfoundland, Canada	oceanic	-22.81cm	15.98	21	Charman & Warner, 1997

Table 8.2 Published estimates of *Hyalosphenia subflava* WA optima and tolerance values

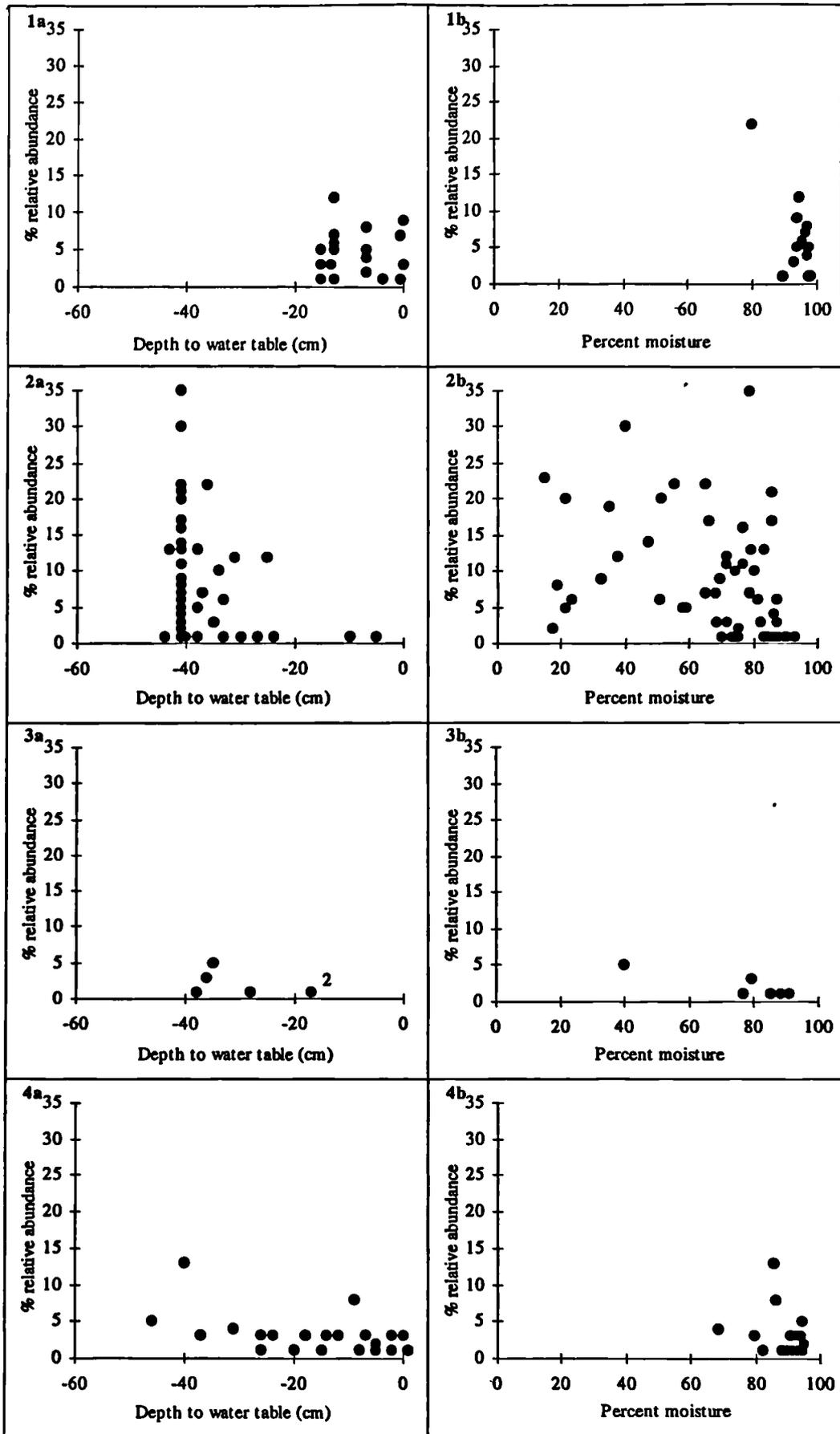


Figure 8.5 *Hyalosphenia subflava* response to hydrology from published studies. 1a & 1b UK, Woodland (1996); 2a & 2b NE Ontario, Canada, Charman and Warner (1992); 3a & 3b NW Ontario, Canada, Warner and Charman (1994), where 2 represents two samples; 4a & 4b Newfoundland, Charman and Warner (1997). Raw data presented with permission from the authors.

The distributional differences from these data sets may represent bias due to single-shot sampling and the sample taken may be unrepresentative compared to mean annual data. The mean annual data from northeastern Ontario (Charman and Warner, 1992) is the data set most likely to represent real differences, although the dominance of water table depths of -41cm remains inexplicable at present.

The difference in hydrological optima for *H. subflava* may also be related to regional differences. Table 8.2 shows the WA estimates of *H. subflava* optima and tolerances from the four studies. Tolerances are a measure of the variance of the water table data, similar to a standard error, but based on the effective number of occurrences (Charman and Warner, 1997). The British data set has the highest water table optimum for *H. subflava* at -14.94cm. The lowest water table optimum is -49.9cm from northwestern Ontario (Warner and Charman, 1994). The British and Canadian data sets are likely to be different, since the British sites were all oceanic and most of the Canadian sites were continental. Thus, the Canadian data will result in drier reconstructed values, since the mires were in drier locations. Only in the NE Ontario data set (Charman and Warner, 1992) and the single-shot sample from northwestern Ontario/Minnesota (Warner and Charman, 1994), do abundances of *H. subflava* reach levels comparable to the 50%+ found in the fossil data from this study. Therefore, these are the nearest analogues at present.

The water table value for *H. subflava* in the British modern analogue data set is likely to be an under-estimate of its actual optimum and tolerance range. It would appear that only part of the hydrological range has been sampled, resulting in an optimum value that is in fact part of the tolerance range. The principal of this can be seen in Figure 8.4 b and c, where the theoretical distribution shows that the optimum is related to the sample range. In order to derive a more realistic optimum value for *H. subflava* from published studies, samples should be comparable to the fossil data set in terms of sample location, *i.e.*, oceanic; mode of data collection *i.e.*, mean annual data for water table depth and have a similar level of abundance in the training set (Section 8.2). All of the published studies have far lower occurrences, both in terms of the number of samples containing *H. subflava* and the percentage occurrence in those samples, than in the fossil data set. None of the published studies consist of both mean annual data from oceanic sites and, therefore, it is not possible to derive a realistic optimum value from these data. Added to this, following the argument of Gehrels and van de Plassche (in press), the possibility

of regional variability between assemblages necessitates the establishment of local training sets for valid palaeoecological interpretations.

To obtain a more robust analogue value for this taxon and the other taxa with poor analogues, drier sites in Britain are required with long-term hydrological data. Studies of such sites will hopefully result in better optima values for xerophilous taxa and may result in taxa being found that cannot tolerate the conditions found in the wet study sites. Work is currently in progress (Woodland, pers. comm.) to address this problem.

8.5 Taxonomic issues

The issues raised as taxonomic problems in Chapter Four (Section 4.1.5), have been addressed by Charman, Hendon and Woodland (in prep.). The identification guide provides a comprehensive dichotomous key for the identification of fossil tests from British oligotrophic peats and seeks to provide a reliable way of identifying fossil specimens that can consistently be repeated between several workers. The present taxonomic state, where species that are similar or identical have been assigned different names, results in confusion. Other genera have also been over-split, resulting in inconsistent identification.

The species descriptions given in Charman, Hendon and Woodland (in prep.) contain lists of synonyms and similar taxa that cannot consistently be separated. Original authorities are given for the first time a species was described, even if it was subsequently moved to a different genus and, if a species has been renamed, the secondary authority is also given. This shows the evolution of the nomenclature changes in the literature, which should minimise future confusion. Photomicrographs are presented for each taxon and SEM images are used to illustrate variations in test construction. This key will inevitably change over time, as more sites are sampled for testate amoebae analyses and a greater range of fossil material is collected. The guide does, however, address the taxonomic problems that have arisen during the course of this research and should serve to provide a more workable and consistent identification of fossil testate amoebae in future research. It is recommended that in future work, references of original authorities are clearly given and described. Previous work has often relied on secondary identification sources and this has contributed to the confusion over taxonomy.

Some of the nomenclature used in Woodland (1996) has changed, because of the taxonomic reclassification by Charman, Hendon and Woodland (in prep.). For example, the taxon recorded as *Diffflugia angulostoma* by Woodland is now recorded as *Diffflugia pristis* type. The reclassifications of taxa are shown in Table 4.4. The nomenclature used in the transfer function (Woodland *et al.*, 1998) is consistent with that used in this study.

Woodland's (1996) concerns about the possibility of differential decay rates of tests, have been shown to be largely unfounded. Some tests may be degraded or broken, but since the species composition change over time, variations in faunal assemblages are more likely to be attributable to habitat conditions changing, rather than to test degradation. Spinose tests such as *Centropyxis aculeata* may have some or all of the spines broken from the posterior region, but this should not hamper identification, since the number of spines is not a diagnostic feature (Charman, Hendon and Woodland, in prep.). The siliceous plates that the *Nebela* spp. are composed of are often not apparent in the fossil forms, which means that determination of whether the plates overlap or not can sometimes be difficult. The *Nebelas* are distinguishable on other features such as size, the presence of pores or a marginal keel, so the ability to see the plate structure acts as confirmation rather than a crucial diagnostic feature. Thus, on the basis of the research described in this thesis, the degradation and decay of tests is not considered to be a problem.

8.6 Conclusions

The methodological issues raised during the course of this study indicate that there are several improvements that can be made to increase the robustness of palaeohydrological reconstructions from peatlands using testate amoebae. The sieve mesh size could be reduced to 200µm to remove a greater proportion of detritus from the microscope slides. This will improve their quality and enhance counting. Smaller taxa such as *Diffflugia pulex* should then be easier to see. However, the clarity of testate amoebae slides is not comparable to that achieved after chemical preparations for pollen analysis. Without such chemical processes, detritus remains, sometimes in large quantities, but to remove this would also entail the loss or degradation of large parts of the faunal assemblage. Reduction of mesh size should be kept under review since some sediments may contain larger taxa.

The transfer function could be substantially improved by expanding the hydrological range of the bogs sampled to include sites at the drier end of the range. Analysing moss polsters from drier parts of bogs should increase the number of taxa included in the transfer function and should enable optimum and tolerance values to be calculated for those species that currently have no or poor analogue values. This would also improve the precision of existing analogue values by more accurately identify optimum values for some taxa. However, this requires long-term hydrological monitoring programs to be established on dry mires, which is currently not undertaken as such sites are perceived to be of lower conservation value than wet mires. There is a possibility that this type of work can be undertaken in conjunction with a research project at Liverpool John Moores University that is looking at the restoration of cut-over bogs (Charman, pers. comm.). Drier taxa are likely to be abundant on the surface of cut-over mires as these sites are drained prior to milling. Monitoring the water table fluctuations of such sites would provide an ideal opportunity to extend the current hydrological range of the training set taxa.

The mis-match between the regression and calibration data sets affects the robustness of the resultant hydrological curves, as the lack of adequate modern analogues for taxa at the drier end of the hydrological range creates a systematic error. Some samples do not have good reconstructed values and, although it is likely that the direction and rate of change in the hydrological reconstructions are reliable, the magnitudes of change are underestimates for dry shifts.

Charman, Hendon and Woodland (in prep.) have largely addressed the taxonomic issues raised by the study of fossil testate amoebae from oligotrophic peatlands, by systematically examining the literature from original citations to the present and comparing descriptions of taxa. A set of criteria for consistent, repeatable identification of fossil specimens has been compiled that should eliminate ambiguous identification for the taxa described within it. This work is subject to change as and when further species are found which are not currently included.

The methodological issues discussed in Chapter Eight must be considered in Chapter Nine, as they affect the interpretation of the data. The water table records are compared at the three scales of study and are used to assess within site and between site variability. These studies are used to separate autogenic hydrological signals from climatic inputs

and guidelines are given for the use of testate amoebae analysis as a proxy climatic indicator.

CHAPTER NINE

Replicability of palaeohydrological reconstructions

9.0 Introduction

The main aim of this study was to evaluate the spatial and temporal variability of the palaeohydrological record derived from testate amoebae analysis of peatlands. The mire types included two intermediate oceanic ombrotrophic mires and a minerogenic valley mire. In order to fulfil the aims, three scales of study were adopted (Figure 3.1). At the micro-scale (1-10m), two closely spaced cores extracted from the centre of an ombrotrophic mire were studied. The meso-scale (100-1000m) involved comparisons between the main elements of a mire, *i.e.* the central mire expanse and mire margins. Four cores from Coom Rigg Moss, two from the centre and two from the mire margins and three cores from Butterburn Flow (one central and two marginal) were analysed to evaluate meso-scale variability. At the macro-scale (1-10km), analysis involved comparisons of the central cores from all three morphologically distinct and hydrologically separate sites. In this study, the macro-scale comparison cores were extracted from sites within a limited geographical district and hence should have been influenced by the same climatic regime throughout the Holocene. Therefore, if climate is the only control on surface wetness, it would be expected that all cores would show the same changes through time.

Palaeoclimatic reconstructions for peatlands are based upon the idea that ombrotrophic sites are directly coupled to climate, as their sole source of nutrients and moisture is from precipitation. Decreasing precipitation or increasing temperatures cause a fall in water table level and *vice versa*. For testate amoebae, the drying out or wetting of the mire surface is reflected in the species composition and therefore calibration of the fossil faunal assemblages with a modern analogue transfer function is used to reconstruct past mire surface wetness (Section 2.5).

Barber (1981) claimed to demonstrate from one site, Bolton Fell Moss, that climate plays a major role in peat formation and postulated that autogenic factors that affect site hydrology, such as drainage, the life-cycles of plants and pool size, are all subordinate to climate. The shifts identified by Barber as 'wet shifts' give only a general idea of hydrological, and hence, climatic change. This provides a broad indication of changes

in mire surface wetness, but smaller shifts are not detected. The use of a single site to infer climate change is questionable, since major stratigraphic changes replicated at only one site may in reality be the product of internal autogenic factors, albeit acting over a large part of the mire expanse. The three levels of study investigated here provide a 'nested' approach which enable an assessment of the relative contribution of allogenic hydrological influences, derived mainly from climatic inputs and the autogenic hydrological signal, resulting from internal bog dynamics, in controlling testate amoebae faunas and hydrology over long time scales.

Multiple cores from several sites were required to evaluate the relative contribution of both allogenic and autogenic hydrological influences. If the overall pattern of change as measured by the direction, rate and magnitude of change in the water table reconstructions are the same at each site, it is likely that climatic forcing is the major hydrological influence. If the water table record is different at each site, autogenic processes such as mire development and morphology are likely to be the principal contributors to surface wetness. Closely spaced cores from the centre of the same mire are used to assess the replicability of the water table record over a short distance. This micro-scale study allows quantification of errors at the broader scales of study, although it may be an under-estimate of these. If the micro-scale cores have a similar record, it is likely that the same hydrological inputs have influenced the testate record. At the meso-scale, if the main cores are the same and the edges are different, it is likely that internal bog dynamics have influenced the water table record at the mire margins. A shift in the direction of the water table will be regarded as climatic if it is replicated across the region at the macro-scale of study.

9.1 Error estimation in chronology and water table reconstructions

Water table reconstructions are compared at three scales of study. Since the moisture reconstructions are less robust than those for depth to water table, they are not discussed further here. The reasons for this are fully explained in Chapters Four and Eight. Evaluation of the replicability of the water table records at each scale of study involves comparison of the rate, magnitude and synchronicity of the reconstructed water table curves from all cores in a variety of combinations (Table 3.2). If the major shifts in the hydrological reconstructions are coincident within the confidence limits (*c.f.* Bennett, 1994) of the interpolated ^{14}C chronology, they may be regarded as synchronous changes.

Assessment of the replicability of the water table reconstructions are made within the confidence limits of inferred water tables derived from bootstrapping (Section 4.2).

The water table curves are plotted at the calibrated median interpolated age, but the actual date may fall anywhere within the calibrated age range (Stuiver and Reimer, 1993a,b) (Section 4.1.5). Linear interpolation of sample ages was adopted, since using the R^2 regression line between dates would have put too much emphasis on the end dates (*i.e.* basal date and uppermost date), even though linear regression produced excellent R^2 values (*e.g.* 0.9989 for BBF I) and the differences calculated between linear interpolation and R^2 regression were minor. Any estimate of 2σ error for interpolated ages does not take into account errors from the interpolation process *i.e.* that the interpolation line and equations may be incorrect and, that the possible range of ages are not precise, but are estimates.

Stuiver and Reimer (1993a) recommended that calibrated radiocarbon ages are rounded to the nearest 10 years, since rounding to the nearest year may be too precise in some instances. However, because it is recognised that the actual date of peat accumulation may fall within a range, the dates have been rounded to the nearest year and plotted at this point.

The smaller the confidence limits that are calculated on the ^{14}C chronologies, the more precise the reconstruction. Pilcher (1991, 1993) defines the precision of a date as the closeness of the confidence intervals. He also describes the accuracy of a date as being as close to the date of the actual event as is possible. Precision of dating is also addressed by Baillie (1991) and Oldfield *et al.* (1997). Baillie (1991) identifies the problems of smearing, where a truly synchronous event may have gone unrecognised by dating and is smeared into a 'period' and conversely, where loosely dated events may be 'sucked-in' and used to explain a wide spread of observations. Both are potential problems in the comparison of water table curves in this study.

An improvement to the chronology would have been to take smaller size samples for dating to reduce the period of peat accumulation and hence the confidence intervals on each date. However, Shore *et al.* (1995) point out that the smaller the sample dated, the greater the effect of any contaminants contained within it. The width of the sample is an

important factor (*c.f.* Pilcher, 1993) since a sample 5cm in length may represent 50-75 years peat accumulation. This will affect the precision of the radiocarbon date.

The range of radiocarbon ages within which the water table curves fall allows assessment of events within an error range. This provides a more realistic basis for interpretation, rather than interpreting the water table curves against only the median age. Because the relationship between ^{14}C and calendar age is not linear, 2σ errors vary considerably between different radiocarbon ages, even if the laboratory counting error is the same. Where interpolated ages are being compared, the precise 2σ error is impossible to determine, but a conservative estimate would be that the error due to calibration will be at least as large as the largest error of the dates used for interpolation.

The confidence intervals on the water table values are derived from bootstrapped error estimates of the mean water table reconstructions, taking into account the tolerance ranges of the taxa in each species assemblage (Sections 2.5 and 4.2). This is an advance on the work of Woodland (1996), who tested the transfer function in a fossil context on a short core from Bolton Fell Moss, but did not calculate 95% confidence intervals on the mean water table by bootstrapping. At present, the transfer function used to reconstruct palaeohydrological records from testate amoebae analysis results in assemblages dominated by fauna at the drier end of the 'wetness scale' having underestimates of the depth to water table. The direction of change is accepted, but the magnitude of change in dry shifts appears to be too small on the basis of information available about particular taxa from other studies (Section 8.2). This limitation is acknowledged, but since all assemblages based on drier taxa are similarly affected, direct comparisons should be possible. The low water table areas will be particularly subject to refinement when the transfer function is re-developed and analogues are found for taxa such as *Diffugia pulex*, that currently do not have values. Improvement of the estimate for optimum and tolerance ranges of poor-analogue taxa, such as *Hyalosphenia subflava*, may also improve the match between parts of the cores and give more realistic estimates of dry shifts.

In the following discussion of the water table curves, wet and dry shifts are defined as directional changes of varying magnitudes and are assigned the date at the point where the direction of change begins. Each shift is labelled with a letter code for comparing changes at the various scales of study. Because of the sample spacing (10cm at >1m

depth and 5cm at <1m depth), the exact point of wet or dry shift may not be precisely located and this may be another reason for slight age differences between similar shifts in each core.

These studies are used to test the suitability of testate amoebae analysis as a palaeohydrological indicator. Testate amoebae analysis can only be regarded as a useful proxy-climatic indicator if the records are reliable and replicable in a number of cores from several sites. The confidence intervals on both the water table depths and age ranges of samples are important for comparing the records at the various scales of study.

9.2 Micro-scale comparisons

A micro-scale (1-10m) comparison was undertaken to see if cores from the centre of a mire have replicable water table records. In palaeoecological studies it is often assumed that a single core from a mire is representative of the site as a whole and no account is taken of local variations (*e.g.* Barber *et al.*, 1994a; Stoneman, 1993) (Section 3.1). Barber (1994) regarded multiple coring from one site to be time-consuming and relied on the replicability of the data collected by Moore (1977) and Smart (1982) which he considered to have shown a good degree of synchronicity. However, these studies do not have radiocarbon chronologies and are compared on the basis of depth. Smart (1982) points out that mire surface features are three dimensional which results in stratigraphic profiles that are not identical. She also suggests that apparently synchronous levels in the profiles do not necessarily represent contemporary surfaces because of differential decay and the compression of peat. This study has shown that comparisons against depth are an unreliable substitute for well constrained chronologies (Section 9.3.2) and, since synchronicity can only be discussed in terms of time not space, Barber's reliance on these data seems to be doubtful. While some degree of replicability between cores has been shown at a broad scale (*e.g.* Svensson, 1988), for quantitative studies it is necessary to know exactly what the differences in magnitude and timing of shifts are, so that this source of error can be calculated and included in surface wetness reconstructions. Tallis (1994) recommends the use of closely spaced multiple cores to compensate for chance variations in the abundance of *Sphagnum* macrofossils, so that the general patterns of change can be determined.

Cores CRM I and CRM IV were extracted approximately 10m apart, from the centre of Coom Rigg Moss, to provide an assessment of the replicability of the hydrological record. These closely spaced cores within the central portion of the mire were used to assess the heterogeneity of the water table record over a short distance.

At the centre of the mire the sole source of water is precipitation, it is therefore the most likely location for a strong climatic signal from the peat record. However, other factors affecting ombrotrophic mire development; vegetation succession and structure, microtopography and microclimate, are superimposed upon the climatic hydrological signal (Figure 3.1). The expansion and contraction of microtopographical features may be recorded in the peat stratigraphic and testate amoebae records and therefore the study of closely spaced cores enables quantification of this source of error so that it may be taken into account in the interpretation of broader scales of study.

Coom Rigg Moss is a low relief bog with no pronounced hummocks or hollows and a greater uniformity would be expected here than at many sites with more obvious microtopographic features. Chapman and Rose (1991) suggested that there has been some loss of microtopographical variation such as shallow pools over the deeper areas of peat since the late 1950s. This is attributed to afforestation adjacent to the site. The plot for the first two axes of the Detrended Correspondence Analysis (DCA) sample ordination for CRM I and CRM IV is presented in Figure 9.1 and shows the degree of overlap between the species assemblages in these cores. Outliers 0cm and 10cm were removed from CRM I and outliers 25cm, 30cm, 80cm and 85cm were removed from CRM IV. There is a good degree of overlap between the cores which suggests the faunal assemblages are similar in general terms.

Figure 9.2 shows the reconstructed water tables for CRM I and CRM IV from 4000BC, with a larger scale comparison of the past 1500 years presented in Figure 9.3. The basal section of CRM I does not have an equivalent age section in CRM IV. The base of CRM I (370cm) has a median age of 3572BC. There is a gap in the record between 2898BC and 2223BC, which represents the beginning of the continuous record from CRM I. The gap was caused by exceptionally low test concentrations at 320cm and 330cm. The base of CRM IV has a median age of 2669BC. The age ranges of the basal 25cm of CRM IV (375-400cm) all fall within the confidence limits of the basal sample of the continuous record from CRM I (310cm = 2383-2049BC).

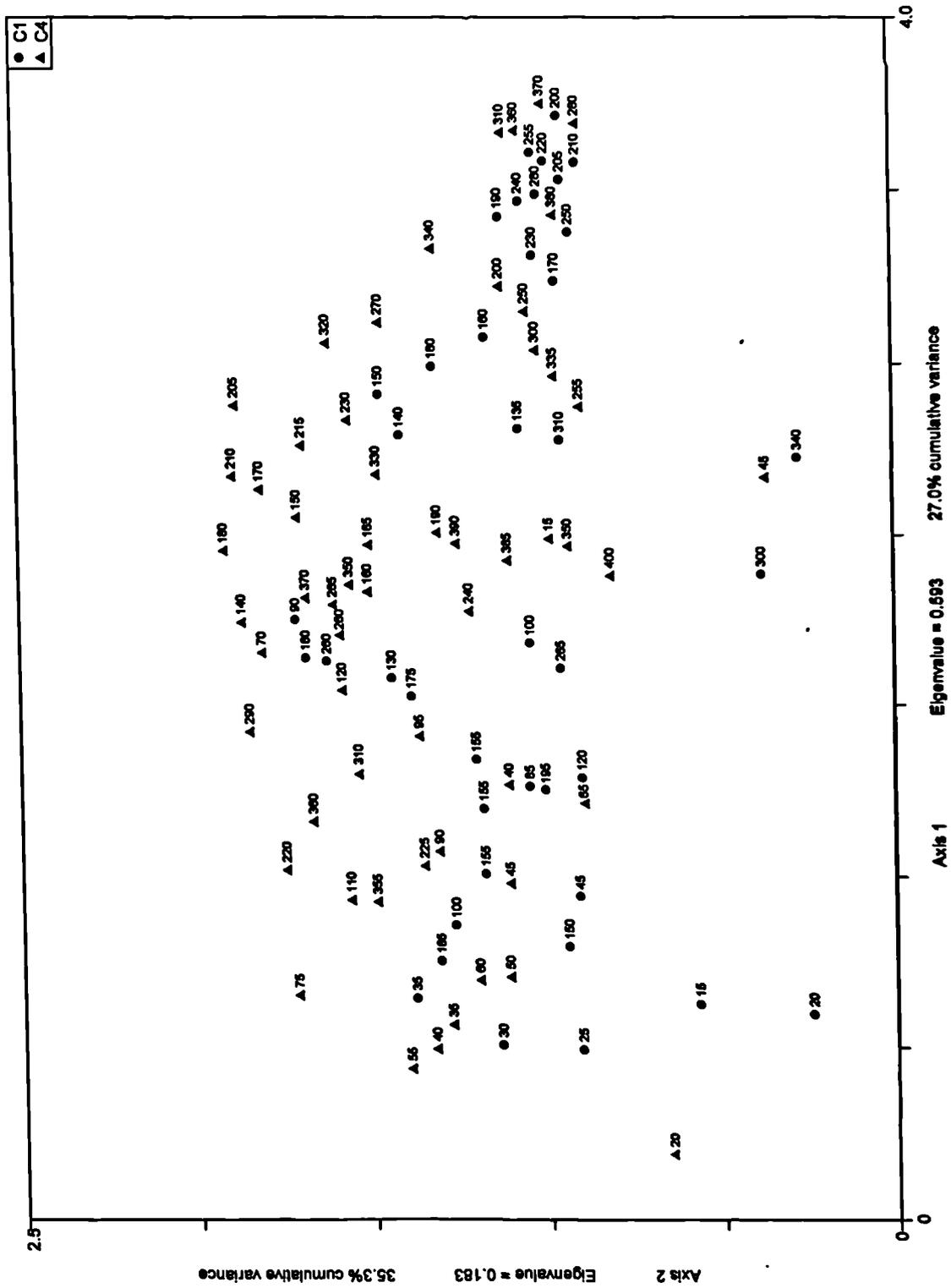


Figure 9.1 Micro-scale ordination plot for CRM I and CRM IV

There is divergence in the water table reconstructions at base of these cores but the records converge at *ca.* 2000BC (point A), with both mean water table and age error estimates coinciding: CRM I = -8.3cm, falling to -16.1cm; CRM IV = -6.5cm, falling to -14.3cm. This dry shift is coincident in both cores, suggesting a lowering of the water table across the central mire surface. Above this (point B), both cores have a wet shift from a mean water table of *ca.* -16cm in both cores to -7.5cm at *ca.* 1460BC.

From 1235BC to 629AD in CRM I, the hydrological curve indicates a low and stable water table, possibly suggesting a persistent feature such as a hummock. The equivalent time period for CRM IV (1391BC to 446AD), exhibits a much more fluctuating curve, where the mean water table shows a greater degree of variation. However, there are only three points in CRM IV that do not overlap within the confidence limits of the water table curve of CRM I. These are dry shifts at points C₁ (-3.4cm (861BC) to -15.7cm (808BC)), at C₂ (-4.6cm (702BC) to -11.6cm (543BC)) and, at D (-1.8cm (65BC) to -10.5cm (65AD)). The latter two initially high water tables are associated with peaks in *Amphitrema flavum* in the testate amoebae record, which are probably associated with microtopographical variations on the mire surface. Directional, but minor shifts are present in CRM I (C -14.9cm to -16cm; D -12.6cm to -13cm) but are more pronounced in CRM IV (C₁ -3.4cm to -15.7cm; C₂ -4.6cm to -11.6cm; D -1.8 to -10.5cm). It is probable that CRM IV occupied an intermediate position between hummock and hollow at this time and that CRM I was a hummock and therefore drier and less sensitive to hydrological fluctuations. The greater degree of fluctuation in the water table record for CRM IV is unlikely to be attributable to errors in the chronology or sample spacing, as the magnitude of the shifts are so large.

The curves from 500AD are presented separately in Figure 9.3 so that hydrological fluctuations over the historical period can be seen clearly and with higher temporal resolution. This corresponds to the wetter section of the reconstructions and hence should be more robust, as there are better analogues for taxa at the wetter end of the scale of wetness (Section 8.2).

At *ca.* 630AD, there is a wet shift in both cores (point E), but this directional change may have begun earlier in CRM IV at point E₁ (-14.4cm (386AD) to -8.5cm (446AD)). In CRM I (629AD), the water table rises from -11.9cm to -4.7cm at 699AD. Point E₂ in

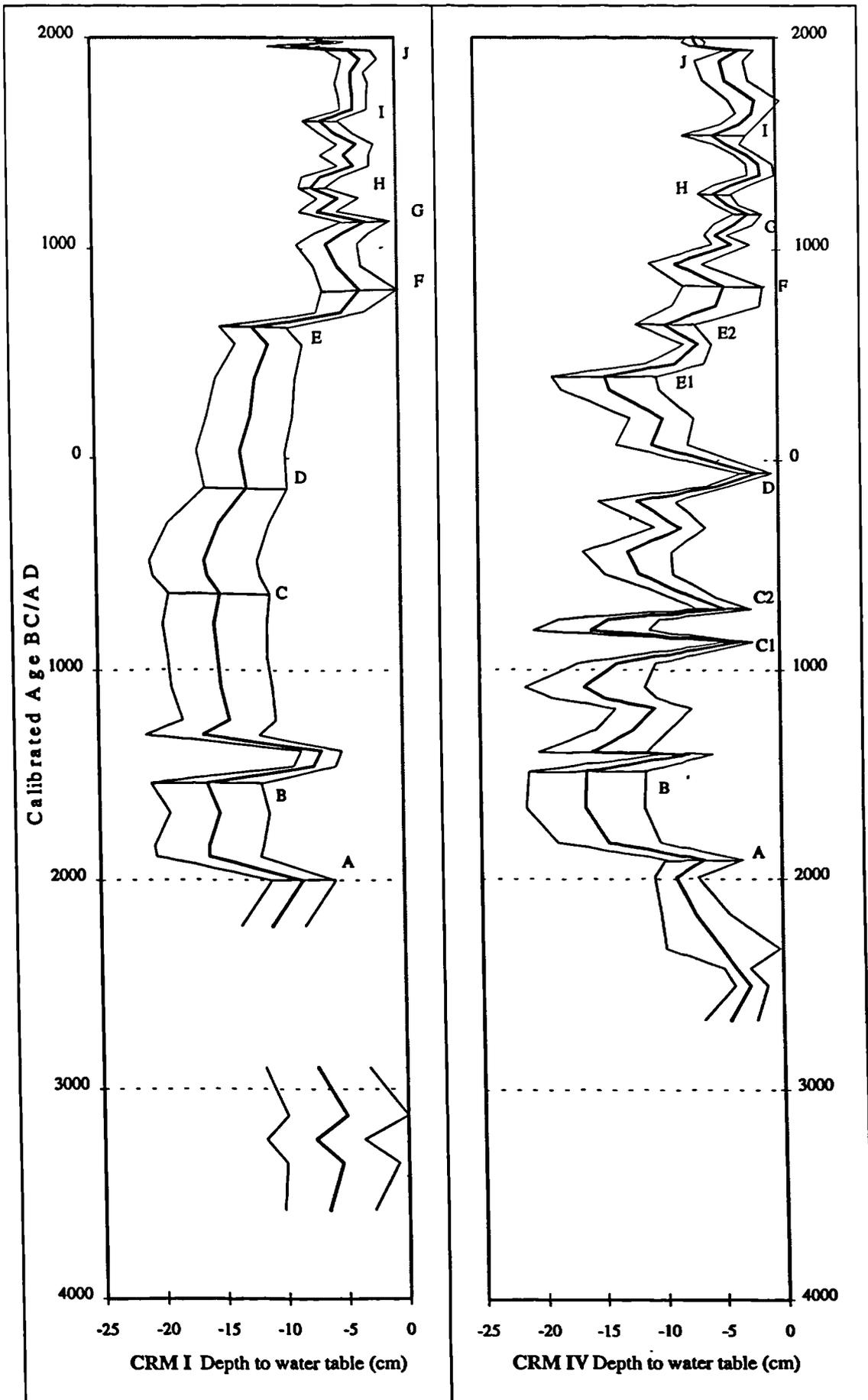


Figure 9.2 Micro-scale water tables 4000BC to present

CRM IV (636AD) rises from -9.3cm to -5.1cm. This wet shift (point E₂, CRM IV) is within the age range and confidence limits of the water table reconstructions for both cores.

Point F represents a dry shift. In CRM I the depth to water table falls from -3.1cm (805AD) to -5.7cm (911AD). In CRM IV at 826AD, the depth to water table falls from -4.4cm to -8.5cm at 874AD. The dry shift is of a larger magnitude, over a shorter time period in CRM IV, but this point exhibits a good degree of similarity within the confidence intervals for timing and water table depth.

Point G also represents a dry shift. In CRM I the water table falls from -2.5cm at 1123AD to -6.4cm at 1177AD. In CRM IV, the water table falls from -2.4cm at 1159AD to -4.0cm at 1207AD. This dry shift is similar in timing and magnitude in both cores.

At *ca.* 1260AD, there is a wet shift in both cores from -6.9cm to -3.5cm in CRM I (1283AD) and from -5.1cm to -1.3cm in CRM IV (1255AD) (point H). The lower water table in CRM IV is probably related to microtopographical variations because CRM I is a drier location, but direction and magnitude of change are similar.

Point I marks a wet shift. In CRM I at 1602AD, the water table rises from -6.1cm to -3.4cm at 1656AD. In CRM IV at 1540AD the water table rises from -5.1cm to -3.0cm at 1588AD. Although the median age of this event is slightly later in CRM IV, the age ranges of the dates have a good degree of overlap (CRM I 1421-1899AD; CRM IV 1371-1819AD).

Point J represents a major dry shift in the early 20th century. In CRM I the water table was -2.9cm at 1900 and falls to -8.4cm in 1957. In CRM IV, the water table falls from -4.6cm in 1885 to -6.7cm in 1958 (Table 9.1). In CRM I, the drop in water table appears to be more extreme than that in CRM IV, but the confidence limits of the reconstructions overlap. Species diversity increases in the surface zone and the surface reconstructions may be complicated due to vertical zonation of living tests in the acrotelm (Meisterfeld, 1977).

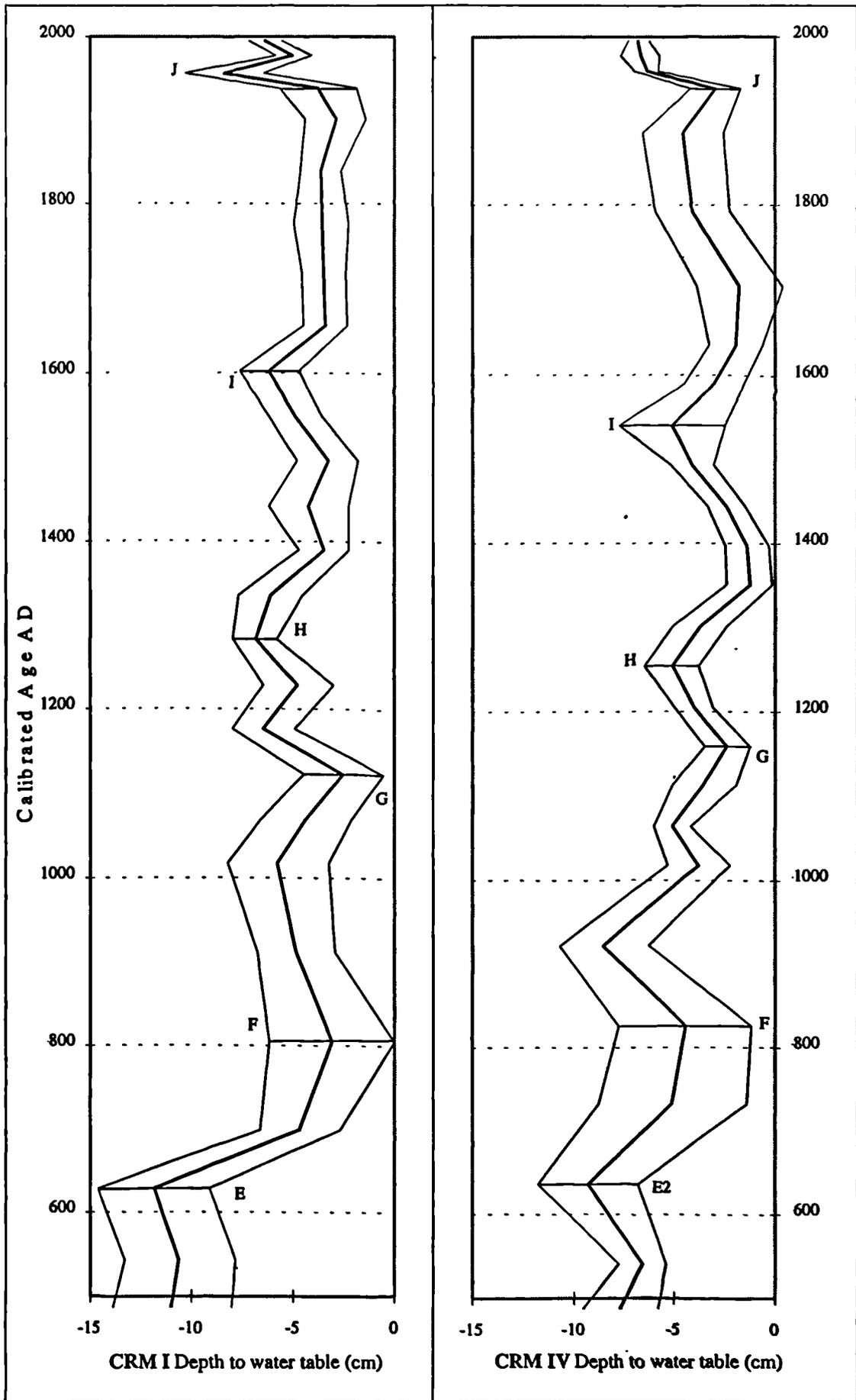


Figure 9.3 Micro-scale water table comparisons 500AD to present

From 500BC to the present, there is a better match between both the mean water table reconstructions and the median calibrated radiocarbon age. This may be because the fauna in these sections of the cores are characteristic of wetter conditions and hence have better analogues and more robust reconstructions. Sites should also become 'more' ombrotrophic over time as they become totally dependent on allogenic inputs such as precipitation and are less influenced by factors such as runoff. From 130cm peat depth, cores CRM I and CRM IV have similar ages. The top metre of CRM I and CRM IV are closely related in age, although errors in the radiocarbon dating of recent peats must be considered. Samples at 100cm depth in CRM I and CRM IV both have a median interpolated age of 1017AD. Both have fairly high water tables of -5.7cm and -3.7cm for CRM I and CRM IV respectively.

The accumulation rates for both cores CRM I and CRM IV (Tables 5.11 and 5.12) show that periods of more rapid peat accumulation correspond with the rise in water table levels at point E. In CRM I, the accumulation rate increases from an average of 12.5 years per centimetre to 11 years per centimetre after point E. In CRM IV, the accumulation rate increases from 11 years per centimetre to 10 years per centimetre after E. The radiocarbon dates were taken at these depths (CRM I 130-135cm; CRM IV 160-165cm - Table 4.5) because of major changes in the composition of the species assemblages at these depths.

The water tables show that CRM IV is a wetter site by about 1cm on average throughout the depths of the cores. This is probably due to the micro-elevational differences between the core locations, but the important point is that the relative changes in the direction and rate of water tables fluctuation are similar.

Pollen and hydrology at the micro-scale

Vegetation is an important influence on the micro-scale palaeohydrological record. Microclimate, management practices, competition, succession and structure may all result in local differences in vegetation composition, which may affect evapotranspiration and therefore surface wetness. Comparison of the pollen spectra for cores CRM I and CRM IV can be used to evaluate the significance of the vegetation history on the micro-scale palaeohydrological record.

The pollen spectra for CRM I and CRM IV are generally very similar, although they are relatively crude, as pollen analysis was undertaken for correlation purposes only (Figures 5.25 and 5.28). Age estimates on the pollen spectra are approximate, as sample spacing is 20cm below the anthropogenic *Pinus* rise, which represents *ca.* 200 years between samples. The pollen spectra suggest that differences in the vegetational history of the two cores are not a major influence on the palaeohydrological record.

The Cyperaceae (sedge) rises in CRM I and CRM IV both correspond with the increased occurrence with *Hyalosphenia subflava* in the same horizons. These horizons (310cm and 350cm for CRM I and CRM IV respectively) occur asynchronously, at 2223BC and 1821BC. There is no overlap in the age ranges of these samples, but there is only a 51 year difference between the minimum age of the CRM I date and the maximum age of the CRM IV date. This suggests that the lack of age range overlap may be related to sampling resolution rather than a real difference in age. The association of Cyperaceae pollen, a species group which prefers wet or aquatic conditions (Stace, 1995) and the testate amoebae *H. subflava*, a taxon favouring drier conditions appears to be contradictory, although 'drier' conditions for testate amoebae may still be regarded as relatively wet (see discussion of relative wetness in Section 4.2.2). Cyperaceae pollen is likely to be composed of *Scirpus cespitosus* (Deergrass), *Eriophorum vaginatum* (Cotton Grass, Hare's Tail) and *E. angustifolium* (Common Cotton Grass), as found in the stratigraphic record (Tables 5.1 and 5.8) and, according to Tallis (1994), its presence may be evidence for open-water conditions. This is probably an over-simplification, since Cyperaceae is such a broad group. Tallis (1994) considers high Cyperaceae values to indicate either expanses of bare peat, resulting from the erosion of low-lying areas of the mire surface, or the drying out of open water pools by lowering of the general water table. There is no evidence of surface haggling in the stratigraphy of Coom Rigg Moss and the Pennine peats studied by Tallis (1994) are from rather different system types to that found at Coom Rigg Moss. In the conditions found in cores CRM I and CRM IV, with an increasing xerophilous faunal assemblage, drying out of open water pools is a more likely cause.

The Ericaceae record is high throughout both cores. The Ericaceae are likely to include *Erica tetralix* (Cross-leaved Heath) an indicator of wettish conditions and *Calluna vulgaris*, which prefers drier conditions. These were not differentiated in the pollen record and so interpretation of the ericads in terms of hydrology is limited.

The anthropogenic *Pinus* rise (APR) corresponds to the lowering of the water table in the 20th century (Point J, Figure 9.3). This may be coincidental, but is possibly related to the drying of the bog surface resulting from greater interception of precipitation by adjacent trees, losses through the uptake by tree roots and by evapotranspiration. Marginal areas are probably more affected than the centre of the mire (Chapman and Rose, 1991), although Coom Rigg Moss is a relatively small bog. This will be evaluated in the meso-scale analysis, Section 9.3.

Conclusions for micro-scale comparisons

This study of the replicability of two closely spaced cores from the centre of the mire show that generally, there is a good degree of homogeneity between the hydrological reconstructions. The magnitudes of change in the depth of water table are sometimes different, but the directions are very similar for the last 1500 years. Minor fluctuations are not replicated, probably due to a combination of autogenic influences and a lack of modern analogues for taxa such as *Diffflugia pulex* and a poorer analogue than is potentially available for *Hyalosphenia subflava* (Section 8.4.1). CRM I has a mean water table generally lower than CRM IV by about 1cm. CRM IV contains a greater abundance of *D. pulex* in association with *H. subflava* than CRM I and this may result in a better reconstruction for CRM I, because although *H. subflava* has a poor analogue value, it is better than none at all. The main directional changes in water table appear to correlate well, with wet and dry shifts occurring synchronously within the range of radiocarbon ages.

The hypothesised model of factors affecting ombrotrophic water table depth (Figure 3.1), shows that the four major factors at the micro-scale are vegetation, succession, micro-climate and microtopography. At Coom Rigg Moss, since the planting of the Kielder Forest, there have been marked changes in both the structure and composition of mire surface vegetation (Chapman and Rose, 1991). This is likely to have contributed to the fall in water table depth in the 20th century. Prior to this, vegetation succession and its relationship with microtopography was probably of greater importance to mire surface wetness.

The main period where the water table records do not match is between about 1200BC and 600AD. Based on Barber's (1981, 1994) hypothesis of expanding and contracting hollows, it is possible that CRM IV occupied a marginal position between hummock

and hollow for this period and therefore exhibits more fluctuation than CRM I. CRM I was probably the location of a hummock during this time, showing a less sensitive record of water table depth. Subsequently, both cores are equivalent micro-topographic locations. There is a good match between hydrological reconstructions at the micro-scale and major variations appear to be forced by large scale changes in peat surface wetness.

9.3 Meso-scale comparisons

At the meso-scale (10-1000m), cores are compared between the central mire expanse and the margins of the same mire. The distance between cores will be dependent on the size of the mire. The variability of the palaeohydrological record within a site is influenced by mire expansion, which is a major factor affecting mire development (Figure 3.1). Mire expansion is influenced by human impact, vegetation succession, topography and micro-climate. Vegetation differences may be present due to competitive interactions and micro-climate. Two comparisons of this kind have been made at Coom Rigg Moss and Butterburn Flow.

9.3.1 Coom Rigg Moss

The marginal cores CRM II and CRM III were 450m apart (Figure 3.3), so the distances between the cores are well within the limits established as the meso-scale. CRM I was located approximately 10m to the west of CRM IV.

Figure 9.4 is a DCA ordination plot of the sample depths for all four cores from Coom Rigg Moss, with samples in the age range 500BC to present. This represents the time span where the cores from Coom Rigg Moss overlap. Samples 205cm to 370cm inclusive have been removed from the ordination analyses for CRM I and samples 250cm to 400cm inclusive have been removed from CRM IV as the median age of these samples exceeds 500BC. Axis 1 is related to depth and therefore, also to hydrology, as the wetter samples are generally found closer to the surface and samples with a lower water table are found at depth. The samples from the four cores overlap and therefore the faunas contained in the samples are comparable in general terms.

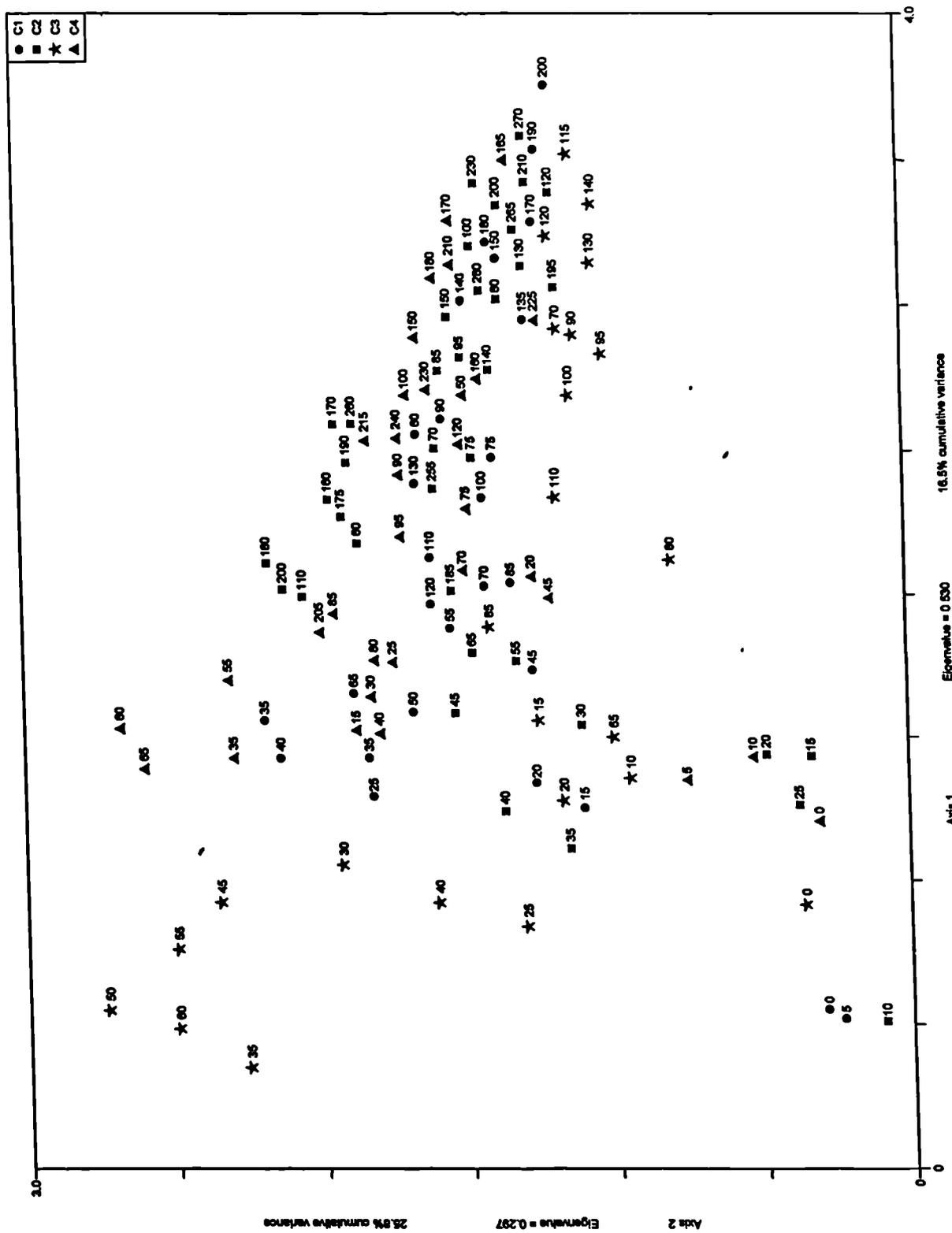


Figure 9.4 Meso-scale ordination plot for Coom Rigg Moss

The water table reconstructions for 500BC to the present from the four cores from Coom Rigg Moss are presented in Figure 9.5. Comparisons between cores CRM I and CRM IV were discussed in detail in Section 9.2.

Core CRM II has a much more variable hydrological signal than either CRM I or CRM IV. The base of CRM II at 226BC overlaps with the confidence intervals for water table depth and age ranges in CRM I and CRM IV at this time.

Point D marks the first shift in water table that is replicated in cores CRM I, CRM II and CRM IV. The peat in CRM III is not old enough to have recorded this event. The dry shift marked by point D is more similar in CRM II and CRM IV than in CRM I. In CRM II the water table falls from -6.0cm at 22AD, to -14.4cm at 125AD. In CRM IV, the drop is from -1.8cm at 65BC, to -10.5cm at 65AD. The overlap in the age range of this event is good and the magnitude of change is similar in both cores (*ca.* 8.5cm), but there is no overlap in the 2σ confidence intervals on the water table reconstructions. CRM II is a drier site at this point and the closeness of the confidence intervals in both cores at this point indicates that the reconstructions are robust. The confidence limits for point D in CRM I overlap with CRM II, but CRM I is also drier than CRM IV - there is no overlap between these cores. Between 0-500AD, CRM II has a reasonably stable hydrological record and although the mean water table is lower than that for either CRM I or CRM IV, the confidence intervals of both cores overlap.

Point E marks the base of a pronounced wet shift in all four cores. In CRM II the water table rises from -15.5cm at 565AD, to -3.5cm at 614AD. In CRM I the water table rises from -11.9cm to -4.7cm between 629AD and 699AD. Taking E₂ as the wet shift in CRM IV, as this spans the same time period as the wet shifts in the other cores, the water table rises from -9.3cm to -5.1cm between 636-684AD. This event has a median date that is slightly later in CRM III, from 762AD to 816AD and the water table rises from -15.2cm to -8.4cm. The age ranges of this event overlap for every core but better simultaneity may have been recorded by reducing the sample intervals. Cores CRM II and CRM III have mean water tables that are lower than CRM I or CRM IV, but the confidence intervals do overlap in all four cores at point E. This is a major event that is replicated across the mire surface. The lower water tables in the marginal cores suggest that there is some internal mechanism affecting water table depth. At particular locations, the shift to a wetter mire surface would appear to be caused by

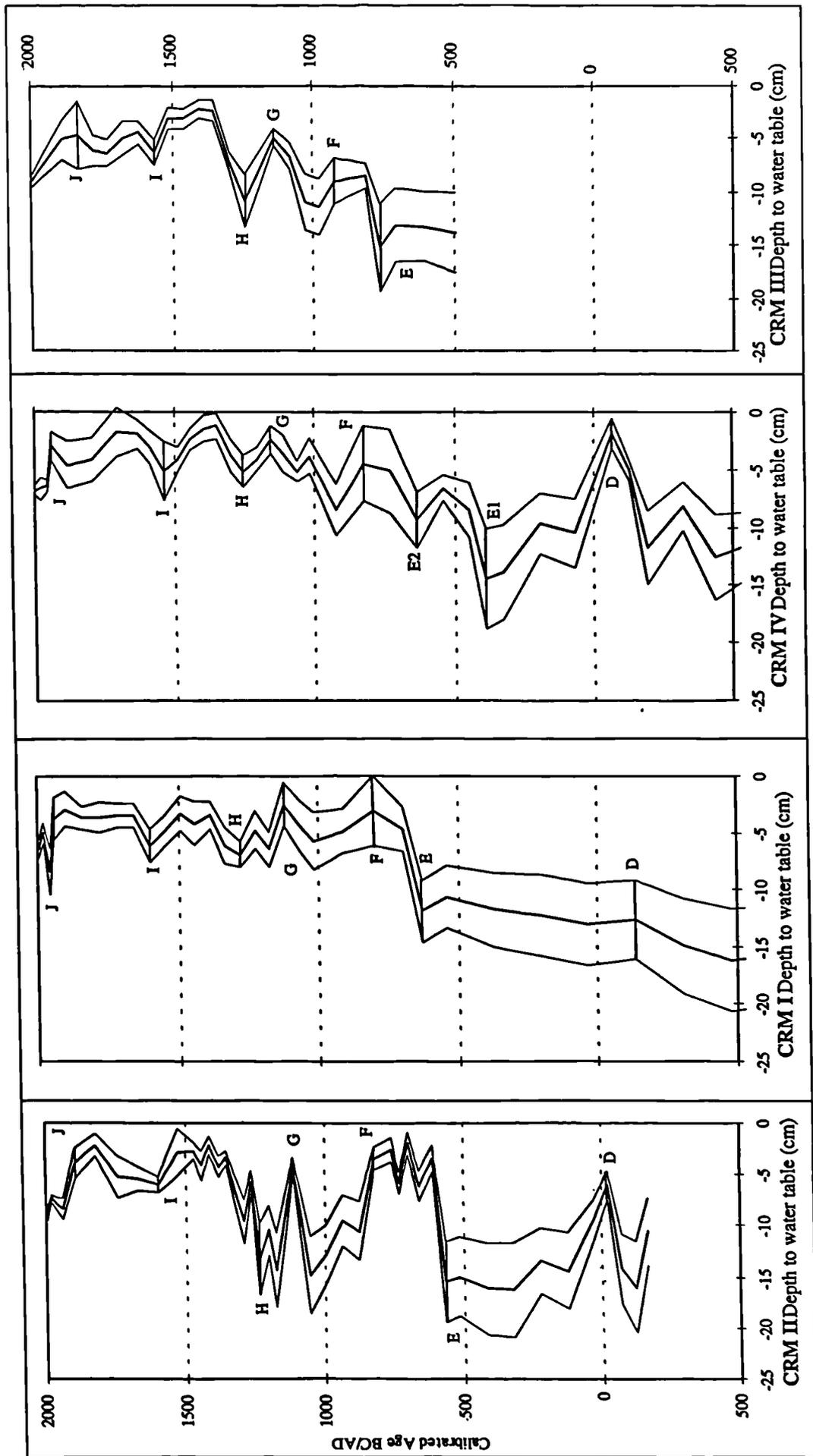


Figure 9.5 Meso-scale water tables from Coom Rigg Moss, 500BC to present

some factor influencing the entire mire surface. This could be climatic in origin, or it could be mire expansion or internal drainage, for example, if an outflow from the mire was blocked.

This wet phase persists until point F, when there was a dry shift. CRM II and CRM III are markedly drier than CRM I or CRM IV, where only a slight dry shift is registered in both cores (CRM I -3.1cm to -4.9cm; CRM II -3.4cm to -10.5cm; CRM III -8.9cm to -11.3cm; CRM IV -4.4cm to -8.5cm). The marginal cores, CRM II and CRM III, have water table ranges which overlap with each other, but not with the hydrological curves from the centre of the mire. This dry phase continues until 1266AD for CRM II and 1352AD for CRM III, where the water table levels rise to a similar depth to CRM I and CRM IV.

In the middle of the drier phase, there is a synchronous wet peak evident in all four cores (point G), prior to a return to low water table conditions. The wet peak occurs between 1120-1160AD in all cores. The two central cores have mean water tables approximately 2cm wetter than that attained at the mire margins (CRM I -2.5cm to -6.4cm; CRM I -4.3cm to -14.4cm; CRM III -4.4cm to -10.7cm; CRM IV -2.4cm to -5.1cm). There is a greater magnitude of drop in the water table levels in the marginal cores than at the mire centre. The fall in water table could be climatically forced, as it is evident across the mire surface or could also be related to changes in the drainage of the mire. This idea will be tested in Section 9.5, the macro-scale comparisons.

Point H represents a wet shift. The rise in water table is synchronous in all four cores at *ca.* 1280AD. The median age of the initial wet shift in CRM II is more closely related to the wet shifts in the other cores than the slightly later shift at 1385AD. The rise in water table is between 3-4cm in all cores, although CRM III has a lower water table, where the confidence intervals do not overlap with any of the other cores.

There is a synchronous rise in water table level at point I between 1540-1600AD. The rise is of between 2-3cm in all four cores and the confidence limits of the reconstructions are close at this point and overlap, showing a good degree of replicability in this part of the core. This magnitude of rise in CRM II takes place over a longer period of time. With closer sampling intervals at point I, the rise in water table

may be more precisely located. However, this is a synchronous rise, of similar magnitudes across the mire surface.

Core	Year	Water Table (cm)	Year	Water Table (cm)
CRM I	1901	-2.9	1995	-6.4
CRM II	1893	-4.0	1995	-8.9
CRM III	1888	-5.1	1995	-8.8
CRM IV	1885	-4.6	1995	-6.9

Table 9.1 Reconstructed mean water tables at CRM core locations prior to and since the planting of the Kielder Forest

There is a synchronous fall in water table levels across the mire surface in the early- to mid-20th century (Table 9.1), which is marked by point J on the water table curves. The fall is not as dramatic in CRM III because sample 55cm, which is contemporaneous, had a testate amoebae concentration that was too low to count.

A qualitative assessment of the species assemblages shows that the species composition of the marginal cores is different from those found in the central cores. This suggests that different assemblages can produce similar records of surface wetness and that better analogues for taxa at the drier end of the wetness scale could result in more dramatic variations between the drier, marginal cores and the wetter, central cores. The direction and rate of change is modelled accurately, but the magnitude of change for dry shifts are underestimated. The CRM II record suggests marginal locations can be sensitive, as it is in many ways more similar to the water table record of CRM IV, which is thought to represent a marginal position between hummock and hollow, than to CRM III, the other marginal core.

Pollen and hydrology

The Cyperaceae rise in CRM I and CRM IV (Figures 5.25 and 5.28) was discussed in Section 9.2. The Cyperaceae rise occurs in the centre of the mire more than 3000 years before it is registered in marginal locations. The Cyperaceae rise is synchronous in CRM II and CRM III (Figures 5.26 and 5.27), suggesting that conditions suitable for colonisation occurred at the same time at either end of the mire. There are, however,

problems relating to the lack of differentiation between the various species that comprise Cyperaceae, but a crude assessment may be that the hydrological records (Figure 9.5) show that it is drier at the edges of the bog than in the centre. The testate amoebae record in the same horizons as the Cyperaceae rise for both CRM II and CRM III show an increase in the abundance of *Amphitrema flavum*, a wet indicator taxon and follows the decline in abundance of *Hyalosphenia subflava*.

The APR correlates with lower water tables at the edges by 2cm more than in the centre of the site. Table 9.1 presents water table levels prior and subsequent to the planting of the Kielder Forest and shows that the fall in water table depth was slightly greater in the marginal cores than in the mire centre. CRM I and CRM IV fell by 3.5cm and 2.3cm and CRM II and CRM III fell by 4.9cm and 3.7cm. The edge effect of the forestry plantation on mire surface wetness is likely to have been greater than in the mire centre, due to increased interception, uptake and evapotranspiration.

9.3.2 Butterburn Flow

The rationale for the meso-scale study at Butterburn Flow was the same for that at Coom Rigg Moss. The influence of mire expansion and development on the testate amoebae record and water table models can be evaluated from a multiple core study and the relative influence of autogenic and allogenic inputs assessed. The topography of a mire will affect the nature and strength of the testate amoebae and vegetation response to climate change, as it affects the retention of water. Butterburn Flow is an intermediate ombrotrophic mire and three cores were extracted from the northern part of the site. Coring locations were shown in Figure 3.7.

Figure 9.6 is a DCA plot of meso-scale comparisons for Butterburn Flow. For BBF I, only samples from the surface to 650cm (6437BC) are plotted as these have an equivalent age range in cores BBF II and BBF III. Outliers at 270cm and 340cm were removed from BBF II and BBF III respectively. There is a good degree of overlap between the samples from these cores, which suggests that the faunas contained in the samples are comparable. Depth is related to hydrology, with wetter samples at the surface and drier samples at deeper points in the core.

The period between 6500-3000BC is shown only in cores BBF I and BBF III. Some fluctuations occur in BBF I which are not registered in BBF III. This is probably attributable to sampling resolution. The record for BBF I had much denser sample spacing than BBF III (Figures 6.25 and 6.27), because the record in BBF I extends over a greater depth (650cm) than BBF III (350cm). Therefore, the same sampling interval in BBF III is stretched out over a longer period of time, which results in a less sensitive record than for BBF I. Confidence intervals overlap and some major shifts are replicated *i.e.* there is a dry shift after 4000BC and a wet shift at *ca.* 3000BC. In BBF I, this period is dominated by *Diffugia pulex*, which has no analogue value. A dominant taxon in BBF III is *Cyclopyxis arcelloides* type, which has very narrow tolerance range (Figure 4.2) and hence should result in a reliable reconstruction. Another factor which may also result in a less sensitive record for BBF III is the microtopographical location of the core, BBF III may have been a complacent location over this period in a similar way to CRM I. The lack of variation in the water table record may also be attributable to core location at the centre and edge of the mire. BBF I was located in the central part of the mire and is therefore more likely to have a strong climatic signal in the peat record.

The water table reconstructions (Figure 9.7) show that point K marks the beginning of a wet shift that is found in all three cores from Butterburn Flow (BBF I 1697-1358BC; BBF II 1711-1337BC; BBF III 1848-1588BC). The magnitude of change is similar in all three cores but there is no overlap in the confidence intervals of the water tables between any of the cores. BBF II has a significantly lower water table (rising from -15.8cm to -12.9cm) than BBF I and BBF III by 10cm and 7cm respectively. BBF I has the highest water table rising from -6.3cm to -3.8cm. This event is replicated across the mire but the differences in size of the wet shift probably indicate some internal mechanisms controlling the depth to water table across the mire. Point K is followed by a dry shift.

Point L marks the start of a dry shift that is evident in BBF I and BBF III at *ca.* 815BC, but is not evident at the same time in BBF II, probably due to the sampling intervals, since the dry shift occurs about 500 years too early in BBF II at 1405BC. The confidence intervals of the water tables for BBF I and BBF III show a good degree of overlap with BBF I falling from -10.1cm to -16.5cm and BBF III falling from -10.6cm to -12.8cm.

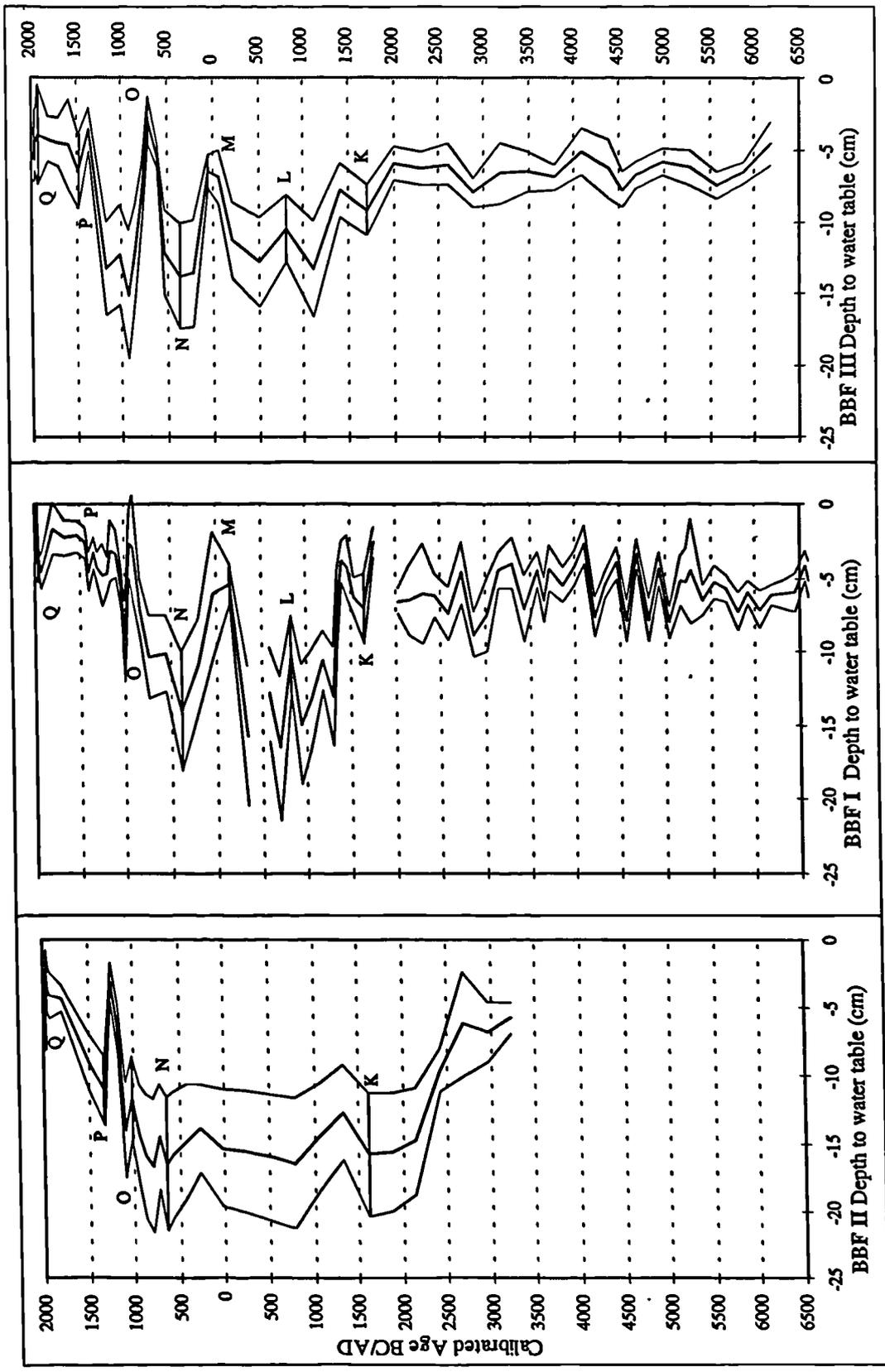


Figure 9.7 Meso-scale water tables for Butterburn Flow, 6500BC to present

Point M marks the beginning of a dry shift which is pronounced in BBF I and BBF III, but is barely registered in BBF II. This may again be related to sample spacing, or it may be that BBF II is a less sensitive location where the change in water table level found in the other two cores has not registered. The age ranges of this point overlap well at the BC/AD boundary.

Figure 9.8 shows the high temporal resolution meso-scale water table comparisons for Butterburn Flow from 0AD. Point N marks the beginning of a wet shift. The wet shift occurs synchronously in BBF I and BBF III and slightly later in BBF II. There is a 7cm rise in water table level in BBF I and BBF III and a 5cm rise in BBF II. The confidence intervals of BBF I and BBF III overlap, but there is no overlap with BBF II, which has a significantly lower water table.

At point O, a dry shift, the age ranges of BBF I and BBF III overlap, but there is no overlap with BBF II (BBF I 778-1079AD; BBF II 1123-1307AD; BBF III 604-811AD). The fall in water table level is approximately -3cm in all cores and occurs first in BBF III and last in BBF II. This may be a truly asynchronous event, but this is unlikely since the magnitude of shift is similar in all three cores and the lack of overlap in age ranges is less than 50 years in BBF I, but is >300 years in BBF III. This suggests that the lack of overlap is related to either sampling intervals or lack of precision in the chronologies. Thus it may be a climatically-induced event, or may be related to a change in surface wetness across the whole mire surface, attributable to an internal mechanism such as drainage.

Point Q marks the fall in the water table level at the beginning of the 20th century (Figure 9.8) (Table 9.2). The fall is 2-3cm in all three cores and may be associated with the planting of the Kielder Forest. However, the forest was not planted in such close proximity to Butterburn Flow as it was at Coom Rigg Moss and the fall in water table may actually be due to reduced precipitation. This could be associated with climate change, with climatic amelioration after the Little Ice Age and 20th century warming (*c.f.* Bradley and Jones, 1993) (Section 9.7).

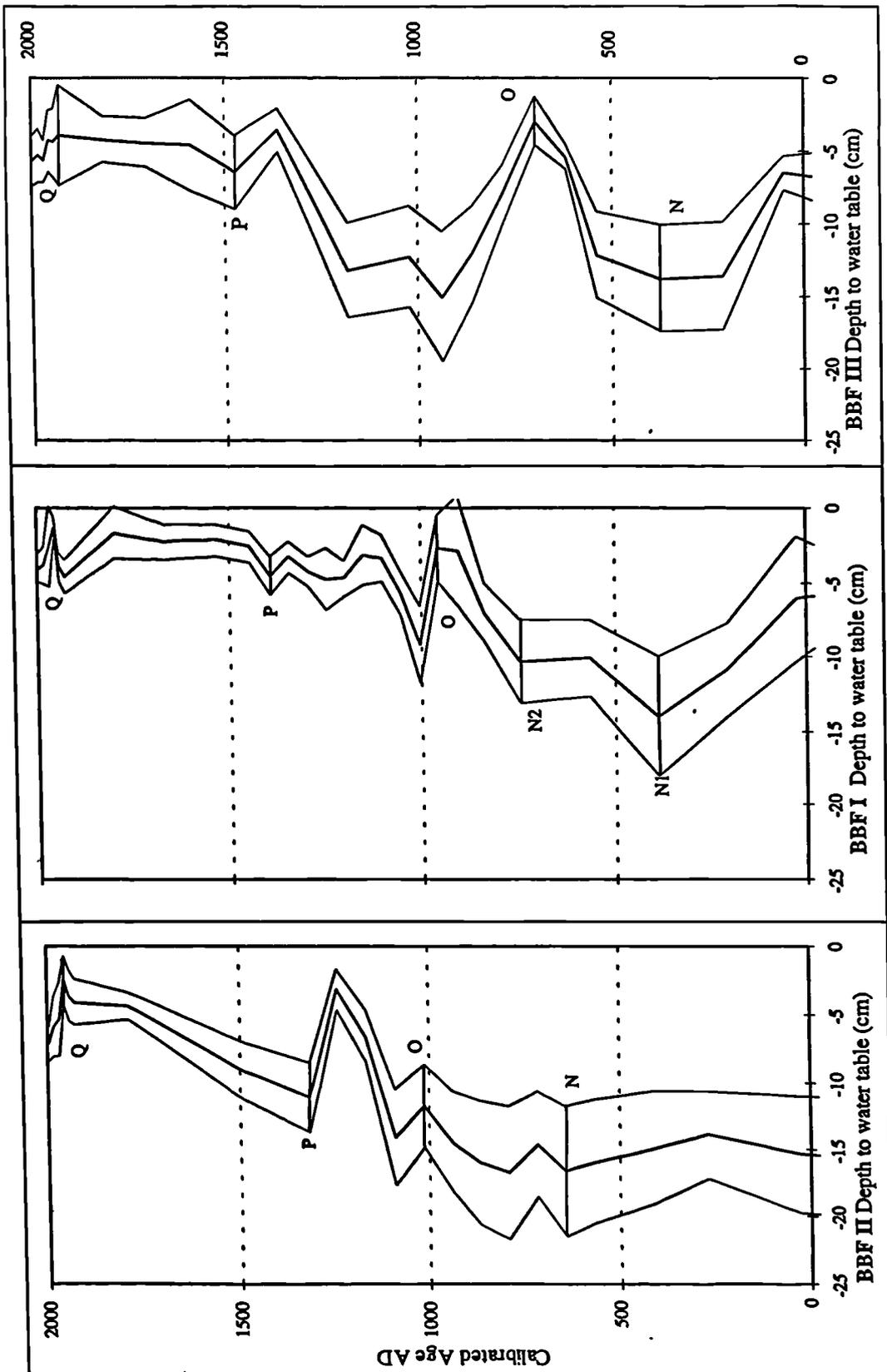


Figure 9.8 Meso-scale water tables for Butterburn Flow, OAD to present

Core	Year	Water Table (cm)	Year	Water Table (cm)
BBF I	1799	-1.7	1995	-3.9
BBF II	1787	-4.4	1995	-7.2
BBF III	1816	-4.2	1995	-5.7

Table 9.2 Reconstructed mean water tables at BBF core locations prior to and since the planting of the Kielder Forest

At Butterburn Flow, the testate amoebae record extends much further down the cores than at Coom Rigg Moss. In all three cores, the depth of peat without a countable testate amoebae record was less than 15cm to the base. Test preservation was better at the base of the Butterburn Flow cores than the base of the Coom Rigg Moss cores. The basal dates for the cores from Butterburn Flow are also more representative of early peat development, since the testate amoebae record extends further down the profile and so the water table records are representative of the entire peat profile, whereas at Coom Rigg Moss the water table record does not extend to the base of the profiles. Therefore, the age of the basal peats is unknown, as peat was dated only to the base of the water table record. Basal peat at Coom Rigg Moss may be similar in age to that at Butterburn Flow but this is impossible to tell.

In BBF III, tests were counted to 340cm, but the peat was of similar age to deposits at BBF I which was 715cm deep. Peat accumulation was therefore slower at BBF III, with less peat over same time range. This may have been influenced by topography. There is a need therefore to have a greater density of sample spacing at BBF III to get the same level of detail of hydrological fluctuations. The water table record from 6500-3000BC, that is found only in cores BBF I and BBF III, also shows a remarkable degree of similarity. BBF I shows a greater level of variation, which may be attributable to sample spacing, but the shifts in water table direction match well and the confidence intervals overlap in time and space.

9.4 Within-site variability

The aim of comparing cores at the meso-scale was to evaluate significance of the internal mire dynamics by comparing cores from the centre of the mire to the mire margins. There are changes that occur in the same direction at the same time, but there

are some large differences, especially at Butterburn Flow. This discussion explores the reasons for these differences with reference to the hypothetical model of factors affecting ombrotrophic mire surface wetness, Figure 3.1. There is a limited body of literature dealing specifically with autogenic and allogenic inputs to the mire hydrological system (e.g. Payette, 1988; Winkler, 1988; Foster and Wright, 1990; Hu and Davis, 1995). Wheeler (1992) and Belyea and Warner (1996) discuss some autogenic and allogenic influences on mire systems, but these are not necessarily hydrological factors. The relative roles of autogenic and allogenic controls in peatlands remains a debatable issue (Hu and Davis, 1995) and the arguments are complex and often contradictory.

CORE	<	>	<	<	>	<	<	>	>	<
	A	B	C	D	E	F	G	H	I	J
CRM II				+	+	+	+	+	+	+
CRM I	+	+	x	x	+	+	+	+	+	+
CRM IV	+	+	+	+	+	+	+	+	+	+
CRM III					+	+	+	+	+	+
		K	L	M	N	O			P	Q
BBF II		+			+	+			+	+
BBF I		+	+	+	+	+			+	+
BBF III		+	+	+	+	+			+	+

Table 9.3 Wet and dry shifts in the meso-scale core comparisons, where A-J are codes for CRM cores and K-Q are codes for BBF cores. x indicates very minor shift, > indicates wet shifts and < indicates dry shifts.

The wet and dry shifts which have been noted in the previous section (Table 9.3) are discussed here in the context of allogenic and autogenic hydrological inputs to the mire. The alignment of shifts between Coom Rigg Moss and Butterburn Flow implies synchronicity as they occur within similar time-spans.

Human impact is unlikely to be a major factor affecting mire surface wetness at either Coom Rigg Moss or Butterburn Flow. At Coom Rigg Moss, the mire was subject to low level grazing and autumn burning to remove dead grass up until the 1950s. The conditions that existed in the area prior to the expansion of sheep farming in the 17th and

18th centuries are unknown (Chapman and Rose, 1991). At Butterburn Flow, sheep grazing still occurs at low intensities. These factors have been considered with respect to changes in the vegetation composition at Coom Rigg Moss by Chapman and Rose (1991). Neither site has been subject to peat cutting and no marginal bog bursts are evident in the stratigraphic record, so the complete record of peat accumulation is assumed to have been recovered.

There is a remarkable degree of similarity between the four cores from Coom Rigg Moss. Shifts A, B and C occur only in cores CRM I and CRM IV since the records from CRM II and CRM III do not extend back far enough to record these shifts. There are no major shifts which occur only at the margins or only in the mire expanse.

The meso-scale study at Coom Rigg Moss appears to agree to a certain extent with the view of Kilian *et al.* (1995). They suggest that autogenic mechanisms may result in drier conditions at mire margins, as cooling and wetting will raise the water table in central, flatter parts of the bog due to a lower gradient in hydraulic potential and will raise the water table later in marginal zones. The marginal cores, CRM II and CRM III, have mean water tables that are generally lower than the central cores, but the temporal lag at the margins described by Kilian *et al.* (1995) is not evident at Coom Rigg Moss. This may be because Coom Rigg Moss is not a classic raised mire site, but is an intermediate ombrotrophic mire. However, the chronological precision may also not be high enough to show this.

CRM II shows a similar degree of shift at point D as CRM IV, with CRM I exhibiting only a very minor decrease in water table level. This fall in water table level appears to occur across the mire surface, but CRM I is a less sensitive location. Point E represents an increase in surface wetness across the mire, as this wet shift is found in all four cores. A shift of such magnitude that occurs synchronously may be attributable to increased inputs to the mire system, possibly allogenic. This will be discussed at the macro scale (Section 9.5). An increase in surface wetness across the mire, which is the result of autogenic factors, may occur due to blocked outflows or impeded drainage at more than one point in the mire system.

Point F represents a dry shift across the mire surface, which may be attributable to better drainage, as the largest drop in water table is in CRM II. H and G represent minor

fluctuations that occur in all four CRM cores under relatively high water table conditions. These small-scale fluctuations may be attributable to an increase in surface patterning and microtopography, with an increasing abundance of hollows and pools making up the surface pattern, although Ivanov (1981) suggested that surface patterns are a source of hydrological stability rather than instability.

As the peatland spreads laterally, it tends towards a broader ellipse (Ingram, 1982). As the central, flat part of the mire increases in size and height resulting in a 'more' ombrotrophic fossil record, the domed area is less likely to be influenced by groundwater and surface runoff. Spatial differences in the record of the upper peats are also less likely, as the area becomes more hydrologically stable. The record is more likely to be related to climate over time as shown by the assessment of the cores at the micro-scale. The record in the upper peats, over the past 500 years, are more similar in the CRM cores. Below 1500AD, CRM III maintains a similar record to CRM I and CRM IV, but CRM II shows a greater degree of sensitivity to fluctuations.

At Butterburn Flow, the water table records for BBF I and BBF III are more similar than they are for BBF II. In all BBF cores, the water table is higher and less variable, but the sample spacing means that the BBF records show less variation than may be evident with a closer sampling interval. BBF II is persistently drier than cores BBF I and BBF III. BBF II also shows a less sensitive water table record, with some fluctuations either not evident or not as pronounced. This suggests that there are autogenic factors affecting peat development at BBF II. There is a lack of contemporary surface microtopographic features on this part of Butterburn Flow. BBF II was located on the banks of the River Irthing. This may result in this location having better drainage than BBF III, which does not have such an extreme marginal location. Discharge across the mire boundary and processes within the mire regulate flow towards the boundary (Ingram, 1983).

Autogenic factors are those that result from internal bog dynamics and include, vegetation, microclimate, mire expansion, human impact and site drainage. Autogenic processes affecting mire surface wetness occur as portions of the mire pass through critical stages of bog development, which may be controlled by morphology, hydrology or peat depth (*c.f.* Foster and Wright, 1990) and are responsible for changes in vertical accretion, lateral expansion and the consequent shape of the peatland (Ingram, 1982;

Winston, 1994; Almquist-Jacobson and Foster, 1995). The upward growth of peat due to autogenic factors usually takes place where there are only small vertical fluctuations in the water table. The theoretical model developed by Almquist-Jacobson and Foster (1995) combined internal bog dynamics with the external factors of local substrate, regional temperature and moisture conditions. The model suggested that the geometry of raised bogs will adjust to climate change regardless of the stage of bog development or direction of climate change. Almquist-Jacobson and Foster (1995) concluded that all aspects of mire development appear to be closely related to climate. Hu and Davis (1995) contradicted this point of view in a gross scale of study, by concluding that allogenic influences should be interpreted as overlays of autogenic signals and that it is important to account for the autogenic signal when using peatland palaeoecological data to detect palaeoclimatic signals. Also, it has been argued that in a suitable climate, autogenic processes are the dominant factors controlling mire development (Walker and Walker, 1961; Tolonen *et al.*, 1985; Foster and Wright, 1990), since atmospheric water supply is in excess.

Payette (1988) argued that autogenic succession may be identified only after external factors and their associated vegetation events have been properly evaluated. From this study of palaeohydrological records, there is a clear need to assess allogenic and autogenic factors together to see which dominates the record. To do this, multiple cores from multiple sites are necessary. It is not possible to separate these signals from one core.

Winkler (1988) found synchronous hydrologic and vegetation changes in a broad scale study from Washburn Bog and Hook Lake Bog after 6500BP. Pollen and plant macrofossil analysis was used to show lower water levels at both sites. This suggests that bog development is a function of climate and that bogs have developed as effective moisture has increased. This is similar to the research at Caribou Bog, Maine by Hu and Davis (1995), who found that the major transitions reflect the regional climatic history, but that autogenic changes affecting hydrology probably also played a major role in peatland development. These changes were mostly chronologically heterogeneous at different localities in the peatland after 3500BP. The heterogeneity of shifts highlights major difficulties in inferring palaeoclimates from peatlands, especially from a single locality. The synchronous changes across the mire at CRM are therefore possible indicators of a climatic influence on peatland development at Coom Rigg Moss but the

replicability of hydrological shifts at the macro-scale (Section 9.5) will establish the validity of this assertion.

There is no way of determining the exact cause of wet or dry shifts, as a number of mechanisms are possible. At the micro-scale, the main differences appear to be attributable to microtopography, related to the sensitivity of the core location. Meso-scale factors causing wet or dry shifts may be related to hydraulic conductivity, compaction and porosity. High water tables may be the result of impeded drainage or blocked outflows and low water tables may be due to throughflow, surface runoff or pipeflow (Ingram, 1983).

9.5 Macro-scale comparisons

The macro-scale study is used to assess the replicability of the palaeohydrological record between sites across a region, at a distance of between 1-10km. Cores from the central expanse of the three sites, Coom Rigg Moss, Butterburn Flow and The Wou are used for the macro-scale comparisons. The mires are hydrologically separate units. Central cores are used as these normally have the longest record and the central area is thought to be the most sensitive part of the mire to climate change. Climate is thought to be one of the most important factors controlling mire surface wetness at this scale, operating through moisture deficit, as a result of the relationship between precipitation and temperature. Changes in mire surface wetness recorded synchronously at a single site are not necessarily climatically forced but may be attributable to internal mire dynamics. Major climatic changes can only be identified by replication at a number of different sites. If the water table records are similar in two or three sites, it is likely that climate is the dominant influence on peat development. If however, the water table records are not comparable across the region, autogenic mechanisms are likely to be the dominant influence on peat development. The autogenic factors affecting mire surface wetness at this scale are mire morphology and internal mire drainage, which are both components of the regional groundwater system (Figure 3.1).

Figure 9.9 is a DCA ordination plot containing all samples from CRM I, CRM IV, BBF I and TW II with a median age within the past 5500 years. The water table record from

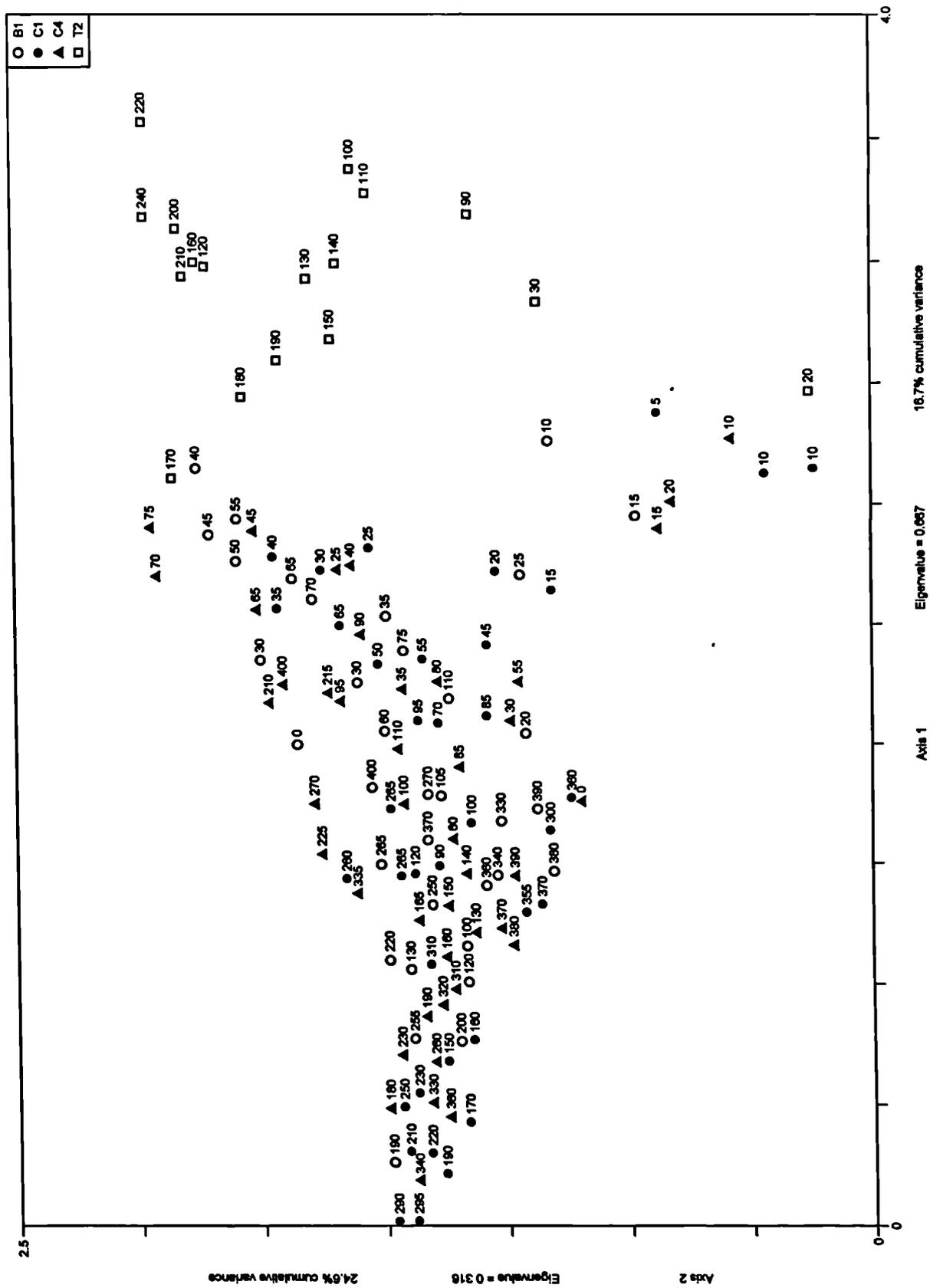


Figure 9.9 Macro-scale ordination plot

TW II extends back as far as 285AD, but the continuous record presented here only extends to 736AD. Plotting samples within the past 5500 years resulted in one sample being removed from CRM I (370cm) and samples between 420-715cm being removed from BBF I. All samples were retained for CRM IV and TW II.

There is a good degree of overlap between CRM I, CRM IV and BBF I, which suggests that these cores contain similar faunal assemblages. The samples from TW II are found further along axis 1, removed from the three other cores and have a larger scatter about axis 2. TW II therefore contains a different faunal assemblage to those found in the other cores. The second axis is related to sample depth, with the widest part of the ordination plot dominated by surface and near-surface samples. This is also related to hydrology, since the wetter samples are found closer to the surface and drier samples found at depth down the cores.

Figure 9.10 shows the water table reconstructions from the central cores from the three sites, cores CRM I, CRM IV, BBF I and TW II. Between 2505-2005BC, the confidence limits of cores CRM IV and BBF I overlap, CRM I shows a falling water table as does BBF I, but to a lesser extent. CRM I does not have a complete record at this point, due to extremely low test concentrations in horizons 320cm and 330cm.

At point A, there is a synchronous fall in water table levels in CRM I and CRM IV. The record is incomplete in BBF I at this point, due to poor test concentrations in sample 300cm. The magnitude of the dry shift at point A was discussed in the micro-scale comparisons, Section 9.2.

There is a synchronous rise in water table level at *ca.* 1530BC (point B). The good match between the direction and rate of change at 1530BC in all three cores suggests that this is a climatically induced change. The confidence intervals of the CRM cores overlap at this point, but BBF I is a wetter site by approximately 10cm and the magnitude of the wet shift is not as much as in the CRM cores. Immediately following this peak in water table level, there is a fall of >6cm in all three cores.

Point C marks a dry shift. Point C in BBF I has a better degree of correlation with C₁ in CRM I than C₂, both occurring between 820-860BC. Conversely, the slight fall in

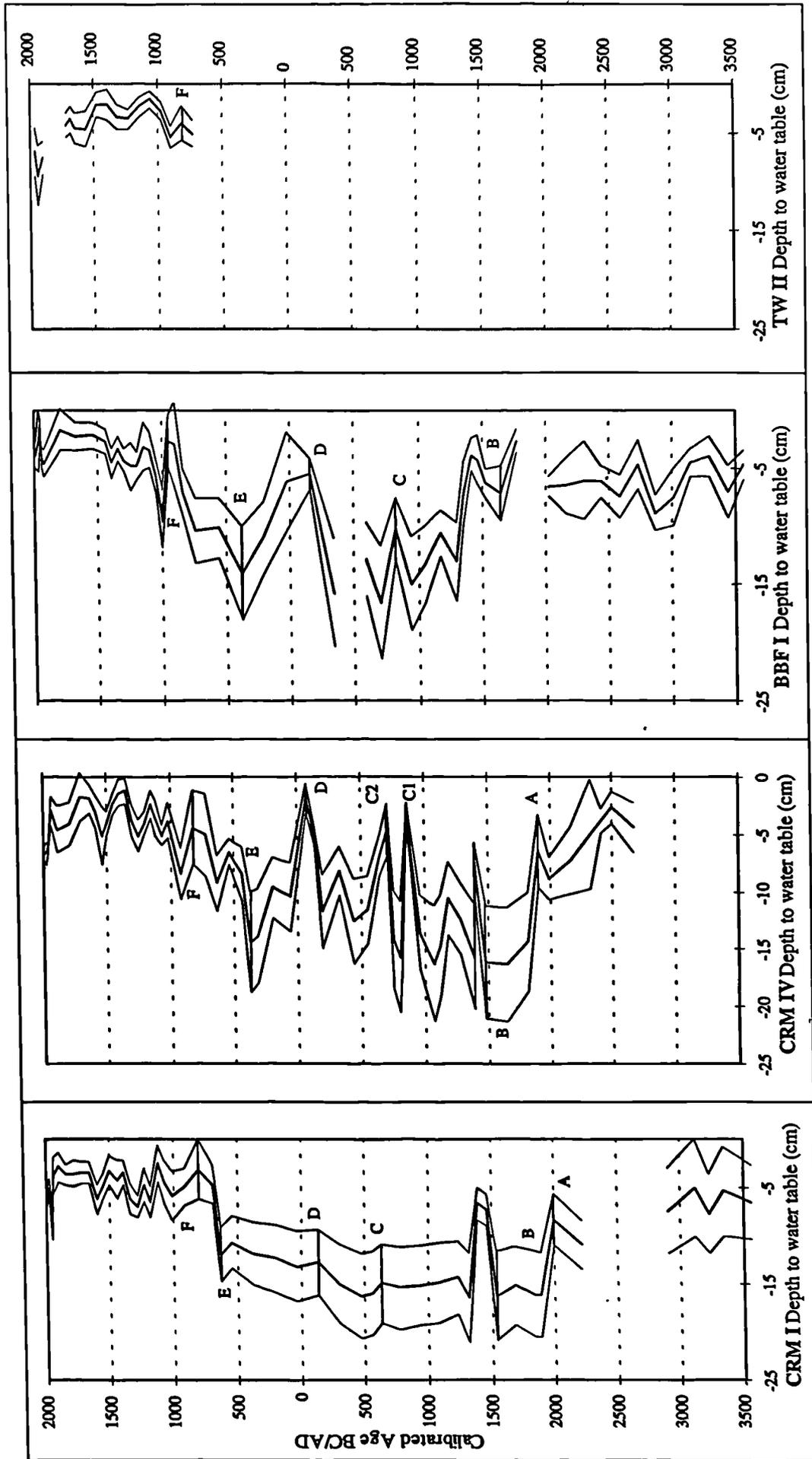


Figure 9.10 Macro-scale water tables 3500BC to present

water table in CRM I has a better match with C₂ in CRM IV at *ca.* 640BC. To improve the match of this dry shift in these cores, a more closely spaced sampling interval would need to be adopted. CRM I has a much more stable mean water table level, although the confidence intervals of all three cores overlap.

Point D marks a fall in the water table level after a significant wet shift. The age ranges of this event show a good degree of overlap, although the median ages of the dry shift are not the same (CRM I 336-15BC: CRM IV 151BC-144AD: BBF I 369BC-152AD). CRM IV has the greatest magnitude shift, as the water table drops by 8cm. The confidence intervals of CRM IV and BBF I overlap at this point, but CRM I has a significantly lower water table level, where there is no overlap in confidence intervals with the other cores at the macro-scale. This fall in water table, although present in CRM I, is not as significant and this may suggest that this is either not a climatically forced hydrological signal, or that there was a local factor overriding a climatic signal at CRM I. Section 9.2 discussed the possibility of CRM I being a less sensitive location during this period, *e.g.* a hummock feature, which is borne out by this scale of comparison. If a shift is replicated across two sites, it suggests that it is local factors which are affecting the surface wetness at CRM I.

Between 0-500AD the confidence intervals of the three cores overlap, although the mean water table level of CRM I shows a slight rise, while cores CRM IV and BBF I both exhibit a drop in the depth to water table.

From 500AD to the present, the water tables for all four cores are presented separately in Figure 9.11, in order to compare the more detailed hydrological record of the historical period at a larger scale. Point E emphasises a marked increase in mire surface wetness. The wet shift is synchronous in CRM IV and BBF I and is of similar magnitude, occurring at 386-387AD in both cores, with a rise in water table level from -14cm to -9/-10cm in CRM IV and BBF I respectively. The wet shift occurs slightly later in CRM I. The size of the shift is between -12cm to -5cm in all cores.

The water table record for TW II begins at 736AD. At 818AD, there is a slight fall in water table level in TW II which corresponds to falls in water table level in the three other cores, at 805AD in CRM I, 826AD in CRM IV and 956AD in BBF I. This is marked as point F in Figure 9.11. The age ranges of this event show a good degree of

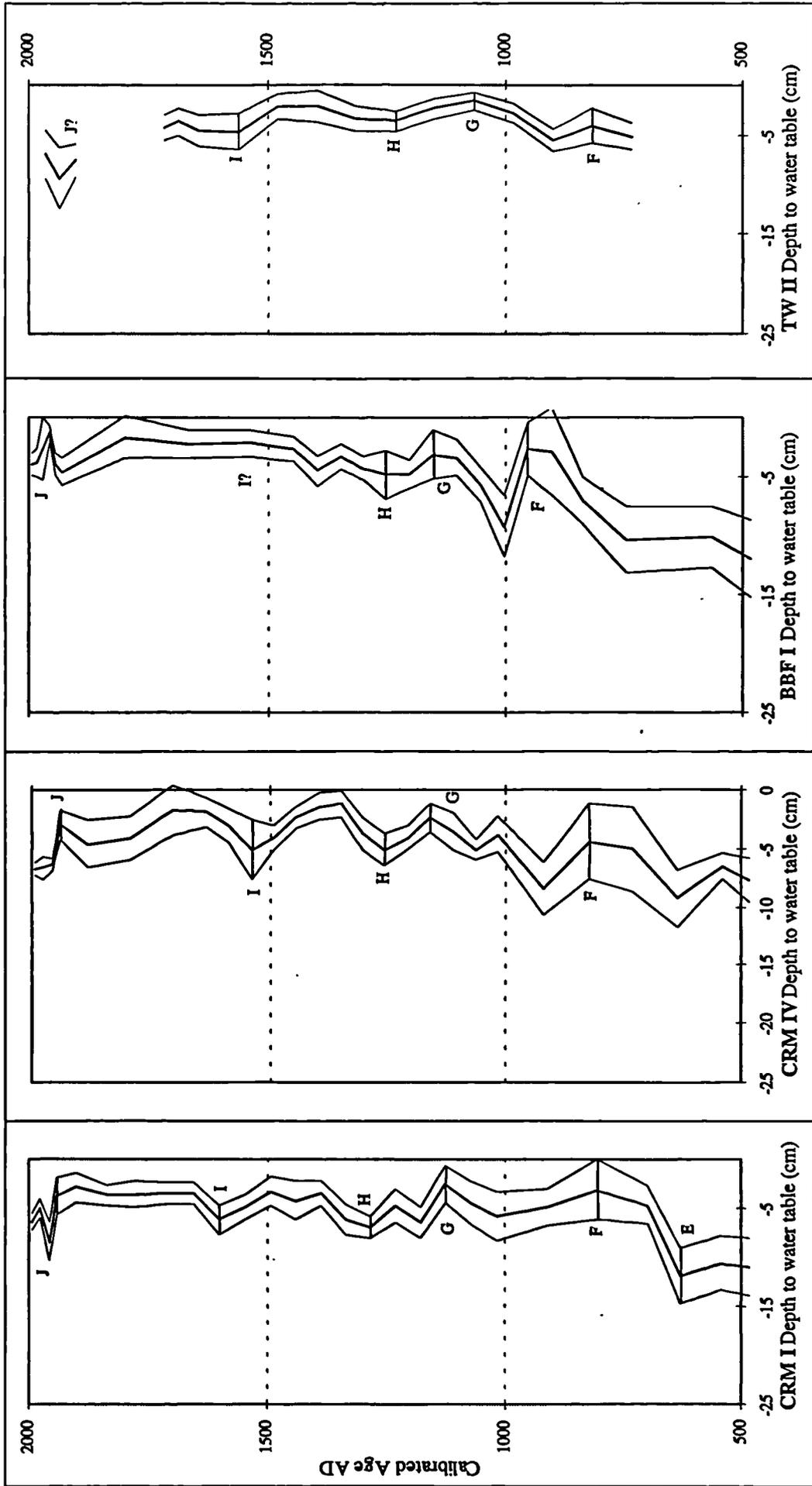


Figure 9.11 Macro-scale water tables 500AD to present

overlap. The shifts are of similar magnitude in CRM IV and BBF I, falling from -4.4cm to -8.5cm and -2.7cm to -9.2cm respectively. Cores CRM I and TW II also have similar magnitudes of drop, from -3.1cm to -4.9cm in CRM I and from -4.0cm to -5.4cm in TW II.

Point G marks the initiation of a dry shift found in all four cores. The median age for this event occurs slightly earlier in TW II (1066AD) and later in the other cores - at 1123AD in CRM I, 1159AD in CRM IV and 1152AD in BBF I. The age ranges of this dry shift overlap. The magnitude of change is between 2-2.5cm in CRM I, CRM IV and BBF I and <1cm in TW II, but the confidence intervals of the water tables overlap in all four cores.

H marks the low water table point prior to a slight wet shift. Point H has a median age between 1231AD (TW II) to 1299AD (BBF I) and the age ranges of this event in all cores show a good degree of overlap. The rise in water table is of the same magnitude in BBF I and TW II, from -4cm to -3cm and is larger in CRM I (-7cm to -3cm) and CRM IV (-5cm to -1cm). However, the confidence intervals for this event also overlap in all four cores.

At *ca.* 1560AD, there is a low in water table level prior to a wet shift in CRM I, CRM IV and TW II (Point I). BBF I does not show a drop in water table level at this point. Point I occurs at 1602AD in CRM I, which is a median age approximately 50 years later than in CRM IV (1540AD) and TW II (1561AD). A similar wet shift occurs earlier in BBF I, with a median samples age of 1250AD (age range 1343-1404). Because the age ranges overlap, it may be regarded as a synchronous event, which may be pin-pointed more precisely with a closer sampling interval in BBF I and a more precise chronology.

There is a relative drop in water table levels in the 20th century (Point J). In the mid-1950s, the water table level of cores CRM I, CRM IV and TW II all fall, whilst concurrently, the water table level of BBF I rises. This is due to the fall being based only a single sample. There is no surface sample for TW II, due to sampling difficulties, so it is not possible to comment on the relative wetness of the present mire surface at The Wou.

9.6 Between-site variability

Climate is the only factor that can reasonably explain synchronous shifts in water tables at this scale of study. Major climatic shifts are evident in all three sites showing a high level of synchronicity in the timing of events and in the confidence intervals of the water table reconstructions. The macro-scale comparison leads to the construction of guidelines for the identification of climatically forced shifts. The directional shifts must be of a similar magnitude, timing and rate of change and this should be replicated in at least three cores from at least two sites. Replication is required from more than one site, because if the shift is found in multiple cores, but only from within one site, it may be internal autogenic factors that are dominating the hydrological signal. More than one core is needed from at least one of the sites for the same reason. However, because it is possible to core in insensitive locations such as CRM I, two cores from two sites may also be acceptable for distinguishing a climatic signal. The wet and dry shifts found at the macro-scale are tabulated in Table 9.4.

CORE	<	>	<	<	>	<	<	>	>	<
	A	B	C	D	E	F	G	H	I	J
CRM I	+	+	x	x	+	+	+	+	+	+
CRM IV	+	+	+	+	+	+	+	+	+	+
BBF I		+	+	+	+	+	+	+	+	+
TW II						+	+	+	+	+

Table 9.4 Presence of wet and dry shifts in the macro-scale core comparisons, x indicates very minor shifts, > indicates wet shift and < indicates dry shifts

Using these criteria for establishing climatically induced shifts it is possible to distinguish climatic shifts at the macro-scale. Point A cannot be regarded as climatic from the available data, since it is only evident in CRM I and CRM IV. It is unfortunate that the sample for BBF I at this time (*ca.* 2000BC) had a concentration which was too low to count. At 1500BC the rise in water table at point B appears to be climatically induced since it occurs in CRM I and CRM IV and in BBF I. The rise in water table may be attributable to increased precipitation and/or reduced evapo-transpiration.

Core TW II from the valley mire, shows a surprising degree of similarity with CRM IV and BBF I. The fact that change is registered at all is remarkable and suggests that climate is an important influence even for valley mires. Generally, the hydrological record from The Wou shows less sensitivity to hydrological fluctuations than the records derived from the ombrotrophic mires. The major changes that are found synchronously in CRM I, CRM IV and BBF I and that are therefore likely to be climatically forced, are found in TW II, but the water table model derived from the valley mire is less sensitive to smaller scale fluctuations. This is probably related to the morphology of the site, because, as a valley mire, water collects along the long axis of the mire from the surrounding catchment and this will mask all but the largest and most dramatic climatic fluctuations. The ombrotrophic mires, receiving inputs mainly from precipitation have a greater level of sensitivity to hydrological change. Whilst it is therefore possible to derive a climatic signal from a valley mire, The Wou is not a sensitive site and comparisons with the other sites are essential to determine whether small magnitude fluctuations in the hydrological signal are likely to be related to climate. Because water is derived from the valley catchment, an excessively dry period must be needed for a dry shift to register in the proxy climatic record. However, there is a better match with the taxa included in the transfer function (Figure 7.2) than the assemblages from Coom Rigg Moss or Butterburn Flow, so it is possible that the smoother hydrological curve is a better representation of events. More work is needed to evaluate this.

Ombrotrophic mires also develop as a result of allogenic inputs, principally climate, as raised mires and the shedding parts of blanket mires are locations where the peat profile is most closely linked to the balance between precipitation and evaporation, rather than other site characteristics. The topography of a mire will affect the nature and strength of vegetation and testate amoebae response to climate change, as it affects the retention of impacting water. It is possible to distinguish between water-shedding and water collecting sites, situated in convex or concave regions of the blanket mire system respectively (Tallis, 1994, 1995). Barber (1981) falsified earlier concepts of autogenic cyclic changes in peatlands by showing that from macrofossil studies, surface wetness patterns occur over entire strata. It may be that autogenic factors are more important in boreal regions with an excess of moisture (Barber, 1994) and it may be that the allogenic and autogenic mires are necessarily mutually exclusive. Barber (1981, 1994) demonstrated the strength of allogenic forcing at Bolton Fell Moss and interpreted pools as hydroclimatic features responding to climatic variations. He considered the relative

area of hummocks and pools on the mire surface to be climatically controlled. In dry periods the relative area of hummocks increases and in moister periods pools form and expand.

Comparing the water table records for Coom Rigg Moss and Butterburn Flow from 500BC to the present, the period for which there is the greatest overlap, it shows that the BBF cores have a much less variable record of fluctuation. The less sensitive record at Butterburn Flow is probably related to sample spacing, because the major trends are similar, but the same depth of peat covers a longer period of accumulation. More closely spaced samples are required to generate a similar degree of sensitivity to shifts in water table level.

9.7 Climate and peatland surface wetness

An allogenic hydrological signal should result in a shift in water table simultaneously across the mire surface in response to broad scale climate change. Autogenic influences would result in more localised hydrological changes in response to crossing critical thresholds of mire growth and expansion. The separation of these signals is central to this study. There is a remarkably good match between the water table records both within and between sites. The possible reasons for these similarities and for the differences, will be discussed in this section.

The horizons that are regarded as climatically forced were discussed in Section 9.5, the macro-scale comparison. Several of the marked horizons identified in the water table records can be compared to published information about climatic events. The three main periods for which there is relevant information are the Dark Ages climatic deterioration at *ca.* 600AD (point E), the Medieval Warm Period (point F) and The Little Ice Age, which began 1400-1500AD (point I). This section compares data from all of the water table curves.

9.7.1 Mire surface wetness before 500AD

Figure 9.12 presents the humification curve from a single core from Talla Moss, an ombrotrophic blanket mire in Scotland (Chambers *et al.*, 1997). This spans the period 3500BC to 1950AD and is equivalent to the time period of the macro-scale comparison

of water table records shown in Figure 9.10. Chambers *et al.* (1997) identified four main wet shifts from these data at *ca.* 3455BP (1405BC), *ca.* 2600BP (550BC), *ca.* 1930BP (20AD) and *ca.* 1095BP (855AD). Another wet shift was identified as commencing at *ca.* 540BP. These inferred wet shifts are marked on Figure 9.12. Climatic inferences were based upon comparison of the humification data with the pollen record and the only wet shift for which climate was thought to be at least partly responsible is at 1070AD. It is not clear how this shift was assigned a climatic influence, when the data are not compared to other mires in the same region. The use of humification data to infer climate means that a relative scale of wetness is derived that is semi-quantitative. It is not clear whether the percentage humification scale implies uniform size shifts in wetness and if it does, what these shifts are. There are no confidence limits generated on humification data, which makes comparisons with other similar data difficult. Humification data from only one core are presented, because of this, it is impossible to determine whether all of the shifts are related to external forcing, or whether the changes in mire surface wetness are related to autogenic mechanisms. Talla Moss is located approximately 60-80km to the north of the field sites used in this study and by comparison to the water table curves from the macro-scale study, it is possible to identify climatically determined shifts in mire surface wetness.

Figure 9.13 shows a wetness curve derived from *Sphagnum* macrofossil analyses from Bolton Fell Moss (Barber *et al.*, 1994a), a Cumbrian peatland within *ca.* 20km of the field sites used in this study. This curve spans a similar period to macro-scale water table curves (Figure 9.10) and the Talla Moss humification data (Figure 9.12). This is an oscillating curve, which is similar in many respects to CRM IV. It does however, have the same limitations as the humification data, in that there are no confidence intervals on the curve and the mire surface wetness is not quantified. Shifts A to F can, nevertheless, be identified in this record and are marked on Figure 9.13.

At approximately 2000BC (4000BP), the water table curves from CRM I and CRM IV show a significant fall in water table level. The humification curve from Talla Moss and the curve derived from *Sphagnum* macrofossils from Bolton Fell Moss both suggest decreased surface wetness at point A. Point B marks a significant wet shift at approximately 1500BC, although this occurs slightly earlier in the macrofossil record. Point C, at *ca.* 700BC represents a distinct dry shift, which is similar in timing in each proxy-hydrological record. At the BC/AD boundary, there is a fall in mire surface

wetness in CRM I, CRM IV and BBF I (Point D). The trend at Talla Moss and at Bolton Fell Moss is similar to this. Point E is also evident at Bolton Fell Moss and Talla Moss at *ca.* 600AD, marking the increased surface wetness of the Dark Ages climatic deterioration (Section 9.7.2).

Thus, whilst some of the shifts indicated by the humification data are seen in the testate amoebae data and may be related to climate, only one of the shifts identified by Chambers *et al.* (1997) as climatic is replicated in the water table curves. This is shift B, at *ca.* 1500BC (1405BC in the humification data). Whilst no one shift is specifically identified by Barber *et al.* (1994a) as climatic, they assumed that the record held a climatic signal. By comparison of these data to the multiple water table curves from Coom Rigg Moss and Butterburn Flow and the humification analyses from Talla Moss, the *Sphagnum* macrofossil record can be seen to contain a regional climatic signal. It is only by comparison to these other data that this is apparent. There is no means of comparing the magnitude of the changes in mire surface wetness as this is not quantified in either the humification or macrofossil data.

The water table records (Figure 9.10), *Sphagnum* macrofossil data (Barber *et al.*, 1994a) and humification data (Chambers *et al.*, 1997), all therefore show similar trends of increasing wetness throughout The Holocene, probably reflecting the late Holocene climatic deterioration (Barber, 1985).

9.7.2 Dark Age deterioration

At *ca.* 600AD (CRM I: 629AD; CRM II: 565AD, CRM III: 762AD; CRM IV: 636AD; BBF I: 567; BBF II: 643; BBF III: 537AD) there is a wet shift in all cores (Point E). The ages of this event overlap well and the direction and rate of change are similar in all profiles. The magnitude of change varies in the cores, the largest shift (12cm) occurs in CRM II, a marginal core and the smallest rise occurs in BBF II, also a marginal core. The small shift in BBF II may be related to the initial low water table, which rose from -17cm to -15cm. Other cores experienced mean shifts of between 3-7cm.

This wet shift coincides with the Dark Ages climatic deterioration (*ca.* 1,400BP/600AD) as identified in humification analyses of five sites by Blackford and Chambers (1991).

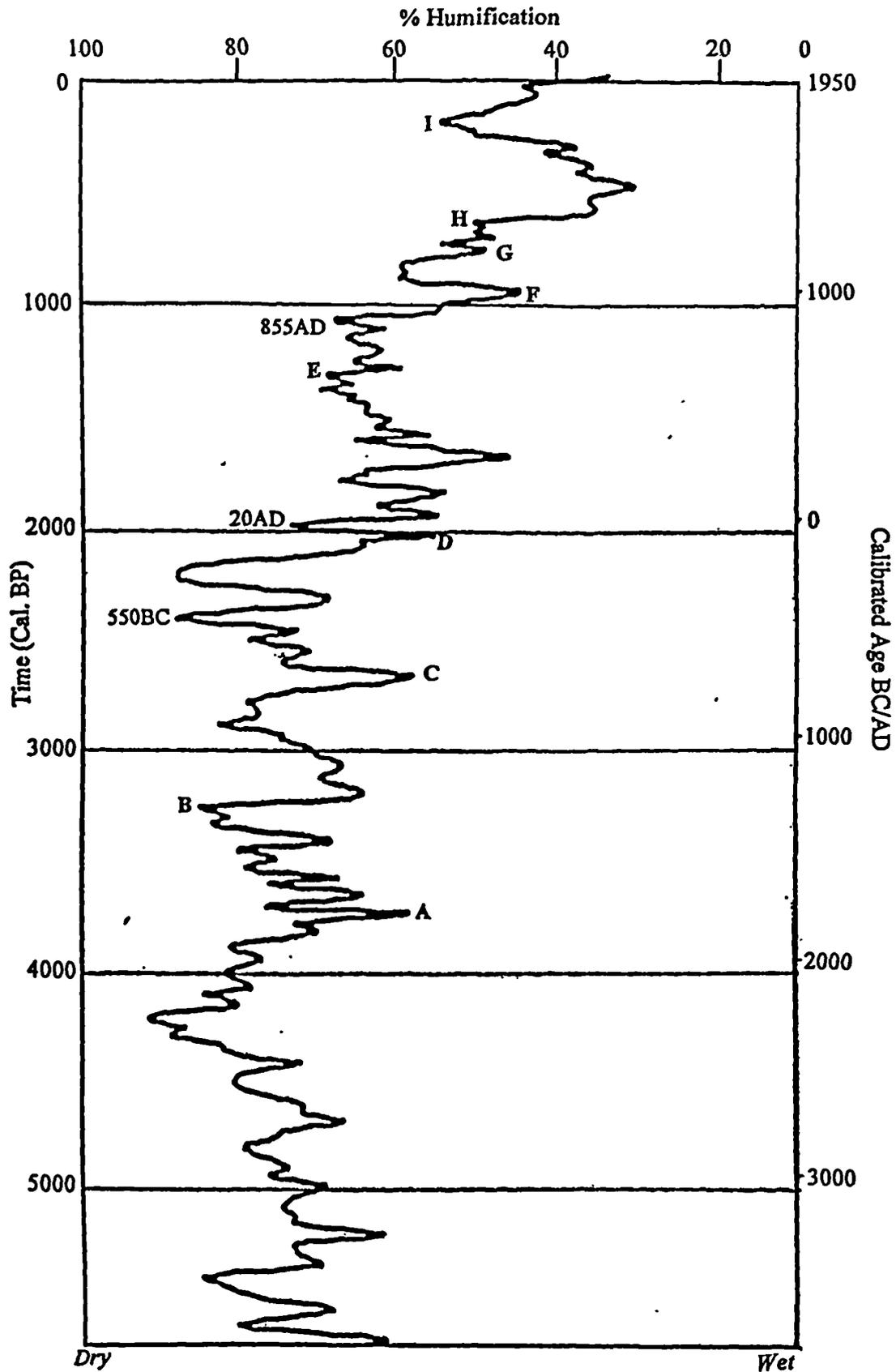


Figure 9.12 Humification analyses from Talla Moss (modified from Chambers *et al.*, 1997), with macro-scale water table shifts marked (Table 9.4)

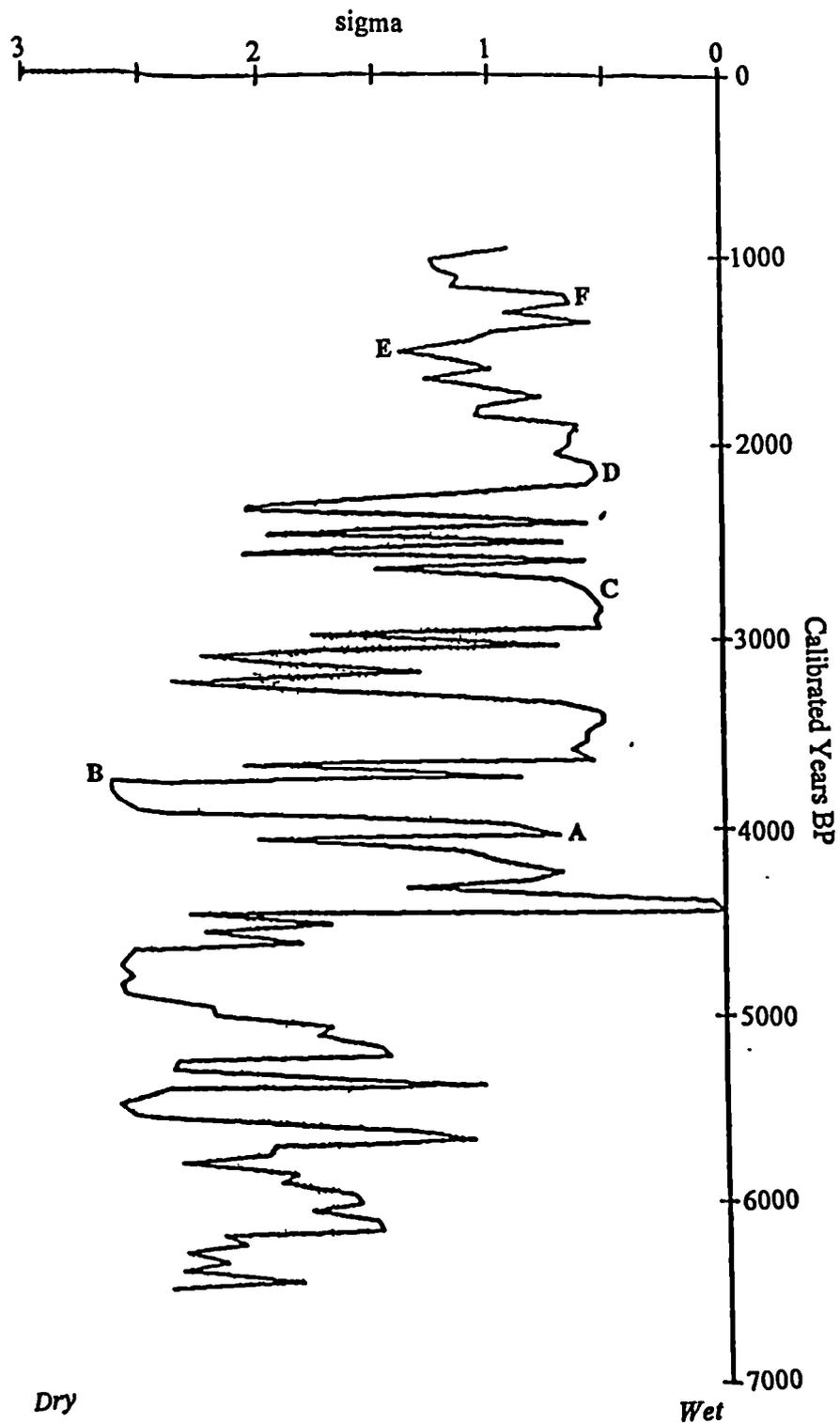


Figure 9.13 Surface wetness curve derived from *Sphagnum* macrofossil analysis from Bolton Fell Moss (Barber *et al.*, 1994a) Macro-scale shifts marked (as Table 9.4)

They could not determine from humification analyses whether the major influence on climatic deterioration was the result of short-lived climatic cooling or more prolonged wetness. This wet shift can also be identified in the humification analyses from Talla Moss (Chambers *et al.*, 1997) (Section 9.7.1). Barber (1985) also found an abrupt peak in surface wetness at Bolton Fell Moss at 1400BP from *Sphagnum* macrofossil analysis. Lamb (1977, 1995) points to documentary evidence that supports the idea of a climatic deterioration in the mid-first millennium AD. This appears to be a major climatic shift, replicated in a number of sites across the British Isles and identified using a variety of palaeoecological techniques.

9.7.3 The Medieval Warm Period

The Medieval Warm Period (MWP), or Little Climatic Optimum (1000-1200AD, Lamb, 1965; 700-1300AD, Barber *et al.*, 1994b; 900-1200AD, Mayes and Wheeler, 1997) was, according to Barber *et al.* (1994b), a period of drier conditions in upland Britain, that is reflected in surface wetness curves from peat bogs derived from *Sphagnum* macrofossil analyses. Point F (Figure 9.11) correlates with the MWP, as all of the cores show a fall in water table level at approximately this time. The water table level over this period is variable and significantly higher than the previous three millennia.

According to Mayes and Wheeler (1997), the MWP is a period for which climatic information is scarce. Blackford and Chambers (1995) present evidence for solar forcing of climatic variability for the MWP and LIA from humification analyses of blanket peats from western Ireland. They suggest that periods of reduced peat decomposition, indicative of cooler or wetter climatic conditions, coincide with periods of reduced sunspot activity and atmospheric ^{14}C anomalies. This adds to the argument that the shifts during the MWP and Little Ice Age evident in the cores were climatically forced.

9.7.4 Little Ice Age

The Little Ice Age (LIA) refers to a period of cooler climatic conditions between the Middle Ages and the warm period of the late 19th - early 20th centuries (Grove, 1988). The exact beginning and end of this event are uncertain, because, as for the MWP, the dates given for the LIA vary from author to author (1550-1800, with a main phase

between 1550-1700 Lamb, 1977; 1250-1920 Porter, 1986; main phase 1570-1730, Bradley and Jones, 1993). Lamb (1995) suggests that the entire period of the LIA may span from 1420, or even 1190 up to 1850 or 1900. It is therefore difficult to define this period. Here, the LIA is taken to begin between 1400-1500 and extends to the end of the 19th century.

The term 'Little Ice Age' is considered to be a misnomer by many (*e.g.*, Grove, 1988), since lower temperatures were not experienced globally and is considered by some to have been insignificant in scale. Bradley and Jones (1993, 1995) suggest that the term LIA be used cautiously since the past 500 years was a period of complex climatic anomalies, where both warm and cold periods were experienced that varied in importance geographically. They showed that this was not one continuous period at all. The period from 1550-1800 is characterised as a time of climatic variability, ranging from severe winters to spells of warm and sunny weather in the summer, but where storms were prevalent (Mayes and Wheeler, 1997). These factors suggest that real evidence for a distinct climatic period is sparse and that the climate of the past 500 years or so was more complex than the term 'Little Ice Age' implies.

The wetter and/or cooler climate of the LIA found in the peat humification record by Blackford and Chambers (1991, 1995), are reflected in high water table levels in the reconstructions and are marked as Point I in Figures 9.3, 9.7 and 9.10. The wetter and/or cooler period between 1660-1720, identified by Blackford and Chambers (1995), may correspond by the low water table point at I. The water table level remains above 5cm depth throughout this period and continues until the early twentieth century. Barber (1982) in study of Bolton Fell Moss from peat stratigraphy, found catastrophic decline into the LIA, with virtual extinction of *Sphagnum imbricatum*. At Bolton Fell Moss, the LIA is reflected in a peak of *Sphagna* that inhabit wetter niches (Barber *et al.*, 1994c).

Bradley and Jones (1993) present records of summer temperature for the LIA from a composite instrumental record. The summer temperatures for central England based on instrumental records (Manley, 1959, 1974) and the composite temperature series for Europe are presented in Figure 9.13. The 19th century was the coolest of past 200-300 years, with the 18th century warmer than 19th century. From composite European record, temperatures were below average from the 1570s to 1690s, were warmer in 18th century

but fell again in 19th century. It is difficult to separate the cool or warm episodes of the LIA identified by Bradley and Jones (1995) or Mayes and Wheeler (1997) with this resolution (5cm sampling intervals) of testate amoebae record, as the fluctuations experienced during the LIA were short-lived perturbations in effective precipitation. However, a hydrological reconstruction based on contiguous 1cm, or higher resolution testate amoebae samples might give a decadal or bi-decadal record of sufficient resolution to determine whether these events can be separated from the overall signal of increased surface wetness derived from independent records of climate change. The wet shift at point I and the dry shift at point J can be seen on the composite European record.

Comparison of Figure 9.14 with the water table records (Figure 9.11) shows however, a rise in summer temperature in both the central England record and the composite record for Europe in the early 1900s. This is supported by Briffa *et al.* (1994) who developed the Monthly Palmer Drought Severity Indices (PDSI) 1892-1991 for Europe and south east Asia. Prior to this, there was a lack of long-term analysis of moisture availability across Europe. The PDSI is based on a simple water balance and considers both moisture supply and demand and is derived using precipitation, evapotranspiration and soil water status. The PDSI show that the 1930s and 1940s were exceptionally dry and that 1943-1952 was the driest decade for which they have data. These data support the theory that the fall in water table at point J (Q for meso-scale comparison of BBF cores) was climatically forced, but it may also have been exacerbated by afforestation in the Kielder Forest area.

9.8 Testate amoebae and palaeohydrological reconstructions on peatlands

In the light of the main findings of this study, discussion of testate amoebae as palaeohydrological indicators can be divided into two main themes - problems and potential. One of the major problems encountered during this study was the lack of adequate modern analogues for xerophilous taxa - those at the drier end of the scale of wetness. The reasons for this were discussed in detail in Section 8.2, but it means that water table reconstructions below *ca.* 500AD, which are dominated by poor or no analogue fauna, do not have as robust reconstructions as the water tables above 500AD.

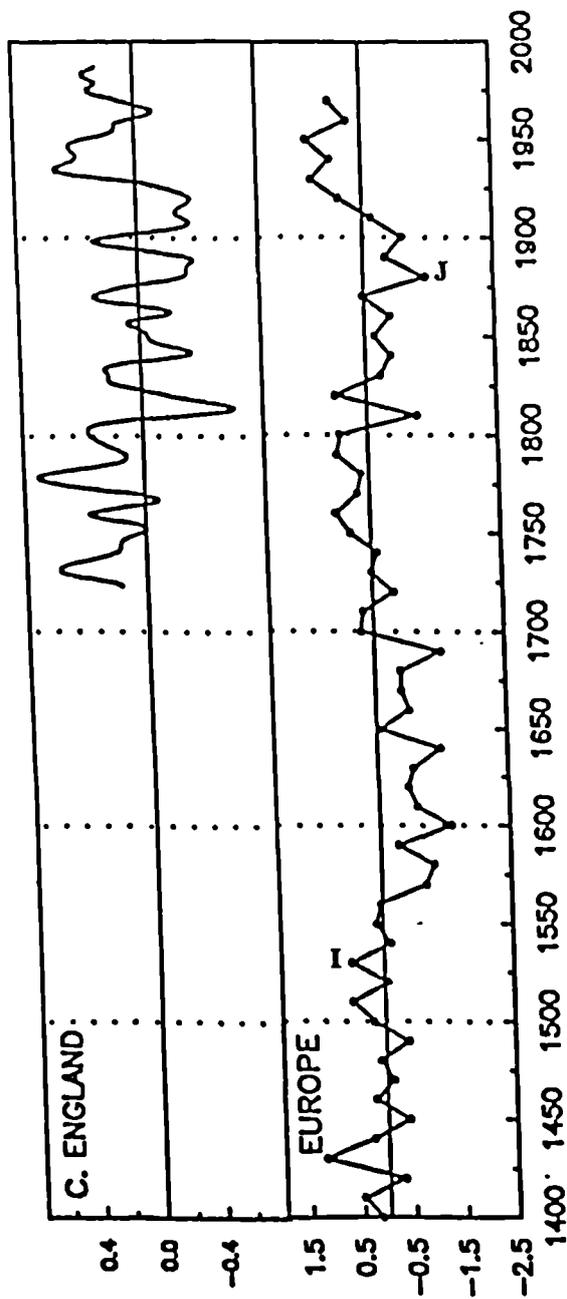


Figure 9.14 Composite summer temperature records for Central England and Europe (modified from Bradley and Jones, 1995) with macro-scale shifts marked (Table 9.4)

The sampling intervals adopted in this study were every 5cm in the top metre and around the sampling points for radiocarbon dates and every 10cm below one metre peat depth. This results in at least 100 years between samples at >1m depth.

This sampling interval was adequate in order to fulfil the aims of this study, but provides only general indications of the trends in water table shifts. More closely spaced, ideally contiguous, sampling would reduce the time period between samples and should more accurately locate the exact beginning and end of shifts and ensure that the entire magnitude of shift is reconstructed. This is especially important for comparing the water table models of the past 1500 years to documentary evidence and independent instrumental records so that fluctuations occurring over a small time-scale are picked up. Higher resolution (*i.e.* <1cm samples) would increase the precision of the water table curves, but this may not always be possible. The quality of the data obtained must be balanced against the time taken to count the samples.

The water table reconstructions are plotted as fractions of centimetres. There is a need for a method of discussing minor shifts without being spuriously precise, as the actual water table level may fall within the range indicated by the bootstrapped error estimates.

The taxonomic problems encountered in this study, resulting from inconsistencies in species description and lack of clarity in the literature have been addressed by the development of a dichotomous key to identification and comprehensive descriptions of taxa found in British oligotrophic peatlands by Charman, Hendon and Woodland (in prep.).

The potential for testate amoebae analysis and palaeohydrological reconstructions will improve once the problems discussed above have been addressed. Testate amoebae analysis has the advantage over other techniques for palaeohydrological reconstructions of mire surface wetness, such as humification analysis and *Sphagnum* macrofossil analysis, in that it is fully quantifiable (currently within the limits of the transfer function). The use of bootstrapped error estimates for 95% confidence intervals means that multiple cores can be compared within the potential range of water table calculated from the optima and tolerances of the taxa contained within each assemblage. The accuracy of these reconstructions may only be fully realised once detailed water table

records for the past 1500 years have been compared to documentary evidence and independent climatic records.

9.9 Implications for palaeoclimatic studies on peatlands

Assessment of the utility of testate amoebae analysis as a proxy climatic indicator was central to the aims of this study. Testate amoebae analysis from a single core can only be regarded as a palaeohydrological signal, *i.e.* a record of past depth to water table from the particular location that the core was extracted. For a palaeoclimatic signal to be derived from testate amoebae analysis there is a need for multiple cores, from multiple sites (Section 9.5) and, for the identification of shifts which are allogenic rather than a result of internal mire processes. This premise applies equally to other proxy climatic indicators.

Future palaeoclimatic reconstructions will therefore require a different approach from that adopted previously and the research described here calls into question the validity of some previous work. Climatic inferences based upon the data from a single core from a single site must be questioned, since there is nothing to compare the record against in order to distinguish fluctuations resulting from autogenic factors from allogenic factors.

Barber (1994) and Barber *et al.* (1994b) regard the layered stratigraphy of moderate relief of many Atlantic bogs or 'flat' stratigraphy, to be more useful and sensitive for climatic reconstruction than a stratigraphy dominated by climatically insensitive hummocks. All of the cores used in this study were extracted from flat locations with no obvious microtopographic features. Cores CRM I and BBF II illustrate well that locations that have had stable or insensitive hydrological records in the past may have much more sensitive records in recent peats. This suggests that it is impossible to tell from the surface what the nature of the record will be at depth. The selection of 'sensitive' sites on the basis of microtopography is likely to be unreliable. Hummocks are shifting features, so it is possible that the mid point between hummock and hollow may provide the best record of climate, as shifts in the expansion and contraction of the hummocks are likely to register there.

9.10 Conclusions

- Water tables derived from testate amoebae analysis are quantitative records of mire palaeohydrology. The 95% confidence intervals on both the chronology and mean water table enable comparisons between the cores to be made within the potential water table and age ranges.
- The comparisons at the micro-scale between CRM I and CRM IV and the interpretation of those records suggest that microtopography is a major influence on the hydrological records at this scale. A marginal position between hummock and hollow may register small-scale fluctuations in mire surface wetness in more detail than an insensitive hummock location. It is not possible to determine from contemporary mire surfaces whether the peat record beneath is a sensitive record or not. This emphasises the need for multiple cores from one mire to take into account the potential for recovering a record from an insensitive location.
- There is a good degree of replicability at the meso-scale from both Coom Rigg Moss and Butterburn Flow. However, the marginal locations generally have lower water tables than in the centre of the mire.
- The water table records show a remarkable degree of replicability both within individual sites and across the region. Major fluctuations are found in all four central cores indicating that some shifts may be climatically forced in origin. In order to determine whether the palaeohydrological records can be interpreted as palaeoclimatic records, at least three cores are required from at least two sites. This is to ensure that shifts resulting from autogenic influences can be separated from the replicable climatic signals. The Wou, the valley mire, has a surprisingly sensitive palaeohydrological record and the fluctuations, although minor, are replicated at the other sites.
- There is a good match between shifts in the depth to water table found in this study compared with the changes in mire surface wetness indicated by the *Sphagnum* macrofossil record from Bolton Fell Moss (Barber *et al.*, 1994a) and the humification data from Talla Moss (Chambers *et al.*, 1997). This suggests that climatic inferences can be made from these data when multiple records are compared.
- From *ca.* 500AD, the water table records are more robust than prior to 500AD, as there is a better match between the faunal assemblages in the transfer function and the

fossil data. This is comparable to the period for which there is independent documentary and instrumental data. Three main climatic events can be seen in the water table data; the Dark Ages climatic deterioration, the Medieval Warm Period and the Little Ice Age. In addition to this, comparisons with published data from other proxy-hydrological studies suggest that shifts similar to those found in this study can also be found in these data.

CHAPTER TEN

Conclusions and future work

10.0 Introduction

This chapter aims to synthesise the data presented in this thesis and is divided into two sections. The first section summarises the main conclusions of this research in the context of the original aims. These conclusions are divided into methodological issues and peatland hydrology and climate reconstructions. The second section discusses the potential for future work that has arisen out of this study.

10.1 Original aims

The overall aim of this research was to establish the usefulness of testate amoebae analysis as a palaeohydrological and palaeoclimatic technique by:

- 1) assessing the replicability of the testate amoebae record within and between mires;
- 2) testing the robustness and precision of percentage moisture and depth to water table reconstructions produced from testate amoebae analysis of Holocene ombrotrophic peatlands;
- 3) separating autogenically and allogenicly forced hydrological signals, in order to assess the influence of climatic change on peatlands.

10.2 Methodological issues

- In order to establish whether testate amoebae analysis could be a useful palaeoclimatic indicator, the best possible preparation technique had to be utilised so that the fossil data set was not impaired by the quality of the microscope slides. The addition of a 15 μ m mesh to back-sieve samples to the standard procedure removed fine fraction detritus (Hendon and Charman, 1997). It is possible that reduction of sieve size to 200 μ m mesh, rather than the 300 μ m sieve that was used in this study would improve slide quality further. Mesh size should be constantly reviewed depending upon the environment and the type of material that testate samples are collected from. The routine use of a small mesh sieve could result in the loss of larger tests which would cause bias in the data set.

- The percentage moisture transfer function was of limited use, since wider confidence intervals were calculated than for the water table reconstructions. This is attributed to the calibration being based on single-shot data, rather than mean annual data (Woodland, 1996; Woodland *et al.*, 1998). The depth to water table transfer function was more robust than the moisture transfer function because it contains a larger number of samples and taxa.
- The training set provided better analogue values for wet taxa than for drier taxa. This was because the sites sampled to develop the transfer function were all wet areas of undamaged extreme oceanic mire (Woodland, 1996; Woodland *et al.*, 1998). The potential full hydrological range of mires was not sampled and hence, seven taxa in the fossil data set had no analogue values and two of the dominant taxa had poor analogue values. It is likely that these taxa do have modern analogues, as specimens were found in the surface samples of cores in this study, albeit in small amounts. The lack of good modern analogues nevertheless affected the robustness of the water table reconstructions, where no- and poor-analogue taxa dominated the faunal assemblages.
- The current inadequate state of the taxonomy has developed from various workers either over-splitting or grouping together taxa and this leads to confusion. A dichotomous key developed by Charman, Hendon and Woodland (in prep.), has addressed the main taxonomic problems encountered during this study and should result in a clarified taxonomy that is consistent between workers. This key will undoubtedly be subject to change if an increased diversity of taxa are found from a wider range of mires. It is recommended that in future work, the original authorities of taxa and any necessary notes on differentiating features are given to avoid any ambiguity.
- The palaeohydrological record derived from testate amoebae analysis provides a quantified value of the depth to water table and estimated error ages. The generation of 95% confidence intervals from bootstrapping provides a useful means of comparing water tables within a possible range of water table depths. Wet and dry shifts can be identified in the water table records and are defined as directional changes of varying magnitudes. Dates are assigned at the point where the direction of change begins. Because of the sample spacing adopted in this study, it is unlikely

that the entire shifts *i.e.* extreme low point and extreme high point, have been picked up.

10.3 Peatland hydrology and climate reconstruction

- The micro-scale study showed that major patterns in the water table records from two centrally located cores were broadly replicable. Variations in the water table records were attributed mainly to microtopographic differences. One core appeared to have been the location of a complacent hummock over much of the period of accumulation. The other core appeared to have been located at the mid-point between hummock and hollow and provided a more sensitive record of mire surface wetness as this feature shifted.
- Within-mire studies at the meso-scale showed a good degree of similarity in the water table records. The marginal cores tended to have lower water tables than the central cores, but the patterns of change were similar across the mire surfaces. At Butterburn Flow, the record was not as sensitive as it was at Coom Rigg Moss. This was attributed largely to sample spacing, because where a shallow depth of peat had accumulated over a long period, subtle changes were not picked up in this study. From this scale of study, it was not possible to ascertain what caused wet or dry shifts. Possible autogenic mechanisms can be postulated, such as impeded drainage or blocked outflows for high water tables and pipeflow, runoff or outflow for low water tables. It is not possible to infer a climatic signal from cores from a single site.
- The macro-scale study was used to assess whether a palaeoclimatic signal could be derived from testate amoebae analysis. Central cores from three sites were analysed, as these normally have the longest record of peat accumulation in a mire and should be more sensitive to climatic inputs than marginally located cores. This assumes a direct coupling of precipitation to ombrotrophic mires. In order to determine that wet or dry shifts in the water table records are climatically influenced, at least three cores from at least two sites within the same geographical region are required. This is so that the allogenic hydrological signal can be separated from autogenic hydrological signals that are a result of internal bog dynamics. Climatic shifts should be of the same direction, of similar magnitude and synchronous in timing and rate of change.

In total, nine shifts fulfil the criteria of climatically induced events. These are shifts B to J (Table 9.4). Shifts in the water table records are comparable with events at the Dark Ages climatic deterioration, the Medieval Warm Period and the Little Ice Age.

10.4 Future Work

Several potential areas for future research have arisen from this study:

- The current transfer function requires modification by the inclusion of drier sites with long term hydrological monitoring programs. This should improve the training set for so called xerophilous taxa and will provide analogues for some, or all of the taxa that currently have no analogue values.
- Documentary evidence and independent records of climate change should be used to calibrate and validate water table reconstructions from testate amoebae analysis. This would help to clarify the link between mire surface wetness and climate. A multiple short-core study should be undertaken, as a climatic signal should be inferred following the guidelines set out above. The top *ca.* 1.5m covers approximately the past 1500 years, from the Dark Ages climatic deterioration to the present. This period also corresponds to the portion of water table reconstructions that have a more robust and reliable water table model, due to better analogues than for taxa found at depth in the cores. As instrumental records rarely span more than the last 150 years, a study of high resolution, contiguous samples of approximately the top 25-30cm peat would be required for a detailed enough record against which to compare the testate amoebae data to the instrumental record. A record of this nature would require ^{210}Pb dating, as recent peats are outside the range of radiocarbon dating. There is also the possibility of using tephra layers as marker horizons.
- The adoption of a multi-proxy approach using microfossils should be evaluated for palaeohydrological reconstructions. Many testate amoebae samples contain diatoms, desmids or rotifers. Samples rarely contain more than one type of additional microfossil and where test concentrations are poor, the other microfossils may provide useful hydrological information. Diatoms should be analysed that have been used as xenosomes in tests and that are valves in samples. Finding an analogue for the rotifer *Habrotrocha angusticollis* is important, since it is abundant in some

samples, although it may be found that it is not abundant in enough samples to obtain an accurate analogue. Work needs to be undertaken to establish whether it responds primarily to hydrology or some other factor. Little palaeoecological work has been undertaken on desmids from peatlands, but they may prove to be useful where testate amoebae concentrations are poor.

- A multi-proxy approach using testate amoebae analysis in conjunction with other palaeohydrological techniques will probably produce more accurate records. At present, *Sphagnum* macrofossil and humification analyses provide semi-quantitative results and, it may be possible to establish more reliable estimates of mire surface wetness than is currently derived from these techniques if they are combined with testate amoebae analysis. From a study such as this, it would also be possible to establish whether there is a relationship between *Sphagnum* species and testate amoebae. A multi-proxy record of this nature would evaluate the lag in response to climate change of different proxies. Testate amoebae probably respond more rapidly to climate change than plants, due to rapid generation times and turnover in populations. Climatic change is normally gradual and testate assemblages should eventually produce a more sensitive record of climatic change than mosses, since the faunal assemblages normally contain a greater number of species than are found in *Sphagnum* macrofossil assemblages.

References & Glossary

References

- AABY, B. (1976) Cyclic climatic variations in climate over the past 5 000 yr reflected in raised bogs. *Nature*, **263** 281-289
- AABY, B. (1986) Palaeoecological studies of mires. In: Berglund, B.E. (ed.) *Handbook of Holocene Palaeoecology and Palaeohydrology*. John Wiley & Sons Ltd. 145-164
- AABY, B. & TAUBER, H. (1975) Rates of peat formation in relation to degree of humification and local environment, as shown by studies of a raised bog in Denmark. *Boreas*, **4** 1-17
- ALMQUIST-JACOBSON, H. & FOSTER, D.R. (1995) Toward an integrated model for raised-bog development: theory and practice. *Ecology*, **76** 2503-2516
- ARAVENA, R. & WARNER, B.G. (1992) Oxygen¹⁸ composition of *Sphagnum* and micro-environmental water relations. *The Bryologist*, **95** 445-448
- ARMSTRONG, A.C. (1995) Hydrological model of peat-mound form with vertically varying hydraulic conductivity. *Earth Surface Process and Landforms*, **20** 473-477
- ARMSTRONG, A.C. (1996) Reply: peat mounds with non-uniform properties. *Earth Surface Process and Landforms*, **21** 769-711
- AUCOUR, A-M., HILLAIRE-MARCEL, C. & BONNEFILLE, R. (1996) Oxygen isotopes in cellulose from modern and Quaternary inter-tropical peatbogs: implications for palaeohydrology. *Chemical Geology*, **129** 341-359
- AUSTIN, M.P. (1990) Community theory and competition in vegetation. In: Grace, J.B. & Tilman, D. (eds.) *Perspectives in plant competition*. San Diego CA Academic Press, 215-238
- BACKÉUS, I. (1991) The cyclic regeneration of bogs - a hypothesis that became an established truth. *Striae*, **31** 33-35
- BAHNSON, H. (1968) Kolorimetriske bestemmelser af humificeringstal I højmoserov fra Fuglso Mose på Djursland. *Meddeland Dansk Geologisk Forening*, **18** 55-63
- BAILLIE, M.G.L. (1991) Suck-in and smear. Two related chronological problems for the 90s. *Journal of Theoretical Archaeology*, **2** 12-16
- BAIRD, A.J. & GAFFNEY, S.W. (1996) Discussion: 'Hydrological model of peat-mound form with vertically varying hydraulic conductivity' by A.C. Armstrong. *Earth Surface Process and Landforms*, **21** 765-767
- BALL, S. & BELL, S. (1994) *Environmental law: The law and policy relating to the protection of the environment*. 2nd Edition. Blackstone Press Ltd, London. pp469
- BARBER, K.E. (1981) *Peat stratigraphy and climatic change. A palaeoecological test of the theory of cyclic peat bog regeneration*. Balkema. Rotterdam.

- BARBER, K.E. (1982) Peat-bog stratigraphy as a proxy climate record. In: Harding, A.F (ed.) *Climatic change in later prehistory*. Edinburgh University Press. 103-113
- BARBER, K.E. (1984) A large capacity Russian-pattern sediment sampler. *Quaternary Newsletter*, 44 28-31
- BARBER, K.E. (1985) Peat stratigraphy and climatic change, some speculations. In: Tooley, M.J. & Sheail, G.M. (eds.) *The climatic scene*. George Allen & Unwin. London. pp.120-136
- BARBER, K.E. (1993) Peatlands as scientific archives of past biodiversity. *Biodiversity and Conservation*, 2 474-489
- BARBER, K.E. (1994) Deriving Holocene palaeoclimates from peat stratigraphy: some misconceptions regarding the sensitivity and continuity of the record. *Quaternary Newsletter*, 72 1-9
- BARBER, K.E., CHAMBERS, F.M., MADDY, D., STONEMAN, R. & BREW, J.S. (1994a) A sensitive high-resolution record of late Holocene climatic change from a raised bog in northern England. *The Holocene*, 4 198-205
- BARBER, K.E., CHAMBERS, F.M., DUMAYNE, L., HASLAM, C.J., MADDY, D. & STONEMAN, R.E. (1994b) Climate change and human impact in north Cumbria: peat stratigraphic and pollen evidence from Bolton Fell Moss. In: Boardman, J. & Walden, J. (eds.) *The Quaternary of Cumbria: field guide*. Quaternary Research Association, Oxford 20-54
- BARBER, K.E., CHAMBERS, F.M., & MADDY, D. (1994c) Sensitive high-resolution records of Holocene palaeoclimate from ombrotrophic bogs. *Palaeoclimate of the Last Glacial/Interglacial Cycle*. NERC Earth Sciences Directorate. 57-60
- BARTLEIN, P.J., EDWARDS, M.E., SHAFER, S.L. & BARKER, E.D. JR. (1995) Calibration of radiocarbon ages and the interpretation of palaeoenvironmental records. *Quaternary Research*, 44 417-424
- BELL, M. & WALKER, M.J.C. (1992) *Late Quaternary environmental change. Physical and human perspectives*. Longman Scientific and Technical, pp273
- BELYEA, L.R. & WARNER, B.G. (1996) Temporal scale and the accumulation of peat in a *Sphagnum* bog. *Canadian Journal of Botany*, 74 366-377
- BENNETT, K.D. (1994) Confidence intervals for age estimates and deposition times in late-Quaternary sediment sequences. *The Holocene*, 4 337-348
- BEYENS, L. (1984) A concise survey of testate amoebae analysis. *Bulletin de la Société Belge de Géologie*, 93 261-266
- BEYENS, L. (1985) On the subboreal climate of the Belgian campine as deduced from diatom and testate amoebae analysis. *Review of Palaeobotany and Palynology*, 46 9-31
- BEYENS, L. & CHARDEZ, D. (1984) Testate amoebae (Rhizopoda: Testacea) from south-west Ireland. *Archiv für Protistenkunde*, 128 109-126

- BEYENS, L. & CHARDEZ, D. (1987) Evidence from testate amoebae for changes in some local hydrological conditions between c.5000BP and c.3800BP on Edgeøya (Svalbard). *Polar Research*, **5** 165-169
- BEYENS, L. & CHARDEZ, D. (1995) An annotated list of testate amoebae observed in the Arctic between the longitudes 27°E and 168°W. *Archiv für Protistenkunde*, **146** 219-233
- BEYENS, L., CHARDEZ, D. & LANDTSHEER, DE R. (1986) Testate amoebae from moss and lichen habitats in the Arctic. *Polar Biology*, **5** 165-173
- BEYENS, L., CHARDEZ, D. & BAERE, DE D. (1991) Ecology of aquatic testate amoebae in coastal lowlands of Devon Island (Canadian High Arctic). *Archiv für Protistenkunde*, **140** 23-33
- BEYENS, L., CHARDEZ, D., BAERE, DE D. & VERBRUGGEN, C. (1995) The aquatic testate amoebae fauna of the Strømness Bay area, South Georgia. *Antarctic Science*, **7** 3-8
- BIRKS, H.J.B. (1995) Quantitative palaeoecological reconstructions, pp 161-254 In, Maddy, D. & Brew, J.S. (eds.) *Statistical modelling of Quaternary science data*. Technical Guide 5, Quaternary Research Association, Cambridge, pp271
- BIRKS, H.J.B. & BIRKS, H.H. (1980) *Quaternary palaeoecology*. Edward Arnold, London.
- BIRKS, H.J.B., LINE, J.M., JUGGINS, S., STEVENSON, A.C. & TER BRAAK, C.J.F. (1990a) Diatoms and pH reconstruction. *Philosophical Transactions of the Royal Society of London B*, **327** 263-278
- BIRKS, H.J.B., JUGGINS, S. & LINE, J.M. (1990b) Lake surface chemistry reconstructions from palaeolimnological data. In: Mason, B.J. (ed.) *The surface waters acidification programme*. Cambridge University Press, 301-313
- BLACKFORD, J.J. (1990) *Blanket mires and climate change: a palaeoecological study based on peat humification and microfossil analysis*. Unpublished Ph.D. Thesis. University of Keele.
- BLACKFORD, J.J. (1993) Peat bogs as sources of proxy climatic data: past approaches and future research. In: Chambers, F, M (ed.) *Climatic change and human impact on the landscape*. *Studies in palaeoecology and environmental archaeology*. Chapman & Hall, London. 47-56
- BLACKFORD, J.J. & CHAMBERS, F.M. (1991) Proxy records of climate from blanket mires: Evidence for a Dark Age (1 400BP) climatic deterioration in the British Isles. *The Holocene*, **1** 63-67
- BLACKFORD, J.J. & CHAMBERS, F.M. (1993) Determining the degree of peat decomposition for peat based palaeoclimatic studies. *International Peat Journal*, **5** 7-24

- BLACKFORD, J.J. & CHAMBERS, F.M. (1995) Proxy climate record for the last 1000 years from Irish blanket peat and a possible link to solar variability. *Earth and Planetary Science Letters*, **133** 145-150
- BLYTT, A. (1876) *Essay on the immigration of the Norwegian flora during alternating rainy and dry periods*. Kristiana. Cammermeyer
- BOBROV, A.A., YAZVENKO, S.B. & WARNER, B.G. (1995) Taxonomic and ecological implications of shell morphology of three testaceans (Protozoa: Rhizopoda) in Russia and Canada. *Archiv für Protistenkunde*, **145** 119-126
- BRADLEY, R.S. & JONES, P.D. (1993) 'Little Ice Age' summer temperature variations: their nature and relevance to recent global warming trends. *The Holocene*, **3** 367-376
- BRADLEY, R.S. & JONES, P.D. (1995) *Climate since A.D.1500*. Routledge, London & New York, pp706
- BRADY, N.C. (1990) *The nature and properties of soils*. 10th Ed. Macmillan Publishing Company, New York, pp621
- BRENNINKMEIJER, C.A.M., GEEL, B VAN, & MOOK, W.G. (1982) Variations in the D/H and ¹⁸O/¹⁶O ratios in cellulose extracted from a peat bog core. *Earth and Planetary Science Letters*, **61** 283-290
- BRIFFA, K.R., JONES, P.D. & HULME, M. (1994) Summer moisture variability across Europe, 1892-1991: an analysis based on the Palmer Drought Severity Index. *International Journal of Climatology*, **14** 475-506
- BROOKS, S.J., MAYLE, F.E. & LOWE, J.J. (1997) Chironomid-based Lateglacial climatic reconstruction for southeast Scotland. *Journal of Quaternary Science*, **12** 161-167
- BURLTON, F.W.E. (1995) *The Border Mires approach*. The Peatlands Convention, Edinburgh, Scotland
- BURLTON, F.W.E. (1996) *Border Mires management plan, 1996-2001*. Forest Enterprise, Kielder District.
- BURLTON, F.W.E. (1997) The Border Mires approach. In: Parkyn, L., Stoneman, R.E. & Ingram, H.A.P. (eds.) *Conserving peatlands*. CAB International, Oxford. 271-279
- BUTLER, A., WARNER, B.G., GROSVERNIER, P. & MATTHEY, Y. (1996) Vertical patterns of testate amoebae (Protozoa: Rhizopoda) and peat-forming vegetation on cutover bogs in the Jura, Switzerland. *New Phytologist*, **134** 371-382
- CASH, J. & HOPKINSON, J. (1909) *The British freshwater Rhizopoda and Heliozoa*. Vol II Rhizopoda, part 2. The Ray Society. London pp166.
- CHAMBERS, F.M. (1993) Late-Quaternary climate change and human impact: commentary and conclusions, In: Chambers, F.M. (ed.) *Climate change and human impact on the landscape*. Chapman & Hall, 247-259

- CHAMBERS, F.M., BARBER, K.E., MADDY, D. & BREW, J. (1997) A 5500-year proxy-climate and vegetation record from blanket mire at Talla Moss, Borders, Scotland. *The Holocene*, **7** 391-399
- CHAPMAN, S.B. (1961) *The hydrology and ecology of Coom Rigg Moss*. Unpublished Ph.D. Thesis, University of London.
- CHAPMAN, S.B. (1964a) The ecology of Coom Rigg Moss, Northumberland: I Stratigraphy and present vegetation. *Journal of Ecology*, **52** 299-313
- CHAPMAN, S.B. (1964b) The ecology of Coom Rigg Moss, Northumberland. II The chemistry of peat profiles and development of the bog system. *Journal of Ecology*, **52** 315-321
- CHAPMAN, S.B. (1965) The ecology of Coom Rigg Moss, Northumberland. III Some water relations of the bog system. *Journal of Ecology*, **53** 371-384
- CHAPMAN, S.B. & ROSE, R.J. (1991) Changes in vegetation at Coom Rigg Moss National Nature Reserve within the period 1958-1986. *Journal of Applied Ecology*, **28** 140-153
- CHARMAN, D.J. (1992) Blanket mire formation at the Cross Lochs, Sutherland, northern Scotland. *Boreas*, **21** 53-72
- CHARMAN, D.J. (1994) Patterned fen development in northern Scotland: developing a hypothesis from palaeoecological data. *Journal of Quaternary Science*, **9** 285-297
- CHARMAN, D.J. (1997) Modelling hydrological relationships of testate amoebae (Protozoa: Rhizopoda) on New Zealand peatlands. *Journal of the Royal Society of New Zealand*, **27** 465-483
- CHARMAN, D.J. (1998 in press) Testate amoebae and the fossil record: issues in biodiversity. *Journal of Biogeography*,
- CHARMAN, D.J. & SMITH, R.S. (1992) Forestry and blanket mires of Kielder Forest, Northern England: Long-term effects on vegetation. In: Bragg, O.M, Hulme, P.D., & Robertson, R.A. (eds.) *Peatland ecosystems and man: an impact assessment*. University of Dundee, 226-230
- CHARMAN, D.J. & WARNER, B.G. (1992) Relationship between testate amoebae (Protozoa:Rhizopoda) and the micro-environmental parameters on a forested peatland in northeastern Ontario. *Canadian Journal of Zoology*, **70** 2474-2482
- CHARMAN, D.J. & WARNER, B.G. (1997) The ecology of testate amoebae (Protozoa: Rhizopoda) in oceanic peatlands in Newfoundland, Canada: modelling hydrological relationships for palaeoenvironmental reconstruction. *Écoscience*, **4** 555-562
- CHARMAN, D.J., ROE, H.M. & GEHRELS, W.R. (1998, in press) The use of testate amoebae in studies of sea-level change: a case study from the Taf estuary, South Wales, UK. *The Holocene*, **8**

- CHARMAN, D.J., HENDON, D. & WOODLAND, W.A. (in prep.) *The identification of testate amoebae (Protozoa:Rhizopoda) from British oligotrophic peats.*
- CHARMAN, D.J., HENDON, D. & PACKMAN, S. (in prep.) Multi-proxy surface wetness records from replicate cores on an ombrotrophic mire: implications for palaeoclimatic records.
- CHILDS, E.C. (1969) *An introduction to the physical principles of soil water phenomena.* Wiley, London.
- COLLINS, E.S., MCCARTHY, F.M.G., MEDIOLI, F.S., SCOTT, D.B. & HONIG, C.A. (1990) Biogeographic distribution of modern thecamoebians in a transect along the Eastern North American Coast. In: Hemleben, C., Kaminski, M.A., Kuhnt, W. & Scott, D.B. (eds.) *Paleoecology, biostratigraphy, paleoceanography and taxonomy of agglutinated foraminifera.* Kluwer Academic Publishers, The Netherlands. 783-792
- COULSON, J.C. & BUTTERFIELD, J. (1978) An investigation of the biotic factors determining the rates of plant decomposition on blanket bog. *Journal of Ecology*, **66** 631-650
- CLYMO, R.S. (1983) Peat. In: Gore, A.J.B. (ed.) *Mires: swamp, bog, fen and moor.* 4B. Ecosystems of the World. Regional Studies. Elsevier Scientific. Amsterdam.
- CLYMO, R.S. (1984) The limits to peat bog growth. *Philosophical Transactions of the Royal Society of London.* B **303** 605-654
- CLYMO, R.S. (1991) Peat growth. In: Shane, L.K.C. & Cushing, E.J. (eds.) *Quaternary Landscapes.* Bellhaven Press, London. 76-112
- CLYMO, R.S. & HAYWARD, P.M. (1982) The ecology of *Sphagnum*. In: Smith, A.J.E. (ed.) *Bryophyte ecology.* Chapman and Hall, London and New York, 229-291
- COMMITTEE ON SYSTEMATICS AND EVOLUTION OF THE SOCIETY OF PROTOZOOLOGISTS: LEVINE, N.D., CORLISS, J.O, COX, F.E.G., DEROUX, J., GRAIN, J., HONIGBERG, B.M., LEEDALE, G.F., LOEBLICH III, A.R., LOM, J., LYNN, D., MERINFELD, E.G., PAGE, F.C., POLJANSKY, G., SPRAGUE, V., VAVRA, J., & WALLACE, F.G. (1980) A newly revised classification of the Protozoa. *Journal of Protistology*, **27** 37-58
- CORBET, S.A. (1973) An illustrated introduction to the testate Rhizopods in *Sphagnum* with special reference to the area around Malham Tarn, Yorkshire. *Field Studies*, **3** 801-838
- CUMMING, B.F., SMOL, J.P. & BIRKS, H.J.B. (1992) Scaled Chrysophytes (Chrysophyceae and Synurophyceae) from Adirondack drainage lakes and their relationship to environmental variables. *Journal of Phycology*, **28** 162-178
- DANIELS, R.E. & EDDY, A. (1985) *Handbook of European Sphagna.* Institute of Terrestrial Ecology. NERC.
- DE GRAAF, F. (1956) Studies on Rotaria and Rhizopoda from the Netherlands. *Biologisch Jaarboek Dodonea*, **23** 145-217

- DECLOITRE, L. (1962) Le genre *Euglypha* Dujardin. *Archiv für Protistenkunde*, **106** 51-100
- DECLOITRE, L. (1976) Le genre *Arcella* Ehrenburg. Compléments á jour au 31. Décembre 1974 de la monographie du genre parue an 1936. *Archiv für Protistenkunde*, **118** 291-309
- DEFLANDRE, G. (1928) La genre *Arcella* Ehrenburg. Morphologie-Biologie. Essai phylogénétique et systématique. *Archiv für Protistenkunde*, **64** 152-287
- DEFLANDRE, G. (1953) Ordres des Testacealobosa, Testaceafilosa, Thalamia ou Thécamoebiens (Rhizopoda Testacea). *Traité de Zoologie*. I 97-148. Paris
- DIERSSEN, K. (1982) *The major plant communities of north-west European mires*. Conservatoire et Jardin Botaniques. Geneva.
- DUMAYNE, L., STONEMAN, R.S., BARBER, K.E. & HARKNESS, D. (1995) Problems associated with correlating calibrated radiocarbon-dated pollen diagrams with historical events. *The Holocene*, **5** 118-123
- DUPONT, L.M. (1986) Temperature and rainfall variation in the Holocene based on comparative palaeoecology and isotope geology of a hummock and a hollow (Bourtangerveen, the Netherlands). *Review of Palaeobotany and Palynology*, **48** 71-159
- DUPONT, L.M. & MOOK, W.G. (1987) Palaeoclimate analysis of $^2\text{H}/^1\text{H}$ ratios in peat sequences with variable plant composition. *Chemical Geology*, **66** 323-333
- DU RIETZ, G. (1954) Die mineralbodenwasserzeigergrenze als Grundlage einer natürlichen Zweigliederung der nord-und mitteleuropäischen Moore. *Vegetatio*, **5-6** 571-585
- DWYER, R.B. & MITCHELL, F.J.G. (1997) Investigation of the environmental impact of remote volcanic activity on north Mayo, Ireland, during the mid-Holocene. *The Holocene*, **7** 113-118
- EDWARDS, K.J. (1983) Quaternary palynology: consideration of a discipline. *Progress in Physical Geography*, **7** 113-125
- EFRON, B. & GONG, G. (1983) A leisurely look at the bootstrap, the Jackknife and cross-validation. *The American Statistician*, **37** 36-48
- ELLISON, R.L. & OGDEN, C.G. (1987) A guide to the study and identification of fossil testate amoebae in Quaternary lake sediments. *International Review of Hydrobiology*, **72** 639-652
- FINLAY, B.J., CORLISS, J.O., ESTEBAN, G. & FENCHEL, T. (1996) Biodiversity at the microbial level: the number of free-living ciliates in the biosphere. *The Quarterly Review of Biology*, **71** 221-237
- FINLAY, B.J. (1997) The global diversity of protozoa and other small species. *10th International Congress of Protozoology*, Sydney, Australia

- FOSTER, D.R. & WRIGHT, H.E. JR. (1990) Role of ecosystem development and climate change in bog formation in Central Sweden. *Ecology*, **71** 450-463
- GAUCH, H.G. & WHITTAKER, R.H. (1981) Hierarchical classification of community data. *Journal of Ecology*, **69** 537-557
- GAUTHIER-LIÈVRE, L. & THOMAS, R. (1958) Les genres *Diffflugia*, *Pentagonia*, *Maghrebica* et *Hoogenraadia* (Rhizopodes testacés) en Afrique. *Archiv für Protistenkunde*, **103** 241-370
- GEHRELS, W.R. & VAN DE PLASSCHE, O. (1998) The use of *Jadammina macrescens* (Brady) and *Balticammina pseudomacrescens* Brönnimann, Lutze and Whittaker (Protozoa: Foraminiferida) as sea-level indicators. *Palaeogeography, Palaeoclimatology, Palaeoecology*, in press
- GODWIN, H. (1946) The relationship of bog stratigraphy to climate change and archaeology. *Proceedings of the Prehistoric Society*, **1** 1-11
- GODWIN, H. (1952) Recurrence surfaces. *Dansmark Geologiske Undersølgelse, III Række*, **80** 22-30
- GOLEMANSKY, V.G. (1982) Thécamoebiens (Protozoa: Rhizopodea) interstitiels du supralittoral Grec de la mer Égée. *Biologia Gallo-Hellenica*, **9** 271-276
- GOLEMANSKY, V.G. (1991) Thécamoebiens mésopsammiques (Rhizopoda: Arcellinida, Gromida & Monothalamida) du sublittoral marin de l'Atlantique dans la région de Roscoff (France). *Archiv für Protistenkunde*, **140** 35-43
- GOLEMANSKY, V.G. (1992) Thécamoebiens interstitiels (Rhizopoda: Arcellinida, Gromida et Monothalamida) du supralittoral français de l'Atlantique dans la région du Roscoff (Bai de Morlaix). *Acta Zoologica Bulgaria*, **45** 3-13
- GOODE, D.A. (1973) The significance of peat and peatlands. *Proceedings of the International Peat Society*. Symposium, Glasgow.
- GOODE, D.A. & RATCLIFFE, D.A. (1977) Peatlands In: Ratcliffe, D.A. (ed.) *A nature conservation review*. Cambridge University Press. **1** 249-287
- GORDON, A.D. & BIRKS, H.J.B. (1972) Numerical methods in Quaternary palaeoecology. I. Zonation of pollen diagrams. *New Phytologist*, **73** 221-249
- GORE, A.J.P. (ed.) (1983) Introduction. *Mires: swamp, bog, fen and moor. General Studies*. 4A. Ecosystems of the World. Elsevier Scientific, Amsterdam. 1-34
- GRANLUND, E. (1932) De svenska hogmossarnas geologi. *Sveriges Geologiska Undersökning Scrinium C26* no. 373
- GRIMM, E.C. (1982) TILIA & TILIAGRAPH (Software). Illinois State Museum, Springfield, Illinois, USA.
- GRIMM, E.C. (1987) CONISS: A FORTRAN 77 program for stratigraphically constrained cluster analysis by the method of incremental sum of squares. *Computers and Geosciences*, **13** 13-35

- GRIMM, E.C. (1988) Data analysis and display. In: Huntley, G.B., & Webb, T, III (eds.) *Vegetation history: handbook of vegetation science 7*. Kluwer Academic publishers, Dordrecht. 43-76
- GROSPEITSCH, TH. (1955) Die testaceen Rhizopoden der Hochmoore und ihre Bedeutung für die Moorforschung. *Gewasser und Abwasser*, 6 5-19
- GROSPEITSCH, TH. (1958) *Wechseltierchen (Rhizopoden). Einführung in die Kleinlebewelt*. Kosmos. Stuttgart.
- GROVE, J.M. (1988) *The Little Ice Age*. Methuen, London.
- HAINES-YOUNG, R. & PETCH, J. (1986) *Physical geography: its nature and methods*. Paul Chapman Publishing Ltd. pp 230
- HARNISCH, O. (1927) Einige Daten zur rezenten und fossil testacean Rhizopoden-Fauna der Sphagnen. *Archiv für Hydrobiologie*, 18 246-360
- HASLAM, C. (1987) *Late Holocene peat stratigraphy and climate change - A macrofossil investigation from the raised mires of Western Europe*. Unpublished PhD Thesis, University of Southampton.
- HEAL, O.W. (1961) The distribution of testate amoebae (Rhizopoda. Testacea) in some fens and bogs in northern England. *Journal of the Linnean Society. (Zoology)*. XLIV, 369-382
- HEAL, O.W. (1962) The abundance and micro-distribution of testate amoebae in *Sphagnum*. *Oikos*, 13 35-47
- HEAL, O.W. (1963) Morphological variation in certain testacea (Protozoa: Rhizopoda). *Archiv für Protistenkunde*, 106 351-368
- HEAL, O.W. (1964) Observations on the seasonal and spatial distribution of testacea (Protozoa: Rhizopoda) in *Sphagnum*. *Journal of Animal Ecology*, 33 395-412
- HEAL, O.W. (1965) Observations on testate amoebae (Protozoa: Rhizopoda) from Signy Island, South Orkney Islands. *British Antarctic Survey Bulletin*, 6 43-47
- HEATHWAITE, A.L., GÖTTLICH, K.H., BURMEISTER, E.G., KAULE, G. & GROSPEITSCH, TH. (1993) Mires: definitions and form. In: Heathwaite, A.L. & Göttlich, K.H. (eds.) *Mires, process, exploitation and conservation*. John Wiley & Sons Ltd. Chichester, 2-75
- HEDLEY, R.H. & OGDEN, C.G. (1973) Biology and fine structure of *Euglypha rotunda* (Testacea: Protozoa). *Bulletin of the British Museum, Natural History (Zoology)*, 25 119-137
- HEDLEY, R.H., OGDEN, C.G. & MORDAN, N.J. (1977) Biology and fine structure of *Cryptodiffugia oviformis* (Rhizopoda: Protozoa). *Bulletin of the British Museum, Natural History (Zoology)*, 30 311-328
- HENDON, D. & CHARMAN, D.J. (1997) The preparation of testate amoebae (Protozoa: Rhizopoda) samples from peat. *The Holocene*, 7 199-205

- HOBBS, N.B. (1986) Mire morphology and the properties and behaviour of some British and foreign peats. *Quarterly Journal of Engineering Geology*, **19** 7-80
- HOOGENRAAD, H.R. (1935) Studien über die sphagnicolen Rhizopoden der niederländischen Fauna. *Archiv für Protistenkunde*, **84** 1-100
- HILL, M. O. (1979) *DECORANA - A FORTRAN program for detrended correspondence analysis and reciprocal averaging*. Ecology and Systematics, Cornell University, Ithaca, New York, 14850, 52pp.
- HILL, M. O. & GAUCH, H. G. JR (1980) Detrended Correspondence Analysis: an improved ordination technique. *Vegetatio*, **42** 47-58
- HU, F.S. & DAVIS, R.B. (1995) Postglacial development of a Maine bog and paleoenvironmental implications. *Canadian Journal of Botany*, **73** 638-649
- HUGHES, J.M.R. & HEATHWAITE, A.L. (1995) Introduction. In; Hughes, J.M.R. & Heathwaite, A.L. (eds.) *Hydrology and hydrochemistry of British wetlands*. John Wiley & Sons Ltd, 1-20
- HUNTLEY, B. (1992) Rates of change in the European palynological record of the last 13,000 years and their climatic interpretation. *Climate Dynamics*, **6** 185-191
- HUNTLEY, B. (1996) Quaternary palaeoecology and ecology. *Quaternary Science Reviews*, **15** 591-606
- HUNTLEY, B. & BIRKS, H.J.B. (1983) *An atlas of past and present pollen maps of Europe 0-13,000 years ago*. Cambridge University Press, London.
- IMBRIE, J. & KIPP, N.G. (1971) A new micropaleontological method for quantitative palaeoclimatology: application to a Late Pleistocene Caribbean core. In: Turekian, K.K. (ed.) *The Late Cenozoic Glacial Ages*. Yale University Press, New Haven and London, 71-181
- IMBRIE, J. & WEBB, T. III (1981) Transfer functions: calibrating micropaleontological data in climatic terms. In: Berger, A. (ed.) *Climatic variations and variability: facts and theories*. D. Riedel, Dordrecht, pp. 125-134
- INGRAM, H.A.P. (1982) Size and shape in raised mire ecosystems: a geophysical model. *Nature*, **297** 300-303
- INGRAM, H.A.P. (1983) Hydrology. In Gore, A.J.P. (ed.) *Mires: swamp, bog, fen and moor. General Studies*. 4A. Ecosystems of the World. Elsevier Scientific, Amsterdam, 67-158
- IVANOV, K.E. (1981) *Water movement in mirelands*. Academic Press. London
- JANSSENS, J.A. (1983) A quantitative method for stratigraphical analysis of bryophytes in Holocene peat. *Journal of Ecology*, **71** 189-196
- JOHNSON, L.J. & DAMMAN, A.W.H. (1991) Species-controlled *Sphagnum* decay on a south Swedish raised bog. *Oikos*, **61** 234-242

- JUGGINS, S. (1992) Diatoms in the Thames Estuary, England: ecology, palaeoecology and salinity transfer functions. *Bibliotheca Diatomologica*. Band 25. Cramer, Berlin
- JUGGINS, S., BATTERBEE, R.W. & FRITZ, S.C. (1994) Diatom/salinity transfer functions and climate change: an assessment of methods and applications to two Holocene sequences from the northern Great Plains, North America. *Palaeoclimate of the Last Glacial/Interglacial Cycle*. NERC Earth Sciences Directorate, 37-41
- JUNG, W. (1936) Thekamoban urprunglicher, lebender deutscher Hochmore. *Abhandlungen Landesmuseum der Provinz Westfalen Museum feur Naturkunde*, 7 1-87
- KENT, M. & COKER, P. (1992) *Vegetation description and analysis. A practical approach*. Bellhaven Press. London, pp 363
- KENT, M., GILL, W.J., WEAVER, R.E. & ARMITAGE, R.P. (1997) Landscape and plant community boundaries in biogeography. *Progress in Physical Geography*, 21 315-353
- KILIAN, M.R., VAN DER PLICHT, J. & VAN GEEL, B. (1995) Dating raised bogs: new aspects of AMS ¹⁴C wiggle matching, a reservoir effect and climatic change. *Quaternary Science Reviews*, 14 959-966
- KORSMAN, T. & BIRKS, H.J.B. (1996) Diatom-based water chemistry reconstructions from northern Sweden: a comparison of reconstruction techniques. *Journal of Palaeolimnology*, 15 65-77
- KOUWETS, F.C. (1984) The taxonomy, morphology and ecology of some smaller *Euastrum* species (Conjugatophyceae, Desmidiaceae). *British Phycological Journal*, 19 333-347
- KOVACH, W. (1991) *Multivariate Statistical Package (MVSP)*, Version 2. University College of Wales, Aberystwyth, Wales.
- KOVACH, W. (1995) Multivariate data analysis. pp1-38 In, Maddy, D. & Brew, J.S. (eds.) *Statistical modelling of Quaternary Science data*. Technical Guide 5, Quaternary Research Association, Cambridge, 271pp.
- LAMB, H.H. (1965) The early Medieval warm epoch and its sequel. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 1 13-37
- LAMB, H.H. (1977) *Climate, present, past and future. Vol. II: Climate, history and the modern world*. Methuen & Co. Ltd. London. pp 433
- LAMB, H.H. (1995) *Climate, history and the modern world*. 2nd Ed. Routledge, London.
- LINE, J.M. & BIRKS, H.J.B. (1990) WACALIB version 2.1 - a computer program to reconstruct environmental variables from fossil assemblages by weighted averaging. *Journal of Palaeolimnology*, 3 170-173

- LINE, J.M., TER BRAAK, C.J.T. & BIRKS, H.J.B. (1994) WALCALIB version 3.3 - a computer program to reconstruct environmental variables from fossil assemblages by weighted averaging and to derive sample-specific errors of prediction. *Journal of Palaeolimnology* 10 147-152
- LINDHOLM, T. & MARKKULA, I. (1984) Moisture conditions in hummocks and hollows in virgin and drained sites on the raised bog Laaviosuo, southern Finland. *Annales Botanici Fennici*, 21 241-255
- LINDSAY, R.A. (1995) *The ecology, classification and conservation of ombrotrophic mires*. Scottish Natural Heritage, pp120
- LINDSAY, R.A. RIGGALL, J., & BURD, F. (1985) The use of small scale surface patterns in the classification of British peatlands. *Aquilo Seria Botannica*, 21 69-79
- LINDSAY, R.A., CHARMAN, D.J., EVERINGHAM, F., O' REILLY, R.M., PALMER, M.A., ROWELL, T. A., & SHROUD, D.A. (1988) *The Flow Country: The peatlands of Caithness and Sutherland*. Nature Conservancy Council. Peterborough
- LINE, E.M. & BROOKS, A.J. (1980) *Desmids of the English Lake District*. Freshwater Biological Association Scientific Publication 42.
- LOEBLICH, A.R. JR & TAPPAN, H. (1964) Sarcodina, chiefly "Thecamoebians" and Foraminiferida. In: Moore, R.C. (ed.) *Treatise on Invertebrate Paleontology*, Part C, Protista 2. C1-510a: Geological Society of America and University of Kansas Press, 1-31
- LOUSIER, J.D. & PARKINSON, D. (1981) The disappearance of empty tests of litter and soil testate amoebae (Testacea: Rhizopoda). *Archiv für Protistenkunde*, 124 312-336
- LOWE, J.J. & WALKER, M.J.C. (1997) *Reconstructing Quaternary environments*. 2nd Edition, Longman. London
- LOWE, S. (1993) *Border Mires. Redefinition of hydrological boundaries (1992-1993)*. Unpublished report, English Nature North-East Region.
- MAHER, L.J. JR (1972) Nomograms for computing 0.95 confidence limits of pollen data. *Review of Palaeobotany and Palynology*, 13 85-93
- MAHER, L. J. JR (1992) Depth-Age conversion of pollen data. *INQUA Working Group on Data-Handling Methods. Newsletter* 7.
- MANLEY, G. (1959) Mean temperature of Central England 1698-1952. *Quarterly Journal of the Royal Meteorological Society*, 79 242-261
- MANLEY, G. (1974) Central England temperature data 1941-1979. *Quarterly Journal of the Royal Meteorological Society*, 100 389-405
- MAYES, J. & WHEELER, D. (1997) Regional perspectives on climate variability and change. In: Wheeler, D. & Mayes, J. (eds.) *Regional climates of the British Isles*. Routledge, London & New York, 279-331

- MCCARTHY, F.M.G., COLLINS, E.S., MCANDREWS, J.H., KERR, H.A., SCOTT, D.B. & MEDIOLI, F.S. (1995) A comparison of postglacial arcellacean ("Thecamoebian") and pollen succession in Atlantic Canada, illustrating the potential of arcellaceans for paleoclimatic reconstruction. *Journal of Paleontology*, **69** 980-993
- MEDIOLI, F.S. & SCOTT, D.B. (1983) Holocene arcellacea (Thecamoebians) from Eastern Canada. *Cushman Foundation Special Publication No. 21*, 5-63
- MEDIOLI, F.S. & SCOTT, D.B. (1985) Designation of *types*, for one genus and nine species of arcellaceans (Thecamoebians), with additional original reference material for four other species. *Journal of Foraminiferal Research*, **15** 24-37
- MEDIOLI, F.S. & SCOTT, D.B. (1988) Lacustrine thecamoebians (mainly arcellaceans) as potential tools for palaeolimnological interpretations. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **62** 361-386
- MEDIOLI, F.S., SCOTT, D.B. & ABBOTT, B.H. (1987) A case study of protozoan intraclonal variability: taxonomic implications. *Journal of Foraminiferal Research*, **17** (1) 28-47
- MEDIOLI, F.S., SCOTT, D.B., COLLINS, E.S. & MCCARTHY, F.M.G. (1990) Fossil thecamoebians: present status and prospects for the future. In: Hemleben, C., Kaminski, M.A., Kuhnt, W. & Scott, D.B. (eds.) *Paleoecology, biostratigraphy, paleoceanography and taxonomy of agglutinated foraminifera*. Kluwer Academic Publishers, The Netherlands. 813-839
- MEISTERFELD, R. (1977) Die horizontale und vertikale verteilung der Testacean (Rhizopoda: Testacea) in *Sphagnum*. *Archiv für Hydrobiologie*, **79** 319-356
- MEISTERFELD, R. (1979) Contribution to the systematik of testacea (Rhizopoda, Testacea) in *Sphagnum* A SEM investigation. *Archiv für Protistenkunde*, **121** 246-269
- MERRICKS, P. (1995) *Coom Rigg Moss National Nature Reserve management plan*. English Nature, Northumberland, Unpublished Internal Report.
- MIGNOT, J-P. & RAIKOV, I.B. (1992) Evidence for meiosis in the testate amoeba *Arcella*. *Journal of Protozoology*, **39** 287-289
- MOORE, P.D. (1977) Stratigraphy and pollen analysis of Claish Moss, North-west Scotland: significance for the origin of surface pools and forest history. *Journal of Ecology*, **65** 375-397
- MOORE, P.D. (1984) *European mires*. Academic Press. London
- MOORE, P.D. (1991) Ups and downs in peatlands. *Nature*, **353** 299-300
- MOORE, P.D. & BELLAMY, D. (1974) *Peatlands*. Elek Science. London
- MOORE, P.D., WEBB, J.A. & COLLINSON, M.E. (1991) *Pollen analysis*. 2nd edition. Blackwell Scientific Publications, Oxford

- N.C.C (1984) *The Wou: SSSI notification document*. Nature Conservancy Council, Northumberland.
- NEWSON, M.D. & WHITE, A.D. (1993) *Hydrology and management options for a selection of Border Mires Conservation Units*. Newcastle University report to English Nature North East Region.
- NORTHUMBERLAND WILDLIFE TRUST (1993) *Management Plan for The Wou*. NWT. Unpublished Internal Report
- OGDEN, C.G. (1980) Shell structure in some pyriform species of *Diffflugia*. (Rhizopodea). *Archiv für Protistenkunde*, **123** 455-470
- OGDEN, C.G. (1983) Observations on the systematics of the genus *Diffflugia* in Britain (Rhizopoda, Protozoa). *Bulletin of the British Museum (Natural History)*. Zoology Series, **44** 1-73
- OGDEN, C.G. (1984) Shell structure of some testate amoebae from Britain. *Journal of Natural History*, **18** 341-361
- OGDEN, C.G. & COÛTEAUX, M-M. (1989) Interstitial marine rhizopods (Protozoa) from littoral sands on the east coast of England. *European Journal of Protistology*, **24** 281-290
- OGDEN, C.G. & HEDLEY, R.H. (1980) *An atlas of freshwater testate amoebae*. British Museum (Natural History). Open University Press. Oxford 222pp.
- OKSANEN, J. & MINCHIN, P.R. (1997) Instability of ordination results under changes in input data order: explanations and remedies. *Journal of Vegetation Science*, **8** 447-454
- OLDFIELD, F. (1963) Pollen analysis and man's role in the ecological history of the southeast Lake District. *Geografiska Annaler*, **45** 23-40
- OLDFIELD, F. (1993) Forward to the past: changing approaches to Quaternary palaeoecology. In: Chambers, F.M. (ed.) *Climate change and human impact on the landscape*. Chapman & Hall. 13-21
- OLDFIELD, F., THOMPSON, R., CROOKS, P.R.J., GEDYE, S.J., HALL, V.A., PILCHER, J.R., RENBURG, I. & RICHARDSON, N. (1997) Radiocarbon dating of a recent high-latitude peat profile: Stor Åmyrån, northern Sweden. *The Holocene*, **7** 283-290
- OLSSON, I.U. (1986) Radiometric Dating. In: Berglund, B.E. (ed.) *Handbook of Holocene palaeoecology and palaeohydrology*. John Wiley & Sons Ltd. 273-312
- OSVALD, H. (1923) Die vegetation des hochmores Kosmosse. *Svenska vaxtsociol. sällsk Landl I*. 1-436

- OVERBECK, F. (1947) Studien zur Hochmoorentwicklung im Niedersachen und die Bestimmung der Hummifizierung bei stratigraphisch-pollenanalytischen Mooruntersuchungen. *Planta*, **35** 1-56
- PAGE, F.C. (1966) *Cryptodifflugia operculata* n. sp. (Rhizopodea: Arcellinida, Cryptodifflugiidae) and the status of the genus *Cryptodifflugia*. *Transactions of the American Microscope Society*, **85** 506-515
- PATTERSON, R.T., MACKINNON, K.D., SCOTT, D.B. & MEDIOLI, F.S. (1985) Arcellaceans ("Thecamoebians") in small lakes of New Brunswick and Nova Scotia: Modern distribution and Holocene stratigraphic changes. *Journal of Foraminiferal Research*, **15** 114-137
- PAYETTE, S. (1988) Late-Holocene development of subarctic ombrotrophic peatlands: allogenic and autogenic succession. *Ecology*, **69** 516-531
- PEET, R.K., KNOX, R.G., CASE, J.S. & ALLEN, R.B. (1988) Putting things in order: the advantages of detrended correspondence analysis. *The American Naturalist*, **131** 924-934
- PENARD, E. (1902) *Faune Rhizopodique du Bassin du Léman*. Genève. pp700
- PILCHER, J.R. (1991) Radiocarbon dating for the Quaternary scientist. *Quaternary Proceedings No. 1*. 27-33
- PILCHER, J.R. (1993) Radiocarbon dating and the palynologist: a realistic approach to precision and accuracy. In: Chambers, F.M. (ed.) *Climate change and human impact on the landscape*. Chapman & Hall, 23-32
- PODANI, J. (1997) On the sensitivity of ordination and classification methods to variation in the input order of data. *Journal of Vegetation Science*, **8** 153-156
- POPPER, K.R. (1972) *Conjectures and refutations*. Routledge
- PORTER, S.C. (1986) Pattern and forcing of Northern Hemisphere glacier variations during the last millenium. *Quaternary Research*, **26** 27-48
- POWER, M. (1993) The predictive validation of ecological and environmental models. *Ecological Modelling*, **68** 33-55
- PRENTICE, I.C. (1986) Vegetation responses to past climate changes. *Vegetatio*, **67** 131-141
- PRICE, G.D., MCKENZIE, J.E., PILCHER, J.R. & HOPER, S.T. (1997) Carbon-isotope variation in *Sphagnum* from hummock-hollow complexes: implications for Holocene climate reconstruction. *The Holocene*, **7** 229-233
- RATCLIFFE, D. (ed.) (1977a) *A nature conservation review*. Volume 1. Cambridge University Press.
- RATCLIFFE, D. (ed.) (1977b) *A nature conservation review*. Volume 2, Site Accounts. Cambridge University Press.

- ROBINSON, N.A. (1993) *Site Quality Monitoring: Butterburn Flow. Air photo interpretation, condition of surface in 1975/76 and 1991*. Unpublished report, English Nature, North West Region.
- RODWELL, J.S. (ed.) (1991) *British plant communities. Volume 2, Mires and heaths*. Cambridge University Press, Cambridge. pp 628
- SERNANDER, R. (1906) On the evidence of postglacial changes of climate furnished by the peat-mosses of northern Europe. *Geologiska Foreningens I.*
- SCHÖNBORN, W. (1962) Zur ökologie der sphagnikolen bryokolen un terrikolen Testacean. *Limnologica*, 1 231-254
- SCHÖNBORN, W. (1963) Die stratigraphie lebender Testaceenim Sphagnetum der Hochmoore. *Limnologica*, 1 315-321
- SCHÖNBORN, W. (1965) Untersuchungen uber die zoochlorellen-Symiose der Hochmoor-Testaceen. *Limnologica*, 3 173-176
- SCHÖNBORN, W. (1967) Taxozöntik der beschalten Süßwasser-Rhizopoden: eine raumstruturanalytische Untersuchung über Lebensraumerweiterung und Evolution bei der Mikrofauna. *Limnologica*, 5 159-207
- SCHÖNBORN, W. (1984) Studies on remains of testacea in cores of the Great Woryty Lake (NE-Poland). *Limnologica*, 16 185-190
- SCHÖNBORN, W. (1990a) Analysis of subfossil; shelled protozoa in the sediments of a small acid forest lake (Northern GDR). *Limnologica*, 21 137-145
- SCHÖNBORN, W. (1990b) Shell polymorphism and habitat structure in testacea (Rhizopoda). *Journal of Protozoology*, 37 62A
- SCHÖNBORN, W. (1992a) Adaptive polymorphism in soil inhabiting testate amoebae (Rhizopoda): Its importance for delimitation and evolution of asexual species. *Archiv für Protistenkunde*, 142 139-155
- SCHÖNBORN, W. (1992b) The role of protozoan communities in freshwater and soil ecosystems. *Acta Protozoologica*, 31 11-18
- SCHÖNBORN, W. (1992c) Comparative studies on the production biology of protozoan communities in freshwater ecosystems. *Archiv für Protistenkunde*, 141 187-214
- SCHÖNBORN, W., PETZ, W., WANNER, M. & FOISSNER, W. (1987) Observations on the morphology and ecology of the soil-inhabiting testate amoeba *Schoenbornia humicola* (Schönborn, 1964) Decloitre, 1964 (Protozoa: Rhizopoda). *Archiv für Protistenkunde*, 134 315-330
- SCHÖNBORN, W. & PESCHKE, T. (1990) Evolutionary studies on the *Assulina-Valkanoria* complex (Rhizopoda: Testaceafiliosea) in *Sphagnum* and soils. *Biology and Fertility of Soils*, 9 95-100
- SCOTT, D.B. & MEDIOLI, F.S. (1983) Agglutinated rhizopods in Lake Erie: modern distribution and stratigraphic implications. *Journal of Paleontology*, 57 809-820

- SHORE, J.S., BARTLEY, D.D. & HARKNESS, D.D. (1995) Problems encountered with the ^{14}C dating of peat. *Quaternary Science Reviews (Quaternary Geochronology)*, **14** 373-383
- SJÖRS, H. (1961) Surface patterns in Boreal peatlands. *Endeavour*, **20** 217-227
- SLEIGH, M.A. (1989) *Protozoa and other protists*. 4th Edition. Edward Arnold, London.
- SMART, P.J. (1982) Stratigraphy of a site in the Munsary Dubh Lochs, Caithness, Northern Scotland: development of the present patterns. *Journal of Ecology*, **70** 549-558
- SMITH, A.J.E. (1978) *The moss flora of Britain and Ireland*. Cambridge University Press, Cambridge
- SMITH, B.M. (1985) *A palaeoecological study of raised mires in the Humberhead Levels*. Unpublished Ph.D. Thesis, University of Wales (Cardiff).
- SMITH, H.G. (1974) A comparative study of protozoa inhabiting *Drepanocladus* moss carpet in the South Orkney Islands. *British Antarctic Survey Bulletin* No. 38, 1-16
- SMITH, H.G. (1986) The testate amoebae rhizopod fauna of *Drepanocladus* moss carpet near Rothera Station, Adelaide Island. *British Antarctic Survey Bulletin* No. 72, 77-79
- SMITH, H.G. (1987) A species-poor testate rhizopod fauna on Brabant Island. *British Antarctic Survey Bulletin* No. 77, 173-176
- SMITH, H.G. (1992) Distribution and ecology of the testate rhizopod fauna of the continental Antarctic zone. *Polar Biology*, **12** 629-634
- SMITH, H.G. & WILKINSON, D.M. (1986) Biogeography of testate rhizopods in the southern temperate and Antarctic zone. *Colloque les Écosystemes Terrestres Subantarctiques*, **58** 83-96
- SMITH, R.S. & CHARMAN, D.J. (1988) The vegetation of upland mires within conifer plantations in Northumberland, Northern England. *Journal of Applied Ecology*, **25** 579-594
- STACE, C. (1995) *New flora of the British Isles*. Cambridge University Press. Cambridge.
- STEINECKE, F. (1927) Leifformen und Leitfossilien der Zehlanbruches: die Bedeutung der fossilen mikro - organism für Erkenntniss der Nekrozonosen eines Moores. *Botanisches Archiv Konisb*, **19** 327-344
- STOCKMARR, J. (1971) Tablets with spores used in absolute pollen analysis. *Pollen et Spore*, **13** 615-621
- STONEMAN, R.E. (1993) *Late Holocene peat stratigraphy and climate: extending and refining the model*. Unpublished Ph.D. thesis, University of Southampton

- STONEMAN, R.E., BARBER, K.E. & MADDY, D. (1993) Present and past ecology of *Sphagnum imbricatum* and its significance in raised peat-climate modelling. *Quaternary Newsletter*, **70** 14-22
- STREEFKERKE, J.G. & CASPARIE, W.A. (1989) *The hydrology of bog ecosystems. Guidelines for management*. Staatbosbeheer, pp120
- STUIVER, M. & REIMER, P.J. (1993a) *CALIB User's Guide Rev 3.0*. University of Washington, Quaternary Isotope Laboratory, 1-24
- STUIVER, M. & REIMER, P.J. (1993b) Extended ^{14}C database and revised CALIB 3.0 ^{14}C age calibration program. *Radiocarbon*, **35** 215-230
- SVENSSON, G. (1988) Bog development and environmental conditions as shown by the stratigraphy of Store Mosse mire in southern Sweden. *Boreas*, **17** 89-111
- TALLIS, J.H. (1994) Pool-and-hummock patterning in a southern Pennine blanket mire II. The formation and erosion of the pool system. *Journal of Ecology*, **82** 789-803
- TALLIS, J.H. (1995) Climate and erosion signals in British blanket peats: the significance of *Racomitrium lanuginosum* remains. *Journal of Ecology*, **83** 1021-1030
- TALLIS, J.H. (1997) The pollen record of *Empetrum nigrum* in southern Pennine peats: implications for erosion and climate change. *Journal of Ecology*, **85** 455-465
- TALLIS, J.H. & LIVETT, E.A. (1994) Pool-and-hummock patterning in a southern Pennine blanket mire I. Stratigraphic profiles for the last 2800 years. *Journal of Ecology*, **82** 775-788
- TANSLEY, A.G. (1939) *The British Islands and their vegetation*. Vol. II. Cambridge University Press. Cambridge.
- TAUSCH, R.J., CHARLET, D.A., WIEXELMAN, D.A. & ZAMUDIO, D.C. (1995) Patterns of ordination and classification instability resulting from changes in input data order. *Journal of Vegetation Science*, **6** 897-902.
- TAYLOR, J.A. (1983) The peatlands of Great Britain and Ireland. In: Gore, A.J.B (ed.) *Mires: swamp, bog, fen and moor*. Regional Studies, 4B. Ecosystems of the World. Elsevier Scientific. Amsterdam, 1-46
- TER BRAAK, C.J.F. (1985) Correspondence analysis of incidence and abundance data: properties in terms of a unimodal response model. *Biometrics*, **41** 859-873
- TER BRAAK, C.J.F. (1987-1992) *CANOCO - a FORTRAN program for Canonical Community Ordination*. Microcomputer Power, Ithaca, NY USA
- TER BRAAK, C.J.F. (1988) Partial canonical correspondence analysis. In: Bock, H.H. (ed.) *Classification methods and related methods of data analysis*. Amsterdam, North Holland, 551-558

- TER BRAAK, C.J.F. & BARENDREGT, L.G. (1986) Weighted averaging of species indicator values: its efficiency in environmental calibration. *Mathematical Biosciences*, **78** 57-72
- TER BRAAK, C.J.F. & VAN DAM, H. (1989) Inferring pH from diatoms: a comparison of old and new calibration methods. *Hydrobiologia*, **178** 209-223
- TER BRAAK, C.J.F. & PRENTICE, I.C. (1988) A theory of gradient analysis. *Advance in Ecological Research*, **18** 271-317
- TER BRAAK, C.J.F. & JUGGINS, S. (1993) Weighted averaging partial least squares regression (WA-PLS): an improved method for reconstructing environmental variables from species assemblages. *Hydrobiologica*, **269/270** 485-502
- TOLONEN, K. (1966) Stratigraphic and rhizopod analyses on an old raised bog, Varrassuo, in Hollola, South Finland. *Annales Botanica Fennici*, **3** 147-166
- TOLONEN, K. (1986) Rhizopod Analysis. In: Berglund, B.E. (ed.) *Handbook of Holocene palaeoecology and palaeohydrology*. John Wiley & Sons Ltd. Chichester. 645-666
- TOLONEN, K., HUTTUNEN, P., JUNGER, H. (1985) Regeneration of two coastal raised bogs in Eastern North America. *Annales Academia Scientiarum Fennicae*. III. Geologica-Geographica. **139 A**. 5-51
- TOLONEN, K., WARNER, B.G. & VASANDER, H. (1992) Ecology of testaceans (Protozoa: Rhizopoda) in mires in Southern Finland: I. Autoecology. *Archiv für Protistenkunde*, **142** 119-138
- TOLONEN K., WARNER, B.G. & VASANDER, H. (1994) Ecology of testaceans (Protozoa: Rhizopoda) in mires in Southern Finland: II. Multivariate Analysis. *Archiv für Protistenkunde*, **144** 97-112
- TROELS-SMITH, J. (1955) Characterisation of unconsolidated sediments. *Danmarks Geologiska undersogelse IV Raekke*, Bd, 1-73
- VAN GEEL, B. (1978) A palaeoecological study of Holocene peat bog sections. *Review of Palaeobotany and Palynology*, **25** 1-120
- VAN GEEL, B. & MIDDLEDORP, A.A. (1988) Vegetational history of Carbury Bog (co. Kildare, Ireland) during the last 850 years and a test of the temperature indicator value of $^2\text{H}/^1\text{H}$ measurements of peat samples in relation to historical sources and meteorological data. *New Phytologist*, **109** 377-392
- VAN DER MOLEN, P.C. & HOEKSTRA, S.P. (1988) A palaeoecological study of the hummock-hollow complex from Engbertsdijksveen, in the Netherlands. *Review of Palaeobotany and Palynology*, **56** 213 - 274

- VAN DER MOLEN, P.C., VAN'T VEER, R., & WIJMSTRA, T.A. (1995) Palaeoecology of hummock-hollow complexes on raised bogs in the Irish Midlands. In: Van der Molen, P.C. (ed.) *Hummock - hollow complexes on Irish raised bogs. A Palaeo / Actuo ecological approach of environmental and climatic change*. Academisch Proefschrift. pp. 83-113
- VON POST, L. & SERNANDER, R. (1910) Pflanzen-physiognomische studien auf Torfmooren in Närke. *Livret des excursion en Suede du 11^{eme} Congress Geologie Internationale*, 14 1-18
- VON POST, L. (1946) The prospect for pollen analysis in the study of the earth's climatic history. *New Phytologist*, 45 193-217
- WALKER, D. (1970) Direction and rate in some British post-glacial hydroseres. In: Walker, D. & West, R.G. (eds.) *Studies in the vegetational history of the British Isles*. Cambridge University Press, 117-139
- WALKER, D. & WALKER, P.M. (1961) Stratigraphic evidence of regeneration in some Irish bogs. *Journal of Ecology*, 49 169-185
- WANNER, M. & MEISTERFELD, R. (1994) Effects of some environmental factors on the shell morphology of testate amoebae (Rhizopoda: Protozoa). *European Journal of Protistology*, 30 191-195
- WARDENAAR, E.C.P. (1987) A new hand tool for cutting peat profiles. *Canadian Journal of Botany*, 65 1772-1773
- WARNER, B.G. (1987) Abundance and diversity of testate amoebae (Rhizopoda, Testacea) in *Sphagnum* peatlands in southwestern Ontario, Canada. *Archiv für Protistenkunde*, 133 173-189
- WARNER, B.G. (1990) Testate Amoebae (Protozoa). *Methods in Quaternary ecology*. Geoscience, Canada 5. Geological Association of Canada. 65-74.
- WARNER, B.G. (1991) Fossil testate amoebae (Protozoa) and hydrological history of an ombrotrophic bog in northwestern Ontario, Canada. In Spigarelli, S.A. (ed.) *Proceedings of an International Symposium on Peat/Peatland Characteristics and Uses*. Minnesota, Bemidji State University, 5-14
- WARNER, B.G. & CHARMAN, D.J. (1994) Holocene changes on a peatland in northwestern Ontario, based on testate amoebae (Protozoa) analysis. *Boreas*, 23 270-279
- WARNER, B.G. & CHENGALATH, R. (1991) *Habrotrocha angusticollis* (Bdelloida: Rotifera): A new palaeoecological indicator in Holocene peat deposits. *Verhandlungen Internationale Vreinigung Limnologie* 24 2738-2740
- WHEELER, A.J. (1992) Vegetational succession, acidification and allogenic events as recorded in Flandrian peat deposits from an isolated Fenland embayment. *New Phytologist*, 122 745-756
- WHEELER, B.D. (1984) British fens: a review. In: Moore, P.D. (ed.) *European mires*, Academic Press, London 237-281

- WHITE, J.W.C., CAIS, P., FIGGE, R.A., KENNY, R. & MARKGRAF, V. (1994) A high-resolution record of atmospheric CO₂ content from carbon isotopes in peat. *Nature*, **367** 153-256
- WHITE, M. (1994) *Border Mires Part I. The Spadeadam Mires, re-definition of hydrological boundaries*. Unpublished report, Northumberland Ecological Services.
- WILKINSON, D.M. (1994) A review of the biogeography of the protozoan genus *Nebela* in the southern temperate and Antarctic zones. *Area*, **26** 150-157
- WINKLER, M.G. (1988) Effect of climate on development of two *Sphagnum* bog in south-central Wisconsin. *Ecology*, **69** 1032-1043
- WINSTON, R.B. (1994) Models of the geomorphology, hydrology and development of domed peat bodies. *Geological Society of America Bulletin*, **106** 1594-1604
- WIMBLE, G.A. (1986) *The palaeoecology of lowland coastal raised mires of south Cumbria*. Unpublished PhD. Thesis, University of Wales (Cardiff).
- WOODLAND, W.A. (1996) *Holocene palaeohydrology from testate amoebae analysis: developing a model for UK peatlands*. Unpublished Ph.D. Thesis, University of Plymouth.
- WOODLAND, W.A., CHARMAN, D.J. & SIMS, P.C. (1998) Quantitative estimates of water tables and soil moisture in Holocene peatlands from testate amoebae. *The Holocene*, **8** (1) in press

Glossary

Technical terms are defined here in the context of this study. Clarification and definition of terminology is essential where the meaning may not always be clear.

General Terms

Bootstrapping	cross-validation used to derive Root Mean Square Estimate of Precision (RMSEP) for individual fossil samples. Generating 95% confidence intervals
Calibration	The opposite of regression. Modelled responses are used to infer the past environmental variables from the composition of fossil assemblages
Climate	the characteristic pattern of weather elements in an area over a long period (<i>i.e.</i> >30 years)
Climatic forcing	changes in the global climate that have an effect on the allogenic inputs to a mire system, <i>e.g.</i> , volcanic activity and solar irradiance
Complacent	tranquil, flat, with little variation
Holocene	Post-Glacial, the past 10Ka BP, a warm period
Indicator value	the value of the environmental variable most preferred by a species
Precision	the degree of refinement of measurement (accuracy)
Regression	The opposite of calibration. The modelling of the responses of modern taxa to the environment, and involves the development of a training set
Reliable	sound and consistent, in which reliance or 'confidence' may be put; yielding concordant results when repeated
Replicable	repeatable, the state/condition/property of being experimentally replicable
Robustness	strong, valid
Shifts	wet and dry shifts are directional changes of varying magnitudes and are assigned the data at the point of change begins
Taxonomy	the delimitation, nomenclature (naming) and classification of groups, <i>e.g.</i> organisms, according to their morphology

Peatlands

Acrotelm	surface layer of bogs (typically the top 10-15cm) with actively growing <i>Sphagna</i> , water permeable, with high hydraulic conductivity. The peat-forming layer.
Allochthonous	[peat] of sedimentary origin <i>i.e.</i> , not formed <i>in situ</i>
Allogenic	hydrological forcing or development produced by factors or influences external to the mire itself, <i>e.g.</i> climate - exogenous
Autochthonous	[peat] formed <i>in situ</i>
Autogenic	hydrological forces resulting from internal processes in the bog, <i>e.g.</i> , the accumulation of peat modifying the hydrological regime; internal drainage - endogenous
Blanket Bog	an extensive mire type over undulating terrain, not confined to depressions and usually formed in response to a humid climate
Bog	formed of plant communities growing upon constantly wet acid peat.
Catotelm	sub-surface layer of peat bog, constantly saturated and anaerobic (below 15cm depth)
Cupola	domed central area of a raised bog
Diplolelmic	composed of two layers, the acrotelm and catotelm
Endogenous	from within the system - autogenic
Exogenous	from outside the system - allogenic
Eutrophic	mineral-rich nutrient status
Fen	minerotrophic mire usually having a wider range of vascular plants than bogs, water is derived from outside their own immediate limits
Intermediate ombrotrophic mire	mires which fall between raised and blanket, a largely unrecognised state
Lagg	the wet marginal zone of a raised bog, where water flowing from the mire mixes with runoff from the adjacent mineral soil
Macrotope	combined mire units <i>e.g.</i> a blanket mire and a raised mire joined together
Mesotope	a mire unit - a body of peat which has developed as a simple hydrological entity
Meteoric water	derived from atmosphere (see telluric water supply)
Microtope	an arrangement or combination of several surface features, <i>e.g.</i> hummocks and pools
Microform	an individual surface feature <i>e.g.</i> a single hummock
Minerotrophic	peat body whose water is derived from lakes or soil by throughflow, <i>e.g.</i> , valley mires
Mire	a generic term which includes ombrotrophic peatland types (namely bogs) and minerotrophic types such as fens.
Moisture	percent water content, wet weight of peat
Oligotrophic	mineral - poor mire, poor in basic salts
Ombrotrophic	mire fed exclusively from rainwater, producing oligotrophic conditions, <i>e.g.</i> , raised or blanket bog
Ontogeny	developmental history of a bog
Paludification	forming a mire system over what was previously grassland, forest or bare rock, mire formation where ground that was once dry becomes wet
Polster	surface sample of moss
Primary peat	formed in basins or depressions (Moore & Bellamy, 1974)

Pluvials	phases of higher rainfall
Raised bog	convex cupola of ombrotrophic peat raised a few metres above the level of the surrounding land, (German: Hochmoor);
eccentric -	primary peats developed with horizontal surface conforming with the water levels in the basin, hummocks and hollows aligned parallel to the contours of the bog surface
concentric -	convex masses of peat in both open and closed basins, with concentric surface patterns of hummocks and hollows
Rand	the margin or border of a raised bog
Recurrence	(Granlund, 1932) 'recurrence' from repetition in sequence of similar climatic
Surfaces	events believed to be contemporary, causing striking change in the conditions of peat formation across a number of bogs (Rekurrensytor)
Regeneration complex	an area on a bog with supposedly cyclic process of bog growth <i>e.g.</i> , hummock - hollow - hummock
Secondary peat	developed beyond the physical confines of the basin or depression (Moore & Bellamy, 1974)
Soligenous mires	formed where drainage water becomes localised along tracks (<i>e.g.</i> , flush mires)
Telluric water	derived from surrounding rocks and soils (see meteoric water supply)
Terrestrialisation	formation of a mire system by the infilling of a water body with organic matter
Tertiary peat	peat that develops above the limits of the ground water table, the peat holds a volume of water by capillarity above the level of the main ground water
Topogeneous mires	where local relief results in a permanently high water table in depressions, <i>e.g.</i> , valley mires
Valley mires	develop in small, shallow valleys or channels of minerogenic peat
Water table	top of saturated zone in a soil or peat, an equilibrium surface at which fluid pressure in the voids is equal to atmospheric pressure

Testate amoebae

Autecology	study of ecology at the level of the species, environmental factors to which taxa are sensitive enabling description of ecological niche of organism
Agglutinated	a test united as with glue (see xenosomic), material secreted by the organism
Biocoenosis	life assemblage, association of organisms forming a community
Cytoplasm	part of the protoplasm which stores food materials
Encysted	forming a cyst as protection against inhospitable conditions
Eurytypic	species which can tolerate a wide range of conditions
Extant	still existing
Filose	pseudopodia thin, pointed and often branching
Hyaline	transparent test
Hydrophiles	testate amoebae inhabiting plants submerged in water
Hydric	containing or using water
Hygrophiles	testate amoebae living in moist habitats, subject to desiccation

	less frequently than xerophiles
Idiosomic	test formed of plates secreted by the cytoplasm
Lanceolate	test tapering to a point in the aboral region (<i>e.g. Diffflugia lanceolata</i>)
Lobose	pseudopodia finger-like with rounded distal ends
Meiosis	reduction division
Morphospecies	organisms which have a similar shape, but which can not be considered to be species in the true sense because of uniparental reproduction
Necrocoenoses	death assemblage
Protoplasm	living contents of a cell, consists of nucleus and plasma (cell) membrane
Pseudochitin	a proteinaceous or mucopolysaccharide material manufactured within the cytoplasm
Pseudopodia	flowing cytoplasm used for locomotion and feeding
Pseudostome	mouth-like opening or aperture
Pyriform	pear-shaped test
Spinose	test with spines (<i>e.g. Centropyxis aculeata</i>)
Stenotypic	species that show a clearly marked preference for a particular environment
Subfossil	where little or no chemical change has occurred subsequent to death
Test	shell or lorica enclosing the protoplasm of a testate amoebae
Tyrofoxene	young, beginner, testate amoebae (<i>e.g. Hyalosphenia subflava</i>) thought to colonise drained, disturbed or forested areas, but not indigenous to living mires
Xenosomic	tests constructed from material taken from the substrate <i>e.g.</i> , mineral particles, diatom frustules or fungal hyphae (see agglutinated)
Xerophiles	testate amoebae living in relatively dry habitats, they must be capable of withstanding desiccation