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UNIVERSITE DE NEUCHÂTEL FACULTE DES SCIENCES

# TESTATE AMOEBAE AND OTHER MICRO-ORGANISMS IN *SPHAGNUM* PEATLANDS : ECOLOGY, PALEOECOLOGY AND IMPACT OF CARBON DIOXIDE ENRICHMENT.

THESE

Présentée à la Faculté des Sciences de l'Université de Neuchâtel
pour l'obtention du grade de docteur ès sciences
par

**EDWARD A. D. MITCHELL**

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**Testate amoebae and other micro-organisms in *sphagnum* peatlands: ecology, paleoecology and impact of carbon dioxide enrichment**

de M. Edward A.D. Mitchell

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**Mitchell, E. ; Buttler, A. ; Grosvernier, Ph. ; Rydin, H. ; Albinsson, C. ; Greenup, A.L. ; Heijmans, M.M.P.D. ; Hoosbeek, M.R. ; Saarinen, T.** – Relationships among testate amoebae (*Protozoa*), vegetation and water chemistry in five *Sphagnum*-dominated peatlands in Europe. RESEARCH New Phytol., 145: 95-106 (2000).

**Mitchell, E. ; Van der Knaap, W.O. ; Van Leeuwen, J.F.N. ; Buttler, A. ; Warner, B.G. ; Gobat, J.-M.** – The palaeoecological history of the Praz-Rodet bog (Swiss Jura) based on pollen, plant macrofossils and testate amoebae (*Protozoa*). The Holocene 11, 1: 65-80 (2001).

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# Ecology of testate amoebae (Protozoa: Rhizopoda) in *Sphagnum* peatlands in the Jura mountains, Switzerland and France[1]

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*Abstract*: Testate amoebae (Protozoa) living in *Sphagnum* peatlands are important environmental and paleoecological indicators. The distribution of these animals is closely related to soil moisture variables. This study examines the ecology of sphagnicolous testate amoebae near the southern limit of bogs in Europe. A total of 64 samples were collected for analysis of testate amoebae from six peatlands in the Jura region of Switzerland and France. Eleven site-specific ecological variables, six of which were soil-moisture related variables, were measured at each site. The data were subjected to weighted averaging, jack-knifing, cluster analysis, canonical correspondence analysis, and the indicator value method to model relationships between testate amoebae distributions and environmental variables. Testate amoebae abundance showed a direct relationship with peat pH and depth to water table. Strong relationships were with sites that had a water table less than 41 cm deep. In drier sites with water table depth greater than 41 cm, other factors such as soil porosity and water holding capacity were more important compared to the wetter sites. Though there was a strong relationship between testate amoebae faunas and soil moisture content and porosity, these two variables could not be confidently predicted. Testate amoebae in peatlands in this region appear to be sensitive to peat pH and water tables. Further work is needed to explore relationships between testate amoebae, soil moisture, and porosity.
*Keywords*: testate amoebae, Protozoa, *Sphagnum*, peatlands, Europe.

*Résumé* : Les thécamoebiens (Protozoa) des tourbières à *Sphagnum* sont d'importants indicateurs environnementaux et paléoécologiques. La distribution de ces animaux est étroitement liée à des variables d'humidité du sol. Cette étude aborde l'écologie des thécamoebiens sphagnicoles non loin de la limite méridionale des haut-marais en Europe. Un total de 64 échantillons ont été récoltés dans six tourbières du Jura, en Suisse et en France pour l'analyse des thécamoebiens. Onze variables écologiques spécifiques aux sites, dont six étaient des variables liées à l'humidité du sol, ont été mesurées dans chaque site. Les données ont été analysées par différentes méthodes : le calcul des moyennes pondérées, les méthodes du jackknife et des groupements, l'analyse canonique des correspondances et la méthode des valeurs indicatrices afin de modéliser les relations existant entre les distributions des thécamoebiens et les variables environnementales. Les abondances de thécamoebiens présentent une relation directe avec le pH et la profondeur de la nappe. Les relations étaient fortes dans les sites ayant une profondeur de nappe inférieure à 41 cm. Dans les sites plus secs, avec une nappe plus basse que 41 cm, d'autres facteurs comme la porosité du sol et la capacité de rétention en eau étaient plus importants par rapport aux sites plus humides. Malgré une forte relation entre les faunes thécamoebiennes et l'humidité du sol et la porosité, ces variables n'ont pas pu être prédites précisément. Les thécamoebiens semblent sensibles au pH et à la profondeur de la nappe dans les tourbières de la région. D'autre études sont nécessaires pour explorer les relations entre les thécamoebiens, l'humidité du sol et la porosité.
*Mots-clés* : thécamoebiens, Protozoa, *Sphagnum*, tourbières, Europe.

## Introduction

Protozoa are an abundant component of the soil microfauna (Sleigh, 1989). One group of amoeboid protozoa, the testate amoebae, is ubiquitous in damp soil, forest floor litter, and mossy habitats, especially bogs and fens where they live in water films on the stems and leaves of *Sphagnum* plants. Most of these animals occupy specialized ecological niches that are regulated by water, temperature, oxygen, pH, and light. Most of the ecological work has been on the sphagnicolous faunas in Europe (Harnisch, 1929; Overbeck, 1975; Meisterfeld, 1977; 1979; Tolonen, 1986; Foissner, 1987). Jung (1936) made an early attempt to fit testate amoebae to a relative scale of soil moisture content, the F-scale (*i.e.,* Feuchtigkeitsgrat). Schönborn (1962) and Meisterfeld (1979) subsequently refined the F-scale. In more recent years, studies in Europe and in North America on the ecology of testate amoebae distributions and a wide range of environmental variables has been published using more sophisticated statistical techniques (Warner, 1987; Tolonen, Warner & Vasander, 1992; 1994; Warner & Chmielewski, 1992; Charman & Warner, 1992; 1997; Warner & Charman, 1994). All of these studies confirm the importance of soil moisture variables of the microhabitat. However, whether testate amoebae can be related to precise soil moisture contents and an "F-scale" requires ecological studies of testate amoebae in a wide geographic range of peatland types.

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The diagnostic features of the shell, their abundance and widespread occurrence in narrow ecological niches, the durability of their shells after death, and the relative ease with which the fossilized shells can be extracted from peat soils, make them a useful group of environmental and paleoecological proxy indicators (Harnisch, 1927; Tolonen, 1986; Warner, 1990; Warner *et al.*, 1994, Charman & Warner, 1997). It has been shown that testate amoebae can be used to effectively reconstruct short and long-term histories of plant community succession and peatland development. Buttler *et al.* (1996) were able to establish plant succession patterns over the last 100 years to determine patterns of natural regeneration of secondary peat sequences on abandoned cut-over bogs in Switzerland. Testate amoebae have been applied to entire Holocene peat sequences to reconstruct peatland development (Tolonen, 1986), yet testate amoebae are probably more powerful paleoecological indicators than hitherto has been demonstrated (Gobat, Aragno & Matthey, 1998).

This paper is a continuation of our on-going efforts to understand the ecology of northern peatland testate amoebae faunas (Tolonen, Warner & Vasander, 1992; 1994; Charman & Warner, 1992; 1997; Warner *et al.*, 1994; Warner & Chmielewski, 1992). The bogs in the Jura region offer the opportunity to examine the ecology of peatland faunas near the southern limit of their range in Europe. Studies on testate amoebae in this region have a long history (Bénier, 1988). Most of the focus has been on the large lake faunas. By comparison, peatland faunas have received little attention.

In view of the importance of soil moisture factors reported in the ecology of sphagnicolous testate amoebae, we studied in more detail a range of soil moisture variables, hitherto unexplored, in order to gain further insights into relationships between testate amoebae distributions and more specific soil moisture parameters.

## Material and methods

### FIELD SAMPLING

Moss samples were collected from representative monospecific swards of *Sphagnum* or other mosses in six peatlands in the Swiss and French Jura (Figure 1; Table I). The samples were taken at the end of August, during a dry period (*i.e.*, one week without any rain). Vegetation cover estimates (percent cover) were made at the time of sampling. Of the 64 samples collected, 48 were collected by gently pushing a tin can cylinder into the living moss carpet. The cylinder measured 12 cm high and 10 cm diameter, was open at one end and had a small hole in the opposite end to allow air to escape and not compress the mosses. These tin can samples were used to estimate water content, water retention, and soil porosity, which are quantitative estimates of water availability that are independent of time-dependent variables such as water table depth and moisture content (Overbeck & Happach, 1956). A replicate sample taken

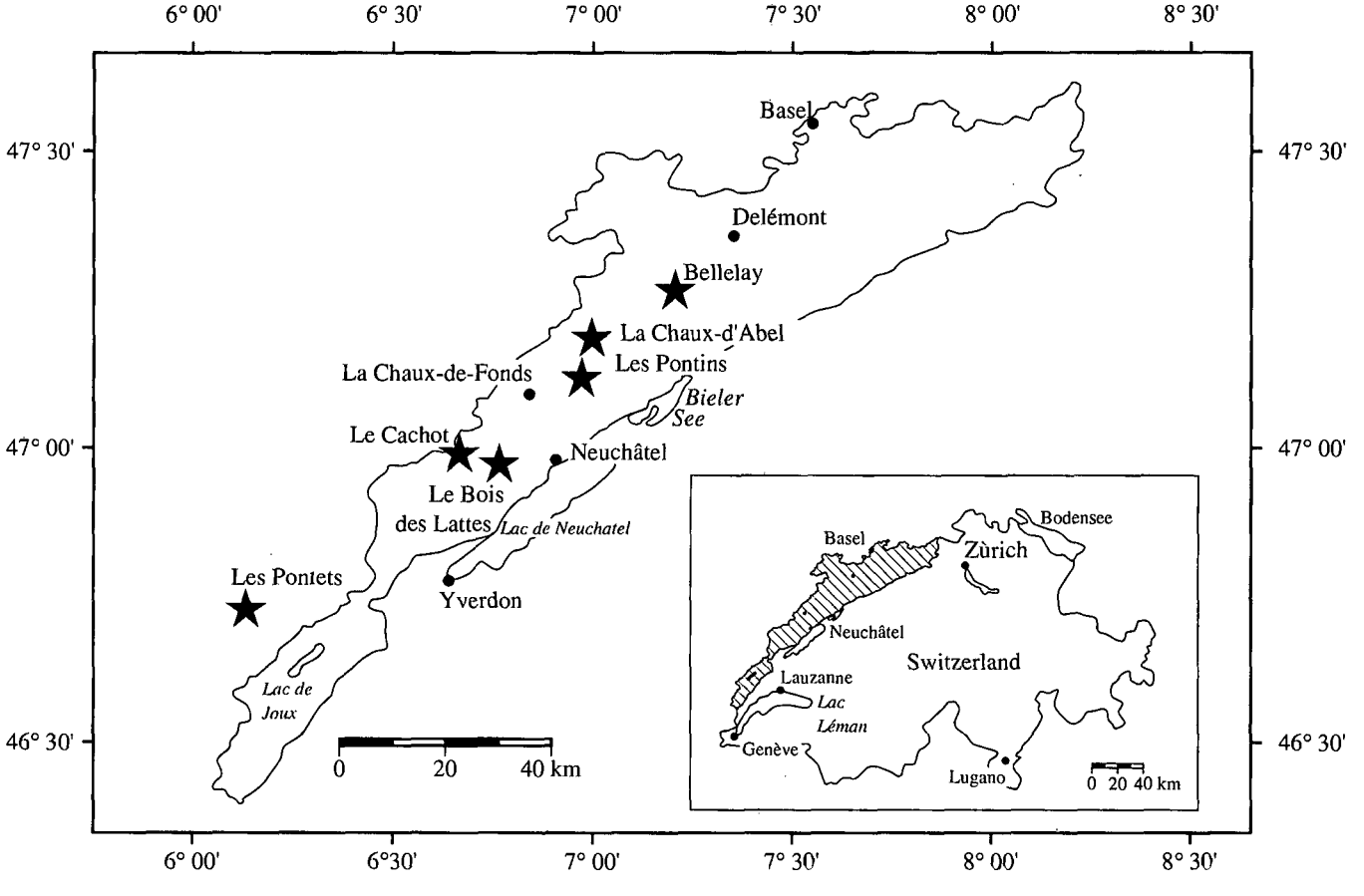


FIGURE 1. Map showing the location of the sampling sites in bogs (black stars) in the Jura region of Switzerland and France.

TABLE I. Site characteristics of the samples analysed

| Sample | Group | Species | Mire | Swiss national maps coordinates | Altitude (m.a.s.l.) | Habitat type |
|---|---|---|---|---|---|---|
| 1 | 1 | *Sphagnum warnstorfii* | Les Pontets (F) | 174.1-502.3 | 1005 | Fen 40 m from the lake shore, small hummock |
| 2 | 1 | *S. teres* | Les Pontets (F) | 174.1-502.3 | 1005 | Fen 40 m from the lake shore |
| 3 | 1 | *S. contortum* | Les Pontets (F) | 174.1-502.3 | 1005 | Fen 40 m from the lake shore |
| 4 | 1 | *S. contortum* + *S. subsecundum* | Les Pontets (F) | 174.1-502.3 | 1005 | Fen 40 m from the lake shore |
| 5 | 5 | *S. magellanicum* | Le Cachot (CH) | 541.2-206.4 | 1050 | Center of the bog, *Sphagnum* lawn |
| 6 | 5 | *S. magellanicum* | Le Cachot (CH) | 541.2-206.4 | 1050 | Center of the bog, *Sphagnum* lawn |
| 7 | 5 | *S. angustifolium* | Le Cachot (CH) | 541.2-206.4 | 1050 | Center of the bog, *Sphagnum* lawn |
| 8 | 5 | *S. angustifolium* | Le Cachot (CH) | 541.2-206.4 | 1050 | Center of the bog, *Sphagnum* lawn |
| 9 | 2 | *S. fuscum* | Le Cachot (CH) | 541.2-206.4 | 1050 | Center of the bog, large hummock |
| 10 | 2 | *S. fuscum* | Le Cachot (CH) | 541.2-206.4 | 1050 | Center of the bog, small hummock |
| 11 | 5 | *S. rubellum* | Le Cachot (CH) | 541.2-206.4 | 1050 | Center of the bog, small hummock |
| 12 | 5 | *S. subsecundum* | Le Cachot (CH) | 541.2-206.4 | 1050 | Center of the bog, small pool |
| 13 | 2 | *S. magellanicum* | Le Cachot (CH) | 541.2-206.4 | 1050 | Center of the bog, hummock under *Pinus rotundata* |
| 14 | 2 | *S. angustifolium* | Le Cachot (CH) | 541.2-206.4 | 1050 | Center of the bog, hummock under *P. rotundata* |
| 15 | 5 | *S. cuspidatum* | Le Cachot (CH) | 541.2-206.4 | 1050 | Large *Scheuchzeria palustris* bog pool |
| 16 | 2 | *S. capillifolium* | Le Cachot (CH) | 541.3-206.3 | 1050 | Tall *P. rotundata* forest, hummock |
| 17 | 2 | *S. magellanicum* | Le Cachot (CH) | 541.3-206.3 | 1050 | Tall *P. rotundata* forest, hummock |
| 18 | 3 | *S. angustifolium* | Le Cachot (CH) | 541.3-206.3 | 1050 | Tall *P. rotundata* forest, hummock |
| 19 | 3 | *Hylocomnium splendens* | Le Cachot (CH) | 541.3-206.3 | 1050 | Tall *P. rotundata* forest |
| 20 | 3 | *Dicranum polysetum* | Le Cachot (CH) | 541.3-206.3 | 1050 | Tall *P. rotundata* forest |
| 21 | 3 | *Polytrichum strictum* | Le Cachot (CH) | 541.1-206.4 | 1050 | Cutover bog surface |
| 22 | 4 | *S. centrale* | Les Pontins (CH) | 566-219.8 | 1095 | Meadow |
| 23 | 2 | *S. centrale* | Les Pontins (CH) | 566-219.8 | 1095 | Meadow |
| 24 | 3 | *S. girgensohnii* | Les Pontins (CH) | 565.8-219.8 | 1095 | *Sphagno-Piceetum* on the side of a drainage ditch |
| 25 | 3 | *S. girgensohnii* | Les Pontins (CH) | 565.8-219.8 | 1095 | *Sphagno Piceetum* |
| 26 | 2 | *S. magellanicum* | Les Pontins (CH) | 565.8-219.8 | 1095 | *Sphagno-Piceetum* on the side of a drainage ditch |
| 27 | 3 | *S. magellanicum* | Les Pontins (CH) | 565.8-219.8 | 1095 | *Sphagno Piceetum* |
| 28 | 5 | *S. cuspidatum* | Les Pontins (CH) | 566-219.7 | 1095 | Center of the bog, pool |
| 29 | 5 | *S. tenelum* | Les Pontins (CH) | 566-219.7 | 1095 | Center of the bog, side of a pool |
| 30 | 5 | *S. cuspidatum* | Les Pontins (CH) | 566-219.7 | 1095 | Center of the bog, pool |
| 31 | 5 | *S. magellanicum* | Les Pontins (CH) | 566-219.7 | 1095 | Center of the bog, hummock |
| 32 | 5 | *S. rubellum* | Les Pontins (CH) | 566-219.7 | 1095 | Center of the bog, hummock |
| 33 | 5 | *S. fallax* | Les Pontins (CH) | 566-219.7 | 1095 | Center of the bog, pool |
| 34 | 5 | *S. fallax* | Les Pontins (CH) | 566-219.7 | 1095 | Depression on the edge of the bog |
| 35 | 2 | *S. fuscum* | Les Pontins (CH) | 566-219.7 | 1095 | Center of the bog, small hummock |
| 36 | 5 | *S. cuspidatum* | Les Pontins (CH) | 566.2-219.7 | 1095 | Cutover bog, ditch |
| 37 | 5 | *S. cuspidatum* | Les Pontins (CH) | 566.2-219.7 | 1095 | Cutover bog, wet conditions |
| 38 | 4 | *S. fallax* | Le Bois des Lattes (CH) | 545.3-203.7 | 1000 | Side of a peat extraction ditch |
| 39 | 4 | *S. centrale* | Le Bois des Lattes (CH) | 545.3-203.7 | 1000 | Side of a peat extraction ditch |
| 40 | 4 | *S. fallax* | Le Bois des Lattes (CH) | 545.3-203.7 | 1000 | Side of a peat extraction ditch |
| 41 | 3 | *S. capillifolium* | Le Bois des Lattes (CH) | 545.3-203.7 | 1000 | Dry bog with *Betula nana* and *Calluna vulgaris* |
| 42 | 4 | *S. teres* | Le Bois des Lattes (CH) | 545.3-203.7 | 1000 | Side of a peat extraction ditch |
| 43 | 4 | *S. teres* | Le Bois des Lattes (CH) | 545.3-203.7 | 1000 | Side of a peat extraction ditch |
| 44 | 4 | *S. palustre* | Le Bois des Lattes (CH) | 545.3-203.7 | 1000 | *Betula* forest near a peat extraction ditch |
| 45 | 4 | *S. centrale* | Le Bois des Lattes (CH) | 545.3-203.7 | 1000 | Side of a peat extraction ditch |
| 46 | 3 | *S. centrale* | Le Bois des Lattes (CH) | 545.3-203.7 | 1000 | *Betula pendula* forest |
| 47 | 4 | *S. palustre* | Le Bois des Lattes (CH) | 545.3-203.7 | 1000 | *B. pendula* forest |
| 48 | 4 | *S. magellanicum* | Le Bois des Lattes (CH) | 545.3-203.7 | 1000 | Side of a peat extraction ditch |
| 49 | 5 | *S. cuspidatum* | Le Cachot (CH) | 541.2-206.4 | 1050 | Large *Scheuchzeria palustris* bog pool |
| 50 | 5 | *S. cuspidatum* | Le Cachot (CH) | 541.2-206.4 | 1050 | Path on the side of a large bog pool |
| 51 | 3 | *Pleurozium schreberi* | Le Cachot (CH) | 541.1-206.4 | 1050 | Tall *P. rotundata* forest |
| 52 | 8 | *Eriopharum vaginatum* litter | Les Pontins (CH) | 566.2-219.7 | 1095 | Secondary peat - dry site |
| 53 | 8 | Bare peat with algae | Les Pontins (CH) | 566.2-219.8 | 1095 | Secondary peat - dry site |
| 54 | 6 | Central part of an *E. vaginatum* tussock | Les Pontins (CH) | 566.2-219.9 | 1095 | Secondary peat - dry site |
| 55 | 6 | *P. schreberi* on the side of an *E. vaginatum* tussock | La Chaux d'Abel (CH) | 562.8-225.2 | 1000 | Secondary peat - dry site |
| 56 | 6 | *S. fallax* | La Chaux d'Abel (CH) | 562.8-225.2 | 1000 | Secondary peat - dry site |
| 57 | 6 | *E. vaginatum* litter on the side of a tussock | La Chaux d'Abel (CH) | 562.8-225.2 | 1000 | Secondary peat - dry site |
| 58 | 7 | *S. fallax* | La Chaux d'Abel (CH) | 562.8-225.2 | 1000 | Secondary peat - dry site |
| 59 | 6 | *E. vaginatum* litter on the side of a tussock | La Chaux d'Abel (CH) | 562.8-225.2 | 1000 | Secondary peat - dry site |
| 60 | 6 | Bare peat on cutover surface | Le Cachot (CH) | 541.1-206.4 | 1050 | Secondary peat - dry site |
| 61 | 6 | *Polytrichum strictum* | Le Cachot (CH) | 541.1-206.4 | 1050 | Secondary peat - dry site |
| 62 | 7 | *S. fallax* saturated | Bellelay (CH) | 580-233.7 | 930 | Secondary peat - wet site, early stage of regeneration |
| 63 | 7 | *S. fallax* | Bellelay (CH) | 580-233.7 | 930 | Secondary peat - wet site, intermediate stage |
| 64 | 7 | *S. fallax* | Bellelay (CH) | 580-233.7 | 930 | Secondary peat - wet site, final stage |

immediately next to the tin can sample, along with an additional 16 samples from other sites, were collected for analysis of testate amoebae and measurement of peat pH. The depth to the water table (*DWT*) was measured at the time of field sampling at all sampling sites. Taxonomy follows Tutin *et al.* (1964-1980) for vascular plants, Isoviita (1967) for *Sphagnum*, and Smith (1980) for other mosses.

### LABORATORY ANALYSES

Tin can samples were used to quantify water content and water retention capacity of the living moss and peat layers by the following procedure:

(*i*) tin can samples were weighed to determine fresh weight (*FR*);
(*ii*) tin can was then filled with distilled water to determine saturated weight (*SAT*) of the samples;
(*iii*) tin can samples were left in the open for 12 days and reweighed to determine evaporated weight (*EV*);
(*iv*) remaining water was allowed to drain from the tin can and then weighed after one hour to determine drained weight (*DR*);
(*v*) tin can samples were then placed in an oven at 105°C for 24 hours before reweighing to determine dry weight (*DW*).

Water content of the fresh samples (*WFr*) was calculated by the following:

$$WFr = FR\text{-}DW \quad [1]$$

Water content of the evaporated samples (*WEv*) was calculated by the following:

$$WEv = EV - DW \quad [2]$$

Water content of the drained samples (*WDR*) was calculated by the following:

$$WDR = DR - DW \quad [3]$$

*WFr*, *WEv*, and *WDR* were expressed as either percent free volume (*WFr*/*V*, *WEv*/*V*, *WDr*/*V*) or as percent dry weight (*WFr*/D, *WEv*/D, *WDr*/D). Total porosity was calculated using the following formula, where *PORO* = total porosity, *d* = density of water:

$$PORO \text{ (percent volume)} = 100 * d\,(SAT - DW)/V \quad [4]$$

Peat pH was measured in two ways: (*i*) in a 1:1 solution with distilled water (true acidity, pH [$H_2O$]), and (*ii*) in a 1:1 solution with 1 M KCl (potential acidity, pH [KCl]).

### TESTATE AMOEBAE ANALYSIS

Subsamples of 5 $cm^3$ were boiled five minutes in water to dissaggregate the samples and release the shells from the mosses, then sieved on a 300 µm mesh sieve (Tolonen, 1986; Tolonen, Warner & Vasander, 1992). A drop of the concentrate was placed in glycerine oil and safranine stain on a slide and covered with a cover slip (20 mm × 20 mm). The entire cover slip was scanned at 400× magnification. All testate amoebae were identified and counted to a mean total of 264 shells (min. = 146, max. = 418, SD = 63). The following references aided with identification: Penard (1902), Deflandre (1936), Grospietsch (1958; 1964), Corbet (1973), and Ogden & Hedley (1980). The bdelloid rotifer *Habrotrocha angusticollis*, commonly found with testate amoebae, was also included in the tabulations.

### STATISTICAL ANALYSES

All testate amoebae counts were transformed using the logarithm to reduce the weight of dominant taxa such as *Pseudodifflugia fulva* and *Cryptodifflugia oviformis*, because the dominance of such taxa is not necessarily proportional to their value as bioindicators or to their ecological importance. In the case of testate amoebae whose shells range from 10 µm to over 200 µm in length, important differences in numbers may be related to the range of sizes of the animals.

### RELATIONSHIP BETWEEN TESTATE AMOEBAE AND ENVIRONMENTAL VARIABLES

Relationships between testate amoebae and five selected environmental variables (Table II) were quantified by calculating weighted averages (*WA*) and weighted standard deviations (*WSD*) using the following formulae (Tolonen, Warner & Vasander, 1992; Warner & Charman, 1994), where $n$ = total number of samples; $X_j$ = value of the environmental variable $X$ for sample $j$; $P_{ij}$ = abundance of species $i$ in sample $j$; $N_i$ = total abundance of species $i$ in all the samples; $WA_iX$ = weighted average of species $i$ for variable $X$; $WSD_iX$ = weighted standard deviation of species $i$ for variable $X$:

$$P'_{ij} = 1n\,(P_{ij} + 1) \quad [5]$$

$$N_i = \Sigma_{j=1 \text{ to } n}\,(P_{ij}) \quad [6]$$

$$WA_iX = (1/N_i) * \Sigma_{j=1 \text{ to } n}\,(P'_{ij} * X_j) \quad [7]$$

$$WSD_iX = (1/N_i) * \Sigma_{j=1 \text{ to } n}\left(P'_{ij}\,(X_j - WA_iX)^2\right)^{-2} \quad [8]$$

### JACK-KNIFING PROCEDURES

Quantitative relationships between species abundance and environmental variables can be modeled to predict either existing environmental variables or to infer environmental conditions. However, the performance of such models can be tested using the "jack-knifing" cross validation technique (Juggins, 1992; Birks, 1995; Charman & Warner, 1997). In this procedure, a transfer function is derived from all samples except one and is then applied to that sample to produce predicted values that can in turn be compared with observed values for the sample. The WA of the species is, therefore, slightly different for every repetition. This cross validation was applied to selected environmental variables (Figure 2). As the transfer function is derived from all samples except one, taxa occurring only once were excluded from the analysis.

### CLUSTER ANALYSIS

Cluster analysis was used to determine the level of similarity (or dissimilarity) between testate amoebae communities (*Q*-mode analysis) and environmental variables (*R*-mode analysis), using the programs in the *r* package (Release 3.0; Legendre & Vaudor, 1991). The program SIMIL was used to obtain similarity matrices that were then used by the program GROUPEMENT to proceed to cluster analysis. Preliminary dendrograms were produced using this method. Similarity matrices were calculated using the Steinhaus similarity index (Legendre & Legendre, 1998) for comparison with species abundance analysis (Figure 3a). The Pearson correlation was used for comparisons of

TABLE II. Weighted average (*WA*) and weighted standard deviation (*WSD*) of 45 testate amoebae species and the rotifer *Habrotrochoa angusticollis* for pH($H_2O$), depth to the water table (*DWT*), water in fresh samples (% of volume; *WFr/V*), total porosity (*PORO*), and water content after one hour drainage (% of volume; *WDr*1h/*V*)

| | | pH($H_2O$) | | *DWT* (cm) | | *WFr/V* (% Vol) | | *PORO* (% Vol) | | *WDr*1h/*V* (% Vol) | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | *N* | *WA* | *WSD* | *WA* | *WSD* | *WA* | *WSD* | *WA* | *WSD* | *WA* | *WSD* |
| *Amphitrema flavum* | 20 | 4.2 | 0.4 | 11 | 7 | 61 | 19 | 90 | 3 | 67 | 13 |
| *Amphitrema wrightianum* | 10 | 4.1 | 0.2 | 9 | 5 | 59 | 20 | 90 | 3 | 64 | 16 |
| *Arcella arenaria* | 22 | 5.2 | 0.7 | 30 | 21 | 30 | 13 | 92 | 3 | 49 | 9 |
| *Arcella artocrea* | 7 | 4.1 | 0.1 | 14 | 7 | 52 | 18 | 90 | 2 | 63 | 13 |
| *Arcella gibbosa* | 5 | 5.3 | 0.7 | 21 | 10 | 35 | 11 | 90 | 1 | 55 | 9 |
| *Assulina muscorum* | 44 | 4.3 | 0.3 | 59 | 49 | 34 | 19 | 91 | 3 | 54 | 11 |
| *Assulina seminulum* | 24 | 4.0 | 0.1 | 38 | 33 | 38 | 18 | 91 | 4 | 55 | 13 |
| *Bullinularia indica* | 10 | 4.0 | 0.2 | 35 | 48 | 57 | 23 | 88 | 4 | 66 | 15 |
| *Centropyxis aculeata* | 16 | 4.9 | 0.7 | 16 | 6 | 40 | 13 | 90 | 2 | 54 | 9 |
| *Centropyxis aerophylla* | 24 | 4.6 | 0.3 | 31 | 37 | 43 | 14 | 89 | 2 | 54 | 5 |
| *Centropyxis platystoma* | 9 | 5.3 | 0.6 | 22 | 15 | 39 | 14 | 92 | 3 | 51 | 9 |
| *Corythion dubium* | 44 | 4.3 | 0.4 | 58 | 53 | 34 | 18 | 90 | 3 | 53 | 12 |
| *Cryptodifflugia oviformis* | 14 | 4.1 | 0.3 | 35 | 36 | 51 | 20 | 87 | 2 | 65 | 11 |
| *Cyclopyxis arcelloides* | 8 | 4.3 | 0.2 | 18 | 18 | 48 | 13 | 90 | 2 | 57 | 7 |
| *Euglypha ciliata* | 38 | 4.2 | 0.3 | 37 | 39 | 42 | 21 | 89 | 3 | 57 | 13 |
| *Euglypha compressa* | 8 | 4.1 | 0.1 | 24 | 7 | 36 | 11 | 92 | 2 | 58 | 7 |
| *Euglypha cristata* | 8 | 4.8 | 0.3 | 15 | 6 | 41 | 11 | 90 | 1 | 52 | 5 |
| *Euglypha laevis* | 29 | 4.2 | 0.4 | 28 | 29 | 49 | 21 | 89 | 3 | 62 | 12 |
| *Euglypha rotuda* | 30 | 4.5 | 0.4 | 31 | 24 | 34 | 15 | 90 | 2 | 52 | 9 |
| *Euglypha strigosa* | 25 | 4.3 | 0.4 | 53 | 42 | 36 | 19 | 89 | 4 | 55 | 12 |
| *Heleopera petricola* | 33 | 4.2 | 0.3 | 44 | 37 | 39 | 21 | 90 | 3 | 56 | 13 |
| *Heleopera rosea* | 28 | 4.4 | 0.7 | 30 | 26 | 38 | 14 | 90 | 3 | 57 | 10 |
| *Hyalosphenia elegans* | 19 | 4.1 | 0.2 | 18 | 7 | 48 | 16 | 90 | 3 | 63 | 11 |
| *Hyalosphenia minuta* | 5 | 3.9 | 0.1 | 16 | 7 | 61 | 14 | 89 | 4 | 71 | 7 |
| *Hyalosphenia papilio* | 20 | 4.4 | 0.7 | 14 | 9 | 49 | 20 | 92 | 3 | 59 | 15 |
| *Hyalosphenia subflava* | 6 | 4.0 | 0.2 | 59 | 51 | 48 | 20 | 87 | 3 | 62 | 12 |
| *Nebela bohemica* | 7 | 5.6 | 0.8 | 40 | 34 | 31 | 11 | 92 | 2 | 53 | 12 |
| *Nebela carinata* | 5 | 4.2 | 0.2 | 10 | 5 | 64 | 13 | 88 | 1 | 67 | 8 |
| *Nebela collaris* | 5 | 5.8 | 0.6 | 24 | 7 | 29 | 11 | 94 | 3 | 47 | 13 |
| *Nebela dentistoma* | 10 | 5.1 | 0.6 | 48 | 38 | 31 | 13 | 91 | 2 | 52 | 7 |
| *Nebela griseola* | 17 | 4.1 | 0.1 | 16 | 7 | 50 | 18 | 90 | 2 | 64 | 11 |
| *Nebela marginata* | 9 | 4.2 | 0.2 | 9 | 4 | 62 | 15 | 89 | 2 | 65 | 12 |
| *Nebela militaris* | 40 | 4.1 | 0.3 | 48 | 40 | 38 | 19 | 89 | 3 | 56 | 12 |
| *Nebela penardiana* | 9 | 4.7 | 0.8 | 21 | 15 | 37 | 10 | 91 | 2 | 55 | 10 |
| *Nebela tincta* | 48 | 4.2 | 0.3 | 58 | 44 | 34 | 18 | 89 | 3 | 54 | 11 |
| *Nebela tubulosa* | 8 | 5.5 | 0.9 | 15 | 6 | 47 | 13 | 91 | 2 | 61 | 11 |
| *Nebela wailesi* | 6 | 4.5 | 0.4 | 17 | 19 | 52 | 13 | 89 | 2 | 59 | 9 |
| *Phryganella acropodia* | 38 | 4.4 | 0.4 | 70 | 51 | 32 | 16 | 89 | 3 | 53 | 10 |
| *Placocista spinosa* | 8 | 4.0 | 0.2 | 22 | 28 | 58 | 19 | 88 | 2 | 67 | 12 |
| *Pseudodifflugia fulva* | 25 | 4.0 | 0.2 | 14 | 19 | 68 | 14 | 87 | 1 | 73 | 8 |
| *Quadruella symmetrica* | 5 | 5.8 | 0.4 | 33 | 18 | 23 | 8 | 94 | 3 | 42 | 8 |
| *Sphenoderia lenta* | 7 | 5.0 | 0.5 | 25 | 26 | 39 | 11 | 87 | 3 | 53 | 6 |
| *Tracheleuglypha dentata* | 15 | 4.9 | 0.5 | 20 | 17 | 42 | 14 | 90 | 2 | 55 | 7 |
| *Trigonopyxis arcula* | 21 | 4.1 | 0.3 | 60 | 42 | 28 | 13 | 92 | 4 | 49 | 10 |
| *Trinema sp.* | 31 | 4.7 | 0.4 | 63 | 42 | 27 | 13 | 91 | 2 | 51 | 8 |
| *Habrotrochoa angusticollis* | 15 | 4.3 | 0.6 | 30 | 27 | 39 | 12 | 90 | 3 | 57.9 | 7.4 |

environmental variables. All cluster analyses were made using the Lance and Williams algorithm with the option "proportional weight" (Legendre & Legendre, 1998).

### CANONICAL CORRESPONDENCE ANALYSIS

A canonical correspondence analysis (CCA; CANOCO release 3.11; ter Braak, 1988-1992) was used to model the relationship between testate amoebae distributions and environmental variables. All testate amoebae taxa were included in these analyses. An initial forward selection analysis was made to select the strongest relationships. The results, together with the results of the cluster analysis of the 18 environmental variables, identified the main environmental variables for the CCA (Figure 3a, 3b; Tables III and IV).

Abundances were used to calculate the ordination of the samples, as in the correspondence analysis, but the ordination axes were constrained to be linear combinations of the environmental variables (ter Braak, 1987). This ensures that the canonical axes are optimally related to the environmental descriptors.

Partial CCA was applied to check the reliability of the selected environmental variables (Table V). The percentage of variation explained by a given environmental variable and shared with the other four variables was assessed by comparing its eigenvalue from a first CCA, in which only one variable was considered with its eigenvalue from a second CCA where the effect of the other variables was excluded. In the second CCA, one variable is used as the environmental variable and the others are treated as covariables.

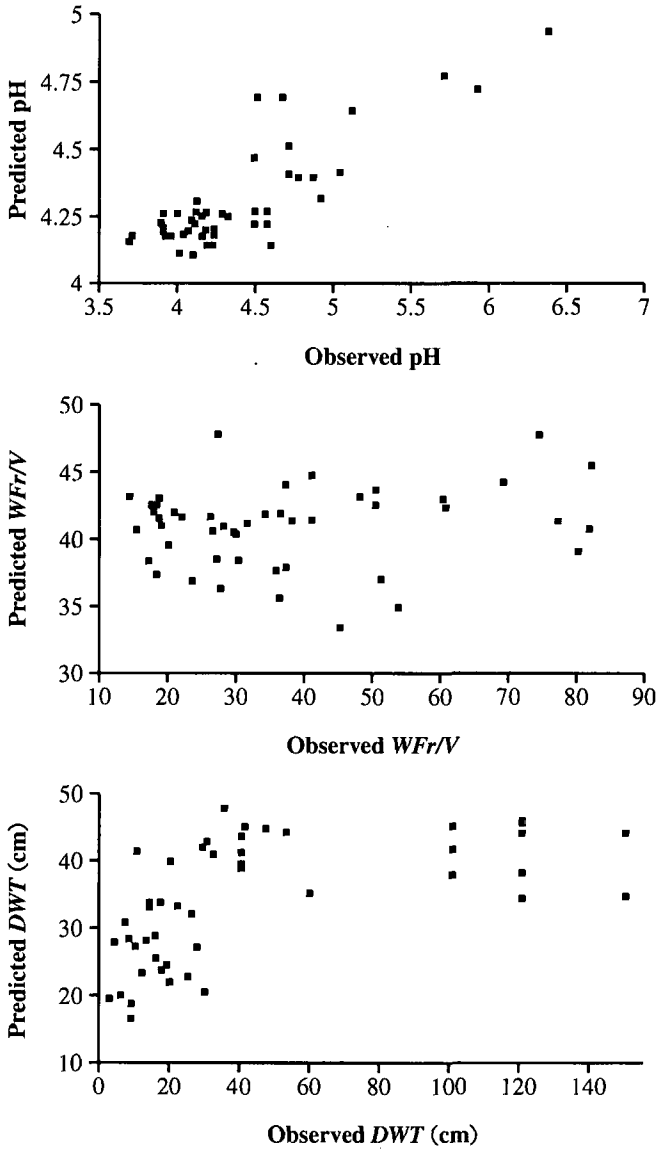


FIGURE 2. Observed parameters for pH ($H_2O$), depth to water table (*DWT*), water content of fresh samples (% volume; *WFr/V*) plotted against predicted values using the jack-knifing procedure.

A down-weighting of rare taxa and a down-weighting of extreme samples by giving them a weight of 0.1 were used in both CCA analyses.

### INDICATOR VALUE OF TAXA

Indicator values (program IndVal; Dufrêne & Legendre, 1997) were used to identify taxa that are characteristic of each group of samples included in a single level in a dendrogram of the hierarchical classification. This program produces an indicator value (*IV*; maximum value 100%) for each taxon and for each level of the dendrogram (Figure 4). The *IV* for each taxon $i$ in each sample group $j$ is calculated as the product of $A_{ij}$, the quotient of the mean abundance of taxa $i$ in the samples of group $j$ ($N$ specimens $ij$) and abundance of taxon $i$ in all samples in the study ($N$ specimens $i$), by $B_{ij}$, the relative frequency of occurrence of taxa $i$ in the samples of group $j$ as follows:

$$A_{ij} = (N \text{ specimens } ij \,/\, N \text{ specimens } i) \qquad [9]$$

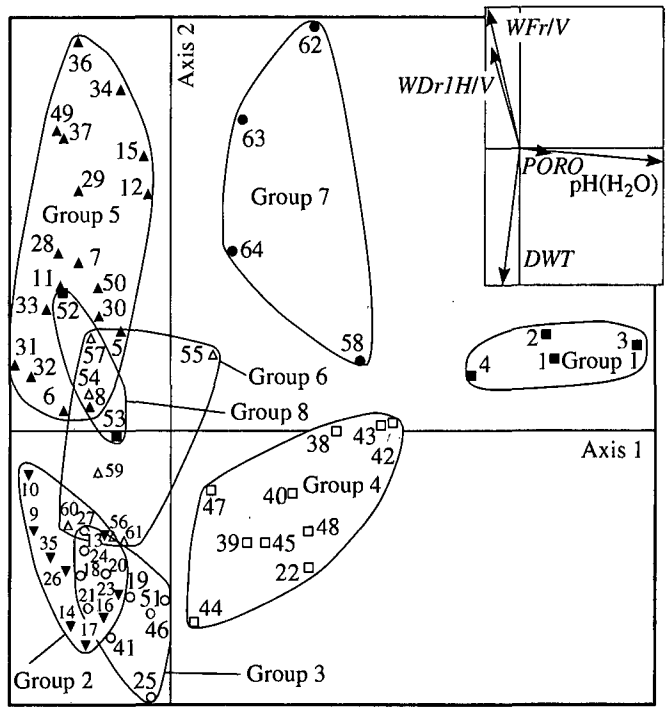


FIGURE 3a. CCA ordination results of axis 1 and axis 2 for testate amoebae taxa using forward selection of environmental variables. The environmental variables selected in the forward selection procedure corresponding to axes 1 and 2 is shown in the inset. Scatter diagram of the samples grouped according to the clustering.

$$B_{ij} = (N \text{ samples } ij \,/\, N \text{ samples } j) \qquad [10]$$

$$IV_{ij}\,(\%) = A_{ij} * B_{ij} * 100 \qquad [11]$$

The IndVal method identifies indicator species for types of ecological samples obtained by any hierarchical or non-hierarchical classification procedure. It is independent of the classification. The *IV* of a taxon will be highest for a classification based on species abundances. We used a dendrogram resulting from the cluster analysis of habitats based on testate amoebae abundance. Only the groups represented by a minimum of three samples and taxa present in at least two samples were used in the analysis. This selection resulted in

TABLE III. Summary of the canonical correspondence analysis

| | Axis 1 | Axis 2 | Axis 3 |
|---|---|---|---|
| Eigenvalues | 0.312 | 0.182 | 0.068 |
| Species-environment correlations | 0.937 | 0.813 | 0.737 |
| Cumulative percentage variance: | | | |
| of species data | 16.6 | 26.3 | 29.9 |
| of species-environment relation | 49.5 | 78.3 | 89.2 |

TABLE IV. Correlations of the five variables for the three axes of the CCA

| | Axis 1 | Axis 2 | Axis 3 |
|---|---|---|---|
| pH($H_2O$) | 0.741 | -0.048 | 0.012 |
| *DWT* | -0.088 | -0.551 | 0.203 |
| *PORO* | 0.162 | -0.019 | -0.403 |
| *WFr/Sat* | -0.169 | 0.551 | 0.190 |
| *WDr1h/S* | -0.151 | 0.414 | 0.145 |

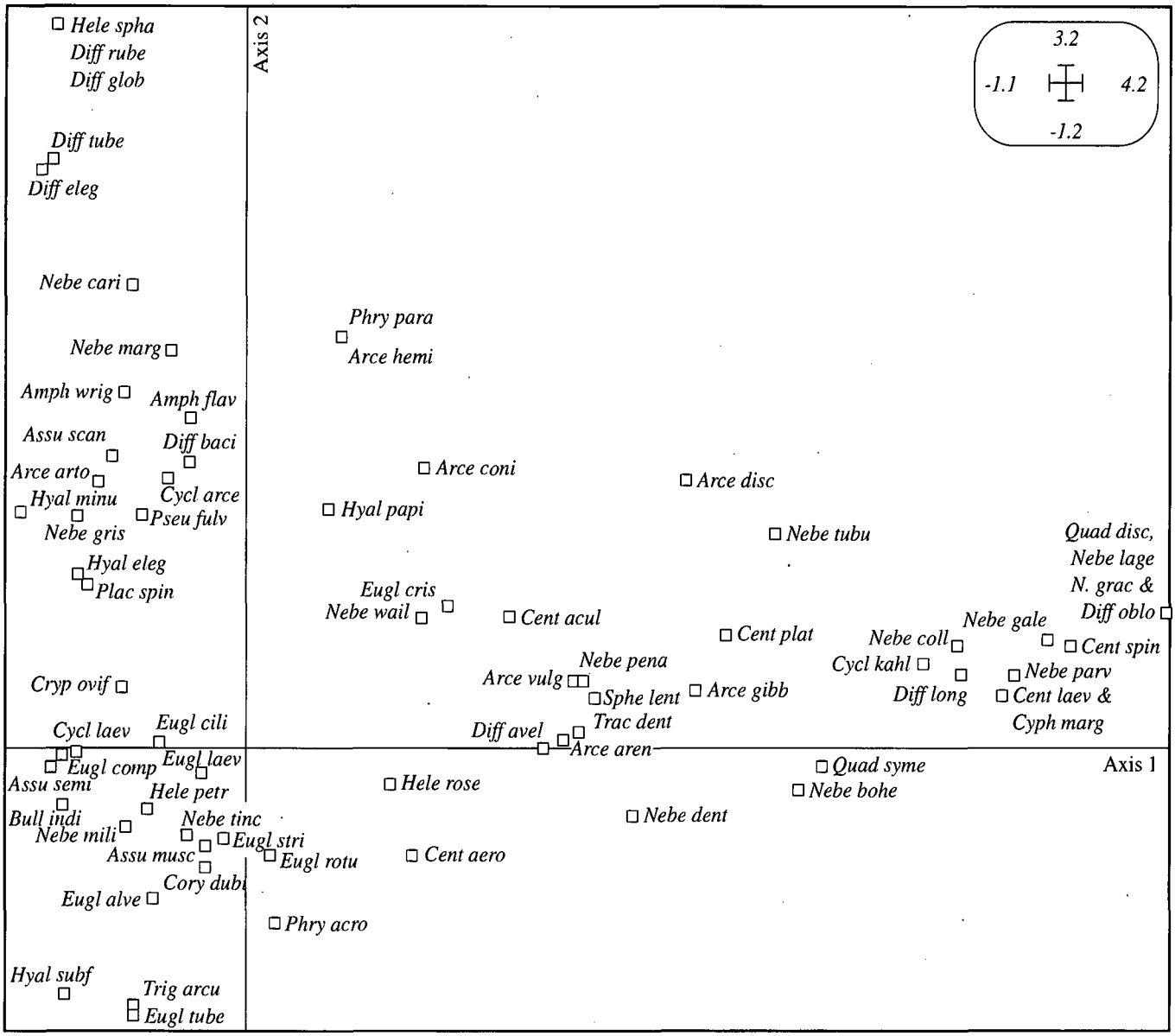


FIGURE 3b (concluded). Scatter diagram of the taxa, axes 1 and 2. Full names are given in Table II.

a modified matrix with a total of 57 taxa in 51 samples, which were used for the identifying indicator species. A given taxon is most characteristic at the level of the dendrogram at which its *IV* is highest. The statistical significance of the *IV* was assessed by ranking the observed value in the randomly generated distribution in decreasing order (permutational probability, 999 permutations).

## Results

### ECOLOGICAL CENTROID OF TAXA

Five environmental variables emerged most strongly from the forward selection of all 11 environmental variables in the canonical correspondence analysis. The same five environmental variables were also representative of the main groups identified by the cluster analysis. The environmental variables in order of strength are: pH ($H_2O$), depth to water table (*DWT*), water in fresh sample

TABLE V. Summary of the partial canonical correspondence analyses of testate amoebae data

| | CCA+ | | Partial CCA* | | % of eigenvalue |
|---|---|---|---|---|---|
| | Eigenvalue (A) | % of total inertia | Eigenvalue (B) | % of total inertia | shared with the othe four variables # |
| pH | 0.308 | 16.4 | 0.278 | 14.8 | 9.7 |
| *WFr/V* | 0.158 | 8.4 | 0.075 | 4.0 | 53 |
| *DWT* | 0.149 | 7.9 | 0.057 | 3.0 | 62 |
| *WDr 1h/V* | 0.107 | 5.7 | 0.046 | 2.4 | 57 |
| *PORO* | 0.069 | 3.7 | 0.044 | 2.3 | 36 |
| Total inertia | 1.878 | | | | |

+ Analysis with only one variable in the model. The % of total inertia indicate the proportion of the variation of the species data explained by the variables.

* Partial analysis with one variable in the model and 4 covariables. The proportion of the variation explained by the variable is lower because a part of the variation explained by the variable is also explained by the other four variables.

# Calculated as: 100*(A-B)/A.

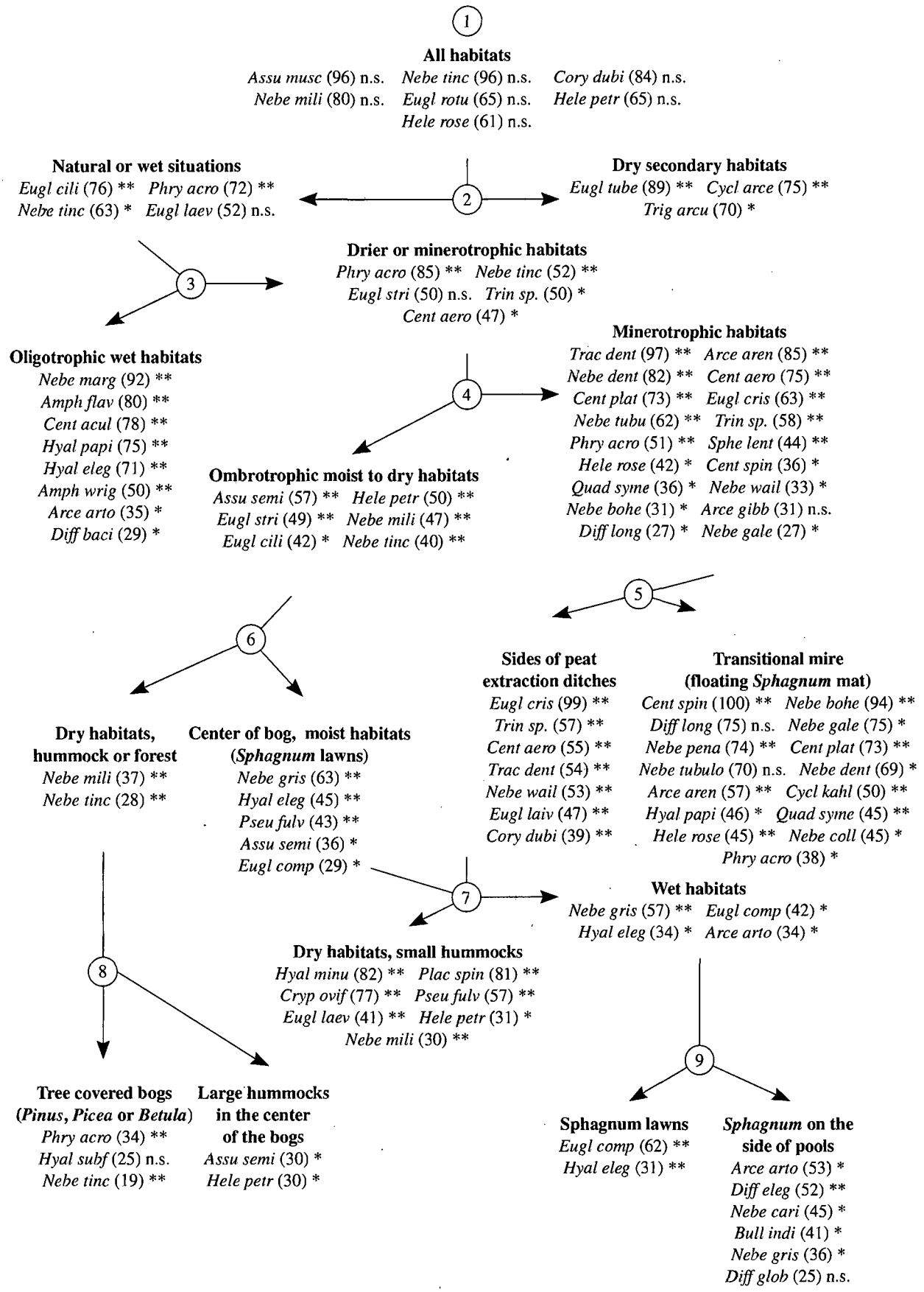


FIGURE 4. Common testate amoebae faunas in relation to site types found in this study with their indicator value (*IV* in %) using IndVal. Full names are given in table II. Bold characters indicate maximum indicator value for the species. *P*-values are indicated as follows: **: $p < 0.01$; *: $p<0.05$; n.s.: $p> 0.05$.

(*WFr/V*), total porosity (*PORO*), and water in sample drained one hour (*WDr/V*). Other environmental variables obtained from the evaporation and drainage experiments correlated closely to one of these five variables and were excluded from further analyses.

Weighted averages (*WA*) and weighted standard deviations (*WSD*) for 45 testate amoebae taxa and the rotifer *Habrotrocha angusticollis* using the five selected variables are closely linked to the number of samples in which the taxa occurred (Table II). Thus, only taxa that occurred in at least five samples are presented in the tables. *WSD*s for the various taxa can be used to identify the most important indicators for the different environmental variables.

Peat pH preferences range from 3.9 (*Hyalosphenia minuta*, a taxon characteristic of small ombrotrophic hummocks) to 5.8 (*Nebela collaris* and *Quadruella symmetrica*, two taxa indicative of minerotrophic wet habitats; Table II, Figure 4). Five taxa appear to be good indicators of pH as suggested by their low *WSD*: *Hyalosphenia minuta, Assulina seminulum, Nebela griseola*, and *Arcella artocrea*.

Water depth preferences range from 9 cm (*Nebela marginata, Amphitrema wrightianum*, two taxa characteristic of oligotrophic wet sites) to 70 cm (*Phyryganella acropodia*, a taxon of dry minerotrophic sites; Table II, Figure 4). Thirteen taxa emerge as good indicators of water table depth as suggested by the low *WSD*: *Amphitrema wrightianum, Centropyxis aculeata, Euglypha cristata, Nebela carinata, N. marginata, N. tubulosa, Amphitrema flavum, Arcella artocrea, Euglypha compressa, Hyalosphenia elegans, H. minuta, Nebela collaris*, and *N. griseola*.

*WA*s for *WFr/V* range from 68% (*Pseudodifflugia fulva*, a taxon common in small ombrotrophic hummocks) to 23% (*Quadruella symmetrica*; Table II, Figure 4). High values for *WFr/V* indicate that water content was close to maximum capacity when the samples were collected and low values indicate that much of the available volume was filled with air. Seven taxa appear to be good indicators of *WFr/V* as suggested by their low WSD: *Arcella gibbosa, Euglypha compressa, E. cristata, Nebela bohemica, N. collaris, Sphenoderia lenta*, and *Quadruella symmetrica*.

*WA*s for porosity (*PORO*) range from 87% (*Hyalosphenia subflava, Pseudodifflugia fulva, Cryptodifflugia oviformis, Sphenoderia lenta*, taxa which are common in tree-covered peatlands or minerotrophic habitats in the Jura) to 94% (*Quadruella symmetrica, Nebela collaris*; Table II, Figure 4). Four taxa appear to be good indicators for *PORO* as suggested by their low *WSD*: *Arcella gibbosa, Euglypha cristata, Nebela carinata*, and *Pseudodifflugia fulva*.

*WA*s for *WDr/V* range from 42% (*Quadruella symmetrica*) to 73% (*Pseudodifflugia fulva*; Table II, Figure 4). Eight taxa appear to be good indicators for *WDr/V* as suggested by their low *WSD*: *Centropyxis aerophylla, Cyclopyxis arcelloides, Euglypha compressa, E. cristata, Hyalosphenia minuta, Nebela dentistoma, Sphenoderia lenta*, and *Tracheleuglypha dentata*.

The results of the jack-knifing procedures, in which predicted and observed values are compared for selected environmental variables, reveal mixed reliability of transfer functions (Figure 2). A clear pattern emerges for peat pH but predicted values are, in most cases, lower than the observed values. *WFr/V* predictions appear unreliable, which is surprising considering its importance in the CCA analysis (see below). For *DWT*, two groups are recognized (Figure 2). For samples with a shallow *DWT*, predictions appear reasonable, whereas for deeper *DWT*, predictions are poor. The *DWT* data suggest a segmented model where the slope ($a$), the intercept of the linear segment ($b$), and the point of contact ($x = c$) were tested with NLIN of SAS. The resulting equations were:

$$\text{For } x < \text{or} = c \qquad y = ax + b \qquad [12]$$

$$\text{For } x > \text{or} = c \qquad y = ac + b \qquad [13]$$

The point of contact ($c$) was calculated to be $x = 41$ cm. This result confirms that deeper water tables cannot be predicted using our data set. The model overestimates *DWT* by about 10 cm between 0 and 41 cm and underestimates deeper *DWT*s.

The reliability of predictions for the other environmental variables is even less reliable than those for *DWT*.

### Habitat types based on testate amoebae assemblages

The results of the CCA show Axis 1 ($P = 0.001$) explains 16.5% of the variance and is best explained as a pH gradient ($r = 0.94$; Figures 3a, b). Axis 2 ($P = 0.001$) explains 9.6% of the variance and is best explained as a moisture gradient *WFr/V* ($r = 0.52$) and *DWT* ($r = -0.69$). Axis 3 ($P = 0.03$) is negatively correlated with *PORO* ($r = -0.58$) and explains 3.7% of the variance (Tables III and IV).

The eight groups of samples resulting from the cluster analysis independent of the CCA are represented on the first two axes of the scatter diagram (Figure 3a). Four samples taken in minerotrophic sites form Group 1. Groups 2 and 3 contain samples from more acidic sites. Group 2 represents large hummocks in the center of undisturbed peatland sites and Group 3 includes sites with an extensive tree and shrub cover. Group 4 contains minerotrophic sites either on the sides of drainage ditches, in an open forest, or open meadows. Group 5 represents all samples taken in moist to wet sites in the center of undisturbed peatlands, and Group 6 represents secondary sites on cut-over peatlands. The two samples comprising Group 8 represent sites in early successional stages in the paludification process of secondary successional sequences (Grosvernier, Matthey & Buttler, 1995). Group 7 contains four samples taken on new secondary peat grown on old cut-over bog surfaces.

The partial CCA (Table III) shows the level of independence of the five environmental variables. pH is the most independent variable. The three moisture-dependent variables, *WFr/V*, *WDr/V*, and *DWT*, show close dependency with each other. Porosity appears to be weakly related to the other variables.

### Indicator value of taxa

The nine groups of samples resulting from the second cluster analysis of the modified species × sample matrix (Figure 4) are similar to those resulting from the first unconstrained cluster analysis (Figure 3a). The nine levels in the dendrogram separate nine habitat types. The number of taxa range from 0 to 10, with the maximum indicator value varying with the different levels in the dendrogram. For ease of interpretation, additional information related to the vegetation is included in Figure 4 to show the sample groups at the different levels of the dendrogram.

The maximum indicator value (*IV*) is shown in bold on Figure 4 along with the *IV* for all taxa, even if it is not significant. Some taxa have significant *IV*s for more than one level in the dendrogram and thus it appears more than once. For example, *Hyalosphenia elegans* is mainly an indicator of oligotrophic wet habitats where it occurs with *Nebela marginata, Amphitrema flavum, Centropyxis aculeata, H. papilio, A. wrightianum, Arcella artocrea,* and *Difflugia bacillifera.* However, it also occurs with *Nebela griseola, Pseudodifflugia fulva, Assulina seminulum,* and *Euglypha compressa* as an indicator of oligotrophic moist to dry habitats in the center of bogs. Taxa such as *Assulina muscorum, Nebela tincta, N. militaris, Corythion dubium, Euglypha rotunda, Heleopera petricola,* and *H. rosea* are poor indicators of all types of habitat (Level 1) and do not have any *IV* within the range of types sampled in this study.

The *IV* of a given taxon differs among levels in the dendrogram. Between two successive levels, the difference can be positive, negative, or nil. The sum of positive and negative *IV* differences between two successive levels for all taxa can be used to cross-check the degree to which taxa can differentiate habitats (Figure 5). If the sum is negative, the two groups of samples representing two types of samples at this level cannot be separated with confidence according to Dufrêne & Legendre (1997). The sum of the differences is greatest at the fourth clustering level that separates ombrotrophic moist and dry habitats from minerotrophic habitats (Figure 4). It appears that testate amoebae have their greatest *IV* for differentiating ombrotrophic and minerotrophic habitats within the range of habitats sampled in this study.

## Discussion

### RELATIONSHIPS BETWEEN TESTATE AMOEBAE AND ENVIRONMENTAL FACTORS

In the forward selection procedure of the CCA analysis, pH emerged as the strongest factor determining testate amoebae distributions. This agrees with laboratory and field studies in Britain (Heal, 1961; 1962; 1964). Heal (1962) showed that in the laboratory, *Difflugia tuberculata* was unable to reproduce at pH lower than 4.5. In Sweden, Paulson (1952) found only a weak relationship, although her study was based on a small number of samples taken from only a few site types with relatively narrow pH range.

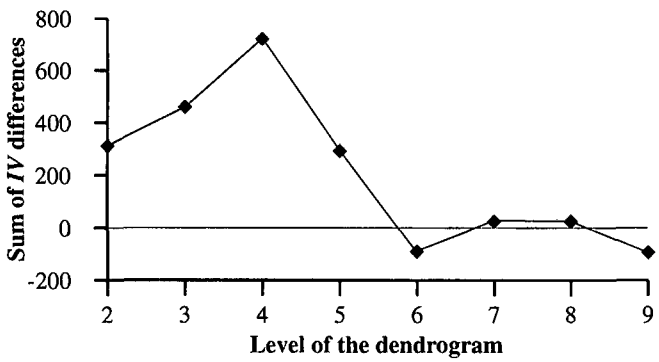


FIGURE 5. Sum of indicator value (*IV*) plotted against successive levels of the dendrogram. Each value represents the difference of the sums of indicator values over all species between two successive levels of the dendrogram. Positive values indicate levels of the dendogram for which testate amoebae can be used with confidence tc separate different types of habitats.

The strong relationship between testate amoebae distributions and water table depth in this study agrees with previous work in Finland and North America (*i.e.,* Minnesota and Ontario; Charman & Warner, 1992; 1997; Tolonen, Warner & Vasander, 1992; 1994; Warner & Charman, 1994). Given that this is the first study to include environmental variables such as *WFr/V*, *WDr/V*, and PORO, we were surprised that these variables did not emerge more strongly than they did in the analysis. We felt that *WFr/V*, *WDr/V*, and *PORO* are more accurate characterizations of the living environment of testate amoebae that reside in water films on the *Sphagnum* stems. For this reason we expected these variables to be stronger than *DWT* in the analysis. Several taxa such as *Nebela carinata, N. griseola,* and *N. marginata,* which emerged as sensitive environmental indicators, agree with observations in Canada (Charman & Warner, 1997).

*WFr/V* was selected by the forward selection in the CCA as the third strongest environmental variable, whereas *WFr/*D was much less informative. *WFr/V* was also negatively correlated to *DWT* ($r$ = -0.56). *WFr/V* correlated well ($r$ = 0.9) with *WDr/V.* This suggests that the carpet structure of mosses closely controls water content, and thus water from rain or fog is important in addition to the water table (*i.e., DWT*; Buttler *et al.,* 1996; Grosvernier, Matthey & Buttler, 1995; 1997, Gobat, Aragno & Matthey, 1998). This observation on importance of water availability reaffirms previous work on testate amoebae (Warner, 1987; Charman & Warner, 1992; 1997; Tolonen, Warner & Vasander, 1992; 1994; Warner & Charman, 1994). Ecological studies on *Sphagnum* itself shows water to be an important factor controlling distribution of these mosses (Overbeck & Happach, 1956; Clymo & Hayward, 1982; Rydin, 1985; Grosvernier, Matthey & Buttler, 1995; 1997). *DWT* and *WFr/V* are worthy of further work. It may be that one factor may emerge stronger than the other in bogs in other geographic regions.

The environmental characteristics of testate amoebae in our sites in the Jura are in line with observations in peatlands elsewhere in Europe and North America, although detailed comparisons are difficult given the different sampling procedures used in the various studies. Our *DWT* preferences correspond closely with the relative F-scale of Jung (1936) and with measurements taken in Finland (Tolonen, Warner & Vasander, 1992; 1994), in the U.S.A. and Canada (Warner, 1987; Warner & Charman, 1994; Charman & Warner, 1997). These results show that for the most part, testate amoebae taxa have similar ecological tolerances in peatlands across the northern hemisphere. Exceptions do exist, however, for taxa such as *Hyalosphenia subflava* (Charman & Warner, 1992; Warner & Charman, 1994).

*PORO* emerged as another important environmental variable on the third axis of the CCA and was negatively correlated to the *WFr/V* ($r$ = -0.56) and to *WDr*1h/*V* ($r$ = -0.47). This implies that the rain and fog water-retaining capacity of the moss carpet is an important environmental variable for testate amoebae. Porosity is related to permeability: peat with higher porosity tends to be much more permeable compared to peat with lower porosity, smaller pore spaces, and

lower permeability (Hayward & Clymo, 1982). As moisture content and *DWT* measurements reflect field conditions only at the time of sampling, PORO might be a more integrative measure of potential site moisture conditions for longer time periods. We suggest that future studies include PORO measurements to test this hypothesis. In our study, the sites exhibited a relatively narrow range for *PORO* and this might account for the weaker-than-expected correlation in the statistical analyses.

Other measures of water content, such as percent water content, have been used in ecological studies of peatlands. In a recent study in Canada, Charman & Warner (1997) used moisture (percent dry weight, percent wet weight, and percent volume) in addition to water table, but also found water table to have the strongest relationship with testate amoebae species assemblages. We feel that some other variable should explain testate amoebae assemblages better than water table depth because no direct relationship exists between minute organisms living in the first few centimeters of *Sphagnum* mosses and the water table level some 10 to 40 cm below.

It is possible that some other environmental variables not included in this study could show relationships stronger than those included here, although this study is one of the most comprehensive ecological surveys undertaken on bog testate amoebae faunas.

### Ecological groups of testate amoebae

Defining ecological groups is difficult because of the co-occurrence of eurytopic and stenotopic taxa in the same samples. Bonnet (1961; 1964) applied techniques developed for phytosociological studies with success to define testate amoebae communities. The IndVal program (Dufrêne & Legendre, 1997) provides the software and fills the gap in analytical capabilities for identifying clear testate amoebae ecological groups. A common alternative has been the TWINSPAN program, which uses a divisive algorithm and does not allow reallocations among sample groups. TWINSPAN produces groups that are more homogeneous than perhaps they really are. The IndVal program overcomes these limitations. It uses an indicator value index based only on within-species abundances and occurrence comparisons, thereby avoiding the problem of individual indicator values that are dependent on another taxon's relative abundance. Further, IndVal ranks taxa according to the indicator value (Dufrêne & Legendre, 1997). Our study confirms the more generalized applications offered by IndVal, which relies on taxa distributions (as used in this study), *a priori* ecological variables, or sampling structures.

### Assessing the reliability of the transfer functions

Our model underestimates peat pH, especially at the extreme basic end of the scale (Figure 2). This may be due to the high number of samples taken in more acidic sites, which are more typical in Jura peatlands.

Our model for *DWT* is most reliable for water tables shallower than 41 cm, even if *DWT* is predicted deeper than observed and predictions become progressively less reliable as the water table becomes shallower. The model can thus be used to identify two groups. The first group contains sites characterized by *DWT* shallower than 41 cm where there is a close relationship between the observed *DWT* and the *IV* of the taxa. The second group contains sites characterized by *DWT* greater than 41 cm, which tends to be secondary sites that have been drained and are covered by secondary vegetation and/or trees (Table I). The high degree of disturbance of these sites is likely responsible for poorer or less clear relationships between environmental parameters and testate amoebae faunas. This is not to say, however, that testate amoebae are poor indicators of secondary or disturbed sites because the study by Buttler *et al.* (1996) clearly establishes that this is not the case.

The model of *DWT* becomes better when sites with water tables deeper than 41 cm are excluded from the analysis. Charman & Warner (1997) found a similar relationship for sites with water tables deeper than 30 cm in peatlands in Canada.

Predictive models for *WFr/V* (Figure 2), *WDr/V*, and PORO are less reliable than for peat pH or *DWT*. Although most water related variables are not strong environmental parameters in this study, water table depth is probably the single most useful ecological factor even though *DWT* is not especially strong in the secondary sites.

This study has shown that testate amoebae are abundant and exhibit widespread distributions that can be explained by various environmental factors characterizing site moisture conditions. Although depth to the water table is important, we suggest that more work should focus on a wider suite of parameters for site moisture conditions than depth to water table alone.

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# The palaeoecological history of the Praz-Rodet bog (Swiss Jura) based on pollen, plant macrofossils and testate amoebae (Protozoa)

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**Abstract:** Stratigraphy, radiocarbon dating and analyses of pollen, plant macrofossils and testate amoebae were used to reconstruct the development and ecology of a small raised bog in a karst-dominated landscape in the Swiss Jura Mountains. Special focus was on past vegetation and on the history of *Pinus rotundata* in relation to anthropogenic and climatic influences. Testate amoebae were used to reconstruct past local soil pH and water-table depth. The inferred development of the Praz-Rodet bog typifies a classic hydroseral terrestrialization of a small basin. Two features are specific for this site. First, the bog was much wetter than today for a long period; according to our hypothesis, this only changed as a consequence of human activities. Second, two hiatuses are present at the coring location (Younger Dryas–early Preboreal, and 4700–2800 cal. yr BP), the former probably caused by low lake productivity due to cold temperatures and the latter by the erosional activity of the adjacent small river. The date of 2800 cal. yr BP for renewed peat accumulation may be related to climatic change (Subboreal–Subatlantic transition). Pollen indicators failed to show one hiatus: an apparently complete pollen sequence is therefore no guarantee of an uninterrupted sediment accumulation. Evidence of early minor human impact on the vegetation in the Joux Valley dates back to c. 6850 calendar years, congruous with the early Neolithic in the Jura Mountains. The history of *Pinus rotundata* appears to be more complex than previously believed. Human activity is clearly responsible for the present abundance of this species, but the tree was naturally present on the bog long before the first evidence of important human disturbance of the site (1500 cal. yr BP). It is suggested that, in karst-dominated landscapes, dense forests growing on mineral soils around raised bogs may significantly reduce summer evapotranspiration by acting as windbreaks. Forest clearance results in increased evapotranspiration, causing a lowering of the water table on the bog and a modification of the vegetation cover. This hypothesis has implications for the management of similar small raised bogs in karst-dominated landscape.

**Key words:** pollen, plant macrofossils, testate amoebae, Lateglacial, Holocene, peat bog, human impact, *Pinus rotundata*, Switzerland.

A HOLOCENE RESEARCH PAPER



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## Introduction

Ombrogenous peatlands are not common in central and southern Europe. Continental and subcontinental climates with prolonged warm and dry summers are not suitable for widespread peat formation and bog development. This holds also for the Jura Mountains, where in addition the hydrogeomorphic conditions (karst) and the calcareous bedrock are unfavourable. Human activities have further eliminated or severely degraded bog remnants. The Joux Valley in western Switzerland and adjacent France nevertheless preserves a number of living bogs, which are among the most southern in Europe.

In this region, it is not clear to what degree humans have had an influence on shaping existing bog ecosystems. Is it possible that some modern bog plant communities are natural and have not been affected by humans? The origins of *Pinus rotundata* (= *P. uncinata* = *P. mugo s.l.*) and the dominant vegetation community on the bogs today (*Pino mugo-Sphagnetum*) have been topics of special interest. Some studies suggest that this community is natural and has remained intact since deglaciation (Chastain, 1952; Richard, 1961; Matthey, 1964; Royer *et al.*, 1978; Julve, 1983; Sandoz, 1987). Others have speculated that *P. rotundata* was introduced onto the bogs in the last two or three centuries and is not a postglacial relict (Feldmeyer-Christe, 1990; Reille, 1991).

The latitudinal position of the Jura Mountains near the southern limit of bogs in Europe suggests that bogs in this region are sensitive to environmental changes, both natural and human-induced. In this region, bogs suffer from summer droughts and are therefore likely to respond to global warming and changes in the pattern of summer precipitation. Furthermore, calcareous terrains with minerogenous waters and with well-developed karst represent unusual conditions for peatlands.

In an attempt to shed some light on these questions and to compare past communities unaffected by human activities against modern bog communities, a detailed palaeoecological investigation was conducted on a representative bog remnant. A record spanning the last 11 000 years was found to exist in the Praz-Rodet bog, one of the few remaining little-disturbed bogs in the Jura Mountains. Stratigraphic relationships, radiocarbon dating and analyses of pollen, plant macrofossils and testate amoebae were undertaken on a sediment core. While pollen represents both a regional and a local palaeoecological signal, this study focuses on local indicators from the pollen, plant macrofossils and testate amoebae to reconstruct a detailed history of local bog communities. This study is the first well-dated postglacial multiproxy palaeoenvironmental record from the Jura Mountains and contributes to an understanding of the age and development of these rare ecosystems in this part of Europe.

## Study site and regional setting

Praz-Rodet is a small bog about 5 ha in size situated at the southwestern end of the Joux Valley near the western border of Switzerland (46°34′00″ N lat, 6°10′25″ E long; 1035 m a.s.l.; Figure 1). The bedrock is pure calcareous sedimentary rock with well-developed karst. Praz-Rodet occupies a basin behind a terminal moraine from the last glaciation (Aubert, 1943; Bruckert and Gaiffe, 1980). Soligenous calcareous water flows along the edges of the bog basin. Dolines (karst holes) drain the periphery of the mire. The surface at the centre is raised and is influenced only by ombrogenous water. Abundant precipitation (annual average

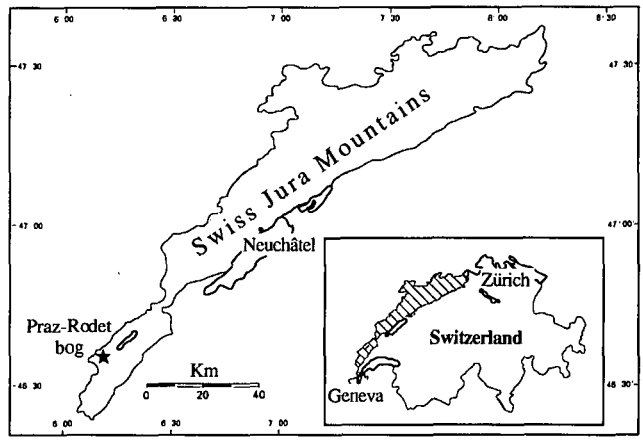


**Figure 1** Map of Switzerland, showing the coring locality.

1500 mm) and cool mean temperatures (annual average <5° C) in this region have been important for sustaining bog conditions.

The central and highest part is characterized by a raised bog community with pine (*Piceo-Vaccinienion uliginosi*), an open raised bog community (*Sphagnion magellanici*), and a bog pool community (*Caricion lasiocarpae*). A *Sphagno-Piceetum* community exists around the periphery. A small stream cuts through the southeast edge. Open pasture (*Cynosurion*) surrounds the bog at the northeastern to northwestern side and a small river (Orbe) marks the limit of the mire at the southeastern side (Figure 2). Plant community nomenclature follows Delarze *et al.* (1998).

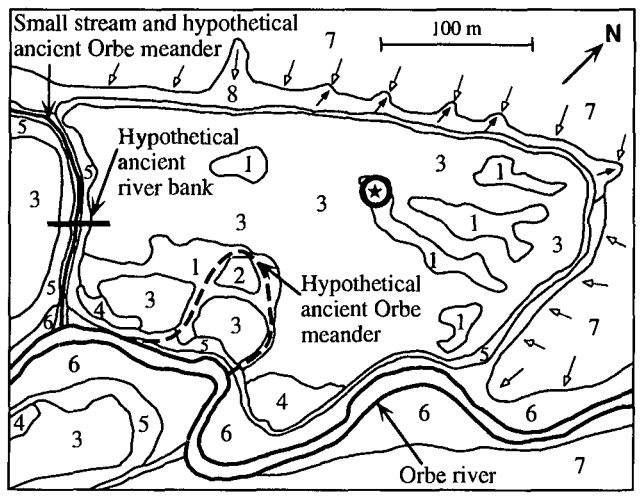


**Figure 2** Site map of the Praz-Rodet bog (redrawn from Gallandat, 1982). Vegetation types are: 1 = open raised bog community (*Sphagnion magellanici*); 2 = bog pool community (*Caricion lasiocarpae*); 3 = raised bog community with pine (*Piceo-Vaccinion uliginosi*); 4 = *Betulion pubescentis* raised bog community; 5 = small sedge fen (*Caricion davallianae* and *Caricion fuscae*); 6 = tall nitrophilous grass and willow communities (*Filipendulion*); 7 = pasture (*Cynosurion*); 8 = wet meadow subject to natural nutrient input (*Calthion*). The circled star indicates the coring location. The Orbe river is outlined in bold. The dashed bold line shows the hypothetical past position of the river based on the vegetation pattern (Gallandat, 1982) of which the present *Caricion lasiocarpae* community (2) is believed to be a remnant. The small stream running at the southwestern side of the mire (shown in bold) is believed to represent the remnant of another hypothetical past meander of the river. The hypothetical ancient river bank is situated at the limit between vegetation types 3 and 5 (Gobat, 1984). The horizontal line at the southwestern end of the mire indicates the location of the transect study of Gobat (1984). Small arrows indicate the flow of water flowing through the wet meadow and into the dolines. Open arrows = calcareous water; closed arrows = bog water.

Human activities in the Joux Valley date back to prehistoric times (Guignard, 1972). The valley was important as a trade route and for glass manufacturing during Roman times (Rod, 1953; Guignard, 1984; 1985; 1987). The first permanent settlements, traced to the tenth and eleventh centuries, were at the northeast end of the valley about 15 km from the study site. In the Jura Mountains, bogs were a minor source of fuel peat since the sixteenth century (Chastain, 1952) but this changed in the eighteenth century when wood became scarce and was substituted by peat as the primary source of fuel. Up to this time, bogs were widespread throughout the Jura Mountains. Subsequently, many bogs were drained, converted to agriculture land, and used for pasture by livestock. The bog studied here, however, has remained untouched.

## Material and methods

### Field coring

A core was taken in 1993 near the centre and highest part of the bog (Figure 2) with a large diameter (8 cm) piston corer (Wright *et al.*, 1984). The upper 1 m was collected in 1994 using a Wardenaar sampler (10 × 10 cm; Wardenaar, 1987). The 1993 core was split longitudinally. One half was used for detailed stratigraphic analyses, pollen subsampling and radiocarbon dating, and the other half was used for testate amoebae and plant macrofossil subsampling. The surface 1 m core was used for $^{210}$Pb and geochemical analyses. Two additional cores, one near the north edge and another near the south edge of the bog, were taken for stratigraphic analyses and comparison with the central core. They suggest that the topography of the underlying impermeable layer is relatively flat, which was confirmed by a radio-magneto-telluric study (Mitchell, 1995).

### Dating and palaeoecological analyses

A total of 18 levels were radiocarbon dated. Radiocarbon ages were calibrated to calendar years (cal. yr BP, present taken as 1950) using CALIB version 3.0.3c (Stuiver and Reimer, 1993). The $^{210}$Pb ages have been published elsewhere (Appleby *et al.*, 1997; Shotyk *et al.*, 1997; van der Knaap *et al.*, 2000).

Samples for pollen analysis were prepared using standard procedures (Faegri *et al.*, 1989). Exotic *Lycopodium clavatum* spores were added to samples from 0 to 1 m for the determination of pollen accumulation rates (Stockmarr, 1971). Pollen and spores were identified using Punt (1976), Punt and Clarke (1980; 1981; 1984), Punt and Blackmore (1991), Punt *et al.* (1988; 1995), and Reille (1992). All pollen percentages were calculated on the basis of a pollen sum that includes tree, shrub and herb pollen but excludes aquatic and peatland pollen.

Subsamples of 20 cm$^3$ were measured by displacement in a graduated cylinder and washed with warm water over a 300 μm mesh sieve. The residue was sorted under a dissecting microscope and all identifiable plant remains were picked and stored in stoppered vials. Six categories of remains were recorded semi-quantitatively according to Aaby and Berglund (1986). Plant remains were identified to the lowest possible taxonomic level with the aid of Lévesque *et al.* (1988) and Grosse-Brauckmann (1972; 1974) for vascular plants, and Janssens (1983) and Daniels and Eddy (1990) for mosses. *Pinus* needles were identified to species with the aid of Sandoz (1987). Charcoal and insect remains were noted but not identified. Plant taxonomy follows Corley *et al.* (1981) for mosses and Tutin *et al.* (1964–80) for vascular plants.

Subsamples of 2 cm$^3$ were analysed for testate amoebae following Tolonen (1986) and Warner (1990). A minimum of 200 shells was achieved for most samples except for some samples at the bottom of the core. Percentages are based on the total number counted per sample. Other invertebrate fossils encountered with the testate amoebae were recorded.

All diagrams were generated using TILIA and TILIAGRAPH (Grimm, 1991).

### Numerical analyses

For numerical analyses, logarithmic transformations were applied to pollen and testate amoebae percentage data in order to reduce the influence of dominant taxa. For testate-amoebae data, only samples with 50 or more shells were included in the analyses. Presence-absence data were used for the plant macrofossil data.

For zonation, pollen (P), plant macrofossil (M) and testate amoebae (T) data were submitted to a depth-constrained clustering using the program CHRONO from the R package release 3.0 (Legendre *et al.*, 1985; Legendre and Vaudor, 1991). This method is non-hierarchical and the algorithm used is agglomerative with a proportional link. Each fusion between groups was tested for significance with a Monte-Carlo permutation. Poller zones were determined separately for regional taxa (regional zones, Pr) and peatland taxa (local zones, Pl). Canonical correspondence analysis (CCA) was performed on the fossil testate amoebae data and on a set of samples of modern testate amoebae from an independent study (Mitchell *et al.*, 1999) using the program CANOCO (ter Braak, 1988–92). Only taxa that occurred in both data sets were included. The ordination space was defined by modern samples and associated environmental variables, with the fossil samples added as passive samples. Samples are grouped according to the depth-constrained clustering results on the CCA scatter diagram.

Past pH and water-table depths were inferred using a two-way weighted averaging procedure in which the modern data are used to estimate the optima of the species. These optima were then used to infer modern values (*sensu* Birks *et al.*, 1990). This double averaging resulted in a shrinkage of the inferred values that was corrected by an inverse linear deshrinking procedure where the observed values are regressed on the initial estimated value. The ecological optima of the species and the performance of the transfer functions (using slightly different methods) are given in Mitchell *et al.* (1999). The performance of the model we used is as follows: water-table depth: RMSEP-WA(tol) –20.28 cm, $r^2$ = 0.58, mean difference between predicted and observed values –14.8 cm; pH: RMSEP-WA = 0.28, $r^2$ = 0.64, mean difference between predicted and observed values = 0.25.

## Results and interpretation

### Stratigraphy and age

Details on the sediment stratigraphy are given in Table 1. Of the 18 radiocarbon dates obtained (Table 2), the three basal dates

**Table 1** Lithostratigraphy of the Praz-Rodet core

| Depth (cm) | Lithostratigraphy |
|---|---|
| 0–5 | Living mosses and litter |
| 5–47 | Well-preserved *Sphagnum*-dominated peat |
| 47–58 | Strongly decomposed peat |
| 58–179 | Mixed *Sphagnum* and herbaceous peat |
| 179–195 | Transition |
| 195–260 | Less-decomposed *Sphagnum*-dominated peat |
| 260–320 | Decomposed *Sphagnum*-dominated peat |
| 320–350 | Transition |
| 350–405 | Compact coarse-detritus gyttja |
| 405–650 | Lake deposits: silt and clay |
| Below 650 | Glacial deposits: mixed coarse gravel and finer material (not studied) |

**Table 2** Radiocarbon dates of the Praz-Rodet core

| Depth (cm) | Thickness (cm) | Laboratory number (1) | Method | Conventional radiocarbon age BP (2) | $\delta^{13}C$ ‰ | Material dated | Calibrated age BP (1$\sigma$) |
|---|---|---|---|---|---|---|---|
| 53 | 0.5 | UtC-4939 | AMS | 257 ± 46 BP | -28.9 | *Sphagnum magellanicum* | 213 ± 213 |
| 97 | 0.5 | UtC-4938 | AMS | 1144 ± 34 BP | -28.3 | *Andromeda polifolia* twig + leaves | 1026 ± 40 |
| 130 | 4 | B-6493 | decay | 1620 ± 40 BP | -24.2 | *Sphagnum magellanicum* | 1479 ± 60 |
| 162 | 4 | B-6494 | decay | 2130 ± 30 BP | -26.4 | *Sphagnum magellanicum* | 2095 ± 41 |
| 180 | 1 | UtC-4936 | AMS | 2589 ± 35 BP | -25.7 | *S. magellanicum* + *S.* Sect. *cuspidata*, amorphous | 2736 ± 19 |
| 188 | 4 | B-6495 | decay | 4220 ± 40 BP | -27.9 | *S. magellanicum* + *S.* Sect *cuspidata*, + *S.* Sect. *acutifolia* | 4743 ± 95 |
| 216 | 4 | B-6496 | decay | 4670 ± 80 BP | -27.8 | *Sphagnum capillifolium* | 5435 ± 133 |
| 260 | 4 | B-6497 | decay | 5210 ± 60 BP | -27.1 | *S. magellanicum* + *S. capillifolium* | 6036 ± 128 |
| 288 | 4 | B-6498 | decay | 5800 ± 80 BP | -26.7 | *Eriophorum vaginatum* + *S. magellanicum* | 6609 ± 104 |
| 318 | 1 | UtC-4052 | AMS | 6270 ± 60 BP | -27.6 | 4.5 *Potentilla palustris* seeds + 1 other seed | 7128 ± 93 |
| 350 | 1 | UtC-4053 | AMS | 7330 ± 90 BP | -26.7 | 6 *Carex* seeds + 4.5 *Potentilla palustris* seeds | 8075 ± 93 |
| 370 | 1 | UtC-4937 | AMS | 7630 ± 47 BP | -27.8 | amorphous peat | 8385 ± 30 |
| 380 | 1 | UtC-4054 | AMS | 7400 ± 70 BP | -26.9 | Cyperaceae leaves | 8165 ± 142 |
| 392 | 2 | UtC-4055 | AMS | 9560 ± 80 BP | -26.3 | seeds | 10684 ± 200 |
| 403 | 1 | UtC-4056 | AMS | 9780 ± 60 BP | -26.3 | herbs | 10956 ± 48 |
| 425 | 1 | UtC-4057 | AMS | 4780 ± 70 BP | -26.8 | one piece of charcoal | 5465 ± 129 |
| 453 | 1 | UtC-4058 | AMS | 5560 ± 50 BP | -26.9 | one piece of charcoal | 6354 ± 50 |
| 473.5 | 2 | UtC-4059 | AMS | 7780 ± 60 BP | -24.1 | leaf fragments | 8492 ± 61 |

(1) Laboratory designations are: UtC = R.J. Van de Graaff laboratory, Utrecht, The Netherlands; B = Radiocarbon-Laboratory, Bern.
(2) Dates are corrected for isotopic fractionation.

(UtC-4057, UTC-4058, UTC-4059) are too young based on the well-established pollen chronology for this region (Welten, 1982; Ammann and Lotter, 1989). These dates are on charcoal and charred vascular plant leaf remains. Dates on charcoal are often problematic because of possible absorption of young carbon. The radiocarbon dates indicate a hiatus in the sediment at 184 cm.

The chrono-stratigraphy of the Lateglacial part of Praz-Rodet bog is based on biostratigraphic correlation of pollen zones from sites at Les Cruilles (1035 m a.s.l.), 15 km NE in the same valley, and Le Marais des Amburrex (1300 m a.s.l.), 5 km ESE in an adjacent valley (Wegmüller, 1966). In the case of Le Marais des Amburnex, however, we correlate Wegmüller's Firbas zone IIa (first part of Allerød) with Firbas zone Ibc (Bølling), assuming synchrony of this biozone with the similar biozone Firbas zone Ibc in Les Cruilles. Firbas zone III, the Younger Dryas, is absent from Praz-Rodet bog, which suggests the occurrence of another hiatus at 406 cm.

An depth-age curve was constructed for four separate sections (Figure 3, left), as follows.

(1) 0–184 cm: ages for the surface 50 cm are based on the $^{210}Pb$ age estimates. Ages and sediment-accumulation rates of the corresponding levels were calculated by linear interpolation. The chronology of the section 50–184 cm was modelled with PSIMPOLL (Bennett, 1993), using a four-term polynomial function, and using all calibrated radiocarbon dates in this section and the $^{210}Pb$ age estimate at 50 cm.
(2) 184–370 cm: PSIMPOLL was used with a three-term polynomial function on the calibrated radiocarbon dates for this core segment.
(3) 370–406 cm: PSIMPOLL was used to interpolate linearly between the calibrated radiocarbon dates at 370 and 403 cm. The radiocarbon date at 380 cm appears too young. The apparent Younger Dryas hiatus extends for about a half millennium into the Preboreal period.
(4) 406–472 cm: ages were linearly interpolated between the approximate ages used for the beginning and end of the Allerød as established in the GISP2 Greenland ice core (Stuiver *et al.*, 1995) (13000 cal. yr BP at 406 cm; and 14000 cal. yr BP at 430 cm). The ages of samples older than Allerød time are extrapolated.

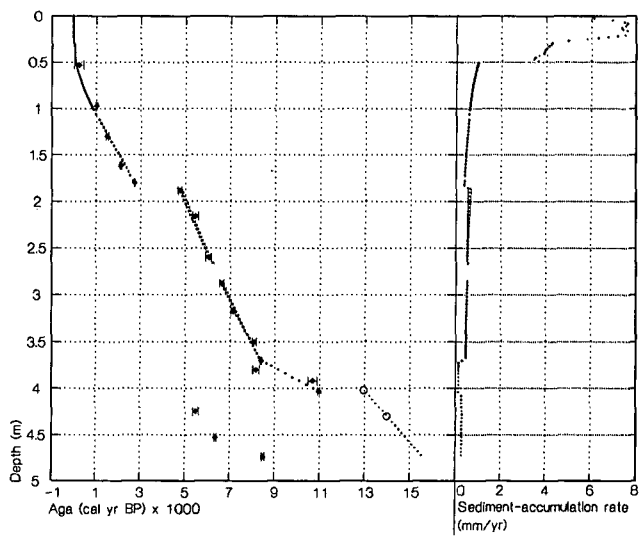


**Figure 3** Depth-age relationship (left) and sediment-accumulation rates (right) for the Praz-Rodet bog based on 18 calibrated radiocarbon dates and two biostratigraphic dates. Ages are expressed as cal. yr BP = calendar years before AD 1950. Calibrated radiocarbon dates are depicted as large diamonds with standard deviations, biostratigraphic dates as open circles, and pollen samples as small diamonds with confidence intervals.

The Firbas zones for the Holocene given in Table 3 are based on biostratigraphic correlation of pollen zones with those in Les Cruilles and Le Marais des Amburnex. As a result, the ages of some of our biostratigraphic Firbas zones differ slightly from chronostratigraphic Firbas zones as defined by Mangerud *et al.* (1974).

Sediment-accumulation rates are low in the early Holocene, and increased markedly at 8500 cal. yr BP. This is similar to average rates in 25 lakes and mires studied for pollen in Switzerland, showing a marked increase *c.* 9000 cal. yr BP (van der Knaap and Ammann, 1997).

**Table 3** Summary and interpretation of regional pollen diagram of the Praz-Rodet bog

| ZONATION: regional site zones | | CHRONO-STRATIGRAPHY | | POLLEN STRATIGRAPHY | | PALAEO-VEGETATION | |
|---|---|---|---|---|---|---|---|
| Pollen zone | Lower zone boundary | Age of lower zone boundary (cal yr BP) | Firbas zone | Increasing (or maximum) pollen percentages | Decreasing (or minimum) pollen percentages | Upland vegetation types | Anthropogenic vegetation: human impact |
| Pr-20 | 21.5 cm | -14 | X (Sub-atlantic) | *Betula, Fraxinus* | *Plantago lanceolata* | Some forest regeneration | Part of fields abandoned |
| Pr-19 | 48 cm | 50 | | *Pinus, Fraxinus, Rumex acetosa* | *Fagus, Cannabis* | Forest clearance | Modern forestry, mainly meadows |
| Pr-18 | 54 cm | 100 | | *Juglans, Olea, Cannabis, Secale*, Gramineae, *Plantago lanceolata, P.media* | *Picea, Abies* | | More meadows, more fields |
| Pr-17 | 96 cm | 780 | | *Pinus*, Gramineae, *Plantago lanceolata, Cannabis*, Cerealia | *Fagus, Alnus glutinosa-type* | | |
| Pr-16 | 114 cm | 1170 | IX (Sub-atlantic) | *Cannabis*, Cerealia, Conifers | Minimum of most deciduous trees | Exploited forest | More meadows, more cereal + hemp fields |
| Pr-15 | 134 cm | 1630 | | *Carpinus, Fraxinus, Pinus, Secale* | | | Meadows, more fields, forest exploitation |
| Pr-14 | 162 cm | 2300 | | *Alnus viridis, Castanea, Juglans*, Chenopodiaceae, *Rumex, Achillea*, Gramineae, *Pteridium, Urtica* | *Abies, Fraxinus, Tilia* | Mixed forest | More meadows, more fields |
| Pr-13 | 184 cm | 2800 | VIII (Sub-boreal) | *Fagus, Carpinus*, Cerealia, *Plantago lanceolata, Urtica* | *Ulmus, Tilia, Taxus, Fraxinus, Pinus* | | |
| Hiatus | 184 cm | 4700 | | | | | |
| Pr-12 | 216 cm | 5270 | (Sub-boreal) | *Fagus, Picea* | *Abies, Tilia, Ulmus* | Conifer-dominated mixed forest | Forest grazing, some meadows |
| Pr-11 | 232 cm | 5550 | | *Abies, Picea, Fagus, Plantago lanceolata*, (Cerealia) | *Fraxinus, Ulmus, Tilia* | *Abies* -dominated mixed forest | Some fields |
| Pr-10 | 276 cm | 6200/6600 | VII (Atlantic) | *Abies, Fagus, (Picea)* | *Betula, Corylus, Tilia, Fraxinus* | Mixed forest with much *Abies* | Forest grazing, first meadows : 6850 cal yr BP |
| Pr-9 | 320 cm | 7300 | | *Abies, Alnus glutinosa*- type, *Fagus, Taxus*, Cruciferae, *Plantago lanceolata* : 298 cm | Gramineae | Mixed forest | |
| Pr-8 | 332 cm | 7550 | | *Betula, Hedera, Allium, Caltha, Potentilla, Valeriana officinalis* | *Pinus, Corylus* | Mixed-oak forest | Wet grassland: grazed? |
| Pr-7 | 371 cm | 8500 | VI (Atlantic) | *Fraxinus, Quercus, Ulmus, Tilia, Acer, Alnus, Abies* | *Corylus* | Mixed-oak forest with *Corylus* | none |
| Pr-6 | 382 cm | 9300 | V (Boreal) | *Corylus, Ulnus, (Tilia, Quercus)* | *Pinus, Betula, Gramineae* | *Corylus-Ulmus* forest | |
| Pr-5 | 406 cm | 11000 | IV (Pre-boreal) | *Pinus, Betula, (Corylus, Quercus)* | *Juniperus, Hippophae, Artemisia, Gramineae, Helianthemum* | Pinus woodland | none |
| Hiatus | 406 cm | 13000 | | | | | |
| Pr-4 | 418 cm | 13600 | IIb (Allerød) | *Pinus* | *Juniperus, Hippophae, Betula, Helianthemum, Artemisia, Gramineae* | Treeless vegetation + open woodland | none |
| Pr-3 | 430 cm | 14000 | IIa (Allerød) | *Pinus, Betula, Selaginella* | *Juniperus, Hippophae, Salix* | Open woodland + treeless vegetation | |
| Pr-2 | 458 cm | 15000 | Ibc (Bølling) | *Betula, Juniperus, Hippophae*, Gramineae, many herbs | *Artemisia, Ephedra*, Chenopodiaceae, *Helianthemum, Pinus* | Closed herb vegetation with shrubs | |
| Pr-1 | 472 cm | 15500 | Ia (Oldest Dryas) | *Artemisia*, Gramineae, *Ephedra, Helianthemum*, Chenopodiaceae | *Betula* | Open herb vegetation | |

## Pollen

The vegetation is reconstructed in two ways. Pollen and spores representing the regional vegetation are presented in Figure 4 and Table 3 and from local sources in Figure 5. Pollen of Cyperaceae can be from both regional and local sources. Also, some pollen types can represent taxa that once grew outside the peatland basin but may have migrated onto the peatland as the surface became dry, e.g., *Pinus*. These are presented in both figures. Pollen zones identified in this study refer to this site only.

## Plant macrofossils

A total of 11 zones were recognized based on plant macrofossils (Figure 6). Needles of *Pinus rotundata* were found at 128 cm (1500 cal. yr BP) and 93 cm depth (720 cal. yr BP). Zones M-1 and M-2 contain fen indicators. Above 320 cm, in zone M-3, *Sphagnum magellanicum* (present in most samples above this level), *Scheuchzeria palustris* and *Eriophorum vaginatum* suggest oligotrophic conditions. Indicators of ombrotrophic conditions (*S. capillifolium* and *Vaccinium*

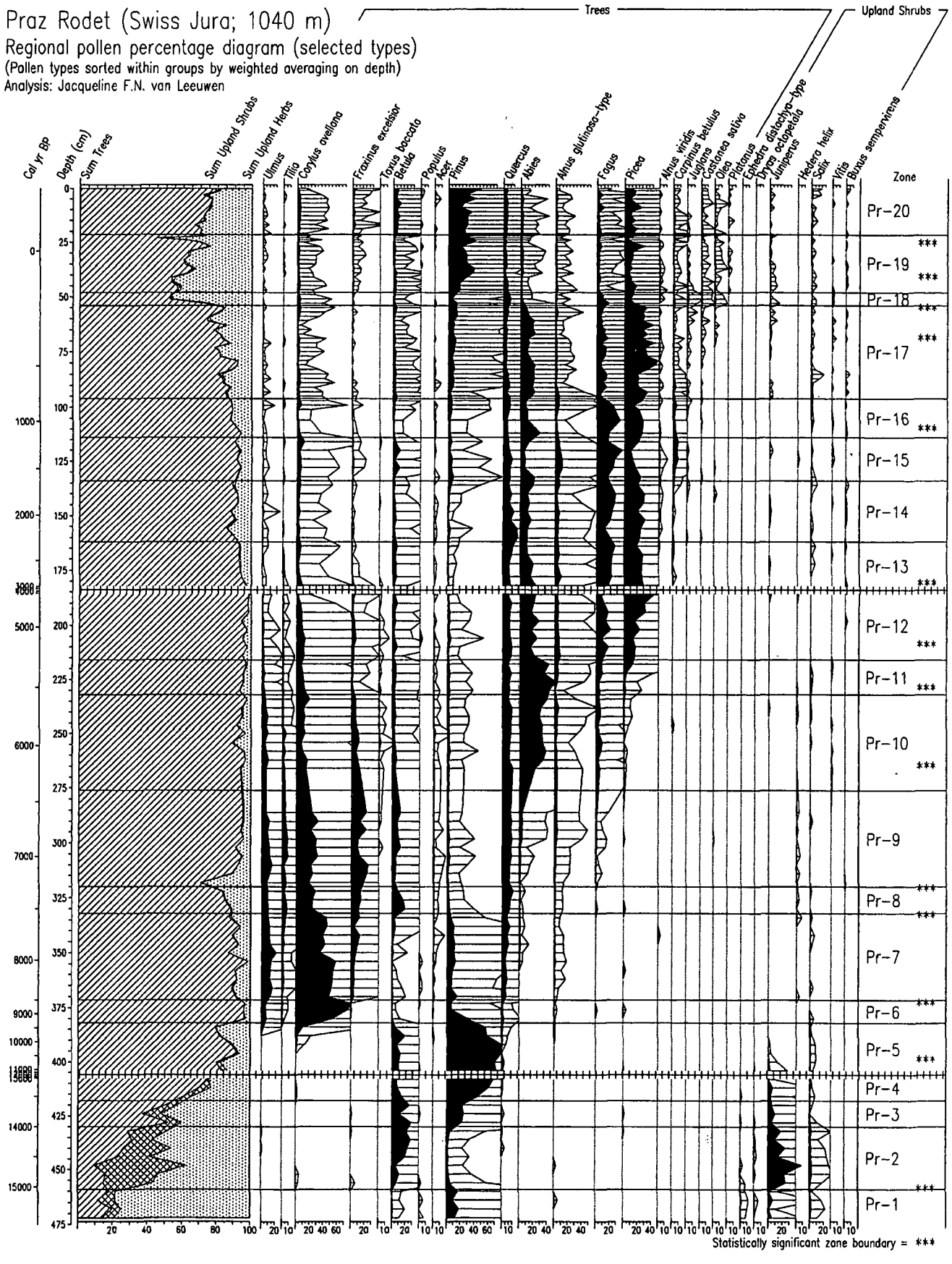


**Figure 4** Pollen percentage diagram of the Praz-Rodet bog showing regional pollen types. Zone boundaries are as follows: dashed line = hiatus; drawn line = other zone. *** = statistically significant zone boundary ($P < 0.05$).

*oxycoccos*) appear in zone M-4. In zone M-6 bog pool species are recorded. Zone M-8 contains indicators of ombrotrophic bog (*V. oxycoccos*) and drier conditions (*Andromeda polifolia*). In zone M-9 *S. cuspidatum, S. tenellum, S. palustris* and *Eriophorum* indicate wet conditions but these species disappear in zone M-10 which suggests drier conditions. In zone M-11 *S.* cf. *rubellum* and *V. oxycoccos* indicate moderately dry ombrotrophic conditions. The final zone M-12 may represent

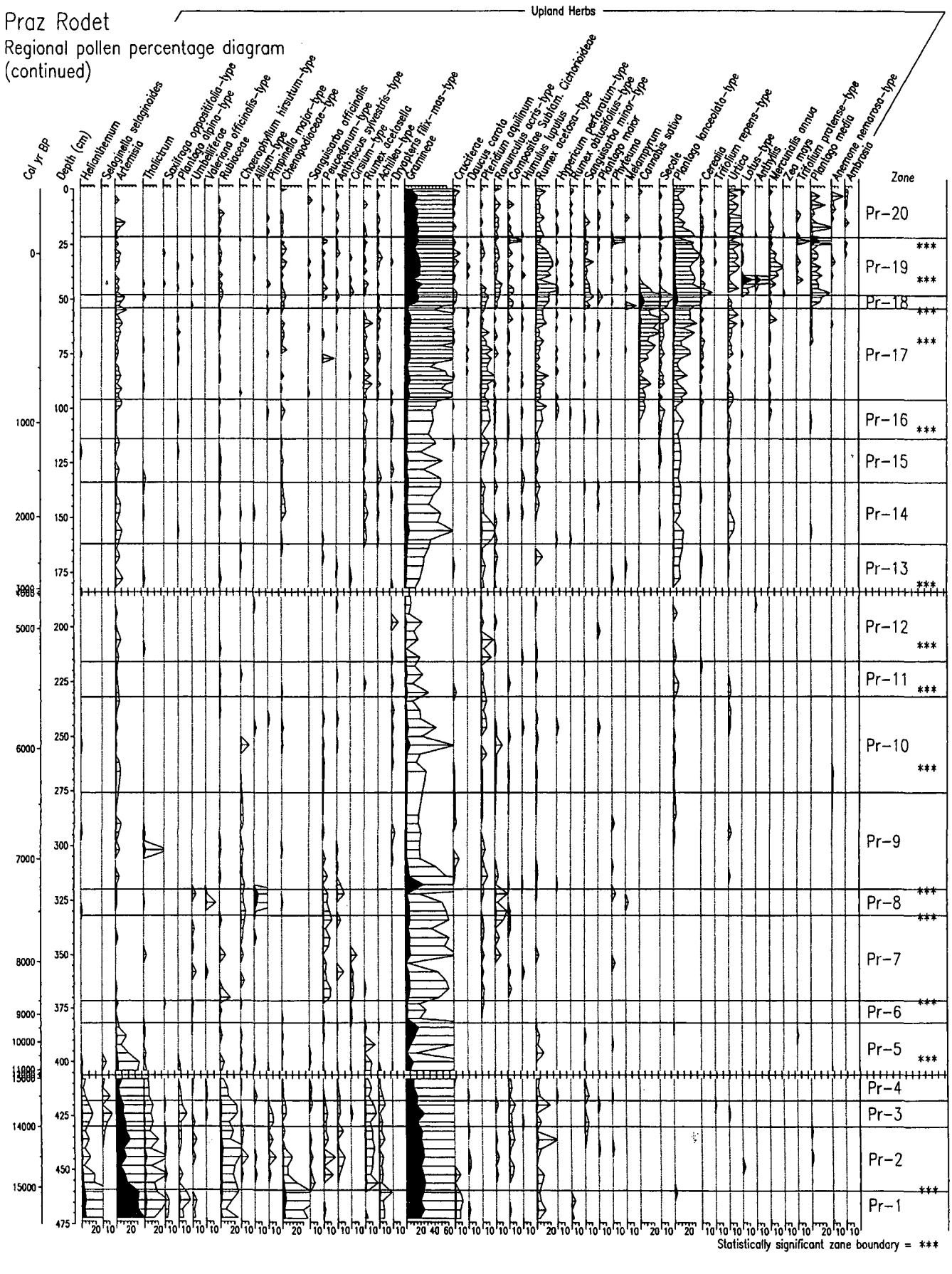


**Figure 4** Continued.

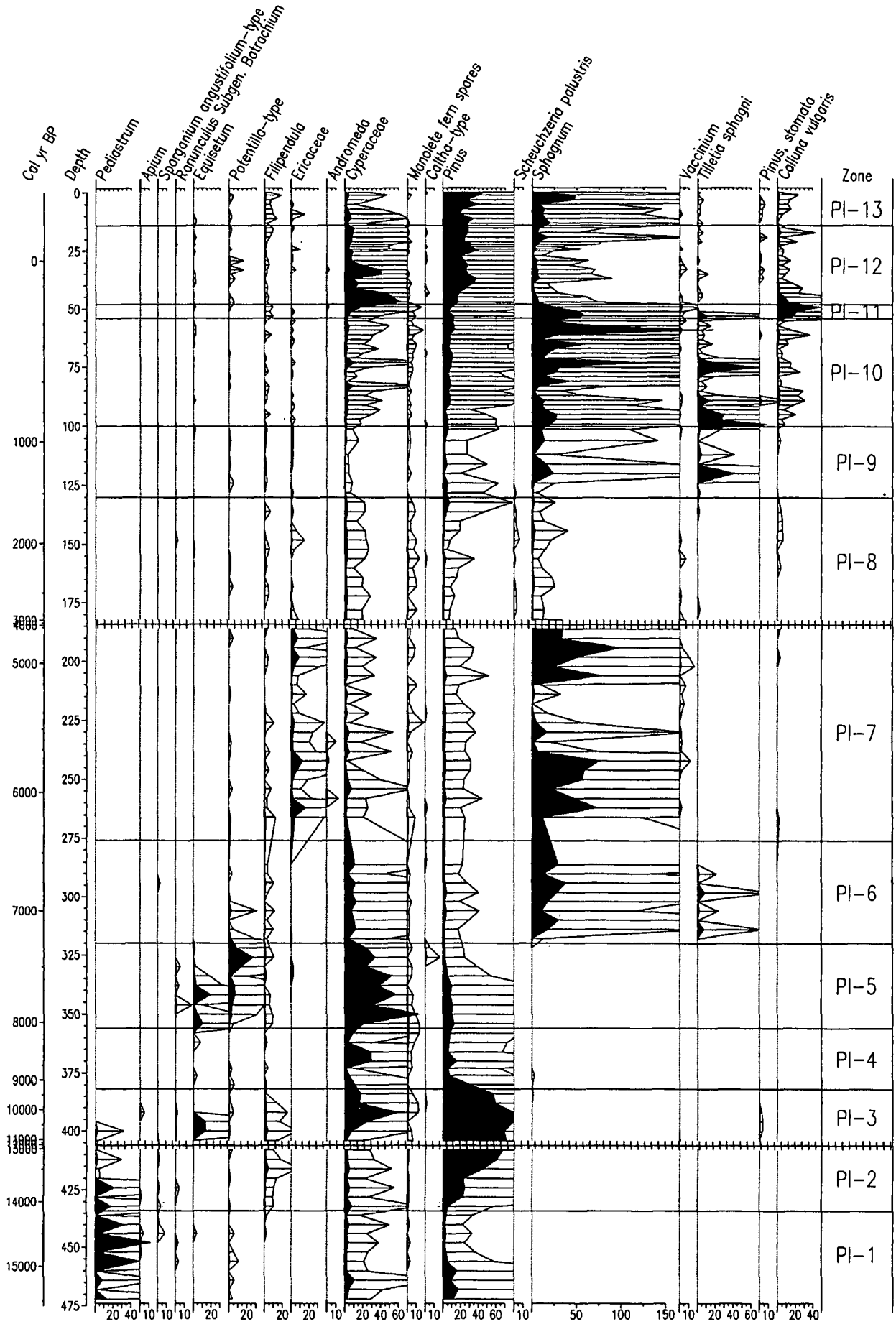


**Figure 5** Pollen percentage diagram of the Praz-Rodet bog (Swiss Jura; 1040 m) showing local pollen types. Zone boundaries are as follows: dashed line = hiatus; drawn line = statistically significant zone boundary ($P < 0.05$). Analysis: Jacqueline F.N. van Leeuwen.

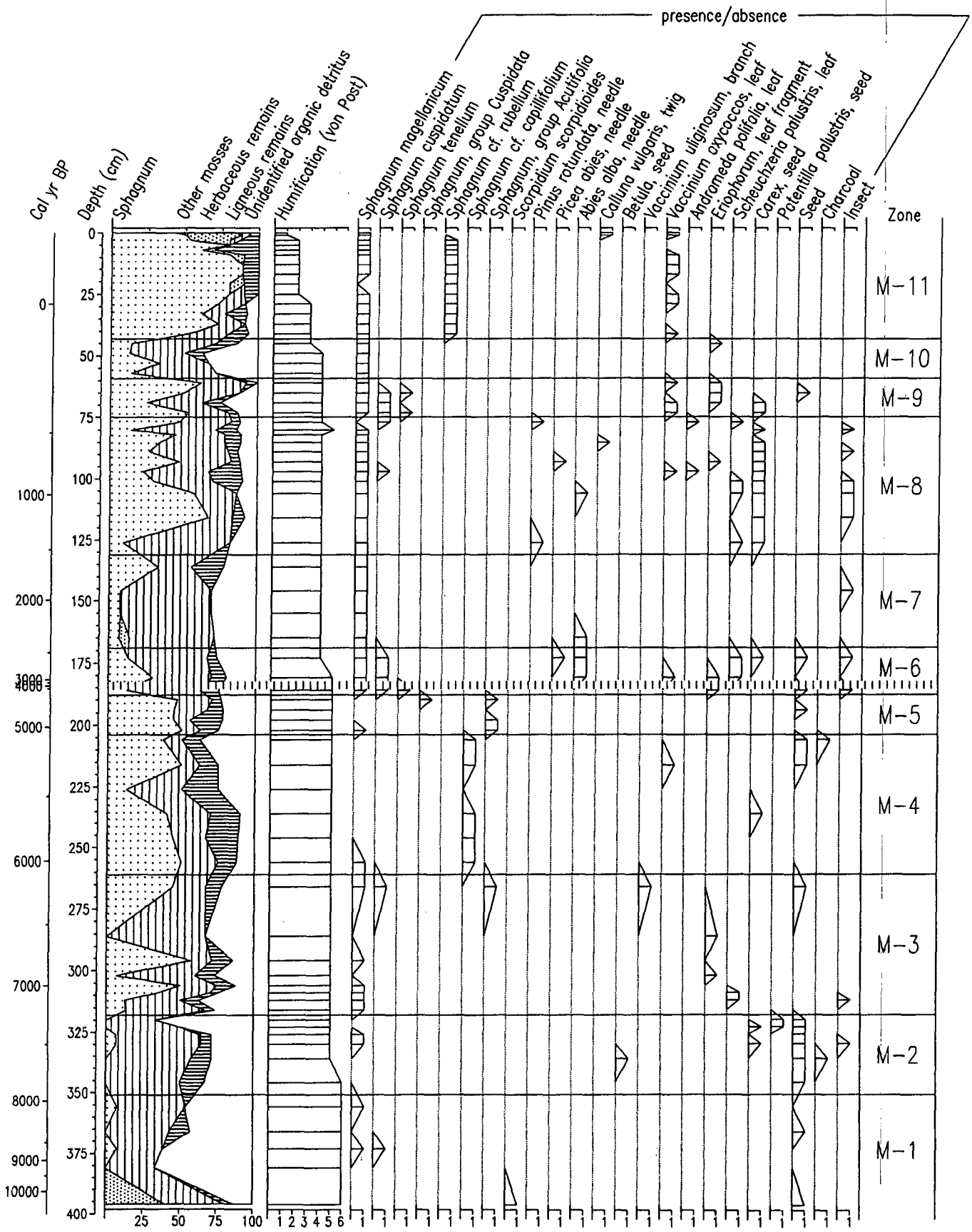


**Figure 6** Plant macrofossil diagram of the Praz-Rodet bog (Swiss Jura; 1040 m). Zone boundaries are as follows: dashed line = hiatus; drawn line = statistically significant zone boundary ($P < 0.05$). Analysis: Edward A.D. Mitchell.

a recent shift in the vegetation towards much drier conditions as suggested by *Calluna vulgaris*.

### Testate amoebae

Results of the testate amoebae analysis are given in Figure 7 and Table 4. *Amphitrema flavum* and *Hyalosphenia papilio* are characteristic of oligotrophic wet habitats such as bog hollows. *A. wrightianum* is characteristic of wetter situations than *A. flavum* and *H. papilio*. *Assulina seminulum* is characteristic of ombrotrophic moist to dry habitats. *Cryptodifflugia oviformis* is characteristic of relatively dry habitats (small hummocks). *Trigonopyxis arcula* is characteristic of dry habitats such as drained sites. *Heleopera rosea, Nebela tincta, N. militaris* and *A. muscorum* are present in all habitats within raised bogs and transitional mires (Tolonen, 1986; Mitchell *et al.*, 1999).

In the canonical correspondence analysis (CCA), four environmental variables were found to be significant (Monte-Carlo test, 999 permutations) by the forward selection procedure. These were, in order of importance, pH ($P = 0.001$), water-table depth ($P = 0.001$), water content of fresh samples expressed as percentage of free volume ($P = 0.002$) and water content of the samples after one hour drainage expressed as percentage of free volume ($P = 0.017$). Together, these four variables explain 30.1% of the total variation in the modern testate amoebae data set. The first three ordination axes are significant ($P \leq 0.05$). Axes 1 and 2 are represented in Figure 8. Testate amoebae and other taxa are represented in Figure 8a. Figure 8b represents fossil types and modern types from surface samples. Most zones are well separated in the ordination diagram. The positions of fossil samples relative to modern samples used to define the ordination space and relative to the environmental variables illustrate the ecological history of the coring site. The overall main trends are towards a wetter bog with minor changes (zones T-2 to T-6) followed by dramatic change towards dry conditions (zones T-7 and T-8).

## Discussion

### Chronostratigraphy and hiatuses in the stratigraphic record

Our chronology is in general in agreement with Firbas zones shown in Table 3. The close agreement is good if we consider that the Firbas zones were established by Wegmüller (1966) as biozones rather than chronozones in a time when few radiocarbon dated pollen diagrams with a similar biostratigraphy were available.

The present record at Praz-Rodet is the best dated bog sequence in the Jura. The age-depth model indicates a complex history of sediment and peat accumulation. One hiatus in the stratigraphic record (Younger Dryas and early Preboreal; 406 cm) is obvious in the pollen stratigraphy and coincides with a change in lithology. The lack of a record may be due to very little sediment accumulation in a highly unproductive lake resulting from the generally low temperatures in this period. A similar situation has been observed by Wegmüller (1966) at Les Cruilles 15 km to the northeast, in which the Younger Dryas is represented by a thin layer of clay and lake marl.

The other hiatus, dated 4700–2800 cal. yr BP (184 cm), is detected on radiocarbon dating only. This observation suggests that hiatuses in peat sequences may go undetected if detailed radiocarbon dating is not available. There is no reason to believe that this hiatus is related to human activities. The most probable explanation is that the Orbe River eroded some peat when it was at or very close to the coring site at some time in the past. Two independent lines of evidence indeed suggest that the position of the Orbe river shifted in the past. The present vegetation pattern suggests that the large *Caricion lasiocarpae* pool community (code 2 in Figure 2) might be a remnant of an ancient meander of the river (Gallandat, 1982). Similarly, soil chemical characteristics such as pH and calcium content show a clear vertical limit at the southwestern margin of the bog (Figure 2) suggesting that the peat was eroded by an ancient meander of the Orbe river (Gobat, 1984). The renewed peat accumulation at 2800 cal. yr BP may be related to another more recent shift in the course of the Orbe river. This event is possibly connected to the rapid climatic change to cooler and moister conditions discussed by van Geel and Renssen (1998) and van Geel *et al.* (1996; 1998a; 1998b), with which the high water table inferred from testate amoebae would also agree.

### Development of the Praz-Rodet bog

Sedimentation began in the centre of the Praz-Rodet basin at the end of the Older Dryas time. Initially the site was a lake with little aquatic vegetation. By Allerød time, well-developed shore vegetation with such species as *Filipendula ulmaria* surrounded the lake. Conditions during the Younger Dryas and early Preboreal are not known because of a lack of sedimentary record. When sediment accumulation resumed in the middle Preboreal, shallow open water existed as indicated by a number of aquatic plants typical of shallow lakes or wetlands with open water. This developed into a fen with less extensive open water between 9300 and 7250 cal. yr BP. During the latter part of this phase (7600–7300 cal. yr BP) pollen suggests the presence of taxa typical of a wet grassland. High proportions of *Allium*-type, *Valeriana officinalis*-type and *Caltha*-type pollen suggest that these plants grew close to the coring site. This wet grassland community resembles riparian communities along the Orbe river (Gallandat, 1982), which may have been much closer to the coring site than today. Plant macrofossils confirm the existence of a fen during this period.

By about 7300 cal. yr BP, a *Sphagnum* mire began to form at the coring site replacing the earlier fen. The period 7300–6200 cal. yr BP is a transitional phase where the fen was gradually replaced by ombrogenous raised bog. This is especially clear in the testate amoebae and in the stratigraphic change from compact detritus peat to *Sphagnum*-dominated peat. The first evidence of human activity occurred at around 6850 cal. yr BP as shown by the occurrence of *Plantago lanceolata*-type, which indicates grazing. This date agrees with the time of the early Neolithic period in the Jura Mountains (SPM II, 1995).

From about 6200 cal. yr BP to the second hiatus starting at 4700 cal. yr BP, pollen, testate amoebae and the peat stratigraphy indicate a raised bog. Plant macrofossils show the presence of raised-bog vegetation by 5530 cal. yr BP. Testate amoebae suggest a relatively high water table until 5200 cal. yr BP. This was followed by a phase with lower water table, which may have been the cause for the disappearance suggested by pollen of the typical raised-bog species *Andromeda polifolia* at 5550 cal. yr BP. This drier period coincides with modest human activity around the basin in the form of forest grazing, presence of some pastures and for the first time some arable fields. Early signs of forest clearance and soil erosion were also recorded by Shotyk *et al.* (1998), in another peatland of the Jura Mountains, as increased deposition of atmospheric lead and scandium suggesting enhanced rates of soil erosion.

After 2800 cal. yr BP, *Scheuchzeria* and *Drosera* pollen and testate amoebae such as *Amphitrema flavum, A. wrightianum* and *Difflugia globulosa* suggest the presence of hollows on a raised bog. *Plantago lanceolata*-type and Gramineae indicate that human impact outside the mire increased more strongly than before.

The three lines of evidence show a shift towards dryness on the bog surface at different temporal and spatial scales. The first is represented by the appearance of *Pinus rotundata* macrofossils that confirm the presence of this tree on the bog since 1500 cal. yr BP, which coincides with an inferred drying trend based on

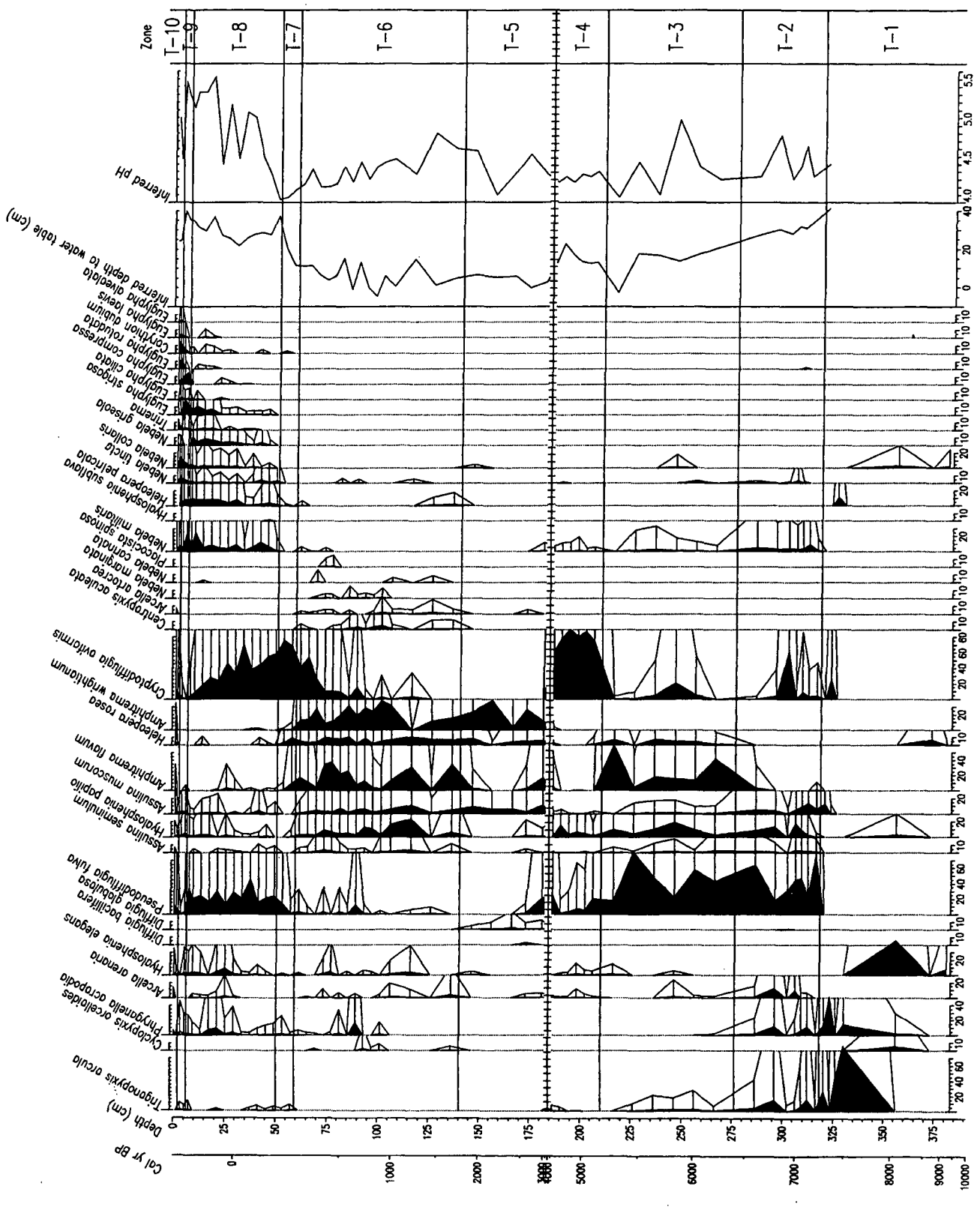


**Figure 7** Testate amoebae percentage diagram of the Praz-Rodet bog (Swiss Jura; 1040 m) with indication of inferred peat pH and water-table depths. Zone boundaries are as follows: dashed line = hiatus; drawn line = statistically significant zone boundary ($P < 0.05$). Analysis: Edward A.D. Mitchell.

**Table 4** Summary and interpretation of testate amoebae diagram from the Praz-Rodet bog

| ZONATION | | CHRONOSTRATIGRAPHY | | | TESTATE AMOEBAE STRATIGRAPHY | | OTHER TAXA | PALAEO-ECOLOGICAL INTERPRETATION |
|---|---|---|---|---|---|---|---|---|
| amoebae zone | Lower zone boundary | Age of lower zone boundary (cal.yr BP) | Corresponding pollen zone(s) regional | local | Testate amoebae percentages: Increasing (or maximum) | Decreasing (or minimum) | | |
| T-8 - T 10 | 51 cm | 65 - -44.0 | Part of Pr-18, Pr-19 & Pr-20 | Part of Pl-11, Pl-12 & Pl-13 | *C. oviformis*, *H. petricola*, *P. acropodia*, *N. militaris*, *N. collaris*, *N. tincta*, *N. griseola*, *C. dubium*, *E. strigosa* | *H. rosea* -type, *A. wrightianum*, *A. flavum* | Abundant Acari only at the top | Vertical micro-distribution in living mosses<br>Stable phase of dry bog, less acid |
| T-7 | 59 cm | 160 | Part of Pr-17 & Pr-18 | Part of Pl-10, & Pl-11 | *P. fulva*, *C. oviformis* | *H. papilio*, *A. flavum*, *A. wrightianum*, *A. muscorum*, *A. seminulum*, *A. arenaria*, *A. artocrea* | Absent | Drying out of the bog, increasing acidity |
| T-6 | 141 cm | 1800 | Part of Pr-14, Pr-15, Pr-16 & part of Pr-17 | Part of Pl-8, Pl-9 & part of Pl-10 | *H. papilio*, *A. wrightianum*, *A. flavum*, *C. aculeata*, *H. rosea* -type, *C. oviformis* | *N. militaris*, *T. arcula* | Less Acari, Copepoda, Cladocera & *H. angusticollis* | Wet bog increasingly acid |
| T-5 | 184 cm | 2800 | Pr-13 & part of Pr-14 | Part of Pl-8 | *A. wrightianum*, *A. muscorum*, *D. globulosa* | *H. papilio*, *C. oviformis*, *P. fulva*, *N. militaris*, *T. arcula* | Abundant Acari, Copepoda, Cladocera & *H. angusticollis* | Very wet acid bog, possibly a hollow |
| Hiatus | 184 cm | 4700 | | | | | | |
| T-4 | 211 cm | 5200 | Part of Pr-12 | Part of Pl-7 | *C. oviformis* | *A. flavum*, *A. muscorum*, *T. arcula*, *H. rosea* -type | Absent | Drier acid bog |
| T-3 | 276 cm | 6200/ 6600 | Pr-10, Pr-11 & part of Pr-12 | Part of Pl-7 | *A. flavum*, *H. papilio* | *P. fulva*, *T. arcula* | Absent | Raised bog, fluctuating low pH |
| T-2 | 318 cm | 7250 | Part of Pr-9 | Pl-6 | *P. fulva*, *A. flavum*, *H. papilio* | *A. arenaria*, *A. muscorum*, *P. acropodia*, *T. arcula*, *C. oviformis* | Few occurrences, only at the bottom of the zone | Transitional mire leading to a raised acid bog |
| T-1 | 381 cm | 8650 | Pr-6, Pr-7, Pr-8 & part of Pr-9 | Pl-4 & Pl-5 | *T. arcula*, *P. acropodia*, *H. elegans*, *A. muscorum* | *A. discoides*, *N. collaris*, *H. rosea* -type (all present in few samples) | Decreasing Turbellaria & Cladocera | Transition from a wet fen to a drier acid and more oligotrophic wetland |

other fossil indicators. The second shift occurred after 860 cal. yr BP, when Ericaceae (*Calluna, Vaccinum*) pollen suggests a dry raised bog on which *Pinus* started to expand. Testate amoebae and macrofossils (*Sphagnum cuspidatum, S. tenellum*), however, indicate that the coring location remained wet up to *c.* 160 cal. yr BP and 240 cal. yr BP, respectively. The coring location probably remained a hollow or pool. However, differences in environmental inferences based on testate amoebae and on pollen may be explained by the heterogeneity of the bog surface and differences in spatial scale. Testate amoebae and plant macrofossils are extremely local in origin whereas pollen is derived from more distant sources. The combination of results suggests that wet hollows existed within an otherwise dry raised bog, a situation frequently encountered in the Jura bogs today. The third shift to drier conditions occurred after *c.* 50–65 cal. yr BP. Two lines of evidence, however, differ in detail. Testate amoebae suggest that

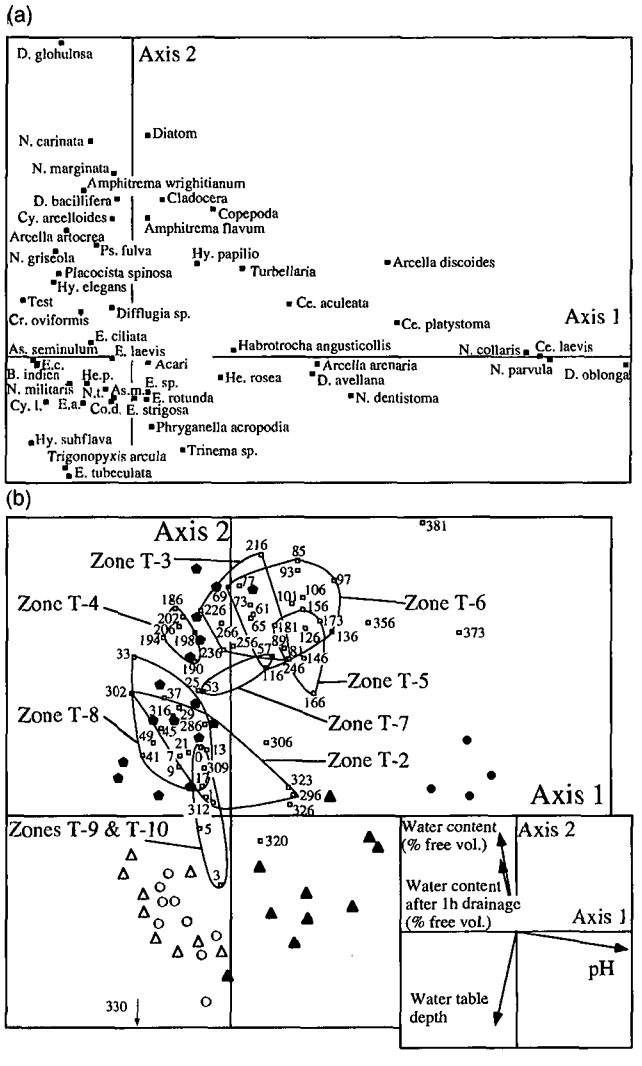


**Figure 8** Canonical correspondence analysis (CCA) scatter diagram of testate amoebae samples from the Praz-Rodet core. The ordination space is a combination of ecological variables derived from a previous study on modern samples (Mitchell *et al.*, 1999). (a) Position of testate amoebae species. (b) Position of samples. Ten zones resulting from the depth-constrained clustering are also represented. The fossil samples are projected passively in this ordination showing their successive position. Numbers indicate the depth (in cm) of the samples. Axes 1 and 2 represent together 24.6% of the total variance. Symbols represent ecological groups of modern samples: filled pentagons = bog centre, wet sites (e.g., *Sphagnum cuspidatum* pools); open triangles = bog centre, hummocks (e.g., *Sphagnum fuscum*); open circles = tree-covered bog (*Pinus rotundata*); filled triangles = minerotrophic sites either on the side of peat extraction ditches, in an open forest, or open meadow; filled circles = minerotrophic and moist sites (transitional *Sphagnum* mirc). As. = *Assulina*; As.m. = *A. muscorum*; B. = *Bullinularia*; Ce. = *Centropyxis*; Co. = *Corythion*; Cr. = *Cryptodifflugia*; Cy. = *Cyclopyxis*; Cy.l. = *C. laevigata*; D. = *Difflugia*; E. = *Euglypha*; E.a. = *E. alveolata*; E.c. = *E. ciliata*; He. = *Heleopera*; He.p. = *H. platystoma*; Hy. = *Hyalosphenia*; N. = *Nebela*; Ps. = *Pseudodifflugia*; Test = unidentified testate amoebae genus.

the bog became drier between 160 and 65 cal. yr BP which was followed by a short period of fluctuating dry conditions up to the present. Pollen suggest a dry bog surface with *Calluna* between 100 and 50 cal. yr BP, followed by a period with a slightly less dry surface on which *Pinus rotundata* expanded.

## Apparent timelag between pollen and testate amoebae data

There appears to be a slight discrepancy in the timing of change indicated by pollen and by testate amoebae. The upper and lower limits for testate amoebae (zone T-7, 160–65 cal. yr BP) differ from those of pollen (zone Pl–11, 100–50 cal. yr BP). This might be attributed to a timelag in the pollen signal of 15 to 60 years (3 to 5 cm in the peat) compared to testate amoebae. As soil organisms, testate amoebae are sensitive to changes in soil moisture and chemical conditions (Gobat *et al.*, 1998; Mitchell *et al.*, 2000a; 2000b) and may respond faster to changes than plants (Buttler *et al.*, 1996; Gilbert *et al.*, 1998).

## Canonical correspondence analysis of modern and fossil testate amoebae data

The ordination technique of canonical correspondence analysis (CCA) is used to complement the palaeoecological interpretation on two points: (1) to quantify the proportion of the variance in species data explained by each environmental variable and to test the significance of these variables; and (2) to visualize in two dimensions the development of the site in relation to well-documented modern sites and to environmental variables measured in these sites (Figure 8b).

The three significant environmental variables explained 30% of the variance. The results show that most sample groups (zones) are well separated from both the preceding and following group. Interestingly, although a clear trend towards drier conditions appears, even in the period of driest conditions (zones T-8 to T-10) the coring site hardly reached the driest conditions encountered in natural open peat bogs today such as *Sphagnum fuscum* hummocks. Also, after the hypothesized erosion phase of the bog by the Orbe river (zone T-5), conditions remained closer to oligotrophic wet conditions comparable with present-day *Sphagnum cuspidatum* pools than to present-day *Sphagnum*-dominated transitional minerotrophic mires.

CCA can also be used as a tool for predicting past values of environmental variables based on modern samples. However, for precise inference, a different analysis should be done for each variable separately.

## History of human impact and origin of *Pinus rotundata*

Pollen data (Table 3) suggest that humans were present in the valley long before the first known permanent settlements of the tenth or eleventh centuries and before the Middle Ages when humans used the valley for glass production. Pollen suggest that grazing in the forests and some of the first pastures could have existed as early as 6850 cal. yr BP. Humans appear to have had little or no direct impact on the bog until the middle of the eighteenth century when the forest was cleared to create extensive pasturelands. After this time, the bog surface became drier and *Pinus rotundata* expanded on the bog. There is no evidence from existing studies of a change in summer climate at the times when the bog became drier. Increasing temperatures at the end of the 'Little Ice Age' may have contributed to the drying-out of the bog once it was exposed to desiccating winds as a result of deforestation.

The presence of *Pinus rotundata* on Jura bogs has long been believed to be a natural relict from Lateglacial times. Furthermore, ecological studies have suggested that the *Piceo-Vaccinion uliginosi* community is the final successional stage in bog development (Richard, 1961; Matthey, 1964; Royer *et al.*, 1978, Julve, 1983; Sandoz, 1987). In contrast, a more recent hypothesis suggested that *Pinus rotundata* was introduced about two or three centuries ago in the Jura Mountains (Feldmeyer-Christe, 1990; Reille, 1991). However, ecological studies have shown that *Pinus rotundata* on the Jura bogs fills a specific ecological niche at the periphery of ombrogenous areas and in fens (Freléchoux, 1997). The growth of pine in the central parts of the peatlands seems to have been enhanced by local forest clearance as confirmed by dendroecological studies (Freléchoux *et al.*, 2000). Indeed, *Pinus* can survive long periods under marginal conditions without

producing significant amounts of pollen (Edelman, 1985). Reille (1991) concluded that *P. rotundata* expanded on bogs in the Jura Mountains and elsewhere one or a few centuries ago as the result of recent introduction, even though he discusses macrofossil evidence showing much earlier presence of *Pinus* sp. on the same bogs probably as small patches or as isolated individuals. According to Bégeot and Richard (1996), *P. rotundata* was not considered to be a valuable tree by foresters and therefore it was never planted on the peat bog of Frasnes (French Jura). However, *P. rotundata* was planted in the Hautes Vosges (Alsace, France) by German forest managers prior to 1914 (Bégeot and Richard, 1996). The same authors further conclude that the recent increase in *P. rotundata* on peat bogs is a consequence of draining and peat harvesting.

Our palaeoecological results do not support any of these hypotheses. Our findings of *P. rotundata* macrofossils in peat about 1500 cal. yr old show this species neither to be glacial relict nor an anthropogenic introduction on the bog. We therefore consider the presence of *P. rotundata* on the Praz-Rodet bog as natural, though not old enough to be a glacial relict. We hypothesise that a dry bog surface and the present abundance of *Pinus* on the bog are due to the clearance of the forest on the mineral soil around the bog. The forest had functioned as a windbreak reducing evapotranspiration on the bog, but there was (and is) no direct hydrological link in the soil between these two environments. Such a protection must have been considerable, because the Praz-Rodet bog is quite small. When the protection disappeared, the mesoclimate was altered and the bog adapted to new conditions.

In northwestern Europe and North America, forest clearance has often induced paludification through raising groundwater tables (Warner *et al.*, 1989). The case of Praz Rodet is opposite from this situation because: (1) the hydrology of the mire is independent from its surroundings as far as groundwater is concerned because of the karstic character of the landscape; and (2) summer winds are much hotter and drier and desiccate more strongly than in northwestern Europe due to (a) a more continental climate and (b) a more southerly position. Indeed, the development of the Praz-Rodet bog is unusual, but similar cases may exist elsewhere in analogous mesoclimatical and geomorphological conditions.

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# Relationships among testate amoebae (Protozoa), vegetation and water chemistry in five *Sphagnum*-dominated peatlands in Europe

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SUMMARY

To study the relationships between groups of organisms and the degree to which these relationships are consistent across major climatic gradients, we analysed the testate amoeba (*Protozoa*) communities, vegetation and water chemistry of one peatland in five countries: Switzerland, The Netherlands, Great Britain, Sweden and Finland, as part of the BERI (Bog Ecosystem Research Initiative) project. The relationships between the different data sets and subsets were investigated by means of detrended correspondence analysis, canonical correspondence analysis and Mantel permutation tests. The comparison of data on vegetation and testate amoebae showed that inter-site differences are more pronounced for the vegetation than for the testate amoebae species assemblage. Testate amoebae are a useful tool in multi-site studies and in environmental monitoring of peatlands because: (1) the number of species in *Sphagnum*-dominated peatlands is much higher than for mosses or vascular plants; (2) most peatland species are cosmopolitan in their distributions and therefore less affected than plants by biogeographical distribution patterns, thus differences in testate amoeba assemblages can be interpreted primarily in terms of ecology; (3) they are closely related to the ecological characteristics of the exact spot where they live, therefore they can be used to analyse small-scale gradients that play a major role in the functioning of peatland ecosystems. This study revealed the existence of small-scale vertical gradients within the vegetation and life-form niche separation in response to water chemistry. The deep-rooted plants such as *Carex* spp. and *Eriophorum* spp. are related to the chemistry of water sampled at or near the ground water table, whereas the mosses are not. Testate amoebae were

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shown to be ecologically more closely related to the chemistry of water sampled at or near the water table level and to the mosses than to the deep-rooted plants.

Key words: peatland, vegetation, testate amoebae, water chemistry, biogeography, microenvironmental gradients.

## INTRODUCTION

Hydrodynamics and hydrochemistry are determinant factors for peatland development (Bridgham *et al.*, 1996). Peatlands are characterized by gradients of nutrients (eutrophic–oligotrophic), hydrology (ombrogenous–geogenous) and acidity. The relationships to environmental gradients are well known for vegetation (Glaser *et al.*, 1990), especially for *Sphagnum* (Clymo, 1973; Andrus, 1986; Rydin, 1993), and for animal communities, especially invertebrates (Borcard & Vaucher-von Ballmoos, 1997). These different groups of organisms respond to, and can be indicative for, these variables. However, less is known about the degree to which the relationships between these structuring groups are consistent across major climatic gradients, and to what extent they react to environmental differences.

In conservation biology there is growing interest in relationships in species diversity of high-order taxa, but the results are highly variable (Prendergast *et al.*, 1993; Prendergast & Eversham, 1997). Studies of species composition among such taxa could reveal the degree to which they are dependent on one another and the same or different environmental variables, and help to explain the variability in species diversity. Very few studies of community composition include species from different high-order taxa (e.g. phytosociological relevés compared with analyses of diatoms; de Sloover *et al.*, 1996).

Among the different groups of microorganisms, the testate amoebae (Protozoa; Rhizopoda) are both abundant and diverse in *Sphagnum* mosses (Warner, 1987). Their well defined ecological preferences in relation to important ecological variables governing peatlands (such as water table depth and the concentration of ions) have long been recognized (for review see Tolonen, 1986) and have made them useful in ecological studies (Charman & Warner, 1992; Tolonen *et al.*, 1992, 1994). In addition, testate amoebae produce shells which are well preserved in peat and allow paleoenvironmental reconstruction (Warner & Charman, 1994; Mitchell, 1995; Buttler *et al.*, 1996). Testate amoebae have been shown to be sensitive to micro-habitat variation (i.e. a mire's surface with the transition from a *Sphagnum* lawn to hummock) and to macro-scale variation between geographical regions (Warner, 1987; Mitchell *et al.*, 1999). Furthermore, they are small (10–300 μm long) and most abundant in the upper few centimetres of the moss carpet, in the living part of *Sphagnum* mosses and in the poorly decomposed litter below. Recent studies on the effect of nitrogen fertilization on microorganisms in a *Sphagnum*-dominated peatland have shown that testate amoebae have a central position in the microbial trophic network and react rapidly to environmental changes (Gilbert *et al.*, 1998a,b).

In this study we examined the relationships between three independently collected data sets (testate amoebae, vegetation and water chemistry) originating from five *Sphagnum*-dominated peatlands across Europe. Our aims were (1) to improve understanding of the factors affecting testate amoebae communities; and (2) to determine the scale at which testate amoebae are sensitive to environmental factors, thus improving the precision of inferences that may be drawn from amoebae in ecological and paleoecological studies.

## MATERIALS AND METHODS

### *Study sites*

We chose five sites of representative lawn communities in ombrotrophic or near-ombrotrophic peatlands, in the major climates where *Sphagnum* peatlands occur in Europe (Fig. 1, Table 1). These sites were chosen as they allowed delivery of $CO_2$ needed in the BERI project (Hoosbeek *et al.*, 1995).

*Boreo–nemoral (southern Sweden).* The Kopparås Mire, in the boreo–nemoral zone of southern Sweden, is mainly open with scattered, small trees of *Pinus sylvestris*. The mire is weakly minerotrophic, but smaller spots are ombrotrophic. The water supplies are both soligenous and, to a lesser extent, topogenous. The mire surface slopes slightly (1:164) towards the south-south west. The lawn vegetation of the area studied is dominated by *Eriophorum angustifolium, Calluna vulgaris, Andromeda polifolia, Narthecium ossifragum* and *Scirpus caespitosus*. Predominant peat mosses are *Sphagnum magellanicum, S. papillosum* and *S. rubellum*.

*Continental–boreal (Ilomantsi, eastern Finland).* The Salmisuo Mire, Ilomantsi, Finland is mainly open with scattered, small trees of *P. sylvestris*. Most parts are weakly minerotrophic, but small ombrotrophic spots exist. The water supply is both soligenous and, to a lesser extent, topogenous. The mire surface slopes slightly (1:200) towards the west. The vegetation is dominated by graminoids such as *Eriophorum vaginatum* and *Carex pauciflora* and, to a lesser extent, by dwarf shrubs such as *A. polifolia, Empetrum nigrum, Chamaedaphne calyculata* and *Vaccinium oxycoccos*. Scattered shoots of *Carex*


**Fig. 1.** Map of Europe showing the location of the five sites. 1, Kopparås mire, south Sweden; 2, Salmisuo mire in Ilomantsi, eastern Finland; 3, Roudsea bog, north-west England; 4, peat from Dwingelo mire transplanted to Wageningen; 5, La Chaux-des-Breuleux, Swiss Jura.

*lasiocarpa* can also be found. On lawn communities, the dominant peat mosses are *Sphagnum balticum* and *S. papillosum* with the subdominants *S. magellanicum* and *S. rubellum*. Scattered hummocks are dominated by *S. angustifolium*, *S. fuscum*, *Polytrichum strictum* and *Aulacomnium palustre*.

*Nemoral, strongly Atlantic* (*north-west England*). At Roudsea, on the edge of the English Lake District National Park, the mire surface slopes slightly towards the west. The site has been drained, but the drainage ditches were blocked and secondary vegetation is well established. Most of the surface is covered by lawn communities with isolated hollows. The vegetation is dominated by *E. vaginatum*, *S. caespitosus*, *Erica tetralix* and *S. papillosum*.

*Nemoral, mild Atlantic* (*The Netherlands*). The site is a small (150 × 50 m) peat area in the State Forestry Dwingeloo, province of Drenthe. The mire developed in a depression (part of a late glacial brook system in and along which pingos arose) and rests on loamy sand and boulder clay. Up to 1955 the site was used by local farmers for peat cutting. Today the vegetation consists of a mosaic of secondary successional stages including pools, carpets and hummocks. Common species are *E. tetralix*, *V. oxycoccos* and *S. magellanicum*.

*Subalpine* (*Jura, Switzerland*). La Chaux-des-Breuleux lies in the subalpine zone in the Jura mountains. The mire developed on the bottom of a shallow valley, on impermeable marl deposits. The mire was drained and peat was mined until the end of World War II. The mire surface slopes slightly (1:200) towards the south. The drainage ditches are colonized by *Sphagnum fallax*, *Carex rostrata*, *E. angustifolium* and *Potentilla palustris*. Between the ditches a bog vegetation has re-established through a natural regeneration process (Grosvernier *et al.*, 1995) and a mosaic of lawn, hummocks and depressions is now well developed with *E. vaginatum*, *Carex nigra* and *V. oxycoccos*. The dominant mosses are *S. fallax* and *P. strictum*.

### *Vegetation analysis*

At each site, 20 plots (10 in Britain), 1 m in diameter, were randomly selected in a visually homogeneous part of the mire. The vegetation was analysed using two methods: point-intercept measurements and classical vegetation relevés. The point-intercept method (Buttler, 1992) was chosen in order to obtain a quantitative, objective measure of abundance for

**Table 1.** *Location, climatic data and nitrogen deposition at the five sites*

| Country | Name, location and height above sea level of field site | Climate* | Nitrogen deposition† | Water table depth (mm)‡ |
|---|---|---|---|---|
| Sweden | Kopparås mire, 57° 7.5′ N, 14° 30′ E, 225 m | 16°C, −2°C, 800 mm, 80–120 d snow | Medium | 102 |
| Finland | Salmisuo in Ilomantsi, 62° 47′ N, 30° 56′ E, 155 m | 16°C, −10°C, 650 mm, 150–200 d snow | Low | 106 |
| Britain | Roudsea bog, 54° 14′ N, 3° 1′ W, 5 m | 13°C, 1°C, 1800 mm, <20 d snow | Medium | 106 |
| Netherlands | Dwingelo, 52° 50′ N 6° 40′ E, 13 m | 18°C, 3°C, 750 mm, <10 d snow | High | 92 |
| Switzerland | La Chaux-des-Breuleux, 47° 13′ N, 7° 3′ E, 1000 m | 15°C, −5°C, 1390 mm, 80–120 d snow | Medium | 324 |

*Mean daily temperature in warmest and coldest month, annual precipitation, number of days with snow cover.
†Low: <1 g $m^{-2}$ $yr^{-1}$; medium: 1–3 g $m^{-2}$ $yr^{-1}$; high >3 g $m^{-2}$ $yr^{-1}$.
‡Average over 3 yr, 1996–98 weekly measurements of 20 plots during the growing season.

the species. We chose a homogeneous subplot (35 × 22.5 cm) with a square grid of 2.5 cm pitch which gave a total of 150 points. At each point a sharp needle (1 mm diameter) was lowered vertically into the vegetation. As the needle was lowered, the contacts of plant species with the tip of the needle were noted. Frequencies expressed as percentages were calculated for each species, giving a quantitative measurement of cover. The vegetation relevés were made on the entire plots of 0.79 $m^2$ to obtain a general description and a better assessment of rare species. In this method the percentage cover of all species was estimated by eye. All data were collected at the peak biomass period. Authorities for plant species follow Corley *et al.* (1981) for mosses, Grolle (1983) for hepatics, and Tutin *et al.* (1964–80) for vascular plants.

### *Water samples*

Water samples were collected from all plots at the five sites using Millipore soil-moisture samplers (Rhizon, Eijkelkamp BV, The Netherlands). The samplers were inserted in the moss carpet as close as possible to the water table, and connected to pre-evacuated glass bottles. The water samples were taken at the beginning of the 1996 growing season and in spring, summer and autumn, 1997 and analysed for dissolved organic carbon (DOC), pH, total N and P, and major cations and anions ($Na^+$, $K^+$, $NH_4^+$, $Ca^{2+}$, $Mg^{2+}$, $Fe^{3+}$, $Al^{3+}$, $NO_3^-$, $Cl^-$, $SO_4^{2-}$) at Wageningen Agricultural University, following Buurman *et al.* (1996). The three data sets from 1997 were used to check for seasonal variations. Similarity matrices (Euclidian distance on centred-reduced data) were significantly correlated (Mantel permutation tests between pairs of matrices, $P < 0.001$). Therefore, although the concentrations of different chemical species varied during the year, the similarity between pairs of samples remained comparable.

### *Testate amoebae sampling and analyses*

At the beginning of the 1996 growing season 5–10 *Sphagnum* mosses were extracted from each plot. Each moss was cut at 3 and 5 cm depth, and testate amoeba shells were extracted from the 3–5 cm section following Warner (1990). Moss samples were boiled in water to detach the amoebae, and filtered (mesh diameter 300 μm). The shells were then concentrated by centrifugation and the samples stored in vials. All shells living and dead were identified and counted by the same person (E. M.) to a minimum number of 150. Frequencies expressed in percentage were calculated for each species. Nomenclature follows Tolonen (1986).

### *Numerical analyses*

(1) Data on vegetation (point-intercept and cover-estimation relevés) and testate amoebae were first submitted to separate detrended correspondence analyses (DCA: CANOCO Program, ter Braak, 1988–92) to show variations of species assemblages in relation to the sites. Both analyses were carried out using the same option in the program: detrending by 26 segments, no data transformation.

(2) Partial canonical correspondence analyses (CCA: CANOCO Program) were used to determine how much of the variation in the data sets for testate amoebae and vegetation (point-intercept data only) was explained by the water chemistry data. The significance of the water chemistry variables was tested by means of a Monte Carlo permutation test in the forward selection procedure. No data transformation was applied. Four samples out of 90 (one from Switzerland and three from The Netherlands) with extreme values, detected by CANOCO as having an extreme influence on the regressions, were deleted. Five dummy variables (coded 0/1) representing the five sites were used as covariables, and permutations were limited within these five blocks. Testate amoebae and plant species occurring only once in the data set were omitted in order to reduce the noise in the data set and thus reduce the total variation in the matrix. This reduced the number of testate amoeba species to 40. The point-intercept vegetation data were subdivided into three sets: all plants, 31 species; deep-rooted vascular plants (*Carex* spp., *Eriophorum* spp., *E. tetralix*, *C. vulgaris*, *E. nigrum*, *S. caespitosus*, *N. ossifragum* and *Rhynchospora alba*, 11 species); mosses, lichens and liverworts (hereafter cryptogams, 12 species).

(3) Mantel permutation tests (Mantel, 1967) were performed between pairs of similarity matrices (Legendre & Fortin, 1989) to test the overall relationships between all combinations of the following four data sets: deep-rooted vascular plants (point-intercept data only); cryptogams (point-intercept data only); testate amoebae; water chemistry. The Steinhaus similarity index was used for the amoeba and vegetation matrices (transformed to a distance matrix for comparison) and the Euclidean distance for the water chemistry matrix (Legendre & Legendre, 1998). These computations were made using the R package for data analysis (Legendre & Vaudor, 1991). The permutations were restricted within five blocks representing the sites. As for the CCA analyses, testate amoebae and plant species occurring only in one sample were deleted.

## RESULTS

### *Water chemistry*

From the water chemistry data (Table 2), the five sites could be classified along two main large-scale

**Table 2.** *Water chemistry of the five sites*

| Chemistry | Sweden | Finland | Britain | Netherlands | Switzerland |
|---|---|---|---|---|---|
| pH | 4.73 | 4.43 | 4.47 | 4.72 | 4.80 |
| $Ca^{2+}$ | 2.29 | 0.30 | 1.53 | 0.49 | 0.34 |
| $Mg^{2+}$ | 0.88 | 0.13 | 0.84 | 0.55 | 0.12 |
| $Na^{+}$ | 3.93 | 0.35 | 6.95 | 3.84 | 0.39 |
| $K^{+}$ | 0.62 | 0.29 | 0.54 | 1.68 | 1.25 |
| $NH_4^{+}$ | 0.03 | 0.00 | 0.46 | 0.92 | 0.00 |
| $Fe^{3+}$ | 0.85 | 0.24 | 0.75 | 1.76 | 0.23 |
| $Al^{3+}$ | 0.13 | 0.02 | 0.27 | 0.06 | 0.01 |
| $NO_3^{-}$ | 1.47 | 0.38 | 1.55 | 0.13 | 0.18 |
| $Cl^{-}$ | 8.43 | 0.00 | 11.6 | 7.98 | 1.21 |
| $SO_4^{2-}$ | 21.5 | 0.03 | 16.6 | 0.00 | 0.01 |
| $N_{tot}$ | 0.33 | 0.14 | 1.14 | 1.50 | 0.14 |
| P | 0.00 | 0.01 | 0.09 | 0.01 | 0.01 |
| DOC* | 21.5 | 18.1 | 41.3 | 39.1 | 15.4 |

Mean concentrations (mg $l^{-1}$, except pH) of major cations, anions and elements in the water collected from the five sites. $n = 20$, except for Britain, $n = 10$.
*Dissolved organic carbon.

**Table 3.** *Mean percentage cover of plant species in the five sites*

| Plant species | Sweden | Finland | Britain | Netherlands | Switzerland |
|---|---|---|---|---|---|
| *Andromeda polifolia* | 3.9 | 6.5 | 3.9 | 0.1 | 0.2 |
| *Calluna vulgaris* | 2.7 | | 6.5 | 0.3 | 0.2 |
| *Carex nigra* | | | | | 2.9 |
| *Carex pauciflora* | | 1.0 | | | |
| *Drosera rotundifolia* | 5.7 | 0.7 | | 0.8 | |
| *Erica tetralix* | 0.1 | | 12.9 | 4.9 | |
| *Eriophorum angustifolium* | 17.7 | | 0.3 | 2.0 | 0.9 |
| *Eriophorum vaginatum* | 2.6 | 9.3 | 13.9 | 0.1 | 2.7 |
| *Narthecium ossifragum* | 3.3 | | <0.1 | | |
| *Rhynchospora alba* | 1.3 | | | 0.1 | |
| *Scheuchzeria palustris* | | 1.6 | | | |
| *Scirpus cespitosus* | 0.4 | 0.2 | 2.2 | | |
| *Vaccinium oxycoccos* | 2.4 | 3.6 | 0.2 | 4.4 | 1.3 |
| *Aulacomnium palustre* | | | | 0.3 | 1.2 |
| *Polytrichum strictum* | | | | | 57.5 |
| *Sphagnum balticum* | 2.8 | 63.4 | | | |
| *Sphagnum fallax* | | | | 0.2 | 88.5 |
| *Sphagnum magellanicum* | 80.5 | 1.9 | | 96.3 | |
| *Sphagnum papillosum* | 10.4 | 34.9 | 78.5 | 0.8 | |
| *Sphagnum rubellum* | 1.7 | | | <0.1 | |
| Number of vascular plant species | 13 | 12 | 9 | 11 | 9 |
| Number of cryptogam species | 6 | 6 | 4 | 8 | 6 |
| Total number of plant species | 19 | 18 | 13 | 19 | 15 |
| Total number of plant species in the point-intercept relevés | 18 | 12 | 13 | 15 | 8 |

Only species with cover $\geq 1\%$ in any site are included. Total number of species includes all species recorded.
The following species were found at lower abundance: *Betula nana, B. pubescens, Calliergon stramineum, Carex lasiocarpa, C. limosa, C. rostrata, Cephalozia connivens, Cladonia* sp., *Empetrum nigrum, Equisetum palustre, Hypnum cupressiforme, Odontoschisma sphagni, Picea abies, Pinus sylvestris, Pleurozium schreberi, Polytrichum commune, Potentilla erecta, Rubus chamaemorus, Sphagnum capillifolium, S. fuscum, S. majus, S. pulchrum, S. tenellum.*

gradients: from oceanic (Britain, Sweden and The Netherlands) to continental (Finland and Switzerland), as reflected by Na, Cl and Mg, and from low atmospheric pollution (Finland, Switzerland and Sweden) to high (The Netherlands and Britain), as reflected mainly by increasing total N and $NH_4^{+}$ levels. These gradients add to the large-scale climatic gradients (Table 1).

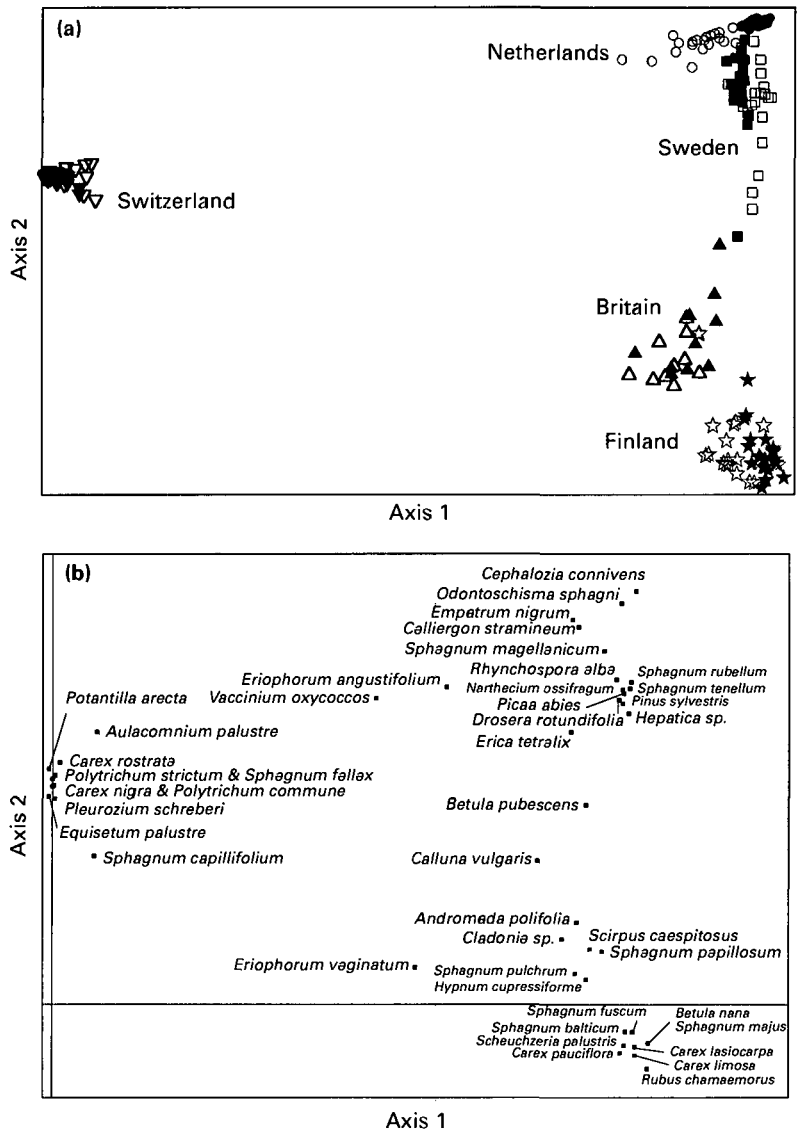


**Fig. 2.** (a) Detrended correspondence analysis (DCA) scatter diagram of point-intercept (open symbols) and cover-estimation (filled symbols) relevés of vegetation for the five sites. Samples from the different sites are represented by symbols: Switzerland, triangles base uppermost; Finland, stars; Netherlands, circles; Sweden, squares; Britain, triangles apex uppermost. Axes 1 and 2 represent 60% of the total variance (eigenvalues 0.949 and 0.708, respectively, total inertia = 2.781). (b) DCA scatter diagram of the plant species.

*Vegetation*

A total of 44 plant species was recorded. Plant species present at all sites are *E. vaginatum*, *V. oxycoccos* and to a lesser extent *A. polifolia*. The different sites clearly differ in vegetation composition (Table 3). Most species were present in only one or two sites. The total number of species was low in the British and Swiss sites (13 and 15 species), and almost equal in the other three sites (18 and 19 species). The number of species in the point intercepts was lower or equal to that of the cover estimations in the relevés, but most of the species absent from the point intercepts were either rare or of little interest in the context of this study (seedlings of *Picea*, *Betula*, etc.).

The position of point-intercept and cover-estimation relevés in the DCA scatter diagram revealed an almost complete separation of sites in the species assemblages (Fig. 2a). The within-site variation was much smaller because plots were placed in homogeneous areas within the sites. The Netherlands and Sweden are close together in the scatter diagram, reflecting their many common species, often with similar abundance, especially for *S. magellanicum* (Table 3). Similarly, Britain and Finland shared a high percentage of *S. papillosum* and *E. vaginatum*, and the two groups overlapped on the ordination. Switzerland was far off from the other four countries, which reflects the abundance of three species (*S. fallax*, *P. strictum* and *C. nigra*) rare or absent from the other sites.

*Testate amoebae*

A total of 54 species were recorded. Each site appeared to have either several characteristic species (usually rare in Sweden, The Netherlands and Britain), or different frequencies of some common species, as compared with other sites (Table 4). Total species number also varied between the sites. The Swedish site showed the highest number of species with 40; the Swiss site was the poorest (16 species); and the three other sites had 29–31 species. These differences resulted in a partial separation of the different sites on the DCA scatter diagram of testate amoebae data (Fig. 3a). As in the vegetation ordination, Switzerland was distinct from the other four sites, but the overlap among the other sites was much higher than in the vegetation ordination. Britain and Finland were well separated in the testate amoebae ordination but not in the vegetation ordination. Three species showed highly contrasting relative abundance between the two countries: *Nebela tincta* var. *major* which was very abundant in the British site (29%) and *Hyalosphenia elegans* and *Hyalosphenia papilio* which were very abundant in the Finnish site (14% each).

*Testate amoebae, vegetation and water chemistry: multivariate analyses*

In general, the significant water chemistry variables explained only a small part of the total variance (2–6%, Table 5). Nitrate, calcium and sulphate were found to be significant in the CCA of testate amoebae data, and these variables explained 6% of the total variance. In the CCA of all plants and that of deep-rooted plants, DOC was found to be significant, explaining 4 and 6% of the total variance, respectively. In the CCA of cryptogams, iron was significant and explained 4% of the total variance. The percentage variance explained by all chemistry variables was highest for deep-rooted plants (17%), almost equal for all plants and testate amoebae (13%) and lowest for cryptogams (10%). The importance of the site effect for the different data subsets varied: it was greatest for the cryptogams (89%), high for all plants (79%), low for deep-rooted vascular plants (57%), and lowest for testate amoebae (51%). Interestingly, the data subsets which were found to have a low site effect also had a higher fraction of their variance explained by the water chemistry.

Mantel tests with limited permutations (Fig. 4) revealed significant relationships between the water chemistry and deep-rooted vascular plants, and between the water chemistry and testate amoebae. Furthermore, the relationship between the cryptogam and testate amoebae data was marginally significant ($P = 0.07$). For the other three pairs of data sets, the relationships were clearly not significant.

## DISCUSSION

Important floristic differences exist between the five sites, but these are due in part to plant distribution patterns. Many of the species occurring only in one or two sites are absent or rare in the other countries. The oceanic species *N. ossifragum* was found only in Britain and Sweden. *Rubus chamaemorus* is a northern species, the English Lake District and The Netherlands are outside the range of *Betula nana*, and *E. tetralix* is not indigenous to Switzerland. However, most species (*Carex limosa*, *C. lasiocarpa*, *C. nigra*, *R. alba*, *P. strictum*, *S. fallax*, *S. papillosum*, *S. tenellum*) are absent from some sites while they do occur in the region, suggesting that the sites differ in their ecology.

By contrast, differences in assemblages of testate amoebae are less pronounced among the sites studied across Europe. Interestingly, testate amoebae appear to reflect the pollution gradient (axis 2, Fig. 3a) from the least polluted site (Finland), through the intermediate site (Sweden) and the more polluted sites in Britain and The Netherlands. This suggests that the existing differences could well reflect ecological differences between the sites, and testate amoebae may be less dependent than plants on differences in distribution pattern. For instance, *Corythion dubium* and *N. tincta* are very abundant at the Swiss site but much rarer at the other sites. These species are very common in mosses and humus, and are therefore not typical peatland species (Chardez, 1965). Their abundance in the Swiss samples is related to the history of the site where both plant and animal communities have not yet fully recovered from the peat exploitation. On the other hand, several species occurring only in Sweden are characteristic for very wet microhabitats such as minerotrophic pools (*Difflugia elegans*, *D. microstoma*, *Euglypha cristata*, *Nebela dentistoma*, *N. gracilis*, *Sphenoderia fissirostris*) (Jung, 1936; Mitchell *et al.*, 1999). Three species present only in the Dutch site (*Arcella vulgaris*, *Centropyxis eurystoma* and *Difflugia globulosa*) are characteristic for minerotrophic and wet conditions. Among the species occurring only in Britain, *Hyalosphenia subflava* is an indicator of dry conditions (the site was drained until recently), and *Nebela flabulellum* could represent an exception to the general rule that peatland testate amoebae are cosmopolitan – this species has been found only in oceanic peatlands on both sides of the northern Atlantic (Charman & Warner, 1997). However, there are not yet sufficient data on distributions of testate amoebae to interpret with confidence the negative evidence of species distribution patterns.

To some extent the different groups of organisms behave similarly: the Swiss site differs from the others both in amoeba composition and in vegetation. The reason might be its successional status. On the other hand, in accordance with suggestions

**Table 5.** *Summary of the partial canonical correspondence analyses of testate amoebae and vegetation data from the five sites*

| Analysis | Cryptogams | All plants | Deep-rooted plants | Testate amoebae |
|---|---|---|---|---|
| Sum of all eigenvalues (*a*) | 2.325 | 2.590 | 2.323 | 2.468 |
| Sum of all eigenvalues after fitting covariables (*b*) | 0.256 | 0.547 | 1.001 | 1.218 |
| Site effect (%) (*c*)* | 89 | 79 | 57 | 51 |
| Sum of all canonical eigenvalues if all variables are accepted in the model (*d*) | 0.026 | 0.074 | 0.166 | 0.161 |
| Percentage of variance explained by all variables (*e*)† | 10.2 | 13.5 | 16.6 | 13.2 |
| Significant variables | Fe | DOC | DOC | Ca, $NO_3$, $SO_4$ |
| Sum of all significant canonical eigenvalues (*f*) | 0.006 | 0.019 | 0.064 | 0.070 |
| Percentage of variance explained by the significant variables (*g*)‡ | 2.3 | 3.5 | 6.4 | 5.7 |
| Significance of axis 1 and correlation of significant variable(s) | 0.037<br>$r$(Fe) = 0.73 | 0.040<br>$r$(DOC) = 0.60 | 0.010<br>$r$(DOC) = 0.61 | 0.001<br>$r$(Ca) = 0.15;<br>$r(NO_3)$ = 0.06;<br>$r(SO_4)$ = 0.10 |
| Significance of axis 2 and correlation of significant variable(s) | – | – | – | 0.01<br>$r$(Ca) = 0.11;<br>$r(NO_3)$ = 0.23;<br>$r(SO_4)$ = 0.18 |
| Significance of axis 3 and correlation of significant variable(s) | – | – | – | ns<br>$r$(Ca) = −0.10;<br>$r(NO_3)$ = −0.14;<br>$r(SO_4)$ = 0.45 |

Five dummy variables representing the sites were used as covariables.
*Calculated as: $c = 100\ (a-b)/a$.
†Calculated as: $e = 100\ (d/b)$.
‡Calculated as: $g = 100\ (e/b)$.

physiological characteristics and phenology. For example, *E. vaginatum* grows and flowers very early in the growing season and also has an early senescence, whereas *C. nigra* has a later phenology.

The Mantel tests reveal interesting relationships between the different subsets of data (Fig. 4). Deep-rooted vascular plants are significantly related to water chemistry, but cryptogams are not. For testate amoebae the situation is somewhat different: they are related to water chemistry and also (marginally significantly) to the mosses in which they live, but not to plants rooted as much as 40 cm below the surface. Thus testate amoebae reflect the chemistry of the ground water and to a lesser extent the botanical composition of the moss carpet in which they live. Lacking roots, mosses are more directly affected by their immediate surroundings as compared to vascular plants. The growth of *Sphagnum* mosses depends mainly on the ecological condition at the level of the capitulum. Even subtle micro-environmental changes such as shading can affect *Sphagnum* growth (Buttler *et al.*, 1998). In addition, although water can reach the capitula by capillarity, *Sphagnum* mosses modify the chemical characteristics of water by active uptake and exchange of cations, thus reducing the nutrient supply to vascular plants (Clymo & Hayward, 1982; Van Breemen, 1995). *Sphagnum* mosses therefore create a chemical gradient which adds to the gradient due to chemical differences between rain water and that of the water table. Thus a marked vertical ecological (mainly trophic) gradient appears within the acrotelm, the aerobic upper layer of *Sphagnum* peatlands. Deep-rooted plants and mosses may respond to different factors and can be considered as two different functional groups. Such differences are more marked in relatively dry situations. This is most obvious in the Swiss site where the deep-rooted plants (*E. vaginatum*, *E. angustifolium*, *C. nigra* and *C. rostrata*) have their roots in mineralized peat formed when the peatland was drained and cut. Soil chemical properties at this depth differ from those closer to the surface.

These results bring to light an aspect of peatland ecosystems that is often overlooked: the existence of vertical as well as horizontal ecological small-scale gradients below the surface. This relates to the crucial distinction between ombrotrophic (rainwater-fed) and minerotrophic (influenced by surrounding mineral soil) conditions of mires: deeply rooted species may be exposed to minerotrophic conditions while the bryophytes at the

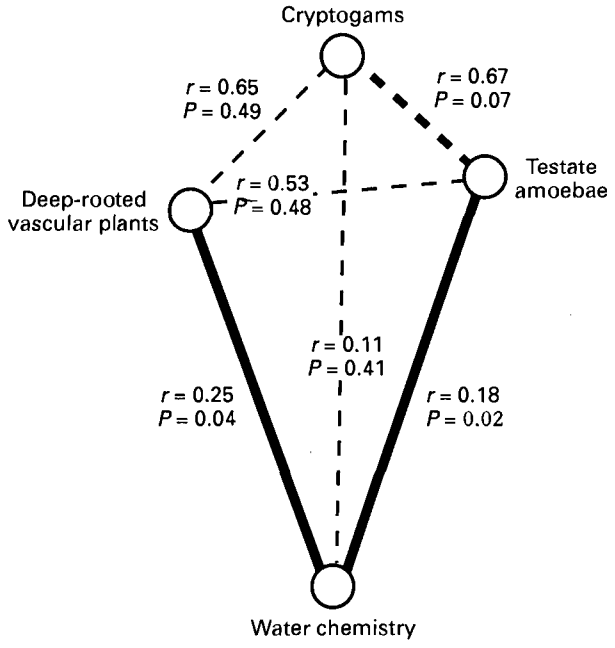


**Fig. 4.** Schematic representation of relationships between the four data sets based on the Mantel statistics. The line lengths are proportional to the Mantel statistic (short lines indicate strong relationships). Broad, unbroken lines, significant relationships ($P<0.05$); broad, dashed lines, marginally significant relationships ($0.1>P>0.05$); narrow, dashed lines, non-significant relationships ($P>0.1$).

surface may undergo ombrotrophic conditions. For the plants this is an excellent case of life-form niche separation (Grubb, 1977), enabling resource acquisition from different sources. At or near the surface, the importance of small-scale ecological gradients for the growth of mosses has recently been established in Swiss peatlands (Grosvernier *et al.*, 1995, 1997; Buttler *et al.*, 1998), but what happens below the surface is also important for the functioning of peatland ecosystems.

From a global perspective, a good understanding of below-ground processes is crucial for predictions of the response of peatlands to environmental change (Lee, 1998). The results of a recent study on the effect of nitrogen deposition on the microbial loop in a French peatland (Gilbert *et al.*, 1998a,b) show that testate amoebae are one of the dominant groups in terms of biomass, that they react quickly to nitrogen fertilization, and that they appear to play a key role in the cycling of matter and energy. Therefore testate amoebae could be an invaluable bioindication tool for ecologists.

From a modelling perspective, Peterson *et al.* (1998) have recently stressed the importance of process and structure variations across the spatial and/or temporal scales in order to understand ecological resilience ('a measure of the amount of change or disruption that is required to transform a system from being maintained by one set of mutually reinforcing processes and structures to a different set of processes and structures'). These authors argue that understanding the interactions between scaling of species and scaling of ecological processes should be a central goal of ecology, especially in the context of global change. Given the importance of peatlands in the global carbon cycle, the modelling of peatland–atmosphere exchanges is crucial for global change scenarios; recognition of the vertical gradients in peatlands may assist in better modelling of their functioning.

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