

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 hydrosere 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.

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 11000 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

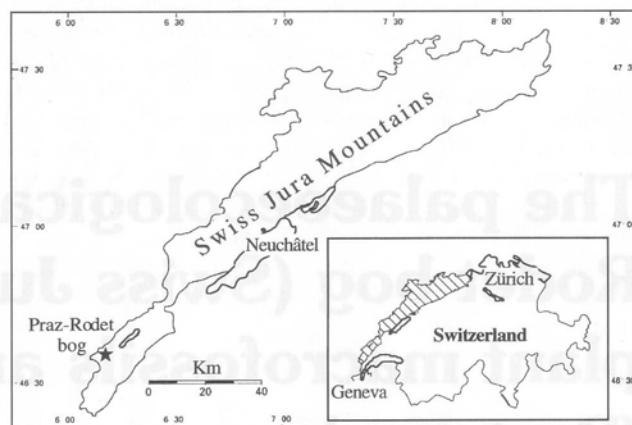


Figure 1 Map of Switzerland, showing the coring locality.

1500 mm) and cool mean temperatures (annual average $<5^{\circ}$ 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).

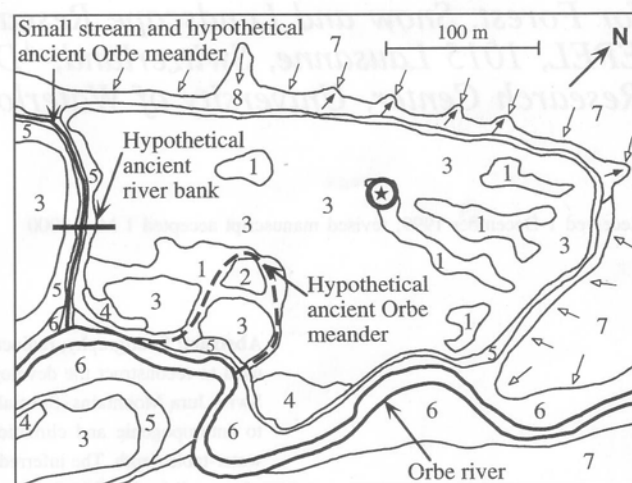


Figure 2 Site map of the Praz-Rodet bog (redrawn from Gallandat, 1982). Vegetation types are: 1 = open raised bog community (*Sphagnion magellanici*); 2 = bog pool community (*Caricion lasiocarpae*); 3 = raised bog community with pine (*Piceo-Vaccinienion uliginosi*); 4 = *Betulia pubescentis* raised 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 cm³ 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 cm³ 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.

Post 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 <i>Sphagnum</i> -dominated peat
47–58	Strongly decomposed peat
58–179	Mixed <i>Sphagnum</i> and herbaceous peat
179–195	Transition
195–260	Less-decomposed <i>Sphagnum</i> -dominated peat
260–320	Decomposed <i>Sphagnum</i> -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)	$\delta^{13}\text{C} \text{‰}$	Material dated	Calibrated age BP (1 σ)
53	0.5	UtC-4939	AMS	257 \pm 46 BP	-28.9	<i>Sphagnum magellanicum</i>	213 \pm 213
97	0.5	UtC-4938	AMS	1144 \pm 34 BP	-28.3	<i>Andromeda polifolia</i> twig + leaves	1026 \pm 40
130	4	B-6493	decay	1620 \pm 40 BP	-24.2	<i>Sphagnum magellanicum</i>	1479 \pm 60
162	4	B-6494	decay	2130 \pm 30 BP	-26.4	<i>Sphagnum magellanicum</i>	2095 \pm 41
180	1	UtC-4936	AMS	2589 \pm 35 BP	-25.7	<i>S. magellanicum</i> + <i>S. Sect. cuspidata</i> , amorphous	2736 \pm 19
188	4	B-6495	decay	4220 \pm 40 BP	-27.9	<i>S. magellanicum</i> + <i>S. Sect. cuspidata</i> , + <i>S. Sect. acutifolia</i>	4743 \pm 95
216	4	B-6496	decay	4670 \pm 80 BP	-27.8	<i>Sphagnum capillifolium</i>	5435 \pm 133
260	4	B-6497	decay	5210 \pm 60 BP	-27.1	<i>S. magellanicum</i> + <i>S. capillifolium</i>	6036 \pm 128
288	4	B-6498	decay	5800 \pm 80 BP	-26.7	<i>Eriophorum vaginatum</i> + <i>S. magellanicum</i>	6609 \pm 104
318	1	UtC-4052	AMS	6270 \pm 60 BP	-27.6	4.5 <i>Potentilla palustris</i> seeds + 1 other seed	7128 \pm 93
350	1	UtC-4053	AMS	7330 \pm 90 BP	-26.7	6 <i>Carex</i> seeds + 4.5 <i>Potentilla palustris</i> seeds	8075 \pm 93
370	1	UtC-4937	AMS	7630 \pm 47 BP	-27.8	amorphous peat	8385 \pm 30
380	1	UtC-4054	AMS	7400 \pm 70 BP	-26.9	Cyperaceae leaves	8165 \pm 142
392	2	UtC-4055	AMS	9560 \pm 80 BP	-26.3	seeds	10684 \pm 200
403	1	UtC-4056	AMS	9780 \pm 60 BP	-26.3	herbs	10956 \pm 48
425	1	UtC-4057	AMS	4780 \pm 70 BP	-26.8	one piece of charcoal	5465 \pm 129
453	1	UtC-4058	AMS	5560 \pm 50 BP	-26.9	one piece of charcoal	6354 \pm 50
473.5	2	UtC-4059	AMS	7780 \pm 60 BP	-24.1	leaf fragments	8492 \pm 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 Amburrex, 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

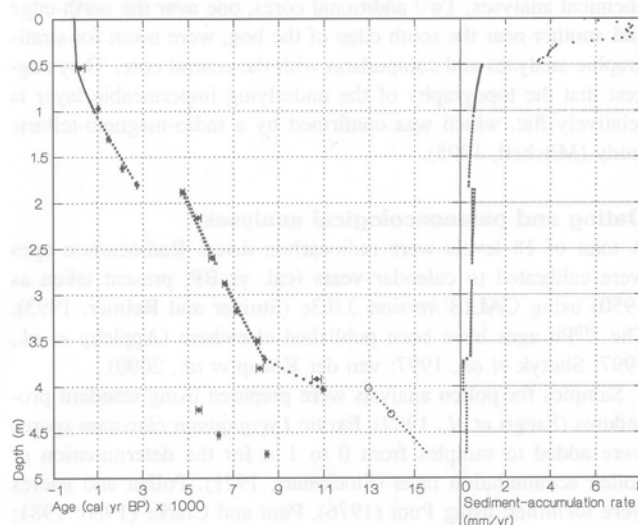


Figure 3 Depth-age relationship (left) and sediment-accumulation rates (right) for the Praz-Rodet bog based on 18 calibrated radiocarbon dates and two biostratigraphic dates. Ages are expressed as cal. yr BP = calendar years before AD 1950. Calibrated radiocarbon dates are depicted as large diamonds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

14000 cal. yr BP at 430 cm). The ages of samples older than Allerød time are extrapolated.

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

Praz Rodet (Swiss Jura; 1040 m)

Regional pollen percentage diagram (selected types)

(Pollen types sorted within groups by weighted averaging on depth)

Analysis: Jacqueline F.N. van Leeuwen

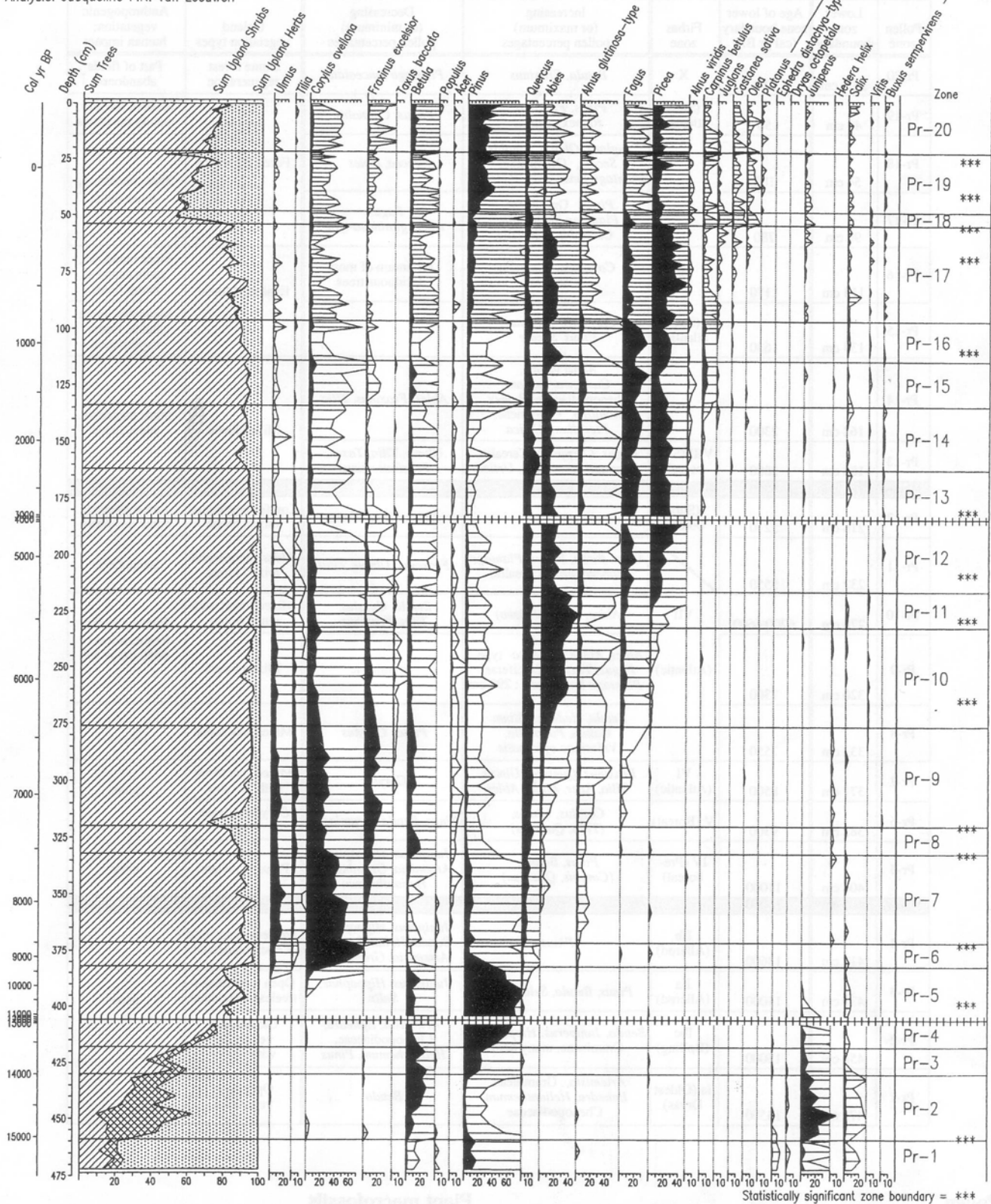


Figure 4 Pollen percentage diagram of the Praz-Rodet bog showing regional pollen types. Zone boundaries are as follows: dashed line = hiatus; drawn line = other zone. *** = statistically significant zone boundary ($P < 0.05$).

oxycoccus) appear in zone M-4. In zone M-6 bog pool species are recorded. Zone M-8 contains indicators of ombrotrophic bog (*V. oxycoccus*) and drier conditions (*Andromeda polifolia*). In zone M-9 *S. cuspidatum*, *S. tenellum*, *S. palustris* and *Eri-*

ophorum indicate wet conditions but these species disappear in zone M-10 which suggests drier conditions. In zone M-11 *S. cf. rubellum* and *V. oxycoccus* indicate moderately dry ombrotrophic conditions. The final zone M-12 may represent

Praz Rodet

Regional pollen percentage diagram
(continued)

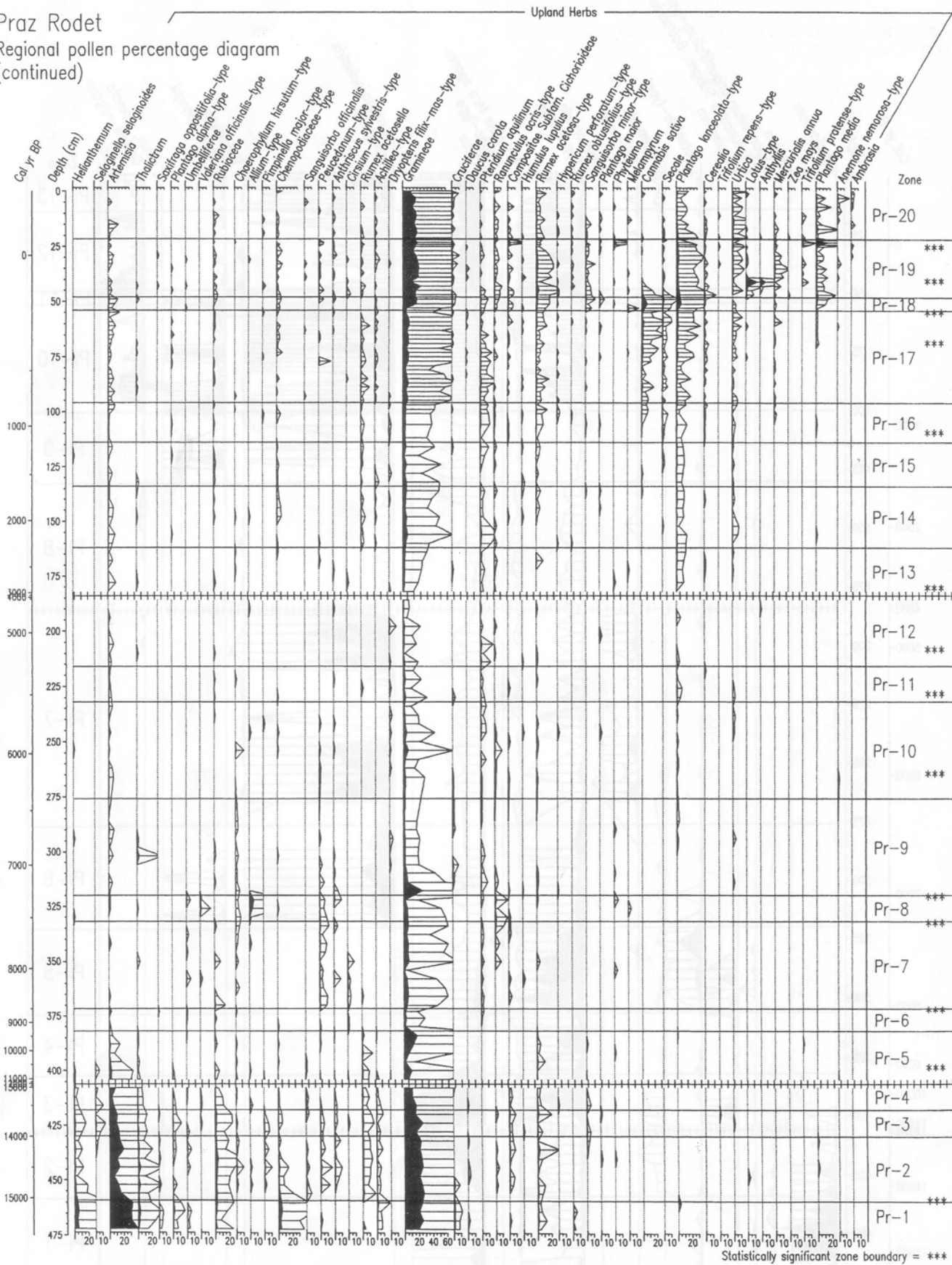


Figure 4 Continued.

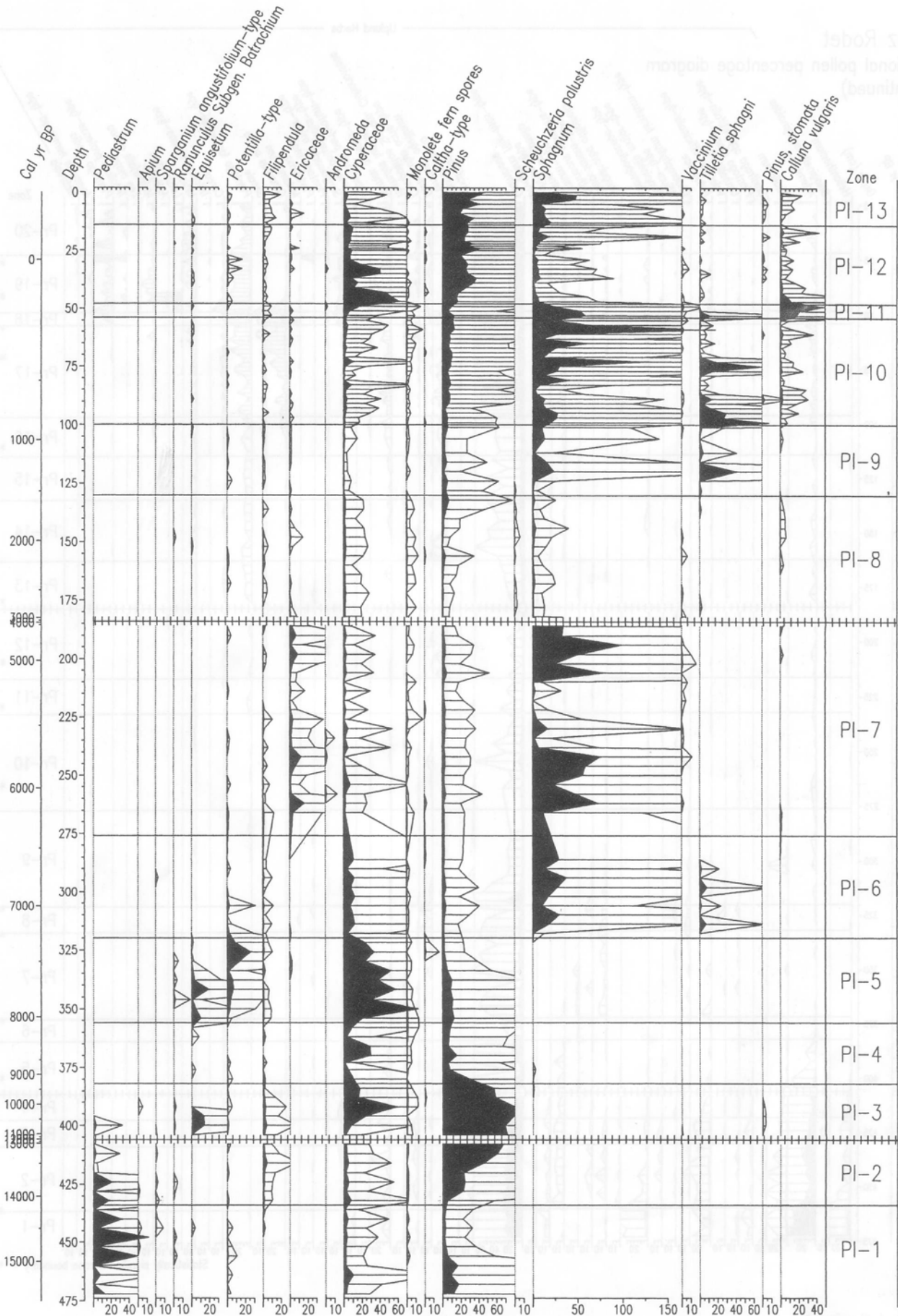


Figure 5 Pollen percentage diagram of the Praz-Rodet bog (Swiss Jura; 1040 m) showing local pollen types. Zone boundaries are as follows: dashed line = hiatus; drawn line = statistically significant zone boundary ($P < 0.05$). Analysis: Jacqueline F.N. van Leeuwen.

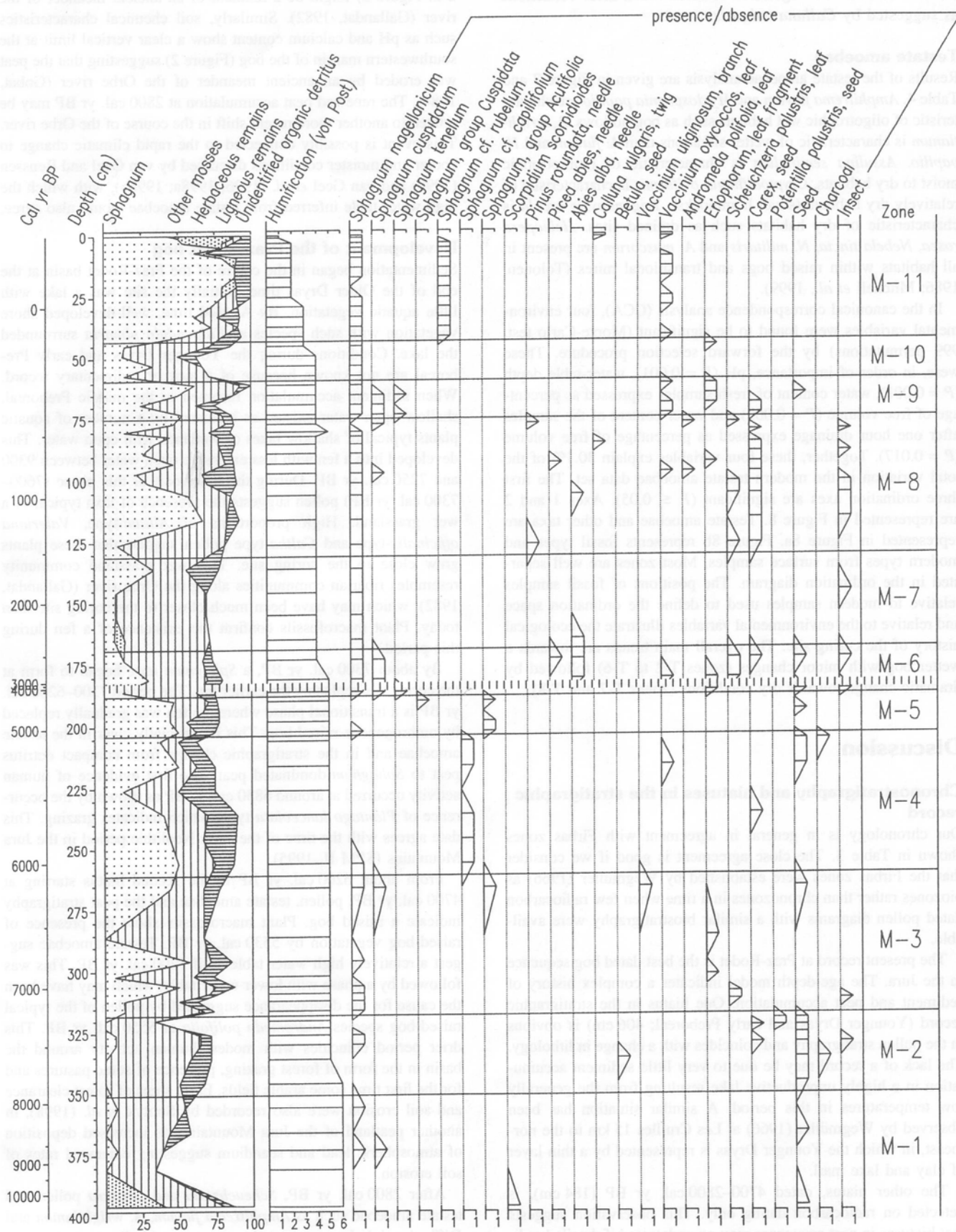


Figure 6 Plant macrofossil diagram of the Praz-Rodet bog (Swiss Jura; 1040 m). Zone boundaries are as follows: dashed line = hiatus; drawn line = statistically significant zone boundary ($P < 0.05$). Analysis: Edward A.D. Mitchell.

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. *Cryptodiffugia oviformis* is characteristic of relatively dry habitats (small hummocks). *Trigonopyxis arcuata* is characteristic of dry habitats such as drained sites. *Heleopera rosea*, *Nebela tinctoria*, *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 *Diffugia 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

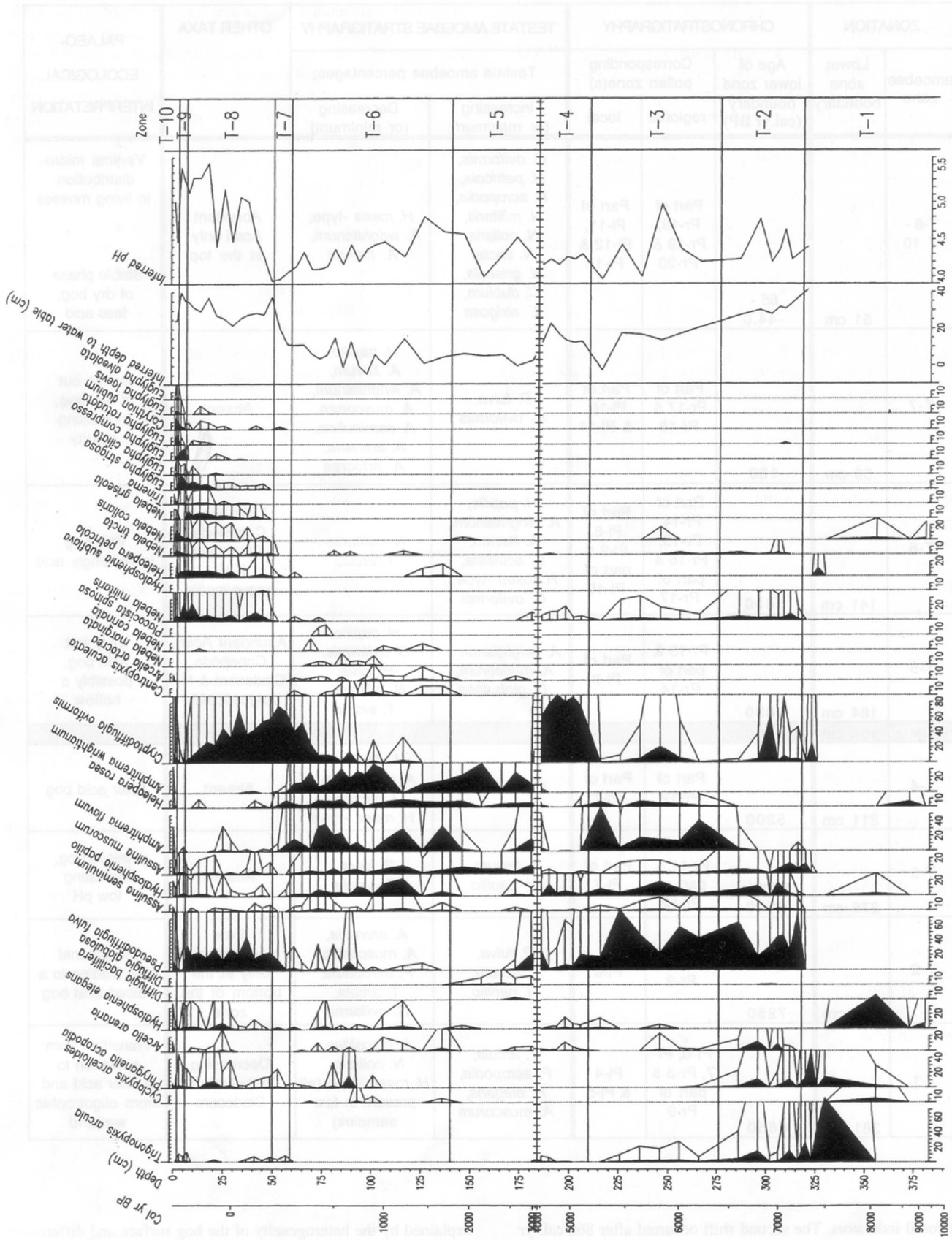


Figure 7 Testate amoebae percentage diagram of the Praz-Rodet bog (Swiss Jura; 1040 m) with indication of inferred peat pH and water-table depths. Zone boundaries are as follows: dashed line = hiatus; drawn line = statistically significant zone boundary ($P < 0.05$). Analysis: Edward A.D. Mitchell.

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)		Testate amoebae percentages:			
			regional	local	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 PI-11, PI-12 & PI-13	<i>C. oviformis</i> , <i>H. petricola</i> , <i>P. acropodia</i> , <i>N. militaris</i> , <i>N. collaris</i> , <i>N. tincta</i> , <i>N. griseola</i> , <i>C. dubium</i> , <i>E. strigosa</i>	<i>H. rosea</i> -type, <i>A. wrightianum</i> , <i>A. flavum</i>	Abundant Acari only at the top	Vertical micro- distribution in living mosses Stable phase of dry bog, less acid
T-7	59 cm	160	Part of Pr-17 & Pr-18	Part of PI-10, & PI-11	<i>P. fulva</i> , <i>C. oviformis</i>	<i>H. papilio</i> , <i>A. flavum</i> , <i>A. wrightianum</i> , <i>A. muscorum</i> , <i>A. seminulum</i> , <i>A. arenaria</i> , <i>A. artocrea</i>	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 PI-8, PI-9 & part of PI-10	<i>H. papilio</i> , <i>A. wrightianum</i> , <i>A. flavum</i> , <i>C. aculeata</i> , <i>H. rosea</i> -type, <i>C. oviformis</i>	<i>N. militaris</i> , <i>T. arcua</i>	Less Acari, Copepoda, Cladocera & <i>H.</i> <i>angusticollis</i>	Wet bog increasingly acid
T-5	184 cm	2800	Pr-13 & part of Pr-14	Part of PI-8	<i>A. wrightianum</i> , <i>A. muscorum</i> , <i>D. globulosa</i>	<i>H. papilio</i> , <i>C. oviformis</i> , <i>P. fulva</i> , <i>N. militaris</i> , <i>T. arcua</i>	Abundant Acari, Copepoda, Cladocera & <i>H.</i> <i>angusticollis</i>	Very wet acid bog, possibly a hollow
Hiatus	184 cm	4700						
T-4	211 cm	5200	Part of Pr-12	Part of PI-7	<i>C. oviformis</i>	<i>A. flavum</i> , <i>A. muscorum</i> , <i>T. arcua</i> , <i>H. rosea</i> -type	Absent	Drier acid bog
T-3	276 cm	6200/ 6600	Pr-10, Pr-11 & part of Pr-12	Part of PI-7	<i>A. flavum</i> , <i>H. papilio</i>	<i>P. fulva</i> , <i>T. arcua</i>	Absent	Raised bog, fluctuating low pH
T-2	318 cm	7250	Part of Pr-9	PI-6	<i>P. fulva</i> , <i>A. flavum</i> , <i>H. papilio</i>	<i>A. arenaria</i> , <i>A. muscorum</i> , <i>P. acropodia</i> , <i>T. arcua</i> , <i>C. oviformis</i>	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	PI-4 & PI-5	<i>T. arcua</i> , <i>P. acropodia</i> , <i>H. elegans</i> , <i>A. muscorum</i>	<i>A. discoides</i> , <i>N. collaris</i> , <i>H. rosea</i> -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*, *Vaccinium*) 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

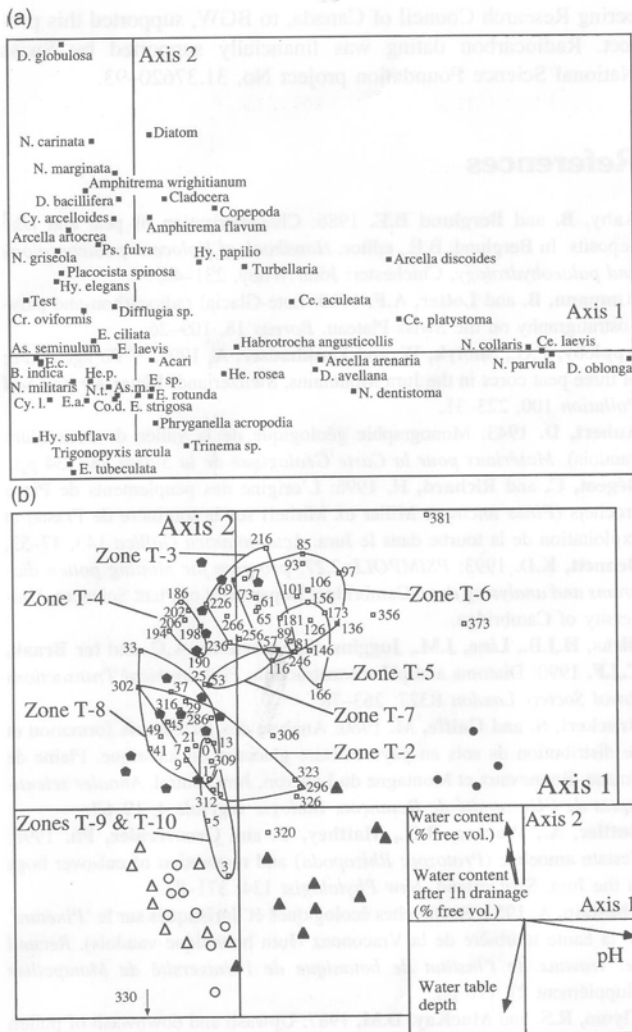


Figure 8 Canonical correspondence analysis (CCA) scatter diagram of testate amoebae samples from the Praz-Rodet core. The ordination space is a combination of ecological variables derived from a previous study on modern samples (Mitchell *et al.*, 1999). (a) Position of testate amoebae species. (b) Position 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* mire). As. = *Assulina*; As.m. = *A. muscorum*; B. = *Bullinularia*; Ce. = *Centropyxis*; Co. = *Corythion*; Cr. = *Cryptodifflugia*; Cy. = *Cyclopyxis*; Cy.1. = *C. laevigata*; D. = *Diffugia*; 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 P1–11, 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 pastures. 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 (Freléhoux, 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 (Freléhoux *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 Frasnés (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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