The relationship of modern pollen spectra, vegetation and climate along a steppe-forest-tundra transition in the Western Sayan Mts., southern Siberia, explored by decision trees

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Abstract

We studied the relationships among the composition of surface pollen spectra, vegetation and selected climate characteristics along a strong gradient of climatic continentality across the Western Sayan Mts., southern Siberia. Representation of 111 pollen taxa in 81 surface samples from steppe, forest and tundra was related to the vegetation composition at various distances from the sampling point and to mean annual precipitation and mean July and January temperatures. These relationships were assessed by an exploratory analysis – the decision tree models. The results show: 1. which vegetation types are well recognisable by their pollen spectra even to the community level, 2. which vegetation types are strongly similar in their pollen spectra and therefore their reconstruction from fossil pollen spectra should be carefully considered, 3. the considerably tight relationship between surface pollen spectra and the selected climate characteristics illustrates that the past climatic conditions can be reasonably predicted by the fossil pollen spectra, and 4. the important role of relatively weak pollen producers for the assignment of pollen spectra to a certain vegetation type or particular values of climate characteristic. We find the decision trees suitable for analysis of pollen/vegetation relationship because they enable us to: 1. formally and precisely assign the pollen spectra to vegetation/landscape types or climatic variables by means of easy-to-interpret graphs, 2. identify the pollen taxa with the highest importance for distinguishing a particular vegetation type, landscape type or climate characteristics. We compare the decision tree models to other approaches and suggest their further use.

Keywords: classification and regression trees, vegetation types, landscape types, pollen/vegetation relationship, surface pollen samples

Introduction

Much of the current research in palynology focuses on evaluation of the relationship between various vegetation types and their pollen deposition. Understanding this relationship is crucial for reliable reconstructions of the past landscapes from fossil pollen assemblages (von Post 1916, Sugita 1994).

Two major approaches have been applied in search for a “vegetation/deposited pollen” converter. The modelling approach (Parsons and Prentice 1981, Prentice and Parsons 1983, Sugita 1994) has brought many interesting results (Calcote 1995, Broström et al. 1998, Sugita et al. 1999, Nielsen 2004, Broström 2004, Bunting et al. 2005, Sugita 2007), especially in estimating the relevant source area of pollen (RSAP) for various regions and vegetation types (Sugita 1994). However, the available models have specific demands on data. They work best on regional scale, with few species well-represented in both pollen and vegetation (typically trees or grasses), and so far do not account for the landscape topography to a desired level. The best results in modelling the regional vegetation/pollen deposition relationship were achieved for large lakes (Sugita 2007), which are rare in many countries. Modelling also requires reliable estimates of pollen productivity, which are quite sparse (Sugita 2007) or not available for many species. Thus a universal usage of modelling approach is still rather limited.

The second approach lies in relating modern pollen deposition to vegetation, land-cover, land-use and environmental features, in order to search for common patterns. The statistical techniques used most commonly include correlation (Liu et al. 1999), regression (Webb et al. 1981, Bradshaw 1981, Bradshaw and Webb 1985), and multivariate methods, such as cluster analysis (Hoyt 2000, Stutz and Prieto 2003) and ordination (eg Gaillard et al. 1992, Gaillard et al. 1994, Brayshay et al. 2000, Odgaard and Rasmussen 2000, Fontana 2005). Apart from these, Prentice et al. (1996) introduced a method of biomization. Biomization is based on presumption that each pollen spectrum has an affinity to one or more biomes. The pollen taxa occurring in a certain pollen sample are assigned to biomes via broader plant functional types. Each taxon is then assigned to the biome with the highest affinity score. Usually, pollen taxa with representation 0.5% are included in the process. Biomization was widely used, for fossil as well as for the modern spectra (Tarasov et al. 1998, Ge Yu et al. 1998, Edwards et al. 2000, Prentice and Jolly 2000, Williams et al. 2000, Tarasov et al. 2001, Elenga et al. 2004).

Both the multivariate methods and biomization provide a useful insight into the pollen/vegetation relationship, but face the same problem with zero and close-to-zero values in percentage pollen data. Vegetation usually contains few strong pollen producers, and many weak pollen producers (especially herbs) or species with poorly dispersed pollen, which attain values lower than 1% in most pollen samples. Weak pollen producers have a low weight in the analysis, in spite of their potentially strong indicative meaning. Moreover, when using percentages, we have to be aware of the well known “Fagerlind effect” (cf. Fagerlind

1952), which means low pollen percentages do not necessarily mean few plants and vice versa. To obtain a balanced data set, the poorly represented pollen taxa are often excluded from the analysis. This is not a serious problem if we wish to reconstruct vegetation only on some rough scale. However, percentage pollen spectra of several structurally distinct vegetation types, eg an open hemiboreal forest and meadow steppe, can be quite similar. To distinguish between such vegetation types in the past, we would either need a macrofossil record (Birks and Birks 2000) or a good knowledge of the modern analogues, their indicator species and pollen spectra.

In this study, we use decision trees (Breiman et al. 1984) to investigate and visualize the relationship between surface pollen spectra and vegetation composition or environmental characteristics in various vegetation types. Decision tree is a technique of the exploratory data analysis. Its main advantage lies in applicability to "typical" ecological data, which are often complex, unbalanced, contain missing values, high-order interactions and non-linear relationships between variables (De'ath and Fabricius 2000). Pollen and vegetation proportions fit this characteristic well, with their non-linear relationship and large numerical differences in representation of pollen taxa.

For our study we chose the Western Sayan Mts. and adjacent areas in southern Siberia. This region, together with the adjacent Altai Mts., may be the closest modern analogue of landscapes and vegetation types of Central Europe in the full and late glacial period. The climate of the area is considerably spatially variable due to the mountainous topography, and the local climates of different parts of these mountains are analogous to the palaeoclimates of Central Europe in different periods of the Pleistocene or early Holocene (cf. Frenzel et al. 1992). The flora of these mountains includes many species with Euro-Siberian distribution ranges (Meusel et al. 1965–1992) with possible historical biogeographical links to Central Europe. Three major biomes, which supposedly occurred widely in the Pleistocene landscapes of Central Europe (Lang 1994, Willis et al. 2000, Jankovská et al. 2002, Jankovská 2006), meet in the Western Sayan Mts.: taiga, steppe and tundra. These form mosaics depending on local topography, altitude and the sharp gradient of climate continentality, running from the northern windward slopes to the southern intermountain valleys (Polikarpov et al. 1986). Therefore the study of the modern pollen/vegetation/environment relationships in this landscape provides a unique opportunity to improve our understanding of the Pleistocene landscape history of Central Europe and to refine its interpretations based on fossil pollen data.

In this paper, we address following questions:

1. To what degree of precision is it possible to predict studied vegetation types on the basis of surface pollen spectra for the sampling point and the landscape in its surroundings?
2. Which pollen taxa contribute most significantly to the prediction?
3. How well do the modern pollen spectra reflect the present climate characteristics in a dry and winter-cold continental area?
4. What are the advantages of decision trees in palynology with regard to other methods?

Chapter 2

Study area

The study area is situated in southern Siberia (Russia) between the towns of Abakan and Minusinsk in the north and the Russian-Mongolian border in the south (50°43'–53°33' N, 91°06'–93°28' E). It includes the mountain range of the Western Sayan and adjacent areas of the Minusinskaya Basin, Central Tuvinian basin and the Tannu-Ola Range. The mountains range in altitude from 350 to 2860 m and have predominantly rugged topography. The basins are flat or gently undulating, Minusinskaya at altitudes of 300–600 m and Central Tuvinian Basin at 550–1100 m.

Macroclimate of the study area is continental, but the northern front ranges of the Western Sayan are relatively warmer and more humid than elsewhere in Siberia (Polikarpov et al. 1986). At lower and middle altitudes, January temperature is –11 to –22 °C, July temperature 16–19 °C and annual precipitation 500–900 mm (Gidrometeoizdat 1966–1970). The abundant winter snow cover reaches up to 1.5 m. At the north-facing, windward slopes of the main ridge of the Western Sayan, annual precipitation is approximately 1600 mm. Southern part of the Western Sayan, Central Tuvinian Basin and the Tannu-Ola Range are in the area of rain shadow. Their climate is arid and continental, with annual precipitation below 400 mm. January temperature is –27 to –34 °C and July temperature 16–18 °C.

Central parts of both basins are located in the steppe zone, where tree stands only survive as narrow galleries along the rivers. Minusinskaya Basin is dominated by a meadow steppe with many Euro-Siberian species. Slightly humid places in this area are occupied by patches of *Betula pendula* or *Populus tremula* woodlands or *Caragana*-*Spiraea* steppic scrub. Central Tuvinian Basin, located at higher altitudes with drier and cooler climate, is covered with dry steppe consisting mainly of central Asian (Mongolian) species. Small woodland patches are mainly dominated by *Larix sibirica*. *Caragana*-*Spiraea* scrub is scattered at relatively humid sites.

Forest-steppe forms a transitional zone between the continuous forests on humid mountain ranges and steppes in the basins. Here, steppe regularly occurs on south-facing slopes and forest on north-facing slopes. In the northern part of the study area, forests in the forest-steppe zone are usually dominated by *Betula pendula* and/or *Pinus sylvestris*, while in the southern part by *Larix sibirica* (Chytrý et al. 2007b).

Forest zone occupies humid areas at middle and higher altitudes, especially on the northern side of the Western Sayan. Forests of the study include hemiboreal forests, occurring at drier and summer-warm sites (often in the forest-steppe zone), and taiga, occurring at wetter, summer-cool sites. Hemiboreal forests include *Betula pendula-Pinus sylvestris* mesic forest in the northern part of the study area, *Larix sibirica* dry forest in the southern part, and *Pinus sylvestris* dry forest on south-facing slopes of the northern part. Taiga includes *Abies sibirica-Betula pendula* wet forest on valley bottoms and footslopes in the northern part, *Abies sibirica-Pinus sibirica* mesic forest on slopes in the northern part, and *Pinus sibirica-Picea obovata* continental forest in cool and dry places throughout the study area, often near the timberline (see Chytrý et al. 2007b for details).

Alpine tundra zone is developed above the timberline (ie above 1600 m on humid northern ridges and above 2000 m on drier southern ranges; Zhitlukhina 1988). The most widespread vegetation type is dwarf-shrub tundra with *Betula rotundifolia* (dwarf birch from the *B. nana* group), *Vaccinium myrtillus* and *V. vitis-idaea*. Tall-forb vegetation occurs along the mountain streams.

Human population is concentrated in scattered villages in the basins and on the mountain foothills, where the steppe or forest-steppe is used for livestock grazing. In contrast, the mountain areas of the Western Sayan are almost without any permanent settlements. This area harbours primeval vegetation, although forest fires occur frequently and various stages of post-fire succession are common.

Materials and Methods

Data sampling

Vegetation of the study area was sampled in summers 2003 and 2004 as a part of a broader ecological study of the southern Siberian mountains. Sampling units were 307 plots of 10 × 10 m, in which complete lists of plant species with their cover-abundances and other characteristics were recorded (Chytrý et al. 2007a). Plots were classified, based on their species composition, by the divisive classification of the TWINSPAN program (Hill 1979). Separate analyses of forest and treeless plots resulted in six vegetation types of the former (described in Chytrý et al. 2007b) and eight types of the latter.

We collected surface pollen samples in each sampling plot, as five subsamples subsequently merged into one. The area of a subsample was ca 10 × 10 cm. We collected either up to 3 cm of humus and topsoil (in steppe and xeric scrub) or the polsters of ground-dwelling bryophytes (in forests, alpine tundra, alpine scrub and meadow steppe). In order to cover all main vegetation types, we refrained from restricting our samples only to places with moss polsters available (cf. Gaillard et al. 1994, Brayshay 2000), even though sampling in these two trapping media may be a source of slight inaccuracy.

We selected 81 samples from a set of those plots which represented the widest possible variety of vegetation and landscape types. We excluded pollen samples from subalpine tall-forb vegetation due to low pollen content, and merged two similar types of alpine tundra (*Vaccinium myrtillus* tundra, *Betula rotundifolia-Vaccinium vitis-idaea* tundra) because of few sampled sites. Thus, vegetation plots and corresponding pollen samples were divided into 12 vegetation types, each containing 5 to 11 plots/samples (Table I). The samples were dried at room temperature and prepared for analysis by standard methods (Faegri and Iversen 1992).

Pollen grains and spores were identified with help of a reference collection and keys (Moore et al. 1991; Reille 1995–1999; Beug 2004). Altogether, we identified 111 pollen taxa and counted minimum 500 grains/sample in 88% of samples. The lowest pollen sum accepted was 290 grains in one of the samples. Spores were not included in statistical analysis. All pollen counts were converted into percentages. To assess an approximate representation of the pollen taxa in the vegetation, we assigned all recorded plant species to pollen taxa and averaged their cover-abundances in all sampled plots for each of the twelve vegetation types (Table II). Pollen taxa relevant for results of our study are listed in Table III, together with corresponding plant species.

In order to obtain vegetation characteristics of the landscape surrounding the sampling points, we used the land-cover data prepared by expert interpretation of satellite images. We defined 13 land-cover classes. Their interpretation was assisted by the ERDAS IMAGINE software (http://gi.leica-geosystems.com/) and ground-proved during the fieldwork. The area of each land-cover class in two concentric rings with radius of 300 and 5000 m around each pollen sample was calculated, using the ArcGIS 8.3 software (http://www.esri.com/).

Table I Short description of vegetation and landscape types used in the classification tree models in Figures 1, 2a and 2b. The number of pollen samples analysed per each vegetation/landscape types is shown. Only land-cover classes with representation > 10% are mentioned in the description of landscape types.

Vegetation types in the area of 100 m^2 around the sampling point	**Pollen samples**	**Characteristic location**
Betula pendula-Pinus sylvestris mesic hemiboreal forest	5	Forest-steppe zone, N part (more oceanic)
Larix sibirica dry hemiboreal forest	7	Forest-steppe zone, S part (more continental)
Pinus sylvestris dry hemiboreal forest	8	Forest-steppe zone, dry slopes in N part
Abies sibirica-Betula pendula wet taiga forest	11	Forest zone, valley bottoms in N part
Abies sibirica-Pinus sibirica mesic taiga forest	5	Forest zone, slopes in N part
0*Pinus sibirica-Picea obovata* continental taiga forest	10	Forest zone, cool and dry areas
Alpine tundra with *Vaccinium myrtillus* or *Betula rotundifolia* and *Vaccinium vitis-idaea*	5	Tundra zone above the timberline
intblXeric scrub with *Caragana* sp. and *Spiraea* sp.	5	N-facing slopes in the forest-steppe zone
Species-rich meadow steppe (*Festuco-Brometea*)	7	Steppe and forest-steppe zone, N part
Dry Eurosiberian steppe (*Festuco-Brometea*)	7	Steppe zone, N part
Dry Mongolian steppe (*Cleistogenetea squarrosae*)	6	Steppe and forest steppe zone, S part
Dry rocky Mongolian steppe (*Cleistogenetea squarrosae*)	5	Steppe and forest-steppe zone, S part
Landscape types at the distance of 300 m from the sampling point		
Mosaic of *Larix* forest (46%), *Pinus sibirica* forest (22%) and deciduous forest with *Betula pendula* (13%)	18	
Mosaic of xeric scrub (32%), dry steppe (30%) and *Larix* forest (22%)	22	
Mosaic of species-rich meadows (31%), *Pinus sylvestris* forest (25%), *Betula pendula* forest (24%) and xeric scrub (16%)	22	
Mosaic of *Abies* taiga (46%), *Betula pendula* forest (24%) and *Pinus sibirica* forest (10%)	19	
Landscape types at the distance of 5000 m from the sampling point		
Mosaic of *Larix* forest (49%), *Pinus sibirica* forest (17%) and xeric scrub (12%)	17	
Mosaic of *Larix* forest (30%), dry steppe (28%), xeric scrub (25%) and alpine scrub (10%)	20	

Vegetation types in the area of 100 m^2 around the sampling point	**Pollen samples**	**Characteristic location**
Mosaic of species-rich meadows (28%), *Pinus sylvestris* forest (27%), *Betula pendula* forest (23%) and xeric scrub (15%)	20	
Mosaic of *Abies* taiga (35%), *Betula pendula* forest (21%), *Pinus sibirica* forest (14%) and *Larix* forest (11%)	24	

The land-cover data were further classified by cluster analysis, using Euclidean distance and Ward's clustering method in the STATISTICA 7.1 software (http://www.statsoft.com/), separately for 300-m and 5000-m circles. Clusters of each classification were interpreted separately as four landscape types with a different relative representation of the original land-cover classes (Table I).

Mean annual precipitation, mean summer and winter temperatures for sample sites were obtained from a climatic model based on the interpolation of measured data from climatic stations combined with standard precipitation-altitude charts and adiabatic lapse rate estimation (Chytrý et al. 2007b).

Data analysis

We used general classification/regression tree models included in the STATISTICA 7.1 software (http://www.statsoft.com/) to analyze how well the composition of surface pollen samples reflects the surrounding vegetation type, landscape type and climate. Decision tree is a statistical method that relates several explanatory variables to a response variable, which can be either categorical (classification tree) or continual (regression tree). A tree is grown by hierarchical splitting of the data into two mutually exclusive groups by means of a simple splitting rule based on a single explanatory variable. The splitting rule is set to maximize the homogeneity of the groups and minimize the within-group variation in the response variable at the same time.

The percentage proportions of 111 pollen taxa and percentage AP sum (consisting of 26 pollen taxa) in surface pollen samples were used as explanatory variables in all models. Vegetation composition in sample plots of 100 m^2 and landscape type (separately in 300-m and 5000-m circles) were defined as categorical response variables, whereas the climate characteristics were defined as continuous response variables. We ran the models three times, twice with transformed pollen abundances (square root and logarithmic transformation), in order to shrink differences in abundance of common and rare pollen taxa. However, the results stayed unaffected.

When growing a decision tree, it is necessary to decide about the right size of the tree, which is a matter of balance between explained variability in the response variable and reasonable amount of samples in terminal nodes. For this, we used 10-fold cross-validation. Following Breiman et al. (1984), we selected the resulting trees according to the standard error (SE) rule. 1-SE rule was used for prediction of vegetation types and 0-SE rule for the models with other response variables, where 1-SE rule lead to very simple trees. Variation in the response variable explained by each tree was calculated from the resubstitution relative error, corresponding to the residual sum of squares.

The accuracy of the classification tree models, that is their ability to classify new samples correctly, could not be tested on a test data set, due to lack of samples. Therefore we tested by

Table II Average cover-abundance ± standard deviation of pollen taxa in sampling plots (10 × 10 m) averaged over each of twelve vegetation types. The values are in %. The nomenclature largely follows Beug (2003).

Non-forest vegetation types	Alpine tundra with *Vaccinium myrtillus* or *Betula rotundifolia* and *V. vitis-idaea*	Xeric scrub with *Caragana* sp. and *Spiraea* sp.	Species-rich meadow steppe (*Festuco--Brometea*)	Dry Eurosiberian steppe (*Festuco--Brometea*)	Dry Mongolian steppe (*Cleistogenetea squarrosae*)	Dry rocky Mongolian steppe (*Cleistogenetea squarrosae*)
Abies	0.26 ± 0.86					
Aconitum/Delphinium	0.29 ± 0.64	0.50 ± 0.99	3.10 ± 5.34	0.34 ± 1.00		0.07 ± 0.45
Allium	0.19 ± 0.60	1.50 ± 1.04	2.00 ± 1.15	1.97 ± 1.10	1.71 ± 3.04	1.82 ± 2.68
Alnus viridis type	0.26 ± 1.44					
Androsace		0.72 ± 0.89	1.40 ± 0.97	0.66 ± 0.94	0.34 ± 0.80	0.64 ± 0.93
Anemone type	0.35 ± 0.84	0.11 ± 0.47	0.50 ± 1.08	0.31 ± 0.72		0.07 ± 0.45
Apiaceae	1.10 ± 1.94	1.78 ± 1.06	2.70 ± 2.06	1.26 ± 1.65	0.74 ± 0.95	1.93 ± 1.34
Artemisia		9.94 ± 10.50	9.30 ± 7.59	6.17 ± 5.62	13.71 ± 15.50	9.04 ± 8.08
Astragalus/Oxytropis	0.23 ± 0.72	0.44 ± 0.92	1.20 ± 1.03	2.37 ± 3.47	0.77 ± 1.17	1.00 ± 1.71
Berberis		0.61 ± 1.09			0.06 ± 0.34	0.20 ± 0.66
Betula nana	14.26 ± 21.88					
Betula pendula				0.29 ± 1.69		0.18 ± 1.19
Boraginaceae	0.29 ± 0.78	2.22 ± 1.17	3.20 ± 0.92	1.91 ± 1.01	1.03 ± 1.15	2.38 ± 1.34
Brassicaceae	0.23 ± 0.72	0.56 ± 0.92	1.20 ± 1.32	1.03 ± 1.22	1.26 ± 1.09	1.96 ± 1.17
Bupleurum	0.55 ± 1.89	2.39 ± 4.09	4.00 ± 2.79	2.69 ± 3.16	0.40 ± 0.81	1.22 ± 1.83
Caltha type	1.03 ± 3.28				0.17 ± 0.51	0.13 ± 0.50
Campanulaceae	0.39 ± 0.80	0.72 ± 1.07	0.30 ± 0.67	0.49 ± 0.85		
Cannabis/Humulus		0.06 ± 0.24			0.06 ± 0.34	
Caragana		5.61 ± 4.57	9.90 ± 11.38	2.69 ± 3.54	4.83 ± 3.63	5.96 ± 5.53
Carduus/Cirsium type	0.23 ± 0.72	0.22 ± 0.65		0.03 ± 0.17		
Caryophyllaceae	0.26 ± 0.73	0.11 ± 0.47	1.00 ± 1.15	0.54 ± 0.85		0.24 ± 0.71
Cerastium type	0.71 ± 1.16	0.83 ± 1.10	1.10 ± 1.20	0.34 ± 0.80	0.09 ± 0.37	0.47 ± 0.87
Chelidonium majus		0.39 ± 0.78	0.20 ± 0.63		0.11 ± 0.47	0.09 ± 0.42
Chenopodiaceae			0.20 ± 0.63	0.09 ± 0.37	3.09 ± 7.00	0.38 ± 0.78

Non-forest vegetation types	Alpine tundra with *Vaccinium myrtillus* or *Betula rotundifolia* and *V. vitis-idaea*	Xeric scrub with *Caragana* sp. and *Spiraea* sp.	Species-rich meadow steppe (*Festuco-* *-Brometea*)	Dry Eurosiberian steppe (*Festuco-* *-Brometea*)	Dry Mongolian steppe (*Cleistogenetea squarrosae*)	Dry rocky Mongolian steppe (*Cleistogenetea squarrosae*)
Compositae subfam. Asteroideae	3.16 ± 5.32	2.00 ± 1.64	5.20 ± 2.94	4.97 ± 3.45	1.40 ± 1.19	3.24 ± 3.56
Compositae subfam. Cichorioideae	0.48 ± 1.03		5.10 ± 3.63	2.14 ± 1.94	0.60 ± 0.91	0.87 ± 1.29
Convolvulus				0.11 ± 0.47	0.71 ± 1.05	0.22 ± 0.64
Cyperaceae	4.94 ± 2.95	23.39 ± 14.55	7.20 ± 5.14	8.31 ± 9.17	1.49 ± 3.36	9.78 ± 13.02
Dianthus	0.29 ± 0.78	0.83 ± 0.99	1.60 ± 0.84	1.37 ± 0.91	0.80 ± 0.96	1.73 ± 0.78
Echinops					0.17 ± 0.62	
Ephedra distachya type				0.20 ± 0.58	1.57 ± 3.10	1.00 ± 1.15
Epilobium type		0.06 ± 0.24				0.04 ± 0.30
Euphorbia		0.39 ± 0.78		0.20 ± 0.41	0.23 ± 0.65	0.44 ± 0.81
Fabaceae			1.20 ± 1.03	0.91 ± 1.20	0.17 ± 0.62	0.09 ± 0.42
Filipendula				0.31 ± 1.43		
Gentiana pneumonanthe type	0.39 ± 0.84		0.40 ± 0.84	1.20 ± 1.11		0.18 ± 0.58
Gentianaceae	0.90 ± 1.25	0.22 ± 0.65	0.20 ± 0.63	0.97 ± 1.18	0.03 ± 0.17	0.18 ± 0.58
Gentianella type		0.11 ± 0.47	0.60 ± 0.97	0.11 ± 0.47		
Geranium	0.87 ± 2.05	0.50 ± 0.92	0.20 ± 0.63	0.26 ± 0.66	0.03 ± 0.17	0.07 ± 0.45
Gypsophila		0.11 ± 0.47		0.71 ± 1.02	0.97 ± 1.04	0.22 ± 0.74
Hedysarum/ Onobrychis	0.26 ± 0.68			1.49 ± 2.12	0.03 ± 0.17	
Heracleum	0.03 ± 0.18			0.03 ± 0.17		
Hypericum			0.30 ± 0.67	0.03 ± 0.17		
Iris		1.00 ± 1.19	4.20 ± 2.90	2.94 ± 4.47	0.34 ± 0.76	0.84 ± 1.46
Juniperus	1.03 ± 3.53					
Lamiaceae		0.44 ± 0.78	1.00 ± 1.05	0.26 ± 0.66	0.57 ± 1.09	0.33 ± 0.83
Larix	0.84 ± 1.92		0.20 ± 0.63	0.46 ± 1.88		
Lathyrus/Vicia	0.06 ± 0.36	0.89 ± 1.18	2.20 ± 1.23	0.54 ± 1.20	0.63 ± 1.52	0.42 ± 1.03
Liliaceae	0.23 ± 0.62	0.61 ± 1.04	2.60 ± 2.55	0.37 ± 0.84		0.13 ± 0.50
Linnaea borealis	0.39 ± 0.80					

Non-forest vegetation types	Alpine tundra with *Vaccinium myrtillus* or *Betula rotundifolia* and *V. vitis-idaea*	Xeric scrub with *Caragana* sp. and *Spiraea* sp.	Species-rich meadow steppe (*Festuco-* *-Brometea*)	Dry Eurosiberian steppe (*Festuco-* *-Brometea*)	Dry Mongolian steppe (*Cleistogenetea squarrosae*)	Dry rocky Mongolian steppe (*Cleistogenetea squarrosae*)
Linum				0.23 ± 0.65		
Lonicera	0.84 ± 1.29	0.17 ± 0.71		0.06 ± 0.34		
Mentha type		0.67 ± 1.14	1.40 ± 2.50	0.77 ± 1.11	0.31 ± 0.80	2.40 ± 3.54
Orchidaceae	0.45 ± 0.93	0.17 0.51		0.09 ± 0.37		0.04 ± 0.30
Orobanche				0.14 ± 0.43		0.07 ± 0.33
Oxalis	0.06 ± 0.36					
Paeonia		0.11 ± 0.47		0.06 ± 0.34		
Papaver	0.06 ± 0.36					
Pedicularis	0.71 ± 1.10		0.20 ± 0.63	0.29 ± 0.71		0.04 ± 0.30
Peucedanum type		0.11 ± 0.47		0.51 ± 0.89		0.04 ± 0.30
Phlomis type		1.11 ± 1.37	0.90 ± 1.20	1.11 ± 1.64		0.27 ± 0.69
Picea	0.35 ± 1.11					
Pinus cembra type	1.97 ± 2.80	0.11 ± 0.47				
Pinus sylvestris type		0.56 ± 1.15				2.36 ± 11.50
Plantago major/media type			0.20 ± 0.63	0.54 ± 1.58		
Plumbaginaceae		0.17 ± 0.51	0.20 ± 0.63	0.71 ± 0.93	1.11 ± 0.96	1.00 ± 0.98
Poaceae	6.39 ± 7.64	6.22 4.41	12.10 ± 9.92	31.11 ± 19.70	15.40 ± 13.54	11.98 ± 8.85
Polemonium coeruleum			0.20 ± 0.63	0.06 ± 0.34		
Polygalaceae		0.11 ± 0.47	1.20 ± 1.03	0.91 ± 1.07	0.40 ± 0.85	0.58 ± 0.89
Polygonaceae					0.40 ± 0.85	0.20 ± 0.66
Polygonum alpinum	0.06 ± 0.36	0.11 ± 0.47	0.80 ± 1.03			0.16 ± 0.52
Polygonum aviculare type	0.61 ± 0.99			0.06 ± 0.34	0.03 ± 0.17	
Populus						0.04 ± 0.30
Portulacaceae	0.16 ± 0.64					
Potentilla type	0.26 ± 0.82	6.56 ± 9.81	4.40 ± 2.12	5.29 ± 6.72	5.94 ± 8.48	5.67 ± 3.71
Primula farinosa type				0.23 ± 0.81		
Prunella type	0.45 ± 1.55	2.06 ± 2.04	2.50 ± 1.27	2.34 ± 3.27	0.60 ± 1.09	0.89 ± 1.53

Non-forest vegetation types	Alpine tundra with *Vaccinium myrtillus* or *Betula rotundifolia* and *V. vitis-idaea*	Xeric scrub with *Caragana* sp. and *Spiraea* sp.	Species-rich meadow steppe (*Festuco-Brometea*)	Dry Eurosiberian steppe (*Festuco-Brometea*)	Dry Mongolian steppe (*Cleistogenetea squarrosae*)	Dry rocky Mongolian steppe (*Cleistogenetea squarrosae*)
Pulsatilla		1.22 ± 1.17	2.90 ± 2.85	1.86 ± 3.45	0.49 ± 0.95	1.69 ± 2.05
Ranunculaceae	0.23 ± 0.62	0.17 ± 0.71				
Ranunculus acris type	0.10 ± 0.40			0.17 ± 0.57		
Ribes	0.23 ± 0.72	0.39 ± 1.14		0.06 ± 0.34	0.06 ± 0.34	
Rosaceae	1.52 ± 2.78	4.17 ± 2.75	4.90 ± 5.90	1.11 ± 1.18	0.34 ± 0.80	2.00 ± 1.91
Rubiaceae		2.00 ± 0.84	3.50 ± 2.32	1.97 ± 1.50	0.34 ± 0.73	1.98 ± 0.89
Rumex acetosa type					0.06 ± 0.34	0.04 ± 0.30
Rumex alpinus type	0.55 ± 0.96					
Salix	4.10 ± 9.92			0.03 ± 0.17		
Sanguisorba officinalis			0.60 ± 0.97	0.31 ± 1.43		0.04 ± 0.30
Saxifragaceae	0.61 ± 1.23					
Scabiosa		0.22 ± 0.65	0.20 ± 0.63	0.94 ± 1.06	0.03 ± 0.17	0.27 ± 0.69
Scrophularia type				0.46 ± 0.95	0.09 ± 0.37	
Scrophulariaceae	0.13 ± 0.50	0.28 ± 0.67	1.70 ± 0.67	0.69 ± 0.96	0.06 ± 0.34	0.29 ± 0.66
Sedum type	5.32 ± 11.46	2.61 ± 4.37	1.60 ± 1.17	0.51 ± 0.92	1.20 ± 1.55	2.44 ± 1.60
Silene type	0.06 ± 0.36	1.06 ± 1.16	1.30 ± 1.16	0.69 ± 0.96	0.37 ± 0.77	1.29 ± 1.18
Spiraea	0.35 ± 0.95	18.78 ± 17.73	12.20 ± 22.89	0.34 ± 0.76	0.11 ± 0.47	2.80 ± 6.75
Thalictrum	0.06 ± 0.36	1.39 ± 1.04	1.60 ± 1.17	1.94 ± 1.78	0.06 ± 0.34	0.80 ± 1.04
Thesium	0.06 ± 0.36	0.39 ± 0.70		0.40 ± 0.74	0.06 ± 0.34	0.27 ± 0.65
Trientalis europaea	0.23 ± 0.72					
Trollius	0.77 ± 1.67			0.09 ± 0.51		
Urtica dioica		0.11 ± 0.47				
Vacciniaceae/ Ericaceae	28.03 ± 22.84	6.67 ± 14.60		0.11 ± 0.68		0.09 ± 0.60
Valeriana officinalis type	0.19 ± 0.60	0.56 ± 0.86	1.00 ± 1.15	0.20 ± 0.58		0.29 ± 1.25
Veratrum	0.48 ± 0.96	0.06 ± 0.24		0.11 ± 0.47		
Vincetoxicum		0.17 ± 0.51			0.43 ± 0.88	0.22 ± 0.64
Viola	0.48 ± 1.52	0.72 ± 0.89	0.60 ± 0.97	0.11 ± 0.47		0.09 ± 0.42

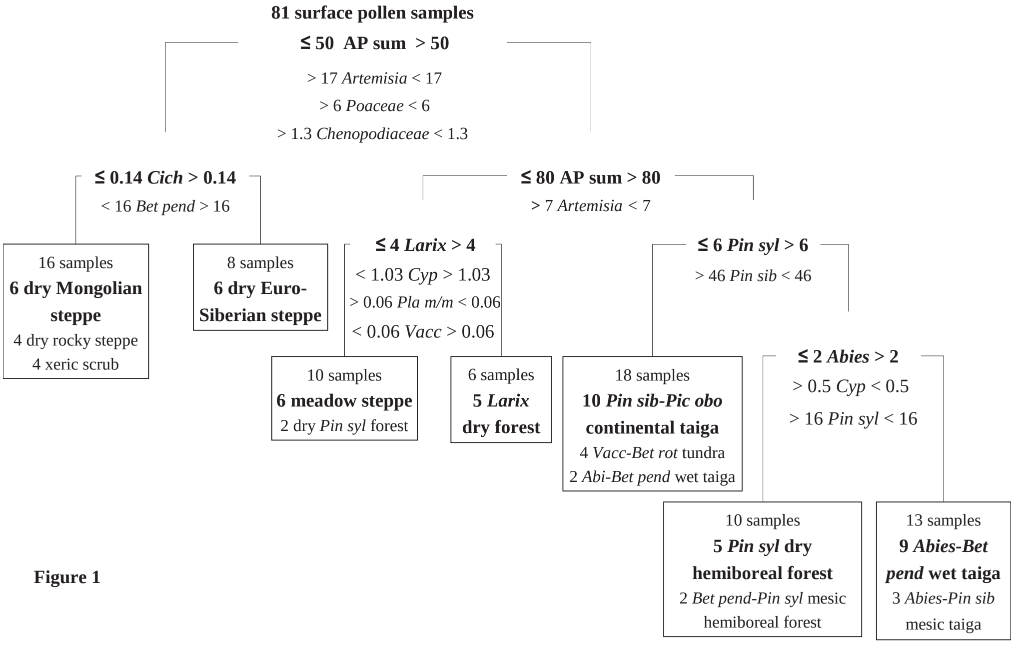


Figure 1

Figure 1. Classification tree showing the relationship between the surface pollen spectra and the local vegetation types at the sampled sites. At each split, the main splitting variable and its split value (pollen percentage) is given in bold. The surrogate variables with associated value of > 0.6 are given under the main splitter. The terminal nodes (framed) show how the division of pollen samples corresponds to the vegetation types at the sampling sites. The boldfaced vegetation types are the ones represented by most samples, the others by at least two samples. For detailed description of vegetation types see Table I. Abies – *Abies sibirica*, AP sum – arboreal pollen sum, Bet pend – *Betula pendula*, Bet rot – *Betula rotundifolia*, Cich – *Compositae* subfam. *Cichorioideae*, Cyp – *Cyperaceae*, Larix – *Larix sibirica*, Pic obo –

deployment, ie by submitting the model the original data set without the information on which sample belonged to which group.

At every step during the tree building process, the program identifies surrogate variables, ie explanatory variables which allocate most cases similarly as the main splitting variable. Each surrogate is assigned a degree of association ranging from 0 to 1. The larger the value of association, the more similar is the split of the samples belonging to the current node, when that particular surrogate is used instead of the main splitter. Surrogates with associated value 0.6 are mentioned in the results.

The relative contribution of each explanatory variable to the prediction of response variable in the tree models is quantified as the predictor's importance. Its value ranges from 0 to 1 and stems both from the variable's role as a splitter and as a surrogate across all nodes of the tree. The most important variable is arbitrarily given the value of 1 (for computational details see Breiman 1984; pp. 147). Explanatory variables with predictor's importance value 0.55 are given in the results.

Fig. 2a

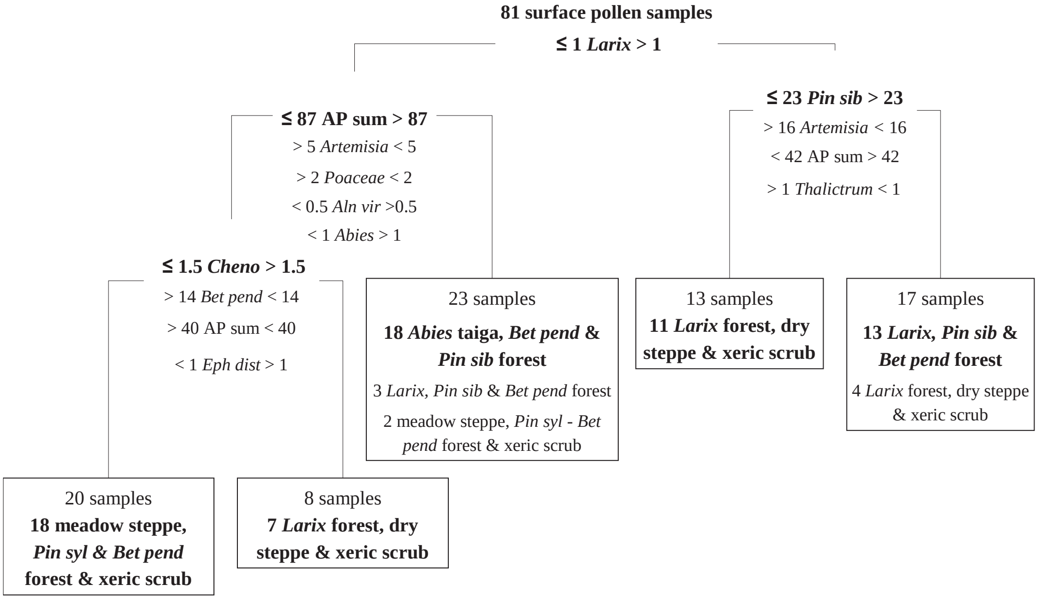


Fig. 2b

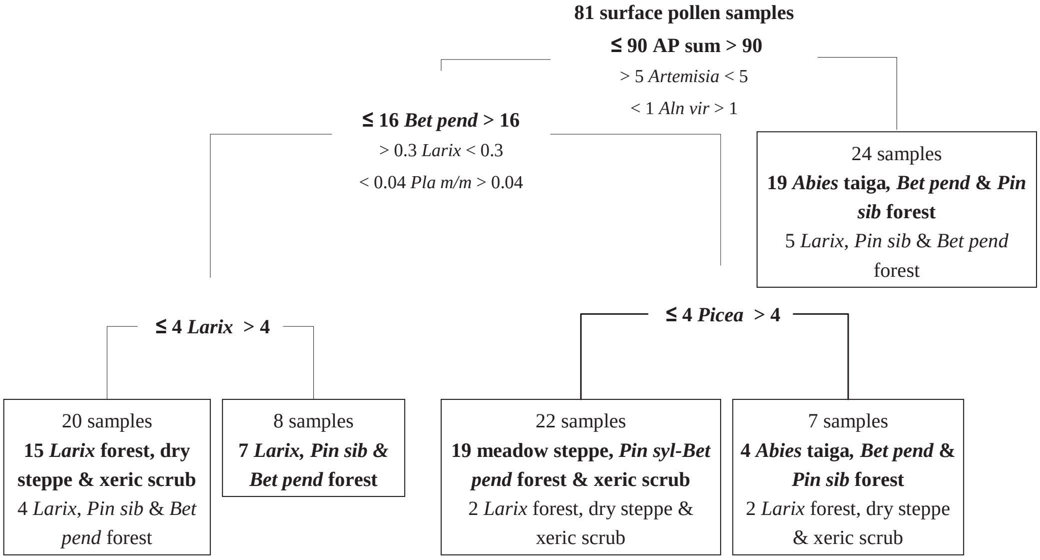


Figure 2. Classification trees showing the relationship between the surface pollen spectra and the landscape types at the distance of 300 m (**2a**) and 5000 m (**2b**) around the sampling site. See Fig. 1 for detailed explanation. The landscape types are defined as mosaics of certain vegetation types (see Table I for details). In the terminal nodes, the boldfaced landscape type is the one represented by most samples, the others by at least two samples.
Abies – *Abies sibirica*, Aln vir – *Alnus viridis* type, AP sum – arboreal pollen sum, Bet pend – *Betula pendula*, Eph dist – *Ephedra distachya* type, Larix – *Larix sibirica*, Picea – *Picea obovata*, Pin sib **–** *Pinus sibirica*, Pin syl – *Pinus sylvestris*, Pla m/m – *Plantago major-media* type.

Results

Prediction of local vegetation types at sampling sites

The classification tree in Figure 1 depicts how well the surface pollen samples reflect vegetation type in 100-m2 plots at the sampling sites (Table I). The tree has seven terminal nodes, in contrast to the original twelve vegetation types. More than half of the vegetation types were successfully distinguished by their surface pollen spectra, even though all terminal nodes did not contain solely samples from one vegetation type. The fist division separated samples from all dry steppe types and xeric scrub on one side and samples from meadow steppe, all types of hemiboreal forests and taiga on the other side. Further, samples from meadow steppe and *Larix* dry hemiboreal forests were separated into terminal nodes, then samples from *Pinus sibirica-Picea obovata* continental taiga and the last division separated samples from *Pinus sylvestris* dry hemiboreal forest and samples from mesic and *Abies-Betula* wet taiga. The accuracy of prediction by this tree was 57% and the explained variation was 50%.

Prediction of landscape types around the sampling sites

The classification tree in Figure 2a shows how the pollen samples reflect the landscape in the area of 300 m around the sampling point. The model distinguished all four landscape types on the basis of the surface pollen spectra. There were five terminal nodes, two of which contained pollen samples from identical landscape type, but were distinguished under different splitting criteria. The left branch of the first division resulted into three terminal nodes: samples surrounded by the mosaic of mesic hemiboreal forest and meadow steppe, samples surrounded by *Larix* forest, xeric scrub and dry steppe, and finally samples from the mosaic of taiga with *Abies* and *Betula pendula* forest. The right branch produced two terminal nodes: one with samples surrounded by *Larix* forest, xeric scrub and dry steppe, and the other with samples from the mosaic of *Larix* and *Pinus sibirica* forest. The accuracy of prediction by this tree was 83% and the explained variation was 76%.

The classification tree in Figure 2b shows how pollen deposition reflects the landscape in the area up to 5000 m around the sampling point. All four landscape types were distinguished like in the previous model. There were five terminal nodes, and samples from the mosaic of *Abies* taiga and *Betula pendula* forests prevailed in two of them. One of these terminal nodes contains seven samples from three different landscape types and supposedly contains samples which were problematic for the model to allocate. However, its existence helped separate other terminal nodes with more precision. This tree model predicted with accuracy of 79% and explained 70% variation in the response variable.

Prediction of climate

The regression tree in Figure 3a visualizes the relationship between composition of surface pollen samples and mean annual precipitation. The left branch of the first division was further divided in three terminal nodes with average values of mean annual precipitation 234, 333 and 668 mm. These terminal nodes contained samples mainly from dry vegetation types, such as dry Mongolian steppe, xeric scrub, species-rich meadow steppe, dry hemiboreal forest or continental taiga forest.

In contrast, the right branch of the tree was gradually divided into four terminal nodes. The average value of mean annual precipitation of the leftmost terminal node was 629 mm and these were samples from dry hemiboreal forest and continental taiga. Next three terminal nodes yielded values of 819, 1123 and 1396 mm and contained samples mostly from moister regions and vegetation types such as wet and mesic taiga, mountain tundra and mesic hemiboreal forest, but also continental taiga. The tree model explained 86% of variability in the mean annual precipitation.

The regression tree in Figure 3b shows the relationship between mean July temperature and composition of surface pollen spectra. The left branch contained mainly samples from taiga forests or mountain tundra, whereas the terminal nodes in the right branch included samples from all kinds of steppe, xeric scrub and hemiboreal forests. The model explained 69% of variability in the mean July temperature.

The regression tree in Figure 3c depicts the relationship between the mean January temperature and surface pollen spectra. Of all three regression tree models, this one was the simplest with only three terminal nodes. The left branch contained mostly samples from continental region in contrast to the right branch with samples from mesic and wet vegetation types. The model explained 57% of variability in the January temperatures.

Predictors' importance

Table IV shows the relative importance of individual pollen taxa for prediction of vegetation composition, landscape types and climate characteristics. The predictors with the highest importance in all the models were almost the same pollen taxa. These were both strong pollen producers (eg *Artemisia*, *Poaceae*, *Betula pendula*, *Pinus sibirica* and *P. sylvestris* and AP sum) and relatively weak pollen producers or species with poorly dispersed pollen (eg *Compositae* subfam. *Cichorioideae*, *Larix*, *Trollius*, *Plantago major-media* type, *Ephedra distachya* type and *Mentha* type). The pollen taxa shown in Table IV that do not appear in the tree graphs are mostly surrogates with associated value 0.5 for any specific division. These may have contributed to quite many divisions, but they cannot distinctively predict any of the terminal nodes in the tree models.

In the classification of vegetation and landscape types, AP sum usually separated forests and meadow steppe from dry scrub, dry steppe and rocky steppe. AP sum also separated *Larix* forests from other types of forest. High values of *Artemisia, Poaceae* and *Chenopodiaceae* indicated dry non-forest vegetation. Higher content of *Artemisia* also differentiated open hemiboreal forests from other forest types. In contrast, varying content of *Pinus sibirica, Pinus sylvestris* and *Abies* pollen separated samples from various types of hemiboreal forests and taiga. Higher content of *Betula pendula* pollen indicated mesic types of hemiboreal forests or mesic taiga in contrast to more extreme taiga types. *Picea* appeared only once as the main splitter and separated the landscape type with prevailing taiga from the mosaic of hemiboreal forests and steppe. Content of *Cyperaceae* pollen was growing towards the hemiboreal forests, either with *Pinus sylvestris* or *Larix sibirica*, where various species of *Carex*, particularly *C. pediformis* s. lat., are quite common.

As for poorly represented pollen producers, growing values of *Alnus viridis* type indicated wet taiga, where *Alnus fruticosa* occurs in the shrub layer (Table III). Occurrence of *Cichorioideae* pollen distinguished between Eurosiberian dry steppe and other more extreme types of dry steppe and xeric scrub. Higher values of *Plantago major-media* type indicated meadow steppe or meadow steppe/hemiboreal forest mosaic, since *P. media* often grows in meadow steppe. Pollen of *Larix* separated *Larix* hemiboreal forests from meadow steppe as well as the mosaic *Larix* forest/steppe from other more forested landscape types. Growing representation of *Vacciniaceae/Ericaceae* pollen differentiated between open hemiboreal forests and the meadow steppe, due to *Vaccinium vitis-idaea* occurring in the undergrowth of

Fig. 3a

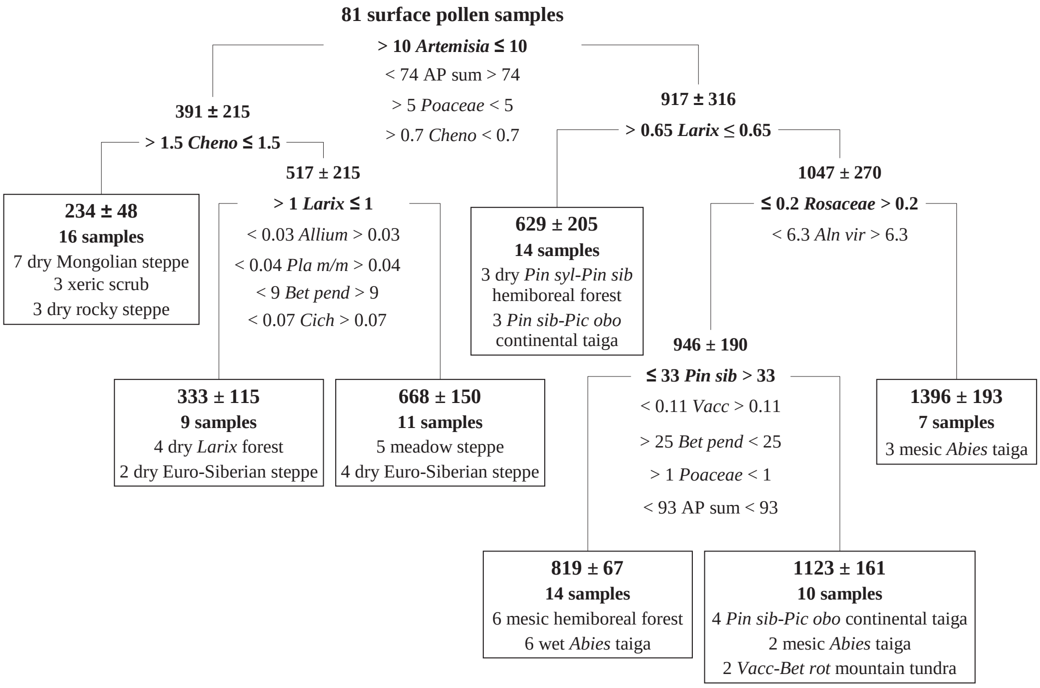
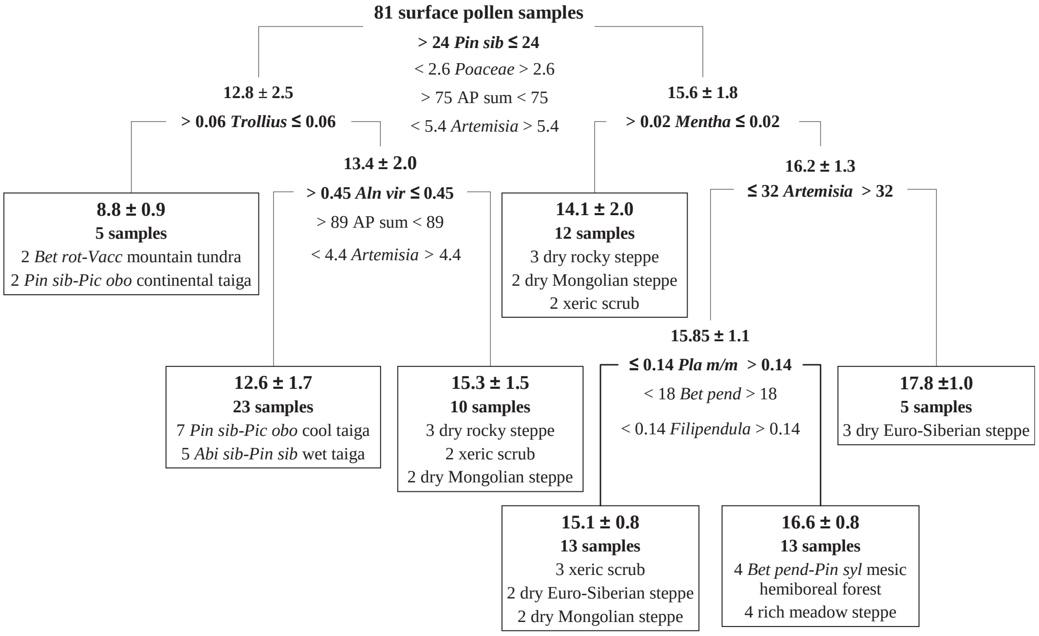


Fig. 3b



open *Larix* forests. Similarly, growing values of *Thalictrum* and *Ephedra distachya* type indicated landscape with *Larix* hemiboreal forest, dry steppe and xeric scrub.

In the regression tree models of climate characteristics, pollen taxa whose high values indicated low mean annual precipitation (*Artemisia, Chenopodiaceae, Poaceae*) or high mean

Fig. 3c

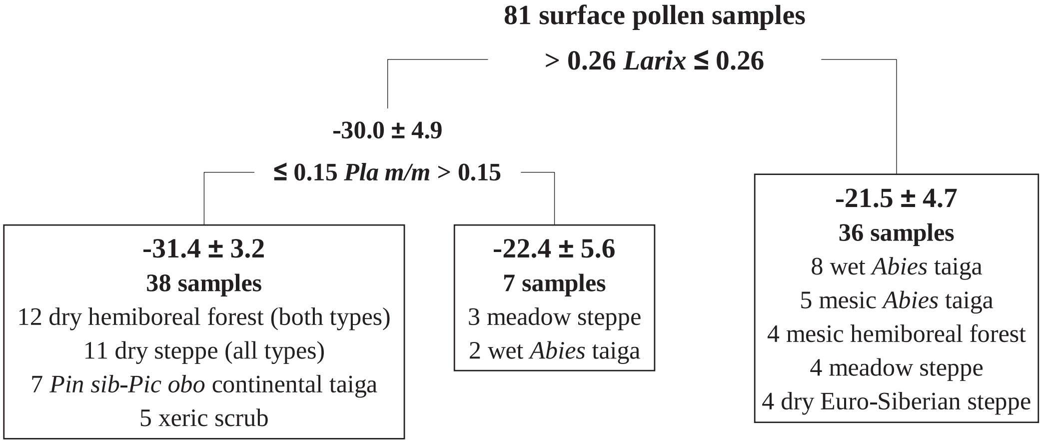


Figure 3. Regression trees showing the relationship between the composition of surface pollen spectra and mean annual precipitation (**3a**, in mm), mean July temperatures (**3b,** in °C) and mean January temperatures (**3c**, in °C), respectively. At each node, mean value of particular response variable ± standard deviation is given. The primary splitting variables with their split value (pollen percentages) are boldfaced. The surrogate variables with associated value of > 0.6 are given under the main splitter. Terminal nodes (framed) show mean value of particular response variable ± standard deviation, number of samples and the vegetation type(s) represented by highest amount of surface samples in that node. Abies, Abi sib – *Abies sibirica*, Aln vir – *Alnus viridis* type, AP sum – arboreal pollen sum, Bet pend – *Betula pendula*, Bet rot – *Betula rotundifolia*, *Cich – Compositae* subfam. *Cichorioideae*, Cheno – *Chenopodiaceae*, Larix – *Larix sibirica*, Mentha – *Mentha* type, Pic obo – *Picea obovata*, Pin sib – *Pinus sibirica*, Pin syl – *Pinus sylvestris*, Pla m/m – *Plantago major-media* type, Trollius – *Trollius asiaticus*, *Vacc – Vacciniaceae/Ericaceae.*

July temperatures (*Artemisia*) were the same ones that indicated dry non-forest vegetation as well. Growing content of *Larix* pollen indicated drier conditions and lower mean January temperatures, which corresponds with the affinity of *Larix* to continental climate. In contrast to continental or very moist conditions, mesic conditions were usually indicated by high values of *Betula pendula*, *Plantago major-media* type or *Filipendula* pollen. Pollen of *Betula* and *Plantago* acted synchronously as predictors. In continental landscapes of central Asia, *Plantago* is an indicator of arid or semi-arid habitats such as steppe, rather than an indicator of human impact (Liu et al. 1999). Higher values of *Pinus sibirica* and AP sum indicated more moisture and lower July temperatures. Samples from localities with the highest mean annual precipitation and nearly lowest mean July temperatures were separated on the basis of *Alnus viridis* type pollen, since *Alnus viridis* grows in mesic types of *Abies* taiga. *Rosaceae* played the same role as *Alnus viridis* type in the prediction of mean annual precipitation.

Samples with the lowest mean July temperatures were separated on the basis of *Trollius* pollen. These originated in mountain tundra or continental taiga with *Pinus sibirica* and *Picea*, where *Trollius asiaticus* occurs in wet places.

Discussion

The central question in interpretation of pollen spectra is the size of the area reflected by these spectra (Jacobson and Bradshaw 1981, Prentice 1985, Sugita 1994). Our model for

Table III Pollen taxa mentioned in the results of the study and related genera/species recorded in 307 vegetation plots sampled in the study area. When there are more than one species in genus, the numbers behind each genus indicate how many species in that genus were recorded. *Pinus sylvestris* type was always considered as *Pinus sylvestris*, since *Pinus mugo* does not occur in the region. *Pinus cembra* type and *Pinus sylvestris* type are denoted as *Pinus sibirica* and *Pinus sylvestris*, respectively, in the text and figures. Plant names follow Cherepanov (1995).

Pollen taxon	**Related genera/species recorded in sampling plots**
Abies	*Abies sibirica*
Aconitum/Delphinium type	*Aconitum* (6), *Delphinium* (3)
Allium	*Allium* (18)
Alnus viridis type	*Alnus fruticosa*
Artemisia	*Artemisia* (17)
Astragalus/Oxytropis	*Astragalus* (10), *Oxytropis* (9)
Betula nana	*Betula rotundifolia*
Betula pendula	*Betula pendula*
Bupleurum	*Bupleurum* (6)
Caryophyllaceae (excl. *Cerastium*, *Dianthus*, *Gypsophila*, *Silene*, *Stellaria*)	*Eremogone meyeri*, *Lychnis sibirica*, *Minuartia* (2), *Moehringia lateriflora*, *Sagina saginoides*
Cerealia	-
Chenopodiaceae	*Chenopodium album*, *Corispermum* spp., *Kochia prostrata*, *Krascheninnikovia ceratoides*, *Nanophyton grubovii*, *Salsola collina, Teloxys aristata*
Compositae subfam. Asteroideae (excl. *Carduus/Cirsium* type)	*Achillea millefolium* s.l., *Antennaria dioica*, *Arctogeron gramineum*, *Aster alpinus*, *Cacalia hastata*, *Doronicum altaicum*, *Erigeron acris* s.l., *Galatella* (2), *Heteropappus* (2), *Inula* (2), *Leibnitzia anandria*, *Leontopodium* (2), *Ligularia sibirica*, *Omalotheca norvegica*, *Ptarmica impatiens*, *Pyrethrum pulchrum*, *Rhinactinidia eremophila*, *Saussurea* (8), *Senecio nemorensis*, *Serratula* (2), *Solidago* (2), *Stemmacantha carthamoides*, *Tanacetum boreale*, *Tephroseris* (2)
Compositae subfam. Cichorioideae	*Cicerbita azurea*, *Crepis* (3), *Hieracium* (7), *Lactuca sibirica*, *Picris davurica*, *Scorzonera* (3), *Sonchus arvensis*, *Taraxacum* spp., *Tragopogon orientalis*, *Trommsdorfia maculata*, *Youngia* (2)
Cyperaceae	*Carex* (22), *Eriophorum brachyantherum*, *Kobresia myosuroides*
Ephedra distachya type	*Ephedra* (2)
Filipendula	*Filipendula ulmaria*
Larix	*Larix sibirica*
Mentha type	*Clinopodium vulgare, Origanum vulgare, Thymus serpyllum s.l.*
Peucedanum	*Peucedanum vaginatum*
Picea	*Picea obovata*
Pinus cembra type	*Pinus sibirica*

Pollen taxon	**Related genera/species recorded in sampling plots**
Pinus sylvestris type	*Pinus sylvestris*
Plantago major-media type	*Plantago media*
Poaceae	*Achnatherum (2), Agropyron cristatum, Agrostis (2), Alopecurus pratensis, Anthoxanthum alpinum, Brachypodium (2), Bromopsis spp., Calamagrostis (5), Cinna latifolia, Cleistogenes (2), Dactylis glomerata, Deschampsia cespitosa, Elymus (6), Elytrigia (4), Festuca (10), Helictotrichon (4), Hierochloe (2), Koeleria (2), Leymus dasystachys, Melica (2), Milium effusum, Phleum (2), Poa (3), Psathyrostachys juncea, Schizachne callosa, Setaria viridis, Stipa (7), Trisetum (2)*
Potentilla type	*Coluria geoides*, *Fragaria* (2), *Potentilla* (16), *Sibbaldia procumbens*, *Sibbaldianthe adpressa*
Rosaceae (excl. *Filipendula*, *Potentilla* type, *Spiraea*, *Sanguisorba officinalis*)	*Agrimonia pilosa*, *Alchemilla* spp., *Chamaerhodos* (2), *Cotoneaster* (2), *Dryas oxyodontha*, *Geum aleppicum*, *Prunus* (2), *Rosa* (2), *Rubus* (3), *Sorbus sibirica*
Rubiaceae	*Cruciata krylovii, Galium (6)*
Salix	*Salix (11)*
Sanguisorba officinalis	*Sanguisorba officinalis*
Spiraea	*Spiraea (5)*
Thalictrum	*Thalictrum (4)*
Trollius	*Trollius asiaticus*
Urtica	*Urtica dioica*
Vacciniaceae/Ericacaeae (incl. Pyrolaceae, Empetraceae)	*Arctous erythrocarpa, Empetrum nigrum, Ledum palustre, Pyrola rotundifolia, Rhododendron (3) Vaccinium (3)*

landscape types at 300 m distance around the sampling point explained most variability (76%) and had the best predictive accuracy (83%). The model for landscape types at 5000 m distance yielded slightly poorer, but similar results (70% explained variability, 79% accuracy). The model for vegetation types in the area of 100 m2 at the sample site gave somewhat weaker results (50% explained variation, 57% accuracy). Although the results of these three classification tree models are not directly comparable and cannot give us a precise estimate of RSAP, they still highlight several important points.

First is the effect of degree of precision in data. If the pollen and vegetation data have a reasonably similar resolution and richness, the matching brings satisfactory results. That is why the so far developed modelling techniques (Sugita 1994, Broström et al. 1998, Sugita et al. 1999, Nielsen 2004, Broström 2004, Bunting et al. 2005, Sugita 2007) work best in the regions with relatively low diversity and few strong pollen producers. Also biomization (Prentice et al.1996) brings good results because it relates pollen taxa to biomes via broadly defined plant functional types and thus can aid the reconstruction of the past landscapes on a rough scale. However, if we wish for more resolution, or we survey areas with high plant diversity, neither biomization nor modelling in its present form is suitable.

The classification tree model in Figure 1 classified the vegetation types derived from the area of 100 m2. These vegetation types were defined formally on the basis of the species composition and species cover-abundance. However, the classification tree had difficulties to distinguish all of the vegetation types by their surface pollen spectra on such a high level of precision.

In some cases the model could not discern between the samples from forest and non-forest vegetation. For example, the samples from meadow steppe in the forest-steppe zone and those from *Pinus sylvestris* dry hemiboreal forest fell into the same terminal node. Similarly, pollen samples from *Pinus sibirica*-*Picea obovata* continental taiga were not distinguished from mountain tundra with *Vaccinium* spp. and *Betula rotundifolia*. In the former case the pollen spectra of meadow steppe with scattered patches of pine or birch and the spectra of open dry hemiboreal forest were quite similar, because the herbs from meadow steppe often occur in the open hemiboreal forests and the pollen of dominant *Pinus sylvestris* and *Betula pendula* is well dispersed and abundant. Therefore these two vegetation types could not be discerned either on the basis of *Pinus sylvestris* pollen, since its pollen productivity and dispersal ability is too high and blurs the difference in the pine's abundance, or on the basis of indicative herb species, since the herb species composition in both of these vegetation types is similar. In the latter case, the pollen spectra of alpine tundra and continental taiga could be similar because the dominant tundra species (*Vaccinium* spp., *Betula rotundifolia*) often occur in the taiga undergrowth. Moreover, due to valley breezes in the local systems of air circulation, the pollen of *Pinus sibirica* and *Picea* can be easily born to the higher altitudes of alpine tundra.

In most other cases, the classification tree for vegetation types (Figure 1) successfully discerned between forest and non-forest, but the distinction of several types within the formation of steppe or forest was problematic. For example, some of the xeric scrub or dry rocky Mongolian steppe samples were misclassified for dry Mongolian steppe. This happened because both types of Mongolian steppe differ mainly in species which cannot be distinguished in pollen, eg grasses. As for xeric scrub, its dominant and insect-pollinated shrubs *Caragana* and *Spiraea* produce little pollen, and the undergrowth is similar in species composition to dry Mongolian steppe. Therefore all these three vegetation types resemble each other in their surface pollen spectra.

In contrast to the above cases of misclassification, the classification tree model distinguished the samples from dry *Festuco-Brometea* meadow steppe from all other types of steppe with high precision. The samples had lower AP sum than those of meadow steppe, but higher content of *Cichorioideae* and *Betula pendula* pollen than dry Mongolian steppe. Another successfully distinguished vegetation type was *Larix* hemiboreal forest. The undergrowth in this forest type may be similar to species-rich meadow steppe. However, *Larix* being the dominant tree, even its low pollen signal was sufficient to separate these two vegetation types. Also *Pinus sibirica-Picea obovata* continental taiga, *Pinus sylvestris* dry hemiboreal forest and *Abies-Betula* wet taiga were satisfyingly classified into separate groups, on the basis of *Abies* pollen and changing ratio of *Pinus sibirica*/*Pinus sylvestris* pollen.

Consequently, there is probably no universal answer to when it is possible to distinguish between vegetation types on community level using surface pollen spectra. It depends on many factors: species composition, physiognomy, patchiness, pollen productivity and dispersal ability, major wind direction, characteristics and distance of surrounding communities (Prentice 1985, Odgaard 1999, Brashay et al. 2000, Broström 2004, Fontana 2005). Moreover, the characteristics of the dominant species matter. If the dominant species is a relatively poor pollen producer such as *Larix*, the presence of *Larix* pollen will be much more significant for assigning the pollen spectrum to vegetation type than would be *Pinus* pollen. Dominant species overrepresented in pollen usually distorts the community

Table IV Importance of predictors in the classification (Fig. 1, 2a and 2b) and regression (Fig. 3a–3c) tree models. Only predictors with the importance value > 0.55 are shown.

Prediction of vegetation type		Prediction of landscape type		Prediction of climate characteristics	
Pollen taxon	**Importance**	**Pollen taxon**	**Importance**	**Pollen taxon**	**Importance**
Compositae subfam. Cichorioidae	1.00	**300 m**		**Mean annual precipitation**	
Betula pendula	0.99	AP SUM	1.00	AP SUM	1.00
Abies sibirica	0.94	*Artemisia*	0.88	Poaceae	0.98
Larix sibirica	0.93	Chenopodiaceae	0.86	*Artemisia*	0.93
Plantago major-media type	0.91	Poaceae	0.80	*Larix sibirica*	0.90
Pinus sylvestris	0.89	*Betula pendula*	0.77	*Abies sibirica*	0.85
Cyperaceae	0.85	*Picea obovata*	0.75	Chenopodiaceae	0.81
Pinus sibirica	0.85	*Plantago major-media* type	0.74	*Pinus sibirica*	0.76
Thalictrum	0.81	*Alnus viridis* type	0.73	*Alnus viridis* type	0.63
Artemisia	0.77	*Pinus sibirica*	0.64	*Thalictrum*	0.63
Chenopodiaceae	0.76	Compositae subfam. Cichorioidae	0.60	*Betula pendula*	0.62
Compositae subfam. Asteroidae	0.76	*Abies sibirica*	0.60	*Bupleurum*	0.61
Poaceae	0.76			Cyperaceae	0.61
Alnus viridis type	0.75	**5000 m**		Rosaceae	0.59
Salix	0.72	*Larix sibirica*	1.00		
Potentilla type	0.71	*Picea obovata*	0.80	**Mean July temperature**	
Bupleurum	0.70	AP SUM	0.78	*Alnus viridis* type	1.00
Vacciniaceae/Ericacaeae	0.68	*Alnus viridis* type	0.78	Poaceae	0.87

Prediction of vegetation type		**Prediction of landscape type**		**Prediction of climate characteristics**	
Pollen taxon	**Importance**	**Pollen taxon**	**Importance**	**Pollen taxon**	**Importance**
Rubiaceae	0.65	*Plantago major-media* type	0.75	Vacciniaceae/Ericacaeae	0.84
Picea obovata	0.65	*Artemisia*	0.72	*Pinus sibirica*	0.83
Spiraea	0.65	*Betula pendula*	0.67	*Urtica dioica*	0.71
Cerealia	0.64	*Pinus sibirica*	0.63	AP SUM	0.67
Sanguisorba officinalis	0.60	Poaceae	0.58	*Plantago major-media* type	0.65
Allium	0.59	Compositae subfam. Cichorioideae	0.56	*Trollius*	0.59
Aconitum/Delphinium type	0.58	*Abies sibirica*	0.56	Compositae subfam. Cichorioideae	0.57
AP SUM	0.57			*Artemisia*	0.55
Caryophyllaceae	0.56			*Betula pendula*	0.55
Astragalus/Oxytropis	0.55				
Peucedanum	0.55			**Mean January temperature**	
				Larix sibirica	1.00
				Betula pendula	0.98
				Plantago major-media type	0.96
				Pinus sylvestris	0.63

representation in its pollen signal, especially if there are no codominants (Brayshay et al. 2000). However, changing ratio in the pollen representation of two overrepresented dominants can act as a diagnostic criterion, too (eg *Pinus sibirica* and *P. sylvestris* in Fig. 1; see also Liu et al. 1999). Presence of diagnostic herb species in the pollen record is also strongly indicative, even if these are weak pollen producers with poor dispersal ability, but ecologically bound to a specific vegetation type.

Secondly, the presented tree models show that even pollen taxa with low representation in studied pollen samples (eg *Larix, Cichorioideae, Ephedra distachya* type, *Alnus viridis* type, *Vacciniaceae/Ericaceae*) are of crucial importance in distinguishing between vegetation or landscape types; they are not less important than the changing ratio of representation of strong pollen producers (eg *Pinus sibirica/Pinus sylvestris*). Note that the mentioned taxa with low pollen productivity do not occur just coincidentally, but are typical of particular vegetation type and really occurred in the sampled vegetation (Tables II and III). Therefore if we omit them from the analysis due to some arbitrarily chosen threshold value, we risk loosing a significant piece of information, especially when using percentage pollen data. In order to exploit maximum information from the pollen samples, we should include as many pollen taxa as possible and use both quantitative and qualitative criteria for assigning the pollen samples to the vegetation types.

As for the pollen/climate relationship, the relative composition of surface samples explained most variability in mean annual precipitation (86%), then in the mean January temperatures (69%) and the least, but still high percentage of explained variability was achieved in mean July temperatures (57%). This indicates that the relationship between pollen spectra and climate characteristics is rather tight, and features of past climates can be reasonably predicted from the fossil pollen spectra.

Regression trees (Figs. 3a–c) highlighted the importance of two tree species, *Larix sibirica* and *Pinus sibirica*, as climate indicators. The former is a weak pollen producer, but its occurrence clearly indicated low winter temperatures and low precipitation, ie a high degree of climatic continentality. The latter indicated low summer temperatures and higher precipitation. These results based on pollen spectra are in accordance with the models of actual distribution of these species in the study area (Chytrý et al. 2007b). They also correspond well with the conclusions of Tinner and Kaltenrieder (2005), who surveyed the responses of high-mountain vegetation to early Holocene environmental changes in the Swiss Alps. Unfortunately, these two species are often overlooked in the fossil pollen spectra. *Larix* might go unnoticed due to its low pollen abundance if small total number of pollen grains is counted, while *Pinus sibirica* (= *P. cembra* s. lat.) is often not distinguished from *P. sylvestris*. In such way important information on the past climate can be lost.

Conclusions

We find the decision tree models suitable for the analysis of pollen/vegetation relationship. Their advantages are: 1. exploiting maximum information from the presence of poorly represented pollen producers, 2. formal, relatively precise and easy-to-interpret assignment of pollen spectra to vegetation or landscape types or particular values of climatic variables,

3. identification of pollen taxa with the highest importance for distinguishing a particular vegetation type, landscape type or climate characteristics.

Some vegetation types were discernable even on the community level (100 m^2 around the sampling point). After the satisfactory results the tree models brought with 81 surface samples, it would be desirable to test their performance on a larger data set in the future.

A considerably tight relationship between the composition of surface pollen spectra and climate characteristics shows that the past climatic conditions can be reasonably predicted by the fossil pollen spectra.

The ambition of this study was not to produce universally applicable decision criteria for assigning pollen samples to vegetation types, landscape types or particular values of climatic variables. For that, a more extensive data set would be needed. Nevertheless, the results illustrate what kind of pollen spectra can be produced by studied vegetation types and on what level of representation of various pollen taxa we can distinguish between the studied vegetation/landscape/climate types.

Since our study was carried out in a region where the human impact is low, the results can aid us when we reconstruct past landscapes where the human impact was also low. Due to the remarkable similarity of some of the modern pollen spectra from the study area with the full and late glacial pollen spectra from Central Europe (Willis et al. 2000, Jankovská et al. 2002, Pokorný 2002, Jankovská 2006), our results can be especially valuable for interpretation of Pleistocene environments of Central Europe.

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Interpretation of the last-glacial vegetation of eastern-central Europe using modern analogues from southern Siberia

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Abstract:

Aim: Interpretation of fossil pollen assemblages may greatly benefit from comparisons with modern vegetation analogues. To interpret the full- and late-glacial vegetation in central Europe we compared fossil pollen assemblages from eastern-central Europe with modern pollen assemblages of various vegetation types of southern Siberia, which presumably include the closest modern analogues of the glacial vegetation of central Europe.
Location: Czech and Slovak Republics (fossil pollen assemblages); Western Sayan Mountains, southern Siberia (modern pollen assemblages).
Methods: 88 modern pollen spectra were sampled in 14 vegetation types of Siberian forest, tundra and steppe, and compared with the last glacial pollen spectra from seven central European localities. We used the principal components analysis for the comparison.
Results: Both full- and late-glacial pollen spectra from the valleys of the Western Carpathians (altitudes 350-610 m) are similar to the modern pollen spectra from southern Siberian taiga, hemiboreal forest and dwarf-birch tundra. The full-glacial and early late-glacial pollen spectra from lowland river valley in Bohemia (altitudes 185-190 m) also indicate presence of patches of hemiboreal forest or taiga as well. Other late-glacial pollen spectra from Bohemia

suggest an open landscape with steppe or tundra or a mosaic of both, possibly with small patches of hemiboreal forest.

Main conclusions: Our results are consistent with the hypothesis that during the full glacial and late glacial, the mountain valleys of the NW Carpathians hosted taiga or hemiboreal forest dominated by *Larix, Pinus cembra, P. sylvestris* and *Picea*, which were partly supplemented by steppic or tundra formations. Forests tended to be increasingly open or patchy towards the west (Moravian lowlands) gradually passing into the generally treeless landscape of Bohemia, with possible woodland patches at locally favourable sites.

Keywords

Fossil and modern pollen spectra, forest, full glacial, late glacial, steppe, surface pollen, tundra, Weichselian

Introduction

Earlier concepts described the periglacial landscapes of central Europe during the last full glacial as an inhospitable steppe, tundra or forest-tundra (Frenzel & Troll, 1952; Lang, 1994). However, recent records of various proxy data are changing this view. These include pollen data from the lowlands adjacent to the northern, western and southern fringes of the Western Carpathians (Rybníček & Rybníčková, 1996; Willis *et al.*, 2000; Jankovská *et al.*, 2002) and charcoal from Upper Palaeolithic sites in central and southern Moravia, north-eastern Austria and the Pannonian Basin, which contained collected and in some cases even *in-situ* wood (Slavíková-Veselá, 1950; Kneblová, 1954; Klíma, 1963; Damblon, 1997; Willis *et al.*, 2000). Charcoal evidence from the archaeological contexts and loess profiles in central Europe is listed and comprehensively summarized by Rudner & Sümegi (2001), Musil (2003), and Willis & van Andel (2004). Although most of the finds represent cold- or drought-tolerant coniferous taxa (*Pinus sylvestris, P. cembra, Larix, Picea, Juniperus*), some mesophilous trees are regularly present as well, including *Abies, Carpinus, Corylus, Fagus, Fraxinus, Quercus, Taxus baccata* and *Ulmus*. For a long time, these finds used to be interpreted in the light of the traditional concept of inhospitable and cold full-glacial tundra. This concept was seriously challenged by the discovery of a full-glacial buried peat dated to 28 ka BP (25,675±2,750 ^{14}C yr BP) at the Bulhary site, Czech Republic (Rybníčková & Rybníček, 1991), which contained a considerable amount of tree pollen. Recently, two other full-glacial pollen profiles from the Western Carpathians were analysed: Šafárka (northern Slovakia), dated between 52–17 ka BP (Jankovská *et al.*, 2002), and Jablůnka (eastern Czech Republic), dated between 45–39 ka BP (Jankovská, 2003). These also suggest local survival of forest species during the full-glacial period. Tree pollen is likewise abundant in the fossil records from the Pannonian Basin of Hungary, dated to the onset of the late glacial (around 17 ka BP at Bátorliget site; Willis *et al.*, 1995). Such an early occurrence of tree pollen indicates the proximity of some full-glacial refugia. Moreover, several pollen profiles located at the transition between the Polish lowlands and the Carpathians indicate coniferous forests with *Pinus cembra* and *Larix* at least during the warmer interstadial of the Weichselian glaciation (Ralska-Jasiewiczowa, 1980; Mamakowa, 2003).

Recent palaeoclimatic simulations of the Stage 3 Project suggest that the full-glacial conditions in eastern-central Europe were not as severe as previously anticipated (Barron & Pollard, 2002; Barron *et al.*, 2003; Pollard & Barron, 2003). Palynological data used in the simulations covered only the maritime, northern European and Mediterranean regions, while eastern and eastern-central Europe was a "white spot" on the map. Since the climatic simulations did not fit along with the underlying concept of treeless tundra, the model was finally rejected (Alfano *et al.*, 2003; Huntley *et al.*, 2003). However, on the basis of the above-mentioned new pollen data, the Stage 3 Project climatic simulations become an object of interest again. Willis & van Andel (2004) suggested that we must acknowledge for full-glacial refugia of many tree or shrub species (*Betula, Carpinus, Corylus, Fagus, Juniperus, Larix, Picea, Pinus, Populus, Quercus, Rhamnus, Salix, Sorbus* and *Ulmus*), situated in the lowlands adjacent to the Western Carpathians. Nevertheless, on the basis of the fossil evidence, we still are not able to decide clearly whether the trees grew in isolated pockets in an otherwise open tundra/steppe landscape or they rather formed a forest-steppe. Furthermore, the related biome model simulations for the last full glacial indicate that the central and eastern European landscape could have supported a true taiga forest (Huntley & Allen, 2003). This opinion is also shared by Willis & van Andel (2004), who proposed that "during the last full-glacial central and eastern Europe was covered by taiga/montane woodland, which in some regions also contained isolated pockets of temperate trees".

The full-glacial aridity was probably a significant limiting factor for tree growth in the eastern-central European loess lowlands (Wright *et al.*, 1993), where most of the previous investigations were accomplished. However, forests were probably common in the Western Carpathians throughout the last glacial, as suggested by palynological (Jankovská *et al.*, 2002; Jankovská, 2003), plant macrofossil (Jankovská, 1984) and malacological data (Ložek, 2006). Orographic precipitation and mesoclimatic humidity may have significantly decreased the climatic stress, especially in the middle altitudes and protected valleys. Contrarily to the Carpathians, the full and late-glacial pollen evidence from the more western and less continental areas (such as the Czech Republic except its eastern part) indicates transitional phases between an open forest-tundra (Pokorný, 2002) and treeless ecosystems (Petr, 2005; Jankovská, 2006).

Our ecological interpretations of the fossil pollen assemblages can be significantly enhanced if we can explore the modern analogues of the central-European full-glacial environments. According to the previous vegetation surveys (Kuminova, 1960; Ermakov *et al.*, 2000; Chytrý *et al.*, 2008), we suggest that the closest modern analogy of the full- and late-glacial vegetation and landscapes of eastern-central Europe can be found in the southern Siberian mountain ranges, namely the Altai and the Western Sayan Mts. Although analogues are never perfect (Williams & Jackson, 2007), this particular one is well supported by the similarity of the present continental climate of the southern Siberian mountains to the last-glacial palaeoclimates of eastern-central Europe (Frenzel *et al.*, 1992). Flora of the southern Siberian mountains includes many species with Euro-Siberian distribution (Meusel *et al.*, 1965–1992) and evident historical biogeographical links to Central Europe. Three major biomes, analogous to the Pleistocene landscapes of Central Europe (Huntley *et al.*, 2003), meet in the southern Siberian mountains: taiga, steppe and tundra. Their distribution reflects local topography, altitude and the sharp climatic gradient of continentality, that increases from the northern windward slopes to the southern intermountain basins (Polikarpov *et al.*, 1986). There is another advantage to these potential southern-Siberian analogues of the full- and late-glacial conditions. It lies in a low human impact on the vegetation, especially in the Western Sayan (Chytrý *et al.*, 2008).

The aim of this paper is to compare the modern pollen assemblages from various vegetation types of the Western Sayan Mountains to the last full- and late-glacial pollen

Table 1. Overview of major vegetation types (codes with F – forest types, codes with N – non-forest types). See Chytrý, *et al.* (2008) for the detailed description of forest types.

Code	No. of pollen samples	Vegetation type
F1	7	***Betula pendula-Pinus sylvestris* mesic hemiboreal forest** occurs in relatively warm, mesic to dry sites. In places, *Larix sibirica* and *Populus tremula* are admixed, the latter in the formerly disturbed sites. This forest is very rich in herbaceous species.
F2	7	***Larix sibirica* dry hemiboreal forest** occurs in very dry and winter-cool areas. In places, *Pinus sibirica* is co-dominating with *Larix*.
F3	8	***Pinus sylvestris* dry hemiboreal forest** is found in the same areas as F1, with relatively warm climate, but it is confined to steeper slopes with well-drained soils.
F4	11	***Abies sibirica-Betula pendula* wet taiga** occurs in relatively warm and precipitation-rich areas, where it occupies lower slopes and valley bottoms. Admixed woody species include *Alnus fruticosa, Picea obovata, Pinus sibirica* and *Sorbus sibirica*. Its richness in herbaceous species is higher than in the other taiga types, and is comparable with the hemiboreal forests.
F5	5	***Abies sibirica-Pinus sibirica* mesic taiga** is typical of north-facing slopes in the summer-cool and precipitation-rich areas. *Picea obovata* often occurs besides the two dominant tree species. This forest type is poor in herbaceous species but rich in bryophytes.
F6	9	***Pinus sibirica-Picea obovata* continental taiga** occurs in areas which are relatively cool in both winter and summer but receive higher precipitation than F2. *Larix sibirica* can co-occur in the tree layer. Herb layer is species-poor but there are abundant bryophytes and lichens.
N1	1	**Subalpine tall-forb vegetation** occurs in stream valleys and on the bottoms of glacial cirques above the timberline, especially in the precipitation-rich areas with a distinctive snow accumulation. It forms dense stands dominated by tall broadleaf forbs.
N2	2	**Short-grass mountain tundra** occurs at drier, often wind-swept sites with shallow soils above the timberline in the precipitation-rich areas. It is a patchy mosaic of short grassland and dwarf heathland of *Vaccinium myrtillus*, with frequent bryophytes and lichens.
N3	5	***Betula rotundifolia-Vaccinium myrtillus-Vaccinium vitis-idaea* dwarf-shrub moutain tundra** occurs above the timberline in topographically wetter places than N2. It contains frequent bryophytes and lichens.
N4	6	***Spiraea media-Caragana pygmaea* xeric scrub** occurs in slightly humid places in the steppe and forest-steppe zone, which are ecologically transitional between steppe and hemiboreal forests. Other common species of this type include shrubs *Cotoneaster melanocarpus* and *Rhododendron dauricum*, grasses such as *Poa* sect. *Stenopoa*, and sedge *Carex pediformis* s. lat.
N5	6	**Species-rich meadow steppe** occurs in relatively warm, mesic to dry sites, often in contact with hemiboreal forests of F1. It forms dense stands of grasses, sedges and dicot herbs. Shrubs typical of N4 also occur locally with low cover. Most species of this steppe have Euro-Siberian distributions.

Code	No. of pollen samples	Vegetation type
N6	6	**Dry Euro-Siberian steppe** is a short grassland occurring in dry and summer-warm areas, dominated by tussocky grasses such as *Stipa, Festuca* and *Koeleria*, tussocky sedge *Carex pediformis* s. lat., sages (*Artemisia* spp.) and other herbs. Most species have Euro-Siberian distributions, but vegetation is species-poorer than the meadow steppe of N5.
N7	5	**Dry Mongolian steppe** is a species-poor, open and short grassland occurring in dry, summer-warm and winter-cool areas, both on slopes and flatlands. It is dominated by short tussocky grasses and low-growing herbs, including *Artemisia* spp., *Chenopodiaceae* and *Ephedra dahurica*. It is species-poorer than the other steppe types and consists mainly of species with central Asian distribution.
N8	8	**Dry rocky Mongolian steppe** is found on rock outcrops or steep slopes in the same areas as N7. It also has a similar structure and species composition as N7, but is richer in the rock-outcrop species (e.g. *Selaginella sanguinolenta*) which increase the overall species richness.

spectra from eastern-central Europe. Further, we discuss the interpretation of the late-Pleistocene vegetation of eastern-central Europe in light of the results and also with respect to the degree of correspondence between the modern pollen spectra and the present southern-Siberian vegetation (Lučeničová *et al.*, subm.).

Material and methods

Modern pollen assemblages

Study area

The study area is situated in southern Siberia (Russia) between the towns of Abakan and Minusinsk in the north and the Russian-Mongolian border in the south (50°43’–53°33’ N, 91°06’–93°28’ E). It includes the Western Sayan Mountains and adjacent areas of the Minusinskaya Basin, Central Tuvinian Basin and the Tannu-Ola Range. The mountains range in altitude from 350 to 2860 m and have predominantly rugged topography. The basins lie in the altitudes of 300–600 m (Minusinskaya) and 550–1100 m (Central Tuvinian).

Macroclimate of the study area is continental, though the northern front ranges of the Western Sayan are relatively warmer and more humid than elsewhere in Siberia (Polikarpov *et al.*, 1986). On the contrary, the southern part of the Western Sayan, Central Tuvinian Basin and the Tannu-Ola Range are in the area of rain shadow. Their climate is arid and continental. Central parts of both basins are covered by steppe, with trees only surviving at narrow galleries along the rivers. Minusinskaya Basin is dominated by meadow- and dry steppe with many Euro-Siberian species (Table 1 & Fig. 8, types N5 and N6). The mesic sites are occupied by patches of *Betula pendula* or *Populus tremula* woodlands or *Caragana*-*Spiraea* steppic scrub (N4). Drier and cooler Central Tuvinian Basin is covered with a dry steppe containing mainly of central Asian (Mongolian) species (N7). Small woodland patches are mainly dominated by *Larix sibirica* (F2). *Caragana*-*Spiraea* scrub (N4) is scattered at relatively humid sites.

Forest-steppe forms a transitional zone between the continuous forests covering the humid mountain ranges and the steppes in the basins. Here, steppe regularly occurs on south-facing slopes and forest on north-facing slopes. In the northern part of the study area, forests in the forest-steppe zone are usually dominated by *Betula pendula* and/or *Pinus sylvestris* (F1, F3), while in the southern part by *Larix sibirica* (F2; Chytrý *et al.*, 2008). Forest zone occupies humid areas at middle and higher altitudes, especially on the northern side of the Western Sayan. Forests are divided into hemiboreal forests at drier and summer-warm sites (often in the forest-steppe zone, rich in herbaceous species and poor in bryophytes), and taiga at wetter, summer-cool sites (poor in herbaceous species and rich in bryophytes (Table 1; see Chytrý *et al.* 2008 for details). Alpine tundra (Table 1; Fig. 8, types N1-N3) is developed above the timberline, i.e. above 1600 and 2000 m on humid northern and drier southern ranges, respectively (Zhitlukhina, 1988).

Human population is concentrated in scattered villages in the basins and on the mountain foothills, where the steppe or forest-steppe is used for livestock grazing. In contrast, the mountain areas of the Western Sayan are almost completely dovoid of any permanent settlements. Thus the area harbours primeval vegetation, although forest fires occur frequently and various stages of post-fire succession are common.

Data sampling and laboratory preparations

Surface pollen samples were collected in 307 plots of 10 × 10 m in the Western Sayan Mountains. The plots were further used for a parallel vegetation survey (Chytrý *et al.*, 2007; 2008). In each vegetation plot, pollen sample was collected as five subsamples, which were merged into one. The area of a subsample was ca 10 × 10 cm. We collected either up to 3 cm of humus and topsoil (in dry steppe and xeric scrub) or polsters of ground-dwelling bryophytes (in forests, tundra, alpine scrub and meadow steppe). In order to cover all main vegetation types, we refrained from sampling only in places with moss polsters available (Gaillard *et al.*, 1994; Brayshay *et al.*, 2000), even though sampling in two different trapping media (soil surface and moss) may slightly reduce comparability among the samples. Vegetation survey plots were classified, based on their species composition, by the TWINSPAN program (Hill, 1979). Separate analyses of forest and treeless plots resulted in six vegetation types of the former (described in Chytrý *et al.*, 2008) and eight types of the latter (see Table 1). Using this vegetation classification, we selected 88 surface pollen samples for analysis in order to cover the fourteen major vegetation types (Table 1). The relationship between these vegetation types and their surface pollen spectra is described in detail by Lučeničová *et al.* (subm.).

All samples were dried at room temperature and prepared by acetolysis (Erdtman, 1960). Besides a reference collection, following keys and atlases were used for pollen identification: Moore et al. (1991), Punt (1976-1996), Reille (1992; 1995; 1998), and Beug (2004). The total pollen sum of AP and NAP was used to calculate percentages. Local pollen (incl. aquatic, mire taxa, *Pteridophyta* and *Cyperaceae*) was excluded from the total pollen sum. The percentages of taxa excluded from the total pollen sum were calculated for each pollen type count relative to the total pollen sum.

Fossil pollen assemblages

Seven fossil pollen assemblages were selected for the comparison with the modern Siberian pollen spectra. All of them are from the Czech Republic (CZ) or Slovakia and dated to the late glacial (sites 1-4, Fig. 3) or the full glacial (sites 5-7; Figs. 4 and 5):

1. Sivárňa (610 m a.s.l.), NE Slovakia (Jankovská, 1998, 2003) lies at the foothill of the Spišská Magura Mountains. According to radiocarbon dating, lower half of the profile covers the late glacial down to 13.7 ka BP.

2. Hrabanovská černava (185 m a.s.l.), central Bohemia, CZ (Petr, 2005) is a profile from an old late-glacial lake in the Labe River floodplain. Oldest parts of the sediment are dated to 13.6 ka BP.

3. Švarcenberk (412 m a.s.l.) S Bohemia, CZ (Pokorný, 2002) is a former lake situated in flat landscape. It is close to the Lužnice River, which probably positively affected humidity in the area, and thereby possibly supported tree survival. There are nearly 5 m of late-glacial sediments with the oldest date 11.7 ka BP, however, the lower parts are probably much older.

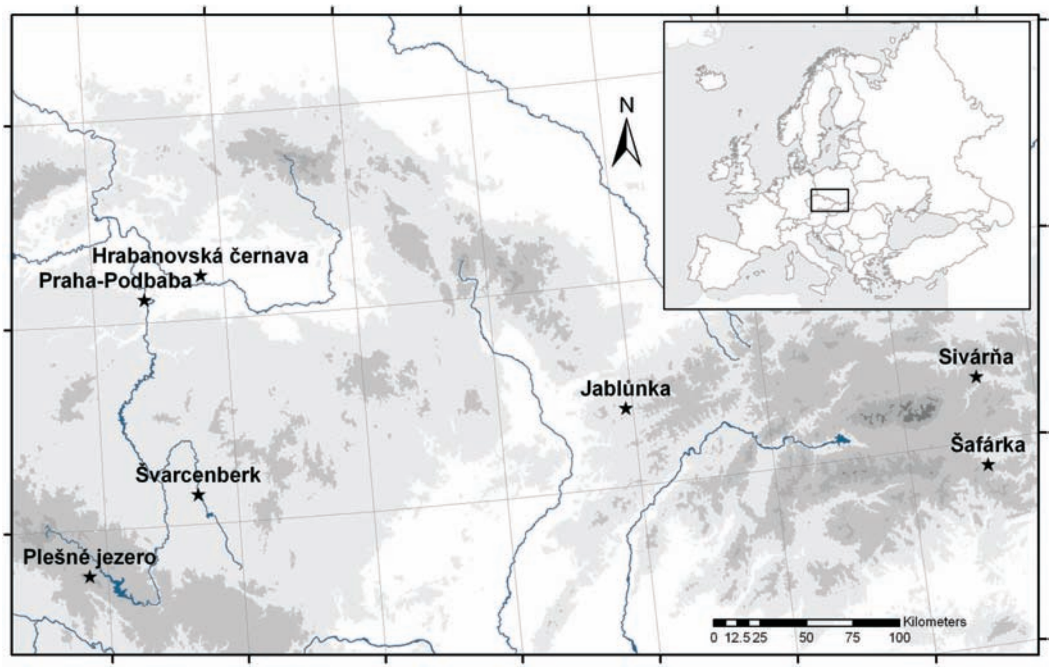


Fig. 1: Fossil pollen sites used in this study, projected on a hypsometric map of eastern-central Europe (Czech Republic, Slovakia, Hungary, Austria, Poland and Germany)

4. Plešné jezero Lake (1090 m a.s.l.), SW Bohemia, CZ (Jankovská, 2006) is a mountain lake of glacial origin. Radiocarbon dating does not cover the late-glacial period, so the late-glacial zone was determined by extrapolation of a depth age model and by biostratigraphic patterns.

5. Šafárka (600 m a.s.l.), NE Slovakia (Jankovská *et al.*, 2002) is a profile from a fossil doline. The radiocarbon age ranges between 17 ka BP and goes beyond limits of measurement (older than 52 ka BP), however, the samples did not retain their stratigraphic position.

6. Jablůnka (350 m a.s.l.), E Moravia, CZ (Jankovská, 2003) is situated in valley of the Vsetínská Bečva River (the westernmost Carpathians). Two AMS radiocarbon dates were obtained and these determined the age of the sediment to 39.7 ka BP and 45 ka BP.

7. Praha-Podbaba (190 m a.s.l.), central Bohemia, CZ (Jankovská & Pokorný, subm.) is situated in a broad valley of the Vltava River. A single peat sample, with an immediate contact with *Picea/Larix* wood (^{14}C date 31 ka BP), was analysed for pollen.

Some of these profiles also contained Holocene samples, which were excluded from the analyses. Overview pollen diagrams (Figs. 3 and 4) were constructed using C2 software (Juggins, 2003). In case of late-glacial profiles, the age-depth models were prepared in Bpeat (Blaauw & Christen, 2005), using linear interpolation between dated layers and one sigma range.

Data analysis

We used multivariate analysis to determine the differences between the fossil pollen spectra and their putative modern analogues. We unified the nomenclature of pollen types of the fossil pollen data and adjusted the pollen nomenclature of several plant taxa with Siberian distribution, whose closely related taxa occurred in central Europe during the last glacial. In particular, this concerned woody species that had undergone a vicariant speciation: *Abies sibirica-A. alba, Alnus fruticosa-A. viridis, Betula rotundifolia-B. nana, Larix sibirica-L. decidua, Picea obovata-P. abies,* and *Pinus sibirica-P. cembra*). We also merged different pollen types within Ericaceae (including *Calluna, Empetrum, Rhododendron* and *Vaccinium* types) and within Compositae subfam. Asteroideae (including *Achillea, Anthemis, Aster* and *Senecio* types). Due to possible divergence in determination by different authors, we did not distinguish between *Pinus cembra/sibirica* and *P. sylvestris*, and *Alnus glutinosa* and *A. viridis* pollen types in the multivariate analysis.

All samples (fossil and modern pollen spectra) have been subject to ordination in the CANOCO program (ter Braak & Šmilauer, 2002). Principle components analysis (PCA) on the covariance matrix with square-root transformed pollen percentages was used to interpret the relationship among samples. This method was selected because it produced rather robust results in the pilot analyses, due to downweighting of the influence of rare pollen types, which tended to occur by chance in few samples and small quantities.

Results

Modern pollen spectra

Percentage histograms (Fig. 2) show differences in composition of the modern surface pollen spectra of the main natural vegetation types in southern Siberia. Differences in the AP/NAP ratio separate forest, subalpine tall-forb vegetation, mountain tundra and species-rich meadow steppe (F1–F6, N1–N3 and N5 in Table 1) on the one hand from xeric scrub and dry steppe (N4 and N6–N8 in Table 1) on the other. This division is mainly caused by varying proportion of *Artemisia,* Graminae and Chenopodiaceae. Changes in the amount of *Pinus sylvestris* and *P. sibirica* pollen separate different types of taiga and hemiboreal forests. *Larix* pollen is the main predictor of hemiboreal *Larix* forests or *Larix* patches in dry or rocky Mongolian steppe. *Betula pendula* pollen proportion is high in mesic hemiboreal forest and wet taiga. Pollen of *Picea* and *Abies* appears rather sporadically, mainly in taiga. *Alnus viridis* pollen type is more abundant in taiga vegetation (F4–F6), where *Alnus fruticosa* often occurs in the shrub layer. However, alder never reaches the 1% threshold in hemiboreal forests (F1–F3).

Late-glacial pollen profiles

Each late-glacial site has a different pollen record (Fig. 3). The AP/NAP proportions suggest varying degree of landscape openness. There are low AP values (under 30–35%) in the profiles from the Bohemian localities Hrabanovská černava and Plešné jezero Lake. These represent extreme situations. Hrabanovská černava is situated in the lowlands, with supposedly dry climate that suppressed tree growth during the younger phases of the late glacial. Plešné jezero Lake is a montane locality (above 1000 m a.s.l.) with a cool climate,

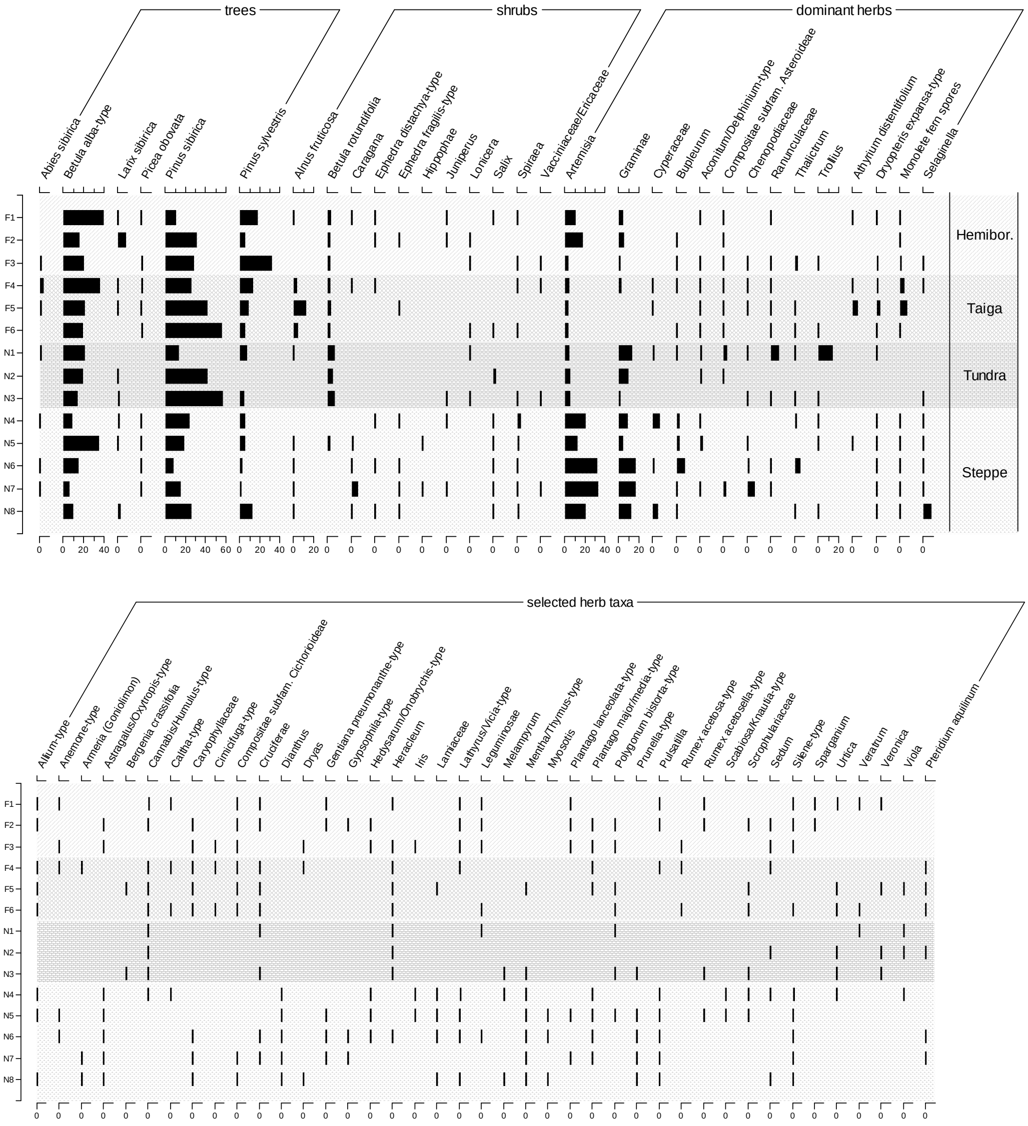


Fig. 2: Modern pollen spectra from the main vegetation types of southern Siberia

which probably did not support trees as well. Moreover, there are many AP/NAP fluctuations in the pollen record of Plešné jezero Lake, which could testify for timberline fluctuations due to strong climatic changes in the late glacial. Open spaces could host *Juniperus* and *Betula nana* in both localities.

At Švarcenberk, even though the AP/NAP ratio was fluctuating, but the AP content stayed above 60% for most of the late glacial. This included considerably high percentage of *Pinus sylvestris* pollen and some *Betula*, which could indicate an occurrence of patchy or open woodlands, similar to the mesic hemiboreal forests of *Betula pendula* and *Pinus sylvestris* in southern Siberia (F1 in Table 1). Pollen curves of *Juniperus* and *Betula nana* attained lower values.

Sivárňa locality, situated in an intermountain basin within the Western Carpathians, had the highest proportions of AP pollen among the late-glacial localities (up to 90%). Compared

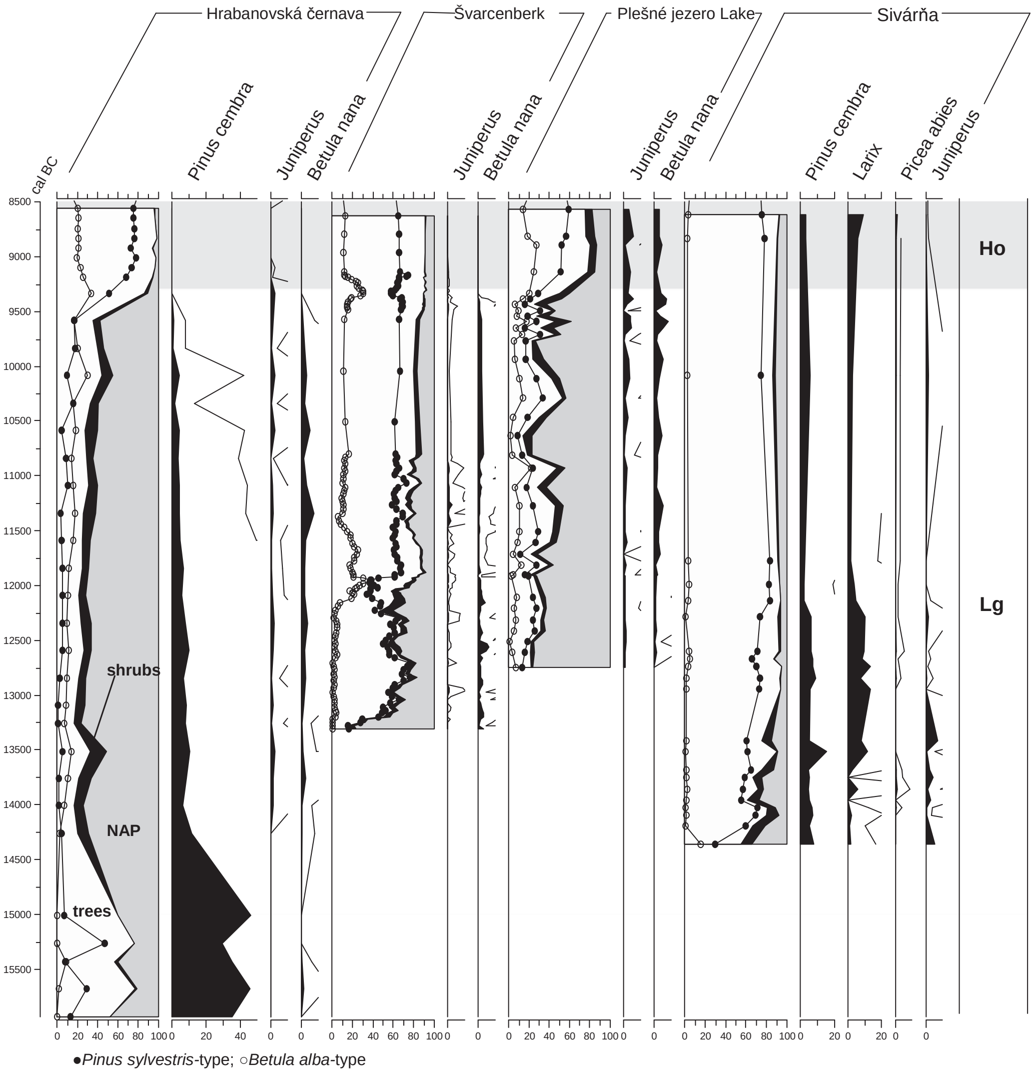


Fig. 3: Percentage pollen diagrams of selected pollen taxa in the late-glacial profiles from central Europe drawn on a joint time axis. Lg – last glacial, Ho - Holocene

to the other localities, this can mean occurrence of closed forest with *Pinus sylvestris, P. cembra* and/or *Larix decidua* and admixture of *Picea abies*. Occurrence of some *Juniperus* pollen can be linked to patchy forest openings at drier sites.

Full-glacial pollen profiles

Pollen profile of the easternmost locality Šafárka has distinct pollen assemblage zones (PAZ; Fig. 4). The AP/NAP proportions were fluctuating but *Pinus cembra* pollen values were rather constant through the time. The two oldest PAZ, with age beyond the limit of radiocarbon dating (over 52 ka BP), attained the lowest AP value. Apart from these two PAZ, the AP content was constantly increasing. There was a considerably high amount of *Betula alba* and *Larix* pollen and even some broadleaf thermophilous taxa, e.g. *Ulmus, Corylus* and *Quercus* (Jankovská *et al.*, 2002). A noticeable change occurred at the beginning of the third PAZ. Percentage values of *Picea* and *Pinus sylvestris* pollen increased, and the AP proportions reached up to 90%. This change happened some time around 30 ka BP and could be connected with climate amelioration. More favourable climatic conditions, especially more moisture, could have induced spreading of spruce into previously established larch-birch open woodlands. According to changes in the AP/NAP ratio, this possibly led to closed spruce-dominated stands with fewer herbs. Further fluctuations in the AP and *Picea* curves, e.g. the decline around the last glacial maximum, might be a result of climate change.

The second full-glacial pollen site, Jablůnka, is a short profile (Fig. 4), but the radiocarbon dates of its upper part (39 ka BP and 45 ka BP) suggest that the record may cover a long period, most likely with several hiatuses. AP values in the lower part of the diagram were fluctuating around 60%. Unfortunately, this section was not directly dated, but according to the stratigraphy, it is most likely older than 45 ka BP. If we accept this assumption, the lower Jablůnka section can be compared with the oldest section of Šafárka, which is probably of similar age. The pollen curves of *Pinus sylvestris*, *P. cembra*, *Larix* and *Betula* are almost constant in the lower section of the Jablůnka profile. By contrast, *Picea* has only low values. Just in a single sample (Jablůnka: 3 cm) it attained 20%, replacing other pollen types such as *Betula* and *Alnus viridis* (Jankovská & Pokorný, subm.). The low values of *Picea* together with occurrence of some broadleaf trees and shrubs (*Tilia, Ulmus* and *Corylus*) can point to a warmer period. In the upper part of the diagram, AP values rise up to 80-90%. These imply a more favourable climate (especially increased humidity) and spreading of woody vegetation.

The last full-glacial record is represented by a single pollen spectrum from Praha-Podbaba site (Jankovská & Pokorný, subm.; Fig. 5). Dated to 31 ka BP, it depicts vegetation of the Bohemian Massif during the last glacial. The relative pollen abundances, especially the AP/NAP ratio, are comparable to Jablůnka site. Forests consisted of *Larix*, which is documented by wood macrofossils, and *Pinus sylvestris*, with an admixture of *Picea* and *Betula pendula*. However, Praha-Podbaba site differs from Jablůnka in lower representation of *Pinus cembra* and also some more demanding taxa (*Corylus, Alnus glutinosa* and *Abies*).

Comparison of fossil and modern pollen spectra

Principal components analysis (PCA) of all (fossil and modern) pollen spectra (Fig. 6) reveals the difference between the forest (upper left) and treeless (lower right) samples. The taiga samples (F4–F6) are situated in the upper left part of the ordination diagram, whereas the samples from drier hemiboreal forests (F1–F3) lie in the central part. The tundra samples (N2 and N3) overlap with the forest samples (both taiga and hemiboreal forests), as well as the samples from meadow steppes (N5) with those of hemiboreal forests. The samples from more arid and more continental steppes (N4, N6-N8) lie in the lower right part of the diagram.

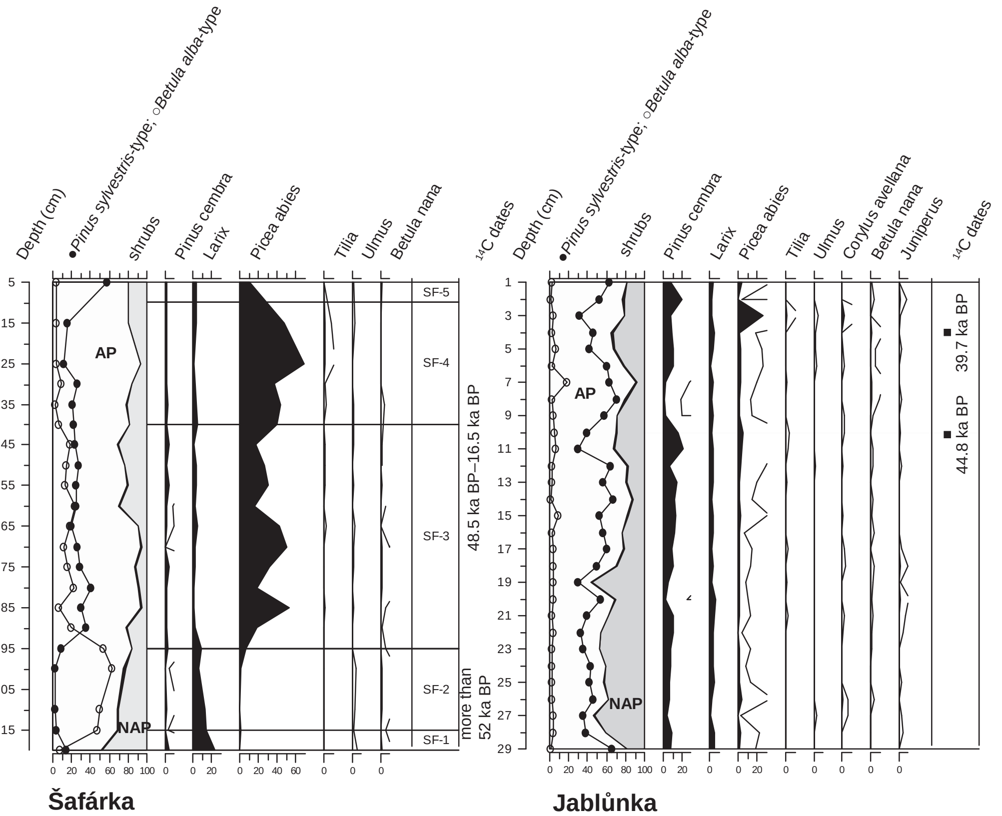


Fig. 4: Percentage pollen diagrams of selected pollen taxa in the full-glacial profiles from central Europe drawn on a joint time axis

Late-glacial profiles are found in the bottom part of the diagram. The samples from Plešné jezero Lake form a distinct group, close to modern Siberian samples of treeless vegetation, especially to dry steppic or shrubby communities (N6, N7 and N8). The upper samples of the Hrabanovská černava profile are also very similar to dry xeric scrub (N4) or dry steppes (N6-N8). Contrastingly, its older samples are similar to the modern pollen assemblages of cool taiga (F6) or mesic hemiboreal forest (F1). Samples from Sivárňa are situated mainly on the left-hand side of the diagram, where the closest modern samples are those of drier forest types, such as continental taiga or dry hemiboreal forest (F6 and F3). Samples of the last late-glacial locality, Švarcenberk, are placed on the transition between the modern samples of mesic hemiboreal forest (F1) and tundra on one side, and of steppic vegetation (more continental to the right) on the other side.

Generally, the full-glacial profiles are similar to the modern pollen samples from forests, tundra and forest-tundra. According to their position, the pollen spectra from Jablůnka should mainly correspond with hemiboreal forests, occurring most likely in a mosaic with shrubby tundra of *Betula nana*. Similarity of Praha-Podbaba pollen spectrum to Jablůnka is confirmed by its position among Jablůnka samples. By contrast, the samples from Šafárka are

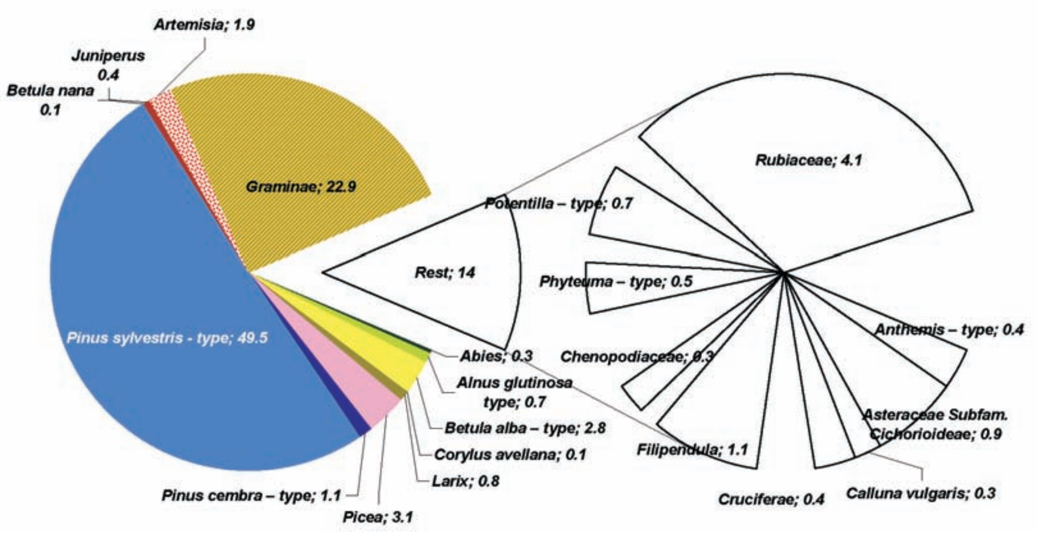


Fig. 5: Full-glacial pollen spectrum from Praha-Podbaba locality

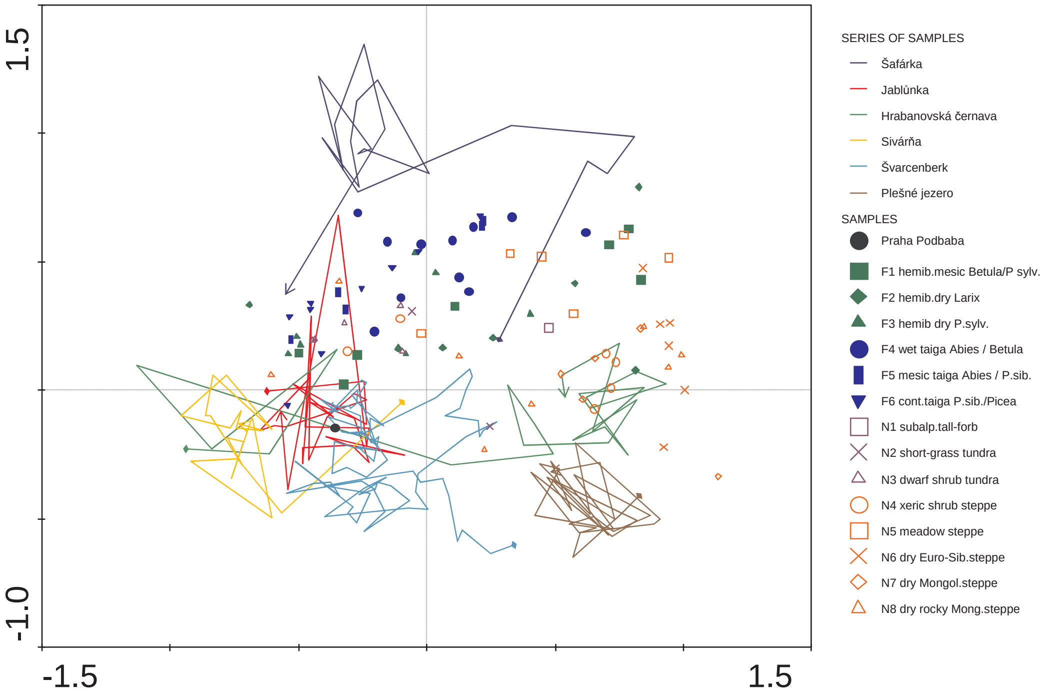


Fig. 6: PCA ordination scatterplot of modern and fossil pollen samples. Full and empty symbols represent the forest and treeless vegetation types of southern Siberia, respectively. Fossil pollen spectra are represented by lines connecting samples of each profile in their stratigraphical order; arrows point from the chronologically oldest to the youngest sample

situated at the top of the ordination diagram, close to the modern samples of taiga vegetation, especially its mesic and wet types (F4 and F5). Only a few of the lowest Šafárka samples are closer to the samples of dry *Larix* dominated hemiboreal forest (F2).

The ordination biplot with both samples and species (Fig. 7) illustrates the main differences in palaeovegetation of the full-glacial sites: *Picea, Larix* and *Abies* prevailed in Šafárka, whereas Jablůnka and Sivárňa were dominated by *Pinus cembra* and *P. sylvestris*.

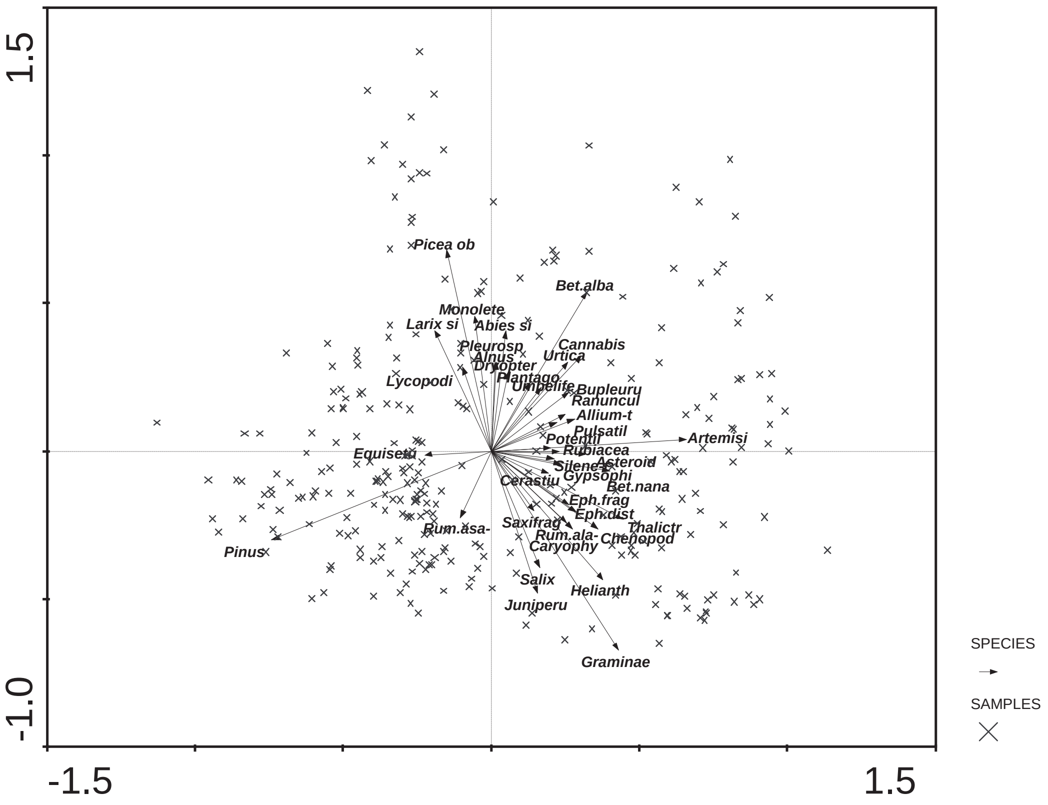


Fig. 7: PCA ordination biplot of pollen spectra and pollen taxa. See Fig. 6 for legend of samples

Discussion

Our analysis has confirmed similarities between the modern pollen spectra from southern Siberia and the fossil pollen spectra from central Europe. There was even some overlap of the fossil and modern samples in the ordination diagram (Fig. 6), although in general each group of samples occupied a different part of the diagram. This is not surprising, given that (1) some pollen types are poorly preserved in fossil records (Sayer *et al.*, 1999), (2) in spite of the considerable similarity, contemporary flora of southern Siberia is not exactly the same as the glacial flora of central Europe, (3) both the Western Sayan and each of the fossil profiles contain some local idiosyncracies that are responsible for differences in pollen spectra (this is reflected by the fact that samples from each of the fossil profiles are clustered in the ordination diagram, with the only exception of Hrabanovská černava samples). However, the proximity of the fossil pollen samples to the modern ones from certain vegetation types can be used for interpretation of palaeovegetation.

Interpretation of late-glacial vegetation

Completely treeless vegetation most occurred probably at Plešné jezero Lake and in the middle part of Hrabanovská černava profile. Hrabanovská černava closely matches the modern dry steppe and shrubby steppe (Fig. 6). Plešné jezero Lake is slightly isolated in the ordination diagram, but still considerably close to some steppic types and one tundra sample. Similarity to modern steppe, indicated by high pollen percentages of e.g. *Artemisia, Chenopodiaceae, Helianthemum* or *Thalicrum*, is surprising at this montane site, like at other montane sites in central Europe where same of these pollen types were also abundant at the beginning of the Holocene (Kuneš *et al.*, 2008). However, high representation of *Betula nana* pollen at Plešné jezero indicates tundra vegetation, most likely in a mosaic with drier grassland patches. The dissimilarity of the Plešné jezero samples and the modern samples of *Betula rotundifolia* (= *B. nana* s. lat.) tundra in southern Siberia could by explained by the fact that most Siberian *B. rotundifolia* tundra sites were sampled in slightly wetter landscapes that harboured at least patches of taiga nearby. More modern pollen samples from Siberian tundra would be probably necessary to obtain a clearer picture.

Švarcenberk site, with its recurrent increase and decline of tree pollen, seems to have supported transitional, but less open vegetation, somewhere between the two above-mentioned cases. Its late-glacial vegetation could have included a mosaic of tundra and steppe (*Betula nana, Salix, Alnus viridis*, *Juniperus, Helianthemum, Chenopodiaceae, Artemisia* and *Thalictrum*) and trees (*Pinus sylvestris, Betula*), even in a form of a patchy woodland. This is supported by its proximity in Fig. 6 to the modern samples from tundra, steppe and hemiboreal forests. The most forested of all late-glacial sites were Sivárňa and the oldest samples of Hrabanovská černava. They are closest to the modern hemiboreal forests and taiga (Fig. 6/F1, F3, F6) dominated by *Betula, Larix, Pinus sylvestris* and *P. sibirica* (= *P. cembra* s. lat). *Picea* and *Abies*, which are commonly present in the moister southern Siberian forests (Chytrý *et al.*, 2008), were absent in the pollen records of these late-glacial sites. This absence suggests a dry character of late-glacial forests.

These results imply that the late-glacial vegetation of the Bohemian sites was rather open steppe or tundra with a slight difference depending on altitude. The sites at lower altitudes (Švarcenberk, Hrabanovská černava) included scattered patches of hemiboreal forests, whereas the sites at higher altitudes (Plešné jezero Lake) were completely treeless. Contrastingly, the pollen record from Sivárňa testifies for forests and is consistent with earlier pollen or macrofossil analyses. These suggest occurrence of extensive hemiboreal forests of taiga with *Larix, Pinus cembra*, *P. sylvestris* and also some *Picea* in the intermountain basins of the Western Carpathians (Jankovská, 1984, 1988; Rybníček & Rybníčková, 1996), in the nearby Bieszczady Mountains of the Polish Carpathians (Ralska-Jasiewiczowa, 1980) and in the northern Tatra foreland (Wacnik *et al.*, 2004).

Interpretation of full-glacial vegetation

Our results are consistent with the hypothesis, that much of the Western Carpathians and some favourable spots in the Bohemian Massif were forested in the full glacial. However, there are differences between the full-glacial sites. Jablůnka contains variable samples corresponding with taiga, hemiboreal forest and tundra, some of them being similar to the samples from the upper section of the late-glacial Švarcenberk profile (Fig. 6). The single sample from Praha-Podbaba lies close to the samples representing a mosaic of treeless and forest vegetation, similar to those from Švarcenberk and the older part of Jablůnka profile. Their pollen spectra can represent patchy woodland vegetation, growing preferably at wind-protected sites with favourable moisture. Even after woody vegetation partially spread, there probably still existed enough open patches, reflected in the presence of light demanding taxa, such as *Betula nana, Hippophaë* and *Juniperus*. Somewhat lower representation of *Pinus cembra* and some more demanding taxa (*Corylus, Alnus glutinosa* and *Abies*) at Praha-Podbaba site could mean a long distance transport, when we take into account considerable landscape openness of this site. Samples from Šafárka show an affinity to the modern pollen spectra of dark taiga. However, the species composition and dominants are slightly different. The upper part of the profile corresponds with taiga dominated by *Picea*, *Betula, Larix, Pinus cembra* and *Pinus sylvestris* (Fig. 6). Two samples from Jablůnka site can be attributed to this category, too. The bottommost samples from Šafárka depict a drier forest dominated by *Larix*, which could form in a mosaic with meadow steppe (N5) and other types of hemiboreal forest.

Apart from the fossil pollen data used in this paper, the occurrence of the full-glacial forests in eastern-central Europe was supported by several recent studies. Pollen analysis of the profile at the former Nagy-Mohos Lake (Magyari *et al.*, 1999) confirmed *Larix*, *Pinus*, and *Picea* occurrence during the last glacial maximum. Late-glacial deposits in three Hungarian lakes (Willis *et al.*, 1995; Willis, 1997; Willis *et al.*, 1997) also suggested cold-stage refugia for these tree species, and even for some broadleaf species (Willis *et al.*, 2000). The pollen diagram from Bulhary site in southern Moravia (Rybníčková & Rybníček, 1991), dated to around 28 ka BP, indicates a coniferous forest containing *Pinus sylvestris, P. cembra, Picea, Larix, Juniperus*. There are also pollen records of temperate deciduous trees like *Ulmus, Corylus, Quercus, Tilia* and *Acer*, however, with low frequencies. Presence of these deciduous trees was repeatedly confirmed also *in-situ* at the Upper Palaeolithic archaeologic sites of Dolní Věstonice (Svobodová, 1991a, b) and Barová Cave (Svobodová & Svoboda, 1988). On the northern foothills of the Carpathians, several pollen profiles provided evidence for stands with *Pinus cembra* and *Larix* during warmer interstadials of the Weichselian pleniglacial (Mamakowa, 2003). Complementary information about the full-glacial vegetation is brought by malacozoological records of some woodland species that survived the extreme full-glacial conditions in the Western Carpathians (Ložek, 2006). Possible mammal refugia in this region have also been discussed (Sommer & Nadachowski, 2006).

By contrast, long profiles spanning the period of the Weichselian glacial bring rather traditional picture of full-glacial vegetation north of the Carpathian range, in the Polish lowlands. They show predominantly treeless vegetation dominated by steppic elements like Gramineae and *Artemisia*, with only slight occurrence of climate-resistant trees or shrubs like *Pinus sylvestris*, *Betula*, and *Juniperus* (Granoszewski, 2003; Mamakowa, 2003). It is the same case west of the Carpathians, where several long profiles spanning the last full glacial also suggest mainly treeless vegetation, which continued throughout the late glacial, (e.g. Füramoos in German alpine foreland; Müller *et al.*, 2003). The only exception in this scenario is the Praha-Podbaba site, which is located close to modern forest sites in the ordination diagram (Fig. 6). Forest patches could survive there due to favourable mesoclimate of a river valley, probably located in an otherwise open landscape. Unfortunately, this deposit does not cover the period of the last glacial maximum around 20 ka BP.


F1


F2

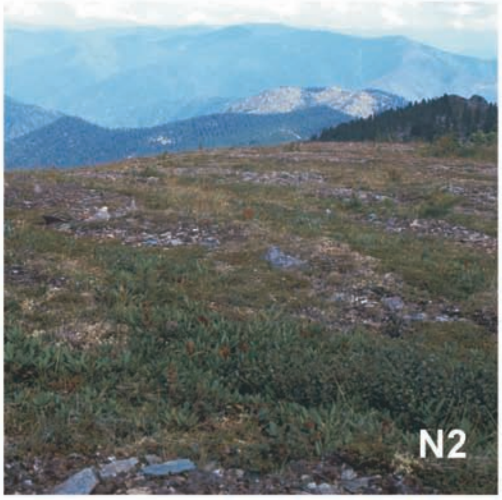

F3


F4

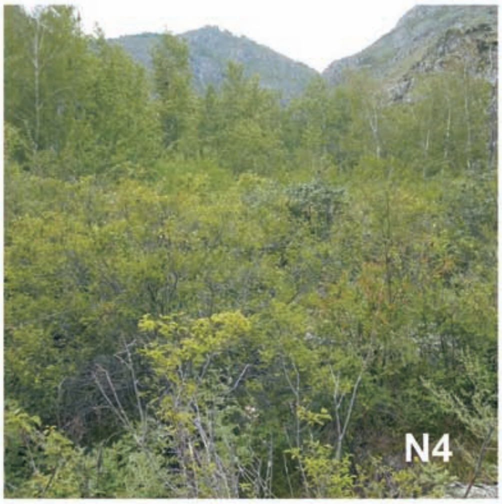

F5


F6

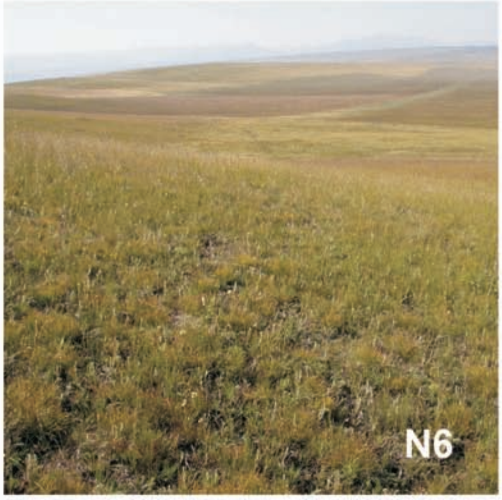

N1


N2


N3


N4


N5


N6

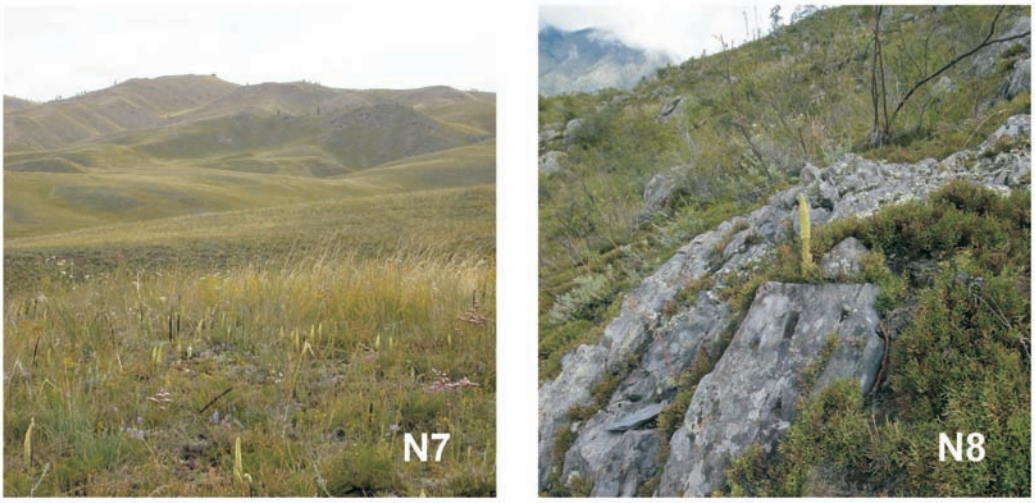


Fig. 8 (page 57–59): Examples of stand structure of main vegetation types (see Table 1 for details). Photos N5, N6 and N7 by Zdenka Otýpková.

An important question remains: how could taiga or hemiboreal forest, perhaps with some of temperate elements, survive extreme and harsh conditions of the full-glacial climate? Stage 3 Project climatic simulations (see Introduction) and our results (occurrence of dark taiga types with moisture demanding species like *Picea*) support the model which presumes that the eastern-central European mountainous regions had more rainfall than southern Europe. This means that relatively warm, moist, and dry continental climatic conditions could meet in the Western Carpathians during the full glacial. Similar situation exists in contemporary landscapes of southern Siberia, where such climatic conditions are the underlying reason for quite remarkable diversity in vegetation types as taiga, hemiboreal forests, steppe and tundra (Chytrý *et al.*, 2007, 2008; Lučeničová *et. al.*, subm.).

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Detection of impact of Early Holocene hunter-gatherers on vegetation in the Czech Republic, using multivariate analysis of pollen data

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Abstract: Pollen data from the Czech Republic was used to detect the Early Holocene impact of hunter-gatherers on vegetation based on a selection of 19 Early Holocene pollen profiles, complemented with archaeological information regarding the intensity of local and regional Mesolithic human habitation. Archaeological evidence was assigned to simple categories reflecting the intensity of habitation and distance from pollen sites. Multivariate methods (PCA and RDA) were used to determine relationships between sites and possible anthropogenic pollen indicators and to test how these indicators relate to the archaeological evidence. In several profiles the pollen signal was influenced by local Mesolithic settlement. Specific pollen types (e.g. *Calluna vulgaris, Plantago lanceolata, Solanum* and *Pteridium aquilinum*) were found to be significantly correlated with human activity. The role of settlement proximity to the investigation site, the statistical significance of pollen indicators of human activity, as well as the early occurrence of *Corylus avellana* and its possible anthropogenic dispersal, are discussed.

Keywords: anthropogenic pollen indicators, Mesolithic, early human impact, *Corylus avellana*, multivariate analysis

Introduction

In the Czech Republic the Mesolithic period of human prehistory lasted from the Preboreal to the Early Atlantic (i.e. from about 10,000 B.P. to 7000 B.P. according to the most accepted contemporary view; Pavlů 2004, Vencl 2006). It was a period during which dramatic changes occurred both in the global climate and in ecosystems. Reacting to these environmental changes, Mesolithic human populations adopted various hunting, gathering and fishing strategies, all of which were generally more specialized than those of the big game hunters of the Paleolithic period. As post-Glacial natural afforestation proceeded, Mesolithic populations started to be less mobile and thus they affected local environments around camp sites more intensively. However, this impact was probably only of a local character and hence could be easily overlooked in pollen diagrams. Moreover, the occurrence of anthropogenic pollen indicators in the sedimentary record may be strongly dependent upon the distance between the settlement and the sampling point (Behling and Street 1999; Wacnik 2005), as well as upon the type of sediment or local geomorphology.

A number of detailed palaeoecological studies concerned with the wider relationships of Mesolithic archaeology have been made (Simmons et al. 1985; Simmons and Innes 1988a; b; Clark 1989; Simmons and Chambers 1993; Turner et al. 1993; Macklin et al. 2000; Innes and Blackford 2003). Important surveys have come from Scandinavia, showing interesting pollen-analytical evidence for local Mesolithic settlements (Hicks 1993; Regnell et al. 1995; Vuorela 1995; Hornberg et al. 2006). A few studies have recently been presented from Western continental Europe (Bos and Janssen 1996; Bos 1998; Behling and Street 1999; Bos and Urz 2003; Bos et al. 2006) and Poland (Wacnik 2005).

The area of the present Czech Republic was selected as a model landscape for our study because of the abundant organic deposits of mire or lacustrine origin. However, very few of them have been studied by means of pollen analysis, and even less go as far back as the Early Holocene or Late Glacial. Up to now, no studies have been undertaken in the Czech Republic that focus on the impact of hunter-gatherers on the vegetation. In general, detailed high-resolution palaeoecological and archaeobotanical studies of this period as undertaken in other countries are missing. In order to perceive more clearly what could possibly be achieved and what should we concentrate on in the future, we have collected the available palynological data from the Czech Republic that includes the Early Holocene and analyzed them using multivariate numerical methods. In this paper we want to show how Mesolithic settlements can be verified or predicted based on pollen analysis, and which plants in particular can be considered as indicators of human presence in the Mesolithic. To achieve this goal, we ask the following questions:

1) Are there patterns in the pollen data that can be attributed to Mesolithic human influence?

2) Are there specific anthropogenic indicators for this period in the pollen assemblages?

3) Is there a relationship between the distance of a Mesolithic settlement from the sampling point and the (anthropogenic) pollen signal?

4) Are there differences in anthropogenic pollen signal between sites of different origin (small/large lakes and mires)?

5) Was human influence important for Early Holocene immigration and spreading of some trees?

Material and methods

Sites selection

The pollen sites for this study were first selected according to information available in the literature (see Table 1). Data were either extracted from the European Pollen Database (EPD – http://www.ncdc.noaa.gov/paleo/epd/epd_main.html) or from the original spreadsheets of the authors. The sites were selected in order to best cover the sequence of the Early Holocene and, in addition, to have sufficient archeological data in the surroundings such as findings of artifacts, or already excavated archaeological sites. Another important criterion for site selection was the possibility of building an absolute chronology for the period of interest. Unfortunately, this could not always be fully achieved due to the generally low number of radiocarbon dates in the available pollen diagrams.

The evidence of habitation around the sampling points was assessed on the basis of published or ongoing archeological surveys and excavations. Basic sources and the first comprehensive lists of Mesolithic sites in different areas have been gathered since 1990 (Vencl 1992; Sklenář 2000; Svoboda 2003; Vencl 2006; Prostředník and Šída 2006). However, these catalogues do not cover the whole area of the Czech Republic equally and survey progress is not at the same level everywhere (Mesolithic evidence in some areas has been discovered only recently and the number of localities is now steadily growing). Many areas are markedly under-represented (e.g. the surroundings of Komořanské jezero, the Elbe region, and certainly the highland and mountain regions). For example, information about Mesolithic settlements around Komořanské jezero originates exclusively from before the Second World War (Skutil 1952), as the lake was later completely destroyed by coal mining. On the other hand the best investigated area nowadays is southern Bohemia (Vencl 2006), but there still remain parts without investigation. Hence our approach was to attempt to estimate a potential Mesolithic habitation, taking into account not only the known localities but also some measure of the intensity of archaeological survey. We expect an increasing concentration of discovered localities in the near future; for this reason we assume the continual growth of the parameters presented. The area of Český ráj provides a good example: the number of Mesolithic localities has increased from only one known in 2002 to 16 in 2006 (Prostředník and Šída 2006).

For our study, 19 profiles were finally selected (Table 1) that represent different vegetation zones, from lowlands to montane ecosystems (the lowest at 170 m, the highest at 1089 m asl), as well as different phytogeographic provinces (according to Hejný and Slavík 1988). The mean annual temperature and precipitation range from 9.2°C and 530 mm in the lowlands to 4.5°C and 1000 mm in the uplands (Culek 1996), respectively. The distribution of survey sites (as indicated in Fig. 1) also reflects many diverse situations with respect to habitation settlement history during the Mesolithic, the state of archaeological survey (as described above), and the preservation of the sites.

Data preparation and numerical analysis

The data from different authors had to be standardized for numerical analysis. First, the nomenclature used in different pollen diagrams had to be unified (achieved using the POLPAL2005 Tabela program, Walanus and Nalepka 1999). The pollen-taxonomic nomenclature used follows Beug (2004) and is partly modified in the case of some plant taxa that are characteristic of the Czech Republic's flora (Kubát 2002). The total sum of upland AP and NAP together was used to calculate percentages. Local pollen and spores (incl. aquatic

Table 1 – List of pollen profiles used for data analysis. (T – terrestrial, L – lacustrine sediments)

code	profile name	author	localization	altitude (m asl.)	available ^{14}C dates B.P. (cm depth)	sediment type	data source
B	Bláto	Rybníčková	N 49° 2’ 30", E 15°11’ 30"	645	10570±150 (250) 11060±250 (277,5)	T	Rybníčková (1974) + EPDB
T	Borkovická blata	Jankovská	N49°13’57.6" E 14° 38’ 0.6"	420	6184±125 (245) 7040±100 (430)	T	Jankovská (1980) + EPDB
E	Červené blato	Jankovská	N 48°51’ 38.6" E 14°48’ 39.3"	470		T	Jankovská (1980) + EPDB
H	Hrabanovská černava	Petr	N 50°12’ 58.1" E 14°49’ 56.5"	185	8660±50 (85) 11310±60 (105) 12500±60 (115) 13630±50 (195)	L+T	Petr (2005)
J	Jestřebské blato	Jankovská	N 50°36’ 30.6" E 14°35’ 57.8"	259		T	Jankovská (1992)
K	Komořanské jezero	Jankovská	N 50°36’ 30.6" E 14°35’ 57.8"	231	1490±70 (30) 2590±70 (90) 6570±80 (117,5) 7770±80 (128,5)	L	Jankovská (1983)
O	Kožlí	Pokorný	N 49°21’ 35.8" E 14° 1’ 18.3"	485	1408±165 (40) 2159±237 (80) 8212±225 (115)	T	Pokorný (unpubl.)

code	profile name	author	localization	altitude (m asl.)	available ^{14}C dates B.P. (cm depth)	sediment type	data source
L	Loučky	Rybníčková	N 49°19’ 26.5" E 15° 32’ 3.2 „	560	10225±145 (202,5)	T	Rybníčková (1974) + EPDB
U	Mělnický úval	Petr	N 50°17’ 56.4" E 14°34’ 44.1"	170	5600±40 (25) 14200±70 (105)	T	Petr (2005)
M	Mistřín	Svobodová	N 48°57’ 56.9" E 17° 4’ 48.7"	175	1810±70 (105,5) 3370±60 (151) 4100±60 (175,5) 4600±65 (186,5) 6620±75 (215,5)	T	Svobodová (1997) + EPDB
Y	Mokré louky	Jankovská	N 49° 1’ 5.2 „ E 14°46’ 16.5"	425	7390±80 (225) 8180±90 (285) 8650±90 (326) 9630±100 (355) 9600±100 (365)	T	Jankovská (1987) + EPDB
N	Palašiny	Jankovská	N 49° 41’ 20" E 15° 29’ 0"	520	9530±270 (95)	T	Jankovská (1990) + EPDB
P	Plešné jezero	Jankovská	N 48°46’ 36.1" E 13°51’ 59.8"	1089	2005±60 (52,5) 3637±60 (106,5) 3949±50 (115,5) 4733±55 (142,5) 8264±65 (235,5)	L	Jankovská (2006)

code	profile name	author	localization	altitude (m asl.)	available ^{14}C dates B.P. (cm depth)	sediment type	data source
R	Řežabinec	Rybníčková	N 49°15’ 0.3 „ E 14° 5’ 26"	372	1220±75 (72,5) 2750±150 (88,5) 3055±195 (110) 4185±245 (115,5) 5280±105 (121,5) 6860±110 (125,5) 8755±140 (130) 8925±300 (150,5) 9095±390 (153,5)	T	Rybníčková and Rybníček (1985) + EPDB
S	Švarcenberk	Pokorný	N 49° 8’ 39.7" E 14°42’ 20.8"	412	4650±100 (151,5) 6350±100 (325,5) 9640±115 (391,5) 10780±115 (521,5) 11750±120 (681,5)	L	Pokorný and Jankovská (2000)
C	Velanská cesta	Jankovská	N 48° 46’ 29" E 14°55’ 44.5"	498		L+T	Jankovská (1980) + EPDB

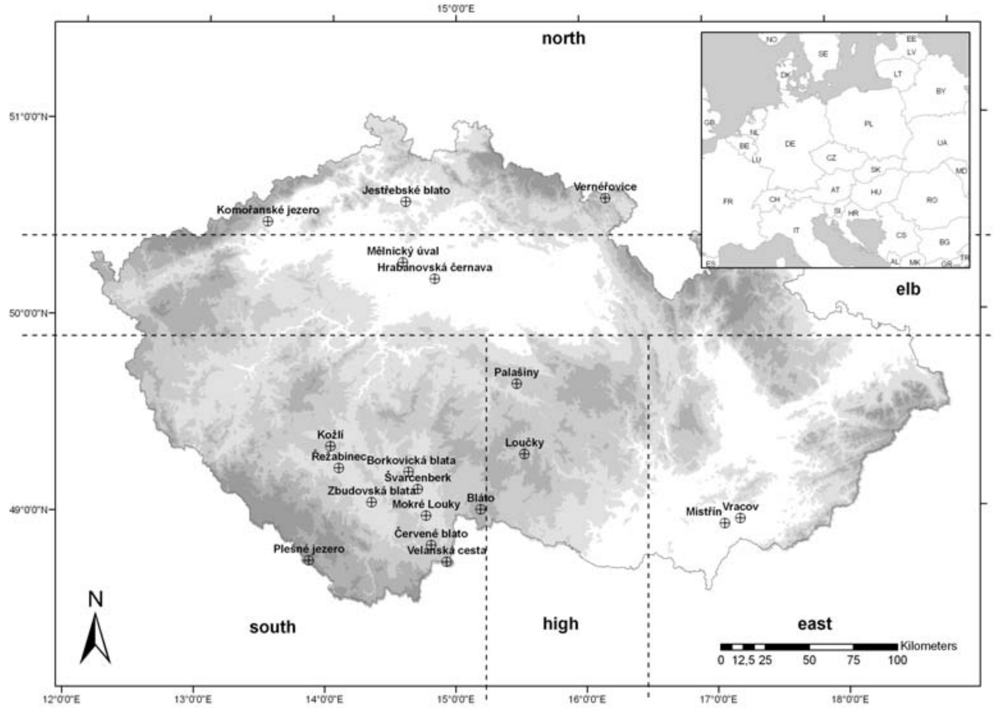


Fig. 1 – Map of the Czech Republic with survey sites (circles). Codes at the right and at the bottom of the map indicate regions (delimited by dotted lines). The same codes are used in the ordination diagrams.

and mire taxa) were excluded from this total sum. The percentages of taxa excluded from the total pollen sum (i.e. local pollen) were calculated based on each respective pollen type count in relation to total sum.

Subsequently, the zonation of all pollen diagrams was made in the POLPAL Diagram program using Constrained Single Linkage analysis (ConSLink) and Principal Component Analysis (PCA) (Nalepka and Walanus 2003). This means that zones were determined by biostratigraphic patterns and their denomination was made according to Firbas (1952). In those cases where available, ^{14}C ages were also used in determining zones and their precision. For each pollen diagram two main pollen-assemblage zones (PAZ) were distinguished that covered the Early Holocene period: Early and Late Mesolithic time slices. For those sites where some part of the record was missing, only one pollen assemblage zone was distinguished.

All samples from a selected PAZ were analyzed stratigraphically unconstrained in the CANOCO program (ter Braak and Šmilauer 2002) to avoid subjectivity in data interpretation. First a Detrended Correspondence Analysis (DCA) with square-root transformed data was performed. As the data were quite uniform among the dominant taxa, the first canonical axis had a gradient length of only 1.895. This confirmed that linear-based models like PCA or RDA (as in Fig. 3) should be used in the analyses. To suppress the influence of dominant taxa, we used a logarithmic transformation of the data percentages. All non-pollen palynomorphs (algae, fungi, charcoal, etc.), *Equisetum,* Cyperaceae and monolete fern spores were excluded from the analyses.

In order to better visualize and interpret the data in further analyses (as in Fig. 3 onwards), an average for each zone was calculated, labeled with a code (I for the older and II for the younger zone). The data prepared in this way were then processed with PCA, using logarithmic transformation of percentage pollen data. To test for significance between environmental (three categories of archaeological evidence according to their distance from the sampling spot) and pollen taxa, Redundancy Analysis (RDA) was used with logarithmic transformation, performing Monte-Carlo permutation tests with the reduced model and using unrestricted permutations.

Assessment of the archaeological evidence

Records of human presence near the pollen sites during the Mesolithic period were assigned to three categories according to their distance from the sampling point (Table 2). The first category includes local archaeology, defined as evidence of human presence just at the study site, which, in our case, meant only finds at the edge of the deposit or in the close proximity (less than 500 metres from the sampling point). The next two categories represent archaeological evidence within 5 and 25 km, respectively; the scale attempts to give a quantitative estimate of intensity of human impact. Data had to be simplified to some extent, and, in some cases, due to their complete absence or inconsistency, extrapolated using analogies from more intensively-studied nearby regions; these possible shortcomings may thus distort the results of the analyses. Only part of southern Bohemia can be considered as widely surveyed. Other regions are hence markedly under-represented, where localities have been found rather fortuitously. According to the sites so-far investigated, Mesolithic settlement in southern Bohemia was very intensive and can be found in every suitable location (including highland areas). Nevertheless, some places had been markedly preferred, such as river confluences, lakes, or large rivers. Extrapolating from these Mesolithic settlements, we assumed that a weak intensity of human presence would be higher in all areas in lowland regions and extremely high around spots distinguished by having a high diversity of ecosystems (e.g. lakes, rivers, confluences). The above-mentioned three categories of intensity of human presence were used in the numerical analyses as environmental variables to interpret the pattern in the pollen data.

Furthermore, a ‘Human Impact Factor’ (HIF) was created, which is a combination of all three categories (for the formula for its evaluation see Table 2), describing the character/extent of human habitation in the surroundings of each sampling point. HIF aims to express the intensity of human impact, which decreases proportionally with increasing distance of an archaeological record from a pollen sampling point.

Anthropogenic indicators in pollen diagrams

Selected pollen types were characterized as human-impact indicators according to Behre (1981). The following pollen types were used to create a sum of anthropogenic indicators for each site: *Calluna vulgaris, Achillea*-type, *Artemisia, Aster*-type, *Avena*-type, *Bupleurum*-type, *Campanula, Cannabis / Humulus,* Caryophyllaceae Subfam. Silenoideae-type, *Cerastium*-type, Cerealia, *Cirsium,* Asteraceae Subfam.Cichorioideae, Cruciferae (Brassicaceae), *Daucus carota, Gnaphalium*-type, *Helianthemum, Heracleum, Hordeum*-type, Chenopodiaceae, *Melampyrum, Peucedanum*-type, *Pimpinella major*-type, *Plantago lanceolata, P. maior*-type, *Pleurospermum austriacum, Polypodium, Pteridium aquilinum,* Ranunculaceae, *Ranunculus* *acris*-type, Rubiaceae, *Rumex*-type, *Secale cereale, Senecio, Silene vulgaris*-type, *Solanum dulcamara, Succisa, Thalictrum, Trifolium*-type, Umbelliferae (Apiaceae), *Urtica,* and *Trapa natans*.

Construction of summary pollen curves

In this study, two summary pollen diagrams with percentage pollen curves from all sites in the analysis were used. Using the spreadsheet program TILIA (Grimm 2004), an age-scale

Profile / Site	*Archaeology*			Human Impact Factor (HIF)
	Local	0.5-5 km	*5-25 km*	
Bláto	0	0	1	1
Borkovická Blata	0	1	2	7
Červené blato	0	1	1	6
Hrabanovská černava	0	1	2	7
Jestřebské blato	0	2	3	13
Komořanské jezero	3	1	1	81
Kožlí	1	2	2	37
Loučky	0	0	1	1
Mělnický úval	0	1	2	7
Mistřín	0	1	1	6
Mokré louky	0	1	2	7
Palašiny	0	0	1	1
Plešné jezero	0	0	1	1
Řežabinec	3	3	2	92
Švarcenberk	3	2	1	86
Velanská cesta	0	1	1	6
Vernéřovice	0	1	2	7
Vracov	0	1	1	6
Zbudovská blata	0	1	2	7

Table 2 - Mesolithic occupation in relation to palynological sites. The 'archaeology' variable indicates four categories of increasing intensity of human presence: 0 – absence; 1 – low; 2 – medium-strength; 3 – intensive habitation. The summary values of the HIF variable are calculated as a distance-weighted intensity of human presence in the landscape using the values of the 'archaeology' variable: (HIF=25*Local + 5*(0.5-5 km) + (5-25 km)).

was reconstructed with linear interpolation between the available uncalibrated radiocarbon dates (see Table 1). This age-scale has to be taken as only a tentative one, since it is based on a very weak chronology.

Results

Archaeological background

The occurrence of Mesolithic settlements around some lakes is well known: Komořanské jezero (Skutil 1952), Švarcenberk (Pokorný et al. in press), Řežabinec (Vencl 2006). Other regions with a high intensity of human presence were investigated with another aim in mind: Mělnický úval and Hrabanovská černava were surveyed by Skutil (1966) and Sklenář (2000), whereas Svoboda (2003), and Prostředník and Šída (2006), focused on sandstone for the last ten years. The site Vernéřovice is located in an area that has never been largely investigated.

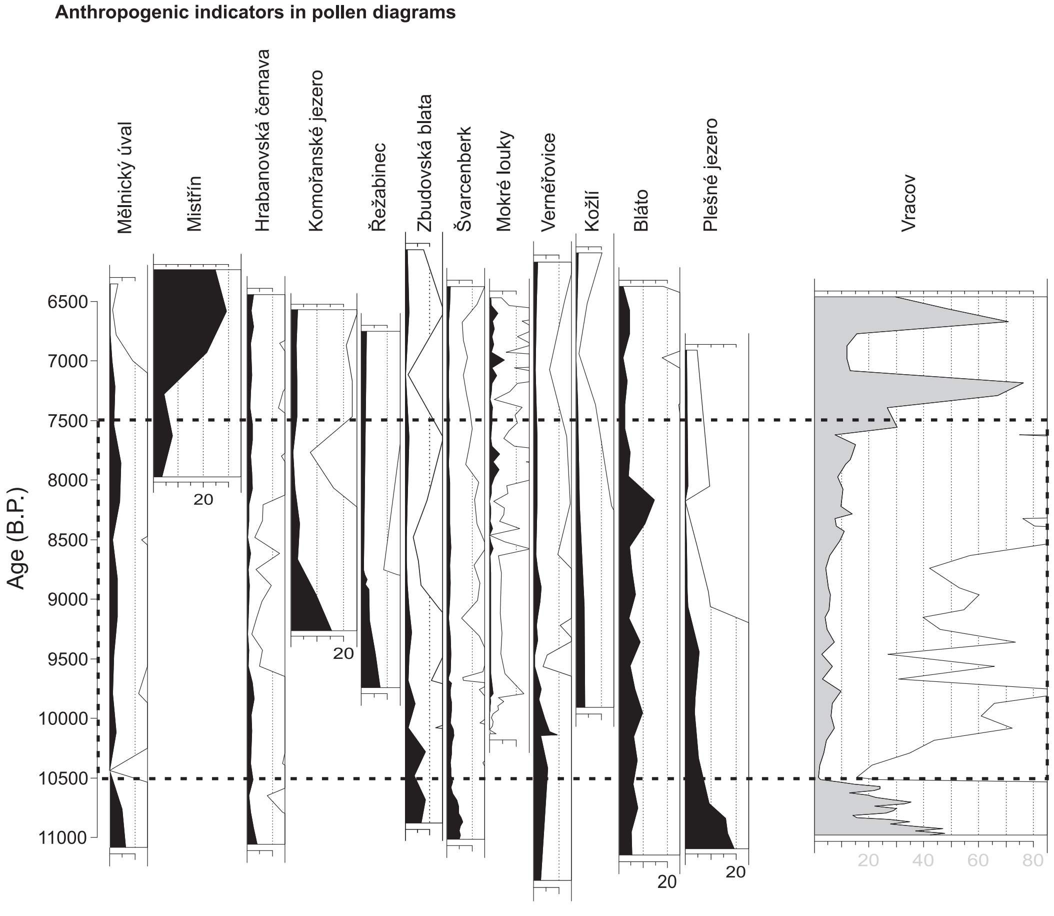


Fig. 2 - Percentage pollen curves made from the sum of potential anthropogenic indicators at sites where chronology could be constructed. Sites are ordered according to increasing altitude from left to right (170 - 1089 m asl). The pollen record from Vracov (at right) is not well dated; the timescale has thus been constructed based on biostratigraphy, but it is used here as a principal lowland reference site.

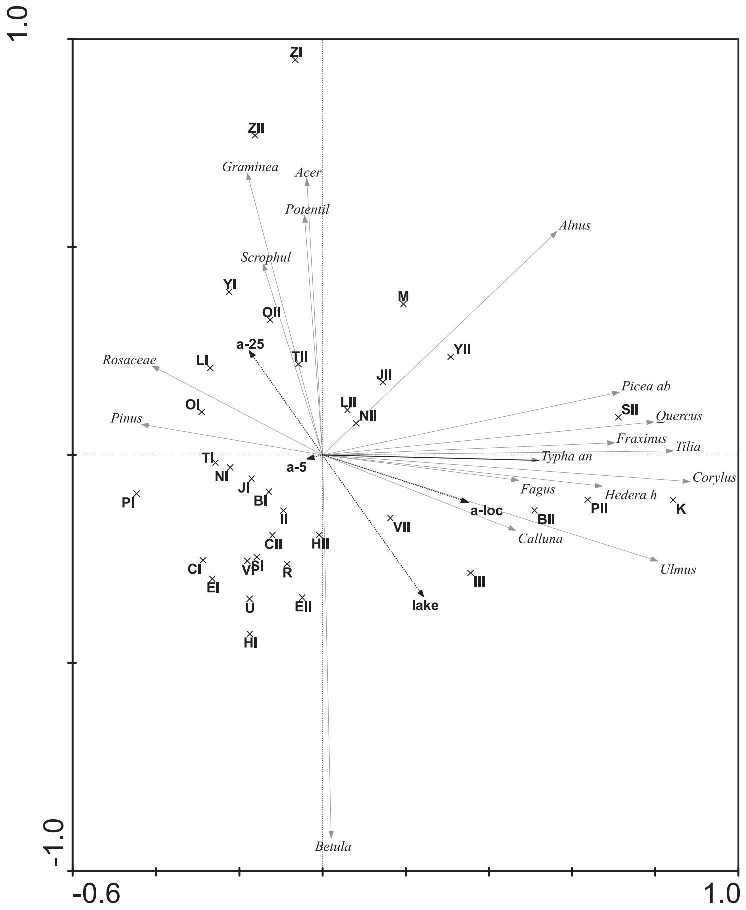
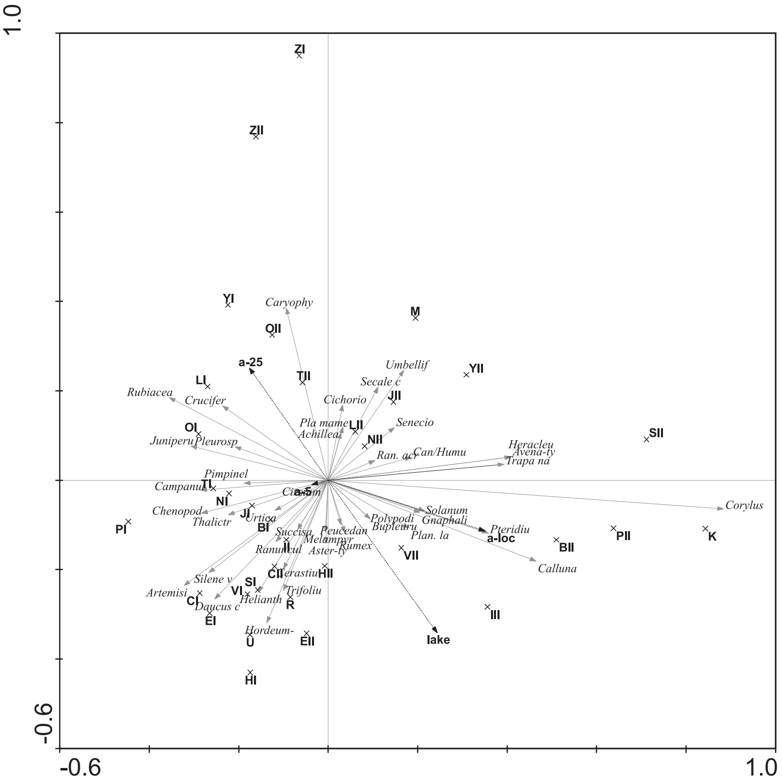


Fig. 3 – PCA triplot of averaged samples over pollen assemblage zones (PAZ), using type of sediment ('lake': lake sediment) and archaeology ('a-loc': local archaeology; 'a-5': archaeology within 5 km; 'a-25': archaeology within 25 km) as environmental variables. Localities (X marks) are labelled following codes in Table 1. Taxa indicated are mainly dominant trees, mostly responsible for the distribution of sites according to the age of each zone.

However, during the last few years some single finds of Mesolithic stone manufacture have appeared (Bronowski 2000), hence archaeological finds are to be expected in this area. Southern Bohemia is the region where a rather intensive Mesolithic archaeological research has been undertaken and consequently has a high index of human impact for all profiles. Southern Moravia has been the poorest in archaeological investigations. Although studies have uncovered several localities (e.g. Valoch 1978), the intensity of human presence is not as high as that around comparable profiles in the Bohemian lowlands. This difference cannot be due to some dissimilar preferences of Mesolithic populations, because the landscape provides similar conditions (e.g. Elbe region). It for this reason that we reconstruct higher numbers of human habitation intensity in southern Moravia.

Table 2 shows the results of the categorization of archaeological finds. Komořanské jezero, Švarcenberk, and Řežabinec could be considered as important Mesolithic settlement sites; all three sites are former lakes. For some of the other sites there is strong regional evidence of Mesolithic occupation, a category represented by profiles in: central Bohemia - Elbe region (Hrabanovská černava, Mělnický úval); sandstone landscapes (Jestřebské blato, Vernéřovice); part of southern Bohemia (Borkovická blata, Kožlí, Mokré louky, Řežabinec, Zbudovská blata); and southern Moravia (Mistřín, Vracov).

Fig. 4 – PCA triplot of averaged pollen assemblage zones using type of sediment and archaeology as environmental variables (codes used as in Fig. 3). Taxa indicated are potential anthropogenic indicators.



Numerical analysis of pollen data

The results of the data analysis for each pollen profile provided the first look into the pollen assemblage zones (PAZ). We combined both ConSLink and PCA to determine the period of the Early Holocene, considering also radiocarbon data. Finally, two pollen-analytical zones in each profile were assigned to Early (I) and Late Mesolithic (II). In the pollen diagrams for Mělnický úval, Mistřín and Řežabinec (I), and Komořanské jezero (II), the analysis resulted in a single period only, according to the age of the samples.

The sums of selected anthropogenic indicators for different pollen profiles are shown in Fig. 2; however, there was no clearly visible pattern between sites during the investigated period of the Early Holocene (i.e. both PAZ I and II). We have therefore chosen more sensitive multivariate statistical methods. The PCA of all pollen samples from the period of interest (Early Holocene) indicated the main distribution of pollen assemblages between and within all sites, and also explained the main trend in the data. A cluster of samples was represented by the sites Švarcenberk, Komořanské jezero, Plešné jezero, and Vernéřovice, the first two of which have strong archaeological evidence for Mesolithic habitation (Table 2); however, using all pollen samples separately made interpretation of the ordination diagram difficult and some important trends may have remained hidden.

The results of the PCA using all the samples but averaged within pollen assemblage zones provided a more coherent view (Fig. 3; Fig. 4); in addition, environmental variables were included, with altitude being used as a covariable. The first ordination diagram (Fig. 3) shows the distribution of both the sites and the abundant (mainly tree) species, the latter being mainly responsible for deciding the principle distribution of samples in the diagram. This means that the first axis of the ordination represents an approximate time axis between the

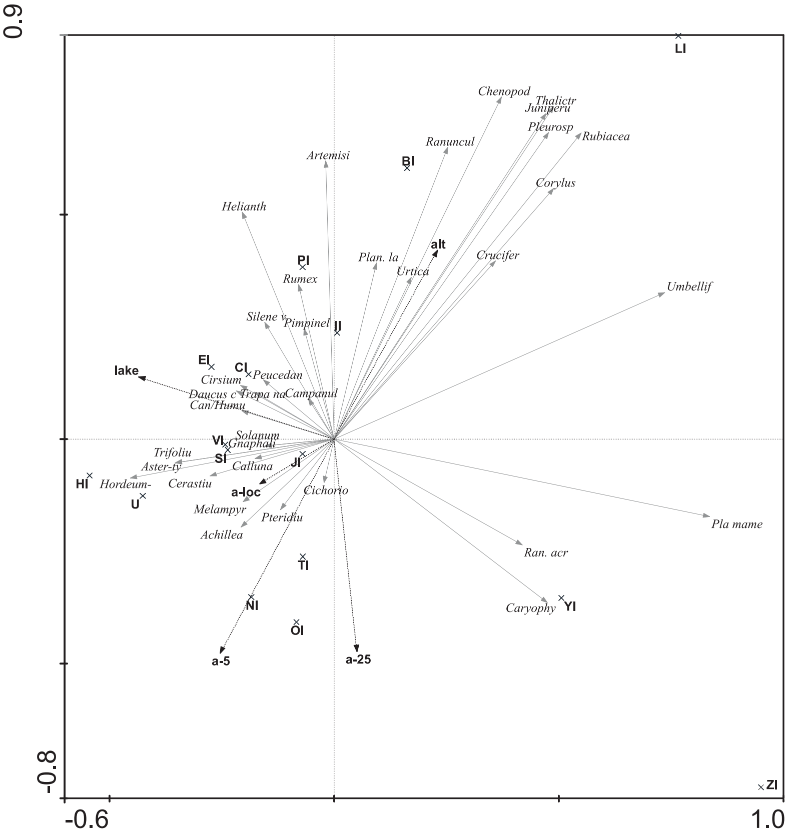


Fig. 5– PCA triplot of Early Mesolithic samples using type of sediment and archaeology (codes used as in Fig. 3), and altitude (‘alt’) as environmental variables.

older (from the left) and younger (to the right) samples. In the second ordination from the same PCA, where only anthropogenic indicators are represented (Fig. 4), certain variables can be seen to be correlated: above all, the environmental variable ‘local archaeology’ with the species *Calluna, Solanum, Pteridium, Plantago lanceolata* and *Corylus* and to a lesser extent with *Trapa natans, Cannabis/Humulus,* and *Rumex*. All these latter taxa are found to the right of the ordination having a strong relation to the sites Komořanské jezero, Plešné jezero, Švarcenberk and Vernéřovice.

A more detailed view was possible by separately analyzing the Early (PAZ I) and Late (PAZ II) Mesolithic samples, which filtered out the major effect of the dominant trees. Two ordination diagrams were produced by PCA, without using any covariables, but with altitude as an environmental variable, in an attempt to determine which of the anthropogenic indicators could point to naturally-opened landscapes. This can be interpreted in the first ordination (Fig. 5) using the averaged samples of the Early Mesolithic (Preboreal) period. Just after the onset of the Holocene, the landscape was continuously overgrown by forest, so that we can expect both primary and secondary open stands. This situation can be seen at the top of the ordination diagram where sites from higher altitudes (Czech-Moravian Upland, Bohemian Forest) are situated; at such altitudes, open stands from the late-glacial period may well have persisted, in this case demonstrated by species of open stands such as *Juniperus, Thalictrum, Artemisia,* and *Helianthemum,* and to a lesser degree by *Rumex, Plantago lanceolata,* and *Urtica,* which can here be considered as indicative of both primary open stands and as anthropogenic indicators. In the bottom left of the diagram are sites correlated with archaeological evidence and thus with possible indicators of human activities such as

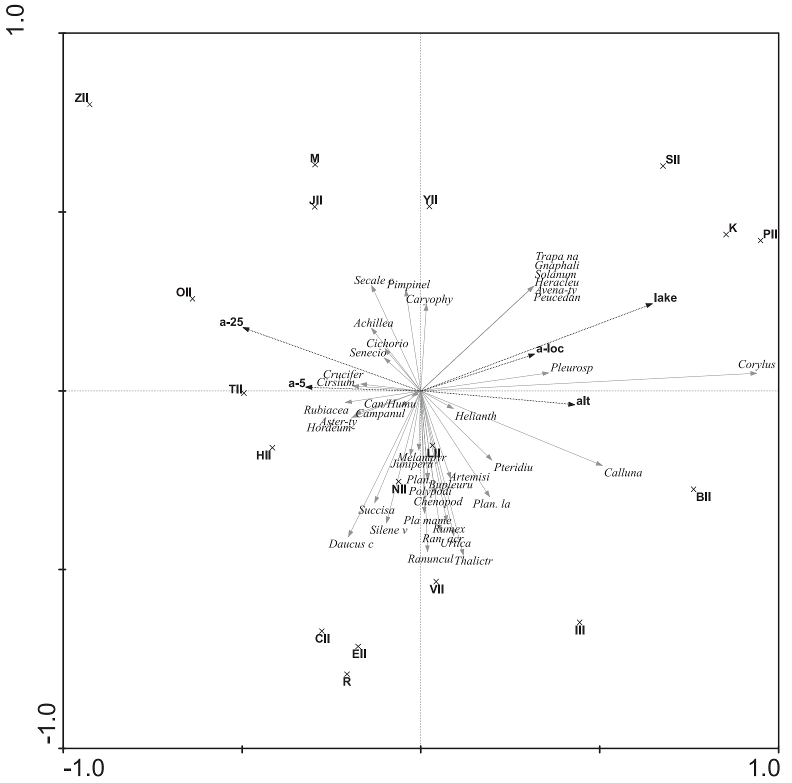
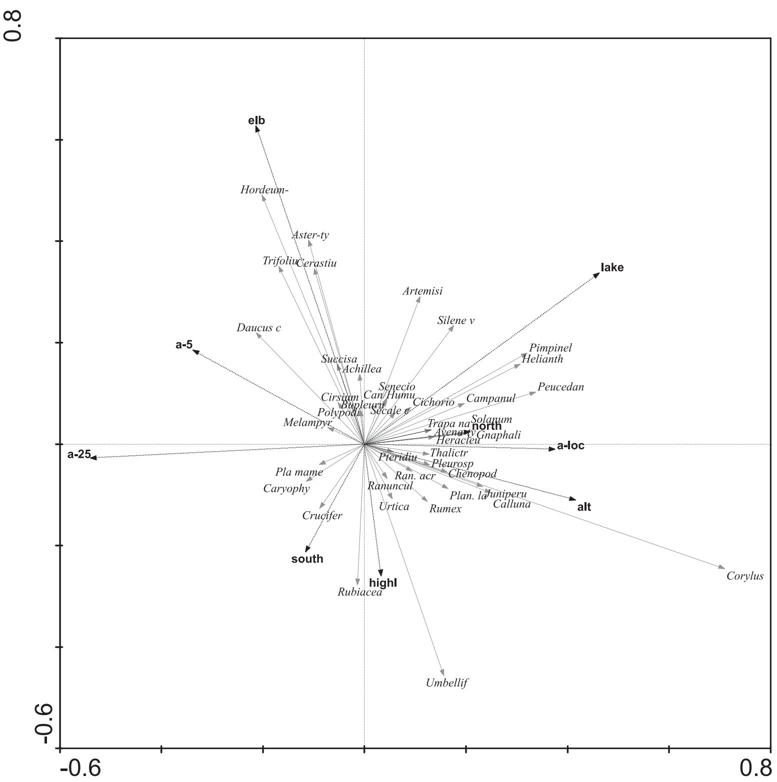


Fig. 6 – PCA triplot of Late Mesolithic samples using type of sediment and archaeology (codes used as in Fig. 3), and altitude (‘alt’) as environmental variables.

Calluna, Cannabis/Humulus, Aster-type*, Solanum, Melampyrum, Pteridium,* and *Achillea*-type. These species were closely related to sites having an archaeological record of local settlement or intensive regional occupation. The next ordination, taken from the Late Mesolithic (Boreal) period (Fig. 6), is less straightforward to interpret. It shows great variability in its samples, represented by a group of lake sites in the top-right corner and a group of terrestrial (mire) sites in the lower part of the diagram. The latter group represents sites with a local and regional archeology that may represent extensively-used landscapes rather than the lake examples with only a local impact. Again one can see certain taxa grouped together, such as *Melampyrum, Pteridium, Plantago lanceolata,* and *Rumex*.

In the subsequent analyses, RDA was used to test the significance of relationships between taxa and environmental variables. The first two RDA figures show the relationships of different taxa to various components of archaeology: one with the effect of altitude (Fig. 7), and one without (Fig. 8), altitude being effectively filtered out as a covariable. The first RDA axis explained 17.4% of the total variance in the fossil pollen data (p-value = 0.034) and the second represented a further 11.8%. A positive correlation could be seen between lake-type sediment and local archaeology. The following potential anthropogenic indicators are correlated with local archaeology: *Calluna, Plantago lanceolata, Solanum dulcamara, Pteridium*, *Helianthemum,* and *Cannabis/Humulus*. Using altitude as a covariable (Fig. 8), there were species that had been quite sufficiently filtered from the effect of altitude and which could be considered both as anthropogenic indicators and primary open landscape indicators at higher altitudes, such as *Juniperus, Urtica,* Chenopodiaceae*, Rumex, Plantago maior/media,* Cruciferae (Brassicaceae), etc.; in the first diagram (Fig. 7) located to the right, and, after elevation has been allowed for statistically, more towards the middle (Fig. 8). Other

Fig. 7 – Redundancy analysis (RDA) biplot of potential anthropogenic pollen indicators found in the Mesolithic period with environmental variables (‘a-loc’: local archaeology; ‘a-5’: archaeology within 5 km; ‘a-25’: archaeology within 25 km; ‘alt’: altitude; ‘lake’: lake sediment; ‘elb’, ‘highl’, ‘south’, ‘north’: 4 regions as indicated on map in Fig. 1).



indicators more likely represented lowland environments (i.e. they were negatively correlated with altitude), which could also be regarded as potentially-settled areas (marked as regional archaeology ‘a-5’, ‘a-25’). Into this category fall, for example, the commonly-prevalent *Melampyrum*, *Aster*-type*, Daucus,* or *Trifolium*-type.

In a further RDA (Fig. 9), we tried to determine those indicators related to human activities in the landscape that do not depend on distance but rather on human impact intensity. In this case, archaeology was expressed as a single environmental variable. The list of potential anthropogenic indicators includes *Artemisia* and *Silene vulgaris*, both of which are probably correlated with human activity in general. An interesting aspect also depicted in the RDA ordinations was the position held by hazel (*Corylus avellana*), which was significantly correlated with local archaeology and archaeology in general.

***Corylus avellana* in pollen diagrams (Fig. 10)**

Fig. 10 shows the percentage curves of *Corylus avellana* pollen at selected sites during the Early Holocene. The sites have been ordered according to altitude (increasing to the right). However, there was no discernible relation in hazel occurrence and dominance, neither was there any relationship to geographical distribution. An earlier occurrence of *Corylus* was documented at the sites of Komořanské jezero, Švarcenberk, Vernéřovice, and Plešné jezero (sites marked with an arrow in Fig. 10). Remarkable at these sites was the abrupt start and the long persistence of high percentages of hazel, which could be related to human habitation at these localities or in their proximity (Skutil 1952; Vencl 2006; Pokorný et al. in press). The occurrence of *Corylus avellana* is significant as tested in the RDA (see above) and was strongly

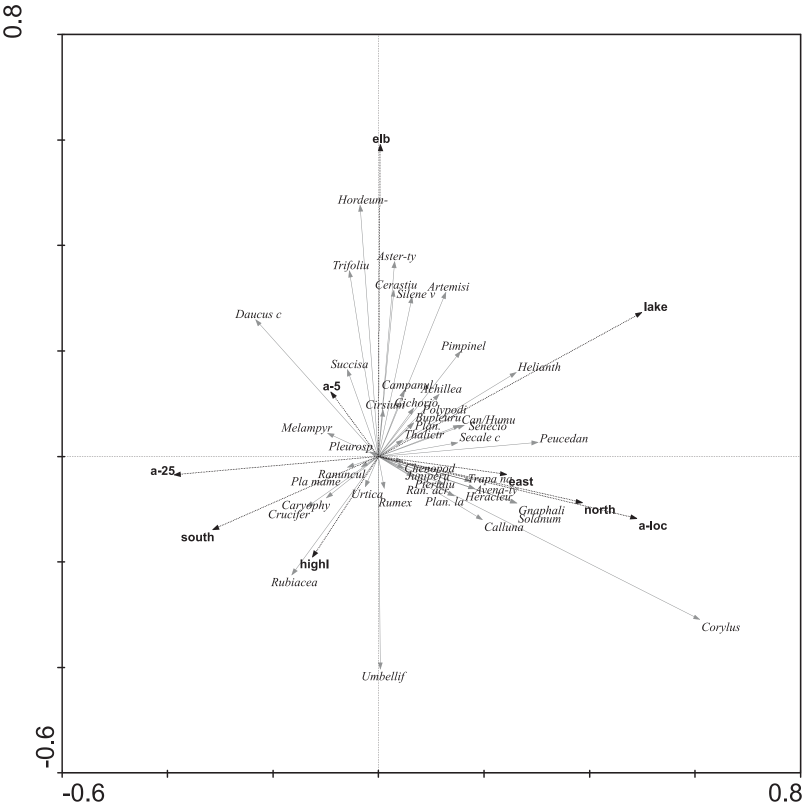


Fig. 8 – RDA biplot of potential anthropogenic pollen indicators found in Mesolithic period with environmental variables as in previous RDA ordination (for codes see Fig. 7) but using altitude as a covariable.

correlated with both local human activities (local archaeological record) and general intensity of human habitation (summed archaeology HIF – Fig. 9).

Discussion

The pollen-analytical data used in this study represent a selection of reference profiles for the area of the Czech Republic. The question of human impact of hunter-gatherers on environments in the Early Holocene and its evidence in the pollen spectra has been a marginal part of previous studies in the Czech Republic (Jankovská 1983; Svobodová 1989; 1997; Jankovská 2000; Pokorný and Jankovská 2000). Some deeper analyses were only carried out in studies that aimed at discussing archaeological theories (Pokorný 2005). In contrast, the present study focuses on vegetation development. Here, we found that some evidence for human impact in the Early Holocene can be demonstrated using data already collected, i.e. already-existing pollen diagrams, and that there is a certain potential for this approach in future studies.

Settlement proximity to investigated pollen sites

We address the problem of human impact intensity being reflected in the pollen record by utilizing a number of sites over a rather large area. Past studies focussed more on the uniqueness of each locality and described the human impact related to specific archaeological finds of various intensity: from intentional landscape management, especially in

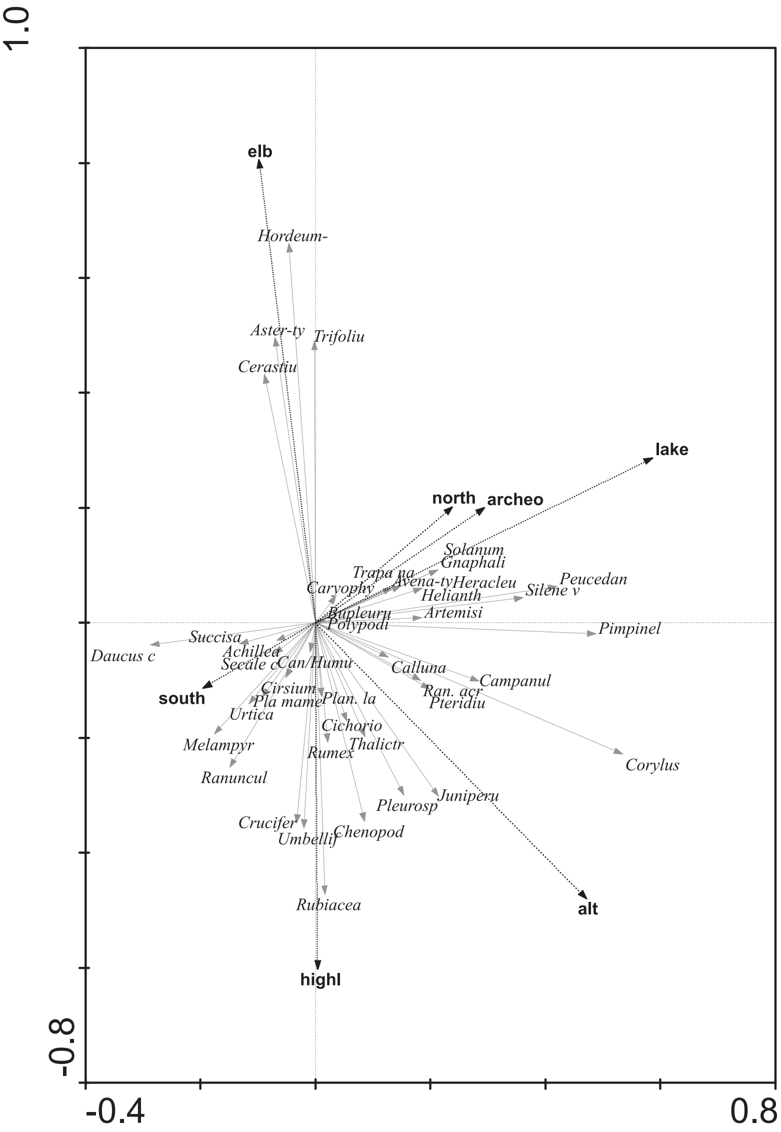


Fig. 9 – RDA biplot using environmental variables as in previous RDA ordination (see Fig. 7 for codes) but using archaeology ('archeo') expressed as one variable (Human Impact Factor - HIF).

north-western Europe (Simmons et al. 1985; Turner et al. 1993; Macklin et al. 2000; Mason 2000) to the presence of humans hardly detectable (Behling and Street 1999). Certainly the possibility of human activities being recorded in the Early Holocene landscape is strongly dependent on the openness of the landscape and on the proximity of pollen sources of anthropogenic indicators (Wacnik 2005). This is also demonstrated by the present quantitative multivariate analyses, where the amounts of anthropogenic indicators are correlated with the local archaeological record (e.g. sediment profiles with Mesolithic archaeological finds on lake shores). At such sites, it then becomes possible to document human-induced changes in vegetation in the form of deforestation and connected events and to record frequent fires (increases in the input of microscopic charcoal particles), which, in fact, might only have been local in character. At a larger scale, a wider picture of human impact can already be more distorted, with potential anthropogenic pollen indicators being

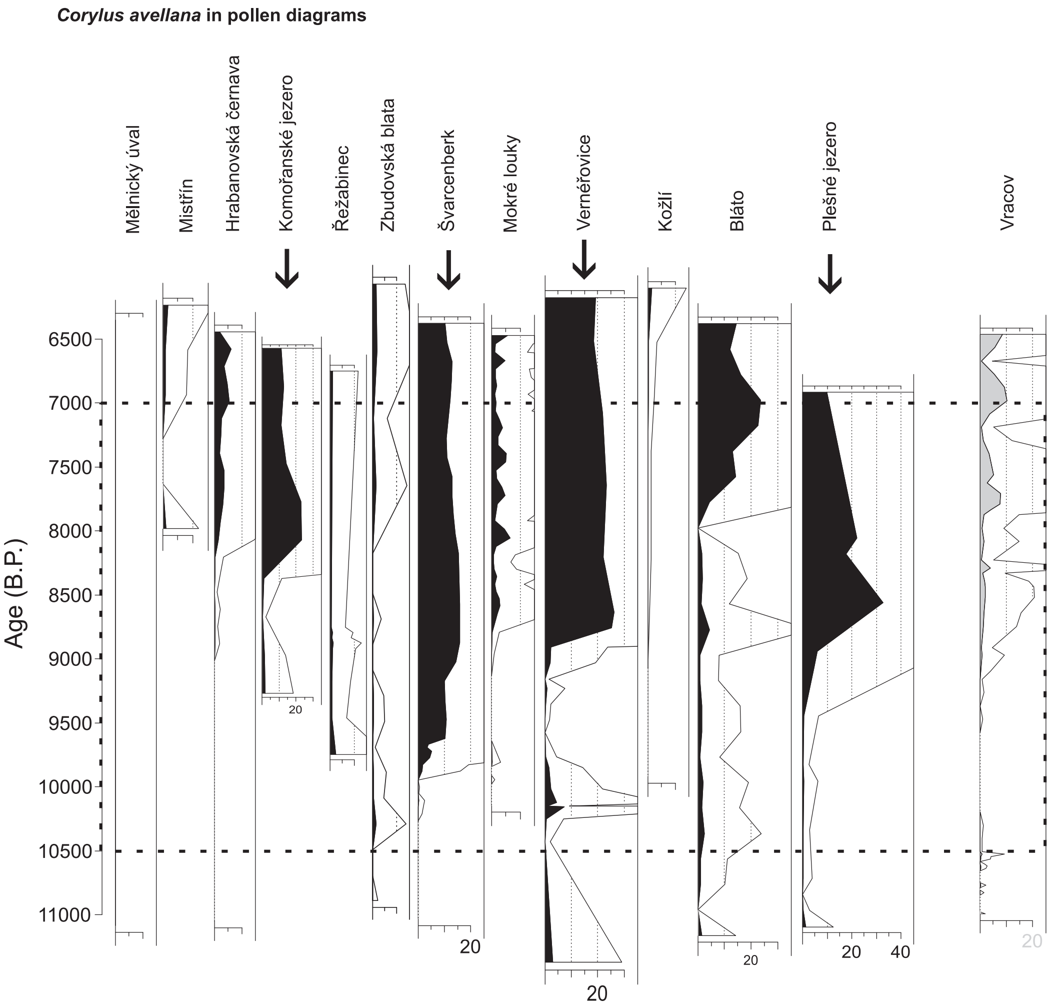


Fig. 10 – Percentage pollen curves of *Corylus avellana* from selected sites. The time-scale is tentative since it is in some cases based on a very weak chronology (see Table 1). Sites are ordered according to increasing altitude from left to right (170-1089 m asl). Vracov is not well dated (time-scale based on the Glacial-Holocene boundary and tree-zonation), but is used here as a lowland reference site.

also those of open landscape. Moreover, the distinction between primary and secondary open stands (as shown by our results of the multivariate analysis) is not unambiguous.

Even very close distances between sampling points and areas of habitation (Behling and Street 1999) or direct evidence of anthropogenic indicators in pollen diagrams (Fig. 2) may not necessarily represent human activity. Most likely these indicators have a more specific and very weak response that is visually hardly detectable in the pollen diagram. Numerical analyses, as presented here, often show the negative correlation of local and regional archaeological variables. This can support the theory of the very local response of pollen indicators to habitation. At sites having only regional evidence of human activities, specific pollen indicators are generally not present. Considering the different pollen source areas of sites with varying size and type of sedimentation (Sugita 1994; Nielsen and Sugita 2005), we may expect some scatter of these groups (mainly lakes and mires) in ordination diagrams. Some trends can be depicted in this bifurcation (Fig. 3). There might be a simple explanation for this, namely that Mesolithic populations would not settle around or in the proximity of mires or swampy areas but rather prefer larger lakes. Our detailed comparative study at the important Mesolithic occupation site Švarcenberk (Pokorný et al. in press) gives supplementary facts about the varying levels of human impact detection. Comparing littoral and central pollen records at this site, the influence of Mesolithic occupation is very heterogeneously recorded in pollen diagrams from different parts of the adjacent lake.

Anthropogenic pollen indicators

In the Czech Republic, correlation with available archaeological data is problematical because of the lack of surveys undertaken. However, recent archaeological excavations show a denser landscape occupation than previously expected (Fridrich and Vencl 1994).

When assessing indicators of Early Holocene human impact in pollen diagrams, there are several other issues we have to deal with. The majority of plant species are insect-pollinated: having low pollen productivity and very local pollen transport in the mainly forested Early Holocene landscape. Moreover, they have an ambiguous ecology when considered as human impact indicators (e.g. *Juniperus, Urtica, Rumex,* etc.). Some studies have used a high-resolution approach (Simmons et al. 1985; Bos and Urz 2003) or non-pollen palynomorphs such as fungal spores or charcoal particles (Innes and Blackford 2003; Bos et al. 2006) in trying to solve this problem. However, they were mainly undertaken in north-western and western Europe, whereas the central-European landscape at the time was probably more forested. For detecting some differences, rarefaction analysis can also be useful (but see also Odgaard 1999); it can show even a doubling of palynological diversity (Poska et al. 2004), but one can not still be sure when judging between human and natural causes.

By using numerical methods and a network of reference sites, in combination with data about landscape habitation during the Mesolithic, we have managed to verify that the indicator pollen response is dependent on human habitation and distance from the pollen source. The next important result is that only some potential pollen indicator types are correlated with Mesolithic settlement. Others may not have only reflected anthropogenic activities but were more likely responding to natural processes in the ecosystems, even if many studies consider them within the group of anthropogenic indicators (Behling and Street 1999; Beckmann 2004; Wacnik 2005). We consider the following taxa (pollen types) as having an important role in the detection of Mesolithic occupation, at least for the Czech Republic: *Calluna vulgaris, Plantago lanceolata, Solanum dulcamara, Gnaphalium*-type*, Trapa natans, Heracleum, Ranunculus acris*-type*, Peucedanum*-type*, Helianthemum, Cannabis/Humulus*-type*, Pteridium aquilinum* and *Corylus avellana*. In spite of the fact that there has been only one single good piece of evidence of microscopic charcoal abundance (Pokorný and Jankovská 2000), the occurrence of all these types could still be explained by deliberate burning and clearances, which subsequently resulted in succession and the occurrence of light- and nitrogen-demanding taxa. Secondary vegetation of open areas is here represented by *Calluna, Helianthemum,* and *Plantago lanceolata*. Regeneration phases after fire disturbances are best represented by *Pteridium aquilinum* and *Plantago lanceolata*. Other pollen types could be indicators of partly nutrient-rich and wetter stands (*Solanum, Peucedanum, Heracleum,* and *Ranunculus*), as a result of settlements being established, or longer human persistence near a wetland site (vicinity of lakes or palaeochannels), and the creation of environments with prevalent herbs and shrubs to attract wild animals (Mellars 1976; Zvelebil 1994; Bos and Urz 2003). Finally, mention should be made of those species connected with the Mesolithic diet or other kind of plant use (Zvelebil 1994; Merlin 2003), especially *Trapa natans*, demonstrably gathered for nuts. *Corylus avellana*, which played an important role in the Mesolithic diet deserves special attention (see discussion below).

The next group of potential indicators that should be discussed are *Juniperus, Thalictrum,* Chenopodiaceae, Rubiaceae, *Pleurospermum, Artemisia, Rumex, Plantago maior/media, Urtica,* and *Silene vulgaris*. These taxa are often used as indicators of mosaic woody landscape or larger open landscape patches, hence also as potential human-activity indicators, e.g. by Beckmann (2004). Taking into account the environment, climatic conditions, and vegetation of the Early Holocene, we must also consider alternative explanations for the occurrence of these taxa. For example, juniper is also often mentioned as an indicator of dry pastures (Behre 1981), but it was common in the Late Glacial and Preboreal patchy landscape. *Juniperus, Thalictrum,* Chenopodiaceae, Rubiaceae, and *Pleurospermum* together form a group in the Preboreal ordination diagram (Fig. 5) and are best explained as indicating natural open stands of the Early Holocene, which is in agreement with their position being determined by increasing altitude. The remaining pollen types represent mainly light-demanding species: *Artemisia, Rumex, Plantago maior/media,* and *Silene vulgaris*. *Urtica* is connected with nutrient-rich soils. It has been suggested to include them as anthropogenic indicators (Behre 1981); however, according to the results of our numerical analyses, they are strongly affiliated with trends other than archaeology in our case. Especially during the Early Mesolithic (Fig. 5), they appear correlated with increasing altitude, which may be interpreted as more or less persistent tundra or tundra/steppe environments, or just a high proportion of open stand vegetation with a relatively high nutrient content. A good example of this are the present-day environments of the continental southern Siberian mountains, where good examples of gradients from species-rich boreal or hemi-boreal forest to steppe or tundra can be found (Ermakov 1998). Similar vegetation conditions could be expected during the Early Holocene in central Europe (Jankovská 1998; Jankovská et al. 2002). This fact has been to a large extent verified by the RDA analysis, which, after partialling out the effect of altitude, showed significant correlation of these pollen indicators to altitude, and hence to natural types of ecosystems, rather than to human-raised environments (Fig. 8). According to our results the interpretation of *Artemisia* pollen is still very debatable: it's occurrence could be connected with some human presence as an indicator of ruderal stands or along footpaths (Behre 1981), a fact partly proved by our data analyses (Fig. 9). On the other hand, an *Artemisia* record may also represent larger, natural, forest-free areas (remains of late-glacial vegetation at higher altitudes, or dry lowlands, or extreme habitats), due to the ability of its pollen to be transported long distances (as shown by our recent pollen studies in southern Siberia; *unpubl. results*).

Anthropogenic use and spreading of *Corylus avellana*

Hazel is traditionally believed to have spread to the area of present-day Czech Republic from its glacial refugia. In most studies, these refugia are often reconstructed to have been more to the south, as well as being in the British Isles or close to south-west Scandinavia (Deacon 1974; Bennett et al. 1991). However, some surveys in the Czech Republic also argue for these glacial refugia to have been in central Europe (Peichlová 1979; Rybníčková and Rybníček 1988). What is undisputable, however, is the mostly sudden appearance and abrupt rise in

Corylus pollen at many Early Holocene sites (Jankovská 2000; 2006). Moreover, at some of these sites, its appearance can be observed as occurring at the very start of the Holocene (Peichlová 1979; Pokorný and Jankovská 2000). Similarly, the very early spread of *Corylus* and its quite high pollen abundance in the Early Holocene has also been detected throughout the rest of Europe (Boyd and Dickson 1986; Simmons and Innes 1988a; b). This fact has quite often been given as being connected with Mesolithic habitation in an area (Hicks 1993; Regnell et al. 1995). On the other hand, this trait could be the product of many ecological factors acting together (Huntley 1993; Tallantire 2002); meanwhile, human populations were just beginning to make use of these same conditions.

The pollen-analytical results from the Czech Republic show that *Corylus avellana* started to spread suddenly at some sites around 8500 ^{14}C B.P., or in some cases even earlier (Švarcenberk around 9500 ^{14}C B.P.; Fig. 10). Our recent studies at the Švarcenberk locality show finds of *Corylus* macrofossils (nuts) in a stratigraphic position just before the pollen curve started to rise. There was no visible relationship between *Corylus avellana* pollen distribution and that of altitude, geographical position, or any other ecological factor tested or taken into account. Also, a comparison of closely-situated localities in southern Bohemia depicted big differences between *Corylus* curves (Fig. 10) (Rybníčková et al. 1975; Rybníčková and Rybníček 1985; Jankovská 1987; Pokorný and Jankovská 2000). This suggests that the pollen records indicate local conditions, which were very different at different localities.

The relationship between *Corylus* pollen and archaeological data tested with RDA indicated a significant relation between local archaeology and the appearance of *Corylus avellana* (Fig. 8), as well as between the human impact factor (HIF; Table 2) and *Corylus* (Fig. 9). Human influence was the only environmental variable tested that could explain the rapid and irregular spread of *Corylus avellana* in the Czech Republic during the Early Holocene. An evaluation of sites that had strong signs of Mesolithic habitation (Fig. 3) enabled us to identify *Corylus* pollen as a rather good anthropogenic indicator. We cannot say, however, whether the spreading of hazel by humans was deliberate, unintentional, or coincidental (e.g. by providing good conditions through deforestation).

Conclusions

The use of pollen diagrams for evaluating the potential impact of Mesolithic settlement on vegetation was examined using multivariate analyses. The selection of 19 profiles from the Czech Republic and their pollen records between 10,500 and 7500 B.P. were processed using PCA and RDA together with some information about the Mesolithic occupation of areas surrounding the pollen sites. Patterns in the data distribution between those sites possibly influenced by Mesolithic habitation were recognized, and also in sites without that evidence. The results of these analyses support the hypothesis that some potential anthropogenic indicators react very specifically, although weakly, to Mesolithic human activity in the landscape. Summary pollen curves of all anthropogenic indicators were reconstructed for each site but did not show any explainable differences between sites. A closer look at certain specific indicators might discover some possible human impact; however, the occurrence of these indicators is generally very sporadic, their percentages low, and they can easily be overlooked in pollen diagrams. Multivariate analysis applied to several pollen sites together proved a better tool for studying this early human impact.

We have also tested the relationship between Mesolithic occupation and its distance from the pollen sampling points. Human activity during the Early Postglacial in central Europe (an area largely forested) was only local in character (of the order of hundreds metres) and can be hardly detected at greater distances.

The early occurrence, rapidly spreading and high initial abundance of *Corylus avellana* was apparent at most of the study sites. However, even if its occurrence has been found to be significantly correlated with human presence, the possibility of an asynchronous spread of hazel in different climatic and edaphic conditions cannot be ruled out.

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Mezolitické osídlení bývalého jezera Švarcenberk (jižní Čechy) v kontextu vývoje přírodního prostředí

Petr Pokorný, Petr Šída, Petr Kuneš, Ondřej Chvojka

Abstract

The extinct Lake Švarcenberk offers an unprecedented quantity of data for the study of the natural environment and its interaction with human settlement for the period of time between 15 000 years BP and 5000 years cal BC. Recently both natural scientific and archaeological excavations have been undertaken here. An extensive Mesolithic settlement was discovered near the lake including settlement remains which had been flooded by a rise in the surface of the water. These remains also included wooden artefacts. Natural scientific methods reflected the presence of this settlement and indicate the early appearance of several varieties (hazel and water nut at the very beginning of the holocene), which could be related to their introduction. For the future the area of Lake Švarcenberk has demonstrated itself to be one of the most promising in our country for the study of the Mesolithic period from mainly an environmental archaeological point of view.

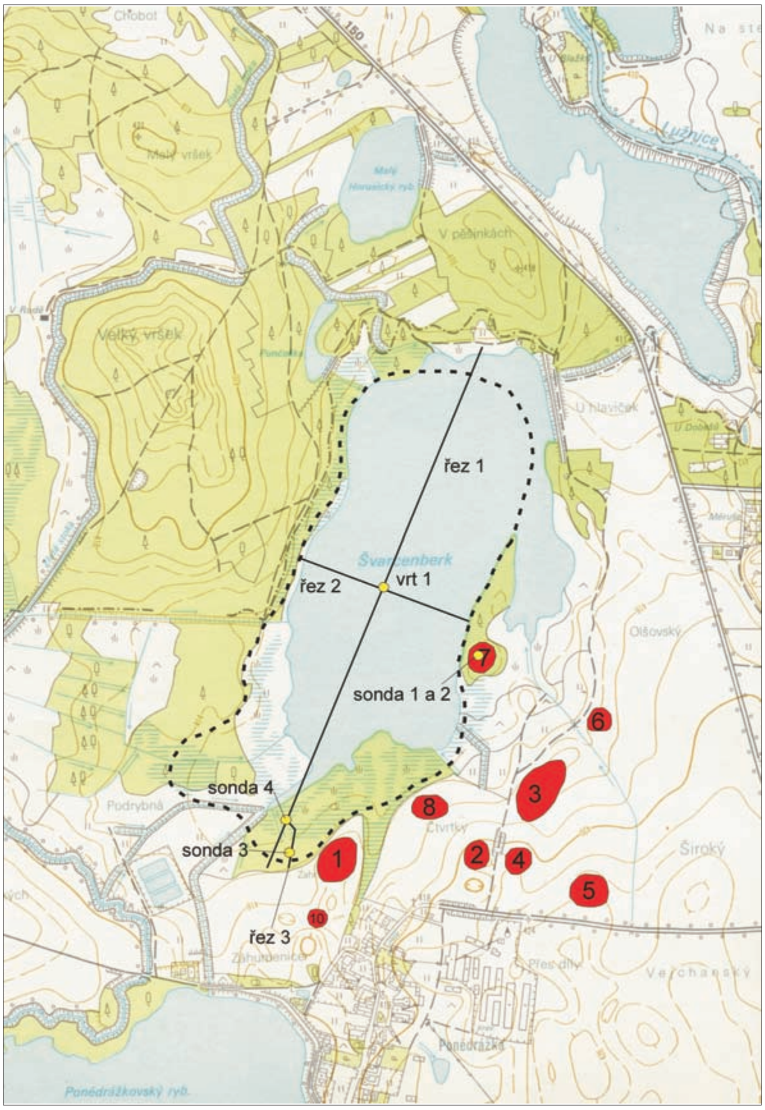
Úvod

Lidská sídla bývají odjakživa vázána na dominantní geomorfologické útvary, které svou přítomností lokálně zvyšují diverzitu přírodních zdrojů, poskytují orientační body v krajině a umožňují societám jistou formu sebeidentifikace. Mezi významné fenomény tohoto druhu bezesporu patří přirozené vodní plochy. Na území České republiky jsou jezera většího rozsahu poměrně vzácným úkazem (*Janský, Šobr et al. 2003*; příspěvek L. Petra v přítomné publikaci). Předpokládáme, že o to výraznější roli mohly takové ojedinělé lokality hrát ve struktuře pravěkého osídlení.

Před téměř deseti lety začal dlouhodobě koncipovaný paleoekologický výzkum zazemněného jezera Švarcenberk. Jezero se nacházelo v severní části Třeboňské pánve, jižně od Veselí nad Lužnicí na katastru obce Ponědrážka (*obr. 1*). Jeho rozsah mírně přesahoval plochu dnešního rybníka vybudovaného zde na přelomu 17. a 18. století. Podle něj dostalo původní jezero název. Náš příspěvek si klade za cíl ve stručnosti a přehlednou formou shrnout dosavadní stav poznání této mimořádné lokality, včetně nejnovějších výsledků archeologického a zejména paleoenvironmentálního výzkumu.

Obr. 1: Rozsah bývalého jezera, poloha jednotlivých archeologických lokalit, vrtů, sond a řezů

Fig. 1: Extent of the former lake, location of the individual archaeological sites, cores, sondages and sections



Objev zaniklého jezera se datuje na počátek 70. let 20. století, kdy *V. Jankovská* zjistila jezerní sedimenty pod vrstvou rašeliny ve výtopě dnešního rybníka (*Jankovská 1976, 1980*). V polovině 90. let jsme na tato zjištění navázali rozsáhlejším stratigrafickým průzkumem. Záhy se ukázalo, že se jedná o původní jezero značného rozsahu a že je uprostřed pánve dochován mocný sled jezerních sedimentů nečekaně vysokého stáří. Dva litorální profily a jeden profil centrální byly postupně zpracovány metodou pylové analýzy, rozboru zbytků řas a makrozbytkové analýzy s cílem popsat postup zazemňování jezerní pánve a dlouhodobou vegetační sukcesi s ním spojenou (*Pokorný – Jankovská 2000*). Chronologie sedimentárního záznamu je postavena na radiokarbonových datech, na nepřímém datování stopovými obsahy rubidia (k této nově vypracované metodě viz *Veselý et al. 2006*, v tisku) a na relativním palynostratigrafickém datování. Centrální profil, jehož spodních 5 metrů vznikalo v průběhu pozdního glaciálu, byl využit k rekonstrukci vývoje vegetace a geochemických změn v povodí jezera v souvislosti s prudkými klimatickými změnami na přelomu pleistocénu a holocénu (*Pokorný 2001, 2002*). Sedimentologický výzkum ověřil přítomnost eolické složky v jezerním souvrství. Stopy eolické činnosti, patrné v jezerních sedimentech, se podařilo korelovat se vznikem dun vátých písků v přilehlé části nivy Lužnice a vysvětlit je jako reakci na klimatické zhoršení, ke kterému došlo na počátku mladšího dryasu (*Pokorný – Růžičková 2000*). Paleoekologický potenciál této mimořádné lokality zdaleka není zmíněnými výzkumy vyčerpán. V sedimentech jsou zachovány například zbytky rybí fauny a dalších vodních organismů, které lze využít k rekonstrukci změn lokálního prostředí a ke studiu klimatických změn regionálního až globálního charakteru. Postupně jsou zpracovávány například zbytky rozsivek (*Bešta 2004*) a vodních korýšů (Cladocera – *K. Nováková*, zatím nepublikováno).

Zajímavé jsou okolnosti objevu mezolitického osídlení v okolí jezera Švarcenberk. Z blízkého okolí Ponědrážky (Bošilec, dvě polohy v Lomnici nad Lužnicí, Ponědraž) jsme znali zatím jen ojedinělé nálezy štípané kamenné industrie patrně předneolitického stáří (souhrnně viz *Vencl et al. 2006*). První archeologický průzkum v bezprostředním okolí rybníka Švarcenberk podnikl v roce 1986 Ivan Pavlů, který zde povrchovým sběrem nalezl jediný úštěp a ve vykopané sondě při jihozápadním okraji rybníka doložil pouze vrstvu rašeliny bez jakýchkoliv artefaktů (*Pavlů 1992*, 8–10; *Vencl et al. 2006*). Odhlédneme-li od tohoto ojedinělého nálezu, bylo rozsáhlé mezolitické osídlení doloženo až nepřímo, a to na základě přítomnosti pylových zrn antropogenních indikátorů a mikroskopických uhlíkových částic v jezerních sedimentech datovaných do raného holocénu (*Pokorný 1999*). V litorálním profilu budily pozornost nálezy oříšků kotvice plovoucí (*Trapa natans*) a zejména semen maliníku (*Rubus idaeus*), která se do jezerních sedimentů mohla stěží dostat přirozenou cestou. Silná nepřímá indikace dávala tušit přítomnost mimořádně hustého osídlení v těsném okolí bývalého jezera, a to minimálně od samého začátku holocénu po jeho střední část. Navazující archeologický průzkum, provedený v roce 2000 S. Venclem (*Vencl 2006*, 208–210) a zejména pak v letech 2005 a 2006 autory tohoto příspěvku, přinesl hojné nálezy štípané kamenné industrie datovatelné rámcově do pozdního paleolitu a především do mezolitu. Podařilo se tak objevit archeologickou lokalitu, která má vzhledem k vazbě na jezerní a bažinné prostředí mimořádný potenciál k aplikaci celé řady environmentálně archeologických metod.

Původ a vývoj jezera

Bývalé jezero Švarcenberk mělo v době svého vzniku plochu zhruba 50 ha a maximální hloubku okolo 10 m (*obr. 2*). Napájely ho především prameny artézské vody, které vystupují podél tektonického zlomu. Jezero se odvodňovalo do nedaleké řeky Lužnice. Jeho vznik před více než 15 000 lety[1]1 zatím nelze vysvětlit běžnými mechanismy. S největší pravděpodobností souvisel s klimatickými podmínkami konce vrcholného glaciálu v kombinaci s příhodnými místními faktory. Maximální ochlazení posledního glaciálu bylo na našem území provázeno přítomností permafrostu. O jeho rozsahu se již dlouhou dobu vedou spory. Pokud pomineme extrémní názory na obou stranách, vezmeme v úvahu hodnoty průměrných ročních teplot rekonstruované pro období vrcholného glaciálu mírně pod bod mrazu (*Wright et al. 1993*), a pokud se navíc spolehneme na recentní analogie, můžeme konstatovat, že panuje konsensus alespoň o přítomnosti permafrostu nesouvislého. Jaké

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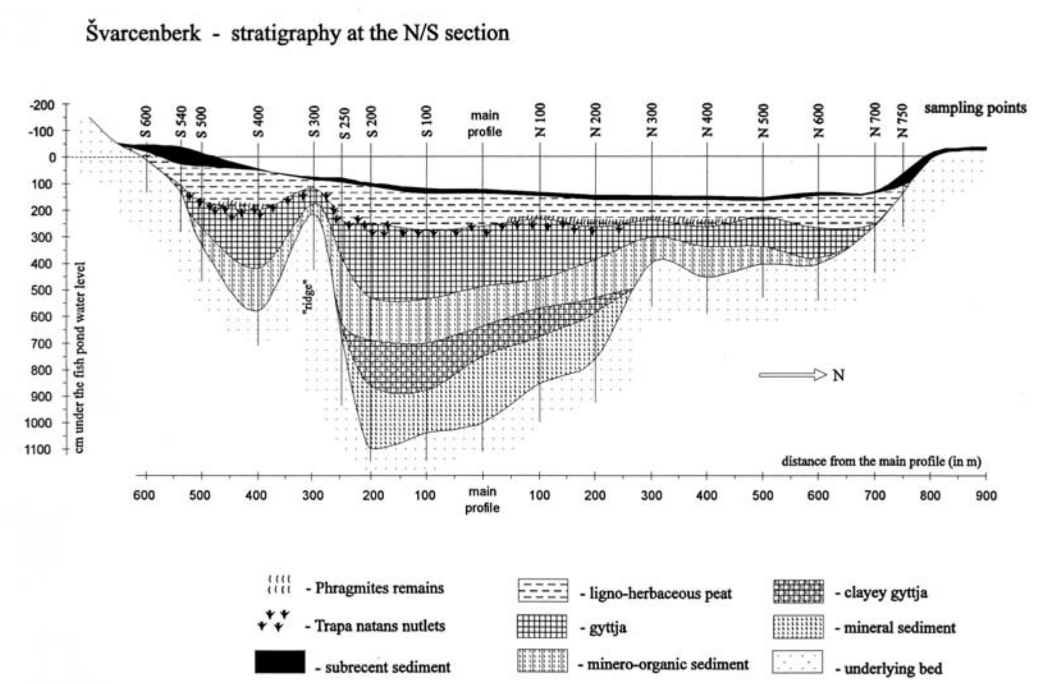
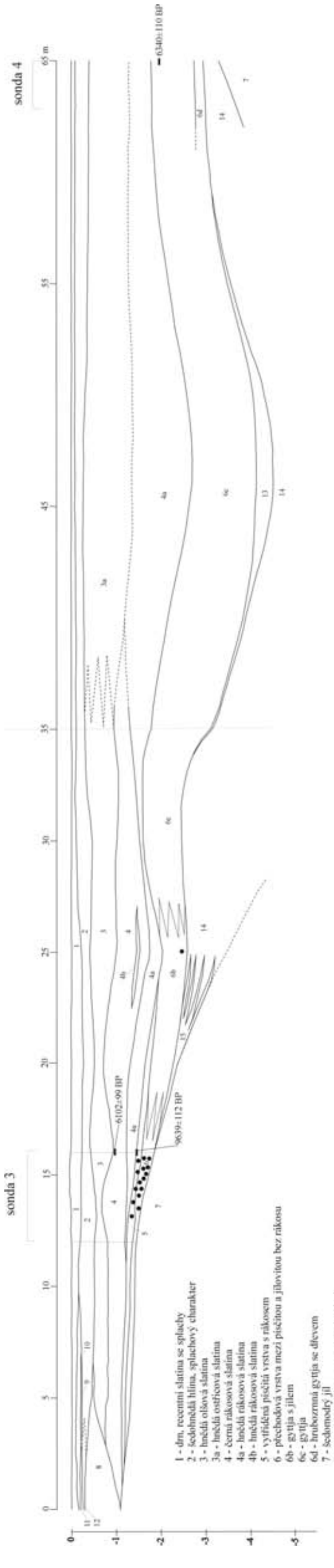
1 Absolutní časové údaje uvádíme pro pozdní glaciál v nekalibrované formě (^{14}C BP) a pro období holocénu ve tvaru kalibrovaném (cal. BC/AD)



Obr. 2: Stratigrafický řez jezerem podél delší osy (řez 1). Vrt 1 je na obrázku označen jako „main profile“
Fig. 2: Stratigraphic section of the lake along the longer axis (section 1). Core 1 is marked on the figure as the “main profile”

důsledky mohlo mít působení artézské vody, tlačící se zespodu do trvale zmrzlého substrátu (v daném případě jílovito-písčitého, tedy měkkého)? Voda v takovém případě tuhne a po čase vytvoří rozměrnou čočku podzemního ledu. Jak čočka narůstá, vytlačuje horninový materiál a celé těleso je na povrchu patrné jako vyklenutý mohutný pahorek. Takové útvary, nesoucí eskymácký název *pingo*, v současných kontinentálních subarktických podmínkách skutečně existují a mohou dosáhnou značných rozměrů, v extrémních případech až osmdesátimetrové výšky (*Washburn 1980*, *Pissart 1988*). Pokud dojde k celkovému klimatickému oteplení, podzemní ledová čočka spolu s permafrostem roztaje a na místě někdejšího *pinga* vznikne jezero charakteristického oválného tvaru. Pánev jezera Švarcenberk je podle všeho útvarem složeným alespoň ze tří takto vzniklých konkávních těles. Na samém dně jezerní pánve jsme ve vrtech nalezli zbytky terestrické vegetace, která zřejmě pokrývala vyklenutý povrch *pinga* ještě v době před jeho kolapsem. V souvislosti s právě popsaným mechanismem vzniku jezera musíme upozornit na jednu nově zjištěnou skutečnost, která naši teorii dále potvrzuje: Na tektonických zlomových liniích v severní části Třeboňské pánve, tedy v podobných geologických situacích, nacházíme více miskovitých sníženin, v nichž se podařilo prokázat jezerní usazeniny. Žádná z dosud prozkoumaných lokalit ovšem nedosahuje rozměrů bývalého jezera Švarcenberk.

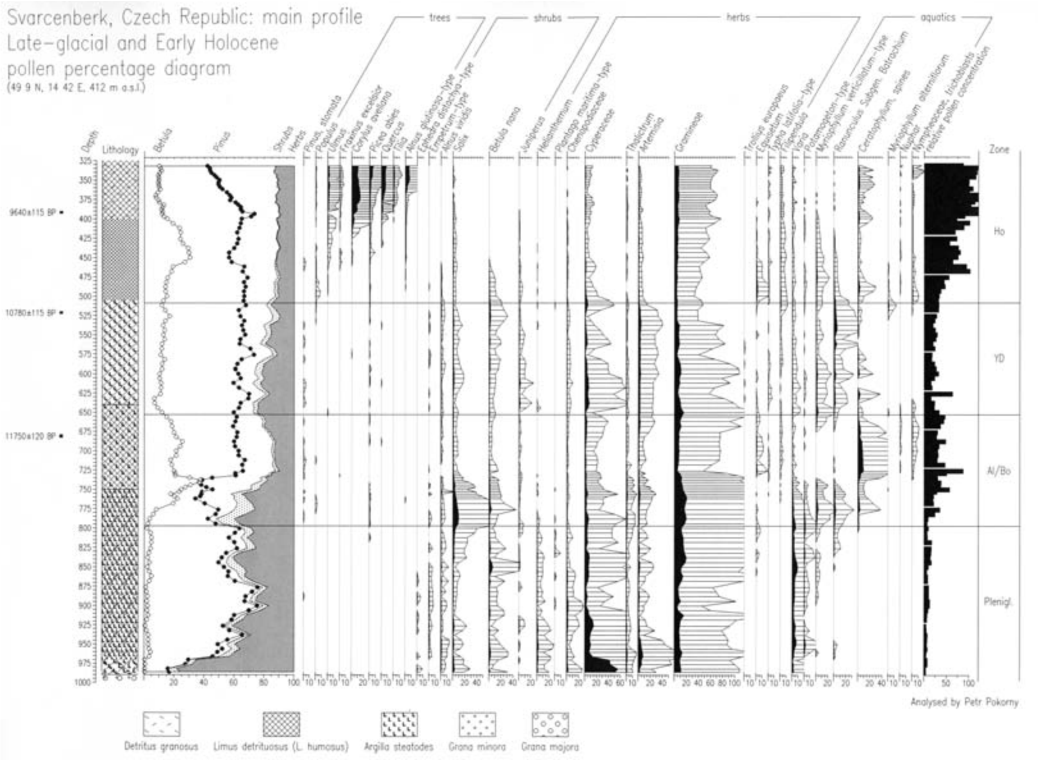
Nyní se ve stručnosti podívejme na historii jezerního biotopu. Hluboké a chladné vody jezera v závěru vrcholného glaciálu umožňovaly život jen nemnoha pionýrským organismům,



Obr. 3: Stratigrafický řez pobřežní zónou jezera (řez 3)
Fig. 3: Stratigraphic section of the bank zone of the lake (section 3)

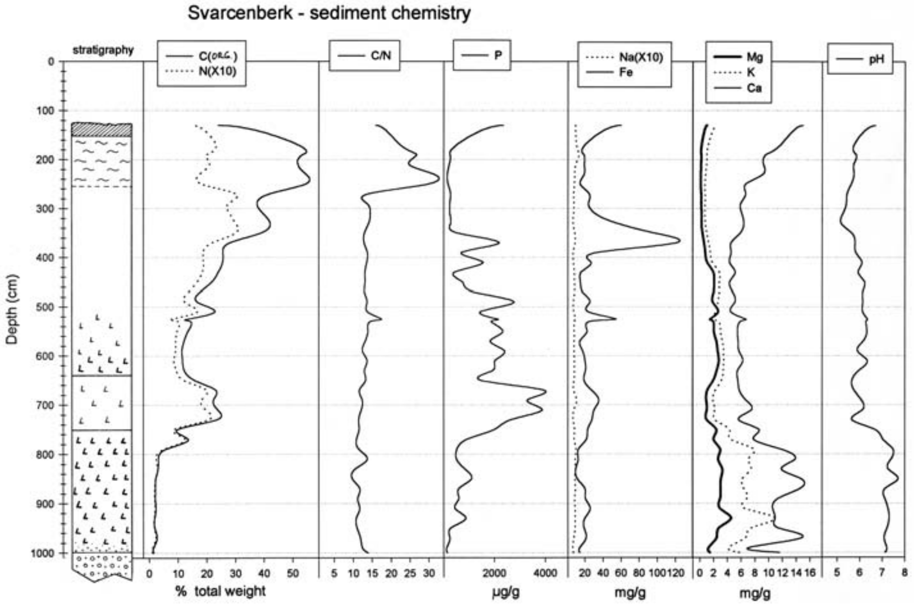
především parožnatkám druhu *Chara strigosa*, rostoucím dnes výhradně ve vysokohorských jezerech a v oblastech kolem polárního kruhu. Jak se postupně oteplovalo, stoupala teplota vody i množství živin v ní rozpuštěných. V hlubších částech jezera začal sedimentovat organický sapropel (*gyttja*). Po prudkém oteplení na počátku pozdně glaciálního interstadiálu (komplex Bölling/Alleröd – 13 000 ^{14}C BP) pokryly hladinu jezera stulíky (*Nuphar lutea, N. pumila*), lekníny (*Nymphaea*) a rdesty (*Potamogeton natans, P. gramineus*). Pod hladinou rostly stolístky (*Myriophyllum spicatum, M. alterniflorum*) a růžkatec ponořený (*Ceratophyllum demersum*). Takové prostředí bylo schopno udržet i první velké populace ryb – v sedimentech nacházíme množství šupin a požerákových zubů okouna (*Perca fluviatilis*). Po dlouhou dobu tvořil okoun jediného zástupce rybí fauny. Teprve v sedimentech datovaných do počátku holocénu se začínají objevovat také zbytky kaprovitých ryb.

Chladná oscilace mladšího dryasu se projevila částečným návratem minerální sedimentace a vymizením teplotně náročnějších rostlinných druhů. Prudké oteplení na počátku holocénu (9250 cal. BC) se na jezeře Švarcenberk projevilo hlubokými změnami celého ekosystému. Rychle vymizely chladnomilné formy řas a vyšších rostlin a byly vystřídány druhy vyžadujícími teploty srovnatelné s dnešními, nebo dokonce ještě mírně vyšší. Hladina jezera zarostla stulíky, lekníny a zejména kotvicí plovoucí (*Trapa natans*). Pod hladinou rostla hustá spleť růžkatců, stolístků a řečanek (*Najas marina, N. minor*). Jezero se od břehů rychle zazemňovalo akumulovanou organickou hmotou. Podél břehů začaly růst orobince a rákos. Tam, kde



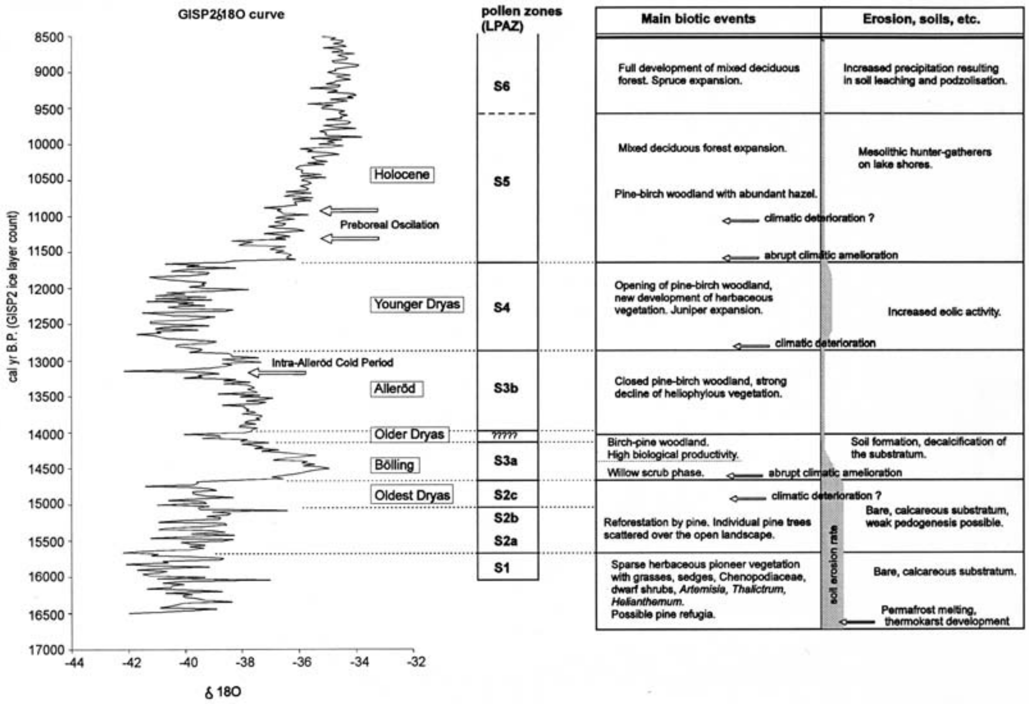
Obr. 4: Pylový diagram profilu ve středu jezerní pánve (vrt 1), spodní část. Diagram zachycuje období pozdního glaciálu a raného holocénu

Fig. 4: Pollen diagram profile in the middle of the lake basin (core 1), lower part. The diagram represents the period of the late glacial and early holocene



Obr. 5: Chemická stratigrafie profilu ve středu jezerní pánve (vrt 1)

Fig. 5: Chemical stratigraphic profile in the middle of the lake basin (core 1)

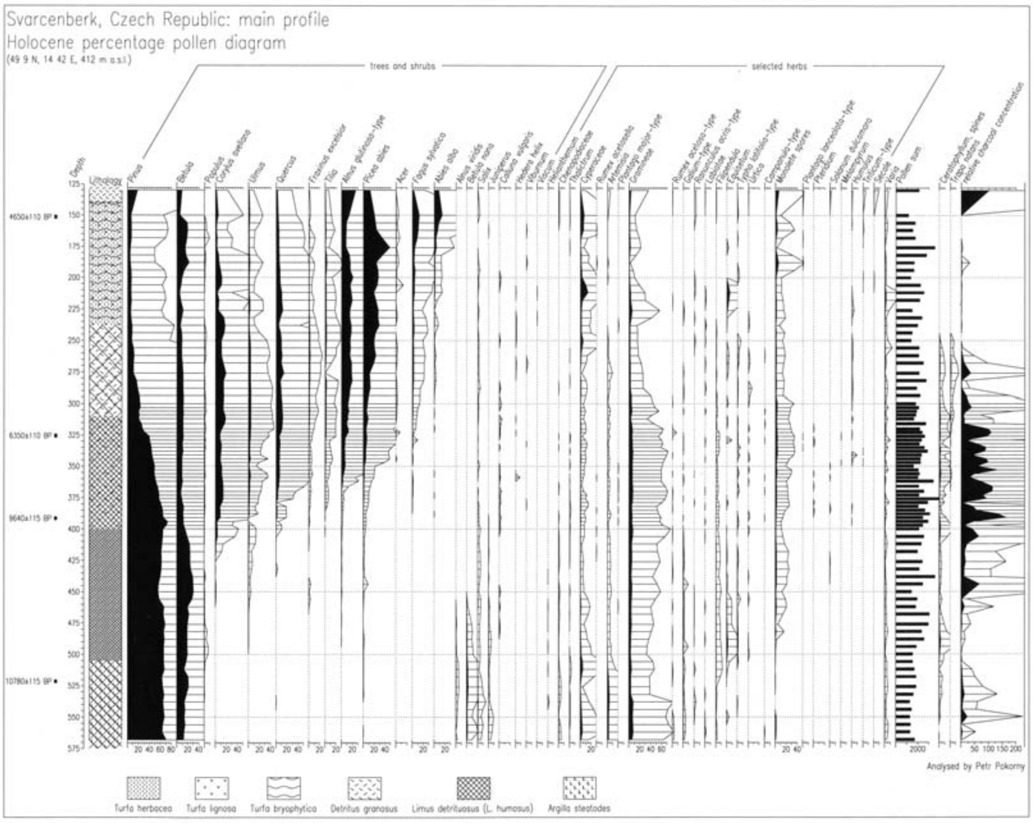


Obr. 6: Korelace biostratigrafického záznamu (LPAZ – lokálních pyloanalytických zón) z profilu ve středu jezerní pánve (vrt 1) se záznamem stabilních izotopů kyslíku v grónském ledovci (vrt GISP)
Fig. 6: Correlation of the biostratigraphic records (LPAZ – local pallenological zones) from the profile in the middle of the lake basin (core 1) with a record of the stable isotopes of oxygen in the Greenland glaciers (core GISP)

vodní hladina již definitivně ustoupila bažinné vegetaci, rostly ostřice a začaly se uchycovat první semenáčky olše lepkavé.

Nejnovější vrty provedené na jaře 2006 v příbřežní zóně na jižním okraji pánve a jejich faciální analýza odhalily významnou regresně-transgresní událost na přelomu pleistocénu a holocénu (*obr. 3*). K oscilaci vodní hladiny muselo dojít v rozsahu asi dvou metrů. Příčinou regrese bylo pravděpodobně ochlazení a klimatické vysušení v mladším dryasu. Následnou transgresi vyvolalo naopak oteplení a nárůst klimatické vlhkosti s nástupem holocénu. Analogie náhlého zvýšení vodní hladiny na počátku holocénu známe z řady jezer ve střední a severní Evropě (souhrnně viz *Harrison – Diggerfeldt 1996*).

V průběhu staršího holocénu pokračoval proces zazemňování vlivem vysoké organické produkce jezerního ekosystému. Před zhruba 5000 lety (cal. BC) zmizely i poslední zbytky volné hladiny a střed bývalého jezera se změnil v rašeliniště. Koberec rašeliníku spolu s dalšími bažinnými rostlinami nenáročnými na živiny (*Scheuchzeria palustris*, *Menyanthes trifoliata*, *Drosera rotundifolia*) začal vytvářet vrstvu rašeliny, která dnes tvoří nadloží jezerních sedimentů. Nejmladší vrstvy rašeliny dochované ve středu pánve pocházejí z období kolem přelomu starého a nového letopočtu. Zbytek souvrství byl zničen v průběhu budování a existence rybníka.



Obr. 7: Pylový diagram profilu ve středu jezerní pánve (vrt 1), horní část. Diagram zachycuje období holocénu
Fig. 7: Pollen diagram profile in the centre of the lake basin (core 1), upper part. The diagram represents the holocene period

Vývoj vegetace v regionu jako důsledek klimatických změn

Jezerní sedimenty jsou mimořádně vhodným objektem k multidiscilinárním výzkumům. Pylová analýza vypovídá o historii vegetace (*obr. 4, 7* a *11*), chemické (*obr. 5*) a sedimentologické analýzy o procesech eroze a tvorby půd v povodí, obsah organických látek a živin zase o celkové produkci ekosystému. Všechny tyto jevy jsou přímo či nepřímo svázány s vývojem klimatu a lze je vzájemně korelovat. Stáří usazenin dochovaných v jezerní pánvi je nezvykle vysoké (na středoevropské poměry) a vysoká byla také rychlost jejich tvorby. Studovaný sedimentární záznam je proto mimořádně podrobný, zvlášť v kombinaci se zvolenou strategií vzorkování po 2 cm. Získané výsledky lze srovnávat se sekvencemi pocházejícími z řady míst západní a severní Evropy (v naší části střední Evropy srovnatelné lokality zatím chybějí), nebo s výsledky rozboru stabilních izotopů kyslíku, například v grónském ledovci (*obr. 6*). Ze srovnání vyplývá, že území Třeboňska bylo postiženo stejnými klimatickými změnami jako oblasti přilehlé Atlantickému oceánu. Pouze chladná oscilace tzv. středního dryasu, málo výrazná i v atlantické oblasti, nebyla v jezerních sedimentech na studované lokalitě zachycena vůbec. Rozdíly jsou i ve způsobu odpovědi živé přírody na prokazatelné klimatické změny. První výraznější oteplení datované do období před 15 000 lety (^{14}C BP) se na charakteru vegetace v západní Evropě nijak znatelně nepodepsalo – stále tam převládají otevřené stepní a tundrové formace. Na Třeboňsku byla situace poněkud odlišná: Oteplení mělo za následek první šíření lesa, i když zatím jen v podobě rozvolněných borových porostů typu řídké tajgy. Příčinou rozdílné odpovědi místní vegetace na klimatické oteplení byla lokální přítomnost refugií borovice, která se po zlepšení podmínek mohla okamžitě šířit.

Jakmile odezněla následující chladná perioda (nejstarší dryas; DR1), přichází nové, již opravdu výrazné oteplení, charakterizované po celé střední Evropě nástupem borobřezové tajgy. Tak je tomu i na Třeboňsku. Rozvoj zapojeného lesa má spolu se zvlhčením klimatu za následek ústup dřívějších otevřených formací trav, pelyňků (*Artemisia*), merlíkovitých (*Chenopodiaceae*), keříčkových vrb (*Salix*), trpasličí břízy (*Betula nana*), olše zelené (*Alnus viridis*), jalovce (*Juniperus*), chvojníků (*Ephedra*) a rakytníku (*Hippopha(rhamnoides*), tedy vesměs zástupců druhově bohaté stepní a tundrové vegetace. Zatímco předešlé období můžeme charakterizovat převahou surového, vápnitého a solemi bohatého substrátu, začíná spolu se šířením tajgových porostů tvorba půd. Jejich pokračující vývoj v pozdně glaciálním interstadiálu měl za následek postupnou změnu chemismu prostředí do té podoby, jakou známe z Třeboňska dnes – začaly vznikat vyloužené, kyselé a na živiny chudé půdy. Ve zkoumaných jezerních sedimentech se tato změna projevuje náhlým poklesem obsahu kationtů (zvláště *Ca*, *K* a *Mg*; *obr. 5*).

Částečný ústup lesa, návrat otevřených formací (tentokrát doprovázených zvlášť hojným jalovcem) a náhlé zvýšení eroze v povodí jezera v době 11 300 ^{14}C BP je zřetelným důsledkem nového klimatického ochlazení. Výrazná chladná oscilace mladšího dryasu (DR3) zasáhla celou Evropu, a je dokonce pravděpodobné, že měla globální charakter (*Peteet 1995*). Nastupující drsné klima mělo za následek odumírání části borobřezových porostů. Mrtvá dřevní hmota byla náchylná k požárům (*Hoek 1997*). Ty se zřejmě nevyhnuly ani Třeboňsku, jak ukazuje výzkum Pískového přesypu u Vlkova (*Pokorný – Růžičková 2000*). Požárová vrstva dochovaná pod souvrstvím vátých písků byla radiokarbonově datována do doby před 11 260 lety (^{14}C BP).

Po oteplení na počátku holocénu pozorujeme v pylových diagramech (*obr. 4* a *7*) vegetační sukcesi, rámcově analogickou všem středoevropským územím s odpovídající nadmořskou výškou. Začíná prudkou expanzí borovice a břízy a pokračuje postupnou imigrací a šířením dřevin smíšených doubrav. Vzhledem ke zvláštnostem půdních poměrů na Třeboňsku si ovšem borovice stále udržuje významnou roli. Není vyloučeno, že přirozenou sukcesi lesního ekosystému v lokálním měřítku blokovala i činnost člověka (*Kuneš et al.*, v tisku).

Poznatky získané nejnovějším archeologickým výzkumem

V roce 2005 se v návaznosti na výše popsané paleoekologické výzkumy a první archeologické nálezy rozeběhl také sídelně geografický průzkum mezolitického osídlení v okolí jezera, který navázal na rozsahem spíše drobné sběry I. Pavlů v roce 1986 a S. Vencla v roce 2000. V této fázi jsme se zaměřili na ověřování platnosti základních východisek pro budoucí intenzivnější výzkum. Soustředili jsme se na zjištění hustoty osídlení, která se na základě poměrně výrazné indikace v environmentálním záznamu zdá značná. Pomocí povrchových sběrů jsme postupně objevili devět lokalit v jihovýchodním segmentu příbřežní zóny jezera (lokality 1–8 a 10; *obr. 1*). Získali jsme tak zatím sice nepočetné, ale rámcově dobře datovatelné kolekce (mezolit, prozatím bez mikrolitů, které se sběry obtížně zjišťují). Na protáhlé vyvýšenině

typ	jaspis	jaspis červený	křemen	křemenec typu Skršín	křišťál	neurčeno	opál	pazourek	celkem	%
amorfní zlomek		3	5		5	3	5		21	*46,7*
čepel	1	1				3			5	*11,1*
jádro				1		1			2	*4,4*
retušovaná čepel z hrany jádra								1	1	*2,2*
škrabadlo dvojité		1							1	*2,2*
trapéz						1			1	*2,2*
úštěp		7	4			1	1	1	14	*31,1*
celkem	1	12	9	1	5	9	6	2	45	*100*
%	*2,2*	26,7	*20*	*2,2*	11,1	20	13,3	4,4	100	

Tab. 1: Švarcenberk, lokalita 7. Typologické a surovinové složení kolekce ze sondy 1/05
Tab. 1: Švarcenberk, site 7. Typological and raw material composition of the collection from sondage 1/05

těsně při břehu bývalého jezera jsme objevili lokalitu 7. Tato poloha není zasažena orbou, avšak byla mezi lety 2004 a 2005 vážně narušena divokou těžbou písku. Vyvýšenina je tvořena zrnitostně nevytříděným pískovým sedimentem a představuje pravděpodobný relikt okrajového valu vzniklého po kolapsu *pinga* jako zbytek horninového materiálu erodovaného z jeho povrchu. Lokalita byla objevena ve stěně malého písečníku díky přítomnosti výrazného zahloubeného objektu. Objekt byl prozkoumán malou sondou na ploše 1,2x0,5 metru, ve které bylo získáno 45 štípaných artefaktů (hustota 75 kusů na metr čtvereční). Největší část kolekce tvoří amorfní zlomky a úštěpy (*tab. 1*). Méně je čepelí a jader. Nástroje jsou doloženy pouze třemi artefakty – retušovanou čepelí, dvojitým škrabadlem a trapézem. Dominantní surovinou je červenavý jaspis, křemen, opál a křišťál, vše patrně jihočeské suroviny. Vedle nich se vyskytují i dálkové importy ze severu (pazourek a křemenec typu Skršín). Vedle kamenné industrie byly získány i dva fragmenty tuhové keramiky z povrchové vrstvy.

Na první zjišťovací sondáž navázala na podzim téhož roku další sonda na ploše 1x9 m (velikost základního dokumentačního čtverce je 0,5x0,5 m). Sonda byla provedena metodikou základního výzkumu, která umožňuje získání maximálního množství informací. Veškerý materiál byl důsledně plaven na sítech. Objekty byly dokumentovány po mechanických úrovních v jednotlivých horizontálních a následně i vertikálních řezech. Celkem jsme prozkoumali tři mechanické vrstvy (po 10 cm), další nemohly být zkoumány kvůli momentálně vysoké hladině spodní vody (dokončení bude následovat v příští vhodné sezoně). Na řezech jsme zdokumentovali celkem šest objektů. Jeden se zahluboval shora do půdní vrstvy a výrazně se odlišoval charakterem výplně (objekt 1 – *obr. 8*). Na základě nálezu tuhované keramiky datujeme tento objekt do středověku až raného novověku. Ostatní

profil, stratigrafická pozice	***Lab. No.***	***metoda***	***druh materiálu***	***naměřené ¹⁴C datum***
vrt 1, 150-153 cm	LuA-4588	AMS	dřevo olše	4650 ± 100 BP
vrt 1, 324-327 cm	LuA-4589	AMS	oříšek kotvice	6 350 ± 100 BP
vrt 1, 390-393 cm	LuA-4590	AMS	dřevo borovice	9 640 ± 115 BP
vrt 1, 520-523 cm	LuA-4591	AMS	gyttja	10 780 ± 115 BP
vrt 1, 680-683 cm	LuA-4738	AMS	gyttja	11 750 ± 120 BP
sonda 3, 64 cm	Crl-6090	konvenční	borová kůra	6102 ± 99 BP
sonda 3, 85-87 cm	Crl-6093	konvenční	dřevo borovice	9639 ± 112 BP
sonda 3, 85-92 cm	Poz-16752	AMS	fragment ratiště šípu	9500 ± 50 BP
sonda 3, 92-100 cm	Poz-16753	AMS	lískový oříšek	9280 ± 50 BP
sonda 4: 200 cm	LuA-4297	AMS	oříšek kotvice	6 340 ± 110 BP
Vlkovský přesyp, 210 cm	LuA-4645	AMS	uhlíky borovice	11 260 ± 120 BP

Tab. 2: Přehled radiokarbonových dat použitých v článku
Tab. 2: Overview of the radiocarbon dates used in the article

objekty vykazovaly tmavě hnědou písčitou výplň a obsahovaly pouze kamennou industrii (*obr. 9*), stejně jako objekt prozkoumaný první sondou. Vznik těchto objektů dáváme do souvislosti s mezolitickým osídlením, jejich účel však neznáme.[2] Ze sondy 2 pochází celkem 195 kusů industrie (hustota 21,7 artefaktu na metr čtvereční). Její výskyt je vázán především na úroveň pohřbené půdní vrstvy a výplně objektů. Při výzkumu jsme získali také 14 fragmentů tuhované keramiky (středověk – raný novověk), jejichž výskyt je vázán pouze na úroveň půdní vrstvy a objekt 1. Dominantní složkou nalezené industrie jsou amorfní zlomky (109 kusů; 55,9 %). Následují úštěpy (51 artefaktů; 26,2 %), čepele (23 artefaktů; 11,8 %) a jádra (2 artefakty; 1 %). Nástrojů je v kolekci doloženo 10 (4 trojúhelníky, 3 škrabadla, 2 rydla a 1 čepel s laterální retuší; 5,1 %). Zajímavý je větší výskyt opálené industrie ve čtvercích CH a I. Pro vyhodnocení planigrafie bylo zatím získáno málo dat, příslušné závěry budeme moci formulovat až po prozkoumání větší plochy lokality.

Prozatím poslední fáze zjišťovacího výzkumu proběhla na jaře roku 2006. Tentokrát jsme se zaměřili na nejméně porušený jižní úsek pobřeží bývalého jezera. Hlavním cílem bylo ověření archeologického potenciálu vlhkých břehových partií a odběr profilu pro

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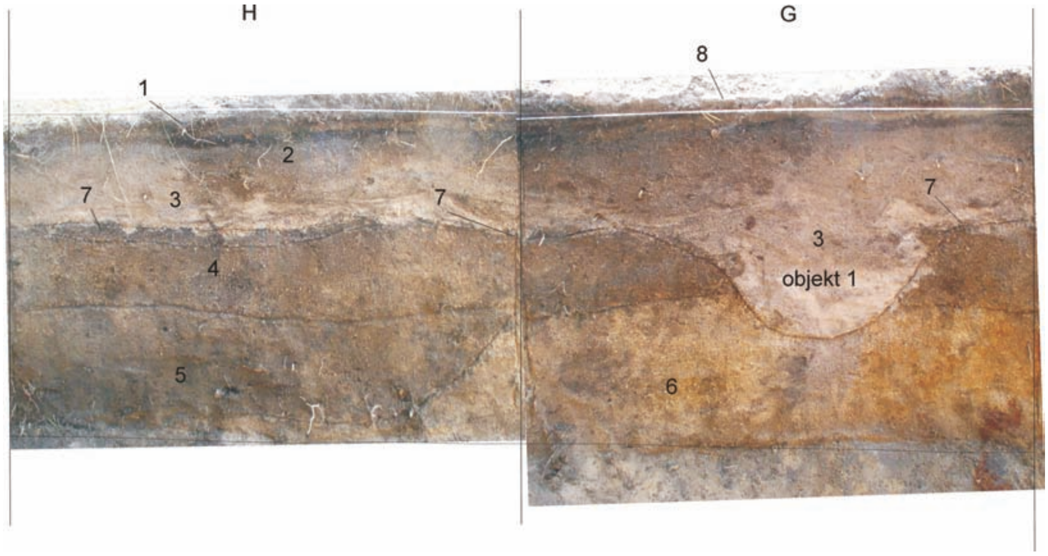
[2] Analogie můžeme nalézt například v Tašovicích (*Prošek 1951*), popřípadě na některých polských lokalitách (Wojnowo 2, Tanowo 3, Wierzchowo 6, Kobusiewicz 1999, 39, 97–8, 100; Bukówna 5, Masojć 2004, 38). Podobné situace mezolitického stáří známe rovněž přímo z jižních Čech z Putimi (*Mazálek 1951; Vencl 2004, Vencl et al. 2006*), Blanice 6, Dolního Poříčí 2 a Strakonic 6b (*Vencl et al. 2006*). Jsou to opět do podloží zahloubené jamky a jámy se štípanými artefakty, jádry, uhlíky a v jednom případě (Dolní Poříčí 2) s vypálenými hrudkami okrového barviva (v podobě limonitického slídnatého pískovce) a se zuhlenatělými kostmi



Obr. 8: Fotografický plán řezu v sondě 2 – jižní profil ve čtvercích G a H.
Fig. 8: Photographic plan of the section in sondage 2 – southern profile in squares G and H.

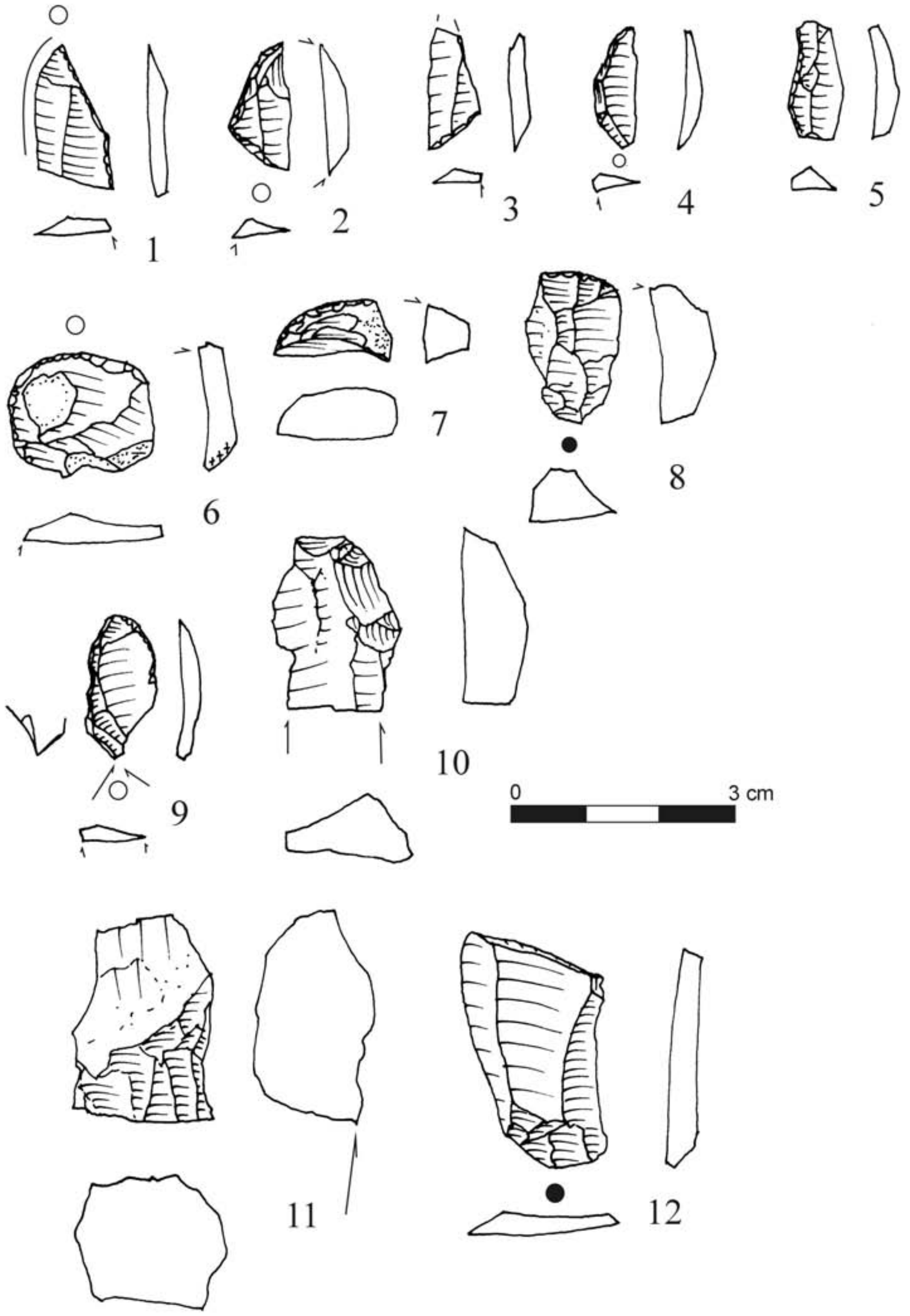
Obr. 10: Foto z výzkumu litorálních partií jezera – sonda 3 (vlevo)
Fig. 10: Photo from the excavation of the littoral area of the lake – sondage 3 (left)
Obr. 12: Detail fragmentů ratiště šípu nalezených v SZ sektoru sondy 3 v pozici 85–92 cm. Nález je radiokarbonově datován 9500±50 BP (po kalibraci mezi 9130 BC a 8630 BC na 95% hladině pravděpodobnosti). Na lomech jsou patrné paralelně orientované letokruhy. Ratiště bylo vyrobeno z většího kusu borového dřeva, pravděpodobně soustružením (vpravo)
Fig. 12: Detail of the fragments of the arrow shaft found in the NW sector of sondage 3 at a position of 85–92 cm. The find has been radiocarbon dated to 9500±50 BP (after calibration between 9130 BC and 8630 BC at a 95% level of probability). There are clearly parallel orientated growth rings in the breaks. The shaft was manufactured from a larger piece of pinewood, probably with a lathe (right)

paleoekologické analýzy. Vrtnou sondáží byl proveden řez od břehu směrem do středu zazemněné jezerní zátoky (*obr. 3*). Na základě faciální analýzy jsme zjistili, že na samém počátku holocénu došlo k transgresi jezera do pobřežní zóny vlivem zvýšení vodní hladiny.

Tato událost se projevuje přítomností inverzní stratigrafie, kdy telmatická fáze vývoje stratigraficky (a tedy i časově) předchází fázi limnické. Takové zjištění skýtá výraznou naději, že mohlo dojít k zatopení některých archeologických situací mezolitického stáří (případně i stáří pozdně paleolitického), a tím k zakonzervování organických materiálů.

Zjišťovací sonda o rozměru 2x4 m (sonda 3; *obr. 10*) zachycuje ve své spodní části pobřežní facii z doby po transgresi vodní hladiny. Toto organické souvrství s jílem a pískem se ukázalo být bohaté na pylová zrna (viz pylový diagram na *obr. 11*) a rostlinné makrozbytky, včetně čerstvého dřeva a velkých kusů uhlíků. Z množství nalezených fragmentů dřev nese 14 nálezů jasné stopy opracování (*obr. 12* a *13*). V některých případech známe jejich pravděpodobnou funkci (ratiště šípu a pravděpodobný jeho polotovar), v jiných případech je funkce zatím nejasná. Fragment ratiště se podařilo radiokarbonově datovat (nedestruktivním způsobem metodou AMS; Poznań Radiocarbon Laboratory, Polsko). Výsledné datum je 9500±50 BP, po kalibraci mezi 9130 BC a 8630 BC (na 95% hladině pravděpodobnosti). Další nalezená dřeva nenesou stopy opracování, jsou však často opálená, a to buďto na celém povrchu, nebo na jednom konci. Pylová analýza prokázala v příslušné části souvrství přítomnost řady bylinných druhů hodnocených jako sekundární antropogenní indikátory. Rovněž některé nálezy rostlinných makrozbytků z této vrstvy – skořápky lískového ořechu a semen maliníku – jsou v jezerních usazeninách překvapivé, protože se jedná o druhy rostoucí na sušších místech. Interpretace je nasnadě: Jedná se zřejmě o zbytky sbíraných potravin. Polovina lískového ořechu nalezená ve vrstvě 92–100 cm byla radiokarbonově datována 9280±50 BP. Po kalibraci vychází rozpětí kalendářního stáří mezi 8640 a 8320 BC (95% pravděpodobnost). Nález považujeme za mimořádný vzhledem ke zjištěnému stáří. Na samém počátku holocénu se líska ve střední Evropě vyskytovala jen sporadicky. Nalezený lískový ořech v kontextu jezerních sedimentů s artefakty tak může být předběžně považován za nepřímý důkaz šíření této dřeviny člověkem. Pylový diagram z místa nálezu (ze sondy 3) ukazuje pro příslušnou dobu pouze ojedinělý výskyt lísky v regionu. Její pylová křivka prudce narůstá až značně později. Na druhou stranu pylová křivka lísky ve vrtu v centru jezera (vrt 1; *obr. 4*) narůstá již dříve. Vzhledem k faktu, že záznam z centra velkého jezera odráží pylový spad více regionálního charakteru, dá se výskyt lísky v širším okolí lokality předpokládat již pro tuto velmi ranou dobu. Vyplývá to také ze srovnání s jinými pyloanalyticky zpracovanými lokalitami, z nichž některé leží i na Třeboňsku (tato analýza je obsahem připravovaného článku *Kuneše et al.*, in prep.). Je možné, že člověk přispíval k šíření lísky donášením sklizených plodů z větších vzdáleností (při sezonním pohybu lovecko-sběračských skupin), rozvolňováním korunového zápoje lesa a není vyloučeno, že i záměrným managementem, což zatím zůstává pouze v rovině hypotézy.

Vrstva rákosové slatiny v nadloží výše popsaného souvrství vznikla až po zazemnění pobřežní zóny, a to zhruba v rozmezí let 9000 a 5000 cal. BC (na základě radiokarbonového datování – viz *obr. 11*). Černé zbarvení horní části této vrstvy je důsledkem přítomnosti velkého množství mikroskopických uhlíků. Podle mikromorfologie uhlíkových partikulí je jejich menší část původem ze spáleného dřeva, větší část pochází z travin. Ve stejné době zřejmě docházelo k požárům pobřežního rákosového porostu, a to opět pod pravděpodobným vlivem člověka (záměrné vypalování?). Pokračuje zde totiž (dokonce se zvyšuje) indikace přítomnosti osídlení v podobě antropogenních pylových indikátorů (*Artemisia*, Chenopodiaceae, Compositae Subfam. Cichorioideae, *Melampyrum*, *Plantago lanceolata*, Rubiaceae, *Solanum dulcamara*)



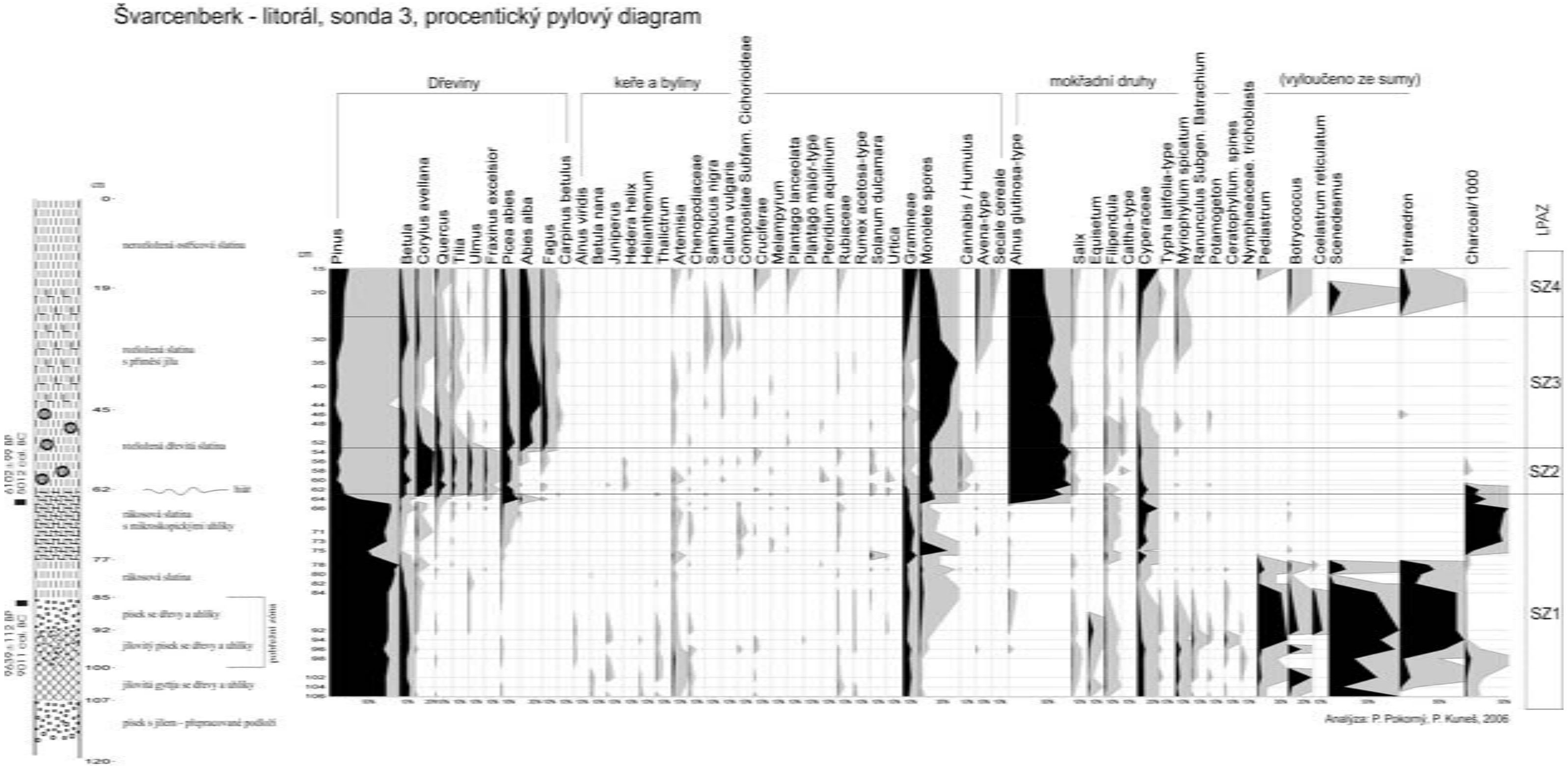
Obr. 9: Výběr industrie ze sondy 2/05. Legenda: 1–3 – trojúhelníky, 4 – segment, 5 – laterálně retušovaná čepel, 6–8 – škrabadla, 9–10 – rydla, 11 – jádro, 12 – čepel
Fig. 9: Selection of the industries from sondage 2/05. Caption: 1 –3 – triangles, 4 – segment, 5 – laterally retouched blade, 6–8 – scrapers, 9–10 – burins, 11 – core, 12 – blade

Další poznatky o mezolitickém osídlení lokality získané paleoekologickým výzkumem – jeho vliv na vegetaci a problém chronologie

Neustále přibývá důkazů o tom, že lovecko-sběračské populace pozdního paleolitu a mezolitu využívaly přírodní prostředí v okolí sídlišť natolik intenzivně, že můžeme toto působení zachytit paleoekologickými metodami, například v pyloanalytických profilech. Významné studie na tomto poli pocházejí z Britských ostrovů (*Simmons – Chambers 1993*; *Macklin et al. 2000*; *Innes – Blackford 2003*), ze Skandinávie (*Hicks 1993*; *Regnell et al. 1995*; *Vuorela 1995*; *Hornberg et al. 2006*), západní Evropy (*Bos – Janssen 1996*; *Behling – Street 1999*; *Bos – Urz 2003*; *Bos et al. 2006*) a z Polska (*Wacnik 2005*). Sedimentární záznam z jezera Švarcenberk je prvním dokladem tohoto druhu na našem území. V sedimentech datovaných do starší poloviny holocénu jsou někdy i pouhým okem patrné vrstvy s vysokým obsahem mikroskopických uhlíkových částic. Jejich kontinuální výskyt (viz příslušnou křivku v pravé části pylových diagramů, *obr. 7* a *11*) indikuje buďto přímo sídelní aktivity (v případě, že uhlíky pocházejí z ohnišť), nebo vypalování lesní či pobřežní vegetace v okolí. Často lze vzájemně odlišit mikroskopické uhlíky pocházející ze dřeva od uhlíků původem z bylin (například z rákosin). Ve studovaném materiálu z jezerních sedimentů jsou pravidelně přítomny obě kategorie nálezů. S přítomností mikroskopických uhlíkových partikulí koreluje zvýšený výskyt pylových zrn některých antropogenních indikátorů. Jedná se o rostliny preferující otevřená travnatá stanoviště (*Thalictrum*, *Rumex acetosella*, *Melampyrum*, *Plantago lanceolata*, Gramineae) a druhy expandující na požárem zasažených plochách (*Pteridium aquilinum, Calluna vulgaris*). Výskyt některých vodních a pobřežních rostlin (*Ceratophyllum*, *Typha latifolia*), případně rostlin vlhkých, dusíkem bohatých stanovišť (*Solanum dulcamara*, *Urtica*) ve stejném období může souviset s eutrofizací, tzn. se zvýšením přísunu živin do jezera a jeho pobřežní zóny. Nálezy některých taxonů (*Artemisia*, Chenopodiaceae, *Plantago major*-typ) lze hodnotit jako důkaz přítomnosti ruderálních stanovišť na sídlištích.

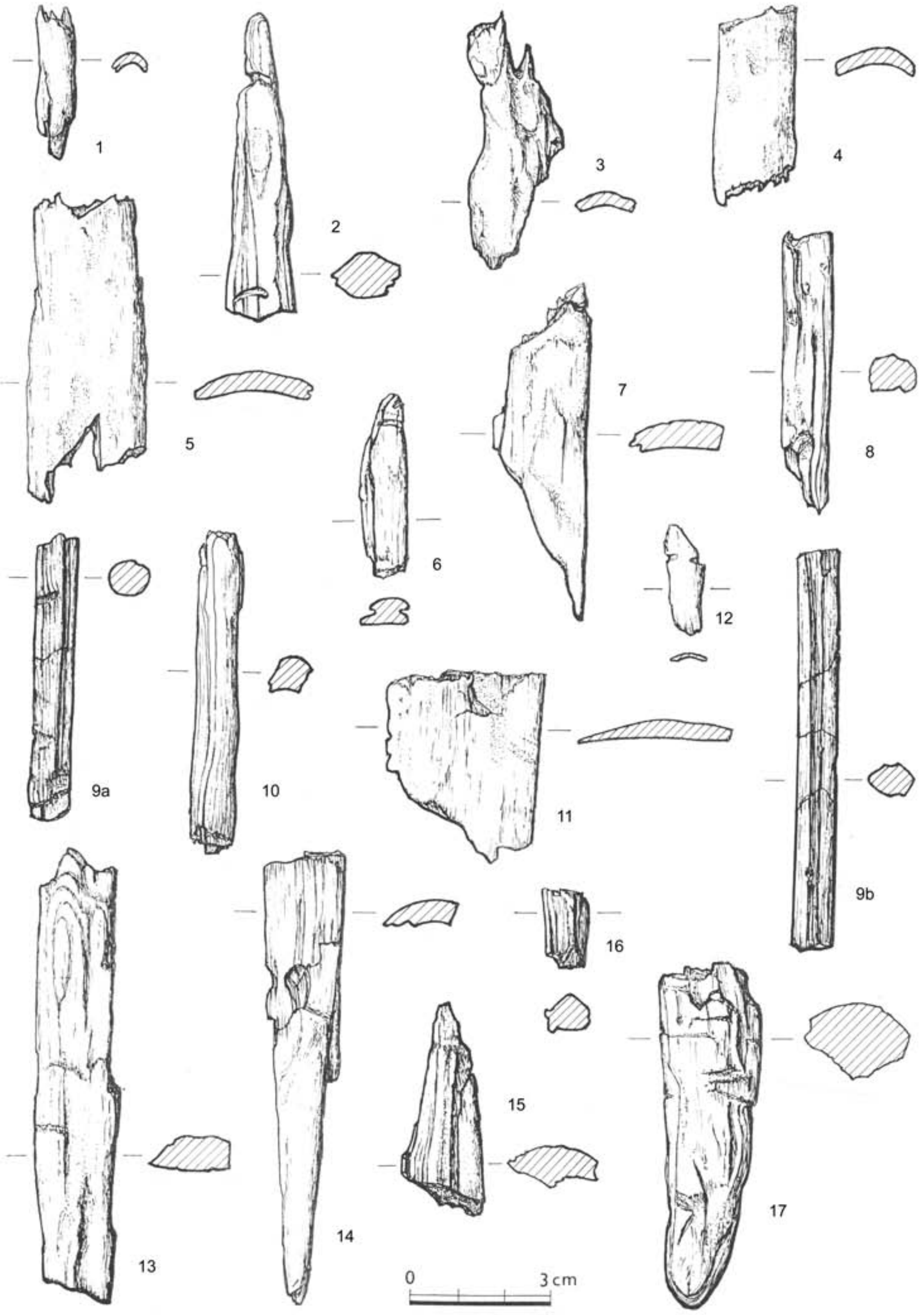
V souvislosti s mezolitickým osídlením není bez zajímavosti výskyt kotvice plovoucí (*Trapa natans*) na studované lokalitě. Ta se v podobě hojných makrozbytků (plodů) a pylových zrn dochovala v jezerních sedimentech. Kotvice je vzplývavá vodní rostlina, jejíž škrobnaté oříšky tvořily významnou součást jídelníčku mezolitického člověka (*Vuorela – Aalto 1982*, *Zvelebil 1994*). Nejstarší nálezy oříšků kotvice v sedimentech jezera Švarcenberk se datují do samého počátku holocénu. Překvapivě časný výskyt této teplomilné rostliny je nejen důkazem příznivého klimatu v příslušné době, ale navíc vyvolává podezření z její záměrné introdukce. Jedná se tedy o podobný případ jako výše popsaný nález lískového ořechu. Zajímavý je rovněž velmi časný výskyt pylových zrn obilovin v pylovém diagramu z centrálního profilu (*Triticum*-typ; *obr. 7*), radiokarbonově datovaný mezi 9050 a 8400 cal. BC. Nálezy tohoto typu nejsou v rámci střední a západní Evropy ojedinělé a někdy bývají interpretovány jako doklad předneolitické domestikace domácích druhů trav (*Zvelebil 1994*, *Regnell et al. 1995*). My se však spíše přikláníme ke střízlivějšímu názoru, který považuje podobné nálezy za výsledek polyploidizace divokých trav, a to buďto spontánní, nebo člověkem jen nepřímo vyvolané rozšiřováním kulturního bezlesí (čímž mohlo docházet k přirozené selekci vitálnějších polyploidů pod vlivem konkurence v porostu).

Na základě indikace v pylových diagramech lze zařadit začátek lidského vlivu na vegetaci v okolí jezera Švarcenberk do samého počátku holocénu (okolo 9200 cal. BC). To ovšem neznamená, že by osídlení nebylo ve starším období přítomno. Pyloanalytická indikace v průběhu pozdního glaciálu je jednoduše nemožná vzhledem k tomu, že části krajiny byly



Obr. 11: Pylový diagram profilu v severozápadním rohu sondy 3. Uvedená kalibrovaná radiokarbonová data jsou střední hodnotou intervalu na hladině pravděpodobnosti 95 %

Fig. 11: Pollen diagram in the north-western corner of sondage 3. The listed calibrated radiocarbon data are a medium value interval at a level of probability of 95%



Obr. 13: Dřevěné artefakty nalezené ve spodní části sondy 3. Všechny nálezy jsou asociovány s organicko-písčitou facií mezi 85 a 107 cm. Fragmenty předmětů byly vyplaveny na pobřeží jezera buďto z volné hladiny, nebo z kulturních vrstev zatopených po transgresi jezera.
Fig. 13: Wooden artefacts found in the lower part of sondage 3. All finds are associated with an organic-sandy facies of between 85 and 107 cm. Fragments of objects were washed up onto the bank of the lake either from the open surface or from culture layers that were submerged after transgressions of the lake

tehdy přirozeně bezlesé a byla v ní přítomna stanoviště s přirozeným výskytem druhů, označovaných v holocenním kontextu za antropogenní indikátory. Pouze budoucí archeologický výzkum, resp. radiokarbonová data získaná jeho prostřednictvím, může přinést důkazy o přítomnosti nebo nepřítomnosti pozdně paleolitického osídlení a o jeho kontinuitě s osídlením mezolitickým. Indikace lidského vlivu končí v centrálním i litorálním profilu ve středním holocénu, a to těsně kolem data 5000 cal. BC. Tehdy došlo k definitivnímu zániku vodní plochy přirozeným zazemněním jezera. To mohlo být bezprostřední příčinou opuštění lokality, protože lovecko-sběračské komunity tím definitivně ztratily možnost rybolovu, lovu vodních ptáků i sběru vodních rostlin.

Přinejmenším překvapivé je poměrně pozdní datum konce kontinuálního osídlení, zatím indikovaného pouze nepřímo v jezerních sedimentech. Na základě radiokarbonového datování paleoenvironmentálního záznamu získáváme datum těsně okolo 5000 cal. BC, které z chronologického hlediska spadá již hluboko do období neolitu rozvinutého v příznivějších oblastech. Třeboňská pánev s kyselými a zamokřenými půdami byla zcela nevhodná pro zemědělské osídlení, a tak není vyloučeno, že zde lovecko-sběračské populace přetrvávaly ještě dlouho po rozšíření zemědělského způsobu života v úrodných nížinách. To velmi dobře odpovídá představě o dlouhém přežívání mezolitiků v periferních oblastech Čech, jak ji formuloval S. Vencl (*Vencl et al. 2006*, 412, 439). Zhruba od data 5000 cal. BC je v pylovém záznamu patrný dočasný hiát v osídlení, a to až do období okolo 3800 cal. BC, kdy se začínají objevovat indikátory zemědělské aktivity v podobě pylových zrn obilovin. Archeologicky je přítomnost mladoneolitických populací v blízkém okolí námi sledovaného území naznačena keramikou lengyelské kultury i několika kamennými artefakty z nedaleké pískovny u Vlkova (*Beneš 1976*, 16, 21).

Právě popsanou chronologii osídlení lokality je nutno považovat za zatím předběžnou. Problematickou zůstává zejména otázka absolutního datování. To je prozatím založeno na poměrně malém množství radiokarbonových dat. Indikace osídlení v pylových profilech je sice poměrně silná, nicméně stále ještě v rovině nepřímých důkazů. Za této situace nezbývá než doufat, že budoucí archeologický výzkum přinese pádnější argumenty pro zatím předběžná zjištění.

Závěr

Výzkum mezolitického areálu v okolí bývalého jezera Švarcenberk představuje šanci zachytit toto osídlení v mimořádné šíři aspektů. Je to možné díky dochování organických artefaktů v jezerním a bažinném prostředí v kombinaci s neporušenými sídlištními situacemi na suchých vyvýšených místech podél pobřeží. Dosavadní stav výzkumu prozatím dovoluje vznést řadu zajímavých otázek, jejichž řešení nás teprve čeká. V současné době před námi stojí řada důležitých dílčích úkolů. Do budoucna je především nutné zajistit účinnou ochranu příbřežních sedimentů bývalého jezera, potenciálně ohrožených hospodářskými aktivitami (děje se tak ve spolupráci se správou ochrany přírody CHKO Třeboňsko) a nalézt dostatečné finanční prostředky i odborné kontakty pro další výzkum této unikátní lokality.

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Summary:

The discovery of the extinct Lake Švarcenberk dates to the beginning of 1970s, when *V. Jankovská* discovered lake sediments under a layer of peat in the flood zone of the present-day lake (*Jankovská 1976, 1980*). In the mid 1990s we followed up this discovery with extensive stratigraphic investigations. Investigations showed that we were dealing with a natural lake of significant size and that in the middle of the basin a massive sequence of lake sediments of an unexpectedly high age had been preserved. Two litoral profiles and a central profile were gradually processed using the methods of pollen analysis, the analysis of algae remains and macro-remains analysis with the aim of describing the progress of the silting up of the lake basin and the long-term vegetational succession connected with it (*Pokorný – Jankovská 2000*). The chronology of the sediment record is based on radiocarbon dates, on indirectly dated traces containing rubidia (for this newly developed method see *Veselý et al. 2006*, in print) and on relative palynostratigraphic dating. The central profile, whose lower 5 metres formed during the late glacial period, was used for the reconstruction of the vegetational development and geochemical changes in the basin of the lake in connection with the severe climatic changes at the turn of the pleistocene and holocene (*Pokorný 2001*, *2002*). Sedimentological research verified the presence of eolithic elements in the lake layers. It was possible to clearly correlate traces of eolithic activities in the lake sediments with the formation of blown sand dunes in adjoining parts of the Lužnice levels and explain them as a reaction to the climatic deterioration, which took place at the beginning of the latter dryas (*Pokorný – Růžičková 2000*). The palaeoeclogical potential of this exceptional site has not by far been exhausted by the above-mentioned research. The remains of fish fauna and other aquatic organisms have been preserved in the sediments for example and they can be used to reconstruct changes in the local environment and for the study of climatic changes of a regional to global character. The remains of diatoms (*Bešta 2004*) and aquatic crustaceans for example have been gradually processed (Cladocera – *K. Nováková*, unpublished).

The circumstances of the discovery of the Mesolithic settlement on the banks of the former Lake Švarcenberk are interesting. Up till now we had only known of individual finds of a chipped stone industry of clearly pre-Neolithic date from the immediate surrounding area (in summary form see *Vencl et al. 2006*, *Pavlů 1992*). If we leave aside these individual finds extensive Mesolithic settlement was only indirectly substantiated on the basis of the presence of pollen grains of anthropogennic indicators and microscopic charcoal particles in lake sediments dated to the early holocene (*Pokorný 1999*). Strong indirect evidence cause us to suspect the presence of an exceptionally dense settlement in the immediate vicinity of the former lake at least from the very beginning of the holocene up to its middle part. The following archaeological investigation, carried out in 2000 by S. Vencl (*Vencl et al. 2006*), and on a larger scale in 2005 and 2006 by the authors of this contribution, produced plentiful

finds of chipped stone industries dated to the late Palaeolithic and mainly to the Mesolithic. With the aid of surface collections we have gradually discovered nine sites in the south-eastern segment of the foreshore zone of the lake (sites 1–8 and 10; *fig. 1*). We have thus in the meantime obtained a small but generally well-dated collection (Mesolithic, so far without microliths, which are difficult to pick up by surface collection). Thanks to the presence of a distinct sunken feature we discovered the plough undisturbed site 7 on an oval rise close by the bank of the former lake. The first exploratory sondage undertaken in autumn 2005 covered an area of 1x9 m. The discovered features were full of a dark brown sandy fill and only contained a stone industry (*fig. 9*). We associate their origin with the Mesolithic settlement. An industry of altogether 195 pieces was produced by the sondages (a density of 21.7 artefacts per square metre). Its dominant components are amorphous fragments (109 pieces; 55.9 %). This is followed by chips (51 artefacts; 26.2 %), blades (23 artefacts; 11.8 %) and cores (2 artefacts; 1 %). So far we have 10 tools in the collection (4 triangles, 3 scrapers, 2 burins and 1 blade with lateral retouching; 5.1 %). Too little data has so far been obtained for the evaluation of the planography – we will be able to formulate appropriate conclusions after the investigation of a larger area of the site.

The as yet final phase of the exploratory excavation took place in spring 2006. This time we concentrated on the least disturbed southern stretch of the bank of the former lake. The main aim was the verification of the archaeological potential of the moist shoreline areas and the taking of profiles for palaeoeclogical analyses. An exploratory sondage of 2x4 m (sondage 3; *fig. 10*) picked up the coastal facies from the period after the transgression of the water surface in its lower part. This organic layer with clay and sand showed itself to be rich in pollen grains (see pollen diagram on *fig. 11*) and plant macro-remains, including fresh wood and large pieces of charcoal. 14 of the discovered fragments of wood bear clear traces of working (*fig. 12* and *13*). In some cases we know their probable function (an arrow shaft and probably its semi-finished product), in other cases the function is still unclear. It has been possible to radiocarbon date the fragment of the arrow shaft. The resulting date is 9500±50 BP, after calibration between 9130 BC and 8630 BC (to a 95 % level of probability). Further wood finds bear traces of working, they are however often burnt either over the whole surface or at one end. In the appropriate parts of the layer pollen analysis shows the presence of a series of types of herbs that have been evaluated as secondary anthropological indicators. Likewise some finds of plant macro-remains from these layers – shells of hazelnuts and raspberry seeds – are surprising in lake sediments, because they represent types that grow in drier areas. The interpretation is obvious: We are clearly dealing with the remains of gathered foodstuffs. Half of the hazelnuts found in a layer of between 92–100 cm have been radiocarbon dated to 9280±50 BP. After calibration we arrive at a calendar age span of between 8640 and 8320 BC (95 % probability). We regard the find as exceptional with regard to its ascertained age. At the very beginning of the holocene hazel only occurs sporadically in central Europe.

The hazelnuts found within the context of lake sediments with artefacts can thus be provisionally regarded as indirect evidence of the diffusion of this wood by man. It is possible, that man contributed to the diffusion of hazel by transporting the harvested fruits over longer distances (during the seasonal movements of hunter-gatherer groups), by reducing the canopy connecting the forest and it is not to be ruled out, by deliberate management as well which for the meantime only remains at the level of a hypothesis.

The layer of reed bogs above the bed of the above described deposit came into being after the silting up of the lakeside zone roughly between 9000 and 5000 cal. BC. (on the basis of radiocarbon dating – see *fig. 11*). The black coloured upper part of this layer is the result of the presence of a large amount of microscopic charcoal. Its continual occurence (see the appropriate graph in the right part of the pollen diagrammes, *fig. 7* and *11*) either indicates direct settlement (in the case that the charcoal came from a fireplace), or the burning down of woodland or lakeside vegetation in the surrounding area. Microscopic charcoal from wood can often be distinguished from charcoal of herbal origin (for example from reeds). Both categories of find are probably present in the studied material from lake sediments. The increased occurence of pollen grains of some anthropogennic indicators correlates with the presence of microscopic charcoal particles. It is a matter of plants which prefer an open grassy environment (*Thalictrum*, *Rumex acetosella*, *Melampyrum*, *Plantago lanceolata*, Gramineae) and types which expand onto fire affected areas (*Pteridium aquilinum, Calluna vulgaris*). The occurence of some aquatic and lakeside plants (*Ceratophyllum*, *Typha latifolia*), or as the case may be plants from damp, nitrogen rich environments (*Solanum dulcamara*, *Urtica*) at the same time could be connected with eutrophysation, that means with an increased supply of nutrients into the lake and its shoreline zone. Finds of some taxons (*Artemisia*, Chenopodiaceae, *Plantago major*-type) can be evaluated as evidence of the presence of ruderal stands at the settlements.

The occurence of water nut (*Trapa natans)* at the studied site is not without interest in connection with the Mesolithic settlement. It has been preserved in the lake sediments in the form of plentiful macro-remains (of fruit) and pollen grains. Water nut is a floating aquatic plant, whose amylaceous nuts formed a significant part of the bill of fare of Mesolithic man (*Vuorela – Aalto 1982*, *Zvelebil 1994*). The oldest finds of water nuts in the sediments of Lake Švarcenberk date to the very beginning of the holocene. The surprisingly early appearance of this warmth-loving plant is not only proof of the favourable climate at the relevant time, but moreover again arouses suspicion of its deliberate introduction.

The relatively late date of the end of the continuous settlement which has for the meantime only been indirectly indicated in the lake sediment is at least surprising. On the basis of the radiocarbon dating of palaeoenvironmental records we obtain a date of closely around 5000 cal. BC, which from a chronological point of view already lies deeply within the Neolithic period that had developed in areas that were more favourable to agriculture. The Třeboň Basin with acidic and waterlogged soils was completely unsuitable for such settlement and thus it cannot be ruled out that a hunter-gathering population persisted here for a long time after the expansion of the agricultural way of life in the fertile lowlands. This corresponds very well to the concept of the long term survival of the Mesolithic in peripheral areas of Bohemia as has been formulated by S. Vencl (*Vencl et al. 2006*). There is a distinct temporary hiatus in settlement in the pollen record from roughly 5000 cal. BC until the period around 3800 cal. BC when indicators of agricultural activity start to appear in the form of cereal pollen grains. The presence of a later Neolithic population in the immediate vicinity of the area under investigation is archaeologically suggested by Lengyel Culture pottery and several stone artefacts from the nearby gravel-pit of u Vlkova (*Beneš 1976*).

Dřevěné artefakty raně holocenního stáří z litorálu zaniklého jezera Švarcenberk.

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Abstract: Filled-in Lake Švarcenberk brings many opportunities to study the environment and its interactions with human occupation during the period 15000 – 7000 BP. Over the last ten years we have started multidisciplinary palaeoecological and archaeological research of the lake and its vicinities. During the field survey of well-preserved southern lake shore we have discovered important regression-transgression cycle that is dated to the Pleistocene-Holocene transition. In the littoral sediments of the transgression phase we have collected several wooden artifacts in association with charcoal and plant macro-remains. This find indicates neighboring wet archaeological site and makes hope for preservation of intact situations in waterlogged environment. Local vegetation development is illustrated by pollen diagram. Intensive Mesolithic occupation had considerable effect to the environment in the surroundings of the lake.

Keywords: mezolit, dřevěné artefakty, starší holocén, jezero (Mesolithic, wooden artifacts, Early Holocene, lake site)

Úvod

Před téměř deseti lety začal dlouhodobě koncipovaný paleoekologický výzkum zazemněného jezera Švarcenberk. Jezero se nacházelo v severní části Třeboňské pánve, jižně od Veselí nad Lužnicí na katastru obce Ponědrážka. Jeho rozsah mírně přesahoval plochu dnešního rybníka vybudovaného zde na přelomu 17. a 18. stol. Podle něj dostalo původní jezero název. Objev zaniklého jezera se datuje na počátek 70. let 20. století, kdy *V. Jankovská* zjistila jezerní sedimenty pod vrstvou rašeliny ve výtopě dnešního rybníka (*Jankovská 1976*; *1980*). V polovině 90. let jsme na tato zjištění navázali rozsáhlejším stratigrafickým průzkumem. Záhy se ukázalo, že se jedná o původní jezero značného rozsahu a že je uprostřed pánve dochován souvislý, až 11 m mocný sled jezerních sedimentů a rašeliny vrcholně glaciálního až pozdně holocenního stáří. Jezero je s největší pravděpodobností termokrasového původu. Dva litorální profily a jeden profil centrální byly postupně zpracovány metodou pylové analýzy, rozboru zbytků řas a makrozbytkové analýzy s cílem popsat postup zazemňování jezerní pánve a dlouhodobou vegetační sukcesi s ním spojenou (*Pokorný - Jankovská 2000*). Chronologie sedimentárního záznamu je postavena na radiokarbonových datech, na nepřímém datování stopovými obsahy rubidia (k této nově vypracované metodě viz *Veselý a kol. 2006*, *v tisku*) a na relativním palynostratigrafickém datování. Profil ve středu jezerní pánve, jehož spodních 5 metrů vznikalo v průběhu pozdního glaciálu, byl využit k rekonstrukci vývoje vegetace a geochemických změn v povodí jezera v souvislosti s prudkými klimatickými změnami na přelomu pleistocénu a holocénu (*Pokorný 2001*; *2002*). Sedimentologický výzkum mimo jiné ověřil přítomnost eolické složky v jezerním souvrství. Stopy eolické činnosti patrné v jezerních sedimentech se podařilo korelovat se vznikem dun vátých písků v přilehlé části nivy Lužnice a vysvětlit je jako reakci na klimatické zhoršení, ke kterému došlo na počátku mladšího dryasu (*Pokorný - Růžičková 2000*). Paleoekologický potenciál této mimořádné lokality zdaleka není zmíněnými výzkumy vyčerpán. V sedimentech jsou zachovány například zbytky rybí fauny a dalších vodních organismů, které lze využít k rekonstrukci změn lokálního prostředí a ke studiu klimatických změn regionálního i globálního charakteru. Postupně jsou zpracovávány například zbytky rozsivek (*Bešta 2004*) a vodních korýšů (Cladocera - *K. Nováková*, zatím nepublikováno).

Mezolitické osídlení okolí jezera

Zajímavé jsou okolnosti původního objevu mezolitického osídlení v okolí zaniklého jezera. Z blízkého okolí Ponědrážky (Bošilec, dvě polohy v Lomnici nad Lužnicí, Ponědraž) jsme dlouho znali jen ojedinělé nálezy štípané kamenné industrie patrně předneolitického stáří (souhrnně viz *Vencl a kol. 2006*). První archeologický průzkum v bezprostředním okolí rybníka Švarcenberk podnikl v roce 1986 Ivan Pavlů, který zde povrchovým sběrem nalezl jediný úštěp a ve vykopané sondě při JZ okraji rybníka doložil pouze vrstvu rašeliny bez jakýchkoliv artefaktů (*Pavlů 1992*, *Vencl a kol. 2006*). Odhlédneme-li od tohoto ojedinělého nálezu, bylo rozsáhlé mezolitické osídlení v těsném okolí bývalého jezera doloženo až nepřímo a to na základě přítomnosti pylových zrn antropogenních indikátorů a mikroskopických uhlíkových částic v jezerních sedimentech datovaných do raného holocénu (*Pokorný 1999*). V litorálním profilu budily pozornost nálezy oříšků kotvice plovoucí (*Trapa natans*) a semen maliníku (*Rubus idaeus*), která se do jezerních sedimentů mohla stěží dostat přirozenou cestou. Silná nepřímá indikace pylovými analýzami dávala tušit přítomnost mimořádně hustého osídlení v těsném okolí bývalého jezera a to minimálně od samého začátku holocénu po jeho střední část. Navazující archeologický průzkum, provedený v roce 2000 S. Venclem (*Vencl a kol. 2006*, 208-210) a zejména pak v letech 2005 a 2006 autory tohoto příspěvku ve spolupráci s *O. Chvojkou*, *J. Michálkem* a *J. Fröhlichem*, přinesl hojné nálezy štípané kamenné industrie datovatelné rámcově do pozdního paleolitu a mezolitu. Podařilo se tak objevit archeologickou lokalitu, která má vzhledem k vazbě na jezerní a bažinné prostředí mimořádný potenciál k aplikaci celé řady environmentálně archeologických metod.

V roce 2005 se v návaznosti na výše popsané paleoekologické výzkumy a první archeologické nálezy rozeběhl také sídelně geografický průzkum mezolitického osídlení v okolí jezera. V této fázi jsme se zaměřili na ověřování platnosti základních východisek pro budoucí intenzivnější výzkum. Soustředili jsme se na zjištění hustoty osídlení, která se na základě poměrně výrazné indikace v environmentálním záznamu zdála hned od počátku značná. Pomocí povrchových sběrů jsme postupně objevili devět lokalit v jihovýchodním segmentu příbřežní zóny jezera (lokality 1-8 a 10; *obr. 1 v kapitole 5*). Získali jsme tak zatím sice nepočetné, ale rámcově dobře datovatelné kolekce (mezolit, prozatím bez mikrolitů, které se sběry obtížně zjišťují). Na protáhlé vyvýšenině těsně při břehu bývalého jezera jsme objevili nejperspektivnější lokalitu 7, která není výrazně porušena zemědělskou činností. Ověřovací sondáže na tomto místě poskytly již početnější kolekce nástrojů včetně mikrolitů. Většina nalezených artefaktů pochází z objektů nepravidelného tvaru zahloubených do písčitého podloží (*Pokorný a kol. v tisku*).

Řez a sonda v zamokřené litorální partii zaniklého jezera.

Zjišťovací výzkum zaměřený na nejméně porušený jižní úsek pobřeží bývalého jezera proběhl na jaře roku 2006. Hlavním cílem bylo ověření archeologického potenciálu vlhkých břehových partií a odběr litorálního profilu pro paleoekologické analýzy. Vrtnou sondáží jsme provedli řez od břehu směrem do středu zazemněné jezerní zátoky (*obr. 3 v kapitole 5*). Na základě faciální analýzy jsme zjistili, že na samém počátku holocénu došlo k transgresi jezera do pobřežní zóny vlivem zvýšení vodní hladiny. Tato událost se projevuje přítomností inverzní stratigrafie, kdy telmatická fáze vývoje stratigraficky (a tedy i časově) předchází fázi limnické. Takové zjištění skýtá výraznou naději, že mohlo dojít k zatopení některých archeologických situací mezolitického stáří (případně i stáří pozdně paleolitického) a tím k zakonzervování organických materiálů. K oscilaci vodní hladiny muselo dojít v rozsahu asi dvou metrů. Příčinou snížené vodní hladiny v pozdním glaciálu bylo s největší pravděpodobností vysušení klimatu v mladším dryasu. Následnou transgresi vyvolal naopak nárůst klimatické vlhkosti s nástupem holocénu. Analogie náhlého zvýšení vodní hladiny na počátku holocénu známe z řady jezer ve střední a severní Evropě (souhrnně viz *Harrison - Diggerfeldt 1996*). V průběhu staršího holocénu pokračoval proces zazemňování vlivem vysoké organické produkce jezerního ekosystému a pobřežních porostů. Před zhruba 5 000 lety (cal. BC) zmizely i poslední zbytky volné hladiny a střed bývalého jezera se změnil v rašeliniště. Koberec rašeliníku spolu s dalšími bažinnými rostlinami nenáročnými na živiny (*Scheuchzeria palustris*, *Menyanthes trifoliata*, *Drosera rotundifolia*) začal vytvářet vrstvu rašeliny, která dnes tvoří nadloží jezerních sedimentů. Nejmladší vrstvy rašeliny dochované ve středu bývalé jezerní pánve pocházejí z období kolem přelomu starého a nového letopočtu. Zbytek souvrství byl zničen v průběhu budování a existence rybníka.

profil, stratigrafická pozice	*Lab. No.*	*metoda*	*druh materiálu*	*naměřené ^{14}C datum*
sonda 3, 64 cm	Crl-6090	konvenční	borová kůra	6102 ± 99 BP
sonda 3, 85-87 cm	Crl-6093	konvenční	větev borovice, na jednom konci opálená	9639 ± 112 BP
sonda 3, 85-92 cm	Poz-16752	AMS	broušený artefakt, fragment ratiště šípu (?)	9500 ± 50 BP
sonda 3, 92-100 cm	Poz-16753	AMS	lískový oříšek	9280 ± 50 BP

Tab. 1: Radiokarbonová data ze sondy 3.
Tab. 1: Radiocarbon measurements from the trench no. 3.

Zjišťovací sonda o rozměru 2 x 4 m (sonda 3, *obr. 3-4*) zachycuje ve své spodní části pobřežní facii z doby těsně po transgresi vodní hladiny na samém počátku holocénu. Toto organické souvrství s jílem a pískem se ukázalo být bohaté na pylová zrna (viz pylový diagram na *obr. 11 v kapitole 5*), rostlinné makrozbytky (včetně čerstvého dřeva a velkých kusů uhlíků) a rovněž fragmenty opracovaných dřev.

V jezerních a pobřežních sedimentech datovaných v sondě 3 do starší poloviny holocénu jsou někdy i pouhým okem patrné vrstvy s vysokým obsahem mikroskopických uhlíkových částic. Jejich výskyt (viz příslušnou křivku v pravé části pylového diagramu, *obr. 11 v kapitole 5*) indikuje buďto přímo sídlení (v případě, že uhlíky pocházejí z ohnišť), nebo vypalování lesní či pobřežní vegetace v okolí. Někdy lze vzájemně odlišit mikroskopické uhlíky pocházející ze dřeva od uhlíků původem z bylin. Ve studovaném materiálu z jezerních sedimentů jsou pravidelně přítomny obě kategorie nálezů. S přítomností mikroskopických uhlíkových částic koreluje zvýšený výskyt pylových zrn některých antropogenních indikátorů. Jedná se o rostliny preferující otevřená travnatá stanoviště (*Thalictrum*, *Rumex acetosa*-typ, *Melampyrum*, *Plantago lanceolata*, Gramineae). Výskyt některých vodních a pobřežních rostlin (*Ceratophyllum*, *Typha latifolia*), případně rostlin vlhkých, dusíkem bohatých stanovišť (*Solanum dulcamara*, *Urtica*) ve stejném období může souviset s eutrofizací, tzn. se zvýšením přísunu živin do jezera a jeho pobřežní zóny. Nálezy některých taxonů (*Artemisia*, Chenopodiaceae) lze hodnotit jako důkaz přítomnosti ruderálních stanovišť na přilehlých sídlištích.

Některé nálezy rostlinných makrozbytků v sondě 3 - skořápky lískového ořechu a semen maliníku - jsou v jezerních usazeninách překvapivé, protože se jedná o druhy rostoucí na sušších místech. Interpretace je nasnadě: Jedná se zřejmě o zbytky sbíraných potravin, které se dostaly jako antropogenní odpad do jezerních usazenin. Polovina lískového ořechu nalezená ve vrstvě 92-100 cm byla radiokarbonově datována 9 280±50 BP. Po kalibraci vychází rozpětí stanoveného stáří vzorku mezi roky 8 640 BC a 8 320 BC (95% pravděpodobnost). Tedy srovnatelné datum jako v případě dřevěného artefaktu - ratiště šípu nalezeného ve stejné vrstvě (viz níže). Nález považujeme za mimořádný právě vzhledem ke zjištěnému vysokému stáří. Na samém počátku holocénu se líska ve střední Evropě vyskytovala jen sporadicky. Nalezený lískový ořech tak může být předběžně považován za nepřímý důkaz šíření této dřeviny člověkem. Pylový diagram z místa nálezu (*obr. 11 v kapitole 5*) ukazuje v příslušné době pouze ojedinělý výskyt lísky v regionu. Její pylová křivka prudce narůstá až značně později. Je možné, že člověk přispíval k šíření lísky donášením sklizených plodů z větších vzdáleností (při sezónním pohybu lovecko-sběračských skupin), rozvolňováním korunového zápoje lesa a není vyloučeno, že i záměrným managementem, což zatím zůstává pouze v rovině hypotézy.

V souvislosti s mezolitickým osídlením lokality není bez zajímavosti ani výskyt kotvice plovoucí (*Trapa natans*). Ta se v podobě hojných makrozbytků (plodů) a pylových zrn dochovala v jezerních sedimentech. Kotvice je vzplývavá vodní rostlina, jejíž škrobnaté oříšky jistě tvořily významnou součást jídelníčku mezolitického člověka (*Vuorela - Aalto 1982*; *Zvelebil 1994*). Nejstarší nálezy oříšků kotvice v sedimentech zaniklého jezera Švarcenberk se datují do samého počátku holocénu. Překvapivě časný výskyt této teplomilné rostliny je nejen důkazem příznivého klimatu v příslušné době, ale navíc vyvolává podezření z její záměrné introdukce. Jedná se tedy o podobný případ jako výše popsaný nález lískového ořechu.

Obr. 3. Jezero Švarcenberk. Letecký pohled na místo nálezu dřevěných artefaktů od jihu.
Fig. 3. Švarcenberk Lake. Aerial view on excavation place with wooden artifacts; facing north.

Obr. 4. Jezero Švarcenberk. Pohled na západní profil sondy 3 v průběhu výzkumu, artefakty byly nalezeny ve spodní šedé vrstvě.
Fig. 4. Švarcenberk Lake. View to the western section of trench 3 during excavation. Artifacts were found in lower grayish layer.

Chapter 6

Dřevěné artefakty

Nálezy dřevěných artefaktů mezolitického stáří jsou ralativně četné v severském prostředí (například Ageröd V – *Larsson 1983*; Tågerup - *Karsten - Knarrström 2001*; Ronæs Skov - *Andersen 1999*), severním Rusku (Zamostje 2 - *Lozovski - Ramseyer 1998*; Vis I - *Burov 1990*) ale i v Nizozemí či severním Německu (Friesack – *Gramsch 1987*; Hardinxveld - *Louwe Kooijmans 2001*; Hohen Viecheln – *Schuld 1954*). Ve střední Evropě zatím srovnatelné nálezy scházely. Severské dřevěné artefakty navíc v naprosté většině pocházejí až z mladší fáze mezolitu (kultura ertebølle). Velké kolekce jsou výjimečné a publikovány bývají hlavně celé a dobře interpretovatelné artefakty. Nález dřevěných artefaktů na Švarcenberku nás staví před problém jejich interpretace. Takto starých dřevěných artefaktů známe zatím velice málo, a proto je obtížné hledat analogie. Velká část artefaktů navíc působí dojmem fragmentů vyřazených jako odpad, což dále stěžuje interpretaci. Z toho důvodu jsme rozdělili artefakty do umělých skupin podle typu opracování.

Soupis nálezů:

- A štěpiny dřeva vybroušené do kulatého průřezu, patrně součásti ratišť
  - 1a fragment slepený ze 4 částí, rozlámán recentně při výzkumu, po konzervaci mírně oválný průřez, těsně po vyjmutí kulatý, na bocích artefaktu dva protiběžné žlábky, letokruhy jsou situovány napříč artefaktem, délka 8,55 cm, průměr 1 – 0,85 cm (*obr. 13:9b v kapitole 5, 7:4*)
  - 1b část stejného artefaktu, která nejde spojit, slepena ze dvou částí, délka 6,1 cm, průměr 1-0,8 cm (*obr. 13:9a v kapitole 5, 7:3*)
  - 2 drobný fragment patrně stejného artefaktu, jeden z lomů starý, průřez oválný, délka 1,7 cm, průměr 1-0,85 cm (*obr. 13:16 v kapitole 5*)
- A1 polotovar typu A
  - 3 štěpina dřeva, ? obvodu vybroušena, okrajové lomy staré, délka 6,8 cm, šířka 1 cm a výška 0,85 cm (*obr. 13:10 v kapitole 5*)
- B artefakty se žlábkem
  - 4 podlouhlý zploštělý artefakt, terminální partie zahrocená, na bázi se artefakt zužuje a přechází do kulatého průřezu (zde staře odlomen), po celém obvodu (kromě báze) vyříznut žlábek 1-3 mm hluboký (patrně hrot šípu), délka 3,9 cm, šířka 1,15 cm a výška 0,7 cm (*obr. 13:6 v kapitole 5, 7:1*)
- C artefakty s dvěma protiběžnými vruby
  - 5 tenký plochý artefakt se dvěma protiběžnými vruby, na ventrální straně vybroušen oválný žlábek (nese stopy po opálení), délka 2,4 cm, šířka 0,8 cm a výška 0,2 cm, součást průvlečky? (*obr. 13:12 v kapitole 5, 7:9*)
- D artefakty s vrubem
  - 6 zahrocený artefakt s vrubem na hrotu, celý artefakt mírně opálen, délka 4,5 cm, šířka 2 cm a výška 1 cm (*obr. 13:15 v kapitole 5, 7:5*)
  - 7 plochá štěpina s vrubem na laterální hraně, délka 5,5 cm, šířka 2 a výška 0,4 cm (*obr. 13:3 v kapitole 5*)
  - 8 zahrocený artefakt s vrubem na hrotu, celý artefakt mírně opálen, délka 6,55 cm, šířka 1,55 cm a výška 1,05 cm (*obr. 13:2 v kapitole 5, 7:2*)

Obr. 7. Jezero Švarcenberk. Nalezené dřevěné artefakty. Popis viz text.
Fig. 7. Švarcenberk Lake. Wooden artifacts from trench 3.

E broušené artefakty
  9 plochá široká štěpina z podkorního prostoru, jedna laterální strana seříznuta pod úhlem 45° a spolu s ventrální stranou byla přebroušena, celý artefakt je mírně opálen, délka 9,75, šířka 1,9 cm a výška 0,9 cm (*obr. 13:13 v kapitole 5*)
  16 plochá štěpina, obě laterální strany jsou zabroušeny do oblého tvaru, délka 6,65 cm, šířka 2,55 cm a výška 0,5 cm (*obr. 13:5 v kapitole 5*)
F artefakty opracované řezáním
  10 hrotitý artefakt se zakulaceným hrotem, hrany seříznuté, celý artefakt mírně opálený, délka 7,5 cm, šířka 2,4 cm a výška 1,7 cm (*obr. 13:17 v kapitole 5, 7:6-7*)
  11 plochá štěpina zahrocená seříznutím, delší z laterálních hran také opracována seříznutím, délka 7,2 cm, šířka 2,05 a výška 0,75 cm (*obr. 13:7 v kapitole 5, 7:8*)
  12 plochá štěpina s laterální hranou seříznutou pod ostrým úhlem do tvaru ostří, délka 4,15 cm, šířka 3,5 cm a výška 0,5 cm (*obr. 13:11 v kapitole 5*)
G štěpiny dřeva
  13 štěpina větve s centrálním letokruhem, délka 6 cm, šířka 1,1 cm a výška 0,9 cm (*obr. 13:8 v kapitole 5*)
  14 štěpina z podkorního letokruhu, délka 4,2 cm, šířka 1,75 cm a výška 0,4 cm (*obr. 13:4 v kapitole 5*)
  15 štěpina z podkorní partie větve, délka 3,3 cm, šířka 0,95 cm a výška 0,3 cm (*obr. 13:1 v kapitole 5*)
  17 štěpina z podkorních partií dřeva, délka 9,7 cm, šířka 1,7 cm a výška 0,6 cm (*obr. 13:14 v kapitole 5*)

Z množství nalezených fragmentů dřev nese 13 nálezů jasné stopy opracování, další čtyři nalezené kusy dřeva byly pouze záměrně fragmentovány. Další dřeva nalezená c sondě 3 nenesou stopy opracování, jsou však často opálená a to buďto na celém povrchu, nebo na jednom konci.

Patrně nejsnáze můžeme určit funkci artefaktů typu A a B, které nejspíše představují fragmenty šípu. Jeden z fragmentů ratiště (č. 1a a 1b) se podařilo radiokarbonově datovat (nedestruktivním způsobem metodou AMS; Poznań Radiocarbon Laboratory, Polsko). Výsledné datum je 9 500 ± 50 BP, po kalibraci mezi 9 130 BC a 8 630 BC (na 95% hladině pravděpodobnosti). Artefakt byl vyroben ze štěpiny borového kmene pomocí řezání a broušení. Při průměru 1 cm v něm můžeme napočítat celkem 14 letokruhů, které jsou velice ploché a téměř dokonale paralelní (*obr. 12 v kapitole 5*), což svědčí o velkém obvodu a stáří použitého stromu.

Relativně je možné také určit funkci artefaktů typu G, které představují štěpiny dřeva získané patrně lámáním a štípáním pomocí kamenné hrubotvaré industrie. Z části jde zřejmě o polotovary, z části o odpad výroby větších dřevěných artefaktů. O funkci typů C až F nemůžeme říci nic určitého. Z etnografických paralel víme, že jednoduchým zahroceným klackem lze stáhnout a naporcovat divoké prase (Papua – Nová Guinea, recent), takže artefakty s ostřím či hrotem mohly sloužit například jako nože či hroty při práci s masem, jejich funkcí ale mohlo být nepřeberné množství a zatím je nejsme sto blíže určit.

Vedle popisovaných artefaktů jsme nalezli i několik větví s opáleným koncem, které pravděpodobně pocházejí z vyhaslého ohniště. Z jedné z nich pochází konvenční radiokarbonové datum (Crl-6093; *tab. 1*).

Xylotomickou analýzu nálezů provedl *Jan Novák*. Všechny nalezené artefakty jsou vyrobeny z borového dřeva. V daném prostoru přichází do úvahy pouze borovice lesní - *Pinus* *sylvestris*. Vzhledem k raně holocennímu stáří nálezů to není nijak překvapivé zjištění. V příslušnou dobu byla borovice lesní zdaleka nejběžnější dřevinou nejen v okolí jezera (což mimo jiné dobře ilustrují pylové analýzy z lokality), ale všude ve střední Evropě. Kromě ní zde běžně rostla bříza a osika, v mokřadech pouze křivolaké vrby. Ze dřevin, které přicházely k výrobě artefaktů v úvahu, bylo dřevo borovice jistě nejlépe dostupné, nejlépe opracovatelné, nejhouževnatější a tudíž nejvhodnější.

Závěr

Studované artefakty nalezené ve zjišťovací sondě pocházejí z pobřežní zóny bývalého jezera, kam byly pravděpodobně přemístěny během transgresní události. Další nehodnotitelné fragmenty dřev jsme spolu s vrbovým proutím zachytili ve vrtu o 10 m dále k severu (25 m na řezu 3 - *obr. 3 v kapitole 5*) a to v podstatně větší hloubce. Právě zde by se mohly nacházet zamokřené archeologické situace z doby před transgresí. V budoucnu bychom chtěli právě do těchto míst položit další zjišťovací sondu, která by měla přítomnost *in situ* dochovaných situací potvrdit či vyvrátit.

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Summary

Former Lake Švarcenberk is situated in the northern part of the Třeboň Basin, south Bohemia. Its former extent was slightly larger than present fishpond that was built in the same place in late 17th century. According to this pond, former lake was named. Its discovery dates to the 70's of the last century, when V. *Jankovská* (*1976*, *1980*) found lake sediments buried under the layer of peat.

Intensive Mesolithic occupation of the site was first evidenced indirectly, based on the results of pollen and microscopic charcoal analyses of the sediments dated to the Early

Holocene (*Pokorný 1999*). Macro-remains of water chestnut (*Trapa natans*) and raspberry (*Rubus idaeus*) in the littoral sediments of the lake gave another indication of the same occupation. In the year 2005 we have started settlement-archaeological survey of former lake shores aimed on the validation of the working hypotheses for the purpose of future intensive investigations. Through the surface artifact survey we have successively discovered nine Mesolithic sites in the SE segment of the area (see Fig. 1 in Chapter 5). This way we gathered not very numerous, but rather well-dated collection of lithic industry. In the elongated elevation along the very shore of the lake we have discovered well-preserved the site no. 7. Test pitting at this place led to the find of numerous collection of artifacts including microlithes, which were concentrated within archaeological features countersunk into the sandy substratum.

During the spring 2006 we have concentrated to the verification of archaeological potential of waterlogged littoral parts of the lake, where we have discovered 13 pieces of small wooden artifacts dated to the Early Holocene. They were all made from pine wood. Their functional interpretation is though difficult. Only some pieces are most probably fragments of an arrow. They were radiocarbon-dated to 9 500 ± 50 BP. After calibration this measurement gives calendar dating to the interval between 9 130 BC and 8 630 BC (95% probability). The arrow was made by chopping and grinding from a sliver of a large pine trunk.

Post-glacial vegetation development in sandstone areas of the Czech Republic

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In the Bohemian territory of the Czech Republic, sandstone areas have always been generally described as small-scale islands with well-defined montane vegetation, situated within landscapes with a mesic or thermic character. These small-scale islands are caused mainly by climatic inversions at the bottom of sandstone gorges, very low irradiation and a very low nutrient content. This is supported by typical sandstone geomorphology, which often forms a very complicated network of narrow valleys and gorges together with small, top plateaus, their margins and steep walls (Fig. 1). The present poor nutrient content in soils and in the sandstone bedrock itself is reflected by a relatively poor vegetation cover (low alpha-diversity *sensu* Whittaker 1972) of sandstone areas (Sýkora and Hadač 1984), mainly characterized by species of poor pine-oak forests (*Avenella flexuosa, Calluna vulgaris, Vaccinium myrtillus, Vaccinium vitis-idaea*), fragments of degraded beech forests (*Calamagrostis villosa, Trientalis europaea*), and microclimatically inverse stands with oreophytic indicators (*Athyrium distentifolium, Cicerbita alpina, Rumex alpestris, Viola biflora*). From the point of view of environmental history, it is clear that individual sandstone areas, in the whole rank of the Bohemian Cretaceous Basin, differ significantly from one another. Some regions could have had much richer nutrient conditions in the past, as documented by malacological investigations in the Kokořínsko region (Ložek 1997) and, most recently, by the first pollen-annalytical data obtained by the present authors from Bohemian Switzerland and areas adjacent to the Kokořínsko region (see below). These sandstone areas had a more nutrient-demanding vegetation cover in the past. Today, this is found in fragments on calcareous sandstones with rare continental species (e.g. *Carex pediformis* and *Sesleria caerulea*) or in steep rubble slopes as humic nitrophillous mixed

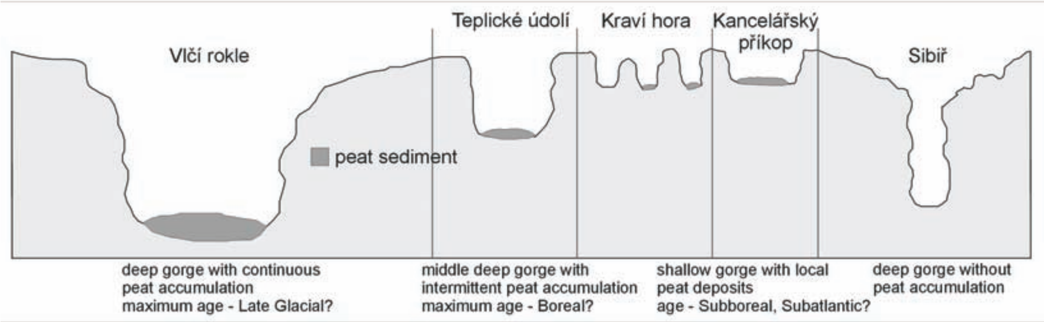

Fig. 1: Geomorphological profileof the Teplické skály Cliffs (schematic view)

forests. After the Middle Holocene climatic optimum, both the nutrient-rich soils and the calcareous bedrock were liable to nutrient loss. This was probably because of climatic changes which were possibly, exacerbated by direct human impact. The influence of human impact, in most sandstone areas, following the massive colonization in the Late Medieval and Modern Periods is unexceptionable.

The following text describes the post-glacial vegetation and landscape development mainly on the basis of direct palaeoecological data – pollen analyses and analyses of plant macroremains. However, the data used was collected with an uneven intensity. Most of it comes from the Broumovsko region in North East Bohemia, which is differentiated from other sandstone regions by its highest inclination towards montane character i.e. highest humidity and highest acidity. It has the most apparently developed climatic inversions in the gorges and the biggest differences between gorges and plateaus due to the height of the rocks. The reconstructions have been made primarily on the basis of data from the area of Broumovsko Basin (Peichlová 1979). Nevertheless, very detailed research has focused on Adršpašsko-teplické skály, addressing a number of individual profiles (Chaloupková 1995; Nováková 2000; Kuneš and Jankovská 2000). From the rest of the sandstone areas there exists only sparse palaeoecological data, represented mostly by malacological analyses from rockshelter sediments (Cílek *et al.*1996) and by one single profile from Jestřebská kotlina (Jankovská 1992). Most recent pollen-analytical investigations focus on the Bohemian Switzerland region (one profile now available) and to the region of acidic terraces of the middle Labe River valley, adjacent to the southeastern segment of the Kokořínsko area (Pokorný 2004).

Palaeoecological record from sandstone areas

When discussing the reconstruction of past vegetation, it is important to be taken into account exactly where the data was collected. This is why some remarks on sedimentology will be useful for the following text. There is a great variety of post-glacial sediments inside sandstone gorges, but only a few of them are useful for the task of obtaining an appropriate palaeoecological record. Most important for the reconstruction of past vegetation is data obtained from continuous peat profiles. But not all peat accumulations bear information of the same quality. An idealized chart of various types of gorges with accumulated material and

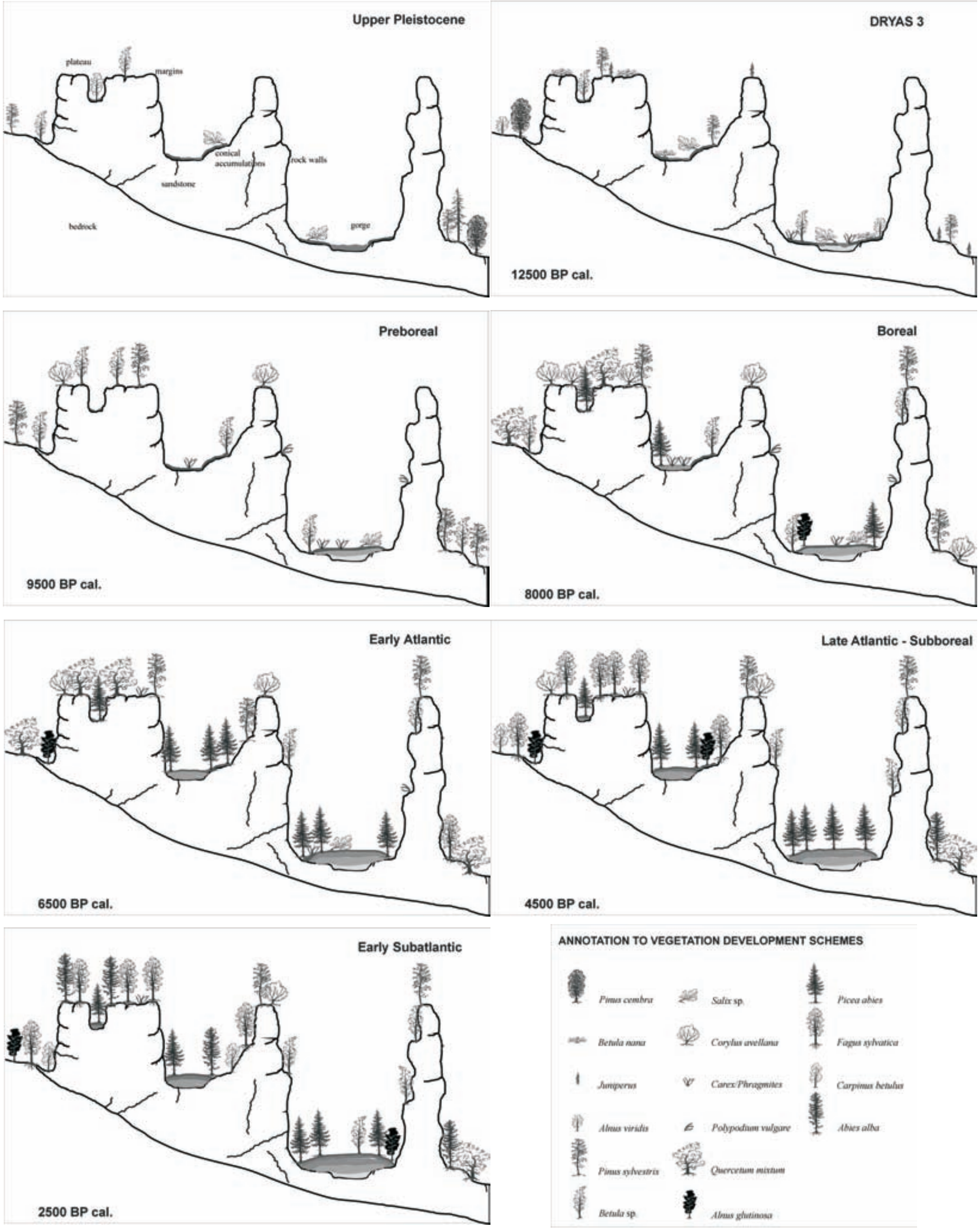

Fig. 2–9: An idealized chart of various habitat types with their typical vegetation during the Late Glacial and Holocene (an example from Adršpašsko-teplické skály Cliffs).

supposed age is shown in an example from Adršpašsko-teplické skály Mts. (Fig. 2–9). In periods with wetter and colder climates, specific hydrological and microclimatic conditions caused the sedimentation of organic material in shallow water reservoirs. The conditions inside gorges might have been differentially influenced by the global climate at various places

Table 1: A list of individual sites with palaeoecological records that represent the source data for interpretation in this paper.

locality	***Sandstone area***	***sediment type***	***data collected***	***reference***
Vlčí rokle	Teplické skály	peat profile	pollen, macrorem.	Fig.11; (Kuneš and Jankovská 2000)
Teplické údolí	Teplické skály	peat profile	pollen	(Kuneš 2001)
Anenské údolí	Teplické skály	peat profile	pollen	Fig. 13
Kancelářský příkop	Teplické skály	peat profile	pollen, macrorem.	(Nováková 2000)
Kraví hora	Teplické skály	peat profile	pollen, macrorem.	(Nováková 2000)
Vernéřovice	Broumovská kotlina close to Teplické skály	peat profile	pollen	(Peichlová 1979)
Heřmánky	Kokořínsko	rock-shelter	pollen	(Svobodová 1986)
Zátyní	Kokořínsko	rock-shelter	molluscs	(Prošek & Ložek 1952)
Jestřebské blato	Jestřebská kotlina close to Kokořínsko	peat profile	pollen	(Jankovská 1992)
Tišice	Middle Labe valley close to Kokořínsko	lake sediments	pollen	(Pokorný 2004)
Jezevčí převis	Bohemian Switzerland	rock-shelter	macroremains	(Pokorný 2003)
Pryskyřičný důl	Bohemian Switzerland	peat profile	pollen	Fig. 12; Pokorný, unpublished results.

and to varying degrees. The deepest parts of each sandstone area ought to preserve a better record of local conditions than the shallower parts, in which the sediment could be easily eroded due to a more prominent cycle of desiccation, subsequent weathering, and washing out. The initial phases of peat growth were usually characterized by very wet conditions derived from a rich water supply of rainfall and percolation through the sandstone. In existence were localised water reservoirs, overgrown by mosses and peat-producing vascular plants. The oldest layers from the bottom of the “Vlčí rokle” profile, date to the Late Glacial (Fig. 11), are formed of grayish-white clay, and probably accumulated in a local pond with oligotrophic, cool water. The sedimentation of both organic and inorganic material is also likely to have taken place in other gorges and,during the earlier period of the Late Pleistocene. Nevertheless, the deposited material could have been washed away during major flood events connected with snow melts, strong downpours, etc. Thus, the microfossils identified in the deepest parts of profiles in clayey or sandy sediment are only residua from originally thicker deposits. Records from other profiles at Adršpašsko-teplické skály support the theory of existing small water reservoirs during the initial phases of organic

Fig. 10: A typical view at a peat-bog situated inside a sandstone valley in the Adršpašsko-teplické skály Mts. Peat growth was stopped by forestry management and the former peat bog is now overgrown by spruce forest.

sedimentation. Basal layers of these sites are formed by organic material, possibly redeposited and mixed together with sand. Continuous peat accumulation began only around 8000-7500 BP i.e. during the Boreal period. These deposits originated from *Sphagnum* and *Polytrichum* moss pollsters surrounded by initial vegetation on sandy substrata (*Chamaenerion angustifolium, Polygonum bistorta, Filipendula*).

Environment during the Würm Late Glacial (about 15 000 – 10 000 BP conv.)

The ideas about the ecosystems covering sandstone landscapes during the Late Glacial period lean on very sporadic records. Most important is a reference profile "Vlčí rokle" situated directly in the heart of Adršpašsko-teplické skály Mts., being elaborated by Vlasta Jankovská (Fig. 11). Another two profiles come from the adjacent Broumovsko basin, an area with such different environmental conditions, that they can only be insecurely extrapolated.

From fragments of probably early Late Glacial sediments (Older Dryas or Alleröd/Bölling) this little known period can be reconstructed. Remains of green algae (coenobia of *Pediastrum kawraiskyi,* an important glacial relict, along with *Pediastrum integrum* and *Botryococcus pila*) lead to the following interpretation: the combination of these species was typical of cold, clear waters of the Late Glacial and Early Holocene (eg. Jankovska 2000). The vegetation of this time was characterized by very low pollen production and the occurrence of *Alnus viridis, Larix,* and *Pinus cembra* (interpreted from the finds of *Pinus haploxylon*-type). Sub-Arctic conditions allowed for only a sporadic occurrence of the above mentioned tree

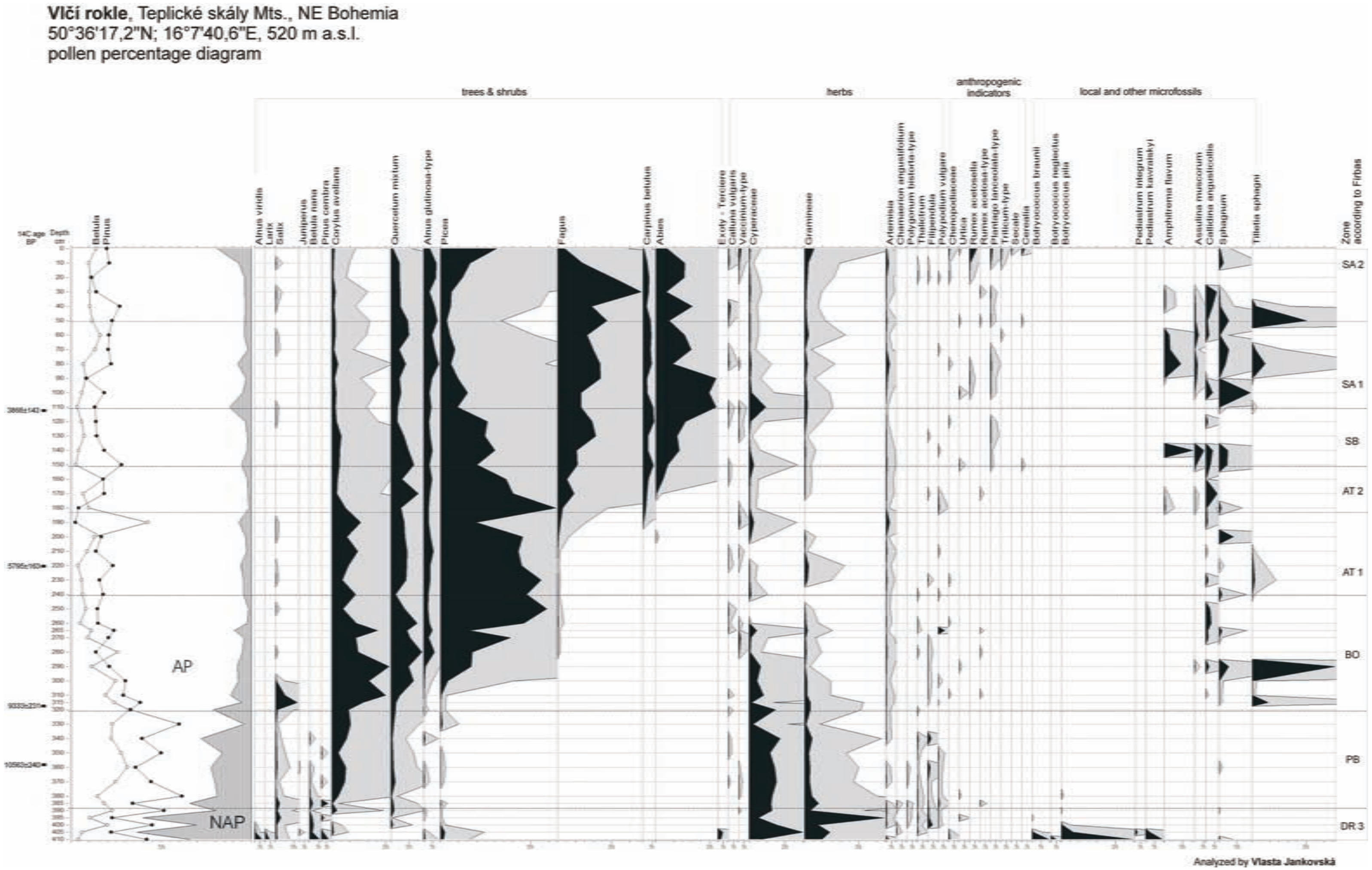

Fig. 11: Pollen diagram from Vlčí rokle, Teplické skály.

species, similar to the contemporary situation at the polar limit of the northern Siberian forest tundra. Small lakes with oligotrophic, cool water (as described above), possibly containing the admixture of dystrophic water from nearby mossy grounds, were probably common at the bottom of individual gorges.

From investigations in the Adršpašsko-teplické skály Mts so far, the first layers of partly organic material correspond to the Younger Dryas (DR3) period. During that time, the area was covered by vegetation of forest tundra with prevailing birch (*Betula pubescens* and most probably also *B. nana*), with both bushy and creeping willows, *Populus tremula, Juniperus* and *Pinus sylvestris*. The bottoms of the gorges hosted wetlands with prevailing mosses, *Carex* and *Eriophorum* species. Due to the absence of closed forest stands during the Late Glacial, the sandstone landscapes were easily accessible to human populations (we have numerous archaeological data demonstrating the presence of Epipaleolithic people in the sandstone areas of Kokořínsko and Bohemian Switzerland (Svoboda 2003). In the studied profiles from the Broumovsko basin, the sporadic presence of pollen grains of *Pinus haploxylon*-type, belonging most probably to *Pinus cembra,* does not necessarily reflect the direct presence of this tree in the area. Pollen grains of *P. cembra* could spread through the treeless Late Glacial landscape of Central Europe over hundreds of kilometers. In spite of this, the possibility of the presence of *P. cembra,* within the northeastern mountain ranges of the Czech territory, during the Late Glacial, cannot be completely excluded. Its local presence is likely to be due to the position of this region at a communication channel along the northern foreland of the Carpathian mountain ridge, which could cause some important differences in species migration chronology as shown below. This is supported by investigations made on the Polish side of the same mountain ranges (Madeyska 1989; Ralska-Jasiewiczowa 1989).

Environment during the Early Holocene (around 10 000 – 7 500 BP conv.)

As in the case of the previous period, the only suitable record of Early Holocene vegetation conditions is from the Adršpašsko-teplické skály region. After the Pleistocene/Holocene transition, the warm climate, more or less corresponding to present one (only more prominent in continentality), supported continuously developing ecosystems. During the Preboreal (PB), the first period of the Holocene, sandstone landscapes had the character of a sparse, mostly birch-rich “taiga” with an admixture of *Pinus sylvestris*. A distinctly developed undergrowth of forbs still contained a mixture of plant taxa typical of tundra (e.g. *Saxifraga* sp., *Polygonum* cf. *viviparum, Huperzia selago*), moist meadows (e.g. *Filipendula, Peucedanum, Phyteuma, Polygonum bistorta, Aconitum, Thalictrum*) and other biotopes with favourable light conditions under the sparse forest cover (*Chamaenerion, Armeria, Melampyrum*). Typical for the end of the Late Glacial and beginning of the Holocene is the common occurrence of ferns that grow under wet condition on sandstone substrata (e.g. *Botrychium, Gymnocarpium dryopteris* and an unidentified fern with Monolete spores). On sandstone outcrops, *Polypodium vulgare* was common at the same time. There is evidence for the expansion of *Corylus* during the Preboreal in the Adršpašsko-teplické skály region, i.e. considerably earlier than in the rest of the Czech Republic and Poland. The presence of hazel has been proven by pollen analysis from the sandstone area, where it could occupy stands on plateaus and their margins. The same evidence, reported amongst radiocarbon dates 11 790 and 10 140 BP (conv.), was found in the nearby area of the Broumovská Kolitna Basin (Peichlová 1979), and in neighboring regions north of Broumovsko (Madeyska 1989). An

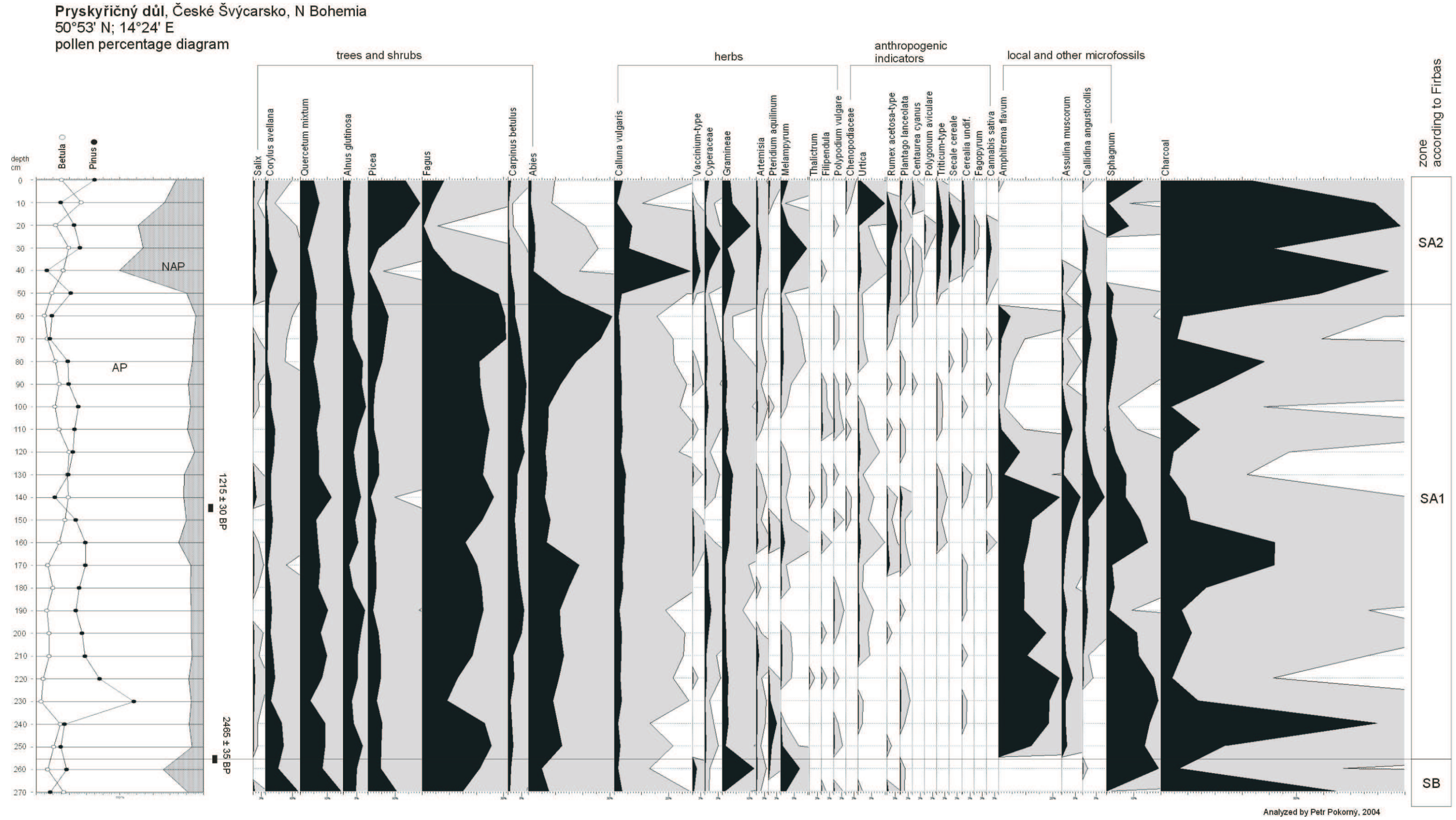

Fig. 12: Pollen diagram from Pryskyřičný důl, Bohemian Switzerland.

explanation of this interesting phenomenon is still difficult. We may speculate about the intentional spread of hazel by Mesolithic hunter-gatherers. Their massive presence is proven for other sandstone areas (Labské pískovce, Českolipsko, see chapter 3), and numerous finds of charred hazelnuts have been made in a Mesolithic context. Nevertheless, there are no corresponding archaeological finds in the Broumovsko region up to now, maybe only as a result of a lack of archaeological investigation. Sandstone landscapes were still "half-open" during the Early Holocene and were easy to pass through and to look over, particularly from high places, which could have been preferred by any hunters of the Late Palaeolithic and Early Mesolithic.

The Boreal (BO) period, with temperatures even higher than the present, resulted in the massive expansion of arboreal vegetation. The spread of *Corylus* into regions with good light and moisture conditions is widely expected, especially in the Broumovsko and Labské pískovce regions, which have the best developed montane character. The expansion of species of mixed oak woods (*Ulmus, Tilia* and *Quercus*) is expected, particularly in regions with lower altitude and a warmer climate e.g. Kokořínsko and Český ráj. Some variations in vegetation cover over geomorphologic gradients in the sandstone landscapes can be observed. In the case of the Adršpašsko-teplické skály Mts. it is possible to reconstruct the spread of hazel at the sandstone margins and on small plateaus, while species of mixed oak woods probably occurred on larger plateaus with mesic conditions and adjacent to sandstone areas. The expansion of *Picea* as well as the gradual spread of *Alnus* took place right inside the sandstone areas and their surroundings, mostly in places with improved hydrology and favourable mesoclimatic conditions. The presence of *Picea abies* is proven for Bohemian Switzerland during the Boreal Period. Spruce charcoal fragments and charred needles were found in the Mesolithic fireplace at Jezevčí převis rockshelter (Pokorný 2003) and were radiocarbon-dated to 8530±150 BP (conv.) Although Peichlová (1979), discussed the possibility of the Broumovsko region as a glacial refugium for *Picea*, its presence during the full Glacial and Late Glacial is unlikely, but still not excluded.

During the Boreal period, sandstone landscapes still contained numerous open places with prevailing stands of forbs. Ferns were abundant and *Polypodium vulgare* was growing on the rock outcrops. A rise of the underground water level (due to increasing precipitation) at the bottoms of sandstone gorges usually resulted in the expansion of *Sphagnum* mosses, which in many places led to peat bog formation (as already described above). In *Sphagnum* peat *Callidina angusticollis* shells are common. This rotatorian species is a good indicator of an oligotrophic environment.

Environment during the climatic optimum (around 7 500 – 4 500 BP conv.)

By the beginning of the Early Atlantic (AT 1), temperate forest communities had finally been established, however, their species structure and richness must have differed considerably across individual sandstone regions. In those defined by montane character (mainly NE Bohemia – Broumovsko) the vegetation reflected colder and wetter conditions. So during the older part of the Atlantic the most noticeable is the massive spread of spruce (*Picea abies*) supported by climatic inversion in the sandstone valleys and gorges together with good hydrological conditions. Its shady stands limited the occurrence of other, more light-demanding, woody species. A decline in ferns is also noticeable.. Spruce reached its maximum distribution during the Early Atlantic, covering entire valleys and their margins.

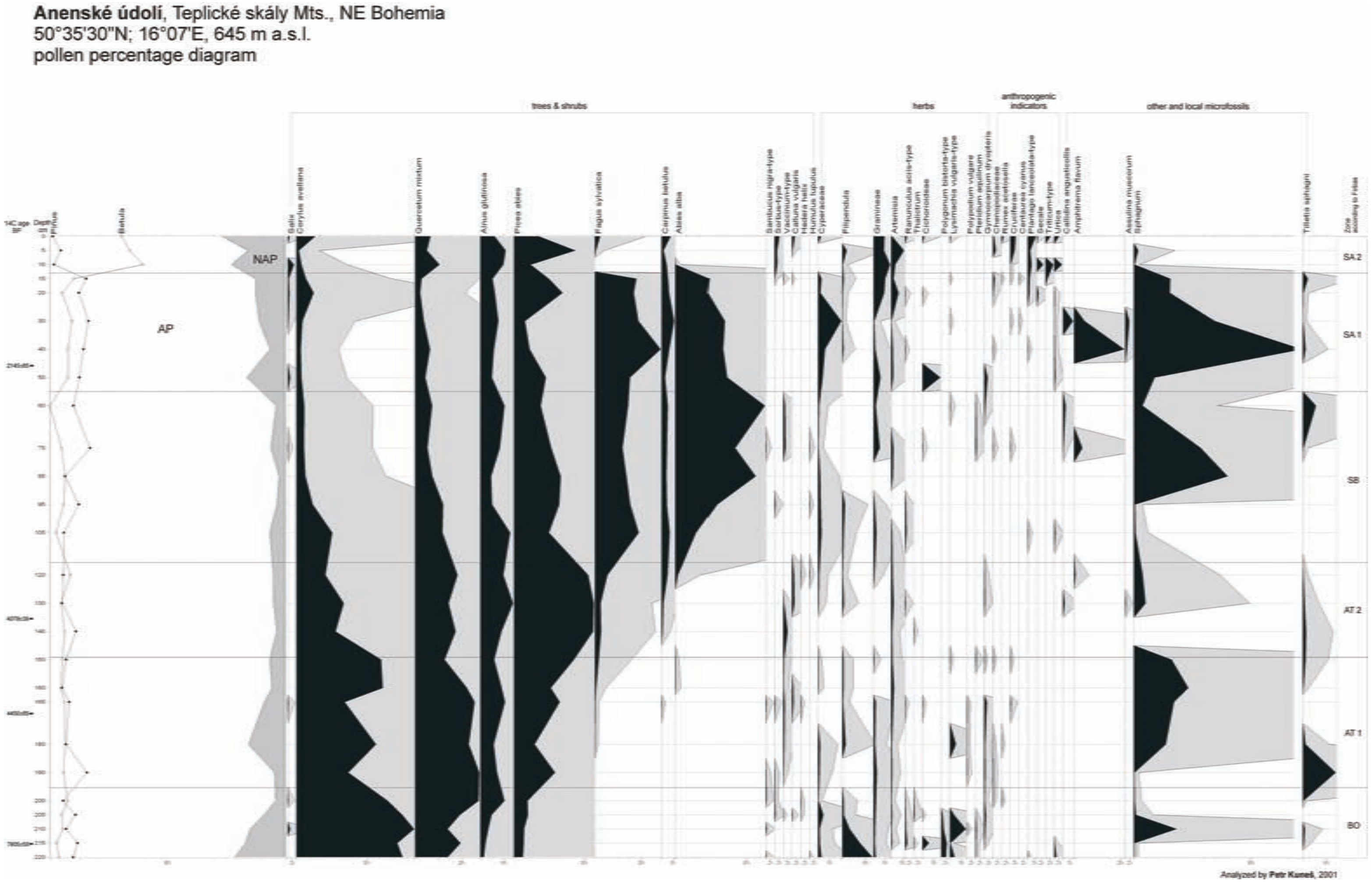

Fig. 13: Pollen diagram from Anenské údolí, Teplické skály.

Other trees (mainly *Pinus, Betula,* and *Corylus*) retreated to extreme habitats on the rocks and small sandstone plateaus. Only hazel showed its permanent larger presence in the area due to sufficient ecotones and a conveniently warm and wet climate. Species of mixed oak woods, which included some newcomers (*Acer, Fraxinus*), were probably the typical vegetation cover of non-sandstone areas around the Adršpašsko-teplické scaly Mts., or large plateaus on the sandstone area itself.

In other sandstone areas, with a warmer climate, the vegetation cover must have developed differently during the same period. Kokořínsko was the region with warmest and driest climate and the lowest elevations.. Unlike the above-described montane regions, mixed oak wood communities probably developed in this area. In contrast to the present, the high nutrient status and carbonate contents in the soils and the bedrock itself allowed the common occurrence of demanding species of moist oak woodlands. Unfortunately, we have no direct evidence (i.e. a pollen record or plant macroremains) of this so far, . Nevertheless, the high biodiversity of ecosystems was shown by the subfossil snail fauna discovered under the rock shelters and dated to the Middle Holocene (Ložek 1997, 2000). The composition of this fauna is close to recent communities on calcareous bedrock. A similar situation could have also occurred in the Bohemian Switzerland region, as supported by the first pollen analyses (Kuneš and Pokorný unpublished) from probably Middle Holocene layers of the "Jelení louže" peatbog. These data show the surprising role of *Tilia*, *Quercus*, *Ulmus*, and *Fraxinus* in the forest cover directly within the sandstone area. The role of pine in this sandstone region must be questioned. Only a minor role can be reconstructed from the results of pollen analyses, from the Adršpašsko-teplické skály region. A greater role can only be reconstructed in the warm and dry areas of Kokořínsko and Český ráj. The results of pollen analyses from Jestřebská kotlina (Jankovská 1992) confirms this hypothesis.

Peculiar vegetation conditions were recorded in the Broumovsko region during the Late Atlantic (AT 2). *Fagus* and *Abies* were the first species that began to spread and compete with spruce and hazel in climatically mesic situations. What is surprising, is the concurrent massive spread of *Carpinus*, which usually appears, in most of the Czech basin, no sooner than at the beginning of the Older Sub-Atlantic (SA 1). The unusually early and diachronous spread of *Carpinus* in the Broumovsko region has its analogy in neighbouring territories of Poland, copying the outer Carpathian foreland (Madeyska 1989; Latałova 1989; Ralska-Jasiewiczowa 1989). The expansion of *Carpinus* was preceded by *Abies* in the Bystrzickie Mts. (Poland) and in the Teplické skály Mts. on the Czech side. Stands with prevailing *Carpinus* were probably localised to the peripheral parts of the sandstone areas or accumulations of eroded sand - sandy colluvia. Local conditions at the peat bogs, in the gorges, remained more or less constant, however, peat accumulations in shallow gorges could have been eroded by heavy rainfall.

Environment during the Late Holocene (around 4 500 BP conv. – present)

With the beginning of the Subboreal (SB), an unstable, more continental climatic setting came, affecting mainly the lower altitude sandstone areas. Simultaneously, at the end of the Bronze Age, areas around Kokořínsko, Českolipsko, Český ráj as well as Labské pískovce underwent the first phase of heavy human influence (Pokorný 2004). That resulted, together with changes towards climatic instability, in the whole rank of northern Central Bohemia in irreversible decalcification, erosion, and changes in the soil chemistry into oligotrophic or extremely oligotrophic in the case of sandstone areas. This was strongly shown in the Kokořínsko region by abrupt changes to the molluscan fauna connected with vegetation changes to poor pine-woods or acid oak-pine woods, which have remained until the present time. The speed and the consequences of this change was equivalne to a local catastrophe, therefore, referred to as the 'Lausitanian Catastrophe' (Ložek 1997; Cílek *et al*. 1996). Vegetation changes, probably connected with the same event, are recorded in the Middle Labe River acidic gravel terraces in the southeastern margin of the Kokořínsko area (Pokorný 2004). In the profile near Tišice, an abrupt shift from mixed oak woods to pine-dominated vegetation has been radiocarbon-dated to the Late Bronze Age, and is connected with the acceleration of human impact. These strong changes were not recorded in the Broumovsko region because of its montane character and the sparsity or absence of human colonisation in prehistory (only minor human activity in the foothills of Broumovsko-sandstones is demonstrated by continuous curves of *Plantago lanceolata* pollen). A fast invasion of *Abies* into existing stands of spruce and beech took place. Newly expanding tree species (*Fagus, Abies*) gradually restricted the expansion of spruce and its presence declined. Spruce probably retained its dominance at the bottom of sandstone gorges and at other inversion sites. What is completely unclear, is the potential occurrence of large, relic, pine-woods stated by many geobotanists to be present during the whole postglacial. From the palaeoecological finds the situation seems to be completely the opposite. Mainly during the end of the Atlantic and in the Subboreal, pine pollen attained very low values, which shows that pine at those times must have been confined to very extreme stands on the rocks with a minimal number of individuals. In Bohemian Switzerland, beech and silver fir forest occupied their maximum area at the same time, although pine was more common here than in the Adršpašsko-teplické skály region (Fig. 12).

The period of the Early Sub-Atlantic (SA 1) should reflect, according to the geobotanical conception, the potential natural vegetation. In the montane areas (Broumovsko and partly Bohemian Switzerland), such "climax" communities were represented by silver fir-beech forests on sandstone plateaus, gentle slopes and wide valleys. On the slopes and at the bottoms of the valleys, spruce and hornbeam were present as an admixture. Spruce-dominated stands were prevalent in the positions with strong climatic inversions, i.e. bottoms of narrow gorges and their slopes. Infrequent hornbeam, oak, lime and probably also maple and ash stands occurred mainly in peripheral parts of the sandstone areas, or in the foothills. The existence of relic pine stands has already been discussed above. A very restricted pine pollen occurrence probably refers to some isolated individuals on the rocks in the Adršpašsko-teplické skály region. In the Bohemian Switzerland area, extreme habitats with acidic pine stands were more common. The opposite situation probably existed in the areas of lower altitude (Český ráj, Kokořínsko), where it is possible to think about a greater importance for pine woods due to the different climate and stronger human impact.

In the first half of the Late Sub-Atlantic (SA 2), the composition of original stands remained unchanged by anthropic influences in montane areas, despite agricultural activity taking place in the foothills. Strong human impact in the forests can be dated to no earlier than the Late Middle Ages and in the Broumovsko area to only the nineteenth century. Timber extraction, resin production, and grazing contributed to deforestation and forest composition changes. Both the pollen record and historical data point to a massive spread of spruce to the prejudice of the originally dominant fir and beech. Spruce was not only favoured by foresters, but probably also by climatic changes that led to colder and wetter conditions during the Late Sub-Atlantic. During the twentieth century the spread of alien species contributed to change e.g. *Pinus strobus* which rapidly colonized a great deal of forest stands in sandstone regions and devastated their undergrowth.

General conclusions: Sandstone vegetation in time – specific features of long-term vegetation ecology in sandstone areas

The most important factor, which distinguished the sandstone vegetation from surrounding areas was, without doubt, the complicated geomorphology and geochemistry. This granted an existence to different and contrasting stands over a very small spatial scale, so that thermophilous communities of sandstone plateaus could exist alongside psychrophilous communities at the bottoms of sandstone valleys and gorges, pioneer vegetation of rock-walls and peat-bogs. This diversity has existed since the end of the Late Glacial. Important diversity also exists between individual sandstone areas within the Czech Republic. This diversity is best expressed in the vegetation development during the Holocene as demonstrated above.

Some authors consider the sandstone regions to be favourable for the survival of several tree species throughout the Full Glacial Period due to increased moisture (*Pinus, Betula, Juniperus, Populus*) and for more demanding species like *Picea* and *Corylus* (Peichlová 1979). The refugia of *Picea* and *Corylus* could be a few individuals surviving in microclimatically wet places protected from strong winds. Nevertheless, this claim is still only speculative, as the occurrence of all of these tree species has not yet been proven by direct evidence.

If compared with the surrounding landscapes, sandstone areas were more liable to invasions of new species into existing plant communities. This was probably due to the high diversity of habitats that did not allow the formation of “climax” communities over a large spatial scale and prevented the population pressure of only a few species to play an important role (the so-called mass effect). Open stands could offer refuges to newly spreading species both in the past (e.g. *Picea abies*, *Fagus sylvatica, Carpinus betulus*) and recently (e.g. *Pinus strobus* - an alien invasive species).

The majority of sandstone regions are under the management of Protected Landscape Areas and one National Park. Future development of their ecosystems should be discussed in the light of their development in the past. Acceptance of the extremely dynamic nature of sandstone ecosystems should help against rash interferences leading to their further degradation through extreme “conservationist” management.

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Holocene acidification process recorded in three pollen profiles from Czech sandstone and river terrace environments

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Introduction

Late Quaternary climatic changes had dramatic effect on the terrestrial biosphere. In temperate mid-latitude regions of the Northern Hemisphere, vegetation belts migrated over several thousands of kilometers. These macroscale vegetational changes were accompanied (and were partly in response to) changes in soil properties. The ways in which soil-vegetation relationships have evolved, and particularly the response of vegetational and pedogenetic processes to climatic change, are of fundamental importance in understanding the dynamics of contemporary ecosystems. Viewed in this light, acidification is a long-term natural process that occurs especially during warm phases of Quaternary climatic cycle (Iversen 1958; Birks 1986). It is characterized by loss of cations (namely bivalent bases – Ca^{2+} and Mg^{2+}) that are normally bound to clay minerals in the soils. Under wet and warm conditions, bases are leached from these complexes, being dissolved in percolating water and transported out of the ecosystem (and finally through the rivers to the sea). This process results in change in species composition and productivity of the ecosystems. The dynamics of acidification is seriously modified by climatic changes, biotic influences, and, during the Holocene, also by human intervention (Bell & Walker 1992).Anthropogenic activities contribute to the acidification through removal of biomass (grazing, mowing, woodcutting, harvesting without subsequent manuring) and through triggering the soil erosion. Positive backbound mechanisms may play an important role in case of biological control of acidification. To give a simple example from Central Europe: At the first stage of acidification coniferous trees (namely *Pinus sylvestris, Picea abies,* and *Abies alba*) spread within broadleaf forests. During the decomposition of coniferous falloff, humic acids are produced in great quantities. Organic compounds in soils change from mull to mor humus. This efficiently speeds up further

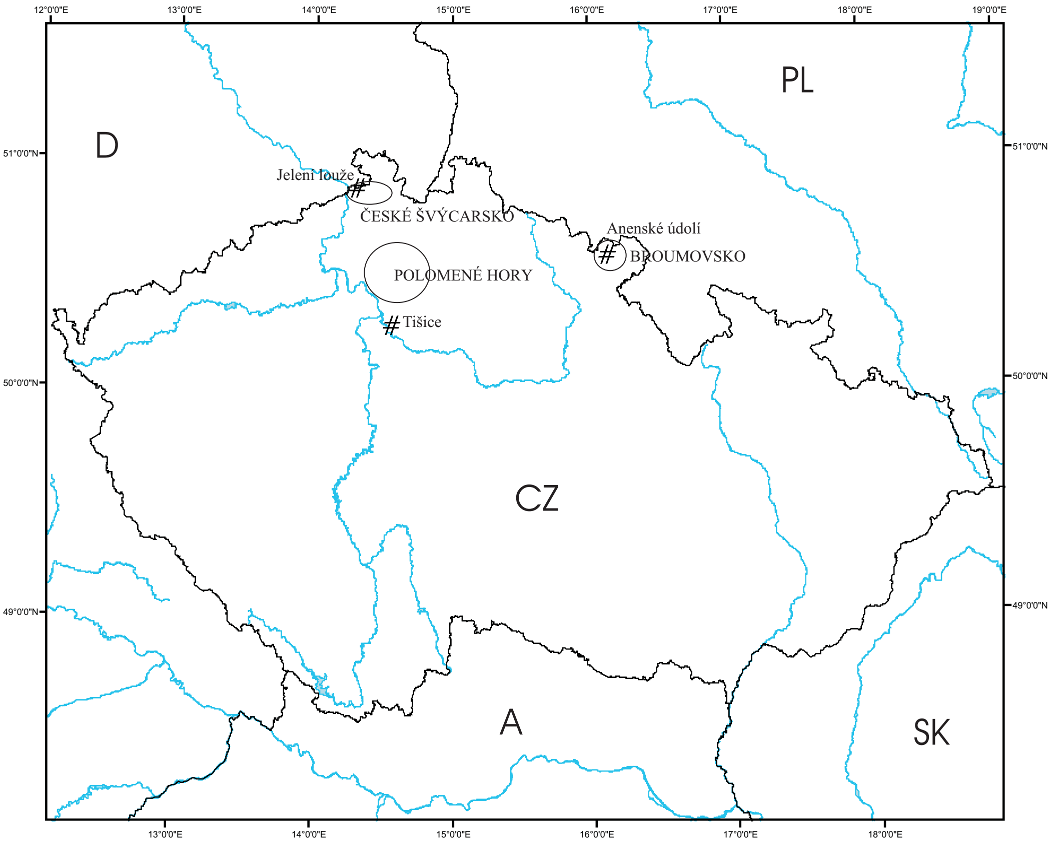

Fig. 1: Territory of the Czech Republic and the location of sites and regions mentioned in the text.

acidification and soils structure is changed in the process called podzolisation. Usually also upperlayer of underlying bedrock is being leached and decalcified.

Due to its long long-term nature, acidification processes can be best studied in secular to millennial time scale. Pollen analysis is appropriate tool for this as it enables to record time scales long enough and because vegetation corresponds directly to local geochemical changes.

The pollen and sediment chemistry evidence

Soils developed on relatively acidic bedrock are often more sensitive to loss of nutrients than those on calcareous substrata. This is why best evidence for Holocene acidification in the Czech Republic comes from sandstone regions and from river environment with extensive cover of acidic sands and gravel. In the following, we will give three examples of profiles, where acidification process can be studied (location of profiles indicated in Fig. 1).

Anenské údolí, Broumovsko sandstone region

The site, a topogenic mire in the bottom of a valley at 645 m a.s.l. altitude, is surrounded by dramatic relief with sandstone rocks and gorges. Present vegetation is dominated by acidic

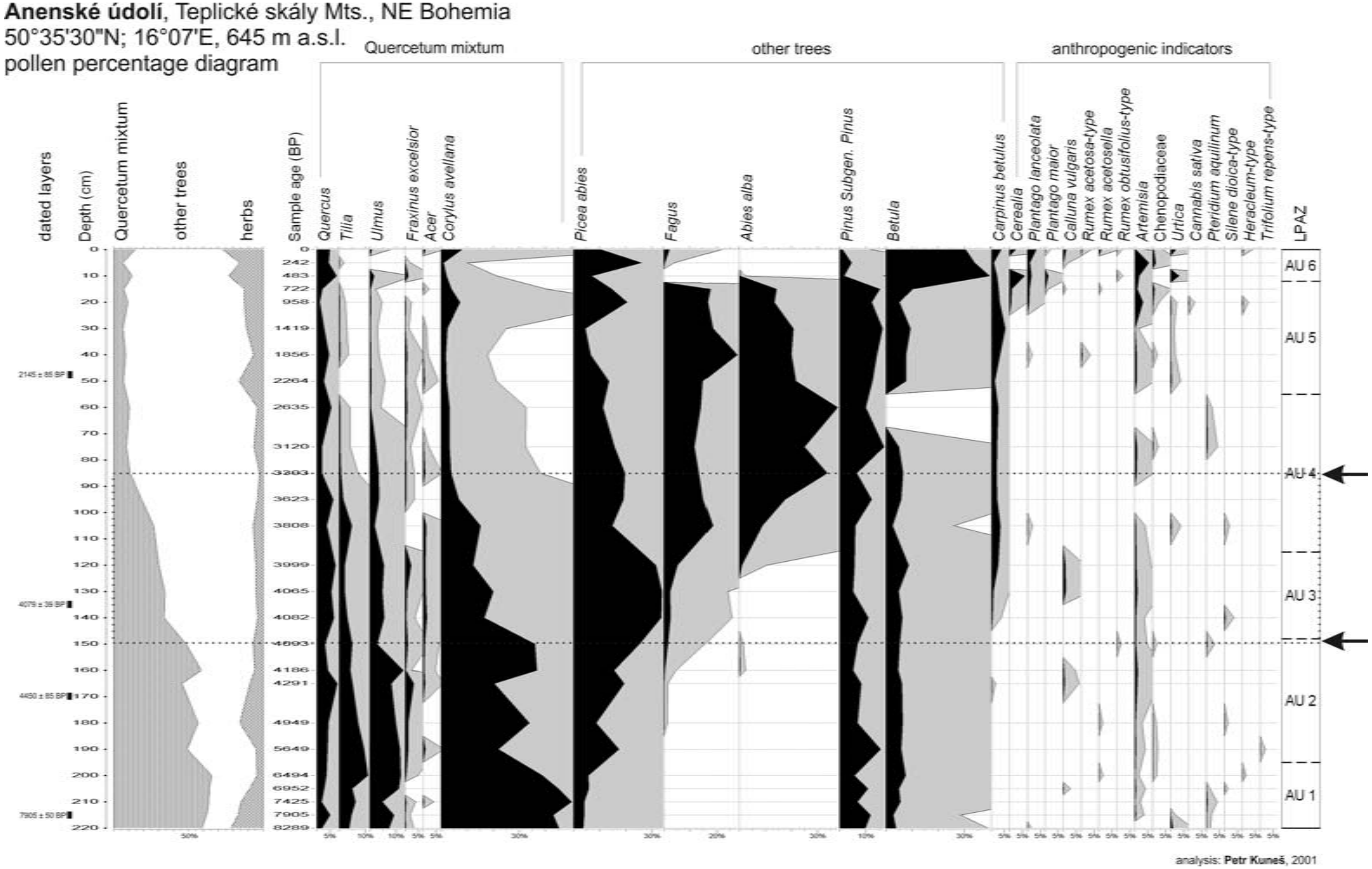

Fig. 2: Simplified percentage pollen diagram from Anenské údolí site. The period of acidification indicated at right.

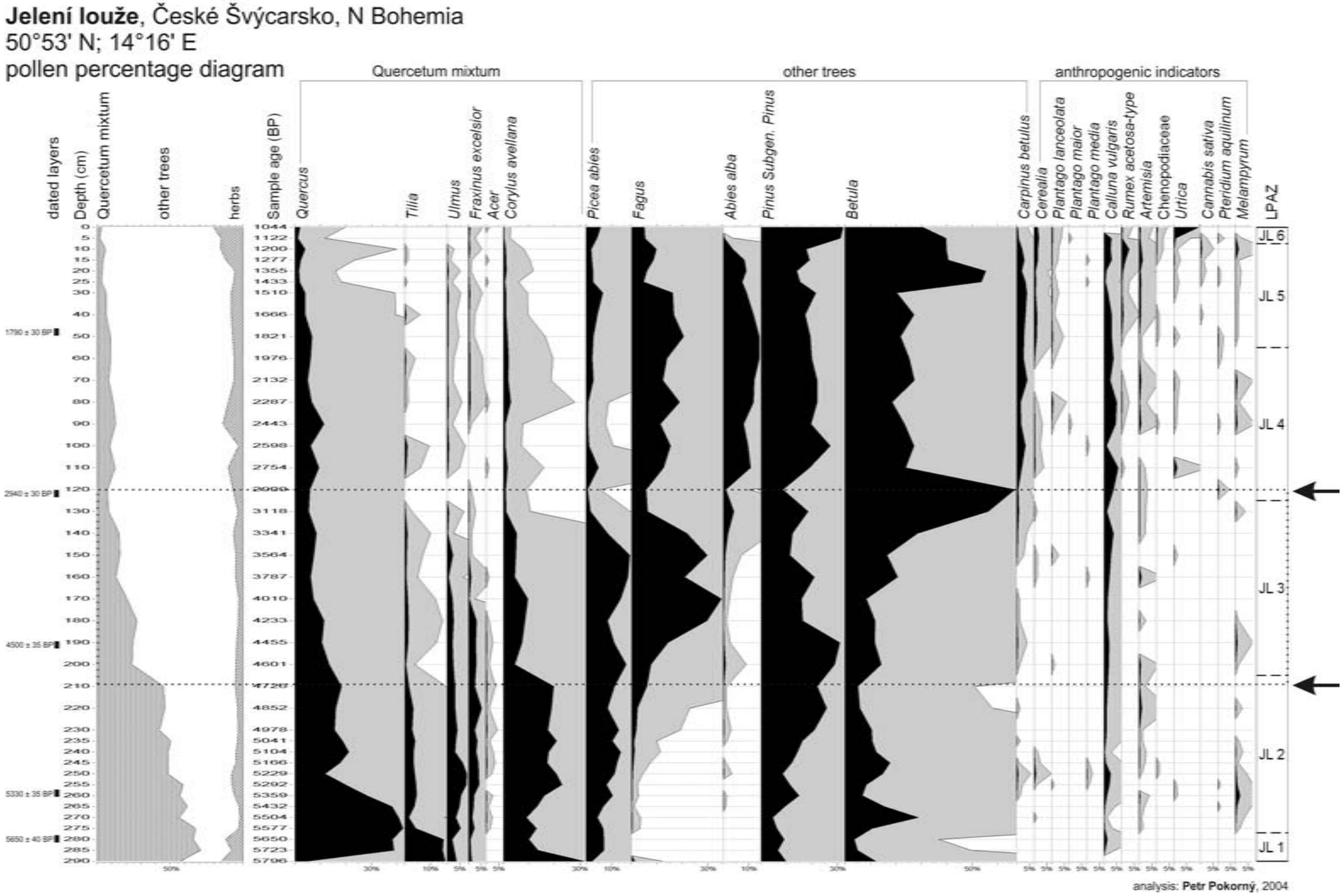

Fig. 3: Simplified percentage pollen diagram from the Jelení louže site. The period of acidification is indicated on the right side.

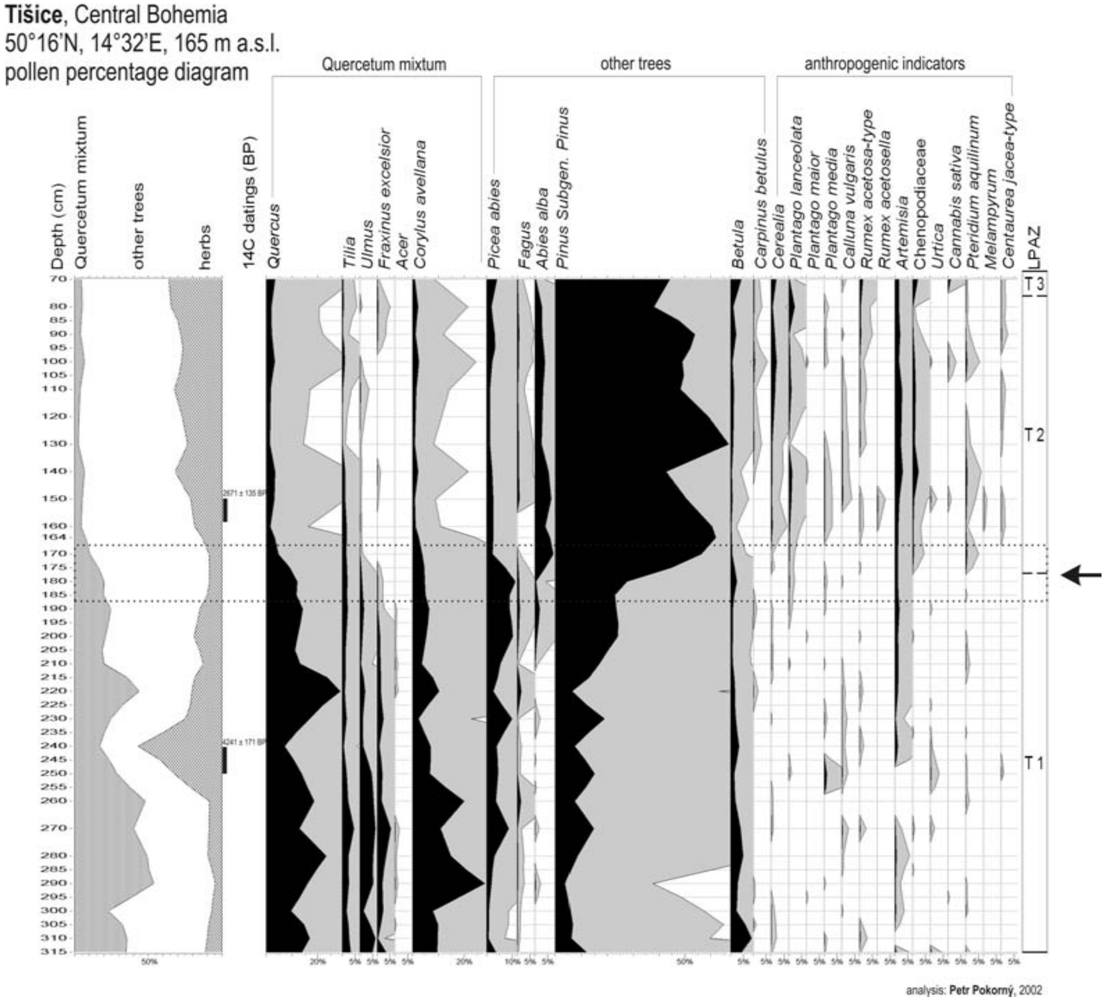

Fig. 4: Simplified percentage pollen diagram from the Tišice site. The moment of acidification is indicated on the right side.

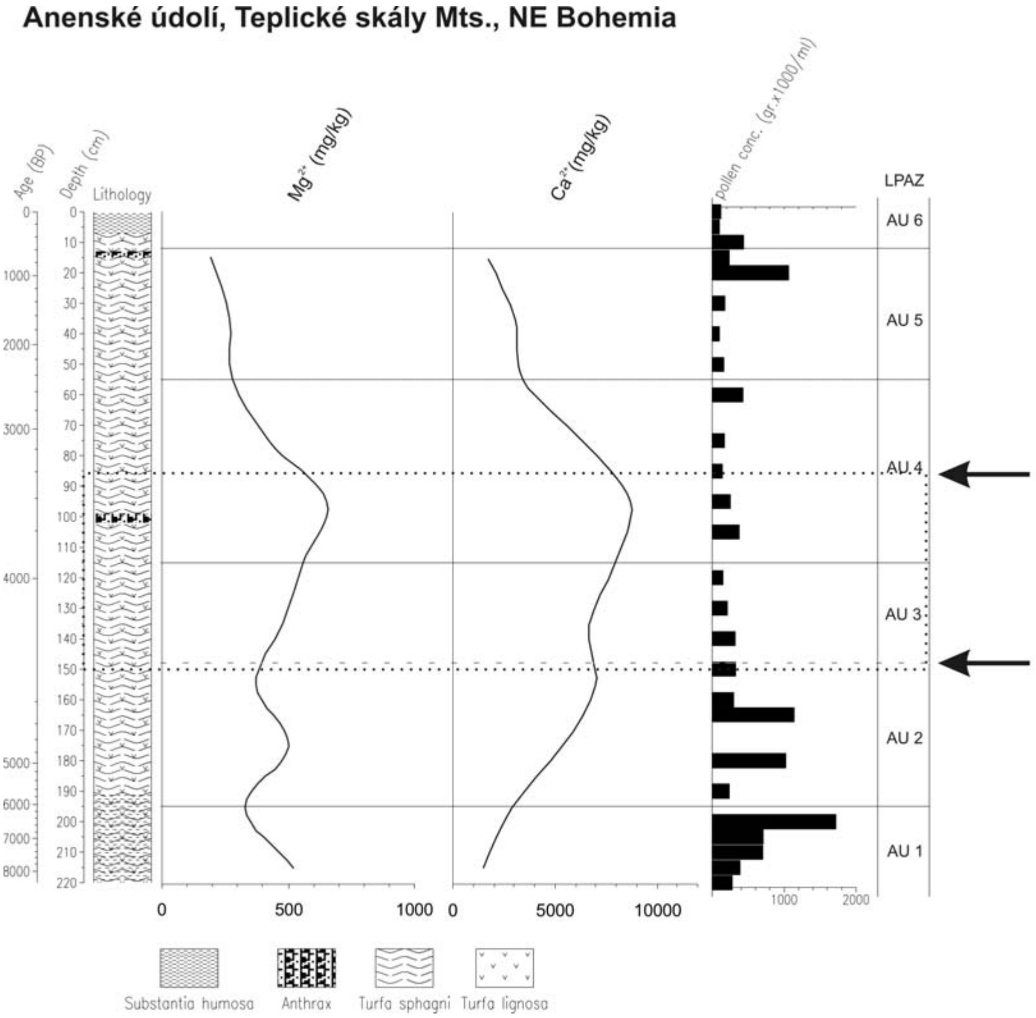

Fig. 5: Ca^{2+} and Mg^{2+} total concentrations diagram from Anenské údolí site. The period of acidification (derived from pollen diagram; Fig. 2) is indicated on the right side

pine woodland in relatively dryer situations and by spruce plantations in the bottoms of the valleys. Climate of the region is oceanic and relatively cold (mean annual temperature around 7°C and rainfall around 800 mm).

In the pollen diagram (Fig. 2) we see gradual vegetation change from mixed oak woodlands to communities dominated by spruce (*Picea abies*), beech (*Fagus sylvatica*), and silver fir (*Abies alba*). This change can be observed between 150 and 85 cm – i.e. between ca 4 100 and 3 400 B.P. according to radiocarbon chronology. While the decrease in demanding tree species is gradual, expansion of constituents of oligotrophic woodland communities is stepwise: In the first step this is the expansion of *Picea abies*, followed by strong increase in *Fagus sylvatica* and *Abies alba*. Also hornbeam (*Carpinus betulus*) appears in this stage. As human impact indicators virtually lacking in the pollen record we may assume that above-described process of acidification was controlled entirely by natural influences in this case.

To get more insight to process of acidification, samples for chemical analysis of Ca^{2+} and Mg^{2+} cations (Fig. 5) were taken directly from above-described peat profile. At first, concentration of both elements steadily rises (from about 190 to 95 cm). This must be the result of increased leaching from the soils in the catchment after invasion of beech (*Fagus sylvatica*). Leached cations were than bound into peat organic matter (Digerfeldt 1972). Maximum concentrations are found at the level of 95 cm – this is probably the result of silver fir invasion (see *Abies alba* curve in pollen diagram). As already described above, the decomposition of coniferous falloff may speed up acidification process. Spread of coniferous forest in the catchment caused more Ca^{2+} and Mg^{2+} to be released from the soils. After the maximum at 95 cm, the concentrations of both Ca^{2+} and Mg^{2+} started to decline as their availability slowly decreased in the catchment. At this time finally, acidification process was completed.

Jelení louže, České Švýcarsko sandstone region

This pollen profile comes from a topogenic mire that is situated in relatively shallow sandstone gorge, about 400 m a.s.l. The site is surrounded by large sandstone plateau bordered by well-developed rock formations. Today, this area is extremely acidic with species-poor vegetation dominated by pine and birch. Surface pollen spectrum (0 cm in the pollen profile) reflects the present vegetation conditions. Local climate is rather oceanic with relatively high annual rainfall (nearby station at Chřipská: 934 mm).

Acidification process is seen in the pollen diagram between the depth of 210 and 120 cm (Fig. 3).This corresponds to the time period between about 4700 B.P. and 2900 B.P. according to radio-carbon dating. As in the case of Anenské údolí site, although final consequences of acidifications are very deep, the process itself is rather gradual. Vegetation response to acidification has a stepwise character. The starting point is the vegetation of rich mixed oak woodlands with significant admixture of hazel (*Corylus avelana*). In the first step, the curves of demanding trees (*Quercus, Tilia, Ulmus, Acer, Fraxinus*, and *Corylus*) decline in favor to expanding beech (*Fagus sylvatica*). During the second step we may observe another decrease demanding broadleaf trees, but also the in *Fagus* that is replaced by silver fir (*Abies alba*). In the same period, anthropogenic indicators are very low in the pollen diagram, excluding again the possibility of anthropogenic control of acidification process.

Tišice, middle Labe region

Unlike the previous two cases, this site is situated at low elevation (165 m a.s.l.) and in very different geomorphologic situation – in a flat landscape within a broad valley of Labe River, adjacent to Polomené hory sandstone area. The valley is filled with sandy and gravel substrata of Pleistocene river terraces. We may trace the history of human impact in the region deep into Neolithic period from the pollen-analytical investigations and according to archaeological excavations (Dreslerová & Pokorný 2004). Today, this is an agricultural landscape with some little remains of acidic pine woodlands. Local climate is warm, dry, and relatively continental (mean annual climatic characteristics of nearby city of Mělník: 8.7 °C, 527 mm).

Older part of the pollen diagram (Fig. 4) is characterized by high pollen curves of *Quercus, Tilia, Ulmus, Fraxinus,* and *Corylus*. Acidification is much more dramatic process than in previous two examples. It is seen in pollen diagram as sudden vegetation change between 185 and 175 cm depth. This period corresponds roughly to 3 000 B.P. according to radiocarbon chronology. Demanding trees of mixed oak woodlands decline in this point and curves of

Pinus and *Abies alba* increase significantly. This event is synchronous with sudden rise in anthropogenic indicators – both arable and grazing indicators. Close correlation of both phenomena suggests an anthropogenic control of acidification process. This was probably the reason why vegetation change is so sharp in this case.

Discussion and conclusions

Sandstone and river terrace landscapes in the Czech Republic experienced considerable changes in their productivity, species richness and composition during the Late Holocene. These areas, today extremely acidic and oligotrophic, were much more nutrient rich during most of their Holocene history. In the example of three pollen profiles we could see how process of acidification may differ in the timing and in its dynamics. These differences are due to different local climatic setting and, more important, due to different human impact histories.

First evidence for Late Holocene acidification Czech sandstone landscapes was given by V. Ložek (1998). His arguments are based on palaeomalacological finds from sedimentary fills of rock shelters at Polomené hory sandstone area. Middle Holocene snail communities were surprisingly rich in species, whereas at present the areas in question are characterized by only very poor communities consisting of few most resistant species. Strong decrease in snail species richness – from 41 species to only 6 in case of a single site – coincides with the Final Bronze Age period (about 3 000 B.P.). This suggests a dramatic transformation of ecosystem during respective time. For the explanation of this phenomenon, Ložek proposes model of environmental collapse induced by climatic change associated with human activity – woodland clearance and grazing. This model corresponds very well to our present data from Tišice site, where vegetation change to more acidic conditions is synchronous with significant increase in human impact. Also the timing of both acidification events is about the same (Late to Final Bronze Age). In contrast to this, pollen evidence from Broumovsko and České Švýcarsko sandstone regions suggests more gradual acidification that took place between ca 4 700 and 3 000 B.P. (Late Neolithic to Final Bronze Age according to archaeological chronology). This difference is probably due to the lack of prehistoric human influence which was negligible in two later mentioned regions.

According to arguments presented in this paper, soil acidification and ecosystem depauperization is a process that is natural under climatic conditions of Central Europe. Sandstone substrata are especially sensitive to loss of basic nutrients. Around 3 000 B.P., natural process of acidification culminated in both sandstone regions under study. This happened obviously without influence of man. Nevertheless, human impact may have been an important factor that speeded up this process. This happened during Late and Final Bronze Age (i.e. at about 3 000 B.P. again) in case of Polomené hory sandstone area and in nearby-situated terraces of Middle Labe River. Woodland clearance, grazing and subsequent soil erosion were probably most important control mechanisms that played a role.

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