Forest vegetation of the last full-glacial period in the Western Carpathians (Slovakia and Czech Republic)

Lesní vegetace v období posledního vrcholného glaciálu v Západních Karpatech

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Palaeobotanical data from last full-glacial period in eastern-central Europe repeatedly confirm the existence of parkland landscapes with coniferous trees at relatively northern latitudes. However, up to now, the absence of fossils prevented a study of the full-glacial vegetation in the mountain areas of the Western Carpathians – a region crucial to determining whether there were refugia for present European forest biota during the Last Glacial period. This paper provides new pollen and macrofossil evidence from this key region, dated to a critical period in the Weichselian full glaciation (between 50 and 16 ka 14C BP). Our data from two study sites in the Western Carpathians (part of today's Slovakia and easternmost Czech Republic – Moravian region) support the hypothesis that well-protected and relatively humid valleys in this mountain range were, as far as climate is concerned, favourable for forest vegetation during the last full-glacial period. These forests were similar to present Siberian coniferous taiga. In the lowlands and highlands that surround the Western Carpathians, there occurred a diversity of parkland landscapes: mosaic of steppe communities and tundra patches. However, we use the example of one site in central Bohemia, near what is the present city of Prague, to show that trees may also have occurred here on sites with a suitable local climate.

K e y w o r d s: coniferous taiga, palaeoecology, pollen analysis, Weichselian Pleniglacial, Western Carpathians

Introduction

Earlier concepts of the environments that existed in Central Europe during the last full-glacial period saw the periglacial landscapes as inhospitable steppe, bush- and forest-tundra. New evidence from different sources has gradually changed this view. This is especially true for results published since the 1950s on from the lowlands to the north, west and south of the Carpathian Range's extension into Central Europe. Charcoal from a number of Upper Palaeolithic archaeological sites in central and southern Moravia and the Pannonian Basin (in both Austria and Hungary) provide evidence of collected and sometimes in-situ wood material (Slavíková-Veselá 1950, Kneblová 1954, Klíma 1963, Opravil in Valoch et al. 1969). Although most of the finds are of cold- or drought-tolerant coniferous taxa (*Pinus sylvestris*, *Pinus cembra*, *Larix*, *Picea* and *Juniperus*), they also regularly include more demanding tree taxa *Abies*, *Corylus*, *Quercus*, *Fagus, Fraxinus*, *Ulmus*, *Taxus* and

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Carpinus. The available charcoal evidence from the last full-glacial period from archaeological sites and loess profiles are listed and comprehensively summarized in Musil (2003), Rudner & Sümegi (2001), Willis & van Andel (2004) and Hajnalová & Hajnalová (2005). For a long time, these finds were interpreted in the light of the traditionally-held concept of an inhospitable, cold, full-glacial mammoth steppe, and were considered unreliable. Serious doubts about the validity of the hypothesis of a "mammoth steppe" environment of Gravettian mammoth-hunters were raised after the discovery of buried peat dated to 25,675±2750 14C yr BP at Bulhary (Rybníčková and Rybníček 1991), not far from the famous Gravettian site of Dolní Věstonice (Czech Republic), where occupation was dated to the same period. The Bulhary pollen diagram indicated not only a coniferous forest vegetation containing *Pinus sylvestris, P. cembra, Picea, Larix* and *Juniperus* but also included sporadic pollen of some temperate deciduous trees like *Ulmus, Corylus, Quercus, Tilia* and *Acer*. If these trees were present locally, which is not certain, this would be a rather surprising find for the full-glacial period at a latitude of 48°50' N. Nevertheless, the Bulhary site is situated in the foothills of the warm Pálavské vrchy hills, which have a complicated relief, high insolation of south-oriented slopes and favourable calcareous rocks. Already in the 1960s, Frenzel (1964a, b) proposed the possibility of the local occurrence of demanding tree taxa in this region. Nevertheless, there is still the possibility of long distance pollen transport.

There is an abundance of tree taxa in pollen diagrams from Hungary, dated to the transition from the Pleniglacial to the Late Glacial period (around 17 ka BP in the case of the Bátorliget site; Willis et al. 2000). Here, the relatively early presence of pollen of broadleaf trees may indicate the proximity of a full-glacial refugia. North of the Carpathians, at the transition to the Polish plain, several pollen profiles have provided evidence of coniferous forests domined by *Pinus cembra* and *Larix* during interstadial periods in the Weichselian Pleniglacial (Ralska-Jasiewiczowa 1980, Mamakowa 2003). Valuable information on vegetation development, climatic conditions and biostratigraphy during the Last Glacial period in NW Europe are given by Behre & Lade (1986) and Behre (1989). For E Europe (Russian Plane), important information on the environmental conditions during 33–24 ka BP interval is in Markova et al. (2002).

Willis & van Andel (2004) argue, on the basis of the above-mentioned data, that in the lowlands surrounding the western extension of the Carpathian range there were full-glacial refugia for many tree species such as *Picea*, *Pinus*, *Larix*, *Juniperus*, *Salix*, *Betula*, *Fagus*, *Ulmus*, *Quercus*, *Corylus*, *Sorbus*, *Carpinus*, *Rhamnus* and *Populus*. However, they found it difficult to establish from the fossil evidence whether these trees grew in isolated patches within an otherwise open steppe-tundra landscape or formed an open-canopy forest. Recent palaeoclimatic simulations of the Stage 3 Project (Barron & Pollard 2002, Barron et al. 2003, Pollard & Barron 2003) suggest that full-glacial conditions in eastern-central Europe were not nearly as severe as previously suggested. Related biome model simulations for the last full-glacial period indicate that the central and eastern-central European landscape could have supported true taiga forest (Huntley & Allen 2003). This interpretation was accepted by Willis & van Andel (2004) and led them to suggest that "during the last full-glacial interval the central and E European landscape was covered by taiga/montane woodland, which in some regions also contained isolated pockets of temperate trees." This climatic cooling during the Last Glacial Maximum changed atmospheric circulation patterns in W Europe and around the Alps. Florineth & Schlüchter

(1998) argue that the winds bringing moisture from the Atlantic Ocean moved to the south of the Pyrenees and the Alps as a result of the southward shifting of the northern polar front. Germany, located on the northern side of the Alps, became much drier as a result. The southern winds were bringing moisture to the southern flanks of the Alps and further to the east into the Carpathians, Pannonian Basin, eastern regions of Austria and Moravia. These regions might have received sufficient moisture from the Mediterranean and Adriatic Seas for trees to survive through the Last Glacial Maximum.

Material and methods

Study sites (Fig. 1)

Šafárka (48°52'55"N; 20°34'30"E; 600 m a.s.l.), NE Slovakia

The site of Šafárka is situated 8 km south from Spišská Nová Ves, on the northern rim of the Slovenské Rudohorie Mountains. Today, the area is generally mild and humid (mean values: July 17°C, January –5°C, annual precipitation 1000 mm). In this area, fossil dolines (sink holes) developed during the Quaternary in the gypsum bedrock of Upper Permian age (Novotný 2002). In one of these dolines, about 20 m wide, 30 m long and nearly 50 m deep, an organic sediment (peat) profile was sampled directly from a wall of strata above the gypsum bedrock. The organic strata were overlain by about 5 metres of mostly inorganic clayey material. Samples for pollen analyses were taken in the field at intervals of 5 cm. At the same time, single samples of plant macrofossils (mainly wood and cones of conifers) were collected, regardless of chronological order. It was impossible to

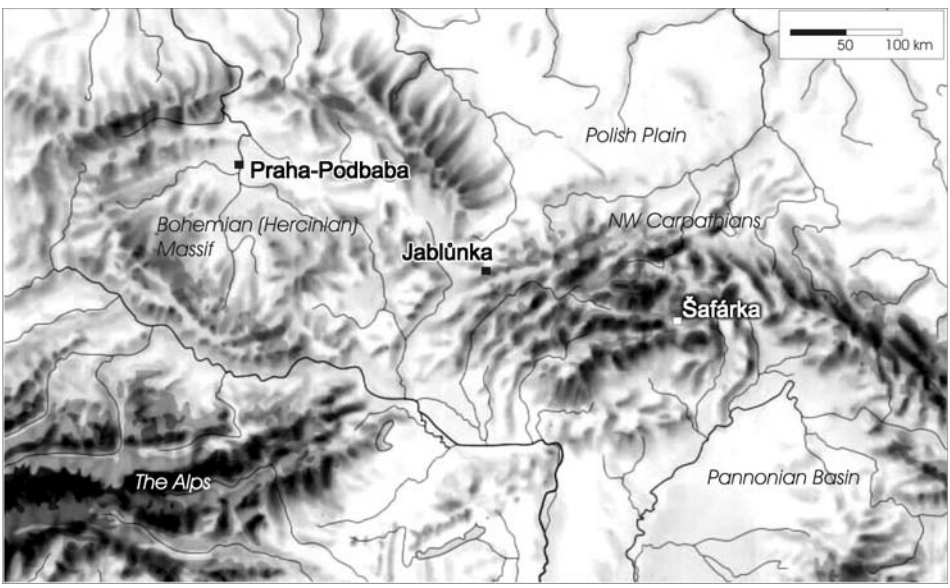

Fig. 1. – Orographic map of eastern central Europe giving the location of the sites investigated. The map includes the Czech Republic, Slovakia, Hungary, Austria, Poland and Germany.

adopt a better way of sampling, as the site was part of an active gypsum quarry and field conditions were very dangerous and complicated. Immediately after sampling the deposit was destroyed by mining. The results for the Šafárka site are published in Jankovská et al. (2002). In this paper, further information on the stratigraphic conditions and palaeoecological interpretation of the results is given.

Six macrofossil samples collected from the profile were 14C dated in the Faculty of Natural Sciences, Charles University, Prague, Czech Republic using the conventional (decay-counting) method. Unfortunately since the material came from an already disturbed site, it is impossible to estimate the samples' original exact position in relation to the pollen sequence. The range of these unstratified radiocarbon dates only permit a determination of the minimum time-span of the profile. Later on, four additional AMS radiocarbon dates were obtained at the Institute of Physics, University of Erlangen-Nürnberg, Germany from another two unstratified *Picea* macrofossils and for material from the bottom part of the sequence (90 and 115 cm; bulk peat samples – for all results see Table 1).

Table 1. – Radiocarbon ages for the Šafárka section.

Lab. no.	Type of material	Stratigraphic position	Radiocarbon age
CU 1600 (conventional)	wood	unknown	16,565 ± 415 BP
CU 1763 (conventional)	*Larix* cone	unknown	18,287 ± 1,512 BP
CU 1656 (conventional)	*Picea* cone	unknown	26,509 ± 480 BP
CU 1655 (conventional)	*Larix* cone	unknown	30,186 ± 1,935 BP
CU 1761 (conventional)	wood	unknown	31,883 ± 3,091 BP
CU 1762 (conventional)	undetermined cone	unknown	32,008 ± 3,593 BP
ERL-7352 (AMS)	*Picea* cone	unknown	44,592 ± 1,112 BP
ERL-7353 (AMS)	*Picea* cone	unknown	48,539 ± 1,484 BP
ERL-4532 (AMS)	wood	90 cm	older than 52,000 BP
ERL-4533 (AMS)	wood	115 cm	older than 52,000 BP

Jablůnka (49°23'N; 17°57'E; 350 m a.s.l.), E Moravia (Czech Republic)

Jablůnka lies 9 km south of Valašské Meziříčí, in the valley of the Vsetínská Bečva river that cuts through the Hostýnsko-Vsetínské Vrchy (a mountain range that represents one of the westernmost projections of the Carpathians) in a north-south direction. The area today is mildly warm and humid (mean annual temperature 7.4°C; annual precipitation 768 mm). The flooding in 1997 removed a layer of coarse-grained colluvial sediments and uncovered a 28 cm thick layer of organic sediment at the river's edge. The peat layer was sampled at 1 cm intervals for pollen analysis and for radiocarbon dating (for results see Table 2).

Prague–Podbaba (50°06'45"N; 14°23'30"E; 190 m a.s.l.), central Bohemia (Czech Republic)

The site is situated within the northern edge of the present capital of the Czech Republic, Prague, within the deeply-cut valley of the Vltava river. The area today is warm and dry (mean annual temperature 8.7°C; annual precipitation just around 500 mm). A 1.2 m thick layer of highly compressed peat, buried under 23 m of colluvium, was discovered by drilling. Unfortunately, the drilling technique used was unable to sample any form of stratified profile. Therefore, peat in immediate contact with *Larix/Picea* wood (dated to 31,012±1,810 BP; see table 2) was sampled for pollen analysis at this single stratigraphic level.

Laboratory work and pollen diagrams

All samples for pollen and other microfossil analyses were treated using the acetolysis method (Erdtman 1960) after pre-treatment in concentrated hydrofluoric acid for 24 hours at room temperature. For pollen identification, a reference collection and the following keys and atlases were used: Faegri & Iversen (1989), Moore et al. (1991), Punt (1976–1996), Reille (1992-1998) and Beug (2004). Pollen nomenclature follows ALPADABA (the Alpine Palynological Data-Base). Pollen frequency was in most cases high and pollen grains well preserved.

Percentage pollen diagrams were compiled using POLPAL software (Walanus & Nalepka 1999). The pollen sum includes arboreal (AP), dwarf-shrubs and herbaceous (NAP) taxa, but not wetland taxa. The percentages of monolete spores, *Cyperaceae* and all non-pollen objects were related to the total pollen.

Results

Šafárka site

The organic material taken from the exposed wall of peat contained large numbers of plant macrofossils, particularly in the lowermost part of the section. These consisted mainly of large pieces of wood, cones and seeds of different tree species – *Picea* sp., *Larix* sp., *Pinus cembra* and *Pinus sylvestris*. Some of these finds were 14C dated (see Table 1) and represent direct evidence of the local presence of these taxa during a given time period, i.e. at least during the radiocarbon time interval between 16 and 48 ka BP. The age of the bottom part of the sequence (90 and 115 cm) is beyond the limit of radiocarbon measurement (older than 52 ka BP). Main attention was given to the pollen analysis of the profile. The pollen diagram (Fig. 2) is divided into five local pollen assemblage zones (LPAZ).

LPAZ SF-1: *Larix–Gramineae*; 115–120 cm.

The age of this zone is unknown as it is beyond the limit of the radiocarbon dating method (radiocarbon age over 52 ka BP was obtained from a small piece of wood found at 115 cm). The single pollen spectrum attributed to this zone represents vegetation conditions, which reflect a cool, continental climate. The absolute dominance of *Larix* pollen, always considerably under-represented in pollen spectra, confirms the dominant role of larch in the tree cover. This interpretation is supported by analyses of modern pollen spectra from the alpine and polar tree limits of NW Siberia (Jankovská 2007a and unpublished data). *Betula*, most likely *B. pubescens*, and *Pinus cembra*, along with *P. sylvestris*, occurred sporadically within the *Larix* stands. *Betula nana* grew in the undergrowth. Analogous boreal forests can be observed nowadays in some areas of continental Siberia. *Larix* is a tree species that today forms the polar tree limit in Siberia around the Arctic Circle. It also forms the alpine tree limit in many Siberian mountain ranges and the xeric forest limit in the transition to the S Siberian steppes (Kuneš et al. 2007). Larch is able to grow in regions with permafrost. Closed stands of larch with stone pine currently occur in Central Europe, e.g. right at the tip of the Aletsch Glacier in Switzerland, at an altitude of about 2000 m a.s.l. Relicts of this larch taiga-like vegetation formation were last extensively distributed

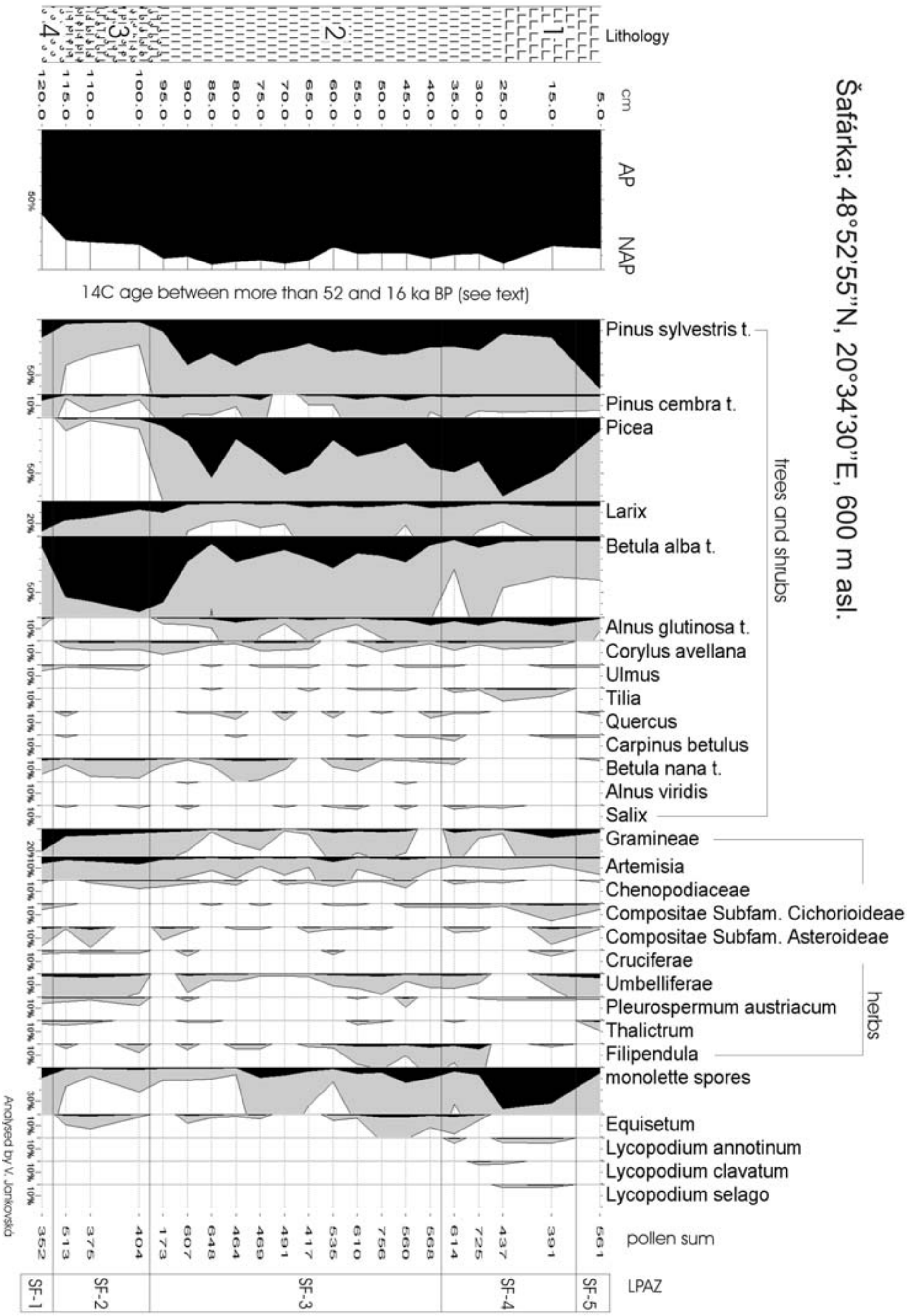

Fig. 2. – Pollen percentage diagram for the Šafárka site. Lithology description: 1 – clay with plant detritus; 2 – peat with remains of herbaceous plants and wood; 3 – peat with large pieces of wood; 4 – peat with wood and sand.

over the NW Carpathians during the Late Glacial. They were replaced during the rapid expansion of spruce at the beginning of the Holocene (Jankovská 1984, 1988). Such larch stands would have had a species-rich herbaceous layer, as in the contemporary vegetation in continental Siberia. Semi-open character of the forest canopy is illustrated by common occurrence of several herbaceous taxa in the profile: *Pleurospermum austriacum*, *Sanguisorba officinalis*, *Thalictrum*, *Polygonum bistorta/Polygonum viviparum*, *Phyteuma*, *Gentiana*, *Cardamine*, *Polemonium* and *Artemisia.*

LPAZ SF-2: *Betula-Larix*; 95–115 cm.

This zone is represented in the profile by a distinct layer of sediment dominated by large and small pieces of wood. The pollen of *Betula alba*-type prevails in the pollen spectra. *Larix* attains pollen values of about 10%, which is still relatively high for a tree with low pollen production and poor dispersal. Taking this into the account, such a pollen assemblage can be interpreted as larch forest with an admixture of birch. The local existence of this vegetation does not exclude the possibility of the occurrence of open habitats within the area – either wetlands or patches of steppe on rocks and steep slopes. These habitats could have been ideal for several plant taxa of an arcto-alpine distribution, growing together with xerothermic elements. The pollen finds of *Artemisia*, *Campanula*, *Centaurea jacea*, *Cerastium*, *Heracleum*, *Pimpinella major*, *Pleurospermum austriacum* and *Saxifraga granulata* fall into this category. A similar combination of taxa is currently present, e.g. within the alpine tree limit of Polar Ural Mts.

The presence, although sporadic, of pollen grains of some climatically demanding broadleaf trees, such as *Corylus*, *Ulmus*, *Quercus* and *Carpinus* is interesting. It supports the hypothesis of Willis et al. (2000) that these trees "must have survived in microenvironmentally favourable pockets", even in times when the boreal taiga dominated the area. Nevertheless, it is unlikely that these broadleaf thermophilous taxa occurred in the vicinity of the study site. The low pollen frequencies could indicate long-distance pollen transport from climatically more favourable regions (that could have been present e.g. in relatively warm and humid limestone areas of Slovakia).

LPAZ SF-3: *Picea-Pinus-Betula*; 40–95 cm.

The lower limit of this zone is marked by a sudden increase in *Picea* and *Pinus sylvestris*-type pollen and a similar sudden decrease in that of *Betula* and *Larix*. From this time on, *Alnus* is continuously present. Pollen of *Corylus*, *Ulmus*, *Quercus* and *Tilia* is regularly present. Sporadic pollen finds of *Fagus* and *Abies* are also recorded, while somewhat more pollen grains of *Carpinus* are present. This very distinct change in vegetation can be regarded as evidence of a climatic amelioration. Linked to the increase in temperature was probably a favourable change in the hydrological situation. The thawing of the permafrost and an increase in precipitation can be assumed to have followed the increase in insolation. The response to the shift to more favourable soil-moisture conditions and warmer climate was the rapid spread of spruce, alder (we may speculate about *Alnus incana* in this case) and also Scotch pine. Shady spruce stands were the main contender to replace the previously more-open, well-lit stands of larch. The same, of course, applies to the herb layer, which largely disappeared from the dark spruce stands.

This forest vegetation recorded within LPAZ SF-3 is probably most similar to the contemporary continental middle to northern spruce taiga.

LPAZ SF-4: *Picea-Alnus* – monolete spores; 10–40 cm.

This zone is characterized by maximum in pollen values for *Picea* and *Alnus*, and minimum value for *Betula alba*-type and *Pinus sylvestris*-type. This reflects the maximum forestation of the region. Spruce forest attained its maximum distribution and the vegetation in the region was probably very similar to that of the intermontane basins in the Carpathians much later, at the beginning of the Holocene climatic optimum (Jankovská 1988, 1991). Shady, closed spruce stands limited the distribution of most other trees. *Betula nana* was practically forced out due to that shading. The forest possessed the character of a coniferous ("middle") taiga, with an undergrowth of ferns and club-mosses (see high values of monolete spores, *Lycopodium annotinum*, *L. clavatum* and *L. selago*). *Larix* and *Pinus cembra* most probably remained an important forest component at those sites where spruce was unable to thrive.

The suggestion of a full-glacial climatic optimum at this time is corroborated by the increase in *Tilia* pollen. This situation currently occurs in SW Siberia, where lime (*Tilia sibirica* and *T. nasczokini*) has its eastern distribution limit and grows within the continental taiga forest belt. Also of interest is the find of a single coenobium of the green alga *Pediastrum simplex*. On the basis of its contemporary ecology, this is a demanding taxon both in terms of temperature and nutrient status (Komárek & Jankovská 2001).

LPAZ SF-5: *Pinus*; 5–10 cm.

This uppermost LPAZ was delimited on the basis of a sharp decrease in both *Picea* and *Alnus* pollen, and an equally sharp increase in the *Pinus sylvestris*-type pollen percentage. It also contains fewer monolete spores. Since this LPAZ is represented by a single pollen spectrum, any interpretation has to be made with caution. It is only possible to speculate that the climate became less favourable. This is what could have caused the retreat of spruce, thus providing more space for pine (maybe also *Pinus mugo*), which has greater light requirements.

The predominantly inorganic material overlying the peat profile is considered by geologists to have resulted from solifluction. Considering this and the radiocarbon data obtained from unstratified macrofossils (Table 1), it is likely that this LPAZ belongs to the onset of a climatically unfavourable phase during the maximum cooling of the Last Glacial Maximum.

Jablůnka site

From two radiocarbon dates obtained from the section (see Table 2), it is likely that this rather short, 28 cm thick sediment profile covers a relatively long time period, or it may alternatively include some hiatuses (Jankovská 2006). The pollen diagram (Fig. 3) indicates that the vegetation did not change much during this period as the pollen curves of the majority of taxa remain more or less constant. Therefore, the pollen diagram was not divided into zones (as was done in the case of Šafárka). Only the sample at a depth of 2 cm was distinctly different. Here *Picea* attains values over 20%, and pollen values of some

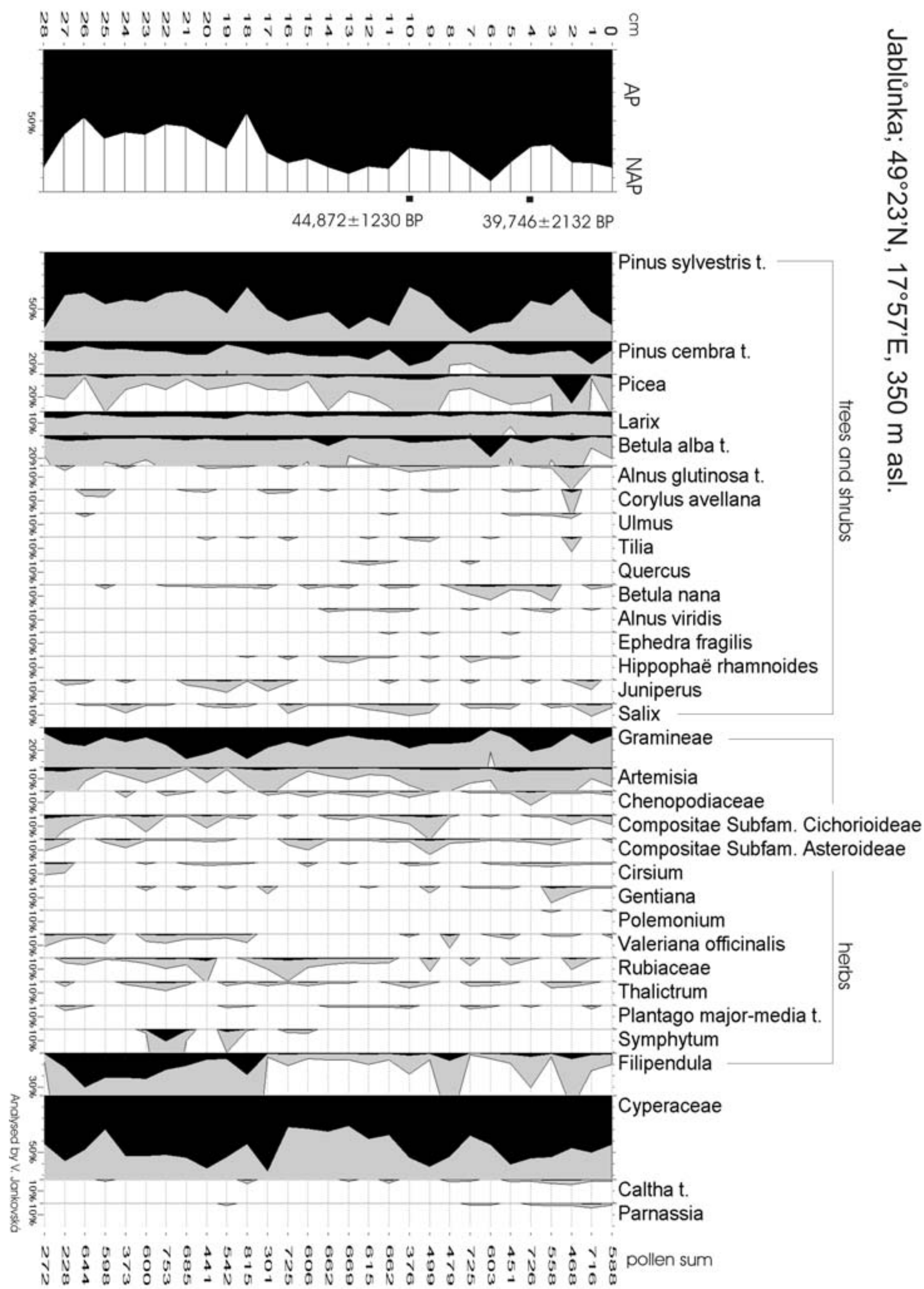

Fig. 3. – Pollen percentage diagram for the Jablůnka site. Lithology: From the bottom to the top a highly compressed and well decomposed peat.

broad-leaved trees (such as *Alnus glutinosa*-type, *Corylus avellana*, *Ulmus* and *Tilia*) are highest. Missing from this layer are *Betula nana* and *Alnus viridis*. All this suggests the occurrence of a warmer period, which resulted in vegetation similar to that observed in LPAZ SF-4 of the Šafárka profile. The landscape in the vicinity of the study site can be, if the above sample is ignored, reconstructed for the whole period (using the pollen diagram) and is analogous to the Siberian taiga forest, although less dense than in the case of Šafárka site (see the differences in the AP/NAP ratio). Differences are also found in relative proportions of the dominant trees. At Jablůnka, *Picea* was significantly less abundant and pine (*Pinus sylvestris*-type and *P. cembra*-type) more so. Furthermore, the values for broad-leaved taxa are lower here, this being most pronounced in the case of *Alnus glutinosa* type and *Corylus avellana* (again, with the exception of the sample at the 2 cm depth). All the above suggests that climatic conditions at Jablůnka were less favourable despite its lower altitude (250 metres less than Šafárka). It is likely it was drier, which limited forest growth – especially the occurrence of spruce, which requires wet conditions.

The occurrence of *Hippophaë rhamnoides*, *Juniperus*, *Betula nana* and a number of herbaceous plants (reaching higher proportions than at Šafárka) reflects the existence of open areas.

Table 2. – Radiocarbon ages for the Jablůnka and Prague–Podbaba sections (Erl – Institute of Physics, University of Erlangen-Nürnberg, Germany, CU – Faculty of Natural Sciences, Charles University, Prague, Czech Republic).

Lab. no.	Type of material	Stratigraphic position	Radiocarbon age
Erl-5837 (AMS)	Jablůnka; Peat-bulk	4 cm	39,746 ± 2,132 BP
Erl-4531 (AMS)	Jablůnka; wood	10 cm	44,872 ± 1,230 BP
CU-1872 (conventional)	Podbaba; *Larix/Picea* wood	2430 cm	31,012 ± 1,810 BP
CU-1875 (conventional)	Podbaba; *Larix/Picea* wood	2510 cm	40,418 ± 4,077 BP

Prague–Podbaba site

An interesting complement to the above data from the Western Carpathians is the pollen and macrofossil analyses of full-glacial peat found within the town of Prague in the Czech Republic. The single pollen spectrum shown in Table 3 comes from the analysis of peat that was extracted from inside a fissure within one of several larch (*Larix* sp.) trunks. This piece of wood was radiocarbon-dated to 31,012±1,810 BP (CU-1872; Table 2). The find of *Larix* trunks itself confirms the occurrence of this taxon in the region at that time. The pollen sample contained all the tree species found at the two sites in the Western Carpathians. The percentages are similar to that at the Jablůnka site, with only the values for *Larix* and *Pinus cembra*-type slightly lower. In addition, pollen of some more demanding species, such as *Abies*, *Alnus glutinosa*-type and *Corylus avellana*, sporadically occur in the pollen spectra. The interpretation of the pollen spectrum from Prague–Podbaba is similar to that for Jablůnka: local vegetation consisted of a more open, parkland taiga, located within a wide and rather deeply-incised valley. Thanks to the direct influence of a big river, increasing both temperature and humidity, this location could have provided refugia for more demanding species. Currently, however, it is unclear what the fate of this vegetation was during the coldest period of the Last Glacial Maximum around 20 ka BP. In order to resolve this problem we require at least some piece of fossil evidence from the Bohemian Massif.

Table 3. – Results of pollen analysis for Prague–Podbaba section; 50°06'45" N; 14°23'30" E; 190 m a.s.l. Pollen analysis by P. Pokorný and V. Jankovská of stratigraphic position 2430 cm; sample associated with wood that was radiocarbon-dated to 31,012±1,810 BP (laboratory no. CU-1872). AP – arboreal pollen, NAP – non-arboreal pollen; t after the names of taxa refers to pollen types.

Pollen taxa		Total count	Percentage
AP	*Abies*	6	0.4
	Alnus glutinosa t.	12	0.9
	Betula alba t.	45	3.3
	Corylus	2	0.1
	Larix	10	0.7
	Picea	41	3.0
	Pinus sylvestris t.	857	62.1
NAP	*Artemisia*	26	1.9
	Calluna vulgaris	2	0.1
	Campanula t.	9	0.7
	Caryophyllaceae	1	0.1
	Compositae subfam. *Asteroideae*	5	0.4
	Compositae subfam. *Cychorioideae*	15	1.1
	Cruciferae	8	0.6
	Eranthis hyemalis t.	2	0.1
	Filipendula	13	0.9
	Gentiana t.	2	0.1
	Gramineae	219	15.9
	Helianthemum	1	0.1
	Chenopodiaceae	4	0.3
	Labiateae	1	0.1
	Melampyrum	1	0.1
	Parnassia t.	1	0.1
	Polygonum bistorta t.	2	0.1
	Ranunculaceae	4	0.3
	Rosaceae	7	0.5
	Rubiaceae	34	2.5
	Scleranthus perennis t.	1	0.1
	Sedum t.	1	0.1
	Thalictrum	1	0.1
	Trifolium pratense t.	1	0.1
	Umbelliferae	9	0.7
	Valeriana dioica t.	2	0.1
	Valeriana officinalis t.	9	0.7
	Viciaceae	4	0.3
	varia	22	1.6
AP + NAP		1380	100%
Hydrophyta	*Cyperaceae*	867	62.9
	Myriophyllum alterniflorum	1	0.1
	Myriophyllum spicatum t.	1	0.1
	Nuphar	1	0.1
	Nymphaeaceae – trichoblast	1	0.1
	Potamogeton	4	0.3
Pteridophyta	*Botrychium*	3	0.2
	Equisetum	1	0.1
	monolete spores	4	0.3
Bryophyta	*Sphagnum*	13	0.9
Algae	Algae (cysts)	12	0.9
	Botryococcus sp.	1	0.1
	Mougeotia t.	2	0.1
	Spirogyra t.	1	0.1

Discussion

In our opinion, the closed hemiboreal forest biome – an analogy of the present Siberian continental taiga – existed in the Weichselian Pleniglacial in the territory of present Slovakia and the westernmost ranges of the Carpathians in the E Czech Republic. Nevertheless, it is uncertain whether this generalization holds for the whole period. Climate at that time was far from stable. Abrupt climatic oscillations are recorded both in Greeanland ice cores (e.g., Dansgaard et al. 1993, Johnsen et al. 1992) and in marine sedimentary records (e.g., Heinrich 1988, Bradley 1999). Although some signs of the same changes are regularly present in terrestrial records (most important of these being in loess sequences), their dating is generally insufficiently accurate for most correlations. This is also the case for our material. Therefore, it was not possible to associate our pollen and macrofossil finds with certain climatic periods (stadials and interstadials) and we present a more general picture.

Our view of the full-glacial vegetation in the region studied is strongly supported by recent malacostratigraphic investigations undertaken in central Slovakia by Ložek (2006). Talus accumulations investigated at two sites are of upland facies, which are equivalent to lowland loess. Their snail assemblages consists of a peculiar mixture of cold- and warm-loving elements, including demanding species, generally considered to be characteristic interglacial faunal elements. Their occurrence together with glacial index species indicates that at the southern foot of the Western Carpathian mountain range a woodland zone persisted during the last full-glacial period. The author of the study, Vojen Ložek, concludes that this forest zone was situated between the lowland loess steppe and alpine grassland belt, providing suitable conditions for survival of a number of warm-loving snail species. The protected and relatively moist valleys of the Western Carpathian mountain ranges must have been much more favourable from a climatic point of view than the dry, loess lowlands and transitional highlands, where most pollen investigations have been undertaken so far, and where aridity was probably a significant factor in limiting tree growth (Wright et al. 1993). Orographic precipitation and relatively high air humidity might have significantly lowered the full-glacial climatic stress on the biota of mid-altitude mountain ranges.

Results of several previous palaeobotanical studies on peat and lake deposits of Late Glacial age have already proved that the development of vegetation in the NW Carpathian region took quite a different path than in the more westerly-situated areas of Central Europe (Jankovská 1984, 1988, 1998; Jankovská et al. 2002; Rybníčková & Rybníček 1996). Also in the Bieszczady mountain range, Polish East Carpathians, in deposits of the Weichselian Late Glacial Period, a continuous pollen curve for *Larix*, up to 7%, is accompanied by numerous macrofossils of the same genera, providing evidence of the dominance of larch in the local vegetation at that time (Ralska-Jasiewiczowa 1980). In the N Tatra Mountains piedmont, larch was apparently present during the Late Glacial and Preboreal periods (Wacnik et al. 2004). Also striking are the findings of high pollen values and macrofossils of *Larix*, *Picea* and *Pinus cembra* in the Late Glacial deposits east and south of the High Tatra mountain range (Hozelec and Sivárňa sites; Jankovská 1984, 1988, 2007b). This indicates that stands similar to the larch-stone pine Siberian taiga (Fig. 4) were extensively present in the NW Carpathians and its piedmont during the Late Glacial and early Holocene. *Picea* and *Pinus sylvestris* (maybe also *P. mugo*) were abundant in these stands. Such data provided the basis for the hypothesis that these tree species survived the Last Glacial Maximum in this area.

Based on pollen analyses of loess profiles at Oberfellabrunn and Stillfried (Lower Austria), Frenzel (1964a) shows that climatic amelioration during the "Stillfried B Interstadial" (perhaps equivalent to "Paudorf Insterstadial") enabled subalpine conifer forests and riverine broad-leaved forests to spread along the rivers and over other suitable places within the still dominant steppe formations on dry loess plateaus. This description fits the picture of the vegetation roughly the same period at Prague–Podbaba.

Important data relevant to the question of full-glacial forest refugia has come from the Pannonian Basin of Hungary and S Moravia. The vegetation situation from between 22 and 9 ka BP has been revealed by the pollen in a profile of sediments of the former Nagy-Mohos Lake (Magyari et al. 1999), which indicates the presence of *Larix*, *Pinus*, and *Picea* during the Last Glacial Maximum. Equally interesting is pollen from Late Glacial deposits in three Hungarian lakes, which indicate cold refugia for the same tree species and even some broad-leaved taxa (Willis et al. 2000). The pollen diagram from the Bulhary site in SE Moravia (Rybníčková & Rybníček 1991), dated to 25,675 ±2750 14C yr BP, indicates a coniferous forest containing *Pinus sylvestris*, *P. cembra, Picea, Larix* and *Juniperus communis*. In addition, sporadic pollen grains of temperate deciduous trees such as *Ulmus*, *Corylus*, *Quercus*, *Tilia* and *Acer* were also found. In the northern foothills of the Carpathians, several pollen profiles indicate presence of tree stands with *Pinus cembra* and *Larix* during warmer interstadial periods of the Weichselian Pleniglacial

Fig. 4. – Montane taiga forest with *Larix sibirica* and *Pinus sibirica* and patches of dwarf shrubby vegetation with *Betula nana* (syn. *B. rotundifolia*), *Alnus viridis* (syn. *Duschekia fruticosa*), and *Rhododendron dahuricum*. Upper forest limit in Western Sayan Mts, 52°27'N, 91°49'E. Photograph: P. Pokorný.

(Mamakowa 2003). Another important line of evidence comes from the great number of charcoal pieces from full-glacial loess and Upper Palaeolithic archaeological sites in the Czech Republic, Austria and Hungary (see Introduction).

Relevant to northern full-glacial refugia of temperate broadleaf trees, is the important data recently provided by detailed phylogenetic studies on European beech, *Fagus sylvatica* (Magri et al. 2006). This indicates that beech expanded in the early post-glacial from scattered nuclei. One important region, for potential proposed by these authors, is located in S Moravia, including the foothills of the Western Carpathians.

North of the Carpathian range, in the Polish plain, deep deposits of peat spanning the period of the Weichselian Glacial indicate a more traditional picture of full-glacial vegetation. A predominantly treeless vegetation dominated by steppe elements like Gramineae and *Artemisia*, with only a low occurrence of cold-resistant trees like *Pinus sylvestris*, *Betula* and *Juniperus* (Granoszewski 1998, Mamakowa 2003). Low pollen frequencies of broadleaf tree species is attributed to long-distance transport. In the territory of the Russian Plane during the last full-glacial period Markova et al. (2002) propose that several biogeographic regions existed, based of the fossil fauna and flora: tundra, forest-tundra, forest-steppe and steppe.

Much further west of the Carpathians, at Füramoos (German alpine piedmont; Müller et al. 2003), a thick profile spanning the period of the last full-glacial, gives a picture of an equally open vegetation, probably with only sparse tree cover composed of *Pinus* and *Betula*. In S Bohemia, at Švarcenberk (SW Czech Republic; Pokorný 2002), during the transitional period at the very beginning of the Late Glacial (around 16 ka BP), it consisted of a parkland landscape with only sparse *Pinus* stands. The only exception to this picture is the recent data from Prague–Podbaba, presented in this article, which indicates forest-steppe vegetation with larch, pine, birch and spruce at a favourable location in a deep river valley. Unfortunately, this deposit does not include the period of the Last Glacial Maximum of around 20 ka BP.

The important question remains, how could a taiga-like forest with some temperate elements survive the extremes of the full-glacial climate in Central Europe? Greenland ice core data for Oxygen Isotope Stages 3 and 2 (57–18 ka BP) show a series of short-term climatic fluctuations of a great amplitude (Dansgaard et al. 1993). Recently, high-resolution climate simulations have been obtained for the early full-glacial and Last Glacial Maximum (LGM) within the Stage 3 Project (Barron & Pollard 2002, van Andel 2002). Pollen-analysis data used in the simulations covered only the maritime, northern and Mediterranean regions, while eastern and eastern-central Europe was a "blank spot" on this map. Since this climatic simulation did not fit the underlying concept of a tree-less tundra, the model was rejected (Alfano et al. 2003, Huntley et al. 2003). In the light of new data presented by, for example, Willis & van Andel (2004), and especially that presented in this paper, the "Stage 3 Project" climatic simulations may be relevant again. According to this model, there were two main continental-scale gradients in the climate of Europe north of the Mediterranean region: a north-south gradient from arctic to cold temperate climates in the foothills of the Central European mountain rim, and a west-east gradient from the maritime Atlantic climate to the continental one in the eastern part of Europe. The model suggests that rainfall in central and eastern regions was much heavier than in S Europe. This means that in the Carpathians, relatively warm (above all in summer), moist and continental climatic conditions occurred. This situation has a modern analogy in central and southern Siberia, where such climatic conditions are known to support a diverse vegetation of the continental southern taiga, sometimes in a complicated mosaic with steppe and tundra habitats.

Conclusions

Data presented in this article, together with that in the literature on the Weichselian full-glacial vegetation of central-eastern Europe, point to the importance of the Western Carpathians as a large-scale forest refugium, where many elements of forest biota survived the Last Glacial Maximum. Due to orographic precipitation and high mesoclimatic humidity in the mountain valleys of this mountain range, this region could have been covered during most of the Weichselian full-glacial by montane forests. *Larix*, *Pinus cembra*, *Pinus sylvestris* and *Picea* dominated a rather dense forest canopy during those times. Current analogy of this vegetation occurs in certain areas of Siberia – those with a continental and still relatively humid climate. Isolated patches of some broadleaf trees like *Corylus avellana*, *Alnus glutinosa/A. incana*, *Tilia*, *Ulmus*, *Quercus*, *Fagus*, *Carpinus*, *Abies* and *Acer* may have existed in more favourable places (e.g., the limestone region of Southern Slovakian Karst), but pollen analyses above cannot prove this firmly. Around the Carpathians, in the Pannonian Basin and Moravian Foredeep, there was a comparable vegetation throughout the last full-glacial. It is likely, however, that the tree stands here had a somewhat more open and patchy character, when compared with those in the valleys of NW Carpathians. This difference is most likely due to drought stress. Even further to the west, the presence of comparable vegetation is supported by evidence from protected river valley in the central Bohemian lowland near Prague.

Souhrn

Paleobotanické údaje z období posledního vrcholného glaciálu opakovaně potvrzují existenci parkové krajiny s významným podílem jehličnatých dřevin ve východní části střední Evropy. Až do nedávné doby znemožňovala absence podobných nálezů studium charakteru vegetace tohoto období v horských a podhorských oblastech Západních Karpat – v regionu, který považujeme za klíčový pro pochopení kvartérní historie současné středoevropské lesní bioty. Náš příspěvek přináší nové pyloanalytické a makrozbytkové údaje právě z tohoto regionu. Naše nálezy jsou datované do kritického období posledního vrcholného glaciálu (mezi 50 a 16 tisíci lety před současností) a plně potvrzují hypotézu, která byla vyslovena již dříve, a to víceméně pouze na základě extrapolace paleobotanických dat z okolních území. Chráněné a relativně vlhké doliny Západních Karpat na území Slovenska a Moravy představovaly stanoviště vhodná k rozvoji zapojených lesů tajgového charakteru v průběhu chladných období posledního vrcholného glaciálu. V celoevropském měřítku tedy Západní Karpaty podle všeho představovaly významné vrcholně glaciální refugium lesní bioty. V nížinách a pahorkatinách obklopujících tyto horské masivy bychom ve stejnou dobu nalezli spíše mozaikovitou parkovou krajinu analogickou stepotundře, lesostepi a chladné stepi. Na příkladu paleobotanického materiálu nalezeného na území současné Prahy však ukazujeme, že areál tajgových dřevin – smrku a modřínu – sahal v posledním vrcholném glaciálu až daleko na západ a že také zde existovala mikroklimaticky vhodná stanoviště k přežívání lesních elementů. Takovými stanovišti byly chráněné polohy na dnech hlubokých říčních údolí.

Na základě dosud získaných paleobotanických dat můžeme dále vyslovit hypotézu, že v lesích tajgového charakteru mohly na určitých mikroklimaticky vhodných stanovištích přežívat teplomilné listnaté dřeviny (například *Corylus avellana, Alnus glutinosa / A. incana*, *Ulmus*, *Quercus*, *Fagus*, *Carpinus*, *Abies*, *Acer*). Vyplývá to z našich výsledků i ze zjištění obsažených ve starší literatuře, avšak na pozadí přetrvávajícího paradigmatu „mamutí stepi“ dosud plně nedoceněných. Musíme však zdůraznit, že dosavadní nálezy, zejména pyloanalytické, mají zatím spíše charakter nepřímých důkazů. Hypotézu bude možné testovat pouze v případě, pokud budou k dispozici

makrozbytková data o příslušných kritických taxonech a to nejlépe v přirozených a stratifikovaných kontextech. Dosavadní nálezy uhlíků listnatých dřevin na archeologických lokalitách situovaných v Panonské nížině a datovaných do pleniglaciální fáze mladšího paleolitu (Gravettien) již určité závažné indicie v tomto směru představují. Významná zjištění poskytují navíc současné fylogenetické studie – v případě buku (*Fagus sylvatica*) jsou na jejich základě rekonstruována glaciální refugia v prostoru jižní Moravy a Západních Karpat (Magri et al. 2006).

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