Holocene history of a *Cladium mariscus*-dominated calcareous fen in Slovakia: vegetation stability and landscape development

Holocenní historie vápnité slatiny s dominantní mařicí pilovitou na Slovensku – vegetační stabilita a vývoj krajiny

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Dedicated to Kamil Rybníček and Eliška Rybníčková on the occasion of their 80th birthdays

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Hájková P., Jamrichová E., Horsák M. & Hájek M. (2013): Holocene history of a *Cladium mariscus*-dominated calcareous fen in Slovakia: vegetation stability and landscape development. – Preslia 85: 289–315.

There are very few palaeoecological studies of thermal springs in central Europe, despite the fact that they are extreme but stable habitats that enabled the long-term survival of certain species and are located in areas for which there is little data about landscape history. In western Slovakia, close to Malé Bielice village at the northern margin of the Pannonian-Carpathian boundary, a peat-forming warm spring is uniquely preserved, and it still harbours a rare plant, *Cladium mariscus*. This site is located in a region that is noteworthy for the occurrence of many rare, light-demanding species that have disjunct distributions or are at the limits of their distributions, which may indicate a long history of treeless habitats there. The geographical position of this study site thus provides a great opportunity to address the perennial debate about in situ relicts and the continuity of grasslands throughout the forest optimum. We analysed a Holocene sediment core for macrofossils of vascular plants, bryophytes and molluscs, and for pollen, which were surprisingly preserved in rather high diversity, which enabled a detailed reconstruction of the landscape history. We further reviewed the archaeological evidence. Using this multi-proxy approach, we were able to confirm (i) the early expansion of mesophilous trees (*Ulmus*, *Fraxinus*, *Tilia* and *Quercus*) in northern parts of the Carpathian-Pannonian boundary, but the onset of this expansion could not be dated precisely, (ii) the continual persistence of the *Cladium mariscus* population in the fen, and (iii) existence of open steppes and/or dry grasslands and open wetlands in this region throughout the Holocene. Since the Bronze Age, there are coincidences in the history of human settlement, local development of the fen and regional changes in the representation of particular habitats, including managed wet, mesic and semi-dry grasslands.

Keywords: grassland persistence, macrofossils, molluscs, multi-proxy, pollen, radiocarbon dating, human influence

Introduction

Thermal springs in central Europe are extreme habitats with stable conditions and potential refugia where light- and warm-demanding wetland species could survive during the whole Holocene or even during former periods (Diaconeasa & Popa 1964). Most thermal springs are utilized for spa purposes and as a consequence the vegetation is destroyed.

In western Slovakia, close to the town of Partizánske (the Malé Bielice village) at the Pannonian-Carpathian interface, one wetland patch around a warm spring still persists and harbours rare fen species such as *Cladium mariscus* and *Schoenus nigricans* (Ambros 1996). These species are rare and strictly protected in several countries in central Europe (Feráková et al. 2001, Piękoś-Mirkowa & Mirek 2006, Grulich 2012). *Cladium mariscus* is a light-demanding species with wide ecological amplitude, growing in both calcium-rich wetlands in areas with a subcontinental climate and on sandy soils in areas with a oceanic climate (Galka & Tobolski 2012). It is assumed that low availability of nutrients (nitrogen, phosphorus) is also important for its occurrence (Balátová-Tuláčková 1991, Pokorný et al. 2010). Because in peat deposits seeds and pollen of *C. mariscus* are usually well preserved and identifiable it is possible to study the population dynamics and continuity of its occurrence (cf. Hafsten 1965, Pokorný et al. 2010, Galka & Tobolski 2012). In central Europe, *C. mariscus* is considered to be a relict from earlier periods of the Holocene (Brande 2008, Pokorný et al. 2010). The fossil records from the middle Holocene are the most frequent and this species is usually not present in the youngest phases of fen development. Further, there is the fossil record from the MIS 3 interstadial period from Belgium (Haest et al. 1986: 38–42 000 uncal. yr BP). It therefore seems that *C. mariscus* could be considered as a warm-stage relict in Europe. In Slovakia, the fossil record is fragmentary with *Cladium* detected in sedimentary fill in a palaeomeander of the river Danube in the La Tène period (Pišút & Procházka 2012) and in the Šúr palaeolake in the Danube lowland south of the Malé Karpaty Mts in the middle Holocene (P. Žáčková, in verb.). The aim of this study is to trace the history of *C. mariscus* populations in Slovakia, where warm springs could have been one of its potential long-lasting refugia.

The study site is located at the southern margin of the Inner Western Carpathians (middle-Nitra Basin), an area for which there is currently no radiocarbon-dated palynological data (cf. Kuneš et al. 2009). Thus, it provides an opportunity to fill the gap in our palaoeocological knowledge of the Pannonian-Carpathian interface. Two important questions can be addressed: the spread of mesophilous trees (*Ulmus*, *Fraxinus*, *Tilia* and *Quercus*) in early Holocene and continuity of grasslands throughout the forest optimum. In the region where the warm spring studied is located, some range-margin disjunct populations of southern elements occur (e.g. *Aethionema saxatile* and *Cotinus coggygria*; Ambros 1996, Čeřovský et al. 1999). Hence, timing of appearance of mesophilous tree pollen in the profile and knowledge of landscape development could bring certain indirect evidence to the question when did these disjuctions originate.

The continuity of temperate grasslands throughout the entire Holocene is the second still unresolved problem. Although older studies did not acknowledge continual survival of steppe elements in central Europe (e.g. Rybníčková & Rybníček 1972), there is a growing body of evidence that human activity played a crucial role in both the formation of grasslands and the alteration of forest composition from Neolithic times onwards (Pokorný et al. 2006, Baumann & Poschlod 2008, Dutoit et al. 2009, Magyari et al. 2010). In the middle Holocene, closed-canopy forests started to spread, whereas heliophilous and open grassland species retreated. The spread of agriculture that started in central European lowlands ca 7500 cal. yr BP had a counteracting effect: landscape was step-by-step deforested and cattle grazing, burning and crop cultivation facilitated the spread of heliophilous species. Thus, in the regions that were colonized during Neolithic and Late Neolithic, the pool of early Holocene heliophilous species may have been preserved and the development of

heliophilous vegetation may have been more or less continuous during the Holocene. Hájková et al. (2011) summarized the evidence supporting this hypothesis for the White Carpathians, another region at the western Carpathian-Pannonian boundary, where species considered to be early Holocene elements disjunctly occur despite the absence of naturally treeless habitats. The study site is located in the early-colonized region with archaeological records since Early Neolithic period (Točík 1970) when human activities could have helped to maintain a treeless vegetation throughout the Holocene forest optimum, which is considered to have been a bottleneck for the survival of light-demanding species (Ložek 2008). Without human influence, treeless vegetation can survive only on sites, which are edaphically unfavourable for tree growth, such as rocky outcrops. Disjunct occurrences of some light-demanding steppe or semi-dry- and mesic-grassland species in the wider surroundings of the study site (e.g. *Crepis sibirica*, *Gypsophyla fastigiata*, *Peucedanum carvifolia* and *Tephroseris integrifolia* subsp. *moravica*; Hlaváček et al. 1984, Ambros 1996, Janišová et al. 2012) resemble the above mentioned White-Carpathian story and indicate that the study profile could be suitable for tracing the Holocene survival of light-demanding species.

Our study thus addresses not only the processes affecting large-scale landscape transformations but also local "ahistoric" processes that resist them and contribute to the formation of recent diversity patterns. We (i) explore the development of local fen habitats and *Cladium mariscus* persistence around warm springs using multi-proxy methods (pollen, macrofossils of plants and molluscs, radiocarbon dating), (ii) document the spread of mesophilous trees since the early Holocene, (iii) search for evidence of continuity of open grassland vegetation, and (iv) trace the history of human settlement in pollen records, with an emphasis on the distribution of grassland habitats.

Methods

Study site

The study site is located near the Malé Bielice village in the middle-Nitra Basin, western Slovakia, which separates Považský Inovec, Strážovské vrchy and Tribeč Mts (Fig. 1) and links with Podunajská nížina lowland in the south. Geomorphologically, it belongs to the Inner Western Carpathian Mts. The study site is 185 m a.s.l. and supplied with warm spring groundwater (about 40 °C). It is one of four recent localities of the relict and critically endangered species, *Cladium mariscus* (Eliáš et al. 2003), even though the water level was reduced by drawing off spring water from this site in the past. Vegetation belongs to the *Magnocaricion elatae* alliance (Oťaheľová et al. 2001). Fen vegetation is overgrown by *Phragmites australis* and is extremelly poor in species, but the population of *Cladium* remains viable. The fen peat is 240 cm thick and accumulated on fluvial sands. Climate at the site is warm and slightly dry with 8–9 °C mean annual temperature and 550–600 mm mean annual precipitation (http://geo.enviroportal.sk/atlassr).

The study site is in the valley of the river Nitra and surrounded by loess slopes on the northern edge and flood terraces in the east (http://mapserver.geology.sk; Fig. 1). This kind of landscape has attracted people since prehistoric times. In central Europe, the first agricultural cultures were at naturally sheltered sites with favourable soil and climatic conditions located mainly on loess terraces and slopes (Hajnalová 2007, Bogaard 2004).

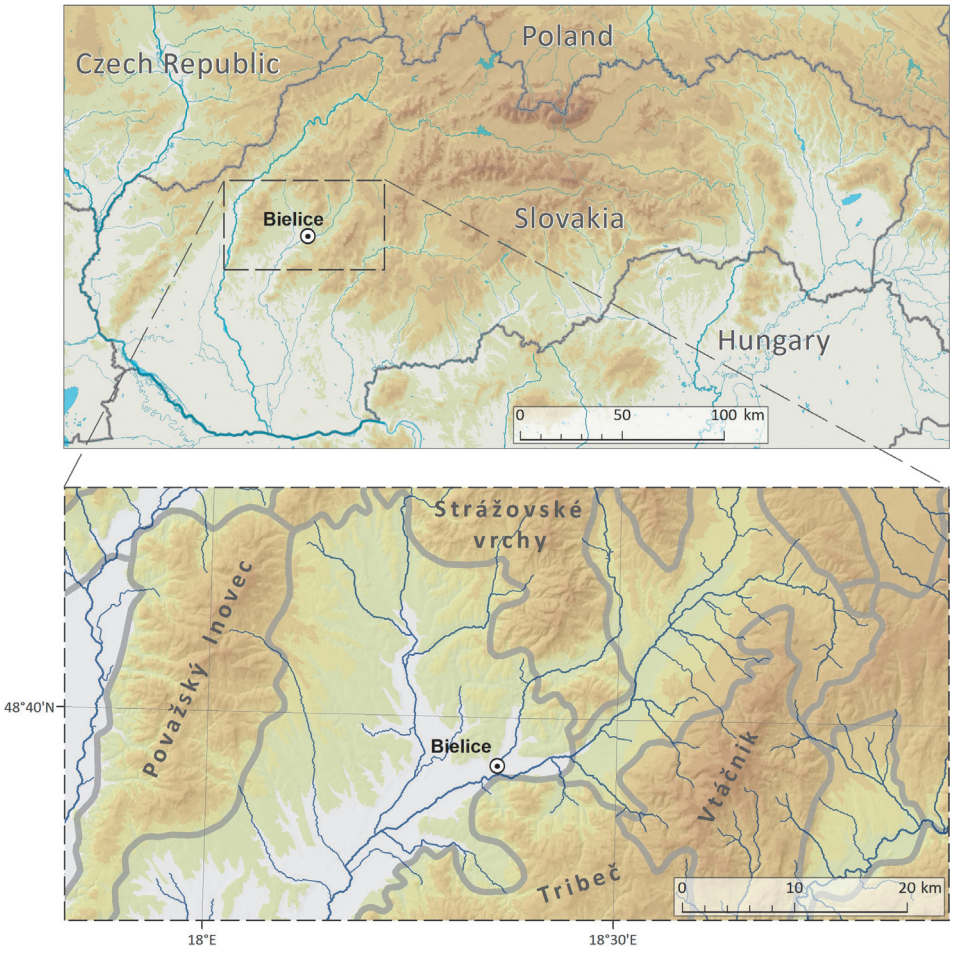


Fig. 1. – Location of the study site in the middle-Nitra Basin (SW Slovakia).

This region is in an old-settlement zone; the oldest known archaeological records are for the middle Pleistocene (Bárta 1965, Kaminská 2008) and the fossil remains of *Mammoth primigenius* were discovered near the study site (Bárta 1965).

The oldest known agricultural settlements in the vicinity of the site date back to the Early Neolithic (Linear Pottery culture; ~5700–5000 BC; 7650–6950 cal. yr BP) through Late Neolithic (Lengyel III; ~4700–4400 BC; 6650–6350 cal. yr BP) and Bronze Age onwards (Lusatian Culture 1300–700 BC; 3250–2650 cal. yr BP) (Točík 1970, Veliačik 1988). Rich settlement records are dated to the Iron Age (Hallstatt, ~700–450 BC; 2650–2400 cal. yr BP; La Tène; ~450–0 BC; 2400–1950 cal. yr BP) and they probably occur there because of the occurrence of iron ore and gold in the nearest mountains (Wiedermann 1985, Veliačik 1988, Vangľová 2008). Human occupation of this landscape continues through Slavic Time (6th–12th the century AD; 1250–650 cal. yr BP) up to the present. First written evidence about the nearest villages is for the second half of the 13th century AD; 550 cal. yr BP (Kropilák et al. 1977–1978).

Sediment sampling and analyses

Material for palaeoecological analyses was collected using a Russian-type peat-corer (Eijkelkamp, Giesbeek, The Netherlands) to obtain two cores that were collected close to each other. The physical properties of the sediments were described following Troels-Smith (1955; for detail see Table 1). Profiles of all proxies were divided into developmental zones based on results of constrained cluster analysis based on sum of squares (Coniss analysis, implemented in Tilia program; Grimm 2011).

Table 1. – Stratigraphy and description of fen peat in the Malé Bielice profile. Components: Tb (Hyp) – moss peat, Th – herbaceous peat, Tl – wood peat, Dh – herbaceous detritus, Dl – wood detritus, GCa – calcium carbonate precipitation, Ga – sand, [A] – charcoal.

Depth (cm)	Troels-Smith system	Description
0–40	Th3, GCa1, Dh+	sedge peat with an admixture of $CaCO_3$, root zone
40–55	Th4, Tb+, Dh+	sedge peat without $CaCO_3$
55–120	Th3, GCa1, Tb (Hyp)++, Dh+	brown-moss/sedge peat with $CaCO_3$ precipitation
120–240	Th2, Tl2, Tb(Hyp)+, Dh+, Dl+, [A]	sedge/wood peat with small admixture of bryophytes and charcoal; 235–240 cm increased amount of charcoal
240–250	Ga4, Tl+, Th+, [A]	sand with small pieces of wood and plant tissue
Below 250	Ga4	sand

Material for pollen analyses from both profiles were subsampled (volume of 1 cm^3) at 10 cm intervals along the profile and processed using standard techniques (Faegri & Iversen 1989) with *Lycopodium* added as a marker (Stockmarr 1971). In the bottom part of the profile, where the depth-age model indicated that 40 cm spaned almost five thousand years, we sampled certain sequences at 2 cm intervals (207–197 cm) and 3 cm intervals (198–187 cm) in order to identify or rule out a possible hiatus.

Samples containing clastic material were pretreated with cold concentrated HF (hydrogen fluoride) for 24 hours and then KOH (potassium hydroxide) solution before acetolysis. At least 500 pollen grains of terrestrial plants per sample were identified using Beug (2004), Punt & Clark (1984) for the family *Apiaceae*, or pollen atlases (Reille 1992, 1995, 1998). For the identification of non-pollen palynomorphs van Geel et al. (1980–1981) and van Geel et al. (2003) were used. The nomenclature of pollen types follows Punt & Clark (1984) and Beug (2004). The concentration of microscopic pieces of charcoal was determined using particle counts and compared with *Lycopodium* counts (Whitlock & Larsen 2001, Tinner & Hu 2003).

Pollen data are presented in two percentage pollen diagrams. In the first the development of forests, ruderal and dry habitats is presented. In the second is the pollen of species that grow mainly in wetland and wet meadow habitats. Spores and non-pollen palynomorphs (NPP) are also included in the second pollen diagram. The percentages of the different pollen taxa was based on pollen sums of arboreal and non-arboreal pollen (AP+NAP = 100%). The percentages of wetland taxa, spores and non-pollen palynomorphs were related to the extended sum (i.e. AP+NAP+wetland+spores+NPP = 100%). In addition to classic pollen diagrams, we constructed a synoptic diagram, in which particular pollen taxa were classified into groups according to the habitat requirements of the plant species involved. We created these groups in order to trace the changes in the representation of

open habitats, especially particular types of grasslands. We classified all pollen taxa. Collective pollen taxa, especially those at the family level, were merged into the group of unclassified herbaceous taxa named "indifferent ecology". This group also includes *Poaceae*, because they may dominate dry grasslands, wetlands and open Carpathian forests; but some authors use *Poaceae* as indicators of grasslands. Nevertheless, the majority of this group is considered to grow in open habitats, including steppes. *Chenopodiaceae*, which are used as steppe indicators (Magyari et al. 2010), were placed in the group "open-country ruderals", because macrofossils of *Chenopodium album* agg. were found at the study site. This group may also indicate steppe and halophytic habitats, especially in the first phase of the Holocene. We are aware that some taxa are difficult to classify, but we believe that using this approach led to a more objective assessment of landscape changes than relying on particular pollen taxa. For the list of taxa included in each of the groups and comments on species classification see Electronic Appendix 1. For photographic documentation of *Cladium* pollen and *Sporormiella*-t. spores see Electronic Appendices 2 and 3. All pollen diagrams were constructed using Tilia software v. 1.7.16 (Grimm 2011).

Five centrimeters wide samples for macrofossil and mollusc analyses (50 cm^3) were taken discontinuously apart at 5 cm intervals and sieved into three fractions (200–630 μm, 0.630–1 mm, > 1 mm). Larger fractions were analysed using a dissection stereomicroscope at magnifications of 10–40× and each slide (1 cm^3 of the finest fraction) was examined at 100–400× magnification to identify small seeds (e.g. *Juncus*) and oogonia of *Chara vulgaris*. Seeds and plant tissues were determined according to Mauquoy & van Geel (2007), Velichkewicz & Zastawniak (2008), Cappers et al. (2012) and other available identification literature. Macrofossils were also checked against the reference seed collection of the Institute of Botany, Academy of Sciences of the Czech Republic. Schweingruber (1978) was used for determining wood fragments and Hedenäs (2003) for bryophytes. Values are presented as absolute numbers (seeds, bryophytes, molluscs) or as volume percentages (plant tissues and woods). Mollusc shells were separated from other macrofossils and identified according to Ložek (1964) and M. Horsák's personal reference collection, using a dissection stereoscopic microscope. Remnants of slugs were not considered. Nomenclature of vascular plants follows Marhold & Hindák (1998), that of bryophytes Hedenäs (2003) and molluscs Horsák et al. (2010). Both macrofossil and mollusc diagramms were created using C2 software (Juggins 2003).

Chronology

Based on distinct changes in pollen diagrams we identified eight layers that were AMS radiocarbon dated. Dominant plant macrofossils were isolated from respective layers and sent for dating to the Centre for Applied Isotopes Studies, University of Georgia, Athens, GA, USA (UG-) (Table 2). A depth-age relationship model was constructed using OxCal 4.1 (Bronk Ramsey 2009; Fig. 2). An IntCal09 calibration curve (Reimer et al. 2009) was used to calibrate radiocarbon dates. In the main text, age of each sample refers to centre of interpolated calibrated age before year AD 1950 (i.e. BP=0), with a 95.4% probability. In the archaeological context, we additionally use also years BC/AD. Dating of samples (single seeds of *Schoenoplectus*) from the depths of 205–207 cm (6250 cal. yr BP) and 225–227 cm (6623 cal. yr BP) gave results that do not correspond with pollen spectra indicating an early Holocene age. Because both these dates are based on a single seed, we considered

Table 2. – Results of ^{14}C dating of the Malé Bielice peat profile. *UGAMS 12321 and 12322 according to the pollen record (for detail see Chronology section in the Methods) are not reliable and were not included into the depth-age model (see Discussion for details). Identity of seeds used for dating: [1]*Schoenoplectus*, *Cladium*; [2]*Schoenoplectus*; [3]*Schoenoplectus*, *Cladium*, *Lycopus*.

Samples	Depth (cm)	Dating method	Age in uncal. yr BP	Cal. yr AD/BC (95.4% c.i.)	Cal. yr BP (95.4% c.i.)	Material
UGAMS 12327	37–39	AMS	1860 ± 20	85–222 AD	1865–1728	Seeds[1]
UGAMS 12326	75–77	AMS	2620 ± 25	826–776 BC	2776–2726	Seeds[2]
UGAMS 12325	107–109	AMS	3040 ± 30	1406–1213 BC	3356–3163	Seeds[1]
UGAMS 12324	125–127	AMS	3480 ± 25	1885–1740 BC	3835–3690	Seeds[1]
UGAMS 12323	185–187	AMS	5620 ± 20	4499–4368 BC	6449–6318	Seeds[3]
*UGAMS 12322	205–207	AMS	5440 ± 20	4342–4259 BC	6292–6209	Seeds[2]
*UGAMS 12321	225–227	AMS	5830 ± 40	4790–4556 BC	6740–6506	Seeds[2]
UGAMS 12763	223–224	AMS	10000 ± 30	9743–9356 BC	11693–11306	bulk

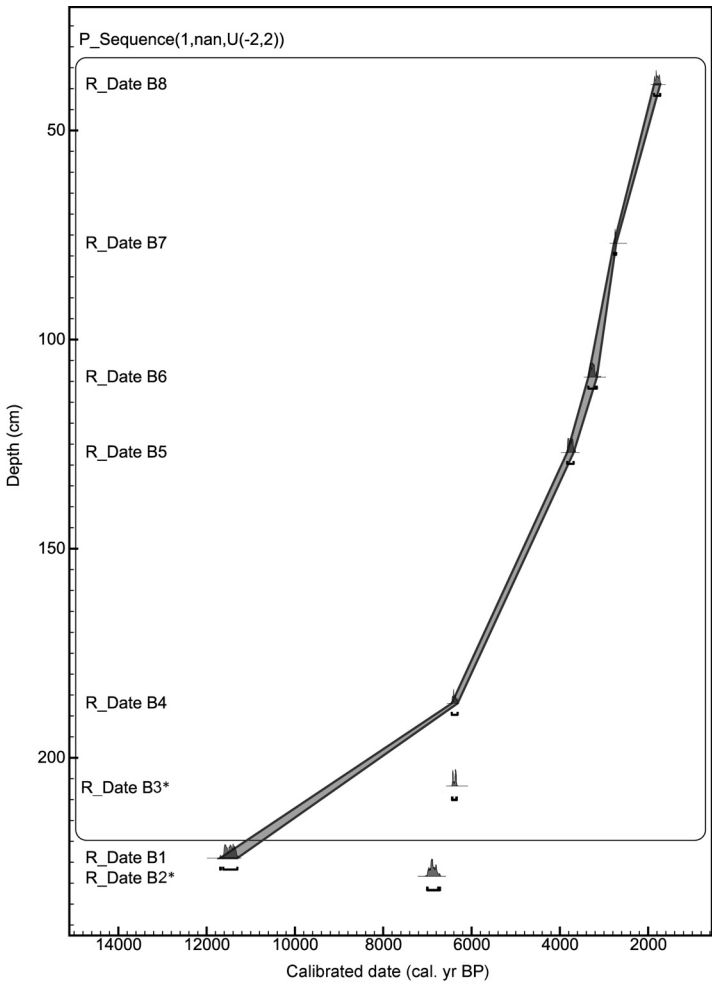


Fig. 2. – Depth-age relationship for the Malé Bielice profile based on six radiocarbon dates.

these results to be a product of bioturbation processes in grazed spring fens and as a consequence rely more on bulk dating (see Discussion for further argumentation). That is why we did not include these two dates in the depth-age model and decided instead to date a bulk sample from the bottom layer.

Results

Stratigraphy

The peat is mainly composed of sedge peat (*Cladium*, *Schoenoplectus*) and in the upper part there is a slight admixture of calcium carbonate (0–120 cm) and mollusc shells (0–150 cm). Large quantities of wood fragments are present in the lower peat layers (125–240 cm). Generally, the peat is characterized by a rather high decomposition rate, probably promoted by hot water (cf. Taylor & Dykstra 2005). Bryophytes occur in low quantities in the middle part of the profile and are not very-well preserved. The core used for macrofossil and mollusc analyses was about 15 cm longer than that used for pollen analysis, because the oldest (bottom) layer was slightly thicker. For detailed information about the stratigraphy and peat composition see Table 1 and Fig. 3 (macrofossils).

Pollen

Based on cluster analysis, the pollen diagram was divided into the four main phases and two subphases (Figs 4, 5).

1. The first zone Bpa1 (227–212 cm; 11, 475–9568 cal. yr BP) is characterized by the dominance of *Pinus* with an admixture of *Larix*, *Juniperus*, *Betula* and *Salix.* Among the different pollen types of herbaceous plants, *Poaceae* and *Artemisia* dominated. Pollen of *Picea* and mesophilous trees (*Quercus*, *Ulmus* and *Corylus*) is also present. Pollen of trees makes up almost 75% of the total pollen sum (TS), but the presence of species such as *Poaceae*, *Rubiaceae*, *Chenopodiaceae*, *Artemisia*, *Matricaria*-t*. and Cladium mariscus* clearly indicate the presence of open habitats.

2. The second zone Bpa2 (212–182 cm; 9568–6174 cal. yr BP) is characterized by a great increase in the pollen of mesophilous trees (*Alnus*, *Ulmus*, *Tilia*, *Quercus* and *Fraxinus*), decline in that of *Pinus* and complete disappearance of that of *Larix* from the pollen record. Pollen of light-demanding *Corylus* shrubs also significantly increases. Pollen grains of *Fagus* occur sporadically. Among the pollen of herbaceous plants, species of wet habitats (e.g. *Senecio*-t., *Petasites*, *Peucedanum palustre*-t. and *Primula farinosa*-t.) occur in higher quantities. *Cyperaceae* markedly increase and taxa indicating open water appear (*Lemna* and *Alisma*-t.).

3. In the subzone Bpa3a (182–112 cm; 6174–3640 cal. yr BP) pollen of *Fagus*, *Carpinus* and *Abies* is present. Pollen of herbaceous plants indicates the presence of dry and mesic meadows (*Cephalaria/Dipsacus*, *Jasione montana*-t., *Falcaria vulgaris*-t. and *Plantago lanceolata*-t.), wetlands (*Cladium mariscus*) and nutrient-rich habitats (S*olanum dulcamara*, *Chelidonium majus* and *Urtica* and *Bidens*). *Cerealia* pollen (*Triticum*-t.; found at the end of this zone) indicates human settlement. In the wetland, green algae *Botryoccoccus* rapidly increases and *Cyperaceae* decline.

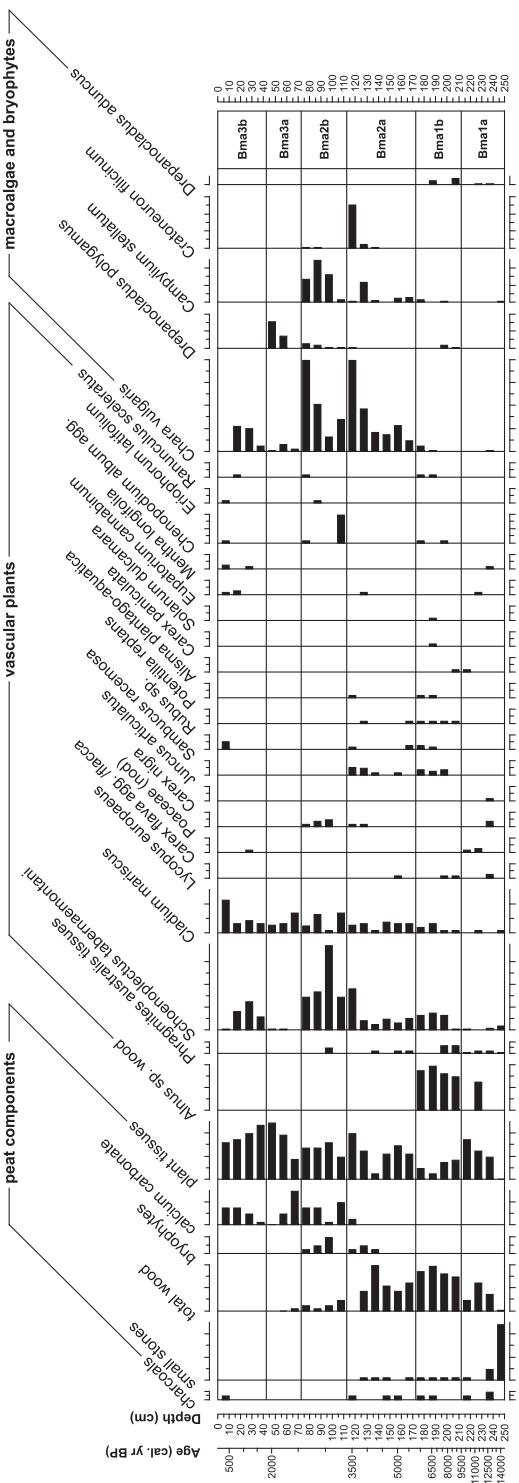


Fig. 3. – Macrofossil diagram. Main components of the peat are placed at the beginning of the diagram and presented in relative percentages. Countable plant remains are given in absolute numbers (seeds of vascular plants, oogonia, bryophyte stems), uncountable material (wood, plant tissues) in percentages in terms of volume. Oogonia of *Chara vulgaris* and seeds of *Juncus articulatus* were counted in 1 mL of the finest fraction of the sediment.

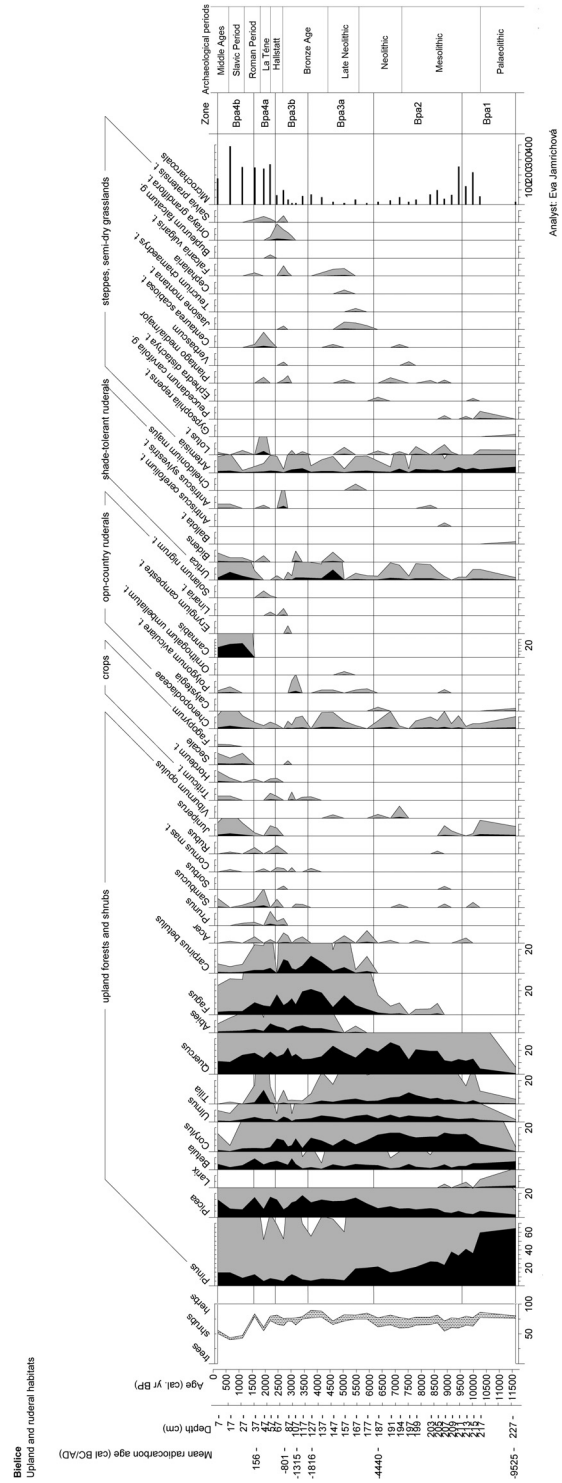


Fig. 4. – Percentage pollen diagram of trees, ruderals and dry-grassland species. The percentages of of individual pollen taxa are based on pollen sums of arboreal and non-arboreal pollen (AP+NAP = 100%).

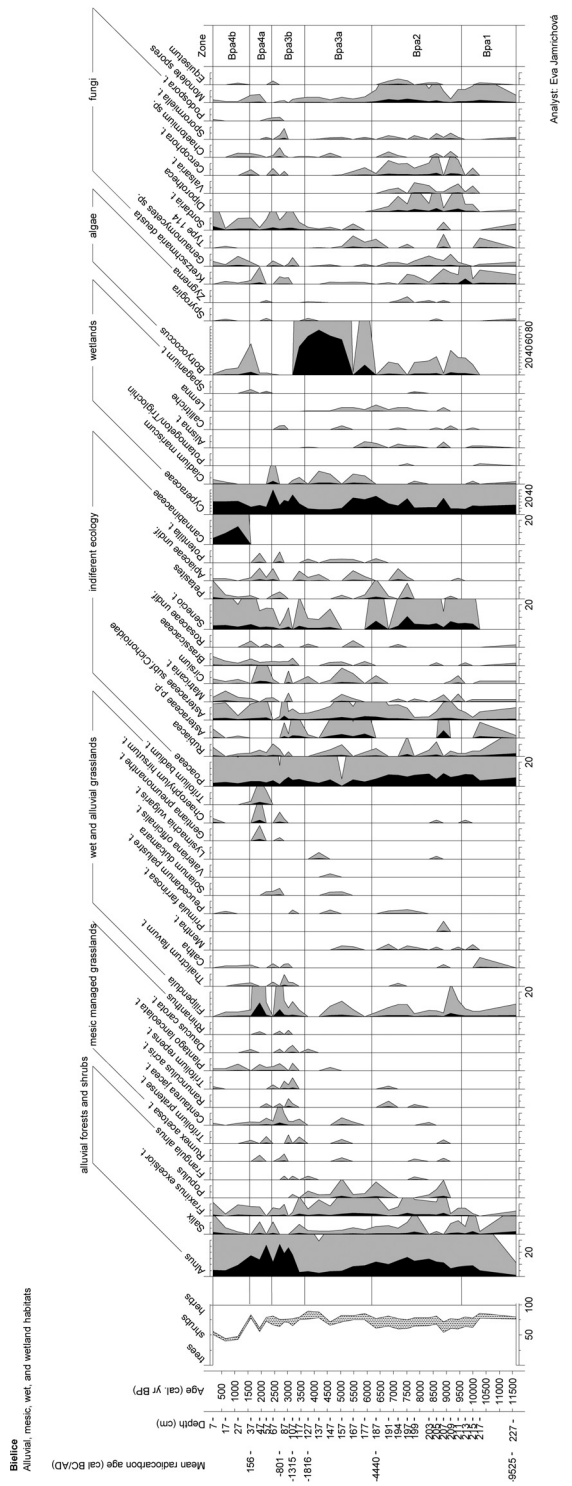


Fig. 5. – Percentage pollen diagram of species preferring wetland and wet meadow habitats. Spores and non-pollen palynomorphs (NPP) are also included. The percentages of individual pollen taxa are based on pollen sums of arboreal and non-arboreal pollen (AP+NAP = 100%). The percentages of wetland taxa, spores and non-pollen palynomorphs are based on the extended sum (i.e., AP+NAP+wetland+spores+NPP = 100%).

In the subzone Bpa3b (112–62 cm; 3640–2392 cal. yr BP) pollen of *Fagus*, *Carpinus* and *Tilia* clearly declines, whereas that of *Alnus* rapidly increases. Higher quantities of *Betula* are also recorded. Among the pollen of herbaceous plants the increase in that of cereals (*Triticum*-t. and *Secale*), ruderals (*Polygonum aviculare*-t.) and pasture plants (e.g. *Eryngium campestre*-t., *Orlaya grandiflora*-t. and *Plantago lanceolata*-t.) indicates presence of dry-grasslands and pastures. Concerning local taxa, *Botryococcus* suddenly declines and *Cyperaceae* increases, which indicates a lowering of the water table.

4. At the beginning of the subzone Bpa4a (62–32 cm; 2392–1563 cal. yr BP), the amount of pollen of *Cerealia*, ruderal-, meadow- and pasture-indicating taxa increases and *Juniperus* reappears, implying the spread of pastures. In the second part of the zone, there is a marked decrease in the amount of *Cerealia* and *Juniperus* pollen and increase in that of wet-meadow species (*Filipendula*, *Trifolium badium*-t. and *Gentiana pneumonanthe*-t.). *Botryococcus* reappears and *Cyperaceae* decline and the quantity of microcharcoals increases.

The last pollen subzone Bpa4b (32–7 cm; 1563–405 cal. yr BP) is characterized by a decline in tree pollen (AP decreases to 50%) and an increase in that of vegetation associated with the presence of humans; pollen of *Fagopyrum* is recorded for the first time and that of *Secale* increases continuously from the beginning of this zone. Of the ruderal species, a large quantity of *Cannabis* pollen is recorded. The increase in pollen of taxa indicating nutrient-rich habitats is also recorded (*Urtica*, *Bidens* and *Chenopodiaceae*).

Macrofossils

On the basis of cluster analysis, we divided the macrofossil diagram into three main phases and three subphases (see Fig. 3). The local vegetation remained stable throughout the time span of this profile; seeds of *Schoenoplectus tabernaemontani* and *Cladium mariscus* are present continuously.

1. Subzone Bma1a (250–215 cm; 14 396–9886 cal. yr BP according to the depth-age model used: see Chronology section for details) represents the oldest phase of fen development. Seeds of *Cladium mariscus*, *Schoenoplectus tabernaemontani*, *Eupatorium cannabinum*, *Mentha longifolia* and *Lycopus europaeus*, sedges *Carex flava* agg. and *C. nigra* are present, but in low quantities. Small amounts of *Alnus* wood indicates presence of alder-carr in the vicinity of the fen or scattered trees growing directly in the fen, but we cannot exclude underground origin of the pieces of wood, which implies that *Alnus* may not have been present at this stage in the development of the fen.

In subzone Bma1b (210–175 cm; 9409–5898 cal. yr BP) the abundance of seed of *Cladium* and *Schoenoplectus* increases. Seeds of *Rubus* and *Sambucus* indicate shrubby vegetation in the vicinity. Seeds of other fen (*Juncus articulatus* and *Carex paniculata*) or nitrophilous wetland species growing on disturbed fen peat (*Ranunculus sceleratus*, *Chenopodium album* agg. and *Potentilla reptans*) are also present. These species together with the moss *Drepanocladus aduncus* indicate fluctuating and seasonally strongly decreasing water level. There is an increase in the quantity of *Alnus* wood, indicating a more closed canopy. A small quantity of oogonia of *Chara vulgaris* is recorded at the end of this zone.

2. Subzone Bma2a (170–115 cm; 5652–3452 cal. yr BP) is similar to the previous one, but there is a greater abundance of oogonia of *Chara vulgaris*, which indicates wetter

conditions, probably small fen pools. Bryophytes are less abundant (*Campylium stellatum*, *Cratoneuron filicinum*).

At the beginning of the subzone Bma2b (110–75 cm; 3358–2691 cal. yr BP) there is a greater quantity of *Chenopodium album* agg. seeds, which together with the decrease in the quantity of wood recorded could indicate the presence of humans. At that time trees were probably being felled and the fen disturbed or grazed. There is also an increase in precipitation of calcium carbonate and in the abundance of heliophilous species such as *Schoenoplectus tabernaemontani* (seeds) and *Campylium stellatum* (stems with leaves).

3. Subzone Bma3a (70–45 cm; 2601–1927 cal. yr BP) is characterized by the strong decrease of seeds of *Schoenoplectus tabernaemontani*. There is a markedly lower abundance of oogonia of *Chara vulgaris*, which indicates a decrease in water level. Further, there is a strong decrease in the total amount of bryophytes and *Campylium stellatum* is replaced by *Drepanocladus polygamus*. There is a decrease in precipitation of calcium carbonate at the end of this period.

At the beginning of subzone Bma3b (40–5 cm; 1854–171 cal. yr BP), *Schoenoplectus* seeds and *Chara vulgaris* oogonia increase in abundance. Later, in the most recent part of this zone, oogonia disappear and *Schoenoplectus* seeds disappear almost completely, indicating a decrease in water level. In contrast, the seeds of *Cladium mariscus* become more abundant.

Molluscs

Based on the cluster analysis, four mollusc assemblage zones were distinguished (Fig. 6). Most of the interpretations are based more on changes in species abundances than on species turnover, as the latter is likely to be linked with suboptimal conditions for shell preservation in most layers. Unfortunately, shells in layers from a depth of 140 cm down to the bottom (entire zone Bmo1 and the oldest part of the zone Bmo2) were extremely poorly preserved due to the low concentration of calcium carbonate and a high quantity of wood, which provided only very limited material for reconstruction.

1. In the first zone Bmo1 (250–155 cm; 14 396–4955 cal. yr BP) there is only extremely poor material, consisting of only a few shells in only some layers. The species recorded, *Vallonia pulchella* and *Vertigo pygmaea*, are characteristic of fully open habitats, which indicates the existence of an open-fen at this site.

2. In the second zone Bmo2 (150–115 cm; 4709–3452 cal. yr BP), *Clausilia pumila*, a species of wet and alluvial habitats, is present. This might indicate, along with the absence of typical open habitat species in the deeper layers of this zone, an increase in the abundance of shrubs. At the end of this zone, two open-habitat species appear and in the subsequent layer *C. pumila* disappears completely.

3–4. In the zones Bmo3 (110–45 cm; 3358–1927 cal. yr BP) and Bmo4 (40–5 cm, 1854–171 cal. yr BP), several wetland species (e.g. *Oxyloma elegans* and *Vertigo antivertigo*) are very abundant, particularly in the third zone, which indicates a high and stable water table and succession into stable open calcareous fen. Another fen species, *Vertigo moulinsiana*, which is sensitive to intensive grazing, is also present in one layer of the zone Bmo3. Zones 3 and 4 differ in the dominance of the open-country snail *Vertigo pygmaea*, which is more abundant in the youngest layers.

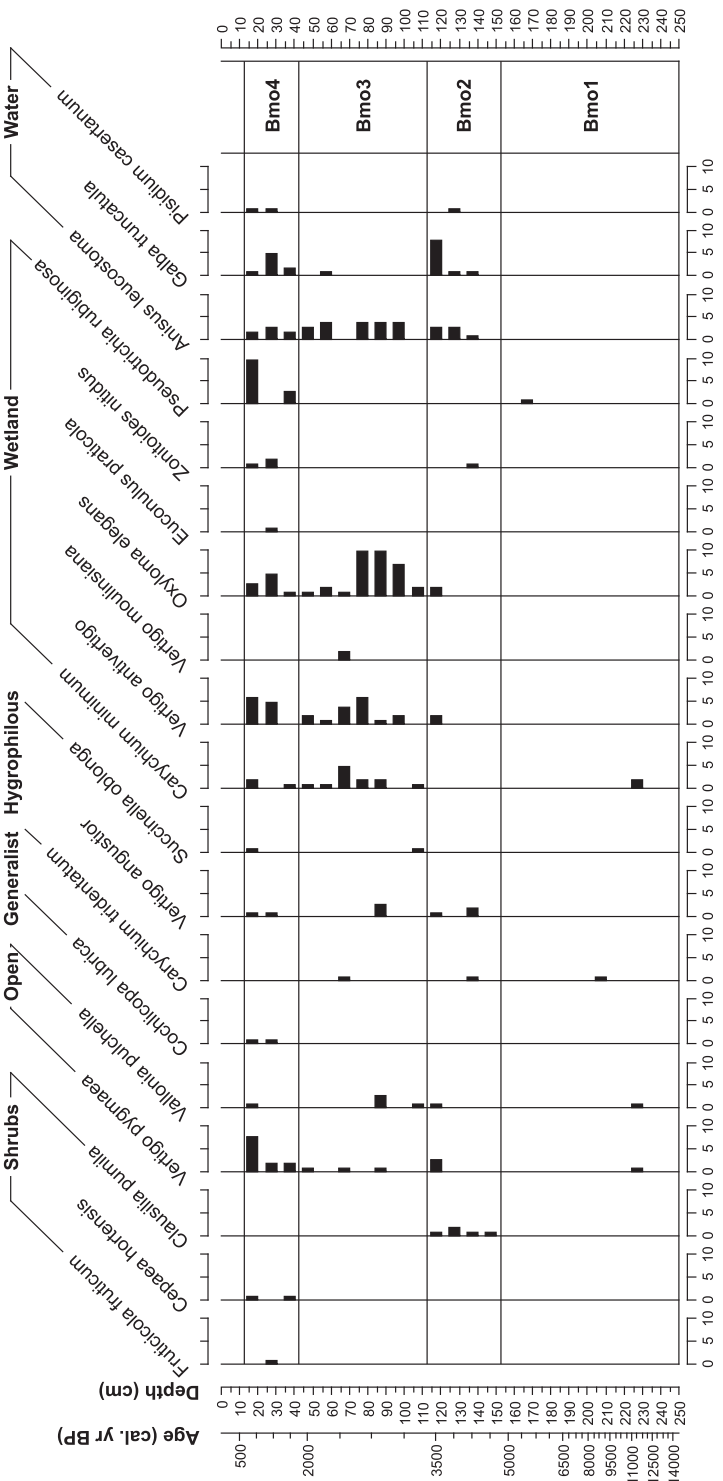


Fig. 6. – Mollusc diagram. Data are in absolute numbers of shells. Species are classified into main ecological groups according to Ložek (1964).

Discussion

Chronology

Our presumption that the basal layers are of early-Holocene age, as indicated by the bulk dating (11,500 cal. yr BP), is supported by two pieces of evidence. First, early Holocene is indicated in the record by a steep and rapid decline in the dominance of *Pinus*. In central Europe *Pinus* was also locally dominant in the middle Holocene (e.g. Pokorný & Kuneš 2005) but only in areas where the edaphic conditions were unsuitable for other trees, which is not our case. In addition, we do not know of a steep decline in the abundance of *Pinus* occurring around 6500 cal. yr BP anywhere else and the results from other profiles at the Carpathian-Pannonian border clearly indicate that in the middle Holocene, *Pinus* pollen is also not abundant (Magyari et al. 1999, 2001, Petr et al. 2013, unpublished data of E. J.). Second, early-Holocene age is indicated by an uninterrupted pollen curve for *Larix* up to 211 cm. Current information indicates that *Larix* disappeared in the region of the Carpathian-Pannonian border prior to the middle Holocene (Magyari et al. 1999, 2001, unpublished data of E. J.) and its occurrence during middle and late Holocene is documented only in northern Slovakia, in the Tatra Mts (Rybníčková & Rybníček 2006), Orava, Spiš, Liptov and Horehronie regions (Jankovská 1988, Hájek et al. 2011, Rybníček & Rybníčková 2002, unpublished data of E. J.), in the Slovenský raj Mts and the Turčianska kotlina basin. Also data from the Mitická slatina site (located ca 25 km from the study site), based on AMS dating of more seeds, suggest that *Larix* occurred together with an abundance of *Pinus* and some mesophilous trees in the late glacial (12,900 cal. yr BP) but disappered during the early Holocene.

The difference between single-seed and bulk dating may be due to a bioturbation that transported seeds from upper to lower layers. This might include root growth of reed (*Phragmites australis*), activity of invertebrates generally living in rather deep layers in spring fens or frequent grazing, which is well-documented in our fossil record. Contamination during coring also cannot be excluded. The hard-water effect (Grimm et al. 2009) is probably of little importance in this case, because (i) we dated fen and not aquatic bulk deposits (note that fen vegetation usually photosynthesizes above the water-table), (ii) the bulk sample did not contain grains of calcium carbonate or snail shells, (iii) our results for other spring fens in the Western Carpathians are very similar in terms of the dates for bulk and seed samples (our unpublished data). Note that seed redeposition could happen very easily, because the bottom layer is very compressed with 40 cm equivalent to almost five thousand years. We do not know the reason for the different rates of accumulation in bottom layers and the rest of profile, but high mineralization due to lower water supply is a possible explanation.

As a result of dating constraints, the age of the early-Holocene sequence (up to ca 7000 cal. yr BP) is only inferred from the depth-age model and not based on individual AMS dates obtained for material within this zone. The pollen spectrum (absence of *Carpinus*, *Abies* and crops and high representation of *Pinus*, *Corylus* and *Tilia*) conforms to the prediction of the depth-age model and indicates an early-Holocene age, but the fossil record in this sequence may not be complete. Scarce occurrence of *Fagus* could point to a hiatus in the record, but the amount of pollen is rather low. Moreover, pollen of *Fagus* occurs in early Holocene sequencies in the profile collected at Šúr (western Slovakia; Petr et al. 2013) and Santovka (south-western Slovakia; Petr et al. 2012), which indicates the occurrence of beech during the early-Holocene period in the foothills of the Western Carpathians.

Local vegetation

Our results indicate the continual presence of *Cladium mariscus* at the study site. Similarly, *C. mariscus* seeds are recorded in different Holocene periods in fens in north-eastern Poland (Galka & Tobolski 2012), northern Germany (Michaelis 2002), central Bohemia (Hrabanovská černava; Petr 2005), north-western Bohemia (Pokorný et al. 2010) and southern Slovakia (P. Žáčková, in verb.), which indicate its continuous presence in calcareous fens in Europe during the Holocene. As the distribution of this species is limited by low winter temperatures of below 2 °C, which damage its meristems (Conway 1938), and a low number of frost-free days (Salmina 2004), it was probably not widespread during the glacial periods, but direct palaeoecological evidence is scarce. Thermal springs may have been refugia during the glacial period, but our fossil record cannot indicate whether it was present before the start of the Holocene. This species probably spread after the climate improved in the early Holocene and its decline probably did not start before the formation of the High Medieval landscape, when sedimentation of nutrient-rich flood loams caused by errosion after human-deforestation started (Pokorný et al. 2010). Further, eutrophication and drainage during the last decades resulted in a strong reduction in the number of localities for *Cladium* in central Europe (Eliáš et al. 2003, Pokorný et al. 2010).

The community with *C. mariscus* studied was rather stable with only small changes connected with fluctuating water level. The presence of *Alnus* wood, *Eupatorium cannabinum*, *Mentha longifolia*, *Potentilla reptans* and *Ranunculus sceleratus* seed in the period between ~13,700 and 6000 cal. yr BP is characteristic of a fluctuating water level and higher nutrient supply. *Alnus* wood in the bottom part of the profile (up to 175 cm; ~6000 cal. yr BP), along with pollen and seeds of light-demanding plants, indicate alder carr with an open canopy or a mosaic of open fen habitat and scattered *Alnus* trees. Later, the level of the water increased and then remained stable (~5100 cal. yr BP), which is indicated by the presence of a high abundance of *Chara vulgaris* oogonia and *Botryococcus* characteristic of calcareous-fen pools. This change may be due to a change in the position of the spring or to climate moistening, the latter is documented as occurring in this period (~5500–5000 cal. yr BP) in the Eastern Carpathians (Magyari et al. 2009, 2013) and Great Hungarian Plain (Magyari et al. 2010; increase in *Fagus* associated with an increase in humidity). During this period the vegetation consisted of reed swamp dominated by tall graminoids (*Cladium*, *Schoenoplectus* and *Phragmites*) and tall herbaceous plants (*Eupatorium* and *Lycopus*), but lacked a well-developed bryophyte layer. It probably corresponds to the present-day vegetation of the *Magnocaricion elatae* Koch 1926 alliance, which is the most common current vegetation type with *Cladium mariscus* (Eliáš et al. 2003). The important finding is that of *Primula farinosa* (see comment on this pollen type in Electronic Appendix 1) in the early-Holocene period. This species prefers ancient *Caricion davallianae* calcareous fens which initiated in the late glacial or early Holocene (Hájek et al. 2011), but till present there was no direct evidence of its occurrence in those periods in the Western Carpathians. Its occurrence in the profile studied suggests that low-sedge brown-moss vegetation coexisted in a mosaic of *Cladium* stands. Such a mosaic may also have developed in younger phases of fen development, even if it is not documented by pollen, because pollen record of entomogamous herbaceous plants might mirror a very local pattern.

The site was probably repeatedly influenced by human activities (probably grazing) occurring at the latest from the Bronze Age, which is indicated by the high presence of *Chenopodium album* seeds. Another explanation could be that the origin of the *Chenopodium* seeds is natural and due to disturbance by wild herbivores or drying out of fen peat; *Chenopodiaceae* can grow on exposed mudflats or dessicated surfaces of fens (e.g. Magyari et al. 2010, 2012). These natural events might explain the occurrence of *C. album* seeds in older parts of the profile. Grazing by domesticated or wild herbivores is further indicated by the presence of spores of coprophilous fungi (*Sporormiella*-t.) and absence of the calcareous-fen snail *Vertigo moulinsiana* (cf. Ausden et al. 2005) from all but one layer of the profile. Grazing could increase the input of nutrients into the ecosystem, which probably limited the occurrence of low-productive *Caricion davallianae* vegetation. High-productive vegetation consisting of tall graminoids and tall herbaceous plants might be further supported by the high water temperature of the warm springs, which probably increases the mineralization rate (Taylor & Dykstra 2005) and the associated nutrient release. A high rate of decomposition might also account for the flat depth-age curve in the basal part of the profile.

The most recent change in vegetation caused by an anthropogenic water-level decrease is reflected in the disappearance of *Schoenoplectus tabernaemontani*, whose seeds are present in the subrecent sample collected from 5–10 cm below the surface, and recent spread of *Phragmites australis.* As a disturbed water regime is considered to be the reason for the recent extinction of *Cladium mariscus* at many sites (Eliáš et al. 2003), the future of this species at the study site is uncertain.

Early spread of mesophilous trees

As expected, we documented the occurrence of some mesophilous trees (*Ulmus*, *Fraxinus*, *Tilia* and *Quercus*) from the beginning of sediment accumulation, dated roughly to the early Holocene, even though the abundances of these trees was less than those reported for more southern locations: northern Hungary (Magyari et al. 2010) and southern Slovakia (Petr et al. 2013, unpublished data of E. J.). Occurrence of local glacial refugia for these trees more to the north is suggested by Magri (2008) and Willner et al. (2009) but not verified, thus it is likely that mesophilous trees spread from Pannonian glacial refugia (e.g. Birks & Willis 2008, Sümegi et al. 2013) northwards to a small basins surrounded by mountain ranges (Tribeč Mts, 829 m a.s.l. and Považský Inovec Mts, 1042 m a.s.l. in our case). Later, these mesophilous trees increased in abundance, probably after an improvement in climate when, simultaneously, open-country species (*Artemisia* and *Chenopodiaceae*) decreased and *Poaceae* increased. However, in deciduous forests at the Pannonian-Carpathian boundary there is characteristically also a great abundance of *Poaceae* (e.g. *Brachypodium pinnatum*). Because the dating of the basal layer of the profile is somewhat uncertain and of poor resolution (see section Chronology in Discussion), further research is needed to reconstruct more precisely the spread of mesophilous trees in the region studied.

Continuity of treeless vegetation

Landscape openness is usually measured in terms of the AP (arboreal pollen) and NAP (non-arboreal pollen) ratio in pollen records. Generally, if AP makes up more than 80% of

total pollen, it indicates forest vegetation, less than 70% forest-steppe and lower percentages (less or equally to 50%) steppe (Svenning et al. 2002, Magyari et al. 2010). Using other palaeoecological proxies, such as macrofossils of plants and snails, may also be used to determine the level of landscape openness (Svenning et al. 2002), though they may reflect rather local conditions. Our pollen diagram indicates that arboreal pollen prevailed from the beginning of the accumulation of organic matter (about 80%). A similar AP:NAP ratio is recorded during the Pleistocene/Holocene transition at the Vracov site (southern Moravia, north-western margin of the Pannonian lowland; Rybníčková & Rybníček 1972). The AP percentages are greater than 75% in most of the profile, which might indicate a densely forested landscape. Nevertheless, this contradicts not only the clearly open character of local wetland vegetation (indicated by the plants *Cladium mariscus*, *Schoenoplectus tabernaemontani*, and snails *Vallonia pulchella* and *Vertigo pygmaea*) but also clear evidence of the presence of open-grassland and steppe patches (Fig. 4). Indeed, recent studies indicate that the relationship between the AP percentage and representation of forests is more complicated than previously thought (e.g. Sugita et al. 1999, Pelánková et al. 2008, Magyari et al. 2010). Recent surface samples from floodplains in wooded steppe, where improved moisture conditions result in the development a local forest, often contain > 75% of AP and as a consequence it is difficult to distinguish continuous forest from wooded steppe (Magyari et al. 2010). This may also apply to the site studied, which is situated in a waterlogged basin where *Picea*- and *Alnus*-forests were probably abundant (Fig. 4). The results from southern Siberia indicate that pollen spectra consisting of between 50–80% AP are recorded not only in open *Larix* and *Pinus sylvestris* forests, but also in meadow steppes in a forest-steppe landscape (Pelánková et al. 2008). We conclude that in the Pleistocene/Holocene transition and early Holocene in the area studied there were open coniferous forests with *Pinus sylvestris* and *Larix*, similar to those reconstructed in other regions of the Western Carpathian mountains (Jankovská 1988, Jankovská & Pokorný 2008) and Pannonian Basin (Sümegi et al. 2001), where they occurred in a mosaic with treeless habitats such as fens and steppes. These forests may have been similar to the southern-Siberian *Pinus-Larix* hemiboreal forests, which are rather open, with many light-demanding species and high species richness (Chytrý et al. 2012). They dominated the landscape, but the exact ratio of forested and treeless habitats cannot be assessed accurately.

The AP percentages remained stable during the entire prehistoric period, even if the composition of forest species changed; this is caused by differences in production of pollen among different species of trees (e.g. Prentice 1985, Sugita 1994, Sugita et al. 1999), the large proportion of light-demanding shrubs in the AP sum in most periods, and changing ratio of local (floodplain) and regional (upland) pollen influx. Because even some types of Carpathian-Pannonian deciduous forests usually have an open structure and many light-demanding species are present (Roleček 2005) it is difficult to distinguish between a mosaic of large areas of steppe with forested patches and open forests. Our data suggests that early- and middle-Holocene forests (~9500–6500 cal. yr BP; see section Chronology for discussion on dating) were composed mainly of light-demanding *Quercus* with an admixture of *Corylus*. They should be open, because both hazel and oak seedlings need high light intensities to survive. These *Quercus-Corylus* forests were kept open by various natural factors. First, climate in the Pannonian lowland was rather dry and relatively warm (Magyari et al. 2010, unpublished data of E. J.). Second, edaphic factors (soil properties, nutrient

availability, geomorphology) might codetermine the existence of species-rich open forests (Svenning 2002, Bradshaw et al. 2005, Sümegi et al. 2012). Third, disturbances caused by large native herbivores (Vera 2000), natural fires (Chytrý et al. 2010) or human activity in the Mesolithic (Tallantire 2002, Kuneš et al. 2008) could also have contributed to keeping forests open enough for survival of light-demanding species. The high number of particles of microcharcoal found in this period indicates that fires were important regardless of whether they were started by man during the Mesolithic (Mason 2000) or by natural events. Grazing by large herbivores is well indicated by the presence of spores of coprophilous fungi (*Sporormiella* genus) in organic deposits (Ahmed & Cain 1972), even though present in low amounts of below 1% (Davis & Shafer 2006). We recorded *Sporormiella*-t. spores from the Pleistocene/Holocene transition, which indicates possible influence of large herbivores in a pre-agriculture period. Concerning steppe vegetation, it surely existed in central-European lowlands before man established settlements there (Wallis DeVries et al. 2002) at least on south facing slopes and dry plateaus (Dúbravková & Hajnalová 2012). In the study area, continental steppe vegetation probably persisted on loess loams situated on slopes close to the study site (http://mapserver.geology.sk), whereas wet and mesophilous meadows occurred in the floodplain. Steppe occurrence is well indicated by *Artemisia* and *Chenopodiaceae*. Although these taxa may indicate human settlements, their occurrence before the Neolithic is likely to be connected with either steppes or halophytic habitats in the steppe zone (Eliáš et al. 2013).

After 4000 cal. yr BP (the Bronze Age), the AP frequencies started to fluctuate, probably as a consequence of an increasing representation of species of managed grasslands, crops and some dry-grassland species, and spread of *Fagus* and *Carpinus*. The synoptic pollen diagram (Fig. 7) reveals that around 3700 cal. yr BP the most important bottleneck for light-demanding species occurred. It is indicated by a decline of all grassland, open-country ruderal and open-wetland species, and unlike the previous bottleneck at the Boreal/Atlantic boundary around 7500 cal. yr BP it was further associated with a decline in pollen of unclassified non-arboreal taxa (including *Poaceae*) and an increase of upland forests. This period corresponds to the expansion of *Fagus* and *Carpinus*, which is generally attributed to soil deterioration due to nutrient leaching (Berglund 1986, Pokorný & Kuneš 2005), fluctuating human activity (Pokorný 2005) and/or increase in the availability of moisture during the growing-season in the Pannonian lowland (Magyari et al. 2010). This phase of the Holocene was apparently also crucial for the survival of light-demanding species in another region at the Pannonian-Carpathian boundary, the White Carpathians (Hájková et al. 2011). In the study region and the White Carpathians, *Fagus* and *Carpinus* expansion is closely associated with agriculture intensification at the onset of the Bronze Age. In the profile studied, enhanced human activity between 3700 and 3500 cal. yr BP is indicated by the occurrence of coprophilous fungi (*Sporormiella*-t., *Sordaria*-t., *Chaetomium* sp.), the plant *Plantago lanceolata* (indicating managed grasslands), and a general increase in species of all grassland types (wet, mesic and dry) and open-country ruderals (Fig. 7).

Coincidence between pollen and archaeological records

The human settlement of the study area is documented by archaeological records since the Early Neolithic (~5700–5000 BC; Točík 1970) but there is no clear pollen evidence such as presence of *Cerealia* pollen or increase in microcharcoals. There are records of a Neolithic

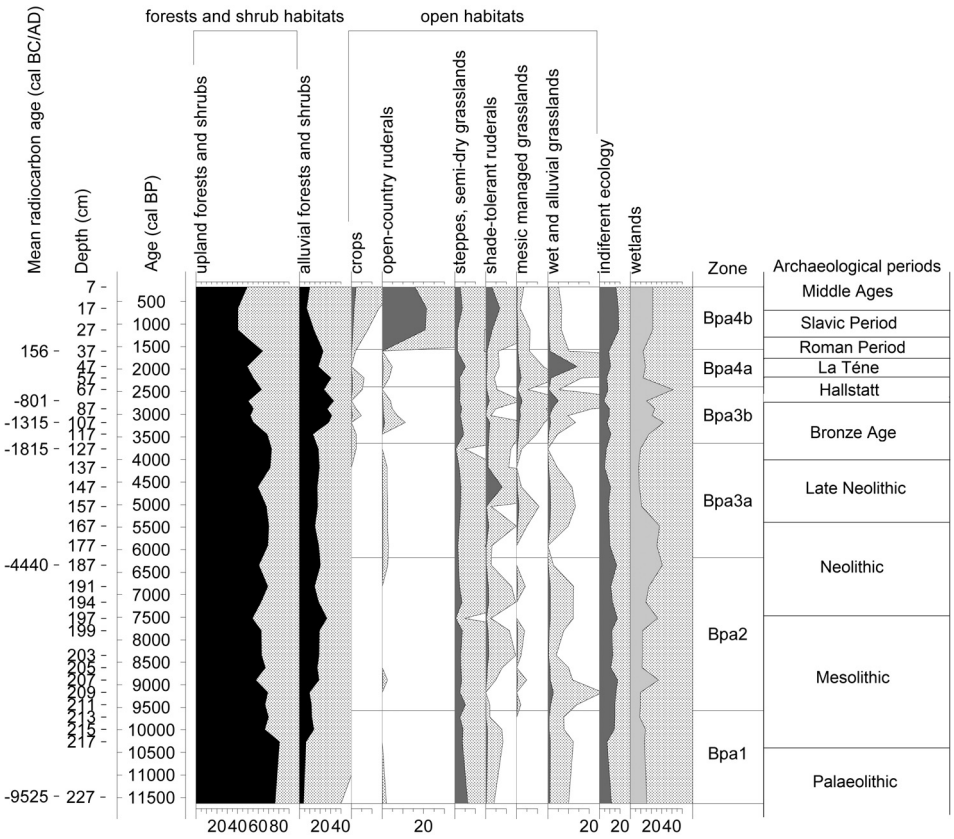


Fig. 7. – Synoptic pollen diagram. All pollen taxa are classified into groups according to habitat requirements of the plant species involved. Group "wetlands" is not included in the total sum. For the list of taxa belonging to particular groups and comments on species classification see Electronic Appendix 1.

settlement ~3 km from the site analysed, but the small-scale garden agriculture typical of that period (Bogaard 2004) probably accounts for the absence of *Cerealia* in pollen records. As the population density of Neolithic farmers was sparse, they did not have a marked effect on the landscape. Moreover, the first farmers tended to settle in naturally treeless areas in those parts of central Europe covered with loess (Bogaard 2004, Hajnalová 2007), therefore deforestation was not required (Willis 2007). During Late Neolithic (Eneolithic), agricultural practices were developed (Hajnalová 2007), but there is still no evidence of the presence of *Cerealia* during that time in the study area, possibly the distance from the human settlements at that time limited the input of crop pollen (E. Jamrichová et al., unpublished data). Dreslerová & Pokorný (2004) document that even large water bodies in a less geomorphologically structured landscape can have catchment areas of only 800–1000 m in radius and that small water bodies catch only local pollen. Even though we did not record cereals for this period, changes in the composition of grassland species indicate human activity, mainly grazing, in the surrounding landscape, during the Late Neolithic.

The first occurrence of *Triticum*-t. pollen is dated to ca 4000 cal. yr BP (127 cm, 3765 cal. yr BP; 1816 BC Bronze Age). The Bronze Age (~4250–2650 cal. yr BP; 2300–700 BC; Bárta 2009) is characterized by an improvement in farming techniques (use of ard and yoke; Hajnalová 2012), ore mining and metal processing, which markedly affected the landscape. The decline in mesophilous trees (*Fagus* and *Carpinus*) and increase in *Alnus* after 3500 cal. yr BP might be due to an increase in human pressure. Deforestation and tillage resulted in soil erosion in the area of loessic hilly lands (Stankoviansky 2008, Smetanová 2011) and development of *Alnus* carrs (cf. Pokorný 2005). On the other hand, deforestation of south-exposed slopes allowed the development of dry grasslands (Dúbravková & Hajnalová 2012). This process may account for the gradual spread of dry-grassland species, especially those recorded in the pollen diagram that indicate disturbance (*Orlaya grandiflora*-t. and *Eryngium campestre*-t.). Dry grasslands were grazed, mown or burned to keep them open in order to obtain hay for livestock (Bylebyl 2007). Woodlands were probably grazed as well, which led to a decrease in canopy cover and spread of the light-demanding shrubs *Cornus mas*, *Frangula* and *Sambucus* (cf. Moskaldel Hoyo 2013). According to Marinova & Thiébault (2008), presence of *Cornus mas* together with *Sambucus* is associated with human activity, such as canopy opening and, in the case of *Sambucus*, nutrient enrichment and disturbance. Alternatively, light-demanding shrubs might have survived in forests not affected by human activity but growing on shallow soils in limestone rocky places in the Strážovské vrchy Mts. Forest grazing probably also resulted in open oak forests (oak pollen increased) and suppressed shady beech forests in that period (Fig. 4: zone Bpa3b).

Further intensification of agriculture occurred in the Iron Age (67 cm; 2500 cal. yr BP, 560 BC), i.e. the period when numerous settlements are recorded in the study region. At that time settlement intensity increased due to iron and gold ore mining in the closest mountains (Vangľová 2008). There is evidence of prehistoric mining on the north-eastern slopes of the Považský Inovec Mts, only ~25 km from the study site (Lukačka 2006). The increase in the concentration of microcharcoal in the pollen diagram probably reflects strong exploitation of the surrounding landscape (deforestation and metallurgy). During the La Tène period (around 80 BC), human activity around fortified settlements increased (Vangľová 2008), which might account for the in situ decline in *Cerealia* associated with a clear peak in species indicating wet and alluvial grasslands. Dry-grassland species also increased, but less so. These changes may suggest a general change from crop cultivation to grassland management. Because the stability of wet grasslands is more dependent on mowing than dry grasslands (Galvánek & Lepš 2009), the changes recorded for the La Tène period might suggest the presence of hay meadows in the study area, which corresponds to the results of the meta-analysis of western and central European archaeobotanical data (Hodgson et al. 1999).

After temporary decline in agriculture, the representation of grassland and open-country ruderal species steeply increased, coinciding with Slavic settlement of the region.

Conclusions

The warm-spring fen-peat profile collected close to the Malé Bielice village contained not only macrofossils of plants and molluscs, but also an extraordinary high number of pollen

taxa, which is an uncommon feature of calcium-rich lowland fens. Our multi-proxy palaeoecological study of this profile confirmed (i) the early spread of mesophilous trees (*Ulmus*, *Fraxinus*, *Tilia* and *Quercus*) into the northern part of the Carpathian-Pannonian boundary, but unfortunately it was not possible to date it accurately, (ii) the survival of *Cladium mariscus* population throughout the Holocene, (iii) the Holocene persistence of open-country habitats (calcareous fens, dry grasslands) in the region, which may explain the occurrence of rare light-demanding species, and (iv) the coincidences between the history of human settlement and the spread of particular types of grassland at the Pannonian-Carpathian boundary.

See www.preslia.cz for Electronic Appendices 1–3

Acknowledgements

We dedicate this study to Eliška Rybníčková and Kamil Rybníček, who conducted one of the first multi-proxy palaeoecological studies on the Pannonian-Carpathian boundary, on their 80th birthday. We are grateful to Libor Petr and Stanislav Němejc for help with the profile sampling, Zuzana Formánková for laboratory work and three reviewers for valuable comments. The research was funded by grant GAČR P504/11/0429, institutional support of Masaryk University and long-term research development project no. RVO 67985939.

Souhrn

Historie slatin na teplých pramenech je ve střední Evropě téměř neprobádaná (s výjimkou teplých pramenů v Rumunsku), přestože jsou to extrémní stanoviště se stabilními podmínkami, které mohou umožňovat dlouhodobé přežívání druhů. Studovali jsme vápnitý sediment, který se začal ukládat na začátku holocénu u Malých Bielic (u města Partizánske na západním Slovensku) na vývěru teplého pramene s teplotou okolo 40 °C. Tato lokalita se zachovala do současnosti a vyskytuje se na ní vzácný druh *Cladium mariscus*. Důležité je, že se nachází v oblasti, odkud paleoekologická data dosud zcela chyběla a kde se v současnosti vyskytují vzácné světlomilné druhy, které zde mají izolované výskyty nebo jsou zde na okraji svého areálu rozšíření. Jejich přežívání během klimatického optima, kdy expandoval v krajině les, není doposud plně vysvětleno a právě paleoekologické metody mohou přispět k vysvětlení současného prostorového uspořádání výskytu těchto druhů. Studované území v kotlině řeky Nitry představuje také severní výběžek panonské nížiny do Západních Karpat, což bylo důležité pro šíření mezofilních dřevin v raném holocénu. Detailní mezioborové studium tohoto slatinného sedimentu zahrnující analýzu pylových zrn, rostlinných makrozbytků, schránek měkkýšů a stratigrafii doplněnou radiokarbonovým datováním nám umožnila potvrdit (1) časnou expanzi mezofilních dřevin (*Ulmus*, *Fraxinus*, *Tilia*, *Quercus*) v severních částech karpatsko-panonské hranice; (2) reliktní charakter a dlouhodobé přežívání izolované populace *Cladium mariscus* na slatiništi, syceném teplým pramenem; (3) kontinuální výskyt otevřených stanovišť (slatiny, stepi/suché trávníky) v krajině během celého holocénu, což mohlo významně ovlivnit přežívání vzácných světlomilných druhů v krajině a (4) vliv lidské činnosti na šíření jednotlivých typů nelesní vegetace na karpatsko-panonské hranici, který se významně projevoval od doby bronzové. Člověk začal v krajině intenzivněji působit právě v okamžiku rozmachu bukových a habrových lesů a pravděpodobně tak zabránil vyhynutí řady světlomilných druhů.

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Received 21 March 2013
Revision received 7 July 2013
Accepted 8 July 2013