Reevaluation of the palaeoenvironmental record of the former Komořanské jezero lake: late-glacial and Holocene palaeolimnology and vegetation development in north-western Bohemia, Czech Republic

Nové zhodnocení paleoenvironmentálního záznamu z Komořanského jezera – paleolimnologická rekonstrukce a postglaciální vývoj vegetace v severozápadních Čechách

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

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The main goal of this article is to summarize results of palaeoecological investigations of a classical and iconic site in the Czech Republic, the former Komořanské jezero lake. This lake persisted in north-western Bohemia from at least the Weichselian Late Glacial until quite recently. Pollen and palaeoalgological analyses of coccal green algae were carried out on several sedimentary sequences sampled within the framework of palaeobotanical and archaeological salvage research from 1970s to 1990s. The results are published here jointly for the first time. They make it possible to reconstruct both the lacustrine environment and upland vegetation in the wider surroundings of the lake. The Komořanské jezero lake in the late-glacial period was cold and oligotrophic. Its nutrient status gradually changed and became mesotrophic and dystrophic locally in the early Holocene and eutrophic from the Middle Holocene onwards. Unfortunately, big differences in geomorphology and environmental conditions together with long-distance (and likely even fluvial) transport of pollen make the reconstruction of upland vegetation somewhat difficult. Immigration of climatically demanding species into the area started already in the Preboreal period (before 8200 uncal. yr BP). Maximum expansion of broadleaved forests occurred in the Atlantic period (between 6000 and 7000 uncal. yr BP). At the same time, afforestation spreading from the lowlands (200 to 400 m altitude) up to the mountain ridges (around 1000 m a.s.l.) of the Krušné hory Mts attained its maximum level. Based on continually increased presence of non-arboreal pollen we hypothesize that open grassland biotopes (continental-type steppe vegetation) persisted in the wider region from the late glacial throughout the entire Holocene. First clear evidence of a human effect on vegetation in promoting expansion of secondary grasslands is dated in pollen diagrams to around 4000 uncal. yr BP (i.e. the Subboreal period).

Keywords: central Europe, continental forest-steppe zone, palaeoalgology, palaeoecology, pollen analysis, vegetation history

Introduction

The former Komořanské jezero lake is situated in the south-eastern foothills of the Krušné hory Mts (approximate center of the lake basin: 50°32'N; 13°33'E; 230 m a.s.l.; Fig. 1) and was supplied with water draining off the slopes and summit plateau. According to Hurník

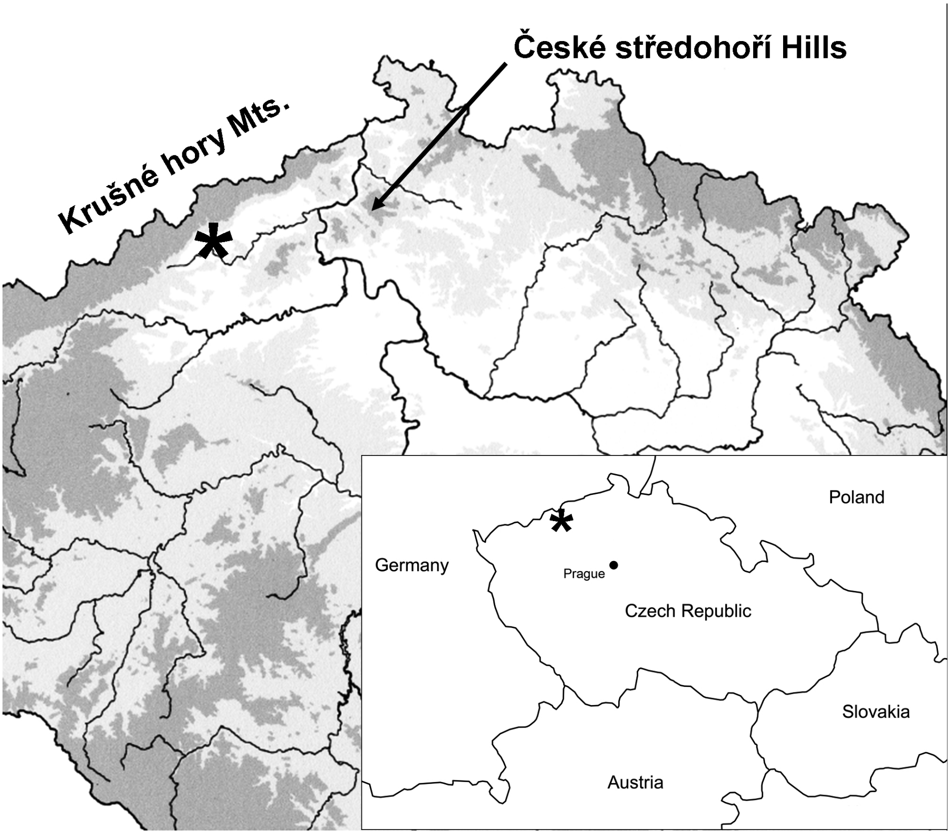

Fig. 1. – Location of Komořanské jezero lake in the Czech Republic (study site marked by asterix).

(1969), the origin of the Komořanské jezero lake was tectonic (through subsidence of Podkrušnohorská pánev basin – a submontane basin in the Krušné hory Mts). It is also likely that in addition to Komořanské jezero lake there were several other similar, though smaller lakes in this area (Kruta & Vencl 1973). Stratigraphy of the sedimentary fill in this basin is thoroughly described by Hurník (1969). According to him, the sand and gravel basal sediment is up to 4 m deep. It originated from reworked terraces along the river Bílina during the last full-glacial period. In the late glacial the sediment deposited consisted of fine-grain silt with an organic admixture. Sedimentation of mainly organic material started at the beginning of the Holocene, and in the course of early and middle Holocene, diatomite and gyttja accumulated. Thickness of these younger organic deposits does not exceed 1.8 m in the center of the basin. Lake sediments were covered, particularly in areas of the littoral zones of the previous lake, by peat that attained a thickness of up to 3 m.

In historic times, free water occurred only in scattered places within the basin of Komořanské jezero lake (as seen in a Military survey map of AD 1780; Fig. 2). Open water occupied an area of 5.75 km^2 in 1789 (Klement & Enz 1940 in Řeháková 1986), while the lake area shown on a map by Wolf (1880), was about 25 km^2. According to Rudolph (1926), the water level in the lake fluctuated greatly, increasing when the basin

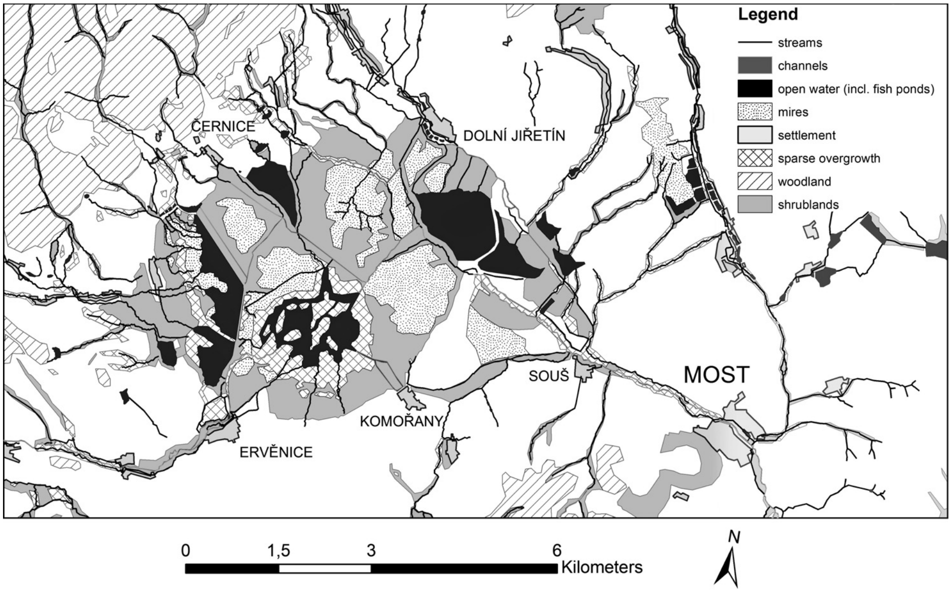

Fig. 2. – The area around Komořanské jezero lake area in the late 18th century, before extensive brown coal extraction started. Land-use categories are based on the interpretation of the First Military Survey Map (AD 1780 approx.). *Open water*, *mires*, *sparse overgrowth* and *shrubland* categories (the last one also includes some alder woods) show the approximate extension of the original lake, which at that time had already been drained and managed. Author of the reconstruction: Vladimír Bruna.

filled with water after snowmelt in the Krušné hory Mts or periods of heavy rain. Thus, there exist rather contradictory opinions on the lake's historical physical parameters.

The artificial drying out of the lake basin in AD 1831–1834 resulted in the origin of the so-called Jezerní louka ("Lake Meadow"; Březák & Klápště 1983). Today, Komořanské jezero lake does not exist as its environs have been completely altered by mining of brown coal. The last remnants of lacustrine sediments were completely destroyed in the last decades of the 20th century, bringing to an end one of the most valuable post-glacial sedimentary archives in the Czech Republic.

The former Komořanské jezero lake was definitely the largest natural lake in the current territory of the Czech Republic. It was the only significant lowland natural water body existing in this country until recent times. Nevertheless, the existence of several other ancient lakes in the Czech Republic is confirmed by palaeobotanical research (Petr & Pokorný 2008). Recently, further evidence was obtained that supports the idea that the landscape of the Czech Republic formerly was marked during the late glacial and early Holocene by the rather common occurrence of small lakes (Jankovská 2001). There is an illustrative case of such a lake bordering a retreating glacier at high altitudes in the Labský důl Valley in the Krkonoše Mts (the Giant Mts), which was only recently discovered using palaeobotanical methods (Engel et al. 2004, Jankovská 2004) and is similar to extant ones on the Polish side of the Krkonoše Mts (the Welki and Mali Staw lakes) and in the Bohemian Forest (Čertovo jezero, Černé jezero, Prášilské jezero and Plešné jezero lakes). A landscape characterized by the presence of lakes existed also north of the Bohemian

Massif at the end of the Pleistocene and early Holocene. The sediments of these silted lakes have provided information on landscape development and human colonization, e.g. those from the locality Reichwalde in neighbouring Saxony, Germany (Friedrich et al. 2001).

First palaeobotanical research carried out at the site of the former Komořanské jezero lake was that of Rudolph (1926) followed by Losert (1940). The main goal of this research was to link the archaeological and pollen-analytical chronologies for this site. Following the post-WWII exploratory investigations of Pacltová & Žertová (1959) the first detailed studies were published in the eighties of the 20th century (Jankovská 1983a, 1984) along with pollen analyses of material collected from archaeological sites excavated around the Lake (Neustupný 1985, Jankovská 1988). The results of the pollen analyses of the profile PK-1-B were only published in an abbreviated form (Jankovská 1983a, 1984), as were conclusions of palaeoecological research on the profile PK-1-E (Jankovská 2000). Analyses of the diatoms in the sediments of Komořanské jezero lake sediments were published by Řeháková (1962, 1983, 1986).

Historical developments in the area of Komořanské jezero lake were the subject of studies by Schlesinger (1871) and Pokorný (1963) and aspects of the geology of the basin by Hurník (1969). More recently, Březák & Klápště (1983) reconstructed the geomorphological and hydrological conditions in the former Komořanské jezero lake and present the first topographic reconstructions of this former Lake. Klápště (1988) also compiled a systematic map of the locations of the prehistoric as well as medieval and early modern archaeological finds. A further study by Klápště (1985) reveals the local network of long-distance roads that existed in the Early-Medieval period. Finally, Klápště (1994) summarizes the archaeological and historical evidence about the nature of the landscape and human settlements in this region during the Medieval period.

Material and methods

Fieldwork

Sections of sediment in profiles exposed during brown coal surface mining were sampled by the first author (V. Jankovská, with J. Kyncl). Section PK-1-B was sampled on 14 April 1977 in the western part of the former lake, to the east of the settlement of Dřínov (within the area of the "Rudé armády" mine, close to the "Eliška" mine). Not far from there, profile PK-1-D was also sampled and analyzed for pollen for purposes of environmental-archaeological research (Neustupný 1985, Jankovská 1988). Section PK-1-E was sampled in the close vicinity of the former lake (mine "Obránců míru"). Precise localization of this profile is not now possible due to lack of data that arose from both technical and administrative difficulties of sampling at that time. The same is unfortunately true for the PK-1-CH profile.

Laboratory methods

Subsamples from all the profiles studied were prepared for pollen and palaeoalgological analyses by means of standard acetolysis treatment (Erdtman 1960, Fægri & Iversen 1989). The mineral components (silicates) were disintegrated by means of hydrofluoric acid for 24 hours.

Pollen was determined using published keys and atlases (e.g. Punt 1976, Punt & Clarke 1980, 1981, 1984, Punt & Blackmore 1991, Reille 1992–1998, Punt et al. 1998, 1995, Beug 2004) and a reference collection of slides of modern pollen housed in the Institute of Botany, Brno, the Czech Republic. The pollen frequency was generally very high and preservation excellent. The number of pollen grains of upland trees and herbaceous plants fluctuated around 1000 and only in exceptional cases (lower profile layers with low pollen concentration values) were they between 300 and 400 (PK-1-B) and 100 and 150 (PK-1-E).

Pollen diagrams (Figs 3–10) were calculated and drawn in Tilia and TiliaGraph programs (developed by Eric Grimm, Illinois State Museum, Illinois, USA). Wetland pollen taxa (like *Alnus*, *Salix*, *Cyperaceae* and all hydrophytes) were excluded from the calculation sum. The values AP + (NAP – wetland pollen taxa) = 100% were used as the basis for the calculation of percentage values of local pollen taxa and also of non-pollen objects.

Algal remains were determined according to Sulek (1969) and with the help of J. Komárek (Institute of Botany, Czech Academy of Sciences). Remains (colonies as well as individual cells) of coccal green algae were determined and counted on the same slides as those used for counting pollen grains. Despite of the progress attained recently in the determination of findings of subfossil coccal green algae (Jankovská & Komárek 1982, 2000, Komárek & Jankovská 2001), some determinations remain at the level of knowledge prevailing in the eighties and nineties of the 20th century, when most of these analyses were performed. *Pediastrum alternans* together with *P. boryanum* var. *longicorne* were classified as belonging to the same group at that time (see pollen diagrams under designation *). In profile PK-1-CH *P. alternans* and *P. boryanum* var. *longicorne* were determined separately. It is likely that the taxon *Botryococcus braunii* includes other species of the genus *Botryococcus* (*B. pila*, *B. neglectus*, *B.* spec. div.), which were not specifically identified at that time.

Radiocarbon dating

Conventional radiocarbon data were obtained for four samples of sediment (bulk) from the profile PK-1-B at University of Wisconsin, Madison, USA (WIS designations in Table 1). Profile PK-1-CH was dated using bulked samples of sediment at AMS Laboratory of the Center for Applied Isotope Studies, University of Georgia, USA (UGAMS designations in Table1). It was impossible for technical reasons to arrange for samples from the profiles PK-1-D and PK-1-E to be dated. Dating results are reported here in an uncalibrated form (uncal. yr BP).

Table 1. – Results of radiocarbon dating of the profiles studied.

Profile label; depth	Lab. no.	Result (uncal. yr BP)
PK-1-B; 30 cm	WIS-1410	1490±70
PK-1-B; 90 cm	WIS-1411	2590±70
PK-1-B; 116–119 cm	WIS-1412	6570±80
PK-1-B; 128–129 cm	WIS-1413	7770±80
PK-1-CH; 154 cm	UGAMS-3164	3820±25
PK-1-CH; 162 cm	UGAMS-3165	3730±25
PK-1-CH; 172 cm	UGAMS-3166	4270±25
PK-1-CH; 190 cm	UGAMS-3167	5890±25
PK-1-CH; 204 cm	UGAMS-3168	6720±30
PK-1-CH; 218 cm	UGAMS-3169	8200±30

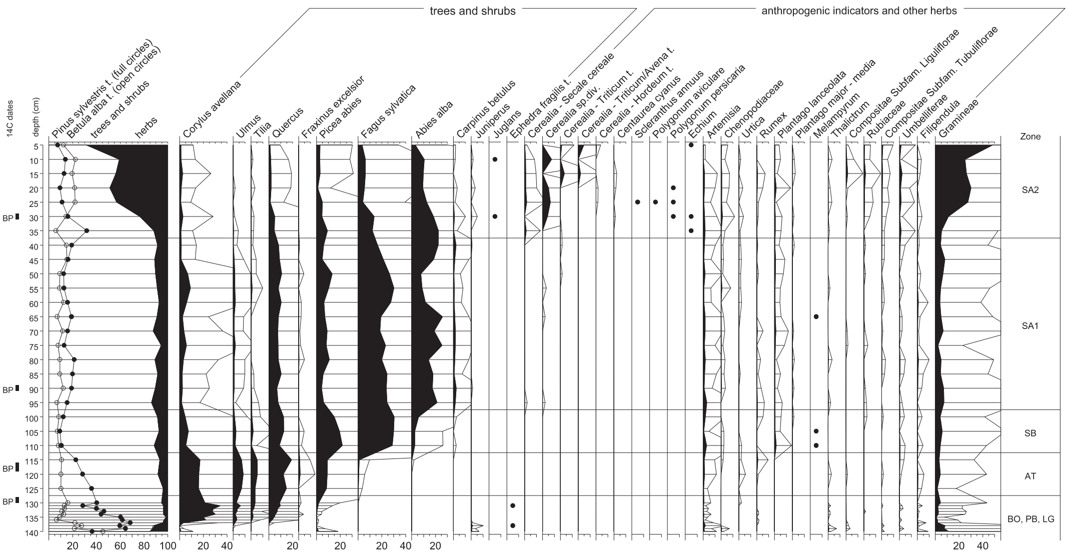

Fig. 3. – Percentage pollen diagram for PK-1-B section of the Komořanské jezero lake, which is based on an analysis done by Vlasta Jankovská. All taxa are included in the sum.

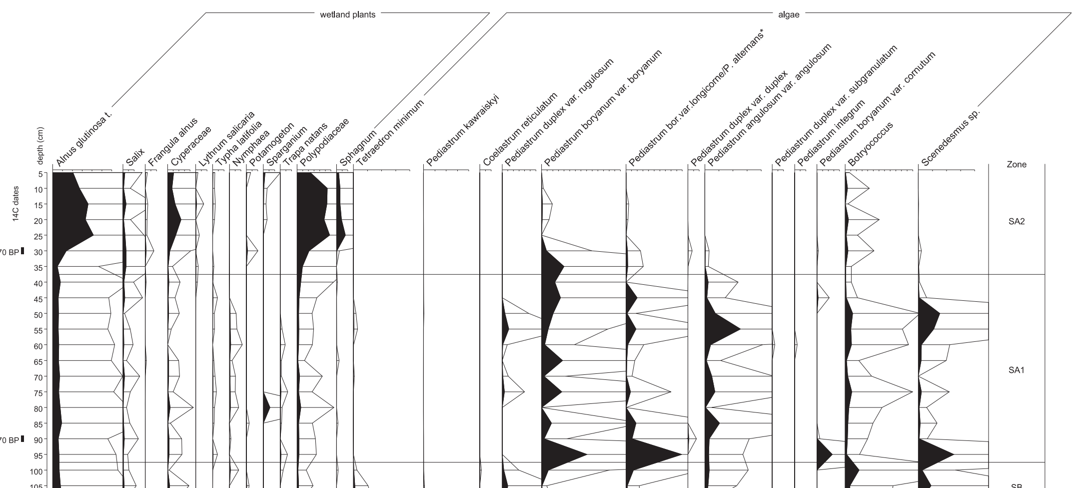

Fig. 4. – Diagram of local pollen and non-pollen objects recorded in the PK-1-B section of the Komořanské jezero lake. Note variable x-axis scales. The analysis was done by Vlasta Jankovská. Percentages of all taxa are related to upland pollen sum.

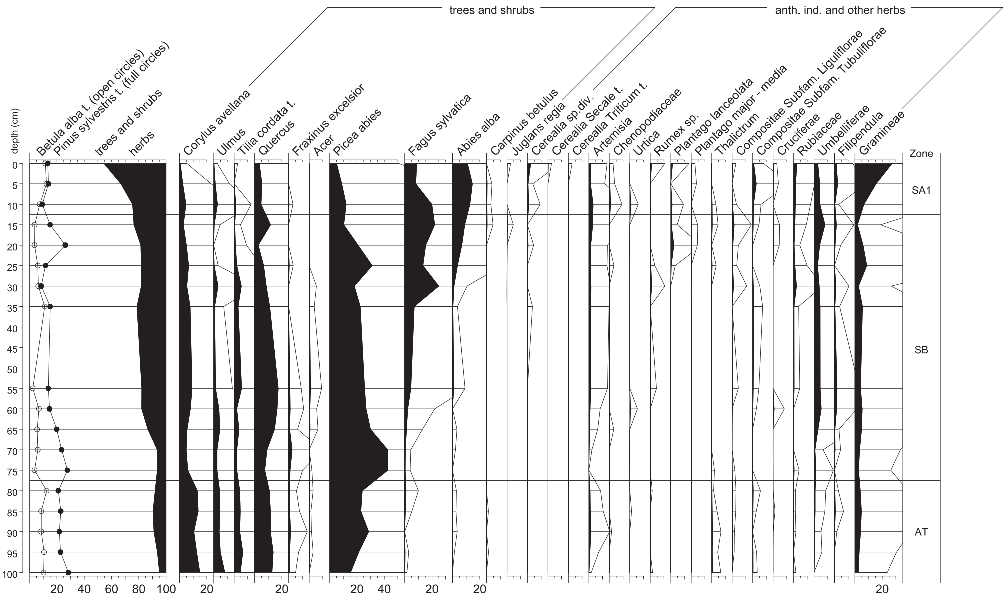

Fig. 5. – Percentage pollen diagram for PK-1-D section of the Komořanské jezero lake, which is based on an analysis done by Vlasta Jankovská. All taxa are included in the sum.

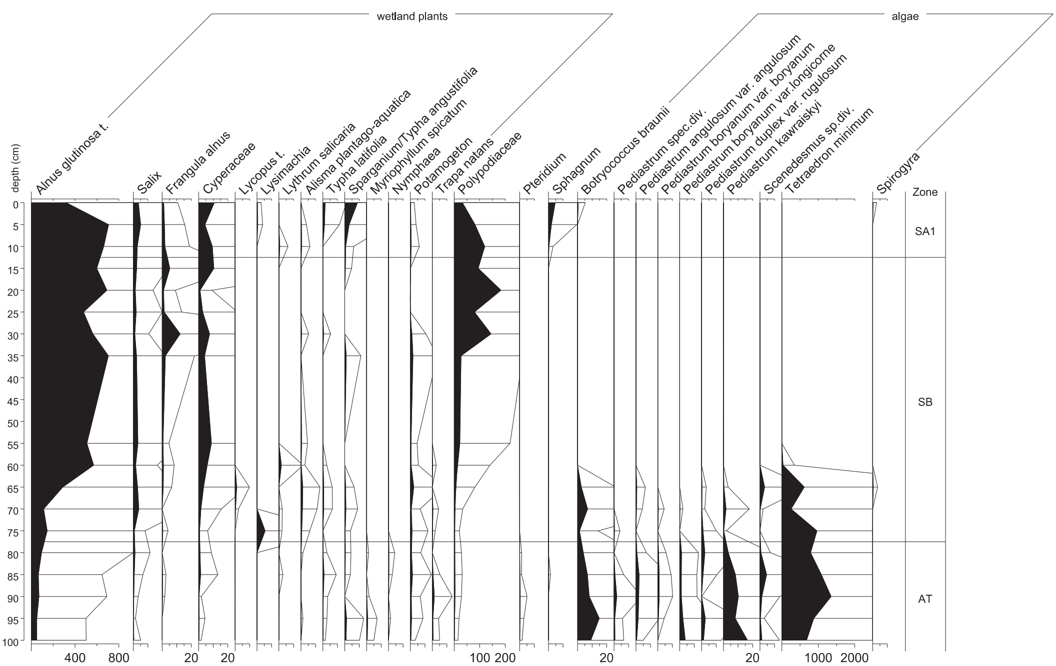

Fig. 6. – Diagram of local pollen and non-pollen objects recorded in the PK-1-D section of the Komořanské jezero lake. Note variable x-axis scales. The analysis was done by Vlasta Jankovská. Percentages of all taxa are related to upland pollen sum.

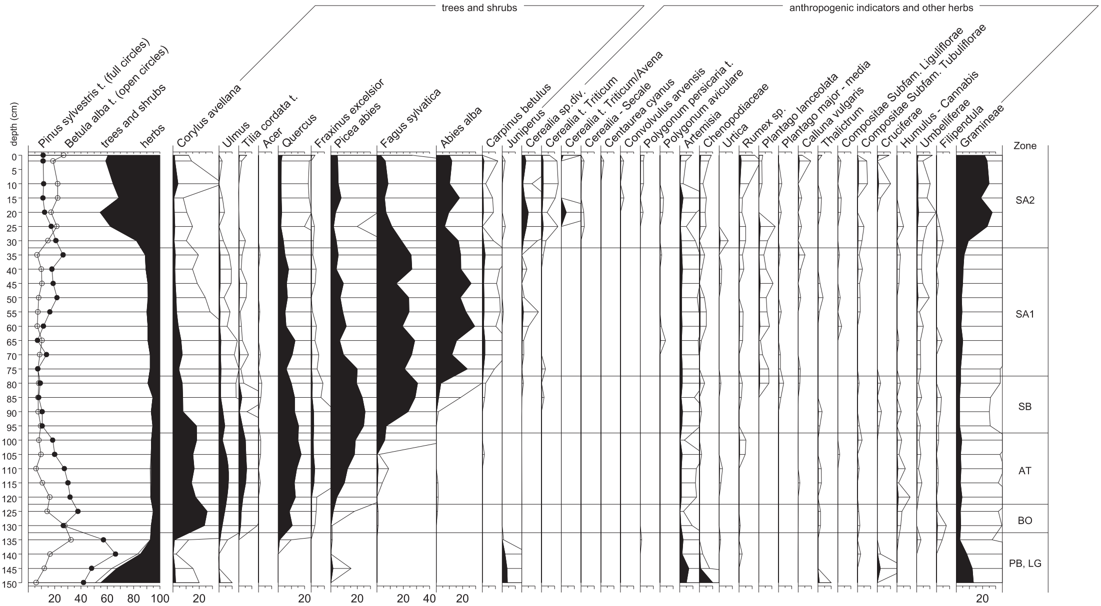

Fig. 7. – Percentage pollen diagram for PK-1-E section of the Komořanské jezero lake, which is based on an analysis done by Vlasta Jankovská. All taxa are included in the sum.

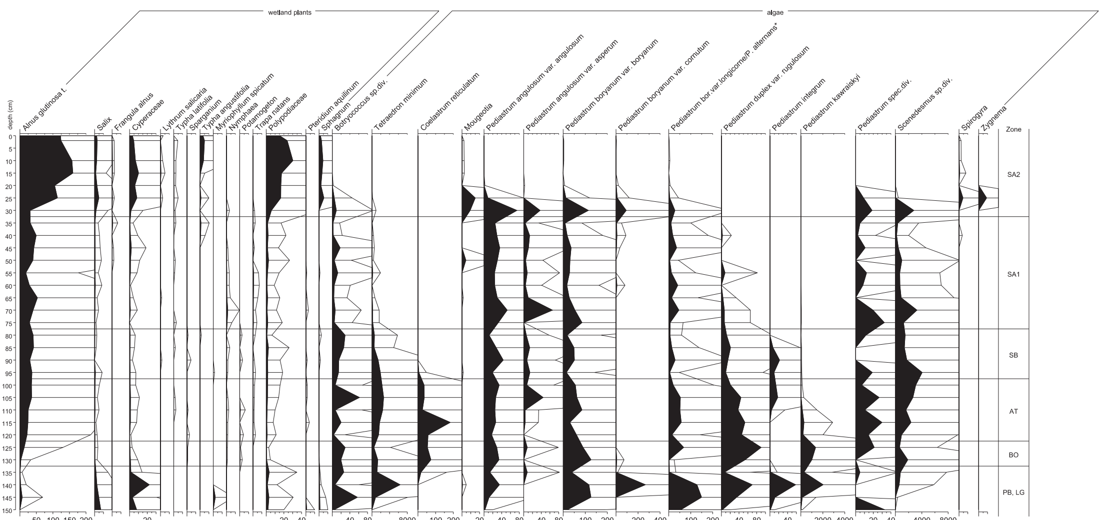

Fig. 8. – Diagram of local pollen and non-pollen objects recorded in PK-1-E section of the Komořanské jezero lake. Note variable x-axis scales. The analysis was done by Vlasta Jankovská. Percentages of all taxa are related to upland pollen sum.

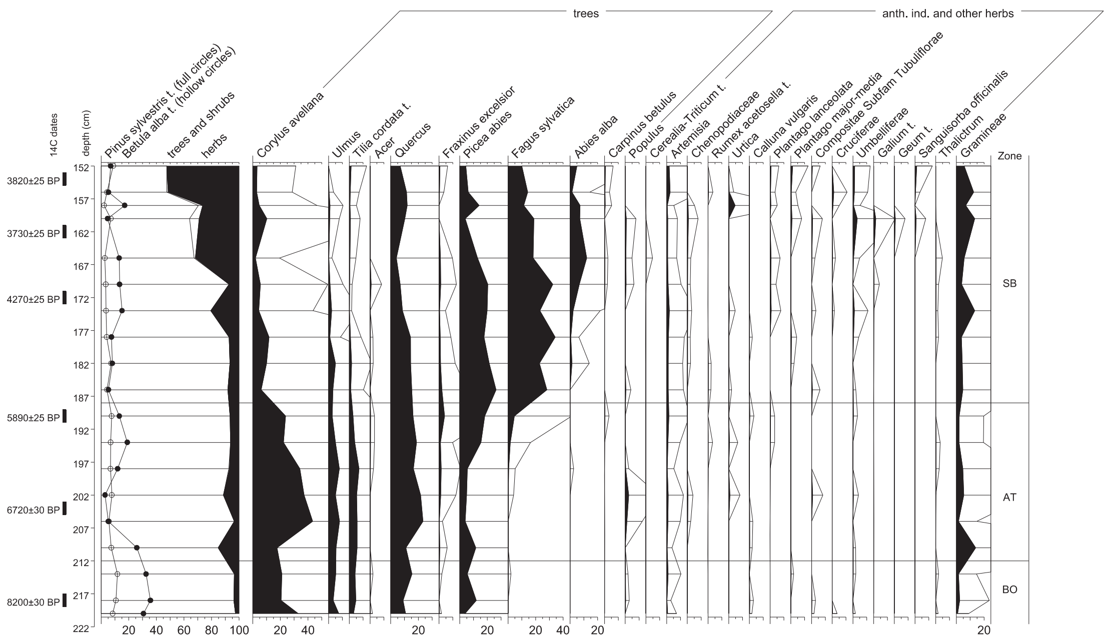

Fig. 9. – Percentage pollen diagram for PK-1-CH section of the Komořanské jezero lake, which is based on an analysis done by Vlasta Jankovská. All taxa are included in the sum.

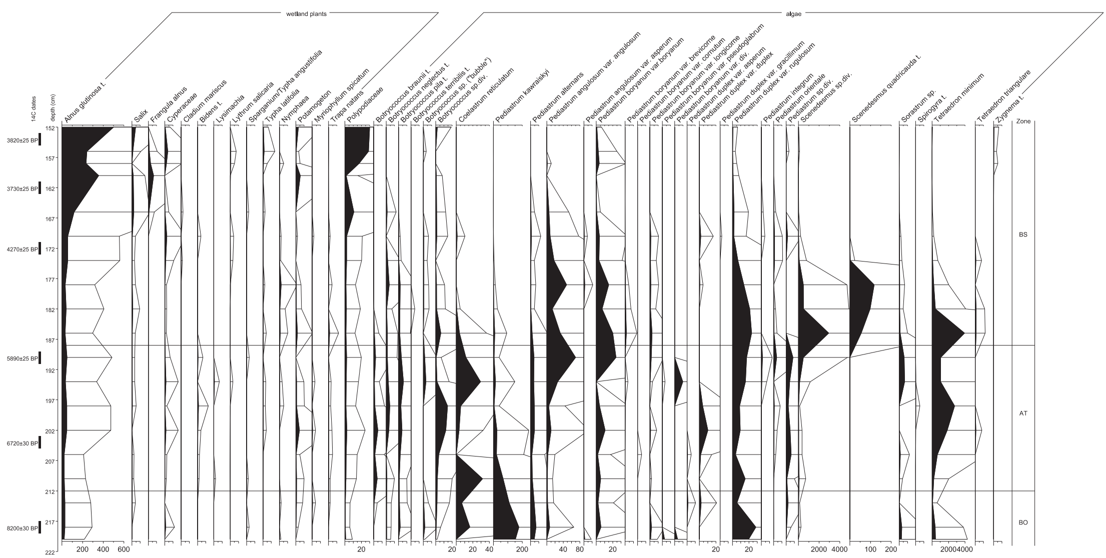

Fig. 10. – Diagram of local pollen and non-pollen objects recorded in PK-1-CH section of the Komořanské jezero lake. Note variable x-axis scales. The analysis was done by Vlasta Jankovská. Percentages of all taxa are related to upland pollen sum.

Results

Basal minerogenic sediments occurring in all sections studied yielded a mixed pollen spectrum of palynomorphs of Tertiary and Quaternary age. The following Tertiary arboreal taxa were most frequently recorded: *Carya*, *Engelhardtia*, *Keteleeria*, *Liquidambar*, *Nyssa*, *Platycarya*, *Pterocarya*, *Sequoia*, *Symplocos*, *Taxodiaceae/Cupressaceae*, *Tsuga*, *Zelkova/Ulmus*. Pollen grains of a number of Arcto-Tertiary trees and shrubs (*Alnus glutinosa*-t., *Ulmus*, *Tilia*, *Corylus avellana)* were also found. These can be classified as Tertiary based on differences in appearance and coloring resulting from prolonged fossilization processes. A considerable part of the conifer pollen, particularly of *Pinus sylvestris*-t. and *Abies alba*, is likely also to be of Tertiary age. However, it was difficult to differentiate reliably some palynomorphs of the Tertiary and Quaternary periods. This is why we did not include the results for these basal layers in the interpretations and start describing the results from the level in which the redeposition of pollen from Tertiary bedrock formations became negligible, i.e. the end of the late-glacial period.

All pollen and other microfossil diagrams are presented in Figs 3–10. The description below of the results is organized according to palyno-stratigraphic subdivisions (zonation) in the diagrams. Biostratigraphic terminology is adapted from Firbas (1949, 1952).

Late glacial to Preboreal (LG–PB)

Late glacial and Preboreal pollen spectra were recorded only within thin layers in the lowermost parts of PK-1-B (Fig. 3) and PK-1-E (Fig. 7) profiles. Further subdivision of this period is thus impossible. The biostratigraphically delimited late-glacial and Preboreal phase unfortunately has not been radiocarbon dated, due to the low content of organic matter.

P a l a e o l i m n o l o g y. Within the sediments of late-glacial to Preboreal age were high values of *Pediastrum kawraiskyi*, *P. boryanum* var. *boryanum* and *Tetraedron minimum* (Figs 4, 8). The highest values in the lowermost sample of the PK-1-E profile were for *Pediastrum boryanum* var. *longicorne*/*P. alternans*. *Pediastrum kawraiskyi*, *P. integrum*, *P. duplex* var. *rugulosum*, *P. boryanum* var. *cornutum* and *P. angulosum* var. a*ngulosum* were numerous in sample taken by 10 cm above. An increased occurrence was also noted for *Pediastrum angulosum* in profile PK-1-E (Fig. 8). This species is known to grow on submerged stems of water plants such as *Sparganium*, *Nymphaea*, *Typha* and even *Equisetum*. It is likely there were wetlands with *Cyperaceae*, *Filipendula*, *Typha* and perhaps some *Phragmites* growing in the littoral zone. The vegetation of submerged water macrophytes was very poor. Scarce pollen grains of the following taxa were identified: *Myriophyllum spicatum*, *M. alterniflorum*, *Nymphaea* and *Sparganium* (see Figs 3 and 7).

U p l a n d v e g e t a t i o n. In contrast to the limited diversity of woody species (*Betula*, *Pinus*, *Salix*, *Juniperus* and *Ephedra fragilis* are recorded), the vegetation of herbaceous plants was very rich. It is likely the forest-tundra communities became mountain tundra on the summit plateau of the Krušné hory Mts. However, the much warmer and drier České středohoří hills were probably covered by open steppe (see high pollen values of *Artemisia* and *Chenopodiaceae* in Fig. 7) with a scattered occurrence of *Pinus sylvestris.*

Pollen grains of mesophilous arboreal taxa (*Alnus glutinosa*-t., *Picea abies* and *Corylus avellana*) occur regularly in basal sediments of both profiles of this period (PK-1-B, PK-1-E; Figs 3 and 7). In the absence of macroremains, which could be radiocarbon-dated, it is impossible to confirm or disprove the local occurrence of these taxa. It cannot be excluded that the pollen grains of *Alnus glutinosa*-t., *Picea abies* and possibly of some other species of trees could have originated from reworked Tertiary deposits (the possibility of contamination from layers deposited later is unlikely since profiles were sampled from exposed walls).

Boreal (BO)

The Boreal period is distinctly manifested in profiles PK-1-B, PK-1-E (Figs 3, 7) and also the lowermost part of PK-1-CH (Fig. 9). From this point in time the record is generally well stratified and independently radiocarbon-dated (8200±30 uncal. yr BP in PK-1-CH and 7770±80 uncal. yr BP in PK-1-B). The most likely reason for the increased rate of accumulation of sediment was an improvement in the climate, which resulted in an increased production of both phyto- and zooplankton in the lake and formation of an organic sediment (gyttja).

P a l a e o l i m n o l o g y. The lake was still oligotrophic (as indicated by *Pediastrum kawraiskyi*, *P. integrum*, *P. boryanum* var. *longicorne*, *P. alternans*). *Coelastrum reticulatum* indicates a somewhat increased trophic status (Figs 8 and 10). The change in water environment from cold and oligotrophic to warm and mesotrophic is further indicated by the decline in the abundance of *Pediastrum kawraiskyi* at the end of this period. The occurrence of *P. angulosum* var. *angulosum* is also quite common. According to its current ecology, this species is associated with alkaline water environments and the presence of submersed macrophytes on the surface of which it lives. Indeed, further increases in water plants (*Potamogeton*, *Nymphaea*, *Sparganium*, *Trapa natans*) are recorded in the pollen diagrams (Figs 4, 8, 10).

U p l a n d v e g e t a t i o n. In the littoral zones of the lake, tall sedge communities, reed beds and peat meadows occurred. Willow stands started to be succeeded by *Alnus glutinosa* (see increasing curve in Figs 4 and 8). Sporadic growth of *Picea abies* was also possible in hydrologically favourable places. Characteristic of the Boreal period is a rapid increase in the number of species of trees of mixed oak woodland communities (see increase in *Quercus*, *Ulmus*, *Tilia* and *Fraxinus excelsior* curves; Figs 3 and 7). In the České středohoří hills (a low-altitude and warm volcanic chain) and on the southern slopes of the Krušné hory Mts, light-demanding *Corylus avellana* must have been an important forest element. In the same period, open formations generally decreased in occurrence (note NAP curves reached their minimum values). However, České středohoří hills were probably still covered with forest-steppe with *Pinus sylvestris* woods and maybe some isolated stands of broad leaved trees. This is indicated by the continued presence of pollen of some NAP taxa, namely that of *Artemisia* (Figs 3, 7 and 9).

Atlantic (AT)

P a l a e o l i m n o l o g y. *Pediastrum kawraiskyi* is not present in profile PK-1-E (Fig. 8). In contrast, the occurrence of *Coelastrum reticulatum* increased in AT (Figs 8 and 10), which together indicate that the water environment became distinctly eutrophic possibly due to an increase in water temperature. Pelagic *Pediastrum duplex* var. *duplex*, *P. duplex* var. *rugulosum* and periphytic *P. angulosum* indicate that the surface of the water was still free of vegetation above the deeper, central parts of the Lake. This also possibly accounts for the presence of an abundance of planktonic diatoms (Řeháková 1986). Water macrophytes

Trapa natans, *Nymphaea*, *Potamogeton*, *Myriophyllum spicatum*, *M. verticillatum* and *Sparganium* considerably increased in abundance in the lake. *Typha latifolia* and *T. angustifolia* grew in the shallower water. Some pollen grains designated as *Gramineae* were probably those of reed (*Phragmites*), but have not been determined yet. Nevertheless, the values are relatively low as are those for *Cyperaceae*.

Upland vegetation. The climate optimum in the Holocene is characterized by the spread of climatically demanding trees that replace less efficient competitors. The spread of *Alnus glutinosa* into the littoral zone of the lake, which started at the end of the Boreal period, continued. *Salix* and *Filipendula* grew in alder stands and locally there could have been also *Humulus*, *Urtica*, *Rumex*, *Umbelliferae*, *Cyperaceae* and *Gramineae*. In hydrologically favourable places within the basin there grew *Picea abies* and this species also probably occurred in the Krušné hory Mts. In the lowlands communities of mixed oak stands with dominant *Quercus* and different proportions of *Ulmus*, *Tilia*, *Fraxinus excelsior*, *Acer* and undergrowth of *Corylus avellana* prevailed. Of similar composition were probably also the forest stands in the České středohoří hills. Deep soils were used for agriculture since Neolithic times and anthropogenic transition to secondary steppe must have occurred already at the onset of Atlantic period. It is likely that *Pinus sylvestris* occurred on steep slopes with more favourable light conditions and thus a more suitable environment in terms of competition. The levels of *Corylus avellana* pollen started to decline at the beginning of AT (Figs 3 and 7). It is likely that a great proportion of the *Picea abies* pollen originated in Krušné hory Mts, which is indicated by the analysis of the summit plateau site "Fláje" (Jankovská et al. 2007), where spruce was dominant in the Atlantic period. On the other hand, a considerable presence of *Picea abies* at lowland sites situated in the area of the lower reaches of the river Ohře is also recorded by Pokorný (2004) and Albert & Pokorný (2012). Nevertheless towards the end of this period, *Fagus sylvatica* became a strong competitor of spruce.

Subboreal (SB)

Palaeolimnology. There are nearly no indicators of the presence of cold and oligotrophic water, such as *Pediastrum kawraiskyi*, *P. integrum* and *Coelastrum reticulatum*, after the start of this period (Figs 4, 6, 8 and 10). The periphytic *P. angulosum* var. *angulosum* and *Scenedesmus* remained relatively abundant whereas *Tetraedron minimum* declined in abundance. Interesting results, almost identical with ours, came from the analyses of diatoms by Řeháková (1986). According to her, the frequency of planktonic forms decreases towards the end of AT and in SB, whereas the periphyton in the littoral zone became quantitatively prevalent. According to the results of pollen analyses of samples from profiles close to the lake's edge (Jankovská 1988) considerable areas in littoral zones of Komořanské jezero lake were occupied by stands of alder. The silting up of the lake was due not only to the alders, willows, reeds with *Typha* and tall sedge communities, but also the accumulation of phytoplankton and remains of submerged vegetation, which consisted of *Trapa natans*, *Nymphaea*, *Potamogeton*, *Sparganium* and *Myriophyllum spicatum*.

Upland vegetation. Extensive stands of mixed oak forest occupied medium altitudes in the Krušné hory Mts. In the České středohoří hills, particularly on exposed slopes of eruptive rocks, it is likely there were stands of *Quercus pubescens*. As in other places in central Europe, the immigration of the main forest trees ceased in SB. The particularly strong increase in the abundance of *Abies alba* is likely to have resulted in a slight decrease in *Picea abies* and *Fagus sylvatica* in mountainous localities. It is likely that *Abies alba* occurred at low altitudes (see Pokorný 2003b, Sádlo & Pokorný 2003). The spread of *Carpinus betulus* in this area and its probable penetration into existing oak woods also began in SB. A conspicuous characteristic of SB pollen spectra is the decrease in the occurrence of all components of mixed oak woods (*Corylus avellana*, *Quercus*, *Ulmus*, *Tilia*, *Fraxinus excelsior*) and low values for *Pinus sylvestris.* SB is the first period in which the pollen spectra of Komořanské jezero lake clearly reveal anthropogenic activities. Anthropogenic pollen indicators of crop plants (cereals) and synanthropic species occur constantly in pollen spectra from this period onwards.

Early Subatlantic (SA1)

Palaeolimnology. The finds of *Pediastrum* in SA1 are dominated by *P. angulosum* var. *angulosum* and those of *P. angulosum* var. *asperum* (in PK-1-E) are also numerous. Both these species indicate presence of submerged macrophytes. Planktonic types (*P. duplex*) occurred only sporadically. The occurrence of *P. boryanum* var. *cornutum* increased in the PK-1-E profile towards the end of SA1 (Fig. 8). This may indicate presence of open water. The enhanced occurrence of *P. boryanum* var. *longicorne* is probably associated with humification of plant materials in the stands of alder. Among the planktonic algae, *Scenedesmus* dominate over *Tetraedron*, which might indicate they competed with one another. The process of lake infilling is indicated by finds of filamentous algae (*Conjugatophyceae*) of the genera *Mougeotia*, *Spirogyra* and *Zygnema* that grow in shallow pools at the margins of lakes. In the littoral zones there were extensive alder carrs with *Frangula alnus*, *Salix* sp. div., together with ferns and herbaceous plants (*Filipendula*, *Lythrum salicaria*). This situation is also documented by the pollen diagrams for the littoral zones published by Jankovská (1988).

Upland vegetation. Only the climax forest in the region of the Krušné hory Mts can be reconstructed, since the lower lying landscapes in both the basin beneath the Krušné hory Mts and the České středohoří hills were settled and markedly affected by humans. The dominant trees in the Krušné hory Mts were *Fagus sylvatica*, *Abies alba* and *Picea abies*. *Picea abies* grew at the highest localities in the mountains and spruce forests dominated the whole top plateau of the mountain range (Jankovská et al. 2007). In the basin beneath the Krušné hory Mts, other than in the wetlands and synanthropic biotopes, mixed-oak woods with *Quercus*, *Tilia*, *Ulmus*, *Fraxinus excelsior*, *Acer* and newly occurring *Carpinus betulus* prevailed. The mountain stands of *Pinus mugo* may be the main source of *Pinus sylvestris*-type pollen transported from the Krušné hory Mts. Nevertheless, the values for pollen of *Pinus sylvestris*-type in the sediments of Komořanské jezero lake are generally rather low. Their slight increase in SA1 may indicate deforestation in the České středohoří hills (*Pinus sylvestris* is a pioneer species). *Abies alba* was probably common in the lowlands along with *Picea abies* at sites with favourable hydrological conditions. There are also relatively high quantities of pollen of *Abies alba* in SA1 sediments in a profile from the alluvium of the Bílina river in the area of the old town of Most (Jankovská 1995a).

Late Subatlantic (SA2)

At a depth of 30 cm in profile PK-1-B (Fig. 3), there are indications of a sudden change in the vegetation that occurred 1490±70 uncal. yr BP. After calibration (performed in CALPAL software; http://www.calpal-online.de), the calendar age is approximately AD 540±74. Nevertheless, the composition of the pollen spectrum (see *Centaurea cyanus* and *Cerealia-Secale*-t. in Fig. 3) corresponds biostratigraphically with the High Middle Ages in most lowland Czech sequences (like that at the Zahájí site near Budyně nad Ohří; Pokorný 2004) with the exception of Vranský potok near Peruc, where the beginning of extensive *Centaurea cyanus* (9.7% max.) and *Secale*-t. (6.5% max.) occurrence is also corroboratively dated to just after AD 500 based on radiocarbon measurements (see Albert & Pokorný 2012).

P a l a e o l i m n o l o g y. The beginning of SA2 marks the end of the existence of a large, permanent lake. In some places open water undoubtedly persisted and became more noticeable after snow melt and periods of heavy rainfall (Kynčl 1992). The occurrence of both planktonic and periphytic algae of the genera *Pediastrum*, *Scenedesmus* and *Tetraedron* ceased (Figs 4 and 8). Zygospores of filamentous algae (*Desmidiales* and *Conjugatophyceae*) and *Mougotia*, *Zygnema* and *Spirogyra* indicate presence of shallow water pools. This is corroborated by the marked occurrence of pollen grains of *Alisma plantago-aquatica*, *Sparganium*, *Typha latifolia*, *T. angustifolia*, *Gramineae* (probably *Phragmites*) and *Cyperaceae*. These taxa were also components of extensive alder stands overgrowing the lake from its shores already in the Boreal period. The original area of the lake was colonized in the 13^{th} century and exploited as pastures, hay meadows and (sometimes) arable fields.

U p l a n d v e g e t a t i o n. The pollen diagrams reveal the strong effect humans had on the vegetation. In particular, the extent of the original mixed oak woodland decreased substantially in the basin beneath the Krušné hory Mts and on the lower parts of the mountain slopes, where deforestation affected mainly stands of *Abies*, *Fagus* and *Picea.* The history of Komořanské jezero lake, which was an important feature of the landscape beneath the Krušné hory Mts for thousands of years, came to an end in 1834, when it was drained. The landscape in the area of the former Komořanské jezero lake was again recently completely changed by brown coal mining.

Discussion

Palaeolimnological reconstructions based on fossil algae

The counts of coenobia and individual algal cells that are presented graphically in Figs 4, 6, 8 and 10 show considerable fluctuations, which are likely to have been due to many factors not yet fully understood in terms of palaeoecology. Algae respond to changes in the quality of the environment much faster than long-lived higher plants. It is therefore not necessary to evaluate every deviation but rather the general trends. Fluctuations in the numbers of algal finds also probably reflects the results of competition for light, nutrients, etc.. For instance, the numbers of *P. kawraiskyi* increased while those of *P. integrum* simultaneously decreased in the Boreal biostratigraphic zone of PK-1-E profile (Fig. 8). Is it possible that at this time *P. kawraiskyi* and, e.g. *P. duplex* var. *rugulosum* were more efficient competitors than *P. integrum* or can it be attributed to changes in water temperature and/or nutrient status? This can only be resolved by actuo-ecological studies of the behaviour of algal communities. Unfortunately, the low temporal resolution of the samples from the profiles studied did not allow a direct reconstruction of seasonal variations.

Although the composition of the algae in sedimentary sequences investigated is highly dynamic, the qualitative indicator value of a few taxa is still sufficient for the reconstruction of the environment (Jankovská & Komárek 1982, 2000, Komárek & Jankovská 2001). The presence of *Pediastrum kawraiskyi* for instance indicates clear, cold stenotherm water bodies, mainly in only slightly eutrophicated (oligotrophic or mesothrophic) lakes in colder areas of temperate zones. This indication is also confirmed by the occurrence of *P. integrum*, which occurs in oligotrophic to dystrophic water bodies. Similar biotopes are also indicated by *P. alternans.* This taxon was classified at the time of the analyses along with the morphologically similar *P. boryanum* var. *longicorne*. Although coenobia of the last named taxon were found during a later revision of the results, it is still a fact that *P. alternans* prevailed in Komořanské jezero lake. Thus, the water in this lake in the late glacial was distinctly cold and clear and largely oligotrophic. In the Holocene, a dystrophic environment prevailed only in some peripheral, peaty parts of the lake (see occurrence of *Sphagnum* in Figs 4 and 8).

Problems related to local pollen taphonomy

The development of Komořanské jezero lake and the surrounding landscape after the end of the late glacial can be evaluated on the basis of results of the pollen analysis presented above. It is likely that the lake existed already in an earlier period of the last full-glacial Period (Weichselian, Würmian). This is indicated by the relatively thick (4 m) mineral sediment of sand and gravel (see Hurník 1969). These sediments contain a mixed spectrum of palynomorphs of Tertiary and Quaternary age (Rudolph 1926 and Losert 1940). According to our opinion, it is conceivable that in this case we are dealing with the resedimentation of eroded Tertiary bedrock that occurred over the period last glacial to early Holocene. Numerous Tertiary pollen grains are also recorded in the basal part of late-glacial age at Reichwalde by Knipping (Friederich et al. 2001), in the Švarcenberk Lake in southern Bohemia (Jankovská 1980, Pokorný 2002, Pokorný et al. 2010) and in the Krkonoše Mts (Engel et al. 2004).

It is accepted by some pollen analysts that the great amounts of pollen and spores in sedimentary basins were transported there by rivers (see classical studies by Peck 1973, Bonny 1978, Pennington 1979). Recently, Brown et al. (2007) performed an extensive modern-analogue study of this process, demonstrating how important this knowledge is to pollen-based reconstructions of vegetation. He also showed that the sedimentation of pollen and spores floating on water is especially important during floods (just following the peak of maximum flow). These findings were recently successfully applied to the interpretation of pollen spectra from alluvial sites in central Bohemia (Albert & Pokorný 2011).

We believe that the implications of these findings for our present study can be especially important. The sediments in the lake basin were undoubtedly influenced by fluvial sediment brought into the basin by the river Bílina and numerous small creeks. The evidence for this is regular, though very variable occurrence of fine silt in the sections of sediment studied. Using the database that is currently available to us, it is impossible to quantify the "airborne" and "waterborne" (both terms used by Brown et al. 2007) components of individual pollen spectra. Such a study would require a detailed sedimentological characterization of each sample of sediment (LOI, granulometry, etc.). Nevertheless, it is likely that a significant proportion of the pollen grains recorded on our pollen slides were fluvially transported. This assumption is especially important in the case of the Komořanské jezero lake pollen record. The catchment of this lake is characterized by very different environments, ranging from warm and dry lowlands to a cold and moist subalpine belt in the Krušné hory Mts. The possibility of fluvial transport of pollen and spores into Komořanské jezero lake from the mountains must be especially emphasized as the catchment of this lake is very asymmetrical. The largest volume of water entering the basin comes from mountainous subenvironment of the catchment.

As a result, the reconstruction of the local development of the vegetation in the lowland environment, in which the Lake is situated, must be significantly blurred by the long-distance transport of "waterborne" pollen from areas with very different conditions, the slopes and summit plateau of the Krušné hory Mts. In other words, we must seriously consider the possibility that the pollen signals reflecting changes in the local environment are much weaker than in the records for most other pollen-analytical sites, namely peat bogs, where purely autochtonous organic sedimentation occurs and pollen spectra are subjected to very different taphonomic transformations (almost only transport by air).

These taphonomic considerations most probably do not influence the interpretation of the local environments of wetlands.

Glacial refugia for temperate trees?

It is necessary to mention here some stimulating conclusions of Losert (1940) regarding possible glacial refugia for some temperate trees. This author very precisely palaeobotanically studied several profiles from intact deposits in Komořanské jezero lake. He has published his analysis of phase 1a, which is equivalent to our Preboreal biostratigraphic zone based on pollen analysis. This analysis indicates the sporadic existence around the lake of temperate elements of *Quercetum mixtum*: namely *Quercus*, *Tilia* and *Ulmus*. He also states that *Picea abies* was also a regular forest component at the end of this period. First population expansion of *Alnus glutinosa* also could have occurred at this time. Indeed, pollen grains of *Alnus glutinosa*-t. and *Picea abies* occur regularly in two of our pollen-analytically studied profiles (PK-1-B, PK-1-E) in sediments corresponding to the Preboreal biostratigraphic zone. However, with no finds of macroremains, which could be radiocarbon dated, it is impossible to confirm or disprove this occurrence. Moreover, it cannot be excluded at present that the pollen grains of *Alnus glutinosa*-t., *Picea abies* and possibly of some other species of trees could have originated from reworked Tertiary deposits.

In the case of spruce, there were glacial refugia at several sites in the Western Carpathians (see, e.g. Magyari et al. 1999, Willis et al. 2000, Jankovská et al. 2002, Jankovská & Pokorný 2008). Therefore, it is not impossible that there were also glacial refugia for *Picea* in the area of inner Bohemia. In this connection it is noteworthy that macroremains (needles and wood) of *Picea abies* were found in a fireplace of Early Mesolithic Age in Czech Switzerland, north Bohemia (Pokorný 2003a). This find is reliably dated using the AMS method to 8530±150 uncal. yr BP, i.e. to the Preboreal/Boreal boundary.

Continuity of continental steppe grasslands throughout the Holocene?

For nearly 100 years discussions have continued about the possibility of indigenous xerothermic grasslands (variant of continental steppes) occurring in central Europe. The key question is whether areas of steppe survived the period of a few centuries between the beginning of the presumably humid Atlantic period and the onset of Neolithic farming. An important milestone in this discussion is "Steppenheidetheorie" proposed by Gradmann (1933) and further discussed by Firbas (1949). According to this theory, large patches of xerothermic grassland have persisted in warm and dry regions of central Europe since the last-glacial period throughout early Holocene until Neolithic times. It is proposed that at this point in time (i.e. at the onset of Neolithic agriculture), anthropogenic deforestation facilitated the expansion of natural steppes and further enriched their biodiversity by the introduction of new species from southern Europe and the Near East.

Today, there is common consensus among biogeographers about the occurrence of the forest-steppe biome in the Czech Republic and also in the wider region of central Europe (Chytrý 2012). Forest-steppes are found today in two lowland areas in the Czech Republic that are characterized by a dry and warm climate: northern and central Bohemia in the rain shadow of the Krušné hory Mts (i.e. the very region where Komořanské jezero is located) and southern Moravia. The first region is considered to be an isolated extrazonal occurrence, while the second is at the edge of a continuous forest-steppe area extending from the Pannonian Basin through eastern Austria and south-western Slovakia. Local forest elements include *Quercus pubescens* and *Q. petraea* forests on dry soils. Treeless vegetation includes various types of grasslands, ranging from rock-outcrop steppe through short-grass steppe with *Festuca* and *Stipa* to semi-dry tall-grass steppe with *Brachypodium pinnatum* (Chytrý 2012).

With climatic amelioration in the early Holocene, the area under steppes decreased as it was gradually colonized by forest, but it is likely this trend was reversed by human activity that began in the Neolithic. It is currently accepted that since the onset of the Neolithic, i.e. over the last 7500 years, local upland vegetation has been continuously managed by humans (Jiráň & Venclová 2007–2008). Large areas of steppes occurring on deep soils were converted into arable land and the area of forest was reduced. Therefore, it is difficult to estimate the relative extent of forested and open areas in pre-Neolithic natural conditions solely on the basis of actuo-ecological data. However, it is possible that many, if not most, species of Czech dry steppes are Pleistocene relicts, which survived the Middle Holocene bottleneck. Moreover, there are now good reasons for thinking that the pre-Neolithic human activity in the territory of the present Czech Republic, in particular the use of fire by Mesolithic hunter-gatherers had a significant effect in terms of reducing forest vegetation (Kuneš et al. 2008, Pokorný et al. 2010).

The results of pollen analyses sometimes do not support the above interpretation (Krippel 1982, Lang 1994, Rybníček & Rybníčková 1994). This method of analysis is strongly criticized, because of its poor taxonomic and spatial resolution and the fact that pollen representation of trees is greatly overestimated in pollen diagrams. On the other hand, continuous presence of steppe snails in the fossil record at some sites in northern Bohemia and southern Moravia and recent occurrence of many plant species of continental steppe (some of them showing disjunct ranges) suggest that steppe vegetation was continuously present from Holocene not only on rocky outcrops, but even on deep soils (Sádlo et al. 2005, Ložek 2011, Chytrý 2012). There is an area where there are few woodland molluscs in the fossil record in the České středohoří hills, which is close to Komořanské jezero lake (Ložek 1963, 1964a, b, 2005). The strength of the evidence for the absence of Holocene woodland molluscs in this area is enhanced by comparison with fully developed woodland mollusc faunas of the Middle Pleistocene (Kovanda 2005). According to these investigations, several strictly woodland species occurred commonly during the Middle Pleistocene interglacials but rarely in the Holocene. The others went extinct and are not present in the Holocene.

Despite these serious taphonomic problems, our pollen record for Komořanské jezero lake seems to support the continuous presence of steppe vegetation throughout the entire duration of the Holocene. This is best documented by the high and continuous occurrence of *Artemisia* pollen in the critical period of the Mesolithic-Neolithic transition (profiles in Figs 3, 7 and 9; the PK-1-E profile has unfortunately not been independently radiocarbon dated). Also some other NAP taxa show continuous occurrences, but these are more difficult to interpret as evidence of steppe grassland elements due to insufficient taxonomic resolution.

Reconstructing the history of human settlement

The oldest archaeological finds from the area of Komořanské jezero lake belong to the Late Palaeolithic settlement represented by the so-called "Federmesser" complex (Vencl 1970a). These people were bound by their settlements to lowlands, rivers, brooks and lakes. Vencl (1970b) presumes that the possible transfer of the "Federmesser" lithic industry into Bohemia was associated with the decrease in temperature that occurred during the Younger Dryas. During this event, part of the population living north of the Krušné hory Mts might have moved to the area around Komořanské jezero lake. An extensive interdisciplinary study carried out at Reichwalde in neighbouring Germany, also corroborates the presence of human settlements around lakes in the Palaeolithic and Mesolithic (Friedrich et al. 2001). Unfortunately, it is impossible to prove that man was present in this area in the late-glacial (Late Palaeolithic) period from the pollen diagrams. Enhanced pollen values for *Artemisia* and *Chenopodiaceae*, that are "anthropogenic indicators", are unfortunately also natural components of the vegetation in this period.

The landscape in the area studied had in the early Holocene a rather open character and was easily passable. Komořanské jezero lake was the dominant of the region between the steeply rising Krušné hory Mts and the low hills of České středohoří. It is no wonder that there is evidence of settlements there in the Mesolithic (Vencl 1970a, b, 1994, 2007) as the lake and its surroundings was a source of fish, birds and game. In addition, *Trapa natans* grew in the lake and may have served as food in the Mesolithic (see Vuorela & Aalto 1982, Jankovská 1995b, Kuneš et al. 2008, Pokorný et al. 2010). In addition in the BO and at the beginning of AT1 there were extensive stands of *Corylus avellana* in the nearby Krušné hory Mts, which also probably served as an important source of food (Jankovská 1995b). The presumed influence of Mesolithic populations on the landscape was probably not very strong and its expression in the sediments of Komořanské jezero lake masked by the regional rain of pollen from woody species, which is a general methodological problem when interpreting pollen data especially that obtained from large lakes (Prentice 1985).

Lakes other than Komořanské jezero occurred in the basin beneath the Krušné hory Mts. The possible existence of a lake at Jezerka from Late Pleistocene to modern times (Kruta & Vencl, 1973), which is 26 km south-west of Komořanské jezero lake, is based on Late Palaeolithic and Mesolithic archaeological finds (Vencl 1970a, b). The finds of Mesolithic industry in the area of Reichwalde are also dated to the Late Boreal period (Friedrich et al. 2001).

Rich archaeological finds are also recorded for the AT period. Neolithic settlements were found located close to the lake (Neustupný 1985, Jankovská 1988). Archaeological research (Neustupný 1985) revealed evidence of LBK, Funnel-necked beaker-, Baden pottery- and Corded-ware cultures. This area was also settled at the end of the Sub-boreal by people of the Únětice culture (Early Bronze Age).

In his classical study, Losert (1940) dates the first occurrence of cereal pollen in Komořanské jezero lake to the Neolithic period. However, it is most likely that the record of *Cerealia* pollen in his pollen diagrams begins no sooner than in the Bronze Age. Results of pollen analyses from the limnic and peat bog sediments of the former Komořanské jezero lake associated with exactly localized finds of ceramics at archaeological sites were the main object of the study by Jankovská (1988). She carried out a pollen analysis of a 100 cm deep profile (PK-1-D), including sediments AT, SB I, SB II, SA1 and SA2. Neustupný (1985) evaluated these results from the point of view of archaeology. The profile contained evidence for the periods of the following archaeologically cultures: StB, TRB**,** Baden culture, Wave culture, Únětice culture**,** Medieval period. Two pollen diagrams in the form of of histograms illustrate the results of the pollen analyses of 32 samples in the context of the finds of ceramic material of the above-mentioned cultures.

For the Neolithic period there is no significant evidence of a human effect in pollen spectra. The first clear evidence of agricultural activity is remains of pollen preserved in deposits dated to the SB period. Cereal pollen (*Cerealia*, *Cerealia-Triticum* type) are recorded along with high counts of the pollen of *Plantago lanceolata* and *P. major-media* in the diagrams. *Urtica*, *Rumex* and *Humulus*, which are ”anthropogenic indicators”, were probably natural components of the vegetation in alder stands, so the informative value of this in terms of the existence of human settlement around Komořanské jezero lake is doubtful. The thick lake sediments dated to SA1 show enhanced pollen values of *Plantago lanceolata*, *P. major-media* and *Cerealia.* Unmistakable indicators of an anthropogenic effect are the pollen values for *Polygonum aviculare* and *Chenopodiaceae*.

The most conspicuous human effect is recorded in the pollen diagrams for SA2 in which there are high values for cereals. In addition to *Cerealia-Triticum* type, *C.-Triticum/Avena* type and *C.-Hordeum* type, there is the simultaneous occurrence of *Secale* and *Centaurea cyanus* pollen. Based on the experience gained from the pollen related research of objects from archaeological sites in the Late-Medieval town of Most (Jankovská 1983b, 1985, 1995a, Klápště 1997) it is likely that this record of cereal pollen indicates Late-Medieval settlement.

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Souhrn

Dolování hnědého uhlí v průběhu 20. století bylo příčinou zániku i posledních zbytků největšího přirozeného jezera na území České republiky – Komořanského jezera v Podkrušnohorské pánvi. Jeho sedimenty, dnes již v terénu nedochované, poskytují důležitý záznam vývoje od pozdního glaciálu až téměř do současnosti. Několik profilů jezerními sedimenty, které byly průběžně vzorkovány od 70. do 90. let 20. století v souvislosti ze záchrannými paleoekologickými a archeologickými výzkumy, bylo analyzováno na přítomnost pylových zrn a na zbytky chlorokokálních zelených řas. Tento článek poprvé podává jejich souhrnné paleoekologické zhodnocení zaměřené na vývoj jezerního prostředí a suchozemské vegetace v okolí. Ukazuje se, že pozdně glaciální jezero bylo chladné a oligotrofní. Jeho živinové poměry se ve starším holocénu postupně měnily na mezotrofní a lokálně též dystrofní, v průběhu středního holocénu až na eutrofní. Charakter vegetace v okolí jezera závisel na konkrétní pozici v rámci ostrých mezoklimatických a environmentálních gradientů v rozsáhlém povodí jezera. Tento fakt poněkud komplikuje rekonstrukci na základě pylových analýz, zejména v souvislosti s předpokládaným dálkovým vodním transportem pylových zrn skrz přítoky, které odvodňovaly prostor nedalekých Krušných hor. Imigrace klimaticky náročných rostlinných druhů do studovaného území začala již v období preboreálu (nesporně již před datem 8200 nekalibrovaných let BP). Šíření smíšených listnatých lesů dosáhlo vrcholu v průběhu atlantiku (mezi 6000 a 7000 nekalibrovaných let BP). Postihlo nejen nížiny (tj. oblasti mezi 200 a 400 m n.m.), ale postupovalo až do podhorských poloh (okolo 1000 m n.m.) Na základě trvalého výskytu indikátorů bezlesí (zejména vysokých pylových hodnot *Artemisia*) je možné spekulovat o kontinuitě xerotermního bezlesí (vegetace kontinentálních stepí) od pozdního glaciálu až po současnost. Archeologická data ukazují na trvalé osídlení prostoru Komořanského jezera od pozdního paleolitu až do současnosti. Vliv tohoto osídlení na vegetaci je ve slabé míře doložitelný až od nejstaršího zemědělského pravěku (neolitu). Tento vliv výrazně narůstá v průběhu subboreálního období, kdy se v nížiných polohách šířila xerotermní vegetace sekundárních stepí.

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