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LONG-TERM VEGETATION DYNAMICS AND THE INFILLING PROCESS OF A FORMER LAKE (ŠVARCENBERK, CZECH REPUBLIC)

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Abstract: Natural lakes are a rare phenomena within extraglacial areas of Central Europe. Almost all have been completely terrestrialized during the Holocene. This paper deals with one such former lake, located in southern Bohemia. Its extensive lacustrine and peat deposits were subjected to a multidisciplinary study that resulted in high-resolution pollen, macrofossil, algal and sediment-chemistry data interpreted in terms of past climate, geomorphology, soil, and regional vegetation development over the last 16,000 years. Against the background of these large-scale processes, local development took place, comprising the lake's ontogeny from an arctic-type ecosystem hosting pioneer aquatic communities, through a highly diversified mosaic of eutrophic hydrosere habitats (shallow pools, *Phragmites* and *Carex* fen, alder carr), towards an oligotrophic mire that started to dome over the terrestrialized lake. At every individual development stage, specific processes characterized ecosystem function and composition: during the Late-Glacial with its rapid climatic changes, external forces induced the major stresses; while during the Holocene, autogenic changes of the wetland ecosystem played the most important role.

INTRODUCTION

The recent discovery of thick, buried lake sediments of former Lake Švarcenberk in the Třeboň Basin, South Bohemia, presents an exceptional opportunity to study the regional vegetation and climatic development, as well as the local environmental succession of a lake basin. A high-resolution investigation of pollen, plant macrofossils, algal remains, and sediment composition for the Late-Glacial and Early to Middle Holocene sediments of the former lake yielded well-founded palaeoclimatic and palaeovegetation data. The profile is unique in the Czech Republic in having an extensive and well-stratified Late-Glacial record. High sediment-accumulation rates allowed the study of brief Late-Glacial climatic oscillations, so that a comparison could be made with western and northwestern Europe (POKORNÝ, in prep.).

The goal of the present study is to describe local vegetation changes against the background of abiotic settings (climate, nutrient cycling in the catchment, geomorphology) in order to reveal their possible driving forces. Thanks to the absence of significant human influence, and water level fluctuations, the Švarcenberk basin represents an ideal site for the study of natural changes in wetland communities. These changes could be the result of climatic stress

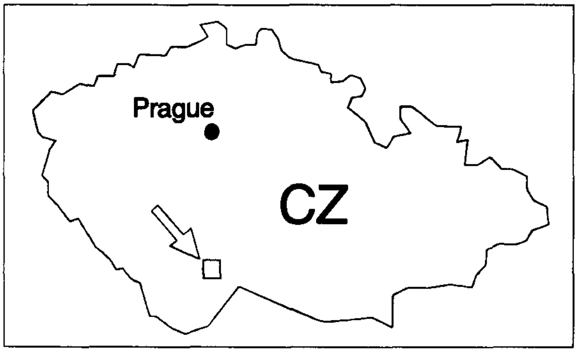


Fig. 1. Location of the study area within the Czech Republic.

or autogenic lake development. Autogenic processes leading finally to peat-bog formation were first described by WEBER (1908). Since that time, the seral development of wetland plant communities in present and former lake basins has been investigated repeatedly using palaeoecological methods (e.g. WALKER 1970, RYBNÍČEK 1983, TALLIS 1983). The advantage of a spatial approach involving more than one sampling point has been appreciated by several authors (more recently, for example, AMMANN 1989, BOS 1998). This approach is adopted in this paper, which aims to interpret lake basin history both on temporal and spatial scales.

STUDY AREA AND SITE

The study site is situated in South Bohemia in the flat landscape of the Třeboň Basin, which has an area of about 1,360 km^2 and a relief which varies by no more than 20–30 m (DEMEK 1987). Sandy and clayey Cretaceous sediments with locally superimposed Tertiary sediments constitute the principal geological substratum. Depressions are filled with Quaternary alluvial silt and gravel, aeolian sands, and particularly peat bogs. The clay content in soils generally increases with depth, and soil aeration is reduced accordingly. The soil nutrient content is generally poor: calcium carbonate deficiency is common, potassium is sufficient only in deep soil horizons, nitrogen content is low, and that of available phosphate is medium (HUSÁK & HEJNÝ 1978). Most soils are leached and show a tendency towards podzolization. The soil reaction is mostly highly acidic (pH down to 3.3). Various types of podzols and sandy or peaty gleys prevail.

The present climate is suboceanic determined by prevailing westerly air masses. The region is somewhat sheltered by the Bohemian Forest highlands. Mean annual precipitation is 622 mm (January being the driest month), and the mean annual temperature is 7.4 ^{o}C. Macroclimatic conditions are somewhat modified by the presence of extensive wetlands and by temperature inversions (CULEK et al. 1995).

The Třeboň Basin, originally an inaccessible swampy area, remained largely a wilderness until the 13th century. During the Late Medieval, it developed into a cultural landscape of fish culture and forest plantations, and fishponds still constitute a characteristic element of the landscape. Significant human impact on the lake/bog ecosystem was likely absent up to the Late Medieval period.

The first palynological investigation of the area was carried out by RUDOLPH (1917). While his primary focus was the investigation of plant macrofossils in several peat bogs, he supplemented his results by the analysis of some types of arboreal pollen. According to this, the basal age of some investigated deposits was later established to be of "Kiefern-Zeit" (*Pinus* era; RUDOLPH & FIRBAS 1922). The early postglacial age of most peat deposits in the Třeboň Basin was later confirmed by KLEČKA (1926, 1928) and ŠTĚPÁNOVÁ (1930). Small pollen counts and an exclusive focus on arboreal pollen were the main disadvantages of these early investigations. In the early 1960's, the second author of this paper started her palaeoecological investigations of the Třeboň Basin, using modern approaches. More recently, the first author continued this work in greater detail, giving it a more multidisciplinary character.

The former Lake Švarcenberk (49° 9' N, 14° 42' E, 412 m a.s.l.) is situated 4 km south of the town of Veselí nad Lužnicí. Limnic sediments are overlain by peat, which formed after the terrestrialization of the lake at approx. 5,500 BP, according to ^{14}C dating. Nowadays, the site is heavily influenced by intensive management: between 1698 and 1701 a dammed fishpond was constructed directly on the site, flooding the peat almost completely. The only presumed remnant of the original vegetation are small patches of tall sedge and *Sphagnum* communities (*Eriophorion gracilis* and *Rhynchosporion albae*) in the western part of the basin.

Several strong artesian springs influence the local hydrology. The spring water rich in iron oxides ascends along a deep tectonic fault. The former lake was presumably supplied almost exclusively by this water. The water supply was apparently continuous, since the lake level remained almost constant over the millennia. The lake drained into the nearby Lužnice River.

The existence of the former Lake Švarcenberk was first noted in the early 1970's by the second author. In her study focused on the vegetation development of the Třeboň Basin (JANKOVSKÁ 1980), she presented a pollen diagram, and a macrofossil diagram from an open profile (JC-7-B) of about 1.5 m of lake sediments, inferring that this was the littoral facies of a larger lake. No further stratigraphic data were obtained at that time. The present study confirms this original assumption.

METHODS

Field methods, sediment description, and subsampling

During a pilot study, the extension and stratigraphy of the former lake basin was studied by coring in a 100 × 100 m grid (sampling distances were reduced along the shores). A boat was used for subaquatic coring. Two reference stratigraphic sections (shown in Fig. 2) cross at right angles in the centre of the basin, where the "main profile" is located. The cores are labeled according to the distance in metres and the wind direction to this transect crossing. Depths in the cores are measured from the fishpond water level. The coring was performed with a 5-cm in diameter Russian-type corer (JOWSEY 1966), a device allowing complete recovery of each core drive.

The "main profile" was selected as the standard profile, having the longest and most continuous record without hiatuses. It consists of seven separate parallel cores taken close together in order to obtain enough material, correlated visually on the basis of lithostratigraphy. The original pollen and macrofossil data of profile JC-7-B (JANKOVSKÁ 1980) are used in this publication. The exact location of this profile's original sampling point (given as "SW margin of the former lake") was reconstructed by making a detailed stratigraphic investigation in the SW part of the basin. A site with an almost identical stratigraphy as that of profile JC-7-B is assumed to be a close approximation (Fig. 2). The second littoral sampling point, S500, was studied on an open-hand dug profile. The limno-thelmatic contact between 160 and 240 cm has been subjected to further analyses. This section is important for comparison with other profiles, as it comprises the complete hydrosere.

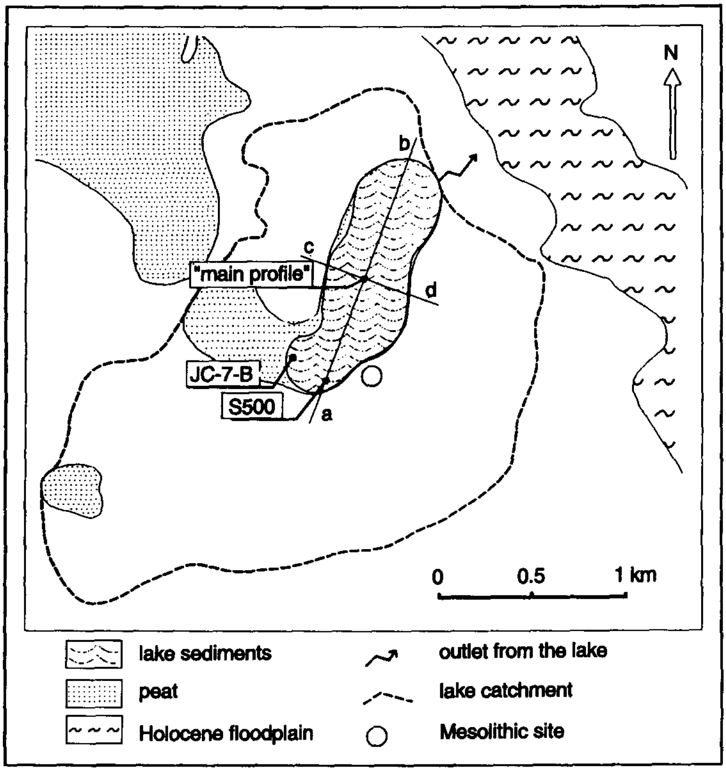


Fig. 2. Quaternary geology and topography of the Švarcenberk lake basin. a–b, c–d – two cross-sections (presented in Fig. 3) used for stratigraphical investigation. Location of selected profiles discussed in the text is shown.

The sediment description follows TROELS-SMITH (1955) as modified by AABY & BERGLUND (1986). The subsampling strategies depended on the required temporal resolution and the sample volume needed for each analysis.

Pollen analysis

The samples used for pollen and other microfossil analyses were prepared by a modified acetolysis method, as follows: Late-Glacial sediments having a more or less mineral character were pre-treated with 35% cold hydrofluoric acid (HF) for 24 hours (FAEGRI & IVERSEN 1989, MOORE et al. 1991). Extracted microfossils were lightly stained by 0.3% safranin and mounted in liquid glycerol-water (1 : 1). A minimum of 1,500 pollen grains was counted in each sample, but 500–700 grains were found in some Late-Glacial samples poor in pollen. For pollen identification, the following keys were used besides a reference collection: FAEGRI & IVERSEN (1989), MOORE et al. (1991) and PUNT (1976–1996). Pollen nomenclature follows the ALPADABA (Alpine Palynological Data-Base, housed at the Geobotanical Institute, Bern).

Algae and other microfossils were identified with VAN GEEL et al. (1981, 1983, 1989), JANKOVSKÁ (1983), JANKOVSKÁ & KOMÁREK (1982), and after personal consultation with Jiří Komárek (Třeboň).

Table 1. AMS radiocarbon dates from Švarcenberk littoral (S500) and central ("main profile") profiles.

Lab. No.	Core label/depth	Type of material	Measured ^{14}C age
LuA-4297	S500: 200 cm	*Trapa natans* nut	6,340 ± 110 BP
LuA-4588	"main p.": 150–153 cm	woody stem fragment	4,650 ± 100 BP
LuA-4589	"main p.": 324–327 cm	*Trapa natans* nut	6,350 ± 100 BP
LuA-4590	"main p.": 390–393 cm	woody stem fragment	9,640 ± 115 BP
LuA-4591	"main p.": 520–523 cm	gyttja	10,780 ± 115 BP
LuA-4738	"main p.": 680–683 cm	alkali soluble fraction from gyttja	11,750 ± 120 BP

The selection of types included in the pollen sum is an important part of the interpretation. Percentage values were calculated on the basis of an AP+NAP pollen sum (Arboreal + Non-Arboreal Pollen), excluding submerged and floating-leaf aquatics but including Monolete fern spores and *Equisetum* spores (in many plant communities, these taxa have an ecological role equivalent to that of higher plants). Concealed, corroded, degraded, and well-preserved but indeterminable pollen grains were combined as *Varia*. The pollen diagram for profile JC-7-B was prepared on the basis of the original counts (Jankovská 1980), using the same pollen sum as for the other two pollen diagrams. Diagrams were printed using the TILIA computer program, written by E.C. Grimm (Springfield).

Pollen diagrams were zoned visually, on the basis of presence/absence and on abundance of individual taxa. A more formalized approach to delimit the local pollen assemblage zones (LPAZ) was also applied on the basis of three different constrained classification procedures implemented in the computer program ZONE (Lotter & Juggins 1991). Consistency among results provided a basis for further specification of visually delimited LPAZ.

Core correlation

The combination of core correlation and radiocarbon dating resulted in relative and absolute temporal frames for local events. Correlation among profiles across the basin was first achieved by visual stratigraphy. For selected cores, this correlation was further confirmed and improved on the basis of trends in regional pollen types (for this purpose, a Holocene regional pollen diagram for the "main profile" is presented in Fig. 6). Corresponding pollen and macrofossil zones were named after zones in the "main profile". In one case, correlation based on biostratigraphy was confirmed by two, almost identical radiocarbon dates in different cores ("main profile" and S500; Tab. 1).

Macrofossil analysis

The material remaining after subsampling for other analyses was used for macrofossil analysis. 10 cm long contiguous samples were cut, and sample volume was determined (ranging around 250 ml in all cases). Samples were heated for 5 minutes in 5% potassium hydroxide (KOH) and sieved with running water over 200, 300 and 700 µm. The residues were examined under a dissecting stereomicroscope. Numbers counted were recalculated to a standard volume of 500 ml fresh sediment. For determination of the seeds/fruits, a reference collection and an atlas of macrofossils (Kac et al. 1965) were used. For profile JC-7-B (Jankovská 1980), a new macrofossil diagram was prepared based on the original analysis.

Plant nomenclature follows Tutin et al. (1964–1980).

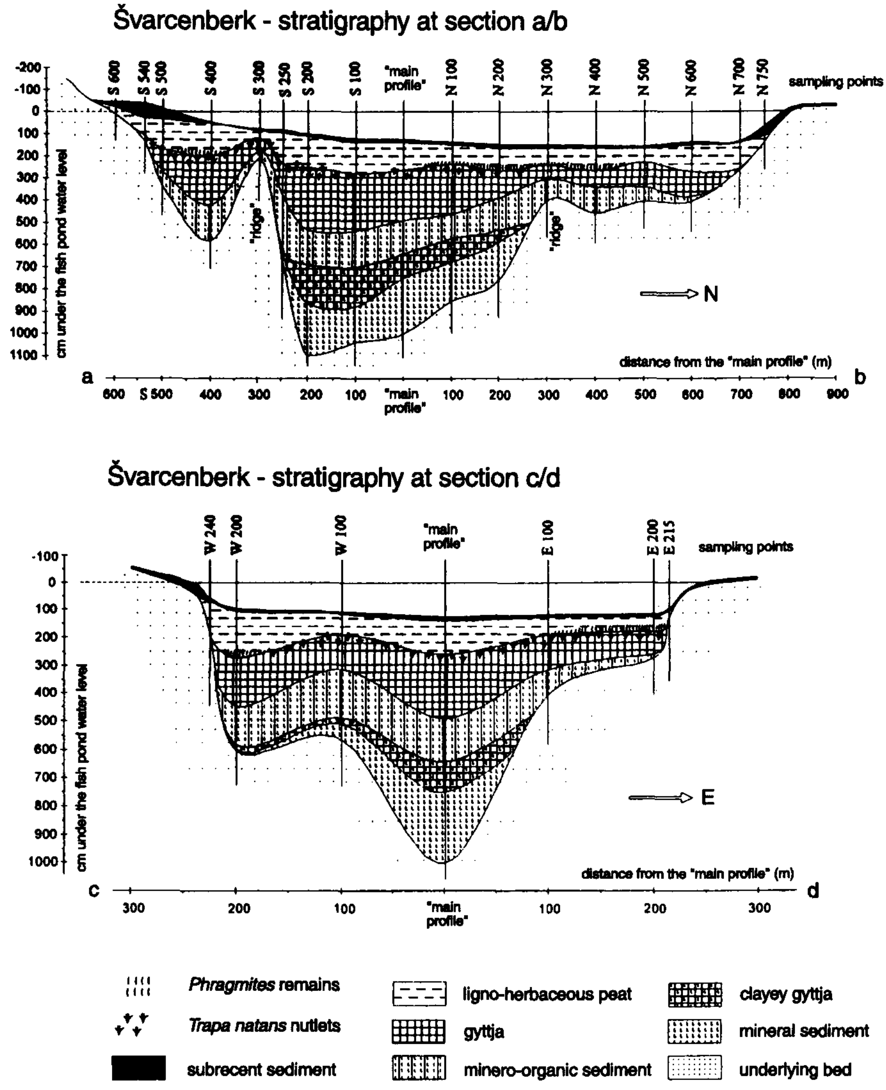


Fig. 3. Two orthogonal stratigraphic cross-sections (their position shown in Fig. 2) through the Švarcenberk Lake basin.

Sediment chemistry and radiocarbon dating

Numerous palaeolimnological studies have shown how sediment chemical properties may be interpreted in terms of processes acting within the lake basin and the surrounding catchment. These processes are often directly or indirectly related to general climatic parameters, ontogenetic development of the lake basin, or human impact. Their understanding may enable further environmental reconstruction (Engstrom & Wright 1984, Dearing 1991). The deepest profile in the centre of the basin ("main profile") was used for sediment chemistry measurements and absolute dating.

Total carbon and nitrogen was determined by combustion at 950 °C in pure oxygen for 3 minutes, followed by a conductivity measurement of C and N oxides (using a Heraeus CHN-Rapid Analyzer of the Analytical Laboratory of the Institute of Botany, Academy of Sciences of the Czech Republic). After dissolution of 0.5 g sample in 0.5 M hydrochloric acid and subsequent boiling for 20 minutes, the carbonate content was measured by sodium hydroxide titration to neutral pH (after HAMMARLUND & BUCHARDT 1996). The total organic carbon content was calculated as the difference between total carbon and carbonate carbon.

Ca, Mg, and K were analyzed by atomic emission spectrometry in the Analytical Laboratory of the Institute of Botany, Academy of Sciences of the Czech Republic, using a Unicam 9200X AAS instrument.

Total phosphorus was determined in the same laboratory as follows: Samples were extracted in Olsen's reagent (OLSEN et al. 1954). The resulting phosphate-phosphorus was reduced in ascorbic acid. A "molybdenum blue" complex was formed in ammonium molybdate-sulphuric acid reagent. The colour intensity was measured by spectrophotometer on 630 nm.

Sediment pH was determined in fresh sediment immediately after its recovery. The sediment sample was stirred in a small volume of distilled water and the pH of the suspension was measured after two minutes by a portable electronic pH-meter.

AMS radiocarbon dating was performed on bulk sediment samples and individual plant macrofossils (see Tab. 1). In the Late-Glacial part of the studied core, insufficient terrestrial plant macrofossils were present for dating. Dating performed on gyttja, clayey lake sediment, or on aquatic plant macroremains may overestimate the ages due to hardwater effects (TÖRNQVIST et al. 1992). In the present study, the hardwater effect may be relatively small, as the sediments contain negligible amounts of carbonates. Radiocarbon dating was carried out by the Radiocarbon Dating Laboratory, Department of Quaternary Geology, Lund, Sweden. The samples were pretreated with HCl and NaOH. Age calculations are based on a ^{14}C half-life of 5,568 years. Dates are expressed in uncalibrated ^{14}C years before present (BP) unless otherwise stated.

RESULTS AND DISCUSSION

Origin of the lake

The former lake had a maximum surface area of 0.51 km^2, and a ratio of surface to drainage basin of about 1 : 8 (Fig. 2). Two lithological cross-sections (Fig. 3) show the morphometry and the sediments that have infilled the depression.

Striking features of the lake basin morphology are its kidney-shaped form, surprising depth and declivity (the presence of unusually steep slopes), and the relatively great age of its infilling. The age of the basal sediments is estimated to around 16,000 BP on the basis of the pollen stratigraphy. The origin of such a structure can best be explained as the remnant of a huge Pleniglacial ground-ice lens – an open-system pingo. A similar thermokarst origin has been suggested for several semicircular depressions in the Netherlands, Belgium, France, Germany, and Poland (WASHBURN 1980, DE GANS 1988, HOEK 1997). The sandy geological substratum, the presence of strong artesian springs and the location close to a river are factors known to favour pingo formation (PISSART 1988, DE GANS 1988). The absence of a distinct rampart around the former lake is not surprising, as the original geomorphology of the site has been completely disturbed by human action, especially during the construction of the fishpond in the 17th century. Moreover, some pingos do not dome very high over the terrain, even if they are relatively large in diameter (WASHBURN 1980) and do not form a distinct rampart after collapse. In view of the unusually large size of the depression, and the presence of ridges (see Fig. 2) dividing the basin into three main parts, the origin of the lake can be best viewed as the remnant of some kind of compound pingo structure.

Response of aquatic vegetation to rapid climatic changes during the Late-Glacial

In the littoral parts of the former lake basin, only a thin layer of Late-Glacial sediments is present, and deposits older than the Younger Dryas are completely lacking. This can be explained by an intensive reworking of sediments along the shores during the Late-Glacial rather than as a result of lower lake levels during this period. On the other hand, the "main profile" contains as much as 5 metres of Late-Glacial sediments.

The Late-Glacial pollen stratigraphy of the "main profile" is subdivided into eight local pollen assemblage zones (LPAZ, Figs. 4, 5). Because of problems of terminology (e.g. AMMANN & LOTTER 1989, WALKER 1995), we have subdivided the diagram in this way rather than into regional Firbas pollen zones. The absence of analogous results over a wider region discourages the use of this regional pollen zonation. The LPAZ are compared with European climatostratigraphical units according to MANGERUD et al. (1974) and AMMANN & LOTTER (1989), as well as with the $\delta^{18}O$ curve of the Greenland ice core GISP2 (STUIVER et al. 1995). This comparison is presented in Fig. 11, giving an idea of the rate and amplitude of climatic changes during this period. The response of the aquatic ecosystem to these climatic changes is briefly discussed below.

Late Pleniglacial (zones S1 and S2)

The maximum depth of the lake was about 9.5 m during this period. Fossil evidence suggests the development of a pioneer lake-bottom vegetation, shortly after the formation of the lake. Pollen from submerged water plants is absent, while large quantities of *Charophyta* oospores (cf. *Chara strigosa*, a pioneer with subarctic modern distribution, preferring clear oligotrophic water) are found. Rare finds of *Ranunculus* subgen. *Batrachium* and *Potamogeton* cf. *gramineus* seeds point to the presence of floating-leaf and submerged macrophytes in the lake. However, their occurrence was so limited (probably restricted to the shores), that it allowed the development of a carpet of charophytes on the bottom. This initial stage was soon succeeded (in the transition to zone S2) by submerged aquatic vegetation (*Potamogeton*, *Myriophyllum*, *Ranunculus* subgen. *Batrachium*), which probably outcompeted the charophytes on the lake bottom.

High values of sedimentary Mg, K, and Ca during the entire pre-Bölling (Late Pleniglacial) may be explained by the erosion of the unstable substratum. N, P and organic C is very low (see Fig. 12). The low nutrient status of the lake together with the low productivity must have been primarily caused by a low energy input. Silty FeS-coloured sediments in the centre of the basin suggest anoxic conditions, as iron-sulfide deposition usually occurs under prolonged or permanent stratification of a lake (ENGSTROM & WRIGHT 1984).

Planktic algal communities include *Pediastrum* taxa characteristic of oligotrophic to dystrophic, cold and clear waters (KOMÁREK & JANKOVSKÁ 2000): *Pediastrum integrum* and *P. boryanum* var. *longicorne*. Among other *Pediastrum* taxa, *P. orientale* is the most interesting. This conspicuous species was first described on subfossil material from Lake Švarcenberk (JANKOVSKÁ & KOMÁREK 1995). According to both recent and subfossil records, *P. orientale*

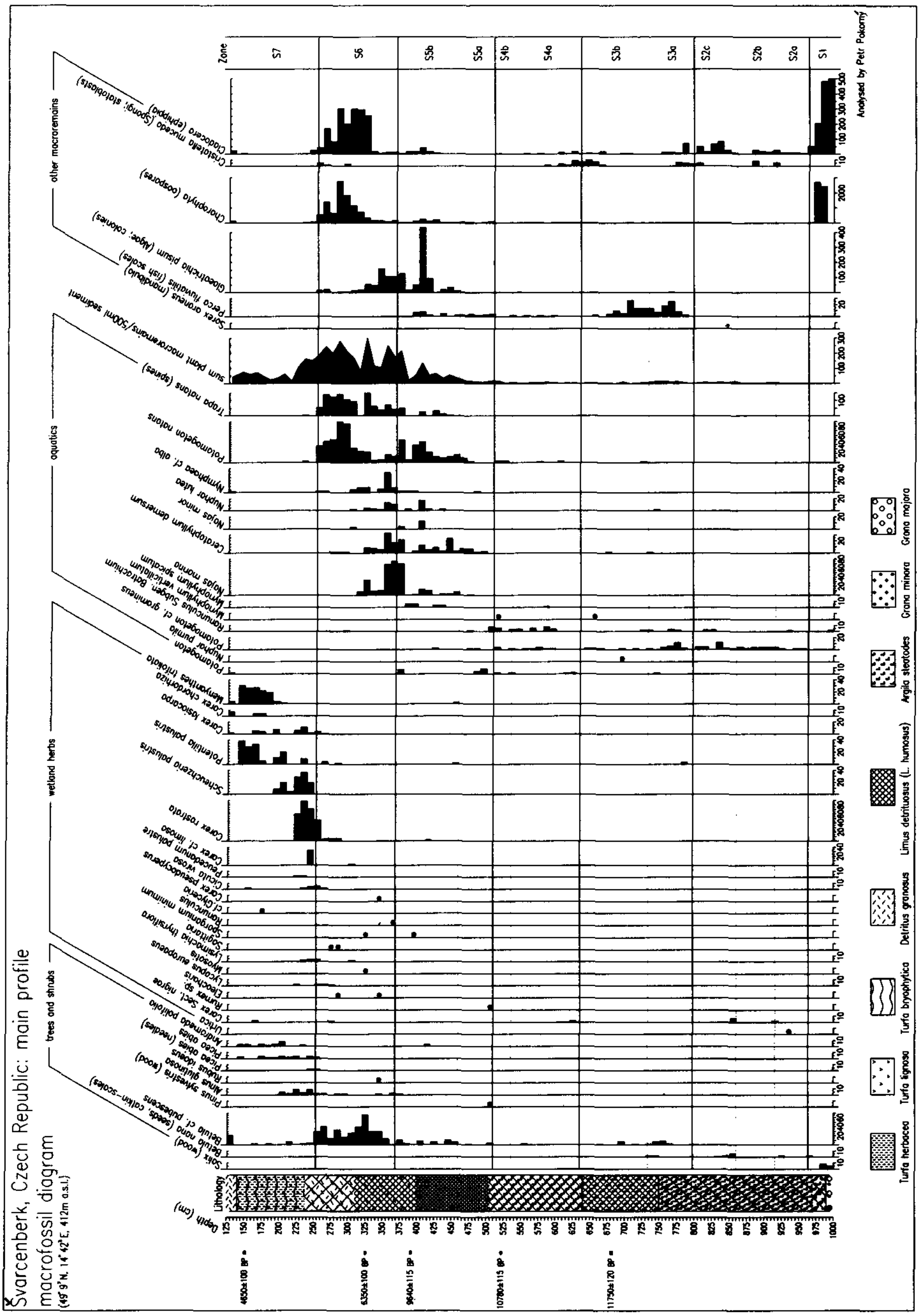


Fig. 4. Late-Glacial and Holocene macrofossil diagram of the "main profile". All finds represent seeds unless otherwise stated. Unit: number/500 ml.

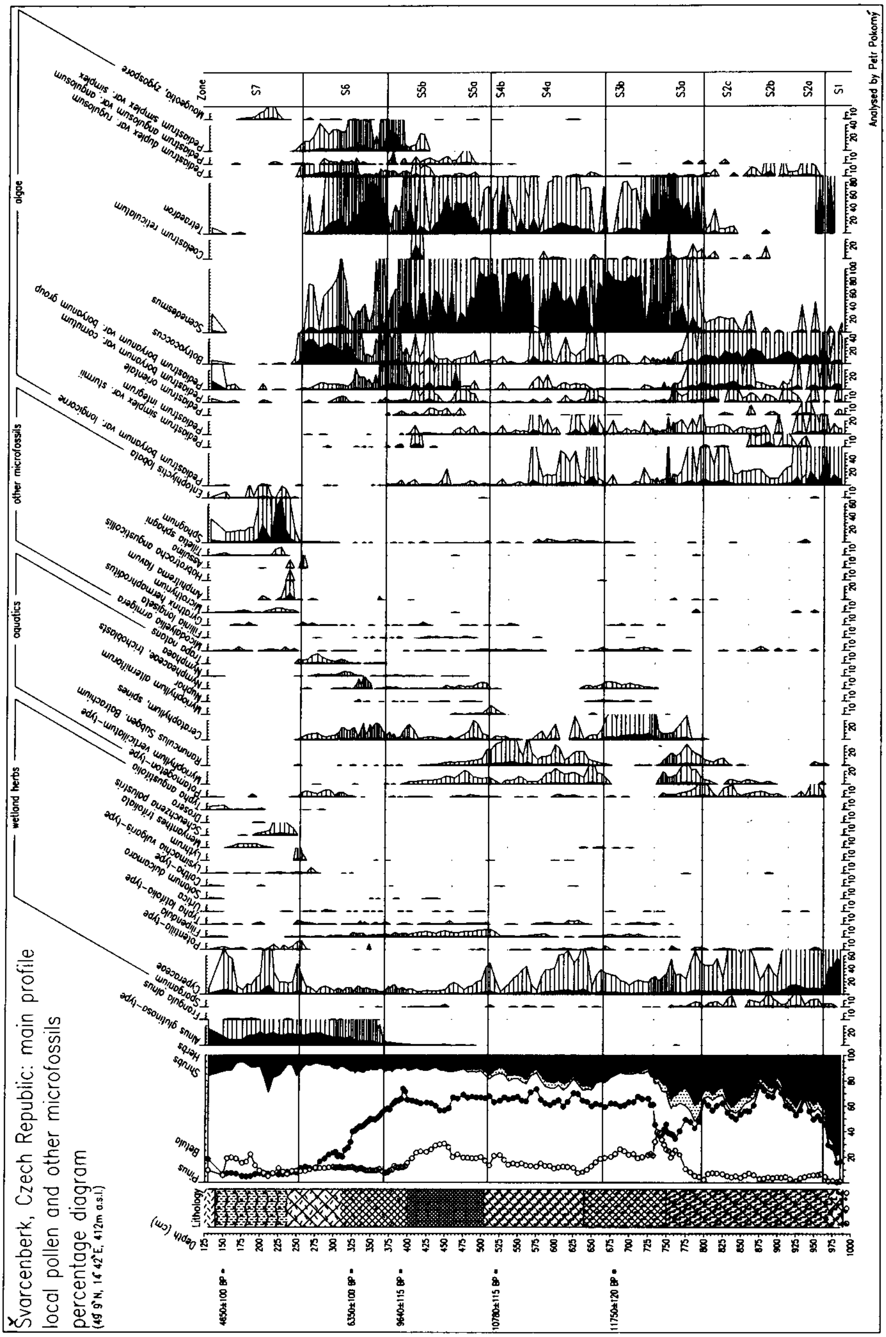


Fig. 5. Late-Glacial and Holocene local pollen and other microfossil diagram of the "main profile". Only selected types are included. For a sediment stratigraphy description, see Fig. 4.

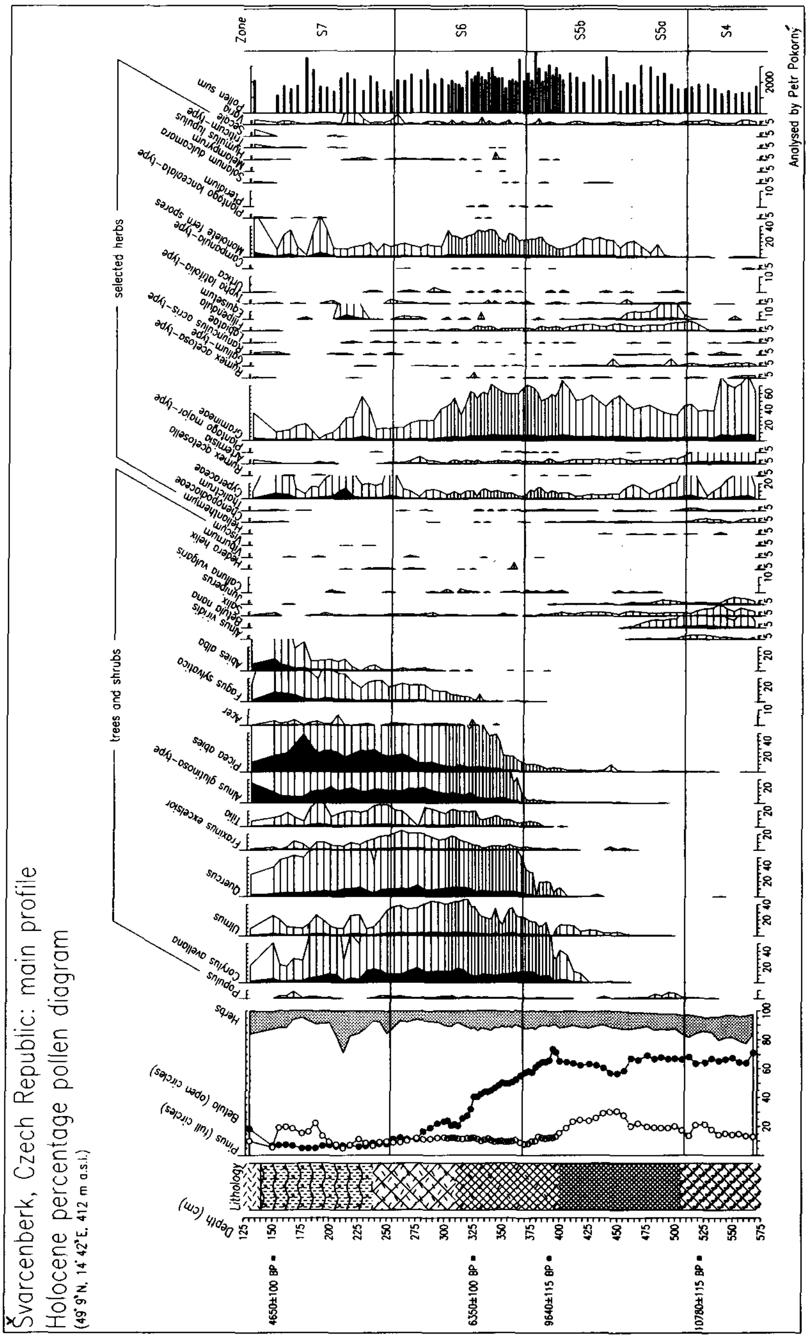


Fig. 6. Holocene regional pollen diagram of the "main profile" used for correlation purposes. For a sediment stratigraphy description, see Fig. 4.

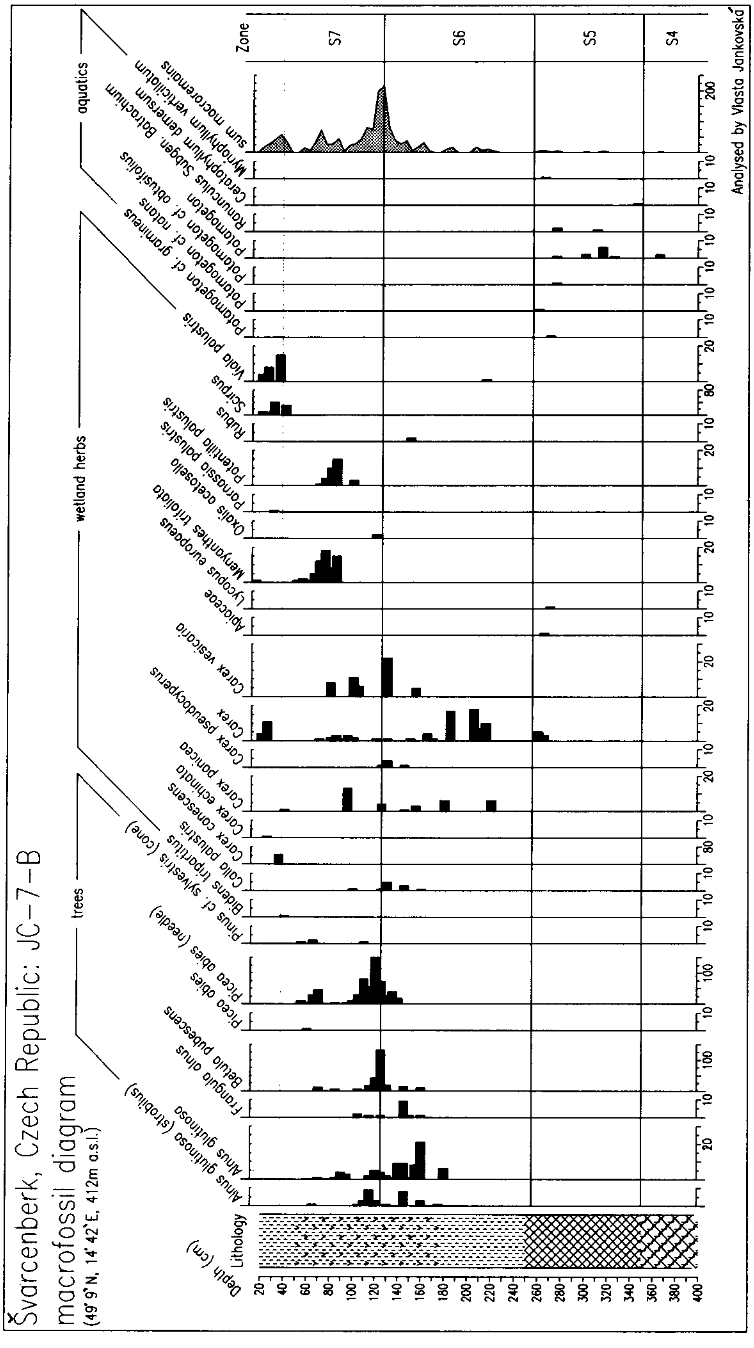


Fig. 7. Macrofossil diagram of JC-7-B profile. All finds represent seeds unless otherwise stated. Unit: number/100 ml. For sediment stratigraphy description, see Fig. 4.

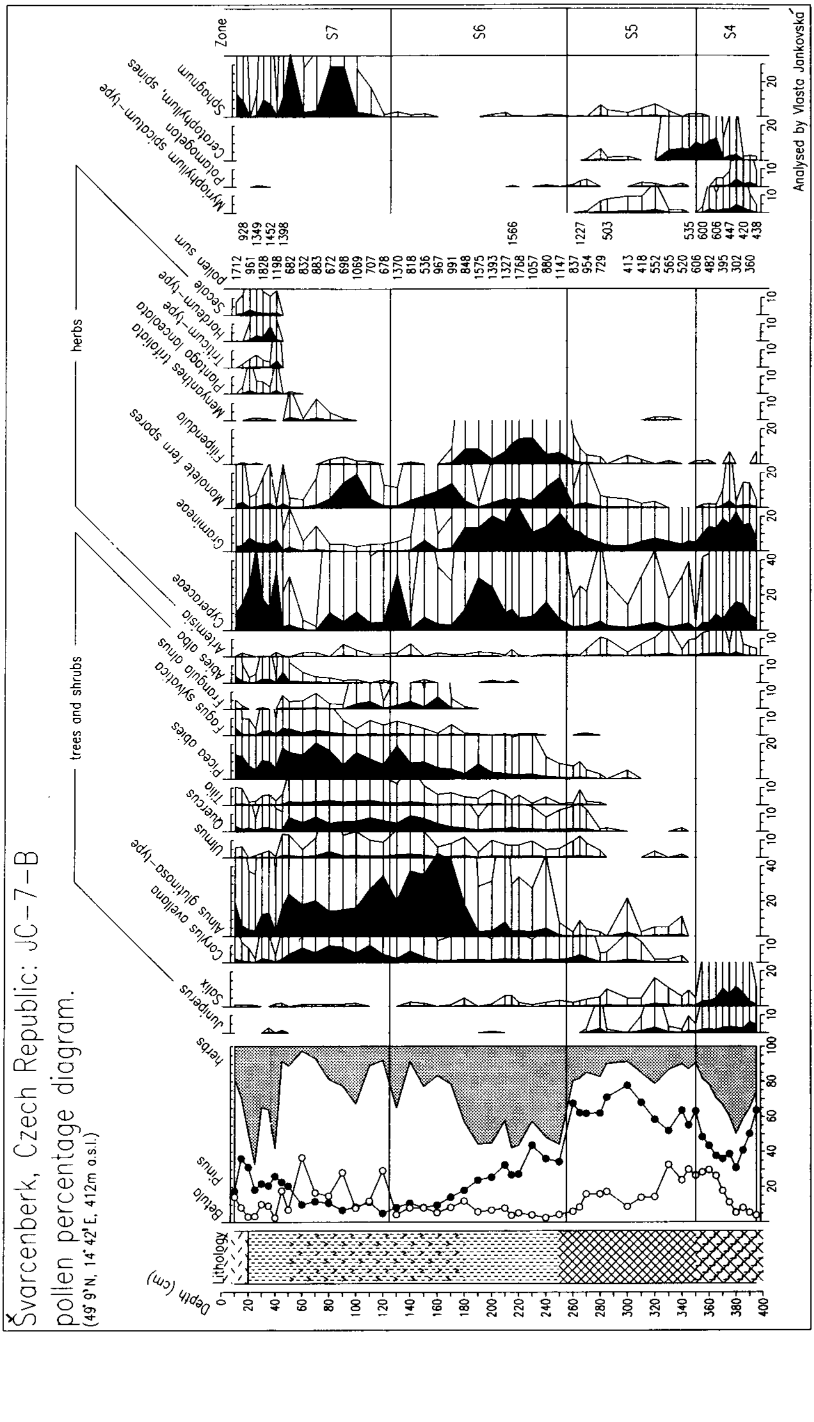


Fig. 8. Pollen diagram of JC-7-B profile. Only selected types are included. For a sediment stratigraphy description, see Fig. 4.

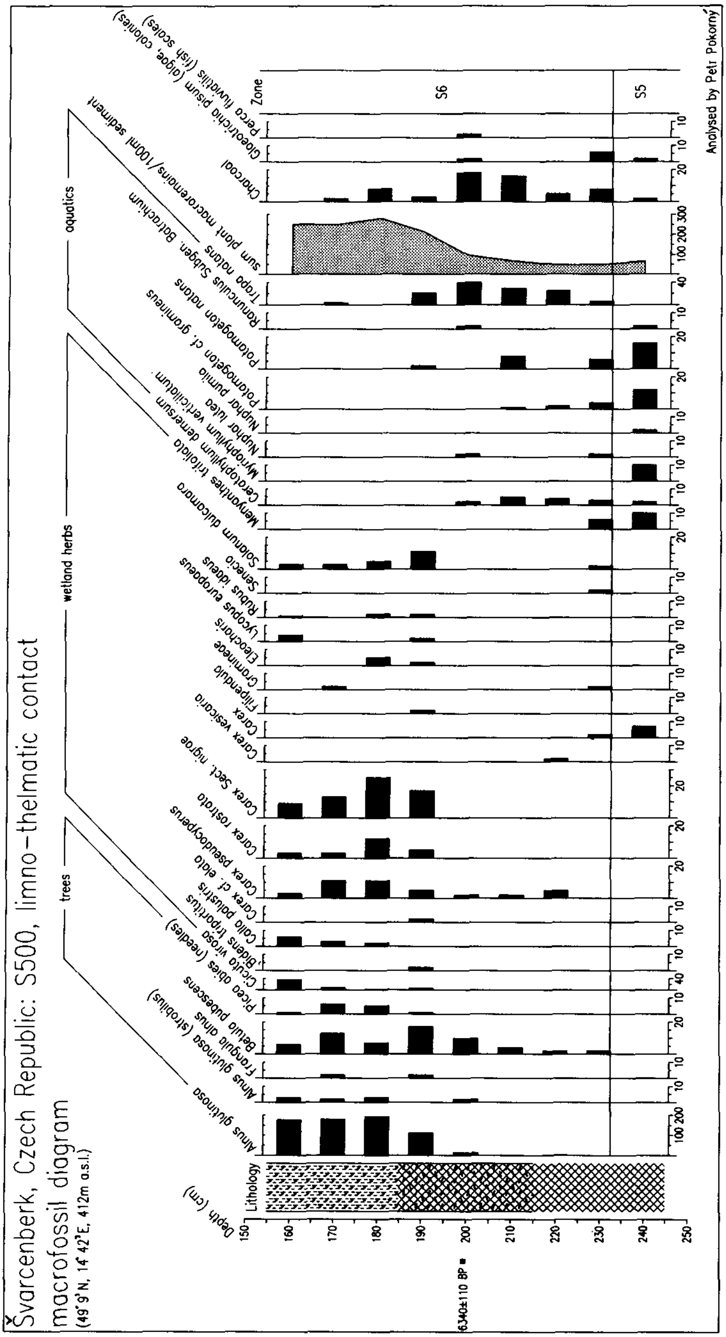


Fig. 9. Macrofossil diagram of S500 profile. All finds represent seeds unless otherwise stated. Unit: number/100 ml. For a sediment stratigraphy description, see Fig. 4.

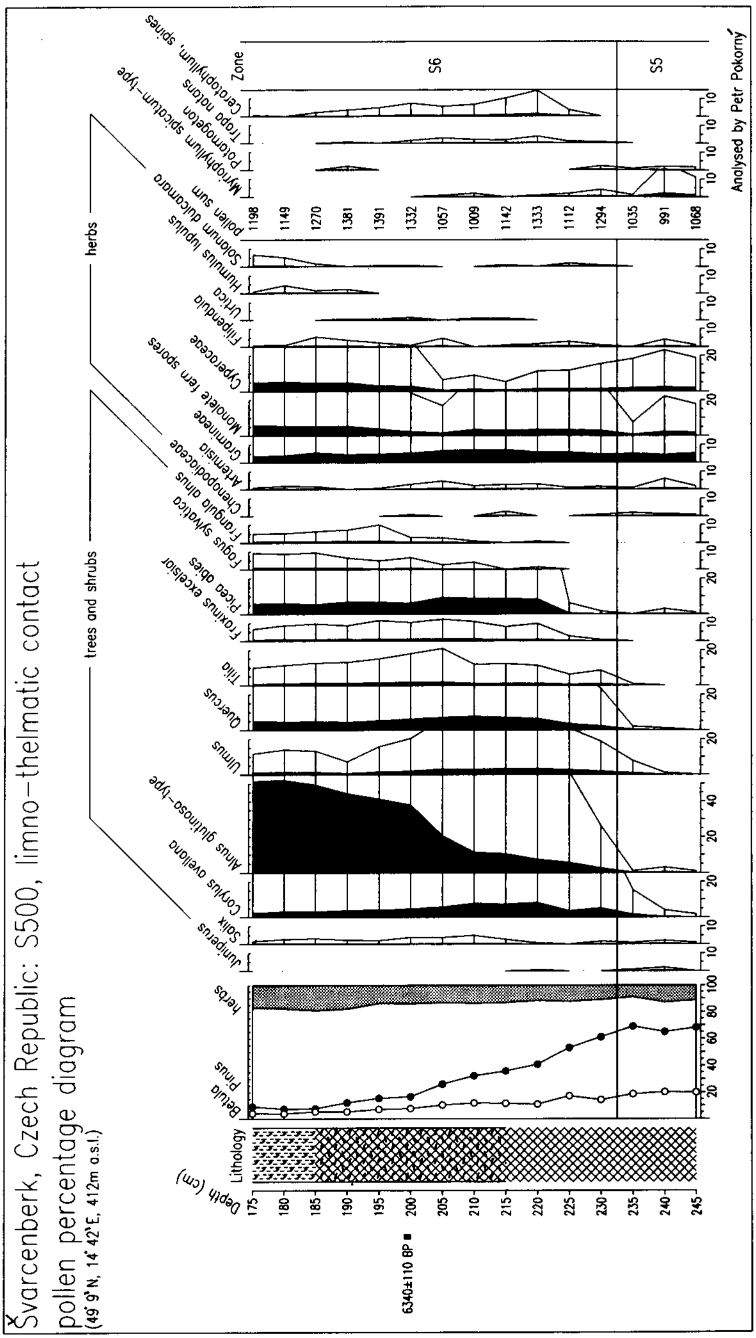


Fig. 10. Pollen diagram of S500 profile. Only selected types are included. For a sediment stratigraphy description, see Fig. 4.

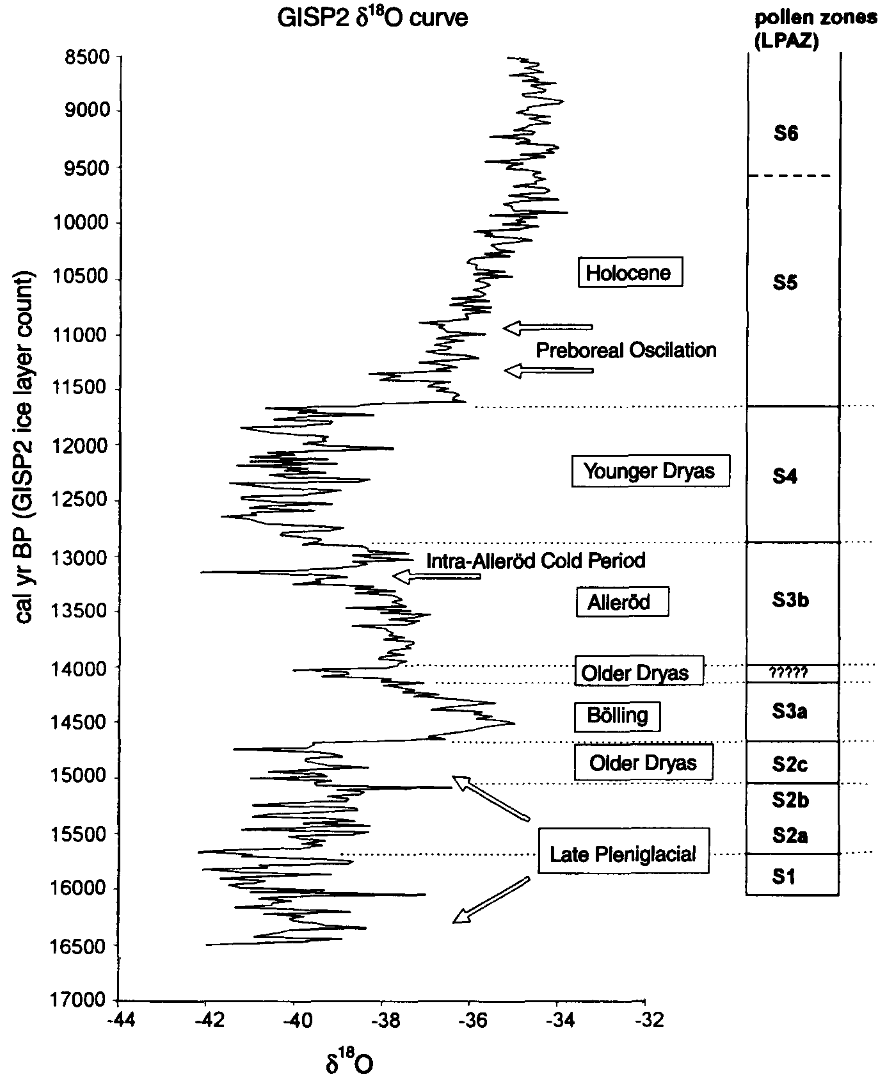


Fig. 11. Local pollen assemblage zones (LPAZ) compared with a bidecadal $\delta^{18}O$ curve of the Greenland ice core GISP2 (data measured by W.O. VAN DER KNAAP from STUIVER et al. 1995). This cross-correlation should be considered as a suggested scheme only. Absolute time scale (cal yr BP; yearly ice-layer counts before A.D. 1950) and chronozones follow STUIVER et al. (1995) with exception of "Preboreal oscillation" derived from AMMANN & LOTTER (1989).

also prefers clear and cool waters (KOMÁREK & JANKOVSKÁ 2000). Probably due to the low nutrient status of the lake water *Scenedesmus* and *Tetraedron minimum* are found either in low quantities or are absent.

Late-Glacial Interstadial (zone S3)

Marked climatic amelioration characteristic of the onset of the Late-Glacial Interstadial resulted in significantly increased organic production, as reflected in the sharp transition from minerogenic to organic sedimentation (see increased organic carbon, nitrogen, and phosphorus;

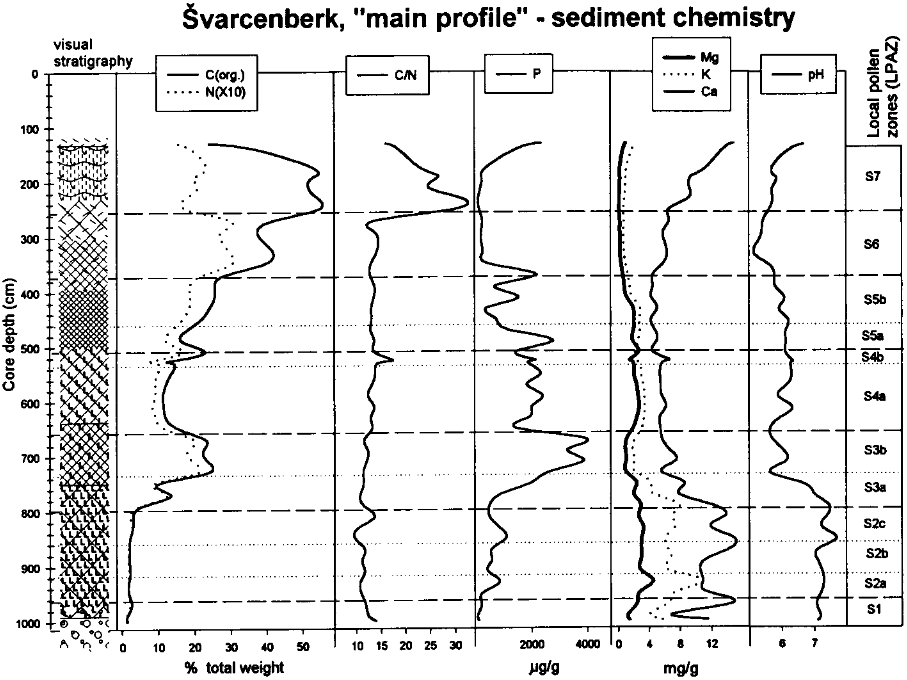


Fig. 12. Sediment chemistry of the "main profile" correlated with local pollen zonation. For visual sediment stratigraphy, see Fig.4.

Fig. 12). In the aquatic environment, submerged macrophytes (*Potamogeton, Myriophyllum, Ranunculus* subgen. *Batrachium*) expanded immediately in response to climatic warming. The submerged aquatic *Ceratophyllum demersum* invaded the lake for the first time and became dominant during the second half of the Interstadial (subzone S3b, i.e. Alleröd chronozone), when also *Nuphar* (probably *N. lutea* according to an isolated macrofossil) expanded in the shallower parts of the lake. The occurrence of these two aquatic plants and the expansion of *Typha latifolia* and *Filipendula* in the littoral zone and along the shore indicate minimum July temperatures of at least 12 °C (Huizer & Izarin 1997).

The massive occurrence of perch (*Perca fluviatilis*) scales is characteristic for Interstadial sediments within the entire Švarcenberk basin. Perch is a less-demanding fish that can survive even in subarctic lakes. The fry is produced in large quantities and feed on planktic or benthic organisms. Adults can feed mostly on their own young and reach high population densities, a cannibalistic food chain described from several contemporary Siberian lakes (Holčík 1977, Karasev 1987) that is assumed also for Lake Švarcenberk during the Late-Glacial Interstadial. Maximum water depth was about 7.5 m.

Reforestation of the surrounding landscape by birch and pine led to initial soil development and to a decrease of erosion as seen from the progressive decline in sedimentary Mg and K. During episodes of relatively stable soils, deep weathering of mature soil profiles should diminish the base content of mineral material prior to its erosive removal and sedimentation in lake basins (Engstrom & Wright 1984). Decalcification of the substratum continued up to its completion (see the decline in Ca down to values comparable with those of the Holocene – Fig. 12).

As a result of changes in the nutrient status of the lake, the composition of algal planktic communities had changed. All *Pediastrum* species had declined, responding probably to the competitive pressure of *Scenedesmus* and *Tetraedron minimum*, which developed so massively that they form the main bulk of the sediment (algal gyttja). Competition among algae in planctic communities may also explain why the ecologically rather indifferent *Pediastrum borynum* var. *boryanum* and *P. borynum* var. *cornutum* had declined (KOMÁREK & JANKOVSKÁ 2000).

Younger Dryas (zone S4)

Vegetation change reflecting climatic deterioration was indicated by a decrease of *Ceratophyllum* spines, and the absence of *Nympheaceae* trichoblasts and *Nuphar* pollen in favour of a massive occurrence of *Myriophyllum verticillatum* and *Ranunculus* subgen. *Batrachium* (both pollen and macrofossils). The presence of *Typha latifolia* pollen in the entire zone suggests minimum July temperatures of at least 12 °C (IVERSEN 1954, AMMANN 1989), i.e. similar to those inferred for the preceding Interstadial zone. This might suggest that the inferred climatic deterioration comprised an increase in continentality rather than a decrease in summer temperatures.

The sediment again became more minerogenic (with significantly less organic carbon, N and P). A slight increase in sedimentary erosion indicators (Mg, K) is observed as well. Maximum water depth was about 5.5 m. The change in water chemistry is reflected in the algal communities, with *Pediastrum* increasing. *Pediastrum integrum* and *P. boryanum* var. *longicorne*, characteristic of oligotrophic, cold, and clear waters (KOMÁREK & JANKOVSKÁ 2000), reached a dominance that was never achieved later in the Holocene.

Start of the Holocene (zone S5)

Organic sediment (algal gyttja), rich in macrofossils, started to accumulate in the basin again at the beginning of the Holocene. Maximum water depth was about 4 m. Sedimentary phosphorus fluctuates but is generally low during the Early Holocene. Further study of phosphorus forms would be necessary to explain this.

The rapid temperature rise during the very beginning of the Holocene is shown by a new expansion of *Ceratophyllum demersum* and *Nuphar* in the lake, and by a massive occurrence of macroscopic colonies of the thermophilous blue-green alga *Gloeotrichia pisum* (VAN GEEL et al. 1989). The first occurrences of *Najas marina* and *Trapa natans* macrofossils are very early in the Holocene (about 9,800 BP; based on linear interpolation between ^{14}C dates). *Najas minor* macrofossils were also found. It occurs usually together with *Najas marina*, but subfossil finds are much less common in Europe (BACKMAN 1951). *Najas marina* suggests a mean July water temperature not less than 15 °C (LOTTER 1988), and *Trapa natans* even more: according to GAMS (1926) and JORGA et al. (1982), water chestnut requires a mean July water temperature not less than 20 °C and in May, when it starts flowering, at least 12 °C. This suggests that present-day temperatures were reached as early as about 9,800 BP, some few hundred years after the end of theYounger Dryas. This is in accord with ^{18}O results of the Greenland ice core GISP2 (STUIVER et al. 1995; see Fig. 11). It is possible that the rapid spread of *Trapa natans* in the Early Holocene was aided by human populations of hunter-gatherers, translocating over long distances in Europe. Several aquatic plants (e.g. *Trapa natans, Nymphaea, Typha, Sagittaria*) are known from archaeological investigations to be utilized as food sources by Mesolithic populations (ZVELEBIL 1994, KUBIAK-MARTENS 1996). Archaeological evidence for Mesolithic settlement was indeed found near the shores of the former Lake Švarcenberk and palaeoecological evidence (pollen and charcoal) dates human occupation on the site to the very beginning of the Holocene, synchronous with the first *Trapa natans* occurrence.

Warm, shallow, and nutrient-rich water allowed the development of *Pediastrum simplex* var. *simplex*, a taxon commonly distributed in naturally eutrophic lakes. This taxon is usually abundant in climatically favourable periods that enabled the development of lake biotopes with naturally eutrophic waters (BOTTEMA 1974, KOMÁREK & JANKOVSKÁ 2000). On the other hand, most *Pediastrum* taxa that were abundant during cold periods of the Late-glacial, now became rare. A more significant occurrence of *Pediastrum angulosum* var. *angulosum* at the beginning of the Holocene has probably no direct climatic or water-quality explanation. It is rather a consequence of the massive development of submerged macrophytes in the lake. This is in accord with the interpretation of KOMÁREK & JANKOVSKÁ (2000).

Vegetation succession during final terrestrialization of the lake basin

In this section, vegetation succession accompanying the final infilling of the lake is described and discussed on the basis of pollen and macrofossils in three profiles (the "main profile", JC-7-B and S500; see Fig. 2). Climatic conditions were so stable during the period involved (Early and Middle Holocene; e.g. DANSGAARD 1980, FRENZEL 1983, HUNTLEY & PRENTICE 1993) and human impact so small that we assume a mainly autogenic vegetation succession connected with lake basin infilling. This assumption is supported by sediment-chemical analysis. The results are presented in Fig. 13A–E; main features are discussed in the text below.

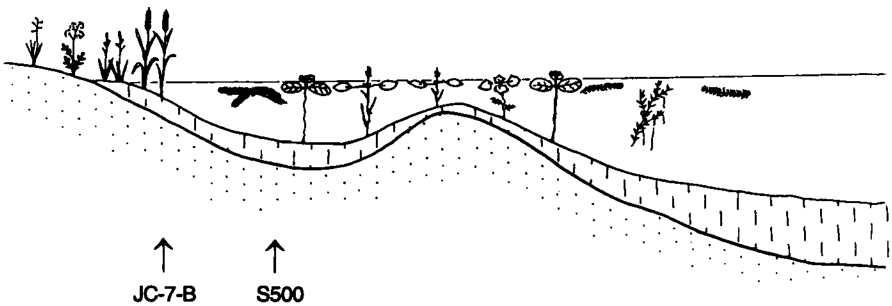
The final stage of terrestrialization of the lake lasted about 3,000 years (8,500–5,500 BP). Individual parts of the basin crossed the ecological boundary (hydrosere) from aquatic to semi-terrestrial environment at different moments, followed by a characteristic vegetation succession (data in Fig. 6–10 and Fig. 11; interpretation in Fig. 13). This succession is a typical eutrophic hydrosere as described by LANG (1994) and ELLENBERG (1996). For the transitional stage, shallow pools with dense aquatic vegetation dominated by *Trapa natans, Potamogeton natans* and charophytes (mainly *Nitella flexilis*) are characteristic. *Trapa natans* is virtually absent in the littoral profile JC-7-B, where only a single pollen grain was recorded. This is most likely due to the early terrestrialization of this part of the basin, before the massive expansion of *Trapa natans* in the lake.

The transition from aquatic to semi-terrestrial environment is best reflected in the sharp decline of algae in the "main profile". *Pediastrum duplex* var. *rugulosum* developed shortly before this event, during the stage characterized by floating-leaf aquatics. This ecology is also described by KOMÁREK & JANKOVSKÁ (2000).

Following the terrestrialization, a eutrophic *Carex* fen (dominated locally by *Carex pseudocyperus, C. rostrata* or *C. vesicaria*) developed and peat accumulation began. These communities were soon succeeded by alder carr with some spruce and birch in the littoral facies, while the centre of the basin developed into an oligotrophic *Sphagnum* peat-bog as the surface raised over the surrounding terrain. As a result, this part of the basin became isolated from the runoff of the catchment and from the ground water. A vegetation gradient developed from the edges to the centre of the basin, reflecting a gradient in nutrient availability. The isolation of the central part is well-reflected in the chemical record of the "main profile". The nutrient status (N and especially P) of the *Sphagnum* peat is very low and the C/N ratio sharply increased, compared with underlying lake sediments. The pH is low (pH = 5), as the

A — **subzone S5b, about 9,500 BP**

location (core label):	JC-7-B	S500	"main profile"
characteristic taxa:	*Potamogeton, Ranunculus* subgen. *Batrachium, Ceratophyllum demersum, Myriophyllum verticillatum*	*Nuphar, Potamogeton, Ranunculus* subgen. *Batrachium, Ceratophyllum demersum, Myriophyllum verticillatum*	*Najas marina, Najas minor, Nuphar, Nymphaea, Trapa natans, Potamogeton natans, Ceratophyllum demersum, Myriophyllum spicatum*
Interpretation:	open water	open water	open water



B — **zone S6 - first half, about 6,500 BP**

location (core label):	JC-7-B	S500	"main profile"
characteristic taxa:	*Carex, Carex panicea, Viola palustris, Filipendula*	*Nuphar, Potamogeton, Ceratophyllum demersum, Trapa natans*	*Najas marina, Nuphar, Nymphaea, Trapa natans, Potamogeton natans, Ceratophyllum demersum*
Interpretation:	fen	shallow pools	open water

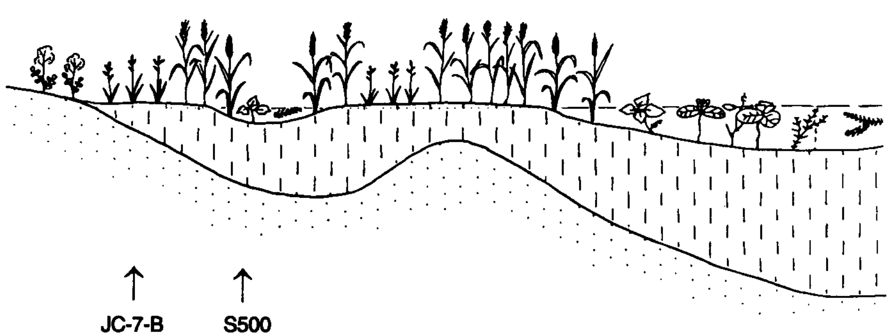
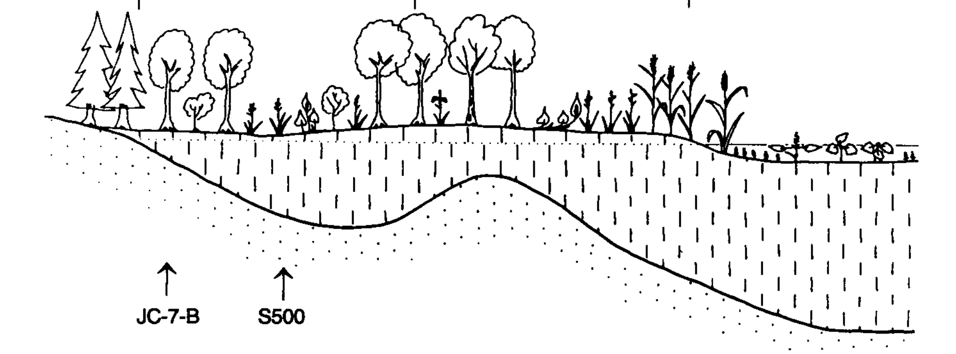


Fig. 13A–B. Time/spatial reconstruction of Lake Švarcenberk basin during the Holocene. Pollen zone labels and absolute time estimates (as BP – years before present) are indicated in headings.

C **zone S6 - second half, about 6,000 BP**

location (core label):	JC-7-B	S500	"main profile"
characteristic taxa:	*Alnus glutinosa, Betula pubescens, Frangula alnus, Carex vesicaria, C. panicea, C. pseudocyperus, Calla palustris*	*Alnus glutinosa, Betula pubescens, Frangula alnus, Carex rostrata, C. sect nigrae, C. pseudocyperus, Calla palustris, Eleocharis, Solanum dulcamara, Lycopus europaeus*	*Potamogeton natans, Trapa natans, Nymphaea, Ceratophyllum demersum, Charophyta, Pediastrum duplex* var. *rugutosum*
Interpretation:	*Carex* fen / alder car	*Carex* fen / alder car	shallow water



D **zone S7 - first half, about 5,200 BP**

location (core label):	JC-7-B	S500	"main profile"
characteristic taxa:	*Alnus glutinosa, Betula pubescens, Picea abies, Frangula alnus, Carex vesicaria, C. panicea, Calla palustris, Sphagnum*	?	*Carex rostrata, C. lasiocarpa, Scheuchzeria palustris, Potentilla palustris, Sphagnum*
Interpretation:	forested fen / bog (?)	forested fen / bog (?)	*Sphagnum* bog

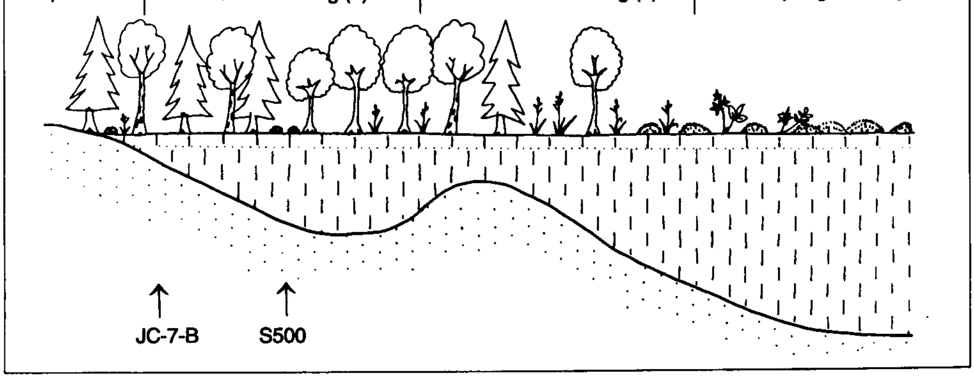


Fig. 13C–D. Time/spatial reconstruction of Lake Švarcenberk basin during the Holocene. Pollen zone labels and absolute time estimates (as BP – years before present) are indicated in headings.

E			zone S7 - second half, about 4,500 BP
location (core label):	JC-7-B	S500	"main profile"
characteristic taxa:	*Menyanthes trifoliata, Potentilla palustris, Sphagnum*	?	*Potentilla palustris, Carex lasiocarpa, C. chordorhiza, Menyanhes trifoliata, Andromeda polifolia, Sphagnum*
Interpretation:	*Sphagnum* bog	*Sphagnum* bog (?)	*Sphagnum* bog

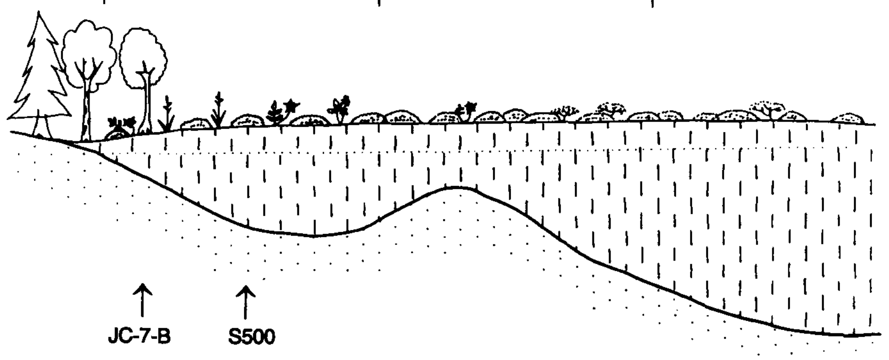


Fig. 13E. Time/spatial reconstruction of Lake Švarcenberk basin during the Holocene. Pollen zone labels and absolute time estimates (as BP – years before present) are indicated in headings.

invasion of *Sphagnum* caused active acidification (Tallis 1983). *Menyanthes trifoliata, Potentilla palustris, Scheuchzeria palustris,* and *Andromeda polifolia* grew in the *Sphagnum* carpet. In small bog pools, *Mougeotia* filamentous algae formed a surface growth.

During the next ca. 1,000 years, oligotrophic bog communities spread towards the periphery of the mire. The sedimentary record ends in the middle of the basin, around 4,500 BP, and in the littoral parts it becomes fragmented, probably comprising some hiatuses. The later development of the mire can not be assumed, but a continued existence until the 13th century, when the area wås first colonized can be. Peat-cutting and finally fishpond construction interrupted the natural development.

The uppermost sediment sample of the "main profile" represents subrecent fishpond bottom sediment (sapropel). Its chemical composition is directly influenced by management (liming, fertilization, intensive fish production, etc.). Cations and phosphates have penetrated downwards. This explains the rise in P and Ca (together with a pH rise) in the uppermost peat. Deep penetration especially by calcium carbonate (artificially supplied in large quantities), which enrich the peat to a depth of about 1.5 m is observed.

Further details of the vegetation succession during individual stages of the lake basin terrestrialization are shown in Fig. 13A–E. A comparison of pollen and macrofossil analyses in the same profile and among profiles allows methodological conclusions on the suitability of both methods to reconstruct spatial patterns in the vegetation. This is, however, not pursued here.

CONCLUSIONS

More than 12,000 radiocarbon years of the environmental history of a medium-sized lake basin could be reconstructed using palaeoecological methods. The results show that the character and rate of overgrowth of the lake were dominated by local factors including trophic conditions of the lake and its catchment, the plant-geographical situation, the area, shape and bathymetry of the lake, and the topography of the surroundings. Changes in vegetation composition, lake production, and sediment/water chemistry during the Late-Glacial that were conspicuously synchronous with regional vegetation and soil development are ascribed to major climatic changes during this highly unstable period. On the other hand, the development during the Holocene has been governed predominantly by the ecological dynamics inherent in the wetland ecosystem itself. For this period, we conclude that autogenic changes played a major role in the terrestrialization and in the formation of the mire ecosystem on the infilled lake.

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