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PALEOEKOLOGIE BÝVALÉHO JEZERA ŠVARCENBERK A VÝVOJ OKOLNÍ KRAJINY V POZDNÍM GLACIÁLU A HOLOCÉNU.

PALAEOECOLOGY OF A FORMER LAKE ŠVARCENBERK AND THE DEVELOPMENT OF THE SURROUNDING LANDSCAPE DURING THE LATE-GLACIAL AND THE HOLOCENE.

(Doktorská dizertační práce)
(A dissertation)

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PŘEDMLUVA

Přítomná doktorská dizertační práce je souborem dosud publikovaných, k tisku přijatých a k recenznímu řízení odeslaných článků vzniklých především jako výsledek studia jezerních sedimentů zachovaných v severní části Třeboňské pánve. Studium mimořádně detailního paleoekologického záznamu zahrnujícího navíc poměrně dlouhou časovou periodu od konce pleniglaciálu po mladší holocén si od počátku vyžádalo multidisciplinární přístup za spolupráce specialistů z více oborů. Práce na zhodnocení rozsáhlého materiálu v podobě jezerních sedimentů na lokalitě Švarcenberk proto dosud zdaleka není u konce a mnohé aktivity budou formou úzce zaměřených projektů pokračovat i v budoucnu.

Jednotlivé články tvořící předkládanou doktorskou dizertační práci jsou tematicky seřazeny v logickém sledu (viz. OBSAH): Do ÚVODU je zařazen populární text, který většinu problematiky stručně shrnuje a uvádí ji do společného kontextu. Vlastní jádro práce tvoří série odborných článků. Jejich text je ponechán v původním znění, pouze grafická úprava je pro celou práci zvolena jednotně a literární odkazy jsou citovány ve společném seznamu literatury. Nejprve je diskutován lokální vývoj jezerní pánve a jejího povodí (kapitoly I. a II.), poté následuje podrobný rozbor vývoje okolní krajiny v pozdním glaciálu a ranném holocénu (kapitoly IV. a V.) spolu s rozborem nejstarších dokladů o působení lidských populací na krajinu (kapitola VI.).

V souvislosti s výzkumem okrajových částí jezerní pánve jsme narazili na závažný problém sedimentačních hiátů, které se zpravidla vyskytují v souvislosti s přítomností dřevité slatiny s obsahem zbytků olše (*Alnus glutinosa*). Řešení této problematiky na lokalitě Švarcenberk tak podnítilo snahu o vyhledávání nového studijního materiálu, jehož zpracování by do problému vneslo více světla. Takový, z metodologického hlediska vhodnější, materiál se podařilo nalézt na lokalitě Na Bahně (okr. Hradec Králové). Výsledek tohoto studia je do předkládané dizertační práce proto rovněž zařazen (jako PŘÍLOHA), opět ve formě odborného článku.

Na samý závěr práce je umístěn soubor několika ilustračních fotografií, které se do odborných článků z úsporných důvodů nemohly dostat.

V Třeboni, 3. 2000

PODĚKOVÁNÍ

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I. ÚVOD

[Pokorný, P. (2000, in press): Osudy zaniklého jezera. 16 000 let historie v jezerních usazeninách. *Vesmír* 79/4.]

Pustá krajina zrádých bažin a mokvajících pramenišť, širokých niv líných toků, rozsáhlých, jen těžko prostupnch blat - to je obraz Třeboňska v době prehistorické. Teprve koncem středověku byly mnohé bažiny přeměněny v rybníky a mnohá blata byla odvodněna, aby sloužila člověku k užitku. Ruční těžba rašeliny, která probíhala na Třeboňsku až do poloviny 20. století, byla zdrojem paliva pro několik sklářských hutí i pro většinu místních domácností. Odumřelé zbytky různých organismů, ukryté ve vrstvách rašeliny, byly přitom dlouho na pokraji zájmu. Teprve počátkem dvacátého století si jich začali všímat někteří přírodovědci. První z nich byl Karl Rudolph, botanik německého původu, narozený v Teplicích v Čechách a působící jako profesor na Pražské německé univerzitě. Ten využíval makroskopických zbytků rostlin k rekonstrukci dávné vegetace a nálezy doplňoval také analýzou pylových zrn některých dřevin. Tak se stala třeboňská rašeliniště jednou z kolébek později tolik využívané metody pylové analýzy. Na Rudolphovu práci navázal jeho univerzitní žák Franz Firbas, pozdější autor světoznámé monografie o vývoji evropské vegetace. Také v poválečné době bylo Třeboňsko středem zájmu paleobotaniků. Tak například Marie Puchmajerová prozkoumala s pomocí pylové analýzy řadu nových ložisek a na základě svých nálezů razila teorii o původu třeboňsých rašelinišť zazemněním bývalého třetihorního jezera, teorii, která se zanedlouho ukázala být mylnou.

Počátkem šedesátých let, ještě za svých univerzitních studií, se k jedinečnému materiálu třeboňských rašelinišť vrátila palynoložka Vlasta Jankovská, která již pracovala podstatně modernějšími a přesnějšími metodami. Významná část její práce byla zaměřena na sever Třeboňské pánve, do oblasti rozsáhlého komplexu Borkovických blat a do míst výskytu drobnějších rašelinných ložisek v okolí Horusického rybníka a rybníka Švarcenberk, vzniklých na vývěrech spodních vod. Právě tato část Třeboňska je vůbec nejrozmanitější a přírodovědecky zřejmě nejcennější - na poměrně malé ploše se tu setkávají rozsáhlá prameniště, duny vátých písků, izolované žulové výchozy, meandrující řeka Lužnice a suchá temena oblých pahorků, porostlá borovými lesy. V roce 1969, při odběru materiálu z ručně kopané sondy ve výtopě rybníka Švarcenberk, narazila Vlasta Jankovská na pozůstatky jezerních usazenin, pohřbené pod několika metry rašeliny. Přítomnost zbytků řas, semen a pylových zrn vodních rostlin tuto domněnku posléze potvrdila. Objev pozůstatků zaniklého jezera neznamenal ovšem návrat k jezerní teorii M. Puchmajerové: Sedimenty se ukázaly být postglaciálního stáří a jen na samé bazi ležela tenká vrstva, datovaná do závěru poslední doby ledové - pozdního glaciálu. Přesto byl nový nález významný, protože přirozeně vzniklá jezera jsou na našem území zcela mimořádným jevem.

Studium jezerních sedimentů, u nás tolik vzácných, může přinést nenahraditelné poznatky o stavu vegetace, krajiny i klimatu v době svého vzniku. Jezerní pánev jako sběrnice shromažďuje informace o událostech ve svém okolí a uchovává je ve vrstvách usazenin jako v přírodním archivu. Dnes již známe značné množství různých způsobů jak v takových přirozených archivech číst. Některé z nich využívají nejmodernějších technických prostředků, dříve nedostupných. Nastal proto čas znovu se k jezerním sedimentům na Třeboňsku vrátit, aby mohl být plně využit jejich potenciál. Před pěti lety proto začal výzkum na lokalitě Švarcenberk znovu. První otázka přirozeně zněla: Jaký skutečný rozsah mělo zaniklé jezero? Byla to jen malá nádrž, či rozsáhlá vodní plocha s mnohametrovou hloubkou? Brzy se ukázalo, že k vyřešení otázky je zapotřebí rozsáhlého terénního průzkumu a to navíc pod hladinou rybníka, který většinu bývalé jezerní pánve zatopil. Výsledky téměř sto padesáti ručních vrtů pak odhalily jezerní pánev ledvinovitého tvaru o rozměrech 450 x 700 metrů s překvapivě prudce se zahlubujícími okraji. Jezerní sedimenty přitom dosahují maximální mocnosti přes deset metrů a jsou překryty ještě asi třemi metry rašeliny, která vznikla poté, co se původní jezero zazemnilo. Následující výzkum ukázal, že vrstvy usazenin začaly vznikat před více než 16 tisíciletími a že se skutečně jedná o mimořádný přírodní archiv, obsahující záznam vývoje přírody od vrcholné fáze posledního glaciálu téměř až po naše dny. Na základě nálezů zbytků různých vodních organismů, makroskopických i mikroskopických zbytků rostlin (hlavně pylových zrn a semen), chemického složení sedimentů a radiokarbonového datování tak můžeme sledovat nejen vznik, vývoj a zánik samotné jezerní pánve, ale i mnohé události, ke kterým došlo v okolí za dlouhá tisíciletí její existence.

Zaniklé jezero a jeho osudy.

Bývalé jezero Švarcenberk mělo v době svého vzniku plochu asi 51 ha a maximálni hloubku okolo deseti metrů. Napájely ho silné prameny artézské vody, vystupující podél tektonického zlomu. Jezero se odvodňovalo do nedaleké řeky Lužnice a jeho povodí nebylo příliš rozsáhlé - ne více než 5 km^2. Již samotný proces vzniku jezera před téměř 17 000 lety byl velmi neobvyklý. Souvisel s klimatickými podmínkami konce vrcholného glaciálu v kombinaci s příhodnými místními faktory: Maximální ochlazení posledního glaciálu bylo na našem území provázeno přítomností trvale zmrzlé půdy - permafrostu. Místy permafrost dosahoval hloubek mnoha desítek metrů. Třeboňsko v tomto směru jistě nebylo výjimkou. Představme si teď, jaké důsledky bude mít přítomnost artézské vody, tlačící-se zespodu do trvale zmrzlého jílovito-písčitého substrátu: Voda bude tuhnout a po čase vytvoří rozměrnou čočku podzemního ledu. Jak čočka narůstá, vytlačuje okolní substrát a celé těleso je na povrchu patrné jako zakulacený, do výšky čnějící pahorek. Takové útvary, nesoucí eskymácký název "pingo", v současných arktických podmínkách skutečně existují a mohou dosáhnou výšky až osmdesáti metrů. Pokud dojde k celkovému klimatickému oteplení, podzemní ledová čočka spolu s permafrostem roztaje a na místě někdejšího pinga vznikne nevelké, ale obyčejně hluboké jezero zvané "alas".

Právě takovým způsobem s největší pravděpodobností vzniklo naše jezero. Jeho hluboké chladné vody zpočátku umožnily život jen nemnoha pionýrským organismům, především drobným trsům parožnatek druhu *Chara strigosa*, rostoucím dnes výhradně ve vysokohorských jezerech a v oblastech kolem polárního kruhu. Jak se postupně oteplovalo, stoupala teplota vody i množství živin v ní rozpuštěných. Po prudkém oteplení před 13 000 lety pokrývají hladinu jezera již první stulíky (*Nuphar lutea, N. pumila*), lekníny (*Nymphaea*), rdesty (*Potamogeton natans*), pod hladinou rostou stolístky (*Myriophyllum spicatum, M. alterniflorum*) a růžkatec ponořený (*Ceratophyllum demersum*). Takové prostředí bylo schopno udržet i první populace ryb - v sedimentech nacházíme veliké množství šupin a požerákových zubů okouna (*Perca fluviatilis* - mnohdy se jedná o zbytky statných jedinců). Je zajímavé, že po dlouhou dobu tvořil okoun výhradního zástupce rybí fauny. Teprve o 4 000 let později se začínají objevovat zbytky dalších, převážně kaprovitých ryb. V této souvislosti nás napadne otázka: Jak mohla hustá populace dravého okouna přežít v jezeře zcela izolována? Odpověď můžeme hledat v některých současných arktických jezerech. Osamocené okouní populace v nich rovněž dosahují vysokých hustot a to díky neobvyklému způsobu obživy: Okouni produkují veliké množství potěru. Ten se živí přisedlými bezobratlými a hmyzem napadaným na vodní hladinu. Dospělí jedinci ovšem požírají výhradně vlastní potomstvo.

Rovnováha takového nezvyklého potravního řetězce je udržována rozdíly v chování mladých a starých jedinců, kteří jsou nejaktivnější v různou denní dobu.

Začátek doby poledové - holocénu (před cca 10 000 lety) je charakterizován dalším prudkým oteplením. To se na našem jezeře podepsalo hlubokými změnami celého ekosystému. Během pouhých dvou set let vymizely chladnomilné formy řas a vyšších rostlin a byly vystřídány druhy, vyžadujícími teploty srovnatelné s dnešními, nebo dokonce ještě mírně vyšší. Hladina jezera se pokrývá listy stulíků, leknínů a trsy kotvice plovoucí (*Trapa natans*). Pod hladinou roste hustá spleť růžkatců, stolístků a řečanek (*Najas marina, N. minor*). Tehdy se jezero začíná postupně zazemňovat: Podél břehů se zelenají trsy orobinců, za nimi vítr češe porosty rákosu. Tam, kde vodní hladina již definitivně ustoupila souši, rostou chomáče ostřic a začínají se uchycovat první semenáčky olše lepkavé. Jednotlivé vegetační zóny tak jako obruče víc a víc svírají zanikající jezero. Když před 5 500 lety mizí i poslední zbytky volné hladiny, mění se střed bývalé jezerní pánve v rašeliniště. Koberec rašeliníku spolu s dalšími rostlinami nenáročnými na živiny (blatnicí bahenní - *Scheuchzeria palustris*, vachtou trojlistou - *Menyanthes trifoliata*, nebo rosnatkou okrouhlolistou - *Drosera rotundifolia*) vytvářejí rychle vrstvu rašeliny, která jako obří poklička pokrývá usazeniny bývalého jezera a vyklenuje se do výšky. Z období kolem přelomu letopočtu pocházejí nejmladší dochované vrstvy rašeliny, zbytek byl zřejmě zničen při stavbě rybníka, nazvaného podle tehdejšího majitele panství - Švarcenberk. Jeho nízká hráz byla navršena mezi léty 1689 a 1701 zhruba v místech, kde malý potůček opouštěl bažinatou sníženinu.

Přírodní archiv.

Nejen informace o vývoji samotného jezera, ale i sled událostí v okolí je v jezerních sedimentech zaznamenán jako v knize. Studujeme-li jednotlivé vrstvy, jako bychom listovali dějinami vývoje krajiny. Pylová analýza vypovídá o historii vegetace, chemické a strukturní analýzy sedimentů o procesech eroze a vzniku půd v povodí, obsah organických látek a živin zase o celkové produkci ekosystému. Všechny tyto jevy jsou přitom přímo či nepřímo svázány s parametry klimatu. Protože stáří usazenin, zachovaných v jezerní pánvi je nezvykle vysoké a vysoká byla také rychlost jejich tvorby, je historický záznam mimořádně podrobný. Rozborem vzorků v intervalu po dvou centimetrech tak bylo dosaženo rozlišení kolem dvaceti let! Získané výsledky lze pak srovnávat s podobnými nálezy pocházejícími z několika míst západní Evropy, nebo s výsledky studia vrtů v gronském ledovci (viz. Vesmír 72, 624, 1993/11). Ze srovnání vyplývá, že území Třeboňska bylo postiženo stejnými klimatickými změnami jako území přilehlá Atlantickému oceánu. Rychlost a amplituda těchto klimatických změn přitom již delší dobu vyráží odborníkům dech. Jejich příčiny bývají obvykle spatřovány ve funkci oceanického výměníku, který pod vlivem odledňování severní polokoule katastroficky přecházel mezi "glaciálním" a "interglaciálním" způsobem fungování (viz. Vesmír 72, 368, 1993/7). Teploty na západě evropského kontinentu se měnily v rozmezí několika stupňů během pouhých několika desítek let a takových prudkých pozdnoglaciálních oscilací bývá zaznamenáno alespoň pět. Výsledky studia sedimentů zaniklého jezera Švarcenberk ukazují, že vliv takových klimatických zvratů sahal až do samého srdce střední Evropy. Ovšem až na jednu výjimku: Chladná oscilace v rámci teplé, tzv. interstadiální periody - "starší dryas", málo výrazná i v atlantické oblasti, nebyla na Třeboňsku zachycena vůbec. Rychlost a itenzita ostatních klimatických změn je jinak srovnatelná. Zásadní rozdíly jsou ale ve způsobu odpovědi živé přírody na tyto změny. První výraznější oteplení je například datováno do období před 15 000 lety. Zachyceno je v záznamu gronského ledovce a projevuje se také ústupem kotinentálního zalednění, které po sobě zanechalo rozsáhlé ústupové morény v Pomořansku. V západní Evropě se na charakteru vegetace nijak znatelně nepodepsalo - stále tam převládají otevřené stepní a tundrové formace. Na Třeboňsku je ale situace odlišná: Výše popsané oteplení má za následek první šíření lesa, i když zatím jen v podobě rozvolněných borových porostů typu řídké tajgy. Příčinou rozdílné odpovědi místní vegetace na klimatické oteplení je pravděpodobně lokální řítomnost borovice, která se po zlepšení podmínek mohla okamžitě šířit. Svou roli zřejmě sehrály také příznivé mikroklimatické podmínky vlhké bažinaté pánve.

Poté, co odezněla následující chladná perioda zvaná "nejstarší dryas", přichází nové, již opravdu výrazné oteplení, charakterizované po celé střední Evropě nástupem boro-březové tajgy. Tak je tomu i na Třeboňsku. Rozvoj zapojeného lesa má spolu se zvlhčením klimatu za následek ústup dřívějších otevřených formací trav, pelyňků (*Artemisia*), merlíkovitých rostlin (*Chenopodiaceae*), keříčkovitých vrb, trpasličích bříz (*Betula nana*), olší zelených (*Alnus viridis*), jalovců (*Juniperus*), chvojníků (*Ephedra*), rakytníků (*Hippophaë rhamnoides*) a další bohaté stepní a tundrové vegetace. Zatímco předešlé období můžeme charakterizovat převahou surového, vápnitého a solemi bohatého substrátu, začíná spolu s příchodem tajgy tvorba prvních skutečných půd. Jejich pokračující vývoj v době před 13 000 až 11 500 lety měl za následek celkovou změnu chemismu prostředí do té podoby, jakou známe z Třeboňska dnes - všude začaly převládat vyloužené, kyselé a chudé půdy. V sedimentech jezerní pánve se tato změna projevuje náhlým poklesem obsahu některých kationtů (zvláště Ca, K a Mg).

Částečý ústup lesa, návrat otevřených formací (tentokrát doprovázených zvláště hojným jalovcem) a náhlé zvýšení eroze v povodí jezera před 11 300 lety je zřetelně důsledkem nového klimatického zvratu. Zhoršení klimatu se projevuje především zvýšením kontinentality - prohloubením rozdílů mezi teplou a studenou polovinou roku. Tato oscilace, nazývaná "mladší dryas", zasáhla celou Evropu a není ani vyloučeno, že měla globální charakter. Nastupující drsné klima mělo za následek hromadné odumírání části boro-březových porostů. Rozsálé oblasti Evropy následně zasáhly požáry mrtvých stromů. Usuzujeme tak z poloh ulíků, které nacházíme na mnoha místech a které jsou shodně datovány do doby kolem 11 000 let před současností. Požáry se zřejmě nevyhnuly ani Třeboňsku, jak ukazuje výzkum známého Pískového přesypu u Vlkova, provedený v souvislosti se studiem nedalekého jezera Švarcenberk. Více než pětimetrová vrstva vátých písků pod sebou totiž pohřbila primitivní půdu s vrstvou borových uhlíků na povrchu. Uhlíková vrstva byla radiokarbonově datována do doby před 11 260 lety. Celkové ochlazení tehdy spolu s požáry způsobilo ústup lesa a obnažilo tak půdu větrné erozi. Vznik přesypu vátých písků u Vlkova spadá právě do tohoto dramatického období.

Mladší dryas končí zhruba před 10 000 lety a po pozdnoglaciální éře klimatického chaosu konečně nastupuje stabilnější perioda současného teplého období - holocénu.

Fenomén jménem Švarcenberk.

Vnik jezera, jeho vývoj a posléze i zánik, jeho význam pro život celé řady vodních a bažiných organismů, jeho vztah k okolní krajině - to je spleť mnoha jednotlivých jevů, navzájem složitě provázaných v prostoru i čase. Také tvářnost současné krajiny je existencí dávného jezera nepřímo ovlivněna. Přes svou jedinečnost, nebo právě díky ní, na sebe jezero vázalo mnoho osudů a jak uvidíme, výjimkou nebyly ani osudy člověka. Archeologické doklady z Třeboňska jsou ovšem velmi sporé a jen několik víceméně náhodných nálezů dovoluje sledovat mlhavou stopu kamsi do období mladšího paleolitu (starší doby kamené). Bylo by však s podivem, kdyby existence významné vodní plochy nepřitahovala pozornost člověka, a to zvláště v době, kdy rybolov spolu s lovem vodních ptáků tvořil důležitou součást obživy malých loveckých tlup, porůznu tánoucích zalesněnou střední Evropou. Tuto skutečnost si uvědomovala již sama objevitelka zaniklého jezera Vlasta Jankovská, která na základě svého nálezu iniciovala první archeologický průzkum. Ten byl ovšem neúspěšný, zřejmě díky nedostatečným informacím o plošném rosahu jezerní páve. Během nejnovějších výzkumů se však v sedimentech časně holocénního stáří začaly objevovat náznaky přítomnosti člověka, a to v podobě pylových zrn rostlin, idikujících otevřené plochy, a ve formě nápadně častého výskytu mikroskopických uhlíků, pocházejících z lesních požárů či z blízkých táborových ohňů. Znovu vyvstala potřeba důkladného archeologického průzkumu. V červenci 1998 proto navštívil břehy zaniklého jezera anglický archeolog českého původu Marek Zvelebil. Jeden z předních odborníků na období mezolitu tehdy místo usilovného rytí v zemi zamyšleně postával před naši terénní základnou a drahnou dobu s ním nebyla řeč. Poté se probudil z hlubokého zadumání, ukázal na malý pahorek v poloze mezi obcí Ponědrážka a břehem bývalého jezera a prohlásil: "Myslím, že by se mělo hledat tam na tom poli." Při nejbližší příležitosti, po podzimní orbě, jsem se na označený pahorek vypravil. Jaké bylo překvapení, když se po krátkém hledání objevilo opracované pazourkové jádro, několik drobných úštěpů a v zápětí také dvě drasadla, na první pohled mezolitického stáří! Artefakty jsou vyrobeny z baltské suroviny a z materiálu pocházejícího z pravěkých dolů v dnešním Bavorsku. Nejnovější pyloanalytické výsledky v kombinaci se studiem uhlíků a s radiokarbonovým datováním ukazují, že mezolitický člověk navštěvoval břehy jezera zhruba v době mezi 8 000 a 4 500 př. Kr. První náznaky lidské přítomnosti přitom nápadně dobře souhlasí s nejstarším prokázaným výskytem kotvice plovoucí. Podle analogií s některými severoevropskými archeologickými nalezišti se můžeme domnívat, že také zde sloužily škrobnaté oříšky kotvice jako významný zdroj potravy. V dané souvislosti není proto vyloučeno, že mezolitický člověk tuto dnes vzácnou vodní rostlinu záměrně šířil a pěstoval.

Dlouhodobá vazba člověka k zaniklému jezeru je dalším důvodem, proč můžeme tento mimořádný přírodní úkaz povýšit na úroveň skutečného ekologického fenoménu a to i přesto, že se nám z něj dochovaly již jen zbytky v podobě usazenin.

Příloha : Původní jezera v Čechách a na Moravě.

Naprostá většina území Čech a Moravy leží v oblasti, která nebyla během čtvrtohor nikdy přímo postižena zaledněním, v tzv. extraglaciální, nebo přesněji periglaciální zóně. Pouze temena našich nejvyšších pohraničních pohoří byla v minulosti opakovaně zaledněna, což se projevilo na jejich morfologii. Součástí někdejších ledovcových karů jsou občas menší horská jezera - plesa. Některá jsou dosud živá, jiná již téměř podlehla zazemnění (např. jezero Laka na Šumavě, které zůstalo zachováno jen díky umělé hrázi). Výjimečné je rovněž ústí Moravské brány - v minulosti k nám tudy několikrát nahlédl severský ledovec a zanechal u samých hranic s Polskem stopy v podobě morén a usazenin někdejšího jezera. Na nikdy nezaledněné většině našeho území jsou původní jezera velikou vzácností, odhlédneme-li od malých nádrží v nivách řek s obvykle jen krátkým trváním - slepých ramen nebo jezírek vytvořených činností bobrů (savců u nás kdysi běžných, během středověku však zcela vyhubených). Ostatní, ve většině případů rovněž drobnější jezera, vznikala buď v krasových oblastech nadržením vody před travertinovými kaskádami (nevětší tohoto typu je zřejmě tzv. Měňanské jezero v Českém krasu, objevené V. Ložkem a podrobně prozkoumané J. Kovandou), nebo působením vátých písků, které v pozdním glaciálu přehradily některý vodní tok či ústí nějakého prameniště (takového původu jsou některé polabské černavy či bývalé jezero Vracov na jižní Moravě, popsané K. a E. Rybníčkovými). Kromě jezera Švarcenberk bylo na Třeboňsku objeveno (opět V. Jankovskou) ještě jedno menší, rovněž zaniklé jezero, tentokrát při samých hranicích s Rakouskem na místě zvaném Velanská Cesta. O jeho původu však zatím mnoho nevíme. Totéž platí také o dalším bývalém jezeře na místě dnešní rezervace Soos u Františkových Lázní.

Nesporně největší původní jezero na našem území bylo tzv. Komořanské jezero v Mostecké pánvi. Vzniklo zřejmě vlivem tektonických pohybů v součinosti s usazováním vátých písků, které přehradily nevelký tok řeky Bíliny. Nebýt dobývání hnědého uhlí, dochovaly by se části rozsáhlé vodní nádrže o původní ploše 1 200 ha až do našich dnů. Důl Československé armády však nedávno zničil i poslední zbytky jezerních sedimentů. Jejich nejcennější partie byly odtěženy ještě dávno předtím, než mohly být spolehlivě odebrány a archivovány. Byl tak natrvalo zničen jeden z nejvýznamnějších přírodních archivů ve střední Evropě, který mohl být pouze z části využit paleobotaniky a archeology (Rudolph, Losert, Jankovská, Vencl, Neustupný). Komořanské jezero na sebe po celou dobu své existence vázalo přítomnost člověka. Archeologické nálezy ležely mnohdy přímo v jezerních usazeninách. Až do minulého století tvořily zbytky jezera s rozsáhlými plochami rákosin na jeho zazemněných okrajích krajinnou dominantu Podkrušnohoří a měly zřejmě nemalý vliv na klima Mostecké pánve i přilehlých Krušných hor.

Tímto článkem jsem se jednoduchou formou pokusil shrnout některé dosavadní poznatky o zaniklém jezeře Švarcenberk, druhé největší dosud zjištěné přirozené vodní nádrži u nás. Věřím, že ještě další zásadní překvapení čekají na své objevitele - odborníky z mnoha různých oborů. Práce na zhodnocení jedinečného přírodního archivu v podobě jezerních sedimentů není totiž zdaleka u konce.

Chtěl bych poděkovat všem svým kolegům a přátelům, kteří mi během práce pomáhali. Většiny výsledků bylo dosaženo díky jim a díky podpoře Grantové agentury České Republiky (skrze grant č. 206/98/0727).

II. LONG-TERM VEGETATION DYNAMICS AND INFILLING PROCESS OF A FORMER LAKE ŠVARCENBERK.

[Pokorný, P., Jankovská, V. (submitted): Long-term vegetation dynamics and infilling process of a former lake (Švarcenberk, Czech Republic). *Folia Geobotanica et Phytotaxonomica*.]

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Keywords: Climatic changes, Subfossil algae, Hydrosere, Lake terrestrialization, Macrofossils, Palaeoecology, Palaeolimnology, Pollen analysis, Vegetation ecology

Abstract: Natural lakes are rare phenomena within the extraglacial areas of Central Europe. Moreover, almost all of them have been completely terrestrialized during the course of the Holocene. This paper deals with one such former lake, located in the southern Czech Republic. Its extensive lacustrine and peat deposits were subjected to a multidisciplinary study that resulted in high-resolution data about climatic, geomorphic, soil and regional vegetation development over the last 16 thousand 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, towards an oligotrophic mire that started to dome over the now terrestrialized lake. At every individual development stage, specific processes characterized ecosystem function and composition: during the Late-Glacial period of rapid climatic changes, external forces were inducing the major stresses; while during the Holocene, autogenic changes inherent in the wetland ecosystem itself played the most important role.

INTRODUCTION

The recent discovery of thick buried lake sediments in the Třeboň Basin, South Bohemia, presents an exceptional opportunity to study a 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 Švarcenberk yielded well-founded palaeoclimatic and palaeovegetational data that can be compared with similar results from other parts of Europe. The profile under study is a unique example in the Czech Republic with an extensive and well-stratified Late-Glacial record. High sediment-accumulation rates permitted the detection of brief Late-Glacial climatic oscillations, so that comparison can bee made with numerous results from western and northwestern Europe (POKORNÝ 2000, *in press*).

The goal of the present study is to describe local vegetation and environmental changes against the background of abiotic settings in order to reveal their possible driving forces. Thanks to the absence of significant human influences, either direct or indirect, and to the absence of significant water level fluctuations during the period involved, the Švarcenberk basin represents an ideal site for the study of natural changes in wetland communities. These changes can be the result of climatic stresses or can be caused by autogenic factors inherent in the nature of lake basin ontogeny. Autogenic processes finally leading to peat-bog formation were first described by WEBER (1908). Since that time, the seral development of wetland plant communities in yet-existing 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 interprete lake basin history both in temporal and in spatial scales.

THE 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 700 km^2 and a relief which varies by no more than 20 - 40 m). 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 content of clay 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 phosphate medium (HUSÁK & HEJNÝ 1978). Most soils are leached and show a tendency towards podzolization. The soil reaction is mostly highly acidic (pH up to 3.3). Various types of podzols and sandy or peaty gleys prevail.

The present climate is suboceanic and is determined by prevailing westerly air masses. The region is somewhat sheltered by the Bohemian Forest highlands. Annual mean precipitation is 622 mm (January being the driest month), annual mean temperature is 7.4 °C.

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. This can be considered as an advantage of the site under study, that entirely no human impact to the natural development of the lake/bog ecosystem can be expected up until 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 his results, the basal age of some investigated deposits was later established to be of „Kiefern-Zeit" (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 palynological investigations. In the early 1960's, the second author started her palaeoecological investigations of the Třeboň Basin, using modern approaches. More recently, the first author continued her work in greater detail, giving it more multidisciplinary character.

The former Lake Švarcenberk is situated 4 km south of the town of Veselí nad Lužnicí (49° 9'N, 14° 42'E) at 412 m. a.s.l. Limnic sediments are overlain by peat, which formed after the final 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 has been constructed directly on the site, and its waters almost completely flood over the peat and underlying lake sediments. The only presumed remnant of original vegetation cover are small patches of tall sedge and *Sphagnum* communities (*Eriophorion gracilis* and *Rhynchosporion albae*) in the western part of the locality.

As for local hydrology, the presence of several strong artesian springs is characteristic. The underground water ascends along a deep tectonic fault and is rich in iron oxides. The former lake was presumably supplied almost exclusively by this artesian water. The activity of underground water sources was apparently independent of general climatic fluctuations in the past. As a result, the lake water level had remained almost constant over the millennia. The lake had drained into the nearby Lužnice River.

The existence of the former Lake Švarcenberk was noted for the first time by the second author in the early 70s. In her study, which focused on the vegetation development of Třeboň Basin (JANKOVSKÁ 1980), she presented a pollen diagram and the results of a macrofossil analysis obtained from a profile (designated JC-7-B) sampled from an open pit. Her profile comprised about 1.5 m of lake sediments, and she correctly assumed that she dealt with the littoral facies of a larger lake. Unfortunately, no stratigraphic data were obtained at that time. The present study, undertaken mostly by the first author in the last four years, fully confirms Jankovská's original assumption.

METHODS

Field methods, sediment description, and subsampling

During the pilot study, the extension and stratigraphy of the former lake basin was studied by coring in a 100 m x 100 m grid (sampling distances were reduced along the shores). For subaquatic coring a boat was used. Two right-angled transects across the basin were chosen as reference stratigraphic sections (shown in Fig. 2). These transects cross at the centre of the basin, where the 'main profile' is situated. The distances in metres and the geographical position (N, S, E, W) in relation to this zero point is given by the core labels. The cores were levelled according to fishpond water level. The coring was performed with a Russian-type corer (JOWSEY 1966) 5 cm in diameter.

The core in the centre of the former lake (the 'main profile' in Fig.2) was selected as the standard profile, as it will most probably show the longest and most continuous record without hiatuses. This 'main profile' actually consists of seven separate parallel cores taken close together in order to obtain enough material for all kind of analyses. The coring was again performed by the Russian-type corer 5 cm in diameter. This type of device permits complete recovery of the section penetrated. All cores comprising the 'main profile' were correlated according to their visual lithostratigraphy. This correlation only confirmed the satisfactory accuracy of parallel sampling.

The first littoral sampling point, JC-7-B, was investigated by Vlasta Jankovská in the early 70's. The results of pollen and macrofossil analyses are described in her original publication (JANKOVSKÁ 1980). Primary data from this publication has been extracted and remastered to the form of the new pollen and macrofossil diagrams. Unfortunately, the exact location of the original sampling point was not recorded during fieldwork, only the position beeing somewhere in the SW margin of the former lake had been noted. This is why a detailed stratigraphic investigation in the SW part of the basin was undertaken in connection with the present study. It revealed a site with an almost identical stratigraphy as that of the original profile JC-7-B. In this manner, is assumed that the location of the original sampling site (see Fig. 2) has been detected with satisfactory accuracy.

The second littoral sampling point, S500 (see Fig. 2), was also opened by way of a hand-made pit. Only a selected part of the profile, the limno-thelmatic contact between 160 and 240 cm, has been subjected to further analyses. This part of the sediment column is the most important from the palaeoecological point of view, particularly for comparison with other profiles, as it comprises the transitional period with the complete terrestrialization hydrosere record.

Sediment description follows the system of 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 analyses

The samples used for pollen and other microfossils analyses were prepared by modified acetolysis method. As the Late-Glacial sediments had a more or less mineral character, the samples were pre-treated with concentrated (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) mixture. At least 1500 pollen grains were counted in each sample, except for only 500 - 700 grains in some Late-Glacial samples that were 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 ALPADABA (*Alpine Palynological Data-Base*, housed at the Geobotanical Institute, Bern).

Algae and other microfossils were identified with the help of the publications of VAN GEEL *et al.* (1981, 1983, 1989), JANKOVSKÁ (1983), JANKOVSKÁ & KOMÁREK (1982), and after personal consultations with Jiří Komárek.

The selection of types included in the pollen sum is always an important stage in the interpretation of palynological results. In this case, percentage values were calculated on the basis of the AP+NAP pollen sum, excluding only submerged and floating-leaf aquatics but including monolete and *Equisetum* spores (in many plant communities, these taxa usually have an ecological role equivalent to that of higher plants). Concealed, corroded, degraded, and well preserved but indeterminable pollen grains were put together and labeled „varia" in the pollen diagram. The pollen diagram for the JC-7-B sampling point was prepared on the basis of the data presented in the original publication of 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 both presence and abundance of individual taxa. A more formalized approach to delimit the local pollen assemblage zones (PAZ) was also applied on the basis of three different constrained classification procedures implemented in the computer program ZONE (LOTTER & JUGGINS 1991). Consistency among results from these three different zonation procedures provided the basis for confirmation and further specification of visually delimited local PAZ.

Core correlation

Correlation of the cores in combination with the results of ^{14}C analyses allowed the establishment of a relative as well as absolute temporal frame for individual local events.

Correlation between individual profiles across the basin was first achieved by visual stratigraphic description. For the selected cores discussed in the present study, this correlation was further confirmed and improved on the basis of pollen-analytical results. General trends in regional pollen types were taken into account for this purpose. Corresponding levels were given the same labels (derived from local pollen zones of the 'main profile') in pollen and macrofossil diagrams to facilitate comparison between individual data-sets. In one remarkable case, pollen-analytical correlation was confirmed by the results of radiocarbon measurements as two samples from two different cores (the 'main profile' and S500 profile) gave almost identical ages (Tab. 1).

Macrofossil analyses

After subsampling for other analyses, the remaining material was used for macrofossil analyses. Contiguous samples 10 cm long were cut, and the volume of each was determined (it ranged around 250 ml in all cases). Macrofossils were extracted by heating each sample for 5 minutes in 5% potassium hydroxide (KOH) solution and sieved with running water. Sieves with mesh sizes of 200 µm, 300 µm and 700 µm were used. The residues were examined under a dissecting stereomicroscope. The absolute number of each kind of macrofossil was recalculated to a standard volume of 500 cm^3 fresh sediment. For determination of the seeds/fruits, a reference collection and an atlas of macrofossils (KAC *et al.* 1965) were used. For the littoral sampling point, JC-7-B, studied by JANKOVSKÁ (1980), a new macrofossil diagram was prepared using the data presented in the original publication.

Sediment chemistry and ^{14}C analyses.

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 reconstructions (ENGSTROM & WRIGHT 1984, DEARING 1991). For sediment chemistry measurements and absolute dating, the deepest profile in the centre of the basin ('main profile') was used.

Total carbon and nitrogen content was determined by combustion at 950 °C in pure oxygen, with subsequent conductivity detection of C and N oxides (using a Heraeus CHN-Rapid Analyser). Carbonate content was measured by sodium hydroxide titration to neutral pH after dissolution of 0.5 g sample in 0.5 M hydrochloric acid and subsequent boiling for 20 minutes (after HAMMARLUND & BUCHARDT 1996). Total organic carbon content was calculated from the difference between total carbon and carbonate carbon.

The elements 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 content was determined in the same laboratory after extraction of each sediment sample in Olsen's reagent (OLSEN *et al.* 1954). The resulting phosphate-phosphorus was than determined using the method based on the formation of the 'molybdenum blue' complex in ammonium molybdate-sulphuric acid reagent after reduction in ascorbic acid. Resulting colour intensity was measured spectrophotometricaly using a wavelength of 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 measured after two minutes by portable electronic pH-meter.

Radiocarbon dates used in the present study are all AMS (Atomic Mass Spectrometry) dates determined from bulk sediment samples and individual plant macrofossils (for sample description see Tab. 1). The disadvantage for the Late-Glacial sequence under study is the absence of enough terrestrial plant macrofossils for dating purposes. The dates from gyttjas, clayey lake sediments, and aquatic plant macroremains are known to give ages which usually exceed those obtained from terrestrial macrofossils (TÖRNQVIST *et al.* 1992). This effect is often ascribed to hardwater error. In the present study, hardwater error is expected to be relatively small, as the sediments contain negligible amounts of carbonates. Radiocarbon analyses were 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 5568 years. For the purposes of simplicity and comparability, dates are expressed in uncalibrated ^{14}C years before present (BP) unless otherwise stated.

RESULTS AND DISCUSSION

Origin of the lake

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

The striking feature of the lake basin morphology is its kidney-shaped form, surprising depth and declivity (the presence of unusually steep slopes), and the relatively great age of its infilling. Unfortunately, no radiocarbon date exists for the basal sediments, but their age is estimated to be around 16,000 BP on the basis of the pollen-analytical results. Considering these finds, 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 on the site, and its location close to a river, are factors known to be favorable for 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, although they are relatively large in diameter (WASHBURN 1980). These structures do not form a distinct rampart after they collapse. What is more surprising in the case of the former Lake Švarcenberk is the unusually large size of its depression. Considering this fact and the observation of 'ridges' (Fig. 2b) 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 of the Late-Glacial

In the littoral parts of the former lake basin, only a thin layer of Late-Glacial sediments is present, completely lacking deposits older than the Younger Dryas. This can be explained by an intensive reworking of 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 an extensive record of the Late-Glacial period: as much as the lowermost 5 metres of sediments formed during this period of rapid climatic changes.

The Late-Glacial pollen stratigraphy of the 'main profile' has been subdivided into eight local pollen assemblage zones (PAZ). Because of problems of terminology (e.g. AMMANN & LOTTER 1989, WALKER 1995), we have decided to subdivide the diagram in this way rather than into Firbas pollen zones, as is traditionally done in central Europe. The absence of analogous results over a wider region discourage the use of this regional pollen zonation. The local PAZ are compared with European climatostratigraphical units according to MAAGERUD *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. Below this section, the response of the aquatic ecosystem to these climatic changes is briefly discussed.

Late Pleniglacial (zones S1 and S2)

Shortly after the formation of the lake, fossil evidence suggests the development of a pioneer lake-bottom vegetation: pollen from submerged water plants is absent, while Charophyta oospores (cf. *Chara strigosa*, a pioneer species with subarctic modern distribution) are found in large quantities in the sediment. 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 (restricted probably to the shores), that it allowed the development of a carpet of light-demanding charophytes on the bottom. This initial stage was soon succeeded (in the transition to the S2 zone) by the development of submerged aquatic vegetation (*Potamogeton, Myriophyllum, Ranunculus* subgen. *Batrachium*), which probably outcompeted the charophytes on the lake bottom. Maximum depth of the lake was about 9.5 m during this period.

High values of sedimentary Mg, K, and Ca during the entire pre-Bôlling (Late Pleniglacial) period may be explained as beeing derived from eroding, unstable soils. N, P and organic C content of the sediments is very low (see Fig.12). The low nutrient status of the lake together with its low productivity must have been primarily caused by a low energy input into the ecosystem. The silty FeS-coloured sediments that had formed in the centre of the basin suggest anoxic conditions, as iron-sulfide deposition usually occurs under a prolonged or permanent state of stratification within a lake (ENGSTROM & WRIGHT 1984).

Planctic algal communities growing in the lake were characterized by the presence of *Pediastrum* taxa that are characteristic of oligotrophic to dystrophic, cold and clear waters (KOMÁREK & JANKOVSKÁ 2000, *in press*): *Pediastrum integrum* and *P. boryanum* var. *longicorne*. Among other *Pediastrum* taxa, *P. orientale* is the most interesting. This species was first described thanks to finds of subfossil cenobia in the sediments of Lake Švarcenberk (JANKOVSKÁ & KOMÁREK 1995). According to both recent and subfossil records of this conspicuous species, *P. orientale* also prefers clear and cool waters (KOMÁREK & JANKOVSKÁ 2000, *in press*). Probably due to the low nutrient status of the lake water, *Scenedesmus sp.* and *Tetraedron minimum* are found in low quantities in the sediment, or they are even completely absent.

Late-Glacial Interstadial (zone S3)

Marked climatic amelioration is characteristic for the onset of the Late-Glacial Interstadial. Climatic warming resulted in significantly increased organic production in the lake basin, as reflected in the sharp transition from minerogenic to organic sedimentation - see increased organic carbon, nitrogen and phosphorus content of the sediment (Fig. 12). In the aquatic environment, submerged macrophytes - *Potamogeton, Myriophyllum, Ranunculus* subgen. *Batrachium* - responded immediately to climatic warming by their expansion. *Ceratophyllum demersum* invaded the lake for the first time. It became the dominant submerged aquatic during the second half of the Interstadial (S3b subzone, i.e. Allerôd chronozone), when also *Nuphar* (probably *N. lutea* according to isolated macrofossil find) expanded in the shallower parts of the lake. The occurrence of *Ceratophyllum demersum* and *Nuphar lutea* in the lake, and the expansion of *Typha latifolia* and *Filipendula* in the littoral and longshore zones, is the result of minimum July temperatures having risen to a value 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 an unambitious fish genus that can survive even in subarctic lakes. The fry are produced in large quantities and feed on planktic or benthic organisms. Adults can feed mostly on their own young and reach high population densities. Such an interesting cannibalistic food chain has been described from several contemporary Siberian lakes (HOLČÍK 1977, KARASEV 1987) and is assumed also for Lake Švarcenberk during the period of the Late-Glacial Interstadial. Maximum depth of the lake was about 7.5 m during this period.

Reforestation of the surrounding landscape by birch and pine resulted in a process of initial pedogenesis. Soil development under forested conditions led to a decrease in erosion rates 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 maximum extent (see the decline in Ca down to the values comparable with those of the Holocene - Fig. 12).

Thanks to the changes in the nutrient status of the lake, the composition of algal planctic 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 between algae in planctic communities may also explain why the ecologically rather indifferent *Pediastrum* species - *P. borynum* var. *boryanum* and *P. borynum* var. *cornutum* had declined (KOMÁREK & JANKOVSKÁ 2000, *in press*).

Younger Dryas (zone S4)

Vegetation change reflecting temporal climatic deterioration is recorded in the lake: *Ceratophyllum* spine values decrease, and Nympheaceae trichoblasts and *Nuphar* pollen are even completely lacking in favor of the massive occurrence of *Myriophyllum verticillatum* and *Ranunculus* subgen. *Batrachium* (both recorded also as macrofossils). The presence of *Typha latifolia* pollen in the entire zone can be considered as circumstantial evidence for minimum July temperatures of at least 12 °C (IVERSEN 1954, AMMANN 1989), i.e. at the same range as those inferred for the preceding Interstadial zone. This might suggest that climatic deterioration was an increase in continentality rather than a decrease in summer temperatures.

The sedimentation character in the lake basin changes to beeing more minerogenic (with significantly lower organic carbon, N and P content) again. A slight increase in sedimentary erosion indicators (Mg, K) is observed as well. Maximum depth of the lake was about 5.5 m during this period. The change in water chemistry is again reflected in the algal communities, where *Pedistrum* green algae develop in higher quantities again. Among them, *Pediastrum integrum* and *P. boryanum* var. *longicorne*, the taxa that are characteristic of oligotrophic, cold and clear waters (KOMÁREK & JANKOVSKÁ 2000, *in press*), reached a dominant position that was never achieved later in the Holocene.

Start of the Holocene (zone S5)

The rapid temperature rise during the very beginning of the Holocene is indicated in the lake environment by the new expansion of *Ceratophyllum demersum* and *Nuphar*. The rapid change to warmer climatic conditions is also evidenced by the massive occurrence of macroscopic colonies of the thermophillous blue-green alga *Gloeotrichia pisum* (VAN GEEL *et al.* 1989). The first occurrence of *Najas marina* and *Trapa natans* macrofossils is dated very early to the Holocene - to about 9,800 BP (calculated by linear extrapolation between the two adjacent ^{14}C dates). *Najas minor* is another aquatic species, whose macrofossils were found in the sediments. This species is usually found together with *Najas marina*, but its subfossil finds are much less common in Europe (BACKMAN 1951). *Najas marina* suggests a mean July 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 circumstancial evidence suggests that present-day temperature values were reached as early as about 9,800 BP, some few hundred years after the end of theYounger Dryas cold episode. This evidence is in accord with the results of δ^{18}O measurements of the Greenland ice core GISP2 (STUIVER *et al.* 1995; see Fig.11). It is not out of the question that the rapid geographical spreading of certain aquatic macrophytes (namely *Trapa natans*) in the Early Holocene had been 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). And, indeed, archaeological evidence for Mesolithic settlement was found near the shores of the former Lake Švarcenberk and palaeoecological evidence (pollen and charcoal) dates human occupation on the site from the very beginning of the Holocene (synchronously with the first *Trapa natans* occurrence on the lake).

Organic sediment (algal gyttja), rich in macrofossils, started to accumulate in the basin again. Maximum depth of the lake was about 4 m at the beginning of the Holocene. Sedimentary phosphorus content fluctuates but is generally relatively low during the Early Holocene. The exact explanation of this phenomenon is still not possible without more data beeing available (further study of phosphorus forms is necessary).

Warm, shallow, and nutrient-rich water allowed the development of *Pediastrum simplex* var. *simplex*, the green algal species that seems to be commonly distributed in naturally eutrophic lakes. Abundant subfossil finds of this species usually indicates climatically favourable periods that conditioned the development of lake biotopes with naturally eutrophicated waters (BOTTEMA 1974, KOMÁREK & JANKOVSKÁ 2000, *in press*). Similarly, in this case, *P. simplex* var. *simplex* behaves as a typically 'thermophilic species' that invaded the lake after the onset of the Holocene climatic optimum. On the other hand, most of the *Pediastrum* types 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 - rather it is as a consequence of the massive development of submerged macrophytes in the lake. This is in accord with the interpretation of KOMÁREK & JANKOVSKÁ (2000, *in press*).

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, based on the study of pollen and macrofossils in three inter-correlated cores (the 'main profile', JC-7-B and S500; see Fig. 2a) that are radiocarbon-dated at some levels. 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 to the ecosystem was apparently so negligible, that we may assume the vegetation changes to be mainly due to autogenic forces connected with the sole process of lake basin ontogeny. This assumption is further supported by the results of sediment chemical analyses. For the purpose of clarity and simplicity, the results are presented in the form of five synoptic tables (Tab. 2 - Tab. 6) and only the main features of the process are discussed in the text below.

The final stage of terrestrialization of the lake lasted from about 8,500 BP to 5,500 BP, i.e., about 3,000 years in total. During this process, individual parts of the basin crossed the ecological boundary (hydrosere) from aquatic to semiterrestrial environment, followed by characteristic vegetation succession (for the evidence, see Fig. 6 - Fig. 11; for the interpretation, see Tab. 2 - Tab. 6). This succession can be characterized as a typical example of an eutrophic hydrosere as described by LANG (1994) and ELLENBERG (1996). For the transitional stage, shallow water pools with dense aquatic vegetation dominated by *Trapa natans, Potamogeton natans* and charophytes (mainly *Najas flexilis*) are characteristic. *Trapa natans* remains are almost completely absent in the littoral core JC-7-B, only a single pollen grain was recorded (JANKOVSKÁ 1980). This is most likely due to the early terrestrialization of this part of the basin, which occurred 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'. Shortly before this event, during the stage characterized by the development of floating-leaf aquatics, *Pediastrum duplex* var. *rugulosum* developed. This is in agreement with the opinion of KOMÁREK & JANKOVSKÁ (2000, *in press*), who noted the same ecological attributes in the case of this particular species.

After the final terestrialisation of the lake, the accumulation of peat began. Individual parts of the basin developed successively into a eutrophic *Carex* fen (dominated locally by *Carex pseudocyperus, C. rostrata* or *C. vesicaria*). These communities were soon succeeded by alder carr stands with some spruce and birch in the littoral facies, while the centre of the basin developed into an oligotrophic *Sphagnum* peat-bog as the peat surface started rising over the surrounding terrain. This part of the basin remained isolated from the direct influence of runoff from the former lake catchment and from the direct influence of the underground water table. A spatial vegetation gradient has developed from the edges to the centre of the former lake basin, reflecting the existence of a sharp gradient in nutrient availability. The process of isolation of the central part of the mire from external influences is well-reflected in the chemical record of the 'main profile': nutrient status (N and especially P content) of the *Sphagnum* peat is very low and C/N ratio sharply increased, if compared with underlying lake sediments. The pH value of the sediment is low (pH 5), as the invasion of *Sphagnum* mosses brought about an active acidification of the substratum (TALLIS 1983). *Menyanthes trifoliata, Potentilla palustris, Scheuchtzeria palustris* and *Andromeda polyfolia* grew amid the *Sphagnum* carpet. In small pools filling the hollows of the bog surface, *Mougeotia* filamentous algae formed a surface growth.

During the next ca. 1,000 years, oligotrophic bog communities expanded from the centre of the mire towards its periphery. At about 4,500 BP, the sedimentary record terminates in the middle of the basin, and in the littoral parts it is only fragmented, probably comprising some hiatuses. The further development of the mire can not be followed from that time onwards, but the mire's continued existence until the 13th century, when the area was first colonized, can be assumed. Peat-cutting and finally fishpond construction terminated the natural development of the former lake basin.

The uppermost sediment sample of the 'main profile' represents subrecent fishpond bottom sediment ('sapropel'). Its chemical composition is directly influenced by the management of the artificial water body - liming, fertilization, intensive fish production, etc.. Solutions rich in cations and phosphates further penetrated from the surface downwards through the sediment column. The rise in P and Ca content (together with pH rise) in the uppermost peat column is most likely caused by this effect. Deep penetration is observed especially in calcium carbonate (artificially supplied into the fishpond in large quantities), which enrich the peat to a depth of about a metre and a half.

For details of the vegetation succession during individual stages of the lake basin terrestrialization, see Tables 2 - 6. Comparison of the results of pollen and macrofossil analyses of the same profile, and between different profiles, also allows some methodological conclusions about the ability of both methods to reveal patterns in the spatial vegetation mosaic. Nevertheless, this comparison is not the subject of the present paper and the reader is referred to Figs. 4 - 10, where the original data can be consulted.

CONCLUSIONS

More than 12,000 years of the environmental history of a medium-sized lake basin could be traced by means of palaeoecological methods. From the results of this study, it is obvious that the character and rate of overgrowth of the lake was strongly governed by local historical factors: trophic conditions of the lake itself and its catchment area, the plant-geographical situation, the area and shape of the lake, and the topography of its bottom and surroundings. Nevertheless, some changes in vegetation composition, lake production, and sediment/water chemistry were conspicuously synchronous with regional vegetation and soil development. These changes can be ascribed to major climatic changes, namely during the highly unstable period of the Late-Glacial. On the other hand, development during the Holocene has been governed predominantly by the ecological dynamics inherent in the wetland ecosystem itself. For this period of the lake basin development, we can conclude that autogenic changes played a major role in the final terrestrialization process described, as well as in the formation of a transient mire ecosystem over an infilled lake.

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TABLES AND FIGURES

Tab. 1: Radiocarbon dates from Švarcenberk littoral (S500) and central ('main profile') cores.

Lab. No.	*Core label/depth*	*Method*	*Type of material*	*Measured ^{14}C age*
LuA-4297	S500: 200 cm	AMS	*Trapa natans* nut	6 340 ± 110 BP
LuA-4588	„main p.“: 150- 153 cm	AMS	Woody stem fragment	4650 ± 100 BP
LuA-4589	„main p.“: 324-327 cm	AMS	*Trapa natans* nut	6 350 ± 100 BP
LuA-4590	„main p.“: 390-393 cm	AMS	Woody stem fragment	9 640 ± 115 BP
LuA-4591	„main p.“: 520-523 cm	AMS	Bulk gyttja sample	10 780 ± 115 BP
LuA-4738	„main p.“: 680-683 cm	AMS	Alkali soluble fraction from gyttja	11 750 ± 120 BP

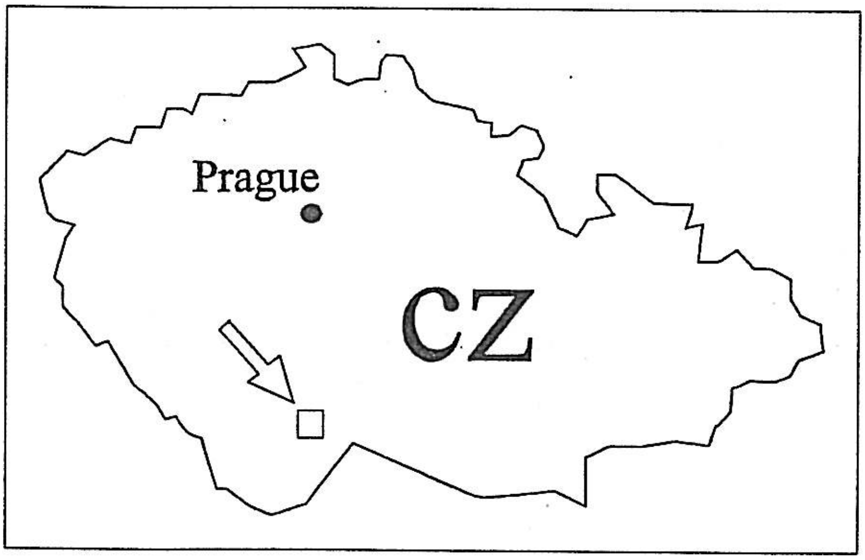


Fig.1: Location of the study area within the Czech Republic.

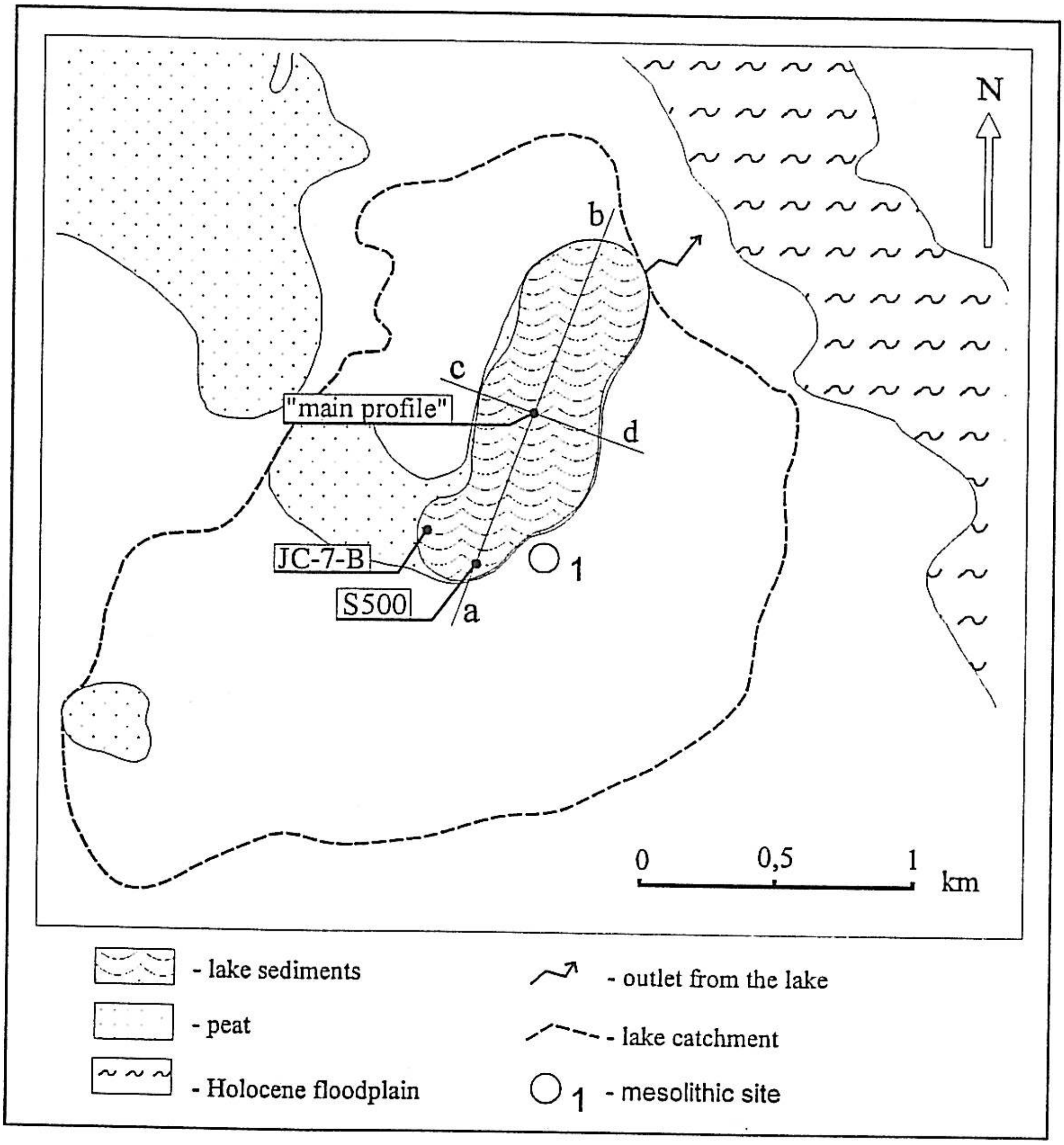


Fig.2: Quaternary geology and topography of the site. a,b,c,d - two cross sections used for stratigraphical investigation. Location of selected cores discussed in the text is dispayed.

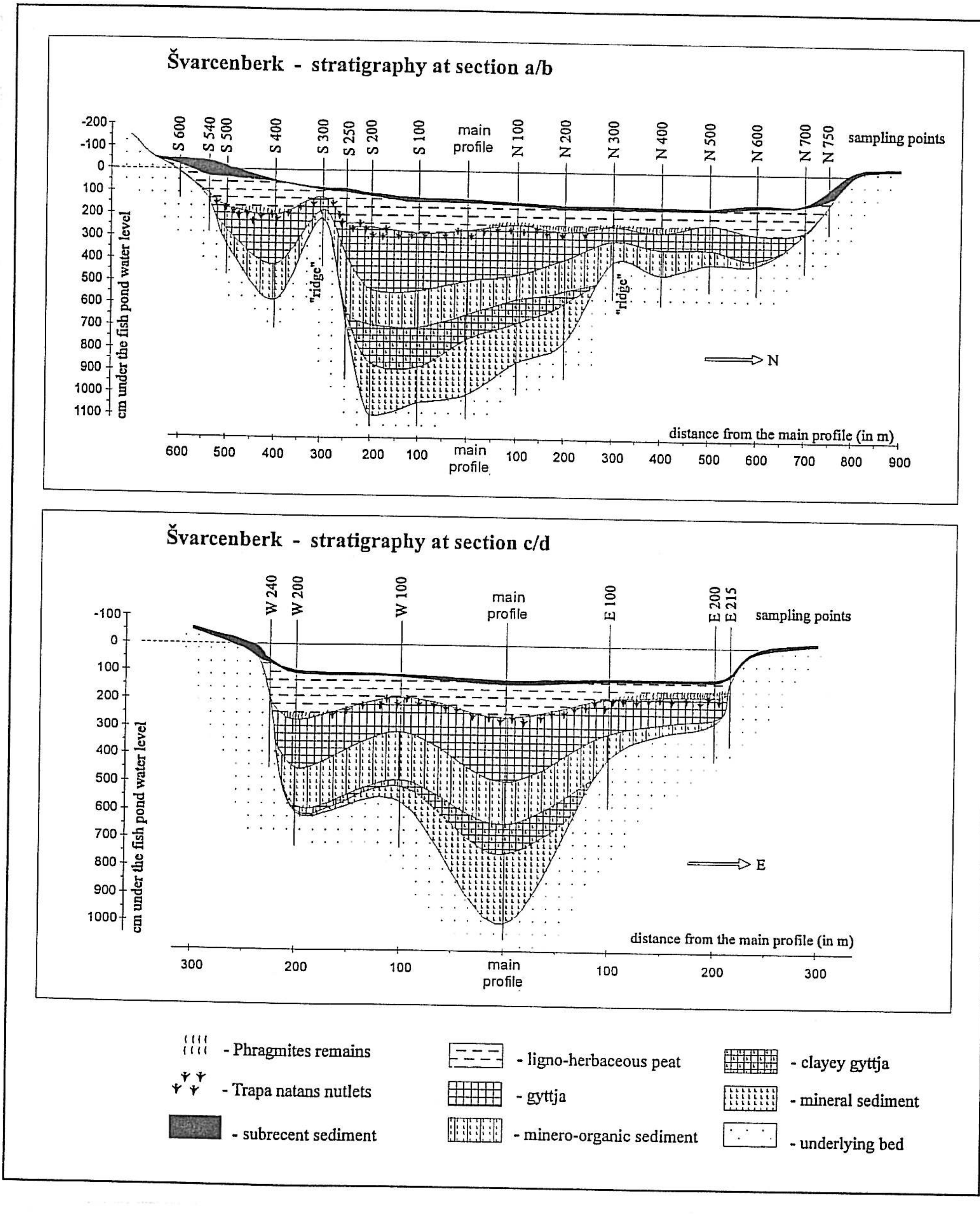


Fig. 3: Two selected orthogonal stratigraphic cross-sections through the Švarcenberk Lake basin.

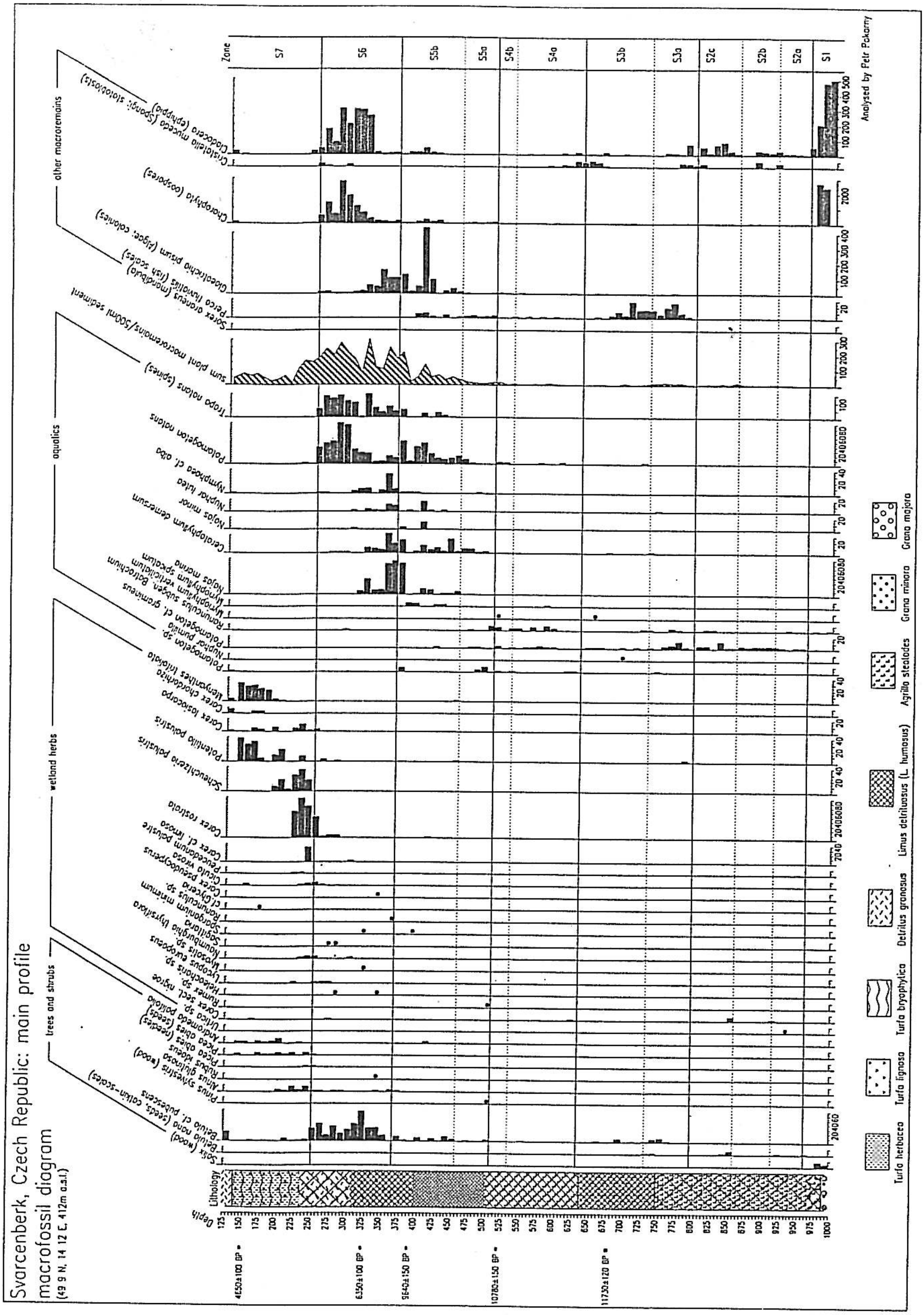


Fig.4: Late-Glacial and Holocene macrofossil diagram of the 'main profile'. If not stated differently, all finds represent seeds.

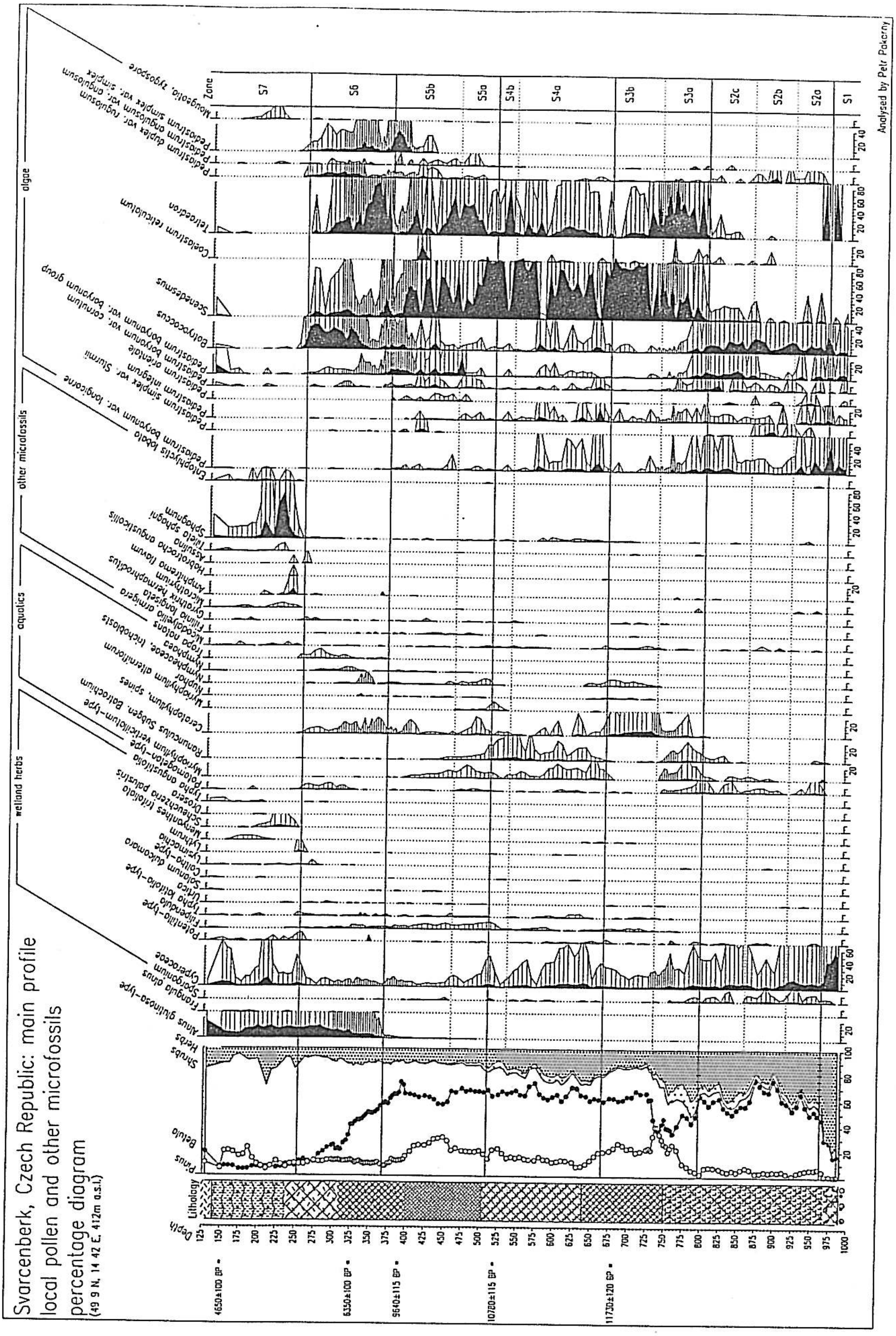


Fig.5: Late-Glacial and Holocene local pollen and other microfossil diagram of the 'main profile'. Only selected types are included. For sediment stratigraphy description, see Fig. 4.

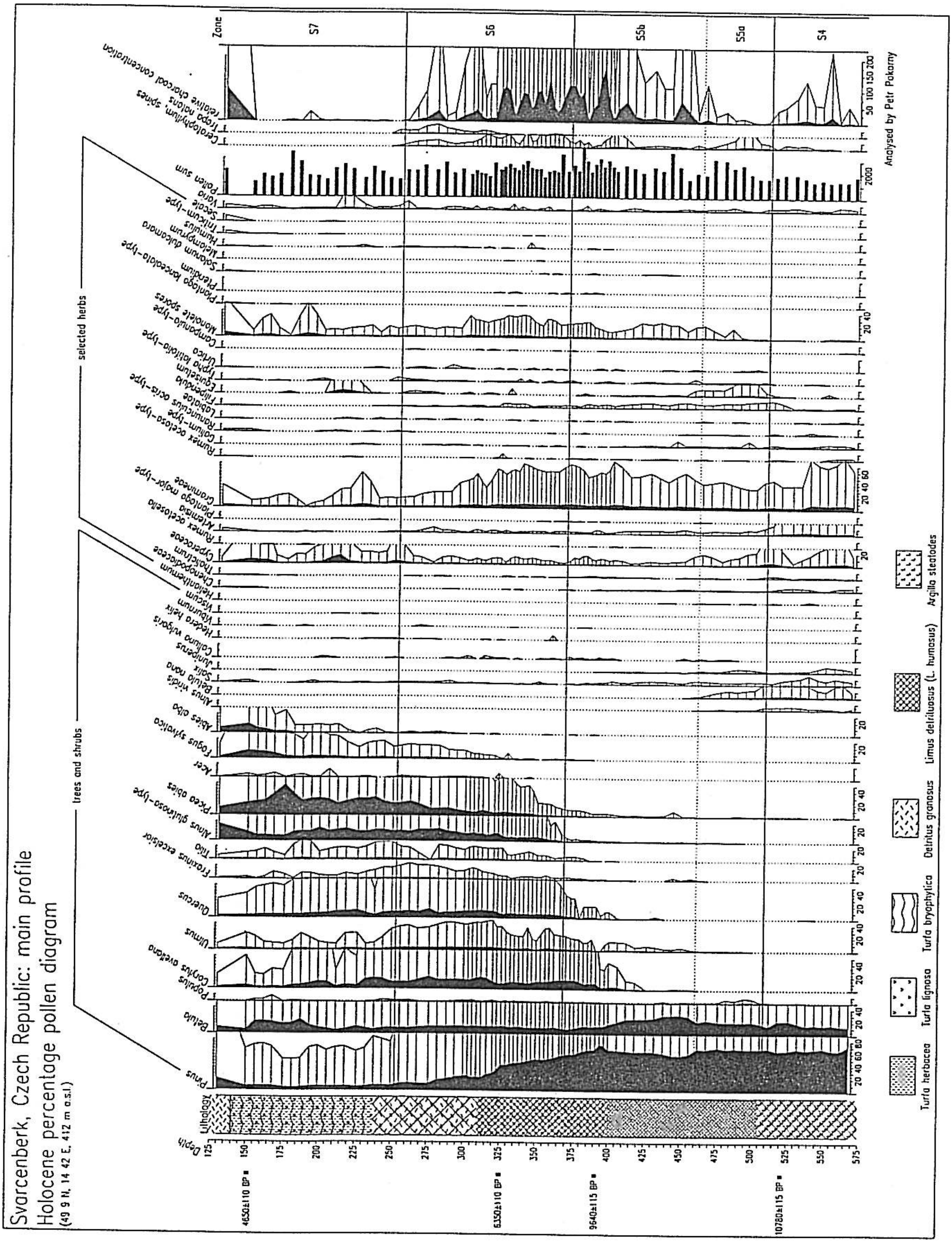


Fig.6: Holocene regional pollen diagram of the 'main profile' used for correlation with other profiles.

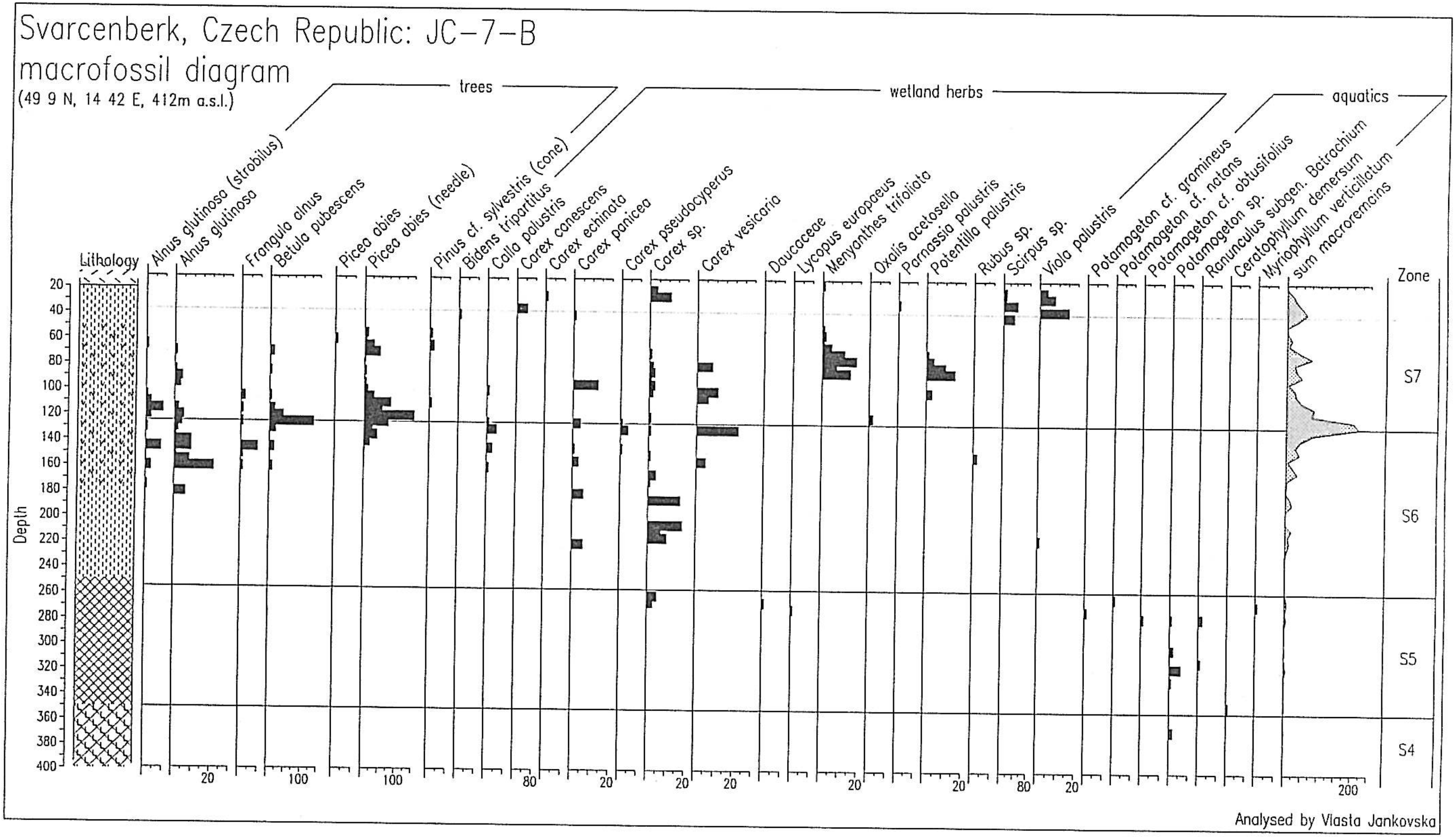


Fig.7: Macrofossil diagram of JC-7-B profile. For sediment stratigraphy description, see Fig. 4.

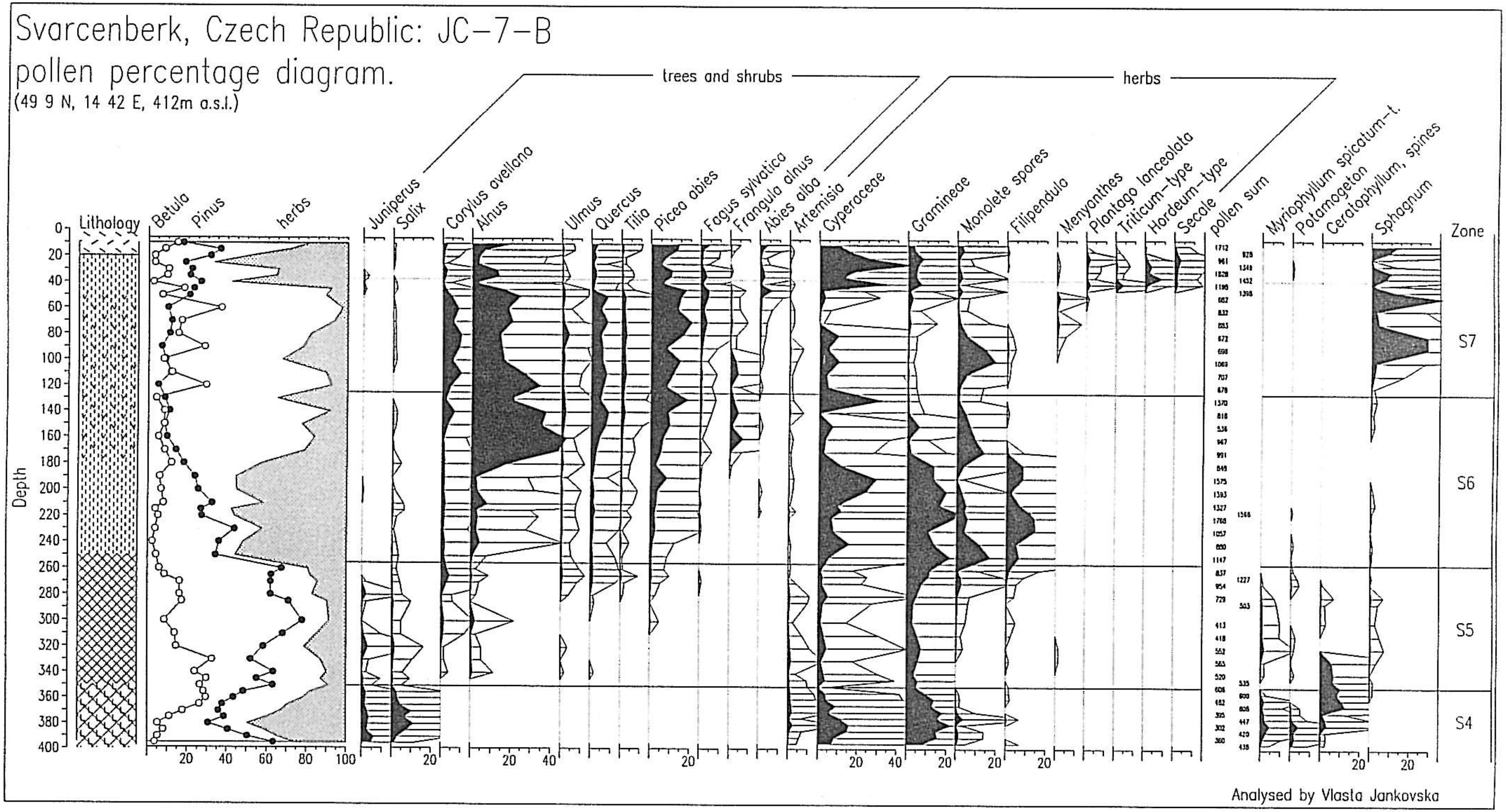


Fig.8: Pollen diagram of JC-7-B profile. Only selected types are included. For sediment stratigraphy description, see Fig. 4.

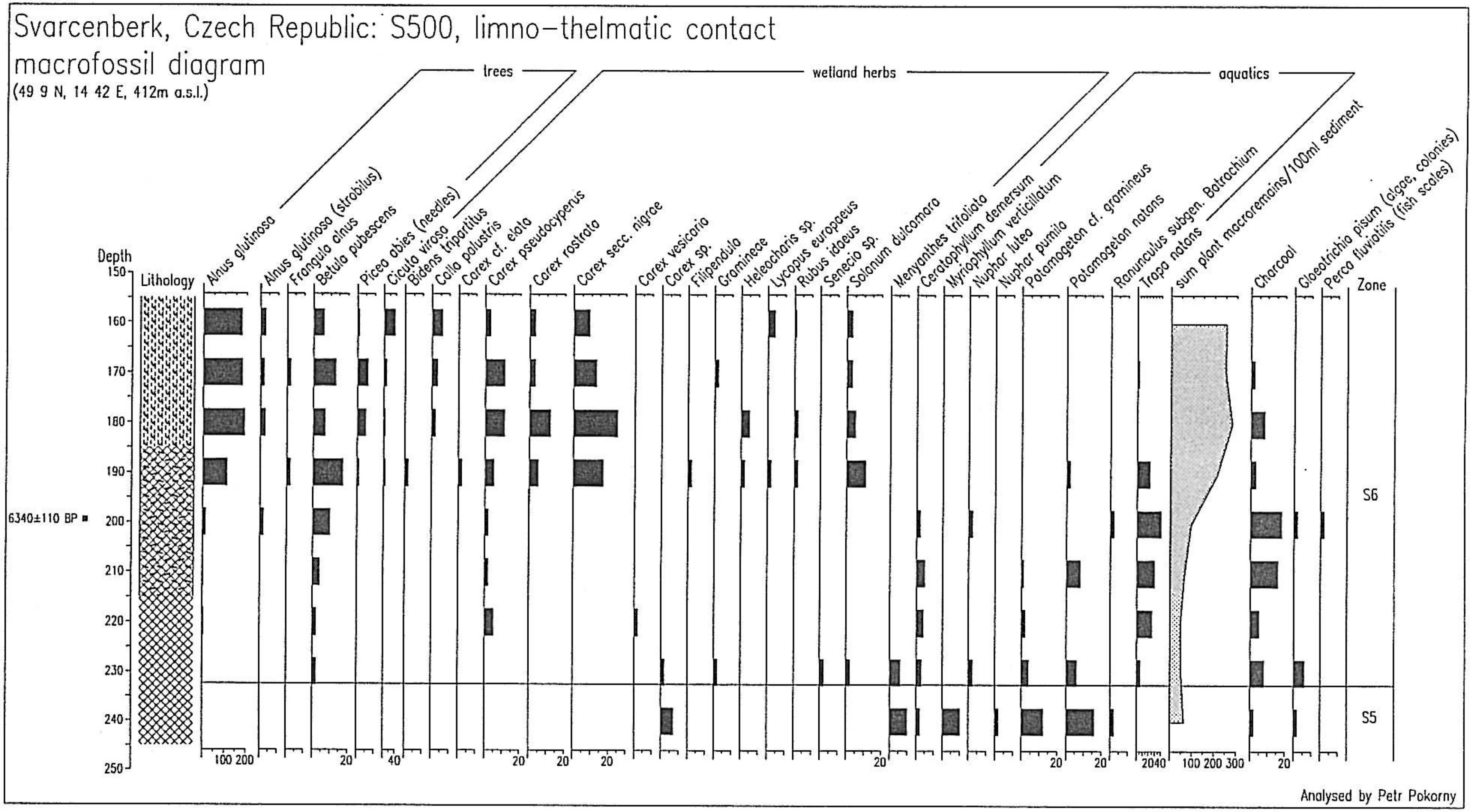


Fig.9: Macrofossil diagram of S500 profile. For sediment stratigraphy description, see Fig. 4.

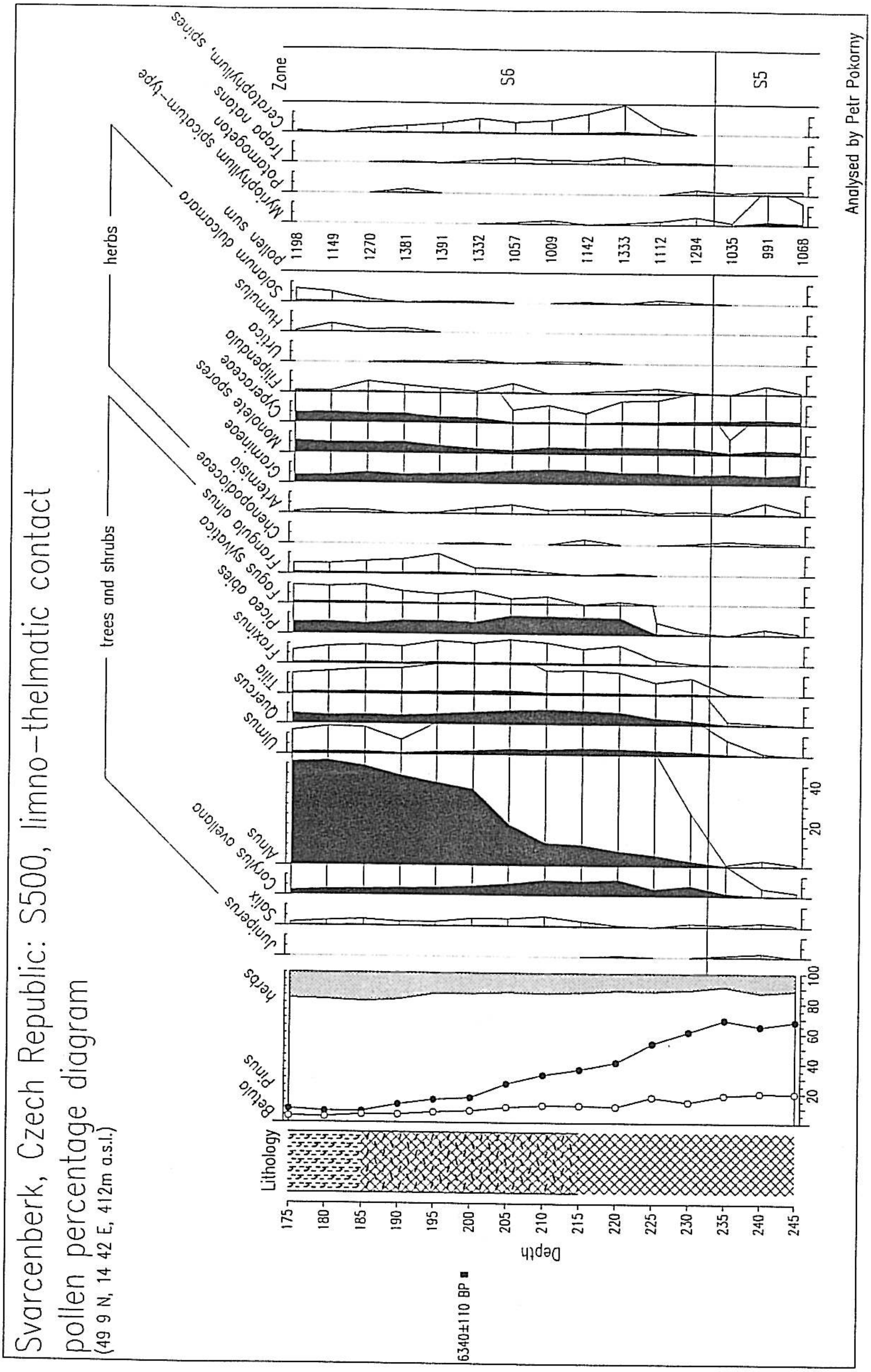


Fig.10: Pollen diagram of S500 profile. Only selected types are included. For sediment stratigraphy description, see Fig. 4.

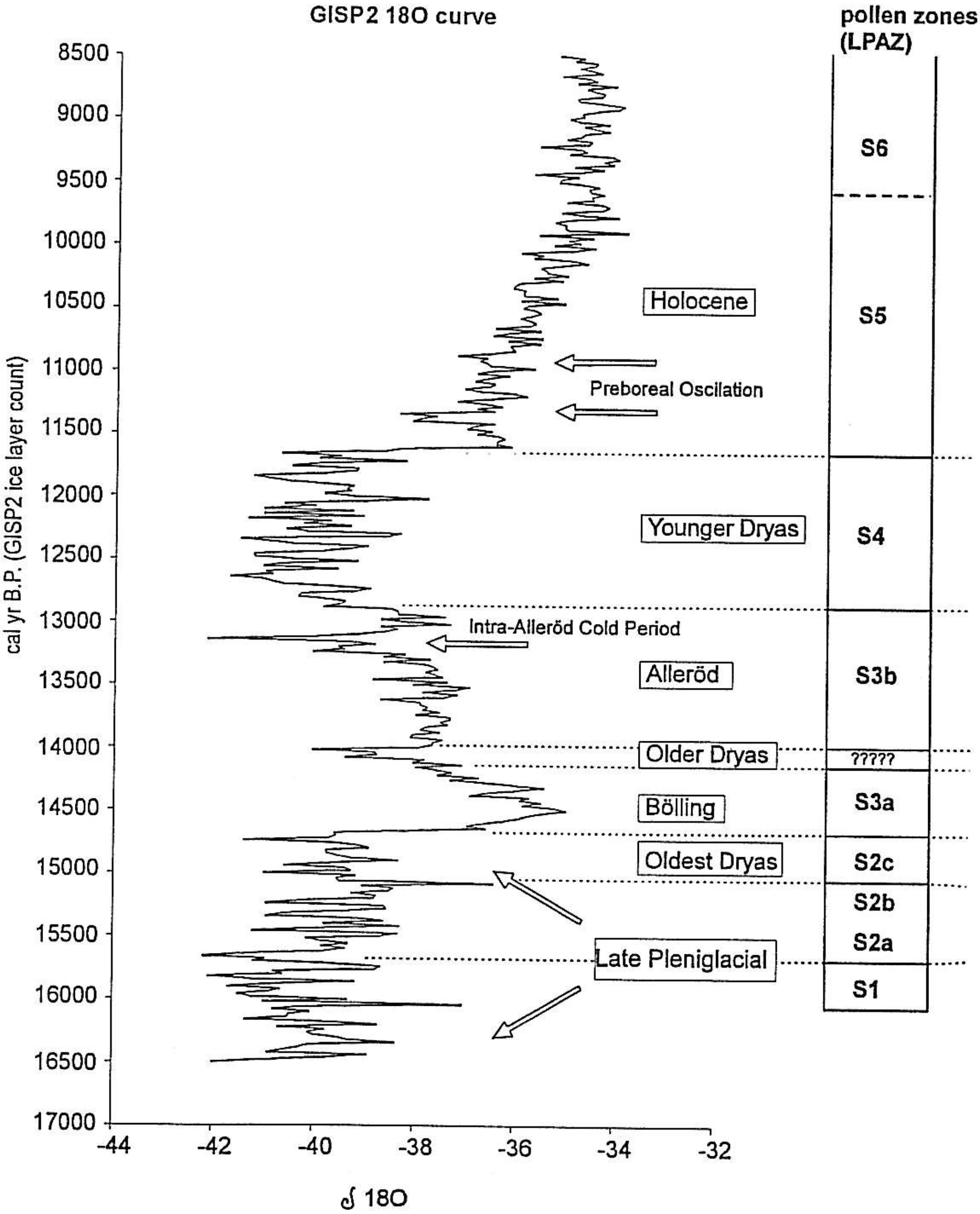


Fig.11: Local pollen assemblage zones (LPAZ) compared with bidecadal $\delta^{18}O$ curve of the Greenland ice core GISP2 (data measured by hand by W.O. van der Knaap from graph presented in Stuiver *et al.* 1995). This cross-correlation should be considered as a suggested scheme only. Absolute time scale (cal yr B.P.; yearly ice-layer counts before A.D. 1950) and chronozones follow STUIVER *et al.* (1995) with exception of 'Preboreal oscilation' derived from AMMANN & LOTTER (1989).

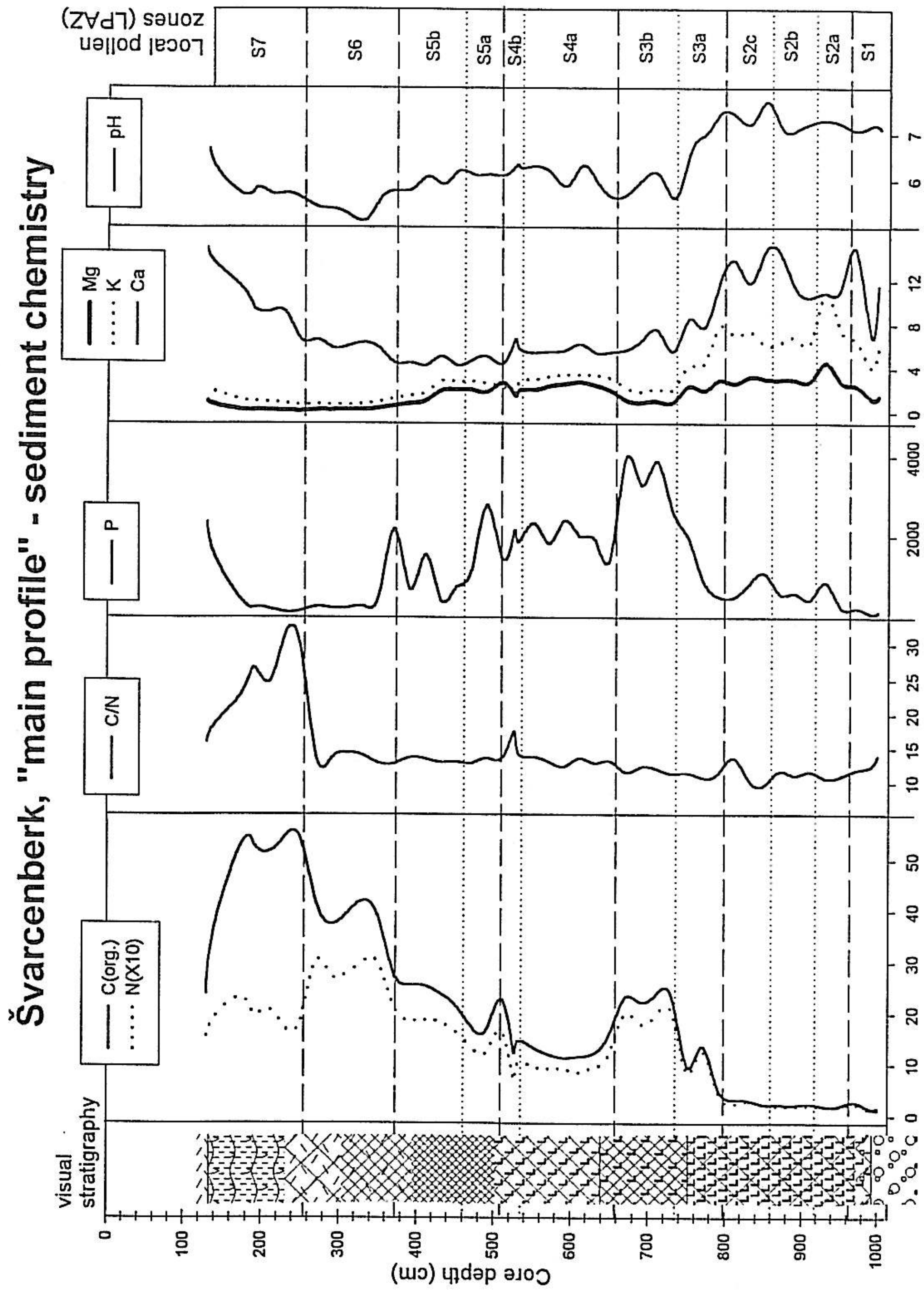
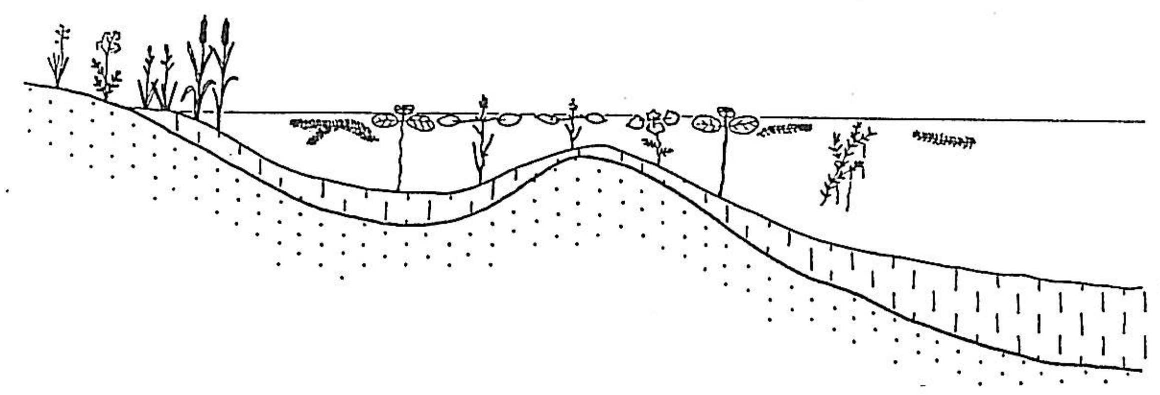


Fig.12: Sediment composition of the „main profile" correlated with local pollen zonation. For sediment stratigraphy description see Fig.4.

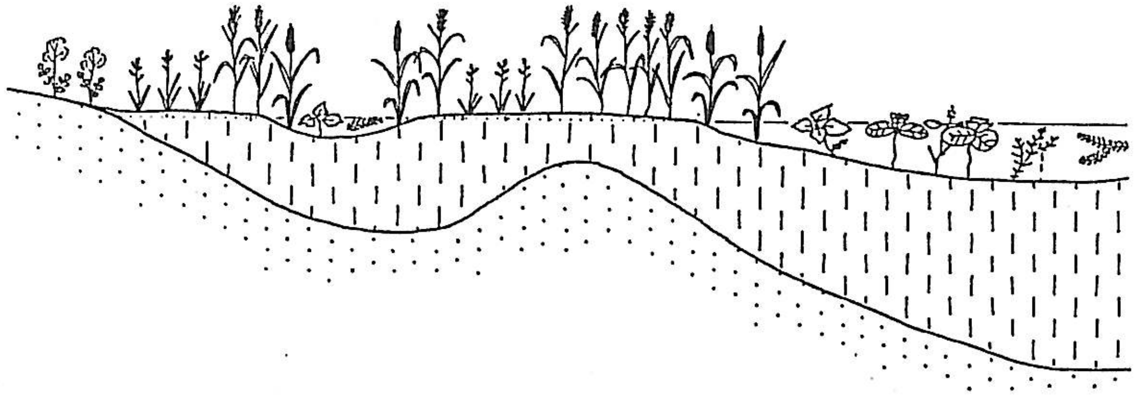
Appendix:

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

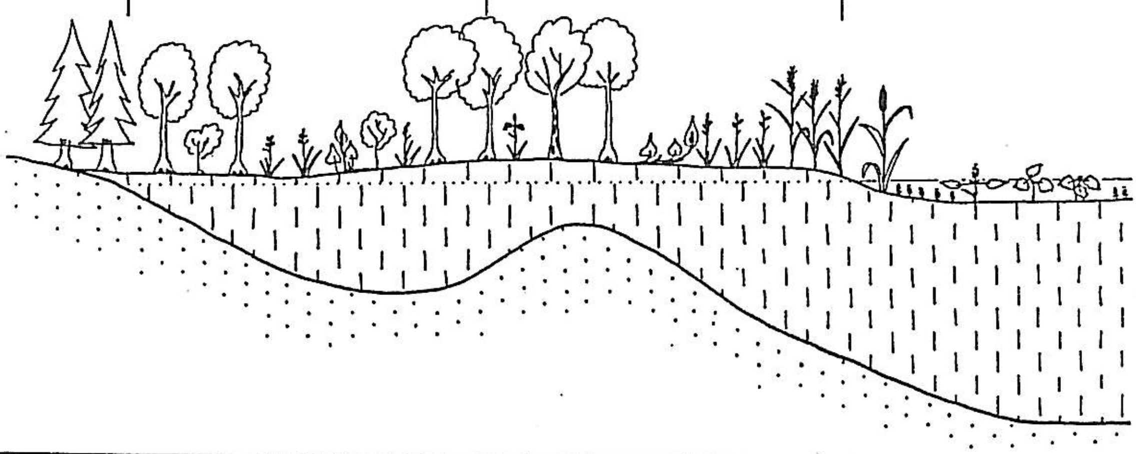
S5b subzone, about 9 500 BP			
location (core label):	**JC-7-B**	S500	**„main profile“**
characteristic taxa:	*Potamogeton* sp., *Ranunculus* subgen. *Batrachium*, *Ceratophyllum demersum*, *Myriophyllum verticillatum*	*Nuphar*, *Potamogeton* sp., *Ranunculus* subgen. *Batrachium*, *Ceratophyllum demersum*, *Myriophyllum verticillatum*	*Najas marina*, *Najas minor*, *Nuphar*, *Nymphaea*, *Trapa natans*, *Potamogeton natans*, *Ceratophyllum demersum*, *Myriophyllum spicatum*



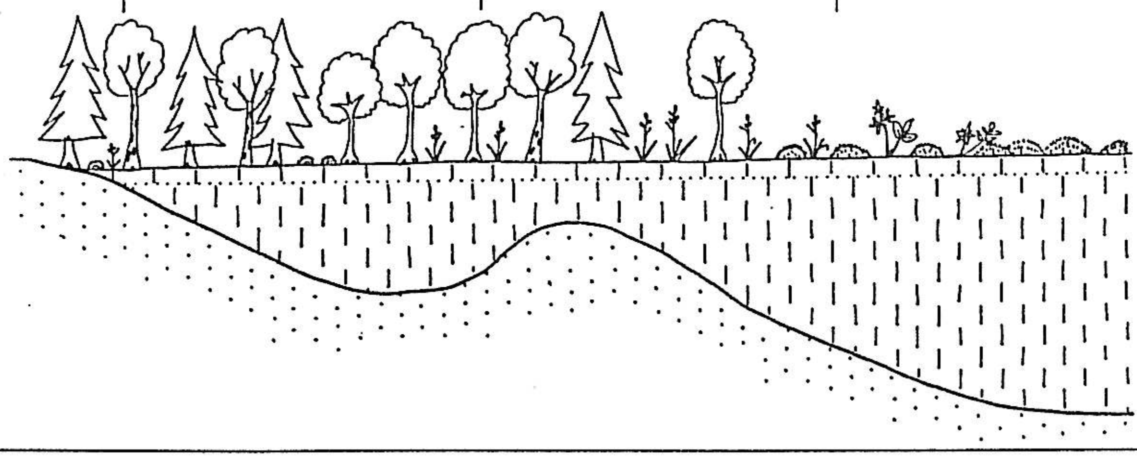
S6 zone - first half, about 6 500 BP			
location (core label):	**JC-7-B**	S500	**„main profile“**
characteristic taxa:	*Carex sp.*, *Carex panicea*, *Viola palustris*, *Filipendula*	*Nuphar*, *Potamogeton* sp., *Ceratophyllum demersum*, *Trapa natans*	*Najas marina*, *Nuphar*, *Nymphaea*, *Trapa natans*, *Potamogeton natans*, *Ceratophyllum demersum*



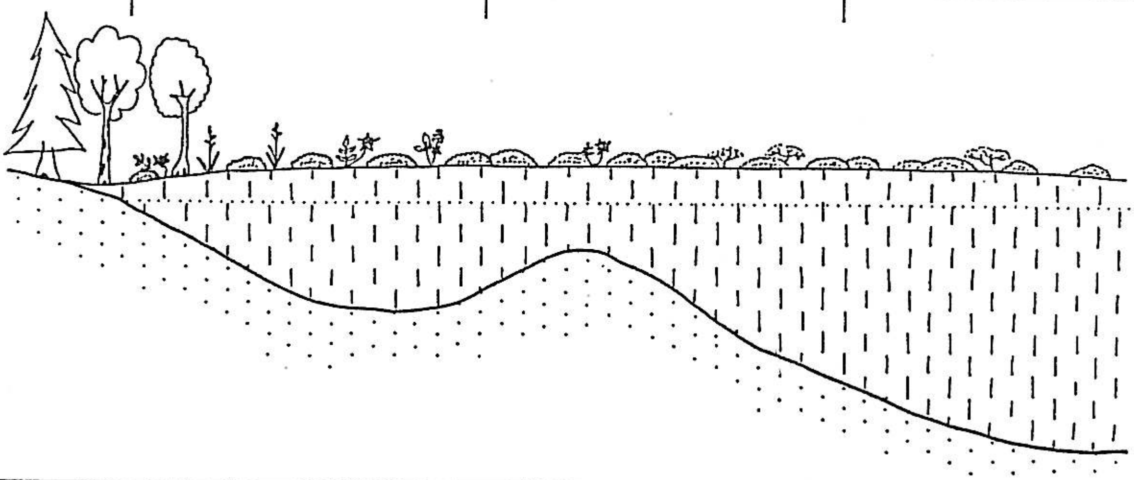
S6 zone - second half, about 6 000 BP			
location (core label):	**JC-7-B**	S500	**„main profile"**
characteristic taxa:	*Alnus glutinosa, Betula pubescens, Frangula alnus, Carex vesicaria, C. panicea, C. pseudocyperus, Calla palustris*	*Alnus glutinosa, Betula pubescens, Frangula alnus, Carex rostrata,, C.* secc. *nigrae, C. pseudocyperus, Calla palustris, Heleocharis* sp., *Solanum dulcamara, Lycopus europaeus*	*Potamogeton natans, Trapa natans, Nymphaea, Ceratophyllum demersum,* Charophyta



S7 zone - 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*



S7 zone - second half, about 4500 BP			
location (core label):	**JC-7-B**	**S500**	**„main profile“**
characteristic taxa:	*Menyanthes trifoliata, Potentilla palustris, Sphagnum*	?	*Potentilla palustris, Carex lasiocarpa, C. chordorhiza, Menyanthes trifoliata, Andromeda polifolia, Sphagnum.*



III. NUTRIENT DISTRIBUTION CHANGES WITHIN THE LAKE AND ITS CATCHMENT AS RESPONSE TO RAPID CLIMATIC OSCILLATIONS.

[Pokorný, P. (2000, in press): Nutrient distribution changes within a small lake and its catchment as response to rapid climatic oscillations. In: Vymazal, J. (ed.): *Nutrient Cycling in Wetlands*. Blackhuys Publishers, Leiden.]

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Abstract: Natural lakes are rare phenomena in extraglacial areas of Central Europe. Moreover, almost all of them have completely terrestrialized in course of the Holocene. The present article deals with one such former lake, located in southern Czech Republic. Its extensive lacustrine and peat deposits were subjected to multidisciplinary research that brought about high-resolution data about climatic, geomorphic, and regional vegetation changes over the last 16 000 years. On the background of these large-scale processes, local changes in nutrient distribution within the lake and its catchment could be traced. Input of individual elements into the lake depended on the intensity of weathering and erosion in the catchment, momentary state of soil development (building-up of raw humus and the leaching of deeper soil horizons), and the retention capacity of lake littorals. Different proportion between the intensity of these various processes during individual successional phases of the last glacial/interglacial transition has been observed. This observation is then compared with Iversen's cyclic model of glacial/interglacial development of temperate ecosystems and the hypothetical role of human activities in the alteration of this development is discussed.

INTRODUCTION

Accumulation of sediments at the lake beds leads to the formation of a „natural archives" of material transported from surrounding water catchment areas. Numerous palaeolimnological studies have shown how sediment chemical properties may be interpreted in terms of processes acting within lakes and their catchments. These processes are often directly or indirectly related to climatic parameters and their understanding may enable further generalisations about the role of climate in nutrient distribution within the surrounding landscape. Intensity of weathering and erosion processes, status of soil development, biological productivity, specific composition of the biota - all these factors interlink momentary climatic setting with nutrient distribution in the ecosystems. Unfortunately, it is usually difficult to identify the precise nature of some processes from fossil sediment record. E.g. Na, K and Mg content in sediments is known to reflect the intensity of weathering and erosion in the catchment (Engstrom & Wright 1984, Dearing 1991), as they are relatively insoluble and usually travel into the lake together with eroded material. However, the intensity of erosion is related to several factors, such the transporting energy in the catchment, availability of sediment for erosion (the factor often connected with the intensity of pedogenetic processes), or momentary development of lake littorals, whose vegetation can have a large sediment-retention capacity.

The need for a long-term record of nutrient distribution changes which would cover at least a half of the last glacial-interglacial cycle comprising the periods of abrupt climatic oscillations has lead to the use of sediment profile form former lake Švarcenberk, situated in relatively flat landscape of northern Třeboň Basin, south Bohemia. This profile is unique example in the Czech Republic with extensive and well-stratified Late-glacial record. The detection of brief Late-glacial climatic oscillations is allowed by high sediment-accumulation rates. Local pollen record has been correlated with regional climatostratigraphical units according to Magerund et al. (1974) and Ammann & Lotter (1989). This correlation was further confirmed by five radiocarbon dates in order to enable comparison with numerous results from western and north-western Europe, where the basic biostratigraphic and climatostratigraphic concepts has been developed (Iversen 1954; Magerund et al. 1974, Watts 1979). As postulated by Rudimann & McIntire (1981) and later recognised in terrestrial record within the areas adjacent to the North Atlantic (e.g. Lowe et al. 1994, Walker 1995), the rapid climatic changes during the last glacial-interglacial transition can be largely ascribed to large-scale shifts in the position of the oceanic Polar Front and have amphi-Atlantic or even global occurrence (e.g. Peteet 1995). The biostratigraphic data from Švarcenberk sediments has already shown (Pokorný 2000), that these concepts can be applied also to the investigated area with some minor limitations. Chronostratigraphic terminology according to Magerund et al. (1974) and Ammann & Lotter (1989), widely used in Europe, is than followed also in this paper and is used as a framework for discussion of the results of sediment analyses.

STUDY SITE

The existence of former lake Švarcenberk has been noted for the first time by Vlasta Jankovská in late 70'th. In her study, focused on vegetation development of Třeboň Basin (Jankovská 1980), she gives the pollen diagram and macrofossil analysis obtained from an open pit. Her profile comprised about meter and half of lake sediments and Jankovská has correctly assumed that she deal with littoral facies of some larger lake. Unfortunately, no stratigraphic data were at the dispose that time. These were obtained only later in connection with the present study and confirmed fully Vlasta Jankovská's original assumption. The extend of lake deposits was mapped in detail by approximately 120 hand borings. The altitude of sediment surface was obtained by levelling. The former lake was found to have a maximum surface 0.51 km^2 and the ratio of the surface to drainage basin about 1:8 (Fig. 2). The striking features of the basin geomorphology is its kidney-shaped form, surprising depth and declivity (the presence of unusually steep slopes) and relatively high age of its infilling (the basal age in the „main profile" is about 16 000 BP). On the basis of these finds, the origin of such structure can be best explained as the remnant of a huge Pleniglacial ground-ice lens - the open system pingo (Pokorný 2000).

The former lake Švarcenberk is situated 4km south of the city Veselí nad Lužnicí (49° 9'N, 14° 42'E) at 412 m. a.s.l.(Fig. 1). Today, the limnic sediments are overlaid by peat that formed after the terrestrialisation of the lake (it has completely filled-in at approx. 5 500 BP according to ^{14}C dating). After the final infilling of the lake, oligotrophic peat started to accumulate.

The investigated site is situated in area which remained only little affected by human activity until Late Medieval colonisation in 13th century AD. This fact enable the separation of processes induced naturally from those induced by human impact. Between 1698 and 1701 a dammed fishpond was constructed directly on the site and its waters almost completely overflooded the peat deposits together with underlying lake sediments.

For local hydrology the presence of several strong arthesic springs is characteristic. Underground water is ascending along the deep tectonic fault and is rich in iron oxides. The former lake has been intensively supplied by this arthesic water. The activity of underground water sources was apparently independent on general climatic fluctuations in the past. As the result, lake water-level remained almost constant over millennia. The lake has drained into nearby Lužnice river. Along the river floodplain, numerous eolic deposits are situated. One of the biggest and most prominent sand dunes, „Vlkov sand dune“ is situated not far from the former lake basin (about 1200 m) and its formation is dated to Younger Dryas, the period considered to be characterised by increased eolic activity (Pokorný 2000).

Sandy and clayey Cretaceous sediments with locally superimposed Tertiary sediments constitute the principal geological substratum in the former lake catchment. The character of these substrates determines that of the soils. In these, the content of clay particles generally increases with depth and the soil aeration is reduced accordingly. Soil nutrient content is generally poor: Calcium carbonate deficiency is common, potassium is relatively sufficient but only in deep soil horizons, nitrogen content is low, that of phosphate is medium (Husák & Hejný 1978). Most soils are leached and show a tendency towards podzolisation. The soil reaction is mostly highly acidic (pH up to 3.3).

The present climate is suboceanic and is determined by prevailing westerly air passages across central Europe. The region is somewhat sheltered by the Šumava (Bavarian Forest) highlands. Macroclimatic conditions are modified by presence of extensive wetlands: Frequent occurrence of fog is typical for the region. Annual mean precipitation is 622mm (January being the driest), annual mean temperature is 7.4 °C.

METHODS

The core in the centre of the former lake basin has been selected as the standard profile for the following reasons: The central core will most probably show a continuous record without occurrence of serious sedimentation hiatuses and it is more likely to give an „average“ picture of the events in the basin and its catchment (without the background of local „noise“ which is assumed to be greatest along the shores). This „main profile“ actually consist of seven separate parallel cores taken close together in order to obtain enough material for all kind of analyses. The coring has been performed by Russian-type corer, 5 cm in diameter. This type of instrument does not cause serious sediment compression resulting in core shortening. All cores comprising the „main profile“ were correlated according to their visual litostratigraphy. This correlation only confirmed the satisfactory accuracy of parallel sampling.

Biostratigraphy.

Pollen and macrofossil analyses has been performed according to standard methods. Primary pollen data were elaborated into the form of pollen diagrams that were divided into different local pollen assemblage zones (PAZ). The biostratigraphic data are not followed in detail in this paper as they form only one part of an overall picture needed for discussion of the main subject.

The lowermost Late-glacial and particularly Pleniglacial sediments contained a lot of reworked Tertiary pollen. An attempt for reliable separation of these pollen grains was made in order to avoid possible misinterpretations of Late-glacial pollen spectra and in order to obtain a tool for assessment of erosion rates in lake shores and lake catchment. It is assumed, that reworked pollen grains embedded in Late-glacial and Holocene sediments originated primarily from eroded Tertiary subsoil sediments of lake catchment, including lake shores. Some of the Tertiary taxa are easily recognised according the pollen morphology (e.g. Engelhardtia, Carya, Liquidambar), but some are difficult or even impossible to separate in the morphological basis only. Fortunately, the state of preservation of the Tertiary pollen is relatively bad in our material, giving pollen grains a „ghosty“ appearance. It has been assumed, that different degree of fossilisation resulted in different chemical composition and physical properties of pollen wall. Considering this assumption, a simple method has been developed to confirm the Tertiary origin of some pollen grains: Pollen preparations, already stained by 0.3% safranin, were differentiated in 40% ethanol for 60 seconds. After that, the pollen preparations were centrifuged and transferred to glycerol-water mounting medium. As the result of this procedure, all pollen grains were bleached to different degree, but the Tertiary ones became almost completely transparent and hence well-separable from the Late-glacial ones.

Sediment chemistry and ^{14}C analyses.

Total carbon and nitrogen content was determined by combustion at 950 °C in pure oxygen with subsequent conductivity detection of C and N oxides (in Heraeus CHN-Rapid Analyser in the Analytical Laboratory of the Institute of Botany, Academy of Sciences of the Czech Republic). Carbonate content was measured by sodium hydroxide titration to neutral pH after dissolution of 0.5 g sample in 0.5 M hydrochloride acid and boiling for 20 minutes (after Hammarlund & Buchardt, 1996). Total organic carbon content was calculated from the difference between total carbon and carbonate carbon content.

Total phosphorus content was analysed after extraction of sediment sample in Olsen's reagent (Olsen et al. 1954). The resulting phosphate-phosphorus was than determined. This method is based on the formation of the „molybdenum blue“ complex in ammonium molybdate-sulphuric acid reagent after reduction in ascorbic acid. Resulting colour intensity was measured spectrophotometricaly using 630 nm wave length.

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

Radiocarbon dates used in the present study are all AMS (Atomic Mass Spectrometry) dates from bulk sediment samples and individual plant macrofossils (for position and description of ^{14}C samples see Tab. 1). The disadvantage of the Late-glacial sequence under the study is the absence of enough terrestrial plant macrofossils for the dating purposes. The dates from gyttjas, clayey lake sediments and aquatic plant macroremains are known to give the ages which usually exceed those obtained from terrestrial macrofossils (Törnqvist et al. 1992). This effect is often ascribed to the hardwater error. In our case, the hardwater error is expected to be relatively small as the sediments contain negligible amount of carbonates. Radiocarbon analyses were carried out by the Radiocarbon Dating Laboratory, Department of Quaternary Geology, Lund, Sweden. Age calculations are based on a ^{14}C half-life of 5568 years. For the purposes of simplicity and comparability, dates are expressed in ^{14}C years before present (BP) unless otherwise stated.

RESULTS AND DISCUSSION

The results of chemical analyses of central sediment core form the former Švarcenberk lake are presented in Fig. 3. Biotic and climatic context to the results is given in form of seven synoptic tables, each for a particular period under discussion. These summarise the results of pollen and macrofossil analyses that were put into wider chronological and spatial context using absolute time control achieved by the application of biostratigraphical correlation together with ^{14}C analyses and detailed geological investigations in the field. For the description of symbols used in reconstructions see Appendix.

Initial warming after the last Glacial maximum - the setting conditions.

The lowermost sediments in the centre of lake basin consist of fine silt with some coarser sand particles. They are dark-coloured as they contain FeS. This suggest anoxic conditions as iron sulphide deposition usually occur under prolonged or permanent stratification of the lake (Engstrom & Wright 1984). The formation of these sediments antedate the period of rapid Late-glacial climatic warming at about 13 000 BP. Their pollen spectra are characterised by high non-arboreal pollen (NAP) values, suggesting an open herbaceous vegetation. Grasses, Cyperaceae, Chenopodiaceae, Betula nana, Alnus viridids, Salix (most likely some dwarf willow species), Thalictrum and Artemisia were important components of the vegetation. The occurrence of Ranunculus subgen. Batrachium can be used as climatic indicator for minimum July temperatures, suggesting those to be at least 10 °C, while Hippophaë rhamnoides presence (found exclusively as pollen) suggest at least 11 °C (Huizer & Izarin, 1997).

Very low sedimentary organic carbon content (values not exceeding 3%) suggest low productivity in the lake as well as in its catchment (see also very low N and P values during that time). Low nutrient status together with small productivity was primarily caused by low energy input into the ecosystem. An interesting find of Urtica dioica seed together with Urtica pollen between 930 and 950 cm is somewhat controversial from this point of view. This nitrophillous plant, requiring mean July temperatures at least 8 °C (Bos 1998), is distributed in eutrophic habitats in modern times. This is in sharp contrast with general picture of Late Pleniglacial period pointing to prevailing oligotrophic and distrophic conditions in the lake and its catchment. There probably must have existed some favourable, nutrient-rich microhabitats, where Urtica dioica could have prospered.

High content of Na, K and reworked Tertiary pollen suggest high erosion rate in lake catchment during this period. This can be ascribed to sever, highly continental and unstable climatic conditions implicating intensive surface cryogenic processes, slope outwash and rilling. Furthermore, the absence of stable soils in the catchment caused good availability of sediment for erosion. Slightly lower values of all erosion indicators in the lowermost approx. two decimetres of sediment core is apparently the result of high relative proportion of coarse sediment fraction (consisting mostly of quartzite grains), rather than lower allogenic sediment fraction input to the lake basin.

Relatively high Helianthemum percentages (up to 3%) point to the presence of bare, calcareous substratum (Hoek 1997). This accord well with the results of sediment chemical analyses, showing high Ca content. This find is in sharp contrast with present-day conditions in the area under study, where most soils are leached, highly acidic, almost completely lacking calcium carbonate.

The rise in Pinus pollen percentages up to values higher than 60% between 870 and 910 cm indicates the period of local pine expansion. Individual pine trees must have been scattered more or less sporadically in the landscape of steppe and tundra-like character. Pine expansion suggest some temporal climatic amelioration. At about that time (cca.15 000 BP), weak traces of initial pedogenesis are described from lowlands of Central Europe. The same period is characteristic in European loess plateaus by a short break in eolic deposition suggesting slightly warmer and wetter climate (Tyráček 1995). In our sediment chemistry record, no evidence for intensive pedogenetic processes has been found for the critical period.

A warm oscillation of Late-glacial Interstadial.

An abrupt climatic amelioration is recorded in many areas of the World at around 13 000 BP (e.g. Lowe et al. 1994). Reforestation by birch and later by pine is recorded over the most of NW and Central Europe during this time. The lower limit of mean July temperatures needed for tree birch colonisation is usually taken as 10 °C, but 12 °C is the optimum for the development of Betula pubescens woodland (Birks 1993). Similar development can be traced also in the area under study: Reforestation by birch and pine resulted in decline of most of pioneer heliophyllous herbs, that were characteristic for the preceding period. In aquatic environment, abrupt climatic amelioration caused the expansion of submerged macrophytes including Ceratophyllum demersum, which appears for the first time in the lake. Nymphaea, Nuphar, Filipendula and Typha latifolia occurrence also point to minimum July temperatures at least 12 °C (Huizer & Izarin 1997).

Late-glacial Interstadial appears to be a period with significantly increased organic production, as reflected in sharp transition from minerogenic to organic sedimentation: Organic-rich gyttja („sapropel“) with organic carbon content exceeding 15% started to accumulate ($C_{org.}$ content reaches 25% during the later - Alleröd phase of the Interstadial). Sedimentary organic carbon curve is synchronous with the curve of sedimentary N. Also phosphorus content in the sediments seems to be a good indicator of past nutrient status of the lake (for discussion of problems associated with phosphorus uptake and postdepositional changes see Engstrom & Wright 1984).

The onset of warm, less continental climate (connected with the decline of cryogenic and slope processes) has lead to significantly decreasing erosion rates in lake catchment obvious from the progressive decline in sedimentary Mg, K and sharp decline in reworked Tertiary pollen. Intensive soil development under forested conditions has probably been the major factor affecting the transport of above mentioned cations into the lake. During episodes of relatively stable soils, deep weathering of mature soil profiles and formation of clay minerals should diminish the base content of mineral material prior to its erosive removal and sedimentation in lake basin (Engstrom & Wright 1984). Decalcification of the developing soils continued up to the maximum extent during this period as seen from the decline in sedimentary Ca to values comparable with those characteristic for the Holocene. The decalcification of soil horizons together with competitive pressure of expanding forest were probably two most important factors responsible for complete decline of Helianthemum and Plantago maritima-type from regional vegetation (as seen from the pollen record). The period of first intensive soil development is also recorded for the Late-glacial Interstadial in lowland loess plateaus of the Czech Republic: Loess formation, which was characteristic of Late Pleniglacial, terminates during Bölling phase (the first half of the Late-glacial Interstadial) and initial pedogenesis takes place during that time (Ložek & Cílek 1995).

Younger Dryas climatic reversal.

The Younger Dryas as a biozone has been widely recognised over the most of Europe. Concerning the duration and the amplitude, this climatic oscillation was the most important during the whole Late-glacial period (Lotter et al. 1992). Younger Dryas climatic deterioration, dated roughly between 11 and 10 ka BP, is correlated with a readvance of polar waters into the North Atlantic. Although the problems of absolute dating accompany the recognition of Younger Dryas event (the „^{14}C plateau" occurrence; Ammann & Lotter 1989), it has been described from many sites in the world and today is believed to be a global event (Peteet 1995). At site under present study, clear evidence of climatic deterioration is also dated to Younger Dryas chronozone. However, this climatic oscillation did not resulted in complete deforestation. The pine-birch woodland became only somewhat more open, whereas the importance of heliophyllous herbs and dwarf shrubs - Alnus viridis, Salix, Betula nana, Chenopodiaceae and Artemisia newly increased. Proxy-evidence suggest, that climatic deterioration was rather increase in continentality than decrease in summer temperatures (see also Ammann 1989): Reconstructed minimum July temperatures are still at least 12 °C, e.i. the same value as reconstructed for western Poland (Walker 1995).

During the Younger Dryas episode, sedimentation character in the lake basin changes to more minerogenic again. Organic carbon content decreases to about 10%, accompanied by fall in N and P, suggesting period of lower productivity. Slight increase in erosion indicators (Mg, K, reworked Tertiary pollen) is observed during the same time. This increase is only indistinctive, suggesting that soil development was not interrupted completely during Younger Dryas and the destruction of yet-formed soils has not been significant.

Early Holocene climatic amelioration (Preboreal and Boreal periods).

There is abundant evidence throughout Europe for a rapid rise in temperature at around 10 000 BP, although precise dating of this event is difficult as another „radiocarbon plateau" occurs at about that time. Over many areas of central and north-west Europe, Younger Dryas open communities were replaced within less than 500 years by Betula/Pinus/Corylus woodland (Walker 1995). The preservation of Pinus-dominated forest in the area under study during the whole Early Holocene and relatively late development of deciduous forest, was connected with the persistence of continental climate during that time and generally low nutrient status together with the sandy character of soils. Pinus forest persisted in the area until the increase in humidity during the onset of Boreal period (for evidence see later), although deciduous forests started to develop in favourable locations somewhat earlier. The rapid temperature rise during Preboreal is indicated in lake environment by early occurrence of *Najas marina, Najas minor* and *Trapa natans* macrofossils. Najas marina suggest a mean July temperature not below 15 °C (Lotter 1988), *Trapa natans* even more. According to Gams (1926) and Jorga et al. (1982), water chestnut requires mean July water temperature not below 20 °C and in May, when it starts flowering, at least 12 °C. The rapid change to warmer climatic conditions is also evidenced (according to Van Geel et al. 1989) through appearance of macroscopic colonies of thermophillous blue-green algae *Gloeotrichia pisum*. This proxy-evidence suggest that the present-day temperature values were reached as early as about 9 800 BP.

Organic sediment (gyttja), rich in macrofossils, started to accumulate in the basin again. The short decrease in organic production at 480 cm is problematic to attribute to some climatic oscillation without exact time control available. Sedimentary phosphorus content fluctuate but is generally low during Early Holocene. It suddenly fall to very small values during Boreal period. The exact explanation of this phenomenon is not still possible without more data available (the study of phosphorus forms would be necessary).

The Early Holocene sediment record from Švarcenberk lake comprises a prominent Fe peak, dated to around 8 600 BP. It may be best explained as the reflection of intensive leaching caused by sudden humification of climate (Engstrom & Wright 1984, Starkel 1991). In the pollen record, the same period is characterised by Picea abies expansion. There is probably some connection between these two phenomena, as spruce grows preferably on waterlogged soils and is able to produce highly acidic, raw humus, promoting intensive leaching. The gradual development of nutrient-poor, acid soils was an important factor in the Holocene vegetation development, as emphasised by Iversen (1958, 1964). The building-up of raw humus on the soil surface and resulting reducing conditions may have released Fe from the soil and it travelled to the lake in solution or bound in organic complexes. Resembling ferrugineous peak has been described from lowland areas of the Czech Republic, where Early Holocene debris are cemented by limonite and goethite (Ložek & Cílek 1995). Also in Polland, the beginning of Holocene is characterised by inwashing of dissolved iron into the lakes and this is interpreted as the first stage of intensive soil leaching (Pawlikowski et al. 1982). In southern Sweden, the Fe content of several Early Holocene lake sediments is very high. Diggerfeld (1972, 1975) attributes this ferrugineous peak to early leaching from Late-glacial soils in the catchment and subsequent transport by groundwater to the lake.

Holocene climatic optimum (Atlantic).

The climatic optimum sediment record is strongly affected by local environmental change - the final terrestrialisation of the lake basin. After terestrialisation of the lake, the centre of the basin has developed into a eutrophic march - reed swamp surrounded by alder carr. Accumulation of peat began that time. As the peat surface started doming over the surrounding terrain, the wetland has successively developed into oligotrophic Sphagnum peat-bog, isolated from direct influence form former lake catchment. This process is well-reflected in sediment chemical record: Nutrient status of the peat is very low and C/N ratio sharply increase if compared with underlying lake sediments.

The uppermost sediment sample used for chemical analysis represents a probe from modern fishpond bottom sediment (sapropel). Its composition is directly influenced by management of the artificial water body - liming, fertilisation, intensive fish production, etc.. Solutions rich in cations and phosphates further penetrate from surface downwards through the sediment column. The rise in P, Fe and Ca content (together with pH rise) in the uppermost peat is most likely caused by this effect. Deep penetration is observed especially in calcium carbonate (supplied into the fishpond in large quantities), which enrich the peat to depth about meter and half.

Final Conclusions: Natural versus human-induced nutrient cycling patterns.

In 1958, Johannes Iversen proposed a simple cyclic model for glacial-interglacial development of temperate ecosystems. He has divided glacial-interglacial cycle into different phases, each of them characterised by particular attributes and processes (see Fig. 4). Investigated lake sediments from former lake Švarcenberk represent a palaeoecological record which has appeared to be representative for at least a part of Iversen's cycle. Several basic principles of this model can be demonstrated on results presented in this article:

Cryocratic stage: Open herbaceous communities growing on bare, base-rich, calcareous substratum. Ruderal ecological strategies prevail. High erosion rates disable the development of soils. Geodivesity of the landscape is high. Low energy input into the ecosystem results in low biological productivity.

Protocratic stage: Open communities are replaced by boreal woodlands with different degree of canopy integration. First soils develop under favourable climatic and vegetation conditions. Unleached soils has basic reaction and are rich in cations. Erosion intensity significantly decreased relatively to the preceding phase. Biological productivity is high.

Mesocratic phase: Mixed deciduous forest became established. Shade-giving trees outcompeted most light-demanding plants. Competitive ecological strategies generally prevail. Matured brown forest soils with mull humus develop. Their reaction is neutral. High biological productivity is responsible for terestrialisation of many water bodies.

Oligocratic phase (recorded only marginally at the site under investigation): Leaching of weathered bases from soils lead to a shift from neutral to acid soils (podzols). These conditions favour trees like spruce or silver fir. Once established, conifers produce further soil acidification as their fallen needles produce acid mor humus. Stress-tolerant ecological strategies are characteristic for this period.

This is only a general picture emerging from the most general interpretation of the results. If we look into the palaeoecological record using somewhat smaller time-resolution, more complicated picture emerge, comprising several reversal phases, phases of more rapid or slower development and Iversen's phases may eventually overlap each others.

Our present interglacial (the Holocene or the Postglacial) significantly differ from its predecessors: Holocene is the period when modern human culture emerge. The development of agriculture (with crop fields as a type of human-managed ecosystems) has far-going consequences to natural environment. We can compare palaeoecological record of glacial-interglacial environmental changes with those caused by human activity during the second half of the Holocene and particularly in modern times. Soil destruction, large-scale deforestation, accelerated erosion and rapid nutrient runoff are characteristic consequences of intensive agricultural management. As obvious from the results of palaeoecological investigations, human activity represents an agent which in many respects simulate natural processes during cryocratic (glacial) stages of glacial-interglacial cycles. The natural mechanisms switching between individual phases of glacial-interglacial climatic cycles we fairly do not understand. They are acting in a complicated web of relationships that apparently does not have a deterministic character. Due to that, human-induced changes causing a „glacial“ settings of some ecosystem characteristics, may have unexpected global consequences which may eventually emerge in a catastrophic form.

Acknowledgements

My sincere thanks belongs to Andrea Kolmanová, Láďa Rektoris, Jiří Šetlík and other colleagues and friends, who assisted in the fieldwork. I am especially grateful to Jan Pokorný and Jan Květ for their practical support and several useful discussions and to Vlasta Jankovská, who helped with the identification of problematic pollen and algal specimens.. Jitka Klimešová is greatly acknowledged for drawing the final versions of reconstructions used in tables. Grant Agency of the Czech Republic supported this study through grant project No. 206/98/0727.

TABLES AMD FIGURES

Tab. 1: Radiocarbon dates for Švarcenberk central core. Core depths are the same as referred for the results of chemical analyses (Fig. 3).

Lab. No.	Core depth	Measured ^{14}C age	Method
LuA-4588	150-153 cm	4 650 ± 100 BP	AMS
LuA-4589	324-327 cm	6 350 ± 100 BP	AMS
LuA-4590	390-393 cm	9 640 ± 115 BP	AMS
LuA-4591	520-523 cm	10 780 ± 115 BP	AMS
LuA-4738	680-683 cm	11 750 ± 120 BP	AMS

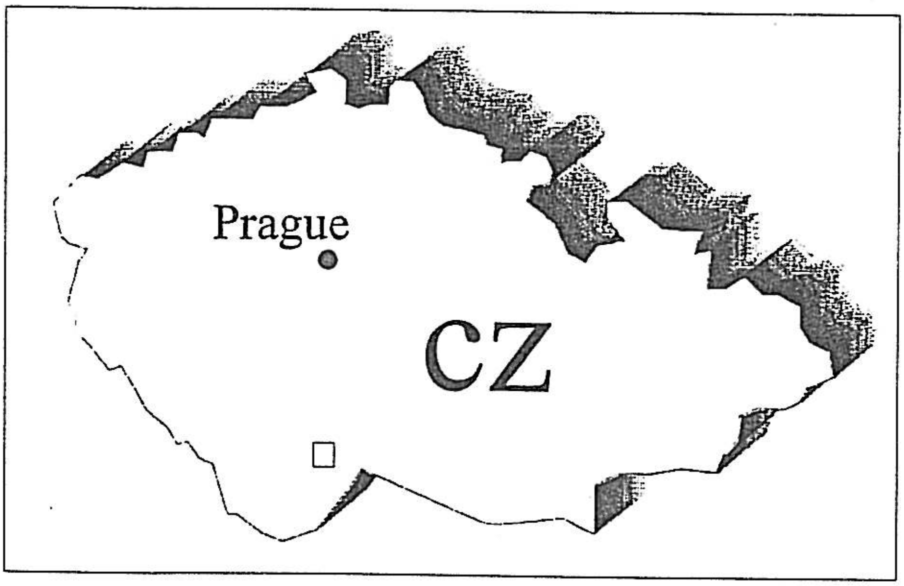
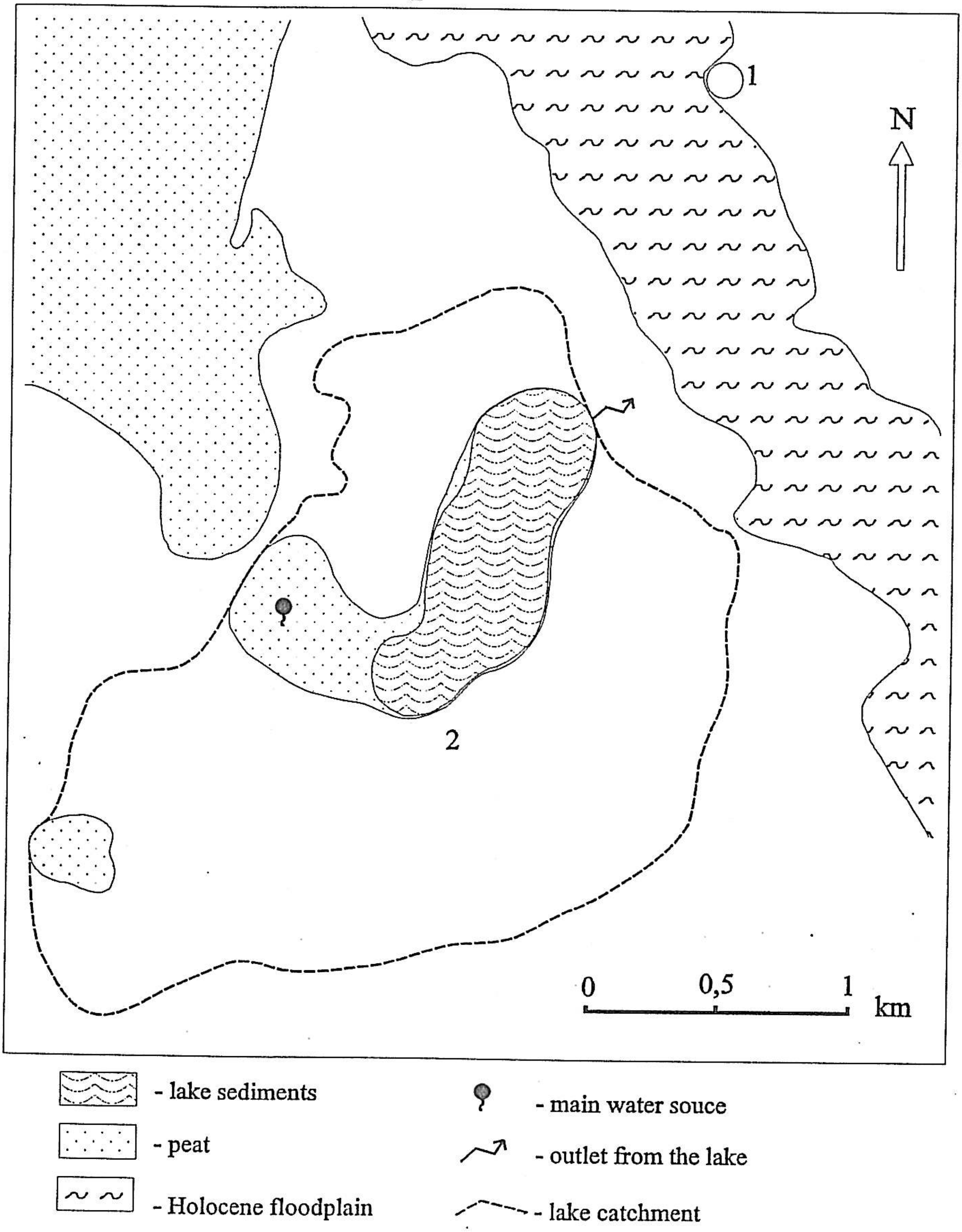


Fig.1. Location of investigated site within the Czech Republic.

Fig. 2. Quaternary geological map of investigated site. 1- „Vlkov sand dune“ eolic structure, 2- archaeological site with Mesolithic artefacts.

Švarcenberk landscape domain



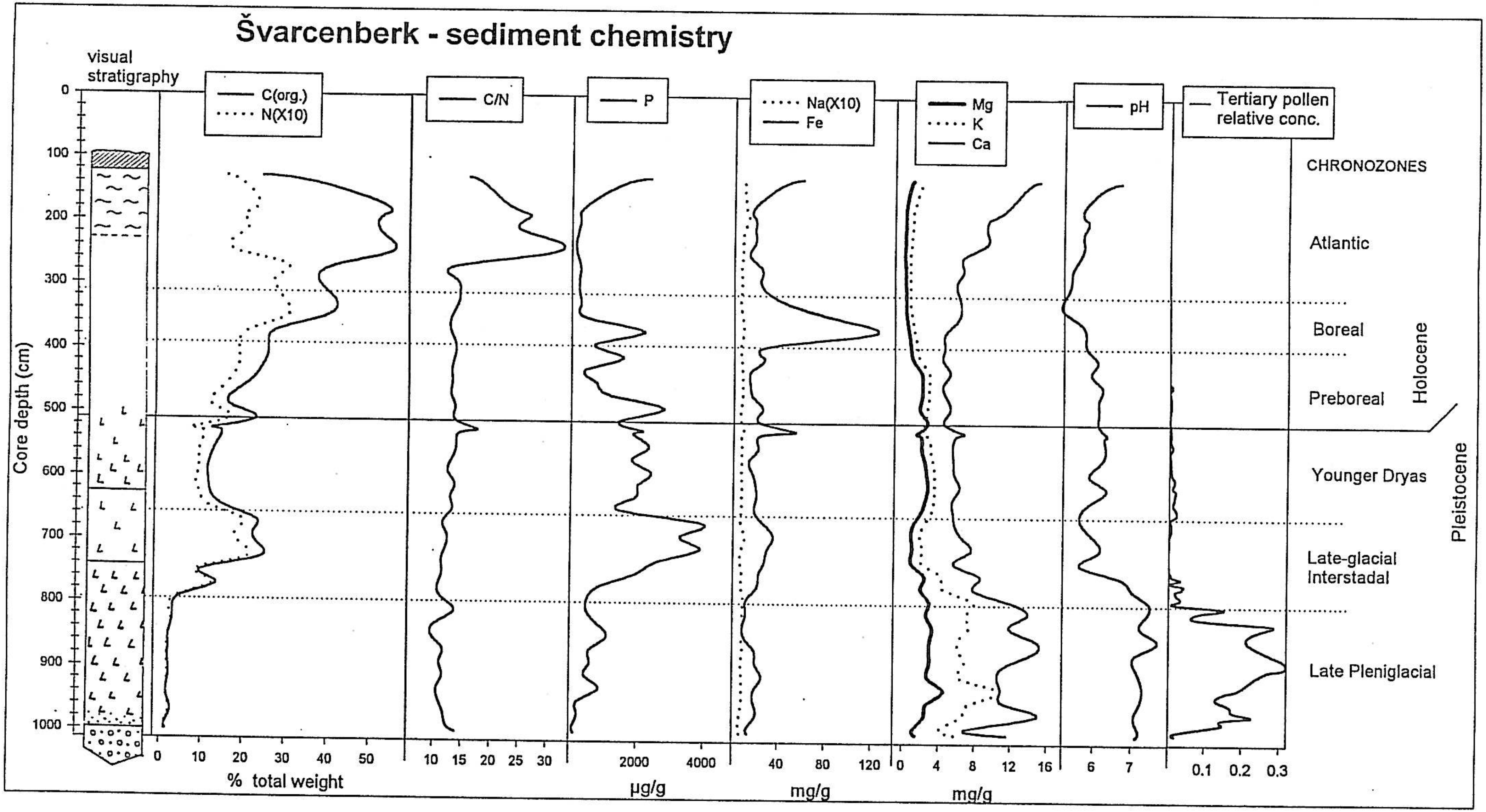


Fig. 3. The diagram of chemical composition of Švarcenberk central sediment core correlated with chronostratigraphic subdivision of Late Pleistocene and the Holocene. Tertiary pollen concentrations in sediments are expressed relatively to the number of all Quaternary pollen grains.

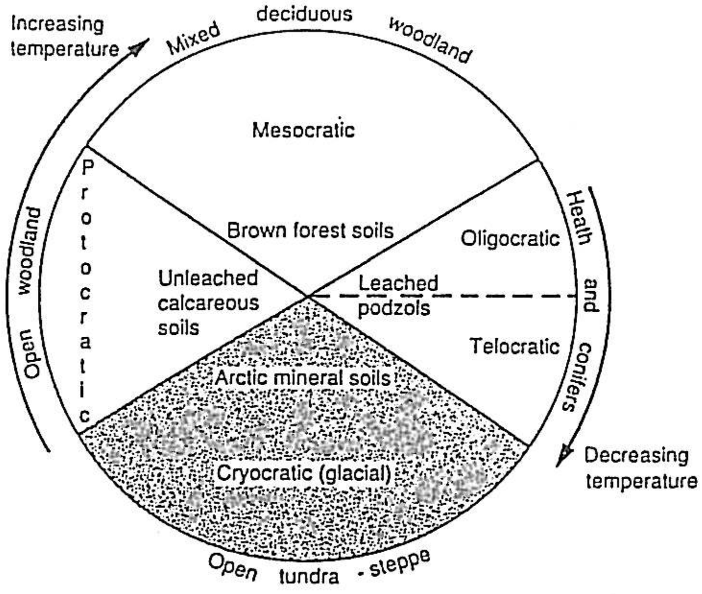
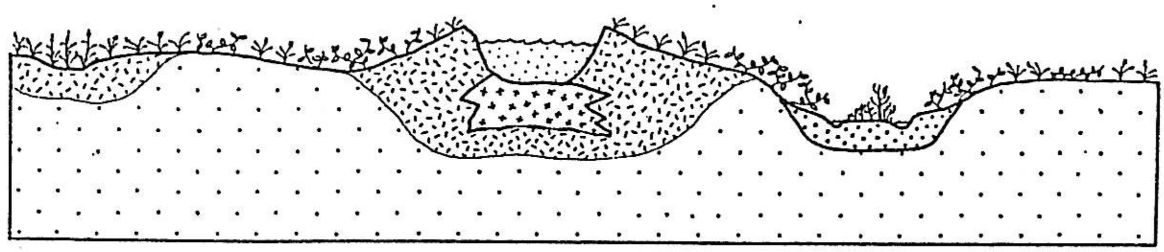


Fig. 4. The glacial-interglacial cycle model. (Modified from Iversen 1958).

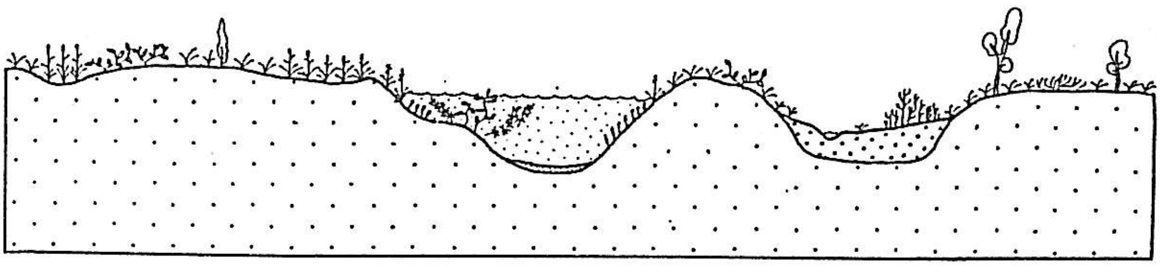
Tab.2.

Initial warming	**after 18 ka BP**
	
Reconstructed climate, soils, *etc.*	Warming from initial mean annual temperatures of about -1°C. Melting of the discontinuous permafrost. Continental climate. Bare, calcareous substratum, high erosion rate.
Reconstructed regional vegetation	Sparse herbaceous pioneer vegetation with grasses, Cyperaceae, Chenopodiaceae, dwarf shrubs (*Salix, Betula nana, Alnus viridis*), *Artemisia, Thalictrum, Helianthemum*. Possible pine refugia.
Lake basin development	Thermokarst (pingo) collapse is giving the lake its form. Pioneer aquatic vegetation dominated by Charophyta. Low lake productivity, minerogenic accumulation.

Tab.3.

Late Pleniglacial

15-13 ka BP

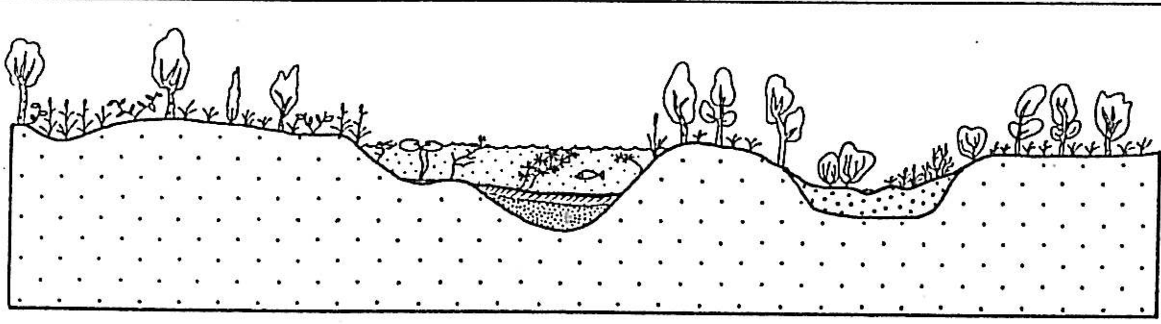


Reconstructed climate, soils, *etc.*	Mean July temperatures at least 11 °C, continental climate. Bare, calcareous substratum, high erosion rate. Weak initial pedogenesis possible in more stable periods.
Reconstructed regional vegetation	Prevailing sparse herbaceous vegetation with heliophyllous herbs and dwarf shrubs (dwarf willows, birch, alder and juniper). Individual pine trees scattered over the open landscape. *Hippophaë rhamnoides* on fresh gravel substrates.
Lake basin development	Anoxic conditions under maximum water depth of cca 9 m. Sparse submerged and floating-leaf aquatic vegetation. Low lake productivity, minerogenic accumulation.

Tab.4.

Late-glacial Interstadial

13-11 ka BP

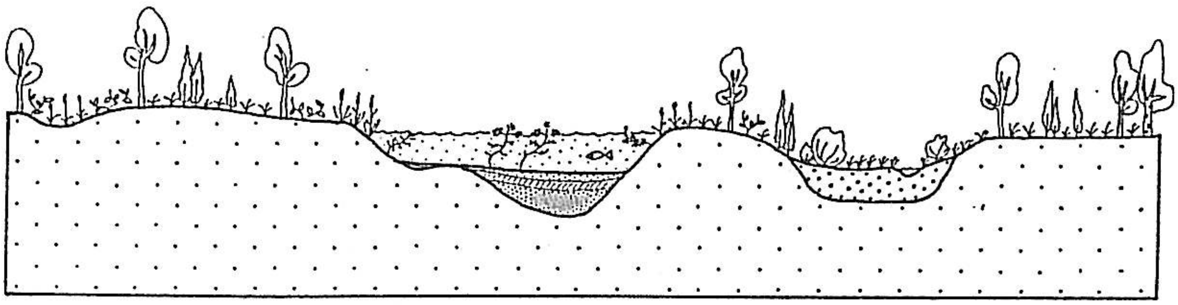


Reconstructed climate, soils, *etc.*	After abrupt climatic warming, mean July temperatures at least 12 °C. Less continental climate. Decalcification of the substratum, soil formation. Low erosion rate. Onset of peat formation at some sites.
Reconstructed regional vegetation	Reforestation of the landscape by birch and pine after the pioneer phase dominated by willow shrubs. Closing of the woodland resulted in decline (but not extinction) of heliophyllous vegetation.
Lake basin development	Dense submerged and floating-leaf aquatic vegetation in littoral. Increased lake productivity, onset of organic accumulation. Rich perch population in the lake. Maximum water depth about 6 m.

Tab. 5.

Younger Dryas

11-10 ka BP

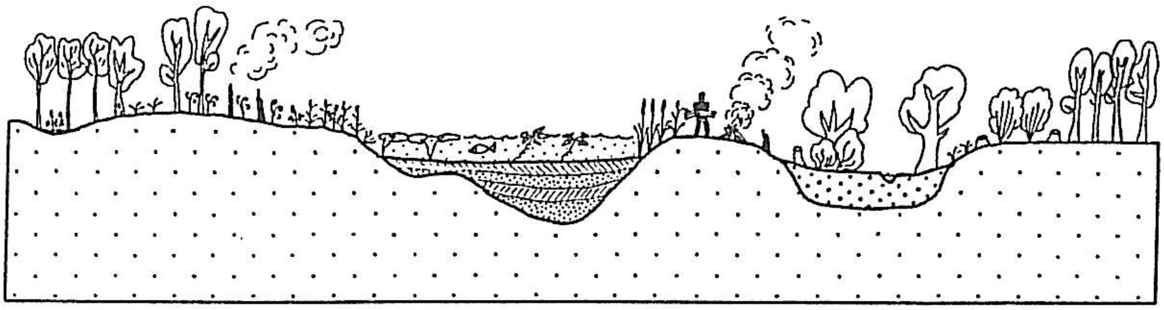


Reconstructed climate, soils, *etc.*	Climatic deterioration - increase in continentality. Minimum mean July temperatures about 12 °C. Slight increase in soil erosion and runoff. Increased eolic activity.
Reconstructed regional vegetation	Opening of pine-birch woodland, new development of pioneer herbaceous vegetation including dwarf shrubs. Juniper expansion on sites that were left open.
Lake basin development	Change in aquatic vegetation reflecting climatic deterioration. Decrease in lake productivity. Minerogenic accumulation.

Tab. 6.

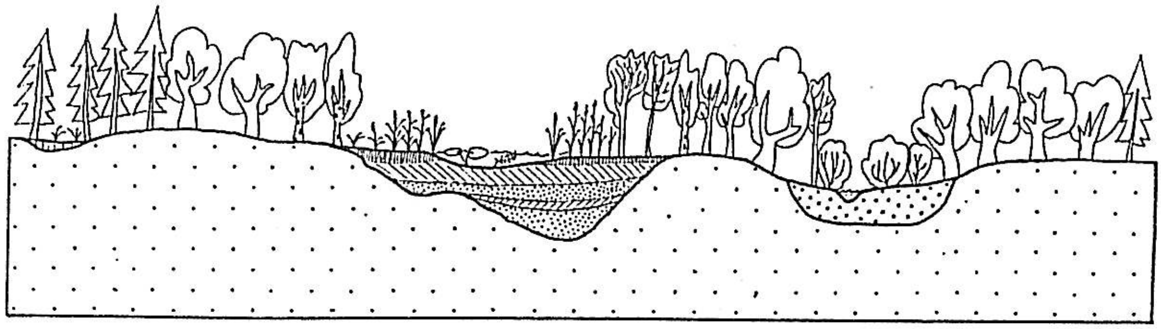
Early Holocene - Preboreal, Boreal

10-8 ka BP

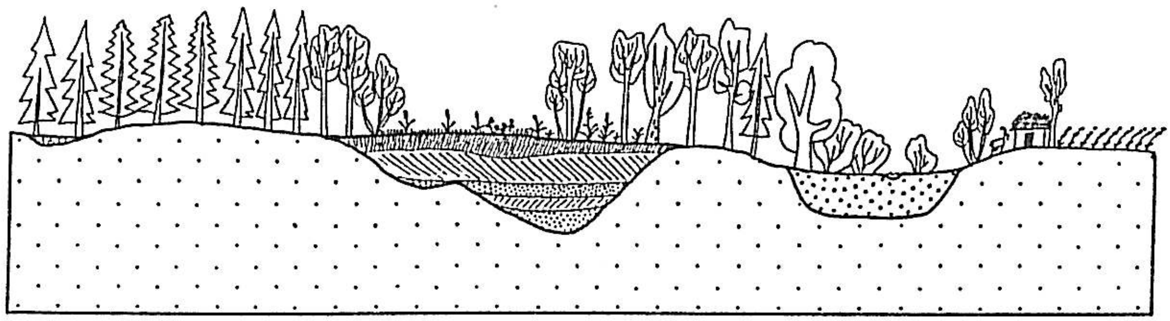


Reconstructed climate, soils, *etc.*	After abrupt climatic warming, mean July temperatures reached at least 15°C. Climate less continental compared to Younger Dryas, but relatively dry. Intensive soil development, low erosion rates.
Reconstructed regional vegetation	Initial period of *Populus* expansion followed by complete reforestation by pine and birch. *Pinus* and *Betula*- dominated forest than slowly replaced by mixed deciduous forest with transitional phase of hazel dominance. Remnants of Late-glacial open vegetation only on peat-bogs and eolic sand dunes. Vegetation development is only slightly modified by human action (fire).
Lake basin development	Demanding aquatic vegetation on lake (*Najas marina, Trapa natans* dominated). High productivity in the lake resulted in organic accumulation. Mesolithic hunter-gatherers on the shores. Maximum water depth about 3m.

Tab. 7.

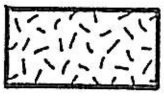
Holocene climatic optimum - Atlantic 8-5 ka BP	
	
Reconstructed climate, soils, *etc.*	Increase in oceanity, onset of warm and wet climate. Full soil development under stable climatic conditions followed by leaching and podzolisation. New peat formation at some sites.
Reconstructed regional vegetation	Full development of mixed deciduous forests. Pine stands only on sandy substratum. Expansion of *Picea abies* on waterlogged sites. Extinction of many open vegetation elements from the regional flora.
Lake basin development	Infilling of the lake from the margins. Alder carr expansion to the marginal fens. The site has been left abandoned by Mesolithic populations.

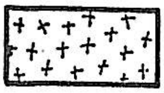
Tab. 8.

Holocene climatic optimum - Late Atlantic 5-4 ka BP	
	
Reconstructed climate, soils, *etc.*	Still warm, but less stable climate with some dry oscillations. Most soils are leached. Neolitic farmers affected the area only marginally.
Reconstructed regional vegetation	Expansion of *Abies alba* and *Fagus sylvatica* into mixed deciduous forests. *Ulmus* decline.
Lake basin development	After infilling of the lake, eutrophic fen started doming above surrounding terrain and changed into the oligotrophic, *Sphagnum*-dominated peat-bog.

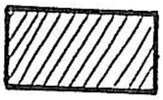
Appendix

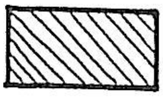
Descriptions of symbols used in reconstructions (included in synoptic tables):

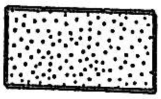
 - permafrost

 - underground ice

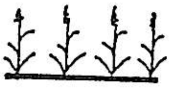
 - peat

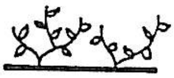
 - Interstadial organic mud (gyttja)

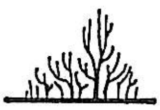
 - Holocene organic mud (gyttja)

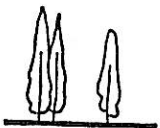
 - minerogenic sediments

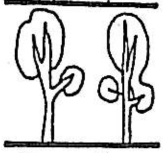
 - grass communities

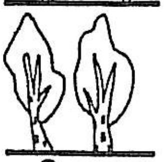
 - sedges

 - dwarf shrubs

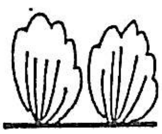
 - *Hippophaë rhamnoides*

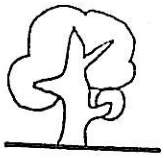
 - *Juniperus*

 - *Pinus*

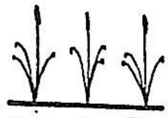
 - *Betula*

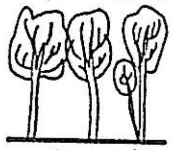
 - *Salix*

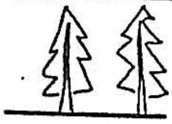
 - *Corylus avellana*

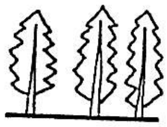
 - mixed oak wood

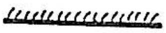
 - *Pteridium aquilinum*

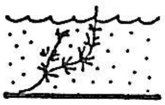
 - *Phragmites* (reed swamp)

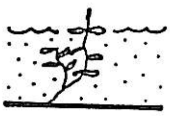
 - Alnus glutinosa

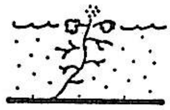
 - Picea abies

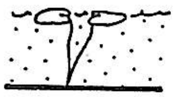
 - Abies alba

 - *Sphagnum* mosses

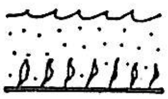
 - *Myriophyllum*

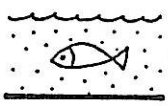
 - *Potamogeton*

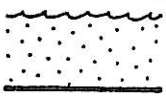
 - aquatic *Ranunculus*

 - *Nymphaea* or *Nuphar*

 - *Trapa natans*

 - Charophyta

 - fish (perch)

 - open water

IV. A HIGH-RESOLUTION RECORD OF LATE-GLACIAL AND EARLY HOLOCENE CLIMATIC AND ENVIRONMENTAL CHANGES.

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Abstract: Recent discovery of thick buried lake sediments in the Třeboň Basin, South Bohemia, presents an exceptional opportunity to study the Late-glacial history of eastern part of Central Europe. High-resolution investigation of pollen, plant macrofossils, algal remains, and lithology for the Late-glacial and early-Holocene sediments of former Lake Švarcenberk yielded a well-founded palaeoclimatic and palaeovegetational data that can be compared with tresults from other parts of west-east European transect, taking into account the oceanic/continental gradient and its influence to palaeoenvironmental conditions. The results demonstrate that the effect of North Atlantic oceanic changes during the last glacial-interglacial transition extended to the investigated area. Nevertheless, significant differences in timing, intensity, and character of vegetational response to these climatic changes have been found between area under study and western part of Central Europe. These differences can be ascribed to increased sesonality, specific regional mesoclimatic and soil conditions, and possible local glacial refugia for pine. The results of sediment chemical analyses indicate a close correspondence between climatic, vegetational, and soil development in lake catchment.

INTRODUCTION

Organic deposits suitable for palaeoecological research usually began to form about 13 ka BP in western and north-western Europe, being classified in different Late-glacial phases by pollen analysis. In non-glaciated, continental regions of Central Europe this subdivision is usually not possible, either because minerogenic sediments contain no pollen or because sediments simply did not accumulate at this time. Particularly lacustrine sequences are very rare in these regions. The profile under study in the Czech Republic is a unique example with extensive and well-stratified Late-glacial record. High sediment-accumulation rates permit the detection of brief Late-glacial climatic oscillations, so that comparison can be made with numerous results from western and northwestern Europe, where the basic biostratigraphic and climatostratigraphic concepts have been developed (Iversen, 1954; Magerund *et al.*, 1974; Watts, 1979). As postulated by Ruddiman and McIntyre (1981) and later recognised in terrestrial records within the areas adjacent to the North Atlantic (e.g. Lowe *et al.*, 1994; Walker, 1995), the rapid climatic changes during the last glacial-interglacial transition can be ascribed to large-scale shifts in the position of the oceanic Polar Front, which have amphi-Atlantic or even global effects (e.g. Peteet, 1995).

The goal of the present study is to test the validity of some of these concepts as applied to the eastern part of Central Europe. The great distance from North Atlantic and from major ice sheets, as well as the high degree of regional environmental diversity, are the most important factors that could cause certain differences in climate and provoke distinct biotic responses to climatic changes in the area under study. It is well known that the response of populations (e.g. plant populations) to climatic change is likely to be greatest near the margin of their distributional limits (Watts, 1979). Rapid climatic changes during the last glacial-interglacial transition usually affected only local populations and did not permit long-distance migrations (Ammann, 1989). This caused a high degree of inter-regional biological diversity, depending on local availability of species. For example, in the intermontane basins of Western Carpathians, some 250 km east of the study area, local populations of *Pinus cembra, P. sylvestris, Larix decidua*, and *Picea abies* responded to the onset of Late-glacial climatic amelioration by expansion to higher altitudes from their locally present glacial refugia (Ralska-Jasiewiczova, 1980; Jankovská, 1984; Rybníček and Rybníčková, 1994). This pattern is completely different from any other recognised in Europe north from the Alps, which probably had no local glacial refugia.

In spite of the problems with absolute dating of Late-glacial events due to the occurrence of ^{14}C plateaus, the biostratigraphic subdivision of NW European Late-glacial is today well fixed on absolute time scale (Ammann and Lotter, 1989; Wohlfarth, 1996, Hoek, 1997). In this paper, detailed correlation of recognised biostratigraphic boundaries with events described from other parts of Europe is not possible on an absolute chronological basis due to the lack of more AMS radiocarbon dates of terrestrial plant remains. Biostratigraphical terminology is therefore followed in this paper. Local pollen assemblage zones (PAZ) are correlated with regional climatostratigraphical units according to Magerund *et al.* (1974) and Ammann and Lotter (1989). This correlation is only roughly confirmed by available ^{14}C dates.

The study area and site

The study site is situated in South Bohemia in the flat landscape of the Třeboň Basin (which has an area about 700 km^2 and maximum relief undulation of 20 - 40 m). 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 content of clay 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 phosphate is medium (Husák and Hejný, 1978). Most soils are leached and show a tendency towards podzolization. The soil reaction is mostly highly acidic (pH up to 3.3). Various types of podzols and sandy or peaty gleys prevail.

The present climate is suboceanic and is determined by prevailing westerly air masses, already significantly reduced in moisture by passage across central Europe. The region is somewhat sheltered by the Šumava-Bavarian Forest highlands. Macroclimatic conditions are strongly modified by presence of extensive wetlands: Frequent occurrence of fog is typical for the region. Annual mean precipitation is 622mm (January being the driest), annual mean temperature is 7.4 °C (see climatic diagram, Fig.1b).

The potential vegetation of the Třeboň Basin would generally be silver fir-oak woodlands (*Abieti-Quercetum*), in waterlogged areas bird cherry-pendulate oak and -alder woodlands (*Quercus robur-Padus avium* and *Alnus glutinosa- Padus avium* communities), alder carrs (*Carici elongatae-Alnetum*), reed swamps and tall-sedge communities (*Phragmito-Magnocaricetea*) (Neuhäuslová *et al.*, 1998). Vast transitional peat bogs are still dominated by forests of Bog-pine (*Pinus rotundata*). Acidophillous pine (*Pinus sylvestris*) forests with oak (*Quercus robur*), birch (*Betula pubescens*), and spruce (*Picea abies*) prevail on dry soils of river terraces and aeolian sands.

The Třeboň Basin, originally an inaccessible swampy area, remained largely a wilderness until the 13th century. During Late Medieval, it developed into the cultural landscape of fish culture and forest plantations, and fishponds still constitute a characteristic element of the landscape.

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 analysis of some types of arboreal pollen. According to his results, the basal age of some investigated deposits was later established to be of „Kiefern-Zeit" (Rudolph and Firbas, 1922). The early postglacial age of most peat deposits in Třeboň basin was later confirmed by Klečka (1926, 1928) and Štěpánová (1930). Small pollen counts and exclusive focus on arboreal pollen were the disadvantages of these early palynological investigations. In the early 1960's, Jankovská started her palaeoecological investigations of Třeboň Basin, using modern approaches. Her work (Jankovská, 1980) forms the basis of our knowledge of the area.

The former lake Švarcenberk is situated 4 km south of the city of Veselí nad Lužnicí (49° 9'N, 14° 42'E) at 412 m. a.s.l.. Limnic sediments are overlain by peat, which formed after the terrestrialisation 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 has been constructed directly on the site, and its waters almost completely flooded over the peat and the underlying lake sediments. The only presumed remnant of original vegetation cover are the small patches of tall sedge and *Sphagnum* communities (*Eriophorion gracilis* and *Rhynchosporion albae*) in western part of the locality.

For local hydrology the presence of several strong artesian springs is characteristic. The underground water ascends along a deep tectonic fault and is rich in iron oxides. The former lake was presumably supplied almost exclusively by this artesian water. The activity of underground water sources was apparently independent of general climatic fluctuations in the past. As a result, lake water-level remained almost constant over the millennia and can't be used as a climatic indicator, unfortunately. The lake has drained into nearby Lužnice River. For evaluating the regional pollen rain on the site, close vicinity to the river floodplain is an important fact.

Along the river floodplain, numerous eolian deposits are situated. One of the biggest and most prominent sand dunes, „Vlkovský přesyp", is situated not far from the former lake basin (1200 m). Its relative height over surrounding terrain (6 meters), its size (60 X 80 m), and the unvegetated character make it a prominent structure on the landscape. According to its morphology, „Vlkovský přesyp" sand dune was formed by an easterly wind. The material constituting it is derived directly from nearby river floodplain (carried by wind for tens or hundreds of meters) according to the mineralogical analyses of Chábera (1982).

The existence of former Lake Švarcenberk was noted for the first time by Vlasta Jankovská in late 70s. In her study, which focused on the vegetational development of Třeboň Basin (Jankovská, 1980), she presents a pollen diagram and macrofossil analysis obtained from an open pit. Her profile comprised about 1.5 m of lake sediments, and she correctly assumed that she dealt with the littoral facies of a larger lake. Unfortunately, no stratigraphic data were obtained. The present study fully confirmes Jankovská's original assumption.

METHODS

Field methods, sediment description, and subsampling

During the pilot study, the extension and stratigraphy of the former lake basin was studied by coring in a 100m X 100m grid (sampling distances were reduced along the shores). For subaquatic coring a boat was used. Two right-angle transects across the basin were chosen as reference sections (shown in Fig. 1c and 2). They have their crossing point in the centre of the basin, where the „main profile" is situated. The distances in metres and the geographical position (N, S, E, W) in relation to this zero point is given by the core labels. The cores were levelled according to fishpond water level. The coring was performed with Russian-type corer (Jowsey, 1966) 5 cm in diameter. The sampling point S500 was opened by hand-made pit. Correlation of the individual cores across the basin was achieved by visual stratigraphic description and further confirmed by pollen analysis in some cases.

The core in the centre of former lake was selected as the standard profile for the following reasons: The central core will most probably show a continuous record without hiatuses, and it is more likely to give an „average" picture of the events in the basin and its catchment (without the background of local „noise", which is assumed to be greatest along the shores). This „main profile" actually consist of seven separate parallel cores taken close together in order to obtain enough material for all kind of analyses. The coring was again performed by the Russian-type corer 5 cm in diameter. This type of device permits complete recovery of the section penetrated. All cores comprising the „main profile" were correlated according to their visual lithostratigraphy. This correlation only confirmed the satisfactory accuracy of parallel sampling.

Sediment description follows the system of Troels-Smith (1955) as modified by Aaby and Berglund (1986). The colours were determined according to standard (Munsell) soil colour charts. The subsampling intervals depended on the required temporal resolution and the sample volume needed for each analysis. Closer subsampling was undertaken in order to get enough material for additional analyses if needed (as advised by Moore *et al.*, 1991).

The stratigraphy of „Vlkovský přesyp" sand dune was studied in an open ditch.

Macrofossil analysis

After subsampling for other analyses, the remaining material was used for macrofossil analysis. Contiguous samples 10 cm long were cut, and the volume of each was determined (it spanned around 250 ml in all cases). Macrofossils were extracted by heating each sample for 5 minutes in a 5% potassium hydroxide (KOH) solution and sieved with running water. Sieves with mesh sizes of 200 µm, 300 µm and 700 µm were used. The residues were examined under a dissecting stereomicroscope. The absolute number of each kind of macrofossil was recalculated to a standard volume of 500 cm^3 fresh sediment. For determination of the seeds/fruits a reference collection and the atlas of macrofossils (Kac *et al.*, 1965) were used.

Pollen analysis

The samples used for pollen and other microfossils analysis were prepared by a modified acetolysis method. As the Late-glacial part of the core had more or less mineral character, the samples were pre-treated with concentrated (35%) cold hydrofluoric acid (HF) for 24 hours (Faegri and Iversen, 1989; Moore *et al.*, 1991). The extracted microfossils were lightly stained by 0.3% safranin and mounted in liquid glycerol-water (1:1) mixture. In each sample at least 1500 pollen grains were counted, except only 500 - 700 grains in the lowermost samples poor in pollen. For pollen identification, the following keys were used besides a reference collection: Faegri and Iversen (1989), Moore *et al.* (1991) and Punt (1976-1996). Pollen nomenclature follows ALPADABA (*Alpine Palynological Data-Base*, housed at the Geobotanical Institute, Bern).

An attempt was made to subdivide *Alnus viridis* and *Betula nana* in the pollen diagram. *Alnus viridis* pollen was found to be relatively easily separable in my material. More difficulties were connected with *Betula nana* pollen identification. As the difference in pollen morphology between *Betula nana* and arboreal birch species is largely quantitative (Birks, 1968; Usinger, 1975), the exact separation was impossible in all cases. When uncertainties occurred, problematic pollen was ranked as „*Betula* indet.". This category represents typically about 30% of total *Betula* pollen in the Late-glacial sequence. It is included in the pollen sum but is not shown in pollen diagram.

Algae and other microfossils were identified with the help of publications of Van Geel *et al.* (1981, 1983, 1989), Jankovská (1983), and Jankovská and Komárek (1982).

Absolute pollen concentrations were estimated by volumetric method (Davis, 1965). As the volumetric method has been proved by Walker *et al.* (1994) to give the results with a relatively high standard deviation, pollen-concentration determinations were not used for pollen-influx calculations. The pollen-concentration curve has been included only in the main pollen diagram (Fig. 3) to give a rough idea about absolute pollen content of the sediment.

The lowermost Late-glacial and particularly Pleniglacial sediments contained a lot of reworked Tertiary pollen. An attempt for reliable separation of these pollen grains was made in order to avoid possible misinterpretations of Late-glacial pollen spectra and in order to obtain a tool for assessment of erosion rates within the lake basin and its catchment. In this approach it is assumed that reworked pollen grains embedded in Late-glacial and Holocene sediments originated primarily from eroded Tertiary subsoil sediments in the lake catchment, including lake shores. Some of the Tertiary taxa are easily recognised according the pollen morphology (e.g. *Engelhardtia, Carya, Liquidambar*), but some are difficult or even impossible to separate in a morphological basis only. Fortunately, the state of preservation of the Tertiary pollen was relatively poor in my material, giving pollen grains a „ghosty" appearance. It has been assumed that different degree of fossilisation resulted in different chemical composition and physical properties of the exine. Consider with this assumption, a simple method was developed to confirm the Tertiary origin of some pollen grains: Pollen preparations, already stained by 0.3% safranin, were bleached in 40% ethanol for one minute. Than they were centrifuged and transferred to glycerol-water mounting medium again. As the result of this procedure, all pollen grains were bleached to different degree, but the Tertiary ones became almost completely transparent and hence easily separable from the Late-glacial ones.

The standard pollen diagram

The selection of types included in the pollen sum is always an important stage in the interpretation of palynological results. Excluded from the sum are therefore types potentially produced by the local aquatic and marsh vegetation of the lake. In the case of the Late-glacial however, it is difficult to evaluate exactly the role of certain wetland taxa (e.g. Cyperaceae, *Equisetum, Salix*) in the regional vegetation cover, as we do not have exact modern analogues to the Late-glacial communities (Watts, 1979; Moore, 1979). Percentage values were therefore calculated on the basis of the AP+NAP pollen sum, excluding only submerged and floating-leaf aquatics but including monolete and *Equisetum* spores (in many plant communities, these taxa usually have an ecological role equivalent to that of higher plants). Concealed, corroded, degraded, and well preserved but indeterminable pollen grains were put together and labeled „varia“ in the pollen diagram. Printing of the diagrams was made with the TILIA computer program, written by E. C. Grimm (Springfield).

The pollen diagram was zoned visually, on the basis of both presence and abundance of taxa. A more formalised approach to delimit the local pollen assemblage zones was also applied on the basis of three different constrained classification procedures implemented in the computer program ZONE (Lotter and Juggins, 1991). Consistency among results from these three different zonation procedures provided the basis for confirmation and further specification of visually delimited local PAZ.

Sediment chemistry and ^{14}C analyses

Numerous palaeolimnological studies have shown how sediment chemical properties may be interpreted in terms of processes acting within the lake and the surrounding catchment (e.g. Na, K, and Mg content in sediments directly reflect the intensity of weathering and erosion). These processes are often directly or indirectly related to climatic parameters, and their understanding may enable further climatic reconstructions (Engstrom and Wright, 1984; Dearing, 1991).

Total carbon and nitrogen content was determined by combustion at 950 °C in pure oxygen, with subsequent conductivity detection of C and N oxides (in Heraeus CHN-Rapid Analyser). Carbonate content was measured by sodium hydroxide titration to neutral pH after dissolution of 0.5 g sample in 0.5 M hydrochloride acid and boiling for 20 minutes (after Hammarlund and Buchardt, 1996). Total organic carbon content was calculated from the difference between total carbon and carbonate carbon.

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

Radiocarbon dates used in the present study are all AMS dates determined from bulk sediment samples and individual plant macrofossils (for sample description see Tab. 1). The disadvantage for the Late-glacial sequence under the study is the absence of enough terrestrial plant macrofossils for the dating purposes. The dates from gyttjas, clayey lake sediments, and aquatic plant macroremains are known to give ages which usually exceed those obtained from terrestrial macrofossils (Törnqvist *et al.*, 1992). This effect is often ascribed to the hardwater error. In the present study a hardwater error is expected to be relatively small, as the sediments contain negligible amounts of carbonates. Radiocarbon analyses were carried out by the Radiocarbon Dating Laboratory, Department of Quaternary Geology, Lund, Sweden. The samples have been pretreated with HCl and NaOH. Age calculations are based on a ^{14}C half-life of 5568 years. For the purposes of simplicity and comparability, dates are expressed in uncalibrated ^{14}C years before present (BP) unless otherwise stated.

Multivariate data analysis

In an attempt to study the similarities among individual pollen spectra, a detrended correspondence analysis (DCA) was made for a complete Late-glacial and Early Holocene data set. Pollen percentages of individual taxa were used as input data for the CANOCO 3.10 (ter Braak, 1990) program. DCA results, plotted as ordination diagrams on DCA axes 1 and 2, show the overall trends in the data (Fig. 7). Similar samples are close together and dissimilar samples are far from each other.

To study the relationship between the composition of individual pollen spectra and sediment chemical composition, a canonical correspondence analysis (CCA) (ter Braak, 1986) was made for the combined data set, including pollen percentages and chemical data. Program CANOCO 3.10 was again used. Plot of the centroid of sediment-chemistry variables in the intersection of CCA axes 1 and 2 was constructed (Fig. 8) in order to summarise the results graphically.

RESULTS

Lake basin, its origin and stratigraphy

The extend of lake deposits within the basin was mapped in detail by approximately 120 hand borings. The altitude of individual stratigraphic transitions was obtained by relative levelling. The former lake was found to have a maximum surface 0.51 km^2, and the ratio of the surface to drainage basin to be about 1:8 (Fig. 1a). Two lithological cross sections (Fig. 2) show the morphometry and the infilling of the depression. Correlation of the individual cores across the basin was achieved by visual stratigraphy, which reflects well the environmental conditions during the time of sedimentation (e.g. Younger Dryas sediments are characterised over the entire basin by the presence of three distinct yellowish layers of eolian material, each about 1 cm thick). The borders distinguished between several litostratigraphic units can therefore be assumed to be roughly time-parallel. In two littoral sampling points, S500 and JC-7B (the latter made and studied in SW part of the basin by Jankovská, 1980), pollen analysis confirmed this assumption. Only the limno-thelmatic contact, marking the time of final infilling of the lake, was expected to be metachronous over the basin. Radiocarbon dating in the littoral part (sampling point S500, with a date of 6 340±110 BP directly at the limno-thelmatic contact) and the central part of the lake (the „main profile", with an almost identical date of 6 350±100BP at a level significantly under the limno-thelmatic contact) confirmed this expectation.

The striking features of the basin morphometry is its kidney-shaped form, surprising depth and declivity (the presence of unusually steep slopes), and relatively great age of its infilling. Unfortunately, no radiocarbon date exists from the basal sediments, but their age is estimated around 16 000 BP from the pollen-analytical results. On the basis of these finds, the origin of such structure can be best explained as the remnant of a huge Pleniglacial ground-ice lens - an open-system pingo. The absence of a distinct rampart around the former lake is not surprising, as the original geomorphology of the site was 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, although they are relatively large in diameter (Washburn, 1980). These structures do not form a distinct rampart after they collapse. What is more surprising in case of former lake Švarcenberk is the unusually big size of its depression. Considering this fact and the observation of the „ridges" (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 a compound pingo structure.

In the littoral parts of the former lake basin, only a thin layer of Late-glacial sediments is present, completely lacking deposits older than Younger Dryas. This can be explained by intensive reworking of the shores during Late-glacial rather being the result of lower lake levels during this period. As the lake was fed almost exclusively by artesian water, water-level remained constant over the entire period of its existence, and water-level reconstructions can't be used as a climatic indicator, unfortunately. After the final infilling of the lake (dated to approx. 5 500 BP), oligotrophic peat started to accumulate.

Main biostratigraphic events and geomorphic processes

Pollen stratigraphy of the „main profile" has been subdivided into six local pollen assemblage zones (PAZ) and eleven subzones, which are used as a framework for the discussion of the results. Because of terminological problems (e.g. Ammann and Lotter, 1989; Walker, 1995) I have decided to subdivide the diagram in this way rather than into Firbas (1949) pollen zones, as is traditionally done in Central Europe. The absence of analogous results over a wide region discourage the use of regional pollen zonation. The local PAZ are later compared (Fig. 9) with European climatostratigraphical units according to Maagerud *et al.* (1974) and Ammann and Lotter (1989) and with the $\delta^{18}O$ curve of the Greenland ice core GISP2 (Stuiver *et al.*, 1995).

Zone S1

The lowest sediments of the lake-basin infill consist of fine silt with coarser sand. Absolute pollen concentrations in the sediment are low. The zone is characterised by high NAP values, suggesting an open herbaceous vegetation. Grasses, Cyperacese, Chenopodiaceae, *Betula nana, Alnus viridis, Salix* (most likely some dwarf willow species), *Thalictrum*, and *Artemisia* were important components of the vegetation. Macroscopic stem fragments of *Salix sp.* were found in the sediment. Sporadic pollen finds of *Ephedra* (both *Ephedra distachya* and *E. fragilis* types) are difficult to interpret, as this type of pollen can be dispersed over long distances (Huntley and Birks, 1983; Lang, 1994). *Pinus* values are below 30%, *Betula* values do not exceed 5%, and both can be ascribed to long-distance transport as well. *Helianthemum* is indicative of bare, calcareous substratum (Hoek, 1997). The abundance of Cyperaceae pollen in relation to *Artemisia* pollen indicate prevailing moist conditions for zone S1. This can be the result of the presence of permafrost and its progressive decay from the surface. Pollen of submerged water plants is absent, and the seeds of *Ranunculus* subgen. *Batrachium* and *Potamogeton* cf. *gramineus* are rare, while Charophyta oospores (cf. *Chara strigosa*, a pioneer species with subarctic distribution) are exceptionally abundant. *Ranunculus* subgen. *Batrachium* is a climatic indicator for maximum July temperatures of at least 10 °C, while *Hippophaë rhamnoides* presence (found as pollen) suggests at least 11 °C (Huizer and Izarin, 1997). Due to the absence of plant macrofossils suitable for ^{14}C dating and the mineral character of the sediment, absolute dating of this zone unfortunately was not possible. The age is only roughly estimated to be around 16 000 BP.

Very low organic content of the sediments suggest low productivity in the lake as well as in its catchment. The lower Mg, Ca, and K content, if compared to the S2 zone, is most likely the result of high proportion of coarse sediment (and high accumulation rates), rather than lower allogenic sediment input to the lake basin.

All the results point to severe climatic conditions, the absence of well-developed soils, and an open, treeless vegetation of steppe and tundra during S1 zone. A significant difference in the character of the vegetation between this and the higher zones was confirmed also by

DCA results (Fig. 7), for the samples of the S1 zone are plotted in the ordination diagram far from the main „cloud" of samples, indicating significantly different composition of their pollen spectra.

Zone S2

This zone starts with a rise in *Pinus* pollen percentages up to 50%, together with a decrease in *Cyperaceae* and a prominent *Artemisia* peak. Pollen of submerged water plants occur for the first time. *Betula* pollen curve is continuous during the entire zone, but still too low (under 5%) to suggest the local occurrence of tree birch. As in the previous zone, grasses, Cyperaceae, Chenopodiaceae, *Alnus viridis,* dwarf willow, *Thalictrum, Artemisia,* and *Betula nana* were important components of the vegetation. Seeds and catkin-scales of dwarf birch (*Betula nana*) were found in the sediment. *Empetrum* pollen percentages around 1% suggest local presence but not the development of extensive *Empetrum*-dominated heaths (acording to quantitative criteria given by Huntley and Birks, 1983). Relatively high *Helianthemum* percentages (up to 3%) point to the presence of calcareous substratum. This accords well with the results of sediment chemical analyses, showing high Ca content. This find is in sharp contrast with present-day conditions in the area under study, for most soils are leached, highly acidic, and almost completely lacking calcium carbonate. The absolute pollen concentrations in the sediment are still low during this zone.

The silty FeS-coloured sediments in the centre of the basin suggest anoxic conditions, as iron-sulphide deposition usually occurs under prolonged or permanent stratification of the lake (EngstromandWright, 1984). Sediment organic content is only around 3% and reflects low productivity in the lake and its catchment. High content of Na and K and of reworked Tertiary pollen suggest high erosion rates and the absence of stable soils in the catchment.

Subzone S2a

The rise in *Pinus* percentages up to values around 60% suggest the onset of pine expansion in the area as the result of some climatic amelioration. Individual pine trees must have been scattered more or less sporadically in the landscape of steppe or tundra-like character. The rise in *Artemisia* shortly before this time can be also considered as the first signal of warming. The find of *Urtica dioica* seed (together with *Urtica* pollen) is particularly interesting from the point of environmental reconstruction, for this nitrophillous plant, requiring mean July temperatures at least 8 °C (Bos, 1998), is distributed in eutrophic habitats today. This is in sharp contrast to the general picture of the S2 subzone, which points to prevailing oligotrophic and distrophic conditions in the lake and its catchment (see also the low sedimentary N content). There must have existed some favourable, nutrient-rich microhabitats (bird-manured patches, for example), where *Urtica dioica* could have prospered.

Subzone S2b

The signs of progressive climatic amelioration are traceable from the pollen record during the onset of S2b subzone as *Pinus* values rise up to 75%. The local presence of pine is confirmed also by the find of *Pinus* stomata. Pine became a successful competitor for light with the heliophyllous vegetation. Overshading occurred in moist habitats, as seen from the decline of *Salix* and Cyperaceae pollen percentages, but also in drier habitats, as *Artemisia* and Gramineae declined during *Pinus* maxima as well. If we compare the pollen concentration curve (attached to the pollen diagram in Fig.3) for S2b subzone with the others, particularly S3 and S4, zones, it become obvious, that the rise in *Pinus* is not due to the percentage effect caused by generally low regional pollen production (Moore *et al.*, 1991). The dating of this subzone is unfortunately uncertain, due to the absence of appropriate material for ^{14}C analysis again. It is only roughly estimated to range between 15 000 and 14 000 BP.

Subzone S2c

The decline of pine and new expansion of heliophyllous herbs in this subzone can be correlated with Oldest Dryas chronozone (sensu Stuiver *et al.*, 1995). Unfortunately, exact ^{14}C dating of this event is again missing. In the upper half of S2c subzone, a new pine expansion anticipates the transition to S3 zone. An interesting macrofossil find, a shrew (*Sorex* cf. *araneus*, det. by I. Horáček) mandible, was made within this subzone. The mandible comes from adult specimen, but its size is unusually small. Its phenotypic appearance significantly differs from contemporary populations. Shrews were in general rare constituents of late Pleistocene faunal assemblages. This find is particularly interesting from palaeoecological point of view, for shrews are characteristic for sparsely wooded landscapes (I. Horáček, pers. comm.), consistent with the palaeobotanical results that suggest sparse tree cover during that time.

Zone S3

Marked vegetation changes are characteristic for this zone. Reforestation of the landscape by birch and pine resulted in decline in heliophyllous herbs. Absolute pollen concentrations in the sediment are now about three times higher than in the underlying zone. Soil development under forested conditions led to the decrease in erosion rates (see progressive decline in sedimentary Mg and K and sharp decline in reworked Tertiary pollen). Decalcification of the substratum continued up to the maximum extent (see the decline in Ca down to the values comparable with those in the Holocene). Increased organic production resulted in gyttja sedimentation. Abundant perch (*Perca fluviatilis*) scales were found in the sediment. Perch is an anambitious fish genus that can survive even in subarctic lakes. The fry are produced in large quantities and feed on planktonic or benthic organisms. Adults feed mostly on their own young and reach high population densities. Such an interesting cannibalic food chain has been described from several contemporary Siberian lakes (Holčík, 1977; Karasev, 1987).

Subzone S3a

This subzone starts with a rise in *Salix* pollen percentages, followed by *Betula* increase. *Salix* probably formed the shrub belt in front of the *Betula* forest-line (Gaillard, 1985; Hoek, 1997), so high values of *Salix* may be expected in advance of a *Betula* expansion. In the second half of S3a subzone, tree birch became dominant in the pollen spectra in place of NAP and *Pinus*. *Betula* cf. *pubescens* seeds and catkin-scales were found in the sediment. This assemblage reflects the development of an open boreal birch woodland with dispersed pine trees. The lower limit of mean July temperature needed for tree birch colonisation is usually taken as 10 °C, but 12 °C is the optimum for the development of *Betula pubescens* woodland (Birks, 1993). An open character of the forest can be inferred from the pollen diagram, for most of the heliophyllous herbs typical for steppe and tundra communities are still abundant. In the aquatic environment, abrupt climatic amelioration caused the expansion of submerged macrophytes, including *Ceratophyllum demersum*, which appears for the first time in this subzone.

The S3a subzone is correlated with the Bôlling chronozone.

Subzone S3b

The basal spectrum of this subzone coincides with a strong decrease in Betula from 40% to about 20% and a new increase in *Pinus* up to values about 60%. The forest cover became more closed, as reflected by a decrease in all open-communities indicators. *Helianthemum* and *Plantago maritima*-type disappeared from the spectra completely. *Filipendula, Typha latifolia, Nymphaea*, and *Nuphar* appeared in and around the lake, pointing to minimum July temperatures at least 12 °C (Huizer and Izarin, 1997). *Ceratophyllum demersum* became the dominant submerged aquatic. Gradual *Betula* decrease is recorded during the upper half of this subzone.

S3b subzone is correlated with the second half of the Late-glacial interstadial - the Allerôd chronozone. This correlation has been confirmed by the radiocarbon date 11 750 ± 120 BP.

Zone S4

The values of *Betula* decrease to about 10%, whereas *Pinus* percentages are generally the same if compared with the preceding zone. *Alnus viridis, Salix, Betula nana,* Chenopodiaceae, and *Artemisia* values increase again, suggesting a new climatic deterioration. Similar increase, but even more prominent, is recorded in the *Juniperus* curve. Juniper percentages reach a maximum in this zone. Vegetation change reflecting climatic deterioration is recorded also in the lake: *Ceratophyllum* spines values decrease, and Nympheaceae trichoblasts and *Nuphar* pollen is even completely lacking in favour of massive occurrence of *Myriophyllum verticillatum* and *Ranunculus* subgen. *Batrachium* (both recorded also as macrofossils). The presence of *Typha latifolia* pollen in the entire zone can be considered the proxy for minimum July temperatures of at least 12 °C (Iversen, 1954; Ammann, 1989), i.e. at the same range as those inferred for the preceding zone. This suggest that climatic deterioration was rather an increase in continentality than a decrease in summer temperatures. Absolute pollen concentrations are lowered relatively to S3 zone, and the sedimentation character changes to more minerogenic again (with lower organic carbon content). Slight increase in erosion indicators (Mg, K, reworked Tertiary pollen) is observed as well.

Although clear evidence of climatic deterioration (manifested most likely as the increase in continentality) is found in this zone, this climatic oscillation did not result in complete deforestation. The pine woodland only became somewhat more open. S4 zone is correlated with the Younger Dryas chronozone, and this correlation is confirmed by the ^{14}C date 10 780±115 BP obtained from the position slightly below the upper zone limit. It is obvious from DCA ordination diagram (Fig. 7), that climatic deterioration led to vegetational revertence, as can be concluded from the shifted position of the samples along the main ordination axis (x-axis in the diagram).

The stratigraphical investigation of „Vlkovský přesyp“ sand dune has revealed a fossil soil buried under more than five meters of eolian sands. A distinctive layer of pine charcoal fragments buried by eolian sands is dated 11 260 ± 120 BP and implies that the formation of „Vlkovský přesyp“ sand dune dates to very beginning of theYounger Dryas period.

Subzone S4a

This subzone is quite uniform, with only slight fluctuations in *Pinus* values and some more or less synchronous fluctuations in Cyperaceae and Gramineae that are difficult to interpret.

Subzone S4b

Slightly higher values of *Betula nana, Artemisia*, and *Ranunculus* subgen. *Batrachium* mark the lower limit of the subzone. When these herbs then decrease, first possible evidence of climatic improvement is recorded by the increase in *Filipendula* and onset of *Populus* rational limit.

Zone S5

The transition from S4 to S5 zone is characterised by a decrease in all NAP taxa, especially *Alnus viridis, Betula nana*, Chenopodiaceae, and *Artemisia* among the most important. At the same time, *Betula, Populus, Filipendula*, and *Equisetum* percentages rise, while those of *Salix* decrease. Most of the thermophyllous trees have their empirical limits (*sensu* Faegri and Iversen, 1989) at the beginning of this zone, and the development of mixed deciduous forest is observed during its second half. *Picea abies* already occurs in low percentages much earlier (during the entire Late-glacial), but these early finds can be ascribed to long-distance transport of easily dispersed pollen rather than local occurrence. Organic production generally increases, and erosion rate is low. Organic sediment (gyttja), rich in macrofossils, accumulated again in the basin.

This zone is correlated with the beginning of Holocene, the Preboreal chronozone.

Subzone S5a

The peak of *Populus* and *Equisetum* and the relatively high *Filipendula* values are characteristic for this zone, pointing to the development of wet meadows. *Populus tremula* may have been favoured as a pioneer tree in areas that were left open during the preceding period (Ammann *et al.*, 1994). *Alnus viridis* and *Betula nana*, the most characteristic tundra elements surviving from the preceding zone, were gradually outcompeted by developing forests, and their values fall to zero. As in the preceding period, pine was still dominant in the regional forest cover, but during the transition to S5b subzone birch started expanding in place of *Pinus*. The short decrease in organic production at 480 cm can not be attributed to any climatic oscillation without exact time control.

Subzone S5b

Boreal forest dominated by birch started being slowly replaced by mixed deciduous forest in this subzone. This change is reflected by the gradual decrease in the *Betula* curve to 10%. On numerous sites with unfavourable sandy soils, *Pinus* stands still occurred, being favoured in competition with arriving thermophyllous trees. Pine forest persistence could also be attributed to prevailing continental character of the climate. Numerous macrofossil finds of *Najas marina, Najas minor*, and *Trapa natans* are dated to about 9 800 BP (calculated by linear extrapolation from the two adjacent dates), permitting climatic reconstruction for this period. *Najas marina* suggest a mean July temperature above 15 °C (Lotter, 1988), *Trapa natans* even more. According to Gams (1926) and Jorga *et al.* (1982), water chestnut requires mean July water temperature not below 20 °C and in May, when the flowers develop, at least 12 °C. The rapid change to warmer climatic conditions is also evidenced by appearance of macroscopic colonies of the thermophillous blue-green alga *Gloeotrichia pisum* (Van Geel *et al.*, 1989).

Possible palynological evidence for the short Preboreal cold climatic oscillation was found, but it is weak: a short *Pinus* peak accompanied by the fall in *Corylus, Ulmus*, and *Quercus* percentages is dated slightly before 9 640±115 BP. Another explanation may bee the opening of the vegetation by fire, but this hypothesis was not confirmed by higher presence of charcoal particles in the corresponding layer.

Zone S6

Full expansion of mixed deciduous forest started in this zone. The pollen curve of *Pinus*, hitherto very high, started decreasing as the result of competition with deciduous trees even on poor substrates, where soils had developed since the beginning of the Holocene. Alder carr developed on infilling margins of the lake, as reflected in strong rise of *Alnus glutinosa* pollen curve and the occurence of alder wood and seeds in the littoral sediments (correlated with the main profile by pollen analysis and ^{14}C dating). The development of highly productive alder stands around the lake probably contributed to increased organic deposition (increased organic carbon content).

At the beginning of the zone, a prominent Fe peak dated to about 8 600 BP may be explained as the reflection of intensive leaching caused by a more humid climate in conjunction with the build-up of raw humus on the soil surface (Engstrom and Wright, 1984;

Starkel, 1990). In the pollen diagram, the same period is characterised by *Picea abies* expansion.

The zone S6 lower boundary can be correlated with the beginning of the Boreal period.

DISCUSSION

Initial warming

The origin of former lake Švarcenberk can be best explained as the remnant of a huge Pleniglacial ground-ice lens, the 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 several strong artesian springs on the site, and its location close to the river are the factors known to be favourable for pingo formation (Pissart, 1988; de Gans, 1988). The occurrence of such thermokarst phenomena has certain climatic significance and may be used for mean annual air temperature reconstruction, suggesting this to be -1 °C or lower (Mackay, 1988). The presence of pingo remnant with depth of almost 12 meters indicates also a minimum permafrost thickness of this much. By *ca.* 16 ka BP, the advanced state of warming is recorded in the eastern Alps, for at least some glaciers had receded more than two-thirds of their original glacial maximum length (Lundqvist and Saarnisto, 1995). In the Swiss Alps, a very fast decay of glacier ice must have occurred between about 18 and 15 ka BP (Ammann *et al.*, 1994). At about that time, North American and Scandinavian ice sheets were at their full retreat (Lundqvist and Saarnisto, 1995; Tyráček, 1995). Thermokarst lakes are usually the first indicators of climatic amelioration in the periglacial zone (Lundqvist and Saarnisto, 1995). The basal age, estimated to be around 16 000 BP for the bottommost sediments of Švarcenberk central core, represents the minimum possible age of the lake that originated by permafrost thawing. This suggests the change from high-arctic to somewhat warmer conditions. The vegetation cover during this time can be reconstructed from the pollen spectra: Treeless vegetation of steppe and tundra character prevailed in the area.

Pinus percentages ranging between 60% and 75% are characteristic for S2 local PAZ. Relatively straightforward evidence of climatic amelioration is present especially in S2b subzone, when *Pinus* percentages reach their maximum. Pine by then was a successful competitor for light against the heliophyllous vegetation, for indicators of certain open communities declined. Reconstructed vegetational cover during S2b subzone can be characterised as a mixture of shrub-heath and steppe patches with scattered pine trees. From this point of view, the macrofossil find of a shrew (*Sorex* cf. *araneus*) mandible in the lake sediments is particularly interesting, for shrews are characteristic of sparsely wooded landscapes (I. Horáček, pers. comm.).

High *Pinus* percentages recorded at Švarcenberk during the pre-Bôlling period notably exceed those found elsewhere in Europe at that time and suggest the local occurrence of *Pinus* stands. Huntley and Birks (1983) conclude that pollen values >50% indicate for local dominance of pine. Ammann *et al.* (1994) suggested the Oldest Dryas *Pinus* percentages around 20% originated from long-distance transport. Increase of *Pinus* from 20% to 65% is defined as the rational limit by Ammann and Lotter (1989) and Lotter *et al.* (1992). Surface pollen samples of the woodland-steppe ecotone in Inner Mongolia suggest *Pinus* pollen percentages exceeding 70% indicate dense local pine woodland (Liu *et al.*, 1999). In the ecotone itself and in the edge of the steppe zone these values decrease to 30% or lower. According to Poser (1984) the poleward limit of forest in Europe approximates the 10 °C isotherm for July (inferred minimum July temperatures for S2 zone are 11 °C). In the Alpine region, and also elsewhere in western Central Europe, pine expands about 13 000 BP or even later in Allerôd chronozone (e.g. Watts, 1979; Hoek, 1997; Bos, 1998). This pine expansion is not accompanied by other indicators of climatic warming and therefore is considered to be caused by lagged immigration (Gaillard, 1984a; 1985). The early pine expansion in the area under study can be ascribed to the rapid response of *Pinus* populations expanding from locally present glacial refugia shortly after climatic amelioration. Favourable mesoclimatic conditions in the marshy area of Třeboň basin (high local humidity) might have played a significant role in early reforestation as well. In continental parts of Central Europe, *Pinus sylvestris* and possibly some other demanding species might have persisted locally through the entire glacial maximum. Pine is known to tolerate and even reproduce under extremely severe climatic conditions (usually in dwarf forms), either dry, windy, or cold. Unfortunately, it is usually not possible to discriminate between a pollen peak caused by a population invading from another region and one caused by local expansion of the species previously present but climatically little favoured (Watts, 1979). This is true mainly in the case of pine pollen transported from a long-distance.

Unfortunately, exact dating of the period of first pine expansion is missing, although it certainly antedates the Bôlling chronozone and ranges approximately to the period between 15 000 and 14 000 BP. This result is consistent with similar evidence from southwestern European pollen records (Beaulieu and Reille, 1984; Jalut *et al.*, 1992; Beaulieu *et al.*, 1994) and the finds from northwestern Norway (Vorren *et al.*, 1988; Alm and Birks, 1991), where early signs of climatic amelioration occur around 15 ka BP. In northern Germany (Meiendorf Interval) and The Netherlands (Epe Interval), there is also evidence for some short-lived warmer oscillation around 15 ka BP (Menke, 1968; Kolstrup, 1980). At about that time, weak traces of initial pedogenesis in the eastern part of Central Europe indicate a short break in loess deposition during the period of slightly warmer and wetter climate (Tyráček, 1995).

The terminal phase of S2 zone, reflected in pollen diagram from Švarcenberk as the period of new *Pinus* decline and a new expansion of open-communities indicators, can be interpreted as the episode of certain climatic deterioration and can be correlated with the Oldest Dryas chronozone (sensu Ammann *et al.*, 1994 and Stuiver *et al.*, 1995). In the Alps as well as in Scandinavia and North America, the Oldest Dryas is known to be a period of temporary glacier readvance (Lundqvist and Saarnisto, 1995).

High values of sedimentary Mg, K, and Ca during the entire pre-Bôlling period may be explained as derived from eroding, unstable soils. Low nutrient status of the lake and its catchment together with low productivity (N and organic C values are very low during that time) were primarily caused by low energy input into the ecosystem. The local PAZ boundaries recognised in the pre-Bôlling record from lake Švarcenberk are compared (in Fig. 9) with $\delta^{18}O$ curve of the Greenland ice core GISP2 (Stuiver *et al.*, 1995). A certain degree of correspondence exist between these two.

Late-glacial Interstadial

An abrupt warming is recorded in the areas adjacent to the North Atlantic around 13 ka BP, during Oldest Dryas - Bôlling transition (Lowe *et al.*, 1994). Reforestation by birch and later by pine is recorded over most of NW and Central Europe during that time. Closing of the immigrating forest canopy is usually anticipated by the period of *Juniperus* expansion. Juniper was an important pioneer shrub after a period of prevailing herbaceous vegetation, and its phase is prominent especially in the Alpine region and in Britain. Farther to the east, this shrub appears to be much less significant in the Late-glacial vegetation (Huntley and

Birks,1983). In the area under study, juniper plays only a minor role, for no *Juniperus* peak (or only an ambiguous one) occurs during the Oldest Dryas - Bôlling transition. Instead of that a prominent *Salix* peak characterise this transitional phase in our case. Local edaphic conditions (prevailing waterlogged soils) may have played a role, decreasing the importance of juniper and favouring moisture-demanding pioneer willow shrubs. For the lack of finds of *Salix* macrofossils the species represented by the pollen are not known. Gaillard (1985) suggested that *Salix caprea* may have grown as a pioneer species before expanding birch woodland. The *Betula nana* peak accompanying that of *Salix* is most likely also the result of climatic improvement, reflecting shrub-heath development prior to the closing of forest canopy. This resembles the *Betula nana* phase during the very beginning of the Late-glacial Insterstadial in the Swiss Alps (Lotter *et al.*, 1992; Ammann *et al.*, 1994). The response of locally present species to climatic amelioration precedes the immigration of species and shows entirely no lag-phase.

In the second half of S3a subzone, tree birch became dominant in the pollen spectra in favour of NAP and *Pinus. Betula*-dominated forest developed, outcompeting most of the heliophyllous plant communities. *Betula* and *Pinus* pollen percentages are almost the same, indicating the diminished role of pine in fully developed Interstadial forests. Shortly after, the marked transition is recorded in the pollen diagram: *Betula* percentages suddenly decrease again in favour of *Pinus*, pointing to the change of proportion between these two in the regional forest cover. Heliophyllous herbs generally decrease to their Late-glacial minima during this *Pinus* phase, indicating that this vegetation change was a progressive closing of the forest canopy. *Pinus* expansion may indicate increasingly severe conditions, particularly in winter, i.e. increase in continentality (Walker, 1995). This event can be correlated with the Bôlling - Allerôd transition, which appears to be abrupt in the pollen record. No distinct transitional phase attributable to Older Dryas is present. If this oscillation occurred in the area under study, it had only a small impact on the vegetation. A short-lived climatic deterioration for the Older Dryas is generally recognised in central and western Europe (e.g. Walker, 1995), although in some sites its recognition is out of temporal resolution of the analyses or out of the climatic threshold of plant communities involved. It is well known, that the response of a plant population to climatic change is likely to be greatest near the margin of its tolerance (Watts, 1979). For example, in Switzerland the Older Dryas (often correlated with the „Aegelsee oscillation“ in this region) is not detectable at low-lying sites but is more apparent at higher altitudes (above cca 600 m a.s.l.), where the climatic limits of indicator species have been crossed (Lotter *et al.*, 1992; Ammann *et al.*, 1993). During the Late-glacial Interstadial, marked climatic gradients developed over Europe, with temperature differences as much as 6-7 °C within a few hundred kilometres (Lowe *et al.*, 1994). Under these conditions, the response of vegetation to climatic changes must have been very diverse in relation to geographical position of the site.

The Late-glacial Interstadial appears to be a period with significantly increased organic production, as reflected in the sharp transition from minerogenic to organic sedimentation (with high organic carbon and nitrogen content in the sediment). The declining values of Mg and K in the Interstadial sediments are the result of the formation of clay minerals in the soil horizons, as soils developed progressively in the lake catchment: 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 and Wright, 1984). The same process of soil development is recorded also in lowland loess plateaus of the Czech Republic: Loess formation, which is characteristic of late Pleniglacial, generally terminates during Bôlling phase, and initial pedogenesis takes place during that time (Ložek and Cílek, 1995). The decalcification of soil horizons (see the decrease in sedimentary

Ca) together with expanding forest were responsible for ultimate decrease in *Helianthemum* percentages.

Younger Dryas

The Younger Dryas as a biozone is widely recognised over the most of Europe. Concerning the duration and amplitude, this climatic oscillation is the most important during the whole Late-glacial period (Lotter *et al.*, 1992). YD climatic deterioration, dated roughly between 11 and 10 ka BP, is correlated with a readvance of polar waters into the North Atlantic. Although the consequences of this event are registered more strongly at the sites near the ocean fringes of northern Europe, it is apparent today that regional changes in climatic regime may have been just as great in southern and eastern regions of Europe as in northern part of this continent (Lowe and Watson, 1993; Beaulieu *et al.*, 1994, Khotinsky and Klimanov, 1997). Although the problems of absolute dating accompany the recognition of Younger Dryas event (the „^{14}C plateau"; Ammann and Lotter, 1989), it has been described from many sites in the world and today is believed to be a global event (Peteet, 1995). For the territory of the Czech Republic, almost no reliable between-site comparison has been possible for the Younger Dryas. Only at Vracov, southern Moravia (Rybníčková and Rybníček, 1972), it is marked by a small *Juniperus* and *Salix* rise after 10 765 BP, but its identification is difficult.

At the present study site, clear evidence of climatic deterioration is ascribed to Younger Dryas chronozone. The values of *Betula* decrease, whereas those of *Alnus viridis, Salix, Betula nana,* Chenopodiaceae, and *Artemisia* increase. Proxy evidence suggests that climatic deterioration was an increase in continentality rather than decrease in summer temperatures (see also Ammann, 1989), for reconstructed minimum July temperatures are at least 12 °C. The same values are reconstructed for western Poland (Walker, 1995). The sedimentation character changes back to more minerogenic, and erosion intensity rises. The increase in erosion indicators is only indistinct, suggesting that soil development was not interrupted completely during this time. TheYounger Dryas can be subdivided in the Švarcenberk standard profile into two phases, indicating climatic amelioration (increase in humidity ?) some time before the onset of Holocene warming. The subdivision of Younger Dryas into older phase with colder and more arid climate and the younger phase with warmer and wetter climate has been also reported from some other sites in Europe (from Norway and Poland; Birks *et al.*, 1994; Goslar *et al.*, 1993), while in the Alps and in most of Western Europe the younger phase has been suggested to be somewhat drier (Walker, 1995).

The formation of extensive eolian deposits in the region under study is dated to the beginning of Younger Dryas chronozone: Stratigraphic investigation of one of the most prominent sand dunes („Vlkovský přesyp", situated near Švarcenberk lake basin) has revealed a fossil soil buried under eolian sands with a distinctive layer of pine charcoal fragments on its surface. This situation resembles conditions in The Netherlands, where the „Usselo soil layer" formed during the Allerôd period of lower eolian activity. „Usselo-layer" has been dated from surface charcoal fragments to between 11 400 and 10 300 BP, with average date around 11 000 BP (Hoek, 1997). These results resemble those from „Vlkovský přesyp", where a radiocarbon date 11 260 ± 120 BP has been obtained from very similar stratigraphical situation. The formation of soils during the Allerôd period required stable climatic conditions with less eolian activity and relatively dense vegetation cover. On the other hand, the formation of eolian sand dunes require severe climatic conditions and sparse vegetation cover. Acceleration of eolian activity during the Younger Dryas accord well with the results of pollen analysis, which point to a certain opening of the forest relatively to the preceding Allerôd period. The morphology of sand dunes points to prevailing easterly winds in time of their formation.

Early Holocene

There is abundant evidence throughout Europe for a rapid rise in temperature at around 10 000 BP, although precise dating of this event is difficult because of another „radiocarbon plateau“ at about that time. Over many areas of central and northwestern Europe, Younger Dryas open communities were replaced within less than 500 years by *Betula/Pinus/Corylus* woodland (Walker, 1995). The preservation of *Pinus*-dominated forest in the area under study during the whole early Holocene and relatively late development of deciduous forest was connected with the persistence of a continental climate during that time and generally low nutrient status together with the sandy character of soils. Pine-dominated forests persisted in the area until the Boreal increase in humidity (see later), although deciduous forests started to develop in favourable locations somewhat earlier. The rapid temperature rise during the Preboreal is indicated in lake environment by the early occurrence of *Najas marina, Najas minor*, and *Trapa natans* macrofossils. *Najas marina* suggests a mean July temperature not below 15 °C (Lotter, 1988), *Trapa natans* even more. According to Gams (1926) and Jorga *et al.* (1982), water chestnut requires mean July water temperature not below 20 °C and in May, when it starts flowering, at least 12 °C. This proxy evidence suggests that the present-day values were reached as early as about 9 800 BP.

In a number of proxy records from mainland Europe, there are indications of a cold climatic oscillation during the first millennium of the Holocene: the „Preboreal oscillation“ of the Swiss Plateau (Lotter *et al.*, 1992) or the „Youngest Dryas“ of northern Germany (Behre, 1978). In western Norway, a readvance of the Josteldalsbreen ice cap has been dated to ca. 9 100 BP (Nesje *et al.*, 1991), while an abrupt fall in snow accumulation (associated with a fall in North Atlantic seasurface temperatures) is recorded in the GISP2 Greenland ice core some 400 years after the end of the Younger Dryas (Alley *et al.*, 1993). Equivalents of European Preboreal oscillation are supposed to be found also in North America (Lowe *et al.*, 1994). Possible palynological evidence for Preboreal climatic oscillation has been found also at Švarcenberk site, but it is relatively weak: a short *Pinus* peak accompanied by the fall in *Corylus, Ulmus*, and *Quercus* percentages and dated slightly before 9 640±115 BP can be the result of some short cooling episode.

The early-Holocene sediment record from Švarcenberk lake comprises a prominent Fe peak dated to around 8 600 BP. It may be best explained as the reflection of intensive leaching caused by sudden climatic humification (Engstrom and Wright, 1984; Starkel, 1991). In the pollen diagram, the same period is characterised by *Picea abies* expansion. There is probably some connection between these two phenomena, as spruce grows preferably on waterlogged soils and is able to produce highly acidic, raw humus, promoting intensive leaching. The gradual development of nutrient-poor acid soils was an important factor in the Holocene vegetation development, as emphasised by Iversen (1964). The building-up of raw humus on the soil surface and resulting reducing conditions may have released Fe from the soil, and it travelled to the lake in solution or bound in organic complexes. A similar peak in Fe has been described from lowland areas of the Czech Republic, where early-Holocene debris is cemented by limonite and goethite (Ložek and Cílek, 1995). Also in Poland, the beginning of the Holocene is characterised by inwash of dissolved iron into the lakes, and this is interpreted as the first stage of intensive soil leaching (Pawlikowski *et al.*, 1982). In southern Sweden, the Fe content of several early-Holocene lake sediments is very high. Digerfeld (1972, 1975) attributed this peak to early leaching from Late-glacial soils in the catchment and subsequent transport by groundwater to the lake.

CONCLUSIONS

The results of present study permit the following conclusions:

1. The Late-glacial biostratigraphy of the investigated site can be subdivided into different local pollen assemblage zones (PAZ). These biostratigraphical units can be correlated with general chronostratigraphic and climatostratigraphic subdivision of the last glacial-interglacial transition as established in Europe.

2. Three distinct cold events interrupted the Late-glacial climatic amelioration: The first occurred before 13 000 and is correlated with the Oldest Dryas. Another regressive phase left only a weak signal and subdivides the Late-glacial Interstadial into distinct *Betula* and *Pinus* phases. It is correlated with the Older Dryas. The third regression, corresponding to the Younger Dryas chronozone, is the most prominent one. It resulted in the reduction of the regional forest cover and a new expansion of open herbaceous communities. Eolian activity accelerated during this time. The continental character of the climate continued for about 500 years after the onset of Holocene warming. It is likely that the observed Late-glacial and early-Holocene climatic oscillations can be attributed to the same processes that acted in the western parts of Europe, i.e. the large-scale shifts in the position of the North Atlantic Polar Front (Ruddiman and McIntyre's model).

3. The response of regional vegetation to the Late-glacial climatic changes was different from much of NW and western part of Central Europe. The main difference is the early development of primaeval pine forest during climatic amelioration antedating the onset of the Late-glacial Interstadial. Pine dominance is then characteristic for the entire Late-glacial and early-Holocene in the investigated area, while juniper is only of minor importance. The role of *Juniperus* as a pioneer shrub was therefore adopted by willow species.

4. There is strong correspondence between vegetational development, soil development, and the intensity of geomorphic processes acting within lake and its surroundings. The synchroneity of these processes has been primarily provoked by external climatic forcing.

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TABLES AND FIGURES

Tab. 1: Radiocarbon dates from Švarcenberk litoral (S500) and central („main profile“) cores and „Vlkovský přesyp“ sand dune (LuA-4645).

Lab. No.	*Core label/depth*	*Method*	*Type of material*	*Measured ^{14}C age*
LuA-4297	S500: 200 cm	AMS	*Trapa natans* nut	6 340 ± 110 BP
LuA-4589	„main p.“: 324-327 cm	AMS	*Trapa natans* nut	6 350 ± 100 BP
LuA-4590	„main p.“: 390-393 cm	AMS	Woody stem fragment	9 640 ± 115 BP
LuA-4591	„main p.“: 520-523 cm	AMS	Bulk gyttja sample	10 780 ± 115 BP
LuA-4738	„main p.“: 680-683 cm	AMS	Alkali soluble fraction from gyttja	11 750 ± 120 BP
LuA-4645	Surface of a fossil soil.	AMS	*Pinus* charcoal fragments	11 260 ± 120 BP

Fig.1: The study site. a) Location of the study area within the Czech Republic. b) Climatic diagram for Třeboň (cca. 15 km south from the site) derived from 50 years of observations. c) Quaternary geology and topography of the site. 1 - „Vlkovský přesyp“ eolian sand dune, a,b,c,d - two cross sections used for stratigraphical investigation. Their crossing point is in the centre of the basin, where the „main profile“ is situated.

FIGURE ON THE NEXT PAGE

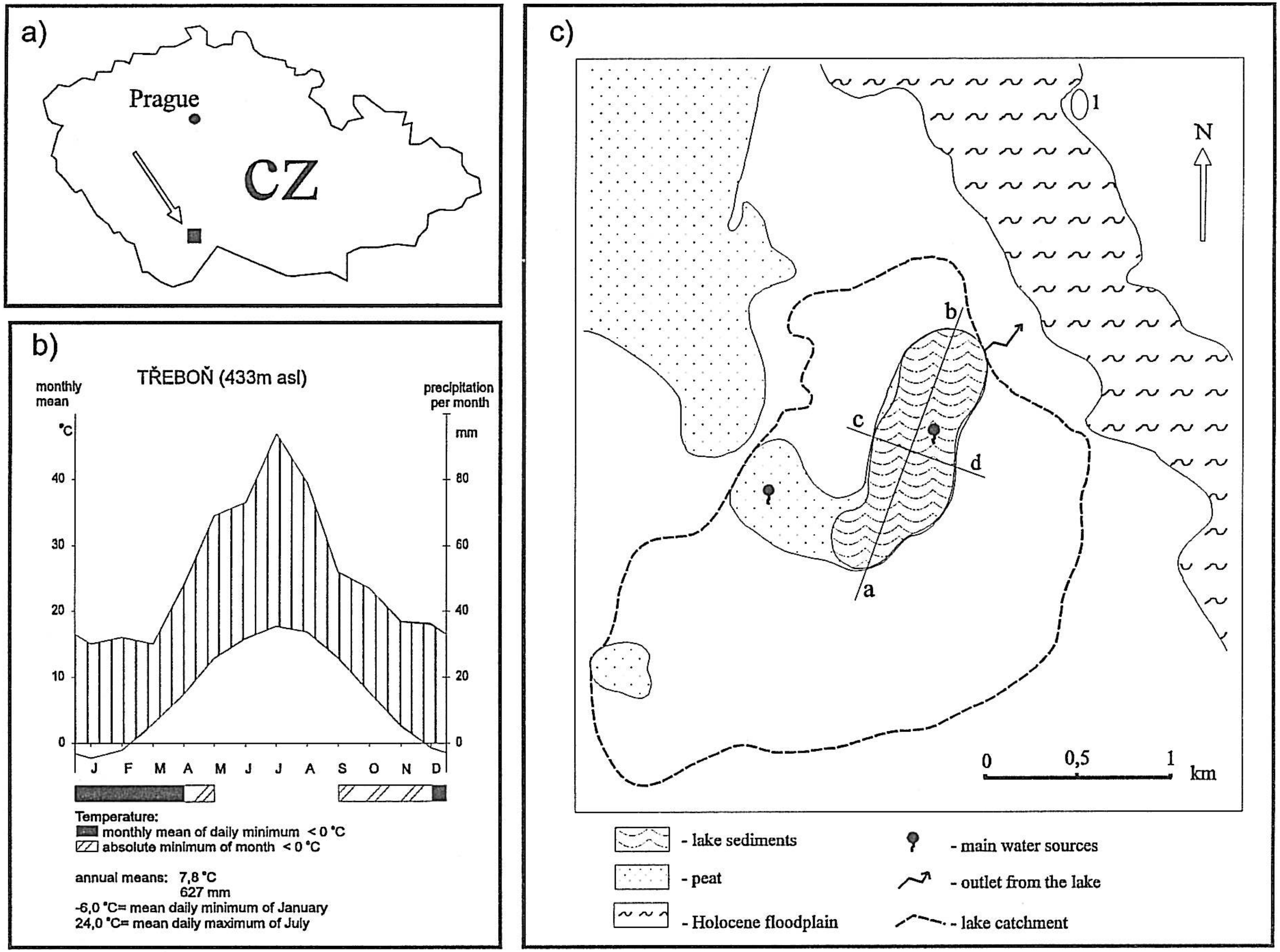
a)
Prague
CZ
b)
TŘEBOŇ (433m asl)
monthly mean
°C
precipitation per month
mm
J F M A M J J A S O N D
Temperature:
monthly mean of daily minimum < 0 °C
absolute minimum of month < 0 °C
annual means: 7,8 °C
627 mm
-6,0 °C= mean daily minimum of January
24,0 °C= mean daily maximum of July
c)
N
0 0,5 1 km
- lake sediments
- peat
- Holocene floodplain
- main water sources
- outlet from the lake
- lake catchment

Fig.1.

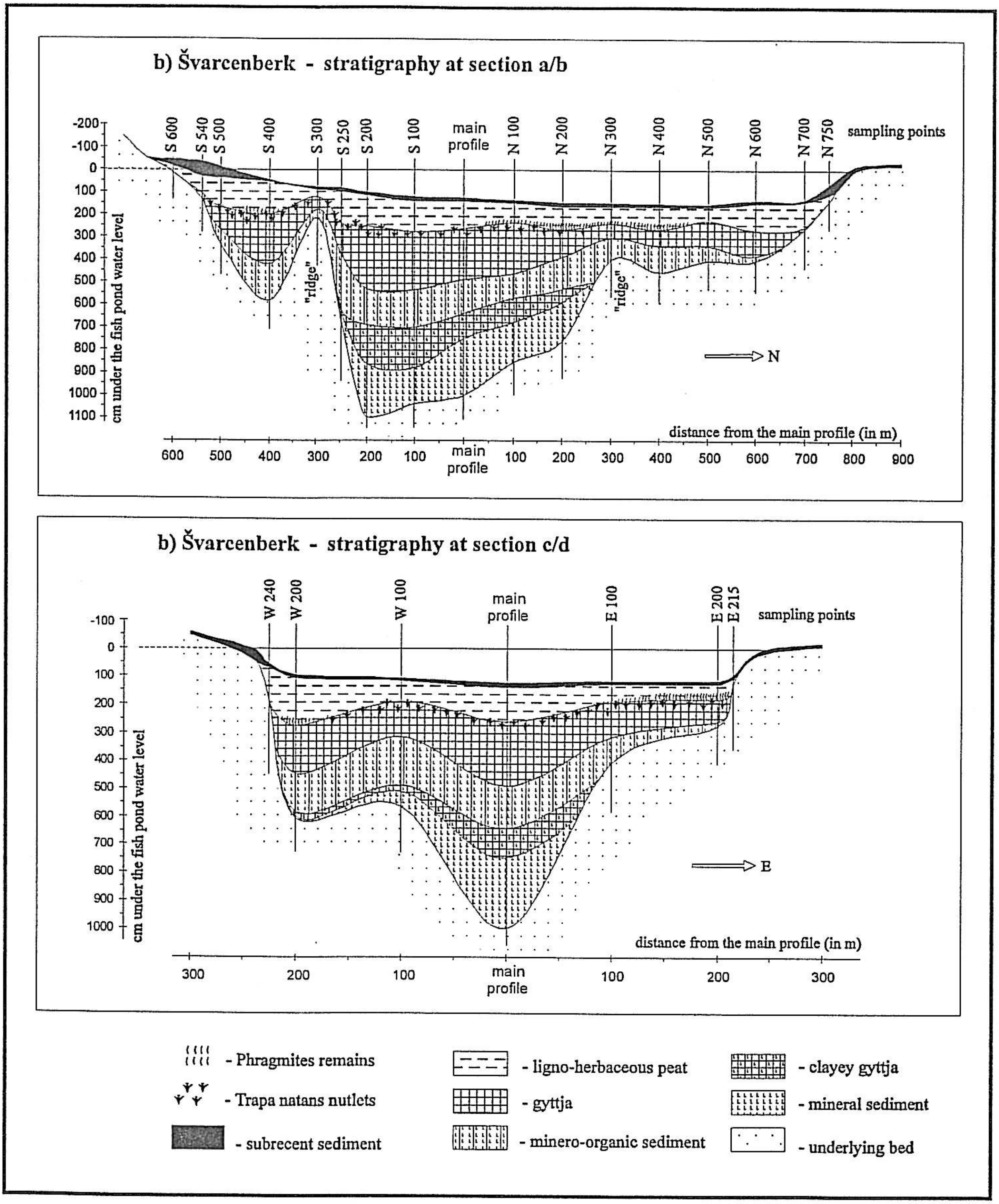

Fig.2: Two selected orthogonal stratigraphic cross-sections (their position described on Fig.1) through the Švarcenberk lake basin.

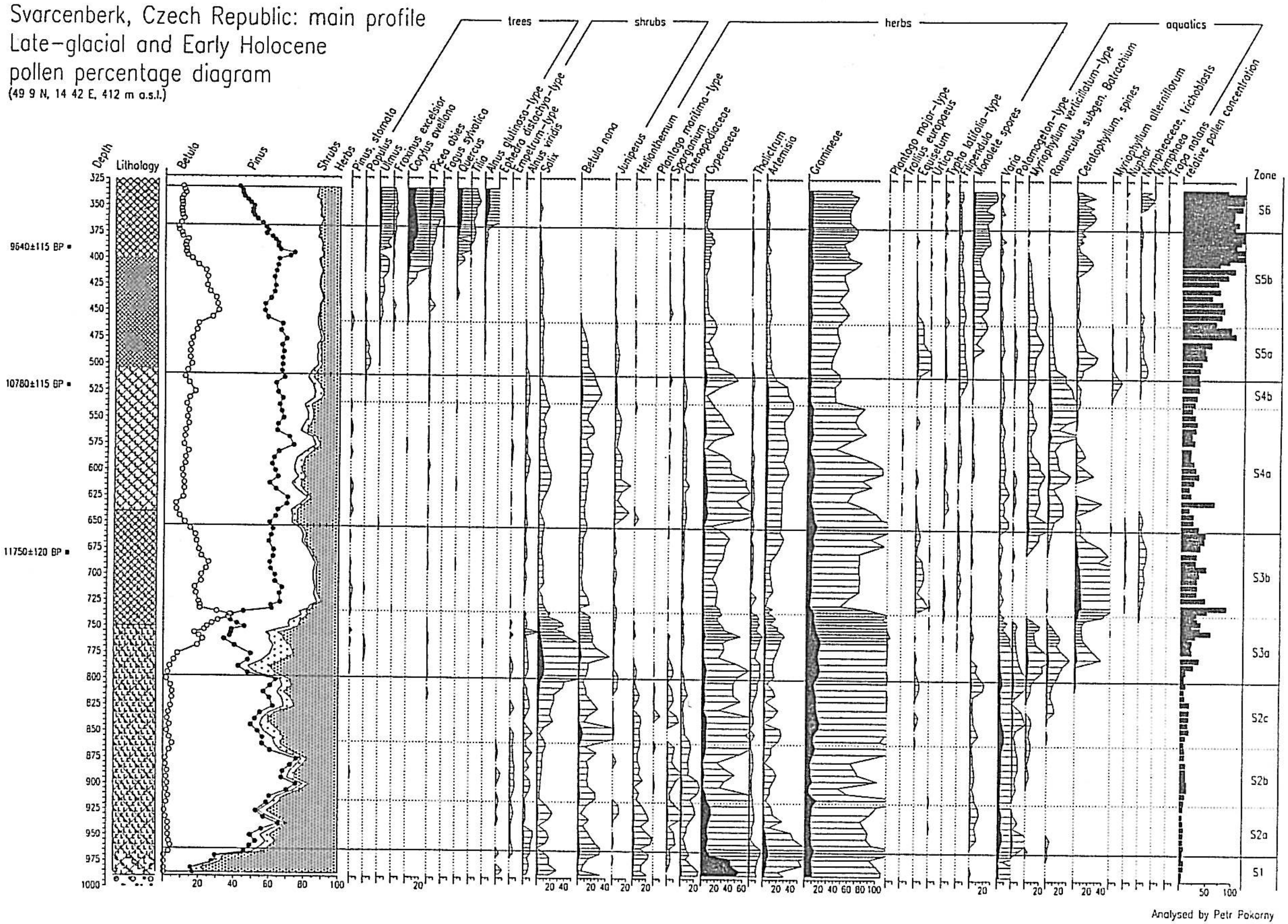

Fig.3: Late-glacial and Early Holocene pollen diagram of the „main profile". Only selected types are included.

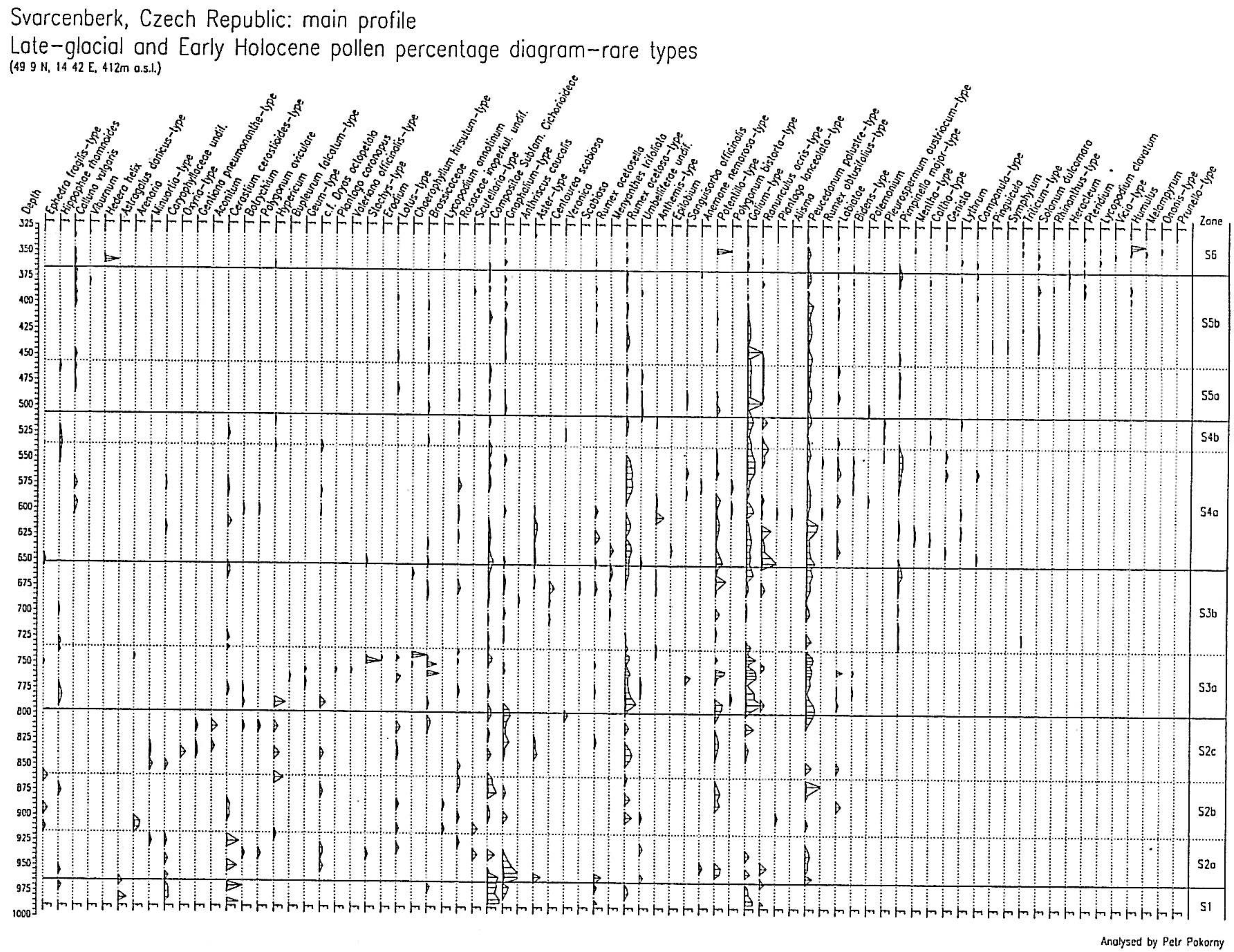

Fig.4: Late-glacial and Early Holocene pollen diagram of the „main profile". Rare pollen types ordered according to results of weighted everaging.

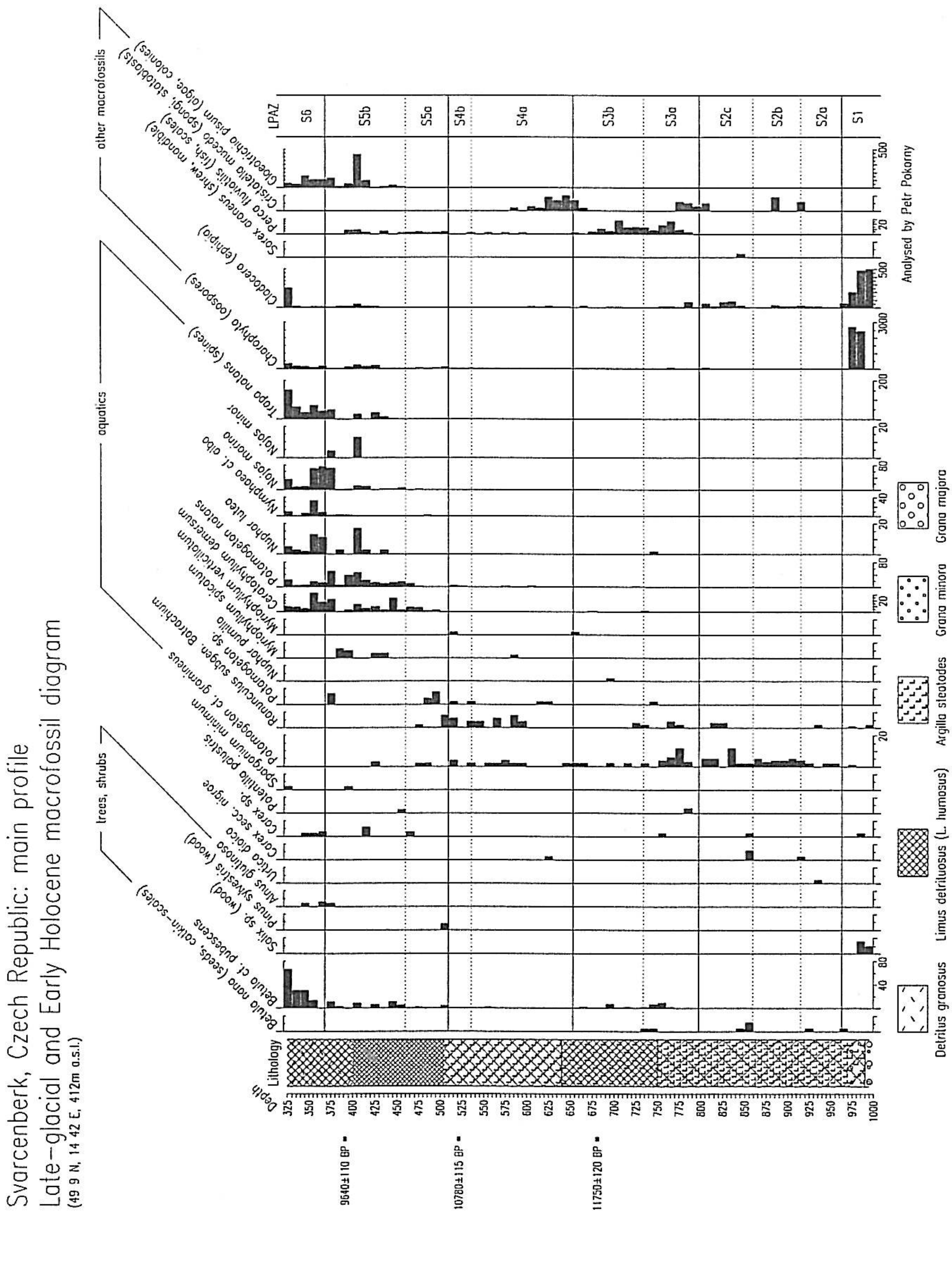

Fig.5: Late-glacial and Early Holocene macrofossil diagram of the „main profile". Absolute numbers of the finds were recalculated to standard volume of 500 cm^3 of fresh sediment. If not stated differently, all finds represents seeds.

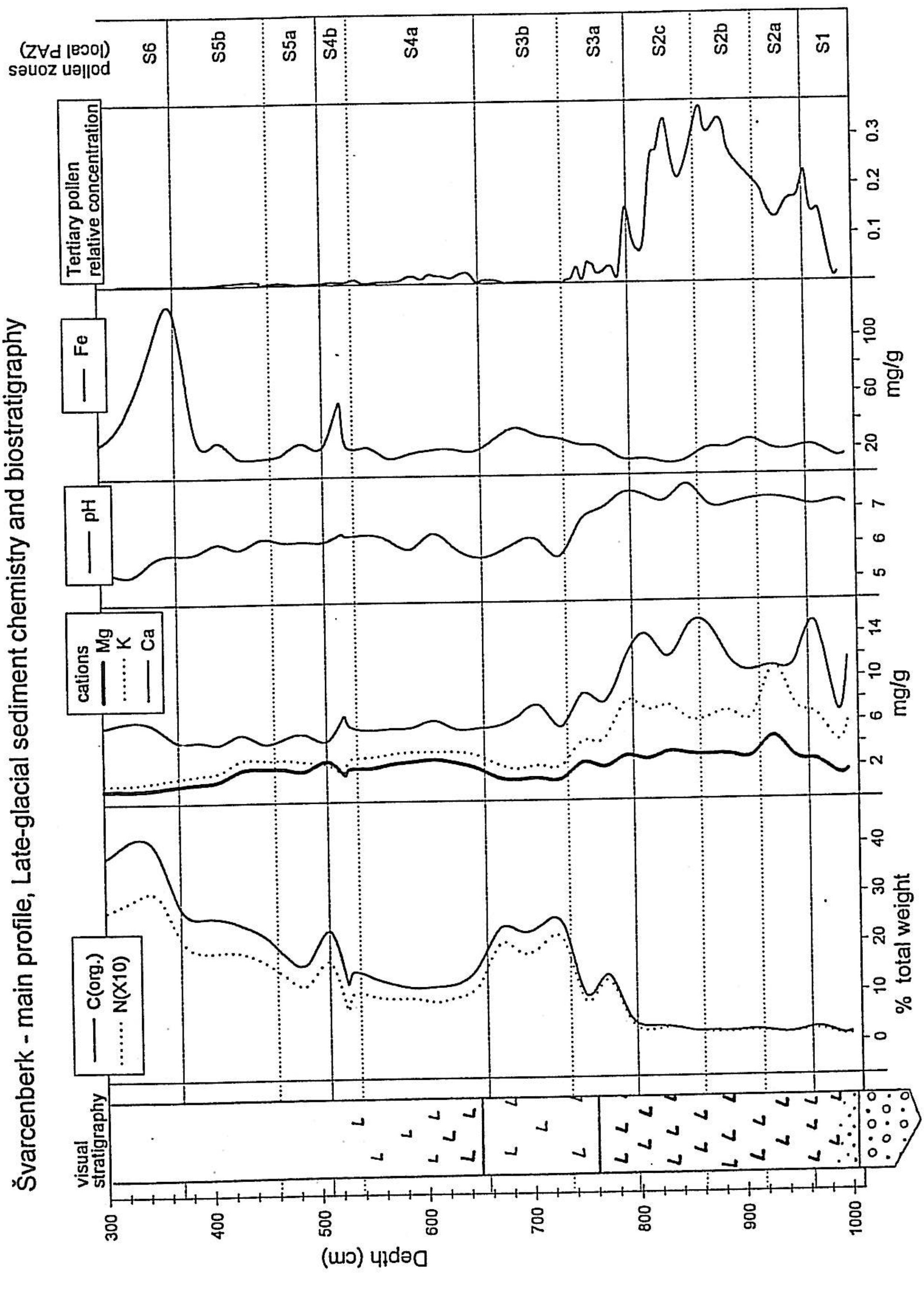

Fig.6: Sediment composition of the „main profile“ correlated with local pollen zonation. Simplified stratigraphical column shows different proportion of sand (dots and circles) and silt (angles) components in organic sediments.

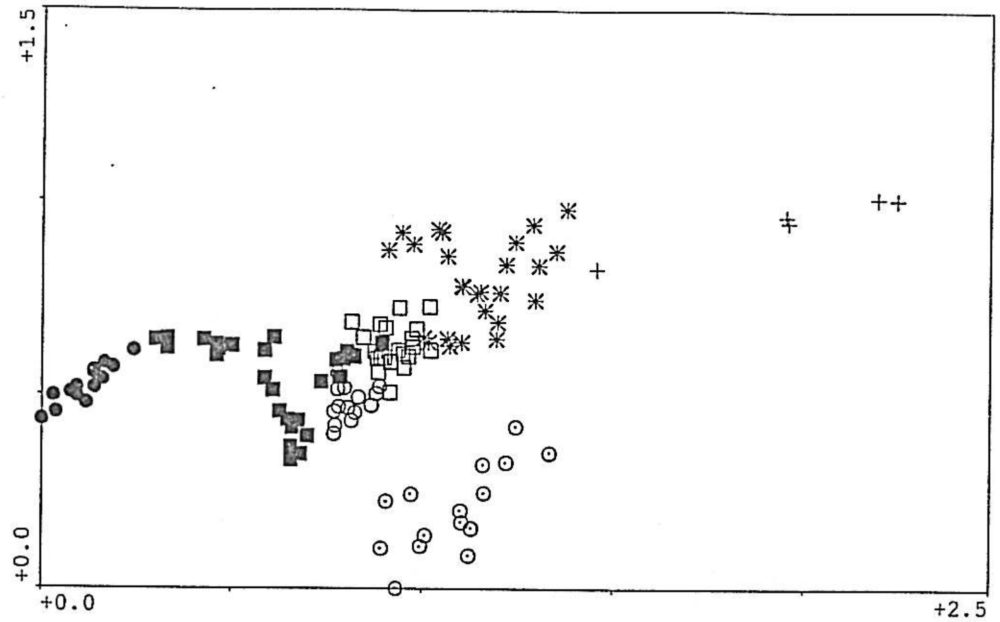

Fig.7: DCA ordination results of percentage pollen data from the "main profile". The use of the symbols follows pollen zonation (LPAZ): Full circles - zone S6, full squares - zone S5, open squares - zone S4, open dotted circles - subzone S3a, open circles - subzone S3b, stars - zone S2, crosses - zone S1.

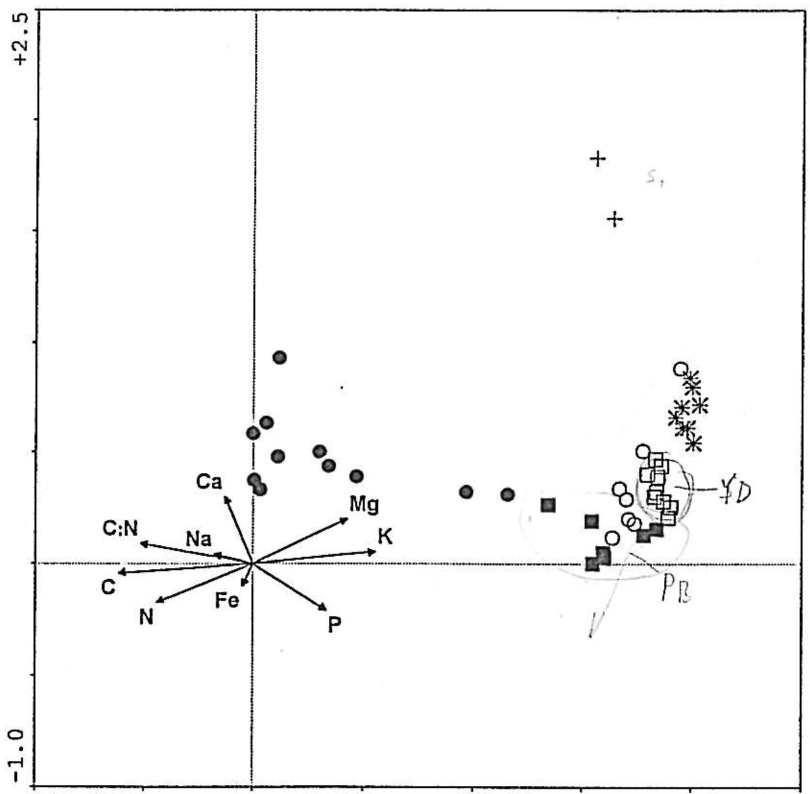

Fig.8: CCA ordination results. Percentage pollen data together with sediment chemistry data (as environmental variables) have been used. The use of the symbols follows pollen zonation (LPAZ): Full circles - zone S6, full squares - zone S5, open squares - zone S4, open circles - zone S3, stars - zone S2, crosses - zone S1.

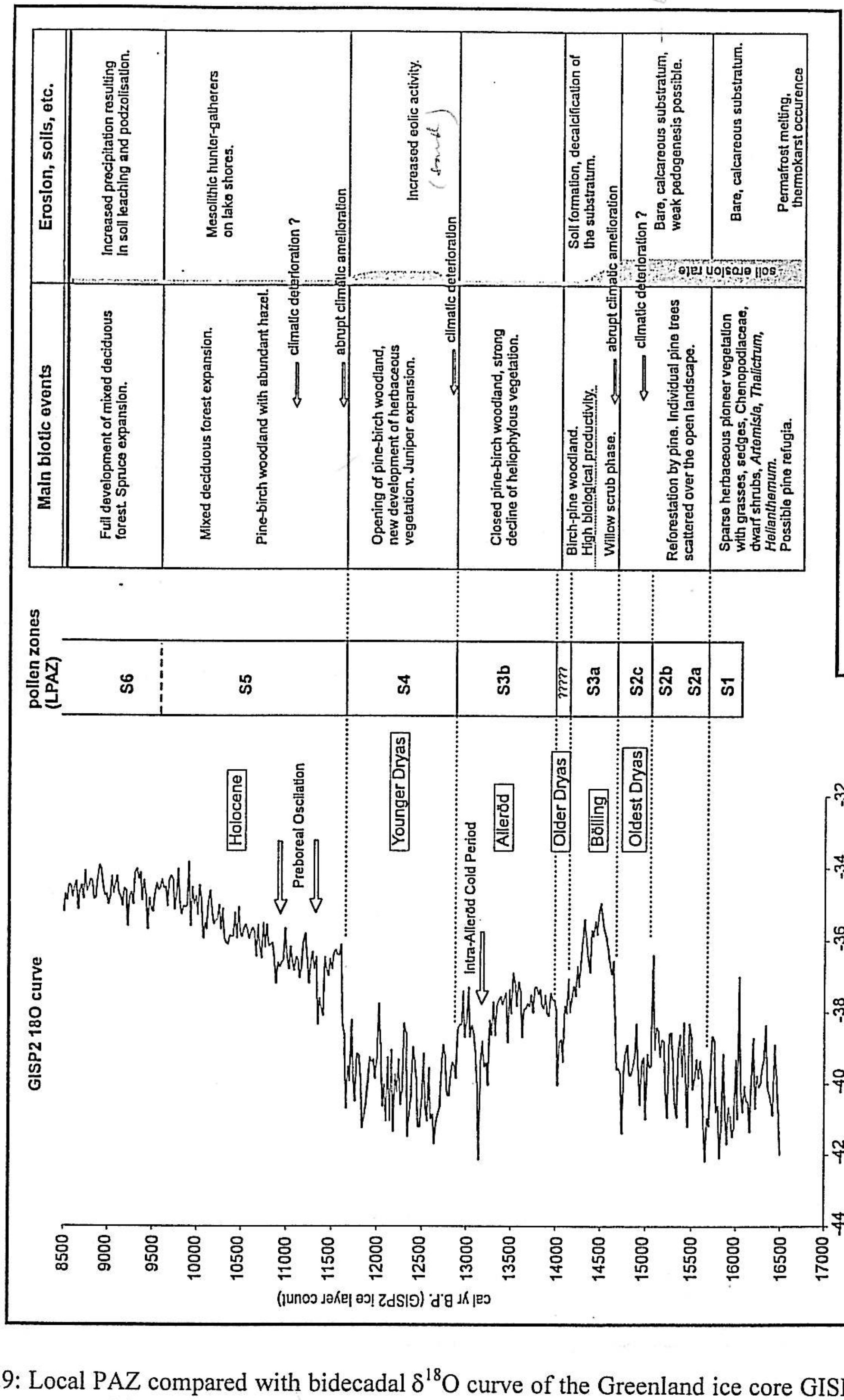

Fig.9: Local PAZ compared with bidecadal $\delta^{18}O$ curve of the Greenland ice core GISP2 (data measured by hand by W.O. van der Knaap from graph presented at Stuiver *et al.*, 1995). This cross-correlation should be considered as a suggested scheme only. Absolute time scale (cal yr B.P.; yearly ice-layer counts before A.D. 1950) and chronozones follow Stuiver *et al.* (1995) with exception of „Preboreal oscilation“ derived from Ammann et Lotter (1989). A synoptic table of the main events for the site of present study is attached from the left.

V. EOLIZOVANÉ KLASTY KŘEMENE V KLASTICKÉ SLOŽCE ULOŽENIN JEZERA ŠVARCENBERK.

[Pokorný, P., Růžičková, E. (2000, in press): Eolizované klasty křemene v klastické složce uloženin jezera Švarcenberk. ***Zprávy o geologických výzkumech v roce 1999.*****]**

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Keywords: *Holocene sediments, Clastic lacustrine sediments, Aeolian sediments*

Jezerní sedimenty patří na území České republiky mezi vzácně se vyskytující typ kvartérních uloženin. Zaniklé jezero Švarcenberk bylo objeveno v místě dnešního rybníka Švarcenberk v severní části Třeboňské pánve. Náleží ke skupině jezer, jejichž vznik a existence jsou vázány na silné prameny artézkých vod. Stratigrafie zazemněné jezerní pánve byla studována pomocí téměř 120 ručních vrtů. Vrt (S-HP) středem pánve, zvolený za standardní, byl dále podroben chemickým, pylovým, makrozbytkovým a v nejnovější době také prvním granulometrickým analýzám. Na základě radiokarbonového datování bylo rámcově určeno stáří bazální výplně pánve na 16 000 let BP (nekalibrováno). Nadložních více než 5 metrů jezerních uloženin vzniklo v období pozdního glaciálu, které je možno na biostratigrafickém základě dále podrobně členit. Rozloha jezera v době jeho vzniku byla cca 51 ha, maximální ověřená hloubka činila v prům. 10 m.

V sedimentární výplni jezer tohoto typu následkem zazemňování ubývá směrem do nadloží klastické terestrické složky souhlasně se zvyšujícím se podílem organických, příp. chemických uloženin. Klastická složka bývá do jezera transportována převážně vodní cestou (splach, občasné menší povrchové vodoteče), částečně jinými méně obvyklými způsoby, např. eolickým transportem. Složení klastického materiálu odpovídá především charakteru zvětralin splachovaných z bezprostředního okolí do pánve.

Tato charakteristika platí rovněž pro zkoumané uloženiny jezera Švarcenberk. Studiem granulometrie vybraných vzorků z vrtu S-HP (11 vzorků z hloubky od 4,5 do 10 m) byl potvrzen rychlý úbytek terestrické klastické komponenty směrem do nadloží. Zatímco na bázi výplně jezera, v hloubce 9,9 m, je jí téměř 100 %, ve vzorku z hloubky 4,5 m pouze okolo 5 %. Úbytek klastické minerální složky není ovšem plynulý, objevují se nepravidelné podřadné polohy s jejím zvýšeným obsahem. Z granulometrie sedimentů jednotlivých vzorků vyplývá, že se většinou jedná o jemný jílovitý prach o průměru zrnitosti od 4 do 10 μm. Vyšší hodnoty dosahuje bazální vrstva (18 μm) a sediment vzorků z hloubek 5,5 a 5,9 m, které obsahují velké množství agregátů jílu, organické hmoty a sloučenin Fe a k jejichž úplnému rozdružení nepomohl ani níže zmíněný postup.

Nedaleký výskyt eolických sedimentů z duny Pískový vrch u Vlkova (1,2 km vzdušnou čarou od okraje bývalého jezera), jejichž stáří je určeno pomocí radiokarbonového datování uhlíků z povrchu podložní fosilní půdy na 11 260 ±120 BP (nekalibrované datum získané metodou AMS), byl jedním z důvodů, abychom se pokusili zjistit přítomnost eolizovaných klastů

křemene v sedimentech jezera. Vzhledem k vysokému podílu organické a chemické komponenty v těchto sedimentech jsme museli provést rozdružení a čištění vzorků chemickou cestou, abychom získali křemenné klasty pro orientační studium na SEM. Současně s křemennými klasty ze vzorků z jezerních uloženin byl na elektronovém mikroskopu studován též tvar a povrch křemenných klastů eolických sedimentů z lokality Pískový vrch pro možnost vzájemného srovnání. Vzhledem k časově náročné přípravě vzorků, byl k orientačnímu porovnání zvolen vzorek s nesporně eolickým materiálem z duny se vzorkem jezerních sedimentů s nejvyšším podílem klastické složky tj. z báze (9,9 m).
Charakter tvaru klastů frakce 0,125 – 0,25 mm z lokality Švarcenberk a z lokality Pískový vrch u Vlkova je téměř shodný, malé množství dokonale zaoblených klastů obou vzorků svědčí o nepříliš dlouhém eolickém transportu. Zřetelnou eolickou skulpturaci vykazuje také povrch klastů křemene frakce 0,25 – 0,5 mm z obou lokalit.
Ze získaných orientačních výsledků můžeme zatím konstatovat, že ve vzorku z výplně pánve jezera Švarcenberk byla identifikována eolická složka. Další výzkum bude zaměřen na kvantifikaci obsahu této složky a korelaci jejího výskytu s biostratigrafickými daty.

VI. VLIV MEZOLITICKÝCH POPULACÍ NA KRAJINU A VEGETACI: NOVÉ NÁLEZY ZE STARŠÍHO HOLOCÉNU TŘEBOŇSKÉ PÁNVE.

[Pokorný, P. (1999): Vliv mezolitických populací na krajinu a vegetaci: Nové nálezy ze staršího holocénu Třeboňské pánve. Zprávy ČAS, Suppl. 38, pp 21-22.]

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Úvod

Současní paleoekologové se rozcházejí v názoru na počátky intenzivního působení člověka na přírodní prostředí. Kořeny dnešní, člověkem formované krajiny střední Evropy bývají tradičně spatřovány v neolitu. Vznik zemědělské plochy jakožto člověkem řízeného ekosystému tehdy nesporně znamenal zcela novou kvalitu v naší přírodě a měl na její přeměnu hluboký dopad. Do jaké míry měla předzemědělská krajina střední Evropy přirozený, t.j. člověkem neovlivněný charakter, však zůstává stále nevyřešenou otázkou. Tradiční názor na vliv mezolitických populací na vegetaci je velmi skeptický: „Tento vliv byl zanedbatelný a je srovnatelný s vlivem jiných velkých býložravých zvířat. Změny v lokální vegetaci většinou nelze zachytit tradičními paleoekologickými metodami" (Rybníček et Rybníčková, 1992). Krajina předneolitického holocénu bývá nazývána „panenskou" (Rybníčková et Rybníček, 1985) a možnosti palynologické indikace jsou obecně považovány za velmi omezené (Kloss, 1987; Berglund, 1988). V poslední době se však množí důkazy o tom, že mezolitické lovecko-sběračské populace nevyužívaly přírodní prostředí pouze extenzivně. Docházelo k záměrnému mamagementu lísky (*Coryllus avellana*), určitých druhů trav, merlíků (*Chenopodiaceae*), šťovíků (*Rumex*), kotvice plovoucí (*Trapa natans*), orobince (*Typha*) a dalších druhů vodních rostlin (Zvelebil, 1994). Největší dopad na krajinu mělo nesporně vypalování. Výsledkem této záměrné činnosti bylo potlačení lesa a následkem toho zvýšení diverzity stanovišť a rozmanitosti zdrojů obživy (Mellars, 1976). Kontinuální výskyt mikroskopických uhlíků v sedimentech je v současnosti považován za nejspolehlivější indikátor lidské aktivity v době předzemědělského holocénu (Tolonen, 1986; Vuorela, 1995; Regnell et al., 1995). Vypalování mohlo vést k první domestikaci rostlin, ikdyž zpočátku nezáměrné, neboť potenciální užitkové rostliny s vysokou produkcí biomasy vyžadují otevřené plochy s dostatečným přístupem světla.

Výsledky paleoekologického studia jezerních sedimentů na lokalitě Švarcenberk

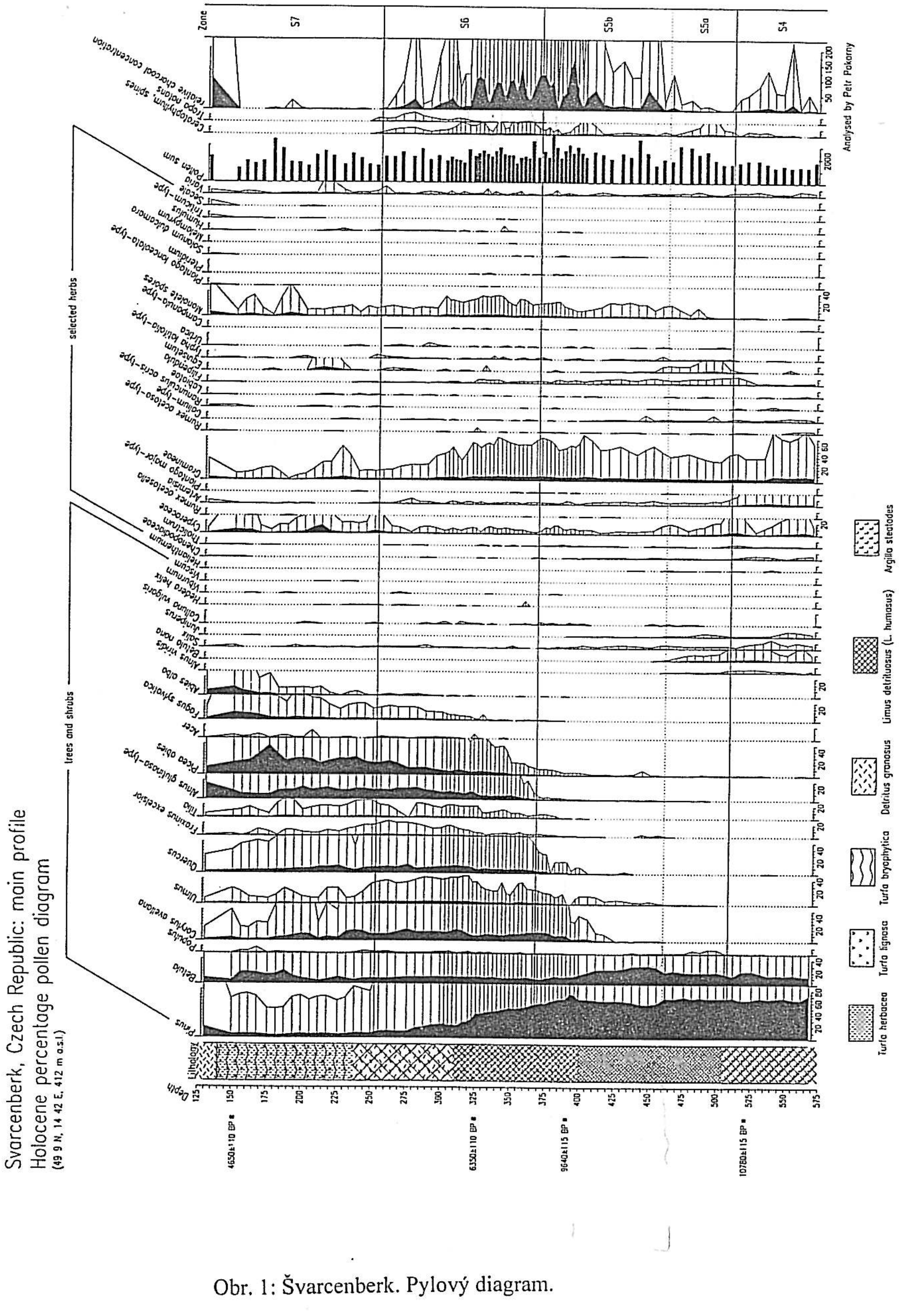
Přiložený pylový diagram prezentuje výsledky pylové analýzy jako jeden z výstupů rozsáhlého výzkumného projektu probíhajícího na místě bývalého jezera Švarcenberk v severní části Třeboňské pánve. Vysoké časové rozlišení a statistická průkaznost pylové analýzy jezerních sedimentů v kombinaci s radiokarbonovým datováním dovolují učinit některé závěry o působení mezolitických populací na okolní krajinu. V okolí zaniklého jezera byl nedávno proveden také povrchový archeologický průzkum, který přinesl štípanou pazourkovou industrii koncentrovanou na nízkém pahorku v těsném sousedství bývalé vodní plochy.

Intenzivní vypalování okolí lokality ve starším holocénu indikuje vysoká koncentrace mikroskopických uhlíků v sedimentu. S výskytem uhlíků korelují pylové křivky některých rostlinných druhů preferujících otevřená stanoviště a lesní okraje (žluťucha - *Thalictrum*, vřes obecný - Calluna vulgaris, kyselka obecná - *Rumex acetosella*, jitrocele - *Plantago major*-typ a *Plantago lanceolata*, trávy - *Gramineae*), případně požárem zasažené plochy (hasivka - *Pteridium*). Výskyt některých vodních a pobřežních rostlin ve stejném období může souviset s eutrofizací (t. zn. se zvýšením přísunu živin) jezera a jeho břehů (růžkatec - *Ceratophyllum*, orobinec širokolistý - *Typha latifolia*, kopřiva - *Urtica*). Zajímavý je výskyt kotvice plovoucí (*Trapa natans*) - vodní rostliny, jejíž škrobnaté oříšky mohly tvořit významnou součást jídelníčku mezolitického člověka (Vuorela et Aalto, 1982; Zvelebil, 1994) Výskyt kotvice plovoucí na jezeře Švarcenberk byl prokázán i hromadným nálezem plodů, radiokarbonově datovaných již do samého počátku holocénu (těsně po 10 000 BP). Překvapivě časný výskyt této teplomilné rostliny je nejen důkazem příznivého klimatu v příslušné době, ale navíc vyvolává podezření z její záměrné introdukce. Zajímavý je rovněž časný nález pylových zrn obilovin (*Triticum*-typ), radiokarbonově datovaný 9640±115 BP. Nálezy tohoto typu nejsou v rámci střední a západní Evropy ojedinělé a ukazují na možnost předneolitické domestikace některých domácích druhů trav (Zvelebil, 1994; Regnell et al., 1995).

Chronologicky lze zařadit nástup období časného antropogenního impaktu v okolí jezera Švarcenberk do samého počátku holocénu (10 000 BP). Mozaikovitá, polootevřená krajina pozdního glaciálu tak byla působením člověka nadále aktivně udržována, alespoň na určitých vymezených plochách. Nepřímá indikace přítomnosti mezolitických populací končí ve středním holocénu (cca 6 000 BP), kdy došlo k defenitivnímu zániku vodní plochy přirozeným zazemněním jezera. Lovecko-sběračské populace tím definitivně ztratily možnost rybolovu, lovu vodních ptáků i sběru kvalitní potravy v podobě vodních rostlin. V následující fázi je v pylovém záznamu patrný dočasný hiát v osídlení a to až do období okolo 5 000 BP, kdy nastupují první sporadické indikátory zemědělské aktivity.

Závěr

Přítomný příspěvek představuje jen velmi zkratkovitý přehled nových poznatků o historii nejstaršího působení člověka na krajinu a vegetaci, získaných studiem jezerních sedimentů dochovaných v severní části Třeboňské pánve. Přirozených vodních ploch bylo na našem území jen velmi málo a proto není divu, že přítomnost většího jezera přitahovala pozornost lovecko-sběračských skupin. Nové výsledky naznačují, že vliv mezolitických populací na okolní přírodu mohl být poměrně značný a že již ve starším holocénu mohla na určitých plochách vznikat kulturní krajina v pravém slova smyslu.



Obr. 1: Švarcenberk. Pylový diagram.

PŘÍLOHA (APPENDIX): LATE HOLOCENE HISTORY AND VEGETATION DYNAMICS OF THE ALDER CARR COMUNITY.

[Pokorný, P., Klimešová, J., Klimeš, L. (2000, in press): Late Holocene history and vegetation dynamics of a floodplain alder carr - a case study from eastern Bohemia, the Czech Republic. *Folia geobotanica et Phytotaxonomica* 35/1]

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Keywords: *Alnus glutinosa*, Cyclic succession, Floodplain mires, Palaeoecology, Pollen analysis, Vegetation ecology.

Abstract: Vegetation development in the lowland floodplain alder carr "Na Bahně" (eastern Bohemia, the Czech Republic) has been studied by means of pollen and macrofossil analyses and combined with vegetation analysis performed over the last 70 years. Local successional changes started with an oxbow lake (160 cal BC) which has later terrestrialised (630 cal AD). Then it changed from a typical alluvial fen into a *Sphagnum*-dominated spring mire (950 cal AD) supplyed by water arising from river terrace surrounding the locality from three sites. In the centre of this wetland a small patch of alder carr developed (1000 cal. AD), showing some tendency towards cyclic succession. The alder carr alternated several times with an open *Carex* fen (1100 cal AD to recent). The last fen-to-alder carr transition has been documented by direct observation during this century. Possible autogenic and allogenic factors driving the succession are discussed. The model of autogenic cyclic succession corresponds well with direct field observations and can be used to interpret alder carr structure, its dynamics, and function.

INTRODUCTION

Woodlands dominated by *Alnus glutinosa* occur usually on wet minerotrophic (*Alnion glutinoso-incanae* according to Zürich-Montpellier phytosociological system) or organic substrates (*Alnetea glutinosae*; the term "alder carr" is usually confined for this type). Phytosociological classification of alder carrs is well-established in Europe (DÖRING-MEDERAKE 1991, PRIEDITIS 1993, 1997), but little is known about their long-term dynamics (JENÍK 1980). Alder carrs have a limited distribution, being restricted to floodplains, where the natural hydrological regime has not been strongly modified by human action.

Numerous palaeoecological studies found alder carrs to be a successional stage that is later replaced by climax forests (TALLIS 1983, WALKER 1970), but others found them to be rather stable and long-persisting systems (MAREK 1965). Fortunately, in wetland woodlands several approaches can be combined, such as direct observations, dendrochronology, pollen and macrofossil analysis (FOSTER et al. 1996, DELCOURT & DELCOURT 1991). Using these approaches, the factors responsible for long-term vegetation changes can be identified. However, some limitations should be taken into account:

(1) The peat deposits under alder carrs usually undergoing mineralisation. Peat is aerated in the root layer of the alder and as a result, mineralization speeds up (JENÍK 1980, BENNETT & BIRKS 1990). Originally flat surface of the fen therefore develops into hummocks and hollows. This is the case of most alder carrs described in literature. The hummocks can be up to 1 m high (PRIEDITIS 1997). In extreme cases peat is mineralised nearly completely. Mineralization of the peat may be one of the factors responsible for the occurence of stratigraphic hiatuses recorded in the stable, wet climate of Middle Holocene (RYBNÍČEK & RYBNÍČKOVÁ 1987). The peat is preserved only exceptionally under alder-carr communities, when a stable water level prevents aeration, so that anoxic conditions are maintained throughout the year. This particular situation on the site of the present study is indicated by a flat, permanently wet soil surface, without hummocks and hollows microtopography (KLIMEŠOVÁ & KLIMEŠ 1996).

(2) Floodplain environments has been changing markedly during the Holocene in central Europe, because of changing periods of sedimentation and erosion (OPRAVIL 1983, ELLENBERG 1996, BROWN 1997). Periods of low sedimentation were characterised by the development of soils, fens, and cultural horizons, whereas periods of prevailing accumulation resulted in these layers beeing covered by gravel and clay, often with embedded trunks (RŮŽIČKOVÁ & ZEMAN 1994). During erosional periods, the fens developping in terrestrialised oxbows are often destroyed, resulting in loss of pollen and macrofossils-containing sediment needed for study the history of alluvial alder carrs. Well-preserved, long-term palaeoecological records are therefore quite rare in contemporary floodplains (DÖRING-MEDERAKE 1991; PRIEDITIS 1993, 1997).

The locality "Na bahně" (E. Bohemia) is an example of an alluvial alder carr featuring well-preserved and relatively long palaeoecological record. The topography of the surroundings suggest the locality was originally an oxbow lake (SITENSKÝ 1891, MIKYŠKA 1926). Numerous springs at the foot of the terrace, situated around the locality on three sides, ensure a stable water regime and permanently high water-level. The vegetation cover of the locality has been repeatedly studied during the last 70 years (MIKYŠKA 1926, 1964, KLIMEŠOVÁ & KLIMEŠ 1996), so a comparison between palaeoecological and phytosociological data can be made.

MATERIAL AND METHODS

The study site

The alder carr "Na bahně" covers an area of about 1 ha below the youngest (Weichselian) terrace on the left bank of the Orlice River, about 8 km E of its entrance to the Labe (Elbe) River (240 m a. s. l., 50° 12' N, 15° 58' E; Fig.1). The terrace, about 5 m high, surrounds the alder car from the S, SE, and SW. It is covered with mixed forest dominated by *Quercus robur*. In the north, the alder carr is bordered by wet abandoned meadows, which are gradually beeing invaded by alder. At the foot of the terrace several strong springs are situated, stabilising the water regime of the locality. Their discharge is independent of year-to-year climatic variability and of smaller fluctuations of the water level in the nearby river (personal observations during the last 10 years). The site is situated about 150 m from present river channel. Peat accumulation has recently resulted in the doming over the surrounding terrain. This has led to a certain degree of emancipation of the locality from the direct influence of the river.

The bedrock of the locality and its surroundings is Cretaceous (Turonian) calcareous marl covered with acid sandy and gravel sediments. Mean annual air temperature is 7.8 ^{0}C, and annual precipitation is 602 mm (1901 to 1950, Nový Hradec Králové Meterological Station, 8.5 km E of the locality; VESECKÝ 1961).

The site under study is dominated by *Alnus glutinosa,* with scattered *Betula pubescens* trees. The following plants prevail in the herb layer (ordered according to their decreasing frequency): *Cardamine amara, Solanum dulcamara, Lycopus europaeus, Urtica dioica, Thelypteris palustris, Myosoton aquaticum, Calamagrostis canescens, Cirsium oleraceum, Chrysosplenium alternifolium, Oxalis acetosella, Athyrium filix-femina, Carex elongata, Mentha aquatica, Poa palustris*. Phytosociologically, the alder carr belongs to a nitrophilous variant of *Carici acutiformis-Alnetum* (SÁDLO, pers. comm.).

Data collection

A series of exploratory borings was performed in early spring of 1997 at the centre of the locality. Peat from nearly 2.5 to about 5 m thickness was found in the area recently covered by alder carr. Fine-grained mineral flood loam with organic detritus underlay the peat. Approximately 16 metres from the edge of the eroded terrace the peat deposit reaches its maximum depth.

Sediment sequence 5 m long was taken with a Russian-type corer (JOWSEY 1966) 5 cm in diameter for litho-stratigraphic examination, ^{14}C dating, macrofossil and pollen analysis. The sediments were analysed for their components according to AABY & BERGLUND (1986).

Three levels were radiocarbon-dated. Few pieces of alder wood were selected for each radiocarbon analysis. One sample (Lu4529) was dated by decay counting and two others by AMS method at the Radiocarbon Dating Laboratory, Department of Quaternary Geology, Lund, Sweden. Age calculations were based on a ^{14}C half-life of 5568 years. The results were calibrated (after STUIVER & REIMER 1993) and are reported on the calibrated calendar time scale.

The samples used for pollen (and other microfossil) analysis were prepared by modified acetolysis method (ERDTMAN 1943). As the lower part of the core had more or less mineral character, the samples were pre-treated with concentrated (35%) coldhydrofluoric 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 mixture. In each sample an average of 1500 pollen grains was counted. For pollen identification, the following keys as well as a reference collection were used: FAEGRI & IVERSEN (1989), MOORE et al. (1991), PUNT (1976-1995).

The core from which the samples for ^{14}C and pollen analysis were taken was subsampled also for macrofossil analysis: Contiguous samples 20 cm long were cut, and the fresh volume of each was determined. Macrofossils were extracted by heating each sample for 5 minutes in a 5% potassium hydroxide (KOH) solution and sieved with running water. Sieves with mesh sizes of 200 µm, 300 µm and 700 µm were used. The residues were examined under a dissecting stereomicroscope. For the macrofossil diagram, the absolute number of each taxon was recalculated to a standard volume of 500 cm^3 fresh sediment.

Plant nomenclature follows TUTIN et al. (1964-1980), pollen nomenclature follows ALPADABA (*Alpine Palynological Data-Base*, housed at the Geobotanical Institute, Bern).

Data analysis

In the pollen diagram local elements were distinguished from regional ones according to the following method (after RYBNÍČKOVÁ & RYBNÍČEK 1971 and HULME & SHIRRIFFS 1994): Taxa present in both the pollen and macrofossil data-sets were considered as local ("gravity component" of the pollen spectra according to FAEGRI & IVERSEN 1989), whereas pollen taxa not present among the macrofossils were considered to be of extralocal, regional, or extraregional ones. Pollen belonging to one or several strictly wetland species was considered as part of the local component, nevertheless it was not recorded as a macrofossil. Broad pollen types, which include at least one species growing in mesic or dry habitats, were excluded from the local diagram to avoid possible misinterpretations. Percentage values were calculated on the basis of the regional pollen sum (for the list of regional pollen types see the Appendix). Concealed, corroded, degraded, and well preserved, but indeterminable pollen grains were included under "varia". Printing of the diagrams was performed with TILIA computer program, written by E. C. GRIMM (Springfield).

Zonation of the pollen and macrofossil diagrams was made visually, using both presence and the abundance of the taxa. A more formalised approach to delimit the zones was also applied, using Detrended Correspondence Analysis - DCA (HILL 1979, TER BRAAK & ŠMILAUER 1998). DCA belongs to a group of multidimensional scaling methods designed to detect the underlying pattern in the data. It is an extension of correspondence analysis (CA), eliminating the arch effect that is produced by CA if data are sampled along long gradients (WARTENBERG et al. 1987). DCA results, presented as ordination diagrams, show the overall trends in the data. Similar samples are close together and dissimilar samples are far from each other. If data are more or less continuous, an ordination diagram is a more useful tool than cluster analysis, because it reflects better the inherent, complicated structure in the data.

Log-transformed percentages of individual pollen and macrofossils taxa were used as input data in our case. Before analysis, some macrofossil taxa were combined into higher pollen taxa; e.g. all macrofossil finds of *Carex* species were lumped together because pollen grains of individual species are not determinable at the species level.

In the scatter diagram, the samples were grouped into "zones" using the following procedure: Three pollen samples were randomly selected from adjacent depths. All other pollen samples located in the range of the three chosen samples were included into the selection. The selection process was continued by including aditional samples until there were no overlapping zones in the selected pollen samples. Then, macrofossil samples were selected from the same depths as the previously-selected pollen samples. If necessary, the macrofossil selection was continued in the same way as that of the pollen samples. After completing the macrofossil selection, the pollen selection was adjusted to include samples from corresponding depths. This iterative procedure continued until the pollen and macrofossil selections included contiguous samples from the same depths. Finally, the same procedure was performed for samples so far not included into any selection. Thus, an equal number of non-overlapping envelopes, which included samples from the same depths, was obtained for pollen and macrofossils. The whole procedure was repeated 100 times in order to determine alternative zonations.

RESULTS

The results of the pollen and macrofossil analyses are presented in the form of diagrams (Figs. 2 and 3). Separation of local elements of the pollen rain follows the criteria described above. Pollen types that did not fall into the local pollen diagram are listed in the

Appendix. Four local zones were distinguished on both pollen and macrofossil diagrams. Absolute ages of the zone boundaries can be roughly estimated by linear interpolation from three available radiocarbon dates (Tab. 1).

If the pollen and macrofossil data are used simultaneously for DCA analysis, only two zones can be distinguished in the ordination diagram (Fig. 4). Further division would result in an overlap of envelopes, including samples belonging to individual zones. The lower zone corresponds to the visually delimited zone NBL-1 (oxbow lake phase; 160 cal BC - 610 cal AD). The remaining samples form a group that can be further divided if the taxa are weighted or if a different approach gives more weight to the dominant taxa. For example, zone NBL-2 is differentiated from the other zones by the abundant *Filipendula* and *Caltha* macrofossils and *Filipendula* pollen, zone NBL-3 by *Equisetum* and *Sphagnum* spores, and zone NBL-4 by abundant Cyperaceae pollen and *Betula* fruits.

Zone NBL-1 (oxbow lake phase; 160 cal BC - 610 cal AD)

This zone is characterised by the finds of indicators of permanent water bodies, suggesting that a small oxbow lake has been present. According to the finds of aquatic plant remains (*Myriophyllum spicatum, Ranunculus* Subgen. *Batrachium, Potamogeton, Nuphar lutea, Ceratophyllum demersum* and *Nymphaea alba*) its depth was about 1.5 m. The occurrence of Nympheaceae and *Ceratophyllum* has been confirmed by the finds of trichosclereids and leaf-spines, respectively (determination after VAN GEEL 1978). High diversity of aquatic macrophyte vegetation indicates that the oxbow lake was not completely shaded by trees (PRACH et al. 1996). The occurence of *Mougeotia* zygospores (chlorococcal algae) indicate permanent, shallow-water conditions as well (JANKOVSKÁ & KOMÁREK 1982). Chlorococcal algae (e.g., *Pediastrum*, the genera frequently found in pollen preparations from lake environments) grew in low quantities in the pond, as is true also for many recent oxbow lakes (PITHART et al. 1996). Macroscopic statoblasts of *Cristatella mucedo* (Bryozoa) also indicate permanent water conditions, either stagnant or slowly flowing.

Amphibious plants such as *Alisma gramineum, Polygonum amphibium,* and *Sagittaria sagittifolia* formed the littoral vegetation, which passed to the telmatic belt formed by sedges (predominantly *Carex rostrata*) and by other common marsh plants (*Lycopus europaeus, Lythrum salicaria, Cicuta virosa, Ranunculus flammula, Solanum dulcamara*). An alder stand occurred near the oxbow lake (see abundant finds of *Alnus glutinosa* seeds). Pine (*Pinus*), hornbeam (*Carpinus betulus*), and lime (*Tilia cordata)* probably grew on the adjacent terrace slope situated 16 m or more from the sampling site.

Zone NBL-2 (fen phase; 610 cal AD - 930 cal AD)

After the oxbow lake had filled up, an eutrophic fen dominated by *Filipendula ulmaria* and *Caltha palustris* has developed. Sedges (*Carex vesicaria, C. pseudocyperus, C. echinata*) were relatively infrequent. Accumulation of peat began that time. Comparison of pollen and macrofossils shows a high coincidence in *Filipendula* pollen and seeds occurrence. This corresponds to the results of other authors (JANKOVSKÁ 1980; FAEGRI & IVERSEN 1989), who concluded that the gravity component prevails in the pollen rain of this entomogamous plant, with unusually high pollen production. Although *Alnus glutinosa* pollen is abundant in the entire zone NBL-2, the number of macrofossils slowly decreases, probably indicating that alder declined locally.

Zone NBL-3 (*Sphagnum* mire phase; 930 cal AD - 1100 cal AD)

An abrupt vegetation change took place at the onset of NBL-3zone. *Sphagnum* mire, dominated by *Equisetum* and *Calla palustris* replaced the previous eutrophic fen. Among the mosses, *Sphagnum palustre* dominated, *S. squarrosum* was less common. Leaf remains of mosses from the Amblystegiaceae family (*Drepanocladus* and *Calliergon*) were also present in the sediment. Occurrence of *Tilletia sphagni*, a parasitic fungus forming spores in the capsules of *Sphagnum*, correlates with the *Sphagnum* spores occurence (as also noted by KUHRY 1997 and VAN GEEL 1978).

The vegetation change at the transition between zones NBL-2 and NBL-3 indicates that the site became more oligotrophic. Since this time, the river activity contributed only little to the sedimentation process at the site and the effect of local springs at the foot of the terrace started dominate.

Zone NBL-4 (alder carr phase; 1100 cal AD to present)

Another abrupt vegetation change occurred during the transition between zones NBL-3 and NBL-4. The *Sphagnum*-dominated mire changed into a fen with *Potentilla palustris, Lycopus europaeus, Cicuta virosa, Carex echinata,* and *Caltha palustris.* The decline of mosses was likely caused by the invasion of birch trees (through the overshading). The surface became more nutrient-rich after the mosses declined and this enabled colonisation of the site by alder. Finally, a closed alder carr had developed.

During the next 900 years the alder carr declined and re-established repeatedly. In the pollen record four stages dominated by alder were associated with few heliophilous wetland herbs, mostly grasses and Cyperaceae (different *Carex* species according to the macrofossil data). Similar tendency is observed also in the macrofossil diagram, where three alder-dominated stages can be distinguished as well. Some chronological displacement between pollen and macrofossil record is probably caused by the fact that the core was subsampled contiguously for macrofossil analysis, whereas for pollen analysis a discontinuous subsampling has been performed.

The uppermost two samples of the pollen diagram comprise approximately the last 70 years, for which direct botanical observations are available (MIKYŠKA 1926, MIKYŠKA 1964, RYDLO 1981, KLIMEŠOVÁ & KLIMEŠ 1996). In the *Sphagnum* peat layer (16-27 cm), several mosses indicating mesotrophic to eutrophic habitats are recorded (*Sphagnum palustre, S. recurvum,* and *Calliergon cordifolium* were abundant, and *Sphagnum squarrosum* and *Rhizomnium punctatum* were infrequent). This layer, formed by species indicating an open vegetation, corresponds to the situation recorded by MIKYŠKA (1926) in the 1920s. The current situation of the locality, which is completely covered with alder carr, is reflected by the pollen and macrofossil sample taken from a surface moss polster.

DISCUSSION

Taphonomy of the pollen spectra

In the dynamic environment of a river floodplain where the position of the river bed is not fixed and where erosion and accumulation periods alternate, a long, well-preserved, and undisturbed palaeoecological record has rarely been studied. We have found a profile with a continuous sedimentation from about 160 BC up to recent. It is a pertinent question to what extent this profile was disturbed by the nearby river and influenced by accumulation of flood loams. The deposition of redeposed pollen and macrofossils may complicate the interpretation of the palaeoecological record. The lowermost one third of the profile was formed predominantly by finely granular clayey material, which represents a flood deposit. One reason why such deposits were avoided in palaeoecological studies in the past was the fear that the pollen would be selectively transported by water either into or out of the site. The ecological coherence of floodplain diagrams suggest that this is not an insurmountable problem in most cases (BROWN 1997). This seems to be true also in our case as there was no significant change in the regional pollen record at the transition from floodplain sedimentation to autochthonous organic sedimentation. In adition, direct observations showed (BROWN 1985) that while flood waters often contain a high concentration of pollen, flood deposits contain very little due to the constant turbulence, which does not allow pollen to settle out. Because of this, we consider our results comparable to those obtained from any peat-bog and equally reliable.

Zonation of the pollen and macrofossil diagrams

We used two approaches to evaluate the diagrams. Visual zonation is the commonly used one whereas multivariate analyses are less frequently used, however it is an efficient and well-established approach (PRENTICE 1986). The advantage over subjective visual evaluation is its repeatability (using the same data and the type of analysis, the same results are obtained by any researcher). However, the process of multivariate analysis does not include any information outside the analysed data set. Thus, no experience of the researcher is used in the interpretation of primary data. As a result, the zonation based on a multivariate analysis reflects well the pattern in the data-se, but its predictive power is usually lower than that of the traditional visual zonation.

Visual evaluation of our diagrams resulted in four zones differing in species composition and abundance. To establish individual zones more weight was given either to species composition (transition of zones NBL-1/2) or to the dominance of selected taxa (transition of zones NBL-2/3 and NBL-3/4). Using the ordination axes I and II, DCA procedure separated individual pollen and macrofossil samples quite well. Further separation of any group consisting of a minimum of 3 samples based on both pollen and macrofossils was possible in one way only, with a zone boundary placed between sample Nos. 17 and 18. Any other division would result in an overlap between envelopes enclosing groups of samples based on pollen, macrofossil data, or both.

Local vegetation succession

It has been shown in numerous palaeoecological studies that vegetation succession during the terrestrialisation of freshwater lakes is rarely determined by a single factor. Numerous autogenic as well as allogenic factors cause the probabilistic character of the transition between individual succession stages (WALKER 1970; TALLIS 1983; SINGER et al. 1996; YU et al. 1996). The main factors responsible for successive vegetation development in the site under the present study seem to be the changing hydrological regime of the locality (effects of the river and artesic springs), and chnges in nutrient availability (competition for nutrients between *Sphagnum* mosses, herbs, and seedlings of woody plants). The fast transition between individual successional stages has been promoted by a high accumulation rate of the peat (2.4 mm/year, on average). The effect of allogenic factors prevailed at the beginning of succession, later autogenic factors became dominant. Over the last nine centuries autogenic factors contributed significantly to the characteristic successional pattern in the alder carr community as described below.

The dynamics of the alder carr

Forests dominated by alder have been present in Central Europe since Early Holocene (HUNTLEY & BIRKS 1983, LANG 1994, BERGLUND et al. 1996). They represent an important successional stage of terrestrialisation of freshwater bodies. In wet, oceanic climate they are a characteristic transient vegetational stage on eutrophic lake basins that had filled up. Later, they often develop into oligotrophic *Sphagnum* mires (WALKER 1970, TALLIS 1983). According to some authors (e.g. MAREK 1965), alder-dominated forests may persist continuously at one site over thousands of years. However, the character of alder life cycle (MC VEAN 1953, 1956a) makes this idea uncertain. Long-term persistence of alder-dominated stands require continuous alder regeneration. Alder carrs require nearly full light conditions for their establishment. Most alder-dominated stands with a canopy cover of 30 - 50 % are not suitable for surviving of alder seedlings (KORPEĽ 1995, TUCKER & FITTER 1981). The light regime in a closed alder carr is insufficient even for regeneration from the bases of dead mother trunk, so daughter trees have a low vitality and die soon. Seedlings and basal shoots can develop and contribute to the canopy only in a swamp carr on a floating mat where trees are short (2 to 3 m tall, with little foliage) and sparse (MC VEAN 1956b).

Another factor adversely affecting the establishment of alder seedlings in alder-dominated stands is often too high a soil moisture (MCVEAN 1956a). In an alder carr, mineralisation of the peat results in increased soil moisture and waterlogging. The age structure of most alder stands also raices doubts about their long-term persistence. Even-aged alder populations, indicating a short single period of alder establishment, are usually found (PIGOTT & WILSON 1978, TUCKER & FITTER, 1981). Therefore, the natural regeneration of alder in an alder carr seems to be unlikely.

In the case of "Na bahně" site, we have found alder carr persisting over several centuries. However, it was found in the palaeoecological record to be a dynamic system with a tendency towards cyclic development. Closed-canopy alder carr alternated several times with open vegetation dominated by sedges and *Sphagnum*. It resembles the hypothesis of cyclic development made for various types of forests (MÍCHAL 1983; DELCOURT & DELCOURT 1991; KORPEĽ 1995; SCHMIDT 1998).

The second half of the last alder carr cycle has been recorded on the site by several botanists and documented since the 1920s. In the centre of the locality, MIKYŠKA (1926) described a mire surrounded by young alder carr forming a belt close to the terrace edges. In his second paper (MIKYŠKA 1964), he described the vegetation of the same locality after 38 years. The central part of the mire was already overgrown by young alder forests. At present alder forms a homogeneous stand in the whole surface of the site (KLIMEŠOVÁ & KLIMEŠ 1996), differing only in the age of the trees between the centre and the margin (KLIMEŠOVÁ et al. 1997). The results of the botanical studies carried out in the last 75 years accord well with the pollen and macrofossil analyses. The observed pattern of long-term cyclic development can be explained using one of the following models:

a) Allogenic model - direct human disturbance

The decline of the tree canopy could be associated with cutting. Decomposition of alder trunks and stumps is relatively fast, so their absence in the peat noted by us during the pilot study cannot serve as an evidence against cutting. However, the timing of the individual successional cycles of the alder carr does not correlate with that of anthropogenic impact, as evidenced by pollen analysis (POKORNÝ & BENEŠ, in prep.). Therefore the hypothesis of direct human disturbance is not supported by any evidence.

b) Other allogenic impacts

Changes in water-level and nutrient availability, either human- or climatically-induced, may also stimulate or prevent the establishment of alder and eventually cause a dieback of fully matured stand. Human-induced changes of hydrological conditions resulting in dieback of alder-dominated forest have been described by BROCK et al. (1989). JANSSEN et al. (1995) explained the dieback and new establishment of an alder stand by fluctuations in water-level caused by long-term changes in river discharge. It is difficult to reject any of these hypotheses in our case. However, the results of the pollen and macrofossil analyses and the continuous character of the sedimentation indicate that abrupt hydrological changes did not occur during critical periods in the development. The same holds for nutrient availability.

c) Autogenic model

As alder cannot regenerate in closed-canopy stands, a massive dieback of even-aged alder trees can be expected at an age of 100-150 years, depending on their vitality. Increased light availability may stimulate the development of an open mire covered with light-demanding plants and intensively accumulating the peat. The more substrate has been mineralised during previous alder phase, the longer is the stage of open vegetation, because the mineralisation resulted in an increased soil moisture. Thereto, the evapotranspiration rate decreases as the result of tree layer dieback, also contributing to general waterlogging of the site. Only when the newly formed peat layer starts doming over the groundwater table again (as a whole or by forming the tussocks), alder seedlings may establish on the site and the cycle is completed. Newly established alder stand is even-aged because the establishment took place during a short time. This development can be further complicated by fluctuation of water-level.

If the peat layer is repeatedly mineralised during alder carr phase, the cycle can hardly be inferred from palaeoecological data. In case of larger alder stands the cyclic development may take place in a mosaic of patches. Even in this case pollen analysis does not represent a suitable approach for studying the long-term cyclic development, because of the noise caused by dispersal of pollen between individual patches. WIEGERS (1985) proposed a similar pattern of cyclic succession for floating fen woodlands albeit with one more factor: vertical movement of the whole surface below the water table caused by the weight of the trees. In the central part of the "Na bahně" site, where the core has been taken, peat mineralisation is a slow process due to the high and stable water level resulting from the local springs. Thus the exceptional hydrological conditions resulted in a well-preserved palaeoecological record. Cyclic development directed by autogenic factors was still possible here: the high water-level further increased after a dieback of the tree layer, and later on, when the mire vegetation formed relatively dry hummocks, establishment of alder was again made possible.

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TABLES AND FIGURES

Table 1. Radiocarbon dates from Na Bahně site.

Lab. No.	Depth	Measured ^{14}C age	Calibrated age	Method
LuA-4528	110-112 cm	890±90 BP	1168 cal AD	AMS
Lu-4529	330 cm	1440±70 BP	635 cal AD	decay
LuA-4551	450 cm	2020±110 BP	2 cal BC	AMS

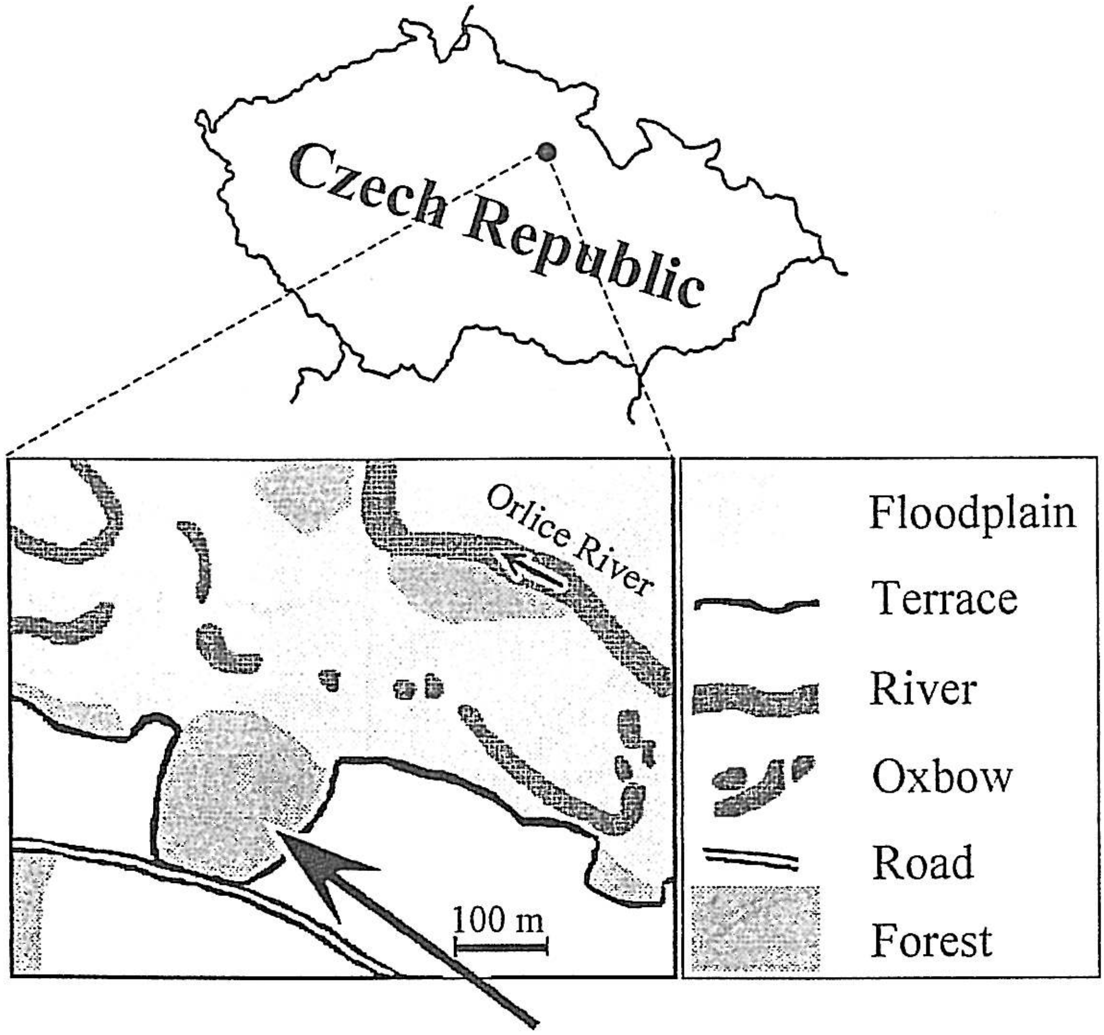

Fig. 1. Location of the study area within the Czech Republic.

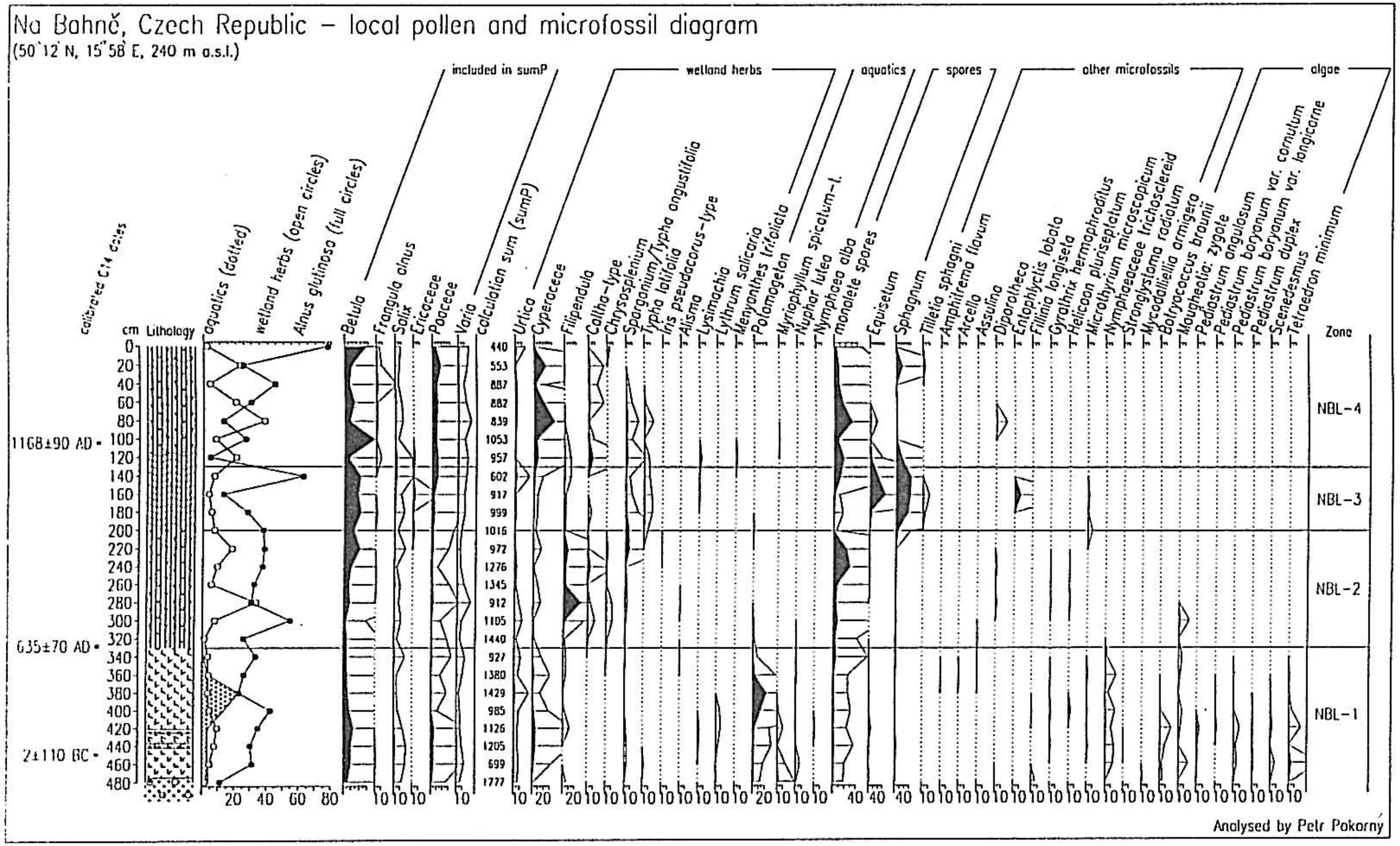

Fig. 2. Percentage pollen diagram from the alder carr "Na bahně". Only the taxa representing local vegetation elements are selected. For sediment description, see Fig.3.

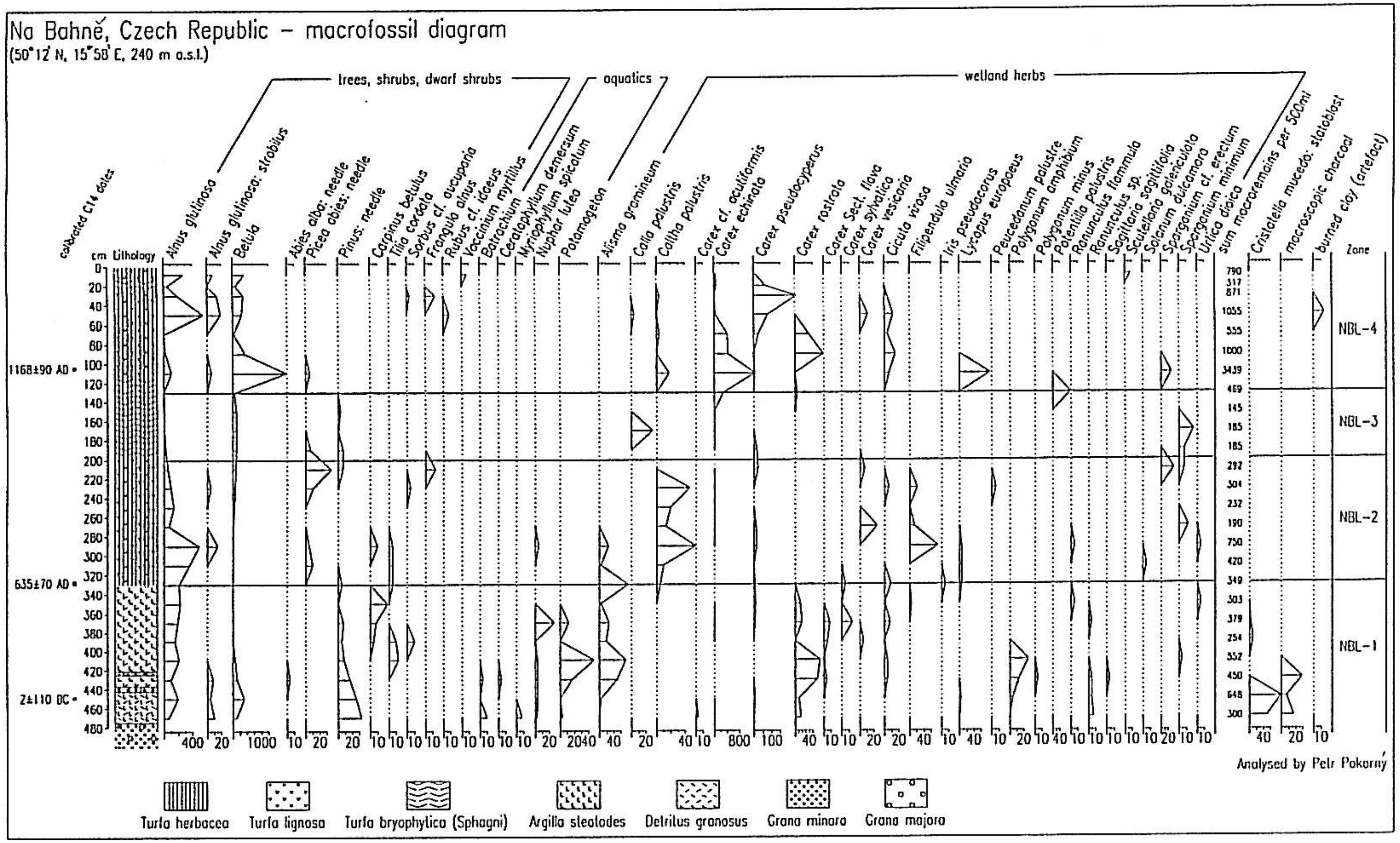

Fig. 3. Macrofossil diagram from the alder carr "Na bahně". Absolute number of the finds was recalculated to a standard volume of 500 cm^3 of fresh sediment. If not stated differently, all finds represents seeds.

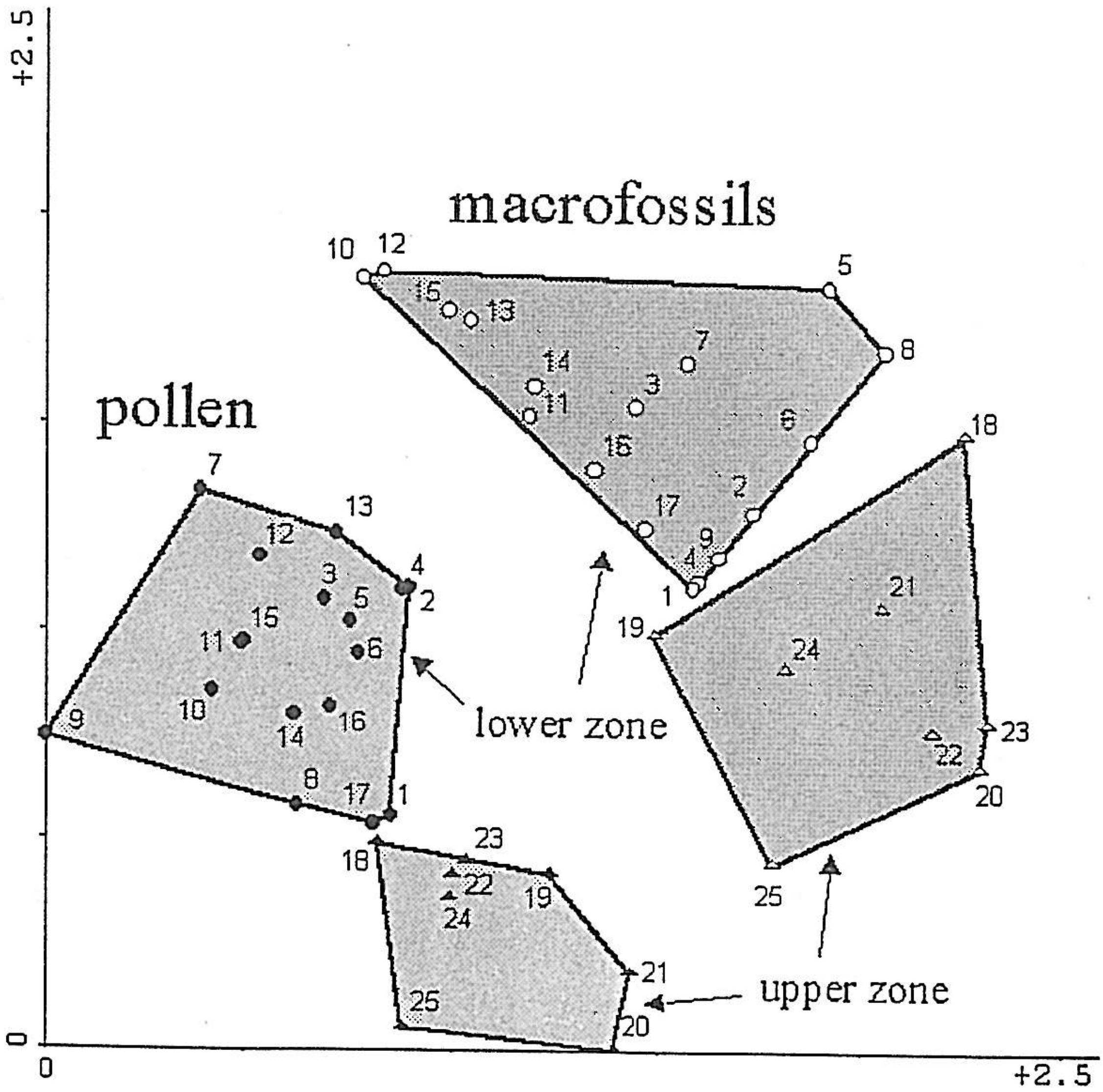

Fig. 4. DCA ordination of pollen and macrofossil data from the alder carr "Na bahně". Full symbols - pollen samples, open symbols - macrofossil samples, circles - lower zone, triangles - upper zone. Numbers denote the order of samples from the surface (1) to the bottom (25). The two zones were delimited using the procedure described in the methods.

Appendix: The list of pollen types not included in local pollen diagram (for separation criteria see methods)

Trees and shrubs: *Abies alba, Acer, Carpinus betulus, Cornus sanguinea, Corylus avellana, Euonymus europaeus, Fagus sylvatica, Fraxinus excelsior, Hedera helix, Juglans, Juniperus, Picea abies, Pinus sylvestris, Quercus, Sambucus nigra, Tilia, Ulmus, Viburnum opulus, Viscum album.*
Anthropogenic indicators: *Cannabis sativa, Centaurea cyanus,* Chenopodiaceae, *Convolvulus arvensis, Plantago lanceolata, Plantago major/media, Polygonum aviculare, Rumex acetosa*-type, *Rumex acetosella*-type, *Secale cereale, Triticum*-type, *Zea mays.*
Herbs: Compositae Subfam. Cichorioideae, Compositae Subfam. Asteroideae, Cruciferae, *Galium*-type, Umbelliferae, Caryophyllaceae, Gramineae, *Calluna, Calystegia, Campanula, Centaurea jacea*-type, *Epilobium, Euphorbia, Helianthemum nummularium*-type, *Humulus lupulus, Impatiens,* Labiatae, *Lotus*-type, *Melampyrum, Mentha*-type, Papilionaceae, *Polygonum persicaria*-type, *Ranunculus*-type, Rosaceae, *Rubus, Sanguisorba officinalis, Stachys*-type, *Symphytum, Trifolium, Valeriana officinalis*-type, *Veronica*-type, *Viola palustris*-type.
Spores: *Anthoceros punctatus, Lycopodium annotinum, Polypodium.*

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FOTOGRAFICKÁ PŘÍLOHA

Foto 1: Pohled na jižní zátoku rybníka Švarcenberk se společenstvy rákosin v místě profilu „S500“.

Foto 2: Letecký snímek rybníka Švarcenberk s vyznačením plošného rozsahu jezerních sedimentů. Křížkem je označeno temeno pahorku, kolem kterého je koncentrován výskyt pazourkových artefaktů.

Foto 3: Odběr profilu jezerními sedimenty z plovoucí vrtné plošiny.

Foto 4: Profil jezerními sedimenty krátce po odběru.

Foto 5: Jezerní sediment s plody kotvice (*Trapa natans*). Kopaná sonda „S500", 210 cm.

Foto 6: Rostlinné makrozbytky z jezerního sedimentu boreálního stáří („hlavní profil", 370 cm). *Ceratophyllum demersum, Potamogeton natans, Najas marina, Nuphar lutea, Nymphaea* cf. *alba*, trny *Trapa natans*.

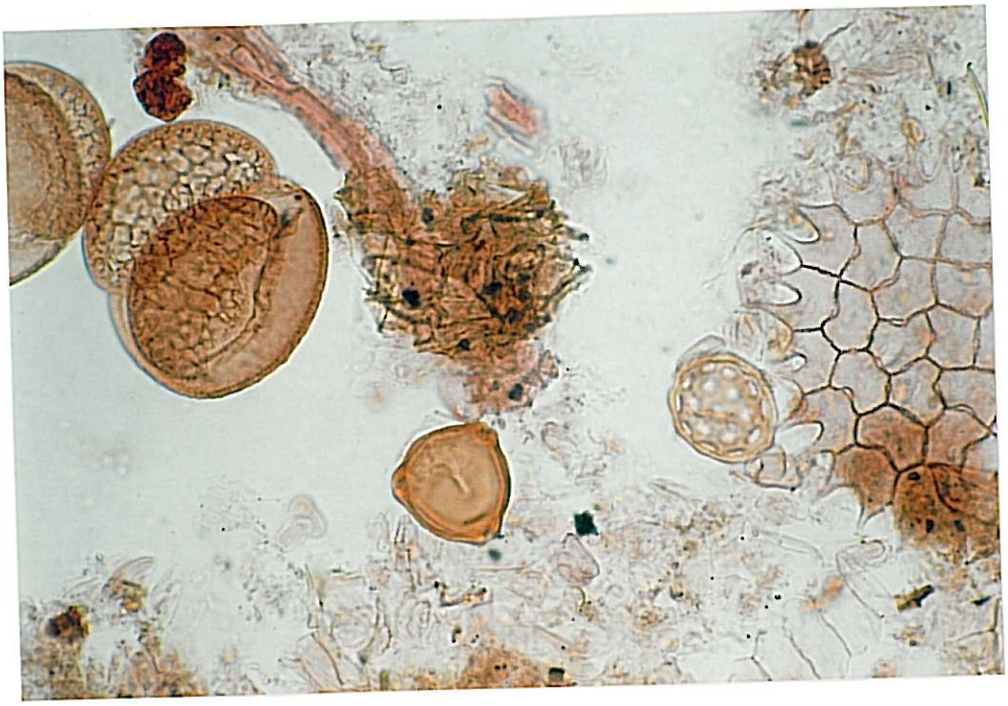

Foto 7: Pylová zrna Chenopodiaceae, *Betula, Pinus* a chlorokokální řasa *Pediastrum boryanum* var. *boryanum* v sedimentu interstadiálního stáří („hlavní profil“, 770 cm). Zv. 700X.

Foto 8: Pylové zrno *Myriophyllum alterniflorum* ze sedimentu datovaného do přelomu pozdního glaciálu a holocénu („hlavní profil“, 510 cm). Zv. 1000X.

Foto 9: Chlorokokální řasa *Pedistrum integrum* - indikátor chladnějšího klimatu (mladší dryas, „hlavní profil“, 600 cm). Zv. 1000X.

Foto 10: Pylová zrna *Trapa natans, Ulmus* a *Pinus* v sedimentu atlantického stáří („hlavní profil“, 270 cm). Zv. 700X.

Foto 11: Letecký snímek oblasti nivy řeky Lužnice se zatopenými pískovnami a pozdnoglaciální dunou vátých písků „Pískový přesyp u Vlkova". V pozadí rybník Švarcenberk s vyznačením rozsahu bývalého jezera v době vzniku Pískového přesypu.

Foto 12: Z výzkumu Pískového přesypu u Vlkova.