HABILITAČNÍ PRÁCE

Fosilní dřevo
a jeho význam pro paleobotanický výzkum:
případové studie z oblasti středních a sz. Čech

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Obsah

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1. Předmluva

„Čím dále v les, tím více dřev."
české přísloví

Fosilní dřevo se díky své povětšinou odolné povaze nachází v geologickém záznamu velmi často a ve velkém množství a představuje tak důležitou složku rostlinných fosilií (Poole & van Bergen 2006). Jeho význam pro vývoj paleobotaniky dobře ilustruje fakt, že dokonce Kašpar Maria hrabě ze Šternberka se v r. 1820 obsáhle věnuje tzv. „stromu potopy" z Jáchymova na úplně první straně svého velkolepého díla *„Flora der Vorwelt"* (Sternberg 1820), které fakticky pokládá základy moderní paleobotaniky (Kvaček 1982). Šternberk si pak především všímá významu, který má jáchymovské dřevo pro pochopení procesu vzniku zkamenělin jako takových. Paleoxylotomie, jak můžeme označit vědu, která fosilní dřeva studuje, se postupně díky svým vynikajícím zástupcům jakými byli např. profesoři Heinrich Göppert (1800–1884), Richard Kräusel (1890–1966), či Édouard Boureau (1913–1999) stala pevnou součástí paleobotaniky (Taylor *et al.* 2009). V současnosti se vedle čistě systematických studií dostává do popředí možnost využití fosilního dřeva při rekonstrukci klimatu (např. Wiemann *et al.* 1999), jakož i při získávání dalších obecnějších informací z geologické minulosti. O tento přístup, totiž vyváženost mezi úzce zaměřeným taxonomickým pohledem a širším přesahem při studiu fosilních dřev, se snaží i moje práce. Doufám jenom, že alespoň částečně úspěšně.

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2. Poděkování

Na prvním místě bych rád poděkoval svému příteli a nejvýznamnějšímu dodavateli zkamenělých dřev, rovněž jejich znalci, obdivovateli a sběrateli, geologovi z Dolů Bílina, Zdeňkovi Dvořákovi. Díky němu jsem měl většinu dřev k dispozici pro studium. Vedle něj bych rovněž poděkoval následujícím kolegům, sběratelům a milovníkům zkamenělých dřev: Bořkovi Zasadilovi, Frantovi Foltýnovi, Jirkovi Svejkovskému, Karlovi Machovi, Josefu Ševčíkovi, Pavlovi Coufalovi, Oldovi Janečkovi, Mirkovi Radoňovi, Vláďovi Rapprichovi, Michalovi Řehořovi, Rosťovi Nedbálkovi, Frantovi Jechovi, Jiřímu Zajíčkovi a dalším.

Rovněž bych rád vyjádřil vděk všem svým kolegům a studentům za přínosné odborné diskuze, které měly příznivý vliv na výslednou práci a určitě ji obohatily. Jedná se především o prof. Zlatka Kvačka z mého mateřského Ústavu geologie a paleontologie a Catherine Gill, Maître de Conférences pracující v době aktivní kariéry v Laboratoři paleobotaniky a paleoekologie Univerzity Pierra a Marie Curieových (Paris 6), tj. na pracovišti, kde jsem absolvoval DEA a doktorská studia a se kterým i nadále zůstávám v těsném kontaktu. Z dalších kolegů bych chtěl ještě poděkovat doc. Vláďovi Grycovi, vedoucímu Ústavu nauky o dřevě Mendelovy univerzity v Brně, za dlouhodobou plodnou odbornou spolupráci a jeho přátelství.

Závěrem bych rád poděkoval svojí rodině, speciálně pak svojí ženě Líbě, za klidné a pohodové zázemí a za její lásku a podporu, díky nimž jsem se mohl nerušeně soustředit na vyhotovení práce.

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3. Úvod

Předkládaná habilitační práce myšlenkově navazuje na moji disertační práci, ve které jsem se před deseti lety snažil přiblížit tzv. celostní přístup se speciálním zřetelem na fosilní dřeva pro oblast třetihor severozápadních Čech (Sakala 2004). Přes obdobný charakter obou prací, kdy jádro tvoří již publikované odborné práce s relativně kratším doprovodným textem, došlo v habilitační práci k určitým změnám.

Z formálního hlediska je potřeba především zmínit fakt, že práce je psána česky a publikované články jsem tentokrát umístil až na konec práce coby přílohy. Myslím si, že tato změna pomůže zpřehlednit text, který se tímto stává samostatným blokem, díky češtině navíc srozumitelnějším širšímu okruhu možných zájemců. Vědecké publikace jsou tentokrát citovány podle vzoru časopisu *Bulletin of Geosciences* s tím, že zkratky pro označení stran a typ nepublikovaných prací uvádím česky. Konečně, bylo rovněž potřeba na formální úrovni zohlednit vývoj Mezinárodního kódu botanické nomenklatury, především vzhledem k existenci „morfotaxonů" a aplikaci celostního přístupu. *Vídeňský kód* z r. 2006 (viz McNeill *et al.* 2006) přinesl široký koncept „fosilních taxonů", které v sobě morfotaxony zahrnovaly už pouze coby podskupinu. Následně, na základě série připomínek (Cleal & Thomas 2010a, b) je v současnosti platném *Melbournském kódu* z r. 2012 (viz McNeill *et al.* 2012) celý koncept morfotaxonů opuštěn a všechny taxony, které jsou definovány na fosilních typech, samozřejmě včetně zkamenělých dřev, jsou nadále označovány výlučně jako „fosilní taxony". Pokud navíc několik fosilních taxonů prokazatelně náleží jediné rostlině, měly by si jejich jména konkurovat zcela ve smyslu běžného pravidla o prioritě (McNeill & Turland 2011). Tento formální předpis tak nově upravuje pojmenování fosilních rostlin v rámci celostního přístupu.

Co se týče rozdílu ve vymezení práce, tak je studovaná oblast tentokrát rozšířena na střední a sz. Čechy, které coby unikátní území vedle kenozoických (třetihorních) dřev poskytují i ta mezozoická (svrchnokřídová) a paleozoická (svrchnokarbonská). K tomuto posunu jsem byl veden především snahou o zhodnocení svojí pedagogické aktivity, která vedle třetihorních dřev (diplomové práce J. Boudové a K. Fischlové 2010–2012 a V. Kouteckého 2011–2014) byla výrazně zaměřena i na dřeva svrchnopaleozoická (diplomové práce P. Matysové 2004–2006, V. Mencla 2005–2007 a J. Holečka 2009–2011). Konečně, část o křídových dřevech je vyjádřením dlouhodobé spolupráce s Ústavem nauky o dřevě v Brně a především pak s již zmiňovaným doc. V. Grycem.

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4. Fosilní dřevo

Pro pochopení významu fosilního dřeva pro paleobotanický výzkum je nejdříve potřeba termín „fosilní dřevo" jednoznačně definovat. Obecně platí, že pokud někdo v geologické a sběratelské komunitě zmíní, že se zajímá o „fosilní dřeva", má většinou na mysli mohutnější zkamenělé stonky obecně, bez ohledu na to, zda vytvářejí sekundární xylém (obr. 1, zelené názvy), či ne (obr. 1, červené názvy), často rozličným způsobem zachované (zuhelnatělé nebo permineralizované). Naproti tomu, pokud stejný výrok pronesete v běžném životě, lidé většinou pochopí, že se zaobíráte výlučně ,kamenným' druhotným dřevem moderního typu, tj. tím, které je charakteristické pro dnešní jehličnany a listnaté dřeviny. Podobný typ dřeva je i u vymřelého rodu *Archaeopteris* (obr. 1). Tento zdánlivý rozpor řeší následující část 4.1. Další části se pak týkají významu dřeva v evoluční historii (4.2.) a rovněž podávají přehled fosilních nálezů z popisovaného území (4.3.).

Lepidodendron   **Archaeopteris**   **Calamites**   **Psaronius**   **Tempskya**   **Livistona**
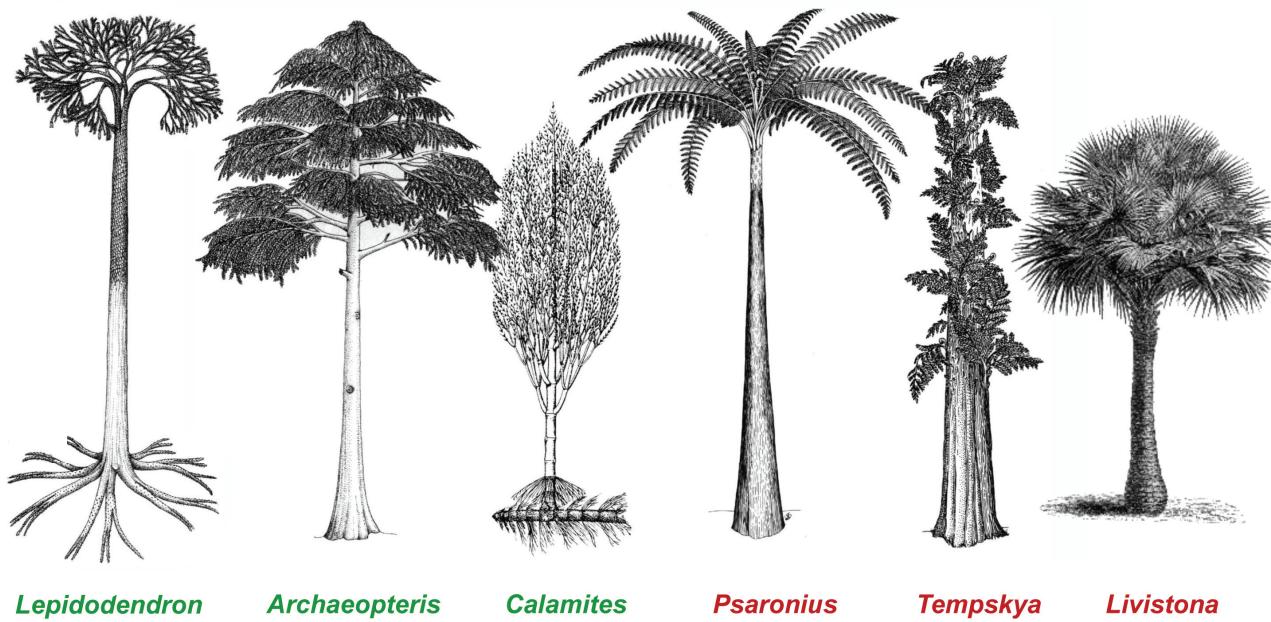
Obr. 1 – *Ukázka stromovitých typů rostlin: pozdnědevonská prvosemenná* Archaeopteris*, karbonský plavuňovitý* Lepidodendron *a přesličkovitý* Calamites *vytvářejí sekundární xylém (zeleně), zatímco kapradinovité rostliny – karbonský* Psaronius *a pozdněkřídová* Tempskya*, jakož i recentní palma* Livistona *sekundární xylém netvoří a vytvářejí stromovité typy jen díky primárním pletivům (červeně). Velikosti nejsou proporcionální.*
(lehce upraveno podle Donoghuea 2005 s použitím internetového zdroje č. 1 pro obraz palmy)

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4.1. Definice termínu

V češtině termín „dřevo" označuje v nejobecnějším botanickém smyslu xylém (Němec 1921), tj. část cévního svazku složenou z cév, popř. cévic, dřevního parenchymu a sklerenchymatické pochvy (Slavíková 1990), jehož hlavní funkcí je rozvádět roztoky anorganických látek z kořenů přes stonek do listů. Nicméně tento význam je vysoce odborný a v češtině se používá především coby přídavné jméno nahrazující *xylém* coby *dřevní* část cévního svazku. V běžném smyslu je pod termínem „dřevo" chápáno výhradně „druhotné dřevo", tj. takové, které vzniká činností druhotného meristému – kambia. V tomto významu (dřevo = sekundární xylém), který je podpořen i cizojazyčnými ekvivalenty slova *dřevo* v němčině (*das Holz*), francouzštině (*le bois*) nebo angličtině (*the wood*), bude tento termín chápán a používán v celé předkládané práci.

Přídavné jméno „fosilní" pak odpovídá „zkamenělým" organismům v nejširším smyslu slova (Pokorný *et al.* 1992). V případě dřev se tak jedná nejen o ta běžně známá ‚kamenná' zachovaná díky prostupujícím roztokům anorganických látek tzv. procesem *intuskrustace* (permineralizace), ale i ta zachovaná díky přeměně původních organických látek za nepřítomnosti vzduchu procesem *karbonizace* (zuhelnatěním), či navíc souběžně probíhajícím trouchnivěním, kdy uhelná hmota oxidovala, často pak vlivem lesních požárů, a docházelo k *fuzitizaci* a vytváření vláknitého (dřevěného) uhlí (Dopita *et al.* 1985); patří sem ale i další méně obvyklé typy zachování jako např. *mumifikace*. Termín „fosilní dřevo" všude v textu tak označuje celou škálu zachování *sekundárního xylému* díky souhrnným procesům *fosilizace*.

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4.2. Evoluční význam dřeva

Evoluce xylému obecně provází vývoj suchozemských rostlin, jelikož jeho přítomnost je nezbytná pro příjem vody a anorganických látek rostlinou pro přežití na suché zemi (Kenrick & Crane 1997). Vedle vedení látek má xylém, resp. jeho jednotlivé elementy, význam i pro mechanickou pevnost rostliny. Obecně platí, že čím rostlina lépe vede vodu (má vyšší specifickou vodivost), tím jsou její vodivé elementy méně mechanicky pevné. Vše ještě komplikuje fakt, že odolnost vodivých elementů vůči kavitaci (ucpání vlivem embolie) je přímo úměrná mechanické pevnosti, ale nepřímo úměrná specifické vodivosti (viz obr. 2).

Obr. 2 – *Diagram ‚něco za něco (angl. 'trade-off') znázorňující vzájemnou souvislost („+" přímá a „–" nepřímá úměra) specifické vodivosti, mechanické pevnosti a odolnosti vůči kavitaci u vodivých elementů xylému (upraveno podle Baase et al. 2004).*

Ve vývoji suchozemských rostlin měl xylém zprvu funkci výlučně vodivou a stabilitu rostlin zajišťoval u těch nejstarších turgor, o něco později (ve stř. devonu) speciální typ kolenchymaticko-sklerenchymatického pletiva, tzv. hypodermálního steromu na vnější straně stonku (Bateman *et al.* 1998; Rowe & Speck 2004). Přes objevení se sekundárního xylému se na mechanické pevnosti stále podílely různé typy dalších pletiv (např. primární a sekundární kůra u stromovitých plavuní řádu Lepidodendrales, viz obr. 9E,F), která vedle zhroucení zabraňovala i kavitaci (Sperry 2003). Další vývoj u dřeva moderního typu (skupina Lignophyta) se ubíral spíše směrem minimalizace ztráty pevnosti při zachování vodivosti prostřednictvím zdokonaleného systému teček umožňujících komunikaci vodivých elementů mezi sebou (Beck *et al.* 1982).

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Dřevo se poprvé objevuje už v raném devonu, jak vyplývá z nových nálezů bazálních euphyllophyt z několika lokalit Francie a Kanady (přehled viz Strullu-Derrien *et al.* 2013), nicméně později nezávisle ještě asi čtyřikrát: u heterosporických plavuňovitých (Lepidodendrales), přesličkovitých (Sphenophyllales, Calamitales), vyhynulých blízce příbuzných kapradin (Cladoxylopsida, Zygopteridales, Rhacophytales) a skupiny Lignophyta (Hoffman & Tomescu 2013; Strullu-Derrien *et al.* 2013, viz obr. 3).
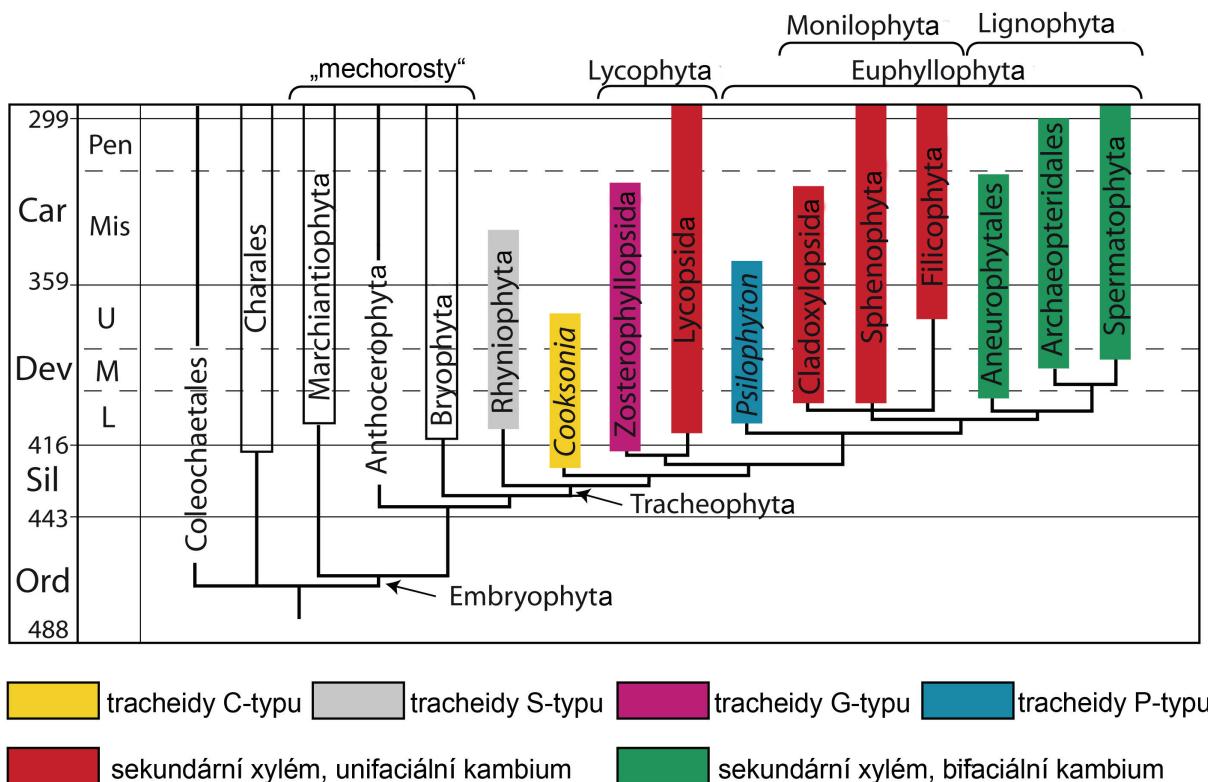

Obr. 3 – *Zjednodušené fylogenetické schéma s hlavními skupinami suchozemských rostlin a typem jejich xylému (upraveno podle Strullu-Derrien et al. 2013).*

Právě u skupiny Lignophyta, zahrnující prvosemenné a semenné rostliny, je přítomen významný odvozený znak, tzv. bifaciální kambium (obr. 4), které vedle produkce sekundárního xylému centripetálně produkuje i sekundární floém centrifugálně. Zároveň se iniciály tohoto svazkového kambia antiklinálně dělí a celý prstenec tak průběžně reaguje na zvětšování průměru stonku (Donoghue 2005). Přítomnost bifaciálního kambia, přesněji sekundárního floému u rodu *Sphenophyllum* (Eggert & Gaunt 1973), či *Astromyelon* (Wilson & Eggert 1974), je dnes zpochybňována (Taylor *et al.* 2009).

Přestože jsou v rámci skupiny Lignophyta obecně považovány jednoděložné rostliny za druhotně netloustnoucí (obr. 5), jsou známy případy specifického sekundárního růstu, převážně pak u řádu Asparagales (např. Schoute 1902; Cheadle 1937; Tomlinson & Zimmermann 1969; Rudall 1991; Carlquist 2012). Tento typ se však netýká nálezů fosilních palem, které jsou zmíněny v předkládané práci.

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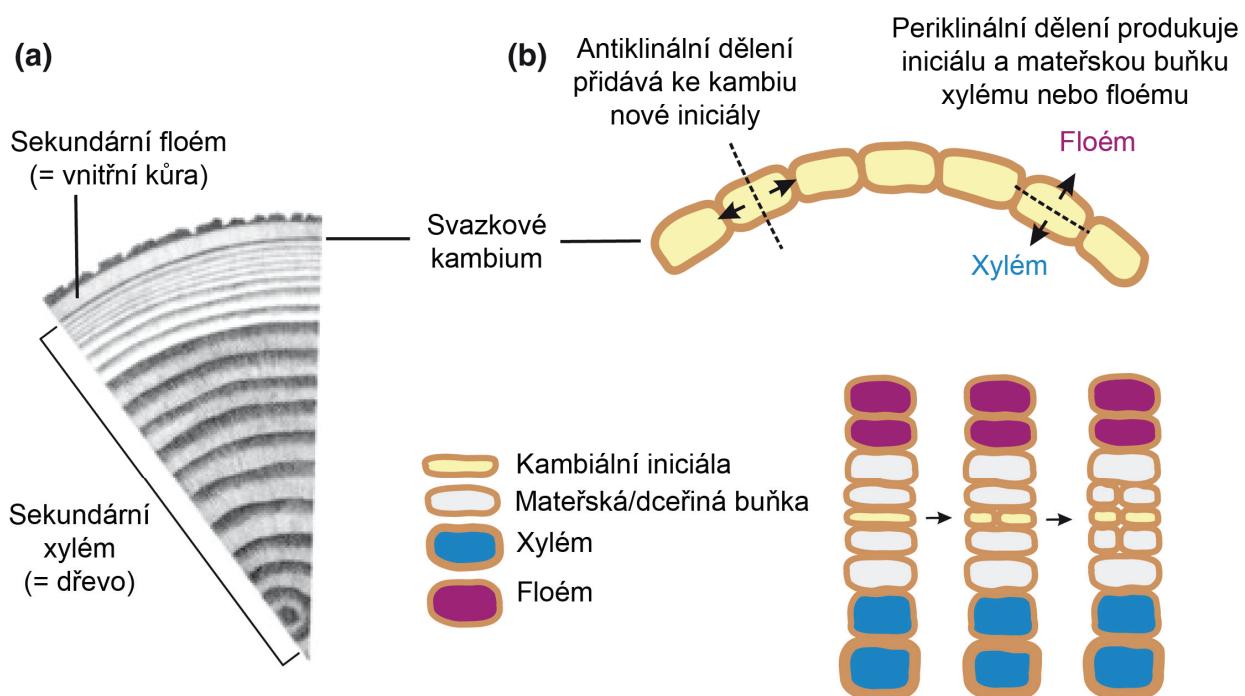
Obr. 4 – *Bifaciální kambium produkuje sekundární xylém centripetálně a sekundární floém centrifugálně. Iniciály se zároveň antiklinálně dělí a kambium tak může zvětšovat svůj průměr (upraveno podle Spicerové & Groovera 2010).*
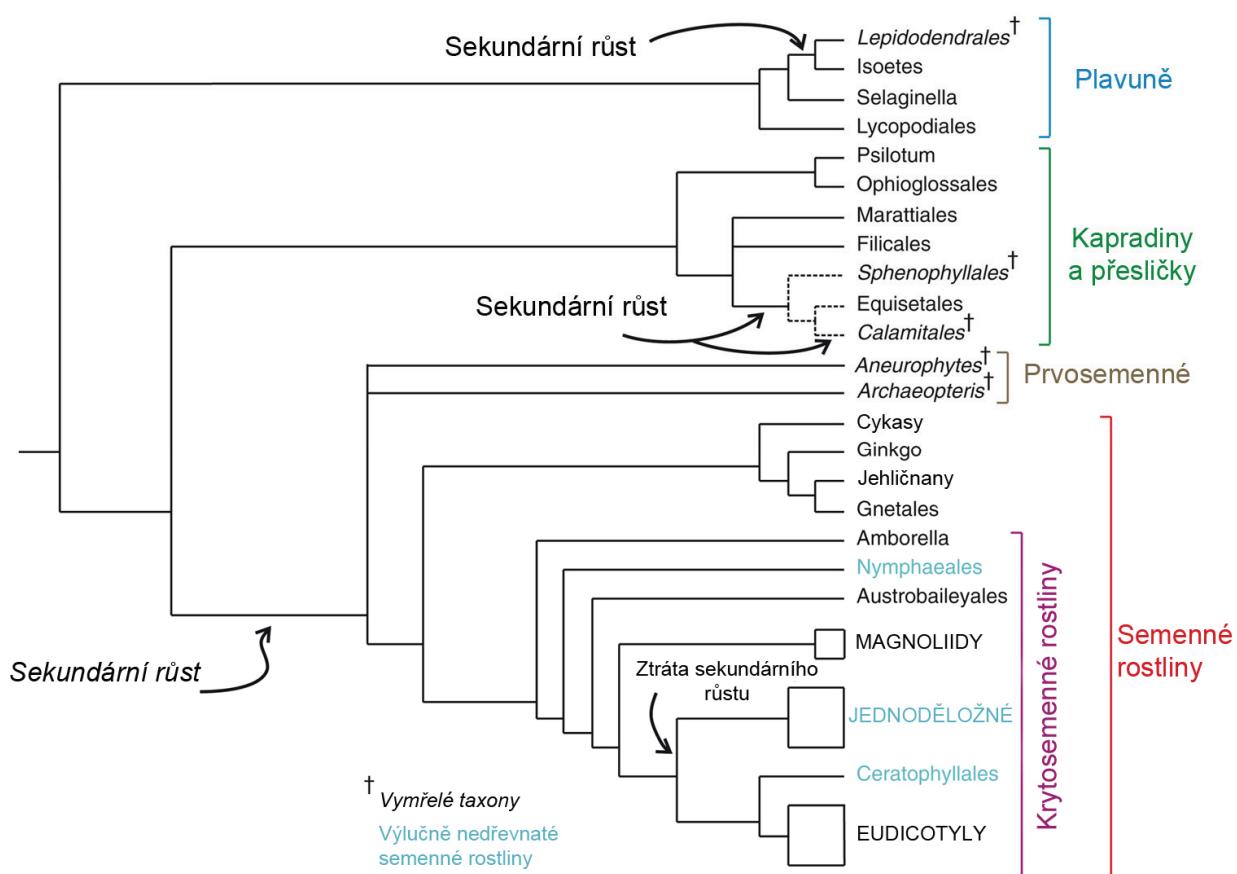
Obr. 5 – *Fylogeneze cévnatých rostlin ve vztahu k několikanásobnému objevení se svazkového kambia. U všech skupin, vyjma Lignophyt (viz* Sekundární růst *kurzívou), se jedná o kambium unifaciální produkující pouze sekundární xylém (upraveno podle Spicerové & Groovera 2010).*

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4.3. Přehled výskytu ve studované oblasti

Přehled výskytu zkamenělých dřev na území bývalého Československa podává do roku 1970 v detailní formě Březinová (1970). Následující stať tak spíš odkazuje na novější práce, které si výskytu dřev všímají, popřípadě zmiňuje ty popisy a zmínky, které byly dříve opominuty. Výčet je pro studované území řazen stratigraficky od prvohorních přes křídová po kenozoická, resp. terciérní dřeva.

kladensko-rakovnická pánev

Výskyt a historii výzkumu v této oblasti detailně popisuje Holeček (2011) ve svojí diplomové práci, stejné jako jsou tyto informace součástí dvou následných publikací (Mencl *et al.* 2013a, b). Obecně platí, že zdaleka nejrozšířenějším typem dřev, který se
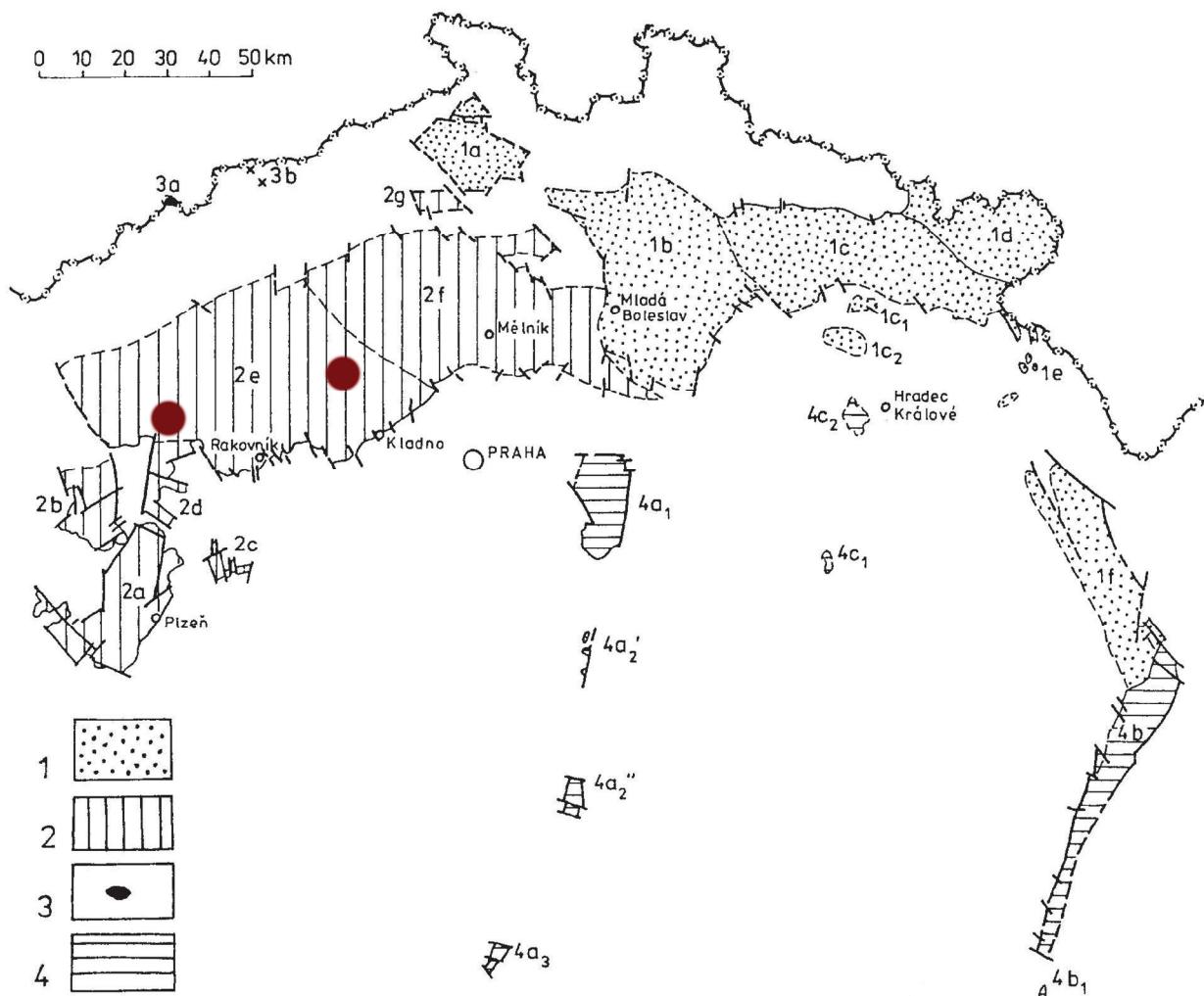

Obr. 6 – *Limnický svrchní karbon a perm Českého masívu se dvěma vyznačenými výskyty fosilních dřev (hnědá tečka vlevo Bílenec, vpravo Klobuky) v kladensko-rakovnické pánvi (2e); vysvětlivky: 1 – sudetské mladší paleozoikum, 2 – středočeské a západočeské mladší paleozoikum, 3 – krušnohorské mladší paleozoikum, 4 – mladší paleozoikum brázd*
(mapa převzata z Chlupáče & Vrány 1994, detailní legenda viz Chlupáč & Štorch 1992).

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vyskytuje nejenom v tradičních ,červených' souvrstvích, ale i v souvrství kladenském a slánském, jsou tzv. „araukarity", tj. dřeva typu *Agathoxylon* (*Dadoxylon*) (Mencl *et al.* 2013b), která odpovídají kordaitům a vlastním jehličnanům. Vedle nich byla v okolí Bílence (obr. 6) popsána dřeva typu *Arthropitys* produkovaná unifaciálním kambiem vymřelých přesliček (Mencl *et al.* 2013a, viz část 5.1.1.). Vedle těchto typů jsou popisovány, např. z okolí Očihova, nepoměrně vzácnější nepravé kmeny rodu *Psaronius* (Dvořák & Švancara 2003; internetový zdroj č. 2), které však dřevo netvoří. Další typy, jako např. kmeny rodu *Medullosa*, se zatím nepodařilo potvrdit. Coby zcela specifická pak musí být ještě zmíněna tzv. „zkamenělá rašelina" z okolí Klobuk (obr. 6), která kromě jiného obsahuje velké množství silicikovaných, zatím blíže neurčených stonků (Dvořák & Švancara 2003; internetový zdroj č. 2).

česká křídová pánev

Výskyty dřev zde nejsou moc hojné; nejběžnějším nálezem, který dřevo připomíná, ale fakticky není přítomno, jsou silicifikované nepravé kmínky stromovitých kapradin rodu *Tempksya* nalézané především v okolí Pecínova (obr. 7), ale i jinde (Dvořák 2005;


Obr. 7 – *Křída Českého masívu se dvěma vyznačenými výskyty fosilních dřev (zelená tečka vlevo nahoře Bílé Horky, vpravo dole Pecínov) v rámci ohareckého (1e), resp. vltavo-berounského (1f) vývoje české křídové pánve; vysvětlivky: 1 – česká křídová pánev, 2 – osoblažská křída, 3 – jihočeské pánve, 4 – další výskyty křídy*
(mapa převzata z Chlupáče & Vrány 1994, detailní legenda viz Chlupáč & Štorch 1992).

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Svoboda & Sakala 2014). Vedle toho Greguš *et al.* (2013) zrevidovali nálezy otisků obdobných druhotně netloustnoucích kmenů stromovitých kapradin rodů *Protopteris* a *Oncopteris*. Co se týče fosilního dřeva, asi první detailní anatomický popis pochází z pera Prakashe & Březinové (1970), kdy popisují krytosemennou rodu *Bridelioxylon* ze středního turonu lokality Bílé Horky (popř. Bílá Horka) u Loun (obr. 7). Podobný typ dřeva byl popsán z cenomanu lokality Pecínov (obr. 7) jako *Paraphyllanthoxylon* Grycem *et al.* (2009), viz část 5.2.1. Z Pecínova byla ještě popsána dřeva fuzitická (Falcon-Lang *et al.* 2001; Oakley & Falcon-Lang 2009), jedno silicifikované dřevo jehličnatých identifikované jako *Cupressinoxylon* Falcon-Langem *et al.* (2001), několik zatím neurčených dřev krytosemenných (Z. Dvořák, osobní sdělení 2014) a konečně je znám i benetitový kmínek typu *Cycadeoidea* uložený v NM v Praze (internetový zdroj č. 3). Podobný typ kmenu benetitu byl Němejcem (1968) zmíněn a zdokumentován od Slaného.

terciér sz. Čech (mostecká pánev, České středohoří a Doupovské hory)

Aktualizovaný historický přehled s použitím práce Březinové (1970) přepisuji ve svojí disertační práci (Sakala 2004) se zaměřením na mosteckou pánev, České středohoří a Doupovské hory (obr. 8), tedy na oblast, kterou popisuje i tento odstavec. Nejnověji pak historický přehled pro obě vulkanické oblasti podává Koutecký (2014) ve svojí diplomové práci. Novější publikované práce, kde jsem spoluautorem, tj. Havelcová *et al.* 2013; Sakala 2007, 2011; Sakala *et al.* 2010; Teodoridis & Sakala 2008, jsou součástí příloh 3 až 7 a jsou detailně popsány v části 5.3. Z dalších publikovaných prací je třeba zmínit studie týmu RNDr. M. Řehoře, které se věnují mineralizaci dřev a kmenů obecně, např. stonku palmy z lokality Nechranice (Řehoř & Nedbálek 2013). Konečně problematice tzv. jáchymovského „stromu potopy", jehož uložení asi jen vzdáleně souvisí s vulkanity Doupovských hor, se věnují Dupéron *et al.* (2008) a Sakala *et al.* (2012). Co se týče nepublikovaných prací, K. Fischlová ve svojí diplomové práci popisuje fuzitická dřeva ze střední lávky hlavní uhelné sloje na Dole Bílina (Fischlová 2012). Na stejné lokalitě pak ve svojí diplomové práci J. Boudová analyzuje xylitická dřeva kmenů v původních růstových pozicích, které se nacházejí v těsném nadloží hlavní sloje (Boudová 2012). Do třetice již zmiňovaný Koutecký (2014) popisuje nová fosilní dřeva ze 4 lokalit: z Vrbice a Nechranic (obě Doupovské hory) jehličnan *Glyptostroboxylon rudolphii* a pět zástupců listnatých dřevin *Cinnamomoxylon seemannianum*, *Alnus tschemrylica*, *Ulmoxylon* cf. *kersonianum*, *Grewioxylon ortenburgense* a jeden taxon, který nebyl pro nedostatek identifikačních znaků blíže určen a byl označen jako Xylotyp: Nechranice 1.

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Na další lokalitě Divoká rokle (České středohoří) byl identifikován taxon *Manilkaroxylon* sp. z čeledi Sapotaceae, konečně vzorky z lokality Bečov (České středohoří) byly určeny jako *Glyptostroboxylon rudolphii* a *Taxodioxylon gypsaceum*, přičemž u druhého zmíněného byly rozpoznány dva subtypy pracovně označeny jako dřevo kmene a kořene (Koutecký 2014).
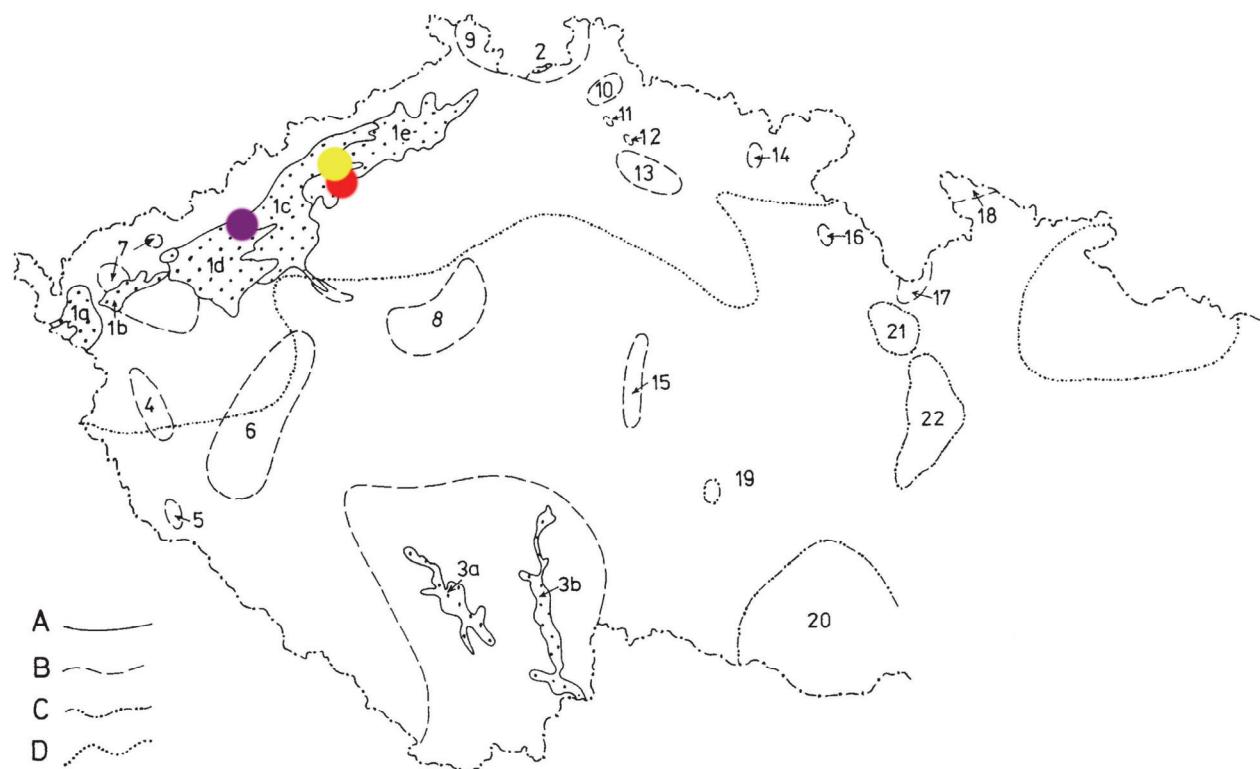
Obr. 8 – *Terciér Českého masívu se třemi vyznačenými výskyty fosilních dřev (fialová tečka Kadaň - Zadní vrch, červená tečka Kučlín, žlutá tečka Bílina) v Doupovských horách (1d), Českém středohoří (1e) a mostecké pánvi (1c); vysvětlivky: A – pánve a vulkanické horniny, B – areály s relikty sladkovodních sedimentů, C – areály s relikty karpatských (převážně marinních) sedimentů, D – jižní okraj rozšíření rozptýlených vulkanitů*
(mapa převzata z Chlupáče & Vrány 1994, detailní legenda viz Chlupáč & Štorch 1992).

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5. Případové studie

Jak již bylo řečeno v úvodu, oblast středních a sz. Čech byla vybrána záměrně, protože poskytuje na relativně malé rozloze, často v těsné blízkosti, dřeva svrchnokarbonská, svrchnokřídová a třetihorní. S tím souvisí odlišný způsob jejich systematického zpracování, kdy je pro každé z nich potřeba zohlednit vlastní strukturu (unifaciální vs. bifaciální kambium), doprovodný paleobotanický obsah (hodně vymřelých taxonů na úrovni rodů i čeledí v karbonu a křídě vs. přítomnost recentních rodů v terciéru), ale i rozdílné nálezové okolnosti (nálezy karbonských dřev převážně roztroušené v eluviu na poli vs. hlavně přímo v profilu v křídě a terciéru). Práce tak může nabídnout relativně komplexní ukázku systematického studia fosilních dřev a jejich významu pro paleobotanický výzkum obecně.

Vedle toho jsem výběrem tématu zohlednil svoji pedagogickou aktivitu, především pak vedení diplomových a disertačních prací, za posledních 11 let, které uplynuly od obhajoby mojí vlastní disertační práce. Domnívám se totiž, že úspěšná pedagogická aktivita je důležitou podmínkou pro získání vědecko-pedagogické hodnosti „docent". Od svého původního tématu terciérních dřev jsem se nejprve odklonil ke dřevům permokarbonským při vedení prací P. Matysové, V. Mencla a J. Holečka (Matysová 2006; Mencl 2007, 2014; Holeček 2011). Později jsem se k nim vrátil při vedení diplomových prací J. Boudové, K. Fischlové a V. Kouteckého (Boudová 2012; Fischlová 2012; Koutecký 2014) a dnes pokračuji jak v rámci terciéru (disertační práce V. Kouteckého), tak i křídy (probíhající práce S. Venclové a J. Greguše). Co se týče křídových dřev, jak již bylo rovněž zmíněno, je část 5.2.1. vyjádřením dlouhodobé spolupráce s doc. V. Grycem z Mendelovy univerzity v Brně.

Následuje 5 případových studií (**příklady 1–5**), které jsou shrnuty ve 3 větší časově oddělené celky uvozené stručným jednostránkovým popisem (**paleozoická, mezozoická a kenozoická dřeva**). Těžištěm každého příkladu je vždy jeden (**příklady 1, 2 a 4: kladensko-rakovnická pánev, česká křídová pánev a České středohoří**), nebo dva články (**příklady 3 a 5: mostecká pánev a Doupovské hory**), které jsou všechny k nalezení v **přílohách 1–7**. Každý příklad je v textu krátce popsán s ohledem na hlavní teze odpovídajícího článku a jeho paleobotanicko-stratigrafické zařazení. Zároveň jsou u každého příkladu vyzdviženy vždy tři z něj vyplývající obecnější otázky formou samostatných odstavců. Ve výsledku, obdobně jako v disertační práci (viz Sakala 2004), tak tato habilitační práce podává **15 obecných aspektů** souvisejících se studiem fosilních dřev.

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5.1. Paleozoická dřeva

Paleozoikum je ve vývoji dřev a růstových typů rostlin obecně asi nejdůležitějším obdobím. První dřevo se objevuje už v raném devonu (viz 4.2.), ale stromovité typy až později. Nejstaršími jsou zástupci kapradinám příbuzné skupiny Pseudosporochnales (tzv. *Gilboa tree*) ze stř. devonu, ty nicméně neměly listy a jen omezený kořenový systém (viz obr. 9A,B); první moderní typy stromů s listy, tloustnoucími větvemi a kořeny (viz obr. 9C,D) a bifaciálním kambiem se objevují až v pozdním devonu a jsou vázány na rod *Archaeopteris* (Meyer-Berthaud & Decombeix 2007). Obecně, vývoj základních typů organizace těla rostlin je hotov už v mississippu (DiMichele & Bateman 2005).
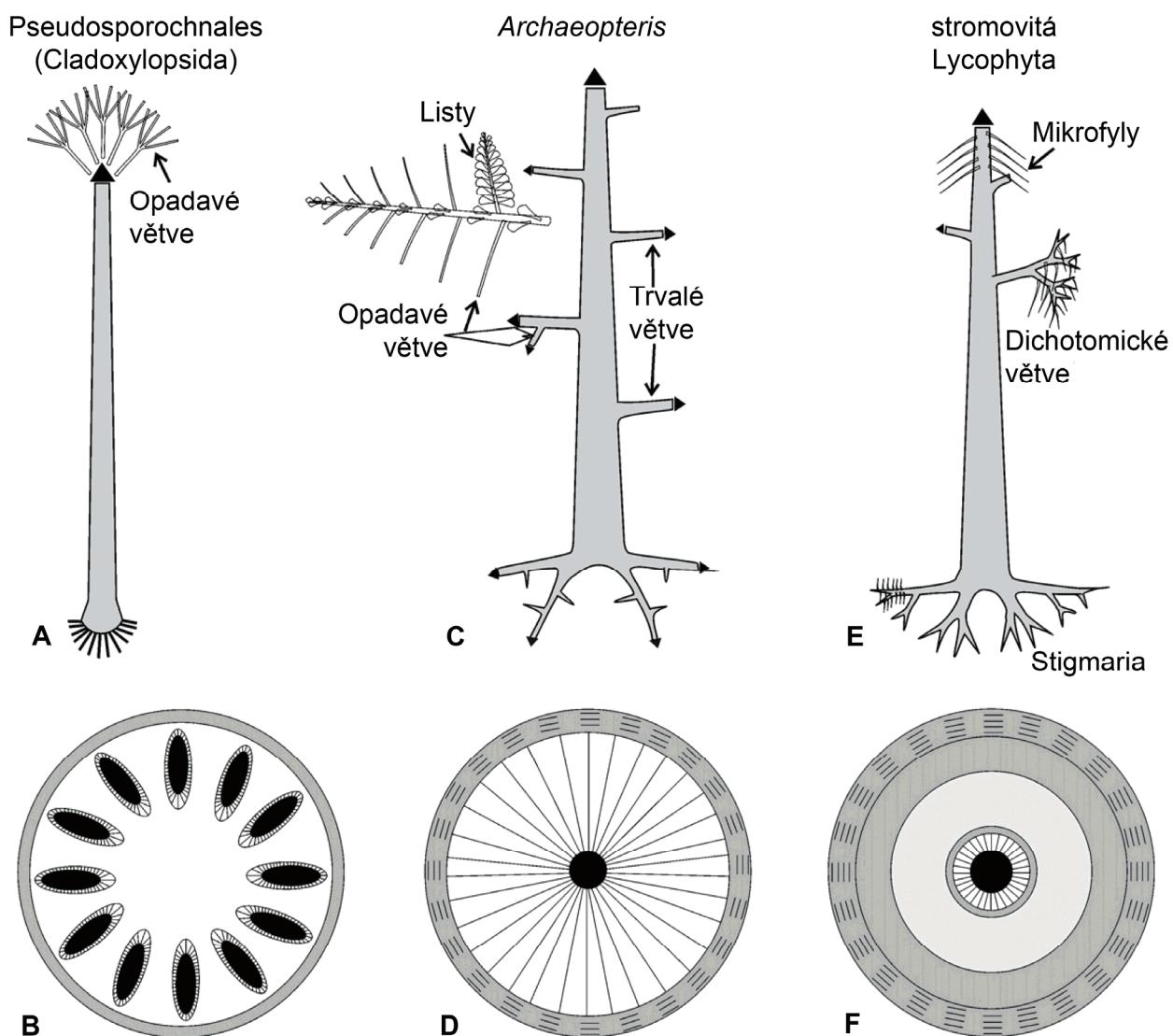
Obr. 9 – *Srovnání charakteristik 3 základních stromovitých typů devonu. A–B: Cladoxylopsida, C–D: Archaeopteridales a E–F: Lycophyta, ukázka stavby (A, C, E) a příčných řezů kmenů (B, D, F). Černá: primární vodivá pletiva; šedivá: kůra; čárkovaně: druhotná pletiva (na bílém podkladu = dřevo; na šedivém podkladu = druhotná kůra).*

(upraveno podle Meyer-Berthaudové & Decombeixové 2009)

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5.1.1. Příklad 1: *kladensko-rakovnická pánev*
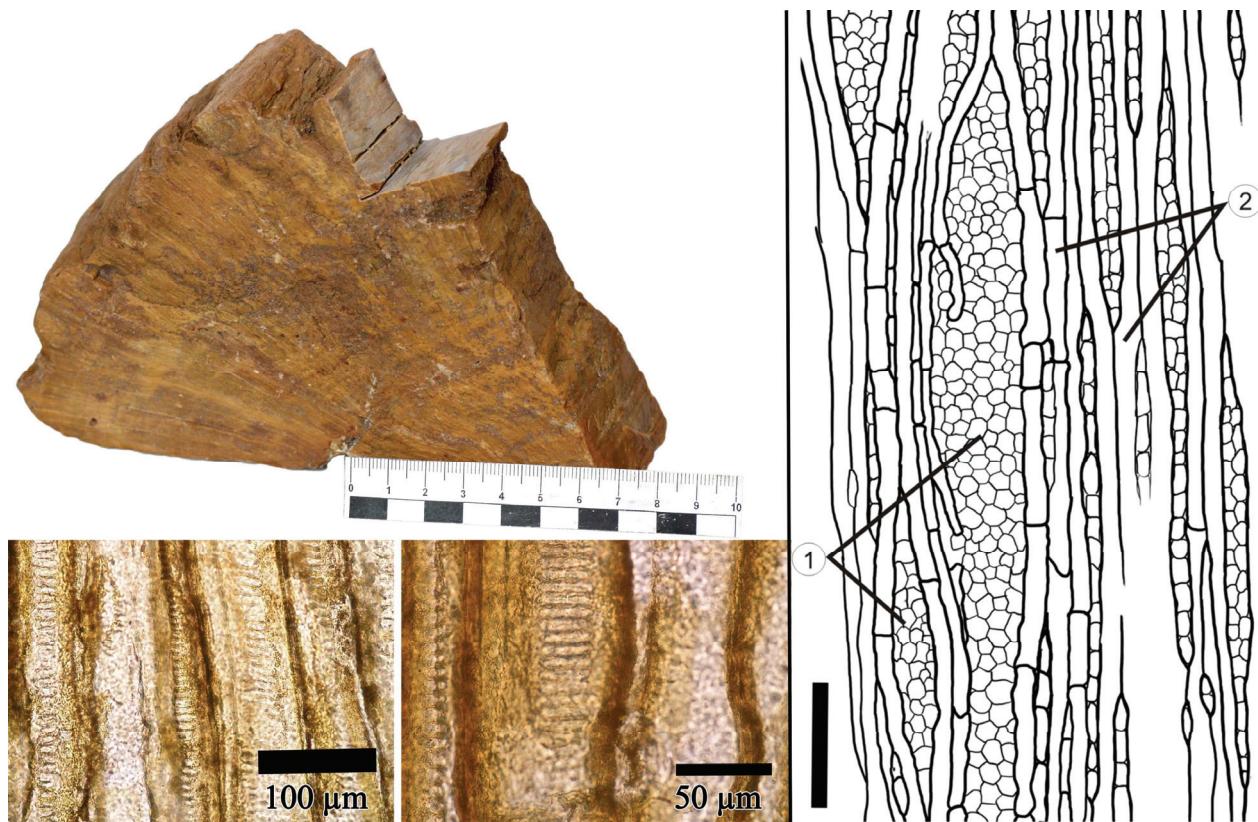
Obr. 10 – *Ukázka přesličky* Arthropitys *cf.* bistriata *z kladensko-rakovnické pánve (vzorek č. ZAJ004/1). Vlevo: vlastní vzorek se dvěma detaily skalariformních dvojteček na radiálních stěnách tracheid; vpravo: náčrtek tangenciálního řezu se širšími interfaskulárními dřeňovými paprsky (1) a fascikulárními zónami s užšími paprsky (2), měřítko odpovídá 0,5 milimetru. (upraveno podle Holečka 2011 a Mencla et al. 2013a)*

Kladensko-rakovnická pánev je součástí oblasti středočeského a západočeského mladšího paleozoika. V posledních letech se studiu dřev z této širší oblasti vedle již zmiňovaného J. Holečka v jeho diplomové práci a následných publikacích (Holeček 2011; Mencl *et al.* 2013a, b) věnují též J. Bureš s ohledem na systematiku (Bureš 2011, 2013) a okrajově též P. Matysová ve svojí právě připravované disertační práci, jejíž výsledky zaměřené především na mineralizaci byly již zčásti publikovány (např. Matysová *et al.* 2010). Litologický obsah je tradičně rozdělen na 4 souvrství, na 2 tzv. *šedá* (na *spodní* kladenské a *svrchní* slánské) a 2 tzv. *červená* (*spodní* týnecké a *svrchní* líňské), která se vzájemně střídají (viz např. Pešek *et al.* 2001). Zcela nejnovější komplexní přehled oblasti středočeského a západočeského mladšího paleozoika v širším rámci permokarbonu Českého masívu pak podávají Schneider *et al.* (2014). Líňské souvrství, kde se nachází nejvíce zkamenělých dřev, je v kontextu hranice karbon/perm popsáno Opluštilem *et al.* (2013). Přesličky (obr. 10) se pak nacházejí hlavně v týneckém, částečně pak líňském souvrství (Holeček 2011; Mencl *et al.* 2013a).

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úplnost fosilního záznamu a role sběratelů

Fakt, že je fosilní záznam nekompletní, se zdůrazňuje od dob Darwinových dodnes jako hlavní omezení paleontologie při rekonstrukci vývoje života a systematických vztahů mezi jednotlivými organismy (např. Kutschera & Niklas 2004; Taylor *et al.* 2009). Přes tuto objektivní skutečnost je někdy neúplnost záznamu přeceňována a nedostatek vlastních nálezů se pak používá jako omluva absence vlastního nového výzkumu. Dobrou možností jak získat unikátní materiál, která se osvědčila v kladensko-rakovnické pánvi, ale i jinde (a to nejenom v případě fosilních dřev, ale i třeba i bezobratlých při výzkumu doc. Fatky ve spodním paleozoiku Barrandienu, či doc. Košťáka v české křídové pánvi), je těsná spolupráce se sběrateli. Díky tomuto vztahu plnému oboustranného respektu mohli Holeček (2011) a následně i Mencl *et al.* (2013a) nejen potvrdit, že dřeva obecně se nacházejí ve všech čtyřech souvrstvích, ale především získat a popsat dřeva přesliček, která by jinak zůstala pro odbornou komunitu neznámá.

unifaciální vs. bifaciální kambium

Jak již bylo řečeno výše (viz část 4.2.), patří stromovité přesličky do skupiny druhotně tloustnoucích rostlin s unifaciálním kambiem. Z toho vyplývá, že antiklinálním dělením nezvětšující se prstenec kambia zabraňuje neomezenému zvětšování průměru kmene. Přes toto zjevné omezení mají přesličky z Rakovnicka průměr několik decimetrů (viz např. obr. 10) až dokonce vice než 0,6 m (F. Jech, osobní sdělení 2015), což přesahuje zatím největší zaznamenaný průměr u druhu *Arthropitys ezonata* (Rößler & Noll 2006). Toto zjištění navazuje na výsledky týmu z Chemnitz pod vedením Dr. R. Rößlera (Rößler & Noll 2006; Rößler *et al.* 2012), který u raněpermských zástupců druhů *Arthropitys ezonata* a A. *bistriata* uvádí neobvykle velké mocnosti dřeva, resp. způsob větvení a jen potvrzuje, že zažitá představa o životě a architektuře stromovitých přesliček musí být částečně revidována.

vliv prostředí na způsob zachování

Prakticky všechna permineralizovaná paleozoická dřeva Českého masívu, snad vyjma těch z tzv. prokřemenělých rašelin a poloh ploužnického obzoru, vznikala ve fluviálním až lakustrinním prostředí bez vlivu vulkanismu ve smyslu Matysové *et al.* (2010) a prodělala určitý transport. Ve výsledku se tak nezachovala extraxylární pletiva vně kambiálního prstence a vzorky jsou většinou tvořeny pouze sekundárním xylémem. Tento jev, který se týká i popisovaných přesliček, představuje určité omezení ve vztahu k možné interpretaci větvení a dalším detailům stavby kmenů (viz např. Mencl 2014).

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5.2. Mezozoická dřeva

Mezozoikum je vývoji rostlin obdobím přechodným, kdy dochází k ústupu „kapraďorostů" a rozvoji mnoha moderních, ale i vyhynulých skupin „nahosemenných", jejichž dřeva mají z dnešního pohledu často neobvyklou kombinací znaků. Příkladem může být problematický rod *Xenoxylon* (obr. 11A, B, D, viz Marynowski *et al.* 2008; Oh *et al.* 2015), umělá skupina jehličnanů Protopinaceae (obr. 11C3, viz Miller 1977), či vymřelé Cheirolepidiaceae (Alvin 1982). Na konci mezozoika, v průběhu křídy, pak vzniká a diverzifikuje se skupina nová, která posléze zcela ovládne období následující – rostliny krytosemenné.
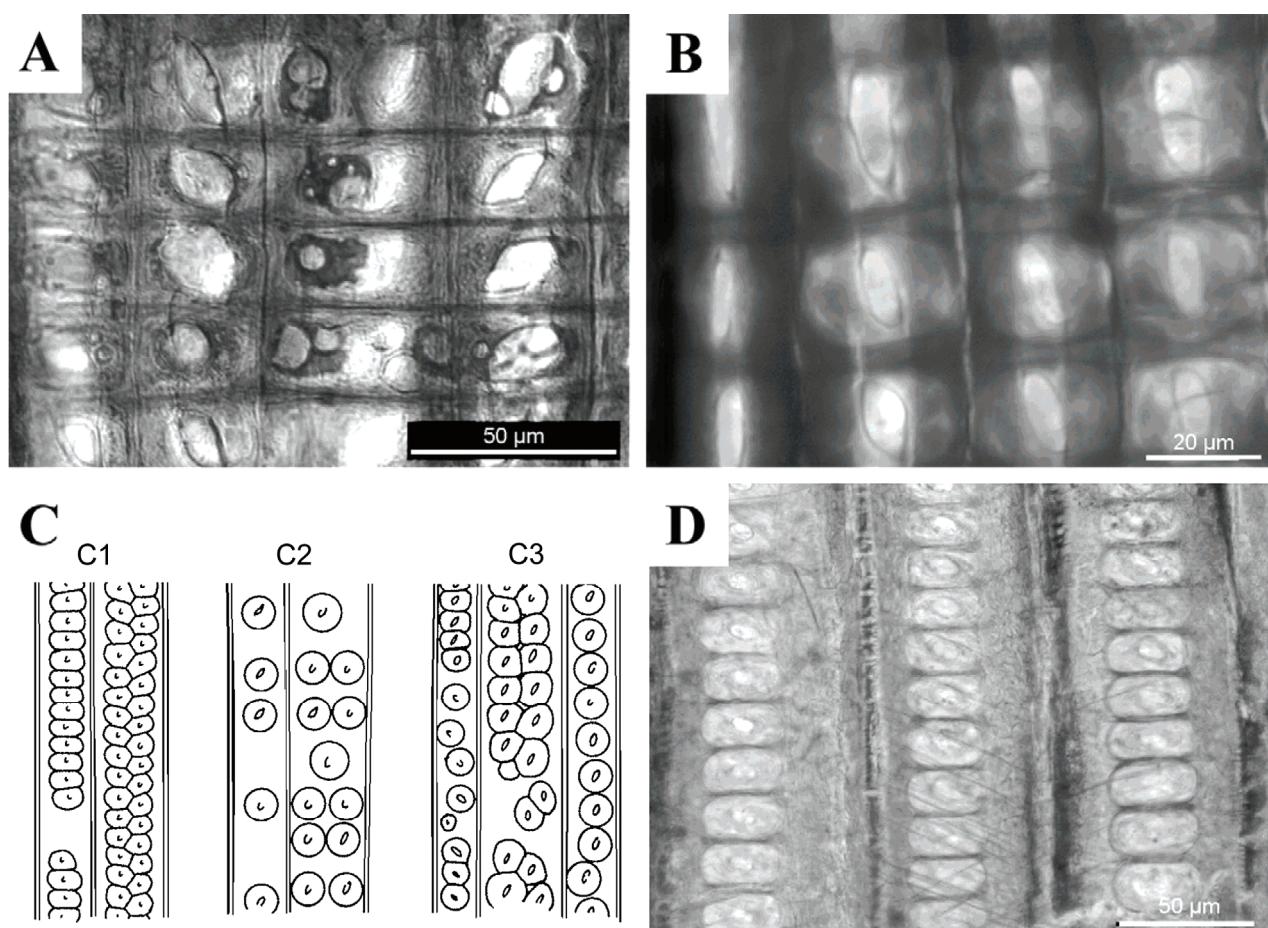
Obr. 11 – *Ukázka dřev mezozoických jehličnanů s charakteristickými tečkami (ztenčeninami) křížových polí (A, B) a dvojtečkami (dvůrkatými ztenčeninami) na radiálních stěnách tracheid (C, D): A)* Xenoxylon phyllocladoides *Gothan, phyllocladoidní tečky; B)* X. phyllocladoides*, podokarpoidní tečky; C) Tři základní typy uspořádání dvojteček: araukarioidní (C1), abietoidní (C2) a smíšený neboli tzv. „protopinoidní" (C3), který Kräuselovi (1917) umožnil charakterizovat skupinu „Protopinaceae"; D)* X. latiporosum *Gothan, speciální „spláclé" xenoxylní dvojtečky.*
(fotky A, B, D zástupců rodu Xenoxylon *ze Špicberků převzaty z Philippa & Bamfordové 2008; schéma C převzato z Philippa 1992)*

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5.2.1. Příklad 2: *česká křídová pánev*

Obr. 12 – *Profil na Pecínově s červenou šipkou vyznačenou fosiliferní pískovcovou polohou celku 5A* (Unit 5A) *podle Uličného et al. (1997); tento celek prostředím svého vzniku odpovídá tidální deltě s dominancí odlivových proudů* (ebb-tidal delta). *Vedle hojných nepravých kmenů stromovitých kapradin rodu* Tempskya *se zde nacházejí i zkřemenělá dřeva jehličnanů a listnáčů – na obrázku vlevo nahoře zde nalezená krytosemenná druhu* Paraphyllanthoxylon *aff.* utahense*, konkrétně vzorek č. UK 102/04 (viz Gryc et al. 2009).*
(obě fotografie poskytl Z. Dvořák v r. 2008)

Česká křídová pánev představuje nejrozsáhlejší intrakontinentální pánev Českého masívu, je pozdně křídového stáří, kdy vznikala v jediném sedimentačním cyklu (cenoman až santon) a v době své existence vytvářela mořské propojení mezi boreální a tethydní oblastí. Nejnovější souhrn stratigrafie a paleogeografie podává Čech (2011). Ve spodní části, v tzv. perucko-korycanském souvrství, je sedimentární výplň charakterizována kontinentálními vlivy a z paleobotanického hlediska pak především obsahuje světoznámou cenomanskou flóru (přehled viz Kvaček *et al.* 2006), která je dlouhodobě studována Dr. J. Kvačkem z NM v Praze. Bohužel dřevy se systematicky nikdo nezabývá: vedle práce Oakleyho & Falcona-Langa (2009) o fuzitických dřevech existuje pouze jediná anatomická studie o cenomanském permineralizovaném dřevě rodu *Paraphyllanthoxylon* (Gryc *et al.* 2009). V tomto ohledu se jako ideální jeví lokalita Pecínov (obr. 12), kde jsou dřeva obou typů zachování nalézána společně s doprovodnou flórou, zároveň se jedná o dobře přístupný a na fosilie bohatý profil.

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vytváření thyl a jejich význam

Thyly jsou vakovité vychlípeniny protoplastu průvodních parenchymatických buněk, které vrůstají do cév a ucpávají je. Jedná se o standardní fyziologický proces, který je typický pro jádrové dřevo listnáčů a jehož vznik souvisí s nižším obsahem vody, či poraněním (Panshin & de Zeeuw 1980). Jak již bylo uvedeno Wheelerovou (1991: 661–662), *Paraphyllanthoxylon* obsahuje velké množství thyl a nejinak je tomu i u našich vzorků z Pecínova. Přestože bylo prokázáno, že thyly se mohou tvořit za velmi specifických podmínek i ve dřevě bělovém po odebrání vzorku ze živého stromu (u dubu viz Murmanis 1975), či u poraženého stromu, který normálně jádrového dřevo nevytváří (u buku viz Jurášek 1956), vzhledem k vysokému stupni zathylování cév u našeho fosilního dřeva předpokládáme, že je jednalo o vzorek z vnitřní jádrové části.

### kmenová vs. korunová skupina taxonu

Dřeva zařaditelná do fosilního rodu *Paraphyllanthoxylon* systematicky odpovídají několika botanickým čeledím (viz Gryc *et al.* 2009). Náš cenomanský zástupce má velmi blízko k vavřínovitým (Lauraceae), navíc z Pecínova jsou známy další zástupci této čeledi (Eklund & Kvaček 1998), včetně fuzitických děv, která jsou s vavřínovitými srovnávána (Oakley & Falcon-Lang 2009). Důležitý systematický znak však chybí: ve dřevě nejsou přítomny idioblasty, tj. zvětšené olejové, popř. slizové buňky (viz Mantzouka *et al.* podáno k publikování). Alternativní vysvětlení absence idioblastů, které podpořil i J. A. Doyle (osobní sdělení 2008), spočívá v možnosti, že se v případě cenomanských vavřínovitých jedná o tzv. kmenovou linii, která ještě nevykazuje všechny znaky typické pro dnešní zástupce tzv. korunové skupiny (např. Judd *et al.* 2007: 176). Tento koncept umožňuje vysvětlit pozici i dalších problematických taxonů, které nejsou jednoznačně zařaditelné do žádné z dnešních čeledí (např. *Doliostrobus* viz část 5.3.2.).

široké pojetí fosilních rodů u děv

Paraphyllanthoxylon představuje typický příklad široce pojatého fosilního rodu, např. Thayn & Tidwell (1984: Table 4) uvádějí rody ze 14 čeledí, kterým může částečně odpovídat. Ve výsledku je tento rod nezařaditelný do jediné konkrétní čeledi, což je situace v hierarchické klasifikaci neobvyklá. Zajímavostí je, že se diagnóza tohoto fosilního rodu naprosto překrývá se dvěma diagnózami mladšími: u rodů *Burseroxylon* Prakash & Tripathi (viz Wheelerová 1991) a *Canarioxylon* (viz Gryc *et al.* 2009), který byl definován Prakashem *et al.* (1974) z lipnického souvrství jižních Čech. Tyto dva fosilní rody jsou tak fakticky mladšími synonymy názvu *Paraphyllanthoxylon*.

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5.3. Kenozoická dřeva

V kenozoiku, především pak od neogénu dál, je už naprostá většina dřev srovnatelná s dnešními rody (obr. 13). Vedle systematického výzkumu, kdy se uplatňuje srovnání s nejbližšími žijícími zástupci, je možné dřeva využít pro rekonstrukci klimatu. Zde se především uplatňují statistický Wiemannův model založený na fyziognomii (Wiemann *et al.* 1998, 1999, 2001) pro dřeva listnáčů a tzv. koexistenční přístup založený na přesném systematickém určení pro dřeva obecně (viz např. Böhme *et al.* 2007).
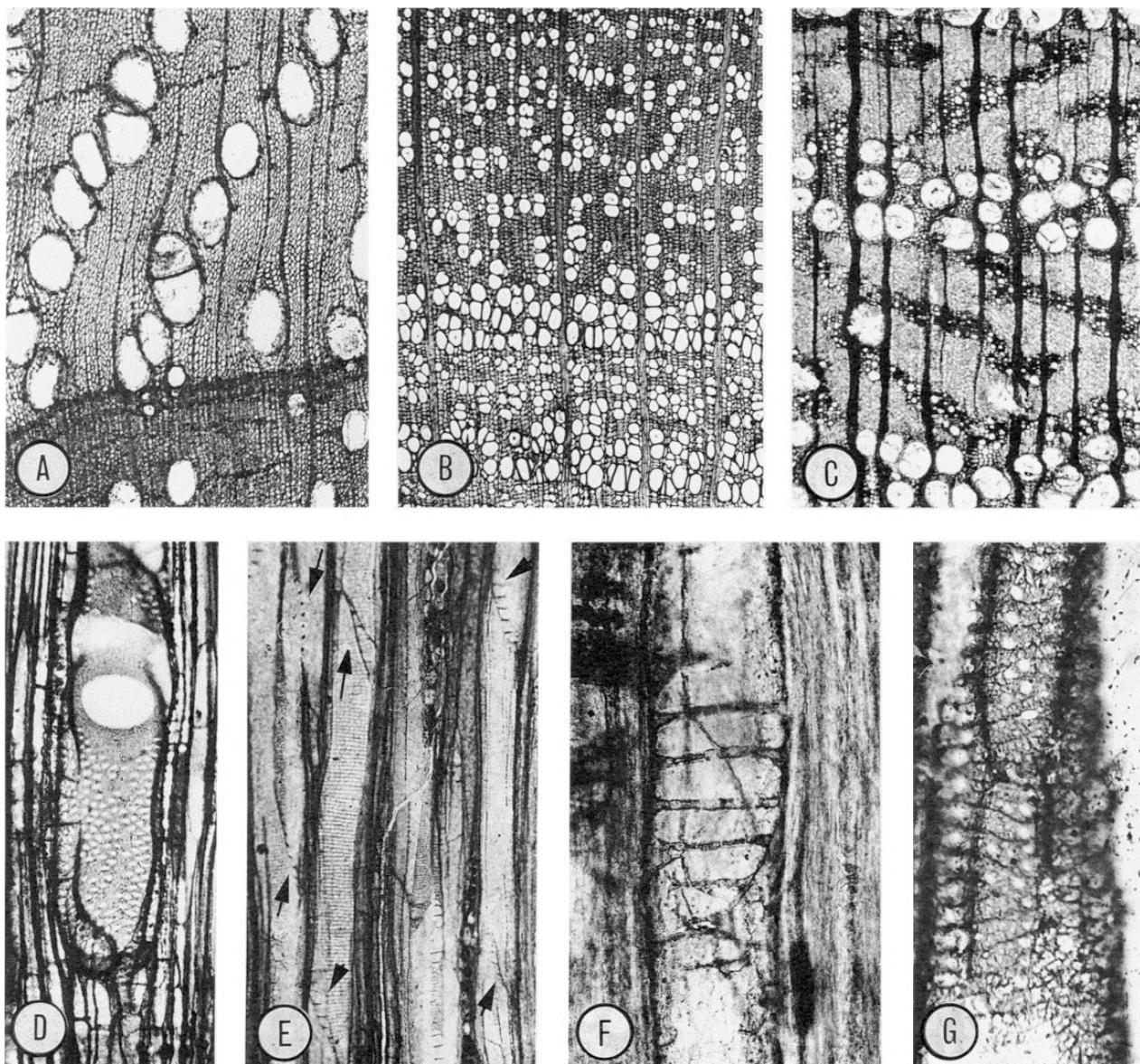
Obr. 13 – *Ukázka amerických kenozoických dřev: polokruhovitě až kruhovitě pórovitá dřeva s cévami různým způsobem seskupenými A)* Pterocaryoxylon*, B) Araliaceae, C)* Robinia*; D) jednoduchá perforace u cévy neurčeného listnáče; E) a F) žebříčkovité perforace u cév druhu* Plataninium haydenii*; G) spirální ztluštěniny na vnitřní stěně cévy neurčeného listnáče; stáří A, B, D–G: střední eocén, C: miocén.*

(zbytek obrázku a rozšířená legenda, viz Wheelerová & Baas 1993: Figure 1)

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5.3.1. Příklad 3: *mostecká pánev*

Obr. 14 – *Tzv. „pařezový horizont" (č. 31) v těsném nadloží hlavní uhelné sloje na Dolech Bílina, ve kterém vystupují xylitické kmeny v růstových pozicích* (in situ)*. Postava na snímku je vedoucí oddělení geologie Severočeských dolů a.s. ing. K. Mach, Ph.D.*
(foto jsem pořídil při exkurzi dne 29. 5. 2015)

Mostecká pánev, ohraničená Doupovskými horami na západě, Krušnými horami na severu a Českým středohořím na jihovýchodě, je největší z terciérních pod-krušnohorských pánví. Prostor pánve začal fungovat už v eocénu, kdy se usazoval materiál přinášený řekami (starosedelské souvrství), přes celý oligocén v převážně vulkanismem ovlivněném režimu (střezovské s.) až do raného miocénu, kam spadá hlavní část sedimentace včetně tvorby uhelné sloje (mostecké s.). Obecné shrnutí podávají Pešek *et al.* (2010), vedle toho pak Matys Grygar & Mach (2013) řeší korelaci a stratigrafii, především pak v nadložních libkovických vrstvách a konečně Mach *et al.* (2014) studují vývoj paleogeografie a paleoekologických aspektů pánve. Již několik let jsou hlavní lokalitou pro výzkum dřev v pánvi, ale i paleobotanický výzkum obecně, Doly Bílina (obr. 14). Ty poskytují unikátní kombinaci vysoké prostudovanosti, snadné dostupnosti, bohaté doprovodné flóry a v neposlední řadě dobré odborné a lidské spolupráce. Výsledkem je několik studií, které pokrývají hlavní specifika fosilních dřev mostecké pánve (Sakala 2002; Teodoridis & Sakala 2008; Havelcová *et al.* 2013).

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rozdílný potenciál zachování dřeva a dalších orgánů

Vliv prostředí na způsob zachování dřeva byl již diskutován výše (viz část 5.1.1.). V případě mostecké pánve je zjevné, že zde dochází k umělému ochuzení dřev zástupců krytosemenných. Prakticky všechna nalezená dřeva za posledních několik desítek let náleží jehličnanům, z listnáčů jsou známy tak 2–3 typy (přehled viz Sakala 2004) a to přesto, že na základě olistění a rozmnožovacích orgánů je jenom z Dolů Bílina známo přes 100 druhů angiosperm, převážně pak druhotně tloustnoucích (Kvaček *et al.* 2004). Tato nesrovnalost z velké míry souvisí se skutečností, že se často jedná o porosty na kyselých rašelinných půdách, kde se dřeva jehličnanů, hlavně ta zuhelnatělá, zachovají snáze (Březinová 1970). Je však třeba ještě zohlednit rozdílný potenciál zachování jednotlivých orgánů: např. dřevo vavřínovitých se zachovává snadno (Wheeler & Manchester 2002: 62), naproti tomu jejich pyl se rozpadá a do fosilního záznamu se tak fakticky nepromítá (R. Zetter osobní sdělení 2003).

jarní vs. letní dřevo

Identifikaci celé řady permineralizovaných (Teodoridis & Sakala 2008) a fakticky všech xylitických (Boudová 2012; Havelcová *et al.* 2013) dřev jehličnanů ztěžoval fakt, že jarní dřevo bylo deformováno. Ve výsledku tak bylo možné pozorovat jen znaky v letním dřevě, které díky užším tracheidám s tlustší sekundární stěnou vykazuje jiné radiální dvojtečky (Bailey & Faull 1934: 239) a tečky křížových polí (Gromyko 1990). Není tak vhodné pro srovnání s typickými popisy, jak jsou běžně uváděny právě na základě znaků dřeva jarního. Srovnávací studie anatomických znaků, jak se mění u příbuzných taxonů v rámci letokruhu, se objevují jen zřídka (např. Gromyko 1982), a proto bylo určování provázeno zvýšenou obezřetností a určitou mírou nejistoty.

významný fosilní taxon 1/2: *Taxodioxylon gypsaceum*

T. gypsaceum, známý z mostecké pánve, je ve třetihorách Evropy velmi běžným fosilním druhem (viz Březinová 1981). Jak poznamenávají van der Burgh & Meijer (1996: 373), "…*T. gypsaceum* je vysoce variabilní polyfyletický druh" a fakticky tak odpovídá výrazné variabilitě u dnešního druhu *Sequoia sempervirens* (viz Bailey & Faull 1934), se kterým je tradičně srovnáván (např. Privé-Gill 1977). V případě mostecké pánve se ale vzhledem k nepřítomnosti zbytků rodu *Sequoia* domnívám, že se v případě tohoto fosilního taxonu jedná o dřevo sekvoji příbuzného vymřelého jehličnanu, konkrétně druhu *Quasisequoia couttsiae* (Teodoridis & Sakala 2008). Obecně možnost, že *T. gypsaceum* může odpovídat nějakému vymřelému typu, zmiňuje už Huard (1966).

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5.3.2. Příklad 4: *České středohoří*
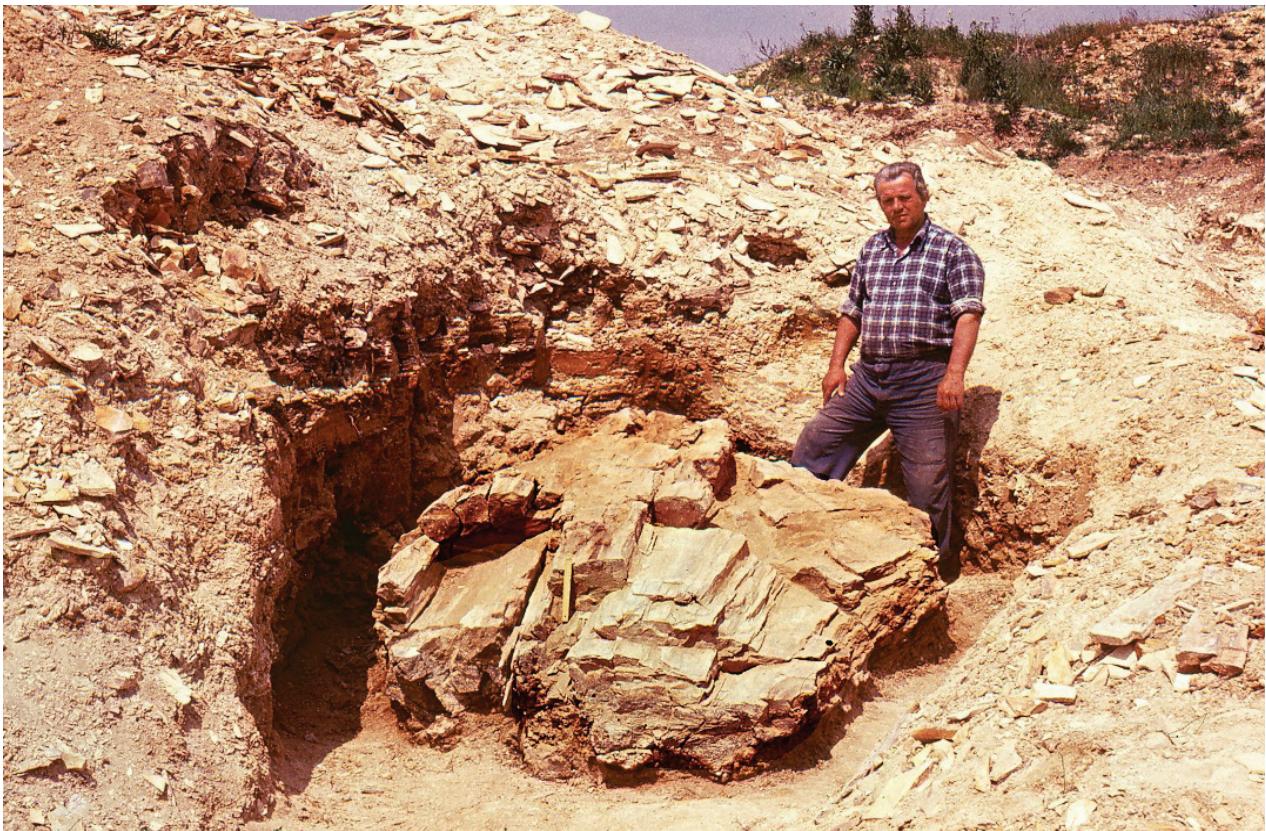
Obr. 15 – *Odkrytí zkamenělého kmene na lokalitě Kučlín v roce 1976. Na snímku od M. Mága z teplického muzea je p. řidič Rybola.*
(foto zapůjčil Z. Dvořák v r. 2015)

České středohoří tvoří rozsáhlý vulkanosedimentární komplex s vulkanity stáří eocén až miocén s těžištěm v oligocénu, přednostně vázanými na hlavní zlomy oherského riftu, a četnými intravulkanickými sedimenty s uhelnými a diatomovými vložkami, bohatými na fosilie. Obecný přehled, včetně většiny literárních zdrojů, předkládá Kopecký (2010). Ve svojí práci se pak geologii s ohledem na některé lokality s fosilními dřevy (Divoká rokle, Bečov) věnuje i Koutecký (2014). Hojná zkamenělá dřeva jsou jak historicky popisována, tak jsou i předmětem moderního výzkumu (viz Březinová 1970; Sakala 2004; Koutecký 2014). V následující stati se zaměřuji na známou pozdněeocenní lokalitu Kučlín (viz např. Kvaček & Teodoridis 2011), především pak na unikátní 7,5 m dlouhý kmen (obr. 15), který zde v roce 1976 objevil Dr. F. Holý. Dřevo tohoto jehličnanu bylo komplexně studováno Březinovou *et al.* (1994), později se mu věnuji ve dvou samostatných ryze systematických publikacích (Sakala 2003, 2011). Následující strana dobře ilustruje možná úskalí v souvislosti se třemi základními částmi odborného systematického příspěvku na téma fosilních dřev, kterými jsou: 1) detailní anatomický popis, 2) část věnovaná pojmenování fosilie a konečně 3) stať o botanické příslušnosti.

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jednoznačnost odborné terminologie

Při anatomickém popisu dřev jehličnanů se vždy snažím vycházet z obecně přijímané terminologie, v daném případě z IAWA Committee (2004), aby byla vyloučena případná nedorozumění. Bohužel některé anatomické znaky, které se v popisech zkamenělých dřev běžně používají, nejsou v této práci definovány. Příkladem můžou být typy teček křížových polí jako glyptostroboidní, či podocarpoidní, kdy ten druhý je právě důležitý při interpretaci a srovnání kučlínského dřeva (Sakala 2011). Existující definice podocarpoidního typu navíc není jednoznačná a zdá se, že se výklady různí dokonce mezi jednotlivými xylotomickými školami, konkrétně mezi německou a francouzskou (Dolezych & Sakala 2007); zajímavostí pak je, že ke stejnému výsledku dříve dospěli i Bamfordová & Philippe (2001).

názvy fosilních dřev

Pro pojmenování terciérních dřev se jména současných botanických rodů používají jen zřídka a jedná se především o americkou paleoxylotomickou školu. Jak ukázali Sakala & Privé-Gill (2004: 376) na příkladu středního eocénu Oregonu (Wheelerová & Manchester 2002), je tento přístup u vymřelého zástupce problematický. Většinová evropská paleoxylotomická tradice naproti tomu používá především fosilní rody s příponou *–xylon*, kdy předpona většinou ukazuje na čeleď, někdy na jediný rod, např. *Laurinoxylon* je dřevo vavřínovitých, *Quercoxylon* odpovídá dubu. U fosilního rodu *Podocarpoxylon*, jak bylo kučlínské dřevo zprvu označeno (Březinová *et al.* 1994), toto neplatí a předpona spíš poukazuje na podocarpoidní aspekt dřeva než na jeho příbuznost s Podocarpaceae, jak např. chybně uvádí Böhme *et al.* (2007).

významný fosilní taxon 2/2: *Doliostrobus*

Při zjišťování botanické příslušnosti fosilního kučlínského kmene šlo v posledku o to, zda se jedná o dřevo žijícího rodu *Tetraclinis*, nebo vymřelého r. *Doliostrobus*, tedy dvou jehličnanů, které jsou na Kučlíně známy díky olistění a reproduktivním orgánům (Kvaček & Teodoridis 2011). Přestože se osobně kloním k první z možností (Sakala 2011), je situace vzhledem ke špatnému zachování důležitých znaků (tečky křížových polí) stále otevřená. *Doliostrobus* je dnes vydělený do samostatné čeledi (Kvaček 2002). Ta spolu s Geinitziaceae představuje v současnosti vymřelý relikt v rámci kenozoických jehličnanů (Farjon 2008), sdílí nicméně podobnost s Araucariaceae a Cupressaceae s.l. (Kvaček 2002). Ve světle koncepce kmenové linie je ale otázkou, zda *Doliostrobus* není součástí právě takové linie cypřišovitých v tom nejširším fylogenetickém smyslu.

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5.3.3. Příklad 5: *Doupovské hory*

Obr. 16 – *Výkop zkamenělého kmene v areálu Kadaňské nemocnice. Na snímku od J. Prokopa z r. 2003 je ing. F. Foltýn.*

Vulkanický komplex Doupovských hor je obdobně jako České středohoří vázán na aktivitu oherského riftu a jeho dnešní podoba je rovněž výrazně ovlivněna denudací. Obecný přehled je nejnověji k nalezení v diplomové práci Kouteckého (2014), moderní odborná geologická syntéza však neexistuje. Doupovským horám se tak věnují jednotlivé kratší články, jejichž vznik je především vázán na probíhající geologické mapování (např. Hradecký 2003; Cajz *et al.* 2006; Rapprich 2011). V paleobotanice je situace obdobná a publikace o fosilních dřevech (Prakash *et al.* 1971; Sakala & Privé-Gill 2004; Sakala *et al.* 2010) tak fakticky představují jediný podrobnější soubor systematických studií. Za zmínku stojí fakt, že východní okraj Doupovských hor, konkrétně Kadaň a blízké okolí, představuje nejbohatší naleziště zkamenělých dřev v oblasti bývalého Československa, co se diversity týče (Sakala 2007).

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definice „typu dřeva"

Wiemann *et al.* (1998) vymezují „typ dřeva" (*wood type*) coby základní taxonomickou jednotku pro klimatický model založený na systematickém zhodnocení anatomických znaků dřev listnáčů; jedná se tak o *„…nejčastěji rod, ale občas druh nebo skupinu druhů, pokud anatomické rozdíly umožní takové vydělení"*. Spíše než jednoznačnou definici uvádí pro lepší pochopení příklad 30 druhů severoamerických dubů mírného pásma, které je možné rozdělit na 3 „typy dřev": stálezelené, červené a bílé duby (Wiemann *et al.* 1998: 85). V systematické studii dřev Doupovských hor jsem tuto kategorii použil také (Sakala *et al.* 2010), především pro sloučení dřev, o nichž jsem se domníval, že přes rozdílná zařazení Prakashem *et al.* (1971) patřila jednomu biologickému typu.

subjektivní vs. objektivní metody

Metody paleoklimatické rekonstrukce založené na fosilních rostlinách je možné rozdělit na 2 skupiny: na ty, které vyžadují systematické zařazení rostlin, jako např. koexistenční přístup s využitím nejbližšího žijícího příbuzného a na ty, které to nevyžadují, převážně pak různé typy fyziognomických metod jako jsou CLAMP pro listy, či Wiemannův model pro dřeva (Sakala 2007). Pro správnou aplikaci první skupiny metod jsou velmi důležité zkušenosti klasifikátora a tyto metody jsou tak výrazně „subjektivní". Naproti tomu fyziognomické metody by měly být relativně nezávislé na osobě, která paleoklimatickou rekonstrukci provádí, a mohou tak být klasifikovány jako „objektivní". Při praktické aplikaci „objektivního" Wiemannova statistického modelu se nicméně ukazuje, že je zde důležitý první „subjektivní" krok, který opět vyžaduje odborné zkušenosti, totiž výběr typů dřev. Například z 22 popsaných fosilních druhů z německé lokality Rauscheröd jsem vybral 16 typů dřev (Sakala 2007: Table 1), ale jiný kolega/kolegyně může udělat odlišný výběr, který ovlivní i výsledné klimatické hodnoty.

omezení pro Český masív

Naše v současnosti nejbohatší lokalita Kadaň-Zadní vrch obsahuje pouze 6 pro Wiemannův statistický model použitelných typů dřev (Sakala *et al.* 2010). Tento počet je bohužel nedostatečný pro získání spolehlivých výsledků v situaci, kdy Wiemannem *et al.* (1999) analyzované fosilní lokality při prezentaci modelu mají minimálně 16 typů dřev. Obecně platí, že v rámci Evropy jsou lokality s dostatečným počtem dřev listnáčů spíše vzácností (např. již zmíněný Rauscheröd), a tak by určitou možností mohlo být slučování několika ekologicky srovnatelných a stejně starých lokalit dohromady (Sakala 2000).

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6. Shrnutí

Základem předkládané habilitační práce, která formou i obsahem navazuje na moji disertační práci (Sakala 2004), je **7 vědeckých článků** (Mencl *et al.* 2013; Gryc *et al.* 2009; Teodoridis & Sakala 2008; Havelcová *et al.* 20013; Sakala 2011, 2007; Sakala *et al.* 2010). Články jsou připojeny v úplném znění na konci textu coby přílohy (**přílohy 1– 7**). Vlastní text práce tvoří obecný úvod, kde charakterizuji předmět studia (fosilní dřevo) a zájmovou oblast (střední a sz. Čechy), a jednotlivé případové studie. Stejně jako v disertační práci jsem představil 5 případových studií (**příklady 1–5**). Každá případová studie odkazuje buď na jeden (příklady 1, 2 a 4: **kladensko-rakovnická pánev**, **česká křídová pánev** a **České středohoří**), nebo na dva články (příklady 3 a 5: **mostecká pánev** a **Doupovské hory**). V textu u jednotlivých příkladů pak popisuji hlavní teze odpovídajících článků, jejich paleobotanicko-stratigrafické zařazení a vždy tři obecnější otázky, které s výzkumem fosilních dřev souvisejí.

 Příklad 1 (viz **Příloha 1**) je zaměřen na paleozoická dřeva přesličkovitých rostlin typu *Arthropitys*, která byla nově popsána ze západní části **kladensko-rakovnické pánve** díky nálezům sběratelů. Mohla tak být velmi dobře demonstrována výhoda dobré spolupráce s nimi (**úplnost fosilního záznamu a role sběratelů**). Některé stromovité přesličky vytvářely velké množství sekundárního xylému jen díky unifaciálnímu kambiu a přestavují tak určitou výzvu tradičnímu modelu (**unifaciální vs. bifaciální kambium**). V důsledku transportu fosilií bylo možno studovat pouze sekundární xylém bez dalších detailů vnější stavby (**vliv prostředí na způsob zachování**).

 Příklad 2 (viz **Příloha 2**) popisuje dřevo listnáče rodu *Paraphyllanthoxylon* z lokality Pecínov **české křídové pánve**. Dřevo je charakteristické velkým množstvím thyl (**vytváření thyl a jejich význam**). Rovněž vykazuje pro moderní dřeva netypickou kombinaci anatomických znaků a jeho jednoznačné přiřazení k některé z dnešních čeledí je tak problematické (**kmenová vs. korunová skupina taxonu**). Samotný *Paraphyllanthoxylon* je pak velmi široce pojatý fosilní rod a dobře ukazuje, že u fosilních dřev existuje často výrazný rozpor mezi pojetím rodu fosilního a tradičního botanického (**široké pojetí fosilních rodů u dřev**).

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Příklad 3 (viz **Přílohy 3** a **4**) se zaměřuje na dřeva jehličnanů z **mostecké pánve**. Přestože je zde na základě olistění a reproduktivních orgánů známo několik desítek rozdílných druhů rostlin, náleží fosilní dřeva v naprosté většině ke 2–3 fosilním druhům jehličnanů (**rozdílný potenciál zachování dřeva a dalších orgánů**). Jejich zuhelnatělá dřeva jsou pak ve většině deformována, kdy pro systematické zařazení důležité jarní dřevo prakticky chybí (**jarní vs. letní dřevo**). V závěru tohoto příkladu zmiňuji pro evropské třetihory **významný fosilní taxon 1/2:** *Taxodioxylon gypsaceum*.

Příklad 4 (viz **Příloha 5**) si všímá jediného zkřemenělého kmene jehličnanu z lokality Kučlín z **Českého středohoří**. Při anatomickém popisu dřeva se ukázalo, že některé typy teček křížových polí nejsou jednoznačně definovány (**jednoznačnost odborné terminologie**). Pro popis fosilních dřev se tradičně používají jména s příponou *–xylon*, předpona ale nemusí vždy ukazovat na skutečnou systematickou příbuznost (**názvy fosilních dřev**). U tohoto příkladu zmiňuji další **významný fosilní taxon 2/2:** *Doliostrobus*, který jako jeho možný původce s kučlínským dřevem úzce souvisí.

Příklad 5 (viz **Přílohy 6** a **7**) se zaobírá především dřevy listnáčů z východního okraje **Doupovských hor** z okolí města Kadaň a jejich využitím pro paleoklimatickou rekonstrukci. Statistická metoda rekonstrukce, založená pouze na fyziognomii dřev listnáčů, používá „typ dřeva" jako svoji základní jednotku; ta se osvědčila i pro systematické studie (**definice „typu dřeva"**). Přes svoji objektivitu má tato metoda důležitý „subjektivní" první krok: právě výběr a počet „typů dřev" (**subjektivní vs. objektivní metody**). Jejich počet, který pro většinu českých třetihorních lokalit není dostatečný, tak pro aplikaci této metody způsobuje výrazné **omezení pro Český masív**.

Studovaná oblast středních a sz. Čech poskytuje dřeva nejen kenozoická (třetihorní), ale i mezozoická (svrchnokřídová) a paleozoická (svrchnokarbonská). Jejich studium tak vedle širokého systematického záběru ukazuje problematiku fosilních dřev v celé její složitosti. Věřím tak, že předkládaná habilitační práce, která vznikla jako spojení mojí vědecké činnosti při popisu dřev a pedagogické aktivity při vedení závěrečných prací, tuto součást paleobotanického výzkumu dostatečně a jasně přibližuje.

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Summary

The present habilitation thesis called *"Fossil wood and its importance in palaeobotanical research: case studies from the area of Central and NW Bohemia"* picks up the threads of my PhD thesis (Sakala 2004). It is based on **7 scientific papers** (Mencl *et al.* 2013; Gryc *et al.* 2009; Teodoridis & Sakala 2008; Havelcová *et al.* 20013; Sakala 2011, 2007; Sakala *et al.* 2010), which can be found unabridged at the end of the thesis as annexes (**Annexes 1–7**). The text of the thesis itself is composed of a general introduction, which characterizes both the field of study (fossil wood) and the area of interest (Central and NW Bohemia), and individual case studies. Similarly to the PhD thesis, there are 5 case studies (**examples 1–5**), each of them refers either on one (examples 1, 2 and 4: **Kladno–Rakovník Basin**, **Bohemian Cretaceous Basin** and **České středohoří Mts.**), or two papers (examples 3 and 5: **Most Basin** and **Doupovské hory Mts.**). In the text of each example, there are main ideas of the corresponding paper/s with its palaeobotanical and stratigraphical context and three more general aspects, which are related to the fossil wood studies.

Example 1 (see **Annexe 1**) is focused on Palaeozoic calamitalean stems of the *Arthropitys* type, which were newly described from the western part of the **Kladno–Rakovník Basin** thanks to amateur fossil collectors. Consequently, the advantage of such cooperation can be demonstrated (**completeness of fossil record**). Some arborescent sphenopsids formed a great amount of secondary xylem with unifacial cambium alone, so they represent a kind of challenge to the traditional model (**unifacial vs. bifacial cambium**). Due to transport of fossils, we could study only secondary xylem without any other detail of extraxylary tissues (**influence of environment on mode of preservation**).

Example 2 (see **Annexe 2**) describes a dicot wood of the fossil genus *Paraphyllanthoxylon* from the locality Pecínov in the **Bohemian Cretaceous Basin**. The wood presents abundant tyloses (**formation of tyloses and its significance**), and also shows an unusual combination of anatomical features, which makes its unambiguous attribution to some modern family problematic (**stem vs. crown group**). *Paraphyllanthoxylon* as a widely defined fossil genus demonstrates well that there is often an important discrepancy between fossil and modern genus concept (**wide concept of fossil genera in wood**).

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Example 3 (see **Annexes 3** and **4**) concentrates on fossil conifer wood from the **Most Basin**. There are several tens of fossil species based on leaves and reproductive structures, but the fossil wood is represented there by only 2 or 3 chiefly conifer species (**different potential of preservation for wood and other organs**). Their xylitic woods are almost all deformed, where the systematically important earlywood part is practically missing (**early vs. late wood**). Finally, already in the context of the European Tertiary, I notice an **important fossil taxon 1/2: *Taxodioxylon gypsaceum***.

Example 4 (see **Annexe 5**) takes note of the silicified conifer trunk from the locality Kučlín in the **České středohoří Mts.** During anatomical description of the wood, I realised that some types of cross-field pitting were not unequivocally defined (**unambiguity of scientific terminology**). Traditionally, there are names with suffix –*xylon* to denominate fossil woods, but the prefix does not have to always point to their true botanical affinity (**names of fossil woods**). Here, there is another **important fossil taxon 2/2: *Doliostrobus***, which is closely linked to the Kučlín wood as its possible mother plant.

Example 5 (see **Annexes 6** and **7**) deals mainly with dicot woods from the eastern edge of the **Doupovské hory Mts.** from the vicinity of the town of Kadaň and their utilization in palaeoclimate reconstruction. Statistical method of reconstruction, which is based on physiognomic features of dicot woods, uses the "wood type" as its main unit; this distinction was effective for the systematical studies as well (**definition of "wood type"**). Despite its objectivity this method requires an important first "subjective" step: selection of "wood types" (**subjective vs. objective methods**). Their number, which is insufficient for the majority of the Czech Tertiary localities, represents a serious **limitation for the Bohemian Massif** for a correct application of this method.

The study area of Central and NW Bohemia provides woods, which are not only Cenozoic (Tertiary), but also Mesozoic (Upper Cretaceous) and Paleozoic (upper Carboniferous). Consequently, their study offers a wide systematical range and also shows how the fossil wood issue is complex. I believe that the presented habilitation thesis, which was prepared as a conjunction of scientific and pedagogic aspects of my work, can show clearly and sufficiently this specific part of palaeobotanical research.

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Seznam příloh

kladensko-rakovnická pánev

1. MENCL, V., HOLEČEK, J., RÖßLER, R. & **SAKALA, J.** 2013. First anatomical description of silicified calamitalean stems from the upper Carboniferous of the Bohemian Massif (Nová Paka and Rakovník areas, Czech Republic). *Review of Palaeobotany and Palynology 197*, 70–77.

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2. GRYC, V., VAVRČÍK, H. & **SAKALA, J.** 2009. Cenomanian angiosperm wood from the Bohemian Cretaceous Basin, Czech Republic. *IAWA Journal 30*, 319–329.

mostecká pánev

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Doupovské hory

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Příloha 1

Research paper

First anatomical description of silicified calamitalean stems from the upper Carboniferous of the Bohemian Massif (Nová Paka and Rakovník areas, Czech Republic)

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ABSTRACT

Silicified stems are very abundant in the upper Palaeozoic basins of the Czech Republic. The results of an anatomical study of the silicified calamitalean stems from the Krkonoše Piedmont and Kladno–Rakovník basins are presented here for the first time. In the Krkonoše Piedmont Basin, there are various silicified plant remains, but the presence of calamitalean wood is restricted to only one stratigraphic unit, to the so-called "Ploužnice Horizon". Only a few data on the systematics of permineralised or petrified stems from the Kladno–Rakovník Basin are available, anatomical descriptions are largely lacking and fossilised calamitalean stems were unknown. The fossils can be attributed to two species: the common Arthropitys cf. bistriata and the rare Calamitea striata; the occurrence of the latter is limited to the Krkonoše Piedmont Basin.

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1. Introduction

The Carboniferous–Permian of the Krkonoše Piedmont area is historically well known for its abundant fossil stems. Their frequency and aesthetic value attracted the attention of local and foreign researchers (Březinová, 1970), but a modern systematic overview is still lacking. One might even say that in the past decades only collectors have shown their interest. The fossil stems were illustrated in several popular books on fossil plants (e.g., Dernbach, 1996; Dernbach et al., 2002). Only Matysová and Mencl in their MSc theses (Matysová, 2006; Mencl, 2007) and three consecutive papers (Matysová et al., 2008; Mencl et al., 2009; Matysová et al., 2010) presented the first detailed systematical and geochemical data, mainly focused on the "Dadoxylon" type of wood. Holeček in his MSc thesis (Holeček, 2011) studied the succession in the Kladno–Rakovník Basin in Central/Western Bohemia, which also contains abundant fossil wood and can be correlated with the succession in the Krkonoše Piedmont area.

The present contribution summarises new and old evidences of silicified calamite stems from the upper Carboniferous of the Czech Republic and provides the first anatomical description with special emphasis on the Krkonoše Piedmont Basin as well as the Kladno–Rakovník Basin, from which calamite stems were previously unknown. We apply the taxonomic concept recently developed for calamitaleans from the early Permian petrified forest of Chemnitz, Germany (Rößler and Noll, 2006, 2007, 2010; Rößler et al., 2012a).

2. Historical research

2.1. Krkonoše Piedmont Basin

Silicified stems in the Nová Paka region (Fig. 1A) were mentioned by many authors, probably first by Maloch (see Heber, 1844). The first scientific descriptions of silicified plant remains from localities such as Nová Paka, Pecka and Kozinec are by Goeppert (1858), who described the conifer wood Araucarites schrollianus (=Dadoxylon saxonicum; synonym: Dadoxylon schrollianum), Calamites and Psaronius. Frič (1912) noticed several types of silicified stems from Nová Paka and Lázně Bělohrad (stem types Medullosa, Psaronius and "Dadoxylon") and silicified peat. He paid special attention to insect borings on the woods, and to small axes of the climbing fern Ankyropteris brongniartii, which were preserved inside the root mantle of Psaronius trunks. Common findings of silicified wood in the Nová Paka and Pecka surroundings were also mentioned by Jokély (1861), Feistmantel (1873a,b,c) and Purkyně (1927). Several pieces of silicified stems ("Dadoxylon", Psaronius, Medullosa) were found in the village of Pecka; mostly as loose pieces but some of them in outcrops, although not in upright position (Purkyně, 1927). The age of these findings was initially considered

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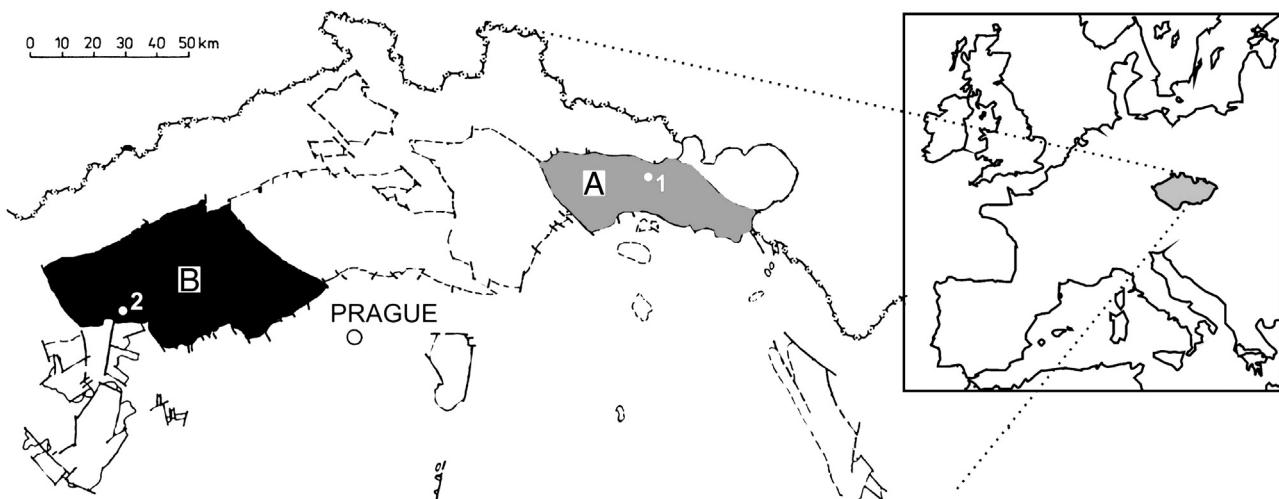
Fig. 1. Carboniferous–Permian basins of the Czech Republic with the position of the Krkonoše Piedmont Basin (A) and Kladno–Rakovník Basin (B) and two studied localities Nová Paka (1) and Bílenec (2) with most abundant fossil wood.

to be early Permian (Feistmantel, 1873a,b,c), but is now regarded to be Kasimovian–Gzhelian (Matysová, 2006; Mencl, 2007; Mencl et al., 2009). No detailed anatomical descriptions of calamitalean stems were published to date, only the historical report by Goeppert (1858), some photos by Němejc (1963, Plates XXXII–XXXIII), a few notes by local collectors (e.g., Soukup, 1997) and a short note by Sakala et al. (2009).

2.2. Kladno–Rakovník Basin

Findings of silicified wood in the Kladno–Rakovník Basin (Fig. 1B) are not as common as in the Krkonoše Piedmont Basin. The first study was carried out by Feistmantel (1873b). He described silicified wood from localities such as Rakovník, Lubná, Hředle, Řevničov, Klobuky and Krušovice as *Araucarites schrollianus* and *Psaronius*. Frič (1912) mentioned sandy strata with silicified wood near Kněževes. Purkyně (1927) provided a summary of findings from Bohemia, including the new localities Očihov and Kryry; he also mentioned an occurrence of black silicified wood from Slaný Formation. The most recent petrological study was performed by Skoček (1970), who divided the petrified wood in two categories: dark wood with organic matter and lighter wood without organic matter. Skoček (1970) assumed that the dark wood was deposited in swamps or marshes in a wet climate regime, while the more common pale-coloured wood was regarded as being deposited under dry climatic conditions. Finally, a short note about the silicified peat and fossil wood in the Kloubuky area was recently published by local collectors (Dvořák and Švancara, 2003). It can be said that the research in the Kladno–Rakovník Basin was not as thorough as in the Krkonoše Piedmont Basin.

3. Geological settings

3.1. Krkonoše Piedmont Basin

The Krkonoše Piedmont Basin is situated in the northern part of the Czech Republic, at the foot of the Krkonoše–Jizerské hory crystalline complex (Fig. 1A) and belongs to a system of post-orogenic extensional/transtensional basins of the Bohemian Massif. Continental deposits in the Krkonoše Piedmont Basin are early Moscovian (Asturian) to Early (or even Middle) Triassic. The maximum thickness of the succession is about 1800 m (Pešek et al., 2001). Despite the fact that occurrences of "*Dadoxylon*" type of wood are confirmed from three stratigraphic levels (Mencl et al., 2009), silicified remains of calamitaleans (*Arthropitys*, *Calamitea*), ferns (*Psaronius*) and seed-ferns (*Medullosa*) are restricted

to a single stratigraphic level — the so-called "Ploužnice Horizon" (Fig. 2, right column).

The Ploužnice Horizon belongs to the middle part of the Semily Formation and is Gzhelian (Stephanian C) in age. It is known from the southern part of the basin, only from a number of localities that are situated approximately around Syřenov, Stará Paka, Nová Paka (with the well-known Balka locality), Borovnice and Pecka. This unit is usually up to 100 m thick and sediments are mostly lacustrine (Pešek et al., 2001). They consist of fine-grained, reddish mudstones and siltstones with limestone-enriched horizons, calcareous and silicic concretions, and intercalations of tuff and tuffitic sandstones that were deposited as bedload (Stárková et al., 2009). Common occurrences of silicified wood and nodules of carnelian are restricted to the lower part of the Ploužnice Horizon. Silicified stems in growth position have never been observed. They are very rarely found in outcrops, but they are always transported and redeposited in lacustrine and fluvial sediments. Most of fossil trunks are split into pieces and found in eluvial sediments.

3.2. Kladno–Rakovník Basin

The Kladno–Rakovník Basin is situated in the central and northwestern part of the Czech Republic (Fig. 1B). It was also formed as part of a post-orogenic extensional/transtensional basin of the Bohemian Massif. The oldest sediments are early Moscovian and the youngest are Gzhelian in age. These mostly lacustrine sediments are usually divided into four formations, i.e. the Kladno, Týnec, Slaný and Líně formations. Silicified wood is usually found in all formations, but it is most abundant in the Týnec and Líně formations (Fig. 2, left column).

The Týnec Formation (Kasimovian) is typified by coarse-grained reddish sediments, without or with little volcanic material. Up to 10 m long silicified trunks were described from this formation by Pešek et al. (2001). The Týnec and the Líně formations are separated by a hiatus. The Líně formation (Gzhelian) was deposited in a drier environment and primarily consists of reddish to crimson-coloured siltstones and claystones. Tuffs and tuffites are more common than in the underlying Týnec Formation. Three horizons can be distinguished within the Líně Formation: the Zdětín, Klobuky and Stránka horizons (Pešek et al., 2001). Unfortunately, there are no outcrops of this formation in the Kladno–Rakovník Basin and all fossil trunks have been found in eluvium. Whole trunks are extremely rare, petrified wood is often fragmented into small pieces without branches. Therefore, we suppose that the trees were transported by rivers and eventually buried far from their original place of growth.

AGE				Kladno-Rakovník Basin		Krkonoše Piedmont Basin	
				FORMATION	MEMBER	FORMATION	MEMBER
TRIASSIC						Bohdašín	upper
							lower
PERMIAN	LOPINGIAN		Changsinghian			Bohuslavice	
			Wuchiapingian				
	GUADALUPIAN		Capitanian			Trutnov	Suchovršice
			Wordian				Havlovice
			Roadian				Vlčice
	CISURALIAN		Kungurian				Horní Staré Město
						Chotěvice	
			Sakmarian			Prosečné	upper
							lower
			Asselian			Vrchlabí	upper
							lower
CARBONIFEROUS	PENNSYLVANIAN		Gzhelian	Líně	🪵	Semily	upper
							middle ➡️ 🪵
							lower
				Slaný	Kamenný Most	Syřenov	
					Kounov		upper
					Ledce		
					Hředel		
					Mšec		lower
					Jelenice		
			Kasimovian	Týnec	🪵	Kumburk	Štikov arkoses
			Moscovian	Kladno	Nýřany		Brusnice
					Radnice		

Fig. 2. Stratigraphy of the Kladno–Rakovník Basin in comparison with the Krkonoše Piedmont Basin; positions of the silicified calamitalean stems are figured by three small logs, the arrow shows the position of the Ploužnice Horizon.

4. Materials and methods

The samples from the Krkonoše Piedmont Basin are either from the palaeontological collections of the Municipal Museum Nová Paka, which have been collected during the last 100 years (signature P) and the Museum of Eastern Bohemia in Hradec Králové (abbreviation H), or by a private collector (specimen DVO5/XLVI). One specimen of *Calamitea striata* is from the Leuckart collection at Museum für Naturkunde Chemnitz (signature K). The samples from the Kladno–Rakovník Basin were provided exclusively by private collectors (abbreviations SVE, REH, ZAJ, DVO).

Only the best preserved samples were selected for further study. Cross sections of several dozens of well-preserved samples were polished and examined in reflected light with a Leica EZ 5 stereomicroscope and a Nikon Eclipse LV100Pol microscope. Several samples were selected for thin sectioning and transverse, tangential longitudinal and radial longitudinal sections were studied microscopically in transmitted light.

Thin sections were studied with an Olympus BX-51 microscope. Images were made with Olympus Camedia 3030 and Canon D500 digital cameras and processed with imaging software AnalySIS and NIS-Elements, with the help of Microsoft Excel 2007–2010.

5. Results

5.1. Systematics

Class: Sphenopsida.
Order: Equisetales.
Family: Calamitaceae.

Arthropitys Goeppert.
Arthropitys cf. *bistriata* (Cotta) Goeppert emend. Rößler, Feng and Noll (Fig. 3; Plates I, II).
Material: P1584, P1591, P1952, P1992, P3207, P4672, P5072, P5657, P5956, H74692, H74697 and DVO5/XLVI from the Krkonoše Piedmont Basin and SVE001/1, SVE002/1, SVE003/1, SVE004/1, SVE005/1, REH002/1, ZAJ004/1 and DVO5/XXXIII from the Kladno–Rakovník Basin.

Macroscopic description: all samples are small; pieces are only several centimetres long. Samples from the Krkonoše Piedmont Basin are dark, red-brown or orange (Plate I, 5; Plate II, 3, 6), only few are beige or whitish. On the other hand, samples from the Kladno–Rakovník Basin are mostly beige to greyish (Plate II, 1, 4), with one exception (ZAJ004/1) that is brown-yellow. Some samples (P1584, DVO5/XLVI) show nodes and another one (SVE005/1) nodes and a branch trace.
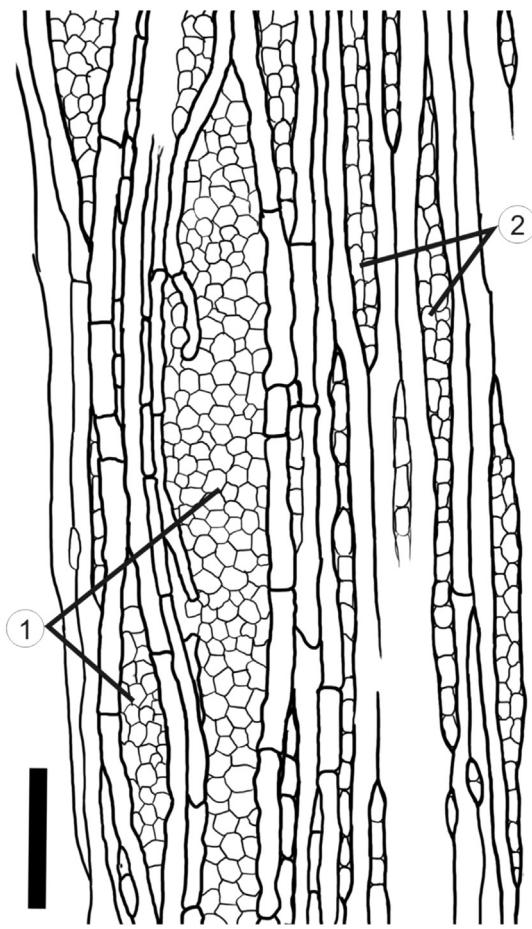
Fig. 3. Drawing showing the zones of wider interfascicular rays (1) and narrower fascicular rays (2), see Plate I/7 (specimen ZAJ004/1, Kladno–Rakovník Basin). Scale bar = 0.5 mm.

Microscopic description: well-preserved secondary xylem tracheids separated by interfascicular rays were observed in all studied samples (Plate II, 5). Sometimes also the primary vascular system with carinal canals and poorly preserved metaxylem in the external part of the pith cavity is preserved (Plate I, 2, 3, 6). The amount of parenchyma is about 46%. Interfascicular rays are distinguishable through the whole secondary xylem thickness (Plate I, 7; Fig. 3).

All specimens show one type of tracheid; tracheids are arranged in radial rows, slightly varying in size and shape in each row (Plate II, 5). Tracheids close to the pith are usually oval, square or brick-shaped in cross-section, and slightly elongated in radial direction; they are 25–100 μm (mean 56 μm) in diameter in radial direction and 22–76 μm (mean 44 μm) in tangential direction. Parenchyma cells in the fascicular rays are usually oval, square or brick-shaped, 22–108 μm (mean 57 μm) in diameter. Tracheids are arranged in five to eighteen files separated by interfascicular rays. These rays are distinguishable to the very edge of the specimens and consist of one to seven rows of parenchyma cells, rectangular, brick-shaped and obviously elongated in radial direction. Tracheids in the external parts of the stems are slightly widened compared to those in the internal part, which are 50–100 μm (mean 70 μm) radially and 45–60 μm (mean 51 μm) wide tangentially. Scalariform pitting is visible in radial longitudinal sections (Plate I, 4). The pits are bordered and the distance between two neighbouring ones is 2–4 μm. Carinal canals and the surrounding metaxylem are sometimes preserved next to the pith cavity (Plate I, 6). Carinal canals are usually circular in transverse section, and 105–171 μm (mean 140 μm) in diameter. Metaxylem elements are rectangular, arranged in two to three rows surrounding the carinal canals and are 15–57 μm (mean 27 μm)

in diameter. The samples interpreted as roots lack carinal canals and have pith parenchyma cells preserved (Plate II, 2ab).

Discussion: thin sections were prepared from specimens P4672, P5956, SVE001/1, SVE002/1, REH002/1 and ZAJ004/1. They all show the same anatomical characteristics. There is only one type of tracheid; all tracheids are oval, square to brick-shaped in transverse section and some of them have bordered scalariform pits in their radial walls as illustrated in Marguerier (1970). Generally, fascicular and interfascicular rays consist of parenchyma cells and almost 50% of the secondary body consists of parenchyma. Moreover, it is possible to distinguish fascicular and interfascicular zones up to the periphery of the wood and the tracheids have scalariform pitting (Rößler and Noll, 2006, 2010; Rößler et al., 2012a). After a detailed comparison with the Chemnitz material, we think that all samples belong to the most common calamitalean *Arthropitys bistriata*. However, because the typical branching pattern of this species (Rößler et al., 2012a) is not recognised in our material, we identify our fossils as *Arthropitys* cf. *bistriata*.

Calamitea Cotta emend. Rößler and Noll.
Calamitea striata Cotta (Plate III).
Material: P3173, P2660A, P2660C, and K2121, all from the Krkonoše Piedmont Basin.

Macroscopic description: only small parts of secondary xylem with badly preserved external portions of the central pith and carinal canals are present. Other parts of plant tissues (e.g., phloem, cortex) are not preserved. The colour of all specimens varies from dark, red-brown or orange to light, whitish or beige. The size of the samples ranges from 50 to 100 mm.

Microscopic description: the secondary xylem consists of two different types of tracheids, one having a larger diameter than the other (Plate III, 5, 6). Both tracheid types are arranged in radial files and are separated by thin continuous rays. The tissues are sometimes deformed during fossilisation. Wide tracheids (SX1) are present in front of the carinal canals and alternate with zones of narrow tracheids (SX2) which the fill lateral parts of secondary xylem fascicles. The two types of tracheids differ in colour (Plate III, 1–4); note that wide (SX1) and narrow (SX2) tracheids correspond to "large-diameter tracheids" and "small-diameter tracheids" sensu Rößler and Noll (2007). Type 1: wide tracheids are mostly in dark, brown-red. This part of secondary xylem has more parenchyma than the Type 2, but the exact shape and size of these parenchyma cells forming fascicular rays cannot be estimated due to poor preservation. Tracheids are variously polygonal with circular to oval lumen in transverse section; the radial rows are usually less deformed. Tracheid diameters vary from 39 to 173 μm (mean 61 μm) radially and from 49 to 120 μm (mean 67 μm) tangentially. Brick-shaped parenchyma cells are mostly poorly preserved (Plate III, 6).

Type 2: these narrow tracheids are usually preserved as lighter parts of secondary xylem and occur on both sides of the Type 1 tracheids toward the interfascicular ray; they are arranged in regular, often deformed radial rows (Plate III, 6). The tracheids are polygonal in transverse section and slightly elongated in radial direction; their diameter varies from 26 to 54 μm (mean 38 μm) radially and from 24 to 51 μm (mean 36 μm) tangentially.

Tracheid pitting in radial walls has not been observed due to the poor preservation.

Interfascicular rays are usually 11–37 μm (mean 25 μm) wide and are composed of one to four rows of cells. Rays are enlarged from the pith to the periphery of the wood cylinder, often deformed and visible as darker zones in the middle of the lighter portions of the secondary xylem Type 2 (see Plate III, 7). Rectangular, thick-walled cells of interfascicular rays are obviously elongated in radial direction. Their diameter varies from 31 to 73 μm (mean 42 μm) in radial direction and from 11 to 22 μm (mean 17 μm) tangentially.

Discussion: only small pieces of secondary tissues were available, but two types of tracheids and ray parenchyma cells are conspicuous. More delicate details like tracheid pitting in radial walls could not
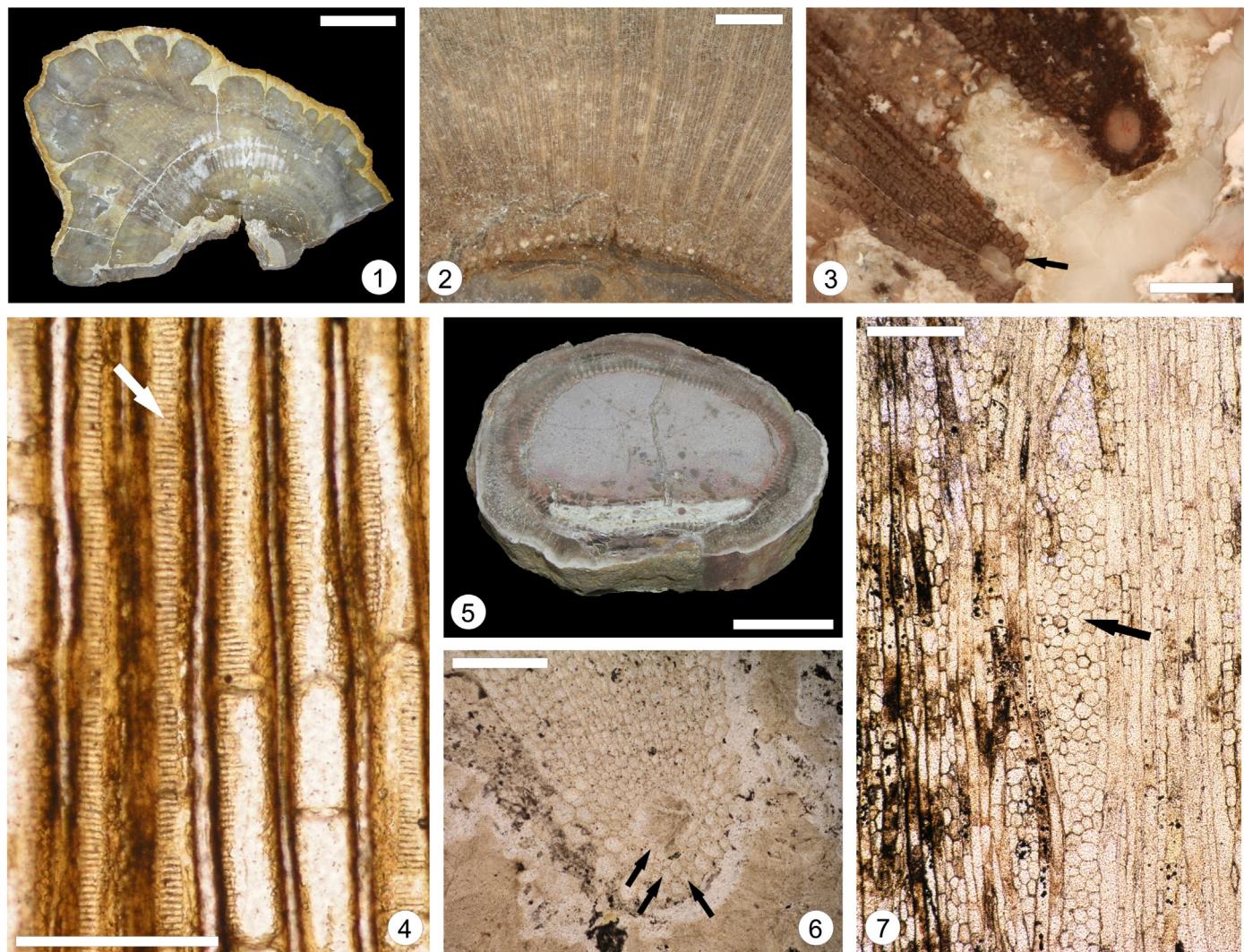
Plate I. *Arthropitys* cf. *bistriata* from the Kladno–Rakovník Basin and the Krkonoše Piedmont Basin.

1. General view of one of the biggest specimens from the Kladno–Rakovník Basin, TS (specimen DVO5/XXXIII). Scale bar = 40 mm.
2. Pith periphery surrounded by secondary xylem composed of fascicular wedges and interfascicular rays, TS (specimen SVE004/1, Kladno–Rakovník Basin). Scale bar = 2 mm.
3. Detail of the central pith secondary filled, TS (specimen P1992, Krkonoše Piedmont Basin), showing pith periphery, detail of innermost interfascicular ray, fascicular secondary xylem and two carinal canals surrounded by badly preserved tracheids of metaxylem (arrow). Scale bar = 0.5 mm.
4. Tracheids of secondary xylem with scalariform bordered pitting (arrow), RLS (specimen ZAJ004/1, Kladno–Rakovník Basin). Scale bar = 0.2 mm.
5. Large central pith secondary filled surrounded by a narrow secondary xylem composed of fascicular wedges and interfascicular rays, TS (specimen P5956, Krkonoše Piedmont Basin). Scale bar = 30 mm.
6. Detail of the previous picture with a carinal canal surrounded by three rows of metaxylem tracheids (arrows). Scale bar = 0.3 mm.
7. A multiseriate interfascicular ray (arrow) among tracheids and fascicular rays, TLS (specimen ZAJ004/1, Kladno–Rakovník Basin). Scale bar = 0.5 mm.

TS = transverse section; TLS = tangential longitudinal section; RLS = radial longitudinal section.

be studied due to the poor preservation of the specimens and low contrast of the structures when observed with stereomicroscope; in fact, it was not possible to make additional thin longitudinal sections because of the rarity of the museum specimens. However, all observed features, mainly the differences in shape of various types of tissue and thickness of their walls, are typical of *Calamitea striata* (Rößler and Noll, 2007). The samples from the Krkonoše Piedmont Basin differ in colour from those of the Permian petrified forest of Chemnitz; all samples from the Krkonoše Piedmont Basin typically show wide, dark-coloured tracheids, whereas narrow tracheids are lighter. On the other hand, the samples from the type locality Chemnitz (except for sample MfNC K 5204: Rößler and Noll, 2007, Plate I, 6) are coloured reversely: narrow tracheids are dark and wide tracheids are light (Rößler and Noll, 2007). This is probably caused by different conditions during taphonomic processes.

5.2. Taphonomy

The silicification of trees represents a very complex process, which involves both the filling of pore spaces in the wood (permineralization) and the replacement of the organic cellular tissue with SiO_2 under various conditions (Ballhaus et al., 2012) and its complete understanding and detailed description are over the scope of the present paper. According to Matysová et al. (2010) silicification can take place in four different palaeoenvironments: (1) in fluvial sediments, (2) in fluvial facies with volcanic influence, (3) in lacustrine facies with volcanic influence, and (4) in environments under direct influence of diverse volcanic emplacement events.

In the Krkonoše Piedmont Basin, silicified stems occur in at least four stratigraphic levels, but only one, the Ploužnice Horizon, shows volcanic influence. According to Matysová et al. (2010) this unit can
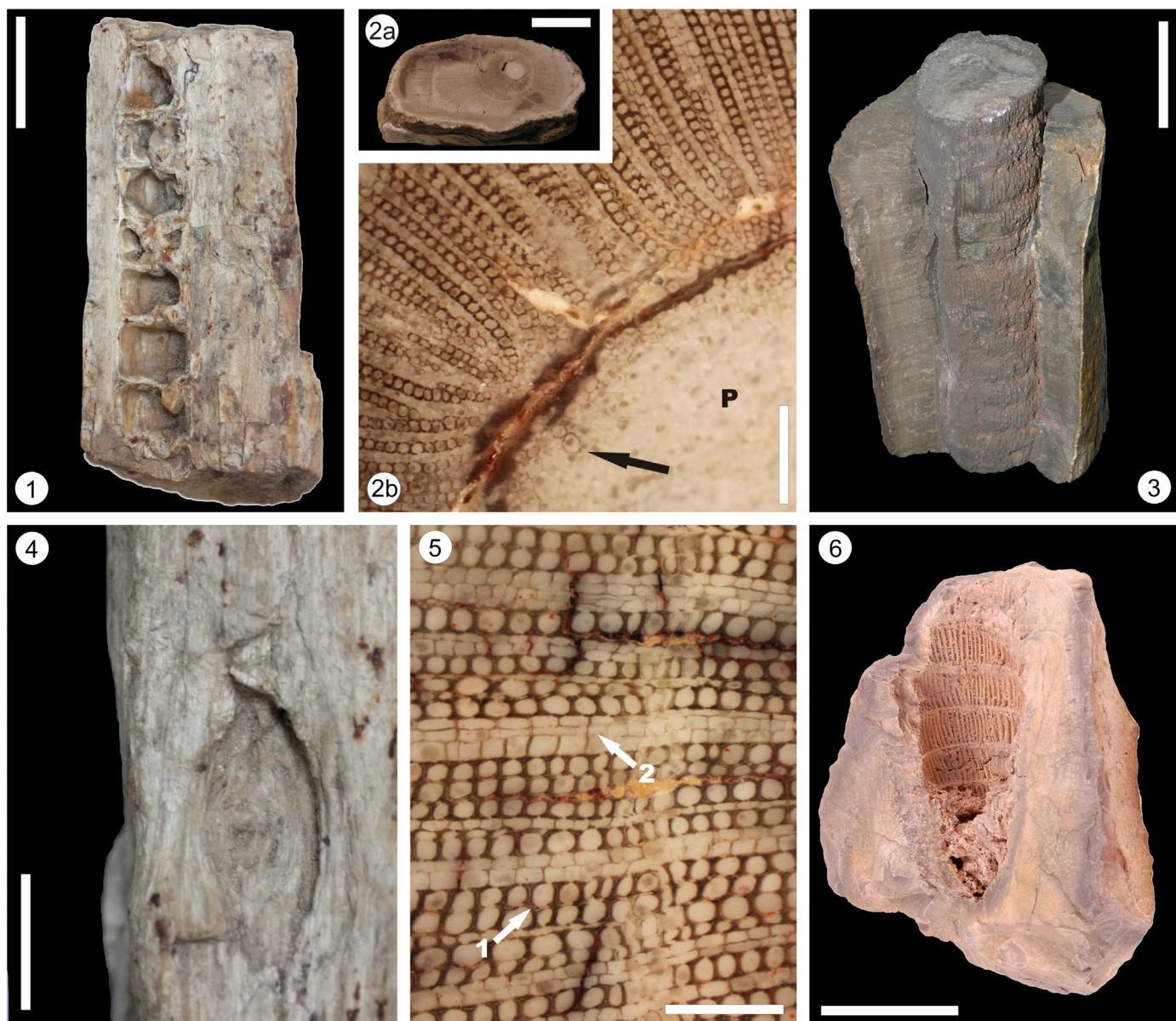
Plate II. *Arthropitys* cf. *bistriata* from the Kladno–Rakovník Basin and the Krkonoše Piedmont Basin.

1. Pith cavity with short internodes and diaphragms at levels of nodes (specimen SVE005/1, Kladno–Rakovník Basin). Scale bar = 30 mm.
2. Small root — general view (a) and detail (b) of its central, solid parenchymatous pith (P), showing parenchyma inside (arrow), and pith periphery without carinal canals but with curved both rays and rows of secondary xylem tracheids, TS (specimen H74692, Krkonoše Piedmont Basin). Scale bars in 2a = 10 mm and in 2b = 0.5 mm.
3. Unusual sample showing both well preserved pith cast and secondary xylem (specimen P1584, Krkonoše Piedmont Basin). Scale bar = 30 mm.
4. Single branch scar as seen on reverse side of the specimen illustrated in Plate II, 1 (specimen SVE005/1, Kladno–Rakovník Basin). Scale bar = 5 mm.
5. Detail of circular-shaped tracheids of secondary xylem (1) and elongated, rectangular parenchyma cells (2) of multiseriate interfascicular rays, TS (specimen H74697, Krkonoše Piedmont Basin). Scale bar = 0.5 mm.
6. Well preserved pith cavity with longitudinal striation of short internodes and transverse diaphragms of a basal tapering portion of the vertical stem (specimen P5657, Krkonoše Piedmont Basin). Scale bar = 50 mm.

TS = transverse section.

be interpreted as a lacustrine environment with influence of volcanism. This horizon contains a much more varied assemblage of silicified stems than the other strata, but the preservation of anatomical detail is often rather poor. The sediments of the Kladno–Rakovník Basin do not contain significant amounts of volcanic material and the fossiliferous sediments are purely lacustrine to fluvial. Silicified stems are known from several units and their anatomy is usually much better preserved than in the specimens from the Krkonoše Piedmont Basin or the Intra Sudetic Basin (Mencl, 2007; Mencl et al., 2009). Finally, the Chemnitz Petrified Forest can be mentioned as comparative example of an environment under direct influence of volcanism. Surprisingly, there is a very high percentage of well-preserved petrified trunks, although there was a direct influence of explosive and therefore destructive volcanic events (Rößler et al., 2012b).

6. Conclusions

Silicified calamitalean stems are reported from two Carboniferous–Permian basins in the Czech Republic.
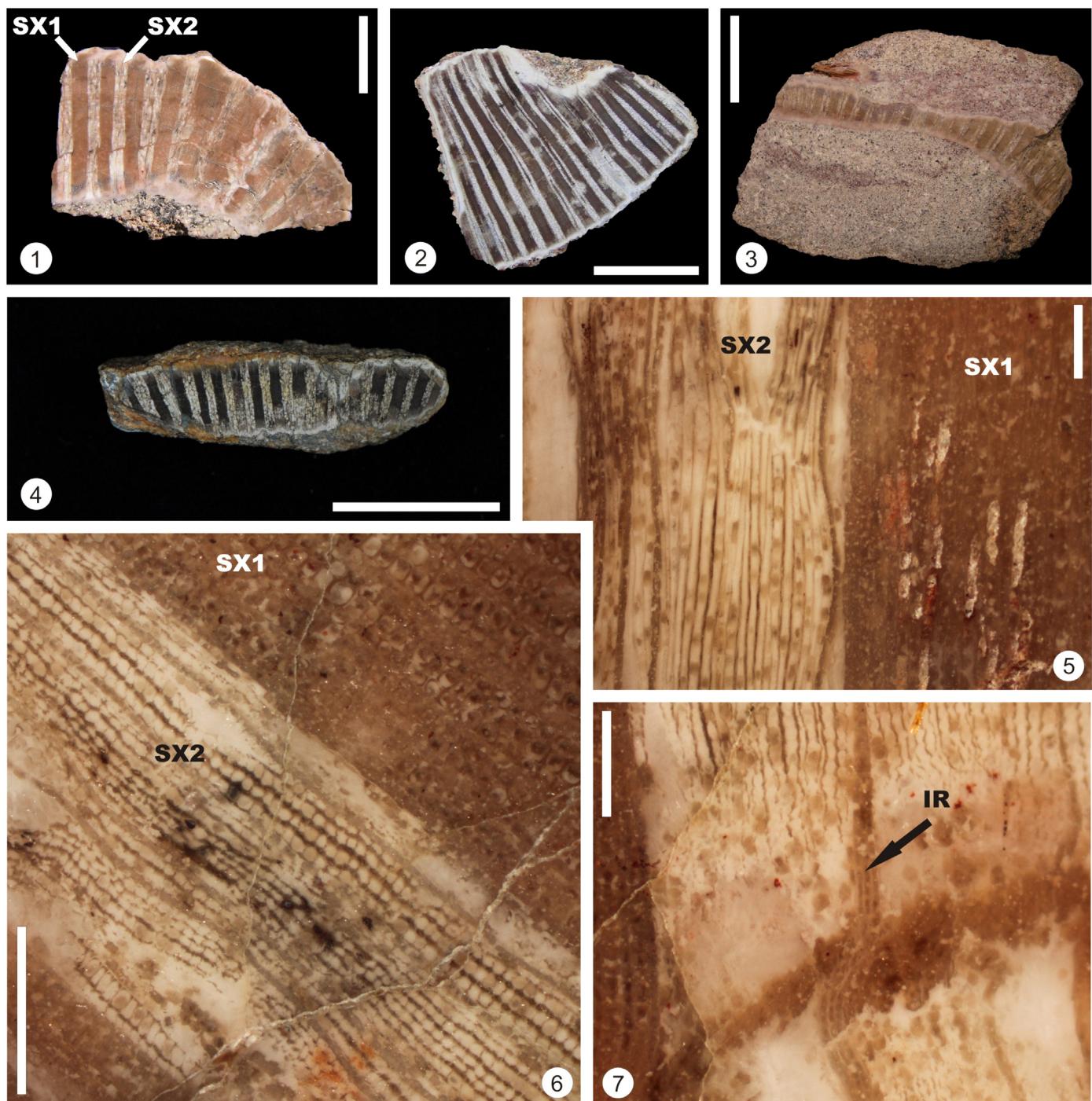
Plate III. *Calamitea striata* from the Krkonoše Piedmont Basin.

1.–4. General view showing the difference in colouration of darker wide (SX1) and lighter narrow (SX2) tracheids, TS (specimens P3173, P2660A, P2660C, K2121). Scale bars in 1 = 10 mm and in 2, 3 and 4 = 20 mm.
5. Detail showing difference between wide (SX1) and narrow (SX2) tracheids, TLS (specimen P3173). Scale bar = 0.25 mm.
6. Detail showing two types of tracheids (SX1, SX2), arranged in slightly deformed rows, TS (specimen P3173). Scale bar = 0.5 mm.
7. Rectangular parenchyma cells of interfascicular ray (IR), TS (specimen P3173). Scale bar = 0.25 mm.

TS = transverse section; TLS = tangential longitudinal section.

In the Krkonoše Piedmont Basin, several hundred specimens have been found, but only few were suitable for anatomical studies. After an evaluation of all available samples we recognise two taxa. *Arthropitys* cf. *bistriata* is very common, whereas *Calamitea striata* is rather rare. The attribution of the former is based on the similarity in parenchyma ratio, the presence of scalariform pitting and interfascicular rays running continuously through the entire wood. The latter was identified on the basis of the two types of tracheids found in the secondary xylem and the small proportion of parenchyma. This type represents only about 1% of all calamitalean stems in the Krkonoše Piedmont Basin, but is also very rare in other coeval fossil forests. Contrary to the "*Dadoxylon*" type of wood, silicified stems of calamitaleans and other "pteridophytes" are in the Krkonoše Piedmont Basin strictly limited to a single stratigraphic unit that contains volcanics. The fossils are usually

fragmented and preserved without branchlets or extraxylary tissues, but are less damaged than "*Dadoxylon*" stems in other stratigraphic levels. They were probably transported by rivers and streams as bedload before they were deposited. Moreover, most of the woody tissue is strongly recrystalised and cell structures are damaged considerably.

In the Kladno–Rakovník Basin, calamitalean stems, although being the second most abundant after the common "*Dadoxylon*" type, are quite rare; other types, such as *Psaronius* or *Medullosa* are very scarce. Stems can mainly be found in two stratigraphic levels, but most of them are found in the Týnec Formation. Both stratigraphic levels are without any volcanic content. The trunks are usually fragmented without branches or extraxylary tissue. They were probably transported and finally embedded in fluvial sediments. Calamitaleans are rarer than "*Dadoxylon*" stems; bigger specimens are not mentioned in literature. The fragmentary nature of the specimens can be related to the nature of the wood that was parenchyma-rich, soft and therefore more prone to destruction. However, we cannot exclude that calamitalean wood remains unidentified in private collections. All samples were found in the field in eluvium. Therefore, the stratigraphic position of the source strata is assumed from the general geological situation.

The present contribution fills a gap in giving the first anatomical description of silicified calamitalean stems from the upper Carboniferous of the Bohemian Massif, which represents a classical area of palaeobotanical interest, well studied both in the past and present, but without a modern systematic overview on fossil wood and petrified stems in general.

Acknowledgements

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Příloha 2

CENOMANIAN ANGIOSPERM WOOD FROM THE BOHEMIAN CRETACEOUS BASIN, CZECH REPUBLIC

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SUMMARY

The first permineralized angiosperm wood from the Cenomanian of the Bohemian Cretaceous Basin (Czech Republic) is described. The wood is diffuse porous, with vessels solitary and in radial multiples of 2–5, perforation plates are exclusively simple, and tyloses abundant. Rays are usually 4–7-seriate and heterocellular, narrower rays are rare. The fossil is designated as *Paraphyllanthoxylon* aff. *utahense* Thayn, Tidwell *et* Stokes. Other occurrences of *Paraphyllanthoxylon* are reviewed and the equivocal botanical affinity of the taxon is discussed.

Key words: *Paraphyllanthoxylon*, permineralized angiosperm wood, Cenomanian, Bohemian Cretaceous Basin, Czech Republic.

INTRODUCTION

Angiosperms dominate modern vegetation with more than 90% of plant diversity. Their fossil evidence goes back to the start of the Cretaceous, but the first record of angiosperm wood is not older than Aptian/Albian (Baas *et al*. 2004). As the major diversification of angiosperms occurred across the Cenomanian-Turonian boundary, any study focusing on this time slice is of particular interest. We describe a fossil angiosperm wood from the Bohemian Cretaceous Basin which encompasses this interval. During most of its existence, the Bohemian Cretaceous Basin, a system of sub-basins filled with deposits of the Cenomanian through the Santonian age (Kvaček *et al*. 2006), was a shallow seaway connecting the Boreal and Tethys realms (Fig. 1A). The lowermost part of the Cenomanian strata, called the Peruc-Korycany Formation, is represented by diverse deposits of fluvial, estuarine, shoreface or off-shore facies and contains fossil fauna (*e.g.*, Fejfar *et al*. 2005) and one of the best preserved and the richest Cenomanian floras in the world (for summary see Kvaček *et al*. 2006). Five different units and sedimentary regimes can be distinguished within the Peruc-Korycany Formation (Uličný *et al*. 1997a, b) at the Pecínov quarry, situated to the west of Prague (Fig. 1B). Here various studies have been conducted on this Formation including sedimentological studies (*e.g.* Uličný *et al*. 1997a), stable isotope analyses (*e.g.* Nguyen Tu *et al*. 2002), a charcoal analysis (*e.g.* Falcon-Lang *et al*. 2001) and systematic studies of plant mesofossils (*e.g.* Eklund & Kvaček 1998) and palynomorphs (*e.g.* Svobodová *et al*. 1998). Within the ebb-tidal

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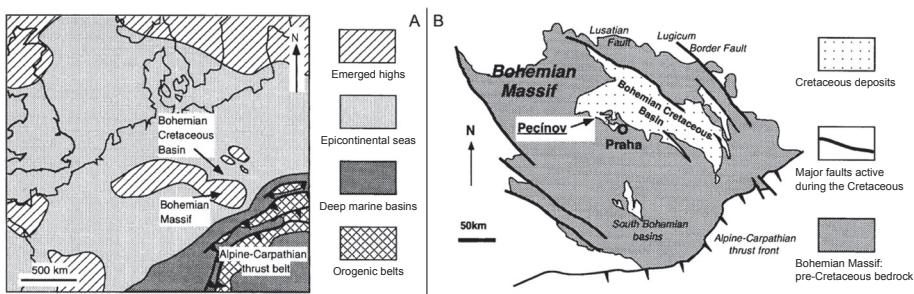
Figure 1. Palaeogeographical position of the Bohemian Cretaceous Basin in Central Europe during the early Turonian peak flooding (A) and the Bohemian Cretaceous Basin in the tectonic framework of the Bohemian Massif with the position of the Pecínov quarry (B) (from Uličný *et al*. 1997a).

delta deposits of Unit 5A (Uličný *et al*. 1997b) sandstones have preserved pseudotrunks of the fern *Tempskya*, rare permineralized gymnosperm wood, and charcoalified wood fragments (identified as *Cupressinoxylon* by Falcon-Lang *et al*. 2001). Recently several silicified wood specimens have been found (by Z. Dvořák) and they provide the first evidence of permineralized angiosperm wood from this age in the Bohemian Cretaceous Basin.

MATERIAL AND METHODS

Silicified wood (two specimens UK 102/04 & UK 103/04) was thin-sectioned in compliance with the standard techniques (Hass & Rowe 1999) and studied using compound light microscopy. The anatomical description is in accordance with the IAWA Hardwood List (IAWA Committee 1989). Remains of the original specimens and thin sections described herein are housed in the Chlupáč Museum of Earth History at the Faculty of Science of the Charles University in Prague.
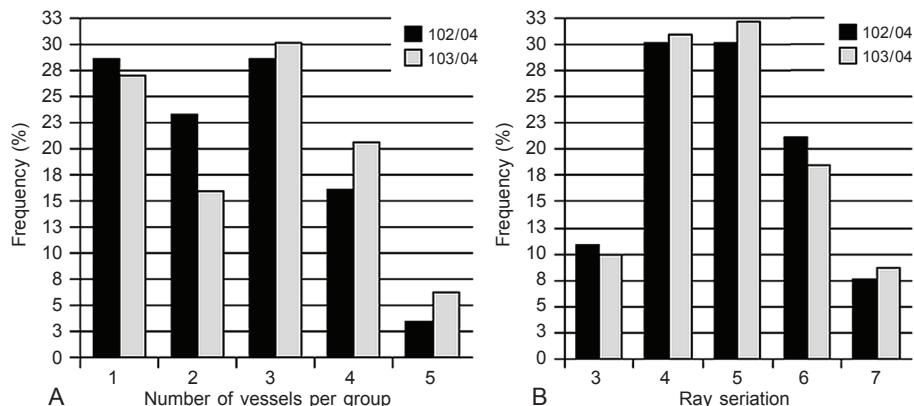
Figure 2. Frequency of solitary vessels and vessels in radial multiples of 2, 3, 4, and 5 (A) and ray widths (B) for samples 102/04 and 103/04.
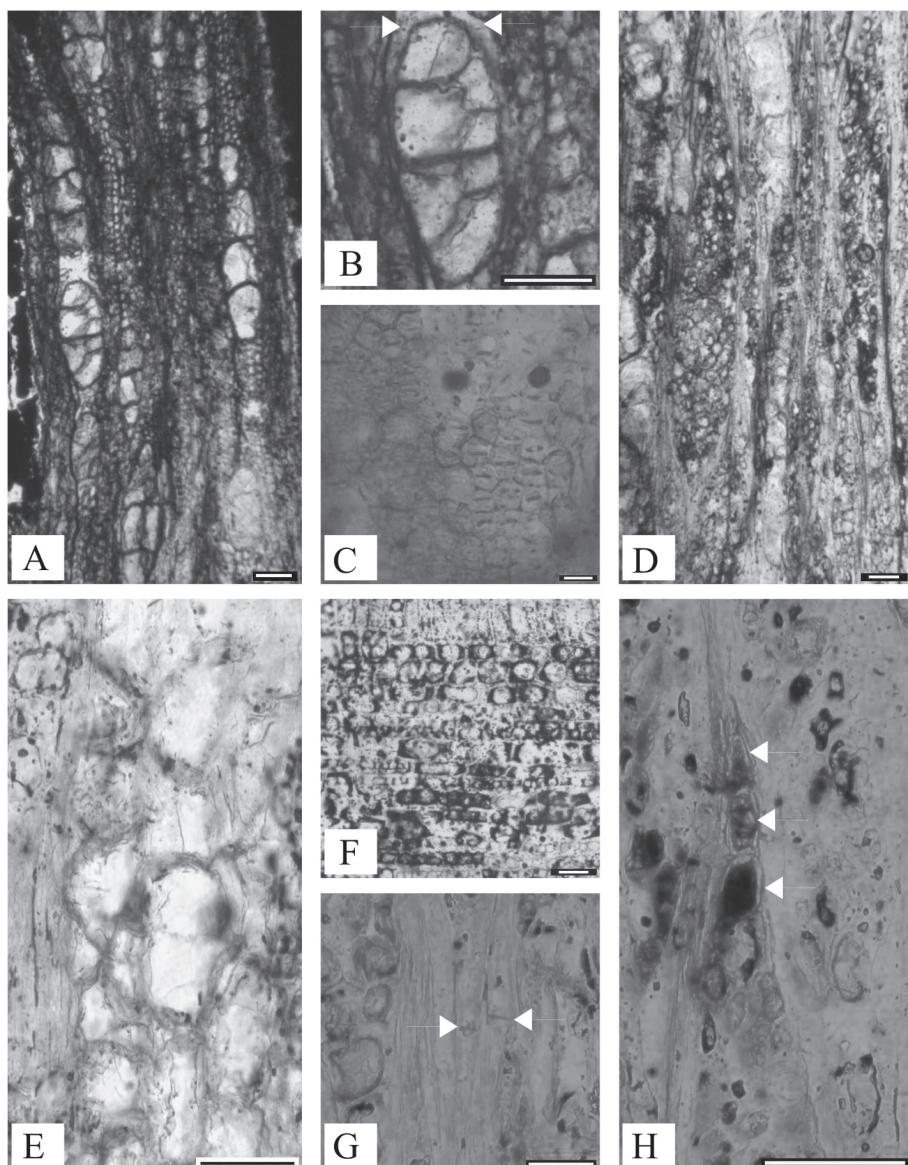
Figure 3. *Paraphyllanthoxylon* aff. *utahense* (A–H: No 102/04). – A: Diffuse porous wood, TS. – B: Vessels in radial multiples with tyloses and scanty paratracheal parenchyma (arrows), TS. – C: Alternate intervessel pits, TLS. – D: Moderately wide rays, TLS. – E: Tyloses within vessels, RLS. – F: Heterocellular rays, RLS. – G: Septate fibres (arrows), TLS. – H: Detail of ray with three marginal rows (arrows), TLS. — Scale bars = 100 μm in A, B, D, E, F, H; 10 μm in C, G.

Table 1. Descriptive statistics of tangential vessel diameter.

	Sample	
	102/04	103/04
N	40	40
Mean (μm)	95	84
Median (μm)	95	81
Standard deviation (μm)	10	16
Minimum (μm)	77	52
Maximum (μm)	122	115
Coefficient of variation (%)	11	19

RESULTS

Family inc.
Paraphyllanthoxylon Bailey
Paraphyllanthoxylon aff. ***utahense*** Thayn, Tidwell *et* Stokes — Fig. 2, 3; Table 1

Material: UK 102/04, UK 103/04
Locality: the Pecínov Quarry
Stratigraphic horizon: Unit 5a of the Bohemian Cretaceous Basin, Czech Republic
Age: Cenomanian

Macroscopic description: Two silicified pieces of fossil wood (UK 102/04 dimensions: 16 × 10.5 × 5 cm, UK 103/04 dimensions: 31 × 7 × 7 cm), beige-brown-rust-coloured, interpreted as samples of trunk.

Microscopic description: *Growth rings:* absent. — *Wood:* diffuse-porous. — *Vessels:* 16–25 per square mm, solitary (29%) and in radial multiples of 2–5 (generally 2–4; Fig. 2A; 3A, B); tangential diameter 52–122 μm (Table 1); outline of solitary vessels round to oval; vessel walls thin; perforation plates exclusively simple with oblique end walls; tyloses abundant (Fig. 3B, E); intervessel pits alternate and polygonal in shape, about 10 μm across (Fig. 3C). — *Rays:* heterocellular up to 7 cells wide (100 μm), commonly 4–6-seriate (Fig. 2B; 3D, H) and 560–990 μm high, uniseriate rays very rare, body of multiseriate rays composed of procumbent and upright cells (Fig. 3F); marginal rows 1–4 of upright cells (Fig. 3H arrows); no crystalliferous elements observed; pits between vessels and rays not observed. — *Axial parenchyma:* scanty paratracheal (Fig. 3B arrows). — *Fibres:* pits not seen, predominantly non-septate, but sometimes septate (Fig. 3G arrows); medium-thick walls.

DISCUSSION

Both samples lack well-defined growth rings, and have vessels solitary and in radial multiples with simple perforation plates, abundant tyloses and alternate intervascular pitting, heterocellular rays up to 7 cells wide, scanty paratracheal axial parenchyma and

septate fibres. Unfortunately, no vessel-ray pitting was observed. This combination of features is characteristic of the fossil morphogenus *Paraphyllanthoxylon*.

Summary of *Paraphyllanthoxylon* species

The morphogenus *Paraphyllanthoxylon* was established by Bailey (1924) from the Cenomanian of Arizona, USA, with the type species *P. arizonense*. In the following decades, many other species were established to accommodate specimens of various ages described from many parts of the world: *P. idahoense* (Spackman 1948) from the Cretaceous of Idaho, USA; *P. capense* (Mädel 1962) from the Upper Cretaceous of South Africa; *P. keriense* (Dayal 1968) from the Tertiary of India; *P. yvardi* (Koeniguer 1970) from the Miocene of France; *P. alabamense* (Cahoon 1972) from the Cenomanian of Alabama, USA; *P. teldense* (Privé 1975) from the Oligocene of France; *P. lignitum* (Daniou & Dupéron-Laudoueneix 1978) from the Eocene of France; *P. romanicum* (Petrescu *et al.* 1978) from the Upper Cretaceous of Romania; *P. utahense* (Thayn *et al.* 1983) from the Lower Cretaceous of Utah, USA; *P. kobense* (Suzuki 1984) from the Miocene of Japan; *P. palaeoemblica* (Prakash *et al.* 1986) from the Tertiary of India; *P. illinoisense* (Wheeler *et al.* 1987) from the Upper Cretaceous of Illinois, USA; *P. abbottii* (Wheeler 1991) from the Paleocene of Texas, USA; *P. marylandense* (Herendeen 1991) from the Lower/Upper Cretaceous of Maryland, USA; *P. anasazi* (Wheeler *et al.* 1995) from the Upper Cretaceous of New Mexico, USA; *P. bacense* (Iamandei & Iamandei 2000) from the Upper Cretaceous/Early Tertiary of Romania; *P. cenomaniana* and *P. obiraense* (Takahashi & Suzuki 2003) from the Upper Cretaceous of Japan; *P. mennegae* and *P. coloradensis* (Martínez-Cabrera *et al.* 2006) from the Miocene of Mexico.

Mädel (1962) transferred several species previously assigned to different genera to *Paraphyllanthoxylon*: *P. pseudohobashiraishi* (Ogura) Mädel from the Palaeogene of Japan (*Phyllanthinium pseudohobashiraishi* - basionym by Ogura 1932 and another specimen by Watari 1943), *P. tertiarum* (Ramanujam) Mädel from the Tertiary of India (*Glochidioxylon tertiarum* by Ramanujam 1956), *P. sahnii* (Prakash) Mädel from the Tertiary of India (*Glochidioxylon sahnii* by Prakash 1959) and *P. pfefferi* (Platen) Mädel from the Neogene of California, USA (*Carpinoxylon pfefferi* by Platen 1908). Iamandei and Iamandei (2000) also proposed a new combination, *Paraphyllanthoxylon bangalamodense* (Navale) Iamandei & Iamandei, based on *Phyllanthinium bangalamodense* described by Navale (1962) from the Mio-Pliocene of India. Conversely Thayn and Tidwell (1984) removed a species of *Paraphyllanthoxylon*, *P. keriense* to the morphogenus *Bridelioxylon* Ramanujam, to make a new combination *Bridelioxylon keriense* (Dayal) Thayn & Tidwell. Finally, Prakash *et al.* (1986) proposed a very narrow concept of *Paraphyllanthoxylon*, applicable for fossil woods of *Phyllanthus* only. This is, however, in contradiction to what a morphogenus implies and the original diagnosis of Bailey.

Other authors have referred their specimens to described species of *Paraphyllanthoxylon*: Oakley and Falcon-Lang (2009) described charcoalified material from Pecínov as *P. marylandense*, Wheeler and Lehman (2000) designated their samples from the Upper Cretaceous of Texas, USA as cf. *P. anazasii* and Meijer (2000) described a fossil

wood from the Upper Cretaceous of Belgium as *P.* cf. *marylandense*. Some simply noted the resemblance to *Paraphyllanthoxylon* at the generic level only, *e.g.* Cevallos-Ferriz and Weber (1992) from the Upper Cretaceous of Mexico or Falcon-Lang *et al.* (2001) from the Cenomanian of the Czech Republic.

Comparison with the described species

There are differences between the species of *Paraphyllanthoxylon* in mean tangential diameter of the vessels (range from 65 μm in *P. teldense* to 175 μm in *P. arizonense* or even 234 μm in specimens of *P. abbottii*), the number of vessels per radial multiple (predominantly solitary or rarely in groups of two in *P. bacense* up to 10 in *P. pfefferi* and 11 in *P. lignitum*) and maximum ray width (2- or rarely 3-seriate in *P. bacense* up to 9-seriate in *P. palaeoemblica*).

It is hard to attribute our fossil woods to existing species of *Paraphyllanthoxylon* because of great variability and overlapping of the features. We see similarities in mean tangential diameter with *P. marylandense*, *P. anasazi*, *P. pfefferi*, *P. utahense*, *P. obiraense*, *P. pseudohobashiraishi*, *P. idahoense* and perhaps with *P. palaeoemblica* if the mean can roughly be estimated from the range given by Prakash *et al.* (1986). On the other hand, the number of vessels per radial multiple and ray width of *P. teldense*, *P. arizonense* and *P. sahnii* are the most similar. These three species belong to the "species group B" (*sensu* Herendeen 1991) and cannot therefore be compared with our woods from the "species group A" (see below). In addition, *P. arizonense* has significantly wider vessels (mean tangential diameter of 175 μm according to Wheeler 1991; Wheeler & Lehman 2009, this issue) and *P. teldense* sometimes possesses scalariform perforation plates. Therefore, we consider *P. utahense* as the most similar to our woods although not completely identical; *P. utahense* has slightly narrower rays with more uniseriate marginal rows. We refer to these Czech fossil woods as *Paraphyllanthoxylon* aff. *utahense* Thayn, Tidwell *et* Stokes.

The differences in ray dimensions and vessel diameters between our samples and the published species of *Paraphyllanthoxylon* as well as the differences between the species can also be explained by the generally very variable structure of wood which depends on local environmental and climatic parameters (*e.g.*, Schweingruber 1993; Preston *et al.* 2006) or on the relative position in the tree (Desch 1932; Panshin & De Zeeuw 1980; Carlquist 1988; Leal *et al.* 2007; Gryc *et al.* 2008).

The abundance of tyloses in *Paraphyllanthoxylon,* as well as their more general significance, has already been discussed by Wheeler (1991: 661–662). We observed tyloses in all sections. The tyloses are formed not only in a standing living tree but also in the sapwood taken from the living tree (Murmanis 1975). Formation of tyloses depends on the time of taking the samples and temperature in the laboratory. In the samples of the red oak (*Quercus rubra* L.), the tyloses formed under optimal conditions (20 °C) in a very short time (about two hours) in the samples taken from the outer parts of the trunk during the growing period. Jurášek (1956, 1958) confirmed that tyloses occurred in the woods without 'true coloured' heartwood, *i.e.*, sapwoods (*Fagus sylvatica* L.). He observed that the formation of tyloses occurred under specific physical conditions:

slow desiccation and temperatures between 15–40 °C (optimal 25 °C). Sufficient diameter (bigger than 10 μm) of the pits between the ray parenchyma and vessel is also necessary for tyloses formation (Jurášek 1956) and this suggests that vessel-ray parenchyma pits in these fossils were big enough. However, it is hard to say whether our fossil wood represents heartwood or sapwood.

Botanical affinities

The botanical affinities of *Paraphyllanthoxylon* remain elusive and continue to be discussed (*e.g.* Martínez-Cabrera *et al.* 2006). When Bailey (1924) first described this morphogenus he noted that there was no single feature that allowed referring it to a particular family. He noted that it had a combination of features seen in the extant euphorbiaceous genera *Bridelia* and *Phyllanthus* of the subfamily Phyllanthoideae (Bailey 1924). Mädel (1962) in her detailed overview of the modern and fossil woods of the Euphorbiaceae placed *Paraphyllanthoxylon* in the *Glochidion* group together with several modern genera from the subfamily Phyllanthoideae and *Acalypha*. Other authors have noted that *Paraphyllanthoxylon* has features found in more than one family, *e.g.* Thayn and Tidwell (1984: Table 4) indicated fourteen families with features of *Paraphyllanthoxylon* and even Mädel (1962: 288) noted that there were six other families with wood sharing anatomical similarities. Wheeler *et al.* (1987) and Herendeen (1991) suggest there are two main groups within *Paraphyllanthoxylon*: 1) species group A characterized by few and short marginal rows of upright cells in the multiseriate rays and rare uniseriate rays and thus resembling Anacardiaceae, Burseraceae, Elaeocarpaceae, Lauraceae and Verbenaceae and 2) species group B with long marginal rows and numerous uniseriate rays resembling Euphorbiaceae, Flacourtiaceae (now Salicaceae), Simaroubaceae, Ulmaceae and Violaceae.

According to Westra and Koek-Noorman (2004) Euphorbiaceae *s.l.* comprise more than 300 woody genera spread mostly in (sub)tropical areas and it is beyond the scope of this study to cover this diversity. If we first compare our fossil woods with the Phyllanthoideae, using the most recent published data (Mennega 1987; Martínez-Cabrera *et al.* 2006), we can say the general pattern is quite similar to our woods except for 'markedly heterocellular' rays in living representatives (Wheeler *et al.* 1987). The Czech fossil woods with short marginal rows and rare uniseriate rays belong to species group A *sensu* Herendeen (1991). It is tempting to suggest these woods are related to the lauraceous leaves, inflorescences and flowers present at the Pecínov quarry (*e.g.*, Uličný *et al.* 1997b; Eklund & Kvaček 1998). Moreover, numerous pieces of charcoalified wood were described from Pecínov and compared to *P. marylandense* (Falcon-Lang *et al.* 2001; Oakley & Falcon-Lang 2009). Herendeen (1991) demonstrated the affinity of *P. marylandense* to Lauraceae based on the similarity between its juvenile wood (diameter of the stem was 3.6 mm with maximum 1 mm wide zone of juvenile wood) and wood of the inflorescence axes of *Mauldinia mirabilis* (0.75–1.25 mm in diameter with 0.2 mm wide zone of xylem). Such juvenile wood can show some 'primitive' features (P. Baas pers. comm.). It can be only very approximately compared with 'normal' mature trunk wood that standard photographic atlases and internet databases such as

InsideWood (2004–onwards) show. Wood of Lauraceae, both extant (*e.g.*, Tupper 1927; Richter in Metcalfe 1987) and fossil (Dupéron-Laudoueneix & Dupéron 2005; Dupéron *et al*. 2008), often has oil or mucilage cells (idioblasts); these are however absent in our woods. However, some extant lauraceous woods have no secretory cells as emphasized by Herendeen (1991), but we can also speculate that our wood belongs to the 'stem group' of Lauraceae, which could lack this feature (J.A. Doyle pers. comm.).

Similarity of *Paraphyllanthoxylon* with other morphogenera

This paper presents the first description of fossil permineralized angiosperm wood from the Bohemian Cretaceous Basin and the Cretaceous of the Czech Republic as a whole and so adds to the picture of the Peruc Korycany flora and Cretaceous vegetation of Europe. Prakash *et al*. (1974) described some angiosperm wood from the Lipnice Formation (South Bohemian Basins, Czech Republic), at that time considered to be Oligocene. The wood they described as *Canarioxylon* is similar to the *Paraphyllanthoxylon* described herein. Moreover, the generic diagnosis of *Canarioxylon* (Prakash *et al*. 1974: 112) fits perfectly the diagnosis of *Paraphyllanthoxylon* and there was no need to create the new morphogenus *Canarioxylon*. J. Hladil provided us recently with additional material from South Bohemia (SPOL-R1 and SPOL-R2) and these samples also are similar to the *Paraphyllanthoxylon* described in this paper. Malkovský (1995) based on analogy in lithology considers that the Lipnice Formation is not Tertiary but Late Cretaceous in age. We suggest that all material from South Bohemia belongs to the Upper Cretaceous. This would logically explain the overall warm character of the flora. It is worth noticing that Wheeler (1991: 662) came to the similar conclusion with the diagnoses of *Burseroxylon* Prakash & Tripathi and *Paraphyllanthoxylon*.

CONCLUSIONS

Paraphyllanthoxylon, more exactly *P. utahense*, the species our woods most closely resembles is important in being one of the two oldest types of angiosperm wood and has simple perforation plates (Baas *et al*. 2004). As already emphasized by Wheeler (1991), Martínez-Cabrera *et al*. (2006) and others, this widely defined morphogenus has characteristics seen in several families which makes any systematic comparison difficult. In the case of the Czech Cenomanian wood, we are unfortunately unable to find any exact living relative at the specific, generic or even familial level.

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Příloha 3

Early Miocene conifer macrofossils from the Most Basin (Czech Republic)

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With 5 figures and 1 table

Abstract: A systematic overview of the conifer macrofossils (leaves, cones, seeds and wood) from the Lower Miocene of the Most Basin (Czech Republic) is presented and nine natural units (botanical species) are defined, belonging to three species of *Pinus* L. and one species of *Pseudolarix* Gordon, *Quasisequoia* Srinivasan & Friis emend. Kunzmann, *Taxodium* Richard, *Glyptostrobus* Endlicher, *Tetraclinis* Masters and *Cupressospermum* Mai emend. Kunzmann. Seeds of the latter taxon have been firstly described from the Most Basin. Different organs are rarely directly attached (pollen/seeds cones attached to a twig, a cone scale with seeds), but rather found in direct (close) or indirect (distant) association. The conifers are also characterized in environmental context as elements of several different vegetation types.

Key words: conifers, macrofossils, morphology, xylotomy, holistic approach, palaeoenvironment, Early Miocene, Most Basin, Czech Republic.

1. Introduction

The Most Basin (formerly the Northern-Bohemian Basin) is one of the most famous Tertiary palaeobotanical sites in the Czech Republic that has been continuously studied since the first half of the 19th century (e.g., Sternberg 1825). Sediments of the Most Basin have yielded over 160 various species of plant macrofossils (e.g., Kvaček et al. 2004a,b; Kvaček & Teodoridis 2007) and more than 100 species of pollen and spores (e.g., Konzalová 1976). Occurrences of conifers, due to their great quantity as well as their eye-catching, have been well collected and documented from different localities (Engelhardt 1876a, b; Menzel 1901; Brabenec 1909; Bůžek & Holý 1964; Kvaček 1976, 1989; Kvaček & Hurník 2000; Sakala 2000 etc.). The present

study tries to summarize and evaluate existing data according to carpological, leaf morphological and xylotomic aspects following a holistic approach. It means to associate detached leaves and reproductive organs (cones and seeds) with fossil wood in order to reconstruct the whole plant as complete as possible (as it really looked like and lived in the area of the Most Basin in Early Miocene). The principles of this holistic approach, known also as a "Whole-Plant" concept, have been demonstrated by Kvaček (2004) for leaves and reproductive organs or by Sakala (2004) for association of wood with other organs. Recently, Martina Dolezych in her PhD Thesis (Dolezych 2005) and related papers (Dolezych et al. 2001; Dolezych & van der Burgh 2004; Dolezych in Junge et al. 2005; Dolezych & Schcneider 2006, 2007) sheds new light on relation

between different wood morphotaxa and their botanical affinities. The aim of the xylotomical part of the present paper is to re-evaluate the wood of Cupressaceae s.l. from the Most Basin in perspective of these new studies.

2. Geology, stratigraphy and dating of the Most Basin

The Most Basin is one of the five sedimentary basins of the Eger Graben and represents the largest freshwater sedimentary body of the Cenozoic in the Bohemian Massif. The total thickness of the younger part of the basin fill (i.e., Most Formation sensu DOMÁCÍ 1977) is about 500 m in the center (KVAČEK et al. 2004a). The base of the Most Formation has been estimated at the Oligocene/Miocene boundary (BUCHA et al. 1987; LOTSCH et al. 1994; TEODORIDIS 2002; SUHR 2003). The volcanic rocks underlying the Most Formation belong to the Střezov Formation sensu DOMÁCÍ (1977), which consist of mostly deeply weathered lava flows and associated volcanogenic deposits. From the basin periphery, rivers and streams transported pebble, sand, silt and clay material into the basin. Deposits of the streams formed a relatively large belt of fluvial sandy facies ("Hlavačov Gravel and Sand" sensu VÁNĚ 1985) heading from central Bohemia and entering the basin near Žatec, then leaving the basin probably near Chomutov (RAJCHL & ULIČNÝ 2005; TEODORIDIS 2004) or across the České středohoří Mts (SUHR 2003). These sediments formed the Duchcov Member of the Most Formation (DOMÁCÍ 1977), i.e. Underlying Formation sensu HURNÍK & MAREK (1962). They include well-known vertebrate localities, namely at Skyřice, Ahníkov and Tuchořice, all dated into the zone MN 3 (FEJFAR 1989). During the Early Miocene, increasing subsidence of the basin caused spreading of flatland with the formation of swamps and shallow lakes (e.g., RAJCHL 2006). In most parts of the basin, deposits of this period belong to the Holešice Member of the Most Formation (DOMÁCÍ 1977). At first, only occasional flooding inundated wetlands. These transferred into periodically or steadily inundated local mires, where plant biomass accumulated as peat. This type of landscape stabilized in the basin during the formation of the Main Coal Seam. During flooding events the fluvial facies spread over large areas into the basin forming clayey-sandy layers in the peat. In the area of the larger vicinity of Žatec, where most streams discharged, sandy deposits prevailed due to lowering of the river gradient (cf. RAJCHL & ULIČNÝ 2005), so that the conditions for peat formation were only limited and short-termed (known as "Žatec Delta" facies). Later, a partial stream reached the environs of Bílina, where a delta body originated (e.g., MACH 1997; RAJCHL et al. in press). As already stated above, these deposits containing lignite seams and equivalent sandy-clayey delta bodies have been included into the Holešice Member (DOMÁCÍ 1977). Generally, the above-mentioned sandy-clayey deposits, i.e. Lower Sandy-Clayey Beds with Basal Coal Seam, Lower Interseams Beds, Upper Interseam Beds sensu HURNÍK & MAREK (1962), divided the Main Coal Seam into the Lower Seam Beds, Middle Seam Beds and Upper Seam Beds sensu HURNÍK & MAREK (1962). The clay/claystone facies (Overlying Formation sensu HURNÍK & MAREK 1962) spread over the mire and buried the peat layer. These mighty strata have been included into the Libkovice Member (DOMÁCÍ 1977). In the Bílina area, the base of this member is built of the Břešťany Clay. While the Bílina Delta ceased to exist, several small streams entered the basin from the north (e.g., at Jezeří) and some others existed at Ústí nad Labem and Žatec. Northern streams transported less extensive sands but influenced the character of clay layers deposited in the lake by bringing traces of mica. Later the lake extended probably well beyond today's limits of the basin. In the area of the "Žatec Delta", the Libkovice Member is developed partly in the sandy-clayey facies, e.g., at the locality Přívlaky (TEODORIDIS 2006). At about 17-18 Ma (BUCHA et al. 1987; MALKOVSKÝ 1995), the lake was already almost filled and shallow swamp and mire conditions reappeared in the environs of Lom in the central part of the basin. This uppermost part of the Most Formation is defined as the Lom Member sensu DOMÁCÍ (1977). It represents an incomplete denudation relict of limited extent and contains the Lom Seam.

3. Material and methods

The fossil leaf and carpological material studied here has been collected at different times and by various people. The first critical revision of leaf and cone material from the Most Formation was published by MENZEL (1901). Additional material was collected during a previous fieldwork in sixties and seventies of the last century, by Č. BŮŽEK and F. HOLÝ from the opencast mines of J. Šverma, J. Fučík, Bílina and Maxim Gorkij and from the cores: Břežánky (B 1, B 4), Droužkovice (Do 201, Do 206, Do 210, Do 211, Do 215), Chomutov (Co 199, Co 201, Co 210, Co 215, Co 225, Co 228), Chotěbudice (Cht 8), Havráň (Hň
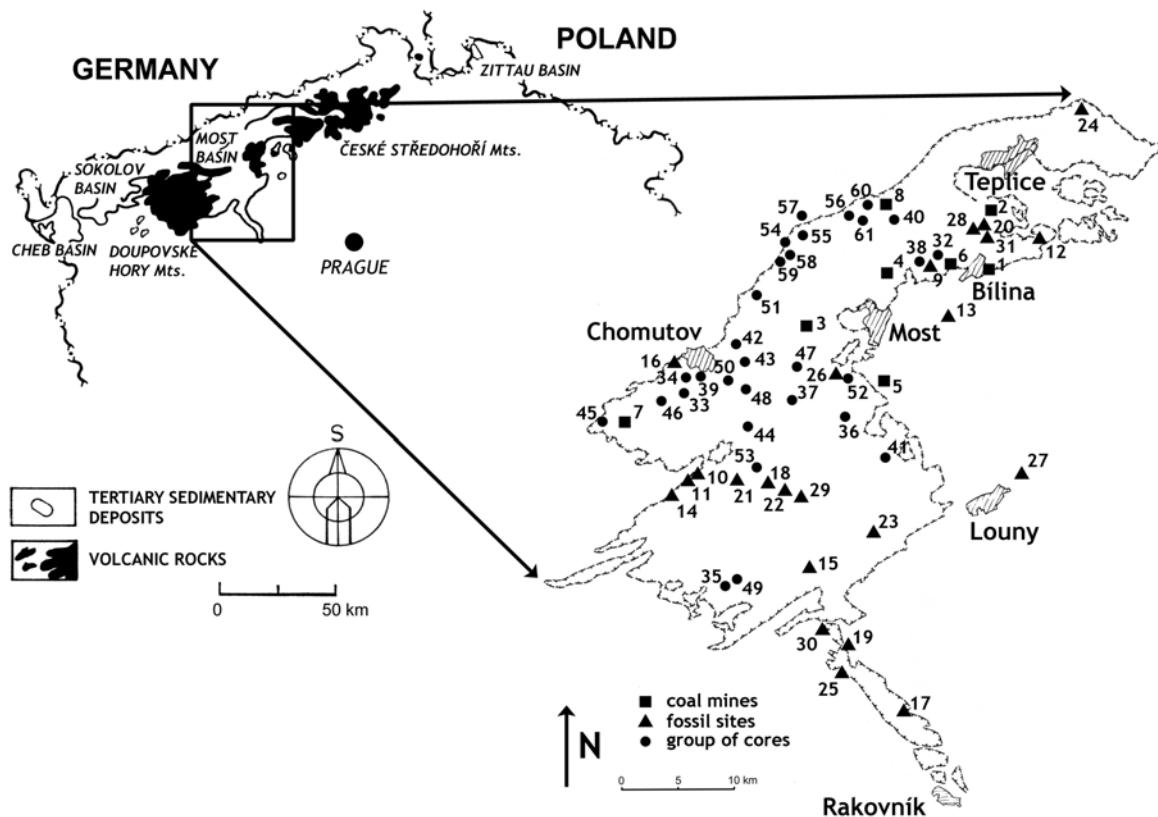
Fig. 1. Location of the fossil plant material studied from coal mines, fossil sites and cores in the area of the Most Basin and the "Hlavačov Gravel and Sand". – i.e., 1. Bílina Mine, 2. J. Fučík Mine, 3. J. Šverma Mine, 4. Ležáky Mine, 5. Marianna Mine, 6. Maxim Gorkij Mine, 7. Nástup-Tušimice Mine, 8. S. K Neumann Mine, 9. Břešťany, Břežánky, 10. Čermníky, 11. Chotěnice, 12. Chuděřice, 13. Dobrčice, 14. Dolany, 15. Holedeč, 16. Hradiště near Černovice, 17. Nesuchyně, 18. Přívlaky, 19. Sádek, 20. Straky, 21. Stranná, 22. Stroupeč, 23. Tuchořice, 24. Varvažova near Chlumec, 25. Velká Černoc, 26. Vršany, 27. Vršovice, 28. Zabrušany, 29. Záhoří near Žatec, 30. Želeč, 31. Želénky, 32. Břežánky (cores: B 1 and B 4), 33. Droužkovice (cores: Do 201, Do 206, Do 210, Do 211 and Do 215), 34. Chomutov (cores: Co 199, Co 201, Co 210, Co 215, Co 225 and Co 228), 35. Chotěbudice (core Cht 8), 36. Havráň (cores: Hň 35 and Hň 36), 37. Hošnice (core Hš 4), 38. Jenišův Újezd near Bílina (core Jú 224), 39. Kralupy near Chomutov (core Kr 11), 40. Libkovice (cores: Lb 77 and P 542), 41. Moravěves (cores: Ma 6 and Ma 8), 42. Otvice (cores: Ot 27 and Ot 36), 43. Pesvice (cores: Pe 18, Pe 19 and Pe 21), 44. Přečáply (core Pč 4), 45. Prunéřov (cores: Pn 130 and Pn 138), 46. Spořice (core Sp 95), 47. Strupčice (cores: Sr 39, Sr 40 and Sr 53), 48. Škrle (core Šk 3), 49. Široké Třebčice (core Štb 43), 50. Údlice (cores: Úd 80 and Úd 81), 51. Vysoká Pec (cores: VP 14, VP 15 and VP 16), 52. Vršany (cores: Vr 20 and Vr 22), 53. Vysočany (core Vy 1), 54. Černice (core CN 54), 55. Horní Jiřetín (core HJi 142), 56. Horní Litvínov (core LiH 13), 57. Janov (core Ja 28), 58. Jezeří (cores: JZ 42, JZ 44, JZ 47 and PVJK 234), 59. Kundratice (cores: KU 108, KU 114, KU 115, KU 116 and KU 127), 60. Lom (core LOM 16), 61. Mariánské Radčice (cores: MR 58 and MR 59).

35, Hň 36), Hošnice (Hň 4), Jenišův Újezd near Bílina (Jú 224), Kralupy near Chomutov (Kr 11), Libkovice (Lb 77, P 542), Moravěves (Ma 6, Ma 8), Otvice (Ot 27, Ot 36), Pesvice (Pe 18, Pe 19, Pe 21), Přečáply (Pč 4), Prunéřov (Pn 130, Pn 138), Spořice (Sp 95), Strupčice (Sr 39, Sr 40, Sr 53), Škrle (Šk 3), Široké Třebčice (Štb 43), Údlice (Úd 80, Úd 81), Vysoká Pec (VP 14, VP 15, VP 16), Vršany (Vr 20, Vr 22), Vysočany (Vy 1), Chuděřice (dug pit) – partly published in Bůžek & Holý (1964). The other studied leaf, carpological and xylotomic samples come from elsewhere, i.e. Břešťany and Břežánky – see Unger (1841-1847, 1852, 1861, 1864, 1866), Ettingshausen (1866, 1868, 1869),

Čermníky (Bůžek 1971), Chotěnice (Bůžek 1971), Chuděřice, Dobrčice (Kvaček & Hurník 2000), Dolany (Bůžek 1971), Holedeč (Brabenec 1904; Teodoridis 2002), Hradiště near Černovice (Engelhardt 1877), Nesuchyně (Němejc 1949; Teodoridis 2002), Přívlaky (Teodoridis 2006), Sádek (Teodoridis 2002), Straky (Kvaček & Hurník 2000), Stranná, Stroupeč (Konrádová 1959), Tuchořice (Kvaček & Bůžek 1982), Varvažova near Chlumec, Velká Černoc (Teodoridis 2002), Vršany (Kvaček & Hurník 2000), Vršovice (Velenovský 1881, Kvaček & Hurník 2000), Zabrušany (Kvaček & Hurník 2000), Záhoří near Žatec (Teodoridis 2003), Želeč

Hurník and Marek 1962			Domácí 1977		age
P R O D U C T I V E	Overlying Fm.		M O S T	Lom Mb. **a1**	Early
				Libkovice Mb.	
				a2	
S E A M	Upper Seam Beds **b**		F O R M A T I O N	Holešice Mb.	Miocene
	Upper Interseam Beds **c**				
S E R I E S	Middle Seam Beds **d**				
	Lower Interseam Beds **e**				
	Lower Seam Beds **f**				
	Lower Sandy-Clayey Beds with Basal Coal Seam **g**				
	Underlying Fm.			Duchcov Mb. **h**	
Volcano-detritic Series			Střezov Fm.		Oligocene
Basal Series			Staré sedlo Fm.		Eocene

Fig. 2. Summary of the stratigraphical classification of the Most Basin sediments (modified to KVAČEK & HURNÍK 2000).

(TEODORIDIS 2002), Želénky (KVAČEK & HURNÍK 2000), from other cores, i. e., Černice (CN 54), Horní Jiřetín (HJi 142), Horní Litvínov (LiH 13), Janov (Ja 28), Jezeří (JZ 42, JZ 44, JZ 47, PVJK 234), Kundratice (KU 108, KU 114, KU 115, KU 116, KU 127), Lom (LOM 16), Mariánské Radčice (MR 58, MR 59) – see in detail KVAČEK & BŮŽEK (1982), TEODORIDIS & KVAČEK (2006), and from still working (w) or former mines of Bílina (w), Nástup-Tušimice (w), Ležáky, Marianna and SK Neumann – for detailed location see Fig. 1.

The above-mentioned fossil material is housed in the paleobotanical and geological collections of the National Museum, Prague (NM), the Institute of Geology and Palaeontology, Faculty of Science, Charles University in Prague (UK), Bílina Mine (DB), Nástup-Tušimice Mine (DNT), Regional Museum of Teplice (RMT), Museum of Mineralogy and Geology in Dresden, Germany (MMG PB) and in private collections of Mr. Z. DVOŘÁK and Mr. J. VYKYDAL.

The fossil carpological material represents compressed, carbonaceous and three-dimensionally preserved fossils and was obtained from the cores mainly by washing. The leaf fossils studied are preserved both as impressions and as compressions with cuticle remains also preserved. The wood is preserved either permineralized (mainly silicified but also impregnated by other minerals as siderite, limonite or dolomite) or lignified as a hard xylite. All xylotomical observations were based on standard thin mineralogical sections cut following three planes: transversal, tangential and radial. In the case of several fragile xylitic specimens, the material was hardened before cutting by resin.

The comparative extant material was obtained from the herbaria of the Charles University, Prague (PRC) and National Museum, Průhonice (PR), W. Szafer Institute of Botany, Polish Academy of Sciences, Kraków (KRA) and

Fig. 3. 1-2. *Pinus rigios* (UNGER) ETTINGSHAUSEN. 1. Three-needle fascicle, locality the Nástup-Tušimice Mine, DNT 201, scale bar 10 mm. 2. Incomplete 3-needle fascicles terminally attached to a branch, locality Břešťany, MMG PB Bn 406, scale bar 10 mm. **3-5.** *Pinus engelhardtii* MENZEL, locality Břešťany. 3. Two seed cones sub-oppositely attached to a branch, MMG PB Bn 355, scale bar 10 mm. 4. Complete seed cone, MMG PB Bn 390, scale bar 10 mm. 5. Complete seed cone, MMG PB Bn 348, scale bar 10 mm, (originally described as *P. horrida* MENZEL 1901, pl. 4, fig. 1). **6-7.** *Pinus urani* (UNGER) SCHIMPER, locality the Nástup-Tušimice Mine. 6. Incomplete seed cone, DNT 209, scale bar 10 mm. 7. Basal part of incomplete seed cone, DNT 213, scale bar 10 mm. **8-10.** *Pinus ornata* (STERNBERG) BRONGNIART, locality Břešťany. 8. Incomplete seed cone, MMG 321, scale bar 10 mm. 9. Apical part of seed cone, RMT PA 1458, scale bar 10 mm. 10. Incomplete basal part of seed cone, RMT PA 1457, scale bar 10 mm. **11-13.** *Pinus* sp. indet., complete winged seeds, locality the Bílina Mine. 11. DB 2-79, scale bar 5 mm. 12. DB 11-80, scale bar 5 mm. 13. DB 71-74, scale bar 5 mm. **14-15.** *Pinus* sp. 1, cylindrical male cone, locality the Bílina Mine. 14. DB 73-78, scale bar 5 mm. 15. DB 11-78, scale bar 5 mm. **16.** *Pinus* sp. 2, five-needle fascicle, locality Velká Černoc, UK VČ-64, scale bar 5 mm. **17-18.** *Pseudolarix schmidtgenii* KRAEUSEL, locality Nesuchyně. 17. Isolated complete cone scale, UK Nn-50, scale bar 10 mm. 18. Incomplete winged seed, UK Nn-51, scale bar 5 mm. **19.** *Pseudolarix* sp., needle fragment, locality Nesuchyně, UK Nn-8, scale bar 10 mm. **20.** *Cupressospermum saxonicum* (MAI) KUNZMANN, seed, locality Jenišův Újezd (core JÚ 224, depth 151.2 m), NM G08555, scale bar 500 μm.
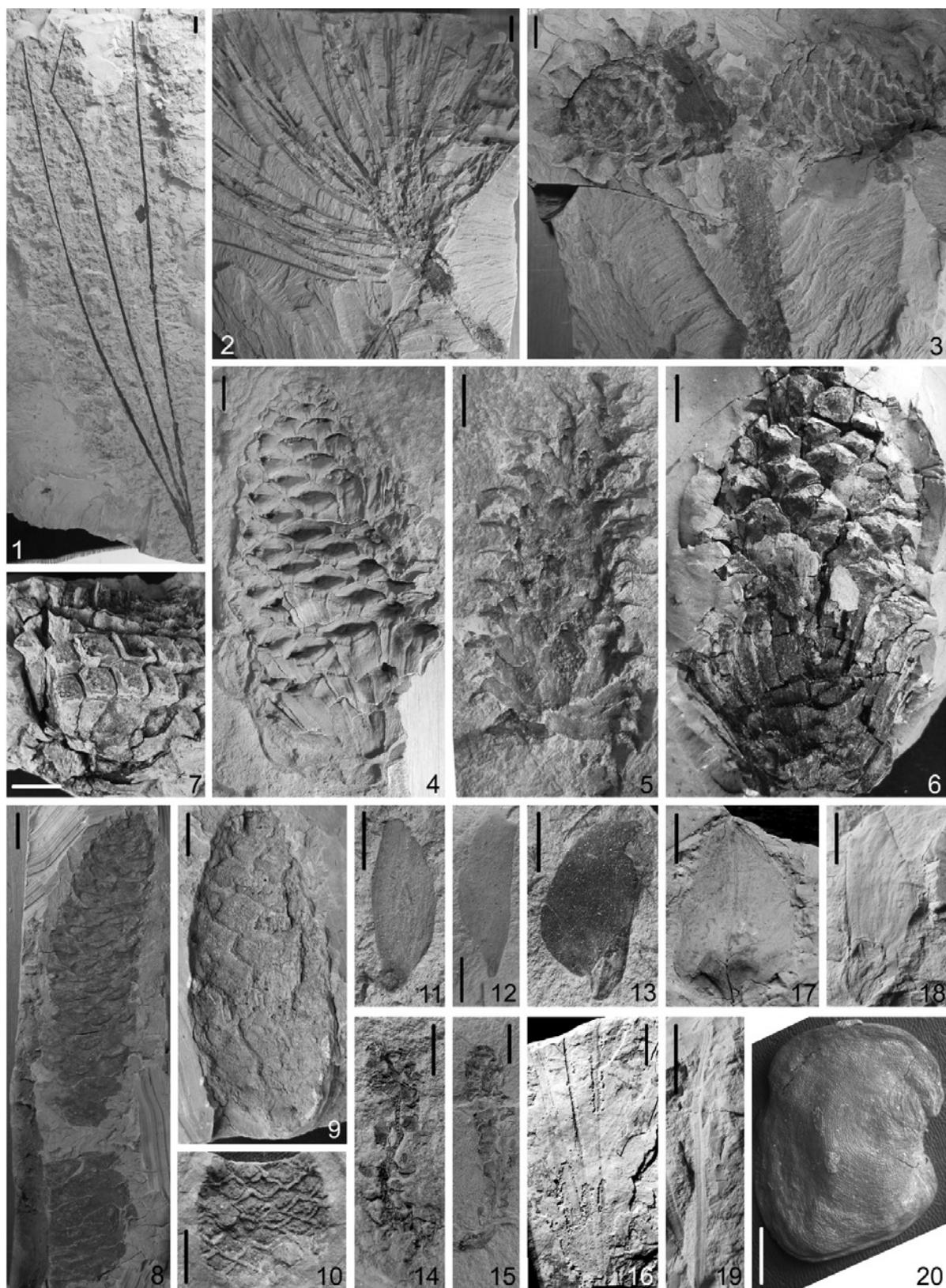
Fig. 3 (Legend see p. 290)

Institut de Botanique, Université de Montpellier II, Montpellier (MPU) and the comparative xylotomical collections of the Laboratoire de paléobotanique et paléoécologie (UPMC, Paris).

Basic observations were made using a binocular microscope. A digital camera Panasonic DMC-FZ8 was used for documentation of the leaf and cone macrofossils. An electron microscope (SEM) was used for detailed studies and documentation. The specimens were examined using a Jeol JSM – 6380 LV scattered electron microscope at 15 kV (Institute of Geology and Palaeontology, Faculty of Science, Charles University in Prague). Currently accepted morphological terminology follows FARJON (2005a, b) for leaves, cones and seeds and IAWA COMMITTEE (2004) for softwood anatomy.

Symbols "a, b, c, d, e, f, g, h" are used in the next text to mark different stratigraphical levels of the Most Basin (Fig. 2) and follows mainly informal stratigraphy given by HURNÍK & MAREK (1962): Underlying Formation (h) – i.e., Duchcov Member sensu DOMÁCÍ (1977); Lower Sandy-Clayey Beds with Basal Coal Seam (g), Lower Seam Beds (f), Lower Interseams Beds (e), Middle Seam Beds (d), Upper Interseam Beds (c) and Upper Seam Beds (b) – i.e., Holešice Member sensu DOMÁCÍ (1977) and Overlying Formation (a) – i.e., Libkovice Member (a2) and Lom Member (a1) sensu DOMÁCÍ (1977). Symbols "E1 (herbs), E2 (shrubs and lianas), E3 (trees under 25 m high) and E4 (trees over 25 m high)" are used for distinguishing vegetative storeys in environmental reconstruction.

4. Systematic part

Pinaceae ADANS.
Pinus L.

1. *Pinus engelhardtii* plant

1.1. *Pinus engelhardtii* MENZEL 1901 emend. MAI 1986 (cones and seeds)
Fig. 3.3-3.5

1877   *Pinus hordacea* (ROSSM.). – ENGELHARDT, p. 372, pl. 1, fig. 4.
1877   *Pinus oviformis* (ENDL.). – ENGELHARDT, p. 371, pl. 1, fig. 1.
1901   *Pinus engelhardtii*. – MENZEL, p. 57, pl. 3, fig. 28.
1901   *Pinus oviformis* (ENDL.) ENGELHARDT. – MENZEL, p. 50, pl. 2, fig. 1.
1901   *Pinus hordacea* ROSSM. – MENZEL, p. 52, pl. 2, fig. 5, pl. 3, figs. 23-27 (pro parte).
1986   *Pinus engelhardtii* MENZEL. – MAI, p. 582, pl. 46, figs. 3-9, pl. 47, figs.1-3, pl. 50, fig. 5, text-fig. 4.

Material: Incomplete seed cones and their fragments (C) and winged seeds (S) – localities: Břešťany, Břežánky [a2] (C), Bílina Mine [a2, b] (C, S), Hradiště near Černovice [a2] (C), Nástup-Tušimice Mine [a2] (C) and Varvažova near Chlumec [a2] (C); – cores: Kundratice /KU 115, depth 93-96.9 m [a2] (C), KU 116, depth 105-108 m [a2] (C)/ and Jezeří /PVJK 234, depth 83-84 m [a2] (C)/.

Description: Seed cones middle sized, slightly asymmetric, ovate in outline, 45.7-(101.5)-132.5 mm long and 21.2-(58.9)-67.9 mm broad, apophysis broadly rhombic, robustly conic to distinctly arched or uncinate, 7.9-(17.9)-20.4 mm long and 9.2-(10.1)-12.4 mm broad, maximal height up to 9.2 mm; umbo short, blunt, centromucronate, mucro small, often indistinct. Seed cones rarely sub-oppositely attached to a branch. Seeds winged, broadly oval in outline, 35 mm long and 6 mm broad (in the middle part), seed part broadly oval, 7 and 10 mm long, 4 and 5 mm broad, located basipetally and symmetrically to wing, wing apex obtuse, striation not preserved.

Remarks: MENZEL (1901: 57, pl. 3, fig. 28) typified this taxon on the cone material from the locality Trmice (Thürmitz). An older and more common synonym of *P. engelhardtii* was *Pinus oviformis* (ENDL.) ENGELHARDT known from the localities Hradiště near Černovice (ENGELHARDT 1877: 371, pl. 1, fig. 1; MENZEL 1901: 50, pl. 2, fig. 3b) and Břešťany, Věšťany near Teplice and Lipenský háj near Teplice (MENZEL 1901: 50, pl. 2, figs. 1, 2, 3a, 4). However, cone material of *P. oviformis* from Staré Sedlo (ENDLICHER 1847: 287) shows morphological similarity to *P. stroboides* (ROSSM.) MAI – e.g., MAI (1986), KNOBLOCH et al. (1996), BŮŽEK et al. (1996). MENZEL (1901, pl. 2, fig. 5, pl. 3, figs. 23-27) described incomplete cone and 5 isolated scales including 2 incomplete winged seeds (in situ) as *P. hordacea* from Břešťany. This carpological material shows also an affinity to *P. engelhardtii*. RANIECKA-BOBROWSKA (1962) noted a cone impression of *P. engelhardtii* from the Early Miocene locality Osieczow upon Kwisą (ZASTAWNIAK, personal communication 2008) and calculated *P. roxburghii* SARG. from mountain forests of the Himalayas as a living analogue. MAI (1986: 583) excluded this species as well as other pines from section *Sula* sensu MAYER because of longer seeds (over 20 mm) and centromucronate umbo of the fossil material, which matches better to pines of subsections *Pinaster* or *Australes* sensu FARJON (2005a). *P. engelhardtii* often co-occurs with leaves of *P. rigios* (UNG.) ETT. – see below. According to this fact, living pines of subsection Australes from the USA, Mexico and the Caribbean (e.g., *P. taeda* L. or *P. rigida* MILLER) are comparable to *P. engelhardtii* – e.g., KVAČEK et al. (2004b). Recently, DIENI & MAI (2007) re-described *Pinus priabonensis* OMBONI from the Upper Oligocene of NE Italy together with a detailed key of other "centromucronate" pines.

1.2. *Pinus rigios* (UNGER 1850) ETTINGSHAUSEN 1866 (leaves)
Fig. 3.1-3.2

1850   *Pinites rigios* UNGER, p. 362.
1852   *Pinites rigios* UNGER, p. 25, pl. 13, fig. 3.
1866   *Pinus rigios* (UNG.). – ETTINGSHAUSEN, p. 41, pl. 13, figs. 11-12.
1877   *Pinus hordacea* ROSSM. – ENGELHARDT, p. 373, pl. 1, figs. 10-11.
1901   *Pinus rigios* UNG. – MENZEL, pp. 61-62, pl. 3, figs. 1-4.

Material: Rarely complete or incomplete fascicles of needles and their fragments (N) rarely attached to a branch – localities: Břešťany, Břežánky [a2], Bílina Mine [a2, b], Hradiště near Černovice [a2] and Nástup-Tušimice Mine [a2].

Description: Isolated 3 - needled fascicles, needles 145.6 to 347.6 mm long and 2.2 to 2.6 mm broad, straight or slightly curved, primarily triangular in transversal section, secondarily compressed, apex acute to attenuate (rarely preserved), sheath 12.4-(18.8)-27.9 mm long and 2.86-(4.1)-5.1 mm broad, base rounded, margin entire, venation consisting of one medial vein (till 0.33 mm broad), parallel striation observed. Fascicles rarely attached to a branch.

Remarks: This species has a rather cumulative character due to its broad stratigraphical range and relatively large area, i. e. from the Late Oligocene to the Pliocene of Europe. MAI (1999: 15) commented the great morphological affinity to other fossil species, e. g., *P. gracilis* SAPORTA, *P. trichophylla* SAPORTA, *P. taedaeformis* (UNG.) HEER, *P. palaeotaeda* ETT. etc. *P. rigios* is typified on the leaf material from Bílina (UNGER 1850: 362), which was figured by UNGER (1852: 25, pl. 13, fig. 3). ETTINGSHAUSEN (1866) described the leaf material of *P. rigios* from Břešťany and Břežánky in association of one cone (ETTINGSHAUSEN 1866: 41, pl. 13, fig. 15) having probably affinity to *P. engelhardtii*. MENZEL (1901) figured new material from Břešťany and Sokolov (Falkenau) and commented possible leaf similarity with *P. hordacea* ROSSM. (ENGELHARDT 1877: 373, pl. 1, figs. 10-11) from Hradiště near Černovice. MAI (1999: 15) added an anatomical and epidermal characteristics of *P. rigios* from the Spremberg sequence from the second brown coal horizon in the Lausitz region (also in BŮŽEK et al 1996). However, he noted the dentate leaf margin and described his leaves as *Pinus* cf. *rigios*. It is possible to assume the association of these leaves and cones of the above-described species of *P. engelhardtii* based on the co-occurrence of both species in localities of Břešťany (Bílina Mine), Nástup-Tušimice Mine and Hradiště nearČernovice. Leaves of *P. rigios* are also known from the Cheb and Sokolov basins (RŮŽIČKA & BENEŠ 1951; BŮŽEK et al. 1996). According to the leaf morphological analysis, *P. rigios* shows an affinity to extant species of *P. taeda* L. and *P. rigida* MILL. (e. g., ETTINGSHAUSEN 1866) and/or other species from section *Pinaster* (MAI 1999). BŮŽEK et al. (1996) compared the fossil material of *P. rigios* from the Cypris Shale to extant *P. taeda* based on the needle length. However, this living species possesses dentate needles, which is not the case of the material from the Cypris Formation as well as the type area at Bilina.

2. *Pinus ornata* plant

2.1. *Pinus ornata* (STERNBERG 1825) BRONGNIART 1828
Fig. 3.8-3.10

1825   *Conites ornatus* STERNBERG, p. 39, pl. 55, figs. 1-2.
1828   *Pinus ornata* (STERNBERG). – BRONGNIART, p. 107.

1876a   *Pinus ornata* STERNBERG. – ENGELHARDT, p. 61, pl. 10, fig. 4.
1877   *Pinus ornata* STERNBERG. – ENGELHARDT, p. 47, pl. 2, fig. 4.
1901   *Pinus ornata* STERNBERG. – MENZEL, p. 54, pl. 2, figs. 6-7, 9.
1968   *Pinus ornata* (STERNBERG) BRONGNIART. – NĚMEJC, p. 384, pl. 39, figs. 2-3.
1994   *Pinus ornata* (STERNBERG) BRONGNIART. – MAI, p. 213, pl. 3, figs. 1-3, text-fig. 1b.

Material: Incomplete seed cones and their fragments (C) – localities: Břežánky [a2], Nástup-Tušimice Mine [a2] and Hradiště near Černovice [a2].

Description: Seed cones symmetric, oblong ovate to cylindric, 81.8-(112.3)-132.5 mm long and 28.4-(45.4)-61.3 mm broad, apophysis rhombic, flattened (mainly in the basal cone part) to slightly arched, 3.9-(4.6)-5.5 mm long and 5.5-(6.5)-8.2 mm broad, distinctly keeled and radially striated, umbo flattened to slightly arched, excentro-denticulatomucornate, mucro small and indistinctly erected.

Remarks: This taxon was originally typified on the cone material from the Oligocene locality Valeč by STERNBERG (1825: 39, pl. 55, figs. 1-2). Unfortunately, the holotype disappeared from the collection of the Osek Monastery during the end of 19th century. ENGELHARDT (1876a: 61, pl. 10, fig. 4) described an incomplete cone associated with fragmentary needles (Pl. 10, figs 5-7) from the "Leitmeritzer Mittelgebirge" (i. e., České středohoří Mts). ENGELHARDT (1877: 47, pl. 2, fig. 4) described an additional incomplete cone from the locality Hradiště near Černovice (Tschernowitz). MENZEL (1901: 54, pl. 2, figs. 6-7, 9) described some other cones from the localities Valeč and Břešťany. Additional cone material is known from the localities Staré Sedlo, Český Chloumek and Žitenice (ENGELHARDT 1876b; KNOBLOCH 1962; KNOBLOCH et al. 1996). Later on NĚMEJC (1968: 384, pl. 39, fig. 3) refigured besides others the MENZEL's cone from Valeč which was marked as suitable material for the neotype by Z. KVAČEK & J. KVAČEK (1992, pl. 4, fig. 1). MAI (1986: 575) classified *P. ornata* into group No 15. "Merkussi" based on the flattened apophysis in the basal cone part and the character of relatively long stalk (till 2 cm). MAI (1986: 575, 1994: 213) has included to this group 11 other fossil species and their synonyms, mainly from French Miocene. The *P. ornata* cone and associated needle analysis shows a xerophytic *P. halepensis* MILL. (from the Mediterranean Zone and West Asia) and *P. merkusii* JUNG. & DE VRIES (from Vietnam, Laos, Cambodia, China, Philippines, Malaysia and Indonesia) as the most comparable extant species. KVAČEK et al. (2004b) note *P. massoniana* LAMB. from Taiwan and China as a possible extant equivalent. But this species shows shorter cones (only 4-(2.5)-7 cm long), which are also more shortly stalked (FU et al. 1999) than *P. ornata*.

2.2. *Pinus hepios* (UNGER 1850) HEER 1855 sensu MENZEL (1901)

Discussion: Seed cones of *P. ornata* are usually associated with relatively short needles in 2- needled fascicles of *Pinus hepios* (Unger) Heer (e.g., Engelhardt 1876a; Menzel 1901). *Pinus hepios* (Unger) Heer was usually used as a cumulative taxon name for pines with two-needle fascicles. However, the leaf material from the locality Valeč (sensu Menzel 1901: 64f., pl. 3 fig. 4) has a direct relation to the type cone material of *P. ornata*. The leaves of *Pinus hepios* (Unger) Heer were typified by Unger (1850, 1852) from the locality Parschlug (e.g., Kovar-Eder et al. 2004). Menzel (1901: 65) noted the additional material from the locality Žitenice and Hradiště near Černovice. Bůžek (1971: 37, pl. 7, fig. 8) revised one sample of two-needle fascicle (incomplete needles 70 mm long, 10 mm and 20 mm broad) as *Pinus* sp. from the "overlying" sediments of the locality Čermníky (Libkovice Member of the Most Formation). This material was originally described as *P. rigios* by Procházka (1954). Unfortunately, the above-mentioned fossil material from the Most Basin is missing. Mai (1999: 14, pl. 8, figs. 9-11, pl. 9, figs. 1-4) noted the leaf material described as *Pinus* cf. *hepios* (Unger) Heer from Lusatia.

3. *Pinus urani* plant

3.1. *Pinus urani* (Unger 1850) Schimper 1872
Fig. 3.6-3.7

1850   *Pinites urani* Unger, p. 363.
1852   *Pinites urani* Unger, p. 98, pl. 37, fig. 5.
1872   *Pinus urani* (Unger). – Schimper, p. 262.
1901   *Pinus laricio* Poir. – Menzel, p. 55, pl. 2, figs. 10-14.
1986   *Pinus urani* (Unger) Schimper. – Mai, p. 587, pl. 51, figs. 11-13, pl. 52, figs. 1-5, pl. 53, figs. 1-4, pl. 59, figs. 8-9, text-fig. 8.

Material: Seed cones and their fragments (C) – localities: Břešťany [a2] and Hradiště near Černovice [a2]; – cores: Kundratice /KU 114, depth 42-73 m [a2], KU 115, depth 93-96.9 m [a2], KU 116, depth 105-108 m [a2]/ and Jezeří /PVJK 234, depth 83-84 m [a2]/

Description: Seed cones relatively small (up to 9 cm), asymmetric, widely oval or ovate in outline, rarely rounded, 36.1-(52.8)-66.9 mm long, 23.2-(33.5)-46.9 mm broad, apophysis widely rhombic to pentagonal, 2.9-(4.1)-5.1 mm long, 3.5-(6.8)-9.3 mm broad, distinctly keeled, umbo radially striated, flattened and slightly striated or uncinate to knobbed and broadly rhombic with a distinct diagonal keel (mainly in the middle cone part), excentromucronate, mucro small, denticulate, rarely erect, often indistinct in the basal cone part.

Remarks: These relatively smaller cones are known only from core material of the micaceous psammite facies occurring along the Krušné Hory Mts fault between Vysoká Pec and Albrechtice (Teodoridis & Kvaček 2006) and from the quartzite sandstone of Hradiště near Černovice (Purberg, Tschernowitz) – Engelhardt (1877) and Menzel (1901). The preservation of the core material is not so perfect (worn

out apophysis) therefore the identification is in some cases equivocal. The main diagnostic features are rhombic to knobbed umbo and small to middle sized cones. *P. urani* is based on a single cone from the Sarmatian locality Radoboj (Middle Miocene, Croatia). This incomplete cone occurring with a seed on one sample was firstly noted by Unger (1850) and later figured in Unger (1852: 98, pl. 37, figs. 5-6 /seed/). Mai (1986: 587f.) revised this taxon occurrences including some older synonyms and seeds mainly from the Late Miocene localities, e.g., Weisweiler near Düren (*P. stelwagii* Kinkelin and *P. weylandii* Kirchheimer), Zülpich (*P. urani* and *P. schultzii* Klipper) and Konin-Patnów (*Pinus* sp.). Menzel (1901) described and partly refigured a relatively abundant cone and cone scale material as *P. laricio* from several different localities, i.e., Hradiště near Černovice (pl. 2, figs. 10-11, 14), Davidovo údolí (pl. 2, fig. 12), Mokřina (pl. 3, fig. 22) and Valeč (pl. 2, fig. 13) in association with isolated seeds from Břešťany (pl. 3, fig. 7), Kundratice (pl. 3, fig. 8), Mokřina (pl. 3, fig. 10) and Jehličná (pl. 3, fig 9) – see below. The cone scale from the locality Mokřina figured by Menzel (1901, pl. 3, fig. 22) bears to 2 seeds in situ. Recently, Němejc et al (2003: 126, pl. 2, figs. 1-3) described incomplete cones as *Pinus* cf. *urani* (Ung.) Schimper complex from the quartzite of Býkov near Plzeň – originally in Purkyně (1911: 2). Similar single cones are known from the Cypris Shale (Bůžek et al. 1996 – as *Pinus* sp.). Fossil cones of *Pinus urani* match well extant cones of *Pinus nigra* J. F. Am subsp. *larico* (Poir.) Maire from mountain forests of Corsica, S Alps and N Pyrenee.

4. Additonal material related to *Pinus* L.

4.1. *Pinus* sp. 1 (pollen cones)
Fig. 3.14-3.15

Material: 12 isolated pollen cones (M) – Břešťany and Bílina Mine [a2].

Description: Pollen cones primarily cylindrical, secondarily compressed, 18.9-24.9 mm long 4.2 to 5.7 mm broad, apex obtuse, base narrowed rounded, sporangiophores spirally attached on stalk (up to 0.59 mm broad) bearing 2 anthers, anther oblong to rounded along the adaxial side, 1.24-1.52 mm long, 0.72-0.96 mm broad, pollen in situ unknown.

Remarks: An assignment of the above-described pollen cone from the Bílina Mine to the species level is problematic. Menzel (1901) described and figured similar material from localities Davidovo údolí (Sokolov), Mokřina and Břešťany (Menzel 1901: 60f., pl. 3, figs. 13-14). Menzel (1901) assumes affinity of the pollen cone from Břešťany to the extant *P. halepensis* Mill. and *P. larico* Poir., which can be correlated to *P. urani* (see above). However, a detailed taxonomy of the above-described pollen cones is equivocal in spite of evident similarity with Menzel's original material from Břešťany. Morphologically comparable material is known from the Cypris Shale of the Cheb and Sokolov basins (Bůžek et al. 1996: 10, pl. 2, fig. 3). We can exclude an affinity to the most common

pine cones of *P. engelhardii* due to their similarity to recent pollen cones of *P. taeda* L. or *P. rigida* MILLER (see above) and co-occurrences in the Libkovice Member of the Most Formation.

4.2. *Pinus* sp. 2 (leaves)
Fig. 3.16

1953   *Pinus* sp. – NĚMEJC, p. 14, pl. 2, figs. 3-4.

Material: Incomplete needle fascicle (N) – locality Velká Černoc [h-g].

Description: Five-needled fascicle, needles incomplete, 31 to 33 mm long and 1 mm broad; sheath 5 mm long and 3 to 2 mm broad in basal part, upper surface poorly preserved, rarely one medial vein and parallel striation observed.

Remarks: One, incomplete impression and its counterpart of needles from the locality Velká Černoc (TEODORIDIS 2002) can be compared with fossil *Pinus pseudostrobus* BRONGNIART based on the number of needles in fascicle. This fossil taxon is relatively common in Late Oligocene to Pliocene of Europe and is related to extant species from sections *Cembra* and *Strobus* (MAI 1997; CZAJA 2003).

4.3. *Pinus* sp. indet. (leaves)

Material: Incomplete needles and their fragments (N) – cores: Kundratice /KU 108, depth 71.2-76.7 m [a2] (?N), KU 115, depth 90-99.2 m [a2], KU 116, depth 105-108 m [a2]/, Jezeří /JZ 42 65-66 m [a2], JZ 44, depth 57-58 m [a2], JZ 47, depth 53-57 m [a2]/, Černice /CN 54, depth 56-60 m [a2]/, Horní Jiřetín /HJi 142, depth 89-123 m [a2]/, Janov /Ja 28, depth 36.3-49.2 m [a2] (?N)/, Horní Litvínov /LiH 13, depth 42-57 m [a2]/ and Mariánské Radčice /MR 58, depth 111.5-143.3 m, MR 59, depth 99.0-135.0 m [a2] (N)/.

Remarks: Incomplete needles and their fragments from the above-mentioned cores have been assigned as inde-terminated species of *Pinus* L. (KVAČEK in TEODORIDIS & KVAČEK 2006). It is possible to estimate an affinity to the cone material of *P. urani* and *P. engelhardtii* due to their co-occurrence. However, an assignment to other conifer genera in the case of the fragmentary material is not ex-cluded.

4.4. *Pinus* sp. indet. (seeds)
Fig. 3.11-3.13

1901   *Pinus laricio* POIR. – MENZEL, p. 55, pl. 3, figs. 7-10.
1901   *Pinus* sp. – MENZEL, p. 59, pl. 3, figs. 5-6.
1901   *Pinus pseudonigra* ENGELHARDT. – MENZEL, p. 60, pl. 3, fig. 11.

Material: 2 different types of isolated seeds (S) – locali-ties: Břešťany [a2], Bílina Mine [a2].

Description: Type A – An isolated winged seed broadly oval in outline, 16.7 mm long and 5.9 mm broad, seed broadly oval, 4.4 mm long and 3.1 mm broad, located basipetally and asymmetrically to wing, apex obtuse, striation indistinct and parallel. Type B – Isolated winged seeds broadly oblong to oval in outline, 16.6, 13.8 and 19.8 mm long and 4.1, 5.1 and 6.1 mm broad, seed oval to rounded, 2.21, 1.4 and 1.4 mm long and 1.0, 1.3 and 0.70 mm broad, located basipetally and symmetrically to wing, wing apex obtuse, striation indistinct and parallel.

Remarks: Pine seeds are not so common in the Most Basin. We just recognized only two forms. The relatively large seed asymmetrically surrounded by a broad wing is characterizing as the form A. MENZEL (1901, pl. 3, fig. 7) described this seed belonging to *P. laricio* POIR. from Břešťany. He also associated this type of seeds (MENZEL 1901, pl. 3, figs. 7-10) to the same named seed cones, which correspond to *P. urani*. Contrary to the MENZEL's opinion, MAI (1986, 1994) indicates twice bigger seeds of *P. urani* from Weisweiler (MAI 1986: 587, pl. 59, figs. 8-9) and Val d'Arno Superiore (MAI 1994: 215, pl. 4, figs. 4-7). On the other hand, the seed morphology of our type A is very similar to the seeds from Schoenneg (ETTINGSHAUSEN 1890: 13, pl. 1, figs. 80-82 – *P. taeaformis* UNG.) and from the locality Mokřina and the Cypris Shale of the Cheb and Sokolov basins (BŮŽEK et al. 1996: 10, pl. 2, fig. 2 – *Pinus* sp.). BŮŽEK et al. (1996) noted a probable morphological affinity to seeds of living *P. taeda* L., *P. rigida* MILL… etc. associated to the fossil leaf species of *P. rigios* and/or seed cones of *P. engelhardtii*, which match the seed size data published in MAI (1986: 582, pl. 60, fig. 5). The B type with a less symmetrical seed is identical to the material from the Cypris Shale figured by MENZEL (1901, pl. 3, figs. 11-12) and BŮŽEK et al. (1996, pl. 10, pl. 2, fig. 5). BŮŽEK et al. (1996) noted a similarity with fossil seeds of *P. palaeo-strobus* ETT. and *P. prae-pumilo* ETT. (ETINGSHAUSEN 1890: 14, pl. 1, figs. 76-79) and pointed out that many modern pine species or other conifers, e.g., *Keteleeria* CARRIÈRE, produced a similar seed type.

Pseudolarix GORDON

5. *Pseudolarix schmidtgenii* plant

5.1. *Pseudolarix schmidtgenii* KRAEUSEL 1938 (cone scales, seeds)
Fig. 3.17-3.18

1938   *Pseudolarix schmidtgenii* KRAEUSEL, p. 26, pl. 3, fig. 7, text-fig. 4m-p.

Material: 26 cone scale (Sc) and 2 seeds (S) – locality Nesuchyně [h-g].

Description: Seed scale ovate in outline, 18.1-(22.5)-24.2 mm long and 11.2-(16.2)-20.3 mm broad, maximally in the first third of scale, apex obtuse or rarely acute, base cordate to rounded; midrib obvious on the concave adaxial side, strong and straight, narrowed to acute stalk at basal

scale part, 2 seed imprints or even winged seeds situated along midrib; bract visible in central part of the scale base on the convex abaxial side. Seed winged, oval in outline, 22.2 mm and 19.3 mm long, 7.1 mm and 6.2 mm broad, venation parallel following wing shape around margin areas, seed oval, 6.1 mm and 5.2 mm long, 3.1 mm and 2.5 mm broad.

Remarks: The cone scales, seed and fragmentary needles are known only from the locality Nesuchyně (NĚMEJC 1949; BŮŽEK & KVAČEK 1989; TEODORIDIS 2002) that belongs to the sedimentary belt of the "Hlavačov Gravel and Sand" (VÁNĚ 1985). This important taxon occurring in association of *Fagus saxonica* KVAČEK & WALTHER proved a phytho-stratigraphical correlation with the Floristic Assemblage of Thierbach sensu MAI & WALTHER (1991) and with the sediments of the lowermost part of the Duchcov Member of the Most Formation sensu DOMÁCÍ (1977) – see in detail Walther in LOTSCH et al. (1994) and TEODORIDIS (2002, 2004). An assignment of seed material to *Pseudolarix schmidtgenii* KRÄUSEL is based on morphological comparison with the seeds, which were described by KRAEUSEL (1938) from the locality Mainz-Kastel (Early Miocene). However, probably the first note about the fossil occurrences of *Pseudolarix* seed scale was published by FLORSCHÜTZ (1925) under the name of *P. kaempferi* GORGON *fossilis* FLORSCHUETZ from Reuver (Upper Pliocene).

P. schmidtgenii can be interpreted as a mesophytic conifer associated with the fluvial and/or extrabasin environment that corresponds to extant species *Pseudolarix amabilis* (J. NELSON) REHDER that enters the Mixed Mesophytic and the Mixed Montane Conifer Angiosperm Forests in East China (FARJON 1990, 2001).

5.2. *Pseudolarix* sp. (leaves)
Fig. 3.19

Material: Needle fragments – locality Nesuchyně [h-g].

Description: Needle incomplete 24.2-(45.3)-65.1 mm long and 1.1-(2.3)-3.1 mm broad, straight to slightly curved, narrowing, apex acute, basal part not preserved, distinct and relatively sunken medial vein dividing needle into 2 groves, margin entire, no cuticles preserved.

Remarks: Determination of associated fragmentary needles from locality Nesuchyně is problematic without evidence of cuticular analysis. The main argument is the fact that the needles are closely associated with the scales and seeds of *Pseudolarix schmidtgenii* KRAEUSEL and match in morphology those of the extant species *P. amabilis*.

Cupressaceae GRAY sensu FARJON 2005b

Quasisequoia SRINIVASAN & FRIIS emend. KUNZMANN

6. *Quasisequoia couttsiae* plant

6.1. *Quasisequoia couttsiae* (HEER 1862) KUNZMANN 1999 (leaves, cones, seeds)
Fig. 4.1-4.4

1862   *Sequoia couttsiae* HEER, p. 1051ff., pls. 59-61.
1866   *Taxodium dubium* (STERNB.) HEER. – ETTINGSHAUSEN, p. 34, pl. 10, figs. 8-9, 20-22 (pro parte).
1881   *Sequoia langsdorfii* BRONGN. – VELENOVSKÝ, p. 16, pl. 1, figs. 30-35 (pro parte).
1884   *Athrotaxis couttsiae* (HEER). – GARDNER, p. 90f., pl. 6, figs. 1-9, pl. 10, figs. 6-9.
1901   *Sequoia couttsiae* HEER. – MENZEL, p. 91, pl. 5, figs. 17-25.
1901   *Sequoia langsdorfii* BRONGN. – MENZEL, p. 89, pl. 5, figs. 26-28.

Fig. 4. 1-4. *Quasisequoia couttsiae* (HEER) KUNZMANN. 1. Two complete seed cones attached to sub-oppositely branched sterile twig seed cones, locality the Bílina Mine, DB 02-81, scale bar 10 mm. 2. Complete seed cone attached to sterile twig, locality the Bílina Mine, DB 11-82, scale bar 10 mm. 3. Complete seed, locality the J. Šverma Mine [b], NM G 08556, scale bar 500 μm. 4. Incomplete seed, locality Strupčice (core Sr 40, depth 85 m), NM G 08557, scale bar 500 μm. **5-11.** *Taxodium dubium* (STERNBERG) HEER. 5. Immature seed cone terminally attached to sterile twig, locality the Bílina Mine, DB 01-76, scale bar 10 mm. 6. Twig, locality Břešťany, MMG PB Bn 417, scale bar 10 mm (originally described as *Athrotaxidium bilinicum* MENZEL 1901, pl. 5, fig. 4). 7. Pollen cones arranged in long drooping clusters, locality the Bílina Mine, DB 24-70, scale bar 10 mm. 8. Seed cone scale with undulate umbo including upper submarginal row of distinct, sharp and isolated tubercles, locality the Bílina Mine, DB 21-59, scale bar 5 mm. 9. Incomplete seed cone, locality the Bílina Mine, DB 21-57, scale bar 5 mm. 10. Incomplete seed, locality the Bílina Mine, DB 2-63, scale bar 1 mm. 11. Seed, locality Vysoká Pec (core VP 14, depth 48.5 m), NM G 08558, scale bar 1 mm. **12-18.** *Glyptostrobus europaeus* (BRONGNIART) UNGER. 12. Two complete seed cones sub-oppositely attached to sterile twig, locality Břešťany, MMG 292, scale bar 10 mm (originally described as *Glyptostrobus europaeus* BRONGNIART by MENZEL 1901, pl. 5, fig. 2). 13. Three complete seed cones alternately attached to sterile twig, locality Břešťany, DB, scale bar 10 mm. 14. Pollen cones terminally or subterminally attached to sterile twigs, locality the Bílina Mine, DB 30-84, scale bar 10 mm. 15. Complete seed, locality Vršany (core Vr 22, depth 72 m, NM G 08559, scale bar 1 mm. 16. Complete seed, locality Vysoká Pec (core VP 14, depth 59.5 m, NM G 08560, scale bar 1 mm. **17-18.** *Tetraclinis salicornioides* (UNGER) KVAČEK, locality the Bílina Mine. 17. Incomplete foliage twig including sub-oppositely branched branchlets, DB 24-85, scale bar 10 mm. 18. Isolated two flattened branchlets, DB 30-86, scale bar 5 mm.
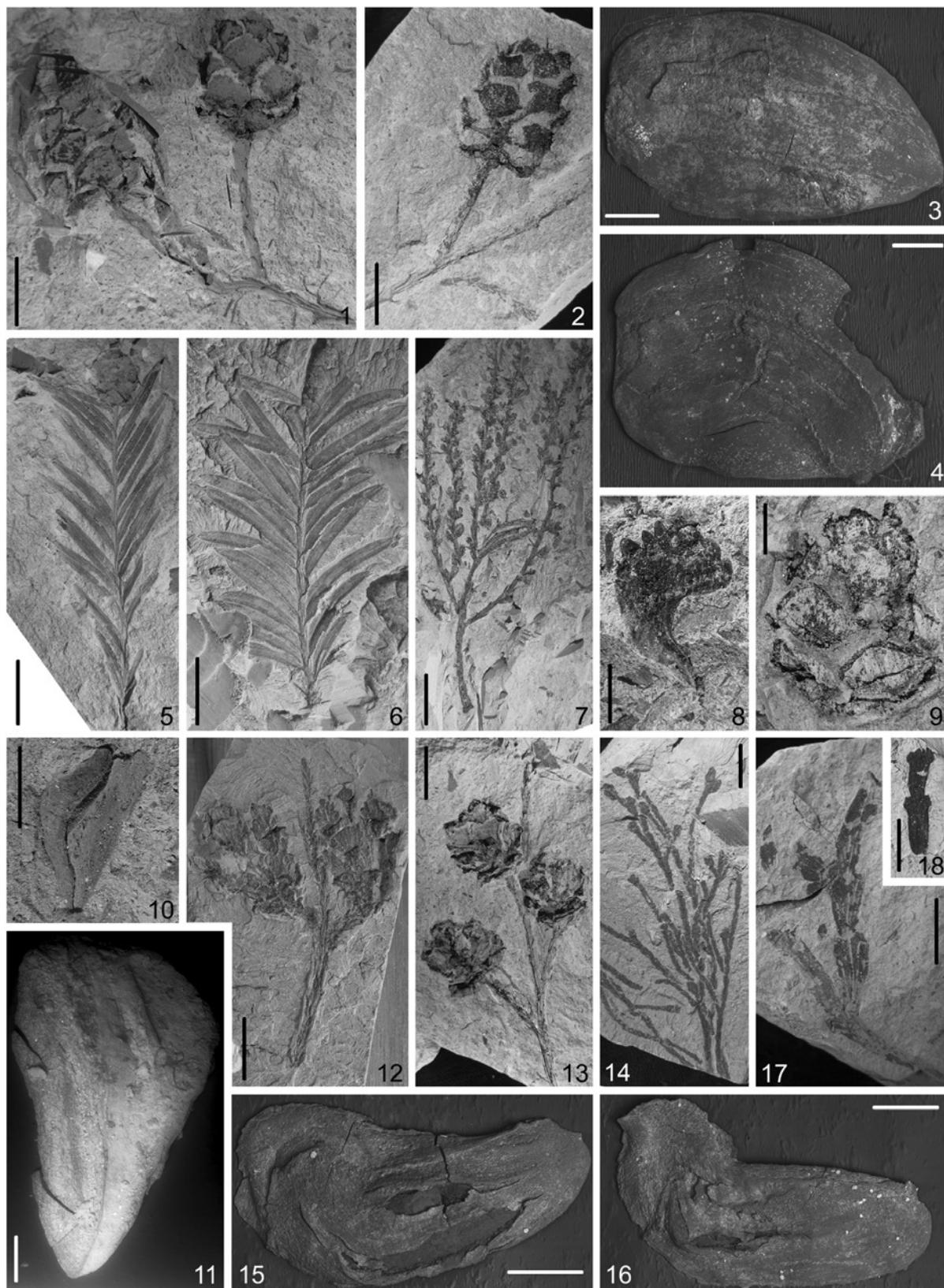
Fig. 4 (Legend see p. 296)

1964   *Sequoiadendron* cf. *couttsiae* (HEER) GRAMBAST. – BŮŽEK & HOLÝ, p. 112, pl. 3, figs. 1-11.
1999   *Quasisequoia couttsiae* (HEER). – KUNZMANN, p. 57, pl. 10, figs. 5-6, pls. 11-13, text-figs. 13-14.

Material: Great quantity of sterile twigs (T), seed cones (F), isolated cone scales (Sc), seeds (S) – localities: Břežánky, Břešťany [a2] (T, F, Sc, S), Bílina Mine [a2-b] (T, F, Sc, S), Dobrčice [c] (T, F), Dolany [c] (T, F), Chuděřice [a2] (T, F), Marianna Mine [c] (T, F), Straky [a2] (F, T), Vršovice [c] (T, F), Záhoří near Žatec [c] (T, F), Želénky [a2] (T), J. Šverma Mine [b, d] (F, Sc, S, T) and J. Fučík Mine [b, d] (F, Sc, S) – cores: Břežánky /B 1, depth 131.1 m [a2] (F, S); M 541, depth 103 m [a2] (Sc, S)/, Chomutov /Co 199, depth 66.3 m [c] (F, S), Co 215, depth 89.9 m [d] (Sc), Co 225, depth 57.8 m [f] (F, Sc), Droužkovice /Do 201, depth 65.6 m [a2] (F, Sc), Do 210, depth 47.5 m [b] (S)/, Hošnice /Hš 4, depth 21.5 m [b] (F, Sc)/, Kundratice /KU 127, depth 64-79 m [a2] (T)/, Libkovice /P 542, depth 94-95 m [a2] (F, Sc, S)/, Lom /LOM 16, depth 54.5-54.6 m [a1] (C, S, T)/, Otvice /Ot 36, depth 38-39.0 m [c] (Sc, S)/, Pesvice /Pe 18, depth 67 m [d] (F, Sc), depth 82.3 m [d] (F, Sc), Strupčice /Sr 39, depth 63 m [c] (Sc, S, T), Sr 40, depth 85 m [d] (Sc, S), depth 90 m [d] (S)/, Údlice /Úd 81, depth 125 m [g] (S)/, Vršany /Vr 20, depth 87.4 m [f] (S), Vr 22, depth 75 m [d] (Sc, S), depth 79-80 m [d] (Sc, S)/ and Vysoká Pec /VP 14, depth 48.5 m [c] (Sc, S); VP 15, depth 95-96 m [f] (S), VP 16, depth 45-46.0 m [c] (F, Sc, S), depth 65.0 m [c] (F, S)/.

Description: Twigs covered by scale-like, spirally arranged leaves, closely adhering to the axis or just slightly protruding. Mature seed cone symmetric, rounded to oval in outline, 13.9-(17.6)-22.8 mm long and 11.2-(12.9)-16.3 mm broad, apex rounded, base rounded to broadly cuneate, composed of 8-12 scales, scale consists of distinctly narrowed stalk centrally attaching peltae apophysis, apophysis rhombic to oval, 2.9-(3.75)-4.9 mm long and 5.25-(5.6)-6.8 mm broad, always broader than longer, abaxial side wrinkled including poorly visible central mucro; immature cones smaller; winged seed ovate to triangular in outline, flat, often slightly curved, 3.18-(3.71)-4.26 mm long and 1.87-(2.3)-2.95 mm broad, base rounded to slightly cordate or rarely broadly cuneate, including slightly concave chalaza, apex acute to blunt containing a small prominent micropyle tip, seed oblong to elliptic, 0.82-(1.1)-1.34 mm broad, bordered by bifacial wings, often symmetric, upper surface poorly preserved, distinct longitudinal rows built by rectangular and oblong pits (100 x 120 μm).

Remarks: A relatively common conifer from coal facies of the Holešice Member and from the Břešťany Clay (e.g., BŮŽEK & HOLÝ 1964; KVAČEK & HURNÍK 2000) are known as seed cones, their isolated scales, seeds and sterile twigs in the Most Basin. Sterile twigs, and pollen fertile twigs are morphologically indistinguishable from *Glyptostrobus europaeus*, however, cuticles of both taxa are different (e.g., KVAČEK 1985; KUNZMANNN 1999; SAKALA 2000). According to PINGEN (1994: 25), it is possible safely define several morphological features of seeds, which help to differentiate this taxon from *Sequoia abietina* (BRONGN. in CUVIER) KNOBLOCH. KUNZMANN (1999: 62) specified the seed morphology based on the "in-situ" material. On the other hand, it is necessary to calculate possible intraspecific seed variability, an aspect also known from seeds of living *Sequoia* ENDL. KUNZMANN (1999: 66-69) discussed possible affinity to the living species of Cupressaceae sensu FARJON (2005b) without finding an extant analogue.

Fig. 5. 1-5. *Taxodioxylon gypsaceum* (GOEPPERT) KRAEUSEL, locality the Bílina Mine. 1. General view with uniseriate medium rays and axial parenchyma with smooth transverse end walls, tangential longitudinal section, UK 012/98, scale bar 100 μm. 2. Partially biseriate ray, tangential longitudinal section, UK 012/98, scale bar 100 μm. 3. Taxodioid cross-field pits with horizontal apertures, mostly 4 per field arranged in one horizontal row (arrows), radial longitudinal section, UK 012/98, scale bar 50 μm. 4. Taxodioid cross-field pits in marginal ray cells arranged in two horizontal rows, radial longitudinal section, UK 013/98, scale bar 50 μm. 5. Triseriate pitting in radial tracheid walls, closely spaced with bars of Sanio (= crassulae), radial longitudinal section, UK 013/98, scale bar 100 μm. 6-12. *Taxodioxylon taxodii* GOTHAN. 6. General view with one very high ray (40 cells), tangential longitudinal section, locality the Bílina Mine, UK 008/98, scale bar 200 μm. 7. Axial parenchyma with nodular transverse end walls and globular resin contents, tangential longitudinal section, locality the Bílina Mine, UK 008/98, scale bar 100 μm. 8. Detail of prominent nodules in transverse end wall of the axial parenchyma (arrow), tangential longitudinal section, locality the Bílina Mine, UK 031/98, scale bar = 50 μm. 9. General view of the outermost part of the section with taxodioid cross-field pits and uni- to biseriate pitting in radial tracheid walls with pronounced bars of Sanio, radial longitudinal section, locality Vršany, UK 6/97, scale bar = 50 μm. 10. General view of growth rings with destroyed earlywood tracheids (darker parts), transverse section, locality Břežánky, UK 3/97, scale bar 500 μm. 11. Detail of four prominent nodules in transverse end wall of the axial parenchyma (arrow), tangential longitudinal section, locality Břežánky, UK 3/97, scale bar 50 μm. 12. Cupressoid cross-field pits with slightly inclined apertures, mostly 1-2 per field arranged in one horizontal row, radial longitudinal section, locality Břežánky, UK 3/97, scale bar 50 μm. 13-15. *Glyptostroboxylon rudolphii* DOLEZYCH & VAN DER BURGH, locality the Bílina Mine. 13. One ray seven cells high with intercellular spaces, here in black, tangential longitudinal section, UK 007/98, scale bar 50 μm. 14. General view with "glyptostroboid" cross-field pits and uni- to biseriate pitting in radial tracheid walls with inconspicuous bars of Sanio, radial longitudinal section, UK 007/98, scale bar 50 μm. 15. "Glyptostroboid" cross-field pits with very wide horizontal apertures, mostly 1-2 per field arranged in 1-2 horizontal rows, radial longitudinal section, UK 007/98, scale bar 50 μm.
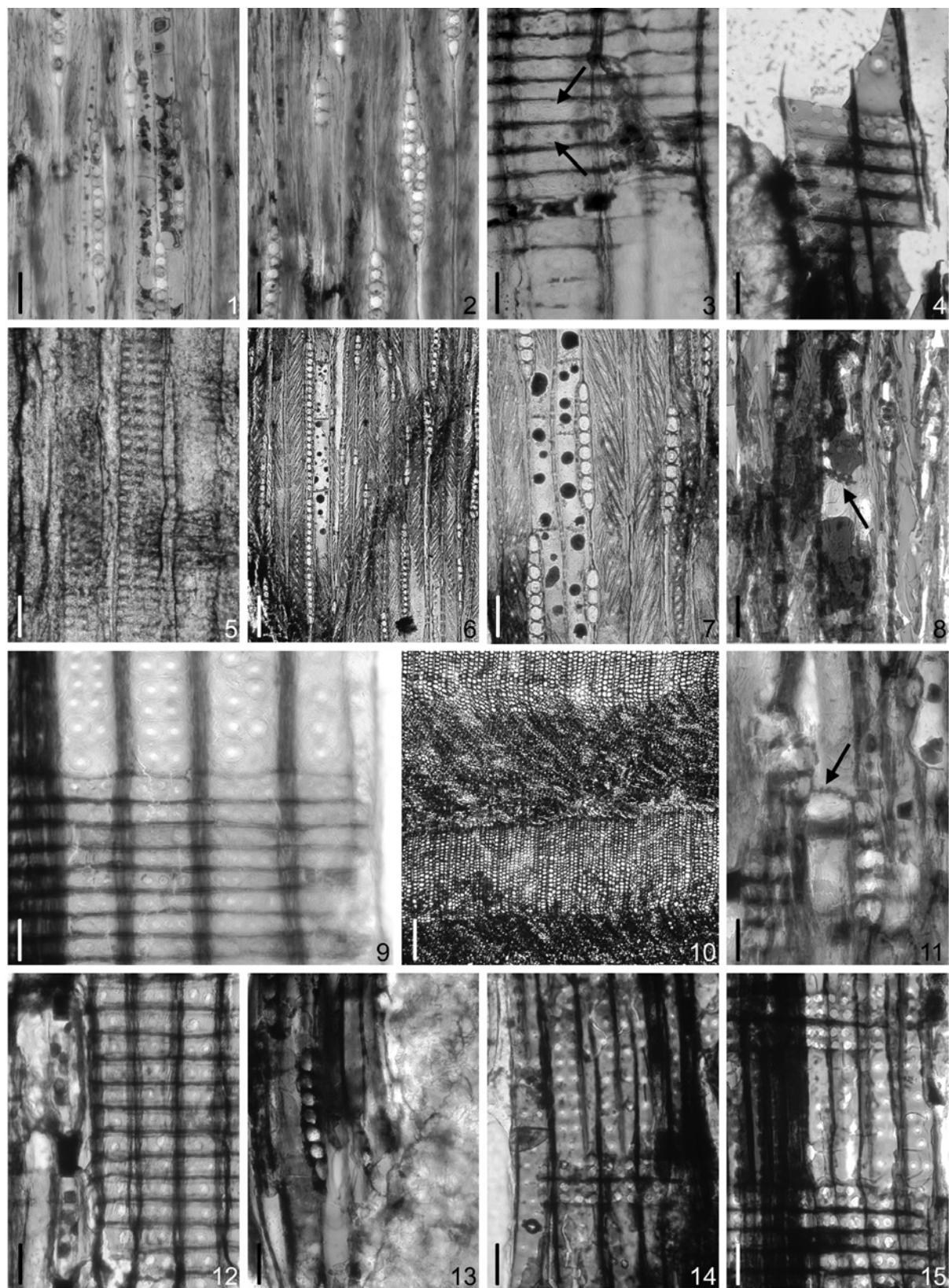
Fig. 5 (Legend see p. 298)

MENEZL (1901: 99, pl. 5, figs. 6-8) noted a leaf and cone evidence of *Widdringtonia helvetica* HEER from the localities Břešt'any, Březno (Priesen), Kučlín, Hradiště near Černovice and Staré Sedlo. Hovever the figured twigs from Břešt'any and Březno (figs. 6-7) show affinity to sterile twigs of *Q. couttsiae* or *G. europaeus* and figured cone (fig. 8) probably related to an endocarp of *Nyssa* sp.

Taxodioxylon HARTIG

6.2. *Taxodioxylon gypsaceum* (GOEPPERT 1842) KRAEUSEL 1949 (wood)
Fig. 5.1-5.5

1842   *Pinites gypsaceus* GOEPPERT, p. 374, pl. 66, figs. 1-2, pl. 67, figs. 4-12.
1949   *Taxodioxylon gypsaceum* (GOEPPERT). – KRAEUSEL, p. 147.

Material: Isolated fragments of permineralized woods – localities: Břežánky [a2], Bílina Mine [a2], J. Šverma Mine [b] and Velká Černoc [h-g].

Description: Transverse section: Growth rings distinct with gradual transition from earlywood to latewood. Tracheids generally polygonal in cross section. Axial parenchyma diffuse or tangentially zonate in latewood. Tangential longitudinal section: Pits on tangential tracheid walls small circular bordered. Rays uniseriate or very rarely partially biseriate and medium to high in height (up to 20 cells, rarely more). Axial parenchyma cells with resin substance and smooth to irregularly thickened transverse end walls. Radial longitudinal section: Pits on radial tracheid walls bordered, circular, 1-3 (rarely up to 4) seriate, opposite, closely spaced with bars of Sanio (= crassulae). Ray tracheids absent. Ray cells procumbent, their horizontal walls thin and smooth, unpitted or very rarely pitted, indentures absent, their end (tangential) walls thin and smooth. Cross-field pits taxodioid, with horizontal to slightly inclined apertures, mostly 2-4 per field arranged in 1 horizontal row (in marginal cells up to 6 per field arranged in 2 horizontal rows).

Remarks: Gymnosperm wood is very common in the Lower Miocene of the Most Basin, however a very few studies are available. ORTMANN (1922) described *Cupressinoxylon krasseri* from Duchcov, which in fact represents the type identical with *Taxodioxylon gypsaceum* according to KRÄUSEL (1949). The genus *Taxodioxylon* is also recorded by BŘEZINOVÁ (1964) from the Vrbenský Mine and by SELMEIER (2001) from the Bílina and Libouš Pruněřov Mines. Finally, HURNÍK-LUFT (1960) identified a conifer wood from Braňany as *Pinus* sp., but with respect to bad preservation and the insufficient description the attribution to Pinaceae remains very problematic. A new re-investigation of thin slides obtained from Z. DVOŘÁK between years 1996-2002 (see descriptions hereafter) reveals that all identifiable specimens belong to Cupressaceae sensu FARJON (2005b), including Cupressaceae sensu stricto and the former Taxodiaceae without *Sciadopitys*. The wood is characterized by absence of normal resin canals and spirals on tracheid walls and by presence of rather abundant axial parenchyma, the abietoid (opposite) type of pitting on radial tracheid walls and cupressoid to taxodioid type of cross-field pitting. Even though the wood of Cupressaceae sensu lato is a very important element of the Tertiary of Europe and comparative anatomical studies of extant members are rather numerous, e.g., HENRY & MCINTYRE (1926), PEIRCE (1936, 1937), PHILLIPS (1948), KRÄUSEL (1949), GREGUSS (1955), GROMYKO (1982, 1990), VISSCHER & JAGELS (2003), there is no consensus on their systematics. Practically, each specialist attributes a different importance to the features observed and a huge amount of wood morphotaxa is in striking contrast with only several elements, based on foliage and reproductive structures.

The specimens, which are here attributed to *Taxodioxylon gypsaceum*, are all characterized by rather abundant axial parenchyma with smooth transverse end walls, closely spaced multiseriate bordered pits with typical crassulae on radial tracheid walls and ray cells with thin unpitted horizontal and end walls and taxodioid cross-field pits with horizontal apertures arranged in horizontal rows. In fact, this morphospecies is one of the most frequent elements in the conifer wood record of the Tertiary of Europe (e.g., PRIVÉ-GILL 1977; BIONDI 1982; VAN DER BURGH & MEIJER 1996; SÜSS & VELITZELOS 1997 with the list of species of *Taxodioxylon*). As also emphasized by VAN DER BURGH & MEIJER (1996: 373) "…*T. gypsaceum* is highly variable polyphyletic species" which reflects a great variation recorded by BAILEY & FAULL (1934) in *Sequoia sempervirens* (D. DON) ENDL.

Discussion: *Taxodioxylon gypsaceum* is traditionally compared with the wood of modern *Sequoia* (e.g., PRIVÉ-GILL 1977; DOLEZYCH & SCHNEIDER 2006). Another possibility, mentioned also by HUARD (1966), is that the wood of *T. gypsaceum* belongs not only to *Sequoia* but also to other extinct plants close to *Sequoia*, as for example *Quasisequoia couttsiae*. This was already suggested by VAN DER BURGH & MEIJER (1996) who found in the Schleenhain opencast mine (Upper Eocene, Germany) a layer with the wood of *T. gypsaceum* and leaves and cones belonging exclusively to *Q. couttsiae*. We believe that this is the only possible solution also in the case of the Most Basin where no leaves, cones or seeds of *Sequoia* (e.g., *S. abietina*) are present in the whole series in comparison with abundant remains of *Quasisequoia*. Hence, we propose *Taxodioxylon gypsaceum* as the wood of *Quasisequoia couttsiae* plant, which grew in Early Miocene in the Most Basin. Most recently, DOLEZYCH proposes in the published version of her PhD Thesis (DOLEZYCH 2005: 256), together with J. VAN DER BURGH, a new genus *Quasisequoioxylon*, which is intermediate between *Cupressinoxylon* GOEPPERT (predominance of cupressoid cross-field pits) and *Taxodioxylon* (bi- to triseriate bordered pits on radial tracheid walls). Based on co-occurrence of this type of wood with remains of *Q. couttsiae* in the mines Piskowitz (Early/Middle Miocene, Germany) and Hambach (Late Miocene, Germany), DOLEZYCH (2005) concludes that this wood belongs to *Q. couttsiae* plant. These two parallel interpretations remain unsolved till the wood is found in direct organic connection with leaves or cones of *Q. couttsiae*.

Taxodium RICHARD

7. *Taxodium dubium* plant

7.1. *Taxodium dubium* (STERNBERG 1823) HEER 1853
(leaves, cones, seeds)
Fig. 4.5-4.11

1823   *Phyllites dubius* STERNBERG, p. 37, pl. 36, fig. 3.
1853   *Taxodium dubium* (STERNB.). – HEER, p. 136.
1866   *Taxodium dubium* (STERNB.) HEER. – ETTINGS-HAUSEN, p. 34, pl. 10, fig. 13, pl. 12, figs. 1-7 (pro parte).
1876a   *Taxodium distichum miocenicum* HEER. – ENGEL-HARDT, p. 15.
1881   *Taxodium dubium* (STERNB.) HEER. – VELENOVSKÝ, p. 14, pl. 1, fig. 27.
1901   *Taxodium distichum miocenicum* HEER. – MENZEL, p. 86.
1901   *Torreya bilinica* SAP. et MAR. – MENZEL, p.104, pl. 5, fig. 4.
1949   *Taxodium distichum miocenicum* HEER. – NĚMEJC, p. 27, pl. 2, fig. 9, pl. 3, fig. 2, pl. 5, figs. 7-10.
1953   *Taxodium distichum miocenicum* HEER. – NĚMEJC, p. 14, pl. 1, figs. 1-2.
1953   *Sequoia langsdorfii* HEER – NĚMEJC, p. 14, pl. 2, figs. 1-2.
1964   *Taxodium dubium* (STERNBERG) HEER. – BŮŽEK & HOLÝ, p. 111, pl. 2, figs. 1-7.

Material: Great quantity of sterile twigs with needles (T), macroblasts (PT), unripe seed cones (F), isolated bract scales (Sc), seeds (S), pollen cones (M) – localities: Bílina Mine [a2-b] (T, PT, F, Sc, M), J. Fučík Mine [a2-b] (T, F), Břešťany, Březánky [a2] (T, PT, F, Sc, M, S), Čermníky [g, c] (T, F, Sc), Chotěnice [c] (T), Chuděřice [a2] (T), Dobrčice [c] (T), Dolany [c] (T), Ležáky Mine [a2-b] (T, F), Holedeč [c] (T), Nesuchyně [h-g] (T), Nástup-Tušimice Mine [e, c, a2] (T, Sc, M), Přívlaky [a2] (T), Stranná [a2] (T), Stroupeč [c] (T), J. Šverma Mine [a2-b] (T, F, Sc, S), Velká Černoc [h-g] (T), Vršovice [c] (T, Sc), Zabrušany [a2] (T), Želeč [g-h] (T) and Želénky [a2] (T); – cores: Březánky /B 4, depth 72.6 m [a2] (T, Sc)/, Droužkovice /Do 206, depth 117.4 m [f] (F, Sc); Do 210, depth 47.5 m [b] (F), Do 215, depth 44.5 m [d] (T, F, Sc)/; Havráň /Hň 35, depth 143 m [f] (S); Hň 36, depth 34.2 m [c] (S)/, Chomutov /Co 210, depth 40.9 m [a2] (T, Sc), depth 99.8 m [c] (T), Co 228, depth 98.75 m [d] (T, Sc), Otvice /Ot 27, depth 74.3 m [f] (Sc, S)/, Pesvice /Pe 18, depth 67 m [d] (Sc), Pe 19, depth 98, 8 m [d] (Sc), Přečaply /Pč 4, depth 80-81 m [e] (S)/, Strupčice /Sr 39, depth 63 m [c] (Sc)/, Široké Třebčice /Štb 43, depth 26.4 m [d] (S)/, Údlice /Úd 81, depth 47 m [b] (S)/, Vršany /Vr 22, depth 79-80 m [d] (Sc)/ and Vysoká Pec /VP 14, depth 48.5 m [c] (Sc, S), depth 50.5 m [c] (Sc), depth 59.5 m [c] (Sc, S); VP 15, depth 96 m [f] (S)/.

Description: Sterile twigs with needles, differently sized, flattened, distichous, alternate at unequal distances, linear to lanceolate, apex acute, base often very shortly petiolate and rounded, venation with strong and distinct midrib, often obvious dense parallel venation, rarely branched; uncommon perennial macroblast with spiral imbricate needles; unripe seed cone ovate to rounded in outline, 52 to 86 mm long, 43 to 63 mm; bract scale complex helicaly arranged, isolated bract scale, pelatate, distally rounded or broadly squared to rhombic, 8 to 12.5 mm high and 5.5 to 11 mm broad, rugose, with distinct transverse ridge caused by the relatively small bract and a sulacate to undulate upper margin, 2 seed imprints visible axillary; seed oblong to irregularly triangular to angular-ovate in outline, flattened, 7.8 to 10.3 mm long and 4.4 to 5.2 mm broad, often bent, base rounded, apex acute, margin undulate to finely cristate, seed cavity central oblong to triangular, often longitudinally furrow distinct, boarder by narrowed wing, densely, finely and longitudinally furrowed; pollen cones oval to rounded in outline, 1.2 to 2.3 mm in diameter, each cone attached in the axis of a small scale-like leaf, arranged in relatively long drooping clusters, sympodially branched.

Remarks: The most common conifer of the Most Basin (e.g., MENZEL 1901, BRABENEC 1909) mainly known from coal and clay facies as well as from the Tertiary fluvial remnants (NĚMEJC 1949, 1953) was typified by KVAČEK (1976: 290-294) including synonymy and as well as comments on affinity of *Taxodium balticum* SVESHNIKOVA & BUDANTSEV (1960). This taxon occurs as sterile deciduous twigs, unripe cones, isolated scales and seeds there. Epidermal characteristic published by e.g., KVAČEK (1976, 1985), SAKALA (2000) helps to safely distinguish *Taxodium* leaves from *Sequoia* ENDLICHER or *Metasequoia* HU & W. C. CHENG leaves however several morphological diacritical features exist (e.g., NĚMEJC 1968; SAKALA 2000). MENZEL (1901: 104, pl. 5, fig. 4) described isolated sterile leaf twig from Břešťany and Zichov as *Torreya bilinica* SAP. & MAR. (pl. 2, fig. 6). *T. dubium* matches morphologically both extant species of *Taxodium* – i.e., *T. distichum* (L.) RICH. occupying swampy regularly flooded forests from the southern-east area of the USA and *T. mucronatum* TEN. known as an element of mountain swampy forests from Mexico. But, the epidermal pattern shows affinity to *T. mucronatum* rather than *T. distichum* (KVAČEK, personal communication 2008). The genus *Taxodium* from the Palaeogene and Neogene of Central Europe was most recently overviewed by KUNZMANN et al. (in press).

Taxodioxylon HARTIG

7.2. *Taxodioxylon taxodii* GOTHAN 1906 (wood)
Fig. 5.6-5.12

1906   *Taxodioxylon taxodii* GOTHAN, p. 164.

Material: Isolated fragments of the permineralized and one xylitic woods – localities: Břežánky [a2], Bílina Mine [a2] and Vršany [c].

Descriptions: Transverse section: Growth rings distinct with gradual transition from earlywood to latewood. Tracheids generally polygonal in cross section. Axial parenchyma diffuse or tangentially zonate in latewood. Tangential longitudinal section: Pits on tangential tracheid walls small

circular bordered. Rays uniseriate or very rarely partially biseriate and medium to very high in height (up to 38 cells). Axial parenchyma cells with resin substance and with typical nodular transverse end walls. Radial longitudinal section: Pits on radial tracheid walls bordered, circular, 1-2 (rarely up to 3) seriate, opposite, closely spaced with bars of Sanio (= crassulae). Ray tracheids absent. Ray cells procumbent, their horizontal walls thin and smooth, un-pitted or very rarely pitted, indentures not observed, their end (tangential) walls thin and smooth. Cross-field pits taxodioid, with horizontal to slightly inclined apertures, mostly 2-3 per field arranged in 1 horizontal row (in marginal cells up to 6 per field arranged in 2 horizontal rows).

Remarks: The woods, attributed here to *Taxodioxylon taxodii*, are in fact similar to the previously characterized *T. gypsaceum*. Both species have muliseriate piting on radial tracheid walls with crassulae, abundant axial parenchyma, and high uniseriate rays with thin smooth both horizontal and tangential walls and mostly taxodioid cross-field pits. The main difference consists in the character of transverse end wall in axial parenchyma which is nodular in *T. taxodii* contrary to smooth or irregularly thickened in *T. gypsaceum*. Other co-occurring differences which we have observed in ray height (generally higher in *T. taxodii* which can exceed 30 cells), pitting on radial tracheid walls (generally biseriate in *T. taxodii* vs. 2-4 seriate in *T. gypsaceum*) and cross-field pits (slightly more numerous per field in *T. gypsaceum*), are consistent with the previous observations (GOTHAN 1906; HUARD 1966; DOLEZYCH 2005, see comparative Table 4 in PRIVÉ 1975: 106-107). Contrary to the previous observations, we did not observe differences in thickness and character of horizontal ray walls (rather thick and pitted in *T. taxodii* according to DOLEZYCH & SCHNEIDER 2007) and size of cross-field pits (bigger in *T. gypsaceum* according to HUARD 1966). The measurement was difficult or even impossible, obscured by permineralization of the specimens studied. However, it should be noticed that there is a difference between palaeobotany and botany in perception of horizontal walls of rays in Cupressaceae sensu lato. Palaeobotanists generally attach importance to their thickness and possible pitting (HUARD 1966; PRIVÉ 1975; VAN DER BURGH 1973; DOLEZYCH 2005). On the other hand, IAWA COMMITTEE (2004: 48) recognizes 'distinctly pitted' walls for some members of Pinaceae only, as opposite to 'smooth unpitted' walls for other conifers. This surely corresponds to the fact that there is no secondary wall in ray parenchyma cells in other than Pinaceae as already noticed by BAILEY & FAULL (1934: 241-242). Similar difference between Pinaceae and other conifers is also present in transverse end walls in axial parenchyma (IAWA COMMITTEE 2004: 39). Finally, one specimen, No 3 (Březánky 3, see Fig. 5.10-5.12), with markedly nodular transverse end walls in axial parenchyma but uniseriate rarely biseriate pitting on radial tracheid walls and only cupressoid crossfield pits was also attributed to *T. taxodii*. In fact, there is no earlywood tracheid preserved in this specimen, they are all folded (see Fig. 5.10). We believe that the differences from the typical form of *T. taxodii* (cupressoid vs. taxodioid crossfield pits, uniseriate vs. biseriate pits on radial tracheid walls) are due to the fact that we observed

features on latewood tracheids only which are obviously narrower. This interpretation is supported by the results of BAILEY & FAULL (1934: 238) on pitting on radial radial tracheid walls or GROMYKO (1990) on cross-field pits.

Discussion: Leaves, cones and seeds of *Taxodium dubium* are morphologically and ecologically similar to both species of extant *T. distichum* and *T. mucronatum* (KVAČEK et al. 2004b). Concerning the fossil wood, there is a general consensus that *Taxodioxylon taxodii* represents the wood of *Taxodium* as well. HUARD (1966) recognized two fossil species related to *Taxodium*, i.e., traditional *Taxodioxylon taxodii* compared with *T. mucronatum* and his new species *Taxodioxylon distichoides* related with *Taxodium distichum*. Differences between the two morphogenera (and the corresponding nearest living relatives) consist according to HUARD (1966) in bigger cross-field pits, thinner horizontal walls in rays and wider ray cells in *T. taxodii* (*Taxodium mucronatum*) comparing to *T. distichoides* (*Taxodium distichum*); data for modern representatives are partly based on GREGUSS (1955) partly on his own observations. The results published by GROMYKO (1982, 1990) do not confirm any unequivocal distinction between *Taxodium distichum* and *T. mucronatum*. Recently, DOLEZYCH & SCHNEIDER (2007) based on their own observations excluded relation of *T. taxodii* to *Taxodium distichum*, which contrary to the fossil species has both cupressoid and taxodioid cross-field pits, anatomical comparison with *Taxodium mucronatum* has however not been made. As a result, we can say that leaves, cones and seeds of *Taxodium dubium* and wood of *Taxodioxylon taxodii* all belong to the single *Taxodium* plant, the exact nearest living relative of which is however uncertain.

Z. DVOŘÁK (personal communication 2007) noticed that in the horizons with the dominance of *Taxodium* remains there were woods containing duxite, a specific type of fossil resin (see in VÁVRA et al. 1997). Our xylotomical analyses prove that all specimens of wood having duxite (with a single exception) can be attributed to *Taxodium*. Hence, we can speculate that the presence of duxite is of systematical importance and *Taxodium dubium* plant can be determined as the duxite producer tree.

Glyptostrobus ENDLICHER

8. *Glyptostrobus europaeus* plant

8.1. *Glyptostrobus europaeus* (BRONGNIART 1833) UNGER 1850 (leaves, cones, seeds)
Fig. 4.12-4.16

1833   *Taxodium europaeum* BRONGNIART, p. 168.
1850   *Glyptostrobus europaeus* (BRONGN.). – UNGER, p. 434.
1866   *Glyptostrobus europaeus* (BRONGN.) UNGER. – ETTINGSHAUSEN, p. 37, pl. 10, figs. 10-12, pl. 12, figs. 3-7, 11-12.
1866   *Glyptostrobus bilinicus* ETTINGSHAUSEN. – p. 39, pl. 11, figs. 1-2, 10.
1876a   *Glyptostrobus europaeus* (BRONGN.) UNGER. – ENGELHARDT, p. 29, pl. 4, fig. 9.

1881   *Glyptostrobus europaeus* (Brongn.) Unger. – Velenovský, p. 15, pl. 1, figs. 21-26.

1901   *Glyptostrobus europaeus* (Brongn.) Unger. – Menzel, p. 87, pl. 5, figs. 1-3.

1901   *Athrotaxidium bilinicum* Menzel, p. 97, pl. 5, figs. 13-16.

M a t e r i a l : Great quantity of sterile twigs (T), seed cones (F), isolated cone scales (Sc), seeds (S), pollen cones (M) – localities: Březánky, Břešťany [a2] (F, M, S, T), Bílina Mine [a2-b] (F, M, S. T), Čermníky [a2, c] (T, F), Dobrčice [c] (T), Dolany [c] (T, F), Holedeč [c] (T, F), Chotěnice [c] (T), Chuděřice [a2] (F, S), Ležáky Mine [a2-b] (T, F), Nástup-Tušimice Mine [a2, c, e, f] (T, F, Sc), Marianna Mine [c] (T, F), Nesuchyně [g-h] (T), Nechranice [a2] (T), Přívlaky [a2] (T), Stroupeč [a2] (T), Tuchořice [g] (T), Velká Černoc [g-h] (T), Vršovice [c] (T), Zabrušany [a2] (T), Záhoří near Žatec [c] (T), Želeč [g-h] (T), Želénky [a2] (T), J. Fučík Mine [a2-b] (T, F), J. Šverma Mine [a2-b] (F, Sc, S, T) and Maxim Gorkij Mine [a2-b] (Sc); – cores: Březánky /B 1, depth 131.1 m [a2] (F), depth 132.4 m [a2] (F)/, Chomutov /Co 199, depth 66.3 m [c] (S), depth 101.8 m [g] (S), Co 201, depth 86.1 m [d] (S), depth 87.0 m [d] (S), Černice /CN 54, depth 56-60 m [a2] (T)/, Droužkovice /Do 201, depth 65.6 m [a2] (F), Do 210, depth 47.5 m [b] (F, S, T), Do 215, depth 44.5 m [d] (Sc)/; Havráň /Hň 35, depth 54 m [c] (F, S), depth 143 m [f] (F)/, Horní Litvínov /LiH 13, depth 42-57 m [a2] (T)/, Hošnice /Hň 4, depth 45.2 m [d] (F, Sc, S, T), depth 60.4 m [e] (Sc)/, Kralupy near Chomutov /Kr 110, depth 98.65 m [f] (F, S, T)/, Kundratice /KU 127, depth 64-79 m [a2] (T), KU 115, depth 90-99.2 m [a2] (T)/, Libkovice /P 542, depth 94-95 m [a2] (F, S)/, Lom /LOM 16, depth 54.5-54.6 m [a1] (C, S, T)/, Mariánské Radčice /MR 58, depth 111.5-143.3 m [a2] (T)/, Moravěves /Ma 6, depth 116.1 m [f] (F), Ma 8, depth 66.5 m [f] (S)/, Otvice /Ot 27, depth 74.3 m [f] (S)/, Pesvice /Pe 18, depth 67 m [d] (Sc, S), Pe 19, depth 82.3 m [d] (Sc), depth 89.9 m [d] (Sc), Pe 21, depth 51.0 m [b] (F, Sc, S), depth 99.0 m [e] (S)/, Přečaply /Pč 4, depth 80-81 m [e] (S)/, Prunéřov /Pn 138, depth 60 m [g] (F, S, T)/, Spořice /Sp 95, depth 110. m [f] (T)/, Strupčice /Sr 39, depth 63 m [c] (S, T), Sr 40, depth 90 m [d] (F, Sc, S), Sr 53, depth 48.0 m [c] (S), depth 50 m [c] (S)/, Škrle /Šk 3, depth 61 m [d] (F, Sc, S)/, Široké Třebčice /Štb 43, depth 26.4 m [d] (Sc, S, T)/, Údlice /Úd 80, depth 45.4-45.7 m [e] (F, S), Úd 81, depth 106 m [f] (S)/, Vršany /Vr 22, depth 75 m [d] (F, S), depth 79-80 m [d] (Sc, S)/, Vysoká Pec /VP 14, depth 48.5 m [c] (S), depth 59.5 m [c] (S), depth 70.5 m [d] (S); VP 15, depth 95-96 m [f] (S), VP 16, depth 65.0 m [c] (S), depth 73 m [d] (S)/ and Vysočany /Vy 1, depth 71.0 m [d] (F, Sc)/.

D e s c r i p t i o n : Sterile twigs with spiral imbricate needles or cryptomeroid leaves (typical of young or fertile twigs). Incomplete seed cones 1.3-1.9 mm long and 8.5-1.2 mm broad, obovate to globular, only basal part usually preserved, apex obtuse, base cuneate to broadly cuneate, consisting of 8 scales (fragmentary), scale complexes rhombic to deltoid, in the lower part formed by bract scale, in the upper part by seed scale. Bract scales wedge-shaped, base narrowed, apical part mucronate, small umbo, abaxial side wrinkled, seed scale rounded or triangular with notched margin, small notches numbering of 6 to 8, sculptured by radial furrows, seed scales overgrow about 2 to 4 mm beyond the bract scale. Seeds 4.6-11.4 mm long and 2.1-4.2 mm broad, apical winged, oblong in outline, distinctly bent, flat, seed bodies oval (1.8 to 2.46 mm long and 0.86 to 1.2 mm broad), often situated in lower third of seeds, finely longitudinally sculptured, seed wings bent, starting at basal parts, forming basal rims, bordered seeds towards obtuse apices, distinct concave sides crest-shaped, descending to convex sides, upper surface hardly visible, formed by elongated to polygonal pits (55.3 to 89.5 µm long and 19.1 to 31.6 µm broad).

R e m a r k s : The genus *Glyptostrobus* Endlicher is a common and well-known coal-forming conifer occurring in the whole area of the Most Basin as well as in Northern Bohemia. The taxon is proved by pollen and seed cones, their isolated scales, seeds and sterile twigs – e.g., Menzel (1901), Bůžek & Holý (1964). The sterile twigs of *Glyptostrobus* are morphologically identical with leaves of *Quasisequoia couttsiae* (Heer) Kunzmann and often co-occur in fossil sites (e. g., Bílina Mine). The difference in the epidermal structure of both taxa is noted by many authors – e. g., Kvaček (1985), Kunzmann (1999), Sakala (2000). Recently, Ma et al. (2007, table 1) summarize epidermal differences of several extant "Cupressaceous" taxa. Mai & Walther (1988: 68, pl. 6, figs. 4-9) newly combined *G. brevisiliquata* (Ludwig) Mai & Walther based on the seed material from the Pliocene localities of Gerstungen und Dorheim / Wetterau. However, associated twigs and cones were described as *G. europaeus*. This seed morphotaxon is common element for the Middle Miocene to Pliocene European localities (e. g., Mai 2000) and is often clearly undistinguishable from seeds of *G. europaeus* due to broad morphological inter-specific variability, which is also distinct in the seedy variability of living plants. Menzel (1901: 97, pl. 5, figs. 13-16.) described leaf and cone material as *Athrotaxidium bilinicum* Menzel from Břešťany. We interprete this material as immature and worn out seed cones of *G. europaeus* (cf. Kunzmann 1999: 60). *G. europaeus* can be interpreted as an autochthonous, predominant element of coniferous peat-forming swamp forest and mixed swamp forest (see below). A single living species *G. pensilis* (Staunton ex D. Don) K. Koch occupies humid biotopes on the riverbanks or near the seacoast in southern China (Sveshnikova 1963) and in southern Vietnam (Farjon 2005b).

Glyptostroboxylon Conwentz emend. Dolezych & van der Burgh

8.2. *Glyptostroboxylon rudolphii* Dolezych & van der Burgh 2004 (wood)
Fig. 5.13-5.15

2004   *Glyptostroboxylon rudolphii* Dolezych & van der Burgh, p. 409, text-figs. 6-7, pl. 2, figs. 1-9, pl. 3, figs. 1-5.

Material: One fragment of sideritic wood – locality: Bílina Mine [a2].

Description: Transverse section: Growth rings distinct with gradual transition from earlywood to latewood. Tracheids polygonal in cross section. Axial parenchyma tangentially zonate in latewood. Tangential longitudinal section: Pits on tangential tracheid walls small circular bordered. Rays uniseriate and medium in height (up to 14 cells). Axial parenchyma cells with unknown character of transverse end walls. Radial longitudinal section: Pits on radial tracheid walls bordered, circular, generally uni- to biseriate, closely spaced opposite with inconspicuous bars of Sanio (= crassulae). Ray tracheids absent. Ray cells procumbent, their horizontal walls thin and smooth, indentures not observed, their end (tangential) walls thin and smooth. Cross-field pits exclusively "glyptostroboid" (= taxodioid with very narrow borders approaching almost pinoid) with horizontal to slightly inclined apertures, mostly 1-2 per field arranged in 1 horizontal row (in marginal cells 3-5 per field arranged in 2 horizontal rows).

Remarks: The morphogenus *Glyptostroboxylon* is characterized by the presence of "glyptostroboid" cross-field pits, which means in terms of the IAWA Committee (2004) taxodioid cross-field pits with very narrow borders (or very wide horizontal to slightly inclined apertures) approaching almost pinoid ones. As already emphasized by Süss & Velitzelos (1997: 16) and Fairon-Demaret et al. (2003: 122), Gothan (1905) was apparently the first who noticed that this feature is typical not only of the recent genus *Glyptostrobus*, but also of *Cunninghamia* R. Brown ex Richard & A. Richard. This was most recently articulated by Dolezych & van der Burgh (2004) who emended the diagnosis of *Glyptostroboxylon* based on the original type material to accommodate fossil woods with affinities to both modern genera: *Glyptostroboxylon tenerum* (Kraus) Conwentz is newly interpreted as a wood of *Cunninghamia* contrary to *G. rudolphii* Dolezych & van der Burgh which represents the wood of *Glyptostrobus*. According to Dolezych & van der Burgh (2004), the type of cross-field pits (glyptostroboid) and transverse end wall of the axial parenchyma (smooth to slightly nodular) cannot help to distinguish these two species. The main differences consist in pitting in radial tracheid walls (biseriate with crassulae in *G. rudolphii*, uniseriate without crassulae in *G. tenerum*) and disposition of cross-filed pits (typically more numerous per field in *G. rudolphii*); the presence of indentures in *G. tenerum* and large intercellular spaces in rays of *G. rudolphii* can be noticed as subsidiary distinctive features. Our fossil wood despite its bad preservation can be related to *G. rudolphii*: numerous "glyptostroboid" cross-field pits correlate with biseriate pitting in radial tracheid walls (Fig. 5.14-5.15) and rays, even if generally badly preserved, seem to have large intercellular spaces present as dark triangles (Fig. 5.13).

Discussion: Generally, there is an interesting disproportion between abundant leaves and cones/seeds of *Glyptostrobus* and only one specimen of wood attributable to this genus. This is emphasized by the fact that *Glyptostrobo-*

xylon is traditionally considered as the main coal-forming element (e. g., Kvaček 1998). A possible interpretation could lie in taphonomy, i. e., in-situ upright stems in close vicinity of the coal seam, which are related to the *Glyptostrobus* association (sensu Kvaček & Bůžek 1982) characteristic of peat-forming swamps and supposed to belong directly to *Glyptostrobus*, are often preserved as xylite. These xylitic specimens are very numerous but they are generally badly preserved. They can hardly be identifiable at the specific or even generic level; we can only identify them as Cupressaceae sensu lato. This, however, does not exclude their affinity to *Glyptostrobus*. Recently, a petrified forest with wood of *Glyptostroboxylon rudolphii* was described from the Middle Pliocene of NW Italy by Vassio et al. (2008).

Tetraclinis Masters

9. *Tetraclinis salicornioides* plant

9.1. *Tetraclinis salicornioides* (Unger 1841) Kvaček 1989 (leaves)
Fig. 4.17-4.18

1841   *Thuites salicornioides* Unger, p. 11, pl. 2, figs. 1-4.
1989   *Tetraclinis salicornioides* (Ung.) Kvaček, p. 48, pl. 1, fig. 11, pl. 2, figs. 2-14, pl. 3, figs. 3-4, text-fig. 1.

Material: Incomplete sterile foliage twigs and their fragments (T) – localities Nesuchyně [h-g], Nástup-Tušimice Mine [a2] and Bílina Mine [a2-b], – core Kundratice KU 127, depth 64-79 m [a2].

Description: Incomplete foliage twigs mostly oppositely branched, up to 450 mm long, branchlets flattened, 6.1-(8.9)-11.3 mm long, base truncate to rounded, apex obtuse with terminal and two lateral incisions, towards apex gradually broaden, at base 1.3-(1.7)-2.1 mm broad and at apex 2.34-(3.86)-4.22 mm broad, individual needles imbricate, markedly flatted, 4 fused in a pseudowhorl, forming a cladode-like segment (cladodium), innervating with distinct midrib and two lateral thin veins.

Remarks: This conifer rarely occurs in the area of the Most Basin. Only fragmentary foliage material has been known from the localities Nástup-Tušimice Mine, Bílina Míne and Nesuchyně contrary to relatively common occurrences of fossil cones, seeds and foliage from Oligocene localities ofČeské Středohoří Mts and Doupovské hory Mts (detailed in Kvaček 1989). Two fossil species have been recognized from the European Tertiary – i. e. *T. salicornioides* (Ung.) Kvaček (Middle Eocene to Early Pliocene) and *T. brachyodon* (Brongniart) Mai & Walther 1978 (Early Eocene to Early Pliocene), although Mai (1997) merges these species to one entity. *T. salicornioides* is typified by sterile twigs from the Middle Miocene (Sarmatian) sediments of Radoboj (Unger 1841), where individual impressions were described as *Thuites salicornioides* Ung. Endlicher (1847) regarded fossil material to

the genus *Libocedrites* ENDLICHER. Similarly HEER (1855) re-assigned those fossils to *Libocedrus salicornioides* (UNG.) HEER. KVAČEK et al. (2000) defined a new variety, *T. salicornioides* (UNGER) KVAČEK var. *praedecurrens* (KNOWLTON) KVAČEK & MANCHESTER typical of the Oligocene and Miocene of western North America. Our material, as well as other material from Europe to Transcaucasia (Middle Eocene to Early Pliocene in age) belongs to variety *salicornioides* (KVAČEK et al. 2000). Generally, *T. salicornioides* is an element of the mesophytic, humid forests along river and basin banks. Extant *T. articulata* (VAHL.) MASTERS occupies warm, summer-dry vegetation of northern Africa, Malta and southern Spain (KVAČEK et al. 2000) that fits better to more xerophytic fossil *T. brachyodon*.

9.2. *Tetraclinoxylon vulcanense* PRIVÉ 1973 (wood)

Discussion: The wood of *Tetraclinis* is unknown from the Most Basin. However, it has been interpreted from the neighbouring volcanic area of the České středohoří Mts. and designated as *Tetraclinoxylon vulcanense* by SAKALA (2003) based on the fossil trunk from the Late Eocene locality Kučlín, described originally as *Podocarpoxylon helmstedtianum* GOTTWALD by BŘEZINOVÁ et al. (1994). Another interpretation of the wood of *Tetraclinis salicornioides* is done by DOLEZYCH (2005: 259) who described a different fossil wood from the clay pit Tetta-Buchholz (Middle Miocene, Germany) as *Cupressinoxylon boureaui* (GRAMBAST) DOLEZYCH & VAN DER BURGH. This new combination points to D o l e z y c h's large concept of the morphogenus *Cupressinoxylon* (see in DOLEZYCH & SCHNEIDER 2006: 180).

Geinitziaceae KUNZMANN

Cupressospermum MAI 1960 emend. KUNZMANN 1999

10. *Cupressospermum saxonicum* plant

10.1. *Cupressospermum saxonicum* (MAI 1960) KUNZMANN 1999

1960　*Cupressospermum saxonicum* MAI, p. 75, pl. 3, figs. 1-5, text-figs. 1-2 (holotypus).
1974　*Cupressospermum saxonicum* MAI. – HOLÝ, p. 15, pl. 2, figs. 2-10.
1977　*Cupressospermum saxonicum* MAI. – KVAČEK & HOLÝ, p. 10.
1999　*Cupressospermum saxonicum* (MAI) KUNZMANN, pl. 92, pl. 21, figs. 1-9, pl. 22, figs. 1-9, pl. 23, figs. 1-9, text.-figs. 18, 21/5.

Material: 7 isolated seeds (S) – core: Jenišův Újezd near Bílina /Jú 224, depth 151.2 m [b]/.

Description: Seed flattened, reniform, cashew-nut shaped to broadly sub-circular in general outline, 1.59-(2.19)-3.2 mm long and 1.28-(1.66)-2.34 mm broad, maximal thickness in transversal plane 0.45 mm, distinctly winged on the dorsal convex side, relatively thick wing (ca. 0.35 mm broad) bordered whole seed excluding ventral concave side, locule campylotropous or amphitropous, rounded on both ends, hilum and micropyle basiventral, micropyle rarely obvious as rounded protuberance, upper surface rugulose, pits quadrangular or polygonal, rarely oblong 10.9-19.1 µm long and 8.2-16.3 µm broad, arranged into regular parallel grooves copying curvature of seeds, structure of testa (MAI 1960: 74 and KUNZMANN 1999: 96)

Remarks. This taxon was defined by MAI (1960: 75, pl. 3, figs. 1-5) on the basis of the seed material from Olbersdorf near Zittau including a second species, i. e., *C. chamaecyparoides* MAI from Hartau near Zittau (MAI 1960: 75, pl. 3, figs. 8-11). KUNZMANN (1999: 91-98) emended the genus and species diagnosis and added a detailed description of seed cones and of the epidermal structure of needle and cone. The above-described seeds give the first evidence of *Cupressospermum saxonicum* (MAI) KUNZMANN in the Most Basin. However, HOLÝ (1974: 15) noted the seed cones, isolated seed scales and seeds from the Kristina Mine (Hrádek part of the Zittau Basin). Similarly KVAČEK & HOLÝ (1977: 10) pointed out *C. saxonicum* from sandy deposits of the Habartov Member of the Sokolov Formation in the Sokolov Basin. This important taxon can be used as a phytostratigraphical marker which could correlate sediments of the uppermost part of the Holešice Member of the Most Formation with the Habartov Member of the Sokolov Formation and the Upper Coal Seams sensu lato of the Hrádek Formation as well as sediments of the Lower Miocene of Lausitz (Saxony, Germany). MAI & SCHNEIDER (1988: 107-110) interpreted *C. saxonicum* as an element of the eutrophic swamp forest associated with *Glyptostrobus* and *Taxodium* or as an element of the association of *Cupressospermum-Comptonia*.

Discussion: DOLEZYCH (2005: 250) described *Juniperoxylon pachyderma* (GOEPPERT) KRAEUSEL from the opencast mine Nochten (Early/Middle Miocene, Germany) as a fossil wood of Cupressaceae sensu lato however without any exact nearest living relative. This wood is characterized by nodular both transverse end walls in axial parenchyma and tangential walls in rays as well as by taxodioid to cupressoid cross-field pits and fits very well the broad concept of the genus *Juniperoxylon* GOTHAN proposed by VAN DER BURGH (1973). Based on co-occurrence of seeds and twigs of *Cupressospermum*, DOLEZYCH (2005) interpreted this wood as belonging very probably to this botanical genus. Unfortunately, such a wood structure is still unknown from the Most Basin.

5. Holistic approach – Whole-Plant Concept

Nine natural units – botanical conifer species (in systematical part numbered and denominated as different 'plants') were defined for the whole area of the Most Basin. They are based on the combination of

Table 1. Summary of the floristic conifer composition in different stratigraphical levels of the Most Basin. – Symbols: a1 (Lom Member sensu DOMÁCÍ 1977), a2 (Libkovice Member sensu DOMÁCÍ 1977), b-g (Holešice Member sensu DOMÁCÍ 1977) – i.e., in the sense of HURNÍK & MAREK (1962): b (Upper Seam Beds), c (Upper Interseam Beds), d (Middle Seam Beds), e (Lower Interseams Beds), f (Lower Seam Beds) and g (Lower Sandy-Clayey Beds with Basal Coal Seam), h (Duchcov Member sensu DOMÁCÍ 1977); F (seed cones), Sc (isolated scales of the female cone), M (pollen cones), S (seeds), L (leaves) and W (wood).

Taxon	Organs	Stratigraphical levels of the Most Basin								
		a1	a2	b	c	d	e	f	g	h
***Pinus engelhardtii* plant**										
Pinus engelhardtii MENZEL	F, S			*	*					
Pinus rigios (UNGER) ETTINGSHAUSEN	L			*	*					
***Pinus ornata* plant**										
Pinus ornata (STERNBERG) BRONGNIART	F			*						
Pinus hepios (UNGER) HEER sensu MENZEL	L			*		*				
***Pinus urani* plant**										
Pinus urani (UNGER) SCHIMPER	F		*							
Additonal material related to *Pinus* L.										
Pinus sp. 1	M			*						
Pinus sp. 2	L								*	*
Pinus sp. indet.	L			*						
***Pseudolarix schmidtgenii* plant**										
Pseudolarix schmidtgenii KRAEUSEL	Sc, S								*	*
Pseudolarix sp.	L								*	*
***Quasisequoia couttsiae* plant**										
Quasisequoia couttsiae (HEER) KUNZMANN	F, Sc, L, S	*	*	*	*	*	*	*		
Taxodioxylon gypsaceum (GOEPPERT) KRAEUSEL	W			*	*				*	*
***Taxodium dubium* plant**										
Taxodium dubium (STERNBERG) HEER	F, Sc, L, S, M			*	*	*	*	*	*	*
Taxodioxylon taxodii GOTHAN	W			*		*				
***Glyptostrobus europaeus* plant**										
Glyptostrobus europaeus (BRONGNIART) UNGER	F, Sc, L, S, M			*	*	*	*	*	*	*
Glyptostroboxylon rudolphii DOLEZYCH & VAN DER BURGH	W		*							
***Tetraclinis salicornioides* plant**										
Tetraclinis salicornioides (UNGER) KVAČEK	L			*	*				*	*
***Cupressospermum saxonicum* plant**										
Cupressospermum saxonicum (MAI) KUNZMANN	S				*					

organs as leaves, cones, seeds and wood (see Table 1), but only two taxa (*Taxodium, Glyptostrobus*) are characterized by all of them. The organs were only very rarely directly attached to each other, e.g., seed/pollen cones attached to twigs. They were rather found in direct (close) association within one place/locality or even indirectly (distantly) associated in one layer/time interval. The combination was then made on their common systematical affinity. The tenth group (additional material related to *Pinus*) is purely artificial and can partly be related to other species of *Pinus*.

6. Palaeoenvironmental signals

We distinguish two types of environmental regimes in the larger area of the Most Basin based on different lithological patterns, i.e., fluvial and/or delta and basin environments. Conifers represent more or less important elements of vegetation in these environ-

ments. Reconstruction of vegetation of the fluvial environment is based on the former floristic analysis of plant assemblages of the fluvial facies from Central and North Bohemia (e. g., Teodoridis 2001, 2002). A basic vegetation type may be interpreted as a relatively temperate riparian forest with predominance of deciduous elements (*Taxodium dubium*, *Fagus saxonica* and representatives of Betulaceae and Salicaceae). The riparian forest overlaps distally with the mixed swamp forest and proximally with the mesophytic forest. The association of the mixed swamp forest shows relatively low dynamic character and was often occupied by "swamp" conifers such as *Glyptostrobus* (E4), *Taxodium* (E4), *Quasisequoia* (E4) and *Cupressospermum* (E4), bound on the stagnant water or periodical, relatively long-lasting flooded biotopes of oxbow lakes in the river system. In the contrary, the mesophytic forests, characterized by zonal, more or less allochtonous, mesophytic elements, has established on relatively dry biotopes with lower water table in wider river vicinity or uplands. This vegetation contains among others zonal conifers, i. e. *Pseudolarix* (E4), *Tetraclinis* (E2) and *Pinus* (E3). For more information about the associated floras and additional plant associations see Teodoridis (2004). The delta environment shows a more or less similar structure as the fluvial environment. However, it is transformed and redistributed in the areas of Pětipsy and the Žatec Delta into a system of anastomosing river with low gradient, resembling recent inland deltas (Teodoridis 2004) and into a "true" delta regime in the Bílina area (Kvaček 1998). Similarly, several partial types of vegetation within the basin environment can be distinguished. An assemblage, the most typical of coal seams, reflects the coniferous peat-forming swamp forest that corresponds to the association of *Glyptostrobus* sensu Kvaček & Bůžek (1982). This association, characterized by a relatively high water table and relatively long-lasting floods changing to permanent floods in the distal part of the basin, contains predominantly *Glyptostrobus* stands (E4) associated with *Quasisequoia* (E4) and other elements in proximal part of basin (e. g., Boulter et al. 1993). A next association overlapping towards waterside is the mixed swamp forest that is comparable to the *Nyssa-Taxodium* association sensu Kvaček & Bůžek (1982). Conifers are important elements there, mainly newly appearing *Taxodium* (E4) and mutually integrated *Quasisequoia* and *Glyptostrobus* from the previous association. Other elements represent a mixture of the angiosperms and

ferns (e. g., Kvaček & Bůžek 1982; Boulter et al. 1993; Kvaček et al. 2004a). The next association characterized by the occurrence of "our" conifers is the evergreen broad-leaved forest. This association occupies extra-basin, mesophytic and acid biotopes, such as crystalline rock elevations of the Krušné Hory Mts. (i. e., sandy and micaceous facies) and containing monotonous *Pinus* (E3) stands and *Tetraclinis* (E2) combined with other angiosperm elements (e. g., Teodoridis & Kvaček 2006).

Acknowledgments

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Příloha 4

"Stump Horizon" in the Bílina Mine (Most Basin, Czech Republic) — GC–MS, optical and electron microscopy in identification of wood biological origin

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ABSTRACT

Numerous coalified tree stumps remained preserved *in-situ* in the so-called "Stump Horizon" (the palaeontologic horizon No. 31), which represents clayey overburden of the main coal seam in the Bílina open cast mine in the Most Basin (Czech Republic). The petrological and chemical composition, palaeobotanical origin and preservation of 24 selected tree stumps were studied by optical and scanning electron microscopy and gas chromatography–mass spectrometry (GC–MS). Composition of the fossil wood is dominated by ulminite, particularly texto-ulminite B. Textinite forms up to 38 vol.% in the decomposed tree stumps. Corpohuminite dominates in bark and root tissues. Partly gelified and deformed woody tissues contain both corpohuminite and resinite fillings. Random reflectance of ulminite ranges from 0.33% to 0.39% and carbon content from 49 wt.% to 78 wt.%. Samples represent pure woody material with small admixtures of clay minerals, siderite, and very rare pyrite. Observations by scanning electron microscopy revealed various levels of deformed secondary xylem with more or less swollen cell walls, conspicuous tracheids, uniseriate rays of a different height, and round or cylinder-like resin or corpohuminite bodies. According to our results and other published data the wood might belong to *Glyptostroboxylon* and *Taxodioxylon* genera that are supposed to belong to *Glyptostrobus* and *Quasisequoia* plants respectively, representatives of the coniferous family Cupressaceae. The biomarker composition in the extracts of the fossil wood includes sesquiterpenoids (α-cedrane, drimane, eudesmane), diterpenoids (abietane, fichtelite, 16α(H)-phyllocladane) and their degraded compounds. The terpenoids are derived from precursors produced by the source plants and microorganisms. The terpenoid signatures support a relationship to the Cupressaceae family with input of microbial species. These characteristics were identical for all studied samples. Significant variations have been observed in sesquiterpenoid α-cedrane and diterpenoid 16α(H)-phyllocladane contents.

1. Introduction

Fossil woods are common constituents in sedimentary sequences worldwide and in the calcified, silicified or charred forms may exhibit a high degree of anatomical preservation. These materials represent an important archive of data for palaeoenvironmental reconstructions (Falcon-Lang, 2005; Figueiral et al., 1999; Jeong et al., 2009; Kunzmann et al., 2009; Teodoridis and Sakala, 2008; Visscher and Jagels, 2003; Witke et al., 2004; Yoon and Kim, 2008). Part of fossil wood forms mummified, humified and gelified wood with variable preserved cell tissue structure, which is problematic for palaeoecological studies (Figueiral et al., 1999; Sweeney et al., 2009). Relationship between gelification, coalification, microscopic appearance, and chemical composition and structure of wood has been described in many Tertiary

deposits, *e.g.*, Victorian brown coal in Australia (Russel, 1984; Russel and Barron, 1984), Greece (Kalaitzidis et al., 2004), Poland (Drobniak and Mastalerz, 2006; Wagner, 1982), Canada (Sykes, 1994), and Hungary (Erdei et al., 2009; Hámor-Vidó et al., 2010). Coalified fossil woods are usually deformed by the hydrostatic pressure of buried sediments, whereas petrified cherts and siderite coal balls preserve the original geometry of fossilized plant tissues (Hámor-Vidó et al., 2010; Sweeney et al., 2009).

The deformation and homogenization of gelified cellular structure caused a problem in the study of wood anatomy and identification of botanical affinity of coalified fossil wood. An effective technique in identification of plant tissue types is the old technique of etching of polished surfaces with oxidizing agents as summarized by Stach et al. (1982) and Taylor et al. (1998). Vassio et al. (2008) or Gryc and Sakala (2010) used a method based on boiling of wood in water for several hours to soften it before preparation of thin sections for a microscopical study in transmitted light. Figueiral et al. (2002) used

laboratory charring of wood specimens followed by taxonomy identification by reflected light microscopy. The botanical affiliation of the fossil wood can be also determined based on the molecular composition of terpenoid hydrocarbons. Chemotaxonomical classification of fossil fragments is based on majority of terpenoids in agreement with pollen elements representing a forest swamp environment (Bechtel et al., 2007; Otto and Wilde, 2001; Stefanova et al., 2005; Zdravkov et al., 2011).

Previous research on coalified fossil wood has largely focused on the chemical and petrographical characterization of organic matter, its deformation, degradation, mineralization, and determination of botanical affiliation of woody materials from the fossil forests or tree stumps and trunks in coal seams (Bechtel et al., 2007, 2008; Hámor-Vidó et al., 2010; Sweeney et al., 2009; Sykes, 1994; Vassio et al., 2008).

This study has investigated petrological and chemical properties of selected coalified woods from the Miocene "Stump Horizon" in the Bílina open pit mine in the Most Basin. The attention was also paid to determination of the palaeobotanical origin and the way of preservation of selected tree stumps using optical and scanning electron microscopy (SEM) and gas chromatography–mass spectrometry (GC–MS) analysis of extracts.

2. Geological settings

Since the opening of the Bílina open cast mine (exploiting 9 million tonnes of brown coal per year) on the top of coal seam 2–5 m thick uniform layer of clay rich in coalified remains of *in-situ* growing trees has been documented. Numerous coalified tree stumps remained preserved *in-situ* in clay overburden up to 5 m thickness of the main coal seam in the Bílina open cast mine in the Most Basin, Czech Republic (Fig. 1). This so called "Stump Horizon" is a clastic time equivalent of the lower half of the upper bench of the main coal seam within the Holešice Member of the Miocene age (Fig. 2). It consists of 2–4 distinguished horizons of stumps. Laterally this layer gradually turns to a clear coal bench. Vertically it gradually changes into prodeltaic laminated clays and a 100 m thick lacustrine deltaic system. This layer covers an area
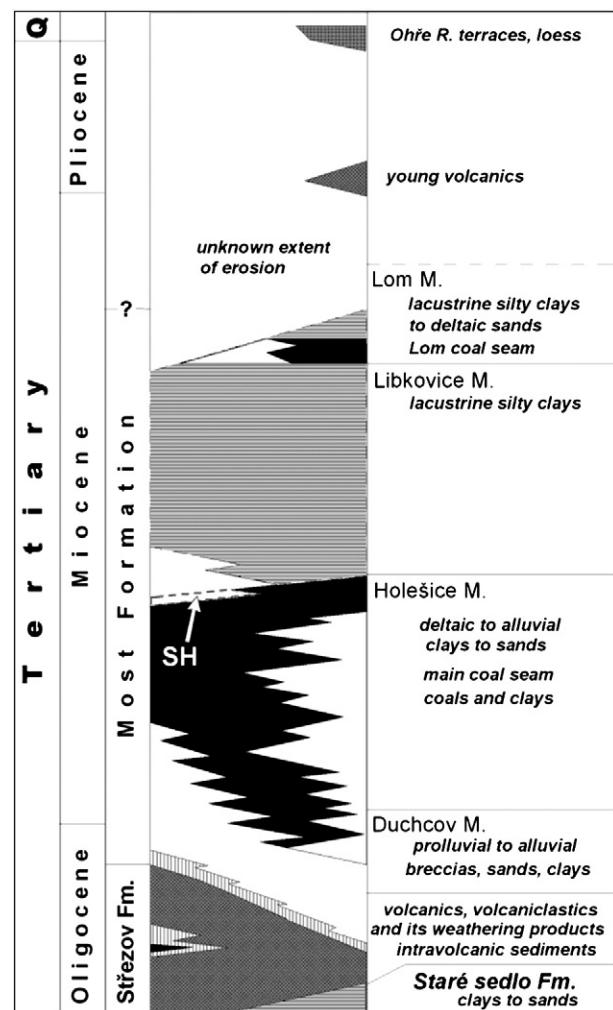

Fig. 2. Stratigraphy of the Most Basin fill. SH – "Stump Horizon" in the Bílina open pit mine.
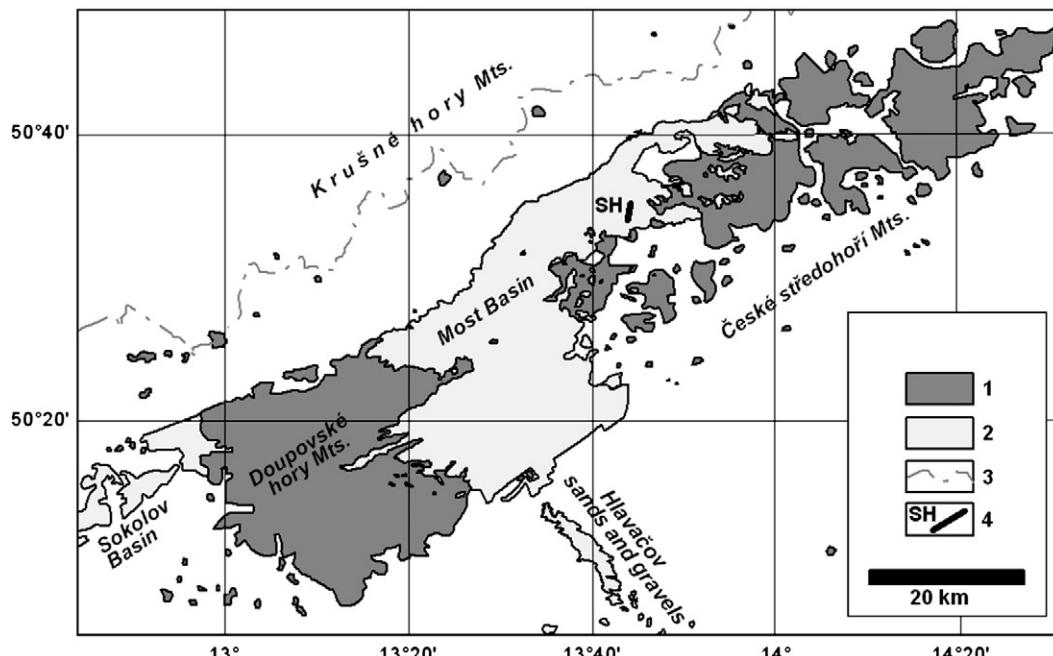
Fig. 1. Sketch map of the Most Basin. 1 – Oligocene volcanics (alkalic basalts, trachytes, phonolites) and its volcanoclastic equivalents; 2 – Lower Miocene sedimentary fill of the Most Basin (sands, clays, coal seam); 3 – state border; 4 – SH - area of "Stump horizon" sampling.

Fig. 3. Position of a stump in the layer of clay.

Fig. 4. Location of the studied subsamples in the one stump.

of 10×1 km. It is interpreted as an early stage of the Miocene development of the Bílina (river) delta. Grey clay sediment conserving coalified stumps and filling hollow trunks is thinly layered by organic detritus containing prevalently coniferous needles, twigs and cones, leafs and root systems of paludal grasses, ferns, floating ferns, *Calamus* palmetto, and several types of angiosperm swampy elements. Among the coniferous macrofossils, the most abundant are remains of leaves and cones of *Glyptostrobus europaeus* (Brongniart) Unger and *Quasisequoia couttsiae* (Heer) Kunzmann (Kvaček, 1998; Teodoridis and Sakala, 2008).

Most of the tree stumps are more or less hollow, around 1 to 5 m high and up to 2 m in diameter. They are exposed in three to four altitudinal subhorizons, mostly in upright position, some of them leaned to the clastic input source line (channel). They are accompanied by abundant siderite concretions.

3. Samples and methods

3.1. Samples

Coalified fossil wood samples from 23 selected stumps were collected (Fig. 3) and analysed. From one of the stumps, 9 sub-samples were taken which represent 8 selected parts of the trunk and roots and one sample of the woody detritus from the surrounding sediment (Fig. 4). Overview of the studied samples, dimensions of the found parts of trees, their characterization, and localization of the samples is given in Table 1.

From characteristic pieces of dull, brown to black-brown fossil wood (xylite), pieces oriented along the transverse, radial and tangential cuts were thoroughly selected and treated. Subsequently, polished sections for optical microscopy and samples for scanning electron microscopy were prepared from them. On polished sections with transverse and radial cuts, detailed exploration of morphology of

Table 1
Overview of the studied fossil wood samples with their general characteristics.

Number of the sample	Tree diameter (m)	Height (m)	Short description of stump	Deformation	Sample
S1–S9	1	1.2	Massive, in the upper part selectively to ribbon-form remnants digested	Medium	8 samples from the whole stump + 1 clay (see Fig. 4)
P1	1.1	1.5	Selectively to ribbon-form remnants digested and massive in the lower part	Medium	Middle part
P2	1.8	>2	Massive, almost without deformation	Low	Upper middle part
P3	1.4	>1	Hollow and deformed	Medium	North side with the lower deformation
P4	0.8	1.2	Selectively to ribbon-form remnants digested	Medium	Middle part
P5	1.2–1.8	1.5	Hollow like bowl-formed and splayed, selectively to ribbon-form remnants digested	medium–strong	Middle part of the "bowl"
P6	1.5	0.7	Strongly deformed lower part	Strong	North side
P7	0.5	0.6	Massive	Medium	Upper part
P8	0.45	0.9	Massive, tip tilted slightly, in the upper partially selectively to ribbon-form remnants digested	Low	North side
P9	0.65	0.6	Massive	Low	North upper part
P10	1.8	1.8	Strongly deformed, in upper part hollow like bowl-formed, in lower massive	Strong	middle part
P11	1	>1	Massive, tilted slightly, selectively sideritized	Low	Upper middle part + pelocarbonate
P12	1	>0.5	Strong deformed, lower part of the stump	Low	Middle part
P13	0.8	>0.5	Massive, tilted 60° to the south	Low	Middle part
P14	1	>0.5	Selectively to ribbon-form remnants digested, strong deformed, tilted 45° to the west, lower part of the stump	Low	Sampled from relatively low deformed part
P15	0.7	>0.5	Selectively to ribbon-form remnants digested, deformed	Medium	Middle part
P16	1.8	>1	Massive, partly deformed, selectively sideritized	Medium	From relatively low deformed part + pelocarbonate
P17	0.8	0.7	Selectively to ribbon-form remnants digested	Medium	North part
P18	1.8	1.3	Seemingly massive, upper part collapsed into the lower hollow digested part (tracheids oriented in various directions)	Strong	Central section of the upper part
P19	1.2	1	Seemingly massive, upper part collapsed into the lower hollow digested part (tracheids oriented in various directions)	Strong	Middle deformed part
P20	1.5	2.5	Massive, slightly tilted to the north, in upper part strongly deformed, in middle part undulating	Low–strong	Middle low deformed part
P21	1.8	>2	Massive, in upper part digested, tilted 45° to north	Medium	Middle part
P22	0.8	1.5	Massive, in upper part digested, tilted 45° to north	Low	Middle part
P23	<1	<1	Selectively to ribbon-form remnants digested	Low	North outer part

Table 2
Results of micropetrographic analysis of stumps P1–23.

Parametr	P1	P2	P3	P4	P5	P6	P7	P8	P9	P10	P11	P12	P13	P14	P15	P16	P17	P18	P19	P20	P21	P22	P23
Rr (%)	0.36	0.37	0.37	0.39	0.36	0.37	0.38	0.37	0.35	0.38	0.38	0.38	0.36	0.36	0.37	0.38	0.39	0.35	0.37	0.38	0.36	0.37	0.38
s	0.04	0.03	0.03	0.05	0.02	0.02	0.05	0.04	0.06	0.04	0.05	0.03	0.03	0.03	0.04	0.05	0.05	0.04	0.05	0.04	0.30	0.05	0.04
R_{TUA} (%)	0.25	0.00	0.00	0.00	0.24	0.23	0.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.23	0.23	0.24	0.23	0.24	0.00	0.00	0.00	0.00
Huminite (vol.%)	**93.7**	**90.4**	**92.1**	**93.9**	**89.5**	**90.4**	**91.7**	**91.7**	**89.0**	**89.4**	**90.6**	**91.8**	**93.0**	**93.7**	**91.7**	**93.5**	**91.3**	**91.2**	**93.8**	**93.4**	**90.8**	**90.6**	**92.5**
Textinite	26.1	6.4	20.3	13.3	15.8	18.9	6.4	14.7	6.1	15.8	5.3	26.3	9.2	2.3	28.4	37.3	5.9	2.9	2.0	9.3	3.2	5.5	5.0
T_A	*1.5*	*0.0*	*0.0*	*0.0*	*0.8*	*0.0*	*0.0*	*0.0*	*0.0*	*0.5*	*0.0*	*0.3*	*0.0*	*0.0*	*0.5*	*0.8*	*0.0*	*0.0*	*0.0*	*0.0*	*0.0*	*0.0*	*0.0*
T_B	*25.0*	*6.4*	*20.3*	*13.3*	*15.0*	*18.9*	*6.4*	*14.7*	*6.1*	*15.3*	*5.3*	*26.0*	*9.2*	*2.3*	*27.9*	*36.5*	*5.9*	*2.9*	*2.0*	*9.3*	*3.2*	*5.5*	*5.0*
Texto-ulminite	48.8	43.9	55.8	66.2	59.6	57.7	67.2	60.6	67.0	55.3	72.2	51.0	72.7	81.6	50.9	43.5	73.5	72.5	78.2	69.7	72.9	69.7	71.6
TU_A	*0.5*	*0.0*	*0.0*	*0.0*	*1.3*	*1.5*	*2.7*	*0.0*	*0.0*	*0.0*	*0.0*	*0.0*	*0.0*	*0.0*	*0.8*	*0.9*	*0.7*	*3.3*	*1.4*	*0.0*	*0.0*	*0.0*	*0.0*
TU_B	*48.3*	*45.9*	*55.8*	*66.2*	*58.3*	*56.2*	*64.5*	*60.6*	*67.0*	*55.3*	*72.2*	*51.0*	*72.7*	*81.6*	*50.1*	*45.4*	*72.8*	*69.2*	*76.8*	*69.7*	*72.9*	*69.7*	*71.6*
Eu-ulminite	4.8	22.6	5.8	3.7	3.3	1.5	5.6	2.0	5.7	5.2	2.2	0.0	0.0	0.0	0.0	0.0	0.0	2.1	2.0	2.5	1.9	2.7	4.2
Attrinite	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Densinite	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Corphuminite	11.6	14.4	10.3	10.7	10.8	12.3	9.6	14.4	10.2	13.1	9.6	14.3	11.1	7.5	11.6	12.7	11.9	12.5	10.3	11.2	11.5	12.7	10.9
Gelinite	2.4	1.1	0.0	0.0	0.0	0.0	2.9	0.0	0.0	0.0	1.3	0.2	0.0	2.3	0.8	0.0	0.0	1.7	1.3	0.7	1.3	0.0	0.8
Liptinite (vol.%)	**5.1**	**7.1**	**4.9**	**5.0**	**6.6**	**6.3**	**5.8**	**6.5**	**5.7**	**6.4**	**5.6**	**5.1**	**5.9**	**3.8**	**6.2**	**5.5**	**7.5**	**4.7**	**4.4**	**5.4**	**5.2**	**6.6**	**5.0**
Sporinite	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cutinite	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Resinite	5.1	7.1	4.9	5.0	6.6	6.3	5.8	6.5	5.7	6.4	5.6	5.0	5.9	3.8	6.2	5.5	7.5	4.7	4.4	5.4	5.2	6.6	5.0
Liptodetrinite	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Inertinite (vol.%)	**0.0**	**2.0**	**0.0**	**0.0**	**0.0**	**0.0**	**0.0**	**0.0**	**0.0**	**0.0**	**0.0**	**2.0**	**0.6**	**0.0**	**0.0**	**0.0**	**0.0**	**0.8**	**0.0**	**0.0**	**0.6**	**0.0**	**0.0**
Fusinite	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Funginite	0.0	2.0	0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.0	0.6	0.0	0.0	0.0	0.0	0.8	0.0	0.0	0.6	0.0	0.0
Minerals (vol.%)	**1.2**	**0.5**	**2.4**	**1.1**	**3.9**	**3.3**	**2.5**	**1.8**	**5.3**	**4.2**	**3.8**	**1.1**	**1.3**	**2.5**	**2.1**	**1.0**	**1.2**	**3.3**	**1.8**	**1.2**	**3.4**	**2.8**	**2.5**
Clays	1.2	0.5	1.5	0.5	3.2	2.6	2.3	1.5	4.8	1.5	3.2	0.7	1.0	1.5	1.9	0.6	0.7	1.9	1.2	1.1	1.6	0.9	1.7
Carbonates	0.0	0.0	0.9	0.5	0.0	0.7	0	0.2	0.3	2.1	0.5	0.3	0.0	1.0	0.0	0.4	0.0	1.4	0.6	0.0	1.8	1.9	0.6
Sulphides	0.0	0.0	0.0	0.1	0.7	0.0	0.2	0.1	0.2	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.5	0.0	0.0	0.0	0.0	0.0	0.2
Quartz	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Other	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.5	0.1	0.1	0.3	0.0	0.2	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0
GI (gelification index)	**2.2**	**10.9**	**3.0**	**5.3**	**4.0**	**3.1**	**11.8**	**4.3**	**11.9**	**3.8**	**14.3**	**1.9**	**7.9**	**35.5**	**1.8**	**1.2**	**12.5**	**26.3**	**40.8**	**7.8**	**23.8**	**13.2**	**15.3**

Significance of bold are main maceral groups.
Significance of italics are sub-maceral groups.

Table 3
Results of micropetrographic analysis of the stump samples S1–S9.

Parameter	S1	S2	S3	S4	S5	S6	S7	S8	S9
R_o (%)	0.36	0.34	0.35	0.34	0.36	0.35	0.36	0.37	0.33
S	0.03	0.03	0.03	0.02	0.02	0.02	0.03	0.03	0.04
R_{TUA} (%)	*0.0*	*0.2*	*0.2*	*0.21*	*0.22*	*0.2*	*0.24*	*0.25*	*0.22*
Huminite (vol. %)	**79.1**	**83.5**	**90.3**	**91.9**	**90.3**	**90.1**	**90.5**	**87.3**	**23.0**
Textinite	1.9	16.5	15.5	38.3	12.3	13.5	5.7	10.8	0.4
TA	*0.3*	*0.8*	*1.5*	*1.9*	*1.1*	*1.4*	*0.9*	*1.6*	*0.3*
TB	*1.6*	*15.7*	*14.0*	*36.4*	*11.2*	*12.1*	*4.8*	*9.2*	*0.1*
Texto-ulminite	41.7	38.8	52.2	33.2	53.4	61.4	70.4	54.6	10.3
TU_A	*0.0*	*2.3*	*2.0*	*0.0*	*0.0*	*0.0*	*1.9*	*2.1*	*2.9*
TU_B	*41.7*	*36.5*	*50.2*	*33.2*	*53.4*	*61.4*	*68.5*	*52.5*	*7.4*
Eu-ulminite	20.3	5.0	6.6	1.2	7.4	1.7	3.8	2.0	1.3
Attrinite	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Densinite	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.1
Corpohuminite	14.4	21.3	15.5	19.2	17.2	13.5	10.6	19.9	8.0
Gelinite	0.8	1.9	0.5	0.0	0.0	0.0	0.0	0.0	0.9
Liptinite (vol. %)	**5.9**	**7.7**	**6.2**	**7.4**	**6.0**	**6.5**	**5.7**	**8.7**	**11.9**
Sporinite	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.7
Cutinite	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4
Suberinite	0.3	0.9	0.0	0.0	0.0	0.2	0.4	0.0	0.5
Resinite	5.6	6.8	6.2	7.4	6.0	6.3	5.3	8.7	5.1
Exsudatinite	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Liptodetrinite	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.6
Inertinite (vol. %)	**0.0**	**2.0**	**0.6**	**0.0**	**2.5**	**0.0**	**0.0**	**0.0**	**0.9**
Fusinite	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Funginite	0.0	2.0	0.6	0.0	2.5	0.0	0.0	0.0	0.9
Minerals (vol. %)	**15.0**	**6.8**	**2.9**	**0.7**	**1.2**	**3.4**	**3.8**	**4.0**	**64.2**
Clays	14.1	4.8	2.0	0.5	1.0	2.9	2.4	3.1	57.6
Carbonates, siderite	0.9	2.0	0.9	0.2	0.2	0.5	1.3	0.8	1.3
Sulphides	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.1	0.2
Quartz	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Other	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	5.1
GI (gelification index)	33.0	2.8	3.8	1.0	4.9	4.7	9.5	5.2	33.0

Significance of bold are main maceral groups.
Significance of italics are sub-maceral groups.

cell tissues, gelification of cell walls, contraction fissures, resinite and corpohuminite forms, mineralization and weathering was performed. The rest of the sample was powdered (<3 mm), reduced in size by quartering, and powdered for optical microscopy (<1 mm) and chemical analyses (<0.2 mm).

3.2. Optical microscopy

Reflectance, as a parameter of coalification, was measured on homogeneous sites of ulminite B on grained polished sections according to ISO 7404 (2009) using a UMSP 30 Petro OPTON-ZEISS microscope, in monochromatic light ($\lambda = 546$ nm), with immersion objectives at 5×, 40×, and 400× magnifications. With the same apparatus, macerals were identified according to ISO 7404 and in accordance with the principles brought forward by Taylor et al. (1998), International Committee for Coal and Organic Petrology (ICCP) (2001), and Sýkorová et al. (2005). Determination of liptinite macerals was performed using the UMSP 30 Petro microscope with a fluorescence system. From the maceral composition, gelification index (GI) was calculated based on a principle of the proportion of gelified and ungelified huminite components, according to the equation proposed by von der Brelie and Wolf (1981):

$$GI = \frac{Gelified\ telohuminite + Gelified\ detrohuminite + Gelinite}{Non\ gelified\ telohuminite + Non\ gelified\ detrohuminite}$$

Attention was paid to discern their botanical characteristics with focus on earlywood and latewood tracheids, rays, and cross-fields, in accordance with scanning electron microscopy studies.

Tissue texture was studied on oriented polished sections using an OLYMPUS BX51 microscope for reflected light with a CRAIC system, dry objectives at 10× and 40× magnifications, and immersion objectives at 5×, 40×, and 100× magnifications.

3.3. Scanning electron microscopy

Scanning electron microscopy was used for detailed anatomical studies and documentation. Samples with well preserved and undistorted structure from selected pieces of wood were processed. The xylitic specimens were observed using a Quanta 450 scanning electron microscope (Institute of Rock Structure and Mechanics, Academy of Sciences of the Czech Republic), and were examined using a Jeol JSM-6380 LV scattered low-vacuum electron microscope at 15 kV (Institute of Geology and Palaeontology, Faculty of Science, Charles University in Prague). The anatomical description is in accordance with the IAWA Softwood terminology (IAWA Committee, 2004).

3.4. Chemical analysis

The elemental organic composition was determined using a CHNS/O microanalyser Flash FA 1112 Thermo Finnigan. For organic geochemistry analyses, wood fragments were powdered and Soxhlet-extracted with dichloromethane for 5 h. The solvent amount was reduced using a vacuum evaporator. The polar compounds were removed from the extracts using column chromatography on silica gel (Kieselgel 60, Merck). The aliphatic and aromatic hydrocarbon fractions were eluted by *n*-pentane and a mixture *n*-pentane:dichloromethane (1:1, v:v). The extracts were analyzed by GC–MS using a Thermo Scientific Trace Ultra DSQ II instrument equipped with a capillary column with a fixed stationary phase DB 5 (30 m × 0.25 mm × 0.25 µm film). The GC oven was heated from 35 °C (5 min) to 300 °C (10 min) at a rate of 4 °C/min. The analysis was carried out in the split mode (1:50). Helium was used as a carrier gas. Mass spectra were recorded at EI 70 eV from 40 to 500 amu in full scan mode. Identification of compounds was based on comparison of spectra with the National Institute of Standards and Technology (NIST) mass spectral library and data from literature (Philp, 1985).

4. Results

4.1. Petrographical characteristics of fossil wood

Reflectance and maceral analyses of 23 representative samples were carried out (Table 2). One stump was studied in detail (Table 3). Reflectance values range from 0.34% R_r to 0.39% R_r in trunk samples. The lowest value 0.33%R_r originates from ulminite of the woody fragments dispersed in carbonaceous clay surrounding the stump S. These values indicate a metatype lignite rank (ECE-UN, 1998). All wood samples dominantly consist of ulminite, particularly texto-ulminite B (Fig. 5). In some cases, dark ulminite A with reflectance lower than 0.25% R_{TUA} has been recognized in the cellular tissues. Textinite comprises up to 38.3 vol.% in the partly decayed tree stump S4 and 37.3 vol.% in P16. Dark textinite was observed in amounts less than 2 vol.% in samples S1–S9 and P1, P5, P10, P12, P15, and P16. Completely gelified cellular tissues occurred irregularly, eu-ulminite dominated in sample S1 and P2. A characteristic feature of the wood samples is the presence of corpohuminite bodies which infill cell lumens and comprise 7.5 vol.% to 21.3 vol.% of the wood. The corpohuminites are solid or finely porous, nonfluorescent, reflecting more than ulminite B, typically round to oval in transverse section, and elongated in oblique or longitudal section. Resinite fillings of cellular and intercellular spaces range between 4.4 vol.% and 8.7 vol.% in S8 sample. Other liptinite macerals sporinite, cutinite, suberinite and liptodetrinite have been found in carbonaceous clayey rock PB9. Inertinite macerals are absent in the sample collection
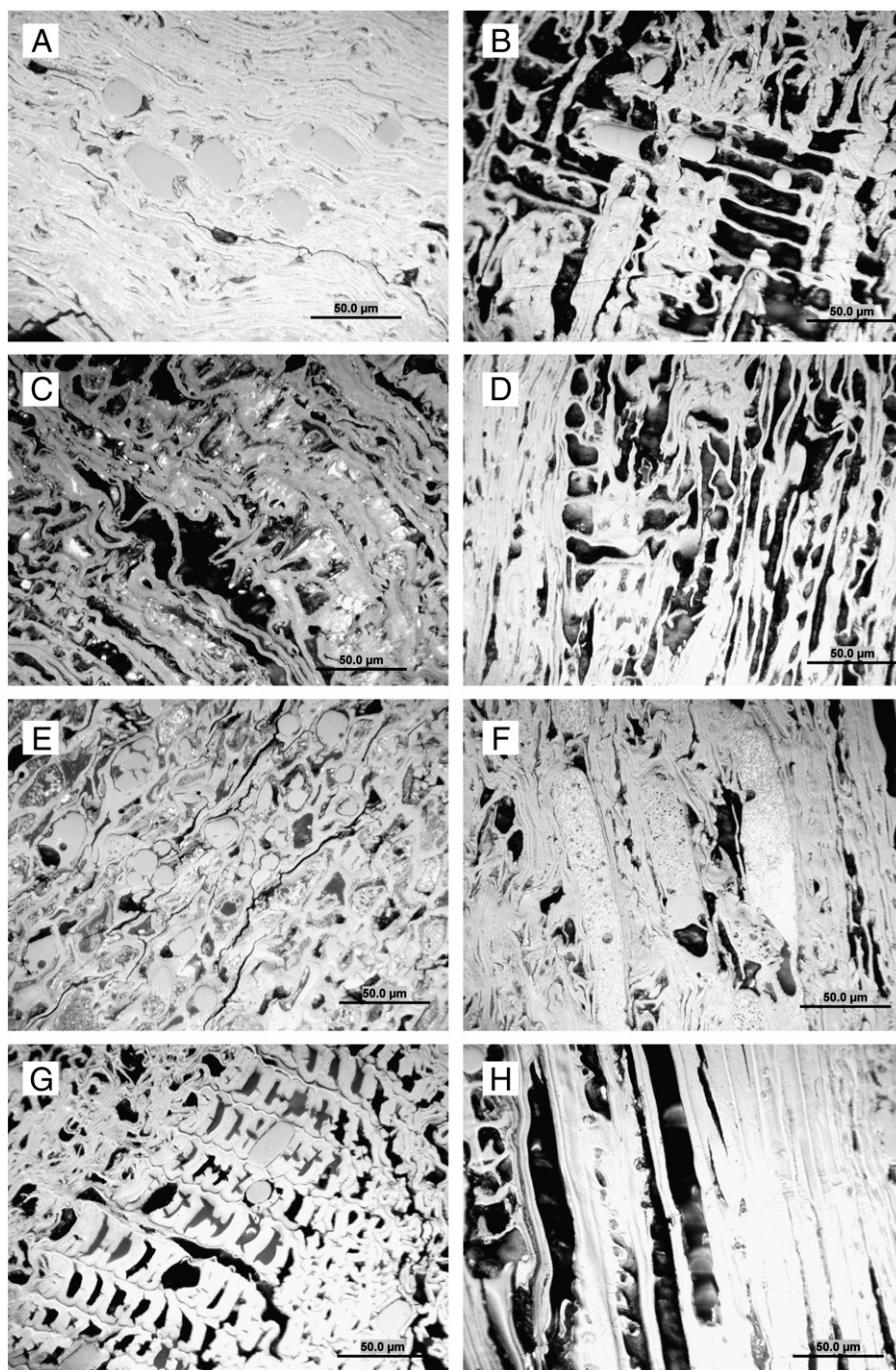
Fig. 5. Reflected light microphotographs of xylite samples showing the range of humotelinite structure preserved in wood tissues of coalified tree stumps. A. Ulminite and corpohuminite – deformed and gelified wood tissue of massive stump P1. B. Ulminite and corpohuminite – deformed and gelified wood tissue of massive stump P1. C. Textinitte B and ulminite B in cross-field in the partly gelified wood tissue in partly decayed stump P6, radial cut. D. Textinite A and transition to ulminite A which are impregnated by resinite, sample P5. E. Ulminite B and textinite in partly gelified wood tissue with deformed uniseriate rays (P9), tangencial cut. F. Corpohuminite and resinite fillings in cell volumes of textinite and ulminite that represent partly swollen cell walls in partly decayed stump P15. G. Ulminite with transition to textinite and elongated fine porous corpohuminite in wood tissue of partly decayed stump P16. H. Textinite to ulminite with corpohuminite and resinite fillings of cell volumes in deformed and partly gelified tissue of earlywood and latewood, partly decayed stump P15, radial cut. I. Ulminite to textinite – poorly saved pits observed in fragment of tracheid. Partly decayed stump P23, radial cut.

with exception of funginite, which has been found in low concentrations in samples S2, S3, S7, S9, P2, P3, P12, P13, P18, and P21 (Tables 2 and 3). Samples represent clean woody material with small admixtures of clay minerals, massive bodies of siderite, and very rare framboidal and crystallic pyrite. The dominance of ulminite, lower contents of textinite and absence of humodetrinite correspond with values of the gelification index GI ranging between 1.0 and 40.8.

4.2. SEM characteristics

The SEM observation of prepared gelified wood fragments revealed various levels of deformed secondary xylem with more or less swollen cell walls with round and cylinder-like resin or corpohuminite bodies with various size (Fig. 6). In spite of an overall bad preservation of the anatomical features, two taxonomical units were identified —
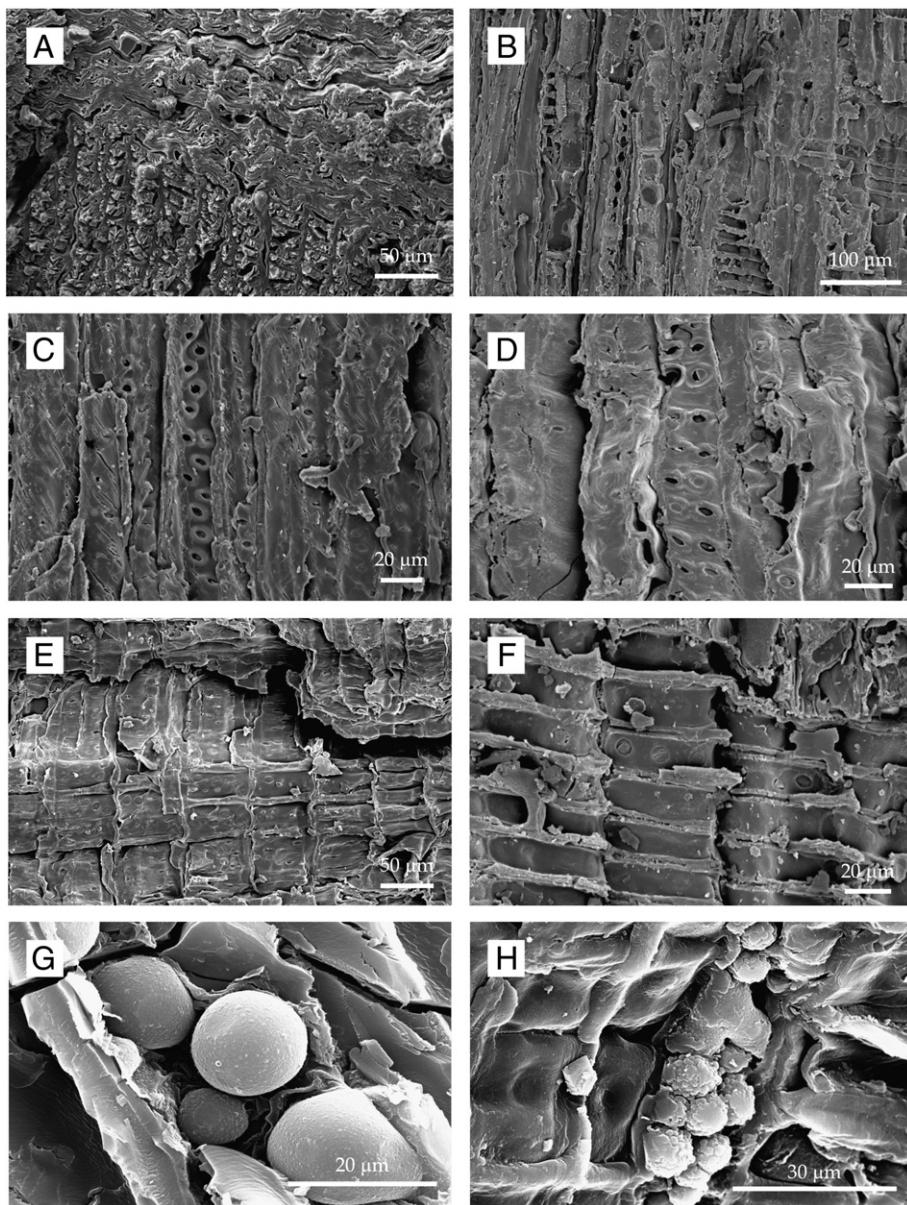
Fig. 6. SEM microphotographs of the microscopic structures of the wood tissues preserved in the coalified tree stumps. TS – transverse section; TLS – tangential longitudinal section; RLS – radial longitudinal section.

Glyptostroboxylon rudolphii:

A TS, sample P15, general view with both early- and latewood, gelified and deformed.
B TLS, sample P9, general tangential view with rays passing radial one demonstrating the deformed structure.
C RLS, sample P8, uniseriate bordered pits in radial tracheid wall.
D RLS, sample P18, regularly arranged biseriate pitting with crassulae.
E RLS, sample S4, irregularly arranged "glyptostroboid" cross-field pits.

Taxodioxylon gypsaceum:

F. RLS, sample P9, taxodioid cross-field pits in regular horizontal rows.
G. RLS, sample P21, detail of spherical and irregular particles of resinite or corpohuminite with relative smooth surface, which are discretely located in cell.
H. RLS, Sample P21, detail of cauliflower-like particles of resinite fixed in cell walls.

Glyptostroboxylon rudolphii Dolezych & van der Burgh and *Taxodioxylon gypsaceum* (Goeppert) Kraeusel. The main criterion was type and regularity of both pitting in radial tracheid walls and cross-field pitting. These wood fragments have been interpreted in accordance with the previous study from the same area (Teodoridis and Sakala, 2008), i.e., *Glyptostroboxylon rudolphii* as wood of *Glyptostrobus europaeus*

and *Taxodioxylon gypsaceum* as wood of *Quasisequoia couttsiae*. Results of SEM studies correspond to the macrofossil record (Kvaček, 1998; Kvaček et al., 2004) of the layer studied.

The samples attributed to *Glyptostroboxylon rudolphii* (S4, S5, P1–P8, P10, P12, P14, P15, P17, and P20–P22) show growth rings, but transition between earlywood and latewood was not observed. Bordered pits

Table 4
Basic chemical characterization of the stump samples S1–S9 (a) and P1–P23 (b).

Sample	%W[a]	%A[d]	%C[daf]	%H[daf]	%N[daf]	%S[daf]	%SOM[daf]
a)							
S1	12.92	10.56	78.11	5.72	1.77	0.50	8.36
S2	20.76	9.12	70.10	5.25	1.58	0.50	15.94
S3	19.62	4.96	64.29	5.11	1.49	0.47	13.71
S4	19.25	1.37	74.40	5.71	1.40	0.42	14.97
S5	16.64	3.27	70.43	5.60	1.55	0.31	10.47
S6	20.40	1.60	73.06	5.62	1.64	0.42	13.32
S7	20.39	6.19	70.39	5.40	171	0.44	9.84
S8	28.71	2.34	70.41	5.47	1.32	0.36	19.51
S9	6.30	71.62	49.79	6.87	1.37	0.39	6.77
b)							
P1	14.20	2.36	71.45	4.98	1.95	0.02	8.44
P2	17.73	1.10	70.36	5.43	1.67	0.01	16.55
P3	15.65	2.66	71.14	5.02	1.83	0.03	9.56
P4	14.64	1.75	69.34	5.05	1.66	0.06	9.65
P5	14.75	1.10	69.53	5.17	1.67	0.03	14.80
P6	14.23	1.40	75.47	5.29	1.72	0.01	12.53
P7	12.28	14.49	71.77	5.27	1.61	0.01	9.64
P8	15.36	2.21	70.97	5.52	1.49	0.01	15.84
P9	13.37	6.16	73.56	5.24	1.66	0.20	11.15
P10	15.79	2.83	71.36	5.45	1.63	0.01	15.63
P11	11.47	5.14	69.59	5.05	0.91	0.39	1.11
P12	11.52	1.94	69.40	5.03	0.78	0.33	8.64
P13	11.23	1.69	63.68	5.04	0.78	0.38	12.67
P14	11.42	3.25	66.12	4.76	0.98	0.32	8.97
P15	10.15	2.39	69.56	5.19	0.65	0.38	10.72
P16	10.71	1.10	69.39	5.05	0.92	0.40	7.91
P17	10.30	1.65	70.56	5.33	0.81	0.40	11.82
P18	11.49	4.24	68.80	4.86	1.15	0.40	7.83
P19	10.66	2.31	68.93	4.94	1.05	0.36	6.54
P20	11.20	1.71	69.94	5.28	1.01	0.39	10.35
P21	10.02	4.10	68.36	5.15	0.77	0.40	10.18
P22	11.33	1.30	69.74	5.29	0.78	0.37	11.36
P23	13.21	3.26	67.79	4.90	1.02	0.37	8.46

%W — percent of moisture.
%A — ash yield.
%C — carbon content.
[a]Analytical sample.
[d]Dry.
[daf]Dry ash free.
SOM Soluble organic matter.

are opposite, circular, in 1–2 irregular vertical rows in radial tracheid walls. Uniseriate rays composed solely of parenchyma cells without ray tracheids are up to 10 cells high with thin and smooth both horizontal and end (tangential) walls. The 1–3 mostly "glyptostroboid" (taxodioid with very narrow borders approaching almost pinoid) cross-field pits per field were irregularly arranged. The axial parenchyma was present often with the resin substance, the type of transverse end walls is unknown.

The samples attributed to *Taxodioxylon gypsaceum* (P9, P11, P13, P16, P18, P19, P23) have growth rings, but transition between early-wood and latewood was not observed. Bordered pits are opposite, circular, in 1–2 regular vertical rows in radial tracheid walls, and crassulae are often present. Uniseriate rays composed solely of parenchyma cells, without ray tracheids, up to 13 cells high with thin or slightly thickened and smooth both horizontal and end (tangential) walls. The 1–3 mostly taxodioid cross-field pits per field were arranged in regular horizontal rows. The axial parenchyma was present often with the resin substance, the type of transverse end walls is unknown.

4.3. Bulk chemical composition

Table 4 demonstrates that there are not significant differences in bulk chemical composition between samples from one trunk (S1–S9)

and samples from 23 stumps (P1–P23). Xylite samples are characterized by variable ash content (A[d]) ranging between 1.30 wt.% and 10.56 wt.%. The highest ash content has been found in carbonaceous clay S9. Total sulphur content (%S[daf]) varies up to 0.5 wt.%, and nitrogen content (%N[daf]) up to 1.95 wt.% (Table 4). The carbon contents higher than 70 wt.% C[daf] were determined in the samples S1–S8 from one stump and in the samples P1–P3, P6–P10, and P17. The highest carbon contents were found in the sample of gelified wood of the root S1 and in the sample of deformed wood P6 (Table 4).

4.4. Organic geochemistry

Examples of two typical chromatograms obtained for the samples P7 and P17 are shown in Fig. 7 (aliphatic fraction) and Fig. 8 (aromatic fraction) together with their detailed description. The total area given by the sum of the areas of all identified compounds was used as a reference for determining the relative content of an individual compound in the samples. The results for aliphatic and aromatic hydrocarbon fractions are shown in Tables 5 and 6, respectively (part a) — wood extracts S1–S9, part b) — wood extracts P1–P23).

5. Discussion

5.1. Gelification index, soluble organic matter, and carbon, nitrogen, sulphur and oxygen contents

The wood, bark and root samples are petrographically distinct, in terms of both maceral and tissue composition. They are dominated by gelified but structurally intact ulminite B with minor and variable proportions of textinite B and corphuminite. The wood contains a low portion of varieties of textinite A and ulminite A with reflectance values lower than 0.25% (Table 2). The origin of both dark varieties of telohuminite can be ascertained from higher cellulose content, lower degree of humification and gelification, lower Eh and pH conditions, and from the type of vegetation and plant tissues (Russel, 1984; Russel and Barron, 1984; Stach et al., 1982; Sykes, 1994). Textinite and ulminite were studied from the anatomical point of view. Differences in petrological and chemical composition have been found among the wood samples from one stump as well as among the individual samples in the set of 23 stumps. Our results show large variability of GI values in the carbon rank range from 49 wt.% to 78 wt.% (Fig. 9).

According to Bechtel et al. (2002), sulphur content is associated with the degree of wood gelification. This does not appear in the studied samples. Fig. 10, Tables 2 and 3 show that all samples can be divided into three groups according to their sulphur contents. Sulphur content higher than 0.3 wt.% has been found in gelified wood with GI lower than 15 and in the group of samples with GI higher than 20. In samples with GI lower than 15, sulphur is present in trace amounts. It can be assumed that sulphur is represented primarily by organic sulphur. No pyrite was detected under optical microscopy in samples P6–P10 with very low sulphur and in the remaining samples it was rare. The stump samples (Fig. 10) were enriched with sulphur, which could be due to selective preservation of sulphur containing compounds (sulphur is largely bound to lignin and its derivatives) or may indicate anaerobic conditions during storage of wood, in the presence of anaerobic bacteria (Bechtel et al., 2002). The relative increase in sulphur may reflect preferential preservation and relative enrichment with sulphur as a result of removal of selected wood components, such as cellulose due to changing edaphic conditions Eh and pH (Drobniak and Mastalerz, 2006). Hatcher et al. (1981), Hatcher (1988), and Stout et al. (1989) found that cellulose is rapidly depleted and removed from organic material during early coalification via biological degradation whereas lignin is somewhat resistant to alteration. Results of the early stage coalification experiments show that both the cellulose and lignin components of the wood could be converted to vitrinite-like substances under pressure and temperature
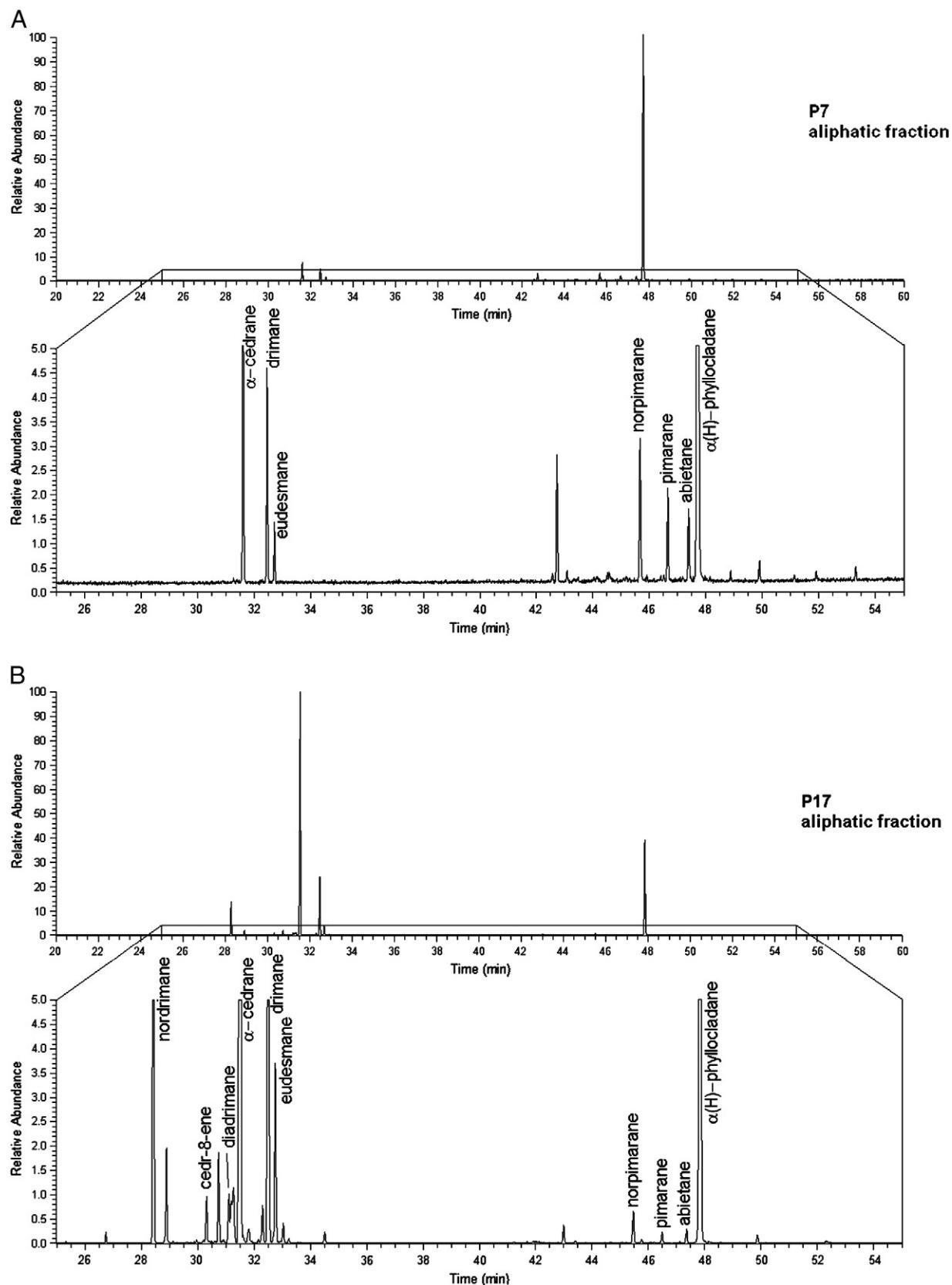
**Fig. 7.** Typical TIC (Total Ion Current) chromatograms of the aliphatic fraction of the sample extracts P7 (A) and P17 (B).

conditions without biochemical processes (Davis and Spackman, 1964; Rollins et al., 1991).

According to Bechtel et al. (2002) there is also a correlation between soluble organic matter (% SOM) and gelification degree (GI) of the sample (the higher extractability is in non-gelified or low gelified wood fragments), and between nitrogen, sulphur and oxygen content (NSO) and gelification (GI) of the sample (the larger GI, the higher NSO). We have not found such dependence. In accordance with
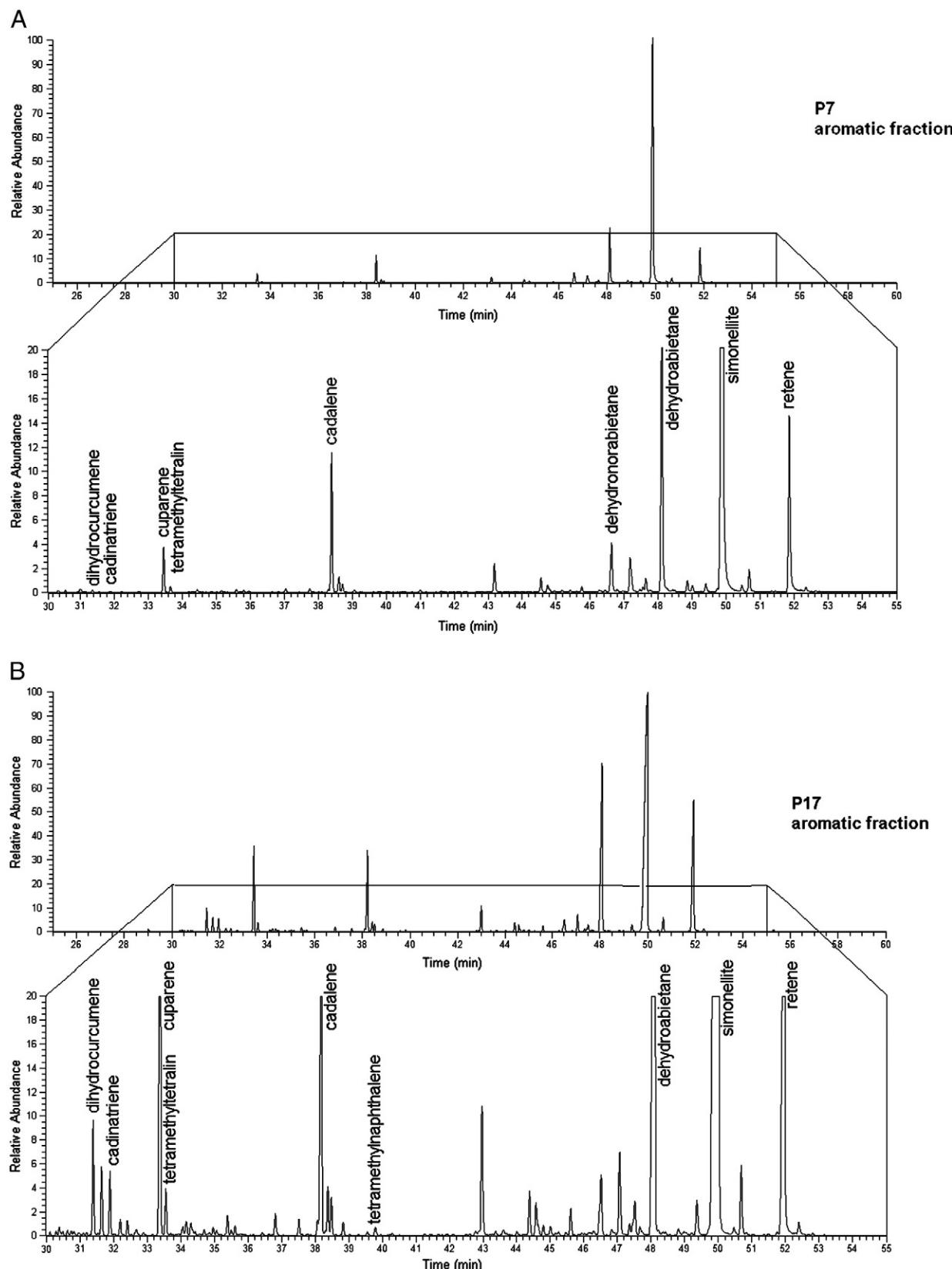
Fig. 8. Typical TIC (Total Ion Current) chromatograms of the aromatic fraction of the sample extracts P7 (A) and P17 (B).

Bechtel et al. (2002, 2003, 2004) and Havelcová et al. (2012) we found a relationship between resinite content and SOM (Fig. 11). Resinite forms round and oval fillings of cellular volumes of tissues and it irregularly fills intercellular spaces. Traces of resinite can be dispersed in cell walls of textinite A and ulminite A.

5.2. Organic compounds

Distribution of *n*-alkanes was similar for all sample extracts: *n*-alkanes with 13 to 32 carbons in the chain have been identified, with a maximum at *n*-C_{23}, and odd-over-even predominance (Fig. 12). The *n*-alkanes are

Table 5
Relative contents of the compounds in the aliphatic hydrocarbon fractions of the stump samples S1–S9 (a) and P1–P23 (b).

a)

Compound	S1	S2	S3	S4	S5	S6	S7	S8	S9
Sesquiterpenoids	0.0	0.0	0.0	0.0	0.0	0.0	2.5	5.8	5.1
Nordrimane									
Cedr-8-ene									
α-cedrane							1.2	3.0	2.3
Drimane							0.8	2.1	1.3
Eudesmane							0.5	0.8	1.5
Diterpenoids	87.1	83.4	84.0	91.6	86.7	89.7	84.3	82.0	82.3
Norpimarane	11.6	10.1	11.0	10.3	10.6	10.2	11.3	11.3	11.7
Norabietane	0.6	0.8	0.6	0.7	0.8	0.8	0.9	0.7	
Isopimarane	1.9	2.1	1.9	2.1	2.2	2.1	2.0	2.0	1.9
Abietane	2.3	2.5	2.4	2.4	2.5	2.4	2.3	2.3	2.2
α(H)-phyllocladane	70.6	67.8	68.1	76.1	70.5	74.1	67.8	65.7	66.5
n-alkanes	12.9	16.6	16.0	8.4	13.3	10.3	13.2	12.2	13.0

b)

Compound	P1	P2	P3	P4	P5	P6	P7	P8	P9	P10	P11	P12	P13	P14	P15	P16	P17	P18	P19	P20	P21	P22	P23
Sesquiterpenoids	99.4	99.7	94.8	98.9	97.7	74.0	9.6	93.8	7.5	93.0	87.3	95.3	95.9	98.7	95.9	30.9	73.2	95.8	95.1	94.3	96.8	93.4	30.2
Nordrimane	3.0	1.6	0.1	2.7	3.2	2.3		1.0		0.9	1.7	2.9	3.0	2.3	3.6	4.7	6.4	2.8	4.4	5.7	4.0	2.4	1.2
Cedr-8-ene	1.6	4.6	0.4	2.4	3.3	0.4		0.4		0.5	0.3	1.8	1.0	0.7	1.0	0.5	0.4	1.3	1.1	1.6	1.2	0.9	0.2
α-cedrane	85.5	85.9	84.2	82.3	78.0	62.2	5.5	84.9	4.1	82.2	78.6	64.5	79.5	84.4	86.0	18.5	53.7	86.5	78.6	71.1	84.1	71.7	24.9
Drimane	5.4	3.2	5.4	6.8	8.5	7.0	3.2	4.4	3.0	7.1	8.6	20.8	10.2	8.8	4.5	8.8	12.4	3.6	5.9	13.8	6.6	16.5	5.3
Eudesmane	2.4	1.8	3.5	2.4	2.8	1.5	0.9	2.1	0.5	1.5	1.0	6.9	3.2	2.5	1.2	1.8	1.8	3.4	6.8	2.4	1.5	2.4	1.5
Diterpenoids	0.4	0.2	1.7	0.7	2.0	25.7	89.3	5.9	91.5	6.5	7.7	0.5	1.4	0.5	3.0	48.9	23.1	2.2	2.6	2.4	1.8	4.0	59.9
Norpimarane			0.5		0.1	0.9	2.4		2.4	0.1	1.3	0.4	0.1		0.1	1.0	0.1	0.2	0.1	0.1	0.1	0.1	2.1
Norabietane																							
Isopimarane							1.4		0.8		0.5					0.1	0.1	0.1	0.1				0.2
Pimarane							1.1		1.6														
Abietane																0.2							0.2
α(H)-phyllocladane	0.3	0.2	1.2	0.7	1.9	24.8	84.3	5.9	86.7	6.4	6.3	0.2	1.4	0.5	3.1	53.8	23.6	2.0	2.5	2.3	1.8	4.0	63.6
n-alkanes	0.2	0.1	3.5	0.4	0.4	0.3	1.1	0.3	1.0	0.5	3.4	2.9	1.7	0.5	0.8	12.5	3.2	1.9	2.1	1.4	1.2	1.2	10.4

Significance of italics is the sum of all sesquiterpenoids (diterpenoids), n-alkanes) - main coumpound groups in the samples.

Table 6
Relative contents of the compounds in the aromatic hydrocarbon fractions of the stump samples S1–S9 (a) and P1–P23 (b).

a)

Compound	S1	S2	S3	S4	S5	S6	S7	S8	S9
Sesquiterpenoids	1.2	2.9	2.5	1.9	4.1	4.6	22.1	29.2	10.7
Dihydrocurcumene									
Cadinatriene									
Cuparene							6.1	11.9	0.4
Tetramethyltetralin									
Cadalene	1.2	2.9	2.5	1.9	4.1	4.6	16.1	17.3	10.3
Diterpenoids	96.7	97.1	97.5	97.2	95.5	95.2	73.1	62.4	89.3
Dehydrobisnorabietane									
Dehydronorabietanes	4.7	1.8	2.7	3.0	2.6	3.5	8.0	7.9	5.2
Dehydroabietane	11.1	18.7	18.3	14.4	13.3	13.1	9.8	6.9	14.2
Simonellite	45.1	67.2	63.5	45.3	50.6	69.1	21.2	12.0	50.0
Retene	35.8	9.4	13.0	34.5	29.0	9.6	34.1	35.5	19.9

b)

Compound	P1	P2	P3	P4	P5	P6	P7	P8	P9	P10	P11	P12	P13	P14	P15	P16	P17	P18	P19	P20	P21	P22	P23
Sesquiterpenoids	22.9	26.5	13.0	24.0	24.3	16.7	7.8	14.9	8.1	22.2	24.7	11.9	9.8	11.3	15.5	1.8	13.7	27.1	27.6	24.0	10.8	28.4	7.5
Dihydrocurcumene	0.7	0.8	0.1	0.5	0.6	0.6	0.1	0.3	0.1	0.5	1.4	0.7	0.2	0.9	0.4		1.4	0.7	0.1	0.4	0.2	0.9	0.1
Cadinatriene		0.5	0.1	0.3	0.4	0.3		0.1		0.3	0.4	0.1	0.1	0.3	0.3		0.3	0.4	0.4	0.4	0.2	0.5	0.1
Cuparene	6.1	6.5	2.0	6.2	8.5	6.3	1.5	3.6	1.7	7.7	7.3	6.3	2.7	1.5	4.4	0.2	5.8	6.1	2.9	8.6	3.3	10.3	1.6
Tetramethyltetralin	1.8	2.9	0.4	1.4	1.8	1.0	0.2	0.8	0.1	1.1	1.6	2.1	0.6	0.3	0.7	0.1	0.6	2.2	1.1	1.4	0.8	1.2	0.2
Cadalene	14.2	15.7	10.5	15.8	13.0	8.4	6.0	10.1	6.1	12.7	14.0	2.9	6.2	8.3	9.7	1.5	5.7	17.7	23.2	13.2	6.2	15.6	5.5
Diterpenoids	77.1	73.5	87.0	76.0	75.7	83.3	92.2	85.1	91.9	77.8	75.3	88.1	91.3	88.6	84.5	98.2	86.3	72.9	72.4	76.0	89.2	71.6	92.5
Dehydrobisnorabietane	0.4	1.5	0.1	0.4	0.6	0.7	0.3	0.7	0.2	0.4	0.5	0.4	0.5	0.6	0.9	0.2	0.5	0.4	0.4	0.2	1.0	0.9	0.4
Dehydronorabietanes	0.4	0.4	0.3	0.4	0.5	1.6	4.0	0.8	1.8	0.3	0.8	0.5	0.4	0.7	0.4	0.2	1.2	0.2	0.3	0.2	0.5	0.5	0.4
Dehydroabietane	0.9	1.8	0.9	1.0	2.3	21.8	11.5	21.2	10.2	14.6	19.3	11.7	10.2	10.0	9.0	7.9	18.2	4.4	2.6	6.9	22.4	26.1	18.3
Simonellite	44.8	36.6	63.5	44.3	43.6	48.7	68.7	50.7	75.0	43.5	32.9	46.5	53.5	34.1	55.0	58.9	53.0	50.5	37.3	51.4	44.1	36.2	57.1
Retene	30.6	33.1	22.2	29.9	28.7	10.6	7.6	11.7	4.7	19.0	21.8	29.0	25.7	43.3	19.3	31.0	13.4	17.4	31.9	17.5	21.2	7.9	16.4
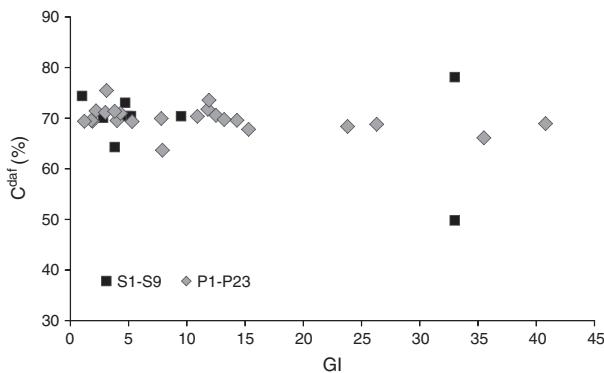
Fig. 9. Relationship between the gelification index (GI) and carbon content (C^{daf}).
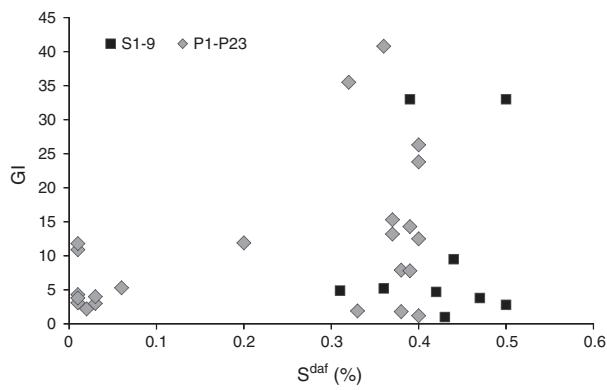
Fig. 10. Relationship between sulphur content (S^{daf}) and gelification index (GI).

characteristic for higher plants, because they originate from their lipids. Carbon Preference Indexes (CPI) (Bray and Evans, 1961) and odd-even predominance (OEP) (Scalan and Smith, 1970) (Table 7) indicate a terrigenous origin of the *n*-alkanes. The lowest values of CPI and OEP have been found in the sample extract P16. The value may have been diminished by geothermal alteration during and after sedimentation or by microbial reworking. The observed *n*-alkane maximum and calculated values (Table 7) correspond to submerged/floating aquatic macrophytes (Ficken et al., 2000; Zheng et al., 2007). Considering the nature and similar storage conditions of the samples, the distribution of *n*-alkanes in the studied samples is associated with a taxon. The similar *n*-alkane distribution in a fossil wood fragment (conifer wood *Protopodocarpoxylon*)
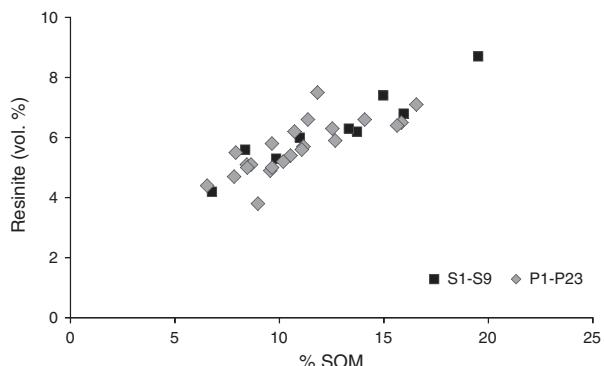
Fig. 11. Relationship between soluble organic matter (SOM) and resinite content.

was identified by Marynowski et al. (2007). Lockheart et al. (2000) and Otto and Simoneit (2001) found that conifer leaves and cones from *Taxodium*, *Sequoia* and *Metasequoia* genera have different distribution of *n*-alkanes compared to other genera.

The results of GC–MS analyses are similar in all wood extracts with regard to terpenoid compounds in the aliphatic and aromatic fractions of the extracts: the most abundant are α-cedrane, 16α(H)-phyllocladane, cadalene, dehydroabietane, simonellite, and retene.

The diterpenoid 16α(H)-phyllocladane makes up the majority of the substances found in the aliphatic extract of the stump samples S1–S9 (65.7–76.1%), followed by *n*-alkanes (8.4–16.6%) and norpimarane (about 11%). Most of the substances found in the aromatic extract of the stump samples S1–S9 are diterpenoids: dehydroabietane, simonellite and retene, all of which are aromatization products of precursors with the abietane skeleton. These substances constitute more than 90% of the aromatic fraction of the extracts in the S1–S6 samples. Sample extracts S7–S9 contain higher amounts of cuparene and cadalene. Sample extracts from the stumps P1–P23 differ among themselves in proportion of 16α(H)-phyllocladane and α-cedrane (Fig. 13). For the stump sample extracts S1–S9 the 16α(H)-phyllocladane/α-cedrane ratio shows minor variations (Fig.14).

There are other differences in isopimarane, pimaranes (pimarane + norpimarane) and abietanes (abietane + norabietane) distributions in sample extracts P1–P23 (Fig. 15). For the stump sample extracts S1–S9 the variation in relative abundances of these compounds is minor (Fig. 16). The agreement in relationship of the 16α(H)-phyllocladane/α-cedrane ratio and terpenoid occurrences in the stump sample extracts S1–S9 is evident. Among the stump sample extracts P1–P23 the most different are the results in the extracts P7, P9, and P16 having opposite 16α(H)-phyllocladane/α-cedrane ratio.

Hopanoids (hopenes), bacterial markers, were detected only in the stump sample extracts S1–S9, and only in very small quantities, indicating little effect of bacteria on the wood. Non-hopanoid pentacyclic triterpenoids, angiosperm markers, have not been found, and thus no samples can be assigned to angiosperm plants. Identified alkylated aromatic compounds – methylnaphthalenes, methylbiphenyles, methylphenanthrenes, tetramethyltetralin – (Fig. 12) are degradation products of original terpenoids (Bastow et al., 1998).

Numerous papers have been published on GC–MS application in the study of organic matter of fossil conifers. A summary can be found in a review article by Otto and Wilde (2001), with a list of sesqui-, di- and triterpenoids, which were found in samples and reported between the years 1950 and 1997. The investigation carried by Otto and Wilde (2001) resulted in division of terpenoid substances according to their occurrence: some compounds (*e.g.*, cadinanes, pimaranes) are nonspecific and can be found in all conifer plants, other (*e.g.*, 16α(H)-phyllocladane) can be found only in some families of conifer plants, and there are also terpenoids typical for one family only (*e.g.*, cuparenes in Cupressaceae).

Cupressaceae s.l. (Cupressaceae s.str. plus former Taxodiaceae without *Sciadopitys*) are recognized as a single family. This unity is independently supported by similarity of terpenoids. This family can be distinguished by the presence of cuparanes (or other sesquiterpenoids, *e.g.*, widdranes), that occur only in the Cupressaceae s.str.. Pinaceae are distinguished from other conifers because they lack some terpenoids (phenolic abietanes, tetracyclic diterpenoids) and contain some special sesquiterpenoids (longicyclanes, sativanes), diterpenoids (cembranes), and also triterpenoids (serratanes, lanostanes). All other papers published after 2001 have been based on the findings presented in the review by Otto and Wilde (2001): Bechtel et al. (2002), Otto et al. (2002), Hautevelle et al. (2006), Otto et al. (2007), Marynowski et al. (2007), and Bechtel et al. (2007).

Terpenoids and their metamorphic derivatives may have different precursors and that is why tracing of their origin in fossil organic matter is complicated. For example, isopimaranes, pimaranes, and abietanes can come from the labdane-derived copalyl pyrophosphate.
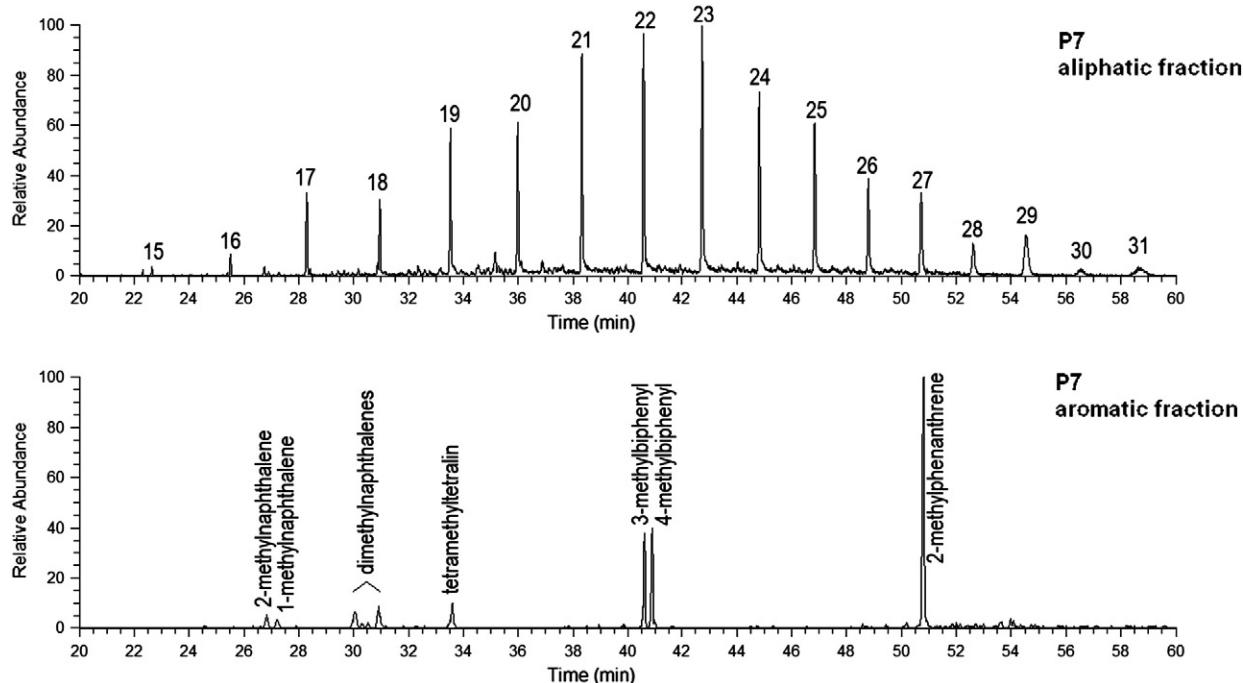
Fig. 12. SIM (Selected Ion Monitoring) chromatograms showing distribution examples of *n*-alkanes (m/z 71) (a) and aromatic compounds (m/z 142, 156, 168, 173, 192) (b). The numbers above peaks indicate carbon numbers of *n*-alkanes.

But they can also come from acids (pimaric, abietic, sandaracopimaric or isopimaric acid), which occur in resins of conifer plants (Otto and Wilde, 2001). The conversion of abietanes then evolves into other compounds — simonellite, retene, and cadalene. But cadalenes may form in an entirely different way, converted from farnesyl pyrophosphate, as well as from α-cedrane or cuparene.

Some of the terpenoid substances found in the studied sample extracts are specific to higher plants and can be assigned to a particular class and family. The occurrence of aliphatic and aromatic biomarkers, arising from native plant materials, depends on conditions during diagenesis of organic matter. Usually, aromatization of plant terpenoids occurs (microbial oxidation, dehydrogenation, and demethylation). If composition of a sample extract is dominated by aliphatic biomarkers, then either the original terpenoid compounds in the plant were special (resistant to degradation) and the storage conditions maintained their status of aliphatics, or the diagenetic conditions were uncommon, reducing primarily production of the aromatic compounds while preserving the aliphatic compounds.

We can assume that the conditions during diagenesis of the plant material were very similar everywhere, and apart from the depositional environment conditions and diagenetical processes also other factors influenced geochemical composition of the material investigated. Differences in the biomarker distribution are related to a conifer family (genus) which original wood has come from. The set of 23 wood fragments is quite representative to exclude random fluctuations in the data. However, among the data from the biomarkers there are at least three samples with more or less intermediate composition.

Staccioli et al. (1993) studied the extracts of the wood of *Taxodioxylon gypsaceum* from Pliocene sediments. The wood revealed the presence of sesqui- and diterpenoid structures, which mainly had cadinane, selinane, and abietane carbon skeletons. The main compounds did not belong to a particular botanical family but also some minor constituents such as α-cedrane were identified. There is a lack of similar data with respect to *Glyptostroboxylon rudolphii*.

According to Otto and Simoneit (2001), cedranes occur only in the family Cupressaceae s.str. and Taxodiaceae, and cuparenes in the family Cupressaceae s.str. and Podocarpaceae of modern wood, and can be used as a characteristic of these conifer plants. Results of the chemical composition analysis show that the studied samples (or at least those with high content of α-cedrane) belong to one order and appear to be representatives of the family Cupressaceae s.l.

Identical composition of saturated and aromatic hydrocarbons from different parts of stumps and coaly clasts from the surrounding sediment can be considered as an evidence of autochthonous origin of the coaly detritus in the "Stump Horizon". It can also serve as an evidence of the same way and intensity of diagenetic change of organic matter near one place. But there is also an opposite possibility that the organic matter was altered significantly, and this diagenetic transformation suppressed slight differences and created new ones due to other effects. With respect to the above stated facts it must be said that all studied samples from the stumps S1–S8 and P1–P23 (*Glyptostroboxylon rudolphii* and *Taxodioxylon gypsaceum*) are more coalified and gelified wood fragments, which testifies about humid and warm environment. Such a climate was suitable for most Cupressaceae s.l. with dominantly preserved huminite and relatively high resinite, as it appears in the summary by Kalaitzidis et al. (2004).

6. Conclusion

Results of the study have shown the diversity in maceral and chemical composition among samples of one stump and among samples in a set of 23 tree stumps from the "Stump Horizon" in the Bílina open cast mine in the Most Basin.

Optical microscopy of the fossil stumps has shown plant textures of ulminite and textinite corresponding to botanical structure typical for conifers. Despite an overall bad preservation of anatomical features, SEM has proved all the microscopic structures and enabled a very detailed study of characteristic visual aspects. Stump samples correspond to the species *Glyptostroboxylon rudolphii* and *Taxodioxylon gypsaceum*.

The sample extracts differ in the relative content of the identified compounds. In the sample extracts different ratios of sesquiterpenoids and diterpenoids – α-cedrane and 16α(H)-phyllocladane, respectively – have been found, and different contents of isopimaranes, abietanes, and pimaranes. The samples can be divided into two or three groups (some results are intermediate). The division into two basic groups of samples according to xylotomical parameters does not match the division

Table 7

Values of parameters calculated from the relative n-alkane distribution in the extracts of wood fragments: CPI (Bray and Evans, 1961), P_{aq} (Ficken et al., 2000), P_{wax} (Zheng et al., 2007), OEP 1 and OEP 2 (Scalan and Smith, 1970). S1–S9 (a) and P1–P23 (b).

Sample	CPI	P_{aq}	P_{wax}	OEP1	OEP2
a)					
S1	1.70	0.91	0.22	1.40	1.49
S2	2.21	0.72	0.39	1.20	1.76
S3	1.94	0.81	0.33	1.12	1.67
S4	2.26	0.68	0.40	1.16	1.64
S5	1.98	0.67	0.45	1.08	1.54
S6	2.12	0.65	0.46	1.10	1.58
S7	1.81	0.76	0.37	1.16	1.54
S8	1.99	0.78	0.34	1.09	1.64
S9	2.27	0.75	0.37	1.13	1.80
b)					
P1	2.03	0.93	0.17	1.44	1.48
P2	1.85	0.91	0.20	1.23	1.35
P3	1.52	0.90	0.21	1.19	1.21
P4	1.75	0.91	0.20	1.37	1.29
P5	1.55	0.92	0.19	1.26	1.15
P6	1.99	0.91	0.21	1.42	1.57
P7	2.25	0.82	0.32	1.49	1.94
P8	1.89	0.93	0.19	1.25	1.42
P9	1.64	0.91	0.20	1.19	1.40
P10	2.01	0.95	0.15	1.33	1.45
P11	1.85	0.83	0.29	1.24	1.45
P12	1.57	0.82	0.29	1.12	1.16
P13	1.47	0.79	0.32	1.14	1.12
P14	1.71	0.73	0.38	1.19	1.27
P15	2.08	0.78	0.34	1.35	1.47
P16	0.96	0.64	0.52	0.96	0.89
P17	2.74	0.64	0.45	1.41	1.75
P18	1.71	0.86	0.26	1.24	1.28
P19	1.39	0.78	0.37	1.15	1.18
P20	1.98	0.85	0.25	1.31	1.40
P21	1.80	0.82	0.29	1.30	1.30
P22	2.02	0.75	0.37	1.28	1.51
P23	2.21	0.71	0.41	1.32	1.65

$CPI = 0.5 * [(C25 + C27 + C29 + C31 + C33)/(C24 + C26 + C28 + C30 + C32) + (C25 + C27 + C29 + C31 + C33)/(C26 + C28 + C30 + C32 + C34)]$.
$P_{aq} = (C23 + C25)/(C23 + C25 + C29 + C31)$.
$P_{wax} = (C27 + C29 + C31)/(C23 + C25 + C27 + C29 + C31)$.
$OEP1 = 1/4 * [(C21 + 6\,C23 + C25)/(C22 + C24)]$.
$OEP2 = 1/4 * [(C25 + 6\,C27 + C29)/(C26 + C28)]$.

according to the study of organic matter composition. In the case of Bílina coniferous "Stump horizon", a GC–MS study of coalified wood has not led to identification of certain genus or species within the family Cupressaceae. The differences in terpenoid composition can be considered as a complex of problems related to diagenetic processes, genus and status of original plant materials that are still subject to further investigation.
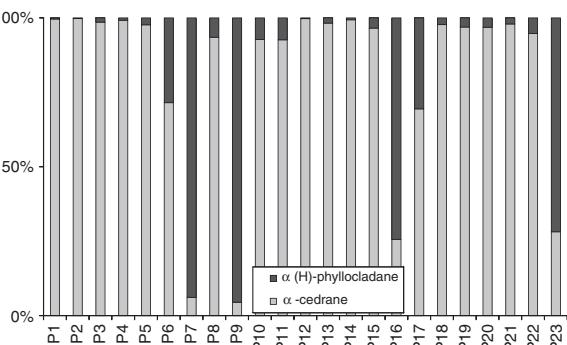
Fig. 13. 16α(H)-Phyllocladane and α-cedrane in samples P1–P23.
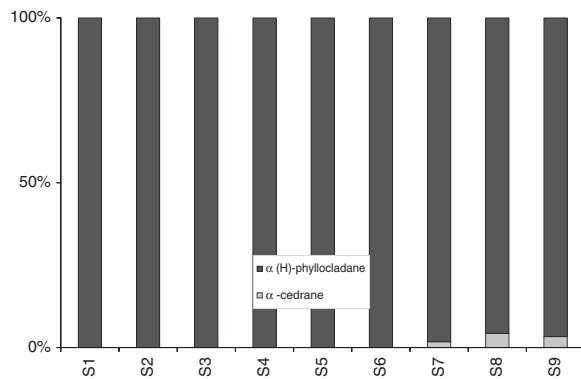
Fig. 14. 16α(H)-Phyllocladane and α-cedrane in samples S1–S9.
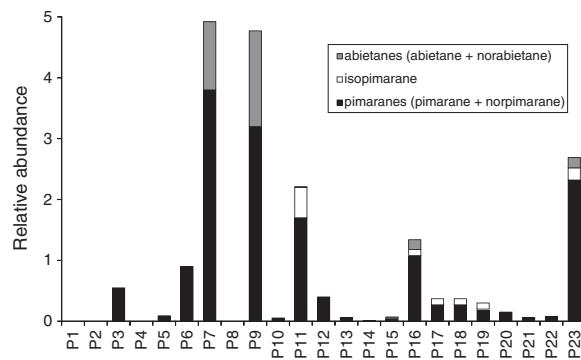
Fig. 15. Relative contents of isopimaranes, pimaranes, and abietanes in samples P1–P23.
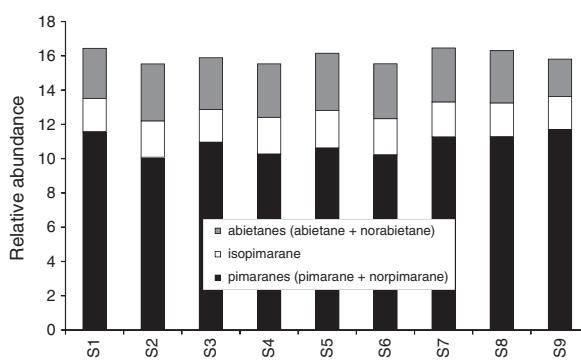
Fig. 16. Relative contents of isopimaranes, pimaranes, and abietanes in samples S1–S9.

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Příloha 5

SILICIFIED STEM FROM THE LATE EOCENE FOSSIL LOCALITY OF KUČLÍN (CZECH REPUBLIC): OVERVIEW AND NEW REMARKS

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Abstract. The silicified stem from Kučlín was first attributed to *Podocarpoxylon helmstedtianum* and linked with the co-occurring remains of *Doliostrobus*. Later it was re-interpreted as *Tetraclinoxylon vulcanense* and associated with twigs and seeds of *Tetraclinis*. The new anatomical comparison reveals that exact botanical affinities of the silicified stem cannot be unequivocally established, mainly with respect to poorly preserved cross-field pitting.

■   fossil conifer wood; *Podocarpoxylon*; *Tetraclinoxylon*; *Doliostrobus*; *Tetraclinis*; Late Eocene; Kučlín; Czech Republic

Introduction

In 1976, a large silicified tree attaining 7.5 m in length was found in the locality of Kučlín by F. Holý (Text-fig. 1). In 1994, the stem was systematically attributed to *Podocarpoxylon helmstedtianum* GOTTWALD and tentatively linked with the co-occurring twigs and cone scales of *Doliostrobus* MARION (Březinová et al. 1994). In 2003, the wood was re-interpreted as *Tetraclinoxylon vulcanense* PRIVÉ and associated with twigs and seeds of *Tetraclinis* MASTERS (Sakala 2003). In fact, *Doliostrobus* and *Tetraclinis* are the only two conifers described in Kučlín (Kvaček 2002, Kvaček and Teodoridis 2011 in this volume), well characterized and unequivocally separated

Text-fig. 1. Historical photo by M. Mag of the discovery of the silicified stem in the locality of Kučlín in 1976 (courtesy Regional Museum Teplice).

based on foliage and reproductive structures. Therefore, the uncertainty, which persists about exact botanical affinities of the silicified stem, is rather problematic.

Historical overview

Březinová in Březinová et al. (1994) described the wood from Kučlín as *Podocarpoxylon helmstedtianum*. The cross-fields, which are of crucial interest for attribution to the morphogenus *Podocarpoxylon* GOTHAN, were characterized as cupressoid and taxodioid. The author, however, noticed they were "usually poorly preserved" (Březinová in Březinová et al. 1994: p. 224). When I re-analyzed the fossil wood (Sakala 2003), I did not observe any "taxodioid" cross-field pit, i.e., with "large, oval to circular, included apertures; the aperture exceeds the width of the border at its widest point" (IAWA Committee 2004: feature 94, p. 53). In fact, all the observed cross-field pits were "cupressoid", i.e., with "elliptical apertures included within the limits of the pit border (contrary to the often extended piceoid pits); apertures are definitely narrower than the border" (IAWA Committee 2004: feature 93, p. 53). However, similarly to Březinová, I could note that the cross-field pits were "poorly preserved" (Sakala 2003: p. 26), in other words, the fact that I did not observe any taxodioid cross-field pit might be also related to the bad preservation or high recrystallisation of the Kučlín wood. I consequently concentrated on features other than cross-field pitting and I realized that, contrary to the previous description (Březinová in Březinová et al. 1994), the tracheids were markedly roundish in cross-section (Text-fig. 2) with characteristic intercellular spaces (Sakala 2003). This feature in combination with other ones (see in Sakala 2003) allowed me to re-attribute the sample to *Tetraclinoxylon vulcanense*, which had originally been described from the Pliocene of Rochefort-Montagne, France by Privé (1973). This fossil morphospecies is considered to describe the wood of *Tetraclinis*, even it differs from the only living representative of *Tetraclinis* – *T. articulata* (VAHL) MASTERS by having both strongly developed crassulae (= Sanio bars) and numerous biseriate parts of pitting in radial tracheid walls (see in Privé 1973: p. 173). Therefore, I associated the fossil wood with twigs and seeds of *Tetraclinis salicornioides* (UNGER) Z. KVAČEK described from the same locality by Kvaček (2002).

In 2005, the trunk wood of *Doliostrobus* was described from the Late Eocene locality of Groitzsch, Germany and a new morphogenus *Doliostroboxylon* was proposed by Dolezych in Junge et al. (2005) to accommodate a unique combination of wood anatomical features. The wood has an overall cupressaceous character (similar to Cupressaceae s.l.) except for the peculiar cross-field pitting; Dolezych in Junge et al. (2005) described cross-field pits as cupressoid,
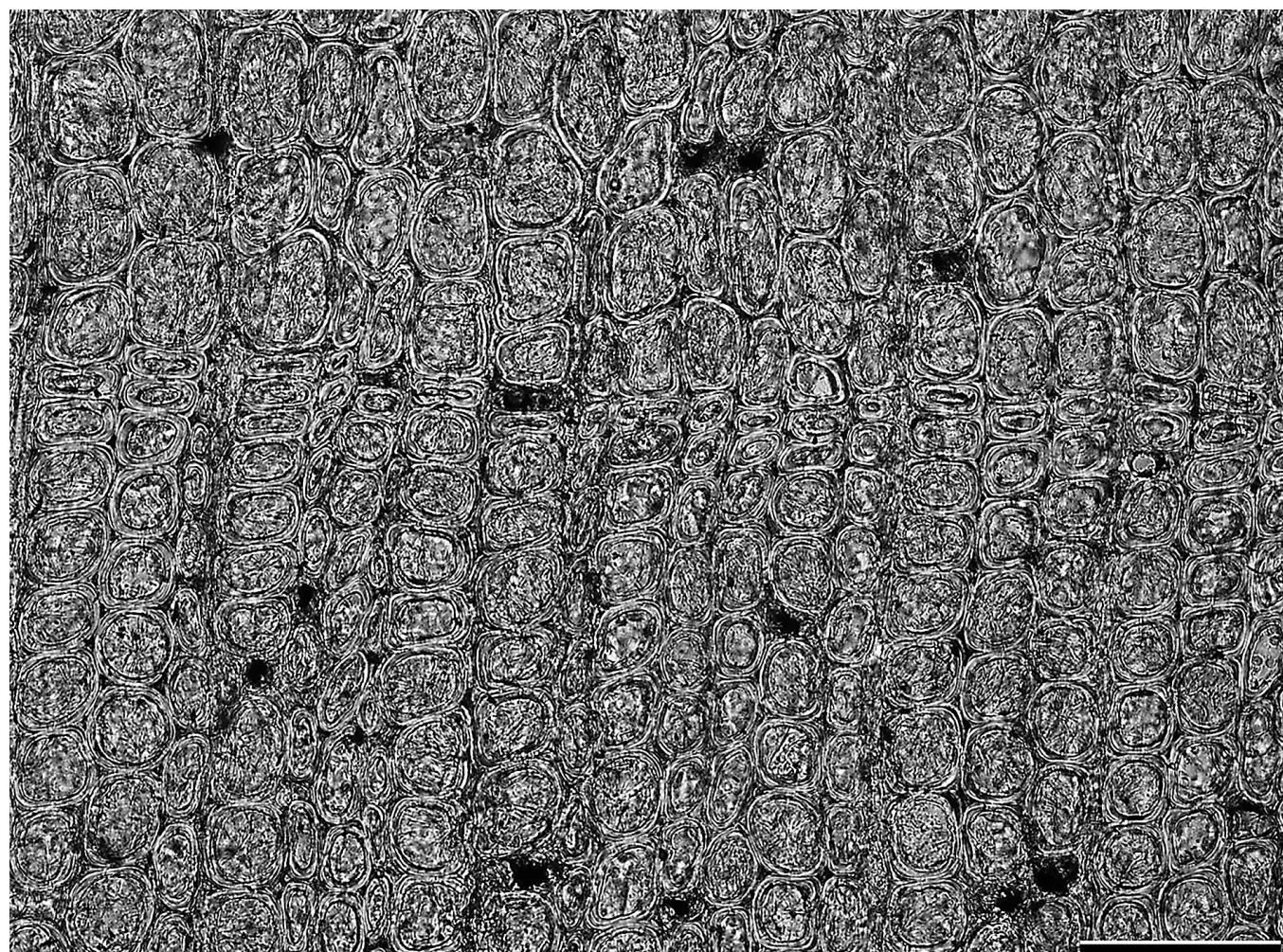
Text-fig. 2: Microscopic photo of the wood from Kučlín (specimen No. G 4723, NM, transverse section) shoving growth ring boundary with markedly rounded tracheids and abundant axial parenchyma (dark cells) present both in late- and earlywood (scale bar = 100 μm).

Table 1. Comparative anatomical table, for more information, see explanation in the text, part called New remarks, note: "height of ray cells" means ratio between the height of ray cells in 1-cell high rays and the height of the middle ray cells in 3- or more-cell high rays; this ratio cannot be determined from the publications about *Doliostroboxylon* and the holotype of *Tetraclinoxylon vulcanense* so there are only total ranges of ray cell height in these two cases.

	Doliostrobus (twig wood)	*Doliostroboxylon* (trunk wood)	*Podocarpoxylon helmstedtianum*	Kučlín wood	*Tetraclinoxylon vulcanense*	*Tetraclinis articulata*
	Geiseltal, Germany Middle Eocene	Groitzsch, Germany Late Eocene	Helmstedt, Germany Middle Eocene	Kučlín, Czech Republic Late Eocene	Rochefort-Montagne, France Pliocene	Recent
	thin slides	Dolezych in Junge et al. 2005	Gottwald 1966 and thin slides	thin slides	Privé 1973	thin slides
tracheid shape in transverse section	angular to polygonal	angular to polygonal	angular to polygonal	rounded	rounded to polygonal	polygonal to rounded
radial diameter of widest tracheid	25 µm	50 µm	35(40) µm	60(70) µm	55 µm	30(40) µm
radial pitting	1-seriate, no crassulae	1(-2)-seriate, crassulae	1-seriate, without crassulae	1-2-seriate, strong crassulae	1-2-seriate, strong crassulae	1-seriate
axial parenchyma	very abundant	abundant	very abundant	abundant	rare	extremely rare
height of ray cells	20-27 µm /15-17 µm	12-40 µm	23-40 µm / 20-30 µm	40-45 µm / 25-30 µm	15-30(-39) µm	25 µm /15-20 µm
cross-field pits	doliostroboid	1-2(-3-4) cupressoid, podocarpoid, pinoid	1-2 ?cupressoid and ?glyptostroboid	1-2(-4) cupressoid, ?podocarpoid	1-2(-4) cupressoid	1-4 cupressoid

podocarpoid and pinoid. This was complementary to a unique cross-field pitting seen in a small leafy branch of *Doliostrobus* from the Middle Eocene locality of Geiseltal, Germany, which was first illustrated by Bůžek et al. (1968), and later formalized by Rüffle and Süss (2001) by defining "doliostroboid" cross-field pits as large, mostly simple pits, 1-5 in number, irregularly disposed in a cross-field and variable in shape. The uniqueness of the cross-field pitting in *Doliostrobus* is still matter of controversy, partly related to its aspect (podocarpoid vs. araucarioid), partly to terminological problems with consensual definition of "podocarpoid" cross-field pit (see in Dolezych and Sakala 2007). However, this debate is beyond the scope of the present overview, especially as the cross-field pits are poorly preserved in the Kučlín wood. Finally, it must be noticed that Rüffle (1976) had already suggested that *Podocarpoxylon helmstedtianum*, described originally from the Middle Eocene locality of Helmstedt, Germany by Gottwald (1966), might in fact be also related to *Doliostrobus*. However, strictly speaking, the only unequivocal and incontestable record of *Doliostrobus* wood is represented today by the small branch from Geiseltal with *Doliostrobus* leaves in direct organic connection; the others are 'only' more (or less) plausible hypotheses.

New remarks

In order to see what the differences are between the above-mentioned woods, I prepared a kind of synoptic table

(see Tab. 1). The published descriptions as well as some original thin slides were used to complete the table; more concretely, the thin slides alone were used in the case of *Doliostrobus* twig, Kučlín wood and extant *Tetraclinis*, combination of both published descriptions and thin slides in *Podocarpoxylon* from Helmstedt, and finally the published description alone in the case of *Doliostroboxylon* from Groitzsch and the holotype of *Tetraclinoxylon vulcanense*. I could observe under microscope the following thin slides: 1) original slides of *Doliostrobus* twig from Geiseltal described in Bůžek et al. (1968) Nos Ge 2/1, 2/2, 2/3, all three sections (courtesy Z. Kvaček), 2) part of Gottwald's type material of *Podocarpoxylon helmstedtianum* from Helmstedt Nos BFA Nr. 12 252 f (holotype), 12 262 f – 12 276 f, 12 278 f – 12 287 f, all three sections (courtesy Z. Kvaček), 3) original slides of *Podocarpoxylon helmstedtianum* from Kučlín described by Březinová in Březinová et al. (1994) Nos G 4700-4710 and G 4715-4726 from the collections of the National Museum in Prague (NM), all three sections (courtesy J. Kvaček) and 4) wood of extant *Tetraclinis articulata* No. 2280 from the collections of Laboratoire de paléobotanique et paléoécologie, UPMC, Paris, all three sections (courtesy C. Privé-Gill).

The results are presented in Tab. 1. I did not see any significant difference between the height of ray cells in 1-cell high rays and that of the middle ray cells of 3- or more-cell high rays, as underlined like typical feature of *Doliostrobus*

wood by Rüffle and Süss (2001: p. 416). Generally, the results clearly show that two woods can be distinguished quite easily by distinct combination of features: *Doliostrobus* twig and extant *Tetraclinis*. The resting four types are rather similar to each other, except for *Podocarpoxylon helmstedtianum* from Helmstedt, which presents narrow tracheids with only uniseriate radial pitting; its cross-field pitting, described by Gottwald (1966), was not confirmed by inspection of the type thin slides. Contrary to *Doliostroboxylon* from Groitzsch, I observed only the cross-field pits with narrow 'slit-like' apertures in the wood from Kučlín; our wood seems to have also more numerous biseriate parts of pitting in radial tracheid walls with more distinct crassulae and more abundant axial parenchyma than the wood from Groitzsch. Moreover, it seems that the Kučlín stem itself is smooth (Text-fig. 1) and does not present typical "burls" on the trunk surface, recorded by Dolezych in Junge et al. (2005: pictures 19-22) in *Doliostroboxylon* from Groitzsch. Finally, the holotype of *Tetraclinoxylon vulcanense* and our wood are very similar, only the former seems have less abundant axial parenchyma. In fact, a reappraisal of the original thin slides of the holotype from France would be the only possibility to quantify this feature.

Conclusions

The fossil wood from Kučlín, originally described as *Podocarpoxylon helmstedtianum* and later re-interpreted as *Tetraclinoxylon vulcanense*, is newly compared to five wood types: *Doliostrobus* from Geiseltal, *Doliostroboxylon* from Groitzsch, *Podocarpoxylon helmstedtianum* from Helmstedt, *Tetraclinoxylon vulcanense* from France and extant *Tetraclinis articulata*. Our wood is the most similar to *Tetraclinoxylon vulcanense*, which is not surprising, but the anatomical feature, indispensable in this context, i.e., cross-field pitting, is poorly preserved. Therefore, the question about its unequivocal systematical attribution or exact botanical affinities is still open.

Acknowledgments

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Příloha 6

The potential of fossil angiosperm wood to reconstruct the palaeoclimate in the Tertiary of Central Europe (Czech Republic, Germany)

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ABSTRACT. The methods in palaeoclimate reconstruction are either taxonomically controlled with the need to identify fossil specimens or not requiring identification of a fossil. The differences between the two types of methods were demonstrated on fossil wood floras from the Tertiary of Central Europe. The Tertiary of northwestern Bohemia (Czech Republic) are unsuitable both for the Coexistence Approach and for Wiemann et al.'s statistical model. On the other hand, the North Alpine Foreland Basin (Germany) is ideal for both methods. The statistical model is applied here for the first time to the famous locality Rauscheröd, using the published xylotomical descriptions only. The minimal values of MAT, calculated as 18°C and 21°C, are lower than those published earlier using the CA and closer to other coeval European localities. Generally, defining wood types to use in Wiemann et al.'s model is an important preliminary step which requires wood anatomical knowledge.

KEY WORDS: fossil angiosperm wood, palaeoclimate reconstruction, Tertiary, Czech Republic, Germany, Central Europe

INTRODUCTION

Fossil angiosperm wood is often neglected as a source of complementary information in palaeoclimate reconstruction. Nevertheless its potential to provide climatic data is great. Climate variables can be determined using the statistical model based on angiosperm wood characters without the necessity of an exact systematic attribution (Wiemann et al. 1998, 1999). However, this model requires more wood types than usually are present at a single locality. On the other hand, the Coexistence Approach (CA), developed by Mosbrugger and Utescher (1997), depends on properly establishing the closest living analogue. The difference between the two methods is demonstrated here using the Tertiary wood floras of two selected model areas from the Czech Republic and Germany.

METHODS IN PALAEOCLIMATE RECONSTRUCTION

There are two main groups of methods for reconstructing palaeoclimate from fossil plants.

The first group is based on finding the systematic affinities of fossil taxa. Generally, this approach reconstructs palaeoclimate using climatic requirements of the presumed living analogues. It is assumed that the fossil taxa and their living analogues have similar climatic requirements. The CA is a good example of the quantification of such an approach (Mosbrugger & Utescher 1997). The CA is based on ecological and climatic requirements of the so-called nearest living relatives (NLR) of the fossil elements. The climatic tolerances of the NLR, i.e., various living plants chosen for equivalents of a given fossil assemblage, are included into a database in form of ranges, and the fossil assemblage is subsequently characterized by the interval, where the maximum of these ranges overlap, i.e., maximum number of NRL can co-exist.

This approach depends on an exact systematic attribution of fossil taxa; however, the right choice of the NLR is often difficult (Kvaček in press). Opinion about the NLR of a fossil can vary depending on the investigator; consequently, the climatic values based on the CA vary as well. Moreover, the existence of the so-called "mosaic" species where each part of the plant shows relationship to a different living relative, makes the application of the CA even more difficult (documented for the fossil elm wood in Bílina, see Fig. 1:1 – for the summary see Sakala 2004).

On the other hand, there is the second group of methods which does not need a precise identification of fossil specimens. These methods take into account the correlation between climate and selected features of the plant structure; these methods include CLAMP (Wolfe 1993), tree ring analysis (Creber 1977) or stable isotopes (van Bergen & Poole 2002). For fossil wood, Wiemann et al. (1998, 1999) developed statistical models for inferring climate from selected wood anatomical characters. The relationships between anatomical features and climate parameters are presented in the form of regression equations. The limitation of this method is that the statistical evaluation requires a large amount of dicot elements (at least 25) within an assemblage or an area (Wiemann et al. 1998, 1999) and this is rare (Sakala 2000). However, this model as well as other methods that are independent of taxonomic attribution should theoretically come to the same results independent of investigator. For that reason, this group of methods can be considered as "objective".

CASE STUDIES

In order to demonstrate different aspects of the two approaches, two areas were chosen. The first is the Tertiary of north-western Bohemia (Czech Republic) focusing on the Most basin (Bílina, early Miocene, Fig. 1:1) and the Doupovské hory Mountains in the vicinity of Kadaň (Oligocene, Fig. 1:2). The second one is the locality Rauscheröd (early Miocene, Fig. 1:3) in the North Alpine Foreland Basin (Germany).

CZECH REPUBLIC

Outcrops of the Tertiary in north-western Bohemia are linked to the Ohře Rift system, a depression zone orientated in SW-NE direction. The Ohře Rift represents a complex volcano-tectonic structure, which can be separated by transverse, NW-SE orientated lines in differently depressed blocks of volcanic centres (České středohoří and Doupovské hory Mts.) and sedimentary freshwater deposits (Most Basin etc.). Generally, the volcanic and sedimentary rocks are mostly late Eocene to early Miocene in age, and there are many fossilifer-
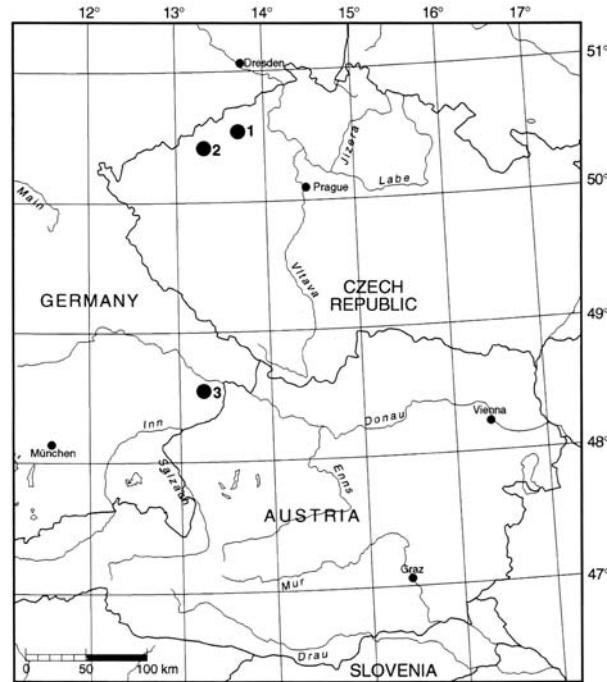

Fig. 1. Geographic position of the compared regions: **1** – Bílina; **2** – Kadaň; **3** – Rauscheröd. (according to Kovar-Eder et al. 2001, slightly modified)

ous localities. The recent state of knowledge and complementary references can be found in Chlupáč et al. (2002).

Coexistence approach (CZ)

The Tertiary of north-western Bohemia have been intensively explored, however, most palaeobotanical investigations have been of fossil leaves, fruits and seeds. Angiosperm wood is also known but uncommon (e.g., the famous "wood of the deluge" from Jáchymov, found in 1557, being originally described as *Ulminium diluviale* by Unger (1842); the original slides were re-discovered and re-described by Dupéron et al. (submitted). Therefore, the palaeoclimate reconstruction based on the CA must uses leaves and reproductive structures.

Statistical model (CZ)

The model developed by Wiemann et al. (1998, 1999) requires a statistically valid sample, i.e., sufficient number of "wood types" sensu Wiemann et al. (1998). However, in the area of Kadaň, i.e., the richest site for fossil angiosperm wood in the Czech Republic, there are only eight different species described (Prakash et al. 1971). New specimens have been collected. The re-examination of the original and new material reveals a total of only seven well defined species (wood types) of fossil dicot-

yledonous angiosperms (Sakala 2006), maybe slightly more. Hence, the vicinity of Kadaň as well as the whole area of the Tertiary of north-western Bohemia remains unsuitable for the statistical model.

GERMANY

Fossil wood record from the early- to middle Miocene sediments of the North Alpine Foreland Basin has recently been summarized by Böhme et al. (in press). With over 1000 samples from 65 localities assigned to 80 taxa this area can be considered as one of the world's richest for silicified wood (Böhme et al. in press). The locality Rauscheröd (Fig. 1:3) from Lower Bavaria was chosen as ideal for the purpose of the present paper. First, there are many angiosperm woods (more than 20 species) at one single site, which is rare for Europe. Second, Rauscheröd is traditionally considered as a locality with markedly tropical character (Selmeier 2000a), which is rather unusual regarding its age (early Miocene, late Ottnangian, MN 4b). Recently, Böhme et al. (in press) characterized Rauscheröd as a paratropical evergreen *Carapoxylon* (*Xylocarpus*) forest. In fact, the main reason of this study was to check "independently" the tropical (or paratropical) character of Rauscheröd using the "objective" statistical model. Geologically, Rauscheröd belongs to the Ortenburg gravel, which represents a delta deposit of the Oncophora Lake. (For further information and additional references see Böhme et al. in press).

Coexistence approach (DE)

Böhme et al. (in press) analyzed Rauscheröd using the CA: NLR together with their corresponding mean annual temperatures (MAT) are summarized in their figure 6:1, then all climatic parameters calculated for all localities studied are presented in their Table 1. Focusing just on MAT, determined for Rauscheröd as 22.2–24.2°C, the genus *Carapoxylon* causes its highest value (Böhme et al. in press). The fossil was compared to *Xylocarpus* / *Carapa* (Böhme et al. in press, appendix tab. 1) and one must recognize that these taxa (e.g. *Carapa guianensis* Aubl., *Xylocarpus mollucensis* (Lamk.) Roem., *X. granatum* Koenig) look very similar (Richter & Dallwitz 2000-onwards, InsideWood 2004-onwards). The second most thermophilic taxon *Bombax* (with about 17°C as the minimal value of the range of MAT,

Böhme et al. in press) was recognized as the nearest living relative to *Bombacoxylon oweni* (Carr.) Gottwald. However, this fossil species is generally placed somewhere between Sterculiaceae and Bombacaceae (Privé-Gill & Pelletier 1981). Similarly, several species of *Grewioxylon*, the variability of which had been described in detail by Selmeier (2000b), were compared to the modern genus *Grewia* (Böhme et al. in press, appendix tab. 1). These species may represent "tilioid" types other than *Grewia*, e.g. *Craigia*, which is very common in the Tertiary of Central Europe based on reproductive structures (Kvaček 2005). The wood of extant *Craigia* was described recently by Manchester et al. (2006) and some fossil woods might represent this genus, e.g. a new find from the area of Kadaň (Sakala 2006). However, *Grewioxylon* and similar fossil tilioid woods lack the helically thickened vessels typical of the modern *Craigia* (Manchester et al. 2006).

The CA of the Rauscheröd xyloflora gives, except for *Carapoxylon,* a broad interval for MAT (Böhme et al. in press). Therefore, it will be important to find exact living analogues to different species of *Carapoxylon*, the most abundant element at Rauscheröd.

Statistical model (DE)

On the other hand, the statistical model, using wood characters only, should prove the possible tropical (paratropical) character of Rauscheröd in rather objective way. Table listing all fossil woods from Rauscheröd (Böhme et al. in press, appendix tab. 2) served after a consultation with A. Selmeier as a basis of the data set. The model of Wiemann et al. (1998, 1999) uses dicotyledonous wood only, so *Palmoxylon* sp. and *Taxodioxylon* sp. are not considered. *Cinnamomoxylon* sp. div., *Laurinoxylon* sp., *Carapoxylon* sp. and *Grewioxylon* sp. were also not included in the data set because their description did not allow defining the woods as distinct taxonomic units. The data set presented in Table 1 consists of 22 fossil species and 13 wood anatomical characters (Wiemann et al. 1998, 1999), the definition of which is found in the caption to Table 1. All characters were based on literature exclusively.

The subsequent step consisted in choosing "wood types" instead of "fossil species". A wood type is the unit in Wiemann et al.'s statistical

Table 1. Dicotyledonous fossil wood from Rauscheröd with 22 fossil species (all lines) representing 16 wood types (lines in grey). Wood anatomical characters (definitions according to Wiemann et al. 1998, 1999): **tang** – tangential arrangement, **mult** – vessels with multiple perforations, **spir** – spiral thickening present in the vessels, **<100 μm** – vessel mean tangential diameter less than 100 μm, **rp** – wood ring-porous, **homo** – rays exclusively homocellular, **> 10ser** – rays commonly more than 10 cells wide, **het4+** – heterocellular rays with 4 or more rows of upright cells, **stor** – rays storied, **para** – axial parenchyma predominantly paratracheal, **marg** – marginal parenchyma present, **abs** – axial parenchyma absent or rare, **sept** – septate fibres; **0** – character absent, **1** – character present, **0/1** – character ambiguous (= cannot be attributed with certainty), **X** – character cannot be used (= character '<100 μm' has no sense for ring porous woods). Data from Gottwald (1997) and Selmeier (1970a, b, 1985, 1989, 1998, 2001)

Family	Taxon	Vessels					Rays				Parenchyma			Fibres
		tang	mult	spir	<100 μm	rp	homo	>10ser	het4+	stor	para	marg	abs	sept
Bombacaceae?	*Bombacoxylon oweni*	0	0	0	0	0	0	0	0	0	0	0	0	0
Ebenaceae	*Eudiospyroxylon* cf. *multiradiatum*	0	0	0	1	0	1	0	0	1	0	0	0	0
	Euebenoxylon polycristallum	0	0	0	1	0	0	0	0	0	0	0	0	0
Ericaceae	*Ericaceoxylon macroporosum*	0	1	0	1	0	0	0	0	0	0	0	0	0
Euphorbiaceae	*Euphorbioxylon ortenburgense*	0	0	0	1	0	0	0	1	0	0	0	1	0
Fagaceae	*Castanoxylon bavaricum*	0	0	0	x	1	1	0	0	0	0	0	0	0
	Castanoxylon zonatum	0	0	0	x	1	1	0	0	0	0	0	0	0
Flacourtiaceae	*Homalioxylon europaeum*	0	0	0	0/1	0	0	0	1	0	0	0	0/1	1
Juglandaceae	*Eucaryoxylon rauscheroedense*	0	0	0	1	0	0	0	0	0	0	0	0	0
Lauraceae	*Cinnamomoxylon areolosum*	0	1	0	1	0	0	0	0	0	1	0	0	0
	Cinnamomoxylon limagnense	0	1	0	0	0	0	0	0	0	1	0	0	0
	Cinnamomoxylon seemannianum	0	1	0	0	0	0	0	0	0	1	0	0	0
	Laurinoxylon annularis	0	1	0	0	0	0	0	0	0	1	0	0	0
	Laurinoxylon cristallum	0	1	0	0	0	0	0	0	0	1	0	0	0
Meliaceae	*Carapoxylon* cf. *ornatum*	0	0	0	0	0	0	0	0	0/1	0	1	0	1
	Carapoxylon ortenburgense	0	0	0	0	0	0	0	0	0/1	0	1	0	1
	Carapoxylon xylocarpoides	0	0	0	0	0	0	0	0	0/1	0	1	0	1
	Cedreloxylon cristalliferum	0	0	0	x	1	0	0	0	0	0	0	0	0
Myricaceae	*Myricoxylon zonatum*	0	1	0	1	0	0	0	0	0	0	0	0	0
Tiliaceae	*Grewioxylon auctumnalis*	0	0	0	0	0	0	0	0/1	0	0	1	0	0
	Grewioxylon neumaieri	0	0	0	0	0	0	0	1	0	0	1	0	0
	Grewioxylon ortenburgense	0	0	0	0	0	0	0	1	0	0	1	0	0

model. It is most often a genus, but "…occasionally a species or group of species if wood anatomical differences permitted such a separation." (Wiemann et al. 1998). In other words, a wood type, still following the examples cited by Wiemann et al. (1998) is a wood with a distinctive combination of characters. In fact, this step requires familiarity with wood anatomy. The wood types here have been chosen based on my judgment (after consultation with C. Privé-Gill) and available literature (descriptions, figures and plates) to reflect natural taxonomic units with distinctive wood anatomy. At Rauscheröd, there are 16 wood types (in comparison with 22 fossil species!), which are marked in grey in Table 1. In spite of the fact that Rauscheröd is a unique locality with many angiosperm woods, this number is still lower than 25 types per locality recommended by Wiemann et al. (1998).

Finally, the MAT was calculated using the same three regression equations as used for the fossil wood localities of Yellowstone, Post, Vantage, Clarno Nut Beds and Fejej (Wiemann et al. 1999). The first regression equation, defined by Wiemann et al. (1998) and based on untransformed data, is the following:

MAT (Wiemann 98) = 13.40 − 0.250(spir) + 0.637(>10ser) + 0.255(het4+) + 0.416(stor) − 0,213(abs), where the values in parentheses are the percent of wood types in an assemblage that have the corresponding character. The other two equations are based on transformed data (arcsine transformation) and were published later by Wiemann et al. (1999):

MAT (Arcsines 12) = 24.78 + 36.57(stor) −15.61(marg) − 16.41(abs)

MAT (Arcsines 15) = 17.07 + 25.23(stor) − 23.17(abs) + 13.79(sept), where the values in parentheses are the arcsines of the square roots of the proportions of the characters.

How to code "axial parenchyma absent or rare" in *Homalioxylon* and "rays storied" in *Carapoxylon* is unclear with respect to equivocal information obtained from the publications so rexamination of the original slides is needed (see Tab.1).

The MAT calculated are the following:

minimal values (*Homalioxylon* with parenchyma absent or rare and neither of the two species of *Carapoxylon* having storied rays)

MAT (Wiemann 98) = 18.0°C
MAT (Arcsines 12) = 20.7°C
MAT (Arcsines 15) = 21.0°C

maximal values (*Homalioxylon* with parenchyma present and both species of *Carapoxylon* having storied rays)

MAT (Wiemann 98) = 24.9°C
MAT (Arcsines 12) = 30.2°C
MAT (Arcsines 15) = 28.9°C

Generally, the minimal values of the MAT obtained for Rauscheröd using the statistical model, i.e., MAT calculated as 18 and 21°C, seem to be more realistic and closer to the values obtained from other Ottnangian(-Karpatian) localities with "Younger Mastixioid Floras" correlated with the assemblage of Eichelskopf-Wiesa sensu Mai (1995) of the Miocene climatic optimum, e.g., Oberdorf, Austria with MAT = 15.7–17.6°C based on CA (Bruch & Kovar-Eder 2003) or the upper part of the Libkovice member of the Most formation, Czech Republic with MAT estimated 19 ± 1°C (Teodoridis & Kvaček 2006).

CONCLUSIONS

1) The Tertiary of north-western Bohemia, Czech Republic, is not suitable for the CA based on fossil angiosperm wood, nor for the statistical model developed by Wiemann et al. (1998, 1999). The information useful for CA is better obtained from the more abundant leaves and reproductive structures. The richest site for fossil angiosperm wood, i.e., town of Kadaň and its vicinity, have only seven well defined wood types of fossil dicotyledonous angiosperms (Sakala 2006). This is not sufficient for a correct application of the statistical model.

2) On the contrary, the North Alpine Foreland Basin, Germany, is ideal both for the CA and the statistical model. Rauscheröd has many angiosperm woods at one single site and the possibility to test its tropical (paratropical) character by the statistical model was chosen as the model example. The MAT there had already been calculated as 22.2–24.2°C using the CA by Böhme et al. (in press). Modern *Carapa / Xylocarpus*, attributed to dominant *Carapoxylon* as its NLR, caused the highest value for MAT (Böhme et al. in press). The exact nearest living relative of *Carapoxylon* remains still unknown. The xyloflora, except for *Carapoxylon*, gives unspecific climate information because the fossil woods are compared to living genera only and not to species. The

NLR of some fossil wood taxa might also be wrong (something between Sterculiaceae and Bombacaceae rather than *Bombax* alone for *Bombacoxylon*, another member of Malvaceae s.l. with tile cells, e.g., *Craigia* instead of *Grewia* for *Grewioxylon*). The statistical model was applied for the first time on Rauscheröd xyloflora. All data were taken from literature, 22 fossil species were reduced to 16 wood types. The results for MAT have a broad range and confirm the results of CA (Böhme et al. in press). The minimal values of MAT calculated here as 18 and 21°C seem to be in accordance with the data published earlier for other localities from the similar time interval. However, the study requires the re-examination of the original slides, mainly *Carapoxylon* and *Homalioxylon*, to determine their characters.

3) Generally, the "objective" (in the sense that it does not require an exact systematical attribution of fossil specimens) statistical model has an important preliminary phase, i.e., choice of the wood types. This requires an experienced xylotomist, who should also look at the original samples from a locality.

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Příloha 7

Fossil angiosperm wood and its host deposits from the periphery of a dominantly effusive ancient volcano (Doupovské hory Volcanic Complex, Oligocene-Lower Miocene, Czech Republic): systematics, volcanology, geochronology and taphonomy

JAKUB SAKALA, VLADISLAV RAPPRICH & ZOLTÁN PÉCSKAY
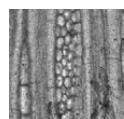
A variety of fossil woods occur on the northern margin of the Doupovské hory Volcanic Complex in the northwestern part of the Czech Republic. The woods were buried by three different processes reflecting three different settings. First, a large area between the towns of Kadaň and Klášterec is covered by an up to 100 m thick sequence of lahar and debris avalanche deposits. These flows and avalanches gathered wood of *Liriodendron*, Lauraceae, *Platanus*, *Cercidiphyllum*, ?*Craigia* and Styracaceae from both the volcanic complex slopes and adjacent plains. Second, a rich assemblage of fossil woods with thermophilous elements such as Lauraceae and palms was preserved on the northern volcanic complex periphery by a Strombolian eruption of a monogenic cone. Third, a shallow lake formed to the side of the volcanic complex, where *Platanus* trunks were fossilized in the travertine. The wood of *Liriodendron* has never been previously recorded in the localities representing volcanic complex foothills, but is common in the local lahar deposits. This distribution leads us to hypothesize that *Liriodendron* forests dominated higher topographic levels of the Doupovské hory Volcanic Complex, reaching, but probably not exceeding 1000 m a.s.l. • Key words: fossil angiosperm wood, systematic palaeobotany, volcanology, taphonomy, geochronology, Tertiary, Czech Republic.

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Volcanic areas often provide excellent settings for preservation of fossil material, especially producing when fine pyroclastic material predominate. Effusive volcanic activity is much less conducive to the fossilization of organic material. Lava-built volcanoes and volcanic complexes undergo weathering and solid rock decay processes. Weathering products may substitute the role of pyroclastic deposits in dominantly effusive volcanoes. Consequently in combination with the topography, debris avalanches, debris flows and mudflows may be produced. Such secondary sedimentary processes bury remains of both fauna and flora (*e.g.*, Cameron & Pringle 1986).

Fossil wood is relatively common in the Tertiary of the northwestern part of the Czech Republic. Most are Cupressaceae *s.l.* (*e.g.*, Teodoridis & Sakala 2008). Angiosperm wood is frequently found in the town of Kadaň and its vicinity, related to Oligocene to early Miocene activity of the Doupovské hory Volcanic Complex (DHVC in the following text). Prakash *et al.* (1971) and Sakala & Privé-Gill (2004) described eight different wood types from this area, hence the locality is one of the richest sites of fossil angiosperm wood in Central Europe (Sakala 2006, 2007). Temporary exposures excavated in the last fifteen years, including construction of the new hospital and digging activity for gas pipe and gas-fixtures in Kadaň, offered the opportunity for new sampling and reassessment of the taphonomic model for the area which was believed to have been dominated by diatreme facies of maar volcanoes (*e.g.*, Kopecký 2010). The aim of our research is to understand how wood fragments were fossilized in settings of a dominantly effusive volcanic complex.
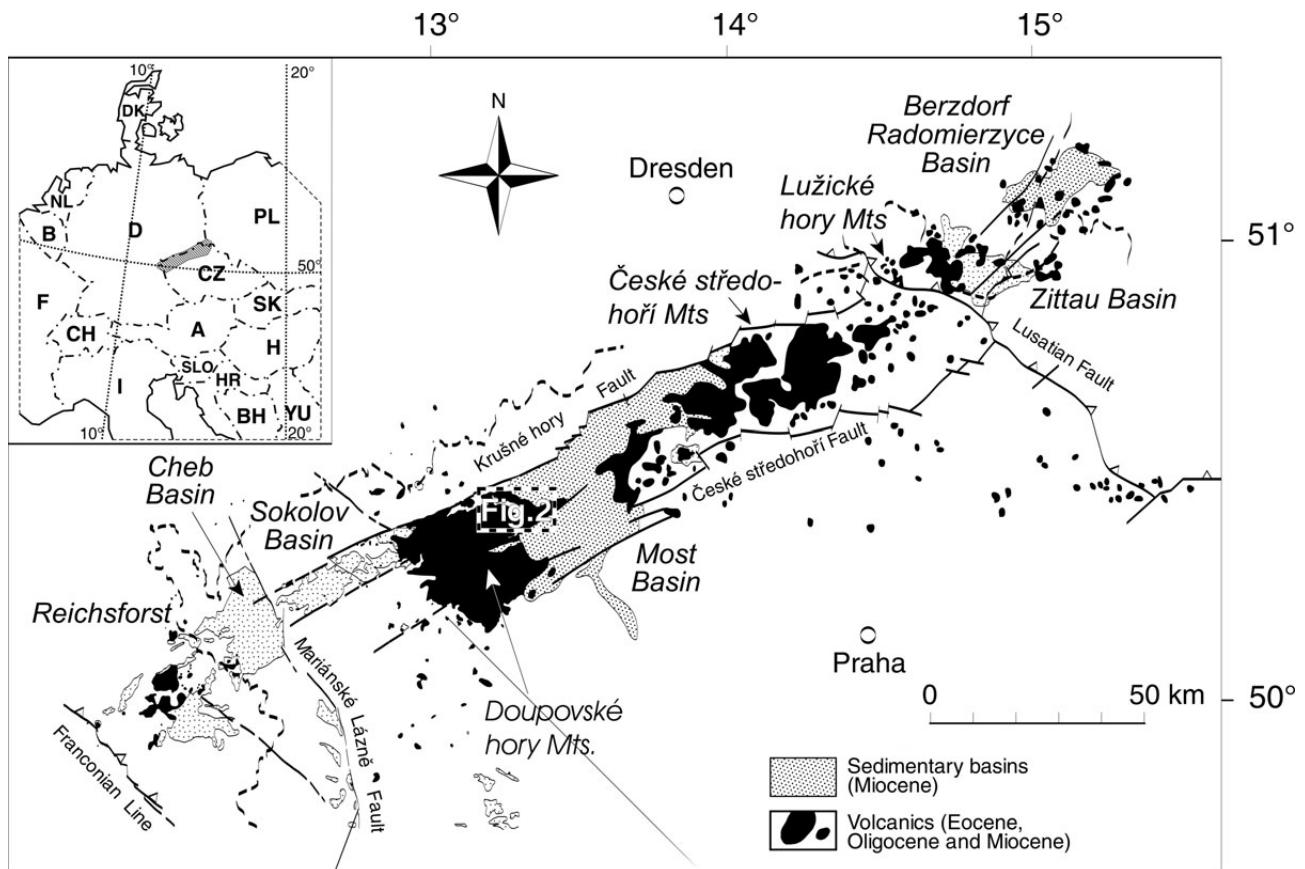
Figure 1. Location of the Doupovské hory Volcanic Complex.

Geological setting

The origin of the Doupovské hory Volcanic Complex (DHVC – Fig. 1) is associated with the formation of the continental Eger (Ohře) Graben and ascent of mantle derived melts (*e.g.*, Ulrych *et al.* 2002) along the boundary between the Saxothuringian and Teplá-Barrandian Domains of the Bohemian massif (Mlčoch 2003). A complex mosaic of crystalline rocks (including amphibolite, paragneisse, orthogneisse, granulite, phylite, variscan granite, *etc*.) form the basement of the DHVC (Mlčoch & Konopásek 2010). The entire DHVC represents an erosional relic of a multiphase volcanic complex. Activity was initiated in the earliest Oligocene (mammal zone MP-21: Fejfar & Kaiser 2005). The early DHVC fine-grained volcaniclastics were produced by basaltic eruptions of the Strombolian and phreato-magmatic style. Pyroclastic material from this activity was deposited in subaerial, swampy and lacustrine environments with a total thickness reaching 80 m (Hradecký 1997a). These deposits currently crop out on the eastern and northeastern margins of the DHVC. The volcanic activity later became predominantly effusive in character (Rapprich & Holub 2008), associated with weak Strombolian and possibly also Hawaiian eruptions. The effusive ac-

tivity continued until the Early Miocene (*ca* 29–22 Ma: Rapprich & Holub 2008). This younger stage formed an extensive complex of foidite/basanite/tephrite lava sequences up to 500 m thick (Hradecký 1997a, Rapprich & Holub 2008). Individual lava units are often accompanied by volcaniclastic debrites. These coarse grained sediments are interpreted as lahar or debris avalanche deposits (*e.g.*, Hradecký 1997b). Hradecký (1997b) described these accumulations from the southern and western margins of the DHVC. In addition, we have documented lahar deposits also on the northern margins of the DHVC. Generally, the lahar deposits occur in various stratigraphic positions within the DHVC, but the debrites on the northeastern margins pre-date the lavas of the Úhošť Hill (Rapprich 2007). The oldest lava at the base of the Úhošť Hill was dated by the K-Ar method as 28.66 ±1.06 Ma (Rapprich & Holub 2008). On the northeastern periphery of the DHVC, a group of eroded remnants of monogenetic cones (23–20 Ma: this paper) occur and appear to represent the most recent volcanic activity of the DHVC in the Lower Miocene (Fig. 2). The sedimentary infill (including coal seams) of the Eger Graben shortly postdates the volcanic activity of the DHVC. This sedimentary period is represented to the northeast of the DHVC by the Miocene Most Basin.
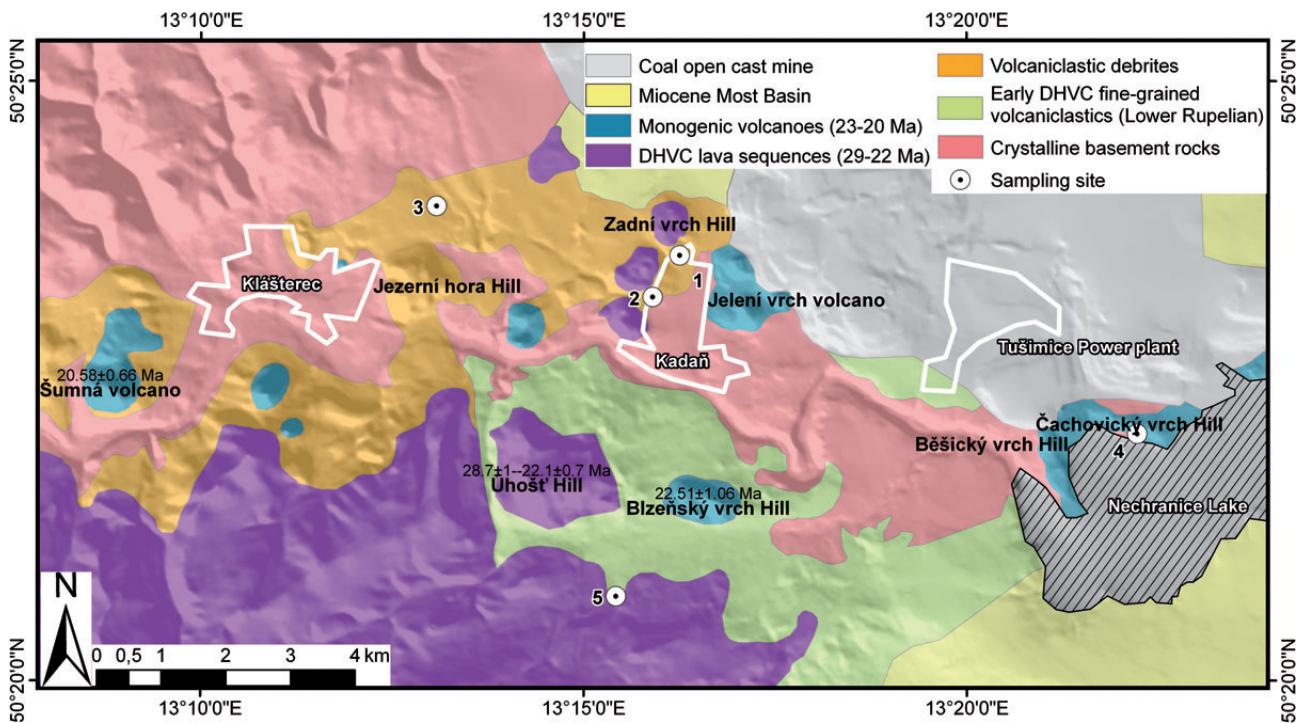
Figure 2. Simplified geological map of the northeastern periphery of the DHVC (adapted from the Digital Geological map of the Czech Republic 1 : 50,000 scale available on http://www.geology.cz/extranet/geodata/mapserver and modified with respect to new data and observations) and location of sampling sites: 1 – Zadní vrch Hill, 2 – Prostřední vrch Hill, 3 – Vernéřov, 4 – Nechranice, 5 – Zvoníčkov. Digital Elevation Model illuminated from southwest.

Material and methods

New specimens of silicified and calcified wood were thin-sectioned in compliance with the standard techniques and studied using compound light microscopy. Anatomical descriptions are in accordance with the IAWA Hardwood List (IAWA Committee 1989). The thin sections described here are partly housed in the National Museum in Prague (those described originally by Prakash *et al.* 1971 and epitype of *Cercidiphylloxylon kadanense*), and partly in the Chlupáč Museum of Earth History in the Faculty of Science of Charles University in Prague (new specimens).

The approximate age of the lahar deposits was determined by their position beneath a lava dated 28.66 ±1.06 Ma (K-Ar: Rapprich & Holub 2008), but the age of the monogenetic volcanism on the northern periphery of the DHVC was not known. Three samples of lavas from monogenic volcanoes (Šumná volcano, Blzeňský vrch Hill, Jelení vrch Hill) on the northern periphery of the DHVC were dated using the K-Ar method. All the three samples were measured as bulk-rocks. Additionally, glass and plagioclase fractions were separated from the groundmass of the Jelení vrch Hill sample to resolve the problem of low potassium content in the bulk-rock sample. Geochronological analyses were carried out in the

ATOMKI Laboratories, Debrecen, Hungary. Potassium concentration was measured using a digitized flame photometer, CORNING 480 machine with a Li internal standard. The analyses were controlled by inter-laboratory standards Asia 1/65, LP-6, HD-B1 and GL-O. Argon was extracted from the samples by high frequency induction heating. A [38]Ar-spike was introduced into the system via a gas pipette before the degassing began. The isotopic ratios were measured on a 15 cm radius magnetic sector-type mass spectrometer under static mode, built in Debrecen, Hungary. Balogh (1985) and Odin (1982) described in detail the methods applied here. The calculation of ages was based on atomic constants suggested by Steiger & Jäger (1977). Analytical errors are quoted for the 68% confidence level (one standard deviation).

Systematic palaeobotany

Angiosperm wood from the DHVC, both newly found specimens and those described by Prakash *et al.* (1971) and Sakala & Privé-Gill (2004), can be subdivided into seven units called "wood types" *sensu* Wiemann *et al.* (1998, p. 85). These are listed using informal names and described in the following section.

Figure 3. Calcified trunk of *Liriodendron* in the lahar deposits exposed during diggingwork for gas-pipes in Kadaň, southern slope of the Prostřední vrch Hill.

Wood type 1 – *Liriodendroxylon*

Family Magnoliaceae

Genus *Liriodendroxylon* Prakash, Březinová & Bůžek

***Liriodendroxylon tulipiferum* Prakash, Březinová & Bůžek**
Figure 4A–C

Material. – Kadaň-Zadní vrch ZV-23 (holotype), 18/98, 53/02; Vernéřov 57/02, 61/02.

Description. –Wood diffuse-porous, growth ring boundaries distinct, vessels rarely solitary mostly in radial multiples and clusters, scalariform perforation plates with about 10 bars, opposite intervessel pits with oval outlines, slightly heterocellular rays mostly 3- to 4-seriate, and marginal axial parenchyma.

Discussion. – Prakash *et al.* (1971) noted that this wood type was similar to modern *Liriodendron tulipifera* L. (see InsideWood 2004–onwards). Marginal parenchyma is visible in slide G4049 of the holotype specimen which

includes both transverse and radial views (Fig. 4A). Other diagnostic features, such as oval opposite intervessel pits are visible in the holotype (Prakash *et al.* 1971, fig. 33) as well as in the new specimens, *e.g.*, 18/98 (Fig. 4C). Leaves and fruits of *Liriodendron* are unknown from the DHVC, but there are occurrences of *Liriodendron haueri* in the České středohoří Mts (Kvaček & Teodoridis 2007).

Wood type 2 – *Laurinoxylon*

Family Lauraceae

**Genus *Laurinoxylon* Felix emend. Dupéron *et al.***

***Laurinoxylon czechense* Prakash, Březinová & Bůžek**
Figure 4D–G

Material. – Kadaň-Zadní vrch CNB-2 (type); ?Nechranice 74/04.

Description. – Wood diffuse-porous, growth ring boundaries distinct, vessels mostly solitary and in radial (and oblique) multiples of 2–3, predominantly simple perforation plates, scalariform perforation plates with 10–15 bars rarely present in narrow vessel elements, heterocellular rays 1- to 3-seriate with some enlarged oil / mucilage cells in the margins, vasicentric axial parenchyma.

Discussion. – Dupéron-Laudoueneix & Dupéron (2005) inventoried the fossil woods assigned to the Lauraceae. The original slides of *Laurinoxylon diluviale* (Unger) Felix, the type species of *Laurinoxylon* known since 16th century as 'Sündfluthholz' from the phreatomagmatic vent breccia at Jáchymov (north of the DHVC, in the Krušné hory Mts/Erzgebirge), were re-discovered in the French Museum of Natural History (MNHN) in Paris and re-described, together with emended generic and specific diagnoses (Dupéron *et al.* 2008). The fossil wood briefly described here has characteristics of the morphogenus *Laurinoxylon*. Prakash *et al.* (1971) recognized it as a distinct

Figure 4. A–C – Wood type 1 – *Liriodendroxylon* (A, B: holotype ZV-23 of *Liriodendroxylon tulipiferum*; C: specimen 18/98). • A – diffuse-porous wood with vessels rarely solitary, usually in multiples and terminal parenchyma in 3-seriate lines, TS/RLS. • B – slightly heterocellular rays mostly 3–4-seriate and scalariform perforation plates with about 10 bars, TLS. • C – opposite intervessel pits, RLS. • D–G – Wood type 2 – *Laurinoxylon* (holotype CNB-2 of *Laurinoxylon czechense*). • D – diffuse-porous wood with paratracheal vasicentric parenchyma, TS. • E – heterocellular 1–3-seriate rays with swollen marginal cells, TLS. • F – ray cells with oil or mucilage content in margin, RLS. • G – detail of a small vessel element with alternate intervessel pits in lower part and scalariform perforation plate in upper part, TLS. • H–M – Wood type 3 – *Platanus* (H, K: holotype CNB-6 of *Platanoxylon bohemicum*; I, L, M: holotype ZV-24 of *Spiroplatanoxylon europeanum*; J: holotype CNB-11 of *Dryoxylon bohemicum*). • H–J – diffuse-porous wood with distinct growth rings and broad rays, TS. • K – broad homocellular rays up to 20 cells wide, TLS. • L – detail of homocellular ray and exclusively scalariform perforation plates with about 20 bars, TLS. • M – helical thickening on the top of a vessel element, TLS. Scale bars = 500 μm in A, B, D, H–K; 200 μm in E, F, L; 50 μm in C, G, M.
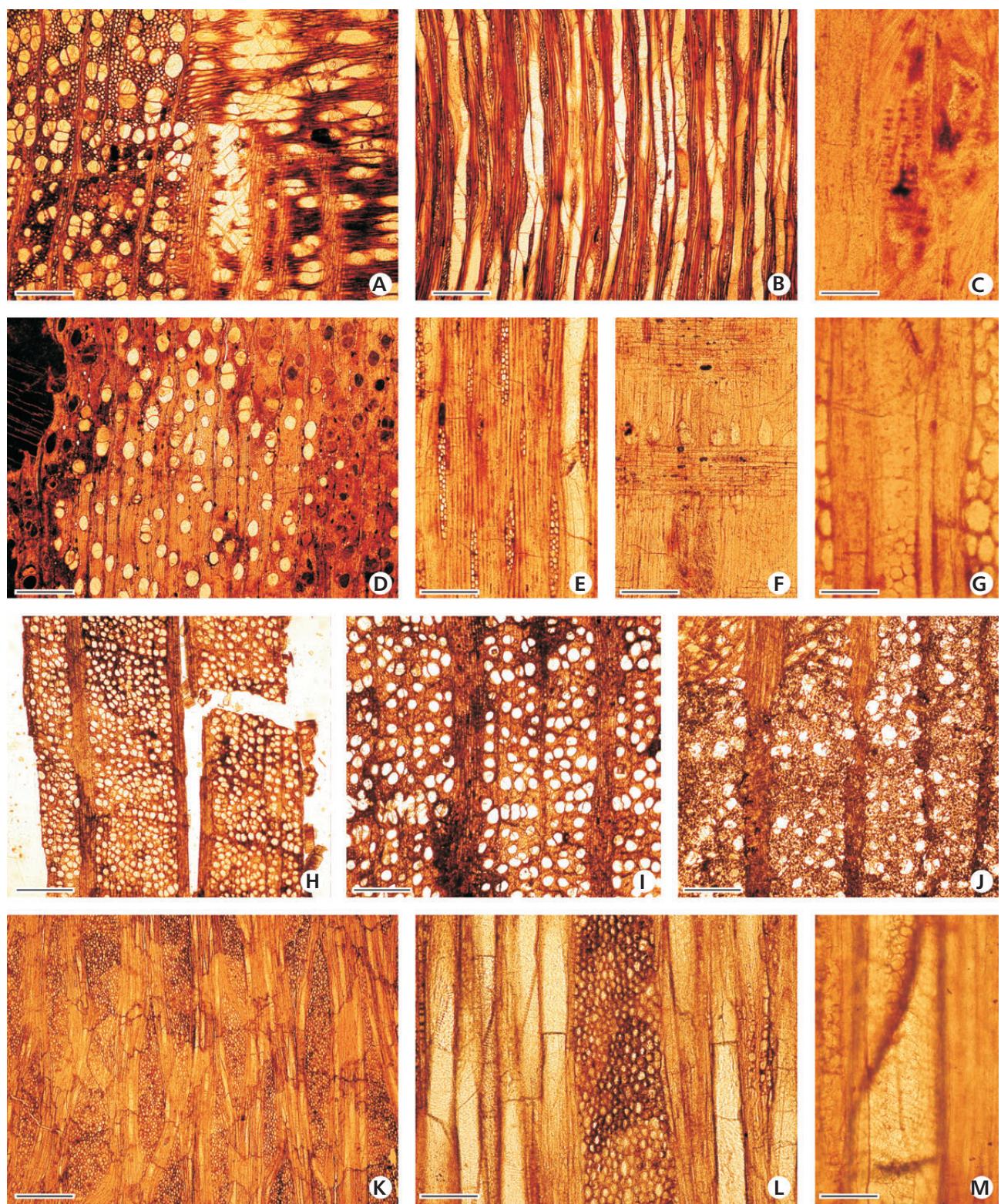
species *L. czechense*. It differs from *L. diluviale* in having generally thinner rays, mainly due to narrower individual ray cells. This difference in ray width can partly be explained by the processes of fossilization which could produce more dilated ray cells in *L. diluviale* (M. and J. Dupéron, pers. comm.). Contrary to Prakash *et al.* (1971), we observed oil cells similar to those in *L. diluviale* (Fig. 4E, F) associated with ray parenchyma only (but not those amongst fibres) and very rarely scalariform perforation plates in narrow vessel elements (Fig. 4G). Therefore, it is not easy to distinguish between these two species. Idioblasts (oil/mucilage cells) associated exclusively with rays are present in several taxa, *e.g.*, *Caryodaphnopsis*, *Litsea chinensis* or the south-American species of *Cinnamomum* (Richter 1987). As vessel-ray pitting is not preserved, it is not possible to use correctly the classification *sensu* Richter (1987). As a result, we cannot attribute our wood to any particular living genus. The periphery of the DHVC has yielded thermophilous floras with *Daphnogene* (Kvaček & Teodoridis 2007), which is considered to be related to the living *Cinnamomum camphora* (L.) J. Presl (Kvaček *et al.* 2004, Kvaček pers. comm.).

Wood type 3 – *Platanus*

Family Platanaceae

Platanoxylon Andreánszky *ex* Prakash, Březinová & Bůžek

Platanoxylon bohemicum Prakash, Březinová & Bůžek
Figure 4H, K

> 1971 *Platanoxylon bohemicum* sp. nov.; Prakash, Březinová & Bůžek, p. 115, pl. 39, figs 44, 46.

Material. – Kadaň-Zadní vrch CNB-6 (type), 73/03; ?Nechranice 109/05, 114/06; ?Vernéřov 64/02.

Spiroplatanoxylon Süss

Spiroplatanoxylon europeanum (Prakash, Březinová & Bůžek) Süss
Figure 4I, L, M

> 1971 *Plataninium europeanum* sp. nov.; Prakash, Březinová & Bůžek, p. 120, pl. 42, figs 59–63.
> 2007 *Spiroplatanoxylon europeanum* (Prakash, Březinová & Bůžek) Süss comb. nov.; Süss, p. 12.

Material. – Kadaň-Zadní vrch ZV-24 (type, CNB-11).

Dryoxylon Schleiden *in* Schmid

Dryoxylon bohemicum Prakash, Březinová & Bůžek
Figure 4J

> 1971 *Dryoxylon bohemicum* sp. nov.; Prakash, Březinová & Bůžek, p. 122, pl. 43, figs 64–67.

Material. – Kadaň-Zadní vrch CNB-11 (type).

Description. – Wood diffuse porous, growth ring boundaries distinct, vessels solitary or in short irregular multiples with scalariform perforation plates only (simple plates not observed) with about 20 bars, sometimes with spiral thickenings, homocellular rays up to 20 cells wide and apotracheal diffuse-in-aggregates and scanty paratracheal vasicentric axial parenchyma, rarely crystalliferous.

Discussion. – The three species recognized by Prakash *et al.* (1971), *i.e.*, *Platanoxylon bohemicum*, *Plataninium europaeum* (= *Spiroplatanoxylon europeanum*) and the very poorly preserved *Dryoxylon bohemicum*, are very similar to each other. They all have large homocellular rays, up to 24 cells wide, and scalariform perforation plates. Although there are several differences between them (*e.g.*, smaller vessel elements in *Platanoxylon bohemicum* type species) they all seem to belong to the same type of platanoid wood whose exact affinity is uncertain. We think the wood must be related to *Platanus neptuni* (Ettingsh.) Bůžek, Holý & Z. Kvaček (Sakala 2006, Kvaček & Manchester 2004), the only member of the Platanaceae present in both volcanic areas of the DHVC and the České středohoří Mts (Kvaček & Teodoridis 2007). *P. neptuni* is otherwise known as a nearly complete plant based on foliage branches, isolated leaves, stipules, staminate inflorescences with pollen *in situ* and infructescences (Kvaček 2008). The specific systematic position of *P. neptuni* within *Platanus* is expressed by a distinct subgenus *Glandulosa* (see in Kvaček *et al.* 2001, table 1) and corresponds well to the specific character of our fossil wood (see here below).

The fossil wood related to *Platanus* is usually classified under the mophogenera *Platanoxylon* or *Plataninium*. As already noticed by Brett (1972) and Wheeler & Manchester (2002, p. 97), the classification of fossil *Platanus*-like woods is not a simple matter because they generally differ from the extant *Platanus*. Firstly, fossil platanoid wood often has scalariform perforation plates only (Wheeler 1995). The only living representative of *Platanus* which bears some resemblence with respect to this feature *i.e.* having a higher portion of scalariform to simple perforation plates, is *P. kerrii* Gagnep., native to Laos and Vietnam (Wheeler 1995). Contrary to Prakash *et al.*'s (1971) description, and in accordance with Süss & Müller-Stoll (1977, p. 50), we have not observed any simple perforation

plates in our samples of platanoid wood. Secondly, as Süss & Müller-Stoll (1977) described, some platanoid woods have spiral thickening in the vessel elements. This feature is unknown among extant *Platanus* woods (Wheeler & Manchester 2002). Süss (2007) recently created a new morphogenus, *Spiroplatanoxylon,* for platanoid wood with spiral thickening and re-interpreted *Platanoxylon* and *Plataninium* from Kadaň as belonging to this genus. We can confirm the presence of spiral thickenings (Fig. 4M) and rare prismatic crystals in axial parenchyma cells in *Plataninium* but not in *Platanoxylon*. Therefore, we use the denomination *Spiroplatanoxylon* only for the *Plataninium* type of wood in which we observed spiral thickening and crystals; as a precaution, we also keep the three morphospecies as separated units. However, we think they all represent the same botanical species.

Wood type 4 – *Cercidiphylloxylon*

Family Cercidiphyllaceae

Genus *Cercidiphylloxylon* Prakash, Březinová & Bůžek

***Cercidiphylloxylon kadanense* Prakash, Březinová & Bůžek**
Figure 5A, B

Material. – Kadaň-Zadní vrch ZV-12 (holotype), G8113 (= 23/98) (epitype).

Description. – Wood diffuse-porous, growth ring boundaries distinct, vessels mostly solitary, with angular outline, scalariform perforation plates with about 40 bars, heterocellular, mostly 2–3-seriate rays with uniseriate marginal rows (tails), which sometimes interconnect several multiseriate ray portions.

Discussion. – This wood type was originally described by Prakash *et al.* (1971) and later reviewed in detail by Sakala & Privé-Gill (2004) with the definition of an epitype and comparative study with the extant Cercidiphyllaceae and Hamamelidaceae. It was noticed that 1) *Cercidiphylloxylon kadanense* slightly differed from extant *Cercidiphyllum* Sieb. & Zucc., 2) it was the oldest record of true *Cercidiphyllum* fossil wood and 3) an older record of *Cercidiphyllum*-like wood of Paleocene/Eocene age had to be related to extinct genera with leaves of *Trochodendroides* Berry emend. Crane and fruits of the *Nyssidium*-type (Sakala & Privé-Gill 2004). Our fossil wood most probably is the wood of *Cercidiphyllum crenatum* (Unger) R.W. Brown which occurs in all Oligocene localities in the České středohoří Mts (Kvaček & Teodoridis 2007). However, its occurrence in the DHVC has not been proven so far. *C. crenatum* is known as a nearly complete plant based on

foliage, fruits, seeds, staminate inflorescences, and *in situ* pollen (Kvaček 2008).

Wood type 5 – *Ulmus*

Family Ulmaceae

Genus *Ulmus* L.

***Ulmus* sp.**
Figure 5C

Material. – Nechranice 75/04.

Description. – A small branch, 2.5 cm in diameter, with bark preserved. Wood ring-porous, growth ring boundaries distinct, earlywood vessels mainly solitary, latewood vessels grouped, forming typical wavy tangential bands, wide exclusively homocellular rays.

Discussion. – This single piece of wood was already mentioned by Sakala (2006). Unfortunately, the very poor preservation only allows its safe attribution to elm wood thanks to the diagnostic pattern seen in cross-section and the homocellular rays seen in radial section. A comparison with the fossil elm wood described from Bílina (Sakala 2002) or with other Ulmaceae (Wheeler & Manchester 2007) is not possible. In the Tertiary of northwestern Bohemia, the genus *Ulmus* is represented by 2 species: *U. fischeri* as leaves in volcanic areas of both the DHVC and the České středohoří Mts and *U. pyramidalis* in the Most Basin based on leaves and fruits (Kvaček & Teodoridis 2007).

Wood type 6 – ?*Craigia*

Family Malvaceae s.l.

Genus *Craigia* W.W. Smith & W.E. Evans

aff. *Craigia* sp.
Figure 5D–G

Material. – Kadaň-Zadní vrch 72/03; Nechranice 70/03, 78/03, 84/04, 89/04, 90/04.

Description. – Wood semi-ring porous, growth ring boundaries distinct, marked by marginal parenchyma, earlywood vessels solitary or in short radial multiples of 2–3, latewood vessels thick-walled, mainly in radial multiples of 2–3, both with simple perforation plates, strongly heterocellular rays up to 10 cells wide with tile cells of the *Pterospermum* type, apotracheal diffuse to

diffuse-in-aggregates and paratracheal vasicentric axial parenchyma.

Discussion. – It was recently suggested by Sakala (2006) that this newly discovered fossil wood could be attributed to Malvaceae s.l. due to its diagnostic tile cells in the rays, and to the extant genus *Craigia*, whose wood was described by Manchester *et al.* (2006). Tile cells occur in Malvaceae s.l. and are sometimes cited as a rare example of synapomorphy based on wood anatomy (Olson 2005, p. 514); however, they are also present in several species of *Hopea* from the Dipterocarpaceae (order Malvales) (*e.g.*, Manchester *et al.* 2006, Selmeier 2000, table 3). In fact, the Czech wood type is similar to both the extant *Craigia* and extinct *Chattawaya* Manchester (1980) in its vessel disposition and character of tile cells. Unfortunately, we did not observe any helical thickening typical of *Cragia*; the seemingly helically thickened vessels in one specimen (Fig. 5G) do not represent true spirals but only "coalescent apertures" of intervessel pits (E.A. Wheeler, pers. comm.). Among fossil representatives, the helical thickening is only present in *Reevesia japonoxyla* Terada & Suzuki (1998). On the other hand, we did not observe crystals, which are very typical of *Chattawaya* (Manchester 1980, Wheeler & Manchester 2002). Therefore, we call our fossil wood "aff. *Craigia* sp.", reflecting the similarity to this genus except for the typical helical thickening. Although unknown in the DHVC, *Craigia* represents an important and abundant element in the České středohoří Mts and also in the Most and Sokolov basins (Kvaček & Teodoridis 2007). It is generally present as dispersed fruit valves, but also as complete fruits at various stages of maturity, dispersed flowers and flower buds with pollen *in situ*, often together with the accompanying foliage of *Dombeyopsis lobata* (Kvaček 2008).

Wood type 7 – *Coryloxylon*

Family Styracaceae

Genus *Coryloxylon* Prakash, Březinová & Bůžek

Coryloxylon nemejcii Prakash, Březinová & Bůžek
Figure 5H–J

> 1971 *Coryloxylon nemejcii* sp. nov.; Prakash, Březinová & Bůžek, pp. 116–118, pl. 40, figs 48–52.

Material. – Kadaň-Zadní vrch CNB-4 (type).

Coryloxylon tertiarum Prakash, Březinová & Bůžek
Figure 5K–M

> 1971 *Coryloxylon tertiarum* sp. nov.; Prakash, Březinová & Bůžek, pp. 118–120, pl. 41, figs 53–58.

Material. – Kadaň-Zadní vrch CNB-3 (type).

Description. – Wood diffuse porous, growth ring boundaries distinct, vessels solitary, but mostly in clusters and radial multiples, scalariform perforation plates with about 15–20 bars, heterocellular uniseriate and multiseriate (mostly 3- to 4-seriate) rays, axial parenchyma diffuse or diffuse-in-aggregates, chambered axial parenchyma with prismatic crystals often present.

Discussion. – The difference in vessel arrangement between *Coryloxylon nemejcii* and *C. tertiarum* do not seem to be systematically significant and can be explained by intraspecific or individual variability. We consider that both woods represent the same wood type, the affinities of which need re-evaluation. We did not observe the aggregate rays described by Prakash *et al.* (1971) so the connection to *Corylus* becomes questionable. Both woods have features seen in the Styracaceae: exclusively scalariform perforation plates, pores solitary or in multiples, both uni- and multiseriate heterocellular rays, diffuse and diffuse-in-aggregates axial parenchyma and prismatic crystals or silica (Dickison & Phend 1985). Prismatic crystals are useful for distinguishing between species within the extant Styracaceae. These are present only in *Bruinsmia*, *Halesia* and *Styrax*: *Bruinsmia* differs strongly from our wood in lacking growth rings, but a clear distinction between *Halesia* and *Styrax* is not possible based only on wood (Dickison & Phend 1985). In the David A. Kribs wood collection housed in the N.C. State University, we observed similar structure in the extant *Halesia macgregorii* Chun (SJRw 29811) from China, however, it lacked crystals. Therefore, we are not able to distinguish between *Styrax* and *Halesia*. In the Tertiary of northwestern Bohemia, the only record of Styracaceae so far comes from the Early Miocene Cypris formation of the Sokolov Basin – there are fruits designated as *Sinojackia* sp. by Bůžek *et al.* 1996 (recorded as *Halesia crassa* in Kvaček & Teodoridis 2007).

Volcanology and sedimentology

Material for study was sampled from five localities (Fig. 2) representing three different volcanogenic sedimentary deposits:

Zadní vrch, Prostřední vrch, Vernéřov (localities 1, 2 and 3 in Fig. 2)

Localities 1, 2 and 3 are situated within the volcaniclastic debrites of the DHVC (Fig. 2). The localities were artificial trenches (length × width × depth = 10 × 1 × 1 m at

Prostřední vrch) and earthworks (length × width × depth = 300 × 200 × 2 m at Vernéřov, 300 × 100 × 1-3 and 300 × 200 × 3 m at Zadní vrch). Similar deposits were observed in all three localities. The sediments form subhorizontal beds up to 2 m thick, represented by a poorly sorted polymictic (fragments of various types of basaltic rocks), coarse-grained (basaltic boulders up to 40 cm in diameter) matrix-supported debrite. The volcanigenic matrix consists of fine basaltic detritus and clinopyroxene crystals. The total thickness of the lahar deposits observed on the Jezerní hora Hill reaches 100 m. Xenolithic clasts occur rarely, they were found in some depositional units of debrites around Klášterec and they consist of horizontally stretched violet clays with quartz crystals, most probably gneiss argillized by weathering already prior to the volcanic activity. The deposits contain abundant tree trunks, up to several meters long and 1 m in diameter, and fragments of tree branches. The trunks are distributed randomly in the host rock and subhorizontally orientated (Fig. 3). The number of trunks exposed during occasional excavations was not high enough to evaluate the possible preferred orientation statistically.

Nechranice (locality 4 in Fig. 2)

Opalized and calcified wood fragments occur at the base of fine- to medium-grained scoriae on the banks of the Nechranice dam on the southern slopes of the Čachovický vrch Hill. The geological classification was reconstructed on the basis of several small outcrops. The lower part of the section is accessible only when the Nechranice Lake is emptied during dry seasons. The basement of the profile consists of the fossil-weathered gneisse overlain by a pyroclastic deposit. Locally, relics of pre-volcanic sediments – sandstones derived from crystalline rocks, are also present. The non-welded, loose pyroclastic rocks do not create a real outcrop there and the thickness can only be estimated as not exceeding 1 m. The pyroclastic deposit consists of basaltic scoria fragments, 1–2 cm in diameter. The fragments of fossilized woods can only be found where pyroclastics occur. The fossilized wood was collected in an area 200 × 20 m, on the banks of the Nechranice Lake. The pyroclastic deposits are overlain by a few meters thick basanitic lava flow, which extends to the site from the top of Čachovický vrch Hill.

Zvoníčkov (locality 5 in Fig. 2)

Calcified tree trunks were found in the abandoned Zvoníčkov village among fragments of lacustrine travertine containing numerous cavities that originated from herbaceous stems. The travertine containing the tree trunks occurs in the valley amidst hills representing remnants of the DHVC lava sequences, but the contact is not exposed at present. We categorize this site as Early DHVC volcaniclastics on the basis of data obtained during the late 18th and early 19th century, when celadonite was exploited in the area of Zvoníčkov and eastern foothills of the Úhošť Hill. Großkopf (1932) and Müller (1936) described the sediments hosting the travertine as a sequence of alternating layers of tuffs, clays and limestone. The lithological scheme is supported by a 114 m deep borehole (Müller 1936).

Geochronology

Three monogenetic volcanoes from the latest phase of volcanic activity on the northern periphery of the DHVC were dated using the K-Ar method: Šumná Volcano, Blzeňský vrch Hill and Jelení vrch Hill. Despite the similar setting of the three volcanoes, their composition differs significantly. The lava of the Šumná volcano has a trachybasaltic composition, a picrobasalt erupted on the Jelení vrch scoria cone, the Čachovický vrch Hill is composed of an altered basanite (not suitable for K-Ar analysis) and a limburgite forms the Blzeňský vrch lava. The trachybasalt of the Šumná Volcano was sampled in the castle-trench on the top of the Šumná Hill (541 m a.s.l.). The remnant of a lava lake inside the scoria cone crater is exposed there. A picrobasalt feeder dyke of a scoria cone remnant crops out on the peak of the Jelení vrch Hill (363 m a.s.l.). Basanite lava was sampled in the active quarry currently occupying the entire Blzeňský vrch Hill. Suitable potassium concentrations produced reasonable data for the Šumná Volcano (20.58 ± 0.66 Ma) and the lava of Blzeňský vrch Hill (22.51 ± 1.06 Ma). The K_2O content in the picrobasalt of the Jelení vrch Hill does not exceed 0.5 %. Hence, acceptable results could be obtained neither by processing a bulk-rock sample nor by processing the plagioclase/glass fraction separated from the groundmass.

The data obtained from Šumná volcano and Blzeňský vrch Hill yield an Aquitanian age and can be correlated with the youngest lava of the Úhošť Hill profile (22.09 ± 0.73 Ma, Rapprich & Holub 2008).

Discussion on taphonomy and stratigraphy

This paper focuses on fossilized wood from five sites from the north-eastern margins of the DHVC, representing three different types of volcaniclastic deposits (Fig. 2).

The area between the towns of Kadaň and Klášterec – where the localities Zadní vrch Hill, Prostřední vrch Hill and Vernéřov are situated (localities 1–3 in Fig. 2) – is mainly composed of polymictic volcanogenic debrites. These polymictic matrix-supported volcanogenic deposits

with horizontally orientated tree trunks reflect sedimentation from debris flow – lahar. The older interpretation by Kopecký (*e.g.*, 2010) considering maar volcanoes is rejected here because the debrites display no signs of phreatomagmatic fragmentation, xenolith content is low and their presence is limited solely to some layers and the debrites comprise subhorizontal beds of thickness up to 2 m. On the other hand, diatreme breccias penetrating crystalline units should contain one type of basaltic rock (not various types of basaltic rocks as from the DHVC) and high content of upper-crustal xenoliths. Numerous types of volcanic rocks would be present only if diatreme penetrated the pre-existing volcanic sequence which is not the case in the northern DHVC periphery.

The lahars must have originated from a terrain with high relative elevation – most likely in the central part of the DHVC. The volcanic complex very probably reached altitudes of 1000 m a.s.l. in its central part at that time (the highest part of the early DHVC edifice is preserved in an erosional remnant on the Pustý zámek Hill, 927 m a.s.l. in the centre of the DHVC). The trees were dragged by the mass flows during their descent down the slopes of the volcano. The process may explain the high species diversity from the Zadní vrch Hill. The lower species diversity of the Prostřední vrch and Vernéřov localities is very probably due to the limited extent of occasional exposures. We consider *Liriodendron*-dominated forests to be typical of higher altitudes on the volcanic complex flanks as this wood type has not been observed in the lowland deposits surrounding the volcanic complex. *Liriodendron* today is a straight, tall tree, which is for two-thirds of the trunk freeof lateral branches and famous for its considerable height; nowadays it is the tallest of all Eastern United States angiosperm trees, and can attain 60 m in height (Beck 1990). We found a piece a trunk 40 cm in diameter (Fig. 3) which would roughly correspond to an at least 30 m tall tree (Beck 1990, table 1). The clastic material of the sediment is derived from the decay of an Early Ruppelian volcanic edifice. The lahars are overlain by a lava remnant (Rapprich 2007) correlated with lava dated 28.66 ± 1.06 Ma (Rapprich & Holub 2008). Hence, we may suppose the age of the lahars as Late Ruppelian.

The lacustrine limestone (travertine) at Zvoníčkov containing platanoid wood forms intercalations in fine-grained volcaniclastics. These deposits are traditionally described as "tuffs", but no modern volcanological study has yet been focussed on them, mainly due to the absence of good exposures. The fine-grained volcaniclastics that underlie the Úhošť lavas can most probably be correlated with the fine-grained volcaniclastics with limestone intercalations known from the southeastern margins of the DHVC (mammal zone MP-21: Fejfar & Kaiser 2005, *i.e.* 34 Ma). The fine-grained volcaniclastics at Zvoníčkov therefore represent products of early DHVC activity in the Early Ruppelian.

The coarse-grained and strongly vesiculated character of the pyroclasts at Nechranice reflects a local low-energy magmatic-gas driven volcanic eruption (Strombolian). The wood assemblage at Nechranice is relatively rich. It contains not only the types described above, but also new unidentified angiosperm wood (with at least three new types, probably related to subtropical Lauraceae and other families) and one silicified palm stem (No. 121/07), which are subject of ongoing studies. The plants were buried rapidly by the pyroclastic fall out. The subsequent lava effusion protected the accumulation from being eroded. The monogenetic volcanism on the northern periphery can be assigned to the Aquitanian according to the new data presented in this paper. However, we were not able to analyze exactly the Běchovický vrch Hill, the surrounding monogenic volcanoes yielding data within the range of 20.58 ± 0.66 to 22.51 ± 1.06 Ma. The monogenic activity on the northern margin of the DHVC was contemporaneous with the youngest lava of the Úhošť profile (Rapprich & Holub 2008).

Conclusions

We have distinguished three types of deposits reflecting three different volcanic environments: 1) lahar deposits on the Zadní vrch Hill, Prostřední vrch Hill and at Vernéřov, 2) pyroclastic deposits of a local monogenic cone at Nechranice and 3) lacustrine sediments on a plain at the foot of the volcano near Zvoníčkov. The obtained K-Ar ages for the monogenic cones on the DHVC northern periphery are the youngest among the volcanic rocks of the entire

Figure 5. A, B – Wood type 4 – *Cercidiphylloxylon* (epitype G8113 of *Cercidiphylloxylon kadanense*). • A – diffuse-porous wood with mostly solitary vessels, angular in outline. TS. • B – detail of a long scalariform perforation plate with about 50 bars, TLS. • C – Wood type 5 – *Ulmus* (specimen 75/04): Outer part of a ring-porous wood with mainly solitary earlywood vessels and latewood vessels in wavy tangential bands, TS. • D–G – Wood type 6 – ?*Craigia* (D–F: specimen 72/03; G: specimen 89/04). • D – Wood semi-ring porous with folded earlywood vessels, TS. • E – strongly heterocellular rays with tile cells, TLS. • F – detail of tile cells of *Pterospermum* type, RLS. • G – coalescent apertures of alternate intervessel pits mimicking helical thickening, TLS. • H–M – Wood type 7 – *Coryloxylon* (H–J: holotype CNB-4 of *Coryloxylon nemejcii*; K–M: holotype CNB-3 of *Coryloxylon tertiarum*). • H, K – diffuse-porous wood with numerous vessels in radial multiples, TS. • I, L – mostly 3–4-seriate strongly heterocellular rays, TLS. • J – two scalariform perforation plates with less than 20 bars in the middle, RLS. • M – scalariform perforation plate with less than 20 bars from a side view, TLS. Scale bars = 500 μm in A, C, D, H, K; 200 μm in E, F, I, L; 100 μm in B, G, J, M.
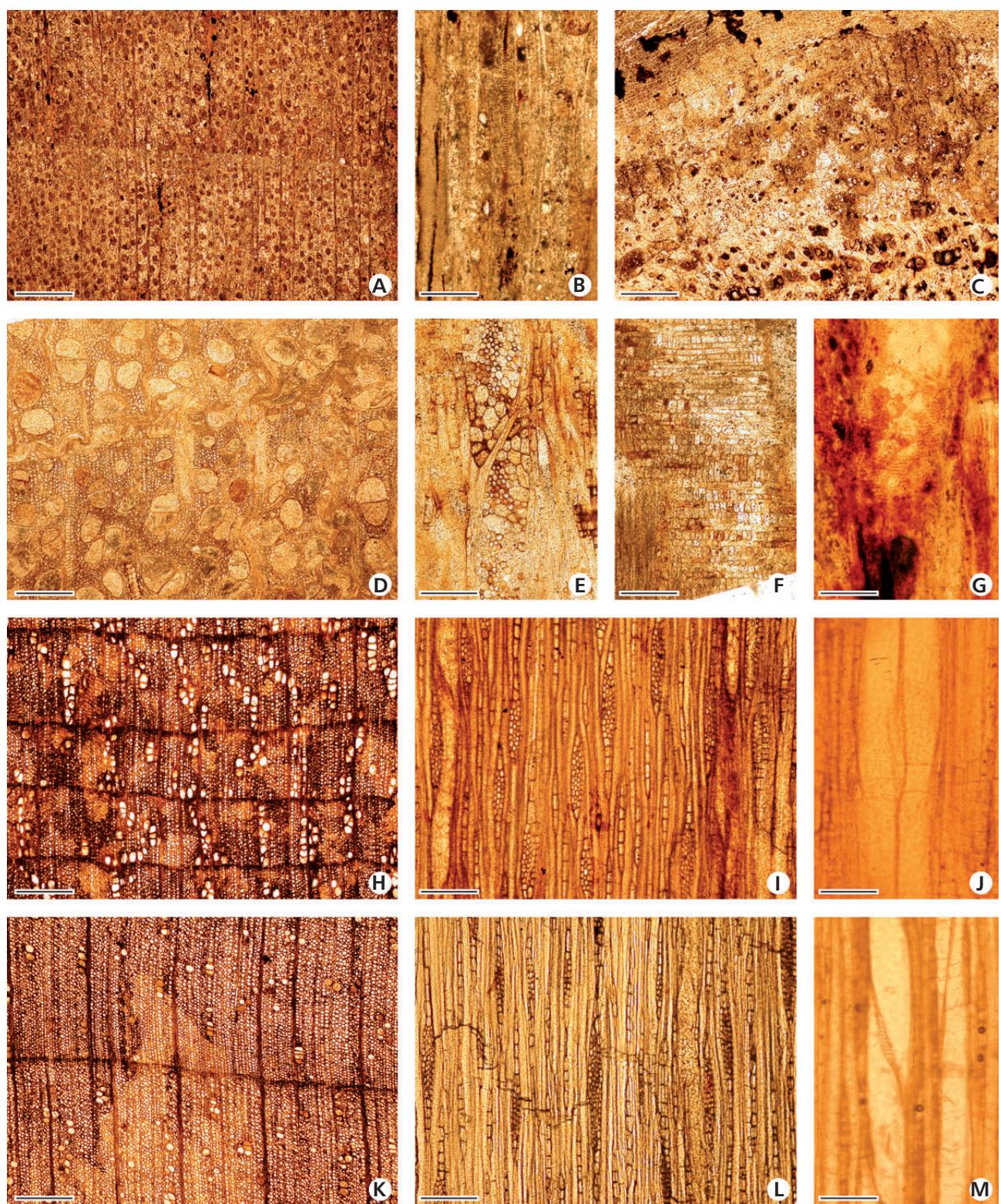
complex. The data confirm the geological position of the monogenic cones and support the stratigraphic classification of the flora from the Nechranice site.

A re-examination of the type material as well as the new collections show that some taxa determined earlier should be combined forming 'natural' taxa. This is the case for *Platanoxylon bohemicum*, *Spiroplatanoxylon europaeum* and *Dryoxylon bohemicum* which belong to one type of platanoid wood, probably related to *Platanus neptuni* and also *Coryloxylon nemejcii* and *C. tertiarum* which represent only one wood type related to the genera *Styrax* and *Halesia* of the Styracaceae. On the other hand, two new types are described: *Ulmus* (Ulmaceae) and tentative *Craigia* (Malvaceae s.l.). As a result, there are at present seven well defined species / types of fossil angiosperm wood recognized in the studied area of the DHVC.

The lahar deposits and the lacustrine limestones appear to be similar in age. We may suppose that during the Rupelian, *Platanus*-type woods dominated lower altitudes whereas *Liriodendron* occupied the slopes and higher altitudes of the repeatedly growing and decaying volcanic complex. The lowlands, represented here by the Nechranice area, show a mixture of various species including some thermophilous elements such as subtropical Lauraceae and palms.

Acknowledgments

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