DOCTORAL THESIS

The 'Whole-Plant' concept in palaeobotany with examples from the Tertiary of northwestern Bohemia, Czech Republic with particular reference to fossil wood

by

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1. Foreword

"How much easier the paleobotanist's work would be if plants were preserved in their entirety." The sentence from the third chapter of their textbook by Stewart & Rothwell (1993) shows clearly the main difficulty of palaeobotany: fragmentary nature of the fossil plant specimens. The fossil plants are mostly recorded disarticulated, as detached organs, isolated leaves, stems, reproductive structures etc. This specificity of the plant fossil record is recognized by the latest edition of the International Code of Botanical Nomenclature (= Saint Louis Code adopted in 1999) in existence of morphotaxa and "for nomenclatural purposes, botanical fossils are now considered to belong in the first place to morphotaxa" (St Louis Code, Preface). A morphotaxon is "as a fossil taxon which, for nomenclatural purposes, comprises only the parts, life-history stages, or preservational states represented by the corresponding nomenclatural type." (St Louis Code, Art. 1.2.) and "the provisions of this *Code* authorize the publication and use of names of morphotaxa." (St Louis Code, Art. 1.3.).

However, the ultimate objective of palaeobotany is to understand the entire organism - the whole fossil plant - and its evolution in time and space. From the taxonomic point of view, the naming of the whole fossil plant in the sense of evolutionary unit is not prescribed by the St Louis Code but several approaches exist (for summary see in Stewart & Rothwell 1993, p. 30 and in Taylor & Taylor 1993, p. 36). It must be only emphasized that a "strict synonymy and therefore priority only operates among morphotaxa of the same kind" (St Louis Code, in Preface referring to Art. 11.7.), so the names of plants (diatoms excepted), which are based on a non-fossil type, have priority over names of the same rank based on a fossil (or subfossil) type (St Louis Code, Art. 11 Note 4).

The idea of the reconstruction of the whole fossil plant is at least as old as palaeobotany. The palaobotanists since Brongniart have tried to pursue this challenge. Such an approach, known today as the 'Whole-Plant' concept (or approach), involves the hypothetical reconstruction of extinct plants from their detached fossils organs. The results of individual palaeobotanical disciplines are taken into account: one discipline, e.g. palaeoxylology, should respect the results based on other palaeobotanical remains such as foliage, seeds, fruits, pollen etc. In this submitted doctoral thesis, I have tried to show the general aspects of the 'Whole-Plant' concept on five concrete examples from the Tertiary of northwestern Bohemia, Czech Republic, with particular reference to fossil wood.

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2. Acknowledgements

First of all, I am deeply indebted to my tutors, Madame C. Privé-Gill from the Laboratoire de Paléobotanique et Paléoécologie de l'Université Pierre-et-Marie of Paris and Mr Z. Kvaček from the Institute of Geology and Palaeontology of Charles University of Prague, who have helped me importantly by their experiences, comments, consultations, suggestive advice, corrections and references to important literal sources.

I am also grateful to all the pedagogic and technical staff of the Institute of Geology and Palaeontology of the Charles University in Prague, as well as to that of the Laboratoire de Paléobotanique et Paléoécologie de l'Université Pierre-et-Marie, namely M and Mme Dupéron, Denise Pons, Madame Salard and Madame Vozenin, who helped me with a good will by their experiences every time I asked them.

Most cordial thanks are due to Mr. Z. Dvořák, geologist from the Bílina Mines, who generously provided the fossil wood material, which he had collected mostly himself, and so practically facilitated this work.

Finally, I would like to thank all my family, especially my wife, for a peaceful and easy-going family background in Prague, thanks to which I could concentrate untroubled on the finalization of this work.

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3. Introduction

The Tertiary of northwestern Bohemia has been intensively explored. The first palaeobotanical data were published already by Sternberg (1820 – 1838), one of the founders of the modern palaeobotany. The systematic research started there in the second half of the 19th century (e.g., Ettingshausen 1866-1869, Engelhardt 1891, Velenovský 1881) and has continued until present. Most palaeobotanical data are based on fossil leaves, fruits and seeds (e.g., Kvaček & Walther 2003, Kvaček et al. 2004). Woods in different states of preservation are however very abundant there and, except for material from the locality of Kadaň – Zadní vrch Hill (see page 12), they have not been studied systematically, have been described only sporadically (see pages 8, 10 and 12) or just recorded in lists without description. Hence, the Tertiary of northwestern Bohemia, where fossil leaves, wood, flowers, dispersed pollen and pollen in situ, fruits and seeds are frequently found in (in)direct association, presents the ideal area for the application of the 'Whole-Plant' concept.

The present doctoral thesis is particularly focused on the fossil wood. Its main intention is to associate detached leaves and reproductive organs with fossil wood (= morphogenera with the typical suffix *-xylon* or older *-inium*) in order to reconstruct the whole plant as complete as possible, as it really looked like and lived in the area of northwestern Bohemia during the Tertiary. The results of the recent systematic publications on the fossil wood (Sakala & Teodoridis 2001, Sakala 2002, 2003a, Sakala & Privé-Gill 2004) are summarized with respect to the 'Whole-Plant' concept. All woods presented hereafter were thin sectioned following the standard techniques and observed with a compound light microscope. This work is closed with the exceptional record of leafy fertile twig of *Decodon* (Kvaček & Sakala 1999) which shows us "how much easier the paleobotanist's work would be if plants were preserved in their entirety", or almost entirety :-)

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4. Geological settings

Map 1: Position of the Czech Republic and the Tertiary of northwestern Bohemia with the three studied regions (from W to E) of the Doupovské hory Mts., the Most Basin and the České středohoří Mts.

The Tertiary of northwestern Bohemia is spread in the northwestern part of the Czech Republic as a continuous zone of magmatic and sedimentary complexes, parallel to the Czech-German boundary. This zone is formed, from west to east, of the Cheb and Sokolov basins, the Doupovské hory Mts., the Most Basin, the České středohoří Mts. and the Žitava Basin. The present study has been limited to the three regions: Doupovské hory Mts., Most Basin and České středohoří Mts. (see Map 1).

Outcrops of the Tertiary in northwestern Bohemia are linked to the Ohře Rift system, a depression zone orientated in SW-NE direction. The Ohře Rift was formed by a tectonic collapse in the NW part of the Bohemian Massif during its vaulting, as an 'echo' of the Alpine orogenetic processes active in the southern Tethys region. 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.). These basins were supplied from the S and SE by rivers, which continued toward the NW. Generally, the volcanic and sedimentary rocks are mostly Late Eocene - Early Miocene in age there. The recent state of knowledge and complementary references can be found in Chlupáč et al. (2002).

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4.1. Most Basin

Map 2: Position of the studied localities in the Most Basin: 3 Velká Černoc; 4 (=5) Bílina.

Most Basin - main characteristics

The Most Basin (the former North Bohemian Lignite Basin) belongs, besides the Cheb and Sokolov basins, to the so-called "Krušné hory Piedmont Basins", and with its area of 1400 km^2, is the largest of them. The Most Basin is limited tectonically in the NW and SE, and in the NE and SW by the neovolcanites of the Doupovské hory and České středohoří Mts. The basin has a single lignite seam, typically 10-30 m thick, which occasionally splits in two or more partial seams. Important detritic bodies of clays and sands correspond to two "deltas" (alluvial fans) near Žatec and Bílina where rivers discharged into the basin from the SE. The clays and sands, mostly wedged into or overlying the main seam, are richly fossiliferous.

Most Basin - stratigraphy

The basement is formed of metamorphic and eruptive rocks of the Krušné hory Mts. crystalline complex, and partly covered by younger sediments of the Permian-Carboniferous or Upper Cretaceous. The Tertiary starts locally with the so-called sandy "Basal Formation", Late Eocene in age. The following Střezov Formation (Early Oligocene - Oligocene-Miocene boundary) is mostly composed of volcanic bodies, tuffites and reworked pyroclastic rocks. The main fill of the basin, including the "Main Seam", its "Underlying Member" and the richly fossiliferous overlying clays and sands, belongs to the Most Formation (Early Miocene, the floor of the main seam dated to MN 3a zone).

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Most Basin - studied localities

The locality of **Velká Černoc** (Map 2, locality 3) belongs to a relatively continuous belt of the Hlavačov gravel and sand. These extra-basinal fluvial deposits, the so-called "Neogene accumulations of Central Bohemia", were the part of a river system which flowed into the basin in the area of Žatec. According to Teodoridis (2002), the flora of the Hlavačov gravel and sand can be correlated with the Upper Oligocene Thierbach floristic complex from the lower part of the Bitterfeld Basin in Germany.

Bílina (Bílina Mine, see Map 2, locality 4=5) is the famous 'classical' locality with the rich and well studied fossil record of plants as well as insects, molluscs, fish, amphibians, reptiles, and exceptional birds and mammals. The main part of the fossiliferous sediments belongs to the Early Miocene Most Formation. The present state of knowledge of geology, palaeobotany and palaeoecology of Bílina is summarized in Bůžek et al. (1992), Kvaček (1998) and Sakala (2000).

Most Basin - palaeontology focused on fossil wood

The Most Basin is paleontologically rich (e.g., Fejfar & Kvaček 1993, Kvaček 2003, Prokop 2003). Important elements of the macroflora with an overview of palaeobotanical research, description of localities, original landscape reconstructions etc. have recently been presented in a detailed monograph (Kvaček et al. 2004).

Concerning the fossil woods, most of them are attributable to the **Taxodiaceae**, and some of them have already been described: *Cupressinoxylon krasseri* Ortmann (1922) from Duchcov (= *Taxodioxylon gypsaceum* (Goeppert) Kräusel after Kräusel 1949), and *Taxodioxylon* from Most (Březinová 1964). Some conifer woods with characteristic resin canals, have been described as **Pinus sp.** (e.g., Hurník-Luft 1960).

Contrary to huge amount of gymnosperm woods, a single angiosperm wood has been described so far in detail from the basinal fill (**Ulmoxylon** from Bílina - see Example 4). A notice by Hurník (2001) refers to **Quercoxylon sp.** coming from the Bílina Mine as well. In the basinal fill, indeterminate fossil fragments of angiosperm wood and **palm stems** were also recorded. In extra-basinal sediments, **Castanoxylon** (see Example 3) has been described from Velká Černoc as a chesnut wood and **Betulinium stagnigenum** Unger by Unger (1850) from Tuchořice as a birch wood. However, the affinity of the latter remains doubtful, and the re-examination of the original specimen will be needed.

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4.2. České středohoří Mountains

Map 3: Position of the studied localities of the České středohoří Mts.: 1 Kučlín; 2b Žichov.

České středohoří Mts. - main characteristics (see Fejfar & Kvaček 1993)

The České středohoří Mts. is a volcanic mountain range situated in the NE part of the Ohře Rift. Its present shape arose due to denudation processes and represents mostly the fill of inflow channels and subsurface bodies, as lacolithes etc. The whole area studied in detail since the 19th century, has become a typical example of the continental alcaline volcanism. In addition to the interesting volcanism and petrology, the České středohoří Mts. have many fossiliferous localities, e.g. diatomites of Kučlín and Bechlejovice.

České středohoří Mts. - stratigraphy

The complex of the České středohoří Mts. is traditionally divided into two major units: the Late Eocene Staré Sedlo Formation, composed mostly of quartzite sandstone, and the České středohoří Complex of alkaline volcanites and intravolcanic deposits, such as diatomites, marls and volcanoclastics, ranging from the Late Eocene to the Early Miocene. Kvaček & Walther (2003) offered a new subdivision into six levels, which reflect the changing ecosystems. In their proposal, every level regroups corresponding localities and is characterized by typical floral elements and members of the ichthyofauna.

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České středohoří Mts. - studied localities

The locality of **Kučlín** (Map 3, locality 1) is a relict of the volcanogenic complex on the top of the Trupelník Hill near Bílina. The deposit with richly fossiliferous diatomite (flora, fossil insects, crayfish, fish and other vertebrates) represents a volcanic facies coeval with the fluvial settings of the Staré Sedlo Formation, Late Eocene in age. Kučlín and the other Late Eocene sites have recently been reviewed in detail by Kvaček (2002a) focusing on ecosystems, environment and palaeoclimate.

At **Žichov** (Map 3, locality 2b), the fossiliferous rock is a diatomite transformed into semiopal, containing fossil fish, insects, foliage and silicified fragments of wood. The site is inaccessible today, but several small isolated pieces of silicified wood have recently been found in nearby fields. The locality, together with volcanoclastics at the Matrý Hill, represents the youngest fossiliferous level of the volcanic region of the České středohoří Mts. and belongs to the Děčín formation, Late Oligocene in age (Kvaček & Walther 2003).

České středohoří Mts. - palaeontology focused on fossil wood

The fossil record of České středohoří Mts. is rich in plants and animals, e.g. fish from Kučlín (Obrhelová & Obrhel 1987) or frogs from Bechlejovice (Špinar 1972). The fossil flora represented mainly by leaves and fruits and seeds has been systematically described from different localities (e.g., Kvaček & Walther 1995, 1998 etc.) as well as regularly presented as general comparative works (Kvaček & Walther 2001, 2003). The most complete overview of the localities of the České středohoří Mts. and their fossil contents can be found in Radoň (2001).

From this area, two gymnosperm woods have been described so far. The first is **Taxodioxylon gypsaceum** described by Březinová in Prakash et al. (1971) from Bečov. The second wood, *Podocarpoxylon helmstedtianum* Gottwald from Kučlín (Březinová et al. 1994), has newly been re-identified as **Tetraclinoxylon** (see Example1). The only angiosperm wood described in detail is **Ficoxylon tropicum** (Schleiden) Felix (1883) from Kostomlaty. The wood was originally described as *Ungerites tropicus* Schleiden (in Schmidt & Schleiden 1855), later studied and re-described as *Ficoxylon bohemicum* Kaiser (1880). There are also two notes about the presence of **Betulinium stagnigenum** in Korozluky (Slavík 1869) and an **?oak wood** near the town of Ústí nad Labem (Procházka 1951). Finally, **Liquidambaroxylon** has newly been described from Žichov (see Example 2).

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4.3. Doupovské hory Mountains

Map 4: Position of the studied locality of the Doupovské hory Mts.: 2a Kadaň - Zadní vrch Hill.

Doupovské hory Mts. - main characteristics

The Doupovské hory Mts. arose in the intersection of the Ohře Rift and the Jáchymov fault zone orientated in the NW-SE direction. Their activity is dated to the Late Eocene - Early Miocene and their today's morphology is influenced a lot by denudation, similarly to the České středohoří Mts. The Doupovské hory Mts. are traditionally interpreted as the largest single stratovolcano in the Czech Republic. However, new studies, burdened by the presence of the military base in the area, show that the main part of the Doupovské hory Mts. is formed by lavas, and not by pyroclastic rocks. Some sites have newly been interpreted as lahars and maars

Doupovské hory Mts. - stratigraphy

Based on the character of the volcanism, the Doupovské hory Mts., as well as České středohoří Mts., belong to the so-called 'main volcanic phase' of the 'rift stage' (Ohře Rift) which is dated to the Late Eocene - Early Miocene. The base of the volcanic complex, which lies on the Late Eocene sediments of the Staré Sedlo Formation, has been palaeontologically dated by mammals from the SE border to the Early Oligocene zone MP 21. Several radiometric dates, e.g., 37.7 ± 1.5 my for Dětaň by K/Ar method (Fejfar 1987), have recently been questioned. Hence, more radiometric data and further biostratigraphic studies, mostly in the central military (= restricted) area, are still needed.

Doupovské hory Mts. - studied locality

The locality of **Kadaň – Zadní vrch Hill** (Map 4, locality 2a) is formed of tuffites. Numerous angiosperm woods were described from this locality (Prakash et al. 1971), which is the richest for fossil angiosperm wood in the Czech Republic. All woods from the locality are calcified. The origin of the locality as a whole is interpreted as a maar relic (P. Hradecký pers. comm., 2003). Its age is believed to be Oligocene.

Doupovské hory Mts. - palaeontology focused on fossil wood

Due to the presence of the military base in the central part of the Doupovské hory Mts., the fossil record has mostly been studied in the peripheral part. There are interesting records of Oligocene mammals in the southern region, in the calcareous tuffites of Dvérce, Dětaň and Valeč (Fejfar 1987, Fejfar & Kvaček 1993). The famous "Wassermaus" from Valeč (now identified as a rodent *Bransatoglis*) represents probably the earliest scientifically described fossil from the territory of the Czech Republic (compare in Chlupáč et al. 2002). Contrary to the České středohoří Mts., fossil leaves and reproductive structures have not been systematically studied there (e.g., Bůžek et al. 1987).

A single publication deals with the fossil wood from the Doupovské hory Mts. area proper. Prakash et al. (1971) described two types of conifer wood of Taxodiaceae - ***Taxodioxylon gypsaceum*** from Kadaň and ***Sequoioxylon*** from Dvérce and Mikulovice. In Kadaň – Zadní vrch Hill, as mentioned above, Prakash et al. (1971) recognized **eight different types of angiosperm wood** including ***Cercidiphylloxylon*** (see Example 2), which has recently been reviewed in detail by Sakala & Privé-Gill (2004).

At Jáchymov, fossil woods have also been described from the tuffs associated to the volcanism of the Doupovské hory Mts. Unger (1842) identified ***Ulminium diluviale***. This species, later placed under various morphogenera, is today considered as a wood of Lauraceae. Lignified woods of ***Taxodioxylon*** **sp.** and ***Quercinium*** **sp.** have also been described from Jáchymov (Frimmel in Becke 1912). The overview of the fossil woods described until 1971 from the Doupovské hory Mts. as well as from the České středohoří Mts. is to be found in the 'Introduction' in Prakash et al. (1971).

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5. Case studies

The main aim of this work is to illustrate different general aspects of the 'Whole-Plant' concept on concrete examples from the Tertiary of northwestern Bohemia with particular reference to fossil wood. Consequently, these 'Case studies' represent the essential part of the doctoral thesis. The five following examples deal succesively with gymnosperm wood, angiosperm wood and with reproductive structures, all from various localities of the Most Basin and the České středohoří and Doupovské hory Mountains.

Every example (**Example 1-5**) is documented in detail by one corresponding publication, which can be found in 'Literature' as well as in its integral form which immediately follows each 'Example'. Hence, the text of this part and the related references are reduced. The text only summarizes the systematic aspect of each example by one illustrative picture and short conclusions. General aspects of each 'Example' relative to the 'Whole-Plant' concept are also presented. Finally, the reader is asked to see further details in the five main publications, the references to which are emphasized by the text in **<u>bold underlined</u>**:

Example 1: *Tetraclinoxylon* from Kučlín   see **<u>pages 17-21</u>** (Sakala 2003a)

Example 2: *Cercidiphylloxylon* from Kadaň and *Liquidambaroxylon* from Žichov

                 see **<u>pages 25-36</u>** (Sakala & Privé-Gill 2004)

Example 3: *Castanoxylon* from Velká Černoc

              see **<u>pages 39-44</u>** (Sakala & Teodoridis 2001)

Example 4: *Ulmoxylon* from Bílina see **<u>pages 47-52</u>** (Sakala 2002)

Example 5: *Decodon* from Bílina see **<u>pages 56-77</u>** (Kvaček & Sakala 1999)

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5.1. Gymnosperm wood

Gymnosperm wood is common in the Tertiary of northwestern Bohemia. In fact, it represents the major part of all fossil wood found there. Most gymnosperm woods, characterized by absence of normal resin canals and spirals on tracheid walls and by presence of axial parenchyma, the abietoid type of pitting on radial tracheid walls and mostly taxodioid type of cross-field pitting, are attributable to Taxodiaceae (newly several subfamilies of Cupressaceae).

However, an exact attribution of these woods is problematic. Even though the taxodiaceous woods are very important in the Tertiary of Europe, there is no consensus today on their systematics. Practically, each specialist attributes a different importance to the features observed. Moreover, a huge amount of wood morphotaxa is in striking contrast with only several elements, based on foliage and reproductive structures. The long-term solution consists in revisions of the original type material (as required for fossil foliage) together with the clarification of the true botanical affinity of wood morphotaxa. In this respect, the Tertiary of northwestern Bohemia is of great importance as taxodiaceous wood occurs together in indirect but close association with leaves, cones and seeds.

As a single example concerning gymnosperm wood, a fossil trunk of Cupressaceae (or Cupressoideae of Cupressaceae) from Kučlín in České středohoří Mts. has been re-identified. This re-identification proposes a new linking of the wood with other remains, which were found (and mostly described) indirectly associated in the locality.

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5.1.1. Example 1: *Tetraclinoxylon* from Kučlín

pages 17-21 - Sakala 2003a
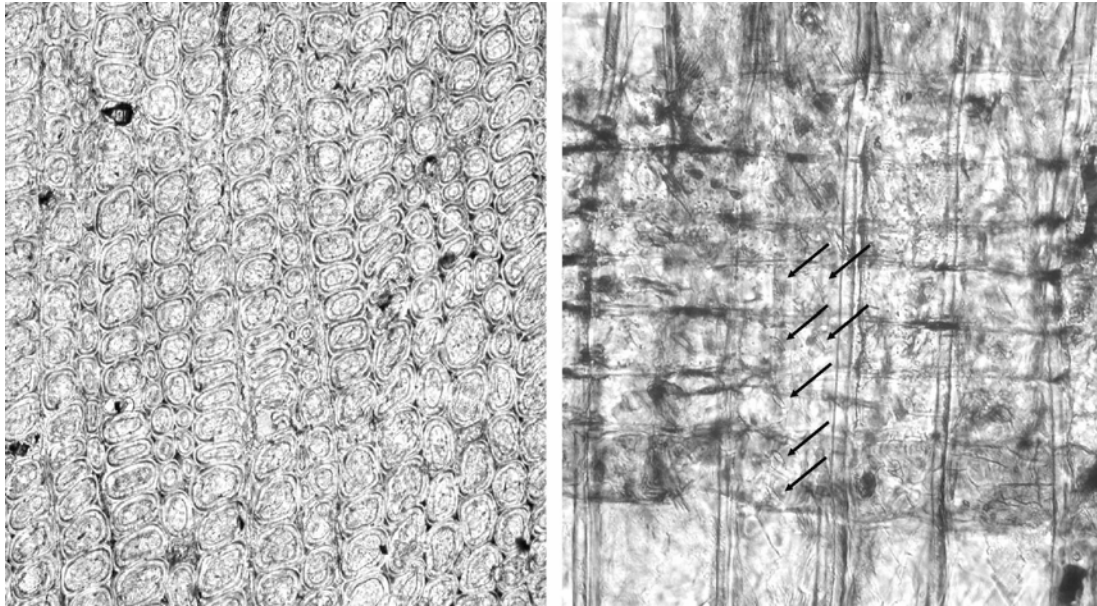
Text-fig. 1: Wood of *Tetraclinoxylon vulcanense* from Kučlín in cross-section with rounded tracheids (left) and in radial section (right) with typically cupressoid type of cross-field pitting (arrows).

Example 1: Systematic part - conclusions

The big silicified trunk from Kučlín (Late Eocene of the České středohoří Mts. – see chapter 4.2.) was reinterpreted as *Tetraclinoxylon vulcanense* Privé (**Sakala 2003a**). This new interpretation is based on features not previously described, i.e., exclusively cupressoid type of cross-field pitting and the markedly roundish shape of the tracheids in cross-section (see Text-fig. 1). The wood was originally identified as *Podocarpoxylon helmstedtianum* Gottwald and preliminarily associated with co-occurring twigs and cone scales of an extinct conifer *Doliostrobus taxiformis* (Sternb.) Z. Kvaček (see in Březinová et al. 1994). However, the new diagnosis of the genus *Doliostrobus* Marion and the new family Doliostrobaceae (Kvaček 2002b) that takes into account the characteristics of secondary wood of twig (Rüffle & Süss 2001) do not support that attribution.

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Example 1: General aspects relative to the 'Whole-Plant' concept

Differences in cross-field pitting between trunk and twig wood

There are significant differences in cross-field pitting between the wood of *Doliostrobus* and the Kučlín trunk wood. Contrary to other features, e.g., different height of rays, they could not be explained by an individual variation between normal trunk (mature) and twig (juvenile) wood. This means that the difference in cross-field pitting must be explained by a different affinity and the trunk from Kučlín cannot be associated with *Doliostrobus*. The wood with typical cupressoid features can be identified as the morphogenus *Tetraclinoxylon* Grambast and associated with rare twigs and seeds of *Tetraclinis salicornioides* (Unger) Z. Kvaček described from the same locality (Kvaček 2002a). The recently found whole twig of this species in Kučlín (Z. Dvořák pers. comm., 2003) supports also this attribution.

Systematical vs. ecological aspects of the nearest living relative

Tetraclinis salicornioides (associated in Kučlín with *Tetraclinoxylon vulcanense*) is systematically similar to modern *Tetraclinis articulata* (Vahl) Masters, a single extant species of genus *Tetraclinis* Masters, which is native to northern Africa, Malta, and southern Spain. Ecologically, the modern *Tetraclinis* is, however, closer to another fossil species *T. brachyodon* (Brongniart) Mai, subhumid "Praemediterranean" species, contrary to *T. salicornioides*, which is rather humid subtropical species (Kvaček 2002a).

Discrepancy between the record of wood and other organs

In the Tertiary of Europe, there are only these two species of *Tetraclinis*, well defined by cones, seeds and foliage: *T. brachyodon* and *T. salicornioides*, the latter extending to western North America (Kvaček et al. 2000). On the other hand, there are six species of *Tetraclinoxylon* Grambast. This discrepancy evokes the question if the species based on wood really represent natural species of *Tetraclinis*. The true botanical affinity of *Podocarpoxylon helmstedtianum* Gottwald as well as that of most records of morphogenus *Podocarpoxylon* Gothan in the European Tertiary (for the list see in Süss & Velitzelos 2000) remains also uncertain.

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J. Sakala

Podocarpoxylon helmstedtianum Gottwald from Kučlín (Late Eocene, Czech Republic) reinterpreted as *Tetraclinoxylon vulcanense* Privé

With one Plate

Summary

A big silicified trunk from the Late Eocene locality of Kučlín was originally identified as *Podocarpoxylon helmstedtianum* Gottwald and preliminarily associated with co-occurring twigs and cone scales of *Doliostrobus taxiformis* (Sternb.) Z.Kvaček. However, the new diagnosis of the genus *Doliostrobus*, recently complemented by the characteristics of secondary wood of twigs, does not support such an attribution. On the basis of a new analysis of wood structures and comparisons, the fossil wood from Kučlín is reinterpreted as *Tetraclinoxylon vulcanense* Privé, and associated with twigs and seeds of *Tetraclinis salicornioides* (Unger) Z.Kvaček, the second conifer recorded at this locality.

Zusammenfassung

Podocarpoxylon helmstedtianum Gottwald aus Kučlín (Obereozän, Tschechische Republik), erneut interpretiert als *Tetraclinoxylon vulcanense* Privé

Ein großer verkieselter Stamm aus dem späten Eozän von Kučlín, ursprünglich bestimmt als *Podocarpoxylon helmstedtianum* Gottwald wurde vorläufig zu den ebenfalls dort vorkommenden Zweigen und Zapfenschuppen von *Doliostrobus taxiformis* (Sternb.) Z.Kvaček gestellt. Eine Neudefinition des Genus *Doliostrobus*, nunmehr durch die Charakterisierung des Sekundärholzes der Zweige vervollständigt, erlaubt eine solche Zuordnung nicht mehr. Aufgrund einer erneuten Analyse der Holzstruktur sowie veschiedenen Vergleichen wird das fossile Holz von Kučlín nunmehr als *Tetraclinoxylon vulcanense* Privé interpretiert, und vergesellschaftet mit Zweigen und Samen von *Tetraclinis salicornioides* (Unger) Z.Kvaček ist dies der zweite Koniferenfund auf dieser Lokalität.

1 Introduction

The Late Eocene locality of Kučlín is situated in the neo-volcanic area of the České středohoří Mountains, in northwestern Bohemia (50°32'N, 13°48'E), in the Czech Republic. This locality together with other Late Eocene sites was recently reviewed in detail by Kvaček (2002a). The diatomite of Kučlín has yielded fossil insects (Prokop in press), cray-fish, fish and other vertebrates, but above all an interesting flora. While Kvaček (2002a) studied fossil leaves, fruits and seeds, the present paper deals with the fossil wood. The single find of a big silicified trunk, originally described from there as *Podocarpoxylon helmstedtianum* Gottwald by Březinová in Březinová et al. (1994), is reinterpreted hereafter as *Tetraclinoxylon vulcanense* Privé.

2 Systematic part

Cupressaceae

Tetraclinoxylon GRAMBAST

Tetraclinoxylon vulcanense PRIVÉ 1973

1973 *Tetraclinoxylon vulcanense* PRIVÉ; PRIVÉ: 174, figs. 2–4, plates 1, 2

1994 *Podocarpoxylon helmstedtianum* GOTT-WALD; BŘEZINOVÁ in BŘEZINOVÁ et al.: 224, plates 1, 3, 4

2.1 Material

Thin sections Nos G 4700–4710 and G 4715–4726 (collections of the Palaeontological department of the National Museum, Prague).

2.2 Description

The following details can be added to the original description done by BŘEZINOVÁ in BŘEZINOVÁ et al. (1994: 224). Contrary to the previous description, I did not observe taxodioid, but exclusively cupressoid cross-field pitting (Plate I, Fig. 6). Generally, the cross-field pitting is badly preserved but not a single taxodioid pit with larger aperture was observed. On the other hand, the tracheids are more markedly roundish in cross-section than seen in the published figures (BŘEZINOVÁ et al. 1994, pl. 3, figs. 1, 2) and are associated with characteristic intercellular spaces (Plate I, Fig. 1).

2.3 Discussion

The wood of the fossil silicified trunk in question was originally described as *Podocarpoxylon helmstedtianum* GOTTWALD by BŘEZINOVÁ in BŘEZINOVÁ et al. (1994) and preliminarily associated with the twigs and cone scales of *Doliostrobus taxiformis* (STERNB.) Z.KVAČEK from the same locality (BŘEZINOVÁ et al. 1994). However, the diagnosis of the genus *Doliostrobus*, recently complemented by the characteristics of secondary wood of a twig (RÜFFLE & SÜSS 2001), contains features, which are absent in the fossil wood studied.

There are several differences, but the most important concerns cross-field pitting. The cross-fields of *Doliostrobus* twigs, as seen in radial section (BŮŽEK et al. 1968, Pl. 35,

Fig. 6; RÜFFLE 1976, Pl. 69, Fig. 6; RÜFFLE & SÜSS 2001, Text-fig. 1, Pl. I, Figs. 3, 4; my own observations), are large, mostly simple, 1–5 in number, irregularly disposed and variable in shape. The pits are called "doliostroboid" (RÜFFLE & SÜSS 2001). On the other hand, the wood from Kučlín has only relatively small, half-bordered cupressoid pits with typical cupressoid alignment, i.e., 1–4 pits per field with 1–2 pits in each vertical and horizontal row (see Plate I, Fig. 6). These differences in cross-field pitting appear very significant. Contrary to other features, e.g., different height of rays, they could not be explained by an individual variation between normal trunk (mature) and twig (juvenile) wood. This means, as already reported by C. PRIVÉ-GILL and J. SAKALA (in KVAČEK 2002b), that the trunk from Kučlín (BŘEZINOVÁ et al. 1994) and the twig from Geiseltal (RÜFFLE & SÜSS 2001) cannot belong to the same conifer. Consequently our fossil wood does not belong to extinct *Doliostrobus* from the new family Doliostrobaceae (KVAČEK 2002b).

Concerning its systematic affinity, the wood clearly shows diagnostic features of the Cupressaceae: cupressoid type of cross-field pitting, presence of parenchyma, and absence of alternate pitting and resin canals. Other characters, i.e., roundish shape of tracheids in cross-section (Plate I, Figs. 1, 2), presence of 1–4 cross-field pits with narrow apertures (Plate I, Fig. 6), thin smooth horizontal walls of parenchyma (Plate I, Fig. 7), tangential pitting of tracheids, smooth horizontal walls of ray cells, and absence of callitroid thickening of tracheids, indentures and juniperoid thickening on tangential walls of procumbent ray cells, allow to identify our fossil as the wood of *Tetraclinis* MASTERS (PEIRCE 1937; KRÄUSEL 1949; GREGUSS 1955; PRIVÉ 1973). Such an attribution is supported by co-occurring impressions of twigs and seeds of *Tetraclinis salicornioides* at Kučlín (KVAČEK 2002a).

In the Tertiary of Europe, the wood of *Tetraclinis* is known under morpho-genus *Tetraclinoxylon* GRAMBAST. Following the generic key of fossil woods of Cupressaceae (VAUDOIS & PRIVÉ 1971: 66), we can attribute the wood from Kučlín to this genus. The only incongruity is in the diagnostic feature "height average of procumbent ray cells less than 25 μm"

(Gʀᴀᴍʙᴀsᴛ 1951: 283). Our fossil has higher procumbent cells, about 27(−30) µm on average. Generally, its ray cells are more vertically elongated (Plate I, Fig. 3) than observed in the modern wood (Plate I, Fig. 5). I think that this slight difference in height of ray cells is not of a great systematic value, and might be due to diagenetic processes. Thus, the wood studied could be unambiguously attributed to the morpho-genus *Tetraclinoxylon*.

Six species of *Tetraclinoxylon* have been recognized: *Tetraclinoxylon boureaui* Gʀᴀᴍʙᴀsᴛ (1951), *T. vulcanense* Pʀɪᴠᴇ́ (1973), *T. anglonae* Bɪᴏɴᴅɪ (1979), *T. velitzelosi* Sᴜ̈ss (1997), *T. lusitanense* (Vᴀʟʟɪɴ) Sᴜ̈ss (1997) syn. *Cupressinoxylon lusitanense* Vᴀʟʟɪɴ (1965), and *Tetraclinoxylon romanicum* S. & E. Iᴀᴍᴀɴᴅᴇɪ (1999). The wood samples studied match quite well the diagnosis of *T. vulcanense* Pʀɪᴠᴇ́ (1973: 174) in having characteristic cross-field pit alignment, biseriate pitting on radial tracheid walls, and very distinct and common Sanio bars (Plate I, Figs. 6, 8). Subtle differences, e.g., in shape of procumbent ray cells (compare Fig. 3 and Fig. 4 from Plate I), are interpreted as secondary without any systematic value.

3 Conclusions

The silicified trunk from Kučlín, originally described as *Podocarpoxylon helmstedtianum* Gᴏᴛᴛᴡᴀʟᴅ by Bʀ̌ᴇᴢɪɴᴏᴠᴀ́ in Bʀ̌ᴇᴢɪɴᴏᴠᴀ́ et al. (1994), is newly re-identified as *Tetraclinoxylon vulcanense* Pʀɪᴠᴇ́ (1973). This interpretation is based on features not previously described, i.e., exclusively cupressoid type of cross-field pitting and the markedly roundish shape of the tracheids in cross-section. The wood must belong to rare twigs and seeds of *Tetraclinis salicornioides* (Uɴɢᴇʀ) Z.Kᴠᴀč̌ᴇᴋ known from the same locality (Kᴠᴀč̌ᴇᴋ 2002a). Generally, in the Tertiary of Europe, there are only two well defined species of *Tetraclinis* Mᴀsᴛ., based on cones, seeds and foliage: *T. brachyodon* (Bʀᴏɴɢɴ.) Mᴀɪ & Wᴀʟᴛʜᴇʀ and *T. salicornioides*, the latter extending to western North America (Kᴠᴀč̌ᴇᴋ 1989; Kᴠᴀč̌ᴇᴋ et al. 2000). On the other hand, there are six species of *Tetraclinoxylon* Gʀᴀᴍʙᴀsᴛ. This discrepancy

evokes the question if the species based on wood really represent natural species of *Tetraclinis*. Finally, the true botanical affinity of *Podocarpoxylon helmstedtianum* Gᴏᴛᴛᴡᴀʟᴅ (1966) as well as that of most records of morpho-genus *Podocarpoxylon* Gᴏᴛʜᴀɴ in the European Tertiary (for the list see in Sᴜ̈ss & Vᴇʟɪᴛᴢᴇʟᴏs 2000) still remain uncertain.

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Explanations to plate I

Plate I

Fig. 1
Tetraclinoxylon vulcanense PRIVÉ (Kučlín specimen, No. G 4723), cross-section: markedly roundish shape of tracheids associated with characteristic intercellular spaces (scale bar = 100 µm)

Fig. 2
Extant *Tetraclinis articulata* (VAHL) MAST. (No. 2280, coll. Laboratoire de paléobotanique et paléoécologie, UPMC, Paris), cross-section: general view (scale bar = 100 µm)

Fig. 3
Tetraclinoxylon vulcanense PRIVÉ (Kučlín specimen, No. G 4724), tangential section: on the left typical vertically elongated rather thin rays, on the right, unusual shorter wider rays (scale bar = 70 µm)

Fig. 4
Tetraclinoxylon vulcanense PRIVÉ (holotype, No. 4933), tangential section: general view of rays (scale bar = 70 µm)

Fig. 5
Extant *Tetraclinis articulata* (VAHL) MAST. (No. 2280, coll. Laboratoire de paléobotanique et paléoécologie, UPMC, Paris), tangential section: general view of rays (scale bar = 70 µm)

Fig. 6
Tetraclinoxylon vulcanense PRIVÉ (Kučlín specimen, No. G 4726), radial section: cupressoid cross-field pits (arrows) with typical cupressoid alignment (scale bar = 50 µm)

Fig. 7
Tetraclinoxylon vulcanense PRIVÉ (Kučlín specimen, No. G 4722), radial section: axial parenchyma with smooth and thin horizontal wall indicated by the arrow (scale bar = 50 µm)

Fig. 8
Tetraclinoxylon vulcanense PRIVÉ (Kučlín specimen, No. G 4726), radial section: biseriate pitting on radial tracheid walls with distinct Sanio bars (= crassulae) (scale bar = 50 µm)
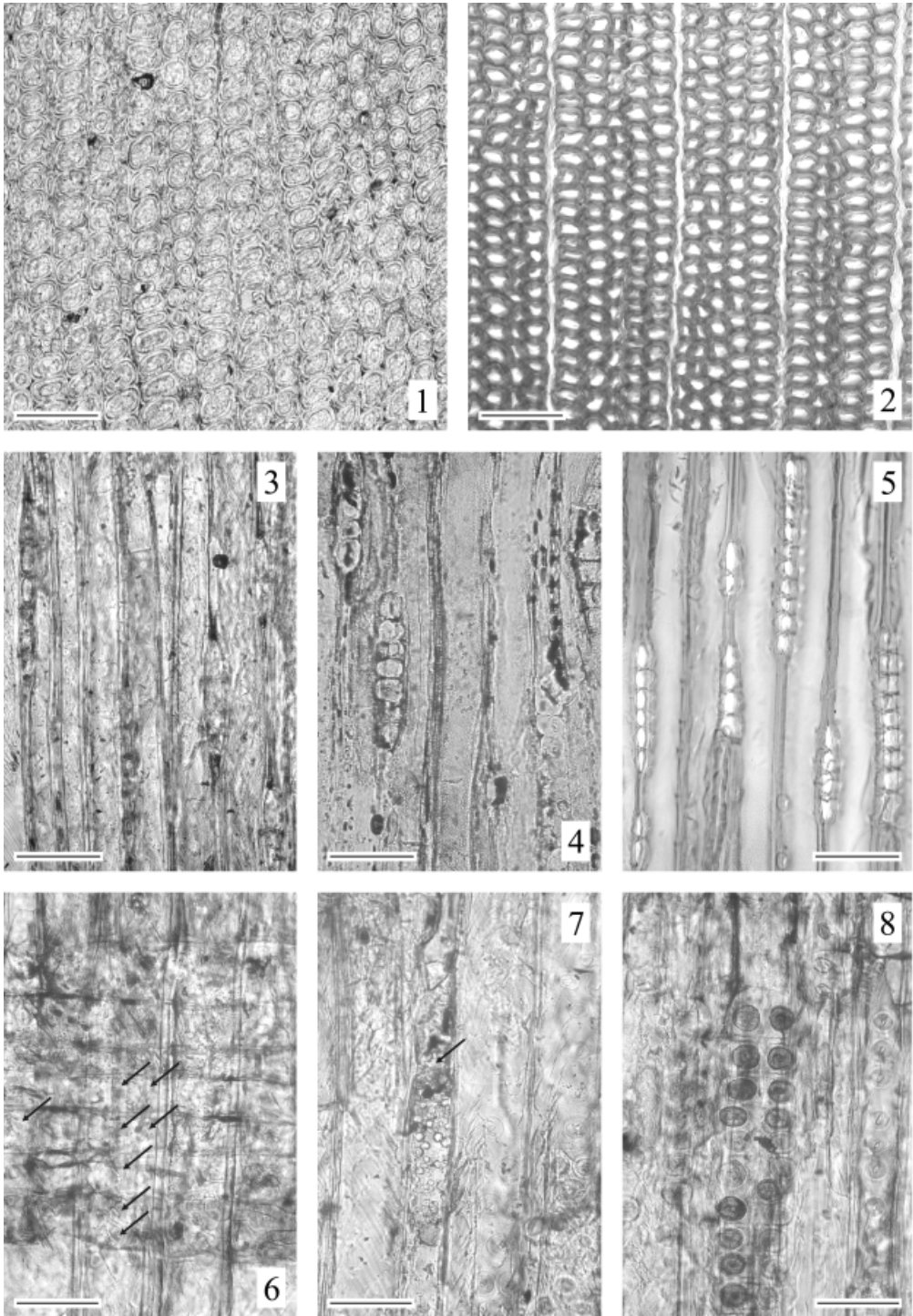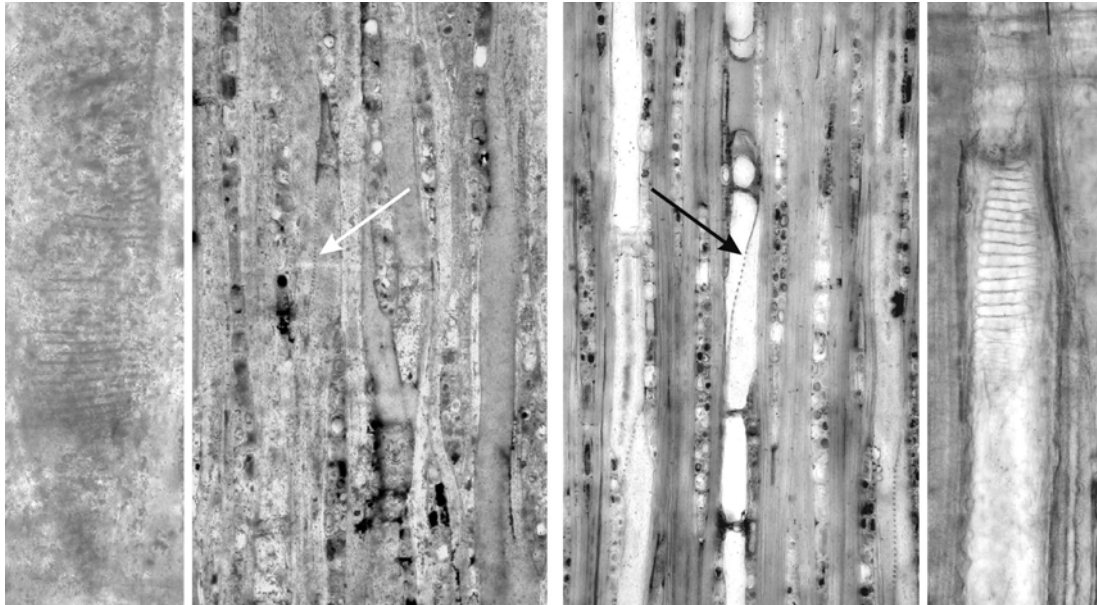
PLATE I

Doctoral Thesis by Jakub Sakala (2004)
The 'Whole-Plant' concept in palaeobotany with examples from the Tertiary of northwestern Bohemia, Czech Republic
with particular reference to fossil wood

5.2. Angiosperm wood

Contrary to the gymnosperm wood, the fossil angiosperm wood is rather rare in the Tertiary of northwestern Bohemia. The locality of Kadaň – Zadní vrch Hill (see chapter 5.2.1.), the only place where the angiosperm fossil wood has been studied systematically, is with eight different types of angiosperm wood the richest site in the former Czechoslovakia (Prakash et al. 1971). However, the less frequent the angiosperm woods are there, the more it is easy to identify them correctly at the generic / specific level. Once well identified, the true botanical affinity of the wood can be found more easily, and the wood can be combined with other fossil organs.

The three following examples describe four wood species from the families of Cercidiphyllaceae (Kadaň – Zadní vrch Hill in the Doupovské hory Mts.), Hamamelidaceae (Žichov in the České středohoří Mts.), Fagaceae (Velká Černoc in the Most Basin) and Ulmaceae (Bílina in the Most Basin). In addition to specific problems related to the systematics of each of these woods, they evoke some interesting general questions about importance of feature in (palaeo)xylotomy, e.g. the number of bars in the scalariform perforation plates or presence of crystalliferous wood parenchyma.

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5.2.1. Example 2: *Cercidiphylloxylon* from Kadaň
and *Liquidambaroxylon* from Žichov
pages 25-36 - Sakala & Privé-Gill 2004

Text-fig. 2: *Cercidiphylloxylon kadanense* from Kadaň – Zadní vrch Hill (two pictures on the left; first in radial, second in tangential section) and *Liquidambaroxylon speciosum* from Žichov (two pictures on the right; first in radial, second in tangential section) with 40 and 20 bars respectively in their scalariform perforation plates.

Example 2: Systematic part - conclusions

New excavations at the locality of Kadaň – Zadní vrch Hill (Oligocene of the Doupovské hory Mts. – see chapter 4.3.) have yielded several specimens of calcified wood. One of them was identified as *Cercidiphylloxylon kadanense* Prakash et al. (**Sakala & Privé-Gill 2004**). Its preservation, which is better than in the holotype specimen, allows its designation as an epitype of *Cercidiphylloxylon kadanense* as well as of *Cercidiphylloxylon*, both defined originally by Prakash et al. (1971) from the same locality. New observations on *C. kadanense* and *Cercidiphylloxylon* are: 1) rays can be up to 4-seriate, 2) the presence of crystals in the rays of *C. kadanense* and 3) the density of bars in the scalariform perforation plates is about 20 bars per 0.1 mm in *C. kadanense* (see Text-fig. 2, left), which is useful also for incompletely preserved scalariform perforation plates. Another fossil wood from Žichov (Late Oligocene of the České středohoří Mts. – see chapter 4.2.), similar to modern *Liquidambar* L. in having fewer and more widely spaced bars, was attributed to the fossil morphospecies *Liquidambaroxylon speciosum* Felix (see Text-fig. 2, right).

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The 'Whole-Plant' concept in palaeobotany with examples from the Tertiary of northwestern Bohemia, Czech Republic
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Example 2: General aspects relative to the 'Whole-Plant' concept

Wood of extinct plants

The wood of *C. kadanense* represents the oldest record of the fossil wood of true *Cercidiphyllum* Sieb. & Zucc. because of its Oligocene age and the occurrence of leaves, fruits, seeds, staminate inflorescences, and pollen of *Cercidiphyllum* in northwestern Bohemia (e.g., Kvaček & Konzalová 1996). All older cercidiphyllaceous woods described so far do not represent the wood of *Cercididiphyllum* but most probably extinct *Cercidiphyllum*-like plants with leaves of *Trochodendroides* Berry emend. Crane and fruits of the *Nyssidium*-type. A similar problem arise in the case of *Doliostrobus* (see Example 1).

Rays vs. scalariform perforation plates

C. kadanense was also compared with modern wood of some species of *Cercidiphyllum* Sieb. & Zucc., *Liquidambar* L., *Altingia* Noronha, *Corylopsis* Sieb. & Zucc., *Distylium* Sieb. & Zucc., and *Hamamelis* L. to determine how to distinguish the wood of *Cercidiphyllum* (Cercidiphyllaceae) from similar woods of Hamamelidaceae. Generally, the number of bars in the scalariform perforation plates of the vessels is a reliable criterion to distinguish the wood of *Cercidiphyllum* Sieb. & Zucc. (about 40 densely spaced bars) from woods of the Hamamelidaceae (about 20 widely spaced bars). On the other hand, the rays among the Cercidiphyllaceae and Hamamelidaceae can vary, even at an intra-specific level.

Similar wood in systematically unrelated taxa

C. kadanense has also some similarity to the wood of modern *Nyssa* Gronov ex L. (Sakala 2003b, Sakala & Privé-Gill 2004). However, *Nyssa* has in contrast to *Cercidiphyllum* and our fossil wood more radial multiples and radial groups of vessels, and no crystals in the rays (Noshiro & Baas 1998). A distinction between the wood of *Nyssa* and *Cercidiphyllum* is very useful because they both represent important elements in the Tertiary of northwestern Bohemia.

OLIGOCENE ANGIOSPERM WOODS FROM NORTHWESTERN BOHEMIA, CZECH REPUBLIC

Jakub Sakala[1,2] **& Catherine Privé-Gill**[2]

SUMMARY

Two species of fossil angiosperm wood are described from the Oligocene of northwestern Bohemia in the Czech Republic. One specimen from Kadaň–Zadní vrch Hill is identified as *Cercidiphylloxylon kadanense* Prakash et al. Because of its superior preservation, the specimen is designated as an epitype to the original holotype specimen of the species and genus. *Cercidiphylloxylon kadanense* is known only from the locality of Kadaň–Zadní vrch Hill, and it represents the oldest fossil wood of true *Cercidiphyllum* Sieb. & Zucc. Three other wood specimens from Žichov are attributed to *Liquidambaroxylon speciosum* Felix. Modern wood of some species of *Cercidiphyllum* Sieb. & Zucc., *Liquidambar* L., *Altingia* Noronha, *Corylopsis* Sieb. & Zucc., *Distylium* Sieb. & Zucc., and *Hamamelis* L. was examined to determine how to distinguish the wood of *Cercidiphyllum* (Cercidiphyllaceae) from similar woods of Hamamelidaceae. The number of bars in the scalariform perforation plates of the vessels is about 40 in *Cercidiphyllum*, and about 20 in the Hamamelidaceae. Rays are variable, even at intra-specific level, and are not suitable for distinguishing these woods. These criteria were found to be useful in evaluating affinities of the fossil woods.

Key words: *Cercidiphylloxylon, Liquidambaroxylon*, fossil wood, Oligocene, Czech Republic, Cercidiphyllaceae, Hamamelidaceae, modern wood.

INTRODUCTION

The Tertiary of northwestern Bohemia, consisting of the volcanics of České středohoří and Doupovské hory Mts. and the sediments of Most basin, is intensively explored. Most palaeobotanical data are based on fossil leaves, fruits and seeds (e.g., Kvaček 1998; Kvaček & Walther 2003). The present paper, dealing with two types of Oligocene angiosperm woods, is part of recent systematic publications on the fossil wood from this region (Sakala & Teodoridis 2001; Sakala 2002, 2003a). Woods in different states of preservation are very abundant there. However, except for material from the Doupovské hory Mts. (e.g., Prakash et al. 1971), they have not been studied system-

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atically, only described sporadically (see the overview in Prakash et al. 1971: 104) or recorded if present (e.g., Radoň 2001). This study of fossil woods from northwestern Bohemia adheres to the so-called 'Whole-Plant' concept (Sakala & Teodoridis 2001) by combining detached leaves and reproductive organs with fossil wood. The woods described hereafter are similar, but they can be distinguished by the number of bars in the scalariform perforation plates of the vessels. They are attributed here to two fossil species and compared to the modern wood of the Cercidiphyllaceae and the Hamamelidaceae.

MATERIALS AND METHODS

The fossil woods described herein were found at two neighbouring localities: Kadaň–Zadní vrch Hill (50° 23' 33" N, 13° 16' 06" E) and Žichov (50° 29' 26" N, 13° 47' 26" E) in northwestern Bohemia, in the Czech Republic. The locality of Kadaň–Zadní vrch Hill belongs to the volcanic complex of the Doupovské hory Mts. The fossiliferous horizon is formed of tufites. Numerous angiosperm woods have been described from this locality, which is the richest for fossil angiosperm wood in the Czech Republic (Prakash et al. 1971). All woods at the locality are calcified. Our wood specimen comes from a 60 × 60 cm trunk, yellow-brown to red in colour. The origin of the locality as a whole is interpreted as a maar relic (P. Hradecký, pers. comm.). Its age is believed to be Oligocene but radiometric dating and further biostratigraphic studies are needed. At Žichov, the diatomite transformed into semiopal has yielded fossil fish, insects and foliage. In 1983, a small silicified fragment of a trunk, 20–25 cm in diameter, was found there and determined by D. Březinová as *Taxodioxylon* sp. (Radoň 2001). Although this site is inaccessible today, several small isolated pieces of silicified wood have recently been found in a nearby field. Based on growth ring curvature, it seems that they came from a trunk or a large branch. The locality, together with volcanoclastics at the Matrý Hill, represents the youngest fossiliferous level of the volcanic region of the České středohoří Mts. and belongs to the Děčín formation, Late Oligocene in age (Kvaček & Walther 2003).

Woods were thin sectioned following the standard techniques. The original pieces and thin sections of the wood described herein are deposited in the National Museum of Prague (one specimen/epitype from Kadaň–Zadní vrch Hill), and in the palaeontological collections of Doly Bílina–Bílina Mines (the three specimens from Žichov). Except for *Cercidiphyllum japonicum* No. 24-Mertz and *Liquidambar styraciflua* No. 708 from the collections of the Laboratoire de Paléobotanique et Paléoécologie, Université Pierre-et-Marie Curie, Paris, all modern woods studied were from the Jodrell Laboratory of the Royal Botanical Garden in Kew. The type specimen of *Cercidiphylloxylon spenceri* was studied and photographed in the palaeontological collections of the Department of Palaeontology in The Natural History Museum of London.

RESULTS

CERCIDIPHYLLACEAE

Cercidiphylloxylon Prakash et al.

Cercidiphylloxylon kadanense Prakash et al. 1971 — Fig. 1A–D, 2A

Material: G 8113 (epitype), collections of the Palaeontological department of the National Museum, Prague.

Locality: Kadaň–Zadní vrch Hill (Oligocene, northwestern Bohemia, Czech Republic).

Growth rings: distinct, 1.3–3.6 mm wide.

Wood pattern: diffuse-porous.

Vessels: mostly solitary, sometimes in tangential and radial pairs, 110–165 pores per mm^2; mostly angular in outline, but also elliptical to rounded; tangential diameter 25–80 μm, mean 50 μm; radial diameter 30–110 μm; vessel walls about 3 μm thick; scalariform perforation plates with (25–)40(–45) bars with a spacing of 19–22 per 0.1 mm; vessel pits on longitudinal walls scalariform, vessel-ray pits also scalariform.

Axial parenchyma: sparse, diffuse; cell dimensions (transverse diameter × height): 15–24 × 70–100 μm.

Rays: heterocellular, 1–4-seriate, mostly 2–3-seriate, about 10–13 per mm; multiseriate rays with uniseriate rows of 1–8 upright and sometimes procumbent cells; multiseriate rays 15–47 μm wide, and up to 55 cells (1300 μm) high; rays often vertically interconnected, composed of several multiseriate portions joined together by uniseriate portions (= end-to-end ray fusion); ray cell dimensions (tangential height × tangential width × radial length) are 10–42 × 9–24 × 18–70 μm; large quadrangular crystals present, mostly in upright ray cells.

Fibres: quadrangular to polygonal in cross-sectional outline, thick-walled (3–8 μm), disposed in 1–6 rather regular radial lines between two rays; tangential and radial diameters 12–33 μm; fibre pits not preserved.

HAMAMELIDACEAE

Liquidambaroxylon Felix

Liquidambaroxylon speciosum Felix 1884 — Fig. 1E–H

Material: specimens No. 02/98, 33/99 and 34/99 (collections of Doly Bílina).

Locality: Žichov (Late Oligocene, northwestern Bohemia, Czech Republic).

Growth rings: distinct, 0.4–4.6 μm wide.

Wood pattern: diffuse porous.

Vessels: mostly solitary, sometimes in tangential multiples of 2 due to overlapping of end walls, very rarely radially grouped, 155–185(–240) pores per mm^2; angular to oval in outline; tangential diameter 20–60 μm, mean 40 μm; radial diameter 20–80 μm; vessel walls 1–2 μm thick; vessel elements 470–650(–800) μm long; scalariform perforation plates with (15–)17–23(–27) bars with a spacing of 13–17 bars per 0.1

mm; bars sometimes (rarely) forked; vessel pitting on longitudinal walls generally in one or rarely in two series of round to horizontally elongated, scalariform pits (6 × 6–12 μm); vessel-ray pits horizontally flattened, 3–5 μm high, up to 15 μm long; tyloses conspicuous.

Axial parenchyma: diffuse, not abundant; up to 7 cells per strand; cell dimensions (tangential diameter × radial diameter × height): 12–18 × 9–23 × 90–120 μm; cell walls 2 μm thick.

Rays: heterocellular, (1–)2-seriate, rarely triseriate, about 20 per mm; uniseriate rays of upright cells, sometimes shorter cells in the middle of the rays; multiseriate rays with marginal rows of 1–6(–10) upright cells and bodies of procumbent cells; uniseriate ray height 1–22 cells (62–640 μm), width 7–18 μm; multiseriate rays 15–30 μm wide (up to 35 μm in very rare triseriate portions), height 3–62 cells (116–1294 μm); rays often interconnected; ray cell dimensions (tangential height × tangential width × radial length) are 9–80 × 6–30 × 15–120 μm; ray cells often with crystal contents, often 2 crystals per one horizontally divided upright cell; ray cells markedly pitted.

Fibres: quadrangular to polygonal, mostly hexagonal in cross-sectional outline; 1–5 rather regular radial rows between two rays; tangential and radial diameters 7–30 μm; thick-walled (3–9 μm), lumen 2–9 μm; pits, observed on radial walls, rounded in outline, in one vertical row, 7–9 μm in diameter with a vertically elongated lumen.

DISCUSSION

The two fossil wood types described here are very similar. Both are diffuse-porous with mostly solitary, angular vessels, and scalariform perforation plates. They also have heterocellular, 2(–3)-seriate rays with uniseriate marginal rows (tails), which sometimes join several multiseriate ray portions together, forming the so-called 'interconnected rays' sensu Carlquist (1988: 202), or 'end-to-end ray fusion' sensu Prakash et al. (1971). The specimen G 8113 from Kadan has slightly wider, mostly 2–3-seriate, less heterocellular rays and more numerous bars (about 40 and more) in the scalariform perforation plates (Fig. 1A–C). The three specimens from Žichov have narrower, mostly biseriate and more heterocellular rays, which are frequently interconnected, and fewer bars (about 20) in the scalariform perforation plates (Fig. 1E–H). This combination of characters (diffuse-porous pattern, angular, mostly solitary vessels with scalariform pitting and perforations, rather thin rays with uniseriate marginal rows sometimes joined together, rare diffuse parenchyma, and presence of crystals in rays) is found in the families Cercidiphyllaceae and Hamamelidaceae (Wheeler & Manchester 2002).

Conspectus of the representatives of the morpho-genus *Cercidiphylloxylon*

The specimen G 8113 from Kadaň belongs to *Cercidiphylloxylon kadanense*, which is the type species of the morpho-genus *Cercidiphylloxylon*. *Cercidiphylloxylon kadanense* was originally defined by Prakash et al. (1971) on a single type specimen (= ZV-12) from the locality of Kadaň–Zadní vrch Hill of the Oligocene of northwestern Bohemia (Czech Republic). Our new specimen (= G 8113) comes from the same locality. As its
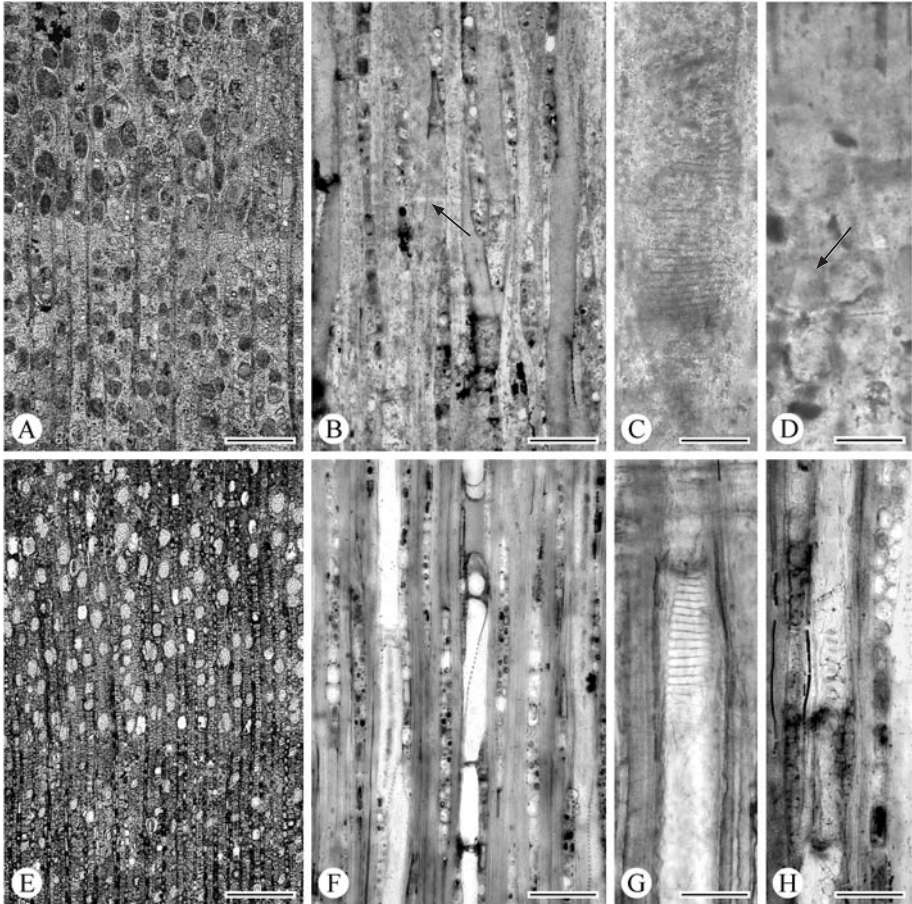
Fig. 1. A–D: *Cercidiphylloxylon kadanense* Prakash et al. (G 8113, epitype). – A: Diffuse-porous wood with mostly solitary vessels, angular in outline, XS. – B: 2–4-seriate rays with some interconnected rays (4-seriate ray lower right), and scalariform perforation plate (arrow), TLS. – C: Scalariform perforation plate with 40 bars, RLS. – D: Crystal in the upright ray cell (arrow), RLS. — E–H: *Liquidambaroxylon speciosum* Felix (02/98). – E: Diffuse-porous wood with mostly solitary vessels, angular in outline, XS. – F: Uni- to biseriate rays with long uni-seriate extremities & frequent interconnected rays, and scalariform perforation plates, TLS. – G: Typical scalariform perforation plate with 20 bars, RLS. – H: Scalariform vessel pitting, TLS. — Scale bars = 200 μm in A, E; 100 μm in B, F; 50 μm in C, D, G, H.

preservation is much better than the original type specimen, we propose designating this new specimen as an epitype of *C. kadanense*, as well as of *Cercidiphylloxylon*. Information from this new specimen complements the original specific / generic diagnosis (Prakash et al. 1971: 112). New observations on *C. kadanense* and *Cercidiphylloxylon* are: 1) rays can be up to 4-seriate, observed in both holotype and newly designated epitype (Fig. 2A, B), 2) the presence of crystals in the rays of *C. kadanense* (Fig. 1D),
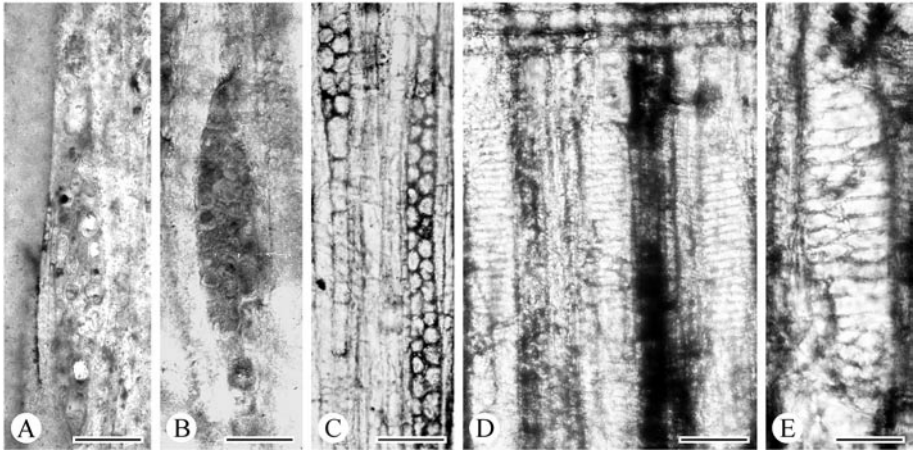
Fig. 2. A & B: *Cercidiphylloxylon kadanense* Prakash et al. (A: G 8113, epitype; B: ZV-12 (= G 4055), holotype). – A: 4-seriate ray (same as shown in Fig. 1B lower right), TLS. – B: 4-seriate ray, TLS. — C–E: *Cercidiphylloxylon spenceri* (Brett) Pearson (C–E: V.23438, one of the syntypes; C: V.23438c; D & E: V.23438b). – C: Biseriate rays with uniseriate marginal rows (tails), TLS. – D: Scalariform perforation plates with 19–25 bars, RLS. – E: Scalariform, often forked, perforation plate with about 20 bars, RLS. — Scale bars = 50 μm in A, B, C; 40 μm in D; 25 μm in E.

and 3) the density of bars in the scalariform perforation plates is about 20 bars per 0.1 mm in *C. kadanense* (Fig. 1C). This last feature, together with the total number of bars (about 40), is diagnostic of *C. kadanense*; the spacing of the bars can be used to help identify specimens where only a part of the scalariform perforation plate is preserved.

The second species of *Cercidiphylloxylon* (*C. spenceri*) is based on the wood described as *Cercidiphyllum spenceri* by Brett (1956) from the Eocene of London Clay, and later transferred to the morpho-genus *Cercidiphylloxylon* by Pearson (1987). Pearson's argumentation is consistent with a more general concept of *Cercidiphylloxylon*, which agrees with the botanical affinities of this morpho-genus, discussed hereafter. Crawley (1989) attributed two specimens from the Palaeocene of Scotland to *C. spenceri*. He also included the wood of *Cercidiphyllum alalongum* Scott & Wheeler (1982) from

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Fig. 3. A & B: *Cercidiphyllum japonicum* Sieb. & Zucc. (No. 24-Mertz, coll. LPP UPMC Paris). – A: Biseriate rays, often interconnected, TLS. – B: Scalariform perforation plate with closely spaced 45 bars, RLS. — C & D: *Liquidambar formosana* Hance (C: 600-69-31275w, coll. RBG Kew; D: Formosa, Hort. Kew, RBG Kew). – C: Uni- to biseriate rays, TLS. – D: Bi- to triseriate rays, TLS. — E & F: *Liquidambar styraciflua* L. (E: SE USA trade 1962, coll. RBG Kew; F: SE USA, coll. RBG Kew). – E: Uni- to biseriate rays, sometimes interconnected, TLS. – F: Scalariform perforation plate with about 25 bars, RLS. — G & H: *Altingia excelsa* Noronha (G, H: specimen from Burma, coll. RBG Kew). – G: Bi- to triseriate rays, TLS. – H: Part of a scalariform perforation plate with 28 bars, RLS. — I & J: *Corylopsis* sp. (I, J: specimen from Wakehurst, coll. RBG Kew). – I: Bi- to triseriate rays, TLS. – J: Scalariform perforation plate
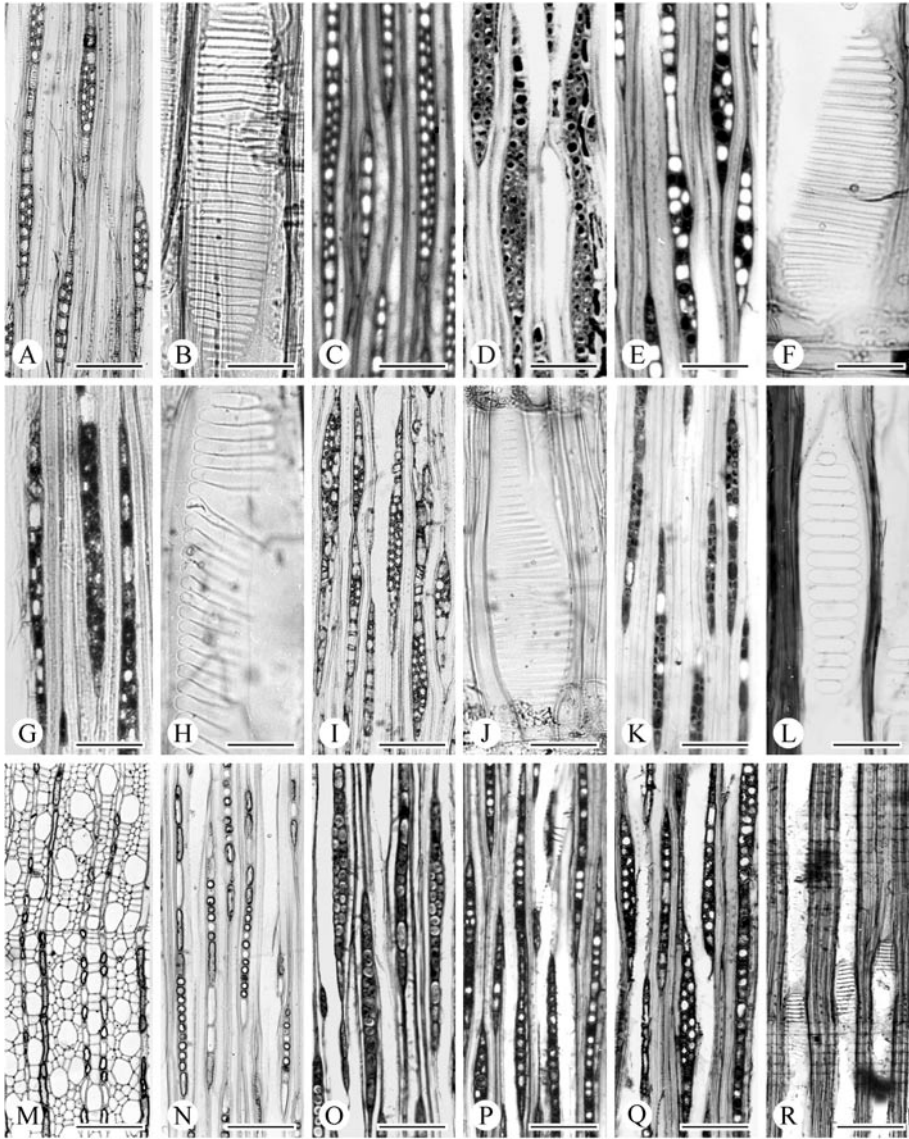
with 24 bars, RLS. — K & L: *Distylium racemosum* Sieb. & Zucc. (K: 6/A/882, Japan, coll. RBG Kew; L: Tl - 4866, Japan, coll. RBG Kew). – K: Mostly uni- to biseriate rays, TLS. – L: Scalariform perforation plate with 16 bars, RLS. — M–O: *Hamamelis japonica* Sieb. & Zucc. (M, N: 1045, Japan, coll. RBG Kew; O: TI-4852, Japan, coll. RBG Kew). – M: Diffuse-porous wood with solitary vessels, angular in outline, XS. – N: Exclusively uniseriate rays, TLS. – O: Uni- to biseriate rays, sometimes interconnected, TLS. — P–R: *Hamamelis virginiana* L. (P: PACw 6078, USA, coll. RBG Kew; Q, R: PACw 7215, USA, coll. RBG Kew). – P: Mostly uniseriate rays with some biseriate portions, TLS. – Q: Frequent biseriate interconnected rays, TLS. – R: Scalariform perforation plates with less than 20 bars, RLS. — Scale bars = 100 μm in A, C–E, G, I, K, M–R; 40 μm in B, F, H, J, L.

the Eocene of the Clarno Formation into the synonymy list of *Cercidiphylloxylon spenceri* (Crawley 1989: 600). Our observations on the type material of *Cercidiphylloxylon spenceri* support the view of Crawley (1989) that all these specimens belong to the same morpho-species, i.e., *Cercidiphylloxylon spenceri* (Brett) Pearson sensu Crawley. All differences seem to be only intraspecific (for a summary, see table 2 in Crawley 1989: 604). The wood recently assigned to *Cercidiphyllum alalongum* Scott et Wheeler by Wheeler and Manchester (2002) would also belong to *Cercidiphylloxylon spenceri*. The only discrepancy between the type and other specimens of *C. spenceri* is in the number of bars in the scalariform perforation plates. In the type, where Brett (1956) counted 25–30 bars, we have seen 27 bars at maximum, generally 19–25 bars, forked sometimes (Fig. 2D, E). This may be due to the type specimen V.23438 being a small fragment with immature (juvenile) wood.

Thus, the morpho-genus *Cercidiphylloxylon* has two species: *C. kadanense* Prakash et al. known only from the Oligocene of the Czech Republic and *C. spenceri* (Brett) Pearson from the Palaeocene and Eocene of the British Isles and the Eocene of the United States. These species may be distinguished, as already pointed out by Crawley (1989), by wider rays and a larger vessel diameter in *C. kadanense*. Ray width is also useful diagnostically: *C. kadanense* has mainly 2–3-seriate, but also 4-seriate rays (Fig. 1B; 2A, B), *C. spenceri* has 1–2-seriate rays (Fig. 2C).

Botanical affinities of Cercidiphylloxylon

The wood of *Cercidiphylloxylon* does not correspond only to *Cercidiphyllum* Sieb. & Zucc., but also to diverse extinct Cercidiphyllaceae.

Cercidiphylloxylon spenceri, only Palaeocene and Eocene in age, undoubtedly represents wood of extinct *Cercidiphyllum*-like plants, known from infructescences and foliage (Crane & Stockey 1986). As pointed out by Kvaček & Konzalová (1996), true *Cercidiphyllum*, based on fruits, is not older than Oligocene (Jähnichen et al. 1980; Meyer & Manchester 1997). Although never found in direct connection, nor closely associated with other organs (Crane 1984), the wood of *C. spenceri* belongs most probably to the plant with leaves of *Trochodendroides* Berry emend. Crane and fruits of the *Nyssidium*-type.

Cercidiphylloxylon kadanense has been recorded at a single locality, at the Kadaň–Zadní vrch Hill, in the Oligocene of NW Bohemia. In the Oligocene and Early Miocene of NW Bohemia, the fossil *Cercidiphyllum crenatum* (Unger) R.W. Brown occurs (Kvaček & Konzalová 1996), and is known from foliage, fruits, seeds, staminate inflorescences, and in situ pollen. Hence, the wood of *Cercidiphylloxylon kadanense* might be associated with this species.

Comparison with extant wood types

Both fossil woods described here are close to the Cercidiphyllaceae and Hamamelidaceae, as stated above. There are numerous descriptive works on the wood of *Cercidiphyllum japonicum* Sieb. & Zucc. (e.g., McLaughlin 1933; Swamy & Bailey 1949; Metcalfe & Chalk 1950; Kribs 1968). However, the wood of *C. magnificum* (Nakai) Nakai

has never been mentioned, except for a note about spiral thickening in the tips of vessels (Ilic 1987: 40). *Cercidiphyllum japonicum* (Fig. 3A, B) is similar to the specimen G 8113, which we assign to *Cercidiphylloxylon kadanense*. However, as pointed out by Prakash et al. (1971), the rays of modern *Cercidiphyllum* (1–2-seriate) and fossil *Cercidiphylloxylon kadanense* (mostly 2–3-seriate) differ. In ray width, the modern *Cercidiphyllum* is closer to *Cercidiphylloxylon spenceri*, which, however, likely represents the wood of extinct *Cercidiphyllum*-like plants.

A similar wood structure, including 1–2-seriate rays, may be observed in *Liquidambar* L. (Fig. 3C–F) of the Hamamelidaceae. Prakash et al. (1971) proposed a distinction between *Liquidambar* and *Cercidiphyllum* based on the number of bars in scalariform perforation plates and the character of rays: *Liquidambar* with less (12–25) bars and occasional interconnected rays, contrary to *Cercidiphyllum* with numerous (20–50) bars and rays frequently interconnected. We studied extant wood material of two species of *Liquidambar*: *L. formosana* Hance (Fig. 3C, D) and *L. styraciflua* L. (Fig. 3E, F). Our observations confirm the difference in interconnected rays, but we believe this to be a rather subjective distinction. The rays of *Liquidambar* are variable; we observed narrower uni- to biseriate rays, sometimes interconnected, with various height of biseriate portions (Fig. 3C, E), but also wider bi- to triseriate rays (Fig. 3D). On the other hand, we found 15–20 bars in *L. formosana*, and up to 25(–30) bars in *L. styraciflua* (Fig. 3F), similar to Prakash et al. (1971). In addition, the bars in perforation plates of *Liquidambar* are more widely spaced: with 15 bars per 0.1 mm in *Liquidambar*, and about 20 bars per 0.1 mm in *Cercidiphyllum*.

We have examined rays and perforation plate number in other Hamamelidaceae: *Altingia* Noronha (Fig. 3G, H), *Corylopsis* Sieb. & Zucc. (Fig. 3I, J), *Distylium* Sieb. & Zucc. (Fig. 3K, L), and *Hamamelis* L. (Fig. 3M–R). Some authors have already compared the rays of some of these genera to *Cercidiphyllum*, e.g., comparison with *Corylopsis* was done by Scott and Wheeler (1982). Our observations of Hamamelidaceae show that their rays are very similar to each other. They are in general rather thin, uniseriate and biseriate with biseriate portions of different form and size and uniseriate marginal rows, with variation in frequency of interconnected rays (Fig. 3G, I, K, N–Q). The rays sometimes vary within one specimen, sometimes significantly within one species, as in *Hamamelis*. One specimen of *H. japonica* has exclusively uniseriate rays (Fig. 3 M, N); the other has uni- to biseriate rays, which are sometimes interconnected (Fig. 3O). Similar variation in ray character also occurs in *H. virginiana* (compare Fig. 3P vs. 3Q). *Cercidiphyllum* can be distinguished from these genera of Hamamelidaceae by the number of bars in the scalariform perforation plates. Hamamelidaceae have about 20 bars (Fig. 3J, L, R) with a maximum of 28 in *Altingia* (Fig. 3H), in contrast to *Cercidiphyllum* with 40 or more bars (Fig. 3B). We have found the perforation plate bar number to be very consistent and we believe it taxonomically useful. Consequently, the second fossil wood from the locality of Žichov, which is similar to modern *Liquidambar* in having fewer and more widely spaced bars, is attributed to the fossil morphospecies *Liquidambaroxylon speciosum* Felix. No other fossil remains of *Liquidambar* are reported from Žichov, contrary to *Cercidiphyllum* leaves (Ettingshausen 1869).

Finally, *Cercidiphylloxylon kadanense* from Kadaň–Zadní vrch Hill has some similarity to the wood of modern *Nyssa* Gronov ex L. (Sakala 2003b). However, *Nyssa* has more radial multiples and radial groups of vessels, and no crystals in the rays (Noshiro & Baas 1998), in contrast to *Cercidiphyllum* and our fossil wood. The presence of crystals in the rays differentiates our wood from *Diplopanax* Hand.-Mazz., another similar wood of the Cornaceae alliance (Noshiro & Baas 1998). Being able to distinguish between the wood of *Nyssa* and *Cercidiphyllum* is useful because they both represent important elements in the Tertiary of northwestern Bohemia. In the Early Miocene of Most basin, *Nyssa* is known by its leaves, endocarps, whole fruits and inflorescences with pollen in situ as a notorious swampy plant (Dašková 2000; Sakala 2000; Sakala et al. in progress). In the Oligocene, there are typical dentate leaves of *Nyssa altenburgensis* Walther & Kvaček from Seifhennersdorf (Kvaček & Walther 1981). This volcanoclastic deposit, situated near the Czech borders in the German part of the České středohoří Mts., is late Early Oligocene in age (Kvaček & Walther 2003).

CONCLUSIONS

The family Cercidiphyllaceae is represented today by a single genus, *Cercidiphyllum* Sieb. & Zucc. (katsura tree) with two species, confined to China and Japan (e.g., Spongberg 1979). However, the family was more diversified in the past, containing some extinct genera based on various plant organs (Crane & Stockey 1986; Kvaček & Konzalová 1996). Fossil cercidiphyllaceous woods have already been described (Brett 1956; Prakash et al. 1971; Scott & Wheeler 1982; Crawley 1989; Wheeler & Manchester 2002; wood mentioned in the taxonomic list as '*Cercidiphyllum* sp.' by Beck 1945 was subsequently described in detail by Prakash & Barghoorn 1961 as '*Liquidambar* cf. *styraciflua*'; S.R. Manchester, pers. comm.). New excavations at the locality of Kadaň–Zadní vrch Hill (Oligocene, northwestern Bohemia, Czech Republic) have yielded several specimens of calcified wood. One of them is identified here as *Cercidiphylloxylon kadanense* Prakash et al. (1971). Its preservation, which is better than in the holotype specimen, allows its designation as an epitype of *Cercidiphylloxylon kadanense* as well as *Cercidiphylloxylon*, both defined originally by Prakash et al. (1971) in the same locality. We conclude that the wood of *Cercidiphylloxylon kadanense* represents the oldest record of the fossil wood of true *Cercidiphyllum* because of its Oligocene age and the occurrence of leaves, fruits, seeds, staminate inflorescences, and pollen of *Cercidiphyllum* in the region.

We compared *Cercidiphylloxylon kadanense* with another similar wood type from the neighbouring locality, treated here as *Liquidambaroxylon speciosum* Felix as well as with similar modern woods from the Cercidiphyllaceae and Hamamelidaceae. Generally, the number of bars in the scalariform perforation plates of the vessels is a reliable criterion to distinguish the wood of *Cercidiphyllum* Sieb. & Zucc. from woods of the Hamamelidaceae. Rays among the Cercidiphyllaceae and Hamamelidaceae can vary, even at intra-specific level, and we believe ray characteristics are not suitable for distinguishing them. However, the co-occurring differences of the rays of two fossil woods, viewed here as a subsidiary feature, corroborate the recognition of two genera.
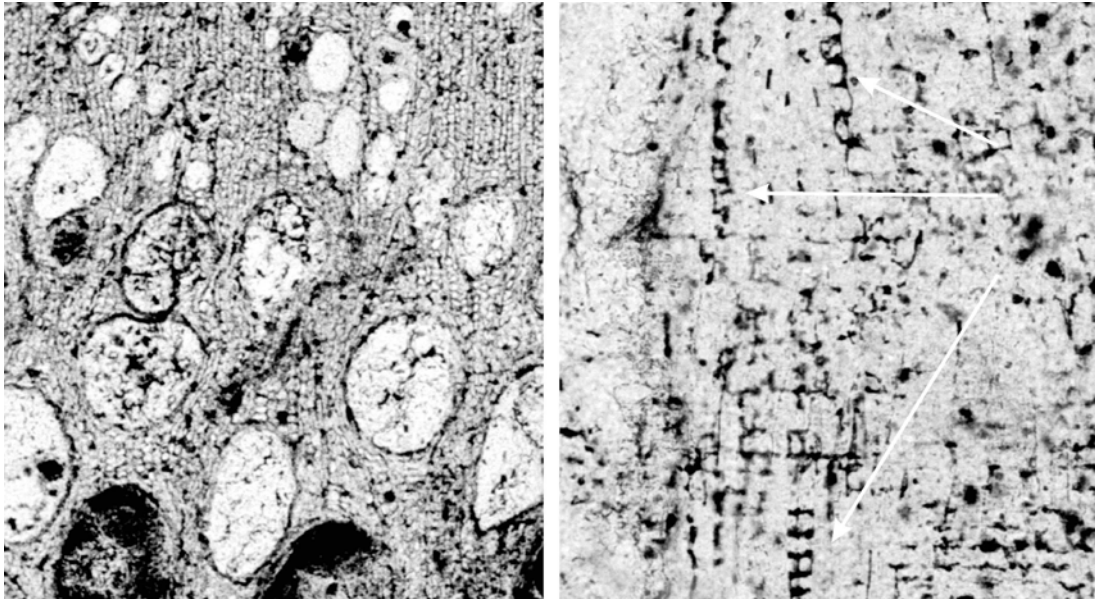
ACKNOWLEDGEMENTS

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Doctoral Thesis by Jakub Sakala (2004)
*The 'Whole-Plant' concept in palaeobotany with examples from the Tertiary of northwestern Bohemia, Czech Republic
with particular reference to fossil wood*

5.2.2. Example 3: *Castanoxylon* from Velká Černoc

pages 39-44 - Sakala & Teodoridis 2001

Text-fig. 3: *Castanoxylon bavaricum* in cross-section (left) with the characteristic flame-shaped arrangement of vessels in the late wood and in radial section (right) showing the crystalliferous septate parenchyma (arrows).

Example 3: Systematic part – conclusions

A big silicified trunk found in the Late Oligocene sediments at Velká Černoc shows characters shared with some Fagaceae in having ring porous wood pattern with relatively large, usually solitary vessels in the early wood, characteristic flame-shaped arrangement of vessels in the late wood, diffuse apotracheal parenchyma and tracheids. The presence of uniseriate to biseriate rays allows its certain safe attribution to the fossil genus *Castanoxylon* Navale, a morphogenus comprised of the fossil woods of *Castanea* Mill., *Castanopsis* Spach and some species of *Quercus* L. and *Lithocarpus* Bl. Concerning possible affinities with modern wood, our fossil must be compared to *Castanea* with respect to its characteristic cross-section with early wood pores in a multiseriate band, often in contact radially (see Text-fig. 3, left). In the specific level, the wood from Velká Černoc can be identified as *Castanoxylon bavaricum* Selmeier (**Sakala & Teodoridis 2001**).

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Example 3: General aspects relative to the 'Whole-Plant' concept

Importance of crystalliferous wood parenchyma

The presence of septate crystalliferous parenchyma in our fossil (see Text-fig. 3, right) seems to have a systematic importance at the specific level. The crystalliferous elements in parenchyma occur today only in *Castanea mollissima* Bl., distributed in northern and central China (Suzuki 1976, Watari & Kuroda 1949). I have examined just only several specimens of *Castanea* and the crystalliferous septate parenchyma was observed only in the specimen called *"C. vulgaris"* (n° MUS IV., Japan - RBG Kew collection). However, the crystals are generally very rare in the modern wood contrary to the fossil one.

Lack of comparative material of rare modern wood

Further additional studies and more extensive living comparative material of *Castanea*, essentially Asiatic including *C. mollissima* are required in order to get the true botanical affinity of the fossil wood. As the morphogenus *Castanoxylon* covers also rare *Quercus* and *Lithocarpus* wood with uni- to biseriate rays, not available for my study. The future studies must include these representatives. Generally, the nearest living relatives of the Tertiary plants of Europe grow often in the regions of Atlantic North America and south China (Mai 1995). Especially Chinese woods are rarely available, but they must be seen for further more detailed studies.

Plausible but uncertain combination of organs

Castanoxylon bavaricum from Velká Černoc and a leaf of cf. *Castanea atavia* Unger sensu Kräusel from the neighbouring locality of Nesuchyně of the same geological formation present both affinities with *Castanea*. It was proposed that the wood and the leaf belonged to the same plant (Sakala & Teodoridis 2001). The single leaf is just fragmentarily preserved, but it represents the only specimen of the *Castanea*-type foliage in the whole formation. The proposal of such a combination is very plausible in spite of the fact that the leaf and the wood were not found in direct connection or even association.

Fossil wood and foliage of *Castanea* (Fagaceae) from the Upper Oligocene of northern Bohemia

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A b s t r a c t . The present article gives the first results of the thesis of Jakub Sakala, concerning an interesting find of wood of *Castanea*-type from the Upper Oligocene sediments of the locality Velká Černoc of northern Bohemia. This locality, together with other localities of the so-called "Neogene accumulations of central Bohemia", was recently studied in detail by Vasilis Teodoridis from the point of view of leaves/fruits and seeds. In the neighbouring locality of Nesuchyně, *Castanea*-type foliage has also been discovered and is described herein by the second author. Therefore, the present study combines the finds of fossil *Castanea*-type wood and leaves coming from neighbouring localities of the same geological formation.

A b s t r a k t . Předkládaný článek přináší první výsledky doktorandské práce Jakuba Sakaly, které se týkají zajímavého nálezu dřeva typu *Castanea* ze svrchně-oligocenních sedimentů severočeské lokality Velká Černoc. Tato lokalita společně s dalšími z tzv. „Neogenních ostrovů středních Čech" byla zcela nedávno detailně zpracována Vasilisem Teodoridisem z hlediska listů, plodů a semen. Na sousední lokalitě Nesuchyně bylo nalezeno též olistění typu *Castanea*. Tento nález je zde popsán druhým autorem. Tato práce tak kombinuje nálezy fosilního dřeva a olistění, obojí typu *Castanea* a pocházející ze sousedních lokalit stejného geologického souvrství.

K e y w o r d s : *Castanea*, wood, foliage, Velká Černoc, Nesuchyně, Upper Oligocene, northern Bohemia, Czech Republic

Introduction

In spite of the fact that the North Bohemian Tertiary as a whole poses a very well documented area from the palaeobotanical-palaeontological point of view, fossil wood has not been studied in detail there yet. In contrast to the important number of studies on leaves / fruits and seeds, only few recent papers on fossil wood have been published. These are the note on a piece of silicified wood from the Most Basin by Březinová (1964), a study dealing with samples from tuffitic strata of the Doupov and České středohoří Mts. by Prakash et al. (1971), the paper by Březinová and Süss (1988) and other related papers on wood remains from the Karlovy Vary area, and finally the paper describing a silicified stem from the locality of Kučlín by Březinová et al. (1994).

The xylotomical research conducted within the Ph.D. thesis of the first author, supervised by Catherine Privé-Gill, attempts to fill this gap. The present article brings the first results of this thesis, concerning a wood of the *Castanea*-type from the Upper Oligocene sediments of the locality of Velká Černoc in northern Bohemia.

This locality, much like other localities of the so-called "Neogene accumulations of central Bohemia" (in the sense of Němejc 1949), was recently studied in detail by the second author (Teodoridis 2000) from the point of view of fossil leaves/fruits and seeds. At Nesuchyně, an another locality of the so-called "Neogene accumulations", *Castanea*-type foliage has been also discovered and is described herein by the second author.

Therefore, the present study combines the finds of fossil wood and leaves, both of the *Castanea* type, while not directly attached to each other, coming from the same geological formation.

Geological setting

The localities of Velká Černoc and Nesuchyně are located in northern Bohemia (Fig. 1) and belong to a relatively continuous belt of the Hlavačov gravel and sand, stretching between the towns of Rakovník and Holedeč. The belt is about 21 km long and 2–3.5 km wide (Váně 1985). Other relics of the Hlavačov gravel and sand were preserved in the area of Želeč and Sádek (railway station). In the area of Holedeč and Měcholupy, the Hlavačov gravel and sand deposits do not occur on the surface, but underlie the Žatec facies of the Most Formation, which belongs to the Most Basin.

The lithological character of the Hlavačov gravel and sand is very typical. Boulder material of gravel facies is highly varied and includes mainly white or yellowish quartz and black lydite. Along the Hlavačov gravel and sand deposit, 1 to 3 clay beds (20–50 cm thick) can be found. They are irregularly distributed and differ in their number and thickness, being frequently represented by isolated fossiliferous lenses (Bretšnajder 1952, Váně 1985). The Hlavačov gravel and sand is typically a fluvial deposit with variable grain size and clay content, cross bedding, erosive boundaries within the accumulation etc. (for details see Gabriel and Valín 1968).

According to Pešek and Spudil (1986), the Hlavačov gravel and sand deposit represents a terminal sedimentary
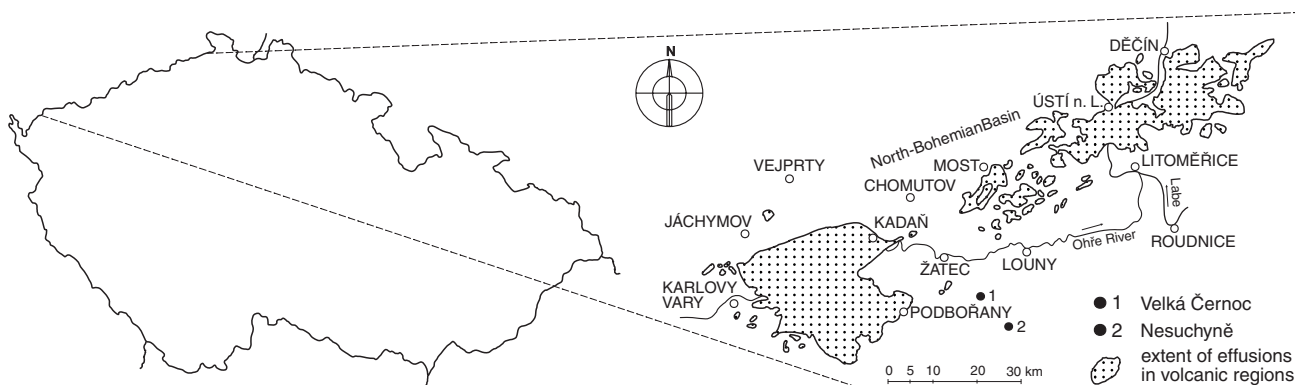
Fig. 1. Position of the localities of Velká Černoc and Nesuchyně.

relict of the so-called "River C". During the Tertiary, this river drained the areas of central and western Bohemia, flowing across the Rakovník area towards the Žatec area (Pešek and Spudil 1986). The Thierbach strata (Bitterfeld Basin) and the Hlavačov gravel and sand (Čadek 1966, Lotsch et al. 1994) can be correlated on the basis of the analogy in heavy mineral standards and their floristic similarity, and suggest sedimentation in a common river system of the same age (Lotsch et al. 1994).

Systematic part

1.) Fossil wood

Fagaceae
Castanoxylon Navale

Castanoxylon bavaricum Selmeier 1970
(Fig. 2, Pl. I/1–3)

1970a *Castanoxylon bavaricum* Selmeier; Selmeier, p. 25, figs. 1–8.
1980 *Castanoxylon bavaricum* Selmeier; Privé-Gill et Watelet, p. 140, pl. 2, figs. 1–9, text-figs. 3,5.
1991 *Castanoxylon bavaricum* Selmeier; Selmeier, p. 151, figs. 1–9.

M a t e r i a l : Fossils from the collections of Z. Kvaček (no. VČ 1 + VČ 2) and Z. Dvořák (no. 27/98).

D e s c r i p t i o n : The specimens are beige to orange silicified blocks of several centimetres in size.

Growth rings–very well pronounced, 850–3500 μm wide.

Wood pattern – ring porous

Vessels–oval, round or elliptical in cross-section; a) in the early wood – mostly solitary, but also in oblique, tangential or radial groups of 2–(3), tangential diameter 130–400 μm (mean 270 μm), radial diameter 150–600 μm; b) in the late wood–rarely solitary, mainly grouped radially, obliquely and tangentially, forming typical

flames, tangential diameter 30–220 μm (mean 75 μm), radial diameter 30–210 μm; vessel walls 5–9 μm thick; vessel elements 180–740 μm long, separated by horizontal or slightly inclined simple perforation plates; intervascular pits bordered, circular, alternate, quite dense, 5–7 μm in diameter; tyloses frequent.

Fibres – 600–750 μm long, polygonal in cross-section in the early wood, quadrangular to elliptical, tangentially flattened in the late wood, forming 2–11 radial regular lines between the rays; tangential diameter 9–36 μm, radial diameter 7–36 μm; fibre walls 3–5 μm thick in the late wood and about 3 μm in the early wood; tracheids with round, bordered and very dense pits, about 7 μm in diameter in the early wood.

Axial parenchyma – abundant, apotracheal, diffuse and in discontinuous tangential aggregates; parenchyma cell dimensions (tangential diameter × radial diameter × height): 20–30 μm × 15–30 μm × 80–90 μm, septate, crystalliferous parenchyma also present, relatively abundant.

Rays–homogeneous, uniseriate (rarely biseriate), 12-30 μm (up to 45 μm in biseriate rays) wide, 55–630 μm (2–25 cells) high; 12–15 in number per tangential horizontal mm; ray cell dimensions (height × width × length): 15–35 μm × 10–30 μm × 35–75 μm.

D i s c u s s i o n : The described wood shows similar characters to some Fagaceae in having relatively large, usually solitary vessels in the early wood, characteristic flame-shaped arrangement of vessels in the late wood, diffuse apotracheal parenchyma and tracheids. The presence of uniseriate to biseriate rays allows its safe attribution to the fossil genus *Castanoxylon*.

Castanoxylon was erected by Navale (1964) as a form genus regrouping the fossil woods of Fagaceae, which present uniseriate to biseriate rays with a flame-shaped arrangement of pores, i.e., *Castanea*, *Castanopsis* and some species of *Quercus* and *Lithocarpus*.

Because of the absence of comparative slides or detailed descriptions of very rare wood of *Quercus* and *Lithocarpus* that present only uni- to biseriate rays, two genera must be mainly considered: *Castanopsis* and *Castanea*.
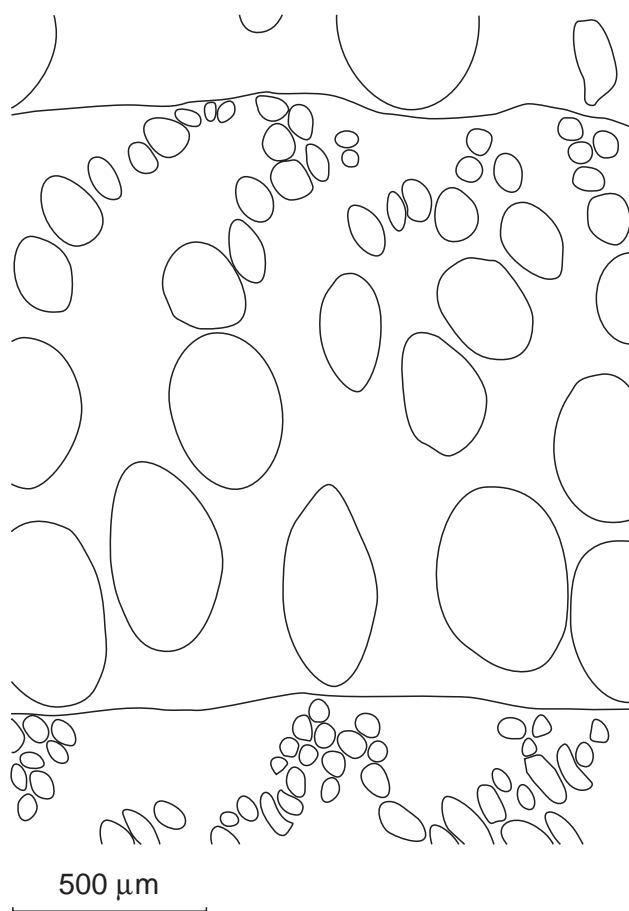
Privé-Gill and Watelet (1980) and Selmeier (1991). This species corresponds quite well to our fossil in all diagnostic features: solitary bigger vessels in the early wood, smaller vessels forming the characteristic flames in the late wood, diffuse apotracheal & septate crystalliferous parenchyma and uni- to biseriate homogeneous rays.

Concerning possible affinities with the extant material, the presence of septate crystalliferous parenchyma in our fossil seems to have a systematic importance. The crystalliferous elements in parenchyma are found today only in *Castanea mollissima* Bl., distributed in northern and central China (Suzuki 1976, Watari and Kuroda 1949). This area of distribution would fit quite well that of the living relatives of numerous Tertiary plant elements. However, it is very difficult to give a more detailed opinion on this question without the sufficient number of comparative extant material that we do not have at our disposal.

We examined only several specimens of *Castanea*: five different specimens of *C. sativa* Mill., and one of each of the following species – *C. crenata* Sieb. et Zucc., *C. dentata* (Marsh.) Borkh. and *"C. vulgaris"*. Crystalliferous septate parenchyma was observed only in the specimen called *"C. vulgaris"* (no. MUS IV., Japan – RBG Kew collection; see Pl. I/4). In contrast to the fossil specimen, the crystals are very rare in the modern wood. The examination of true affinities of *Castanoxylon bavaricum* would require additional studies and more extensive living comparative material, essentially Asiatic including *Castanea mollissima* Bl.

2.) Fossil leaves

Fagaceae
Castanea Mill.

cf. *Castanea atavia* Unger 1850 sensu Kräusel 1938
(Fig. 3, Pl. I/5, 6)

1850 *Castanea atavia* Unger; Unger, p. 34 (164), pl. 10 (31), figs. 5, 7.
1852 *Castanea atavia* Unger; Goeppert, p. 274, pl. 34, fig. 4.
1938 *Castanea atavia* Unger; Kräusel, p. 45, pl. 5, fig. 12, pl. 6. fig. 1, text-figs. 12 a, b.
1969 *Castanea atavia* Unger; Knobloch, p. 94, pl. 41, fig. 5, pl. 42, fig. 9, text-fig. 217.

M a t e r i a l : Leaf fragment no. Nn – 158.
D e s c r i p t i o n : Leaf fragment oblong, 99 mm long and up to 34 mm broad (in the upper third), apex, base and petiole not preserved; margin regularly simple serrated, hooked teeth triangular, sharp and relatively long (2–3 mm); venation simple craspedodromous, primary vein strong and straight, secondary veins slender, alternate, probably numerous (11 pairs preserved), straight in last third broken and slightly curved towards margin, originating at angles of 48 to 63°; tertiary venation and higher-order venation not preserved.
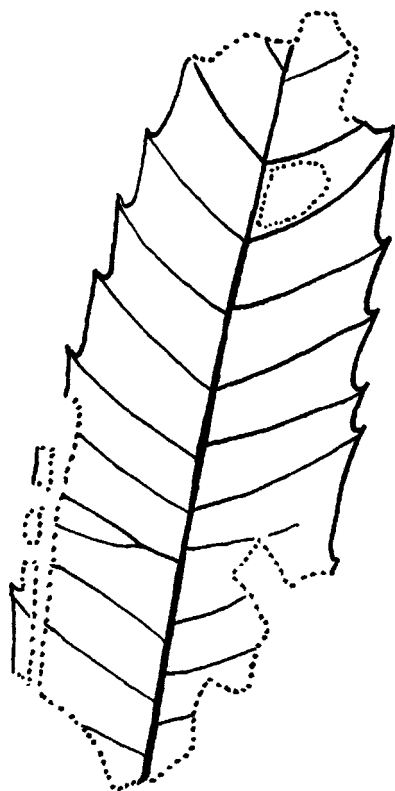

Fig. 2. Schematic cross-section of *Castanoxylon bavaricum* (no. VČ 1).

These two genera can be distinguished, as already stated by Selmeier (1970b, 1992), by their characteristic cross-sections. *Castanea* has early wood pores in a multiseriate band, often in contact radially (= more or less continuous tangential bands) while the early wood pores of *Castanopsis* are all solitary in a single row, i.e., in regularly interrupted tangential bands (e.g., Record 1942, p. 23). Regarding these diagnostic features, our fossil (Fig. 2) must be correlated with the wood of *Castanea*.

As already pointed out by Privé-Gill and Watelet (1980) and Selmeier (1986), the only detailed descriptions of fossil *Castanea* wood, allowing a comparison, are those provided by Watari and Kuroda (1949), Selmeier (1970a), Suzuki (1976), Privé-Gill and Watelet (1980), and finally by Selmeier (1991).

The Oligocene *Castanea protoantiqua* described by Suzuki (1976) cannot be considered because of its high percentage of bi- and triseriate rays (51 % and 9 %, respectively) and significantly smaller vessels (up to 310 μm).

The second Japanese wood, Pliocene *Castanea antiqua* described by Watari and Kuroda (1949) is quite similar to our wood. However, it differs from the Czech fossil in having very abundant parenchyma in regular tangential bands in the late wood.

Our fossil can be identified as *Castanoxylon bavaricum* described by Selmeier (1970a), pointed out by

Fig. 3. Leaf of *Castanea* atavia (no. Nn – 158), × 1.

D i s c u s s i o n : The determination of the species and genus is very difficult in this case because of the incompleteness of the leaf and uniqueness of the occurrence. The method of epidermal analysis cannot be applied because of the preservation of the whole fossil materials from the Hlavačov gravel and sand. The above mentioned fragment Nn – 158 can be assigned to the species *Castanea atavia* Ung. sensu Kräusel on the basis of leaf morphology. The main morphological features for the determination are especially the form and the character of the margin and teeth (Fig. 3). Practically identical fossil material was described from the locality of Sotzka (Unger 1850, pl. 10, figs. 5–7) and from the locality of Mainz-Kastel (Kräusel 1938). Similar leaf impressions are known from the Moravian Tertiary (Knobloch 1969). Morphology of the incomplete leaf shows a certain resemblance with some specimens of *Castanea kubinyi* Kov. ex Ett. (e.g., Ettingshausen 1852). The main morphological differences between *Castanea atavia* and *Castanea kubinyi* are in the number of secondary vein pairs, leaf form and teeth character (see in detail in Knobloch 1969, Knobloch and Kvaček 1976). According to Czecott (1951) *Castanea kubinyi* poses an oak. Differences in the foliage between the genera *Quercus* and *Castanea* were studied in detail by Hummel (1983).

According to Unger (1850), the recent analogue of *Castanea atavia* Ung. is *Castanea pumila* Mill., which is distributed in the Atlantic area of North America (e.g., New Orleans). Knobloch (1969) compared this fossil species to the extant species *Castanea sativa* Mill.

C o n c l u s i o n s : Both localities, i.e., Velká Černoc and Nesuchyně, belong to the same accumulation of the so-called "Hlavačov gravel and sand". Plant fossils are bound to clay lenses irregularly distributed in the gravel and sand. The flora is composed of 2 ferns, 5 conifers and 51 angiosperms (for details see Teodoris 2000, Teodoris in press). The plant association connected with the Hlavačov gravel and sand corresponds to the temperate riparian forest with dominant deciduous elements, e.g. *Fagus saxonica*, *Pseudolarix schmidtgenii*, *Taxodium dubium*, Betulaceae. The flora of the Hlavačov gravel and sand can be correlated with the Upper Oligocene Thierbach floristic complex (in the sense of Mai and Walther 1991) from the lower part of the Bitterfeld Basin in Germany (Lotsch et al. 1994, Teodoris in press).

Both the fossil wood from Velká Černoc and the leaf from the neighbouring Nesuchyně locality present affinities with the genus *Castanea*. We suggest that the wood and the leaf belong to the same species of the genus. The single leaf is just fragmentarily preserved, but represents the only known foliage of *Castanea*-type in the whole sand and gravel accumulation. Therefore, the proposal of such a combination seems plausible to us in spite of the fact that the leaf and the wood were not found in direct connection or even association.

Generally, the North Bohemian Tertiary presents a unique opportunity to combine detached organs (Sakala 2000). This approach, recently shown by Kvaček and Sakala (1999) on the exceptionally well preserved material from the same area, is the only way to reach the ideal "whole-plant palaebotany".

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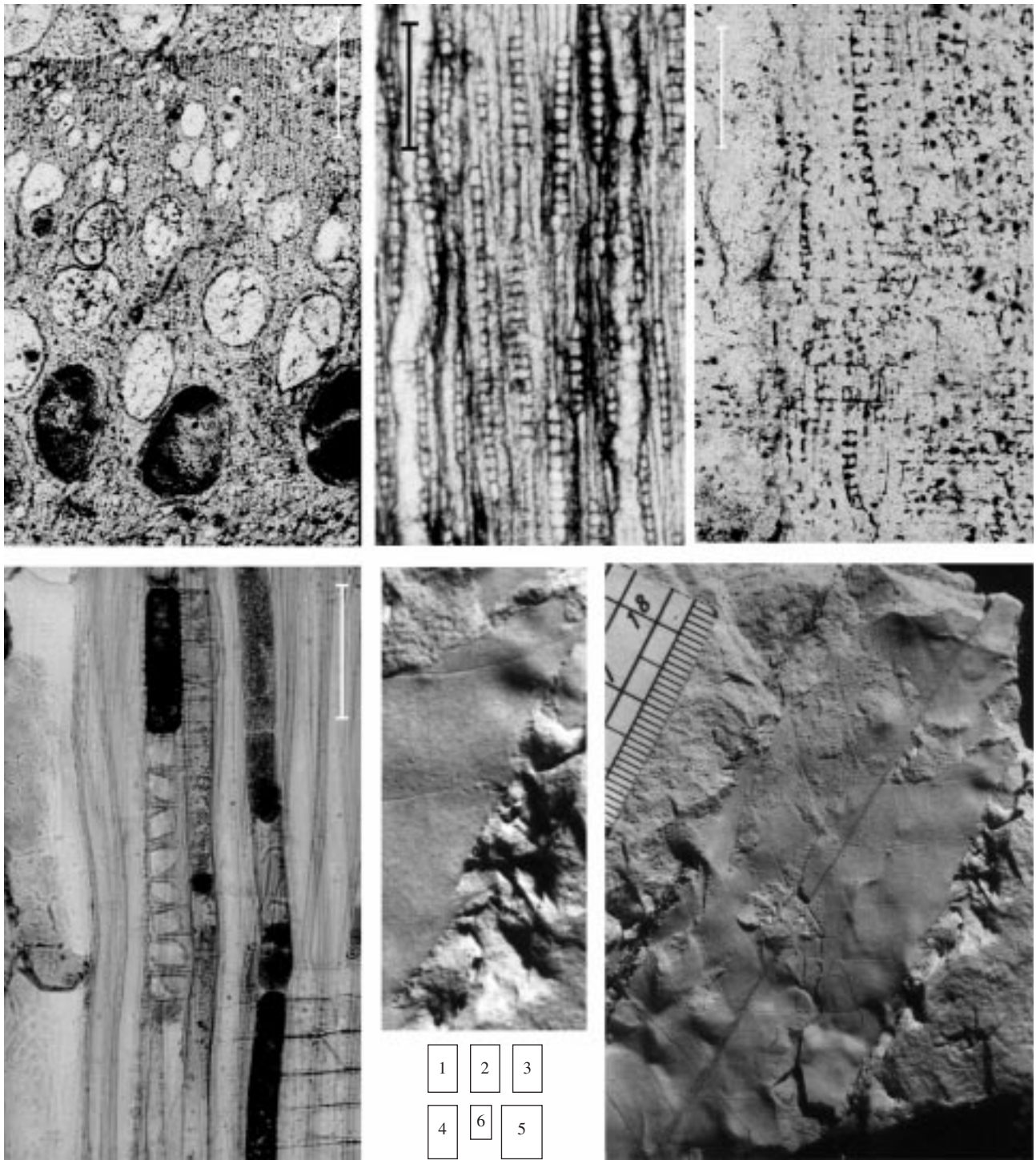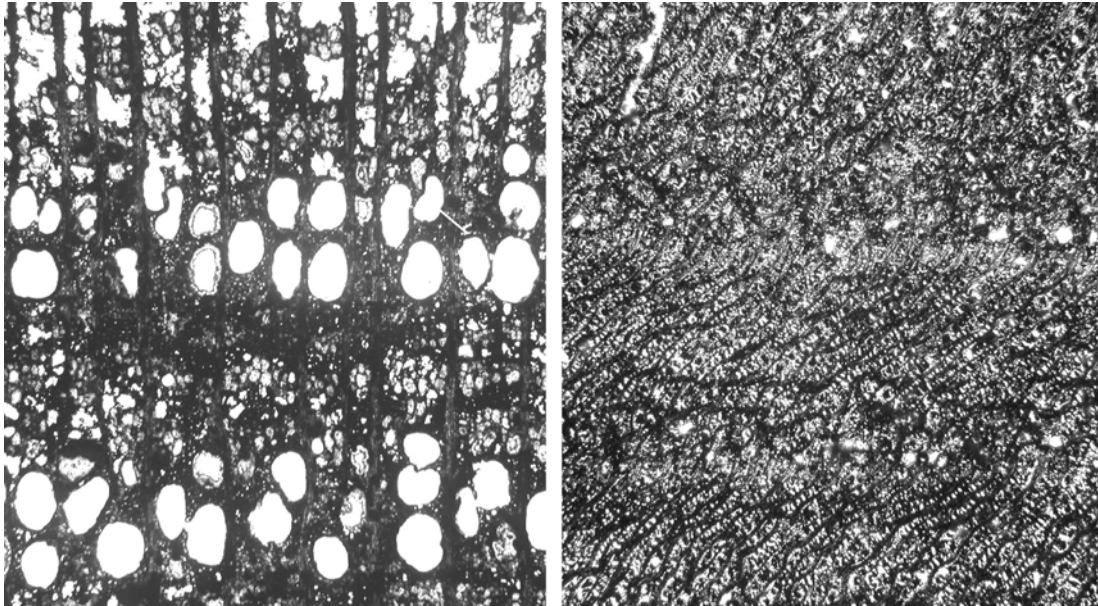
| 1 | 2 | 3 |
| 4 | 6 | 5 |

Plate I

1 – Cross-section of *Castanoxylon bavaricum* (no. VČ 1), scale bar 500 μm.

2 – Tangential section of *Castanoxylon bavaricum* (no. 27/98), scale bar 200 μm.

3 – Radial section of *Castanoxylon bavaricum* with two portions of crystalliferous septate parenchyma (no. 27/98), scale bar 200 μm.

4 – Radial section of modern *Castanea vulgaris* (RBG Kew collection, no. MUS IV., Japan) with a detail of crystalliferous septate parenchyma, scale bar 80 μm.

5 – Leaf of *Castanea atavia* (no. Nn – 158), × 1.

6 – Detail of the same leaf of *Castanea atavia* (no. Nn – 158), × 2.

Photos 5 and 6 by J. Brožek

Doctoral Thesis by Jakub Sakala (2004)
The 'Whole-Plant' concept in palaeobotany with examples from the Tertiary of northwestern Bohemia, Czech Republic
with particular reference to fossil wood

5.2.3. Example 4: *Ulmoxylon* from Bílina

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Text-fig. 4: Two types of preservation of the same wood species of *Ulmoxylon marchesonii* - limonitized (left) and xylitic (right) specimen, both in cross-section.

Example 4: Systematic part – conclusions

A fossil angiosperm wood was described for the first time from Bílina (**Sakala 2002**). It represents a fossil elm wood, attributable at the specific level to *Ulmoxylon marchesonii* Biondi. The fossil wood with prominent ring porous pattern, wavy grouping of late wood pores and early wood pores in 1-3 tangential rows, homocellular rays mostly 4-5 cells wide, and crystalliferous parenchyma can be compared to extant North American soft elms, as well as to *Ulmus macrocarpa* Hance and *U. parvifolia* Jacq. from China and to the European common elm *U. carpinifolia* Gled.

Doctoral Thesis by Jakub Sakala (2004)
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with particular reference to fossil wood

Example 4: General aspects relative to the 'Whole-Plant' concept

Influence of preservation on wood structure

The influence of different types of preservation on fossil wood structure has been demonstrated. The two specimens studied, i.e., permineralized by limonite N° 29/98 and xylitic N° 16/98, are very different from each other at first sight (see Text-fig. 4), especially in cross-section. However, they have been interpreted as a single species of fossil wood after a more detailed analysis (Sakala 2002).

Stem vs. root wood

A similar philosophy has already been applied in the case of two wood specimens from the Eocene of Dangu (France). Even though the specimens were different, they shared some similarities. They were interpreted as two forms (stem vs. root) of the same species (Sakala et al. 1999). Such an approach avoids artificial splitting of taxa and promotes a more natural concept where not every subtle detail is reflected in systematical distinction on the specific or higher levels.

'Mosaic' species

In Bílina, the fossil wood is related to the elm foliage and samaras of *Ulmus pyramidalis* Goeppert (Sakala 2000). This species is characteristic of riparian forests on levées along rivers. The same autecology is, in analogy, supposed for the fossil wood. On the other hand, the botanical affinities of the fossil wood are not exactly the same as those of *U. pyramidalis*. In fact, the fossil elm of Bílina must be considered as a particular extinct species, a kind of 'mosaic' where each part of the plant shows relationship to a different living relative and consequently as a specific fossil elm which is as a whole different from all modern elms. A similar situation, even at the level of family, can be seen in the case of *Doliostrobus* (see Example 1). The extinct conifer *Doliostrobus* presents the affinity with the family of Araucariaceae (Kvaček 2002b), but its branch wood with abietoid pitting of radial tracheid walls and "doliostroboid" cross-field pits does not correspond to the characteristics of this family (Rüffle & Süss 2001).

Paléontologie systématique / Systematic Palaeontology
(Paléobotanique / Palaeobotany)

First record of fossil angiosperm wood (*Ulmoxylon*, Ulmaceae) from the famous locality of Bílina (Czech Republic, Early Miocene)

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Abstract – A fossil angiosperm wood is described for the first time from the famous Early Miocene locality of Bílina. It represents a fossil elm wood, attributed to *Ulmoxylon marchesonii* Biondi. The fossil wood can be compared to extant North American soft elms, also to *Ulmus macrocarpa* Hance and *U. parvifolia* Jacq. from China or to the European common elm *U. carpinifolia* Gled. The wood together with fossil leaves/fruits of *Ulmus pyramidalis* Goeppert forms a single natural fossil species that lived in the Bílina area during the Early Miocene. The influence of two types of preservation, permineralised and xylitic, on the same wood species is also discussed. *To cite this article: J. Sakala, C. R. Palevol 1 (2002) 161–166.* © 2002 Académie des sciences / Éditions scientifiques et médicales Elsevier SAS

Bílina / Czech Republic / Early Miocene / fossil angiosperm wood / type of preservation / *Ulmoxylon marchesonii* / *Ulmus pyramidalis*

Résumé – Première évidence de bois fossile d'angiosperme (*Ulmoxylon*, Ulmaceae) de la célèbre localité de Bílina (République tchèque, Miocène inférieur). Un bois fossile d'angiosperme est décrit pour la première fois dans la célèbre localité de Bílina. Il s'agit d'un orme fossile, attribué à *Ulmoxylon marchesonii* Biondi. Le bois fossile peut être comparé aux ormes tendres (*soft elms*) de l'Amérique du Nord, ainsi qu'à *Ulmus macrocarpa* Hance et *U. parvifolia* Jacq. de Chine ou à l'orme commun d'Europe, *U. carpinifolia* Gled. Le bois forme avec des feuilles et des fruits fossiles, rapportés à *Ulmus pyramidalis* Goeppert, une seule espèce naturelle fossile, qui a vécu à Bílina pendant le Miocène inférieur. L'influence de deux types de préservation, perminéralisé et en xylain, sur la même espèce de bois est aussi discutée. *Pour citer cet article : J. Sakala, C. R. Palevol 1 (2002) 161–166.* © 2002 Académie des sciences / Éditions scientifiques et médicales Elsevier SAS

Bílina / République tchèque / Miocène inférieur / bois fossile d'angiosperme / type de préservation / *Ulmoxylon marchesonii* / *Ulmus pyramidalis*

Version abrégée

1. Introduction

Le gisement de Bílina, situé en Bohême du Nord-Ouest (Fig. 1), est connu depuis Sternberg [22] pour sa richesse en végétaux fossiles. Outre la flore fossile, il recèle une faune diversifiée, y compris des insectes fossiles [12–16].

Contrairement aux autres organes, le bois n'a jamais été étudié à Bílina, à l'exception d'un *Taxodioxylon* [2] d'un gisement voisin. Dans cette note, deux spécimens de bois fossile d'angiosperme, venant de la mine de Bílina, sont décrits.

2. Cadre géologique

Le gisement appartient au bassin de Most. Son âge est attribué au Miocène inférieur. Trois publications font le point sur l'état actuel de la connaissance en géologie, paléobotanique et paléoécologie à Bílina [4, 7, 17].

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3. Partie systématique

Ulmoxylon marchesonii Biondi 1981 (Fig. 2A–H)

Les deux spécimens de bois décrits (limonitisé n° 29/98 et en xylène n° 16/98) sont caractérisés par une zone poreuse, avec des vaisseaux du bois final en bandes tangentielles, des fibres libriformes disposées en désordre, du parenchyme apo- et paratrachéal souvent cristallifère ainsi que des rayons homogènes, larges essentiellement de 4 à 5 cellules.

À première vue, les deux bois sont relativement différents. Néanmoins, ces différences peuvent s'expliquer par les deux types de préservation. Les traits diagnostiques [9, 19] permettent d'identifier les deux bois comme *Ulmus* L. (orme). Après les avoir comparés aux bois fossiles connus [1, 5, 10, 11, 21, 24], ils peuvent être attribués à l'espèce *Ulmoxylon marchesonii* Biondi.

Concernant les affinités avec les bois actuels, on s'est reporté à plusieurs publications comparatives [6, 9, 19, 23, 25, 26] dont deux [25, 26] sur les bois d'Amérique du Nord et de Chine, deux régions importantes pour la paléobotanique du Tertiaire d'Europe [8]. Nos bois peuvent être comparés à *Ulmus americana* L. et *U. rubra* Muhl. [25], à *U. parvifolia* Jacq. et *U. macrocarpa* Hance [26], ou encore à *U. carpinifolia* Gled. [6, 19].

Le bois fossile est sûrement lié à *Ulmus pyramidalis* Goeppert, représenté à Bílina par des feuilles et des samares [3, 17]. Comme cette espèce croît sur les levées le long des rivières [4], nous supposons la même autécologie pour notre bois. Finalement, en tenant compte des affinités du bois fossile avec *Ulmus pyramidalis*, notre bois représente apparemment une espèce éteinte particulière, différente de tous les ormes actuels.

4. Conclusions

C'est la première fois qu'un bois fossile d'angiosperme provenant de la célèbre localité de Bílina est décrit. Il s'agit d'un orme fossile, attribué à *Ulmoxylon marchesonii*. Le bois fossile peut être comparé aux ormes tendres (*soft elms*) de l'Amérique du Nord, ainsi qu'à *Ulmus macrocarpa* Hance et *U. parvifolia* Jacq. de Chine ou à l'orme commun d'Europe, *U. carpinifolia* Gled. Le bois représente, avec les feuilles et les fruits fossiles attribués à *Ulmus pyramidalis* Goeppert, une seule espèce naturelle fossile ayant vécu à Bílina pendant le Miocène inférieur.

Les deux types de préservation, perminéralisé et en xylain, doivent être notés et pris en considération, car ils confèrent aux bois des aspects différents, tout en préservant les caractères essentiels.

Cet article poursuit la publication des résultats obtenus par l'auteur dans le cadre de sa thèse. Outre la description de ce nouveau bois du Miocène inférieur du bassin de Most, un bois fossile de l'Oligocène supérieur, venant des sédiments fluviaux de Bohême du nord, a été publié antérieurement [18]. Le travail a été réalisé dans le cadre du projet international NECLIME.

Note. Entre la soumission et l'acceptation du manuscrit, le même spécimen limonitisé (= No. 29/98) a été décrit comme *Robinioxylon* sp. [20]. Bien qu'il montre une section transversale, typique de l'orme et qu'il ne comporte pas de parenchyme étagé, il a été par erreur rapproché de *Robinia* (faux acacia). Ce genre est complètement inconnu dans la localité [7], tandis que les feuilles et les fruits d'*Ulmus* y sont assez fréquents [17].

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1. Introduction

The locality of Bílina (Bílina Mine), from which the described fossil wood has been recorded, is situated in the Most Basin, in northwestern Bohemia (50°34′N, 13°45′E), in the Czech Republic (see Fig. 1). It represents since Sternberg's times [22] a classical area of palaeobotanical interest. The fossil flora is accompanied there by a rich fauna as fossil insects [12–16], molluscs, fish, amphibians, reptiles, birds, and mammals.

Contrary to other detached plant organs, fossil wood from Bílina has not been studied so far. There is only one paper by Březinová [2] about a silicified piece of *Taxodioxylon* coming from another locality of the Most Basin. The present paper describes for the first time a fossil angiosperm wood (*Ulmoxylon marchesonii* Biondi) from the famous locality of Bílina.

2. Geological setting

The locality as a whole belongs to the Early Miocene fill of the Most Basin. Three overviews of the present state of knowledge of geology, palaeobotany and palaeoecology of Bílina have recently been published [4, 7, 17].

3. Systematic part

Class Magnoliopsida
Family Ulmaceae
Genus *Ulmoxylon* Kaiser
Species *Ulmoxylon marchesonii* Biondi 1981 (Fig. 2)
1981 *Ulmoxylon marchesonii* Biondi; [1, p. 89, figs. 1–4, plates 1–3].

3.1. Material

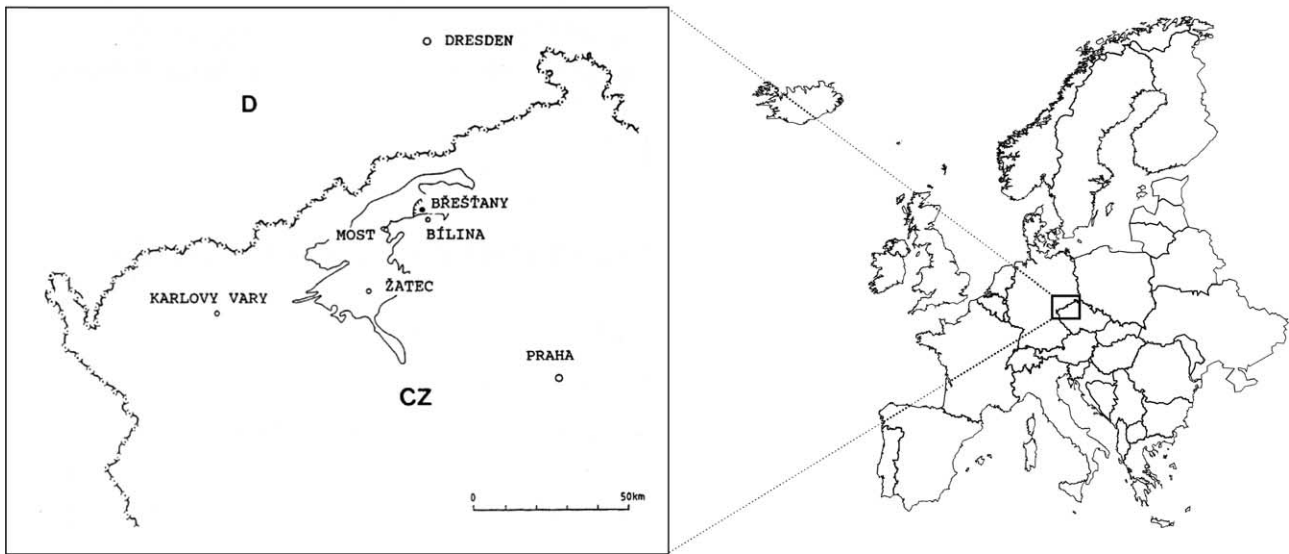Two wood specimens, limonitised (No. 29/98) and xylitic (No. 16/98).

Figure 1. Geographical position of the Bílina Mine in Europe (**CZ**: Czech Republic, **D**: Germany; the uninterrupted line indicates the boundary of the Most Basin), according to Prokop and Nel [15].

Figure 1. Position géographique de la mine de Bílina en Europe, (**CZ** : République tchèque, **D** : Allemagne, la ligne continue indique les limites du bassin de Most ; d'après Prokop et Nel [15].

3.2. Description

3.2.1. Macroscopic

The specimen No. 29/98 is a beige to orange small piece of a dislocated limonitised trunk about 50 × 20 cm in size. The specimen No. 16/98 comes from a horizontally deposited xylitic trunk, 30 cm wide.

3.2.2. Microscopic

Growth rings: well pronounced, 0.5–2 mm wide.
Wood pattern: ring porous.
Vessels: round to oval in cross-section; (a) in the earlywood arranged in one to three tangential rows, mostly solitary, sometimes in tangential or radial groups of two, tangential diameter 65–295 μm (mean 185 μm), radial diameter 80–320 μm; (b) in the late wood rarely solitary, mainly grouped, forming wavy tangential bands, tangential and radial diameter 25–165 μm; vessel walls 5–7 μm thick; spiral thickening present; short vessel elements limited by slightly inclined simple perforation plates; intervascular pits bordered, circular, alternate, quite dense, about 10 μm in diameter.
Axial parenchyma: abundant, apotracheal, diffuse and paratracheal between small latewood vessels; parenchyma cell dimensions (tangential and radial diameter × height): 20–30 × 40–80 μm; crystalliferous septate parenchyma present, abundant; crystal cells enlarged, in radial section 20–40 μm wide, 25–45 μm high.
Rays: exclusively homogeneous, composed of procumbent cells; 1–6 (12–85 μm) cells wide, rarely uni-, mostly 4–5 seriate; high from 4 up to 60 and more cells (55–830 μm); about 6 rays per tangential horizontal mm; ray cell dimensions (tangential height × tangential width × radial length): 8–23 μm × 8–20 μm × 20–70 μm.
Fibres: libriform, polygonal in cross-section, irregularly densely arranged; tangential and radial diameter 10–20 μm; fibre walls 3–5 μm thick; tracheids not observed.

3.3. Discussion

At first sight, the two woods described herein present two different structures. However, with regard to their different states of preservation, this need not be a reason to treat them as two distinct morphospecies.

The first one (No. 29/98) shows typical permineralised preservation by limonite. Its main features are: ring porous pattern, late wood pores in wavy tangential bands, and homogeneous, mostly 4–5 cells wide rays.

In contrast, the second wood (No. 16/98) is preserved as xylite. Its cross-section, not very well preserved, shows a rather diffuse porous pattern, different from the first wood. But a closer look at the cross-section allows to recognise tangential bands composed of small grouped vertical elements and sometimes large solitary, vessel-like, folded or crashed apertures arranged in tangential rows. These two different structures could be interpreted as tangential bands of latewood pores (grouped elements) and earlywood large vessels (folded apertures) in a ring
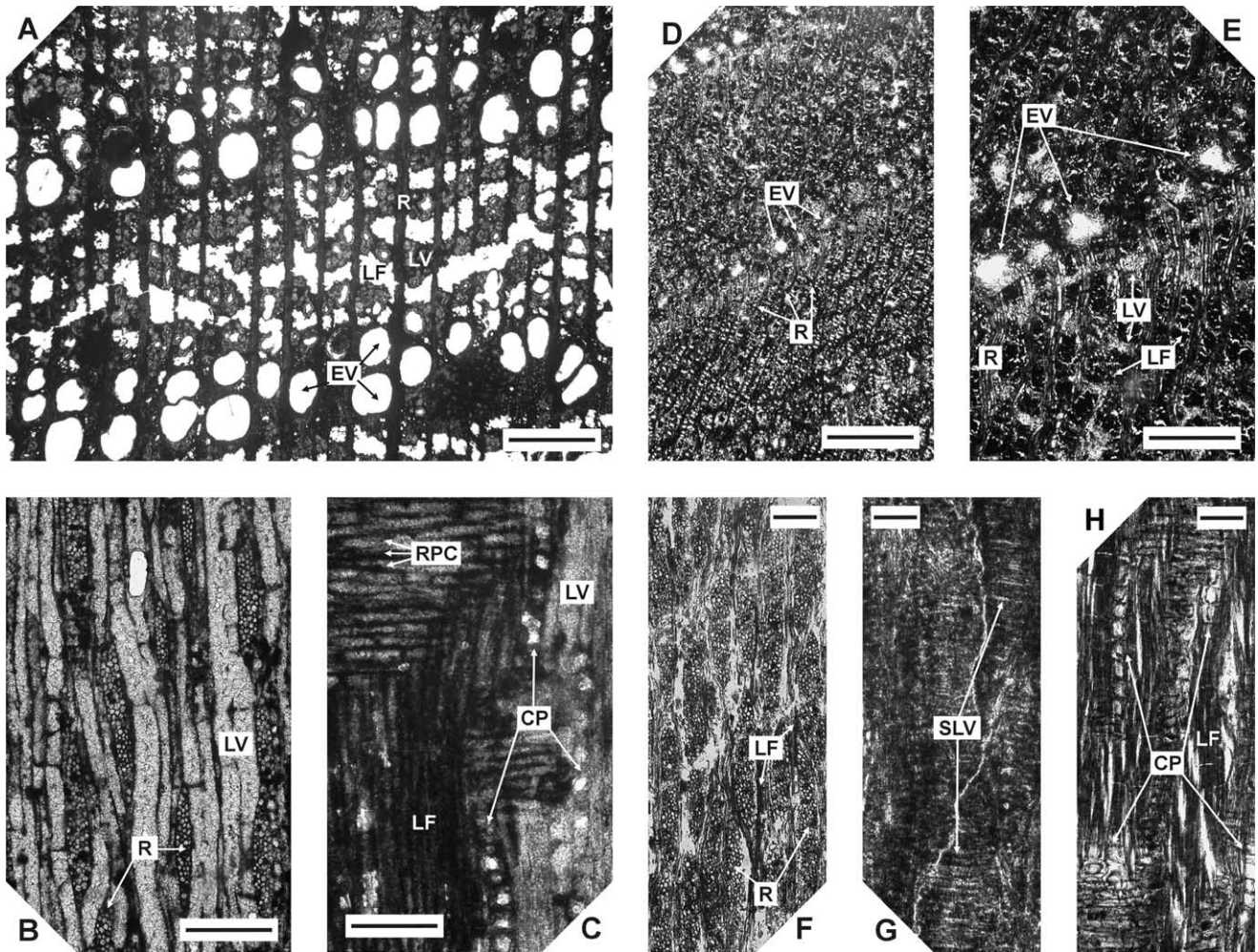
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Figure 2. A–C: *Ulmoxylon marchesonii*; limonitised specimen (No. 29/98). **A.** Cross-section. **EV**, Earlywood vessels; **LV**, latewood vessels in tangential waves; **LF**, libriform fibres (often missing – seen as empty space); **R**, rays. Scale bar = 500 µm. **B.** Tangential section. **R**, rays; **LV**, latewood vessels. Scale bar = 200 µm. **C.** Radial section. **RPC**, procumbent ray cells; **LV**, latewood vessels; **LF**, libriform fibres; **CP**, crystalliferous parenchyma. Scale bar = 100 µm. **D–H** *Ulmoxylon marchesonii*; xylitic specimen (No. 16/98). **D.** Cross-section. **EV**, earlywood vessels; **R**, rays. Scale bar = 500 µm. **E.** Cross-section; detail. **EV**, earlywood vessels; **LV**, latewood vessels; **LF**, libriform fibres; **R**, rays. Scale bar = 200 µm. **F.** Tangential section. **LF**, libriform fibres; **R**, rays. Scale bar = 100 µm. **G.** Tangential section. **SLV**, spirals in latewood vessels. Scale bar = 50 µm. **H.** Radial section. **LF**, libriform fibres; **CP**, crystalliferous parenchyma. Scale bar = 50 µm.

Figure 2. A–C. *Ulmoxylon marchesonii* ; spécimen limonitisé (No. 29/98). **A.** Section transversale. **EV**, vaisseaux du bois initial ; **LV**, vaisseaux du bois final en bandes tangentielles ; **LF**, fibres libriformes (souvent absentes – vues comme espace vide) ; **R**, rayons. Échelle = 500 µm. **B.** Section tangentielle. **R**, rayons ; **LV**, vaisseaux du bois final. Échelle = 200 µm. **C.** Section radiale. **RPC**, cellules couchées de rayons ; **LV**, vaisseaux du bois final ; **LF**, fibres libriformes ; **CP**, parenchyme cristallifère. Échelle = 100 µm. **D–H** *Ulmoxylon marchesonii* ; spécimen en xylain (No. 16/98). **D.** Section transversale. **EV**, vaisseaux du bois initial ; **R**, rayons. Échelle = 500 µm. **E.** Détail de la section transversale. **EV**, vaisseaux du bois initial ; **LV**, vaisseaux du bois final ; **LF**, fibres libriformes ; **R**, rayons. Échelle = 200 µm. **F.** Section tangentielle. **LF**, fibres libriformes ; **R**, rayons. Échelle = 100 µm. **G.** Section tangentielle. **SLV**, spirales dans les vaisseaux du bois final. Échelle = 50 µm. **H.** Section radiale. **LF**, fibres libriformes ; **CP**, parenchyme cristallifère. Échelle = 50 µm.

porous wood. In spite of unsuitable preservation of the cross-section, this wood (No. 16/98) shows several significant features in longitudinal sections: conspicuous spirals in vessels, septate crystalliferous parenchyma and two to six cells wide homogenous rays.

Hence, both woods can be reasonably attributed to the same species, the description of which combines all features observed. Some of them are visible mainly in the specimen No. 29/98, e.g., wood pattern in cross-section, some in the other one No. 16/98, e.g., spirals in vessels and finally some in both of them, e.g., rays, crystalliferous parenchyma, vessel pitting. Because the characteristics are very typical of *Ulmus* L. [9, 19], we regard it as a fossil elm wood. A published comparative overview [11] and C. Privé-Gill's personal database of the fossil wood record were used to help its determination.

Five species show a rather similar wood pattern: *Ulmus crystallophora* Watari from the Miocene of Japan [24], *Ulmus baileyana* Prakash and Barghoorn from the Miocene of USA [10], *Ulmoxylon kersonianum* Starostin and Trelea from the Miocene of Moldavia [21], *Ulmoxylon* cf. *Ulmus carpinifolia* Gled. from the Mio-Pliocene of Hungary [5], and *Ulmoxylon marchesonii* Biondi from the Miocene(?) of Italy [1]. All these species have prominent ring porous pattern with wavy late wood pores and earlywood pores in multiseriate rows, homogeneous rays up to 6–(8) cells wide, and crystalliferous parenchyma, which is not described in one single species [21]. However, they can be distinguished from our fossil wood: *Ulmus crystallophora* differs by its 'striking abundance' of chambered (crystalliferous) parenchyma and 2–4 rows of earlywood pores, *Ulmus baileyana* by its 3–4 rows of earlywood pores, and *Ulmoxylon* cf. *Ulmus carpinifolia* by its large annual rings with relatively small earlywood pores ranges in 2–4 rows. The description of *Ulmoxylon kersonianum*, as stated above, does not include the crystalliferous parenchyma. Moreover, the species has bigger vessels arranged in the earlywood in 2–3 rows. The last species, *Ulmoxylon marchesonii*, is the most similar to our fossil, yet not completely identical. Nevertheless, we propose to attribute our fossil to this species.

Concerning its affinities with the modern *Ulmus* wood, several comparative works have been published: general ones [9, 23], those dealing with European species [6, 19], but above all recent ones dealing with North American and Chinese species [25, 26]. These two regions are generally very important for the Tertiary palaeobotany of Europe [8]. With regard to these publications, the fossil can be compared either to the North American soft elms, allied to *Ulmus americana* L. with one row of earlywood pores and *U. rubra* Muhl. with 2–5 rows of earlywood pores [25], or to *U. parvifolia* Jacq. and *U. macrocarpa* Hance among the Chinese elms of the ring porous Group I [26]. In regard to European elms, the fossil is most similar to the common elm *U. carpinifolia* Gled. [6, 19].

The fossil wood is certainly related to the elm foliage and samaras occurring at Bílina, which both belong to *Ulmus pyramidalis* Goeppert [3, 17]. In the Most Basin, this species is characteristic of riparian forests on levees along the rivers [4]. The same autecology is in analogy supposed for the fossil wood. *U. pyramidalis* is compared to the modern *U. americana* L. or to *U. alata* Michx. [3, 17]. The fossil wood can support the comparison with *U. americana*. However, *U. alata*, as a member of the North American hard elms [25], presents a quite different wood pattern. In this case, the wood serves to correct the affinities of *U. pyramidalis*. In fact, having respect to the affinities of the fossil wood as well as to those of *U. pyramidalis*, the fossil elm of Bílina must be considered as a particular extinct species, different from all modern elms.

4. Conclusions

For the first time, a fossil angiosperm wood is described from the famous Early Miocene locality of Bílina. It represents a fossil elm wood, attributable at the specific level to *Ulmoxylon marchesonii* Biondi. The fossil wood can be compared to extant North American soft elms, also to *Ulmus macrocarpa* Hance and *U. parvifolia* Jacq. from China or to the European common elm *U. carpinifolia* Gled. The wood together with fossil leaves and fruits of *Ulmus pyramidalis* Goeppert form a single natural fossil species, living in the Bílina area during the Early Miocene.

Generally, we encountered here two types of preservation of the same wood species: permineralised and xylitic. Their influence on fossil wood structure must be noticed and taken into consideration.

This article is a continuation of the published results of the author's doctoral thesis. In addition to the wood from the Early Miocene fill of the Most Basin characterised herein, a fossil angiosperm wood from the Late Oligocene fluvial sediments was described [18]. The present work is a part of the international NECLIME project.

Note. In the time between the submission and the acceptance of the paper, the same limonitised specimen (= No. 29/98) was identified as *Robinioxylon* sp. [20]. Although the wood has the cross-section pattern typical of elm and does not contain any storied parenchyma, the fossil specimen was compared erroneously to the wood of modern *Robinia* (locust). This genus is completely unknown from the locality [7], while leaves and fruits of *Ulmus* are quite common [17].

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Doctoral Thesis by Jakub Sakala (2004)
The 'Whole-Plant' concept in palaeobotany with examples from the Tertiary of northwestern Bohemia, Czech Republic
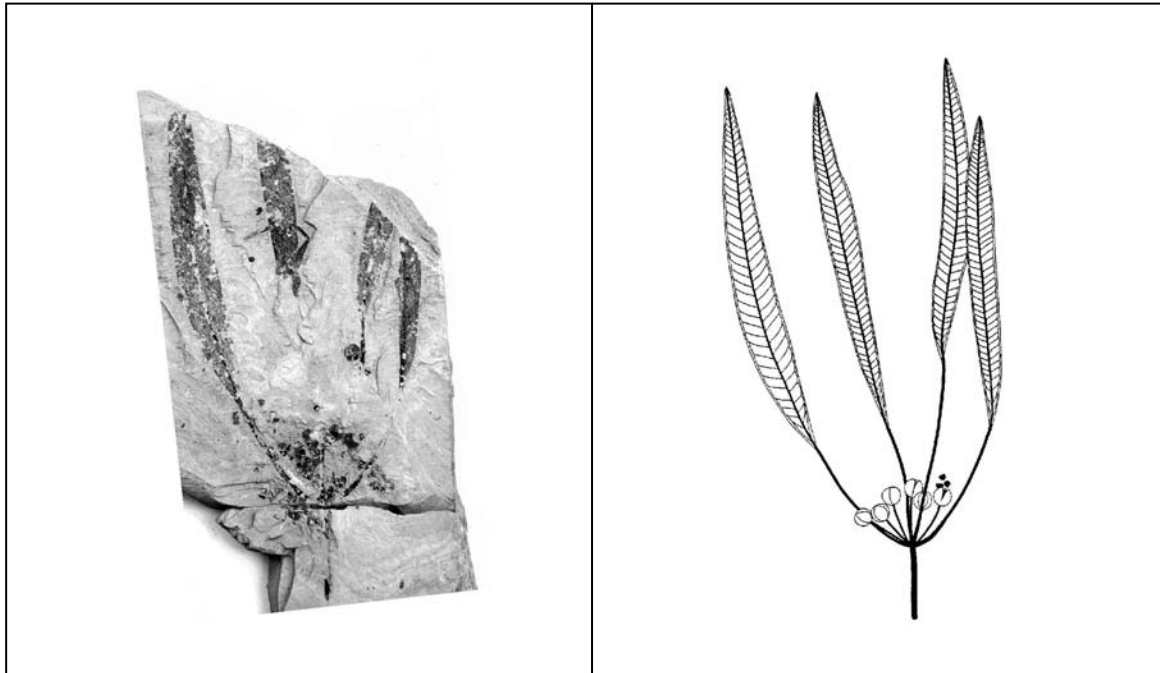*with particular reference to fossil wood*

5.3. Reproductive structures

Reproductive structures are of great importance in the 'Whole-Plant' concept. The leaves or other vegetative organs as wood can be sometimes very similar in systematically unrelated taxa, but the reproductive structures, the most important for taxonomy, should differentiate them. Generally, the reproductive structures represent the ultimate and the most important argument for the systematical attribution.

The last example concerning *Decodon*, single for this part, shows a very rare occasion in fossil plant record where several organs are found in direct organic connection. It was possible, thanks to reproductive structures attached, to find out the true botanical affinity of leaves, which were recorded only isolated till the discovery of this specimen. Unfortunately, these cases where organs are found fragmented and detached prevail in palaeobotany...

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with particular reference to fossil wood

5.3.1. Example 5: *Decodon* from Bílina

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Text-fig. 5: Fertile leafy twig of *Decodon gibbosus* (left) and its reconstruction (right).

Example 5: Systematic part – conclusions

A twig fragment with attached verticillate leaves and capsules with intact seeds was recovered from the roof of the main lignite seam in the Bílina Mine (**Kvaček & Sakala 1999**). The seeds correspond to those known in dispersed condition as *Decodon gibbosus* (E. M. Reid) E. M. Reid in Nikitin, whereas, the foliage matches that which had been called *Ficus multinervis* Heer, and sometimes *Apocynophyllum helveticum* Heer. The whole fossil plant was designated *Decodon gibbosus* (E. M. Reid) E. M. Reid in Nikitin emend. Z. Kvaček et Sakala. This species differs from the only extant species *D. verticillatus* (L.) Ell. from eastern North America by a narrower triangular shape of seeds in transverse section and the thicker spongy layer of the testa on the dorsal side (Sakala in Kvaček & Sakala 1999), the leaves are also slightly different. The associated fossil plant assemblage suggested aquatic to swampy environment, typical of the extant relative as well.

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*The 'Whole-Plant' concept in palaeobotany with examples from the Tertiary of northwestern Bohemia, Czech Republic
with particular reference to fossil wood*

Example 5: General aspects relative to the 'Whole-Plant' concept

Priority principle vs. stability of nomenclature

Isolated leaves with typical intramarginal venation have long been known from the Eurasian Tertiary, but without clarified botanical affinities and knowledge about the corresponding reproductive structures. The foliage similar to our specimen was well defined both macro- and microscopically (Kvaček in Kvaček & Sakala 1999), and the whole plant was assigned to *Decodon gibbosus*. This taxon is based on the seed morphology and reflects diagnostic traits that warrant the natural content. The taxa based on foliage (e.g., *Ficus multinervis*) were published much earlier, but their cuticular structure is not known and they do not reflect safely generic and even specific differences. Hence, they were left as purely artificial units.

Modern endemism of Tertiary Holarctic elements

Decodon J. F. Gmelin is endemic today to Atlantic North America, but in the Tertiary this genus represented an important Holarctic element, recorded mostly as seeds in Pacific North America, Europe, Siberia and Japan (e.g., Matsumoto et al. 1997, Little & Stockey 2003). Generally, the endemism of living plants which had Holarctic distribution in Tertiary is frequent. In the same horizon as *Decodon*, fruits of *Craigia* W. W. Smith et W. E. Evans and associated leaves of *Dombeyopsis* Ung. have been found. The genus *Craigia*, now endemic to southern China and Vietnam, was widespread in the Northern Hemisphere during the Tertiary (Hably et al. 2000, Kvaček et al. 2002).

Ideal state of the 'Whole-Plant' palaeobotany

The discovery of the fertile leafy twig was unexpected. At the beginning only upper parts of the leaves were visible, but after a 'fortunate preparation' (= the specimen fell on the floor:) fruits including seeds of *D. gibbosus* appeared in the lower part attached to the twig together with the leaves (see Text-fig. 5). The unique preservation, as in our case, is rare. Contrary to other combinations of organs described in this work, i.e., indirect association within one locality (*Tetraclinoxylon* and *Ulmoxylon*) or combination of organs between two neighbouring localities (*Castanoxylon*), this last example of *Decodon* with different organs found in direct connection does not leave any doubt about the accuracy of the combination. In fact, this case represents an ideal state in palaeobotany - the top of the 'Whole-Plant' concept.

Twig with attached leaves, fruits and seeds of *Decodon* (Lythraceae) from the Lower Miocene of northern Bohemia, and implications for the identification of detached leaves and seeds

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Abstract

A twig fragment with attached verticillate leaves and capsules with intact seeds was recovered from the Lower Miocene lignitic clay in the Bílina strip mine (northern Bohemia). The seeds correspond to those known in dispersed condition as *Decodon gibbosus* (E.M. Reid) E.M. Reid in Nikitin, while the foliage matches that which has been called *Ficus multinervis* Heer, and sometimes *Apocynophyllum helveticum* Heer. While the determination of the seeds is safe, the identity of the isolated foliage may be less secure. Therefore the name *Decodon gibbosus* is given preference to designate the whole plant. This fossil species differs from the only extant species *D. verticillatus* (L.) Ell. of eastern North America by narrower triangular shape of seeds in transverse section, the thicker spongy layer of the testa on the dorsal side, and by long petiolate leaves that are more variable in shape (from narrow linear-lanceolate to broadly lanceolate) with more densely spaced secondaries and intersecondaries. The leaf cuticular structure matches that of the glabrous form of *D. verticillatus*. The associated plant assemblage suggests aquatic to swampy environment typical of the extant relative. © 1999 Elsevier Science B.V. All rights reserved.

Keywords: Decodon; Miocene; leaves; fruits; seeds; palaeoecology

1. Introduction

Lanceolate, entire leaves with pronounced intramarginal veins have been long known from the Eurasian Tertiary, but their familial and generic affinities have been subject of many different opinions. Examples include: Moraceae — *Ficus*; Apocyna ceae/Asclepiadaceae — *Apocynophyllum*, *Nerium*, *Periploca*; and Myrtaceae — *Myrtophyllum*. Due in part to lack of knowledge about the cor-

responding reproductive structures, the taxonomic affinities of many of these leaves have remained in question. New material from the Lower Miocene of Bílina, northern Bohemia, proves that at least some of these leaves belong to the extant genus *Decodon* of the Lythraceae. A rare twig with mutually attached leaves and fruits including seeds, which is reported herein, unites this type of foliage with the extinct *Decodon gibbosus*, a common Tertiary species based on seeds. In connection with the study of the material from northern Bohemia we offer a brief review of other fossil foliage with similar morphology and

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compare some extant taxa showing convergent venation with the aid of leaf anatomy.

2. Material and methods

The rich site of Miocene plants in the Bílina strip mine (Most Basin, northern Bohemia, Czech Republic) has been the subject of several systematic studies in recent years. (Papers summarising geology, palaeobotany and palaeoecology of this site are referenced in Kvaček, 1998). The lignitic clay immediately overlying the main lignite seam contains a parautochthonous assemblage of plants representing swamp forest and marsh vegetation (Sakala, 1997). Besides plant remains, also fishes and other vertebrate fauna, and insects have been found in the same level (Prokop, 1997, 1998). The site is dated indirectly by the fauna of Ahníkov — Merkur North Mine (Fejfar, 1989) — to the mammal zone MN 3, i.e. Early Miocene.

The first author has participated in this paper by the study of the foliage, palaeoecology and nomenclature; the second author investigated fruits and seeds. The specimens described herewith are kept partly in the collections of the National Museum, Prague, and partly in the Bílina Mine headquarters. Specimens are cited by the National Museum catalogue numbers (prefixed by NM) and by the Bílina Mine collection numbering (prefixed MG). Most of the plant fossils studied are from the dark lignitic clay above the coal seam (layer No. 30 in the local stratigraphy of the Bílina Mine). They are preserved as carbonized compressions. The leaves bear thick but finely cracked coalified substance with preserved cuticles. The seeds appear in fracture surfaces with poorly preserved anatomical details. Several complete seeds have been isolated from the matrix and cleaned in hydrofluoric acid. The single foliage twig with attached fruits was collected in the same level as several detached fruits, and many detached leaves. Additional leaf impressions without cuticles but showing details of venation have been collected in the layers nos. 2, 11 and elsewhere in the same outcrop.

For preparation of cuticles, small pieces were cleaned in hydrofluoric acid, washed in water, and macerated using a short treatment in the Schulze solution, followed by rinsing in weak potassium hydroxide, water and embedding in glycerine directly on the microscope slide. Comparative extant cuticles were prepared by a similar procedure or by longer maceration in 30% hydrogen superoxide.

Fossil seed material for comparison has been studied from the Upper Miocene of Moravia (coll. National Museum, Prague), the foliage of related taxa from the Lower Oligocene of Saxony (coll. Staatliches Museum für Mineralogie und Geologie, Dresden, Charles University, Prague) and Lower–Middle Miocene of Oberpfalz (Bayerische Staatssammlung für Paläontologie und historische Geologie, München, Charles University, Prague). Besides fresh material of the Lythraceae from our own field collections, the herbarium specimens have been made available from herbaria of the Muséum National d'Histoire Naturelle, Paris (P), National Museum, Průhonice (PR) and Charles University, Prague (PRC).

3. Emended characteristics of *Decodon gibbosus* (E.M. Reid) E.M. Reid in Nikitin

Order MYRTALES
Family LYTHRACEAE

Genus *Decodon* J.F. Gmelin

Decodon gibbosus (E.M. Reid) E.M. Reid in Nikitin (Plate I; Plate II; Plate III, 1–5; Plate IV, 1–6; Figs. 1–3)

Synonymy:

?1856 *Ficus multinervis* Heer, p. 63, pl. 81, figs. 6–10; pl. 82, fig. 1.

?1859 *Apocynophyllum helveticum* Heer, p. 91, pl. 154, figs. 2– 3.

1869 *Sapindus bilinicus* Ettingshausen, p. 24, pro parte, pl. 47, fig. 7 (non figs. 4–6).

1920 *Diclidocarya gibbosa* E.M. Reid, p. 82, pl. 4, figs. 23, 25, text-fig. 1 left.

1929 *Decodon gibbosus* (E.M. Reid) E.M. Reid; Nikitin, p. 37, pl. 589, figs. 8–9.

Misapplied names (selected):

1866 *Ficus multinervis* auct. (non Heer); Ettingshausen, p. 68, pl. 20, figs. 5–6.
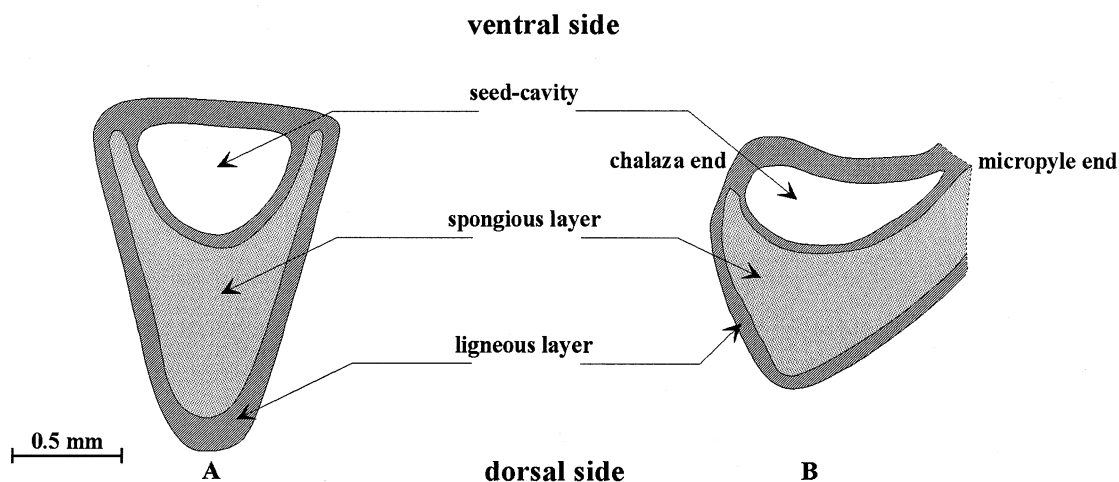
ventral side

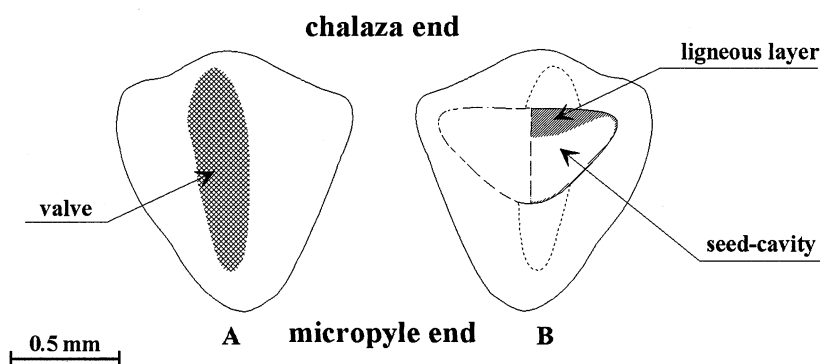Fig. 1. Sections of seeds. (A) Transverse section. (B) Longitudinal section. See Plate I, 7 and 8 right.


Fig. 2. Atypical isolated seed shown in Plate II, 2 and 4. (A) External view on the ventral side. (B) Partly exposed inner part just below the valve.

1891 *Salix angusta* auct. (non A. Braun); Engelhardt, p. 164, pl. 10, fig. 16.

1891 *Dryandroides laevigata* auct. (non Heer); Engelhardt, p. 168, pl. 8, figs. 11–14; pl. 9, figs. 2–4, 14.

1891 *Chrysophyllum palaeocainito* auct. (non Ettingshausen); Engelhardt, p. 173, pl. 9, fig. 16.

1891 *Sapindus bilinicus* auct. (non Ettingshausen); Engelhardt, p. 183, pro parte, pl. 12, figs. 1, 3, 6–9.

1891 *Dodonea salicites* auct. (non Ettingshausen); Engelhardt, p. 185, pl. 9, fig. 7.

1961 cf. *Apocynophyllum helveticum* auct. (non Heer); Hurník, p. 423, pl. 3.

1971 '*Ficus*' *multinervis* auct. (non Heer, 1856); Bůžek, p. 94, pl. 48, figs. 5–8.

1992 '*Ficus*' *multinervis* auct. (non Heer); Bůžek et al., p. 127, fig. 4.2.

1992 Lythraceae; Bůžek et al., p. 130.

1998 *Decodon*; Kvaček, p. 115.

Emended diagnosis: Reproductive branches with verticillate simple leaves and axillary pedicellate capsules. Leaves entire, linear to broadly lanceolate, width : length index 1 : 8 to 1 : 4 (–1 : 3.2), at bases cuneate to long cuneate, long petiolate, amphistomatic, glabrous, venation brochidodromous, with a distinct intramarginal vein, cuticles finely striate, stomata anomocytic, solitary adaxially, common abaxially.
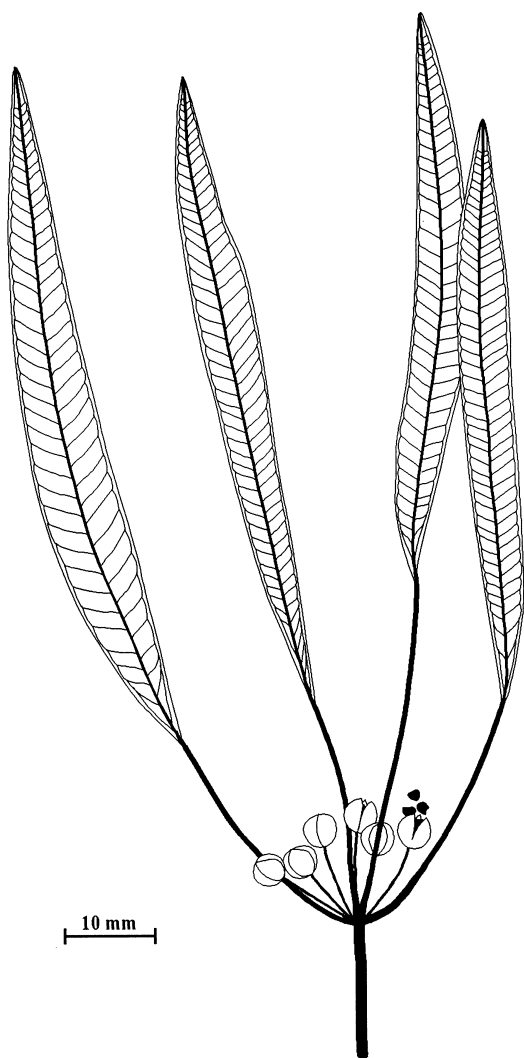
PLATE I
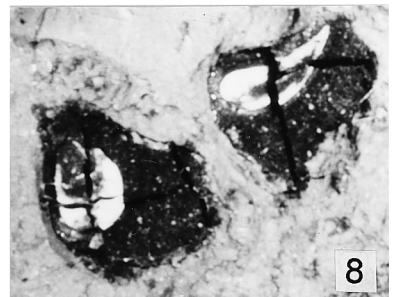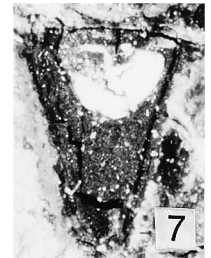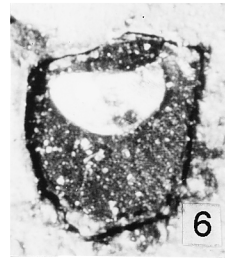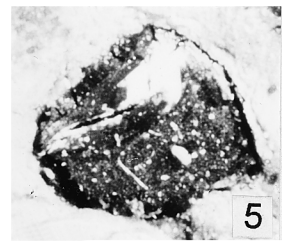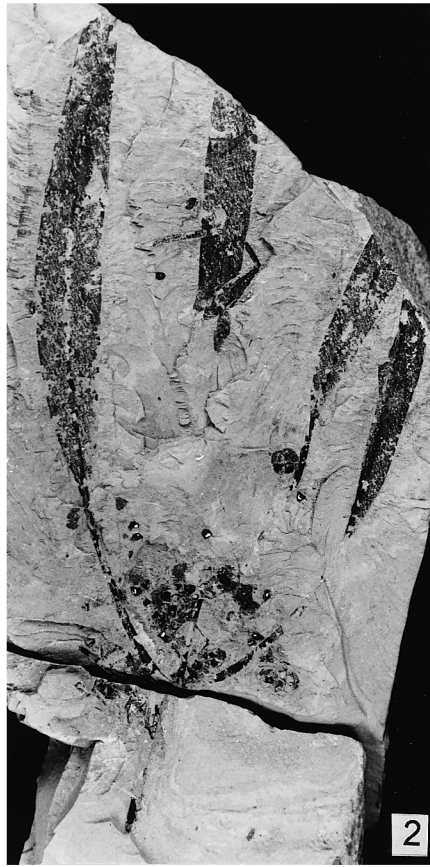
Fig. 3. Hypothetical picture of the fertile leafy twig of *Decodon gibbosus* reconstructed from the specimens nos. NM G 7682a, b (negative and positive part).

Fruits globular, containing seeds irregularly pyramidal in form, with ventral side triangular, flat or slightly concave, partly covered by germination valve; dorsal side convexly rounded to keel-like. Dorsal seed wall much thicker than in other species of *Decodon*.

Description: Specimen No. NM G 7682a, b (Plate I; Plate II, 1–5, Plate IV, 1–3; Figs. 1–3) from horizon 30. A fragmentary twig with four incomplete leaves in a whorl. Petioles up to 30 mm long. Laminae linear-lanceolate, 6–9 mm wide and more than 80 mm long, entire, base long cuneate, slightly asymmetric and decurrent, apex missing. Venation brochidodrome, midvein prominent, secondaries alternate, under 50–85°, straight or slightly curved often near the midvein concave, dense, joined into an intramarginal vein (Plate I, 3), secondaries interconnected by tertiary veins, which form a large quadrangular to polygonal network. Higher-order venation indistinct. Leaves hairless, amphistomatic. Adaxial cuticle very thin, finely striate, more distinctly on the midvein and adjacent areas, showing polygonal straight-walled cells (ca. 25–45 µm across), solitary anomocytic stomata near the midvein, exceptionally near the margin; abaxial cuticle also thin, distinctly striate, ordinary cells polygonal (ca. 25–35 µm across), with anticlinal walls straight to slightly sinuous, stomata anomocytic, narrow elliptic, 20–30 µm long and 10–17 µm wide, with spindle-like outer aperture bordered with slightly thickened ledges (Plate IV, 1–3).
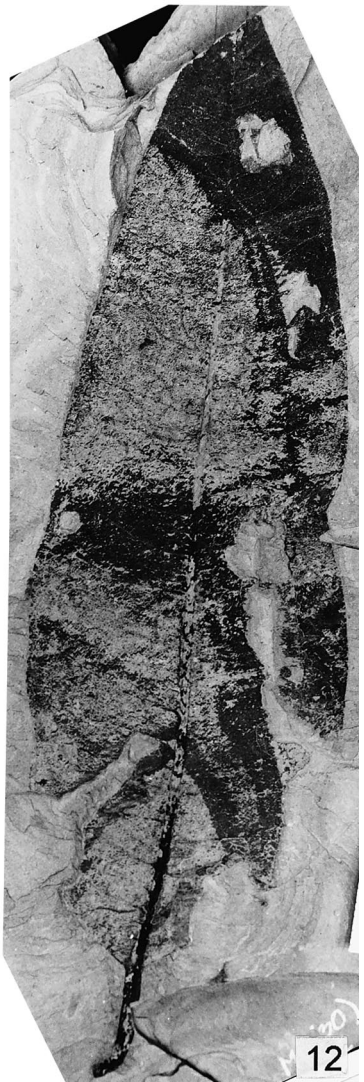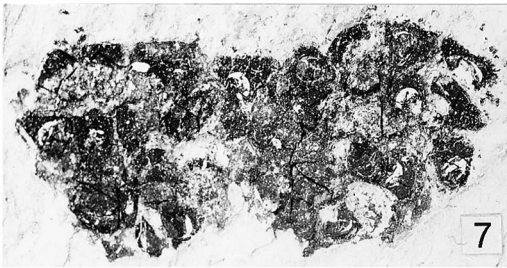
The attached fruits, interpreted as dehiscent capsules, occur in the leaf axils. They are globular, approximately 4 mm across, on pedicels that are enlarged at the point of attachment, 6–9 mm long, The capsules are fragmentary preserved, but contain at least 10 seeds, partly dispersed around (Plate I, 4–8;

PLATE II
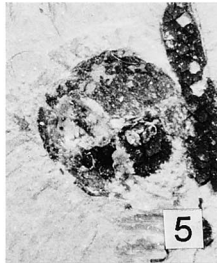
Figs. 1 and 2). The seeds are pyramidal–roundish, up to 2 mm in length, mostly fractured in sections that range from obliquely longitudinal to obliquely transverse. Longitudinal sections show the seed cavity, often in white colour, pyriform with longer axis parallel with the length of the seed situated near one side (ventral margin). The seed wall is thinner on the ventral side and much thicker, keel-like, built of shagreen-dull lustre coal matter (spongy layer) on the dorsal side; both the seed cavity and the spongy layer are coated by black lustre tissue (sclerenchyma) (Fig. 1B). Transverse sections are long triangular showing the seed cavity on the top (ventral side) and the keel-like thickened dorsal side towards the base with dull lustre spongy layer, again both structures coated by black lustre tissue (sclerenchyma) (Fig. 1A).

Specimens nos. NM G 7682, G 7683 a, b (two fruits together), G 7684 (Plate II, 5–7), MG (30) 409 from horizon 30. Detached, rarely stalked capsules rounded to broadly oval 4–8 mm across, packed with 8–15 visible seeds of the same form as those described above.

Specimens nos. NM G 7685-90 (Plate II, 8–12; Plate III, 3–5), MG (30) 283, 348, 379 from horizon 30. Detached leaves linear-lanceolate, 7–18 mm wide and 70–80 mm long to broadly lanceolate, 17–45 mm wide and 60–150 mm long (width : length index 1 : 3.2 to 1 : 8), entire, base cuneate to long cuneate, slightly asymmetric and slightly decurrent, apex long acute; petioles up to 18 mm long. Venation brochidodrome, midvein prominent, secondaries dense, under 50–85°, in wider forms more uniform (70–80°), straight or slightly curved often concave near the midvein, joined into an intramarginal vein, partly giving off an abmedial branch which terminates also into the intramarginal vein, rarely two

secondaries fusing before reaching the intramarginal vein, in wider leaves prominent intersecondaries slightly sinuous, ending in about half of their course to the leaf margin, sometimes continuing up to the intramarginal vein, intramarginal vein gives off thinner side veinlets forming small loops or entering the margin. Secondaries (and intersecondaries) interconnected by perpendicular to slightly oblique tertiary veins, which form large quadrangular to polygonal network.

Epidermal structure of specimens NM G 7686, G 7688, G 7690 (Plate IV, 1–6), MG (30) 348 — adaxial cuticle thin, indistinctly (in larger leaves and near leaf margins) or more distinctly finely striate, showing polygonal straight-walled cells 22–45 μm across, exceptionally indistinct solitary stomata; abaxial cuticle also thin, in narrower leaves more distinctly striate, showing vaguely polygonal ordinary cells, about 25–30 μm across with slightly wavy anticlines, stomata anomocytic, narrow elliptic, 22–32 μm long and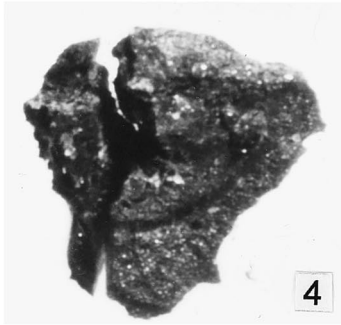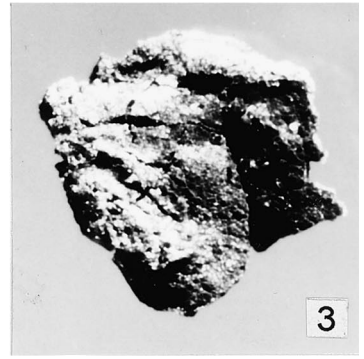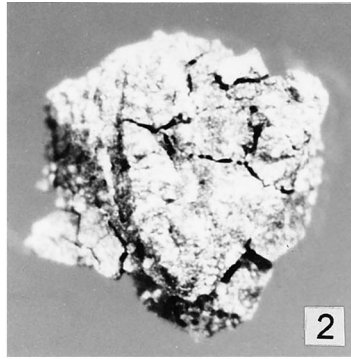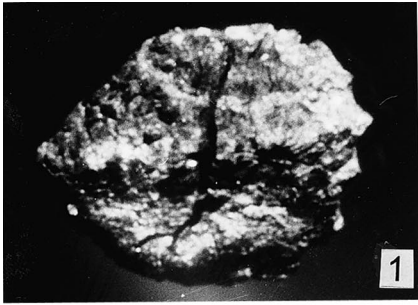 10–25 μm wide, with spindle-like outer aperture, usually narrow, partly widely open, bordered by slightly thickened ledges; striation radial to perpendicularly disposed to the stomata; no trichome bases observed, even on the midvein.

Specimen No. NM G 7691(Plate III, 1, 2) from horizon 11 — impression of a large lanceolate leaf without apex, lamina 35 mm wide and more than 120 mm long, base cuneate, petiole stout, 28 mm long. Venation brochidodromous, midvein almost straight, secondaries nearly perpendicular to the midvein, 4–6 mm apart, gently bent and forming a distinct intramarginal vein, intersecondaries often present, merging with the tertiaries half the distance to the margin. Tertiary veins random reticulate. Higher-order venation connected in small, more or less isometric meshes of various order, indistinct.

PLATE II

Decodon gibbosus (E.M. Reid) E.M. Reid, Lower Miocene, Mine Bílina, northern Bohemia.
1. Lateral view of a seed isolated from the sample shown in Plate I, 2 with a trace of germination valve. ×32.
2, 3. Dorsal and ventral view on an atypical flattened seed isolated from the sample shown in Plate I, 2 (2 see Fig. 2A). ×35.
4. The same seed with partly exposed seed cavity (see Fig. 2B). ×35.
5. Detached fruit on the sample shown in Plate I, 2. ×5.
6. A stalked detached fruit, No. NM G 7684. ×5.
7. Two detached fruits devoid of fruit walls, No. NM G 7683a. ×5.
8–12. Detached leaves, Nos. NM G 7685, G 7686, G 7687a, G 7688a, G 7689. Natural size.

PLATE III
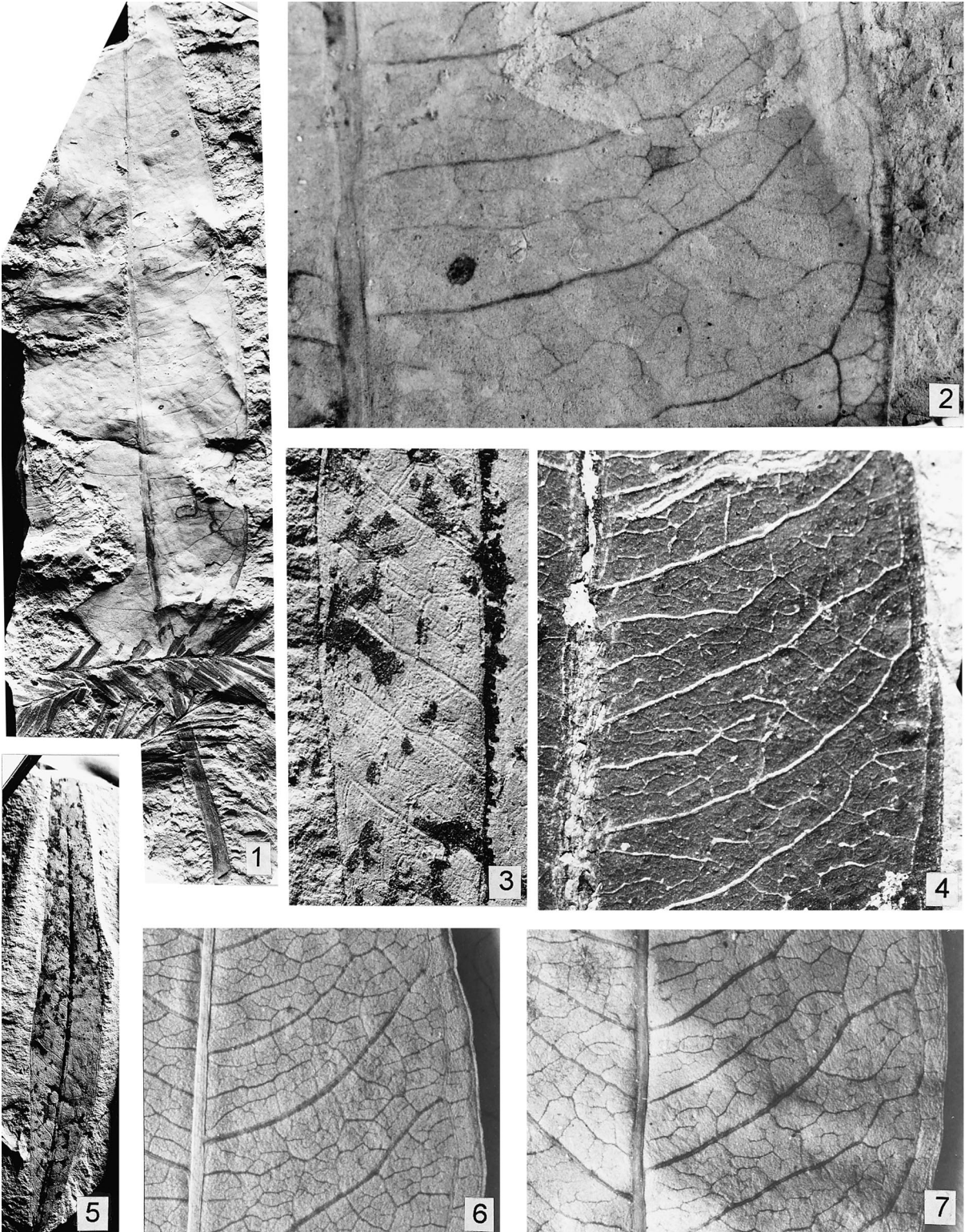
4. Discussion

4.1. Foliage

The foliage is well distinguished from other lanceolate entire leaves occurring in the fossiliferous layers by a prominent intramarginal vein. Such leaves are common at various localities in the Most Basin, but due to poorly preserved venation, such fossils have been partly misinterpreted as other taxa, like *Sapindus* (Ettingshausen, 1869) or willows with entire leaves of the group of *Salix angusta* A. Braun (Engelhardt, 1891). The verticillate phyllotaxy, amphistomatic leaves with finely striate cuticles, anomocytic stomata, together with characters of the attached capsules and their seeds, corroborate the assignment to *Decodon* of the Lythraceae family.

Lanceolate leaves with an intramarginal vein and dense secondary venation occur in several groups of angiosperms and present a typical case of convergence. Such foliage can be found in the Moraceae (*Ficus*), Apocynaceae incl. Asclepiadaceae (e.g. *Periploca*), Myrtaceae and also Lythraceae. In the fossil state, such leaves have been often ascribed to the above mentioned families without safely proving the true affinities. In other regions, studies of similar foliage attached to the fruit-bearing twigs (Iljinskaya, 1986; Manchester et al., 1998) showed that we cannot rely merely on the morphology and venation patterns for generic determination. Leaves with intramarginal veins appeared already in the Upper Cretaceous. Although those of the Bohemian Cenomanian were formerly determined as *Ficus*, *Eucalyptus*, *Myrtophyllum*, etc., epidermal studies indicated that they belong in fact to the Laurales (Kvaček, 1992). In the Tertiary of North America, similar leaves attached to twigs with fruits were assigned to the Myrtaceae and named *Syzygoides* Manchester

et al. (1998). Its tertiary venation is truly myrtoid, dense and very oblique to the secondaries. The twig described above bearing *Decodon* fruits and seeds indicates some of the leaves with intramarginal veins commonly found in the European Tertiary belong in fact to the Lythraceae.

One of the frequently used binomials for similar leaves is *Ficus multinervis* Heer typified by a suite of leaves from the Lower Miocene of the Swiss 'Mollase Grise' [type locality Riantmont (Heer, 1856), indirectly dated to MN 2 (J.-P. Berger, pers. commun.)]. The flora of this locality including the syntypes of *Ficus multinervis* (Museum of Geology, Lausanne) is in need of revision. The morphology, particularly the variation including both narrower and wider forms (Heer, 1856, pl. 81, figs. 6–10; pl. 82, fig. 1) is very similar to that of the leaves from Bílina. It is not surprising that the fossils of this kind from the Most Basin were assigned partly to *Ficus multinervis* by previous authors (Ettingshausen, 1866; Bůžek, 1971). We are not informed, if the seeds of *Decodon gibbosus* are associated in the same levels in Switzerland. *Ficus multinervis* has been widely applied for similar fossils also in other parts of Europe (e.g. Friedrich, 1883 — Stedten, Late Eocene; Takáč, 1974 — Handlova, Middle Miocene; Pilar, 1883 — Sused, Middle Miocene). Givulescu (1994) suggested this species to belong to *Periploca*. It is very questionable if all these records are conspecific.

Lanceolate leaf forms with the intramarginal vein are known also as *Apocynophyllum helveticum* Heer. The type material is from the locality Walkringen near Bern in Switzerland (Heer, 1859, p. 191, pl. 154, fig. 2), although Heer assigned another leaf from Bagnasco in Italy (Heer, 1859, p. 191, pl. 154, fig. 3) to the same entity. The type specimen shows opposite phyllotaxy and does not differ much in leaf

PLATE III

1–5. *Decodon gibbosus* (E.M. Reid) E.M. Reid, Lower Miocene, Mine Bílina, northern Bohemia, detached foliage and detailed venation.
1.   Impression of an extremely large leaf, No. NM G 7691. Natural size.
2.   The same specimen, venation. ×5.
3.   Venation of a narrow leaf shown in Plate III, 5. ×5.
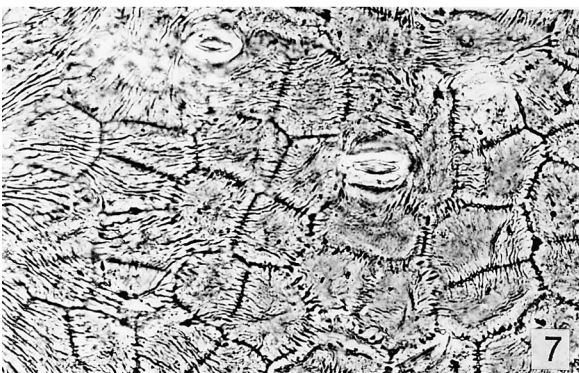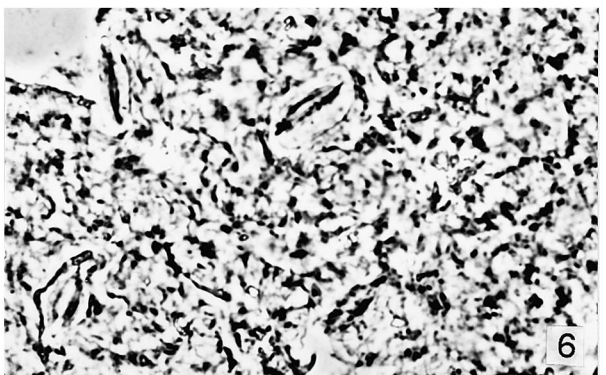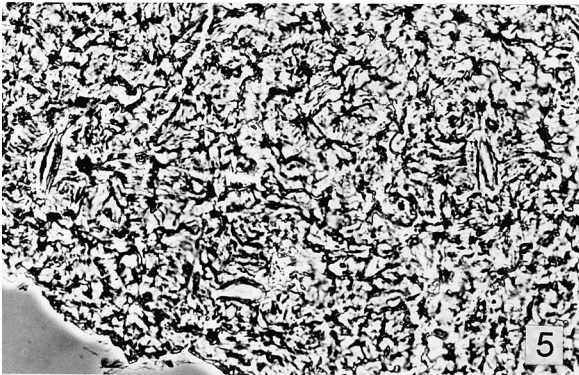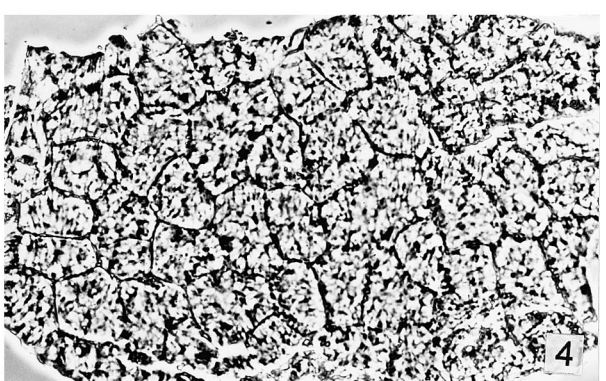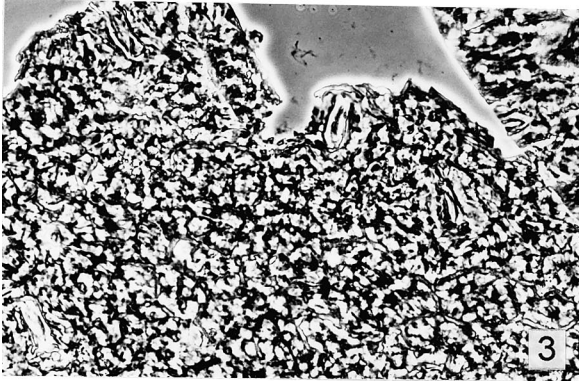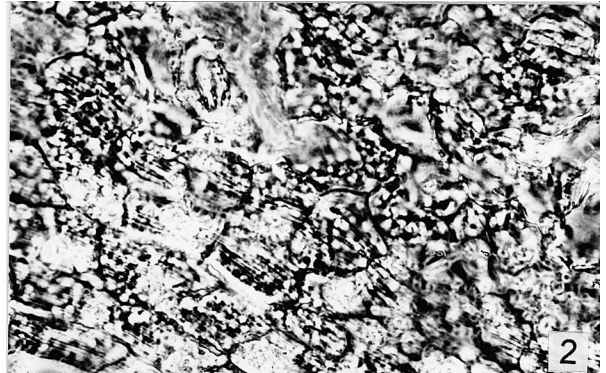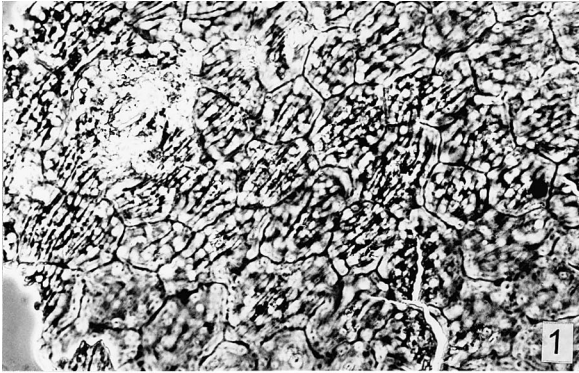4.   Venation of a broader leaf shown in Plate I, 11. ×5.
5.   A narrow leaf, No. NM G 7687b. Natural size.
6.   *Decodon verticillatus* (L.) Ell., venation for comparison. ×5.
7.   *Periploca graeca* L., venation for comparison. ×5.

PLATE IV

morphology from *Ficus multinervis* (see also Bůžek, 1971). The associated flora has not been studied in detail. The locality may be of Late Oligocene to Early Miocene age.

Abundant leaf fossils referred to *Apocynophyllum helveticum* were reported from the Lower Miocene of Altmittweida in northwestern Saxony in Germany (Beck, 1882). They probably correspond to our fossils because this locality belongs to the same stratigraphical level as the Bílina Mine [floristic zone Ng. IV, or Brandis in the sense of Mai and Walther (1991) or Bílina–Brandis in the sense of Mai (1995)]. Seeds of *Decodon gibbosus* and *D. tetraedriformis* have been obtained from the coal clay, exposed temporarily in 1965 at this locality (Mai and Walther, 1991).

Another occurrence of *A. helveticum* was published by Heer (1869) from the Baltic Lower Oligocene. New excavations in this area (Budantsev and Sveshnikova, 1964) yielded fragmented leaf compressions variable in form, with only adaxial cuticular structure preserved. Seeds of *Decodon gibbosus* have been recorded from the same clay lens as the leaves (Dorofeev, 1963).

An identical leaf form occurs in masses at the locality Zmiev in Ukraine (Zhilin, 1986). Zhilin considers this species as an index fossil of the Oligocene (Zhilin, 1984, 1989) and ranges this locality into the Upper Oligocene. Leaf fossils assigned to *A. helveticum* have been reported also from Kazakhstan, where they occurred in the Late Eocene to Late Oligocene floras (Zhilin, 1984, 1989). The associated seed flora is not known.

A common occurrence of the *Apocynophyllum helveticum*-like foliage has been recorded by Matthiesen (1975) from the Middle Miocene of Central Jutland, Denmark (locality Moselund). Judging from the published drawings the leaf shape and venation patterns are very similar to the North Bohemian

leaf material (dense secondaries, long petioles, long cuneate bases). Matthiesen was unable to prepare cuticles of any of the studied specimens. His interpretation of small dots observed on the leaf surface as 'hardened latex' is probably wrong — they may represent rather fungal bodies. At this locality no information is available as to the carpological record, but abundant seeds of *Decodon gibbosus* have been known in the same area and the same formation (Friis, 1985).

Leaf forms assigned to *Apocynophyllum helveticum* but deviating from the type specimens by narrower lamina and much denser secondaries and intersecondaries (Plate VI, 1) occurred in masses in levels of aquatic plants in the German Early Oligocene Haselbach flora (Mai and Walther, 1978). In morphology (narrow forms with dense secondary venation) they correspond exactly to *Apocynophyllum neriifolium* Heer, 1861 from the Upper Eocene strata of the same region. They were compared with the Apocynaceae (Kräusel and Weyland, 1950), but this assumption was not corroborated by the study by Walther (in Mai and Walther, 1978). These leaves occur regularly associated with common seeds of an extinct Lythraceae *Microdiptera parva* Chandler and may represent its foliage. In epidermal structure they differ from the specimens from the Bílina Mine by stomata occasionally showing paracytic type and rare trichome bases. We have examined topotypical specimens from Haselbach and found cuticular structure not very different from the Lythraceae — the cuticles are finely striate, stomata are occasionally paracytic, but the anomocytic type prevails (Plate VI, 2).

Lanceolate leaves from the Middle Eocene of Geiseltal, described as *Apocynophyllum echitiforme* (Rüffle et al., 1976) have cuticles, which differ decidedly from the North Bohemian material and suggest affinity with the Ericaceae (*Vaccinioides*

PLATE IV

1–6. *Decodon gibbosus* (E.M. Reid) E.M. Reid, Lower Miocene, Mine Bílina, northern Bohemia, cuticular structures.
1, 2. Adaxial cuticle with striation and solitary stomata of the specimen No. NM G 7682b shown in Plate I, 2. ×300.
3.   Abaxial cuticle with striation and stomata of the same specimen. ×300.
4.   Adaxial cuticle of the specimen No. NM G 7688a shown in Plate II, 11. ×300.
5.   Abaxial cuticle of the same specimen. ×300.
6.   Abaxial cuticle of a leaf No. NM G 7690a. ×500.
7, 8. *Decodon verticillatus* (L.) Ell. var. *laevigatus* Torr. et Gray, adaxial and abaxial cuticle for comparison, Pretz 2126, Allentown (PRC). ×300.

PLATE V
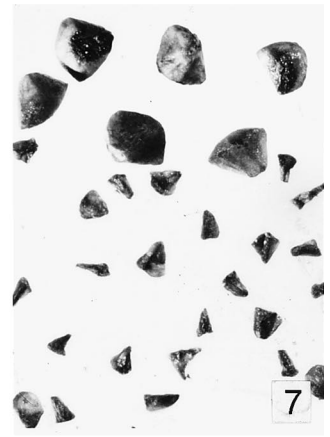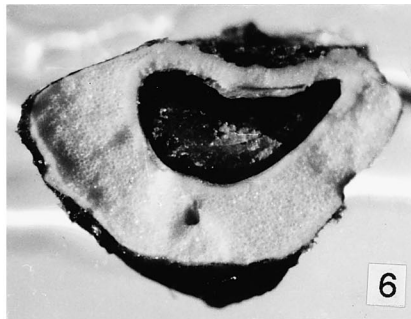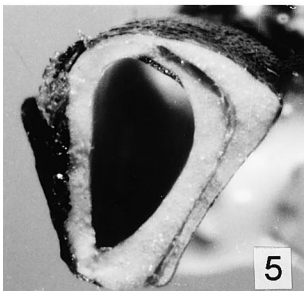
echitiformis (Rüffle, Müller-Stoll et Litke) Kvaček, Walther et Wilde in Kvaček and Walther, 1990). On the other hand, forms determined as *Apocynophyllum helveticum* (Rüffle et al., 1976) match rather the Lythraceae, namely *Decodon*, in anomocytic stomata and striate cuticles. The seeds of the Lythraceae have not been reported from the Middle Eocene of this locality (Mai, 1976). The Upper Eocene strata of Geiseltal (Kayna-Süd 14) furnished leaf fossils reported under the name *Apocynophyllum neriifolium* Heer by Rüffle et al. (1976), which are very similar to those from Haselbach both in leaf morphology and epidermal structure. The illustrated 'Gummikör-per' (Rüffle et al., 1976, pl. 39, fig. 6) are doubtful structures and need revision of authentic prepara-tions. *Apocynophyllum neriifolium* is also associated with the seeds of *Microdiptera parva* at this locality of Geiseltal (Mai and Walther, 1985).

Broader leaf forms with intramarginal vein, more rounded to slightly cordate at the base, were described as *Dicotylophyllum jungii* Knobloch et Kvaček, 1976 from the Lower–Middle Miocene of the Murnerweiher Mine near Schwandorf, Germany (Plate VI, 3). The cuticles are very fragmentary, but in general they correspond to the foliage of *Decodon* (Plate VI, 4, 5). The seeds of Lythraceae occur-ring in these deposits belong to *Decodon globosus* (Gregor, 1980, pers. commun.). The same type of foliage was assigned to the taxon No. LVIII sensu Ferguson (1971) pro parte. (Two entities were mixed up in this taxon — the leaf No. Utrecht 4148 in fig. 40D deviates from the Lythraceae in the struc-ture of cuticles and differs from the rest of the material of taxon LVIII in details of venation.) The specimen figured by Ferguson (1971) in fig. 40B matches best *D. jungii*. *Decodon globosus* has been also reported from the Kreuzau flora (Pingen, 1987; Ferguson et al., 1998). Considering its leaf morphol-

ogy, *Periploca kryshtofowichii* Kornilova (Kornilova, 1960; Zhilin, 1974; Pn'ova, 1986) from the Lower Miocene of Kazachstan can hardly be distinguished from *Dicotylophyllum jungii*. Information on its cu-ticular structure and any associated seeds is unfortu-nately lacking.

A complete review of all the fossil foliage with in-tramarginal venation, that is comparable to the above described fossils is beyond the scope of this paper. However, such fossil impressions have been often identified in the Tertiary as *Apocynophyllum* Unger (see above), *Eucalyptus* (Iljinskaya, 1986), *Myrto-phyllum* Heer (Chelidze, 1970), *Neritinium* Unger (Unger, 1866), *Nerium* (Saporta, 1879), *Periploca* (Kornilova, 1960; Kutuzkina, 1964; Zastawniak, 1978), etc. and may mostly represent the Lythraceae.

Previously, fossil foliage determined as *Decodon* has been described so far only from the North Amer-ican Tertiary. *Decodon alaskanus* Wolfe et Tanai, 1980 from the Miocene floras of Seldovia Point, Alaska and Collawash, Oregon matches the extant *D. verticillatus* in wider, more arch-like secondaries. *D. brownii* Meyer et Manchester, 1997 from the Oli-gocene of the John Day Formation, Oregon, is dis-tinguished by non-looped course of the intramarginal vein, a feature shared with other members of the Lythraceae, e.g. *Cuphea*. Because of the lack of epidermal preservation and clearly associated fruits or seeds, these identifications must be regarded as tentative.

The foliage of *Decodon gibbosus* usually called *Ficus multinervis* or *Apocynophyllum helveticum* from the Bílina Mine matches well that of the ex-tant *D. verticillatus* in size and shape variation, and venation patterns, particularly in the shallow arch-like course of the intramarginal vein. However, the petioles average much longer than those of the ex-tant species. *D. verticillatus* has slightly broader and

PLATE V

1.   *Periploca graeca* L., abaxial epidermis for comparison, cult. (PRC). ×300.
2–7. *Decodon verticillatus* (L.) Ell. for comparison.
2.   Abaxial cuticle with trichomes (var. *verticillatus*), Redmondt 306, Maryland (P). ×300.
3.   Flowering leafy branch (var. *laevigatus* Torr. et Gray), Biltmore Herb. 3765a, Tennessee (P). Natural size.
4.   Stalked capsule enclosed in the hypanthium. ×5.
5.   Longitudinal section of a seed showing raphe in the dorsal seed wall (right). ×25.
6.   Transverse section of a seed showing raphe as a point in the dorsal seed wall (down). ×25.
7.   Variation in seed size and form within one fruit. ×5.

PLATE VI
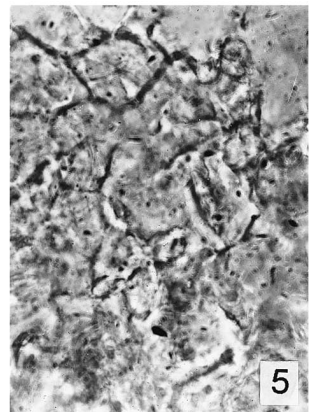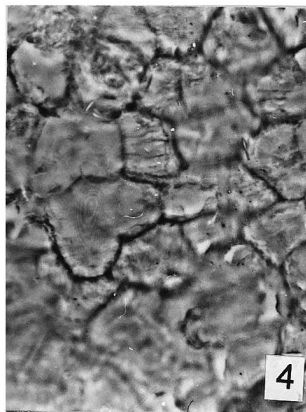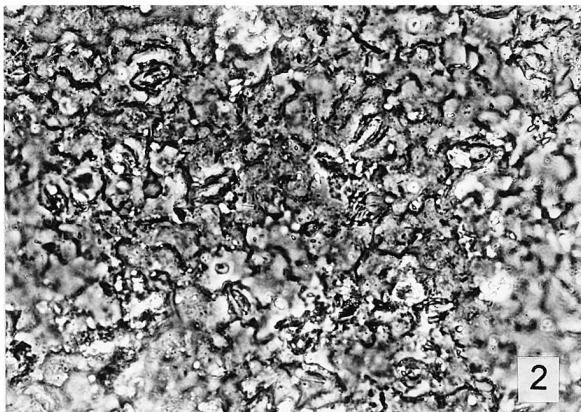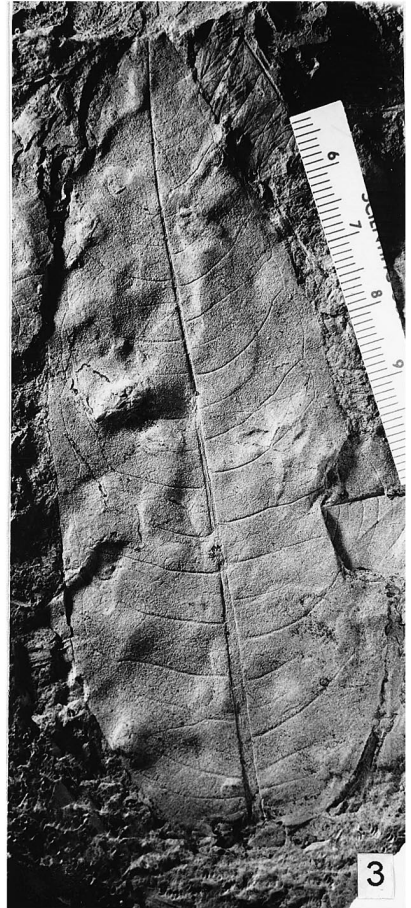
less variable leaf blades (width : length index usually 1 : 6.5 to 1 : 3) but compares well in leaf size (Plate V, 3). The size variation may reflect position of leaves on the stems. The fossil leaves are hairless contrary to mostly hairy to densely hairy leaves of *D. verticillatus* with characteristic uniseriate simple or branched trichomes (Plate V, 2). However, a glabrous form of *D. verticillatus* (var. *laevigatus* Torr. et Gray) distributed more frequently in the northern part of its range (Graham, 1964) perfectly matches *D. gibbosus* in epidermal structure. Both the adaxial and abaxial cuticles are finely striate, and show polygonal cells with straight (to slightly sinuate abaxially) anticlines. Stomata are anomocytic, as in most Lythraceae, very similar in their form and structure (Plate IV, 7, 8).

Leaves of *Periploca* and many other members of the Apocynaceae/Asclepiadaceae, converge closely with those of *Decodon* and cannot be distinguished on the basis of the venation alone (Plate III, 6, 7). However, *Periploca* differs in its epidermal structure (Plate V, 1), namely by paracytic stomata (with occasionally subdivided subsidiary cells), and laticiferous tubes in the mesophyll tissue (Metcalfe and Chalk, 1950).

4.2. Seeds and fruits

First figured by Reid and Reid (1907), then described as a fossil genus of unknown affinities, *Diclidocarya*, by E.M. Reid (1920, 1923) and finally recognized as *Decodon* by Nikitin (1929), the fossil seeds of the genus *Decodon* are among the most typical elements in the Eurasian Tertiary seed floras (e.g. Dorofeev, 1977; Friis, 1985; Mai, 1985, 1995). Together with allied extinct taxa they have been treated in a number of taxonomic studies (for taxonomic reviews see Eyde, 1972; Holý, 1976; Mai

and Walther, 1978; Tiffney, 1981; Cevallos-Ferriz and Stockey, 1988).

Generally, the seeds are anatropous, bisymmetric with a characteristic flat or concave germination valve on the ventral side (Nikitin, 1929; Friis, 1985). This germination valve is very important from a systematic point of view: its concavity led Reid (1920) to re-examine hers and her husband suggestion (Reid and Reid, 1915) about the affinity of the fossil seeds to the recent genus *Stocksia* of the Sapindaceae, which has, unlike the fossils, a convex germination valve (Reid, 1920). Whereas the ventral side of the seed is more or less the same in shape as in the extant *Decodon verticillatus*, the dorsal side varies considerably from prolonged triangular-pyramidal or rounded in shape to slightly rounded or almost flat. These differences in shape, together with a proportional relation of size (height, length, width) were employed to separate fossil seed species (forms) within the fossil representatives of *Decodon* (Reid, 1920; Dorofeev, 1955; Raniecka-Bobrowska, 1956; Chandler, 1963; Dorofeev, 1977).

Among the studied specimens from the Bílina Mine the most important one is the specimen No NM G 7682 a, b, which represents a fragment of the fertile leafy twig (Plate I, 1, 2). It was recovered by chance. The leaves (their upper parts) were found first. After an unintended 'preparation', caused by the specimen falling on the floor, stalked fruits with seeds directly attached in leaf axils became exposed in the lower half of the specimen. This specimen with the fruits/seeds of the *Decodon*-type definitely proved the lythraceous affinities of the foliage.

Unlike common dispersed fossil seeds, which are mostly three-dimensionally preserved in sandy deposits, the studied seeds (and also fruits) are generally flattened and broken in such a way that one half

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PLATE VI

1, 2.   *Apocynophyllum neriifolium* Heer (i.e. *A. helveticum* sensu Mai et Walther), a possible foliage of *Microdiptera parva* Chandler, Lower Oligocene, Haselbach Mine, Saxony.

1.   Detailed venation of a leaf, (PRC). ×7.

2.   Abaxial cuticle of the same specimen. ×300.

3–5.   *Dicotylophyllum jungii* Knobloch et Kvaček, a possible foliage of *Decodon globosus* (E. M. Reid) Nikitin, Lower–Middle Miocene, Murnerweiher Mine near Schwandorf, Oberpfalz.

3.   Holotype, No. Sch 691 (coll. Bayer. Staatssamml. Paleontol. Hist. Geol., München). Natural size.

4.   Adaxial cuticle showing faint striation, No. Sch 691B/2 (PRC). ×500.

5.   Abaxial cuticle with a stoma, No. Sch 691B/2 (PRC). ×500.

remains on the positive and the other on the counterpart of the fossil. Such a mode of fossilization shows longitudinal, oblique and transverse sections of seeds (Plate I, 5–8), as they were described and figured in the literature (Reid, 1920; Nikitin, 1929; Raniecka-Bobrowska, 1956; Friis, 1985).

The sections show pyriform or simply oval areas, often white in colour, surrounded by the black coal matter of the seed wall. This type of structure matches well those described in earlier works (Reid, 1920; Nikitin, 1929; Raniecka-Bobrowska, 1956). The white area can be interpreted as a seed cavity. It is long, pyriform, viewed in the longitudinal section (Fig. 1B) and short, oval, viewed in the transverse section (Fig. 1A).

The longitudinal sections occur more rarely than the transverse ones. Their shapes, characterized by a very prolonged dorsal side, recall the shapes of the type specimens of *Decodon gibbosus*. The transverse sections, more numerous, vary more widely in shape: straight or concave in their upper (ventral) sides; rounded, more or less extended, to narrow triangular in their lower (dorsal) parts. In view of the most extreme, very narrowly triangular forms (Plate I, 6; Fig. 1A), the *Decodon gibbosus* type of seeds matches best. Shorter, more rounded sections represent probably transverse sections in the micropyle (lower) part of the seed, which is narrower. Extremely long, narrowly triangular sections are situated in the chalaza (upper) part, which is wider.

The whitish seed cavity is surrounded by black carbonized matter of the seed wall. It is composed of two types of tissue: dull lustre (shagreen), forming most of the dorsal part of the seed under the seed cavity, and not structured, lustre, coating both the seed cavity and the dull lustre area (Fig. 1). The dull lustre structure represents certainly spongy tissue in the sense of Nikitin (1929), aerenchyma in sense of Raniecka-Bobrowska (1956), mesotesta in the sense of Friis (1985) and the middle integumentary zone in the sense of Cevallos-Ferriz and Stockey (1988). According to our own observations of the extant material, it is characterized by relatively big thin-walled oval to polygonal cells. Shagreen texture of this fossil tissue reflects the relief of cells. The black lustre tissue, coating the spongy layer and the seed cavity, must be the ligneous thick layer

that surrounds the spongy tissue on the dorsal part of the seed (Nikitin, 1929), i.e. sclerenchyma in sense of Raniecka-Bobrowska (1956) and outer and inner integumentary zone in sense of Cevallos-Ferriz and Stockey (1988). This tissue, dorsally with the intercalated spongy layer, originates by splitting of the second (lower) layer of the external integument which is continuous on the ventral part of the seed (Nikitin, 1929).

Due to the mode of fossilization we were unable to observe the black structureless mucous layer described by Raniecka-Bobrowska (1956) on the surface of seeds and employed as a diagnostic trait. It represents the upper epidermal layer of the external integument of the seed testa of Nikitin (1929). Also due to the fossilization such details as raphe canal, hilum, micropyle or chalaza, have not been observed in cross-sections in the material studied.

Several complete, but fractured and very fragile seeds have been separated from the matrix (Plate II, 1–4). Their external characters agree mostly with those viewed on the transverse section — the seeds are generally high, often asymmetrical, with an oblong to slightly triangular prolonged dorsal side and a narrow ventral side. The surface is smooth, not structured, the valve is not always present — if so, it is narrow, made up of black shiny non-ornamented, probably ligneous tissue.

The majority of the studied seeds, mostly preserved in oblique transverse sections, shows typical features of the fossil *Decodon gibbosus*: a very prolonged dorsal part, narrow ventral side and the height of seed exceeding the width. However, among several complete seeds separated from a fruit one is different (Plate II, 2–4; Fig. 2). It may not be fully ripe and may represent an undeveloped stage. This seed is dorso-ventrally flattened, symmetric, more angular in its form and in the concave outline of the lateral margins, more similar to those of the modern *Decodon* or rather of its most closely related fossil ancestor *D. globosus* (E.M. Reid) Nikitin. The valve is present and forms a narrow oval, remarkably risen above the ventral seed surface (probably due to the absence of the upper epidermal layer, which is mostly absent in fossil seeds — see Kirchheimer, 1957). The dorsal side is slightly oblong, but rather flat. In transverse view, the seed is flattened, slightly convex on the ventral side, mostly due to the risen

valve. In internal view below the valve, a section of the seed cavity, coated by sclerenchyma, can be seen (Plate II, 4; Fig. 2B). This view represents a longitudinal section of the seed cavity, more or less parallel to the ventral seed surface. The section of the cavity is probably oval (only one half has been exposed), oriented perpendicularly to the long axis of the valve. A comparable arrangement can be observed in *D. verticillatus*. This type of the longitudinal section, parallel to the ventral seed surface, has not been usually figured. At first sight, it reminds transverse sections, already published by Reid (1920), Nikitin (1929) and Raniecka-Bobrowska (1956). However, in true transverse sections, the upper side of the seed cavity and its surrounded sclerenchyma are always marginal on the ventral side (Fig. 1A). On the other hand, the longitudinal section parallel to the ventral seed surface shows the sclerenchyma coating of the seed cavity on the chalaza end of the seed (Fig. 2B). In this time, the sclerenchyma is not marginal.

Three main differences between the extant and fossil seeds of *Decodon* can be noticed regarding the development of the testa, the form and size of the seeds.

The first differences in the testa, noted by Nikitin (1929), is observed in our material: the fossils seeds have the external part (i.e. closer to the seed surface) of the ligneous dorsal layer (= lower layer of the external integument) thicker than the internal one, situated closer to the seed cavity (Fig. 1). The external layer in the extant seeds is thinner.

Differences in the form can be also observed: The transverse sections and several isolated seeds studied are dorsally very prolonged (Plate I, 6, 7; Fig. 1A) with a narrow ventral side and the height exceeding the width. This form is characteristic of *Decodon gibbosus* (incl. '*Decodon globosus*' sensu Raniecka-Bobrowska, 1956) — contrary to the recent *Decodon verticillatus* with a broad valve and the width exceeding the height (Plate V, 6; E.M. Reid in Nikitin, 1929; Raniecka-Bobrowska, 1956). The difference in the outline of the lateral margin, mentioned by Nikitin (1929), seems to us not sufficiently clear — we prefer the interpretation of Kirchheimer (1957), who characterized the extant forms as generally more angular in relation to the more rounded fossil forms.

Sometimes differences in size of seeds have been used to help distinguish the species. Nikitin (1929) described fossil seeds of *D. globosus* as "somewhat smaller in size" than the recent ones. Also Raniecka-Bobrowska (1956) stated the fossil seeds be generally smaller than the seeds of *D. verticillatus*. As we have observed in samples of *D. verticillatus* (Plate V, 7) the seeds vary in size within one fruit considerably (from 'typical', normally developed to 'unusual', aborted, according to the position in the capsule). This disproportion in size may be due to immaturity of some seeds and logically affect also the fossil material. So we prefer not to stress distinction between the extant and fossil seeds based on their relative sizes, as E.M. Reid in Nikitin (1929) and Raniecka-Bobrowska (1956) did. In this case, one must keep always in mind that transitions from typical to unusual or aborted forms could influence drastically the resulting taxonomy (see also Chandler, 1960, p. 232; Meller, 1998, p. 538).

The fruits of recent *D. verticillatus* (Plate V, 4) are dry 3- (or 4-) loculed globose thin-walled capsules, loculicidally dehiscent, 5–6 mm in diameter, basally enclosed in persistent hypanthium, containing 20–30 seeds (Koehne, 1903; Nikitin, 1929; Kirchheimer, 1957; Zomlefer, 1994). The fossil fruits of *Decodon* were described and figured by Raniecka-Bobrowska (1956, 1959). These capsules bear often remains of the calyx and the stalk. They contain one, two, four or more seeds on a central axis. Depending on the number of seeds in the capsule, Raniecka-Bobrowska (1956) recognises several seed forms ranging from well developed rounded seeds coming from one-seeded capsules to lateral flat irregularly shaped seeds coming from more-seeded capsules. This remark, which matches very well our own observations of the recent material, is very important considering the natural variability of seed forms linked to the position of seeds in the capsule. Nikitin (1929) described a group of 20–30 seeds 5.5–6 mm across and interpreted as a possible fruit without preserved walls. Gregor (1980) illustrated several globular fruits of *D. globosus*, partly in cross sections, containing more than 10 seeds, also usually without fruit walls.

The studied fossil fruits are well rounded, approximately 4–8 mm across, without preserved hypanthium, calyx or other details, such as dehiscent lines. They are placed on stalks, 7–9 mm long, which are

often fragmented, enlarged at the attachment place at the stalk base. At least five fruits are present in the specimen No. NM G 7682, one of them directly attached by a non-fragmented stalk in the leaf axil. Because of that, we suppose that they formed clusters, placed in the leaf axils (Fig. 3). The number of seeds per capsule can not be precisely estimated because the seeds are not limited to the fruit only, but they are also found nearby, forming a mixture with the seeds coming from the other neighbouring fruits. At least 8–15 seeds have been seen on the surface of the compressions of the isolated capsules. In spite of poor preservation of capsule walls the fruits compare favourably with those of extant *Decodon*. Delicate fruit walls probably decayed quickly in the water. Only in specific permineralized state such details may preserve in the *Decodon* fruits (e.g. Cevallos-Ferriz and Stockey, 1988; Manchester, 1994).

4.3. Nomenclature and form taxa

The priority principle does not contribute much to the stability of nomenclature, as it is apparent from the latest policy development of the nomenclature committee (Greuter et al., 1994; Anonymous, 1998). In fossil plants, which occur usually as disarticulated fossils, another problem arises, when a unification of natural and form taxa should be made. In our case, we prefer to adhere to a species with natural content, i.e. *Decodon gibbosus*, which is based on an organ (the seed) reflecting more precisely specific differences. The taxa of the foliage ('*Ficus*' *multinervis* or *Apocynophyllum helveticum*), published much earlier, are based on leaf fossils without known cuticular structure and do not reflect safely natural specific and even generic differences. Hence their identity with our material is not fully guaranteed. We recommend to employ these names as purely artificial units.

5. Palaeoecology and sociology

Like many of the Lythraceae, also *Decodon verticillatus* grows on damp habitats today. This North American endemite is confined to the eastern United States and Canada (from Florida to Nova Scotia). It is suffrutescent in growth habit and forms dense stands in shallow water. According to our own ob-

servations, it prefers open non-arborescent vegetation on margins of standing waters and marshes (e.g. Paynes Prairie near Gainesville) or clearings in the *Taxodium–Nyssa* swamp forests (e.g. Okifenokee swamp). Judging from the fossil assemblages containing abundant remains of *Decodon* and related Lythraceae, its Tertiary relatives must have had similar autecology.

D. gibbosus occurs in a few Early Miocene localities of the Most Basin in northern Bohemia. Several fossiliferous levels have been distinguished within the section of the Bílina Mine, which yielded most of the studied material (Bůžek et al., 1992; Kvaček, 1998). The *Decodon* foliage, fruits and seeds are more frequent in the level No. 30, in which whole branches of the Taxodiaceae, foliage twigs, large leaves, inflorescences and wing fruits are indicative of parautochthonous origin of the assemblage sensu Behrensmeyer and Hook (1992). *Glyptostrobus*, *Taxodium*, '*Athrotaxis*' *couttsiae*, *Alnus*, *Cercidiphyllum, Nyssa*, *Fraxinus*, *Acer* and *Craigia* prevail among the trees. Vines as *Berchemia* and *Rubus* are also well represented, but herbaceous remains (ferns, monocot leaves) are rare (Sakala, 1997). The dark colour, the presence of pyrite, fish skeletons and intact insects are evidence for anoxic conditions. The assemblage is ranged into the *Taxodium–Nyssa* association in sense of Bůžek and Kvaček (see Boulter et al., 1993) and reflects a deep muddy swamp covered for most of the year by water, where *Decodon* grew in undergrowth. Another rich occurrence of the *Decodon* foliage is found higher in the exposure (levels No. 2, 11, etc.), where alluvial sandy–clayey deposits prevail. Several levels of aquatic free-floating plant assemblages dominated by *Salvinia* remains interchange with the levels of the *Salix*-, *Taxodium*-, *Alnus*- or *Sabal*-dominated arboreal assemblages. Among them, levels overfilled with strap-like leaves of monocots (*Spirematospermum*, *Typha* and others) and the foliage of *Decodon* form transitional stages between these two extremes and reflect sedge belts. Hurník (1961, 1973) described a similar aquatic plant assemblage from the same area in the former strip mines Maxim Gorkij I at Braňany, and Ležáky at Most. Also there aquatic and swamp plants including *Salvinia*, *Typha*, *Potamogeton* and other monocots were associated with the foliage of *Decodon* (i.e. cf. *Apocynophyllum*

helveticum sensu Hurník). He matches these assemblages with vegetation of reed marshes, mudflats and freshwater marshes in the Mississippi delta.

Another well known site of *D. gibbosus* from the Baltic Oligocene (Heer, 1869) is Svetlogorsk (see also Dorofeev, 1963; Budantsev and Sveshnikova, 1964). Although older in age, the flora at the generic level is not much different from that of Bílina: arboreal *Taxodium*, *Alnus*, *Populus*, *Nyssa*, in shrub layer with *Myrica*, *Calamus*, *Spirematospermum* and *Decodon*. Again a flooded riparian–swamp forest can be expected near the depositional site.

The Søby–Fasterholt fruit and seed assemblages in the Danish Middle Miocene (Friis, 1979, 1985) are partly allochthonous. In a layer of fine sand intercalated between the two uppermost coal layers in the C. Nielsen A/S Mine near Fasterholt, a parautochthonous assemblage occurred, which included abundant seeds of *Decodon gibbosus*. Friis (1985) interprets this element as a rooted plant with floating stems comparable with the extant *D. verticillatus*, a constituent of aquatic and wetland communities bound to fresh water marshes of the Atlantic Coastal Plain of North America. The Fasterholt flora is very diversified (more than 150 species), the assemblage is dominated by woody *Sequoia*, *Taxodium*, *Glyptostrobus*, *Platanus*, *Alnus* vel *Betula*, *Myrica*, *Pyracantha*, *Rubus*, *Epacridicarpum*, and herbaceous *Salvinia*, *Brasenia*, *Pistia*, *Typha* and Cyperaceae.

A similar case of occurrence of *D. gibbosus* has been recorded in the Lower Miocene of Köflach, Austria (Meller, 1998). The levels rich in its seeds (samples ME-Ob-90-3 and 5) are close to lignite sedimentation and contain abundant fruits/seeds of *Sequoia*, *Cercidiphyllum*, ?*Cleyera*, *Myrica*, *Rubus* and *Sparganium*. Meller interprets the assemblage ME-Ob-90-5 as a wetland forest with stream-side and peat bog elements. The associated leaf fossils include common *Cercidiphyllum* together with *Acer tricuspidatum*, *Alnus*, Betulaceae, Leguminosae, *Myrica*, *Sequoia* and *Cephalotaxus*.

The connection of *Decodon globosus* with mostly swamp vegetation is also apparent from the statistical evaluation of the carpological record by Günther and Gregor (1989, 1993). These authors recognized several types of assemblages. Among them those connected with the coal or clay facies and con-taining *Decodon* are usually dominated by aquatic and swamp plants (their carpofloras B3b, B3c, E2a, E2b, E3a–d) or a more diversified riparian-mesophytic vegetation (Z1b, Z2a–c, Z2g, Z3b–c). *Decodon* is more rarely represented also in the sandy allochthonous facies (F3a, F3b). *Decodon globosus* occurs abundantly in the Lower Pliocene of the strip mine Hambach, Germany in deposits of fluviatile origin. The typical *Decodon*-rich associations are there dominated by *Carex*, *Dulichium*, *Scirpus*, *Alisma*, *Apium*, *Boehmeria*, *Oenanthe*, *Rubus*, *Urtica*, and arboreal *Alnus*, *Liriodendron* and *Pterocarya*, i.e. an alder carr with open grass- and reedland vegetation (Van der Burgh and Zetter, 1998, samples Nos. 14132, 14380, 14381).

In the Haselbach flora (Mai and Walther, 1978), the extinct Lythraceous *Microdiptera parva* is regularly associated with the foliage of *A. neriifolium* (Haselbach Mine, collection points 1, 3, Waltersdorf Mine, Schleenhain Mine). The most common forest vegetation connected with its occurrence is the *Taxodium–Nyssa* swamp forest with *Tetraclinis* and '*Athrotaxis*', aquatic and swamp associations with *Salvinia*, *Azolla*, *Eichhornia* but also the Mixed Mesophytic Forest (Mai and Walther, 1978).

Mai (1981, 1985) mentioned *Decodon* and *Microdiptera* in the European Tertiary as constituents of the undergrowth storey in the riparian forests and of the Fern–Monocot riparian coal-forming vegetation on mesotrophic, usually river-side flatland mires. Although the accompanied vegetation changed during the Palaeogene to Pliocene in its composition, it is mostly azonal, physiognomically very consistent, well comparable to that of the extant relictual species. Fossil *Decodon* obviously tolerated climatic fluctuations from subtropical to temperate humid regimes like today in the Atlantic North America.

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Doctoral Thesis by Jakub Sakala (2004)
The 'Whole-Plant' concept in palaeobotany with examples from the Tertiary of northwestern Bohemia, Czech Republic
with particular reference to fossil wood

6. Conclusions

The ultimate objective of palaeobotany is to understand the entire organism - the whole fossil plant - and its evolution in time and space. However, in fossil record the plants are present mostly disarticulated in isolated organs. The approach known today as **the 'Whole-Plant' concept** combines the detached organs in order to reconstruct the whole plant as it really looked like and lived in the past.

The Tertiary of northwestern Bohemia (Czech Republic) was chosen as the ideal area to illustrate the principles of the 'Whole-Plant' concept with particular reference to fossil wood. There were two main reasons for this choice. First, various plant organs such as fossil leaves, wood, flowers, dispersed and in situ pollen, fruits and seeds are frequently found there in (in)direct association. Secondly, the Tertiary of northwestern Bohemia represents a classical area of palaeobotanical research, which is, except for fossil wood, intensively explored up to the present.

The Tertiary of northwestern Bohemia is spread in the northwestern part of the Czech Republic as a continuous zone of magmatic and sedimentary complexes, parallel to the Czech-German boundary. The present study has been limited to three regions: from west to east **the Doupovské hory Mts., the Most Basin and the České středohoří Mts.**, which are all bound to the Ohře Rift system, a depression zone orientated in SW-NE direction. The age of the fossiliferous rocks varies mostly between Late Eocene and Early Miocene.

The concrete examples and the general aspects of the 'Whole-Plant' concept were demonstrated in **five case studies**: the first example dealt with gymnosperm wood, the three following described angiosperm woods and the last one was about reproductive structures. **Five publications** (1 - Sakala 2003a, 2 - Sakala & Privé-Gill 2004, 3 - Sakala & Teodoridis 2001, 4 - Sakala 2002, 5 - Kvaček & Sakala 1999), which can be found in their integral form in the text represent an essential part of each example (case study) as well as of the whole doctoral thesis.

Example 1 - The big silicified trunk from **Kučlín** (Late Eocene, České středohoří Mts.), which was believed to be a wood of extinct conifer *Doliostrobus*, has newly been reinterpreted as a wood of *Tetraclinis* - **Tetraclinoxylon**. This revision is based on the exclusively cupressoid type of cross-field pitting and the markedly roundish shape of the tracheids in cross-section. The wood was associated with rare twigs and seeds of *Tetraclinis salicornioides* from the same locality.

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Concerning the **general aspects of Example 1** relative to the 'Whole-Plant' concept, the cross-field pitting between our wood and the twig of *Doliostrobus* were too different to be interpreted as ***differences in cross-field pitting between trunk and twig wood*** of the same species. The difference between ***systematical and ecological aspects of the nearest living relative*** was also shown when *Tetraclinis salicornioides*, associated in Kučlín with *Tetraclinoxylon vulcanense*, was compared systematically to modern *Tetraclinis articulata*. This taxon is however ecologically closer to the second fossil species - *T. brachyodon*. Finally, the general problem of ***discrepancy between the record of wood and other organs*** was demonstrated on *Tetraclinis* from the Tertiary of Europe with two species well defined by cones, seeds and foliage compared to six species of *Tetraclinoxylon*.

Example 2 - A calcified trunk from **Kadaň – Zadní vrch Hill** (Oligocene, Doupovské hory Mts.) was identified as ***Cercidiphylloxylon kadanense*** and designated as an epitype of *C. kadanense* as well as of *Cercidiphylloxylon*, both defined earlier from the same locality. The modified diagnosis of *C. kadanense* and *Cercidiphylloxylon* mentions wider rays, and for *C. kadanense* the presence of crystals in the rays and the density of bars in the scalariform perforation plates. The wood of *C. kadanense* can be associated with *Cercidiphyllum crenatum* known in the Tertiary of northwestern Bohemia from foliage, fruits, seeds, staminate inflorescences, and in situ pollen. A similar fossil wood from **Žichov** (Late Oligocene, České středohoří Mts.) with fewer and more widely spaced bars was attributed to ***Liquidambaroxylon speciosum***, representing the wood of *Liquidambar*.

Concerning the **general aspects of Example 2** relative to the 'Whole-Plant' concept, the second species of *Cercidiphylloxylon* - *C. spenceri* reminds us that in the Tertiary of Europe we can still meet the ***wood of extinct plants***, which represent botanical genera that do not exist any more. The observation of the ***rays and scalariform perforation plates*** revealed the number of bars in the scalariform perforation plates as a reliable criterion to distinguish the wood of modern *Cercidiphyllum* from similar Hamamelidaceae. Finally, the problem of ***similar wood in systematically unrelated taxa*** was demonstrated on the similarity between the wood of *Nyssa* and *Cercidiphyllum*, both important elements in the Tertiary of northwestern Bohemia.

Example 3 - A big silicified trunk found in **Velká Černoc** (Late Oligocene, Most Basin) with a ring porous wood pattern with relatively large, usually solitary vessels in the early wood, characteristic flame-shaped arrangement of vessels in the late wood, uniseriate to biseriate rays, diffuse apotracheal parenchyma and tracheids can be attributed to the

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morphogenus ***Castanoxylon***, which regroups the fossil woods of *Castanea*, *Castanopsis* and some species of *Quercus* and *Lithocarpus*. At the specific level, the wood was identified as *Castanoxylon bavaricum*, similar to the modern *Castanea*.

Concerning the **general aspects of Example 3** relative to the 'Whole-Plant' concept, it seems that in *Castanea* there is a systematic ***importance of crystalliferous wood parenchyma*** at the specific level. The problem of ***lack of comparative material of rare modern wood***, especially Chinese woods, arose during the searching of the nearest living relatives for *Castanoxylon bavaricum*. Finally, the wood of *C. bavaricum* was associated with the leaf fragment of cf. *Castanea atavia* the neighbouring locality of Nesuchyně. As the leaf and the wood were not found in direct connection or even association, this is a ***plausible but uncertain combination of organs***.

   Example 4 - A fossil angiosperm wood was described for the first time from **Bílina** (Early Miocene, Most Basin). The fossil wood with prominent ring porous pattern, wavy grouping of late wood pores and early wood pores in 1-3 tangential rows, homocellular rays mostly 4-5 cells wide, and crystalliferous parenchyma was attributed to ***Ulmoxylon - U. marchesonii***. The fossil can be compared to extant North American soft elms, as well as to *Ulmus macrocarpa* and *U. parvifolia* from China and to *U. carpinifolia* from Europe. In Bílina, the fossil wood was associated with the foliage and samaras of *Ulmus pyramidalis.*

Concerning the **general aspects of Example 4** relative to the 'Whole-Plant' concept, it was showed how important can be the ***influence of preservation on wood structure*** in the case of two specimens of *U. marchesonii*, very different from each other at first sight. Another kind of non-systematical differences has already been described between the ***stem and root wood*** on the fossil material from the Eocene of the Paris Basin. Finally, the fossil elm of Bílina demonstrated a typical ***'mosaic' species*** where each part of the plant showed relationship to a different living relative.

   Example 5 - A twig with attached leaves and capsules containing seeds was recovered in **Bílina** (Early Miocene, Most Basin) and identified as ***Decodon***. The seeds correspond to *Decodon gibbosus*, the foliage matches that which had been called *Ficus multinervis* or *Apocynophyllum helveticum*, and the whole fossil plant was designated *Decodon gibbosus*. This species differs from the modern *D. verticillatus* from eastern North America by a narrower triangular shape of seeds in transverse section and the thicker spongy layer of the testa on the dorsal side. The leaves are also slightly different. Concerning the **general aspects of Example 5** relative to the 'Whole-Plant' concept, two main principles of nomenclature, ***priority principle and stability of nomenclature***,

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were compared in order to attribute a correct name to the entire fossil twig. During searching for the nearest living relative of the fossil *Decodon*, the **modern endemism of Tertiary Holarctic elements** was pointed out as a rather frequent phenomenon. Finally, the leafy twig of *Decodon* represents a rare case of interattached organs in the fossil record and **the ideal state of the 'Whole-Plant' palaeobotany**.

The example of the Tertiary of northwestern Bohemia presented several aspects of the complexity of the 'Whole-Plant' concept, including some obstacles to be avoided. The main purpose of this approach is to deduce the systematic reconstitution of fossil plants. However, any subsequent method, no matter how sophisticated (reconstruction of climate, various analyses etc.), cannot lead to correct conclusions without accurate systematic description and attribution.

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Le concept de 'Plante Entière' en paléobotanique
appliqué au Tertiaire
de la Bohême du Nord-Ouest, République Tchèque,
avec une référence particulière au bois fossile

- Résumé -

L'objectif ultime en paléobotanique est la reconstitution d'un organisme complet - la plante fossile entière - et de son évolution dans le temps et l'espace. Néanmoins, les plantes sont présentes dans les couches fossiles principalement à l'état désarticulé sous forme d'organes isolés. L'approche connue actuellement comme **le concept de 'Plante Entière'** combine les organes détachés pour reconstituer la plante entière, comme elle a réellement existé et a vécu dans le passé.

Le Tertiaire de la Bohême du Nord-Ouest (République Tchèque) a été choisi comme une région idéale pour illustrer les principes du concept de 'Plante Entière' avec une référence particulière au bois fossile. Il y a deux raisons principales à ce choix. Premièrement, divers organes de plante tels que feuilles fossiles, bois, fleurs, pollen dispersé et in situ, fruits et graines y sont fréquemment présents en association (in)directe. Deuxièmement, le Tertiaire de la Bohême du Nord-Ouest représente un territoire classique de la recherche paléobotanique, qui a été, à l'exception du bois fossile, étudié de façon intensive jusqu'à présent.

Le Tertiaire de la Bohême du Nord-Ouest s'étend dans la partie Nord-Ouest de la République Tchèque comme une zone continue de complexes magmatiques et sédimentaires, parallèle à la frontière Tchéco-Allemande. Cette étude s'est limitée à trois régions : de l'Ouest à l'Est **les Montagnes de Doupovské hory, le Bassin de Most et les Montagnes de České středohoří**, qui sont tous liés au système du graben d'Ohře, une zone de dépression orientée dans la direction SO-NE. L'âge des roches fossilifères se situe principalement entre l'Éocène supérieur et le Miocène inférieur.

Les exemples concrets et les aspects généraux du concept de 'Plante Entière' consistent en **cinq études de cas** : le premier exemple traite d'un bois de gymnosperme, les trois études suivantes ont décrit des bois d'angiospermes et le dernier concerne des structures reproductives. **Cinq publications** (1 - Sakala 2003a, 2 - Sakala & Privé-Gill 2004, 3 - Sakala & Teodoridis 2001, 4 - Sakala 2002, 5 - Kvaček &

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Sakala 1999), qui peuvent etre trouvées en forme intégrale dans le texte représentent une partie essentielle de chaque exemple (étude de cas) ainsi que de la thèse en général.

Exemple 1 - Le grand tronc silicifié de **Kučlín** (Éocène supérieur, Montagnes de České středohoří), que l'on croyait etre le bois d'un conifère éteint *Doliostrobus*, a été nouvellement réinterprété comme un bois de *Tetraclinis* - **Tetraclinoxylon**. Cette révision repose sur les ponctuations de champs de croisement de type exclusivement cupressoide et sur la forme des trachéides qui est sensiblement ronde dans la coupe transversale. Le bois est associé avec de rares branches et graines de *Tetraclinis salicornioides* dans le même gisement.

Concernant les **aspects généraux de l'Exemple 1** liés au concept de 'Plante Entière', les ponctuations de champs de croisement entre notre bois et la branche de *Doliostrobus* sont trop différentes pour être interprétées comme des ***différences dans les ponctuations de champs de croisement entre le bois de tronc et de branche*** de la même espèce. La différence entre les ***aspects systématiques et écologiques du taxon équivalent moderne le plus proche*** apparaît aussi si l'on considère que *Tetraclinis salicornioides*, associé à Kučlín avec *Tetraclinoxylon vulcanense*, a été systématiquement comparé au moderne *Tetraclinis articulata*. Du point de vue écologique, ce taxon est cependant plus proche de la seconde espèce fossile - *T. brachyodon*. Finalement, le problème général de la ***divergence entre l'évidence fossile du bois et des autres organes*** apparaît sur *Tetraclinis* du Tertiaire d'Europe qui présente deux espèces bien définies par des cônes, graines et feuillage alors que l'on recense six espèces de *Tetraclinoxylon*.

Exemple 2 - Un tronc calcifié de **Kadaň – Zadní vrch** (Oligocène, Montagnes de Doupovské hory) a été identifié comme ***Cercidiphylloxylon kadanense*** et désigné en tant qu'un épitype de *C. kadanense* ainsi que de *Cercidiphylloxylon*, les deux taxons ayant été définis précédemment dans le même gisement. La diagnose modifiée de *C. kadanense* et *Cercidiphylloxylon* mentionne des rayons plus larges, et pour *C. kadanense* la présence de cristaux dans les rayons et la densité des barres dans les perforations scalariformes. Le bois de *C. kadanense* peut être associé avec *Cercidiphyllum crenatum* connu dans le Tertiaire de la Bohême du Nord-Ouest par des feuilles, fruits, graines, inflorescences mâles et pollen in situ. Un bois fossile similaire de **Žichov** (Oligocène supérieur, Montagnes de České středohoří), avec des barres moins nombreuses et moins denses, a été attribué à ***Liquidambaroxylon speciosum***, qui représente le bois de *Liquidambar*.

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Concernant les **aspects généraux de l'Exemple 2** liés au concept de 'Plante Entière', la seconde espèce de *Cercidiphylloxylon - C. spenceri* nous rappelle que dans le Tertiaire d'Europe on peut toujours rencontrer le ***bois de plantes éteintes***, appartenant à des genres botaniques qui n'existent plus. L'observation des ***rayons et des perforations scalariformes*** a révélé que le nombre de barres dans les perforations scalariformes présentait un critère fiable pour différencier le bois de *Cercidiphyllum* actuel des bois similaires des Hamamelidaceae. Finalement, le problème du ***bois similaire dans les taxa non apparentés systématiquement*** a été démontré en évoquant la similarité entre le bois de *Nyssa* et celui de *Cercidiphyllum*, deux éléments importants de la flore du Tertiaire de la Bohême du Nord-Ouest.

Exemple 3 - Un grand tronc silicifié de **Velká Černoc** (Oligocène supérieur, Bassin de Most), avec un bois à zones poreuses, des vaisseaux relativement grands, solitaires pour la plupart dans le bois initial, un arrangement caractéristique en flammes des pores dans le bois final, des rayons unisériés à bisériés, du parenchyme apotrachéal diffus et des trachéides, peut être attribué au morphogenre ***Castanoxylon***, qui regroupe les bois fossiles de *Castanea*, *Castanopsis* et quelques espèces de *Quercus* et *Lithocarpus*. Au niveau spécifique, le bois a été identifié comme *Castanoxylon bavaricum*, similaire au *Castanea* actuel.

Concernant les **aspects généraux de l'Exemple 3** liés au concept de 'Plante Entière', il semble que dans le cas de *Castanea*, il y a une ***importance du parenchyme crystallifère*** au niveau systématique spécifique. Le problème du ***manque de matériel comparatif des rares bois actuels***, surtout des bois de Chine, est apparu pendant la recherche du taxon équivalent moderne le plus proche de *Castanoxylon bavaricum*. Finalement, le bois de *C. bavaricum* a été associé avec un fragment de feuille de cf. *Castanea atavia* du gisement voisin de Nesuchyně. Comme la feuille et le bois n'ont pas été trouvés en connexion directe meme pas associés, il s'agit d'une ***combinaison d' organes plausible mais incertaine***.

Exemple 4 - Un bois fossile d'angiosperme a été décrit pour la première fois à **Bílina** (Miocène inférieur, Bassin de Most). Le bois fossile à zones poreuses avec des pores du bois final en forme de vagues et les pores du bois initial en 1-3 bandes tangentielles, des rayons homogènes larges de 4-5 cellules et du parenchyme crystallifère, a été attribué à ***Ulmoxylon*** - *U. marchesonii*. Le fossile peut être comparé aux ormes tendres ("soft elms") de l'Amérique du Nord, ainsi qu'à *Ulmus macrocarpa* et *U. parvifolia* de Chine ou à *U. carpinifolia*, l'orme commun d'Europe. A Bílina, le bois fossile a été associé avec les feuillage et samares d'*Ulmus pyramidalis.*

Concernant les **aspects généraux de l'Exemple 4** liés au concept de 'Plante Entière', il a été démontré dans le cas des deux spécimens de *U. marchesonii*, très différents l'un de l'autre à première vue, à quel point l'***influence de la préservation sur la structure de bois*** peut être importante. Un autre type de différences non-systématiques a déjà été décrit entre le ***bois de tige et de racine*** sur le matériel fossile de l'Éocène du Bassin de Paris. Finalement, l'orme fossile de Bílina a indiqué une ***espèce en 'mosaïque'*** typique où chaque partie de la plante présente des affinités avec un taxon analogue actuel différent.

Exemple 5 - Une branche avec des feuilles et des capsules à graines attachées a été découverte à **Bílina** (Miocène inférieur, Bassin de Most) et identifiée comme ***Decodon***. Les graines correspondent à *Decodon gibbosus*, les feuilles correspondent bien avec celles qui ont été appelées *Ficus multinervis* ou *Apocynophyllum helveticum*, et la plante fossile entière a été désignée *Decodon gibbosus*. Cette espèce diffère de l'espèce actuelle *D. verticillatus* de la partie orientale de l'Amérique du Nord, par la forme en triangle plus étroit des graines en coupe transversale et par la couche spongieuse plus épaisse de la testa sur son côté dorsal. Les feuilles sont aussi légèrement différentes.

Concernant les **aspects généraux de l'Exemple 5** liés au concept de 'Plante Entière', deux principes fondamentaux de la nomenclature, les ***principes de priorité et de stabilité de nomenclature***, ont été appliqués pour pouvoir attribuer un nom correct à la branche fossile entière. A propos de la recherche du taxon équivalent moderne le plus proche du *Decodon* fossile, l'***endémisme actuel des éléments à distribution Holarctique dans le Tertiaire*** a été remarqué comme un phénomène plutôt fréquent. Finalement, la branches à feuilles et à capsules de *Decodon* présente une des rares évidences fossiles et ***l'état idéal en paléobotanique de la notion de 'Plante Entière'.***

L'exemple du Tertiaire de la Bohême du Nord-Ouest a présenté quelques aspects de la complexité du concept de 'Plante Entière' y compris les obstacles à éviter. L'objectif principal de cette approche est la reconstitution systématique d'une plante fossile. Néanmoins, sans description et attribution systématiques précises, aucune des applications postérieures quel que soit leur degré de sophistication (reconstitution du climat, analyses diverses etc.) ne peut aboutir à des conclusions correctes.

Celostní přístup v paleobotanice
na příkladu třetihor severozápadních Čech
se speciálním zřetelem na fosilní dřeva

- Shrnutí -

Konečným cílem paleobotaniky je rekonstrukce úplného organismu - celé fosilní rostliny - a jeho vývoje v čase a prostoru. Nicméně rostliny jsou ve fosilním záznamu v naprosté většině přítomny coby jednotlivé izolované orgány. Přístup v současnosti známý jako **celostní přístup** tyto jednotlivé orgány kombinuje a snaží se zrekonstruovat celou rostlinu tak, jak kdysi skutečně vypadala a žila.

Třetihory severozápadních Čech byly zvoleny coby oblast ideální pro ilustraci základních principů celostního přístupu se speciálním zřetelem na fosilní dřeva. Pro tento výběr byly dva základní důvody. Především se zde hojně nacházejí rozličné rostlinné orgány jako fosilní listy, dřevo, květy, disperzní pyl a pyl in situ, plody a semena společně v (ne)přímé asociaci. Za druhé pak třetihory severozápadních Čech představují klasickou oblast paleobotanického výzkumu, která je až do dnešních dnů intenzívně studována, snad jen s výjimkou fosilních dřev.

Třetihory severozápadních Čech se rozkládají v severozápadní části České republiky coby souvislé pásmo magmatických a sedimentárních hornin, rovnoběžné s česko-německou hranicí. Předkládaná práce se omezila na tři oblasti: od západu na východ **Doupovské hory, mostecká pánev, České středohoří**, které jsou všechny vázány na systém oherského riftu, depresní zóny JZ-SV směru. Stáří fosiliferních hornin se zde převážně pohybuje mezi pozdním eocénem a raným miocénem.

Konkrétní příklady, jakož i obecné aspekty celostního přístupu, byly demonstrovány v **pěti studiích**: první z nich si všímá dřeva nahosemenné dřeviny, následující pět popisuje dřeva listnatých dřevin a konečně poslední se týká rozmnožovacích orgánů. **Pět publikací** (1 - Sakala 2003a, 2 - Sakala & Privé-Gill 2004, 3 - Sakala & Teodoridis 2001, 4 - Sakala 2002, 5 - Kvaček & Sakala 1999), které je možné nalézt v úplném znění v rámci textu, představuje nejdůležitější část každého příkladu (studie), jakož i celé doktorské práce.

Příklad 1 – Velký prokřemenělý kmen z **Kučlína** (pozdní eocén, České středohoří), o kterém jsme se domnívali, že představuje dřevo vyhynulého jehličnanu *Doliostrobus*, byl nově interpretován coby dřevo jehličnanu *Tetraclinis* - **Tetraclinoxylon**. Nová

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interpretace se opírá o typ ztenčenin křížových políček, který je výlučně cupressoidní a nápadně kruhovitý tvar tracheid na příčném průřezu. Dřevo bylo dáno do spojitosti s nehojnými větvičkami a semeny *Tetraclinis salicornioides* ze stejné lokality.

Co se týče **obecných aspektů Příkladu 1** ve vztahu k celostnímu přístupu, rozdíl mezi ztenčeninami křížových políček tohoto dřeva a větvičkou *Doliostrobus* je natolik významný, než aby mohl být vysvětlen ***rozdílností ztenčenin křížových políček mezi dřevem kmene a větve*** u stejného druhu. Ukázal se rovněž rozdíl mezi **aspektem systematickým a ekologickým téhož nejbližšího žijícího příbuzného**, když byl fosilní druh *Tetraclinis salicornioides*, spojovaný na Kučlíně se dřevem *Tetraclinoxylon vulcanense*, přirovnáván ze systematického hlediska k dnešnímu druhu *Tetraclinis articulata*. Z hlediska ekologického je však tento žijící druh bližší druhému fosilnímu druhu - *T. brachyodon*. Konečně obecný problém **nesouladu mezi záznamem fosilních dřev a ostatními orgány** byl jasně vidět na příkladu rodu *Tetraclinis* v evropských třetihorách. Jsou známé pouze dva druhy tohoto rodu, velmi dobře definované na šišticích, semenech a olistění, zatímco na základě dřeva jich existuje šest, resp. je šest druhů morforodu *Tetraclinoxylon*.

Příklad 2 – Kalcifikovaný kmen z **Kadaně – Zadního vrchu** (oligocén, Doupovské hory) byl určen jako ***Cercidiphylloxylon kadanense*** a stanoven coby epityp druhu *C. kadanense*, jakož i rodu *Cercidiphylloxylon*, tj. taxonů, které byly definovány dříve ze stejné lokality. Pozměněná diagnóza těchto taxonů uvádí širší dřeňové paprsky a v případě *C. kadanense* přítomnost krystalů v paprscích a hustotu otvorů u schodovitých perforací cév. Dřevo *C. kadanense* je možné spojit se druhem *Cercidiphyllum crenatum* známým ve třetihorách severozápadních Čech svými listy, plody, semeny, samčími květenstvími a pylem in situ. Podobné dřevo z lokality **Žichov** (pozdní oligocén, České středohoří), ale s menším počtem a řidšími otvory u schodovitých perforací, bylo přiřazeno ke druhu ***Liquidambaroxylon speciosum***, které představuje dřevo ambroně (rod *Liquidambar*).

Co se týče **obecných aspektů Příkladu 2** ve vztahu k celostnímu přístupu, druhý druh rodu *Cercidiphylloxylon - C. spenceri* připomíná fakt, že se ve třetihorách Evropy stále setkáváme se ***dřevem vyhynulých rostlin***, které odpovídá již vymřelým botanickým rodům. Srovnávací studie moderních dřev, konkrétně jejich ***dřeňových paprsků a schodovitých perforací cév*** odhalila, že počet otvorů u perforací představuje spolehlivé kritérium pro odlišení rodu *Cercidiphyllum* od podobných zástupců čeledi Hamamelidaceae. Konečně problém ***podobných dřev u systematicky nepříbuzných***

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taxonů byl demonstrován na podobnosti mezi dřevy rodu *Nyssa* a *Cercidiphyllum*, dvou významných elementů květeny třetihor severozápadních Čech.

Příklad 3 – Velký prokřemenělý kmen z lokality **Velká Černoc** (pozdní oligocén, mostecká pánev), se dřevem kruhovitě pórovitým, relativně velkými, převážně samostatnými cévami jarního dřeva a póry pozdního dřeva vybíhajícími do typického tvaru plamenů, se dřeňovými paprsky jedno- až dvouvrstevnými, s apotracheálním roztroušeným parenchymem a s tracheidami, může být přiřazen k morforodu ***Castanoxylon***, který seskupuje fosilní dřeva rodů *Castanea*, *Castanopsis* a několik druhů rodu *Quercus* a *Lithocarpus*. Na druhové úrovni bylo fosilní dřevo určeno jako *Castanoxylon bavaricum*, který odpovídá dnešnímu kaštanovníku (rod *Castanea*).

Co se týče **obecných aspektů Příkladu 3** ve vztahu k celostnímu přístupu, zdá se, že v případě rodu *Castanea* je ***význam přítomnosti krystalů v podélném parenchymu*** systematický, a to na úrovni druhu. Problém ***nedostupnosti srovnávacího materiálu vzácných současných dřev***, především pak těch čínských, vyvstal v průběhu hledání nejbližšího žijícího příbuzného ke druhu *Castanoxylon bavaricum*. Konečně dřevo *C. bavaricum* bylo dáno do spojitosti s fragmentem listu cf. *Castanea atavia* ze sousední lokality Nesuchyně. Jelikož ale list a dřevo nebyly nalezeny v přímém spojení, ale ani ve vzájemné asociaci, jedná se o ***kombinaci orgánů možnou, nicméně nejistou***.

Příklad 4 – Dřevo krytosemenné rostliny bylo vůbec poprvé popsáno z lokality **Bílina** (raný miocén, mostecká pánev). Dřevo kruhovitě pórovité s póry pozdního dřeva uspořádanými ve vlnkách a 1-3 tangenciálními pásy pórů jarního dřeva, s homogenními 4-5 buněk širokými dřeňovými paprsky a s podélným parenchymem s krystaly bylo přiřazeno k rodu ***Ulmoxylon***, druhu *U. marchesonii*. Fosilní dřevo připomíná tzv. "měkké" severoamerické jilmy, rovněž čínské druhy *Ulmus macrocarpa* nebo *U. parvifolia*, popř. běžný evropský habrolistý jilm *U. carpinifolia*. Na Bílině je fosilní dřevo spojováno s olistěním a nažkami druhu *Ulmus pyramidalis.*

Co se týče **obecných aspektů Příkladu 4** ve vztahu k celostnímu přístupu, bylo na příkladě dvou na první pohled velmi rozdílných vzorků druhu *U. marchesonii* zřetelně ukázáno, do jaké míry může být důležitý ***vliv zachování na strukturu dřeva***. Podobná, rovněž ne-systematická, odlišnost byla také popsána mezi ***dřevem stonku a kořenu*** na materiálu z eocénu pařížské pánve. Konečně jilm z lokality Bílina názorně ilustruje typický případ tzv. ***'mozaikového' druhu***, kde každá část rostliny jeví příbuznost s jiným nejbližším žijícím příbuzným.

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Příklad 5 - Větvička s přisedlými listy a tobolkami obsahujícími semena byla nalezena na **Bílině** (raný miocén, mostecká pánev) a určena jako *Decodon*. Semena náleží druhu *Decodon gibbosus*, listy odpovídají olistění tradičně označovanému *Ficus multinervis* nebo *Apocynophyllum helveticum*, celá rostlina pak byla pojmenována *Decodon gibbosus*. Tento druh se liší od jediného současného zástupce rodu, druhu *D. verticillatus* z východní části Severní Ameriky, užším trojúhelníkovitým tvarem semen v příčném řezu a silnější houbovitou vrstvou testy na dorzální straně semene. Fosilní listy jsou rovněž lehce odlišné.

Co se týče **obecných aspektů Příkladu 5** ve vztahu k celostnímu přístupu, dva základní principy nomenklatury, ***princip priority a princip stability nomenklatury***, byly vyhodnoceny tak, aby celá plodná větvička byla nomenklatoricky správně pojmenována. Při hledání nejbližšího žijícího příbuzného fosilního zástupce rodu *Decodon* bylo konstatováno, že ***současný endemismus rostlin s holarktickým rozšířením ve třetihorách*** je jev relativně velmi běžný. Konečně plodná větvička rodu *Decodon*, tj. s listy, plody a semeny v přímém organickém spojení, představuje velice vzácný případ a především pak ***ideální stav celostní paleobotaniky.***

Příklad třetihor severozápadních Čech ukázal celostní přístup v celé jeho složitosti, včetně nástrah, jichž je potřeba se vyvarovat. Hlavním cílem tohoto přístupu je systematická rekonstrukce fosilních rostlin. Nicméně, bez základního systematického popisu a přesné biologické klasifikace přinesou jakékoliv následné aplikace, byť jsou sebesofistikovanější (rekonstrukce klimatu, rozličné analýzy atd.), nepřesné výsledky.