

# 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* Goepfert 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* Goepfert, 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***

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## 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 *Taxodioxydon* [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].

### 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 samaras [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 xylène, 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].

## 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

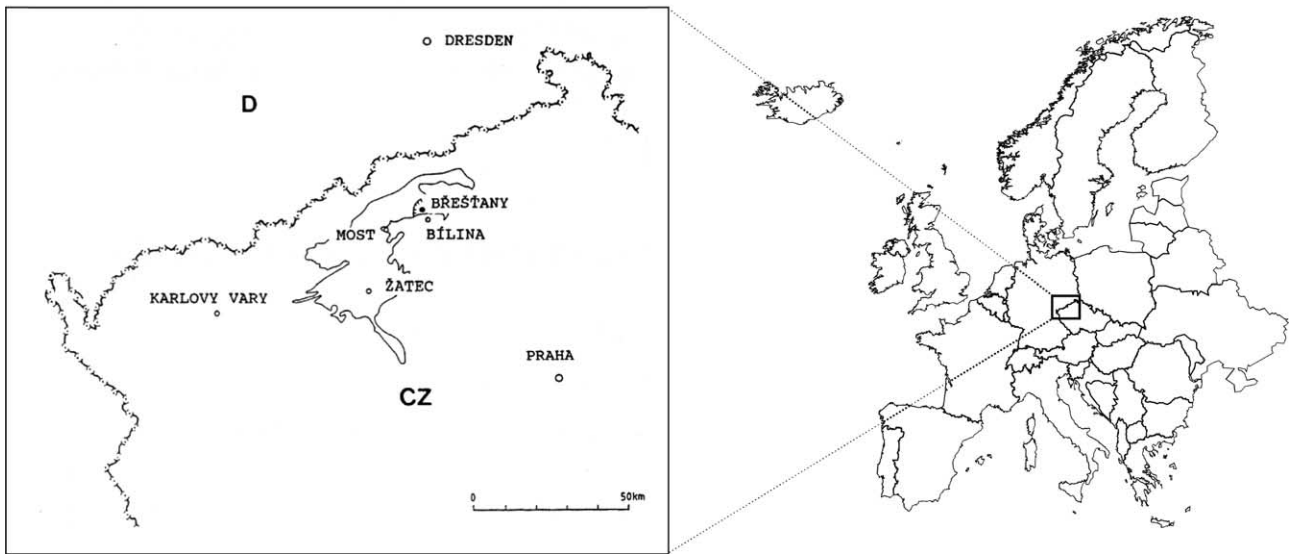
Family Ulmaceae

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 Břilina 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 Břilina 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.

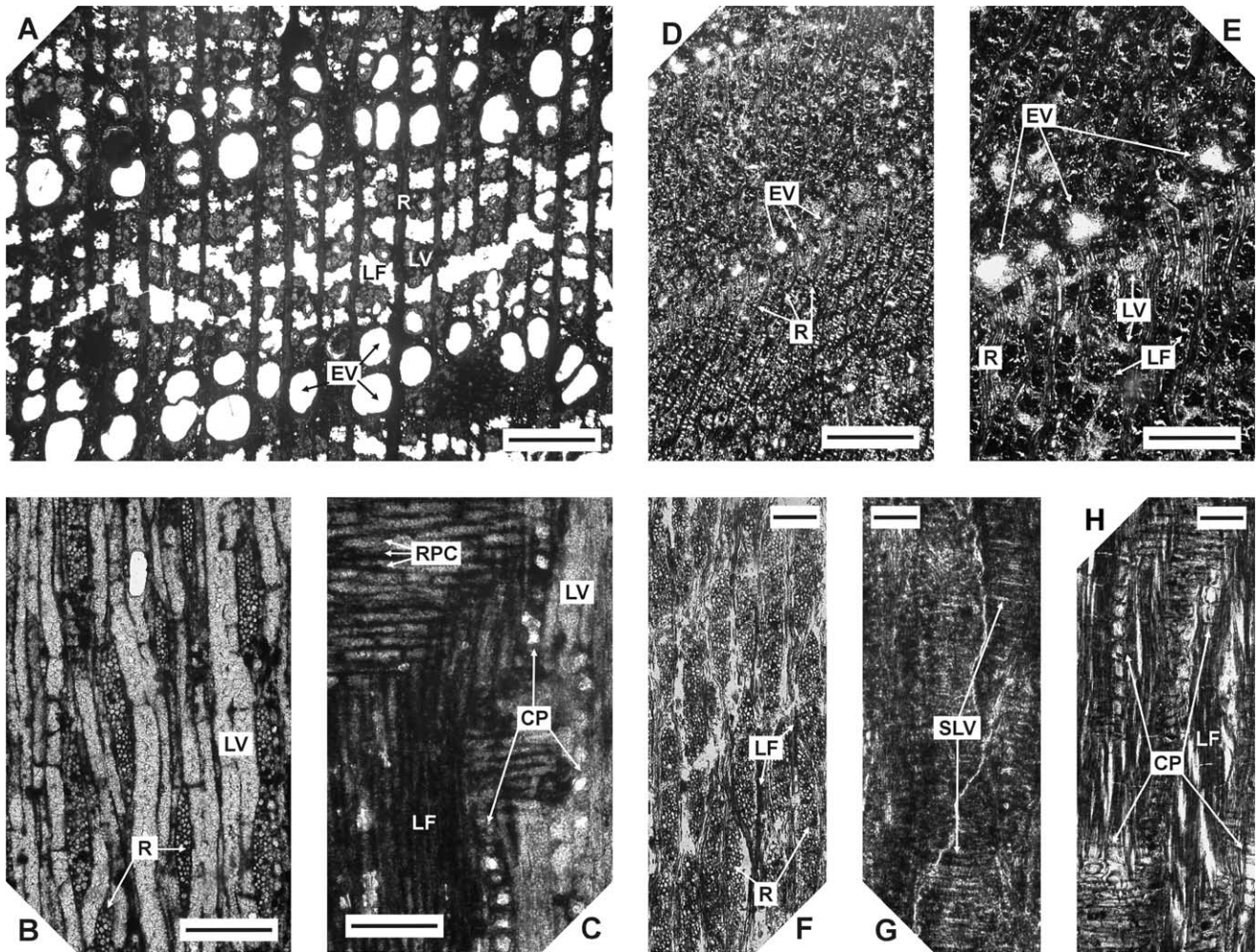
*Fibres:* libriform, polygonal in cross-section, irregularly densely arranged; tangential and radial diameter 10–20 μm; fibre walls 3–5 μm thick; tracheids not observed.

## 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



**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  $\mu\text{m}$ . **B.** Tangential section. **R**, rays; **LV**, latewood vessels. Scale bar = 200  $\mu\text{m}$ . **C.** Radial section. **RPC**, procumbent ray cells; **LV**, latewood vessels; **LF**, libriform fibres; **CP**, crystalliferous parenchyma. Scale bar = 100  $\mu\text{m}$ . **D–H** *Ulmoxylon marchesonii*; xylitic specimen (No. 16/98). **D.** Cross-section. **EV**, earlywood vessels; **R**, rays. Scale bar = 500  $\mu\text{m}$ . **E.** Cross-section; detail. **EV**, earlywood vessels; **LV**, latewood vessels; **LF**, libriform fibres; **R**, rays. Scale bar = 200  $\mu\text{m}$ . **F.** Tangential section. **LF**, libriform fibres; **R**, rays. Scale bar = 100  $\mu\text{m}$ . **G.** Tangential section. **SLV**, spirals in latewood vessels. Scale bar = 50  $\mu\text{m}$ . **H.** Radial section. **LF**, libriform fibres; **CP**, crystalliferous parenchyma. Scale bar = 50  $\mu\text{m}$ .

**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  $\mu\text{m}$ . **B.** Section tangentielle. **R**, rayons; **LV**, vaisseaux du bois final. Échelle = 200  $\mu\text{m}$ . **C.** Section radiale. **RPC**, cellules couchées de rayons; **LV**, vaisseaux du bois final; **LF**, fibres libriformes; **CP**, parenchyme cristallifère. Échelle = 100  $\mu\text{m}$ . **D–H** *Ulmoxylon marchesonii*; spécimen en xylain (No. 16/98). **D.** Section transversale. **EV**, vaisseaux du bois initial; **R**, rayons. Échelle = 500  $\mu\text{m}$ . **E.** Détail de la section transversale. **EV**, vaisseaux du bois initial; **LV**, vaisseaux du bois final; **LF**, fibres libriformes; **R**, rayons. Échelle = 200  $\mu\text{m}$ . **F.** Section tangentielle. **LF**, fibres libriformes; **R**, rayons. Échelle = 100  $\mu\text{m}$ . **G.** Section tangentielle. **SLV**, spirales dans les vaisseaux du bois final. Échelle = 50  $\mu\text{m}$ . **H.** Section radiale. **LF**, fibres libriformes; **CP**, parenchyme cristallifère. Échelle = 50  $\mu\text{m}$ .

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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## References

- [1] E. Biondi, *Ulmoxydon marchesonii* n. sp. di legno fossile rinvenuta sui Monti Sibillini (Appennino Centrale), Studi trent. Sci. nat. 58 (1981) 77–91.
- [2] D. Březinová, Zkřemenělé dřevo z dolu Vrbenský, Geologický výzkum v SHR 1964 (1964) 37–39.
- [3] Č. Bůžek, Tertiary flora of the northern part of Pětipsy area (North-Bohemian Basin), Rozpr. Ústř. Úst. geol. 36 (1971) 1–118.
- [4] Č. Bůžek, Z. Dvořák, Z. Kvaček, M. Prokš, Tertiary vegetation and depositional environments of the 'Bílina delta' in the North-Bohemian brown-coal basin, Čas. Miner. Geol. 37 (1992) 117–134.
- [5] P. Greguss, Tertiary Angiosperm Woods in Hungary, Akadémiai Kiadó, Budapest, 1969.
- [6] D. Grosser, Die Hölzer Mitteleuropas, Springer-Verlag, Berlin, Heidelberg, New York, 1977.
- [7] Z. Kvaček, Bílina: a window on Early Miocene marshland environments, Rev. Palaeobot. Palynol. 101 (1998) 111–123.
- [8] D.H. Mai, Tertiäre Vegetationsgeschichte Europas, Gustav Fischer Verlag, Jena, Germany, 1995.
- [9] C.R. Metcalfe, L. Chalk, Anatomy of the Dicotyledons, Vol. 2, Clarendon Press, Oxford, 1950.
- [10] U. Prakash, E.S. Barghoorn, Miocene fossil woods from the Columbia basalts of Central Washington, II, J. Arnold Arbor. 42 (1961) 347–362.
- [11] C. Privé, R. Brousse, Bois fossiles de la nappe de ponces villafranchienne à la Bastide-du-Fau (Cantal), 8<sup>e</sup> congrès INQUA, Paris, Et. Quat. Monde 1969 (1969) 233–263.
- [12] J. Prokop, S. Bílý, *Dicerca bilinica* sp. n., a new species of buprestid-beetle (Coleoptera: Buprestidae) from Lower Miocene of the Most formation in northern part of the Czech Republic, Acta Soc. Zool. Bohem. 63 (1999) 311–314.
- [13] J. Prokop, M. Boulard, *Tibicina sakalai* n. sp., Cigale fossile du Miocène inférieur de Tchecoslovaquie, EPHE, Biol. Evol. Insectes 13 (2000) 127–131.
- [14] J. Prokop, A. Nel, Tertiary termite from the Bílina mine in northern Bohemia (Isoptera: Hodotermitidae), Klapalekiana 35 (1999) 141–144.
- [15] J. Prokop, A. Nel, *Merlax bohemicus* gen. n., sp. n., a new fossil dragonfly from the Lower Miocene of northern Bohemia (Odonata: Aeshnidae), Eur. J. Entomol. 97 (2000) 427–431.
- [16] J. Prokop, A. Nel, First record of the genus *Lethocerus* Mayr, 1853, from the Lower Miocene of the Most Formation in northern Bohemia, Czech Republic (Heteroptera, Belostomatidae), Bull. Soc. Entomol. France 105 (2000) 491–495.
- [17] J. Sakala, Flora and vegetation of the roof of the main lignite seam in the Bílina Mine (Most Basin, Lower Miocene), Acta Mus. Nat. Pragae, Ser. B, Hist. Nat. 56 (2000) 49–84.
- [18] J. Sakala, V. Teodoridis, Fossil wood and foliage of *Castanea* (Fagaceae) from the Upper Oligocene of northern Bohemia, Bull. Czech Geol. Surv. 76 (2001) 23–28.
- [19] F.R. Schweingrüber, Mikroskopische Holz Anatomie, Eidgenössische Forschungsanstalt für Wald, Schnee und Landschaft, Birmensdorf, Germany, 1978.
- [20] A. Selmeier, Silicified Miocene woods from the North Bohemian Basin (Czech Republic) and from Kuzuluk, district Adapazari (Turkey), Mitt. Bayer. Staatsslg. Paläont. hist. Geol. 41 (2001) 111–144.
- [21] G. Starostin, N. Trelea, Studiu paleoxilologic al florei din Miocenul Moldovei, Anal. științ. Univ. Al. I. Cuza Secț. Ila 15 (1969) 447–451.
- [22] K. von Sternberg, Versuch einer geognostisch-botanischen Darstellung der Flora der Vorwelt, J. Spurny, Gottlieb Haase, Prague (1820–1838).
- [23] E.M. Sweitzer, Comparative anatomy of Ulmaceae, J. Arnold Arbor. 52 (1971) 523–585.
- [24] S. Watari, Dicotyledonous Woods from the Miocene along the Japan Sea side of Honsyu, J. Fac. Sci. Univ. Tokyo III 6 (1952) 97–134.
- [25] E.A. Wheeler, C.A. LaPasha, R.B. Miller, Wood anatomy of elm (*Ulmus*) and hackberry (*Celtis*) species native to the United States, Iawa Bull. n.s. 10 (1989) 5–26.
- [26] Y. Zhong, P. Baas, E.A. Wheeler, Wood anatomy of trees and shrubs from China. IV. Ulmaceae, Iawa Bull. n.s. 13 (1992) 419–453.