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CENOMANIAN ANGIOSPERM WOOD FROM THE BOHEMIAN CRETACEOUS BASIN, CZECH REPUBLIC

Vladimír Gryc[1], **Hanuš Vavrčík**[1] and **Jakub Sakala**[2]

SUMMARY

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

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

INTRODUCTION

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

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1) Mendel University of Agriculture and Forestry in Brno, Faculty of Forestry and Wood Technology, Department of Wood Science, Zemědělská 3, 613 00 Brno, Czech Republic [E-mail: gryc@mendelu.cz].

2) Charles University in Prague, Faculty of Science, Institute of Geology and Palaeontology, Albertov 6, 128 43 Praha, Czech Republic [E-mail: rade@natur.cuni.cz].

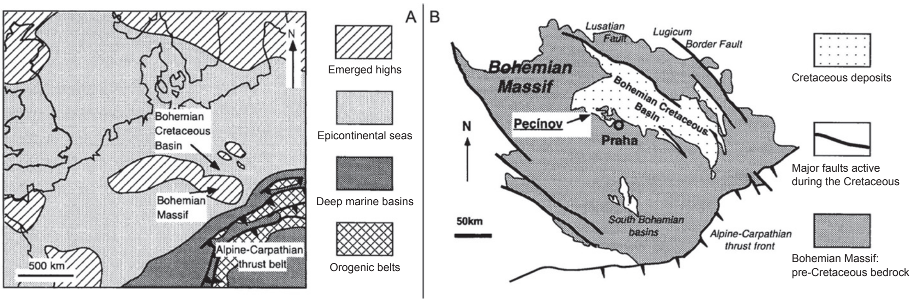

Figure 1. Palaeogeographical position of the Bohemian Cretaceous Basin in Central Europe during the early Turonian peak flooding (A) and the Bohemian Cretaceous Basin in the tectonic framework of the Bohemian Massif with the position of the Pecínov quarry (B) (from Uličný *et al*. 1997a).

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

MATERIAL AND METHODS

Silicified wood (two specimens UK 102/04 & UK 103/04) was thin-sectioned in compliance with the standard techniques (Hass & Rowe 1999) and studied using compound light microscopy. The anatomical description is in accordance with the IAWA Hardwood List (IAWA Committee 1989). Remains of the original specimens and thin sections described herein are housed in the Chlupáč Museum of Earth History at the Faculty of Science of the Charles University in Prague.

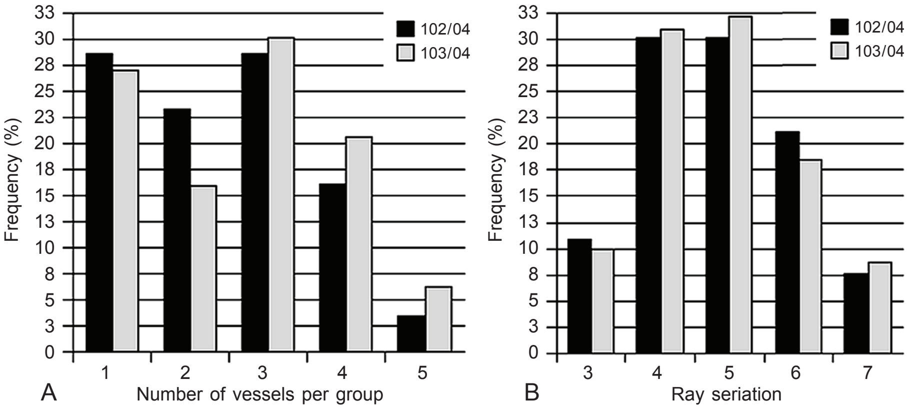

Figure 2. Frequency of solitary vessels and vessels in radial multiples of 2, 3, 4, and 5 (A) and ray widths (B) for samples 102/04 and 103/04.

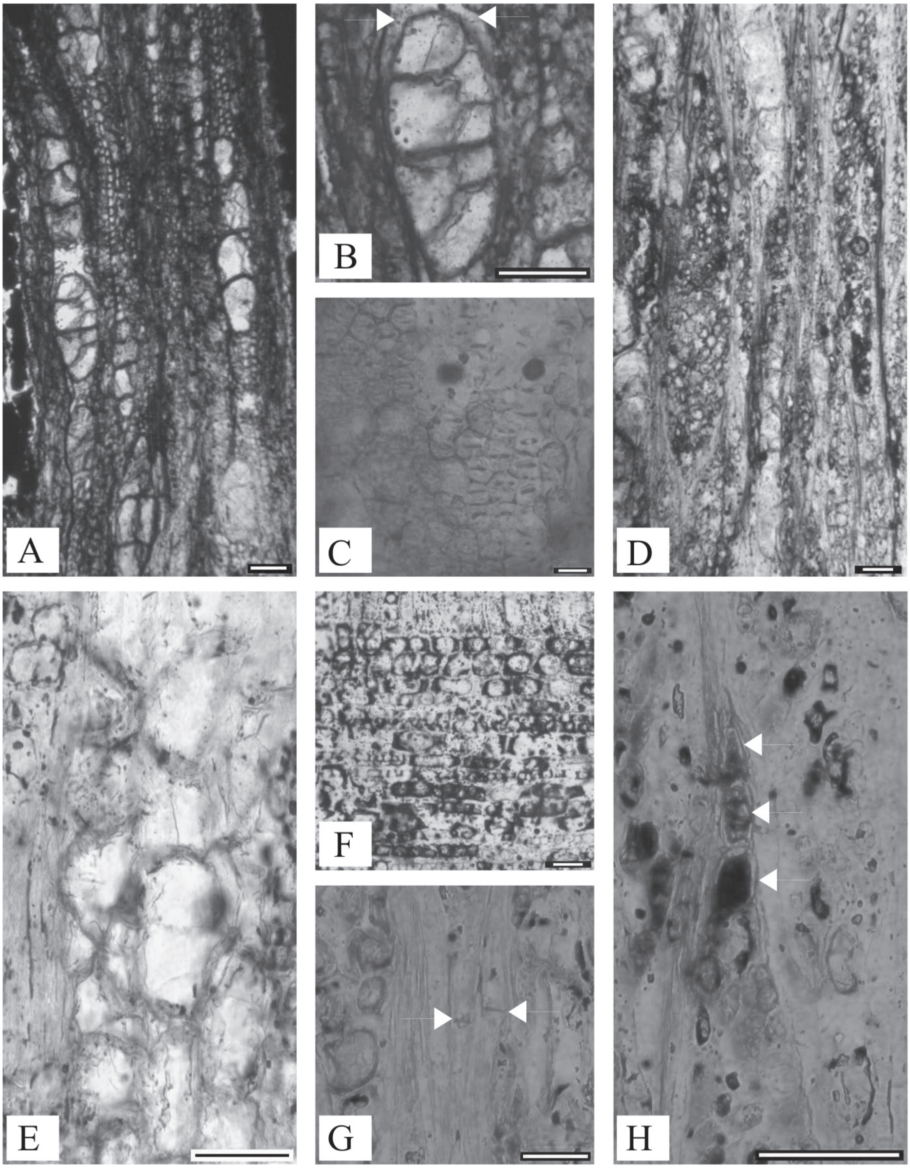

Figure 3. *Paraphyllanthoxylon* aff. *utahense* (A–H: No 102/04). – A: Diffuse porous wood, TS. – B: Vessels in radial multiples with tyloses and scanty paratracheal parenchyma (arrows), TS. – C: Alternate intervessel pits, TLS. – D: Moderately wide rays, TLS. – E: Tyloses within vessels, RLS. – F: Heterocellular rays, RLS. – G: Septate fibres (arrows), TLS. – H: Detail of ray with three marginal rows (arrows), TLS. — Scale bars = 100 μm in A, B, D, E, F, H; 10 μm in C, G.

Table 1. Descriptive statistics of tangential vessel diameter.

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

RESULTS

Family inc.

Paraphyllanthoxylon Bailey

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

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

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

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

DISCUSSION

Both samples lack well-defined growth rings, and have vessels solitary and in radial multiples with simple perforation plates, abundant tyloses and alternate intervascular pitting, heterocellular rays up to 7 cells wide, scanty paratracheal axial parenchyma and septate fibres. Unfortunately, no vessel-ray pitting was observed. This combination of features is characteristic of the fossil morphogenus *Paraphyllanthoxylon*.

Summary of Paraphyllanthoxylon species

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

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

Other authors have referred their specimens to described species of *Paraphyllanthoxylon*: Oakley and Falcon-Lang (2009) described charcoalified material from Pecínov as *P. marylandense*, Wheeler and Lehman (2000) designated their samples from the Upper Cretaceous of Texas, USA as cf. *P. anazasii* and Meijer (2000) described a fossil wood from the Upper Cretaceous of Belgium as *P.* cf. *marylandense*. Some simply noted the resemblance to *Paraphyllanthoxylon* at the generic level only, *e.g.* Cevallos-Ferriz and Weber (1992) from the Upper Cretaceous of Mexico or Falcon-Lang *et al.* (2001) from the Cenomanian of the Czech Republic.

Comparison with the described species

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

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

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

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

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

Botanical affinities

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

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

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

Similarity of Paraphyllanthoxylon with other morphogenera

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

CONCLUSIONS

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

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by **E.A. Wheeler** and **S.R. Manchester**

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