

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

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Received 25 July 2006; accepted for publication 13 December 2006

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

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

## INTRODUCTION

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

## METHODS IN PALAEOCLIMATE RECONSTRUCTION

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

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

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

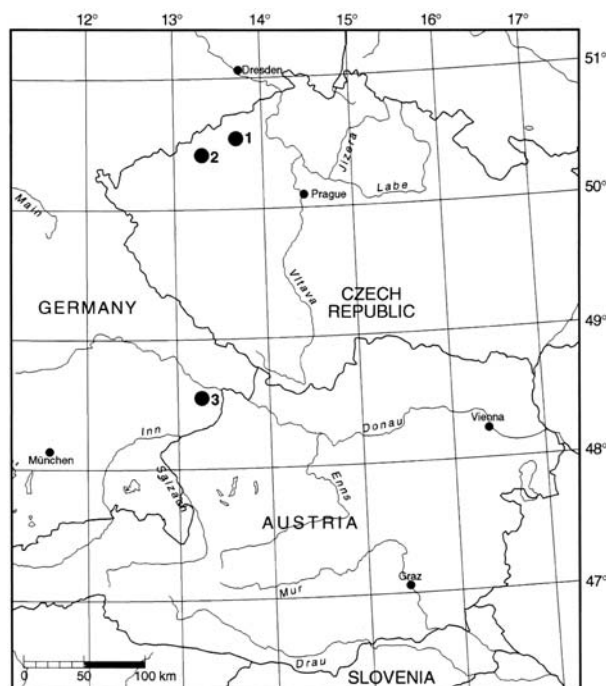
On the other hand, there is the second group of methods which does not need a precise identification of fossil specimens. These methods take into account the correlation between climate and selected features of the plant structure; these methods include CLAMP (Wolfe 1993), tree ring analysis (Creber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

## CASE STUDIES

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

### CZECH REPUBLIC

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



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

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

### Coexistence approach (CZ)

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

### Statistical model (CZ)

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

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

#### GERMANY

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

#### Coexistence approach (DE)

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

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

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

#### Statistical model (DE)

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

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

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

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

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

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

$\text{MAT (Wiemann 98)} = 13.40 - 0.250(\text{spir}) + 0.637(>10\text{ser}) + 0.255(\text{het}4+) + 0.416(\text{stor}) - 0.213(\text{abs})$ , where the values in parentheses are the percent of wood types in an assemblage that have the corresponding character. The other two equations are based on transformed data (arcsine transformation) and were published later by Wiemann et al. (1999):

$\text{MAT (Arcsines 12)} = 24.78 + 36.57(\text{stor}) - 15.61(\text{marg}) - 16.41(\text{abs})$

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

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

The MAT calculated are the following:

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

MAT (Wiemann 98) = 18.0°C

MAT (Arcsines 12) = 20.7°C

MAT (Arcsines 15) = 21.0°C

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

MAT (Wiemann 98) = 24.9°C

MAT (Arcsines 12) = 30.2°C

MAT (Arcsines 15) = 28.9°C

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

## CONCLUSIONS

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

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

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

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

#### ACKNOWLEDGEMENTS

This paper resumes the results presented during the 17<sup>th</sup> International Botanical Congress 2005 in Vienna. The research was supported by the grants GACR 205/04/0099 and MSM 0021620855. I would like to thank C. Privé-Gill for helping me with the Rauscheröd xyloflora and M. Böhme for providing me with the precious publication in press. I have benefited from valuable comments by A. Selmeier, M. Böhme and two anonymous reviewers.

My warmest thanks and gratitude go to Zlatko Kvaček for his unflagging help and support throughout my whole scientific life. I would like to associate with a long queue of congratulators, just saying: “Vážený pane profesore, přeji Vám vše dobré do dalších let, hlavně hodně zdraví, rodinné pohody a at Vám nevysychá inkoust ! Jakub”.

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