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Palaeoclimate Estimates for Selected Leaf Floras from the Late Pliocene (Reuverian) of Central Europe Based on Different Palaeobotanical Techniques

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Abstract: To provide quantitative palaeoclimate estimates based on different palaeobotanical techniques for three contemporaneous Pliocene leaf floras, we applied the Coexistence Approach (CoA), leaf margin analysis (LMA), the Climate Leaf Analysis Multivariate Program (CLAMP) and the European Leaf Physiognomic Approach (ELPA). Furthermore, we compared recently published estimates from an additional locality with our data. The leaf physiognomic techniques yield lower mean annual temperatures than the CoA, which is most likely caused by taphonomic biases. Due to these potential biases we are in favour of the CoA as the most reliable method, and its palaeotemperature estimates show similar temperatures for all localities. These estimates are also in good agreement with previously published data derived from other techniques for other Late Pliocene floras from Western and Central Europe. No longitudinal/latitudinal temperature gradient can be observed for the sites under study.

Key Words: palaeoclimate, Reuverian, Coexistence Approach, Leaf Margin Analysis, Climate Leaf Analysis Multivariate Program, European Leaf Physiognomic Approach

Orta Avrupa’nın Geç Pliyosen (Reuverian)’inden Seçilmiş Yaprak Floraları için Farklı Paleobotanik Tekniklere Dayanan Paleoiklim Tahminleri

Özet: Üç eş yaşlı Pliyosen yaprak florasının, farklı paleobotanik tekniklere dayalı sayısal paleoiklimsel değerlendirmelerini elde etmek için, Birarada Olma Yaklaşımı yöntemi (CoA), Yaprak Kenarı Analizi (LMA), İklim-Yaprak Analiz Değişken Programı (CLAMP) ve Avrupa Yaprak Fizyonomisi Yaklaşımı (ELPA)nı uyguladık. Ayrıca, kendi bulgularımız ile ek bir bölgeden (lokaliteden) son zamanlarda yayınlanan hesaplamalarla karşılaştırdık. Yaprak fizyonomisi teknikleri, büyük olasılıkla taphonomik önyargıların neden olduğu, CoA’dan daha düşük yıllık ortalama sıcaklık dereceleri vermektedir. Bu potansiyel ön yargılar nedeniyle, en güvenilir yöntem olarak CoA tercih edilmiştir ve bu yönteme ait paleosıcaklık ölçümleri tüm bölgeler için benzer sıcaklık dereceleri göstermektedir. Bu ölçümler, Batı ve Orta Avrupa’dan diğer Geç Pliyosen floraları için başka tekniklerden elde edilerek, daha önce yayınlanmış olan veriler ile iyi bir uyum içindedir. Bu çalışmadaki bölgelerde, boylamsal ve enlemsel hiçbir sıcaklık değişimi gözlenememiştir.

Anahtar Sözcükler: paleoiklim, Reuveriyen, Birarada Olma Yaklaşımı Yöntemi, Yaprak Kenarı Analizi, İklim Yaprak Analizi Değişken Programı, Avrupa Yaprak Fizyonomisi Yaklaşımı

Introduction

To understand future climatic changes and their influence on the environment and biodiversity it is of great importance to gain information about past climates (Haywood *et al.* 2008). As the vast climatic oscillations typical of the Quaternary had already started during the Pliocene (Zachos *et al.* 2001; Haywood *et al.* 2009), it is that period which is of special interest in understanding the transition from a global greenhouse to icehouse climate. The reconstruction of global scale palaeoclimate e.g., based on marine or ice records, is easier than regional palaeoclimate estimates from continental deposits because stratigraphic correlation and age determination of many continental deposits is more complicated. The reconstruction of climatic characteristics on continents is furthermore hampered by the patchiness of deposits containing appropriate proxies. However, the good preservation and diversity of plant macrofossils, i.e. leaves and seeds, at some sites allows for climate reconstruction in the terrestrial realm (e.g., Utescher *et al.* 2000; Mosbrugger *et al.* 2005; Uhl *et al.* 2007a), thus providing information that is important for our understanding of continental palaeoclimate development, not only on a global but especially on a regional and local scale.

To evaluate the quality of palaeoclimatic estimates derived from Cenozoic leaf floras it is necessary to apply different quantitative techniques under a wide variety of different 'boundary conditions' (i.e. depositional setting, stratigraphic age, geographical source area) (e.g., Liang *et al.* 2003; Uhl *et al.* 2003, 2006, 2007a, b; Yang *et al.* 2007; Teodoridis *et al.* 2009). For this purpose we have chosen the (more or less) contemporaneous Pliocene leaf floras of Willershausen (Lower Saxony/Germany) and Berga (Saxony-Anhalt/Germany) because the taxonomic composition of both floras is well known and they are both relatively diverse (Willershausen: Knobloch 1998; Knobloch & Gregor 2000; Gregor & Storch 2000; Berga: Mai & Walther 1988). Additionally, we analysed a third flora (Frankfurt am Main, Hesse/ Germany [the so called 'Klärbecken Flora']) which is also believed to be almost contemporary with the former two floras, but which has not been revised taxonomically since the monograph by Mädler (1939). We have chosen this particular flora to test the influence of the 'quality' of taxonomic revisions on the different approaches (assuming that many determinations by Mädler (1939) are probably not valid in terms of modern taxonomy; e.g., Teodoridis *et al.* 2009). For comparison we also included previously published climate data derived from the recently revised leaf flora of Auenheim (Alsace/France), as the taxonomic composition of this particular flora is very similar to all three floras analysed in this study (Kvaček *et al.* 2008; Teodoridis *et al.* 2009).

Localities

Stratigraphy

We herein follow the formal ratification recently presented by Gibbard *et al.* (2010) in which the base of the Pleistocene has been revised to 2.58 Ma, so that the Pleistocene now includes the Gelasian Stage.

Based on the floral composition of the individual floras, Mai & Walther (1988) assigned Willershausen and Berga to the Reuver Floral Assemblage (~Reuverian/ Piacenzian, Late Pliocene; cf. Popescu *et al.* 2010), whereas Frankfurt and Auenheim were assigned to the older Brunssum Floral Assemblage by these and subsequent authors (e.g., Mai 1995). However, based on the recent taxonomic revision of the Auenheim flora (a flora that has significant similarities with the Frankfurt flora) an assignment to the Reuver Floral Assemblage has been suggested for Auenheim and Frankfurt (Kvaček *et al.* 2008; Teodoridis *et al.* 2009). This interpretation implies that all floras considered in this study are of more or less the same age.

Geology and Palaeobotany

Willershausen– The Willershausen clay-pit, yielding an extraordinary (insect-) fauna (e.g., Straus 1967) and flora (e.g., Straus 1930, 1935; Knobloch 1998), is located in the foothills of the Harz mountains in Germany (Figure 1). The plant-bearing sediments were deposited in a small, fault-bounded basin that developed due to local subsurface erosion of Permian salts that intruded Mesozoic sediments (Meischner & Paul 1977, 1982). Based on sedimentological and palaeontological evidence, later authors reconstructed the lake as only about 200 m wide and some 10 m deep.

Previous authors (e.g., Straus 1967) assumed a Piacenzian (Late Pliocene) age for this locality; an assumption supported by the occurrence of the gomphothere *Anancus arvernensis* as well as *Tapirus*, indicating a position within the mammal zone MN 16/17 (Mai 1995).

A recent taxonomic revision of the Willershausen flora has been published by Knobloch (1998) and Ferguson & Knobloch (1998), with subsequent taxonomic additions and comments by Knobloch

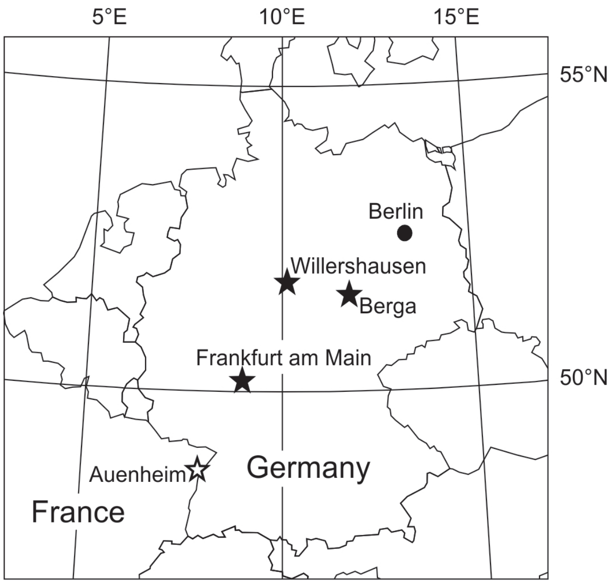

Figure 1. Map showing the geographic position of the three floras investigated in the present study (black stars), as well as the Auenheim locality that has been included for comparison (open star).

& Gregor (2000) and Gregor & Storch (2000). From these works it became evident that the flora represents a Mixed Mesophytic forest. The climate of Willershausen has previously been interpreted as Cfa-type *sensu* Köppen (with tendency to Cfb-type) with mean annual temperature (MAT) 11–13°C, mean temperature of the coldest month (CMMT) 5–9°C, mean temperature of the warmest month (WMMT) ~ 25°C and mean annual precipitation (MAP) >1000 mm (Gregor & Storch 2000). Due to the absence of *Viscum*, Ferguson & Knobloch (1998) suggested oceanic climate conditions with rather cool WMMT (13–17°C) and mild winters with CMMT above freezing point, i.e. similar to present day conditions. Annual precipitation was estimated at 800–1400 mm. Recently, MAT values derived from different techniques have been presented in by Uhl *et al.* (2007b) (cf. Table 1).

Berga This rich flora (>160 taxa of leaves, fruits and seeds) comes from a former clay pit near Berga in Saxony-Anhalt (Middle-Germany), about 60 km southeast of Willershausen (Figure 1). The fossils have been discovered in lacustrine (?) clays and fluviatile (?) silt-bodies that cut into the clays (Mai & Walther 1988; Steinmüller 2003). The sediments were deposited in a small basin that, like Willershausen, can probably be interpreted as a sink-hole formed by subsurface dissolution of salts (Steinmüller 2003).

The macroflora from this locality has been described in detail by Mai & Walther (1988); based on the composition of the flora and lithological comparisons these authors suggested a Late (then: Middle; cf. Gibbard *et al.* 2010) Pliocene age (probably Reuverian) for this flora. According to Mai (1995) the flora represents a Mixed Mesophytic forest with a tendency to a mixed oak-beech-hornbeam-forest. The climate of Berga has previously been interpreted as Cfa-type *sensu* Köppen with MAT 13–14°C, CMMT 0–1°C, WMMT 24–25°C and MAP 1300–1500 mm (Mai & Walther 1988). Recently, Uhl *et al.* (2007b) presented MAT values derived from different quantitative techniques (cf. Table 1).

Frankfurt am Main The so-called 'Klärbecken-Flora' originates from a sandy clay lens and was discovered during excavations for the clearing basin of the sewage treatment plant for the city of Frankfurt am Main (Figure 1) in the years 1885 and 1903 (Mädler 1939). The monograph about this important flora (Mädler 1939) is still the most complete and recent taxonomic work on it. Undoubtedly, a systematic revision is strongly needed (Teodoridis *et al.* 2009).

According to Mai (1995) the flora represents a Mixed Mesophytic forest. The climate of Frankfurt has previously been interpreted as Cfa-type *sensu* Köppen (Mai 1995). Apart from MAT values (Uhl *et al.* 2007b) (cf. Table 1) we are not aware of any published reconstructions for individual palaeoclimatic parameters for this locality.

Methods

During our study we analysed the three floras using three widely used techniques for the reconstruction/estimation of palaeoclimatic parameters: (i) the Coexistence Approach (CoA) (Mosbrugger & Utescher 1997) which is based on the nearest living relative (NLR) concept, (ii) leaf margin analysis (LMA) following Wolfe (1979) and Wilf (1997), and (iii) Climate Leaf Analysis Multivariate Program (CLAMP), a multivariate technique utilising leaf physiognomy, based on a modern calibration data

Table 1. Climate values derived from the different techniques for the three leaf-floras as well as for the contemporary flora of Auenheim (Alsace, France).

		Willershausen	Berga	Frankfurt am Main	Auenheim
MAT [°C]	CoA	13.6–15.6 **	13.6–16.6 **	14.0–15.5 **	13.6–15.6*
	CLAMP	11.2±1.2 **	8.9±1.2 **	12.2±1.2 **	12.1±1.2*
	ELPA	10.8±1.1**	7.4±1.1**	16.5±1.1**	n.a.
	LMA	10.6±1.3 **	8.8±2.6 **	18.3±2.4 **	12.0±2.2 ***
WMMT [°C]	CoA	25.7–26.3	25.7–27.0	23.8–24.8	23.6–24.2*
	CLAMP	19.8±1.6	17.7±1.6	23.3±1.6	19.0±1.8*
	ELPA	19.6±1.9	18.2±1.9	25.4±1.9	n.a.
CMMT [°C]	CoA	0.6–1.7	0.6–1.7	2.7–4.1	0.9–1.7*
	CLAMP	3.2±1.9	0.2±1.9	2.3±1.9	3.9±2.5*
	ELPA	1.6±2.1	−4.3±2.1	6.8±2.1	n.a.
MAP [mm]	CoA	897–1151	897–1297	979–1333	979–1122*

* taken from Teodoridis *et al.* (2009)
** taken from Uhl *et al.* (2007)
*** calculated based on data presented in Teodoridis *et al.* (2009)

set covering mainly North American and East Asian sites (Wolfe 1993, 1995; Wolfe & Spicer 1999). Additionally, we applied another recently developed multivariate leaf physiognomic approach to our floras, which uses a calibration data set compiled from European woody angiosperms (Traiser 2004; Traiser *et al.* 2005, 2007).

Because the major aim of our study is the comparison of different techniques, we focused on climate parameters that can be reconstructed by more than one of the methods used here; i.e. mean annual temperature (MAT), mean temperature of the warmest month (WMMT), and mean temperature of the coldest month (CMMT), plus mean annual precipitation (MAP), a parameter that is only estimated by the CoA.

Coexistence Approach

The Coexistence Approach (CoA) is based on the long known NLR concept and makes use of the climatic ranges of as many as possible NLRs of an individual fossil flora to determine the common interval of a given climatic parameter (e.g., MAT) in which most of the supposed NLRs are in principle able to coexist. The resulting interval is then assumed to represent the range of this particular climatic parameter at the fossil locality. The advantages and disadvantages of this approach have been discussed in detail (e.g., Mosbrugger & Utescher 1997; Mosbrugger 1999; Uhl *et al.* 2003; Kvaček 2007), and so far this reconstruction technique has been successfully applied in several palaeoclimatic studies based on floras from the Palaeogene and Neogene of Europe (e.g., Mosbrugger & Utescher 1997; Pross *et al.* 1998; Utescher *et al.* 2000; Uhl *et al.* 2003, 2006, 2007a, b; Mosbrugger *et al.* 2005; Teodoridis *et al.* 2009), the Neogene of East Asia (e.g., Liang *et al.* 2003), and the Late Cretaceous and Early Palaeogene of Antarctica (Poole *et al.* 2005). Climatic parameters for individual NLRs were taken from the PALAEOFLORA database (Mosbrugger & Utescher 1997–2009). The limiting taxa for the different localities and their climatic ranges are shown in Tables 2, 3 & 4, and the lists of taxa are given in Appendices 1–3.

Leaf Margin Analysis

For almost a century it has been known that in modern vegetation a direct correlation between the proportion of dicot woody species with entire margined leaves and MAT exists (Bailey & Sinnott

Table 2. CoA estimates for Willershausen, including limiting taxa of the palaeoclimatic intervals.

Parameter	Taxon min-value	min-value	max-value	Taxon max-value
MAT [°C]	*Parrotia persica*	13.6	15.6	*Comptonia peregrina*
CMMT [°C]	*Parrotia persica*	0.6	1.7	*Parrotia persica*
WMMT [°C]	*Ulmus alata*	25.7	26.3	*Sorbus* sp.
MAP [mm]	*Liquidambar styracifolia*	897	1151	*Coryllus avellana*

Table 3. CoA estimates for Berga, including limiting taxa of the palaeoclimatic intervals.

Parameter	Taxon min-value	min-value	max-value	Taxon max-value
MAT [°C]	*Parrotia persica*	13.6	16.6	*Zelkova carpinifolia, Zelkova serrata*
CMMT [°C]	*Parrotia persica*	0.6	1.7	*Parrotia persica*
WMMT [°C]	*Ulmus alata*	25.7	27.0	*Aesculus hippocastanea*
MAP [mm]	*Taxodium distichum Liquidambar styraciflua*	897	1297	*Populus tremula*

Table 4. CoA estimates for Frankfurt am Main, including limiting taxa of the palaeoclimatic intervals.

Parameter	Taxon min-value	min-value	max-value	Taxon max-value
MAT [°C]	*Cephalotaxus fortunei*	14.0	15.5	*Prunus spinosa*
CMMT [°C]	*Myrica cerifera* sp.	2.7	4.1	*Betula pubescens*
WMMT [°C]	*Torreya nucifera*	23.8	24.8	*Prunus spinosa*
MAP [mm]	*Pseudolarix amabilis*	979	1333	*Acer monspessulanum Aesculus hippocastanea Buxus sempervirens*

1915, 1916). In recent decades, a number of different modern calibration datasets have been developed which theoretically allow the quantitative estimation of MAT values from fossil dicot leaves (Wolfe 1979; Wilf 1997; Kowalski 2002). Here we use the widely used linear regression equation based on a modern dataset from mesic forests of East Asia (Wolfe 1979; Wing & Greenwood 1993) that describes the correlation between the proportion of woody species with entire-margined leaves in a flora (P) and the mean annual temperature (MAT):

$$MAT = 30.6P + 1.14$$

The regression error of this equation is ± 0.78°C (Wing & Greenwood 1993), but here we report the (generally larger) error due to binomial sampling as calculated by Wilf (1997; his equation 4):

$$\sigma_{MAT} = c \times \sqrt{\frac{P(1-P)}{r}}$$

where *P* represents the proportion of leaf species with entire margins, *r* the total number of species in the flora, and *c* the constant in the regression equation (here 30.6).

Climate Leaf Analysis Multivariate Program

The multivariate leaf physiognomic approach CLAMP (Climate Leaf Analysis Multivariate Program) was introduced by Wolfe (1993) and since then has been developed further by a number of authors (e.g., Wolfe 1995; Kovach & Spicer 1996; Wolfe & Spicer 1999). This technique employs up to 31 physiognomic characters simultaneously (e.g., leaf margin type, details of tooth morphology, leaf size, leaf length to width ratio, leaf shape) and the resulting multivariate physiognomic data set is analysed by Canonical Correspondence Analysis (CCA), a direct ordination method, widely used in plant ecology (Ter Braak 1987). The modern calibration data set (CLAMP3) consists of 173 (CLAMP3A) or 144 (CLAMP3B) samples (localities) respectively, mainly from North America and East Asia. The slightly larger CLAMP3A subset includes a well-defined, so-called subalpine nest of floras from high altitudes or latitudes with leaf physiognomies adapted to freeze-induced drought (Wolfe & Spicer 1999). Although inclusion of the subalpine sites may be important for studies of Tertiary elevation changes (Povey *et al.* 1994; Wolfe *et al.* 1998) and high-latitude Neogene floras (Wolfe 1995), the assumed frost-free conditions during the Late Pliocene of Europe (e.g., Mai 1995) suggest that the subalpine sites should be excluded from the modern calibration set for this study.

All calculations for CLAMP were performed with the software-package CANOCO 4.02 for Windows and the pre-programmed spreadsheet-files provided by R.A. Spicer on the CLAMP web-site (http://tabitha.open.ac.uk/spicer/CLAMP/Clampset1.html).

European Leaf Physiognomic Approach

This method (which is still in a development stage) uses a grid-based (0.5° latitude – 0.5° longitude) modern calibration dataset that currently comprises 1835 synthetic floras (Traiser *et al.* 2005). A synthetic flora at a specific geographical coordinate is defined as the list of taxa that (can) occur at this particular site according to published distribution maps (Klotz 1999; Klotz *et al.* 2003). These synthetic floras have been generated by means of distribution maps of 108 woody angiosperm taxa, which have been physiognomically characterised based on floral manuals. Synthetic floras included in the actual calibration dataset are restricted to grid-cells with more than 25 taxa and an elevation between 0 and 400 m above sea-level. Details of this dataset are discussed by Traiser *et al.* (2005). Physiognomic data and grid-based climatic data (from New *et al.* 1999) are processed with Redundancy Analysis (RDA), an alternative direct ordination technique, using CANOCO 4.02 for Windows in analogy to the CLAMP-procedure (for further details see Traiser 2004; Traiser *et al.* 2007). This method has so far been applied to several palaeofloras from the Palaeogene and Neogene of the Northern hemisphere (Uhl *et al.* 2006, 2007a, b; Traiser *et al.* 2007).

The leaf physiognomic characterisation of the three floras used for the physiognomic approaches is given in Table 5.

Results

For all localities the MATs for the CoA are in good agreement. The main differences are the narrower temperature range for Frankfurt am Main (Table 1, Figure 2) and the slightly higher maximum temperature (16.6°C) for Berga. However, the CLAMP-MAT reconstructed for Berga is significantly colder (8.9±1.2°C) than the CoA-MAT (13.6–16.6°C), whereas, considering the errors, it results in only slightly colder CLAMP-MATs for Willershausen and Frankfurt am Main. Apart from Berga CLAMP-MATs agree well for all localities.

For Auenheim the LMA-MAT (12.0±2.2°C) agrees well with the other two methods, whilst LMA for Willershausen and Berga results in colder MATs than CoA. In contrast, the CoA-MAT of Frankfurt is reconstructed to be warmer than the LMA-MAT (18.3±2.4°C). The same tendency is found for the MATs for these localities comparing ELPA and CoA. For Willershausen and Berga ELPA-MATs are colder than CoA-MATs and CLAMP-MATs, whereas the ELPA-MAT for Frankfurt is warmer than the CLAMP-MAT. In general, apart from Frankfurt, the CoA yields higher MATs than the leaf physiognomic approaches.

Following the CoA, Frankfurt am Main (23.8–24.8°C) and Auenheim (23.6–24.2°C) show slightly colder WMMTs than Willershausen (25.7–26.3°C)

Table 5. Leaf-physiognomic characterisation of the three palaeofloras investigated in the present study.

	Willershausen	**Berga**	**Frankfurt am Main**
Lobed	21	38	15
No Teeth	31	25	56
Teeth Regular	45	41	32
Teeth Close	28	40	14
Teeth Round	34	56	10
Teeth Acute	26	27	34
Teeth Compound	23	6	8
Nanophyll	0	0	0
Leptophyll I	0	0	0
Leptophyll II	0	0	8
Microphyll I	0	3	20
Microphyll II	33	36	56
Microphyll III	37	42	16
Mesophyll I	21	17	0
Mesophyll II	5	2	0
Mesophyll III	4	0	0
Apex Emarg.	2	0	0
Apex Round	49	36	22
Apex Acute	46	64	72
Apex Atten.	3	0	6
Base Cordate	25	32	31
Base Round	52	58	48
Base Acute	22	11	21
L:W<1:1	10	10	4
L:W 1-2:1	56	50	30
L:W 2-3:1	24	36	43
L:W 3-4:1	9	2	11
L:W>4:1	1	2	11
Obovate	10	27	18
Elliptic	64	60	58
Ovate	25	13	24
Total number of species	122	26	40

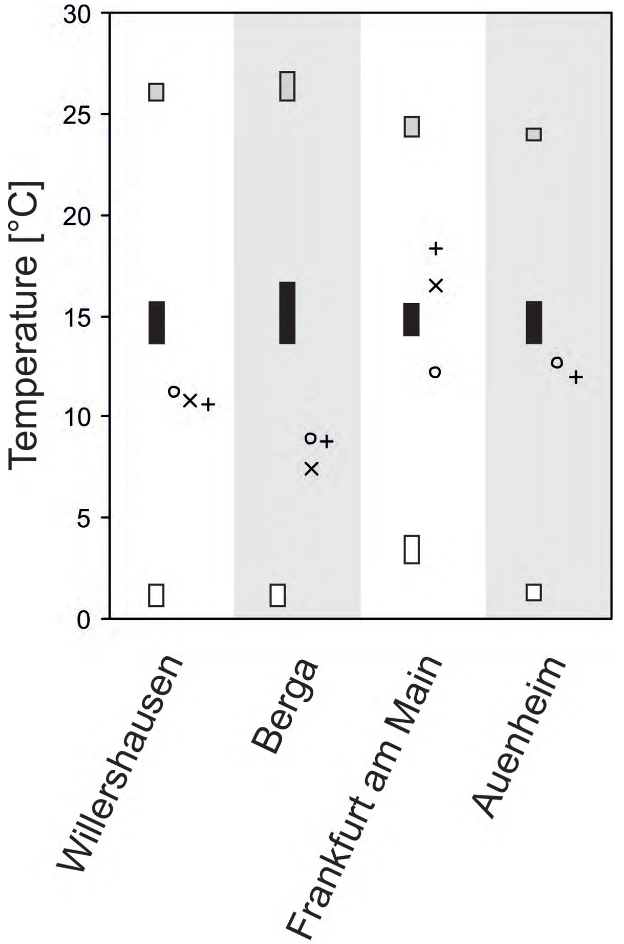

Figure 2. MAT-, WMMT- and CMMT-estimates derived from the different techniques for the floras considered in this study. CoA-MAT– black boxes, CoA-CMMT– white boxes, CoA-WMMT– grey boxes, CLAMP-MAT– o, LMA-MAT– +, ELPA-MAT– ×

and Berga (25.7–27.0°C). For the latter two floras CLAMP-WMMTs are colder than the estimate for CoA, whereas it is in good agreement for Frankfurt am Main and Auenheim. The same is true for ELPA where the WMMTs are in very good agreement with CLAMP.

For Berga and Willershausen CoA-CMMT result in a rather tight temperature range (0.6–1.7°C), which is similar to that of Auenheim (0.9–1.7°C). Frankfurt am Main is reconstructed to have a much warmer CoA-CMMT than the latter two. This estimate agrees with the CLAMP-CMMT, which on the other hand is in disagreement with the CoA-CMMT for Willershausen, resulting in much warmer temperatures. The ELPA-CMMT (1.6±2.1°C) is in accordance with the CoA-CMMT results for Willershausen, while it yields much colder temperatures for Berga –4.3±2.1°C) and significantly warmer temperatures for Frankfurt am Main (6.8±2.1°C).

The reconstruction of MAP is only possible for the CoA and resulted in values around 1000 mm for all localities, with a maximum of 1333 mm for Frankfurt am Main.

Discussion

In all localities, the CoA results are in good agreement, but significant differences are found when comparing the CoA with the temperatures derived from the leaf physiognomic approaches. There is a tendency for lower temperature estimates using the leaf physiognomic approaches, except for the flora of Frankfurt am Main. This might reflect problems with the taxonomy of this flora, i.e. leaf morphotypes as defined by Mädler (1939) may not represent meaningful taxa as seen by modern taxonomy. CLAMP, especially, produces cooler temperature estimates (i.e., MAT and WMMT) than CoA. MATs derived from LMA derived show no such clear trend, but the reliability of this technique has to be questioned due to problems with taphonomic biases influencing the results obtained from this method (Burnham 1994; Uhl *et al.* 2003). The phenomenon of lower palaeotemperatures derived from leaf physiognomic techniques has previously been observed for a number of localities from the European Tertiary, especially the Neogene and Late Palaeogene (e.g., Mosbrugger & Utescher 1997; Utescher *et al.* 2000; Uhl *et al.* 2003, 2006, 2007a). The reasons for these discrepancies are not yet fully understood. Uhl *et al.* (2007a) speculated that the actual correlation between climate and leaf shape may be modified by either long-time evolutionary responses or floral changes, leading to erroneous palaeoclimate estimates when a calibration dataset is used which is not suitable for the region and time-interval under study. Different authors also emphasised the leaf shape dependency on different habitats (Burnham *et al.* 2001; Kowalski & Dilcher

2003). Their data suggest that MATs calculated from leaves derived from wet environments are underestimated compared to dry habitats. The datasets used for physiognomic approaches mainly incorporate dry-land sites, but most macrofossil floras were deposited in wet environments such as floodplain, swamps, lakes, and deltas (Kowalski & Dilcher 2003). This is true for the sites under study and hence the leaf physiognomic approaches are prone to yield lower temperatures.

The CoA-MATs derived from the four Central European floras are more or less in good agreement with climate reconstructions for several Western European localities reconstructed by Fauquette *et al.* (2007), although we cannot observe such clear latitude gradients as these authors. However, the latitude range covered by our localities is only about 3° and the maximum difference would thus be 1.8°C between the southernmost locality (Auenheim) and the northernmost locality (Willershausen) if we assume the same thermal gradient (0.6°C per degree in latitude) as Fauquette *et al.* (2007). Such a comparably small difference is unfortunately beyond the thermal resolution of the methods used in this study.

Formerly, the differences in floral composition of the four localities, interpreting Willershausen and Berga as one and Frankfurt am Main and Auenheim as another group, used to be explained by climatic effects such as east–west gradients (Krutzsch 1988; Mai 1995). However, following the recent taxonomic revision of the Auenheim flora (Kvaček *et al.* 2008) it has been suggested by Teodoridis *et al.* (2009) that all four floras considered in the present study, have very similar taxonomic compositions (in the case of Frankfurt am Main based on a preliminary survey of the flora). The CoA results do not indicate significant differences in palaeotemperatures for any of the localities besides CMMT for Frankfurt am Main.

From what is known (Mai & Walther 1988; Mai 1995), it has to be assumed that the floras are more or less contemporary, i.e. Reuverian. However, in any interpretation of the age of these floras it has to be acknowledged that the Reuverian covers a wide time span which allows for age differences on a scale which is large enough for climatic oscillations as suggested by Zagwijn & Hager (1987). It has also to be noted that, as for almost all continental Pliocene deposits, chronological evidence is missing that would allow for clear assignment of the floras to (sub-)stages. Kemna & Westerhoff (2007) criticised that for the classical Neogene chronostratigraphic system relevant for Central Europe (Zagwijn 1957, 1960, 1963, 1985) quantitative changes in pollen assemblages were interpreted to present climate changes without considering that synchronous deposits can contain different assemblages due to edaphic factors or preservation conditions. In their opinion, scaling up of locally defined zones into regionally applicable chronostratigraphic (sub-) stages causes problems when interpreting palaeoenvironmental data. This is underlined by Donders *et al.* (2007) who presented data indicating that long-distance chronostratigraphical correlations based on the original continental Neogene stages are invalid. Thus it seems problematic to verify that the four floras considered here are really contemporaneous, solely based on their floral similarities and climate data derived from the floral data.

The CMMT estimates for Frankfurt am Main have yielded, independently of the method used, warmer temperatures than the other localities. Also the annual precipitation derived from the CoA shows comparable higher values than those of all other localities. Following Haywood *et al.* (2000, 2009), with the constraint of the rather low resolutions, there ought to be no obvious difference in CMMT and precipitation between the localities presented in our study. Therefore local factors might have influenced these palaeoclimatic parameters, although it seems likely that these differences are (at least partly) due to the outdated taxonomic knowledge about this locality. These results corroborate that all techniques used here are susceptible to change (over time), or differing (between authors) taxonomic concepts, thus complicating the comparison of palaeoclimate estimates based on floras from different and especially older sources.

Conclusions

This study aimed to apply different quantitative palaeobotanical techniques to derive palaeoclimate estimates from leaf floras. We therefore applied the Coexistence Approach and three leaf physiognomic methods. As observed in other studies, the leaf physiognomic techniques yield lower MAT estimates than the CoA, which is most likely caused by taphonomic biases. Due to these potential biases we favour the CoA as the most reliable method. The CoA palaeotemperature estimates point to CfA-type climate *sensu* Köppen, yielding similar temperatures for all localities; no longitude/latitude temperature gradient could be found for the sites under study. Independently of the method applied, Frankfurt am Main shows warmer temperatures; the causes could be local factors or, more likely, problems with the outdated taxonomy of this flora.

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Appendix 1

List of taxa from Willershausen (based on Knobloch 1989 and Gregor & Storch 2000) and NLRs used for CoA (from PALAEOFLORA database).

Willershausen	
Fossil taxa	**NLRs used for CoA**
Abies sp.	*Abies* sp.
Acer aff. *opalus*	*Acer* sp.
Acer aff. *pseudoplatanus*	*Acer* sp.
Acer cf. *palaeosaccharinum*	*Acer sacharinum*
Acer integerrimum	*Acer cappadocicum*
Acer sanctae-crucis	*Acer* sp.
Acer sp. *1*	*Acer* sp.
Acer sp. *2*	*Acer* sp.
Acer sp. *3*	*Acer* sp.
Acer sp. *4 (Acer* aff. *tricuspidatum sub*sp. aff. *lusaticum)*	*Acer rubrum*
Acer sp. vel *Sterculia* sp.	
Actinidia pliocenica	*Actinidia* sp.
Aesculus sp. 1	*Aesculus* sp.
? *Aesculus* sp. 2	*Aesculus* sp.
Aesculus sp. 3	*Aesculus* sp.
Aesculus velitzelosii	*Aesculus* sp.
aff. *Magnolia* sp. 1	
aff. *Tilia* sp. div.	
Alnus cf. *gaudinii*	*Alnus nitida*
Alnus sp. *1*	*Alnus* sp.
Alnus sp. *2*	*Alnus* sp.
Alnus sp. *2* vel cf. *Corylus* sp.	
Alnus sp. *3*	*Alnus* sp.
Alnus sp. *4*	*Alnus* sp.
Ampelopsis cordataeformis	*Ampelopsis* sp.
Aristolochia pliocaenica	
cf. *Aristolochia venusta*	
Asplenium gothani	
Betula cf. *subpubescens*	*Betula pubescens*
Betula hummelae sp.	*Betula* sp.
Betula insignis	*Betula* sp.
Betula sp. 1	*Betula* sp.
cf. *Betula* sp. 2	*Betula* sp.
cf. *Betula* sp. 3	*Betula* sp.

cf. *Betula* sp. 4	*Betula* sp.
cf. *Betula* sp. 5	*Betula* sp.
Betula speciosa	*Betula* sp.
Buxus pilocenica	*Buxus* sp.
Carpinus cuspidens	*Carpinus* sp.
Carpinus grandis	*Carpinus* sp.
cf. *Carpinus grandis*	*Carpinus* sp.
Carpinus sp.	*Carpinus* sp.
Carya minor	*Carya* sp.
Carya serrifolia	*Carya cordiformis*
Cedrela heliconia	*Meliaceae* (*Melia,Cedrela*)
Celtis trachytica	
Cerasus avium	
Cercidiphyllum crenatum	*Cercidiphyllum japonicum*
Chamaecyparis lawsoniana	
Comptonia difformis	*Comptonia peregrina*
Corylus avellana	*Corylus avellana*
Crataegus aff. *dyssenterica*	*Crataegus* sp.
Crataegus aff. *oxyacanthoides*	*Crataegus* sp.
Crataegus cf. *praemonogyna*	*Crataegus* sp.
Crataegus meischneri	*Crataegus* sp.
Crataegus sp. 1	*Crataegus* sp.
Crataegus sp. 2	*Crataegus* sp.
Cydonia sp. vel *Cotoneaster* sp. vel *Capparis*	
Dicotylophyllum actinidiodes	
Dicotylophyllum eucommioides	
Dicotylophyllum microcrenulatum	
Dictotyophyllum kvacekii	
Dictotyophyllum milenae	
Dictotyophyllum pyriforme	
Dictotyophyllum sp. 1 (? *Rosaceae*)	
Dictotyophyllum sp. 10	
Dictotyophyllum sp. 11	
Dictotyophyllum sp. 12	
Dictotyophyllum sp. 2	
Dictotyophyllum sp. 3 (? *Daphne*), *Berberis* sp.	
Dictotyophyllum sp. 4	
Dictotyophyllum sp. 5	
Dictotyophyllum sp. 6	
Dictotyophyllum sp. 7	
Dictotyophyllum sp. 8	

Dictotyophyllum sp. 9 (? *Prunus* sp., ? *Quercus* sp.)	
Dictotyophyllum wegelei	
Dombeyopsis lobata	*Sterculiaceae*
Epimedium praeasperum	
cf. *Eucommia* sp.	*Eucommia ulmoides*
Fagus pliocenica subsp. *multinervis*	*Fagus* sp.
Fagus pliocenica subsp. *willerhausensis*	*Fagus* sp.
Fraxinus pliocenica	
Fraxinus ungeri	
cf. *Fraxinus* sp.	
Glyptostrobus europaeus	
Hedera helix	*Hedera* sp.
Hedera sp. div. (*Hedera* aff. *helix*)	*Hedera* sp.
Juglans acuminata	*Juglans regia*
Laurophyllum sp.	*Lauraceae*
Leguminosites strausii	
Liquidambar europaea	*Liquidambar styraciflua*
Liriodendron procaccinii	
Magnolia sp. 2	*Magnolia* sp.
Malus pulcherrima	
Malus sp.	
Oinus sp.	
Paliurus tiliaefolius	*Paliurus* sp.
Parrotia pristina	*Parrotia persica.*
? *Physocarpus* sp.	
Picea cf. *latisquamosa*	
Picea omoricoides	
Populus aff. *populina*	*Populus* sp.
Populus albiformis	*Populus* sp.
Populus canescentoides	*Populus* sp.
Populus gregorii	*Populus* sp.
Populus sp. div.	*Populus* sp.
Populus willershausensis	*Populus* sp.
Potamogeton spp.	
Pteridium sp.	
Quercus ex gr. *gigas*	*Quercus* sp.
Quercus mohrae	*Quercus* sp.
Quercus praecastaneifolia	*Quercus* sp.
Quercus praeerucifolia	*Quercus* sp.
Quercus roburoides	*Quercus petraea*
Quercus roburoides subsp. *latifolia*	*Quercus petraea*

Quercus roburoides subsp. *roburoides*	*Quercus petraea*
Rosa sp.	
Roseceae gen. et sp. indet. vel *Ulmus carpinoides*	
cf. *Salix* sp. 1	
Salix sp. 2	
cf. *Salix* sp. 3	
Sassafras ferretianum	*Sassafras* sp.
Sequoia abietina	
Sequoia langsdorfii	
Sequoia sp.	
Sorbus ariaefolia	*Sorbus* sp.
Sorbus cf. *uzenensis*	*Sorbus* sp.
Sorbus gabbrensis	*Sorbus* sp.
Sorbus praetorminalis	*Sorbus* sp.
Swida ? *graeffii*	
Taxus baccata foss.	
Tilia cf. *saviana*	
Tilia saportae	*Tilia* sp.
Torreya nucifera foss.	*Tilia* sp.
Tsuga europaea	
Ulmus cf. *carpinoides*	*Ulmus alata*
? *Vitis* aff. *stricta*	*Vitis vulpina*
Vitis sp. vel *Ampelopsis* sp.	
Zelkova zelkovifolia	*Zelkova carpinifolia, Z. serrata*

Appendix 2

List of taxa from Berga (from Mai & Walther 1988) and NLRs used for CoA (from PALAEOFLORA database).

Berga	
Fossil taxa	**NLRs used for CoA**
Abies resinosa	*Abies* sp.
Abies sp. *indet. fol.*	*Abies* sp.
Acer berganum	*Acer* sp.
Acer campestrianum	*Acer* sp.
Acer integerrimum	*Acer cappadocicum*
Acer sp.	*Acer* sp.
Acer tricuspidatum	*Acer sacharinum*
Actinidia faveolata	*Actinidia* sp.
cf. *Actinidia* sp.	
Aesculus hippocastanum	*Aesculus hippocastanea*
Aesculus sp.	*Aesculus* sp.
Ajuga reptans	*Ajuga reptans*
Alisma ovatum	
Alnus gaudinii	*Alnus nitida*
Alnus tambovica	*Alnus* sp.
Ampelopsis macrosperma	*Ampelopsis* sp.
Ampelopsis malvaeformis	*Ampelopsis* sp.
Apium nodiflorum	
Aralia szaferi	
Asarina ruboidea	
Betonica monieri	
Betula cholmechensis	*Betula* sp.
Betula longisquamosa	*Betula* sp.
Boehmeria lithuanica	
Caldesia cylindrica	
Carex binervis	
Carex carpophora	
Carex flagellata	
Carex helmensis	
Carex laevigata	
Carex paucifloroides	
Carex pendula	
Carex pilulifera	
Carex rostrata	
Carex szaferi	

Carpinus betulus	
Carpolithus bergaensis	
Carpolithus mercurialoides	
Carpolithus minimus	
Carya globosa	*Carya* sp.
Cathaya abachasica	
Cathaya loehrii	
Celtis sp.	*Celtis* sp.
Cercidiphyllum crenatum	*Cercidiphyllum japonicum*
Chamaecyparis obtusa	
Chenopodium album	
Chenopodium polyspermum	
Cirsium arvense	
Cirsium palustre	
Cladium mapaninoides	
Corylopsis urselensis	
Corylus avellana	*Corylus avellana*
Cotoneaster gailensis	
Crataegus oxyacantha	
Cyclocarya nucifera	
Decodon globosus	
Dendrobenthiamia tegeliensis	
Dichostylis pliocenica	
Engelhardia macroptera	
Epipremnum reticulum	
Euphorbia platyphyllos	
Fagus attenuata	*Fagus ferruginea*
Fagus decurrens	
Glyptostrobus brevisiliquata	
Glyptostrobus europaeus	
Gratiola officinalis	
Gypsosphila semisphaerica	
Hedera helix	*Hedera* sp.
Humulus scabrellus	
Hypericum calycinoides	
Kalmia minutula	
Lemna trisulca	
Liquidambar europaea	*Liquidambar styraciflua*
Lirodendron geminata	
Ludwigia palustris	
Luronium natans	

Lychnis flos-cuculi	
Lycopus europaeus	
Lysimachia punctata	
Mahonia staphyleaeforme	
Melissa officinalis	
Mentha longifolia	
Mentha pulegium	
Microdiptera sibirica	
Minuartia pliocenica	
Morus ucrainica	
Myosoton aquaticum	
Najas lanceolata	
Najas marina	
Nuphar lutea	
Oenathe aquatica	
Osmunda heeri	*Osmunda* sp.
Ostrya szaferi	
Oxalis corniculata	
Parrotia pristina	*Parrotia persica*
Pentapanax tertiarius	
Peucedanum moebii	
Physalis alkekengis	
Physocarpus europaeus	
Picea rotunde-squamosa	
Pilea bashkirica	
Platanus cf. *platanifolia*	*Platanus* sp.
Poliothyrsis hercynica	
Polygonum persicaria	
Populus cf. *tremula*	*Populus tremula*
Potamogeton cholmechensis	
Potamogeton elegans	
Potamogeton medicagoides	
Potamogeton natans	
Potamogeton perforatus	
Potamogeton polymorphus	
Potentilla erecta	

Potentilla pliocenica	
Potentilla supina	
Proserpinaca europaea	
Proserpinaca reticulata	
Prunella vulgaris	
Prunus fruticosa	
Pterocarya paradisiaca	*Pterocarya fraxinifolia*
Pterocarya pterocarpa	
Quercus pseudocastanea	*Quercus Sekt. Cerris*
Quercus pubescens	*Quercus* sp.
Quercus sp.	*Quercus* sp.
Quercus sp. Typ 1	*Quercus* sp.
Quercus sp. Typ 2	*Quercus* sp.
Quercus sp. Typ 3	*Quercus* sp.
Ranunculus edenensis	
Ranunculus reidli	
Ranunculus repens	
Ranunculus sceleratus	
Ranunculus tanaiticus	
Ranunculus trachycarpoides	
Rosa bergaensis	
Rubus fruticosus	
Rubus idaeus	
Rubus polevskoyanus	
Rumex acetosella	
Salix varians	*Salix bonplandiana*
Salvia cf. *officinalis*	
Sambucus bashkirica	
Sambucus nigra	
Sambucus pulchella	
Sapium mädleri	
Sassafras ferretianum	*Sassafras* sp.
Satureja acinos	
Scirpus isolepioides	
Scirpus mucronatus	
Scirpus radicans	

Scirpus sylvaticus	
Scopolia carniolica	
Selaginella pliocenica	
Sequoia abietina	
Solanum dulcamara	
Sparganium emersum	
Sparganium neglectum	
Stachys sylvatica	
Styrax maxima	
Swida gorbunovii	
Swida kineliana	
Swida sanguinea	
Taxodium dubium	*Taxodium distichum*
Taxodium rossicum	
Teucrium chamaedrys	
Teucrium tatjanae	
Thalictrum simplex	
Thesium nikitinii	
Tilia tuberculata	
Trichosanthes fragilis	
Tsuga Section *Tsuga*	
Typha pliocenica	
Ulmus cf. *carpinoides*	*Ulmus carpinifolia*
Ulmus pyramidalis	*Ulmus alata*
Urtica dioica	
Valeriana pliocenica	
Viburnum hercynicum	
Viola bergaensis	
Viola neogenica	
Viola palustris	
Vitis sylvestris	
Weigela szaferi	
Weigela thuringiaca	
Zelkova ungeri	*Zelkova carpinifolia, Z. serrata*
Zelkova zelkovifolia	*Zelkova carpinifolia, Z. serrata*

Appendix 3

List of taxa from Frankfurt am Main (from Mädler 1939) and NLRs used for CoA (from PALAEOFLORA database).

Frankfurt am Main	
Fossil taxa	**NLRs used for CoA**
Abies pectinata	*Abies* sp.
Abies sclereidea	*Abies* sp.
Acanthopanax sp.	*Acanthopanax* sp.
Acer brachyphyllum	*Acer* sp.
Acer grosse-dentatum	*Acer* sp.
Acer integerrimum	*Acer cappadocicum*
Acer monspessulanum	*Acer monspessulanum*
Acer platanoides	*Acer platanoides*
Acer sp.	*Acer* sp.
Aesculus hippocastanum	*Aesculus hippocastanea*
Ajuga antiqua	*Ajuga reptans*
Alnus sp. cf. *alnobetula*	*Alnus* sp.
Araliaceae, genus indet.	*Araliaceae*
Berberis sp.	*Betula* sp.
Betula brongniarti	*Betula lenta*
Betula longisquamosa	*Betula* sp.
Betula sp. cf. *pumila*	*Betula* sp.
Betula subpubescens	*Betula pubescens*
Buxus sempervirens	*Buxus sempervirens*
Carduus sp. vel *Cirsium* sp.	
Carduus sp. vel *Cnicus* sp.	
Carex sp., sectio *Vignea*	
Carpinus betulus	*Carpinus betulus*
Carpolithes sp. 25	
Carya angulata	*Carya* sp. *(C. cordiformis., C. glabra)*
Carya aquatica	*Carya* sp.
Carya globosa	*Carya* sp.
Carya longicarpa	*Carya* sp.
Carya tomentosa	*Carya tomentosa*
Castanea sp.	*Castanea* sp.
Cephalotaxus francofurtana	*Cephalotaxus* sp.
Cephalotaxus loossi	*Cephalotaxus* sp.
Cephalotaxus pliocaenica	*Cephalotaxus fortunei*
Cephalotaxus rotundata	*Cephalotaxus* sp.

Ceratophyllum submersum	*Ceratophyllum submersum*
Cercidiphyllum crenatum	*Cercidiphyllum japonicum*
Compositae, genus indet.	
Corylopsis urselensis	*Corylopsis pauciflora*
Corylus avellana	*Corylus avellana*
Cyperaceae, genus indet.	
Draba venosa	
Dulichium spathaceum	*Dulichium spathaceum*
Engelhardtia nucifera	
Eucommia europaea	*Eucommia ulmoides*
Euryale lissa	
Fagus decurrens	*Fagus* sp.
Fagus ferruginea	*Fagus ferruginea*
Ficaria sp. cf. *verna*	
Fraxinus sp.	
Ginkgo adiantoides	
Gramineae, genus indet.	
Ilex aquifolium	*Ilex aquifolium*
Juglans cinerea	*Juglans cinerea*, *J. mandshurica*
Juglans costata	
Keteleeria loehri	*Keteleeria fortunei*
Larix europaea	*Larix* sp.
Laubblatt sp. A	
Laubblatt sp. A 1	
Laubblatt sp. A 2	
Laubblatt sp. B cf. *Evonymus* sp.	
Laubblatt sp. C cf. *Stuartia* sp.	
Laubblatt sp. D cf. *Cocculus latifolius*	
Laubblatt sp. E	
Laubblatt sp. F	
Laubblatt sp. G	
Laubblatt sp. H	
Laubblatt sp. J	
Laubblatt sp. K	
Laubblatt sp. L cf. *Celtis japeti*	
Laubblatt sp. M	
Leguminosites gymnocladoides	
Libocedrus pliocaenica	
Liquidambar pliocaenica	*Liquidambar* sp.
Liriodendron tulipifera	*Liriodendron* sp.
Magnolia cor	*Magnolia* sp.

Magnolia moenana	*Magnolia* sp.
Magnolia sinuata	*Meliosma* sp.
Meliosma europaea	
Melissa elegans	
Monocotyledoneae incertae sedis.	
Myrica lignitum	*Myrica cerifera*
Nuphar sp.	
Nyssa disseminata	*Nyssa sylvatica*
Oleaceae, tribus *Jasminoideae,* genus indet.	
Parrotia fagifolia	
Parthenocissus sp.	
Peucedanum moebii	
Picea excelsa	*Picea* sp.
Picea latisquamosa	*Picea* sp.
Picea sp.	*Picea* sp.
Pinus askenasyi	
Pinus brevis	*Pinus mugo*
Pinus laricio	
Pinus ludwigi	
Pinus silvestris	*Pinus sylvestris*
Pinus stellwagi	
Pinus strobus	*Pinus strobus*
Pinus timleri	
Pirus malus	
Pirus sp.	
Podocarpus kinkelini	*Podocarpus* sp.
Polygonum wolfi	*Polygonum* sp.
Populus sp. cf. *nigra*	*Populus* sp.
Potamogeton medicagoides	
Potamogeton sp.	
Prunus aviiformis	*Prunus* sp.
Prunus insititia	*Prunus* sp.
Prunus sp. cf. *aequinoctialis*	
Prunus spinosa	*Prunus spinosa*
Pseudolarix kaempferi	*Pseudolarix amabilis*
Pterocarya denticulata	*Pterocarya* sp.
Quercus sessiliflora	*Quercus* sp.
Rhizomites moenanus	
Salix denticulata	*Salix nigra*
Sciadopitys tertiaria	*Sciadopitys verticilata*
Scirpus sp. 2	

Scirpus sp. 3	
Scirpus spletti	
Scleranthus sp.	
Sequoia langsdorfi	
Sparganium sp.	*Sparganium* sp.
Staphylea pliocaenica	*Staphylea* sp.
Stuartia europaea	*Theaceae.*
Styrax obovatum	*Styrax* sp.
Taxodium distichum	*Taxodium distichum*
Thuja pliocaenica	
Tilia sp. cf. *platyphllos*	*Tilia* sp.
Torreya nucifera	*Torreya nucifera*
Trichosanthes fragilis	*Trichosanthes* sp.
Tsuga europaea	*Tsuga* sp.
Ulmus longifolia	*Ulmus* sp.
Viola sp.	
Viscophyllum miqueli	
Viscophyllum pliocaenicum	
Vitis ludwigi	
Vitis sp.	
Vitis teutonica	
Zelkova ungeri	*Zelkova carpinifolia, Z. serrata*