Pliocene palaeoenvironment and correlation of the Sessenheim-Auenheim floristic complex (Alsace, France)

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Abstract

For the first time modern quantitative techniques have been employed to the Pliocene floristic complex of the Sessenheim-Auenheim area in Northern Alsace, France, in order to objectively assess vegetation reconstruction (IPR vegetation analysis) and palaeoclimatological estimates (CLAMP, CoA) based on the recently revised leaf and carpological assemblages from this area. The data have been compared to the intuitively derived models received by comparisons with analogous modern forest vegetation in East Asia and North America by former authors. The studied floristic spectra have been correlated in similar way with selected Pliocene plant assemblages of comparable age in Europe. The resulting vegetation analysis refers the studied two assemblages into the Mixed Mesophytic Forest for the lower-lying Sessenheim "Saugbagger" carpological assemblage and into the Broad-leaved Deciduous Forest in the case of the Auenheim leaf and carpological assemblage, respectively. Our data potentially suggest a slight decrease of Mean Annual Temperature (MAT) and Coldest Month Mean Temperature (CMMT) between the stratigraphically older "Saugbagger-Flora" (MAT: 15.3–15.6 °C; CMMT: 2.7 °C; both only CoA) and the Auenheim assemblage (MAT: 13.6–15.6 °C [CoA], 12.1 °C [CLAMP]; CMMT: 0.9–1.7 °C [CoA], 3.9 °C [CLAMP]).

Keywords: Macroflora, IPR vegetation analysis, CoA, CLAMP, palaeoclimate, Pliocene, Alsace.

Zusammenfassung

Moderne quantitative Methoden werden erstmals auf den aus dem Pliozän des Elsass, Frankreich, stammenden Florenkomplex der Gegend um Sessenheim und Auenheim angewandt, mit dem Ziel einer objektiven Rekonstruktion der Vegetation (IPR Vegetationsanalyse) und der Abschätzung verschiedener Paläoklimaparameter (CLAMP, CoA). Die vorliegende Arbeit basiert dabei auf aktuellen Revisionen der Blatt- und Karpofloren des Untersuchungsgebiets. Die dabei gewonnenen Ergebnisse werden mit jenen intuitiver Ansätze früherer Autoren verglichen, die vor allem auf Vergleichen mit modernen Analoga aus der Vegetation Ost-Asiens und Nord-Amerikas basierten. Des Weiteren werden die hier untersuchten Floren mit verschiedenen, etwa gleich alten europäischen Pliozänfloren verglichen. Die aus unseren Untersuchungen resultierende Vegetationsanalyse zeigt, dass die untersuchten Floren dem „Mixed Mesophytic Forest" (Saugbagger-Flora von Sessenheim) und dem „Broad-leaved Deciduous Forest" (Auenheim) zugeordnet werden können. Unsere Daten deuten auf einen leichten Rückgang der Mittleren Jahrestemperatur (MAT) und der mittleren Temperatur des kältesten Monats (CMMT) zwischen der Ablagerung der "Saugbagger-Flora" (MAT: 15,3–15,6 °C; CMMT: 2,7 °C; beide nur CoA) und der etwas jüngeren Flora von Auenheim (MAT: 13,6–15,6 °C [CoA], 12,1 °C [CLAMP] und CMMT: 0,9–1,7 °C [CoA], 3,9 °C [CLAMP]) hin.

Contents

1. Introduction

The Pliocene of the so-called "Haguenau terrace" and lowlands of the Rhine River in Northern Alsace, France, has yielded huge quantities of fossil plant and animal remains and has become a classical "Lagerstätte" in Europe (Geissert 1979; Geissert & Ménillet 1979; Geissert et al. 1990). The sites are scattered in the wider surroundings of Haguenau (e. g., Soufflenheim, Sessenheim, Auenheim) in abandoned or active sand and gravel quarries, and pottery clay quarries (Geissert 1987). The present paper summarizes the recently revised palaeobotanical data on leaf and carpological material from the main fossiliferous layer and its adjacent deposits in order to achieve an objective vegetation picture and palaeoclimatic signal for this floral complex. This study may contribute towards the understanding of environmental and climatic development in Western Europe during Pliocene time. Two major treatments serve as a basis for the data presented here – Geissert et al. (1990) for carpology and Kvaček et al. (2008) for foliage, besides several preliminary papers consulted additionally (Kirchheimer 1949; Geissert 1962, 1967, 1972, 1974, 1979, 1987; Geissert & Gregor 1981; Geissert & Nötzold 1979; Gregor 1980). The analyses are based on detailed comparisons of individual elements with the living analogues according to detailed morphological and anatomical studies. For comparisons we employed own observations and the published data on some other floras of similar age in Italy (Ca'Viettone, Sento, Stura) and Germany (Willershausen).

Abbreviations

Abbreviations for climate estimates:

CMMT	coldest month mean temperature
MAP	mean annual precipitation
MAT	mean annual temperature
P-dry	precipitation during the driest month
P-warm	precipitation during the warmest month
P-wet	precipitation during the wettest month
SD	standard deviation
WMMT	warmest month mean temperature

Abbreviations for the "Integrated Plant Record (IPR) vegetation analysis":

AQUATIC	aquatic component
AZONAL WOODY	azonal tree and shrub component
BLD	broad-leaved deciduous woody angiosperm component
BLDF	Broad-leaved Deciduous Forest
BLE	broad-leaved evergreen woody angiosperm component
CONIFER	zonal and extrazonal conifer component
DRY HERB	open woodland and grassland component
F	fruit and carpoflora
FERN	zonal and extrazonal fern component
L	leaf flora
LEG	legume-type woody angiosperm component
MMF	Mixed Mesophytic Forest
MESO HERB	forest undergrowth component
PALM	zonal palm component
REED/SEDGES	wetlands herb and azonal fern component
SCL	sclerophyllous woody angiosperm component

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2. Geological setting of the sites and dating

The fossiliferous deposits in Northern Alsace (Fig. 1) are geographically divided into two sections by neo-tectonic faults. The higher "Haguenau terrace" extends from Haguenau to Soufflenheim parallel to the Rhine River and includes the "classical" exposures of clay quarries from where plant fossils were first described by Hickel (1932) and later also by Kirchheimer (1949). This level was neotectonically shifted by some tens of meters higher than the riverplain, where large sand quarries at Sessenheim, Auenheim, Rountzenheim, and other places have been opened (Geissert 1962, 1969). According to Geissert (1967, 1996) and Geissert et al. (1990), the plant assemblages deriving from the main fossiliferous horizon consisting of clay lenses in the "Haguenau terrace" and the lowland sand quarries differ from those from the lowermost levels of the "Saugbagger-Flora" at Sessenheim in underlying strata (Günther & Gregor 1989). Geissert et al. (1990) recognized four fossiliferous horizons: 1) the lowermost "Saugbagger-Flora" in the Sessenheim sand quarry ("Brunnssumian"), 2) the clayey fossiliferous lenses above sands and gravels in Auenheim and other sites, 3) lignite seamlets in sand quarries of Sessenheim, Soufflenheim and sandy clay in Königsbrück Mine ("Reuverian"), and 4) ortstein psammitic-psefitic deposits with *Mammut borsoni* at Sessenheim and Soufflenheim ("Pliocene final") (Geissert 1996; Kvaček et al. 2008). The younger fossiliferous level of post-Reuverian age, which is spread in the N-S direction, yielded another plant assemblage not treated in this account (Nötzold 1963). Later executed boreholes on oil and drinking water revealed the thickness

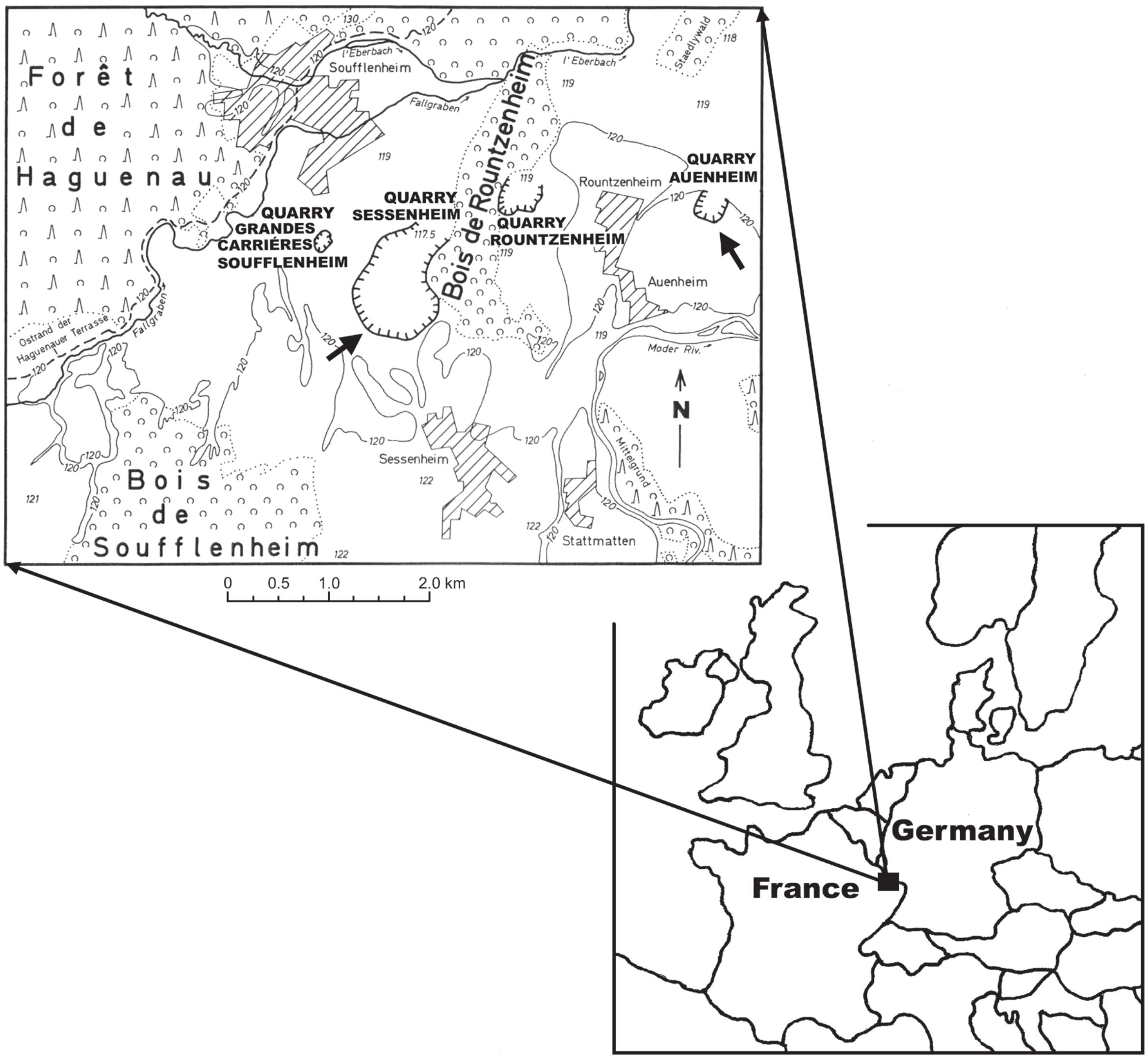

Fig. 1. Location of the studied floras of Auenheim and Sessenheim "Saugbagger-Flora" (arrows) in the Alsace Area (adapted from Geissert 1996).

of the whole Pliocene sedimentary complex which reaches in the "Haguenau terrace" max. 60 m and in the river valley over 200 m. F. Geissert, who carried out most collections and explorations in the Alsace area after the Second World War, was able to recognize several palaeontological horizons of different lithology, floristic content, and age in main exposures at Soufflenheim, Sessenheim, and Auenheim and supplied detailed data on the geological section at Auenheim (Geissert 1974). The so far available dating independent from the palaeofloristic correlation derives from mammals from the upper fossiliferous layer at Soufflenheim and Sessenheim (Geissert 1987) and from freshwater molluscs (Nordsieck 1974; Schlickum & Geissert 1980). Palaeomagnetic data are unfortunately not available.

In the Pliocene correlation chart by Mai (1995), the Pliocene floras of the Alsace area are ranged into the Floristic Assemblages Brunssum and Reuver sensu Mai & Walther (1988). Krutzsch (1988, table in attachment) ranges the level of the "Saugbagger-Flora" into the late Early Pliocene and the Auenheim level into the early Late Pliocene. Gregor (in Kvaček et al. 2008) assigned the Auenheim flora of the main fossiliferous horizon to the Reuverian along with the Willershausen flora, i. e. Middle Pliocene (or Late Pliocene in sense of Zagwijn 1990). The Brunssumian and Reuverian stages in the Netherlands have been assigned to the ages of 3.6 to 2.6 Ma, according to the palaeomagnetic correlation (Kuhlmann et al. 2006).

3. Material and Methods

The leaf material of Auenheim (coll. GEISSERT) is available as compressions separated from "leaf beds", i. e. coaly layers consisting of accumulated and compressed mummified leaves. The leaf compressions were mechanically separated from each other by preparation in water with the aid of hydrogen peroxide and provisionally preserved spread on the bottoms of plastic boxes and kept moistened in glycerol. The epidermal structures are preserved in many cases. The preparations proceeded by routine techniques (KVAČEK et al. 2008).

Most fossil material of Auenheim studied has been transferred to the collections of the Naturmuseum Augsburg, with duplicates to the National Museum, Department of Palaeontology, Prague. Besides, some original material from Auenheim studied by F. GEISSERT has been revised in the collection of the State Museum of Natural History Stuttgart. The reference cuticle collections are housed at the Charles University, Prague. The leaf material of Willershausen that served for our comparisons has been studied in the collections of the State Museum of Natural History Stuttgart. The other data on this flora have been taken from the published monographs (STRAUS 1992; KNOBLOCH 1998). The data from Italy come from various publications by MARTINETTO (1995), MARTINETTO et al. (1997), BERTINI & MARTINETTO (2008) and his personal communications. The carpological material from the localities Auenheim (GÜNTHER & GREGOR 1989; GREGOR personal communication) and Sessenheim (GEISSERT et al. 1990) has partly been revised by E. MARTINETTO, H. J. GREGOR and the first author. The fruits and seeds are partly compressed, carbonaceous and also three-dimensionally preserved and have been obtained from deposits by washing. The material is housed in the collections of the State Museum of Natural History Stuttgart and in the collections of the Naturmuseum Augsburg.

3.1. Integrated Plant Record vegetation analysis (IPR vegetation analysis)

A semi-quantitative evaluation method was developed by KOVAR-EDER & KVAČEK (2007) and KOVAR-EDER et al. (2008) to map integrated fossil plant records (leaf, fruit, and pollen assemblages) in terms of zonal vegetation. This method attempts to incorporate taxonomy, physiognomy and autecological properties of Cenozoic fossil plants for an objective assessment of fossil vegetation. It uses 13 basic taxonomic-physiognomic groups defined to reflect key autecological characteristics (see KOVAR-EDER & KVAČEK 2003, 2007 and KOVAR-EDER et al. 2008). Percentages of different components (i. e., basic taxonomic-physiognomic groups of an assemblage) have been defined to distinguish six modern vegetation types: Broad-leaved Deciduous Forest, Mixed Mesophytic Forest, Broad-leaved Evergreen Forest, Subhumid Sclerophyllous Forest, Xeric Open Woodland and Xeric Grassland or Steppe (for details see KOVAR-EDER et al. 2008, table 4).

3.2. Coexistence Approach (CoA)

Climate and environmental reconstructions based on the assumed nearest living relatives (NLR) of fossil elements are as old as palaeobotany started as a modern science. Whereas early reconstructions were based on the comparison of few selected (climate sensitive) taxa (e. g., HEER 1855, 1856, 1859), many modern approaches have tried to use as many NLRs as possible to get more reliable and reproducible quantitative results. One of these modern approaches, the Coexistence Approach developed by MOSBRUGGER & UTESCHER (1997), is based on a database that includes climatic parameters for more than 750 NLRs of fossil plant taxa from the European Palaeogene and Neogene (UTESCHER & MOSBRUGGER 1990–2007). This approach compares climatic demands of as many NLRs as possible to get climatic intervals in which as many NLRs as possible could theoretically coexist today. It is assumed that these intervals are the best descriptions of the potential palaeoclimatic conditions under which the corresponding fossil flora grew. Arguments for and against this method have been discussed repeatedly (e. g., MOSBRUGGER & UTESCHER 1997; MOSBRUGGER 1999; UHL et al. 2003; UHL 2006; KRAČEK 2007), but its general applicability and reliability have been demonstrated by various authors for the European Palaeogene and Neogene (e. g., PROSS et al. 1998; UTESCHER et al. 2000; UHL et al. 2006, 2007; MOSBRUGGER et al. 2005; BRUCH et al. 2007).

3.3. Climate Leaf Analysis Multivariate Program (CLAMP)

This methodology is based on the multivariate statistical technique for quantitative determining a range of palaeoclimate parameters based on leaf physiognomy of woody dicotyledonous flowering plants. CLAMP has first been introduced by WOLFE (1993) and subsequently this technique has been refined mainly by WOLFE & SPICER (1999), SPICER et al. (2004) and SPICER (2000, 2007). Mathematically, this method is based on Canonical Correspondence Analysis (TER BRAAK 1986). We used suitable spreadsheets provided by SPICER as well as modern calibration datasets, which include 173 modern sample sites (CLAMP 3A), mostly located in North America and Eastern Asia. All materials are free to download on SPICER'S CLAMP website http://www.open.ac.uk/earth-research/

Tab. 1. Percentage of foliar physiognomic characters of the Auenheim flora (45 species).

Foliar physiognomic characters		%
Margin character states	Lobed	31.11
	No teeth	35.56
	Teeth regular	48.89
	Teeth close	20.00
	Teeth round	42.22
	Teeth acute	31.11
	Teeth compound	6.67
Size character states	Nanophyll	0.00
	Leptophyll I	0.00
	Leptophyll II	2.22
	Microphyll I	6.64
	Microphyll II	22.56
	Microphyll III	42.56
	Mesophyll I	21.46
	Mesophyll II	4.44
	Mesophyll III	0.00
Apex character states	Apex emarginate	4.55
	Apex round	47.34
	Apex acute	37.11
	Apex attenuate	10.98
Base character states	Base cordate	26.29
	Base round	41.84
	Base acute	31.84
Length to width character states	L : W <1 : 1	12.22
	L : W 1–2 : 1	58.87
	L : W 2–3 : 1	20.71
	L : W 3–4 : 1	5.16
	L : W >4 : 1	2.96
Shape character states	Obovate	31.11
	Elliptic	38.89
	Ovate	30.00

spicer/CLAMP/Clampset1.html. We use for our analysis the statistical program CANOCO for Windows Version 4.5. The list for the physiognomic score of the Auenheim flora is given in Table 1.

4. Palaeofloristics

The so far described carpological data from the Sessenheim area (e. g., Geissert & Gregor 1981; Günther & Gregor 1989; Geissert et al. 1990) refer to more than 150 species, of which 11 belong to conifers and the rest to angiosperms. The list has been corrected according to new revisions, mainly in *Symplocos* (Mai & Martinetto 2006), *Sargentodoxa* (Mai 2001, Martinetto 2001) and *Fagus* (Denk & Meller 2001) and in this way the number of angiosperms has been reduced to 131 (see Appendix). The carpological assemblage reveals a relatively high content of mesophytic herbs (ca. 15.4 %), mostly native to Europe. Among woody elements those with modern East Asian relatives prevail (e. g., *Cephalotaxus*, *Eucommia*, *Meliosma*, *Phellodendron*, *Sargentodoxa*) with additional elements with Asa-Gray disjunction *(Liriodendron*, *Symplocos*, *Schisandra)* or North American distribution *(Taxodium*, *Sequoia*, *Brasenia*, *Leitneria)*. Extinct or morphogenera are rare *(Epipremnites*, *Scindapsites*, *Tectocarya*, *Carpolithus)*. Among angiosperms, putative shrubs are common, and also several vines and lianas are listed *(Actinidia*, *Ampelopsis*, *Vitis*, *Schisandra*, *Sargentodoxa*, *Toddalia*, *Trichosanthes)*. Ferns and fern-like plants have not been documented so far.

The recently revised plant assemblage of Auenheim consists of 10 gymnosperms and 51 angiosperms (see Appendix). Arboreal elements prevail while fossils of vines and small shrubs are less frequent. Single fossils may represent herbs. Ferns and fern-like plants are lacking. Most fruit remains recovered in the fossiliferous horizon at Auenheim correspond to elements also documented by foliage *(Carpinus*, *Fraxinus*, *Acer*, *Craigia*, *Eucommia)*. The only exception is *Liriodendron*, which is exclusively represented by fruits. Most elements have nearest living relatives in East Asia and Western Eurasia, e. g., *Ginkgo*, *Picea echinata*, *Fagus kraeuselii*, *Buxus*, *Eucommia*, *Parrotia*, *Pterocarya*, *Craigia*, fewer of them are confined to North America today *(Taxodium)* or show an Asa-Gray disjunction *(Pseudotsuga*, *Tsuga*, *Torreya*, *Nyssa*, *Carya)*. The other sites yielded much less diverse plant assemblages and are less relevant to the present analysis.

5. Palaeoenviromental analysis

5.1. Intuitive comparisons with the modern vegetation

The carpological assemblage of Sessenheim "Saugbagger-Flora" is characterized by a higher representation of thermophilous and evergreen elements, such as *Sequoia*, *Symplocos*, *Rehderodendron-Halesia* complex, *Tectocarya* etc., which links this assemblage with warm temperate to subtropical forests in the SE USA and East Asia. Due to the lack of evergreen Fagaceae and Lauraceae, a direct comparison with the subtropical Nothophyllous Evergreen Forest of East Asia seems improbable and even with the typical Mixed Mesophytic Forest sensu

WOLFE (1979) deviates a lot. According to GEISSERT et al. (1990), the Sessenheim "Saugbagger-Flora" reflects best a relatively cooler trend within the subtropical Cfa type and is comparable with the Molasse floras, i. e. MAT (14–16 °C) and MAP (1000–1500 mm). This estimation agrees well with an interpretation of the palaeovegetation of the Floristic Assemblage of Ca'Viettone in Italy, which was estimated as an ancient equivalent of the extant Evergreen Broad-Leaved Forest of China, climatically characterized by MAT = 15–17 °C and MAP = 1300–2700 mm respectively (MARTINETTO 1995). However, the Sessenheim carpoflora differs decidedly by the lack of *Trigonobalanopsis*, fitting better into the Mixed Mesophytic Forest type.

Most of the elements dominating the Auenheim assemblage, i. e., *Fagus*, deciduous *Quercus*, *Carpinus*, Salicaceae, and Ulmaceae belong to the deciduous mesophytic to moist riparian broad-leaved forests outside swampy and flooded habitats. Only a few woody elements are facultative or true swamp plants, i. e., *Taxodium*, *Alnus*, *Nyssa*, and *Fraxinus*. *Taxodium*, a typical tree of swamps of SE and E USA today is not accompanied at Auenheim by other swamp elements of the European Neogene, like *Glyptostrobus*, *Cercidiphyllum*, *Liquidambar*, *Myrica*, etc. or these elements are only represented by single fragmentary fossils *(Alnus*, *Nyssa)*. On the contrary, mesophytic woody elements are better represented, e. g., *Zelkova*, *Acer* spp., *Buxus*, *Carpinus*, and Rosaceae. *Carya* and *Pterocarya* may have entered both mesophytic and riparian non-flooded areas together with *Ulmus*, *Zelkova*, *Fraxinus*, *Gleditsia*, and Salicaceae. Vines *(Trichosanthes)* and shrubs (*Ilex*, cf. Vacciniaceae) are relatively rare, possibly due to taphonomic bias. Also all recorded gymnosperms except *Taxodium*, such as *Ginkgo*, Pinaceae, and *Torreya* belong to mesophytic representatives of mixed coniferous and broad-leaved deciduous forests in the Northern Hemisphere. Thermophilous elements, such as evergreen Fagaceae, Lauraceae, Theaceae, and others, which would indicate the Mixed Mesophytic Forest of East Asia, are largely absent. Exceptions are *Cathaya* and *Craigia*, two relict living genera, which deviate from their ancestors in more thermophilous character. The assemblage of Auenheim can best be compared with forest vegetation spread in Korea and Japan in higher zones of the *Fagus* forests or the northern part of the area of *Taxodium* in the USA. Relatively close affinities can be found also to the Caucasus – Near East refugial forests with *Fagus orientalis*, *Parrotia persica*, *Pterocarya*, *Zelkova*, and *Buxus*.

5.2. IPR vegetation analysis

The Sessenheim "Saugbagger-Flora" is only based on seed and fruit taxa (see Appendix). The IPR vegetation analysis shows a similar ratio of zonal and azonal taxa (i. e. 68.1 % vs 31.9 %) such as that in the Auenheim flora. Besides, there is obviously a distinct increase of percentage in MESO HERB component of zonal taxa (13.5 %) contrary to 1.6 % of Auenheim. The percentages of BLD component of zonal woody angiosperms (76.4 %), of the BLE component of zonal woody angiosperms (20.3 %) and of SCL + LEG component of zonal woody angiosperms (3.3 %), fit to the Mixed Mesophytic Forest (MMF) (see Tab. 2).

The flora of Auenheim with almost 100 taxa is based on the leaf and carpological material (Appendix and Tab. 2), of which 61.6 % are zonal taxa and 38.4 % are azonal. IPR vegetation analysis shows a high percentage of BLD elements of zonal woody angiosperms (89 %) contrary to 4 % BLE elements of zonal woody angiosperms and 7 % SCL + LEG elements of zonal woody angiosperms. This composition corresponds to the Broad-leaved Deciduous Forest (BLDF). This IPR vegetation analysis of the Auenheim flora corroborates our intuitive opinion derived from the scarcity of thermophilous Mixed Mesophytic Forest elements (Lauraceae, evergreen Fagaceae, Symploceae, Styracaceae, etc.). A noticeable feature of the Auenheim flora based on the IPR vegetation analysis is the relatively higher percentage of zonal conifers (16.39 % of zonal elements). Conifers are represented by some more boreal elements, such as *Picea* and *Abies* typical of the mixed coniferous and broad-leaved deciduous forests. This is a characteristic feature of most Late Pliocene floras of Europe. Also characteristic and consistent is the very low percentage of BLE in the zonal part of the assemblage.

6. Palaeoclimatic analysis

CoA estimates for temperature parameters for both studied floras do not differ significantly from each other (see Tab. 3 and 4), although temperature estimates for Sessenheim ("Saugbagger-Flora") are slightly higher than those for Auenheim. Such differences between carpofloras (Sessenheim) and mixed floras dominated by leaves (Auenheim) are known for several other localities from the European Neogene – e. g., MOSBRUGGER & UTESCHER (1997), UTESCHER et al. (2000). Potential reasons for such differences are: 1) carpofloras are usually more diverse than leaf-floras, leading to narrower intervals of coexistence (e. g., MOSBRUGGER & UTESCHER 1997), and 2) in most leaf floras shrubs and herbs (including many elements characteristic of warmer conditions) are underrepresented, e. g., BELZ & MOSBRUGGER (1994), MOSBRUGGER & UTESCHER (1997). The MAT estimate derived by CLAMP for Auenheim (see Tab. 5) is also in approximate agreement with both CoA estimates when the standard deviation of this particular value is taken into account. In the case of CMMT the CoA intervals for both floras do not overlap

Tab. 2. Results of IPR vegetation analysis. For symbols see ‘Abbreviations’!

		ZONAL components									AZONAL components		
			Woody angiosperms										
Locality	Organ	CONIFER	BLD	BLE	SCL	LEG	PALM	DRY HERB	MESO HERB	FERN	AZONAL WOODY	REED/ SEDGES	AQUATIC
Auenheim	L	8	27.5	1.5	2	1	0	0	0	0	12	1	0
	F	2	16.5	0.5	0.5	0	0	0.5	1	0	5.5	3.5	7
	L+F	10	44	2	2.5	1	0	0.5	1	0	17.5	4.5	7
Sessenheim	F	7.5	57.7	15.3	2.5	0	0	0	13	0	13	9	18

Locality	Problematic taxa	Total number of taxa	Total number of zonal taxa	% zonal taxa of total number of taxa	% azonal taxa of total number of taxa	Total number of zonal woody angiosperms	% BLD of zonal woody angiosperms	% BLE of zonal woody angiosperms	% SCL + LEG of zonal woody angiosperms	% ZONAL HERB of zonal taxa	% DRY HERB of zonal taxa	% MESO HERB of zonal taxa	Vegetation formation
Auenheim	6	59	40	67.80	32.20	32	85.94	4.69	9.38	0.00	0.00	0.00	BLDF
	3	40	21	52.50	47.50	17.5	94.29	2.86	2.86	7.14	2.38	4.76	BLDF
	9	99	61	61.62	38.38	49.5	88.89	4.04	7.07	2.46	0.82	1.64	BLDF
Sessenheim	5	141	96	68.10	31.90	75.5	76.42	20.26	3.31	13.54	0.00	13.54	MMF

directly, which corresponds to the IPR vegetation analysis. But the respective CLAMP estimate overlaps with both CoA estimates when the standard deviation of this particular value is taken into account. For WMMT only CoA estimates are in perfect agreement, but the value of CLAMP is lower and closer to the IPR vegetation analysis. Precipitation estimates (CoA), which are notoriously difficult to obtain from fossil plant assemblages, due to the large influence of edaphic (i. e., groundwater) conditions, differ between both floras studied only slightly, but these differences are probably beyond the resolution of this particular method. All in all our CoA estimates for both floras, together with the CLAMP estimates for the Auenheim flora, point to a climate of the Cfa type (sensu Köppen), thus corroborating previous climatic interpretations for the Sessenheim “Saugbagger-Flora” that were based on “intuitive” approaches (Geissert et al. 1990; see above). They are also in good agreement with previously published climate estimates for a number of floras from the Pliocene of Central Europe, e. g., Mosbrugger & Utescher (1997), Utescher et al. (2000), Uhl et al. (2007). Tab. 6 shows MAT estimates for a number of such localities, together with the according estimates derived from CLAMP (if these have been published). The congruity between the CoA estimates is interesting and to some degree surprising when we consider that not all of these floras have been revised taxonomically in recent times. For example, the estimate for the plant assemblage of the Frankfurt Pliocene is based on the taxonomic descriptions provided by Mädler (1939) and there is no doubt that many of his taxonomic determinations would have to be changed in a modern taxonomic revision.

Previously published climate estimates derived from CLAMP and CoA for a number of Pliocene localities show astonishingly similar values to CLAMP data for the locality Auenheim, although some of these estimates (i. e., Berga and Hambach [leaf]) are slightly colder than our own estimates for Sessenheim and Auenheim, whereas CoA estimates for these localities overlap at least with the CoA estimate for Auenheim (Tab. 6, Fig. 2).

A possible explanation for the lower CLAMP estimates for some localities including Auenheim may be the dominance of riparian elements, like in Berga (Mai & Walther 1988). As demonstrated by different authors (e. g., Burnham et al. 2001; Kowalski & Dilcher 2003) modern (and probably fossil) floras originating from wet

Tab. 3. CoA palaeoclimatic estimates for the locality Sessenheim based on the NLRs up to species level including limiting taxa of the palaeoclimatic intervals.

Parameter	Taxon min-value	min-value	Taxon max-value	max-value
MAT [°C]	*Ziziphus* sp.	15.3	*Prunus spinosa* L.	15.6
CMMT [°C]	*Fothergilla* sp.	2.7	*Cornus sanguinea* (L.) Opiz	2.7
WMMT [°C]	*Proserpinaca palustris* L.	23.6	*Lycopus europaeus* L.	25.1
MAP [mm]	*Rehderodendron* sp.	979	*Juglans cinerea* L.	1146
P-wet [mm]	*Rehderodendron* sp.	164	*Lycopus europaeus* L.	167
P-dry [mm]	*Pterocarya rhoifolia* Siebold & Zucc.	37	*Rhederodendron hui* Chun.	38
P-warm [mm]	*Proserpinaca palustris* L.	84	*Pterocarya fraxinifolia* (Poir.) Spach	84

Tab. 4. CoA palaeoclimate estimates for the locality Auenheim based on NLRs up to species level including limiting taxa of the palaeoclimatic intervals.

Parameter	Taxon min-value	min-value	Taxon max-value	max-value
MAT [°C]	*Parrotia persica* C. A. Mey.	13.6	*Juglans cinerea* L.	15.6
CMMT [°C]	*Halesia* sp.	0.9	*Parrotia persica* C. A. Mey.	1.7
WMMT [°C]	*Proserpinaca palustris* L.	23.6	*Ceratophyllum submersum* L.	24.2
MAP [mm]	*Halesia* sp.	979	*Carex rostrata* Stokes	1122
P-wet [mm]	*Torreya* sp.	116	*Acer pseudoplatanus* L.	139
P-dry [mm]	*Nyssa sylvatica* Marshall	43	*Ostrya* sp., *Sparganium* sp.	43
P-warm [mm]	*Proserpinaca palustris* L.	84	*Pterocarya fraxinifolia* (Poir.) Spach	84

Tab. 5. CLAMP palaeoclimate estimates for the locality Auenheim.

Climate characters	value	SD
MAT [°C]	12.1	1.7
WMMT [°C]	19.0	1.8
CMMT [°C]	3.9	2.5

environments tend to have more species with toothed margins and other morphological adaptations that have been assumed to be indicative for colder conditions, than floras from nearby more mesic habitats.

7. Comparison with other selected Pliocene floras

7.1. Germany

The flora of Auenheim shares most elements with the Pliocene flora from the Main River deposits at Frankfurt a. M. (Mädler 1939), e. g., most gymnosperms, Fagaceae, Juglandaceae, Viscaceae, *Liriodendron*, *Eucommia*, *Parrotia*, *Buxus*, *Ilex*, *Trichosanthes.* This well known "Klärbecken-Flora" of Niederrad is not yet revised but preliminary studies suggest that it belongs to the same floral type that was ranged by Mai & Walther (1988) in our opinion incorrectly into the Brunssumian floral assemblage. Krutzsch (1988, table in attachment) assigned the Auenheim and Klärbecken levels to the same time slice. In Auenheim, the flora seems to be impoverished of various exotic plants recorded elsewhere by carpological research *(Stewartia*, *Rehderodendron*, *Tectocarya*, *Toddalia*, *Symplocos).* The Alsacian Pliocene area is not completely uni-

Tab. 6. Previously published MAT estimates for selected Pliocene floras from Central Europe based on CoA and CLAMP.

Locality	Age	CoA MAT [°C]	CLAMP MAT [°C]	Reference
Berga (leaf)	Pliocene	13.3–16.6	8.9	Uhl et al. 2007
Willershausen (leaf)	Pliocene	12.5–16.5	11.2	Uhl et al. 2007
Frankfurt/Main (leaf)	Pliocene	14.4–15.5	12.2	Uhl et al. 2007
Hambach (leaf)	Lower Pliocene	13.3–13.8	8.4	Utescher et al. 2000
Hambach (carpo)	Lower Pliocene	14.1–14.4	–	Mosbrugger & Utescher 1997

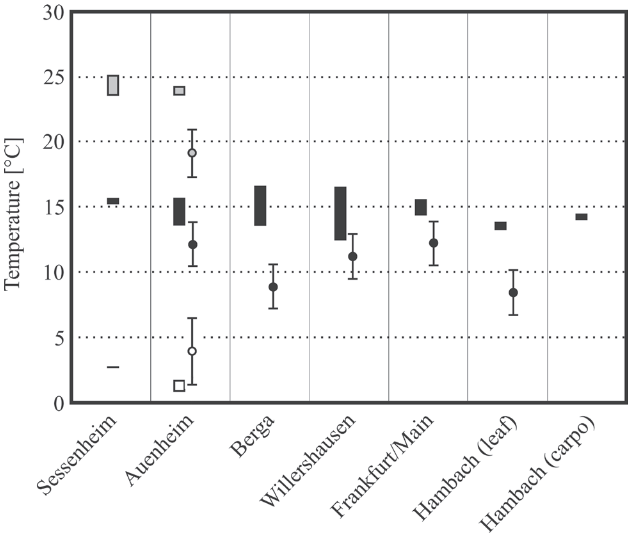

Fig. 2. Comparison of the results obtained by CoA (columns) and CLAMP (circles) for WMMT (grey symbols), MAT (black symbols) and CMMT (open symbols) for the Sessenheim and Auenheim floras and for previously published MAT estimates for selected Pliocene floras from Central Europe (for details see Tabs. 3 to 6).

form and the discussed flora from Auenheim lies stratigraphically above the well known carpological assemblage of the "Saugbagger-Flora" from the Sessenheim quarry that looks more ancient and indeed belongs to the warmer part of the Pliocene, i. e. into the Brunssumian. In their computer analytical study Günther & Gregor (1989) assigned the Frankfurt leaf assemblage to the Late Pliocene but the "Saugbagger-Flora" to the undivided Pliocene. According to the new assessment (Kvaček et al. 2008) the whole complex of the Pliocene floras in the Alsace is dated into the Early to Late Pliocene. However, it is certainly premature to be very precise in ranging these floras into the chronostatigraphical scale without independent dating and such an attempt certainly needs more thorough comparisons as we are trying now. Comparisons with other Pliocene sites in Central Europe are less satisfactory.

Although the flora of Willershausen is poorly known in respect of leaf cuticular data and the sieved three-dimensionally preserved carpological material is practically lacking, noteworthy parallels can be found with the Auenheim leaf assemblage. The angiosperm elements (Straus 1992; Knobloch 1998) are mostly of similar morphology, although their taxonomic interpretation in the Willershausen flora partly deviates from the identifications based on cuticular studies. The occurrence of *Ginkgo* is so far questioned (Straus 1992), while the conifer spectrum is similar (Pinaceae, *Torreya*), only the Cupressaceae are more diversified *(Sequoia*, *Chamaecyparis)*. The problem of exact correspondence of, e. g., Fagaceae, is largely influenced by individual attitude towards splitting or lumping of morpho-types especially in *Quercus*, and collecting mechanism/taphonomical processes (burial of leaf fossils). The main components of the Willershausen flora are deciduous Fagaceae, as it is the case in the Auenheim assemblage. Rare subtropical/evergreen elements occur at both sites. Also typical plants of the European Pliocene *(Sassafras*, *Torreya)* are also present. We may stress a much higher diversity of the Willershausen flora (*Tilia*, Rosaceae, Betulaceae, *Comptonia*, *Aristolochia*, *Aesculus*, *Liquidambar*, *Celtis* etc.), which may be due to long-termed collecting by the late Adolph Straus (Straus 1992) but also due to age difference or taphonomical bias. In spite of the above mentioned differences in the spectrum the Willershausen flora compares well with Auenheim and in our opinion is properly assigned to the Late Pliocene by many authors.

Perhaps the most promising comparisons can be made with the section of the Hambach Mine, Düren (e. g., van der Burgh & Zetter 1998). The assemblages from level 9 ("Rotton") of the local stratigraphy seem to have much in common with the carpological records of Sessenheim. However, the study of the Hambach section is not yet completed, particularly in respect of the leaf assemblages.

A more diversified Pliocene flora of Berga (Mai & Walther 1988) is better comparable to the Auenheim flora than the Sessenheim "Saugbagger-Flora".

7.2. Poland and the Netherlands

The flora of Ruszów, Poland (Hummel 1983, 1991), which includes fewer common elements with Auenheim, is clearly biased by swampy habitats and less diversified in mesophytic woody component. There occur in common only *Taxodium*, deciduous Fagaceae including *Fagus*, *Acer* spp., and *Fraxinus*.

Similar applies to the Reuverian leaf assemblages in the Netherlands, still not revised, but similar in representation of deciduous Fagaceae, Salicaceae and *Acer tricuspidatum* forma *productum* (Laurent & Marty 1923, pl. 3, fig. 10, as *Betula alba foss.*). However, the Reuverian lacks typical "Miocene to Early Pliocene" elements, e. g., *Ginkgo*, *Torreya*, *Craigia*, and others represented in the Auenheim flora.

7.3. Italy

The Sessenheim "Saugbagger-Flora" shows affinity to the floristic assemblage of Ca'Vietone, N-Italy, based on the taxonomic comparison. Nevertheless, it is obviously poorer in frequency of "old" elements except *Tectocarya rhenana* (Mastixioideae). Martinetto (1995) characterized the Ca'Vietone floristic assemblage as a mixture of a rich and diversified record of subtropical and "archaic" elements (similar to the Miocene floras of Central Europe), covering the time interval from 4.7 to 3.6 Ma of the thermal optimum of the Early Pliocene (Zubakov & Borzenkova 1990). Martinetto et al. (1997) grouped the Italian carpofloras of Ca'Vietone and Sento successions in a single floristic assemblage and verified the age of the Early Pliocene based on the mollusc, foraminiferal (Sento) and pollen (Ca'Viettone) datasets (see also in Basilici et al. 1997). These authors note a surprising "Miocene" character of the Italian fossil assemblages and their richness in exotic and subtropical elements corresponding to the "Younger Mastixioid Floras" of Wiesa (Mai 1964) and Wackersdorf in Germany (Gregor 1978, 1980). The Early Pliocene age of the Ca'Vietone Floristic Assemblage helps to correlate it with the carpofloras north of the Alps, e. g., Brunssum (Reid & Reid 1915; Zagwijn 1990) and Krościenko (Szafer 1947) due to the lack of subtropical elements (Martinetto et al. 1997: 243). In contrast, the Auenheim flora (represented by leaf and carpological material, see Appendix) can be better correlated with the Floristic Assemblage of Stura, North Italy, sensu Martinetto (1995). This "younger" floristic assemblage is characterized by occurrences of still very rich "archaic" elements in combination with a distinct decrease of subtropical elements (cf. Martinetto 1995, tabs. 5.2, 5.3). This is in agreement with the fruit and seed floras of the Reuverian of NW Europe (Floristic Assemblage of Reuver sensu Mai & Walther 1988). The mentioned similarity with the Reuverian floras and richness in "old" elements suggest a correlation of this floristic assemblage with the temperate phase of the Middle ("Upper" sensu Zagwijn 1990) Pliocene (Martinetto 1995).

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Appendix. Summary of the floristic compositions of the studied localities Auenheim and Sessenheim "Saugbagger-Flora" including suggestion of the Nearest Living Relatives (NLR). – Symbols: C (cone), F (fruit), L (leaf), S (seed) Sc (isolated cone scale) and Ec (endocarp).

Taxa	Organs	Auenheim	Sessenheim	NLR
Abies cf. *albula* (LUDWIG) MÜLLER-STOLL	L	x		*Abies pectinata* DC.
Acer campestrianum DOROFEEV	F		x	*Acer* sect. *Campestria*
Acer cf. *pseudoplatanus* L.	L	x		*A. pseudoplatanus* L.
Acer cf. *tricuspidatum* BRONN forma *productum* (A. BRAUN) PROCHÁZKA & BŮŽEK	L	x		*A. dasycarpum* L.
Acer gerberi GEISSERT, GREGOR & MAI	F		x	*A. palmatum* THUNB. *A. pseudosieboldianum* (PAX) KOM.
Acer integerrimum (VIVIANI) MASSALONGO	L	x		*A. mono* MAXIM. *A. pictum* THUNB. *A. cappadocicum* GLED.
Actinidia faveolata C. & E. M. REID	S	x	x	*Actinidia melanandra* FRANCH. *A. arguta* (SIEBOLD & ZUCC.) PLANCH. ex MIQ.
Aesculus spinosissima C. & E. M. REID	F		x	*Aesculus hippocastanum* L.

Appendix. Continued.

Taxa	Organs	Auenheim	Sessenheim	NLR
Ajuga antiqua C. & E. M. Reid	F	x	x	*Ajuga reptans* L. *A. genevensis* L.
Alangium deutschmannii Geissert & Gregor	Ec		x	*Alangium longiflorum* Merr. *A. lamarcki* Thwaites
Aldrovanda praevesiculosa Kirchh.	F	x	x	*Aldrovanda vesiculosa* L.
Alnus glutinosa Gaertner *fossilis*	F		x	*Alnus glutinosa* Gaertner
Alnus incana (L.) Moench *fossilis*	F		x	*A. incana* (L.) Moench
Ampelopsis malvaeformis (Schloth.) Mai	S		x	?
Ampelopsis tertiaria Dorofeev	S		x	*Ampelopsis brevipedunculata* (Maxim.) Trautv. *A. megalophylla* Diels & Gilg *A. fargesii* Gagnhep
Aralia sp.	Ec	x		*Aralia sp.*
Aralia szaferi Mai	Ec		x	*A. californica* S. Watson
Asimina brownii P. W. Thomson	S		x	*Asimina triloba* (L.) Dun. *A. parviflora* Michx.
Brasenia victoria (Caspary) Weberbauer	S	x	x	*Brasenia schreberi* J. F. Gmel.
Buxus pliocaenica Saporta	L	x		*Buxus sempervirens* L.
Caldesia cylindrica (E. M. Reid) Dorofeev	F		x	?
Carex flagellata C. & E. M. Reid	F	x	x	*Carex dickinsii* Franch. & Sav. *C. rostrata* Stokes
Carex szaferi Dorofeev	F		x	?
Carpinus sp.	L	x		*Carpinus betulus* L.
Carpinus betulus L. *fossilis*	F	x	x	*C. betulus* L.
Carpolithus alsaticus Geissert, Gregor & Mai	S		x	?
Carpolithus sp.	S		x	?
Carya angulata C. & E. M. Reid	F	x	x	*Carya ovata* (Mill.) K. Koch
Carya askenasyi (Kinkelin) Mai	F		x	?
Carya globosa (Ludwig) Mädler	F		x	*C. aquatica* (F. Michx.) Nutt.
Carya sp.	L	x		? *C. alba* K. Koch *C. diguetii* Dode
Cathaya sp.	L	x		*Cathaya argyrophylla* Chung & Kuang
Cephalotaxus rhenana Gregor	S		x	*Cephalotaxus drupacea* Sieb. & Zucc. *C. harringtonia* (Knight ex Forbes) K. Koch
Ceratophyllum demersum L. *fossilis*	F		x	*Ceratophyllum demersum* L.
Ceratophyllum submersum L. *fossilis*	F	x	x	*C. submersum* L.
cf. *Gleditsia* sp.	L	x		*Gleditsia triacanthos* L.
Cornus mas L. *fossilis*	F		x	*Cornus mas* L.
Corylopsis urselensis Mädler	S	x	x	*Corylopsis spicata* Hemsl. *C. willmottiae* Rehder & E. H. Wilson
Corylus acuminata Geissert, Gregor & Mai	F		x	*Corylus sieboldiana* Blume *C. maxima* Mill.
Corylus avellana L. *fossilis*	F	x	x	*C. avellana* L.
Corylus sp.	L	x		*C. avellana* L.
Crataegus guinieri Geissert, Gregor & Mai	Ec		x	*Crataegus vailliae* Britton
Cyclocarya nucifera (Ludwig) Mai	F		x	*Cyclocarya paliurus* (Batalin) Iljinsk.
Daphniphyllum cylindricum Mai	Ec		x	*Daphniphyllum glaucescens* Blume
Decodon gibbosus (E. M. Reid) Nikitin	S	x		*Decodon verticillatus* (L.) Elliott
Dendrobenthamia tegeliensis Mai	Ec		x	*Cornus capitata* Wall.
Dicotylophyllum cf. *heerii* (Engelhardt) Kvaček & Walther	L	x		*Laurocerasus* spp.
Dicotylophyllum sp. 1	L	x		*Sorbus alnifolia* (Sieb. & Zuccarini) K. Koch
Dombeyopsis lobata Unger	L	x		*Craigia yunnanensis* W. W. Smith & Svand

Appendix. Continued.

Taxa	Organs	Auenheim	Sessenheim	NLR
Dulichium arundinaceum (L.) Britt. *fossilis*	F		x	*Dulichium arundinaceum* (L.) Britt.
Dulichium vespiforme C.& E. M. Reid	F	x		*D. arundinaceum* (L.) Britt.
Epipremnites reniculus (Ludwig) Gregor & Bogner	S		x	?
Eucommia europea Mädler	F	x	x	*Eucommia ulmoides* Oliv.
Eucommia sp.	L	x		*E. ulmoides* Oliv.
Euphorbia cf. *esula* L. *fossilis*	S		x	*Euphorbia esula* L.
Euphorbia helioscopa L. *fossilis*	S		x	*E. helioscopa* L.
Euphorbia palustris L. *fossilis*	S		x	*E. palustris* L.
Fagus deucalionis Ung.	F	x	x	*Fagus sieboldii* Endl. *F. grandifolia* Ehrh.
Fagus kraeuselii Kvaček & Walther	L	x		? *F. sylvatica* L. ssp. *orientalis* (Lipsky) Greuter & Burdet
Fothergilla europaea Szafer	S		x	*Fothergilla gardenii* L.
Fraxinus sp.	F, L	x		*Fraxinus excelsior* L.
Ginkgo adiantoides (Unger) Heer	L	x		*Ginkgo biloba* L.
Glyptostrobus europaea (Brongn.) Heer	S		x	*Glyptostrobus pensilis* (Staunton ex D. Don) K. Koch
Halesia crassa (C. & E. M. Reid) Kirchh.	Ec	x	x	*Halesia carolina* L. *H. parviflora* Michx.
Hartziella rosenkjaeri (Hartz) Szafer	Ec		x	?
Hartziella vindobonensis Szafer	Ec		x	?
Chenopodium sp.	S		x	*Chenopodium* sp.
Ilex aquifolium L. *fossilis* Engelhardt	Ec, L	x		? *Ilex aquifolium* L. *I. cornuta* Lindl. & Pax.
Ilex cantalensis E. M. Reid	Ec		x	*I. crenata* Thunb.
Ilex fortunensis v. d. Burgh	Ec		x	?
Ilex wiesaensis Mai	Ec		x	*I. ambigua* Chapm.
Juglans bergomensis (Balsamo-Crivelli) Massalongo	F	x	x	*Juglans cinerea* L.
Leitneria flexuosa Geissert, Gregor & Mai	Ec		x	?
Leitneria venosa (Ludwig) Dorofeev	Ec		x	*Leitneria floridana* Chapm.
Liquidambar europaea A. Braun	F	x	x	*Liquidambar orientalis* Mill. *L. styraciflua* L. *L. acalycina* H. T. Chang
Liriodendron geminata Kirchh.	F, S	x	x	*Liriodendron chinensis* (Hemsl.) Sarg.
Lycopus europaeus L. *fossilis*	S		x	*Lycopus europaeus* L.
Magnolia cor Ludwig	S	x	x	*Magnolia stellata* (Sieb. & Zucc.) Maxim. *M. salicifolia* Maxim. *M. liliiflora* Desr.
Mahonia staphyleaeformis Mai	S		x	*Mahonia fremontii* (Torr.) Fedde *M. aquifolium* (Pursh) Nutt.
Meliosma pliocaenica (Szafer) Gregor	Ec	x		*Meliosma alba* (Schltdl.) Walp. *M. dilleniifolia* (Wall. ex Wight & Arn.) Walp.
Meliosma wetteraviensis (Ludwig) Mai	Ec		x	*M. alba* (Schltdl.) Walp. *M. veitchiorum* Hemsl.
Menispermum reidii Geissert, Gregor & Mai	Ec		x	*Menispermum canadense* L.
Menyanthes trifoliata L. *fossilis*	S	x	x	*Menyanthes trifoliata* L.
Mespilus germanica L. *fossilis*	Ec		x	*Mespilus germanica* L.
Najas marina L. *fossilis*	S		x	*Najas marina* L.
Nuphar canaliculata Reid	S	x		*Nuphar lutea* (L). Sibth & Sm.
Nuphar lutea (L). Sibth & Sm. *fossilis*	S		x	*N. lutea* (L). Sibth & Sm.
Nyssa disseminata (Ludwig) Kirchh.	Ec	x	x	*Nyssa sylvatica* Marshall
Nyssa sp.	L	x		*N. sylvatica* Marshall *N. sinensis* Oliv.

Appendix. Continued.

Taxa	Organs	Auenheim	Sessenheim	NLR
Olea oleastroides ZABŁOCKI	F		x	*Olea europaea* L.
Ostrya carpnifolia SCOPOLI *fossilis*	F		x	*Ostrya carpnifolia* SCOP.
Ostrya sp.	F	x		*O.* cf. *carpinifolia* SCOP.
Parrotia pristina (ETTINGSH.) STUR	L	x		*Parrotia persica* C. A. MEY.
Phellodendron elegans C. & E. M. REID	S		x	*Phellodendron japonicum* MAXIM.
Physalis alkekengi L. *fossilis*	S		x	*Physalis alkekengi* L.
Picea echinata MÜLLER-STOLL	L	x		*Picea torano* (SIEBOLD ex K. KOCH) KOEHNE
Picea latisquamosa LUDWIG		x		*P. excelsa* (LAMB.) LINK *P. morinda* LINK
Pinus brevis LUDWIG	C		x	*Pinus* sp.
Pinus cf. *latisquamosa* (LUDWIG) GEYLER & KINKELIN	C		x	*Pinus* sp.
Pinus sp. div.	S		x	*Pinus* sp.
Polygonum leporimontanum KIRCHH.	F		x	*Polygonum* sp.
Polygonum wolfii (KINKELIN) MÄDLER	F		x	*Polygonum* sp.
Populus (sect. *Aeigiros* DUBY) sp.	L	x		*Populus nigra* L.
Populus cf. *balsamoides* GÖPPERT sensu lato	L	x		*Populus* L. sect. *Tacamahaca* PAX
Populus cf. *glandulifera* HEER	L	x		*Populus* L. sect. *Leucoides* SPACH
Populus populina (BRONGN.) KNOBLOCH	L	x		*Populus* L. sect. *Populus* (syn. *Leuce* DUBY)
Potamogeton austroeuropaeus NEGRU	Ec		x	*Potamogeton* sp.
Potamogeton cf. *polymorphus* DOROFEEV	Ec		x	*Potamogeton* sp.
Potamogeton palaeocompressus DOROFEEV	Ec		x	*Potamogeton* sp.
Potamogeton planus NIKITIN	Ec		x	*Potamogeton* sp.
Potamogeton praepectinatus NEGRU	Ec		x	*P. pectinatus* L.
Proserpinaca reticulata C. & E. M. REID	S	x	x	*Proserpinaca palustris* L. *P. intermedia* MACK
Prunus avium L. *fossilis*	Ec		x	*Prunus avium* L.
Prunus crassa (LUDWIG) SCHIMPER	Ec		x	*P. napaulensis* STEUD. *P. bracteopadus* KOEHNE
Prunus fruticosa PALLA. *fossilis*	Ec		x	*P. fruticosa* PALLA.
Prunus girardii KIRCHH.	Ec	x		*P. alleghaniensis* PORTER *P. watsonii* SARG.
Prunus girardii KIRCHH.	Ec		x	*P. alleghaniensis* PORTER *P. watsonii* SARG.
Prunus insititia L. var. *pliocaenica* MÄDLER	Ec		x	*P. insititia* L.
Prunus padus L. *fossilis*	Ec		x	*P. padus* L. *P. asiatica* KOM. *P. grayan* MAXIM.
Prunus spinosa L. *fossilis*	Ec		x	*P. spinosa* L.
Prunus tenerirugosa MAI	Ec		x	*P. maximowiczii* RUPR.
Pseudoeuryale europaea DOROFEEV	S	x		? *Euryale* sp.
Pseudoeuryale limburgensis (C. & E. M. REID) DOROFEEV	S		x	? *Euryale* sp.
Pseudotsuga sp.	L	x		*Pseudotsuga menziesii* (MIRB.) FRANCO
Pterocarya limburgensis C. & E. M. REID	F	x	x	*Pterocarya fraxinifolia* (POIR.) SPACH *P. rhoifolia* SIEBOLD & ZUCC.
Pterocarya paradisiaca (UNGER) ILJINSKAYA	L	x		*P. pterocarpa* (MICHX.) KUNTH
Pyracantha acuticarpa (C. & E. M. REID) SZAFER	F		x	*Pyracantha coccinea* M. ROEM. *P. crenulata* (D. DON) M. ROEM. *P. gibbsii* A. B. JACKS.
Quercus cf. *kubinyii* (KOVÁTS ex ETTINGSH.) CZECZOTT	L	x		? *Quercus variabilis* BLUME
Quercus cf. *praeerucifolia* STRAUS	L	x		*Q. pedunculiflora* K. KOCH
Quercus gigas GÖPP. emend. WALTHER & ZASTAWNIAK	L	x		*Quercus* sect. *Cerris* SPACH

Appendix. Continued.

Taxa	Organs	Auenheim	Sessenheim	NLR
Quercus pseudocastanea GÖPP. emend. WALTHER & ZASTAWNIAK	L	x		*Quercus* sect. *Cerris* SPACH
Quercus roburoides GAUDIN	L	x		*Q. petraea* (MATT.) LIEBL.
aff. *Quercus extincta* GREGOR	F		x	?
aff. *Quercus polycarpa* SCHUR vel *Quercus pubesceus* WILLD. *fossilis*	F		x	?
Ranunculus reidii SZAFER	F	x		*Ranunculus lateriflorus* DC.
Rehderodendron ehrenbergii (KIRCHH.) MAI	Ec		x	*Rehderodendron hui* CHUN.
Rubus laticostatus KIRCHH.	S		x	?
Sabia europaea CZECZOTT & SKIRG.	Ec		x	*Sabia leptandra* HOOK. & THOMS. *S. limonica* WALL. *S. japonica* MAXIM.
Salix sp.	L	x		*Salix bonplandiana* HBK.
Salvia cf. *glutinosa* L. *fossilis*	S		x	*Salvia glutinosa* L.
Sambucus lucida DOROFEEV	S		x	*Sambucus chinensis* LINDL. *S. williamsii* HANCE *S. glauca* NUTT. *S. pubens* MICHX.
Sambucus nigra L. *fossilis*	S		x	*S. nigra* L.
Sambucus pulchella C. & E. M. REID	S	x		*S. ebulus* L.
Sapium maedleri GEISSERT, GREGOR & MAI	S		x	?
Sargentodoxa gossmannii (GEISSERT, GREGOR & MAI) MARTTINETO	F		x	*Sargentodoxa cuneata* REHD. & WILSON
Sassafras cf. *ferretianum* MASSALONGO & SCARABELLI	L	x		*Sassafras tzumu* (HEMSL.) HEMSL.
Scindapsites crassus (C. & E. M. REID) GREGOR & BOGNER	S		x	?
Scirpus pliocaenicus SZAFER	S	x		*Scirpus carinatus* (HOOK. & ARN. ex TORR.) GRAY
Sequoia abietina (BRONGN.) KNOBLOCH	C, Sc		x	*Sequoia sempervirens* (D. DON) ENDL.
Schisandra geissertii GREGOR	S		x	*Schisandra chinensis* (TURCZ.) BAILL.
Schisandra kirchheimerii GEISSERT, GREGOR & MAI	S		x	*S. repanda* (SIEBOLD & ZUCC.) RADLK. *S. henryi* S. B. CLARKE
Schoenoplectus lacustris (L.) PALLA *fossilis*	F		x	*Schoenoplectus lacustris* (L.) PALLA
Silene cf. dichotoma EHRH.	S		x	? *Silene dichotoma* EHRH.
Solanum dulcamara L. *fossilis*	S		x	*Solanum dulcamara* L.
Sorbus torminalis (L.) CRANTZ *fossilis*	F		x	*Sorbus torminalis* (L.) CRANTZ
Sparganium minimum WALLR. *fossilis*	Ec		x	*Sparganium minimum* WALLR.
Sparganium neglectum BEEBY *fossilis*	Ec		x	*S. neglectum* BEEBY
Sparganium noduliferum C. & E. M. REID	Ec	x		*S. simplex* HUDS.
Staphylea cf. *trifolia* L. *fossilis*	S		x	*Staphylea* cf. *trifolia* L.
Staphylea colchica STEVEN. *fossilis*	S		x	*S. colchica* STEVEN.
Staphylea pliocaenica KINKELIN	S		x	*S. pinnata* L.
Stewartia beckerana (LUDWIG) KIRCHH.	F, S		x	*Stewartia monadelpha* SIEBOLD & ZUCC. *S. serrata* MAXIM.
Stratiotes intermedius (HARTZ) CHANDLER	Ec		x	*Stratiotes aloides* L.
Stratiotes tuberculatus C. & E. M. REID	Ec	x		*S. aloides* L.
Styrax maximus (WEBER) KIRCHH.	Ec	x	x	*Styrax japonicus* SIEBOLD & ZUCC.
Swida gorbunovii (DOROFEEV) NEGRU	Ec		x	*Cornus alba* (L.) OPIZ *C. sericea* (L.) HOLUB
Swida kraeuselii GEISSERT, GREGOR & MAI	Ec		x	*Cornus controversa* (HEMSL.) SOJÁK *C. alternifolia* (L.) SMALL
Swida sanguinea (L.) OPIZ *fossilis*	Ec		x	*Cornus sanguinea* (L.) OPIZ
Symplocos casparyi LUDWIG sensu MAI & MARTINETTO	Ec		x	*Symplocos* subgen. *Hopea* (L.) C. B. CLARKE

Appendix. Continued.

Taxa	**Organs**	**Auenheim**	**Sessenheim**	**NLR**
Taxodium cf. *dubium* (Sternb.) Heer	L	x		*Taxodium distichum* (L.) Rich.
Taxodium dubium (Sternb.) Heer	C, S	x	x	*T. mucornatum* Ten. *T. distichum* (L.) Rich.
Taxus cf. *baccata* L.	S		x	*Taxus baccata* L.
Tectocarya cf. *lusatica* Kirchh.	Ec		x	?
Ternstroemia dorofeevii Geissert, Gregor & Mai	S		x	*Ternstroemia* sp.
Thalictrum bauhini Crantz *fossilis*	F	x		*Thalictrum bauhini* Crantz
Thalictrum flavum L. *fossilis*	F		x	*T. flavum* L.
Toddalia mai Gregor	S		x	*Toddalia asiatica* L.
Toddalia rhenana Gregor	S		x	*T. asiatica* L.
Toddalia thieleae Gregor	S		x	*T. asiatica* L.
Torreya sp.	L	x		*Torreya* sp.
Trapa sp.	F		x	*Trapa* sp.
Trichosanthes fragilis E. M. Reid	S	x	x	*Trichosanthes palmata* Roxb. *T. kirilowii* Maxim.
Trichosanthes sp.	L	x		*Trichosanthes* sp.
Tsuga (sect. *Hesperopeuce* Engelm.) sp.	L	x		*Tsuga* sp.
Tsuga (sect. *Tsuga*) sp.	L	x		*Tsuga* sp.
Tsuga europaea (Menzel) Szafer	C		x	*Tsuga* sp.
Ulmus carpinoides Göpperet	L	x		*Ulmus carpinifolia* L.
Ulmus pyramidalis Göpperet	L	x		*Ulmus* L. sect. *Chaetoptelea* (Liebm.) Schneid.
Vicia sp.	S		x	*Vicia* sp.
Viola cf. *uliginosa* Szafer	S		x	?
Viscum aff. *ponholzense* Gregor	F		x	*Viscum* sp.
Viscum miquelii (Geyler & Kinkelin) Czeczott	L	x		*V. album* L.
Viscum ponholzense Gregor	F	x		? *V. album* L.
Vitis ludwigii A. Braun	S	x		*Vitis munsoniana* Simpson ex Munson *V. watsoniana* (E. H. Wilson) Bean
Vitis parasylvestris Kirch.	S	x	x	*V. coignetiae* Pulliat ex Planch.
Vitis sylvestris C. C. Gmelin *fossilis*	S		x	*Vitis* sp.
Vitis teutonica A. Braun	S	x	x	*V. balansana* Planch.
Wikstroemia thomasii Geissert & Gregor	S		x	*Wikstroemia* div. sp.
Zelkova zelkovifolia (Unger) Bůžek & Kotlaba	L	x		*Zelkova sicuta* Di Pasquale, Garfi & Quézel *Z. abeliacea* (Lamark) Boiss. *Z. carpinifolia* (Pall.) K. Koch
Ziziphus noetzoldii Geissert, Gregor & Mai	F		x	*Ziziphus nummularia* (Burm. f.) Wight *Z. joazeiro* Mart.