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Palaeoclimate estimates for the Middle Miocene Schrotzburg flora (S Germany): a multi-method approach

Abstract We present a detailed palaeoclimate analysis of the Middle Miocene (uppermost Badenian–lowermost Sarmatian) Schrotzburg locality in S Germany, based on the fossil macro- and micro-flora, using four different methods for the estimation of palaeoclimate parameters: the coexistence approach (CA), leaf margin analysis (LMA), the Climate-Leaf Analysis Multivariate Program (CLAMP), as well as a recently developed multivariate leaf physiognomic approach based on an European calibration dataset (ELPA). Considering results of all methods used, the following palaeoclimate estimates seem to be most likely: mean annual temperature ~15–16°C (MAT), coldest month mean temperature ~7°C (CMMT), warmest month mean temperature between 25 and 26°C, and mean annual precipitation ~1,300 mm, although CMMT values may have been colder as indicated by the disappearance of the crocodile *Diplocynodon* and the temperature thresholds derived from modern alligators. For most palaeoclimatic parameters, estimates derived by CLAMP significantly differ from those derived by most other methods. With respect to the consistency of the results obtained by CA, LMA and ELPA, it is suggested that for the Schrotzburg locality CLAMP is probably less reliable than most other methods. A possible explanation may be attributed to the correlation between leaf physiognomy and climate as represented by the CLAMP calibration data set which is largely based on extant floras from N America and E Asia and which may be not suitable for application to the European Neogene. All physiognomic methods used here were affected by taphonomic biasses. Especially the number of taxa had a great influence on the reliability of the palaeoclimate estimates. Both multivariate leaf physiognomic approaches are less influenced by such biasses than the univariate LMA. In combination with previously published results from the European and Asian Neogene, our data suggest that during the Neogene in Eurasia CLAMP may produce temperature estimates, which are systematically too cold as compared to other evidence. This pattern, however, has to be further investigated using additional palaeofloras.

Keywords Neogene · Palaeoclimate · Taphonomy · Leaf physiognomy · Nearest living relatives

Dedicated to Prof. Dr. Harald Walther, Dresden, on the occasion of his 75th birthday.

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Introduction

Dealing with Global Change may become one of the major challenges for humankind in the 21st century (e.g. Steffen et al. 2004). A critical assessment of the possible impacts of Global Change must not only refer to the reliability of model predictions for the future, but also to information about past climate and environmental changes. In the terrestrial realm the reconstruction of past climatic and environmental conditions and changes is largely based on fossil plant remains. A large number of different methods have been developed to derive environmental data from these plants (e.g. Kershaw and

Nix 1988; Chaloner and Creber 1990; Mosbrugger and Schilling 1992; Jones and Rowe 1999; Klotz et al. 2003). However, only a few of these methods are able to produce quantitative data.

In general, two different approaches exist for the Tertiary, which claim to be able to produce reliable quantitative data based on plant fossils: (1) the nearest living relative (NLR) approach and (2) the leaf physiognomic approach.

The NLR approach has been used by palaeobotanists at least since the days of Sternberg and Brongniart in the early 19th century. Whereas these early authors and even many authors today restrict the NLRs which they use for the estimation of palaeoclimatic conditions to some selected threshold taxa, recent modifications of this approach make use of as many NLR taxa as possible (e.g. Kershaw and Nix 1988; Kershaw 1997; Mosbrugger and Utescher 1997; Zhao et al. 2004). These various methods reconstruct palaeoclimate requirements (intervals for different parameters) of a fossil flora on the basis of the mutual climatic requirements of the individual taxa, which participate in the fossil flora. Especially, the coexistence approach (CA), developed by Mosbrugger and Utescher (1997), has been applied repeatedly to floras (macro and micro) from the European and Asian Tertiary (e.g. Mosbrugger and Utescher 1997; Bruch 1998; Pross et al. 1998; Utescher et al. 2000; Ivanov et al. 2002; Kvaček et al. 2002; Liang et al. 2003; Uhl et al. 2003; Roth-Nebelsick et al. 2004).

In contrast to these NLR approaches, the leaf physiognomic approach makes use of the fact that certain leaf physiognomic traits of extant leaves may be strongly correlated with certain climatic parameters. Widely used in palaeoclimatology research is, for example, the correlation between the type of leaf margin and mean annual temperature (MAT) (e.g. Bailey and Sinnott 1915, 1916; Wolfe 1979; Wing and Greenwood 1993; Wilf 1997; Greenwood et al. 2004). To overcome some of the problems in using only an individual leaf physiognomic trait, Wolfe (1993) has developed the Climate-Leaf Analysis Multivariate Program (CLAMP), which is currently based on 31 leaf physiognomic traits (Wolfe and Spicer 1999).

Although CA and CLAMP have frequently been used for the estimation of palaeoclimatic parameters by various authors (e.g. Wolfe 1994a, b, 1995; Herman and Spicer 1997; Mosbrugger and Utescher 1997; Bruch 1998; Pross et al. 1998; Utescher et al. 2000; Ivanov et al. 2002; Kvaček et al. 2002; Liang et al. 2003), so far direct comparisons between the results obtained by both methods on the basis of the same source-floras are very rare (e.g. Mosbrugger and Utescher 1997; Utescher et al. 2000; Kvaček et al. 2002; Liang et al. 2003; Kvaček and Walther, 2004). In most of these cases, however, the CLAMP estimates for various temperature parameters, as well as the estimates from leaf margin analysis (LMA) for MAT, have been observed to be considerably lower than the estimates from CA. The reason for this discrepancy is absolutely unclear so far. However, for most

of these reconstructions, additional data tend to support the estimates derived from CA rather than those by CLAMP or LMA (e.g. Mosbrugger and Utescher 1997, Kvaček et al. 2002). Especially, it has been argued that probably taphonomic distortions may be the reason for the cooler temperature estimates obtained by the physiognomic approaches (e.g. Liang et al. 2003). Also the fact that lakeside and riverside vegetation, which is commonly the source of the dominating part of fossil floras (e.g. Spicer 1981, 1991; Ferguson 1985), is often characterized by smaller proportions of entire margined taxa than the surrounding vegetation (Burnham et al. 2001; Kowalski and Dilcher 2003), may lead to an underestimation of MAT by leaf physiognomic methods. However, in some cases, leaf physiognomic techniques and CA produced MAT estimates, which were in good agreement with each other (e.g. Uhl et al. 2003; Roth-Nebelsick et al. 2004), although it could be demonstrated that the physiognomic techniques were strongly influenced by taphonomy at some of these localities (Uhl et al. 2003).

Here, we present a detailed investigation based on the fossil macro-flora from the Middle Miocene Schrotzburg locality ("oberes Pflanzenlager" sensu Hantke 1954) in S Germany which includes a variety of palaeoclimate parameters [i.e. MAT, warmest month mean temperature (WMMT); coldest month mean temperature (CMMT), mean annual precipitation (MAP), growing season precipitation (GSP) and the length of the growing season (GSL)], and also a wide array of methods. These methods concern CA, LMA, CLAMP and a recently developed multivariate leaf physiognomic approach based on an European calibration dataset (ELPA) (Traiser 2004; Traiser et al. 2005). Additionally, we present the results of a first survey of the micro-flora from this locality, and CA estimates derived from this micro-flora.

Study site, material and methods

Study site

In the Bohlinger Schlucht, a small gorge located on the northern flank of the Schienerberg in the west of Lake Constance (S Germany) (cf. Fig. 1), sediments are exposed, which have been deposited in the Northern Alpine Foreland basin and which belong to the Middle Miocene Upper Freshwater-Molasse ("Obere Süßwassermolasse", OSM). The sediments at the Bohlinger Schlucht are slightly older than the Upper Oehningen beds (Schreiner 1992), the flora of which has first been described by Heer (1855, 1856, 1859). Sediments from the lower part of the profile exposed at the Bohlinger Schlucht have been attributed to the mammal zone MN-6, whereas the uppermost part ("oberes Pflanzenlager" sensu Hantke 1954), which we considered in the present study, most probably represents the lowermost part of mammal zone MN-7 (uppermost

Badenian–lowermost Sarmatian) (Giersch 2004). The Schrotzburg palaeoflora, most likely representing a riparian forest vegetation, has been studied in detail by Hantke (1954) and Nötzold (1957), about one century after the initial studies by Heer (1855, 1856, 1859). Subsequently, several additional taxonomic publications on the Schrotzburg flora appeared (e.g. Nötzold 1956; Hantke 1965, 1966, 1980; Gregor and Hantke 1980; Gregor, 1982; Herendeen 1992a, b), which dealt with only one or with a few taxa. Despite the fact that there is no modern revision, this flora can still be considered as one of the best-known Miocene floras in Central Europe (e.g. Mai 1995). The macro-flora has yielded about 40 species (including conifers, angiosperm leaves, fruits and seeds) and several thousands of specimens. Although the macro-flora of the Schrotzburg locality has been investigated in great detail, the micro-flora has not been analysed so far.

The plant-bearing sediments of the "oberes Pflanzenlager" (sensu Hantke 1954) are very uniform and consist of marls attaining a thickness of about 4 m (Rutte 1956). The flora has initially been collected from 28 distinct layers, which may be interpreted as individual flooding events, covering a time span of approximately 1,400–1,700 years (Hantke 1954).

Heer (1859) estimated MAT to be about 18–19°C during the entire OSM in S Germany and N Switzerland.

Fig. 1 Map indicating the location of the Schrotzburg locality to the West of Lake Constance (*filled star*)

Hantke (1954) studied the Schrotzburg leaf flora in detail and—based on the climatic requirements of NLRs of a few taxa of the fossil flora—estimated MAT to be about 16°C, CMMT to be about 7–8°C, WMMT to be about 24°C, and MAP to be about 1,300–1,500 mm. More recently, Uhl et al. (2003) gave quantitative estimations of MAT for this locality of 14.4–16.5°C (using CA) and 17.8 ± 2.6°C (using LMA), which are in full agreement with Hantke's (1954) results.

Material

For this study, we considered not only the more than 14,000 macro-specimens which have been investigated by Hantke (1954) and which are stored in the collection of the "Eidgenössische Technische Hochschule Zürich", Switzerland, but for the first time also palynomorphs from this locality.

Concerning the macro-remains, we used a taxonomically slightly revised and with respect to nomenclature updated version of the original taxa list published by Hantke (1954). The revised list and their NLRs are given in Table 1. Important changes that have been made are summarized in Table 2. To investigate the potential taphonomic effects on the multivariate methods applied in this study in detail, we used the florules from 26 individual layers as subsamples of the Schrotzburg flora (for details see: Uhl et al. 2003). With respect to the micro-flora assemblage of the Schrotzburg locality, sediment samples were taken from the marl deposits. For a preliminary study, palynomorphs were extracted from two sediment samples following standard palynological techniques. For this purpose, 10–15 g of the sediment material were decalcified with HCl (33%) and subsequently treated with HF (40%). Oxidation with HNO_3, followed by neutralization with KOH, was used to break down amorphous organic matter obscuring the palynomorphs. After each of these steps, the material was sieved through a 10 μm nylon mesh. Following this procedure, strew mounts were prepared using glycerine gelatine as mounting medium. Two slides (one for each sample) have been counted completely with 280 and 170 grains, respectively. The slides are stored at the Institute of Geosciences, University of Tübingen, Germany. A list of the 31 palynomorph taxa identified in this samples and their NLRs is given in Table 3.

Methods

For the reconstruction of the palaeoclimate parameters represented by the macro- and micro-flora remains, we applied the CA (cf. Mosbrugger and Utescher 1997), LMA (cf. Wolfe 1979; Wing and Greenwood 1993), CLAMP (cf. Wolfe 1993) and a recently developed multivariate leaf physiognomic approach based on an ELPA (cf. Traiser 2004; Traiser et al. 2005). Although most of these methods claim to reliably give estimates

Table 1 List of macro-remains from the Schrotzburg locality, and their corresponding NLRs (NLRs used for the CA$_{macro}$ in **bold**)

Fossil taxon	NLR
Amblystegium schrotzburgense Hantke	*Amblystegium riparius*
Pteridium oeningense (Unger) Hantke	*Pteridium*
Salvinia formosa Heer	***Salvinia natans***
G. europaeus (Brongniart) Heer	*Glyptostrobus lineatus*
Alnus rotundata Goeppert	***Alnus***
Fagus sp.	***Fagus***
Castanea atavia Unger	***Castanea sativa***
Quercus mediterranea Unger	***Quercus ilex,*** ***Quercus coccifera***
Comptonia oeningensis A. Braun	*Comptonia peregrina*
Juglans acuminata A. Braun	***Juglans regia***
Pterocarya castaneaefolia (Goeppert) Menzel	***Pterocarya fraxinifolia***
Populus latior A. Braun	***Populus***
Populus balsamoides Goeppert	***Populus balsamifera***
Salix lavateri A. Braun	*Salix*
Salix angusta A. Braun	*Salix*
Ulmus longifolia Unger	*Ulmus*
? *Parthenocissus* sp.	? *Parthenocissus*
Liquidambar europaea A. Braun	***Liquidambar styraciflua***
Platanus aceroides Goeppert	***Platanus occidentalis***
Magnolia ?rueminiana (Heer) Hantke	***Magnolia acuminata***
D. polymorpha (A. Braun) Ettingshausen	**Lauraceae**
Persea princeps (Heer) Schimper	*Persea*
Phoebe integriuscula (Heer) Hantke	***Phoebe***
Ceratophyllum schrotzburgense Hantke	***Ceratophyllum***
Crataegus longepetiolata Heer	***Crataegus***
Rosa sp.	*Rosa*
Podocarpium podocarpum (A. Braun) Herendeen	Leguminosae
Sapindus falcifolius A. Braun	***Sapindus***
Acer tricuspidatum Bronn	***Acer saccharinum***
Acer angustilobum Heer	***Acer trautvetteri,*** ***Acer pseudoplatanus***
Leguminosae indet.	Leguminosae
Berchemia multinervis (A. Braun) Heer	***Berchemia***
Cornus graeffii (Heer) Hantke	***Cornus***
Diospyros brachysepala A. Braun	***Diospyros virginianum***
Hydromystria expansa (Heer) Hantke	*Hydromystria laevigatum*
Smilax sagittifera Heer emend. Hantke	*Smilax*
Gramineae	Gramineae
Cyperaceae	Cyperaceae
Typha latissima A. Braun	*Typha latifolia*

Table 2 Changes between Hantke's original taxa list (Hantke 1954) used by Uhl et al. (2003) and the modified list used in this study

Hantke (1954)	This study
Fagus attenuata Goeppert	*Fagus* sp.
Zelkova ungeri Kováts	? *Parthenocissus* sp.*
C. polymorphum (A. Braun) Heer	*D. polymorpha* (A. Braun) Ettingshausen
C. polymorphum f. *scheuchzeri*	*D. polymorpha* (A. Braun) Ettingshausen
C. polymorphum f. *retusum*	*D. polymorpha* (A. Braun) Ettingshausen
Gleditischia sp.	*Podocarpium podocarpum* (A. Braun) Herendeen
Podogonium lyellianum Heer	*Podocarpium podocarpum* (A. Braun) Herendeen
Acer trilobatum (Sternberg) A. Braun	*Acer tricuspidatum* Bronn

*Kovar-Eder et al. (2004) explicitly mentioned this as a probable relationship for the specimens figured by Hantke (1954) as *Zelkova ungeri*

Kvaček et al. 2002; Uhl et al. 2003; Roth-Nebelsick et al. 2004; Mosbrugger et al., 2005), but also, at least in one case, for the Neogene of East Asia (Liang et al. 2003). For a detailed discussion of this approach see Mosbrugger and Utescher (1997), Mosbrugger (1999) and Uhl et al. (2003). Here, we calculate the intervals of coexistence for MAT, CMMT, WMMT and MAP for the macro-remains (CA$_{macro}$), as well as for the palynomorphs (CA$_{micro}$). Assignment of NLR's was done according to the data stored in the palaeoflora database on which the CA is based.

The CA$_{macro}$ estimates for MAT, WMMT and CMMT have been calculated for the entire flora, and also for those sub-samples of the individual layers (cf. Uhl et al. 2003) with more than ten taxa (the taxa lists for the individual layers are available upon request from the authors or see Hantke 1954).

for more parameters as included in our study, we restricted our investigation to climate parameters, which at least can be reconstructed by two out of the different approaches.

Coexistence approach

The CA is a recent and largely computer assisted variation of the NLR methodology. It has been introduced by Mosbrugger and Utescher (1997) and has been successfully applied to estimate palaeoclimate parameters not only for the European Neogene and Palaeogene (e.g. Bruch 1998; Utescher et al. 2000; Ivanov et al. 2002;

Leaf margin analysis

Based on studies of modern floras, Bailey and Sinnott (1915, 1916) were the first to observe a direct correlation between the proportion of dicot woody species with entire margined leaves within a flora, and MAT. Subsequently, different modern calibration data sets have been developed which allow the quantitative estimation of MAT values based on fossil dicot leaves (e.g. Wolfe 1979; Wilf 1997; Kowalski 2002). Here, we used a regression equation which is based on a modern dataset from mesic forests of East Asia (Wolfe 1979; Wing and Greenwood 1993), and which describes the correlation between the proportion (P) of woody species with entire-margined leaves in a flora and MAT by:

$$\text{MAT} = 30.6P + 1.14$$

The standard deviation or "sampling error" σMAT of MAT was calculated after Wilf (1997) as:

Table 3 List of palynomorphs extracted from the Schrotzburg locality, and their corresponding botanical affinity and NLRs (NLRs used for CA_{micro} in **bold**)

Fossil taxon	Botanical affinity	NLR
Saxosporis sp.	Anthocerotaceae	
Retitriletes sp.	Lycopodiaceae	*Lycopodium* sect. *Annotina*
Leiotriletes triangulus (Mürringer & Pflug ex Krutzsch) Krutzsch	?	
Corrugatisporites multivallatus (Pflug) Planderova	Lygodiaceae	***Lygodium***
Echinatisporis sp.	Selaginellaceae	*Selaginella*
Lusatisporis perinatus Krutzsch	Selaginellaceae	*Selaginella*
Laevigatisporites haardti (Potonie & Venitz) Thomson & Pflug	?	
Verrucatosporites favus (Potonie) Thomson & Pflug	Dennstaedtiaceae	
Pinuspollenites spp.	Pinaceae	*Pinus*
Piceapollenites spp.	Pinaceae	***Picea***
Cathayapollis sp.	Pinaceae	*Cathaya*
Zonalapollenites robustus Krutzsch ex Kohlman-Adamska	Pinaceae	***Tsuga***
Sciadopityspollenites serratus (Potonie & Venitz) Raatz ex Potonie	Sciadopityaceae	*Sciadopitys*
Cupressacites insulipapillatus (Trevisan) Krutzsch	Cupressaceae	
Inaperturopollenites concedipites (Wodehouse) Krutzsch	**Taxodiaceae**	*Taxodium/Glyptostrobus*
Inaperturopollenites verrupapillatus Trevisan	**Taxodiaceae**	*Taxodium/Glyptostrobus*
Polyvestibulopollenites verus (Potonie) Thomson & Pflug	Betulaceae	***Alnus***
Polyporopollenites undulosus (Wolff) Thomson & Pflug	**Ulmaceae**	*Ulmus/Zelkova*
Intratriporopollenites instructus Mai	Tiliaceae	*Craigia*
Momipites punctatus (Potonie) Nagy	Juglandaceae	***Engelhardia***
Caryapollenites simplex (Potonie) Raatz ex Potonie	Juglandaceae	***Carya***
Pterocaryapollenites stellatus (Potonie) Thiergart	Juglandaceae	***Pterocarya***
Multiporopollenites maculosus (Potonie) Thomson & Pflug	Juglandaceae	***Juglans***
Tricolporopollenites staresedloensis Krutzsch & Pacltova	Hamamelidaceae	*Distylium*
Liquidambarpollenites stigmosus (Potonie) Raatz	Hamamelidaceae	***Liquidambar***
Quercopollenites petraea-type Nagy	Fagaceae	(deciduous) ***Quercus***
Tricolporopollenites wackersdorfensis Thiele-Pfeiffer	Fabaceae	
Nyssapollenites kruschi (Potonie) Nagy	Nyssaceae	***Nyssa***
Ericipites sp.	Ericaceae	
Tubulifloridites sp.	Asteraceae	Asteroidae
? Araliaceoipollenites sp.	Araliaceae?	

$$\sigma\text{MAT} = c\sqrt{\frac{P(1-P)}{r}},$$

with P representing the proportion of leaf species with entire margins of the r species in the flora, and c being the constant in the regression equation (here 30.6).

Climate-leaf analysis multivariate program

The CLAMP technique has been introduced by Wolfe (1993) and has subsequently been refined by Wolfe and co-workers (cf. Wolfe and Spicer 1999). In its current version, this technique considers 31 leaf physiognomic characters. It is based on a modern calibration data set, which includes 144 modern sample sites (CLAMP 3B data set), mostly located in N America and in E Asia. Mathematically, this technique is based on canonical correspondence analysis, a direct ordination method, which is widely used in plant ecology. For our analysis, we used the spreadsheets provided by R.A. Spicer on his CLAMP website (http://www.tabitha.open.ac.uk/spicer/CLAMP/Clampset1.html) and the programme CANOCO 4.02 for Windows. A list of the physiognomic scores for the Schrotzburg flora used for the application of CLAMP and ELPA is given in Table 4.

Table 4 Percentages of leaf physiognomic characters of the Schrotzburg palaeoflora

Leaf character	Percentage
Lobed	17.2
No teeth	37.9
Teeth regular	25.9
Teeth close	25.9
Teeth round	24.1
Teeth acute	36.2
Teeth compound	17.2
Nanophyll	0.0
Leptophyll 1	0.0
Leptophyll 2	2.3
Microphyll 1	14.9
Microphyll 2	46.4
Microphyll 3	23.5
Mesophyll 1	12.6
Mesophyll 2	0.0
Mesophyll 3	0.0
Apex emarginated	0.0
Apex round	12.5
Apex acute	55.4
Apex attenuate	32.1
Base cordate	5.5
Base round	38.9
Base acute	55.5
L:W < 1:1	10.3
L:W 1–2:1	38.8
L:W 2–3:1	26.7
L:W 3–4:1	6.0
L:W > 4:1	18.1
Shape obovate	9.8
Shape elliptic	51.1
Shape ovate	39.1
Leaf simple	83.9

The CLAMP estimates for MAT, WMMT and CMMT have been calculated for the entire flora, and also for those sub-samples of the individual layers (cf. Uhl et al. 2003) with more than ten taxa (the physiognomic scores for the individual layers are available upon request from the authors).

European leaf physiognomy approach

The ELPA has recently been developed at the Institute of Geosciences, University of Tübingen (cf. Traiser 2004; Traiser et al. 2005). This approach uses a grid-based (0.5° lat. to 0.5° long.) calibration dataset covering large areas in Europe. At the moment, this data-set consists of 1,835 "synthetic floras" which are generated on the basis of the distribution maps of 108 extant woody angiosperm taxa that have been physiognomically characterised using floristic manuals. A synthetic flora at a specific geographical co-ordinate is defined exactly by the list of those taxa whose distribution maps cover that locality (Klotz 1999; Klotz et al. 2003; Traiser et al. 2005). So far, the "synthetic floras" included in the actual calibration data-set are restricted to grid-cells with more than 25 taxa and to an elevation between 0

and 400 m above sea-level. Details of this data set are discussed in detail by Traiser et al. (2005). Physiognomic data and climatic data (from New et al. 1999) are processed with Redundancy Analysis (RDA), a linear direct ordination technique, using CANOCO 4.02 for Windows (see Traiser, 2004). Although the underlying database has to be seen as preliminary (cf. Traiser et al. 2005), this approach has been included in our study to evaluate its current and future potential for palaeoclimatic analysis.

The ELPA estimates for MAT, WMMT and CMMT have been calculated for the entire flora, and also for those sub-samples of the individual layers (cf. Uhl et al. 2003) with more than ten taxa (the physiognomic scores for the individual layers are available upon request from the authors).

Results

"Floristic" observations

The taxonomy and palaeoecology related to the macro-flora of the Schrotzburg locality has been analysed in detail by Hantke (1954) and Nötzold (1957). Therefore, we restrict our "floristic" descriptions and observations to a short comparison between the macro- and the micro-flora, and to some preliminary palaeoecological implications inferred from the micro-flora. A detailed investigation of the palynoflora from the Schrotzburg locality is in preparation and will be published elsewhere.

Only a few taxa can be identified in both floras, i.e. *Alnus*, *Juglans*, *Pterocarya*, *Liquidambar*, *Quercus* and maybe *Ulmus* and *Glyptostrobus*, although the pollen of the latter two taxa cannot be distinguished from the pollen of closely related taxa (cf. Table 4). Whereas the macro-flora contains only remains of a single conifer taxon, *Glyptostrobus europaeus*, this group occurs with at least eight pollen types belonging to four different families (Table 4). Most of the source taxa can probably be regarded as elements of the hinterland-flora (i.e. Pinaceae, Sciadopityaceae, Cupressaceae), which are in general poorly represented in the macro-flora from this locality. Other palynomorph-types point to taxa which are common in palaeofloras from the Neogene of Central Europe (e.g. Gregor 1982; Mai 1995), such as *Engelhardia*, *Carya*, *Nyssa* or *Craigia*, but which have not been identified in the Schrotzburg macro-flora so far. Other palynomorph elements, which are not present in the macro-flora, belong to herbaceous forms like liverworts, ferns and Asteraceae.

The observed qualitative differences in the macro- and the micro-floras are also documented on account of the quantitative differences in the climatically limiting taxa when the CA is applied to both floras (cf. Table 5).

Table 5 List of the taxa, which define the limits of the palaeoclimate intervals of coexistence for the macro- as well as for the micro-flora of the Schrotzburg locality

	NLR taxa			
	CA$_{macro}$		CA$_{micro}$	
	Min	Max	Min	Max
MAT (°C)	*Sapindus*	*Populus balsamifera*	*Engelhardia*	*Juglans*
CMMT (°C)	*Quercus ilex Q. coccifera*	*Populus balsamifera*	*Engelhardia*	*Juglans*
WMMT (°C)	*Diospyros virginiana*	*Juglans*	*Engelhardia*	*Nyssa*
MAP (mm)	*Liquidambar styraciflua*	*Populus balsamifera*	*Lygodium*	*Taxodiaceae*

Palaeoclimate estimates

Coldest month mean temperature

Estimates for CMMT differ markedly between the different methods (cf. Table 6, Fig. 2). CLAMP–CMMT is hardly above 0°C (and may fall below this value if the error is included), whereas all the other methods estimate CMMT to be above 0°C. The results from these methods, however, also differ among one another with ELPA estimating the highest values ranging between 6.8 and 10.8°C. This interval, as represented by the standard deviation, slightly overlaps with that of CA$_{micro}$. In contrast, CA$_{macro}$ suggests CMMT values considerably lower than obtained by ELPA and CA$_{micro}$, which overlap with the CLAMP estimate for this parameter.

Mean annual temperature

The MAT estimates obtained from CA$_{macro}$, CA$_{micro}$ and ELPA are in good agreement with one another, suggesting MAT about 16°C (cf. Table 5, Fig. 2). In contrast, the CLAMP and the LMA suggest lower temperatures. In addition, the CLAMP estimate does not overlap with any of the other estimates, whereas the LMA estimate overlaps with the other estimates when taking into account the standard deviation.

The MAT estimates derived by LMA based on the revised macro-flora list (LMA$_{rev}$) used in this study are conspicuously colder than LMA estimates published by Uhl et al. (2003), which were based on Hantke's (1954) original taxa list (LMA$_{orig}$) (Table 7). Values for the complete flora differ by about 5.0°C. LMA$_{rev}$ estimates overlap with CA$_{macro}$ estimates, as it has been observed before for LMA$_{orig}$ estimates (Uhl et al. 2003). The taxonomic changes (cf. Table 1, 2) resulted also in a

slightly lower boundary for CA$_{macro}$ estimates (13.4°C as compared to 14.4°C estimated by Uhl et al. 2003).

Warmest month mean temperature

The WMMT estimates from all approaches are more or less in agreement with one another. All estimates point to WMMT of about 25–26°C, or slightly above this value (cf. Table 6, Fig. 2). The estimate obtained by CA$_{micro}$ is slightly higher than those by both physiognomic approaches, but the lower boundary (26.5°C) overlaps with the upper boundary of CA$_{macro}$ (26.7°C).

Mean annual precipitation

As both physiognomic approaches used in this work cannot reliably estimate MAP, we can only compare the results of CA$_{macro}$ and CA$_{micro}$. Here, CA$_{micro}$ estimates for MAP are slightly higher than those of CA$_{macro}$, suggesting values at about 1,300 mm (cf. Table 6).

Growing season precipitation

Only the two multivariate physiognomic approaches used in this study claim to be able to estimate GSP, suggesting, however, markedly different results (cf. Table 6), with the ELPA estimate (503 mm) three times higher than the CLAMP estimate (167 mm).

Growing season length

Similar to GSP, only the two multivariate physiognomic approaches claim to be able to estimate GSL. The GSL

Table 6 Palaeoclimate estimates for selected palaeoclimate parameters obtained by the different methods used in this study (for LMA see Table 7), and the original estimates from Hantke (1954), which were based on selected NLRs

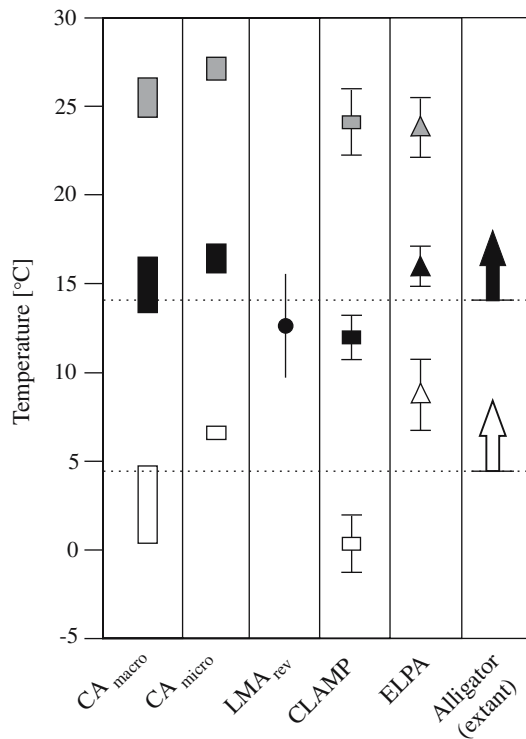|	CA$_{macro}$	CA$_{micro}$	CLAMP	ELPA	Hantke (1954)
MAT (°C)	13.4–16.5	15.6–17.2	12.0 ± 1.2	16.0 ± 1.1	~16
CMMT (°C)	0.4–4.8	6.2–7.0	0.4 ± 1.6	8.8 ± 2.0	7–8
WMMT (°C)	24.3–26.7	26.5–27.8	24.1 ± 1.9	23.8 ± 1.7	~24
MAP (mm)	897–1237	1300–1322			1300–1500
GSP* (mm)			167 ± 33.6	503 ± 81	
GSL* (months)			7.4 ± 0.7	9.7 ± 0.7	

*Temp. > 10°C

Fig. 2 Comparison of the results obtained by the individual methods for WMMT (*grey symbols*), MAT (*black symbols*) and CMMT (*open symbols*) based on the entire flora of the Schrotzburg locality. *Boxes* = CA, *circle* = LMA$_{rev}$, *square* = CLAMP, *triangle* = ELPA, and total ranges are given by standard deviation, *arrows* = crocodilians (base of *arrows* indicate threshold values for modern *Alligator*)

estimate suggested by CLAMP is slightly lower than that by ELPA (cf. Table 6). When the errors of estimation are considered a difference of about one month is suggested.

Taphonomic observations

In a previous study on the Schrotzburg macro-flora it was demonstrated that MAT estimates derived from LMA are strongly influenced by taphonomic distortions, due to the under representation of entire margined taxa in layers with low specimen numbers (Uhl et al. 2003). To investigate the potential influence of such distortions also on the multivariate physiognomic methods CLAMP and ELPA, MAT, WMMT and CMMT estimates for the individual layers with at least ten taxa are compared to the results obtained by LMA$_{rev}$ (only MAT) and CA$_{macro}$ (cf. Table 7, Fig. 3). It could be observed that such taphonomic distortions might have had relatively little influence on CA (e.g. Uhl et al. 2003). Only in layers with very few taxa, the width of the corresponding interval of coexistence was wider for all three climatic parameters (Fig. 3).

In all sub-samples, the WMMT estimates derived from CLAMP and ELPA did overlap and only in some sub-samples were these values below the CA$_{macro}$ estimates. CLAMP estimates did overlap in several cases with those of CA$_{macro}$, especially in layers with a low number of taxa and thus with consequently relative wide intervals of coexistence (Fig. 3). ELPA estimates for WMMT tended to be slightly warmer than those of CLAMP, and therefore did overlap more often with CA$_{macro}$ estimates.

For MAT, with the exception of three layers (5, 6 and 13) the LMA$_{rev}$ intervals spanned by the standard deviation did overlap with the two other physiognomic methods. In these three cases, estimates and errors derived from ELPA were higher than those from LMA$_{rev}$. With the exception of five sub-samples (1–4, 7), MAT values derived from CLAMP were lower than CA$_{macro}$ estimates, whereas all but one (layer 6) of the LMA$_{rev}$ estimates overlapped with CA$_{macro}$ estimates.

Table 7 MAT estimates obtained by LMA, CA$_{macro}$, CLAMP and ELPA for the florules of the individual layers with more than 10 taxa. For further explanations see text. LMA$_{orig}$ refers to the results by Uhl et al. (2003), which were based on the original taxa list published by Hantke (1954), whereas LMA$_{rev}$ refers to the revised list used in this study (cf. Tables 1, 2)

Layer (no. of taxa)	LMA$_{orig}$ (°C)	LMA$_{rev}$ (°C)	CA$_{macro}$ (°C)	CLAMP (°C)	ELPA (°C)
Complete flora (29)	17.8 ± 2.6	12.8 ± 2.8	13.4–16.5	12.1 ± 1.2	16.0 ± 1.1
1 (25)	19.5 ± 2.7	14.6 ± 3.0	12.5–16.5	12.5 ± 1.2	18.0 ± 1.1
2 (15)	19.1 ± 3.7	15.4 ± 3.9	12.5–16.5	12.1 ± 1.2	16.4 ± 1.1
3 (21)	18.4 ± 3.2	14.3 ± 3.3	12.5–16.5	12.0 ± 1.2	16.5 ± 1.1
4 (16)	17.3 ± 3.7	12.6 ± 3.7	12.5–16.5	11.4 ± 1.2	15.7 ± 1.1
5 (19)	17.2 ± 3.3	12.4 ± 3.4	13.4–16.5	11.6 ± 1.2	17.5 ± 1.1
6 (19)	16.4 ± 3.1	9.2 ± 3.1	12.5–16.5	10.0 ± 1.2	15.5 ± 1.1
7 (21)	17.7 ± 3.1	12.8 ± 3.2	12.5–16.5	12.0 ± 1.2	17.0 ± 1.1
8 (22)	17.6 ± 3.0	12.3 ± 3.1	13.4–16.5	11.6 ± 1.2	16.5 ± 1.1
10 (11)	15.0 ± 4.6	12.3 ± 4.4	12.5–16.5	9.5 ± 1.2	14.0 ± 1.1
11 (14)	17.5 ± 3.9	12.1 ± 3.9	13.4–16.5	11.6 ± 1.2	16.2 ± 1.1
12 (11)	17.8 ± 4.6	12.3 ± 4.4	13.4–16.5	10.6 ± 1.2	14.0 ± 1.1
13 (18)	13.0 ± 3.5	9.6 ± 3.2	12.5–16.5	10.1 ± 1.2	16.0 ± 1.1
14 (11)	19.0 ± 4.4	12.3 ± 4.4	12.5–16.5	10.6 ± 1.2	14.5 ± 1.1
17 (12)	13.9 ± 4.4	8.8 ± 3.8	12.5–16.5	9.5 ± 1.2	12.1 ± 1.1
18 (11)	16.4 ± 4.4	12.3 ± 4.4	12.5–16.5	10.1 ± 1.2	14.1 ± 1.1
19 (10)	15.0 ± 4.6	7.3 ± 3.9	12.5–16.5	8.7 ± 1.2	11.7 ± 1.1
26 (20)	19.8 ± 3.1	14.9 ± 3.4	13.4–16.5	13.0 ± 1.2	18.2 ± 1.1

Fig. 3 Comparison between CA$_{macro}$, LMA, CLAMP and ELPA estimates for **a** WMMT, **b** MAT and **c** CMMT based on the florules of the individual layers at the Schrotzburg locality with more than 10 taxa. *Grey boxes* = CA$_{macro}$, *filled circle* = LMA$_{rev}$, *filled square* = CLAMP, *filled triangle* = ELPA and total ranges are given by standard deviation, *dotted lines* = original estimate by Hantke (1954) for the complete flora, *broken lines* = threshold values as inferred from modern *Alligator*
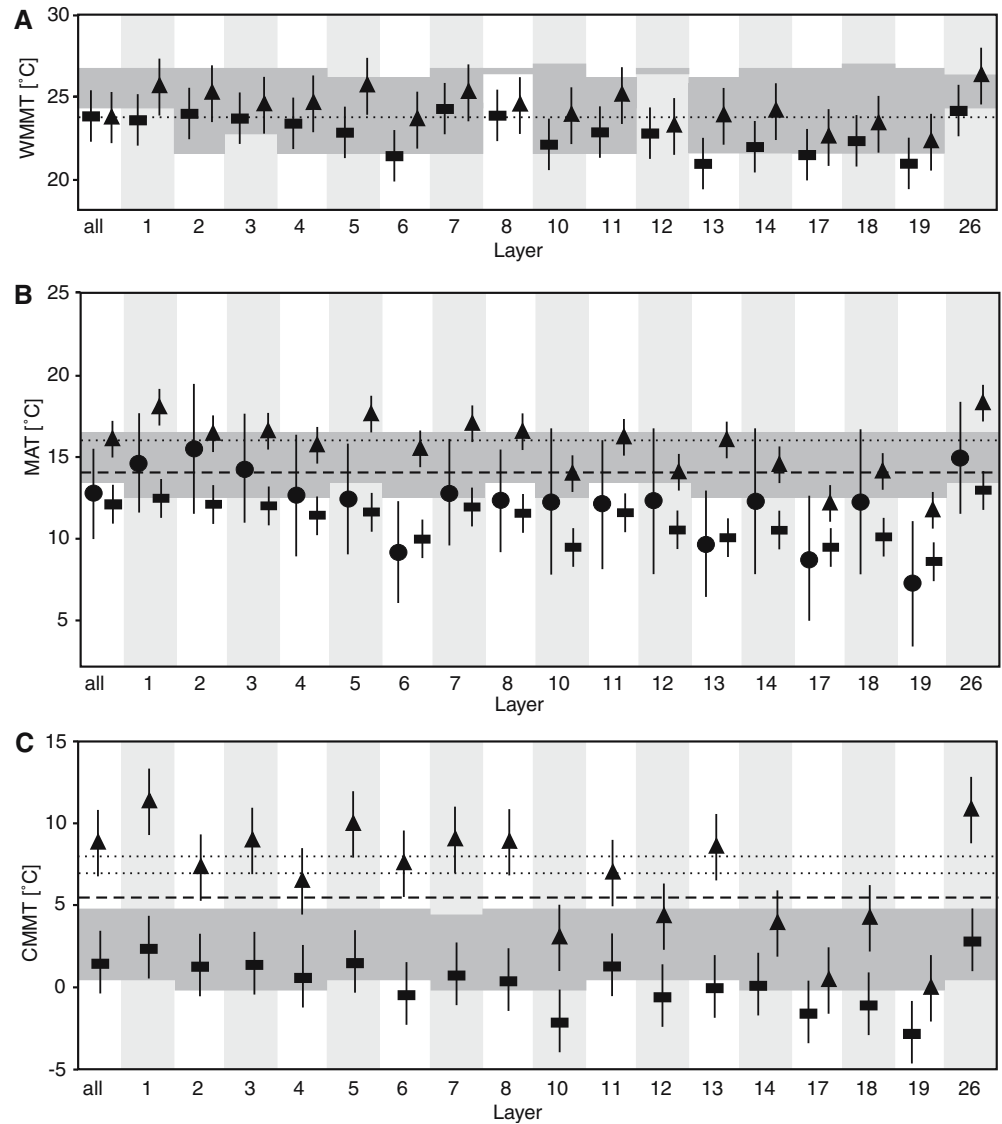
The overlapping estimates were consistently on the colder limits of the CA$_{macro}$ estimates. A similar trend to cooler MAT estimates derived from LMA$_{rev}$ and CLAMP can also be seen for the other layers, although the standard deviations did overlap with CA$_{macro}$ estimates in these cases. Interestingly, all ELPA estimates for MAT are significantly higher than CLAMP estimates. Most of the ELPA estimates overlap with CA$_{macro}$ estimates and the remaining two ELPA estimates, which do not overlap (one, 26), are higher than the CA$_{macro}$ estimates. Furthermore, the lowest ELPA estimates have been derived from the layers with the smallest number of taxa (<14 taxa).

Considering those layers with at least ten taxa (Table 7), the range of MAT as derived from CLAMP (4.3°C) was about half the range of that from LMA (8.2°C), and the range of ELPA values was intermediate between these two ranges (6.5°C). In that case, when layers with fewer than 15 taxa were excluded, these ranges were significantly reduced. The LMA range was reduced to 6.2°C, the CLAMP range to 2.9°C, and the ELPA range even to 2.8°C.

For CMMT, in almost all cases the CLAMP estimates did overlap with those of CA$_{macro}$, although the CLAMP estimates tend to overlap with the cooler part of the CA$_{macro}$ estimates. Only in one case (layer 19) is the CLAMP estimate significantly colder than the CA$_{macro}$ estimate. Except for six ELPA estimates (10, 12, 14, 17, 18, 19), the others were significantly warmer than the CA$_{macro}$ estimates (Fig. 3). These six estimates came from the layers with the lowest numbers of taxa (<14 taxa) (Table 7). For some of these layers, relative wide intervals of coexistence are suggested with respect to WMMT and MAT, with significantly colder lower boundaries than in the other layers.

To test the influence of the type of leaf margin on the reconstruction with CLAMP and ELPA, we correlated MAT values derived from LMA$_{rev}$ with both multivariate leaf physiognomic approaches. As a first result, the values as suggested by LMA$_{rev}$ and CLAMP correlated

rather well (cf. Fig. 4a). For all layers with more than 10 taxa, R^2 is 0.73 ($P < 0.8$) and increases to 0.87 ($P < 0.01$) when those layers with at least 15 taxa are considered. A further increase in the number of taxa, however, did not increase R^2, thus indicating a stable correlation on the basis of at least 15 taxa. Next, the correlation between ELPA and LMA_{rev} did result in R^2-values of 0.52 (≤ 10 taxa, $P < 0.7$) and 0.37 (≤ 15 taxa, $P < 0.4$) (cf. Fig. 4b), thus maybe indicating a slightly reduced influence of the type of the leaf margin on this approach.

Discussion

The taxonomic composition of the macro- and the micro-flora at the Schrotzburg locality differs significantly from each other. As could be expected, more elements from the hinterland and also from herbaceous forms have been found so far in the micro-flora than in the macro-flora. Despite these differences, which can largely be explained by variations in the taphonomic behaviour

Fig. 4 Correlation between LMA_{rev} and CLAMP (a), as well as between LMA_{rev} and ELPA (b) estimates for MAT based on the floras of the individual layers at the Schrotzburg locality. All symbols = layers ≥10 taxa (*dotted regression line*), solid symbols = layers ≥15 taxa (*solid regression line*)

of the different plant organs, most palaeoclimatic estimates based on NLRs for both floras are remarkably similar.

Palaeoclimate signals related to the entire Schrotzburg flora

All methods used in our study are able to estimate comparable values for WMMT for the entire Schrotzburg flora (Fig. 2), which are also in rather good agreement with earlier estimates by Hantke (1954) (cf. Table 6). Reconstructions for MAT and especially for CMMT, however, show some differences between the methods. For both parameters, the CLAMP estimates are lower than those obtained by the other methods. In the case of CMMT, also the CA_{macro} estimates are lower than those of the other methods, overlapping with the CLAMP estimate. This pattern leads to the question on how to decide which of the different methods suggest the most reliable results. In general, there are two ways to deal with this problem: (1) If two or more estimates of the five (more or less) independent methods overlap, it could be assumed that these estimates are most probable. As a result of such a procedure it is suggested that all WMMT estimates, MAT estimates from both CA and ELPA, and from LMA_{rev} if the standard deviation (or sampling error) is taken into account, as well as CMMT from CA_{micro} and ELPA, but alternatively also from CLAMP and CA_{macro} are most probable. Following such an argumentation, the following values for palaeotemperatures would be most likely: MAT ~16°C; CMMT ~7°C; WMMT = 25–26°C. These results are in absolute agreement with previous reconstructions for the Middle Miocene in S Germany and Switzerland (e.g. Gregor 1989; Mai 1995). For MAT, however, also the estimates derived from CLAMP and LMA_{rev} overlap, as well as the CMMT estimates derived from CLAMP and CA_{macro}, and thus may represent possible alternatives to the results of the other methods. (2) Alternatively to such an approach, estimates obtained from absolutely unrelated proxies such as stable isotopes or palaeozoological proxies can be compared to our results as inferred from the different methods used in this study. For the Schrotzburg locality, remains of the crocodilian *Diplocynodon* cf. *ratelli* POMEL, which have been recovered from the lower part of the profile at the Bohlinger Schlucht (Giersch 2004), may be used for this purpose. This taxon is common in the lower part of the profile at the Bohlinger Schlucht (belonging to mammal zone MN-6; Giersch 2004), but becomes gradually more rare towards the top of the profile, disappearing from the fossil record about 65 m below the plant bearing locality considered in our study (Giersch 2004). This author estimated the time between the last occurrence of *Diplocynodon* and our flora to be about 700,000 years. The disappearance of this taxon at the Bohlinger Schlucht roughly coincides with the extinction of this taxon in the Northern Alpine Foreland basin at the end
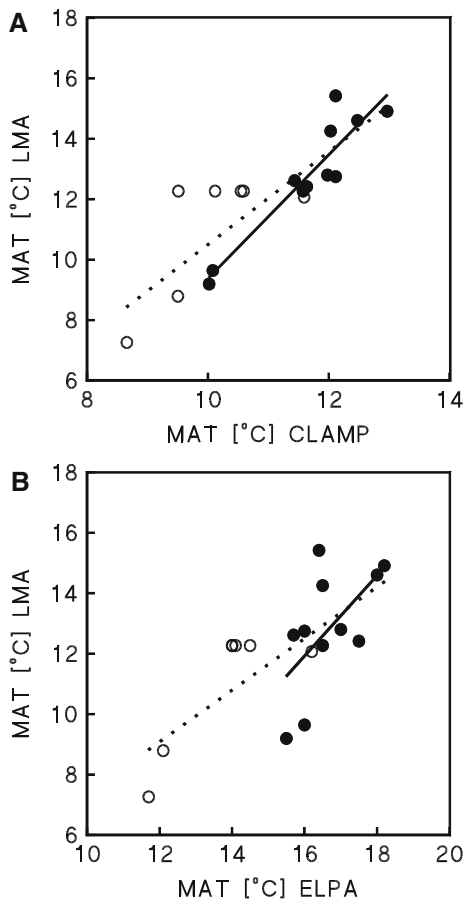
of mammal zone MN-6 (Böhme 2003). This extinction has been correlated with a drop in temperatures (MAT and CMMT) following the Middle Miocene climatic optimum (Böhme 2003) and might give us some threshold information about these parameters.

The most cold-hardy extant crocodilians (*Alligator mississippiensis* and *A. sinensis*) have been considered to show a northern limit, which approximately coincides with a CMMT of about 4.4°C (Neill 1971) (Fig. 2). So far, there is no evidence that crocodilian populations can survive during longer periods of subzero temperatures or of severe frosts (Hutchinson 1982; Markwick 1998). This would suggest CMMT to be probably as cold as indicated by CA_{macro} or even the CLAMP estimate and estimates from all other methods would be rather too warm. In addition, for modern *Alligator* the threshold for MAT is about 14.2°C (Markwick 1998). Again, this would favour the estimates derived from CLAMP, and CA_{macro}, but also LMA, whereas CA_{micro} and ELPA estimates would be too warm for such a threshold. Following such an argumentation we would come to the following conclusions: MAT ~13–14°C; CMMT < 4.4°C; WMMT = 25–26°C.

Nevertheless, such an interpretation is in contrast to other palaeobotanical evidence for the Upper Freshwater Molasse from the Northern Alpine Foreland basin (e.g. Gregor 1982, 1989; Mai 1995), although it is in better agreement with values for minimal temperatures during the coldest month estimated by Böhme (2003), who based her palaeoclimate estimates on the climatic demands of ectothermic vertebrates. How can such a contradiction be solved? In recognition of this dilemma Giersch (2004) argued that maybe *Diplocynodon* had warmer climatic demands than modern *Alligator*. This would result in higher thresholds for *Diplocynodon*, which maybe would lie above the MAT and CMMT values derived from CA_{micro} and ELPA, which are in fact close to the thresholds given by the climatic demands of modern *Alligator* (cf. Fig. 2). Although such an interpretation might be possible, it does not solve our problem concerning the MAT and CMMT values derived from the different methods.

Taking other palaeobotanical evidence from a wide number of contemporaneous localities from the Upper Freshwater Molasse of the Northern Alpine Foreland basin in account (e.g. Gregor 1982, 1989; Mai 1995), the results from our first approach seem to be more likely, than the results indicated by the disappearance of *Diplocynodon* and the temperature thresholds derived from modern alligators (*A. mississippiensis* and *A. sinensis*).

For precipitation (MAP, GSP) and GSL estimates, the palaeoclimate pattern is also far from clear (cf. Table 6). MAP values obtained by both CA methods differ only slightly from each other, with a somewhat higher value by CA_{micro}. This is in good agreement with Hantke's (1954) estimate relying on the precipitation demands of some selected NLRs of the macro-flora. Hantke (1954) based his analysis mainly on the

occurrence of *Daphnogene polymorpha*, determined by him as *Cinnamomum polymorphum*, for which he used the extant *Cinnamomum camphora* as a potential NLR. Although *D. polymorpha* is defined as a morpho-taxon of the Lauraceae which can not be assigned to any extant genus, it is possible that this taxon is closely related to *Cinnamomum* as evidenced by associated fruits which are apparently related to *Cinnamomum* at the Kreuzau locality in the Lower Rhine embayment (Pingen et al. 1994). Nevertheless, we did not use *Cinnamomum* in our analysis because no associated fruits of the *Cinnamomum* type have been found at the Schrotzburg locality so far. If this taxon were excluded from Hantke's climatic analysis, his estimate for MAP would probably have a slightly lower limit and would thus better match our CA_{macro} estimate. Thus, a MAP value of about 1,300 mm or even more seems to be likely for the Schrotzburg locality.

Concerning GSP and GSL, only the two physiognomic methods claim to be able to generate estimates but here CLAMP values are significantly lower than those obtained by ELPA. Only a part of the lower GSP estimate can probably be explained by a reduction in GSL. The results from both physiognomic methods suggest that the greater part of the annual precipitation (ca. 800–1,100 mm, assuming that the CA estimates and Hantke's original estimate are more or less reliable) did not fall during the growing season. Although this is not impossible, it contradicts the results of numerous studies on the climate of the Northern Alpine Foreland basin during the Late Miocene, predicting a climate of the Cfa type (sensu Köppen) with precipitation almost equally distributed throughout the year (e.g. Hantke 1954; Gregor 1982). Hence, it can be concluded that both physiognomic methods fail to produce reliable estimates for GSP, although ELPA seems to be closer to a more realistic value than CLAMP. Taking the error margins into account, both estimates for GSL (CLAMP maximum, ELPA minimum) differ only by about 1 month. Nevertheless, currently it is not possible to decide which of these estimates, if any, is more reliable for GSP and GSL.

All in all, it can be stated that for most palaeoclimatic parameters the estimates derived by CLAMP differ from those derived by most of the other methods used in this study, pointing to colder temperatures and lower precipitation values. A possible reason for this discrepancy of CLAMP may be the fact, that the correlation between leaf physiognomy and climate as it is represented in the calibration data-set of CLAMP (CLAMP 3B data-set) may not be suitable to analyse palaeofloras from the European Neogene. For the univariate correlation between leaf margin type and MAT it has been repeatedly demonstrated that in many cases this correlation varies across different regions of the world (e.g. Wilf 1997; Kowalski 2002; Greenwood et al., 2004; Traiser et al. 2005). Taking into account that the temperature signal in the CLAMP calibration data-set is obviously dominated by leaf margin type (Wilf 1997; this article), it

can probably be concluded that also the multivariate correlation between leaf physiognomy and environment may vary in different parts of the world. This observation was one of the reasons to develop the ELPA, which seems to be better suited to produce reliable estimates for temperature parameters than CLAMP for the European Neogene, although the ELPA database has to be seen as taxonomically incomplete at the moment. Nevertheless, based on the ELPA approach it has been demonstrated by Traiser et al. (2005) that there exist a statistically significant correlation between extant leaf physiognomic patterns and climatic conditions on a European scale.

Influence of the taxonomic revision on palaeoclimate interpretation

The comparison of the results for MAT relying on LMA for the taxonomically revised and for the original flora of the Schrotzburg (cf. Hantke 1954; Uhl et al. 2003) revealed that such a taxonomic revision may have a significant influence on palaeoclimate estimates. Such an effect has also been discussed earlier by various authors (e.g. Wolfe 1999). The LMA, MAT results for the revised and for the original entire Schrotzburg flora differed at about 5°C, and that for the individual layers between 2.7 and 7.7°C. Although the results by LMA_{rev} were consistently lower than that by LMA_{orig}, which primarily reflects the reduction in entire margined taxa, the LMA_{rev} estimates were still in rather good agreement with estimates derived from CA_{macro}. Nevertheless, the resulting intervals of coexistence derived from CA_{macro} were slightly wider (i.e. slightly colder lower limits) following our taxonomic revision.

Palaeoclimate signals related to the individual layers of the Schrotzburg flora

The CLAMP results for the floras of the individual layers suggest that MAT is estimated to be systematically too cold as compared to CA_{macro} and ELPA, and to other independent evidence. Although CLAMP estimates for CMMT and WMMT often overlap with CA_{macro} estimates they are systematically at the lower limits of these estimates, also suggesting a tendency to underestimate these parameters. Despite the potential failure of CLAMP to produce reliable MAT estimates for the Schrotzburg locality, the advantage of such a multivariate approach with regard to taphonomic biasses is still obvious: the range of MAT values as obtained by CLAMP and ELPA is smaller than those obtained by LMA_{rev}, thus indicating that CLAMP is far less influenced by taphonomic biasses than LMA (cf. Uhl et al. 2003). In the case of samples with a rather low number of taxa (< 15), ELPA seems to be slightly more affected by taphonomic distortions than CLAMP. However, when only layers with at least 15 taxa were considered, estimates from both methods exhibited virtually the same variation in MAT values.

With this study it also became obvious that the results from CLAMP are strongly influenced by the proportions of taxa with entire margined leaves, as indicated by the rather high correlation between the MAT estimates from LMA_{rev} and CLAMP (cf. Fig. 4a). In contrast, correlation between LMA_{rev} and ELPA estimates for MAT is less high, thus possibly pointing to a smaller dependence of the latter approach on the type of leaf margin. Wilf (1997) already pointed to the fact that the temperature signal in the CLAMP calibration data set is dominated by leaf margin and that the additional characters used for CLAMP add only minimal statistical precision. Hence, it does not appear to improve the quality of a temperature estimate in practical use. In addition, Wilf (1997) concluded that the univariate LMA approach will give palaeotemperature estimates at least as precise as the multivariate approach, which is more complicated and time consuming. When comparing the results from LMA_{rev} and CLAMP presented in this study, we have on the one hand to agree with Wilf's interpretation, simply because of the fact that CLAMP failed to produce reliable estimates for MAT at the Schrotzburg locality. On the other hand, it could be observed that taphonomy had greater effects on LMA than on CLAMP at this locality. For new collections, some of these taphonomic influences may be significantly reduced by sampling as many taxa, facies types and the longest possible transect per stratigraphical level as possible, as already suggested by Wilf (1997). However, for old collections, especially from localities, which are no longer accessible, as is often the case with "classical" localities in Europe, this may not be practicable. Many of these "classical" localities, whose floras have been described during the 19th or even the 20th century, were related to the commercial exploitation of mineral resources like coals, lignites or limestone. In many cases, the corresponding quarries or mines have long since been abandoned and the fossil-bearing strata are no longer accessible. Well known examples are the Oehningen limestone quarries (Heer 1855, 1856, 1859), or the large open cast lignite mines in Eastern Germany (e.g. Mai and Walther 1978, 1985) which have been renaturalised and are no longer accessible for collecting fossils. In these cases, other solutions have to be found to enable us to extract reliable information about selected palaeoclimatic parameters on the basis of fossil plants. These solutions may include the development of new calibration data-sets for the use of uni- and multivariate leaf physiognomic approaches, as well as the constant improvement of methods based on the NLR approach.

Conclusions

Considering the results of all methods used, as well as of the palaeoclimatic implications of crocodilian remains discovered at the Bohlinger Schlucht, the fol-

lowing palaeoclimate estimates seem to be most likely for the Middle Miocene Schrotzburg locality in SW Germany: MAT ~16°C, CMMT ~7°C, WMMT between 25 and 26°C and MAP ~1,300 mm (although CMMT may have been considerably lower, as indicated by the disappearance of *Diplocynodon* and the threshold derived from modern alligators). Despite the uncertainty concerning CMMT these results are in absolute agreement with earlier estimations for this locality, which were based on the climatic demands of only a few selected NLRs (Hantke 1954). CLAMP estimates were consistently colder than temperature estimates from most other methods used here and additional evidence from other palaeofloras from the Upper Freshwater-Molasse of the Northern Alpine Foreland basin. A possible explanation for this discrepancy may be the fact that CLAMP relies on an extant calibration data-set based on North American and East Asian vegetation. In contrast, the multivariate leaf physiognomic method ELPA, which is based on an (not yet complete) European calibration data-set provided estimates, which are in good agreement with those of the other methods, as well as with independent evidence. Both multivariate methods were less influenced by taphonomic biases at this locality, as compared to the univariate LMA.

All in all, our results suggest in combination with previously published results from other localities from the Neogene in Europe (e.g. Mosbrugger and Utescher 1997; Utescher et al. 2000; Kvaček et al. 2002) and in Asia (Liang et al. 2003), that for the Neogene of Eurasia CLAMP may produce temperature estimates, which are systematically colder as compared to other evidence. However, before the applicability of CLAMP is totally disregarded for the European and maybe also for the Asian Neogene, further studies on palaeofloras from a variety of source vegetations and from depositional settings have to be conducted. Then it can be assessed if the observed deviation of CLAMP estimates has to be considered as the rule, or as the exception for the application on Neogene Eurasian palaeofloras. Additionally, the applicability of the ELPA has to be tested further with the same floras, parallel to its ongoing development and taxonomic completion.

References

Bailey IW, Sinnott EW (1915) A botanical index of cretaceous and tertiary climates. Science 41:831–834

Bailey IW, Sinnott EW (1916) The climatic distribution of certain types of angiosperm leaves. Am J Bot 42:24–39

Böhme M (2003) The Miocene climatic optimum: evidence from ectothermic vertebrates of Central Europe. Palaeogeogr Palaeoclimatol Palaeoecol 195:389–401

Bruch AA (1998) Palynologische Untersuchungen im Oligozän Sloweniens–Paläo-Umwelt und Paläoklima im Ostalpenraum. Tübinger Mikropaläontologische Mitteilungen 18:193pp

Burnham RJ, Pitman NCA, Johnson KR, Wilf P (2001) Habitat-related error in estimating temperatures from leaf margins in a humid tropical forest. Am J Bot 88:1096–1102

Chaloner WG, Creber GT (1990) Do fossil plants give a climatic signal? J Geol Soc 147:343–350

Ferguson DK (1985) The origin of leaf-assemblages–new light on an old problem. Rev Palaeobot Palynol 46:117–188

Giersch S (2004) Die Fauna aus den mittelmiozänen Krokodil-schichten der Bohlinger Schlucht–Ein Beitrag zur Paläoökologie und Biostratigraphie der Oberen Süßwassermolasse am Schiener Berg (Baden-Württemberg). Carolinea 62:5–50

Greenwood DR, Wilf P, Wing SL, Christophel DC (2004) Paleo-temperature estimation using leaf-margin analysis: Is Australia different? Palaios 19:129–142

Gregor H-J (1982) Die jungtertiären Floren Süddeutschlands. Ferdinand Enke, Stuttgart

Gregor H-J (1989) Versuch eines neuen Klima-Modells für die Zeit der Oberen Meeres- Süßwasser-Molasse in Bayern. Documenta naturae 46:34–47

Gregor H-J, Hantke R (1980) Revision der fossilen Legumino-sengattung *Podogonium* HEER (= *Gleditsia* LINNE) im europäischen Jungtertiär. Feddes Repert 91:151–182

Hantke R (1954) Die fossile Flora der obermiozänen Oehninger-Fundstelle Schrotzburg. Denkschriften der Schweizerischen Naturforschenden Gesellschaft 80:27–118

Hantke R (1965) Die fossilen Eichen und Ahorne aus der Molasse der Schweiz und von Oehningen (Süd-Baden). Neujahrsblatt der Naturforschenden Gesellschaft Zürich 1965:108

Hantke R (1966) Die fossilen *Liquidambar*-Reste (Amberbaum) aus der Molasse der Schweiz und von Oehningen (Südbaden). Eclogae Geol Helv 59:981–988

Hantke R (1980) Die Bedeutung der als ausgestorben betrachteten Leguminosen-Gattung *Podogonium* HEER (*Gleditsia* L.) für die Obere Süßwassermolasse und für die Vogesenschüttung im Delsberger Becken (Jura). Eclogae Geol Helv 73:1031–1043

Heer O (1855) Flora tertiara Helvetiae I. Verlag von Wurster und Comp., Winterthur, 116p

Heer O (1856) Flora tertiara Helvetiae II. Verlag von Wurster und Comp., Winterthur, 110p

Heer O (1859) Flora tertiara Helvetiae III. Verlag von Wurster und Comp., Winterthur, 378p

Herendeen PS (1992a) A reevaluation of the fossil genus *Podogonium* Heer. In: Herendeen PS, Dilcher DL (eds) Advances in Legume Systematics: Part 4. The fossil record. The Royal Botanical Gardens, Kew, pp 3–18

Herendeen PS (1992b) *Podocarpium podocarpum* comb. nov., the correct name for *Podogonium knorrii* Heer, nom. illeg. (fossil Fabaceae). Taxon 41:731–736

Herman AB, Spicer RA (1997) New quantitative palaeoclimate data for the Late Cretaceous Arctic: evidence for a warm polar ocean. Palaeogeogr Palaeoclimatol Palaeoecol 128:227–251

Hutchinson JH (1982) Turtle, crocodilian, and champsosaur diversity changes in the Cenozoic of the north-central region of Western United States. Palaeogeogr Palaeoclimatol Palaeoecol 37:149–164

Ivanov D, Ashraf AR, Mosbrugger V, Palamarev E (2002) Palynological evidence for Miocene climate change in the Forecarpathian Basin (Central Paratethys, NW Bulgaria). Palaeogeogr Palaeoclimatol Palaeoecol 178:19–37

Jones TP, Rowe NP (eds) (1999) Fossil plants and spores: modern techniques. Geological Society London, 408pp

Kershaw AP (1997) A bioclimatic analysis of early to Middle Miocene brown coal floras, Latrobe Valley, South-Eastern Australia. Aust J Bot 45:373–387

Kershaw AP, Nix HA (1988) Quantitative palaeoclimatic estimates from pollen data using bioclimatic profiles of extant data. J Biogeogr 15:589–602

Klotz S (1999) Neue Methoden der Klimarekonstruktion—angewendet auf quartäre Pollensequenzen der französischen Alpen. Tübinger Mikropaläontologische Mitteilungen 21:169

Klotz S, Guiot J, Mosbrugger V (2003) Continental European Eemian and early Würmian climate evolution: comparing signals using different quantitative reconstruction approaches based on pollen. Glob Planet Change 36:277–294

Kovar-Eder J, Kvaček Z, Ströbitzer-Hermann M (2004) The Flora of Parschlug (Styria, Austria)—Revision and Synthesis. Annalen des Naturhistorischen Museums Wien 105 A:45–157

Kowalski EA (2002) Mean annual temperature astimation based on leaf morphology: a test from tropical South America. Palaeogeogr Palaeoclimatol Palaeoecol 188:141–165

Kowalski EA, Dilcher DL (2003) Warmer paleotemperatures for terrestrial ecosystems. Proc Natl Acad Sci 100:167–170

Kvaček Z, Walther H (2004) Oligocene Flora of Bechlejovice ar Decin from the neovolcanic area of the Ceske Stredohori mountains, Czech Republic. Acta Musei Nationalis Pragae, Series B, Natural History 60:9–60

Kvaček Z, Velitzelos D, Velitzelos E (2002) Late Miocene Flora of Vegora, Macedonia, N. Greece. University of Athens, Athens Greece, p 175

Liang M-M, Bruch A, Collinson M, Mosbrugger V, Li, Ch-S, Sun Q-G, Hilton J (2003) Testing the climatic estimates from different palaeobotanical methods: an example from the Middle Miocene Shangwang flora of China. Palaeogeogr Palaeoclimatol Palaeoecol 198:279–301 (doi:10.1016/S0031-0182(03)00471-1)

Mai DH (1995) Tertiäre Vegetationsgeschichte Europas. Gustav Fischer, Jena

Mai DH, Walther H (1978) Die Floren der Haselbacher Serie im Weißelster-Becken (Bezirk Leipzig) DDR. Abhandlungen des Staatlichen Museums für Mineralogie und Geologie zu Dresden 28:1–200

Mai DH, Walther H (1985) Die obereozänen Floren des Weißelster-Beckens und seiner Randgebiete. Abhandlungen des Staatlichen Museums für Mineralogie und Geologie zu Dresden 33:1–260

Markwick PJ (1998) Fossil crocodilians as indicators of Late Cretaceous and Cenozoic climates: implications for using palaeontological data in reconstructing palaeoclimate. Palaeogeogr Palaeoclimatol Palaeoecol 137:205–271

Mosbrugger V (1999) The nearest living relative method. In: Jones TP, Rowe NP (eds) Fossil plants and spores: modern techniques. Geological Society, London, pp 261–265

Mosbrugger V, Schilling H-D (1992) Terrestrial paleoclimatology in the Tertiary: a methodological critique. Palaeogeogr Palaeoclimatol Palaeoecol 99:17–29

Mosbrugger V, Utescher T (1997) The coexistence approach—a method for quantitative reconstructions of Tertiary terrestrial palaeoclimate data using plant fossils. Palaeogeogr Palaeoclimatol Palaeoecol 134:61–86

Mosbrugger V, Utescher T, Dilcher DL (2005) Cenozoic continental climatic evolution of Central Europe. Proc Natl Acad Sci 102:14964–14969 (doi:10.1073/pnas.0505267102)

Neill WT (1971) The last of the Ruling Reptiles: Alligators, Crocodiles, and Their Kin. Columbia University Press, New York, NY, p 486

New M, Hulme M, Jones P (1999) Representing 20th century space-time climate variability. Part I: development of a 1961–1990 mean monthly terrestrial climatology. J Clim 12:829–856

Nötzold T (1956) Baptisiaecarpum schrotzburgense n. gen., hülsenartige Früchte aus dem Obermiozän bei der Schrotzburg am Bodensee. Mitteilungen des badischen Landesvereins für Naturkunde und Naturschutz, N.F. 6:372–379

Nötzold T (1957) Miozäne Pflanzenreste von der Schrotzburg am Bodensee. Berichte der Naturforschenden Gesellschaft zu Freiburg 47:71–102

Pingen M, Ferguson DK, Collinson ME (1994) Homalanthus costatus Mai: a new Miocene fruit of Cinnamomum Schaeffer (Lauraceae). Palaeontographica B 232:155–174

Pross J, Bruch A, Kvaček Z (1998) Paläoklima-Rekonstruktionen für den Mittleren Rupelton (Unter-Oligozän) des Mainzer Beckens auf der Basis mikro- und makrobotanischer Befunde. Mainzer geowissenschaftliche Mitteilungen 27:79–92

Roth-Nebelsick A, Utescher T, Mosbrugger V, Diester-Haass L, Walther H (2004) Changes in atmospheric CO_2 concentrations and climate from the Late Eocene to Early Miocene: palaeobotanical reconstruction based on fossil floras from Saxony, Germany. Palaeogeogr Palaeoclimatol Palaeoecol 205:43–67 (doi:10.1016/j.palaeo.2003.11.014)

Rutte E (1956) Die Geologie des Schienerberges (Bodensee) und der Öhninger Fundstätten. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 102:143–282

Schreiner A (1992) Erläuterungen zur Geologischen Karte des Landkreises Konstanz und Umgebung 1:50.000. Geologisches Landesamt Baden-Württemberg, Freiburg

Spicer RA (1981) The sorting and deposition of allochthonous plant material in a modern environment at silwood Lake, Silwood Park, Berkshire, England. US Geol Surv Prof Paper 1143:77p

Spicer RA (1991) Plant taphonomic processes. In: Allison PA, Briggs DEG (eds) Taphonomy: releasing the data locked in the Fossil Record. Topics in Geobiology 9:71–113

Steffen W, Sanderson A, Tyson PD, Jäger J, Matson PA, Moore B III, Oldfield F, Richardson K, Schellnhuber HJ, Turner BL II, Wasson RJ (2004) Global change and the earth system—a planet under pressure. Springer, Berlin Heidelberg New York, p 336

Traiser C (2004) Blattphysiognomie als Indikator für Umweltparameter: eine Analyse rezenter und fossiler Floren. Unpubl. Ph.D. Thesis, University of Tübingen, IV, p 113 (URN: urn:nbn:de:bsz:21-opus-14947)

Traiser C, Klotz S, Uhl D, Mosbrugger V (2005) Environmental signals from leaves—a physiognomic analysis of European vegetation. New Phytol 166:465–484 (doi: 10.1111/j.1469-8137.2005.01316.x)

Uhl D, Mosbrugger V, Bruch A, Utescher T (2003) Reconstructing palaeotemperatures using leaf floras—case studies for a comparison of leaf margin analysis and the coexistence approach. Rev Palaeobot Palynol 126:49–64 (doi:10.1016/S0034-6667(03)00058-7)

Utescher T, Mosbrugger V, Ashraf AR (2000) Terrestrial climate evolution in Northwest Germany over the last 25 million years. Palaios 15:430–449

Wilf P (1997) When are leaves good thermometers? A new case for Leaf Margin Analysis. Paleobiology 23:373–390

Wing SL, Greenwood DR (1993) Fossils and fossil climate: the case for equable continental interiors in the Eocene. Philos T Roy Soc B 341:243–252

Wolfe JA (1979) Temperature parameters of humid zo mesic forests of Eastern Asia and relation to forests of other regions of the Northern hemisphere and Australia. US Geol Surv Prof Paper 1106:1–37

Wolfe JA (1993) A method of obtaining climatic parameters from leaf assemblages. US Geol Surv Bull 2040:1–71

Wolfe JA (1994a) Tertiary climatic changes at middle latitudes of western North America. Palaeogeogr Palaeoclimatol Palaeoecol 108:195–205

Wolfe JA (1994b) An analysis of Neogene climates in Beringia. Palaeogeogr Palaeoclimatol Palaeoecol 108:207–216

Wolfe JA (1995) Paleoclimatic estimates from Tertiary leaf assemblages. Annu Rev Earth Planet Sci 23:119–142

Wolfe JA (1999) Early Palaeocene palaeoclimatic inferences from fossil floras of the western interior, USA—comment. Palaeogeogr Palaeoclimatol Palaeoecol 150:343–345

Wolfe JA, Spicer RA (1999) Fossil leaf character states: multivariate analysis. In: Jones TP, Rowe NP (eds) Fossil plants and spores: modern techniques. Geological Society, London, pp 233–239

Zhao LC, Wang YF, Liu CL, Li CS (2004). Climatic implications of fruit and seed assemblage from Miocene of Yunnan, Southwestern China. Quatern Int 117:81–89