Leaf physiognomy and palaeoenvironmental estimates – an alternative technique based on an European calibration

CHRISTOPHER TRAISER[1*], DIETER UHL[2], STEFAN KLOTZ[1] and VOLKER MOSBRUGGER[1,3]

[1]Institut für Geowissenschaften, Eberhard Karls Universität Tübingen, Sigwartstrasse 10, D-72076 Tübingen, Germany; e-mail: christopher.traiser@uni-tuebingen.de

[2]Palaeoecology, Institute of Environmental Biology, Faculty of Science, Laboratory of Palaeobotany and Palynology, Utrecht University, Budapestlaan 4, 3854 CD Utrecht, The Netherlands; e-mail: dieter.uhl@gmx.de

[3]Forschungsinstitut Senckenberg, Senckenberganlage 25, D-60325, Frankfurt am Main, Germany; e-mail: volker.mosbrugger@senckenberg.de

ABSTRACT. Physiognomic characters of fossil angiosperm leaf assemblages are believed to represent suitable proxies for palaeoenvironment, and particularly for palaeoclimatic reconstruction. To analyse past environments in Europe, a recently developed approach (ELPA: European Leaf Physiognomic Approach) is used to examine the relationship between angiosperm leaf physiognomy and environmental parameters. Transfer functions for different environmental parameters (e.g. mean annual temperature, temperature of warmest and coldest month, number of ground frost days per year, and proportion of evergreen taxa within the vegetation) have been estimated from leaf physiognomic characters using Redundancy Analysis (a multivariate ordination technique). These transfer functions are applied to three fossil floras from the European Paleogene (Monod-Rivaz, Switzerland, Late Oligocene) and Neogene (Schrotzburg in Germany, middle Miocene and Erdőbénye Kővágó-oldal in Hungary, also Middle Miocene). The results obtained are compared to alternative palaeoenvironmental estimates: (1) transfer functions based on multiple linear regression, (2) the coexistence approach (which is based on the "nearest living relative concept"), and (3) palaeoenvironmental estimates from preceding publications on the three fossil floras. The application of the new transfer functions based on the ordination technique to the three European fossil floras shows realistic results, consistent with other palaeoclimatic reconstructions. The leaf physiognomic transfer functions proposed here thus provide alternative techniques that can be applied in palaeoenvironmental research.

KEY WORDS: leaf physiognomy, fossil leaf assemblage, ordination, Redundancy Analysis RDA, evergreen leaves, character syndrome, palaeoclimate

INTRODUCTION

In palaeoenvironmental research two main approaches for reconstructing palaeoenvironmental conditions based on fossil plants can be distinguished, both of which rely on the principle of actualism (Wing & Greenwood 1993): (1) approaches which are based on functional morphological adaptations of plants, regardless of systematic position of the investigated taxa; (2) approaches that use the systematic relationships of fossil and modern plants. The latter method assumes that closely related taxa (a fossil and its nearest living relative – NLR) have similar environmental requirements. Both approaches have their specific advantages and disadvantages, which will not be discussed here in detail. It is noticeable, however, that only a few publications dealing with reconstructing palaeoenvironmental conditions cross-validate the results of these two approaches. To compare different approaches

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* Author for correspondence

Table 1. Leaf physiognomic composition of the three investigated fossil assemblages

No	Leaf character	Abbr.	Definition	[%]		
				Monod-Rivaz	Schrotz-burg	Kővágó-oldal
1	leaf simple	le_simp	leaf is not compound	96.0	83.9	80.9
2	leaf lobed	le_lobe	leaf with lobes	10.0	19.4	22.1
3	leaf margin entire	ma_enti	margin without teeth	68.0	51.6	52.9
4	leaf size: leptophyll 1	ls_lep1	< 20 mm²	2.0	0.0	0.0
5	leaf size: leptophyll 2	ls_lep2	20–80 mm²	2.0	0.0	4.4
6	leaf size: microphyll 1	ls_mic1	80–400 mm²	16.0	9.1	15.6
7	leaf size: microphyll 2	ls_mic2	400–1400 mm²	35.6	31.1	39.1
8	leaf size: microphyll 3	ls_mic3	1400–3600 mm²	33.0	32.7	30.3
9	leaf size: mesophyll 1	ls_mes1	3600–6200 mm²	8.3	17.9	10.3
10	leaf size: mesophyll 2	ls_mes2	6200–10000 mm²	3.0	8.0	0.0
11	leaf size: mesophyll 3	ls_mes3	> 10000 mm²	0.0	0.8	0.0
12	apex of blade: obtuse	ap_obtu	$\alpha > 90°$	33.0	15.6	27.9
13	apex of blade: acute	ap_acut	$\alpha < 90°$	67.0	82.8	72.1
14	apex of blade: emarginate	ap_emar	apex emarginated	0.0	1.6	0.0
15	base of blade: obtuse	ba_obtu	$\alpha > 90°$	63.0	50.2	61.8
16	base of blade: acute	ba_acut	$\alpha < 90°$	34.0	39.8	32.4
17	base of blade: embayed	ba_emba	base cordate	3.0	9.9	2.9
18	blade: length / width < 1:1	lw_1	ratio l/w: < 1:1	4.0	11.3	11.8
19	blade: length / width 1–2:1	lw_2	ratio l/w: 1–2:1	38.0	36.8	40.0
20	blade: length / width 2–3:1	lw_3	ratio l/w: 2–3:1	25.0	23.9	26.8
21	blade: length / width 3–4:1	lw_4	ratio l/w: 3–4:1	16.0	7.5	7.6
22	blade: length / width > 4:1	lw_5	ratio l/w: > 4:1	17.0	20.4	10.3
23	shape of blade: obovate	sh_obov	largest width in upper 1/3 of lamina	5.4	12.9	23.5
24	shape of blade: elliptic	sh_elli	largest width in middle 1/3 of lamina	69.2	43.5	52.9
25	shape of blade: ovate	sh_ovat	largest width in lower 1/3 of lamina	25.4	43.5	20.6

or techniques it is necessary to apply more than one method to an individual flora (Mosbrugger & Utescher 1997, Liang et al. 2003, Uhl et al. 2003, 2006). Such a procedure also enables us to get a more reliable impression of palaeoclimatic as well as palaeoecological conditions (Wing & Greenwood 1993, Uhl et al. 2006). Approaches used in this investigation are based on functional morphological adaptations, comprising leaf physiognomic traits such as leaf size, leaf length/width ratio and leaf shape (Tab. 1). These physiognomic characters are correlated with several environmental parameters, such as mean annual temperature, number of ground frost days, and growing season length. The leaf physiognomic-environmental calibration dataset (ELPA) used here (Traiser et al. 2005) is based on extant European hardwood vegetation, thus conifer needle leaves are excluded from the analysis. In this study the results of palaeoenvironmental estimates for three European fossil floras based on leaf physiognomy are cross-validated with (1) results obtained by the coexistence approach and (2) estimates from previous studies, to compare the different approaches. Moreover, the detailed leaf physiognomic study and comparison of the three fossil leaf assemblages offers an advanced analysis of palaeoecological characteristics such as the proportion of evergreen taxa within a given flora. This is possible because extant broad-leaf evergreen leaves show leaf physiognomic character syndromes that can also be observed in fossil leaf assemblages.

MATERIAL AND METHODS

FOSSIL SITES AND FOSSIL MATERIAL

The three fossil leaf floras investigated in the present study are characterized by relatively high species richness and excellent morphological preservation. The floras are located in the Trans-European Paratethys bioprovince, with Monod-Rivaz (Switzerland) and Schrotzburg (Germany) in the Northern Alpine Molasse Basin, and the flora of Erdőbénye Kővágó-oldal (Hungary) in the northern part of the Pannonian Basin.

Monod-Rivaz (Oligocene, Switzerland)

The floras of Monod and Rivaz were described for the first time by Heer (1855, 1856, 1859) and Delaharpe & Gaudin (1856), and were subsequently merged to "Monod-Rivaz" by Heer (1859) because of the proximity of the localities, near Lake Geneva (370 m a.s.l.) in south-west Switzerland (Fig. 1). The fossils, i.e. leaves

Miocene fluvial sands about 300 m in thickness, with numerous embedded marly lenses, and is uncomfortably overlain by Quaternary moraines. The Schrotzburg flora (approx. 600 m a.s.l.) occurs in a marly lens on the steep northern slope of the mountain (Hantke 1954). The fluvial sediments were deposited in the Northern Alpine Foreland Basin, when a large river system crossed the northern fringe of the rising
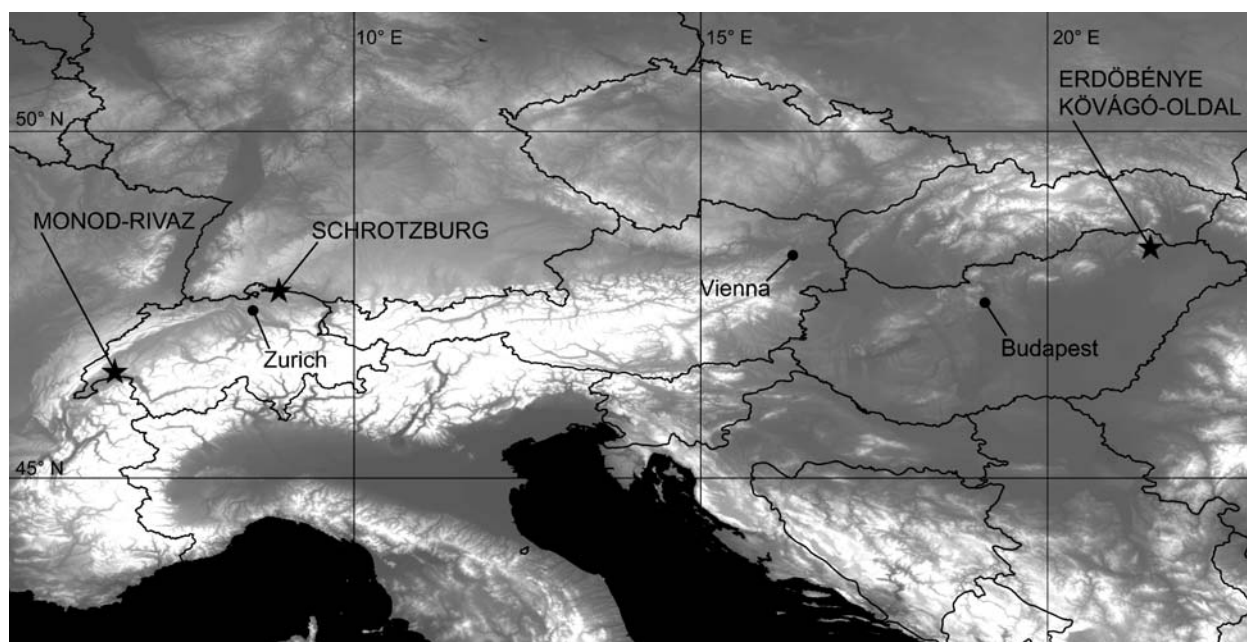
Fig. 1. Location of the investigated fossil sites: Monod-Rivaz (Switzerland) Late Oligocene, Schrotzburg (Germany) middle Miocene, Erdőbénye Kővágó-oldal (Hungary) Middle Miocene

and carpological remains, occur in lacustrine marly sediments. The flora is assigned to the Lower Freshwater Molasse (USM = Untere Süßwassermolasse) and is of latest Oligocene age (Chattian; mammal zone MP 29, Mai 1995). The sediments of the fossil site are part of the sub alpine molasse formation "Poudinges du Pélerin", for which palaeoelevation has been reconstructed to be about 300–800 m (Berger 1989).

According to Mai (1995), the flora of Monod-Rivaz can be correlated with the floral complex Eger-Hausham, and is characterized by laurophyllous taxa and many Eocene and early Oligocene floral relics. The most recent palaeoecological and palaeoclimatological analyses of the Swiss molasse floras are given by Berger (1989, 1990, 1998). The palaeoenvironmental reconstruction presented here (Appendix A). is based on the floral list given by Berger (1994) The leaf physiognomic composition of the fossil leaf assemblage was scored from original voucher specimens at the "Musée Cantonal de Géologie" in Lausanne/Switzerland (Tab. 1). Mostly several specimen of each taxon were scored. However, a few taxa were represented by only one specimen, whereas others could not be scored at all due to fragmentation.

Schrotzburg

Close to the western shore of Lake Constance in southern Germany (Fig. 1) the mountain Schienerberg rises about 300 m above the surrounding area. It is built up of slightly consolidated cross-laminated

alpine chain. The sediments were deposited during the Upper Freshwater Molasse (OSM = Obere Süßwassermolasse). The stratigraphic age of the plant bearing marls is suggested to be at the transition from mammal zone MN 6 to MN 7 (Giersch 2004). The absolute age of the marls was determined to be 14.6 ± 0.6 Ma (Lippolt et al. 1963), using bentonite (Hofmann 1951). Gregor (1982) assigned the Schrotzburg flora to his phyto-stratigraphical zone "OSM-3b", so the flora can be placed stratigraphically in the Early Serravallian (following German Stratigraphic Commission 2002).

The fossil flora has been known for more than 150 years and has been described by Heer (1855, 1856, 1859, 1865), Würtenberger (1906), Hantke (1954) and Nötzold (1957). According to Mai (1995) this flora can be compared with the floral complex Stare Gliwice – Unterwohlbach, which is characterized by deciduous forests with a low proportion of laurophyllous taxa. At this locality, deciduous trees, which are supplemented by some evergreen subtropical trees, dominate the riparian forests (broad leaved deciduous riparian forest; Boulter & Kvaček 1990). The leaf physiognomic composition of the fossil leaf assemblage was scored using photographs and diagnognostic descriptions published by Hantke (1954), collection material of the "Staatliches Museum für Naturkunde Karlsruhe" (Germany) as well as additional material collected by the authors during several field trips to this locality (Tab. 1 and Appendix B). Several specimens of each taxon were scored.

Erdőbénye Kővágo-oldal

Erdőbénye Kővágó-oldal is located in the Tokaj Mountains in north-eastern Hungary (Fig. 1). Due to alpine tectonics, the Carpathian-Pannonian region shows multiple volcanic phases during the Miocene (Csontos 1995), and the Middle Miocene sediments of the Tokaj Mountains are essentially of volcanic origin. The plant fossils of Erdőbénye Kővágó-oldal are embedded in clayey tuffs with lignite lenses. The stratigraphic position of the flora is suggested to be Sarmatian of Central Paratethys stages (Erdei & Hir 2003) and is therefore probably of Late Serravalian age (German Stratigraphic Commission 2002). Hence, it may be somewhat younger than the Schrotzburg flora.

The Miocene floras of the Tokaj Mountains have been investigated e.g. by Ettingshausen (1853), Kováts (1856), Stur (1867), Unger (1870), Andreánszky (1959), Kvaček and Erdei (2001), and Erdei and Hir (2003). Furthermore, palaeoclimatic estimates of Kővágo-oldal based on the nearest living relatives method (see below) are given in Erdei et al. (in press). According to Mai (1995), the flora of Erdőbénye Kővágó-oldal is a part of the floral complex Erdőbénye, which is characterized by sub- and meso-xerophytic, small leaved dry forests. The palaeovegetation of Erdőbénye Kővágó-oldal is dominated by meso phytic elements (Appendix C). The leaf physiognomic composition of the fossil leaf assemblage was scored by Erdei based on specimens of the Natural History Museum in Budapest (Tab. 1).

PALAEOENVIRONMENTAL ESTIMATES

For the reconstruction of palaeoenvironmental parameters from the fossil floras of Monod-Rivaz, Schrotzburg and Erdőbénye Kővágó-oldal, we used different morphological and taxonomical approaches.

Leaf physiognomy

Leaf physiognomy has been used for a long time to extract environmental conditions from fossil plants, particularly with regard to climate. Bailey and Sinnott (1915, 1916) were the first to recognize a strong correlation between the abundance of woody angiosperm taxa with entire margined leaves in the local vegetation and mean annual temperature; leaves with entire margins are more frequent in warm, tropical vegetation than in cooler, middle latitudes. Since these initial reports, a multitude of other leaf physiognomic characters such as leaf size, shape of leaf base and apex and leaf shape have been investigated in relation to environment (e.g. Wolfe 1979, 1993, Jacobs 1999; for a recent overview see Traiser et al. 2005 and citations therein). Environmental estimates based on physiognomic characteristics of fossil leaf assemblages are mainly derived from the CLAMP (Climate Leaf Analysis Multivariate Program) data set (Wolfe 1993, CLAMP website), which includes extant vegetation predominantly from America.

In the present study, a recently developed calibration data set based on European vegetation (ELPA: European Leaf Physiognomic Approach; Traiser et al. 2005) is used to derive estimates for particular palaeoenvironmental conditions. In contrast to the CLAMP data set, ELPA is a grid based data set, which is compiled from synthetic floral lists of 108 European angiosperm hardwood taxa. A synthetic flora is defined as those taxa whose chorologic distribution maps cover that location for a given geographical location (Klotz 1999, Traiser et al. 2005). The data set consists of 1835 grid cells (0.5° × 0.5° latitude/longitude resolution), allowing the comparison of leaf physiognomic and environmental parameters over a large area in Europe (Traiser et al. 2005). Contrary to CLAMP, only 25 different leaf physiognomic characters are taken into consideration for ELPA (Tab. 1). The definition of leaf characters largely follows Wolfe (1993), with one exception: leaves with an attenuate apex are included to leaves with an acute apex. Leaf size is measured according to the leaf size template in Wolfe (1993). Leaflets of compound leaves are treated as single leaves. The leaf physiognomic characters are derived from descriptions in floristic manuals (Götz 1975, Krüssmann 1976–1978, Godet 1986).

The leaf physiognomic composition of 1835 synthetic floras (Traiser & Mosbrugger 2004a) was calibrated with 14 environmental parameters (Traiser & Mosbrugger 2004b) extracted from the global climate grid data set by New et al. (1999) based on the climate period from 1961 to 1990 (Tab. 2). Most climatic parameters are directly provided by the grid data set e.g. mean annual temperature (MAT) and mean annual precipitation (MAP), whereas others such as the growing season length (GSL) or annual temperature sum (T_{sum}) are calculated from the data set. The annual temperature sum, a measurement category often used in phenology, is defined as the summation of all daily maximum temperatures within a year. The growing season length (GSL) is calculated from the sum of all months with mean temperatures of more than 10°C. Ground frost days (FD) are defined as the frequency of grass minimum temperatures below 0°C (5 cm above ground). Precipitation day frequency (PD) is defined as days with precipitation greater than 0.1 mm. The growing season precipitation (PGS) is calculated as the sum of precipitation of those months with mean temperatures of more than 10°C. The mean annual global radiation (RAD) is a measurement for the short-wave solar radiation input.

As an additional ecological character, an examination of the proportion of evergreen angiosperm taxa in the flora was included in our investigation. For this purpose, each taxon was characterized as evergreen or deciduous, based on data from floristic manuals. Transfer functions for 15 environmental parameters were extracted using different multivariate statistical methods such as multiple linear regression and direct ordination. The statistic characteristics of the transfer functions are given in Table 2.

Multiple linear regression (MLR)

MLR transfer functions were obtained from the ELPA data set by the "forward stepwise regression" technique, which allows the identification of four independent variables (Traiser et al. 2005). Additionally we compiled a MLR transfer function for the portion

Table 2. Statistic characteristics of investigated environmental and ecological parameters of the **ELPA** data set. **RDA** (Redundancy Analysis): ordination transfer functions; **MLR** (multiple linear regression): transfer functions; **r²:** coefficient of determination; **SE**: standard error of estimate; **SE$_R$**: range of standard error of estimate.

No.	Parameter	Abbr.	Unit	ELPA					
				RDA			MLR		
				r²	SE	SE$_R$ (%)	r²	SE	SE$_R$ (%)
1	mean temp. of coldest month	T_{min}	°C	0.85	2.0	8.4	0.84	2.1	8.9
2	ground frost days per year	FD	d	0.83	17.2	9.8	0.86	16.0	9.1
3	mean annual temp.	MAT	°C	0.83	1.1	8.2	0.89	0.9	6.6
4	annual temperature sum	T_{sum}	°C	0.79	366.7	8.8	0.85	313.2	7.5
5	growing season lenght (T > 10°C)	GSL	month	0.68	0.7	8.8	0.72	0.6	8.1
6	max. annual temperature range	ATR	°C	0.55	3.7	14.2	0.66	3.2	12.3
7	mean global radiation	RAD	W/m²	0.52	11.2	11.8	0.70	8.9	9.3
8	mean temp. of warmest month	T_{max}	°C	0.39	1.7	13.5	0.55	1.7	11.8
9	precipitation of driest month	P_{min}	mm	0.34	9.8	9.1	0.45	8.9	8.3
10	precipitation of 3 driest consec. months	P_{3min}	mm	0.33	31.2	9.2	0.44	28.4	8.4
11	precipitation days per year	PD	d	0.30	21.6	13.4	0.54	17.5	10.9
12	precipitation of growing season (T > 10°C)	PGS	mm	0.26	81.1	7.8	0.31	78.0	7.5
13	mean annual precipitation	MAP	mm	0.24	145.6	8.0	0.26	143.4	7.8
14	precipitation of wettest month	P_{max}	mm	0.14	18.1	8.9	0.19	17.5	8.6
15	portion of evergreen taxa in the veg.	eg	%	0.85	2.8	6.1	0.86	2.7	5.9

of evergreen angiosperm leaves within the vegetation (Traiser 2004):

[1]   eg = –24.59 + (1.04 * lw_3) +
        + (0.41 * ma_enti) +
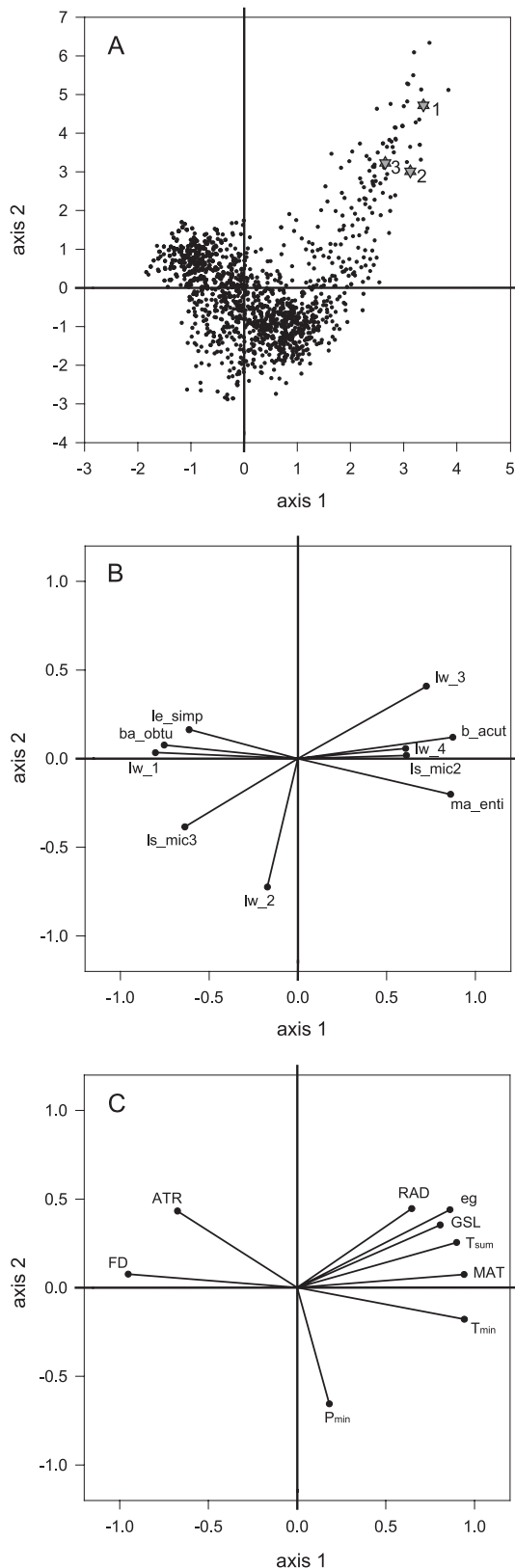   + (0.56 * lw_5) + (1.72 * ls_lep2)

r^2 = 0.86; SE = 2.7; SE$_R$ = 5.9; P-value < 0.00001; F-value = 2845 (abbreviations see text below and Tables 1, 2)

Redundancy analysis (RDA)

In contrast to MLR, ordination methods, such as RDA, analyse the correlation between all leaf physiognomic characters and environmental variables simultaneously. Ordination is the arrangement or "ordering" of data along gradients. Ordination primarily endeavours to represent sample and species relationships as faithfully as possible in a low-dimensional space (Gauch 1982). The main principle of ordination is to project the data from a multidimensional space, spanned by all considered variables, onto fewer dimensions. Thus, ordination is a reduction of dimensions, and data can easily be visualised for analysis of qualitative and quantitative relationships.

In order to choose an adequate ordination technique i.e. a statistically robust method, which separate signals from noise, the response model (monotonic, unimodal, bimodal) of the investigated parameters has to be tested (Jongman et al. 1995). The length of environmental gradients, which are inherent in a data set, plays a decisive role in the determination of the respective response model. The length of environmental gradients is expressed in standard deviation units (SD) of species turnover (ter Braak & Smilauer 1998). It is a measure of the "length" of an ecological gradient or ordination axis, in terms of parameter composition: A gradient length of SD > 4 corresponds to a clear uni-modal distribution of the data, whereas short gradients of SD < 3 represents a monotonic response model (ter Braak & Smilauer 1998). The ELPA-data set is (like the CLAMP-data set) characterized by relatively short environmental gradients (ELPA: SD ~ 0.5). "Thus if the community variation is within a narrow range, the linear ordination methods – Principal Component Analysis (PCA) and redundancy analysis – are appropriate" in ter Braak and Prentice (1988). Even though in univariate statistics many pair plots of leaf physiognomic and environmental parameters, e.g. leaf base cordate – mean annual temperature, show a non-linear relationship (e.g. Green 2006) the response model produced by multivariate ordination methods in ELPA (and also CLAMP) is by construction linear, whether or not the underlying pair wise relationships between the variables are linear. An overview to this topic is recently given in Green (2006). Due to the short environmental gradient length in the ELPA-data set, the data have to be analysed by Redundancy Analysis (RDA), which represents the canonical form of PCA (ter Braak & Smilauer 1998). This direct ordination method was carried out using the software package "CANOCO 4.02". Default settings were used throughout. The ordination plots of the ELPA data are presented in Figure 2. Based on the ordination, 15 environmental and ecological parameters were estimated using polynomial functions of second degree as transfer functions (Wolfe 1993, 1995). By calculating the residuals of the estimation y_{est} and the real value y_{real} of the environmental parameter the quality of each transfer function was evaluated. To quantify the quality of the transfer functions, different parameters of measurement are used: (1) coefficient of determination (r^2), (2) standard error of estimation (SE: formula [2]) and (3) the ratio of SE to the total range of the environmental parameter (SE$_R$: formula [3]), see Table 2.

$$[2] \quad SE = \sqrt{\frac{\sum (y_{est} - y_{real})^2}{n-1}}$$

$$[3] \quad SE_R = \frac{SE}{y_{real(max)} - y_{real(min)}} \times 100\%$$

with

SE	: standard error of estimate
SE_R	: ratio of standard error of estimate
y_{est}	: estimated value of a given environmental parameter
y_{real}	: real value of a given environmental parameter
$y_{real(max)}$	: maximum of the real value in the calibration data set
$y_{real(min)}$	: minimum of the real value in the calibration data set
n	: number of sites in the calibration data set

Nearest living relatives

As an alternative to the use of physiognomic traits of vegetation, nearest living relatives of fossil plants may be used for palaeoclimatic reconstructions (Heer 1859, 1868, MacGinitie 1941, Axelrod & Bailey 1969, Hickey 1977, Chaloner & Creber 1990). Techniques that are based on this approach, such as the coexistence approach (CA) used here (Mosbrugger & Utescher 1997, assume that the climatic requirements of a fossil taxon are more or less–similar to its closest living relative. In case of the CA, the palaeoclimatic estimates are obtained by determining the climatic coexistence interval of as many as possible of the nearest living relatives of the constituent fossil plant community. Climatic parameters for the individual NLRs were taken from the CLIMBOT database on which the CA is based (Mosbrugger & Utescher 1997). In this study, the coexistence intervals of six palaeoclimatic parameters are determined on the basis of the floristic composition of the three fossil floras (see Tabs 3, 4, 5; Appendix A-C).

Estimates based on previous studies

Previously published palaeoclimatic estimates for the three fossil floras (Monod-Rivaz – Heer 1865, Berger 1989; Schrotzburg – Heer 1865, Hantke 1954, 1982; Erdőbénye – Andreánszky 1959) are compared to our results based on the leaf physiognomic and nearest living relative approach.

RESULTS

REDUNDANCY ANALYSIS (RDA) OF LEAF PHYSIOGNOMY

Figure 2 shows the RDA triplot (site scores, leaf character scores and environmental scores) of the analysis of the ELPA-dataset. The first four axes explain $\lambda_1 = 41.0\%$, $\lambda_2 = 11.4\%$, $\lambda_3 = 3.5\%$ and $\lambda_4 = 2.7\%$ of the variance within the data set. To extract the transfer functions all calibrations were carried out based on anal-

Fig. 2. Ordination plots of the first two axes based on Redundancy Analysis (RDA); eigenvalues (**s**): axis 1: s = 0.410, axis 2: s = 0.114; **A** – site scores with 3 fossil sites as passive samples: – **1** Monod-Rivaz, – **2** Schrotzburg, – **3** Erdőbénye Kővágó-oldal; **B** – leaf physiognomic character scores; only characters with eigenvalues |s| > 0.6 are plotted; for abbreviations see Tab. 1; **C** – environmental scores; only parameters with eigenvalues |s| > 0.6 are plotted; for abbreviations see Tab. 2

ysis of axis 1 versus axis 2 because the main information is inherent in these axes (cumulative percentage variance of leaf physiognomic data: 52.4%; cumulative percentage variance of leaf physiognomic-environment relation: 82.9%). All three fossil sites are clearly within the leaf physiognomic character space covered by the ELPA data set, even though they are not close to the origin. With regard to the leaf physiognomic composition, the origin of the triplot corresponds to present day eastern-central European (sub-continental) leaf physiognomy (Traiser 2004). In contrast, the leaf physiognomic compositions of the fossil floras (Fig. 2A) show close similarity to present day Mediterranean vegetation, which is plotted in the upper right quadrant of the triplot (Traiser 2004).

GENERAL LEAF PHYSIOGNOMIC
CHARACTERISTICS OF THE FOSSIL FLORAS

The leaf physiognomic composition of the fossil assemblages is listed in Table 1. Compared with present day European vegetation, all three fossil leaf assemblages are characterized by a relatively high proportion of long narrow leaves (lw_3 and lw_4) with acute leaf bases (ba_acut) and relatively small leaves (ls_mic2 and smaller; Fig. 2A, B). Thus, all investigated fossil floras show high similarity with extant Mediterranean leaf assemblages (Traiser 2004). The physiognomic compositions of the Miocene leaf assemblages (Schrotzburg and Erdőbénye Kővágó-oldal) are quite similar, whereas Monod-Rivaz has a higher proportion of long narrow leaves. The environmental conditions implied by the leaf assemblages include relatively high radiation (RAD), long growing season (GSL) and high temperature sum per year (T_{sum}; Fig. 2A, C). Furthermore, all fossil leaf assemblages are characterized by a relatively high proportion of evergreen taxa (vector *eg* in Fig. 2C). As can be seen from the ordination plots (Fig. 2B, C) evergreen leaves have a characteristic combination of leaf traits consisting of a specific length/width ratio, shape of leaf base, and leaf size. The MLR transfer function for evergreen leaves also includes the proportion of entire leaf margins (ma_enti in formula [1]). This characteristic combination of evergreen leaf traits here is here referred to "evergreen character syndrome". According to Traiser (2004) the proportion of evergreen taxa in the vegetation proves to be a significant eco-

logical parameter in the ELPA data set (see formula [1] and Tab. 2) because of its strong correlation with leaf physiognomic characteristics ($r^2 = 0.85$ (RDA), $r^2 = 0.86$ (MLR)), and therefore seems suitable for use in palaeoecological reconstruction.

PALAEOENVIRONMENTAL ESTIMATES

Monod-Rivaz

Temperature

The estimates of mean annual temperature based on CA and RDA are close or overlap with previous estimates from Berger (1989) for the Lower Freshwater Molasse (see Tab. 3 and Fig. 3). MLR transfer functions predict distinctly warmer conditions for T_{min} and MAT in comparison our estimates. Both leaf physiognomic approaches, RDA and MLR, indicate quite long growing season length (GSL). Heer (1865) predicted significantly higher temperatures in particular for T_{min} and MAT than our palaeoclimatic investigations (with exception of MLR), a trend also observed by other studies (e.g. Gregor 1982).

Precipitation

The estimates of MAP based on CA are in agreement with the prediction by Berger (1989). Estimates of P_{min} and P_{max} from CA, MLR and RDA consistently indicate very dry and very humid months within the year. In general, all precipitation estimates based on the ELPA data set provide significantly lower values than other approaches (Tab. 3).

General characterization of environmental conditions

According to these results, the climatic conditions of the Late Oligocene locality Monod-Rivaz can be qualitatively characterized as warm with (seasonally?) changing humidity. The estimates for precipitation based on the CA and RDA both show dry and humid periods within the year, maybe pointing to a marked seasonality in precipitation. The growing season (GSL) with approximate 11 month was interrupted only for a few weeks in the year and temperatures, which led to ground frost (FD) presumably did not occur (Tab. 3). Owing to the leaf physiognomic composition of the flora, the proportion of evergreen taxa (eg) is estimated by ELPA to be about 40% (MLR) to 45% (RDA), which represents the high-

Table 3. Palaeoclimatic and ecological estimates of 15 parameters of Monod-Rivaz. Abbreviations of parameters see Tab. 2. **CA** – Coexistence Approach; **ELPA** – European Leaf Physiognomic Approach; **MLR** – multiple linear regression; **NLR** – nearest living relative method; **RDA** – Redundancy Analysis; **SE** – standard error of estimate; **USM** – Lower Freshwater Molasse.

| No. | Parameter | Unit | Leaf physiognomy ELPA | | | | NLR CA | | Berger (1989) USM | Heer (1865) USM | New et al. (1999) present day climate |
			MLR	SE	RDA	SE	min	max			
1	MAT	°C	21.6	± 0.9	16.8	± 1.1	15.6 – 16.6		~ 17.0–18.0	~ 20.0–21.0	8.0
2	T_{min}	°C	17.7	± 2.0	8.2	± 2.0	5.0 – 7.0			~ 13.2–13.3	−0.6
3	T_{max}	°C	26.4	± 1.4	25.2	± 1.7	24.7 – 28.1			~ 27.5–28.3	16.8
4	ATR	°C	17.6	± 3.2	28.5	± 3.7					25.8
5	T_{sum}	°C	5131	± 313	6267	± 367					2933
6	FD	days	0	± 16	1	± 17					115
7	MAP	mm	721	± 143	679	± 146	828 – 1327		> 1100		1182
8	P_{min}	mm	0	± 9	9	± 10	5 – 13				87
9	P_{max}	mm	81	± 18	111	± 18	160 – 170				120
10	PGS	mm	309	± 78	524	± 81					537
11	P_{3min}	mm	0	± 28	59	± 31					264
12	PD	days	52	± 18	82	± 22					178
13	GSL	month	11.9	± 0.6	10.7	± 0.7					4.0
14	RAD	W/m²	171	± 9	178	± 11					118
15	eg	%	40	± 2.8	45	± 2.7					4

est value of all three investigated fossil leaf assemblages. The high proportion of evergreen taxa indicates a drastic change in vegetation composition since the Late Oligocene in this region, where today only 4% evergreens are present in the hardwood vegetation (Tab. 3).

Schrotzburg

Temperature

The temperature estimates based on RDA and those published by Hantke (1954, 1982) are in good agreement for MAT, T_{max} and T_{min} (Tab. 4 and Fig. 3). In contrast, CA predicts considerably lower temperatures for T_{min} and higher temperatures for T_{max}. Again, MLR transfer functions predict distinctly warmer conditions for T_{min} and MAT in comparison with most other techniques. The same is true for estimates given by Heer (1865) for the upper fresh water molasses (OSM).

Precipitation

The estimates of MAP based on CA are slightly lower than the prediction by Hantke (1954, 1982) but both indicate high values of more than 1100 mm. P_{min} indicates no month that is markedly dry within the year. Estimates of precipitation derived from RDA and MLR again predict significantly lower values than other approaches (Tab. 4).

General characterization of environmental conditions

The palaeoclimatic condition of the Middle Miocene Schrotzburg locality can be characterized as warm and humid. According to CA, the estimates for precipitation indicate almost no seasonality. The growing season (GSL) is long, thought slightly shorter than in Monod-Rivaz, and ground frost (FD) occurred rarely if ever. This result agrees with estimates given by Hantke (1954) that "frost occurred in this region during the vegetation period scarcely or very seldom". The leaf physiognomic composition of the Schrotzburg flora indicates a proportion of about 1/3 evergreen hardwoods in the vegetation. This is a decrease of about 10% in comparison to the Late Oligocene locality Monod-Rivaz.

Erdőbénye Kővágó-oldal

Temperature

The temperature estimates based on CA and RDA show good agreement (Tab. 5 and Fig. 3). These estimates are slightly lower than the values given by Andreánszky (1959) for Erdőbénye. The predictions based on MLR show lower values for T_{max} and higher values for T_{min} compared with other approaches, whereas the MAT estimate is in good agreement with the predictions of CA and RDA.

Table 4. Palaeoclimatic and ecological estimates of 15 parameters of Schrotzburg. Abbreviations of parameters see Tab. 2.; **CA**: Coexistence Approach; **ELPA**: European Leaf Physiognomic Approach; **MLR**: multiple linear regression; **NLR**: nearest living relative method; **OSM**: Upper Freshwater Molasse; **RDA**: redundancy analysis; **SE**: standard error of estimate; * temperatures reduced to palaeoelevation of 150m a.s.l according to Hantke (1980).

No.	Parameter	Unit	Leaf physiognomy ELPA MLR	SE	RDA	SE	NLR CA min	max	Hantke (1954) Schrotzburg	Hantke (1982) OSM	Heer (1865) OSM	New et al. (1999) present day climate
1	MAT	°C	18.4	± 0.9	16.0	± 1.1	14.4 –	15.6	~ 16	15.5–16.0	~ 18 – 19	* 11.6
2	T_{min}	°C	12.2	± 2.0	8.8	± 2.0	3.7 –	4.4	7–8	5–6	~ 11.8 – 12.8	* 2.5
3	T_{max}	°C	25.5	± 1.4	23.8	± 1.7	25.6 –	26.1	~ 24		~ 25.1 – 25.7	* 20.6
4	ATR	°C	28.4	± 3.2	25.5	± 3.7						25.6
5	T_{sum}	°C	5409	± 313	5843	± 367						3193
6	FD	days	0	± 16	5	± 17						110
7	MAP	mm	817	± 143	774	± 146	1122 –	1237	1300 – 1500	1300 – 1500		999
8	P_{min}	mm	28	± 9	22	± 10	42 –	61				63
9	P_{max}	mm	123	± 18	107	± 18	131 –	134				120
10	PGS	mm	510	± 78	503	± 81						519
11	P_{3min}	mm	96	± 28	88	± 31						192
12	PD	days	86	± 18	103	± 22						181
13	GSL	month	8.1	± 0.6	9.7	± 0.7						5.0
14	RAD	W/m²	172	± 9	164	± 11						110.2
15	eg	%	31	± 2.8	34	± 2.7						2

Precipitation

The estimates of MAP based on CA are slightly higher than the predictions of Andreánszky (1959), whereas RDA and MLR again predict significantly lower values (Tab. 5). According to CA there is seasonality in precipitation but in general the climate remains humid. Compared with Schrotzburg, all methods indicate lower minimum precipitation.

Table 5. Palaeoclimatic and ecological estimates of 15 parameters of Erdőbénye Kővágó-oldal. Abbreviations of parameters see Tab. 2. **CA** – Coexistence Approach; **ELPA** – European Leaf Physiognomic Approach; **MLR** – multiple linear regression; **NLR** – nearest living relative method; **RDA** – redundancy analysis; **SE** – standard error of estimate

No.	Parameter	Unit	Leaf physiognomy ELPA MLR	SE	RDA	SE	NLR CA min	max	Andreánszky (1959) Erdőbénye	New et al. (1999) present day climate
1	MAT	°C	14.8	± 0.9	15.1	± 1.1	15.6 –	16.6	17	9.0
2	T_{min}	°C	11.9	± 2.0	6.6	± 2.0	5.0 –	5.8	9	–3.2
3	T_{max}	°C	19.0	± 1.4	23.6	± 1.7	24.7 –	26.1	26	19.1
4	ATR	°C	13.6	± 3.2	27.2	± 3.7				31.6
5	T_{sum}	°C	4256	± 313	5603	± 367				3434
6	FD	days	26	± 16	23	± 17				120
7	MAP	mm	820	± 143	698	± 146	897 –	1032	857	603
8	P_{min}	mm	16	± 9	19	± 10	8 –	24		30
9	P_{max}	mm	99	± 18	105	± 18	118 –	130		87
10	PGS	mm	270	± 78	487	± 81				339
11	P_{3min}	mm	51	± 28	81	± 31				96
12	PD	days	126	± 18	108	± 22				152
13	GSL	month	8.3	± 0.6	9.3	± 0.7				5.0
14	RAD	W/m²	119	± 9	160	± 11				125
15	eg	%	37	± 2.8	31	± 2.7				2

General characterization of environmental conditions

Altogether, the palaeoclimate at Erdőbénye Kővágó-oldal is similar to that of Schrotzburg and can also be characterized as warm and humid. There is lower precipitation, however than at Schrotzburg, and a clear seasonality. Although the growing season length is similar to that of Schrotzburg, a clear increase of days with ground frost (FD) to approximately one month is suggested by leaf physiognomy, which implies a greater seasonality. Nevertheless, the proportion of evergreen hardwoods in the vegetation (about 1/3) is similar to that of Schrotzburg.

DISCUSSION

LEAF PHYSIOGNOMIC COMPOSITION OF THE FOSSIL FLORAS

With regard to the overall leaf physiognomic composition of the fossil assemblages, Schrotzburg and Erdőbénye Kővágó-oldal are very similar whereas the flora of Monod-Rivaz is distinct (Fig. 2A). This difference in leaf physiognomic composition is mainly the result of different proportion of evergreen leaves in the vegetation (this is discussed below). Nevertheless, there are also similarities between Monod-Rivaz and Erdőbénye Kővágó-oldal with regard to the relative proportion of small leaves whereas the flora of Schrotzburg is characterized by slightly larger average leaf size (Tab. 1). The difference in leaf size may be explained by the seasonality of annual precipitation: both localities Monod-Rivaz and Erdőbénye Kővágó-oldal, which have relatively small leaves, show (according to CA) a change between humid and dry seasons with monthly minimum precipitation of less than 25 mm (cf. Tabs 3–5). In contrast, the precipitation estimates for Schrotzburg, which has relatively large leaves, indicate constant humid conditions throughout the year. Furthermore, the water supply is not a limiting factor within the riparian forest of Schrotzburg so it is reasonable that large leaves were predominant in the palaeovegetation. According to Burnham et al. (2001) and Kowalski & Dilcher (2003) palaeoclimate predictions based on leaf physiognomy (particularly with regard to leaf margin) might underestimate temperature in riparian forests, however, according to our results this effect is not visible within the riparian forest of Schrotzburg.

The composition of leaf sizes of the investigated fossil floras also provides information on density of palaeo-vegetation. According to Parkhurst and Loucks (1972) and Givnish (1979) there is a high portion of large leaves in dense (warm, moist) vegetation types with predominantly indirect sunlight whereas leaf size is small in thin, open (warm, dry) vegetation types. The occurrence of mosses (*Amblystegium schrotzburgense*) and ferns (*Pteridium oeningense*) in the Schrotzburg flora (Hantke 1954) suggests a relatively dense closed canopy forest, whereas the relatively small leaved floras of Monod-Rivaz and Erdőbénye Kővágó-oldal are characterized by a high portion of trees with preference for open and light dominated forests.

EVERGREEN TAXA

The proportion of evergreen angiosperm taxa within a fossil leaf assemblage is a valuable indicator for the ecological interpretation of palaeofloras. Because this trait has so far only been indirectly inferred for fossil plants by comparison with their NLRs, there is a high uncertainty in the determination of the proportion of evergreen taxa in fossil leaf assemblages. Only a few investigations have attempted to use leaf physiognomy to determine whether evergreen or deciduous leaves predominate in fossil leaf assemblages. Usually, only one (leaf margin entire or toothed) or a few physiognomic characters are taken into account (Givnish 1979, Wolfe & Upchurch 1987, Boyd 1990). However, leaf physiognomy as a whole seems to represent a useful tool for the quantitative estimation of the proportion of evergreen taxa within a given (palaeo-)flora. The parameter "proportion of evergreens (eg)" in the ELPA data set shows one of the best correlations with leaf physiognomy ($r^2 = 0.85$) of all estimated parameters (Tab. 2). In vegetation with a high portion of evergreen leaves, specific physiognomic characters such as proportion of relatively small leaves (lept_2, micr_1), medium length/width ratio (lw_3) and leaves with an acute base (ba_acut; Fig. 2B, C) predominate. On the other hand, vegetation that is dominated by deciduous hardwoods shows leaf characters such as broad leaves (lw_2, lw_1), large leaves (micro_3, mesophyll)

and leaves with a cordate base (ba_emba). This implies the existence of specific leaf physiognomic character syndromes for predominantly evergreen and deciduous floras in extant European vegetation. In terms of ordination methods evergreen and deciduous taxa occupy different areas within the leaf physiognomic character space though these areas may also overlap. However, both strategies in leaf abscission can be discriminated be their own leaf physiognomic character syndromes.

The flora of Monod-Rivaz is characterized by the highest proportion of evergreen angiosperm taxa (45% in RDA), whereas Schrotzburg and Erdőbénye Kővágó-oldal have somewhat lower proportions (34 % and 31 % respectively). The decrease of evergreens reflects the overall change of the European palaeovegetation that took place between the Late Oligocene, the Middle Miocene (e.g. Mai 1995) and today. The difference in the proportion of evergreen leaves between the localities of Schrotzburg and Erdőbénye Kővágó-oldal, which have nearly the same age and same latitude, is too small for further interpretations (RDA-standard error of estimate is approximately 3%; Tab. 2). The estimates for the number of ground frost days (FD) give a hint to lower proportion of evergreens in Erdőbénye Kővágó-oldal as it shows on Tables 4 and 5 a higher number of ground frost days (23 days) than Schrotzburg (5 days).

QUALITY OF ESTIMATES OF DIFFERENT APPROACHES

There is the general problem of how to evaluate the reliability of palaeoclimatic estimates. To supply exact evidence of palaeoclimatic estimates is not possible for any method, however, there are some options to evaluate their degree of reliance: (1) The comparison with other palaeoclimatic reconstruction methods (including estimates from preceding publications) enables us to evaluate which estimations in their entirety seem to be more "reliable" than others (Uhl et al. 2006, submitted); (2) The analysis of residuals by the application of transfer functions to present day data sets such as ELPA. For this, the ELPA data set was divided into a training and a testing data set by random sampling. The transfer functions were generated using the training data set and subsequent applied to the testing data set. The residuals calculated from the estimated and real values allow evaluation of the reliability of transfer functions. According to this residual analysis, it can be stated for example that estimates of MAP and all precipitation related parameters are not as "reliable" as temperature related climatic parameters (Tab. 2) because precipitation is not "satisfyingly" reproduced by transfer functions (Traiser 2004, Traiser et al. 2005); (3) The estimates can be proven in relation to their internal consistency. For example, the combination of high mean annual temperature and short growing season is possible but not very probable; high radiation input (RAD) should lead to high annual temperature sum (T_{sum}) and high mean annual temperature (MAT), if not there is a problem of internal consistency. Furthermore, the consistency of different palaeoclimate reconstruction approaches can be proofed. If, for example a series of fossil localities with different ages are investigated by alternative approaches, the palaeoclimatic trends should show the same direction (e.g. a cooling or warming trend). Based on these evaluations of palaeoclimatic estimates the different approaches are discussed below. However, these evaluations should not imply that the authors have decided which results are "true".

MLR

Although the application of MLR transfer functions leads to consistent results with extant leaf physiognomic data (Traiser et al. 2005) their application to fossil leaf assemblages seem to be less reliable. In general, the palaeotemperature estimates based on MLR transfer functions are warmer than estimates derived from other methods, and therefore should probably be treated with caution. The reasons for this discrepancy may be: (1) The climatic character space of the ELPA-calibration data set has its upper boundaries of temperature close to the inferred palaeotemperatures of the fossil sites (e.g. MAT-maximum is 17.5°C in the ELPA data set; Traiser et al. 2005) and thus the estimates have probably been at least partly extrapolated. The relationships between environmental and leaf physiognomic parameters outside the calibrated character space may be non-linear. Thus, MLR reconstructions based on fossil assemblages close to calibration boundaries may produce unreliable values. (2) The MLR transfer functions used in this study consider only four different leaf physiognomic

characters. Accidental or selective differences of some leaf physiognomic characters in the leaf physiognomic composition of fossil leaf assemblages due to taphonomic effects may have serious consequence for palaeoclimatic estimates based on such methods (Greenwood 1992, 2005, Uhl et al. 2003, Spicer et al. 2005). Therefore, the rather inconsistent results of palaeoclimatic estimates based on MLR transfer functions can probably be attributed to the high sensitiveness of this approach to accidental or selective shifts in the leaf physiognomic compositions of the palaeofloras.

RDA

In general, there is good agreement between temperature estimates derived from RDA and CA, as well as with many estimates in previous publications. In contrast to MLR transfer functions, the ordination method turns out to be more robust against (random?) shifts in the leaf physiognomic composition of the palaeofloras. Owing to the consideration of all 25 investigated leaf physiognomic characters in the palaeoclimatic estimates, accidental or selective shifts in the leaf physiognomic composition have probably only slight influence on the results (Herman & Spicer 1997). Nevertheless, within the ELPA data set, the estimation of precipitation seems not to be as reasonable as the estimation of temperature. Possible reasons for the all in all very low estimates of precipitation may include: (1) the very complex distribution pattern of precipitation within Europe (Traiser 2004, Traiser et al. 2005), which is not reflected by the leaf physiognomic composition of the vegetation and (2) the dominant role of edaphic factors, like the water holding capacity of a soil or local and regional drainage patterns, that override signals from precipitation alone (Traiser et al. 2005). Some of the presented climatic parameters are also estimated by CLAMP – using Canonical Correspondence Analysis (e.g. Herman & Spicer 1997). However, estimates of precipitation using CLAMP show low correlations between actual and estimated parameters, too (Kovach & Spicer 1996). The application of RDA to the ELPA data set, however, does provide the ability to estimate some new environmental parameters such as ground frost frequency, annual temperature sum and proportion of evergreen angiosperms in the vegetation. All these new parameters are characterized by high coefficients of determination (Tab. 2) and thus their estimates represent reliable values contrary to estimates of precipitation, which have throughout low coefficients of determination.

A critical point of transfer functions (MLR as well as RDA) derived from the ELPA data set may be their application to fossil floras, which are relatively old in comparison to the modern vegetation used for calibration. To evaluate this, the applicability of RDA transfer functions to Paleogene floras from Spitsbergen was tested and compared to alternative palaeoclimate reconstruction methods (Uhl et al. submitted). For the study presented here it can be stated: the investigated fossil floras are clearly within the leaf physiognomic character space covered by the ELPA data set, at least with regard to the first two ordination axes, which are used to calibrate the RDA transfer functions. Thus the leaf physiognomic composition of the fossil floras is represented by the ELPA data set even though there are only a few (sub)tropical taxa within extant European vegetation. The proportion of NLRs in the extant European vegetation is irrelevant for the application to fossil floras if the fossil leaf assemblages are within the leaf physiognomic character space covered by calibration data set. Nevertheless, to solve the problem if a calibration data set only applies for relative young floras (with a high proportion of modern taxa) or not, additional investigations are needed. For this, we have to distinguish which part of the variance of leaf physiognomic-environmental relationship of a calibration data set is constrained by phylogenetic relationships (i. e. the vegetation history of the calibration area) and which part is really explained by environment. A study, which is estimating the phylogenetic inertia (Diniz-Filho et al. 1998, Desdevises et al. 2003) within the ELPA data set, is in development.

COEXISTENCE APPROACH

As an alternative to the use of leaf physiognomic traits, palaeoclimatic estimates based on CA provide generally similar values to those provided by previous studies and also to the results of RDA applied to leaf physiognomic data. The estimates for MAT of the fossil site Schrotzburg have already been discussed in Uhl et al. (2006). Estimates based on CA generally seem to show a shift of the

minimum (T$_{min}$) and maximum temperatures (T$_{max}$) toward the extremes as compared with ELPA. This is true in particular for estimates of Schrotzburg where T$_{min}$ is cooler and T$_{max}$ is warmer than estimates given by RDA (see Fig. 3).

A popular fallacy is that palaeoclimatic estimates based on the nearest living philosophy such as CA would be invalid or not robust over evolutionary timescales. Fact is that if the method is applied prudent to pre-Quaternary fossil floras the intervals of coexistence simply get broader because (1) NLRs of fossils can be assigned only on genus or family level instead of species level and (2) the number of taxa, which can be analysed decrease because the NLR is unknown (Uhl et al. submitted). Thus, in theses cases the estimates of CA do not give very detailed climatic information (e.g. an

interval of coexistence for MAT from 10–18°C) but the results remain still "realistic".

PALAEOCLIMATE ESTIMATES IN GENERAL

Some general trends in palaeoclimate estimates of the fossil sites can be observed: (1) Estimates for palaeotemperatures based on leaf physiognomy show better agreement with other approaches than estimates for precipitation. This circumstance has already been noted for climate estimates in the extant vegetation of Europe (Traiser et al. 2005). Nevertheless, the general palaeoclimatic trends of the investigated fossil floras are consistent with present theory of European climatic evolution during the Cenozoic (e.g. Mosbrugger et al. 2005). (2) The palaeoclimate estimates in general indicate lower temperatures than former
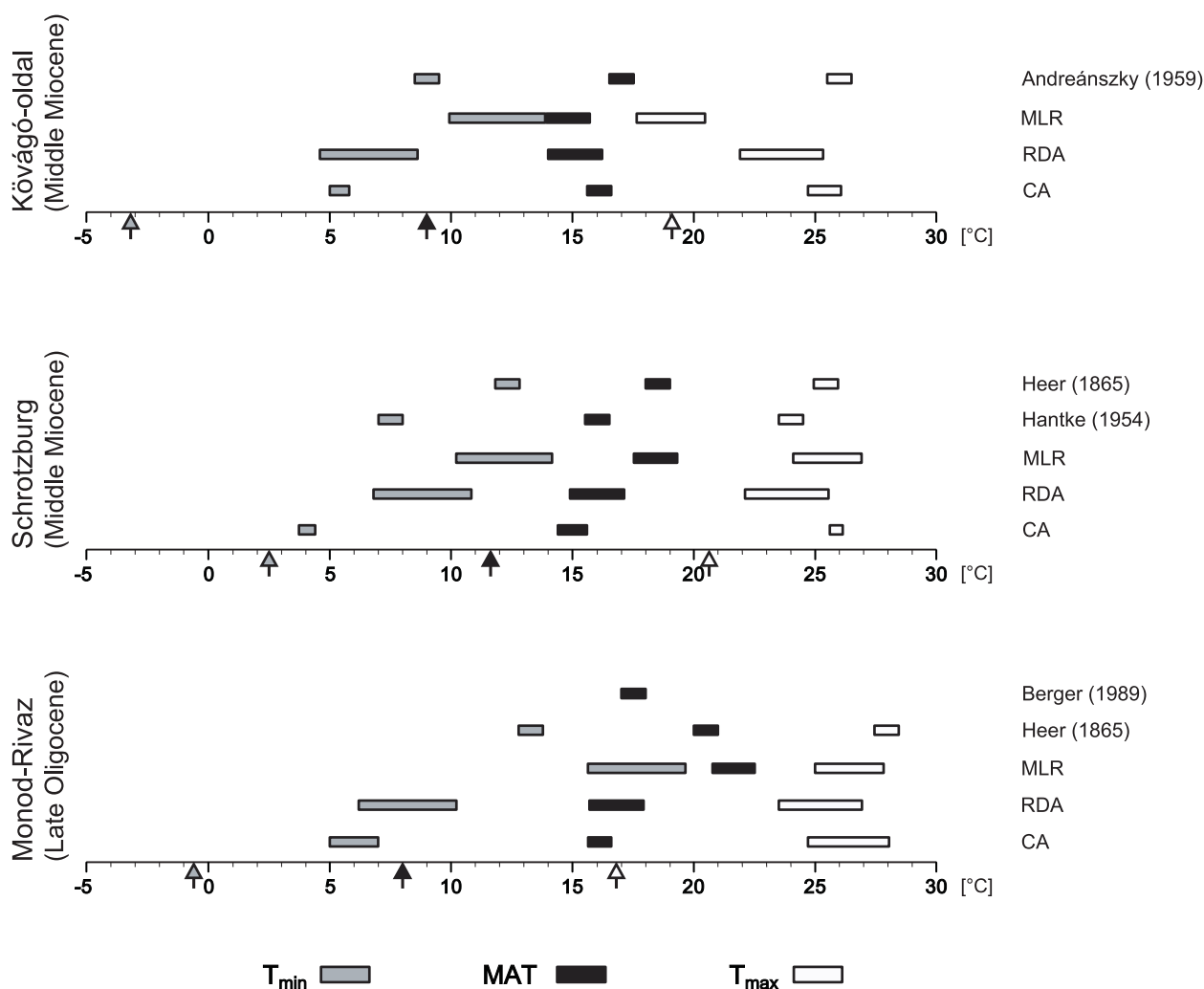
Fig. 3. Palaeotemperature estimates of the three fossil sites according to different methods: T$_{min}$ (mean temperature of coldest month) light grey, MAT (mean annual temperature), black; T$_{max}$ (mean temperature of warmest month), dark grey; CA (Coexistence Approach), RDA (Redundancy Analysis), MLR (multiple linear regression) and previous studies. The arrows on the abscissa indicate the present day values for temperature parameters of the localities

investigations predicted. (3) The highest variance in reconstructed palaeotemperatures occurs between minimum temperatures (T_{min}) whereas MAT and maximum temperatures (T_{max}) show greater consistency (Fig. 3). (4) Although it is not possible to draw far-reaching conclusions from two fossil localities of the Middle Miocene, a European east–west gradient of minimum temperature parameters such as T_{min} and ground frost days probably becomes apparent according to our results. The minimum temperatures show greater differences between the west and the east than maximum temperatures. Correspondingly the minimum precipitation is clearly more affected by this gradient than maximum precipitation. If this climatic east–west gradient is simply accidental or already existent in the Middle Miocene has to be proofed in future investigations.

CONCLUSIONS

The comparison of the palaeoenvironmental estimates based on different approaches shows that leaf physiognomy is a valuable indicator of ancient conditions. In general, estimates based on leaf physiognomy support existing palaeoclimatic studies.

The application of ordination methods such as RDA, based on a newly developed European leaf physiognomic calibration data set (ELPA), seems to be in good agreement with palaeoclimatic estimates derived from other palaeobotanical techniques. Estimates of temperature show better agreements with other approaches than precipitation. Nevertheless, in contrast to their results when applied to extant vegetation, MLR-transfer functions reproduce less reliable palaeoenvironmental estimates as compared to RDA.

Leaf physiognomy contains a lot of "new" information, which is at this time scarcely explored. An example of this is the physiognomic character complex identifying evergreen leaves, which seems successfully to estimate the proportion of evergreens in a flora. Further studies should elucidate whether a similar relationship can also be detected in other regions and calibration data sets.

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198

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APPENDIX A

List of fossil taxa of Monod-Rivaz; column 4 indicate, which taxa are included for leaf physiognomic analysis; column 5 lists only those nearest living relatives (NLRs), which were used in the coexistence approach; * indicate that NLRs or their climatic ranges are unknown.

No.	Fossil taxa (Heer 1855–1859)	Fossil taxa (Berger 1994)	Leaf phys.	NLR
		MONOD-RIVAZ		
1	*Acer dasycarpoides* Heer	*Acer tricuspidatum* Bronn	X	*Acer saccharinum*
2	*Acer rueminianum* Heer	*Acer rueminianum* Heer	X	*Acer*
3	*Alnus nostratum* Unger	*Alnus nostratum* Unger	X	*Alnus*
4	*Carpinus grandis* (Unger) Heer	*Carpinus grandis* (Unger) Heer	X	*Carpinus*
5	*Cinnamomum lanceolatum* (Unger) Heer	*Cinnamomum lanceolatum* (Unger) Heer	X	*Cinnamomum*
6	*Cinnamomum spectabile* Heer	*Cinnamomum* sp.	X	*Cinnamomum*
7	*Clethra helvetica* Heer	? Theaceae	X	Theaceae
8	*Cornus rhamnifolia* O. Weber	*Berchemia multinervis* (A. Braun) Heer	X	*Berchemia*
9	*Dalbergia primaeva* Unger	? *Trigonobalanopsis*	X	*
10	*Dryandroides hakaefolia* Unger	? *Engelhardia*	X	*Engelhardia*
11	*Elaeodendron gaudini* Heer	? Vitaceae	X	*
12	*Eucalyptus oceanica* Unger	*Laurophyllum* sp 1.	X	Lauraceae
13	*Ficus morloti* Unger	*Dicotilophyllum* sp.	X	*
14	*Ficus populina* Heer	*Populus zaddachii* Heer	X	*Populus* sect. *Leucoides*
15	*Ilex sphenophylla* Heer	?	X	*
16	*Juglans bilinica* Unger	*Juglans bilinica* Unger	X	*Juglans*
17	*Laurus primigenia* Unger	*Laurophyllum* sp 2.	X	Lauraceae
18	*Laurus swaszowiciana* Unger	*Laurophyllum* sp 3.	X	Lauraceae
19	*Leguminosites sclerophyllus* Heer	?	X	*
20	*Palaeolobium sotzkianum* Unger	Theaceae, Lauraceae	X	Theaceae, Lauraceae
21	*Planera ungeri* Ettingshausen	*Zelkova zelkovifolia* (Unger) Bůžek & Kotlaba	X	*Zelkova carpinifolia, Z. serrata*
22	*Rhamnus gaudini* Heer	*Alnus gaudini* (Heer) Knobloch & Kvaček	X	*Alnus nitida*
23	*Rhopala aneimiaefolia* Heer	? *Celtis*	X	*Celtis*
24	*Rhus brunneri* Fischer-Ooster & Heer	? *Ulmus drepanodonta sensu* Walther	X	*Ulmus*
25	*Salix arcinervia* O. Weber	? *Salix varians* Goeppert *sensu* Walther	X	*
Sum of taxa			25	15

APPENDIX B

List of fossil taxa of Schrotzburg; column 3 indicate, which taxa are included for leaf physiognomic analysis; column 4 lists only those nearest living relatives (NLRs), which were used in the coexistence approach; * indicate that NLRs or their climatic ranges are unknown.

No.	Fossil taxa (Hantke 1954, 1980)	Current taxonomy	Leaf phys.	NLR
	SCHROTZBURG			
1	*Acer angustilobum* Heer		X	*Acer trautvetteri, A. pseudo-platanus*
2	*Acer trilobatum* (Sternberg) A. Braun	*Acer tricuspidatum* Bronn	X	*Acer saccharinum*
3	*Alnus rotunda* Goeppert		X	*Alnus*
4	*Berchemia multinervis* (A. Braun) Heer		X	*Berchemia*
5	*Castanea atavia* Unger		X	*Castanea sativa*
6	*Cinnamomum polymorphum* (A. Braun) Heer	*Daphnogene polymorpha* (A. Braun) Ettingshausen	X	Lauraceae
7	*Comptonia oeningensis* A. Braun		X	*Comptonia peregrina*
8	*Cornus graeffii* (Heer) Hantke		X	*Cornus*
9	*Crataegus longepetiolata* Heer		X	*Crataeagus*
10	*Diospyros brachysepala* A. Braun		X	*
11	*Fagus attenuata* Goeppert	*Fagus* sp.	X	*Fagus*
12	*Juglans acuminata* A. Braun		X	*Juglans*
13	*Liquidambar europaea* A. Braun		X	*Liquidambar styraciflua*
14	*Magnolia ?rueminiana* (Heer) Hantke		X	*Magnolia acuminata*
15	*Myrica serotina*		X	*Myrica*
16	*Persea princeps* (Heer) Schimper		X	*Persea*
17	*Phoebe integriuscula* (Heer) Hantke		X	Lauraceae
18	*Platanus aceroides* Goeppert		X	*Platanus*
19	*Podogonium lyellianum* Heer	*Podocarpium podocarpum* (A. Braun) Herendeen	X	*
20	*Populus balsamoides* Goeppert		X	*Populus balsamifera*
21	*Populus mutabilis*		X	*Populus euphratica*
22	*Populus populina* (Brongniart) Knobloch		X	*Populus*
23	*Pterocarya castaneaefolia* (Goeppert) Menzel		X	*Pterocarya fraxinifolia*
24	*Quercus mediterranea* Unger		X	*Quercus ilex, Q. coccifera*
25	*Rosa* sp.		X	*
26	*Salix angusta* A. Braun		X	*
27	*Salix lavateri* A. Braun		X	*
28	*Sapindus falcifolius* A. Braun		X	*
29	*Smilax sagittifera* Heer emend. Hantke		X	*
30	*Ulmus longifolia* Unger		X	*Ulmus*
31	*Zelkova ungeri* Kováts	*Zelkova zelkovifolia* (Unger) Bůžek & Kotlaba	X	*Zelkova carpinifolia, Z. serrata*
	Sum of taxa		31	23

APPENDIX C

List of fossil taxa of Erdőbénye Kővágó-oldal; column 3 indicate, which taxa are included for leaf physiognomic analysis; column 4 lists only those nearest living relatives (NLRs), which were used in the coexistence approach; * indicate that NLRs or their climatic ranges are unknown.

No.	Fossil taxa (Erdei & Hir 2003)	Leaf phys.	NLR
	ERDŐBÉNYE KŐVÁGÓ-OLDAL		
1	*Acer integerrimum* (Viviani) Massalongo	X	*Acer cappadocicum*
2	*Acer tricuspidatum* Bronn	X	*Acer saccharinum*
3	*Alnus julianaeformis* (Sternberg) Kvaček & Goly	X	*Alnus japonica, A. trabeculosa*
4	*Berberis andreanszkyi* Kvaček & Erdei	X	*
5	*Buxus pliocaenica* Saporta & Marion	X	*Buxus*
6	*Carpinus grandis* (Unger) Heer	X	*Carpinus*
7	*Carya serraefolia* (Goeppert) Kräusel	X	*Carya cordiformis*
8	*Celtis trachytica* Ettingshausen	X	*Celtis*
9	*Dicotylophyllum* sp.	X	*
10	*Diospyros* aff. *pannonica*	X	*
11	*Diospyros banensis*	X	*
12	*Diospyros brachysepala* A. Braun	X	*
13	cf. *Diospyros* sp.	X	*
14	*Engelhardia orsbergensis* (Wessel & Weber) Jähnichen, Mai & Walther	X	*Engelhardia*
15	*Fagus haidingeri* Kováts	X	*Fagus longipetiolata, F. lucida*
16	*Ilex parschlugiana* Unger	X	*Ilex*
17	Lauraceae gen. et sp.	X	*
18	*Liquidambar europaea* A. Braun	X	*Liquidambar styraciflua*
19	*Parrotia pristina* (Ettingshausen) Stur	X	*
20	*Pistacia lentiscoides* Unger	X	*
21	*Platanus* sp.	X	*Platanus*
22	*Podocarpium podocarpum* (A. Braun) Herendeen	X	*
23	*Populus* sp.	X	*Populus*
24	*Prunus* cf. *laurocerasus*	X	*Prunus laurocerasus*
25	*Pterocarya paradisiaca* (Unger) Il'inskaya	X	*Pterocarya fraxinifolia*
26	*Quercus drymeja* Unger	X	*Quercus*
27	*Quercus kubinyi* (Kováts) Czeczott	X	*Quercus* sect. *Cerris*
28	*Quercus mediterranea* Unger	X	*Quercus coccifera, Q. ilex*
29	Rhamnaceae gen. et sp.	X	*
30	*Sapindus falcifolius* A. Braun	X	*
31	*Ulmus braunii* Heer	X	*Ulmus*
32	*Zelkova zelkovifolia* (Unger) Bůžek & Kotlaba	X	*Zelkova carpinifolia, Z. serrata*
33	*Zizyphus* sp.	X	*Zizyphus*
34	? *Hedera* sp.	X	*
Sum of taxa		34	21