Early Oligocene Continental Climate of the Palaeogene Basin (Hungary and Slovenia) and the Surrounding Area

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Abstract: This paper concentrates on the Early Oligocene palaeoclimate of the southern part of Eastern and Central Europe and gives a detailed climatological analysis, combined with leaf-morphological studies and modelling of the palaeoatmospheric CO_2 level using stomatal and $\delta^{13}C$ data. Climate data are calculated using the Coexistence Approach for Kiscellian floras of the Palaeogene Basin (Hungary and Slovenia) and coeval assemblages from Central and Southeastern Europe. Potential microclimatic or habitat variations are considered using morphometric analysis of fossil leaves from Hungarian, Slovenian and Italian floras. Reconstruction of CO_2 is performed by applying a recently introduced mechanistic model. Results of climate analysis indicate distinct latitudinal and longitudinal climate patterns for various variables which agree well with reconstructed palaeogeography and vegetation. Calculated climate variables in general suggest a warm and frost-free climate with low seasonal variation of temperature. A difference in temperature parameters is recorded between localities from Central and Southeastern Europe, manifested mainly in the mean temperature of the coldest month. Results of morphometric analysis suggest microclimatic or habitat difference among studied floras. Extending the scarce information available on atmospheric CO_2 levels during the Oligocene, we provide data for a well-defined time-interval. Reconstructed atmospheric CO_2 levels agree well with threshold values for Antarctic ice sheet growth suggested by recent modelling studies. The successful application of the mechanistic model for the reconstruction of atmospheric CO_2 levels raises new possibitities for future climate inference from macro-flora studies.

Key Words: Early Oligocene, Palaeogene basin, fossil flora, palaeoclimate, morphometry, carbon dioxide

Paleojen Havzası (Macaristan ve Slovenya) ve Çevresindeki Alanın Erken Oligosen Karasal İklimi

Özet: Bu çalışma, Doğu ve Merkezi Avrupa'nın güney kısmının Erken Oligosen paleoiklimi üzerine yoğunlaşmakta ve yaprak morfolojisi çalışmaları ve stomal ve $\delta^{13}C$ verileri kullanılarak paleoatmosferik CO_2 düzeyinin modellenmesi ile birleştirilmiş ayrıntılı iklimsel analizleri vermektedir. İklimsel veriler Paleojen Havzasının (Macaristan ve Slovenya) Kiscellian floraları ve Merkezi ve güneydoğu Avrupa'dan eş yaşlı topluluklar Birarada Olma Yaklaşımı kullanılarak hesaplanır. Potansiyel mikroiklimsel veya ortam değişimleri Macaristan, Slovenya ve İtalyan floralarından fosil yaprakların şekil ölçüm analizleri kullanılarak değerlendirilmiştir. CO_2'in yeniden kurgulanması, bir yeni tanıtılmış mekanik model uygulamasıyla gerçekleştirilmiştir. İklimsel analizlerin sonuçları, yeniden şekillendirilmiş paleocoğrafya ve paleovejetasyon ile iyi bir uyum içinde olan çeşitli değişkenler için belirgin enlemsel ve boylamsal iklim modellerini ortaya koymaktadır. Genelde hesaplanmış iklim değişkenleri, düşük mevsimsel sıcak, ılık ve buzlanmasız bir iklim düşündürmektedir. Sıcaklık parametrelerindeki bir fark, esas olarak en soğuk ayın ortalama sıcaklığında belirtilmiş Merkezi ve Güneydoğu Avrupa'daki lokaliteler arasında kaydedilmiştir. Şekil ölçü analizlerinin sonuçları, çalışılmış floralar arasındaki mikroiklimsel veya ortam farkını göstermektedir. Oligosen süresince atmosferik CO_2 düzeylerindeki seyrek bilgiyi genişletmek için biz iyi tanımlanmış zaman aralığı için veriler sağladık. Yeniden elde edilmiş atmosferik CO_2 düzeyleri, güncel modelleme çalışmaları tarafından önerilmiş Antartik buz kütlelerinin büyümesi için eşik değerleri ile iyi bir şekilde uyuşmaktadır. Konrad *et al.* (2008) tarafından önerilmiş yeni metodun başarılı uygulaması, gelecekte makro-flora çalışmalarından iklim çıkarımı için yeni olasılıklara yol açmaktadır.

Anahtar Sözcükler: Erken Oligosen, Paleojen havzası, fosil flora, paleoiklim, şekil ölçümü, karbon dioksit

Introduction

The present paper concentrates on Early Oligocene palaeoclimate, based on megafloras representing the vegetation cover of the southern part of Eastern and Central Europe. Previous work (Bruch & Mosbrugger 2002; Erdei *et al.* 2007; Utescher *et al.* 2007; Bozukov *et al.* 2009) dealing with this area focused on climate historical studies using fossil plant assemblages that spanned most of the Neogene or even broader time slices. The main aim of these studies was to enhance both temporal and spatial resolution of palaeoclimate reconstruction. However, the present complex study is focused on localities of well-defined age and region (Figure 1). We endeavoured to give a detailed climatological analysis combined with leaf-morphological studies and modelling of the palaeoatmospheric CO_2 level using stomatal and $\delta^{13}C$ data.

The study of Palaeogene (Early Oligocene) climate, adopting quantitative climate reconstructions and the closely related atmospheric CO_2 concentrations derived from fossil floras, is of significant relevance to the issue raised by the Cenozoic greenhouse-icehouse climate transition. This has been proposed to start as early as the Eocene/Oligocene boundary or even earlier in the Eocene (Shackleton & Kenneth 1975; Zachos *et al.* 2001; Moran *et al.* 2006). Related to the changes of the water cycle, the coincident formation of the Antarctic ice-sheet and circumpolar current, major climatic shifts for the Late Eocene/Oligocene (cooling setting in with the Oi-1 glaciation event at the Eocene/Oligocene transition, the Late Oligocene Warming) have been widely discussed (increasing seasonality in temperature / precipitation in Europe, decreasing mean annual temperatures / cold season temperatures – Prothero & Bergreen 1992; Utescher *et al.* 2000, 2009; Zachos *et al.* 2001; Roth-Nebelsick *et al.* 2004; Mosbrugger *et al.* 2005).

A continental, relatively warm (frost-free) climate, with low annual range of temperature predominated in the Eocene–Early Oligocene of most of Europe (low latitudinal temperature gradient in the Eocene, Greenwood & Wing 1995; Mosbrugger *et al.* 2005; Utescher *et al.* 2011). A quite warm, frost-free climate is suggested by Eocene–Early Oligocene flora lists from Europe, e.g. Messel (Wilde 1989; Grein *et al.* 2011), Geiseltal (e.g., Mai 1976; Krumbiegel *et al.* 1983), Weisselster-Becken (Mai & Walther 1985), Staré Sedlo (Knobloch *et al.*

1996), Ovce Polje (Mihajlovic & Ljubotenski 1994), Tard Clay flora (Hably 1992; Kvaček & Hably 1998; Kvaček *et al.* 2001; Kvaček 2002; etc). Accordingly, the mid-latitudes of Europe were characterized by vegetation types with a dominance or high ratio of evergreen plants, including a diverse spectrum of thermophilous, tropical taxa (Mai 1995; Collinson & Hooker 2003; Utescher & Mosbrugger 2007). During the Oligocene the gradual replacement of evergreen plants by deciduous among them even cool temperate ones had started, although the timing and scale of this floral transition does not seem to be uniform in various regions of Central and Southeastern Europe (Kvaček & Walther 2001).

The Eurasian Late Eocene–Early Oligocene was characterized by significant tectonic activity, mainly linked to the collision of India and Asia, resulting in large-scale palaeogeographic changes. The evolution of the northern Peri-Tethys Platform area was complicated by palaeogeographic reorganizations and basin rearrangements (Meulenkamp & Sissingh 2003). The formation of an isolated Paratethys Sea started during the Eocene/Oligocene transition and the closure of marine seaways culminated during the Early Oligocene. Continentalization of Europe increased; the Turgai Strait closed and the Bering Bridge opened. In its first period (NP 23) the Paratethys was characterized by reduced salinity, anoxic bottom conditions and strong endemism (Báldi 1980; Rusu 1988; Rögl 1999; Schulz *et al.* 2005).

Fossil plant assemblages studied here are preserved in lower Oligocene sediments. Our complex approach estimates palaeoclimate, pCO_2 levels and possible microclimate/habitat variations using various proxies made available by fossil leaf assemblages.

A special focus is placed on Early Oligocene (Kiscellian), well-dated and documented fossil macrofloras preserved in sediments of the Palaeogene Basin which are exposed in Hungary and Slovenia. Climate data calculated using the Coexistence Approach are compared with the results derived from relevant proxy data of coeval assemblages from southern Central and Southeastern Europe (localities from Austria, Bulgaria, Italy, Serbia) and from Central Europe (Germany, Czech Republic).

Adopting a morphometric analysis of leaves we may refine climate data and support potential
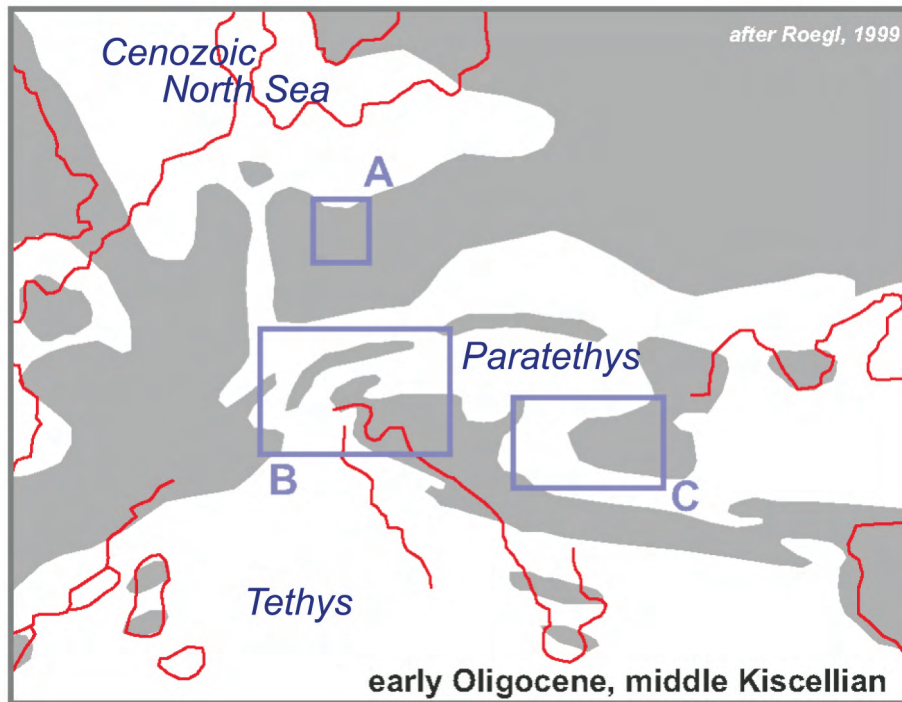
Figure 1. Palaeogeographic map showing study area. (**A**) studied area of the European plate, (**B**) Palaeogene Basin, (**C**) Rhodopes. Red lines indicate present day coast lines.

microclimatic or habitat variations using given climate parameters in the Hungarian, Slovenian, and Italian localities.

Reconstruction of CO_2 level is performed by applying a mechanistic model recently introduced by Konrad *et al.* (2008). The model combines the processes of gas diffusion (CO_2 into the plant, and transpiration) and photosynthesis and an optimum principle that is realized in plants to obtain maximum carbon gain with minimum water loss. By applying stomatal density, stomatal pore length, assimilation parameters, climate data and carbon isotope data as input parameters, the model can be used to calculate CO_2 level (termed C_a throughout the rest of the paper).

The Palaeogene Basins and the Palaeogeographical Settings

Extensive studies have discussed the stratigraphy and tectonic evolution of the Palaeogene Basin (Báldi 1983; Kázmér & Kovács 1985; Nagymarosy 1990; Seifert *et al.* 1991; Csontos *et al.* 1992).

The Mesozoic tectonostratigraphic units of the Intra-Carpathian domain (comprising the North Pannonian and Tisza megatectonic units) evolved during Triassic and Jurassic rifting episodes and several Cretaceous compressional events in the Dinaric and Alpine belt (Figure 2). By the Palaeogene these processes resulted in the tectonic superposition of individual units (Csontos *et al.* 1992). The Inner Carpathian Palaeogene basins (Hungarian, Slovenian and Transylvanian) show no direct geographical connection in their present position (Nagymarosy 1990) with each other, or with the surrounding Inner and Outer Carpathian flysch basins, or the Mediterranean region. However they show many similarities in their Late Eocene–Oligocene depositional history and biostratigraphy, e.g., the Early Oligocene endemic event (Báldi 1986; Nagymarosy 1990). It has been suggested that the Hungarian and Slovenian Palaeogene basins formed part of a possibly elongated single basin that was dissected by wrench faulting (Royden & Báldi 1988; Báldi 1989; Csontos *et al.* 1992).

Probably the drift of the North-Pannonian (Pelso) unit in SW–NE direction along the Balaton and Mid-
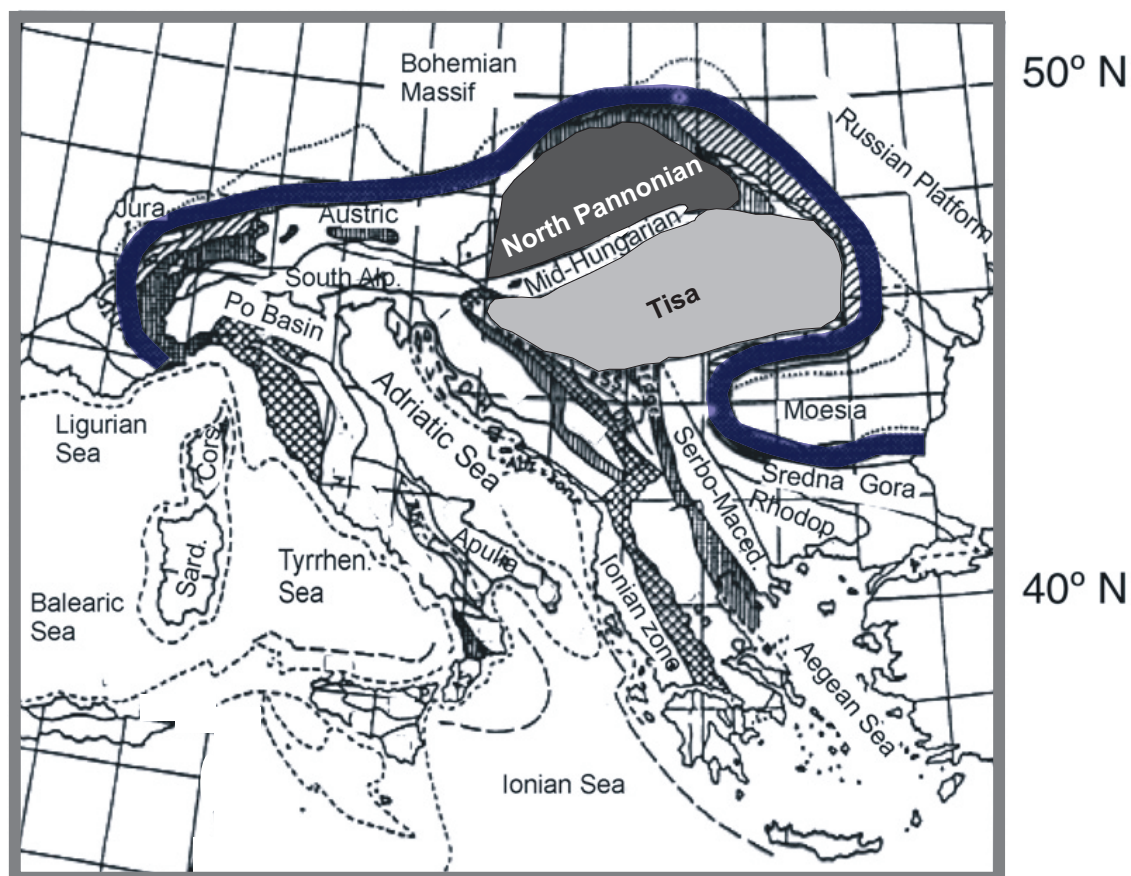
Figure 2. Palaeotectonic map showing the studied area and its Alpine-Carpathian-Dinaric surrounding during the Early Oligocene (after Hably & Kázmér 1996). The North Pannonian and Tisia units are indicated by solid grey colour. The blue line shows position of the Pieniny Klippen Belt.

Hungarian Lines (fault system, Figure 2) accounts for the recent distribution of the Intracarpathian Palaeogene sedimentary basins extending from Slovenia through Hungary to Slovakia (Nagymarosy 1990).

Material

Hungarian and Slovenian Fossil Plant Assemblages

Localities studied here are shown on map (Figure 3) and additional details are listed in Table 1. References used for the compilation of flora lists are given in Table 2.

All the Hungarian fossil floras are preserved in the characteristically laminated organic rich sediments of the Tard Clay Formation, formed in the bathyal

Tard Basin mostly under anoxic conditions. Faunal endemisms and anoxic bottom conditions indicate the first isolation of the Paratethys, extending from the Alpine forelands to the Caucasus-Caspian Basin (Báldi 1980, 1983, 1989). Fossil plants are preserved in the uppermost brackish level characterized by the laminite facies (lower level rich in planktonic foraminifers, the middle 'mollusc' level characterized by a mass of pteropod shales and bentonic molluscs, Báldi 1983) and dated by nannoplanktons to the NP23 zone (Nagymarosy & Báldi-Beke 1988).

The fossil floras generally comprise a wide range of taxa (e.g., Kvaček & Hably 1991, 1998; Hably 1992; Hably & Manchester 2000; Kvaček *et al.* 2001; Kvaček 2002), with thousands of specimens mainly sampled from two areas of the Palaeogene basin in
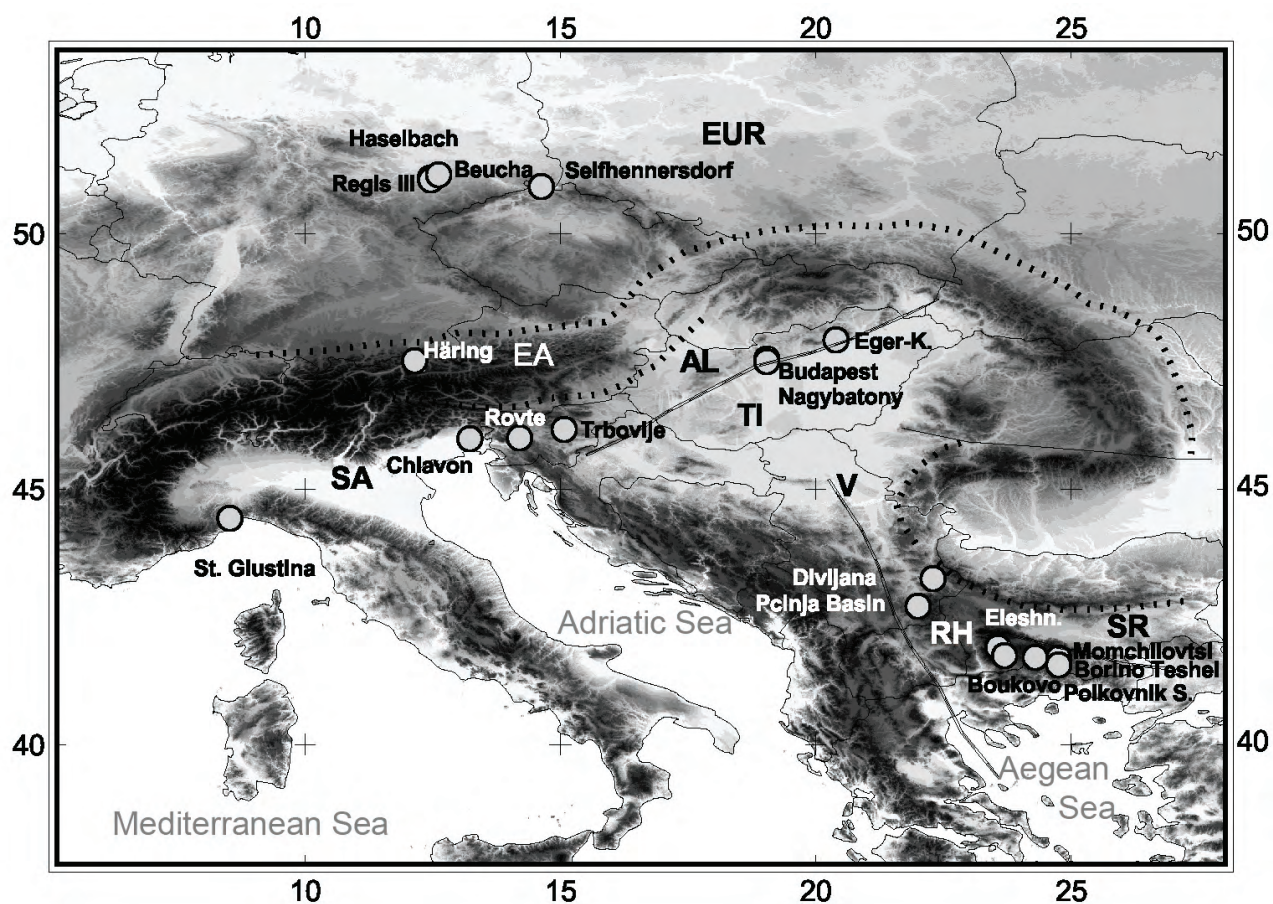
Figure 3. Relief map of the study area showing localities dealt in this paper. Thin broken lines indicate current frontiers, the thick solid black lines represent faults.

northern and northeastern Hungary: (1) fossil floras near Budapest – Nagybátony-Újlak, Vörösvári street, Bécsi street, Kiscell-1 and H- boreholes; (2) those in northeastern Hungary, in the Bükk Mountains – Eger-Kiseged. These fossil assemblages are all well dated using litho- and bio-stratigraphy (nannoplankton) as Early Oligocene (Rupelian; Central Paratethys stage – Kiscellian), NP23 zone (Nagymarosy & Báldi-Beke 1988). For practical reasons (discussed in Methodology) we combined the flora lists of the Vörösvári street, Bécsi street, Kiscell-1 and H-boreholes for climate analyses.

The Socka beds, sediments of the Palaeogene basin which are exposed in Slovenia (Figure 7 in Csontos *et al.* 1992) preserve additional fossil floras. They originate from the upper fish shale level of the Socka beds, like the floras preserved in the upper fish shale level of the Hungarian Tard Clay. Based on

this consideration the age of the fossiliferous layers may be coeval with the Tard Clay layers belonging to the NP23 zone. From Slovenia the floras of Trbovlje (Trifail), Novi Dol (Mihajlovic 1988; Hably & Manchester 2000; Kvaček *et al.* 2001; Walther & Kvaček 2008) and Rovte (Nagymarosy & Kázmér, personal communication) were selected for this study (Figure 3, Tables 1 & 2). Lists from Rovte and Novi Dol were combined due to the relatively low number of taxa.

Assemblages Selected for Comparison

Nearly coeval fossil plant assemblages were selected for comparison from Austria, Bulgaria, Italy and Serbia (Figure 3, Tables 1 & 2). The flora of Häring, (Tirol) Austria, with fossils preserved in bituminous marls of the Häring Formation, is considered to be

Table 1. List of floras with geographical position, age and dating method.

Locality		Longitude	Latitude	Age/method of dating	Reference
Budapest	Nagybátony-Újlak	19°2′	47°32′	biostratigraphy, nannoplankton, NP23 zone	Nagymarosy & Báldi-Beke (1988)
	Bécsi street	19°1′	47°33′	biostratigraphy, nannoplankton, NP23 zone	Nagymarosy & Báldi-Beke (1988)
	Vörösvári street	19°2′	47°32′	biostratigraphy, nannoplankton, NP23 zone	Nagymarosy & Báldi-Beke (1988)
	H- boreholes	19°2′	47°32′	biostratigraphy, nannoplankton, NP23 zone	Nagymarosy & Báldi-Beke (1988)
	Kiscell1	19°2′	47°32′	biostratigraphy, nannoplankton, NP23 zone	Nagymarosy & Báldi-Beke (1988)
Eger-Kiseged		20°24′	47°54′	biostratigraphy, nannoplankton, NP23 zone	Nagymarosy & Báldi-Beke (1988)
Trbovlje		15°3′	46°9′	biostratigraphy, nannoplankton, NP23 zone	Nagymarosy & Báldi (1979)
Novi Dol		12°82′	46°19′	biostratigraphy, nannoplankton, NP23 zone	Nagymarosy & Báldi (1979)
Rovte		14°10′	45°59′	biostratigraphy, nannoplankton, NP23 zone	Nagymarosy & Báldi (1979)
Santa Giustina		11°54′	45°34′	biostratigraphy, nummulites	Lorenz (1969)
Chiavon		13°12′	45°58′	biostratigraphy, nummulites	Lorenz (1969)
Häring		12°7′	47°30′	biostratigraphy, nannoplankton, NP21-22 zone	Mai (1995)
Divljana		22°18′	43°12′	regional stratigraphy, biostratigraphy	Mihajlovic (1985)
Pcinja basin		22°1′	42°40′	regional stratigraphy, biostratigraphy	Mihajlovic (1985)
Beucha		12°35′	51°9′	lithology, sequence stratigraphy	Standke et al. (2005)
Haselbach Seam IV		12°26′	51°4′	lithology, sequence stratigraphy	Standke et al. (2005)
Regis III		12°25′	51°5′	lithology, sequence stratigraphy	Standke et al. (2005)
Seifhennersdorf		14°36′	50°56′	radiogeochronology, K/Ar method	Bellon et al. (1998)
Eleshnitsa		23°34′	41°52′	radiogeochronology, K/Ar method	Ivanov & Černjavska (1972); Harkovska (1983)
Borino Teshel		24°19′	41°40′	palaeobotany, radiogeochronology, K/Ar method	Harkovska et al. (1998)
Momchilovtsi		24°46′	41°40′	palaeobotany, radiogeochronology, K/Ar method	Kitanov & Palamarev (1962); Harkovska et al. (1998)
Polkovnik Serafimo		24°46′	41°31′	radiogeochronology, K/Ar method	Harkovska et al. (1998)
Boukovo		24°59′	41°30′	radiogeochronology, K/Ar method	Harkovska et al. (1998)

Table 2. References used for the compilation of flora lists.

Locality		Reference
Budapest	Nagybátony-Újlak Bécsi street Vörösvári street H-boreholes Kiscell-1	Hably 1992; Kvaček & Hably 1998; Hably & Manchester 2000; Kvaček *et al.* 2001; Kvaček 2002
Eger-Kiseged		
Trbovlje		Mihajlovic 1988; Hably & Manchester 2000
Novi Dol		Kvaček *et al.* 2001
Rovte		Walther & Kvaček 2008
Santa Giustina		Principi 1916, 1921; Hably 2007
Chiavon		Principi 1916, 1921; Hably 2007
Häring		corrected floralist, Ettingshausen 1853; Butzmann & Gregor 2000; Heying *et al.* 2003
Boukovo		Bozukov *et al.* 2008
Borino-Teshel		Bozukov *et al.* 2008
Eleshnitsa II		Bozukov *et al.* 2008
Momchilovtsi		Bozukov *et al.* 2008
Polkovnik Serafimovo		Bozukov *et al.* 2008
Divljana		Mihajlovic 1985
Pcinja basin		Mihajlovic 1985
Beucha E.E. Oligocene		Mai & Walther 1978
Haselbach Seam IV		Mai & Walther 1978
Regis III		Mai & Walther 1978
Seifhennersdorf		Walther & Kvaček 2007

older than the Palaeogene basin floras of Hungary and Slovenia based on nannoplankton and belongs to the NP21-22 zones (Mai 1995; Piller *et al.* 2004). This age was confirmed by Löffler (1999), identifying the NP22 zone at the base of the overlying Paisslberg Formation. The revised flora list is based on the works of Ettingshausen (1853), Butzmann & Gregor (2000) and Heying *et al.* (2003).

The Early Oligocene floras of Borino-Teshel, Boukovo, Eleshnitsa-II, Momchilovtsi and Polkovnik Serafimovo, all from the Rhodope region in Bulgaria, were selected for comparison. The Eleshnitsa and Boukovo floras originate from sediments in the graben structures of the West Rhodopes (Mesta Graben). Leaf bearing strata rest on volcanic rocks radiometrically dated as Rupelian (K/Ar method, 33–28 Ma: Harkovska 1983; Harkovska *et al.* 1998; Pécskay *et al.* 2000). Both floras comprise relatively high numbers of taxa (leaves) and their floral composition supports the radiometric age (Palamarev *et al.* 1999). The Borino-Teshel flora is preserved in continental sediments of the Borino-Teshel Graben (West Rhodopes). Palaeobotanical correlations suggest it is Early Oligocene (Palamarev *et al.* 2001). In the central Rhodopes, the age of the Momchilovtsi flora excavated from sandstones is Early Oligocene, based on floral correlations (Bozukov *et al.* 2009) and

radiometric data (Harkovska *et al.* 1998), while the Polkovnik Serafimovo flora preserved in continental sediments of the Polkovnik Serafimovo Graben is dated as Early Oligocene by means of palaeobotany. Radiometric dating of nearby volcanics suggests a Rupelian age (Harkovska *et al.* 1998). The floral lists used for climate reconstruction are all based on Bozukov *et al.* (2009).

As regards the floral record of Serbia, lists were compiled from the Divljana (Koritnica basin, East Serbia) and the Pčinja basin (Central and South Serbia). The age of the assemblages is based on local and regional biostratigraphy (Mihajlovic 1985). Corrected flora lists were compiled using the work of Mihajlovic (1985).

Two Italian localities, Santa Giustina and Chiavon (Southern Alpine Foreland) were adopted for comparison. The fossil assemblages are preserved in anoxic marine clays dated by biostratigraphy (nummulites) as Early Oligocene (Lorenz 1969). Floral lists are based on latest revisions (Hably 2007; Hably 2010) as well as earlier works of Principi (1916, 1921).

Fossil floras from the stable European Plate were selected from Germany and the Czech Republic (Bohemian Massif). In Saxony (Germany), the Haselbach, Regis and Beucha floras are preserved in the brown coal formations of the Weisselster Basin. The Haselbach flora (sands below Seam IV) is Early Oligocene, while the flora of Beucha (lower part of the Middle Zeitz Sands) is probably somewhat older, early Early Oligocene. The Regis III flora was dated as Early Oligocene, using lithological correlation and sequence stratigraphy, ca. 31.5–33.7 Ma. (cf. Standke *et al.* 2006). Floral lists used in climate analysis are based on Mai & Walther (1978).

The age of the volcanic flora of Seifhennersdorf (Czech Republic) is dated by means of K/Ar dating as Early Oligocene (30.44±1.25 Ma, Bellon *et al.* 1998) and the floral list was compiled by Walther & Kvaček (2007).

Methodology

Quantitative Climate Reconstructions

To obtain quantitative palaeoclimate data the systematics-based Coexistence Approach (CA)

method of Mosbrugger & Utescher (1997) was applied to the fossil floras. The method follows the nearest living relative concept. Based on the climatic requirements of the nearest living relatives (NLRs) of fossil plant taxa in a fossil assemblage it calculates 'coexistence intervals' for various climate parameters allowing a maximum number of NLR taxa to co-exist. By means of thus defined parameter ranges the palaeoclimate can be characterized. For a detailed description of the Coexistence Approach method, see Mosbrugger & Utescher (1997). The following climate parameters were calculated: mean annual temperature (MAT), mean temperature of the coldest month (CMM), mean temperature of the warmest month (WMM), mean annual precipitation (MAP), precipitation in the warmest month (MPwarm), precipitation in the driest month (MPdry), and precipitation in the wettest month (MPwet).

Most fossil assemblages studied here comprise elements of the zonal vegetation which are most relevant for palaeoclimate reconstructions. Taxa used in the analyses and corresponding NLRs are listed in Table 3. Taxa with uncertain botanical affinity are excluded from the analysis. The number of applicable taxa in the individual floras ranges between 9 and 40. Some fossil floras comprise relatively few taxa, especially some of the assemblages in Budapest (Vörösvári street, Bécsi street, Kiscell-1 and H-boreholes; cf. Table 3). These floras are close to each other and represent similar fossil assemblages preserved in similar sediments and facies. In order to obtain narrower coexistence intervals, we combined their flora lists because the significance of the results obtained increases in the number of taxa included in calculations (Mosbrugger & Utescher 1997). Results obtained and specific adjustments performed in the calculation of climate variables are described in 'Results'.

Climate parameters of the Beucha, Haselbach, Regis and Seifhennersdorf floras have already been published by Roth-Nebelsick *et al.* (2004) and Mosbrugger *et al.* (2005) except for the MPdry, MPwet, and MPwarm variables presented by this study. At Seifhennersdorf a revised flora list and palaeoclimate data derived with the CA were provided by Walther & Kvaček (2007). We have repeated CA

Table 3. List of fossil taxa and corresponding nearest living relatives (NLRs). A– Eger-kiseged; B– Nagybátony-Újlak; C– Bécsi street; D– Vörösvári street; E– Kiscell1; F– H-boreholes; G– Häring; H– Rovte/NoviDol; I– Trbovlje; J– Chiavon; K– Santa Giustina; L– Divljana; M– Pcinja.

Fossil taxon	Nearest Living Relative	A	B	C	D	E	F	G	H	I	J	K	L	M
Ailanthus tardensis	*Ailanthus* sp.		x						x				x	x
Calocedrus suleticensis	*Calocedrus macrolepis*	x	x											
Cedrelospermum aquense	Ulmaceae	x	x	x					x		x		x	x
Cedrelospermum flichei	Ulmaceae	x	x					x					x	x
Ceratozamia floersheimensis	*Ceratozamia* sp.		x											
Ceratozamia sp.										x				
Chamaecyparites hardtii	Taxodiaceae				x		x	x	x					
"Comptonia acutiloba"	*Myrica* sp.							x			x	x		
Comptonia schrankii	*Comptonia peregrina*							x	x			x		x
Comptonia sp.	*Comptonia peregrina*	x			x		x							
Craigia bronni	*Craigia* sp.	x	x						x				x	
Dalbergia bella	Leguminosae	x			x	x			x			x		
Daphnogene bilinica	Lauraceae				x									
Daphnogene sp.	Lauraceae	x	x				x	x	x	x	x	x	x	x
Doliostrobus taxiformis var. *hungaricus*	Taxodiaceae	x	x	x	x	x	x	x	x		x		x	
Engelhardtia macroptera	*Engelhardia* sp.			x				x	x	x			x	
Engelhardtia orsbergensis	*Engelhardia* sp.	x	x	x				x	x	x			x	
Eotrigonobalanus andreanszkyi	*Castanopsis, Lithocarpus, Trigonobalanus*	x	x											
Eotrigonobalanus furcinervis	*Castanopsis, Lithocarpus, Trigonobalanus*	x	x	x	x	x	x	x	x	x			x	x
Hooleya hermis	Juglandaceae	x	x						x					
Hydrangea sp.	*Hydrangea* sp.	x			x				x					
Ilex castellii	*Ilex aquifolium*									x				
Lauraceae	Lauraceae			x	x									
Laurophyllum acutimontanum	Lauraceae	x			x		x							
Laurophyllum hradekense	Lauraceae			x		x								
Laurophyllum kvaceki	Lauraceae				x	x	x							
Laurophyllum markvarticense	Lauraceae				x	x	x							
Laurophyllum medimontanum	*Persea* sp.				x		x							
Laurophyllum sp.	Lauraceae							x	x		x	x	x	
Leguminosae gen. et sp.	Leguminosae	x	x					x	x	x	x		x	x
Matudaea menzelii	*Matudaea* sp.	x	x	x										
Myrica lignitum	*Myrica* sp.							x	x		x			
Myrica longifolia	*Myrica* sp.							x	x	x	x		x	x
Palmae	Palmae		x											
Pinus sp.	*Pinus* sp.	x			x	x	x					x	x	x
Platanus neptuni	*Platanus* sp.	x	x		x	x	x	x			x		x	
Platanus schimperi	*Platanus* sp.	x												
Rosa lignitum	*Rosa* sp.							x						
Rosa sp.	*Rosa* sp.	x												
Sabal major	*Sabal* sp.							x	x	x		x		x
Sassafras tenuilobatum	*Sassafras* sp.	x							x					
Sloanea olmediaefolia	*Sloanea* sp.	x			x		x	x	x	x		x	x	
Sloanea eocenica	*Sloanea* sp.			x										
Sloanea peolai	*Sloanea* sp.										x	x		
Smilax weberi	*Smilax* sp.	x										x		
Smilax sp.	*Smilax* sp.										x		x	
Taxodiaceae	Taxodiaceae						x							
Tetraclinis brachyodon	*Tetraclinis articulata*	x	x											
Tetraclinis brogniartii	*Tetraclinis articulata*										x		x	
Tetraclinis salicornoides	*Tetraclinis articulata*	x	x	x	x		x	x						x
Tetrapterys harpyiarum	*Tetrapterys* sp.	x	x	x	x	x	x		x	x				
Zizyphus zizyphoides	*Ziziphus* sp.	x	x	x	x	x	x	x	x	x	x	x	x	x

calculations for this list, using the latest version of the Palaeoflora data base (Utescher & Mosbrugger 1990–2011). Except for MAP and MPwet, data obtained are the same or very close to the results of Walther & Kvaček (2007), and therefore we use them in our study as published. For MAP and MPwet data we use the actual data because calculations yielded considerably higher values than the results of Walther & Kvaček (2007) where 897–971 mm are cited for MAP, and 117–133 mm for MPwet, respectively. Our new results (MAP 1194–1213 mm; MPwet 167–212) are quite comparable to previously published values (Roth-Nebelsick *et al.* 2004; Mosbrugger *et al.* 2005: MAP 979–1250 mm; MPwet 167–225 mm).

In the Bulgarian sites all but one of the climate parameters are based on Bozukov *et al.* (2009), MPwet is calculated in this study.

Most, but not all, prior applications of CA have dealt with Neogene and younger floras. When applying the CA to Palaeogene floras it is appropriate to reconsider/discuss the reliability of the estimates obtained. This method assumes that climatic tolerances of the fossil taxa do not significantly differ from the climatic tolerances of their NLR. This may be less valid for some Palaeogene plant taxa (cf. 'taxa excluded' in the discussion and in Bozukov *et al.* 2009). To overcome this problem we restrict the NLR allocation to higher taxonomic levels (genus/family). In addition, the CA proved its potential and reliability in various studies of Palaeogene floras (e.g., Mosbrugger *et al.* 2005). Based on macrofloras, the authors reconstructed a continental climate record covering the time-span from the Mid-Eocene to the late Pliocene, revealing an evolution largely congruent to data known from marine archives (e.g., Zachos *et al.* 2001). Furthermore, CA studies of middle Eocene temperatures in the Northern Hemisphere based on 47 floras yield interpretable large-scale patterns consistent with various proxies from other sources (Utescher *et al.* 2011). Oligocene MATs reconstructed by the CA are even in good agreement with results obtained from leaf morphology (CLAMP, LMA; cf. Roth-Nebelsick *et al.* 2004) while results do not overlap for most late Oligocene to Pliocene European floras analysed by the above techniques (e.g., Utescher *et al.* 2000; Uhl *et al.* 2007).

Leaf Morphometry

Morphometric measurements have already been successfully used for the comparison of leaf size and shape of given taxa, in order to reveal habitat differences in various localities, or even to establish new morpho-species (Hably *et al.* 2007; Tamás & Hably 2009).

Selected leaves of *Sloanea olmediaefolia* (Unger) Kvaček & Hably (= *Sloanea elliptica*, Hably & Kvaček 2008), and *Eotrigonobalanus furcinervis* (Rossmässler) Walther & Kvaček were investigated using morphometric measurements (Table 4). *Sloanea* leaves were selected from five localities – Santa Giustina (Italy), Nagybátony-Újlak and Eger-Kiseged (Hungary), Rovte and Trbovlje (Slovenia). *Eotrigonobalanus* was obtained from Santa Giustina, Nagybátony-Újlak and Eger-Kiseged.

For leaf size comparisons we used Hill's circular grid method, a simple procedure that is applicable even for analysing fragmentary leaf fossils (Hill 1980). Hill's circular grid is composed of 36 radii. The circular grid should be positioned on the leaf as follows: the line along 0–180° falls on the primary vein, the radius of 0° points towards the apex of the leaf and the line along 90–270° falls on the broadest point of the leaf lamina. Along each radius the distance between the origin and leaf margin is recorded, yielding 36 values if the leaf is intact. For detailed description of the method see Tamás & Hably (2009).

We aimed to measure the greatest possible number of leaves. The only criterion was to have enough intact material from the middle part of the leaf to enable us to measure unequivocally the broadest point of the leaf.

A digital sliding calliper (TIME 110-15 DAB) was used to measure the leaves. To compare leaf sizes, the values measured along radii on the left and right sides were averaged. Based on the length values measured radially and the included angles of radii, the area of triangles is calculable, and the area of 18 triangles approximates the area of the half leaf blade. Statistical comparison of the localities was based on the comparison of areas of the corresponding triangles. The data set did not follow Gaussian Distribution, therefore we used the Kruskal-Wallis

Table 4. Preliminary data on the size of fossil *Sloanea olmediaefolia* and *Eotrigonobalanus furcinervis* leaves.

	Sloanea olmediaefolia					*Eotrigonobalanus furcinervis*		
	Santa Giustina	Nagybátony-Újlak	Eger-Kiseged	Rovte	Trbovlje	Santa Giustina	Nagybátony-Újlak	Eger-Kiseged
Number of leaves measured	24	16	19	2	9	14	21	22
Leaf length average, min.-max. (mm)	139.0 83.6–189.6	121.5 97.2–154.4	98.7 62.9–144.0	78.2 73.5–82.9	92.7 52.7–142.0	186.9 157.5–200.3	162.2 133.4–209.3	154.3 87.2–217.9
Leaf width average, min.-max. (mm)	58.5 38.2–102.2	61.6 36.4–89.7	31.8 20.2–71.8	28.1 17.2 – 39.1	49.8 22.0–85.1	27.3 11.4–49.3	27.8 9.0–88.3	18.5 5.2 – 33.4
Average length/width ratio	2.4	2.0	3.1	2.8	1.9	6.8	5.8	8.3
Average leaf area (mm²)	5407.1	4974.1	2156.1	1537.6	3495.8	2913.0	3101.7	1757.5

Test (Nonparametric ANOVA) with Dunn's Multiple Comparisons Test as a post-test in statistical evaluation (InStat 1998).

Palaeoatmospheric CO_2

The traditional, widely used method for the reconstruction of palaeoatmospheric CO_2 concentration requires the calibration of the stomatal density or index of a plant species against pCO_2. Calibration is usually accomplished by using herbarium material with the relevant atmospheric CO_2 measurements (ice core data) or by conducting greenhouse experiments with extant plants (e.g., Kürschner 1996; Rundgren & Beerling 1999; Wagner *et al.* 1999; McElwain *et al.* 2002). Data of the CO_2 response of extant plants are therefore required to obtain the desired relationship between CO_2 and stomatal data. Stomatal density response to pCO_2 is highly species dependent (Kürschner *et al.* 1996; Royer 2001; Beerling & Royer 2002). Therefore a proper calibration requires that the considered fossil material belongs to still extant species. This circumstance is problematic, since it greatly restricts the range suitable fossil taxa.

Calibration using extant plants is necessary, because the conventional method of reconstructing

C_a by stomatal data considers the mechanism of stomatal density response as a 'black box'. However, the reason for the inverse response of stomatal density (termed SD throughout the rest of the paper) probably lies in the role of CO_2 as substrate for photosynthesis: if C_a increases, the maximum conductance of the epidermis, represented by the product of stomatal density and maximum aperture, can be decreased (Woodward 1987). Inversely, this product has to be increased if C_a decreases. The response is also driven by the fact that water vapour loss by transpiration occurs also through open stomata: any CO_2 uptake means water loss at the same time. Since water is of limited availability at least temporally in most terrestrial environments, a water conservation strategy is mandatory for plants.

To keep water loss as low as possible and to gain as much CO_2 as possible represents an optimization problem. In fact, it was demonstrated several times for extant plants, that an optimization principle is realized in the regulation of stomatal conductance by stomatal aperture change (Hari *et al.* 1986; Aalto *et al.* 2002). The characteristic midday depression which means a decrease in stomatal conductance around noon and the subsequent increase in the afternoon is one consequence of the optimization principle. Since stomatal density is a parameter that contributes to

maximum stomatal conductance, it is reasonable to assume that the inverse change in stomatal density under changing C_a is a part of this optimization principle, working not on the phenotypic level as aperture change but on the evolutionary level and dictating the maximum stomatal conductance. Both stomatal parameters (density and pore size) and aperture can be combined into the conductance parameter of the optimization principle on which the model of Konrad *et al.* (2008) is based.

A detailed description and test of the model approach is provided by Konrad *et al.* (2008). Thus, only a brief description is given here. The model uses the interrelationship between stomatal conductance, assimilation and the CO_2 gradient between leaf interior and the atmosphere. Transpiration depends on stomatal conductance and the humidity gradient between leaf interior and atmosphere (and also on other environmental parameters, such as wind and temperature). Assimilation depends on the CO_2 concentration in the leaf interior, biochemical parameters and temperature. The model then determines the optimum conductance and assimilation and C_a can be derived. A validation of the model calculations is possible via isotope data, since $d^{13}C$ of plant material is dependent on the difference between C_a and CO_2 concentration within the leaf interior (Farquhar *et al.*1989).

Among the model parameters only some are critical (sensitive) which means that they strongly affect the results (Konrad *et al.* 2008). Test calculations on extant taxa and their data sets confirm that the variation of these four critical parameters (temperature, relative air humidity, maximum RuBP-saturated rate of carboxylation and water-availability) is sufficient for calculating the actual C_a (Konrad *et al.* 2008) Thus, the C_a range of a species is calculated by varying the critical parameters. This procedure has to be performed on at least two species for the considered time interval (here: NP23) since the C_a range of a species may be quite large. The resulting overlapping interval should contain the actual C_a.

The input parameters (Table 5) are derived from the fossil material and its environment, such as stomatal density and aperture length and climate data. An exception is the biochemical parameters of assimilation which have to be borrowed from

extant relatives. Model calculation occurs currently via a MAPLE Sheet which is available from the authors (M.G. and A. R.-N.) upon request. MAPLE (Maplesoft, Ontario, Waterloo, Canada) is a tool for solving mathematical approaches, and it also contains a spreadsheet (MAPLE sheet) for convenient calculation of equation systems. In this study, stomatal data of *Sloanea olmediaefolia* are used. A modern species, *Sloanea sinensis* (Hance) Hemsley is suggested as best matching (may be indicated as modern relative) the Early Oligocene *S. olmediaefolia* (Kvaček *et al.* 2001).

Stomatal densities were measured using *Sloanea olmediaefolia* leaves collected from Nagybátony-Újlak (6 specimens) and H-boreholes (5 specimens) in Hungary and Rovte in Slovenia (3 specimens). Only leaves identified as sun leaves (characterized by high stomatal densities) were used, and thus a total number of 7 leaves were considered. Our measurements followed the technique in Poole & Kürschner (1999). On each leaf at least 50 counts were made (in units of 0.032 mm^2). Counting areas were arranged in cuticles prepared from the middle part of the lamina that displayed a sufficiently large area with clearly observable stomata. On the same samples, measurements of stomatal pore length were used to reconstruct stomatal pore area. Biochemical parameters of assimilation were borrowed from extant species of Elaeocarpaceae (Dungan *et al.* 2003; Dungan & Whitehead 2006; Gamage & Jesson 2007; Gamage 2010). The parameters are characteristic for tree species of the subtropical or warm temperate zone.

Results

Climate Analysis (Coexistence Approach)

Seven climate variables (MAT, CMM, WMM, MAP, MPwarm, MPdry, MPwet) were calculated for each flora. The mean annual range of temperature (MART) and the mean annual range of precipitation (MARP) were obtained from the parameter ranges of the relevant climate variables. Results of climate calculations are given in Table 6, and Figures 4, 6, 8, 11, 13, 15 & 16, together with published data taken from Roth-Nebelsick *et al.* (2004), Mosbrugger *et al.* (2005), and Bozukov *et al.* (2009). To visualize

Table 5. Palaeoclimatic, anatomic and photosynthetic data used for mechanistic CO_2-modelling based on fossil *Sloanea olmediaefolia* (Elaeocarpaceae) and resulting C_a-ranges parameters: V_{wind}– wind speed, RH– relative atmospheric humidity, T– mean annual temperature, d_{as}– depth of assimilation tissue, d_{st}– depth of stomatal pore, h_{st}– length of stomatal pore, w_{st}– width of stomatal pore ($h_{st}/2$), l– leaf length, SD– stomatal density, V_{cmax} Maximum RuBP-saturated rate of carboxylation, R_d– mitochondrial respiration rate in the light, c_i/c_a– ratio of leaf-internal to ambient CO_2, calc. C_a– calculated atmospheric CO_2 (bold values constrain the overlapping interval) [1] rough estimate, [2] this study, [3] estimates derived from Dungan *et al.* (2003), Dungan & Whitehead (2006), Gamage & Jesson (2007) and Gamage (2010) for extant Elaeocarpaceae * derived from $\delta^{13}C$ of sun leaves; for Nagybátony-Újlak we took H-boreholes; for C_a reconstruction c_i/c_a was varied ± 0.03 (corresponding to standard deviation of H-boreholes).

Parameter	Unit	H-boreholes (Hungary)	Nagybátony-Újlak (Hungary)	Rovte (Slovenia)	Reference
V_{wind}	m/s	3	3	3	1
RH	%	75–78	77–79	79–81	2
T	°C	15.6–21.1	15.6–22.2	16.5–21.3	2
d_{as}	µm	55	55	55	3
d_{st}	µm	11	11	11	3
h_{st}	µm	2.95	3.31	3.25	2
w_{st}	µm	1.47	1.66	1.62	2
l_{leaf}	cm	11	11	11	2
SD	1/mm²	646	646	700	2
V_{cmax}	µmol/m²s	30–40	30–40	30– 40	3
R_d	µmol/m²s	1	1	1	1, 3
c_i/c_a*		0.81	0.81	0.81	2
calc. C_a	ppm	**503**–1188	283–1028	266–**839**	2

and discuss spatial climate patterns in the study area climate maps were generated for each climate variable using means of CA intervals. We used ARCView GIS to generate interpolated data grids (Figures 5, 7, 9, 10, 12, 14, 17 & 18). The number of NLRs per flora contributing to the analysis with climate data ranges from 9 to 40. In the actual calculations the coexistence level equals 100% in most cases, meaning very robust results in the sense of the method, although occasionally not all taxa may overlap (cf. Table 6). Very narrow coexistence intervals with absolute values below the thermal resolution of the CA (<1°C or even a single value) as obtained for CMM derived from some of the floras (Table 6) can be regarded as an artifact caused by method. Details of the climatic

resolution of the CA and potential sources of error are discussed in Mosbrugger & Utescher (1997). The description of the palaeoclimate data given below refers to both published data and results obtained in this study.

Mean annual temperature ranges between 15.5–25.5°C (Table 6, Figure 4). Coexistence intervals are broader for the Hungarian, Slovenian and Italian localities, because of the relatively low number of applicable taxa compared to the other localities. The lower limits of coexistence intervals are more or less uniform in all cases (15.5–17°C) and show very slightly lower values for the EUR (European Plate: German and Czech) floras. In contrast the upper limits of MAT are much higher (21.5–25.5°C)

Table 6. Results of climate calculations.

Flora	taxa with climate data	MAT min	MAT max	taxa coexisting	CMM min	CMM max	taxa coexisting	WMM min	WMM max	taxa coexisting
this study										
taxa excluded: *Tetraclinis. Comptonia, Matudaea, Ceratozamia*										
Häring	16	16.5	18.9	16	5	12.2	16	26	28.3	16
St. Giustina	9	16.5	25.5	9	4.8	21.4	9	26	28.1	9
Chiavon	9	15.6	25.5	9	2.2	19.8	9	24.7	28.9	9
Rovte Novi Dol	19	16.5	21.3	19	7.7	13.3	19	26	28.1	19
Trbovlje	14	16.5	25.5	14	7.7	21.4	14	24.7	27.9	14
Nagybátony-Újlak	20	15.6	22.2	20	7.7	19.8	19(~*Craigia*)	24.7	28.2	20
Budapest (composit)	32	15.6	22.2	32	7.7	19.8	31(~*Craigia*)	24.7	28.2	32
Eger-Kiseged	24	15.6	21.3	24	7.7	12.2	24	24.7	28.2	24
H-boreholes	14	15.6	21.1	14	7.7	13.2	14	24.7	28.9	14
Bécsi street	10	15.6	24.2	10	7.7	19.8	10	24.7	28.2	10
Vörösvári street	12	15.6	25.5	12	7.7	19.8	12	24.7	28.9	12
Kiscell1	9	13.4	25.5	9	7.7	19.8	9	20	28.9	9
Roth-Nebelsick *et al.* 2004; Mosbrugger *et al.* 2005										
Regis III	18	16.5	21.3		9.6	13.3		26	27.9	
Haselbach Seam IV	23	15.7	16.5		3.4	10.9		23.8	27.6	
Beucha	13	15.6	16.1		5	7.8		24.7	25.6	
Seifhennersdorf	66	15.6	15.9		5	5.2		25.7	25.9	
Utescher *et al.* 2007										
Pcinja Basin	8	16.5	25.5		4.8	21.4		26	28.1	
Divljana	15	15.6	22.2		5	13.6		24.7	28.9	
Bozukov *et al.* 2009										
Eleshnitsa	31	16.4	21.1		12.2	12.6		25.6	28.1	
Borino Teshel	24	17	21.1		12.6	12.6		26	27.9	
Momchilovtsi	10	15.9	21.3		12.2	13.3		25.6	28.1	
Polkovnik Serafimo	40	17	19.5		12.6	12.6		25.6	26.1	
Boukovo	30	15.9	21.3		12.2	12.6		25.4	27.9	

Table 6. (Continued.)

Flora	MAP min	MAP max	taxa coexisting	Mpdry min	Mpdry max	taxa coexisting	Mpwet min	Mpwet max	taxa coexisting	Mpwarm min	Mpwarm max	taxa coexisting
this study												
taxa excluded: *Tetraclinis. Comptonia, Matudaea, Ceratozamia*												
Häring	979	1520	16	7	38	16	204	245	16	149	196	16
St. Giustina	979	1812	9	7	38	9	164	293	9	149	221	9
Chiavon	979	1520	9	7	38	9	164	245	9	149	221	9
Rovte Novi Dol	1194	1362	19	21	38	19	204	245	19	149	187	19
Trbovlje	979	1812	14	8	38	14	204	241	14	149	196	14
Nagybátony-Újlak	1194	1520	20	21	38	20	245	254	20	149	187	20
Budapest (composit)	1194	1520	32	21	38	32	245	245	32	149	187	32
Eger-Kiseged	1194	1520	24	21	38	24	204	240	24	118	187	24 (*Rosa; Sloanea*)
H-boreholes	979	1520	14	11	38	14	164	245	14	149	195	14
Bécsi street	823	1520	10	8	43	10	245	245	10	79	221	10
Vörösvári street	979	1520	12	8	38	12	164	245	12	149	196	12
Kiscell1	506	1520	9	8	43	9	71	245	9	8	196	9
Roth-Nebelsick *et al.* 2004; Mosbrugger *et al.* 2005; Mpdry, -warm, -wet this study												
Regis III	823	1281		22	50		204	265		132	195	
Haselbach Seam IV	1231	1281		29	43		180	193		118	120	
Beucha	823	1058		13	50		115	265		84	145	
Seifhennersdorf	1194	1213		32	43		167	221		118	131	
Utescher et al., 2007												
Pcinja Basin	629	1741		4	43		134	293		73	221	
Divljana	1194	1520		21	38		204	245		149	187	
Bozukov *et al.* 2009; Mpwet this study												
Eleshnitsa	1360	1384		32	43		137	141		105	131	
Borino Teshel	1122	1384		32	38		136	241		90	187	
Momchilovtsi	1360	1613		32	40		193	196		108	196	
Polkovnik Serafimo	1122	1356		32	38		131	241		105	116	
Boukovo	1090	1355		32	38		204	204		108	163	
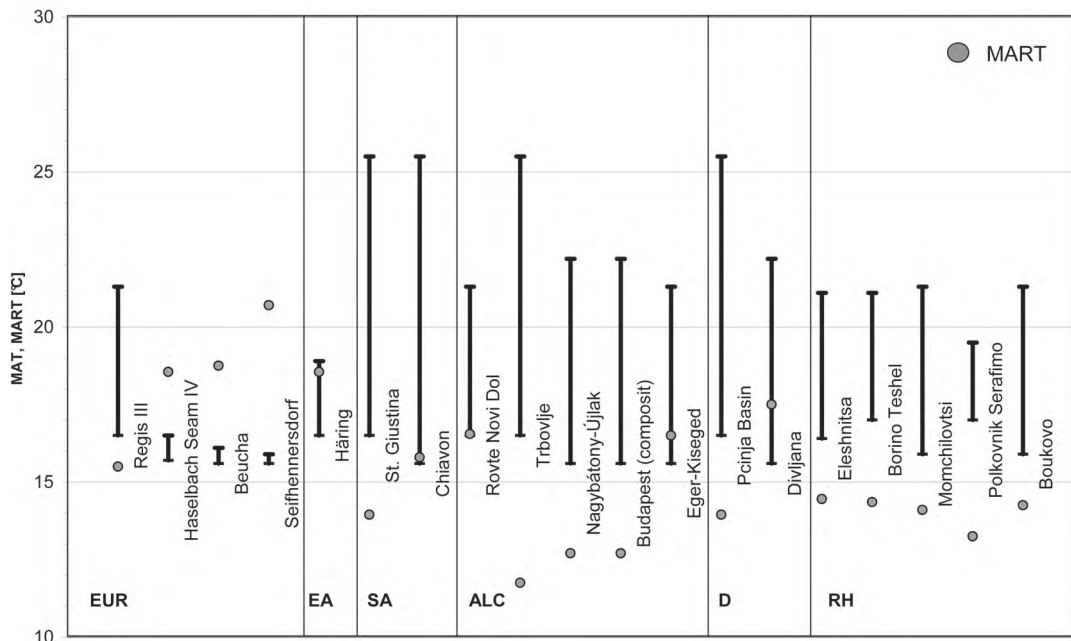
Figure 4. Coexistence intervals for mean annual temperature (MAT). EUR– European plate, EA– Eastern Alpine, SA– South Alpine, ALC– Alcapa, D– Dinarid, RH– Rhodopes.
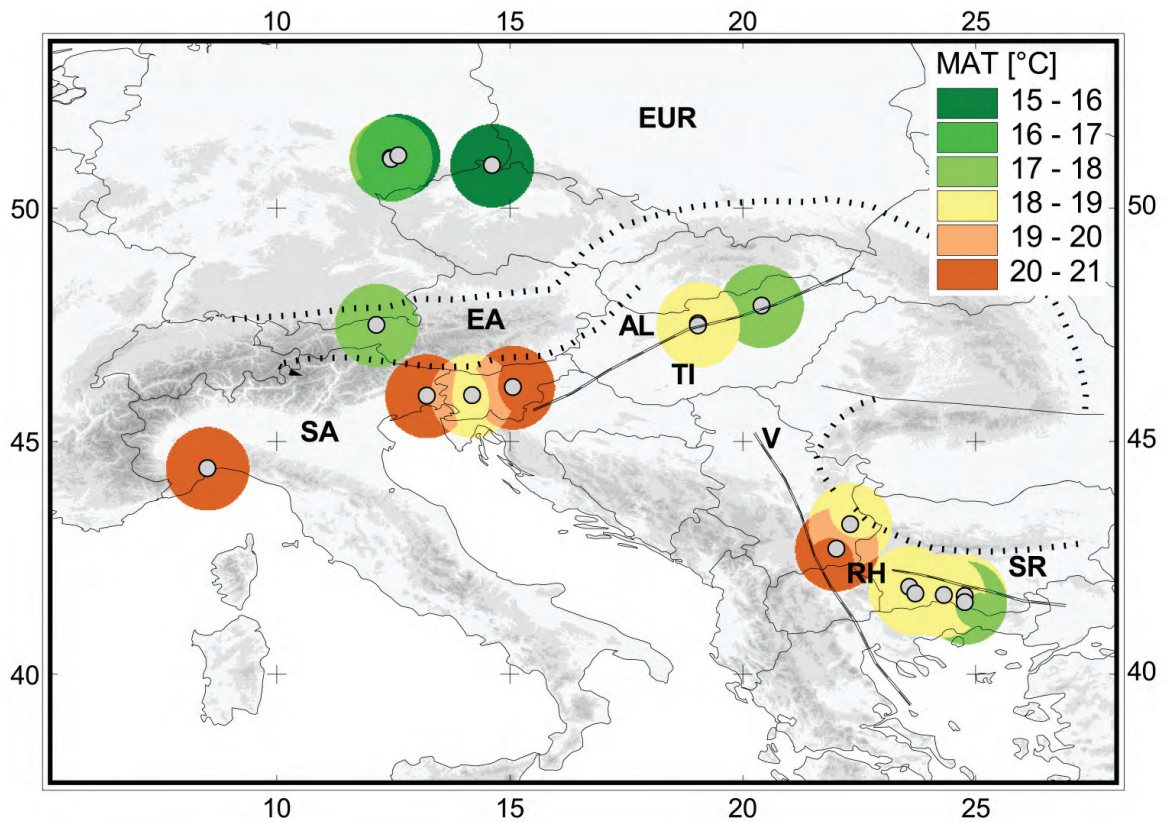

Figure 5. Climate map showing MAT calculated for each floras. EUR– stable European plate, EA– Eastern Alpine area, AL– Alcapa, TI– Tisia, V– Vardar, RH– Rhodopes.
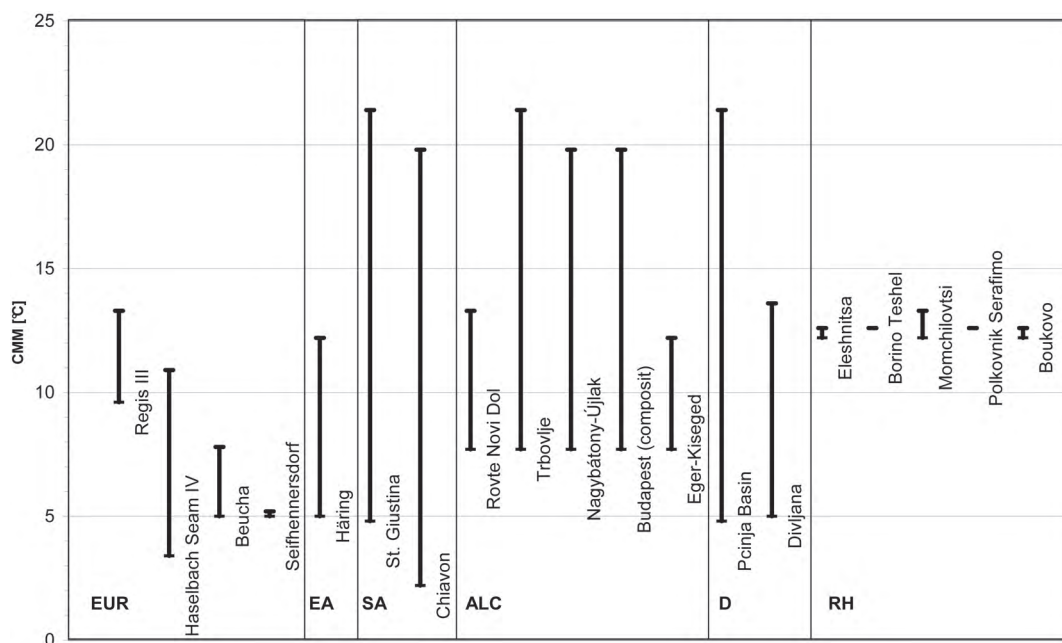
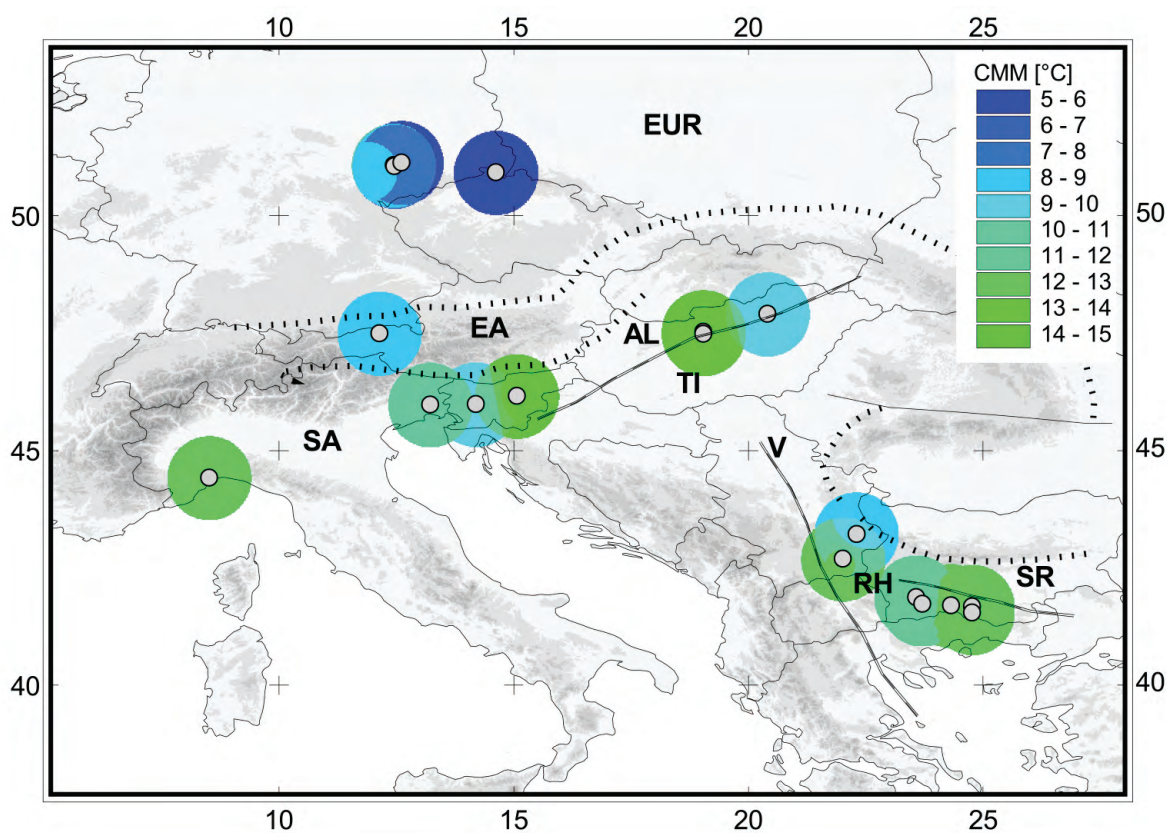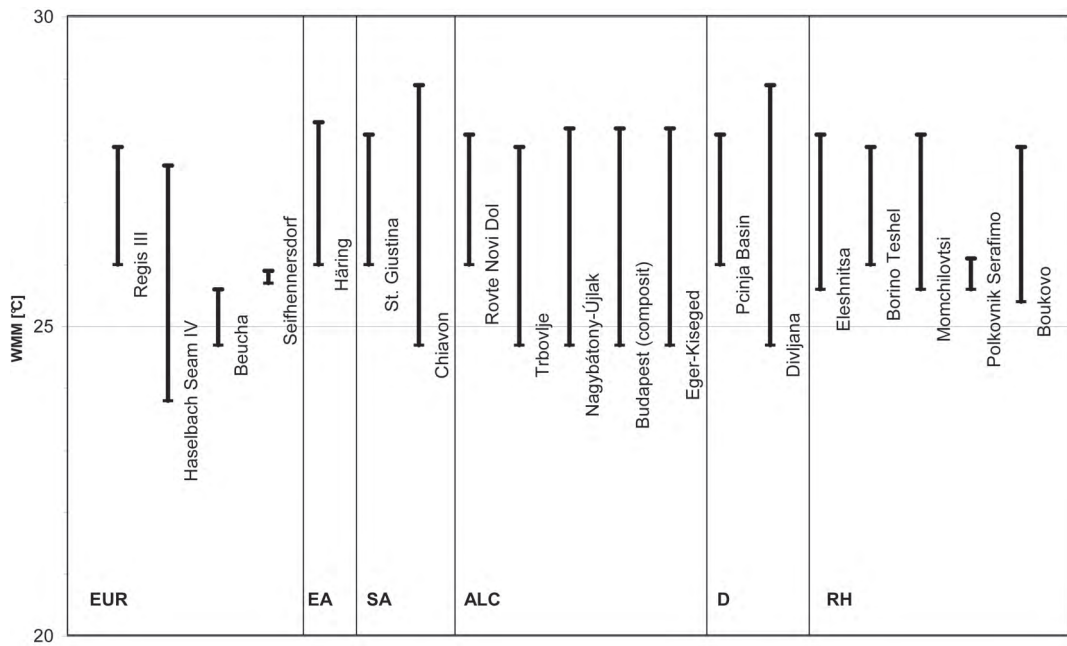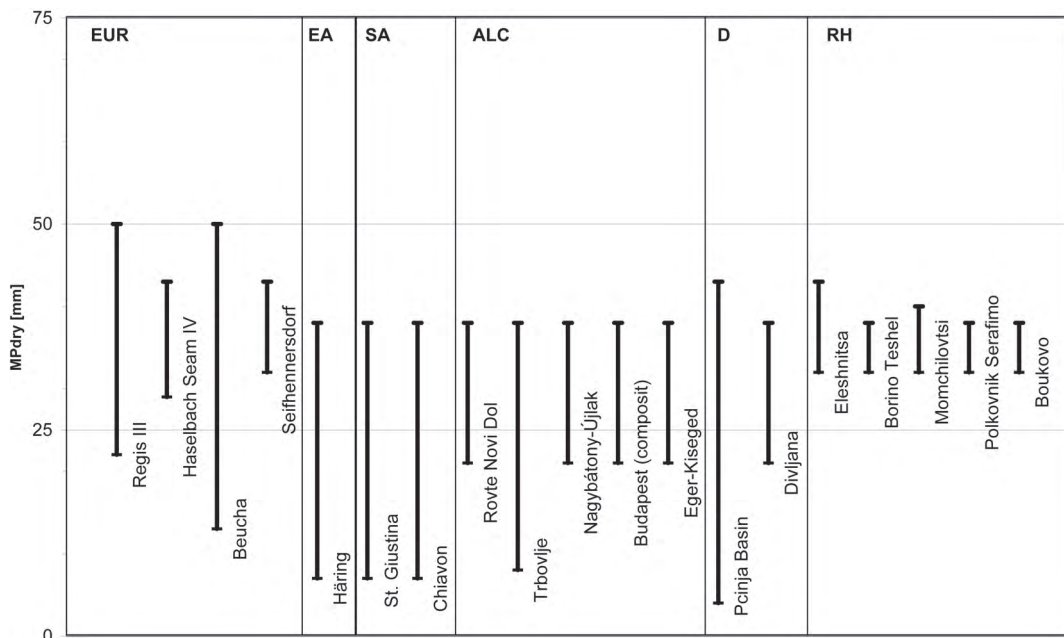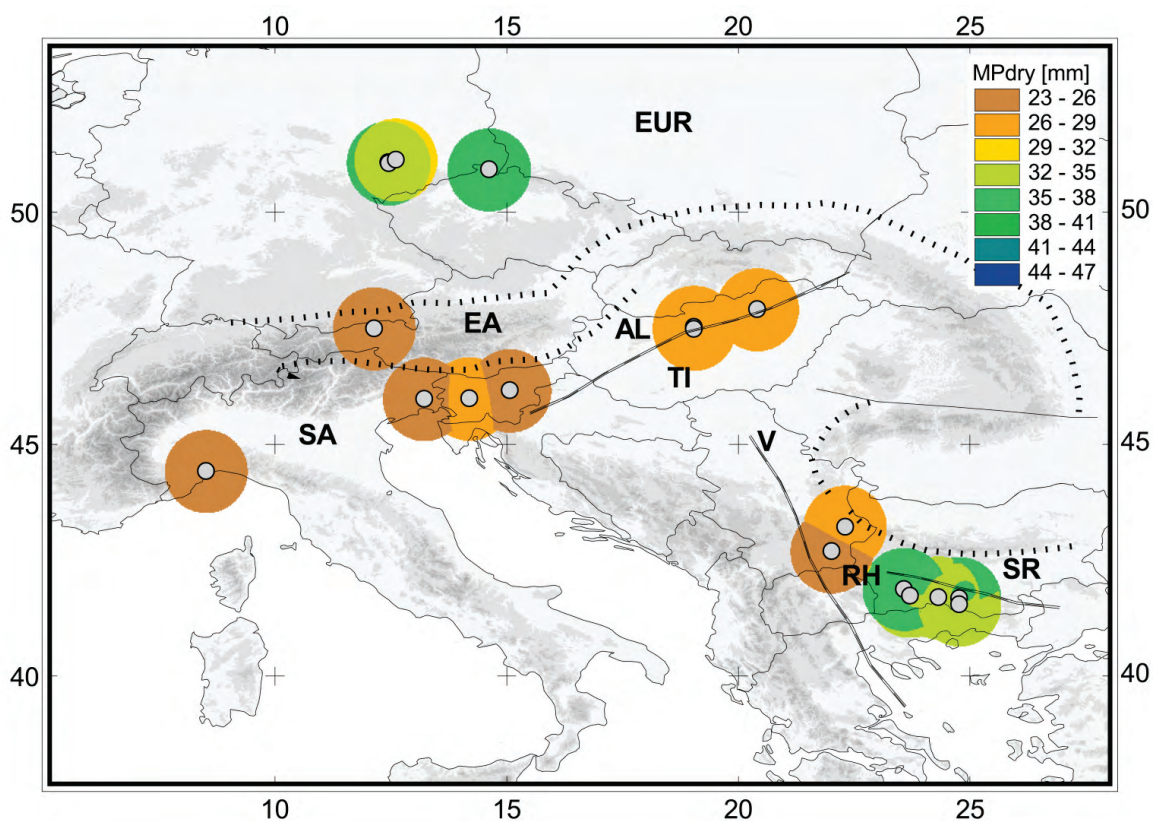**Figure 6.** Coexistence intervals for mean temperature of the coldest month (CMM). Abbreviations as in Figure 4.

Figure 7. Climate map showing CMM calculated for each flora. Abbreviations as in Figure 5.

Figure 8. Coexistence intervals for mean temperature of the warmest month (WMM). Abbreviations as in Figure 4.
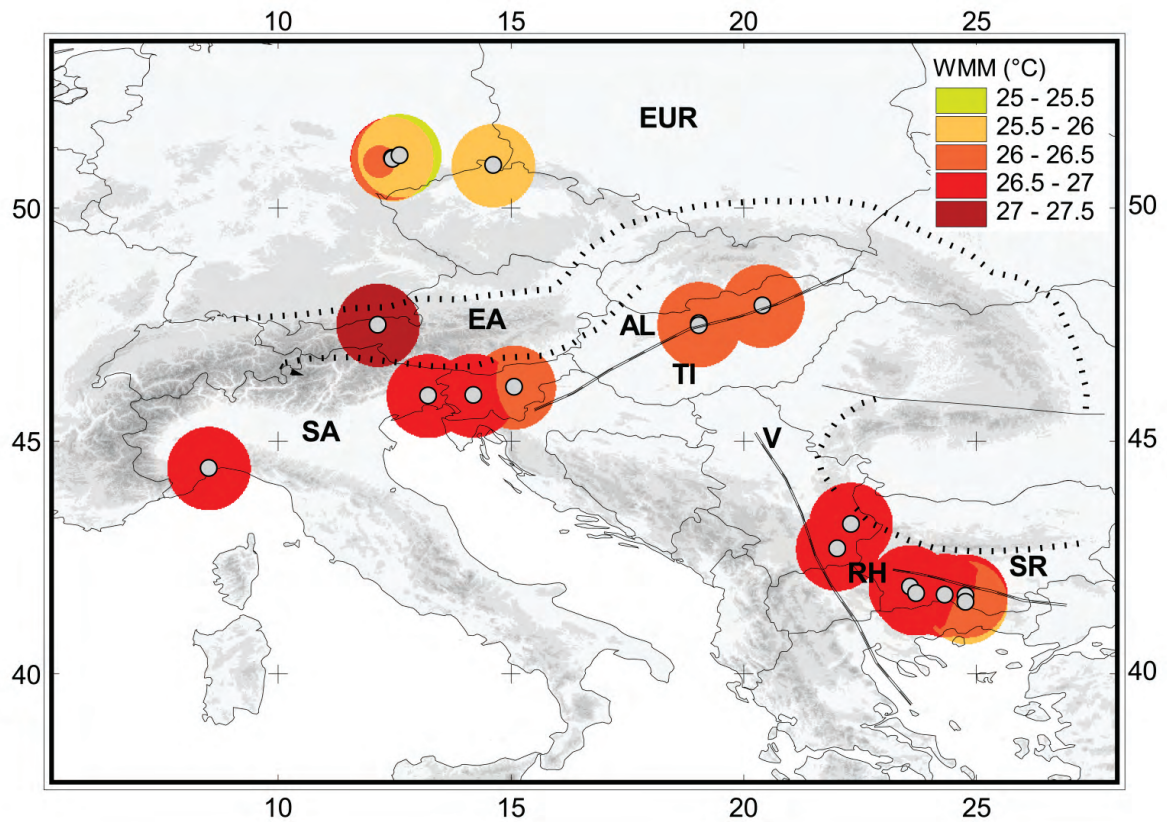
Figure 9. Climate map showing WMM calculated for each flora. Abbreviations as in Figure 5.
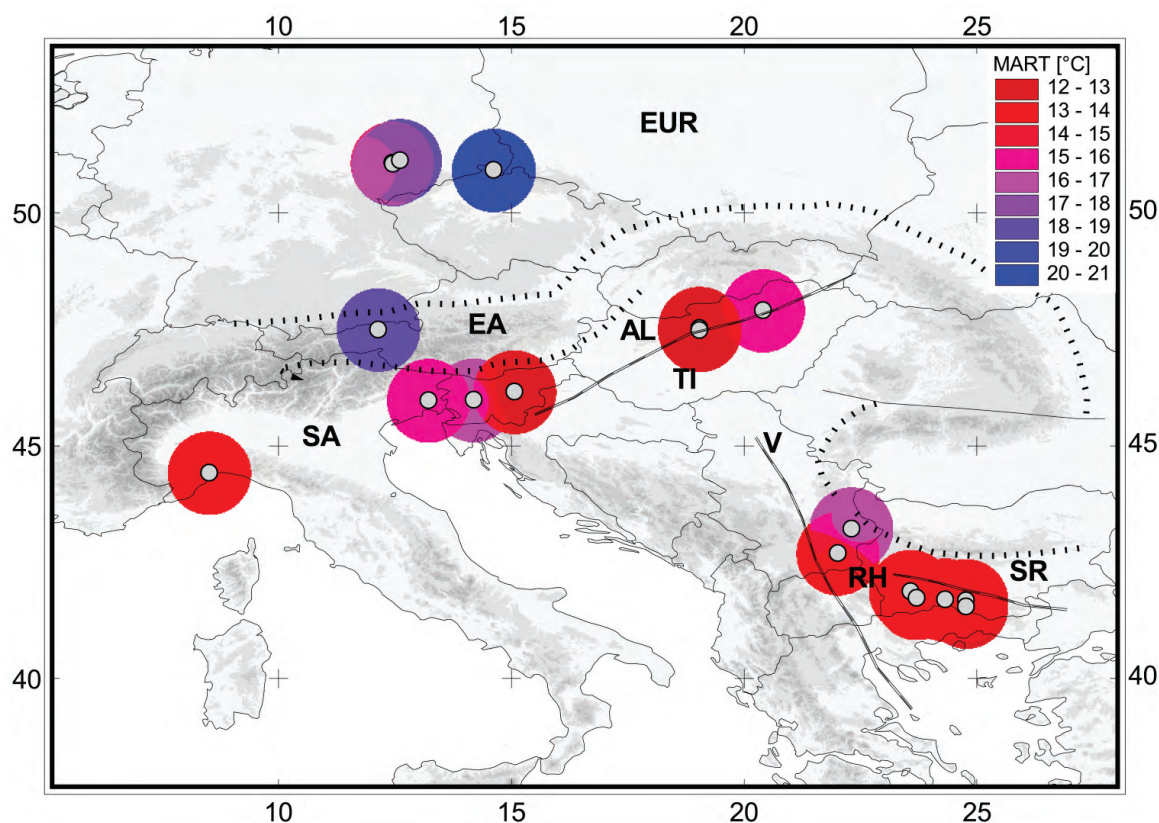
Figure 10. Climate map showing mean annual range of temperature (MART) calculated for each floras. Abbreviations as in Figure 5.
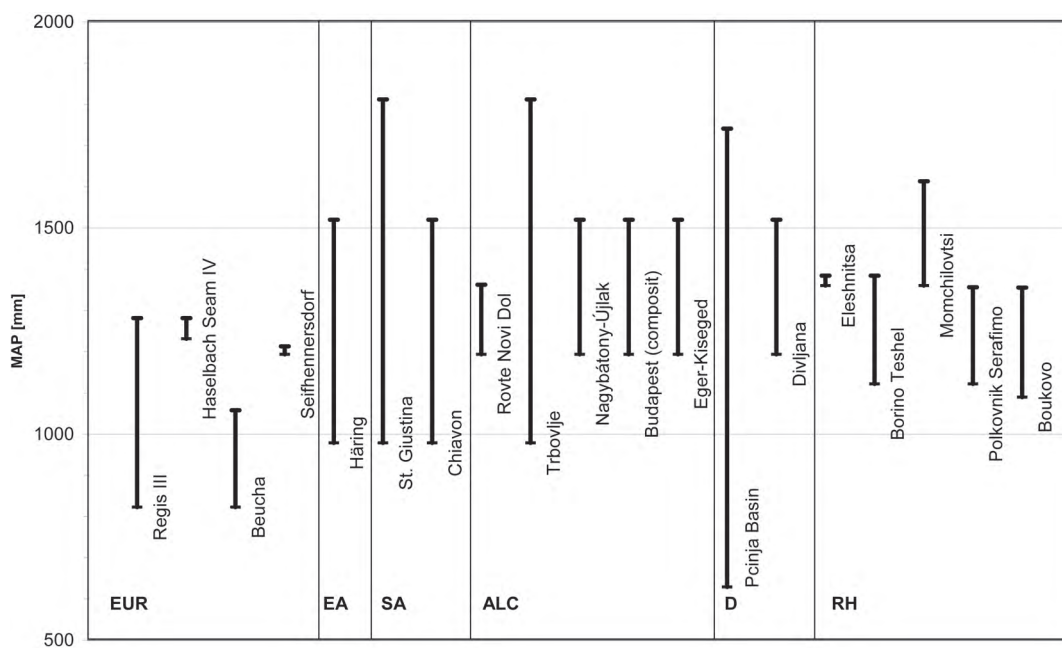
Figure 11. Coexistence intervals for mean annual precipitation (MAP). Abbreviations as in Figure 4.

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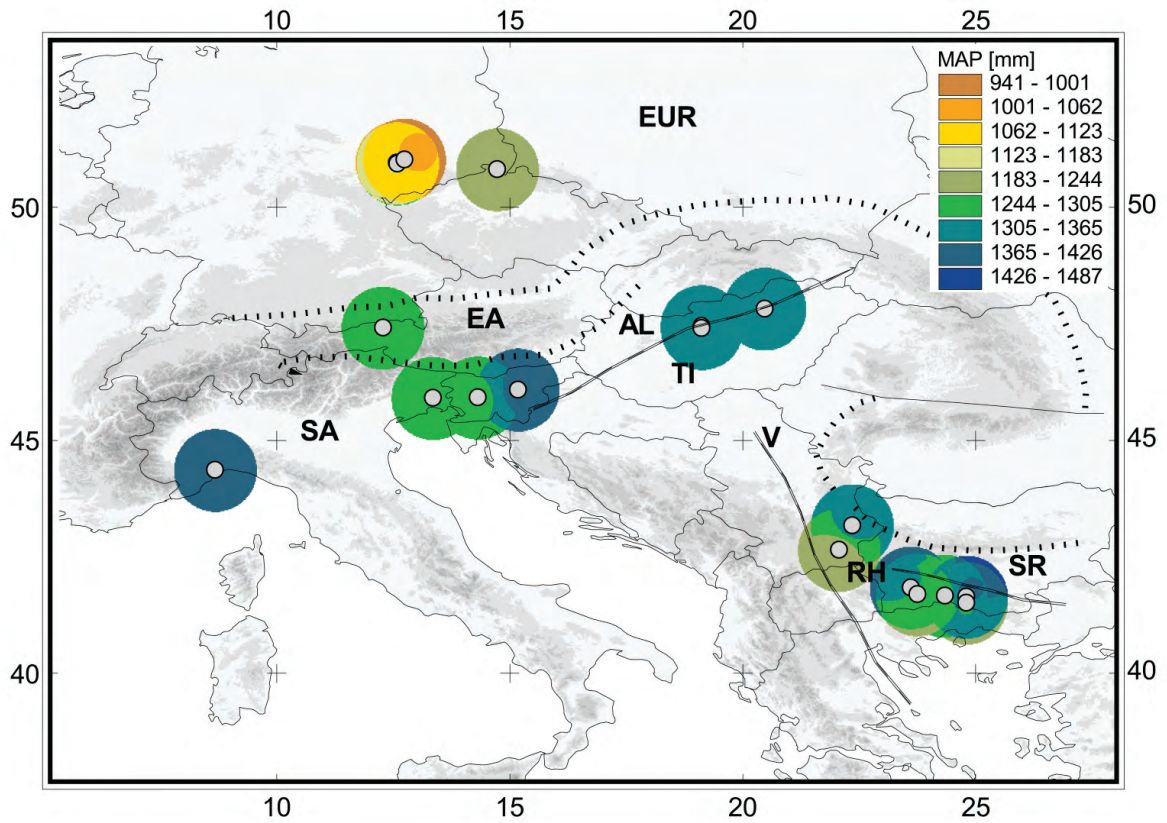
Figure 12. Climate map showing MAP calculated for each flora. Abbreviations as in Figure 5.

Figure 13. Coexistence intervals for mean precipitation of the driest month (MPdry). Abbreviations as in Figure 4.

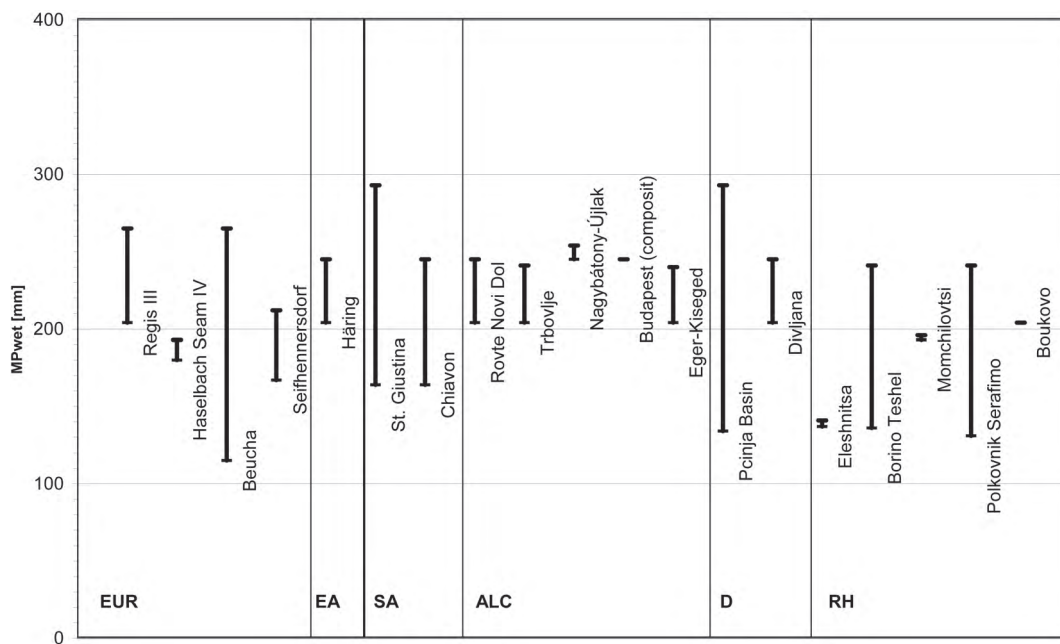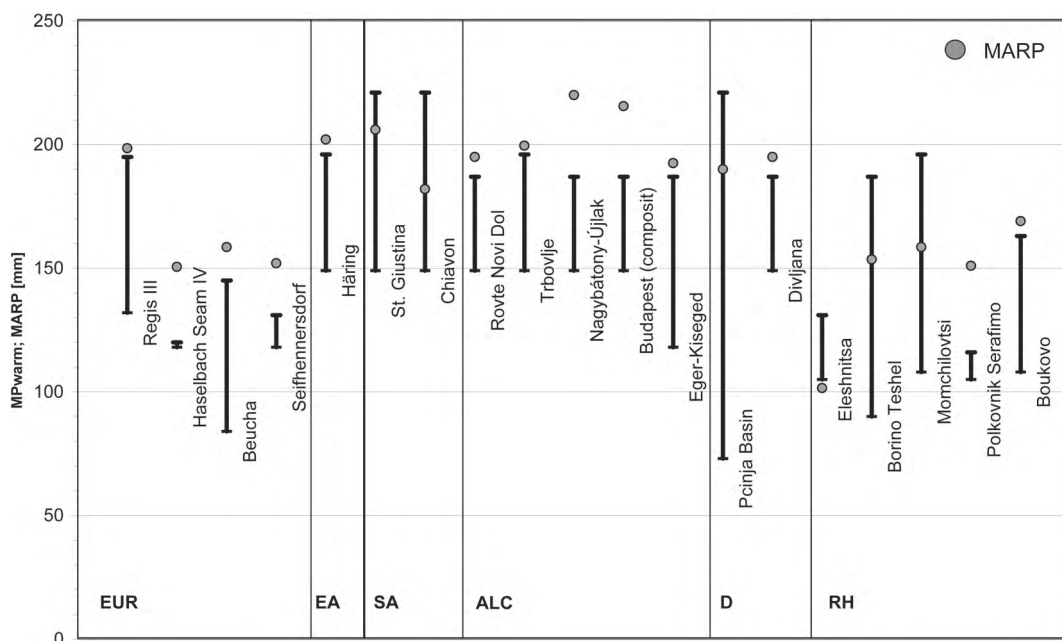**Figure 14.** Climate map showing MPdry calculated for each flora. Abbreviations as in Figure 5.

Figure 15. Coexistence intervals for mean precipitation of the wettest month (MPwet). Abbreviations as in Figure 4.

Figure 16. Coexistence intervals for mean precipitation of the warmest month (Mpwarm). Abbreviations as in Figure 4.
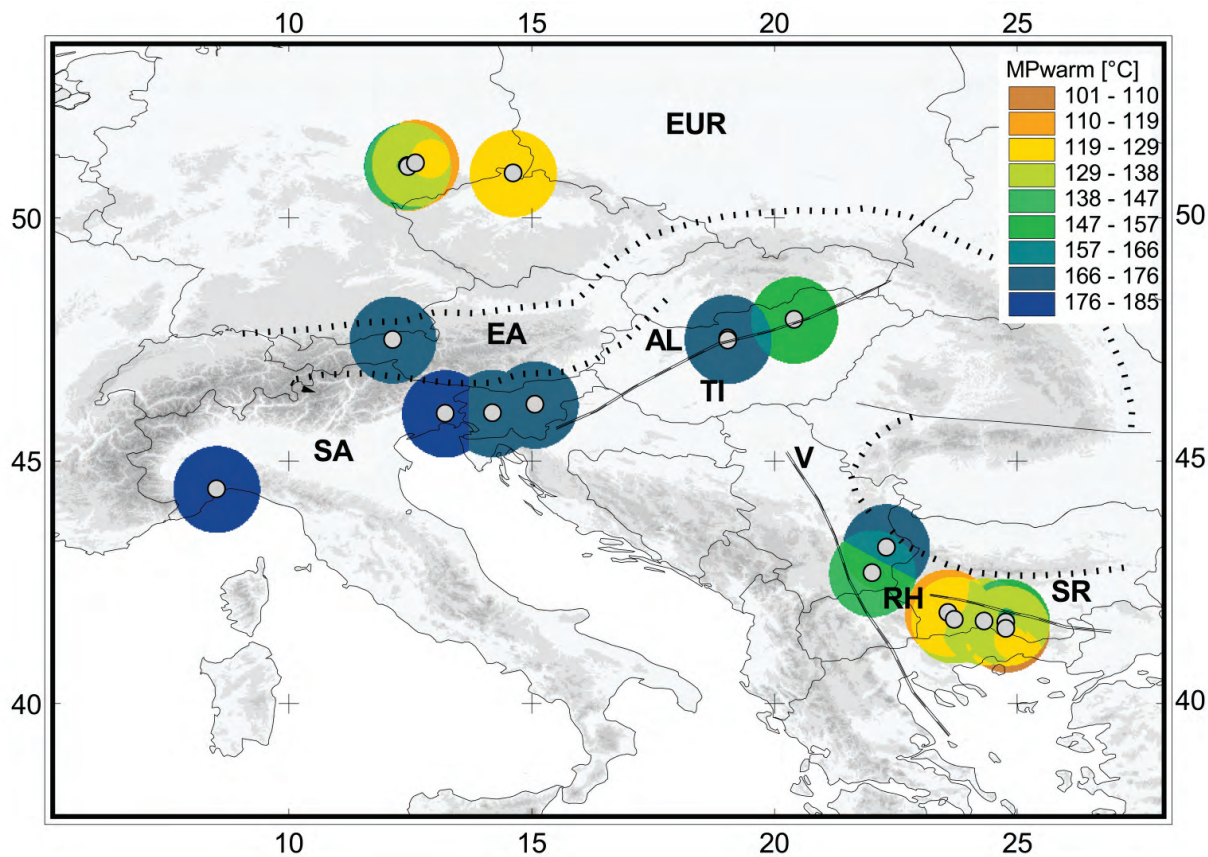

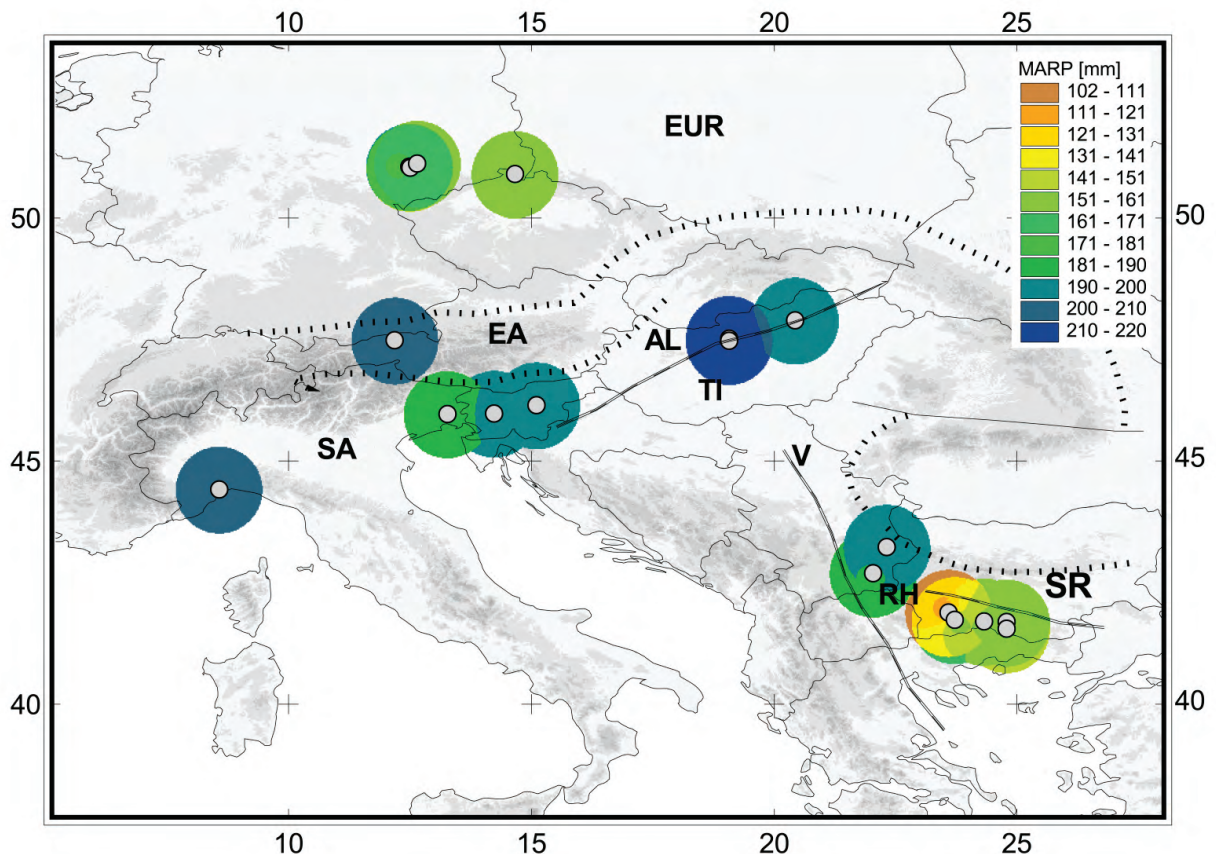**Figure 17.** Climate map showing Mpwarm calculated for each flora. Abbreviations as in Figure 5.

Figure 18. Climate map showing mean annual range of precipitation (MARP) calculated for each floras. Abbreviations as in Figure 5.

for the SA (South Alpine: Italian) and ALC (Alcapa: Hungarian and Slovenian) floras, partly due to the broad intervals. This slight difference is emphasised if we compare the mean values of intervals. Among EUR floras the MAT interval of Regis III shows higher values (16.5–21.5°C), comparable to sites situated to the south of the stable European Plate. The slight differences in MAT between the sites are well demonstrated on a climate map (Figure 5).

Cold month temperatures (CMM) show an even clearer distinction, but prove uniformly a frost-free climate for all localities (Table 6, Figures 6 & 7). CMM ranges between 2–21.5°C and broader intervals were obtained for the ALC floras for the same reason as in the case of MAT. Definitely lower intervals were calculated for the EUR floras (3–11°C), except for the Regis III flora (9.5–13.5°C).

Warm month temperatures (WMM) are quite uniform for all localities, ranging between 23.5–29°C

(Table 6, Figure 8). CMM and WMM results are plotted on maps (Figures 7 & 9).

Mean annual range of temperature (MART) was calculated from the temperature parameters for each flora (Table 6, Figure 4). Definitely higher MART values (15.5–21°C) were obtained for the EUR and EA (Eastern Alpine: Austrian) floras, whereas the ALC, D (Dinarid: Serbian) and RH (Rhodopes: Bulgarian) floras were proved to have more equable temperatures throughout the year with lower MART values (11.5–17.5°C). Distinction in MART is clearly demonstrated on the climate map (Figure 10).

Precipitation values seem to be relatively uniform for the sites, with a MAP ranging between 600–1850 mm (Table 6, Figure 11). This broad interval is mainly due to the Pcinja Basin flora (600–1750 mm). Most of the localities range between 850–1500 mm, with slightly lower values for the EUR floras, as indicated by the climate map (Figure 12).

The mean precipitation of the driest month (MPdry) ranges between 5–50 mm (Table 6, Figure 13). As shown in Figure 14 slightly lower precipitation rates are obtained for the driest month in the ALC, EA and SA floras than for the EUR and RH floras. The mean precipitation of the wettest month (MPwet) ranges between 110–300 mm (Table 6, Figure 15) whereas precipitation values of the warmest month (MPwarm) ranges between 75–220 mm (Table 6, Figures 16 & 17). That means that the warmest month was neither the wettest nor the driest month and it seems to be the case in nearly all floras studied. Mean annual range of precipitation (MARP) was calculated for each of the floras and proved to be relatively low, with values ranging between 100–220 mm (Table 6, Figure 16). As shown by the climate map (Figure 18) no clear distinction is observable between the sites. Slovenian, SA and EA floras tend to have slightly higher values.

Leaf Morphometry

Average dimensions of the leaf fossils are summarized in Table 4 and Figure 19. The Santa Giustina locality is characterized by the largest leaves of *Sloanea olmediaefolia*. Large leaves were also found at Nagybátony-Újlak, with a slightly shorter and wider leaf blade compared to the former locality. Medium-sized leaves were found in Trbovlje and relatively small ones in Eger-Kiseged and Rovte. According to the leaf length/width ratio, the more oval forms are from Trbovlje and Nagybátony-Újlak, while the narrowest ones are from Eger-Kiseged. Statistical evaluation of the leaf area data is summarized in Table 7. There is no significant difference among the localities in the uppermost 3 corresponding triangles. From the fifth triangle onward, there are significantly smaller leaf areas in Eger-Kiseged than in Santa Giustina and Nagybátony-Újlak. Rovte and Trbovlje do not differ significantly from any of the other localities. The reason for this result, at least in part, is the small number of leaves available for comparison.

The largest leaf area of *Eotrigonobalanus furcinervis,* with the least elongated blade forms, is typical at Nagybátony-Újlak. In Santa Giustina there are similar leaf areas but these leaves are longer and narrower. The smallest and narrowest leaves are found in Eger-Kiseged. Statistical evaluation (Table
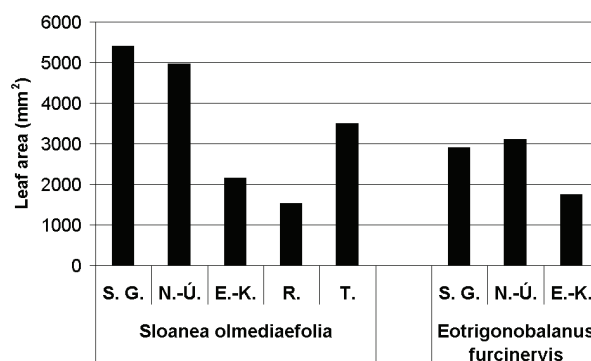

Figure 19. Average leaf area of the studied species. Number of measured leaves are given in Table 4. Abbreviations: S.G.– Santa Giustina, N.-Ú.– Nagybátony-Újlak, E.-K.– Eger-Kiseged, R.– Rovte, T.– Trbovlje.

8) shows that the area of the corresponding triangles in the upper and basal region of the blade does not differ significantly among the studied localities. 4 triangles are significantly smaller in Eger-Kiseged than in Santa Giustina. From the twelfth to sixteenth triangles, there is a significant difference between the smaller leaves of Eger-Kiseged and the bigger leaves of Nagybátony-Újlak. The data from Santa Giustina and Nagybátony-Újlak are similar to each other and show no significant difference.

Palaeoatmospheric CO_2 Levels

Data obtained in this study are the first results for the considered material. The reconstructed C_a values are shown in Table 5 and Figure 20. The range of C_a values of the three sites differs somewhat, with a total range of all three sites from 266 ppm to 1188 ppm. The resulting overlapping interval indicates a C_a between 503–839 ppm during NP23 (Figure 20A).

Discussion

Climate Analysis (Coexistence Approach)

When calculating precipitation variables, *Ceratozamia* Brongn (Vörösvári street, Santa Giustina; Kvaček 2002)*, Matudaea* Lundell (Bécsi street, Eger-kiseged, Nagybátony-Újlak; Kvaček & Hably 1998) and *Tetraclinis* Mast (Bécsi street, Chiavon, Divljana, Eger-kiseged, H-boreholes, Häring, Nagybátony-Újlak, Pcinja, Vörösvári street; Hably 1979; Manchester & Hably 1997; Hably &

Table 7. Area of the triangles of *Sloanea olmediaefolia* leaves from five localities. Numbering of the triangles starts from the apex of leaves. In addition to medians of the values, the statistical groups (= s.g.) of the corresponding triangles (in rows) are also indicated. Letters 'a' and 'b' mean significantly different groups of data according to Dunn's Multiple Comparisons Tests, while 'ab' is intermediate, i.e. does not differ either from the 'a' nor the "b" group. Level of significance: $p < 0.05$. Statistical evaluation is based on all measured leaves of the given localities. Due to the fragmentary state of leaves, more data are available for the middle section of the leaves, i.e. 5–15. triangles than their upper and lower part.

Triangle	Santa Giustina Area (mm²)	s. g.	Nagybátony-Újlak Area (mm²)	s. g.	Eger-Kiseged Area (mm²)	s. g.	Rovte Area (mm²)	s. g.	Trbovlje Area (mm²)	s. g.
1.	211.47	a	104.95	a	111.08	a	55.38	a	77.80	a
2.	137.19	a	79.60	a	75.59	a	33.57	a	78.24	a
3.	89.34	a	70.23	a	61.98	a	21.52	a	68.05	a
4.	144.86	a	159.09	ab	89.13	b	70.62	ab	110.73	ab
5.	115.01	a	156.31	a	47.93	b	49.35	ab	89.77	ab
6.	94.09	a	123.26	a	35.80	b	38.78	ab	78.03	ab
7.	125.34	a	153.40	a	40.89	b	45.54	ab	100.30	ab
8.	100.06	a	139.41	a	32.81	b	34.56	ab	85.32	ab
9.	87.56	a	126.63	a	29.98	b	29.76	ab	81.72	a
10.	94.39	a	134.36	a	30.02	b	28.88	ab	81.04	ab
11.	97.33	a	145.06	a	32.53	b	30.76	ab	80.95	ab
12.	113.97	a	163.87	a	38.99	b	38.31	ab	93.66	ab
13.	101.18	a	130.65	a	32.85	b	33.29	ab	75.78	ab
14.	120.75	a	159.70	a	46.24	b	44.16	ab	103.67	ab
15.	172.74	a	193.26	a	66.73	b	63.19	ab	126.87	ab
16.	118.63	a	108.48	a	45.51	b	42.34	ab	75.75	ab
17.	154.90	a	124.80	a	58.47	b	50.23	ab	84.69	ab
18.	199.85	a	157.42	a	70.74	b	58.55	ab	94.30	ab

Table 8. Area of the triangles of *Eotrigonobalanus furcinervis* leaves from three localities. See Table 7 for notes.

| Triangle	Santa Giustina Area (mm²)	s. g.	Nagybátony-Újlak Area (mm²)	s. g.	Eger-Kiseged Area (mm²)	s. g.
1.	313.86	a	204.23	a	167.55	a
2.	125.41	a	77.90	a	93.35	a
3.	93.44	a	46.87	ab	44.58	b
4.	85.76	a	51.15	ab	37.27	b
5.	40.06	a	30.46	a	18.52	a
6.	24.35	a	19.98	a	11.77	a
7.	24.58	a	26.58	a	14.65	a
8.	20.06	a	17.74	a	11.31	a
9.	19.88	a	16.75	ab	10.26	b
10.	19.86	a	19.35	a	10.15	a
11.	23.04	a	21.82	ab	11.36	b
12.	28.30	ab	33.25	a	15.42	b
13.	28.79	ab	33.37	a	14.12	b
14.	44.14	ab	49.16	a	21.57	b
15.	84.11	ab	95.41	a	40.63	b
16.	70.70	ab	85.00	a	42.72	b
17.	106.61	a	122.26	a	89.71	a
18.	227.30	a	189.49	a	109.23	a
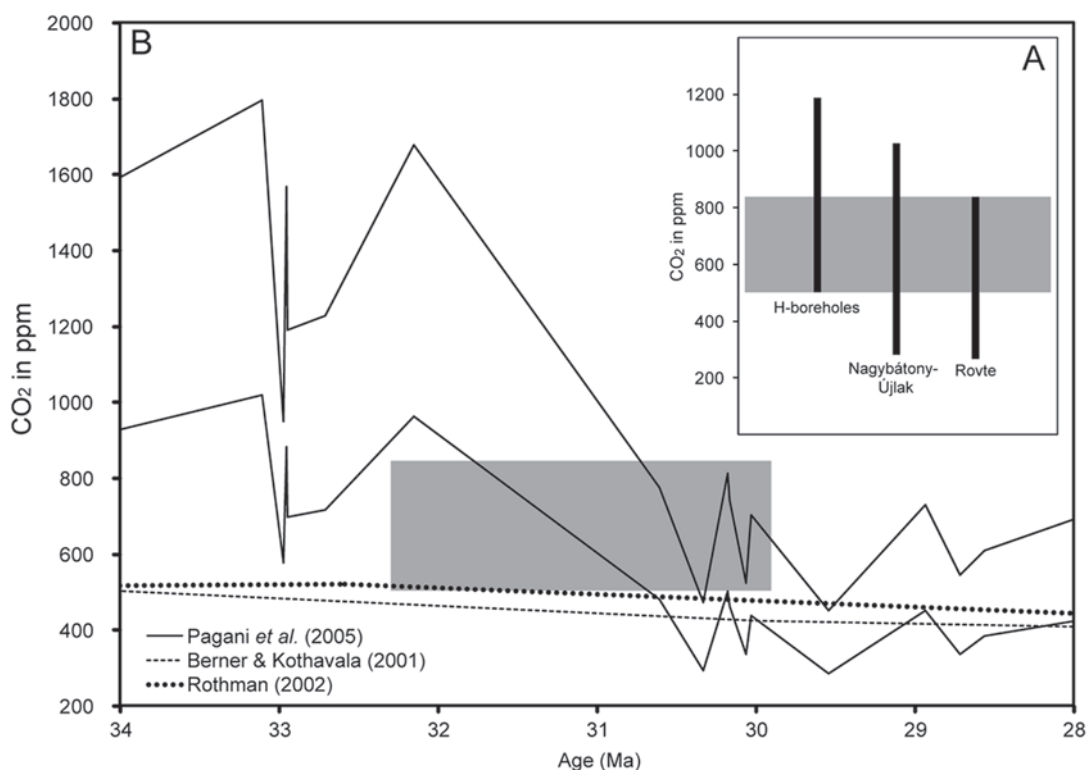
Figure 20. Results of C_a reconstructions obtained within this study applying the mechanistic-theoretical approach of Konrad *et al.* (2008). Calculations are based on stomatal data of *Sloanea olmediaefolia* from H-boreholes and Nagybátony-Ùjlak (both Hungary) and Rovte (Slovenia). **(A)** Single CO_2-ranges in ppm (black rectangles) obtained by varying sensitive parameters and the resulting overlapping interval (grey shaded area). **(B)** Results compared to proxy data and geochemical models: Pagani *et al.* (2005), Berner & Kothavala (2001) and Rothman (2002) with $pCO_2(0)= 280$ ppm (personal communication, D. Rothman, 2010). Grey shaded area– overlapping interval during NP23.

Fernandez Marrón 1998; Kvaček & Hably 1998; Hably & Manchester 2000; Hably *et al.* 2000, 2007; Tamás & Hably 2005) proved to be outliers whereas concerning temperature variables *Ceratozamia* and *Matudaea* indicated rates falling outside the ranges corresponding to most taxa.

Tetraclinis, a widespread conifer genus in the European Palaeogene and Neogene, (considered by some authors to represent an extinct genus, *Libocedrites*, Wilde & Frankenhäuser 1998) is monotypic today with *Tetraclinis articulata* Mast. surviving in a restricted area under warm and dry (winter-rain), Mediterranean type climatic conditions (Krüssman 1960; Farjon 2005). The climatic tolerance of the modern species most probably does not

correspond to that of its fossil representatives known to form outliers in palaeoclimate analysis (e.g., Erdei *et al.* 2007). Cycads (Cycadales) flourished in both hemispheres and showed high diversity in the past but their modern representatives form a relict group. Extant *Ceratozamia* is restricted to Mexico, Guatemala and Belize, mainly in dense, moist woodlands (Norstog & Nicholls 1997). The ecological range of extant cycads may reflect a different climate spectrum to that which these plants must have been adapted to in earlier times. This is supported by the absence of clear correlation between habitat and cuticular characters, e.g., deeply sunken stomata under humid conditions (Erdei *et al.* 2010). Cycads must have been relatively widespread in the

European early Cenozoic, as attested by the fossil record (cf. Erdei *et al.* 2010), in floras of both the stable European plate and the much more southern terranes under various climatic conditions.

The Neotropical *Matudaea* genus occurs in Central America (Mexico, Honduras, Guatemala, Nicaragua) in humid mountain forests (Lundell 1981). Its climatic tolerance is expressed in much higher precipitation rates than those delimiting most other taxa in our record.

The slightly lower values of MAT for the EUR floras (Figure 5) are congruent with the postulated Early Oligocene palaeogeography of Europe.

The palinspastic reconstruction of the external Carpathian flysch nappes (Oszczypko & Slaczka 1985) suggests that the Inner Carpathian domain must have been located several hundred kilometres to the south and west of its present position. The Pieniny Klippen belt was located during the NP23/24 transition some hundred kilometres further southwest (figure 3 in Csontos *et al.* 1992) meaning several degrees further south in latitude.

The Rhodope Massif is considered to be a microplate that has remained attached to Eurasia since the Triassic (Golonka 2004). Since the Late Eocene a northward movement of about 2° latitude was assumed for the Rhodope massif as part of the stable W Eurasian plate (Dilek 2006; Bozukov *et al.* 2009).

The SA floras occupied a transitional position to the Alcapa microplate and their relative location is not clearly defined (Hably 2006).

The slight difference in MAT is mainly due to variations in CMM, i.e. its lower values for the EUR floras resulting in higher MART (Figures 7 & 10). Nevertheless, a frost-free climate is assumed for all localities studied.

Precipitation parameters indicate a relatively humid climate for all floras. The minor difference in warm month and wettest month precipitation values suggests a relatively humid warm season, but low precipitation rates in the driest month proves some seasonality. Based on the calculated parameters, a climate with a humid warm season can be assumed, but with a low annual range of precipitation (Figure 18). Lower MP dry values of the ALC, EA and SA floras express a more pronounced seasonality in

precipitation compared to the EUR and RH floras. Earlier studies presumed a 'subhumid' (seasonality in rainfall or low values of annual precipitation) warm 'subtropical' (Kvaček 2002), or seasonally dry tropical (Hably & Thiébaut 2002) climate, based on the Hungarian floras (Tard Clay floras). Varying humidity conditions in these floras may further be supported by the abundance and diversity of winged fruits and seeds (cf. Kvaček & Hably 1998; Hably & Manchester 2000; Hably & Thiébaut 2002; Hably 2010). Pounden *et al.* (2008) found that dispersal distances of some (bilaterally symmetric) winged seed types may be considerably reduced by collisions with other vegetation in a forest. That suggests that in an open vegetation type these seeds may have more successful dispersal. The ratio of (certain types of) winged seeds and vegetation type seems to bear correlation, which theoretically may imply an influence of humidity.

Our results correspond well to earlier floral studies and vegetation reconstructions. The Palaeogene Basin (Hungary and Slovenia) has a warmth-demanding flora, which contains some exotic taxa but no traces of temperate elements, contrasting with coeval assemblages recorded in Germany and Bohemia, in which temperate/deciduous ('arctotertiary') elements had already had a significant role. In the pre-Neogene palaeogeographic reconstructions discussed above the Intra Carpathian area was sharply separated from the stable European plate, with only some connection to the west. This agrees well with the results of a floral comparison of the Tard Clay floras (Palaeogene Basin, Hungary) and the Santa Giustina flora (Italy) (Hably 2010). The revision by Hably revealed an overlap of taxa of 44% and specific shared elements like *Kydia kräuseli* or *Acherniaephyllum hydrarchos*, which are only known from these areas. This suggests a floral connection of the respective areas as early as the early Oligocene (Hably 2010).

The Bulgarian Early Oligocene vegetation was dominated by evergreen forests (e.g., *Eotrigonobalanus*-Lauraceae forests) developed under 'subtropical' moderately humid and warm conditions with periodic short-term dry climate phases. The sclerophyllous vegetation of the Boukovo site (shrubby vegetation of 'macchia' type dominated by evergreens, Palamarev *et al.* 1999) is explained by the specific combination of high temperatures and

local edaphic and/or orographic conditions (Bozukov *et al.* 2009).

Kvaček & Walther (2001) compared the phytogeographical provinces, the southern Paratethys (~Palaeogene Basin) and the northern Boreal Provinces (~European plate), and distinguished them by the role of subtropical elements. Assemblages of the southern province mostly bound to nearshore environments are characterized by a higher number of thermophilic taxa and the survival of rare ancient elements from the Eocene (e.g., *Doliostrobus* Marion, *Raskya* Manchester & Hably). Arctotertiary elements appeared in the fossil record only later, during the Late Oligocene. In contrast arctotertiary elements are already well represented in the Early Oligocene assemblages of the northern province. The climate analysis of Late Oligocene (Egerian) macrofloras of Hungary (Erdei & Bruch 2004) resulted in lower mean annual and cold month temperatures (9.3–20.5°C / −3.3–13.3°C) compared to Early Oligocene climate data suggesting a cooling of climate. This is nicely supported by the increasing occurrence of temperate (arctotertiary) elements in the Late Oligocene (Egerian) macrofloras of Hungary (Hably 1988, 1994; Kvaček & Hably 1991).

Akhmetiev *et al.* (2009) reconstructed Palaeogene trends in climate and vegetation based on prevailingly mesophytic vegetation from the Far East and Central Europe. Assemblages from the Bohemian Massif (e.g., Kundratice, Behlejovice, Seifhennersdorf, Suletice, etc., equivalent to the Boreal phytogeographic Province in Kvaček & Walther 2001), representing both coal forming and volcanic floras, contain evergreen as well as deciduous elements. Accordingly, zonal vegetation is described as mainly mixed mesophytic forests. Although some taxa are shared between Central European and Palaeogene Basin floras e.g., *Sloanea*, *Eotrigonobalanus*, *Platanus neptuni*, the apparent absence of numerous deciduous elements in the early Oligocene Palaeogene Basin, e.g. Betulaceae, *Salix*, *Acer*, etc. sharply differentiates these floral regions.

Leaf Morphometry

The results of the morphometric study were compared with the variability in leaf size for some modern species published in the literature. The variability in leaf size of the studied fossil species shows a similar order of magnitude to the biological variability of modern woody species. A remarkable difference in leaf area between fossil localities was found in the case of *Sloanea olmediaefolia*. Compared with other woody species, the variability of *Sloanea olmediaefolia* is surpassed only by the highly variable *Metrosideros polymorpha* Gaudich. sampled along an altitudinal gradient (Cordell *et al.* 1998). Leaf size is affected by various climatic factors. Higher humidity results in larger leaf area (Núnez-Olivera *et al.* 1996; Talhouk *et al.* 2000). The amount of light also has a great impact on leaf size and structure (Chazdon 1988). Higher light intensity mainly results in the formation of smaller and thicker leaves (Gratani 1997; Tucić *et al.* 1998; Klich 2000; Coelho *et al.* 2002; Kalapos & Csontos 2003; Westoby & Wright 2003; Aranda *et al.* 2004; Wright *et al.* 2007), but there is evidence for the opposite, as well (Chazdon 1988; Mojzes *et al.* 2003).

Morphometric measurements thus may contribute additional information to our climate calculations. Among *Sloanea* and *Eotrigonobalanus* leaves from the Hungarian, Slovenian and Italian localities having quite uniform floral composition, the smallest and narrowest leaves (= the smallest leaf areas) were measured from Eger-Kiseged (Figure 19). As discussed above, lower humidity or higher light intensity mainly results in smaller leaf area. This may be attributed to altitudinal or habitat differences here, since calculated precipitation parameters do not indicate lower humidity for the Eger Kiseged locality. Edaphic factors e.g., soils, variable exposure to light or wind, or a rain-shadow position of the vegetation may result in habitat difference. A small-scale dry climatic spell to which the vegetation adapts without drastic change in floral composition serves as additional explanation.

Atmospheric pCO$_2$

The C_a values of the single locations (H-boreholes, Nagybátony-Ùijlak and Rovte) obtained in the present study fall within the range of the other C_a reconstruction approaches presented by Pagani *et al.* (2005), Berner & Kothavala (2001) and Rothman (2002) (Figure 20B). The pCO$_2$ values provided by Pagani *et al.* (2005) are based on stable carbon isotopic values of di-unsaturated alkenones obtained

from deep sea cores. The C_a provided by Berner & Kothavala (2001) and Rothman (2002) were obtained by geochemical modelling. Our own results and other proxy data as a whole show a high degree of overlap. The overlapping interval of the three locations obtained with stomatal data from *Sloanea olmediaefolia* ranges from 503 to 839 ppm. The lower limit of our overlapping C_a-range is close to the values of Berner & Kothavala (2001) and Rothman (2002). Furthermore, they overlap with the results of Pagani *et al.* (2005). It is therefore suggested that a data interval of about 500 to 840 ppm represents a realistic range of C_a between 30 to 32 Ma.

The differences between C_a data reconstructed for the three sites may be caused by statistical reasons that are an inherent characteristic of proxy data. Firstly, stomatal parameters show natural variation which affects the margin of the results. Secondly, climate parameters were used as input parameters that were reconstructed by CA, and these show also a statistical error margin caused by various factors (Mosbrugger & Utescher 1997). It is therefore not to be expected that the results from all three sites would be completely identical. As a whole, the data sets overlap to a high degree, indicating that the data are reliable (also indicated by the good agreement with the other proxy data shown in Figure 20).

A C_a value in the Early Oligocene close to 500–840 ppm is much higher than the pre-industrial value. It is much lower than the values that are usually provided for the Eocene, where peak values of 2000 ppm and more are found in several proxy data sets (Pearson & Palmer 2000; Pagani *et al.* 2005). A substantial decrease in C_a from the Eocene to the Oligocene is also in accordance with studies that identify C_a as a triggering agent of Antarctic glaciations (DeConto & Pollard 1983; Tripati *et al.* 2005). Results of recent modelling studies indicate that a C_a threshold of about 750 ppm is required for growth of Antarctic ice sheets (DeConto *et al.* 2008) which is in excellent agreement with the interval of C_a indicated by our and other proxy data.

Conclusions

Our multi-proxy approach provides a detailed insight into the climate of the Early Oligocene using fossil floras. A detailed climatological analysis combined with leaf-morphological studies and modelling of the palaeoatmospheric CO_2 level using stomatal and $\delta^{13}C$ data is given. A special focus was placed on Early Oligocene (Kiscellian), well-dated and documented fossil macro-floras preserved in sediments of the Palaeogene Basin (Hungary and Slovenia). Climate data were obtained by the Coexistence Approach for Kiscellian floras of the Palaeogene Basin (Hungary and Slovenia) and coeval assemblages from Central and Southeastern Europe. Additional precipitation variables were reconstructed for some climate datasets already published. A morphometric analysis of leaves was applied at Hungarian, Slovenian and Italian localities. Finally, CO_2 levels were estimated/inferred using a recently introduced mechanistic model.

Calculated climate variables suggest a generally warm and frost-free climate with a low annual range of temperature. A slight difference in temperature parameters was recorded between localities from Central and southeastern Europe. The lower MAT values of the EUR floras are mainly attributable to the definite difference in the mean temperatures of the coldest month. Consequently, the mean annual range of temperature proved to be higher for the EUR floras. Precipitation parameters are more uniform, suggesting a humid warm season but combined with seasonality in precipitation to various degree in the individual floras. The climate reconstructed for the Palaeogene Basin floras may correspond to the Cfa (without dry season) or Cw (dry cold season) climate types in the Köppen-Geiger climate classification system (Kottek *et al.* 2006; Peel *et al.* 2007). Results of climate analysis support palaeogeographic reconstructions showing the Palaeogene Basin several degrees of latitude farther south than today.

Morphometric analysis reveals differences between leaves from the Hungarian, Slovenian and Italian localities and suggests a definite habitat or small-scale climatic difference for the Eger-Kiseged assemblage.

Extending the scarce information available on atmospheric CO_2 level during the Oligocene we provide data for a well-defined time-interval. Reconstructed atmospheric CO_2 levels fall in the range of previous calculations obtained by various

methods and agree well with threshold values for growth of Antarctic ice sheets suggested by recent modelling studies. The novel method by Konrad *et al.* (2008) raises new aspects of macro-flora studies for the future.

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