Palaeoclimate analysis of the flora of the Klikov Formation, Upper Cretaceous, Czech Republic

ZUZANA VÁCHOVÁ & JIŘÍ KVAČEK

The Late Cretaceous flora of the Klikov Formation (Upper Turonian–Santonian) in South Bohemia comprises 110 species representing pteridophytes, ferns, conifers, angiosperms, macro and mesofossils. Palaeoclimatic analysis of the Klikov Formation Flora using methods of Leaf Margin Analysis, Climate Leaf Analysis Multivariate Program (CLAMP) and the Nearest Living Relative allows us to conclude that this flora experienced a seasonally dry subtropical climate. Mean annual temperature is predicted to have been approximately 15°C. Numerous charcoalified fossils strongly suggest frequent fires typical of a seasonally dry climate. • Key words: flora, Klikov Formation, Late Cretaceous, palaeoclimate, CLAMP, CoA.

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Distribution and physiognomy of plants as well as plant assemblage characteristics are strongly influenced by climate. A number of studies have been published examining this relationship (Bailey & Sinnot 1915; Wolfe 1979, 1993; Wing & Greenwood 1993; Wilf 1997; Mosbrugger 1999; Uhl *et al*. 2007). Two different groups of palaeoclimatical methods are currently used to deduce the influence of climate on plant distribution and characteristics. The first group is based on analyses of morphological characters of woody dicot leaves (Bailay & Sinnot 1915; Wolfe 1979, 1993; Wing & Greenwood 1993; Wilf 1997). The second group is based on choosing the nearest living relatives of the fossil plants (Mosbrugger 1999, Mosbrugger & Utescher 1997, Uhl 2006). Cretaceous plant assemblages contain numerous extinct family and genera. Interpretations of their palaeoecology usually require specific tools and methods. In this case study, we attempt to combine both of the above mentioned approaches: leaf morphology methods, which are usually used in studies of Cretaceous floras (Herman & Spicer 1996; Herman & Kvaček 2002, 2007; Herman *et al*. 2002; Kenedy *et al*. 2002); and the Nearest Living Relative method (NLR), which we used here experimentally bearing in mind that the method has its limits with Cretaceous floras and can produce larger deviations than predicted. Scarcity of living relatives and the degree of relatedness between recent and Cretaceous taxa are the largest problems when using the Nearest Living Relative method. However, we attempted to use both methods in order to demonstrate a comparison between the two. This could help us in understanding the applicability and comparability of both palaeoecological methods in relation to Cretaceous plant assemblages. A comparison of several methods, based on different primary data, generally gives higher credibility of final results. However, we understand that the degree of accuracy of these methods applied to Cretaceous plant assemblages cannot be as high as is usual in the Tertiary. The main problem with the NLR method in Cretaceous plant assemblages is the difficulty of determining the nearest living relative. Another factor decreasing the accuracy of our data is the poor preservation of leaf impressions from the Klikov Formation.

Geological setting

The fossil leaves in this study come from the Klikov Formation, basal member of the South Bohemian Basins. The South Bohemian Basins consist of two parts, the Budějovice and Třeboň Basins, separated from each other by Lišov Horst (Rudolfov Ridge). The basins together occupy an area of 2300 km^2 (Fig. 1). Sedimentation in the basins began in the Late Cretaceous and continued intermittently

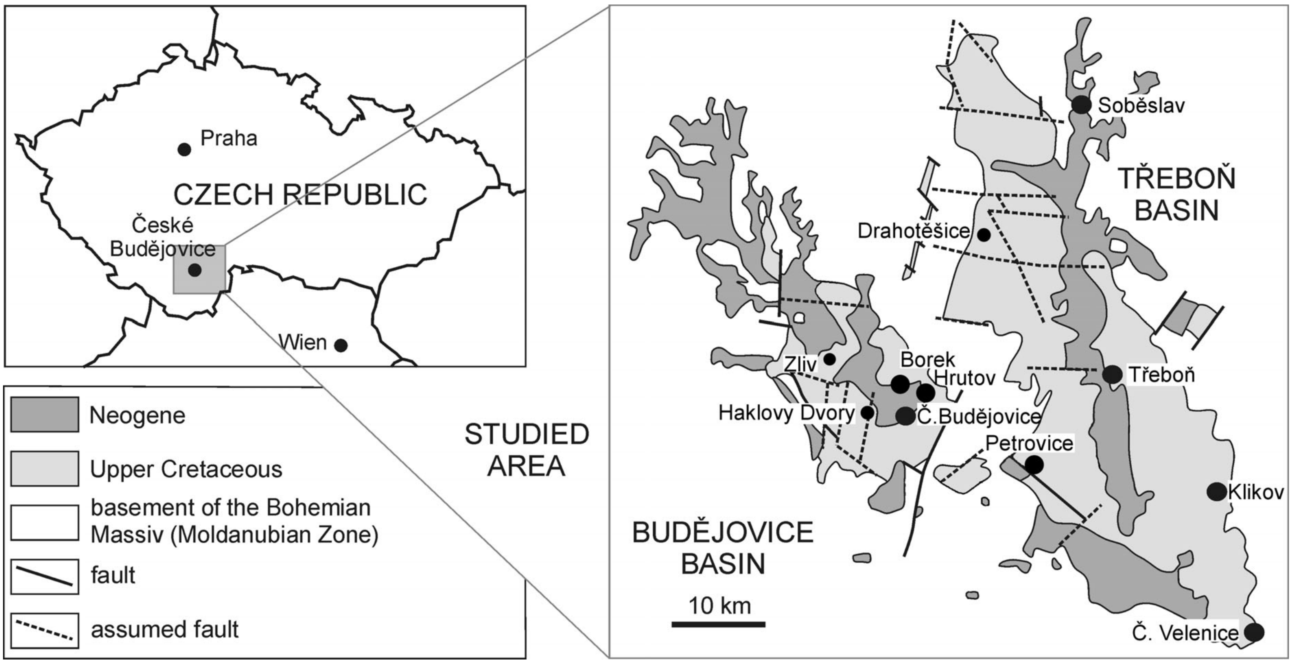

Figure 1. Geological map of South Bohemian Basins according to Slánská (1976) and Ševčík (2007) and position of South Bohemian Basins in the Czech Republic.

until the Pliocene (Malecha *et al.* 1962, Slánská 1974, Ševčík *et al.* 2007).

The sedimentary succession of the Klikov Formation (Upper Turonian–Santonian) was classified according to Slánská (1974, 1976) who recognized three lithological types that constituted an irregular cyclical sequence. The lithological types are: A – light grey (or greenish light grey, yellowish – grey) sandstone beds; B – red beds; and C – grey beds. The red beds consist of poorly sorted sandstones, sandy mudstones or sandy claystones. The grey beds consist of sandstones or claystones, with variable amounts of carbonised plant debris and pigment. Plant fossils occur predominantly in the grey beds, but are also present in the red beds. Sedimentary sequences are interpreted as successions of fluvial and lacustrine deposits (Slánská 1976).

Fossil flora

The flora of the Klikov Formation represents one of the most interesting Late Cretaceous floras in Central Europe. This flora includes macrofossils (leaves), mesofossils (fruits and seeds) and microfossils (pollen), and has been a focus of scientific interest since the 19th century. The main period of intensive study was from the 1950's to the 1980's. The oldest descriptions of this fossil flora were done by Ettingshausen (1852). The limited number of leaf impressions that Ettingshausen (1852) identified indicated that the flora was Tertiary in age. Cretaceous age for the flora was first proposed by Němejc (1938), who interpreted it as Cenomanian. However, micropaleontological studies in the early sixties of the last century by Pacltová (1958b, 1961) revealed a Senonian age. Upper Turonian–Santonian age of the Klikov Formation was established by Pacltová (1981) and supported by Knobloch (1985). We support an Upper Turonian–Santonian age for the Klikov Formation *sensu* Knobloch (1985), which was based on a comparison of palynology, carpology and macroflora. Fossil leaves from the location were described by Němejc (1961), Knobloch (1964) and Němejc & Kvaček (1975). Fruits and seeds were studied in detail by Knobloch & Mai (1984, 1986, 1991). Palynological research was carried out mostly by Pacltová (1955, 1958a, b, 1961, 1981; Němejc & Pacltová 1956). Palaeoecological aspects of the flora were briefly mentioned in palaeoecological comparisons with other Euro-Asian localities by Herman *et al.* (2004).

Angiosperm remains (leaves and reproductive structures) represent over 90% of the Klikov flora. Approximately 1000 dicotyledonous angiosperm leaf impressions and compressions have been recorded from the South Bohemian Cretaceous, which were assigned to 23 species (Figs 2, 5). Reproductive structures of angiosperms were assigned to *ca* 90 species (Knobloch & Mai 1986, 1991). Specimens examined for this study are housed in the collections of the National Museum, and the Czech Geological Survey, both in Prague. Most of the leaf fossils are fragmentary; however, many specimens have well preserved cuticle. Reproductive structures are usually preserved as lignified or charcoalified mesofossils (Table 1).

Table 1. Occurrence of selected taxa from Klikov Formation used for palaeoclimate analysis. A – Branišov GB-3, B – Břidlice L-XIII, C – Borek u Českých Budějovic, D – České Budějovice ČB-4, E – České Budějovice – Budvar, F – Drahotěšice, G – Haklovy dvory Br21/58, H – Haklovy dvory ČB2, I – Hluboká nad Vltavou, J – Hrutov, K – Klikov, L – Lomnice n. L. V-10, M – Nedabyle TsV-6, N – Opatovice Hl-1, O – Třebeč Tj-4a, P – Třebeč TjSv-5, Q – Petrovice, R – Vyškov, S – Vráto Vo-38–Vo-66, T – Zliv – Řídká blana.

	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T
Araliophyllum elongatum Němejc											x									
Cocculophyllum extinctum (Velenovský) Němejc & Kvaček																				x
Debeya cf. *coriacea* (Velenovský) Knobloch																				x
Debeya haldemiana (Saporta & Marion) Knobloch											x									x
Debeya insignis (Hosius & Marck) Knobloch			x								x						x			x
Debeya lusitanica (Teixeira) Knobloch											x							x		
Dicotylophyllum saliciforme Němejc											x									
Dicotylophyllum sp. *Laurophylum affine* Velenovský										x	x						x			x
Dicotylophyllum sp. A																				x
Dicotylophyllum sp. B											x									x
Dicotylophyllum sp. C																				x
Dicotylophyllum sp. D										x										x
Dicotylophyllum sp. E																				x
Dicotylophyllum sp. F																				x
Dicotylophyllum sp. G											x									
Dicotylophyllum sp. H																				x
Ettingshausenia cf. *laevis* (Velenovský) J. Kvaček & Váchová											x							x		x
Ettingshausenia senonensis (Knobloch) J. Kvaček & Váchová						x	x				x						x	x		x
Liriodendron papilliformis Knobloch & Mai				x										x						
Myricophyllum serratum (Velenovský) Němejc										x	x									x
Proteophyllum laminarium Velenovský									x	x	x							x	x	x
Proteophyllum lanceolatum Němejc & Z. Kvaček											x						x			x
Quercophyllum pseudodrymejum (Velenovský) Němejc											x									x
Qurecophyllum triangulodentatum Knobloch																	x			
Sabia menispermoides Knobloch & Mai					x															
Saurauia alenae Knobloch & Mai	x	x						x				x	x	x	x	x			x	
Saurauia antiqua Knobloch & Mai															x	x				

Methods

For palaeoclimatic reconstruction and interpretation of the climate which existed during sedimentation of the Klikov Formation, we have used two major methods: Nearest Living Relative (NLR) and leaf physiognomy. The Nearest Living Relative methods (Heer 1855–1859, Mosbrugger 1999) are based on climate variables necessary for growth of the nearest living relatives of the fossil plants under study. Quantitative taxa-based approaches of NLR methods included a coexistence approach (CoA) by Mosbruger & Utescher (1997) as one of the new versions of NLR. Leaf physiognomy methods are based on correlation between climate variables and leaf physiognomy. Two methods are usually applied: Leaf Margin Analysis (LMA) (Bailay & Sinnot 1915, Wing & Greenwood 1993, Wilf 1997, Wilf *et al.* 1998); and Climate Leaf Analysis Multivariate Program (CLAMP) (Wolfe 1990, 1993; Spicer 2006; Yang *et al.* 2007). CLAMP is a far more precise method for Cretaceous floras, because it does not require living relatives which are extremely uncommon for Cretaceous taxa.

CoA – For the coexistence approach, a dataset [PALAEOFLORA (Utescher 2006)] has been developed containing over 800 Tertiary taxa together with relevant records of mean annual temperatures, cold month mean temperatures and warm month mean temperatures.

LMA – Leaf Margin Analysis is based directly on the work of Bailay & Sinnot (1915), who were the first researches to find a robust relationship between leaf morphology and climate. Wing & Greenwood (1993) refined this method, which now has the advantage of scoring only one character. They defined a mathematical formula for calculation of mean annual tem-

Table 2. Selected taxa from Klikov Formation. CLAMP – taxa used for CLAMP. CoA – taxa used coexistence approach. NLR – taxa identified as nearest living relatives.

	plant organ	CLMAP	CoA	NLR
Araliophyllum elongatum Němejc	leaf	x		
Cocculophyllum extinctum (Velenovský) Němejc & Kvaček	leaf	x		
Debeya cf. *coriacea* (Velenovský) Knobloch	leaf	x		
Debeya haldemiana (Saporta & Marion) Knobloch	leaf	x		
Debeya insignis (Hosius & Marck) Knobloch	leaf	x		
Debeya lusitanica (Teixeira) Knobloch	leaf	x		
Dicotylophyllum saliciforme Němejc	leaf	x		
Dicotylophyllum sp. *Laurophylum affine* Velenovský	leaf	x		
Dicotylophyllum sp. A	leaf	x		
Dicotylophyllum sp. B	leaf	x		
Dicotylophyllum sp. C	leaf	x		
Dicotylophyllum sp. D	leaf	x		
Dicotylophyllum sp. E	leaf	x		
Dicotylophyllum sp. F	leaf	x		
Dicotylophyllum sp. G	leaf	x		
Dicotylophyllum sp. H	leaf	x		
Ettingshausenia cf. *laevis* (Velenovský) Kvaček & Váchová	leaf	x	x	*Platanus* sp.
Ettingshausenia senonensis (Knobloch) Kvaček & Váchová	leaf	x	x	*Platanus* sp.
Liriodendron papilliformis Knobloch & Mai	seed		x	*Liriodendron* sp.
Myricophyllum serratum (Velenovský) Němejc	leaf	x		
Proteophyllum laminarium Velenovský	leaf	x		
Proteophyllum lanceolatum Němejc & Z. Kvaček	leaf	x		
Quercophyllum pseudodrymejum (Velenovský) Němejc	leaf	x		
Qurecophyllum triangulodentatum Knobloch	leaf	x		
Sabia menispermoides Knobloch & Mai	seed		x	*Sabia* sp.
Saurauia alenae Knobloch & Mai	endocarp		x	*Saurauia* sp.
Saurauia antiqua Knobloch & Mai	endocarp		x	*Saurauia* sp.

perature (MAT). Wilf (1997) tested the LMA method against the CLAMP modern-plant database as well as with independently collected data from modern floras (mostly herbarium specimens); he found good correlations between leaf margin type and mean annual temperature, and between leaf area and mean annual precipitation. The temperature is correlated with the percentage of entire margined species in a flora. The disadvantage of the method is its low accuracy and evaluation using only one parameter (MAT).

CLAMP – Climate Leaf Analysis Multivariate Program is a widely used multivariate statistical technique for obtaining palaeoclimatic information (Wolf 1990, 1993; Kovach & Spicer 1995; Wolf & Spicer 1999; Spicer 2000; Kvaček & Teodoridis 2007). The paradigm used by CLAMP correlates the physiognomy of woody dicot leaves with the temperature and amount of precipitation. CLAMP has been used effectively for fossil floras up to 100 million years old (Herman & Spicer 1996, Herman *et*

Figure 2. Angiosperm fossil leaves of the Klikov Formation. Scale bar – 1 cm. • A – *Dicotylophyllum* sp., Zliv – Řídká Blana, F 1728. • B – *Dicotylophyllum* sp., Zliv – Řídká Blana, F 1566. • C – *Proteophyllum laminarium* Velenovský, Zliv – Řídká Blana, F 1674. • D – *Quercophyllum pseudodrymejum* (Velenovský) Němejc, Klikov, F 0070. • E – *Qurecophyllum triangulodentatum* Knobloch, Pertovice, ČGU 809. • F – *Debeya* cf. *coriacea* (Velenovský) Knobloch, Zliv – Řídká Blana, F 1612. • G – *Dicotylophyllum saliciforme* Němejc, Klikov, F1562. • H – *Proteophyllum lanceolatum* Němejc & Z. Kvaček, holotype, Zliv – Řídká Blana, F 1630. • I – *Ettingshausenia* cf. *laevis* (Velenovský) J. Kvaček & Váchová, Klikov, F 0041. • J – *Araliophyllum elongatum* Němejc, lektotyp, Klikov, F 0028. • K – *Cocculophyllum extinctum* (Velenovský) Němejc & Z. Kvaček, Zliv – Řídká Blana, F 1799. • L – *Debeya haldemiana* (Saporta & Marion) Knobloch, Klikov, F 0045. • M – *Ettingshausenia senonensis* (Knobloch) J. Kvaček & Váchová, Zliv – Řídká Blana, ČGU P 1820. • N – *Debeya insignis* (Hosius & Marck) Knobloch, Borek u Českých Budějovic, F1730. • O – *Dicotylophyllum* sp., Zliv – Řídká Blana, F 1632.


A
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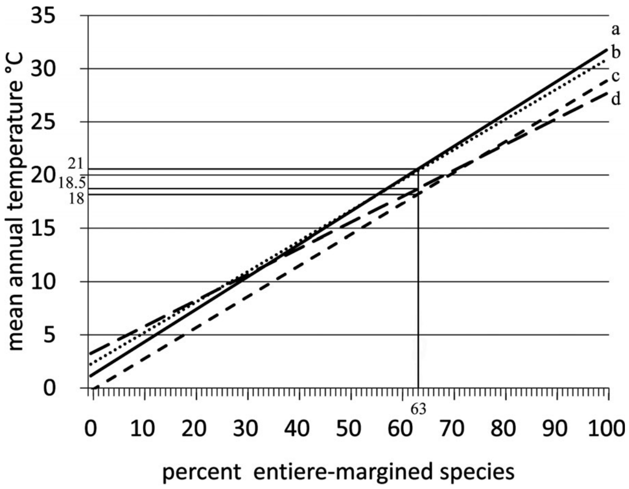


Figure 3. Leaf Margin Analysis. LMAT calculated for 63% of entire marinate leaves. a – plot according to Wolfe 1979 (Wing 1993), b – plot according to Wilf 1997 (Wilf 1997), c – plot according to Wolfe 1993, data for CLAMP were used (Wilf 1997), d – plot according to Wolfe (1993) data for CLAMP were used when 32 sites with the coldest winter temperatures were removed (Wilf 1997).

al. 2002, Kennedy *et al.* 2002, Hayes *et al.* 2006). It works well for leaf palaeoassemblages with more than 20 morphospecies of woody dicot leaves.

In CLAMP the architecture of woody dicot leaves from extant vegetation growing under known climatic conditions is used as a reference data set. The architecture of leaves found in a fossil assemblage is then compared with this data set. There are now several of these datasets which vary in size, geographical and climatic coverage. We selected comparable and appropriate datasets of 173 and 144 modern vegetation sites. Most of these sites are located in the Northern Hemisphere (dataset PHYSG3AR) and are scored for 31 leaf characters and correlated with 8 climate variables (Wolfe 1993, 1995; Herman & Spicer 1996, 1997); see also http://tabitha.open.ac.uk/spicer/CLAMP/Clampset1.html. These variables are: mean annual temperature (MAT), warm month mean temperature (WMMT), cold month mean temperature (CMMT), length of the growing season (GROWSEAS), growing season precipitation (GSP), mean monthly growing season precipitation (MMGSP), precipitation during the 3 consecutive wettest months (3-WET) and precipitation during the 3 consecutive driest months (3-DRY).

The CANOCO program, using Canonical Correspondence Analysis (Ter Baark 1986) is a direct ordination method used here to order site, leaf character and environmental data simultaneously in multidimensional space; sites are ordered by their character scores, characters are ordered by their distribution among the sites. Thus, sites are arranged relative to one another in multidimensional space using the physiognomic characters of the vegetation at that site; environmental data are not used to position the sites.

Table 3. Scoring results (percentage of characters preserved) for CLAMP analysis.

foliar physiognomic characters		Klikov
margin character states	lobed	13%
	no teeth	63%
	teeth regular	25%
	teeth close	10%
	teeth round	4%
	teeth acute	3%
	teeth compound	0%
size character states	nanophyll	0%
	leptophyll I	0%
	leptophyll II	2%
	microphyll I	23%
	microphyll II	46%
	microphyll III	19%
	mesophyll I	9%
	mesophyll II	1%
	mesophyll III	0%
apex character states	apex emarg.	0%
	apex round	0%
	apex acute	100%
	apex atten.	0%
base character states	base cordate	0%
	base round	2%
	base acute	98%
length to width character states	L : W < 1 : 1	0%
	L : W 1–2 : 1	26%
	L : W 2–3 : 1	0%
	L : W 3–4 : 1	11%
	L : W > 4 : 1	63%
shape character states	obovate	19%
	elliptic	81%
	ovate	0%
total number of species		23

Results

Leaf Margin Analysis of 23 dicot leaf morphotypes from the Klikov Formation flora (Table 2) shows that 63% of morphotypes have entire-margined leaves.

For LMA calculation four different mathematical formulas were used. "P" is in all the formulas, and represents percentage of entire-margined leaves. The first formula, LMAT = 1.141 + (P × 0.306) (Fig. 3), was published by Wing & Greenwood (1993), and is based on data collected by Wolfe (1979). When this formula is applied to 63%, the value of MAT is 20.5 °C. The second formula, LMAT = 2.24 + (P × 0.286) (Fig. 3), was published by Wilf (1997),

Table 4. Results of CLAMP, Klikov ecosystem (Upper Turonian–Santonian).

	Standard deviation for A 173	Klikov – A 173 recent sites	Standard deviation for B 144	Klikov – B 144 recent sites
MAT °C – mean annual temperature	1.72	14.19	1.17	11.82
WMMT °C – warm month mean temperature	1.80	23.87	1.58	14.72
CMMT °C – cold month mean temperature	2.54	5.66	1.88	8.02
GROWSEAS months – length of the growing season	0.85	8.04	0.70	6.88
GSP mm – growing season precipitation	318	808.2	336	1332.2
MMGSP mm – mean monthly growing season precipitation	37	104.6	37	108.5
3-WET mm – precipitation during the 3 consecutive wettest months	138	433.7	140	552.8
3-DRY mm – precipitation during the 3 consecutive driest months	89	189.4	93	93.9

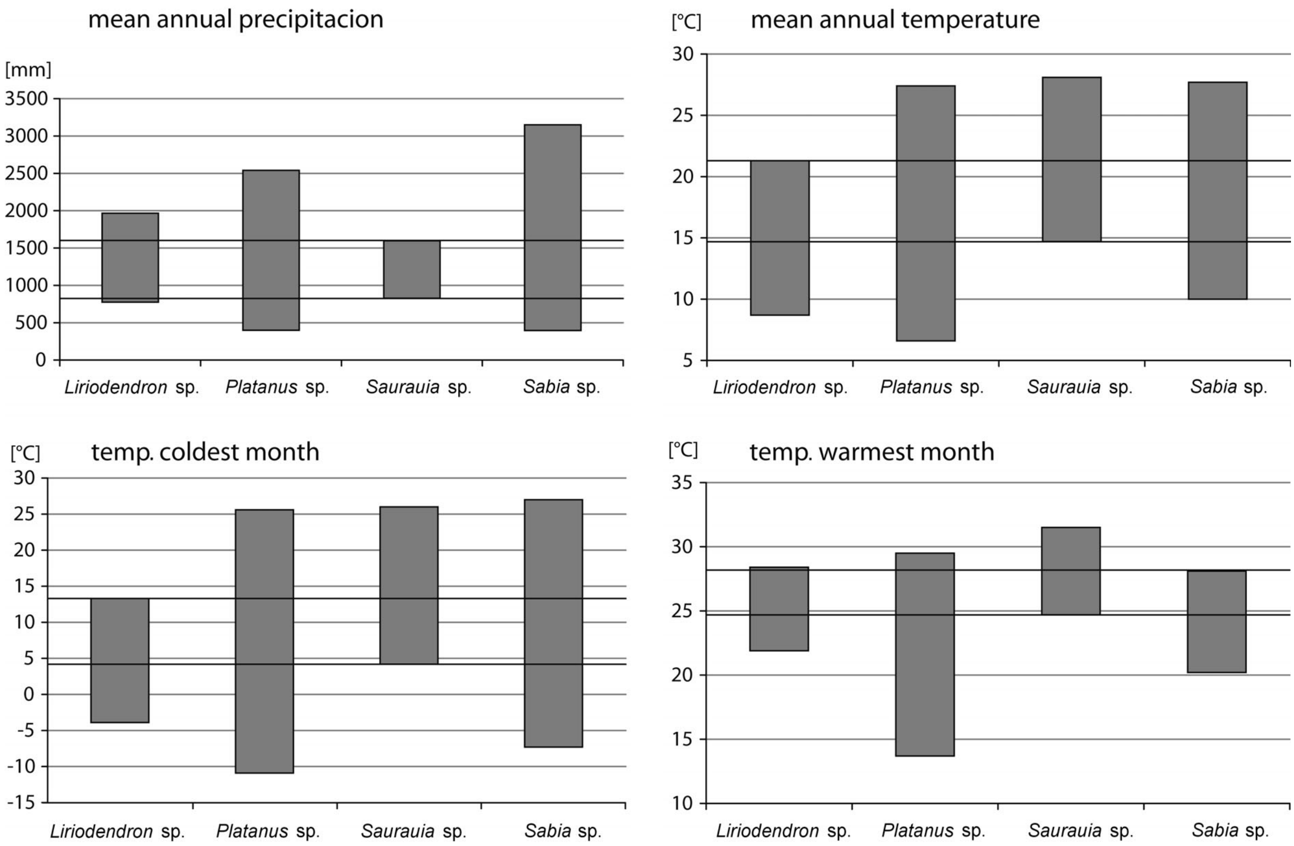


Figure 4. Summarised data from co-existence approach. Four taxa were used for the coexistence approach (*Platanus-Ettingshausenia, Liriodendron, Sabia, Saurauia*). The value limits the interval of coexistence.

and is based on data collected by Wilf (1997). When formula two is applied to 63%, the value of MAT is 20.2 °C. The third formula, LMAT = (P × 0.291) – 0.226 (Fig. 3), was published by Wilf (1997), and is based on data collected by Wolfe (1993) for CLAMP analysis. When this third formula is applied to 63%, the value of MAT is 18.0 °C. The fourth formula, LMAT = (P × 0.244) + 3.25 (Fig. 3), was published by Wilf (1997), and is based on data collected by Wolfe (1993) for CLAMP analysis, but only for a warm climate. When formula four is applied to 63%, the value of MAT is 18.5 °C. Sampling deviation is greater than 3 °C (Wilf 1997); however, with the poor preservation of plant fossils from the Klikov Formation, our deviation could be even larger.

In the present study, 23 leaf morphotypes (Table 2) were scored for 32 characters (Table 3). CLAMP analysis of the flora of the Klikov Formation revealed MAT of 14 °C, WMMT 24 °C, CMMT 6 °C, GROWSEAS 8 months, GSP 800 mm, MMGSP 100 mm, 3-WET 430 mm and 3-DRY 190 mm. The assemblage was scored

Table 5. Preliminary results of CLAMP, Klikov ecosystem, published by Herman *et al.* (2002).

	standard deviation	Klikov, Zliv, Hluboká
MAT C° – mean annual temperature	1.8	15.6
WMMT C° – warm month mean temperature	3.1	22.2
CMMT C° – cold month mean temperature	3.3	9.0
GROWSEAS months – length of the growing season	1.1	8.7
GSP mm – growing season precipitation	280	780
MMGSP mm – mean monthly growing season precipitation	23	88.6
3-DRY mm – precipitation during the 3 consecutive driest months	70	144.1

Table 6. Klikov ecosystem – major palaeoclimatic parameters. LMA – according to formula published by Wilf (1997), based on data collected by Wolfe (1993) for CLAMP analysis. CLAMP – the assemblage was scored according to 173 recent sites. CoA – four taxa (*Platanus-Ettingshausenia, Liriodendron, Sabia, Saurauia*) were used for the coexistence approach.

	LMA	CLAMP	coexistence approach
MAT °C	18.5	15	15–21
WMMT °C		24	24–28
CMMT °C		6	5–15
GSP mm		800	900–1600

according to 173 recent sites. Calibrating our CLAMP analysis with a dataset of 144 recent localities, we obtained extremely low temperatures MAT 12 °C, WMMT 15 °C, CMMT 8 °C. Other data are as follows: GROWSEAS 7 months, GSP 1300 mm, MMGSP 100 mm, 3-WET 550 mm and 3-DRY 100 mm (Table 4). As is the case with other proxy studies of this flora, we do not give high credibility to the extremely low temperatures resulting from these calculations with a dataset of 144 sites.

Most of the living relatives of the studied plants occur in regions with CMMT well below 0 °C (Fig. 4). The only plant which shows CMMT above freezing is the genus *Saurauia* (Fig. 4). However, many species of this genus are freeze hardy (Mai 1970, Soejarto 1980, Behera *et al.* 2002, Anonymus 2008). Therefore, we decided to use the data set of 173 recent localities recommended for calculation of palaeoclimatic variables of temperate floras.

Four taxa were used for the coexistence approach (*Platanus-Ettingshausenia, Liriodendron, Sabia, Saurauia*).

Leaves of *Ettingshausenia senonensis* (Knobloch) J. Kvaček & Váchová and *Ettingshausenia laevis* (Velenovský) J. Kvaček & Váchová are common in the Klikov Formation. They are preserved as leaf compressions and impressions. The Cretaceous genus *Ettingshausenia* is associated with the recent family Plataneaceae (Kvaček & Váchová 2006). Extant members of this family are widespread in warm-temperate regions of the Northern Hemisphere, but they also grow in the subtropics. Cretaceous representatives of this family are also known from regions characterised by a temperate climate.

Liriodendron, Saurauia and *Sabia* are preserved as charcoalified seeds.

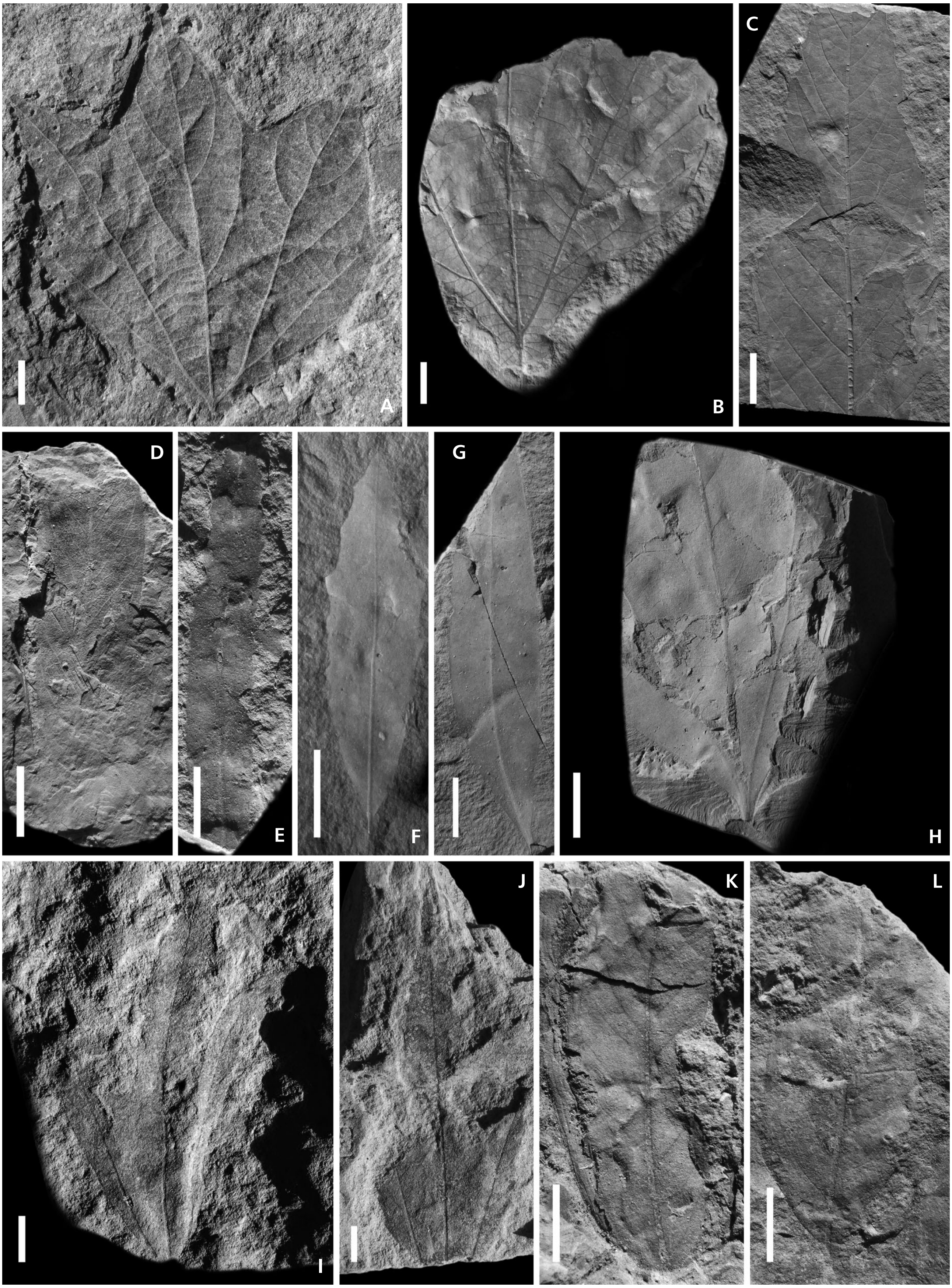
Sabiaceae – the genus *Sabia* is often used for Tertiary NLR analyses. *Sabia menispermoides* Knobloch & Mai represents one of the earliest records of the genus (Knobloch & Mai 1986). The recent Sabiaceae are native to warm tropical temperate regions of southern Asia and the Americas.

Saurauiaceae – the record of the recent *Saurauia* Willdenow in the Klikov Formation is one of the earliest for the family. Tertiary species of *Saurauia* (*S. poolensis, S. crassisperma* and *S. subhercynica*) are very similar to the recent species *S. nudiflora* (Mai 1970). Cretaceous *S. antiqua* has characters very similar to *S. poolensis* (Chandler) Mai, but it is smaller and has a longer raphe (Knobloch & Mai 1986). The recent genus *Saurauia* has approximately 250 species distributed throughout the tropics and subtropics of Asia and both South and Central America.

Magnoliaceae – the genus *Liriodendron* is known since the Cenomanian and is a common element of Cretaceous floras (Frumin & Friis 1999). Material for this study is represented by a single specimen. In this case, we relied on the determination by Knobloch & Mai (1986), who studied more seeds. There are two recent species in the genus: *Liriodendron chinense*, native to China and Vietnam; and *Liriodendron tulipifera*, native to North America. Representatives of this genus grow in subtropical to temperate climates (Beck 1990).

The data and results of our determination of CoA are summarised in Fig. 4. We have identified MAT values from 15 °C to 21 °C and CMMT values from 5 °C to 15 °C. The

Figure 5. The angiosperm fossil leaves of the Klikov Formation. Scale bar – 1 cm. • A – *Ettingshausenia senonensis* (Knobloch) J. Kvaček & Váchová, Zliv – Řídká Blana, ČGU P 1820. • B – *Ettingshausenia senonensis* (Knobloch) J. Kvaček & Váchová, holotype, Zahájí Za1, depth 38.5 m, ČGU P 2960. • C – *Quercophyllum pseudodrymejum* (Velenovský) Němejc, Zliv – Řídká Blana, F 1702. • D – *Proteophyllum laminarium* Velenovský, Zliv – Řídká Blana, F 1674. • E – *Proteophyllum lanceolatum* Němejc & Z. Kvaček, holotype, Zliv – Řídká Blana, F 1630. • F – *Debeya* cf. *coriacea* (Velenovský) Knobloch, Zliv – Řídká Blana, F 1612. • G – *Dicotylophyllum* sp. C, Zliv – Řídká Blana, F 1728. • H – *Cocculophyllum extinctum* (Velenovský) Němejc & Z. Kvaček, Zliv – Řídká Blana, F 1799. • I – *Araliophyllum elongatum* Němejc, Klikov, F 0033. • J – *Araliophyllum elongatum* Němejc, lectotype, Klikov, F 0028. • K – *Dicotylophyllum sp.*, Zliv – Řídká Blana, F 1632. • L – *Dicotylophyllum* sp., Zliv – Řídká Blana, F1567.


A
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presence of the genus *Saurauia* limits the lowest temperature values for MAT and CMMT. The presence of the genus *Liriodendron* limits the highest temperature values for both MAT and CMMT. WMMT values determined range from 24 °C to 28 °C. The genus *Saurauia* is again responsible for the lowest temperature values and the presence of the genus *Sabia* limits the highest temperature values. Mean annual precipitation values vary from 900 to 1600 mm. This variable is limited by the genus *Saurauia*, which can only grow in areas with a very limited range of precipitation values. These values limit the interval of coexistence, which is the interval in which all of the discussed genera can grow.

These data are in general agreement with other studies carried out on Cretaceous floras. The results for coexistence analysis published by Uhl (2006) for Cretaceous floras are in very good agreement with our interpretations.

Discussion

As a basis for the present palaeoecological reconstruction, we used the CLAMP analysis. Methods of LMA and NLR were used for comparison and clarification of the results. The present work also revised the preliminary results of CLAMP by Herman *et al*. (2002), based on figured specimens by Němejc (1961) and Němejc & Z. Kvaček (1975), who used it in their comparison with the flora of Grünbach. Preliminary data published by Herman *et al.* (2002) based on dataset of 103 modern vegetation sites are: MAT 15.6 °C; WMMT 22.2 °C; CMMT 9.0 °C; GROWSEAS 8.7 months; GSP 780 mm; MMGSP 88.6 mm; 3-DRY 144.1 mm (Table 5).

In the present study, we analyzed all available data (more than 1000 specimens). The number of taxa and their variability allow employment of the CLAMP method, but we must take into account that the shortage of high quality fossils increases climate estimate deviation. Poor preservation (no cuticle or venation preserved) of some entire-margined leaves may have been responsible for low diversity, which could in turn produce quite low temperature values.

The results of CLAMP analyses were compared to the results gathered from LMA, NLR and coexistence methods. In general we agree with the preliminary data published by Herman *et al.* (2002), and by using two major approaches we were able to deduce the major palaeoclimatic parameters shown in Table 6.

The values of MAT (LMA: 18.5 °C, CLAMP: 15 °C, CoA: 15–21 °C) have a large range. This is most likely due to the poor preservation of the flora; however we accept a value for MAT of approximately 15 °C. We put more emphasis on data obtained by CLAMP because it works with more characters than LMA.

The results for WMMT (CLAMP: 24 °C, CoA: 24–28 °C), CMMT (CLAMP: 6 °C, CoA: 5–15 °C) and GSP (CLAMP: 800, NLR: 900–1600 mm) are in agreement for both CLAMP and the coexistence approach. It is normal for LMA to give higher MAT values than CLAMP (compare Herman & Kvaček 2007). However, in the present comparison, CoA also showed higher MAT values. It is striking that WMMT, CMMT and GSP values are in good agreement for all three methods used.

Based on the presence of frequent charcoals, we assume a seasonally dry climate for the Klikov ecosystem. Charcoal is commonly formed under natural conditions during wildfires (Falcon-Lang *et al.* 2001). Fires are common in the dry season of seasonally dry subtropical forests, where accumulated dead plant remains serve as a combustible material which easily burns.

Summary

For the palaeoclimatic interpretation of the Klikov Formation Flora (Upper Turonian–Santonian) leaves, fruits and seeds were used. We used the following methods: LMA, CLAMP and CoA. LMA and CLAMP are based on leaf physiognomy, the CoA is based on environmental requirements of the nearest living relatives of the fossil plants.

Mean annual temperature is estimated to have been approximately 15 °C. Values obtained from CLAMP are 15 °C; values from LMA are 18.5 °C and from the coexistence approach are 15–21 °C. Results obtained using LMA are generally higher than in other analyses. Values obtained using the coexistence approach could be inconsistent due to a shortage of living relatives and their distant relationship to their Cretaceous ancestors. According to CLAMP and the coexistence approach, WMMT was approximately 24 °C and CMMT was approximately 6 °C. Growing season precipitation is estimated to have been approximately 800 mm.

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