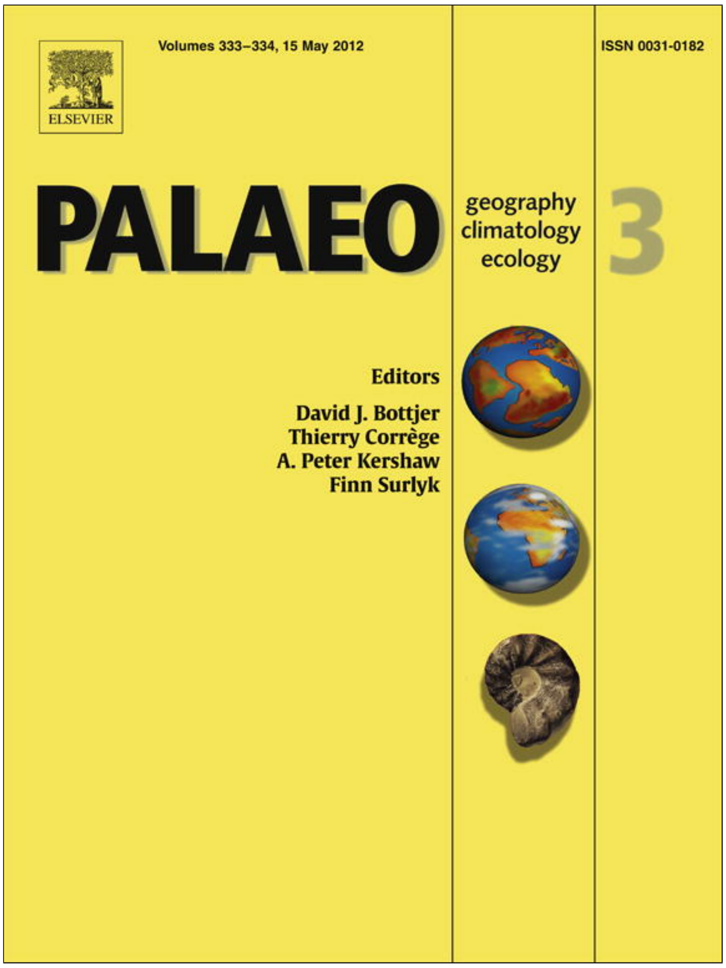
Volumes 333–334, 15 May 2012
ISSN 0031-0182
ELSEVIER
PALAEO
geography
climatology
ecology
3
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Palaeogeography, Palaeoclimatology, Palaeoecology 333–334 (2012) 40–58

Contents lists available at SciVerse ScienceDirect

Palaeogeography, Palaeoclimatology, Palaeoecology

journal homepage: www.elsevier.com/locate/palaeo

Environmental analysis of the mid-latitudinal European Eocene sites of plant macrofossils and their possible analogues in East Asia

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ARTICLE INFO

Article history:
Received 24 September 2011
Received in revised form 27 February 2012
Accepted 10 March 2012
Available online 20 March 2012

Keywords:
European Eocene
Asian modern vegetation
IPR-vegetation analysis
Coexistence Approach
CLAMP

ABSTRACT

Previously known Eocene floras of mid-latitudinal Europe are analysed using statistical methodologies in order to obtain more reliable palaeoclimatological signals to detect possible climatic fluctuations during this time interval. Only macrofossil assemblages have been taken into account and subjected to the statistical evaluation called the Integrated Plant Record (IPR) vegetation analysis, which is based mostly on percentages of various components. Additional palaeoclimatic approaches were employed, namely the Coexistence Approach, based on autecology of the nearest living relatives, and the physiognomic methods of the Leaf Margin Analysis and Climate Leaf Analysis Multivariate Program (CLAMP). The same statistical approaches have been applied to analogous living vegetation of China and Japan for comparative purposes. Additionally, an update of objective statistical tools for the selection of the best-suited modern vegetation CLAMP dataset from 144 site (Physg3br/GRIDMet3br), 173 (Physg3ar/GRIDMet3ar) and 189 (PhysgAsia1/GRIDMetAsia1) extant biotopes is proposed including its "copy & paste" Excel application.

1. Introduction

The present study aims at a re-evaluation of European Eocene floras with the aid of statistical methodologies. The sites described so far are numerous although the quality of the published data is variable. Mai (1995) attempted to survey all available sites and offered a synthesis that divides all European floras into 41 floristic assemblages ("Florenkomplexe") within five palaeogeographical bioprovinces: Atlantic–Boreal, Trans-European–Paratethys, East European–East Paratethys, Caucasian, and Mediterranean-Tethys (see Mai, 1995, pp. 340–429). The latest overview of the European early Palaeogene floras (Kvaček, 2010, Table 1) partly revised Mai's classification, wherein new vegetation units were characterised using a phytosociological (non-statistical) approach. The subdivisions relied on diversity, physiognomy, and leaf size following the actuopalaeobotanical study of living vegetation in East Asia as elaborated by Wolfe (1979). Kvaček (2010) proposed three main mesophytic forest types for the Eocene of Europe: The polar deciduous forest typified by plant assemblages found in Spitsbergen and Mull (e.g., Boulter and Kvaček, 1989), the notophyllous forest type typified by the middle–late Eocene floras of Germany and Bohemia including Messel, Zeitz, Staré Sedlo, and Kučlín (Mai and Walther, 1985; Knobloch et al., 1996; Kvaček et al., 2011) and the quasi-paratropic vegetation type represented by the highly diversified early Eocene floras of the London Clay and a large-leaved assemblage collected in Belleu. Due to several features of both the Messel and Geiseltal sites, these highly diverse assemblages may be intermediate between the notophyllous and the quasi-paratropical type.

Cenozoic vegetation has recently been the focus of methodological studies in order to objectively assess fossil plant assemblages (e.g., Kovar-Eder et al., 2008; Martinetto and Vassio, 2010; Bertini and Martinetto, 2011; Kvaček et al., 2011) and their impact on deriving more precise climatic proxies. To date, the Integrated Plant Record vegetation analysis (IPR-vegetation analysis) method has been applied mostly to floras of the Neogene (e.g., Kovar-Eder et al., 2008; Teodoridis, 2010; Jacques et al., 2011a). In the present paper we employed this technique and Leaf size Analysis, together with palaeoclimatic methods of Coexistence Approach, Leaf Margin Analysis and Climate Leaf Analysis Multivariate Program on a limited area of the mid-latitude European Eocene using updated taxonomy (e.g., Wilde, 1995; Wilde et al., 2005), to reconstruct the general zonal character of ancient environments. A statistical comparative study (cluster analysis) of selected fossil sites of European Eocene with modern subtropical and temperate vegetation types of China and Japan (Teodoridis et al., 2011a) and tropical zone floras from southern China (this paper) may suggest new, more real, conceptions of structure and character for the Eocene vegetation in Europe. We focus on the analyses of living vegetation in East Asia

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doi:10.1016/j.palaeo.2012.03.008

because more components of the European Eocene vegetation survived there until present than anywhere else.

2. Material

2.1. The fossil sites studied

Twenty-nine Eocene floras from the United Kingdom, Germany and the Czech Republic (Fig. 1, Table 1) have been statistically analysed. They were selected according to qualitative criteria, i.e., floristically diverse, reliably determined, well preserved and complete. Following these basic criteria, we compiled several species-poor assemblages from the same stratigraphic levels in the same area to obtain a more reliable basis for our evaluation (e.g., two middle Eocene sites of Profen and Scheiplitz, or twelve small late Eocene floras from the Staré Sedlo Formation, marked here as the flora of Staré Sedlo sensu lato (s.l.) evaluated together — see Appendix 1). To verify this procedure we compared quantitative differences of obtained palaeoclimatic proxies and the results of the IPR-vegetation analysis derived from Staré Sedlo s.l. and the locality Staré Sedlo itself (see Section 6.4). Similarly, we compiled small late Eocene floras from the Weisselster Basin (i.e., Klausa, Knau, Haselbach and Profen) to obtain the CLAMP proxies.

2.2. The studied modern vegetation from East Asia

For our comparison we used forty different modern vegetation types from the subtropical and temperate zones of SE China and Japan described and evaluated by Teodoridis et al. (2011a) and additionally, seven tropical vegetation types from Hainan (Jianfengling) and Yunnan (Xishuangbanna) in southern China (Fig. 2, Table 2).

Jianfengling (Hainan) — Jianfengling Nature Reserve is located between 18°36′ and 18°52′ N, 108°52′ and 109°5′ E. It has a mountainous topography with elevation varying from sea level to 1412.5 m at the

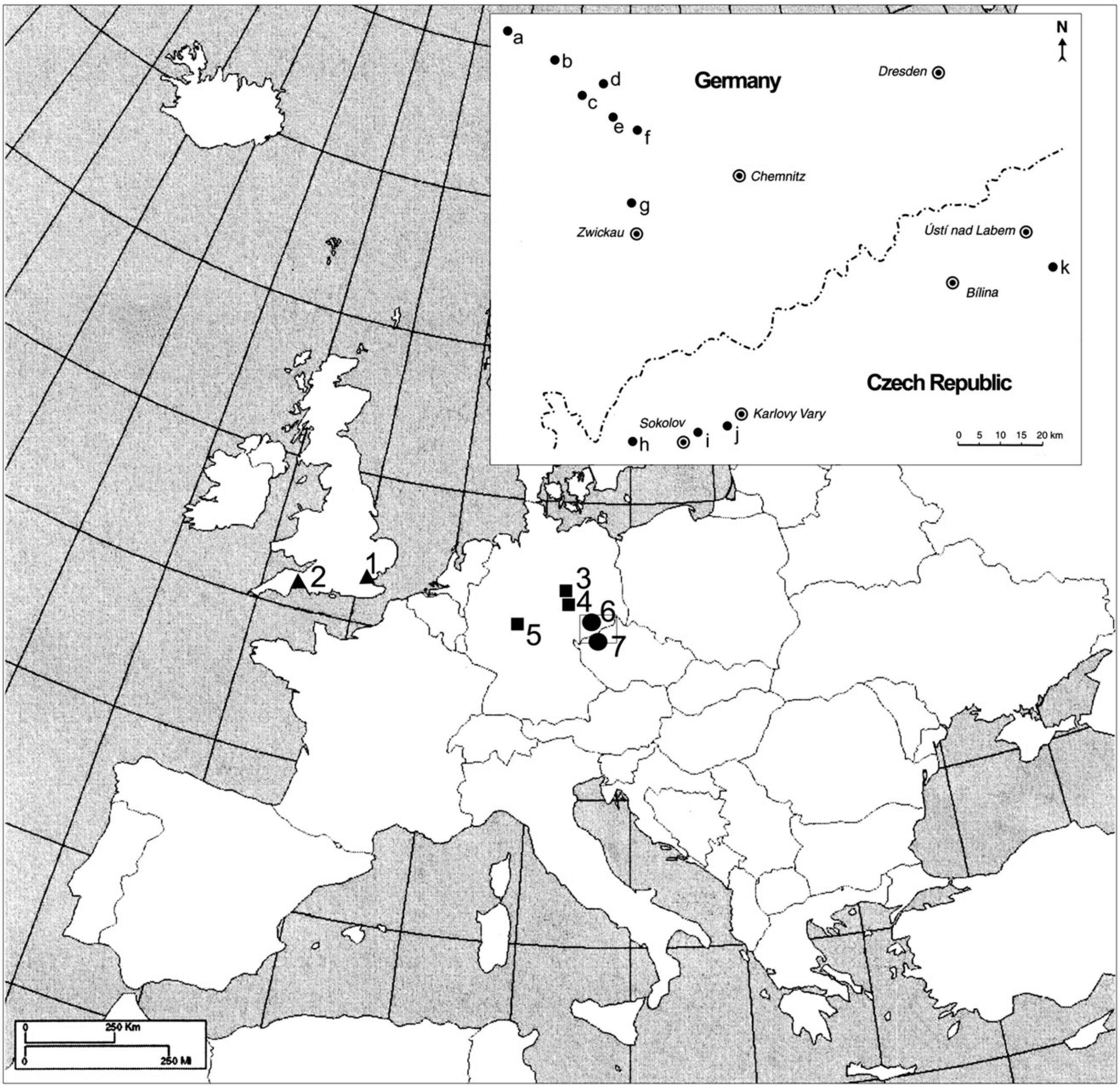

Fig. 1. Location of the studied European fossil sites. Early Eocene (triangle): 1. London Clay, 2. Hampshire Basin (UK). Middle Eocene (square): 3. Geiseltal (Germany), 4. Profen–Scheiplitz (Germany), 5. Messel (Germany). Late Eocene (circle): 6. Weisselster Basin (Germany) — a. Kayna-Süd, b. Profen, c. Phönix-Nord, d. Haselbach, e. Knau, f. Klausa, g. Mosel, 7. Staré Sedlo Fm. (Czech Republic) — h. Nový Kostel, i. Staré Sedlo, j. Český Chloumek, k. Žitenice.

Table 1
Eocene floras considered in the present study and an overview of the employed palaeoenvironmental methods. Abbreviations: IPR (Integrated Plant Record vegetation analysis), LSA (Leaf Size Analysis), LMA (Leaf Margin Analysis), CLAMP (Climate Leaf Analysis Multivariate Program), and CA (Coexistence Approach). Asterisk (*) - indicates the source of published palaeoclimatic proxies.

Locality	Country	Age	Floristic references	Palaeoenvironmental methods	References
London Clay	United Kingdom	Early Eocene	Collinson (1983)	IPR	This paper
Hampshire Basin	United Kingdom	Early Eocene	Collinson (1983)	IPR	
Geiseltal	Germany	Middle Eocene	Mai (1976), Wilde (1995), Kahlert and Rüffle (2007)	IPR, LSA, LMA, CA*	This paper, * Mosbrugger et al. (2005)
Messel	Germany	Middle Eocene	Sturm (1971), Wilde (1989), Wilde et al. (2005)	IPR, LSA, CLAMP, CA*	This paper, * Grein et al. (2011)
Profen–Scheiplitz	Germany	Middle Eocene	Fischer (1991), Mai and Walther (2000)	IPR, LSA, LMA, CLAMP, CA*	This paper, * Mosbrugger et al. (2005)
Haselbach	Germany	Late Eocene	Mai and Walther (1985, 2000)	IPR, LSA, LMA, CLAMP, CA*	This paper, * Roth-Nebelsick et al. (2004)
Kayna-Süd	Germany	Late Eocene	Mai and Walther (1985, 2000)	IPR, LMA, CLAMP	This paper
Klausa	Germany	Late Eocene	Mai and Walther (1985, 2000)	IPR, LSA, LMA, CLAMP	
Knau	Germany	Late Eocene	Mai and Walther (1985, 2000)	IPR, LSA, LMA, CLAMP, CA*	This paper, * Roth-Nebelsick et al. (2004)
Mosel	Germany	Late Eocene	Mai and Walther (1985, 2000)	IPR, LSA, LMA, CLAMP	This paper
Phönix-Nord	Germany	Late Eocene	Mai and Walther (1985, 2000)	IPR, CLAMP	
Profen	Germany	Late Eocene	Mai and Walther (1985, 2000)	IPR, CLAMP, CA*	This paper, * Roth-Nebelsick et al. (2004)
Český Chloumek	Czech Republic	Late Eocene	Knobloch et al. (1996)	IPR, LSA, LMA	This paper
Nový Kostel	Czech Republic	Late Eocene	Knobloch et al. (1996)	IPR, LSA, LMA	
Staré Sedlo	Czech Republic	Late Eocene	Knobloch et al. (1996)	IPR, LSA, LMA, CLAMP, CA*	This paper, * pro parte Uhl et al. (2007)
Žitenice	Czech Republic	Late Eocene	Knobloch et al. (1996)	IPR, LSA, LMA	This paper

mountain top. It experiences conspicuous changes in climate across its altitude. Table 3 provides summarised meteorological and gridded climatic datasets for each studied vegetation types (Liu et al., 1995; Zeng, 1995; New et al., 1999; BRIDGE, 2008). There are four main vegetational types along an altitudinal transect in Jianfengling. The tropical savannah vegetation exists below 200 m altitude which grades into a tropical lowland rain forest in the valleys (between 200 and 800 m) and a tropical semi-evergreen rain forest on its slopes (200–600 m). A tropical montane rainforest is found between 600 and 1000 m, and passes into a montane dwarf forest above (Hu, 1985). Two vegetational types described below and characterised by several sample plots were used in the current study (Table 2). Predominant elements in the studied vegetation are marked in Appendix 2. (a) Tropical lowland rain forest is composed of 3 to 4 indistinct tree layers, of which the uppermost canopy consists largely of emergent trees that grow to heights of 30 to 40 m; the second layer reaches heights of 18 to 30 m with the development of almost a continuous crown; the third, lower layer grows to a height of 5 to 18 m. (b) Tropical montane rain forest is also characterised by three tree storeys of which the uppermost canopy is up to 30 m tall and the middle tree layer is 15 to 20 m tall.

Xishuangbanna (Yunnan) lies between 21°09′ and 22°36′ N, 99°58′ and 101°50′ E. It has a mountainous topography with the mountain ridges running in a north–south direction, decreasing in elevation southward. Its altitude ranges from 480 m at the base of the lowest valley in the south (Mekong River) to 2429.5 m at the tops of the northern mountains. Similarly, Table 3 provides summarised meteorological and gridded climatic datasets for each studied vegetation type (YMB, 1983; New et al., 1999; BRIDGE, 2008). The vegetation of Xishuangbanna is classified into four main vegetation types that include: 1) tropical rainforest, 2) tropical seasonal moist forest, 3) tropical monsoon forest, and 4) tropical montane evergreen broad-leaved forest. The tropical rainforest is further

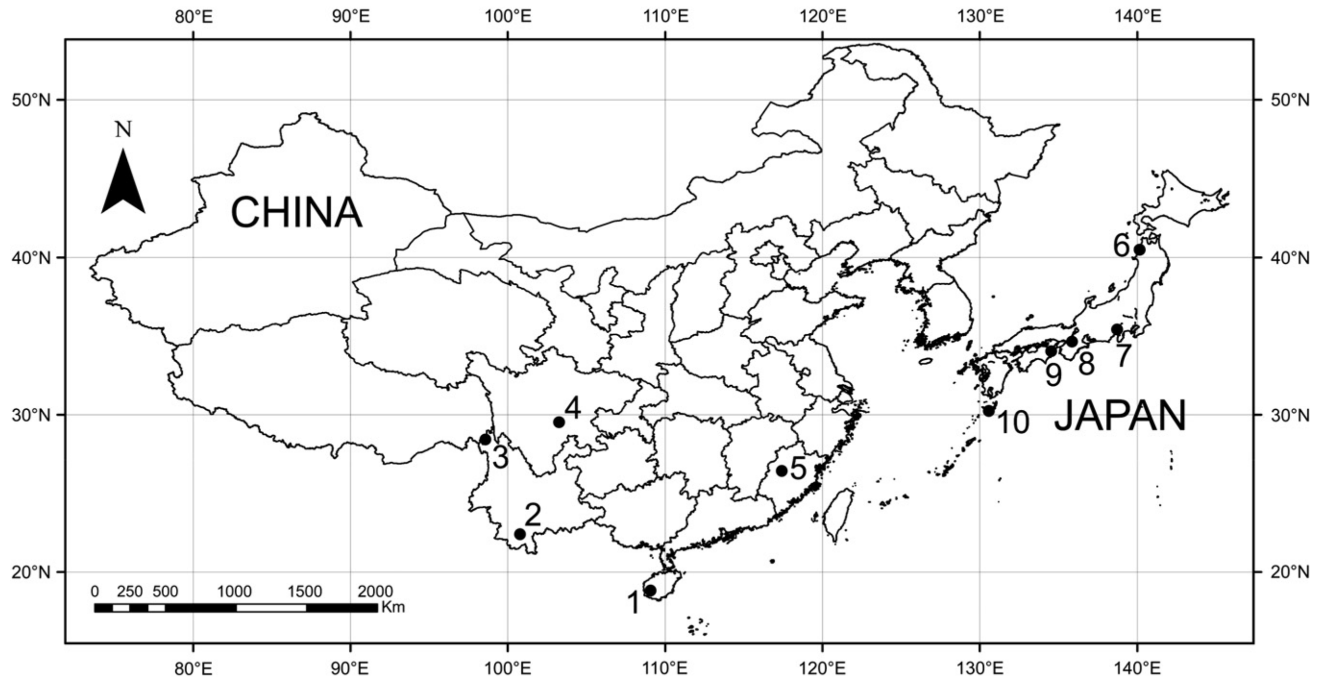

Fig. 2. Location of the studied modern and referred sites in China and Japan (sensu Teodoridis et al., 2011a). 1. Jianfengling (Hainan), 2. Xishuangbanna (Yunnan), 3. Meili Snow Mountain (Yunnan), 4. Mount Emei (Sichuan), 5. Mount Longqi (Fujian), 6. Shirakami Sanchi, 7. Mount Fuji, 8. Nara, 9. Shiroyama, and 10. Yakushima Island.

Table 2
Location of modern tropical, subtropical and temperate vegetation types from the studied areas of China and Japan.

Country	Site	Vegetation assemblage	Reference	Longitude E	Latitude N	Altitude [m]	Number of plots	Plot size [m^2]
China	Jianfengling	Tropical lowland rain forest	Jiang and Lu (1991),	108°59′	18°44′	241 and 256	2	200–600
		Tropical montane rain forest	Fang et al. (2004)	108°53′	18°43′	868 and 893	2	600
	Xishuangbanna	Tropical seasonal rain forest	Zhu (1997, 2005, 2006),	101°12–35′	21°31–59′	600–1100	11	20–250
		Tropical montane rain forest	Zhu et al. (1998)	100°32–33′	21°27–28′	900–1800	2	500
		Tropical seasonal moist forest		101°26–27′	21°52–53′	650–1300	7	250–500
		Monsoon forest		100°22–35′	22°35–47′	480–850	5	500
		Tropical montane broad-leaved evergreen forest		101°12–33′	21°27–34′	900–1800	3	500
	Mt. Emei	Broad-leaved evergreen forest (BLEF)	Teodoridis et al. (2011a)	103°22′	29°34′	750–1500	5	200–600
		Mixed mesophytic forest (MMF)				1660	1	600
						1500–2000	General lists	–
		Broad-leaved deciduous forest (BLDF)				2000–2500	2	400 and 1600
	Meili Snow Mts	Broad-leaved deciduous forest (BLDF)		98°36–52′	28°17–52′	2650–3410	9	100 and 400
		Subhumid sclerophyllous forests (ShSF)				2580–3650	14	100
	Mt. Longqi	Broad-leaved evergreen forest (BLEF)		117°11–21′	26°23–43′	500–1200	General list, 7	400 and 600
Japan	Shirakami Sanchi	Broad-leaved deciduous forest (BLDF)		140°07′	40°28′	0–1000 ?	3	?
	Mt. Fuji	Broad-leaved evergreen forest (BLEF)		138°43′	35°21′	0–2500	General lists	–
		Broad-leaved deciduous forest (BLDF)						–
	Nara	Broad-leaved evergreen forest (BLEF)		135°51′	34°41′	132–285	41	100–400
	Shiroyama	Broad-leaved evergreen forest (BLEF)		134°33′	34°04′	15–70	45	90–150
	Yakushima Island	Broad-leaved evergreen forest (BLEF)		130°23–38′	30°15–23′	8–980	77	80–900
		Mixed mesophytic forest (MMF)				1100–1772	67	

subdivided into two types: a tropical seasonal rainforest in the lowlands and a tropical montane rainforest found at higher elevations (Zhu, 2006; Zhu et al., 2006; Table 2). Predominant elements in the studied vegetation types are marked in Appendix 2.

(1a) Tropical seasonal rain forest (600–1100 m alt.) is found in the lowlands, usually below 900 m in elevation, but can be encountered occasionally in mountain valleys up to an altitude of 1100 m. Similar to equatorial lowland rainforests, the tropical seasonal rainforest has 3–4 indistinct storeys of trees, of which the top storey is composed of emergent trees over 30 m tall (tallest up to 60 m) with about 30% of crown coverage. The second layer is considered the main canopy, and comprises trees that grow up to 30 m tall with almost a continuous crown cover (70–80%), exhibiting the greatest density of stems. The third storey reaches a height between 5 and 18 m and has crown cover of about 40%. This storey consists of small trees and juveniles of species found in the upper layers. (1b) Tropical montane rain forest (900–1800 m alt.) occurs in wet montane habitats found between 900 and 1800 m in elevation. It exhibits a maximum height of 20–30 m and consists of 2–3 tree storeys. The uppermost canopy has a 70–80% crown cover without emergent trees. (2) Tropical seasonal moist forest (650–1300 m alt.) occurs on the middle and upper limestone slopes and may range from 650 to 1300 m in altitude. This vegetation type is adjacent to the seasonal rainforest. In contrast, this forest is evergreen, with two distinct tree layers. The top tier exhibits a crown cover of 40–60% and reaches a height of 15–25 m, whereas the second layer has a denser crown cover (70–80%) and grows to a height between 3 and 15 m tall. Woody climbers are very abundant and vascular epiphytes with small thick leaves are frequent. This vegetation type expresses an extrazonal vegetation type due to its specific substrate with enormous rainfall absorption (see Section 7). (3) Monsoon forest (480–850 m alt.) occurs on the banks of the Mekong River and at wide basinal areas where there is evidently an annual drying controlled by a strong monsoon climate and river discharge. The monsoon forest grows usually to a height of 20–25 m and consists of 1–2 deciduous tree layers. Woody lianas and epiphytes are scarce. The monsoon forest is often a single dominant tree community or consociation (i.e., association having one dominant species of plant). (4) Tropical montane broad-leaved evergreen forest (900–1800 m alt.) is the primary montane vegetational type. It grows on mountain slopes and summits above 900 m altitude and in valleys above 1300 m altitude. The tropical montane evergreen broad-leaved forest has 2 conspicuous storeys of trees, of which the top storey is 15–25 m tall with dense crown coverage and the lower layer is 3–15 m in height with canopy coverage of ca. 50%.

We realise taphonomic problems deriving from the comparison of the multi-storeyed canopy structure of the studied modern vegetation and fossil assemblages (e.g., Burnham, 1989, 1994).

3. Methods

We applied four palaeoenvironmental methods, i.e., Integrated Plant Record vegetation analysis (IPR-vegetation analysis), Leaf Size Analysis (LSA), Climate Leaf Analysis Multivariate Program (CLAMP), and Leaf Margin Analysis (LMA) on the studied fossil floras. We also used published palaeoclimatic proxies for the floras derived from the Coexistence Approach (CA), which was methodologically introduced by Mosbrugger and Utescher (1997). Integrated Plant Record vegetation analysis and Leaf Size Analysis methods were applied to evaluate the studied modern vegetation types from the tropical zone of China. Cluster analysis was used to show relations of the fossil and modern vegetation assemblages from E Asia based on the results of both of the last mentioned methods.

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

The IPR-vegetation analysis is a relatively new semi-quantitative evaluation method developed by Kovar-Eder and Kvaček (2003) to map the integrated fossil plant records (leaf, fruit, and pollen assemblages) in terms of the zonal vegetation (Kovar-Eder and Kvaček, 2007; Kovar-Eder et al., 2008). Methodologically, the IPR-vegetation analysis follows plant taxonomy, physiognomy, and autecological properties to classify them into several zonal and azonal taxonomic–physiognomic groups and/or components, i.e., CONIFER (zonal and extrazonal conifers), BLD (broad-leaved deciduous woody angiosperms), BLE (broad-leaved evergreen woody angiosperms), SCL (sclerophyllous woody angiosperms), LEG (legume-like woody angiosperms), ZONPALM (zonal palms), ARBFERN (zonal arborescent ferns), DRY HERB (open woodland and grassland elements), MESO HERB (mesophytic forest undergrowth), AZONAL WOODY (azonal woody trees and shrubs), AQUATIC (aquatic elements), AZNW (azonal non-woody elements) and PROBLEMATIC taxa.

Table 3
Meteorological and climatic proxy datasets of the studied regions derived from the meteorological stations (YMB, 1983; Liu et al., 1995; Zeng, 1995) and gridded datasets sensu New et al. (1999) and BRIDGE, 2008. Abbreviations: BLDF (broad-leaved deciduous forests), MMF (mixed mesophytic forests), BLEF (broad-leaved evergreen forests), ShSF (subhumid sclerophyllous forests), MAT (mean annual temperature), WMMT (warmest month mean temperature), CMMT (coldest month mean temperature) and MAP (mean annual precipitation).

Country	Areas	Studied vegetation unit	Longitude E	Latitude N	Gridded climatic parameters					Weather stations						Reference
					Altitude [m]	MAT [°C]	WMMT [°C]	CMMT [°C]	MAP [mm]	Name	Altitude [m]	MAT [°C]	WMMT [°C]	CMMT [°C]	MAP [mm]	
China	Jianfengling	Tropical lowland rain forest	108°59′	18°44′	249	23.9	27.7	18.3	1924.5	Jianfengling Town	68	24.5	27.8	19.4	1650	Liu et al. (1995),
		Tropical montane rain forest	108°53′	18°43′	880	20.6	24.3	15.6	1924.5	Tianchi	820	19.7	27.7	15.1	2651	Zeng (1995)
	Xishuangbanna	Tropical seasonal rain forest	101°12–35′	21°31–59′	600	23.5	26.6	18.6	1372.0	Jinghong City	550	21.7	25.3	15.6	1193	YMB (1983)
					1100	20.7	23.8	16.0	1143.0						(740 m alt.)	
		Tropical montane rain forest	100°32–33′	21°27–28′	900	21.8	25.0	16.9	1351.1							
					1800	16.8	19.8	12.3	1351.1							
		Tropical seasonal moist forest	101°26–27′	21°52–53′	650	23.0	26.4	17.6	1322.1							
					1300	19.4	22.8	14.2	1322.1	Nangongshan	1979	15.1	17.9	8.8	2491	
		Monsoon forest	100°22–35′	22°35–47′	480	23.6	27.3	17.4	1300.0						(1979 m alt.)	
					850	21.6	25.3	9.8	1299.7							
		Tropical montane broad-leaved	101°12–33′	21°27–34′	900	21.8	24.9	17.0	1372.0							
		evergreen forest			1800	16.8	19.9	12.4	1372.0							
	Mt. Emei	BLEF	103°20′	29° 31′	750	17.6	26.7	8	969	Emeishan City	447	17	26.8	7.1	1528	Teodoridis et al.
		MMF			1500	14.2	22.7	4.8	969							(2011a)
		BLDF			2000	11.7	20	2.6	969	Jinding	3047	3.1	11.8	−5.6	1756	
					2500	9.3	17.3	0.4	969							
	Meili Snow Mts	BLDF	99° 10′	28° 26′	2200	12.6	18.7	4.9	976	Deqin	3593	4.7	11.7	−3.1	661	
					3800	3.5	10.3	−3.5	976							
		ShSF			2580	10.5	16.7	2.9	976							
					3650	4.3	11	−2.7	976							
	Mt. Longqi	BLEF	117° 10′	26° 54′	580	17.8	26.5	8	1595	Taining	341	17	26.9	5.9	1775	
			117° 10′–21′	26° 30′–36′	1300	14.4	22.6	5	1595	local weather stations	1000	14.6–18.8	–	–	1600–1800	
Japan	Shirakami Sanchi	BLDF	139° 51′	38° 54′	0	11.43	24.9	−0.5	1614	Sakata	3	12.2	–	–	1938	
			139° 59′	40° 23′	1000	6.1	19.7	−5.8	1614	Hachimori	39	11.3	23.9	0.4	1465	
	Mt. Fuji	BLEF	138° 37′	35° 14′	0	15.1	26.1	4.9	1866	Fuji City	8	16.9	35.5	−3	1902	
			138° 27′	35° 10′						Nanbu	141	14.6	26	3.6	2471	
			138° 38′	35° 13′	600	12	23	1.8	1866	Hara	500	12.6	–	−2.2	2153	
		BLDF	138° 34′	35° 23′	1800	5.8	16.9	−4.4	1866	Asagiri	900	9.4	–	–	2671	
	Nara	BLEF	135° 30′	34° 25′	1000	10.3	21.3	−0.1	2345	Nara	104	14.6	26.6	3.8	1333	
	Shiroyama	BLEF	134°34′	34°04′	0	15.7	27.3	4.9	1690	Tokushima	6	16.2	27.4	6	1540	
					1000	10.6	22.1	0.1	1690							
	Yakushima Island	BLEF	130° 33′	30° 14′	0	16.1	25	7.1	2373	Onoaida	0	20.2	27.9	12.5	2941	
					1000	11.1	19.9	2.2	2373		60	20.0	27.4	12.5	3231	
		MMF	130° 33′	30° 13′	1700	7.5	16.27	−1.25	2373	Yakushima	15	18.9	–	–	3514	

The percentages of the various components of zonal woody angiosperms and zonal herb component (i.e., MESO HERB + DRY HERB) of zonal woody components are calculated as follows:

$$\%_{BLD} = \frac{BLD}{\sum(BLD, BLE, SCL, LEG, ZONPALM)} \times 100, \quad (1)$$

$$\%_{BLE} = \frac{BLE}{\sum(BLD, BLE, SCL, LEG, ZONPALM)} \times 100, \quad (2)$$

$$\%_{SCL+LEG} = \frac{SCL + LEG}{\sum(BLD, BLE, SCL, LEG, ZONPALM)} \times 100, \quad (3)$$

$$\%_{MESO\ HERB+DRY\ HERB} = \frac{MESO\,HERB + DRY\,HERB}{\sum(BLD, BLE, SCL, LEG, ZONPALM, CONIFER, MESO\,HERB, DRY\,HERB)} \times 100. \quad (4)$$

These percentages (Eqs. 1–4) have been defined as distinguishing 8 zonal vegetation types including their ecotones (Kovar-Eder and Kvaček, 2007; Teodoridis et al., 2011a; Table 4 — this paper): 1) temperate to warm-temperate broad-leaved deciduous forests (BLDF); 2) warm-temperate to subtropical mixed mesophytic forests (MMF); 3) subtropical broad-leaved evergreen forests (BLEF); 4) subtropical, subhumid sclerophyllous or microphyllous forests (ShSF); 5) ecotone vegetation of BLDF/MMF; 6) ecotone vegetation of BLEF/MMF; 7) xeric open woodlands; and 8) xeric grasslands or steppe (= Xeric grassland). The first four mentioned vegetation types were tested on living assemblages from China and Japan (Teodoridis et al., 2011a) to verify thresholds of the vegetation types originally defined only on the fossil record and their "palaeoenvironmental" habitats. Recently, the new IPR-vegetation database was built to organise and summarise the existing fossil and modern results (Teodoridis et al., 2011b).

3.2. Cluster analysis

A hierarchical tree clustering analysis was processed by STATGRAPHICS (StatSoft, Inc., 2011). According to Teodoridis et al. (2011a), we applied Ward's method as a linkage tree clustering method in which two clusters (x, y) are determined by the analysis of variance, and the method joins the clusters with minimal sums of squares (the Euclidean square distance). The number of the defaulted clusters was five corresponding to main vegetation types from E Asia (tropical rain forest "TRF", broad-leaved evergreen forest "BLEF", mixed-mesophytic forest "MMF", subhumid sclerophyllous forest "ShSF", and broad-leaved deciduous forest "BLDF"). We employed values of % BLD, BLE, SCL + LEG components of the studied fossil and modern sites as the source for the cluster analysis. Fig. 3.1 and Table 5 show clustering of the studied modern tropical vegetation types from southern China (studied here) and former studied vegetation types of the subtropical and temperate zones from SE China and Japan (Teodoridis et al., 2011a). Then we ran the clustering process to include the studied fossil floras to find out their relationship to modern vegetation types (Fig. 3.2).

3.3. Leaf Size Analysis (LSA)

This method determines the ratio of the percentage of leaf size categories (Dilcher, 1973). We follow leaf size categories sensu Webb (1959), i.e. leptophyll (<0.25 cm^2), nanophyll (0.25–2.25 cm^2), microphyll (2.25–20.25 cm^2), notophyll (20.25–45.0 cm^2), mesophyll (20.25–182.25 cm^2) and macrophyll (182.25–1640.25 mm^2). Notophyll and mesophyll categories correspond to mesophyll leaf category sensu Raunkiaer (1934). The categories are comparable to those used by CLAMP (see Appendix 3), where microphyll 3 and mesophyll 1 categories are equal to notophyll leaf size and mesophyll 2 and 3 to macrophyll leaves. The leaf size of fossil morphotaxa was measured in the categories using the leaf size template, which is available on the CLAMP website (Spicer, 2012). We used broad-leaved evergreen and broad-leaved deciduous woody angiosperms. We evaluated only complete or almost complete fossil leaves. In the case of the studied incomplete leaves, we tried to transpose the general outline of the leaves. Leaf fragments were strictly excluded. The number of samples of the studied fossil taxa (see Appendix 4) corresponds to those published in the original floristic (source) papers (Table 1). We did not analyse fossil floras containing less than 10 woody angiosperms. This method was applied also to the studied modern tropical and subtropical vegetation types from China. The leaf size categorisation was based on the personal experience of the third author (ZH), our studies in herbaria, i.e., Herbarium of Xishuangbanna Tropical Botanical Garden (HITBC) and Herbarium of the Institute of Botany, Chinese Academy of Sciences, Beijing (PE), and mainly on the published physiognomic characteristics in Flora of China (Wu et al., 2004). We also applied the hierarchical tree clustering analysis (Ward's method, Euclidean square distance) to compare results obtained from the studied fossil and modern sites (Table 6, Fig. 4). We used values of the percentage of leptophyll and nanophyll, microphyll, notophyll, and mesophyll taxa as the source for the cluster analysis. The number of the defaulted clusters was one.

3.4. Climate Leaf Analysis Multivariate Program (CLAMP)

This methodology is based on the observed quantitative relationship between foliar physiognomic characters of living woody dicots and the relevant climatic parameters at modern biotopes, i.e., 218 modern reference sites defined by physiognomic and climatic parameters distinguished into three separated datasets containing 144, 173 (144 + extra 29) and 189 (144 + extra 45) modern sites. These datasets can then be compared to the foliar physiognomic characters of a fossil flora (Appendix 3) in order to obtain palaeoclimate estimates. CLAMP was first introduced by Wolfe (1993), and subsequently this technique has been refined mainly by Wolfe and Spicer (1999),

Table 4
Zonal vegetation types as defined by IPR-vegetation analysis, namely by percent of zonal woody angiosperms and zonal herbs sensu Teodoridis et al. (2011a, Table 8).

Vegetation type	Zonal woody components			Zonal herbaceous components (fossil record)	Zonal herbaceous components (modern record)
	BLD	BLE	SCL + LEG	MESO + DRY HERB	MESO + DRY HERB
Broad-leaved deciduous forests	>80%			≤30%	40–70%
Ecotone	75–80%	<30%	<20%	<30%	40–55%
Mixed mesophytic forests	<80%				
Ecotone		30–40%			
Broad-leaved evergreen forests		>40%	(SCL + LEG) < BLE	<25%	10–45%
Subhumid sclerophyllous forests			≥20%	<30%	40–55%
Xeric open woodlands		<30%	≥20%	30–40%; MESO HERB > DRY HERB up to 10% of all zonal herbs	n.a.
Xeric grasslands or steppe		<30%		≥40%	n.a.

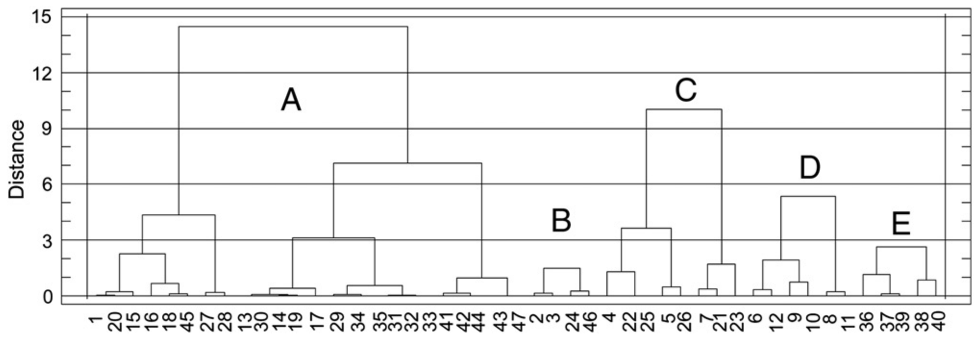

Fig. 3.1. Dendrogram (Ward's method, squared Euclidean distance) showing five defaulted clusters (A to E) based on the percentages of the BLD, BLE, and SCL+LEG components. Numbers represent the studied sites from subtropical and temperate areas of China and Japan (sensu Teodoridis et al., 2011a) and the studied tropical vegetation units in China (data source in Table 5).

Spicer (2000, 2007), Spicer et al. (2009), and Teodoridis et al. (2011c). CLAMP uses 31 different leaf physiognomic parameters (see Appendix 3) to estimate 11 (palaeo)climatic values, i.e., MAT (mean annual temperature), WMMT (warmest month mean temperature), CMMT (coldest month mean temperature), GROWSEAS (length of the growing season), GSP (growing season precipitation), MMGSP (mean monthly growing season precipitation), 3-WET (precipitation during 3 consecutive wettest months), 3-DRY (precipitation during 3 consecutive driest months), RH (relative humidity), SH (specific humidity) and ENTHAL (enthalpy). Mathematically, this method is based on Canonical Correspondence Analysis (CCA) — see Ter Braak (1986). For our study the spreadsheets and modern calibration reference datasets available on the CLAMP website (Spicer, 2012) were used. These include physiognomic and gridded meteorological datasets for 173 modern sample sites (Physg3ar and GRIDMet3ar), for 144 modern sample sites (Physg3br and GRIDMet3br) and for 189 modern sample sites (PhysgAsia1 and GRIDMetAsia1 — Jacques et al., 2011b). The sampling sites are mostly located in Northern America and Eastern Asia. CANOCO for Windows Version 4.5 provided CCA.

CLAMP often produces different results depending on which modern calibration dataset is applied. A statistical tool developed by Teodoridis et al. (2011c, p. 43) can clearly resolve the appropriate use of calibration datasets based on the similarities (i.e., minimum difference MIN $DIFF_i$) of the fossil (studied) and modern (calibration) physiognomic characteristics. To select the relevant CLAMP physiognomic reference datasets from 144, 173 and 189 modern sites and the relevant modern gridded calibration datasets (i.e., Physg3br, Physg3ar and PhysgAsia1; GRIDMet3br, GRIDMet3ar and GRIDMetAsia1), we have to update the original tool, which used only the 144 and 173 calibration datasets. The update is provided by an integration of the 189 reference dataset into a selection process as followed:

(A) Calculate means for all foliar physiognomic characteristics for the 144 modern sites (*MEAN*144) included also in calibration datasets of 173 and 189 sites.
(B) Calculate means for the remaining 29 modern sites (*MEAN*29), i.e., difference of 173 and 144 calibration datasets.
(C) Calculate means for the remaining 45 modern sites (*MEAN*45), i.e., difference of 189 and 144 calibration datasets.
(D) Take the foliar physiognomic parameters of the studied fossils (OUR) — see Appendix 3.

For each foliar physiognomic parameter:

$$DIFF144_i = \frac{ABS(OUR-MEAN144)}{[MAX(ABS(OUR-MEAN144), ABS(OUR-MEAN29)), ABS(OUR-MEAN45)]}, \tag{a}$$

$$DIFF29_i = \frac{ABS(OUR-MEAN29)}{[MAX(ABS(OUR-MEAN144), ABS(OUR-MEAN29)), ABS(OUR-MEAN45)]}, \tag{b}$$

$$DIFF45_i = \frac{ABS(OUR-MEAN45)}{[MAX(ABS(OUR-MEAN144), ABS(OUR-MEAN29)), ABS(OUR-MEAN45)]}, \tag{c}$$

where i = 1 to 31 is a foliar physiognomic parameter.

If $MIN(\sum(DIFF144_i), \sum(DIFF29_i), \sum(DIFF45_i)) = \sum(DIFF144_i)$ then OUR site is closer to the mean calculated from 144 sites and we should use the 144 dataset;

If $MIN(\sum(DIFF144_i), \sum(DIFF29_i), \sum(DIFF45_i)) = \sum(DIFF29_i)$ then OUR site is closer to the mean calculated from 173 sites and we should use the 173 dataset; otherwise we should use the 189 dataset. For the updated "copy & paste" Excel application — see Appendix 5.

3.5. Leaf Margin Analysis (LMA)

Leaf Margin Analysis is a univariate leaf physiognomic technique based on the empirical positive correlation between mean annual temperature (MAT) and the proportions of taxa with toothed vs. taxa with entire leaf margins (woody dicots) of non-pioneer vegetation. Wolfe (1979) devised this method and compiled 34 humid to mesic floras from East Asia, including the reference datasets of Wang (1961), to build a linear regression equation to predict temperature — see Eq. (5). Recently, Su et al. (2010) introduced a new Eq. (6) from humid to mesic forests from China. Sampling error was calculated by Miller et al. (2006) — see Eq. (7).

$$MAT_1 = 30.6 \times P + 1.41, \tag{5}$$

$$MAT_2 = 27.6 \times P + 1.038, \tag{6}$$

$$SE_{MAT} = \sqrt{[1 + \varphi(n-1)P(1-P)] \times \frac{P(1-P)}{n}}, \tag{7}$$

where $\varphi = 0.052$ (dispersion factor); P ($0<P<1$) is the percentage of woody dicots with entire leaves; and n is the total number of woody dicots.

4. Phytosociology of the studied Eocene sites

The early Eocene sites of the London Clay yielded the most diverse macrofossil assemblages of this age in Europe. Phytosociological and palaeoclimatic evaluations, to date, have been undertaken using nearest living relatives. Because of a high proportion of the potentially tropical elements, Collinson et al. (1981, p. 24) compared the cumulative London Clay assemblage with the East Asian paratropical forest sensu Wolfe (1979), where they stressed important differences. These differences

Table 5
Results of the IPR-vegetation analysis and cluster analysis of the studied Eocene floras of Europe and modern tropical, subtropical and temperate vegetation types from China and Japan (sensu Teodoridis et al., 2011a, Table 7; this paper). Data source for the cluster analysis was values of the percentage of BLD, BLE and SCL + LEG components. Abbreviations: BLDF (broad-leaved deciduous forests), MMF (mixed mesophytic forests) BLEF (broad-leaved evergreen forests) and ShSF (subhumid sclerophyllous forests). Percentages of components were calculated following the Eqs. ((1) to (4) — this paper).

Time/zone		Country	Area	Vegetation type – empirical classification	Studied modern vegetation units [region, (sub)community, (sub) association] and fossil floras/studied fossil floras	Cluster analysis: Site numbers (Figs. 3.1–3.2)	Cluster (Fig. 3.1)	Cluster (Fig. 3.2)	IPR-vegetation analysis: Organ	% of BLD	% of BLE	% of SCL + LEG	% of zonal palm	% of zonal herb (DRY + MESO herbs) of zonal taxa	Number of zonal taxa	Number of zonal woody angiosperms	Total number of taxa	Problematic taxa	Classification sensu Teodoridis et al. (2011a) – Table 4
Recent	Subtropical and temperate zone	China	Mt. Emei	BLEF	Plots (Tang and Ohsawa, 1997; Tang et al., 2007)	1	A	A	–	34	66	0	0	–	62	64	64	0	BLEF
				MMF	1 plot (Tang and Ohsawa, 1997)	2	B	B	–	65	36	0	0	–	23	23	24	0	BLEF/MMF
					Vegetation description (Li and Shi, 2007)	3	B	B	–	67	31	1	0	51	637	313	735	0	BLEF/MMF
				BLDF	2 plots (Tang and Ohsawa, 1997)	4	C	C	–	80	17	4	0	–	46	43	47	0	BLDF
			Meili Snow Mts	BLDF	*Betula* spp., *Acer* spp., *Sorbus* spp. comm.	5	C	C	–	100	0	0	0	63	52	19	53	0	BLDF
					Summarised communities of *Hippophae rhamnoides*, *Prunus mira*, *Salix luctuosa* and *Zanthoxylum simulans*, and *Populus haoana* var. *haoana*	6	D	D	–	68	6	26	0	58	37	16	41	0	ShSF
					Summary for BLDF	7	C	C	–	84	3	13	0	56	79	35	83	0	BLDF
				ShSF	*Quercus guyavifolia* comm.	8	D	D	–	56	12	33	0	40	39	24	41	0	ShSF
					Quercus aquifolioides comm., *Q. aquifolioides* and *Pinus armandii* subcomm.	9	D	D	–	55	21	24	0	50	37	19	39	0	ShSF
					Quercus aquifolioides comm., *Q. aquifolioides* subcomm.	10	D	D	–	64	14	22	0	53	72	34	77	0	ShSF
					Quercus aquifolioides comm., *Q. aquifolioides* and *Populus davidiana* subcomm.	11	D	D	–	54	15	31	0	47	30	16	32	0	ShSF
					Summary for ShSF	12	D	D	–	62	12	26	0	49	118	55	124	0	ShSF
			Mt. Longqi	BLEF	*Phoebe bournei* comm.	13	A	E	–	17	80	3	0	30	46	32	47	0	BLEF
					Altingia chinensis comm.	14	A	E	–	14	82	3	0	19	35	31	41	0	BLEF
					Castanopsis fargesii comm.	15	A	A	–	38	60	1	1	30	150	104	160	0	BLEF
					Castanopsis eyrei comm.	16	A	A	–	29	69	3	0	9	44	40	48	0	BLEF
					Castanopsis carlesii comm.	17	A	E	–	17	83	0	0	10	42	36	43	0	BLEF
					Lithocarpus polystachys comm.	18	A	A	–	23	77	0	0	14	42	35	43	0	BLEF
					Plots (He et al., 1998)	19	A	E	–	14	84	2	0	–	59	56	61	0	BLEF
					Summary for BLEF	20	A	A	–	35	64	1	1	26	234	171	249	0	BLEF
		Japan	Shirakami Sanchi	BLDF	*Lindera membranacea*–*Fagus crenata* comm.	21	C	C	–	78	9	13	0	53	178	82	205	2	BLDF/MMF
					Quercus mongolica var. *grosseserrata*–*Lindera umbellata* var. *membranacea* comm.	22	C	C	–	87	6	6	0	47	106	55	122	2	BLDF
					Ilex–*Thuja standishii* comm.	23	C	C	–	77	5	18		39	67	38	72	0	BLDF/MMF
			Mt. Fuji	BLEF	*Camellia japonica* region	24	B	B	–	55	42	3	0	–	38	36	39	0	BLEF
				BLDF	*Fagus crenata* region	25	C	C	–	89	5	6	0	–	104	93	113	0	BLDF
					Vaccinium–*Picea* region	26	C	C	–	95	2	3	0	–	107	97	122	2	BLDF

(continued on next page)

Table 5 (*continued*)

Time/zone	Country	Area	Vegetation type – empirical classification	Studied modern vegetation units [region, (sub)community, (sub) association] and fossil floras/studied fossil floras	Cluster analysis			IPR-vegetation analysis										
					Site numbers (Figs. 3.1–3.2)	Cluster (Fig. 3.1)	Cluster (Fig. 3.2)	Organ	% of BLD	% of BLE	% of SCL + LEG	% of zonal palm	% of zonal herb (DRY + MESO herbs) of zonal taxa	Number of zonal taxa	Number of zonal woody angiosperms	Total number of taxa	Problematic taxa	Classification sensu Teodoridis et al. (2011a) – Table 4
		Nara	BLEF	*Podocarpus nagi* assoc., typical subassoc.	28	A	A	–	38	53	6	4	44	60	35	78	0	BLEF
		Shiroyama	BLEF	*Elaeocarpus sylvestris* var. *ellipticus* assoc.	29	A	E	–	17	73	6	3	25	44	32	52	3	BLEF
		Yakushima Island	BLEF	*Ficus superba* var. *japonica*–*Persea thunbergii* assoc.	30	A	E	–	17	81	2	0	30	87	61	99	1	BLEF
				Tarenna–*Castanopsis sieboldii* assoc.	31	A	E	–	16	80	5	0	30	108	75	122	0	BLEF
				Hydrangea–*Castanopsis sieboldii* assoc.	32	A	E	–	14	80	6	0	31	119	81	134	1	BLEF
				Distylium–*Quercus salicina* assoc., typical subassoc.	33	A	E	–	14	81	6	0	39	62	36	67	0	BLEF
				Distylium–*Quercus salicina* assoc., *Maesa japonica* subassoc.	34	A	E	–	19	76	5	0	45	148	76	172	4	BLEF
				Summary for *Distylium*–*Quercus salicina* assoc.	35	A	E	–	20	75	5	0	44	149	77	172	4	BLEF
			MMF	*Eurya*–*Cryptomeria japonica* assoc., *Dryopteris nippoensis* subassoc.	36	E	D	–	56	32	12	0	52	73	33	87	1	BLEF/MMF
				Eurya–*Cryptomeria japonica* assoc., typical subassoc.	37	E	D	–	56	27	17	0	42	54	29	62	0	MMF
				Eurya–*Cryptomeria japonica* assoc., *Tsuga sieboldii* subassoc.	38	E	D	–	43	42	15	0	49	88	41	105	2	BLEF
				Eurya–*Cryptomeria japonica* assoc., *Carex morrowii* var. *laxa* subassoc.	39	E	D	–	53	31	16	0	43	37	19	45	2	BLEF/MMF
				Summary for *Eurya*–*Cryptomeria japonica* assoc.	40	E	D	–	43	38	19	0	52	103	48	122	2	BLEF/MMF

	Tropical zone	China	Jianfengling	Tropical lowland rain forest	41	A	E	–	5	95	1	1	1	148	146	152	0	BLEF
				Tropical montane rain forest	42	A	E	–	1	98	0	1	1	245	242	254	0	BLEF
			Xishuangbanna	Tropical seasonal rain forest	43	A	E	–	9	89	0	2	1	98	97	99	0	BLEF
				Tropical montane rain forest	44	A	E	–	3	97	0	0	0	59	58	59	0	BLEF
				Tropical seasonal moist forest	45	A	A	–	26	73	1	0	2	74	74	74	0	BLEF
				Monsoon forest	46	B	B	–	59	40	1	0	39	60	37	69	0	BLEF
				Tropical montane broad-leaved evergreen forest	47	A	E	–	9	91	0	0	0	54	54	54	0	BLEF
Fossil		UK	Early Eocene	London Clay	48	–	A	L, F	36	58	0	6	0	118	114	144	16	BLEF
				Hampshire Basin	49	–	A	L, F	40	58	0	2	0	85	83	106	11	BLEF
		Germany	Middle Eocene	Geiseltal	50	–	A	L, F	28	59	6	7	9	64	55	75	1	BLEF
				Messel	51	–	A	L, F	32	58	8	2	10	69	61	78	0	BLEF
				Profen–Scheiplitz	52	–	E	L, F	11	79	3	7	6	36	30	52	2	BLEF
			Late Eocene	Haselbach	53	–	E	L, F	13	83	0	4	5	32	26	49	3	BLEF
				Kayna-Süd	54	–	E	L, F	18	81	0	0	11	22	19	36	0	BLEF
				Klausa	55	–	A	L, F	25	68	0	6	5	19	16	26	0	BLEF
				Knau	56	–	E	L, F	8	92	0	0	5	21	19	30	0	BLEF
				Mosel	57	–	E	L, F	16	83	0	0	0	20	18	21	0	BLEF
				Phönix-Nord	58	–	A	L, F	25	74	1	0	0	41	35	50	0	BLEF
				Profen	59	–	A	L, F	21	77	0	2	0	31	28	45	0	BLEF
		Czech Republic		Český Chloumek	60	–	A	L, F	22	66	0	13	0	17	16	18	0	BLEF
				Nový Kostel	61	–	A	L, F	34	66	0	0	0	30	30	32	0	BLEF
Fossil				Staré Sedlo locality — leaf and carpological record	62	–	A	L, F	25	59	3	14	3	45	38	49	1	BLEF
				Staré Sedlo s.l. — leaf and carpological record	63	–	A	L, F	27	63	2	9	4	64	56	69	1	BLEF
				Staré Sedlo s.l. — pollen record	64	–	B	P	49	40	3	8	16	68	51	85	0	BLEF
				Staré Sedlo s.l. — integrated record	65	–	A	L, F, P	37	52	2	8	10	132	107	154	1	BLEF
				Žitenice	66	–	A	L, F	17	55	0	28	6	17	15	19	0	BLEF

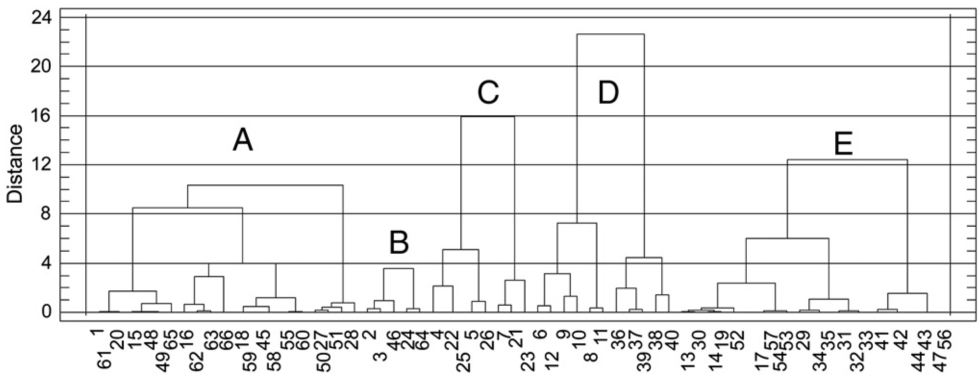

Fig. 3.2. Dendrogram (Ward's method, squared Euclidean distance) showing a relation of the studied fossil floras within the modern studied vegetation types (data source in Table 5) grouped into five defaulted clusters (A to E).

include a high diversity of gymnosperms, seasonality as indicated by growth rings, absence of dipterocarps, and a high proportion of temperate elements. Kvaček (2010) used these characteristics to establish this high diversity Eocene forest vegetational unit, the quasi-paratropical forest.

Among the middle Eocene plant sites in Europe that at Messel attracted much intensive palaeobotanical interest. In the overviews by Wilde (2004) and Collinson et al. (2010), the plant assemblage appears to be highly diverse and includes about 130 species in the carpoflora alone, and even more taxa when using the foliage. The vegetation, when reconstructed, has been compared with paratropical forests (Mai, 1995; Wilde, 2005), but as in the case of the London Clay plant assemblages, more arguments against such an interpretation can be postulated based both on the floristic composition and the physiognomic features of vegetative organs. According to the mean size of leaves corresponding to the notophyllous category, a new term "mid-latitudinal notophyllous broad-leaved evergreen forest" was suggested for the European Eocene (Kvaček, 2010).

The middle to late Eocene site of Geiseltal, also well-known for its preserved fauna, was monographed by Rüffle (1976) and others before the mine was closed and the outcrop flooded in 1993. The occurrences of the middle Eocene flora of Geiseltal (Wilde, 1995) are limited to the thick coal seam. According to the review by Wilde (1995), the leaf assemblage includes representatives of one *Equisetum*, 5 ferns, one cycad, 5 conifers, 33 species of dicots, and 4 species of monocots. Additional studies (Kahlert and Rüffle, 2007) have added further information on leaf-assemblage composition. The carpoflora, according to Mai (1976), includes 2 conifers, 22 dicots, and 4 monocots. The Geiseltal flora is not yet fully understood because the vegetational composition of a collection site was strongly influenced by sedimentology in this coal-forming swamp and tectonic influences (Rüffle and Litke, 2000; Kahlert and Rüffle, 2007). Studies attempting to help resolve these issues have been initiated (Hellmund and Wilde, 2001), but have not been yet completed. Estimates on the Palaeogene palaeoclimate by Krutzsch et al. (1992) stress the presence of a seasonal climate with pronounced dry phases within a warm, subtropical climate.

The middle Eocene of the Weisselster Basin is characterised by a floristic unit termed by Mai and Walther (1983, 2000) the "Scheiplitz floristic assemblage (Florenkomplex)." Besides the type locality at Scheiplitz, this assemblage is also found at Profen (Fischer, 1991), Dörstewitz, and even Bournemouth (Mai and Walther, 2000, p. 44). The vegetation type corresponds to a subtropical evergreen forest with members of the Fagaceae, Lauraceae, Myrtaceae, Theaceae, Myricaceae and Arecaceae predominating. Several of the local assemblages are considered to be "subxerophyllous" due to a smaller leaf size.

According to Mai and Walther (2000, p. 45) most of the late Eocene assemblages in the Weisselster Basin can be characterised as evergreen notophyllous forests. The same applies for the North Bohemian Staré Sedlo (Altsattel) Formation, which encompasses several classical sites (see Knobloch et al., 1996). The coeval diatomite of Kučlín near Bílina and adjacent volcanic sites represents lateral equivalents to the sandy deposits of the ancient Staré Sedlo River (Kvaček, 2002; Kvaček and Teodoridis, 2011). The volcanic assemblages differ in higher diversity but the vegetational type is the same for both Saxony and Bohemia. The Staré Sedlo assemblage differs slightly from that of the Zeitz in the scarcity of *Doliostrobus* and new, partly endemic, dicots such as *Trigonobalanopsis*, *Castaneophyllum*, *Engelhardia*, *Byttneriopsis*, and *Ternstroemites*.

5. Overview of European Eocene palaeoclimatic signals

Zachos et al. (2001, p. 686) referred to the interval from the mid-Palaeocene (59 Ma) to early Eocene (52 Ma), which is included in our study, as the most pronounced Cenozoic warming trend (expressed by a 1.5‰ decrease in $\delta^{18}O$). It peaked with the early Eocene Climatic Optimum (EECO; 52 to 50 Ma). The EECO was followed by a 17 Ma-long trend towards cooler conditions, as expressed by a 3.0‰ rise in $\delta^{18}O$, with much of the change occurring during the early–middle Eocene (50 to 48 Ma) into the early Oligocene (35 to 34 Ma). The cooling trend is interpreted to represent an Ice-free temperature decline in MAT from 12 to 2 °C (Zachos et al., 2008, Fig. 2).

Rough palaeoclimatic estimates are known from European mid-latitudinal floras. Mai (1995, p. 473) estimated the mean annual temperature (MAT) for the London Clay assemblage to be 18–19 °C, with the coldest month mean temperature (CMMT) 8–16 °C and the warmest month mean temperature (WMMT) 15–23 °C. Similarly, Mai (1976, 1995) interpreted the middle coal seam (middle Eocene) at the Geiseltal to have experienced a MAT ranging from 15–19 °C, a CMMT 3–15 °C and a WMMT 15.5–25.5 °C. Later Fischer (1991) estimated a MAT higher than 22 °C and CMMT 10 °C for Profen and Scheiplitz. The late Eocene floras from the Weisselster Basin and Staré Sedlo Formation (i.e., Staré Sedlo s.l.) belonging to the Zeitz floristic assemblage show similar palaeoclimatic estimates; these include a MAT of 15 to 20 °C, CMMT of 6–13 °C, and WMMT of 15–23 °C (Mai and Walther, 1983). Mosbrugger et al. (2005) reconstructed the climate evolution on the Central European continent for the last 45 million years and provided climate proxies for MAT, CMMT, WMMT and mean annual precipitation (MAP) mainly derived from the Coexistence Approach (Tables 1, 7). Their results correspond to the general Cenozoic cooling trend based on the oxygen-isotope records derived from deep-sea cores (Zachos et al., 2001, 2008).

6. Results

6.1. IPR-vegetation analysis

The fossil sites of the European Eocene listed in Table 1 are here evaluated by the IPR-vegetation analysis for the first time (Table 5).

Table 6
Results of the Leaf Size Analysis and cluster analysis of the studied Eocene floras of Europe and modern tropical, subtropical and temperate vegetation types from China and Japan (sensu Mai and Walther, 1985; Ohsawa and Ozaki, 1992; Tang and Ohsawa, 1999; this paper). Data source for the cluster analysis was values of the percentage of leptophyll + nanophyll, microphyll, notophyll, mesophyll, and macrophyll elements. Asterisk (*) - results derived from analysis of broad-leaved evergreen woody angiosperms only.

Age	Country/area		Studied fossil floras	Cluster analysis		Leaf size categories sensu Webb (1959)						References
				Site numbers in the dendrogram (Fig. 4)	Clusters	% of leptophyll and nanophyll	% of microphyll	% of notophyll	% of mesophyll	% of macrophyll	Number of taxa	
Middle Eocene	Germany		Profen–Scheiplitz	1	A	0	49	40	11	0	21	This paper, Appendix 6
			Geiseltal	2	B	0	40	51	9	0	26	
			Messel	3	B	8	30	52	10	0	55	
Late Eocene			Haselbach	4	C	16	62	22	1	0	–	Mai and Walther (1985)
			Klausa	5	C	21	48	28	3	0	–	
			Knau	6	C	35	47	16	2	0	–	
			Mosel	7	A	3	75	20	3	0	–	
			Weisselster Basin s.l.	8	B	0	23	67	11	0	30	This paper, Appendix 6
	Czech Republic		Český Chloumek	9	A	0	39	37	24	0	13	
			Nový Kostel	10	A	0	47	43	10	0	16	
			Staré Sedlo — locality	11	B	0	38	53	9	0	29	
			Staré Sedlo s.l.	12	B	0	41	52	7	0	41	
			Žitenice	13	A	0	33	39	28	0	11	
Modern	China	Jianfengling	Tropical lowland rain forest	14	B	1	27	58	13	0	145	This paper, Appendix 7
			Tropical montane rain forest	15	B	0	27	54	17	1	149	
		Xishuangbanna	Tropical seasonal rain forest	16	D	2	3	35	46	14	94	
			Tropical montane rain forest	17	D	0	9	48	27	16	51	
			Tropical seasonal moist forest	18	D	2	15	46	29	7	70	
			Monsoon forest	19	D	3	22	28	35	13	36	
			Tropical montane broad-leaved evergreen forest	20	D	2	3	51	40	4	52	
		Mt. Longqi	Broad-leaved evergreen forest (BLEF)	21	B	0	28	48	20	3	186	
		Mt. Emei	Broad-leaved evergreen forest (BLEF)	22	D	0	9	51	33	8	60	
			Mixed mesophytic forest (MMF)	23	A	0	43	46	11	0	23	
			Broad-leaved deciduous forest (BLDF)	24	A	8	51	38	3	0	43	
			Broad-leaved evergreen zone (BLEF)*	25	B	0	29	54	17	0	40	Tang and Ohsawa (1999)
			Mixed forest zone (MMF + BLDF)*	26	A	0	48	37	15	0	58	
			Subtropical montane forest (BLEF + MMF + BLDF)*	27	B	0	36	48	16	0	88	
		Meili Snow Mts	Broad-leaved deciduous forest (BLDF)	28	C	17	48	27	9	0	31	This paper, Appendix 7
			Subhumid sclerophyllous forest (ShSF)	29	C	13	22	13	5	1	53	
	Japan	Mt. Kiyosumi	Subtropical/warm-temperate lowland forest*	30	A	8	45	40	8	0	40	Ohsawa and Ozaki (1992)
		Mt. Takakuma	Subtropical/warm-temperate lowland forest*	31	A	9	45	35	9	2	194	
		Mt. Yuwan	Subtropical/warm-temperate lowland forest*	32	A	0	62	30	8	0	63	

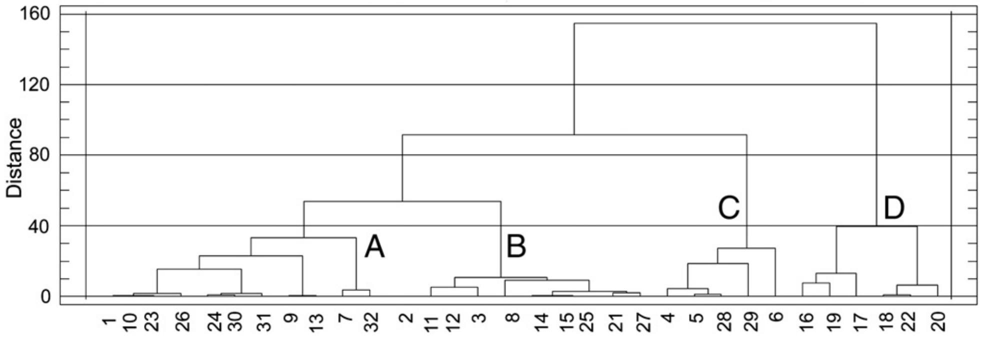

Fig. 4. Dendrogram (Ward's method, squared Euclidean distance) showing one defaulted cluster based on the percentage of leptophyllous and nanophyllous, microphyllous, notophyllous, mesophyllous and macrophyllous leaves/leaflets (sensu Webb, 1959) on the studied fossil and modern sites. Numbers represent the studied sites (data source in Table 6). Four subclusters (A to D) are distinguished.

According to the thresholds of key components for vegetational types established by Teodoridis et al. (2011a, Table 8), Table 4 - this paper, all Eocene assemblages are placed in the broad-leaved evergreen forest category. The number of elements per fossil flora varies from 19 to 144, and Appendix 5 shows how each element is scored for each locality included in this study. The early Eocene floras of the

Table 7
Palaeoclimatic estimates of the studied middle and late Eocene floras based on the Coexistence Approach (sensu Mosbrugger et al., 2005; Roth-Nebelsick et al., 2004; pro parte Uhl et al., 2007; Grein et al., 2011), Leaf Margin Analysis (LMA 1 sensu Wolfe, 1979; LMA 2 sensu Su et al., 2010) and Climate Leaf Analysis Multivariate Program (CLAMP). Abbreviations: MAT (mean annual temperature), WMMT (warmest month mean temperature), CMMT (coldest month mean temperature), GROWSEAS (length of the growing season), GSP (growing season precipitation), MMGSP (mean monthly growing season precipitation), 3-WET (precipitation during 3 consecutive wettest months), 3-DRY (precipitation during 3 consecutive driest months), RH (relative humidity), SH (specific humidity) and ENTHAL (enthalpy), SE (sampling error sensu Miller et al., 2006), and STDEV Residuals (standard deviations — CLAMP).

Age	Locality	Palaeoclimatic estimates										
		Coexistence Approach (CA)								Leaf Margin Analysis (LMA)		
		MAT [°C]		WMMT [°C]		CMMT [°C]		MAP [mm]		LMA 1 — MAT [°C]	LMA 2 — MAT [°C]	Sampling error [°C]
		Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.			
Middle Eocene	Geiseltal	22.9	25.0	26.7	28.1	16.9	23.0	1003.0	2091.0	23.5	20.9	2.5
	Messel	16.8	23.9	24.7	27.9	10.6	19.4	803.0	2540.0	21.9	19.5	2.3
	Scheiplitz	15.7	21.1	23.6	28.1	4.3	13.2	1096.0	1322.0	19.9	17.7	3.1
	Profen	16.5	21.7	27.1	27.5	13.3	14.8	1355.0	1534.0			
Late Eocene	Haselbach	17.5	20.8	27.1	27.9	12.2	13.3	1122.0	1281.0	20.1	17.9	4.7
	Klausa	–	–	–	–	–	–	–	–	21.4	19.1	3.9
	Knau	18.0	18.6	27.1	28.1	13.3	13.3	1096.0	1355.0	24.4	21.7	3.9
	Mosel	–	–	–	–	–	–	–	–	26.9	24.0	3.5
	Profen	17.5	20.8	27.1	28.1	13.3	13.3	1090.0	1355.0	–	–	–
	Český Chloumek	–	–	–	–	–	–	–	–	21.4	19.1	3.9
	Nový Kostel	–	–	–	–	–	–	–	–	26.1	23.3	2.7
	Staré Sedlo	–	–	–	–	–	–	–	–	19.9	17.7	2.9
	Staré Sedlo s.l.	15.7	23.9	25.6	28.1	5.0	13.6	1122.0	1613.0	21.2	18.9	2.4
	Žitenice	–	–	–	–	–	–	–	–	18.6	16.6	5.1

Age	Locality	Climate Leaf Analysis Multivariate Program (CLAMP)										
		Reference datasets	MAT [°C]	WMMT [°C]	CMMT [°C]	GROWSEAS [month]	GSP [cm]	MMGSP [cm]	3-WET [cm]	3-DRY [cm]	RH [%]	SH [g/kg]	ENTHAL [kJ/kg]
Middle Eocene	STDEV Residuals	189 sensu Jacques et al. (2011a)	1.3	1.5	2.6	0.7	21.8	2.5	13.9	4.1	6.0	1.2	0.5
	Messel		16.5	25.1	7.8	9.2	99.1	12.3	55.1	11.5	69.7	8.7	32.4
	Profen–Scheiplitz		20.3	27.1	10.5	11.2	104.4	14.1	52.2	8.7	67.5	9.8	33.2
Late Eocene	Staré Sedlo		16.2	25.9	6.3	9.1	112.2	13.3	59.4	12.0	70.5	8.6	32.4
	Staré Sedlo s.l.		16.1	26.0	6.2	9.0	119.2	14.3	61.5	12.9	71.3	8.7	32.4
	Weisselster Basin s.l.		17.2	24.2	8.4	9.3	85.7	17.8	51.0	9.0	73.5	9.7	32.9

Age	Locality	Range values of palaeoclimatic estimates based on the CA, LMA and CLAMP							
		MAT [°C]		WMMT [°C]		CMMT [°C]		MAP [mm]	
		Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.
Middle Eocene	Geiseltal, Messel, Profen, Scheiplitz	15.7	25.0	23.6	28.1	4.3	23.0	803.0	2540.0
Late Eocene	German floras: Haselbach, Klausa, Knau, Mosel and Profen, Weisselster Basin s.l.	17.2	26.9	24.2	28.1	8.4	13.3	1090.0	1355.0
	Bohemian floras: Český Chloumek, Nový Kostel, Staré Sedlo, Staré Sedlo s.l., Žitenice	15.7	26.1	25.6	28.1	5.0	13.6	1122.0	1613.0

London Clay and Hampshire Basin show relatively low values of the BLE component (58%) compared to the BLD component (36 and 40%). The ZONPALM component equals to 6 and 2%, whereas other significant zonal components (SCL + LEG and ZONAL HERB) are absent. The middle Eocene Geiseltal and Profen-Scheiplitz floristic assemblages show quite different values for BLE and BLD components (i.e., 59 and 79% [BLE] vs 28 and 11% [BLD]), whereas other SCL + LEG, ZONPALM, and ZONAL HERB components show minor differences and comparable values (SCL + LEG = 6 and 3%; ZONPALM = 7%; ZONALHERB = 9 and 6%). Late Eocene floras from the Weisselster Basin (i.e., Haselbach, Kayna-Süd, Klausa, Knau, Mosel, Phönix-Nord and Profen) show a distinct predominance of the BLE component, which varies from 68 to 92%, in contrasts to the percentage of the BLD components that fluctuated from 8 to 25%. The SCL + LEG component is absent except Phönix-Nord (1%), and the ZONPALM and ZONAL HERB components constitute up to 6% (Klausa) and up to 11% (Kayna-Süd). The middle Eocene locality of Messel is comparable with the late Eocene floras of the Staré Sedlo Formation. Here, the BLE and BLD components vary from 55 to 66% vs. 17 to 34%, and the extremely high value of ZONPALM at the Český Chloumek and Žitenice localities (13 and 28%) is due to the relatively low number of elements used in the analysis (18 and 19). Therefore, the values of 8% to 9% (ZONPALM) from the Staré Sedlo s.l. are considered appropriate. The IPR vegetation analysis results based only on the pollen record from Staré Sedlo s.l. shows a typical inverse character of the BLE and BLD components, which is in contrast to the results derived from the macrofossils. This discrepancy is caused by splitting uncertain sporomorph (e.g., *Tricolporopollenites*) into BLE and BLD and/or BLE and SCL groups. This fact also influenced the summarised results of Staré Sedlo s.l., where the pollen record is integrated. The relatively low value of the zonal herbaceous components is taphonomically influenced, i.e., general absence of the herbs in macrofossil record vs. pollen record (16% — Staré Sedlo s.l. — pollen), and caused by the lack of zonal herbaceous-grassland/steppe vegetational types in the European Palaeogene.

Four different types of tropical vegetation from Xishuangbanna and two from the Jianfengling were evaluated using the IPR-vegetation analysis (Tables 2, 5). The number of elements per vegetational unit ranges from 54 to 245 species. Appendix 2 shows scoring of elements within the IPR-vegetation analysis for the studied modern vegetation. Nearly all tropical vegetational types examined in both areas, except the monsoon forest from Xishuangbanna, show a distinct predominance of the BLE components ranging from 98 to 89%, which is in contrast to the percentages of BLD that range from 1 to 9%. Only the tropical seasonal moist forest shows a lower BLE value of 73% and a BLD value of 26%. The percentage of other significant zonal components (i.e., SCL + LEG, ZONPALM and ZONAL HERB) is ignored because of their low values (less than 2%). In contrast, the monsoon forest from Xishuangbanna shows an inverse distribution of BLE and BLD components and a relatively high abundance of zonal herbaceous components (39%). Here, the BLE value is 40% and BLD value is 59%. In sum, these results correspond to the broad-leaved evergreen vegetation type (Table 4).

6.2. Comparison of Eocene European vegetation and modern vegetation types from China and Japan — cluster analysis

Fig. 3.1 and Table 5 show five clusters of the modern tropical vegetation types from southern China studied here and vegetation types of subtropical and temperate zones from China and Japan sensu Teodoridis et al. (2011a), which were used as the template for our analysis of studied fossil vegetation and their affinities to the modern vegetation types (Table 5, Fig. 3.2). Fig. 3.1 shows obviously a relatively close relationship between the broad-leaved evergreen forest vegetation types (BLEF) from China (Mt. Longqi — 13–19; Mt. Emei — 1) and Japan (Nara — 27, 28; Shiroyama — 29, and Yakushima Island — 30–35) and the studied tropical vegetation types from Jianfengling (41, 42) and Xishuangbanna (43–45, 47) grouped in one cluster (Fig. 3.1, cluster "A"). Only a single vegetation type of monsoon forest from Xishuangbanna (46) is clustered separately among mixed mesophytic forests from Mt. Emei (2, 3) and specific BLEF vegetation type of Mt. Fuji (24) with a very low percentage of BLE components (42%) (Teodoridis et al., 2011a, p. 235) - see Fig. 3.1, cluster "B". The above-mentioned close relationship between the studied broad-leaved evergreen forests and tropical vegetation types in China is based on the similarities in the composition of the BLD, BLE and SCL + LEG components. The studied Chinese tropical vegetation originally assigned as paratropical rain forest sensu Wolfe (1969) shows different physiognomical and taxonomic characteristics from the BLEF vegetation types (e.g., greater height of canopy, different taxonomic affinities of dominant representatives, leaf size character, higher percentage of entire-leaved elements, prominent lianas with high diversity). According to Wolfe (1979, pp. 7–11), the Chinese paratropical vegetation is more closely similar to the vegetation of the tropical rain forests rather than to the notophyllous broad-leaved evergreen forests that correspond to BLEF vegetation type defined by the IPR-vegetation analysis (Table 4).

To demonstrate the relationship between the analysed fossil plant assemblages of the European Eocene and the modern studied vegetation types from China and Japan (Table 5), we provided cluster analysis using the studied fossil floras (marked 48–66 in Table 5). Similarly, the dendrogram (Fig. 3.2) presented five different clusters A to E. The first cluster "A" grouped together 13 fossil floras, tropical seasonal moist forest from Xishuangbanna (45) and subtropical assemblages of broad-leaved evergreen forests (BLEF) from Mt. Emei (1), Mt. Longqi (15, 16, 18, 20), Nara (28), and Shiroyama (29). The late Eocene flora of Nový Kostel (61) has a close relation to BLEF vegetation type of Mt. Emei (1) and to the summarised vegetation type of BLEF from Mt. Longqi (20). The studied early Eocene floras of London Clay (48) and Hampshire Basin (49) as well as an integrated flora of Staré Sedlo s.l. (65) show the nearest distance to site 15 (*Castanopsis fargesii* comm.). Next late Eocene floras of Staré Sedlo locality (62), Staré Sedlo s.l. — leaf and carpological record (63) and Žitenice (66) are clustered in one group with modern BLEF from Mt. Longqi (16 — *Castanopsis eyrei* comm.). The next group of the cluster "A" contains late Eocene floras of Klausa (55), Phönix-Nord (58), Profen (59) and Český Chloumek (60) and modern vegetation types of BLEF from Mt. Longqi (18 — *Lithocarpus polystachys* comm.) and tropical seasonal moist forest from Xishuangbanna (45). The tropical forest flora is closest to the flora of Phönix-Nord (58) and these are also grouped together with the flora from Profen (59) and modern vegetation from Mt. Longqi (18). A relatively independent subgroup of the cluster "A" includes two middle Eocene floras of Geiseltal (50) and Messel (51) with a close relationship to the modern BLEF vegetation types of Nara (27, 28). The cluster "B" represents a specific relationship with the vegetation of Staré Sedlo s.l. based on the pollen record only (64), with specific BLEF vegetation of Mt Fuji (24), monsoon forest from Xishuangbanna (46), and MMF vegetation type of Mt. Emei (2, 3). The cluster "C" comprises only modern vegetation types of broad-leaved deciduous forests (BLDF) from Mt. Emei (4), Meili Snow Mts (5, 7), Shirakami Sanchi (21–23) and Mt. Fuji (25, 26) without any affinities to the studied Eocene floras. Similarly, the cluster "D" contains a mixture of the studied modern vegetation types of mixed mesophytic forest (MMF) from Yakushima Island (36–40), broad-leaved deciduous forest (BLDF) and subhumid sclerophyllous forest (ShSF) from Meili Snow Mts (6, 8–12). The fifth cluster "E" groups middle Eocene flora of Profen–Scheiplitz (52), next to late Eocene floras of Mosel (57), Kayna-Süd (54), Haselbach (53), and Knau (56) together with BLEF vegetation types from Mt. Longqi (13, 14, 17, and 19), Shiroyama (29), and Yakushima Island (30–35), and tropical vegetation from Jianfengling (41, 42) and Xishuangbanna (43, 44, and 47). However the first four mentioned fossil floras show the closest affinity with BLEF vegetation of Mt. Longqi (13, 14, 17, and 19) and vegetation of *Ficus superba* var. *japonica–Persea thunbergii* association from Yakushima Island (30). The flora of Knau (56) is most comparable to the tropical seasonal rain forest and the tropical montane broad-leaved evergreen forest from Xishuangbanna (43, 47).

6.3. Result of the Leaf Size Analysis (LSA) from fossil and modern studied vegetation types

The results of the LSA applied on the leaf material from the studied fossil and modern floras are presented in Table 6, and in Appendices 6 and 7, which contain lists of the studied plant elements including their evaluation along with detailed physiognomic characteristics derived mainly from Wu et al. (2004). We had to exclude several fossil floras from the LSA due to an absence of the leaf record (London Clay, Hampshire Basin) or the low representation of the woody angiosperms (less than 10), i.e., Kayna-Süd, Phönix-Nord and Profen.

Similarly, we ran the cluster analysis (Ward's method, squared Euclidean distance) to model a schema of the relationship between the studied fossil and modern sites (Table 6). Focusing on the presented dendrogram (Fig. 4), it is possible to distinguish four subclusters marked A to D. The first subcluster "A" groups together the middle Eocene flora of the Profen–Scheiplitz (1), late Eocene floras of Nový Kostel (10), Český Chloumek (9), Žitenice (13) and Mosel (7) with modern vegetation types of mixed forest zone from Mt. Emei (26), mixed mesophytic forest from Mt. Emei (23), broad-leaved deciduous forest from Mt. Emei (24) and subtropical/warm-temperate rain forests from Japan (30–32). The floras of Profen–Scheiplitz (1) and Mosel (7) show the nearest affinities to the mentioned modern vegetation types of 23 (MMF from Mt. Emei) and 32 (Mt. Yuwan, Japan). The subcluster "B" comprises a set of the remaining middle Eocene floras of Geiseltal (2) and Messel (3) and late Eocene floras of Staré Sedlo locality (11), Staré Sedlo s.l. (12) and Weisselster Basin s.l. (8) linking to a relatively isolated group of modern vegetation types of tropical rain forest from Jianfengling (14, 15), of broad-leaved evergreen zone from Mt. Emei (25) and/or broad-leaved evergreen forest from Mt. Longqi (21) and of subtropical montane forest (27) from Mt. Emei. The subcluster "C" includes the last of the late Eocene floras of Haselbach (4), Klausa (5) and Knau (6) showing nearest relations to the modern vegetation types of broad-leaved deciduous forest (28) and subhumid sclerophyllous forest (29) from Meili Snow Mts. The last subcluster "D" contains only the studied modern tropical vegetation types from Xishuangbanna (16–20) and broad-leaved evergreen forest from Mt. Emei (22).

6.4. Palaeoclimatic signals of the studied Eocene European floras

We have used the published CA proxies from the Eocene sites included in the present study and combined those with newly derived proxies from CLAMP and LMA (Table 1) to provide palaeoclimate estimates derived from different methods during the Eocene (Table 7). As noted in Section 5, the palaeoclimatic proxies for the early Eocene and/or London Clay floras are not available and we accepted rough palaeoclimatic range estimates derived from floristic records and analogues with modern paratropical vegetation (sensu Wolfe, 1979) in south China, i.e., 18–19 °C (MAT), 15–23 °C (WMMT), and 8–16 °C (CMMT). We can summarise the results presented for the middle Eocene (Geiseltal, Messel, Profen–Scheiplitz) to obtain range values of the studied flora and very rough palaeoclimatic proxies as follows: MAT 16–25 °C, WMMT 24–28 °C, CMMT 4–23 °C and MAP 803–2540 mm. These palaeoclimatic estimations correspond to the former studies of Mai (1976, 1995) and Fischer (1991). Focusing on the palaeoclimatic signals, we observed significant differences in the CA and CLAMP results for the Profen–Scheiplitz, and Messel floras. The difference in the value of MAT, WMMT and CMMT parameters is due to different methodologies of both the techniques used. CLAMP estimates are based on leaf physiognomic characteristics, which are influenced by a relatively high abundance of leptophyllous elements in the Messel flora (8.2% — Appendix 3). This effect is also indicated in the results of the IPR-vegetation analysis, where the value of the SCL + LEG component for Messel is 8% (Table 5). The xerophyllous character of leptophyllous fossils from Messel (i.e., *Leguminosae* spp. 1–5) should be linked naturally with a warm subhumid environment during the middle Eocene. On the contrary, CLAMP proxies show the opposite palaeoclimatic character when compared with the Profen–Scheplitz estimates. Similar values for the same leptophyllous leaf size characteristic were measured on several calibration sites from the temperate zones of Northern America and Japan — e.g., Stroudsburg (Pennsylvania, USA), Dannemora (New York, USA), Kannami and Nekko (Honshu, Japan), which are included in the 189 modern reference datasets (PhysgAsia1). Logically, this mentioned effect cannot be detected when using CA and LMA techniques, which are based on analysis of the nearest living relatives (NLRs) and characteristics of the leaf margin (independent from the leaf size characteristics), respectively. The flora of Profen–Scheiplitz shows an interesting congruity in the values of the studied palaeoclimatic proxies derived from LMA, CLAMP, and CA despite a relatively low CMMT minimum-estimate of 4.3 °C (Scheiplitz — CA). The published CA results of Geiseltal (Mosbrugger et al., 2005) correspond to the presented LMA results. The late Eocene floras from both Germany and the Czech Republic exhibit the following range of palaeoclimatical characters: MAT 17–27 °C and 16–26 °C, WMMT 24–28 °C and 26–28 °C, CMMT 8–13 °C and 5–14 °C, and MAP 1090–1355 mm and 1122–1613 mm (see Table 7). Generally, the proxies presented here for the studied late Eocene sites show higher values in contrast to the original estimation for the Zeitz floristic assemblage (Mai and Walther, 1983). If we compare these range values with those derived from the studied middle Eocene floras no significant palaeoclimatic change can be detected. Focusing on the CLAMP results only, i.e., Profen–Scheiplitz, Staré Sedlo and Weisselster Basin (excluding colder estimates for Messel — see above), we can note a temperature decrease in MAT (3–4 °C) and a rise of the mean annual range of temperature (MART = WMMT minus CMMT) except for the floras summarised for the Weisselster Basin. The increase of the MART should indicate that the area experienced higher seasonal temperature fluctuations during the late Eocene. However, we cannot find similar differences in MAT and MART parameters estimated by CA and LMA for the same time interval. Only the CA and LMA proxies of Geiseltal (and Messel for LMA) when compared to those from the studied late Eocene floras show unequivocal palaeoclimatic changes. Some of the LMA results may be biased due to a low total number of elements available from Haselbach, Klausa, Knau, Český Chloumek, and Žitenice. This fact is indicated by the relatively high values for the sampling error (Miller et al., 2006). The values of MAT, derived from LMA 2 sensu Su et al. (2010), correspond better to those derived from CLAMP and CA analyses than to those obtained from LMA 1 sensu Wolfe (1979). The parallel use of the three palaeoclimatic methods presented here to get climatic proxies from the middle to late Eocene equivocally provides (only CLAMP — see above) the cooling trend for this period as expressed by evaluating $\delta^{18}O$ from deep sea deposits (Zachos et al., 2001).

7. Discussion

Two questions that appeared during our studies on fossil and modern plant records are, in our opinion, crucial and are discussed below:

(A) Can we use modern tropical and subtropical vegetation types from E Asia as models for European Eocene floras?
(B) Can we use the IPR-vegetation analysis for Palaeogene floras at all?

(A) Most European Eocene assemblages studied here have generally an azonal character (mainly from Weisselster Basin and Staré

Sedlo Formation) typical of the fossil plant record. From these macrofossil assemblages it is difficult to obtain a complete picture of the upland zonal vegetation. Kvaček (2010) defined two zonal Eocene vegetational types: (1) a mid-latitude quasi-paratropic rainforest for early Eocene floras of the Hampshire Basin and London Clay, and the middle Eocene flora of Messel, and (2) mid-latitude notophyllous broad-leaved evergreen forest that is known from late Eocene floras of Hordle, England, and Kučlín. Otherwise, he also noted several azonal forest types (1) broad-leaved evergreen riparian gallery forest with palms known from the Staré Sedlo Formation and Geiseltal (Zeitz, upper part of Geiseltal section), (2) mixed pine and broad-leaved evergreen swamp forest from coal facies of Geiseltal, and (3) mixed *Doliostrobus* (and/or *Quasisequoia*) and broad-leaved evergreen swamp forest from middle Eocene sites of Helmstedt, Scheiplitz and Profen (Kvaček, 2010). An equivalent of extrazonal vegetation of the mountain coniferous forest, mainly based on the pollen records from the Staré Sedlo Formation and Messel, is a less clear-cut unit and should be considered in the category with zonal vegetation (Kvaček, 2010). The character of this extrazonal assemblage can be compared with modern, high altitude vegetation analogues from the tropical and subtropical zones of China that is predominated by Pinaceae (*Pinus*, *Cathaya*, *Abies*, *Tsuga*). For example, these conifers occur in the coniferous forest zone from 2500 to 3099 m altitude in Mt. Emei (Tang and Ohsawa, 1997).

The differences between the mentioned zonal vegetation types from European Eocene, i.e., mid-latitude quasi-paratropic rainforest and mid-latitude notophyllous broad-leaved evergreen forest, depend only on the age of the assemblages and their floristic composition. The early Eocene quasi-paratropic rainforest is based on the carpological record from marine deposits (London and Hampshire Basins) of mainly extinct genera and species. Its "paratropic" character is difficult to compare with modern vegetation types despite the presence of a polydominance of tropical families, such as the Annonaceae, Cornaceae, Icacinaceae, Lauraceae, Menispermaceae, and Rutaceae (cf. Collinson, 1983). According to the presented results of the IPR-vegetation analysis and cluster analysis from China and Japan (Table 5; Figs 3.1–3.2; Appendixes 2, 4), we can compare the studied fossil sites with the modern vegetation analogous from the subtropical and tropical zones in E Asia. Focusing on IPR-vegetation analysis results only, the studied early Eocene floras from the London Clay and Hampshire Basin show the closest affinity to broad-leaved evergreen forest in Mt. Longqi (*Castanopsis fargesii* comm.). The above-mentioned close relationship of these floras and Staré Sedlo s.l. — integrated record (Fig. 3.2) was caused by a relatively low diversity of the BLE component derived from mixing the leaf and carpological record with pollen spectrum (Appendix 4). Besides, the early Eocene floras from the UK are based mainly on the carpological record often representing extinct elements with unclear affinities to NLR. This fact makes IPR vegetation analysis scoring more difficult, because the scoring must be based on higher taxonomic levels, i.e., genera or families (Kovar-Eder and Kvaček, 2007). The analysed middle Eocene floras of Geiseltal and Messel are close to the modern BLEF vegetation types of Nara. Besides, the flora of Profen–Scheiplitz is comparable to the broad-leaved evergreen forest from Mt. Longqi and Yakushima Island. The studied late Eocene floras also show affinities to the modern reference vegetation types of the broad-leaved evergreen forests from Mt. Emei, Mt. Longqi and Yakushima Island. Only the flora of Knau shows the nearest distance to the tropical seasonal rain forest and the tropical montane broad-leaved evergreen forest from Xishuangbanna. Similarly, the studied modern vegetation type of the tropical seasonal moist forest (Xishuangbanna) presents a close relationship to the late Eocene flora of Profen and also has affinity to other late Eocene floras from cluster "A", i.e., Český Chloumek, Klausa, and Phönix-Nord (Fig. 3.2). Finally, on the basis of the ratio of BLD, BLE, SCL + LEG components, the studied Eocene floras from Europe are comparable to the studied modern subtropical vegetation types of the broad-leaved evergreen forests from China rather than those from the tropical zone in south China.

As we have noted above in Section 6.1, Wolfe (1969) strictly distinguished tropical vegetation types and subtropical broad-leaved evergreen forests based on the differences in canopy structure, element diversity, taxonomic affinity, percentage of the BLE component, and leaf size character. The present study (Section 2.2, Table 5, Appendix 2) and Teodoridis et al. (2011a) supports the independence of tropical vegetation and BLEFs in China based on the mentioned Wolfe's diagnostic differences. However, some features, such as leaf size character, can overlap in some cases of the specific montane tropical vegetation and lowland subtropical BLEF types. The results of the leaf size analysis (Table 6, Fig. 4) show a close relationship between subtropical vegetation of the broad-leaved evergreen forests from Mt. Emei and Mt. Longqi and tropical vegetation from Jianfengling and Xishuangbanna (see clusters "B" and "D"). Fig. 4 shows a subcluster grouping together tropical seasonal moist forest from Xishuangbanna (18), broad-leaved evergreen forest from Mt. Emei (22), and tropical montane broad-leaved evergreen forest (20) from Xishuangbanna. The similarity of leaf size here is probably caused by mutual compensation in altitude and latitude zonation between tropical and subtropical zones as well as the specific abiotic factors of the tropical seasonal moist forest growing on calciferous soils/habitats having extraordinary drainage character (only 73% of BLE component and 15% of microphyllous elements). Similarly, vegetation types of tropical lowland rain forest and tropical montane rain forest from Jianfengling (14, 15) are clustered together with broad-leaved evergreen forest from Mt. Longqi (21), broad-leaved evergreen forest zone from Mt. Emei (25) and cumulative vegetation type of subtropical montane forest from Mt. Emei (27), which summarises vegetation from broad-leaved evergreen and mixed forest zones, i.e., BLEF, MMF and BLDF forests (Tang and Ohsawa, 1999). The leaf size characteristics of the two latter-mentioned vegetation types are based on BLE components analysis only (Tang and Ohsawa, 1999). Clustering of the studied fossil floras shows no time dependence and probably is influenced by environment factors, i.e., azonal vs. zonal elements and/or environments. The studied floras grouped together in cluster B (i.e., Geiseltal, Messel, Staré Sedlo — locality, Staré Sedlo s.l., Weisselster Basin s.l. — Table 6, Fig. 4) present a dominance of the notophyllous and mesophyllous over microphyllous and leptophyllous and nanophyllous elements. This ratio is the closest to those analysed by the tropical vegetation types from Jianfengling (14, 15) and broad-leaved evergreen forests from Mt. Longqi (21), Mt. Emei (25) and summarised vegetation types of Mt. Emei (27). On the contrary, the other studied floras of late Eocene age from Germany (i.e., Haselbach, Klausa, Knau) have distinct microphyllous character that might be caused by their mostly azonal character and taxonomical absence of the "notophyllous" elements such as *Trigonobalanopsis*, *Engelhardia*, *Byttneriopsis* or *Ternstroemites*. These floras are grouped together within the subcluster "C" with close affinity to extrazonal vegetation from Meili Snow Mts (28, 29). Similarly the remaining studied late Eocene floras (Mosel, Český Chloumek, Nový Kostel) and middle Eocene flora of Profen–Scheiplitz show relatively smaller leaf size characteristics that allows those to be grouped with vegetation types of mixed mesophytic forest and broad-leaved deciduous forests from Mt. Emei (23, 24, 26), and subtropical/warm temperate lowland forests from Japan (30–32) sensu Oshawa and Ozaki (1992). The LSA provided for Profen–Scheiplitz and its close affinity to subtropical–warm temperate MMF and BLDF vegetation can also prove the equivocal interpretation described above of the leptophyllous elements (and small leaf size elements in general) in palaeoclimatic and/or palaeovegetational aspects (Section 6.4). The LSA results presented from modern vegetation types from Mt. Emei (Table 6) corroborate also those based on BLE elements only and prove the trend of leaf size decreasing towards higher altitude (Tang and Ohsawa, 1999). The known effect of change in leaf size variation within a forest stratification in modern vegetation (e.g., Tang and Ohsawa, 1999), where canopy trees are composed of predominantly large-size elements, while subcanopy and understorey trees are mainly composed of elements with foliage of smaller size cannot easily be applied to the studied fossil record due to taphonomic bias (e.g., Burnham, 1989, 1994). On the other hand, Teodoridis et al. (2011a) revealed that there are no discrepancies between modern geobotanically (empirically) defined vegetation types from China and Japan (Table 2 — this paper) and palaeobotanical vegetation types following primary experiences in European fossil floras (Table 4). The congruity has proved the independence of the IPR-vegetation analysis on several aspects such as the number and frequency of studied elements (predominant, common, and endemic) or sampling plots vs. general floristic list. These aspects are usually marked as weak points for palaeoenvironmental evaluation of fossil assemblages. The studied lowland vegetation types with multi-storeyed canopies (3 to 4) from the tropical zone of China yielded a high percentage of BLE elements in excess of 87%, which corresponds to those from the vegetation of tropical montane broad-leaved evergreen forest having only two tree-storeys canopy structure. These tropical vegetation types are also grouped in one cluster “A” (Fig. 3.1) together with subtropical BLEF types from Mt. Longqi, Mt. Emei, Nara, and Yakushima Island. Similarly, there are no significant differences in LSA (one subcluster “D”). Therefore, we stress there is a limitation to the use of the IPR-vegetation analysis for distinguishing assemblages with a multi-storeyed canopy structure.

Fang et al. (2002) climatically defined a northern limit to the tropical zone in China as follows: Warmth Index (WI sensu Kira, 1977) is 240 °C per month, which corresponds to MAT 25 °C and/or CMMT of 18 °C. The gridded meteorological datasets as well those values from the climatological stations presented in Table 3 are more or less comparable to the above-mentioned boundary between tropical and subtropical zones in China, however it is necessary to reflect lower values of the studied climatic parameters depending on higher altitudes. Generally, the studied lowland tropical vegetation from Jianfengling and Xishuangbanna (up to 900 m altitude) and subtropical lowland vegetation from Mt. Emei, Mt. Longqi, Nara, Shiroyama, and Yakushima Island (up to 1000 m altitude) can be climatically characterised as followed, i.e., MAT 21.6–23.9 °C and 10.6–17.6 °C, WMMT 25.0–27.7 °C and 19.9–26.8 °C, CMMT 16.9–18.3 °C and 0.1–8 °C, and MAP 1193–2651 mm and 1333–2373 mm (see Table 3). We can simply compare the presented palaeoclimatic estimates derived from CA, CLAMP and LMA for the middle to late Eocene (Table 7), as well as rough estimates for our early Eocene floras (Sections 5 and 6.4) with the above-mentioned range of meteorological values for tropical and subtropical zones of E Asia. It is obvious that the studied Eocene floras show a close affinity to modern subtropical lowland vegetation of broad-leaved evergreen forest. The most significant diagnostic parameter is the values of the CMMT. Only the values of CMMT coexistence interval estimated for the middle Eocene flora of Geiseltal (i.e., 19.9–23.0 °C) exceed the limit. However this interval value does not correspond to those from the other studied middle Eocene floras (Messel, Profen, and Scheiplitz), nor the proxies derived from CLAMP (Messel, Profen–Scheiplitz) and the rough palaeoclimatic estimates (Mai, 1976, 1995; Fischer, 1991) — Table 7.

According to the summarised results of the palaeoenvironmental methods used and the cluster analysis, we stress that the studied middle and late Eocene floras from Europe compare better to modern subtropical vegetation types of broad-leaved evergreen forests from E Asia than to the studied vegetation from the tropical zone in China. The closest modern vegetation analogue is the subtropical lowland broad-leaved evergreen forest characterised by a predominance of larger leaf size elements (i.e., notophyllous to macrophyllous), which grow under climatic conditions with minimum values of MAT and CMMT above 15 °C and 5 °C, respectively. This modern analogous vegetation is typified by the broad-leaved evergreen forests of Mt. Emei sensu Tang and Ohsawa (1997) and Mt. Longqi sensu Li (1994, Figs. 4–7).

(B) Focusing on the results of the IPR vegetation analysis presented in Table 5, there is an obvious discrepancy between the early Eocene floras of the London Clay and Hampshire Basin and those preserved in middle–late Eocene sites. The relatively low value of the BLE components in the early Eocene assemblages indicates that a high number of elements with uncertain taxonomic affinity and therefore uncertain autecological preferences may lower the quality of the results obtained by the IPR vegetation analysis. Accordingly, the reliability of the IPR vegetation analysis decreases with the increase in the age of plant assemblages and results should be interpreted with caution. Similar limitations are found in the application of the actualistic principle and NLR approach, i.e. CA analysis (Kvaček, 2007).

8. Conclusions

The results presented here demonstrate important novelties with reference to the palaeoenvironmental investigation of the mid-latitudinal European Eocene floras and their possible modern analogues from E Asia. We applied two palaeovegetational methods, i.e. the IPR vegetation analysis and leaf size analysis, on 16 fossil floras and on 47 modern reference vegetation types from tropical, subtropical and warm-temperate zones of China and Japan. The hierarchical tree clustering analysis was used to show a relationship between the studied fossil and modern sites (Tables 5, 6; Appendixes 2, 4, 6, 7). To study the palaeoclimatic aspect of the Eocene environment, we used Leaf Margin Analysis and CLAMP techniques, and used the published palaeoclimatic proxies from the Coexistence Approach (Table 7). Additionally, we defined new limits to the IPR vegetation analysis based on the studied early Eocene floras and modern tropical vegetation types. We presented an update tool applied to the CLAMP process (Appendix 5). We can conclude the results to several following bullet points:

- The palaeoclimatic estimates derived from LMA, CLAMP and CA of middle and late Eocene studied floras are presented in Table 7 and show almost the same character. Only CLAMP proved the temperature decrease in MAT (3–4 °C) and the rise of the mean annual range temperature (MART) on the boundary of the middle and late Eocene, which can be compared with the cooling trend for this boundary as expressed by evaluating $\delta^{18}O$ from deep sea deposits (Zachos et al., 2001). However, the unequivocal decrease in both temperature and precipitation as indicated by floristic and/or vegetation changes is not as distinct and steep within terrestrial environments as recorded from the marine realm and should show an oscillational character with a gradual cooling trend.
- The studied middle and late Eocene floras compare better to modern broad-leaved evergreen forests from the subtropical zone of China and Japan rather than to the studied vegetation from the tropical zone of China. The nearest modern analogue is a subtropical lowland notophyllous broad-leaved evergreen forest growing under climate conditions, where the minimum values of MAT and CMMT are not less than 15 °C and 5 °C. The analogous vegetation is the broad-leaved evergreen forest typified in Mt. Emei sensu Tang and Ohsawa (1997) and Mt. Longqi sensu Li (1994, Figs. 4–7).
- Application of the IPR vegetation analysis on the early Eocene and Palaeocene floras shows doubtful results biased by a high number of elements with uncertain taxonomic affinity and autecological preferences. Similarly, IPR vegetation analysis is limited in recognising the multi-storeyed canopy forest types from the tropical zone as well their fossil analogues.
- We introduce a statistical background of the updated version of the objective statistical tools for the selection of the best-suited modern vegetation CLAMP dataset from 144 sampling site (Physg3br/GRIDMet3br), 173 sampling (Physg3ar/GRIDMet3ar) and 189 sampling (PhysgAsia1/GRIDMetAsia1) extant biotopes originally developed

by Teodoridis et al. (2011b) including its "copy & paste" Excel application (Appendix 5).

Supplementary materials related to this article can be found online at doi:10.1016/j.palaeo.2012.03.008.

Acknowledgments

Our thanks are due to our friend Dieter Uhl, who provided the partly published CA estimates (Uhl et al., 2007) from the Weisselster Basin and Staré Sedlo Formation. We are also grateful to the following friends and colleagues for their useful comments: Jian Yang (Chinese Academy of Science, Beijing), Han Xu (National Field Monitoring and Research Station for Forest Ecosystem in Jianfengling, Hainan; Research Institute of Tropical Forestry, Chinese Academy of Forestry), Michaela Grein (State Museum of Natural History Stuttgart), Torsten Utescher (University of Bonn, Bonn), Angela A. Bruch, (Senckenberg Research Institute, Frankfurt a. M.) and Arata Momohara (Chiba University, Chiba). Our special thanks go to Robert A. Gastaldo, Teresa E.V. Spicer and Robert. A. Spicer for their useful comments and linguistic revision. Finally, we would like to thank Johanna Kovar-Eder and Judith Totman Parrish — both reviewers for their constructive comments on the second version of the manuscript.

The study was supported by the grant projects: GA ČR (Grant Agency of the Czech Republic) No. P210/10/0124 and No. P205/08/0643, KONTAKT (Ministry of Education of the Czech Republic) No. ME 09115 and The National Natural Science Foundation of China No. 41071040. This paper is also our further contribution to the NECLIME international project.

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