Oligocene–Miocene CO₂ fluctuations, climatic and palaeofloristic trends inferred from fossil plant assemblages in central Europe

WOLFRAM M. KÜRSCHNER & ZLATKO KVAČEK



Stomatal frequency data from four independently calibrated woody plant species reveal pronounced CO, fluctuations since the Late Oligocene. CO, fluctuations in the Early to Middle Miocene are of such a magnitude that they may have driven much of the temperature variation and major climatic events. Warm intervals such as in the Late Oligocene and the mid-Miocene climatic optimum are characterized by significantly elevated CO, levels of at least about 500 ppmv. Elevated CO, levels may have also increased the diversity in C3 plant communities. The major cooling events in the Early Miocene and the late Middle Miocene are characterized by CO, decreases down to 340 ppmv and 280 ppmv, respectively. A comparison with marine and continental climate records indicates that much of the long-term climate variation was linked to changes in atmospheric CO,. The CO, fluctuations may have influenced ancient diversity of plant communities indirectly via changes in climate parameters, such as temperature or precipitation, seasonality, and/or directly by affecting plant photosynthetic performance. In the Oligocene, the type of vegetation is dominated by thermophilous paratropical-subtropical elements including palms but also with a considerable proportion of deciduous trees. The vegetation during the Oligocene-Miocene transition is slightly impoverished in species richness. There are profound differences in the physiognomy of elements, which are predominantly deciduous. During the Early to early Middle Miocene (15–17 Ma), plant assemblages are characterized by subtropical Notophyllous Evergreen forest vegetation with a maximum in species richness reflecting the middle Miocene climate optimum (Late Mastixioid floras sensu Mai). In the late Middle Miocene (13–14 Ma), the floras are less diversified, the woody elements are mostly dicots, both evergreen and deciduous and the vegetation type belongs to the Mixed Mesophytic Forest with a higher proportion of evergreen elements but with exceptional macrofossils of palms. The youngest flora of the latest Middle Miocene is much less diversified in contrast to the previous time interval. Generally, more diversified deciduous broad-leaved trees predominate while the lauroid elements become much less dominant. The diversity trends in central Europe suggest that the highest diversity found during the Late Oligocene and Middle Miocene most likely resulted from optimal climate conditions that expanded the area available for thermophilous, paratropical-subtropical vegetation into the mid-latitudes. The Oligocene-Miocene vegetation history is hard to explain with permanent low CO, conditions (~200-280 ppmv) as suggested by the marine CO, proxy records. • Key words: vegetation, CO, concentrations, Late Oligocene, Miocene, palaeoclimate.

KÜRSCHNER, W.M. & KVAČEK, Z. 2009. Oligocene–Miocene CO₂ fluctuations, climatic and palaeofloristic trends inferred from fossil plant assemblages in central Europe. *Bulletin of Geosciences 84(2)*, 189–202 (3 figures, 3 tables). Czech Geological Survey, Prague. ISSN 1214-1119. Manuscript received July 14, 2008; accepted in revised form December 11, 2008; published online February 25, 2009; issued June 30, 2009.

Wolfram M. Kürschner, Faculty of Sciences, Section Palaeo-Ecology, Laboratory of Palaeobotany and Palynology, Utrecht University, Budapestlaan 4, 3584 CD Utrecht, Netherlands; w.m.kuerschner@.uu.nl • Zlatko Kvaček, Faculty of Sciences, Charles University, Albertov 6, 128 43 Prague 2, Czech Republic; kvacek@natur.cuni.cz

Anthropogenic greenhouse gas emissions and modification of land surfaces are changing Earth's climate profoundly. IPCC assessments indicate that global temperature will rise by about 3 °C during the next decades and will turn the present day "icehouse climate" into a "greenhouse climate" (Meehl *et al.* 2007). In order to assess the human impact against the natural climate variability, studies of past warm intervals are of pivotal importance. A coupling between atmospheric CO_2 and glacial-interglacial cycles over the past 600,000 years is well documented by ice core analysis (Siegenthaler *et al.* 2005). During this time, however, CO_2 did not exceed the present day level. Therefore, palaeoclimate studies also increasingly focus on older geological periods with presumably elevated CO_2 levels which may represent a better ancient analogue for our future greenhouse world (*e.g.*, Sluijs *et al.* 2007, Zachos *et al.* 2008).

The Miocene is of particular interest for palaeoclimate studies as it represents a period of the Cenozoic which is characterized by extreme climate states such as the Middle Miocene climatic optimum and two major glaciations during the Early and the late Middle Miocene, when the east Antarctic ice sheet was established (e.g., Flower & Kennett 1993, Zachos et al. 2001). The middle Miocene cooling marks the founding of the modern Late Cenozoic cool mode. Associated with these key climatic events are profound vegetation changes such as the expansion of grasslands and C4 plants (Cerling et al. 1997, Jacobs et al. 1999, Stroemberg 2002). Major radiations in large mammalian herbivores have been attributed to changes in the distribution of vegetation and terrestrial primary productivity (Janis et al. 2000, MacFadden 2005). Miocene CO2 reconstructions based on marine geochemical proxies, however, indicate consistently low CO2 since the Early Miocene despite the occurrence of large-scale shifts in climate (Pagani et al. 1999, Pearson & Palmer 2000). Although both climate trends and plant physiological adaptations are thought to be influenced by long-term CO₂ fluctuations (Ehleringer et al. 1991), CO₂ reconstructions and modeling studies have disputed the role of CO₂ as a forcing factor (Shevenell et al. 2004, Pagani et al. 2005).

In addition to the marine geochemical proxy records, the pore (stomata) frequency, preserved on the cuticle of fossil leaf remains, represents a terrestrial proxy for atmospheric CO₂ that is based on the inverse relationship between atmospheric CO₂ and the number of stomata (Woodward 1987). It provides a robust method for estimating CO₂ levels for short (*e.g.*, Wagner *et al.* 2002) and geologically long-time scales (*e.g.*, van der Burgh *et al.* 1993, Royer *et al.* 2001, Beerling *et al.* 2002). Because the stomatal frequency response to CO₂ is species-specific, quantitative estimates of CO₂ are limited to extant species. This method requires good preservation of leaf fossils with cuticles and a good understanding of taxonomy and evolution of those elements that are followed.

The current paper is a sequel to a palaeoatmospheric CO_2 study based on stomatal counts of laurel and *Ginkgo* leaf remains (Kürschner *et al.* 2008). Here we document in detail the taxonomical and biostratigraphic framework as well as the regional palaeofloristic and palaeoclimatic trends from the Late Oligocene to the Late Miocene in central Europe.

Material and methods

We have studied three species of Lauraceae and *Ginkgo*, a total of 70 herbarium and 36 fossil leaf samples (Table 1) for their epidermal cell properties. The species are either ancestors distributed in the European Cenozoic and included into extant genera – *Laurus abchasica*, *Ocotea hradekensis*, *Ginkgo adiantoides* or one extinct morphospecies *Laurophyllum*

 Table 1. Mean raw SI values for herbarium and modern Laurus nobilis
 leaves

sample	age [AD]	location	atm. CO ₂ [ppmv]	SI [%]	S.D.
LN24.1	1866	Unknown	276	19.62	1.48
LN24.2	1866	Unknown	276	18.09	0.87
LN23.1	1870	Abchasicum	276	21.64	1.20
LN23.2	1870	Abchasicum	276	21.01	0.70
LN9.1	1886	Ultraject	292	20.63	1.45
LN9.2	1886	Ultraject	292	20.54	2.48
LN10.1	1905	Hyeres	297	18.26	1.42
LN10.2	1905	Hyeres	297	17.50	2.12
LN10.3	1905	Hyeres	297	17.57	1.70
LN09	1907	Dalmatien	298	18.75	1.28
LN10.1	1907	Kulaniek (Palestina)	299	16.81	0.98
LN10.2	1907	Kulaniek (Palestina)	299	16.47	1.69
LN01.1	1911	Brioni	300	16.37	1.47
LN01.2	1911	Brioni	300	17.10	1.99
LN12	1913	Catalunia (Spain)	300	19.49	0.49
LN12.1	1913	Catalunia (Spain)	300	20.32	0.42
LN17.02	1922	Luganer See (Tyrol)	302	17.27	1.78
LN17.03	1922	Luganer See (Tyrol)	302	18.19	1.16
LN13.1	1935	Korsika	306	18.50	1.83
LN13.2	1935	Korsika	306	18.80	1.40
LN13.4	1935	Korsika	306	18.22	1.38
LN13.5	1935	Korsika	306	18.57	1.75
LN07.1	1955	Mallorca	313	16.56	1.53
LN07.2	1955	Mallorca	313	16.79	1.16
LN07.3	1955	Mallorca	313	16.72	0.98
LN07.4	1955	Mallorca	313	16.81	1.06
LN06.1	1958	Mantauroux	315	17.40	1.06
LN06.2	1959	Mantauroux	315	17.45	0.51
LN06.3	1958	Mantauroux (Fr)	315	17.38	1.01
LN06.4	1958	Mantauroux (Fr)	315	17.63	1.43
LN11.1	1962	Korsika	318	16.91	1.86
LN11.2	1962	Korsika	318	16.93	2.08
LN20.1	1973	Kreta	330	15.47	0.70
LN20.2	1973	Kreta	330	16.76	1.07
LN30.2	2004	Rossum (NL)	378	14.36	1.30
LN30.1	2004	Rossum (NL)	378	14 77	0.95

pseudoprinceps with doubtful affinities. In order to convert the stomatal index (SI) values from the species *L. abchasica*, *O. hradekensis* to CO_2 levels, CO_2 inference models were established from their living equivalents *Laurus nobilis* and *Ocotea foetens* (Fig. 1). The taxonomical relationships have been established by extensive comparative studies on leaf morphology and cuticle anatomy (Ferguson 1974, Bůžek *et al.* 1996). CO_2 estimates from *G. adiantoides–biloba* lineage were based on calibration data by Royer *et al.* (2001). In the absence of a modern equivalent for the extinct species *L. pseudoprinceps*, the SI response of this species has been cross calibrated by using Miocene CO_2 levels inferred from the three other extant species.



Figure 1. Atmospheric CO_2 inference models based on historical series of herbarium sheets for *Ocotea foetens* (open circles) and *Laurus nobilis* (filled circles) (after Kürschner *et al.* 2008, adapted).

Stomatal frequency is preferably expressed as the stomatal index (SI), which is calculated as: SI (%) = $[SD/(SD + ED)] \times 100$, where SD is the stomatal density, and ED epidermal cell density (Salisbury 1927). Since SI normalizes for leaf expansion as observed for example in sun and shade leaf morphotypes, it is largely independent of plant water stress, and is primarily a function of CO₂ (Kürschner 1997). The stomatal and epidermal cell density has been counted using an image analysis system (analy-SIS, Münster) in Utrecht or from digital images taken from an Olympus light microscope in Prague. On average 5-10 stomata bearing alveoles per cuticle sample were measured for epidermal cell density (ED [n/mm²]) and stomatal density (SD [n/mm²]). Most of the fossil cuticle preparations studied (at present housed at the Faculty of Science, Charles University, Prague) come from the material collected in freshwater lignite basins and volcanogenic rocks scattered over the Bohemian Massif and its periphery. The herbarium sheets were provided by the National Herbarium, Leiden. Cuticle samples of the historical herbarium sheets are stored at the Palaeoecology branch of the Institute of Environmental Biology in Utrecht (Laboratory of Palaeobotany and Palynology).

The training dataset (Fig. 1) for the two extant laurel species has been used to establish the following relationships between stomatal index and atmospheric CO₂ concentration (Kürschner *et al.* 2008, for details see there). The stomatal index calibration of *L. nobilis* to atmospheric CO₂ concentrations results in a linear relationship with SI = -0.6724 CO₂ + 38.367 and a coefficient of determination (R²) of 0.64. The stomatal index calibration of *O. foetens* to atmospheric CO_2 concentrations results in a linear relationship with SI = $-0.5448 CO_2 + 30.245$ and a coefficient of determination (R²) of 0.5.

To account for the non-linear response of SI to changing CO₂ concentrations, both herbarium SI data and the historical CO₂ concentrations were log-transformed before fitting a linear response curve through the data sets. For *L. nobilis*, this results in a relationship of CO₂ = $10^{3.173}$ – $[0.5499 \times \log(SI_{fossil})]$ with a coefficient of determination (R²) of 0.78 between the measured and inferred CO₂ values and a root square error (RMSE) of 13.5 ppmv CO₂.

For *O. foetens* the regression curve (Fig. 1) and statistics are: $CO_2 = 10^{1.9624} - [0.4284 \times log(SI_{fossil})]$ with a coefficient of determination (R²) of 0.5 between the measured and inferred CO₂ values and a root square error (RMSE) of 19 ppmv CO₂.

In the absence of a modern equivalent for the extinct species *L. pseudoprinceps*, the stomatal index response of this species has been cross calibrated by using Miocene CO_2 levels inferred from the other three extant species. This results in a relationship of $CO_2 = -46.011 \times SI_{fossil} + 993.37$ with a coefficient of determination (R²) of 0.68. The multiple species stomatal index record based on the three extant species allows the CO_2 values to be independently inferred from the individual species-specific CO_2 inference models and verified for inter-specific coherence.

Stratigraphy of the fossil leaf samples studied

The Oligocene site Markvartice belongs to the Děčín Fm. of the České středohoří Mts and is dated by K-Ar method to be 30.8-24.7 Ma, i.e. late Rupelian to early Chattian (Cajz 2000). The Libkovice Member of the Most Basin has been dated by palaeomagnetic study (Bucha et al. 1987). For the lower part of this member (localities Břešťany and Jezeří with cores KU 285, MR 59, lower part - chron 6) the value 20 Ma is given, for the higher levels (samples from the upper part of the core MR 59 – chron 5e) the age of about 19 Ma can be estimated. The sample from the core JZ 44 below the coal seam belongs to the Duchcov Member. Its age cannot be precisely estimated, but it is tentatively assigned to the Aquitanian. The base of the main seam (i.e. Holešice Member) is dated into the Eggenburgian according to its small mammal content (zone MN 3a for the fauna from the Merkur-North Mine – Fejfar 1974).

For the Cypris Formation in the Cheb Basin, age assessment has been established based on small mammal remains. The plant bearing levels are within or slightly below the fauna of Františkovy Lázně, which corresponds to the lower part of the mammal zone MN 5, correlated with the Karpatian of the Paratethys area (Höck, personal communication 2004). The Mydlovary Formation of the South Bulletin of Geosciences • Vol. 84, 2, 2009

Bohemian basins has been assigned to the Early Badenian on account of the radiometric age of the tectites $14.7 \pm$ 0.7 Ma in the roof of the formation (Genter et al. 1967), small mammals of the MN 5 zone on the base and MN 6 within the formation (Fejfar, personal communication 2004, Ševčík et al. 2007) and the diatom flora (Řeháková in Vrána 1980). The rest of the floras (Hrádek, Wackersdorf, Horní Bříza) are dated according to the regional geological and palaeofloristic correlation and the same applies to the material from the Lusatia Basin and Lower Rhineland Embayment in Germany (see Němejc et al. 2003, Czaja 2003, Ferguson et al. 1998). The fossil cuticle samples from Oberdorf, Styrian Basin in Austria (provided by Johanna Eder-Kovar) are assigned to the Ottnagian based on the mammals of the MN4 zone (Kovar-Eder & Meller 2001). The Bulgarian Sarmatian material from Karbinci that has been used from the published data (Uzunova 1995) is dated by its mollusc fauna to the Bessarabian (ca 10–12 Ma) of the Dacian Basin (Palamarev et al. 1999).

Taxonomical remarks

Ginkgo adiantoides (Unger) Heer

syn. *Ginkgo florinii* Samylina, *Ginkgo occidentalis* Samylina Figure 2A

This is the only representative of *Ginkgo* in the European Neogene. It has been split into smaller entities (Samylina 1967) on account of epidermal features (rare vs. lacking trichomes, thin vs. thicker cuticle, weak vs. distinct papillae), which we consider as only ecotypic variation of a single species. It is true that the ancestors with similar leaf morphology were spread over the whole Northern Hemisphere during the Early Palaeogene. These have been rightly given different species names (for more information see Boulter & Kvaček 1989). The earliest record of Ginkgo adiantoides in central Europe has been enounced from the German locality Wiesa (Mai 2000), but there is some uncertainty, from which layers these fossil compressions come exactly. Most other records have been connected with the warm temperate Mixed Mesophytic forest. This is also the case of Horní Bříza in western Bohemia (Němejc et al. 2003), where Ginkgo is accompanied by Chamaerops and the evergreen Gordonia (Theaceae) but also deciduous oaks, and other Arcto-tertiary elements. More records are available from the Late Badenian and Sarmatian of the Ukraine (Samylina 1967), Poland (Szafer 1967) and many other sites in Europe (for a more complete list of synonyms / records see Palamarev & Petkova 1987). We studied the material from the roof of the Frimmersdorf Seam in the Frimmersdorf Mine, which can be assigned to the Middle Miocene cooling period (Utescher *et al.* 2000). Later on *Ginkgo* was fairly well spread during the Late Miocene and Pliocene in Europe. *Ginkgo adiantoides* is not fully identical, at least with respect to epidermal anatomy (see also Samylina 1967), with the living *Ginkgo biloba* (Fig. 2B), native in East Asia, which is today probably not known in a wild state but widely cultivated in China and elsewhere in the temperate Northern Hemisphere.

Laurus abchasica (Kolakovskii & Shakryl) Ferguson

syn. Laurophyllum abchasicum Kolakovskii & Shakryl; Piliparicutis triangulata Schneider; Litsaeophyllum miocenicum Juchniewicz; ?Laurus pliocenica (Saporta & Marion) Kolakovskii; Laurus canariensis pliocenica Saporta & Marion Figure 2C

This evergreen element of the Lauraceae represents the direct ancestor of two extant laurels distributed today in the Mediterranean (L. nobilis – Fig. 2D) and Canary Islands (L. azorica), being more similar to the latter (Ferguson 1974). It is recognizable even in small fragments of the abaxial leaf cuticle (rhomboidal stomatal complexes, omega-shaped fine undulation of anticlinal cell walls). In central Europe it occurs sporadically in the latest Eggenburgian and Ottnangian, mostly as solitary specimens (Most Basin, Libkovice Member - Teodoridis & Kvaček 2006; Oberdorf, Hanging wall sequence - Kovar-Eder & Meller 2001). More regularly it is recorded in Wackersdorf (Knobloch & Kvaček 1976), in the Cheb Basin, Cypris Fm. (Bůžek et al. 1996), the Czech and Polish parts of the Zittau Basin (Hrádek - Kvaček & Bůžek 1966; Turów - Juchniewicz 1975), the Main (Second) Lusatia Coal Seam in Germany (coal mines Greifenhain, Nochten; as Piliparicutis triangulata Schneider 1969, cf. Apollonias canariensis sensu Litke 1966), ranging into the Karpatian-Early Badenian. The last record from central Europe from the Mydlovary Formation in southern Bohemia is still of Badenian age (Ledenice - Knobloch & Kvaček 1996). The same age can be ascribed to the site Kreuzau (Ferguson 1971, as taxon XXIII) in the Lower Rhineland Embayment, based on the floristic correlation (Ferguson et al. 1998). In all mentioned

Figure 2. Abaxial epidermal structures of the studied taxa and the nearest living relatives (all scale bars = $100 \,\mu$ m). • A – *Ginkgo adiantoides*, Middle Miocene, Horní Bříza, No. HB 4. • B – *Ginkgo biloba*, Recent, cult. Praha. • C – *Laurus abchasica*, Lower Miocene, Cheb Basin, No. HV 1-23/1, core HV 1, depth 97.4 m. • D – *Laurus nobilis*, Recent, cult. Athens. • E – *Ocotea hradekensis*, Lower Miocene, Zittau Basin, Hrádek/N., mine Kristina, No. KR 300/1. • F – *Ocotea foetens* – Recent, Tenerife. • G – *Laurophyllum pseudoprinceps*, Oligocene, Markvartice, No. MR 390. • H – *Laurophyllum pseudoprinceps*, Lower Miocene, Cheb Basin, No. HV 4-31/4b, core HV 4, depth 96.7 m.

Wolfram M. Kürschner & Zlatko Kvaček • Oligocene–Miocene CO, fluctuations, climatic and palaeofloristic trends



assemblages *Laurus* is accompanied, in addition to "Arctotertiary" broad-leaved deciduous elements, by other Lauraceae, evergreen Fagaceae (mainly *Trigonobalanopsis*), *Engelhardia* and evergreen Hamamelidaceae (*Distylium*). Later in the Miocene *Laurus abchasica* withdrew southwards (Sarmatian of NW Bulgaria – Uzunova 1995) and survived till the Pliocene in Italy (Fossa – Martinetto, personal communication 2005) and Abkhasia (Kolakovskii 1958).

Ocotea hradekensis (Kvaček & Bůžek) Kvaček

syn. Laurophyllum hradekense Kvaček & Bůžek; Piliparicutis hradekensis (Kvaček & Bůžek) Schneider; Ocotea macrostoma sensu Uzunova & Stojanova; ?Ocotea heerii (Gaudin) Takhtajan; ?Oreodaphne heerii Gaudin Figure 2E

In many ways, this lauroid is similar to the previous case, but less typical in the stomatal pattern. With respect to epidermal anatomy (butterfly-like transparent stomatal complexes with broad and short ledges) and leaf architecture (glands at the base of the lowest secondary veins) and despite subtle differences (Schneider 2005) Ocotea hradekensis is the best candidate for the direct ancestor of Ocotea foetens, a relict in the Canary Island lauri-silvae (Fig. 2F). So far, it was recorded only in the European Neogene, namely at a few sites of the Early-Middle Miocene, first in Wackersdorf (Knobloch & Kvaček 1976), the Cheb Basin, Cypris Fm. (Bůžek et al. 1996), the Zittau and Berzdorf Basins (Kvaček & Bůžek 1966, Schneider 2005), the Main (Second) Lusatia Coal Seam in Germany (Lauraceae 2 sensu Litke 1966), ranging into the Karpatian–Lower Badenian. Its last record from Central Europe is again from the Mydlovary Formation in southern Bohemia (Ledenice - Knobloch & Kvaček 1996). The dispersed cuticles from the Sarmatian in Bulgaria (Ružinci, Karbinci - Uzunova 1995) indicate its migration southwards. Ocotea (usually named O. heerii) was a common evergreen element in the Late Neogene floras of Italy (Fischer & Butzmann 2000, Martinetto, personal communication).

Laurophyllum pseudoprinceps Weyland & Kilpper complex

syn. Laurophyllum undulatum Weyland & Kilpper; Laurophyllum verrucosum Weyland & Kilpper; Ocoteophyllum verrucosum (Weyland & Kilpper) Juchniewicz; Nectandrophyllum czeczottiae Juchniewicz; Ocotea oblanceolata Palamarev & Petkova; Ocotea pseudoprinceps (Weyland & Kilpper) Uzunova & Stojanova; Ocotea undulata (Weyland & Kilpper) Uzunova & Stojanova; Piliparicutis pseudoprinceps (Weyland & Kilpper) Schneider Figure 2G, H

This apparently extinct lauroid was correlated with various members of *Ocotea* (Juchniewicz 1976, Uzunova & Stoja-

nova 1999) without very satisfactory evidence as to the generic affinity. Indeed, Laurophyllum pseudoprinceps is similar in the stomatal pattern to Ocotea s.l., but at the same time, also to other genera, e.g., Aniba, Cryptocarya, which should also be taken into consideration (Kvaček 1971). Particularly the bead-like thickenings on the anticlinal cell walls in combination with the stomatal pattern (finely granular surface of the guard cells) are characteristic for this element. The direct lineage of the fossil towards an extant species, as is the case for Laurus abchasica and Ocotea hradekensis, is broken at the Pliocene, when L. pseudoprinceps became extinct in Europe. The first record comes from the Late Eocene sandstone in North Bohemia (Knobloch & Kvaček 1996). Then this lauroid becomes common in warmer parts of the Oligocene (e.g., Markvartice - Bůžek et al. 1976) and Early Miocene in central and Western Europe (Kvaček 1971). The Laurophyllum pseudoprinceps complex consists of two to three morphotypes sometimes considered as independent (sub)species (Weyland & Kilpper 1963, Kvaček in Knobloch et al. 1996). We used in our study only the typical L. pseudoprinceps in order to avoid the influence of different leaf morphotypes, the former representing sun leaves while L. undulatum may represent a shade morphotype. A further interfering factor may arise from polyploidy. In the case of L. macrostoma, a transitional form can be mistaken for Ocotea hradekensis (Uzunova & Stojanova 1999). During the Late Badenian, this species complex migrated southwards and is met again in the Sarmatian and Pannonian of Roumania (Suraru et al. 1978, Givulescu 1975 - partly as Laurophyllum rhomboidale) and the Sarmatian of NW Bulgaria (Uzunova 1995, Uzunova & Stojanova 1999). The European Pliocene records are known so far only from Italy (Martinetto, personal communication 2005).

Considering the role of all three lauroid species in associated assemblages, they are typical components of the subtropical evergreen humid forest types. The diversification of the Lauraceae in Europe coincides with appearance of the "Late Mastixioid Floras" in the Middle Miocene climate optimum. Later on, central and eastern Europe was covered by mixed mesophytic and broad-leaved deciduous forest, in which only more hardy evergreen taxa remained or re-appeared in southerly stations of the Paratethys and Tethys area (Kvaček *et al.* 2006). This is also the time, when *Ginkgo adiantoides* became a common component of the forest vegetation over the whole of Europe.

Various types of the forest vegetation give only approximate palaeoclimatic data and the ratio of deciduous *vs.* evergreen woody elements does not indicate very precisely the variation in the climate / temperature regime. From the studied Czech locations statistical calculations for two levels are available. The CLAMP analysis of the diversified classical flora of the Břešťany (Preschen) Clay (lower part of the Libkovice Member in the Most Basin, Eggen-

sample	age [AD]	location	altitude [m]	atm. CO ₂ [ppmv]	CO ₂ partial pressure [kPa]	SI [%]	S.D.
OF 0801	1865	Madeira	900	289	26.37	13.66	1.43
OF 0802	1865	Madeira	900	289	26.37	14.62	0.71
OF 0803	1865	Madeira	900	289	26.37	13.66	1.75
OF 0901	1865	Madeira	900	289	26.37	16.42	1.07
OF 0902	1865	Madeira	900	289	26.37	17.07	0.47
OF 0903	1865	Madeira	900	289	26.37	17.40	1.34
OF 0301	1869	Hortus Utrecht	0	289	29.09	13.79	1.07
OF 0302	1869	Hortus Utrecht	0	289	29.09	14.92	0.74
OF 0601	1906	Palma Los Tiles	400	296	28.56	16.62	0.67
OF 0602	1906	Palma Los Tiles	400	296	28.56	16.31	1.16
OF 0603	1906	Palma Los Tiles	400	296	28.56	14.81	0.81
OF 0701	1906	Palma Los Tiles	400	296	28.56	14.19	0.55
OF 0702	1906	Palma Los Tiles	400	296	28.56	13.62	1.18
OF 0703	1906	Palma Los Tiles	400	296	28.56	15.11	0.62
OF 0401	1908	Hortus Antibes	0	299	30.1	12.86	0.54
OF 0402	1908	Hortus Antibes	0	299	30.1	13.61	0.75
OF 0201	1908	Teneriffe	0	299	30.1	14.10	2.02
OF 0202	1908	Teneriffe	0	299	30.1	15.62	1.14
OF 0203	1908	Teneriffe	0	299	30.1	15.29	1.82
OF 0201	1923	Teneriffe	0	303	30.1	14.09	1.25
OF 1401	1968	Madeira Funchal	0	324	32.61	11.28	1.01
OF 1402	1968	Madeira Funchal	0	324	32.61	11.09	0.78
OF 1403	1968	Madeira Funchal	0	324	32.61	10.49	1.43
OF 10.1	1972	Canary Islands	600	328	30.96	12.96	0.71
OF 10.2	1972	Canary Islands	600	328	30.96	13.38	0.95
OF 10.3	1972	Canary Islands	600	328	30.96	12.95	0.73
OF 12.1	1972	Canary Islands	600	328	30.96	13.07	1.45
OF 12.2	1972	Canary Islands	600	328	30.96	13.05	0.83
OF 12.3	1972	Canary Islands	600	328	30.96	14.67	1.19
OF 0401	1997	Madeira	900	364	33.22	11.90	1.45
OF 0402	1997	Madeira	900	364	33.22	14.05	1.22
OF 0403	1997	Madeira	900	364	33.22	12.56	0.86

Table 2. Mean raw SI values for herbarium and modern Ocotea foetens leaves

burgian) indicate the following proxy data (Teodoridis & Kvaček 2006): Mean Annual Temperature (MAT) 15.9 ± 1.2 °C; mean temperature of the warmest month (WMMT) 25 ± 1.6 °C; mean temperature of the coldest month (CMMT) 7 ± 1.9 °C. According to the co-existence analysis of the Badenian assemblage of Horní Bříza (data provided by D. Uhl), similar climate data have been derived: MAT 15.7–16.5 °C, WMMT 26.4–26.7 °C, CCMT 5.0–6.2 °C.

Results and discussion

Oligocene-Miocene CO, trends

Since the late Oligocene (Kürschner *et al.* 2008), the SI records of all four species (Fig. 3A) (*Ginkgo adiantoides, Laurus abchasica, Ocotea hradekensis, Laurophyllum* *pseudoprinceps*) show pronounced fluctuations. Three intervals can be recognized in the present record: During the oldest part, the Late Oligocene to Early Miocene (between 25 and 20 Ma), the SI of *L. pseudoprinceps* shows a significant increase from about 9% to 15% and remains high during the Early Miocene (until 20 Ma). During the middle part, the late Early to early Middle Miocene (between 20 and 16 Ma), *L. pseudoprinceps* shows a decrease in the SI from 15% to 12%. A simultaneous decline in SI is found for two other laurel species, *L. abchasica* and *O. hradekensis*, from 12% to 10% and from 12% to 8%, respectively. In the youngest part of the present study, the Middle Miocene (between 16 and 12 Ma), *L. abchasica* and *G. adiantoides* show pronounced changes from 10% to 20% and 8% to 15%, respectively.

The stomatal index record by Kürschner *et al.* (2008) reveals prominent changes in CO_2 since the Late Oligocene (Fig. 3B). From initially high CO_2 values of about

600 ppmv during the Late Oligocene, CO2 declines drastically to about 340 ppmv during the early Miocene. It remains low until the mid-Early Miocene, 20 Ma and increases again to reach a maximum of about 500 ppmv in the early Middle Miocene, about 15.5 Ma. Superimposed on this increasing trend are several smaller temporary CO₂ oscillations with an amplitude of ~50 ppmv. A second major decline in CO₂ to 280 ppmv occured during the Middle Miocene, between about 15.5 and 14 Ma which is followed by a slight increase to about 340 ppmv during the Late Miocene. It should be noted that SI data from North American Ginkgo leaf remains (Royer et al. 2001, Retallack 2002) correspond perfectly with the present study. Our data are, however, in contrast with stomatal frequency measurements on 3 dicotyledonous species (Eotrigonobalanus furcinervis, Laurophyllum pseudoprinceps, L. acutimontanum) from Late Eocene to Early Miocene sediments in the Weisselster Basin in Saxony, Germany (Roth-Nebelsick et al. 2004). The discrepancy may be partly explained by the insufficient stratigraphic resolution of their material. They combined SI data from different localities / stratigraphic units which may have biased original variations in SI. Another reason could be the use of leaf remains of the Laurophyllum pseudoprinceps complex which is a synthetic morphotaxon consisting of several lauroid leaf morphotypes with doubtful botanical affinity (see our taxonomical remarks above). Mixing SI data from different leaf morphotypes may yield misleading results by omitting species-specific variance of absolute SI values and SI response rates. In the present study only SI data from one leaf morphotype, L. pseudoprinceps Weyland & Kilpper sensu *stricto* has been used for palaeoatmospheric CO₂ estimates. During the course of our study it appeared necessary to constrain the SI analysis to only one of these lauroid leaf types as the combination of all 3 morphotypes resulted in random variance without any temporal trends in SI, which is similar to the results reported by Roth-Nebelsick et al. (2004). The variance in epidermal cell parameters of the Laurophyllum pseudoprinceps complex is subject to further investigations (Kürschner et al. in prep.).

The present leaf based CO_2 reconstruction, however, shows some similarities with the marine CO_2 proxy records as for example the CO_2 decline at the Oligocene–Miocene transition (Pagani *et al.* 2005, Pearson & Palmer 2001). But it deviates significantly from the alkenone based CO_2 record throughout the course of the Miocene, which shows consistently low CO_2 levels (200–280 ppmv) despite the presence of major Miocene climate events. The boron isotope based CO_2 reconstruction (Pearson & Palmer 2000) shows CO_2 variations very similar to our study although the absolute values are significantly lower, by about 200 ppmv.

Consistently low CO_2 levels during the Miocene as inferred from marine proxy records has led to the concept of a decoupled climate – carbon cycle relationship (*e.g.*, Pagani *et al.* 2005). Our new results provide evidence that CO_2 fluctuations may have considerably contributed to the Miocene long-term climate evolution as recorded in marine temperature proxy records (Zachos *et al.* 2001).

Quantitative continental climate data, such as for example mean annual temperature (MAT), mean annual precipitation (MAP), coldest and warmest month means (CMM, WMM respectively), has been documented from European megafloras by the coexistence approach (Utescher et al. 2000, Mosbrugger et al. 2005). Both, the Late Oligocene warming and the Mid-Miocene Climate Optimum are characterized by significant increases in MAT by about 3 °C. The warming trends are even more pronounced (up to about 5 °C) in the coldest month mean (CMM). By comparison of this continental climate record with the marine CO_2 proxy records available at that time, Mosbrugger and co-workers came to the conclusion that CO₂ was not a major driving force in Cenozoic climate evolution. The present data, however, show that in fact CO₂ may well have contributed to the climate fluctuations. The radiative forcing of the CO₂ fluctuations in the global surface temperature, calculated according to equations by Kothavala et al. (1999) is shown in Fig. 3C. A 2-3 °C warming of the mean global surface temperature is indicated for the Late Oligocene and the Mid-Miocene climatic optima resulting from elevated CO₂ levels. The high CO₂ levels during the climate optima may represent conservative values as the extrapolation of the SI response function beyond the calibration interval results in an underestimation by about 200 ppmv of the actual value. In fact, CO₂ levels may have been about 650-700 ppmv and 800-900 ppmv during the Middle Miocene and Late Oligocene climatic optima, respectively (Kürschner et al. 2008).

Palaeofloristic trends

The CO_2 fluctuations may have influenced ancient diversity of plant communities indirectly via changes in climate parameters, for example temperature or precipitation, seasonality, and / or directly by affecting plant photosynthetic performance. Fossil plant assemblages do not fully reflect the species richness, being highly influenced by taphonomic processes and preservation potential of various plant organs. Therefore, only general characteristics of the sites studied or time sectors are discussed as a first order approximation (Fig. 3D). More detailed studies including both macrobotanical and palynological data will improve the present picture.

The Oligocene floras (sites Markvartice, Suletice, Proboštov – Bůžek *et al.* 1976, Radoň *et al.* 2006) are predominantly woody, with only four conifers and *ca* 50 arboreal dicots and lianas. Herbaceous monocots are represented by



Figure 3. Adapted after Kürschner *et al.* 2008. • A – SI (SI) of fossil leaf remains between 25 Ma and 12 Ma (late Oligocene until the late middle Miocene) collected mainly from several brown coal basins in the Czech Republic (Most and Zitttau basins, S Bohemia) supplemented with some material from Austria (Köflach, Styria) and Germany (Lower Rhine Embayment, Lusatia Basin). The circles represents SI data of *Laurophyllum pseudoprinceps*, the triangles those for *Laurus abchasica*, the diamonds of *Ocotea hradekensis*, and the squares of *Ginkgo adiantoides* with error bars $2 \times s.d$. The age error bars indicate the minimum and maximum age of the sample. The stratigraphic framework is established by vertebrate biostratigraphy and magneto-stratigraphy (further details in the Material and methods section and Table 3). • B – reconstructed late Oligocene–middle Miocene palaeoatmospheric CO₂ levels based on individual independently calibrated tree species. • C – modeled temperature departure of global mean surface temperature from present day calculated from mean *p*CO₂ estimates using a CO₂-temperature sensitivity study (Kothavala *et al.* 1999). • D – relative changes in floral diversity based on the macrofossil content of the locations studied.

a few morphotypes of foliage. The type of vegetation is rather thermophilous, containing paratropical – subtropical elements, such as Icacinaceae, *Engelhardia*, *Sloanea*, evergreen Oleaceae, well diversified Lauraceae, but also a considerable proportion of deciduous trees of Betulaceae, *Acer, Carya, Ailanthus*, Ulmaceae, Tiliaceae and Vitaceae. Legumes are probably also well represented but due to highly uniform leaves, their diversity is less certain with about 5 morphotypes. Palms are represented by 1–2 species.

The sites at the latest Oligocene-Miocene boundary are rare (one site in the Duchcov Mb.). The floras of this time sector belong to the Thierbach type (Teodoridis 2004). With only five conifers and about 35 dicotyledonous arboreal elements are thus slightly poorer in species richness than the previous period. Profound differences however are in the physiognomy of elements, which are predominantly deciduous. Fagus and Pseudolarix are diagnostic for long-distance correlation. Evergreen plants are represented in the shrub storey (Mahonia, Myrica) rather than in the canopy. More diversified assemblages occur in Saxony (Mai & Walther 1991) and contain remnants of subtropical evergreen plants (Mastixia, evergreen Fagaceae, Lauraceae, Theaceae), if a broader concept of this palaeofloristic unit is accepted. Vegetation is predominantly riparian, although parts may form transitions to the Mixed Mesophytic Forest. Aquatic herbaceous plants are common (Lythraceae, Cyperaceae, *Stratiotes*).

The Early Miocene flora of the Břešťany clay (bottom of the Libkovice Mb. - Teodoridis & Kvaček 2006) does not differ profoundly from the previous part of the Most section. Conifers are richer, with four Cupressaceae and three species of Pinus. Woody dicots include slightly over 35 species, partly deciduous, partly evergreen. Subtropical elements slightly increased and palms again entered the riparian settings. An enigmatic index fossil Schenkiella (Wójcicki & Kvaček 2002) allows a long-distance correlation with the Brandis type of floras (Mai & Walther 1991). Vegetation of this assemblage corresponds to the mixed mesophytic forest on peripheral slopes and lowland intrabasin swamp forest. The sandy facies (Přívlaky - Teodoridis 2006) yielded purely deciduous riparian broadleaved elements (ca 20 species) similar in composition to the flora from the Oligocene-Miocene boundary. The adjacent underlying layers contained diversified remains of aquatic plants and grasses (Kvaček et al. 2004).

Higher in the Libkovice Mb. (19 Ma) the assemblages

come from the core samples – hence no long-term collection and not objectively reflecting species richness. The flora consists of prevailing evergreen woody taxa (diversified Lauraceae, Fagaceae, *Engelhardia*, Theaceae, *Platanus neptuni*). The horizon in the cores may laterally coincide with or slightly overlap carpological assemblages on the basin periphery, which are even richer in exotic elements (*Symplocos*, Theaceae, *Myrica*, *Toddalia*, *Mastixia*) and can form subtropical Notophyllous Evergreen green forest (Teodoridis & Kvaček 2006).

Early to early Middle Miocene floras reflect the Mid-Miocene climate optimum and belong to the Late Mastixioid floras sensu Mai (1964). Locations with the Late Mastixioid floras are frequent, including the Cypris Shale flora of the Cheb Basin, Wackersdorf at Schwandorf in Oberpfalz, Germany, the upper part of the Žitava (Zittau) Basin (Hrádek/N., Hartau, Turów) and adjacent Lusatia (Wiesa). Based on all published records including foliage and carpofloras (Mai 1964; Knobloch & Kvaček 1976; Gregor 1978, 1980; Bůžek et al. 1996; Mai 2000; Czaja 2003) this type of floras called the Wiesa-Eichelskopf Complex (Mai 1995), is the richest in species of all Miocene plant assemblages in Europe. Conifers reached the highest diversity including 10 Pinaceae, three Cupressaceae and two Taxaceae. Woody dicotyledons are by far the prevailing form, being represented by well over 80 species. Palms are represented by only a few species. The floral spectra depend greatly on the sedimentary settings so that the assemblages from fluviatile facies may contain a considerable mixture of riparian deciduous woody taxa. Herbaceous vegetation mostly consists of wetland and aquatic elements (Lythraceae, Aldrovanda, Alismataceae, Cyperaceae). Various and diversified Mastixiaceae may serve for long-distance correlation. The vegetation type is apparently subtropical Notophyllous Evergreen Forest according to the leaf size category with many exotic elements with tropical affinities. Assemblages of the same age and the same aspects are known from the Styrian Basin in Austria (Meller et al. 1999, Kovar-Eder & Meller 2001). The diversity of woody dicots is again high, over 60 species. Herbaceous dicot families make up less than 10%. Herbaceous monocts are mostly represented by wetland Cyperaceae and Sparganium.

The early Middle Miocene is characterized by transitional floras to the previous period. The South Bohemian assemblages dated to the MN6 zone correspond in a greater part to the Late Mastixioid Floras *sensu* Mai (Holý 1976, Knobloch & Kvaček 1996, Ševčík *et al.* 2007). They are assigned to the Kleinleipisch Complex of the Berzdorf Basin in Upper Lusatia (Czaja 2003). Conifers survived as several species of Cupressaceae and Pinaceae. Woody dicots are slightly less diversified in comparison with the Wiesa type, attaining about 50 species. The vegetation becomes more open as documented by the presence of wetland herbaceous plants, both dicots and monocots, with at least 20 species each including *Stellaria, Ranunculus, Teucrium* etc. The vegetation type corresponds to the Mixed Mesophytic Forest with remnants of mastixioid and other thermophilous elements.

During the late Middle Miocene (13-14 Ma) the palaeofloras from the Lower Rhine Embayment (Ville Fm.) document further floristic changes. The carpological record from the Garzweiler seam in the Zukunft-West mine at Eschweiler includes several conifers (including Juniperus) (van der Burgh 1983, 1987, 1988; Günther & Gregor 1989). The woody elements are mostly dicots, partly evergreen, partly deciduous, slightly over 40 species (the number has been updated according to the revision of Symplocos by Mai & Martinetto, 2006) are all dicots, partly evergreen and partly deciduous. Herbaceous dicots (Umbelliferopsis) and monocots (Cyperaceae, Araceae) are much less common. The vegetation type belongs to the Mixed Mesophytic Forest with a higher proportion of evergreen elements. In physiognomic terms it does not differ much from the previous Kleinleipisch type and still includes some remnants of mastixioids but hardly any macrofossils of palms.

The youngest record in our study comes from Karbinci, NW Bulgaria (Uzunova 1995) and is of latest Middle Miocene - Bessarabian age. The flora is less diversified contrary to the previous time interval of the Sarmatian, called the Volhynian (Palamarev et al. 1999). Of 58 so far described species, a considerable part belongs to woody dicots, including some elements of sub-humid aspects (legumes, sclerophyllous oaks). Generally, the lauroid element declines and more diversified deciduous broad-leaved trees predominate, both in riparian and mesophytic settings. Evergreen woody plants were probably limited to the undergrowth. In addition, also swamp forest of Glyptostrobus -Byttneriophyllum - Nyssa type, and wetland herbaceous communities can be reconstructed. Herbs tend to increase in the pollen spectra. Thermophilous elements, like mastixioids and palms survived in these southern locations.

The above described palaeofloristic trends fit with quantitative estimates of woody plant diversity on a broader scale during the Miocene that have been evaluated by meta-analysis of the available Eurasian palaeobotanical records (Utescher et al. 2007, Kovar-Eder et al. 2008). Our brief, rather qualitative essay on diversity trends in central Europe (Fig. 3) suggests that the highest diversity is found during the Late Oligocene and Middle Miocene, most likely as a result of optimal climate conditions that expanded the area available for thermophilous, paratropical-subtropical vegetation into the mid-latitudes. At present we leave the question open whether the observed maxima in plant diversity are the result of climate optima alone or also caused by elevated CO₂ levels. Elevated CO₂ levels may have fertilized plant growth and facilitated the expansion of high-diversity forest. However, in our opinion, the Oligocene-Miocene vegetation history as summarized above

Wolfram M. Kürschner & Zlatko Kvaček • Oligocene-Miocene CO fluctuations, climatic and palaeofloristic trends

Table 3. Mean raw SI values of fossil leaf remains studied. ¹ Uzunova (1995), ² Palamarev *et al.* (1999), ³ Schäfer *et al.* (2004), ⁴ Knobloch & Kvaček (1996), ⁵ Litke (1966), ⁶ Bůžek *et al.* (1996), ⁷ Kovar-Eder & Meller (2001), Kovar-Eder *et al.* (2001), ⁸ Mai (1995), ⁹ Knobloch (1989), ¹⁰ Bucha *et al.* (1987), ¹¹ Němejc *et al.* (2003), ^{12, 13} Royer *et al.* (2001), ¹⁴ Kvaček & Bůžek (1982), ¹⁵ Kvaček & Walther (2003)

species	sample	locality	stage	age	biostratigraphy	SI	SD
Laurus abchasica	Literature ¹	Ruzinci	Bessarabian ²	11.6 ± 0.6		15.19	1.45
Laurus abchasica	MM2	Zukunft-W	Late Badenian	13.9 ± 0.4	MN6 ³	17.72	0.40
Laurus abchasica	MM3	Zukunft-W	Late Badenian	13.9 ± 0.4	MN6 ³	20.02	1.62
Laurus abchasica	MM8	Zukunft-W	Late Badenian	13.9 ± 0.4	MN6 ³	20.21	0.95
Laurus abchasica	MY18	Ledenice ⁴	Early Badenian ⁴	15.7 ± 0.7		8.84	1.15
Laurus abchasica	Literature ⁵	Lusatia	Early Badenian ⁵	15.7 ± 0.7		10.05	2.01
Laurus abchasica	HV1-25/1	Cheb (Eger) Basin	Karpatian ⁶	16.8 ± 0.4	E. MN5	9.70	0.59
Laurus abchasica	HV1-28/1	Cheb (Eger) Basin	Karpatian ⁶	16.8 ± 0.4	E. MN5	10.37	1.41
Laurus abchasica	1993/28/32/2	Oberdorf	Ottnangian ⁷	17.6 ± 0.4	MN4	12.83	0.34
Laurus abchasica	1993/28/34A/1	Oberdorf	Ottnangian ⁷	17.6 ± 0.4	MN4	11.47	2.49
Laurus abchasica	1993/29/26B/3	Oberdorf	Ottnangian ⁷	17.6 ± 0.4	MN4	12.82	1.55
Laurus abchasica	KR76/1	Hrádek nad Nisou	Ottnangian ⁸	17.6 ± 0.4		12.35	1.08
Laurus abchasica	Sch 672/1	Wackersdorf	Ottnangian ⁹	17.6 ± 0.4		11.39	
Laurus abchasica	MR59-5	Most Basin core MR59	Eggenburgian ¹⁰	19.0 ± 0.5		10.90	0.13
Ocotea hradekensis	MY26	Ledenice	Early Badenian ⁴	15.7 ± 0.7		6.97	1.13
Ocotea hradekensis	HV11-31	Cheb (Eger) Basin	Karpatian ⁶	16.8 ± 0.4	E. MN5	8.44	0.86
Ocotea hradekensis	KR300/1	Hrádek nad Nisou	Ottnangian ⁸	17.6 ± 0.4		11.49	1.14
Ginkgo adiantoides	GA	Zukunft-W	Late Badenian	13.9 ± 0.4	MN6	14.64	1.43
Ginkgo adiantoides	HB2/1	Horní Bříza	Early Badenian ¹¹	15.7 ± 0.7		7.68	0.46
Ginkgo adiantoides	HB2/2	Horní Bříza	Early Badenian ¹¹	15.7 ± 0.7		7.86	0.75
Ginkgo adiantoides	Literature	49Camp	Early Badenian ¹²	15.8 ± 0.02		7.6	1.3
Ginkgo adiantoides	Literature	Juliaetta	Early Badenian ¹³	16.5 ± 1		8.14	
Laurophyllum pseudoprinceps	Kau.U/Crd	Kamenný Újezd	Early Badenian ⁴	15.7 ± 0.7		11.39	0.77
Laurophyllum pseudoprinceps	HV4-31/4B	Cheb (Eger) Basin	Karpatian ⁶	16.8 ± 0.4		11.99	0.73
Laurophyllum pseudoprinceps	KR508/1	Hrádek nad Nisou	Ottnangian ⁸	17.6 ± 0.4		14.09	1.30
Laurophyllum pseudoprinceps	KR181/1	Hrádek nad Nisou	Ottnangian ⁸	17.6 ± 0.4		12.63	1.78
Laurophyllum pseudoprinceps	Sch469/1	Wackersdorf	Ottnangian ⁹	17.6 ± 0.4		12.13	0.54
Laurophyllum pseudoprinceps	Sch673/1	Wackersdorf	Ottnangian ⁹	17.6 ± 0.4		13.72	1.80
Laurophyllum pseudoprinceps	MR59-14	Most Basin core MR59	Eggenburgian ¹⁰	19.0 ± 0.2		11.25	1.08
Laurophyllum pseudoprinceps	MR59-24	Most Basin core MR59	Eggenburgian ¹⁰	19.0 ± 0.2		11.96	1.8
Laurophyllum pseudoprinceps	MR59-26	Most Basin core MR59	Eggenburgian ¹⁰	20.0 ± 0.3		13.58	
Laurophyllum pseudoprinceps	MR59-36	Most Basin core MR59	Eggenburgian ¹⁰	20.0 ± 0.3		14.45	1.92
Laurophyllum pseudoprinceps	MR59-49	Most Basin core MR59	Eggenburgian ¹⁰	20.0 ± 0.3		14.58	1.62
Laurophyllum pseudoprinceps	VJK237-12A	Most Basin core JZ44	Aquitanian ¹⁴	22.1 ± 1.5		14.36	1.2
Laurophyllum pseudoprinceps	MR390	Markvartice	Late Oligocene15	25.0 ± 1		9.65	0.99
Laurophyllum pseudoprinceps	MR322	Markvartice	Late Oligocene ¹⁵	25.0 ± 1		7.96	1.28

is in contradiction with permanent low CO_2 conditions (~200–280 ppmv) as suggested by the marine CO_2 proxy records (Pagani *et al.* 1999, 2005). Moreover, the low CO_2 scenario has been assessed physiologically with plant photosynthetic models. These modeling experiments show that photorespiration rates under a warm climate and low CO_2 would drastically reduce the Carbon assimilation rates of C3 land plants (Cowling 1990). In fact, plant growth would have been drastically limited and plant richness would have been much lower than indicated in the fossil record. Further vegetation and climate model experiments may shed new light on the significance of CO_2 fluctuations on the evolution of Cenozoic terrestrial ecosystems.

Acknowledgements

We are thankful to Jakub Sakala and Vasilis Teodoridis (Prague) for research assistance and for climatic proxy data to Dieter Uhl (Frankfurt). Peter Baas (Leiden) is acknowledged for providing herbarium leaf material. WMK acknowledges and appreciates the financial support of the Alexander von Humboldt foundation. The study was carried out within the projects No. 205/04/0099 and 205/08/0643 of the Grant Agency of the Czech Republic with additional financial support from the research schemes of CR No. MSM 0021620855 and CR No. MSM 113100006, the European Science Foundation "Environments and Ecosystem Dynamics of the Eurasian Neogene" (EEDEN).

References

- BEERLING, D.J., LOMAX, B.H., ROYER, D.L., UPCHURCH, G.R., JR. & KUMP, L.R. 2002. An atmospheric pCO₂ reconstruction across the Cretaceous-Tertiary boundary from leaf megafossils. *Proceedings of the National Academy of Sciences USA 99*, 7836–7840. DOI 10.1073/pnas.122573099
- BOULTER, M.C. & KVAČEK, Z. 1989. The Palaeocene flora of the Isle of Mull. *Palaeontology Special Papers* 42, 1–149.
- BUCHA, V., ELZNIC, A., HORÁČEK, J., MALKOVSKÝ, M. & PAZDEROVÁ, A. 1987. Paleomagnetic timing of the Tertiary of the North Bohemian Brown-Coal Basin. Věstník Ústředního ústavu geologického 62, 83–95.
- BŮŽEK, Č., HOLÝ, F. & KVAČEK, Z. 1976. Tertiary flora from the Volcanogenic Series at Markvartice and Veselíčko near Česká Kamenice (České Středohoří Mts.). Sborník geologických věd, Paleontologie 18, 69–132.
- BÚŽEK, Č., HOLÝ, F. & KVAČEK, Z. 1996. Early Miocene flora of the Cypris Shale (western Bohemia). Acta Musei nationalis Pragae, Series B – historia naturalis 52, 1–72.
- CAJZ, V. 2000. Proposal of lithostratigraphy for the České středohoří Mts. volcanics. Věstník Českého geologického ústavu 75, 7–16.
- CERLING, T.E., HARRIS, J.M., MACFADDEN, B.J., LEACEY, M.G., QUADE, J., EISENMANN, V. & EHLERINGER, J.R. 1997. Global vegetation change through the Miocene/Pliocene boundary. *Nature* 389, 153–158. DOI 10.1038/38229
- COWLING, S.A. 1999. Plants and temperature-CO₂ uncoupling. *Science* 285, 1500–1501.

DOI 10.1126/science.285.5433.1500

- CZAJA, A. 2003. Paläokarpologische Untersuchungen von Taphozönosen des Unter- und Mittelmiozäns aus dem Braunkohletagebau Berzdorf/Oberlausitz (Sachsen). *Palaeontographica*, *Abteilung B 265*, 1–148.
- EHLERINGER, J.R., SAGE, R.F., FLANAGAN, L.B. & PEARCY, R.W. 1991. Climate change and the evolution of C4 photosynthesis. *Trends in Ecology and Evolution 6*, 95–99. DOI 10.1016/0169-5347(91)90183-X
- FEJFAR, O. 1974. Die Eomyiden und Cricetiden (Rodentia, Mammalia) des Miozäns der Tschechoslowakei. *Palaeontographica Abteilung A 146*, 100–180.
- FERGUSON, D.K. 1971. The Miocene flora of Kreuzau Western Germany. 1. The leaf – remains. Verhandelingen der Koninklijke Nederlandse Akademie van Wetenschappen, Afd. Natuurkunde, Tweede Reeks 60(1), 1–197.
- FERGUSON, D.K. 1974. On the taxonomy of recent and fossil species of *Laurus* (Lauraceae). *Botanical Journal of the Linnean Society* 68, 51–72. DOI 10.1111/j.1095-8339.1974.tb01747.x
- FERGUSON, D.K., PINGEN, M., ZETTER, R., & HOFMANN, C.-C. 1998. Advances in our knowledge of the Miocene plant assemblage from Kreuzau, Germany. *Review of Palaeobotany and Palynology 101*, 147–177.

DOI 10.1016/S0034-6667(97)00074-2

FISCHER, T.C. & BUTZMANN, R. 2000. Die neogene Flora von Meleto (Valdarno, Italien), Paläobotanik, Palöökologie und Paläoklima. *Documenta naturae*, *Flora tertiaria mediterranea* V(6), 1–187.

FLOWER, B.P. & KENNETT, J.P. 1993. The middle Miocene transi-

tion: East Antarctic Ice sheet development, deep ocean circulation and global carbon cycling. *Palaeogeography, Palaeoclimatology, Palaeoecology 108*, 537–555. DOI 10.1016/0031-0182(94)90251-8

- GIVULESCU, R. 1975. Fossile Pflanzen aus dem Pannon von Delureni (Rumänien). Palaeontographica, Abteilung B 153, 150–182.
- GENTER, W., KLEINMAN, B. & WAGNER, G.A. 1967. New K-Ar and fisshion-track ages of impact glasses and tektites. *Earth and Planetary Science Letters* 2, 83–86. DOI 10.1016/0012-821X(67)90104-5
- GREGOR, H.-J. 1978. Die miozänen Frucht- und Samen-Floren der Oberpfälzer Braunkohle. I. Palaeontographica, Abteilung B 167, 8–103.
- GREGOR, H.-J. 1980. Die miozänen Frucht- und Samen-Floren der Oberpfälzer Braunkohle. II. Palaeontographica, Abteilung B 174, 7–94.
- GÜNTHER, T. & GREGOR, H.-J. 1993. Computeranalyse neogener Frucht- and Samenfloren Europas. *Documenta naturae* 50(4), 1–190.
- HOLÝ, F. 1976. Representatives of the family Mastixiaceae Calestani 1905 in the Bohemian Tertairy. Acta Musei nationalis Pragae, Series B – historia naturalis 31(3–5), 123–147.
- JACOBS, J.C., KINGSTON, J.D. & JACOBS, L.L. 1999. The origin of grass dominated ecosystems. Annals of the Missouri Botanical Garden 86, 590–643. DOI 10.2307/2666186
- JANIS, C.M., DAMUTH, J. & THEODOR, J.M. 2000. Miocene ungulates and terrestrial primary productivity: where have all the browsers gone. *Proceedings of the National Academy of Sciences USA 97*, 7899–7904. DOI 10.1073/pnas.97.14.7899
- JUCHNIEWICZ, K. 1975. Flora kopalna Turowa koło Bogatyni w swietle analizy nablonkowej I. Prace Muzeum Ziemi 24, 65–132.
- KNOBLOCH, E. 1989. Die biostratigraphische Stellung der tertiären Blattfloren von Seussen und Wackersdorf (Oberpfalz). Documenta naturae 55, 79–89.
- KNOBLOCH, E. & KVAČEK, Z. 1976. Miozäne Blätterfloren vom Westrand der Böhmischen Masse. *Rozpravy Ústředního geolo*gického ústavu 42, 1–131.
- KNOBLOCH, E. & KVAČEK, Z. 1996. Miozäne Floren der südböhmischen Becken. Sborník geologických věd, Paleontologie 33, 39–77.
- KNOBLOCH, E., KONZALOVÁ, M. & KVAČEK, Z. 1996. Die obereozäne Flora der Staré Sedlo-Schichtenfolge in Böhmen (Mitteleuropa). *Rozpravy Českého geologického ústavu 49*, 1–260.
- KOLAKOVSKII, A.A. 1958. Pervoe dopolnenie k duabskoi pliotsenovoi flore. *Trudy Sukhumskgo botanicheskogo sada 11*, 311–397.
- KOTHAVALA, Z., OGLESBY, R.J. & SALTZMAN, B. 1999. Sensitivity of equilibrium surface temperature of CCM3 to systematic changes in atmospheric CO₂. *Geophysical Research Letters 26*, 209–212. DOI 10.1029/1998GL900275
- KOVAR-EDER, J. & MELLER, B. 2001. Plant assemblages from the hanging wall sequence of the opencast mine Oberdorf N Voitsberg, Styria (Austria, Early Miocene, Ottnangian). *Palaeontographica Abteilung B 259*, 65–112.
- KOVAR-EDER, J., KVAČEK, Z. & MELLER, B. 2001. Comparing Early to Middle Miocene floras and probable vegetation types of Oberdorf N Voitsberg (Austria), Bohemia (Czech Republic),

and Wackersdorf (Germany). *Review of Palaeobotany and Palynology 114*, 83–125.

DOI 10.1016/S0034-6667(00)00070-1

- KOVAR-EDER, J., JECHOREK, H., KVAČEK, Z. & PARASHIV, V. 2008. The integrated plant record: An essential tool for reconstructing Neogene zonal vegetation in Europe. *Palaios* 23, 97–111.
- KÜRSCHNER, W.M. 1997. The anatomical diversity of recent and fossil leaves of the durmast oak (*Quercus petraea*, Lieblein / *Q. pseudocastanaea* Goeppert) – implications for their use as biosensors of palaeoatmospheric CO₂ levels. *Review of Palaeobotany and Palynology 96*, 1–30. DOI 10.1016/S0034-6667(96)00051-6
- KÜRSCHNER, W.M., KVAČEK, Z. & DILCHER, D.L. 2008. The impact of Miocene atmospheric carbon dioxide fluctuations and the evolution of terrestrial ecosystems. *Proceedings of the National Academy of Sciences USA 105*, 449–453. DOI 10.1073/pnas.0708588105
- KVAČEK, Z. 1971. Fossil Lauraceae in the stratigraphy on the North Bohemian Tertiary. Sborník geologických věd, Paleontologie 13, 47–86.
- KVAČEK, Z. & BŮŽEK, Č. 1982. Tertiary assemblages of the North Bohemian brwon-coal basin in connection with the lithofacial setting (Třetihorní společenstva severočeské hnědouhelné pánve ve vztahu k litofaciálnímu vývoji). MS report, Ústav geologie a geotechniky ČSAV, Praha.
- KVAČEK, Z. & WALTHER, H. 2003. Reconstruction of vegetation and landscape development during the volcanic activity in the České středohoří Mountains. *Geolines* 15, 60–64.
- KVAČEK, Z., BÖHME, M., DVOŘÁK, Z., KONZALOVÁ, M., MACH, K., PROKOP, J. & RAJCHL, M. 2004. Early Miocene freshwater and swamp ecosystems of the Most Basin (north Bohemia) with particular reference to the Bílina Mine section. *Journal of the Czech Geological Society* 49, 1–40.
- KVAČEK, Z., KOVAR-EDER, J., KOVÁČ, M., DOLÁKOVÁ, N., JE-CHOREK, H., PARASHIV, V., SLAMKOVÁ, M. & SLIVA, L. 2006. Evolution of landscape and vegetation in the Central Paratethys area during the Miocene. *Geologica Carpathica* 57(4), 295–310.
- LITKE, R. 1966. Kutikularanalytische Untersuchungen im Lausitzer Unterflöz. Paläontologische Abhandlungen 2(2), 327–426.
- MAI, D.H. 1964. Die Mastixioideen-Floren im Tertiär der Oberlausitz. *Paläontologische Abhandlungen* 2(1), 1–192.
- MAI, D.H. 1995. *Tertiäre Vegetationsgeschichte Europas*. 691 pp. Gustav Fischer Verlag, Jena.
- MAI, D.H. 2000. Die untermiozänen Floren aus der Spremberger Folge und dem 2. Flözhorizont in der Lausitz. IV. Palaeontographica, Abteilung B 254, 65–176.
- MAI, D.H. & MARTINETTO, E. 2006. A reconsideration of the diversity of *Symplocos* in the European Neogene on the basis of fruit morphology. *Review of Palaeobotany and Palynology 140*, 1–26. DOI 10.1016/j.revpalbo.2006.02.001
- MAI, D.H. & WALTHER, H. 1991. Die Oligozänen und Unter-miozänen Floren NW – Sachsens und des Bitterfelder Raumes. Abhandlungen des Staatlichen Museums für Mineralogie und Geologie zu Dresden 38, 1–230.
- MACFADDEN, B.J. 2005. Terrestrial mammalian herbivore response to declining levels of atmospheric CO₂ during the Cenozoic: Evidence from North American horses (family Equidae), 273–292.

In EHLERINGER, J.R., CERLING, T.E. & DEARING, M.D. (eds) A history of atmospheric CO₂ and its effects on plants, animals, and ecosystems. Ecological Studies 177. Springer Verlag, Berlin.

- MEEHL, G.A., STOCKER, T.F., COLLINS, W.D., FRIEDLINGSTEIN, P., GAYE, A.T., GREGORY, J.M., KITOH, A., KNUTTI, R., MURPHY, J.M., NODA, A., RAPER, S.C.B., WATTERSON, I.G., WEAVER, A.J. & ZHAO, Z.-C. 2007. Global climate projections, 747–845. In SOLOMON, S., QIN, D., MANNING, M., MAR-QUIS, M., AVERYT, K., TIGNOR, M.M.B., LEROY MILLER, H. JR. & CHEN, Z. (eds) Climate Change 2007: the physical science basis. Contribution of Working Group 1 to the fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge.
- MELLER, B., KOVAR-EDER, J. & ZETTER, R. 1999. Lower Miocene leaf, palynomorph, and diaspore assemblages from the base of the lignite-bearing sequence in the opencast mine Oberdorf, N Voitsberg, Styria, Austria) as an indication of "Younger Mastixioid" vegetation. *Palaeontographica, Abteilung B 252*, 123–170.
- MOSBRUGGER, V. & UTESCHER, T., 1997. The coexistence approach a method for quantitative reconstructions of Tertiary terrestrial palaeoclimate data using plant fossils. *Palaeogeography, Palaeoclimatology, Palaeoecology 134*, 61–86. DOI 10.1016/S0031-0182(96)00154-X
- MOSBRUGGER, V., UTESCHER, T. & DILCHER, D.L. 2005. Cenozoic continental climatic evolution of Central Europe. *Proceedings of the National Academy of Sciences USA 102*, 14964–14969. DOI 10.1073/pnas.0505267102
- NĚMEJC, F., KVAČEK, Z., PACLTOVÁ, B. & KONZALOVÁ, M. 2003. Tertiary plants of the Plzeň Basin (West Bohemia). Acta Universitatis Carolinae, Geologica 46(4, 2002), 121–176.
- PAGANI, M., ARTHUR, M.A. & FREEMAN, K.H. 1999. Late Miocene atmospheric CO₂ concentrations and the expansion of C4 grasses. *Science* 285, 876–878. DOI 10.1126/science.285.5429.876
- PAGANI, M., ZACHOS, J.C., FREEMAN, K.H., TIPPLE, B. & BO-HATY, S. 2005. Marked decline in atmospheric carbon dioxide concentrations during the Paleogene. *Science* 309, 600–603. DOI 10.1126/science.1110063
- PALAMAREV, E. & PETKOVA, A.S. 1987. Les fossiles de Bulgarie VIII.1. La macroflore du Sarmatien. 275 pp. Academie Bulgare des Sciences, Sofia.
- PALAMAREV, E., IVANOV, D. & BOZUKOV, V. 1999. Paläoflorenkomplexe im Zentralbalkanischen Raum und ihre Entwicklungsgeschichte von der Wende Oligozän/Miozän bis ins Villafranchium. *Documenta naturae, Flora tertiaria mediterranea VI*(5), 1–95.
- PEARSON, P.N. & PALMER, M.R. 2000. Atmospheric carbon dioxide concentrations over the past 60 million years. *Nature 406*, 695–699. DOI 10.1038/35021000
- RADOŇ, M., KVAČEK, Z. & WALTHER, H. 2006. Oligocene megafossil plant remains and environment from the newly recovered locality of the Holý Kluk hill near Proboštov (České středohoří Mountains, Czech Republic). Acta Universitatis Carolinae, Geologica 47, 95–124.
- RETALLACK, G.J. 2002. Carbon dioxide and climate over the past 300 Myr. *Philosophical Transactions of the Royal Society in London A* 360(1793), 659–673. DOI 10.1098/rsta.2001.0960

- ROTH-NEBELSICK, A., UTESCHER, T., MOSBRUGGER, V., DIESTER-HAASS, L. & WALTHER, H. 2004. Changes in atmospheric CO₂ concentrations and climate from the Late Eocene to Early Miocene: palaeobotanical reconstruction based on fossil floras from Saxony, Germany. *Palaeogeography, Palaeoclimatology, Palaeoecology 205*, 43–67. DOI 10.1016/j.palaeo.2003.11.014
- ROYER, D.L., WING, S.L., BEERLING, D.J., JOLLEY, D.W., KOCH, P.L., HICKEY, L.J. & BERNER, R.A. 2001. Paleobotanical evidence for near present-day levels of atmospheric CO₂ during part of the Tertiary. *Science 292*, 2310–2313. DOI 10.1126/science.292.5525.2310
- SALISBURY, E.J. 1927. On the causes and ecological significance of stomatal frequency, with special reference to the woodland flora. *Philosophical Transactions of the Royal Society of London B 216*, 1–65.
- SAMYLINA, V.A. 1967. On the final stages of the history of the genus *Ginkgo* L. in Eurasia. *Botanicheskii Zhurnal* 52, 303–316.
- SCHNEIDER, W. 1969. Cuticulae dispersae aus dem 2. Lausitzer Flöz (Miozän) und ihre fazielle Aussage. Freiberger Forschungshefte C 222, 1–75.
- SCHNEIDER, W. 2005. Cuticulae dispersae in der Lausitz (Ost-Deutschland). *Documenta naturae* 155, 1–41.
- ŠEVČÍK, J., KVAČEK, Z. & MAI, D.H. 2007. A new mastixioid florula from tektite-bearing deposits in South Bohemia, Czech Republic (Middle Miocene, Vrábče Member). *Bulletin of Geosciences* 82(4), 429–426.

DOI 10.3140/bull.geosci.2007.04.429

- SHEVENELL, A.E., KENNETT, J.P. & LEA, D.W. 2004. Middle Miocene southern ocean cooling and Antarctic cryosphere expansion. *Science* 305, 1766–1770. DOI 10.1126/science.1100061
- SIEGENTHALER, U., STOCKER, T.F., MONNIN, E., LUETHIM, D., SCHWANDERM, J., STAUFFERM, B., RAYNAUD, D., BARNOLA, J.-M., FISCHER, H., MASSON-DELMOTTE, V. & JOUZEL, J. 2005. Stable Carbon cycle – climate relationship during the Late Pleistocene. *Science* 310, 1313–1317. DOI 10.1126/science.1120130
- SLUIJS, A., BRINKHUIS, H., SCHOUTEN, S., BOHATY, S.M., JOHN, C.M., ZACHOS, J.C., REICHART, G.-J., SINNINGHE DAMSTÉ, J.S., CROUCH, E.M. & DICKENS, G.D. 2007. Environmental precursors to rapid light carbon injection at the Palaeocene/Eocene boundary. *Nature* 450, 1218. DOI 10.1038/nature06400
- STROEMBERG, C.A.E. 2002. The origin and spread of grass-dominated ecosystems in the late Tertiary of North America: preliminary results concerning the evolution of hypsodonty. *Palaeogeography, Palaeoclimatology, Palaeoecology 177*, 59–75. DOI 10.1016/S0031-0182(01)00352-2
- SURARU, M., SURARU, N. & GIVULESCU, R. 1978. Sarmatianul din Valea Baita si paleoflora lui. *Nymphaea* 6, 65–92.
- SZAFER, W. 1961. Miocene flora from Stare Gliwice in Upper Silesia. Instytut Geologiczny Prace 33, 1–205.
- TEODORIDIS, V. 2004. Floras and vegetation of Tertiary fluvial sediments of Central and Northern Bohemia and their equivalents in deposits of the Most Basin (Czech Republic). Acta Musei nationalis Pragae, Series B historia naturalis 60(3–4), 113–142.
 Transport V. 2006 E. dia and the sedimentation of the sedimentation of the sedimentation.

TEODORIDIS, V. 2006. Tertiary flora and vegetation of the locality

Přívlaky near Žatec (Most Basin). Acta Universitatis Carolinae, Geologica 47, 165–177.

- TEODORIDIS, V. & KVAČEK, Z. 2006. Palaeobotanical research of the Early Miocene deposits overlying the main coal seam (Libkovice and Lom Members) in the Most Basin (Czech Republic). *Bulletin of Geosciences 81(2)*, 93–113. DOI 10.3140/bull.geosci.2006.02.093
- UTESCHER, T., ERDEI, B., FRANCOIS, L. & MOSBRUGGER, V. 2007. Tree diversity in the Miocene forests of Western Eurasia, *Palaeogeography, Palaeoclimatology, Palaeoecology 253*, 226–250. DOI 10.1016/j.palaeo.2007.03.041
- UTESCHER, T., MOSBRUGGER, V. & ASHRAF, A.R. 2000. Terrestrial climate evolution in northwest Germany over the last 25 million years. *Palaios* 15, 430–449.
- UZUNOVA, K.G. 1995. Dispersed cuticles of Sarmatian sediments in northwestern Bulgaria. Lauraceae. *Phytologia Balcanica 1*, 13–17.
- UZUNOVA, K. & STOJANOVA, R. 1999. Anatomically grounded new taxonomical point of view to *Laurophyllum pseudo*princeps-complex. Documenta naturae 126, 7–19.
- VAN DER BURGH, J. 1983. Allochthonous seed and fruit floras from the Pliocene of the Lower Rhine Basin. *Review of Palaeobotany and Palynology* 40, 33–90.

DOI 10.1016/0034-6667(83)90004-0

- VAN DER BURGH, J. 1987. Miocene floras in the lower Rhenish Basin and their ecological interpretation. *Review of Palaeobotany and Palynology* 52, 299–366. DOI 10.1016/0034-6667(87)90064-9
- VAN DER BURGH, J. 1988. Some local floras from the Neogene in the lower Rhenish basin. *Tertiary Research* 9, 181–212.
- VAN DER BURGH, J., VISSCHER, H., DILCHER, D.L. & KÜRSCH-NER, W.M. 1993. Palaeoatmospheric signatures in Neogene fossil leaves. *Science* 260, 1788–1790. DOI 10.1126/science.260.5115.1788
- VRÁNA, S. Ed. 1980. Vysvětlivky k základní geologické mapě ČSSR 1 : 25 000, 22-44. Hluboká nad Vltavou. Ústřední ústav geologický, Praha.
- WAGNER, F., AABY, B. & VISSCHER, H. 1999. Rapid atmospheric CO₂ changes associated with the 8,200-years-BP cooling event. *Proceedings of the National Academy of Sciences USA 99*, 12011–12014. DOI 10.1073/pnas.182420699
- WEYLAND, H. & KILPPER, K. 1963. Kritische Untersuchungen zur Kutikularanalyse Tertiärer Blätter VI. Palaeontographica, Abteilung B 113, 93–116.
- WÓJCICKI, J.J. & KVAČEK, Z. 2002. Schenkiella genus novum, thorny disseminules of unknown affinities from the Early Miocene of Central Europe. Acta Palaeobotanica 42(2), 109–116.
- WOODWARD, F.I. 1987. Stomatal numbers are sensitive to increases in CO₂ from pre-industrial levels. *Nature* 327, 617–618. DOI 10.1038/327617a0
- ZACHOS, J.C., PAGANI, M., SLOAN, L., THOMAS, E. & BILLUPS, K. 2001. Trends, rythms, and aberrations in global climate 65 Ma to present. *Science* 292, 686–693. DOI 10.1126/science.1059412
- ZACHOS, J.C., DICKENS, G.R. & ZEEBE, R.E. 2008. An early Cenozoic perspective on greenhouse warming and carbon-cycle dynamics. *Nature* 451, 279–283. DOI 10.1038/nature06588