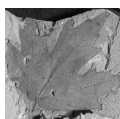


Palaeoenvironmental evaluation of Cainozoic plant assemblages from the Bohemian Massif (Czech Republic) and adjacent Germany

VASILIS TEODORIDIS & ZLATKO KVAČEK



We summarize palaeoclimatic oscillations recognizable in Cainozoic floras and vegetation of the Bohemian Massif and adjacent regions in Germany during the time span late Eocene to early Pleistocene. Statistical evaluation using Leaf Margin Analysis, Climate Leaf Analysis Multivariate Program and Coexistence Approach together with the Integrated Plant Record Vegetation Analysis has been employed to reconstruct climatic parameters (mainly Mean Annual Temperature, Mean Temperature of the coldest and the warmest months and Mean Annual Precipitation). Results of individual techniques have been compared and used for constructing curves that illustrate climatic trends. These methods can augment other sources of data to understand better the extent and timing of palaeoclimatic oscillations in Central Europe during the Cainozoic. • Key words: flora, vegetation, palaeoclimate, Cainozoic, Bohemian Massif, Germany.

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In the present overview we summarize results of palaeoenvironmental research carried out in the last few decades based on the fossil plants recovered from Palaeogene and Neogene freshwater and volcanogenic deposits of the Bohemian Massif and available since the 19th century (see reviews by Kvaček & Teodoridis 2007 and Pešek *et al.* 2010, 2014). We focus in more detail on palaeovegetation and palaeoclimatic changes and use simultaneously several palaeoclimatic techniques and discuss the resulting palaeoclimatic estimates in connection with syntaxonomical study (phytosociological approach *sensu* Mai 1995) and palaeoclimatic estimates previously published – see Kvaček & Walther (2004), Teodoridis & Kvaček (2006), Kvaček & Teodoridis (2007, 2011), Walther & Kvaček (2007), Holý *et al.* (2012), Teodoridis *et al.* (2012) and Kvaček *et al.* (2014). We have added several geographically and stratigraphically adjacent sites from the periphery of the Bohemian Massif in Saxony, Lusatia and Thuringia as well as the Paratethys with the aim to reconstruct a wider picture of palaeoenvironmental evolution in Central Europe (Fig. 1, Appendix 1).

Material and methods

Twenty-nine sites of late Eocene to early Pleistocene age from the Czech Republic and thirty sites from Germany are briefly characterized below. The plant assemblages have been selected according to qualitative criteria, *i.e.*, taxonomic and/or floristic diversity, reliable taxonomic treatment, good preservation, completeness of the studied taphocoenoses (autochthonous or parautochthonous *vs* allochthonous) and the environments, from which they are inferred to have originated (for detailed accounts see Appendix 1). To obtain independent palaeoenvironmental estimates for comparison and validation, four different palaeoenvironmental methods – the Integrated Plant Record vegetation analysis (IPR-vegetation analysis), Leaf Margin Analysis (LMA), Climate Leaf Analysis Multivariate Program (CLAMP) and Coexistence Approach (CA) have been used and discussed based on the published results (see Appendix 1).

The IPR vegetation analysis is a semi-quantitative fossil-based evaluation method, which has been usually

applied to Neogene and Palaeogene leaf, fruit and pollen floras (Kovar-Eder & Kvaček 2007, Kovar-Eder *et al.* 2008). The method is generally used for the classification of fossil floras in terms of zonal vegetation type and has been recently critically updated by its validation based on the modern vegetation sites from China and Japan (Teodoridis *et al.* 2011b, 2012) and by building an internet platform with interactive database (Teodoridis *et al.* 2011a). Leaf Margin Analysis (LMA) is a univariate leaf physiognomic technique based on the empirical positive correlation between mean annual temperature (MAT) and the proportions of toothed *vs* entire leaf taxa (woody dicots) of non-pioneer vegetation (Bailey & Sinnott 1916). Wolfe (1979) devised this method and compiled 34 humid to mesic floras from East Asia to build a linear regression equation to predict MAT. Recently, several equations of linear regression based on the different vegetation are used and listed in Appendix 5 including values of sampling errors. Climate Leaf Analysis Multivariate Program (CLAMP) is based on the multivariate statistical technique for quantitative determining for a range of palaeoclimate parameters based on leaf physiognomy of woody dicotyledonous flowering plants. CLAMP has first been introduced by Wolfe (1993) and subsequently this technique has been refined (Wolfe & Spicer 1999; Spicer *et al.* 2004; Spicer 2000, 2007), methodologically modified (*e.g.*, Yang *et al.* 2011; Teodoridis *et al.* 2011c, 2012; Yang *et al.* in press) and updated using gridded meteorological data (Spicer *et al.* 2009) and new CLAMP calibration data (*e.g.*, Jacques *et al.* 2011, Srivastava *et al.* 2012). Mathematically, this method is based on Canonical Correspondence Analysis (CCA) – see Ter Braak (1986). Coexistence Approach follows the description of the method provided by Mosbrugger & Utescher (1997) and Utescher *et al.* (2014). Climate data for the Nearest Living Relatives identified for the fossil taxa were retrieved from the current version Palaeoflora Database (Utescher & Mosbrugger 2013). Based on these data, the CA “core-program” – CLIMSTAT has been used to determine intervals of coexistence for a number of (palaeo)climatic parameters. Different palaeoclimatic approaches are purposely used simultaneously because some authors doubt the reliability of the listed techniques. For example, the Coexistence Approach has been challenged due to changes in autecology of nearest living relatives and the influence of certain environmental conditions, *e.g.*, mountainous regions in particular (*e.g.*, Kvaček 2007; Grimm & Denk 2012 *vs* Utescher *et al.* 2014), and the CLAMP approach has been seriously questioned (*e.g.*, Kennedy *et al.* 2002; Greenwood *et al.* 2004; Royer *et al.* 2005; Little *et al.* 2010; Peppe *et al.* 2010, 2011).

The list of plant taxa recovered from the studied assemblages/sites and their scoring according to the IPR-vegetation analysis is shown in Appendix 2, while physiognomic

characteristics of the studied plant assemblages for CLAMP are presented in Appendix 3.

Palaeofloristic overview

Late Eocene sites within the Bohemian Massif occur in the Cheb Basin, Sokolov Basin, České středohoří Mts, and Doupovské hory Mts. They mostly belong to fluvial deposits of the Staré Sedlo Formation (Kvaček & Teodoridis 2007), only rarely to volcanogenic facies. The Staré Sedlo Formation (Knobloch *et al.* 1996 – see Fig. 1B) is found in a limited area at Nový Kostel on the western border of the Cheb Basin and several localities, namely Staré Sedlo, Jehličná, Český Chloumek and the Erika Mine in the Sokolov Basin and reaches as far as Litoměřice in the České středohoří Mts. The floras of the Staré Sedlo Formation were monographed by Knobloch *et al.* (1996) and recently revised by Teodoridis *et al.* (2012, Appendix 1). They include several phytostratigraphical markers, such as *Steinhauera subglobosa*, *Rhodomyrtophyllum reticulatum*, *Gordonia saxonica* and *Laurophyllum syncarpifolium* associated with the predominant *Eotrigonobalanus furcinervis*/*E. andreanszkyi* (Fagaceae) and *Daphnogene* (Lauraceae). Their composition shows clear connections to the late Eocene floristic assemblage Hordle–Zeitz *sensu* Mai (1995). The late Eocene flora of Kučlín from the lower part of the volcanic complex of the České středohoří Mts differs from the flora of the Staré Sedlo Formation due to its distinct facies (volcanic *vs* fluvial). The former includes some other important elements, such as *Doliosporus taxiformis*, *Cedrelospermum leptospermum*, *Byttneriopsis*, *Sterculia crassinervia*, *Sloanea nimrodi*/*S. manchesteri*, *Raskya vetusta* and *Hooleyia hermis* (Kvaček 2002, Kvaček & Teodoridis 2011). Several comparable late Eocene sites occur in the area of the Weissenster Basin of Germany (Mai & Walther 1985, 2000; Kunzmann & Walther 2002; Hennig & Kunzmann 2013), *e.g.*, Haselbach, Kayna-Süd, Klaus and Knau (Fig. 1B, Appendix 1). A latest Eocene assemblage in North Bohemia has been recovered at Roudníky (Bellon *et al.* 1998) at the border of the Most (North Bohemian) Basin. It deviates from all the other Eocene sites by the presence of *Juniperus pauli*, which is also found at Větruše (Kvaček 2002), and the predominance of Arctotertiary elements as in most Oligocene floras of the same region (Kvaček *et al.* 2014).

From the lowermost limestone deposits belonging to the Doupov volcanic complex, Bůžek *et al.* (1968, 1987) reported a rare occurrence of *Doliosporus*, which is an important marker related to the Eocene/Oligocene boundary in the Bohemian Massif and to the floristic assemblage of Bembridge *sensu* Mai (1995). Thin-bedded and volcano-clastic material from the localities Valeč, Dvorce and Vrbice belongs to higher parts of the Doupov complex, the

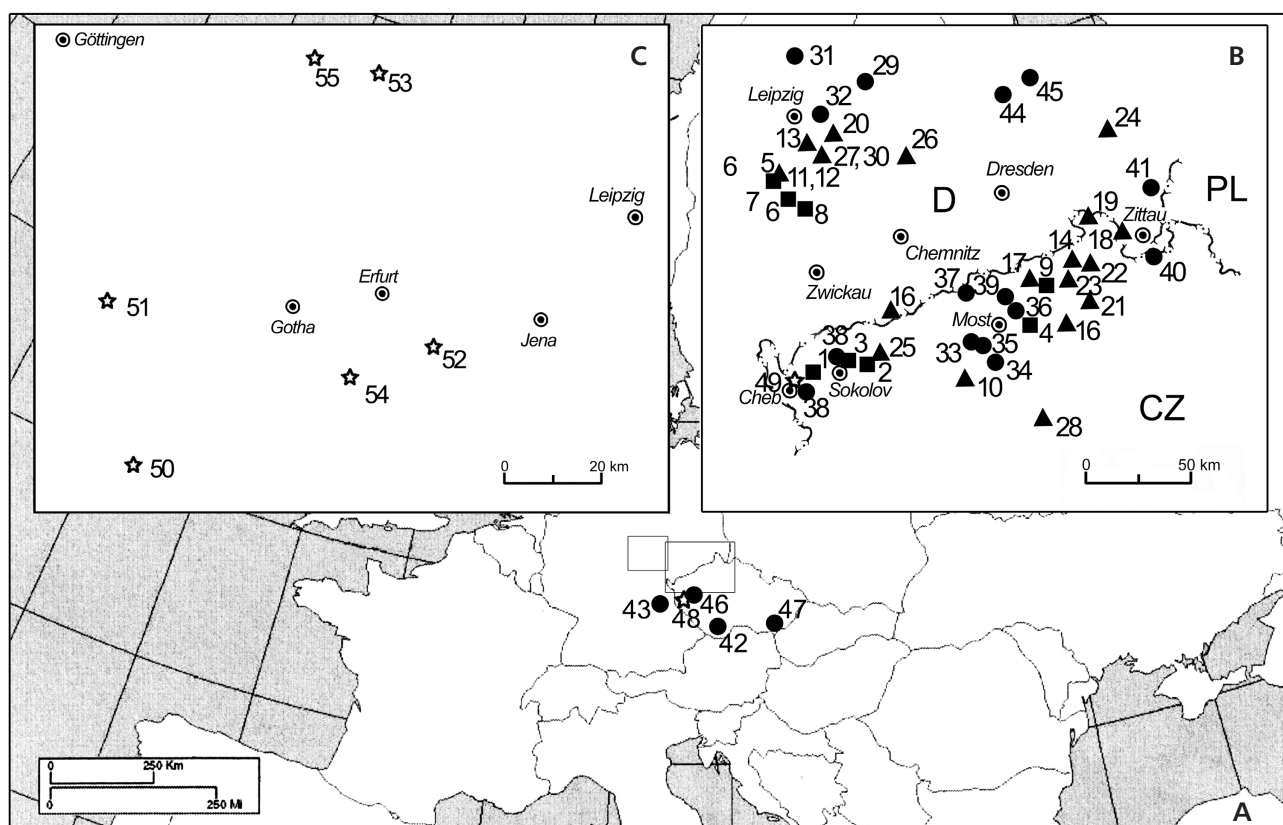


Figure 1. Location of the studied floras in Europe (A), in the NW part of the Czech Republic and Saxony (B), and in Lusatia (C). Symbols: “square” – Eocene sites, “triangles” – Oligocene sites, “circles” – Miocene sites, “star” – Pliocene–Pleistocene sites; floras/sites: 1. Nový Kostel, 2. Český Chloumek, 3. Staré Sedlo, 4. Kučlín, 5. Haselbach, 6. Klaus, 7. Kayna-Süd, 8. Knau, 9. Roudníky, 10. Valeč, 11. Haselbach, 12. Regis, 13. Beucha, 14. Bechlejovice, 15. Kundratice, 16. Hammerunterwiesenthal, 17. Holý Kluk, 18. Seifhennersdorf, 19. Knížecí–Hrazený, 20. Nerchau, 21. Sulečice–Berand, 22. Markvartice–Veselíčko, 23. Matry, 24. Kleinsaubernitz, 25. Počerny–Podlesí, 26. Bockwitz, 27. Borna-Ost, 28. Hlavačov Gravel and Sand, 29. Mockřena, 30. Witznitz, 31. Bitterfeld, 32. Brandis, 33. Čermnky, 34. Holedeč, 35. Přivlaky, 36. Břeštany, 37. Kundratice–Jezeří (micaceous facies), 38. Cypris Formation in the Cheb and Sokolov basins, 39. Horní Litvínov–Mariánské Radčice, 40. Hrádek/N. (Kristina Mine), 41. Wiesa, 42. Mydlovary Formation in the Třeboň and České Budějovice basins, 43. Wackersdorf, 44. Berzdorf 2 (Kleinleipisch), 45. Klettwitz, 46. Horní Břiza, 47. Moravská Nová Ves, 48. Tachov Graben, 49. Vildštejn Formation (Vonšov and Nová Ves Member) in the Cheb Basin, 50. Kaltensundheim, 51. Gerstungen, 52. Kranichfeld, 53. Berga, 54. Rippersroda, 55. Nordhausen.

base of which is dated by mammals (MP 21 – Fejfar & Kvaček 1993). The available floras show an early Oligocene character proved by the occurrences of *Alnus rhenana* (syn. *A. rostaniana*) and *Pinus ornata* associated with *Tetraclinis salicornioides*, *Platanus neptuni* and *Eotrigonobalanus furcinervis* (Bůžek *et al.* 1990a). A similar flora from Hammerunterwiesenthal in Saxony adjacent to the Doupov complex is radiometrically dated to the early Oligocene (Rupelian, 30.5 My – Walther 1998) and is correlated with the floristic assemblage of Seifhennersdorf–Kundratice *sensu* Kvaček & Walther (1998). The most diversified early Oligocene floras are known from the magmatic complex of the České středohoří Mts, namely those of Bechlejovice (Kvaček & Walther 2004), Kundratice (Kvaček & Walther 1998), Knížecí–Hrazený (Knobloch 1961, partly revised), Sulečice–Berand (Kvaček & Walther 1995), Holý Kluk (Radoň *et al.* 2006) and Markvartice–Veselíčko (Bůžek *et al.* 1976). All belong to

the Ústí Formation (Cajz 2000) and include typical conifers, such as *Torreya bilinica*, *Taxus engelhardtii*, *Cephalotaxus parvifolia*, *Calocedrus suleticensis* together with thermophilous broad-leaved, partly evergreen elements, such as *Platanus neptuni*, *Sloanea olmediifolia*/*S. engelhardtii*, *Palaeohosiea bilinica*, *Engelhardia orsbergensis*/*E. macroptera*, *Laurophyllum acutimontanum* *etc.* and the debut of deciduous (Arctotertiary) elements, such as *Alnus gaudinii*, *Acer palaeosaccharinum*, *Acer angustilobum*, *Cercidiphyllum crenatum*, *Carya fragiliformis*, *Betula alboides*/*B. dryadum*, *Ostrya atlantidis*, *Carpinus*, *Craigia*, *Zelkova*, *Ulmus fischeri* *etc.* (Akhmetiev *et al.* 2009). Based on the invasion of the above-mentioned deciduous elements associated with persisting Lauraceae and other thermophilous palaeo-subtropical elements, such as *Engelhardia*, *Sloanea* and *Palaeohosiea*, these floras are correlated with the floristic assemblage of Seifhennersdorf–Kundratice *sensu* Kvaček

& Walther (1998). The recently revised flora of Seiffenhensdorf from the periphery of the Zittau Basin in Saxony and Varnsdorf in the Czech Republic (Walther & Kvaček 2007) belongs also to this floristic assemblage (Kvaček & Walther 2001, 2003).

The next studied locality of Matřý (Radoň 2001, Soukupová 2004) belongs stratigraphically to the Děčín Formation of the České středohoří Mts (late Oligocene) and its flora includes new elements, such as *Ulmus pyramidalis*, *Acer crenatifolium* and *Betula brongniartii*. Further only partly revised late Oligocene floras of Počerny and Podlesí near Karlovy Vary from the Sokolov Basin are mastixioid, characterized by the first occurrences of *Fagus saxonica*, *Cathaya* sp., *Mastixia amygdaliformis* (= *M. venosa*) and *Carya costata* (Holý 1984, Kvaček & Walther 2001). They are correlated with the late Oligocene (Egerian) floristic assemblages of Linz–Krumvíř *sensu* Kvaček & Walther (2001) and Thierbach *sensu* Mai & Walther (1991). In the present study we have also analysed several Oligocene sites from Germany, such as Haselbach, Regis, Beucha, Nerchau, Kleinsaubernitz, for comparative purposes (Mai & Walther 1978, 1991; Walther 1999; Fig. 1B, Appendix 1). The German floras of Haselbach, Regis and Beucha, which belong to the Haselbach FA, contain the first appearance of *Boehlensipollis hohlui* indicating the oldest Oligocene strata in central Germany *sensu* Krutzsch (2011). But there is no connection to the marine biostratigraphic record and their position to the Eocene/Oligocene boundary is uncertain (Kunzmann pers. comm. 2015). Therefore the stratigraphical correlation of the studied German and Bohemian floras from the late Eocene to early Oligocene period is problematic. Kunzmann *et al.* (in press, text-fig. 1) presented the correlation scheme of these floras in context of their phytostratigraphy and lithological data from the Weissenster, Cheb and Sokolov basins and České středohoří Mts.

Late Oligocene to early Miocene sediments of the Most Basin yielded many rich floras (Fig. 1B, Appendix 1), which are most comparable and palaeogeographically linked with those from Saxony and Lusatia (Mach *et al.* 2014). These deposits belong to the Most Formation, which is divided into the Duchcov, Holešice, Libkovic and Lom Members (see Domáci 1977 and Matys Grygar & Mach 2013). Palaeobotanical data from the Duchcov Member are very scanty (*e.g.*, a florula of Jeníkov, drill core Je 96 – Kvaček & Bůžek 1983). Additionally, palynological spectra from deeper horizons of the basin deposits show, besides common Oligocene and Miocene elements, a maximal abundance of *Fagus* pollen in sediments of the Duchcov Member (Konzalová 1976). More abundant plant macrofossils are known from extra-basinal fluvial deposits of the Hlavačov Gravel and Sand *sensu* Váně (1985), which are typified by the occurrence of *Pseudolarix* and *Fagus saxonica* associated with several

broad-leaved elements, such as *Tilia*, *Acer* spp., *Mahonia*, *Ailanthus*, *Daphnogene* and *Trigonobalanopsis* (Němejc 1949; Bůžek & Kvaček 1989; Teodoridis 2002, 2010). These plant assemblages show close palaeobotanical and geochemical affinity to sediments of the Thierbach layers characterized mainly by the floras of Bockwitz and Borna-Ost (Mach *et al.* 2014) and are assigned to the floristic assemblage of Thierbach *sensu* Mai & Walther (1991). According to Mach *et al.* (2014), the floras of Mockrehna near Eilenburg (micaceous sands underlying the Bitterfeld Main Coal Seam – Mai & Walther 1991) and Witznitz near Borna (coaly clay of the Thierbach layers – Mai & Walther 1991) are not exactly correlatable with those of the Most Basin. They have been placed in the Oligocene/Miocene floristic assemblage of Mockrehna–Witznitz *sensu* Mai & Walther (1991), which is currently regarded as being questionable (Roth-Nebelsick *et al.* 2014).

The Holešice Member of the Most Formation is distinctly richer in plant macrofossils than the Duchcov Member. The floras are taxonomically uniform with prevailing swamp elements, *i.e.*, mainly predominance of Cupressaceae s.l. (*Glyptostrobus europaeus*, *Taxodium dubium*, *Quasisequoia couttsiae*) associated with frequent occurrences of *Stratiotes kaltennordheimensis*, *Spirematospermum wetzleri*, *Myrica* spp., *Calamus daemonorops*, *Salvinia*, *Decodon*, *Rubus* spp., *Sparganium* spp., *Nyssa bilinica*, *Alnus julianiformis*, *Quercus rhenana*, *Cercidiphyllum*, *Proserpinaca*. Several more-or-less mesophytic allochthonous elements, such as *Ternstroemia* sp., *Toddalia maii*, *Liriodendron aptera*, *Eurya stigmosa*, and *Laurophyllum saxonicum* co-occur (Bůžek & Holý 1964, Bůžek 1971, Kvaček & Teodoridis 2007). Plant assemblages of the deltaic and fluvial environments from the Žatec Delta are documented mainly by records from Čermníky (Bůžek 1971, Teodoridis 2004), Holedeč (Brabenec 1904, Teodoridis 2002) and Záhoří near Žatec (Teodoridis 2003a). Floristically similar assemblages in Saxony are known from the upper part of the Bitterfeld Main Coal Seam and its overlying clay (“Deckton”) as well as analogous horizons from the open cast mine Delitzsch-NW (Mach *et al.* 2014). They belong to the floristic assemblages of Bitterfeld and Brandis *sensu* Mai & Walther (1991). The assemblages of the Bílina Delta are slightly younger. More than 110 species are known from 65 fossiliferous horizons (Bůžek *et al.* 1992, Boulter *et al.* 1993, Kvaček 1998, Dvořák pers. comm. 2013) and belong to the associations of *Parrotia-Ulmus pyramidalis* and *Nyssa-Taxodium* (*sensu* Kvaček & Bůžek 1983). However, noteworthy aquatic, partly endemic plants (*Elephantosotis dvorakii*, *Hydrochariphyllum buzekii*, *Lemna cestmirii* – Kvaček 1998, 2003; *Schenkiella credneri* – Wójcicki & Kvaček 2002, *Smilacinites ungeri* – Kvaček *et al.* 2004) occur there associated with thermophilous elements, such

as *Blechnum dentatum*, *Tetraclinis salicornioides*, *Engelhardia orsbergensis*, *Sabal lamanonis*, *Platanus neptuni*, *Symplocos casparyi* and an azonal extinct conifer *Cupressospermum saxonicum*.

The above-mentioned sites of the Bílina Delta correspond stratigraphically to the lower part of the Libkovice Member *sensu* Domáci (1977; *i.e.*, the upper part of the Holešice Member *sensu* Matys Grygar & Mach 2013), while those from the younger part of the Most Basin are represented by the assemblages of the Břešťany Clay (Ettingshausen 1866, 1868, 1869; Teodoridis & Kvaček 2006), Přívklady (Teodoridis 2006) and micaceous facies in the vicinity of Jezeří and Kundračice (Teodoridis & Kvaček 2006). That of the Břešťany Clay is characterized as a mixture of coal-forming elements, such as Cupressaceae s.l. (*Glyptostrobus*, *Taxodium* and *Quasisequoia*), *Alnus julianiformis*, *Nyssa bilinica*, *Laurophyllum saxonicum*, *Quercus rhenana*, *Acer tricuspidatum*, *Craigia* and *Cercidiphyllum* associated with abundant riparian and mesophytic elements that primarily occupied delta and upland environments, *e.g.*, *Cinnamomum polymorphum*, *Laurophyllum* spp., *Podocarpium*, *Liquidambar*, *Parrotia*, *Salix haidingeri*, *Carya*, *Populus populina*, *Ulmus*, *Zelkova*, *Rosa*, “*Sapindus*” *falcifolius*, *Acer angustilobum*, *Acer integrilobum*, *Fraxinus bilinica*, *Trigonobalanopsis rhamnoides*/T. *exacantha* and *Pinus* (associations of *Engelhardia-Taxodium* and *Comptonia-Pinus oviformis sensu* Kvaček & Bůžek 1983). The flora of Přívklady from the Žatec Delta includes similar riparian elements known from the Bílina Mine (*Liquidambar*, *Ulmus*, *Parrotia*, *Salix*, *Acer*, *Diospyros*, *Zelkova*, *Carya*, *Rosa*, *Comptonia* and *Podocarpium*) with an interesting re-appearance of *Fagus saxonica*. The assemblages of the micaceous facies show a distinctly more thermophilous character proved by occurrences of *Vaccinioides lusatica*, *Gordonia hradeckensis*, *Symplocos volkeri*, *Mastixia lusatica*, *Symplocos casparyi*, *Schisandra moravica* associated with some aquatic, wetland and zonal elements such as *Azolla* spp., *Cladiocarya*, *Cladium*, *Dulichium*, *Potamogeton*, *Sparganium*, *Spirematospermum*, *Stratiotes*, *Myrica* spp., *Glyptostrobus*, *Comptonia*, *Engelhardia*, *Eurya*, *Meliosma*, *Pinus* spp., *Pterocarya*. The sediments just underlying the Lom Coal Seam (formally belonging to the uppermost part of the Libkovice Member *sensu* Domáci 1977 – Mach *et al.* 2014), contain several drill-core assemblages from Horní Litvínov and Mariánské Radčice (MR58, MR59, LIH13). They are characterized by mostly palaeosubtropical elements, such as *Laurus abchasica*, *Laurophyllum pseudovillense*, *Laurophyllum pseudo-princeps*, *Laurophyllum markvarticense*, *Quercus kubinyi*, *Cedrelospermum* sp. and *Gordonia hradeckensis*, besides the persisting thermophilous elements, *e.g.*, *Lygodium* and *Platanus neptuni* (Teodoridis & Kvaček 2006). The flora from the Lom Coal Seam is fragmentarily

known from the drill cores LOM 15, 16, OS 9 and MR 59 and shows a predominance of aquatic and swamp elements, such as *Salvinia*, *Azolla* spp., *Hemitrapa*, *Potamogeton*, *Pronephrium*, *Glyptostrobus*, *Quasisequoia*, *Myrica undulatissima*, *Nyssa gmelinii*, *Decodon* sp., *Alnus* sp., *Salix* cf. *varians*, Poaceae vel Cyperaceae gen. et sp. indet. – see Teodoridis & Kvaček (2006). According to Mach *et al.* (2014), a new florula from the clay overlying the Lom Seam (drill core OS 16) includes several thermophilous elements, such as *Ceratozamia hofmannii*, *Laurophyllum nobile*, *Myrica lignitum* and *Pinus* sp. (Kvaček 2014). The floras from the underlying sediments of the Lom Coal Seam and the Lom Member can be correlated with the floristic assemblage of Eichelskopf-Wiesa *sensu* Mai (1995) and/or the floristic assemblage Františkovy Lázně–Kleinleipisch *sensu* Mai (1995) and Czaja (2003) showing affinity to the floras of Hrádek/N. (the Kristina Mine and drill cores in its vicinity – Teodoridis 2003b, Holý *et al.* 2012) and the Cypris Formation in the Sokolov and Cheb basins (Bůžek *et al.* 1996). The flora of the Cypris Formation *sensu* Reuss (1852) is also thermophilous with a similar but richer floristic composition of *Mastixia*, *Cinnamomum polymorphum*, *Ocotea hradeckensis*, *Laurus abchasica*, *Laurophyllum* spp. div., *Gordonia* and *Platanus neptuni* and newly appearing *Quercus kubinyi* (Bůžek *et al.* 1996). Our study includes additional early to middle Miocene sites from Germany (Fig. 1A, B), *i.e.*, Wiesa, Wackersdorf, Kleinleipisch and Klettwitz (*e.g.*, Knobloch & Kvaček 1976; Gregor 1978, 1990; Mai & Walther 1991; Günther & Gregor 1993; Mai 1995, 2000, 2001a, b; Czaja 2003 – Appendix 1), which define the above-mentioned floristic assemblages or show close stratigraphical and palaeoenvironmental affinities.

Several important Miocene plant assemblages of the Bohemian Massif are known outside the Ohře Graben, namely from sedimentary relicts of the Neogene river system of Central and Western Bohemia and the České Budějovice and Třeboň basins in South Bohemia (Fig. 1A). Those from the fluvial relicts within the Plzeň area (Ejpovice, Kyšice, Dobříč, Horní Břiza and Býkovský les) were reported by Hurník & Knobloch (1966). Němejce *et al.* (2003) completely revised them including micro-palaeobotanical analysis except those of Kyšice and Ejpovice (see Kvaček *et al.* 2006). The flora of Horní Břiza includes a mixture of rare thermophilous elements (*Chamaerops*, *Laurophyllum pseudovillense*, *Gordonia*) and deciduous woody elements (*Ginkgo adiantoides*, *Platanus leucophylla*, *Quercus pseudocastanea*), which suggest a middle Miocene, probably Badenian age. The upper parts of sedimentary fills of the České Budějovice and Třeboň basins belong mostly to the Neogene. The Mydlovary Formation (localities Mydlovary, Ledenice, Hluboká and Kamenný Újezd) is characterized by a

thermophilous mastixioid flora with *Mastixia amygdalaeformis*, *Eomastixia hildegardis*, *Trigonobalanopsis rhamnoides* and *Engelhardia orsbergensis* with additional *Ziziphus paradisiaca*, *Ailanthus*, *Myrica lignitum* and *M. vindobonensis* showing affinities to the flora of Františkovy Lázně (Cheb Basin – Holý 1977b) and the Cyprus Formation in general. However, in addition to the mastixioids, new younger (Badenian) elements, i.e. *Magnolia liblarensis*, *Smilax sagittifera* and *Illipophyllum thomsonii* appear for the first time in the Bohemian Massif (Knobloch & Kvaček 1996) and stress the middle Miocene age of the Mydlovarý Formation (Kvaček & Teodoridis 2007). A mastixioid assemblage recovered in tectite-bearing deposits at Vrábče (Ševčík *et al.* 2007) also fits into the Miocene Climatic Optimum.

We also treat sites in the Czech Republic belonging to the Paratethys, which continue our sequence of the Miocene. Knobloch (1969) described several macrofloras from the Moravian part of the Vienna Basin of late Miocene (Pannonian) age from the localities of Poštorná, Dubňany and Moravská Nová Ves. They show a more temperate character indicated by the predominance of deciduous elements, such as *Alnus*, *Betula*, *Carpinus*, *Ulmus*, *Carya*, *Fagus haidingeri*, *Quercus kubinyii*, *Q. gigas* and *Acer* spp. associated with *Laurophyllum* sp., *Daphnogene pannonica*, *Craigia bronnii* – *Dombeyopsis lobata*, and *Myrica* sp. Leaves of *Buxus pliocenica* and *Ginkgo adiantoides* are also present there, suggesting a correlation with the flora of Horní Břiza in the Plzeň Basin (Němejc *et al.* 2003).

Pliocene and Pleistocene sediments of the Vildštejn Formation (Fig. 1B), which yielded the youngest fossil plant assemblages of the Bohemian Massif, were deposited after a long hiatus in the Cheb Basin (Bůžek *et al.* 1985). The plant-bearing fluvio-lacustrine deposits have been dated to 4.5–1.5 Ma with the aid of palaeomagnetic measurements (Špičáková *et al.* 2000; *cf.* Bucha *et al.* 1990). According to Teodoridis *et al.* (in press), the lower part of the Vildštejn Formation (the Vonšov Member – Pluto Clays, the Nová Ves Member – Nero Clay) is characterized by the occurrence of *Glyptostrobus* and other conifers (*Taxodium*, *Chamaecyparis*, *Pinus* cf. *spinosa*, *Picea* cf. *echinata*, *Pseudolarix*) as well as of angiosperms (*Liriodendron*, *Ampelopsis*, *Acer* cf. *tricuspidatum*, *Viburnum* cf. *dilatatum*, *Weigela*, *Leucothoe narbonnensis*, *Epipremnites*) known from the early Pliocene (Brunsumian–Reuverian, Piacenzian) of Europe, e.g., Frankfurt a. M., Willershausen, Berga, Auenheim and Stura (Mädler 1939, Mai & Walther 1988, Straus 1992, Martinetto 1995, Knobloch 1998, Kvaček *et al.* 2008, Teodoridis *et al.* 2009). On the other hand, plant assemblages from the upper part of the Nová Ves Member are distinctly cool temperate with *Picea omoricoides*, *Chamaecyparis*, *Vaccinioideae* (including *Chamaedaphne*, *Oxycoccus*),

Menyanthes, *Scheuchzeria* and other herbs (Teodoridis *et al.* in press). Bůžek *et al.* (1985) compared these floras with the Praetiglian (early Pleistocene). This palaeofloristic correlation may indicate an age of the boundary between the Vonšov and Nová Ves Members *sensu* Bůžek *et al.* (1985) and/or the lower and middle parts of Nová Ves Beds (Pluto Clay/lignite beds of Nová Ves Beds) *sensu* Teodoridis *et al.* (in press) approximately at 2.6 Ma. Floras known from fluvial relicts of the Tachov (Cheb-Domažlice) Graben (the river “F” – *sensu* Pešek & Spudil 1986) outliers of the Cheb Basin (Konzalová in Bůžek *et al.* 1985) have an older floristic character due to frequent remains of *Glyptostrobus*, *Corylopsis*, *Symplocos* and *Microdiptera* which would suggest an affinity to the early Pliocene (Zanclean) flora of Europe, e.g., Brunssum, Sessenheim, Krościenko, Ca’Vietone and Sento (Reid & Reid 1915, Szafer 1947, Zagwijn 1959, Martinetto 1995, Martinetto *et al.* 1997, Kvaček *et al.* 2008, Teodoridis *et al.* 2009). Besides the above-mentioned flora of Berga, five other Pliocene to Pleistocene sites from Thuringia (Nordhausen, Rippersroda, Kranichfeld, Gerstungen and Kaltensundheim – Mai & Walther 1988, Fig. 1C, Appendix 1) are evaluated here to show trends in vegetation and palaeoclimatic changes in Central Europe.

Results of palaeovegetation analysis

Results of the newly developed IPR-vegetation analysis of 56 sites from the Bohemian Massif, Saxony and Lusatia are presented in Appendix 6 and Fig. 2A, B (for a detailed taxa scoring see Appendix 2). Kvaček (2010) noted a zonal vegetation type of Mid-latitude Notophyllous Broad-leaved Evergreen Forest as a possible vegetation analogue for the late Eocene assemblage of Kučlín based on the phytosociological (intuitive) approach (e.g., Mai 1995). This fossil zonal vegetation type can be interpreted as the upland vegetation analogue for several azonal late Eocene plant assemblages known from the Staré Sedlo Formation and the Weissester Basin assigned by Kvaček (2010) to the Broad-leaved Evergreen Riparian Gallery Forest with palms (sites of the Staré Sedlo Formation) and the mixed *Doliosirobus* and/or *Quasisequoia* and Broad-leaved Evergreen Swamp forests (sites from the Weissester Basin). The results of the IPR-vegetation analysis of the studied late Eocene sites from the Staré Sedlo Formation, the Weissester Basin (detailed in Teodoridis *et al.* 2012) and Kučlín (Kvaček & Teodoridis 2011) corroborate the phytosociological results given by Kvaček (2010) and assign these plant assemblages to the Broad-leaved Evergreen Forest (“BLEF”) vegetation type. However, the late Eocene assemblages of the BLEF type from the Weissester Basin are characterized by a relatively high percentage of BLE components, which varies from 65% to 82% (! the assemblage

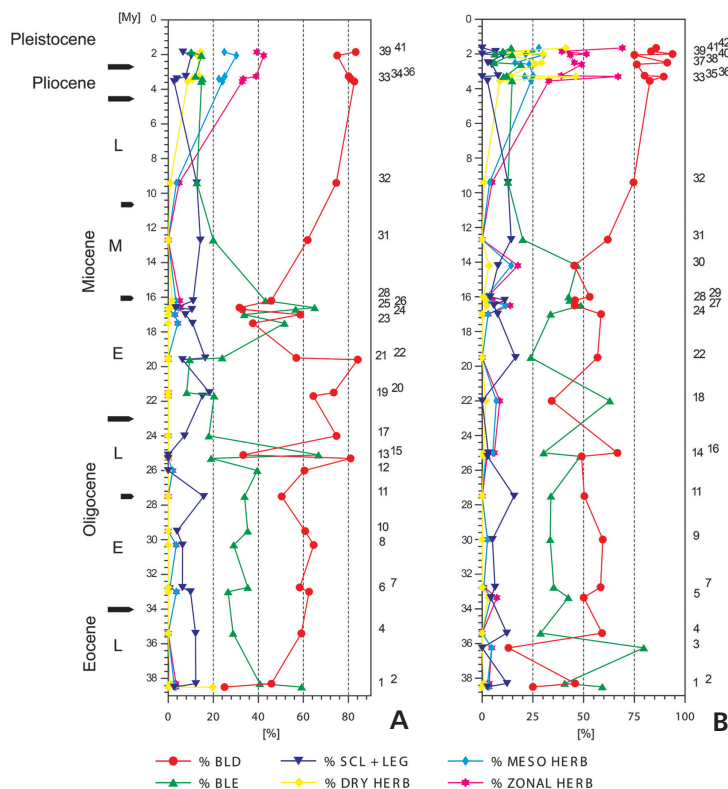


Figure 2. General vegetation changes and trends based on the selected IPR-vegetation results of the studied floras during the late Eocene to early Pleistocene period in the Bohemian Massif (A) and Central Europe (B). Symbols: BLD (broad-leaved deciduous woody angiosperms), BLE (broad-leaved evergreen woody angiosperms), SCL+LEG (sclerophyllous woody and legume-like woody angiosperms), DRY HERB (open woodland and grassland elements), MESO HERB (mesophytic forest undergrowth elements), and ZONAL HERB (DRY HERB + MESO HERB); sites: 1. Staré Sedlo, 2. Kučlín, 3. Haselbach (Zeitz Sand and/or Floristic Assemblage), 4. Roudníky, 5. Haselbach, 6. Bechlejovice, 7. Kunderatice, 8. Holý Kluk, 9. Seifhennersdorf, 10. Knižecí-Hrazený, 11. Sulečice-Berand, 12. Markvartice-Veselíčko, 13. Matry, 14. Kleinsaubernitz, 15. Počerný-Podlesí, 16. Bockwitz, 17. Hlavačov Gravel and Sand, 18. Brandis, 19. Čermníky, 20. Holedeč, 21. Přivlaky, 22. Břešťany, 23. Kunderatice-Jezí (micaceous facies), 24. Cypris Formation 25. Horní Litvínov-Mariánské Radčice, 26. Hrádek/N. (Kristina Mine), 27. Berzdorf 1 (Wiesa), 28. Mydlovary Formation, 29. Wackersdorf, 30. Berzdorf 2 (Kleinleipisch), 31. Horní Břiza, 32. Moravská Nová Ves, 33. Tachov Graben, 34. Vonšov Mb. (Vildštejn Formation) – Pluto Clay, 35. Kaltensundheim, 36. Nová Ves Mb. (Vildštejn Formation) – Nero Clay, 37. Kranichfeld, 38. Berga, 39. Nová Ves Mb. (Vildštejn Formation) – lignite beds, 40. Rippersroda, 41. Nová Ves Mb. (Vildštejn Formation) – upper part, 42. Nordhausen.

of Knau included even 92% – see Teodoridis *et al.* 2012) and relatively low abundances of BLD component (23% to 18%) contrary to those from the Staré Sedlo Formation (BLE component 59% to 66%, BLD component 25% to 22%) as well as Kučlín (BLE 41%, BLD 46% – Appendix 6, Fig. 2A, B: Nos 1–3). The late Eocene vegetation type of Roudníky (Fig. 2A, B: No. 4) is characterized by 29% and 59% of BLE and BLD components, respectively, which assigns it to the Mixed Mesophytic Forest (MMF). Besides, the vegetation types of Kučlín and Roudníky show also a high percentage of sclerophyllous and legume-like elements (both 12%), which is rarely the case in the late Eocene floras of Europe (Fig. 2A). Teodoridis *et al.* (2012) noted as a modern living vegetation analogue for both of them the subtropical broad-leaved evergreen forest of Mt. Emei (Sichuan, China). This comparison is based on the results of a cluster analysis that compares 47 modern vegetation types from the subtropical and tropical zones of China and Japan and 14 late Eocene fossil vegetation sites from the Weisselster Basin and the Staré Sedlo Formation (see Teodoridis *et al.* 2012, fig. 3.2). According to results of the cluster analysis presented in Kvaček *et al.* (2014), the late Eocene vegetation of Roudníky and Kučlín shows a close affinity to the early Oligocene vegetation of Bechlejovice (see below). These fossil vegetation types are related to the modern vegetation associations of *Eurya-Cryptomeria japonica* (Mixed Mesophytic Forest type) from the Yakushima Island in Japan (Kvaček *et al.* 2014, fig. 13).

Early Oligocene sites from the Doupovské hory Mts (locality Valeč) and from the České středohoří Mts (Bechlejovice, Kunderatice) document a distinct decrease of the BLE components (26% and 35%) and an increase of the BLD component at the Eocene/Oligocene boundary, which corresponds to an enormous immigration of riparian deciduous broad-leaved elements from Asia to Europe (Kvaček & Teodoridis 2007). This trend is also reported from the above-mentioned sites of Roudníky (latest Eocene – 35.4 Ma according to Bellon *et al.* 1998) and Větruše (74% of BLD component *vs* 26% of BLE component – Kvaček *et al.* 2014, Appendix 1), as well as the studied early Oligocene assemblages from Saxony, where the retreat of evergreen elements is more significant (34% – Seifhennersdorf). The vegetation character can be interpreted as the Mixed Mesophytic Forest “MMF” (Bechlejovice) and the ecotonal vegetation type of Broad-leaved Evergreen Forest “BLEF” and MMF (Kunderatice, Hammerunterwiesenthal, Seifhennersdorf). Only the early Oligocene assemblage of Haselbach contains 42% of BLE. This value allows it to be assigned to the BLEF vegetation type; however, the decrease of percentage of BLE elements, compared to the studied late Eocene sites from the Weisselster Basin, is more than 30% (Appendix 6, Fig. 2A, B: Nos 5–9). These vegetation types provided by the IPR-vegetation analysis are comparable with those based on the phytosociological approach, which postulated a Mixed Mesophytic Forest for Bechlejovice (Kvaček &

Walther 2004, p. 51), Kundratice (Kvaček & Walther 1998, p. 31), Hammerunterwiesenthal (Walther 1998, p. 252) and Seifhennersdorf (Walther & Kvaček 2007, p. 131). Kvaček & Walther (2001) presented new azonal vegetation types called the *Nyssa-Taxodium* swamp forest, aquatic *Salvinia* association and riparian forests with broad-leaved deciduous trees (*Alnus*, *Populus*, *Carya*, *Carpinus*, *Ulmus*, *Liquidambar*, *Acer*), lianas and shrubs (*Ampelopsis*, *Vitis*) for the lower Oligocene Haselbach Series. These vegetation units are also typical for the partially compiled assemblages of Haselbach, Schleenhain, Regis and Beucha, which were described by Mai & Walther (1978). Kvaček & Walther (2001) assumed that the poorly characterized plant assemblage of Valeč (Bůžek *et al.* 1990a) was the zonal vegetation equivalent for these azonal units. The re-appearance of thermophilous elements (documented by an increase of the BLE elements and palms – Appendix 6) is connected with a warming trend, which started in the late early Oligocene and continued throughout the Oligocene (sites of Holý Kluk – 29%, Sulečice–Berand – 34%, Markvartice–Veselíčko – 40%; on average 36% of BLE components) and culminated in the late Oligocene with the plant assemblages of Kleinsaubernitz (48%), Počerny–Podlesí (67%) showing on average 57.5% of BLE components comparable to the modern subtropical zone. The results of the IPR-vegetation analysis for the studied vegetation of the late early and late Oligocene sites correspond to MMF, ecotonal vegetation type of MMF/BLEF [or Broad-leaved Evergreen Forest vegetation type] (Appendix 6, Fig. 2A, B: Nos 10–15). The previous phytosociological studies of Sulečice–Berand (Kvaček & Walther 1995), Holý Kluk (Radoň *et al.* 2006), Markvartice and Veselíčko (Bůžek *et al.* 1976) also predicted the Mixed Mesophytic Forest vegetation type as an analogue for the studied zonal fossil plant assemblages. The maar flora of Kleinsaubernitz shows affinity to the modern ecotone between MMF and BLEF (Walther 1999, p. 152). The IPR vegetation results from a carpoflora of Nerchau shows relatively high abundances of BLE and MESO HERB components, which may be caused by the lack of riparian elements documented by leaf material and by *Selaginella* records (4 species – see Appendix 2).

The boundary between late Oligocene and early Miocene is characterized by a re-appearance of deciduous elements corresponding to an increase of the BLD component, *i.e.* Bockwitz, Borna-Ost (Thierbach layers) – 67% and 57%, Hlavačov Gravel and Sand – 75% (see Appendix 6, Fig. 2A, B: Nos 16, 17), which can be interpreted as a slight cooling event under a humid warm temperate climate. A prediction of vegetation types based on the IPR-vegetation analysis of these sites fluctuated from BLEF through MMF to transitional vegetation type of Broad-leaved Deciduous Forest “BLDF” and Mixed Mesophytic Forest. However, the assemblages of the Thierbach layers (Mai & Walther

1991) and the Hlavačov Gravel and Sand (Teodoridis 2004) have a riparian character, which is physiognomically characterized by the predominance of deciduous elements. Therefore, the predicted IPR-vegetation types can be partly influenced by this riparian character of the plant assemblages as well as the palaeoclimate estimates derived from the physiognomic techniques (LMA and CLAMP – see below). The same situation is evident in the assemblage of Matřý (Radoň 2001, Soukupová 2004), which shows an anomalously high percentage of BLD components (81%, BLDF estimated by IPR vegetation analysis) contrary to the other studied early late Oligocene assemblages. The Oligo-Miocene assemblages of Mockrehna and Witznitz (Mai & Walther 1991) may represent vegetation types of BLEF as demonstrated by a lower abundance of BLD components (53% and 22%) linked with increasing BLE components (43% and 78%). The vegetation character of the early Miocene sites of Čermníky and Holedeč can be interpreted as MMF (rates of BLE 64% and 73%, BLD 20% and 8%) with a relatively high percentage of the SCL+LEG component (15% and 18%). The Saxonian analogues of Bitterfeld and Brandis (Mach *et al.* 2014) exceed the threshold value of the BLE component for BLEF (Appendix 6, Fig. 2A, B: Nos 18–20). The IPR-results agree with the predicted vegetation types based on the phytosociological approach (Bůžek 1971; Teodoridis 2002, 2010; Mai & Walther 1991). Younger early Miocene floras from the Most Basin, *i.e.*, those of Břešťany, Přívklady, micaceous facies, as well as Horní Litvínov–Mariánské Radčice and their phytostratigraphical equivalents from the other areas of the Bohemian Massif and Germany (assemblages from the Cypris Formation, Berzdorf 1 (Wiesa), Hrádek/N., the Mydlovary Formation, Wackersdorf, Klettwitz 3 and Berzdorf 2) are typical of a significant increase of the BLE elements and abundant occurrences of mastixioid elements, *e.g.*, Berzdorf 1 (Wiesa) – Czaja (2003), Hrádek/N. (Kristina Mine) – Holý (1974, 1977a, b, 1978), Holý *et al.* (2012); Mydlovary Fm. – Knobloch (1986), Knobloch & Kvaček (1996); Wackersdorf – Knobloch & Kvaček (1976), Gregor (1978, 1990) – see Appendix 6, Fig. 2A, B: Nos 21–29. This trend is also known from the early/middle Miocene assemblages of Berzdorf 2 (Kleinleipisch) and Klettwitz 3 (Czaja 2003; Mai 2000, 2001a, b) – see Appendix 6, Fig. 2B: No. 30. The predicted vegetation type for almost all the mentioned sites is the BLEF. Only the assemblages of Břešťany, Přívklady and those of the Cypris Formation belong to different vegetation types, *i.e.* MMF, BLDF and the ecotone of MMF/BLEF (Appendix 6, Fig. 2A, B: Nos 21, 22, 24). The assemblage of Přívklady displays a riparian character (Teodoridis 2006); therefore the BLDF predicted by IPR vegetation analysis as possible zonal vegetation equivalent is unacceptable and represents more probably an “azonal” vegetation type occupying wet soils. The Břešťany flora includes a relatively high value of

SCL+LEG component (legumes, *Myrica*, *Berberis*, *Mahonia*, *Pungiphyllum*) that could cause the low value of BLE. Teodoridis & Kvaček (2006) suppose a zonal Evergreen Broad-leaved Forest type mixed with pine stands for areas outside the basin (sandy and micaceous facies) for the sites within the Libkovice Member; however, the assemblage of the Břešťany Clay is more azonal because it is characterized by a mixture of azonal elements and Mixed Mesophytic Forest elements and thus belongs to the MMF type. According to the proportion of entire and dentate (non-entire) leaf morphotypes/species (40% vs 60%) and the floristic composition, Bůžek *et al.* (1996) presumed an ecotonal vegetation of the Notophyllous Evergreen Broad-leaved Forest and the Mixed Mesophytic Forest *sensu* Wolfe (1979) as a modern living analogue for the mesophytic forests of the Cypris Formation (Shale). Knobloch & Kvaček (1976) reported the same living analogues for Wackersdorf. The middle Miocene sites of Horní Bříza and Klettwitz 12 as well as the late Miocene site of Moravská Nová Ves are characterized by the decreasing BLE component in favour of BLD elements (Appendix 6, Fig. 2A, B: Nos 31, 32). The results of the IPR vegetation analysis classify these assemblages as the vegetation types of MMF, BLDF and the ecotone of MMF/BLDF.

According to Teodoridis *et al.* (in press), the results derived from the Pliocene of the Vonšov Member (Pluto Clay) and the Nová Ves Member (Nero Clay) show a relatively high abundance of arboreal elements (BLD component 81% and 80%, BLE component 15% and 12%), associated with relatively low values for zonal herbs (33% and 39%). Such proportions of the key components correspond more or less to those for BLDF vegetation types (Appendix 6, Fig. 2A, B: Nos 34, 36). The values of the zonal herb component exceed 30% (the threshold for the BLDF vegetation types according to Teodoridis *et al.* 2011b). The sites from the Tachov (Cheb–Domažlice) Graben show almost identical results, where the values of BLD, BLE and zonal herb components are 83%, 15%, and 33%, respectively (Fig. 2A, B: No. 33). The result of Kaltensundheim (BLD 89% and BLE 11%), which corresponds to the vegetation type of BLDF, can be partly influenced by a very low number of zonal woody angiosperms (only 10) – see Teodoridis *et al.* (2011a) and Appendix 6, Fig. 2B: No. 35. However, the parameters of DRY HERB and MESO HERB (46% and 21%, respectively) are more reliable, because they are calculated based on the total number (*i.e.* 57) of zonal elements. The results of the IPR vegetation analysis correspond to syntaxonomical results previously published by Bůžek *et al.* (1985), where the assemblages of the Vonšov Mb. and the Tachov Graben were interpreted as mesic Mixed Coniferous and Broad-leaved Deciduous Forests with a predominance of Pinaceae overlapping into azonal riparian and swampy vegetation types characterized by

Cupressaceae, Betulaceae, *Pterocarya*, *Liquidambar*, *Nyssa*, and by abundant wetland herbaceous elements (*e.g.*, Ericaceae, Polypodiaceae, *Osmunda*, *Sparganium*). The late Pliocene floras of Kranichfeld, Berga and Gerstungen from Thuringia show results close to the assemblages of the Vildštejn Formation (Appendix 6, Fig. 2A, B: Nos 37, 38). The BLD, BLE, SCL+LEG components allow the assemblages to be assigned to the vegetation types of BLDF (Berga), MMF/BLDF (Kranichfeld) or MMF (Gerstungen); however, the ZONAL herbs components exceed 40% at the Berga and Kranichfeld sites. The late Pliocene sites of the Nová Ves Member (Fig. 2A, B: Nos 39, 41), and Rippersroda (Fig. 2B: No. 40) are characterized by a distinct increase in relative diversity of the zonal herb component, generally exceeding 39%. These herbaceous elements are associated with taxa of the SCL+LEG component in the Nová Ves Member only, which are represented by relatively high numbers (10% to 7%), and with BLD and BLE elements in the following percentages: 75%, 83%, 94% (Rippersroda) and 15%, 10% and 7%. The assignment of the studied assemblages from the lignite beds of the Nová Ves Member to particular vegetation types is equivocal and may correspond to three possible types – Xeric Grasslands or Steppe, transitional vegetation of BLDF/MMF and/or vegetation of MMF. The assemblage of Rippersroda shows an affinity to an open BLDF vegetation type and/or Xeric Grasslands or Steppe. The studied sites from the upper part of the Nová Ves Member have been excluded from the analysis because of the low number of zonal angiosperms elements (only 7). For the same reason, the assemblage of Nordhausen (Thuringia, Fig. 2B: No. 42) is also neglected. They may correspond to open BLDF vegetation type and/or xeric grassland or steppe.

The more open forest environments of the BLDF or MMF vegetation types with high abundances of DRY HERB component exceeding the threshold of 40% for the xeric grasslands or steppe vegetation type (*e.g.*, Kovar-Eder *et al.* 2008) have been predicted by the IPR vegetation analysis for most studied late Pliocene to early Pleistocene assemblages (Appendix 6). This type of vegetation was corroborated by phytosociological interpretations published by Bůžek *et al.* (1985) and Mai & Walther (1988). Bůžek *et al.* (1985, fig. 4.3) characterized vegetation of the Nová Ves Member (lignite beds) as mesotrophic transitional moor with Cyperaceae, *Scheuchzeria*, *Menyanthes* associated with *Pinus cf. spinosa*, overlapping in its oligotrophic areas to vegetation dominated by Ericaceae (*Andromeda polifolia*, *Chamaedaphne calyculata*, *Oxycoccus*) and in alluvial parts to forest vegetation characterized by *Picea omoricoides* and *Chamaecyparis cf. pisifera*. Analogous modern vegetation types are *e.g.*, the Northern broad-leaved and Weymouth Pine forests in the USA (Knapp 1965, p. 85), the wet rock habitats with *Picea omorika* in the Drina valley at 800–1000 m alt. in Bosnia

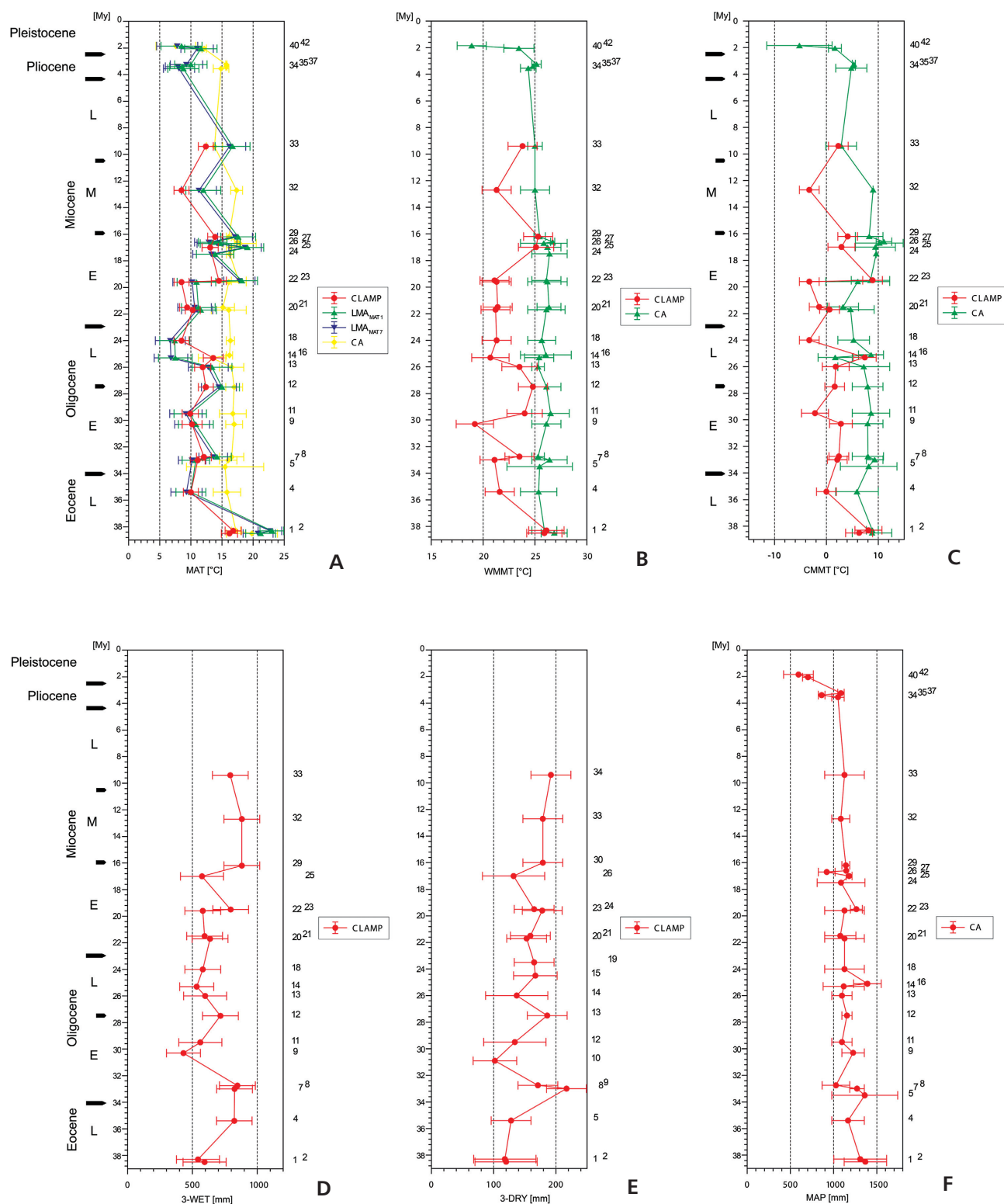
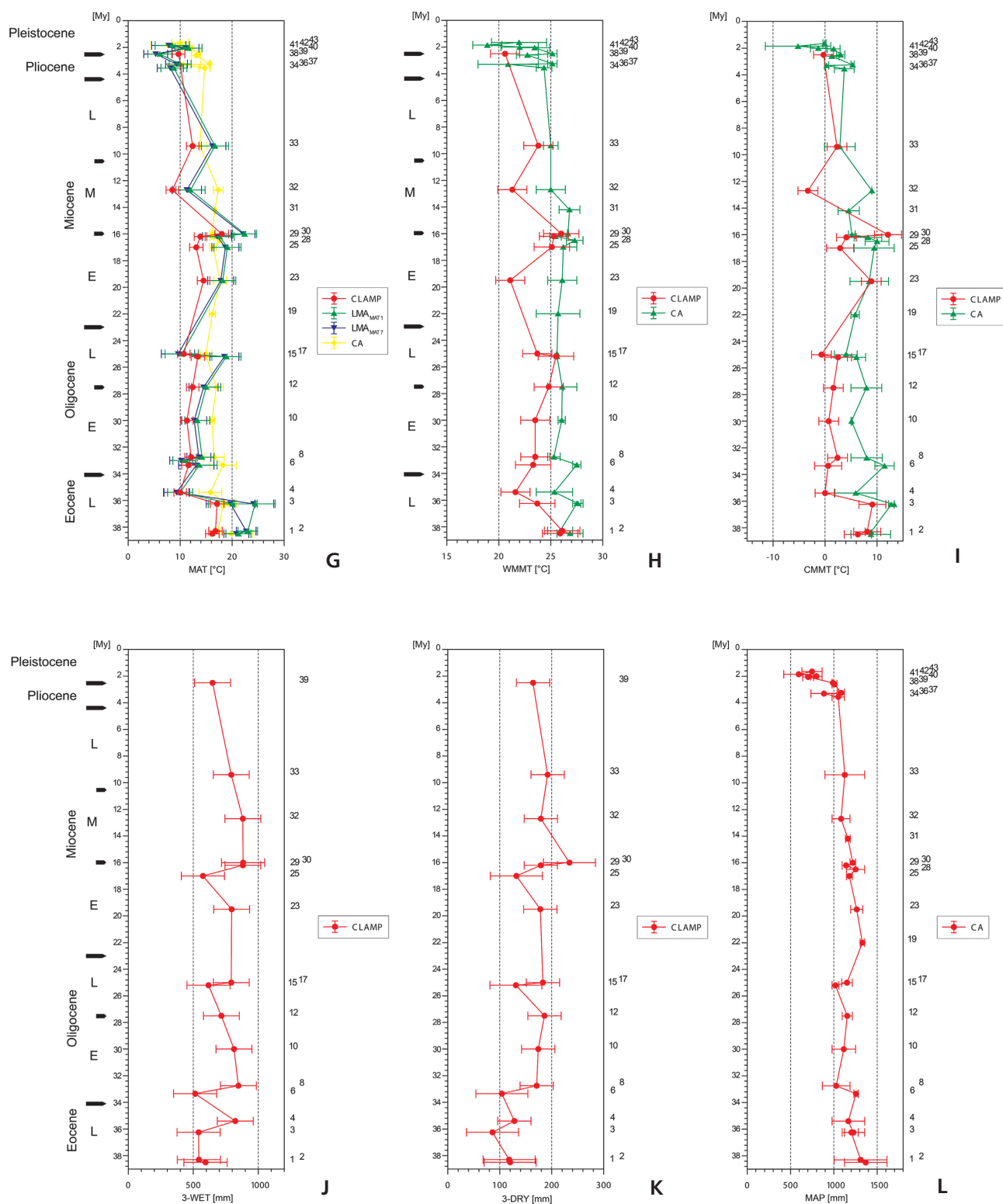


Figure 3. Palaeoclimatic changes and trends within the studied parameters derived from the Climate Leaf Analysis Multivariate Program (CLAMP), Leaf Margin Analysis (LMA) and Coexistence Approach (CA) techniques based on selected floras/sites from Central Europe (A–F) and Bohemian Massif (G–L). Dataset source (Appendices 7, 8). Abbreviations and symbols: MAT (mean annual temperature), WMMT (warmest month mean temperature), CMMT (coldest month mean temperature), 3-WET (precipitation during 3 consecutive wettest months), 3-DRY (precipitation during 3 consecutive driest months), and MAP (mean annual precipitation); sites: 1. Staré Sedlo, 2. Kučlín, 3. Haselbach and Knau (Haselbach FA – CLAMP), 4. Roudný, 5. Valeč, 6. Haselbach, 7. Bechlejovice, 8. Kundračice, 9. Holý Kluk, 10. Seifenhennersdorf, 11. Knížecí-Hrazený, 12. Sulečice–Berand,



13. Markvartice–Veselíčko, 14. Matřý, 15. Kleinsaubernitz, 16. Počerný–Podlesí, 17. Bockwitz, 18. Hlavačov Gravel and Sand, 19. Brandis, 20. Čermníky, 21. Holeděč, 22. Přivlaky, 23. Břešťany, 24. Kunderatice–Jezeří (micaceous facies), 25. Cypris Formation, 26. Horní Litvínov–Mariánské Radčice, 27. Hrádek/N. (Kristina Mine), 28. Berzdorf 1 (Wiesa), 29. Mydlovary Formation, 30. Wackersdorf, 31. Berzdorf 2 (Kleinleipisch), 32. Horní Bříza, 33. Moravská Nová Ves, 34. Tachov Graben, 35. Vonšov Mb. (Vildštejn Formation) – Pluto Clay, 36. Kaltensundheim, 37. Nová Ves Mb. (Vildštejn Formation) – Nero Clay, 38. Kranichfeld, 39. Berga, 40. Nová Ves Mb. (Vildštejn Formation) – lignite beds, 41. Rippersroda, 42. Nová Ves Mb. (Vildštejn Formation) – upper part, 43. Nordhausen.

and Herzegovina and Serbia (Horvat *et al.* 1974), and/or the lowland peat bogs with *Chamaedaphne calyculata* in Finland (Overbeck 1975). The vegetation of the upper beds of the Nová Ves Mb. represents a coniferous forest vegetation type dominated by pines (*Pinus* cf. *halepensis*, *Pinus* cf. *sylvestris*) in association with *Picea omoricoides*, *Abies* sp., and *Juniperus* cf. *communis*. The forest probably overlapped with riparian vegetation with *Alnus* cf. *rugosa* and *Salix* and moor and aquatic vegetation with *Menyanthes* cf. *trifoliata*, *Elatine alsinastrum*, *Andromeda polifolia*, *Artemisia*, Cyperaceae *etc.* This vegetation type is comparable with modern vegetation known from the Taiga zone (Bůžek *et al.* 1985).

Palaeoclimatic analyses

The temperature and precipitation estimates from of palaeoclimatic analyses for 54 sites studied are presented in Appendices 5, 7, 8 and Fig. 3A–L (see also Teodoridis *et al.* 2012 and Kvaček *et al.* 2014). The late Eocene estimates (Appendices 5, 7, 8; Fig. 3A–L: Nos 1–4) except Roudníky (Fig. 3A–L: No. 4) show comparable results for all the used palaeoclimatic techniques – MAT: 16.2–17.1 °C (CLAMP), 22.1 °C (LMA_{MAT 1–9} – averaged value), 15.7–23.9 °C (CA); WMMT: 23.7–26.1 °C (CLAMP), 24.7–28.1 °C (CA); CMMT: 6.3–9.1 °C (CLAMP), 5–13.3 °C (CA); 3-WET: 54–59 mm (CLAMP); 3-DRY: 9–12 mm (CLAMP); and MAP: 1003–1613 mm (CA). The results of LMA from Haselbach, Klaus, Knau and Český Chloumek have been excluded because of the limited number of available taxa (9, 10 and 13) and values of the sampling errors (SE_{1 MAT}, SE_{2 MAT}) exceeding 3.9 °C (Appendix 5). The employed techniques have unequivocally proved for the latest Eocene site of Roudníky a decreasing trend in all studied parameters – MAT: 10.0 °C (CLAMP), 9.1 °C (LMA_{MAT 1–9} – averaged value), 13.6–18 °C (CA); WMMT: 21.6 °C (CLAMP), 23.6–27.1 °C (CA); CMMT: 0 °C (CLAMP), 1.8–10.0 °C (CA); 3-WET: 82 mm (CLAMP); 3-DRY: 12 mm (CLAMP); and MAP: 979–1355 mm (CA). An additional palaeoclimatic parameter of mean annual range of temperature (MART = WMMT – CMMT) based on the CLAMP estimates rose from 15.8 °C (Weisselester Basin s.l.) to 22.2 °C (Roudníky) and, based on the CA estimates, increased from 14.3 °C (Knau) to 19.5 °C (Roudníky).

Kvaček *et al.* (2014) described palaeoclimatic trends in the Bohemian Massif and Saxony during the early Oligocene as follows: The climatic proxies derived by CA for Valeč (the earliest Oligocene studied site) has a very approximate value due to the long range of the CA intervals (MAT and CMMT parameters exceeding 10 °C); however, it also shows a significant decreasing trend, in comparison with the late Eocene sites from the Bohemian Massif (*e.g.*,

difference of 4.3 °C in MAT parameter /CA/ compared with those of Staré Sedlo, 3.7 °C Haselbach, and 0.3 °C Roudníky /based on the studied late Eocene sites/ – Appendix 8). The mean value of MAT estimate for Valeč (15.5 °C) seems to be very low in comparison with the average value of MAT (17.7 °C) estimated for the early Oligocene floras of the Haselbach Series (*i.e.*, Haselbach, Regis and Beucha – Appendix 8). Therefore, the above-mentioned decrease in MAT at the late Eocene/early Oligocene boundary needs to be corrected by 2–3 °C. This MAT interval also corresponds to the averaged mean value of the MAT differences between the studied late Eocene assemblages and Valeč (2.6 °C). The correction results in better MAT estimates for Bechlejovice (mean value of MAT 16 °C /CA/, a MAT difference of 2.1 °C). Kvaček & Walther (2004) published palaeoclimatic estimates based on the CLAMP and CA analyses for Bechlejovice. These original values show warmer characteristics and have been re-evaluated using the expanded NLR's database (CA) as well the gridded meteorological reference datasets (see above). The obtained palaeoclimatic values for the other early Oligocene sites from the Bohemian Massif and Germany, *i.e.*, Haselbach, Bechlejovice, Kundratice, Hammerunterwiesenthal, Holý Kluk, Seifhennersdorf, Knížecí–Hrazený, Sulečice–Berand and Markvartice–Veselíčko, are similar (Appendices 5, 7, 8; Fig. 3A–L: Nos 6–13), corresponding to a general warming trend from the early to late Oligocene periods documented also by the palaeovegetation results (increase of the BLE elements). The LMA and CLAMP estimates are cooler than those resulting from CA (*i.e.*, Holý Kluk, Knížecí–Hrazený and late Oligocene site of Matřý). The averaged values of the palaeoclimatic parameters of the studied early Oligocene sites summarizing LMA, CLAMP and CA estimates (Appendices 5, 7, 8) are characterized as follows – MAT: 11.3 °C (CLAMP), 11.7 °C (LMA_{MAT 1–9}), 15.0–18.4 °C (CA); WMMT: 23.1 °C (CLAMP), 25.3–27.1 °C (CA); CMMT: 0.9 °C (CLAMP), 6.0–10.2 °C (CA); 3-WET: 66.3 mm (CLAMP); 3-DRY: 15.6 mm (CLAMP); and MAP: 1063–1245 mm (CA). The palaeoclimatic estimates for the late Oligocene follow the warming trend corroborated by the re-appearance of thermophilous elements (not always entire-margined leaf taxa) that cause an increase of MAT, CMMT and MAP values in the sites Matřý, Nerchau, Kleinsaubernitz and Počerný–Podlesí (Appendices 5, 7, 8; Fig. 3A–L: Nos 14–16). Even if the averaged values of the palaeoclimatic parameters of the late Oligocene sites are similar to those from the early Oligocene, *i.e.*, MAT: 13.5 °C (CLAMP), 12.3 °C (LMA_{MAT 1–9}), 13.4–16.3 °C (CA); WMMT: 23.1 °C (CLAMP), 23.3–26.7 °C (CA); CMMT: 5 °C (CLAMP), 3.3–7.7 °C (CA); 3-WET: 66.1 mm (CLAMP), 3-DRY: 17 mm (CLAMP) and MAP: 956–1330 mm (CA), the increase of MAT (CLAMP, LMA), CMMT (CLAMP, CA)

and MAP (CA) parameters is unequivocal. Palaeoclimatic estimates based on CLAMP and LMA derived from Bockwitz, Borna-Ost (Thierbach layers) and the Hlavačov Gravel and Sand (Fig. 3A–L: Nos 17, 18) show distinctly lower values when compared with the late Oligocene site of Kleinsaubernitz (Fig. 3A–C, F: No. 15). Differences in the mean values for Bockwitz, Borna-Ost and the Hlavačov Gravel and Sand are MAT (3.9 °C /CLAMP/, 10.4 °C /LMA/), WMMT (2.7 °C /CLAMP/) and CMMT (4.9 °C /CLAMP/). This trend may be caused by the azonal character of the studied assemblages (see above) and does not affect the results derived from CA, which show higher mean values of MAT (15.1–16.4), WMMT (25.1–26.2 °C) and almost the same values for CMMT (2.6–7.2 °C) compared to those of Kleinsaubernitz. The late Oligocene flora of Počerny–Podlesí, which is a mastixoid one (Holý 1984), gives higher CA estimates.

The mentioned differences between the CA and CLAMP temperature estimates are obviously caused by the “riparian effect” (Teodoridis 2004, Mach *et al.* 2014), with higher frequencies of non-entire margined foliage (typical of riparian vegetation) resulting in colder palaeoclimatic estimates based on the physiognomic techniques of LMA and CLAMP. On the other hand, distinctly higher values of MAT (18.6 °C /averaged/ and 14.6 °C), WMMT (25 °C) and CMMT (4.2 °C) estimated by LMA and CLAMP for the Oligo-Miocene site of Witznitz (see above) may be caused by low diversity of the plant assemblage (see Appendix 5). The “riparian” effect is also demonstrated in the early Oligocene site of Flörsheim (Germany), which is characterized by a high abundance of entire-margined and “large-sized” leaves of woody angiosperms caused by selective taphonomic processes (for details, see Kvaček 2004). Results of the IPR vegetation analysis (BLD 37.7%, BLE 52.4%, SCL+LEG 7.3%, ZONPLM 2.6%, DRY HERB 1%, MESO HERB 4.5% – for details see Appendix 4) are comparable with those of thermophilous assemblages of late Oligocene and early Miocene (Appendix 6). Hence, the LMA and CLAMP estimates, *i.e.* MAT (19.3 °C /averaged/ and 17.4 °C), WMMT (26.7 °C) and CMMT (7.5 °C), are much higher compared those from the isochronal sites of Markvartice–Veselíčko using the same reference dataset file containing 189 modern sites (Appendices 4, 5, 7) and also match the estimated intervals of CA – *i.e.*, MAT (15.6–16.9 °C), WMMT (25.6–28.1 °C), CMMT (5.6–10.0 °C) and MAP (979–1355 mm). The “cooling event” in late Oligocene and/or at the boundary of late Oligocene/early Miocene, which is usually connected with the re-appearance of deciduous elements under a humid warm temperate climate, may also be a consequence of the riparian effect characterized above.

The climate during the early Miocene was characterized by a gradual increase of temperature as revealed by the LMA, CLAMP and CA estimates. The previously studied

assemblages of Bitterfeld, Brandis, Čermníky and Holedeč (corresponding to the Whole Basin Swamp phase *sensu* Mach *et al.* 2014) are mainly azonal being bound to the coal and delta; therefore CLAMP and LMA estimates indicate lower temperatures. On the other hand, slight warming trends are recognizable, contrary to assemblages of the Thierbach layers and Mockrhena (Witznitz). Palaeoclimatic conditions during the early Miocene (Appendices 5, 7, 8; Fig. 3A–L: Nos 19–21) are characterized as follows – MAT: 9.4–11.6 °C (CLAMP), 10.8 °C (averaged LMA_{MAT 1–9}), 14.5–18.4 °C (CA); WMMT: 23.6–28.5 °C (CLAMP), 24.9–27.8 °C (CA); CMMT: –1.4–0.8 °C (CLAMP), 2.6–8.2 °C (CA); 3-WET: 64.4 mm (CLAMP), 3-DRY: 16.1 mm (CLAMP) and MAP: 1071–1323 mm (CA). The increasing warming has also been proved in the assemblages of the Břešťany Clay and the micaceous facies (Kundratice–Jezeří), which are characterized as follows: Břešťany – MAT: 14.5 °C (CLAMP), 17.1 °C (averaged LMA_{MAT 1–9}), 16.5–18.9 °C (CA); WMMT: 21.1 °C (CLAMP), 16.5–18.9 °C (CA); CMMT: 8.9 °C (CLAMP), 4.8–12.2 °C (CA); 3-WET: 76.5 mm (CLAMP), 3-DRY: 17.8 mm (CLAMP); MAP: 1194–1333 mm (CA); Kundratice, Jezeří (CA) – MAT: 15.7–16.8 °C, WMMT: 24.7–28.1 °C, CMMT: 9.6–9.6 °C, MAP: 810–1362 mm (Appendices 5, 7, 8; Fig. 3A–L: Nos 23, 24). The assemblage of Přívěky (Teodoridis 2006) includes riparian elements only; hence the CLAMP and LMA estimates derived from this site are distorted. The relevant CA results numerically corresponding to those of Holedeč and Čermníky possess also lower values (Appendices 5, 7, 8; Fig. 3A–L: No. 22), although the site of Přívěky is surely younger than that of Břešťany based on geochemical analysis (Mach *et al.* 2014). The above-mentioned climatic change, distinctly culminating during the late early Miocene in the Bohemian Massif and Saxony, is linked to an increase of atmospheric CO₂ concentration (Kürschner *et al.* 2008) during the deposition of stratigraphically comparable sediments within the Libkovice Member of the Most Formation. It was previously used to define the Early Miocene Optimum *sensu* Teodoridis & Kvaček (2006), which have recently been shifted on account of new results of palaeomagnetic analysis and cyclostratigraphy (Matys Grygar *et al.* 2013) to the time interval of 16.5 to 16.7 Ma (late Burdigalian or latest Karpatian – M4b, see Rögl *et al.* 2003). This time period corresponds to the beginning of the Miocene Climatic Optimum (*e.g.*, Zachos *et al.* 2001, Mach *et al.* 2014). The climatic optimum in the studied area is also linked to the above-mentioned increase of BLE elements (mastixioid floras). Generally, the climatic and vegetation effects are detected in the sites of Horní Litvínov–Mariánské Radčice, Wiesa, Cypris Formation, Hrádek/N. (Kristina Mine), Mydlovary Formation, Wackersdorf, Klettitz 3, Berzdorf 2 (Kleinleipisch) – see Appendices 5–8; Fig. 2: Nos 25–30; Fig. 3A–L: Nos

26–31. These assemblages produce comparable palaeoclimatic estimates derived from CLAMP, LMA, CA, *i.e.*, MAT: 13.1–18.0 °C (CLAMP), 15.8 °C (averaged LMA_{MAT 1–9}), 15.2–20.5 °C (CA); WMMT: 25.1–26.0 °C (CLAMP), 23.6–28.1 °C (CA); CMMT: 2.9–12.1 °C (CLAMP), 2.5–14.8 °C (CA); 3-WET: 77.9 mm (CLAMP), 3-DRY: 18.2 mm (CLAMP); and MAP: 823–1362 mm (CA). The climatic parameters are close to modern subtropical climatic conditions.

Subsequent climatic deteriorations, cooling trends expressed also in changes of vegetation (increase of BLD elements – Appendix 5) can be traced at various places in Central Europe at different time intervals. Hence, these changes seem to have had a diachronic character (Kvaček *et al.* 2006, Kovar-Eder *et al.* 2008) gradually starting during the middle Miocene. This diachronic cooling trend can be proved climatically by results of CLAMP and LMA from the studied assemblage of Horní Bříza, characterized by MAT: 8.5 °C and 11.0 °C (averaged LMA_{MAT 1–9}), WMMT: 21.3 °C, CMMT: –3.3 °C, 3-WET: 88.1 mm, and 3-DRY: 17.9 mm. On the other hand, the CA results from Horní Bříza and Klettwitz 12 (MAT: 16.4–18.3 °C and 15.7–16.3 °C, WMMT: 23.6–29.4 °C and 25.7 °C, CMMT: 9.0 °C and 4.7–6.2 °C, and MAP: 979–1187 mm and 979–1355 mm, respectively, show distinctly higher values, which better correspond to those of late early Miocene sites, such as Hrádek/N. (Kristina Mine) or Wiesa (*cf.* Appendices 5, 7, 8; Fig. 3A–L: No. 33 and Nos 27, 28). Therefore the physiognomic estimates are probably influenced again by the above-mentioned riparian effect.

A distinct decrease of mean temperature parameters and initial cooling trends were detected in the Paratethys area in South Moravia, namely in the late Miocene site of Moravská Nová Ves (Knobloch 1969, Doláková & Kováčová 2008; Fig. 3A–L: No. 33). There the climate estimates are characterized as MAT: 12.4 °C (CLAMP), 15.6 °C (averaged LMA_{MAT 1–9}), 12.5–15.1 °C (CA); WMMT: 23.8 °C (CLAMP), 24.3–25.7 °C (CA); CMMT: 2.3 °C (CLAMP), –0.1–5.8 °C (CA); 3-WET: 79.2 mm (CLAMP), 3-DRY: 19.2 mm (CLAMP); and MAP: 897–1355 mm (CA). They correspond in fact with much older early Oligocene sites in the České středohoří Mts (*e.g.*, Kundratice) except for the assemblages affected by the “riparian” effect. However, the CA results for the South Moravian area are distinctly colder and do not correspond to any of the sites from the Bohemian Massif and Saxony.

According to Teodoridis *et al.* (in press) the late Pliocene to early Pleistocene assemblages of the Vildštejn Formation in the Cheb Basin and the early Pliocene assemblages of the Tachov (Cheb–Domažlice) Graben (Appendices 5 and 8), together with the CA estimates from Lusatia, are characteristic for further palaeoclimatic development in Central Europe. The early Pliocene climate estimates from the Tachov (Cheb–Domažlice) Graben and

Kaltensundheim (Fig. 3A–C, F–I, L: Nos 34, 36) are characterized by MAT: 8.0 °C (averaged LMA_{MAT 1–9}), 13.6–15.8 °C (CA) and 7.2–13.9 °C; WMMT: 23.6–25.1 °C and 18.0–23.8 °C; CMMT: 1.8–5.6 °C and –0.1–0.7 °C; and MAP: 979–1122 mm and 735–1036 mm. Late Pliocene climatic conditions estimated by CA for the sites of the Vonšov Member (Pluto Clay) and Nová Ves Member (Nero Clay), Kranichfeld and Berga show slightly lower values – MAT: 12.2–15.8 °C, WMMT: 21.7–25.6 °C, CMMT: –0.1–5.6 °C, and MAP: 823–1122 mm (see Appendices 5, 7, 8; Fig. 3A–C, F–L: Nos 35, 37–39). However, these values are still comparable with those obtained from the studied sites of early Pliocene and late Miocene age (see Appendices 5, 7, 8). The assemblage of Berga has also been analysed by CLAMP and LMA techniques showing lower estimates (mainly in MAT parameter) – MAT: 9.7 °C and 5.4 °C (averaged LMA_{MAT 1–9}), WMMT: 20.6 °C, CMMT: –0.3 °C, 3-WET: 64.8 mm, and 3-DRY: 16.4 mm. A distinct cooling change is proved by CA and LMA estimates from the Nová Ves Member (lignite beds and upper part), Rippersroda and Nordhausen, which is characterized by averaged values of MAT 9.2 °C (averaged LMA_{MAT 1–9}), 7.4–11.0 °C (CA); WMMT: 19.0–22.9 °C; CMMT: –4.9–0.5 °C; and MAP: 596–831 mm (see Appendices 5, 8, Fig. 3A–C, F–L: Nos 40–43). The sites of the Nová Ves Member (lignite beds and upper part) provided data that are close to the present day situation with MAT of 7 °C and CMMT of about –3 °C. Only summer temperatures (WMMT) were slightly higher than the present day value of 16 °C (meteorological station of Cheb – Teodoridis *et al.* in press).

Discussion on palaeoenvironmental trends

The accuracy of the employed palaeoenvironmental approaches is apparently dependent on the accuracy of taxonomical analyses of studied plant assemblages (Appendix 1) even in those cases using leaf physiognomical traits. It is always necessary to recognize exactly the sets of elements used in the analyses. One conclusion is apparent from our studies: The geochronologically older and systematically more difficult plant fossils are, the less accurate the recognizable systematic units and their relationships become for their analyses and statistical evaluation (Kvaček 2007, Teodoridis *et al.* 2012). According to S.R. Manchester (*pers. comm.* 2015), it is also because leaves of thermophilic plants even today display more convergence and are very difficult to identify with confidence. The succession of the Cainozoic assemblages analysed by the same palaeovegetation and palaeoclimatic techniques offers an opportunity to discuss relative advantages and sensitivity of the individual methods and compare the obtained palaeoclimatic trends with generally accepted data (Zachos *et al.* 2001,

2008). We have focused on several palaeoenvironmental events such as the Eocene/Oligocene boundary, Oligocene warming trend, Early/Middle Miocene Climatic Optimum, and Pliocene and Pleistocene deterioration.

Zachos *et al.* (2001, 2008) characterized palaeoclimatically the Eocene period beginning with a significant peak of the Early Eocene Climatic Optimum (EECO, 52 to 50 Ma), which is expressed by a 1.5‰ decrease in $\delta^{18}\text{O}$. This event was followed by a 17 Ma-long trend towards cooler conditions (3.0‰ rise in $\delta^{18}\text{O}$), with many of the changes occurring during the early–middle Eocene (50 to 48 Ma) to the early Oligocene (35 to 34 Ma). The cooling trend is also proved in the studied area by the presented changes in palaeovegetation (enormous immigration of BLD (Arctotertiary) elements from Asia to Europe and a decrease of thermophilous BLE elements (see Appendix 6, Fig. 2), as well as a deterioration of the palaeoclimate during the late Eocene and/or at the boundary of late Eocene/early Oligocene (Appendices 5, 7, 8, Fig. 3) in the Bohemian Massif (*i.e.*, Staré Sedlo, Kučlín, Roudníky) as well as in Saxony (Knau, Haselbach and/or Böhlen – see Mosbrugger *et al.* 2005). As we note above, the floras from Saxony have serious problems of dating and makes comparison with those of Northern Bohemia speculative (Kunzmann *et al.* in press).

According to Kvaček *et al.* (2014), the published CA estimates of Böhlen from the Weissester Basin (37 Ma) show comparable palaeoclimatic estimates derived by CA (MAT: 15.6–19.9 °C, WMMT: 25.7–28.1 °C, CMMT: 7.1–12.3 °C and MAP: 1308–1355 mm) with those from Roudníky (Appendices 5, 7, 8). However, the CA estimates are equivocal, because they are based on 9 taxa only. The floristic character of Böhlen does not correspond to the mentioned trend in vegetation change and shows a mixture of coniferous and BLE elements (*Chamecyparites*, *Tetraclinis*, *Phoebe*, *Visnea*, and *Zenobia*), of which only *Tetraclinis* is shared with the contemporaneous flora of Roudníky (*cf.* Mai & Walther 2000, Kvaček *et al.* 2014). According to Zachos *et al.* (2001), the early Oligocene is characterized by cooling and a rapid expansion of Antarctic continental ice-sheets proved by a relatively high value of deep-sea $\delta^{18}\text{O}$ (2.5‰) corresponding to a bottom temperature of 4 °C. The ice sheets persisted until the latter part of the Oligocene (26 to 27 Ma), when a warming trend reduced the extent of Antarctic ice. Our palaeoclimatic estimates based on multi-technique analyses of terrestrial ecosystems within the Bohemian Massif and Saxony confirm this global palaeoclimatic trend and show distinct decreases in MAT, WMMT and CMMT (equalling to 2–4 °C) during the latest Eocene (Roudníky, Böhlen – see above) at the late Eocene/early Oligocene boundary. This event is also linked with the above-mentioned immigration of BLD elements and distinct decrease of BLE elements (Haselbach, Bechlejovice, Kundratice). In the next time

slice, the re-appearance of thermophilous elements (*e.g.*, palms) indicates a slight warming trend that started in the early Oligocene and continued throughout the Oligocene (Sulečice, Holý Kluk, Markvartice), culminating in the late Oligocene (mastixoid flora of Počerný–Podleší).

The “cooling event” in late Oligocene and/or at the boundary of late Oligocene/early Miocene, which is usually connected with the re-appearance of deciduous elements under a humid warm temperate climate, might be influenced by the specific physiognomic character of the riparian vegetation assemblages (non-entire leaf margin – *e.g.*, assemblages of the Thierbach layers, Hlavačův Gravel and Sand, see Appendices 5, 6 and 7 vs Appendix 8). This vegetation change and the climate deterioration has been predicted by Zachos *et al.* (2001), who call it as Mi-1 glacial event at the Oligocene–Miocene transition. Grein *et al.* (2013) noted, basing on study of stomatal density, cooling and high seasonality for Kleinsaubernitz and Bockwitz/Borna-Ost while temperatures increase towards the Oligocene/Miocene boundary (Witznitz), which corresponds to increase in number of months in the growing season (9, 7 vs 11). The fluctuation of seasonality is traceable also in our CLAMP estimates, when values of mean annual range of temperature (MART) decrease from 23 °C (Kleinsaubernitz) to 20.8 °C (Witznitz) – Appendix 7.

A gradual increase of temperature and precipitation is detected during the early Miocene and might be linked with a low amount of global ice volume in Antarctica and seawater temperature with the exception of several brief periods of glaciation (*e.g.* Zachos *et al.* 2001, 2008). This global warming trend continued and peaked in the Middle Miocene Climatic Optimum (17 to 15 Ma). This warming trend is expressed in vegetation of the studied area by a massive representation of thermophilous and later also palaeo-subtropical elements (*e.g.*, sites at Hrádek/N., Wiesa, Wackersdorf, Kleinleipisch) during the late early to middle Miocene. It defines, palaeobotanically, the beginning of the Middle Miocene Climatic Optimum during the latest early Miocene in the Bohemian Massif (Mach *et al.* 2014).

According to Zachos *et al.* (2001, 2008) a gradual cooling and reestablishment of a major ice-sheet on Antarctica is expressed by gently rising mean values of $\delta^{18}\text{O}$ through the late Miocene (10 Ma) until the early Pliocene (6 Ma) including an indication of additional cooling and small-scale expansion of the ice sheets on west-Antarctica and in the Arctic (Thiede & Vorren 1994). This event and/or cooling trend is linked to terrestrial ecosystems of the studied area with a distinct vegetation change characterized by a rapid rise of deciduous woody elements (Horní Bříza, Klettwitz 12, Moravská Nová Ves, the Vildštejn Formation and Lusatia – Appendices 5–8) from the late middle Miocene to early Pliocene. Belz & Mosbrugger (1994) reported a similar trend derived from the late Neogene sites of the Rhineland. During the early Pliocene Zachos *et al.* (2001)

noted a subtle warming until 3.2 Ma, when $\delta^{18}\text{O}$ again increased reflecting the onset of the Northern Hemisphere Glaciation (NHG). Similarly, this climatic event based on the isotopic analysis of deep-sea deposits, can be analogous to floristic/vegetation change characterized by appearance of more open vegetation assemblages, such as open forests with numerous herbaceous elements in the Bohemian Massif (assemblages of the Nová Ves Member) and Germany (Rippersroda, Nordhausen) – Appendix 6. This vegetation change approximately reflects the boundary between the late Pliocene and early Pleistocene. The climatic deterioration detected by CA estimates in the mentioned sites (Appendix 8) corresponds to the general palaeoclimate trends (Zachos *et al.* 2001, 2008).

Conclusions

Results of the IPR vegetation analysis (Appendix 6) and the employed palaeoclimatic techniques of LMA (Appendix 5), CLAMP (Appendix 7) and CA (Appendix 8) indicate that in the period from late Eocene to early Pleistocene several important vegetation and palaeoclimatic trends and changes took place in the Bohemian Massif, Saxony and Lusatia. These conform only partly to palaeoclimatic changes indicated by other sources. Three important points from this work are:

- 1) The known cooling event in the latest Eocene occurred in the northern part of central Europe slightly earlier than in the Paratethys. The Eocene/Oligocene boundary is thus not connected with a sharp environmental change in central Europe; contrary to southern Europe, warming trends from the early to late Oligocene are easily recognizable.
- 2) The cooling in late Oligocene/early Miocene is connected with the re-appearance of deciduous elements and linked with high seasonality in central Europe.
- 3) The Miocene Climatic Optimum in the Czech Republic started before the middle Miocene contrary to other parts of Europe and peaked in the middle Miocene; the late middle Miocene to early Pliocene cooling trend is well documented by the influx of deciduous forest elements.
- 4) The late Pliocene/early Pleistocene boundary, in the sense of the present chronostratigraphy, is connected with a stepwise decline in warm temperate forests and the appearance of cool temperate vegetation.

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Appendices 1–4. Available online on: <http://www.geology.cz/bulletin/contents/art1553>

Appendix 1. An overview of the studied floras from the Bohemian Massif and Saxony including summarized references with floristic, dating, and palaeoenvironmental results.

Appendix 2. List of plant taxa occurring in the studied floras and their scoring according to the IPR-vegetation analysis.

Appendix 3. Percentage scores for the foliar physiognomic characters of the studied fossil floras.

Appendix 4. Results of the IPR vegetation analysis, palaeoclimatic estimates based on Leaf Margin Analysis (LMA), Climate Leaf Analysis Multivariate Program (CLAMP) and Coexistence Approach (CA) for the fossil flora of Flörsheim including percentage scores for the foliar physiognomic characters.

Appendix 5. Palaeoclimatic estimates of mean annual temperature (MAT) derived from Leaf Margin Analysis (LMA) including sampling errors (SE_{1MAT} , SE_{2MAT}). Values of MAT and sampling errors are calculated using the presented equations. Symbols: n (total species number), P (proportion of n species with entire margin, $0 < P < 1$), c (slope of the MAT vs leaf margin regression, equals 30.6), and ϕ (dispersion factor, equals 0.052).

A – MAT (LMA 1) = $1.41 + 30.6 P$, ($r^2 = 0.98$) *sensu* Wolfe (1979) [$^{\circ}\text{C}$]; B – MAT (LMA 2) = $27.6 P + 1.038$, ($r^2 = 0.79$) *sensu* Su *et al.* (2010) [$^{\circ}\text{C}$]; C – MAT (LMA 3) = $28.6 P + 2.240$, ($r^2 = 0.94$) *sensu* Wilf 1997 [$^{\circ}\text{C}$]; D – MAT (LMA 4) = $29.1 P - 0.266$, ($r^2 = 0.76$) *sensu* Wilf 1997 [$^{\circ}\text{C}$]; E – MAT (LMA 5) = $31.6 P - 0.059$, ($r^2 = 0.89$) *sensu* Gregory-Wodzicki (2000) [$^{\circ}\text{C}$]; F – MAT (LMA 6) = $27.0 P - 2.120$, ($r^2 = 0.63$) *sensu* Greenwood *et al.* (2004) [$^{\circ}\text{C}$]; G – MAT (LMA 7) = $31.4 P + 0.512$, ($r^2 = 0.60$) *sensu* Traiser *et al.* (2005) [$^{\circ}\text{C}$]; H – MAT (LMA 8) = $29.0 P + 1.320$, ($r^2 = 0.91$) *sensu* Miller *et al.* (2006) [$^{\circ}\text{C}$]; I – MAT (LMA 9) = $30.6 P + 1.14$, ($r^2 = ?$) *sensu* Kowalski & Dilcher (2003) [$^{\circ}\text{C}$]; J – $SE_{1MAT} = c \sqrt{[P(1-P)/n]}$ *sensu* Wilf (1997); K – $SE_{2MAT} = \sqrt{([1 + \phi (n-1) P(1-P)] \times (P(1-P))/n)}$ *sensu* Miller *et al.* (2006).

Age	Studied floras	Leaf Margin Analysis (LMA)												
		n	P	A	B	C	D	E	F	G	H	I	J	K
early Pleistocene	Nová Ves Mb. (Vildštejn Formation) – upper part	15	0.23	8.5	7.5	8.9	6.5	7.3	6.8	7.8	8.1	8.3	3.2	3.3
	Nová Ves Mb. (Vildštejn Formation) – lignite beds	30	0.33	11.6	10.2	11.8	9.4	10.5	9.5	11.0	11.0	11.3	2.7	2.6
late Pliocene	Berga	23	0.15	6.1	5.2	6.6	4.2	4.7	4.6	5.3	5.7	5.8	2.4	2.3
	Nová Ves Mb. (Vildštejn Formation) – Nero Clay	43	0.28	10.0	8.7	10.2	7.9	8.8	8.0	9.3	9.4	9.7	2.3	2.1
	Vonšov Mb. (Vildštejn Formation) – Pluto Clay	43	0.24	8.6	7.5	9.0	6.6	7.4	6.9	7.9	8.2	8.4	2.1	2.0
early Pliocene	Tachov Graben	27	0.24	8.8	7.7	9.1	6.7	7.5	7.0	8.1	8.3	8.5	2.5	2.5
late Miocene	Moravská Nová Ves	35	0.50	16.7	14.8	16.5	14.3	15.8	14.0	16.2	15.8	16.4	2.8	2.6
middle Miocene	Horní Břiza	29	0.34	12.0	10.6	21.1	9.8	20.8	9.8	11.3	11.3	11.7	2.7	2.8
early Miocene	Wackerdorf	50	0.69	22.5	20.0	21.9	19.7	21.7	19.1	22.1	21.3	22.2	2.0	2.3
	Mydlovary Formation	35	0.53	17.6	15.6	17.4	15.1	16.6	14.8	17.1	16.6	17.3	2.6	2.8
	Hrádek/N. (Kristina Mine)	60	0.39	13.5	11.9	13.5	11.2	12.4	11.2	12.9	12.8	13.2	1.9	2.3
	Horní Litvínov–Mariánské Radčice	23	0.43	14.7	13.0	14.7	12.4	13.7	12.3	14.2	13.9	14.4	3.1	3.2
	Cypris Formation	44	0.58	19.1	17.0	18.9	16.6	18.3	16.2	18.7	18.1	18.9	2.2	2.6
	Kundratice–Jezeří (micaceous facie)	27	0.41	13.9	12.3	13.9	11.6	12.8	11.5	13.3	13.1	13.6	2.9	3.0
	Břešťany	50	0.55	18.2	16.2	18.0	15.7	17.3	15.4	17.8	17.3	18.0	2.2	2.5
	Přívlačky	21	0.31	10.9	9.6	11.1	8.7	9.7	8.9	10.2	10.3	10.6	3.1	3.1
	Holedeč	29	0.32	11.3	9.9	11.4	9.1	10.1	6.2	10.6	10.6	11.0	2.7	2.7
	Čermníky	40	0.33	11.6	10.2	11.8	9.4	10.5	9.5	11.0	11.0	11.3	2.3	2.5
	Bitterfeld	14	0.36	12.3	10.9	12.5	10.1	11.2	10.2	11.7	11.7	12.1	3.8	3.9
late Oligocene / early Miocene	Witznitz	15	0.60	19.8	17.6	19.4	17.2	18.9	16.7	19.4	18.7	20.5	3.8	3.9
	Hlavačov Gravel and Sand	25	0.20	7.4	6.4	7.8	5.4	6.1	5.8	6.7	7.0	7.1	2.4	2.4
late Oligocene	Borna-Ost	17	0.18	6.8	5.9	7.3	4.9	5.5	5.3	6.1	6.4	6.5	2.7	2.8
	Bockwitz	19	0.29	10.3	9.0	10.5	8.2	9.1	8.3	9.6	9.7	10.0	3.1	3.2
	Kleinsaubernitz	35	0.57	18.9	16.9	18.6	16.4	18.0	16.0	18.5	18.0	18.7	2.6	2.8
	Matřý	20	0.20	7.5	6.6	8.0	5.6	6.3	5.9	6.8	7.1	7.3	2.7	2.7
early Oligocene	Markvartice–Veselíčko	23	0.39	13.4	11.8	13.4	11.1	12.3	11.1	12.8	12.7	13.1	3.1	3.2
	Sultice–Berand	36	0.44	15.0	13.3	15.0	12.7	14.0	12.5	14.5	14.2	14.8	2.5	2.8

Age	Studied floras	Leaf Margin Analysis (LMA)												
		n	P	A	B	C	D	E	F	G	H	I	J	K
early Oligocene	Knížecí–Hrazený	29	0.28	9.9	8.7	10.1	7.8	8.7	8.0	9.2	9.3	9.6	2.6	2.6
	Seifhennersdorf	49	0.39	13.3	11.7	13.3	11.0	12.2	11.0	12.7	12.6	13.0	2.1	2.4
	Holý Kluk	26	0.31	10.8	9.5	11.0	8.7	9.7	8.8	10.2	10.2	10.6	2.7	2.8
	Kundratice	61	0.42	14.2	12.6	14.2	11.9	13.2	11.8	13.6	13.4	13.9	1.9	2.3
	Bechlejovice	52	0.31	10.8	9.5	11.0	8.7	9.7	8.8	10.2	10.2	10.6	2.0	2.2
	Haselbach 1, Beucha (Haselbach FA)	20	0.40	13.7	12.1	13.7	11.4	12.6	11.3	13.1	13.0	13.4	3.3	3.4
late Eocene	Roudniky	34	0.28	10.0	8.7	10.2	7.9	8.8	8.1	9.3	9.4	9.7	2.5	2.4
	Knau	10	0.75	24.4	21.7	23.7	21.6	23.6	20.8	24.1	23.1	24.1	4.2	3.9
	Klausau	13	0.65	21.4	19.1	21.0	18.8	20.6	18.2	21.0	20.3	21.1	4.0	3.9
	Haselbach (Zeitz Sand)	9	0.61	20.1	17.9	19.7	17.5	19.3	17.0	19.7	19.0	19.8	5.0	4.7
	Haselbach, Klausau, Knau (Zeitz Floristic Assemblage /FA/)	18	0.69	22.7	20.2	22.1	19.9	21.9	19.3	22.3	21.5	22.4	3.3	3.3
	Kučlín	78	0.71	23.0	20.5	22.4	20.3	22.2	19.6	22.7	21.8	22.7	1.6	1.9
	Staré Sedlo	44	0.65	21.2	18.9	20.8	18.6	20.4	18.0	20.8	20.1	21.0	2.2	2.4
	Český Chloumek	13	0.65	21.4	19.1	20.9	18.8	20.6	18.2	21.0	20.3	21.1	4.0	3.9
	Nový Kostel	18	0.81	26.1	23.3	25.3	23.2	25.4	22.3	25.8	24.7	25.8	2.9	2.7

Appendix 6. Results of the IPR vegetation analysis from the studied floras of Bohemian Massif and Saxony from late Eocene to Plio-Pleistocene. Percentages of the BLD (broad-leaved deciduous woody angiosperms), BLE (broad-leaved evergreen woody angiosperms), SCL+LEG (sclerophyllous woody and legume-like woody angiosperms), DRY HERB (open woodland and grassland elements), MESO HERB (mesophytic forest undergrowth elements) components were calculated following the equations published in Kovar-Eder *et al.* (2008). Abbreviations: BLDF (temperate to warm-temperate broad-leaved deciduous forests), MMF (warm-temperate to subtropical mixed mesophytic forests), BLEF (subtropical broad-leaved evergreen forests), BLDF/MMF (ecotone vegetation between BLDF and MMF), and BLEF/MMF (ecotone vegetation between BLEF and MMF).

A – % of BLD; B – % of BLE; C – % of SCL + LEG; D – ZONPALM; E – % DRY HERB; F – % MESO HERB; G – % of ZONAL herbs

Age	Localities	IPR-vegetation results							Vegetation type <i>sensu</i> Teodoridis <i>et al.</i> (2011b)
		A	B	C	D	E	F	G	
early Pleistocene	Nordhausen	85.71	14.29	0.00	0.00	41.17	27.93	69.11	? BLDF (open forests), Xeric grasslands or steppe
	Nová Ves Mb. (Vildštejn Formation) – upper part	83.21	10.22	6.57	0.00	14.40	24.92	39.32	? BLDF (open forests)
	Rippersroda (Perrier-Rippersroda FA)	93.85	6.15	0.00	0.00	29.99	21.41	51.40	? BLDF (open forests), Xeric grasslands or steppe
	Nová Ves Mb. (Vildštejn Formation) – lignite beds	75.00	14.76	10.24	0.00	13.20	30.22	43.41	? BLDF/MMF (open forest) or ? MMF (open forest), Xeric grasslands or steppe
late Pliocene	Berga	91.22	5.94	2.84	0.00	29.27	16.22	45.50	? BLDF (open forest), Xeric grasslands or steppe
	Kranichfeld	76.19	19.50	4.76	0.00	25.42	22.69	48.12	? MMF/BLDF (open forest), Xeric grasslands or steppe
	Gerstungen	72.22	25.00	2.78	0.00	11.80	7.85	19.65	MMF
	Nová Ves Mb. (Vildštejn Formation) – Nero Clay	80.08	12.10	7.82	0.00	13.88	25.15	39.03	? BLDF (open forest)
	Vonšov Mb. (Vildštejn Formation) – Pluto Clay	80.99	15.17	3.84	0.00	10.79	22.49	33.28	? BLDF (open forest)
early Pliocene	Kaltensundheim (Ceyssac FA)	89.47	10.53	0.00	0.00	46.07	20.91	66.98	? BLDF (open forests), Xeric grasslands or steppe
	Tachov Graben	82.62	14.77	2.61	0.00	8.72	24.12	32.84	? BLDF (open forest)
late Miocene	Moravská Nová Ves	74.60	12.70	12.70	0.00	0.91	3.68	4.89	BLDF/MMF
middle Miocene	Klettitz 12 (Schipkau FA)	81.85	15.75	2.40	0.00	17.30	13.86	31.16	BLDF
Miocene	Horní Bříza	61.90	20.00	14.29	3.81	0.00	0.00	0.00	MMF

Age	Localities	IPR-vegetation results							Vegetation type <i>sensu</i> Teodoridis <i>et al.</i> (2011b)
		A	B	C	D	E	F	G	
early Miocene / middle Miocene	Klettwitz 3 (Klettwitz FA)	53.68	40.24	6.80	0.00	10.38	15.21	25.60	BLEF
	Berzdorf 2. Kleinleipisch (Kleinleipisch FA)	45.40	46.79	7.81	0.00	3.29	14.30	17.58	BLEF
early Miocene	Wackersdorf	52.99	42.62	3.98	0.40	0.60	2.40	2.64	BLEF
	Mydlovary Formation	45.76	43.17	11.70	0.00	1.72	3.43	5.15	BLEF
	Hrádek/N. (Kristina Mine)	31.65	65.01	3.33	0.00	0.93	4.45	5.38	BLEF
	Berzdorf 1. Wiesa – Wiesa FA	45.61	48.59	5.80	0.00	2.29	11.49	13.79	BLEF
	Cypris Formation	58.61	33.75	7.64	0.00	0.00	2.99	2.99	MMF/BLEF
	Horní Litvínov–Mariánské Radčice	32.89	56.58	10.53	0.00	0.00	0.00	0.00	BLEF
	Kundratice–Jezeří (micaceous facie)	37.57	51.62	10.81	0.00	0.00	4.26	4.26	BLEF
	Přívlačky	84.13	9.52	6.35	0.00	0.00	0.00	0.00	BLDF
	Břešťany	56.85	23.97	16.44	2.74	0.00	0.00	0.00	MMF
	Brandis (Brandis FA)	34.29	62.86	0.00	2.86	1.72	6.94	8.66	BLEF
	Holedeč	73.47	8.22	18.31	0.00	0.00	0.00	0.00	MMF
	Čermníky	64.42	20.39	15.19	0.00	0.00	0.00	0.00	MMF
early Miocene / late Oligocene	Bitterfeld (Bitterfeld FA)	56.95	40.00	3.50	0.00	2.49	17.50	19.99	BLEF
	Witznitz (Mockrhena–Witznitz FA)	22.35	77.65	0.00	0.00	0.00	0.00	0.00	BLEF
	Mockrehna (Mockrhena–Witznitz FA)	53.13	42.69	4.19	0.00	0.00	12.77	12.77	BLEF
late Oligocene	Hlavačov Gravel and Sand	74.70	18.70	7.23	0.00	0.00	0.00	0.00	BLDF/MMF
	Borna-Ost (Thierbach FA)	57.23	42.77	0.00	0.00	0.00	3.79	3.79	BLEF
	Bockwitz (Thierbach FA)	66.67	30.30	3.30	0.00	0.75	5.28	6.20	BLEF/MMF, MMF
	Počerny–Podleší	33.33	66.67	0.00	0.00	0.00	0.00	0.00	BLEF
	Kleinsaubernitz	49.02	48.37	2.61	0.00	0.70	1.77	2.47	BLEF
early Oligocene	Matrý	80.95	19.50	0.00	0.00	0.00	0.00	0.00	BLDF
	Markvartice–Veselíčko	60.47	39.53	0.00	0.00	0.00	2.00	2.00	MMF/BLEF
	Sulečice–Berand	50.36	33.89	15.75	0.00	0.00	0.00	0.00	MMF/BLEF
	Nerchau	17.27	76.58	6.15	0.00	0.00	18.19	18.19	BLEF
	Knížecí–Hrazený	60.78	35.29	3.92	0.00	0.00	0.00	0.00	MMF/BLEF
	Seifhennersdorf	59.44	33.54	5.10	1.92	0.00	2.65	2.60	MMF/BLEF
	Hammerunterwiesenthal	54.64	36.08	3.90	6.19	0.00	0.00	0.00	MMF/BLEF
	Holý Kluk	64.56	29.90	6.36	0.00	0.00	3.56	3.56	MMF
	Kundratice	58.37	35.29	6.34	0.00	0.00	0.84	0.84	MMF/BLEF
	Bechlejovice	62.51	26.60	9.92	0.93	0.00	3.64	3.64	MMF
late Eocene	Haselbach (Haselbach Floristic Assemblage /FA/)	50.03	42.48	4.26	3.23	2.90	4.35	7.25	BLEF
	Roudníky	59.09	28.79	12.12	0.00	0.00	0.00	0.00	MMF
	Kayna-Süd	18.42	81.58	0.00	0.00	0.00	11.36	11.36	BLEF
	Klaus	23.53	64.71	0.00	11.76	0.00	5.41	5.41	BLEF
	Profen	21.43	76.79	0.00	1.79	0.00	0.00	0.00	BLEF
	Haselbach (Zeitz Sand)	12.96	79.63	0.00	7.41	0.00	4.69	4.69	BLEF
	Kučlín	45.81	40.65	12.26	1.29	0.81	2.64	3.45	BLEF
	Staré Sedlo	25.00	59.21	2.63	13.61	0.00	3.37	3.37	BLEF
	Český Chloumek	21.88	65.63	0.00	6.91	0.00	0.00	0.00	BLEF
	Nový Kostel	33.90	66.10	0.00	0.00	0.00	0.00	0.00	BLEF

Appendix 7. Palaeoclimatic estimates based on Climate Leaf Analysis Multivariate Program (CLAMP) for the studied floras from the Bohemian Massif, Saxony and Lusatia. Abbreviations: MAT (mean annual temperature), WMMT (warmest month mean temperature), CMMT (coldest month mean temperature), 3-WET (precipitation during 3 consecutive wettest months) and 3-DRY (precipitation during 3 consecutive driest months). Values of the STDEV are presented in brackets by the estimates.

Age	Studied floras	CLAMP calibration datasets	Palaeoclimatic estimates (CLAMP)				
			MAT [°C] (STDEV)	WMMT [°C] (STDEV)	CMMT [°C] (STDEV)	3-WET [cm] (STDEV)	3-DRY [cm] (STDEV)
late Pliocene	Berga	144	9.7 (1.2)	20.6 (1.4)	−0.3 (1.9)	64.8 (13.8)	16.4 (3.2)
late Miocene	Moravská Nová Ves	144	12.4 (1.2)	23.8 (1.4)	2.3 (1.9)	79.2 (13.8)	19.2 (3.2)
middle Miocene	Horní Břiza	144	8.5 (1.2)	21.3 (1.4)	−3.3 (1.9)	88.1 (13.8)	17.9 (3.2)
early Miocene	Wackersdorf	189	18.0 (1.3)	26.0 (1.7)	12.1 (2.6)	88.3 (16.6)	23.4 (5.0)
	Mydlovary Formation	144	13.9 (1.2)	25.3 (1.4)	4.1 (1.9)	88.1 (13.8)	17.9 (3.2)
	Cypris Formation	189	13.1 (1.3)	25.1 (1.7)	2.9 (2.6)	57.4 (16.6)	13.2 (5.0)
	Přívlaky	144	8.5 (1.2)	21.3 (1.4)	−3.3 (1.9)	58.0 (13.8)	16.5 (3.2)
	Břešňany	144	14.5 (1.2)	21.1 (1.4)	8.9 (1.9)	79.5 (13.8)	17.8 (3.2)
	Holedeč	144	9.4 (1.2)	21.4 (1.4)	−1.4 (1.9)	59.4 (13.8)	15.9 (3.2)
	Čermnínky	144	10.3 (1.2)	21.2 (1.4)	0.6 (1.9)	63.6 (13.8)	15.3 (3.2)
	Bitterfeld	144	11.6 (1.2)	20.6 (1.4)	0.8 (1.9)	70.2 (13.8)	17.1 (3.2)
late Oligocene / early Miocene	Witznitz	189	14.6 (1.3)	25.0 (1.7)	4.2 (2.6)	57.2 (16.6)	11.0 (5.0)
	Hlavačov Gravel and Sand	144	8.5 (1.2)	21.3 (1.4)	−3.3 (1.9)	58.0 (13.8)	16.5 (3.2)
late Oligocene	Borna-Ost	144	9.4 (1.2)	23.5 (1.4)	−3.2 (1.9)	78.3 (13.8)	20.5 (3.2)
	Bockwitz	144	10.7 (1.2)	23.7 (1.4)	−0.7 (1.9)	79.2 (13.8)	18.3 (3.2)
	Kleinsaubernitz	189	13.4 (1.3)	25.5 (1.7)	2.5 (2.6)	61.7 (16.6)	13.1 (5.0)
	Matrý	173	13.6 (1.6)	20.7 (1.8)	7.4 (2.2)	53.3 (13.1)	16.7 (3.5)
early Oligocene	Markvartice–Veselíčko	189	11.9 (1.3)	23.5 (1.7)	1.8 (2.6)	59.8 (16.6)	13.7 (5.0)
	Sulečice–Berand	144	12.4 (1.2)	24.8 (1.4)	1.6 (1.9)	71.6 (13.8)	18.6 (3.2)
	Knížecí–Hrazený	189	9.9 (1.3)	24.0 (1.7)	−2.2 (2.6)	56.1 (16.6)	13.4 (5.0)
	Seifhennersdorf	144	11.3 (1.2)	23.5 (1.4)	0.7 (1.9)	81.3 (13.8)	17.4 (3.2)
	Holý Kluk	173	10.2 (1.6)	19.2 (1.8)	2.8 (2.2)	43.1 (13.1)	10.2 (3.5)
	Hammerunterwiesenthal	144	11.3 (1.2)	25.4 (1.4)	−1.5 (1.9)	66.4 (13.8)	18.0 (3.2)
	Kundratice	144	12.1 (1.2)	23.5 (1.4)	2.4 (1.9)	84.7 (13.8)	17.1 (3.2)
	Bechlejovice	144	11.1 (1.2)	21.1 (1.4)	2.1 (1.9)	82.5 (13.8)	21.7 (3.2)
	Haselbach, Beucha (Haselbach FA)	189	11.6 (1.3)	23.3 (1.7)	0.6 (2.6)	51.4 (16.6)	10.4 (5.0)
late Eocene	Roudníky	144	10.0 (1.2)	21.6 (1.4)	0.0 (1.9)	82.3 (13.8)	12.8 (3.2)
	Haselbach, Klaus, Knau (Zeitz Floristic Assemblage /FA/)	189	17.1 (1.3)	23.7 (1.7)	9.1 (2.6)	54.1 (16.6)	8.6 (5.0)
	Kučlín	189	16.8 (1.3)	26.1 (1.7)	8.1 (2.6)	54.3 (16.6)	11.8 (5.0)
	Staré Sedlo	189	16.2 (1.3)	25.9 (1.7)	6.3 (2.6)	59.4 (16.6)	12.0 (5.0)

Appendix 8. Palaeoclimatic estimates based on Coexistence Approach (CA) for the studied floras from the Bohemian Massif, Saxony and Lusatia. Abbreviations: MAT (mean annual temperature), WMMT (mean temperature of the warmest month), CMMT (mean temperature of the coldest month), and MAP (mean annual precipitation). VF – Vildšteín Formation

Age	Studied floras	Palaeoclimatic estimates (CA)							
		MAT [°C]		WMMT [°C]		CMMT [°C]		MAP [mm]	
		min. value	max. value	min. value	max. value	min. value	max. value	min. value	max. value
early Pleistocene	Nordhausen	8.4	11.6	19.3	24.6	−0.4	0.2	631.0	864.0
	Nová Ves Mb. (VF) – upper part	4.4	10.8	17.5	20.3	−11.5	1.1	422.0	766.0
	Rippersroda (Perrier-Rippersroda FA)	9.1	10.5	20.2	23.8	−2.8	0.2	735.0	864.0
	Nová Ves Mb. (VF) – lignite beds	11.8	12.5	22.0	24.9	0.4	2.9	641.0	766.0
late Pliocene	Berga	13.3	13.9	24.7	25.6	2.2	3.8	979.0	998.0
	Kranichfeld	12.2	13.9	21.7	23.8	−0.1	2.7	979.0	1036.0
	Nová Ves Mb. (VF) – Nero Clay	15.6	15.8	24.7	25.6	5.0	5.6	1048.0	1122.0

Age	Studied floras	Palaeoclimatic estimates (CA)							
		MAT [°C]		WMMT [°C]		CMMT [°C]		MAP [mm]	
		min. value	max. value	min. value	max. value	min. value	max. value	min. value	max. value
late Pliocene	Vonšov Mb. (VF) – Pluto Clay	15.6	15.8	24.7	24.9	5.0	5.6	823.0	900.0
early Pliocene	Kaltensundheim (Ceyssac FA)	7.2	13.9	18.0	23.8	−0.1	0.7	735.0	1036.0
	Tachov Graben	13.6	15.8	23.6	25.1	1.8	5.6	979.0	1122.0
late Miocene	Moravská Nová Ves	12.5	15.1	24.3	25.7	−0.1	5.8	897.0	1355.0
middle Miocene	Klettowitz 12 (Schipkau FA)	15.7	16.3	25.7	25.7	4.7	6.2	979.0	1355.0
	Horní Břiza	16.4	18.3	23.6	26.4	9.0	9.0	979.0	1187.0
early Miocene / middle Miocene	Klettowitz 3 (Klettowitz FA)	18.0	18.0	25.7	27.8	9.6	10.9	1231.0	1355.0
	Berzdorf 2. Kleinleipisch (Kleinleipisch FA)	16.5	16.8	25.8	27.8	2.5	6.6	1134.0	1190.0
early Miocene	Wackersdorf	15.7	16.6	26.6	26.7	4.5	5.8	1187.0	1250.0
	Mydlovary Formation	15.7	16.5	24.9	26.0	5.6	10.9	1096.0	1187.0
	Wiesa	17.2	18.0	26.5	28.1	7.7	12.3	1146.0	1355.0
	Hrádek/N. (Kristina Mine)	17.0	18.0	26.5	26.9	9.6	12.6	1146.0	1146.0
	Horní Litvínov–Mariánské Radčice	15.2	20.5	23.6	28.1	5.6	14.8	823.0	1018.0
	Cypris Formation	15.7	17.0	24.9	27.5	5.6	13.3	1146.0	1213.0
	Kundratice–Jezeří (micaceous facie)	15.7	16.8	24.7	28.1	9.6	9.6	810.0	1362.0
	Břešťany	16.5	18.9	24.7	27.5	4.8	12.2	1194.0	1333.0
	Přívlačky	13.3	18.9	24.3	28.1	−0.1	12.2	897.0	1355.0
	Holedeč	13.3	17.0	25.2	27.5	0.2	6.2	897.0	1258.0
	Čermníky	13.3	18.9	24.3	27.9	0.1	9.2	897.0	1355.0
	Brandis	15.6	16.8	23.6	27.8	5.0	6.6	1304.0	1355.0
	Bitterfeld (Bitterfeld Main Seam)	15.7	20.8	26.6	27.9	5.0	10.9	1187.0	1322.0
late Oligocene / early Miocene	Mockrheha	15.3	16.7	25.8	26.0	3.7	6.6	1231.0	1355.0
	Hlavačov Gravel and Sand	15.7	17.0	24.3	27.0	2.2	8.3	897.0	1355.0
late Oligocene	Borna-Ost	15.7	16.1	25.4	26.0	3.8	7.1	1096.0	1355.0
	Bockwitz	13.8	16.1	25.6	25.6	1.8	6.2	1090.0	1213.0
	Počerný–Podlesí	15.7	16.7	23.6	28.5	6.2	11.0	1231.0	1551.0
	Kleinsaubernitz	14.0	16.1	25.6	25.6	4.3	7.8	979.0	1058.0
		12.6	16.7	20.1	26.0	4.3	7.1	735.0	1355.0
	Matrý	11.2	15.6	24.0	26.8	−1.6	5.0	879.0	1355.0
early Oligocene	Markvartice–Veselíčko	14.6	18.5	24.7	25.9	2.2	12.2	979.0	1213.0
	Sulečice–Berand	15.6	18.3	24.7	27.5	5.0	10.9	1096.0	1213.0
	Nerchau	15.7	17.0	26.5	26.8	4.3	5.8	1194.0	1194.0
	Knížecí–Hrazený	14.6	18.9	24.7	28.3	5.0	12.2	979.0	1213.0
	Seifhennersdorf	15.6	16.6	25.7	26.4	5.0	5.2	979.0	1250.0
early Oligocene	Holý Kluk	15.6	18.3	24.7	27.5	5.0	10.9	1096.0	1355.0
	Hammerunterwiesenthal	11.2	17.0	–	–	–	–	–	–
	Kundratice	14.6	18.5	24.7	25.9	5.0	11.0	867.0	1187.0
	Bechlejovice	14.6	17.4	24.7	28.1	7.7	10.9	1187.0	1355.0
	Haselbach Floristic Assemblage /FA/	15.6	16.1	24.7	25.6	5.0	5.8	897.0	1206.0
	Beucha	16.5	23.9	26.0	27.9	9.6	13.6	1187.0	1281.0
	Regis	15.7	20.8	27.1	27.9	12.2	13.3	1231.0	1281.0
	Haselbach 1	9.3	21.7	22.3	28.6	2.7	13.6	979.0	1741.0
late Eocene	Valeč	13.6	18.0	23.6	27.1	1.8	10.0	979.0	1355.0
	Roudníky	18.0	18.6	27.1	28.1	13.3	13.3	1096.0	1355.0
	Knau	17.5	20.8	27.1	27.9	12.2	13.3	1122.0	1281.0
	Haselbach (Zeitz Sand)	16.5	18.0	24.7	27.1	7.7	10.0	1003.0	1613.0
	Kučlín	15.7	23.9	25.6	28.1	5.0	12.6	1122.0	1613.0
	Staré Sedlo								