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# THE MIDDLE MIOCENE CENTRAL EUROPEAN PLANT RECORD REVISITED; WIDESPREAD SUBHUMID SCLEROPHYLLOUS FORESTS INDICATED

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**Abstract:** The Middle Miocene plant record from the wider Central Paratethys region (Central Paratethys, the North Alpine Foredeep, Carpathian Foredeep, the Swabian Alb and southern parts of the Bohemian Massif) was analysed by the Integrated Plant Record (IPR) vegetation analysis to assess major vegetation types. The plant assemblages at 27 sites accumulated under very different sedimentological settings and reflect heterogeneous environments. Although of very different origin, the plant record delivers a fairly consistent signal towards subhumid sclerophyllous forests (ShSF) as the most likely major zonal vegetation unit for the Langhian/Serravallian. Today, such forests develop under seasonal climate with pronounced seasonal changes in precipitation. The floristic characteristics are outlined and the record is compared to that of the preceding and the following Miocene periods.

**Key words:** zonal vegetation, Integrated Plant Record vegetation analysis, Middle Miocene, Central Europe

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## Introduction

The Middle Miocene, currently dated to 15.97–11.63 m.a. (Cohen et al. 2013 [updated 2017]), was a period of severe abiotic and biotic changes both on a global and regional scale. Two events partly fall into this period: the Mid-Miocene Climatic Optimum (approximately 17–15 m.a.) as well as the Middle Miocene Climate Transition at 14.2 to 13.8 m.a., which is linked to the expansion of the Antarctic ice sheet (Shevenell et al. 2004). The Central Paratethys region underwent several transgressional cycles, a severe sea-level drop of up to 120 m probably related to the afore-mentioned growth of the Antarctic ice shield, and the demise of marine conditions in the North Alpine Foredeep during the Badenian (Harzhauser and Piller 2007).

The fossil plant record of this period has been interpreted more controversially than for any other Miocene period ranging from "Buschsteppe", "Savanne" and "Macchia- und Hartlaubgewächse mediterraner Prägung" (Berger and Zabusch 1953) and Mediterranean-like vegetation (Andreánszky 1959, Szafer 1961) to deciduous mesophytic forests under (semi) humid-temperate climate (Cfa sensu Köppen) for plant assemblages from the Alpine Foredeep (Gregor 1980, 1982).

For the Late Badenian and Middle Pannonian, Kvaček et al. (2006) traced the vegetation of the Paratethys region on palinspastic palaeogeographic maps, thus only partly covering the here-discussed region and time interval. Further studies considered whole western Eurasia. These include the vegetation assessments performed by Kovar-Eder and Kvaček (2007) and Kovar-Eder et al. (2008) based on the Integrated Plant Record (IPR) vegetation analysis and by Utescher et al. (2007) evaluating plant functional types. Most recently, Henrot et al. (2017) deduced the vegetation from climate models for the Middle Miocene.

Attempts to assess climatic evolution are based on diverse resources such as herpetofauna (e.g. Böhme 2003, Böhme et al. 2008, 2011), mammals (e.g. Van Dam and Utescher 2016) and plants (Erdei et al. 2007, Bruch et al. 2011). The results of those studies are partly also very controversial, assuming distinctly drier conditions in the Langhian/Serravallian compared to the earlier and later periods (Böhme et al. 2011), while concluding very high precipitation in the Langhian and lower precipitation with seasonal changes in the Serravallian (Bruch et al. 2011). Other attempts are too imprecise to decipher regional features (e.g. Henrot et al. 2017). Here, we reinvestigate the rich Middle Miocene plant record of the wider Central Paratethys region by applying the IPR vegetation analysis to assess zonal vegetation units, i.e. vegetation at low altitudes under mesic conditions.

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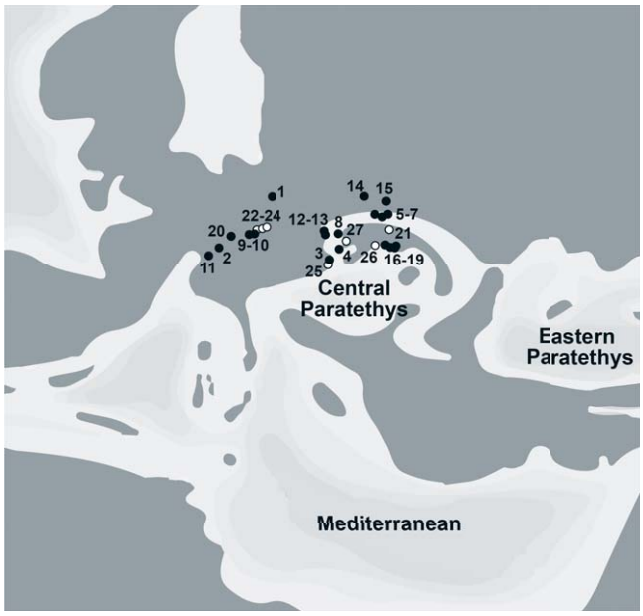
## Material and methods

From the Langhian/Serravallian, 31 plant assemblages (leaves, fruits, pollen) from 27 sites were selected from the wider Central Paratethys region. This includes the Central Paratethys, the Carpathian and the North Alpine Foredeeps, the Norian Depression, the Swabian Alb, and the southern Bohemian Massif (Text-figs 1, 2, Tab. 1). Strong emphasis is put on independent dating (i.e. dating by means other than by plant remains) to achieve reliable resolution in time. The depositional facies range from maar lake deposits at Randeck Maar and lacustrine sediments in the impact crater lake at Steinheim on the Swabian Alb to lacustrine sediments (Parschlug, Weingraben) and fluvio-lacustrine deposits (e.g. Kirrberg, Entrischenbrunn, Schrotzburg, Młyny and Stawiany) as well as marine/brackish (e.g. Wieliczka, Erdőbénye, Türkenschanze, Hernals) and floodplain settings (Gratkorn). Some sites were previously examined applying the IPR vegetation analysis when the time interval 14–17 m.a. was studied (Kovar-Eder and Kvaček 2007, Kovar-Eder et al. 2008). Such sites are included here again due to the modified spatio-temporal focus of this study.




**Text-fig. 1. Palaeogeographic map of the Langhian/Badenian according to Harzhauser and Piller (2007) and location of the fossil-bearing sites. Numbers of sites correspond to those in Table 1. Black circles – IPR vegetation analysis applied, white circles – IPR vegetation analysis not applicable.**

## The Integrated Plant Record (IPR) vegetation analysis

This method was developed to assess major vegetation types. It applies a semi-quantitative evaluation based on the autecology of taxa and leaf physiognomy (Kovar-Eder and Kvaček 2003, 2007, Kovar-Eder et al. 2008, Teodoridis et al. 2011a, b). The fossil plant record is usually strongly influenced or even dominated by intrazonal taxa (mainly wetland taxa), masking zonal taxa which are characteristic of mesophytic environments. The fossil flora of Parschlug serves as a showcase in this respect, where a few wetland taxa are most abundant and mask the true nature of this assemblage (Kovar-Eder et al. 2004). A major feature of the IPR vegetation analysis is, therefore, to exclude intrazonal taxa to the degree possible to uncover the true composition of the mesophytic vegetation. This is important because the latter is essential for extracting climate signals.

In performing the IPR vegetation analysis, all taxa of an assemblage are assigned to the components described in detail in Teodoridis et al. (2011a). The major vegetation types are assessed by the percentages of broad-leaved deciduous (BLD), broad-leaved-evergreen (BLE) and sclerophyllous plus legume-like (SCL+LEG) components of zonal angiosperm taxa. We are aware that the assessment of some taxa (e.g. *Quercus kubinyii* (Kováts ex Ettingsh.) Czeczott) may be equivocal and autecology of fossil taxa may differ from the most similar living relatives. Since the reliability of the results depends on the number of zonal taxa available in an assemblage, here we raise the former threshold from a minimum of 10 zonal taxa (Kovar-Eder et al. 2008) to 15 for the application of the IPR vegetation analysis. The major vegetation types as defined for the IPR vegetation analysis are illustrated in Table 2. Refining the thresholds of components (Teodoridis et al. 2011a) caused slight differences compared to the evaluation results presented earlier by Kovar-Eder and Kvaček (2007) and Kovar-Eder et al. (2008). Taxonomic updates were made prior to the IPR vegetation analysis (Appendix 1).

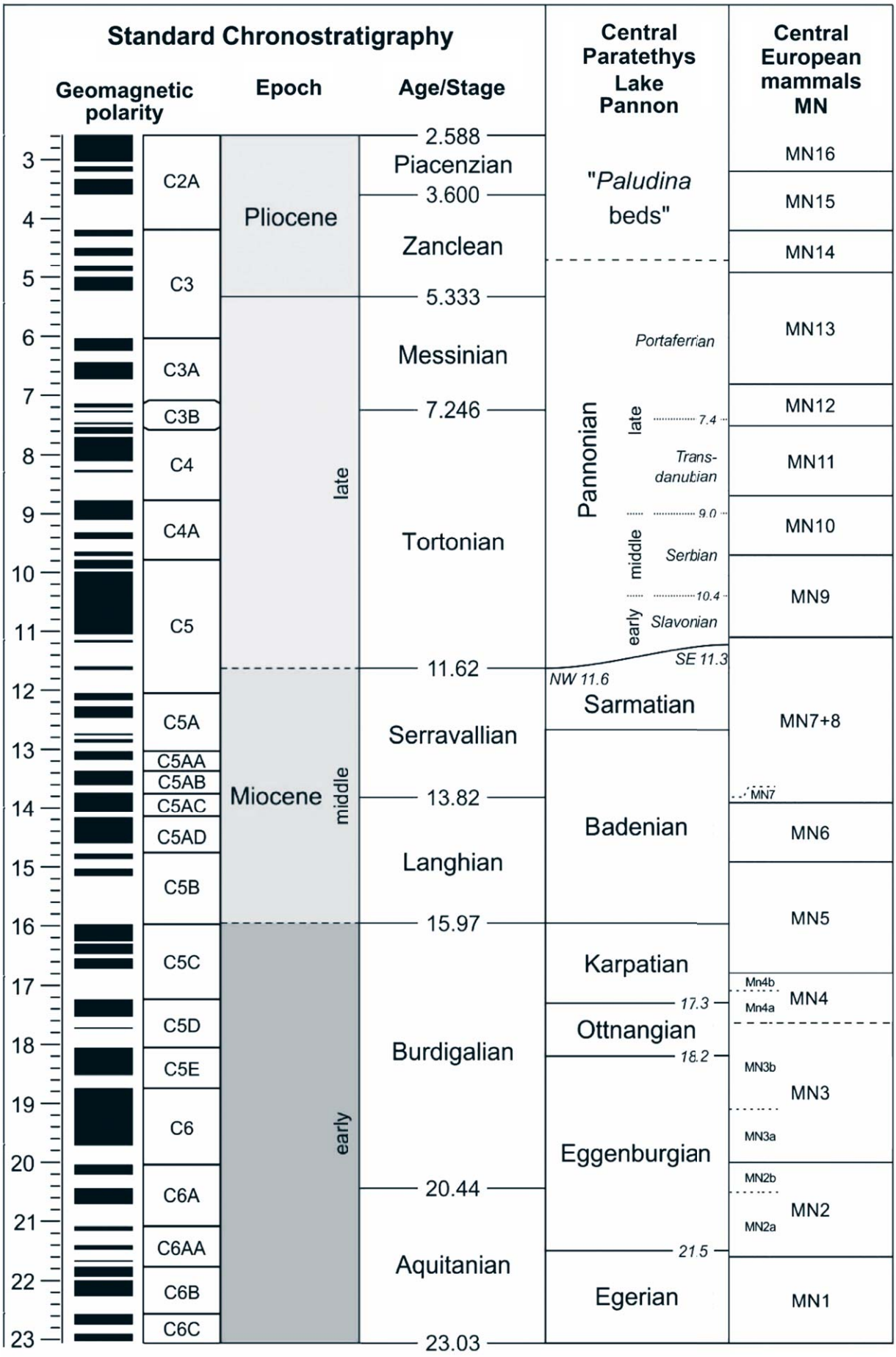
## Cluster analysis

A hierarchical tree clustering analysis was performed applying the STATGRAPHICS program in which the fossil record is clustered in the context of modern vegetation units from China and Japan (Teodoridis et al. 2011a, 2012). Ward's method was applied as a linkage tree clustering method in which two clusters (x, y) are determined by the analysis of variance, and the method joins the clusters with minimal sums of squares (the Euclidean square distance). The number of the defaulted clusters was one. The percentages of the BLD, BLE and SCL+LEG components of the studied fossil and modern sites derived by the IPR vegetation analysis served as a source for cluster analysis (Appendix 2). The dendrogram shows the relationships between modern vegetation from tropical, subtropical and temperate zones of SE China and Japan (Teodoridis et al. 2011a, Teodoridis et al. 2012) and of the here-studied fossil floras (Text-fig. 3).

Abbreviations: IPR vegetation analysis – Integrated Plant Record vegetation analysis, BLD component – broad-leaved deciduous component, BLE component – broad-leaved evergreen component, SCL component – sclerophyllous component, LEG component – legume-type component, BLDF – broad-leaved deciduous forest, BLEF – broad-leaved evergreen forest, MMF – mixed mesophytic forest, ShSF – subhumid sclerophyllous forest.

## Results

Twenty of 27 sites (24 assemblages of fruits, leaves, pollen) are suitable for the IPR vegetation analysis (Tab. 1).




**Text-fig. 2. Stratigraphic correlation table for the Miocene and Pliocene according to Neubauer et al. (2015).**

**Table 1. Studied sites listed stratigraphically, key data, stratigraphic correlation and references.**

| No in Text-fig. 1 | Site | Country | Depositional facies | Sediment type | Dated by | Formation/ Lithostratigraphy | Epoch/Age | Central Paratethys stage/Regional stages | Biostratigraphical stage | References |
|---|---|---|---|---|---|---|---|---|---|---|
| 1 | Horní Bříza, Plzeň Basin | Czech Republic | fluviatile | bituminous paper shale | flora | – | Middle Miocene | – | – | Hurník and Knobloch (1966), Němejc et al. (2003), Kvaček et al. (2006) |
| 2 | Randeck Maar, Swabian Alb | Germany | maar lake, lacustrine | dysodil, laminates of marlstones and clay | small mammals | – | – | – | MN 5, late Orleanian | Rüffle (1963), Gregor (1982), Kottik (2002), Rasser et al. (2013) |
| 3 | Parschlug, Norian Depressian | Austria | lignite basin, lacustrine | marlstone-ironstone (Toneisensteinbänke) | approx. 15–16 m.a., correlation of tuffites dated to 14.9 m.a. above lignites in adjacent basins (Sachsenhofer pers comm. 2018) | – | – | (Karpatian/)Early Badenian | – | Unger (1841-1847), Ettingshausen (1878), Sachsenhofer et al. (2001), Kovar-Eder et al. (2004), Sachsenhofer pers comm. (2018) |
| 4 | Weingraben, Oberpullendorf Basin of the Pannonian Basin system | Austria | lacustrine | oilshales | regional geology, pollen, formainifera | Hochriegelschichten | – | Middle Badenian | Sandschalerzone | Bachmayer et al. (1991), Draxler and Zetter (1991), Jechorek and Kovar-Eder (2004) |
| 5 | Wieliczka, Carpathian Foredeep | Poland | marine | evaporites (salt)/sandstone | regional geology, flora | – | – | Middle Badenian/ Wielician | – | Łańcucka-Środoniowa and Zastawniak (1997) |
| 6 | Swoszowice, Carpathian Foredeep | Poland | ? | gypsiferous beds | regional geology | "Tortonian gypsiferous beds" | – | Middle Badenian/ Wielician | – | Iljinskaja (1964) |
| 7 | Gdów Bay | Poland | marine/fluviatile | sands, silts, marls, evaporitic | regional geology, fauna | – | – | Middle Badenian/ Wielician | – | Łańcucka-Środoniowa (1966) |
| 8 | Devínska Nová Ves, Pannonian Basin system, Vienna Basin | Slovakia | marine | clay | foraminifera, nannoplankton, ostracods, molluscs | – | – | early Late Badenian | *Bulimino-Bolivina* foraminifera zone | Berger (1951), Švagrovský (1978), Sitár and Kováčová-Slamková (1999) |
| 9 | Kirrberg in Balzhausen, North Alpine Foredeep | Germany | fluviatile-lacustrine | clay, marl | micro mammals | Upper Freshwater Molasse | – | – | MN 6, Phytozone OSM 3b | Riederle and Gregor (1997), Seehuber (2008) |
| 10 | Entrischenbrunn, North Alpine Foredeep | Germany | fluviatile-lacustrine | marls | flora | Upper Freshwater Molasse | – | Late Badenian | Phytozone OSM 3b | Schmitt and Butzmann (1997) |
| 11 | Schrotzburg/Öhningen, North Alpine Foredeep | Germany | fluviatile-lacustrine | marls | – | Upper Freshwater Molasse, "Oeningian" | Middle Serravallian | Late Badenian | – | Heer (1855-1859), Hantke (1954), Doppler et al. (2005), Berger et al. (2005) |
| 12 | Türkenschanze, Pannonian Basin system, NW margin of the Vienna Basin | Austria | marine-brackish | clay | molluscs | Rissoenschichten | – | Early Sarmatian | – | Berger and Zabusch (1953) |
| 13 | Hernals, Pannonian Basin system, NW margin of the Vienna Basin | Austria | marine-brackish | – | molluscs | ? Rissoenschichten | – | Early Sarmatian | – | Ettingshausen (1851), Stur (1867), Berger (1953) |

**Table 1. continued.**

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| **14** | Stare Gliwice | Poland | fluviatile-lacustrine | clay | marine molluscs | – | – | Early Sarmatian/ Buhlovian | – | Szafer (1961), Krach et al. (1974) |
| **15** | Młyny, Holy Cross Mts., Carpathian Foredeep | Poland | shallow marine | micritic limestones and clay | marine molluscs | – | – | Early Sarmatian | – | Zastawniak (1980) |
| **15** | Stawiany, Holy Cross Mts., Carpathian Foredeep | Poland | shallow marine | limestone | foraminifera | – | – | Early Sarmatian | *Anomalinoides dividens* (i.e. *Cibides badensis*) zone | |
| **16** | Erdőbénye-Barnamáj, Tokay Mts., Pannonian Basin | Hungary | volcanic/ brackish marine | clayey tuffite with lignitic lenses | reg. stratigraphy, marine molluscs | Galgavölgy Rhyolitic Tuff Fmt. | – | Middle Sarmatian | – | Kóvats (1856a, b), Andreánszky (1959), Erdei and Hír (2002) |
| **17** | Erdőbénye-Kővágó-oldal, Tokay Mts., Pannonian Basin | Hungary | volcanic/ brackish marine | | reg. stratigraphy, marine molluscs | Galgavölgy Rhyolitic Tuff Fmt. | – | Middle Sarmatian | – | |
| **18** | Tállya, Tokay Mts., Pannonian Basin | Hungary | volcanic | silicified layers among rhyolitic tuff and tuffite | – | – | – | Middle Sarmatian | – | |
| **19** | Erdőbénye Ligetmajor, Tokay Mts., Pannonian Basin | Hungary | volcanic/ lacustrine | pelitic tuffite, diatomateous earth | reg. stratigraphy, diatoms | Galgavölgy Rhyolithic Tuff Fmt. | – | Late Sarmatian | – | |
| **20** | Steinheim, Swabian Alb | Germany | impact crater lake, lacustrine | calcareous marls | mammals | *sulcatus*-Schichten | Serravallian | – | MN 7/8 | Heizmann and Reiff (2002), Kovar-Eder and Schweigert (in press) |
| **Sites not suitable for the application of the IPR vegetation analysis (number of zonal taxa too low)** | | | | | | | | | | |
| **21** | Nógrádszakál, Pannonian Basin | Hungary | volcanic | clays, tuffitic beds | – | Baden Clay Formation | – | Middle Badenian | NN 5 | Andreánszky (1959), Nagymarosy (1980), Kordos-Szakály (1984) |
| **22** | Burtenbach, North Alpine Foredeep | Germany | fluvio-lacustrine | – | regional geology, plants | Upper Freshwater Molasse, Mittlere Serie Dehm´s | Late Langhian/ Early Serravallian | – | *knorrii-hessigii* Verband, Phytozone OSM 3b | Gregor (1982), Schmid (1983) |
| **23** | Derching, North Alpine Foredeep | Germany | fluvio-lacustrine | – | regional geology, plants | Upper Freshwater Molasse, Mittlere Serie Dehm´s | Late Langhian/ Early Serravallian | – | *knorrii-hessigii* Verband, Phytozone OSM 3b | Schmidt (1976, 1980), Gregor (1982) |
| **24** | Gallenbach, North Alpine Foredeep | Germany | fluvio-lacustrine | – | regional geology, plants | Upper Freshwater Molasse, Mittlere Serie Dehm´s | Late Langhian/ Early Serravallian | – | *knorrii-hessigii* Verband, Phytozone OSM 3b | Schmid and Gregor (1983) |
| **25** | Gratkorn, Pannonian Basin system, Styrian Basin | Austria | fluvio-lacustrine | clay | mammals, gastropods, magnetostratigraphy | Gleisdorf Formation | – | Sarmatian | – | Harzhauser et al. (2008), Gross et al. (2014), Hably and Meller (2017) |
| **26** | Felsőtárkány, Bükk Mts., Pannonian Basin | Hungary | – | rhyolitic tuff | reg. stratigraphy, vertebrates in overlying sediments | – | – | Late Sarmatian ? | MN 8 | Erdei and Hír (2002) |
| **27** | Sopron-Piusz puszta, Sopron-Kismarton Basin | Hungary | prodeltaic | laminated coaly clay | molluscs, ostracods, foraminifera | – | – | Late Sarmatian | – | Erdei and Lesiak (1999-2000), Erdei and Hír (2002) |

**Table 2. Zonal vegetation types as defined by the IPR vegetation analysis sensu Teodoridis et al. (2011a: tab. 8).**

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

**Table 3. Summary of scoring results. Note that for sites included in previous studies (Kovar-Eder and Kvaček 2007, Kovar-Eder et al. 2008), some results have slightly changed due to refining the thresholds between the vegetation units (Teodoridis et al. 2011a).**

| Site/Asemablage | BLD | BLE | SCL+LEG | Zonal palms | Number of taxa | Number of zonal woody angiosperms | 1 taxon accounts for approx. X % | Test | Vegetation type |
|---|---|---|---|---|---|---|---|---|---|
| Horní Bříza | 62 | 15 | 20 | 4 | 32 | 24 | 4.2 | 100 | MMF/ShSF |
| Randeck Maar-leaves | 40 | 28 | 26 | 6 | 49 | 33 | 3.1 | 100 | ShSF |
| Randeck Maar-fruits | 65 | 11 | 24 | 0 | 47 | 20 | 4.9 | 100 | ShSF |
| Randeck Maar-pollen | 48 | 35 | 15 | 2 | 54 | 24 | 4.2 | 100 | MMF/BLEF |
| **Randeck Maar integrated record** | **49** | **26** | **22** | **3** | **150** | **77** | **1.3** | **100** | **ShSF** |
| Parschlug | 48 | 18 | 34 | 0 | 74 | 54 | 1.9 | 100 | ShSF |
| Weingraben-leaves-fruits | 37 | 26 | 37 | 0 | 37 | 29 | 3.5 | 100 | ShSF |
| Weingraben-pollen | 57 | 31 | 12 | 0 | 57 | 23 | 4.4 | 100 | MMF/BLEF |
| **Weingraben integrated record** | **46** | **28** | **26** | **0** | **94** | **52** | **1.9** | **100** | **ShSF** |
| Wieliczka | 57 | 34 | 9 | 0 | 170 | 101 | 1.0 | 100 | MMF/BLEF |
| Swoszowice | 78 | 9 | 12 | 0 | 27 | 16 | 6.2 | 100 | BLDF/MMF |
| Gdów Bay | 86 | 9 | 5 | 0 | 58 | 20 | 5.1 | 158 | BLDF but > 30 % Meso+Dry herb |
| Devínska Nová Ves | 62 | 27 | 11 | 0 | 78 | 36 | 2.8 | 100 | MMF |
| Kirrberg | 62 | 22 | 16 | 0 | 40 | 27 | 3.7 | 100 | MMF |
| Entrischenbrunn | 51 | 15 | 34 | 0 | 20 | 15 | 6.5 | 100 | ShSF |
| Schrotzburg | 58 | 18 | 25 | 0 | 43 | 26 | 3.9 | 100 | ShSF |
| Türkenschanze | 30 | 12 | 58 | 0 | 55 | 38 | 2.6 | 100 | ShSF |
| Hernals | 34 | 29 | 37 | 0 | 27 | 19 | 5.2 | 100 | ShSF |
| Stare Gliwice | 77 | 9 | 13 | 1 | 150 | 63 | 1.6 | 100 | MMF/BLDF |
| Młyny | 48 | 5 | 47 | 0 | 52 | 31 | 3.3 | 100 | ShSF |
| Młyny and Stawiany | 51 | 5 | 44 | 0 | 55 | 32 | 3.1 | 100 | ShSF |
| Erdőbénye Barnamáj | 55 | 9 | 36 | 0 | 31 | 21 | 4.7 | 100 | ShSF |
| Erdőbénye Kővágó-oldal | 55 | 10 | 35 | 0 | 43 | 30 | 3.3 | 100 | ShSF |
| Erdőbénye Ligetmajor | 57 | 14 | 26 | 4 | 29 | 29 | 3.5 | 100 | ShSF |
| Tállya | 68 | 4 | 28 | 0 | 30 | 24 | 4.1 | 100 | ShSF |
| Steinheim | 61 | 6 | 32 | 0 | 44 | 28 | 3.5 | 100 | ShSF |

The total number of all taxa per site varies between 20 (Entrischenbrunn) and 170 (Wieliczka) (Tab. 3). The number of zonal woody angiosperms is lowest in Entrischenbrunn (15) and highest in Wieliczka (101). In calculating the different components, a single taxon accounts for about 6.5 % in the least confident calculation (Entrischenbrunn) to 1.0 % in the most reliable results (Wieliczka). The BLD component varies between 30 % (Türkenschanze) and 78 % (Swoscowice). The BLE component is lowest in Tállya (4 %) and highest in Randeck Maar-pollen (35 %); mostly it does not exceed 30 %. Exceptions are Randeck Maar-pollen, Weingraben-pollen, and Wieliczka. At 15 sites (17 assemblages), the values of the BLE component are lower than that of the SCL+LEG component. This involves most sites correlated to the Sarmatian. The value of the SCL+LEG component is lowest for Gdów Bay (5 %) and highest for Türkenschanze (58 %). At 6 sites (8 assemblages) this component accounts for < 20 %, which is the threshold towards ShSF according to the IPR vegetation analysis. These sites/assemblages are Randeck Maar-pollen, Weingraben-pollen, Wieliczka, Swoszowice, Gdów Bay, Devínska Nová Ves, Kirrberg and Stare Gliwice. At Horní Bříza the SCL+LEG component makes up 20 %. At all other sites (assemblages) the SCL+LEG component significantly exceeds the 20 % threshold.

The IPR vegetation analysis yields a signal directed towards ShSF as the most likely major zonal vegetation unit for most sites (14 sites/15 assemblages). For the other

**Table 4. Floristic characteristics of the studied sites.**

| Site | Dominant woody taxa | Conifers | *Podocarpium podocarpum* | Further shared taxa contributing to the SCL+LEG component | Diversity of oaks | Diversity of maples | Sapindalean taxa with compound leaves | Thermophilous elements | Broad-leaved deciduous newcomers |
|---|---|---|---|---|---|---|---|---|---|
| **Horní Bříza** | – | *Glyptostrobus*, *Pinus* | absent | *Buxus pliocenica*, *Celtis*, *Ulmus* cf. *plurinervia*, *Zelkova* | *Quercus* cf. *drymeja*, *Q. kubinyii*, *Q. pseudocastanea* | none | *"Sapindus" falcifolius* | *Chamaerops* cf. *humilis*, *Gordonia* cf. *hradekensis*, *Laurophyllum pseudovillense* | *Ginkgo adiantoides*, *Platanus leucophylla*, *Quercus pseudocastanea* |
| **Randeck Maar** | *Podocarpium podocarpum*, *Berchemia parvifolia*, *Zelkova zelkovifolia* | Cupressaceae | abundant | *Cedrelospermum*, *Celtis*, *Zelkova* | *Quercus kubinyii* (formerly *Castanea atavia*) | *A. integrilobum*, *A.* sp. | *Ailanthus*, *Koelreuteria*, *"Sapindus" falcifolius* | *Cedrelospermum*, *Daphnogene*, Lauraceae, Arecaceae | – |
| **Parschlug** | *Glyptostrobus europaeus*, *Myrica lignitum*, *Liquidambar europaea* | ? *Cathaya*, ? *Cupressus*, *Glyptostrobus*, *Pinus* | present | *Celtis*, *Ulmus plurinervia*, *Zelkova* | *Quercus drymeja*, *Quercus mediterranea*, *Quercus zoroastri* | *A. integrilobum*, *A. pseudomonspessulanum*, *A. tricuspidatum* | *Ailanthus pythii*, *A. confucii* | *Daphnogene*, *Engelhardia orsbergensis/macroptera*, *Saportaspermum* | *Platanus leucophylla* |
| **Weingraben** | ? | ? *Cathaya*, ? *Cupressus*, *Glyptostrobus*, *Pinus* | present | *Zelkova* | *Quercus drymeja*, *Q. kubinyii* | *Acer integrilobum* | ? *Sapindus* sp. | *Cedrelospermum*, *Eostangeria* cf. *ruzinciniana*, *Engelhardia orsbergensis/macroptera*, *Laurophyllium markvarticense*, *Saportaspermum* | – |
| **Wieliczka** | ? | *Abies*, *Cephalotaxus*, *Chamaecyparis*, *Cunninghamia*, cf. *Cupressus*, *Glyptostrobus*, *Pinus*, *Taxodium*, *Tetraclinis*, *Thuja* | no | *Celtis* | *Quercus* sp. div. | *Acer* sp. div. | *Koelreuteria margaritifera* | evergreen Fagaceae, Theaceae, Mastixiaceae, Lauraceae, Rutaceae, etc. | – |
| **Swoszowice** | ? | *Taxodium*, *Sequoia* | no | – | *Quercus gigas* (formerly *Castanea atavia*, *Quercus grandidentata*) | *Acer integerrimum* | – | *Daphnogene* | *Platanus leucophylla* (former *P. aceroides*) |
| **Gdów Bay** | ? | *Abies*, *Cephalotaxus*, *Glyptostrobus*, *Juniperus*, *Pinus*, *Taxodium*, *Tetraclinis* | no | *Buxus sempervirens* | – | *Acer* sp. | – | – | *Ginkgo adiantoides* |
| **Devínska Nová Ves** | ? | *Pinus* | no | – | *Quercus kubinyii*, *Q. mediterranea* (? unfig.), *Q. pseudocastanea* | *Acer* sp. | *Sapindus falcifolius* | *Daphnogene* | *Platanus leucophylla*, *Quercus pseudocastanea* |
| **Kirrberg** | *Daphnogene*, *Populus balsamoides*, *"Quercus mediterranea"* and *"Zelkova zelkovifolia"* (taxonomic assignment ambiguous) | none | present | – | ?, assignments problematic | *A. angustilobum* | *Sapindus falcifolius* | *Daphnogene*, *Smilax sagittifera* | *Pungiphyllum cruciatum* |
| **Entrischenbrunn** | *Daphnogene*, *Populus mutabilis*, *Podocarpium podocarpum* | none | abundant | *U.* ? *plurinervia* (former *U. pyramidalis*) | *Quercus drymeja* (former cf. *Myrica* sp.) | none | – | *Daphnogene* | *Pungiphyllum cruciatum* |

**Table 4. continued.**

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| **Schrotzburg** | *Liquidambar europaea*, *Ulmus pyramidalis*, *Platanus leucophylla* | *Glyptostrobus*, *Pinus* | abundant | *Zelkova* | *Quercus* sp. (former *Castanea atavia*), *Quercus mediterranea* | *A. angustilobum*, *A. tricuspidatum* | *Sapindus falcifolius* | *Daphnogene*, *Laurophyllum* sp. (former *Persea princeps*), *Smilax sagittifera* | *Platanus leucophylla* |
| **Türkenschanze** | *Zelkova zelkovifolia* | *Cephalotaxus* (?), *Pinus* | ? present | *Buxus pliocenica*, *Ulmus plurinervia*, *Zelkova* | ? *Quercus drymeja*, *Q. mediterranea* | *A. integrilobum* | *Sapindus falcifolius* | *Daphnogene* | – |
| **Hernals** | *Daphnogene* | *Glyptostrobus*, *Pinus* | no | *Zelkova* | cf. *Quercus drymeja*, *Q. kubinyii*, *Q. mediterranea* | none | *Sapindus falcifolius* | *Daphnogene*, *Smilax sagittifera* | – |
| **Stare Gliwice** | ? | *Abies*, *Cunninghamia*, *Glyptostrobus*, *Juniperus*, *Pinus*, *Pseudotsuga*, *Quasisequoia*, *Sequoia*, *Taxodium*, *Tetraclinis*, *Tsuga* | – | *Buxus pliocenica*, *Zelkova zelkovifolia* | – | – | – | *Castanopsis pyramidata*, *Symplocos casparyi* | *Ginkgo adiantoides*, *Quercus gigas* |
| **Młyny** | *Ulmus* and *Alnus* (specific assignments ambiguous) | *Pinus*, *Tetraclinis salicornioides* | abundant | *Buxus pliocenica*, *Ulmus plurinervia*, *Zelkova* | *Quercus pseudorobur* | *A. integerrimum*, *A.* ? *vindobonensis* (former *A. tricuspidatum*) | – | – | *Acer* ? *vindobonensis* (former *A. tricuspidatum*), *Alnus ducalis* (?), *Quercus pseudorobur*, *Fagus haidingeri* (former *F. orientalis*) |
| **Stawiany** | *Ulmus* type *carpinoides*, *Platanus leucophylla* | none | absent | *Ulmus plurinervia* (assignment ambiguous) | – | none | – | – | *Alnus ducalis* (?), *Fagus haidingeri* (former *F. orientalis*), *Platanus leucophylla* |
| **Erdőbénye-Barnamáj** | *Zelkova zelkovifolia*, *Podocarpium podocarpum*, *Quercus kubinyii* | Cupressaceae, *Glyptostrobus*, *Pinus* | abundant | *Celtis*, *Ulmus braunii*, *Zelkova* | *Quercus drymeja*, *Q. kubinyii*, *Q. mediterranea*, *Q. pseudocastanea* | *A. integerrimum*, *A.* sp. | "*Sapindus*" *falcifolius* | – | *Fagus haidingeri*, *Quercus pseudocastanea* (former *Q. pseudorobur*) |
| **Erdőbénye-Kővágó-oldal** | *Zelkova zelkovifolia*, *Podocarpium podocarpum*, *Quercus kubinyii*, *Q. mediterranea*, *Carpinus grandis* | Cupressoideae, *Glyptostrobus*, *Pinus*, *Tetraclinis*, Taxodioideae | abundant | *Buxus*, *Celtis*, *Ulmus braunii*, *Zelkova* | *Quercus drymeja*, *Q. kubinyii*, *Q. mediterranea* | *A. integerrimum*, *A. tricuspidatum*, *A.* sp. | *Ailanthus confucii*, "*Sapindus*" *falcifolius* | *Engelhardia orsbergensis* | *Ginkgo adiantoides*, *Fagus haidingeri* |
| **Tállya** | *Zelkova zelkovifolia*, *Podocarpium podocarpum*, *Quercus kubinyii* | *Pinus*, *Tetraclinis brachyodon* | abundant | *Celtis*, *Ulmus braunii*, *Zelkova* | *Quercus kubinyii*, *Q. gigas* (former *Q. pontica miocenica*) | *A. integerrimum*, *A.* cf. *palaeosaccharinum*, *A.* sp. | "*Sapindus*" *falcifolius* | – | *Ginkgo adiantoides*, *Quercus gigas* (former *Q. pontica miocenica*) |
| **Erdőbénye-Ligetmajor** | *Zelkova zelkovifolia*, *Podocarpium podocarpum*, *Quercus kubinyii* | Cupressaceae, *Pinus* | abundant | *Celtis*, *Ulmus braunii*, *Zelkova* | *Quercus drymeja*, *Q. kubinyii*, *Q. mediterranea*, *Q. pseudocastanea* | *A. integerrimum* | "*Sapindus*" *falcifolius* | cf. *Daphnogene*, Lauraceae | *Fagus haidingeri* |
| **Steinheim** | *Podocarpium podocarpum*, ? *Quercus* sp. | none | abundant | *Buxus pliocenica*, *Celtis*, *Zelkova* | *Quercus drymeja*, *Quercus* ? *gigas*, *Quercus kubinyii*, *Q. mediterranea*, *Q. pseudocastanea* | *Acer pseudomonspessulanum* vel *integrilobum*, *A. tricuspidatum* vel *angustilobum* | Sapindales sp. 1, 2, ? *Ailanthus* sp. | cf. *Daphnogene* | *Quercus* ? *gigas*, *Quercus pseudocastanea* |

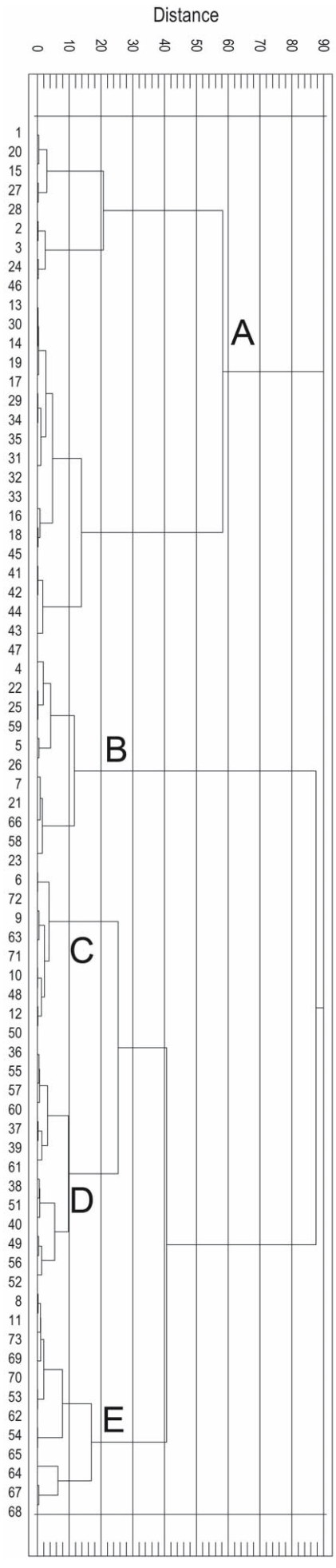
**Table 4. continued.**

| | Sites not suitable for the application of the IPR vegetation analysis (number of zonal taxa too low) | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| **Nógrádszakál** | *Populus, Acer, Ulmus, Parrotia* | ? | no | ? | *Quercus gigas* (former *Q. pontica miocenica*), *Q.* sp. div. | ? | ? | ? | *Quercus gigas* (former *Q. pontica miocenica*) |
| **Burtenbach** | *Daphnogene polymorpha, Podocarpium podocarpum, Populus balsamoides, Salix* | none | abundant | ? | ? | ? | ? | *Daphnogene, Smilax sagittifera* | *Pungiphyllum cruciatum* |
| **Derching** | *Daphnogene polymorpha, Ulmus pyramidalis* (former *U. longifolia*) | none | ? | – | *Quercus* | none | *Ailanthus, Koelreuteria macroptera* | – | – |
| **Gallenbach** | *Podocarpium podocarpum, Populus mutabilis* (?), *Ulmus pyramidalis* (former *U. longifolia*) | none | abundant | *Celtis* | *Castanea kubinyii* (? *Quercus*, unfigured) | none | none | *Daphnogene, Zanthoxylum wemdingense* | *Platanus leucophylla* |
| **Gratkorn** | *Salix* | none | common | *Buxus pliocenica* | none | *A. integrilobum* | none | none | none |
| **Felsőtárkány** | *Glyptostrobus europaeus, Ulmus pyramidalis*, cf. *Salix varians, Alnus cecropiifolia, Acer tricuspidatum* | *Glyptostrobus* | no | none | *Q. gigas* (former *Q. pontica miocenica*), *Quercus kubinyii* | *A. integerrimum, A. tricuspidatum, A.* sp. | none | none | *Quercus gigas* (former *Q. pontica miocenica*) |
| **Sopron-Piusz puszta** | ? | *Picea, Pinus,* Taxodioideae | no | *Buxus pliocenica* | none | none | none | Lauraceae, *Toddalia* | – |

sites the results indicate BLDF (Gdów Bay), ecotone BLDF/MMF (Swoszowice, Stare Gliwice), MMF (Devínska Nová Ves, Kirrberg) or ecotone MMF/BLEF (Randeck Maar-pollen, Weingraben-pollen, Wieliczka). The results for Horní Bříza suggest a transition between MMF/ShSF.

Regarding the floristic composition, the dominant taxa at the different sites are rather variable and no congruent pattern can be identified (Tab. 4). For example, Parschlug is dominated by *Glyptostrobus europaeus* (Brongniart) Unger, *Myrica lignitum* (Unger) Saporta and *Liquidambar europaea* A.Braun, which is related to the lignite-forming environment there. In Schrotzburg, the most abundant taxa – *Liquidambar europaea*, *Ulmus pyramidalis* Göppert, *Platanus leucophylla* (Unger) Knobloch, along with *Populus balsamoides* Göppert and *P. populina* (Brongniart) Knobloch – reflect its fluviatile character. The fluviatile influence is also evident at Młyny and Stawiany (Holy Cross Mts.) where *Ulmus*, *Alnus* and *Platanus leucophylla* are most common. In the Paratethys region, at Türkenschanze (Vienna Basin) and the sites in the Tokay Mountains (Erdőbenye-Barnamáj, Erdőbénye-Kővágó-oldal, Erdőbénye-Ligetmajor, Tállya), *Zelkova zelkovifolia* (Unger) Bůžek et Kotlaba is most abundant. In the Tokay Mountains, other common taxa are *Podocarpium podocarpum* (A.Braun) Herendeen and *Quercus kubinyii*. In the leaf assemblages, generally, conifers presumably not bound to wetland habitats are largely restricted to pines, except for rare findings of *Tetraclinis salicornioides* (Unger) Kvaček (Weingraben, Wieliczka, Gdów Bay, Stare Gliwice, Erdőbénye Kővágó-oldal, Młyny, Tállya). Sites lacking any records of conifers are Kirrberg, Entrischenbrunn, Stawiany, and Steinheim. Conifer diversity is higher in the pollen and fruit record. At many sites, *Podocarpium podocarpum* is abundant, at few sites it is at least present (Parschlug, Weingraben, ? Türkenschanze), whereas records are lacking from Horní Bříza, Wieliczka, Swoscowice, Gdów Bay, Devínska Nová Ves, Stare Gliwice, Hernals, Stawiany, Nógrádszakál, Felsőtárkány and Sopron-Piusz puszta.

Furthermore, the following taxa are present at many sites: *Buxus pliocenica* Saporta et Marion, *Celtis*, *Quercus drymeja* Unger, *Q. kubinyii*, *Q. mediterranea* Unger, *Ulmus* type *plurinervia* Unger/*braunii* Heer, and *Zelkova zelkovifolia*. Oak diversity, including both acutely toothed, partly sclerophyllous forms as well as roburoid ones (type *Q. pseudocastanea* Göppert), is highest in Steinheim (5), Erdőbénye-Barnamáj and Erdőbénye-Ligetmajor (4 each). In the leaf record, entire-margined maples (such as *Acer integrilobum* Weber sensu Walther, *A. integerrimum* Viviani et Massalongo, *A. pseudomonspessulanum* Unger) occur at more sites (Randeck Maar, Parschlug, Weingraben, Swoszowice, Hernals, Türkenschanze, Młyny, Erdőbénye-Barnamáj, Erdőbénye-Kővágó-oldal, Ligetmajor, Tállya, Steinheim, Gratkorn, Felsőtárkány) than maples with toothed margins (*A. tricuspidatum* Bronn and/or *A. angustilobum* Heer), which are documented from Parschlug, Kirrberg, Schrotzburg, Młyny, Erdőbénye-Kővágó-oldal and Steinheim. No maples have been recorded from Horní Bříza, Entrischenbrunn, Stawiany, Sopron-Piusz puszta, Derching and Gallenbach. This may be an artefact for the latter three sites due to low number of taxa recorded there. Furthermore, many sites share the presence of taxa with compound leaves




of probable Sapindalean affinity (*Ailanthus*, *Koelreuteria*, "*Sapindus*" and others).

Those sites that did not allow application of the IPR vegetation analysis because they include mainly intrazonal taxa and the number of zonal ones is too low, provide additional signals relevant in this context. Gratkorn (Hably and Meller 2017) includes only 3 taxa (out of 23) that may be regarded primarily as zonal. These are *Podocarpium podocarpum*, *Buxus pliocenica* and *Acer integrilobum*, indicating a close relationship to the plant assemblages richer in zonal taxa. Burtenbach and Gallenbach yield *Podocarpium podocarpum*; in the latter this legume is abundant. In Felsőtarkany (Erdei and Hír 2002), out of 20 taxa, only *Quercus kubinyii*, *Quercus gigas* Göppert emend. Walther and Zastawniak (former *Q. pontica miocenica* Kubát) and *Acer* cf. *palaeosaccharinum* Stur may be regarded as primarily zonal ones.

**Results of the cluster analysis**

The comparison of the studied European fossil record with 47 modern vegetation units from temperate to tropical zones of China and Japan (Teodoridis et al. 2011a, 2012) is shown in Text-fig. 3 and Appendix 2. None of the studied fossil sites cluster with subcluster A representing modern BLEF (including MMF of Mt. Emei – 2, 3) and tropical vegetation from SE China and Japan. Swoszowice (58), Gdów Bay (59), and Stare Gliwice (66) belong to subcluster B, representing a close affinity to living BLDF of Mt. Emei (4), Meili Snow Mts. (7), modern *Lindera membranacea-Fagus crenata* (21), and *Ilex-Thuja standishii* (23) plant communities of BLDF from Shirakami Sanchi and modern *Fagus crenata* and *Vaccinium-Picea* regions of Mt. Fuji (25, 26) from Japan. The fossil vegetation units of Tállya (72), Schrotzburg (63) and Erdőbénye Ligetmajor (71) are very close to each other and belong to subcluster C, integrating also modern BLDF (6) and several plant communities of the ShSF dominated by *Quercus* and *Pinus* (9), (10), (12) from Meili Snow Mts. (Yunnan, China) sensu Ou et al. (2006). Subcluster D shows close affinity of the fossil sites Randeck Maar (49–52), Devínska Nová Ves (60), Kirrberg (61), Wieliczka (57) and Weingraben-pollen (55) as well as Weingraben-integrated record (56) to modern *Eurya-Cryptomeria japonica associations* of MMF (36–40) from Yakushima Island (Japan). Subcluster E summarises the fossil assemblages of Steinheim (73), Erdőbénye Barnamáj (69), Erdőbénye Kővágó-oldal (70), Parschlug (53), Entrischenbrunn (62), Weingraben-leaf and -fruit record (54), Hernals (65), Türkenschanze (64), Młyny (67), and Młyny and Stawiany (68) with the modern "*Quercus*" communities of ShSF from Meili Snow Mts. (8, 11).

**Text-fig. 3. Results of the cluster analysis based on Ward's method and squared Euclidian distance. Dendrogram showing 5 subclusters (A–E). Cluster analysis is based on the percentages of the BLD, BLE, and SCL+LEG components. Numbers 1–40 sites studied by Teodoridis et al. (2011a), Nos 41–47 by Teodoridis et al. (2012), Nos 48–73 Middle Miocene sites in the wider Central Paratethys region, studied here. The data source is provided in Appendix 2.**

## Discussion

This study is deliberately designed on a rather narrow time interval of about 4 million years with a strong regional focus in order to uncover regional vegetational and climatic peculiarities. The dating of the plant assemblages does not allow for higher resolution in time. No estimations are available regarding how much time is reflected in the individual plant-bearing sediments, nor is an estimation possible as to whether, and to what degree, plant taphocoenoses accumulated with an overlap in time.

The strong signal towards ShSF derives from the sites in the Pannonian Basin, the North Alpine and Carpathian Foredeeps, the adjacent Parschlug Basin, and the Swabian Alb. Ecotone between MMF/BLEF, indicated by Wieliczka, Randeck Maar-pollen, and Weingraben-pollen, contrasts with the leaf and fruit record from Randeck Maar and Weingraben, which signals ShSF. Such differences in the pollen versus the leaf and fruit signal are probably related to the lower taxonomic resolution of the pollen record and to the fact that pollen assemblages may be much more strongly influenced by long-distance transport than the macro record (Kovar-Eder and Kvaček 2007). Note for Wieliczka, Randeck Maar-pollen and Weingraben-pollen that the results (ecotone MMF/BLEF) differ from the formerly presented ones (BLEF; Kovar-Eder and Kvaček 2007, Kovar-Eder et al. 2008). This is due to the fine-tuning of the IPR vegetation analysis, i.e. raising the threshold of the BLE component from 30 % to 40 % for BLEF (Teodoridis et al. 2011a). Dated by the flora, the age of the assemblage from Horní Bříza, which points to the ecotone MMF/ShSF, is less confident. No further interpretation of this result should be advanced at this time.

In the Carpathian Foredeep, the differences in vegetation proxies from the Badenian sites (Wieliczka ecotone MMF/BLEF, Swoszowice and Stare Gliwice ecotone BLDF/MMF, Gdów Bay BLDF) compared to the Early Sarmatian ones (Młyny, Młyny and Stawiany both ShSF) may be related to differences in age. Our results for Stare Gliwice are somewhat contradictory to Szafer's (1961), who recognised a distinct "Mediterranean" element there (e.g. *Juniperus*, *Buxus*, *Cotinus*). These taxa are, however, by far outnumbered by broad-leaved deciduous ones, explaining the results of the IPR vegetation analysis. The signal from the Carpathian Foredeep (BLDF to ecotone MMF/BLEF) compared to the other regions at that time may reflect regional vegetation differentiation due to either more humid and/or a more equal year-round distribution of precipitation there.

In the North Alpine Foredeep, *Podocarpium podocarpum* is a characteristic element of the floras assigned to phytozone OSM 3b sensu Gregor (1982). The understanding of *P. podocarpium* as a wetland-species and indicative of humid climatic conditions assumed that it is closely related to *Gleditsia aquatia* Marshall and *G. heterophylla* Bunge (Gregor and Hantke 1980). Herendeen (1992) has, however, demonstrated that *P. podocarpum* has no contemporary equivalent. In the fossil record, *P. podocarpum* occurs not only in plant assemblages of strong intrazonal character such as the sites in the North Alpine Foredeep, but is also abundant at sites that mainly reflect zonal environments such as Randeck Maar, the Erdőbénye sites, and Steinheim. This explains our interpretation of it being a mainly zonal taxon with a wide ecological range.

The here-presented results in which ShSF is the dominant zonal vegetation unit in this region contrasts with those obtained for preceding and later Miocene periods (Kovar-Eder and Kvaček 2007, Kovar-Eder et al. 2008, and see below). ShSF as an important zonal vegetation unit in the Paratethys region during the Middle Miocene was not clearly recognised by Kovar-Eder et al. (2008) because the time interval 17–14 m.a. (late Early Miocene to early Middle Miocene) was not suitable and, covering the entire area of Western Eurasia meant that study was on too large a scale.

### Vegetation characteristics during the Middle Miocene

Due to the ongoing discussions regarding the vegetation and climate in the Langhian/Serravallian (e.g. Hably and Meller 2017), we here attempt to outline a feasible picture of the landscape and vegetation. In the Langhian/Serravallian time interval, the Central Paratethys was highly dissected by islands and the arising Carpathians (Text-fig. 1); tectonic activity was connected to volcanism. The fossil record is rich, i.e. from former islands in the Pannonian Basin (Tokay Mountain sites related to volcanism), the Carpathian Foredeep (Wieliczka, Swoszowice, Gdów Bay, Stare Gliwice, Młyny, Stawiany), from western parts of the Pannonian Basin system (Weingraben, Devínska Nová Ves, Sopron-Piusz puszta, Türkenschanze, Hernals), from floodplain environments at the NW margin of the Styrian Basin (Gratkorn), and the Parschlug lignite basin in the Norian depression. Along the North Alpine Foredeep, in its western part, fluviatile-lacustrine domains prevailed (e.g. Schrotzburg, Entrischenbrunn, Kirrberg). On the Swabian Alb, which was a karst plateau at that time, maar lake deposits (Randeck Maar) and the deposits of an impact crater lake (Steinheim) record the surrounding vegetation. Finally, the flora from Horní Bříza represents the record from fluvio-lacustrine sediments of the Plzeň Basin in the southern part of the Bohemian Massif (Text-fig. 1, Tab. 1).

Intrazonal vegetation developed along streams, braided rivers, floodplains, and lakes. Characteristic are, among others, *Acer tricuspidatum*, *A. angustilobum*, Juglandaceae, *Liquidambar europaea*, *Platanus leucophylla*, *Populus*, *Salix* and *Ulmus pyramidalis*. In particular braided river systems and floodplains probably occupied vast regions with very diverse habitats ranging from almost mesophytic to riparian and floodplain forests, to swampy and aquatic habitats. These environments, which are best represented in the fossil record, were most dynamic due to major factors such as water discharge, tectonics and sea level changes.

Including the pollen record, Kvaček et al. (2006) were able to delineate the altitudinal vegetation zonation. Conifers (e.g. *Abies*, *Keteleeria*, *Pseudotsuga*) and mainly broad-leaved deciduous woody taxa formed extrazonal forests at higher altitudes. Such vegetation is reflected in the pollen record of Randeck Maar, Weingraben and Devínska Nová Ves. ShSF developed as zonal vegetation in mesophytic colline and lowland environments. Northwards, zonal vegetation turns into the ecotones between MMF/BLDF and MMF/BLEF. ShSFs were characterised by broad-leaved deciduous trees and shrubs (BLD component mainly

around 45–60 %), trees and shrubs with sclerophyllous and legume-like foliage (SCL+LEG component around 20–40 %) and broad-leaved evergreen ones (BLE component around 5–29 %). They differ in composition from that of earlier and later periods in several aspects. Oak diversity is high, including a mixture of both broad-leaved deciduous (*Quercus gigas*, roburoid oaks type *Q. pseudocastanea*) and more or less sclerophyllous, probably also deciduous ones (*Q. mediterranea*, *Q. drymeja*, *Q. kubinyii*), including both more ancient (*Q. drymeja*) and younger (*Q. gigas*, *Q. pseudocastanea*) species. *Podocarpium podocarpum* is among the most common species, often occurring in great quantities (e.g. Randeck Maar, Erdőbénye sites, sites along the North Alpine Foredeep, Steinheim). For Hungary, Hably (1992) lists the following additional occurrences: Gyöngyöspata, Szurdokpüspöki and Sajómercse (all Badenian) and Bánhorváti, Bújak, Diósgyoőr and Füzérradvány (all Sarmatian in age). Further taxa occurring at numerous sites and often abundant are elms with small-sized foliage of the type *Ulmus plurinervia*/*U. braunii* and *Zelkova zelkovifolia*. *Buxus pliocenica*, *Celtis* and entire-margined maples (*Acer integerrimum*, *A. integrilobum*, *A. pseudomonspessulanum*) occur commonly but usually are not abundant. Taxa with compound leaves of Sapindalean affinity (such as Rutaceae, Simaroubaceae, Sapindaceae) but of yet often uncertain generic assignment occur at many sites; their leaflets are sometimes abundant (e.g. Steinheim, Randeck Maar). Conifers are both scarce and low in diversity, except for pines. A remarkable feature of the Middle Miocene plant record is the first occurrence of broad-leaved deciduous taxa such as *Acer vindobonensis* (Ettingshausen) Berger, *Ginkgo adiantoides* (Unger) Heer, *Platanus leucophylla* and *Quercus pseudocastanea* (Kovar-Eder et al. 1994). Some ancient taxa such as *Engelhardia orsbergensis* (Weber) Jähnichen, Mai et Walther/*macroptera* (Brongniart) Unger, Lauraceae (especially *Daphnogene*), and *Tetraclinis salicornioides* may also occur. Records of palms are extremely rare, restricted to the oldest sites Horní Bříza and Randeck Maar and to Stare Gliwice. The zonal vegetation was diversified depending on the soil type, sun exposure, and altitude. Erdei et al. (2007) recognised this unique floristic character in the Hungarian Sarmatian, stressing also its "subxerophytic" aspect and suspecting that this may be related to the volcanic environments. We demonstrate here that this vegetation type had a wider spatio-temporal distribution, although it appears restricted to the (latest Early) and Middle Miocene. Kovar-Eder et al. (2012) demonstrated that the vegetation during the late Early and early Middle Miocene was characterised by an increased proportion of anemochorous woody taxa and, vice versa, decreasing endozoochorous taxa, contrary to that of preceding periods. These shifts in dispersal syndromes indicate changes in diet sources for herbivores. We suspect that these trends would appear even more pronounced if the Early and Middle Miocene records were separated properly, as done here.

Comparing the fossil record to modern vegetation in China and Japan by applying the cluster analysis and/or IPR vegetation analysis, the Middle Miocene plant record shows a close affinity to ShSF vegetation (Meili Snow Mt., Yunnan, China), which is distributed at 2,580–3,650 m alt. This vegetation type is characterised by sclerophyllous oaks, i.e. *Quercus aquifolioides* Rehder et E.H.Wilson, *Q. gilliana* Rehder et E.H.Wilson, *Q. guyavifolia* Rehder et E.H.Wilson and *Q. rehderiana* Handel-Mazzetti in association with *Rhododendron*, *Populus*, *Myrsine*, *Lonicera*, *Dipelta*, *Rosa*, *Salix*, *Urtica*, *Rubus*, *Picea*, *Larix* and *Drynaria*. Such forests are relatively frequent in northwest Yunnan and western Sichuan and are comparable to sclerophyllous forests in the Mediterranean region (Wu et al. 1987, Ou et al. 2006) and in California, USA (Tang 2006).

The here-presented results support the view expressed by several authors (e.g. Jing 1981, Zhou et al. 2003, Tang 2006) that modern evergreen sclerophyllous oak forests in China presumably evolved from sclerophyllous *Quercus* forests in the former Tethys region after the uplift of the Himalayas.

**The Middle Miocene plant record compared to the Early and Late Miocene**

Separating the Early Miocene from the Middle Miocene plant assemblages (compare Kovar-Eder et al. 2008: appendix 6) reveals that the former usually differ by having higher proportions of the BLE component and lower ones of the SCL+LEG component. This explains BLEF or MMF, respectively, as the major vegetation units. The flora from Randeck Maar, which is correlated to MN 5, indicates that ShSF probably started to spread in the outgoing Early Miocene/earliest Middle Miocene. We assume that the time frame 17–14 m.a. set for the afore-mentioned study was not suitable to detect these changes in the dominating vegetation unit from BLEF/MMF in the Early Miocene to ShSF in the here-studied region in the Middle Miocene.

In both Early and Middle Miocene plant assemblages, the BLD component is similarly low. The first occurrences of several broad-leaved deciduous taxa such as *Acer vindobonensis*, *Alnus ducalis* Gaudin emend. Knobloch, *Fagus*, *Ginkgo adiantoides*, *Platanus leucophylla*, and *Quercus pseudocastanea* (Kovar-Eder et al. 1994) do, however, indicate dynamic changes in the composition of the BLD component during the Middle Miocene. In the Late Miocene the BLD component is usually distinctly higher, often exceeding 80 %. The LEG+SCL component is similarly low in the Early Miocene and Tortonian but distinctly higher in the Langhian/Serravallian. Due to the diversity of broad-leaved evergreen taxa of Fagaceae, Lauraceae, Magnoliaceae, Theaceae, and Symplocaceae, the BLE component is usually highest in plant assemblages from the Early Miocene. In contrast, its values are similarly low in the Langhian/Serravallian and Tortonian. Our interpretation is that the increase of sclerophyllous and legume-type taxa occurred at the cost of broad-leaved evergreen ones from the late Early Miocene onwards. The increase of broad-leaved deciduous taxa occurred in the Tortonian more at the cost of sclerophyllous and legume-type taxa than of broad-leaved evergreen ones. *Podocarpium podocarpum* already appeared in the Early Miocene, e.g. Čermníky (Bůžek 1971), and developed a bloom in the Langhian/Serravallian. It became extinct during the Early Pannonian (Hably 1992). In the Tortonian, the diversity of deciduous broad-leaved Betulaceae, Fagaceae, Hamamelidaceae, Juglandaceae, Sapindaceae (*Acer*), and others accounts for the overall

higher values of the BLD component (Kovar-Eder et al. 2008). In Late Miocene taphocoenoses, the proportion of the BLD component is usually higher than that in the Early and Middle Miocene assemblages. In contrast, the SCL+LEG component is distinctly lower than in the plant assemblages from the Langhian/Serravallian: its values are more similar to those retrieved from most Early Miocene sites.

**Comparison with existing vegetation reconstructions**

Kvaček et al. (2006) presented palinspastic maps of the Miocene evolution of landscape and vegetation. These maps clearly indicate "sub-humid aspects" in southern parts of the Paratethys (Hungary, Serbia, Romania) and an increase in broad-leaved deciduous elements in more northern regions of the Paratethys during the Late Badenian. Utescher et al.'s (2007) assessment of tree diversity and vegetation, scoring the Miocene plant record to functional types (PFT), is more difficult to compare. This is because the PFTs are not congruent with the components defined for the IPR vegetation analysis. Moreover, the plant record is treated in an undifferentiated manner to assess the overall vegetation, contrary to the IPR vegetation analysis, which differentiates plants according to the presumable autecology of the taxa. We assume that "PFT 9 broadleaved evergreen – warm temperate/dry season" is similar to the SCL component in the IPR vegetation analysis. Cluster analysis of the PFT scores groups Öhningen (comparable to Schrotzburg), Randeck Maar, Türkenschanze, Erdőbénye-Ligetmajor and Młyny in cluster (M2). In this cluster, PFT 9 is of significance, indicating elevated values of woody plants adapted to seasonal drought, similar to the results of the IPR vegetation analysis. Otherwise, the PFT approach delivers distinctly higher proportions of broad-leaved deciduous taxa than obtained by the IPR vegetation analysis. This most likely reflects the undifferentiated treatment of the zonal and intrazonal taxa by the PFT analysis. Accordingly, the vegetation assessment based on the PFT approach is considered less convincing.

In the context of the modern vegetation units of China and Japan, as applied here, the Tortonian plant assemblages from Crete (Gavdos, Makrilia, Pitsidia) also plot with ShSF (Mantzouka et al. 2015) as does most of the Langhian/Serravallian record from the wider Central Paratethys region. Floristically, especially Makrilia and Pitsidia show distinct similarities to our Central European record as reflected by the diversity of oaks and the occurrence of *Buxus pliocaenica*, *Podocarpium podocarpum* and others (Sachse et al. 1999, Zidianakis et al. 2010). This highlights the evolutionary linkage between ShSF vegetation in both regions.

**Vegetation evolution signals climate change**

Although the IPR vegetation analysis is not designed for direct climate assessment, the resulting vegetation development not only reflects regional landscape development and related vegetation change, but also points to overall climate change in this region.

Today, ShSFs are bound to climates with pronounced seasonal changes in precipitation. Based on the here-studied record, the Langhian/Serravallian period experienced more marked precipitation seasonality than the preceding and following periods. The onset of such climatic conditions occurred around the turn of the Early to Middle Miocene, documented by the fossil floras from Randeck Maar (MN 5). The Swabian Alb may have been suitable for the early appearance of ShSF due to the hydrological regime characterising karst plateaus.

The development of the BLD component (similarly low values in the Early and Middle Miocene, distinctly higher ones in the Tortonian) points to a stronger temperature drop around the turn of the Middle/Late Miocene than in the preceding Miocene time. This supports Böhme's (2003) assumption that the changes in the precipitation regime (towards a seasonal dry climate) in the Early Badenian were probably less linked to changes in the temperature regime. The first records of several broad-leaved deciduous woody plants (see above) in the wider Central Paratethys region cannot be further resolved stratigraphically to underpin a drastic drop in mean annual temperature around the Langhian/Serravallian turn as assumed by Böhme (2003).

Based on the herpetofauna, Böhme (2003) and Böhme et al. (2008, 2011) suggest strong seasonality in precipitation in the Early Langhian, dry climatic conditions in the later Langhian, and dry conditions during the interval Late Serravallian/Early Tortonian. For the wider Central Paratethys region, the plant record indicates seasonal drought, but the stratigraphic resolution is insufficient to recognise possible oscillations.

Based on the Coexistence Approach (CA) (Mosbrugger and Utescher 1997), the record of fossil wood from the North Alpine Foredeep in southern Germany served for another attempt to reconstruct the vegetation and climate (Böhme et al. 2007). Those results indicate an almost equal distribution of precipitation year-round and, overall, humid conditions from the Late Ottnangian through the Middle Badenian. Our results, which include several plant assemblages from the North Alpine Foredeep, do not confirm such climatic conditions for the Badenian.

Bruch et al. (2011) presented precipitation estimates for Central Europe throughout the Miocene based on the evaluation of 169 plant-bearing sites by the CA. Several of the sites they evaluated palaeoclimatically are also included in our study. Those authors, however, arrive at very high humidity during the Langhian, followed by slightly lower humidity and seasonality in the Serravallian and slightly increased precipitation and seasonal changes during the Tortonian. Their results for the Langhian in particular are not in agreement with ours nor with those derived from the herpetofauna (Böhme et al. 2011). Otherwise, their compilation is too rough for deciphering variability in humidity at smaller regional and shorter time scales. We assume that the CA proxies reveal high humidity values and minor variability because this method neglects autecological differentiation. Furthermore, it relies on so-called "nearest living relatives", which more precisely should be termed "most similar living relatives" because though most similar, they may not be the closest relatives. Taxa of unknown or problematic taxonomic affinity must be excluded from the CA. Such taxa are, however, not uncommon in the Miocene (e.g. *Cedrelospermum*, "*Sapindus*" *falcifolius* (A.Braun) A.Braun), and especially small-sized, sclerophyllous leaves are often of unknown taxonomic affinity. In contrast, the IPR

vegetation analysis includes such taxa to the extent possible, evaluating leaf physiognomy.

## Conclusions

The Middle Miocene plant record in the wider Central Paratethys region provides a consistent signal pointing to vegetation adapted to seasonal changes in precipitation. This signal was already recognised by many authors for the Early Sarmatian (e.g. Berger and Zabusch 1953, Andreánszky 1959, Szafer 1961, Gregor 1982) and, subsequently, was interpreted very controversially both in terms of vegetation and climate. Our study of mainly independently dated fossil floras with the spatio-temporal focus on the Langhian/Serravallian of the Central Paratethys region reveals that ShSF was a wide-spread vegetation unit at low altitudes during that period (i.e. zonal vegetation). Its spread may have already started there during the latest Early Miocene. Constraints on stratigraphic correlation hinder, however, tracing possible oscillations in vegetation and climate.

Forest dynamics, namely floristic composition, must be envisioned as depending mainly on soil type and sun exposure, but also on altitude. Broad-leaved taxa preferred more humid sites (e.g. north-exposed slopes) than sclerophyllous and legume-type taxa. The Langhian/Serravallian record of likely zonal taxa differs both floristically and leaf-physiognomically from that of both preceding and later Miocene periods. This becomes evident only when the fossil record, which is usually strongly dominated by intrazonal taxa, is differentiated according to taxa preferring zonal or intrazonal habitats. Intrazonal environments (along river systems, floodplains, swamps, lake margins, etc.) and their specific plant communities occupied vast regions, e.g. in the North Alpine Foredeep. Extrazonal vegetation (vegetation at higher altitudes) is mainly reflected in the pollen record.

The zonal vegetation of the Langhian/Serravallian is comparable to that occurring today under natural conditions in the northern hemisphere with a climate at the transition between Cs to Cfa/Cfb (sensu Köppen).

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**Appendix 1. Scores for the individual Middle Miocene European sites according to the IPR vegetation analysis. Numbers corresponding to those in Table 1.**

Appendix 1 is available on-line on the journal website.

**Appendix 2. Results of the IPR-vegetation analysis and of the cluster analysis of the studied Middle Miocene European floras and modern tropical, subtropical and temperate vegetation types from China and Japan. Data from Teodoridis et al. (2011a) (site Nos 1–40), Teodoridis et al. (2012) (site Nos 41–47) and the here-studied fossil sites (Nos 48–73). The percentages of BLD, BLE and SCL+LEG components are the data source for the cluster analysis. BLEF/MMF – transitional vegetation (ecotone) between BLEF and MMF, BLDF/MMF – transitional vegetation (ecotone) between BLDF and MMF.**

| Time/Zone | Country | Area | Vegetation type – empirical classification | Studied modern vegetation units [region, (sub)community, (sub)association] and fossil floras / studied fossil floras | Cluster analysis | | IPR vegetation analysis | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | Site numbers (Tab. 1) | Subcluster (Text-fig. 3) | % of BLD | % of BLE | % of SCL+LEG | Number of zonal woody angiosperms | Total number of taxa | Classification |
| SUBTROPICAL and TEMPERATE ZONE (sensu Teodoridis et al. 2011a) | China | Mt. Emei | BLEF | plots (Tang and Ohsawa 1997, Tang et al. 2007) | 1 | A | 34 | 66 | 0 | 64 | 64 | BLEF |
| | | | MMF | 1 plot (Tang and Ohsawa 1997) | 2 | A | 65 | 36 | 0 | 23 | 24 | BLEF/MMF |
| | | | | vegetation description (Li and Shi 2007) | 3 | A | 67 | 31 | 1 | 313 | 735 | BLEF/MMF |
| | | | BLDF | 2 plots (Tang and Ohsawa 1997) | 4 | B | 80 | 17 | 4 | 43 | 47 | BLDF |
| | | Meili Snow Mts | BLDF | *Betula* spp., *Acer* spp., *Sorbus* spp. comm. | 5 | B | 100 | 0 | 0 | 19 | 53 | BLDF |
| | | | | summarized communities of *Hippophae rhamnoides*, *Prunus mira*, *Salix luctuosa* and *Zanthoxylum simulans*, and *Populus haoana* var. *haoana* | 6 | C | 68 | 6 | 26 | 16 | 41 | ShSF |
| | | | | Summary for BLDF | 7 | B | 84 | 3 | 13 | 35 | 83 | BLDF |
| | | | ShSF | *Quercus guyavifolia* comm. | 8 | | 56 | 12 | 33 | 24 | 41 | ShSF |
| | | | | *Quercus aquifolioides* comm., *Q. aquifolioides* and *Pinus armandii* subcomm. | 9 | C | 55 | 21 | 24 | 19 | 39 | ShSF |
| | | | | *Quercus aquifolioides* comm., *Q. aquifolioides* subcomm. | 10 | C | 64 | 14 | 22 | 34 | 77 | ShSF |
| | | | | *Quercus aquifolioides* comm., *Q. aquifolioides* and *Populus davidiana* subcomm. | 11 | E | 54 | 15 | 31 | 16 | 32 | ShSF |
| | | | | Summary for ShSF | 12 | C | 62 | 12 | 26 | 55 | 124 | ShSF |
| | | Mt. Longqi | BLEF | *Phoebe bournei* comm. | 13 | A | 17 | 80 | 3 | 32 | 47 | BLEF |
| | | | | *Altingia chinensis* comm. | 14 | A | 14 | 82 | 3 | 31 | 41 | BLEF |
| | | | | *Castanopsis fargesii* comm. | 15 | A | 38 | 60 | 1 | 104 | 160 | BLEF |
| | | | | *Castanopsis eyrei* comm. | 16 | A | 29 | 69 | 3 | 40 | 48 | BLEF |
| | | | | *Castanopsis carlesii* comm. | 17 | A | 17 | 83 | 0 | 36 | 43 | BLEF |
| | | | | *Lithocarpus polystachys* comm. | 18 | A | 23 | 77 | 0 | 35 | 43 | BLEF |
| | | | | plots (He et al. 1998) | 19 | A | 14 | 84 | 2 | 56 | 61 | BLEF |
| | | | | Summary for BLEF | 20 | A | 35 | 64 | 1 | 171 | 249 | BLEF |
| | Japan | Shirakami Sanchi | BLDF | *Lindera membranacea-Fagus crenata* comm. | 21 | B | 78 | 9 | 13 | 82 | 205 | BLDF/MMF |
| | | | | *Quercus mongolica* var. *grosseserrata-Lindera umbellata* var. *membranacea* comm. | 22 | B | 87 | 6 | 6 | 55 | 122 | BLDF |
| | | | | *Ilex-Thuja standishii* comm. | 23 | B | 77 | 5 | 18 | 38 | 72 | BLDF/MMF |

**Appendix 2. continued.**

| | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| SUBTROPICAL and TEMPERATE ZONE (sensu Teodoridis et al. 2011a) | Japan | Mt. Fuji | BLEF | *Camellia japonica* region | 24 | A | 55 | 42 | 3 | 36 | 39 | BLEF |
| | | | BLDF | *Fagus crenata* region | 25 | B | 89 | 5 | 6 | 93 | 113 | BLDF |
| | | | | *Vaccinium-Picea* region | 26 | B | 95 | 2 | 3 | 97 | 122 | BLDF |
| | | Nara | BLEF | *Podocarpus nagi* assoc., typical subassoc. | 27 | A | 33 | 57 | 6 | 25 | 60 | BLEF |
| | | | | *Podocarpus nagi* assoc. | 28 | A | 38 | 53 | 6 | 33 | 78 | BLEF |
| | | Shiroyama | BLEF | *Elaeocarpus sylvestris* var. *ellipticus* assoc. | 29 | A | 17 | 73 | 6 | 32 | 52 | BLEF |
| | | Yakushima Island | BLEF | *Ficus superba* var. *japonica-Persea thunbergii* assoc. | 30 | A | 17 | 81 | 2 | 61 | 99 | BLEF |
| | | | | *Tarenna-Castanopsis sieboldii* assoc. | 31 | A | 16 | 80 | 5 | 75 | 122 | BLEF |
| | | | | *Hydrangea-Castanopsis sieboldii* assoc. | 32 | A | 14 | 80 | 6 | 81 | 134 | BLEF |
| | | | | *Distylium-Quercus salicina* assoc., typical subassoc. | 33 | A | 14 | 81 | 6 | 36 | 67 | BLEF |
| | | | | *Distylium-Quercus salicina* assoc., *Maesa japonica* subassoc. | 34 | A | 19 | 76 | 5 | 76 | 172 | BLEF |
| | | | | Summary for *Distylium-Quercus salicina* assoc. | 35 | A | 20 | 75 | 5 | 77 | 172 | BLEF |
| | | | MMF | *Eurya-Cryptomeria japonica* assoc., *Dryopteris nippoensis* subassoc. | 36 | D | 56 | 32 | 12 | 33 | 87 | BLEF/MMF |
| | | | | *Eurya-Cryptomeria japonica* assoc., typical subassoc. | 37 | D | 56 | 27 | 17 | 29 | 62 | MMF |
| | | | | *Eurya-Cryptomeria japonica* assoc., *Tsuga sieboldii* subassoc. | 38 | D | 43 | 42 | 15 | 41 | 105 | BLEF |
| | | | | *Eurya-Cryptomeria japonica* assoc., *Carex morrowii* var. *laxa* subassoc. | 39 | D | 53 | 31 | 16 | 19 | 45 | BLEF/MMF |
| | | | | Summary for *Eurya-Cryptomeria japonica* assoc. | 40 | D | 43 | 38 | 19 | 48 | 122 | BLEF/MMF |
| TROPICAL ZONE (sensu Teodoridis et al. 2012) | China | Jianfengling | | Tropical lowland rain forest | 41 | A | 5 | 95 | 1 | 146 | 152 | BLEF |
| | | | | Tropical montane rain forest | 42 | A | 1 | 98 | 0 | 242 | 254 | BLEF |
| | | Xishuangbanna | | Tropical seasonal rain forest | 43 | A | 9 | 89 | 0 | 97 | 99 | BLEF |
| | | | | Tropical montane rain forest | 44 | A | 3 | 97 | 0 | 58 | 59 | BLEF |
| | | | | Tropical seasonal moist forest | 45 | A | 26 | 73 | 1 | 74 | 74 | BLEF |
| | | | | Monsoon forest | 46 | A | 59 | 40 | 1 | 37 | 69 | BLEF |
| | | | | Tropical montane broad-leaved evergreen forest | 47 | A | 9 | 91 | 0 | 54 | 54 | BLEF |
| FOSSIL | | | | Horní Bříza | 48 | C | 62 | 15 | 20 | 24 | 32 | MMF/ShSF |
| | | | | Randeck Maar-leaves | 49 | D | 40 | 28 | 26 | 33 | 49 | ShSF |
| | | | | Randeck Maar-fruits | 50 | C | 65 | 11 | 24 | 20 | 47 | ShSF |
| | | | | Randeck Maar-pollen | 51 | D | 48 | 35 | 15 | 24 | 54 | MMF/BLEF |
| | | | | Randeck Maar integrated record | 52 | D | 49 | 26 | 22 | 77 | 150 | ShSF |
| | | | | Parschlug | 53 | E | 48 | 18 | 34 | 54 | 74 | ShSF |
| | | | | Weingraben-leaves-fruits | 54 | E | 37 | 26 | 37 | 29 | 37 | ShSF |
| | | | | Weingraben-pollen | 55 | D | 57 | 31 | 12 | 23 | 57 | MMF/BLEF |
| | | | | Weingraben integrated record | 56 | D | 46 | 28 | 26 | 52 | 94 | ShSF |
| | | | | Wieliczka | 57 | D | 57 | 34 | 9 | 101 | 170 | MMF/BLEF |

**Appendix 2. continued.**

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| FOSSIL | Swoszowice | 58 | B | 78 | 9 | 12 | 16 | 27 | BLDF/MMF |
| | Gdów Bay | 59 | B | 86 | 9 | 5 | 20 | 58 | ? BLDF |
| | Devínska Nová Ves | 60 | D | 62 | 27 | 11 | 36 | 78 | MMF |
| | Kirrberg | 61 | D | 62 | 22 | 16 | 27 | 40 | MMF |
| | Entrischenbrunn | 62 | E | 51 | 15 | 34 | 15 | 20 | ShSF |
| | Schrotzburg | 63 | C | 58 | 18 | 25 | 26 | 43 | ShSF |
| | Türkenschanze | 64 | E | 30 | 12 | 58 | 38 | 55 | ShSF |
| | Hernals | 65 | E | 34 | 29 | 37 | 19 | 27 | ShSF |
| | Stare Gliwice | 66 | B | 77 | 9 | 13 | 63 | 150 | MMF/BLDF |
| | Młyny | 67 | E | 48.49 | 4.91 | 46.6 | 31 | 52.47 | ShSF |
| | Młyny and Stawiany | 68 | B | 50.9 | 5 | 44.41 | 32 | 55.47 | ShSF |
| | Erdőbénye Barnamáj | 69 | E | 54.52 | 9 | 36.48 | 21 | 30.96 | ShSF |
| | Erdőbénye Kővágó-oldal | 70 | E | 54.55 | 10.3 | 35.15 | 30 | 42.98 | ShSF |
| | Erdőbénye Ligetmajor | 71 | C | 56.56 | 13.79 | 25.51 | 29 | 28.98 | ShSF |
| | Tállya | 72 | C | 67.83 | 3.74 | 28.42 | 24 | 29.97 | ShSF |
| | Steinheim | 73 | E | 61.48 | 6.46 | 32.06 | 28 | 43.98 | ShSF |