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Miocene evolution of landscape and vegetation in the Central Paratethys

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Abstract: The digital elevation model (DEM) helps to express Neogene landscapes and vegetation on palinspastic maps with reconstructed orography. To reconstruct ancient vegetation cover, basic zonal vegetation formations and their characteristics have been defined based on diversity and proportions of zonal woody evergreen, deciduous, sclerophyllous and legume-type elements, besides intrazonal (azonal, e.g. coal-forming, aquatic and riparian) and extrazonal (montane conifer-rich) vegetation. Three time intervals have been analysed — Karpatian to Early Badenian, Late Badenian to earliest Sarmatian and Early to Middle Pannonian. After evaluating respective local sites of leaf, fruit/seed and spore/pollen assemblages, paleogeobotanical maps have been constructed for the area of the Central Paratethys and its periphery.

Key words: Miocene, Central Paratethys, paleogeography, palinspastic maps, digital elevation models, vegetation mapping.

Introduction

It is a common task of geobotany today to express interpreted vegetation over larger areas on maps, because the extent of various types of plant communities is an important factor, for example, in tracing human influence or migrations of terrestrial animals. However, several aspects of such studies are different considering Neogene vegetation (Kovar-Eder et al. submitted). The paleogeographic configuration of land and sea was different from the present situation. The regional relief changed in connection with orogeny processes. The floristic spectra included elements mostly extinct or no longer living in Europe. The time slices for the respective maps are many million years distant from the Recent. Global climate, atmospheric circulations and the world ocean varied depending on the time interval studied. To overcome these problems a team of specialists is needed. The paleogeographic background with an approximate demarcation of sea, basins and approximate relief is the first premise to attempt such a paleogeobotanical mapping.

Complex and well determined spectra of plant elements from the reference sites with both megafossil and spore/pollen records are most relevant. The megafossil record usually reflects the situation near the site and is differentiated according to the lithofacies. It also reflects the presence of plants producing poorly preservable pollen (e.g. Lauraceae) and indicates more strongly floristic changes than the spore/pollen spectra. Leaves may convey information on the vegetation physiognomy. Fruits and seeds are better indicators of systematic affinities. Pollen and spores may undergo long distance transport by wind and their spectra thus include information on the composition and changes of upland vegetation, which usually consists of mountain conifer-rich forests. It is problematic to transfer frequencies of any kind of plant organs in the fossil spectra into true abundances of plants in a community or landscape, because the fossil record is biased either by overproduction of fossil organs (e.g. pollen, diaspores) and taphonomic processes (e.g. deciduous vs. evergreen foliage, more rapid decay of delicate leaves). In our analyses, we relied mostly on qualitative proportions of elements, that is the floral diversity, within the given assemblage.

A synthetic view over a large area that includes several countries should be obtained based both on own experiences including authentic knowledge of plant fossil sites and the review of the published data. In the latter cases, it is often a difficult task to critically re-evaluate older taxonomical interpretations, both in the megafossil and pollen spectra. Particularly the interpretations of various pollen types within the natural system look very different today from the traditional morphological or semi-natural systems used previously (or even at present). Particularly by efforts of large-scale comparisons with living plants (Stuchlik 1994) and electron scanning microscopy (Walther & Zetter 1993; Ferguson et al. 1998; Zetter 1998; Liu et al. 2001), surprising solutions for several sporomorphs have been suggested and important natural affinities have been recognized (e.g. *Mastixia*, i.e. *Cornaceaepollis satzveynsis*, *Trigonobalanopsis*, i.e. *Castaneoipollenites pusillus*, etc.). Studies of pollen *in situ* and co-occurrence with megafossils are also important. Thus it has recently become obvious that the tilioid pollen does not belong in most cases to *Tilia*, a deciduous zonal element, but to *Craigia* & *Dombeyopsis lobata* or *Banisteriaecarpum* & *Byttneriophyllum tiliaefolium* (alias "*Alangium*") plants both intrazonal, frequent constituents of the *Glyptostrobus* swamp forests (e.g. Kvaček et al. 2002).

This paper introduces a new methodology of the Neogene paleogeobotanical mapping presenting it on three time slices of the Neogene in the Central Paratethys.

Methodology

Digital Elevation Models (DEMs) of the Central Paratethys (Fig. 1) in individual time intervals of the Miocene, which help us to express landscapes with expected orography, were constructed on the basis of present knowledge of geodynamic evolution of the Alpine-Carpathian-Pannonian region (Csontos et al. 1992; Kováč et al. 1993, 1997, 2001, 2002; Meulenkamp et al. 1996; Baráth et al. 1997; Plašienka et al. 1997; Plašienka & Kováč 1999; Bezák et al. 2002; Konečný et al. 2002; Soták & Kováč 2002; Bielik et al. 2004), existing palinspastic maps (Kováč et al. 1989, 1998, 2003; Magyar et al. 1999; Kováč 2000; Popov et al. 2004), as well as burial and uplift history of sedimentary or other rock complexes (Horváth et al. 1988; Dunkl 1992; Kováč et al. 1994; Hurai et al. 1995; Dunkl & Demény 1997; Danišík et al. 2004, etc.).

Models of the Central Paratethys vegetation (Figs. 2–4) use a simplified system of vegetation units (formations), which are usually sufficient to get tentative pictures of paleovegetation in space. Our attention has been paid to distinguish zonal, intrazonal (azonal) and extrazonal formations on the basis of autecology and leaf physiognomy of elements, whose grouping has been attempted in this respect (Kovar-Eder & Kvaček 2003; Kovar-Eder et al. submitted). The characteristics of the elements have been mostly derived from autecologies of their nearest living relatives or analogues. Reference fossil localities/plant assemblages often included taxa of different vegetation formations, of which zonal elements are relevant for the maps of the reconstructed fossil vegetation. However, it is apparent from the sedimentary settings that assemblages dominated by intrazonal elements prevailed in the record of megafossils, mainly from the basin deposits. Extrazonal conifer-rich mountain vegetation was represented in pollen spectra, exceptionally in megafossil records from the intra-montane basins. Not only altitude, but also the direction of exposure of mountain slopes and substrate may have influenced the composition of the conifer stands. Volcanic settings are the best environments to bring information on zonal vegetation of mesic habitats. Percentages of zonal herbs as well as Non Arboreal Pollen (NAP) as a whole in pollen spectra may refer to close canopy forests versus open woodland to steppe vegetation. Even intrazonal elements can bring information on the character of climate (e.g. the presence of palms), although the intrazonal assemblages usually bear "cool" aspects due to higher proportion of deciduous arboreal elements.

For the purpose of the presented paleovegetation maps several formations have been distinguished and characterized mostly based on the proportion of broad-leaved deciduous, broad-leaved evergreen, sclerophyllous and legume-type components of zonal woody angiosperms (Kovar-Eder et al. submitted).

Zonal formations

1. (Warm-) temperate Broad-leaved Deciduous Forest with very low proportion of evergreen woody elements (vegetation unit 1) includes more than 80 % of zonal deciduous woody elements of angiosperms, such as *Parrotia*, *Zelkova*, *Ostrya*, *Acer angustilobum* etc.
2. Warm-temperate Mixed-Mesophytic Forest (vegetation unit 2) includes less than 80 % deciduous woody elements of zonal angiosperms, less than 30 % evergreen broad-leaved woody taxa of zonal angiosperms and less than 20 % sclerophyllous and legume type elements, regular admixture of *Tetraclinis salicornioides* and other thermophilous elements, less than 30 % of zonal herbs of zonal angiosperms.
3. Subtropical Broad-leaved Evergreen Forests including the "Younger Mastixioid Floras" *sensu* Mai (1964) (vegetation unit 3) includes equal or more than 30 % broad-leaved evergreen and thermophilous elements, represented mainly by Lauraceae, Theaceae, Mastixiaceae, Symplocaceae, Sapotaceae, *Engelhardia*, and evergreen Fagaceae (represented in pollen spectra by morpho-species *Castaneoideoipollenites pusillus*, *Quercoidites henrici*, *Quercoidites microhenrici* — types) and less than 25 % of zonal herbs among zonal angiosperms.
4. Subtropical Sub-humid Sclerophyllous Forest (vegetation unit 4) includes more than 20 % sclerophyllous taxa (*Quercus mediterranea*, *Quercus drymeja*) and legume-type microphyllous woody elements of zonal angiosperms.

Intrazonal formations

5. Swamp forest and coal-forming mire (not expressed by patterns on maps, vegetation unit 7) is dominated by coal-forming woody and herbaceous elements (e.g. *Glyptostrobus* and other Taxodiaceae, *Byttneriophyllum*, *Nyssa*, *Myrica*, *Calamus*, *Spirematospermum*, etc.).
6. Marsh and aquatic vegetation (not expressed by patterns on maps, vegetation unit 8) is dominated by aquatic herbs and helophytes (Cyperaceae, *Typha*, *Potamogeton*, *Stratiotes*, etc.).
7. Deciduous riparian forest (not expressed by patterns on maps, vegetation unit 9) is dominated by woody elements of moist substrates (*Taxodium*, *Alnus*, *Salix*, *Populus*, *Fraxinus*, *Acer tricuspidatum*, etc.).

Extrazonal formations

8. Mountain conifer-rich forest is dominated (mostly in pollen records, vegetation unit 10) by Pinaceae (including *Cedrus*, *Tsuga*, *Picea*, *Cathaya*, etc.).

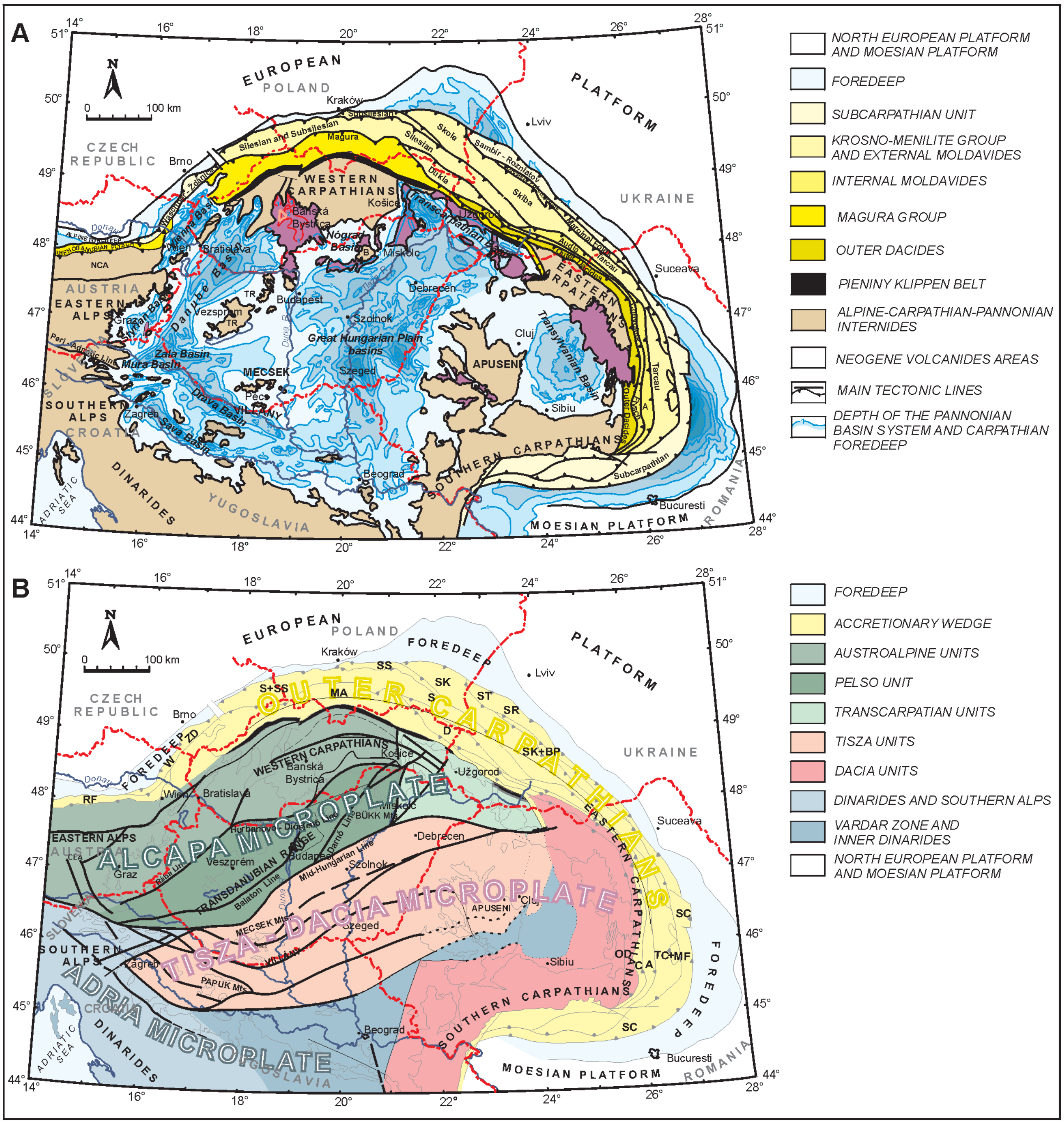

Fig. 1. Geological maps: **A** — Alpine-Carpathian-Pannonian region, **B** — Position of the ALCAPA and Tiszia Dacia microplates.

The network of localities is quite loose and does not sufficiently cover the study area. Thus the gaps between them have been only tentatively extrapolated according to the reconstructed relief. The construction of the maps proceeded in two steps. First, circles of reference sites have been placed on palinspastic maps that include reconstructed sea depths and orography. The sites received name abbreviations (e.g. MA for Mataschen.), which are included in the explanations of the figures and in the review of the sites (available in the digital form on request). Different colours of circles have been used to designate the vegetation formations. The presence of extrazonal mountain conifers in the palynospectra has been marked as a blue-green rim, all kinds of intrazonal vegetation as the brown centre or brown full circle. Colours of zonal vegetation have been divided as follows: light green for the Deciduous Broad-leaved Forest (unit 1), green for the Mixed Mesophytic Forest (unit 2), dark green for mostly evergreen forests (unit 3), and orange for sub-humid, partly sclerophyllous forest types (unit 4).

In the next step, we used various raster patterns (as specified in the explanations of the maps) to depict probable vegetation formations between and around the reference sites. The intrazonal vegetation was omitted because of its limited extent compared with the scale of the maps. The approximate position of extrazonal conifer belts has been placed according to the nearby palynodata and orography.

Early Miocene — model of the Karpatian landscape and vegetation of the Central Paratethys

During Early Miocene, the Central Paratethys was situated at least 200–300 km to the south of its present position. The sea, located along the southern slopes of the European platform, covered the southwestward dipping subduction zone in front of the developing Alpine-Carpathian orogene. The accretion wedge, build up by external Alpine and Carpathian Flysch Belt units, was marked in that time only with islands, forming an archipelago along the platform margin. The uplifted islands, composed of units of the Outer Carpathian nappe pile, were surrounded by residual flysch troughs with turbidite deposition. Toward the south, the epicontinental sea stretched over a large part of the internal zones of the Alpine and Carpathian mountain chains, included the northern lithosphere fragment of ALCAPA and the southern fragment of Tisza-Dacia (Csontos et al. 1992; Csontos 1995). The lithospheric fragments (or microplates) moved towards the subduction zone separately, their amalgamation set at first since the Middle Miocene. The southern boundary of the Central Paratethys Sea was represented by the Dinaride mountain chain, dividing it from the Mediterranean Sea.

In late Early Miocene, the subduction gradually converted to a collision from the west to the east. The weight of the overriding Carpathian orogene front and deep subsurface load of the submerging plate led to development of a flexure on the platform margin. The foredeep basin developed along the whole front of the Outer Carpathian accretion wedge. The evolution of the accretion wedge was associated with compression, controlling folding and thrusting of the Flysch Belt nappe piles (Kováč et al. 1998).

The internal units of the Carpathians, belonging to the ALCAPA and Tisza-Dacia microplates, started to collapse due to stretching in consequence of the subduction pull (Royden 1993a,b), as well as due to asthenospheric mantle upheaval in the western part of the back-arc region. The extension led to initial rifting of the Pannonian basin system (Horváth 1993). By basin opening, besides normal and low angle faults, strike slip faults also played an important role (Vass et al. 1988, 1993; Tari et al. 1992; Fodor 1995; Kováč et al. 1998; Konečný et al. 2002). In the west a sinistral shear dividing the Alpine and Carpathian orogenes opened the Vienna Basin, in the east a dextral shear along the external and internal Carpathians boundary (Pieniny Klippen Belt) opened the Transcarpathian Basin towards the northern part of the East Slovak Basin. Extension in the western part of the back-arc region led to beginning of the formation of the Danube Basin, associated with structural unroofing of the deepest Alpine-Carpathian structural units.

During the Karpatian, a new marine connection opened between the Central Paratethys and the Mediterranean Sea. This connection is supposed through the trans-Dinaride corridor situated in the area of Slovenia and northern Croatia (Rögl 1998). Apart from tectonics, the global sea-level rise during the late Burdigalian had an important role in the development of this seaway (TB 2.2 cycle, *sensu* Haq et al. 1988; Hardenbol et al. 1998; Kováč et al. 2001). The sea transgression, with new elements of marine fauna and flora, flooded the present territory of the Drava and Sava Basins (Pavelić 2001), from where the sea penetrated into the Mura, Zala and Styrian Basins. The NE oriented flooding then followed the way between the northern margin of the Mecsek Mts and the southern margin of the Transdanubian Range reaching the North Hungarian–South Slovak sedimentary area. Northwards, the sea spread to the Bánovská kotlina Depression, the Vienna Basin, the Váh river valley and the East Slovak Basin (Kováč et al. 1993). The Karpatian sea covered especially the western part of the Carpathian Foredeep, in the east the sea extended especially over the area of the present Outer Carpathian units of accretionary wedge with wide marine connections into the East Slovak Basin (Rudinec 1989, 1990; Kováč et al. 1995).

The DEM paleogeographical model of the Central Paratethys during the Karpatian (Fig. 2) documents the beginning of the Carpathian orogene uplift. The ratio between continental and marine environments (ratio of land and surface covered by the sea) can be very roughly interpreted due to the enormous erosion of the Early Miocene sediments at the begin of the Middle Miocene (Kováč et al. 2003). The erosion is documented by a total absence of marginal facies particularly in northern areas of the Central Western Carpathians and by very sporadic findings of the Karpatian sediments in the Outer Carpathians, folded together with the Flysch Belt deposits (Cieszkowski 1992; Oszczypko 2003). The results of study of fluid inclusions also confirm erosion of 2 to 5 km thick pile of deposits (Hurai et al. 2002), as well as an important angular unconformity between the Karpatian and Badenian strata at many places in the Pannonian basin system.

The Carpathian paleo-relief was probably low at this time. In many places, the pre-Tertiary basement units were covered by Paleogene and Early Miocene sediments, much larger in extent than those preserved today in the Paleogene and Neogene basins. In the Western Carpathians, for example, a continuous sedimentary area covering the territory from the Bánovská kotlina Depression to the Vienna Basin has been recorded (Kováč et al. 1993), without indication of an uplift of the Považský Inovec core mountain (Kováč et al. 1994, 1997).

The paleo-river net started to develop in areas with higher relief. The Eastern Alps belonged to such places, where rivers fed deltas in the Alpine Foredeep and the southern part of the Vienna Basin (Aderklaa Formation), and later in the uplifted parts of both the Central Western Carpathians and the Outer Carpathians in the western segment of the Carpathian collision zone (Kováč 2000).

Considerations about prevailing low paleo-relief are also supported by the paleobotanical study, which docu-

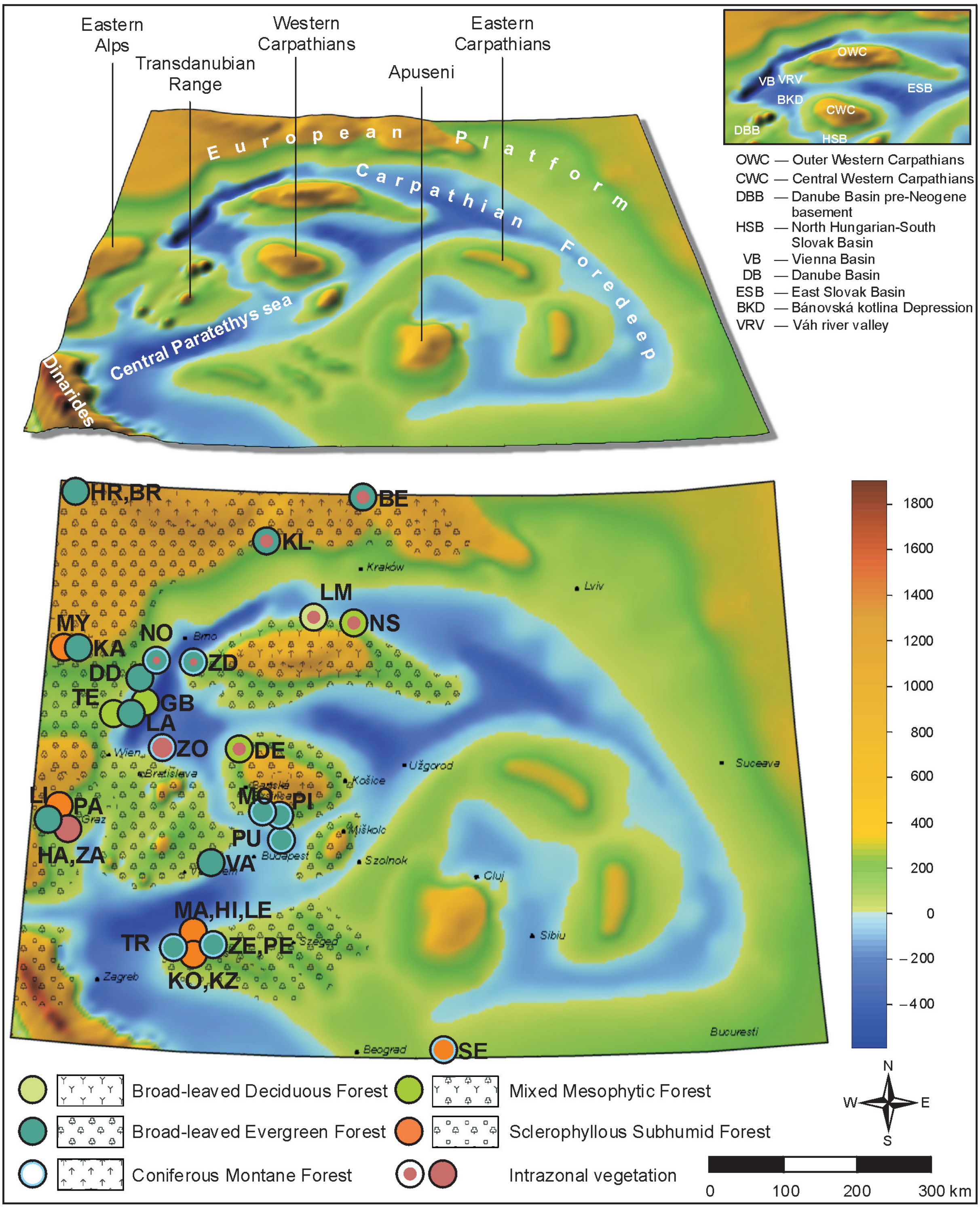

Fig. 2. DEM of the Central Paratethys: landscape & vegetation cover during the Karpatian. Abbreviations of the localities with numbers of vegetation units: **BE** — (3, 8) Bełchatów, KRAM-P 211/214; **BR** — (3, 9) Berzdorf; **DD** — (3) Dolní Dunajovice, Slup, Hevlín; **DE** — (3, 7) Dežerice; **GB** — (3, 10) Core Gbely 139, depth 650–660 m; **HA** — (9) Haiden; **HI** — (3, 9) Core Hidas 53, 1071.0–763.3 m; **HR** — (3, 7) Hrádek/N., Kristina Mine, Turów; **KA** — (3) Kamenný Újezd, Olešník, Hluboká; **KL** — (3, 10) Kłodnica area, Biała and Twardawa cores; **KO** — (4, 9, 10) Core Komló 120; **KZ** — (3, 9, 10) Komló-Zobák puszta; **LA** — (3) Laa/Thaya; **LE** — (3, 10) Leánykö; **LI** — (3, 9) Lintsching; **LM** — (1, 7, 8) Lipnica Mała; **MA** — (4) Magyaregregy; **MO** — (3, 7, 8, 10) Modrý Kameň, Stredné Plachtince, Ďurkovce, Dolné Príbelce; **MY** — (4) Mydlovary; **NO** — (3, 7, 9) Core Nosislav 3, 368–345 m; **NS** — (2, 7, 8) Nowy Sącz; **PA** — (4, 9) Parschlug; **PE** — (9) Core Pécsvárád 44; **PI** — (3, 8, 9) Core Piliny 8; **PU** — (3, 8, 10) Core Püspäkhatran 4; **TE** — (3, 9) Core Tekeres 1; **TR** — (2, 8, 9) Teiritzberg; **VA** — (3, 9, 10) Core Várpalota 133; **ZA** — (7) Zangtal near Voitsberg; **ZD** — (3, 9, 10) Cores Ždánice 67, depth 765–858 m, Ždánice 68, depth 700–820 m; **ZE** — (3, 9, 10) Core Zengővárkony 59; **ZO** — (9, 10) Core Zohor 1, depth 1495–1500 m.

ments an altitudinally not much differentiated character of vegetation in the whole Carpathian-Pannonian region during the Karpatian. Similarly, no obvious latitudinal and longitudinal changes were observed there. Some zonation marks, indicated by the diferentiation of the paleovegetation cover, are visible in the lowlands and margins of the marine sedimentary area.

Karpatian vegetation (Fig. 2) is documented by reference sites, of which only some have been dated by marine fauna. The age of the others is indicated by the mammalian MN5 Zone and thus may overlap with the Early Badenian. In other cases the boundary to the Ottnangian may also be uncertain (MN4 Zone).

Three zonal forest formations were spread over the Central Paratethys region during the Karpatian. Subtropical broad-leaved forests with high to medium proportion of evergreen elements were spread in the western part and continued into the Boreal Province westwards in the form of the typical Younger Mastixioid Floras *sensu* Mai (1964). The corresponding phytostratigraphic unit of the Boreal Province has been called the Floral Assemblage ("Florenkomplex") Františkovy Lázně — Kleinleipisch (Mai 1995, 2001; Czaja 2003), but direct dating to the lower part of the MN5 Zone is available only for Františkovy Lázně in the Cheb Basin outside the Central Paratethys. Domination of thermophilous elements (*Engelhardia*, *Platycarya*, Sapotaceae, Symplocaceae, evergreen Fagaceae, such as *Trigonobalanopsis*, in pollen records expressed by *Castaneoideaepolis pusillus*-, *Castaneoideaepolis oviformis*-, *Tricolporopollenites liblarensis*-, *Quercoidites henrici*- types, etc.) is apparent for the Karpatian–Early Badenian time span (Planderová 1990, Zone MF5; Doláková & Slamková 2003). Only in the central and northern parts near mountains (e.g. Lipnica Mała, Nowy Sącz), the proportion of the broad-leaved deciduous elements increased resulting in the warm-temperate Mixed Mesophytic and Broad-leaved Deciduous Forest types. Some sites (Mydlovary — Knobloch & Kvaček 1996; Parschlug — Kovar et al. 2004; Magyaregregy — Hably 2002) have a sub-humid character (subtropical forests with high proportion of sub-humid and sclerophyllous elements). This may indicate some heterochronity, which we are unable to resolve from the paleobotanical record and short-time fluctuation of perhumid and seasonal climate, as proposed by exothermic vertebrates (Böhme 2003). A distinct East-West gradient is apparent, when broader parts of Europe are compared (Kovar-Eder et al. submitted).

Extrazonal mountain zones with conifers were probably as high as 1500–2000 m a.s.l. and more. The upland forests were dominated by *Pinus*, *Abies*, *Cathaya* and only at still higher altitudes with the admixture of *Cedrus*, *Tsuga*, and *Picea*, as demonstrated in the pollen spectra (Nagy 1992; Doláková & Slamková 2003). Various Pinaceae (*Pinus*, *Cathaya*) and *Sciadopitys* entered also intrazonal lowland formations.

Intrazonal coal-forming forests appeared mainly in the inter-Alpine basins (Leoben-Bruck Basin, Parschlug, Fohnsdorf, and Mecsek Mts — Hably 2002, p. 92). Besides *Glyptostrobus* these thermophilous communities occasionally included palms, e.g. *Calamus*-type at Teiritzberg, evergreen oaks, *Nyssa*, *Myrica*, *Cyrilla* (Zittau Basin), and not yet clarified enigmatic *Rhoipites pseudocingulum* (= *Rhus*-type). Among other mostly intrazonal elements, ferns of Gleicheniaceae, Schizaeaceae (*Lygodium*), *Osmunda* and Polypodiaceae *sensu lato* (including, e.g. *Pronephrium*) were well represented. Pollen of *Avicennia* (Korneuburg Basin) suggests the presence of impoverished mangrove shrubs in the NW part of the Central Paratethys.

Paleobotanical data are lacking for this time interval from the eastern part of the studied region because of unfavourable conditions for the preservation of fossil plants there (Syabryaj 2003). Assemblages from the upper part of the Smoliarka Horizon (Rylova et al. 1999) and Rozhok (zone IV FC *sensu* Yakubovskaya 1993) in Belarus give evidence that the subtropical vegetation of the mastixioid type may have extended north-eastwards from the Central Paratethys.

Middle Miocene — model of the Late Badenian landscape and vegetation of the Central Paratethys

During the Middle Miocene, the active collision/subduction in front of the Carpathians shifted eastwards due to gradual break-down of the submerging slab (Tomek & Hall 1993). In the west, this process led to the termination of collision between the orogene and the European platform, followed by gradual uplift of the Outer Carpathian accretionary wedge and by the migration of foredeep depocentres from the Western Carpathian foreland towards the Eastern Carpathians (Jiříček 1979). The sea flooding in the front of the Carpathian orogene gradually schifted from west to east. At the end of the Early Badenian, the sea abandoned the western part of the foredeep (Czech Republic), marine sedimentary areas extended only in the northern front of the Western Carpathians and in the front of the Eastern Carpathians. The foredeep at the edge of the Western and Eastern Carpathians reached its maximum extent during Late Badenian–Early Sarmatian time, when 2500 m of sediments were deposited (Meulenkamp et al. 1996). The Sarmatian compression associated with uplift of the Outer Western Carpathians draw the sea away from the northern part of the Carpathian Foredeep for ever (Kováč et al. 1998). A connection between the Carpathian Foredeep and the Pannonian basin system remained preserved only in the Eastern Carpathian region (Kováč 2000; Kováč et al. 1998).

The Middle Miocene development of the back-arc basin region was controlled by two geodynamic factors: in the western and central parts of the Pannonian basin system it was upheaval of asthenosphere mantle masses, in the eastern part it was stretching of an overriding plate induced by subduction pull in front of the Eastern Carpathians. In the western part of the back-arc basin, subsidence of the Vienna and Danube Basins caused depocentres above the thinned crust and lithosphere associated with volcanic activity in the hinterland of the Central Western Carpathians (Wernike 1985; Nemčok & Lexa 1990; Tari et al. 1992; Konečný et al. 2002). In the east, orogene that was parallel to the back-arc basin depocentres opened in the area of the Transcarpathian and Transylvanian Basins. Mighty acid and later also "island arc" type volcanic activity appeared in a belt along the eastern border of the back-arc region in the hinterland of the Eastern Carpathians (Konečný et al. 2002).

Synrift subsidence of the back-arc basin in the Pannonian basin system was associated with mighty acid and calc-alkaline volcanic activity (Kováč 2000; Konečný et al. 2002). Individual depocentres formed in the extensional tectonic regime. The main types were grabens and half-grabens associated with normal and low angle faults, although some pull apart basins opened along active strike-slip faults (Vass et al. 1988, 1993; Tari et al. 1992; Fodor 1995; Kováč et al. 1998; Konečný et al. 2002; Kováč 2000).

The Badenian marine conection of the Central Paratethys with the Mediterranean Sea is supposed through a trans-Dinaride corridor (Rögl 1998), at a similar place as during the Karpatian. The Early Badenian sea-level rise, which can be correlated with the early Langhian global sea-level change (TB 2.3 cycle *sensu* Haq et al. 1988; Hardenbol et al. 1998), is documented only in the SW part of the Pannonian basin system — from the Styrian Basin (Rögl et al. 2002). In the northern parts of the back-arc region wide-ranging erosion of Early Miocene deposits is observed. In depressions (future basin depocentres), fan deltas or terrestrial red coloured sediments were deposited during this time.

The Early Badenian tectonically-controlled transgression, followed by rapid subsidence (deep sedimentary environment), started about 15 Ma. The basins were filled by clastics transported by rivers running from uplifted areas of the Eastern Alps and the Western Carpathians. After sea-level fall (documented by erosion of the Early Badenian carbonate platforms in the SW part of back-arc basin — Vienna and Styrian Basins), the "Middle Badenian" transgression, which can be correlated with the global sea-level change in late Langhian (TB 2.4 cycle *sensu* Haq et al. 1988; Hardenbol et al. 1998), took place. The Central Paratethys sea reached the present extent in the intra-Carpathian Neogene basins, except the uplifted North Hungarian–South Slovak sedimentary area. Since that time, a gradual filling up of the Pannonian basin system by deltas has been observed, leading to shallowing of sedimentary environment and development of isolated depocentres. Basins situated in the north and east suffered from isolation. A salinity crisis took place in the Carpathian Foredeep as well as in the Transcarpathian and Transylvanian Basins.

The Late Badenian transgression, which can be correlated with the global sea-level change at the Langhian/Serravalian boundary (TB 2.5 cycle, *sensu* Haq et al. 1988; Hardenbol et al. 1998; 13.65 Ma.) represents the last full marine flood of the Central Paratethys. Since the end of the Late Badenian (12.7 Ma), an isolation of epicontinental sea in the Intra-Carpathian region can be documented and a direct connection of the Central Paratehtys with the Mediterranean is not expected. The Sarmatian flood, from the Eastern Paratethys region, can be correlated with the late Serravalian global sea-level change (TB 2.6 cycle *sensu* Haq et al. 1988; Hardenbol et al. 1998). The sedimentary environment was dominantly shallow marine with decreased salinity.

The DEM model of the Central Paratethys during the Late Badenian (Fig. 3) documents uplift of the Western Carpathians, including accretionary wedge in front of the orogene and broad marine flood in the back-arc basin region. The intra-Carpathian region gained the characteristic features of an archipelago sea, with many small islands surrounded by shallow epicontinental sea. The paleogeography was still strongly influenced by tectonic processes (Styrian phase), as it is well marked by rapid changes of subsiding depocentres (sea bays, small basins) and position of the coastal line.

The paleo-relief of the Carpathians significantly changed during the Middle Miocene, due to strong tectonic influence. The belt of the Outer Carpathians, bordered by internal parts of the orogene, started to be uplifted. The land surface was also strongly differentiated by volcanic activity, some stratovolcanoes reached heights of 2000 to 3000 m a.s.l. The river net transporting eroded clastic material headed mostly towards the back-arc area.

Fair-sized altitudinal differences between lowlands and mountains are documented by paleobotanical studies. Mixed pollen spectra with mountain and lowland vegetation taxa indicate only seemingly the decrease of thermophilous taxa and the increase of more dominant temperate taxa (Sitár & Kováčová-Slamková 1999; Slamková 2004). The Badenian vegetation in the Central Paratethys can generally be characterized as thermophilous without dominance of typical boreal plant elements. Hence, we cannot document sufficiently a gradual cooling of climate indicated in the literature (Böhme 2003) that influenced the European flora from the Late Badenian onwards.

Late Badenian vegetation (Fig. 3) has been documented from sites more often dated by marine fauna (due to an extensive marine transgression), but also from some others that are dated by mammals to Zone MN6 or by regional correlation. The differentiation of the levels within the Badenian has not always been accomplished and such sites are exceptionally included into the map. Some sites overlap with the lowermost Sarmatian, which is floristically hardly distinguishable (see Syabryaj & Stuchlik 2004; merged into a single "Florenkomplex" Stare Gliwice-Unterwohlbach by Mai 1995).

The southernmost sites in Romania, Serbia and Hungary differ from the remaining ones by thermophilous, partly sub-humid aspects under subtropical climatic conditions, which continued from previous times. A general cooling trend appears in other sites by an increasing role of deciduous elements, while thermophilous plants withdrew stepwise southwards and only a part survived, mainly *Tetraclinis*, *Amentotaxus*, *Magnolia*, Lauraceae, *Engelhardia* and others. This is in the contrast to the preceding "Wieliczien" thermophilous humid mastixioid assemblage even in the Polish part of the Carpathian Foredeep (Łancucka-Środoniowa & Zastawniak 1997). From the differentiation of vegetation in the Late Badenian it is obvious that the climatic gradient between the southern and northern parts of the Central Paratethys increased at that time, partly due to altitudinal differenciation, as noted above. A noteworthy forest-forming tree was *Fagus* accompa-

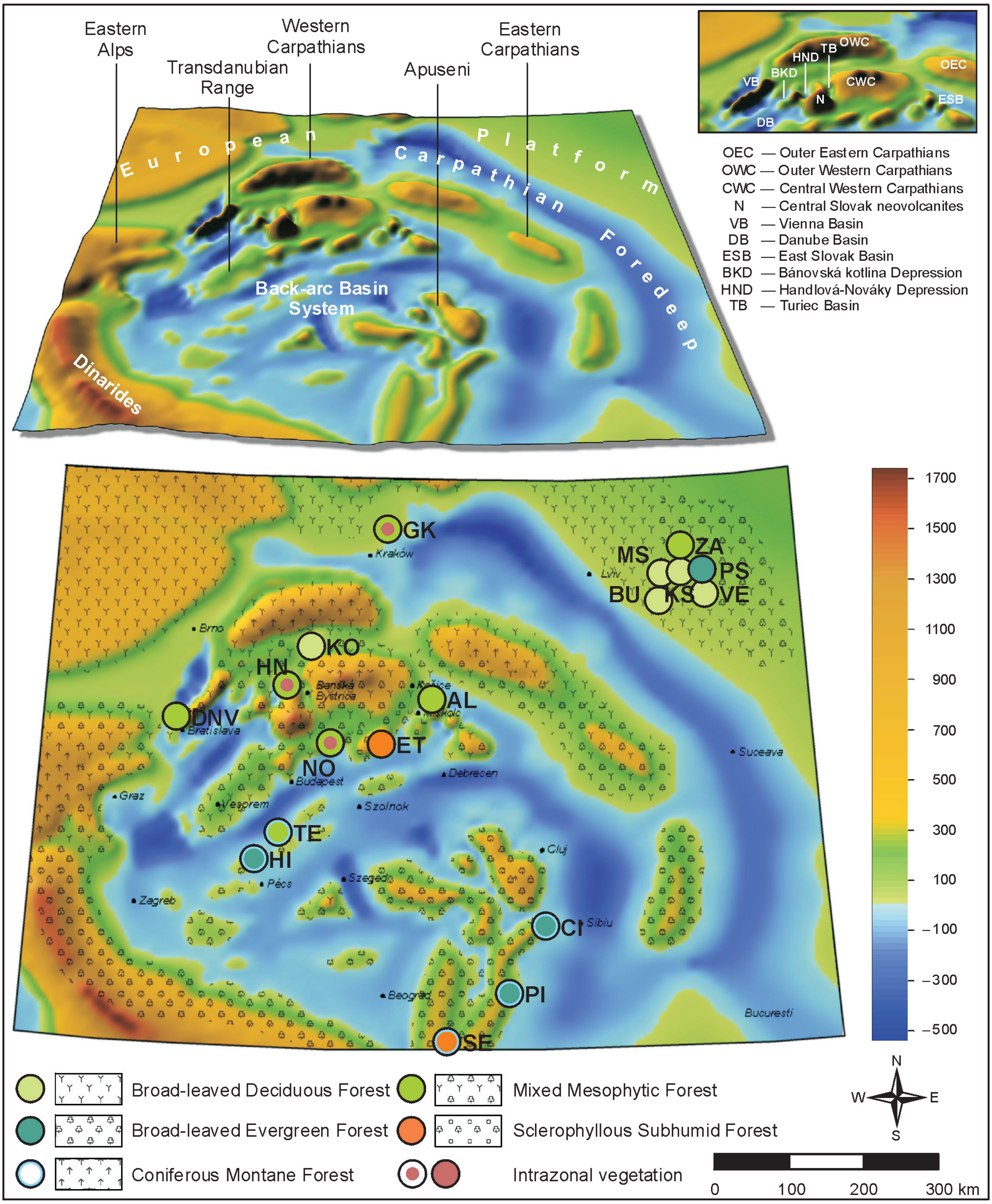

Fig. 3. DEM of the Central Paratethys: landscape & vegetation cover during the Late Badenian. Abbreviations of the localities and numbers of vegetation units: **AL** — (2) Core Alsóvadász 1; **BU** — (1, 9) Burkalo; **CI** — (3) Ciocadia; **DNV** — (2, 7, 10) Devínska Nová Ves — brickkiln; **ET** — (4) Eger-Tihamér; **GK** — (2, 8, 9, 10) Gdów area, core Kłaj 1, depth 30–405 m; **HI** — (2, 10) Core Hidas 53; **HN** — (2, 7, 9) Handlová-Nováky; **KO** — (1, 9) Kolisky; **KS** — (1, 9) Kosov; **MS** — (1, 7) Myshin; **NO** — (2, 9) Nográdszakál, Páris valley; **PI** — (3) Pirlage; **PS** — (3) Pistynka; **SE** — (4) Selishte; **TE** — (2, 10) Core Tengelic 2; **VE** — (1, 9) Verbovets; **ZA** — (2, 9) Zalescy.

nied by other deciduous Fagaceae. *Acer* was diversified in several species, among which *Acer aegopodifolium* (syn. *A. quercifolium* — see Ströbitzer-Hermann 2002; Walther & Zastawniak 2005) appears for the first time in the Central Paratethys (Kovar-Eder et al. 1994), together with *Ginkgo*, *Eucommia* both arriving from Asia via the Turgay migration route. Over most of the Central Paratethys, warm-temperate Mixed Mesophytic Forest thrived, only in the Western Carpathians and the Transcarpathian Ukraine some sites already acquired the character of Broad-leaved Deciduous Forest, probably due to influence of mountains or due to cooling effect of intensive volcanic activity (Navrotskaja et al. 1991; Syabryaj 1992). The proportion of herbs was generally low, not indicating lowland open vegetation (Syabryaj & Stuchlik 2004).

Extrazonal mountain forests are well discernible in pollen assemblages, as at Devinská Nová Ves (Sitár & Kováčová-Slamková 1999), where the coniferous belt reflected by the dominant pollen of *Pinus* includes additional high-mountain elements, such as *Cedrus* and *Tsuga*. Its lower boundary may have decreased towards 1200 m a.s.l. However, this guess is only inferred from the analogous Recent situation in the Colchis area (Stuchlik & Kvavadze 1987; Klotz 1990).

In the intrazonal *Glyptostrobus* peat-forming forests, *Byttneriophyllum* and *Alnus* constituted a basic community, which became wide spread later in the Neogene. Among riparian elements, *Platanus leucophylla* is occasionally present. Lignite-forming communities are typically developed in intra-montane depressions (e.g. Handlová and Nováky) and they are also common in the lowlands outside the Paratethys area in Poland and Germany (Lusatia seam 1). The corresponding phytostratigraphical level in the Boreal Province is probably represented by the Floral Assemblage Schipkau-Konin *sensu* Mai (2001), but this correlation is opposed by Krutzsch (2000.) The paleofloristic differentiation around the Late Badenian and Early Sarmatian boundary has been discussed with little success to give clear-cut differences based on plant megafossils (Němejc 1951, 1967; Shvareva 1965; Sitár 1967, 1982). It is still uncertain, which Early Miocene elements did not enter the Sarmatian flora, where broad-leaved deciduous trees predominate. In her pollen assemblages, Planderová (1990) created a transitional Zone MF7 for this type of flora in the Slovak Neogene. Its pollen spectra include a very low proportion of or no thermophilous Symplocaceae, Sapotaceae and Cyrillaceae.

Late Miocene — model of the Middle Pannonian landscape and vegetation of the Central Paratethys

During the Late Miocene, the area of the Central Paratethys gained paleogeographical features similar to the present situation in the Carpathian-Pannonian region. The main difference was represented by flooding of the intra-Carpathian region and the foredeep depocentres, which were restricted to the southeastern foreland of the Eastern Carpathians in that time (Jiříček 1979; Meulenkamp et al. 1996). Thus a connection of the brackish Eastern Paratethys with the Lake Pannon originated (Magyar et al. 1999).

The Late Miocene geodynamic development of the Carpathians can be characterized by termination of collision between the Western Carpathian and the European platform and reinforced collision connected with subduction in front of the Eastern Carpathians. This process was followed not only by the uplift of the accretionary wedge loop, but also by the uplift of the whole Carpathian orogene mountain chain.

Pull of the active subduction in front of the Eastern Carpathians southern edge led to the "second" rifting phase in the back-arc basin at the begining of the Pannonian, followed by thermal post-rift subsidence (Lankreijer et al. 1995; Kováč 2000; Konečný et al. 2002). Among the Late Miocene basins of the intra-Carpathian domain formed in an extensional regime, flexural basins without important fault activity prevailed, although in the Early Pannonian normal and strike slip faults allowed development of small pull-apart basins (Vass et al. 1988, 1993; Tari et al. 1992; Fodor 1995; Kováč et al. 1998; Kováč 2000; Konečný et al. 2002). The Lake Pannon — the Pannonian basin system was gradually filled up by deltaic deposits, generally from the northwest toward the southeast. The sedimentary environment gradually changed from a brackish deepwater to a shallow water — lake environment due to isolation from the Mediterranean and Eastern Paratethys (Magyar et al. 1999). At the northern margin of the Lake Pannon, marshes, swamps and deltaic systems spread in an ever-larger extent. Due to the retreat of the coastal line the lacustrine environment changed generally into alluvial also in the Late Pannonian. Later, in the Pliocene a broad area of lowlads appeared in the hinterland of the Carpathian chain. Scattered mountains (e.g. the Transdanubian Range Mts, Bükk Mts, Apuseni Mts) and basalt volcanoes formed higher morphological elevations.

At the end of the Late Miocene, tectonic inversion of the basin system (Horváth 1993, 1995; Horváth & Cloetingh 1996) led to the retreat of the aquatic sedimentary environment in the whole intra-Carpathian area, exept the central and southeastern regions. Uplift of the Eastern Alps, the Western and Eastern Carpathians was associated with angular unconformity between the Middle and Late Miocene (or younger) strata.

The architecture of the Late Miocene fill of the Pannonian basin system was distinctly influenced by paleogeographical changes. From the sequence stratigraphy and depositional systems point of view, the succession of the Late Miocene sediments can be characterized at first by a dominant portion of proximal deltaic deposits (A–C zones, *sensu* Papp 1951), which pass upward into distal deltaic to basinal fine-grained clay–silt–sandy facies (D, E zones). Fluvio-lacustrine sediments with coal seams (F–H zone) formed the terminal part of the Pannonian. The overlying Pliocene strata were deposited mostly in an alluvial sedimentary environment. The Pannonian cyclicity can be correlated by global changes Tor-1 cycle (11.6–9.3 Ma, *sensu* Hardenbol et al. 1998) and Tor-2 cycle (9.3–7.2 Ma, *sensu* Hardenbol et al. 1998).

The DEM model of the Central Paratethys during the Middle Pannonian (Fig. 4) documents the extinction of the sedimentary area of the Carpathian Foredeep, except its southeastern part and uplift of the Carpathian mountain chain. At that time, a maximum extent of brackish seawaters covered the intra-Carpathian domain.

The expected paleo-relief of the Carpathian orogenic chain in the Late Miocene began to match the present-day situation, characterized by the presence of both mountains and lowland areas. A difference can be seen in the more elevated belt of the Outer Carpathian accretionary wedge, which formed a natural barrier between flat territories of the European platform and the ever-subsiding Pannonian basin system covered by the Lake Pannon. During the Pannonian and Pliocene, basalt volcanic activity also participated in paleo-orography of the back-arc region (Kováč et al. 1998; Kováč 2000).

The Middle Pannonian vegetation (Fig. 4) corresponds to the warm temperate climatic zone with evidence of sporadically present termophilous and evergreen taxa. A higher percentual proportion of non-arboreal pollen (10 to 14 %) indicates local vegetation of partly open woodland (i.e. woods with open canopy). An increase of halophytic taxa documents the presence of coastal lagoons and marshlands during the lowstand of the brackish sea. Swamp vegetation, which grew directly on swamp substrates, is characterized mainly by noteworthy Taxodiaceae trees. They are often present in the association with Myricaceae and subordinary Nyssaceae. The riparian forest elements subdominantly occurred with *Alnus* and *Ulmus.* The extrazonal vegetation of the mountain areas with *Picea*, *Tsuga*, *Abies*, *Cedrus* is well represented in the pollen spectra.

During the Late Pannonian, the Western Carpathian paleogeography started to change. The Lake Pannon withdrew southwards, the nothern margin of the back-arc basin was slightly uplifted with the progradation of deltaic and alluvial facies, especially in lowlands. These areas were often covered by hygrophilous plants: *Myrica*, *Salix*, *Ulmus*, *Alnus.* Herbs were represented by Chenopodiaceae, Asteraceae, Ericaceae, Poaceae and *Artemisia.* Unevenly high moutain relief of the uplifted mountain chains created ideal conditions for the mixed mesophytic forests with *Carya*, *Quercus*, *Craigia*, *Carpinus*, *Fagus*, *Picea*, *Abies*, *Tsuga* and *Pinus.*

The reference sites considered on the map have been assigned to the Pannonian zones C–E *sensu* Papp 1951, namely the time slice before the major spreading of the lignite facies over the Pannonian Basin (zone F). The dating is based mostly on molluscs or regional correlation, rarely on mammals (MN9 Zone). Additional sites of Early Pannonian age (zones A–B) are shown in brackets on the map. They indicate the previous vegetation type at the Sarmatian/Pannonian boundary. Most leaf assemblages of Pannonian age are at least partly intrazonal and it is difficult to obtain a true picture of zonal vegetation from them. Most spore/pollen assemblages, mainly from the Hungarian Pannonian, have not been revised and the stratigraphic position of pollen samples remains partly uncertain.

At the very beginning of the Pannonian, subtropical conditions returned to some parts of the Central Paratethys. The thermophilous vegetation from southern Austria (Mataschen, Styrian Basin, Pannonian B — Kovar-Eder 2004) can also be found to the north-western periphery outside the Paratethys (Gozdnica) and may correspond to the Floral Assemblage ("Florenkomplex") Düren *sensu* Mai (1995) in western Europe with the latest occurrences of mastixioid plants. However, the dating of Gozdnica is still under dispute (see Dyjor et al. 1992, 1998; Mai, personal communication).

Later in the Pannonian, thermophilous evergreen, partly sub-humid vegetation remained in the south and south-eastern parts (Serbia, southern Hungary, the Borod Basin in Romania). In the Middle Pannonian, broad-leaved deciduous and Mixed Mesophytic warm-temperate to temperate forests with a low proportion of evergreen elements generally became widespread over the Central Paratethys (Styrian Basin, Molasse Zone, Vienna Basin). Characteristic elements in these communities included *Fagus haidingeri–pliocenica* complex, *Quercus* (?*Castanea*) *kubinyii*, *Quercus pseudocastanea–pseudorobur* complex, *Carpinus* sp. div., *Betula*, *Acer integrilobum*, *Acer vindobonense* and *Acer subcampestre* (syn. *Acer jurenakyi*) (Kovar-Eder 1988; Ströbitzer-Hermann 2002; Ströbitzer-Hermann & Kovar-Eder 2003). Cooling trends can be traced in spore/pollen spectra from the cores in the Pannonian Basin (Nagy & Planderová 1985; Nagy 1992). At some sites (Alsóvadász, Suchohrad) somewhat higher frequencies of Chenopodiaceae and *Artemisia* (max. 15 %) may indicate patches of herbaceous vegetation on marshes within broad-leaved deciduous forests. However, high mean annual precipitation (Bernor et al. 2003) prevented the development in this aera of open woodland and grassland vegetation like that suggested for south-eastern to southern Ukraine outside the Central Paratethys (Syabryaj 1999, 2003). Temperate purely deciduous broad-leaved forests were also spread during the Middle Pannonian in the Western Carpathians (e.g. sites at Nové Ustie in the Orava Basin and Martin in the Turiec Basin). In most cases these assemblages include a considerable proportion of intrazonal elements, both woody and aquatic (*Trapa*). Characteristic riparian woody elements were Salicaceae, *Platanus leucophylla*, *Alnus ducalis*, *Alnus cecropiifolia*, and partly intrazonal *Quercus gigas* and *Pterocarya paradisiaca.* The dominant peat-forming community during the whole Pannonian consisted mostly of the *Glyptostrobus-Byttneriophyllum-Alnus* swamp forest. This swampy coal-forming vegetation reached its widest distribution over the Pannonian Basin during the Late Pannonian, as the large extension of the lignite facies in Hungary, southern Moravia, Slovakia and Serbia corroborates (Knobloch 1969; Givulescu 1992; Pantić & Dulić 1993; Hably 2003).

Extrazonal montane conifers of all kinds (including *Tsuga*, *Cedrus*, *Picea*, *Abies*, *Keteleeria*) were found in pollen spectra throughout the Pannonian Basin as regular accessories. In the intra-montane basins macrofossils of these conifers were also formed (Nove Ustie, Martin). Therefore we may expect high mountain conifer belts reaching over 1500 m a.s.l. on the Carpathian and Alpine ridges and descending to medium altitudes, mixed with deciduous broad-leaved elements.

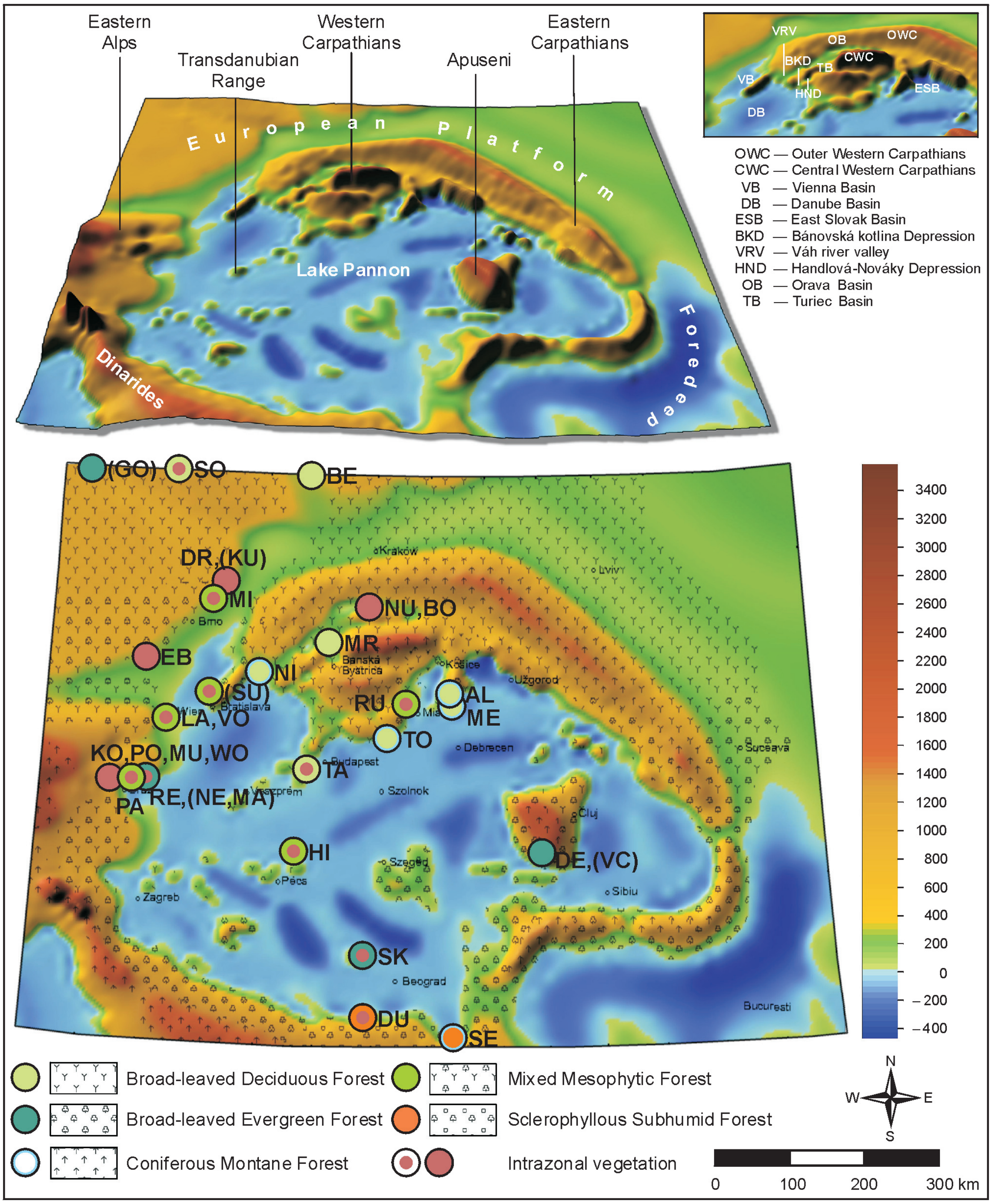

Fig. 4. DEM of the Central Paratethys: landscape & vegetation cover during the Middle Pannonian. Abbreviations of the localities (in brackets earliest Pannonian, not considered for raster pattern) and numbers of vegetation units: **AL** — (1, 10) Core Alsóvadász 1, depth 155.8–240 m, Cszerehát environment; **BE** — (1, 8, 9, 10) Belchatow, upper level (section VI.1, KRAM-P 17, Stawek-1A); **BO** — (9, 10) Bobrov, core V 6; **DE** — (3) Delureni; **DU** — (4, 9) Dubona I; **EB** — (9) Ebersbrunn; **(GO)** — (3, 8, 9, 10) Gozdnica; **HI** — (2, 8, 9, 10) Core Hidas 53, depth 298–367 m; **(HO)** — (8, 9) Höllgraben; **KO** — (9) Kogelwald, core KO 4; **(KU)** — (7, 8) Kunovice, cores KU 1, depth 42-46 m, KU 2, depth 109–174 m; **LA** — (2, 9) Laaerberg; **(MA)** — (3, 8) Mataschen near Fehring; **ME** — (1-2, 9, 10) Core Megyaszó 1, depth 52–206 m; **MI** — (2, 8) Mistřín, DV 4 Mine; **MR** — (1, 8, 9) Martin, Turiec Basin; **MU** — (7, 9) Münzengraben, core MÜ 21; **(NE)** — (3) Neuhaus/Klausenbach; **NI** — (1, 8, 10) Nitra environs, Vozokany, core N-7, Rohoznica, core N-8, Mechenice, core B-23, Pohranice, core B-25; **NU** — (8, 9) Nové Ustie, Orava Basin; **OR** — (7, 8) Ořechov, Polešovice, cores UH 18, depth 11.3 m, UH 19, depth 14.1–29.4 m; **(PA)** — (2, 8, 9) Paldau; **PO** — (7, 9) Pöllau, core PÖ 2; **RE** — (3, 8, 9) Reith near Unterstorcha; **RU** — (2, 7, 9) Rudabánya; **SK** — (3, 9) Sremska Kamenica; **SO** — (1, 8, 9) Sośnica; **(SU)** — (2, 9, 10) Core Suchohrad 32, depth 625–638 m; **TA** — (1, 9, 10) Tata, Core TVG 26 depth 7–39m; **TO** — (1, 9, 10) Core Tököl 1, depth 688.5–730 m; **(VC)** — (3, 4) Valea Crisului; **VO** — (2, 8, 9) Vösendorf; **WO** — (8, 9) Wörth near Kirchberg/Raab.

Paleoclimatic trends

Palaeoclimatic proxies are available for many sites considered in the presented maps (see Mai 1995). Most of them have been derived from "intuitive" comparisons with extant vegetation, while the objective co-existence and leaf physiognomical (CLAMP) methodologies have not been largely applied so far.

Broad-leaved evergreen forests, including the "Late Mastixioid Floras", were usually compared with similar forests in monsoon East Asia. In general, the climate corresponding to this type of vegetation was humid to per-humid (annual sum of precipitation about 1000 to 3000 mm), with heavy rains prevailing in the summer, but without any month with a humidity deficit. The temperature of the coldest month varied between 4–10 °C and absolute minima rarely reached under zero. The Mean Annual Temperature (MAT), according to various estimates (e.g. Mai 1995) varied in larger spans, according to the percentage of evergreen taxa, from 13 to almost 20 °C. The climate must have been quite equable, with a range of temperature less than 25 °C. This is a prevailing condition in the Karpatian to Lower Badenian stages over the Central Paratethys. Only in some parts, high summer mean temperatures over 20 °C and also dry substrate caused a relative humidity deficit and local expansions of sub-humid sclerophyllous (microphyllous) evergreen forests. This type of forest has nothing to do with the etesian (Mediterranean-type) climate and was probably more similar to the microphyllous montane forests in drier parts of the Himalayas today.

The cooling trends expressed by the decline of MAT in the Late Badenian over northern and eastern parts of the Central Paratethys caused changes in the forests. Evergreen elements mostly withdrew southwards and only less frost-sensitive trees remained forming the Mixed Mesophytic Forest with high representation of deciduous taxa. MAT, under which this type of vegetation optimally thrives, is variously estimated, depending on what type of forests is brought for comparison — East Asiatic or North American (Wolfe 1979). While in the former, the Coldest Month Mean Temperature (CMMT) is usually quite low (up to –2 °C), the latter thrives in warmer, subtropical conditions (northern Florida — mean annual temperature ca. 20 °C, January mean up to 10 °C). In general, the following estimation of the decline in temperature can be expected for the Central Paratethys from the published data (e.g. Mai 1995) — MAT 16(–?10) °C, that is lowering by about 3 °C in comparison with the Karpatian, and adequate lowering of the January mean, which may have been even stronger, because of decrease of climatic equability. The sum of Mean Annual Precipitation (MAP) remained high enough for humid conditions in any case, also thanks to the colder climate. Such warm temperate conditions predominated during the Late Badenian and the Middle Pannonian. In the Pannonian in northern and easterly parts of the area studied, particularly near the mountains, the Deciduous Broad-leaved Forests indicate still more severe deterioration of climatic conditions. These temperate forests dominated by deciduous oaks and beech and intermixed with various Pinaceae withstood decrease of CMMT up to –10 °C, particularly on higher altitudinal habitats. The impact of such severe winters was certainly milder due to heavy snows, as is the case today in East Asia, particularly in Japan. Equally high precipitation throughout the year also prevented expansion of herbaceous steppe vegetation, although patches of it can be noticed in the pollen record within deciduous broad-leaved forests in the Middle Pannonian. Due to high humidity of climate, extensive lignite deposits originated over most of the Paratethys area and its north and west periphery.

Conclusions

After having compiled the presented Miocene geobotanical maps according to the methodology applied above, the following conclusions can be drawn for the future research in other areas and time slices of the Cenozoic.

Contrary to various models of ancient Cenozoic vegetation that rely on the physiognomy and composition (diversity) as well as abundance of elements (e.g. Wolfe 1979; Mai 1995), the presented system of vegetation units is much more simplified. It surely suffers from various deficiencies. It neglects abundance. But this parameter is, in our opinion, not objectively derivable from frequencies of fossils in a given site or core level. Another weak point of the system employed above is that individual elements with a broader ecological span can enter more units or they are transitional and their foliar physiognomy (evergreen vs. deciduous) cannot be precisely identified (e.g. *Symplocos*, *Engelhardia*). The defined vegetation formations were certainly not profoundly clear-cut in ancient landscapes and transitions between them existed. Still the diversity percentages are most objective characteristics for a given assemblage and can be verified any time, the assignment into the system of the defined vegetation formations as characterized above (see also Kovar-Eder et al. submitted) is easy and mostly unequivocal.

According to our experience, it is advisable to use paleogeographical and geobotanical maps of narrow time slices, because they reveal better consistent patterns of vegetation and its dynamics in spite of fewer reference localities. When a longer time interval has been considered, local differences between the sites sometimes expressed trends in time rather than climatic gradients in space (see Fig. 3 for the Early-Middle Pannonian).

Megafossil and spore/pollen plant records were combined, whenever feasible, to gain better understanding of taxonomy and ecology of elements composing assemblages. Of course, great problems exist, concerning how to transfer spore/pollen diagrams with various enigmatic plant elements into a formation with known physiognomy. In the fututre, it would be desirable to unify views on the taxonomy of those elements of uncertain affinities both in megafossil and spore/pollen records.

Older data of paleobotanical and palynological research have not been neglected but revised and transferred to a common nomenclature, when the documentation (illustrations, preparations) was available and re-studied. In many cases, such assemblages and their elements were wrongly interpreted, or wrongly assigned to the natural system. Yet the current progress in knowledge of whole fossil plants is improving these inconsistencies. Actuopalynological studies of Recent vegetation (e.g. Stuchlik & Kvavadze 1987; Kvavadze & Stuchlik 1990, 1993) offered important clues for converting spore/pollen spectra into various types of real vegetation. It would be worth attempting to apply for the same sets of fossil data the new methodology presented in this account, which is based on proportions of components and diversity, along with that currently employed by palynologists, which uses abundance percentages of elements.

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