Available online at www.sciencedirect.com
ScienceDirect
PALAEO
Palaeogeography, Palaeoclimatology, Palaeoecology 253 (2007) 131 – 156
www.elsevier.com/locate/palaeo

Neogene flora and vegetation development of the Pannonian domain in relation to palaeoclimate and palaeogeography

Boglárka Erdei [a,*], Lilla Hably [a], Miklós Kázmér [b], Torsten Utescher [c], Angela A. Bruch [d]

[a] *Botanical Department, Hungarian Natural History Museum, H-1476, P.O.Box 222, Budapest, Hungary*
[b] *Department of Palaeontology, Eötvös Lóránd University, H-1518, P.O.Box 120, Budapest, Hungary*
[c] *Institut für Geologie, Nussallee 8, 53115 Bonn, FRG, Germany*
[d] *Senckenberg Research Institute, Senckenberganlage 25, 60325 Frankfurt am Main, FRG, Germany*

Received 28 February 2005; received in revised form 26 February 2007; accepted 5 March 2007

Abstract

A survey of the Neogene flora and vegetation pattern of the Pannonian domain based on selected fossil plant assemblages is given. The paper aims to reveal the complex interrelation of tectonic-palaeogeographic evolution, climate, flora and vegetation development through the Neogene of the Pannonian domain. Flora and vegetation patterns are based on well-documented and studied fossil plant assemblages (macrofloras, primarily leaves). There are time intervals well-represented in the fossil record, e.g. the Pannonian or the Sarmatian and others with relatively few localities, e.g. the Badenian. A general but slow cooling trend is definitely observable after the Early Miocene as reflected by both quantitative climate reconstructions and floristic change, i.e. decrease of diversity, slow disappearance of thermophilous and exotic elements, as well as decrease in the variety of vegetation types. A significant decline of coldest month temperatures (as compared to warmest month temperatures) must have played a defining role in forming flora and vegetation through the Neogene. As compared to climate estimates for the Middle/Late Miocene fossil floras, warmer climate conditions are indicated by the Ipolytarnóc flora and vegetation comprising an extremely high number of thermophilous taxa as well as complex vegetation structure. The Early and Middle Miocene fossil assemblages bear a significant relevance to the tectonic pattern of the Pannonian domain. A transitional character in both flora and vegetation is indicated by the Karpatian Magyaregregy locality. Knowledge of the Badenian flora and vegetation is limited to the Middle Badenian Nógrádszakál assemblage indicating cooler climate conditions which contrasts with global climate change. In contrast to the relatively poor azonal vegetation of Nógrádszakál and most Pannonian localities, the more diverse Sarmatian and Pliocene floras display a strong relation to each other — attributable to palaeogeographic constraints.

Keywords: Fossil flora and vegetation; Palaeoclimate; Palaeogeography; Tectonics; Neogene; Pannonian domain; Hungary

1. Introduction

Several palaeovegetation and climate studies concentrating on limited time intervals or regions of the Neogene in the Pannonian domain have been published so far, e.g. first studies by Andreánszky (Andreánszky, 1963a, 1964); Pannonian/Pliocene (Hably and Kvaček, 1997,

* Corresponding author. Tel.: +36 1 2101330; fax: +36 1 3141483.
E-mail addresses: erdei@bot.nhmus.hu (B. Erdei), hably@bot.nhmus.hu (L. Hably), kazmer@ludens.elte.hu (M. Kázmér), utescher@geo.uni-bonn.de (T. Utescher), abruch@senckenberg.de (A.A. Bruch).

0031-0182/$ - see front matter © 2007 Elsevier B.V. All rights reserved.
doi:10.1016/j.palaeo.2007.03.036

1998; Hably, 2003), Sarmatian (Andreánszky, 1959; Erdei and Hír, 2003), however, a modern survey of the Miocene/Pliocene vegetation pattern discussed in the context of quantitative climate analysis for the Pannonian domain, as well as plate tectonics and palaeogeography is presented for the first time. The Pannonian and the Carpathian Basins are relatively young, formed after the Middle Miocene (Neoalpine structural stage, Kovács et al., 1996–97), therefore we apply the term "Pannonian domain" in the sense as it is used by Kovács et al. (1996–97).

The main purpose of this study is the complex evaluation of temporal and spatial vegetation and floristic changes, like appearance of temperate elements, disappearance of thermophilous ones, variation of diversity, as well as, results of quantitative climate analysis with a suggested plate tectonic framework and development of the area. Detailed studies on the geology, stratigraphy, tectonics and palaeozoology of the area are instrumental in evaluating fossil plant assemblages.

The parallel adoption of a plant functional approach (cf. Utescher et al., 2007-this volume) for the vegetation analysis of numerous fossil assemblages discussed here (e.g. Nógrádszakál, the Erdőbénye floras) offers an opportunity for a comparison of various methods established for vegetation reconstruction.

Applying the Coexistence Approach (Mosbrugger and Utescher, 1997) as a "standard" method for quantitative climate analyses of the fossil plant assemblages in the Pannonian domain will contribute to the climate data basis inevitable for the comparison of local and regional terrestrial palaeoclimates.

Earlier attempts at quantitative reconstruction of palaeoclimate or to obtain climate data are scanty (Andreánszky, 1963a, 1964; Hably and Kvaček, 1998). Climate studies have been mostly qualitative characterizing climate in a subjective, intuitive manner based on the vegetation or certain elements of the flora, e.g. Andreánszky's xerophytic flora elements (Andreánszky, 1963b,c) suggesting a climate similar to the recent mediterranean type.

2. Palaeogeography and tectonic structure of the Pannonian domain

2.1. Plate tectonic background

The area is composed of tectonic units (Alcapa, Tisza and Dacia) characterized by disparate developmental histories (Fig. 1). The palaeogeographic position of the Alpine–Carpathian–Pannonian (ALCAPA) and Tisza terranes during the Cenozoic is a matter of current debate. The large-scale plate tectonic framework is clear: an approaching Africa and Europe slowly and surely close the Tethys ocean (Dercourt et al., 1993), squeezing the enclosed microplates, terranes in various directions. Contrasting palaeogeographic reconstructions (for a review see Csontos, 1995, fig. 9) can be constrained by palaeomagnetic control. Measured declination data – describing rotation of terranes – are increasingly used (see e.g. Csontos and Vörös, 2004), while inclination – a function of latitude, among others – is not. There are embarrassing results of extremely southern palaeolatitudes for certain terranes (e.g. Anatolia: Kissel et al., 2003), placing them next to Africa even during Eocene time. Sceptics maintain that these extremely low latitudes are due to diagenetic compaction, to anomalies of the terrestrial dipole field, or to statistical error (for a review see Krijgsman and Tauxe, 2004). We present data corroborating that vegetation and the inferred palaeoclimate

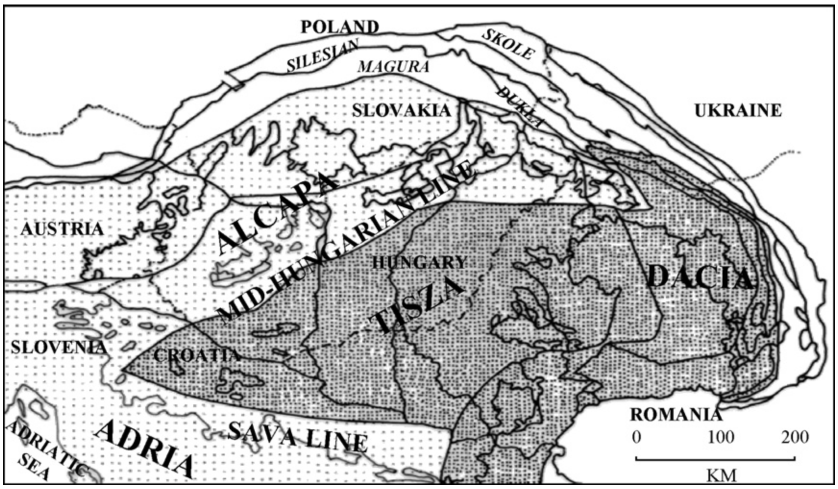

Fig. 1. Major tectonic units in the Pannonian domain (after Csontos, 1995, modified).

has changed in line with inferred palaeopositional change of at least one terrane, the ALCAPA block of the Carpathians.

2.2. Miocene–Pliocene palaeogeography of the Pannonian domain

After the first isolation of the Paratethys during the Early Oligocene (Báldi, 1980) the palaeogeography of the Pannonian domain had been fundamentally related to the subsequent isolations and regressional–transgressional phases of the Paratethys. Likewise, connected to the Cenozoic tectonic evolution of the area, intense volcanic activity accompanying or following the main Neogene orogenic phases had a crucial effect on the palaeo-environment of the Pannonian domain area during the Neogene. The main phases and chronology of the Neogene volcanic events have been studied in detail by numerous authors (Gyarmati, 1977; Balogh et al., 1983, 1985; Pécskay et al., 1986; Hámor et al., 1987; Pécskay and Balogh, 1987; Ravasz, 1987; Csontos, 1995; Márton and Pécskay, 1995; Pécskay et al., 1995).

Detailed surveys of the Intra-Carpathian Miocene–Pliocene (Neogene) palaeogeography, the orogenic phases, subsequent isolations and opening of marine connections were published in numerous works (e.g. Hámor and Bérczi, 1986; Bérczi et al., 1988; in a larger geographic/spatial context e.g. Rögl, 1998; Harzhauser and Piller, 2007-this volume). Data relevant to the palaeogeographic evolution (see also Harzhauser and Piller, 2007-this volume) will be detailed in appropriate parts of the paper.

3. Material and methods

3.1. Fossil assemblages and stratigraphy

Neogene fossil plant assemblages included in this study (Figs. 2 and 3) are well-documented and dated by independent means (radiometric data, biostratigraphy, etc.; e.g. Ipolytarnóc, Gérce). Nevertheless, to obtain higher resolution, i.e. to compile data for most Neogene stages, additional floras (e.g. Karpatian flora of Magyaregregy) dated on the basis of lithostratigraphy were included (for standard chronostratigraphy see Harzhauser and Piller, 2007-this volume). There are time intervals well-represented in the fossil record, such as the Sarmatian or the Pannonian, both with numerous fossil plant assemblages like Erdőbénye, Tállya, Felsőtárkány, Sopron

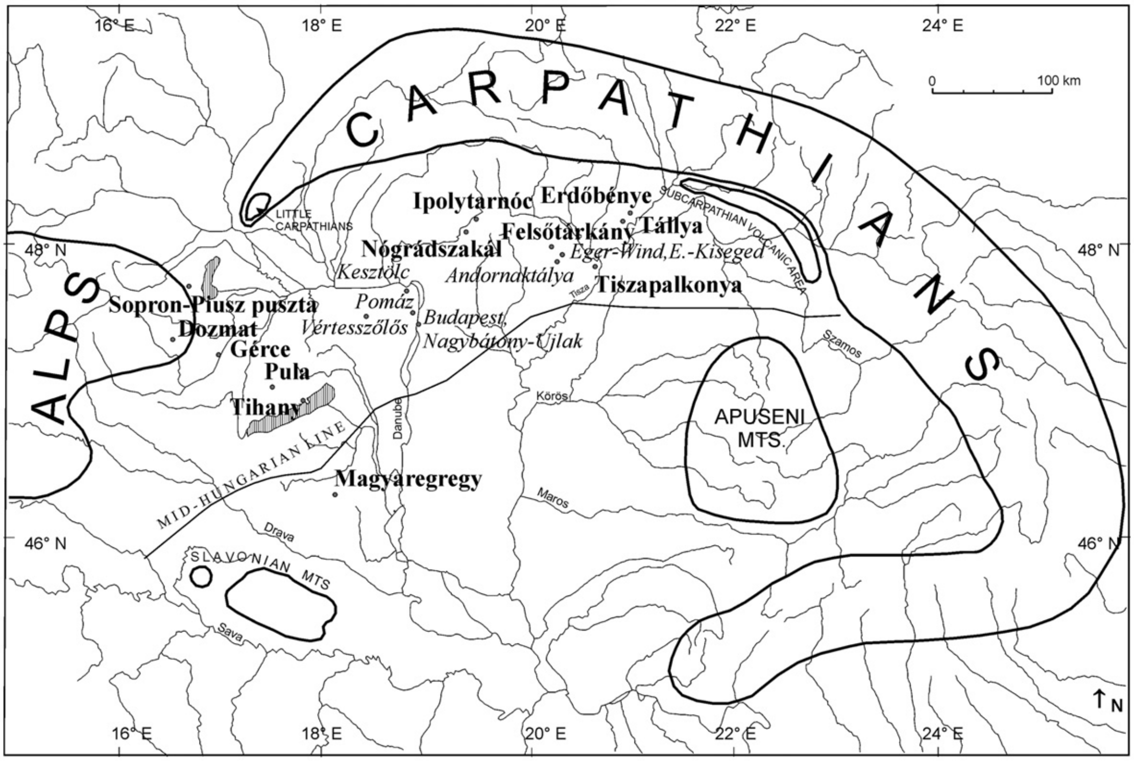

Fig. 2. Map indicating selected fossil plant assemblages of the Pannonian domain. Localities indicated with italic format represent Egerian sites that were also used in climate analysis.

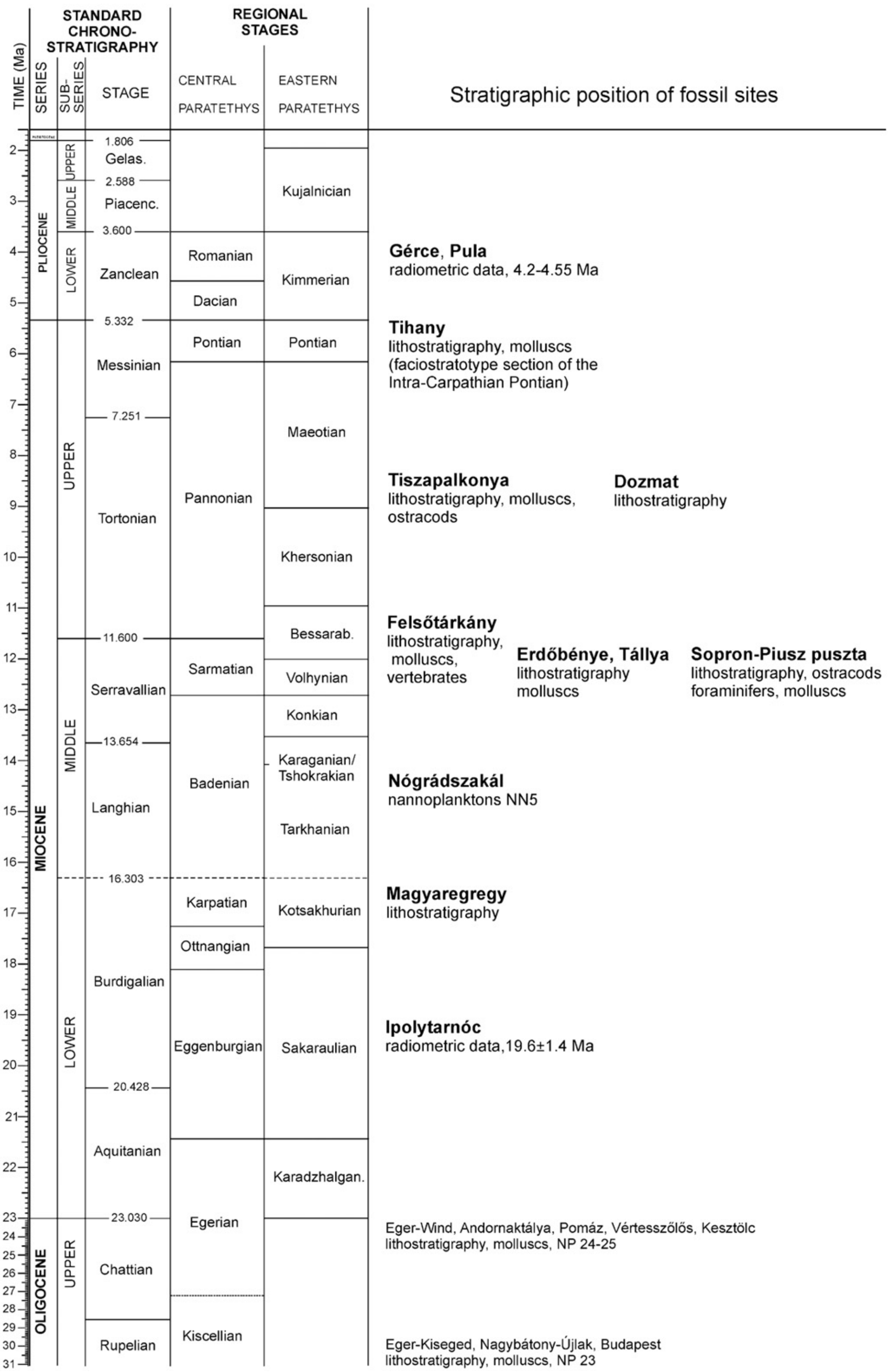

Fig. 3. Stratigraphic range of fossil sites involved in the present study. (Stratigraphic column after Harzhauser and Piller, 2007-this volume).

Piusz puszta, Dozmat and Tiszapalkonya and others with relatively few localities like the Badenian with the flora of Nógrádszakál. Localities involved represent mostly the northern and western parts of the Pannonian domain and comprise mainly leaf floras, rarely fossil fruits and seeds or dispersed material.

The Ipolytarnóc fossil assemblage (Gyulakeszi Rhyolitic Tuff Formation, N Hungary) is of Early Miocene age (Bartkó, 1985); based on radiometric dating the rhyolitic tuff comprising the flora is of 19.6±1.4 Ma (Balogh in Bartkó, 1985; Eggenburgian/beginning of Ottnangian, see Harzhauser and Piller, 2007-this volume). The fossiliferous rhyolitic tuff was deposited in a terrestrial (fluviatile) environment. The rather poor fossil flora of the underlying sandstones which is well-known for its mammal and bird foot-prints is not included in the present study. The fossil leaf assemblage comprises macromorphologically preserved imprints of leaves (Hably, 1985).

The younger Magyaregregy flora (Mecsek Mts, SW Hungary) is of Early Miocene age (Karpatian, lithostratigraphy of the so-called fish scale marl, Budafa Formation; Barabás, 1994). The extensive deposits were formed during the same time slice, in similar facies.

A modern survey of the Early Miocene flora of Magyaregregy has not been published so far. However, a great amount of information has accumulated based on a huge collection of fossil plants involving more than 3000 specimens (Staub, 1882; Pálfalvy, 1953; Andreánszky, 1955; Pálfalvy, 1961; Hably, 2001, 2002; Hably and Thiébaut, 2002). Fossil plant assemblages of the fish scale marl (Magyaregregy – known for a long time/ Pálfalvy, 1953; Andreánszky, 1955/; Kisbattyán – fossils have been collected for the last 10 years by Hably) were transported from the former vegetation cover into the sedimentary basins in a similar way and indicate the same character. An additional assemblage, discovered and collected just recently in Kisbeszterce, represents the same time slice but in volcanic facies. The assemblage is composed of imprints and, very rarely, compressions of leaves, fruits and seeds.

The fossil flora of Nógrádszakál (Baden Clay Formation, N Hungary; Kordos-Szakály, 1984) comprising mainly leaves is preserved by clays (NN5, Nagymarosy, 1980; Middle Badenian, see Harzhauser and Piller, 2007-this volume), as well as intercalated tuffitic beds.

Sarmatian and Pannonian are the best timeslices represented by fossil floras in the Neogene of the Pannonian domain. The Erdőbénye (Kõvágó oldal, Barnamáj, Ligetmajor), Tállya, and Sopron–Piusz puszta floras are all preserved in sediments deposited during the Sarmatian as indicated by lithostratigraphy, microfossils, and molluscs. The Erdőbénye and Tállya assemblages, the so-called volcanic floras, were fossilized in shallow marine and limnic facies, in an environment characterized by intense volcanism, whereas in Sopron–Piusz puszta dispersed organic plant material was preserved by sediments of a prograding delta-system. The flora of Felsőtárkány, deposited in a lacustrine environment, occupies a transitional position — stratigraphic data (lithostratigraphy, vertebrates, molluscs) suggest late Sarmatian or even Early Pannonian (Erdei and Hír, 2003).

Pannonian and Pontian fossiliferous deposits are widely distributed over the area of the Pannonian domain, especially the Transdanubian region and northeastern Hungary, with fossil plant localities known from opencasts, as well as boreholes. The most representative assemblages involved here are Dozmat (Hably and Kovar-Eder, 1996) — plants preserved in clays overlying lignites, Tihany-Fehérpart (Hably, 1992a; the faciostratotype section of the Intra-Carpathian Pontian: Müller and Szónoky, 1989) and Tiszapalkonya (boreholes; Hably, 1992b). Pannonian formations attaining vast extent and thickness (even 6000 m in the Great Hungarian Plain) include mainly the clayey–sandy and lignitic deposits of the Pannonian Lake, as well as fluvial deposits. Its subdivision, however, has raised great problems and resulted in various classifications, e.g. Pannonian s. l. and Pannonian s. str. (for a review see Magyar and Hably, 1994).

The Pliocene (Romanian) floras from Gérce and Pula (Hably and Kvaček, 1997, 1998) have a quite clear stratigraphic position. Young (Pliocene–Pleistocene) basaltic volcanism played a significant role in forming the environment. During intense volcanic activity (starting with explosive eruptions) tuff rings were formed around craters followed by filling of some craters with alginite oil-shale and associated basalt bentonite (Solti in Hably and Kvaček, 1998 — Gérce 4.55 Ma, Pula 4.2 Ma) which preserved remains of the surrounding flora and vegetation.

3.2. Quantitative climate analysis

In the scope of the NECLIME programme, a quantitative climate analysis adopting the systematics based Coexistence Approach established by Mosbrugger and Utescher (1997) was applied to Neogene and Palaeogene fossil floras of the Pannonian domain, i.e. Romanian (Gérce, Pula), Sarmatian (Erdőbénye floras, Tállya, Felsőtárkány), Badenian (Nógrádszakál), Karpatian (Magyaregregy), Eggenburgian (?Ottnangian, Ipolytarnóc), Egerian (Eger-Wind, Pomáz, Kesztölc, Vértesszőlős, Andornaktálya; Erdei and Bruch, 2004) and

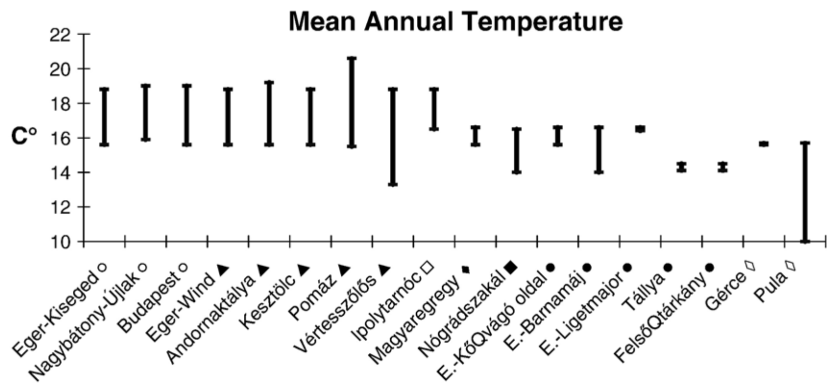

Fig. 4. Intervals for mean annual temperature (MAT), mean temperature of the coldest (CMT) and warmest (WMT) months, and mean annual precipitation (MAP) through the Neogene adopting the Coexistence Approach to fossil plant assemblages (see text for more details). Meaning of symbols: ○ — Kiscellian; ▲ — Egerian; □ — Eggenburgian; ♦ — Karpatian; ■ — Badenian; ● — Sarmatian; ◊ — Romanian.

Kiscellian (Eger-Kiseged, Nagybátony-Újlak, Budapest) floras (Fig. 2). In order to obtain a more extensive temporal survey of climate results of the quantitative climate, analyses applied to Egerian and Kiscellian floras were also included.

Most fossil assemblages included in the analysis comprise elements of the zonal vegetation which are most relevant for palaeoclimate reconstructions.

Some of the fossil floras do not meet the requirements of a climate analysis adopting the Coexistence Approach (few taxa appropriate for the analysis), i.e. Tihany (Pontian), Dozmat and Tiszapalkonya (Pannonian), Sopron–Piusz puszta (Sarmatian).

3.3. Palaeovegetation — Conventional classification and the plant functional approach

Reconstruction of palaeovegetation may be approached by means of various methods, e.g. qualitative and quantitative methods like the analysis of plant functional type diversity (PFTs) (see Utescher et al., 2007-this volume). Plant associations are classified and reconstructed here by means of a conventional interpretation of vegetation types which gives an opportunity to compare its results with those of the plant functional approach (see Utescher et al., 2007-this volume). Due to the higher level of subjectivity of the conventional method it does not give a consistent basis for plotting vegetation cover of extended areas on palaeogeographic maps. However, it may be quite useful for comparing palaeovegetation of various regions or time intervals and for confirming results obtained by other methods. On the other hand the conventional classification often results in a more detailed picture of the vegetation, in contrast to the comparatively crude picture of the PFT method employing diversities of different tree PFTs to classify fossil floras. The classes obtained are then interpreted in terms of major biomes.

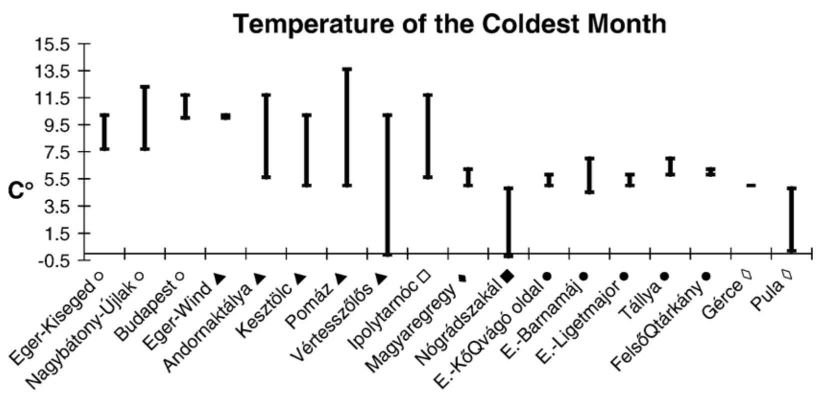

Fig. 5. Intervals for mean annual temperature (MAT), mean temperature of the coldest (CMT) and warmest (WMT) months, and mean annual precipitation (MAP) through the Neogene adopting the Coexistence Approach to fossil plant assemblages (see text for more details). Meaning of symbols: ○ — Kiscellian; ▲ — Egerian; □ — Eggenburgian; ♦ — Karpatian; ■ — Badenian; ● — Sarmatian; ◊ — Romanian.

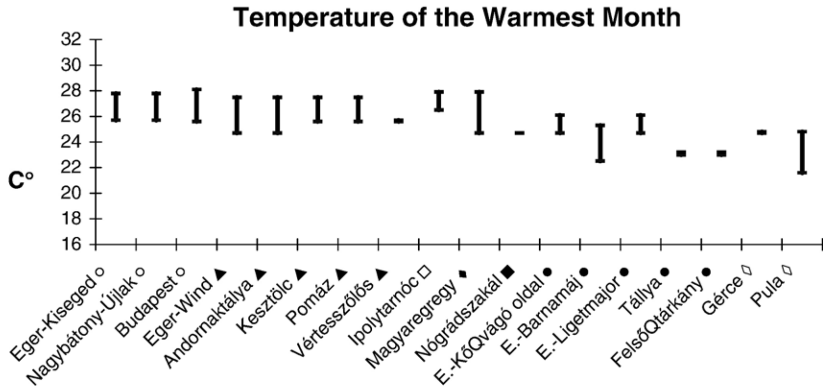

Fig. 6. Intervals for mean annual temperature (MAT), mean temperature of the coldest (CMT) and warmest (WMT) months, and mean annual precipitation (MAP) through the Neogene adopting the Coexistence Approach to fossil plant assemblages (see text for more details). Meaning of symbols: ○ — Kiscellian; ▲ — Egerian; □ — Eggenburgian; ♦ — Karpatian; ■ — Badenian; ● — Sarmatian; ◊ — Romanian.

Thus, combining the results obtained from both methods may improve our knowledge.

4. Results

4.1. Results of quantitative climate analysis

The charts (Figs. 4–8, Table 1) display intervals of values for four of the six climate variables estimated by adopting the Coexistence Approach (CA; Mosbrugger and Utescher, 1997), i.e. mean annual temperature (MAT), mean temperature of the warmest (WMT) and coldest (CMT) months, and mean annual precipitation (MAP) through the Early and Late Oligocene, Early, Middle and Late Miocene and Pliocene based on fossil plant assemblages of the Pannonian domain (Erdei et al., 2007). All three temperature variables (Fig. 4–6, 8) show a definite declining trend after the Eggenburgian/Ottnangian towards younger floras. The low values of CMT recorded by the Badenian flora of Nógrádszakál should be accepted with reservations since remains of the azonal vegetation is likely to be preserved in the fossil assemblage based on palaeovegetation reconstructions adopting the conventional method (see later). When analyzing azonal communities by the CA, broader coexistence intervals are expected, e.g. riparian forest with many pioneers and other taxa characterized by wide climatic ranges. Results obtained by the plant functional approach (Utescher et al., 2007-this volume) similarly indicate a cooler climatic aspect of the vegetation for the Badenian Nógrádszakál assemblage.

Although temperature variables display more or less the similar pattern, values for CMT (Figs. 5, 8) indicate a slightly larger decline than those of MAT

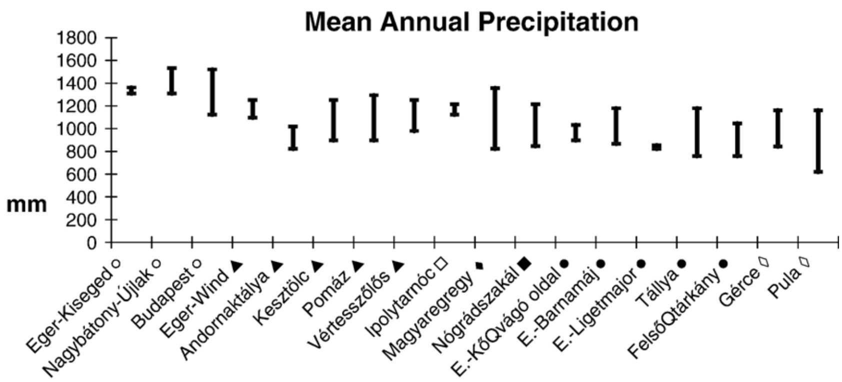

Fig. 7. Intervals for mean annual temperature (MAT), mean temperature of the coldest (CMT) and warmest (WMT) months, and mean annual precipitation (MAP) through the Neogene adopting the Coexistence Approach to fossil plant assemblages (see text for more details). Meaning of symbols: ○ — Kiscellian; ▲ — Egerian; □ — Eggenburgian; ♦ — Karpatian; ■ — Badenian; ● — Sarmatian; ◊ — Romanian.

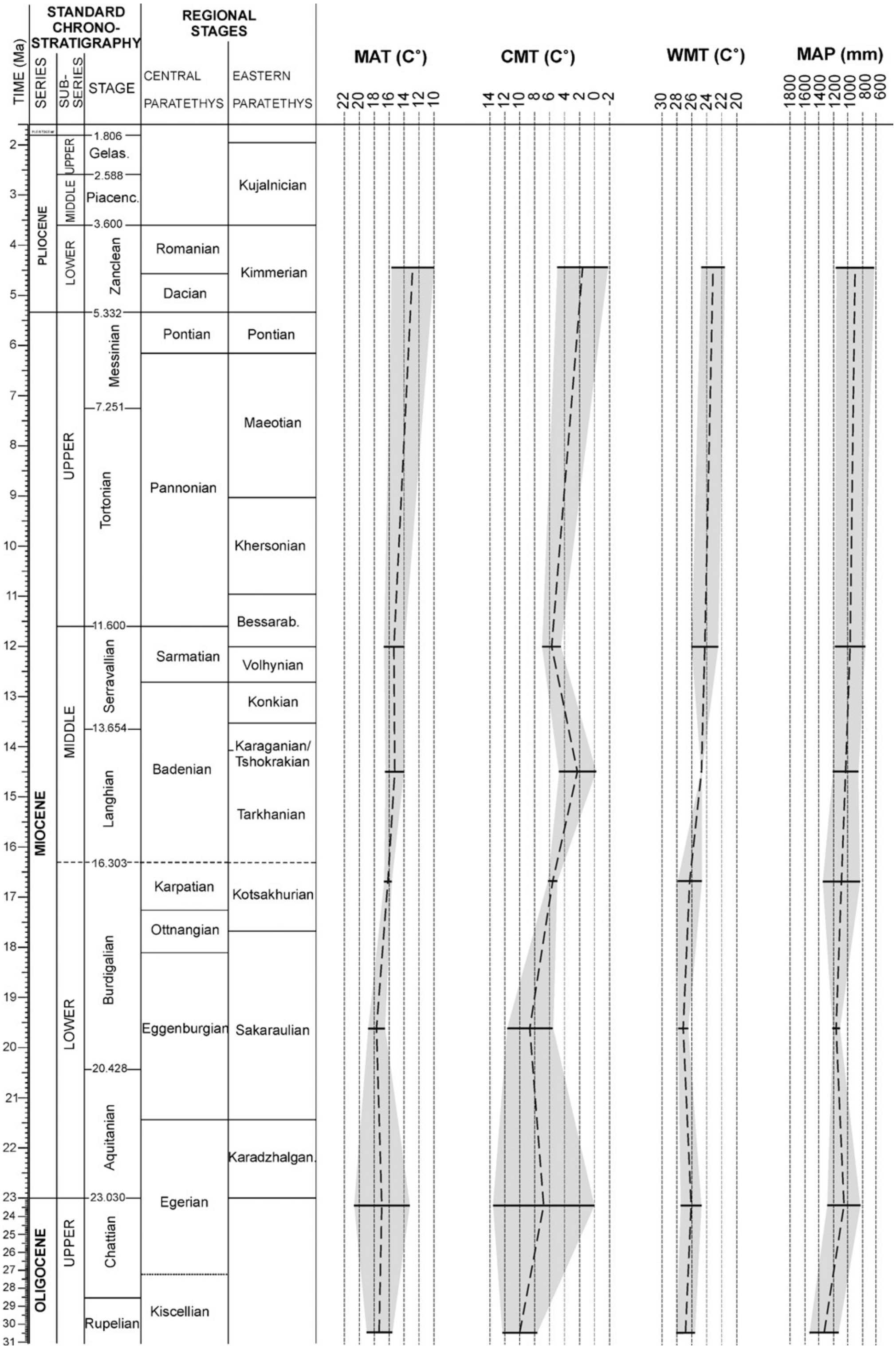

Fig. 8. Trend of climate variables (MAT, CMT, WMT and MAP) during the Kiscellian–Romanian time slice. Intervals are calculated cumulatively from intervals of the localities per each stage. Mean of intervals calculated for fossil floras per each stage are indicated. (Stratigraphic column after Harzhauser and Piller, 2007-this volume).

Table 1
Results of climate estimates adopting the Coexistence Approach (Mosbrugger and Utescher, 1997) to fossil plant assemblages of the Pannonian domain

Chronostratigraphy	Fossil assemblage	Mean annual temperature (MAT, °C)	Temperature of the coldest month (CMT, °C)	Temperature of the warmest month (WMT, °C)	Mean annual precipitation (MAP, mm)
Romanian	Gérce	15.6–15.7	5	24.7–24.8	843–1160
	Pula	10–15.7	0.2–4.8	21.6–24.8	619–1160
Sarmatian	Erdőbénye-Kővágó oldal	15.6–16.6	5–5.8	24.7–26.1	897–1032
	E.-Barnamáj	14–16.6	4.5–7	22.5–25.3	867–1179
	E.-Ligetmajor	16.4–16.6	5–5.8	24.7–26.1	823–854
	Tállya	14.1–14.5	5.8–7	23–23.2	759–1179
	Felsőtárkány	14.1–14.5	5.8–6.2	23–23.2	759–1046
Badenian	Nógrádszakál	14–16.5	−0.2–4.8	24.7	846–1213
Karpatian	Magyaregregy	15.6–16.6	5–6.2	24.7–27.9	823–1356
Eggenburgian	Ipolytarnóc	16.5–18.8	5.6–11.7	26.5–27.9	1122–1213
Egerian	Eger-Wind	15.6–18.8	10–10.2	24.7–27.5	1096–1250
	Andornaktálya	15.6–19.2	5.6–11.7	24.7–27.5	823–1018
	Kesztölc	15.6–18.8	5–10.2	25.6–27.5	897–1250
	Pomáz	15.5–20.6	5–13.6	25.6–27.5	897–1294
	Vértesszőlős	13.3–18.8	−0.1–10.2	25.6–25.7	979–1250
Kiscellian	Eger–Kiseged	15.6–18.8	7.7–10.2	25.7–27.8	1308–1362
	Nagybátony–Újlak	15.9–19	7.7–11.7 excluding Ceratozamia 12.2–12.3 excluding Quercus Sect. Cerris	25.7–27.8	1308–1531
	Budapest	15.6–19	10–11.7	25.6–28.1	1122–1520

(Figs. 4, 8) and especially of WMT (Figs. 6, 8) through the Neogene. It suggests a higher role of minimum temperatures in determining palaeoflora and vegetation. The trend of temperature variables calculated for the Kiscellian–Egerian floras is not totally consistent. It is probably caused by a number of factors. In Kiscellian floras both exotic NLR (Nearest Living Relative) taxa, like *Platanus kerrii* and *Sloanea*, and none exotic ones like *Quercus* and *Smilax* should be considered in the climate analysis which cause wider ranges of the climate variables. At the same time NLR taxa of higher taxonomic level both in Kiscellian and Egerian floras had a similar effect on the coexistence intervals. (The relatively high /Pomáz/, and low / Vértesszőlős/ intervals of both MAT and CMT, are contrasting each other as well as data obtained for other Egerian floras and are probably not representative of Egerian climate, e.g. the high number of taxa of higher taxonomic level or few taxa appropriate for climate analysis, etc.).

Ranges of the precipitation variable (MAP, Figs. 7, 8) are higher for the Kiscellian than for younger floras (with respect to rainfall estimates some NLR taxa, like *Ceratozamia* with drier conditions than our results, or the monotypic *Tetraclinis* are outliers in calculations). After the Eggenburgian–Karpatian a slight decrease of MAP is observable.

4.2. Flora and vegetation development and related climatic evolution during the Miocene and Pliocene of the Pannonian domain

4.2.1. Ipolytarnóc — Evidence for warm climate conditions in the Early Miocene

During the Early Miocene of the Pannonian domain, marine areas were restricted mainly to its north central part and the Bükk region. After transgressive–regressive cycles through the Late Egerian–Eggenburgian–Ottnangian, a considerable decline of marine influence ensued for the Late Ottnangian. The “lower rhyolite tuff,” preserving the Ipolytarnóc assemblage, was deposited as the result of intense volcanic activity (Hámor and Bérczi, 1986, Bérczi et al., 1988). Throughout most of the Ottnangian a marine connection to the Mediterranean existed in the Central Paratethys and by the end of the stage the sea regressed from the Alpine–Carpathian Foredeep (Rögl, 1998; see Harzhauser and Piller, 2007-this volume).

Characteristic floral elements and tentative plant associations of the Ipolytarnóc fossil plant assemblage are indicated in Table 2. Warm climate conditions are well-reflected by the composition of the flora, with a high number of lauraceous and other thermophilous elements, like Palmae, and a high morphological diversity of the leaves (Fig. 9) (Hably, 1985) as well

Table 2
Floral elements and tentative plant associations in Neogene fossil plant assemblages of the Pannonian domain

	Floral elements		Plant associations	
Fossil assemblage	Dominant and frequent elements	Rare elements	Zonal types	Azonal types
Gérce Pula	*Quercus kubinyii*, *Q. pseudorobur*, *Zelkova zelkovifolia*, *Ulmus braunii*, *Acer* div. sp., *Carpinus* div. sp., *Populus populina*, *Buxus pliocenica*	*Carya serriifolia*, *Pterocarya paradisiaca*, *Engelhardia orsbergensis*, *Sassafras* sp.,	1. *Quercus–Zelkova–Ulmus–Carpinus–Acer–Buxus–*(*Juniperus–Torreya–Tsuga*) (mesophytic)	
Dozmat Tiszapalkonya (Tihany)	*Byttneriophyllum tiliifolium*, *Glyptostrobus europaeus*, *Alnus ducalis*, *Cercidiphyllum crenatum*			1. *Glyptostrobus–Osmunda–Alnus–Byttneriophyllum* (swamp) ?*Cercidiphyllum*
Felsőtárkány	*Osmunda parschlugiana*, *Pteris palaeoaurita*, *Glyptostrobus europaeus*, *Byttneriophyllum tiliifolium*, *Cercidiphyllum crenatum*, *Quercus pontica miocenica*, *Alnus cecropiifolia*, *Salix* sp., *Acer* div. sp.	*Ulmus* div. sp., *Quercus kubinyii*, *Populus populina*, *Musophyllum tárkányense*	1. *Quercus–Ulmus–Acer* (mesophytic)	2. *Glyptostrobus–Osmunda–Alnus–Byttneriophyllum* (swamp) 3. *Alnus–Cercidiphyllum–Acer–Ulmus–Quercus–Musophyllum* (riparian)
Sopron–Piusz puszta	*Pinus* sp., *Picea* sp., Lauraceae, *Toddalia* sp. *Buxus* sp.			
Erdőbénye, Tállya	*Glyptostrobus europaeus*, *Quercus drymeja*/*Q. mediterranea*, *Q. kubinyii*, *Podocarpium podocarpum*, *Zelkova zelkovifolia*, *Carpinus* div. sp., *Pinus* div. sp., *Ulmus braunii*, Juglandaceae, *Alnus* sp., *Populus populina*, *Acer* div. sp., *Parrotia* sp.	Lauraceae, *Pistacia* sp., *Ilex* sp., *Fagus* sp., *Rosa* sp., *Smilax* sp., *Liquidambar* sp.	1. *Quercus–Carpinus–Podocarpium–Zelkova–Ulmus–Acer–Parrotia* (mesophytic)	2. *Glyptostrobus* (swamp) 3. *Pterocarya–Carya –Acer–Ulmus–Populus–Alnus–Vitis* (riparian)
Nógrádszakál	*Equisetum* sp., *Parrotia pristina*, *Ulmus* div.sp., *Populus* sp., *Acer* div. sp., *Quercus* div. sp., (*Q. kubinyii*), *Alnus* sp., Cornaceae, *Daphnogene* sp., *Carya* sp., *Salix* sp.	*Platanus* sp., *Vitis* sp., Juglandaceae, Leguminosae, *Zelkova zelkovifolia*, Palmae	??? 1. *Quercus–Acer–Daphnogene–Zelkova–*Leguminosae–Palmae	2. *Equisetum–Ulmus–Populus–Acer* ? *Parrotia* (swamp/riparian)
Magyaregregy	*Glyptostrobus europaeus*, Lauraceae, *Zizyphus paradisiacus*, *Cedrelospermum* sp., *Myrica lignitum*, *Podocarpium podocarpum*, *Zelkova zelkovifolia*, *Ulmus* sp., *Ailanthus* sp., *Engelhardia orsbergensis*, *Carya* sp., *Celastrus* sp.	*Quercus kubinyii*, *Fagus* sp., *Rosa* sp., *Acer* sp., *Nyssa* sp., Salicaceae	1. Leguminosae–*Zizyphus*–*Celastraceae*–*Ailanthus*–Palmae 2. Lauraceae–Juglandaceae–Ulmaceae (subxerophytic, mesophytic)	3. *Glyptostrobus–Nyssa–Myrica* (swamp) 4. *Salix–Populus–Acer–Ulmus* (riparian)
Ipolytarnóc	*Tetraclinis salicorniodes*, *Pinus* div. sp., Lauraceae div. sp., *Daphnogene* div.sp., *Engelhardia orsbergensis*, *Cyclocarya* sp., *Platanus neptuni*, "*Quercus*" *cruciata*, "*Oreopanax*" *protomulticaulis*, Palmae div. sp.	Leguminosae, *Acer tricuspidatum*, *Smilax* sp.	1. *Platanus neptuni* 2. *Engelhardia orsbergensis–Cyclocarya* sp.–*Calamus noszkyi–Daphnogene bilinica* 3. "*Quercus*" *cruciata–Calamus noszkyi–Daphnogene bilinica*	

as temperature estimates (Figs. 4–6, 8). Rainfall estimates indicate a slightly higher mean value of MAP than for younger (after the Karpatian) floras (Figs. 7, 8). The extremely laurophyllous and thermophilous flora is dominated by *Tetraclinis salicorniodes*, *Pinus* div. sp., Lauraceae div. sp., *Daphnogene* div.sp., *Engelhardia orsbergensis*, *Cyclocarya*, *Platanus neptuni*, *Pungiphyllum cruciatum* ("*Quercus*"

Fig. 9. Characteristic taxa and morphologic range of leaves in the flora of Ipolytarnóc.

cruciata), "*Oreopanax*" *protomulticaulis*, Palmae div. sp. (*Calamus*, *Sabal*). Temperate elements, like *Acer tricuspidatum* (*Ulmus* in the underlying sandstone), had a subordinate role; these appeared in smaller numbers than even in the older Egerian floras. This phenomenon is not in complete accordance with the global

Fig. 10. Characteristic taxa and morphologic range of leaves in the flora of Magyaregregy.

temperature record as shown by Zachos et al. (2001) where the Eggenburgian is characterized as a cooler time-period between the warm interval at the beginning of the Miocene and the Mid-Miocene Climate Optimum. Other factors like the disparate palaeogeographic (latitudinal) position of the sites, facies (volcanic), or even the combined effect of these factors have to be taken into account.

Tentative plant associations (Table 2) are based on the parautochtonous assemblages collected from various sample plots (Hably, 1985). The mass co-occurrence of lauraceous leaves, needle leaves and cones of Pinaceae (and palms) indicate extensive lauraceous forests with abundant Pinaceae near the shore — it may be compared with the modern Lauraceae and *Pinus canariensis* forests of Tenerife representing different altitudinal zones. Other sample plots are characterized by the mass occurrence of *Platanus neptuni* accompanied by numerous lauraceous elements or by the abundance of *Engelhardia orsbergensis* with lauraceous elements, palms and *Pungiphyllum cruciatum*.

4.2.2. Magyaregregy — Transition between Palaeogene and younger Neogene flora and vegetation

Related to the Styrian orogenic phase, palaeogeography of the Karpatian stage characterized by a transgressive–regressive cycle changed significantly, i.e. the ratio of marine sedimentation increased, and lagoonal environments became frequent by the end of the stage (Bérczi et al., 1988).

Floras from the various sample plots (fish scale marl and volcanic tuffs) of the Mecsek area consistently indicate the same flora and vegetation. The flora (Fig. 10), though, comprising a high number of thermophilous taxa, gives evidence of the increasing role of temperate elements like *Ulmus*, *Acer*, *Rosa*, or *Salix*. At the same time diversity (number of taxa) of the fossil assemblage remains relatively high (e.g. Ulmaceae family — *Cedrelospermum*, *Ulmus*, *Zelkova*) as compared to younger subsequent fossil floras. The composition of the Magyaregregy flora may serve as a link between the older Palaeogene and the younger Neogene floras (Fig. 11). Similar to the preceding Eggenburgian/Ottnangian flora (Ipolytarnóc), Lauraceae still makes up a significant part of the fossil assemblage with *Daphnogene* and *Laurophyllum* species. *Glyptostrobus europaeus*, which displays mass occurrence later in the Pannonian, can be regarded as a frequent element already in Magyaregregy. As compared to the earlier Cenozoic floras of Hungary, the abundant occurrence of Leguminosae is a noteworthy new character of the fossil assemblage. The first appearance of *Podocarpium*, an extinct genus of Leguminosae

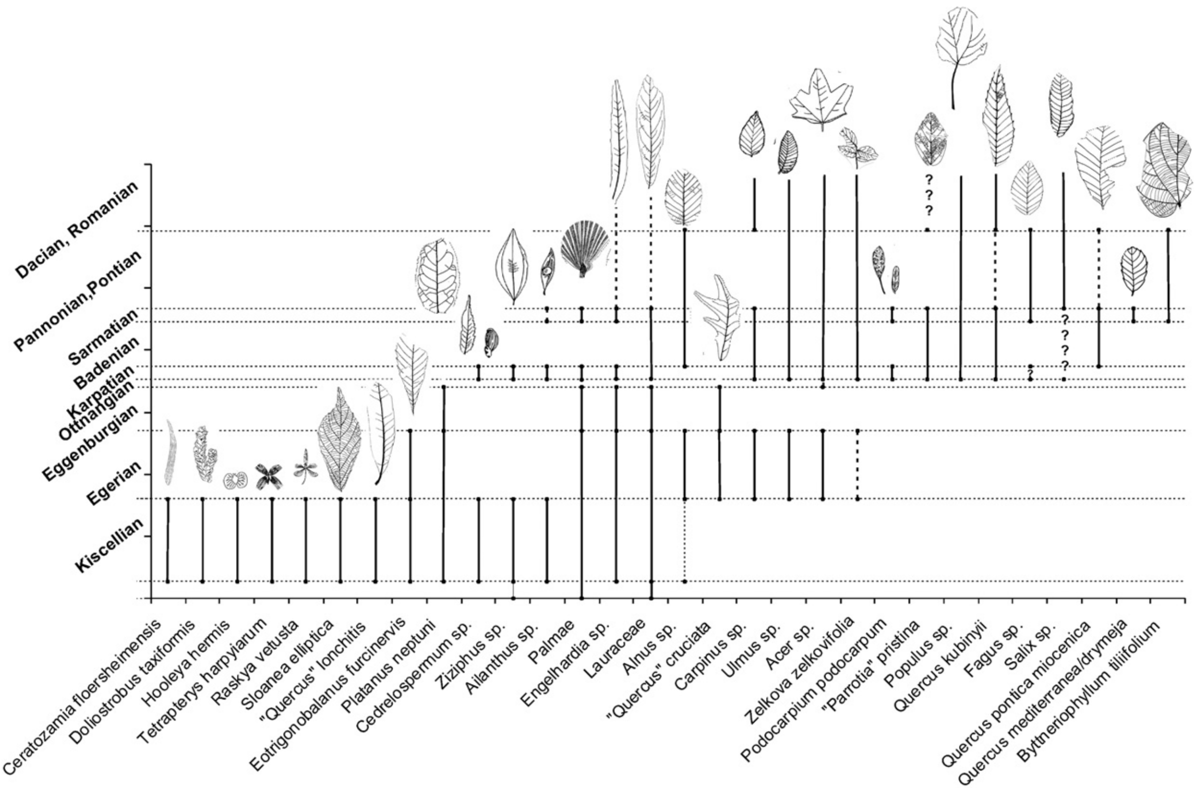

Fig. 11. Fossil record of selected taxa in the Pannonian domain during the Kiscellian–Romanian time interval. (Data for the Kiscellian–Egerian are included to provide a more complete record of thermophilous and exotic elements disappearing during the Neogene) Broken lines indicate fossil record but with extremely low number of specimens. Question marks refer to uncertain records.

and predominating element of subsequent fossil assemblages, gives further importance to the Magyaregregy assemblage. Temperate taxa, however, still belong to the relatively rare elements. The special character of the Magyaregregy flora, i.e. the co-occurrence of floral elements of both older and younger floras is nicely reflected by climate estimates for the Karpatian (Fig. 8). Temperature variables (MAT, and WMT) occupy a transitional position between estimates for the Eggenburgian and Badenian (and younger stages). Interval of CMT is transitional between Eggenburgian and Badenian but its values are not higher than those for the Sarmatian.

Tentative plant associations (Table 2) are outlined as swamp, riparian (composed of numerous temperate taxa) and mesophytic types, the latter with subxerophytic character which is attributable to the appearance of *Zizyphus*, Leguminosae and Celastraceae formed the presumably scanty forest vegetation. The relatively high number of winged fruits also supports the presence of a more open vegetation. At the same time a vegetation type requiring higher annual or more evenly distributed rainfall might have been formed of Lauraceae, Juglandaceae and Ulmaceae.

4.2.3. Nógrádszakál — A cooler climate period during the Badenian of the Pannonian domain?

Maximum transgression causing a peak in marine sedimentation affected a significant part of the Pannonian domain during the Badenian (Hámor, 1984; Hámor and Bérczi, 1986; Bérczi et al., 1988). Though marine sedimentation continued in the Middle Badenian, regression and related widespread desiccation occurred in the Carpathian foredeep and eastern intramountain basins. In the Late Badenian the last event of marine flooding covered the entire region of the Patratethys, probably as a result of a re-opening of Indo-Pacific seaways (Rögl, 1998).

The Badenian flora of Nógrádszakál (Fig. 12) provided the first mass occurrence of temperate elements during the Neogene, with higher ratio than that in older or even the younger Sarmatian floras. Besides *Parrotia*, species of *Ulmus*, *Populus* and *Acer* predominate in the assemblage, whereas thermophilous taxa, like Palmae and Lauraceae are subordinate (Kordos-Szakály, 1984). However, it should not be ignored that most of the remains may represent azonal (swamp or riparian) vegetation types (Table 2), which may be in compliance with the existing palaeogeography of the area. Climate estimates for the Badenian based on data from the Nógrádszakál flora (Figs. 4–6, see above) indicate comparatively cool conditions, i.e. CMT proved to have the lowest range of values among Miocene floras analysed and even values of MAT are similar to those calculated for the Sarmatian. Results obtained by adopting the plant functional approach for vegetation reconstruction also refer to a cooler climatic aspect for the flora (Utescher et al., 2007-this volume).

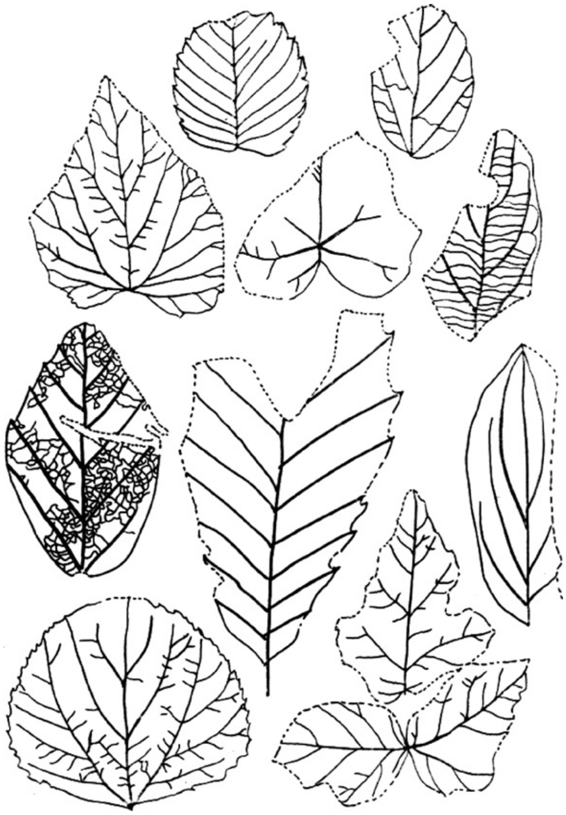

Fig. 12. Characteristic taxa and morphologic range of leaves in the flora of Nógrádszakál.

4.2.4. Sarmatian floras — The Late Miocene Cooling

The Early Sarmatian is characterized by a similar palaeogeography of the Pannonian domain as in the Late Badenian. Later in the Sarmatian, due to the regression of the Paratethys, nearshore environments and sedimentation gained a greater importance (sediments with gypsum, halite, etc. content, Hámor and Bérczi, 1986; Bérczi et al., 1988). During the Late Miocene the Paratethys was isolated from any marine influence and progressively became more fresh (Rögl, 1998).

The Sarmatian is well-documented with fossil assemblages (Fig. 3), and so-called “volcanic floras” are preserved mainly in volcanic environments (Erdei and Hír, 2003). Most of them are dominated by *Quercus* species (*Q. drymeja*/*Q. mediterranea* and *Q. kubinyii*), *Podocarpium podocarpum*, *Zelkova zelkovifolia*, *Carpinus* species and Juglandaceae (Fig. 13). Besides temperate elements, e.g. *Acer*, *Ulmus*, *Populus*, etc., numerous

Fig. 13. Characteristic taxa and morphologic range of leaves in the Erdőbénye floras.

thermophilous taxa, though playing a subordinate role still exist, e.g. Lauraceae, *Engelhardia*, *Toddalia* or Palmae (Table 2). A dominance of *Quercus* species similar to that recorded in the Sarmatian volcanic assemblages appears neither in younger nor in older studied floras of the Pannonian domain. The last occurrence of numerous taxa, mostly thermophilous or "exotic" elements, in the Pannonian domain are from the Sarmatian volcanic floras, i.e. Palmae, *P. podocarpum*, *Q. drymeja*/*mediterranea*, *Ailanthus* (*Engelhardia* and Lauraceae are recorded in small numbers even from younger, Pliocene floras) (Fig. 11). Both zonal and azonal vegetation types are well represented with minor disparities of the individual assemblages (Table 2). A subxerophytic aspect (?due to a volcanic environment) may be indicated by small-leaved *Quercus* species and *Pistacia*.

Contrary to the volcanic assemblages, the flora of Felsőtárkány (Fig. 14) represents a transitional type to younger, Pannonian floras — comprising characteristic elements of both Sarmatian and Pannonian flora and vegetation, e.g. *Byttneriophyllum tiliaefolium*, *Alnus cecropiifolia*, etc. (Table 2).

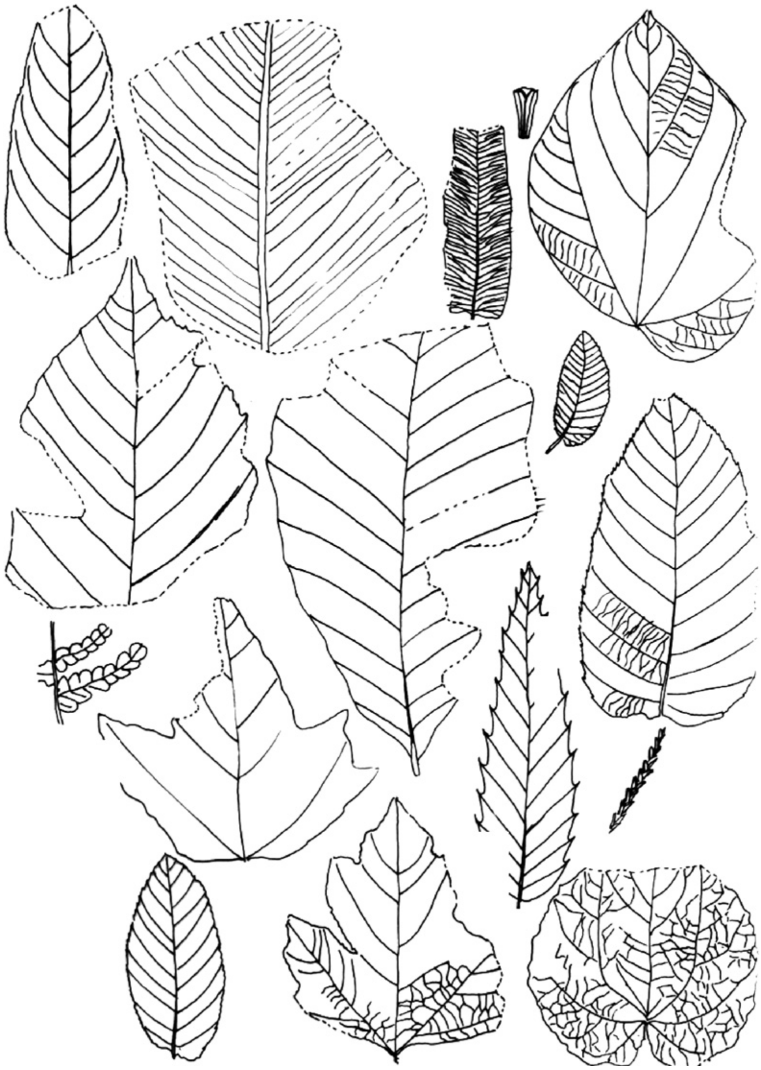

Fig. 14. Characteristic taxa and morphologic range of leaves in the flora of Felsőtárkány.

Climate variables were estimated for five assemblages, i.e. the Erdőbénye floras (Kővágó oldal, Barnamáj, Ligetmajor), Tállya and Felsőtárkány, adopting the coexistence approach (Figs. 4–8). Temperature variables show lower coexistence intervals as compared to those estimated for older floras (with the exception of the Badenian Nógradszakál: intervals of MAT are similar, whereas CMT represents even lower values, than those of Sarmatian floras; discussed above). This result compares well with the floristic change detailed above. Annual rainfall estimates (MAP) indicate slightly lower ranges than for older floras.

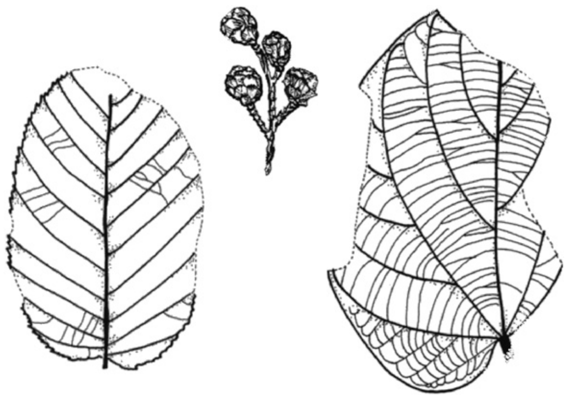

Fig. 15. Characteristic taxa and morphologic range of leaves in the Pannonian floras.

4.2.5. Pannonian and Pontian floras — The effect of palaeogeography

Due to the accelerated subsidence of the Pannonian Basin (domain), more and more areas were flooded by

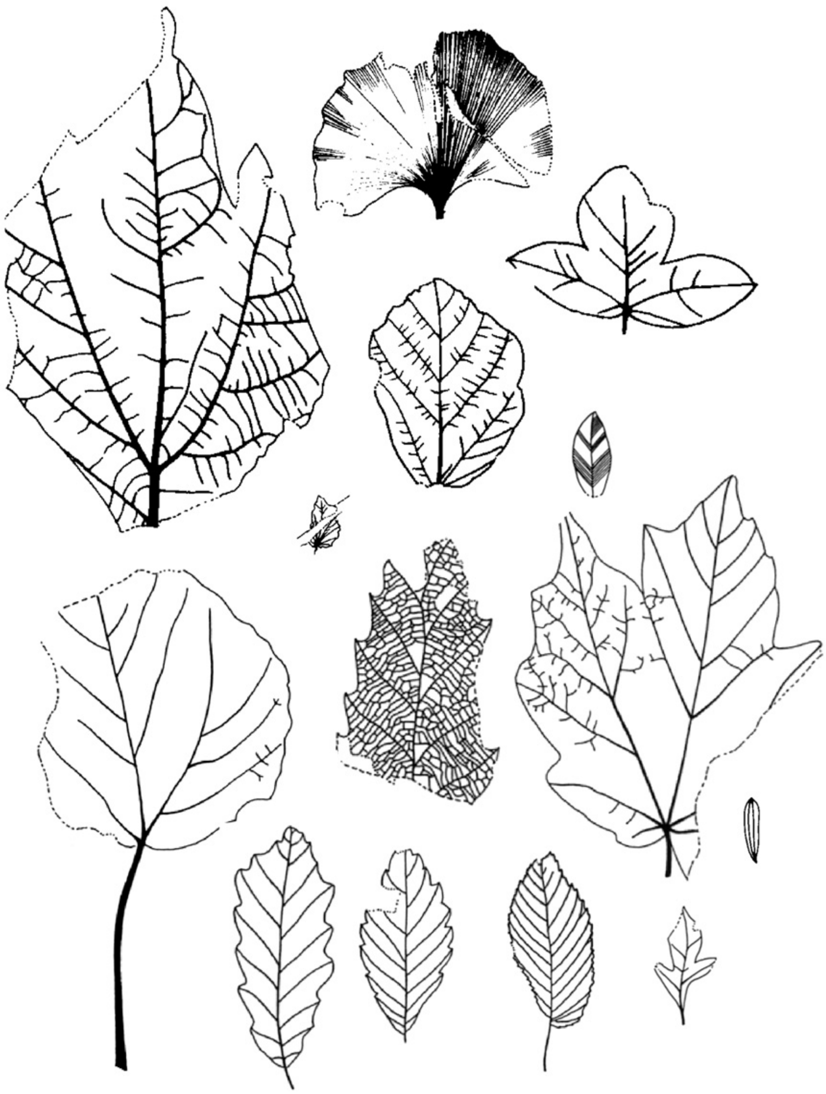

Fig. 16. Characteristic taxa and morphologic range of leaves in the Pliocene floras.

the Pannonian Lake. The extension of the concomitant swampy areas increased, which provided unfavourable conditions for the expansion of mesophytic forests, so they drew back continuously (Hably and Kvaček, 1998). The evidence of this phenomenon may be seen in Rudabánya. Though this flora needs to be revisited, it should be cited here.

Most of the Late Miocene (Pannonian) localities are characterized by the monotonous azonal association of *Glyptostrobus europaeus*, *Alnus cecropiifolia* and *Byttneriophyllum tiliaefolium* (Fig. 15, Table 2) both in the western and eastern parts of the basin, e.g. Dozmat, Tiszapalkonya as well as in Transylvania (Givulescu, 1991; Hably, 1992b; Hably and Kovar-Eder, 1996). In addition, the monotypic assemblage of Sé (western Hungary) is characterized by the mass occurrence of *Salix* leaves (Hably, 2003). The Pontian flora from Tihany provided a relatively rich assemblage suggesting a riparian forest with *Liquidambar europaea*, *Platanus leucophylla*, *Alnus ducalis*, *A. gaudinii*, *Juglans acuminata*, *Populus* div. sp., *Smilax weberi* (Hably, 1992a).

Few remains of the zonal vegetation were recorded in marginal areas, e.g. Rudabánya, in “inselbergs” like Aranyosgadány (Mecsek Mts.), or Neuhaus (southern Burgenland, Kovar-Eder et al., 1995). This is well supported by palaeogeographic reconstructions (Magyar et al., 1999) assuming that the Pannonian Basin was inundated by the freshwater of the Pannonian Lake, there were no extended terrestrial areas allowing the significant settlement of the zonal vegetation.

Azonal vegetation types are inadequate indicators of climate. However, *Byttneriophyllum* is thermophilous among predominating elements, as well as the occurrence of *Daphnogene* and *Engelhardia* in the northern and western marginal areas, e.g. Rudabánya and Neuhaus (Kovar-Eder et al., 1995), prove the existence of thermophilous taxa.

4.2.6. The Pliocene (Romanian) crater lakes — Retreat of Sarmatian flora elements

The Upper Miocene and Pliocene delta formations had a decisive role in the Neogene infilling of the Pannonian Basin on the basis of seismic stratigraphy, seismic faciology and sedimentology. The Hungarian part of the Pannonian Basin was filled up by sediments of prograding delta-systems and connected environments from the margins of the basin (Pogácsás and Révész, 1987).

The flora and vegetation of the Pliocene crater lakes in Gérce and Pula (Fig. 16, Table 2) is essentially disparate from that of the preceding uppermost Miocene (Pannonian/Pontian). In contrast, Pliocene and Sarmatian flora and (zonal) vegetation share similar features, i.e. assemblages from Erdőbénye and the alginite of Gérce and Pula share some dominant, frequent or characteristic taxa like *Quercus kubinyii*, *Q. pseudorobur*, *Zelkova zelkovifolia*, *Carpinus* div. sp., *Ulmus braunii*, *Populus populina*, *Celtis trachytica*, *Acer* div. sp., *Carya serrifolia*, *Pterocarya paradisiaca*, *Parrotia pristina* and *Engelhardia* (Hably and Kvaček, 1998).

The retreat of Sarmatian flora and vegetation is attributable to both palaeogeography and palaeoenvironment, i.e. facies (Hably and Kvaček, 1998). Significant volcanic activity characterized the area during both time intervals. The zonal vegetation of the Sarmatian volcanic areas must have survived the Pannonian inundation in restricted refugia and appeared again in Pliocene volcanic areas, however, with fewer thermophilous taxa. During the uppermost Miocene and Pliocene only minor movements of the tectonic units are assumed to have taken place, thus presumably insignificant from the point of view of flora and vegetation development.

The minor role of thermophilous taxa is nicely shown by climate estimations (Fig. 8); all temperature variables (MAT, CMT and WMT) have significantly lower ranges than those calculated for the Sarmatian. Rainfall estimates (MAP) were slightly lower for Gérce and Pula than for older floras.

5. Discussion

5.1. Climatic trends during the Neogene of the Pannonian domain

5.1.1. Temperature

The temporal variation of the three temperature variables (Fig. 8, Table 1) indicates a cooling of the climate after the Eggenburgian (MAT: 16.5–18.8 °C) up to the Romanian (MAT: 10–15.7 °C). Since temporal and spatial resolution of climate estimations is still far from being complete, negative or positive temperature shifts cannot be excluded. Floristic change during the Neogene is attributable in part to a considerable decline in the temperature of the coldest month (in contrast to WMT). A decrease in CMT of 5.6–11.7 °C during the Eggenburgian to 0.2–5 °C in the Romanian was estimated. The largest drop in CMT is shown — even to negative values during the Badenian. Contrary to this, a warming trend connected to a global warming during the Early Badenian (NN4; Nógrádszakál is dated as NN5, cf. chapter 3) is estimated in the Central Paratethys related to a mass occurrence of marine organisms (e.g. larger foraminifera, algal–coral patch reefs, tropical molluscs, see in Rögl, 1998). This so-called Mid-Miocene Climate Optimum is well reflected in continental climate records from various regions such as the Northwest German Tertiary and Tertiary Basins of Ukraine (Utescher et al., 2000; Syabryaj et al., 2007-this volume). This climate optimum is not obvious from the Hungarian fossil floral record or may be overprinted by other effects such as tectonic processes (see above). Middle Badenian cold temperatures (MAT: 14–16.5 °C; CMT: −0.2 °C) should be supported by additional estimates from other fossil floras that comprise remains of the zonal vegetation. After the Middle Badenian the Late Miocene Cooling coupled with the final expansion of the East Antarctic Ice Sheet (see Zachos et al., 2001) as well as a global change in the ocean deep water current systems, are indicated (Rögl, 1998). Mean annual temperature calculated for the Sarmatian (MAT: 14–16.5 °C) represents a decrease as compared to data of the Karpatian (15.6–16.6 °C).

Jiménez-Moreno et al. (2005) estimated values of temperature and precipitation applying the “climatic amplitude method” on Karpatian–Sarmatian pollen assemblages of the borehole “Tengelic 2” (Hungary). A decrease in mean annual temperature from about 18–20 °C during the Badenian to ca. 16 °C in the Sarmatian was calculated. They interpreted the decrease in temperature accompanied by a decrease also in precipitation as a climatic cooling during the “Monterey Cooling Event”, correlated with the expansion of the East Antarctic Ice Sheet. These values, especially those for the Badenian, are definitely higher than those of MAT obtained by the Coexistence Approach (Fig. 8).

Studying volcanic floras of the Pliocene crater lakes in Gérce and Pula, Hably and Kvaček (1998) estimated a mean annual temperature of 10–13 °C (and a mean annual precipitation of 1000 mm or less).

Based on fossil floras from Hungary, Andreánszky (1964, p. 360, Abb. 5.) reconstructed the temporal pattern of temperature from the Kiscellian up to the Pliocene. His chart indicates a general cooling trend with some negative and positive shifts. A temperature maximum is postulated for the Early Miocene and a negative shift during the Sarmatian.

Kordos et al. (1987) described ecozones for the Neogene of the Carpathian Basin based on palaeontological and palaeogeographical data. During the Early Badenian a period of stability of terrestrial environments is supposed related to the sea of uniform salinity and temperature covering large areas. They indicated changing salinity and probably decreasing temperature as factors governing the disappearance of coral reefs after the Badenian.

Palynological data (Nagy in Kordos et al., 1987) indicate a cooling trend in the Early Pannonian. The Late Pannonian is characterized by extreme ecotypes, i.e. thermophilous associations (subtropical plants) within swamps of the basin, while on adjacent hillsides drier forests flourished.

5.1.2. Rainfall

According to data obtained by the quantitative analysis of rainfall variables (mean annual precipitation, MAP) adopting the Coexistence Approach for the Cenozoic fossil floras of the Pannonian domain (Fig. 8; Table 1), after the Karpatian a slightly declining trend of MAP is observable (Karpatian: 823–1356 mm; Romanian: 619–1160 mm). Except for some floras (e.g. Ipolytarnóc, E.-Ligetmajor, E.-Kővágó oldal) rather wide intervals were calculated (Fig. 7) which means that all the NLR (nearest living relative) taxa of the fossil floras tolerate comparatively wide ranges of MAP raising problems when evaluating precipitation data. Intervals, both higher and lower limits of values, slightly decline after the Badenian. The Sarmatian and Romanian partly appear drier in the annual average than the previous time-periods which seems to be supported floristically, i.e. mainly volcanic floras comprising subhumid/xerophytic elements, however, data do not provide information on the seasonal distribution of rainfall.

Jiménez-Moreno et al. (2005) estimated values of precipitation applying the "climatic amplitude method" on Karpatian, Badenian and Sarmatian pollen assemblages from the borehole "Tengelic 2" (Hungary). A decrease in mean annual precipitation from about 1200–1400 mm during the Badenian to 1100 mm during the Sarmatian was estimated. These values are slightly higher than the mean values of the intervals of MAP calculated with the Coexistence Approach (Fig. 8).

Based on the systematic composition of fossil macrofloras mean annual precipitation for Sarmatian floras has been estimated at 800–1000 mm with a winter-maximum, and for the Felsőtárkány and Pannonian floras higher amounts of rainfall, even above 1500 mm, distributed year-round (Andreánszky, 1963a, 1964, p. 361, Abb. 6.).

The occurrence of subhumid/xerophytic elements in the individual fossil assemblages may reflect a seasonal distribution of rainfall. Andreánszky (1963b) was the first to postulate the occurrence of so-called dry-elements, like "dry-oaks" (e.g. *Q. mediterranea*), some Leguminosae, *Sapindus*, various gymnosperms, etc. in younger Cenozoic (first of all in Sarmatian) floras of Hungary as unambiguous evidence of a mediterranean type climate (see also the Madrean–Tethyan theory of Axelrod, 1958; 1975). However, later studies have not confirmed this theory, since the doubtful systematic affinity of numerous taxa, e.g. some gymnosperms or *Sapindus*, does not allow their adoption for climatic interpretation.

The morphology (shape of leaf lamina, ?coriaceous structure) of "*Quercus*" *cruciata* (presumably corresponding to *Pungiphyllum cruciatum* (Al. Braun) Frankenhäuser & Wilde; Frankenhäuser and Wilde, 1995) which is recorded in high numbers in the Ipolytarnóc flora may suggest drier climatic conditions (xerophytic element in Krutzsch, 1992). However, this is in contrast to the abundant occurrence of leaves with a similar morphology (*Pungiphyllum waltheri* Frankenhäuser & Wilde) in the Middle Eocene flora of Eckfeld (Frankenhäuser and Wilde, 1995; Wilde and Frankenhäuser, 1998) and to the frequency of leaves with drip tips in the flora of Ipolytarnóc (Hably, 1985).

Andreánszky (1959) supposed that the aridity of the climate may be indicated by the high abundance of Leguminosae coupled with a declining ratio of Lauraceae. Distribution of legumes (Hably, 1992c) is most prominent in the Egerian, (Late Ottnangian) Karpatian and Sarmatian. The number of legume specimens through the Hungarian Cenozoic (Fig. 17) suggests that legumes were abundant through the Oligocene–Miocene of Hungary with a significant drop in the Late Eggenburgian–Early Ottnangian. The data were based on the flora of Ipolytarnóc which besides the almost lack

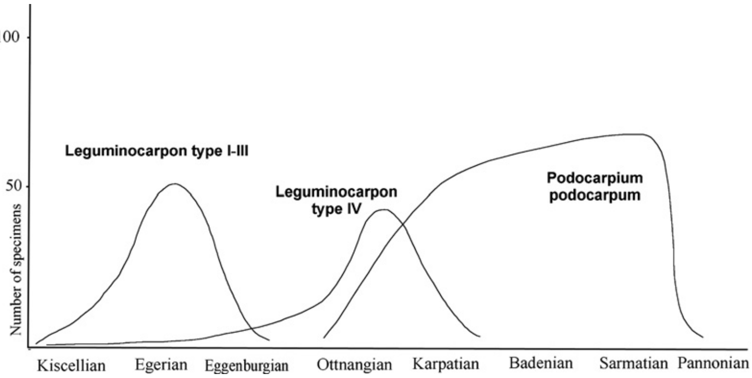

Fig. 17. Distribution of legumes in the Hungarian Cenozoic (after Hably, 1992c).

of legumes possess a high abundance of Lauraceae. Considering the diversity of legume types and not their absolute numbers, the highest diversity (3–4 taxa) was recorded from the (Late Kiscellian) Egerian (Eger-Wind, Pomáz) and the Karpatian (Magyaregregy) whereas the Eggenburgian is extremely poor in legumes (one taxon in the sandstone flora of Ipolytarnóc). Badenian/Sarmatian assemblages have 1–2 taxa of legumes, though often in extremely high numbers (*Podocarpium podocarpum* in Sarmatian fossil floras). Both absolute number of specimens and number of legume taxa have the lowest values in the Eggenburgian (/Ottnangian) Ipolytarnóc flora. Nevertheless, the abundance of legumes and seasonal distribution of rainfall or drier climatic periods do not seem to coincide, e.g. the floral composition of the Eger-Wind assemblage which has the highest legume diversity does not have any other indicators of arid climatic conditions.

Schweitzer (1997) assumes three warm/hot and dry spells (during MN 12, Turolian, 8–7 Ma BP; MN13, Turolian, corresponding to the Messinian salinity crisis, 6.3–5 Ma BP; Mn 16–17 Villanyian, 3–2 Ma BP) in the Carpathian Basin after the Sarmatian mainly supported by sedimentological (grey sand, carbonates, reddish clay, geomorphological features, e.g. desert crusts, desiccation cracks), geochemical and palaeontological data (faunal elements indicating steppe like gazelles, desert mice, ostrich and camel). According to Schweitzer (1997) siliceous desert crusts similar to those described from sediments of the dry intervals are formed today under climates with a MAP of ∼130 mm and a MAT of 16–24 °C. Pannonian and Pliocene (Romanian) macro-floras from the Pannonian domain are not coeval with any of the supposed dry intervals or cannot be dated with enough accuracy (e.g. Pannonian floras). Nevertheless, MAP calculated for Gérce and Pula have much higher values (Fig. 7) than 130 mm. Thus they do not confirm dry or even desert climatic conditions. However, drier climates should not be excluded. On the one hand, due to the extent of inundated areas during the Pannonian, there is a dominance of azonal vegetation which is not really indicative of climate and, on the other hand, local flora and vegetation surrounding the Pliocene crater lakes were found in Gérce and Pula that do not give detailed information about the regional plant cover.

Kordos et al. (1987) proposed a dry period at the end of the Miocene which they related to the Messinian salinity crisis (filling up of the Pannonian Lake, normal fluvial regime, possible increase in wind erosion, increasing role of steppe dwelling vertebrate fauna). Inferred from vertebrate fauna the late Pliocene was characterized by a peak in humidity — a wet period with high temperature followed by a drier period.

5.2. Floristic change, floral elements, diversity and vegetation types

General trends observed in the Neogene fossil plant assemblages of the Pannonian domain are 1. – the disappearance of thermophilous and exotic elements accompanied by the appearance of temperate elements and 2. – a decreasing diversity of vegetation types. However, changes in both trends (e.g. the retreat of thermophilous elements in Pliocene floras and the poor diversity of vegetation types in the Badenian) may be the result of climatic and palaeogeographic factors. The latter has important implications when adopting climate analysis.

The appearance and disappearance of selected taxa during the Cenozoic of the Pannonian domain are indicated on Fig. 11. A definite floristic change is well-documented by the Karpatian Magyaregregy assemblage — numerous ancient-type taxa have their last (e.g. *Cedrelospermum*, *Zizyphus*, *Saportaspermum*) or last abundant occurrence (e.g. *Ailanthus*, *Engelhardia*) accompanied by the appearance of taxa that predominate in younger floras (e.g. *Zelkova zelkovifolia*, *Quercus kubinyii, Podocarpium podocarpum*).

The highest ratio of thermophilous elements as well as the highest diversity and variety of vegetation types during the Neogene of the Pannonian domain is indicated by the Ipolytarnóc assemblage (Table 2). Relative peaks of diversity and diversity of vegetation types may be observed during the Sarmatian and Pliocene whereas negative shifts are displayed by Badenian and Pannonian assemblages.

An increasing ratio of thermophilous floral elements indicated after the Badenian based on palynological data (Nagy in Kordos et al., 1987) agrees well with our results.

5.3. Floristic change and climate in relation to Early–Middle Miocene microplate pattern and palaeogeography

Evolution of the major tectonic units in the Pannonian domain (Fig. 1) must have played a significant role in the regional development of the flora and vegetation.

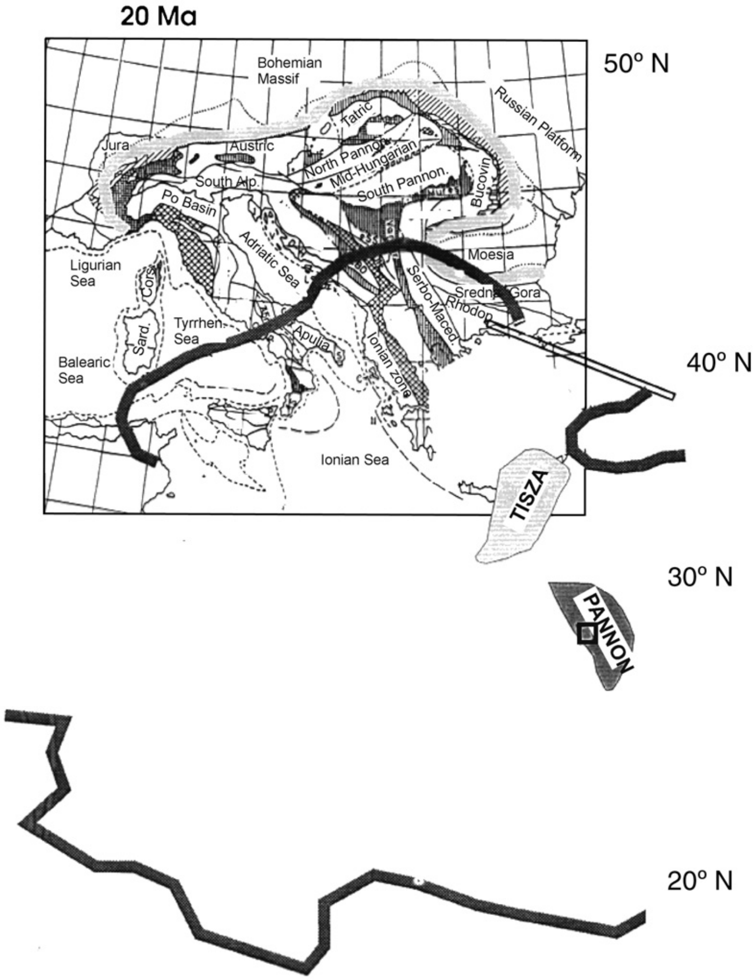

Fig. 18. Palaeopositions of ALCAPA (Pannon) and Tisza terranes within the Tethys during the Neogene. Thick lines: palaeoposition for the southern margin of the continental portion of the Alpine–Carpathian sector of the European plate and the northern margin of the African plate at 20 Ma, 15 Ma, and today (calculated after Besse and Courtillot, 1991 and Dercourt et al., 1993). Positions of ALCAPA and Tisza terranes are restored by assessing rotation and latitudinal shift from paleomagnetic data (Refs. see text). Further terranes are omitted. Present-day arrangement of tectonic units is given for orientation (after Kázmér).

A large palaeomagnetic data set (e.g. Márton and Fodor, 1995; Márton et al., 1996; Márton, 2001) suggests palaeopositions for ALCAPA (Pannon) and Tisza terranes at 20 Ma and 15 Ma, respectively (Figs. 18–20).

Details of the process which led to a significant northward shift (~10° in latitude) in 4 million years are still unclear. During this time both microplates were emplaced in the Carpathian embayment, followed by the well-documented extension in the Pannonian backarc basin (Márton and Fodor, 2003). High activity of explosive acidic and intermediary volcanism – which preserved the Ipolytarnóc flora – is wittness to a major reorganization of microplate pattern.

The extreme abundance of laurophyllous and thermophilous elements in the Ipolytarnóc assemblage (bound to the ALCAPA unit), and its disparate character (e.g. lower ratio, or even absence of temperate "arctotertiary elements") from coeval Western and Central European floras (e.g. Bilina, young "mastixioid floras" — Niederlausitz/Kleinleipisch, Hessen/Eichelskopf, Sachsen/Wiesa, Cheb basin/Františkove Láznì, S Moravia/Znojmo, Luzern; see flora complexes of Mai, 1995) may be related

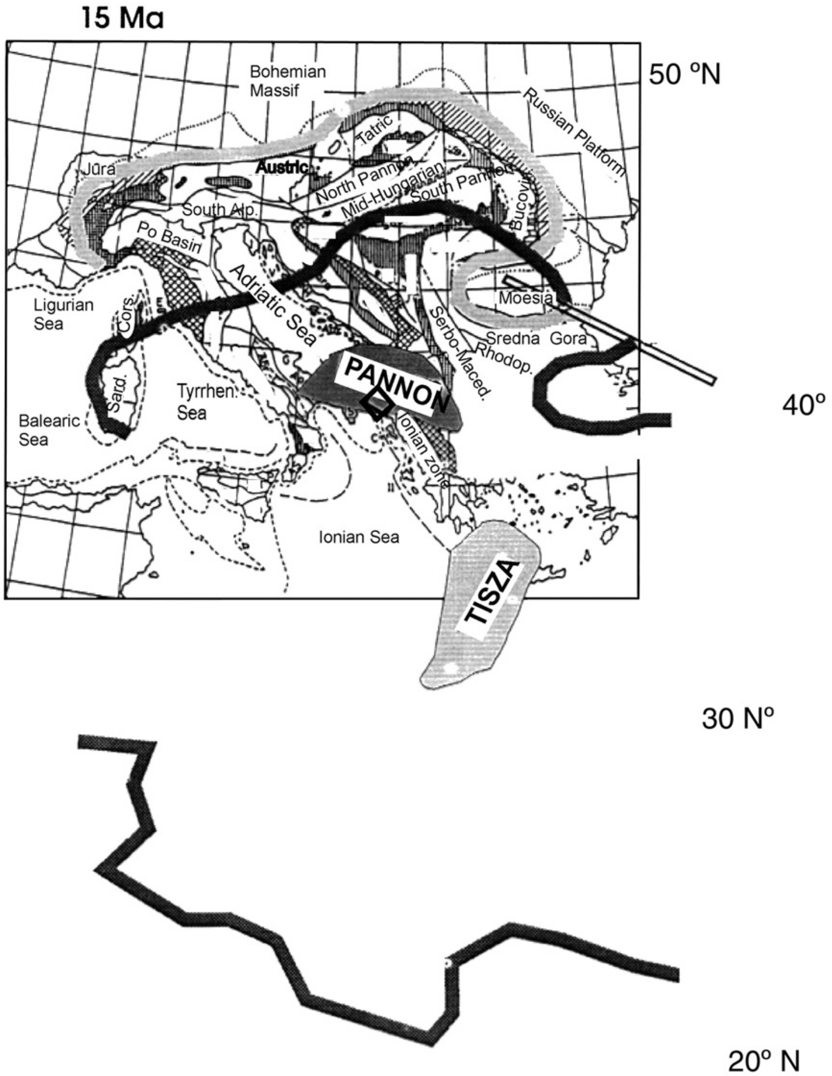

Fig. 19. Palaeopositions of ALCAPA (Pannon) and Tisza terranes within the Tethys during the Neogene. Thick lines: palaeoposition for the southern margin of the continental portion of the Alpine–Carpathian sector of the European plate and the northern margin of the African plate at 20 Ma, 15 Ma, and today (calculated after Besse and Courtillot, 1991 and Dercourt et al., 1993). Positions of ALCAPA and Tisza terranes are restored by assessing rotation and latitudinal shift from paleomagnetic data (Refs. see text). Further terranes are omitted. Present-day arrangement of tectonic units is given for orientation (after Kázmér).

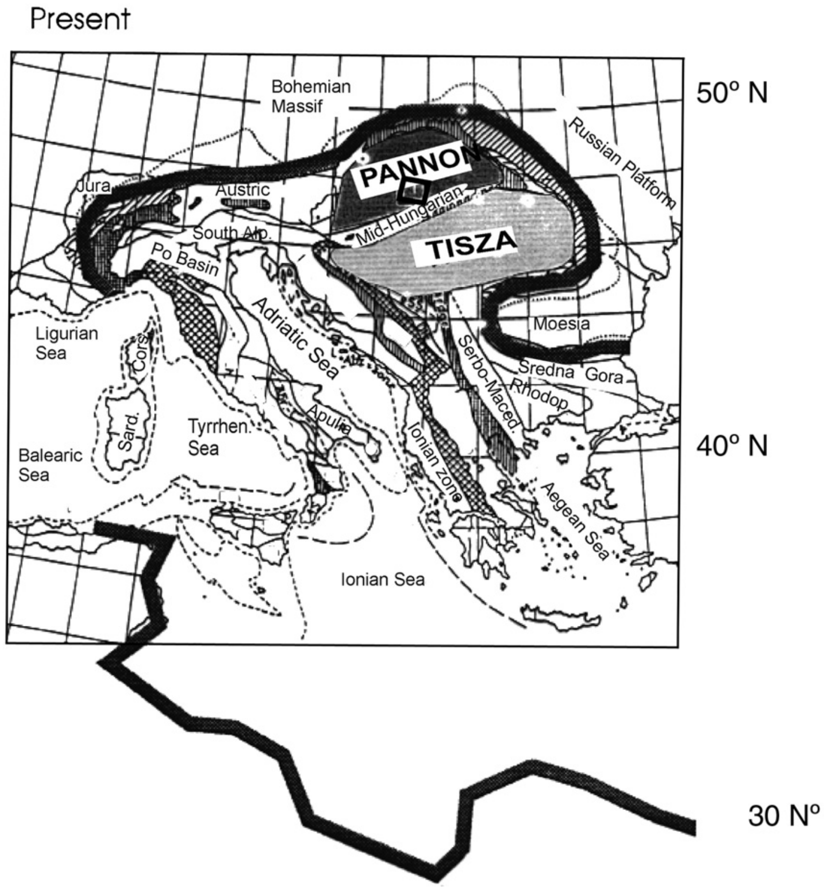

Fig. 20. Palaeopositions of ALCAPA (Pannon) and Tisza terranes within the Tethys during the Neogene. Thick lines: palaeoposition for the southern margin of the continental portion of the Alpine–Carpathian sector of the European plate and the northern margin of the African plate at 20 Ma, 15 Ma, and today (calculated after Besse and Courtillot, 1991 and Dercourt et al., 1993). Positions of ALCAPA and Tisza terranes are restored by assessing rotation and latitudinal shift from paleomagnetic data (Refs. see text). Further terranes are omitted. Present-day arrangement of tectonic units is given for orientation (after Kázmér).

to and support the suggested microplate pattern. An increasing abundance of "palaeotropical elements" coupled with the repeated reappearance of "mastixioid elements" characterized the Neogene floras of Western and Central Europe during periods with optimal climatic conditions (Mai, 1995). Contrary to this, the absence of "mastixioid elements" in Neogene floras of the Pannonian domain provides additional support for the plate tectonic history.

A closer position to the stable European plate (Fig. 19) must have been conducive to the appearance of temperate floral elements, as their mass occurrence is well-documented in the Badenian flora of Nógrádszakál.

The temperature decline as observed in the record from the Eggenburgian (on Figs. 4, 8) most probably reflects in part the pronounced northward movement of the ALCAPA microplate by more than 10 (~12) degrees during the Eggenburgian–Badenian (?Sarmatian) time interval. If we accept the reconstruction given in Figs. 18–20, a decline of mean annual temperature of at least 4.0 (~4.8) °C could be expected by tectonic forcing alone when a zonal gradient of 0.4° per 1° latitude is assumed. Consequently, interpretations of the data calculated in the context with global climate change have to be treated with care. Both temporal and spatial variations of temperature and floristic trends must have been influenced by the regional tectonic evolution and palaeogeography.

Palaeogeography had a significant role in the appearance of Pannonian floras with extremely low diversity of the flora and vegetation types. Due to the accelerated subsidence of the Pannonian Basin the extension of the concomitant swampy areas increased providing unfavourable conditions for the expansion of mesophytic forests.

During the Romanian the retreat of Sarmatian flora and vegetation is mainly attributable to palaeogeography. The zonal Sarmatian vegetation must have survived the Pannonian inundation in refugia and appeared again in volcanic areas but with less of the thermophilous taxa. During the uppermost Miocene and Pliocene movements of the tectonic units are presumably insignificant from the point of view of flora and vegetation development.

Acknowledgements

The authors express their thanks to the program ”Neogene Climate Evolution in Eurasia — NECLIME” for providing significant data of this work. The Hungarian Scientific Research Fund (OTKA T037200) also provided a considerable support for the first and second authors. The authors are grateful to Dr. Mike Pole for language corrections.

References

Andreánszky, G., 1955. Neue Pflanzenarten aus der unterhelvetischen Stufe von Magyaregregy. In: Andreánszky, G., Kovács, É. (Eds.), Gliederung und Ökologie der jüngeren Tertiärfloren Ungarns. Annales Instituti geologici publici hungarici, vol. 44, pp. 152–153.

Andreánszky, G., 1959. Die Flora der Sarmatischen Stufe in Ungarn. Akadémiai Kiadó, Budapest.

Andreánszky, G., 1963a. A növényföldrajzi táj változásai Eger környékén a harmadidõszak folyamán. Egri Múzeum 1963. évi 1. évkönyve, 39–53.

Andreánszky, G., 1963b. Das Trockenelement in der Jungtertiären Flora Mitteleuropas. Vegetatio Acta Geobotanica 11, 154–172.

Andreánszky, G., 1963c. Das Trockenelement in der Alttertiären Flora Mitteleuropas auf Grund Paläobotanischer Forschungen in Ungarn. Vegetatio Acta Geobotanica 11, 95–111.

Andreánszky, G., 1964. Zur Floren-und Vegetationsgeschichte des ungarischen Tertiärs. In Kommission bei Springer-Verlag, Wien/New York, Wien.

Axelrod, D.I., 1958. Evolution of the Madro-Tertiary Geoflora. Botanical Review 24, 433–509.

Axelrod, D.I., 1975. Evolution and biogeography of Madrean–Tethyan sclerophyll vegetation. Annals of the Missouri Botanical Garden 62, 280–334.

Balogh, K., Pécskay, Z., Széky-Fux, V., Gyarmati, P., 1983. Chronology of Miocene volcanism in North–East Hungary. Annuaire de l'Institut de Geologie et de Geophysique 61, 149–158.

Balogh, K., Árva-Sós, E., Pécskay, Z., Ravasz-Baranyai, L., Jámbor, Á., Partényi, Z., Solti, G., Nusszer, A., 1985. K/Ar dating of post-Sarmatian alkaline basaltic volcanic activity in Hungary. 8th Congress of the RCMNS, Hungarian Geological Survey, pp. 82–83.

Barabás, A., 1994. Neogene Formations of the Mecsek Mts (SW. Hungary). Manuscript.

Bartkó, L., 1985. Geology of Ipolytarnóc. Geologica Hungarica. Series Palaeontologica 44, 49–71.

Báldi, T., 1980. The early history of the Paratethys. Bulletin of the Hungarian Geological Society 110 (3-4), 468–471.

Bérczi, I., Hámor, G., Jámbor, Á., Szentgyörgyi, K., 1988. Neogene sedimentation in Hungary. In: Royden, L.H., Horváth, F. (Eds.), The Pannonian Basin. AAPG, Memoir, vol. 45. American Association of Petroleum Geologists, Tulsa, Okla, USA, pp. 57–67.

Besse, J., Courtillot, V., 1991. Revised and synthetic apparent polar wander paths of the African Eurasian, North American and Indian plates, and true polar wander since 200 Ma. Journal of Geophysical Research 96, 4029–4050.

Csontos, L., 1995. Tertiary tectonic evolution of the Intra-Carpathian area: a review. Acta Vulcanologica 7 (2), 1–13.

Csontos, L., Vörös, A., 2004. Mesozoic plate tectonic reconstruction of the Carpathian region. Palaeogeography, Palaeoclimatology, Palaeoecology 210, 1–56.

Dercourt, J., Ricou, L.-E., Vrielynck, B., 1993. Atlas Tethys. Palaeoenvironmental Maps. Gauthier-Villars, Paris. 307 pp.

Erdei, B., Hír, J., 2003. Vegetation and climate reconstruction of Sarmatian (Middle Miocene) sites from NE and W Hungary. Proceedings of the EEDEN/NECLIME joint workshop. Acta Universitatis Carolinae Geologica, vol. 46 (4), pp. 75–84.

Erdei, B., Bruch, A., 2004. A climate analysis of Late Oligocene (Egerian) macrofloras from Hungary. Studia Botanica Hungarica 34, 5–23.

Frankenhäuser, H., Wilde, V., 1995. Stachelspitzige Blätter aus dem Mitteleozän von Eckfeld (Eifel). Abhandlungen des Staatlichen Museums für Mineralogie und Geologie zu Dresden 41, 97–115.

Givulescu, R., 1991. Les forêts marécageuses du Miocène supérieur de Roumanie: un paléobiotope d'exception et sa végétation dans le Miocène supérieur de l'ouest de la Roumanie. In: Kovar-Eder, J. (Ed.), Palaeovegetational development in Europe and regions relevant to its palaeofloristic evolution. Proceedings of PEPC, Vienna, pp. 147–151.

Gyarmati, P., 1977. A Tokaji-hegység intermedier vulkanizmusa. Annals of the Hungarian Geological Survey 58, 195.

Hably, L., 1985. Early Miocene plant fossils from Ipolytarnóc, N. Hungary. Geologica Hungarica. Series Palaeontologica 45, 77–255.

Hably, L., 1992a. The flora of Tihany–Fehérpart (faciostratotype of the Intra-Carpathian Pontian), West Hungary. Geophytology 22, 199–205.

Hably, L., 1992b. Early and late Miocene Floras from the Iharosberény-I and Tiszapalkonya-I Boreholes. Fragmenta Mineralogica et Palaeontologica 15, 7–40.

Hably, L., 1992c. Distribution of legumes in the Tertiary of Hungary. In: Herendeen, P.S., Dilcher, D.L. (Eds.), Advances in Legume Systematics: Part 4. The Fossil Record. The Royal Botanic Gardens, Kew, pp. 169–187.

Hably, L., 2001. Fruits and leaves of *Ailanthus* Desf. from the Tertiary of Hungary. Acta Palaeobotanica 41 (2), 207–219.

Hably, L., 2002. The Middle Miocene flora of Magyaregregy — as shown by a study of recent collections. 6th European Paleobotany–Palynology Conference, Athens, Greece, pp. 91–92.

Hably, L., 2003. Late Neogene vegetation and climate reconstruction in Hungary. Proceedings of the EEDEN/NECLIME joint workshop. Acta Universitatis Carolinae Geologica, vol. 46 (4), pp. 85–90.

Hably, L., Kovar-Eder, J., 1996. A representative leaf assemblage of the Pannonian Lake from Dozmat near Szombathely (Western Hungary), Upper Pannonian, Upper Miocene. Advances in Austrian–Hungarian Joint Geological Research 69–81 Budapest.

Hably, L., Kvaček, Z., 1997. Early Pliocene plant megafossils from the volcanic area in West Hungary. In: Hably, L. (Ed.), Early Pliocene volcanic environment, flora and fauna from Transdanubia, West Hungary. Studia Naturalia, vol. 10, pp. 5–152.

Hably, L., Kvaček, Z., 1998. Pliocene mesophytic forests surrounding crater lakes in western Hungary. Review of Palaeobotany and Palynology 101, 257–269.

Hably, L., Thiébaut, M., 2002. Revision of *Cedrelospermum* (Ulmaceae) fruits and leaves from the Tertiary of Hungary and France. Palaeontographica Abteilung B Paläophytologie 262 (1-4), 71–90.

Hámor, G., 1984. Palaeogeographic reconstruction of Neogene plate movements in the Paratethyan Realm. Acta Geologica Hungarica 27 (1-2), 5–21.

Hámor, G., Bérczi, I., 1986. Neogene history of the central Paratethys. Giornale di Geologia Ser. 3 48 (1-2), 323–342.

Hámor, G., Ravasz-Baranyai, L., Halmai, J., Balogh, K., Árva-Sós, E., 1987. Dating of Miocene acid and intermediate volcanic activity in Hungary. Annals of the Hungarian Geological Survey 70, 149–154.

Harzhauser, M., Piller, W.E., 2007. Benchmark data of a changing sea — Palaeogeography, Palaeobiogeography and Events in the Central Paratethys during the Miocene. Palaeogeography, Palaeoclimatology, Palaeoecology 253, 8–31 (this volume). doi:10.1016/j.palaeo.2007.03.031.

Jiménez-Moreno, G., Rodríguez-Tovar, F.J., Pardo-Igúzquiza, E., Fauquette, S., Suc, J.-P., Müller, P., 2005. High-resolution palynological analysis in the late early–middle Miocene core from the Pannonian Basin, Hungary: climatic changes, astronomical forcing and eustatic fluctuations in the Central Paratethys. Palaeogeography, Palaeoclimatology, Palaeoecology 216, 73–97.

Kissel, C., Laj, C., Poisson, A., Görür, N., 2003. Paleomagnetic reconstruction of the Cenozoic evolution of the Eastern Mediterranean. Tectonophysics 362, 199–217.

Kordos, L., Hajós, M., Müller, P., Nagy, E., 1987. Environmental change and ecostratigraphy in the Carpathian Basin. Annales Instituti geologici publici hungarici 70, 377–381.

Kordos-Szakály, M., 1984. New data to the Miocene flora of Nógrádszakál (Hungary). Annales Historico-Naturales Musei Nationalis Hungarici 76, 43–63.

Kovács, S., Szederkényi, T., Árkai, P., Buda, Gy., Lelkes-Felvári, Gy., Nagymarosy, A., 1996–97. Explanation to the terrane map of Hungary. In: Papanikolau, D. (Ed.), IGCP Project No 276. Terrane maps and Terrane Descriptions. Annales Géol. Pays Hellénique, 37, pp. 245–270.

Kovar-Eder, J., Hably, L., Derek, T., 1995. Neuhaus/Klausenbach — eine miozäne (pannone) Pflanzenfundstelle aus dem südlichen Burgenland. Jahrbuch der Geologischen Bundesanstalt 138 (2), 321–347.

Krijgsman, W., Tauxe, L., 2004. Shallow bias in Mediterranean paleomagnetic directions caused by inclination error. Earth and Planetary Science Letters 222, 685–695.

Krutzsch, W., 1992. Paläobotanische Klimagliederung des Alttertiärs (Mitteleozän bis Oberoligozän) in Mitteldeutschland und das Problem der Verknüpfung mariner und kontinentaler Gliederungen. Neues Jahrbuch für Geologie und Paläontologie. Abhandlungen 186, 137–253.

Magyar, I., Hably, L., 1994. Stratigraphic position of late Neogene palaeobotanical sites in Hungary: Miocene or Pliocene? Acta Palaeobotanica 34 (2), 195–203.

Magyar, I., Geary, D.H., Müller, P., 1999. Paleogeographic evolution of the Late Miocene Lake Pannon in Central Europe. Palaeogeography, Palaeoclimatology, Palaeoecology 147, 151–167.

Mai, D.H., 1995. Tertiäre Vegetationsgeschichte Europas. Fischer, Jena.

Márton, E., 2001. Tectonic implications of Tertiary paleomagnetic results from the PANCARDI area (Hungarian contribution). Acta Geologica Hungarica 44, 135–144.

Márton, E., Fodor, L., 1995. Combination of palaeomagnetic and stress data — a case study from North Hungary. Tectonophysics 98, 43–57.

Márton, E., Fodor, L., 2003. Tertiary paleomagnetic results and structural analysis from the Transdanubian Range (Hungary): rotational disintegration of the Alcapa unit. Tectonophysics 363, 201–224.

Márton, E., Pécskay, Z., 1995. The Tokaj–Vihorlát–Oas–Ignis Triangle: Complex Evaluation of Palaeomagnetic and Isotope Age Data from Neogene Volcanics. Proceedings of the XV. Carpat-Balkan Geological Congress, Spec. Publ. Geol. Soc. Greece, p. 30.

Márton, E., Vass, D., Túnyi, I., 1996. Rotation of the South Slovak Paleogene and Lower Miocene rocks indicated by paleomagnetic data. Geologica Carpathica 47, 31–41.

Mosbrugger, V., Utescher, T., 1997. The coexistence approach — a method for quantitative reconstructions of Tertiary terrestrial palaeoclimate data using plant fossils. Palaeogeography, Palaeoclimatology, Palaeoecology 134, 61–86.

Müller, P., Szónoky, M., 1989. Faciostratotype the Tihany–Fehérpart (Hungary) ("Balatonica Beds", by Lőrenthey, 1905). Chronostratographie und Neostratotypen. Pliozän P11. Pontian. Zagreb-Beograd, pp. 427–436.

Nagymarosy, A., 1980. A magyarországi badenien korrelációja nannoplankton alapján. Bulletin of the Hungarian Geological Society 110 (2), 206–245 (with English Abstract).

Pálfalvy, I., 1950. Középső-miocén növények Magyaregregy környékéről. (Plantes Miocenes mayennes des environs de Magyaregregy). Annual Report of the Hungarian Geological Survey, pp. 175–180.

Pálfalvy, I., 1957. Új növények a mecseki középső-miocén rétegekből. (Neue Pflanzenarten aus den mecseker mittleren miozänen Schichten). Annual Report of the Hungarian Geological Survey, pp. 401–415.

Pogácsás, Gy., Révész, I., 1987. Seismic stratigraphic and sedimentological analysis of Neogene delta features in the Pannonian Basin. Annales Instituti geologici publici hungarici 70, 267–273.

Pécskay, Z., Balogh, K., Széky-Fux, V., Gyarmati, P., 1986. Geochronological investigations on the Neogene volcanism of the Tokaj Mountains. Geologicky Zbornik 37 (5), 635–655.

Pécskay, Z., Balogh, K., 1987. A Tokaji hegység miocén vulkánosságának K/Ar geokronológiája. Bulletin of the Hungarian Geological Society 117 (3), 237 Budapest.

Pécskay, Z., Lexa, J., Szakács, A., Balogh, K., Seghedi, I., Konecny, V., Kovács, M., Márton, E., Kaliciak, M., Széky-Fux, V., Póka, T., Gyarmati, P., Edelstein, O., Rosu, E., Zec, B., 1995. Space and time distribution of Neogene–Quaternary volcanism in the Carpatho–Pannonian Region. Acta Vulcanologica 7 (2), 15–28.

Ravasz, Cs., 1987. Neogene volcanism in Hungary. Annales Instituti geologici publici hungarici 70, 275–279.

Rögl, F., 1998. Palaeogeographic considerations for Mediterranean and Paratethys Seaways (Oligocene to Miocene). Annalen des Naturhistorischen Museums in Wien. Serie A für Mineralogie und Petrographie, Geologie und Paläontologie, Anthropologie und Prähistorie 99, 279–310.

Schweitzer, F., 1997. On late Miocene — early Pliocene desert climate in the Carpathian Basin. Zeitschrift für Geomorphologie N.F. 110, 37–43.

Staub, M., 1882. Baranyamegyei mediterrán növények. Magyar Királyi Földtani Intézet Évkönyve 6, 23–42.

Syabryaj, S., Utescher, T., Molchanoff, S., Bruch, A.A., 2007. Vegetation and palaeoclimate in the Miocene of Ukraine. Palaeogeography, Palaeoclimatology, Palaeoecology 253, 169–184 (this volume). doi:10.1016/j.palaeo.2007.03.038.

Utescher, T., Mosbrugger, V., Ashraf, A.R., 2000. Terrestrial climate evolution in Northwest Germany over the last 25 million years. Palaios 15, 430–449.

Utescher, T., Erdei, B., Francois, L., Mosbrugger, V., 2007. Tree diversity in the Miocene forests of Western Eurasia. Palaeogeography, Palaeoclimatology, Palaeoecology 253, 242–266 (this volume). doi:10.1016/j.palaeo.2007.03.041.

Wilde, V., Frankenhäuser, H., 1998. The Middle Eocene plant taphocoenosis from Eckfeld (Eifel, Germany). Review of Palaeobotany and Palynology 101, 7–28.

Zachos, J.C., Pagani, M., Stone, L., Thomas, E., Billups, K., 2001. Trends, rhythms, and aberrations in global climates 65 Ma to present. Science 292, 686−293.

All climate data provided here are accessible by the world data base PANGAEA under the reference.

Erdei, B., Hably, L., Kázmer, M., Utescher, T., Bruch, A.A., 2007. Oligocene to Pliocene palaeoclimate reconstructions from 18 sites in Hungary. PANGAEA. doi:10.1594/PANGAEA.587448.