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Pannonian (Upper Miocene) Vegetational Character and Climatic Inferences in the Central Paratethys Area

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(With 2 figures)

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Abstract

Vegetation and climate are investigated based on leaf-, pollen- and seed-floras from the Central Paratethys region correlated to the Pannonian (Upper Miocene, Central Paratethys chronostratigraphical stage).

Waterplant-communities, reed facies, riparian forests and swamp forests can be distinguished along with forests comparable to mixed-mesophytic ones rich in species with dominance of deciduous taxa over evergreens and conifers. The percentage of evergreen species increases towards the southeast part of the investigated area. Conifer taxa are supposed to be of prevailing importance in mountainous forests.

Arguments for either xeromorphic mediterranean-like vegetation or for steppe-like conditions (extensive dry grassland) are scarce and probably invalid.

The fossil plant record indicates a warm-temperate climate without remarkable dry season (Cfa-type sensu KÖPPEN).

Zusammenfassung

Blatt-, Pollen- und Samenflora aus dem Pannon (Ober-Miozän) des Zentralen Paratethysgebietes werden vergleichend und zusammenfassend betrachtet. Sie dokumentieren die Existenz von Wasserpflanzengesellschaften, Röhricht, Au- und Moorwäldern sowie von Wäldern vergleichbar den mixed-mesophytic forests. Letztere sind durch das Überwiegen laubwerfender Taxa gegenüber immergrünen und Koniferen gekennzeichnet. In höher gelegenen Gebieten ist verstärktes Auftreten von Koniferen anzunehmen.

Bisher gibt es keine hinreichend fundierten Nachweise für die Existenz xeromorpher Vegetation vom Mittelmeer-Typ oder von Steppe (ausgedehntes Grasland) im Gebiet der Zentralen Paratethys während des Pannon.

Die Wälder des Pannon gediehen unter warm-gemäßigtem Klima ohne ausgeprägte trockene Jahreszeit (Cfa-Typ sensu KÖPPEN).

Introduction	118
Floral record of the different regions	119
Rumania	119
Hungary	121
Poland	122
ČSSR	123

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Austria	123
Western Germany	124
Climate	125
Results	127

Introduction

Several attempts have been made to characterize vegetational changes during the Neogene in different European regions (MAI 1967, KNOBLOCH 1975, HOCHULI 1978, STUCHLIK 1979, GIVULESCU 1980, GREGOR 1982). MAI (1981) reconstructed the vegetational succession in Middle Europe during the Tertiary. However, considerable difficulties arise in attempting to correlate the results both with each other and with palaeoclimatic interpretations obtained by faunistic investigations. There is still no consensus on vegetational oscillations during the Miocene for large parts of Europe. These difficulties arise both as a result of the problems in correlating and dating many fossil floras and different interpretations of climatic and floristic terms such as "warm-temperate", "subtropic", "arid" or "steppe". This paper attempts to clarify our interpretation of miocene terrestrial ecosystems of the Central Paratethys area during the Pannonian. It reviews the leaf-, pollen- and seed-floras that complement each other and provide the basis for interpreting the vegetation. A consistent model of vegetational characteristics and climate is presented for this region during the Upper Miocene (Pannonian, Central Paratethys stage; see fig. 2). Throughout the paper the KÖPPEM-system of climatic classification is used. The fossil floras are dealt according to regions.

Table 1. The investigated floras, their age and the authors. ¹⁾ leaf-flora, ²⁾ pollen-flora, ³⁾ seed-flora. The numbers correspond to that in fig. 1.

locality	author	flora	age
1 Valea Neagra	GIVULESCU 1962	l ¹⁾	Pannon (early)
2 Delureni	GIVULESCU 1975	l	Pannon B
3 Cornitel	GIVULESCU 1957	l	Pannon
4 Beznea	GIVULESCU 1961	l	Pannon (early)
5 Sirbi, Sig, Fizes	DIACONEASA & al. 1968	p ²⁾	Pannon
6 Hidas	NAGY 1984	p	Pannon
7 Tököl	NAGY 1984	p	Pannon
8 Papa	NAGY 1984	p	Pannon
9 Rudabanya	NAGY & PALFALVY 1961	l + p	Pannon
	KRETZOI & al. 1976		Pannon (early)
10 Megyaszó	NAGY 1984	p	Pannon
11 Alsovadasz	NAGY 1984	p	Pannon
12 Koniowka	STUCHLIK 1979	p	Pannon
13 Czarny Dunajez	STUCHLIK 1979	p	Pannon
14 Nove Ustie	KNOBLOCH 1980	l + s ³⁾	Sarmat/Pannon
15 Nitra	SNOPKOVA 1960	p	Pannon
	PLANDEROVA 1984	p	Pannon
16 Dubravica	PLANDEROVA & al. 1960	p	Sarmat/Pannon
17 Kunovice	KNOBLOCH 1976 a	s	Pannon B

locality	author	flora	age
18 Temice	KNOBLOCH 1967, 1976 b	s	Pannon C
19 Orechov	KNOBLOCH 1967, 1976 b	s	Pannon C
20 Mistrin	KNOBLOCH 1967, 1976 b	s	Pannon C
21 Cejc	KNOBLOCH 1967, 1976 b	s	Pannon B
22 Postorna	KNOBLOCH 1967, 1976 b	s	Pannon E
23 Hodonin	KNOBLOCH 1967, 1976 b	s	Pannon E
24 Laaerberg	BERGER 1955 b	l	Pannon E
25 Vösendorf	BERGER 1952, 1955 a	l	Pannon E
26 Ebersbrunn	KOVAR-EDER in press	l	Pannon
27 Schneegattern	KOVAR-EDER in press	l	Pannon
28 Großenreith	KOVAR-EDER in press	l	Pannon
29 Lohnsburg	KOVAR-EDER in press	l	Pannon
30 Leonberg	GREGOR 1982	l + s	phytozone OSM 4, MN 9
	JUNG & MAYR 1980		
31 Hammerschmiede	GREGOR 1982	s	phytozone OSM 4, MN 9
	JUNG & MAYR 1980		

Floral record of the different regions

Rumania

Leaf- and pollen-floras (Beznea, Cornitel, Delureni, Valea Neagra, Sirbi, Sig, Fizes – GIVULESCU 1957, 1961, 1962 a, b, 1975, DIACONEASA & NORICI 1968) have so far been evaluated. They are less rich than Pontian ones (mainly Chiuzaibaia).

Based both on Pannonian and Pontian floras GIVULESCU (1980: 42) characterizes the Pannonian-Pontian vegetation as “forêts mixtes mésophytiques riches en essences des régions collinaires à diverses altitudes et expositions”. A swamp community with *Glyptostrobus* and *Myrica* at the shore of the Pannonian Lake has been documented in Beznea (GIVULESCU 1961: 346). A riparian forest community with *Sequoia*, *Salix*, *Alnus*, *Juglans*, *Quercus*, *Pterocarya*, and plants typical of a mixed-mesophytic forest have been elaborated from Valea Neagra. The mixed-mesophytic forest elements include *Fagus*, *Castanea*, *Carpinus*, *Ulmus*, *Zelkova*, *Carya*, *Sassafras*, *Aceraceae*, *Parrotia*, *Prunus*, *Cornus* and *Ilex* and are thought to reflect a forest comparable to that between the Alleghany Mountains and the Atlantic coast in southeastern North America (GIVULESCU 1962 a: 172).

Evidence for a *Nerium-Arbutus-Laurus-Pistacia*-association (GIVULESCU 1962 a: 173) implying mediterranean-type xeromorphic vegetation is not well founded. Only a single specimen of *Nerium* was described and it may probably be misidentified. Only three leaves were assigned to *Arbutus* and two to *Pistacia* (GIVULESCU 1962 a: 155, 163, 165). Even if they have been determined correctly they would not necessarily be a proof of xeromorphic vegetation (see “Climate”).

The climatic conditions indicated by the Valea Neagra flora are characterized as Cfa-climate of the “Virginia-type” (GIVULESCU 1962 a: 175f.). Generally the Pannonian floras from the Boroder Basin (Beznea, Cornitel, Valea Neagra, Delureni) show a somewhat warmer character than those of Western and Northern

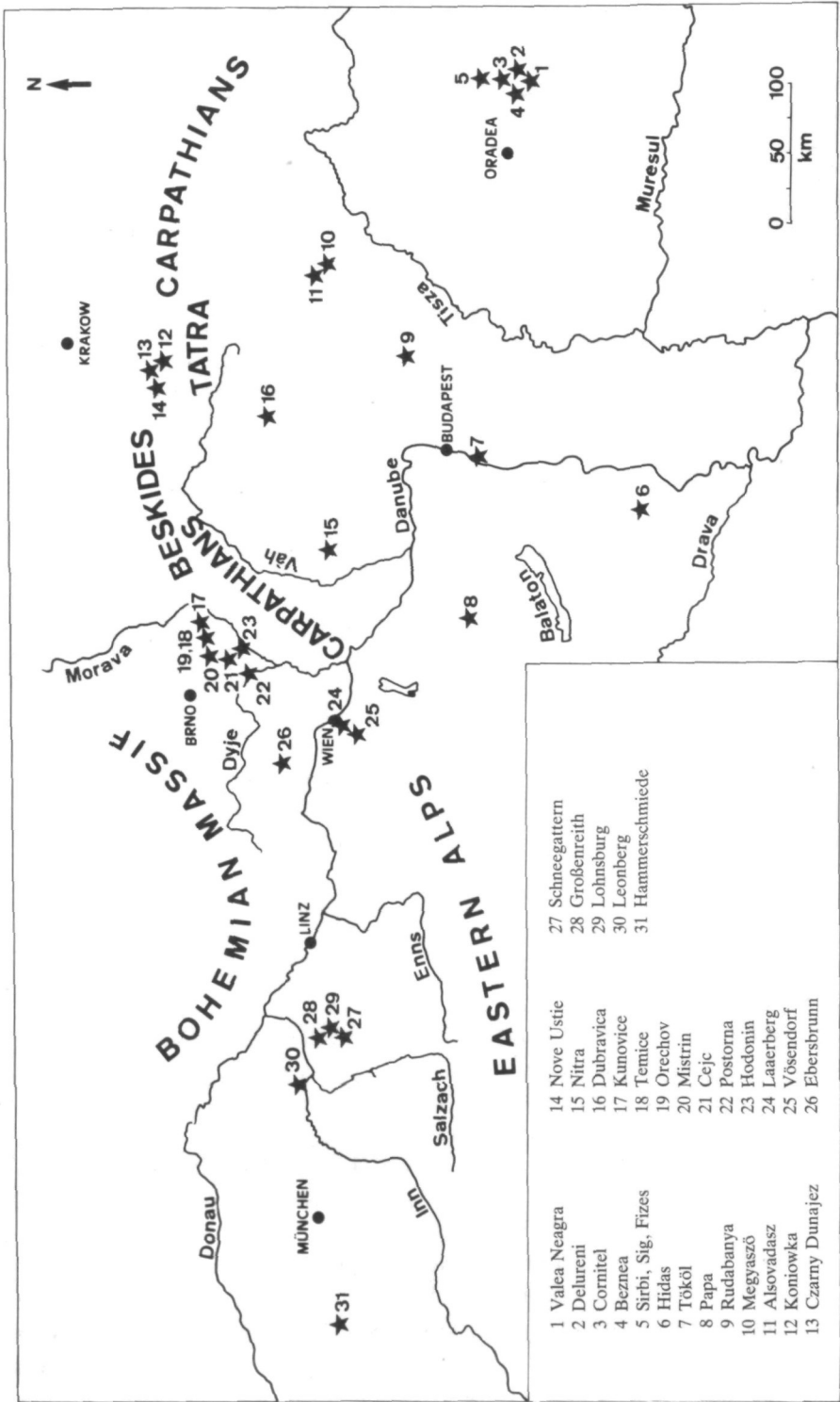


Fig. 1. Geographical map showing the investigated Pannonian plant-localities.

MILL. YEARS	EPOCHS	PARATETHYS		EUROPEAN MAMMAL-ZONES MEIN, 1979	PHYTO-ZONES GREGOR, 1982	
		CENTRAL	EASTERN			
6	E LATE	PONTIAN	PONTIAN	MN 13	OSM 4	
7				MN 12		
8				MN 11		
9	PANNONIAN s. str.	E	MAEOTIAN	SARMATIAN s.l.		
10		D	KHERSONIAN			MN 10
11		C	BESSARABIAN			MN 9
12		A/B			Uj	MN 8
13	MIDDLE	SARMATIAN s. str.	VOLHYNIAN	MN 7	OSM 3b	

Fig. 2. Middle to Upper Miocene stratigraphic correlation table of the Paratethys area (after RÖGL & STEININGER 1983, modified after RÖGL pers. comm.).

Central Paratethys areas. During the Pannonian *Libocedrites salicornioides*, *Engelhardia* and *Lauraceae* are almost restricted to this region (in contrast to their wider distribution in the older Paratethys-floras). This may be due to favourable climatic conditions in the Boroder Basin that is situated at the Southern slopes of the Rez Mountains (GIVULESCU 1962 b: 409, KNOBLOCH 1975: 389).

Hungary

The Hungarian Pannonian contains only a small number of floras (KNOBLOCH 1973: 260). NAGY (1984) characterized the Pannonian¹⁾ vegetation of Hungary based on pollen from bore-hole sections in the Mecsek Mountains (Hidas), in the northwest foreland of the Bakony Mountains (Papa), in the northwest marginal zone of the Hungarian Plain (Tököl) and from North Hungary (Alsóvadasz and

¹⁾ The "lower Pannonian" in NAGY (1984) corresponds to the Pannonian s. str. and belongs to the Miocene (see fig. 2).

Megyaszö). Vegetational types recognized included swamp forests (e. g. Tököl, Hidas) with *Taxodium* and *Myrica*. Similar assemblages were also found in Papa, Megyaszö and Alsóvadász. From Megyaszö NAGY (1984) recognized a freshwater gallery assemblage with *Sparganium*, *Alnus*, *Salix*, *Carya*, *Pterocarya* and ferns. Further landward under somewhat drier – but not “arid” NAGY (1984) – conditions there existed rich forests in Tököl consisting of *Tilia*, *Ulmus*, *Zelkova*, *Acer*, *Carpinus* with *Corylus*, *Ostrya*, *Ericaceae* and *Elaeagnaceae* in the undergrowth and shrub layer. In Megyaszö the mixed warm-temperate deciduous forest is represented by *Tilia*, *Castanea*, *Celtis*, *Elaeagnus*, *Zelkova* and *Quercus* with subtropical understories of *Rhus* and *Ostrya*. From Megyaszö even palms have been reported. Forests of *Abies*, *Picea*, *Pinus*, *Keteleeria* and *Cedrus* were dominant at middle altitude on the mountains (e. g. Hidas).

In the flora of Rudabanya (NAGY & PALFALVY 1957/58, KRETZOI & al. 1976) representatives of water and swamp communities prevail over other plant associations. *Stratiotes*, *Myriophyllum*, *Potamogeton*, *Trapa* and *Nymphaeaceae* represent water plants. The reed facies is documented by *Typha* and *Phragmites* as well as by *Menyanthes* and *Carex*. Temporarily flooded swamp forests included *Glyptostrobos*, *Taxodium*, *Byttneriophyllum*, *Alnus*, *Betula*, *Liquidambar*, *Nyssa*, *Carya* and *Myrica*. Even more rarely flooded than stands of *Salix* and *Alnus* were forests of *Ulmus*, *Zelkova*, *Fraxinus*, *Alnus* and *Quercus*. Middle altitude mountain forests comprised *Tilia*, *Acer*, *Cercidiphyllum*, *Quercus*, *Fagus*, *Carpinus*, *Engelhardia*, *Ginkgo*, *Pinus*, *Cedrus*, *Keteleeria*, *Sciadopitys*, *Tsuga*, *Picea*, *Abies*, *Podocarpus*, *Ilex* and *Corylus*.

KRETZOI & al. (1976: 386f.) also postulate the existence of extensive dry grassland interrupted by tree groups (“ausgebreitete, trockene Graslandgebiete”) because of the presence of *Gramineae*, *Cyperaceae*, *Artemisia*, *Salvia* and *Scabiosa*. They neither give percentages of NAP nor discuss the possibility that at least the pollen of *Cyperaceae* may represent wetland plants. Furthermore the pollen record from Rudabanya does not bear any other support for this interpretation of KRETZOI & al. (1976). So the existence of extensive dry grassland interrupted by tree groups is to be considered doubtful as the presence of swampy facies and the richness of the mixed-mesophytic forest – postulated by the same authors – more likely exclude the presence of this kind of biotope even in the further surrounding of the Rudabanya Lake.

Poland

Pannonian pollen floras have been described in the bore-hole sections of Czarny Dunajec and Koniowka (Nowy Targ Basin) by OSZAST & STUCLIK (1977) and STUCLIK (1979). These authors interpret the vegetation to include: Swamp forests composed of *Glyptostrobos*, *Cunninghamia*, *Taxodium* and *Nyssa* which had extended over large parts of the Nowy Targ – Orava Basin before the Pannonian disappeared as well as *Engelhardia*, *Carya* und *Sequoia*. Pollen of *Picea* and herbaceous plants increases. *Aralia*, *Decodon*, *Parthenocissus*, *Platycarya*,

Staphylea, *Sterculiaceae* and *Symplocos* are not present in the Pannonian (STUCHLIK 1979: 1175f.).

The climate is characterized by STUCHLIK (1979: 1176) as "basically temperate with alternating warmer oscillations, comparatively dry".

ČSSR

The Pannonian vegetation of the Czech part of the Central Paratethys is mainly documented by seed- and pollen-floras while leaf-floras are rare (only Nove Ustie).

Kunovice, Cejc, Mistrin, Temice, Orechov, Postorna, Hodonin and Nove Ustie (KNOBLOCH 1963, 1976 a, b, 1980, 1985) have been interpreted as indicating a wide spectrum of Pannonian plant communities. Waterplants include *Trapa*, *Stratiotes*, *Potamogeton*, *Euryale*, *Nymphaeaceae*, *Ceratophyllum*, *Damasonium*, *Alisma* and *Caldesia*. The reed facies is documented by *Sparganium*, *Typha*, *Scirpus* and *Carex*. Swamp forest elements are *Glyptostrobus*, *Byttneriophyllum*, *Myrica*, *Decodon*, *Diclidocarya*, *Spirematospermum*, *Vitis*, *Ampelopsis*, *Swida*, *Rubus*, *Paliurus* and *Sambucus*. These interpretations are supported by the pollen-flora of Dubravica (near Banska Bystrica, PLANDEROVA & SNOPKOVA 1960). From Nove Ustie leaf remains from *Ginkgo*, *Platanus*, *Ulmus*, *Castanea*, *Fagus*, *Acer* and *Carpinus* and further taxa known from pollen as *Betula*, *Quercus*, *Pterocarya*, *Juglans*, *Engelhardia*, *Tilia*, *Pinus*, cf. *Larix*, *Picea* and *Abies* from Dubravica indicate members of a mixed-mesophytic forest. The pollen-flora from Nitra (SNOPKOVA 1960) agrees with these results. PLANDEROVA & SNOPKOVA (1960) interpret *Cedrus*, *Tsuga* and *Rhus* to have occurred on drier ground in Dubravica. Decrease of subtropical species and dominance of temperate plants as well as high percentage of herbs is characteristic of the Pannonian in southwest Slovakia according to PLANDEROVA (1962: 156). But neither systematic details nor the abundance of herbs have been documented by her.

In contrast to the foregoing results PLANDEROVA (1984) postulates a dry climate with steppe character for the Pannonian based on two borehole sections from the surrounding of Nitra. She states richness of herb species in the pollen-spectra (*Gramineae*, *Compositae*, *Umbelliferae*, *Artemisia*) but also mentions among others *Betulapollenites*, *Alnipollenites*, *Myricipites*, *Pterocaryapollenites*, *Quercoidites* div. sp., *Faguspollenites* div. sp. and *Salixpollenites* div. sp. to be "most frequent" (PLANDEROVA 1984: 132). Details of percentages are missing. The pollen-flora seems more likely to be indicative to the existence of mesophytic forests than of steppe conditions.

Austria

The leaf-floras of the southern part of the Vienna Basin (Laaerberg and Vösendorf, BERGER 1952, 1955 a, b) provide a detailed insight into the Pannonian vegetation in this part of the Central Paratethys region. The flora of Vösendorf appears relatively autochthonous. Waterplants are present with *Ceratophyllum* as

well as reed facies. Swamp and riparian forests are indicated mainly by *Taxodium*, *Glyptostrobus*, *Myrica*, *Nyssa*, *Salix*, *Populus*, *Platanus*, *Zelkova* and *Pterocarya*. From Laaerberg and Vösendorf *Fagus*, *Carpinus*, *Betula*, *Ulmus*, *Acer*, *Alnus*, *Populus*, *Platanus*, *Ginkgo*, *Quercus*, *Juglans*, *Liquidambar*, *Tilia* and *Vitaceae* provide evidence for the existence of a rich mesophytic forest as known from other parts of the Central Paratethys region.

BERGER (1955 b: 108) mentions plants of mediterranean xeromorphic character which he has determined as *Quercus* cf. *wislizeni*, *Buxus*, *Laurus*, *Paliurus* and *Smilax*. The single leaf determined as *Qu.* cf. *wislizeni* probably belongs to the genus *Platanus*. Even BERGER (1955 b: 97) regards the determination of cf. *Buxus pliocenica* as doubtful. The presence of *Smilax* is not indicative to mediterranean xeromorphic vegetation (as proposed by BERGER). Only two of about 300 living *Smilax* species live in the Mediterranean and the others in the subtropics and tropics. Furthermore *Smilax* is present in many Lower and Upper Tertiary floras from Europe and Northern America.

Further west from the Vienna Basin there are several leaf-floras in the Molassezone north of the Alps that are progressively further from the Pannonian Lake (Ebersbrunn, Schneegattern, Lohnsburg, Großenreith; KOVAR-EDER in press). Riparian forest is well documented in Schneegattern by *Salix*, *Alnus*, *Platanus* and *Ulmus*. *Fagus*, *Quercus*, *Acer*, *Ulmus*, *Zelkova*, *Populus*, *Liquidambar*, *Juglandaceae*, *Liriodendron*, *Carpinus* and *Ginkgo* represent members of the mesophytic forest. Conifers like *Glyptostrobus*, *Sequoia* and *Pinus* are not abundant.

Western Germany

Floras from the German part of the Molassezone correlated to the phytozone OSM 4 and mammal stage MN 9 (JUNG & MAYR 1980, GREGOR 1982) and therefore equivalent with the Pannonian are rare. The Hammerschmiede (near Kaufbeuren) and Leonberg (near Markt/Inn) floras contain seeds of waterplants and swampy facies like *Nymphaea*, *Potamogeton*, *Ceratophyllum*, *Trapa*, *Caldesia*, *Mneme*, *Decodon*, *Sparganium*, *Carex*, *Stratiotes*, *Proserpinaca*, *Swida*, *Vitis*, *Spirematospermum* and *Sambucus*. In Leonberg a few taxa indicate the existence of a mesophytic forest: *Acer*, *Carpinus*, ? *Fagus*, *Liquidambar* (GREGOR 1982: 46f., 56). The important floras from Massenhausen (JUNG 1963), Aubenham (UNGER 1983) and Achldorf (KNOBLOCH 1986) have been correlated to the MN 8 (JUNG & MAYR 1980) and to the phytozone OSM 4 (GREGOR 1982) (see text-fig. 2). The stratigraphical relevant faunas of the MN 8 to which the fossil floras have been correlated are equivalent to the Sarmatian. Therefore these floras are excluded from this investigation.

GREGOR (1982) reconstructs the climate for the Bavarian part of the Paratethys area during the phytozone OSM 4 (details are given under "Climate").

Climate

In the Pannonian the climatic conditions indicated by the fossil floral record may be characterized as warm-temperate: Laaerberg, Vösendorf (BERGER 1955 b: 110f., 1955 c: 16f., 27), Dubravica (PLANDEROVA & SNOPKOVA 1960: 190), Nitra (SNOPKOVA 1960: 194), Koniowka and Czarny Dunajec (STUHLIK 1979: 1176), Hungary (NAGY 1984). Sometimes it is compared to the Cfa-climate sensu KÖPPEN (Virginia climate or climate of the musonic type in the Southeast of Northern America): Cornitel (GIVULESCU 1957: 104), Valea Neagra (GIVULESCU 1962: 173ff.), Molassezone north of the Alps, Bavaria (GREGOR 1982: 191).

The Cfa-climate sensu KÖPPEN is defined as follows: warm-temperate climate with no remarkable dry season, temperature of the coldest month between -3°C ($26,6^{\circ}\text{F}$) and $+18^{\circ}\text{C}$ ($64,4^{\circ}\text{F}$) and average temperature of the warmest month $>22^{\circ}\text{C}$ ($71,6^{\circ}\text{F}$) (in BLÜTHGEN & WEISCHET 1980: 668ff.).

GREGOR (1982: 191) gives a more detailed climatic interpretation of the Cfa-climate for the Bavarian part of the Molassezone for the phytozone OSM 4 which he has correlated to the mammal stage MN 8/9 and the Sarmatian/Pannonian chronostratigraphical stage. GREGOR estimates a mean annual temperature of $12\text{--}15^{\circ}\text{C}$ ($53,6\text{--}59^{\circ}\text{F}$), mean January temperature of $>0^{\circ}\text{C}$ (32°F), mean July temperature of $\leq 25^{\circ}\text{C}$ (77°F) and annual precipitation of about 1000–1200 mm. These conditions may not reflect exactly those closer to the Pannonian Lake as the large water body presumably had a moderating influence on the climate of the surrounding area.

Although of Pontian age the climatic evaluation of the flora from the Matra Mountains (NAGY 1958: 259f.) may provide a good model for the slightly older floras in the Pannonian Lake area. NAGY's study is the only one that considers the microclimates of the single habitats. The composition of the flora does not differ principally from those of the Pannonian so that these results have at least some validity for the Pannonian. The following interpretations are presented:

1. swamp forests: mean annual temperature $14\text{--}20^{\circ}\text{C}$ ($57,2\text{--}68^{\circ}\text{F}$), mean July temperature $25\text{--}28^{\circ}\text{C}$ ($77\text{--}82,4^{\circ}\text{F}$), mean January temperature $2\text{--}12^{\circ}\text{C}$ ($35,6\text{--}53,6^{\circ}\text{F}$).

2. riparian forests: mean annual temperature $12\text{--}19^{\circ}\text{C}$ ($53,6\text{--}66,2^{\circ}\text{F}$), mean July temperature $20\text{--}28^{\circ}\text{C}$ ($68\text{--}82,4^{\circ}\text{F}$), mean January temperature $2\text{--}8^{\circ}\text{C}$ ($35,6\text{--}48,4^{\circ}\text{F}$). For stands of *Sequoia* separate dates are given: mean annual temperature $11\text{--}15^{\circ}\text{C}$ ($51,8\text{--}59^{\circ}\text{F}$), mean temperature of warmest month $15\text{--}20^{\circ}\text{C}$ ($59\text{--}68^{\circ}\text{F}$) and of the coldest month $6\text{--}12^{\circ}\text{C}$ ($42,8\text{--}53,6^{\circ}\text{F}$).

3. mesophytic forests of low altitudes ("Zone des am Bergfusse stehenden Waldes"): mean annual temperature $8\text{--}12^{\circ}\text{C}$ ($48,4\text{--}53,6^{\circ}\text{F}$), mean July temperature $23\text{--}26^{\circ}\text{C}$ ($73,4\text{--}78,8^{\circ}\text{F}$) and mean January temperature -3 to $+5^{\circ}\text{C}$ ($26,6\text{--}41^{\circ}\text{F}$).

4. mountain forests (of about 500–600 m till 1300–1400 m above sea level): mean annual temperature $6\text{--}11^{\circ}\text{C}$ ($42,8\text{--}51,8^{\circ}\text{F}$), mean July temperature $17\text{--}22^{\circ}\text{C}$ ($62,6\text{--}71,6^{\circ}\text{F}$) and mean January temperature $-6^{\circ}\text{--}0^{\circ}\text{C}$ ($21,2\text{--}32^{\circ}\text{F}$).

Perhaps the most critical element in these interpretations is the possibility that while some microclimates may have experienced considerable frosts others may have been mere or less frostfree. THENIUS (1982: 698) has recently dealt with the issue of frost in the Pannonian climates. Based in part on the evidence of *Pinus halepensis* and *Pinus canariensis* (KLAUS 1977, 1982) THENIUS suggests a more or less frostfree climate. However the interpretation of *P. halepensis* as frost sensitive (KLAUS 1977: 65) needs to be revised based on the research of FALUSI & al. (1985: 130f.) who studied the effects of frost on buds, needles and stems of *P. halepensis* over 4–5 year periods. Frost hardiness to temperatures of -12°C ($10,4^{\circ}\text{F}$) throughout the whole winter was demonstrated and even lower temperatures could be withstood for short periods. PANETSÓS (1981) has already recorded temperatures of less than -10°C (14°F) in some regions of the natural distribution area of *P. halepensis*.

In addition more attention should be paid to possible microclimatic differences caused by topographical factors such as differences in elevation, extension of mountains as well as distance from stream and river banks and the Pannonian Lake. NAGY'S (1958: 259f.) climate analysis of the flora from the Matra Mountains clearly illustrates possible differences in microclimate in different habitats. It offers interpretation of climatic favoured areas and climatic variation associated with elevation.

Postulated climatic demands of fossil organisms mainly are indicative of the microclimate of their habitat and may be of limited relevance to the macroclimate. Therefore sensitivity to frost of living *Pinus canariensis* as interpreted by KLAUS (1982: 83) may not necessarily indicate a completely frostfree macroclimate. It may instead indicate merely a frostless microclimate of the fossil *P. canariensis* habitat at the border of the Vienna Basin.

A dry climatic period during the lowermost Pannonian suggested by land gastropods (LUEGER 1978) cannot be ascertained by the fossil floras currently known. The rare floral records interpreted to indicate a dry Pannonian climate (PLANDEROVA 1984, KRETZOI & al. 1976) are all doubtful (see above). Furthermore exact correlation of these floras (Nitra, Rudabanya) with the lowermost Pannonian is not possible. All floras of definite lower Pannonian age (seed-floras from Cejc, Kunovice: Pannonian B and Mistrin, Temice, Orechov: Pannonian C; leaf-flora of Cornitel: Pannonian B) consist of water-, wetland-plants and taxa comparable to those of mixed-mesophytic forests.

SUC'S (1984: 429) investigations on the origin of mediterranean vegetation provide evidence that *Phillyrea*, *Olea*, *Cistus*, *Quercus ilex*, *Pistacia* – taxa characteristic of recent mediterranean vegetation did not form spezialized associations in the northwest Mediterranean until the upper Pliocene. In the Pontic area they are still associated with deciduous forests of *Quercus*, *Pterocarya* and *Fagus orientalis* under humid conditions today. In this context it is problematic to extrapolate the ecological demands of Mediterranean taxa to fossil floras. Only recent investigations on Mediterranean Upper Miocene floras (Northern Greece) indicate the existence of forests comparable to mixed mesophytic ones in this region at that

time (VELITZELOS & GREGOR 1986: 38). Similar conditions are postulated for Western Georgia (USSR) by SHATILOVA & RAMISHVILI (1984: 425). They recognize rich subtropical vegetation during the Sarmatian (Eastern Paratethys stage, see tab. 1) and starting from that time an increasing percentage of temperate plants in the Meotian and Pontian.

Results

Plant associations representing different habitats provide the basis for interpreting the vegetation of the Central Paratethys region during the Pannonian. These habitats can be recognized in numerous fossil floras (leaf-, seed- and fruit- as well as pollen-floras) in the Central Paratethys region. The fossil floras complement each other. Waterplant communities, reed facies, riparian forests and swamp forests can all be distinguished along with forests comparable to mixed-mesophytic forests rich in species with dominance of deciduous taxa over evergreens and conifers. The percentage of evergreen species rises towards the SE part of the area and in the mountainous forests conifer taxa are supposed to be of prevailing importance.

Records on steppe-like vegetation (KRETZOI & al. 1976: 386f., PLANDEROVA 1984) as well as interpretations of mediterranean xeromorphic vegetation (BERGER 1955 b: 97) are scarce and probably invalid.

The climatic conditions may be characterized as Cfa-climate *sensu* KÖPPEN which is generally defined as warm-temperate climate without dry season, temperature of coldest month between -3°C and 18°C ($26,6^{\circ}\text{F}$ and $64,4^{\circ}\text{F}$) and mean temperature of warmest month $>22^{\circ}\text{C}$ ($71,6^{\circ}\text{F}$). A more precise characterisation has been given by GREGOR (1982: 191) for the phytozone OSM 4 (Sarmatian/Pannonian) in the Molassezone north of the Alps (Bavaria). The available evidence suggests that the vegetation during the Pannonian in the Central Paratethys Region was similar to that during the Pontian of the Matra Mountains-flora. NAGY'S (1958: 259f.) microclimatic analysis may therefore apply almost equally well to slightly older floras in the Central Paratethys region.

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