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Notes on the contemporary vegetation of the southeastern United States  
and the Pliocene vegetation of the West Carpathian Mountains in Europe

An attempt at comparison \*

by

Kazimierz ZARZYCKI

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\* In memory of Professor Władysław Szafer (1886-1970), on the tenth anniversary of his death

## 1. Introduction

The International Phytogeographic Excursions - Internationale Pflanzengeographische Exkursionen - (IPE), founded in 1908 by A.G. Tansley (Oxford) and E. Rübel (Zürich), have a long and distinguished tradition. The stimulating impact of the IPE on the development of vegetation science in Europe has been enormously important.

The 16th IPE (1978) through the SE United States was of particular interest to the European scientists. "The vegetation of the Carolinas contains such grandesse in general and such outstanding peculiarities in numerous places that this fieldtrip, attempting a cross section through the highlights of the vegetation became an overwhelming experience in itself" was emphasized by LIETH and LANDOLT (1979). I can only add that I agree wholeheartedly with their views.

This excursion gave the European participants the opportunity to make observations and to enjoy unusual forms of insectivorous plants, such as the venus fly-trap (*Dionaea muscipula*) and pitcher plants (*Sarracenia* sp. div.), exotic *Sabal palmetto* and many others in their natural environment.

I was totally absorbed in the rich flora, vegetation, and fascinating ecological studies. Whilst crossing the coastal plain and the mountains of the Carolinas I thought I was wandering through my own country - Poland - some millions of years ago. I remembered that, when I was a student, Professor Szafer told us during his lectures, that the Pliocene forest at the foot of the Pieniny Mts. in the Carpathians, contained such trees as I now observed in the Congaree Swamps; enormous specimens of *Platanus occidentalis* reaching 166 ft. (56 m), *Liquidambar styraciflua* (42 m), *Carya cordiformis* (45 m), *Nyssa sylvatica* var. *biflora* (37 m) and others (GADDY 1977).

It was not only a wonderful trip to the fantastic swamps and the vast forests of the Smoky Mountains but also a journey to the remote past, to the Tertiary period.

I thought about it especially intensively when, during the field trip to the Nantahala Mountains, we admired an enormous specimen of tulip poplar. I

therefore decided to prepare a short essay about the contemporary vegetation of the southeastern United States and the Pliocene vegetation in the West Carpathian Mts. Volume I of "Contributions to the knowledge of flora and vegetation in the Carolinas" helped me very much in my work.

I concentrated on the role of North American element in the rich fruit-and-seed Pliocene flora from Krościenko described by SZAFER (1938, 1946, 1947). The results of this investigation are of great importance for the reconstruction of the Pliocene vegetation and climate in the West Carpathians, as well as for my present work on the relic and endemic plant species in this region (ZARZYCKI 1976).

### Acknowledgements

I wish to express my grateful appreciation to the Rübel Foundation (Zürich) as well as to the Polish Academy of Sciences (Warszawa) for giving me the opportunity to participate in the 16th IPE through the SE United States. My own particular gratitude is due to Professors: Dr E. Landolt (Zürich) and Dr H. Lieth (Osnabrück) and all American colleagues from the Universities and Laboratories of the southeastern United States for their excellent guidance, hospitality and stimulating discussions. I also wish to thank Dr M. Łańcucka-Środoniowa and Dr A. Środoń as well as my collaborators for their help.

Last, but not least, I would like to extend my thanks to all my friends, who participated in that truly memorable field trip, for the creation of a pleasant and constructive atmosphere. The 16th IPE made me feel closer, not only to the exotic landscapes and flora of the SE United States, but also to the people of the US and of the different European countries and it enabled me to understand more fully the vegetation of my home country.

## 2. Materials and methods of comparison

### *2.1. The region of the United States visited by the 16th IPE (August 1978)*

The 16th International Phytogeographical Excursion enabled the participants to acquire a closer acquaintance with the landscapes and vegetation of North Carolina, South Carolina and some places in Tennessee and Georgia. This region



(approximately 32-37° N and 75-84° W) is situated between subtropical Florida and the temperate zone of the NE United States (LIETH 1979).

We crossed the Carolinas starting from sea level (the Atlantic Ocean) to the highest peaks of the Smoky Mts. and visited among others:

1. The Green Swamp on the Coastal Plain of North Carolina (ca 20 m a.s.l.) - Deciduous Bay Forest (Community Class: *Taxodium-Acer-Nyssa/Cyrilla-Lyonia-Ilex*; KOLOGISKI 1977, BRINSON 1978).
2. Piedmont vegetation in the Duke Forest near Durham, N.C., 130-160 m) (OOSTING 1942, KORNAS 1965, PEET and CHRISTENSEN 1980).
3. The *Abies fraseri* subalpine forest on the higher elevation mountains of the Southern Appalachians (1700-1940 m) (PITTILLO and SMATHERS 1979).

## 2.2. Climate, vascular flora and vegetation of the region

The part of the United States we have visited has a broad spectrum of climates (ROBINSON 1979) (cf. tables 1 and 2).

Table 1. Mean annual temperatures and sum-total of precipitation in the Carolinas (after LIETH 1979)

Station	Mean annual	
	temperatures (°C)	sum-total precipitation (mm)
Charleston, S.C. (3 m)	19.2	1168
Atlanta, Ga. (272 m)	16.8	1248
Raleigh, N.C. (132 m)	15.5	1145
Boone, N.C. (1016 m)	10.9	1384

Table 2. Average temperatures in North Carolina (°C) (after ROBINSON 1979)

Station	Winter			Summer		
	Minimum	Mean	Maximum	Minimum	Mean	Maximum
Coastal Plain	2	10	13	21	27	32
Piedmont	-1	7	10	18	24	32
Mountains	-4	4	10	15	21	29

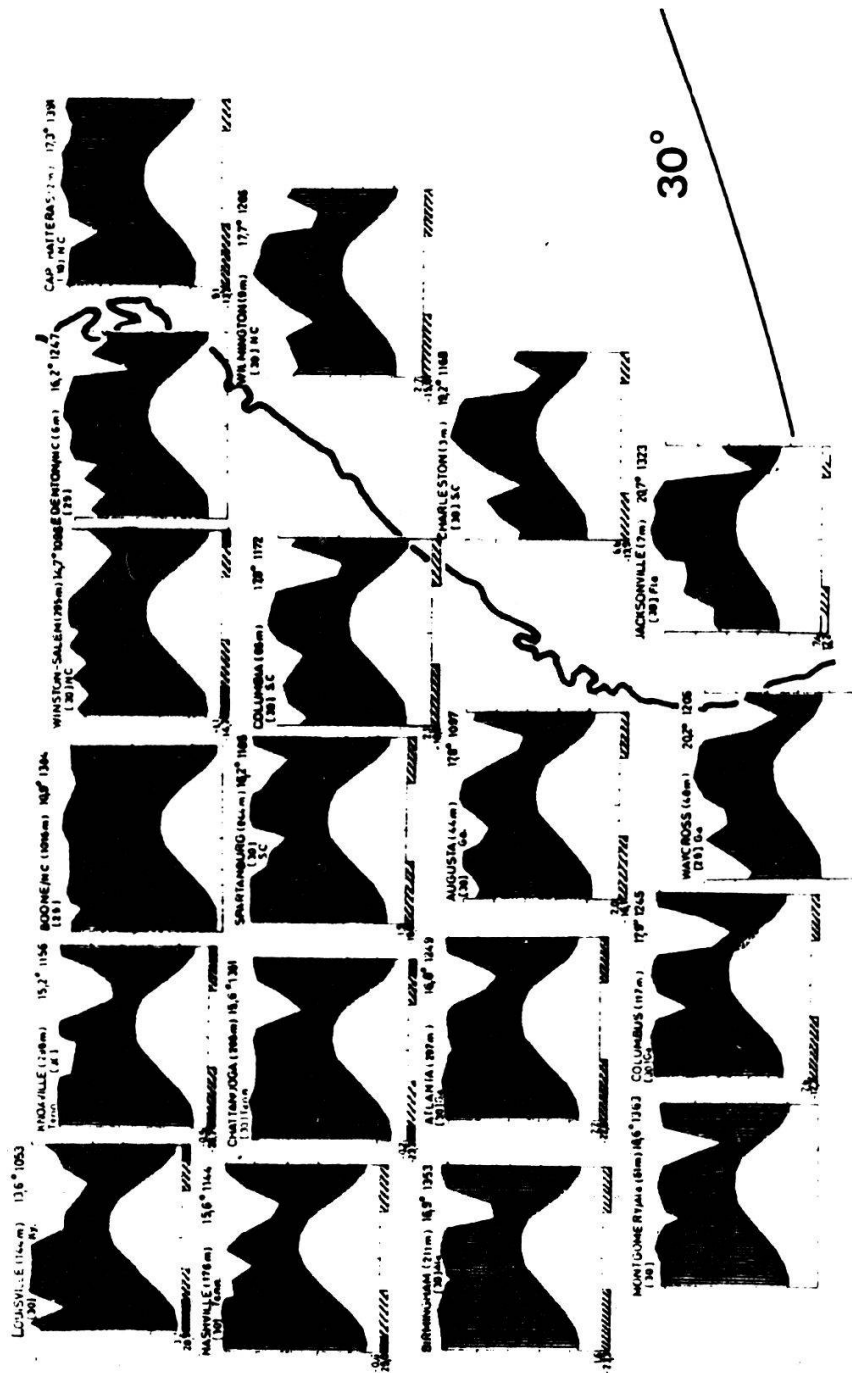


Fig. 1. The climate diagrams for the SE United States (after WALTER et al. 1975)

The climate of the Carolinas belongs to the moist, warm temperate type 5 in the definition of WALTER and LIETH (1961). This type is found (LIETH 1979) "in the northern hemisphere going eastward in isolated spots in Portugal, Spain, France, Italy, the Balkan peninsula, south of the Caucasus, on the south slopes of the Himalaya range, in the middle and northern China, Korea and southern Japan".

Various types of climates within the area of the southeastern United States can be seen in figure 1.

The distribution of the plant species and communities as well as the vegetation history of the region have already been studied (RADFORD et al. 1978, BRAUN 1950, WHITTAKER 1956, LITTLE 1971, KNAPP 1965, DELCOURT and DELCOURT 1979, LIETH and LANDOLT 1979 and references). A bibliography of the vegetation of the Carolinas has been published by PEET (1979).

The vascular flora of the Carolinas is relatively rich. The difference in elevation from the sea level at the coastal plain to more than 2000 m at the peaks of several mountains provides climatic analogues from subtropical climate to the boreal one. It is therefore logical, that several northern species find their southern limit in the Carolinas. Otherwise numerous species of the South reach their northern limits in the coastal plain of North Carolina. One of the most interesting species, seen during the 16th IPE, is *Sabal palmetto* which has its northernmost locality in the south-east corner of North Carolina (cf. fig. 3 in the paper of LIETH 1979, p. 38).

The knowledge of the recent flora and vegetation as well as the climatic features of the southeastern region of North America is based on my personal observations and data obtained during the field trips, and from non-published materials and published papers (see above).

The paper of WHITTAKER (1956, cf. fig. 2) and ecological studies of PITTILLO and SMATHERS (1979; table 3) and KOLOGISKI (1977; fig. 3) are very useful for the reconstruction of the Pliocene climate in Europe.

A number of species found in the forest communities of the Duke Forest near Durham, N.C. (KORNAŚ 1965) as well as the corresponding forest communities of the Cracow Jurassic Upland (MEDWECKA-KORNAŚ 1952; table 4a and 4b) was used to evaluate the number of the plant species of Krościenko in Pliocene.

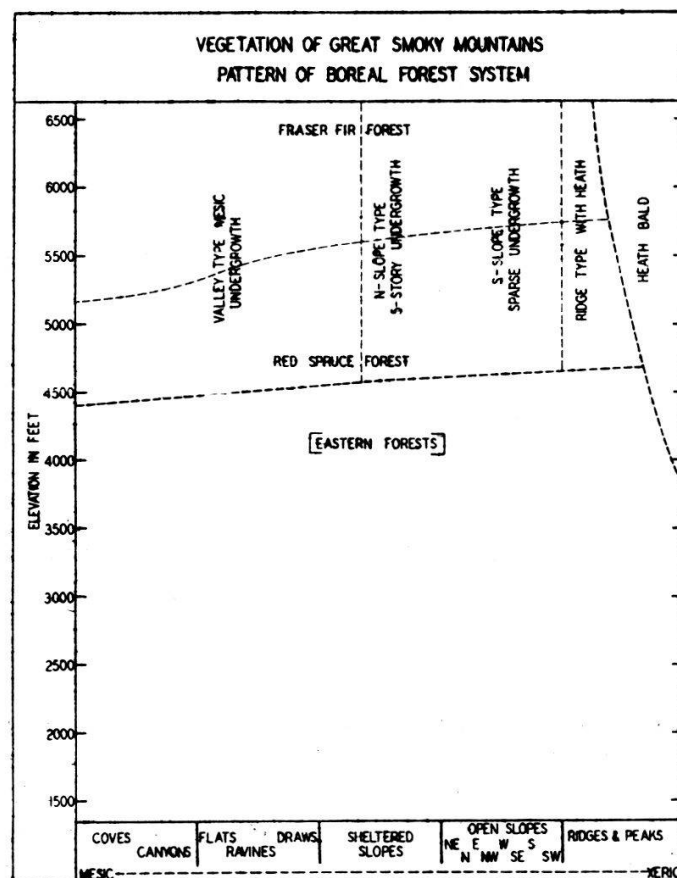
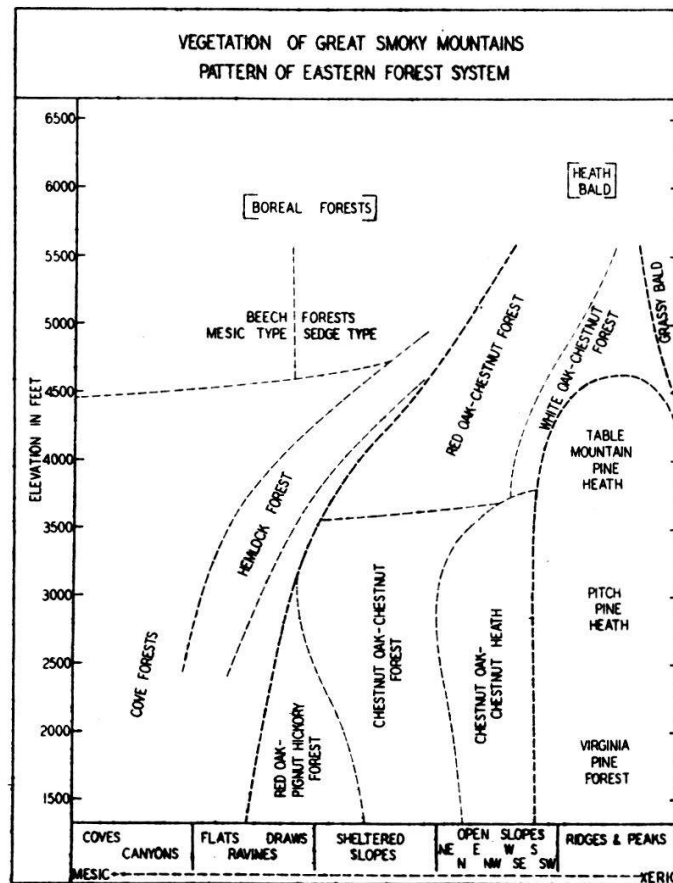


Fig. 2. Types of vegetation of the Smoky Mountains (after WHITTAKER 1956)



Photo 1. General view of the forest in the Great Smoky Mts.



Photo 2. An enormous specimen of *Liriodendron tulipifera* - "Wasylik Champion" (circumference 8.6 m) and the participants of the 16th IPE (1978). From left to right: C.D. Pigott (Lancaster, UK), B. Wagoner (Chapel Hill, N.C., USA), L. Ilijanić (Zagreb, Yugoslavia), Gisela Jahn (Göttingen, FRG), E. Landolt (Zürich, Switzerland), Lena Hämet-Ahti (Helsinki, Finland), H. Doing (Wageningen, Netherlands), K. Zarzycki (Kraków, Poland), H. Lieth (Osnabrück, FRG). The Natahala Mountains, Cherry cove area. Thursday. 10th August, 1978).

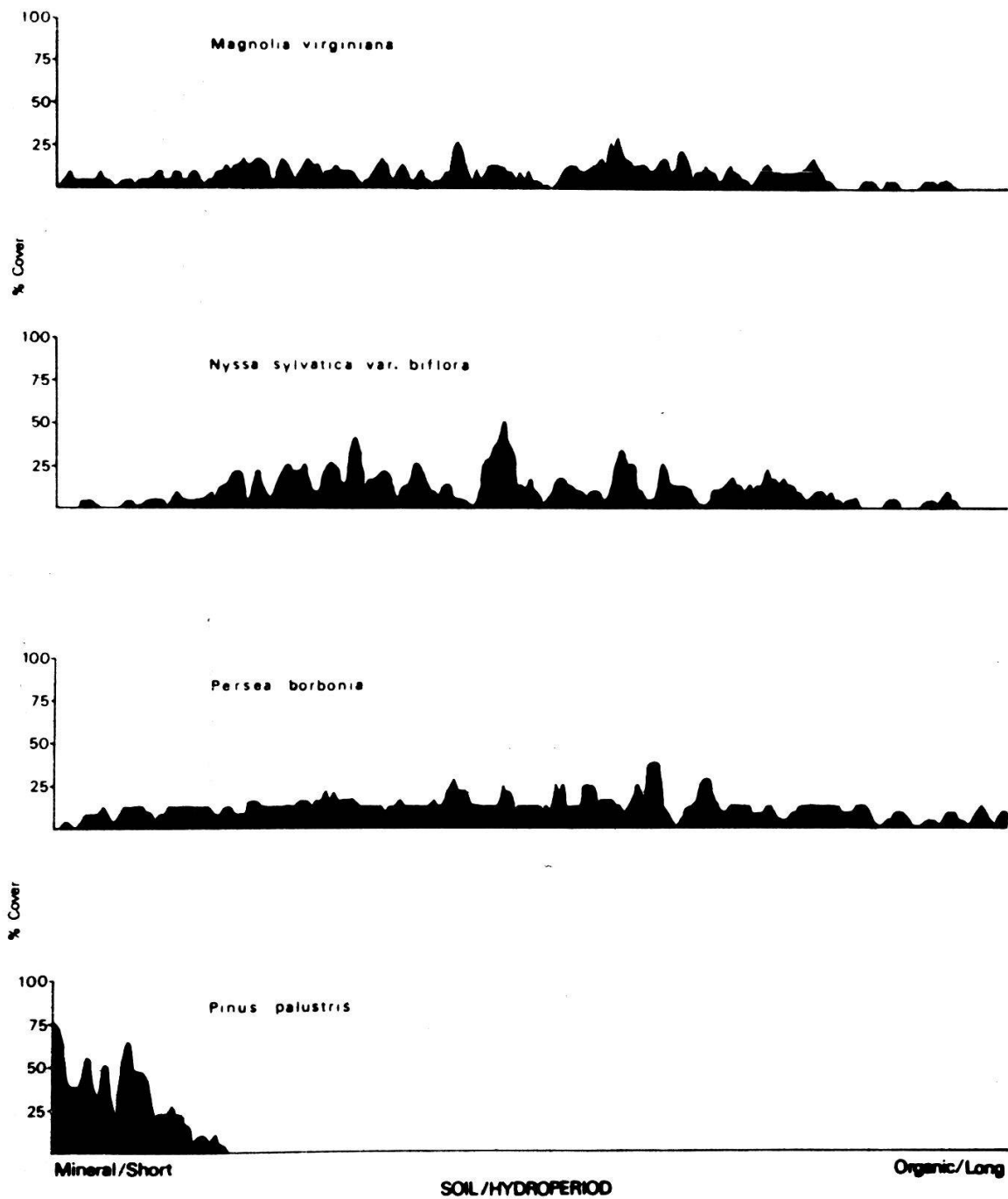


Fig. 3. Dominant species cover values in relation to the soil/moisture gradient (the Green Swamp, North Carolina). This gradient ranges from mineral soils with short hydroperiods to organic soils with long hydroperiods (after KOLOGISKY 1977).

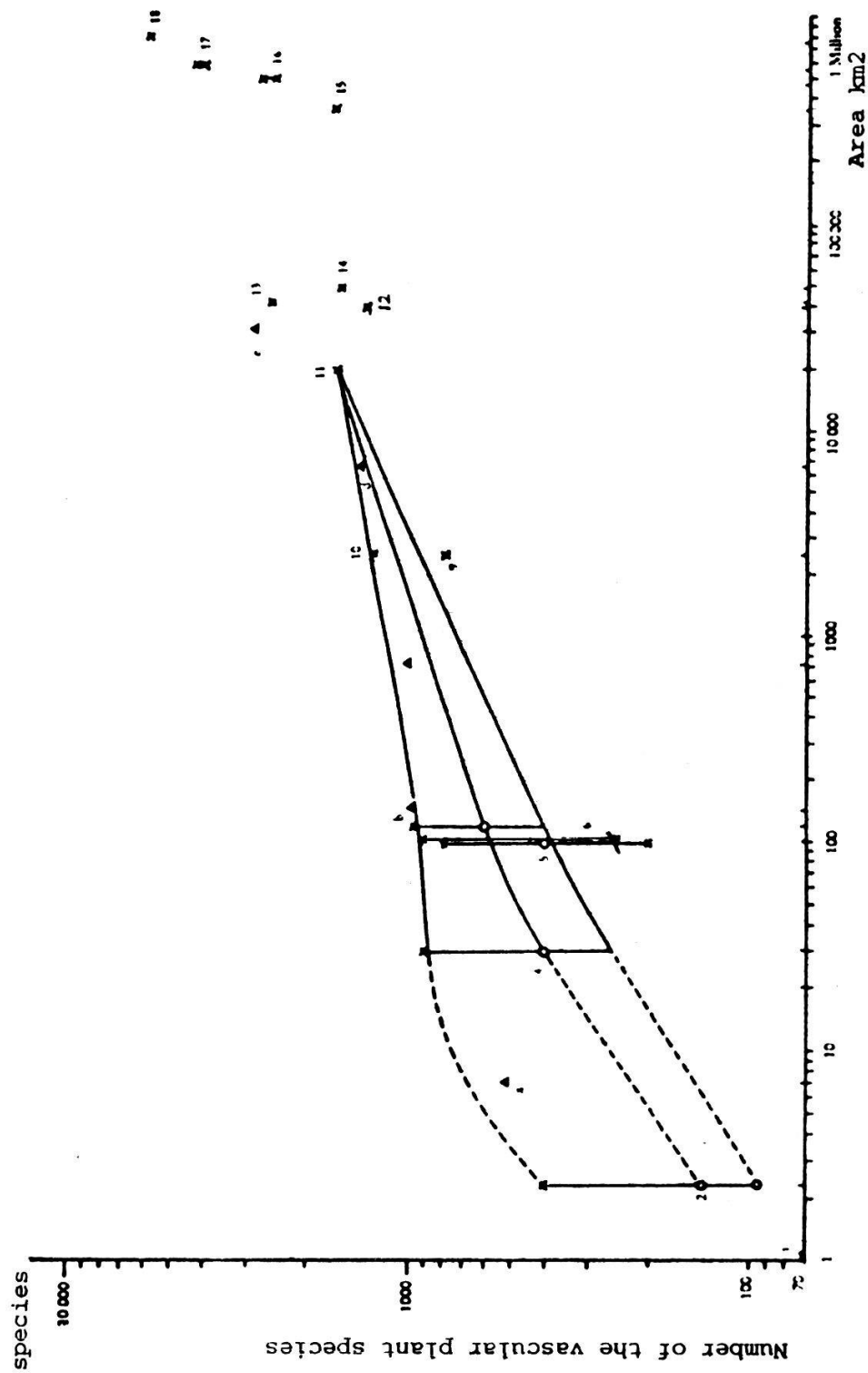


Fig. 4. The relationship of the number of the vascular plant species versus the size of the investigated area in Central Europe (after HAEUPLER 1974, slightly modified). The different numbers correspond to the investigated localities.

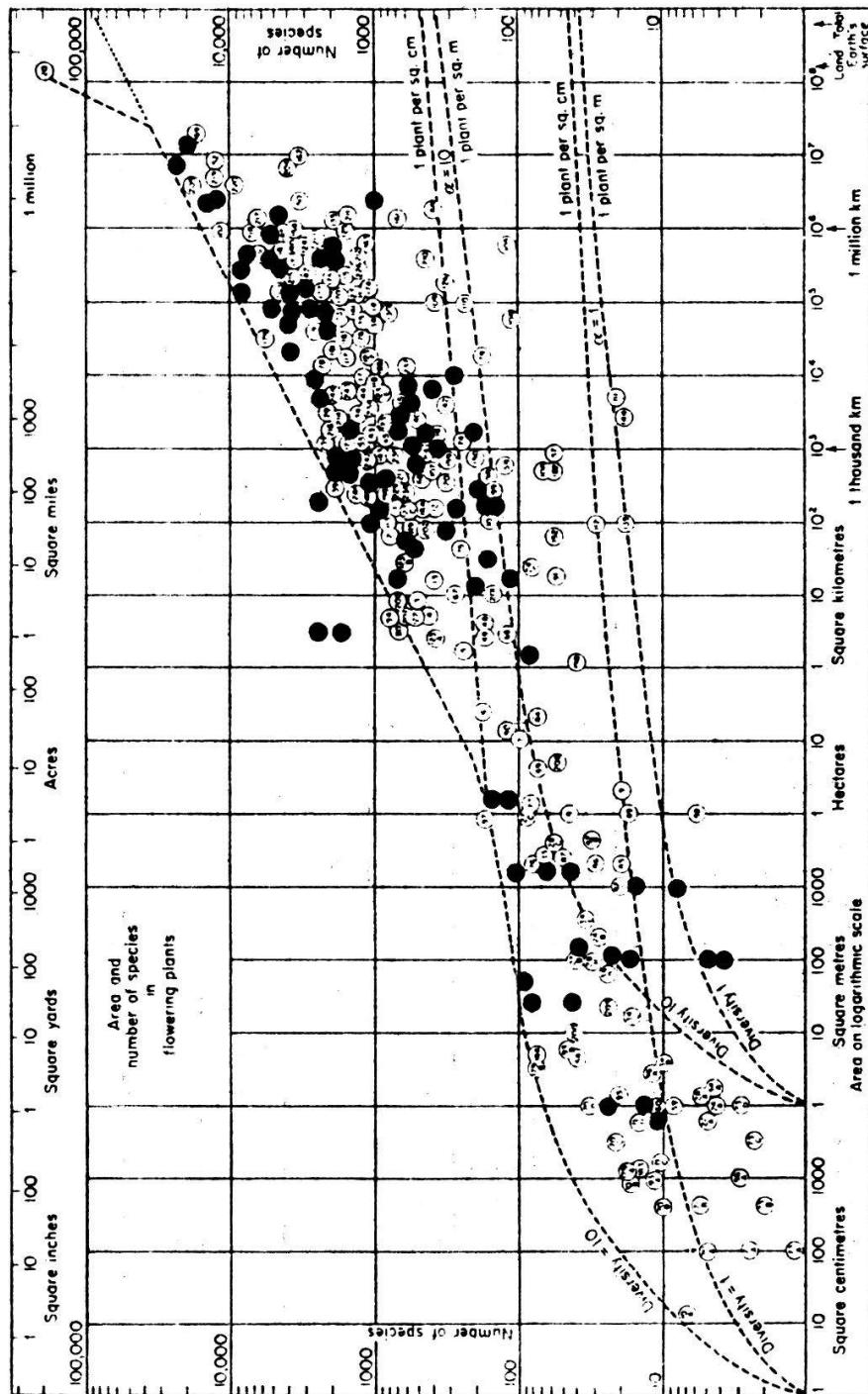


Fig. 5. Area and number of species in flowering plants from different parts of the world (after WILLIAMS 1964, slightly modified) black dots = tropical floras



Table 3. Relative coverage estimates for trees of the Balsam Mountains along the Blue Ridge Parkway (after PITILLO and SMATHERS 1979)

Species	Community*							
	FP	Oak		Cove		Bf	SF	Su
<i>Abies fraseri</i>							43.2	
<i>Acer pensylvanicum</i>			3.4	0.5		21.5	0.4	
<i>A. rubrum</i>		4.9	8.2	3.4	2.3	1.3	1.0	4.3
<i>A. saccharum</i>				19.4				
<i>A. spicatum</i>						16.6	4.7	
<i>Aesculus octandra</i>				16.2			1.9	
<i>Amelanchier arborea</i>		1.8	3.1			1.3	0.4	
<i>Betula alleghaniensis</i>			7.4		2.3	54.6	4.3	
<i>B. lenta</i>		0.4	0.4	0.5				
<i>B. nigra</i>	8.1							
<i>Carpinus caroliniana</i>	9.5			0.6				
<i>Carya cordiformis</i>				1.0				
<i>C. glabra</i>	8.1	2.9	0.4					1.3
<i>C. ovata</i>				2.9				
<i>C. tomentosa</i>		2.1						
<i>Castanea dentata</i>		1.8	4.7	0.9				
<i>Cornus florida</i>	1.8	3.5		21.1				49.5
<i>C. alternifolia</i>							2.6	
<i>Crataegus flabellata</i>						0.9		
<i>Diospyros virginiana</i>		0.7						
<i>Fagus grandifolia</i>			1.7				2.4	2.5
<i>Fraxinus americana</i>			0.3	0.5		1.3		
<i>Halesia carolina</i>	13.1		1.2					
<i>Hamamelis virginiana</i>			1.0					
<i>Ilex ambigua</i> v. <i>montana</i>	1.8		1.7	2.4			0.6	
<i>I. opaca</i>								2.6
<i>Juglans nigra</i>		2.9						
<i>Liriodendron tulipifera</i>	15.4	0.7		18.7				29.4
<i>Magnolia acuminata</i>	1.8		0.2					
<i>Malus coronaria</i>	1.8							
<i>Morus rubra</i>	1.8							
<i>Nyssa sylvatica</i>		10.4		0.5				1.3
<i>Oxydendrum arboreum</i>		0.4	1.7					
<i>Picea rubens</i>					14.0		35.5	
<i>Pinus rigida</i>		3.3						
<i>P. virginiana</i>		0.4						6.9
<i>Platanus occidentalis</i>	24.4							
<i>Prunus pensylvanica</i>		0.2					1.2	
<i>P. serotina</i>	5.9	0.3	0.7	0.5				1.3
<i>Quercus alba</i>		24.6	2.3	2.4				
<i>Q. alba</i> x <i>prinus</i>			0.3					
<i>Q. coccinea</i>		0.7						
<i>Q. muehlenbergii</i>	1.8							
<i>Q. prinus</i>		12.2	5.1	7.3				
<i>Q. rubra</i>		4.6	48.3	0.5		1.3		
<i>Q. velutina</i>	2.7	7.1						2.0
<i>Robinia pseudo-acacia</i>		1.4	0.8	0.5				
<i>Sassafras albidum</i>	1.8	2.0	1.3	0.5				1.3
<i>Sorbus americana</i>							4.5	
<i>Tilia heterophylla</i>						1.3		
<i>Tsuga canadensis</i>					81.4			

\* Bf = boulder field Ha = cove hardwood Mes = mesic oak SF = spruce fir  
 FP = floodplain He = cove hemlock Xer = xeric oak Su = successional

Statistics of the vascular flora of the Carolinas and Poland are given in table 5. Figure 4 presents the relationship of the number of vascular species to the area of Central Europe (cf. HAEUPLER 1974, p. 66-67). The number of species of flowering plants, recorded in floras from all parts of the world, see fig. 5.

Numerous contacts and discussions with the guides and participants of the 16th IPE turned out to be helpful to clear many doubts and questions.

Table 4a. The number of the vascular plant species in the corresponding forest communities of Duke Forest near Durham, N.C. (36°N, 79°W, max. 195 m a.s.l.) (according to the phytosociological tables, 18 relevés of KORNÁŠ 1965).

	Number (and per cent) of species			Total (100%)
	Deciduous	Intermediate	Evergreen	
Trees	35 (15.1)	0	3 (1.3)	38 (16.4)
Shrubs	24 (10.3)	1 (0.4)	1 (0.4)	26 (11.2)
Vines	8 ( 3.4)	3 (1.3)	1 (0.4)	12 ( 5.2)
Herbs and shrubless	-	-	-	156 (67.7)
Total	67 (28.9)	4 (1.7)	5 (2.2)	232 (100 )

Table 4b. The number of the vascular plant species in the corresponding forest communities of Cracow Jurassic Upland (50°07'N, 19°47'W, max. 504 m a.s.l.) (according to the phytosociological tables, 18 relevés of MEDWECKA-KORNÁŠ 1952).

	Number (and per cent) of species			Total (100%)
	Deciduous	Intermediate	Evergreen	
Trees	16 (10.2)	0	5 (3.2)	21 (13.4)
Shrubs	24 (15.3)	0	1 (0.6)	25 (15.9)
Vines	0	0	0	0
Herbs and shrubless	-	-	-	111 (70.7)
Total	50 (31.8)	0	6 (3.8)	157 (100 )

Table 5. Statistics of the contemporary vascular floras of the Carolinas\* and Poland\*\*

Countries latitude area	Number (and per cent) of species				Total (100%)
	Trees	Shrubs	Pterido- phytes	Other herbs	
The Carolinas 32°-37°N, 75°-84°W 217.000	160(5)	329(10)	89(3)	2683(82)	3.360
Poland 49°-54°50'N, 14°07'- 24°08'E 312.700	66(2.5)	219( 8)	65(2.5)	2321(87)	2.670

\* According to RADFORD et al. (1978)

\*\* according to SZAFER et al. (1967) (in both cases native and synanthropic, incl. cultivated, species are considered).

### 2.3. The Pliocene floras of the Polish West Carpathians - general remarks

For a number of years the Neogene deposits of the Nowy Targ - Orawa Basin (fig. 6) have been the object of palaeobotanical and geological research (OSZAST and STUCHLIK 1977). The fruit and seed flora from the Pliocene deposits of Krościenko were first described by SZAFER (1938, 1946, 1947), who then studied the flora of Huba and Mizerna (SZAFER 1954<sup>x</sup>).

The results of the research on the Pliocene deposits from Domański Wierch have also been published: the results of the palynological investigations (OSZAST 1973), as well as the results of the study of the foliaceous flora (ZASTAWNIAK 1972) and partly the results of the determinations of the fruits and seeds (ŁAŃCUCKA-ŚRODONIOWA 1965).

### 2.4. The North American element in the Pliocene floras of the West Polish Carpathians

The North American plant species (or taxa closely related) found in the

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x) The flora from Huba was considered to be the Upper Miocene age (OSZAST 1973).

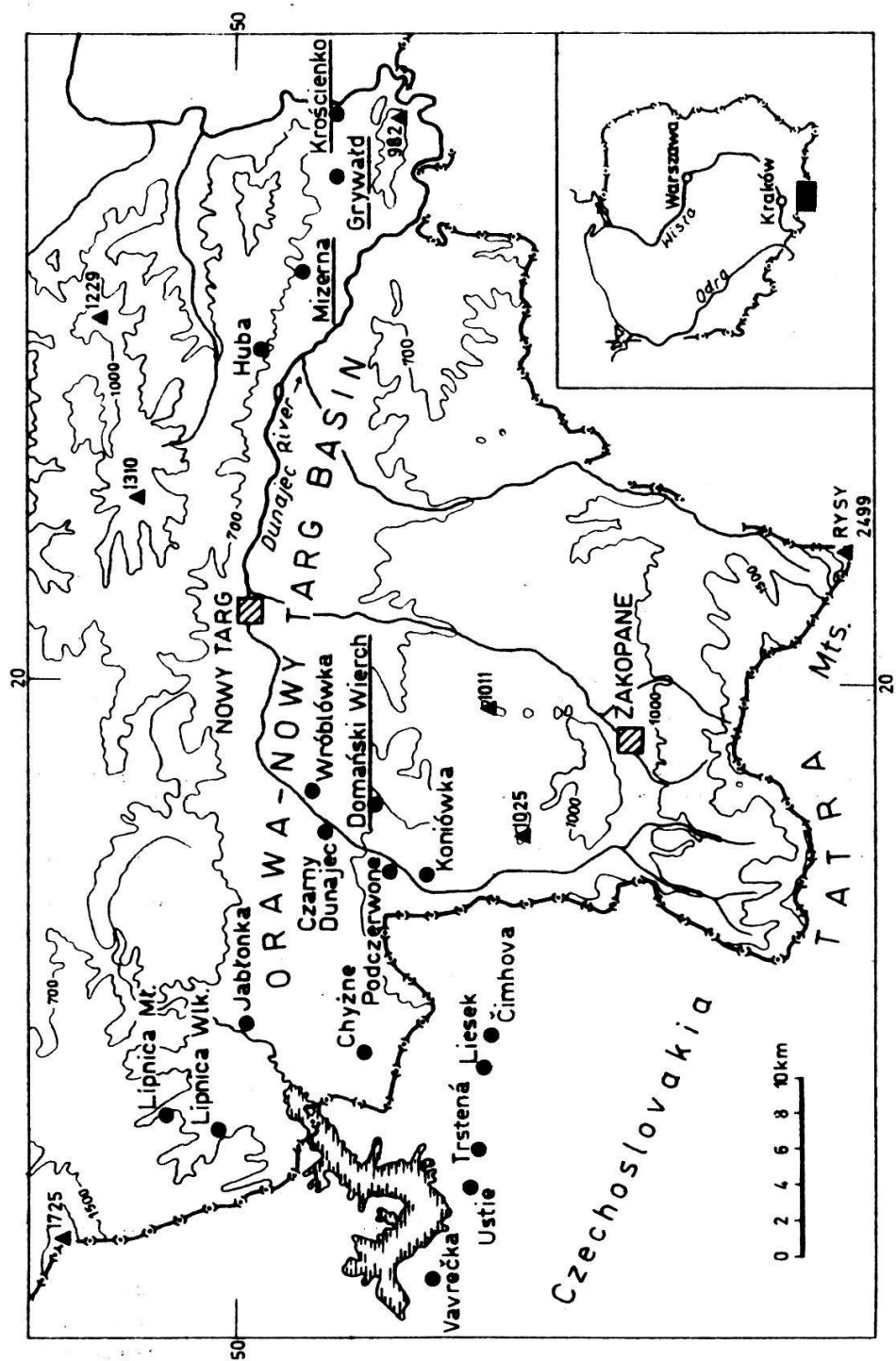


Fig. 6. The localities of Neogene floras in the Nowy Targ-Orawa Basin in the West Carpathian Mts. (after OSZAST and STUCHLIK 1977). The names of the localities of the Pliocene floras are underlined.

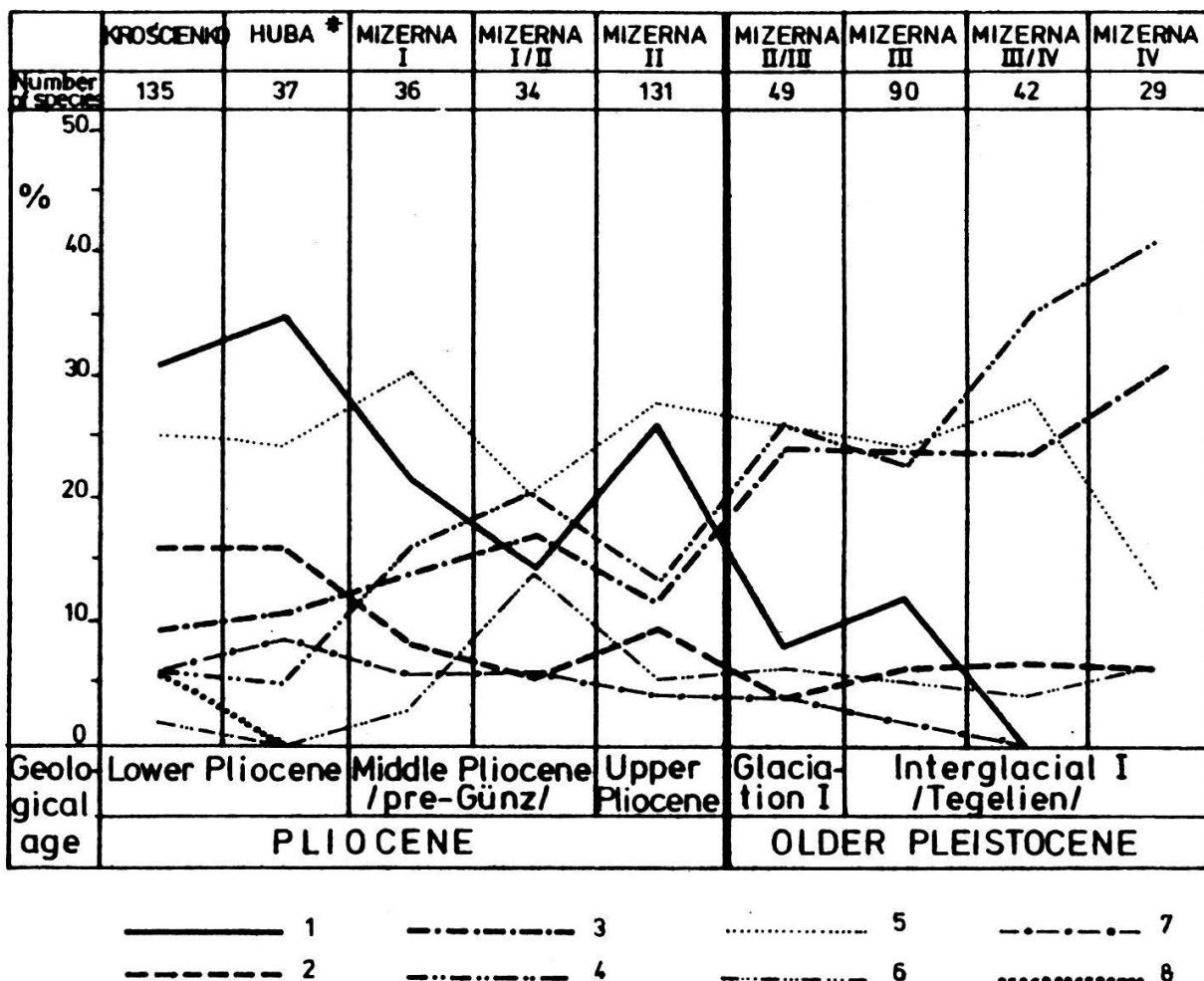


Fig. 7. Geographical-floristic elements in the floras of different ages (after SZAFER 1954).

1 = the East Asiatic element, 2 = the North American element, 3 = the Holarctic element, 4 = the Euroasiatic element, 5 = the European element, 6 = the dispersed Cosmopolitan element, 7 = the Balkan-Colchidian element, 8 = the tropical and subtropical element.

\* The flora from Huba was considered to be of the Upper Miocene age (OSZAST 1973)

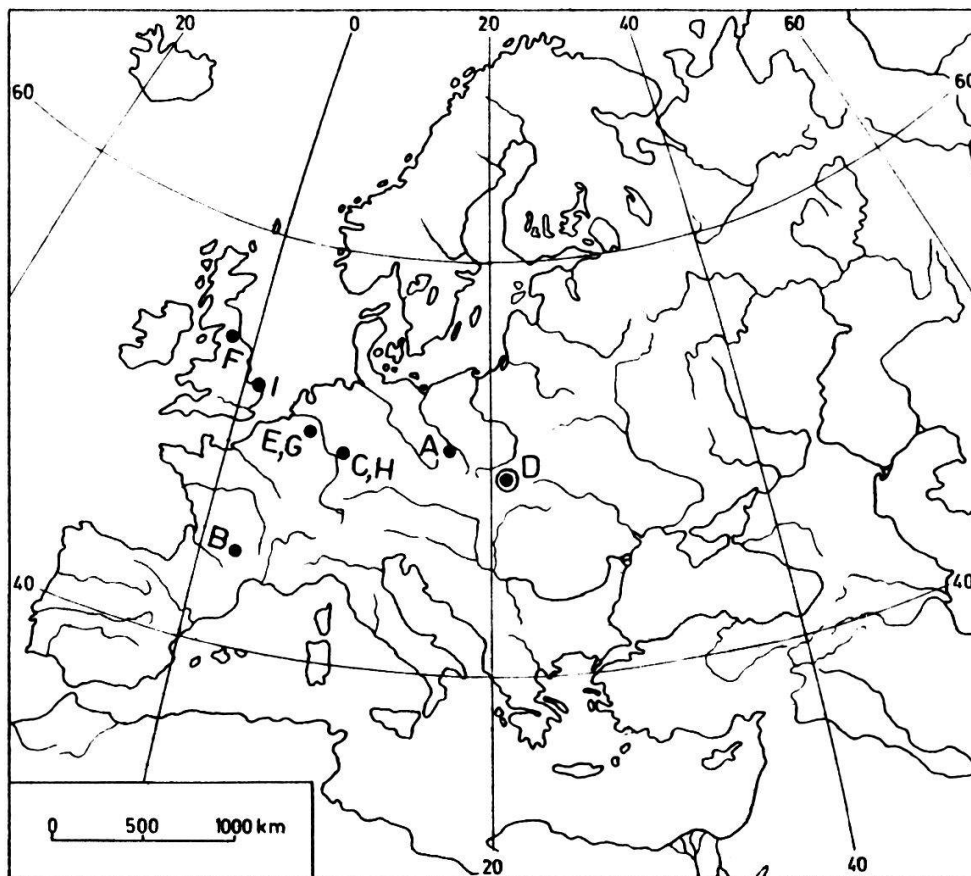


Fig. 8. Localities of the floras of different ages compared by SZAFER (1946, 1947).

A = Sośnica (actually considered as the Lower Pliocene; ŁAŃCUCKA-ŚRODONIOWA, personal comm.). B = Pont-de-Gail. C = Frankfurt a.M. D = Krościenko. E = Reuver. F = Castle Eden. G = Tegelen. H = Schwaheim. I = Cromer.

Pliocene flora of Krościenko, Grywald and Mizerna (SZAFER 1938, 1946, 1947) are listed in tables 6 and 7.

The flora from Krościenko approaches in various degrees other European Pliocene floras because of its floristic composition (fig. 7 and 8, SZAFER 1946: 120 - table III and the references). A comparison of the Pliocene and the early Pleistocene flora in the neighbourhood of the Pieniny Mts. with other similar floras in Europe was made by SZAFER (1954).

The North American species grew in Krościenko in the Lower Pliocene, together with many others, representing different geographical elements. I quote only some examples: *Keteleeria* (x), *Picea* (xxx), *Pseudolarix amabilis* (xx), *Alnus glutinosa* foss., *A. incana* foss., *Salix* and *Populus* (xxx), *Carpinus betulus* (xxx), *Pterocarya fraxinifolia* (xxx), *Corylopsis urselensis* (xxx), *Magnolia* (xxx), *Sinomenium* (xx), *Phellodendron* (xx), *Vitis* (*Ampelopsis*) *ludwigii*, *Sambucus* (xxx), *Carex* (xxx). Of particular interest is the occurrence of *Podestemonites corollatus* (SZAFER 1952), as well as *Hemiptelea* and *Weigela* (ŁAŃCUCKA-ŚRODONIOWA 1967).

The samples taken from a deep bore-hole, situated at the summit of Domański Wierch, contained about 80 plant forms. They were arranged into the following groups (ŁAŃCUCKA-ŚRODONIOWA 1965):

Trees: *Abies*, *Acer campestre*, *A. palmatum*, *A. sp.*, *Betula*, *Carpinus betulus*, *Cephalotaxus*, *Fagus*, *Liquidambar europaea*, *Liriodendron*, *Magnolia Kobus*, *M. sinuata*, *Meliosma europaea*, *Morus*, *Ostrya*, *Parrotia fagifolia*, *Phellodendron*, *Picea*, *Pinus*, *Populus*, *Prunus*, *Pterocarya*, *Quercus*, *Styrax*, *Taxus*, *Tsuga*, *Zelkova Ungerii*.

Shrubs: *Aralia*, *Berberis* (?), *Cornus*, *Corylus*, *Crataegus* (?), *Hamamelis*, *Ilex* (?), *Juniperus* (?), *Sambucus*, *Staphylea*, *Rosa*, *Rubus*, *Viburnum*.

Lianas: *Actinidia faveolata*, *Clematis* (?), *Vitis teutonica*, *V. sp.* *Terastigma*.

Field and ground layer: *Ajuga*, *Alchemilla*, *Caryophyllaceae*, *Euphorbia*, *Hypericum*, *Labiatae*, *Lycopus*, *Potentilla*, *Ranunculus*, *Selaginella pliocaenica*, *Solanaceae*, *Thalictrum*, *Urtica*, moreover *Musci* (*Trachycytis Szaferi*) and *Fungi* (*Polyporites*, *Rosellinites*, *Trematosphaerites*).

March vegetation: *Carex*, *Cyperaceae*, *Decodon globosus*, *Diclidocarya Menzelii*,

Table 6. A list of the North American vascular plant species of the Pliocene flora of Krościenko and the notes on the distribution of those species (or closely related taxa) in the southeastern United States (chiefly in the Carolinas)

Fossil species (taxa)	Relative abundance in fossil remains	Remarks: contemporary distribution within the SE United States
* <i>Tsuga europaea</i> (Menzel) Szafer	xxx	<i>T. canadensis</i> and <i>T. caroliniana</i> : mts., cool and moist conditions
<i>T. caroliniana</i> Engelm. foss.		
<i>Picea rubra</i> Link	xxx	intermediate between <i>P. rubens</i> and <i>P. omorica</i> (STUCHLIK, pers. comm.)
<i>Corylus</i> cf. <i>rostrata</i> Ait. ( <i>C. cornuta</i> )	x	mts. and pied., dry rocky woods
<i>Fagus ferruginea</i> Ait. foss. ( <i>F. grandifolia</i> )	xx	chiefly pied. and mts., rich damp woods
<i>Juglans cinerea</i>	x	chiefly mts.
<i>Carya</i> sp.	x	pollen grain only
<i>Liriodendron tulipifera</i> L. foss.	xxx	mts. and pied., rich or low woods
* <i>Proserpinaca reticulata</i> Reid	xx	genus <i>Proserpinaca</i> chiefly cp., marshes, bogs, pools, ditches
<i>Staphylea</i> cf. <i>trifolia</i> L.	x	chiefly pied.
<i>Nyssa silvatica</i> Marsh. foss.	x	var. <i>sylvatica</i> - throughout upland and low woods, var. <i>biflora</i> - chiefly cp., bogs, bay forests and pocosins
* <i>Dulichium vespiforme</i> Reid.	x	<i>D. arundinaceum</i> - bogs, scattered, throughout SE
* <i>Scirpus pliocenicus</i> Szafer	xxx	

- NOTES: 1. The extinct species are marked with an asterisk (\*)
2. In case of those fossil species which show a great similarity to the ones existing now, but which cannot be regarded as identical with them, the word "confer" (cf.) was added before a specific name.
3. The word "fossilis" (foss.) was added to the name of fossil species if there was no difference between the fruits and/or seeds of the compared species. It is most probable that the majority of them are identical with those now existing (cf. SZAHER 1946, p.99).



4. Relative abundance of the Pliocene forms in the fossil remnants is calculated from Szafer's data (SZAFER 1947):

x : one to few fruits, seeds or their fragments  
 xx : not numerous " " " "  
 xxx : numerous " " " "

5. Remarks on the present distribution of the species chiefly according to RADFORD et al. (1978).

Abbreviations: mts. = mountains, cp. = coastal plain, pied. = piedmont

6. Scientific names of the plants in the tables 6 and 7 as well as in the quotations (in extenso) from the original papers; the names of the plants in text without abbreviations of the author's names (in tables in brackets) follow RADFORD et al. (1978).
7. The following species quoted by SZAFER (1946, 1947) as representing the North American element were omitted because their determination was not correct (cf. LAŃCUCKA-ŚRODONIOWA 1966, 1979 and unpublished data): *Betula* cf. *populifolia* Ait., *Liquidambar europaea* A.Br., *Rubus* cf. *occidentalis* L., *Acer floridanum*, *Ceanothus americanus* L.s.l. foss., *Vitis cordifolia* Michx. foss., *Viburnum* cf. *prunifolium* L.

Table 7. A list of the North American species present in the Pliocene flora of Mizerna (for explanations and abbreviations see table 6)

Fossil species (taxa)	Relative abundance in fossil remains	Remarks: contemporary distribution within the SE United States
<i>Quercus</i> cf. <i>borealis</i> Michx. ( <i>Q. rubra</i> var. <i>borealis</i> ) (SZAFER 1954, p.83)	x	var. <i>rubra</i> - abundant in mts., less in pied., rare in cp. var. <i>borealis</i> - high mts. of N.C.
<i>Carya</i> cf. <i>tomentosa</i> Nuttall foss. (SZAFER l.c., p. 25, 83)	x	throughout SE, dry woods
<i>Prunus</i> cf. <i>lusitanica</i> L. (SZAFER l.c.: 83)	x	?

*Juncus*, *Menyanthes*, *Potamogeton*, *Polygonum*, *Scirpus*, *Sparganium ramosum*, *S.* sp., *Typha* (?).

A characteristic feature of the above flora is the scarcity of conifers. In the whole column of sediments there have been found only single (1-4) needles of *Abies*, *Tsuga*, *Pinus*, *Picea* and *Juniperus* (?), and one indeterminable cone. In the superficial outcrops at Domański Wierch only two not determined needles have been found, one seed of *Taxus*, and one seed of *Cephalotaxus*, and one damaged cone of *Picea* or *Keteleeria*.

The Pliocene leaf flora from Domański Wierch was studied by Ms. E. ZASTAWNIAK (1972). On the basis of the morphological features, 389 specimen were determined as belonging to 14 families (*Equisetaceae*, *Betulaceae*, *Fagaceae*, *Juglandaceae*, *Salicaceae*, *Ulmaceae*, *Hamamelidaceae*, *Platanaceae*, *Aceraceae*, *Vitaceae*, *Cornaceae*, *Cyperaceae*, *Gramineae*, and *Typhaceae*), 22 genera, and 28 species - only two of them - *Liquidambar europaea* A.Br. and *Platanus plataniifolia* (Ettl.) Knobl. - represent the North American element (contemporary related species are *Liquidambar styraciflua*\* and *Platanus occidentalis* respectively).

## 2.5. Opinions on the Pliocene vegetation and climate of the West Carpathians

### 2.5.1. The North American element in the European Pliocene floras

SZAFER (1946, 1954) distinguished eight geographical elements in the European Pliocene floras (cf. fig. 7 and 8). I quote, in extenso, his opinion on the subject (SZAFER 1947, p. 102): "Judging from the floristic relationship and from the climate resemblance, the Pliocene flora of Krościenko comes near the area of the southeastern part of the United States of North America. In a still higher degree it approximates certain ranges of East Asia, but the statistics of their contemporary flora are not known well enough".

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\* "However, it should be noted that leaves of the Asia Minor species *L. orientalis* Mill. are characterized by considerable variability (...). Sometimes leaves closely resembling in shape leaves of *L. styraciflua* (MAKAROVA 1957), also occur in this species" (ZASTAWNIAK 1972, p. 42).

Table 8.. The number of the seed plant species growing in the neighbourhood of Krościenko in Pliocene (calculated by SZAFER 1946, p. 102-103)

Number of seed plant species			
Trees and shrubs		Herbaceous	Total
Dicotyledonous	Gymnosperm		
100	20	380	500

In his later paper SZAFER (1954, p. 184) quoted from Mizerna the following numbers: Gymnospermae: 13 species, Dicotyledones: 140 species, Monocotyledones: 34 species. (Total: seed plants + Fungi + Musci + Filicinae + Equisetinae + Lycopodine + Selaginellales = ca. 240 ).

#### 2.5.2. The Pliocene plant communities in the West Carpathians (the vicinity of Krościenko)\*

"The forest in the vicinity of Krościenko in Pliocene may be characterized as one with a predominance of deciduous trees and evergreen conifers. In higher locations up the mountains this forest passed into one with prevalence of conifers. It consisted of many layers. The rich soil with humus with microflora peculiar to it (the abundance of sclerotia of fungi is striking!) was covered with a layer of mosses, ferns, and other herbs which, however, have left comparatively few remnants preserved in fossil state, much like the layer of higher herbs and suffrutescent plants. The third layer of shrubs, and the uppermost fourth one, composed of trees, have left numerous fossil remnants. The presence of low trees and tall shrubs points to the fact that there was a double layer of trees. The forest lianas formed a separate ecological group very richly developed. Among them were represented: *Vitis* (and) *Ampelopsis*, ... *Actinidia*, ... *Trichosanthes*, ... and *Solanum dulcamara*; ...

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\* I quote, in extenso, from the English summary, some of Szafer's opinions which are still scientifically valid. The considerations, published in palaeobotanical papers, are also interesting from the ecological and phytosociological point of view. Some species in the quotations are omitted.

the genus *Rubus*. There must have been numerous epiphytic mosses on the trunks and branches of the trees, as is proved by abundant remains of the genus *Neckera*.

"A striking feature of the Pliocene forest in Krościenko was the scarcity of evergreen foliage trees and shrubs. They are represented for certain only by sporadic fragments of the genera *Ilex*, *Hedera* and *Olea Zablockii*. ... some species of the genus *Rubus* should be reckoned among them, as well as certain herbaceous plants of the first and second layer, which kept their ground leaves in winter (such as for instance *Ajuga*), much as we see it today in the present carpet of deciduous or mixed forest in the temperate climate. The same scarcity of evergreen Angiosperms characterizes also the Pliocene flora of Frankfort on Main (about 5%), while the Reuverian (Lower Rhine) counts more of them (about 20%). This should be explained by the mildening influence of the submarine climate. Much more abundant are the remnants of the evergreen Angiosperms in the zones II and III\*. There are 24 species of them in the Pliocene in the vicinity of Sofia, that means about 38%, 16 species or 34% in Borsec, and 30 species of about 50% on the lower Rhone. This fact is in accordance with the climatic differences of these localities, caused by their geographical position and by the effect of waters covering vast areas in the zones II and III mildening the winter-climate. The above percentages are of course only approximately.

"Since we assume that the fossil flora of Krościenko, lying now at the altitude of 450 m a.s.l., was occurring more or less at the same altitude in Pliocene, we must admit that above this flora as well as underneath there were developed at least two more altitudinal stages of vegetation. ...

"From the foregoing remarks it results that we may form ideas about the vertical stages of the Pliocene flora in the western Carpathians only by analogy to the present conditions, and on ground of the general character of the forest vegetation. Starting from this point we may speak of the existence of

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\* Zone I: Outer zone with the Pliocene floras: Pont-de-Gail, Frankfurt a.M., Krościenko, Reuver, Castle Eden (cf. fig. 8).

Zone II: Inner zone with the following Pliocene floras: Borsec (Rumania), Podgumer and Kurilo (Bulgaria).

Zone III. Southern zone: Delta of the Rhone (SZAFER 1946, p. 33 and 120)

two distinct stages in Krościenko: the lower one with the prevalence of deciduous trees, and the upper one with conifers predominating.

"In the first or lower stage there prevailed: hornbeams (*Carpinus Betulus*, *C. cf. Tschonoskii*, *C. laxiflora*, *Pterocarya fraxinifolia*, *Alnus glutinosa*, *Liriodendron tulipifera*, *Vitis silvestris* and *Styrax obovatum*. Rather rarely appeared here: *Fagus decurrens*, *F. ferruginea*, *Ostrya carpinifolia*, *Phellodendron amurense*, *P. japonicum*, *Acer palmatum*, *A. japonicum*, *A. cf. pictum*, *A. campestre*, *Zelkova serrata*, *Corylus avellana*, *C. maxima*, *C. rostrata*, *Juglans cinerea*, *Fothergilla europaea*, *Sinomenium Dielsi*, *Actinidia faveolata*, *Stewartia europaea*, *Pirus communis*, *P. malus*, *Prunus spinosa*, *P. aff. echinata*, *P. domestica*, *Ilex sp.*, *Staphylea colchica*, *S. pliocaenica*, *S. cf. trifolia*, *Cornus controversa*, *Nyssa silvatica*, *Aralia sp.*, *Acanthopanax sp.*, *Pieris sp.*, *Olea Zablockii*, *Solanum dulcamara*, *Physalis pliocaenica*, *P. Alkekengi* and *Trichosanthes fragilis*. As for the conifer trees and shrubs there thrived only sporadically: *Chapaecyparis*, *Juniperus sp.*, very rare were also here: *Picea excelsa*, *P. omoricoides*, *P. rubra*, *Tsuga europaea*, *T. caroliniana*, *Pinus Peuce* and *Larix ligulata*. Here, too, almost all water and palustrine plants have their centre.

"In the upper stage the following conifers were predominant: *Picea rubra*, *P. Glehni*, *P. excelsa*, *Tsuga europaea*, *T. caroliniana*, *Abies sp.*, *Pinus montana*. Among the deciduous trees there appeared more often: *Fagus cf. silvatica*, *Alnus incana*. The lack of water- and palustrine-plants is characteristic here.

"The species which grew abundantly in both stages were: *Corylopsis urselensis*, *Sambucus pulchella*, *S. cf. ebulus*, *S. cf. racemosa* and *Vitis (Ampelopsis) Ludwigii*, the last one being especially characteristic for the whole complex of the Pliocene deposits in Krościenko.

"... Speaking about the ecological peculiarities of the Pliocene flora, the plant communities must not be passed over in silence. Up till now diametrically different opinions were expressed in this matter. On one side the scientists supposed the existence of an "indifferentiated deciduous forest climate" (BRAUN 1935) in the Tertiary; on the other side one went as far as to designate the pliocenic communities by conceptions taken from the contemporary

sociology plants. So did STRAUS (1935), who in Willershausen accepted the existence of an association of beech forests, peculiar for the Harz Mountains of today, which he calls *Fagetum subhercynicum pliocaenicum*. Sociological investigations, as far as they concern fossil flora, are, according to my opinion, better left to the future. This is the more advisable, since we are still far from being able to work on contemporary plant communities by one uniform method, and up till now we know almost nothing about the forest associations in the refugial regions situated either in the Atlantic part of North America or in Transcaucasia or East Asia. If, I still venture to speak here about "plant communities" of the Pliocene flora in the vicinity of Krościenko, I do it because I want to prove that in the Pliocene, as much as in the Holocene, there existed a rich differentiation of the flora into strictly distinguishable plant associations (as BRAUN-BLANQUET understands them).

"It is beyond doubt that: 1) in the basin of the foot of the northern Pieniny, where waters spread and partially stagnated, there developed various communities of water vegetation of some *Potamion*-union (this is proved by the remnants of the genera *Nuphar*, *Euryale*, *Potamogeton* and *Trapa*); 2) the shores of these waters were covered by communities belonging to the combinations of the order *Phragmitetalia* (the presence of the *Magnocaricion*-union is confirmed by *Carex pseudocyperus*, *Cicuta virosa*, *Oenanthe aquatica*, and of the *Phragmition* by the presence of *Sparganium ramosum* and *Sagittaria sagittifolia*); 3) the shrubs and forests, which covered almost the whole neighbourhood of Krościenko with a dense coat, reaching up to the top of the mountains around it (they still attain the height of over 1200 m!), were differentiated into numerous forest associations.

"Very little can be said here about Pliocene forest communities, even when we satisfy ourselves merely with stating their higher systematical units, that is of classes, orders and unions. BRAUN-BLANQUET et al. (1939), in a new work on the conifer forests of the class *Vaccinio-Piceeta* in the Eurosyberian North American region, do not mention any such forest communities in this class in which the conifers of our upper stage (see above) would play a part, namely *Picea rubra*, *Tsuga canadensis* or *T. caroliniana*, which today form vast forests especially in the Appalachian Mountains. According to BRAUN-

BLANQUET's opinion, "the forests of the southern Appalachian Mountains are different from the orders *Vaccinio-Piceetalia*".

"As for the deciduous (and mixed) forests from the lower stage (see above), they, no doubt, belonged to various unions. May be that a distinct forest community was formed by *Nyssa silvatica*, *Liriodendron tulipifera*, *Carya*, *Fagus ferruginea* and *Liquidambar*, growing together in wet places, because to-day also they thrive side by side in the southern part of Atlantic America forming a separate forest "type" along the rivers, and were frequently described by American investigators. On the other hand, each of these trees may be met also in other "types" of forests, and this circumstance makes such a supposition dubious. The abundance of fossil remnants of *Alnus glutinosa* and *Solanum dulcamara* points in sociological respect to the presence of forests from the order *Alnetalia*. Also *Pterocarya fraxinifolia* ought no doubt to be placed in some forest community of this union, as well as *Vitis silvestris*. The species of the genera *Acer*, *Carpinus*, *Ulmus* and *Fagus*, together with *Prunus spinosa*, *Crataegus monogyna*, *Physalis Alkekengi* and perhaps also *Agrimonia pliocaenica* indicate the presence of forests from the class *Querceto-Fagetea*, especially from the union *Fraxinio-Carpinion*.

"I will not develop further such risky deliberations. I close them expressing the conviction that a very detailed analysis, both quantitative and qualitative, of the Pliocene remnants of forest flora pursued in particular layers (or lenses) of water deposits, founded upon the detailed knowledge of forest communities living contemporarily in the refugian regions of eastern Asia, Atlantic America and Transcaucasia, will enable in future the creation of a real nucleus of paleosociology of plants".

ŚRODON (1973) discusses the genesis of sediments of the Pliocene flora of Krościenko, Mizerna and Huba. He concludes that these sediments probably " ... originally exceeded their present sites by at least 100 m; from there they were redeposited to the foot of the slopes of the Gorce mountain range in the Pleistocene". In connection with this ŚRODON quotes (p. 304 in Polish text) the long list of plants which in Pleistocene could have been members of communities of forbs and high mountainous natural meadows (?grass balds). In fact, there are many "non-forest" plant species on the list in SZAFER's paper (1954, p. 72-78). Especially striking for me are the following ones:



*Dianthus* sp., *Thalictrum* cf. *minus*, *Ranunculus* cf. *polyanthemos*, *Plantago* sp., *Scabiosa* cf. *columbaria*, *Aster* sp. and *Centaurea* sp. (now those plants in Central Europe chiefly grow on meadows and on rock outcrops, but not in shaded forests). Thus either the Pliocene deposits were periglacially redeposited or the enumerated species grew within the Pliocene forest clearings, on the rock outcrops, or rocky ridges; many water and bog plants of SZAFER's list could occur within the small water basins and on their margins, or close to the streams.

### 2.5.3. *The Pliocene climate in the West Carpathians*

"It is impossible to determine precisely, on a floristic basis, the climate conditions under which the Pliocene vegetation in the vicinity of Krościenko lived, but a general characteristic of them is quite possible" (SZAFER 1946, p. 132). Afterwards (p. 145-146) "... we may accept with considerable probability that in the vicinity of Krościenko in the stage of deciduous (and mixed) forests, the climate in the Middle Pliocene was about 9°C warmer than today, and, in the annual mean rose to about 15.7°C. The July mean temperature was probably about 25.4°C (higher than today by 9.6°C), and the January mean was about 6°C, thus being about 11°C higher than in present times.

"As far as the climate of the upper stage, that of conifers, in the vicinity of Krościenko is concerned, with the predominance of *Tsuga europaea*, *T. caroliniana* and *Picea rubra*, and also with *Picea polita* and *Pinus Peuce*, it probably corresponds approximately to the arithmetic mean temperatures of the thermal curves of the stations Linville and Fuji. Here the difference in relation to Krościenko amounts to about 9° (8.4°C) in the annual mean, about 6° (6.3°C) in the July mean, and about 9° (9.4°C) in the January mean.

"The essential difference between the present and the Pliocene climate in the vicinity of Krościenko, as far as temperature is concerned, depends not only on its mean value which was about 9°C higher in the Pliocene, but also on much smaller oscillations (weaker amplitude), which result from the comparison of absolute and mean maxima and minima partly represented in table 4 (cf. p. 66). The thermal climate of the Pliocene was therefore not only warmer, but also more "maritime", than the now existing, which was due to a



different distribution of land, seas and mountains in Middle Europe in the period of the Middle Pliocene.

"... As for the annual sum of rainfall, one may accept, I believe, that in the Middle Pliocene in the vicinity of Krościenko it approximated the arithmetical mean of the annual sum (...) was about twice as high as the present sum of precipitation (833 : 1492 mm).

"Considering the above determined peculiarities of the Pliocene climate in the vicinity of Krościenko we must state that it was different from the contemporary climate of any region in Europe. A similar climate is to be found no nearer than on the southern slopes of the Caucasus in Transcaucasia.

"... The general climate was locally transformed into a habitat-climate, changeable according to the rich morphology of the territory, the character of the geological substratum, the exposition, the density of the plant communities, etc.; this habitat-climate, together with edaphic and biological factors, decided, much like today, upon the distribution of plants on a small area, and influenced the development of natural plant communities".

In the next paper SZAFER (1954, p. 203-204) suggested that the Pliocene climate of Krościenko was similar to that of Kieonkiang (Fokien), i.e. that it was characterized by the following qualities: average annual temperature approx.  $17^{\circ}\text{C}$  to  $18^{\circ}\text{C}$ , average temperature of the warmest month (July) approx.  $29^{\circ}\text{C}$ , average temperature of the coldest month (January) approx.  $4^{\circ}\text{C}$  to  $5^{\circ}\text{C}$ , total annual precipitation approx. 1500 mm (on the graphic, p. 128 in the Polish text - mean annual temperature is  $18^{\circ}\text{C}$  and annual sum-total of precipitation 1800 mm).

According to Miss E. ZASTAWNIAK's (1972, p. 61) opinion about the Upper Pliocene climate, "the climate requirements of the trees and shrubs, which built the forest associations of Domański Wierch, indicate the temperate or warm-temperate character of the climate and its considerable humidity; presumably, it was similar to the climate of the terrains on which relict forests of the Talysh and Elbrus Mts. grow today. The climate on the northern slopes of the Elbrus is characterized by a mean annual temperature of  $13^{\circ}$  to  $15^{\circ}\text{C}$ , and abundant rainfall with a maximum in the autumn months (mean annual about 1500 mm), and mild winters with frosty periods. ...".

### 3. The author's comments and opinions

#### 3.1. *The North American element in the Carpathian Pliocene flora*

The studied Pliocene floras of the West Carpathians are similar in their composition to the contemporary floras of the area of the Caspian Sea, the south of the Caucasus (the Talysh Mts.), the south slopes of the Himalaya range, the middle and northern China, Korea, and the southern Japan, as well as of the Balkan peninsula. The role of the North American element in Carpathian Pliocene floras is relatively small in comparison with the Miocene Period (TRAN DINH NGHIA 1974, OSZAST and STUCHLIK 1977). The list of the North American plant species and/or closely related taxa (tables 6 and 7), which are critically discussed and compared with the unpublished materials of Mrs. ŁAŃCUCKA-ŚRODONIOWA, contains approx. 15 species\*. Some of them have probably their corresponding taxa in Asia or in the Balkan peninsula (e.g. *Picea rubra* Link. - cf. table 6 and *Liquidambar europaea* A.Br. - cf. footnote p. 91). There is a similarity between the ecological conditions and the general features of the vegetation in the SE United States and the other chief refuges of the Tertiary forest flora of the Northern Hemisphere (cf. LIETH 1979 and fig. 9).

#### 3.2. *The richness of the Carpathian Pliocene floras*

The following relationships were used to evaluate the richness of the Pliocene flora and to compare it with the contemporary vascular flora of Poland:

$$\frac{\text{the area of Poland}}{\text{the number of vascular plant species growing within the area}} = \frac{312\,700 \text{ km}^2}{2670} = 117$$

and adequately:

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\* The fact, that some species from SZAFER's publications have not been included in my following considerations (ca. 10 taxa of the North American element) does not influence the general opinion about the Pliocene flora, vegetation and climate in the West Carpathians.

$$\frac{\text{the area of the Carolinas}}{\text{the number of the vascular plant species in the area}} = \frac{\text{ca. } 217\,000 \text{ km}^2}{3360} = 65.$$

There is a positive correlation between the area and the number of the vascular plant species in Central Europe and in the whole world (cf. figs 4 and 5) (HAEUPLER 1974, WILLIAMS 1964).

Thus, if we accept that:

- a. the contemporary flora of the Carolinas has a similar number of the vascular plant species as the Pliocene flora of Poland
- b. there exists a strong correlation between the area and the number of vascular plant species growing in this area
- c. the number of species of a given area of tropical and subtropical regions is considered to be greater than the corresponding one in temperate regions (cf. fig. 5 - black dots, representing tropical floras, are grouped chiefly in the higher part of the graphic) - then, we can assume that the Pliocene flora in Poland was approximately twice as rich as the contemporary one ( $117 : 65 = 1.8$ ).

We come to a similar conclusion while analyzing the number of the vascular plant species growing in the corresponding forest communities of the Duke Forest near Durham, N.C. and the forests communities of the Cracow Jurassic Upland, S. Poland (table 4a and 4b -  $232 : 157 = 1.5$ ). It would be much better to compare the number of plant species of certain ranges in SE Asia, but unfortunately the statistics of their contemporary floras are not known well enough.

In the Carpathian Pliocene forests grew many different tree species (probably ca. 160 in comparison with 66 in contemporary Poland) and various woody vines (table 9).

### 3.3. *The Pliocene vegetation in the West Carpathians*

The most striking features of the Pliocene flora of Krościenko are the following ones:

- a) small number of evergreen trees and shrubs

Table 9. The number of trees, shrubs and woody vines in the Carolinas and Poland (cf. tables 4 and 5)

Number of species				
	The Duke Forest	The Carolinas	The Cracow Jurassic Upland	Poland
Trees	38	160	21	66
Shrubs	26	274	25	215
Vines (woody)	12	55	0	4

- b) the occurrence of water plants (incl. termophilous) as well as the plants of bogs and marshes (relatively small abundance of *Euryale*, *Brasenia*, *Podostemum*, *Proserpinaca*, *Dulichium*, *Scirpus*)
- c) the occurrence of deciduous trees and shrubs (*Fagus grandifolia*, *Juglans cinerea*, *Carya* cf. *tomentosa*, *Nyssa sylvatica*, *Corylus* cf. *cornuta*, *Staphylea* cf. *trifolia*) as well as the boreal trees (*Tsuga*, probably two species, and *Picea* cf. *rubens*). Gymnosperm remains are richly represented in fossil materials of Krościenko, very poorly in Domański Wierch.
- d) a small number of "calcophilous" plants (? *Scabiosa* cf. *columbaria*, ? *Aquilegia vulgaris*).

Based on the composition of the Pliocene flora of Krościenko and on the ecology and distribution of the contemporary vegetation in the SE United States it is possible to make an attempt to reconstruct the Pliocene vegetation in the West Carpathians.

The Pliocene landscape in the eastern part of the Nowy Targ - Orawa Basin and its vicinity (intramontainous depression close to the Pieniny Klippen Belt on its northern marginal flysch zone - Magura Nappe) resembled the contemporary one. The subsidence and deposition (about 15 m/Ma to about 100 m/Ma\*) in this region was calculated by BIRKENMAJER (1978). In Pliocene the vicinity of Krościenko (ca. 450 to 500 m a.s.l. today) was probably surrounded by

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\* The mean deposition rate gives a value of increase of the sediment pile in meters per million years (m/Ma)

mountains which reached more than 1000 m (BIRKENMAJER, personal comm.), All palaeobotanical (incl. palynological) studies suggest (cf. OSZAST and STUCHLIK 1977) that in the Pliocene there were two different zones of vegetation in the region of Krościenko.

In the lower zone deciduous trees dominated, in the higher, - hemlock, spruces and firs. It seems that this coniferous forest formed a narrow band along the higher Beskidy Mts. and ridges, analogous to that observed in the Appalachian Mts. (cf. VANKAT 1979).

It is probable that the Pliocene Carpathian forest represented in the fossils of Krościenko was situated in a transitional zone where plants of coniferous, mesophilous forests and flooded woods met.

Hemlock (*Tsuga canadensis*), a typical component of the North American northern hardwood forests, attains its largest size near streams on the slopes. Along the southern fringes of its range, it often occurs in widely isolated, outlying situations, which are completely surrounded by ecologically unrelated vegetation. Several disjunct occurrences of *Tsuga canadensis* in Alabama and in North Carolina were reported as occurring in ravines with other Appalachian species (OOSTING and HESS 1956). When the 16th IPE visited the splendid Joyce Kilmer Memorial Forest (August 19th, 1978) in the small area near the stream I noted, at random, *Liriodendron tulipifera*, *Acer rubrum*, *Magnolia fraseri*, *M. acuminata*, *Betula allegheniensis*, *Tsuga canadensis*, *Fagus grandifolia*.

I could imagine similar trees growing together during the Pliocene in West Carpathian Mts., in the neighbourhood of Krościenko.

### 3.5. The climate of the West Carpathians in Pliocene

The Pliocene climate in Krościenko and in the West Carpathians, by analogy to the one of the SE United States, was warm and moist: in the lower zone the average annual temperature was probably ca. 16°C, the mean annual precipitation sum-total 1100 to 1300 mm (cf. two upper rows of the climate diagrams of fig. 1; the two lower rows are, in opinion, rather similar to the climate of the Miocene). At higher elevations, the climate was cooler (average

annual temperature probably about  $10^{\circ}\text{C}$ , cf. the diagram of Boone, N.C.).

My conclusions are in accordance with the results of the research of ZASTAW-  
niak (1972, p. 61; cf. p. 100 of this paper).

It is not, at present, possible to make a more precise determination of climatic conditions using floristic materials. In the Carpathians the differences in means annual temperatures between the northern and southern slopes are from  $0.7$  to  $1.2^{\circ}\text{C}$  (KOSTRAKIWICZ, personal comm.).

#### 4. Final remarks

The 16th IPE (1978) through the SE United States visited one of the chief refuges of Tertiary forest flora in the Northern Hemisphere (fig. 9). This fieldtrip gave participants not only the opportunity to make observations and to enjoy the exotic plant species, landscapes, and vegetation but also to examine some problems of general importance such as the problem of rare, endemic and endangered plant species as well as questions of corresponding taxa and ecological equivalents in the floras of Eurasia and North America.

The contemporary flora of Europe shows very close connections with the flora of Asia. These connections are, however, considerably weaker as far as the flora of North America is concerned. DIELS (see SZAFER 1946, p. 155) states that the flora of Atlantic North America does not possess a single genus exclusively in common with Europe, but instead it has at least 30 genera in common solely with East Asia. Those Tertiary survivors which now live in Europe show taxonomic affinities with Asia rather than North America. We do not speak, of course, about the new invaders: many weeds as well as meadow and pasture plants!

Modern paleobotanical researches have completely confirmed the opinions of many European botanists (cf. SZAFER 1946, p. 158) that the flora of Central Europe was, in the Tertiary Period, only a prolongation of the flora of Asia, and formed the western wing of the uniform Eurasiatic Holarctic flora.

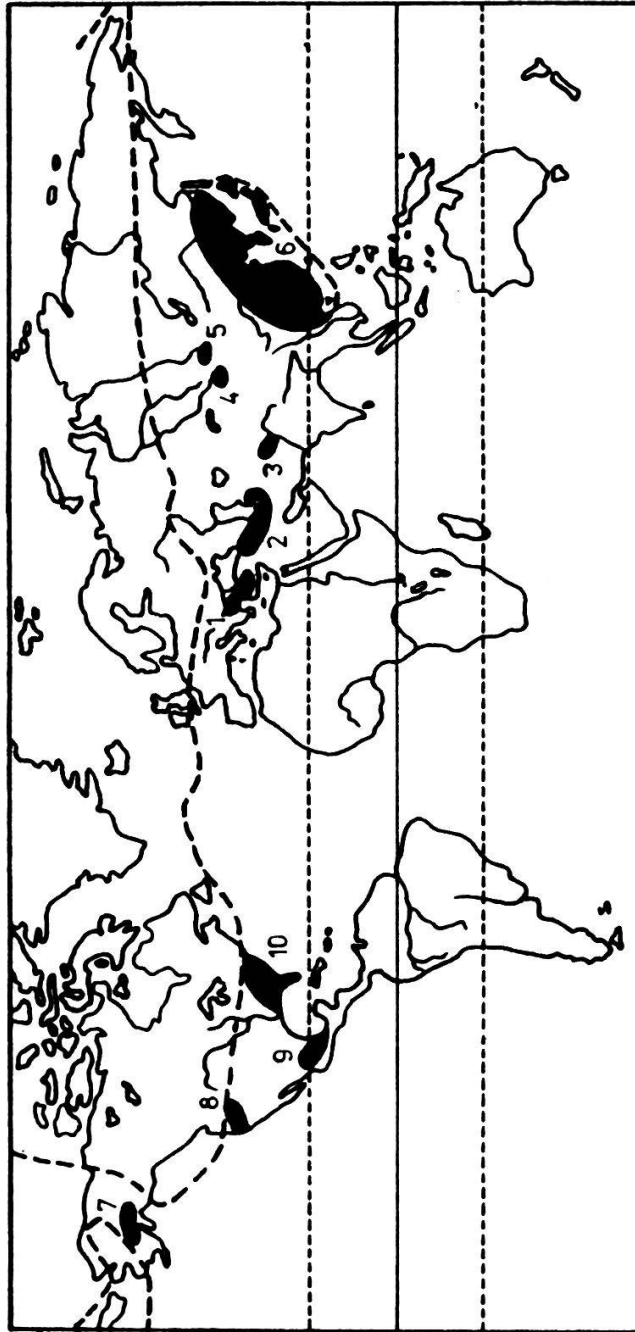


Fig. 9. Chief Pleistocene refuges of forest flora and fauna in which genera and species of plants and animals from the Tertiary period survive. 1. Balkan-Black Sea refuge. 2. Armenian-Persian refuge. 3-5. Central-Asian refuges. 6. Eastern-Asiatic refuge. 7-10. North American refuges. The discontinuous line indicates the maximum range of Pleistocene glaciation (after REINIG, redrawn from SZAFFER 1975).

These floristical connections were relatively strong in the Miocene but weak in the Pliocene.

Although the role of the North American element in the Carpathians and in other European Pliocene floras is not important, the climate and vegetation of the mountainous and submountainous zones in the south Appalachian Mts. closely resemble the Pliocene climate and vegetation in Europe. Modern ecological studies, climate diagrams (WALTER and LIETH 1961-1967, WALTER et al. 1975), as well as the data in the paper of LIETH (1979 although recondited under the modest title "Introduction to the report volumes for the 16th IPE"), containing comparisons of the climate of the SE United States visited by the 16th IPE and similar climates in other parts of the world, are of great value for paleobotanists in their attempts to reconstruct the vegetation and the ecological conditions of the Neogene are.

The European botanists who visit temperate and relatively warm zones of North America, especially its eastern part, are always strongly impressed by a great similarity of the forest flora of both continents: there are many corresponding taxa as well as the ecological equivalents (MEDWECKA-KORNAŚ 1961, GRANDTNER 1963, KNAPP 1965, KORNAŚ 1965, 1972).

The general conclusion made by KORNAŚ (1972, p. 57) is significant for further palaeoecological studies. "Nearly all series of closely related taxa in forests of temperate Eurasia and North America consist of ecologically corresponding components which have similar ranges of tolerance, occupy similar habitats and grow in strictly analogous plant communities. The ecological constitution of such groups must be very ancient and very rigid. Even those nemoral taxa which are separated into morphologically distinct species have undergone no noticeable ecological changes since their isolation some 10-15 million years ago" (KORNAŚ l.c.).

Corresponding taxa of the temperate and warm Holarctic forest flora are certainly excellent material for ecological-evolutionary studies, as it was demonstrated by JENTYS-SZAFEROWA (1958, 1975), who has described the history of genus *Carpinus* in Holarctic. There is still necessity to develop palaeobotanical and ecological research in order to describe climatic changes as well as the changes of vegetation through time and space. Such studies can



only be carried out through longterm co-operation between palaeobotanists and plant ecologists of Europe, Asia and North America.

### Summary

The Pliocene floras of the West Carpathian Mts. are similar in their composition to the contemporary floras of the areas of the Caspian Sea, the south of Caucasus, the Balkan Peninsula and SE Asia. The role of the North American element in the Carpathian Pliocene floras is relatively small. But there is a similarity between the climatical conditions and the general features of the vegetation in the SE United States and the Pliocene climate and vegetation of the West Carpathians. The flora in the Pliocene period in the West Carpathians is approximately twice as richer as the contemporary one. The Pliocene climate of Krościenko (the West Carpathians) was moderately warm and moist: in the lower mountainous zone the average annual temperature was probably approximately 16°C, the mean annual sum-total of precipitation 1100 to 1300 mm; in higher elevations the climate was cooler (average annual temperature approximately 10°C).

### Zusammenfassung

Die Pliozänfloren der Westkarpaten haben viele gemeinsame Züge, vor allem mit den heutigen Floren von Südostasien. Die von SZAFER (1938, 1946, 1947, 1954), LANCUCKA-SRODONIOWA (1965), OSZAST (1973), OSZAST und STUCHLIK (1977), ZASTAWNIAK (1972) u.a. studierten Pliozänfloren enthalten nur wenige nordamerikanische Elemente (vgl. Tab. 7). Die zahlreichen ökologischen und pflanzengeographischen Untersuchungen im Südosten des nordamerikanischen Refugiums der Tertiärfloren ermöglichen die Rekonstruktion der pliozänklimatischen und der Vegetationsverhältnisse in den Westkarpaten und in Europa.

Im Pliozän war die Flora in den Westkarpaten wahrscheinlich zweimal so reich wie heutzutage; die Jahresmitteltemperaturen in niedrigen Lagen waren ungefähr 16°C und die Niederschläge schwankten zwischen 1100 bis 1300 mm pro Jahr, in höheren Lagen waren die Temperaturen niedriger (Jahresmittel ungefähr 10°C).

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