Acta Paleobot. 34(2): 165–194, 1994

DEVELOPMENT OF FLORA AND VEGETATION OF THE UKRAINIAN EASTERN CARPATHIANS AND POLISH WESTERN CARPATHIANS IN THE NEOGENE

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ABSTRACT. On the basis of palynological studies of the Neogene sediments in the Transcarpathians and Polish Western Carpathians main trends of development of flora and vegetation in the whole Carpathians have been clarified with regard to geographical, geological-tectonic and palaeoclimatic conditions. The results have been compared with other palaeobotanical data from other Carpathian regions and a reconstruction of the origin and development of the whole Carpathian flora and vegetation is given. Continuity of altitudinal zonation of vegetation in the Western and Eastern Carpathians from the beginning of the Neogene is explained from the palaeobotanical point of view. Explosive orogenic volcanism is seen to be a very important local climate forming factor influencing vegetation development in this region during the Neogene.

KEY WORDS: Carpathians, Neogene vegetation, palynology

INTRODUCTION

The Carpathian Mountains are divided into several parts: the Eastern Carpathians with the Transcarpathians in the territory of the Ukraine, the Western Carpathians belonging to Slovakia and Poland and the Roumanian South Carpathians. The flora of the outer Carpathians, (Western Carpathians and Eastern Carpathians with the Transcarpathians) has a transitional position between Eastern and Western Europe flora and contains more than 2300 plant species including about 140 endemics. Some of them survived in the Carpathains as relicts.

To properly understand the history of the recent flora and vegetation, their dynamics, state, zonation and tendency of future changes caused by natural and anthropogeneous factors it is necessary to ascertain their composition in all stages of the Neogene, Pleistocene and Holocene. The history of the flora in Carpathians was studied irregularly. There are practically no data on the stage by stage development of the flora and vegetation, or on climatic changes in early and middle Miocene, which are the initial stages of the development of the recent flora in this region.

Previous work on leaf imprints of Neogene plants were studied in the Carpathians includes Stur (1867), Staub (1890), Wiśniewski (1899), Pax 1909), Lilpop (1957), Baykovskaya (1953), Teslenko (1954), Mchedlishvili (1956), Il'inskaya (1960, 1968), Shvareva (1963, 1983), Zastawniak (1972) whilst fossil fruits and seeds were studied by Szafer (1946, 1947, 1954), Dorofeev (1966), pollen and spores by Shchekina (1957, 1960), Rybakova (1964, 1968), Oszast (1970, 1973), Oszast and Stuchlik (1977), Syabryay (1970, 1975, 1978, 1980, 1983, 1985), Syabryay and Shchekina (1983).

The goal of this paper is to clarify the origin, formation and tendency of development of the Neogene flora and vegetation in the Carpathians, to establish the nature of their changes in the geological past.

For stratigraphical purposes we use the stratigraphical scheme for the Paratethys region published by Steiniger and Rögl (1983).

MATERIAL AND METHODS

The main material for our studies comes from the mollasian marine sediments of the Miocene in the north-eastern part of the Central Paratethys, the eastern outskirts of the Pannonian Basin and sediments of the Dacian-Levantinian lacustrine marsh basin. The samples were taken from bore-holes and natural outcrops. In addition for comparison, some samples of Neogene sediments from Slovakia, Hungary, Bulgaria and Eastern Germany were studied. More than 900 samples were evaluated. In general pollen-spore spectra from bottom sediments of lakes and sea characterize land vegetation better than those from terrestrial deposits (Groot & Groot 1966), and reflect the composition of vegetation of surrounding coastal plain areas (Vronsky 1984). They reflect mostly arboreal vegetation of greater surrounding areas without disturbances of the local herbaceous vegetation (Kvavadze & Stuchlik 1990).

Nevertheless a pollen drift takes place in hypsometrically different altitudinal zones, in mountain areas. Generally the drift of pollen and spores from lower vertical zones to upper ones is known but in mountains close to the sea an opposite drift from upper vertical zones lower down to the sea shore also occurs. (Stuchlik & Kvavadze 1987).

Pollen spectra of marine and lacustrine sediments of the lower reaches of mountain rivers, lakes and seas include pollen from the costal plain areas as well as from the surrounding mountains drifted by wind, washed out from soils by rains and transported by rivers into the sea and lakes. These pollen spectra include pollen of plants from all vegetation zones. However there are some areas especially in mountains, namely in the Transcarpathian area, where the setting excludes pollen drift from the Carpathians beyond the Transcarpathians. This basin was surrounded on three sides by eastern outskirts of the Western Carpathians and by Eastern Carpathians and on the fourth side by the arch of Volcanic Carpathians. Thus the Neogene sea of the Transcarpathian area was a natural trap for palynomorphs of plants growing in the Carpathians.

Palynological studies of bottom sediments of the Black Sea in Western Georgia show that the spore-pollen spectra include palynomorphs of plants from all mountain forest belts and reflect adequately the composition of the cenoses (Shatilova 1974).

The samples we have studied are dominated by woody plants (85–90%) and the majority of specimens belongs to the 10 so called "transit taxa" (Blyakhova & Zaklinskaya 1984) which have no stratigraphic significance. The main criterion used to infer changes in the Neogene flora and vegetation composition is a quantitative assessment of groups (Krutzsch & Majewski 1967) with their ecological tolerances deduced from the ecology of their modern analogues. To make the reconstruction of paleoflora more complete results of macrofloristic investigations have been evaluated. The studied sediments are dated quite well using foraminifer, mollusc and ostracod faunas.

POLLEN-SPORE COMPOSITION OF THE NEOGENE SEDIMENTS

In the studied pollen- spore complexes of the Neogene sediments in the Transcarpathian and Western Carpathian areas more than 290 different taxa have been found. The main group are woody plants of the gymnosperms and angiosperms. Among others, ferns are represented by some ancient tropical families *Cyatheaceae, Schizaeaceae* and *Gleicheniaceae* as components of woody tropical flora. These are mostly relicts from the Danian-Paleocene period where they were abundant and well developed. In Neogene sediments they are found only sporadically and not in all profiles, because of the low migration capacity of woody ferns. This group is more common in the Transcarpathians than in Neogene profiles of Polish Western Carpathians. The *Lycopodiales* are more common and represented by *Lycopodium* and *Selaginella* in both Transcarpathians and Western Carpathians. Other ferns especially *Polypodiaceae* sensu lato were well developed during the Paleogene and Neogene. Such genera as *Dryopteris* and *Asplenium* developed mainly during the Neogene, becoming predominant at the end of Pliocene.

The *Ginkgoaceae* family was represented only by one species *Ginkgo adianthoides* whereas *Cycadaceae* was absent in the Paleogene-Neogene sediments and the *Ephedraceae* were very rare in both the Transcarpathians and Western Carpathians. Conifers, namely *Pinaceae*, of low diversity in the Paleogene evolved significantly in the Neogene. Pollen representation of this family was rather monotonous at the genus level. Within pollen of *Pinus* two types the most common and abundant *P. sylvestris* type and in lower quantities *P. haploxylon* type, are distinguished. Pollen forms close to the modern species *Picea abies* appeared in early Miocene, but became abundant in late Pannonian forming its own vegetational belt in the mountains. The genus *Tsuga* shows some species diversity (*T. canadensis* and *T. diversifolia* types) at the beginning of the late Miocene, whereas *Abies* was identified sporadically throughout the Miocene but was more common in the Pliocene. The *Pinaceae* family represents plants of great ecological diversity without stratigraphical significance. A wide distribution of *Pinaceae* in the earlier stages of the Paleogene and even in late Cretaceous was diminished before the Pliocene by disappearance of several forms. *Taxodiaceae – Cupressaceae* group is taxonomically and ecologically monotonous and is facies controlled. During the Neogene no new genera and species evolved (Andreánszky 1956).

The angiosperms are the most variable group with woody, bush and herbaceous plants of great ecological diversity. Increase in pollen diversity serves as evidence of appearance of new genera and species during the Neogene. The same taxa found of various localities in synchronous sediments indicate their migration ability.

In the Paleogene angiosperms were represented by various tropical and subtropical forms which are replaced by temperate genera in the Neogene. A rapid diversification of angiosperms resulted in appearance of many forms are characteristic for the Paleogene and partially for the Neogene flora and vegetation. In this respect the *Fagaceae* family is indicative. Pollen of *Fagus* appeared in the middle Miocene complexes with some species variety (*Fagus orientalis*, *F. sylvatica* and *F. japonica* – types). Remain of leaves of *F. orientalis F. sylvatica* and *F. hertae* were found in the Neogene.

In Hungary Boros (1955) described leaves of three species of *Fagus – F. sylvatica, F. orientalis* and *F. moesiaca*. The latter species according to Karpati (Boros 1955) being a hybrid between *F. sylvatica* and *F. orientalis* exists in Hungary and in adjacent countries nowadays. *Quercus* occurs throught the whole section of the Neogene. However species close to contemporary ones appear in the late Pliocene. The same is with members of the *Betulaceae* family – pollen of *Carpinus betulus* – type, *C. orientalis* – type and *Betula* sp. (*B.* cf. *pendula, B.* cf. *pumila, B.* cf. *pubescens*) appeared in spectra in late Levantinian. Pollen resembling the modern species of *Alnus incana* and *A. glutinosa* appeared in the early Sarmatian, whereas *A.* cf. *viridis* occurred only since the beginning of the Pleistocene.

Almost all species close to modern members of the *Juglandaceae* family appear in the late Miocene and only *Pterocarya* cf. *serrata* appears in the late Pliocene. Among the *Ulmaceae, Ulmus* pollen occurs in all Neogene complexes with pollen close to *U. laevis* appearing in the earlier Sarmatian and becoming wide spread in the late Pliocene and the beginning of the Pleistocene. *Tilia* forms close to modern species appeared in the Sarmatian: *T.* cf. *cordata* in the early Sarmatian. *T.* cf. *platyphylla* and *T.* cf. *tomentosa* in the late Sarmatian.

Almost all woody species which were included in the list were present in floristic complexes since the beginning of the Neogene in quantities. All together 11 spores-pollen floristic complexes have been distinguished for characterizing sediments of Egerian, Eggenburgian, earlier and late Badenian, Dorobratowskaya, Lukowskaya and Almaschskaya suites of Sarmatian, Pannonian, Levantinian and Chopskaya suite for the Transcarpathian with 7 complexes for the Western Carpathians.

THE HISTORY OF DEVELOPMENT OF THE NEOGENE FLORA AND VEGETATION

The Ukrainian Eastern Carpathians and Western Carpathians were formed in the transitional period between the Paleogene and the Neogene. Following uplift of these mountains there was immigration of plant formations from adjacent areas which originated in the Paleogene and subsequently changed as a result of geological and climatic processes.

Prior to the Neogene period, among the Danian-Paleocene flora there were forms close to the contemporary ones of temperate zones such as members of the *Juglandaceae* family, *Pinus, Picea* along with ancient angiosperms producing pollen of the *Normapolles* group. Their role was increasing during the Paleogene. The presence of pollen grains of *Rhus, Palmae, Engelhardtia, Castanea, Carya, Pterocarya, Myrica, Podocarpus, Cedrus* and spores of *Lygodium, Gleicheniaceae* in polytopic spores-pollen complexes from lower Eocene sediments in the Skib and Marmarosh areas of the Carpathians is indicative of the existence of a considerable number of warm-temperate elements in a subtropical flora (Portnyagina 1973). There were elements of various ecological demands which indicate the existence of various altitudinal zones.

Floristic complexes of Eastern Carpathian Oligocene include a considerable quantity of pollen of temperate species very close to their conventional homologues at generic level. The presence of warm-temperate elements in the Eocene and Oligocene floristic composition in the area of Central Paratethys was noted by many scientists (Unger 1951, Krutzsch & Majewski 1967, Planderová 1973, Snopková 1980 and others).

The Carpathian fold system an area of strong oscilatory movements; the process of orogenesis continued up to the Quaternary period. Along with the process of general uplift there was an area of sinking where a large inland basin of the Paratethys was formed north-west of the Tethys zone. The Ukrainian Carpathians as well as the whole Carpathian region are a part of the Central region of the Paratethys and the influence of this sea was apparent during its existence. As a result of intensive oscillatory movements volcanic activity increased in the inner zone of the Ukrainian Carpathians. Configuration and size of the basin changed costantly. All this affected the formation and development processes of the flora and vegetation considerably.

THE EARLY MIOCENE

The Egerian. Polytopic complexes of the Egerian sediments in the inner and auter Carpathian zones include pollen of plants requiring different ecological conditions which could not have grown in one and the same community. There were vegetation assemblages located at different altitudes which was conditioned, among other factors by the raising Carpathians. At the beginning the raised Ukrainian Carpathians were low mountains slightly higher than 1000 m and the Western Carpathians were small mountains. Vegetation differentiation according to the altitude became apparent immediately as a heritage of the Paleogene during which vertical zonation already existed. With climate changing the vegetation zones transformed dynamically. Dislocation of zones and changes in paleocenosis structure were different in the inner and outer zones of the Ukrainian Carpathians. It is likely that at the beginning of the Egerian altitudinal zonation was not clearly distinguished but there was vertical differentiation of natural vegetation.

Certain differences existed in the composition of flora and vegetation of inner and outer zones in every period of the Neogene. Flora and vegetation of lower altitudes especially coastal area of the sea basin, were similar inspite of the absence of some thermophylous elements (*Palmae*) in the north macroslope and in higher zones where this distinction became quite evident.

Subtropical forests including areas of swamp forests with abundance of *Myricaceae* on the outskirts, grew on plains. Ferns including members of subtropical and tropical flora (*Schizaeaceae*, *Gleicheniaceae*, *Cyatheaceae*, *Matoniaceae*, *Dicksoniaceae*) are characteristic for both inner and outer zones.

In coniferous-broadleaved and broadleaved forests of the inner zone members of the family *Juglandaceae*, mainly subtropical ones, play the main role. Chestnut forests were also widely spread.

In the Polish Western Carpathians there is no evidence of fossil floras of Egerian and

Eggenburgian, but probably the development of vegetation, was similar to that of the outer zone of the Eastern Carpathians.

The Eggenburgian. This is the time of the beginning of the formation of the Transcarpathians foredeep of intensive sinking and transgression of warm sea which reached the border of Western Carpathians (Fig. 1). In that time, like in the Egerian, in Eastern Carpathians there were small woody communities with *Taxodium, Nyssa.* The area of subtropical forests, with *Lauraceae* (remains of *Laurus* have been described by Baykovskaya 1953), *Sapotaceae*, *Palmae*, *Myrtaceae*, apparently sclerophylous *Quercus* became wider. In broad-leaved forests *Engelhardtia* was abundant along with numerous other members of the family *Juglandaceae*.

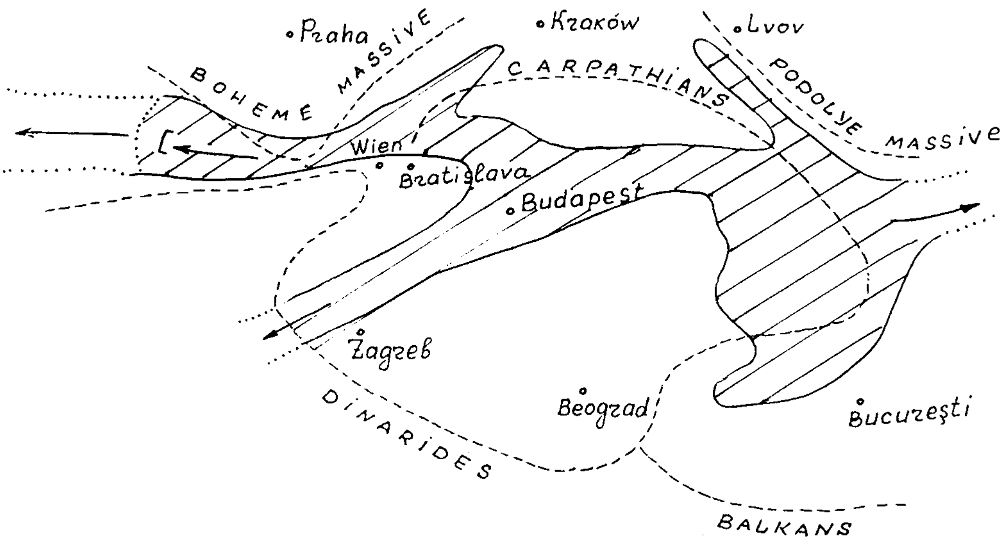

Fig. 1. Palaeogeographic scheme of the Central Paratethys in the Egerian-Eggenburgian (Seneš & Marinescu 1974)

In coniferous forests the role of *Picea, Abies, Tsuga* and *Podocarpus* increased. The latter taxon was spread wider also in forests on the north-eastern part of Carpathians. The role of *Pinus* increased on account of decreasing of other coniferous elements there.

Broad-leaved forests were rich in thermophylous species, chestnut forests being more important in contrast to *Quercus*. Areas of swamp forests widened. A number of thermophylous ferns increased. In forests of the inner as well as of the outer zone of the Carpathians herbaceous plants were of no importance. It is likely that there were open areas only near the sea shore on plains, the habitat of halophytes with predominance of the *Chenopodiaceae* family. Climate was warm and humid in all of the Carpathians.

THE MIDDLE MIOCENE

Ottnangian-Karpatian. During the Ottnangian the sea covered a considerable part of the Eastern Carpathians (Fig. 2), and transgressed to the west in a shape of a narrow gulf, reaching the region Nowy Targ in the Polish Western Carpathians (Ney et al. 1974). Spore and pollen were not found in the Tereshul conglomerates. According to poor spores-pollen spectra only some changes in plant composition were noted in the outer Carpathians zone. *Nyssa* disappeared from swamp-forest assemblages and *Magnolia* disappeared from humid forests of foothills. In broad-leaved forests *Fagus* and *Liquidambar* appeared. Open, possibly coastal areas widened and halophytes spread away from sea-water influence. At the end of the Eggenburgian the foredeep started to sink and volcanic activity intensified in the Transcarpathian area (the first stage of orogenic volcanism) and large tufas formed (Novoselitsk, Apshin, Danilov and Klobuk). Floristic characteristics for the Ottnangian-Karpatian in this region and in Polish Western Carpathians are not known.

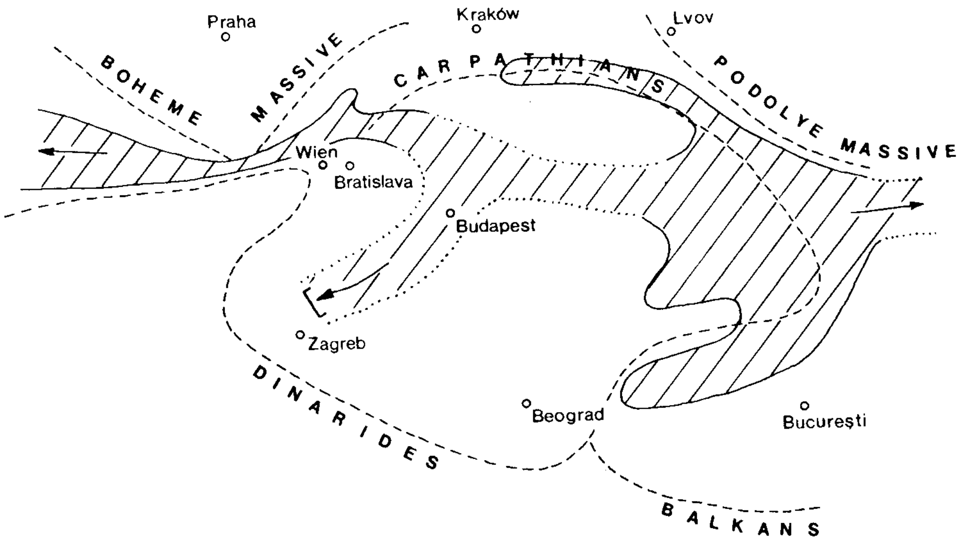

Fig. 2. Palaeogeographic scheme of the Central Paratethys in the Ottnangian (Seneš & Marinescu 1974) emended after Neay et al. (1974)

Early Badenian. This is a period of expending transgression of the Paratethys as a result of which sea water covered the whole Transcarpathians foredeep and in the Western Carpathians the sea expended over the Krosno-Jasło, Nowy Sącz and Nowy Targ-Orawa basins reaching the Morawa Gate and to the north the Holly Cross Mountains (Fig. 3). In coniferous forests of that time *Pinus* was diverse, its subgenus *Diploxylon* dominated and other evergreen coniferous elements occurred often. *Ginkgo* grew sporadically on mountains. Broad leaved forests expanded, *Ulmus* and *Castanea* occurred often, *Engelhardia* was numerous. The abundance of *Castanea atavia* leaves (Il'inskaya

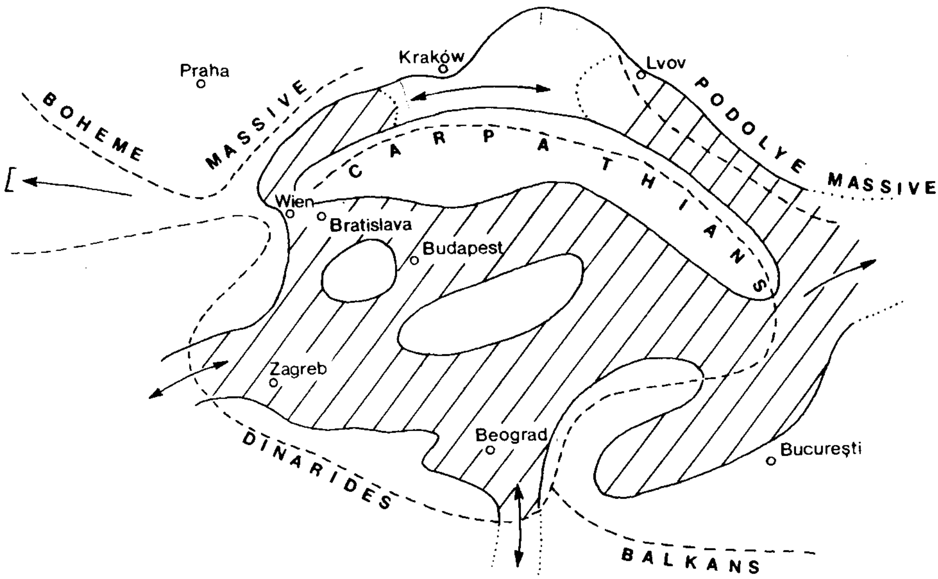

Fig. 3. Palaeogeographic scheme of the Central Paratethys in the Karpatian–Badenian (Seneš & Marinescu 1974) emended after Ney et al. (1974)

1960) in the Badenian sediments are indicative of local chestnut forests. For the first time *Liquidambar* and *Fagus* appeared in the forests of the inner zone of the Ukrainian Carpathians (according to pollen and leaf remains). In the early Badenian thermophylic species decreased in number, the genus *Engelhardtia* was the exception. Swamp forests were not characteristic. In forests of the low zone *Cinnamomum* grew. The warm basin favoured the existence of thermophylic ferns. Climate was rather warm and humid. Many large leaves indicate humidity (Il'inskaya 1960). In south Poland, in the Carpathians Foreland a lower Badenian flora from Swoszowice, Wieliczka and Gdów Bay with a considerable amount of thermophylous elements (e.g. *Mastixia, Eurya, Laurus* and others) represents the last phase of the so called mastixioidean flora (Łańcucka-Środoniowa, 1963, 1966). A distinctive flora existed in the mountain and in the outer zone where the role of *Picea* in coniferous forests and *Ulmus* in broad leaved forests increased. Thermophylous species decreased in number, *Sapotaceae*, *Myrica*, and *Rutaceae* disappeared completely. Climate was cooler in comparison with that of the inner zone and the Carpathian Foreland.

Late Badenian. In Eastern Carpathians after the regressive cycle in the Tereblinsk stage there was a new wide transgression and periodic volcanic activity (Maleev 1964). Water temperature of the sea was rather high as is proved by *Borelis* remains (Venglinsky 1975). In coastal forests thermophylous ferns were still numerous. There were subtropical forests with *Cinnamomum polymorphum* and various *Myrica*. In mixed forests with *Juglans, Engelhardia, Tilia, Acer, Castanea, Fagus, Quercus* and *Platycarya* (the latter not numerous) the genera *Zelkova* and *Ulmus* were of importance.

The role of dark coniferous species increased, *Tsuga* became not so numerous, *Keteleeria* appeared. In the middle mountain zone beech-oak and oak-chestnut forests expanded. Members of the *Juglandaceae* family including its thermophylous forms – *Engelhartia* and *Platycarya* – remained. The shrub layer became richer (*Lonicera, Diervilla, Elaeagnus, Corylus, Cornaceae).* Subtropical assemblages with *Cinnnamomum, Myrtaceae*, leather-leaved *Quercus* and thermophylous ferns slightly diminished. Humid coastal and valley forests with *Carya, Pterocarya, Liquidambar,* and *Alangium* play an important role. In the south-eastern part of the Transcarpathian swamp forests with *Taxodium* expanded. An increased number of herb pollen occurred in the complex among which were members of mountain-meadow communities indicating the presence of open areas on high altitude of the raised mountains.

Gradual falling of temperature and decreasing of humidity continued causing only the diminishing of the leaf size, but changes of the total flora composition. In subtropical communities of the north-eastern part of the Ukrainian Carpathians there were plenty of evergreen elements: *Quercus drymeja, Ficus* (Mchedlishvili 1956) *Myrtaceae, Sapotaceae, Palmae* (Shchekina, 1957), *Cinnamomum* and other *Lauraceae* (Shvareva 1983). *Fagus, Quercus, Carya, Ulmus, Liquidambar, Pterocarya, Platanus* and *Rhododendron* formed a large part of forest composition. In the foothills large areas were occupied by river valley swamp forests with *Taxodium* and abundant *Alnus.* Valley forests were characteristic for the outer zone of the Ukrainian Carpathians in that period (Shvareva 1983). Various *Myricaceae* grew in drying peat-bogs which, in the late Badenian, were the initial material for brown coal beds formed here. The climate was warm and equable soft. Smaller leaves of plants indicate same water deficite during the growing season.

In the Western Carpathians during the late Badenian transgression the Paratethys covered the Nowy Sącz and Nowy Targ-Orawa Basins to the Morava-Gate (Fig. 4). The later Badenian flora indicates cooler conditions with the predominance of gymnosperms over angiosperms and a successive decline of more thermophylous elements (Oszast & Stuchlik 1977). The late Badenian flora in the vicinity of Tarnobrzeg at the northern margin of the Paratethys (Oszast 1967) indicates somewhat warmer conditions. This flora is somewhat similar to the lower Badenian floras of the Carpathian Foreland (Swoszowice, Wieliczka, Gdów) but a high proportion of shrubs in the vegetation cover is remarkable.

In the middle Miocene regression and isolation of sea basins took place in the Precarpathians and Transcarpathians areas, which led to changes in floral composition of these regions in the late Miocene. The flora of the outer zone was more influenced by the sea and as a result was impoverished in thermophylous elements at the end of early Sarmatian.

Our palynological studies have proved the continuity of the late Badenian flora into the Sarmatian. In south Poland the flora and vegetation of the early Sarmatian retains the main features of the late Badenian floras (Oszast 1973, Oszast & Stuchlik 1977). Il'inskaya (1960) admits that the late Badenian flora is closer to the early Sarmatian flora than to early Badenian one according to systematic composition and general features.

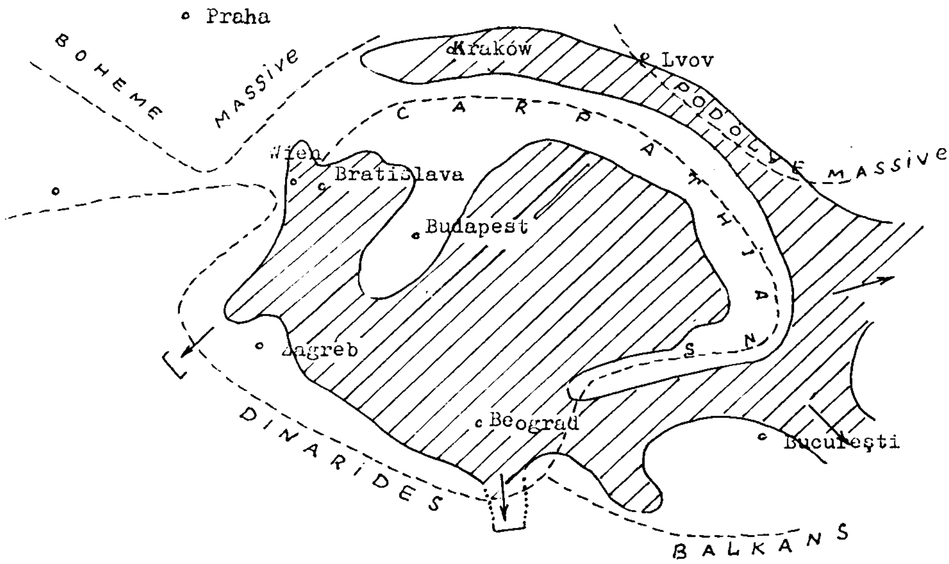

Fig. 4. Palaeogeographic scheme of the Central Paratethys in the Badenian-Sarmatian s. str. (Seneš & Marinescu 1974)

THE LATE MIOCENE

Early Sarmatian. The Sarmatian was characterized by an intensive regime of oscillatory movement, sea transgression in the south-western part of the Transcarpathians, final sea transgression in Western Carpathians and by a second phase of volcanism.

In the Carpathians coniferous forests with spruce and spruce-fir assemblages and various *Tsuga* were developed. *Tsuga* cf. *canadensis* might have grown also in coniferous – broad-leaved forests. However by the end of early Sarmatian, the role of coniferous forests decreased.

An abundance of pollen and leaf remains of beech shows that broad-leaved formations including beech forests in addition to oak-beech and beech-chestnut assemblages expanded. In this time *Fagus orientalis* appeared. Deciduous forests with *Juglans, Carya, Zelkova, Ulmus, Carpinus, Tilia, Acer, Liquidambar, Platanus, Alnus, Populus* and *Pterocarya* were well represented. The early Sarmatian was the last stage when *Lauraceae* existed in the Ukrainian Carpathian and northern Paratethys areas of Poland. Subtropical communities were concentrated in the lower zone and up to the end of the early Sarmatian their number slightly decreased. *Taxodium* and *Nyssa* were growing in swamp areas with *Myrica* on periferal areas.

In south Poland the Sarmatian vegetation belongs to three different geobotanical provinces (Stuchlik 1980). The vegetation of the mountain province represented by the flora of Nowy Targ – Orawa Basin is more or less uniform and characterized by predominant coniferous forests. In the flora of the vicinity of Chmielnik (Zastawniak 1980), on the northern margin of the Paratethys belonging to the north-European lowland province, angiosperms with large proportion of small-leaved forms distinctly prevailed over gymnosperms. In the flora of Stare Gliwice (Szafer 1961, Oszast 1960), which belongs to the west-European province, the gymnosperms prevailed over the angiosperms and more thermophylous elements were recognized.

The early Sarmatian flora, like the late Badenian one, was characterized by small leaves (Il'inskaya 1960). New volcanic activity along with diminishing of sea basin had led to a slight temperature fall and probably also to a deficit of air moisture.

The middle Sarmatian. Reduction of the sea basin, which began in the early Sarmatian, continued in the beginning of middle Sarmatian.

At this time the sea definitely retreated from the territory of south Poland but sedimentation still took place in the Ukrainian Carpathian Foredeep where the formation of the Almash suite began.

Freshwater lagoons were formed and peat formation began. This initiated developing of *Taxodium* swamp forests characteristic for the whole Almash period. Among numerous *Myrica* more ancient forms disappeared toward the end of the Miocene. Hydrophytic communities expended in freshwater basins. Short-lived transgression of the warm sea and decrease in volcanic activity had led to an increase of temperature which allowed return of some subtropical communities with *Engelhardtia*, *Platycarya*, *Platanus*, *Magnoliaceae* (*Liriodendron*), *Sapotaceae* and various ferns e.g. *Gleicheniaceae*. Areas of deciduous forests, including beech forests, expanded. In coniferous forests *Pinus*, *Picea*, *Abies*, *Tsuga*, *Podocarpus*, and *Sciadopitys* predominated but the proportions were different from the early Sarmatian. The middle Sarmatian was characterized by a rich mycoflora, which is usual for coal-forming situations. Climate was subtropical, close to warm-temperate, humid. There is no evidence for the existence of a dry phase during the middle Sarmatian. Remains of algae such as *Tetraporina*, *Triporina*, *Ovoidites*, and diatoms (Syabryay & Vodopyan, 1976), among which are many freshwater species, don't suggest increase of salinity which would be expected during a dry period. In south Poland freshwater sedimentation was continuing and the development of the flora was similar to that in lower Sarmatian. Sarmatian plant associations in the Western Carpathians (Poland) contained warm-temperate species, few sclerophylous forms and mediterranean leather-leaved oaks (Zastawniak 1980). These give no support to suggestions of a long dry warm period during the Sarmatian in this region.

The early Pannonian. The regression of the Paratethys and formation of the isolated Pannonian basin marked the beginning of this period. Territories of swamp forests and peat-bogs decreased. Certain thermophilous species did not survive cold winters and disappeared, *Liquidambar* occurred rarely, *Carya* became dominant only in the coastal and valley forests. Littoral-aquatic assemblages of freshwater basins and open herbaceous communities spread widely. Broad-leaved forests were as wide spread as in the Sarmatian, but elements of the temperate deciduous flora became dominant, the quantity of coniferous species increased.

THE PLIOCENE

The early Pliocene. (the beginning of late Pannonian s.l. – Pontian). In this period a short-term transgression took place in the Ukrainian Eastern Carpathians. As the result of this, in lower Pliocene sediments, ostracodes similar to those from the Pontian layer in the Crimea-Caucasus area appeared (Sheremeta 1958). The second stage of orogenic volcanism with ashes explosions was ending. Vegetation sharply changed in the whole Carpathians. Pine-forests with other coniferous species have formed a separate zone. In these assemblages *Picea* cf. *excelsa* appeared for the first time and *Abies* and *Tsuga* became more diverse in species. Broad-leaved forests grew at lower altitude than in the late Miocene. Swamp forests existed only in local areas. Open space areas expanded, subtropical species disappeared altogether. Gradual temperature fall, which began in the early Pannonian, continued in the beginning of the late Pannonian. Temperature fall was probably the result of volcanic activity. A decrease of solar irradiance due to ashes and sufficient air humidity promotes the growth of shade and humid requiring coniferous forests, and herbaceous plant communities.

Middle – late Pliocene. Dacian – Levantinian. Towards the end of the Dacian the Pannonian basin disintegrated into lagoons and late disappeare completely. Only small lakes remained with reed-marsh during the late Dacian in the Transcarpathian area. In the territory of the Western Carpathians only freshwater sedimentation and lignite formation took place.

Formation of the Vygorlat-Gutin mountain ridge began in the beginning of the late Pliocene (early Levantinian). To the south-west of it shallow lacustrine-marsh basins were formed. Intensive peat-forming processes resulted in the formation of the lower coal-bearing level (V and VI coal-seams) and the lignite formation in the Western Carpathians. The composition of mountain forest communities indicate that temperature rose during the Dacian. Swamp and humid coastal forests with *Taxodium, Nyssa* cf. *aquatica, Osmunda,* various *Alnus* with single *Myrica* admixture expanded. In wet forests on the plain and coastal area *Betula* and *Alnus* are predominant together with *Carya, Liquidambar, Pterocarya, Platanus, Magnoliaceae* and single *Diospyros*. In coniferous mixed forests *Castanea* and *Platycarya* appeared and the role of *Quercus*, *Fagus*, *Engelhardtia*, *Tilia* and *Celtis* increased. During the Dacian the climate was rather humid and warmer than in Pontian. Palynological data give no evidence that the Levantinian flora was different from the Dacian one. On the whole, the generic composition of the flora characteristic for the period of accumulation of the lower Levantinian coal-bearing level did not change in comparison to the Dacian. Quantity and composition of high-altitude vegetation zones changed insignificantly. Swamp forests in which the role of *Nyssa* decreased, became more extensive. Areas of beech forests, with dominant *Fagus* cf. *sylvatica* expanded.

In the Polish Western Carpathians (Domański Wierch and Krościenko areas) coniferous forests dominated by *Picea* mixed with *Pinus* and Tertiary relict *Sciadopitys* were abundant. In broad-leaved forests cold-loving elements were dominant but the genus *Pterocarya* was represented quite well (Oszast 1973, Oszast & Stuchlik 1977, Szafer 1946, 1954).

The late Levantinian. (formation of upper coal-bearing level of the Ilnitskaya suite). This is the period of formation of the III, II and I coal layers. In the beginning of the late Levantinian the third stage of volcanic orogenesis took place. Mountain forests became poorer during the period of accumulation of the third coal layer. More thermophylous elements like *Celtis, Platanus, Hamamelis, Myrica* and *Castanea* disappeared. In coniferous forests the quantity of *Abies, Picea* and *Tsuga* slightly increased. Swamp forests expended luxuriantly probably due to the products of volcanic activity accumulated at the foot of stratovolcans. Such process is observed nowadays in areas of modern volcanic activity (Kamchatka, Indonesia).

At the time of formation of the first and the second coal seams plant communities became rich again, only swamp forests remained unchanged. In broad-leaved forests *Castanea*, *Platycarya*, *Engelhardtia* and *Celtis* appeared again, the latter grew on sunny slopes. *Betula* became numerous, areas of oak forests expanded. *Fagus* cf. *orientalis* disappeared and the beech forests were formed by *Fagus sylvatica*. In coniferous forests *Picea* and *Abies* were dominants. Towards the end of Pliocene the late Levantinian flora became poorer. Among the Quaternary elements *Picea, Abies, Pinus sylvestris, Betula, Corylus, Alnus, Carpinus Quercus, Fagus sylvatica, Salix, Ulmus, Tilia* were dominant (70–75%).

In the Polish Western Carpathians the youngest Pliocene flora from Mizerna (Mizerna I/II and Mizerna II stages) is very similar to the late Levantinian flora of the Eastern Carpathians.

OROGENIC VOLCANISM AND ITS INFLUENCE ON THE VEGETATION COVER

The Transcarpathians was an area of intensive acid explosive volcanism with enormous quantity of volcanic ashes. Four stages of volcanism took place there (Maleev 1964).

The first stage of volcanism in the Transcarpathians began at the end of the Eggenburgian and lasted till the Badenian. It had a catastrophic effect. The area of the Transcarpathians was 3500 km^2, the volume of pyroclastic material in the beginning of this stage was 1 050 km^3 (Maleev 1964). The whole volume of pyroclastic material in the first stage was 4 000–5 000 km^3. The ashes scatter no more than 300 km. Therefore air pollution was local and decline in solar radiation was local too. In the Transcarpathians, at the end of the Karpatian – beginning of the Badenian the flora was less warm-temperate than in the contiguous territories where, at that time, the young mastixioidean flora occurred and volcanism was not so intensive. The thickness of ashes-tuff seams was far less in these territories than in the Transcarpathians.

The second stage of volcanism in the late Badenian–early Sarmatian was not intensive and considerable temperature fall was not appeared in the Transcarpathians. The absence of volcanism, as well as a short-term transgression in the middle Sarmatian, stimulated a warm period at that time. Explosive volcanism of the second stage, at the end of early Pannonian, preceded the temperature fall and changing of flora and vegetation in the Pontian.

The third stage in the early Levantinian caused the impoverishment of the flora at the time of accumulation of the third coal seam and coaly-clays over the coal seam.

In the fourth stage 11 stratovolcanos, six small monogenic volcanoes, 127 extrusives and other centres of volcanism (Maleev 1964) were active and their action strengthened the Pretiglian temperature fall in Transcarpathians.

In the beginning of the Neogene we have recorded a vertical zonation observed for the whole period. Composition and high-altitude boundaries changed depending on tectonic and climatic changes, location of sea basin and intensity of volcanism. Lava flows and volcanic gases were responsible for vegetation destruction in local areas.

During the Neogene there was a gradual change in the vegetation composition of high-altitude zones. Quaternary freezing deepened differences between the modern and Neogene composition of the flora and vegetation. Nevertheless the vertical differentiation which appeared in the Neogene, remains in the vegetation of the whole Carpathians even nowadays.

COMPARISON OF THE CARPATHIAN NEOGENE FLORA WITH OTHER CENTRAL PARATETHYS REGIONS AND ADJACENT TERRITORIES

Flora formation in the Central Paratethys region is connected with the history of development and elevation of the Carpathians at different times, their division into many parts by the seas of the Paratethys basin and the volcanic activity. This caused a certain difference in floristic composition of these areas.

The Egerian. At the Oligocene Miocene boundary in the eastern part of the Western Carpathians woody flora and vegetation was widely spread. The role of warm-temparate deciduous elements was more prominent in comparison to the Oligocene. In newly formed mountains of middle and northern Slovakia (Snopková 1961, Pacltová 1963 b, Planderová 1978), Northern Hungary (Nagy 1979, Hably 1982) as well as in Ukraine, the percentage of warm-temperate elements, particularly *Amentiferae* families, was rather high. Conifers were characteristic for floristic complexes of these regions (*Pinus, Picea, Abies, Podocarpus*), *Taxodium* was not numerous. Subtropical representatives were important in this period.

Subtropical forests with abundant *Lauraceae*, *Palmae* and *Dryophyllum* were characteristic of the Roumanian part of the Carpathian depression. This flora also included deciduous elements (*Ulmus, Juglans, Carya, Salix, Carpinus*), but they were not as pronounced as in the northern regions. There were swamp assemblages with *Taxodium, Nyssa, Spirematospermum* and *Myrica* (Givulescu 1974, 1980). R. Givulescu (1980) considers that the climate of the Egerian resembles the modern climate in south-eastern Asia characterized by regular precipitation especially in summer.

The flora of southern Slovakia was formed under the influence of the Alpine flora and it included numerous warm-temperate deciduous genera (*Acer, Alnus, Juglans, Carya, Quercus* etc.), evergreen subtropical plants (*Daphnogene*, other members of *Lauraceae*, *Pittosporum, Cassia, Eugenia, Ficus*) were more numerous (Nemejc 1970, Sitar

1980). South Hungarian floras included many tropical and subtropical plants along with less numerous deciduous ones. The presence of *Ginkgo, Keteleeria, Sciadopitys, Platycarya, Engelhardtia* and *Zelkova* indicates connections with Eastern Asia (Nagy 1970).

In the Egerian the flora of the South Carpathians developed under the influence of the Balkan and Dynarid mountain floras, which were characterized by a great number of species, and dominated by tropical and subtropical plants. The south Carpathians were isolated from other Carpathian regions by the Paratethys sea (Seneš & Marinescu 1974) (Fig. 1). The presence of plants with narrow leathery leaves, and presence of *Lauraceae* and *Papilionaceae* in the flora, indicate hot climate in the early Miocene in South-east Europe (Weyland et al. 1958, Mihailovič 1978). In this region B. Milakovič (1961) observed a few warm-temperate elements of broad leaved forests characteristic of the northern hemisphere which grew in mountains on higher altitudes.

The existence of various (depending on altitude) vegetational communities in various altitudinal belts (coniferous forests in mountains and subtropical broad-leaved forests in lower zones), were characteristic for the whole Carpathian region which was still separate. The deciduous plants were prominent at higher altitudes and they formed deciduous forest communities. Both south and north of the Paratethys basin there were swamp-communities with *Taxodium, Nyssa, Myricaceae*, on the north sea coast they were more widespread. In coastal forests thermophylous ferns were numerous. Seasonal periodicity and geographic differentiation took place especially toward the end of the Egerian. Climate of the whole region may be characterized as subtropical with heavy summer rains, warmer in south and south western parts of the region.

The Eggenburgian. The temperature rise and increased humidity noted in the Ukrainian Carpathians were recorded for the whole Carpathian region but in different degrees.

In the middle of the region including the Ukrainian Carpathians the number of thermophylous elements increased (subtropical ferns). The number of deciduous elements decreased insignificantly, the role of some moisture-requiring plants (*Alnus, Pterocarya, Carya)* rather increased (Planderová & Snopková 1970). In middle Slovakia the deciduous elements changed with new forms *(Salix, Populus, Acer, Carpinus, Juglans)* (Sitar 1980).

In the south-western part subtropical and tropical elements became more numerous and toward the end of the Eggenburgian the number of thermophylous elements decreased considerably (Gabrielová 1973, Klaus 1955). Coniferous forests were characterized by composition diversity. Areas of swamp forests expanded and mesophytic forests grew in drier areas. Subtropical macrothermal elements (*Lauraceae, Palmae, Sabal*-type) were not numerous. The presence of Sabal was typical for floras of the Eggenburgian in Middle Europe (Klaus 1955, Thenius 1961, Bůžek 1977). According to Scimoncsics (1967 a, b) the temperature in January in this period was +11° and in July +25, annual precipitations was 1200 mm, distributed uniformly.

A characteristic feature of vegetation in the Eggenburgian was widespread plane-tree forests (Andreánszky 1952), that grew at an altitude of 1000–1400 m. This is documented by numerous remains of *Platanus platanifolia* (Rutt.) Knobl. The general temperature rise and increased humidity manifested themselves in the Karpatian more from the middle of the Eggenburgian.

The Ottnangian-Karpatian. The process of increasing temperature and humidity began in the Eggenburgian and during the Ottnangian and Karpatian was more pronounced in the south-western part where mastixioid flora flourished (Hably 1979). It was a period of extensive development of marsh vegetation promoted by warm climate and heavy precipitation. (Kedves 1959), Simoncsics 1969, 1970), there were many reed marshes and swamp forests with *Taxodium, Nyssa, Osmunda, Clethraceae,* with *Lygodium, Glyptostrobus* and *Myrica* in drier areas. Paludal forests of such type were characteristic of the Carpathian area in Poland (Łańcucka-Środoniowa1979), western Poland (Raniecka-Bobrowska 1974), Czech and Slovak Republics (Planderová 1962, 1967, 1973, 1978, Konzalová & Stuchlik 1983) and Austria (Knobloch 1977). Under conditions of humid subtropical climate, lacking a dry season, forest assemblages grew with numerous varied *Lauraceae* resembling laurel forests of south-eastern China. The presence of *Platanus neptunii* (Ett.) Bůžek et al. (1967) known from the middle Oligocene (its analogoue exists now only in Laos) is notable within the flora.

In the Western Carpathians in Poland, deciduous and mixed forests with numerous thermophylous species grew in elevated areas, along with marsh associations. Mastixioid flora was almost absent (Łańcucka-Środoniowa 1979).

The Badenian. During the Karpatian and early Badenian the mountain area of the Carpathian region expanded, the majority of the South Carpathians were elevated (Fig. 2), but were still separated from the Eastern Carpathians. Towards the beginning of the early Badenian the thermal regime changed. It became cooler. A number of deciduous elements increased again. Floral composition of the inner zone was quite different from that of the outer one in both the Eastern Carpathians and the eastern part of the Western Carpathians. In the outer zone, in between-mountain hollows and north to the plain, swamp *Taxodium* forests were wide spread (Oszczypko & Stuchlik 1972). Alder forests and assemblages with *Carya* and *Pterocarya* were typical for this region. Aquatic-marsh grass assemblages were wide spread in the Ukrainian Carpathian Foredeep. Mountain slopes were covered by oak-lime forests, spruce and pines grew higher. Thermophylous elements are not as numerous as in the flora of the inner part of Carpathians (Łańcucka-Środoniowa 1979). Climate of the outer zone was cooler than the inner part, in which there were elements occurring nowadays from the Mediterranean area to South China (*Engelhardtia, Zelkova,* etc.).

In the south-western part of the Carpathians the role of thermophylous species (Knobloch 1969, 1972, Nemejc 1967) rose and broadleaved forests were more subtropical and resembled forests in China, Laos, Vietnam. E. Knobloch has referred to this flora as deciduous with a sufficient amount of laurels (Knobloch & Kvaček 1976).

In the central region, in the territory of the Middle Slovakia *Populus balsamoides, Juglans, Carya, Pterocarya, Engelhardtia* etc. (Sitar 1980) were most common. Light-coniferous forests with rare dark-coniferous elements became wide spread. Areas of swamp forests diminished (Gabrielová & Planderová 1967). In the south, in Hungary, where vegetation communities had been thermophilic in character, deciduous elements became more numerous. Mastixioid flora had already disappeared from there (Nagy 1970). In the early Badenian *Carpinus* and *Pterocarya* occurred for the first time in this region.

In the early Badenian the South Carpathians and Balkans belonged to one and the same region being separated by Paratethys seas from the rest of the Carpathians. In the South Carpathians, like in Bulgaria (Palamarev 1971), humid subtropical forests with abundant thermophylous elements, (namely various *Lauraceae*) grew. In the mountain flora there were also deciduous species along with thermophylous ones (Givulescu & Ticleanu 1977). Regional differentiation was becoming stronger and the north south gradient of increasing macrothermal forms is very clear.

Towards the end of the Badenian the whole Carpathians were united (Seneš & Marinescu 1974) (Fig. 3) and separated from the Balkans by the Paratethys, the water of which reached the Carpathians on the north, east and south. From this time the Carpathians existed as united mountains but the floristic differentiation, founded in the beginning of the Neogene, persisted during the whole Neogene. In basins of the outer zone of the Western Carpathians in Poland (Nowy Targ-Orawa basin), as in Ukrainian Carpathians, areas of swamp-forest vegetation diminished, but areas with alder forests increased. *Picea, Abies* and *Tsuga* made up a considerable part of mountain forests, broad-leaved deciduous species, especially *Amentiferae*, with warm-requiring forms, were wide spread (Oszast 1960, Oszast & Stuchlik 1977). At this time *Fagus* aff. *orientalis* appeared in this region (Łańcucka-Środoniowa 1966).

In forests of the inner part of the Western Carpathians, as well as of the Ukrainian Carpathians (middle region), the role of *Fagaceae*, particularly of *Fagus* and *Quercus*, increased (Planderová 1978, Snopková 1961, Brezinová & Gabrielová 1974).

The appearance in Badenian palynocomplexes, of numerous herbaceous pollen among which were alpine forms, indicates that an open mountain landscape began to be formed in this part of Carpathians as in the Ukrainian Carpathians.

More thermophylous assemblages existed in the south-western region in which *Lauraceae* family were still numerous (Nemejc 1967, Knobloch1972, 1981). Towards the end of Badenian their number sharply decreased.

Thermophylous species were still abundant in the Hungarian Badenian flora (Nagy 1962, 1974, Knobloch 1972) along with an increase of deciduous and coniferous elements. To the south, nearer the Hungarian lowland, plant assemblages were more xerophylous in character.

During the Badenian rich subtropical thermophylic flora with numerous and varied *Lauraceae* and other thermophylous forms with deciduous elements, was typical for the South Carpathians. Among gymnosperms there were *Araucarites taxiformis* (Sternb.) Knobloch (Givulescu & Ticleanu 1977), and various *Pinaceae* including coniferous species. All the vegetation composition indicates on the existence of vertical zonation in the South Carpathians.

The Badenian flora included many North American and east Asian elements. A gradual development of this flora, with clear tendency to increasing of deciduous summer elements, was typical for the Badenian.

The Sarmatian. In all regions of the Carpathians continuity of the early Sarmatian flora from the late Badenian one was noted. According to recent data on absolute age of flora-bearing rocks the floras of Ipoly river valley (Besterce and Paris-flow) previously dated to the Sarmatian (Andreánszky 1959) are proved to be Badenian even to its different stages (Kordos-Szakaly 1984). This emphasizes once again a continuity of development of Badenian – Sarmatian floras.

In Slovakia, and south Poland, the flora and vegetation ofthe early Sarmatian has the main features of the late Badenian ones (Oszast 1973, Oszast & Stuchlik 1977, Sitar 1973, Planderová 1967). coniferous forests with numerous genera, namely *Picea* (Sitar 1973) in the upper forest zone, were typical for the whole area of the middle region, but the lower zone has some distinguish features. There were more subtropical elements. The presence of *Cinnamomophyllum* and leather-leaved *Quercus* similar to that growing in the Caucasus and Asian mountains indicates similarity of the Sarmatian flora from south and south-western Slovakia to the synchronous floras of Hungary (Hajos & Palfalvy 1962, Simoncsics 1963, Nagy 1974, Andreánszky & Kovacs 1955, Andreánszky 1959).

According to Andreánszky (1959) the presence of *Alangium hungaricum* in the Hungarian floras (Erdöbenye and Gylyodéllö near Dédestapolcsánu) and South Slovakia floras (Cabov and Usbi) makes these comparable and indicates their unusual common features. At the same time Andreánszky (1959) described many lather-leaved *Quercus* and other mediterranean elements – *Hakkea, Myrsine, Podogonium* etc. – in the Erdöbenye flora of the late Sarmatian. There were also temperate deciduous forms. According to Andreánszky the presence of plants with *Leguminosae*-type leaves indicate the existence of mediterranean dry forest. He considered that this is indicated the existence of "savanna" biotope along with vast flood plains forests (*Platanus, Zelkova, Liquidambar, Populus, Carya* etc.). Palfalvy described dry forests of mediterranean type with biotopes of coastal and flood plain forests, leather-leaved bushy forests including communities of savanna type probably influenced by Andreánszky's hypothesis (Hajos & Palfalvy 1962).

According to our data on the Ukrainian Carpathians (Syabryay 1978) there was no dry warm period during the Sarmatian.

Mesophytic woody deciduous vegetation of the Sarmatian including swamp-forest communities and *Lauraceae*, was described by Nagy. She noted that the number of *Fagus* and *Quercus* increased (Nagy & Bodor 1982). Mixed forests, with East Asian and North-American elements, were typical for the late Sarmatian (s. str.), which we compare with the Almash time in Transcarpathians.

Thermophylic and hydrophylic elements (*Ficus tiliaefolia, Sassafras, Myrsinaceae, Cercidiphyllum)* were present within various vegetation assemblages. Gregor (1979) analysed ecological characteristics of groups described by Andreánszky (1959) and came to the conclusion that there was no dry biotope but nearly vegetation communities like those of warm-temperate, deciduous, broad-leaved forest of China which grow in dominantly humid climate zones. Simoncsics (1963) described deciduous broad-leaved forests, vast marsh forests, and peatbogs transformed later into coal (Damack, Hungary).

There is also no evidence for the existence of a dry period in the Roumanian part of the Carpathians during Sarmatian. Plant communities were unchanged in comparison to the Badenian ones. This composition remained unchanged up to the middle Sarmatian (Givulescu & Ticleanu 1977, Ticleanu & Givulescu 1981). Various members of *Lauraceae* and other thermophylic species (*Sapotaceae*, *Sapindaceae*, *Myrsinaceae*) and mediterranean *Quercus* flourished along with deciduous elements. Givulescu (1980) described the Sarmatian vegetation as mixed mesophytic forest with admixture of xerophytes. He emphasised topographic control on climate and considered any apparent arid zones to be due to topographic setting.

Summing up we conclude that, in the Carpathians, there was no period of increased dryness with high temperatures in the middle Sarmatian such as that described by Andreánszky. *Pinaceae, Salicaeae, Betulaceae, Fagaceae* and *Aceraceae*, members of which are important in modern Carpathian forests, were already the main part of the Sarmatian flora.

The Pannonian. For comparison and correlation with Pannonian floras of the whole Carpathian region we made an attempt to associate the known floras with Papp's zones (1951) and with the developmental stages of the Pannonian flora in the Ukrainian Carpathians. As a result of disintegration of the Paratethys the isolated Pannonian basin was formed. It played a considerable part in development of flora and vegetation in the inner zone of the Carpathians. This is reflected in the systematic composition and extent of various plant communities.

In the inner zone of the Western Carpathians as well as in the Ukrainian Carpathians coniferous – broad-leaved and broad-leaved forest with numerous Amentiferae – mainly members of *Juglandaceae* family (*Carya, Juglans*) – dominated in the early Pannonian s.l. or in the end of late Miocene. Plain forests and flood plain-riverine forests without thermophylic elements, but with plenty of the Miocene forms were well developed (Planderová Snopková 1960, Planderová 1962, Nemejc 1967). Areas of swamp forests began to decrease. *Taxodium* and attendant species formed small swamp-woody assemblages (Planderová 1962 & Snopková 1961) like in the early Pannonian of the Ukrainian Carpathians.

At the end of the late Miocene, coniferous (pine-spruce) forests were well developed in the outer zone of the Western Carpathians. In the broad-leaved forests *Amentiferae* species dominated. *Castanea* were numerous. Abundance of remains of *Magnolia* and *Liriodendron* leaves and *Magnolia* pollen indicate that these genera were spread in the lower woody zone. In warm freshwaters, in hollows, associations of aquatic *Brasenia, Euryale, Trapa* and *Nuphar* occurred. Plain riverine forests with numerous *Alnus, Carya, Pterocarya, Liquidambar* and *Salix* were typical for this region (Oszast 1973, Oszast & Stuchlik 1977).

In coniferous – broad-leaved forests of south-western extensions of the Western Carpathians thermophylous elements were numerous as in earlier periods (Knobloch 1963, 1967, 1972, 1980).

The age of the rich Pannonian floras found in many places in Roumania (Givulescu 1963, Givulescu at al. 1984) varies from the Pannonian to the problematic Pontian. Givulescu (1962, 1974) described only a relative temporal sequence of these floras using proportions of North American, East-Asian and European elements.

The Pannonian flora of this part of the Carpathians was very exotic. At the beginning of the Pannonian humid woody assemblages with *Glyptostrobus* and *Myrica* surrounded numerous lakes. On mountain spurs broad-leaved forests grew with rich shrub layers including subtropical *Quercus* and *Lauraceae* (*Persea, Laurus* etc.). Broad-leaved and coniferous-broad-leaved forests included *Ulmus, Fagus, Carpinus, Castanea, Pterocarya, Juglans* etc. and various *Pinus* (Givulescu 1962). Mountain coniferous forests included *Abies, Libocedrus* and *Pseudotsuga* (Ticleanu 1970).

The early Pannonian (late Miocene) flora of the Transcarpathians, as well the flora of eastern part of the Western Carpathians, indicates the tendency for climate to be more temperate. Under these conditions almost all the more ancient Miocene forms disappeared.

In south-western parts of the Carpathians occurred Miocene forms more often, while in the south part of the eastern Carpathians (Roumania) the floras retained Miocene elements.

Impoverishment of plant communities of the Western Carpathians in Slovakia, due to decreasing macrothermal elements, spreading of coniferous forests, and decrease of broad-leaved forests, was typical for the next stage of the Pannonian (Planderová 1962, 1967, Pacltová 1961, Sitar 1958). This stage corresponds to the period of accumulation of the lower part of the Koshelevskaya suite in the Transcarpathian (Pontian, zone E. of Papp, 1951). Swamp forests were not typical for this time. It is a period of coniferous forests spreading in the south-western part (Morawia). In lower altitude zones areas of broad-leaved forests remained unchanged and humid forests with *Glyptostrobus, Nyssa* and *Salix* and coastal associations with *Stratiotes tuberculata* and *Spirematospermum wetzleri* were wide spread (Sitar 1958, Bůžek 1962).

In Hungary broad-leaved and coniferous – broad- leaved forests surrounded freshwater basins with rich algal flora. Higher mountain areas were covered by coniferous forests with dominance of *Picea* and *Abies* (Nagy 1958).

In the Western Carpathians of Poland (outer zone) coniferous forests flourished, dominated by *Picea*, with *Abies* and *Tsuga* along with *Sciadopitys*. Evident impoverishment of broad-leaved forests with dominance by Quaternary elements took place (Oszast 1973). Among the latter *Alnus* was dominant (Oszast & Stuchlik 1977). Rather numerous *Pterocarya* and rarer *Carya, Liquidambar* and *Salix* with alder, grew in river valleys. Herbaceous cover was formed mainly by ferns *Polypodiaceae.* Swamp-woody communities were not typical for this region.

The Pontian. The Pontian plant assemblages of the Eastern Carpathians and the South Carpathian in Roumania differed considerably. In the Eastern Carpathian region – Tara Oasului, Satu Mare, Sinersig, Visag (Ticleanu et al. 1975), which is a continuation of the Ukrainian Carpathians, coniferous forests were wide spread. Broad-leaved forests of mountain slopes were composed of warm-temperate species (*Carpinus, Fagus, Ulmus, Acer, Corylus, Juglans, Zelkova* etc.). *Lauraceae* were absent, swamp woody assemblages were rare.

In depressions of the South Carpathians swamp-forests with numerous *Taxodium* grew, in the drier areas – *Glyptostrobus* and *Myrica* developed. In valley forests *Carya* dominated with numerous *Alnus, Cyclocarya cyclocarpa* and *Eucommia ulmoides*, *Byttneriophyllum aqualifolium* (Goep) Giv. appeared. In the lower mountain zone certain members of *Lauraceae* occurred. Woody vegetation distributed according to altitudes was typical for this stage too. Coniferous elements were not important.

On the whole for the Carpathians warm-temperate and humid climate was typical at this stage. It is likely that in south parts of this region summer temperature was higher.

The Dacian – Levantinian. The rising in temperature in the Dacian in the Transcarpathians caused the existence of richer and more varied flora and vegetation in comparison to the Pontian. Temperature rose throughout the inner zone of the Carpathians but to varying extents. The late Pannonian flora and vegetation in Hungary was the most rich and varied. Decreasing size and reduced salinity resulted in only isolated large freshwater lakes remaining in the Pannonian basin. Abundant hydrophytic plant communities were surrounded by swamp forests in which *Taxodium* was replaced by *Alnus* and large peatbog areas. *Carya, Pterocarya, Liquidambar,* numerous *Alnus, Salix, Betula* and others grew in humid coastal forests. Broad-leaved forests (*Quercus, Fagus orientalis, Castanea, Ostrya, Carpinus, Engelhardtia, Tilia, Juglans, Fraxinus, and Ulmus)* grew in the lower mountain zone (Nagy 1958, 1959, 1974). Temperature rose considerably so that *Cinnamomophyllum, Quercus drymeja* Ung. and *Ficus tiliaefolia* appeared again among bush vegetation (Hajos & Palfalvi 1962, Andreánszky & Kovacs 1955). *Ginkgo, Abies, Sciadopitys* and *Cryptomeria* grew in montane broad-leaved- coniferous assemblages at higher altitude.

Single forms of *Laurus* and *Cinnamomum* occurred in the late Pontian woody communities and in the south-western part of the Carpathians (Knobloch 1963) as in Hungary where North-American and East-Asian elements were numerous. *Glyptostrobus, Nyssa disseminata, Alnus,* grew there, and *Byttneriophyllum aequalifolium* is on obligatory element of Pliocene floristic complexes in the southern part of this region. This thermophylic plant of the marsh biotope (Givulescu 1970, Knobloch & Kvaček 1965) is a Miocene relict which disappeared in the Pleistocene.

In the northern area of the inner zone of the Carpathians (Slovakia) as well as in the Ukrainian Carpathians there were woody swamp communities with *Taxodium, Nyssa,* broad-leaved forests with abundant *Quercus, Fagus, Carpinus, Betula, Alnus, Salix* more numerous *Castanea* and *Rhus*. Such thermophylous elements as *Sapotaceae, Symplocaceae* and *Lygodium* were absent. In montane coniferous forests *Picea* and *Abies* dominated (Snopková 1961, Planderová 1978).

The late Pannonian flora and vegetation in Satu-Mare area (Givulescu & Edelstein 1981) was almost identical to that in the Ukrainian Carpathians. *Carpinus* species (*C. grandis, C. pyramidalis, C.* aff. *betulus*), *Acer* aff. *campestre* and numerous *Fagus* including *F.* cf. *orientalis* were characteristic for the Roumanian Eastern Carpathians in the zone of temperate forests, where European elements were dominant.

The similarity of floristic complexes existing at the end of middle Pliocene and at the beginning of the late Pliocene in the Ukrainian Carpathians as well as in the Western

Carpathians (Poland, Slovakia) (Snopková 1961, Pacltová 1963, Planderová 1978, Stuchlik 1982) does not enable separation of the Dacian and Levantinian floras.

Southward of the Eastern Carpathians synchronous floras differ slightly from those of northern areas especially in the lower mountain zone, for example Borsek (Pop 1936). In this area mixed forests with dominant North-American elements (*Pinus* cf. *taeda* and probable *P.* cf. *nigra,* various *Juglandaceae, Hamamelidaceae, Acer trilobatum, Zelkova,* certain *Castanea* and *Quercus*) grew around the large Pliocene lake. Bushes of south European xerotic type covered sunny slopes. Miocene relicts – single *Cinnamomum, Leguminosae* of subtropical-tropical type and probable *Sterculia* grew in ecological settings outside their usual requirements. In coniferous forests *Tsuga* and *Keteleeria* occurred, *Picea, Larix* and *Taxus* grew at higher altitude. The presence in the Borsek flora of about 5% of endemic Balkan species and 37% of mediterranean elements the main part of which grow nowaday in the Balkans is characteristic. This is evidence of ancient connections between the floras of the South Carpathians and the Balkans. Prior to the Badenian these mountain massives were one and the same land which was separated by the Paratethys sea from the northern part of the Carpathians (Seneš & Marinescu 1974) (Fig. 1–3).

The flora of the inner zone of the Eastern Carpathians, namely in hollows, included more Miocene relicts and the process of replacement of both North-American and East-Asian elements by modern European ones was more gradual in the inner zone by comparison with the flora of the outer part (Pop 1936). Such conservative character of the flora may be explained by the presence of a warm lacustrine-marsh basin which prevented continentalization of climate. Warm-temperate and humid climate with high precipitation was typical of the whole inner zone of the Carpathians. According to Köppen the climate may be classified as Cfa type with average annual temperature of 17–19° and precipitation of 1000–1400 mm (Ticleanu et al 1981). The climate of the whole Carpathian region may be considered as of this type with the exception of a slight temperature drop in northern areas of this mountain country.

The late Levantinian. Flora and vegetation of the Levantinian differed from that of the Dacian-Levantinian. The role of Quaternary elements increased (74–75%). However the presence of a warm lacustrine-marsh basin in the inner part of the Carpathian region, including the Ukrainian Carpathians, slowed down the process of continentalization of climate during this stage.

There were many Reuver elements and *Taxodium* was numerous in vegetational composition in this areas. These elements disappeared as a result of the Pretiglian temperature fall (Pacltová 1963). Leschik (1954) considered these floras to be more ancient but the facies controlled *Taxodium* is not indicative of age merely of an ecological contrast which existed in different time periods.

Dacian-Levantinian and Levantinian floras in the northern part of Roumania, in the Transcarpathians and east Slovakia are more prominant. At that time the Vigorlat-Gootin volcanic ridge formed. It isolated the above mentioned three areas as a separate territory with specific microclimate and vegetation. Low volcanic mountains were covered by broad-leaved forests. The ridge was like a bridge via which vegetational interchange took place. In this territory volcanic processes, namely ash throws, affected the processes of soil formation.

The same conditions of geological structure, soil and climate are the reason for the overall similarity and specificity of the Pliocene vegetation in the Volcanic Carpathians. Nowadays specific species composition and regularities of distribution of vegetation also occurs in this area with humid atlantic climate.

CONCLUSION

1. The main direction in evolution of woody flora and vegetation in the Carpathians was determined by a general regime of falling temperature. This mainly gradual process was complicated by tectonic and climatic conditions resulting from development of the mountain region. This was asynchronous and of varied intensity in different area of the mountain country. Rhythmic climatic fluctuations of different duration and intensity become evident with temperature fall. Periods of temperature fall – the Egerian, the late Badenian – early Sarmatian, the Pontian – gave way to periods of temperature rise: the Eggenburgian, the Ottnangian-Karpatian, the middle Sarmatian, the Dacian-Levantinian. Within these large scale rhythms microrhythms, were established. The local temperature fall in the middle Levantinian was one of this microrhythms.

2. Differences in floral composition between the north-eastern and south-western macroslopes of the Ukrainian Carpathians are more prominent since the Badenian with the loss of connections between the Transcarpathian and Precarpathian basins. Development of the Precarpathian flora was influenced to a considerable degree by the adjacent platform land. This resulted in a more temperate composition of the Precarpathian flora.

3. The compositions of the Neogene floras of the Western and Eastern Carpathians are very similar but at that time the South Carpathian Neogene flora included more exotic elements. This could be explained by the influence of the Balkan flora. The southern Carpathians were developed separately from the other part of Carpathians, but were more close to the Balkan Mountains. At least during the Badenian-Sarmatian stages the Southern part of Carpathians was separated from the Balkan but joined to other parts of Carpathians

Some differences in the Eastern and Western Carpathian flora existed in spite of their resemblances. The floras of the Polish and Ukrainian Precarpathians are very close and differ from the Transcarpathian flora, which is characterized by greater diversity and abundance of ferns, which was also found in Roumanian part of the Eastern Carpathians.

4. High-altitude differentiation of the vegetation in the Carpathians has existed since the early Miocene persisted throughout all the studied periods. The boundaries of high altitude zones changed periods during the Neogene under the influence of tectonic and climatic conditions, volcanism and changes in coast line. Towards the beginning of the Pleistocene the vegetation of the mountain country was richer and more diverse than the modern one. Nevertheless a high altitude zonation in the Polish and Ukrainian Carpa-

thians as well as in the whole Carpathian region, has existed since the Miocene and remains up to present days.

5. The Neogene flora and vegetation of the Carpathians were formed as a result of changes of climate – from subtropical to temperate – under the influence of primary dynamic factors (orogenesis, transgression, regression). This flora included azonal and intrazonal subtropical communities, the extent of which is difficult to define.

6. The Volcanic Carpathians (Vigorlat-Gootin ridge) stretched from Slovakia through Ukraine to the Gootin mountains (North Roumania) separated these areas and formed united territory which was characterized by common geological structure, soil and microclimate. These conditions are reflected in the common character of floristic complexes in Slovakia, the Transcarpathians and North Roumania.

7. Development of the Carpathian flora and vegetation in the Neogene and changing paleoclimate were influenced by the changing dimension and location of sea basins (the Paratethys and later – the Pannonian basin). Additional influences were lacustrine-marsh basins, mountain formation and volcanism. Four stages of orogenic explosive volcanism, which took place in the Transcarpathians, may be considered as local climate-forming factors.

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