THE UGOLSKY MASSIF – A REFUGE OF THERMOPHILIC FLORA IN THE UKRAINIAN CARPATHIANS

I. L. NAVROTSKAYA¹, S. V. SYABRYAJ¹, L. G. BEZUS'KO¹; L. STUCHLIK² and L. A. TASENKEVICH³

- N. G. Kholodny Institute of Botany, Academiy of Sciences of the Ukrainian S.S.R., Repin 2, 252601 Kiev GSP-1, USSR
- W. Szafer institute of Botany Polish Academy of Sciences, Lubicz 46, 31-512 Kraków, Poland
 The Lvov Department of the N. G. Kholodny Institute of Botany, Academy of Sciences of the Ukrainian S.S.R., Chaikovsky 17, 290000 Lvov, USSR

ABSTRACT. The existence of a refuge of nemoral thermophilic flora on the territory of the Ugolsky beech forest massif in the Ukrainian Carpathians is suggested on the basis of analysing and generalizing the results of floristic (both higher plants and lichenoflora), phytocenological and paleopalynological studies. The application of a complex approach was allowed to assume that this territory had played the role of a refuge as early as Miocene.

KEY WORDS: refugium, Neogene, flora, Ukrainian Carpathians

INTRODUCTION

Cyclic climatic changes in the Carpathians which can be traced back to the beginning of Neogene brought about cyclic changes in the flora and vegetation composition of this region. Low temperature periods lead to decreases of subtropical element content in the Neogene flora, whereas high temperature periods were marked by its increases. As a rule, there was no complete restoration of flora of the previous warm period, but a large part of subtropical floral elements which had vanished during cold times did return after the recurrence of warmth (Syabryaj 1986).

This phenomenon in the Carpathian region is evidently not linked to processes of migration from warmed areas. Conditions existing in the mountains are likely to provide for the preservation of more thermophilic elements during cold periods in certain refuges within the territory of this region.

The question of refuges has long been and still is a central one among pressing and complicated problems of botany (Lavrenko 1938, Kleopov 1941, Artyushenko & Romanowa, 1984 and others). Many researches noted the existence of thermophilic flora refuges in the Carpathians during glatiations (Firbas 1949, Bertsch 1953, Środoń 1959, Stoyko 1966 and others).

The successful resolution of the question of existence, time of origin and location of refuges depends on the availability of paleobotanical data, and the use of a complex approach to this question provides for optimum reliability of the conclusions.

This article is a generalization of results of floristic (both higher plants and lichenoflora), phytocenological and paleopalynological studies carried out on the territory of the Ugolsky massif of the Carpathian State Preserve which had been organized with the aim of preserving the natural complex of the Carpathian virgin beech forests. It is situated on the Southern macroslope in the Gorgan Mountains (Tyachiv district of the Transcarpathian region) and occupies an area of 4734 hectars.

GEOLOGIC AND GEOGRAPHIC SETTLING

The territory of the preserve massif lies on the Southern sprus of the Menchul Mountain (1487 m above sea level) in the basins of Mala and Velyka Ugolka rivers within the altitude range of 400–1350 m. The climatic conditions within the preserve are very favourable for beeches. The climate here is warm ad humid. The mean annual temperature reaches +7°C, The average temperature of July is +17°C, that of January is -4.5°C, the average annual precipitation is 948 mm.

The geological structure of the investigated region is as follows: molasse formations from Miocene rest upon Paleogene flysh: these are mainly Badenian deposits. They are represented by aleurites, clays, sandstones, argillites. Found inside lime clays are carbonized detritus, streaks and lenses of coal. The volume of Badenian deposits is cut through by several vast layers of tuff.

A specific feature of this region is the presence of large ancient limestone boulders on the soil surface, the area of some of the reaching 1.5 sq.km.

The soil cover of the preserve massif is represented by brown soils typical for the Transcarpathian forests, soils which were formed upon flysh and limestones. Most soils belong to groups of dark and light brown light podzol moutain forest soils.

The Ugolsky beech forests are the largest and best preserved unique massif of virgin forests of *Fagus sylvatica* L. for both the USSR and Central Europe. This region is the only place where virgin beech forests were preserved in such fine conditions. This is the result of climatic, soil and historical conditions which have prevailed there.

From the geobotanical point of view the investigated region is interesting since it has preserved representatives of relic Neogene dendroflora (Taxus baccata L., Juniperus sabina L., Holocene nidi of Quercus petraea Liebl.).

PALEOBOTANICAL INVESTIGATION

Badenian deposits in the Solotvyn kettle are exposed along beds of streams and brooks and are uncovered by boring wells N 4 by the village Uglya and N 997 (Grendesh stretch). We studied samples from cores of these wells and from exposures along

beds of streams Vulkhovchik and Soleny. The wells uncovered rocks starting with the Solotvyn suite and including Badenian tops (the Teresvyn and the Baskhiv suite). Along beds of streams there are exposures of the Teresvyn suite. Early Badenian deposits (Helvetian s.l., including "lower" Tortonian) are exposed along beds of brooks and streams Ukorny, Peryavytsa and by the village Tyachevo. Numerous stratigraphic works of recent times have introduced substancial changes to the dating scheme of Carpathian Miocene deposits. According to the scheme from 1962 (O. Vyalov, L. Pishanova, M. Petrashkevich, G. Grishkevich), the lower Tortonian strata continuously rest upon Burdigalian-Helvetian ones as a part of the Burkalov suite. According to present-day data the Burkalov suite dates back to Burdigalian (Eggenburgian, according to the regional zonation of Central Paratethys), while the low Tortonian belongs to Ottnangian-Carpathian and partly to lower Badenian (the Vodytska and Tereblyn suites, i.e. Helvetian s.l.).

Judging by the composition of the spore-pollen spectra, lands which surrounded the sea basin during early Badenian were covered by forests at different altitudes. As compared to early Miocene, the content of representatives of deciduous moderate flora (Juglans, Carpinus, Ulmus, Castanea, Pterocarya, Platanus, Carya, Zelkova) increased while the participation of thermophils, which still included representatives of Sapotaceae, Rutaceae, Myrtaceae, decreased. The genus Engelhardia was still rather important. It should be noted that Fagus appeared for the first time in the Badenian forests. Marsh associations are not characteristic of early Badenian. Isolated representatives of Taxodium and Nyssa occured in the excessive humidity zone; numerous Myricaceae grew on the warm sea coast.

The results of microremnant studies show that Lauraceae grew in forests by Velyka Ugolka river and the stream Burkalo, in particular Cinnamonum, characteristic of which is a localized remnants deposition. In this case the question is: when exactly did forests such composition exist?

So, the broad-leaved floras of Velyka Ugolka and Burkalo from the Khustsuite that we studiet are more ancient ones than those of Tortonian (according to Ilinskaya 1960). This is not contradicted by their systematic composition, the abudance of *Lauraceae*, their broad-leaved type. Most probably this is early Badenian flora (Helvetian s. l.) similar to the one that Knobloch (1972) described for Austria, characterizing it as a summer green flora with substancial participation of the *Lauraceae*.

The Tyachiv suite is assigned to the upper, not lower, Tortonian (Ilinskaya 1960) i.e. to upper Badenian, in the 1962 scheme as well. Naturally, the floral composition characteristic of these deposits is different. These deposits are separated by a thick layer of volcanic tuffs – a result of the first phase of orogenic volcanism which discharged vast ammounts of ash into the atmosphere. Such events, according to the opinion of Brooks (1952), may trigger off very powerful outbursts of cold, even the coming of glaciers. Truly, the mentioned phenomen brought about a very significant drop of temperature and, consequently, changes in the systematic composition of flora. The climate-shaping role of eruptive acid volcanism is discussed by Lebedev (1982).

The Lauraceae pollen that we found in palynocomplexes from rocks of the upper Badenian Tyachiv subsuite of the Teresvyn suite indicates the presence of Lauraceae

representatives in the vegetation (well 4y). At the some time no Lauraceae pollen was found in deposits of the some Tyachiv subsuite (exposures of rivers Solena and Vulkhoychik, well 997 at the Grendesh stretch in the Solotvyn kettle), as well as in the Upper Badenian deposits of the Chop-Mukachiv kettle - well 911. We analysed Upper Badenian deposit samples from the region Devinska Nova Ves in Slovakia and Polish Carpathians (Table 1). In the spectra from Slovakia, just like the drill core complex from well 4y, we detected pollen of Lauraceae representatives. Judging by the thickness of the tuffs in Slovakia (70-80 m versus 600 m in the Transcarpathian region), here the ash pollution of the atmosphere was much less severe and did not entail a fall of temperature. The Lauraceae are not characteristic of the late Badenian plant communities of Polish Western Carpathians, where light coniferous and broad-leaved forests with prevailance of arctotertiary elements were widespread at that time (Oszast & Stuchlik 1977). All these facts point to a special differentiation of floristic groups under the influence of the local climate-forming factor - orogenic volcanism. These facts provide a basis for the suggestion that during the cold period of the late Badenian a refuge of more thermophilic flora could exist in the Ugolsky massif.

Table 1. Spore and pollen deposits composition from the upper Badenian Tyachiv subsuite of the Teresvyn suite

Location Systematic composition	Well 4y, village Uglya	Vulcovchic, Solenyj	Well 911 Chop- Mukachiv kettle	Well 997, Grendesh stretch	Devinska Nova Ves (Checho- Slovakia)	Czarny Dunajec Koniówka
1.	2	3	4	5	6	7
Ginkgo		+		·		
Pinus	+++	+++	+++	+++	+++	+++
Picea	++	+	++	+	++	+
Tsuga	+	o	+	o	+	+
Abies	+	o	o	o	+	o
Cedrus	o					
Taxodiaceae	++	o	o	o	++	+
Sabalpollenites	o					
Palmae					o	
Salix		o	o	o		0
Myrica	++				+	o
Comptonia		o	o			
Juglans	+	++	+	++	+	.0
Engelhardia	++	o	o	+	++	+
Platycarya	+	o		o	+	+
Pterocarya	+	0	0	0		+++
Carya	++	+	o	+	++	+
Carpinus	o				o	o
Alnus	+	+	+	+	+	+
Betula	o	+	+	o		+

Table 1. Continued.

1	2	3	4	5	6	7
Fagus	+	+	0	+	+	+
Quercus	+	o	o	0	+	+
Castanea	++	+	o	0	++	0
Ulmus	++	+	+	+	+	+
Zelkova	+			0	o	
Magnoliaceae	0					
Liriodendron					o	
Lauraceae	o				o	
Liquidambar	+	o	o	0	o	0
Eucommia		o		o		
Rhus	+			0	+	
Cyrilla					o	o
Ilex	+					o
Celastraceae		o	o			
Aceraceae	o	o	o	o	o	0
Tilia			o	0	o	0
Myrtaceae	+				+	0
Sapotaceae	+				+	
Oleaceae	o	o		U		
Ericaceae	+	o	o	0		0
Nyssa		o		0		0
Tricolporopollonites cingluum spp.fusus	o				o	
T.cinglum	o	o	o	0	o	0
Lycopodium	0		0	o		0
Cyatheaceae	o	o	0	o	o	o
Dicsonia	0	o		o	o	
Polypodiaceae	+	+	0	+	+	+
Polypodium	o	0	0	0	o	o
Schizaeaceae				0		
Anemia	o			o	o	
Lygodium	o	o		0	0	
Gleicheniaceae	+	+	o	o	+	0

Occurence: +++ most frequent, ++ substancial, + constantly present (the quantity varies), o isolated representatives

It should be noted that the Ugolsky massif is a part of the Rodnyansky Alps (this name was used by Popov (1949)), a region with utmost concentration of relics during present times, where, as Popov wrote, echoes of the Sudetes flora, a component of the Neogene core of the Carpathian flora, are most felt. It is interesting that it was a region adjacent to the Rodnyansky Alps, on the north-eastern macroslope, that Shvaryova found *Cinnamonum* remnants inside a polytope complex of Upper Badnian deposits (by Pistynka and Kosiv). Plant remains in these complexes show signs of a long-distance

transfer (Shvaryova 1983), which does not contradict the suggestion of their having grown in one of mountain refuges of the Rodnyansky Alps, especially as the warm sea basin occupied the teritory of both flexures and was not yet divided in two (Senes & Marinescu 1974).

All the invstigated deposits are characterized by different faunal groups and are accurately linked to certain ages.

Unfortunately, there does not exist a single complete section of Neogene deposits in the Ugolsky masiff area, and hence we can estimate the Sarmatian and Pannonian floral composition only on the basis of palynological studies of Neogene deposits in the vicinities of villages Iza, Vyshkove, Velyatyno (the Solotvyn kettle).

The development of flora and vegetation during Neogene was conditioned by the whole geological and tectonic situation. The presence on the territory of the Transcarpathian flexure of a marine basin during Miocene and lake-bog basin during Pliocene created conditions favorable for the existence during the whole Neogene of moderately thermophilic flora, in which subtropical elements played a rather significant role. During Neogene there was a tendency of reduction of macrothermic elements and of a growing dispersal of moderately thermophilic species. Manifestations of orogenic volcanism phases played an important part in the occuring climatic changes (Syabryaj 1986).

The most drastic change in the composition of flora and vegetation was the result of the Pre-Tiglian fall of temperature, the effect of which was enhanced in the Transcarpathian region by phase 4 of orogenic volcanism. Swamp forests disappear during the period, only in deep valleys isolated specimens of Taxodium could exist. Representatives of the Juglandaceae were no longer forest-forming species. In the Mesophytic interglacial forests the role of the family Betulaceae (in particular Betula, Alnus, Carpinus) raised dramatically; a significant role in the composition of forest groups was, like during ealier periods, played by Fagus cf. sylvatica L. Oak-beech and pure beech forests become widespread. Ulmus was quite important. Subtropical plants virtually vanished. The existence of more sparse forests and open spaces resulted in a broad development of the shrub and grass layers.

Unfortunately, we do not possess palynological data from Pleistocene deposits of the Ugolsky area. Available is only fragmentary information on the flora and vegetation of the Eastern Carpathians during Pleistocene (Koziy 1950, Artyushenko 1950, Zerov 1952, Zerov & Artyushenko 1961 and others).

The study of the spore-pollen deposits from a beech forest bog in the Ugolsky region (530 m above the sea level) (Bezus'ko & Tasenkevich 1987) has allowed to determine the main stages in the development of the vegetation cover, starting at the end of middle and during late Holocene. In general, trends of vegetation formation coincide with those in the Eastern Carpathians (Koziy 1950, Artyushenko 1950, Zerov & Artyushenko 1961 and others). The spreading of broad-leaved-spruce forest during middle Holocene is clearly traced. During late Holocene, the participation of silver fir is increased while spruce is replaced by beech. This is characteristic of Eastern Carpathians forests during late Holocene. And the specific feature of the investigated region is that, contrary to other regions, even during middle Holocene the participation of beech in the spore-pol-

len complex was rather high (up to 29%).

The growing role of beech in the plant cover during late Holocene was naturally reflected in the spore-pollen complex composition of late Holocene deposits (up to 48.3%). Another peculiarity of forest vegetation of the Ugolsky massif during middle and late Holocene was the participation in it of some representatives of moderately thermophilic Neogene flora – Morus sp., Juglans sp., Ilex sp. A number of thermophilic Neogene relicts, the majority of which are calciphiles – Lunaria redidiva L., Phyllitis scolopendrum (L.) Newin, Taxus baccata L., Juniperus sabina L., Coronilla elegans Panc., part of present-day flora of limestone cliffs in this region.

Also of interest is the fact that the Ugolsky massif is one of rare for the Ukrainian Carpathians locations where groups of alpine species were found as a part of low mountain forest belt vegetation cover. The process of mountain belts lowering which took place during Neogene reoccured many times during glacial periods of Athropogene. The arctoalpine (Empertum nigrum L.) and alpine elements (Saxifraga paniculata Mill., Thesium alpinum L., Atragene alpina L., Cotoneaster integerrima Medik., Trisetum alpestre (Host.) Beauv., Sesleria heufleriana Schur and others) are probably relics and have remained on the limestone cliffs since the Würm (Valdai) Glaciation. The conclusion about the glacial relics dating back to Würm is supported by data of palynological and radiocarbon analyses performed for deposits of the middle Würm interstade of the Milk Stone cave situated in the belt of modern beech forests of the Ugolsky massif. According to palynologic data 25530±350 (GrN - 7761) years ago a substancial lowering of the subalpine and the alpine belts took place. The alpine belt lowered to 500-700 m above sea level. There was a marked spreading of alpine vegetation representatives. Very sparse forests of Pinus sylvestris L. with the participation of Pinus cembra L., Larix sp. and, probably, elfin woodland of Pinus mugo Turra dominated in areas where at present there exists a belt of beech forests. Limestone cliffs were covered with vegetation close to that of the subalpine and the alpine belt (Gladilin & Pashkevich 1977). A substancial lowering of the subalpine and the alpine belts down to 300-700 m above sea level within the time interval of 25-30 thousand years ago is also noted by Polish researchers (Mamakowa & Środoń 1977).

GEOGRAPHIC ANALYSIS OF THE MODERN FLORA

Let us now turn to the characterization of modern flora and vegetation of the reservation. The geographical anlysis was performed according to criteria proposed for analysing the flora of the Ukrainian Carpathians by Makarevich (1963) and Malinovsky (1969). The results indicate that the modern flora of the Ugolsky massif (with the exception of limestone cliff flora) is composed of the following geographical elements: arctoalpine, boreal, nemoral, alpine, mountain, boreal-mountain, nemoral-mountain, arid, azonal. The limestone cliff flora is represented by arctoalpine, boreal, nemoral, alpine, mountain, boreal-mountain, nemoral-mountain, arid and azonal geographical elements. Nemoral and nemoral-mountain elements comprise the largest part of the modern cliff

flora, as well as of the whole massif in general (110 species, or 56.4%). The study of the limestone cliff flora showed that it is composed of 195 higher plant species, of which 121 species (62%) occurs in the surrounding forests, while 74 species (38%) grow on the cliffs alone. No other relic congrigations of alpine species are known to exist in the lower mountain forest belt of the Ukrainian Carpathians (Tasenkevich 1979). The plant groups and separate species which retreated from the high areas as a result of the fall of temperature must have been preserved in this refuge on limestone cliffs till our days.

LICHENOLOGY ANALYSIS

Quite interesting and demonstrative is the composition of beech forest lichenoflora in the Ugolsky massif, in which 195 species were found among them the nemoral element prevails (36.0%) (Navrotskaya 1979, 1982). By its genesis this element is a derivative of mesophylic forest flora of the turgai - type (according to Krishtofovich 1946, 1947) and combines species disjunctively located in the Holarctic zone, which reflects the present-day fragmentary character of the zone of broad-leaved forests. The pannemoral type of area in the investigated forests is represented by hygrophilous, so-called "suboceanic" species which require high air humidity (Degelius 1935). These are relic nemoral species, such as Parmelia leavigata (Sm) Ach., P. revoluta (Flot.) Flk., Heterodemia speciosa (Wulf.) Trevis, and Normandina pulchella (Borr.) Nyl. P. laevigata - a rather rare species which grows under increased humidity conditions on the bark of leaf-bearing trees and on moss-covered cliffs. In Europe it grows in the western part of the continent; as far as Asia is concerned, there is information about it growing in Japan; it is also reported to occur in North America. Outside the Holarctic zone this species grows, with large disjunctions in tropical and subtropical regions (Africa; Central and South America; South-East Asia - Java, Ceylon; Australia with Polynesia). We found this lichen in a beech forest of the Ugolsky massif at an altitude of 500-750 m above sea level. Makarevich (1963) asssigns it to relics of the Poltava flora in the Ukrainian Carpathians. It is apparently a remnant of ancient subtropical flora with populated the Carpathians immediately after they had been formed.

Parmelia revoluta grows under the same ecological conditions as P. leavigata does, often occuring on leaf-bearing trees in the Ukrainian Carpathians, from mountaimn foothills and up to an altitude of 1200 m above sea level. In the north-western part of Europe this species grows under both plain (Scandinavia, England, France) and mountain conditions (the Pyrenees, Germany).

In Eastern Europe (territory of the USSR) it is known to grow under plain conditions in the vicinities of Leningrad, Lvov and Kiev, and in the Ternopol region. It also occurs in Asia (the Himalayas), South Africa, China, Ceylon, Polynesia, Central and South Amereica. In the Ugolsky massif this lichen grows at altitudes from 500 to 800 m above sea level upon the bark of leaf-bearing trees. *P. revoluta* is a lichen with a discontinious habitat, also a representative of the ancient Carpathian subtropical flora among lichens of the Ukrainian Carpathians.

Heterodermia speciosa is an especially hygrophilous species; the character of its habitat resembles that of Parmelia revoluta and P. laevigata, but its northward penetration is much more pronounced. Oxner (1946) lists this species as one of the Chukotka sector of the Arctic zone (mouth of the Anadyr river). It is found in forest areas of Western, Middle and Southern Europe, and in Asia. The Eurasian part of its area spreads, with disjunctions, from the Atlantic coast to the Pacific littoral. It is known to grow under plain conditions in North America. In Alps it reaches 1800 m above sea level, in the Himalayas – 2000 m. Outside the Holarctic zone it grows in Central and South America. In the investigated beech forests of the Ugolsky massif this lichen was found at altitudes 440 and 800 m above sea level on the bark of leaf-bearing trees and on mosses. Heteroderma speciosa is a relic species of Mediterrenian origin.

Normandina pulchella is also a hygrophilous species, it grows on moss-covered tree stems, on moss-grown stone substrate and on thalli of other lichens. In Europe the area of this species spreads alng the Atlantic coast from the western and southern parts of the British Isle to Portugal; it was also observed under plain conditions in Denmark and the western part of Scandinavia. On the European continent, with the exception of its northern part, N. pulchella mainly grows at low altitudes in the mountains, reaching as far southward as the Adriatic coast of the Balcan Peninsular and as far eastward as the Seventown and the Crimea (Degelius 1935, Kopachevskaya 1961). The Holarctic area of this lichen is of a pronouncedly discontinous nature: in Europe it grows in the Crimean Mountains, in Asia - in the southern and middle parts of the Urals, Mountain Shoria, the Altai, the Krasnoyarsk, Khabarovsk, Primorye territories and in Japan. In North America it was found in the northern States and on the eastern coast of the USA. primarily in mountains. Outside the Holarctic zone the lichen also has a discontinous area; it is known to grow in Africa and neighbouring islands, on the Small Antilles, in South America down to Terra del Fuego, in New Zealand and on the Hawaii. N. pulchella occurs rather frequently in the beech forests of the Ugolsky massif at altitudes from 500 to 1000 m above sea level. Oxner (1946, 1977) regarded this species as a turgai one on the basis of peculiarities of its discontinuous habitat (the existence of numerous elementary areas linked to refuges). Makarevich (1963) suggested a more ancient origin of N. pulchella, having assignated it to Poltava flora relics. Judging by its modern habitat, this species is the most ancient one among the described species and may even be a relic of Paleogene subtropical flora.

Found among the lichens of the Ugolsky massif of the Carpathian State Preserve were several interesting and rare species which usually grow in the alpine belts. One of these is Sphaerophorus fragilis (L.) Pers., which has assigned to the arctoalpine (more precisely, to the arctoalpine-antarctic) element by Makarevich (1963) who pointed out to the fact that this species has a discontinuous alpine part of its area, growing also under mid-altitude mountain conditions. In the Ukrainian Carpathians it was found by Hazslinszky (1884), Hruby (1925), Suza (1926), Szatala (1927), Servít and Nádvorník (1936) on silicate cliffs and on rocky soil in the subalpine and the alpine belts. We found it on the territory of the Ugolsky massif in the lower mountain forest belt (1240 m above sea level), on stones almost by the upper forest boundary (the polonina Menchul), and

this is another evidence of the lovering of the subalpine and the alpine belts detected by the spore-pollen analysis discussed above.

So, the finding of a number of relic hydrophylous nemoral lichens in the Ugolsky massif also favors the suggestion of the existence of nemoral flora refuge in that place.

The attachment of the thermophilic flora refuge to the southern macroslope of the Carpathians is quite natural. The Western, Eastern and Southern Carpathians were one mountain region as early as late Badenian-Sarmatian. Protection by mountains on the north and north-east, opportunities for penetration of warm Atlantic air, the presence of a warm sea basin (later warm lakes) - these factors retarded the process of climate continentalization during late Miocene and Pliocene in the whole Transcarpathian region. Peculiarities of geographical and tectonic conditions also predetermined to a large extent the preservation of such a refuge in this particular part of the Ukrainian Carpathians. Having risen at the junction of Oligocene and Miocene, the Carpathians had varying tectonic regimes during Neogene. Whereas in the outer part of the Carpathians (northern macroslope) both Miocene and Pliocene folds had a relief-forming significance, in the inner part the Miocene folding was most substancial, while the later phases were much less pronounced (Andrusov, 1960). The main relief formation ended during Badenian early Samatian some mountain massif date back to Paleogene. The Gargans rose 200 m after Badenian (Hofshtein 1964). The Badenian Sea was the last one to reach the territory of the current Ugolsky Preserve. Thus, no mayor changes occurred in this region since the end of Badenian-Sarmatian, and therefore most ancient relics concentrated there. The result was the unique richness of the Ugolsky massif flora, especially as conditions favoring the preservation of more thermophilic flora date back to Neogene. The existence of an interesting, from the phytohistorical point of view, refuge on the investigated territory has olready been suggested by Stoyko (1966) and Bezus'ko and Tasenkevich (1978).

The results of the complex study provide grounds for the suggestion that the Ugolsky massif area had repeatedly been a refuge for thermophilic flora during some late Cainozoic stages when natural conditions had worsened.

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