CO-EVOLUTION OF THE HIPPARION FAUNA AND VEGETATION IN THE PARATETHYS REGION

L.K. Gabunia and K.I. Chochieva
Institute of Paleobiology
Academy of Sciences of the Georgian SSR
Potochnaia 4A
380004 Tbilisi
Georgia
USSR

Received May 11, 1978; January 11, 1981

ABSTRACT: The authors observe the close dependence of the evolution of the Hipparion fauna, in the Paratethys region in the Miocene and early Pliocene, on change in the vegetation. In the early Miocene floras the elements of the Oligocene evergreen humid-subtropical floras were still of great importance, whereas beginning with the middle Miocene their significance sharply decreased and mesophyllous forms began acquiring a dominant position. The widespread expansion of the Anchitherium fauna reflects the conditions of this mesophyllous silvan flora. There was a widespread development of open spaces occupied by herbaceous vegetation in most of the Paratethys region during the middle and late Sarmatian and Meotian. The spreading of ostriches, hipparions, gazelles, and other inhabitants of relatively dry localities fully corresponds to the presence of elements of a typical steppe flora. In the vegetal cover of the western region of the Paratethys the predominance of mesophyllous forests was maintained until the end of the Meotian; the relative conservatism of these complexes of the Hipparion fauna evidently conforms to this fact.

* * * * * * *

The powerful influence of the development of the herbaceous vegetation of open spaces on mammalian evolution was shown for the first time in the classical investigations of V.O. Kowalevsky, who depicted the impressive picture of the gradual adaptation of different types of ungulates to a coarse herbaceous food causing significant transformations in the animal kingdom. Despite the rather scanty paleobotanical data of the sixties and seventies of the last century Kowalevšky (1956) neverthless succeeded in establishing the thesis that throughout Europe vegetative formations of open spaces with relatively low humidity became widespread approximately in the middle of the Tertiary period, stimulating the evolution of ungulates for life in an environment unusual for them.

Kowalevsky showed that together with the occupation of herbaceous plains by different groups of ungulates and their adaptation to a coarse food, major changes occurred in the whole organization of these animals. These changes manifested themselves most distinctly in the transformations experienced by the dentition, the skull, and the structure of the limbs: the height of the tooth crowns increased; tooth cement appeared; the structure of their trituration surface became complicated; the skull elongated; the position of the orbits changed; the limbs, especially their distal segments, elongated; the number of digits declined; and so on.

Consequently Kowalevsky convincingly demonstrated in his works the close correlation between the process of evolution of herbaceous plains and the evolutionary changes occurring in the mammalian fauna occupying these plains; he proved that both of these large groups - the herbaceous vegetation and ungulates feeding on it, artiodactyls and perissodactyls - belonged to one ecosystem.

Kowalevsky's idea concerning the co-evolution of ungulates and the herbaceous vegetation has been taken up by many authors, but nobody has studied this problem specially. Meanwhile after Kowalevsky much valuable material has been accumulated, confirming and adding detail to his principal theses.

We shall briefly consider here only a small part of this material, mainly concerning the ecosystem of the late Miocene and early Pliocene mammalian faunas and the vegetation of the Paratethys region (Fig.1).

* * * * * * *

Evolutionary Theory 6: 1-13 (March, 1982)
The editors thank D.I. Axelrod and J. Damuth for help in evaluating this paper.
© 1982, The University of Chicago; rights owned by author.

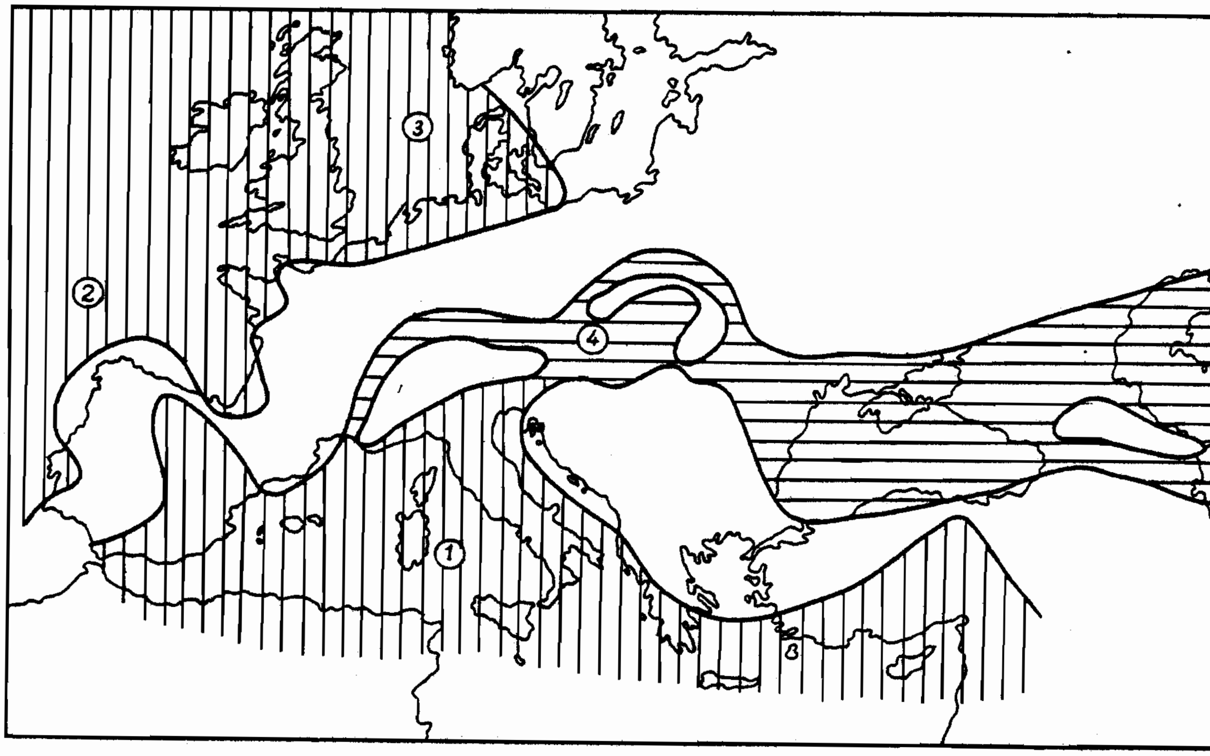

Fig.1. Distribution of bioprovinces in Europe in the Late Tertiary
1 — Mediterranean bioprovince — Tethys; 2 — Celt Lusitanian bioprovince; 3 — Boreal bioprovince; 4 — Transeuropean bioprovince — Paratethys (Cicha 1970)

According to A.I. Tolmachev (1955) the pre-Tertiary origin of monocotyledons is undoubted. He assumes that the formation and early stages of evolution even of such a progressive group as grasses occurred in the Cretaceous period. At the same time Tolmachev shows rather convincingly that the herbaceous vegetation of modern open landscapes is genetically associated with the silvan vegetation and represents the product of the evolutionary development of the herbaceous plants in the forests.

We consider it possible that it was the appearance of grasses and some other herbs during Cretaceous time that initiated the ecological differentiation of the early representatives of placentals. Although we have to be very careful when speaking about the food and habitat of the ancient condylarths (Webb,1977), it is possible to make certain affirmations as to the adaptations to relatively coarse food and life in semi-open spaces and sparse forest of some late Paleogene mammals (Plagiolophus, Indricotherium,Allacerops,Ardynia,Palaeohypsodontus, and others).

However, the herbaceous vegetation of forests couldn't apparently have had any controlling influence on the character of evolution of phytophagous mammals either in the Paleogene or at the very beginning of the Neogene - at the epoch during which the so-called anchitherian fauna became widely distributed. Neverthless it should be mentioned that the appearance of some mesohyposodont forms at the beginning of the Miocene (Table I) is indicative of the fact that at this time feeding on silvan herbs already began to have a decisive formative influence upon the animals, this influence becoming stronger in the middle of the Miocene (Table II). A noticeably increasing number of inhabitants of open spaces testifies to it.

As far as the basic ecological groups of Tertiary terrestrial mammals are concerned, we are very aware of the fact that it is difficult to evaluate with any degree of certainty their mode of life, especially those of the early Cenozoic period. In spite of this, when we observe a clear tendency toward the development of mesohypsodont teeth in forms such as, for example, the Oligocene rhinoceros Ardynia, in which the cheek teeth are somewhat higher than those of the majority of its extremely brachyodont contemporaries, we may classify these forms in the group of

Table I: Ecologically central mammal complexes of the basal lower Miocene (after Flerov and Yanovskaya, 1974; Bendukidze, 1977)

Inhabitants of forests and swampy areas	Inhabitants of open or semi-open areas and silva ráre
Palaeocastor acridens Matth.	Eumysodon spurius (Arg.)
Palaeocastor sp.	Protalactago borissiaki Arg.
Propalaeocastor aff. cumbulakensis Lyts.	Paraceratherium prohorovi (Boriss.)
Desmatolagus aff. gobiensis Matth. et Gr.	Aceratherium aralense Boriss.
Sinolagomys sp.	Aprotodon borissiaki Belj.
Agyspelagus simplex (Arg.)	Prodremotherium sp.
Steneofiber sp.	
Eucricetodon aff. deploratus (Shev.)	
Aralomys gigas Arg.	
Conohyus sp.	
Brachypotherium sp.	
Amphitragulus sp.	
Eumeryx sp.	
Lophiomeryx sp.	

****

inhabitants of semi-open areas, feeding primarily on forest grasses. At the same time, we must keep in mind that not all mammals, even the fully developed mesohypsodont ones, were grazers (for example, the peculiarly specialized amynodonts, paraceratheres, and others). However, when even a slight increase in height of the cheek teeth is accompanied by a clear elongation of the distal parts of the limbs and a reduction of the side toes, we find it possible to consider such mammals as inhabitants of open and semi-open areas, feeding on grass and shrubs (Allacerops, Prodremotherium, and others). It is especially difficult to decide in which ecological group ancient Rodentia and Carnivora belong. For these groups of animals we are sometimes forced to base our conclusions on weak evidence coming for the most part from the mode of life of their recent relatives, which have but a far-off relationship with these fossils. And finally, the main lack in our material is the almost total absence of data on the relative abundance of individuals of the species which compose the group under consideration (such data exist for only two or three fossil localities). This naturally leads to a levelling of characteristics. Indeed, it is one thing to

****

Table II: Ecologically central mammal complexes of the basal middle Miocene (after Gabunia, 1973)

Inhabitants of forests and swampy areas	Inhabitants of open or semi-open areas and silva ráre
Palaeocricetus caucasicus Arg.	Percrocuta abessalomi Gab.
Amphicyon caucasicus Gab.	Paranchitherium karpinskii Boriss.
Laphyctis sp.	Dicerorhinus caucasicus Boriss.
Pseudaelurus sp.	Chilotherium sp.
Gomphotherium sp.	Palaeotragus sp.
Platybelodon danovi Boriss.	Paratragocerus caucasicus Sok.
Bunolistriodon sp.	Kubanotragus sokolovi Gab.
Kubanochoerus robustus Gab.	Hypsodontus miocenicus Sok.
Dorcatherium sp.	
Lagomeryx sp.	
Paradicrocerus flerovi Gab.	
Heteroprox sp.	

note the presence of Hipparion verae, and quite another to indicate that the number of individuals of this species is greater than 30% of the total number of individuals of all species included in this fauna. The taphonomic uniformity of the majority of fossil localities formed on the slopes of old basins can hardly be considered as a sufficient justification for such a simplification of the general picture of the changing ecological composition of mammal faunae, especially since the fossil localities studied here are very unevenly distributed in the Paratethys area, the overwhelming majority of them being concentrated in Moldavia and the Ukraine. Even so, the indirect indications bearing on the gradual increase during the Miocene of the role of herbaceous vegetation, based on fragmentary and incomplete information about these mammal faunas, fully conform to paleobotanical data.

From the point of view of taxonomy the Miocene floras of the Paratethys represent very likely one of the richest and the most peculiar types of the paleofloras of Eurasia. The content of elements of the evergreen humid-subtropical floras of the Eocene and Oligocene in the floras of the early Miocene and the beginning of the middle Miocene is so large that they seem to be more closely connected in origin with the former ones than with the floras of the late Miocene. However, the beginning of the second half of the Badenian is marked both by the reduction of the systematic variety of these taxa and the degree of their participation in the formation of the vegetative cover and by the gradual, but steady, establishment of the predominance of mesophyllous wood species. It sees quite natural that this process did not go on simultaneously and with the same rate throughout the vast territory of the Paratethys and countries contiguous to it. In the Transcarpathian region, for example, the remains of evergreen angiosperms are found in the lower parts of the Miocene not only in a considerable amount, but in some cases (the flora of Burkola) they exceed the number of the deciduous plants (Iljinskaja,1960). According to P.I. Dorofeev (1966) it was in the middle Badenian that the forest composed of Carpinus, Fagus, Castanea, Quercus, and Liquidambar occupies a dominating position in central Europe, but Laurus and Cinnamomum were still widespread there at that time.

From the middle Miocene, mesophyllous deciduous hardwood forests became dominant in the vegetation of the Paratethys. The increasing number of representatives of the Pinacea (Abies, Tsuga, Picea, Cedrus, Pinus) reaching dominance in some pollen spectra (Ananova, 1973; Brezinova, Gabrielova, 1974), is also indicative of it. It was in the Miocene too that the formation of montane floras (the Alps, the Carpathians, the Caucasus) of this territory with more fractionated spatial and high-altitude differentiation mostly took place. And, finally, many taxa of herbaceous plants apparently originated during the Miocene. Their part in the formation of the vegetative cover of the Paratethys varies considerably in time and space. Thus in the lower Miocene (upper Maikopian) deposits of the eastern Peri-Caucasus, along with rich and diverse pollen of Gymnospermae and Amentiferae and single pollen grains of evergreen angiosperms, one can come across pollen of Gramineae, Rosaceae, Chenopodiaceae, and Labiatae. But according to A.N. Gladkova (1956) the latter types of pollen occur seldom and in small amount. The pollen of herbs (Chenopodiaceae, Gramineae, Compositae, Potamogetonaceae, Sparganiaceae) is observed in a small amount in the lower Miocene pollen spectra of the Oksko-Donskaja depression (Grishchenko and Glushchenko, 1965). According to M.N. Grishchenko (1966) it is only in the upper Miocene palynological spectra of this region that the content of pollen of Chenopodiaceae and Gramineae markedly increases. In the Precarpathian region the first appearance of the pollen of Gramineae, Chenopodiaceae, Cyperaceae, and other herbaceous plants in observed in a small amount in the upper Badenian deposits. This fact allows N.A. Shchekina (1960) to express the opinion that on the generally silvan background at that time there were only few strips of land with xerophile herbaceous vegetation there and that the steppe landscape was not typical for the Miocene in the Precarpathian region. The Transcarpathian region is presumably characterized by the same picture: forests with concomitant herbs. The latter are traced here at present beginning with the

Table III: Ecologically central mammal complexes of the upper middle Miocene (after Thenius, 1959; Pavlovich, 1969)

Inhabitants of forests and swampy areas	Inhabitants of open or semi-open areas and silva ráre
Tungurictis sp.	Gobicyon macrognathus Colb.
Gomphotherium angustidens Cuv.	Percrocuta miocenica Pavlov. et Then.
Taucanamo sansaniensis (Lart.)	Anchitherium aurelianense (Cuv.)
Listroidon michli (Parask.)	Eotragus sansaniensis (Lart.)
Lagomeryx sp.	Hypsodontus serbicus Pavlov.
Giraffokeryx punjabensis Pilgr.	

****

upper Badenian - lower Sarmatian deposits near Gorbki village: Alismataceae, Hydrocharitaceae, Sparganiaceae, Gramineae, Cyperaceae (Shchekina, 1960). At the same time it is noteworthy that in the lower Miocene floras of the Trugay district (Boitsova and Pokrovskaya, 1956; Kornilova, 1960) the herbs are characterized by a fairly large proportion of the total pollen (6-32%) and by a striking diversity: Cruciferae, Umbelliferae, Gramineae, Ranunculaceae, Rosaceae, Caryophyllaceae, Leguminosae, Plumbaginaceae, Chenopodiaceae, Artemisia.

The transformation of the vegetative cover and the adaptive changes of the terrestrial mammals caused by them stood in close relation to tectonic processes going on during the Miocene (Nemkov et al., 1974) which changed the geographical configuration of the whole vast region of the Paratethys. The elevation of mountains, the increase of the subdivision of relief, the change of the configuration of the basins forming the Paratethys, the appearance of new areas of the littoral and new connections of formerly separated land, and other changes of the abiotic environment stimulated a considerable differentiation of the vegetation, the appearance of varied types of vegetation complexes, including those associated with grass. For instance, the presence of mesohypsodont bovines among the anchitherian fauna, widespread at this period, and a few other inhabitants of open spaces testify to the existence of forest-prarie landscapes. The data concerning the Tschokrakian and Karaganian floras of the eastern Peri-Caucasus (Gladkova, 1956) and the south of the Ukraine (Mitsul, 1973a) fully conform to such an assumption. In the pollen spectra of the former the content of the herbaceous plants varies from 2 to 22% and in the latter it reaches 17%. The sharp increase of the content of the shrub and herbaceous vegetation observed in the Tschokrakian and Karaganian was presumably called forth, according to Gladkova (1956), by the extension of littoral areas. In this territory, according to the view developed and summarized in the papers by M.M. Ilyin (1937, 1946) the formation of the desert-xerophytic and halophytic representatives of flora took place, beginning in ancient times. The elements of the herbaceous vegetation are

****

Table IV: Ecologically central mammal complexes of the lower Sarmatian (after Thenius, 1959; Dubrovo and Kapelist, 1979)

Inhabitants of forests and swampy areas	Inhabitants of open or semi-open areas and silva ráre
Deinotherium aff. giganteum (Kaup)	Machairodus sp.
Gomphotherium angustidens Cuv.	Anchitherium aurelianense (Cu.)
Brachypotherium brachypus Lart.	Miotragocerus monacensis (Kr.)
Listriodon splendens Meyer	Protragocerus chantrei Dep.
Dicrocerus sp.	Gazella sp.

marked also in the early Badenian of the central Paratethys , but here they are apparently less important than in the middle Miocene of the east Paratethys. The close connection of the herbaceous vegetation with the forest, with its borders and glades, is apparently preserved also at the beginning of the late Miocene. Thus in the southwest of the Ukraine the wood species became dominant in the pollen spectra from the middle of the middle Sarmatian. In the central Paratethys this predominance of wood species is traced even up to the upper Pannonian, and in the north Caucasus, Georgia, and some other regions of the Paratethys it is also marked up to the middle of the middle Sarmatian. Therefore there is no wonder that the anchitherian fauna with its mainly silvan forms continues to exist in the late Badenian and the early Sarmatian (Tables III, IV). This does not mean, however, that in the early gramineous plains serving as the means of existence for many representatives of the Hipparion fauna, which become widespread in the middle Sarmatian.

It is to be supposed that the evolution of gramineous plains preceded to a certain extent the process of their occupation by herbivorous animals, and the period of time during which this occupation (and at the same time the formation of the Hipparion faunas) took place could be observed even geologically. However, a marked increase of the content of herbs begins to manifest itself, as has already been mentioned, in the middle and, according to some data, beginning with the middle of the middle Sarmatian, i.e. from the moment which the Hipparion fauna has already appeared in the Paratethys (Tables V, VI). Thus according to the E.Z. Mitsul's data (1973a,b) the second half of the Sarmatian and nearly the whole period of the Meotian were characterized in Moldavia by a combination of wooded and woodless landscapes. According to Shchekina (1978) the predominance of woodless landscapes, beginning with the end of the middle Sarmatian, also occurs in the territory of the eastern Ukraine. One may gain an impression that the dispersion of faunas of the new type could have taken place simultaneously with the change of the landscape. In any case all this is indicative of a close relation of the evolution of herbivorous mammals to the development of open spaces, occupied by the herbaceous vegetation (Fig.2).

There exists an opinion according to which in the western region of the east Paratethys and in the central Paratethys mesophyllous forests continued to be dominant in the second half of the middle Sarmatian at the time when hipparions and some of their nearest companions appeared here for the first time (basal Pannonian of the central Paratethys). Nevertheless an evidently increased role of the herbaceous vegetation points with certitude to the fact that it was already occupying rather considerable spaces even in these western regions (Berger and Zabusch, 1953). To such a differentiation of landscapes corresponds the presence in the middle Sarmatian mammalian complexes both of relatively low-crowned and massive forms of hipparions, with which anchitheres and some other representatives of the middle Miocene mammalian fauna could co-exist in humid habitats, and of more hypsodont and slender forms associated most likely with open landscapes (Gabunia, 1959,1970).

In the late Sarmatian the predominance of the herbaceous vegetation is marked in many regions of the Paratethys. So, for instance, in the pollen spectra of the upper Sarmatian of Don-Sal-Manych steppes the content of the pollen of herbaceous and shrub vegetation reaches 97% (Ananova,1954). A very high percentage (up to 95%) of the pollen being from herbs is also found in Moldavia (Mitsul, 1973a) and other regions. However, for Moldavia also, the north Caucasus, and especially for the Transcaucasus, complexes with a high content of wood species are also marked; they indicate a considerable afforestation and, accordingly, a humid environment characterizing some sections of the territory under consideration. Apparently in some cases, particularly in the north Caucasus (Dorofeev, 1964) and in the east Transcaucasus (Dzhabarova, 1967,1976; Fataliev, 1964) these complexes may correspond to the silvan flora typical of montane countries with a diversity of habitats. In others, Moldavia and the Ukraine, they were possibly growing in the valleys of rivers, at some distance from which one could find open plains

Table V: Ecologically central mammal complexes of the lower middle Sarmatian (after Godina and David, 1973; Dubrovo and Kapelist,1979)

Inhabitants of forests and swampy areas	Inhabitants of open or semi-open areas and silva rare
Ictitherium sp.	Citellus sp.
Deinotherium aff. giganteum Kaup.	Percrocuta sp.
Choerolophodon pentelici (Gaud. et Lart.)	Hipparion sarmaticum Lungu
Schizochoerus vallesiensis Crusaf. et Lav.	Dicerorhinus sp.
Lagomeryx flerovi Lungu	Aceratherium aff. incisivum Kaup.
Cervavitus bessarabiensis Lungu	Palaeotragus expectans (Boriss.)
	Miotragocerus pannoniae (Kr.)
	Eomellivora sp.

****

covered with herbaceous vegetation. It should be mentioned that the Hipparion fauna of the late Sarmatian (Table VII) reflects as a rule the forest-steppe environment; alongside many undoubtedly silvan forms, such as choerolophodon, gomphothere, microstonyx, palaeotragus, and others, the representatives of a different ecological grouping peculiar to open woodless landscapes (hipparions, gazelles, ostriches, and others) form a part of it. In some late Sarmatian localities the representatives of silvan communities predominate, apparently reflecting local conditions. That is the case particularly in Eldar, East Georgia, where the predominance of silvan forms is strongly evident. Even hipparions are represented here by a form, similar to the archaic H. primigenium, characterized by relatively brachyodont dentition and massive metapodials suggesting a humid environment (Gabunia,1959). Moreover, the paleobotanical data for the upper Sarmatian deposits of the divide between the Kura and the Iori indicate, according to R.A. Fataliev(1964), a climate with high humidity, abundant precipitation, and without strongly marked seasonality, thus agreeing well enough with the peculiarities of the Eldarian fauna. However, according to H.S. Dzhabarova (1967), the picture changes here abruptly in the second half of the late Sarmatian; the pollen spectra of Chobandag, in which the proportion of herbs reaches 67%, undoubtedly testify to it. The hipparion from the upper horizon of the Eldarian series reflects possibly this abrupt change of environment (Gabunia,1959); the relatively long protocone of its upper molar teeth evidently indicates adaptation to coarse fodder.

By the end of the Sarmatian and in the Meotian in most of the Paratethys region the widespread development of open spaces, occupied by herbaceous vegetation, is already beyond any doubt. According to the data of Mitsul (1973a), in the pollen

****

Table VI: Ecologically central mammal complexes of the upper middle Sarmatian (after Godina and David,1973; Dubrovo and Kapelist,1979)

Inhabitants of forests and swampy areas	Inhabitants of open or semi-open areas and silva rare
Ictitherium tauricum Boriss.	Percrocuta sp.
Deinotherium aff. giganteum Kaup.	Hipparion sebastopolitanum Boriss.
Choerolophodon sp.	Hipparion sp.
Gomphotherium sp.	Aceratherium zernovi Boriss.
Zygolophodon sp.	Dicerorhinus sp.
Lagomeryx flerovi Lungu	Palaeotragus expectans (Boriss.)
Dicrocerus sp.	Tragocerus sp.
	Miotragocerus leskevitschi (Boriss.)
	Tragoceras sp.

Table VII: Ecologically central mammal complexes of the upper Sarmatian (after Gabunia,1959;Korotkevich,1970;Godina and David,1973; Dubrovo and Kapelist,1979)

Inhabitants of forests and swampy areas	Inhabitants of open or semi-open areas and silva ráre
Mesophithecus pentelici Wagn.	Orycteropus gaudryi F. Maj.
Ictitherium robustum Nord.	Percrocuta eximia (Roth. et Wagn.)
Ictitherium hipparionum (Gerv.)	Hipparion verae Gab.
Deinotherium sp.	H. giganteum Grom.
Gomphotherium sp.	Dicerorhinus sp.
Choerolophodon pentelici (Gaud. et Lart.)	Aceratherium sp.
	Chilotherium berislavicus Korot.
Zygolophodon sp.	Procapreolus sp.
Tetralophodon longirostris (Kaup.)	Palaeotragus berislavicus Korot.
	Samotherium sp.
Ancylotherium sp.	Miotragocerus leskevitschi (Boriss.)
Microstonyx major (Gerv.)	Tragocerus sp.
Cervavitus sarmaticus Korot.	Procapra brevicornis Roth.et Wagn.
Protragelaphus sp.	Gazella schlosseri Pavl.
	Grecoryx sp.
	Tragoreas sp.

****

spectra of the Meotian of the southern part of the Ukraine, according to Shchekina (1966,1973), herbaceous plants are also already of much importance (the proportion of herb pollen in the corresponding complexes amounts to 18-50%), and their importance evidently increases in the eastern parts of this country. Summarizing the evolution of the vegetation of the Ukraine during the Meotian the author notes, in particular, that whereas at the beginning of the Meotian in the south of the Ukraine herbaceous vegetation does not yet occupy vast areas, at the end of the stage herbaceous plains become developed and the climate becomes more arid than in the early Meotian.

The data obtained with the help of the early Pliocene pollen floras of the northern part of the Black Sea basin (Karmishina and Kovalenko,1976) are of much interest. The proportion of herbs (47%) in these pollen floras is greater than the proportion of arboreal species. A very considerable part of these floras (22%) is formed by Chenopodiaceae. The rest - Gramineae (13%), Compositae (6%), Artemisia (3%), Scrophulariaceae (1%), Sparganiaceae (1%) - are represented more poorly. The high proportion of herb pollen in the pollen spectra of Kerch is noted by I.V. Maslova (1961) as well. The same picture is observed in northern Priaralye, Mangyshlak, northern Prikaspi (northern Caspian region)(Valueva,1973;Timoshina,1973) and some other regions of the eastern Paratethys and neighboring areas (Pulatove, 1972; Pakhomov and Penkova,1978).

The flourishing of the Hipparion fauna (Table VIII), reaching at this time exceptionally widespread expansion and diversity, must be associated with the evolution in the Meotian of herbaceous plains. In the Meotian complexes of the Hipparion fauna the dwellers of herbaceous plains now acquire special significance: besides ostriches and rather numerous hipparions these are - gazelles, procobuses, palaeoryxes, protoryxes, palaeoreases, oioceroses and others (Godina and David, 1973; Dubrovo and Kapelist,1979).

It should be observed here that the abundant material of the Hipparion fauna from different horizons of the Meotian (Tables IX,X) allows us to trace its evolution during the Meotian stage (Gabunia,1959,1970). It turns out that not only hipparions but also other groups of mammals evolved to become better adapted to life in the open landscapes. These observations of the Meotian mammalian complexes fully conform to the data discussed above on the corresponding pollen floras. It is remarkable that in the central Paratethys the middle Pannonian mammalian faunas

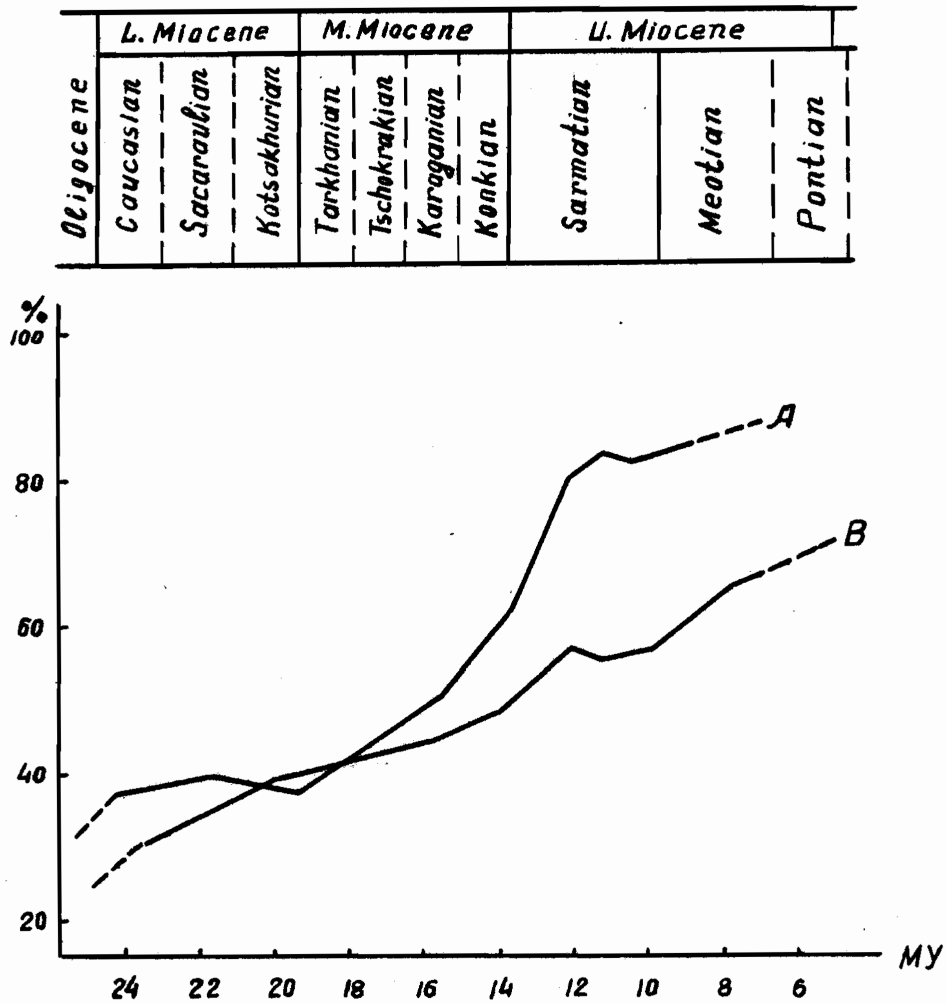

Fig. 2 A graph illustrating co-evolution of herbaceous plants (A) and grazing mammals (B)

****

(Thenius,1959), correlated to the Meotian, are represented mainly by associations of silvan forms, indicative of a persisting environment that is also indicated by the available information of the early and middle Pannonian flora, which reflects a humid environment (Rybakova,1966,1977).

It should be noted that the observations expressed here concerning the landscapes and mammalian fauna of the Meotian do not conform to the views of P.I. Dorofeev, who has devoted to this problem a number of interesting publications. Dorofeev (1966) thinks that in the Meotian of the Ukraine mixed woods, including deciduous and coniferous species, were of greater importance than in the late Sarmatian, and that it was the particular combination of silvan biocoenoses with an open landscape that could represent a cause of mass deaths of the Hipparion fauna, numerous large accumulations of their remains pointing to this.

We believe that P.I. Dorofeev is strongly exaggerating the significance of silvan biocenoses in the Meotian. Evidence for this comes not only from the pollen data of the Meotian deposits adduced here but also from the information of the Hipparion faunas of the Meotian themselves, in the composition of which the dwellers of open spaces acquire much more significance than in the Sarmatian. In our opinion his idea of a degradation of the Hipparion fauna in the Meotian is also incorrect, as is his view that mass deaths give evidence for such a decline. The enormous concentrations of the remains of this fauna in the Meotian deposits of different regions of the Paratethys testify exactly to the fact that the Hipparion fauna was at that time exceptionally widely spread and flourishing.

We confine ourselves here to a consideration of the Sarmatian-Meotian stage of the history of the Hipparion fauna, as very little is yet known about its Pontian representatives. However, even what little we know (Gabunia,1970;Alekseeva,1977;

Table VIII: Ecologically central mammal complexes of the lower Meotian
(Godina and David,1973;Dubrovo and Kapelist,1979)

Inhabitants of forests and swampy areas	Inhabitants of open or semi-open areas and silva ráre
Mesopithecus ucrainicus Grem.	Proochotona eximia (Chom.)
Ictitherium hipparionum Gerv.	Alilepus lascarevi Chom.
Promephitis maeotica Alex.	Lepus sp.
Perunium ursogulo Orl.	Orycteropus gaudryi F. Maj.
Plesiogulo sp.	Percrocuta eximia (Roth.et Wagn.)
Metailurus boodon Weit.	Machairodus cultridens Cuv.
Deinotherium giganteum Kaup.	Hipparion verae Gab.
Tetralophodon longirostris (Kaup.)	H. giganteum Grom.
Microstonyx major (Gerv.)	Aceratherium incisivum Kaup.
Cervavitus sp.	Chilotherium schlosseri (Web.)
Protragelaphus skouzesi Weit.	Palaeotragus rouenii Gaud.
	Procapra brevicornis (Roth.et Wagn.)
	P. deperdita (Gerv.)
	Gazella schlosseri Pavl.
	Palaeoryx majori Schl.

****

Dubrovo and Kapelist,1979) of it is indicative of further interactive evolution of the vegetative cover and mammalian faunas, leading to the development of real steppes with the associations of herbivorous mammals characteristic of them (progressive forms of Hipparion, Paracamelus, Urmiabos, and others).

Finally, we note that the wide dispersal of the Hipparion faunas in close relation to the evolution of floras, could not but affect in its turn the development of the vegetative cover. The powerful influence of phytophagous mammals on the formation of the landscape was not once emphasized (Lillegraven,1972). We shall venture to remind a reader only of Darwin's (1952:133) wonderful observations of heather fields of Staffordshire, where the change in the native vegetation of the enclosed planted part of the heath was most remarkable, more than is generally seen in passing from one

****

Table IX: Ecologically central complexes of the middle Meotian
(after Godina and David,1973; Dubrovo and Kapelist,1979)

Inhabitants of forests and swampy areas	Inhabitants of open or semi-open areas and silva ráre
Ictitherium hipparionum Gerv.	Percrocuta eximia (Roth.et Wagn.)
Lycyaena parva Chom.	Machairodus schlosseri Neit.
Promephitis sp.	Hipparion moldavicum Grom.
Deinotherium giganteum Kaup.	H. platygeny Grom.
Zygolophodon turicensis (Schin.)	Aceratherium incisivum Kaup.
Tetralophodon longirostris (Kaup.)	Dicerorhinus sp.
Microstonyx major (Gerv.)	Diceros pachygnathus (Wagn.)
Cervavitus variabilis (Alex.)	Procapreolus rouenii Gaud.
	Samotherium boissieri F. Maj.
	Tragocerus amaltheus Gaud.
	Procapra deperdita (Gerv.)
	Procobus brauneri Chom.
	P. melania Chom.
	Oriotherium argaloides F. Maj.
	Grecoryx sp.
	Tragoreas oryxoides Schl.
	Palaeoryx majori Schl.

Table X: Ecologically central mammal complexes of upper Meotian (after Godina and David,1973; Dubrovo and Kapelist,1979)

Inhabitants of forests and swampy areas	Inhabitants of open or semi-open areas and silva ráre
Sciurotamias gromovi Top.	Alilepus sp.
Parapodemus sp.	Prolagus sp.
Steneofiber sp.	Microtoscoptes sp.
Ictitherium hipparionum Gerv.	Microspalax compositodontus Top.
Plesiogulo crassa (Teilh.)	Percrocuta eximia (Roth.et Wagn.)
Zygolophodon sp.	Hipparion tudorovense Gab.
Tetralophodon grandincisivum (Schles.)	Chilotherium sp.
	Aceratherium simplex Kroc.
	Dicerorhinus sp.
	Procapreolus flerovi Korot.
	Tragocerus frolovi Pavl.
	Procapra deperdita (Gaud.)
	Palaeoryx majori Schl.
	Protoryx sp.
	Camelidae

****

soil to another quite different (six species of insectivorous birds, twelve new species of plants, not counting grasses and sedges, and Scotch firs were springing up in multitudes so close together that all could not live). Yet the unenclosed heath was so extensive and so extremely barren that, according to Darwin's words, no one would ever have imagined that cattle would have so closely and effectually searched it for food.

However, Pachosky (1917) later showed that the influence of mammals on the vegetative cover manifests itself not only in eating some plants, but also in trampling. It is neverthless impossible, for instance, to explain by trampling alone the almost complete absence of toxic plants in the grassy plains.

This significant phenomenon is considered by Prokhanov (1965) as a result of the intensive eating up of desiccated or frost-bitten plants in winter (or in drought), at times of food shortage, on the one hand, and effectively unlimited amount of pasture during the season of vegetative growth, on the other. And for the plants themselves the winter eating of their remains is not only harmless but also vitally necessary.

Thus the formation of modern steppes with their characteristic absence of inedible plants and typical associations of grasses (Ellison,1960) apparently occured in close relation to the mammalian influence upon them.

Therefore one can think also that the dispersal of the Hipparion faunas in the Paratethys region not only was a result of the appearance of open landscapes but that it itself favored their formation.

****

REFERENCES

Alekseeva, L.I. 1977. Teriofauna Rannego Antropogena Vostochnoi Evropy. Moscow: "Nauka".214pp.

Ananova, E.N. 1954. Palynologicheskie Dannye k Voprosu o Proiskhozhdenii Stepei na Iuge Evropeiskoi Ravniny.Botan. Zhurn.39:343-356.

_______________ 1973. [The pollen flora from the early Sarmatian deposits of the northern Azov region and the lower Don River Basin.] In [The Palynology of the Cenophytic]. Pp. 165-170. Moscow.

Bendukidze,O.G.1977. O Biostratigrafii Miocenovykh Otlozhenii Severo-Sapadnogo Poberszhya Aral'skogo Morya.XXI Nauchn. Sessiya Sektora Paleobiologii Akad. Nauk Gruzinskoi SSR. Tesisy Dokladov.Pp.8-12.Tbilisi.

Berger,W., and Zabusch, F. 1953. Die obermiozäne (sarmatische)Flora der Türkenschanze in Wien.Neues Jahrb.Geol.Paläontol.Abhandl.98:226-276.
Boitsova,E.P., and Pokrovskaya,I.M.1956.Miocenovye Sporovo-pyl'zevye complexy Turgaiskoi Vpadiny. In Atlas Miocenovykh Sporovo-ply'zevykh Complexov Raslichnykh Raionov SSSR.Pp.77-83.Moscow.
Březinová,D.,and Gabrielová,N.1974.A paleobotanical research of Neogene sediments in the environs of the village of Stojcin.Sb.Nar.mus.Praze,30:35-48.
Darwin,C. [1952]. The Origin of Species. London: Watts & Co. 434 pp.
Dorofeev,P.I. 1964.Sammatskaya Flora g.Apsheronska.Dokl.Akad.Nauk SSSR,156:82-87.
__________ 1966.O Flore Epochi Gippariona. Paleont. Zhurn.(1966):124-134.
Dubrovo,I.A., and Kapelist,K.V.1979. Katalog Mestonakhozhdenii Tretichnykh Posvonochnykh SSSR.Moscow: "Nauka". 58pp.
Dzabarova, H.S.1967. Flora i Rastitel'nost' Sapadnogo Azerbaidzhana v Verkhnemiocenovoe Vremya (Po palinologicheskim dannym). Baku.87pp.
__________ 1976. [The stages in the development of the upper Paleogene and Neogene of Azerbaijan]. In [Palynology in the USSR].Pp.105-108.Moscow, "Nauka".
Ellison,L.1960. Influence of grazing on plant succession of rangelands.Bot.Rev., 26:1-78.
Fataliev,R.A.1964. Verkhnesarmatskaya Flora gory Catar v Mezhdurechie Kury i Iory. Avtoreferat dissertacii.Leningrad. 17pp.
Flerov,K.K., and Yanovskaya,N.M.1974. Mlekopitayushchie posdnego Oligocena. Trudy Paleont. Inst. Akad.Nauk SSSR, 146:210-215.
Gabunia,L.K.1959. K Istorii Gipparionov.Moscow. Izd.Akad. Nauk SSSR. 570pp.
__________ 1970. Sur la signification des faunes de Mammifères du Miocène supérieur et du Pliocène de la région Ponto-Caspien. Gior. di Geologia(2)35:161-170.
__________ 1973. Belomechetskaya Fauna Iskopaemykh Posvonochnykh. Tbilisi: "Metsniereba". 138pp.
Gladkova,A.N.1956. Miocenovye Sporovo-pyl'cevye Complexy Vostochnogo Predkavkazya. In Atlas Miocenovykh Sprovo-pyl'cevykh Compexov Raslichnykh Raionov SSSR, pp.28-38. Moscow.
Godina, A.J., and David, A.I. 1973. Neogenovye Mestonakhozhdenia Posvonochnykh na Territorii Moldavskoi SSR. Kishinev.107pp.
Grishchenko,M.N., and Glushchenko, E.I. 1965. O miocenovoi Flore Ergenishkoi Tolshchi. Oksko-Donskoi nizmennoisti.Dokl. Akad.Nauk SSSR,69:1365-1367.
Grishchenko, M.N. 1966.[Stratigraphy of the Neogene of the Oksko-Donskaya lowland (According to Paleobotanic Material)]. In [The Importance of Palynological Analysis for Stratigraphic and Paleofloristic Investigation],pp.168-173.Moscow.
Ilyin, M.M. 1937. K Proiskhozhdeniu Flory Pustyn' Srednei Asii.Sovrem.Botan.6:95-109.
__________ 1946.[Some results gained by studying the formation of flora in the deserts of Central Asia]. In [Materials on the History of the Flora and Vegetation of the USSR], 2:197-256. Moscow.
Ilyinskaya,I.A.1960. Neogenovye Flory Sakarpatskoi Oblasti SSSR. In Flora i Fauna Karpat,pp. 77-86. Moscow.
Karmishina, G.I., and Kovalenko, N.D. 1976. K Voprosu o Sopostavlenii Pliocenovykh Otlozhenii Severnogo Pricaspiya i Severnogo Prichernomorya. In Voprosy Stratigrafii i Paleontologii, 2:138-149. Saratov.
Kornilova,V.S. 1960. Nizhnemiocenovaya Flora Kushuka (Turgaiskii Progib).Alma-Ata. 128pp.
Korotkevich,E.L. 1970. Mlekopitayushchie Berislavskoi Posdnesamatskoi Gipparionovoi Fauny. In Prirodnaya Obstanovka i Fauny Proshlogo, 5:24-124.
Kowalevsky,V.O. [1956]. Sobranie Nauchnych Trudov,2.Moscow:Izd.Akad.Nauk SSSR.448pp.
Lillegraven, J.A. 1972. Ordinal and familial diversity of Cenozoic mammals. Taxon,21:261-274.
Maslova, I.V. 1961. Resultaty Sporovo-pyl'cevogo Analisa Pliocenovykh Otlozhenii Kerchenskogo Poluostrova. Dokl. Akad. Nauk SSSR, 137:387-390.
Mitsul, E.Z. 1973a. Palynologicheskaya Kharakteristica Miocenovykh Otlozhenii Moldavii.Avtoreferat Dissertacii. Kiev,18pp.

____________ 1973b. [Palynological characteristics of the Sarmatian deposits of Moldova]. In [The Palynology of the Cenophytic], pp.170-173. Moscow.

Nemkov, G.I., Muratov, M.V.,et al. 1979. Istoricheskaya Geologiya. Moscow. 319pp.

Pachosky, I.K. 1917. Opisanie Rastitel'nosti Khersonskoi Gubernii. 2. Stepi. Materialy po Issledovaniu Pochv i Gruntov Khersonskoi Gubernii. Fasc. 13.

Pakhomov,M.M., and Pendova, A.M. 1978. Iskopaemye Flory Pamiro-Alaya kak Pokasateli Izmeneii Klimaticheskikh Uslovii v Kainozoe. Izv. Akad. Nauk SSSR, Ser. Geograf., 4:89-97.

Pavlovic, M.B. 1969. Miozän-Säugetiere des Poploca-Beckens. Belgrade. 394pp.

Prokhanov, Y.I. 1965. [Herblands and the latest desert, their nature and origin.] In [Problems of the phylogeny of plants], pp. 124-154. Moscow.

Pulatova, M.Z. 1972. Sporovo-pyl'cevaya Kharakteristika Pogranichnykh Sloev Paleogena i Neogena Yuzhnogo Sclona Gissarskogo Khrebta. In Litologia i Stratigrafia Neftegasonosnykh Tolshchi Tadzhikskoi Depressii, pp.162-183.Dushanbe.

Rybakova, N.O. 1966. [Palynological characteristics of Pannonien deposits in certain sections of the Solotvin Basin in the Transcarpathian district.] In [The Importance of Palynological Analysis for Stratigraphic and Paleofloristic Investigations], pp. 178-184. Moscow.

____________ 1974. Palynologicheskaya Kharakteristika Verkhnemiocenovykh i Pliocenovykh Otlozhenii Sakarpatskoi Oblasti USSR. In Materialy VIII i IX S'ezdov Karpatsko Balkanskoi Associacii, pp. 67-70. Kiev.

Shchekina, N.A. 1960. Istoria Neogenovoi Flory Ukrainskikh Karpat i Prikarpatya. In Flora i Fauna Karpat, pp. 58-74. Moscow.

____________ 1966. [History of the flora and vegetation of the Ukraine in the Pliocene.] In [Importance of Palynological Analysis for Stratigraphy and Paleofloristic Investigation], pp. 184-188.

____________ 1973. [Development of Vegetation in the south of the European part of the USSR in the late Paleogene and Neogene according to the data of spore-pollen analysis.] In [The Palynology of the Cenophytic],pp. 159-162. Moscow.

____________ 1978. Istoria Rasvitiya Rastitel'nogo pokrova yuga Ukrainy v Pozdnem Miocene - rannem Pliocene. Tesisy Dokladov VI Delegatskogo S'ezda VBO, pp. 367-368.

Thenius, E. 1959. Handbuch der stratigraphischen Geologie. Tertiär. Zweiter Teil. Wirbeltierfaunen. Stuttgart. 328pp.

Timoshina, I.A. 1973. [Pliocene flora of the northern Caspian region.] In [Palynology of the Pleistocene and Pliocene], pp. 178-180. Moscow.

Tolmachev, A.I. 1955. K Istorii Rasvitiya Rastitel'nosti Otkrytykh Landshaftov Zemnogo Shara. II Nauchn. Sessiya Sektora Paleobiologii Akad. Nauk Gruzinskoi SSR. Tezisy Dokladov, pp. 11-19. Tbilisi.

Valueva, M.N. 1973. [Development of the late Cenozoic flora of Mangyshlak, Ustiurt, and Priaralye.] In [Palynology of the Pleistocene and Pliocene], pp.181-184.Moscow.

Webb, S.D. 1977. A history of savanna vertebrates in the New World. Part I: North America. Ann. Rev.Ecol. Syst.,8:355-380.