

Inesa Vislobokova¹, Marina Sotnikova² & Andrey Dodonov²

¹ Paleontological Institute, Russian Academy of Sciences, Moscow

² Geological Institute, Russian Academy of Sciences, Moscow

Bio-events and diversity of the Late Miocene-Pliocene mammal faunas of Russia and adjacent areas

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The main dispersal events and changes in biodiversity of the mammalian faunas of Eurasia in the Late Miocene and Pliocene are analyzed based on data from the territory of the Former Soviet Union and Mongolia. New evidence provides a better understanding of the dispersal pattern of some dominant groups of mammals and the influence of these events on the evolution and changes in the biodiversity. There were at least four major dispersal waves of large mammals. The first Late Miocene dispersal wave from Northern America at about 10 Ma brought in Eurasia the first hipparionine horses together with odocoileine cervids. In the middle of the Turolian, the first Canidae came into Eurasia. The *Eucyon* dogs and camelid *Paracamelus* invaded Eurasia during the Messinian crisis. The horses of the genus *Equus* and first elks came from America at the end of the Early Pliocene. The main peaks of diversity of carnivores and dominant ungulate groups coincided in time, being within the MN 13 and MN 16 interval when essential changes of environment and climate occurred.

Correspondence: Paleontological Institute, Russian Academy of Sciences, Profsoyuznaya 123, 117997 Moscow, Russia, e-mail: ivisl@paleo.ru; Geological Institute, Russian Academy of Sciences, Pyzhevskii 7, 109017 Moscow, Russia, e-mail: sotnik@geo.tv-sign.ru, dodonov@geo.tv-sign.ru

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INTRODUCTION

The dynamics of mammalian community diversity was connected with two types of bio-events: evolutionary origins and dispersal events that were closely related to corresponding environmental and climatic changes. The general patterns of evolution of mammal faunas and dominant groups can be reconstructed only on the basis of data from the whole world. But each separate fragment of the evolution of the dominant groups recorded in different territories is very important

for a better understanding of their evolutionary trends and dispersal and can be useful for a further reconstruction of the history and ecology of terrestrial ecosystems. The newcomers enriched the autochthonous faunas and, in some cases, essentially influenced the evolving composition and evolutionary trends of the mammalian faunas. The excellent example of such influence is a well known dispersal event - an arrival of the hipparionine horses in Eurasia during the World Ocean drop at about 11-10 Ma that have led to the

appearance and wide dispersal of the *Hipparion* faunas there. A pan-Eurasian spread of these faunas continued from the beginning of the Late Miocene up to the Middle Pliocene.

The territory of Russia and adjacent countries (Georgia, Ukraine, Moldova, Kazakhstan, Tadjikistan, and Mongolia; in short: the FSU and Mongolia) are very representative for a better understanding of evolution and dispersal of mammals. In the Late Cenozoic, this territory was not only a great area of adaptive radiation and evolution of mammals, but also the place through which many dominant groups migrated. The data on occurrence of some representatives of carnivores and ungulates in the Late Miocene and Pliocene of the studied area allow us to improve the calibration of some well known dispersal events, to receive more definite data on the occurrence and evolution of some genera, and to add several forms to the lists of well known participants of the major dispersal waves. The data from the FSU and Mongolia are based on well studied and, in many cases, magnetostratigraphically calibrated faunas

(Sotnikova *et al.* 1997, Pevzner & Vangengeim 1993, Vangengeim & Pevzner 1993, Vislobokova 1996, etc.) with a revised stratigraphic position in the general geochronological scale. These faunas generally correlate well with the European MN unit system, as well as with the Chinese NMU zones (Figs. 1, 2).

EVOLUTIONARY AND DISPERSAL EVENTS

The penetration of immigrants into Eurasia from North America and Africa caused a number of adaptive radiations there. The diversification of faunas of the territory of the FSU and Mongolia was also affected by faunal exchanges with the Mediterranean Region and China. A number of important dispersal events took place during the late Miocene and Pliocene. The majority of them occurred during the sea level lowering events associated with the advance of Arctic ice, and later with joint Arctic and Antarctic ice advances. Five of these events have been correlated with Global climatic events during the following intervals: 11-10 Ma, 6 Ma,

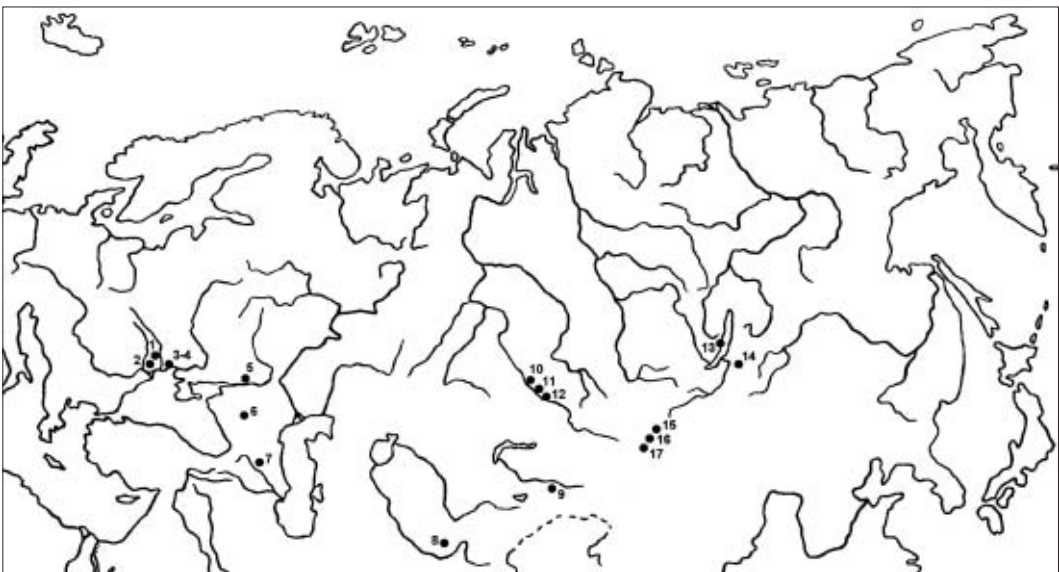


Figure 1 Main Late Miocene-Pliocene localities of mammals of the FSU and Mongolia used in the article. **1** - Kalfa, **2** - Etuliya, **3** - Odessa (Bolshoi Fontan), **4** - Odessa (Catacombs), **5** - Liventzovka, **6** - Kosyakino, **7** - Eldar, **8** - Kuruksay, **9** - Bota Moinak, **10** - Pavlodar, **11** - Lebjazh'e - I, **12** - Podpusk-Lebjazh'e, **13** - Olkhon, **14** - Udunga, **15** - Khirgis-Nur - 2, **16** - Chonok-hariakh, **17** - Oshin.

3.8-3.5 Ma, 3.2-3.1 Ma, and 2.5 Ma (Shackleton & Opdyke 1976; Ciesielski & Weaver 1983).

The most prominent dispersal events during the late Miocene and Pliocene interval concerns the dispersal waves of mammals through Beringia. The faunal exchanges across Beringia influenced the evolution of mammalian communities in both Eurasia and North America. The several waves of dispersals of mammals into Europe from North America across Beringia are traced in the late Miocene and Pliocene (Tedford *et al.* 1987; Woodburne & Swisher 1995; Dawson 1999). Almost all known mammalian taxa passing through Beringia (Tedford *et al.* 1987) are

recognised in the area studied. Moreover, the pattern of occurrence of canids is essentially enriched by the data from Mongolia, and two dispersal events of cervids can be added to known data based on fossil remains from the FSU.

Some genera involved in the Late Miocene and Pliocene trans-Beringian faunal exchange originated in North America. Prior to dispersal events, the members of these families existed only in North America. In the territory of the FSU and Mongolia, seven late Miocene-Pliocene large mammalian dispersal events of this category are recorded: the Equidae (three events), Canidae (three events), and Camelidae (one event). Two

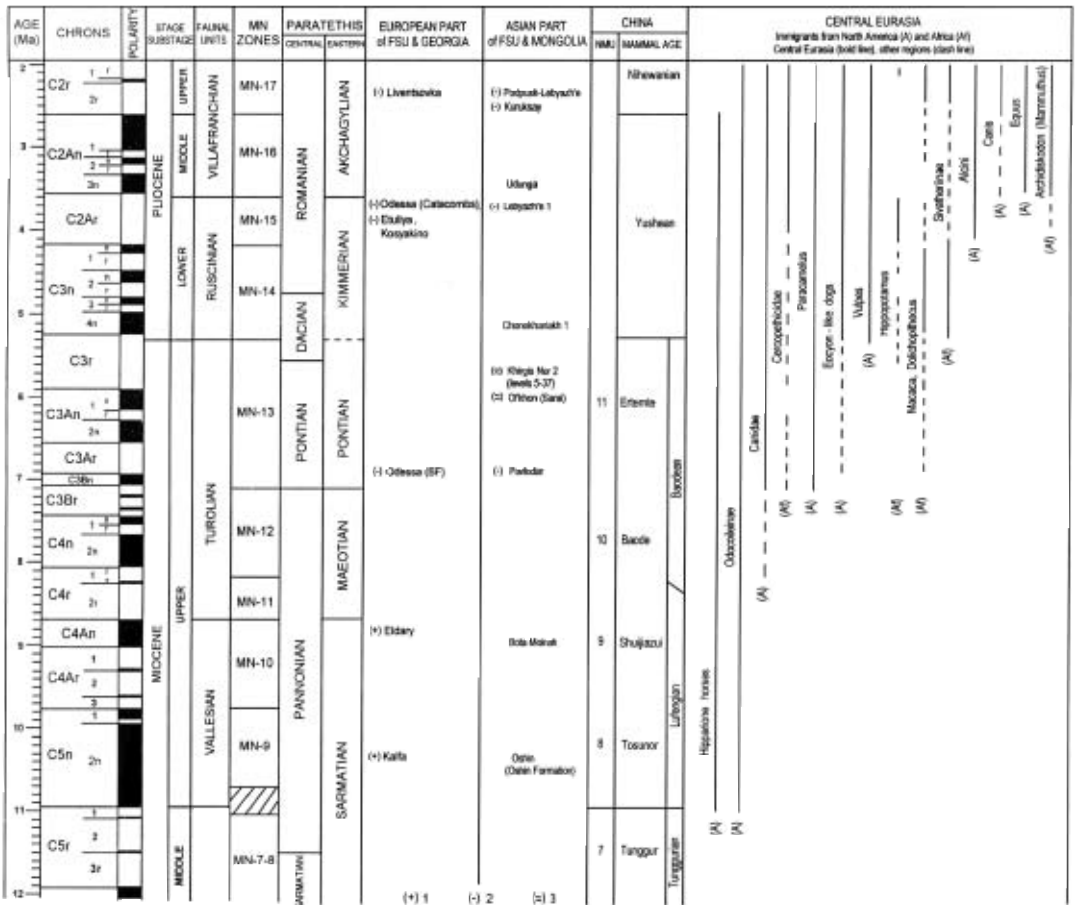


Figure 2 Occurrence of main Late Miocene and Pliocene mammal faunas of the FSU and Mongolia and major dispersal events. Magnetization: **1** - normal, **2** - reversal, **3** - alternated.

other bio-events concerned genera of subfamilies of Asian origin but with a North American history prior to their return westward dispersal: the Cervidae (subfamilies Odocoileinae and Alcinae). All of these events occurred through four or five dispersal waves. Afro-Asian and intercontinental faunal exchanges also influenced the composition of mammalian communities in the territory of the FSU and Mongolia. The Afro-Asian exchange was especially productive in the territory at the beginning of the Pliocene after the Messinian crisis about 6 Ma. It resulted in the appearance of autochthonous African forms (cercopithecoid primates, hippopotamids, and some giraffids) in the northern part of the Black Sea area (Vangengeim *et al.* 1998). The separate fragments of evolution of cercopithecoids and giraffids are further traced in the Pliocene of Kazakhstan, Tadzhikistan, Transbaikalia, and Mongolia.

In Northern Eurasia, the first great dispersal event occurred at the beginning of the Late Miocene when hipparionine horses first invaded the territory. According to different authors, the age of this event is estimated from 11 to 10 Ma (Tedford *et al.* 1987; Bernor *et al.* 1988; Woodburne & Swisher 1995; Woodburne *et al.* 1996; Dawson 1999; Qiu *et al.* 1999). This event coincided with the sea level lowstand in a cool interval at the beginning of the Late Miocene. In that dispersal wave, *hipparionine* horses were accompanied by odocoileine cervids. In the late Late Miocene, another most significant exchanges between North America and Eurasia occurred during the drop in the sea level in the Messinian crisis (Tedford *et al.* 1987; Woodburne & Swisher 1995; Dawson 1999). It was a time when the families Canidae and Camelidae first invaded Northern Eurasia. A considerable faunal renovation at the genus level also occurred at the transition from the early to middle Pliocene (Ruscinian/Villafranchian transition) during the cooling in the interval 3.8-3.5 Ma (Vislobokova *et al.* 1993, 1995 b). In North America, many new genera also appeared

approximately in the same interval: between 4.0 and 3.4 Ma in the early Blancan (Lundelius *et al.* 1987). An intensive faunal exchange between faunas of these continents brought elks and horses of the genus *Equus* from North America into Eurasia. The data on some dominant groups involved in dispersal events are summarized below in the order of their first appearance data (FAD) on the continent.

Family Equidae (Hipparionines)

Eurasian hipparionine horses derived from North American *Cormohipparion* (Bernor *et al.* 1996) and dispersed into Eurasia at the beginning of the Late Miocene at about 11 or 10 Ma (Tedford *et al.* 1987; Woodburne & Swisher 1995; Rögl & Daxner-Höck 1996; Dawson 1999). The dispersal route of hipparionine horses from North America into Eurasia went through the area with temperate climate and woodland dominated. Soon after their arrival, hipparionine horses were radiated into several lineages and became wide spread throughout the continent (Zhegallo 1978; Krakhmalnaya 1996; Forsten 1997, and others).

The FAD of *Hipparion* in the territory of the FSU and Mongolia coincides with that in Europe and is characteristic for faunas correlated to MN 9. In the European part of the FSU, the most ancient hipparionine horses are known from the middle Sarmatian (Bessarabian): *Hipparion sarmaticum* is described from Kalfa, Moldova (Lungu 1973), referred by paleomagnetic data to Chron C5n (Pevzner & Vangengeim 1993; Vangengeim & Pevzner 1993). In Kazakhstan the oldest fauna with *Hipparion* is known from Bota Moinak - Vallesian equivalent (Tleuberdina 1988). In Mongolia, the earliest *Hipparion* found in the Oshin Formation, above the horizon with the ruminant assemblage similar to that of Tunggur, China, belonging to 7 NMU zone by Qiu *et al.* (1999) which corresponds to MN 7-8 zones of Mein (1989, 1999). In China, the earliest hipparionine horses were recorded from the

Amuwusu local fauna, which is correlated with the lower part of the European MN9 (Qiu *et al.* 1999). In southern Asia, FAD of *Hipparion* in the Siwaliks at 10.7 Ma (Pilbeam *et al.* 1996) also confirms a very quick pan-Eurasian dispersal of these equids.

One of the centres of the early adaptive radiation of hipparionine horses was in Central Asia. During the Vallesian stage, *Hipparion* diverged there at least into two lineages, that were represented by *H. elegans* and *H. mogoicum* in the Turolian of Mongolia (Zhegallo 1978). A large radiation of *Hipparion* in Central Eurasia occurred at the beginning of the Turolian; other important evolutionary changes are marked by the appearance of the group of caballoid hipparions at the Turolian/Ruscinian transition. The last event was characteristic mainly for China and Mongolia, but also for the Indian subcontinent and Africa (Zhegallo 1978; Forstén 1997). Bernor *et al.* (1996) discuss their incursion into Central and Western Europe.

Family Equidae (*Equus*)

Contrary to the hipparionine migration event, the dispersal of *Equus* from North America into Eurasia appears to have been more gradual, and the first steps in an Eurasian history were less successful. In Western Europe, FAD of this genus is characteristic for MN 17, and the earliest findings are close in age to 2.5 (Lindsay *et al.* 1980; Forsten 1996) or, with the Cande & Kent 1995 GPS, to 2.6 Ma (Bernor & Armour-Chelu 1999a,b). The dispersal to Africa was delayed nearly 300,000 years (Bernor & Armour-Chelu 1999b). This date of *Equus* dispersal event is widely accepted. However, the invasion of Eurasia by *Equus* appears to have occurred prior to that time. The horses of this genus might come in Eurasia together with alcines.

The earliest *Equus* in Asia is *Equus* sp. from the Lebyzh'e 1 in the southern Western Siberia (Vislobokova 1996). According to paleomagnetic data, the Lebyzh'e 1 fauna might be older than 3.6 Ma and undoubtedly

older than 2.6 Ma (Vislobokova 1996). *Equus* sp. existed in Western Siberia during the cooling that might correspond to that in the intervals 3.8-3.5 or 3.2-3.1 Ma. Other data on an earlier FAD of *Equus* in Europe were obtained in Romania: *Equus* was marked in Malusteni, Berbesti, and Beresti (MN 15) (Samson 1975), but, unfortunately, these data are not taken into account. In the Upper Siwaliks the first appearance for *Equus* was marked at the Tatrot-Pinjor transition (Nanda 1981). According to Opdyke *et al.* (1979), the lowest record of *Equus* has been shown in Pakistan at the base of Matuyama Chron. The very interesting paleomagnetic data of Tandon *et al.* (1984) resulted that the lower part of the Pinjor with finding of *Equus* has mostly normal magnetization (thickness 400 m), which can be interpreted, by our approach, as the Gauss Chron with very characteristic structure. However, Tandon *et al.* (1984) followed a more traditional interpretation of stratigraphical position of *Equus* showing for it unusually very thick interval of the Reunion-Olduvai magnetic events. The data from Siberia allow us to consider that the time gap between the appearance of *Equus* in America and in Eurasia was shorter than it was presumed by Lindsay *et al.* (1980) and Bernor & Armour-Chelu (1999a, b). The most ancient species of the genus (*E. simplicidens*) is present in the Hagerman fauna, which has K-Ar dates from 3.57 to 3.2 Ma and corresponds to the first half of C2An Chron (Gilbert Chron; Bernor & Armour-Chelu 1999a, b). This fauna contained many genera typical also for the contemporaneous faunas of Eurasia.

Family Cervidae (Odocoileinae)

Odocoileines derived from North American blastomerycines (Vislobokova 1990). The first odocoileines invaded Eurasia together with hipparionine horses. Similar to earliest hipparionine horses, they were adapted to open woodland and could go through the Beringian Bridge of that time. Later, these cervids became usual members of *Hipparion*

faunas. In Eurasia they diverged into two lineages (Odocoileini and Capreolini). The earliest Eurasian odocoileines were represented by the genera *Procapreolus*, belonging to the tribe Capreolini. The most ancient *Procapreolus* are known from the Black Sea area (Eldar (Korotkevitch 1988) and from the Pannonian Basin. The adaptive radiation of the Capreolini took place in the late Miocene. An important evolutionary event (the transformation from *Procapreolus* to *Capreolus*) occurred at the Early Pliocene/Middle Pliocene boundary (Vislobokova *et al.* 1995). In Eurasia, the Capreolini survived up-to-date. The first records of Odocoileini, a group close to the ancestor of Recent *Rangifer*, are traced only in the late Miocene of Kazakhstan (Pavlodar, MN 13) and Russia (Baikal, Olkhon, MN 13) (Vislobokova 1990).

Family Cervidae (Alcinae)

Alcines also derived from North American blastomerycines (Vislobokova 1990). But their FAD in Asia is recorded earlier than in North America. The most ancient alcine in Eurasia is known from the late Ruscinian (MN 15) of the Cis-Caucasus (Kosyakino). Another most ancient alcine deer in Eurasia is Alcinae gen. indet. from the early Villafranchian (MN 16) of Transbaikalia (Udunga; Vislobokova *et al.* 1995a). This boreal group of cervids became widespread during the middle Villafranchian (MN 17) when *Libralces* existed in Northern Eurasia from Spain to Tadzhikistan in savannah-like landscapes together with *Archidiskodon* and *Equus* of the *stenonis* group. In the FSU, the remains of *Libralces* were found in the North Black Sea area (Liventzovka) and in Tadzhikistan (Kuruksay).

Family Canidae

The originally American Canidae came to Eurasia in the late Miocene (Turolian). There were several dispersal waves of canids through Beringia associated with dispersal events proposed by Tedford *et al.* (1987). There were two or three dispersal event of

the Canini (?‘*Canis*’, *Eucyon* and, apparently, true *Canis*) and one dispersal event of the Vulpini (*Vulpes*). The FAD of the family in Europe is referred to MN 12. The most ancient European canids are reported from Spain (Concud, Los Mansuetos, and Cerro de la Gariata, MN 12) as ‘*Canis*’ *cipio* (Crusafont 1950; Rook 1992; Ginsburg 1999). This canid is very poorly represented, and has uncertain relationships and no proper ancestral form in the New World. However, Rook (1993) marked some similarity of ‘*Canis*’ *cipio* with a relatively large and contemporaneous canid’s form (‘*Canis*’ sp.) from upper Hemphillian deposits of Northern America.

Eucyon had a long history in America from the Middle Miocene (Tedford & Qui 1996). In Eurasia it appears a bit later, during the Messinian. The earliest *Eucyon* was recorded from Brisighella in Italy, MN 13, as *Eucyon monticinensis* and Venta del Moro in Spain, MN13, as *Eucyon cf. monticinensis* (Rook 1992, 1993).

Recently, the occurrence of the family was stated in the Late Miocene of Mongolia. A *Eucyon*-like dog is determined from the Turolian of the Khirgis Nur II, level 5-37. The diversity of these dogs increased in the Pliocene, and include: *Eucyon* sp. in Italy (Casino, MN 14), Spain (La Galera 1, MN 14), and Greece (La Megalo Emvolon, MN 15); *Eucyon adoxus* in France (Perpignan, MN 15); *Eucyon odessanus* in Ukraine (Odessa Catacombs, MN 15) and Moldova (Etuliya and others, MN 15); and *E. Zhoui* and *E. davasi* from Yushenian (MN 14-16) of China (Rook 1993; Tedford & Qui, 1996; Vangengeim *et al.* 1998). The early Ruscinian *Eucyon*-like dogs and related forms are also recorded in Russia (Baikal Region), Kazakhstan, and Mongolia (Vangengeim *et al.* 1998; Sotnikova personal data). In Europe the occurrence of these dogs was restricted by the Ruscinian, but in Asia they existed up to the Middle Villafranchian where they enjoyed great diversity: *E. minor* (Nihewan, China), *E. kuruksaensis* (Kuruksay,

Tadzhikistan), *Eucyon* sp. (Podpusk-Lebijazh'e, Kazakhstan) (Teilhard & Piveteau 1930; Sotnikova 1989; Tedford & Qui 1996).

Another North American immigrant in Eurasia was the fox *Vulpes*. *Vulpes* is known from the late Miocene in North America. Its arrival in Eurasia might be associated with the dispersal event at the Miocene/Pliocene boundary transition. The most ancient and less advanced form of *Vulpes* has recently been observed in Mongolia (Chonokhariakh, MN 14). In China (Yushe Basin), the earliest fox was described by Qiu & Tedford (1990) as a new species, *V. beihaiensis*, from Mazegou Formation (MN16). The oldest Mediterranean fox, *Vulpes calaticus*, was recently recorded by Ginsburg (1998) in Turkey (Çalta, MN15).

In Europe, a vulpine's FAD referred to the end of the Ruscinian; *Vulpes precorsak* is known from southern Ukraine (Odessa Catacombs) and from a number of the Pliocene sites in Hungary.

In the Pliocene, canids underwent a major adaptive radiation in Asia evidenced by a large diversity of *Eucyon*-like dogs and raccoon dogs *Nyctereutes*. Two species of *Nyctereutes* are recorded in Yushe Basin (China) from upper part of Gaozhuang and from the Mazegou Formation (MN15-16 correlative). Both species, the primitive form *N. tingii* and derived *N. sinensis*, demonstrate the contemporaneous occurrence of two sister taxa in the early Pliocene of Central Asia (Tedford & Qiu 1991). In Europe only one taxa of raccoon-dog *N. donnezani* occurred during the early Pliocene.

Besides these canids, the large wolf-sized *Canis* first appeared in the Middle Pliocene (Early Villafranchian) about 3 Ma in Asia (Yushe Basin, China). In the Middle Villafranchian after 2.5 Ma, its range included northern China (Nihewan) and Tadzhikistan (Kuruksay) (Teilhard & Piveteau 1930; Tedford *et al.* 1991; Rook 1993; Sotnikova *et al.* 1997). In Europe the middle Villafranchian occurrence of the wolf-sized canids is recorded now in Costa

S.Giacomo (Italy), Sèneze (France), Slivnitsa (Bulgaria), Liventzovka (Russia) (Rook 1993; Spassov 1997a, b; Sotnikova *et al.* 2002).

Family Camelidae

Paracamelus, a probable descendant of the North American genus *Procamelus*, dispersed in Eurasia during the Messinian crisis apparently together with *Eucyon*. The dispersal of *Paracamelus* appears to have been rather quick, similar to that of hipparionine horses. But *Paracamelus* was not among dominant forms in the Late Miocene mammal faunas, and its range was restricted to areas with open landscapes and a dry climate. In the FSU, the most ancient remains of this genus are recorded in the Late Miocene of the Northern Black Sea area (Odessa, Bolshoi Fontan, MN 13). The earliest European record of *Paracamelus* is known from the late Miocene of Spain (Venta del Moro and Librilla; Morales *et al.* 1980; van der Made & Morales 1999). The age of Venta del Moro is about 5.8 Ma, and radiometric dates for underlying rocks in Librella range from 6.2(±0.3) to 7(±0.03) Ma (Montenat *et al.* 1975). At the end of the Late Miocene (MN13), *Paracamelus* appears to have inhabited North Africa (Wadi Natun in Egypt; van der Made & Morales 1999).

In the Pliocene the range of *Paracamelus* essentially enlarged eastward and southward and included the territories of the North Black Sea area, southern Western Siberia, Kazakhstan, and China. In China, the first occurrence of camelids is recorded in the early Pliocene of the Yushe Basin (lower part of Gaozhuang Formation) at about 5.4 Ma (Flynn *et al.* 1991; Qui & Qui 1995; Tedford *et al.* 1991). In the northern Black Sea area, the abundance of camelids sharply increased at the Early/Late Ruscinian boundary owing to the increase of the aridity in Central Eurasia. The evolutionary evidence on *Paracamelus* origin and the presence of fossil remains of this genus in southern east European part of the continent better support a presumption of Tedford *et al.* (1987) that

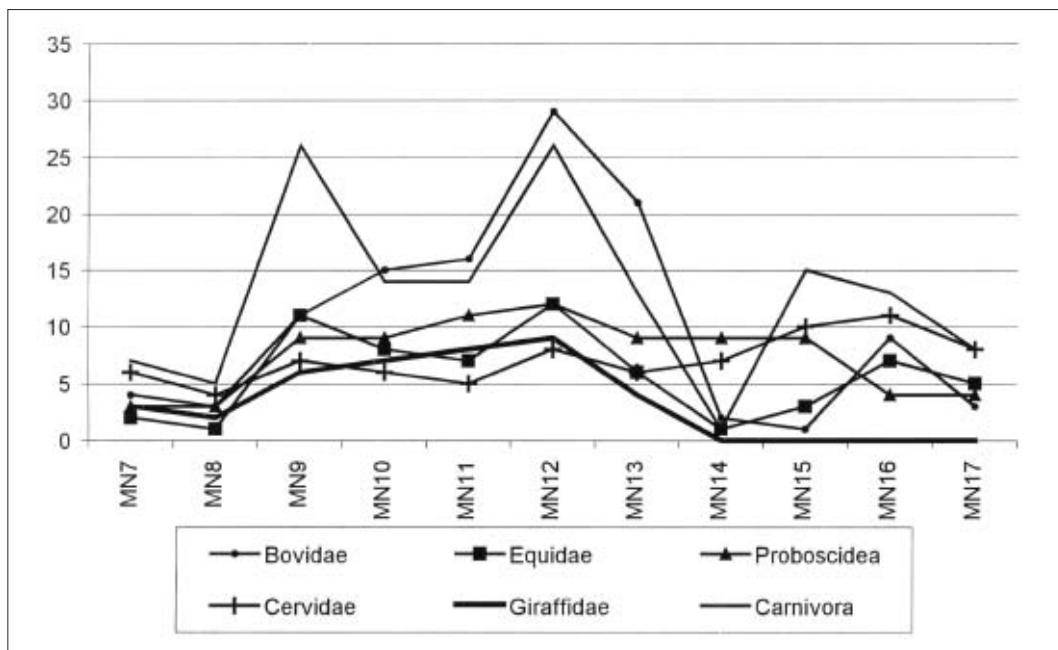


Figure 3 Dynamics of biodiversity of carnivores and ungulates in the European part of the FSU.

Paracamelus came into Western Europe from North America through southern Siberia but not via Africa. The last hypotheses postulated by Morales *et al.* (1980) and Pickford *et al.* (1993). The dispersal could occur through Kazakhstan and then along the northern coast of Black Sea where suitable environmental conditions existed. The future records undoubtedly will help to resolve this problem.

BIODIVERSITY

The preliminary analyses of the data set on the mammals from the FSU and Mongolia according to the NOW (Neogene of the Old World) database (<http://www.helsinki.fi/science/nw/>) revealed that the peaks of diversity of carnivores and dominant ungulate groups (equids, cervids, giraffids, and bovids) coincided in time, being within the MN 13 and MN 16 (Figs. 3, 4). Meanwhile, these peaks are less manifest in the European part of the territory than in the Asian area. This is probably due to an ameliorating climatic inf-

luence of the Paratethys. The main turnover in the composition of the faunal assemblages in the European and Asian parts of the FSU occurred at the Turolian/Ruscinian transition after the Messinian crisis (Vislobokova *et al.* 2001). Other changes in mammal diversity are clearly marked at the end of the Miocene (MN 12/13) and at the Middle/Late Pliocene (MN 16/17) boundaries about 2.5 Ma. The former was associated with well-known Global climatic and environmental shift, which were reflected particularly in the accumulation of the Red Clay and beginning of aeolian sedimentation in China (see Fortelius *et al.* this volume). The latter event was complemented by the onset of the loess forming processes in Central Asia due to the cooling and aridification in the Northern Hemisphere. In Tadzhikistan, the fauna of the middle Villafranchian (MN 17) corresponds to the upper Pliocene loess-paleosol formation.

Taxa with Chinese affinities prevailed in the faunal assemblages of Asia (Baikal Region, Kazakhstan, and Mongolia), while

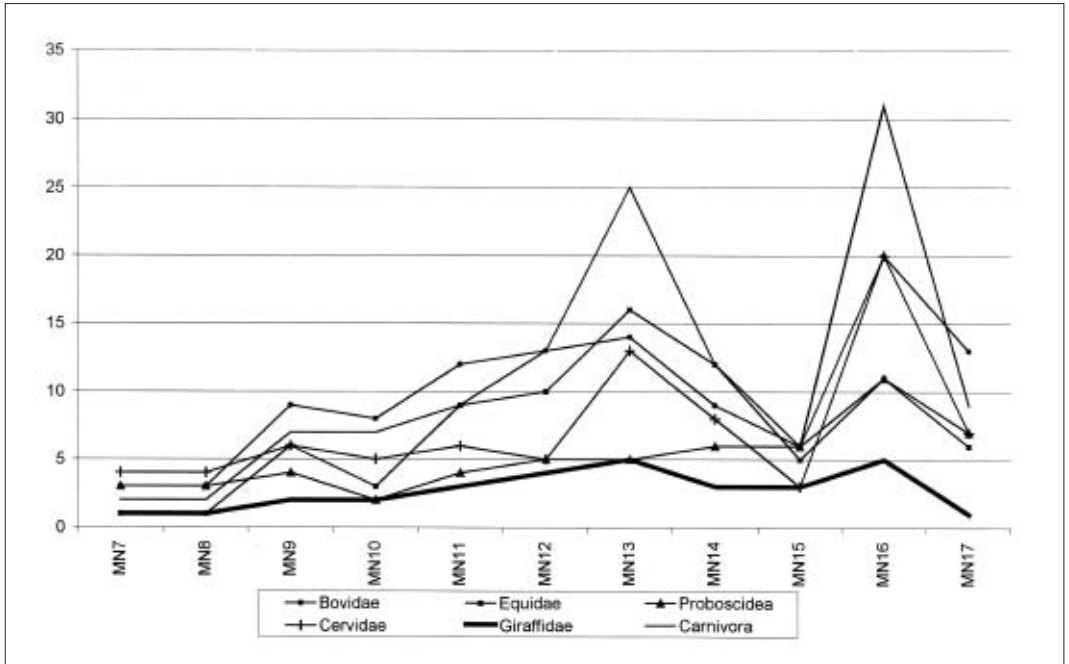


Figure 4 Dynamics of the biodiversity of carnivores and ungulates in the Asian part of the FSU.

the fauna from Tadzhikistan consisted of a mixture of Mediterranean and Asian elements. The mammalian communities of the European part of the area studied were closer in composition to the Mediterranean faunas and included certain endemic forms.

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