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Late Miocene mammal events and biostratigraphy in the Eastern Mediterranean

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A biostratigraphic division of the Neogene in the Eastern Mediterranean is highly necessary. Data from Late Miocene mammalian faunas and absolute dating were collected and used for a first biostratigraphic division. Some important mammalian taxa have been selected and their paleobiogeographic distribution is given. The dispersal events of these taxa are used for the division of the Late Miocene. A preliminary biozonation of the Late Miocene is proposed based on mammalian faunas. However, more data from various countries are necessary in order to obtain a quite reliable biostratigraphy.

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INTRODUCTION

During the Late Miocene, a great number of mammal taxa from Asia and Africa arrived in Europe using Asia Minor and the Balkan Peninsula as access roads. In addition, west-central European mammalian taxa used the same areas for their migration to the east. The importance of migration through these two geographic regions is very large and the various mammalian dispersal events can be used for a biostratigraphic division. The mammalian localities in this area are quite abundant and provide a good knowledge of the faunas. During the last two decades, several new localities have been discovered and new material has been unearthed and determined. The new collections of fossils are well correlated with the stratigraphy, while

the magnetostratigraphy of some of the sections provides quite reliable absolute ages. Certainly, in many cases the available data are limited or few, the determinations are doubtful and the biochronology not precise. Besides all these difficulties: the Eastern Mediterranean is an interesting region for the study of the mammalian migrations and their biochronological significance, and it is quite possible to get some preliminary results which will be enriched in the future with new ones coming from projects in progress, and all together, will give a complete idea about these migrations and biochronology.

In this article, we present data on the paleobiogeographic distribution of some Late Miocene taxa in the Eastern Mediterranean and correlate some of the mammalian events

with the available absolute dating and biostratigraphy in order to arrive at a preliminary biostratigraphic division of the Late Miocene. The Late Miocene was selected because there are several mammalian localities in the Eastern Mediterranean, with well-known faunas and quite precise datation. Moreover, the paleogeography of the area is well known and thus we can check the mammalian migrations.

MATERIAL AND METHODS

The faunal lists and the age of the various Late Miocene localities are issued from the database NOW: www.helsinki.fi/science/now/database.htm. I used the last version that is referred in the text as NOW 2000. For the Greek localities, I also used a personal list. For the Bulgarian localities, NOW 2000 and the lists of Nikolov (1985) were used. For the Turkish localities, the faunal lists of Sickenberg *et al.* (1975) and NOW 2000 were used, as well some personal lists of Dr S. Sen. Additional data were also found in Bonis & Koufos (1999), Lunkka *et al.* (1999), Koufos & Kostopoulos (1997), Korotkevich (1988) and Theodorou *et al.* (this volume). The Late Miocene mammal faunas of the Eastern Mediterranean are very diverse. Consequently, I selected the most common and characteristic taxa with their localities (Appendix 1). The coordinates given in NOW 2000 were used for the location of the various fossiliferous sites in the maps. The geographic term Eastern Mediterranean includes the Balkan Peninsula and Asia Minor, but in the maps, the localities of the neighbouring areas are also included.

Abbreviations

FLA = First Local Appearance, the first occurrence of a taxon in the Eastern Mediterranean.
 LLA = Last Local Appearance, the last occurrence of a taxon in the Eastern Mediterranean.
 NOW = Neogene of the Old World.

PERISSODACTYLA

Hipparion -datum in the Eastern Mediterranean

The appearance of the hipparionine horses, known as *Hipparion*-datum, is a major event indicating the beginning of the Late Miocene in the whole Mediterranean region and Europe. The hipparionine horses are Miocene immigrants with a North American origin. According to Haq *et al.* (1988) a strong sea level drop around 11.0 Ma opened the Beringian landbridge and enabled some north-American mammals to pass into Eurasia. The most important among them is *Hipparion*, which expanded rapidly and conquered the Old World. Concerning the *Hipparion*-datum, two different opinions exist: the first one suggests a synchronous event for the whole Mediterranean region, while the second one supports a diachronous event. Recently, Garces *et al.* (1997) suggests a time-transgressive *Hipparion* dispersal with a short time diachrony.

The age of the *Hipparion*-datum is still an often discussed problem, and two main opinions exist. The first opinion proposes that *Hipparion* occurs between 11.5 and 11.0 Ma, in the upper part of Chron C5r (Agustí *et al.* 1997, Garces *et al.* 1997, Bernor *et al.* 1988). The second opinion suggests that the *Hipparion*-datum can be dated to 10.8-10.3 Ma, in the lower part of Chron C5n (Sen 1990 1997, Pilbeam *et al.* 1996, Swisher III 1996, Kappelman *et al.* 2003). The importance of this event and its dating, makes it necessary to look more precisely at the available data on *Hipparion* from the Eastern Mediterranean.

The only known chronological data on the appearance of *Hipparion* in the Eastern Mediterranean comes from Turkey. The FLA of *Hipparion* is recorded in the Sinap area (Fig. 1) and more exactly in Locality 4, which is correlated to Early Vallesian, MN9 (Lunkka *et al.* 1999). Its age is estimated to be 10.692 Ma, while the MN8/MN9 transition is estimated between the Locality 64 and

Locality 4 at 10.728 Ma (Kappelman *et al.* 2003). This age correlates quite well with the age of 10.7 Ma proposed for the *Hipparion*-datum in the Siwaliks (Pilbeam *et al.* 1996). In Greece, Early Vallesian localities are unknown and the first hipparionine horse is known from the Late Vallesian localities of Kastellios (Crete) and those of the Axios valley (Macedonia, Greece). The Kastellios section is correlated to Chron C4A corresponding to the time span 9.230-9.642 Ma (Sen *et al.* 1986). The first *Hipparion*'s remains were recorded at the level K2 (de Bruijn *et al.* 1972). Its age is estimated at about 9.5 Ma (Sen *et al.* 1986). Similar ages are also estimated for the Vallesian localities of the Axios valley; the oldest locality Xirochori 1 has an age of about 9.6 Ma (Sen *et al.* 2000). Based on these data, the *Hipparion*-datum for the Eastern Mediterranean is dated at 10.7 Ma.

Radiometric dating is known from Höwenegg, Germany. $^{40}\text{Ar}/^{39}\text{Ar}$ dating of the 'tuffites' yielded ages between 10.86 ± 0.04 and 10.29 ± 0.07 Ma, while the Höwenegg deposits are closer to the younger ages (Swisher III 1996). In Austria, the locality of Gaiselberg is considered as being at the beginning of the Vallesian and older than 11.0 Ma (Woodburne *et al.* 1996). In Eastern Europe, the locality of Zeltokamenka includes the co-existence of *Anchitherium* and *Hipparion* (Gabunia 1981). The revised paleomagnetic data suggest an age at about 10.5 Ma for Zeltokamenka (Sen 1997).

Taking into account all the available data from the Eastern Mediterranean, the FLA of the hipparionine horses and consequently the beginning of the Vallesian can be dated at 10.7 Ma. The arrival of *Hipparion* is an important event and besides its short time diachrony, it is a useful tool for correlations. During the Vallesian, the hipparions were common in the area but low in frequency. Later, the genus diversified with the appearance of various species. At the beginning of the Late Vallesian, three different species have been recognized in the Axios valley of Greece (Koufos 2000a). However, the great

development and high frequency of the genus occurred during the Turolian.

Both the largest number of specimens and the highest percentage of individuals is reached during the Turolian where they were commonly represented by more than 50% of the specimens or individuals of a locality. There are important differences between the Vallesian and Turolian hipparions as noted by various specialists. These differences are well expressed in the hipparions of Central and Western Europe. During the Vallesian in the Eastern Mediterranean, the environmental conditions were drier and more open than those of Central and Western Europe (Bonis *et al.* 1992 1999) and consequently the differences between the hipparions from these areas are more expressed. A decrease in the abundance of hipparions is observed during the Pliocene. This may be an artefact of the record because the number of Pliocene localities is still quite low in the Eastern Mediterranean.

The last hipparionine horses are recorded in the locality of Gülyazi, Turkey (Fig. 1) dated to 3.4-2.6 Ma (NOW 2000). In Greece, the last appearance of *Hipparion* is traced in the locality of Apolakkia (Rhodes Island) dated to the Late Ruscinian (MN15). The overlying locality of Damatria, with remains of *Equus*, is dated to the Villafranchian (Benda *et al.* 1977). In Romania, *Hipparion* is recorded in the locality of Malusteni, which is correlated to MN15, and in Georgia from Kvavebi dated to MN16 (NOW 2000). Until now, there is no evidence in the Eastern Mediterranean on the co-existence of *Hipparion* and *Equus*. The hipparionine horses seem to disappear in the area before the end of the Pliocene, while in Africa they existed until the Early Pleistocene. At the moment, the available magnetostratigraphy or radiochronologic data are insufficient for a precise dating of the hipparion's extinction event in the Eastern Mediterranean.

Ceratotherium event

The late Miocene rhinocerotids include the

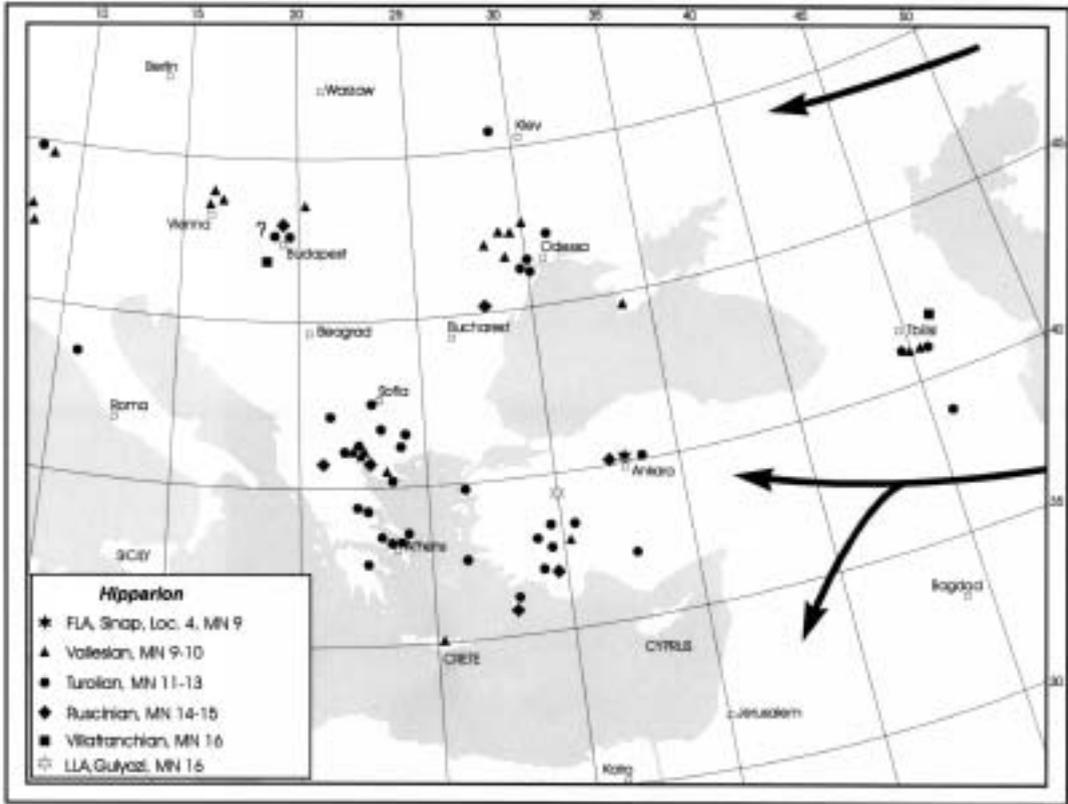


Figure 1 Geographic distribution of *Hipparion* during late Miocene in the Eastern Mediterranean.

genera *Stephanorhinus*, *Ceratotherium*, *Chilotherium* and *Aceratherium*. *Ceratotherium* is quite abundant and common in Late Miocene. Its FLA is traced in the locality of Esme Akcaköy, Turkey dated to the Early Vallesian (MN9, de Bruijn *et al.* 1992). The fauna of Esme Akcaköy is quite similar to or younger than those of the upper levels of the Sinap localities 8A, 8B and 12 (Sen pers. comm. 2001), correlated to upper MN9-lower MN10. *Ceratotherium* existed during the Late Miocene and disappeared at the end of the Turolian. Its LLA is recorded in the locality of Dytiko (Greece), dated to the upper part of the Late Turolian, MN13 (Bonis & Koufos 1999).

RODENTS

Several rodents have been recorded in the various Late Miocene localities of the Eastern

Mediterranean, but generally, the available material is restricted. In fact, the study of the Late Miocene micromammalian faunas in the Eastern Mediterranean is incomplete and the data are quite limited. In the Balkans, the available data comes only from Greece, while they are almost absent from Albania, former Yugoslavia, Bulgaria and Romania. In Turkey, there are some references but again the data are as limited as in Greece. This makes the correlation with the Western Mediterranean difficult. However, the available data will be used in this article, as they include important events, useful in the biostratigraphy of the Late Miocene.

Cricetulodon event

The genus *Cricetulodon* is quite rare in the Eastern Mediterranean. Its FLA is recorded in the locality of Bayraktepe 1 (Turkey) dated to Late Astaracian (de Bruijn *et al.* 1992, NOW

2000). Other occurrences are reported from the Sinap Locality 8A (Turkey) dated at 9.886 Ma and Kastellios (Greece) dated between 9.642 and 9.230 Ma, while its LLA is recorded in the Sinap Locality 84 dated at 9.367 Ma (Lunkka *et al.* 1999, Kappelman *et al.* 2003, Sen *et al.* 1986). In Spain, the taxon is well known and the *Cricetulodon*-zone characterizes the Early Vallesian (Agustí *et al.* 1997). Its first appearance in Spain is recorded in the pre-*Hipparion* levels of Hostalets de Pierola correlated to MN7+8 (NOW 2000), however, its acme zone is from Middle to Late Vallesian (Agustí *et al.* 1997).

***Progonomys* event**

The genus is considered typical for the Vallesian but a clear diachrony can be seen in its distribution (Sen 1990, 1997). In Pakistan *Progonomys* appeared at ca. 12.3 Ma, well before the appearance of *Hipparion* (Pilbeam *et al.* 1996). In the Eastern Mediterranean *Progonomys* appeared quite later. Its FLA is recorded in the Sinap Locality 108 (Sen pers. comm. 2001) dated at 10.135 Ma (Kappelman *et al.* 2003). In Spain, the first local appearance of *Progonomys* is estimated between 9.642–9.740 Ma (Agustí *et al.* 1997) coinciding with the Early/Late Vallesian boundary of 9.64 Ma (Sen 1997).

Progonomys is quite common in the Vallesian of the Eastern Mediterranean (Fig. 2). Except in Sinap (Turkey) it is present in the localities of Bayraktepe II and Karaözü (NOW 2000). The last two localities were dated to Late Vallesian (MN10, de Bruijn *et al.* 1992). Three Greek Vallesian localities contain records of *Progonomys*. The Kastellios locality in Crete includes a poor mammalian fauna but the correlation with the marine forams suggests either a Late Vallesian age (MN10) or an Early/Late Vallesian age (de Bruijn *et al.* 1972, de Bruijn & Zachariasse 1979). The magnetostratigraphy of the Kastellios section suggests an age between 9.642–9.230 Ma (see above in *Hipparion*). The locality of Biodrak (Greece) is also dated to the Late Vallesian (de Bruijn

& van der Meulen 1979).

Magnetostratigraphic data for Biodrak suggests a correlation with Chron C4A and more precisely with the older lower part of the Kastellios section (Sen 1986). The third locality, in which *Progonomys* was found, is that of Ravin de la Pluie, in the Axios valley (Fig. 2) dated to the Late Vallesian (MN10, Bonis & Koufos 1999). Magnetostratigraphic data suggests correlation with Chron C4Ar.1n (9.31–9.23 Ma), while the age of the fossiliferous level is estimated at 9.3 Ma (Sen *et al.* 2000). Finally Lefkon, a locality in the Serres basin (Macedonia, Greece), is referred to the uppermost part of Late Vallesian, MN10 (Mein 1990, de Bruijn *et al.* 1992). *Progonomys* is also reported from the Turkish locality of Cumali, assigned to the end of the Early Turolian (Ünay *et al.* this volume) and representing the LLA of the genus in Eastern Mediterranean.

Progonomys is an Asian immigrant, which arrived in the Eastern Mediterranean slightly later than *Hipparion*, and migrated into Western and Central Europe. It lived in the area until the end of the Early Turolian (Cumali, Turkey). In Central Europe, it is known from the Early Turolian locality of Sumeg, Hungary (NOW 2000). However, the presence of *H. primigenium* in the fauna of Sumeg is an indication for a Vallesian age. Moreover, it is present in the fauna of Kohfidisch (Austria) dated to Late Vallesian, MN10 (NOW 2000). In Spain, it is very common during the Late Vallesian and recorded in the localities Can Llobateres, La Roma, Masia del Barbo, Terassa, Villadecavalls and Can Casablanca (NOW 2000).

Concluding, *Progonomys* appeared at 12.3 Ma in Pakistan, at 10.1 Ma in the Eastern Mediterranean and at 9.7 Ma in Spain. It is interesting that this animal needed about 2.0 Ma to migrate into Asia Minor from Pakistan and then took ~ 0.40 Ma to arrive in Spain. Several hypotheses can be given to explain this diachrony and difference in the migration velocity. Geographic barriers (high mountain chains) do not facilitate an easy migration of

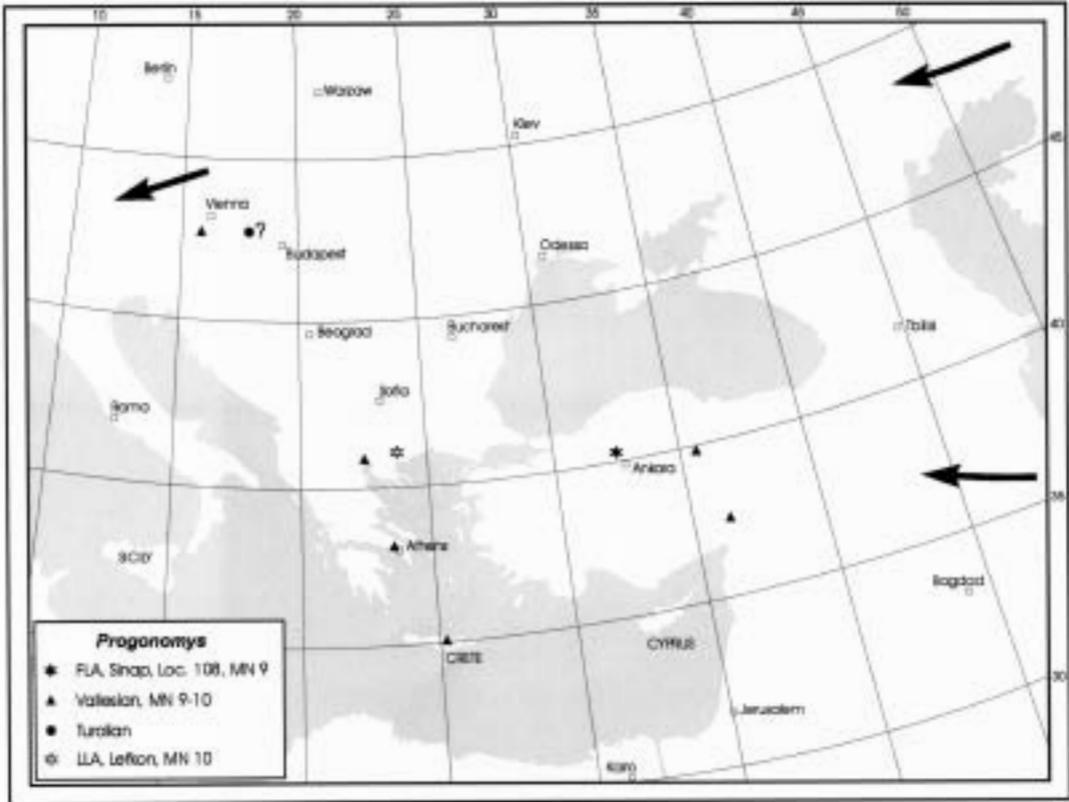


Figure 2 Geographic distribution of *Progonomys* during late Miocene in the Eastern Mediterranean.

Progonomys. However, high mountain chains existed in both areas providing similar difficulties in the migration. The paleoecology is a significant factor for the dispersal of mammals. Certainly, during Late Miocene the paleoecological conditions between Central-Western Europe and Southeastern Europe were different being drier and more open in Southeastern Europe (Bonis *et al.* 1992, Fortelius *et al.* this volume). The more closed and humid paleoenvironments of Central-Western Europe could have favoured the development of *Progonomys* and allowed its rapid expansion into this area. A third hypothesis could be that *Progonomys* either appeared in or migrated into Pakistan where it remained for a long time until it was adapted to the local conditions, diversified and then dispersed westwards.

Parapodemus event

Few Greek and Turkish Turolian localities include *Parapodemus*. The genus has probably migrated into the Balkans from the north because it is known from Vallesian localities of Central Europe (Fig. 3). *Parapodemus* is traced in the locality of Suchomasty (Czech Republic) and Kohfidisch (Austria) both dated to the latest Vallesian (Mein 1990, Fejfar & Heinrich 1990, de Bruijn *et al.* 1992). In Western Europe (Spain), *Parapodemus* appeared at the beginning of the Turolian (de Bruijn *et al.* 1992, van Dam 1997).

The *Parapodemus* bearing localities of the Eastern Mediterranean (Fig. 3) are all dated to Middle Turolian (MN11-12). Its FLA is recorded in the localities of Cumali and Mahmutgazi (Turkey) correlated to the upper part of the Early Turolian (MN11, de Bruijn *et al.* 1992, Ünay *et al.* this volume). Other

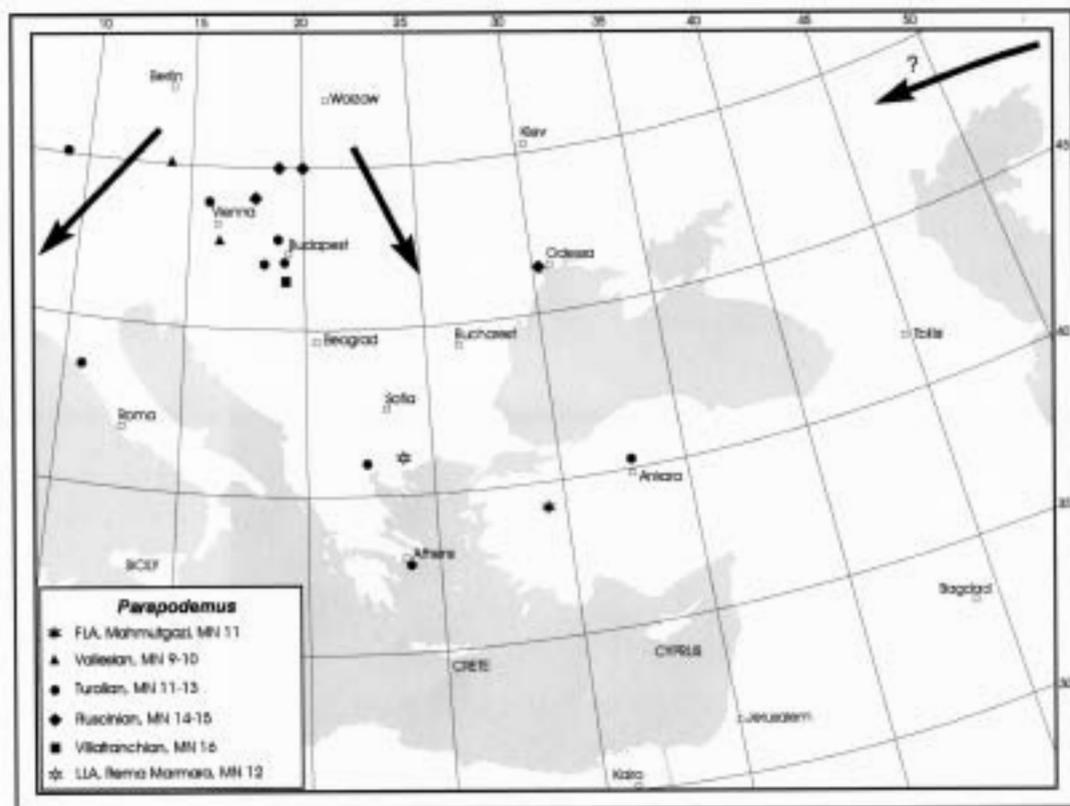


Figure 3 Geographic distribution of *Parapodemus* during late Miocene in the Eastern Mediterranean.

localities such as Cobanpinar (Turkey), Chomateres (Greece), Vathylakkos (Greece) and Rema Marmara (Greece) are all correlated to Middle Turolian, MN12 (de Bruijn *et al.* 1992, de Bruijn 1989, Bonis & Koufos 1999). Magnetostratigraphic data from the Vathylakkos section suggest an age of 7.5 Ma for the corresponding fauna (Sen *et al.* 2000). This record of *Parapodemus* suggests that it is indicative for the Middle Turolian in the Eastern Mediterranean. After the Middle Turolian it disappeared but survived in Central Europe up to the Early Villafranchian, MN16 (Fig. 3).

Other rodents

The genus *Byzantinia* is quite common in the Eastern Mediterranean. Its FLA is traced in the localities of Chrysavgi (Greece), Bayraktepe 1 and Yeni Eskihisar (Turkey) all correlated to the uppermost Astaracian (NOW

2000). *Byzantinia* is present during the Vallesian and Turolian, making its LLA in the locality of Amasya (Sen pers. comm. 2001) dated at the end of the Turolian.

Occitanomys is also an important rodent that is well known in Greece. Its FLA is recorded in Karaözü (Turkey), assigned to the earliest part of Late Vallesian (Ünay *et al.* this volume), while it is also present in Pliocene localities.

Apodemus appeared at the end of the Early Turolian (MN11) in the locality of Cumali, Turkey (Ünay *et al.* this volume) and is still represented in the Eastern Mediterranean by two species. The FLA of *Micromys* is recognized in the Greek localities of Rema Marmara correlated to the end of the Middle Turolian (de Bruijn *et al.* 1992) while it existed in the area until the Villafranchian (MN16) in the Greek locality of Limni-1 (NOW 2000).

PRIMATES

During the Late Miocene several primates, cercopithecids and hominids have been recognized in the Eastern Mediterranean.

Mesopithecus event

The cercopithecid *Mesopithecus* is quite common in the Balkans, absent in Turkey and eastern Black sea, but present in Maragha (Iran) and Molayan (Afghanistan) (Fig. 4). Concerning its first appearance in Europe there are two Vallesian localities, but their age is doubtful. From the first locality, Wissberg (Germany), one isolated tooth is considered to belong to *Mesopithecus* (Delson 1973). However, its age is doubtful, as some workers believe that there is a mixture of the material from the 'Dinotherium-Sands' localities with younger faunal ele-

ments and this tooth may belong to one of them (Andrews *et al.* 1996). The second Vallesian locality with *Mesopithecus* is Grossulovo, Ukraine (NOW 2000). The accompanying fauna has more Turolian than Vallesian characters. In recent lists about the geographic distribution of *Mesopithecus* in Europe, Grossulovo is not mentioned (Andrews *et al.* 1996, Köhler *et al.* 1999).

Delson (pers. comm. 2001) referred to me that "Maschenko (1989) does not list any primate fossils from the Miocene of Grossulovo, but from a Pliocene level (?) (also termed Novopetrovka) there may be a few teeth either of macaque or *Mesopithecus*". Delson has not seen these teeth, but in the collection of the Zoological Institute of Kiev he has seen from this site, some other specimens attributed to *Dolichopithecus*. Krakhmalnaya (pers. comm. 2001) referred to me that "the

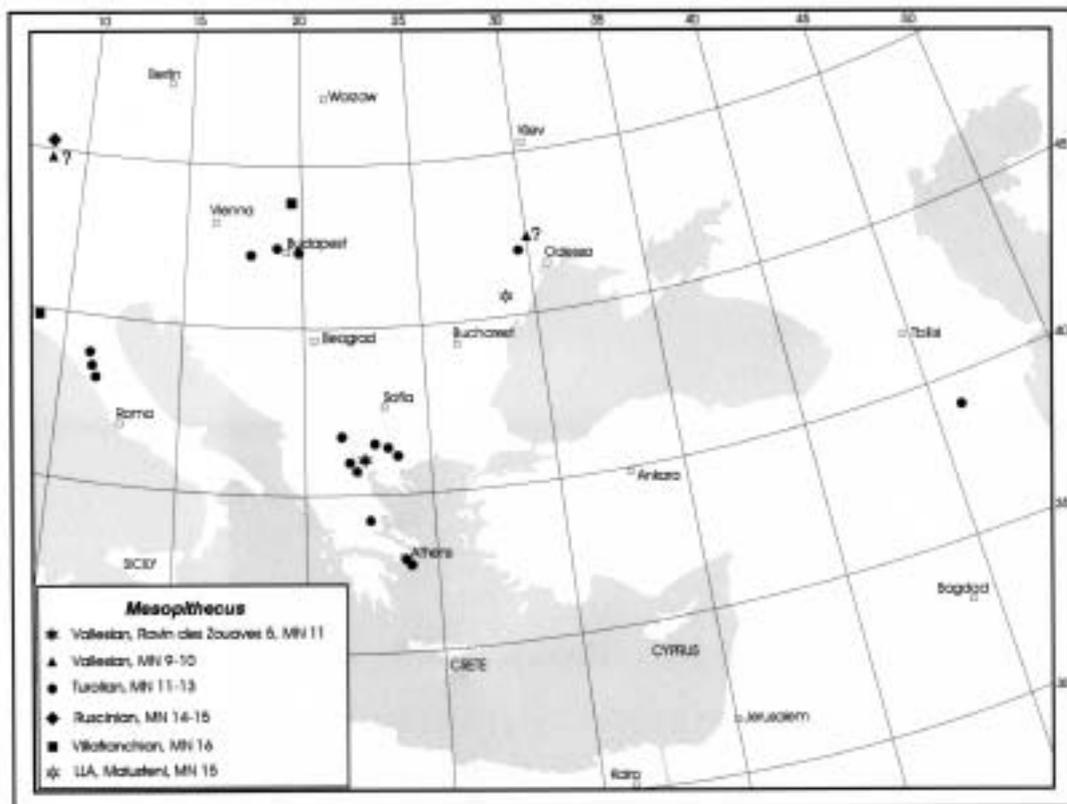


Figure 4 Geographic distribution of *Mesopithecus* during late Miocene in Eastern Mediterranean.

Grossulovo material is stored in Moscow, and Belayeva (1948) dated this to upper Sarmatian (=EarlyTurolian), while she mentioned *Mesopithecus* in her list; later on Pevzner & Vangenheim (1984) attributed Grossulovo to the Late Vallesian (MN10)". This information shows that the Vallesian occurrence of *Mesopithecus* in Europe is questionable and not well documented.

The FLA of the genus in the Eastern Mediterranean is traced in the locality of 'Ravin des Zouaves 5', Macedonia, Greece, dated to the lowermost part of the Early Turolian (MN11), at about 8.2 Ma (Bonis & Koufos 1999, Sen *et al.* 2000). The cercopithecids are absent in Asia Minor and eastern Greece (e.g. Samos). Asia Minor was the most continental part of the area between the Balkans and India and perhaps more drier, thus preventing *Mesopithecus* to live there. In fact, *Mesopithecus* was present in the two extremes of the Greco-Iranian province (Bonis *et al.* 1992) near the big mountain chains of the Alps and Himalayans, where the environment was probably less dry.

Mesopithecus lived in the Eastern Mediterranean during the whole Turolian, many remains occur in all known localities, especially in Pikermi. Its LLA is recorded in the locality of Malusteni, Romania, which is dated to Late Ruscinian (MN15, Mein 1990, NOW 2000).

Hominoids

The hominoids of the Eastern Mediterranean are known from several localities and under various names. They are known from the Middle Miocene Turkish localities of Pasalar (MN5-6) and Çandır (MN6), as well as from the Vallesian of Greece and Turkey under various taxonomic names. During the Late Miocene, two hominoids are known in the Eastern Mediterranean. The genus *Ankarapithecus* found in the Sinap Locality 8A and Locality 12 dated at 9.886 Ma and 9.590 Ma respectively (Kappelman *et al.* 2003). In Greece the hominoid primate *Ouranopithecus* is well known from the loca-

lities Xirochori 1, Ravin de la Pluie and Nikiti-1, which are dated to Late Vallesian (Koufos 2000b, Bonis & Koufos 1999).

Another hominoid mandible under the name *Graecopithecus* is known from the locality of Pyrgos Vassilissis, near Athens with questionable age and morphology. The available data suggest that the Late Miocene hominoids follow *Progonomys* and they were replaced in the Turolian by *Mesopithecus*. It is possible that the extinction of hominoids at the end of Vallesian might be enhanced by the change of the relatively humid and closed environments of the Vallesian, to rather open and dry conditions of the Turolian. The latter paleoenvironmental conditions favoured the development of the cercopithecids.

CARNIVORES

Dinocrocota event

The large hyaenid *Dinocrocota* is known from several localities in the Eastern Mediterranean. Its FLA is reported from Sinap Locality 108 dated at 10.135 Ma (Lunkka *et al.* 1999, Kappelman *et al.* 2003). It is also known from Sinap Locality 12 and Kayadibi (Turkey) dated to Vallesian and lowermost Turolian, respectively (de Bruijn *et al.* 1992, NOW 2000). In Kayadibi the LLA of *Dinocrocota* occurs. In Greece it is known from the locality of Pentalophos tentatively correlated to the lower part of the Late Vallesian (Koufos 1995). Recently, *Dinocrocota* was found in two Bulgarian localities, Nessebr and Blagoevgrad, both dated to Vallesian (Spasov & Koufos 2002). The above-mentioned data indicate that *Dinocrocota* is characteristic for the Vallesian of the Eastern Mediterranean.

Adrocota event

The hyaenid *Adrocota* and the "ictitheres" are the most common carnivores in the Late Miocene localities. The Vallesian occurrence of *Adrocota* is traced in several localities, some of which with questionable age. In Turkey, the Karain fauna includes *Adrocota*

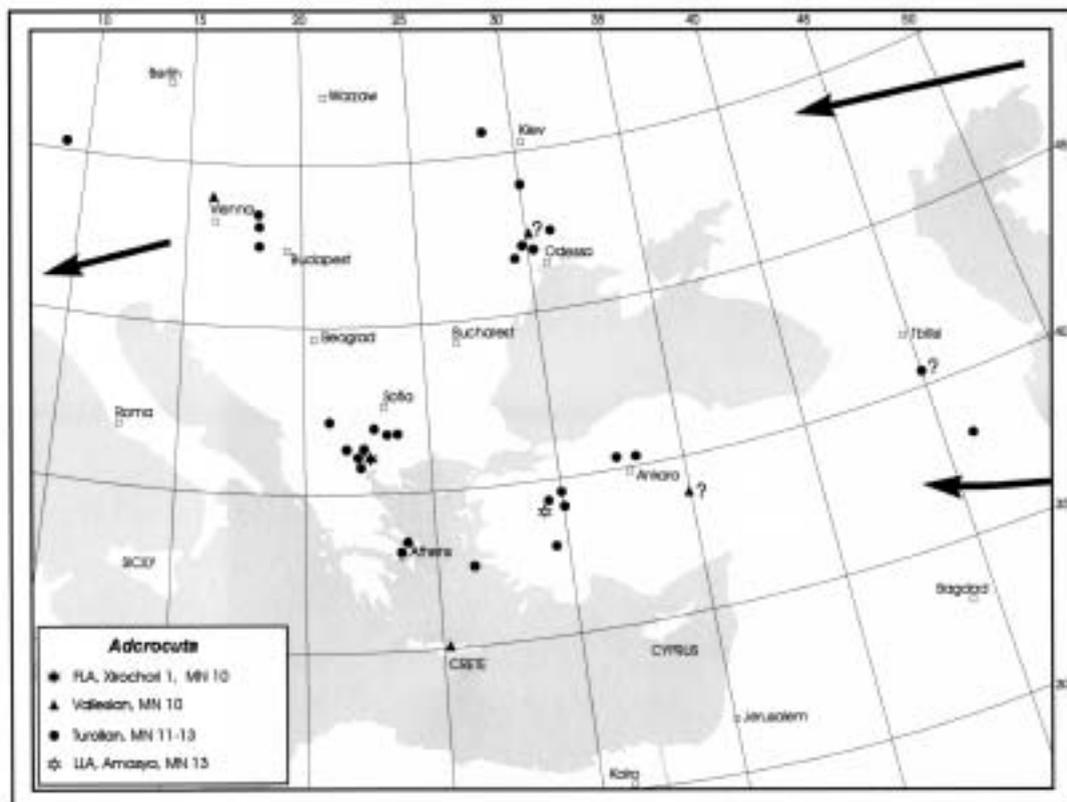


Figure 5 Geographic distribution of *Adcrocuta* during late Miocene in the Eastern Mediterranean.

(Fig. 5) together with *Felis attica* (NOW 2000). However, its poor fauna is not reliable to correlate this locality to Vallesian as previously suggested. In Greece three localities of the lower Axios valley, near Thessaloniki yielded Vallesian *Adcrocuta* (Koufos 2000b, Bonis & Koufos 1999). In the locality of Xirochori 1 (Greece) dated to 9.6 Ma (Sen *et al.* 2000) the FLA of *Adcrocuta* appears. The other localities Ravin de la Pluie and Ravin des Zouaves 1 are slightly younger and their age is estimated at 9.3 Ma (Sen *et al.* 2000). According to Sen (1997), the Early/Late Vallesian boundary is estimated at 9.64 Ma. The age of Xirochori 1 is very close to the beginning of Late Vallesian (MN10). During the Turolian *Adcrocuta* was common in the whole area (Fig. 5). It is very frequent in the Middle Turolian (MN12) but rather scarce in the Late Turolian and disappeared at the end of the Miocene. The LLA of

Adcrocuta is known from the locality of Amasya in Turkey, dated to the uppermost Turolian (Sen & Leduc 1996). Its last occurrence is apparently contemporaneous in the Eastern Mediterranean and Western Europe. This disappearance is probably due to climatic changes observed at the beginning of the Pliocene, as well as to the reduction of the Turolian preys. *Adcrocuta* is an Asian immigrant appearing in the Eastern Mediterranean area at the beginning of the Late Vallesian (ca. 9.6 Ma) and remained in the area until the end of the Miocene. However, it is worth mentioning that the acme of the genus lies in the Middle Turolian.

***Chasmapor thetes* event**

Another interesting Late Miocene carnivore is the hunting hyaena *Chasmaporthetes*. Its FLA is from the locality of Ravin des Zouaves 5, dated to the earliest Turolian at

about 8.2 Ma (Koufos 1987, 1999, 2000b; Bonis & Koufos 1994; Sen *et al.* 2000). The genus is also referred from the Late Turolian (Dytiko, Maramena), Ruscinian (Çalta) and Villafranchian (Dafnero, Gülyazi), (Koufos 1993, 2000b; Schmidt-Kittler *et al.* 1995; Ginsburg 1998; Sickenberg & Tobien 1971).

PROBOSCIDEANS

Choerolophodon event

The Late Miocene proboscideans are represented by few genera among which *Choerolophodon* is very common. The species *C. palaeindicus* is known from the Bugti Beds (Pakistan) correlated to the Middle Aragonian (MN2) at about 20.0 Ma (Tassy 1990). Barry *et al.* (1985) correlated the Bugti fauna to the end of MN3 dated at ~18.3 Ma. Recent data from the Bugti Hills put the presence of *Choerolophodon* in the Late Early Miocene, dated to 17.0-16.0 Ma (Welcomme *et al.* 2001). *Choerolophodon kisumuensis*, is known from the African locality of Buluk which is older than 17.2 Ma (Tassy 1990). Tassy (1983) suggested a possible Southern Asian migration to Africa, circa 16.0 Ma, which brought *Choerolophodon* to Africa. The new data from Buluk allowed him to doubt this hypothesis (Tassy 1990). The new data from the Bugti Hills suggest a younger age about the presence of *Choerolophodon* in Asia and a possible African origin for this. It possibly arrived in Asia during the Proboscidean-datum Event at ~18 Ma with other proboscideans (*Gomphotherium*, *Prodeinotherium*) (Rögl 1999, Koufos *et al.* 2003).

The FLA of *Choerolophodon* in the Eastern Mediterranean is recognized in the locality of Thymiana, Chios Island, Greece. The locality is correlated to Middle Aragonian, MN5 (Bonis & Koufos 1999). Recent paleomagnetic data from Thymiana section indicate that the fossiliferous levels can be dated at 15.5 Ma (Bonis *et al.* 1998). During the Vallesian and Turolian, *Choerolophodon* is quite common in the Eastern Mediterranean (Fig. 6). Its

LLA is known from the locality of Maramena (Schmidt-Kittler *et al.* 1995). The genus *Choerolophodon* is unknown from Central and Western Europe. Its northern limit lies to the southern part of the Balkans and Moldavia (Fig. 6). The two regions show different paleoenvironmental conditions during the Late Miocene (see also Fortelius, this volume).

SUIDS

Microstonyx event

The common suid of the Late Miocene is *Microstonyx*, very well known in the Eastern Mediterranean (Fig. 7) and Europe. *Microstonyx* has been also recognized in Maragha, Iran and Molayan, Afganistan (NOW 2000). If we accept the synonymy of the genus with *Hippopotamodon*, as was proposed by Pickford (1988) and Van der Made (1990), its geographic distribution is extended to the Himalayans. *Microstonyx* appeared in the Eastern Mediterranean during the Vallesian. It is recorded from several localities, Nikiti-1 (Greece), Corak Yerler, Çevril, Gülpınar and Sinap (Turkey) (NOW 2000). Concerning the FLA of *Microstonyx* the available data are not clear. *Microstonyx* is known in the Corak Yerler fauna, which is dated to Late Vallesian (de Bruijn *et al.* 1992, NOW 2000). However, the age of Corak Yerler is questionable. The known material comes from an old collection from two different horizons and the mixture of the material does not allow a definite age determination. Possibly a Late Astaracian or Early Vallesian fauna and another fauna of Late Vallesian or Early Turolian age are mixed (Sen *et al.* 1998). Examination of some new material from Corak Yerler indicates that *Listriodon* is absent, while nothing suggests, neither in the field nor in the new collections that there are two levels (Geraads pers. comm. 2001). Therefore, we cannot assign a definite age to the Corak Yerler locality. The FLA of *Microstonyx* in the Eastern Mediterranean must be that of the locality of Nikiti-1 dated

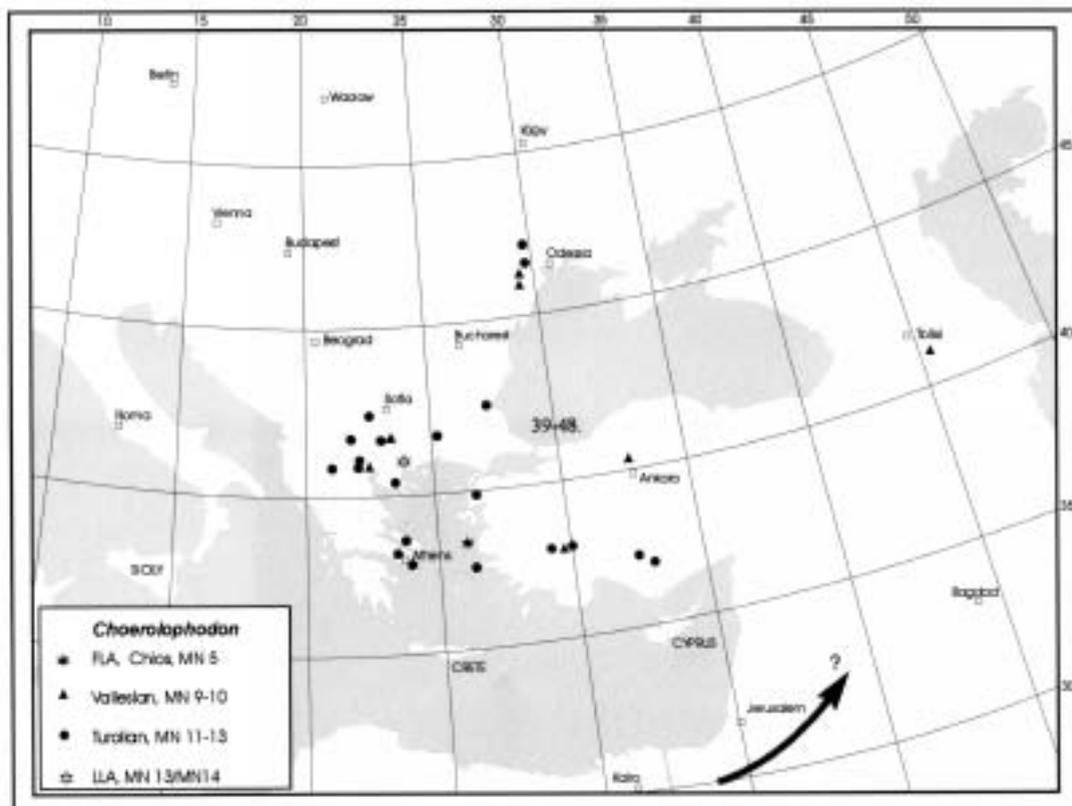


Figure 6 Geographic distribution of *Choerolophodon* during late Miocene in the Eastern Mediterranean.

to the uppermost Vallesian or <9.3 Ma (Koufos 2000c).

In Turkey *Microstonyx* is also found in the Sinap Locality 49 dated by magnetostratigraphy at 9.130 Ma (Lunkka *et al.* 1999, Kappelman *et al.* 2003), in Gülpınar dated to the lower part of Turolian, and in Çevril with questionable age, as *Microstonyx* is the sole faunal element. During the Turolian *Microstonyx* is quite common in all biozones and present in many localities (Pikermi, Samos, Prochoma, Vathylakkos, Ravin des Zouaves 5, Hadjidimovo, Kalimanci, Kayadibi, Mahmutgazi). Its LLA is reported from Dytiko localities (Greece), which are dated to the upper part of Late Turolian (MN13, Bonis & Koufos 1999).

Microstonyx appeared in the Eastern Mediterranean at the end of the Vallesian, while its last occurrence coincides with the

end of the Miocene. In Western Europe (Spain, France) the first record of *Microstonyx* is known from the Late Vallesian localities of Terrassa, Masia del Barbo (Morales *et al.* 1999), Montredon (Ginsburg 1988), Gravitelli (Rook *et al.* 1999) and it persisted until the end of the Middle Turolian (Van der Made *et al.* 1992).

GIRAFFIDS

Several giraffid genera and species are known from the Late Miocene. The giraffids have an African origin and they migrated into Eurasia through the Levant. The first giraffids, *Georgiomeryx*, arrived in the Eastern Mediterranean during the Middle Aragonian at Chios Island (Bonis *et al.* 1997). Later on, several genera arrived in the Eastern Mediterranean through the same passage but

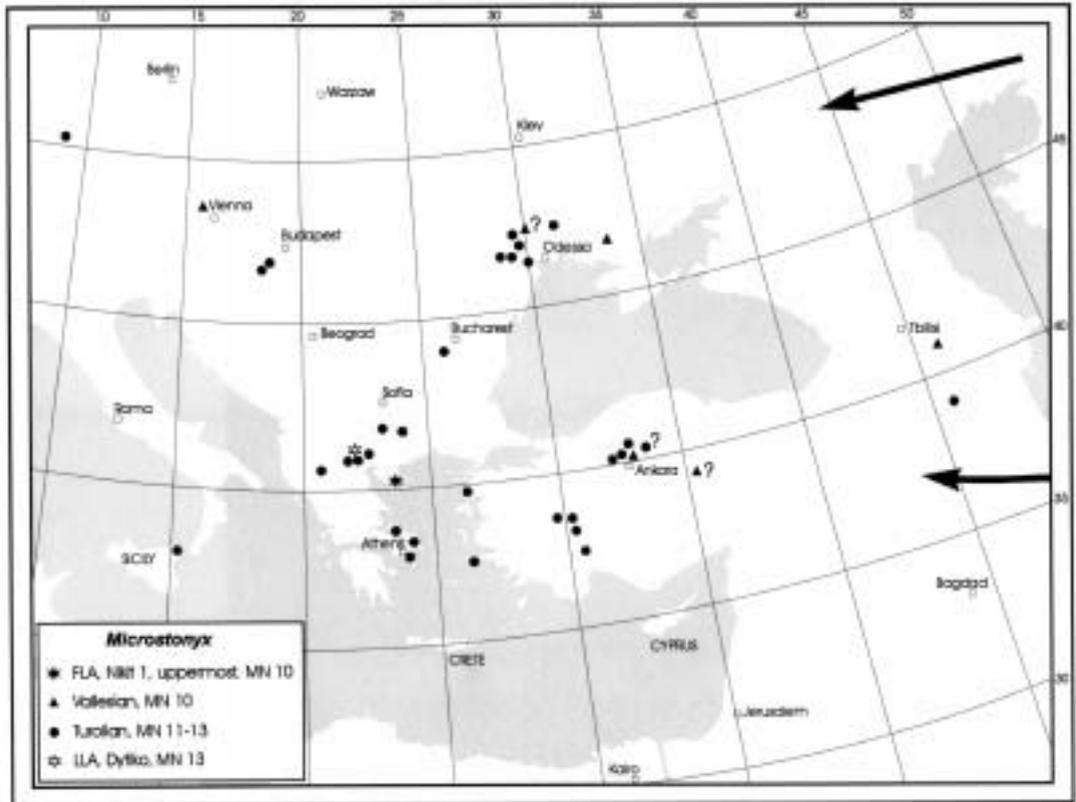


Figure 7 Geographic distribution of *Microstonyx* during late Miocene in the Eastern Mediterranean.

most of them did not migrate to Central or Western Europe. Probably the environmental differences between these regions (Fortelius, this volume) did not favour the dispersion of these giraffids. On the other hand, some high mountains (Alps) may constitute important climatic and topographic barriers for the dispersion of these large animals.

Palaeotragus event

Another interesting event during Late Miocene in the Eastern Mediterranean is the arrival of *Palaeotragus*. The genus is known from the Middle Miocene of Africa (Morocco, Tunisia), Asia (China) and Europe (Spain) (NOW 2000). Until now, it is unknown from this period in the Eastern Mediterranean. The Middle Miocene mammalian localities of the Eastern Mediterranean are scarce with poor faunas and may be this is the reason of the absence of

Palaeotragus. The available data (Fig. 8) indicate that *Palaeotragus* FLA is in the Sinap Locality 4 dated at 10.692 Ma (Lunkka *et al.* 1992, Kappelman *et al.* 2003). The FLA of *Palaeotragus* seems to coincide with that of *Hipparion* in the area. During the Turolian *Palaeotragus* was a common element in Eastern Mediterranean faunas. The LLA of the genus (Fig. 8) is reported from the localities of Dytiko (Macedonia, Greece) dated to the upper part of Late Turolian, MN13 (Bonis & Koufos 1999).

Bohlinia event

Bohlinia is a quite common giraffid in the Late Miocene faunas of Eastern Mediterranean (Fig. 9). Its arrival in the Eastern Mediterranean is reported from the Vallesian localities No 51, 49, 34 of the Sinap area in Turkey (Lunkka *et al.* 1999), as well as from the Greek localities of Ravin de la

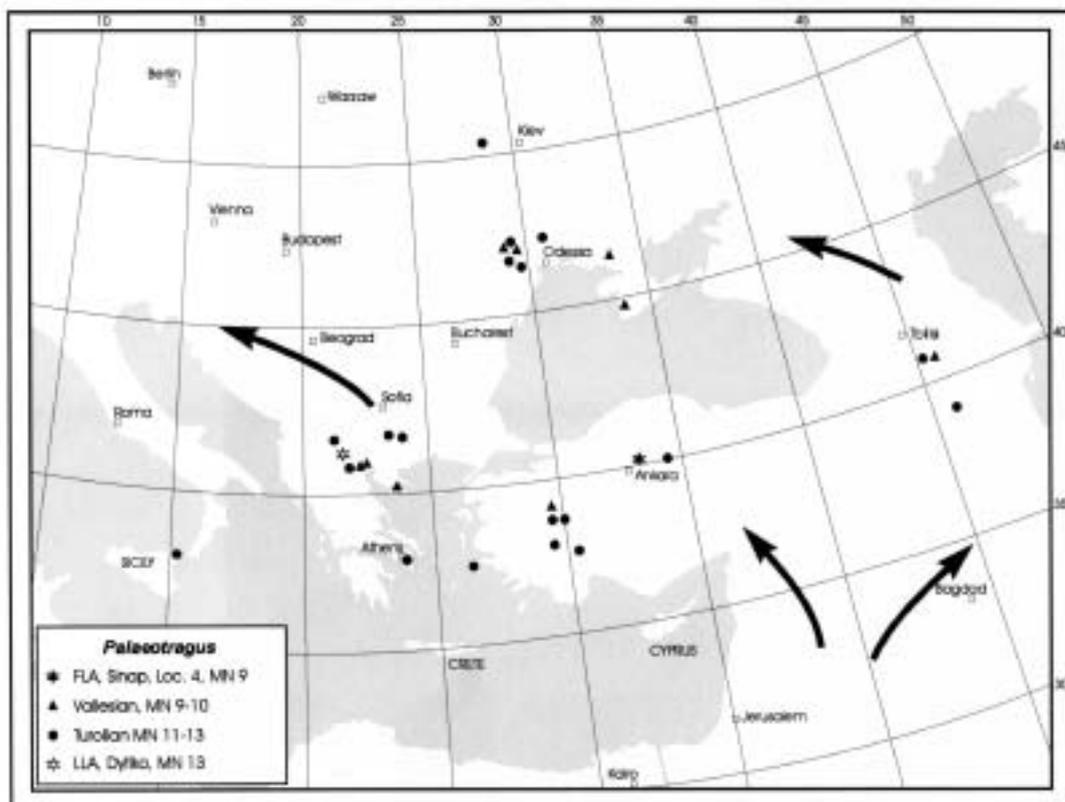


Figure 8 Geographic distribution of *Palaeotragus* during late Miocene in the Eastern Mediterranean.

Pluie and Nikiti-1 (Bonis & Koufos 1999). Ravin de la Pluie is the oldest *Bohlinia* bearing locality with an age of about 9.3 Ma (Sen *et al.* 2000) indicating the early part of the Late Vallesian, (MN10). The Nikiti-1 fauna is younger, expressing the end of MN10 in the area. The Sinop localities are younger and are dated from 9.288–8.440 Ma (Kappelman *et al.* in press). *Bohlinia* is present during the whole Turolian (Fig. 9) and its LLA is reported from Dytiko localities correlated to the upper part of MN13 (Bonis & Koufos 1999).

***Samotherium*-*Helladotherium* event**

Two large-sized giraffids are also known from the Late Miocene of the Eastern Mediterranean: *Samotherium* and *Helladotherium*. *Samotherium* was originally found in Samos, but later also reported from Asia Minor, Georgia, Iran, Ukraine and continental

Greece. Its FLA is known from the locality of Gölpinar, Turkey, which is placed in the Early Turolian (Sen pers. comm. 2001). *Samotherium* is present during the whole Turolian (Fig. 10) of the Eastern Mediterranean with its LLA in the Greek locality of Maramena, which is correlated to the Miocene/Pliocene boundary (MN13/14, Schmidt-Kittler *et al.* 1995).

Helladotherium is also quite common in Late Miocene of the area (Fig. 11). Its FLA is recorded in the locality of Nikiti-1. The faunal assemblage of Nikiti-1 is considered to be latest Vallesian, probably younger than 9.3 Ma (Koufos 2000c). *Helladotherium* is quite common in the Turolian (Fig. 11) and its LLA is in the locality of Ano Metochi assigned to the later part of the Late Turolian (MN13). Both *Samotherium* and *Helladotherium* persisted in the Eastern Mediterranean during the whole Turolian, but they

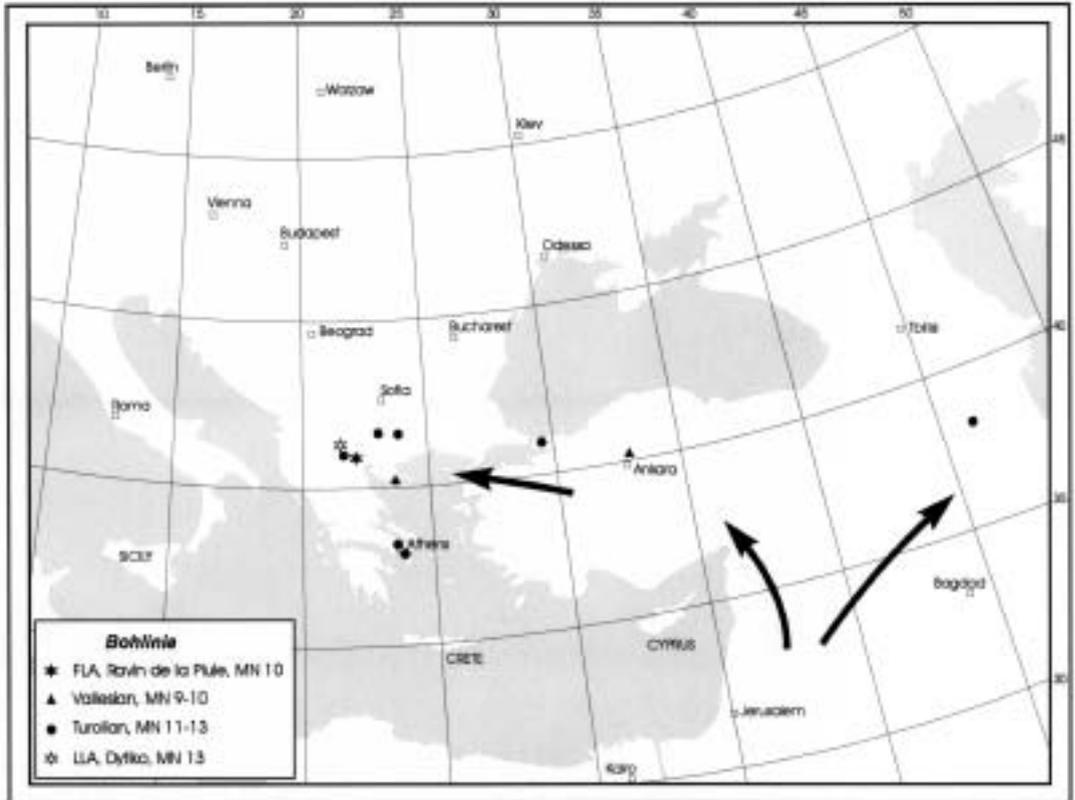


Figure 9 Geographic distribution of *Bohlinia* during late Miocene in the Eastern Mediterranean.

are unknown in Central and Western Europe. *Samotherium* expanded to the north to Kiev, Ukraine (Belka, Novo Elisavetovka, NOW 2000), while *Helladotherium* arrived to Budapest (Hatvan, Polgardi, NOW 2000) (Figs 10,11). As it was referred to above, the different paleoecological conditions between Western-Central and Southeastern Europe works as a barrier restricting the migration of several taxa into Western-Central Europe.

BOVIDS

Tragoportax event

Tragoportax is quite common in the Late Miocene localities of the Circum-Mediterranean region (Fig. 12). Its FLA in the Eastern Mediterranean is recorded in the Sinap Locality 108 (Lunkka *et al.* 1999). The magnetostratigraphy of the Sinap section suggests an age of 10.135 Ma for Locality 108,

which corresponds to the upper part of the Early Vallesian (MN9, Kappelman *et al.* in press). In Turkey *Tragoportax* is also known from the Early Turolian locality of Çorak Yerler (see details about its age in *Microstonyx*) and Gülpınar. In Greece it is traced in the locality of Nikiti-1, which is correlated to the uppermost Vallesian (Koufos 2000c). In the Ukraine two Vallesian localities are known which include *Tragoportax*: Varnitsa and Pokshesty, dated to Early and Late Vallesian, respectively (Mein 1990, NOW 2000). A reconsideration of the magnetostratigraphy of these localities suggests that Varnitsa is correlated to the base of Chron C4A (~9.5 Ma) and Pokshesty to Chron C4An corresponding to an age between 8.7-9.0 Ma (Sen 1997).

In Central Europe *Tragoportax* occurs in the locality of Vösendorf (Austria), dated to the Early Vallesian (de Bruijn *et al.* 1992).

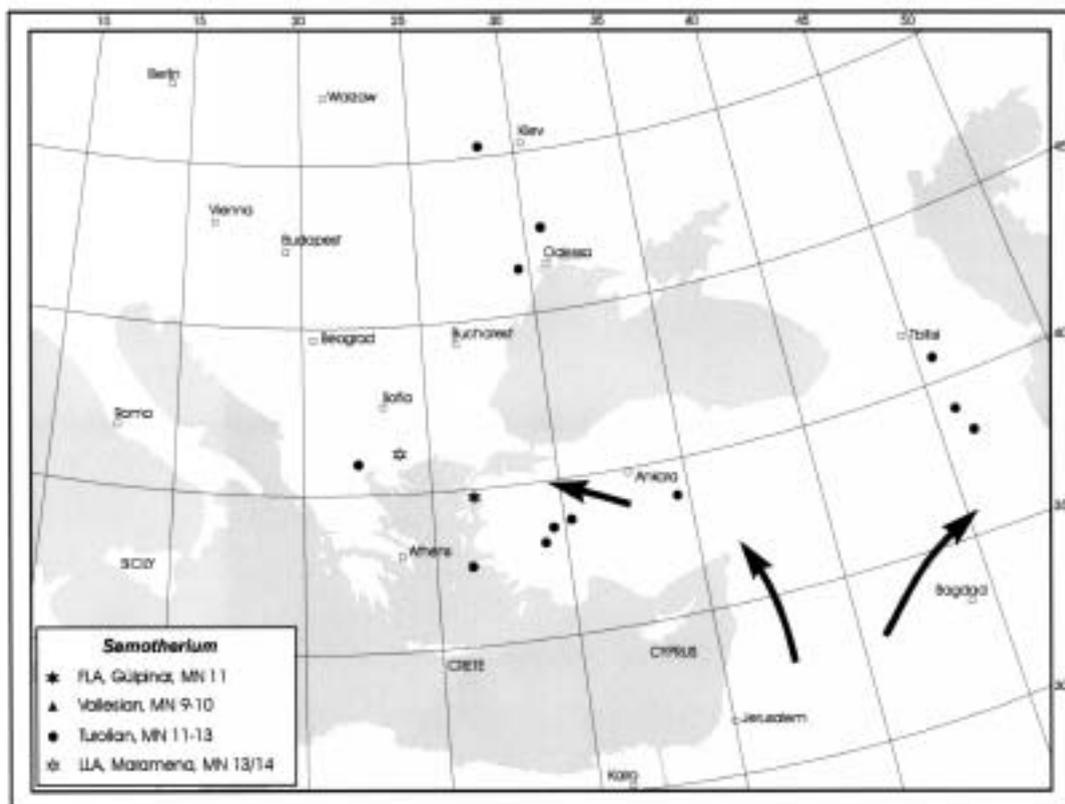


Figure 10 Geographic distribution of *Samotherium* during late Miocene in the Eastern Mediterranean.

The magnetostratigraphic data and their correlation suggest an age of about 10.3 Ma for the fauna (Steininger *et al.* 1996). This estimation is near the age calculated for the FLA of *Tragoportax* in the Eastern Mediterranean. *Tragoportax* is an eastern immigrant, which arrived in Europe in the middle of the Early Vallesian. Its distribution must have been quite rapid, since this bovid runs fast and it travels long distances in order to find food.

In Spain, it is known from the Late Vallesian localities of Villadecavalls and La Roma. Magnetostratigraphic data indicates an age of about 9.6 Ma for Villadecavalls (Agustí *et al.* 1996, Morales *et al.* 1999). Thus, there is a delay of about 0.5 Ma in the distribution of *Tragoportax* from the Eastern to the Western Mediterranean. After its arrival, *Tragoportax* evolved and diversified during the Turolian (Fig. 12), but disappeared at the end of this period. Its LLA is traced in the localities of

Dytiko, dated to the upper part of the Late Turolian MN13 (Bonis & Koufos 1999).

Gazella event

The gazelles are very common in the Neogene/Quaternary mammal localities with several species (Fig. 13). During Late Miocene *Gazella* arrived in the Eastern Mediterranean possibly from Asia and then dispersed into Europe and Africa. The FLA of *Gazella* is recorded in the Sinap Locality 72 dated at 10.080 Ma (Lunkka *et al.* 1999, Kappelman *et al.* in press). *Gazella* is also known from the locality of Nikiti-1 (Greece) correlated to the uppermost Vallesian (<9.3 Ma, Koufos 2000c). During the Turolian *Gazella* is frequently present in all mammalian localities of the Eastern Mediterranean. *Gazella* continues to exist during Pliocene and Pleistocene. Unfortunately, the late Miocene gazelles are not well studied and are

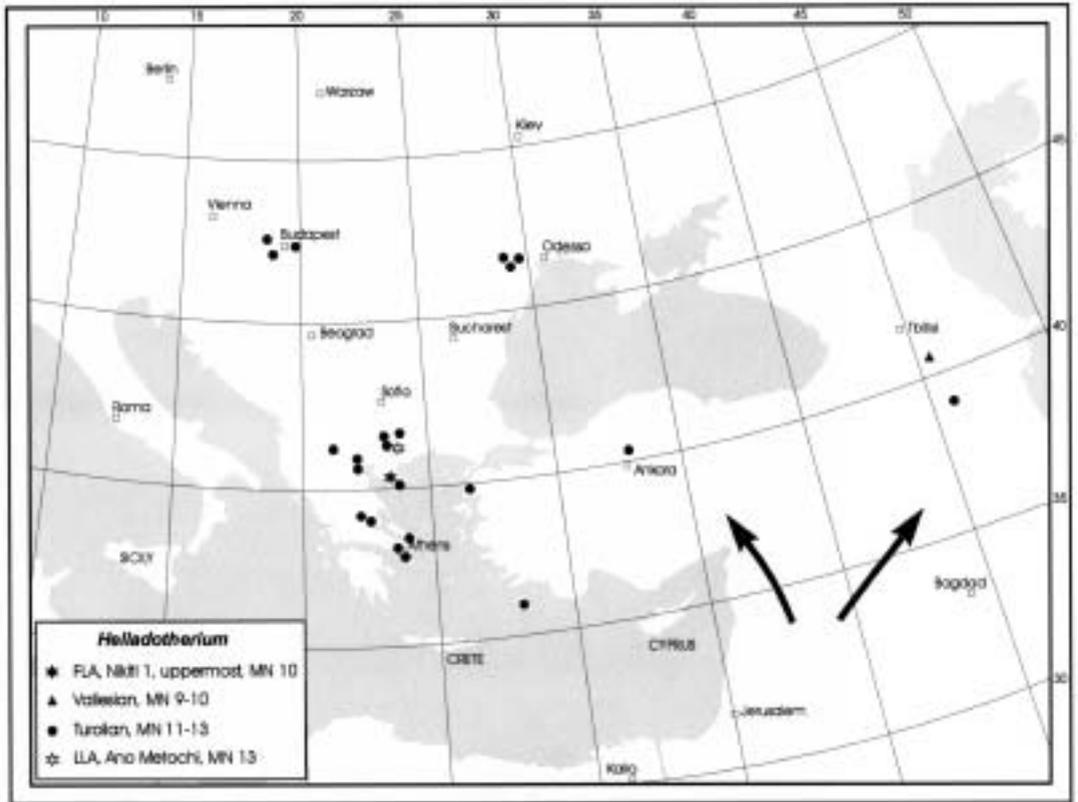


Figure 11 Geographic distribution of *Helladotherium* during late Miocene in the Eastern Mediterranean.

referred as *Gazella* sp. in most localities. In Spain, *Gazella* makes its FLA in the locality of Villadecavalls (dated at the beginning of the Late Vallesian MN10, Morales *et al.* 1999). Agustí *et al.* (1996) suggest for Villadecavalls an age of about 9.6 Ma. Therefore, there is a short diachrony of ~ 0.5 Ma in the dispersion of *Gazella* between the Eastern and Western Mediterranean.

Prostrepsicer os event

In the Eastern Mediterranean *Prostrepsicer os* is common (Fig. 14) and appears at the upper part of the Early Vallesian (MN9). Its FLA is recognized in the Sinap Locality 91 (Turkey) dated at 9.977 Ma (Lunkka *et al.* 1999, Kappelman *et al.* 2003). *Prostrepsicer os* is also known from the locality of Çorak Yerler (Turkey), with an uncertain age assignment (see in *Microstonyx*), as well as from the Late Vallesian localities of Ravin de la Pluie and Nikiti-

1 (Greece). The age of Ravin de la Pluie fauna is estimated at 9.3 Ma (Sen *et al.* 2000), while Nikiti-1 is slightly younger. During the Turolian *Prostrepsicer os* is quite common in the area, but it remains in the Balkans and evidence for migrations towards the west are lacking. To the north, it reaches the southern coast of Ukraine as it is found in the locality of Grebeniki. It seems that *Prostrepsicer os* existed during the whole Turolian. Its LLA is recorded in the locality of Ano Metochi (Greece), dated to the upper part of Late Turolian (MN13). It is also known from Titov Veles (FYROM), which is correlated to MN12-13 (NOW 2000). However, the precise age of the Titov Veles fauna or faunas are uncertain. During the Pliocene *Prostrepsicer os* disappeared, but at the end of the Pliocene *Parastrepsicer os* (a form similar to *Prostrepsicer os*) appeared in the locality of Gerakarou, Greece (Kostopoulos 1998), as well as in Georgia (Vekua 1970).

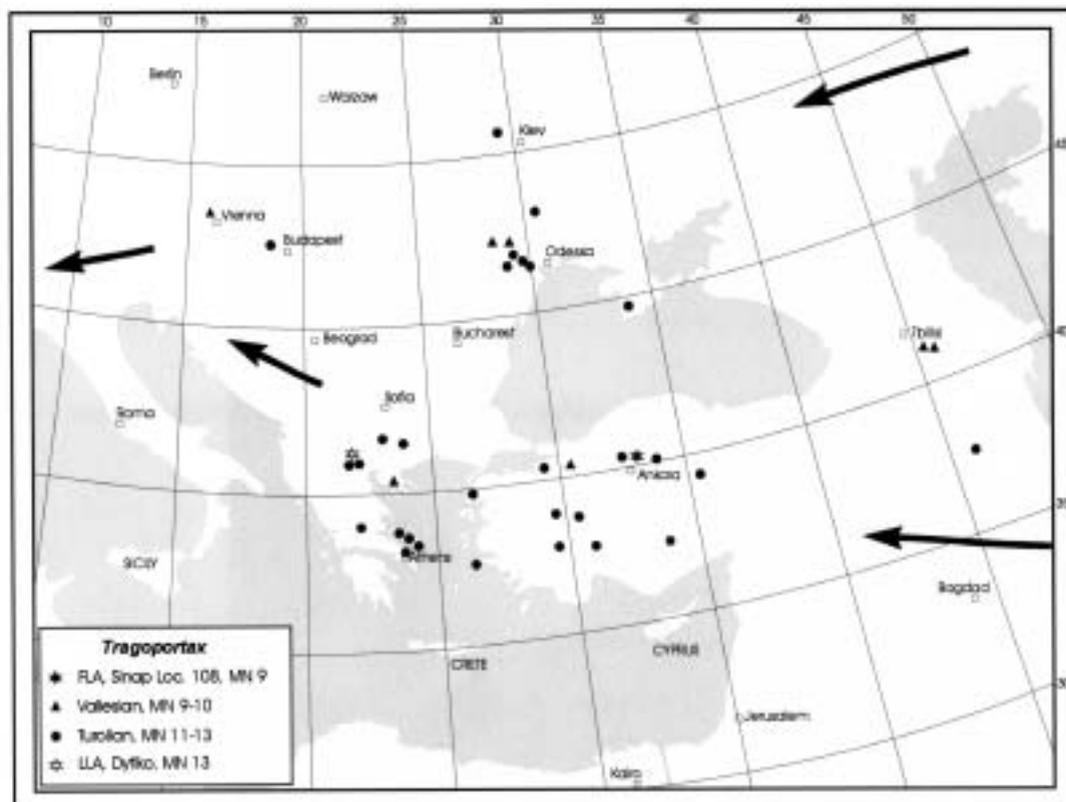


Figure 12 Geographic distribution of *Tragoportax* during late Miocene in the Eastern Mediterranean.

***Nisidorcas* event**

Nisidorcas was originally described as *Antelope cercicapra* or (cf. *Antelope*) *planicornis* from Perim Island (India) and from a level corresponding to Dhok Pathan, India (Bouvrain 1979). New material from the Axios valley (Macedonia, Greece) allowed the erection of the new genus *Nisidorcas* (Bouvrain 1979). *Nisidorcas*, also known from the locality of Kayadibi (Turkey), is described as *Antilospira incarinatus* (Tekkaya 1969), and recently it was recognized in the material of Titov Veles (Fig. 15).

The temporal expansion of *Nisidorcas* is not well known. Its FLA is recorded in the localities of Nikiti-2 (Greece) and Kayadibi (Turkey), which are correlated to the lowermost Turolian (Bonis & Koufos 1999, Mein 1990, de Bruijn *et al.* 1992). In Kayadibi the fossiliferous level is between two ignimbrites dated at 9.4 ± 0.2 Ma for the lower level and

7.95 ± 0.25 Ma for the upper one (Steininger *et al.* 1996). In Greece, the genus is known from five localities of the Axios valley. The locality of Ravin des Zouaves 5 includes a rich collection of *Nisidorcas* and is dated to the lower part of the Early Turolian, MN11 or at 8.2 Ma; Bonis & Koufos 1999, Sen *et al.* 2000). *Nisidorcas* was also found in the three localities of Vathylakkos and in Prochoma, which are younger than the above ones and dated to the beginning of Middle Turolian (MN12, Bonis & Koufos 1999). The magnetostratigraphy of the Vathylakkos 2 section indicates an age of about 7.5 Ma for its fauna (Sen *et al.* 2000). *Nisidorcas* was also recognized in the old material of Titov Veles (Bouvrain 1979) dated to Middle-Late Turolian (NOW 2000). Its LLA is traced in the localities of Vathylakkos and Prochoma (Greece) both dated at about 7.5 Ma (Sen *et al.* 2000). Unfortunately, the old material of

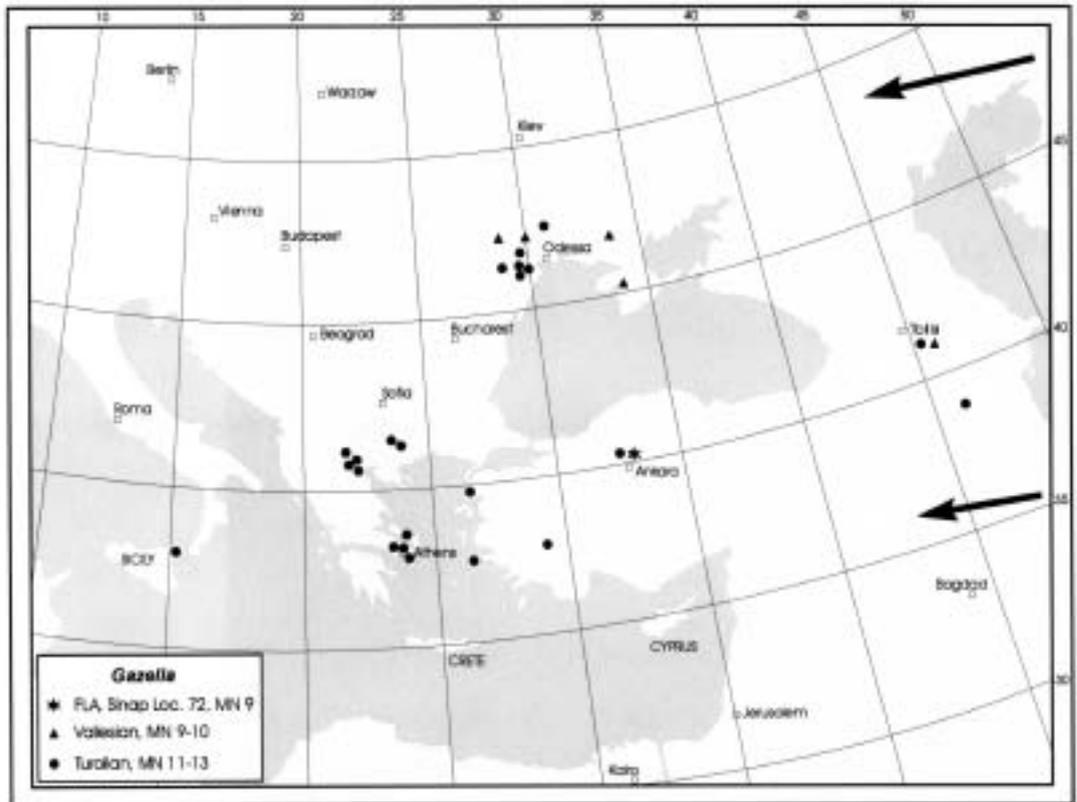


Figure 13 Geographic distribution of *Gazella* during late Miocene in the Eastern Mediterranean.

Nisidorcas from India cannot allow a definite dating. However, its arrival in the Eastern Mediterranean marks the beginning of the Turolian.

CONCLUSIONS

As it was mentioned above, several mammalian taxa have arrived in the Eastern Mediterranean during the Late Miocene. Some of the most important and common were discussed, but of course, more taxa make their FLA in the area. Moreover, the available data increase as research in the area is continuing. During the meeting in Utrecht (in 2001), several new data have been provided by colleagues about the mammalian taxa and localities in the Eastern Mediterranean. The stratigraphic distribution of the above studied taxa in Eastern Mediterranean is given in Appendix 2, while some well-dated

FLA's are given in Appendix 3. The white arrows indicate a magnetostratigraphic calibration of the age. The magnetostratigraphy of the Sinap Tepe is quite important as it includes the whole Vallesian of the area (Kappelman *et al.* 2003). For the Turolian, the known data come from the Greek localities of Axios valley and Samos and from the Turkish locality of Kemiklitepe (Sen *et al.* 1994, 2000). The Samos section is quite thick and the available data quite good (Kostopoulos *et al.* 2003). The age of the other localities is biochronologically calculated, based mainly on their faunal content.

Vallesian

The Astaracian/Vallesian boundary is defined by the *Hipparion*-datum. However, as mentioned above, there are some different opinions about this. In Spain and central Europe, the boundary is considered to be at 11.1-11.2

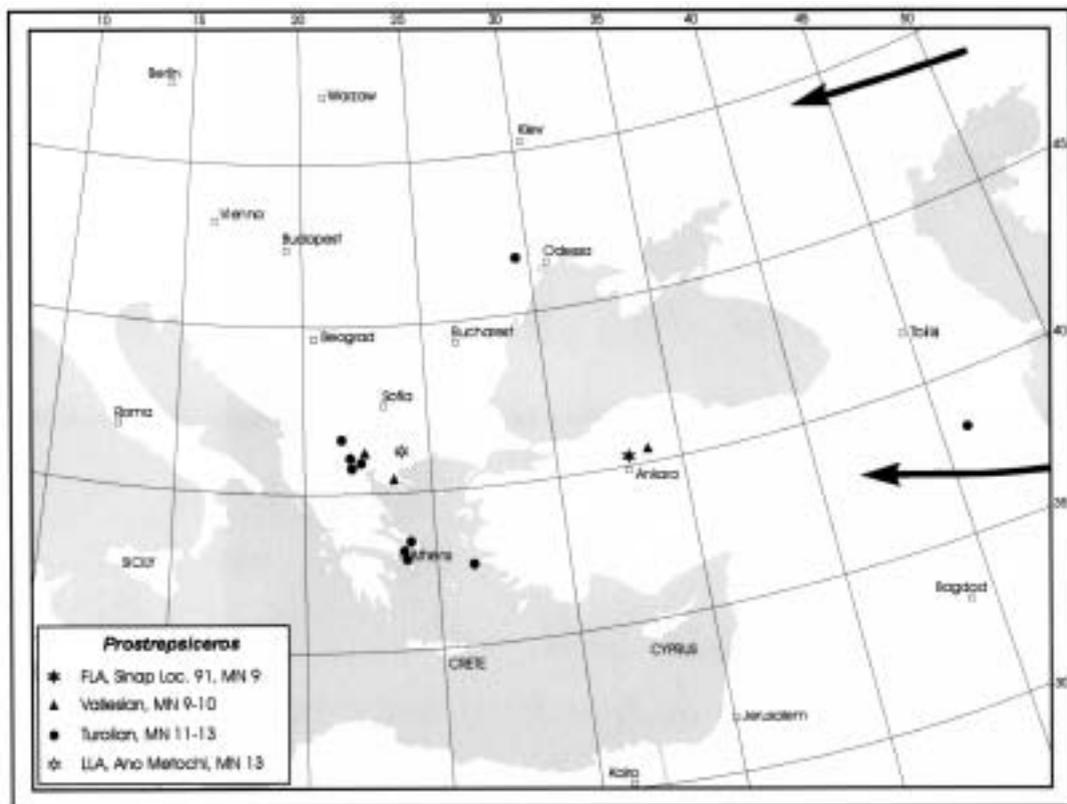


Figure 14 Geographic distribution of *Prostrepsiceros* during late Miocene in the Eastern Mediterranean.

Ma (Garces *et al.* 1997, Steininger *et al.* 1996). On the other hand, in the Eastern Mediterranean the FLA of *Hipparion* is dated at 10.7 Ma in the Sinap Locality 4, defining the Astaracian/Vallesian boundary (Kappelman *et al.* in press, Sen 1997). In the Siwaliks the *Hipparion*-datum has been estimated at ~10.7 Ma (Pilbeam *et al.* 1996). In Central Europe, the *Hipparion*-datum is known from Gaiselberg (Austria) with an estimated age older than 11.0 Ma and from Höwenegg (Germany), which is slightly older than 10.3 Ma (Bernor *et al.* 1996). In Eastern Europe, *Hipparion* and *Anchitherium* occur in the locality of Zheltokamenka, Ukraine (Gabunia 1981). After the reconsideration of the palaeomagnetic data from this locality, the normal polarities obtained for these deposits can be correlated with Chron C5n and an age about 10.5 Ma is possible for Zhelto-

kamenka (Sen 1997). In any case, a new study of the magnetostratigraphy is necessary to provide definite ages. Thus, the entry of *Hipparion* and the Astaracian/Vallesian boundary must be at 10.7 Ma in the Eastern Mediterranean.

Together with *Hipparion*, the giraffid *Palaeotragus* arrived in the area. The Early Vallesian is also characterized by the presence of *Cricetulodon* and *Byzantinia*, but both occur slightly earlier at the end of the Astaracian. During the Early Vallesian, several mammalian taxa arrived in the Eastern Mediterranean such as *Progonomys*, *Tragoportax*, *Gazella*, *Prostrepsiceros*, *Dinocrocota* and the hominoid *Ankarapithecus*.

The Early/Late Vallesian boundary in Spain has been dated at 9.6 Ma (Sen 1997). In the Eastern Mediterranean, the Greek localities

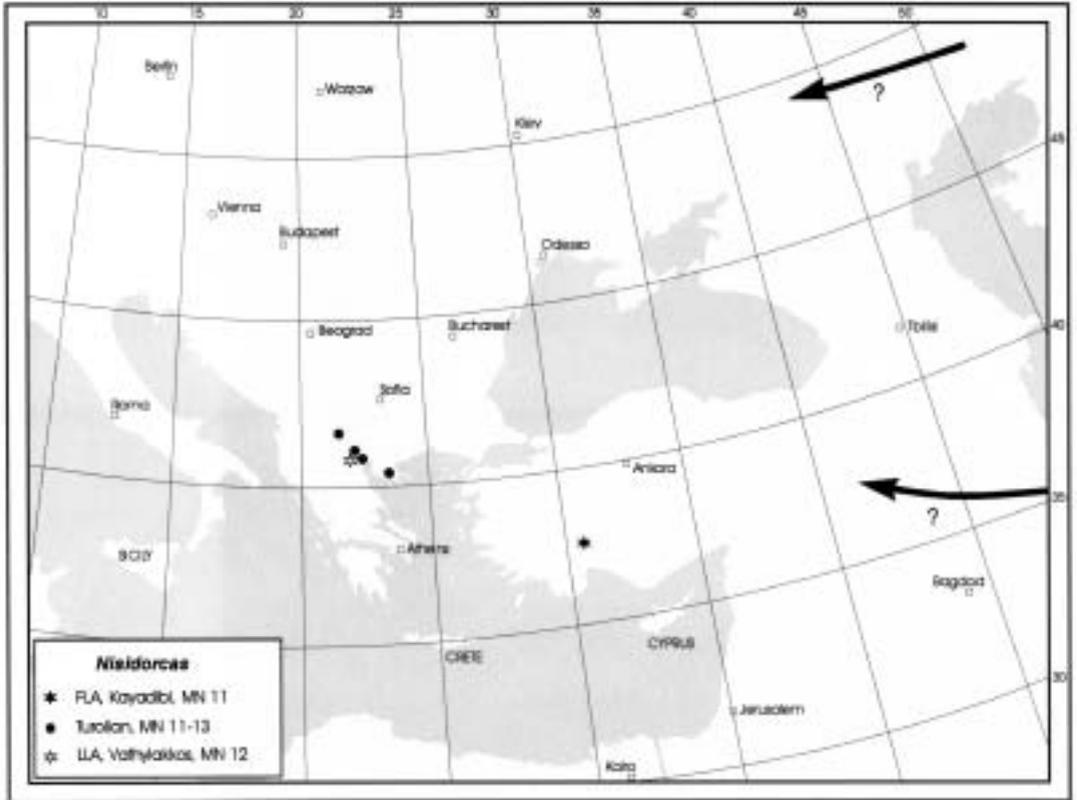


Figure 15 Geographic distribution of *Nisidorcas* during late Miocene in the Eastern Mediterranean.

of Kastellios and Xirochori 1 are of similar age. The FLA of *Adcrocuta* and *Ouranopithecus* characterize this boundary. Late Vallesian includes the FLA of *Occitanomys*, *Bohlinia*, *Helladotherium* and the LLA of the hominoids *Ouranopithecus* and *Ankarapithecus*.

Turolian

The Vallesian/Turolian boundary can be defined by the FLA of the suid *Microstonyx* and the bovid *Nisidorcas*. Another important taxon indicating a Turolian age is *Mesopithecus*, which replaced the large Vallesian hominoid primates. At the same time, the giant hyaenid *Dinocrocuta* disappeared. During the Early Turolian the giraffid *Samotherium* and the hunting hyaena *Chasmapotchetes* entered in the Eastern Mediterranean, while *Progonomys* disappe-

ared at the end of this period.

The beginning of Middle Turolian coincides with the FLA of *Parapodemus*, which is characteristic for this time period. Moreover, the taxa *Apodemus*, *Pliocervus* and *Macrotherium* arrived at the same time. *Nisidorcas* disappeared and until now, there is no evidence for its presence in younger levels.

The Late Turolian is a very characteristic period including an important faunal change that marks the beginning of the Pliocene. The FLA of *Micromys* in the locality of Rema Marmara (Greece) marks the Middle/Late Turolian boundary. Unfortunately for the Middle-Late Turolian the absence of absolute or paleomagnetic ages makes the division more difficult. Several mammalian taxa (*Choerolophodon*, *Adcrocuta*, *Microstonyx*, *Palaeotragus*, *Bohlinia*, *Samotherium*,

Helladotherium, *Tragoportax*, *Prostrepsiceros*) disappeared during the end of the Turolian. All have been replaced by new taxa (*Rhagapodemus*, *Mesocricetus*, *Parabos*, *Paracamelus*, *Korynochoerus*) marking the beginning of the Pliocene. Two Greek faunas (Maramena, Silata) seem to represent the Turolian/Ruscian boundary (Schmidt-Kittler *et al.* 1995, Vassiliadou *et al.* this volume).

Using the available data, it is possible to distinguish some biozones during the Late Miocene (Appendix 3). The boundaries of these biozones are given by dot-lines, meaning that they are not certain (the stratigraphic distribution of the taxa is often changed by new data). As it was mentioned in the introduction, the problems of the Neogene division in the Eastern Mediterranean are large and cannot be solved by this article alone. The main goal of this paper was, after collecting the available data, to give a preliminary division and to point out the main problems, which must be solved. We shall continue the collection of the data for the entire Neogene of the Eastern Mediterranean in order to know what we have and what we need.

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REFERENCES

- Agustí, J., Köhler, M., Moyà Solà, S., Cabrera, L., Garces, M. & Pares, M.J., 1996 - Can Llobateres: The pattern and timing of the Vallesian hominoid radiation reconsidered - *Journal of Human Evolution* 31: 143-155
- Agustí, J., Cabrera, L., Garces, M. & Pares, M.J., 1997 - The Vallesian mammal succession in the Vallés-Penedés basin (northeast Spain): Palaeomagnetic calibration and correlation with global events - *Palaeogeography Palaeoclimatology Palaeoecology* 133: 149-180
- Andrews, P., Harisson, T., Delson, E., Bernor, R.L. & Martin, L., 1996 - Distribution and biochronology of European and southwest Asian Miocene Catarrhines - in: Bernor, R.L., Fahlbusch, V. & Mittmann, H.-W. (eds.) - *The evolution of Western Eurasian Neogene mammal faunas* - pp. 168-207, Columbia University Press, New York
- Barry, J.C., Johnson, N.M., Raza, S.M. & Jacobs, L.L., 1985 - Neogene mammalian faunal change in southern Asia: Correlations with climatic, tectonic and eustatic events - *Geology* 13: 637-640
- Benda, L., Meulenkamp, J. & Van De Weerd, A., 1977 - Biostratigraphic correlations in the eastern Mediterranean Neogene. 3. Correlation between mammal, sporomorph and marine microfossil assemblages from the upper Cenozoic of Rhodes, Greece - *Newsletters on Stratigraphy* 6: 117-130
- Bernor, R.L., Kovar-Eder, J., Lipscomb, D., Rögl, F., Sen, S. & Tobien, H., 1988 - Systematic, stratigraphic and palaeoenvironmental contexts of first-appearing *Hipparion* in the Vienna basin, Austria - *Journal of Vertebrate Palaeontology* 8 (4): 427-452
- Bonis, L. & Koufos, G.D., 1994 - Some hyaenids from the Late Miocene of Macedonia (Greece) and the phylogeny of hunting hyaenas - *Münchner Geowissenschaftliche Abhandlungen* 26: 81-96
- Bonis, L. & Koufos, G.D., 1999 - The Miocene large mammal succession in Greece - in: Agustí, J., Rook, L. & Andrews, P. (eds.) - *Hominoid Evolution and climatic change in Europe, vol. I, The evolution of the Neogene terrestrial ecosystems in Europe* - pp. 205-237, Cambridge University Press, New York
- Bonis, L., Bouvrain, G. & Koufos, G.D., 1999 - Palaeoenvironments of the hominoid primate *Ouranopithecus* in the Late Miocene deposits of Macedonia, Greece - in: Agustí, J., Rook, L. & Andrews, P. (eds.) - *Hominoid Evolution and climatic change in Europe, vol. I, The evolution of the Neogene terrestrial ecosystems in Europe* - pp. 413-435, Cambridge University Press, New York
- Bonis, L., Koufos, G.D. & Sen, S., 1997 - A giraffid skull and mandible from the Middle Miocene of the

- island of Chios (Aegean sea, Greece) – *Palaeontology* 40: 121-133
- Bonis, L., Koufos, G.D. & Sen, S., 1998 - Ruminants (Bovidae and Tragulidae) from the Middle Miocene (MN5) of the island of Chios, Aegean sea (Greece) - *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* 210: 399-420
- Bonis, L., Bouvrain, G., Geraads, D. & Koufos, G.D., 1992 - Diversity and palaeoecology of Greek Late Miocene mammalian faunas – *Palaeogeography, Palaeoclimatology, Palaeoecology* 91: 99-121
- Bonis, L., Brunet, M., Heintz, E. & Sen, S., 1992 - La province greco-irano-afgane et la répartition des faunes mammaliennes au Miocène supérieur. *Paleontologia i Evolucio* 24-25:103-112
- Bouvrain, G., 1979 - Un nouveau genre de Bovidé de la fin du Miocène - *Bulletin Societe Géologique de France* (7) 21(4): 507-511
- De Bruijn, H., 1989 - Smaller mammals from the Upper Miocene and lower Pliocene of the Strimon basin, Greece. Part 1, Rodentia and Lagomorpha - *Bolletino della Societa Paleontologia Italiana* 28: 189-195
- De Bruijn, H. & Van der Meulen, A., 1979 - A review of the Neogene rodent succession in Greece - *Annales Géologiques des Pays Hélieniques Hors Series 1*: 207-217
- De Bruijn, H. & Zachariasse, W.J., 1979 - The correlation of marine and continental biozones of Kastellios Hill reconsidered - *Annales Géologiques des Pays Hélieniques Hors Series 1*:219-226
- De Bruijn, H., Sondaar, P.Y. & Zachariasse, W.J., 1972 - Mammalia and foraminifera from the Neogene of Kastellios Hill (Crete), a correlation of continental and marine biozones - *Proceedings Nederlandse Akademie van Wetenschappen B* 74: 1-22
- De Bruijn, H., Daams, R., Daxner-Höck, G., Fahlbusch, V., Ginsburg, L., Mein, P. & Morales, J., 1992 - Report of the RCMNS working group on fossil mammals, Reisenburg 1990 – *Newsletters on Stratigraphy* 26(2/3): 65-117
- Delson, E., 1973 - Fossil colobine monkeys of the circum Mediterranean region and the evolutionary history of the Cercopithecidae (Primates, Mammalia) - Ph D. dissertation - pp. 1-856, Columbia University, New York
- Fejfar, O. & Heinrich, W.-D., 1990 - Muroid Rodent Biochronology of the Neogene and Quaternary in Europe - in: Lindsay, E. H., Fahlbusch, V. & Mein, P. (eds.) - *European Neogene Mammal Chronology*- pp. 91-117, Plenum Press
- Fortelius M., Eronen, J., Liu, L.P., Pushkina, D., Tesakov, A., Vislobokova, I. & Zhang, Z.Q. (2003) - Continental-scale hypsodonty patterns, climatic paleobiogeography, and dispersal of Eurasian Neogene large mammal herbivores - in: Reumer, J.W.F. & Wessels, W. (eds.) - *Distribution and migration of Tertiary mammals in Eurasia. A volume in honour of Hans de Bruijn - Deinsea 10: this volume*
- Fortelius, M., Werdelin, L., Andrews, P., Gentry, A., Humphrey, L., Mittmann, H.-W. & Viratana, S., 1996 - Provinciality, diversity, turnover and palaeoecology in land mammal faunas of the later Miocene of western Eurasia. - in: Bernor, R.L., Fahlbusch, V. & Mittmann, H.-W. (eds.) - *The evolution of Western Eurasian Neogene mammal faunas* - pp. 414-448, Columbia University Press, New York
- Gabunia, L., 1981 - Traits essentiels de l'évolution des faunes de Mammifères néogènes de la région mer Noire-Caspienn - *Bulletin Muséum National d'Histoire naturelle Paris 4th série* (3): 195-204
- Garces, M., Cabrera, L., Agustí, J. & Pares, M. J., 1997 - Old World appearance datum of *Hipparion* horses: Late Miocene large mammal dispersal and global events - *Geology* 25: 19-22
- Ginsburg, L., 1988 - Contributions à l'étude du gisement Miocène supérieur de Montredon (Hérault), 4. Les Artiodactyles Suidae – *Palaeovertebrata, Mémoire extraordinaire*: 57-64
- Ginsburg, L., 1998 - Le gisement de vertébrés de Calta, Ankara, Turquie. 5. Carnivores - *Geodiversitas* 20: 379-396
- Haq, B.U., Hardenbol, J. & Vail, P.R., 1988 - Mesozoic and Cainozoic chronostratigraphy and cycles of sea-level changes - in: Wilgus, C.K. *et al.* (eds) - *Sea-level changes, an integrated approach* - SEMP special publication 42: 71-108
- Kappelman, J., Duncam, A., Feshea, M., Lunkka, J.-P., Ekart, D., Mcdowell, F., Ryan, T. & Swisher III, C.C., 2003 - Chronology of the Sinap Formation - in: Bernor, R., Kappelman, J., Sen, S. and Fortelius, M. (eds) - *Monograph on the Sinap Formation, Anatolia, Turkey* - Columbia University Press
- Köhler, M., Moya-Sola, S. & Andrews, P., 1999 - Order primates - in: Rössner, G. & Heissig, K. (eds.) - *The Miocene land mammals of Europe* - pp. 91-108, Verlag Dr F. Pfeil, München

- Korotkevich, E.U., 1988 - Istorya formirovaniya gippa rionovoi fauny Vostoshna Evropy - Naukova Dauka - pp. 1-106
- Kostopoulos, D.S., 1998 - *Parastrepsiceros koufosi* n. sp. (Mammalia, Bovidae); note on the possible presence of a *Prostrepsiceros* descendant in the latest Pliocene of northern Greece - Acta Zoologica Cracoviensia 41 (1): 101-109
- Kostopoulos, D.S., Sen, S. & Koufos, G.D., 2003 - Magnetostratigraphy and revised chronology of the Late Miocene mammal localities of Samos, Greece - International Journal of Earth Sciences 92(4): 779-794
- Koufos, G.D., 1987 - *Chasmaporthetes Bonisi*, a new hyaenid (Carnivora, Mammalia) from the Late Miocene of Macedonia (Greece) - Bulletin Société Géologique de France (8) III (5): 913-920
- Koufos, G.D., 1993 - Late Pliocene carnivores from western Macedonia (Greece) - Paläontologische Zeitschrift 67: 357-376
- Koufos, G.D., 1995 - The Late Miocene perocrotas of Macedonia (Greece) - Palaeovertebrata 24: 67-84
- Koufos, G.D., 2000a - New material of Vallesian hipparions (Mammalia, Perissodactyla) from the lower Axios valley, Macedonia, Greece - Senckenbergiana Lethaea 80: 231-255
- Koufos, G.D., 2000b - Revision of the Late Miocene carnivores from the lower Axios valley - Münchner Geowissenschaftliche Abhandlungen (A) 39: 51-92
- Koufos, G.D., 2000c - The hipparions of the Late Miocene locality "Nikiti-1", Chalkidiki, Macedonia, Greece - Revue de Paléobiologie 19 (1): 47-77
- Koufos, G.D. & Kostopoulos, D.S., 1997 - Biochronology and succession of the Plio-Pleistocene mammalian localities of Greece - Proceedings BiochroM 97, Mémoires et Travaux de l'Institut de Montpellier, E.P.H.E. 21:619-634
- Koufos, G.D., Zouros, N. & Mourouzidou, O., 2003 - *Prodeinotherium bavaricum* (Proboscidea, Mammalia) from Lesbos Island, Greece. The appearance of deinotheres in the Eastern Mediterranean - Geobios 36: 305-315
- Lunkka, P.J., Fortelius, M., Kappelman, J. & Sen, S., 1999 - Chronology and mammal faunas of the Miocene Sinap Formation, Turkey - in: Agustí, J., Rook, L. & Andrews, P. (eds.) - Hominoid Evolution and climatic change in Europe, vol. I, The evolution of the Neogene terrestrial ecosystems in Europe - pp. 238-264, Cambridge University Press, New York
- Mein, P., 1990 - Updating MN zones - in: Lindsay, E.H., Falhbusch, V. & Mein, P. (eds.) - European Neogene Mammal Chronology - pp. 73-90, Plenum Press
- Morales Nieto, J., Köhler, M. & Moyà-Solà, S., 1999 - Large mammals from the Vallesian of Spain - in: Agustí, J., Rook, L. & Andrews, P. (eds.) - Hominoid Evolution and climatic change in Europe, vol. I, The evolution of the Neogene terrestrial ecosystems in Europe - pp.113-126, Cambridge University Press, New York
- Nikolov, I., 1985 - Catalogue of the localities of Tertiary mammals in Bulgaria. Bulgarian Academy of Sciences - Palaeontology, Stratigraphy and Lithology 21: 43-62
- Pickford, M., 1988 - Revision of the Miocene Suidae of the Indian subcontinent - Münchner Geowissenschaftliche Abhandlungen 12: 1-92
- Pilbeam, J., Morgan, M., Barry, J.C. & Flynn, L., 1996 - European MN Units and the Siwalik Faunal Sequence of Pakistan - in: Bernor, R.L., Falhbusch, V. & Mittmann, H.-W. (eds.) - The evolution of Western Eurasian Neogene mammal faunas - pp. 96-105, Columbia University Press, New York
- Rögl, F., 1999 - Circum-Mediterranean Miocene Palaeogeography - in: Rössner, G. & Heissig, K. (eds.) - The Miocene land mammals of Europe - pp. 39-48, Verlag Dr F. Pfeil, München
- Rook, L., Abbazzi, L. & Engesser, B., 1999 - An overview on the Italian Miocene land mammal faunas - in: Agustí, J., Rook, L. & Andrews, P. (eds.) - Hominoid Evolution and climatic change in Europe, vol. I, The evolution of the Neogene terrestrial ecosystems in Europe - pp.192-204, Cambridge University Press, New York
- Schmidt-Kittler, N., De Bruijn, H. & Doukas, C., 1995 - The vertebrate locality Maramena (Macedonia, Greece) at the Turolian-Ruscian boundary - Münchner Geowissenschaftliche Abhandlungen A 28: 9-18
- Sen, S., 1986 - Contribution à la magnetostratigraphie et à la paléontologie des formations continentales Néogènes du pourtour Méditerranéen. Implications biochronologiques et paleobiologiques - Thèse Doctorat d'Etat, Université Paris VI, 209 pp.
- Sen, S., 1990 - *Hipparion*-datum and its chronologic evidence in the Mediterranean area - in: Lindsay, E.H., Falhbusch, V. & Mein, P. (eds.) - European Neogene Mammal Chronology - pp. 73-90, Plenum

- Press
- Sen, S., 1997 - Magnetostratigraphic calibration of the European Neogene mammal chronology - *Palaeogeography, Palaeoclimatology, Palaeoecology* 133: 181-204
- Sen, S. & Leduc, P., 1996 - Diversity and dynamics of late Neogene and Quaternary mammalian communities in the Aegean area - *Acta zoologica cracoviensia* 39: 491-506
- Sen, S., Valet, J.-P. & Ioakim, Ch., 1986 - Magnetostratigraphy and biostratigraphy of the Neogene deposits of Kastellios hill (Central Crete, Greece) - *Palaeogeography Palaeoclimatology Palaeoecology* 53: 321-334
- Sen, S., Koufos, G.D., Kondopoulou, D. & De Bonis, L. de, 2000 - Magnetostratigraphy of the late Miocene continental deposits of the lower Axios valley, Macedonia, Greece - in: Koufos, G.D. & Ioakim, Ch. (eds.) - *Mediterranean Neogene cyclostratigraphy in marine-continental deposits* - pp. 197-206, *Bulletin Geological Society of Greece, special publication 9*:
- Sen, S., Seyitoglu, E. Karadenizli, L., Kazanci, N., Varol, B. & Araz, H., 1998 - Mammalian biochronology of Neogene deposits and its correlation with the lithostratigraphy in the Cankiri-corum basin, central Anatolia, Turkey - *Eclogae Geologicae Helveticae* 91: 307-320
- Sickenberg, O., 1975 - Die Gliederung des Höheren Jungtertiärs und Altquartärs in der Türkei nach Vertebraten und ihre Bedeutung für die internationale Neogen-Stratigraphie - *Newsletters on Stratigraphy* 1: 1-167
- Spassov, N. & Koufos, G.D., 2002 - The first appearance of *Dinocrocuta gigantea* and *Machairodus aphanistus* (Mammalia, Carnivora) in the Miocene of Bulgaria - *Mitteilungen der Bayerischen Staatssammlung für Paläontologie und Historische Geologie* 42: 83-101
- Steininger, F.F., Berggren, W.A., Kent, D.V., Bernor, R.L., Sen, S. & Agustí, J., 1996 - Circum-Mediterranean Neogene (Miocene and Pliocene) marine-continental chronologic correlations of European Mammal units - in: Bernor, R.L., Falhbusch, V. & Mittmann, H.-W. (eds.) - *The evolution of Western Eurasian Neogene mammal faunas* - pp. 307-338, Columbia University Press, New York
- Swisher III, C.C., 1996 - New ⁴⁰Ar/³⁹Ar dates and their contribution towards a revised chronology for the late Miocene of Europe and West Asia - in: Bernor, R.L., Falhbusch, V. & Mittmann, H.-W. (eds.) - *The evolution of Western Eurasian Neogene mammal faunas* - pp. 64-77, Columbia University Press, New York
- Tassy, P., 1983 - Les Elephantoidea miocènes du Plateau du Potwar, Groupe de Siwalik, Pakistan - *Annales de Paléontologie* 69: 99-136, 235-298, 317-354
- Tassy, P., 1990 - The "Proboscidean datum event": How many proboscideans and how many events - in: Lindsay, E.H., Falhbusch, V. & Mein, P. (eds.) - *European Neogene Mammal Chronology* - pp. 237-252, Plenum Press
- Tekkaya, I., 1969 - Kayadibi (Konya) bovidae faunası hakkında ön rapor - *Mad. Tet. Ara. Enst. Derg.* 73:155-159
- Theodorou, G., Athanassiou, A., Roussiakis, S. & Iliopoulos, G., 2003 - Preliminary remarks on the Late Miocene herbivores of Kerassía (Northern Euboea, Greece) - in: Reumer, J.W.F. & Wessels, W. (eds.) - *Distribution and migration of Tertiary mammals in Eurasia. A volume in honour of Hans de Bruijn - Deinsea 10: this volume*
- Ünay, E., Bruijn, H. de & Saraç, G., 2003 - A preliminary zonation of the continental Neogene of Anatolia based on rodents - in: Reumer, J.W.F. & Wessels, W. (eds.) - *Distribution and migration of Tertiary mammals in Eurasia. A volume in honour of Hans de Bruijn - Deinsea 10: this volume*
- Van Dam, J.A., 1997 - The small mammals from the upper Miocene of the Teruel-Alfambra region (Spain): Palaeoecology and palaeoclimatic reconstructions - *Geologica Ultraiectina* 156:1-204
- Van der Made, J., 1990 - Palaeobiogeography of *Hippopotamodon* and *Microstonyx* in relation to climate - IXth RCMNS Congress, Barcelona, Abstracts: 223-224
- Van der Made, J., Montoya, P. & Alcalá, L., 1992 - *Microstonyx* (Suidae, Mammalia) from the Upper Miocene of Spain - *Geobios* 25(3): 395-413
- Vassiliadou, K.V., Koufos, G.D. & Syrides, G.E., 2003 - Silata, a new locality with micromammals from the Miocene/Pliocene boundary of the Chalkidiki peninsula, Macedonia, Greece - in: Reumer, J.W.F. & Wessels, W. (eds.) - *Distribution and migration of Tertiary mammals in Eurasia. A volume in honour of Hans de Bruijn - Deinsea 10: this volume*
- Vekua, A., 1970 - New representatives of *Tragelaphini*

- from the Pliocene of Georgia – in: Metsniierba Tbilisi (ed.) - The Mesozoic and Cenozoic fauna of Georgia and its geohistoric significance – pp. 120-136 (in Russian)
- Welcomme, J.-L., Benammi, M., Crochet, J.-Y., Marivaux, L., Metais, G., Antoine, P.-O. & Baloch, I., 2001 – Himalayan forelands: palaeontological evidence for Oligocene detrital deposits in the Bugti Hills (Balochistan, Pakistan) - *Geological Magazine* 138(4): 397-405
- Woodburne, M.O., Bernor, R.L. & Swisher III, C.C., 1996 - An appraisal of the stratigraphic and phylogenetic bases for the "*Hipparion*" datum in the Old World - in: Bernor, R.L., Fahlbusch, V. & Mittmann, H.-W. (eds.) - The evolution of Western Eurasian Neogene mammal faunas - pp. 124-136, Columbia University Press, New York

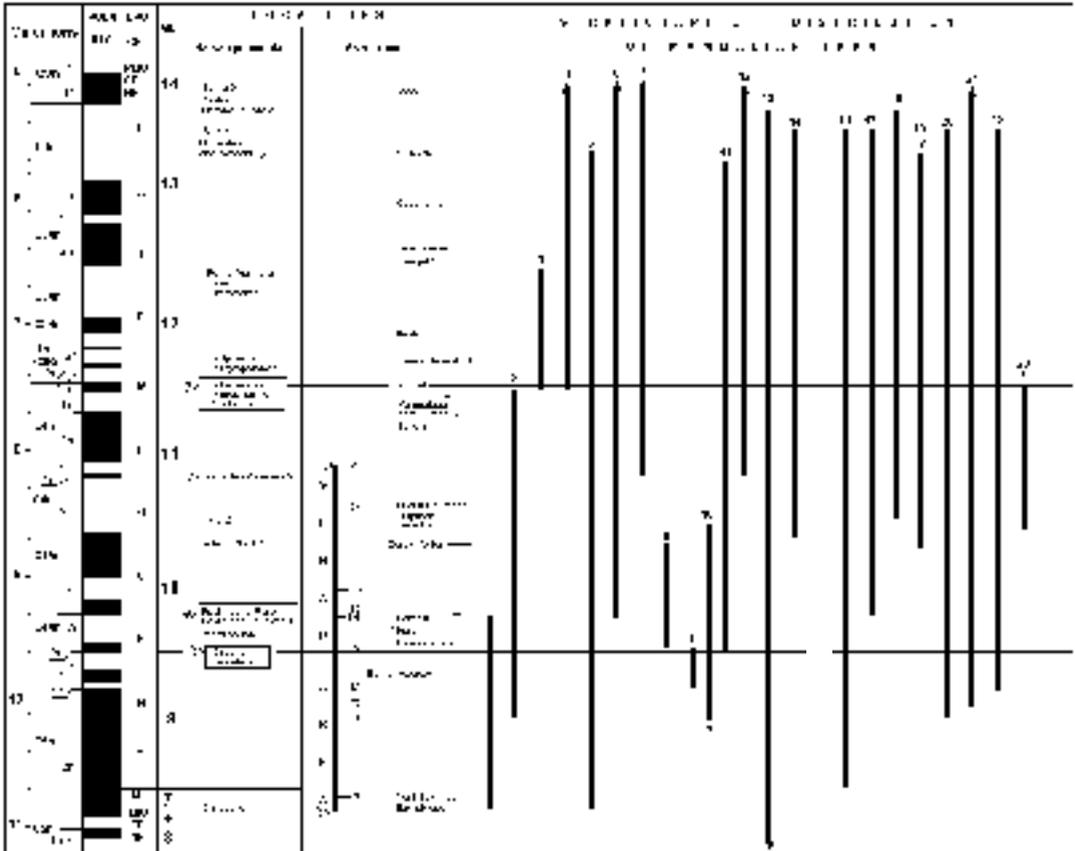
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APPENDIX I Late Miocene mammalian localities of the Eastern Mediterranean including the studied genera.

	1. <i>Cricetodon</i>	2. <i>Progonomys</i>	3. <i>Parapodemus</i>	4. <i>Apodemus</i>	5. <i>Byzantina</i>	6. <i>Occltanomys</i>	7. <i>Mesopithecus</i>	8. <i>Ouranopithecus</i>	9. <i>Ankarapithecus</i>	10. <i>Dicocrotia</i>	11. <i>Adcrocuta</i>	12. <i>Chasmaporthetes</i>	13. <i>Choerolophodon</i>	14. <i>Microstonyx</i>	15. <i>Decennatherium</i>	16. <i>Palaeostragax</i>	17. <i>Bohlinia</i>	18. <i>Samoebrium</i>	19. <i>Helladotherium</i>	20. <i>Tragopriax</i>	21. <i>Gazella</i>	22. <i>Prostrepsiceros</i>	23. <i>Misiodorcas</i>	
Achladion																								
Alifakas																								
Amasya											+													
Ano Metochi 2,3				+		+																+	+	
Bayraktepe 2		+			+																			
Cervit																								
Chomateres			+		+		+						+	+								+	+	+
Cobanpinar			+		+	+							+	+						+		+	+	+
Corak Verler													+	+	+						+	+	+	+
Dytiko							+					+	+	+			+	+			+	+	+	+
Eblio																								
Eski Bayirkoy																								
Esmo-Akcaakoy										+							+							
Garkin													+	+								+		
Gorna Sushitsa							+						+	+								+		
Gulpinar													+	+					+		+	+	+	+
Hadjidimovo							+				+		+	+		+				+	+	+	+	+
Haimyropotamos											+		+	+						+	+	+	+	+
Ihan													+	+								+	+	+
Kaimantsi 2-4							+				+	+	+	+				+		+	+	+	+	+
Karain											+													
Kar'oz?			+		+																			
Kastellos	+	+																						
Kayadibi										+			+	+		+						+		+
Kemiklitepe A-B											+		+				+					+		
Kemiklitepe D													+									+		
Kerassia 1,2,3													+	+		+	+		+	+	+	+	+	+
Kirik											+	+	+			+	+		+	+	+	+	+	+
Kocerinovo																						+		
Kromidovo							+				+						+							
Kucukcekmece																	+							
Kucukyozgat											+											+		
Lefkon		+			+																			
Mahmutgazi			+																					
Malusteni																								
Maragha							+						+	+		+	+	+		+	+	+	+	
Maramena							+	+				+	+								+	+	+	+
Monasteri				+		+															+	+	+	+
Nikiti 1								+					+	+		+	+		+	+	?	+	+	
Nikiti 2													+	+							+	+	+	+
Pentalophos 1										+			+			?	?							+
Perivolaki							+						+								+	+	+	+
Pikermi			+		+	+	+				+	+	+	+		+	+				+	+	+	+
Prochoma											+	+	+								+	+	+	+
Prokopion																								
Pyrgos Vassilissis													+								+	+	+	+
Ravin de la Pluie		+						+			+	+	+	+	+	+							+	+
Ravin des Zouaves 1											+	+									+	+	+	+
Ravin des Zouaves 5							+				+	+	+	+		+				+	+	+	+	+
Rema Mammara			+			+																		
Rhodes																								
Samos MTL																						+	+	+
Samos (old coll.)						+	+				+		+	+		+		+			+	+	+	+
Servia													+	+										
Sinap	+	+			+				+	+		+	+	+	+	+	+			+	+	+	+	+
Tanagra																								
Taskipasa																								
Titov Veles							+				+						+							+
Triada																								
Upper Kavakdere													+											
Vathyakkos			+				+				+	+	+								+	+	+	+
Xirochori 1								+			+	+	+											+

APPENDIX 2 Stratigraphic position of the late Miocene mammalian localities of the Eastern Mediterranean with the stratigraphic distribution of the studied genera. The corresponding numbers of the mammalian taxa are given in Appendix 1.



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