

Miocene/Pliocene mammal faunas of southern Balkans: implications for biostratigraphy and palaeoecology

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Abstract Even though there are numerous late Miocene mammal localities in the southern Balkans, those of late Turolian and early Ruscinian age are uncommon. Using the available data, mainly from Greece and Bulgaria, we compiled information about the faunal and palaeoenvironmental changes at the Miocene/Pliocene boundary. The analysis of the faunal elements indicates that several Miocene taxa disappeared, whereas new taxa appeared. The faunal composition of the mammal zones suggests a decrease of the bovids and giraffids and an increase of cervids and suids from MN 12 to MN 14. The available faunal assemblages from zones MN 12–MN 14 are compared with a set of modern and fossil assemblages from known environments to determine their palaeoenvironment. The results indicate an increase of the closed character of the environment from MN 12 to MN 14, suggesting a gradual increase of the humidity and the development of more forestial conditions. The rodent faunas from northern Greece ranging from MN 13 to MN 14 show a characteristic aridification of the biotopes and the introduction of African elements in the last part of the MN 13 (during the Messinian Salinity Crisis), with a subsequent return of humid-and/or-forested biotopes towards the MN 13/14 boundary. The faunal and sedimentological data

for the Greek localities correlated with the Turolian/Ruscinian boundary suggests a general open landscape with several water spots of variable sizes surrounded by dense forests.

Keywords Turolian/Ruscinian boundary · Mammalian localities · Faunal turnover · Palaeoenvironment

Abbreviations

ASP	Asprogiannos
DIT	Dytiko 2
DKO	Dytiko 3
DRK	Dorkovo
DTK	Dytiko 1
DYTI	Dytiko
HRB	Hrabarsko
KD	Kardia
KES	Kessani
KO1highA and B	Komanos 1 high A and Komanos 1 high B
KO1lowA and B	Komanos 1 low A and Komanos 1 low B
LAV2	Lava 2
MAR	Maramena
MNS	Monasteri
MTH 2 and 3	Ano Metochi 2 and Ano Metochi 3
PLM-A and B	Paliambela A and Paliambela B
PSM	Prosilion-Mercurion
PT1	Ptolemais 1
SLT	Silata
SPL-0 and 1	Spilia 0 and Spilia 1
TE1 and 2	Tomea Eksi 1 and Tomea Eksi 2
VOR1	Vorio 1

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Introduction

Even though the late Miocene mammal localities in the eastern Mediterranean area are abundant, those of latest Miocene-earliest Pliocene are rare. In the southern Balkans, the known mammal localities with an informative fauna from this time slice are a few (Fig. 1; Table 1). The same phenomenon is also observed in Asia Minor, where little is known about the latest Miocene faunas. Furthermore, the mammal faunas present a heteromorphy, as the late Miocene ones include mainly macromammals, whereas the transitional Miocene/Pliocene and the early Pliocene ones have mainly yielded micromammals, hindering any comparison. The best known large mammal localities in eastern Mediterranean are situated in the southern Balkans (Fig. 1; Table 1). The Greek localities of Dytiko in Axios Valley, the localities of Maramena (Serres Basin), Silata (Chalkidiki Peninsula) and Kessani (Xanthi-Komotini Basin) provided the best known late Turolian and Turolian/Ruscinian mammal faunas of the area. In addition, the Greek early Ruscinian mammal faunas of Ptolemais Basin as well as the Bulgarian fauna of Dorkovo provide reliable data.

The end of Miocene and the beginning of Pliocene is an interesting time interval, as it marks the end of the Messinian salinity crisis and is characterised by significant changes in climatic parameters and the palaeoenvironments (e.g. Koufos et al. 2005; Merceron et al. 2005; Koufos 2006a; Hordijk and De Bruijn 2009). The present article is an effort to check the Miocene/Pliocene boundary in the terrestrial fossil mammal record of the southern Balkans, as well as to determine the palaeoenvironment during this time interval.

Material and methods

The available late Turolian–early Ruscinian mammal localities used in the present study are given in Fig. 1 and Table 1 and their faunas are given in Figs. 2, 3 and 4. The pie- and bar-diagrams were made using Excel. The software PAST (Hammer et al. 2001) was used for the correspondence factor analysis given in Fig. 10.

Localities and faunas

The analysed mammal faunas cover the short time interval of the late Miocene to early Pliocene (correlated with the zones MN 13–MN 14) and originate from the southern Balkan area. There is almost no published data from Albania and the European part of Turkey. In FYROM, there are several late Miocene localities in the area of Titov Veles. The old collections are mixed and without clear stratigraphic background, therefore providing questionable taxonomic and biochronologic information. The new collections are not fully published and

the known data are very limited. Furthermore, the well-studied late Turolian (MN 13) fauna from Q5 (Samos Island, Greece) and the Turolian/Ruscinian (MN13/14) micromammalian fauna from Maritsa (or Maritses, Rhodes Island, Greece) are not included in the present analysis, as they both show closer similarity with the Asian faunas than with the Balkan ones.

Thus, the localities used for the present study are restricted to northern Greece and Bulgaria. Their faunal content, age and references for each one of them are presented in Table 1. The numbers in the first column (A/A) correspond to the numbers of the localities in Fig. 1.

The vast majority of the Greek localities (numbers 1–16 in Table 1) have yielded only micromammals (13), three localities have yielded only macromammals, whereas five include both micro- and macro-mammals.

The known Bulgarian localities in the time interval studied are only two (numbers 17–18 in Table 1). Recently, a new locality named Staniantsi was discovered in north-western Bulgaria, which has been correlated with the Turolian/Ruscinian boundary (Böhme et al. 2013), but no detailed faunal list has yet been published and, thus, it cannot be included in our analysis.

Turolian/Ruscinian faunal turnover

The mammal faunas in the focused area show a significant change from the late Turolian towards the early Ruscinian. Several well-known Turolian taxa disappeared at the end of this time period, whereas new taxa appeared. This faunal turnover is mainly evident in the four Greek faunas correlated with the MN13/14 boundary, KES, MTH 2, 3, MAR and SLT, which include a combination of Turolian and Ruscinian taxa (Figs. 2, 3, 4). Many Turolian taxa have their last occurrence in these localities (marked with one asterisk in Fig. 5), whereas only a few of them entered into the Ruscinian (e.g. the murids *Micromys bendai*, *Occitanomys adroveri* and the genera *Gazella* and *Propotamochoerus*). At the same time, many Ruscinian taxa make their first appearance in these localities (marked with two asterisks in Fig. 5), possibly utilising the available niches left behind by the extinct taxa. Finally, many taxa have been until now described only from these four transitional faunas, mainly from MAR, (marked with three asterisks in Fig. 5), giving a unique character to these fossil associations.

Even though many late Turolian–early Ruscinian insectivore assemblages in the studied area are under investigation and may reveal more information, some basic remarks can be made on the biostratigraphic distribution of certain taxa (Fig. 5). Within the erinaceids, the genus *Schizogalerix*, a component of Asian and European faunas since the early Miocene, occurred for the last time in the transitional faunas with the species *S. macedonica*, whereas the extant genus *Erinaceus* first occurred in MAR and SLT. The water-mole



Fig. 1 The late Miocene–early Pliocene localities of the studied area. 1 Dytiko localities, MN 13; 2 Lava 2, MN 13; 3 Asprogiannos, MN 13; 4 Paliambela A, B, MN 13; 5 Monasteri, MN 13; 6 Tomea Eksi 1, 2, MN 13; 7 Prosilion-Mercurion, MN 13; 8 Maramena, MN 13/14; 9 Ano

Metochi 1, 2, MN 13/14; 10 Silata, MN 13/14; 11 Kessani, MN 13/14; 12 Spilia 0, 1, MN 14; 13 Komanos 1, MN 14; 14 Vorio 1, MN 14; 15 Kardia, MN 14; 16 Ptolemais 1, MN 14; 17 Hrabarsko, MN 14; 18 Dorkovo, MN 14

Desmana verestchagini appears for the first time in the faunas of SPL 0, 1 and DRK, thus in the earliest Ruscinian. The latter fauna also includes the first representatives of the mole *Talpa minor*. Finally, the shrews *Amblycoptus jessiae* and *Blarinella dubia*, both present in European late Turolian faunas, vanished at the end of the Miocene, and were replaced by species of the genera *Mafia* and *Deinsdorfia*, present in Europe throughout the Pliocene and until the early Pleistocene.

The rodents show a more dramatic change along the Turolian/Ruscinian boundary in the southern Balkans. Among the flying squirrels, the species *Hylopetes macedoniensis*, first described from MAR and later found in the middle Turolian (MN 12) faunas of Turkey, disappeared after the end of the Miocene, whereas *Pliopetaurista dehneli* and *Miopetaurista thaleri* first appear in the transitional MN 13/14 localities of the focus area. The chipmunk *Tamias atsali* is until now known only from MTH 2, 3 and MAR, and the ground

squirrel *Spermophilinus turolensis*, which appeared during the middle Miocene and showed its widest geographic range during the Turolian, makes its last appearance in the MAR and SLT faunas. The dormice, present in all transitional faunas with one to three species, become less common in the MN 14 faunas.

The best represented family in all faunas is the family Muridae, present with five subfamilies. Within the subfamily Murinae, even though there are only a few disappearances and almost no appearances (except for *Micromys cingulatus*, which is only present in the transitional fauna MAR) along the MN 13/14 boundary, a notably wide variety of species occurs in the transitional MN 13/14 faunas, not to be observed in either MN 13 or MN 14 faunas. The murine genus *Micromys* is represented in most large MN 13 and MN 14 faunas by either the large-sized *M. steffensi* or the medium-sized *M. bendai*. It is of special interest that the genus is present with a different species in each of the

Table 1 The mammalian localities of the southern Balkans, their faunal content (the faunal lists are given in detail in Figs. 2, 3 and 4), their ages and the references that present the original data used for the present study for each one of them

A/A ^a	Locality name (abbreviation)	Faunal content	Age	Mammalian fauna in Figs. 2, 3 and 4 according to:	Additional information in:
1	Dytiko (DYTI) [Dytiko 1 (DTK), Dytiko 2 (DIT), Dytiko 3 (DKO)]	Micro- and macro-mammals	Late Turolian (MN 13)	Koufos (2006b) with amendments according to Bouvrain and de Bonis (2007), Vlachou (2013), Lazarri (GK personal communication 2014), personal observations (GK)	de Bonis et al. (1988, 1990) de Bonis and Bouvrain (1996) de Bonis and Koufos (1999) Kostopoulos et al. (2001) Koufos (1990, 2003, 2009a, 2009b, 2013)
2	Lava 2 (LAV2)	Micromammals	Late Turolian (lower part of MN 13) ~ 6.81 Ma	De Bruijn et al. (1999) Doukas (2005)	Steenbrink et al. (1999)
3	Asprogiannos (ASP)	Macromammals	Latest Turolian, (uppermost MN 13)	Sylvestrou (2002) Sylvestrou and Kostopoulos (2007)	
4	Paliambela A and B (PLM-A and B)	Micromammals	Latest Turolian, (uppermost MN 13)	Sylvestrou (2002) Sylvestrou and Kostopoulos (2007)	
5	Monasteri (MNS)	Micromammals	Latest Turolian, (uppermost MN 13)	De Bruijn (1989) Doukas (1989, 2005) Daxner-Höck (1995) Storch and Dalmann (1995) Sylvestrou and Kostopoulos (2007) Doukas (2005)	
6	Tomea Eksi 1 (TE1) and Tomea Eksi 2 (TE2)	Micromammals	Latest Turolian, (uppermost MN 13) 5.32/5.43 Ma and 5.30/5.40 Ma, respectively	Hordijk and De Bruijn (2009)	Steenbrink et al. (1999)
7	Prosilion-Mercurion (PSM)	Micromammals	Latest Turolian, (uppermost MN 13)	Hordijk and De Bruijn (2009)	
8	Maramena (MAR)	Micro- and macro-mammals	Turolian/Ruscianian boundary (MN 13/14)	De Bruijn (1989) Doukas (1989) Schmidt-Kittler (1995) Schmidt-Kittler et al. (1995) Doukas (2005)	
9	Ano Metochi 2 (MTH 2) and Ano Metochi 3 (MTH 3)	Micro- and macro-mammals	Turolian/Ruscianian boundary (MN 13/14)	Karystinaios (1984) De Bruijn (1989) Doukas (1989) Daxner-Höck (1995) De Bruijn (1995) Doukas et al. (1995) Storch and Dalmann (1995) Wessels (1998, 1999)	Doukas (2005)
10	Silata (SLT)	Micro- and macro-mammals	Turolian/Ruscianian boundary (MN 13/14)	Vassiliadou et al. (2003) Koufos (2006a)	
11	Kessani (KES)	Micro- and macro-mammals	Turolian/Ruscianian boundary (MN 13/14)	Syrides et al. (1997) Vasileiadou et al. (2012)	
12	Spilia 0 (SPL-0) Spilia 1 (SPL-1)	Micromammals	Early Ruscianian (MN 14)	Rümke (1985) Van der Meulen and Van Kolfshoten (1986) De Bruijn (1989) Doukas (1989) Theocharopoulos (1991)	Armour Brown et al. (1977)
13	Komanos 1 low A and B (KO1lowA and B) and Komanos 1 high A and B (KO1highA and B)	Micromammals	Early Ruscianian (MN 14) ~5.23 and ~5.22 Ma, respectively	Hordijk and De Bruijn (2009)	Steenbrink et al. (1999)
14	Vorio 1 (VOR1)	Micromammals	Early Ruscianian (MN 14) ~5.04 Ma	Hordijk and De Bruijn (2009)	Steenbrink et al. (1999)
15	Kardia (KD)	Micromammals	Early Ruscianian (MN 14) ~5.23/5.22 Ma	van de Weerd (1979) Rümke (1985) Doukas (2005) Hordijk and De Bruijn (2009)	
16	Ptolemais 1 (PT1)	Micromammals	Uppermost part of the early Ruscianian (MN 14)	van de Weerd (1979) Rümke (1985) Doukas (2005) Hordijk and De Bruijn (2009)	
17	Hrabarsko (HRB)	Micro- and macro-mammals	Late Turolian (MN 13)	Huguene (1999) Spassov and Ginsburg (1999)	
18	Dorkovo (DRK)	Micro- and macro-mammals	Early Ruscianian (MN 14)	Thomas et al. (1986a, b) Boev (1998) Delson et al. (2005) Rzebik-Kowalska and Popov (2005) Spassov (2005) Spassov et al. (2005)	

^a Numbers in this column correspond to the numbers of the localities in Fig. 1

EULIPOTYPHLA & LAGOMORPHA FAMILIES				Erinaceidae	Talpidae	Soricidae	Leporidae	Ochotonidae
EULIPOTYPHLA & LAGOMORPHA SPECIES				<i>Erinaceus samsonowici</i>	<i>Archaeodesmana getfica</i>	<i>Amblycoptus jessiae</i>	<i>Pliopentalagus sp.</i>	<i>Prolagus sp.</i>
EPOCH	ELMA	MN ZONE	LOCALITIES	<i>Erinaceus sp.</i>	<i>Desmanella dubia</i>	<i>Blarinella dubia</i>	<i>Alilepus turoleusis</i>	<i>Prolagus michauxi</i>
				<i>Schizogalerix macedonica</i>	<i>Desmana verestchagini</i>	<i>Asoriculus gibberodon</i>	<i>Trischizolagus sp.</i>	
				<i>Erinaceidae indet.</i>	<i>Urotrichus sp.</i>	<i>Sorex sp.</i>	<i>Leporidae indet.</i>	
				<i>Archaeodesmana sp.</i>	<i>Talpa fossilis</i>	<i>Petenya hungarica</i>	<i>Soricidae indet.</i>	
				<i>Desmanella dubia</i>	<i>Talpa minor</i>	<i>Deinsdorfia kerkhoffi</i>	<i>Pliopentalagus sp.</i>	
				<i>Desmana verestchagini</i>	<i>Talpidae indet.</i>	<i>Deinsdorfia janossyi</i>	<i>Alilepus turoleusis</i>	
				<i>Urotrichus sp.</i>		<i>Mafia csarnotensis</i>	<i>Trischizolagus sp.</i>	
				<i>Talpa fossilis</i>			<i>Leporidae indet.</i>	
				<i>Talpa minor</i>				
				<i>Talpidae indet.</i>				
				<i>Amblycoptus jessiae</i>				
				<i>Amblycoptus sp.</i>				
				<i>Blarinella dubia</i>				
				<i>Asoriculus gibberodon</i>				
				<i>Sorex sp.</i>				
				<i>Petenya hungarica</i>				
				<i>Deinsdorfia kerkhoffi</i>				
				<i>Deinsdorfia janossyi</i>				
				<i>Mafia csarnotensis</i>				
				<i>Soricidae indet.</i>				
				<i>Pliopentalagus sp.</i>				
				<i>Alilepus turoleusis</i>				
				<i>Trischizolagus sp.</i>				
				<i>Leporidae indet.</i>				
				<i>Prolagus sp.</i>				
				<i>Prolagus michauxi</i>				
PLIOCENE	RUSCINIAN	MN 14	DORKOVO					
			PTOLEMAIS 1 *					
			VORIO 1 *					
			KARDIA *					
			KOMANOS 1 H A & B *					
			KOMANOS 1 L A & B *					
MIOCENE	TUROLIAN	MN 13	SPLIA 0 & 1					
			SILATA					
			MARAMENA					
			ANO METOCHI 2,3 **					
			KESSANI					
			PROSILION-MERCURION					
			TOMEA EKS 2 *					
			TOMEA EKS 1 *					
			MONASTERI					
			PALIAMBELA-A					
			PALIAMBELA-B					
			LAVA 2 *					
			DYTIKO 3					
			DYTIKO 1					
			HRABARSKO					

Fig. 2 Faunal list for the Eulipotyphla and Lagomorpha of the studied localities. The order of the localities does not necessarily coincide with the correct relative chronostratigraphical position among them. The insectivores from most of the localities of the Serbia and Ptolemais Basins have been partially studied (e.g. the Talpidae from KD and PT1 have been studied by Rümke 1985); however, most of the material is still under study by C. Doukas (localities marked with *one asterisk*). The insectivore material from MTH 2,3, initially separately collected and

reported by Doukas (1989), was later included in the material from MAR, described by Doukas et al. (1995), as the two faunas are considered identical (Doukas 2005); here, the faunal content of MTH 2, 3 (marked with *two asterisks*) is shown as initially reported by Doukas (1989). The black box shows definite species presence, the box with diagonal lines shows tentative species identification (cf.) and the box with the checkered pattern shows identification to a similar species (aff.)

four transitional faunas: in KES with the large-sized *M. steffensi*, in MTH 2, 3 with the medium-sized *M. bendai*, in MAR with the medium-sized *M. cingulatus* and in SLT with the small-sized *M. cf. paricioi*.

Occitanomys is also present with many species in the MN 13/14 faunas of the studied area, but with only one species in each fauna. *Occitanomys adroveri* and *O. brailloni* are the species with the greatest geographic distribution, the former spreading from Spain and Morocco to Mongolia and the latter from Spain to Turkey; they are both present in the southern Balkans during the late Turolian and also the early Ruscinian. In contrast, the species *O. debruijni* and *O. (Hansdebruijnina) neutrum*, restricted in Asia and eastern Europe during the Turolian, disappeared at the end of this time interval. Just like with the *Micromys* species, even though only two

Occitanomys species were present in the focus area during both the last part of the Turolian and the first part of the Ruscinian, the transitional faunas show a larger variety, since three different species are present.

The genus *Apodemus* is represented by three species with European affinities that first appeared during the last part of the Turolian (MN 13) and survived across the Turolian/Ruscinian boundary. And again, even though before and after the boundary only one species is present in each fauna (during the late Turolian the large-sized *A. gorafensis* and during the early Ruscinian the medium-sized *A. atavus*), in all four transitional faunas *A. gorafensis* co-exists with *A. atavus*. The situation is simpler with the genus *Rhagapodemus*, since one of the species *R. hautimagnensis* and *R. primaevus* is present in each fauna before and after the boundary. However, in this

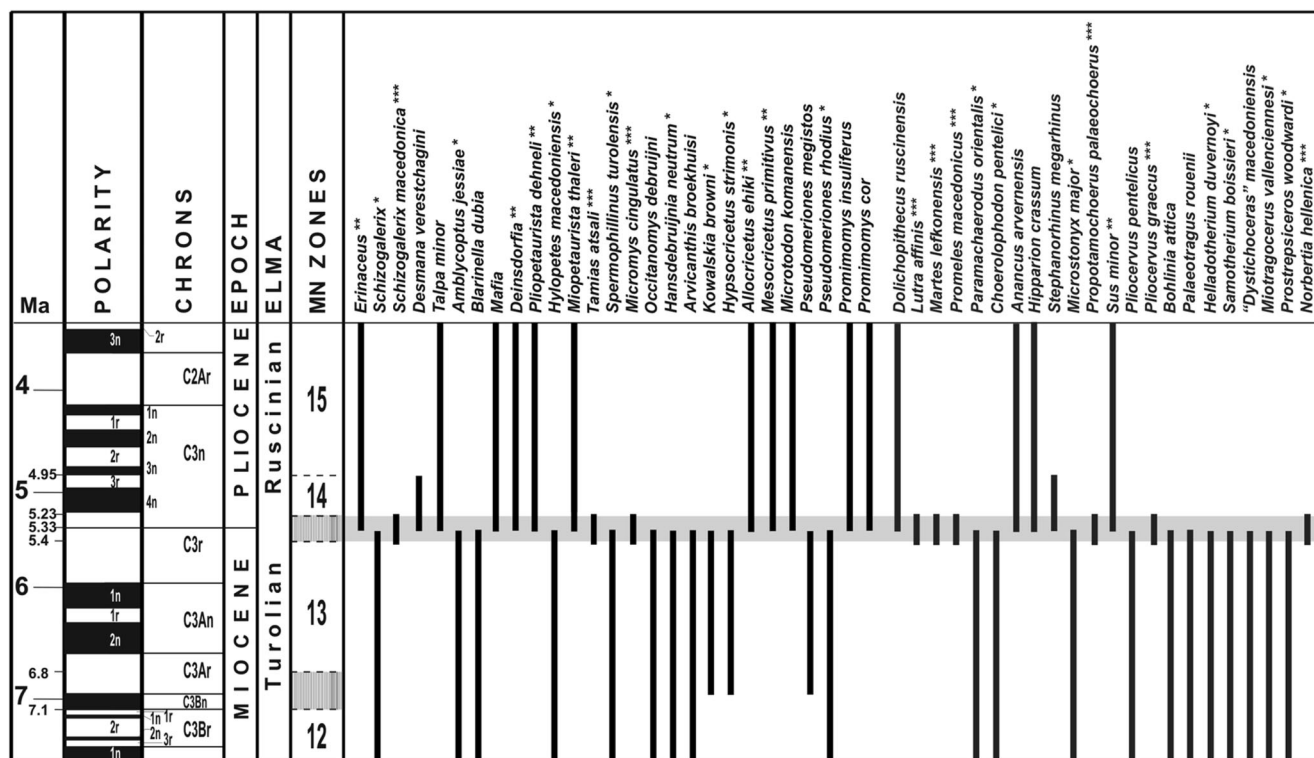


Fig. 5 Biostratigraphic table with the stratigraphic distribution of the main late Turolian- early Ruscinian mammal taxa in the studied area; explanations in the text

elements disappeared from Europe at the end of the Messinian.

The hamsters appear to have changed greatly in this focus interval. The species *Kowalskia browni* and *Hypsocricetus strimonis* disappear, whereas *Allocricetus ehiki* and *Mesocricetus primitivus* appear during the Turolian/Ruscinian boundary. Furthermore, the “microtoid cricetids”, represented by the genus *Microtodon*, first appeared in Europe at the earliest Pliocene (the genus already existed in eastern Asia in the latest Miocene) and are present in the southern Balkans with the species *M. komanensis* and a second species in faunas correlated with MN 14 (Hordijk and De Bruijn 2009).

Pseudomeriones, a genus already present in Asia since the Vallesian and also in the Greek South Aegean Island Samos during the middle Turolian, seems to enter the area of northern Greece during the Messinian salinity crisis (Sylvestrou and Kostopoulos 2007). It appears with two species in the faunas correlated with the last part of the Turolian and with at least one in the transitional faunas. The genus retreats to its original geographic range in Asia at the end of the Miocene and disappears from European faunas. The two species that have been described from Greek faunas, *P. megistos* and *P. rhodius*, disappeared at the end of the Miocene.

The subfamily Arvicolinae has traditionally marked the beginning of the Ruscinian, MN 14. However, the first representative of the voles, the genus *Promimomys*, appeared in

eastern Europe in a fauna correlated with the MN 13 (Fejfar et al. 2011). The genus enters to the studied area at the beginning of Ruscinian with two species, *P. insuliferus* and *P. cor*. According to Fejfar et al. (2011), the former species is more primitive than the latter and is present in faunas correlated with the early part of MN 14, whereas the latter species occurs in faunas correlated with the last part of this zone.

Among the Primates, the colobine monkey *Mesopithecus pentelicus* is present in the Turolian faunas. In the late Turolian DYTI fauna, *M. pentelicus* is present with a form smaller than the typical one from Pikermi whereas another small-sized form co-occurs. The latter is smaller than *M. pentelicus* and close to *M. monspessulanus*, a small-sized colobine, known from the Ruscinian of Europe (Koufos 2009a). In the transitional Turolian/Ruscinian faunas of the studied area, *Mesopithecus* is known from MAR (Kullmer and Doukas 1995), but, as the available material consists of isolated teeth, it is difficult to say if it is represented by one or two forms. The typical Ruscinian cercopithecoids *Dolichopithecus rusciniensis* and *M. monspessulanus* co-exist in the early Ruscinian locality of Dorkovo (Delson et al. 2005).

The main late Miocene carnivore genera (*Adcrocuta*, *Amphimachairodus*, *Paramachaerodus*, *Metailurus*) became extinct, whereas other ones entered in the early Pliocene with new species (*Promeles macedonicus*, *Martes lefkonensis*) and some made their first occurrence (*Lutra affinis*). The presence

of the semi-aquatic carnivore *Lutra* in the Turolian/Ruscianian MAR fauna is an indication that the climate became wetter towards the end of the Turolian.

The common eastern Mediterranean Miocene proboscidean *Choerolophodon pentelici* disappeared and was replaced by *Anancus arvernensis*. In fact, the genus *Anancus* seems to have already appeared before the disappearance of *C. pentelici*, as there is indication of its presence in the late Miocene of Greece and Bulgaria (Markov 2008; Konidaris 2013). The late Miocene hipparions with low enamel plication in the upper cheek teeth and elongated and slender metapodials (running forms eating hard grass) were replaced by forms with highly plicated cheek tooth enamel and relatively short and robust metapodials (more forestrial forms eating soft food), such as *H. crassum*, which is possibly present in the transitional MAR fauna (Sondaar and Eisenmann 1995).

The very common suid *Microstonyx major* disappeared and the more derived genus *Sus* makes its first occurrence in the transitional Turolian/Ruscianian KES fauna (Koufos 2006b). The suid *Propotamochoerus* was represented in the area with the species *P. provincialis* during the early Turolian (de Bonis and Bouvain 1996), which was, at the end of the Miocene, replaced by the more derived *P. palaeochoerus*, present in the Turolian/Ruscianian fauna MAR. The typical Miocene giraffids (*Bohlinia*, *Samotherium*, *Helladotherium*) disappeared at the end of Miocene. The giraffids re-appeared much later, in the early Pleistocene (~2.0 Ma) faunas from Dafnero, Sesklon and Volax with the species *Mitilanotherium martinii* (Kostopoulos 1996; Athanassiou 1998). The genus *Mitilanotherium* is recently considered as synonym to *Palaeotragus* by Athanassiou (2014); if this is true, the Miocene genus *Palaeotragus* re-appeared in the area during the early Pleistocene. The cervids are rare in the late Miocene of the focus area, recorded with the species *Pliocervus pentelicus* (Koufos 2006b). However, in the MAR association, a new species of *Pliocervus* occurred, *P. graecus*, represented by several remains (Azanza 1995). The majority of the Miocene bovids disappeared and most of them make their last occurrence in the Turolian/Ruscianian MAR fauna, whereas the new taxon *Norbertia hellenica* appeared (Köhler et al. 1995) (Fig. 5).

Chronology

Several opinions about the ages of the boundaries between the MN zones have been proposed (Steininger 1999; Steininger et al. 1990; Agustí et al. 2001). However, the correlation and dating of localities with the use of the MN units is problematic on a continental scale but could be still effective on a more regional scale, based on regional biostratigraphy and chronology (Hordijk and De Bruijn 2009; Van der Meulen et al. 2011, 2012).

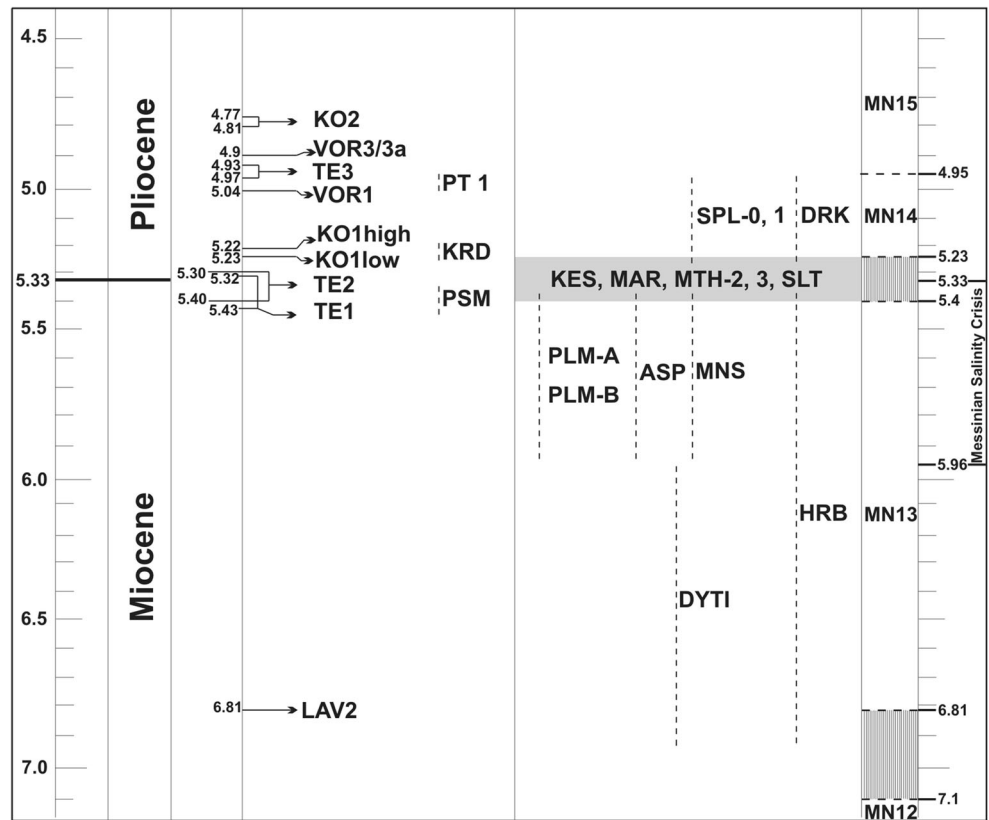
The Serbia and Ptolemais Basins include several localities with well-dated faunas and sediments. A combination of cyclostratigraphy and magnetostratigraphy, together with radiochronology of tephra layers, have provided reliable ages for the faunas of the Serbia and Ptolemais Basins localities (Hordijk and De Bruijn 2009 and references cited therein) (Fig. 6). These authors have established that the minimum age for the MN 12/13 boundary in north-western Greece should be slightly older than 6.81 Ma, below chron C3An.2n and inside chron C3Ar. Considering that the Pikermi fauna (near Athens, Attica, Greece) is dated at ~7.1 Ma, uppermost MN 12 (Koufos 2013), the MN 12/13 boundary for the area should be between 7.1 and 6.81 Ma. It has also been shown that, in the same area, the MN 13/14 boundary must be dated at the interval 5.23–5.40 Ma (but is likely younger than the Messinian/Zanclean boundary at 5.33 Ma), and the MN 14/15 boundary dates approximately at 4.95 Ma, correlated with the upper part of chron C3n.3r (Hordijk and De Bruijn 2009 and references cited therein).

In the present study, we extrapolate the ages given for Serbia-Ptolemais Basins (Hordijk and De Bruijn 2009 and references cited therein) to the whole area of southern Balkans. Below, we will try to approach as close as possible to a numerical age for each of the selected faunas, using stratigraphic and biochronologic observations (Fig. 6).

The three localities of DTYI are correlated with MN 13 since their fauna is more derived than that of Pikermi (~7.1 Ma). Furthermore, the similarities with the fauna from the locality Q5 (Samos Island, East Aegean Sea, Greece), which is dated at 6.9–6.7 Ma (Koufos et al. 2009a), suggest a similar age for DTYI (Koufos 2013 and references cited therein) and consequently a definite pre-Messinian-Salinity-Crisis age. As it is not possible to give a precise age for the fauna, a rough approximation between 7.1 and 6.81 Ma (depending on where the MN 12/13 boundary is) and 5.96 Ma (the beginning of Messinian salinity crisis according to Krijgsman et al. 1999) is assumed (Fig. 6).

The localities PLM-A, PLM-B and ASP of the Katerini Basin are stratigraphically placed in the Makrygialos Fm, which conformably overlies a bed with a characteristic Pontian mollusc fauna. Just above the levels with the mammal remains, there are sand beds that include more than 80 % volcanic clasts from the Almopia volcanic centre (northern Greece), the first activities of which have been radiometrically dated from 5.60±0.10 to 5.05±0.14 Ma (Vougioukalakis 2002; Sylvestrou and Kostopoulos 2007). The presence of a derived large-sized *Pseudomeriones* species in PLM-B suggests that the fauna was accumulated during the last part of the Turolian, more specifically during the Messinian Salinity Crisis. Thus, an age between ~5.96 Ma (beginning of Messinian salinity crisis) and 5.33 Ma (end of Miocene) is quite possible for these three

Fig. 6 Relative chronologic correlations of the studied localities. The data for the chronology of the Ptolemais Basin localities are taken from Hordijk and De Bruijn (2009), Kuiper (2003), Kuiper et al. (2004), Steenbrink et al. (1999) and van Vugt et al. (1998)



localities (Fig. 6). The presence of the same *Pseudomeriones* in the locality MNS indicates a similar age for it (Fig. 6). The Bulgarian locality HRB has yielded a very poor fauna (only two species) and it is impossible to approximate a numerical age for it (Fig. 6).

The localities KES, MAR, MTH 2, 3 and SLT include a mixing of Turolian and Ruscinian faunal elements and thus have been biochronologically correlated to the transition from Miocene to Pliocene. The youngest Turolian fauna in Ptolemais Basin is TE2, dated at 5.40–5.30 Ma, while the oldest Ruscinian one is KO1low dated at 5.23 Ma. Therefore, the localities with the Turolian/Ruscinian faunal elements can be dated at the interval 5.40–5.23 Ma (Fig. 6).

The presence in the fauna from SPL-0, 1 of the arvicolid *Promimomys insuliferus*, which according to Fejfar et al. (2011) characterises the earliest Ruscinian of Europe, implies the correlation of the fauna with the lowermost MN 14; it could possibly be slightly older than the KO1low fauna (5.23 Ma), which includes the slightly more advanced *P. cor* in its fauna. The same arvicolid is present in DRK, which should be of similar age, near the base of MN 14. However, since this indication is not firm enough to date the two faunas, both are here considered to date between 5.40 and 5.23 Ma (depending on where the MN 13/14 boundary is) and 4.95 Ma (the beginning of MN 15 in Ptolemais Basin) (Fig. 6).

Palaeoenvironmental remarks

It is already known, based on the analysis of mammalian faunas, that the palaeoenvironment in south-eastern Europe during the late Miocene was open. Savannah-like landscapes with bushes, shrubs or small trees and grass cover prevailed in the area (de Bonis et al. 1992, 1994; Koufos et al. 2006, 2009b; Kostopoulos 2009; Nagel and Koufos 2009; Koufos and Konidaris 2011). This was the result of the gradual aridity increase from east to west and the replacement of the middle Miocene forests with open savannah-like environments (Koufos 2006c; Ataabadi 2010). The dental microwear analysis of late Miocene herbivores indicates that the environment was open with a thick grass floor in the eastern Mediterranean (Merceron et al. 2004, 2005, 2006, 2007). The study of phytolites from the late Miocene in the area suggests a similar palaeoenvironment (Strömberg et al. 2007). The study of the hypsodonty of herbivore mammals indicates low precipitation and high temperatures in the eastern Mediterranean area during the late Miocene (Eronen and Rook 2004).

Evidence from micromammals

Palaeoenvironmental analysis on the basis of the complete faunal lists (such as cenogram composition) cannot be used for the studied faunal assemblages, as many of their faunal elements are

still under study (e.g. insectivores from many of the localities in the Ptolemais Basin). Several attempts have been made to reconstruct the palaeoenvironment, using proxies based on rodents (Aguilar et al. 1999; van Dam and Weltje 1999; Legendre et al. 2005; Montuire et al. 2006). In order to use such methods, the quantification of assemblages is necessary. Since details about the exact numbers of specimens or Minimum Numbers of Individuals are not known for many of the analysed faunas, comparisons in this context are also not possible. Therefore, we use the mere presence of rodent species and the numbers of species as indications for the habitat and environment.

The selected faunas have been separated in four faunal assemblages: the first faunal assemblage consists of the faunas correlated with MN 13 but accumulated before the Messinian Salinity Crisis (MN 13/a: LAV2 and DYT1), the second comprises of the faunas correlated with MN 13 and accumulated during the Messinian Salinity Crisis (MN 13/b: TE1,2, PSM, PLM, ASP and MNS), the third assemblage consists of the transitional faunas correlated with the MN 13/14 boundary (MN 13/14: KES, MAR, MTH 2,3 and SLT) and the fourth one of the faunas correlated with MN 14 (MN 14: SPL 0,1, KO1 low and high, KRD, VOR1, PT1 and DRK). The percentage of the species number in each rodent family/subfamily and faunal assemblage is given in pie-diagrams (Fig. 7). The

rather high percentage of flying squirrels (26 %), followed by the glirids (17 %), which are represented by two forest dwellers, and the presence of eomyids (8 %) in the MN 13/a faunal assemblage indicates relatively closed conditions for some areas in the southern Balkans during the early part of the late Turolian. The entrance of gerbils (13 %) in the MN 13/b is linked with the dryer conditions during the Messinian Salinity Crisis. However, the presence of a flying squirrel and an eomyid still indicates the presence of local forested patches, even though they were severely reduced during the last part of the Turolian. The transitional Turolian/Ruscinian (MN 13/14) faunal assemblage is characterised by a mixture of indicators of open-dry environments (gerbils and spalacids) and of closed-wet ones (beavers, flying squirrels and eomyids). As several authors have already mentioned, even though the late Turolian has been traditionally considered to be a dry period across the Mediterranean, forested spots and large water bodies persisted in northern Greece (Van der Meulen and Van Kolfshoten 1986; Schmidt-Kittler et al. 1995; Vassiliadou et al. 2003; Koufos 2006c; Koufos and Konidaris 2011). This is also evident from the nature of the fossiliferous sediments, which in all cases are lacustrine and indicate the presence of lakes (ephemeral or larger ones). Such lacustrine deposits are found in the Turolian/Ruscinian

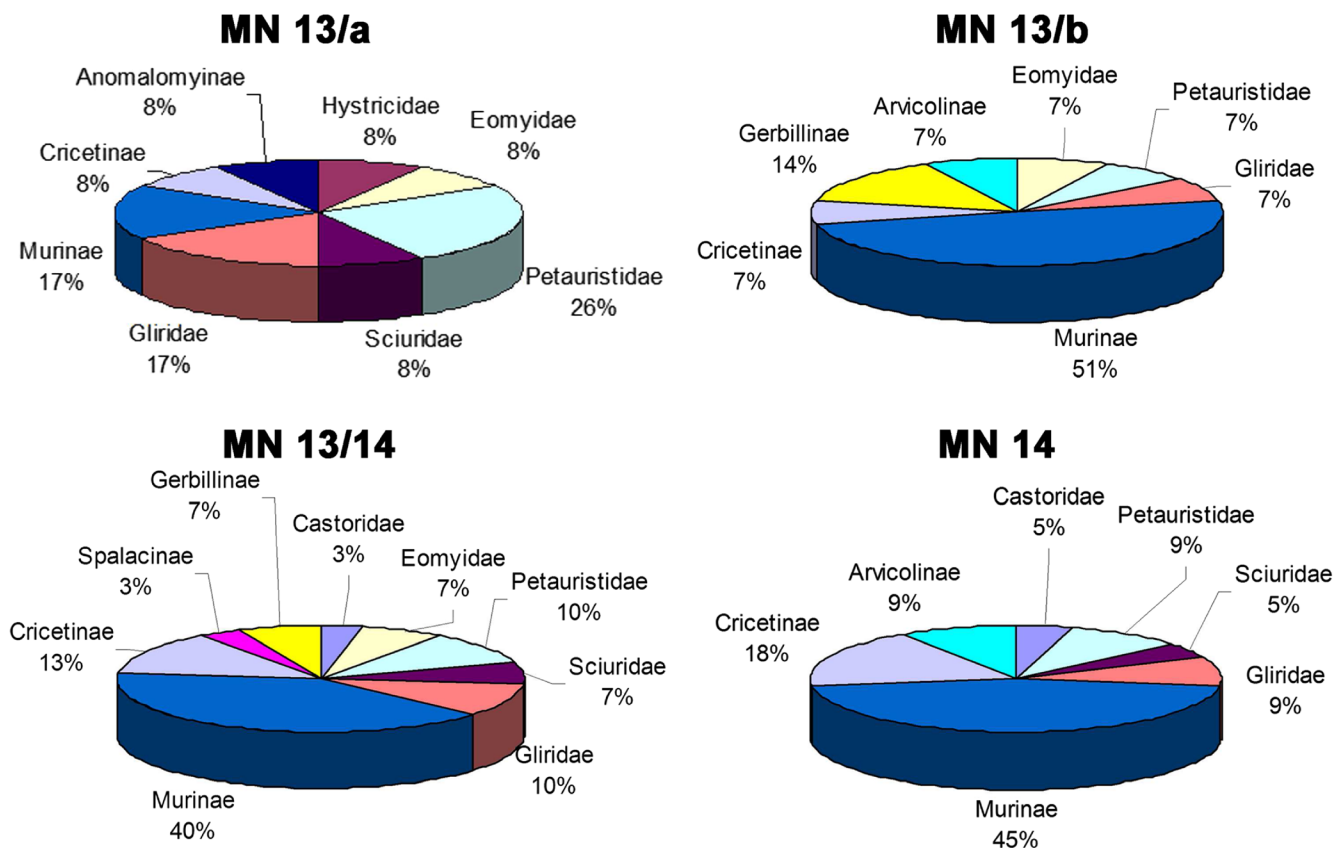


Fig. 7 Faunal composition (% number of species per family or subfamily) of the MN micro-mammalian assemblages

Table 2 Climatic and habitat preferences of fossil rodents (after García-Alix et al. 2008, with changes)

(Sub)family	Species	Climatic preferences				Habitat				Variable		
		unknown	warm	cool	dry	wet	open/ bare	open/ herbaceous	forested	(semi) aquatic	temperature	humidity
Castoridae	<i>Castor fiber</i>					5,9		9	5			
	Castoridae indet.					5,9		9	5			
Hystricidae	<i>Histrix primigenia</i>									5	5	v
Eomyidae	<i>Keramidomys carpathicus</i>					9		9				
	<i>Leptodontomys catalaunicus</i>					9		9				
Petauristidae	<i>Hylopetes macedoniensis</i>					9		9				
	<i>Hylopetes hungaricus</i>		9			9		9				
	<i>Hylopetes</i> sp.		9			9		9				
	<i>Pliopetaurista dehneli</i>		9			9		9				
	<i>Pliopetaurista</i> sp.		9			9		9				
	<i>Miopetaurista thaleri</i>		9			9		9				
	<i>Blackia woelfersheimensis</i>					5		5				
Sciuridae	<i>Tamias atsali</i>					5		5				
	<i>Tamias</i> sp.					5		5				
	<i>Spermophilinus turolensis</i>									9	9	9
	<i>Spermophilinus</i> sp.									9	9	9
	Sciuridae indet.									v	v	v
Gliridae	<i>Myomimus maritsensis</i>					5				5		
	<i>Glis minor</i>					9		9				
	<i>Muscardinus vireti</i>					9		9				
	<i>Muscardinus pliocaenicus</i>					5,9		5,9		1		
	<i>Muscardinus</i> sp.					9		9				
Murinae	<i>Micromys bendai</i>					10,12						
	<i>Micromys cingulatus</i>					10,12						
	<i>Micromys paricioi</i>					2,3,10,12	1			1		
	<i>Micromys steffensi</i>					10,12						
	<i>Occitanomys adroveri</i>		4			4,5	5			5		1
	<i>Occitanomys debruijini</i>					5	5			5		
	<i>Occitanomys neutrum</i>					5	5			5		
	<i>Occitanomys brailloni</i>					5	5			5		
	<i>Occitanomys</i> sp.					5	5			5		
	<i>Castillomys</i> sp.									1	1	1
	<i>Apodemus gorafensis</i>					12				5		5
	<i>Apodemus atavus</i>									1,5	5	5
	<i>Apodemus</i> sp.									5	5	5

Table 2 (continued)

(Sub)family	Species	Climatic preferences				Habitat				Variable		
		unknown	warm	cool	dry	wet	open/ bare	open/ herbaceous	forested (semi) aquatic	temperature	humidity	habitat
	<i>Rhagapodemus primaevus</i>					13						
	<i>Rhagapodemus hautimagnensis</i>					13						
	<i>Arvicanthis broekhuisi</i>		12		12		12					
	Murinae indet. (aff. <i>Arvicanthis</i>)				14		14					
Cricetinae	<i>Kowalskia browni</i>								5		5	5
	<i>Hypsocricetus strimonis</i>					v						
	<i>Allocricetus ehiki</i>								5		5	5
	<i>Mesocricetus primitivus</i>					11		11				
	<i>Mesocricetus</i> sp.					v		v				
	<i>Microtodon komanensis</i>							12				
	<i>Microtodon</i> sp.							12				
Anomalomyinae	<i>Prospalax petteri</i>		15		15							
Spalacinae	<i>Pliospalax macoveii</i>							10				
	<i>Pliospalax</i> sp.							10				
Gerbillinae	<i>Pseudomeriones rhodius</i>					12		12				
	<i>Pseudomeriones megistos</i>					12		12				
	<i>Pseudomeriones</i> sp.					12		12				
Arvicolinae	<i>Promimomys</i> sp.		2,3,6,7,8		2,3,6,7,8		2,3,6,7,8	2,3,6,7,8				
	<i>Promimomys insuliferus</i>		2,3,6,7,8		2,3,6,7,8		2,3,6,7,8	2,3,6,7,8				
	<i>Promimomys cor</i>		2,3,6,7,8		2,3,6,7,8		2,3,6,7,8	2,3,6,7,8				

The species also include assemblages with similarities (cf.) and in the case of *Prospalax petteri*, *P.* aff. *petteri* is also included. The numbers indicate the source of information, as follows: 1 García-Alix et al. (2008); 2 van de Weerd and Daams (1978); 3 Martín Suárez (1988); 4 Martín-Suárez et al. (2001); 5 van Dam and Weltje (1999); 6 Repenning et al. (1990); 7 Fejfar and Repenning (1992); 8 Minwer-Barakat (2005); 9 De Bruijn (1995); 10 van de Weerd (1979); 11 Vassiliadou et al. (2003); 12 Hordijk and De Bruijn (2009); 13 De Bruijn (1989); 14 Vasileiadou et al. (2012); 15 Bolliger (1999); v this paper

localities MAR, SLT and KES, as well as in those of the Servia and Ptolemais Basins, which in most cases include lignites or lignitic clays, indicating the presence of lakes or swamps. The beginning of the Ruscianian, MN 14, is marked by the absence of the gerbils and spalacids and the entrance in the area of the true voles, indicators of wetter but cooler conditions.

Based on the present knowledge on the climatic and habitat preferences of fossil rodent taxa, Table 2 was constructed, with additions and modifications in fig. 3 of García-Alix et al. (2008). The rodents participating in each of the four faunal assemblages are assigned to a category based on their humidity degree preference (dry, wet or variable) and the habitat preference (forested, open, variable or unknown)

(Table 2). Only these two proxies were chosen, as information on others is very limited (e.g. temperature preferences). The numbers of rodent species in each category were counted and the results were plotted in form of bar graphs (Fig. 8). The humidity change graph shows the change from wet to drier conditions during the Messinian Salinity Crisis and the reset of wetter conditions towards the Turolian/Ruscianian boundary, with the humidity increasing further during the Ruscianian. The habitat change graph illustrates the constant presence of relatively closed conditions in the focus area, their important reduction during the Messinian Salinity Crisis and their partial return during the Turolian/Ruscianian boundary and the entire Ruscianian. It is noteworthy that the forested and open as well

as the wet and dry elements are equally represented in the faunal composition (Figs. 7, 8), suggesting a mixed environment with both closed and open landscapes.

Evidence from macromammals

The DYTI macromammalian fauna is one of the best known late Turolian (MN 13) assemblages in the eastern Mediterranean area and its analysis provided a first indication for an environmental change at the late Turolian. Comparison with modern faunas from known environments indicates that the DYTI fauna has, in contrast to the other fossil faunas, its closest similarity with modern forest faunas (de Bonis et al. 1992; Koufos 2006c). Based on dental microwear study, the DYTI bovids are considered to have been either variable grazers or mixed feeders, a result that supports the alternation of wooded and bushy areas with some less widespread grassy ones (Merceron et al. 2005), or, in other words, a mixed environment, more closed than the early-middle Turolian open-dry one. The presence of the tragulids and cervids in the DYTI fauna strengthens the hypothesis for wetter and more closed character of the late Turolian environment.

The macromammalian faunas of the studied area are divided in three faunal assemblages: the first faunal assemblage includes the late Turolian (MN 13) faunas, the second one the Turolian/

Ruscinian (MN 13/14) ones and the third assemblage the Ruscinian faunas (MN 14). The faunal assemblage of the middle Turolian (MN 12) for the focus area is also included in the analysis for comparison, as it is considered to represent the most open-dry conditions. Given the few macromammalian faunas of the uppermost late Turolian, it was not possible to make a distinction between pre- and post- Messinian Salinity Crisis, as we did for the micromammals.

The number of species and the percentage of species per family for the four faunal assemblages (Fig. 9) provide some information for the environment. Note that the early Ruscinian record is poor, as there is only one locality of that age in the studied area. The bovids and giraffids, two important indicators of open environment, constitute a great part ($\geq 25\%$) of the MN 12, MN 13 and MN 13/14 assemblages, indicating relatively open conditions (Fig. 9b). However, their number decreases towards the transitional Turolian/Ruscinian assemblages (Fig. 9a) suggesting a decrease of the open character of the landscape. The percentage of the cervids, although they are represented only by one or two species (the taxonomy of the late Miocene cervids is debated), increases towards the Turolian/Ruscinian boundary, indicating a gradual increase of the closed character for the environment (Fig. 9a, b). Also, the suid percentage increases remarkably (Fig. 9b), supporting the increase of the closed character of the landscape. The equids vary both in the number and percentage of species (Fig. 9), but, more importantly, their morphology changed. The typical running forms (elongated and slender metapodials) of the late Turolian were gradually replaced by forms with short and robust metapodials (Sondaar and Eisenmann 1995 mention a hipparion with short and robust metapodials similar to *H. crassum* in the MN 13/14 MAR fauna) which suggests more closed conditions. Moreover, the increase of the enamel plication in their cheek teeth also suggests softer food and thus higher humidity and relatively closed conditions. The presence of the tapirids in the MN 12 and MN 13 faunas of Bulgaria is noteworthy (Fig. 9). Tapirids are unknown from the late Miocene of Greece; their presence in Bulgaria indicates that the local conditions were wetter, offering a suitable habitat for these animals. This is possibly due to the more northern geographic position or to the topography of the area. Analysis of the terrestrial late Miocene floras of eastern Mediterranean indicated that the mean annual precipitation was 700–800 mm in southern Greece and gradually increased to 1000–1100 mm in the north (Bruch et al. 2006).

The taxonomic composition of the latest Miocene/Ruscinian MN mammal assemblages is compared with modern and fossil faunas from known closed and open environments, using a Correspondence Factor Analysis (Fig. 10). In this analysis, the herbivores of each MN zone are clustered in 11 groups (families or classes) that might correspond to a

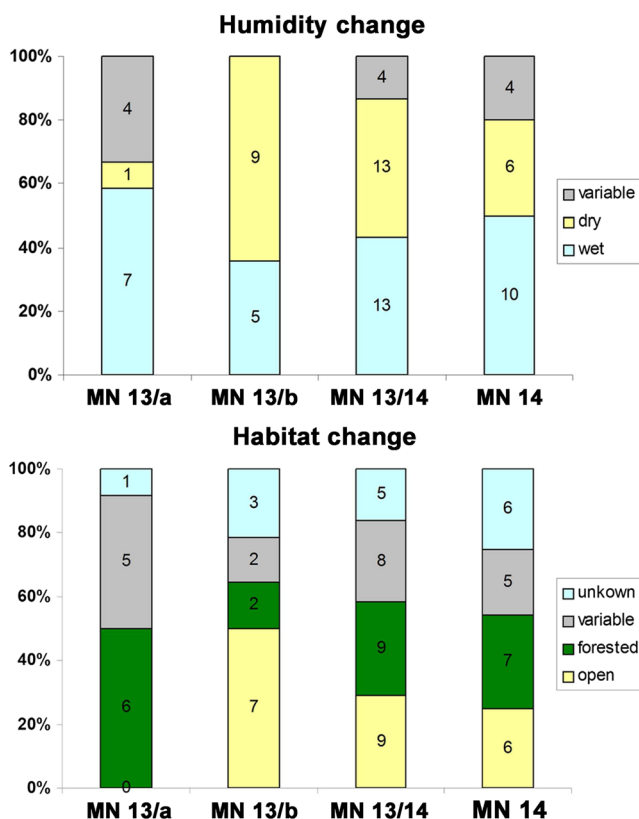


Fig. 8 Humidity (upper) and habitat (lower) change of the MN micromammalian faunal assemblages

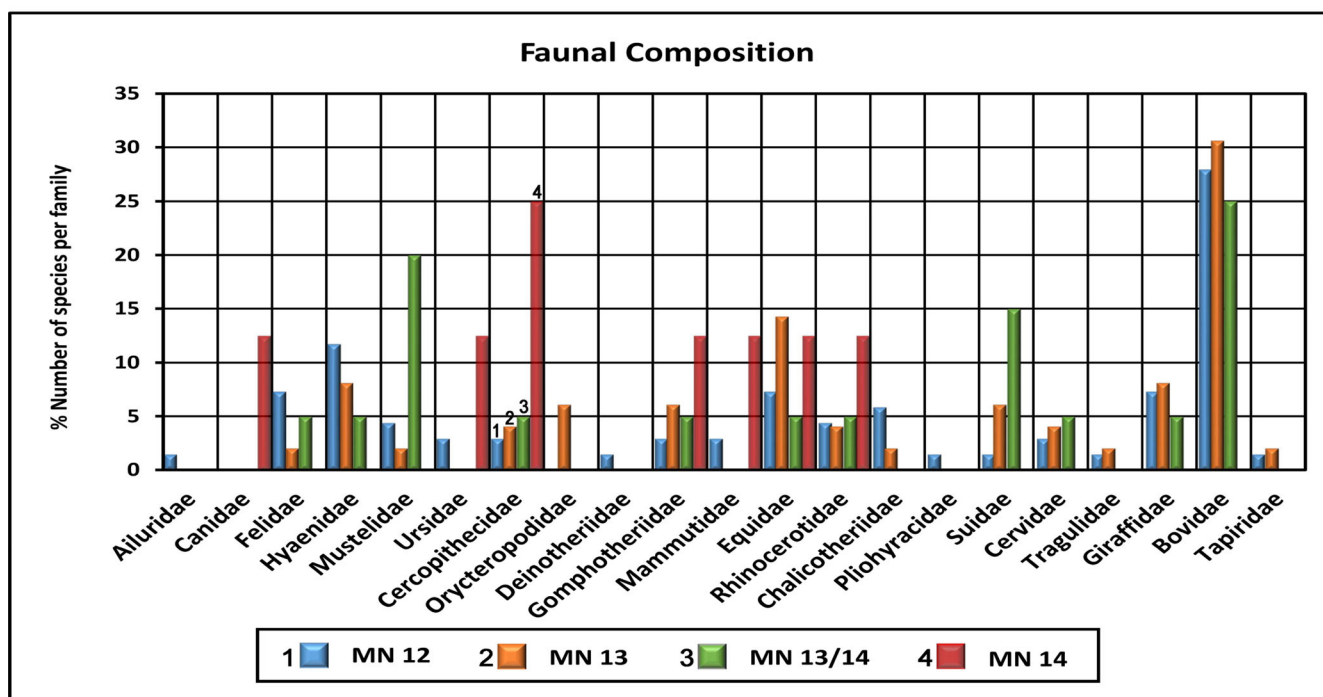
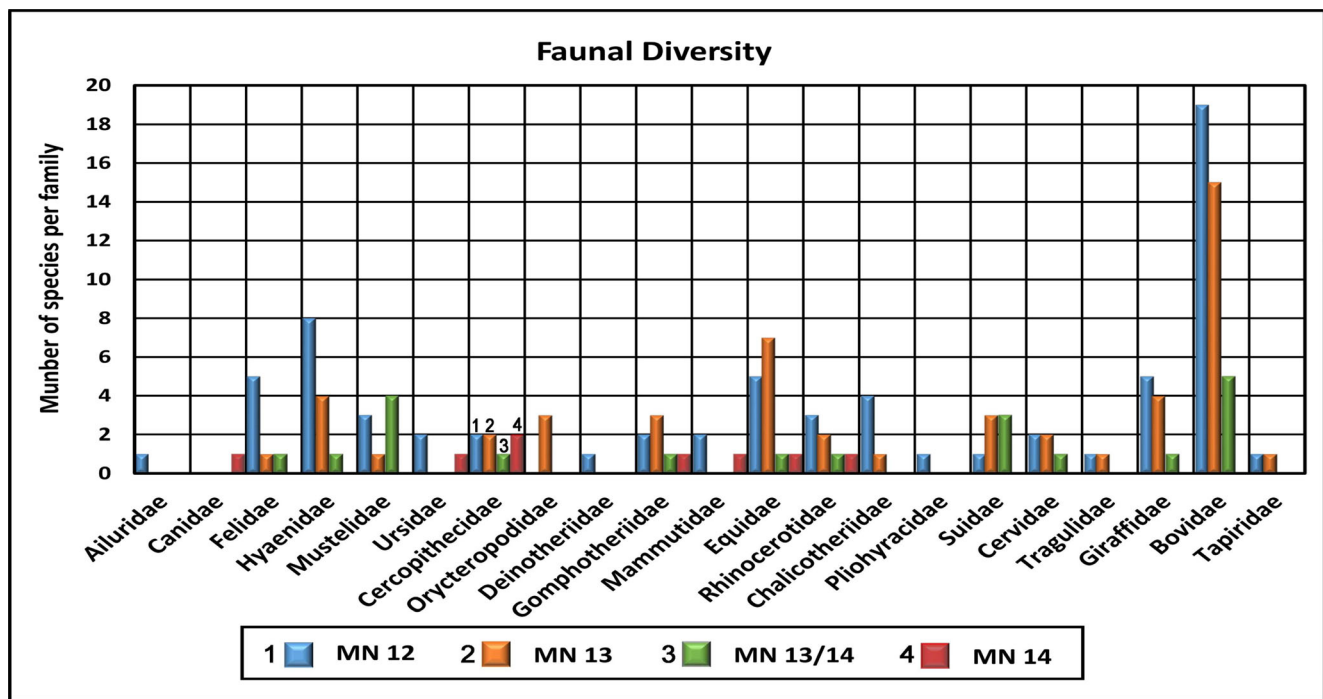


Fig. 9 Faunal diversity (a) and composition (b) of the MN macro-mammalian faunal assemblages

different ecological profile. The fossil faunas are separated geographically to those of western and central Europe (WCE) and to those of eastern Mediterranean (EM). They are also distinguished chronologically into middle and late

Miocene ones. In western and central Europe, the conditions were relatively closed during the middle Miocene-Vallesian (Agusti and Anton 2002), while in eastern Mediterranean conditions were more open, especially in late Miocene (Koufos

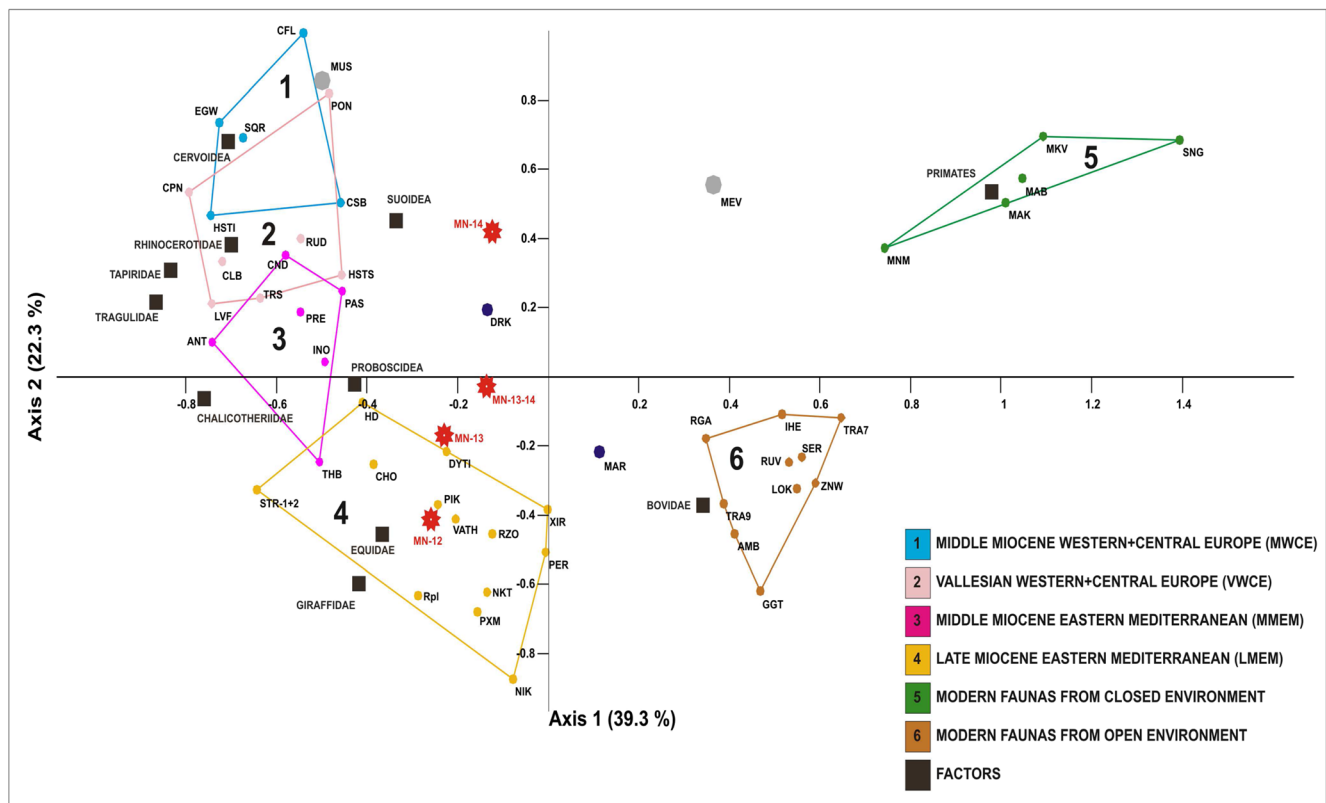


Fig. 10 Correspondence factor analysis of the MN total faunal assemblages of the studied area in comparison with modern and fossil faunas from known environments. Modern assemblages, Closed: 5 MAB La Maboque, MAK Makokou, MKV Mont Kivu, MNM Mont Nimba, SNG Sangmelina; Open: 6 AMB Amboseli, GGT Golden Gate, IHE Ihema, LOK Lokori, RGA Region Gabiro, RUV Rukwa Valley, SER Serengeti, TRA Transvaal, ZNW Zinawe. Fossil assemblages: 1 M. Miocene C+W Europe: CFL Can Feliu, CSB Castell de Barbera, EGW Engelswies, SQR Saint Quirze; 2 Vallesian C+W Europe: CLB Can Llobateres I, HSTI Hostalets inferior, HSTS Hostalets superior, LVF Los Valles de Fuentidueña, PON Can Ponsic, CPN Can Ponsic I, RUD Rudabanya,

TRS Terassa; 3 M. Miocene E. Mediterranean: ANT Antonios, CND Candir, INO Inonu, PAS Paşalar, PRE Prebreza, THB Thymiana-B; 4 L. Miocene, E. Mediterranean: CHO Chomateres, DYTI Dytiko-1,2,3, HD Hadjidimovo, MAR Maramena, NKT Nikiti-1, NIK Nikiti-2, PER Perivolaki, PIK Pikermi, PXM Prochoma-1, RPI Ravin de la Pluie, STR I+2 Strumiani 1+2, VATH Vathylakkos-1,2,3, XIR Xirochori-1. The data for the modern localities are taken from Legendre (1989), for the fossil faunas of Western and Central Europe mainly from NOW (2014), and those from Greek localities from Koufos (2006b) with some personal modifications and for Strumiani 1+2 from Geraads et al. (2011); Dr N. Spassov offered the data for Hadjidimovo

2006c; Atabadi 2010). Hence, four faunas have been recognised: western and central European faunas of the middle Miocene and Vallesian (MWCE and VWCE, respectively) and the middle and late Miocene ones of eastern Mediterranean (MMEM and LMEM). The MWCE, VWCE and MMEM faunas are considered as closed while the LMEM one as open.

In Fig. 10, the modern mammal faunas are split into two groups by axis-2, which separates the closed (upper part) from the open (lower part) faunas, whereas axis-1 separates the modern from the fossil faunas. The fossil faunas from known palaeoenvironments are also well separated, like the modern ones. The closed faunas of MWCE and VWCE are situated above axis-2, correlated well with the modern closed faunas. The MMEM faunas, although closer to the closed ones, have an intermediate position between the closed and open modern faunas, in line with the idea that the open landscapes started to

develop in eastern Mediterranean area from the end of middle Miocene (Koufos 2006c). The LMEM faunas are clearly correlated with the modern open ones situated below axis-2 (Fig. 10). The CFA indicates that there is a clear separation between the closed and the open assemblages, for both modern and fossil faunas. The MN 12 assemblage of the southern Balkans is clearly situated in the area (convex hull) of LMEM indicating relatively open landscape. The MN 13 assemblage is located in the borders of the LMEM area and above MN 12, indicating a trend to less open conditions (Fig. 10). This is clearer for the MN 13/14 assemblage, which is situated near axis 1 and, like the MMEM assemblages, has a transitional character from open to closed environment. Finally, the MN 14 assemblage has positive values on axis-2, correlated clearly with the closed modern and fossil assemblages. This trend is continued until the end of the Ruscian as the two well-known MN 15 mammal faunas of the studied area, Megalon

Emvolon (MEV) and Musselievo (MUS), are clearly correlated with the modern and fossil closed faunas (Fig. 10). This analysis indicates a trend to more closed conditions from MN 12 to MN 14. The transitional faunas (MN 13/14) are characterised by a mixed large mammal content, suggesting a mixed environment, i.e. an open forest or savannah-forest or savannah-bushland.

Conclusions

The late Miocene–early Pliocene mammal localities of the southern Balkans, although not numerous and in some cases with poor faunas, provide interesting data for chronology and palaeoecology. The well-dated deposits and faunas of the Serbia and Ptolemais Basins in western Macedonia allowed a correlation with the other faunas and the estimation for the latter of absolute ages. A number of localities yielded a mixed fauna with Turolian and Ruscinian elements and they are correlated close to the Miocene/Pliocene boundary. Their age coincides with the age of the corresponding faunas of the Ptolemais Basin and the age of the Turolian/Ruscinian boundary is estimated at 5.40–5.23 Ma (fig. 6). The DYTI faunas are considered as pre-Messinian Salinity Crisis, with an age ranging from 7.1 to 6.81 Ma (depending on the age of the MN12/13 boundary) to 5.96 Ma (beginning of the Messinian Salinity Crisis according to Krijgsman et al. 1999). The faunas PLM A, PLM B, ASP and MNS were accumulated during the Messinian Salinity Crisis, with an age from 5.96 Ma to the end of Miocene (5.33 Ma). The localities SPL 0, 1 and DRK are correlated with the early Ruscinian, with an age ranging from 5.33 to 4.95 Ma (the age of the MN 14/15 boundary estimated in the Ptolemais Basin; Fig. 6). The faunal composition of the small and large mammals indicates relatively open conditions in the late Turolian but more closed than the early-middle Turolian ones. The transitional Turolian/Ruscinian faunas indicate a mixed environment with open-dry to closed-wet elements. The humidity and habitat change of the rodents, as well as the comparison of the studied faunas with modern and fossil ones from known environments, confirm these results. In conclusion, during the Mio/Pliocene boundary, the environment was transitional from an open landscape to a forested one. This change seems to have started at the beginning of late Turolian and gradually increased towards the Ruscinian (Fig. 10). During the Turolian/Ruscinian boundary, the conditions were mixed, as the known faunas include both open and forest elements. In a relatively open landscape, there were forest spots mainly near the water (lakes, springs, seasonal lakes, swamps) where the animal remains accumulated. The wetter conditions in the Ruscinian are also confirmed by the extensive deposits of lignites in the area during that time.

Acknowledgements This article is dedicated to our dear friend and colleague Albert van der Meulen, as a memory of the good times we shared with him and as recognition of his contribution to the palaeontological knowledge of the Balkans. Albert, we shall always feel moved for your great passion for the Greek music, especially for “rebetika”. The authors want to express their gratitude to the guest editors of this issue, Lars van den Hoek Ostende, Pablo Peláez-Campomanes and Wilma Wessels, for inviting them to participate in it and for their useful remarks on the manuscript. The constructive comments of the reviewers Sevket Sen and Jordi Agustí Ballester are very much appreciated. (K.V.) Albert, I want to take this opportunity to thank you very much for your great hospitality in your office and for sharing with me your knowledge on voles and micromammalian palaeontology during my first visit to Utrecht as an Erasmus student back in 1997 and every time I visited since then.

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