

Neogene/Quaternary mammalian migrations in Eastern Mediterranean

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ABSTRACT. Palaeogeographic and climatic changes in the Eastern Mediterranean during the Neogene/Quaternary led to extended mammalian migrations and faunal exchanges between Eurasia and Africa. At the same time, the Beringian landbridge was activated several times, and American faunal elements entered Eurasia. It appears that the main factor affecting migration potential and faunal changes/exchanges during the Neogene was palaeogeography, while after the early Pliocene migrations were mainly controlled by climatic changes. Several mammalian migrations can be distinguished, but the most important was that of the middle Orlanian at about 17.0-18.0 Ma when Africa and Eurasia were connected after a long separation and a great number of African faunal elements entered Eurasia and vice versa. Some more important faunal changes also occurred : 1. at ~5.5 Ma, marking the beginning of the Pliocene, 2. at ~2.0-1.8 Ma, marking the beginning of the Pleistocene, and 3. at ~1.0 Ma, defining the early/middle Pleistocene boundary and the establishment of modern mammal fauna. During the Pleistocene, oscillation of glacial and inter-glacial periods caused an alternation of cold-steppic faunas with temperate ones in the Eastern Mediterranean. Endemic late Pleistocene mammalian faunas developed in the Mediterranean islands after their isolation ; "dwarf" elephants, cervids and hippos occurred, as well as giant rodents.

KEY WORDS : Eastern Mediterranean, Neogene/Quaternary, Mammalia, migration, faunal changes, paleobiogeography.

INTRODUCTION

The Eastern Mediterranean is regarded as an important domain for mammal exchanges between Asia, Europe and Africa during the Neogene/Quaternary. The enlarged area of the Eastern Mediterranean includes the Balkan Peninsula, the Aegean Sea, Asia Minor and the Middle East. In this geographic region migration pathways between the three continents crossed. The number of localities for mammal fossils found in the Eastern Mediterranean is quite significant, providing a good base for further comparisons and discussion. The geological age of the faunas and the palaeogeography of the area are already well known from previous and essential works. However, the scarcity of the fossil record and the limited dating of several sites is a great disadvantage to reconstruct the palaeobiogeography.

The main Neogene/Quaternary mammalian migration waves between Eurasia and Africa are associated with important mammal turnovers, climatic and tectonic changes and in some cases also include mammalian forms arrived from America via the Beringian landbridge. The present article combines available data from the mentioned region and neighbouring ones, in order to extract the main migrations, the time spans during which they occurred and the palaeogeographic conditions under which they took place. Our work also focuses on the arrival of some important taxa into Greece and their significance in establishing the evolution of Greek faunas.

MIGRATION FACTORS

The migration of a mammal depends upon various factors. The most important are topographic/physiogeographic and climatic parameters. Geographic barriers, such as high mountain chains and/or sea channels are restrictive for the migration of mammals. Knowledge of the palaeogeography (global or regional) during the various geological periods is essential to extrapolation of migration waves and faunal turnovers. Climatic conditions and the palaeoenvironment of the origin and arrival areas also control migration potential. Animals adapted to warm climatic conditions cannot occupy cool areas and vice versa.

The size of an animal and the migration distance are positively related. A large-sized animal can cover a long migration distance during its life-span, while a micro-mammal (e.g. a rodent) usually needs more generations in order to cover the same distance or to pass a significant topographical barrier. In this case evolution and migration can be simultaneous.

The study of past migrations presupposes a good knowledge of taxonomy and age of the fossils. The taxonomic determination of the mammalian fossils is an important factor for establishing mammal migration and distribution. Differences in the definition of a "biological" and "palaeontological" taxon make the taxonomic determination of fossils more delicate. Geologic timing is another important factor. The age of mammalian faunas is determined either biochronologically (based on the faunal composition and its evolutionary stage) or radiometrically if possible. Magnetostratigraphy also provides good age

resolution, but the method has not been extensively used in continental mammal-bearing deposits. During the last 30 years new methods were developed allowing quite precise age determination for the fossil mammalian faunas providing a good base for comparisons.

GEOTECTONIC BACKGROUND

It is generally accepted that during the entire Neogene/Quaternary there was a continuous connection between Europe and Asia, in the north Caspian region. The South European area and especially its eastern part was definitely formed during this period, by alpine orogenesis, extending the terrestrial communication between Asia and Europe. The following Quaternary tectonism and eustatic movements did not change dramatically the geography of the area, but were mainly of local significance. Neogene was also a time of important geotectonic events that allowed successive connections between Eurasia and Africa, creating great opportunities for faunal exchanges between these continents. The most important Neogene/Quaternary palaeogeographic changes are schematically given in the palaeomaps of STEININGER & RÖGL (1985) and RÖGL (1999), used as background for our work. Geological time is mainly expressed by the system of Mammal Biozones of MEIN (1990, 1999), which permits definition and recognition of small time-units and correlation between neighboring areas (Fig. 1).

AGENIAN-EARLY ORLEANIAN MIGRATION (23.8-18.0 MA)

During the Oligocene/Miocene boundary a deep trough between Arabian and Iranian plates, known as Tethyan Seaway (Fig. 2A), allowed communication of the Mediterranean with the Atlantic and the Indo-Pacific Oceans. The closure of the Tethyan Seaway was gradual, starting at ~19.0 Ma, and continuing until the end of MN 3 at ~18.0 Ma (RÖGL, 1999). At the same time, Asia communicated with America through the Beringian landbridge and an important immigrant, the equid *Anchitherium*, invaded Asia. It rapidly dispersed to Europe as it is known from MN 3 of the Iberian Peninsula (MEIN, 1990). *Anchitherium* is unknown in the Balkan Peninsula, while it appeared in MN 6 of Asia Minor (FORSTEN, 1990 ; NOW 2002). Its absence from the Balkans could suggest that the area was not connected with Asia Minor, or more likely, that it has not yet been found there. Some inner-Eurasian faunal exchanges have also been recognized. In W. Europe the suids *Hyotherium* appeared in MN 1 and *Xenohyus* in MN 2 (MADE, 1990), and the anthracothere *Brachyodus* in MN 3 (MEIN, 1990). The MN 1-3 faunas are very rare in the Eastern Mediterranean. However, the presence of *Brachyodus* is recorded in the locality of Kalimeriani, Greece (MELENTIS, 1966). The sole specimen of *Brachyodus* cannot give a precise age for the locality, but an MN 3-4 age was suggested (BONIS & KOUFOS, 1999). The first spalacid *Debruijnina* is known from MN 3 of Asia Minor, while it was also found in Aliveri, Greece, dated at the base of MN 4 (DE BRUIJN *et al.*, 1992). These data suggest an early connection of Asia Minor with the Balkan Peninsula at the end of MN 3.

During that time the Northern Aegean was a continental domain with low relief (DERMITZAKIS & PAPANIKOLAOU, 1981).

TIME (Ma)	CHRONOS	POLARITY	EUROPEAN LAND MAMMAL		EPOCH		AGES			
			STAGES	MN-ZONES	PLEISTOCENE	PLIOCENE	MIOCENE	MED. CENT. PARA	EAST PARA	
1	C1		VILFRANCHIAN	MNQ 1	EARLY LATE					
2	C2			MN 17	LATE					
3	C2An			MN 16						
4	C3An		RUSCINIAN	MN 15	EARLY					
5	C3n			MN 14						
6	C3r		TUROLIAN (3.8Ma)	MN 13 (1.7Ma)	LATE					
7	C3Ar			MN 12 (1.4Ma)						
8	C3n			MN 11 (0.7Ma)						
9	C4An		VALLESIAN (2.4Ma)	MN 10 (1.0Ma)	LATE					
10	C4Ar			MN 9 (1.4Ma)						
11	C5n		ASTARACIAN (3.9Ma)	MN 7+8 (2.4Ma)	MIDDLE					
12	C5r									
13	C5An									
14	C5Ar									
15	C5ADn									
16	C5ADr									
17	C5Br		ORLEANIAN (5.5Ma)	MN 5 (2.0Ma)	EARLY					
18	C5Cn			MN 4 (1.0Ma)						
19	C5Cr			MN 3 (2.5Ma)						
20	C5Dn									
21	C6An		AGENIAN (5.5Ma)	MN 2 (2.0Ma)	EARLY					
22	C6Ar			MN 1 (1.3Ma)						
23	C6AAn									
24	C6Aa									
	C6Bn									
	C6Br									
	C6Cn									
	C6Cr									
				MP 30						

Fig. 1. – Chronological table for Neogene/Quaternary with the European land mammal stages and MN-Zones. According to MEIN (1990), STEININGER *et al.* (1990) and STEININGER (1999).

MIDDLE ORLEANIAN MIGRATION (18.0-17.0 MA)

The Arabian and Anatolian plates collided at the end of MN 3 (middle Orleanian) re-establishing communication between Africa and Eurasia (Fig. 2B). The landbridge connecting the two continents is known as “*Gomphoth-*

erium-landbridge" (RÖGL, 1999 ; AGUSTI *et al.*, 2001). The closure of the Tethyan Seaway probably provided an earlier connection with Asia as *Pliohyrax*, originating from Africa, was found in India at the end of MN 3 (PICKFORD, 1986). Its presence in the Eastern Mediterranean is reported later in the locality of Pasalar, Turkey, dated to MN 6 (NOW, 2002). This earlier connection is also confirmed by the recent trace of a primitive deinothere *Prodeinotherium* in Lesvos island, Greece. Its dental morphology and the absolute age of the sediments including it, suggest an age of >18.4 Ma (KOUFOS *et al.*, 2003). This means that before the final closure of the Tethyan Seaway, there were some early short or temporary landbridges connecting Africa and Eurasia (before 18.0 Ma), allowing the entrance of some mammals. The Indopacific Seaway to the Eastern Paratethys was closed too. The western part of Paratethys was also closed and thus it became an isolated basin with endemic fauna and reduced salinity (RÖGL, 1999). The Balkan Peninsula was completely connected with Asia Minor (Fig. 2C) except for some lakes or lagoons in the northern Aegean area (DERMITZAKIS & PAPANIKOLAOU, 1981).

A great number of African taxa migrated to Eurasia through the "Gomphotherium-landbridge", while a simultaneous migration is also traced from Eurasia to Africa. The fauna of Negev in Israel, dated to MN 3, corresponds to the first exchange between them as it includes a mixed fauna with African (*Prodeinotherium*, *Gomphotherium*, *Anasipora*, *Dorcatherium*, *Kenyalagomys*, *Megapedetes*) and Asian (*Eotragus*, *Listriodon*, Rhinocerotidae) elements (TCHERNOV *et al.*, 1987 ; AGUSTI *et al.* 2001 ; PICKFORD 2001). Recent radiometric data suggest an age of ~20.7 Ma for this event (RÖGL, 1999). The first African immigrants were the proboscideans ; the gomphotheres and the deinotheres, arriving in India (Bugti Fauna) at ~18.3 Ma (BARRY *et al.*, 1985 ; TASSY, 1990) and in Eastern Mediterranean at ~18.4 Ma (KOUFOS *et al.*, in press). The proboscideans rapidly dispersed in W. Europe as they were found in the Iberian Peninsula at the beginning of MN 4, ~ 18.0 Ma (TASSY, 1990).

Several Asian taxa, such as the bovid *Eotragus*, the suid *Bunolistriodon*, the nimravid *Prosansanosmilus* and the rodents *Megacricetodon*, *Democricetodon*, *Cricetodon*, *Eumyarion* e.t.c. migrated also to Europe and/or to Africa (AGUSTI *et al.*, 2001 and literature listed). The subfamily Democricetodontinae appeared in Asia Minor during the early Miocene (MN 1-2) and then migrated to Africa and Asia (MN 3), as well as to America through the Beringian landbridge (MN 3-4). During MN 4 the subfamily appeared in the Balkans and Western Europe (THEOCHAROPOULOS, 1999).

Many Asian and African immigrants arrived in Greece too. The genera *Megacricetodon*, *Democricetodon* and *Karydomys* are recognized in Aliveri (early MN 4), Karydia and near Komotini (upper MN 4) (THEOCHAROPOULOS, 1999). The first carnivores (*Palaegale*, *Euboictis*) appeared in Aliveri, Evia dated at the base of MN 4 (DE BRUIJN *et al.*, 1992). The genus *Euboictis* has possibly a southern Asian origin and the connection of Asia Minor

with Europe allowed its migration to the Balkans and Central Europe during MN 4 (SCHMIDT-KITTLER, 1999).

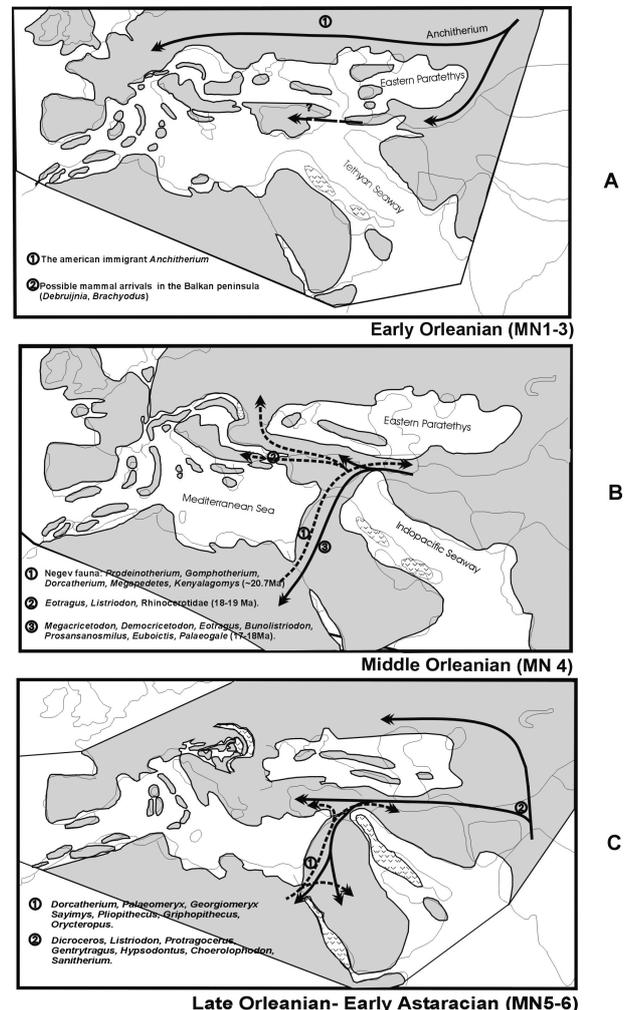


Fig. 2. – Palaeogeographic map of Mediterranean region with the main mammalian migration pathways and arrivals in Eastern Mediterranean.

- a) Agenian-early Orleanian (MN 1-3)
 b) Middle Orleanian (MN 4)
 c) Late Orleanian- Early Astaracian (MN 5-6)
 Palaeogeographic maps from RÖGL (1999).

LATE ORLEANIAN-ASTARACIAN MIGRATIONS (17.0-10.7 MA)

A succession of short-term sea level oscillations during this time interval caused several changes to the palaeogeography of the Eastern Mediterranean. There is evidence of a late Orleanian transgression, re-opening the Tethyan Seaway (RÖGL, 1999). Thus, the landbridge between Africa and Eurasia was active for short periods allowing faunal migrations between the two continents (Figs 2C, 3A). However, such short-term connections between the continents are not confirmed by mammal evidence. In any case three migration waves can be recognized at this time :

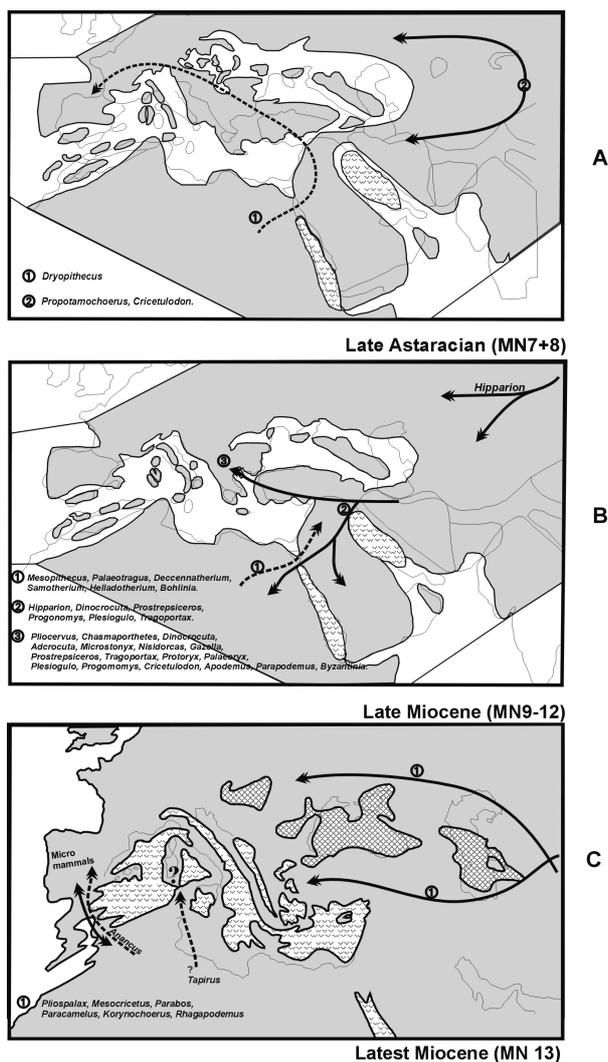


Fig. 3. – Palaeogeographic map of Mediterranean region with the main mammalian migration pathways and arrivals in Eastern Mediterranean.

- a) Late Astaracian (MN 7+8)
- b) Late Miocene (MN 9-12)
- c) Latest Miocene (MN 13)

Palaeogeographic maps from RÖGL (1999) and STEINIGER & RÖGL (1985).

a. During the late Orleanian, MN 5 (17.0-15.0 Ma) a migration wave from Africa arrived in the Eastern Mediterranean. The Greek fauna of Antonios, Chalkidiki dated to MN 4/5 at ~17.0 Ma (KOUFOS & SYRIDES, 1997) fits quite well with it. The Antonios fauna includes a small-sized *Dorcatherium* very close to the small-sized African form described by PICKFORD (2001). The giraffid *Palaeomeryx* is another African element present in Antonios fauna. The sanitheres known from MN 3 of Africa migrated to Asia (PICKFORD, 1984) at the end of MN 3. In the Eastern Mediterranean they appeared firstly in Antonios fauna. These data indicate a short-term mammal invasion, may be before the re-opening of the Tethyan Seaway. The locality of Thymiana, Chios Island, Greece includes strong evidences of a migration from Africa during this time span. The locality is dated to MN 5 or to 15.5 Ma according to magnetostratigraphic data (KONDOPOULOU *et al.*, 1993 ; DE BONIS *et al.*, 1998). The giraf-

fid *Georgiomeryx*, the tragulid *Dorcatherium*, and the ctenodactylid *Sayimys* indicate African origin confirming the above-mentioned connection. The proboscidean *Choerolophodon*, appeared firstly in Chios island coming probably from Asia since it was already present in the Bugti fauna, India, dated to MN 3, or ~18.3 Ma (TASSY, 1990). However, the most important arrival was that of the primates, originating from Africa and invading Eurasia during MN 5. The first primates with the genus *Pliopithecus* are known from the localities of Elgg (Switzerland) and Pontlevoy-Thenay (France) dated to MN 5, and they existed until the end of Vallesian (ANDREWS *et al.*, 1996).

b. A second migration wave from Africa during early Astaracian, MN 6 (15.0-13.5 Ma) brought several immigrants into Eurasia and the Eastern Mediterranean (Fig. 2C). The most important new element was the hominoid *Griphopithecus* of African affinities. It was recognized in the Turkish localities of Pasalar and Candir, as well as in Neudorf-Sandberg, Slovakia, all dated to MN 6. The Eur-Asian *Griphopithecus* is related to the African *Kenyapithecus* known from Maboko, East Africa dated to MN 4 (ANDREWS *et al.*, 1996). The arrival of the aardwark *Orycteropus* in the Eastern Mediterranean is also referred to this wave. The genus has African origin and its oldest remains out of Africa are those from Pasalar, Turkey dated to MN 6 (FORTELIUS, 1990). During MN 6 some asian elements also entered into Europe, such as the hyracoid *Pliohyrax*, the cervid *Dicruceros* and the suid *Listriodon* (THENIUS, 1952 ; MADE, 1990). The hyracoids originated from Africa and entered into the indian subcontinent at the end of MN 3. *Pliohyrax* dispersed eastwards in MN 6, appeared in the Eastern Mediterranean locality of Pasalar Turkey, dated to MN 6 (FORTELIUS, 1990). Several asian bovids (*Protragocerus*, *Tethytragus* and *Hypsodontus*) known from MN 5 of Asia Minor and Chios island migrated to Africa.

c. A third migration wave from Africa seems to have taken place, mainly in MN 8, but the poorly known late Astaracian, MN 7+8 (13.5-10.7 Ma), faunas of the Eastern Mediterranean do not allow detailed conclusions. The most important appearance was that of the hominoid *Dryopithecus* in Europe at about 12.5 Ma ago (Fig. 3A). The Asian suid *Propotamochoerus* entered Europe at that time (MADE, 1999). The genus *Cricetulodon* arrived in the area at the end of MN 7+8 and it is known from Turkey and Greece (KOUFOS, 2003). The genus is known from MN 3 of W-C Europe where it persisted until MN 7+8 (AGUSTI *et al.* 2001 ; NOW, 2002). According to RÖGL (1999) during the late Astaracian there was a seaway between Paratethys and Mediterranean, prohibiting the migrations. These data suggest that at the end of MN 7+8 the connection between Europe and Asia was fully established.

LATE MIOCENE MIGRATION (10.7-6.7 MA)

The arrival of *Hipparion* in Eurasia from America, known as *Hipparion*-datum is a major event used extensively in biostratigraphy and biochronology as a marker of the beginning of the late Miocene (MN 9). A strong sea level drop around 11.0 Ma re-opened the Beringian land-

bridge (HAQ *et al.*, 1988) and some North-American mammals entered Eurasia. However, there are different opinions about the age of *Hipparion*-datum in Europe. The available faunal and magnetostratigraphic data from Spain suggest an age of 11.1 Ma (GARCES *et al.*, 1997). In the Eastern Mediterranean recent magnetostratigraphic data from Turkey suggest an age of 10.7 Ma (KAPPELMAN *et al.*, 2003). Similar dating is also proposed for the *Hipparion*-datum in Pakistan 10.7 Ma (PILBEAM *et al.*, 1996). Thus, the beginning of late Miocene (arrival of *Hipparion*) must be considered at 10.7 in the Eastern Mediterranean, at the moment. The hipparionine horses immediately entered Africa and dispersed rapidly to the whole continent, remaining until the beginning of the Pleistocene.

During the late Miocene there was a short landbridge between Africa and Eurasia (Fig. 3B), while the Red-Sea was more or less formed (RÖGL, 1999). This landbridge allowed faunal exchanges with the most important arrival being that of the cercopithecoid *Mesopithecus*. The genus is very well known in Greece (Pikerni, Axios valley, Marmara), but it is also known in Bulgaria, Former Yugoslavian Republic of Macedonia (FYROM), Afghanistan, and Iran. Its first appearance in the Eastern Mediterranean was recorded in Axios valley, Greece at ~8.2 Ma (KOUFOS, in press.). The giraffids are well represented by several genera, such as *Palaeotragus*, *Bohlinia*, *Samotherium*, *Helladotherium* (Fig. 3B). The different climatic and environmental conditions between South-Eastern and Central-Western Europe did not allow to these large-sized mammals to pass into the occidental part. Only the small-sized *Palaeotragus* migrated to W.-C. Europe.

However, the most important arrivals during the late Miocene were those from Asia. The invasion of *Hipparion* into Eastern Mediterranean was accompanied by the arrival of several Asian mammal immigrants such as the large hyaena *Dinocrocuta*, the icitheres and the extensively known hyaena *Adcrocuta*. The suid *Microstonyx* appeared in the Eastern Mediterranean at the end of MN 10 or more precisely at ~9.0 Ma (KOSTOPOULOS, 1994; KOUFOS, 2000). The carnivores *Plesiogulo* and *Chasmaporthetes* entered Eastern Mediterranean from Asia and were found in the Greek localities of Vathylakkos and Ravin des Zouaves-5, dated at ~7.5 Ma and 8.2 Ma respectively (SEN *et al.*, 2000). The Asian bovid association, arriving at the same time, included many genera, such as *Tragoportax*, *Gazella*, *Prostrepsiceros*, *Nisidorcus*, *Protoryx*, *Palaeoryx*, but most of them did not pass to the west of Europe. Among the small mammals invading the area the genus *Progonomys*, of Asian origin, arrived in the Eastern Mediterranean at ~10.1 Ma (KAPPELMAN *et al.*, 2003). There is a clear diachrony in its distribution as it is known from Pakistan at 12.3 Ma and from Spain at 9.64-9.74 Ma (PILBEAM *et al.*, 1996; AGUSTI *et al.*, 1997). The rodent *Parapodemus* is known from MN 12 of the Eastern Mediterranean, and arrived in the area from the north. Other rodents are the genera *Byzantinia*, *Occitanomys*, and *Apodemus*, all of Asian origin (AGUSTI *et al.*, 2001; KOUFOS, 2003). Thus, an extended bioprovince of savannah character was established from the Balkans to Iran-Afghanistan, named Creco-Iranian Province (BONIS *et al.*, 1993).

During this time-span a significant number of hominoids appeared, representing a local European evolution. BEGUN (2001) proposed that *Dryopithecus*, after its appearance to Europe, evolved and then, during the late Miocene dispersed to the whole of Eurasia, giving rise to various forms, while at the end of the Miocene it re-entered Africa. The genera, *Dryopithecus* in W.-C. Europe, *Oreopithecus* in Italy, *Ankarapithecus* in Turkey, *Sivapithecus* in India and *Lufengpithecus* in China are representatives of the late Miocene group of hominoids. In Greece the hominoid primate *Ouranopithecus macedoniensis* with an age from 9.0-9.6 Ma was found in the localities Ravin de la Pluie and Xirochori of Axios valley and Nikiti 1, in Chalkidiki (DE BONIS & KOUFOS, 1999; KOUFOS, 1993, 1995). *Ouranopithecus* is of special interest as it has strong relationships with the Plio-Pleistocene hominines (DE BONIS & KOUFOS, 2001).

LATEST MIOCENE MIGRATION (6.7-5.3 MA)

Although basin re-organization around the Mediterranean provoked several regional phenomena of isolation already during the middle Late Miocene (late Tortonian, MN 12; KRIJGSMAN *et al.*, 2000), accumulated data from Spain, Italy, Sicily, Gavdos, Crete and Cyprus suggest that a major isochronous palaeoenvironmental change at 6.8-6.7 Ma affected the entire Mediterranean (KRIJGSMAN *et al.*, 2002). This age marks the beginning of MN 13 zone, characterized by an important mammal turnover (AGUSTI *et al.*, 2001). It seems that at 6.1 Ma an ephemeral landbridge between Africa and Europe already existed in the Gibraltar area, caused by the emergence of the Betics intamontane basins, allowed the first terrestrial faunal exchange between these two lands across the Iberian peninsula (GARCES *et al.*, 1998). At 5.9 Ma a climatic trend towards increased aridity and continentality combined with the continuous tectonic convergence between Africa and Europe and the uplift of the Spanish and NW African mountain chains, caused the closure of the Iberian and Rifian Seaways and the definitive isolation of the Mediterranean basin from the Atlantic ocean (STEININGER & RÖGL, 1985; PARTRIDGE, 1997; DINARES-TURELL *et al.*, 1999). Conditions of high evaporation in the Mediterranean led to a significant sea level drop (more than 200m according to deltaic deposits) and the deposition of thick evaporitic beds, starting at 5.96 Ma (KRIJGSMAN *et al.*, 2002). More or less at the same time the Beringian landbridge was re-activated as a result of a global regression, allowing several mammalian taxa to invade Eurasia from N. America (*Alilepus*, ancestor of Leporidae). The Central Paratethys was divided in two intermountain basins: the Dacian Basin in Romania and the Pannonian Basin in Hungary. Sea temperatures in the Mediterranean for that period apparently showed strong fluctuations, with short warm and cold seasons. The relative fall of humidity and temperature in the continent allowed expansion around the Mediterranean of hard-leaved evergreen forests, but the peri-Mediterranean flora was not dramatically changed (SUC, 1986; SUC *et al.*, 1995).

These important physiogeographic transformations provided new migration pathways for mammals, and

allowed more rapid and easy faunal exchanges between Africa and Europe. The main way between Africa and Eurasia in the Middle East remained open, as the Saharo-Arabian channel was not a significant obstacle for large mammals. However, the supposed connection between Africa and Europe across Tunis-Sicily or Sardinia-Corsica-Tuscany was no longer sustainable, since the faunal data from this area indicate a high endemism, plausibly suggesting an insular palaeoprovince (BERNOR *et al.*, 2001). The exchange of mammals between the Iberian Peninsula and Africa is fully substantiated by the study of micromammals (THOMAS *et al.*, 1982, AGUSTI *et al.*, 2001). The communication of the Mediterranean with the Atlantic Ocean by the Gibraltar Seaway became re-established at the end of the Miocene, at about 5.3 Ma. An extensive transgression raised the sea level, and the Mediterranean filled again. Climatic conditions were also changed, being less dry. The presence of tragulids and cervids in the Greek fauna of Dytiko, Macedonia, dated to latest Miocene, is strong evidence for an increase of humidity in the Eastern Mediterranean (DE BONIS *et al.*, 1992). The end of the Miocene is characterized by the disappearance of several mammalian taxa including mastodonts (*Choerolophodon*), carnivores (*Adcrocuta*, *Thalassictis*), suids (*Microstonyx*), giraffids (*Bohlinia*, *Samotherium*, *Helladotherium*), bovids (*Tragoptax*, *Prostrepsiceros*, *Protoryx*, *Palaeoryx*), cervids (*Procacpreolus*), micromammals (*Parapodemus*). This extinction probably resulted from the change in palaeoecological conditions. Few taxa adapted to the newly established environment and entered to Pliocene, e.g. *Gazella*.

The extinction, however, left free ecological space, and new steppic immigrants, mainly from Asia, arrived and dispersed in the Eastern Mediterranean: *Pliospalax*, *Prosimomys*, *Rhagapodemus*, *Mesocricetus*, *Parabos*, *Korynochoerus*, *Nyctereutes*, belong to these immigrants and characterize the beginning of the Pliocene. The earlier camelid *Paracamelus* was previously considered as belonging to this migration wave, but new data confirm an even earlier invasion. Moreover, forest dwellers, possibly of African origin, also arrived. *Tapirus arvernensis* appeared firstly in Italy in MN 13-14 (Now 2002). The mastodont *Anancus*, an African immigrant already mentioned from MN 12 of the Iberian Peninsula, dispersed eastwards and occurred in the Balkans and the Black Sea in MN 14 (Greece, Hungary, Romania, Ukraine). Two Greek faunas (Maramena and Silata) correspond to this transitional period. Their mammal association includes young elements such as the suid *Korynochoerus* and the rodents *Rhagapodemus*, *Mesocricetus*, *Apodemus* and *Micromys* together with Miocene genera such as *Choerolophodon*, *Tragoptax*, *Samotherium* and *Pliocervus*. Both faunas have been dated to the Miocene/Pliocene boundary (SCHMIDT-KITTLER *et al.*, 1995, VASSILIADOU *et al.*, 2003).

EARLY-MIDDLE PLIOCENE MIGRATION (5.3-2.5 MA)

The main palaeogeography of the Mediterranean region changed slightly after the beginning of the Pliocene, being more or less similar to the recent one

(Fig. 4A). The uplift of the Alpine chain separated Northern-Central from Southern Europe distinguishing their biotopes. The Black Sea was restricted more or less at its present limits, while the Caspian Sea formed a larger marine/submarine system; communication between these two basins was possible, but not certain. The continuous northward drift of the Arabian plate allowed definitive opening of the Red Sea, but the African-Middle East migration pathway remained active. Climatic conditions changed to more warm and wet. This is clear from the extended Pliocene lignitic deposits in Greece, Turkey, FYROM and Bulgaria. The great percentage of Desmaninae in the Greek mammalian faunas of this period (Spilia 1, Kardia) confirms this opinion (VAN DER MEULEN & VAN KOLFSCHOTTEN, 1986).

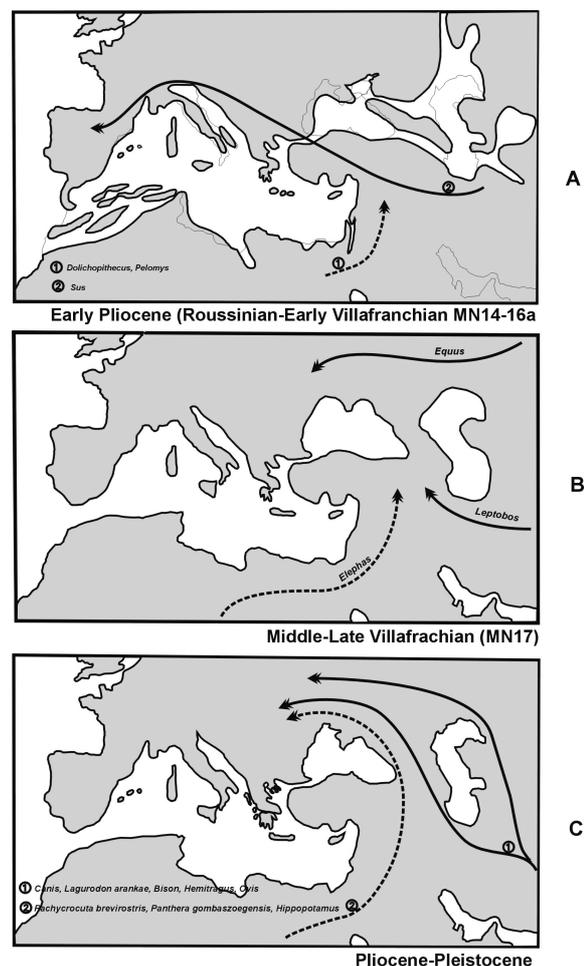


Fig. 4. – Palaeogeographic map of Mediterranean region with the main mammalian migration pathways and arrivals in Eastern Mediterranean.

- a) Early-Middle Pliocene (MN 14-16a)
- b) Middle-Late Villafranchian (MN 17)
- c) Pliocene-Pleistocene

Palaeogeographic maps from STEINIGER & RÖGL (1985).

Pliocene fossil mammal records in the Eastern Mediterranean are, however, scarce. Between 5.3 Ma and ~3.5 Ma ago several new forms arrived in Europe. The cercopithecoid *Dolichopithecus* and the rodent *Pelomys* arrived from Africa via the Middle East. The former appeared in the Eastern Mediterranean in the Greek locality of Meg-

alo Emvolon, dated to the base of MN 15 (KOUFOS & KOSTOPOULOS, 1997). The rodent *Pelomys* arrived earlier at the beginning of the Pliocene, found in the Greek locality of Maritses, Rhodes (DE BRUIJN *et al.*, 1992). Several carnivores, cervids, bovids and rodents migrated to Europe, mainly from Asia. The cervids differentiated rapidly and gave rise to several genera, occupying a significant number of mainly forest ecological niches. The suid *Sus*, most possibly of southern Asian origin, made its first appearance in the Greek locality of Kessani dated to the base of MN 14 (KOUFOS & KOSTOPOULOS, 1997). It rapidly dispersed to the whole of Europe as it is known from MN 14 of Italy, France and Spain (NOW, 2002). Later, it was found in the localities of Apolakkia, Rhodes and Megalo Emvolon dated to MN 15 (KOUFOS & KOSTOPOULOS, 1997). These types of mammalian faunas were partly changed at ~3.2 Ma because of a worldwide climatic cooling, causing a renewal of the mammal communities. Early Villafranchian (3.2 – 2.6 Ma) faunas are, however, poorly known in the Eastern Mediterranean.

THE MIDDLE-LATE VILLAFRANCHIAN FAUNAL TURNOVER (2.6-2.0 MA)

Since the main morphotectonic structures of the peri-Mediterranean region were completely developed, the palaeogeography of the area did not change. Migration and dispersion of the mammals were mainly affected by climatic fluctuations. At ~2.6 Ma (Middle Villafranchian, MN16) a climatic deterioration allowed a more arid phase, which characterized the rest of this period until 1.8 Ma ago. This time-span correlates to the development in the Mediterranean region of the steppic floras characterized by *Artemisia* and *Ephedra* (SUC, 1986 ; SUC *et al.*, 1995), and probably to the first major cool event of the northern hemisphere (TURNER, 1995 ; BLUM, 1997). The character of the mammalian faunas became more steppic, especially in Southeastern Europe. Nevertheless, the palaeoecological conditions changed gradually westwards delaying their presence in the Western Mediterranean. Therefore, during this time interval the palaeoecological conditions appeared to be more arid in the Eastern than in the Western Mediterranean. The middle Villafranchian faunas from Greece, Turkey and neighboring areas already had a more open/dry character than the isochronous faunas from Southwestern Europe as confirmed by the persistence of *Gazella*, giraffids *e.t.c.* (KOSTOPOULOS & SEN, 1999 ; KOSTOPOULOS & KOUFOS, 2000).

The most important arrivals in the Eastern Mediterranean and the whole of Europe are referred to the genera *Elephas*, *Leptobos* and *Equus*, known as *E-L-E event*. The genus *Equus* migrated earlier to Asia from N. America via the Beringian landbridge, but it arrived in the Eastern Mediterranean at the beginning of middle Villafranchian, *c.a.* ~2.6 Ma (AZZAROLI, 1990 ; KOUFOS, 2001). Its possible first appearance in the Eastern Mediterranean has been traced in Damatria, Rhodes Island, Greece. The fauna of Damatria is poor, but a dating to the upper part of early Villafranchian (MN 16b) is possible for it (KOUFOS, 2001). This age corresponds to ~2.6 Ma and fits quite well with the abovementioned first appearance of *Equus* in Europe. The genus dispersed rapidly throughout

Europe, as it is traced in Spain at the same time. *Elephas* arrived from Africa following the Middle East pathway. *Leptobos* is an immigrant from Southern Asia and firstly appeared in the Eastern Mediterranean in the locality of Damatria. At the same time the second dispersal event of arviculids appeared (STEININGER & RÖGL, 1985). During MN 16 several cervids of Asian origin adapted to local conditions providing new species or even genera. From the beginning of MN 17 three cervids *Croizetoceros*, *Eucladoceros* and “*Cervus*” / “*Pseudodama*” appeared in the Eastern Mediterranean. The mountain bovid *Gallogoral* and the slender antelope *Gazellospira*, both possibly of Asian origin, migrated to the Eastern Mediterranean and they were noted at several Greek localities (KOUFOS & KOSTOPOULOS, 1997). Early ovibovines also appeared during this time (SPASSOV, 2000 ; ATHANASSIOU, 2002). In the Eastern Mediterranean and the Black Sea a possible descendant of the late Miocene Palaeotraginae, the giraffid *Mitilanotherium*, is also present (KOUFOS & KOSTOPOULOS, 1997 ; KOSTOPOULOS & ATHANASSIOU, *in press*). Incidentally, the presence of giraffids in W. Europe seems to be underestimated. New data from Spain justify the occurrence of late Pliocene giraffids in this area too (ARRIBAS *et al.*, 2001 and *pers. obs.*).

EARLY PLEISTOCENE MIGRATION (2.0-1.0 MA)

The climatic alternations and their effects on the sea level are the crucial factors of faunal changes during this period, which is characterized by a rapid renewal of the mammalian fauna at ~2.0-1.8 Ma (KOSTOPOULOS & KOUFOS, 2000). The palaeogeography of the Eastern Mediterranean is similar to the recent one (Fig. 4C). During a short time span from 2.0-1.8 Ma several taxa enter Europe via the Balkan Peninsula and the Middle East (SPASSOV, 2000 ; KOSTOPOULOS *et al.*, 2002). Between them the canid *Canis*, the rodent *Lagurodon*, the bovids *Bison*, *Hemitragus* and *Ovis* are Asian immigrants arrived in the Eastern Mediterranean at the beginning of the Pleistocene. The carnivores *Pachycrocuta brevirostris* and *Panthera gombaszoegensis*, as well as *Hippopotamus*, all of African origin, arrived in the area through the Middle East. All these immigrants replaced the typical Villafranchian faunas of the Eastern Mediterranean and Europe. Several old taxa (*Nyctereutes*, *Pliohyaena*, *Gallogoral*, *Procampoceras*, *Leptobos*, *Gazellospira*, *Gazella*, *Sus strozzii*, *Mitilanotherium*, *Croizetoceros* *e.t.c.*) disappeared and were replaced by new ones. This faunal change is well recorded in the Greek locality of Gerakarou and the Bulgarian locality of Slivnitsa, both dated at the end of the Pliocene (KOUFOS & KOSTOPOULOS, 1997 ; SPASSOV, 1997). From the beginning of the Pleistocene (~1.8 Ma) new immigrants, especially from Asia, penetrated further : the characteristic steppic rodent *Allophaiomys pliocaenicus* dispersed in the whole peri-Mediterranean area. The bovids *Pontoceros*, *Praeovibos*, *Soergelia* and the cervid *Praemegaceros* arrived in the Eastern Mediterranean and then dispersed to Europe (AZZAROLI, 1983 ; KOSTOPOULOS *et al.*, 2002). These migration waves are closely related to the expansion of the steppe towards the southwest, including some northern and possibly cooler inhabitants.

MIDDLE-LATE PLEISTOCENE MIGRATION (<1.0 MA)

During the early Pleistocene a large steppic belt was established along Eurasia and N. America. At the beginning of the middle Pleistocene wet climatic conditions allowed an increase of humidity and rehabilitation of the forestial cover. For the next one million years the climatic conditions are characterized by a cyclicity with alternation of cold and temperate periods, establishing the oscillations of the Pleistocene glaciations (AZZAROLI, 1983 ; SUC, 1986 ; TURNER, 1995). During this period no important arrivals are mentioned. Steppic and cold steppic forms of North Asian and American origin such as the bovids *Praeovibos*, *Ovibos*, *Soergelia* and the cervid *Rangifer*, as well as temperate dwellers such as the elephant *Palaeoloxodon*, the rhino *Dicerorhinus* and the large bovid *Bubalus* arrived in the Eastern Mediterranean and then dispersed almost throughout Europe. The expansion of their biomes depended on the alternation of the glacial/interglacial periods. In Southern Europe the so-called "Mediterranean biosystem" was established. The most important migrations followed a N-S and *vice versa* direction, caused by expansion of the glacial cover. However, the uplifted Alpine chain is a significant barrier for most of the mammalian taxa. The Southern European fauna is only affected by the paroxysmal phases of the central European N-S migrations. Cold steppic faunal elements such as *Mammuthus* and the woolly rhino *Coelodonta* are occasionally present there, while temperate dwellers predominated. Both cold and temperate taxa are known from the middle-late Pleistocene of Greece (MELENTIS, 1961 ; MARINOS, 1965).

On the contrary, the Mediterranean islands show a completely different faunal pattern from middle-late Pleistocene. The isolation of the islands due to tectonic movements or/and sea level fluctuations, allowed the development of special endemic faunas. The absence of predators and the dramatic reduction of the living space gave rise to an evolutionary process known as insular endemism. The body mass of the island mammals, adapted progressively to the new conditions, reduced or increased accordingly to their initial size (insular "nanism" in elephants, hippos or "gigantism" in rodents). Several islands in the Eastern Mediterranean (Rhodes, Carpathos, Tilos, Crete, Cyprus e.t.c.) include poor mammalian communities of endemic character with small-sized elephants, hippos and cervids (DERMITZAKIS & SONDAAR, 1978 ; KOTSAKIS *et al.*, 1979 ;).

CONCLUSION

During the Neogene/Quaternary several mammalian migrations and faunal changes have been recognized in the Eastern Mediterranean. The recognized main migrations of this period are : a) the middle Orleanian (18.0-17.0 Ma), b) the late Miocene (10.7-6.7 Ma), and c) the middle Viffafranchian (~2.6 Ma) one. At the same time smaller migration waves from Africa and Asia allowed the entrance of various mammalian taxa into Europe. Two important faunal changes have been recognized : a) the latest Miocene faunal change, which marks the beginning

of the Pliocene, and b) the latest Pliocene change, marking the beginning of the Pleistocene. Known but less significant faunal changes are important for the division of the various stages into smaller time-spans. The migrations and faunal changes of the Neogene are mainly due to palaeogeographic re-organization of the Mediterranean area during the Pliocene and Pleistocene. When the Mediterranean acquired its final palaeogeography and structure, climatic changes became the main factor controlling mammalian migrations. Since the study of Neogene/Quaternary faunas of the peri-Mediterranean region continues new data become available to confirm or modify our ideas.

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