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The Messinian events and the Greek fossil mammal record

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Greek Neogene mammal faunas, being centrally located to the stage of the Messinian play, hold clues to the understanding of this phenomenon. 23 Greek fossil mammal faunas containing 398 taxa, and spanning the period of MN Units 10 to MN15 are analysed, in order to investigate effects the Messinian Events had on Greek Neogene. Updated faunal lists are subjected to cluster statistical analyses for a quantitative estimation of chronological segregation patterns of the faunal assemblages. The Simpson's Faunal Resemblance Index was used as the variable for the faunal correlation. K-Means cluster analysis for two groups distinguished the 3 Samos and the 2 Pikermi faunas as the group with less variation within, than between the two groups in which the 23 faunas were separated. Join cluster analysis' basic pattern did separate the pre- from the post-Messinian faunas, but sampling error due to small faunal size, bias due to skewed sampling of the faunal diversity at the population level, and geographic proximity, could not be factored out. Biochronological (MN Unit) range analysis of 196 species in the faunas showed that the majority of mammals lived in MN12-13 times, and that there was considerable reduction in numbers of large mammal species present in the faunal assemblages after the Messinian. This can be caused not only by the alleged low turn out of (large) Pliocene mammals, but also by sampling error due to insufficient amount of paleontological research done in this time period. Micromammals around the Messinian Stage/Age indicate the presence of variable habitats in the area, dry and wet, forested and open country before, during and after the Messinian. Greek Neogene mammal faunas seem to support the recent understanding that the Messinian 'Event' was lengthy, cyclic in tempo, and diverse in mode.

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INTRODUCTION

For over 30 years earth scientists are trying to describe the events that took place in the Mediterranean Basin during the formation of the Messinian Stage, and to study their climatic and biological effects. The international conference on biotic and climatic effects of the Messinian Event in the Mediterranean, organised in 1995 by the International Institute for Human Evolutionary Research and the Department of Earth Sciences of the University of Garyounis, held in Benghazi Libya, reviewed the data on the Messinian

Event. Recent data show that the Messinian lasted for a long period of time, close to 1.9 My (Hilgen *et al.* 1997), and that it was typified by cyclicality of conditions. The geological age for the onset of the Messinian Stage has been calibrated to 7.26 - 7.12 My (Berggren *et al.* 1995, Vai *et al.* 1993). The beginning of the inflow from the Atlantic to the Mediterranean is dated to c. 5.8 My. Reflooding of the basin dates to 5.0 - 5.3 My (Hodell *et al.* 1994). During this time period, 7 depositional cycles are known to have

occurred in the margins, and about 25 cycles in the center of the basin near Sicily (Butler *et al.* 1995). This is evidenced by the sea-floor seismic reflectors and by the deep-sea cores (Stanley & Wezel 1985). These cycles consisted of changes in water depth and chemistry brought on by evaporation, influx of new water from the Atlantic over the Gibraltar, as well as by additional influx of fresh water from rivers draining into the Mediterranean Basin (Hodell *et al.* 1986). These large rivers cut deep canyons in the circumference of the Mediterranean Basin, as the level of the sea dropped. Geophysical data from northern Sahara confirm the presence of large channels which had cut deep into Tortonian beds before entering the paleo-Sirt Gulf. Some faunal elements indicate a tropical source for these rivers (Gaudant 1987).

Global paleoclimate at the end of the Miocene cooled, as indicated by both deep sea and terrestrial oxygen isotopic records (see Potts 1998). Carbon isotope data indicate that between 8 and 6 My there was a global increase of plant mass using C4 photosynthesis, such as grassland vegetation (Cerling *et al.* 1997). Data from vertebrate paleontological sites in Greece, Libya (Sahabi), Spain and Abu Dhabi seem to support that the Mio/Pliocene time was a period of greater aridity, and that grasslands were widespread. Yet, paleofloral records especially in the northern circum-Mediterranean regions indicate the continued presence of warm-temperate and high humidity vegetation well into the Pliocene (Velitzelos 1995). This apparent contradiction in paleoclimate indicators can be explained by the possible presence of altitudinal and/or latitudinal gradients. Higher elevations could maintain more humid vegetation during arid phases, due to the presence of cloud moisture. Similarly, northern European sites could have had more forest cover than sites located more southerly. Although the oldest paleofloral indications of desert conditions date to the Late Miocene,

desert environments were not widespread before 2.8 My, as indicated by deep-sea records of wind-blown dust off the West Coast of Africa (DeMenocal & Bloemendal 1995). The Messinian was apparently not a period of radical vegetation change, but rather a time of more widespread open vegetation, moderated by climatic oscillations including monsoonal rains.

Zoogeography provides another clue to biotic conditions during the Messinian in the circum-Mediterranean region (see Janis 1993). The taxonomic composition of paleofloras north of the basin clearly shows strong connections with Asia. On the other hand, the macroflora of Sahabi, Libya shows affinities with tropical Africa (Dechamps 1987). The north-south latitudinal gradients implied by the paleofloral pattern, are also shown by the vertebrate faunas (see Hill 1995). Rodent faunas from Asia show affinities with northern and central Spain (Berry 1995). Messinian rodent faunas in the south, however, include the presence of dry-country gerbil species migrating from Africa. In Italy, there are African primates, artiodactyls and *Stegotrabelodon lybicus* of Messinian age in sites in southern Italy, while similarly aged sites in northern Italy lack African elements. Greek Upper Neogene large mammal faunas show open vegetation environments and do not indicate major faunal interchange with Africa. Rather they show connections with contemporaneous sites in Asia, such as Maraghe (Bernor *et al.* 1987, 1996b). The Abu Dhabi fauna on the Arabian Peninsula (Whybrow *et al.* 1999) also shows this latitudinal correlation. It shares many faunal elements with Sahabi, but lacks close connections with similar age sites in the north. For example, the anthracothere *Merycopotamus*, the most common element in the Sahabi fauna (Gaziry 1987), is present in other late Neogene North African sites, such as in Chad, but is absent from Abu Dhabi.

Floral and faunal paleobiogeography during

the Messinian is an active research area, studying such topics as how clear-cut were the apparent latitudinal patterns of vegetation and faunal provinciality during the Messinian. Paleogeography of the Mediterranean basin during the Messinian is also a major research area. The land bridge connecting North Africa and Spain during the Messinian included dry open country and sandy habitats, as indicated by the presence of African gerbils north of Gibraltar (Moya-Sola & Agustí 1989). But more vegetated conditions were probably present as well. African ostriches, monkeys, proboscideans among other species, reached southern Europe while other species, such as micromammals and bears migrated the other way, southwards, inhabiting North Africa.

Finally, the age of the Messinian, c. 7 to 5 My coincides with the estimated Ape - Hominid split. The effect of the Messinian 'Event' on the origin and evolution of early Hominids has passed the stage of being a source of speculation (Brain 1981), and reached the stage of active scientific research (Hill 1995; WoldeGabriel *et al.* 1994). Paleoanthropological field research is coming close to the discovery of definitive hominid fossils in this time period.

The Greek Neogene faunal localities, being centrally located to the stage of the Messinian play, hold clues to the understanding of this phenomenon. Specifically, to the climatological and environmental effects it had to the area, as well as, to the relation of the Messinian to faunal and floral turnover and evolution in the circum-Mediterranean region and beyond. The major mammal faunas on the Greek mainland and islands of Late Miocene to Early Pliocene age will be studied here, in order to investigate aspects of the effects the Messinian had on land mammals.

MATERIAL AND METHODS

A total of 23 Neogene mammal faunas were used in this study consisting of a total of 398

taxa. They were selected based on their chronological proximity to the time period of the deposition of Messinian Stage beds i.e., faunas of Late Turolian to Early Ruscinian Mammal Age, or MN11 to MN15. Second criterion was the sample size. An effort was made to compile the largest possible mammalian faunal samples. Faunal samples with a size of less than 5 taxa were excluded from the study, for reasons of approximation to the populations and for statistical confidence of the analyses. An effort was made to use the most recently taxonomically updated faunal lists. Cf., aff., question-marks (?) and quotes (‘’) in taxa names were omitted. Genera were used without referring to sp. nov., gen. (et sp.) nov. or names in quotes. The compiled faunal assemblages at the species level and the estimated age range in terms of MN Units used in this study are listed below in alphabetical order.

Ano Metochi 2,3

MN 13-14 (partially after Van der Meulen & Van Kolfschoten 1986).

Amblycoptus sp., *Apodemus dominans*, *Apodemus gudrunae*, *Hipparion* sp., *Micromys bendai*, *Myomimus maritsensis*, *Occitanomys adroveri*, *Pliopetaurista dehne* - *li*, *Pliospalax* sp., *Prolagus michauxi*, *Pseudomeriones abbreviatus*, *Rhagapodemus hautimagnensis*, *Schizogalerix* sp., *Tamias* sp. (de Bruijn 1989, Doukas 1989, Steffens *et al.* 1979).

Apollakia

MN 15 (Benda *et al.* 1977)

Apodemus dominans, *Blarinella* sp., *Castor fiber*, *Cervus* aff. *philisi*, *Crocidura* sp., *Dolomys* sp., *Episoriculus gibberodon*, *Gazella* sp., *Hipparion crassum*, *Hyaena pyrenaica*, *Miomys occitanus*, *Ochotonoides* sp. (Van de Weerd *et al.* 1982, Benda *et al.* 1977). *Hipparion crassum* is referred to 'Plesiohipparion' *crassum* by Bernor *et al.* 1996a.

Dytiko 1,2,3

MN 13 (Koufos 1989)

Adcrocuta eximia, *Anomalomys* cf. *rudabanyensis*, *Bohlinia attica*, *Choerolophodon pentelicus*, *Cremohipparion matthewi*, *Cremohipparion mediterraneum*, *Cremohipparion periafricanum*, *Dorcatherium puyhauberti*, *Gazella* sp., *Hispanodorcas orientalis*, *Hystrix primigenia*, *Mesopithecus pentelicus*, *Palaeoreas linder-mayeri*, *Palaeotragus roueni*, *Plesiogulo crassa*, *Pliocervus pentelici*, *Plioviverrops orbignyi*, *Prostrepsicerus* sp., *Protictitherium crassum*, *Protragelaphus theodori*, *Tragoportax gaudryi* (de Bonis *et al.* 1988, Koufos 1989, NOW 1995, Andrews *et al.* 1996, Sen 1996). *Mesopithecus pentelicus* is referred to *M. pentelicus* and/or *M. monspes-sulanus* by Andrews *et al.* 1996.

Halmyropotamos

MN 11 (NOW 1995)

Adcrocuta eximia, *Ancylotherium pentelicum*, *Cremohipparion mediterraneum*, *Deinotherium giganteum*, *Dicerorhinus 'orientalis'*, *Gazella gaudryi*, *Helladotherium duvernoyi*, *Hipparion 'koenigswaldi'*, *Hystrix primigenia*, *Machairodus giganteus*, *Mammuth borsoni*, *Metailurus major*, *Metailurus parvulus*, *Microstonyx major*, *Palaeoreas linder-mayeri*, *Palaeoryx pallasii*, *Pliocervus pentelici*, *Pliohipparion graecus*, *Prostrepsicerus 'woodwardi'*, *Protragelaphus skouzesi*, *Simocyon primigenius*, *Tragoportax amalthea*, *Ursavus ehrenbergi* (Melentis 1969, Koufos 1989, NOW 1995).

KallithiesMN 12 (partially after Sen *et al.* 1978, Sondaar *et al.* 1986)

Byzantinia sp., *Gazella deperdita*, *Gerbilus* sp., *Hipparion* sp., *Ictitherium orbignyi*, *Kowalskia* sp., *Machairodus aphanistus*, *Occitanomys neutrum*, *Paleoreas lindermayeri*, *Paleotragus* sp., *Tragocerus amaltheus* (Sondaar *et al.* 1986).

Megalo Emvolon - KaraburunMN 14-15 (Benda *et al.* 1979, de Bruijn 1984, Steffens *et al.* 1979).

Dolichopithecus ruscinensis, *Gazella bailloudi*, *Nyctereutes* sp., *Oryctolagus laynensis*, *Parabos makedonicus*, *Plesiohipparion longipes*, *Spalax odessanus*, *Sus minor*, *Trischizolagus maritsae* (Koufos & Pavlides 1988, Steffens *et al.* 1979, De Bonis *et al.* 1988, Bernor *et al.* 1996a)

Kardia-Ptolemais IMN14-15 (NOW 1995, Steininger *et al.* 1996)

Apodemus dominans, *Castor fiber*, *Micromys steffensi*, *M. bendai*, *Mimomys davakosi*, *Occitanomys brailloni*, '?*Plesiohipparion*' *crassum*, *Prolagus michauxi*, *Promimomys insulifenus*, *Propotamochoerus provincialis*, *Rhagapodemus hautimagnensis* (Koufos *et al.*, 1988, Van der Meulen & Van Kolfshoten 1986, Bernor *et al.* 1996a, Fejfar & Heinrich 1989).

Kastellios, 1,2,3MN 10 (Steininger *et al.* 1996)

Cricetulodon cf. *sabadellensis*, *Dorcatherium* sp., *Hipparion* sp., *Muscardinus* sp., *Progonomys woelferi*, *P. cathalai*, *Spermophilinus* cf. *bredai* (De Bruijn & Zachariasse 1979).

Limni 1,3,4

MN 14-15 (Van der Meulen & Van Kolfshoten 1986)

Apodemus dominans (1,3,4), *Mimomys occitanus* (3,4), *Myomimus maritsensis* (3,4), *Occitanomys neutrum* (1,3,4), *Promimomys insulifenus* (1) (Van der Meulen & Van Kolfshoten 1986).

MaramenaMN13 (Fahlbush 1996, De Bruijn *et al.* 1996, De Bruijn 1989)

Adcrocuta eximia, *Alilepus turolensis*, *Apodemus gudrunae*, *Choerolophodon pentelicus*, *Hypsocricetus* sp., *Dibolia dekkersi*, *Diceros heumayri*, *Helladotherium duvernoyi*,

Hylopetes macedoniensis, *Kowalskia browni*, *Mustela* sp., *Myomimus* sp., *Occitanomys neutrum*, *Pliopetaurista dehneli*, *Prolagus michauxi*, *Tragelaphus* sp.

(Daxner-Höck 1992, Van der Meulen & Van Kolfschoten 1986, Doukas 1988, De Bruijn 1989).

Maritsa

MN14 (De Bruijn *et al.* 1996, Van der Meulen & Van Kolfschoten 1986)

Apodemus dominans, *Atlantoxenus rhodius*, *Calomyscus minor*, *Castillomys crusafonti*, *Cricetus lophidens*, *Episoriculus gibberodon*, *Keramidomys carpathicus*, *Mesocricetus primitivus*, *Myomimus maritsensis*, *Paraethomys anomalus*, *Pelomys europaeus*, *Pliospalax sotirisi*, *Pseudomeriones rhodius*, *Rhagepodemus vanderweardi*, *Spermophilinus giganteus*, *Trischizolagus maritsae* (De Bruijn *et al.* 1970, Van der Meulen & Van Kolfschoten 1986, Fejfar & Heinrich 1989, Agusti 1989).

Pikermi-Megalo Rema

MN12 (partially after Bernor *et al.* 1996b and Steininger *et al.* 1996)

Aceratherium incisivum, *Adcrocuta eximia*, *Ancylotherium pentelicum*, *Bohlinia attica*, *Bohlinia speciosa*, *Ceratotherium neumayri*, *Choerolophodon pentelicus*, *Cremohipparion mediterraneum*, *Cremohipparion aff. matthewi*, *Deinotherium giganteum*, *Desmanella dubia*, 'Dicerorhinus' *schleiermacheri*, *Enhydriodon laticeps*, *Felis attica*, *Galerix* sp., *Gazella capricornis*, *Graecoryx valenciennesi*, *Helladotherium duvernoyi*, *Hipparion prostylum*, *Hipparion gettyi*, 'Hippotherium' *brachypus*, *Hyaenictis graeca*, *Hyaenotherium wongii*, *Ictitherium viverinum*, *Indarctos atticus*, *Lycyaena chaeretis*, *Machairodus giganteus*, *Mammot borsoni*, *Martes woodwardi*, *Mesopithecus pentelicus*, *Metailurus major*, *Metailurus parvulus*, *Microstonyx erymanthius*, *Miotragocerus monacensis*, *Oioceros rothii*, *Palaeoreas lindermayeri*, *Palaeoryx pallasii*, *Palaeotragus roueni*, *Palaeotragus coelophrys*,

Parapodemus gaudryi, *Plesiogulo* sp., *Pliocervus pentelici*, *Pliohyrax graecus*, *Plioviverrax orbigny*, *Promeles palaeattica*, *Promephitis lartetii*, *Prostrepsicercus rotundicornis*, *Protoryx carolinae*, *Protragelaphus skouzesi*, *Schizogalerix moedlingensis*, *Simocyon primigenius*, *Sinictis pentelici*, *Sporadotragus parvidens*, *Stegotetrabelodon grandincisivus*, *Tragoportax amalthea* (Bernor *et al.* 1996b, Symeonidis *et al.* 1979).

Pikermi-Chomateri

MN12 (Bernor *et al.* 1996c)

Aceratherium sp., *Alilepus* sp., *Byzantinia pikermiensis*, *Chalicotherium* sp., *Choerolophodon pentelicus*, *Cremohipparion mediterraneum*, *Desmanella dubia*, *Galerix moedlingensis*, *G. atticus*, *Gazella depertita*, *Hystrix primigenia*, *Kowalskia aff. lavocati*, *Mesopithecus pentelici*, *Microstonyx major*, *Muscardinus* sp., *Myomimus cf. dehmi*, *Occitanomys provocator*, *Parapodemus gaudryi*, *Pliocervus pentelici*, *Prolagus cf. crusafonti*, *Tragocens amaltheus* (Bernor *et al.* 1996b, NOW 1995, De Bruijn 1976, Lopez Martinez 1976, Rümke 1976, Marinos & Symeonidis 1972).

Prochoma I

MN11 (Steininger *et al.* 1996)

Adcrocuta eximia, *Choerolophodon pentelicus*, *Cremohipparion macedonicum*, *Gazella* sp., *Helladotherium duvernoyi*, *Hipparion dietrichi*, *Ictitherium* sp., *Microstonyx* sp., *Nisidorcas planicornis*, *Plioviverrax orbigny*, *Prostrepsicercus zitteli*, *Tragoportax rugosifrons* (NOW 1995, Kontopoulou *et al.* 1992, Koufos 1989).

Pyrgos

MN10/12 (NOW 1995, Andrews *et al.* 1996)

Bohlinia attica, *Cervus* sp., *Equus cf. stehlini*, *E. stenonis*, *Felis issiodorensis*, *Gazellospira torticornis*, *Graecopithecus freybergi*, *Helladotherium duvernoyi*, 'Jordanomys major', *Leptobos* sp., *Tragoportax amalthea* (Van der Meulen & Van Kolfschoten 1986, NOW 1995).

Ravin de la PluieMN10 (Steininger *et al.* 1996)

Adcrocuta eximia, *Bohlinia attica*, *Choerolophodon pentelicus*, *Cremohipparion macedonicum*, *Decennatherium macedoniae*, *Graecopithecus freybergi*, *Hippotherium pri-migenium*, *Mesembriacerus melentisi*, *Palaeotragus coelophrys*, *P. roueni*, *Pliovivemops orbignyi*, *Progonomys catalai*, *Prostrepsicerus vallesiensis*, *Protictitherium gaillardi*, *Samotragus praecursor* (Koufos 1989, De Bonis *et al.* 1988, NOW 1995, Bernor *et al.* 1996a).

Ravin de Zouaves I

MN10 (NOW 1995)

Adcrocuta eximia, *Choerolophodon pentelicus*, *Cremohipparion macedonicum*, *Helladotherium duvernoyi*, *Ictitherium sp.*, *Mesembriacerus melentisi*, *Ouzocerus gracilis*, *Samotragus praecursor* (Koufos 1989, Bernor *et al.* 1996a).

Ravin de Zouaves 5MN11 (Steininger *et al.* 1996)

Adcrocuta eximia, *Chasmaporthetes bonisi*, *Choerolophodon pentelici*, *Cremohipparion macedonicum*, *Cremohipparion proboscideum*, *Dicero rhinus orientalis*, *Gazella sp.*, *Helladotherium duvernoyi*, *Hipparion dietrichi*, *Hyaenotherium wongii*, *Ictitherium viverrinum*, *Mammuth borsoni*, *Mesopithecus pentelicus*, *Microstonyx sp.*, *Nisidorcas planicornis*, *Palaeoreas zouavei*, *Postpotamochoerus hyotherioides*, *Prostrepsicerus rotundicornis*, *Prostrepsicerus zitteli*, *Tragoportax rugosifrons*, *Zygodolophodon tapiroides* (Andrews *et al.* 1996, Werdelin & Solounias 1996, Bernor *et al.* 1996a, Koufos 1989).

Rema Marmara

MN13/14 (Benda & Meulenkamp 1990)

Micromys bendai, *Occitanomys neutrum*, *O. brailloni*, *Parapodemus gaudryi*, *Prolagus michauxi* (de Bruijn 1989)

Samos - Old Mill BedsMN11 (Bernor *et al.* 1996b)

Cremohipparion mediterraneum, *Gazella capricornis/deperdita*, *Hipparion gettyi*, *H. cf. prostylum*, *?Microstonyx erymanthius*, *Samotherium boissieri*, *Sporadotragus parvidens* (Bernor *et al.* 1996b)

Samos - White SandsMN12 (Bernor *et al.* 1996b)

Adcrocuta eximia, *Bohlinia attica*, *Ceratotherium neumayri*, *Chilotherium samium*, *Cremohipparion nikosi*, *Criotherium argalioides*, *Gazella capricornis/deperdita*, *Hyaenotherium wongii*, *'Hippotherium' giganteum*, *Ictitherium viverrinum*, *?Microstonyx erymanthius*, *Pachytragus crassicornis*, *P. laticeps*, *P. quadricornis*, *Palaeoreas lindermayeri*, *Palaeoryx pallasii*, *Palaeotragus coelophrys*, *Pseudotragus capricornis*, *Samotherium sp.*, *Sporadotragus parvidens*, *Tragoportax rugosifrons* (Bernor *et al.* 1996b).

Samos - Main Bone BedsMN12 (Bernor *et al.* 1996b)

Adcrocuta eximia, *Ancylotherium pentelicum*, *Belbus beaumonti*, *Byzantinia hellenicus*, *Ceratotherium neumayri*, *Chilotherium samium*, *Choerolophodon pentelicus*, *Cremohipparion matthewi*, *C. proboscideum*, *Criotherium argalioides*, *Deinotherium giganteum*, *'Dicerorhinus' schleiermayeri*, *Felis attica*, *Gazella capricornis/deperdita*, *Graecoryx valenciennesi*, *Helladotherium duvernoyi*, *Hipparion dietrichi*, *Hyaenotherium wongii*, *Hystrix primigenia*, *Ictitherium viverrinum*, *Indarctos atticus*, *Lycyaena chaeretis*, *Machairodus giganteus*, *Mammuth borsoni*, *Metailurus parvulus*, *Microstonyx erymanthius*, *Miotragocerus monacensis*, *Muntiacus sp.*, *Occitanomys provocator*, *Oioceros wegneri*, *Orycteropus gaudryi*, *Pachytragus crassicornis*, *P. laticeps*, *P. houtumschindleri*, *Palaeoryx pallasii*, *Paleotragus rounei*, *Parataxidea polakii/maraghana*, *Pliocervus pentelici*, *Pliohyrax graecus*, *Pliospalax sotirisi*, *Pliovivemops orbignyi*, *Promeles paleatica*, *Promephitis lartetii*, *Prostrepsicerus*

rotundicornis, *Protragelaphus skouzesi*, *Pseudomeriones pythagorasi*, *Pseudotragus capricornis*, *Samokeros minotaurus*, *Samonycteris majori*, *Samotherium* sp., *Schizogalerix atticus*, *Spermophilinus bredai*, *Stegotetabelodon grandincisivus*, *Tragoportax amalthea*, *T. curvicornis*, *T. rugosifrons*, *Ursavus depereti* (Bernor *et al.* 1996b).

Vathylakkos

MN12/13 (NOW 1995)

Bohlinia attica, *Ceratherium neumayri*, *Choerolophodon pentelici*, *Cremohipparion macedonicum*, *Dorcatherium puyhauberti*, *Gazella* sp., *Hipparion dietrichi*, *Hyaenotherium wongii*, *Ictitherium viverrinum*, *Microstonyx major*, *Mesopithecus pentelicus*, *Nisidorcas planicornis*, *Palaeoreas lindermayeri*, *Plessiogulo crassa*, *Plioviverrops orbigny*, *Prostrepsicercus zitteli*, *Samotherium boissieri*, *Tragoportax rugosifrons* (Bernor *et al.* 1996a, Koufos 1989, Werdelin *et al.* 1996).

The faunas were subjected to the multivariate statistics of cluster analysis for detecting natural groupings in the data. The primary goal of this test is the estimation of the degree these Greek Neogene mammal faunas are separated into a Pre-Messinian and a Post-Messinian group. It is a gross quantitative estimation of how different the faunas are before and after the Messinian. First, a symmetrical matrix of correlation coefficients between all 23 fossil mammal faunal assemblages was computed. Simpson's formula for Faunal Resemblance Index (SRI, Simpson 1960), was used to produce this input data matrix for the cluster analysis. The SRI formula is: C/N_{\min} , where C is the number of common taxa between two faunas, and N_{\min} the size of the smaller of the two faunas. Cheetham & Hazel (1969) compared the SRI correlation formula with several others, and argued that it showed greater consistency when the size of the faunas vary considerably. Large sample variation is indeed the case

with the fossil faunal assemblages in this study. SRI accomplishes this by dividing the number of common taxa between two faunas, by the number of the smaller of the two samples, thus maximizing similarities between the faunas than differences, as is the case with, among others, the Jaccard formula. [For further discussion on fossil mammal faunal correlation coefficients, see Shuey *et al.* (1978) and Bernor & Pavlakis (1987)]. The statistical program Systat ver. 7 for Windows was used for the calculation and production of the faunal correlation matrix, as well as for the subsequent cluster analysis. The Join or hierarchical method of cluster analysis was used, in which the set of faunas is partitioned into sets of nested groups, with the most similar faunas nested first and closer (for details see Sokal & Sneath 1963). The output of the hierarchical method is a tree or dendrogram.

The pair cross correlation of SRI's was computed as 'distances' between two faunas. These distances are normalised to allow comparison of clustering across widely different SRI values. These pair cross correlation were produced by 4-distance metrics: Euclidean, 1-Gamma coefficient, 1-Pearson correlation coefficient, and Percent disagreement. The Euclidean distance uses the square root of the SRI correlation value of a pair of faunas (mean for more than one faunas in clusters). The Gamma option uses $1-\gamma$, where γ is the Goodman-Kruskal gamma correlation coefficient between two SRI's (pairs of faunas). The Pearson distance is calculated as $1-p$, where p is the Pearson product-moment correlation between two SRI values. The Percentage produces a distance index, which is the percentage of the difference of two SRI values. For more information see Hartigan (1975) and Sokal & Sneath (1963).

For each one of the four-distance metrics, the following linkage clustering methods were used to compute the distance of a cluster to another, in order to decide whether the two

should be merged, in a given step:

- **Single:** the distance between the two closest members in separate clusters is taken as the distance between the two clusters. It produces long, stringy clusters.
- **Complete:** it uses the most distant pair of faunas in two clusters to compute between-cluster distances. It tends to produce compact clusters.
- **Centroid:** it uses the average distance value of all faunas in a cluster as a reference point for distances to other clusters.
- **Average:** it averages all distances between pairs in two clusters to decide how far apart these clusters are.
- **Median:** it calculates the median of all distances between pairs in two clusters to decide how far apart these clusters are.
- Finally, the merging of clusters is decided by the Ward method (Ward 1963), i.e., by producing clusters with minimum variance.

The 23 faunas were also subjected to the K-means clustering method. It assigned faunas to non-overlapping clusters. Two groups of faunas were selected for this study. It split the faunas into two groups by maximizing between clusters variation, relative to the variation within the two clusters (for details see Hartigan 1975). The faunal assemblages were not standardised or ranked in both Join and K-Means statistics. 50 iterations were done for the separation into the two clusters. The 23 mammal Neogene faunas were further analyzed in biochronological and paleoecological context. Specifically, the biochronological range of selected taxa was tabulated to show possible faunal turnover around Messinian times.

RESULTS AND DISCUSSION

The K-means cluster analysis (less SRI variation within clusters than between clusters), produced the following two faunal groups: the first one consists of the Pikermi fauna from Megalo Rema (the main, classical

fauna) and the three Samos faunas (Main Bone Beds, Old Mill Beds and White Sands). The other group contains the rest of the faunas. This first result brings forward the Pikermi and Samos faunas as the reference Greek Neogene fossil mammal faunas. Main reason for this is the large size of the faunal samples. The Pikermi fauna contains 57 taxa, and the Samos (Main Bone Beds) 58, while the next numerous faunal sample has only 23 taxa (Halmyropotamos). An additional reason for this separation is related to taxonomic identification. Both faunas are the best studied and the most recently taxonomically updated. Adequate sample size, which approximates with statistical confidence the extinct animal population, and updated taxonomic identification of the faunal sample, are prime requirements for reconstruction of the paleontological record, biochronological or paleoecological, including that of the Greek Neogene.

The Join cluster analysis produced 26 dendrograms, as described in the methods. In 21 of these diagrams three major factors were detected to have been responsible for the production of clusters: faunal diversity and size, geography and age of the faunas. Only two main faunal groups were almost constantly produced. The main pattern is shown by the dendrogram of Figure 1. It is produced by the Euclidean distance and the minimum variance (Ward) clustering method. This clustering pattern will be described, as the basis for discussing three variations produced by the other dendrograms. One major grouping contains three nested clusters. Ravin, Vathylakos and Prochoma faunas comprise the one cluster, and Samos and Pikermi faunas belong to another cluster. Dytiko and Halmyropotamos are also part of this group. The sister group consists of the rest of the faunas in the study. The faunas of Ano Metochi, Ptolemais and Rema Marmara are nested first, and next cluster with Limni and Maritsa, with the Apollakia fauna outlayer. Additionally, Megalo Emvolo, Maramena, Pyrgos,

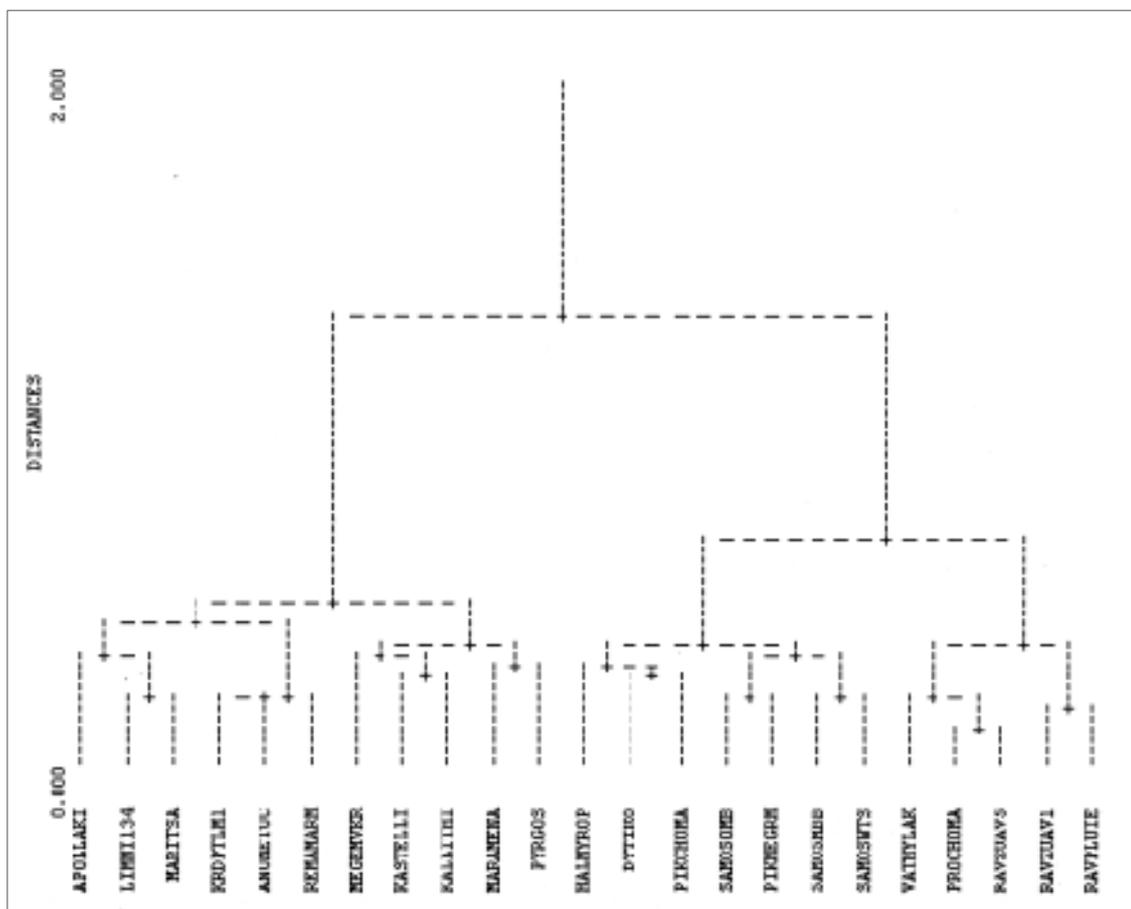


Figure 1 Cluster analysis tree diagram of Greek Neogene faunas studied. Distance metric is Euclidean distance. Ward minimum distance method.

Kastellios and Kallithies cluster together with in this group.

The former of the two major clusters is the solid set of Pikermi-Samos-Axios Valley, large size, taxonomically diverse, Late Miocene, Upper Tortonian-Messinian Stage, Late Turolian Age, MN 11-12, Greek mainland Neogene faunas. The following factors were employed, in order of importance: high faunal diversity and large size of the faunal sample are decisive factors. They make the sample approximate the population and make the statistical analysis reliable. Time and geographical proximity are additional factors that played key role in producing this cluste-

ring. Only Dytiko is younger than the other faunas. It belongs to zone MN11-12.

The second group of faunas is also solid, in terms that, with the exception of a couple of faunas, all cluster runs produce it. This grouping is the result of the high proportion of micromammals in the faunal samples. Time is also a decisive clustering factor. The faunas which belong to this cluster belong mostly to zone MN13 or younger. Only the set of Kastellios and Kallithies faunas are older. Geographic proximity is the next clustering factor (Strimon Basin - Ano Metochi, Maramena, Rema Marmara; Ptolemais; Thessaloniki - Megalo Emvolo; Rhodos).

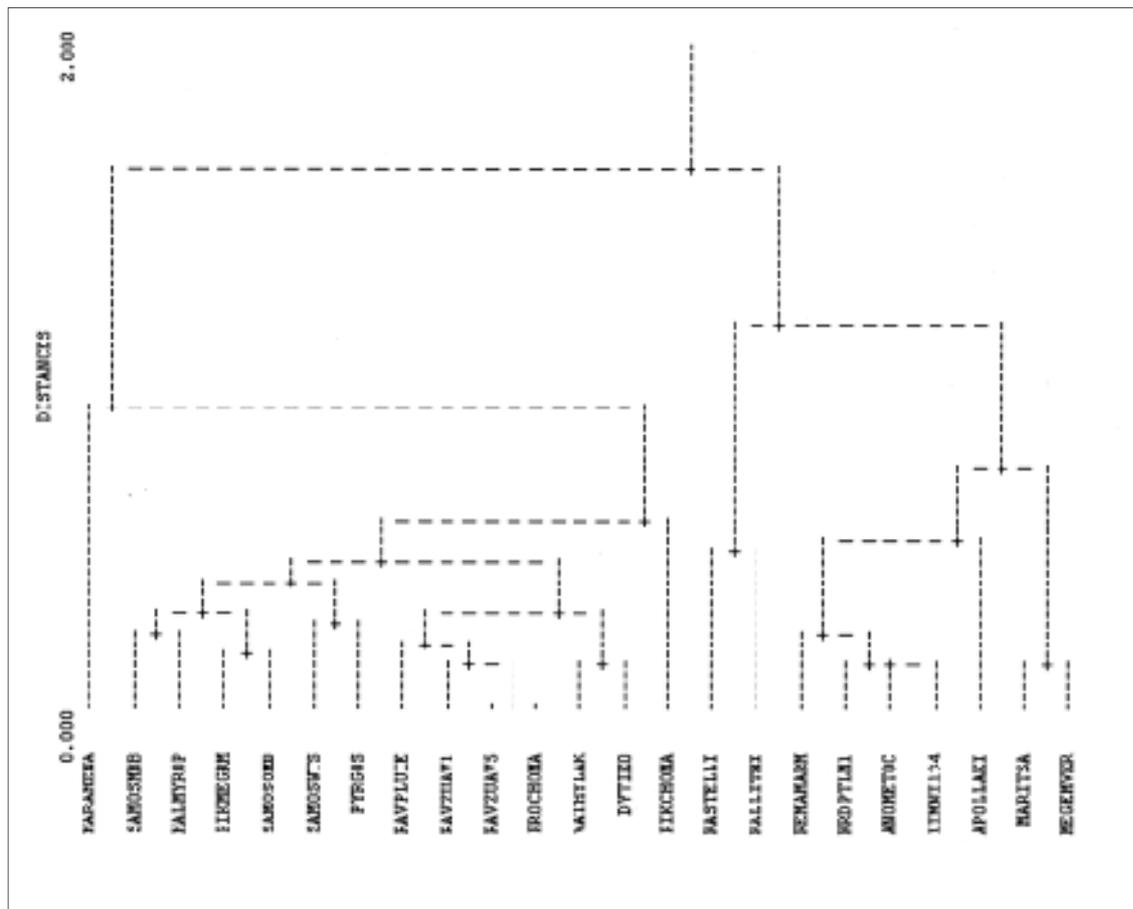


Figure 2 Cluster analysis tree diagram of Greek Neogene faunas studied. Distance metric is I-Gamma coefficient. Average linkage method.

Pyrgos interchanges groups as outlayer in the other runs. It is not an adequately sampled and studied faunal assemblage. In Figure 2 we have the same division into two groups, with the Pyrgos fauna clustering with the MN11/12 faunas. In this dendrogram, Maramena fauna is an outlayer to the early age group. In Figure 3 we have the clearest separation of the faunas into a group dating less than or equal to MN 13 (pre-Messinian) and a group younger than MN13 (post-Messinian). The only exceptions are the Kastellios fauna, which clusters with the young faunas, and the Dytiko fauna, which clusters with the older. Finally, in Figure 4 we have a slightly different cluster arrangement, and perhaps the most realistic. While

the two pre- and post-Messinian basic faunal groupings are still distinct, the problematic faunas of the three previous patterns are outlayers to both major groupings. These five faunas are the oldest Kastellios (MN10), the Pyrgos fauna of uncertain age (MN10-12), and the Maramena, Kallithies and Megalo Emvolo faunas. In Figure 4, therefore, only the Dytiko fauna violates the clear-cut division of the 23 (or 18) faunas into a pre-Messinian and a post-Messinian group. Geographic proximity with the rest of the Axios Valley faunas played the decisive role in the Dytiko clustering.

Biased sampling of the true animal diversity in the extinct population, is a possible cause

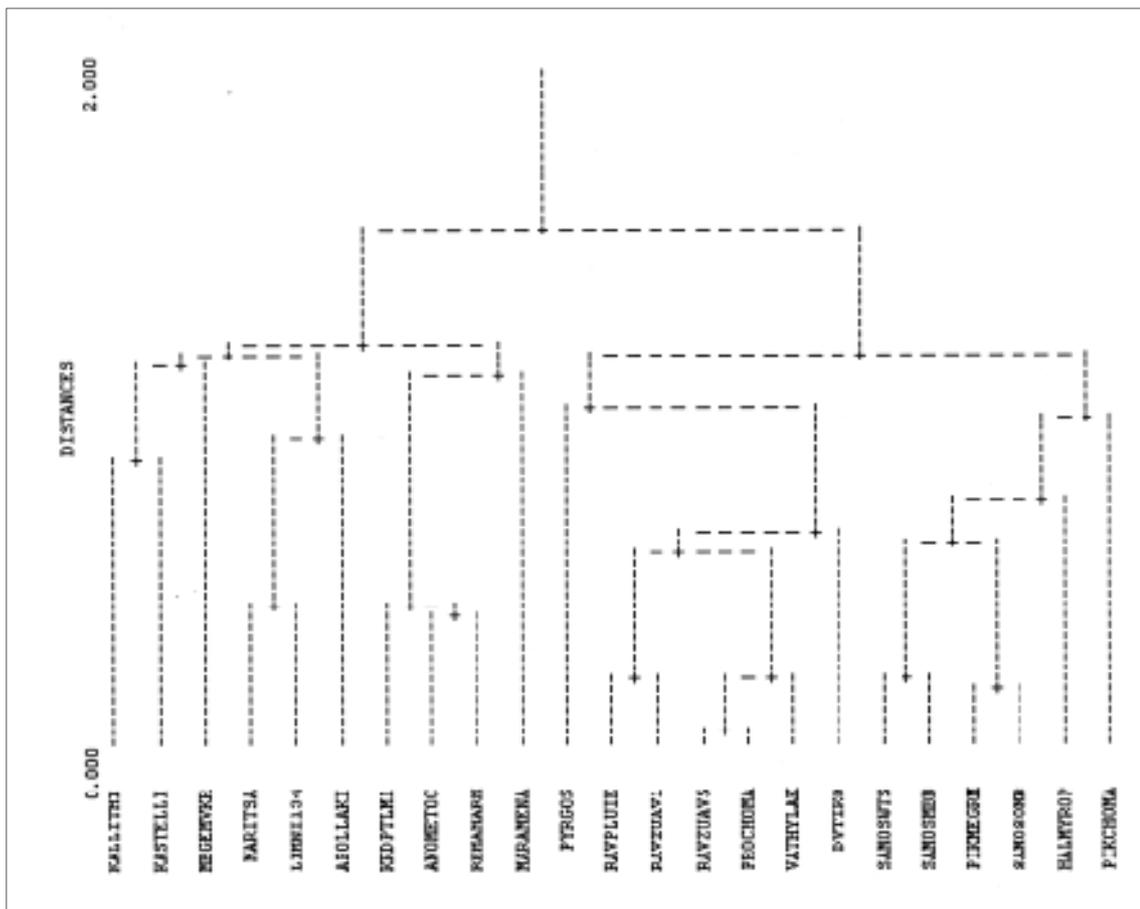


Figure 3 Cluster analysis tree diagram of Greek Neogene faunas studied. Distance metric is 1-Pearson correlation coefficient. Complete linkage method.

of sampling error; an ever-present problem in paleobiology. Sampling error cannot be excluded in the paleofaunas used in this cluster analysis. Beyond this factor, geographic and age proximity are the two factors causing the two major faunal clusters. In order to further investigate the effects the Messinian had on Greek mammal faunas, biochronological ranges of specific species of major mammalian orders have been constructed, with the MN Unit biochronological system as a reference scale. Figures 5 to 11 tabulate the MN biochronological range of 196 species, present in the 23 Greek mammal Neogene faunas. This is a recording of the presence of each species in the MN Unit range 10 to 15

and not a species FAD and LAD in the fossil record. Filling-in was used if a taxon was present in the one MN Unit before and the one after the unit where the taxon was missing. The majority of the bovids in the 23 faunas belong to MN 12. The biochronological distribution of equids and rhinos, as well as that of carnivores, range mostly between MN 11 and 13. There is an apparent considerable number of species reduction at the onset of the Pliocene. That the environment changed around the Messinian, 7-4 My ago, and that this change was caused by a trend for colder and dryer climate worldwide, has been sufficiently documented. Potts (1998) provides a complete treatment of recent data used in

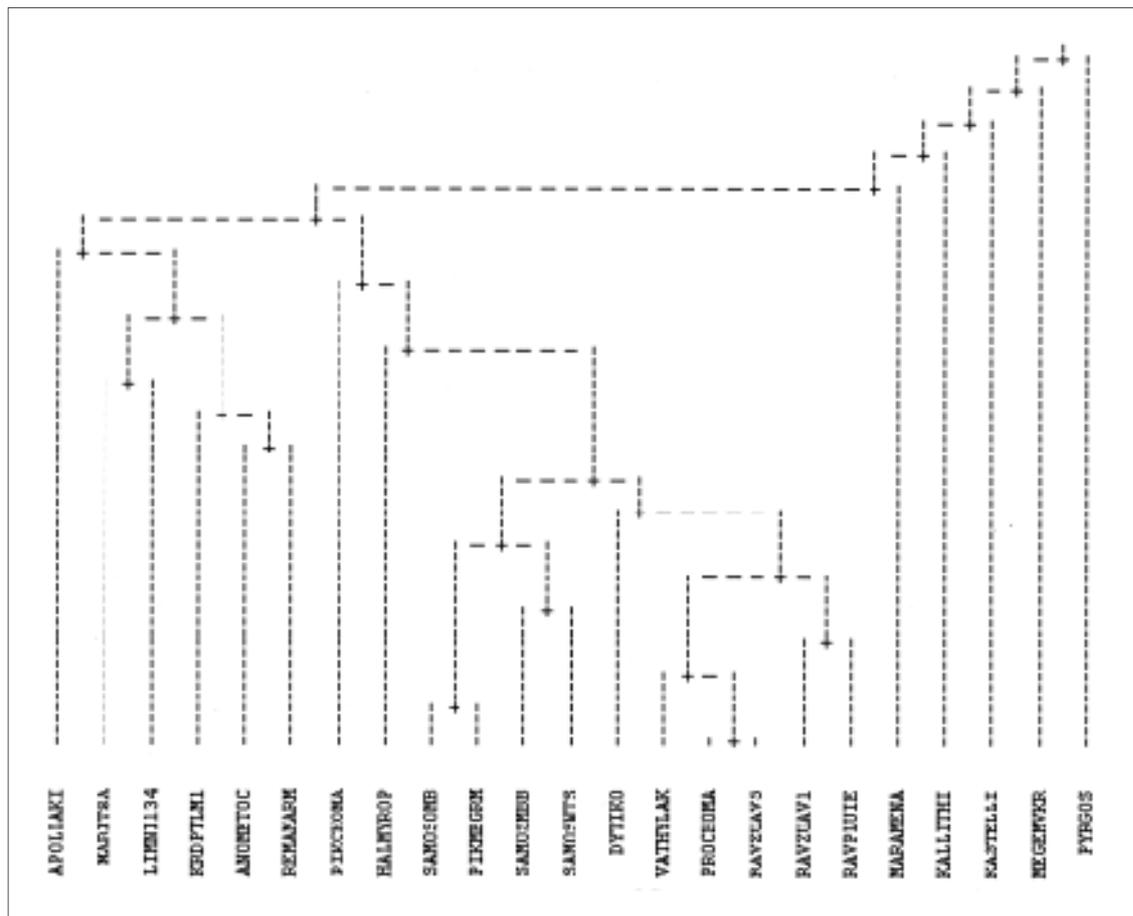


Figure 4 Cluster analysis tree diagram of Greek Neogene faunas studied. Distance metric is I-Pearson correlation coefficient. Median linkage method.

paleoenvironmental reconstruction. Environments, however, always change. And, however low is the turn-out of mammals in the Pliocene, certainly there were mammals around. No study, to my knowledge, equates the effects of the Messinian 'Event' with the major effects of the bolide impact at the end of Cretaceous. The large-mammal distribution is shown in Figures 8-11, with many species not making it after the Messinian, and few new ones appearing. In addition to the known environmental changes after the Messinian mentioned above, this is also due to sampling error and to poor taxonomic identification for some faunal assemblages collected long ago.

Finally, looking at the micromammals (Figs. 5-7), their record in the Greek Neogene is better than that of the large mammals. Moreover, small mammals are environmental indicators. The disadvantage is that they can only tell the environment in a small area. The record of Insectivora is mostly pre-Messinian. *Blarinella* and *Crocidura* have a late presence in Apollakia. Squirrels of all three types are present (flying, tree and ground). The flying squirrel *Hylopetes* is present in Maramena (MN13), and *Tamias* is present in ? post-Messinian Ano Metochi (MN13-14). Most of the Cricetidae and Muridae do not generally support a single widespread dry or wet environment after the

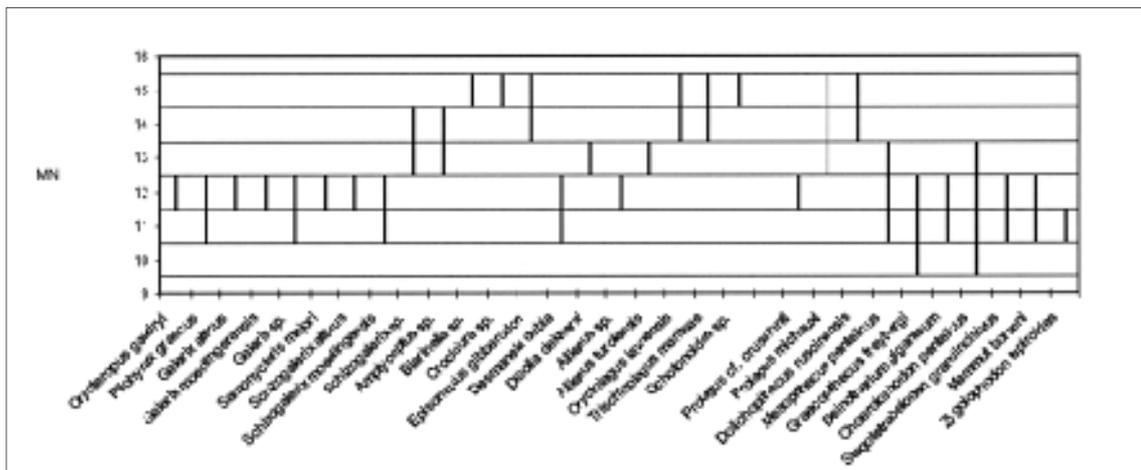


Figure 5 Biochronological range in MN Units of specific Insectivora, Lagomorpha, Primates and Proboscidea present in the studied Greek Neogene faunas.

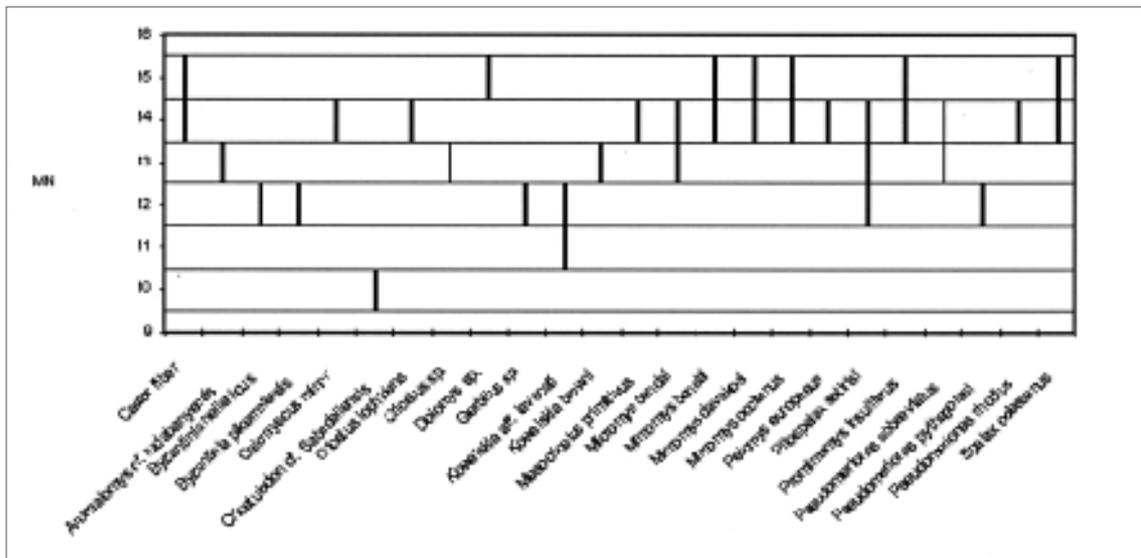


Figure 6 Biochronological range in MN Units of specific Cricetidae (Rodentia) present in the studied Greek Neogene faunas.

Messinian. Instead, the rodents tell us that there were trees, as well as open country, dry sandy ground, wet, as well as dry environments in the area before, during, and after the Messinian. This is supported also by paleobotanical studies in the Greek mainland (Velitzelos 1995). It is obvious today (due to the multidisciplinary research done) that the Messinian effect on the circum-Mediterranean area is more complex than was previously

believed. It is now known that it was not a single and short-lived event. The effects, therefore, to the mammalian faunas must also be far more complex than a direct simple effect on them by a unique, unidirectional trend of environmental change. More scientific data out of fieldwork and a study of paleontological museum collections work will further explain the Messinian phenomenon and its effects on the Greek Neogene mammal faunas.

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