New excavations in the Neogene mammalian localities of Mytilinii, Samos Island, Greece

George D. KOUFOS, George E. SYRIDES, Dimitris S. KOSTOPOULOS, Kalliopi K. KOLIADIMOU, Ioanna A. SYLVESTROU, George Ch. SEITANIDIS and Theodora D. VLACHOU

Aristotle University of Thessaloniki, Department of Geology and Physical Geography, Laboratory of Geology and Palaeontology, 54006 Thessaloniki (Greece)

Koufos G. D., Syrides G. E., Kostopoulos D. S., Koliadimou K. K., Sylvestrou I. A., Seitanidis G. Ch. & Vlachou T. D. 1997. — New excavations in the Neogene mammalian localities of Mytilinii, Samos Island, Greece. *Geodiversitas* 19 (4): 877-885.

ABSTRACT

KEY WORDS mammals, stratigraphy, Late Miocene, Turolian, Greece. In the present article the first data from the new campaign of excavations in the Neogene mammalian localities of the Mytilinii Basin (Samos island, Greece) are given. The faunal composition of five different fossiliferous sites, as well as the first stratigraphic and biochronological data on their deposits are also presented. The mammal faunas newly collected in five sites are all early-middle Turolian age.

RÉSUMÉ

MOTS CLÉS mammifères, stratigraphie, Miocène supérieur, Turolien, Grèce. Dans cet article sont présentés les premiers résultats des nouvelles recherches sur les localités de mammifères de Samos. La composition faunique de cinq gisements fossilifères, ainsi que la stratigraphie des dépôts sédimentaires de la région permettent de proposer des corrélations avec la biochronologie mammalienne de l'Europe. Les nouvelles faunes que nous avons récoltées dans cinq sites à Samos sont datées du Turolien inférieur et moyen.

INTRODUCTION

The fossiliferous deposits of the Mytilinii Basin in Samos island were known since the second half of the last century (Forsyth Major 1894). A great amount of mammalian fossils has been unearthed from several localities, housed now in various museums of Europe and United States. Numerous papers referring to fossils, stratigraphy and chronology of the Mytilinii Basin have been published. However, the main problem, when the old collections are concerned, is that fossils collected from different localities are mixed. As a result, it is difficult, or at least doubtfull, to correlate mammalian taxa with the localities and consequently with the local stratigraphy. Sometimes the number of the determined species from one locality is very high. For example, the faunal list of Quarry 1 (Q1) enumerates sixteen species of bovids (Solounias 1981), a number which is unusual for a single locality. In the Late Miocene localities of Macedonia, Greece, the maximum observed number of bovids is seven in the locality "Ravin des Zouaves 5" RZO (Bonis et al. 1992). Most of the old collectors of Samos were not palaeontologists and they collected fossils for selling them. So the informations on the exact locality where they have been found remain very poor. Brown's collection has locality indications but the relocation and correlation of the old quarries with the recent collections are questionable. Solounias (1981) tried to relocate the old fossil quarries and to identify the collections and taxa related to them in different museums and universities in Europe and United States; consequently, he established faunal lists for most of the old fossil quarries. More recently Bernor et al. (1996) used these relocations to propose correlations of the Samos faunas with the European Neogene mammal chronology. Some micromammals collected from two sites of the basin with clear locality indications are also known (Black et al. 1980).

Prof. J. Melentis excavated in 1963 in the Andrianos ravine and his collection is now stored in the Mytilinii Museum. In the same locality the first author (G. D. K.) was digging in 1986, together with Prof. J. Melentis. This locality is named as MTLA in the present paper.

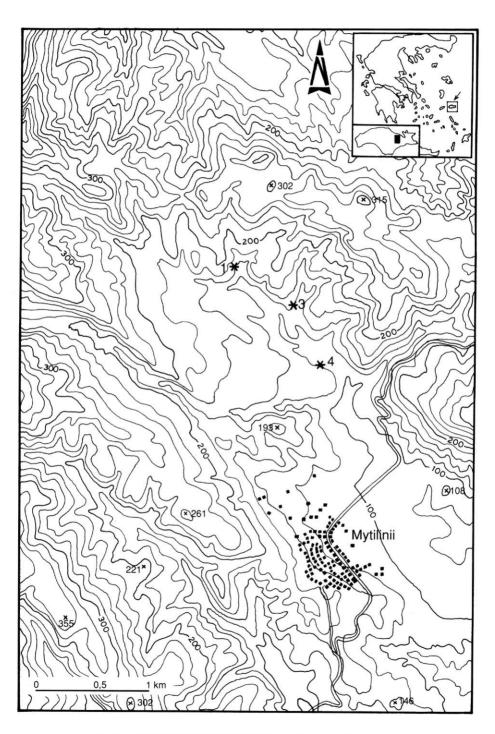
Concerning the age of the Samos fauna there are also different opinions. According to Gentry (1971) and Sondaar (1971) there are two different faunas in the Samos material, dated as early and late Turolian. Solounias (1981) considers that the Mytilinii Formation, including the fossiliferous layers, was deposited in a very short time interval and that the faunal differences are due to seasonal or very minor time differences or to ecological changes.

The mixing of the Samos material, the difficulties in the relocation of the old quarries and consequently of their stratigraphic position, as well as their questionable correlation with the old collections, raise a series of problems, doubts and questions related with systematics, faunal composition, chronology and palaeoecology.

Considering all the above mentioned problems, it is necessary to have new collections from certain fossiliferous levels which can provide more precise stratigraphic information. For this reason we decided to start our work in Samos from "zero point" with a new series of excavations, together with a detailed study of the stratigraphy. Our field work started in 1993 and an extensive prospection allowed us to locate several fossiliferous sites. During 1994 and 1996, excavations in some of them were decided, while a new study of the stratigraphy was initiated in 1996. This paper presents new data on the mammal localities and their faunal content, along with some stratigraphical and biochronological observations.

LOCALITIES

The localities in which excavations were carried out are situated NW of the village of Mytilinii (Fig. 1). In Adrianos ravine – ravine of Stefanidis according to Melentis (1969) – three different fossiliferous sites have been recognized. The locality was named "Mytilinii 1", MTL and its three sites are abbreviated as MTLA, MTLB and MTLC. The latter two sites are new. Their stratigraphical relationships are discussed below. Two other fossiliferous sites were found in the ravine of Potamies and were named "Mytilinii 3" (MYT) and "Mytilinii 4" (MLN; Fig. 1). Several



 $\label{eq:Fig.1.} \textbf{Fig. 1.} \textbf{— Topographic map of the Mytilinii area with the fossiliferous sites.}$

scattered bones have also been found in various sites of the basin but without enough concentration to be investigated. According to the relocation of the old quarries given by Solounias (1981), the locality MTL is probably equivalent to Q1 or QA, while MYT and MLN possibly correspond to Q3 and Q4 respectively.

STRATIGRAPHY

The Neogene stratigraphy of the Mytilinii Basin was studied by several authors (Meissner 1976; Theodoropoulos 1979; Solounias 1981; Weidmann *et al.* 1984). According to the last two papers, the Neogene deposits of the area are divided in five formations. Fossil bones are found in the Mytilinii Formation and more precisely in its two members "Old Mill Beds" and "Main Bone Beds".

Our aim is to study the detailed stratigraphy of the fossiliferous area and to locate the relative position of the various fossiliferous sites from which we collected fossils. The study of the local stratigraphy is very difficult because the area is strongly faulted of and marked lateral facies changes make difficult to follow lithologic horizons. Moreover, the alternation of beds with similar lithology makes the conditions more complicated. We begin to study various outcrops starting with those in which the localities "Mytilinii 1" (MTL) and "Mytilinii 3" (MYT) were found.

The "Mytilinii 1" (MTL) outcrop is situated in Adrianos ravine about 2.5 km NW of the village of Mytilinii (Fig. 1). At the base, the deposits consist of sands and silts with lenses of rounded pebbles from the preneogene basement, of volcanic rocks and of the older Neogene marly limestones (Fig. 2). This lithology is continuing toward the top of the outcrop with several intercalations of marly limestones and volcanoclastics. A fault cuts the outcrop and provides difficulties to follow laterally the fossiliferous level. In the northwestern bank of the ravine the bones are situated near the bottom of the ravine (Fig. 2) in a hard silty sandstone (MTLA). In 1996, in a higher level about 5-6 m above MTLA, the remains of an old excavation have been found.

from which several bones sometimes complete, have been collected. These remains indicate that the old excavators were only interested in collecting skulls and mandibles, while they broke and disposed of the others; consequently, their collections are selected and biased. In the south-eastern flank of the ravine, two fossiliferous sites have been discovered: one at the bottom of the ravine (MTLC) and another near the top, about 25 m higher than the first one (MTLB). Taking into account all these observations, two hypotheses are possible: (1) if there is not any fault along the Andrianos ravine, three different fossiliferous levels should have occured; (2) if there is a fault, at least two different levels can be distinguished. This situation confirms the difficulties to correlate the old fossiliferous sites. The old material labelled as Q1 or QA was probably collected from our locality MTL. But the question whether Q1 and QA belong, or not, to the same horizon is still open. If they are stratigraphically

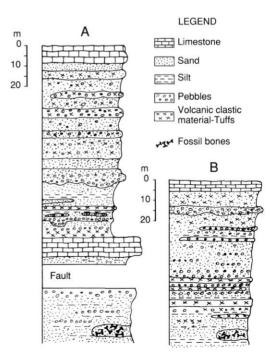


Fig. 2. — Stratigraphic column of "Mytilinii 1", MTL (A) and "Mytilinii 2", MYT (B) outcrops.

different, which of them can be correlated with the fossiliferous sites of MTL? In Kemiklitepe, Turkey, two fossiliferous levels with a height difference of less than 15 m have been dated as MN11 and MN12 respectively (Sen *et al.* 1994). It is also interesting to note that the localities MTLA and MTLB yielded some cores of land snails (Helicidae).

The other outcrop "Mytilinii 3" (MYT) is situated in the area of Potamies, about 2 km from the village of Mytilinii (Fig. 1). The lithology is similar to that of MTL, with sands and silts, and intercalations of volcanoclastics and marly limestones. However, the coarse material predominates in the MYT outcrop. The horizon with bones is situated near the bottom of the outcrop.

FAUNA

VERTEBRATE TAXA

The collected and prepared material from MTLA includes complete skulls and mandibles of rhinocerotids, ictitheres, bovids and suids, as well as several complete postcranial elements allowing a quite accurate determination. The sample from MYT is not so good, but the occurence of some taxa is well argued. From the other localities found during the last field campaign, only few specimens have been unearthed; they are often badly preserved because of the surface weathering. These localities will be better investigated in the future. The determination of the available material from each locality gives the following faunal lists:

MTLA. Pseudomeriones cf. pythagorasi, Promeles sp., Hyaenotherium wongii, Orycteropus gaudryi, Hipparion cf. proboscideum, Hipparion sp., Dicerorhinus pikermiensis, Microstonyx major, Samotherium boissieri, Miotragoceros monacensis, Tragoportax cf. rugosifrons, Gazella sp., Protoryx carolinae, Pseudotragus parvidens, Antilopinae indet., Bovidae indet.

MTLB. Hipparion sp., Dicerorhinus cf. piker-miensis, Samotherium boissieri.

MTLC. Hipparion sp., Dicerorhinus sp., Samotherium boissieri.

MYT. Hipparion sp., Hipparion cf. proboscideum, Dicerorhinus cf. pikermiensis, Samotherium bois-

sieri, Protoryx cf. laticeps, Protoryx sp., cf. Pseudotragus.

MLN. Hipparion sp., ? Protoryx sp., ? Tragoportax sp.

The presence of *Pseudomeriones* in MTLA is significant because small mammals have been found together with the large ones for first time in Samos mammal localities. This taxon is already known in Samos from the sites S2-3 from which N. Solounias washed sediments (Black *et al.* 1980). Our material consists of an hemimandible with m1-2, a right m1 and a right M1; we plan to pursue washing-screening more sediment from MTLA during the next field season in order to check if there are more micromammals or if they are accidentaly occuring.

INVERTEBRATE TAXA

During the stratigraphic investigation in various places on the field, several invertebrate fossils have been collected: in the limestones of Ano Vathy, Planorbis sp., ? Melanopsidae indet. and ? Lymnaeidae indet.; in the limestones east of Pythagorion, Melanopsidae indet; in the mammal localities MTLA and MTLB some cores of Helicidae indet.; Brotia cf. graeca (Stefani) in the lime-stones with Phragmites of Stefana Hill, near Mytilinii; in the marls and limestones, near the village of Mavratzei, Planorbis sp. and Lymnaeidae indet.; in the green marls north of Mavratzei a small faunule with Bithynia sp., ? Lymnaea sp., ? Planorbis sp. and Hydrobiidae indet. Another small faunule including Hydrobiidae indet., Planorbis sp. and ostracodes has been found in the limestones near the monastery of Timiou Stavrou.

COMPARISON OF THE FAUNA

The MTLA collection is the richest one and good comparisons can be drawn with other equivalent aged localities. The carnivores are represented by a skull and some mandibular remains of an ictithere refered to as *Hyaenotherium wongii* based on the morphology and size. The skull and mandible from MTLA is similar to those of "Ravin des Zouaves 5" and Vathylakkos 2, 3 in Axios Valley dated to early Turolian. An isolated m1 is reported to *Promeles* sp. It has the typical morphology of *Promeles* from Pikermi but it is

slightly longer. The rhinocerotids are well represented in the MTLA material by skulls, mandibular fragments and postcranial elements. Their morphology shows strong resemblance to that of Dicerorhinus pikermiensis from Pikermi. The hipparions are poorly represented and the material consists of some maxillary and mandibular remains and postcranial elements. The occurrence of two species is supposed. A large one is metrically close to H. proboscideum, but because of the lack of cranial remains it is referred to as H. cf. proboscideum. Some other hipparion remains correspond to small to middle-sized species. They represent either one species with its extremes values or two species. More material is needed to check their systematic position, hence their attribution to Hipparion sp. Abundant postcranial bones of giraffids have been found in MTLA, and all belong to Samotherium boissieri, the well-known giraffid of Samos. The bovids are numerous and some of them are represented by well preserved skulls and other cranial remains. Their preliminary comparison with those from the Late Miocene localities of Axios Valley, Macedonia, Greece, suggests similarities with the early Turolian forms.

CHRONOLOGY OF SAMOS FAUNA

As we mentioned above, controversial opinions have been expressed about the age and time span of the Samos mammal faunas. The initial opinion envisaged that there are two different faunas dated as early Turolian (MN11) and late Turolian (MN13) respectively (Gentry 1971; Sondaar 1971). It is necessary to mention here that van Couvering & Miller (1971) have calculated, for the tuffs included in the Mytilinii Formation, an approximate K/Ar age of 8.5 Ma (early Turolian). The other opinion is that the Turolian mammals from Samos localities might be considered as belonging to a single fauna, while the Mytilinii Formation which includes the fossiliferous beds was accumulated in less than 0.5 Ma (Black et al. 1980; Solounias 1981). Later on, Weidmann et al. (1984) provided several K/Ar datings on sanidines and biotites from different tuffaceous horizons of the Mytilinii Formation, and thus showed that the fossiliferous horizons are bracketed between 8.5 and 6.2 Ma, which means a duration of more than 1.5 Ma for the Samos faunas. In the recent calibration of the MN zones (Steininger *et al.* 1996), this time interval recovers MN11, MN12 and the base of MN13. The magnetostratigraphic study of the upper part of the Mytilinii Formation suggests that the upper mammalian fossiliferous levels are included in the time span from 6.4-6.1 Ma (Sen & Valet 1986). Using the single crystal 39 Ar/ 40 Ar dating on sanidine, the lower fossiliferous level ("Old Mill beds") was dated as 8.33 ± 0.05 Ma and the upper fossiliferous level ("Main Bone Beds") as > 7.1 Ma (Swisher III 1996).

The available new material from Samos localities is still insufficient to give complete biochronological results. However the material from MTLA is abundant enough to be compared with other localities and to provide information about the age of the locality. The MTLA fauna is compared at specific level (Table 1) with two sets of faunas, both from recent excavations and with precise stratigraphical informations. The first set includes the faunas of two localities in Macedonia, Greece, "Vathylakkos 3", VAT and "Ravin des Zouaves 5", RZO; both have been dated as early Turolian, MN11 (Bonis et al. 1988; Koufos 1990). The other set includes the localities "Kemiklitepe D", KTD and "Kemiklitepe A-B", KTA-B from western Turkey; the first one is dated as early Turolian (MN11) while the second as middle Turolian (MN12) (Bonis et al. 1994; Sen et al. 1994).

The composition of the MTLA fauna presents strong similarities with those of Kemiklitepe localities, suggesting an early-middle Turolian age (Table 1). Its comparison with that of RZO shows that half of the genera recognized in MTLA occurred also in RZO, while several species are shared with both faunas (Table 1). The similarity of the MTLA fauna, both at generic and specific levels with that of 'Vathylakkos 3" is also remarkable; among others we stress the presence of Samotherium boissieri in both localities (Table 1) as demonstrative. Consequently, an early Turolian age is possible for the MTLA fauna. The material from the locality MYT is still poor, although it shares faunal similarities with MTLA.

Table 1. — Faunal composition of MTLA in comparison with other Turolian localities from eastern Mediterranean. The names of the localities are abbreviated as: MTLA, Mytilinii 1A, Samos Island; VAT, Vathylakkos 3, Macedonia, Greece; RZO, Ravin des Zouaves 5, Macedonia, Greece; KTD, KTA-B, Kemiklitepe, sites D and A-B in western Turkey.

Genera	Species	MTL-A	VAT	RZO	KTD	KTA-B
Mesopithecus	delsoni	_	120	+	_	_
Mesopithecus	pentelicus	_	cf.	_	_	_
Pseudomeriones	pythagorasi	cf.	_	-	_	sp.
Hystrix	primigenia	_	_	-	_	+
? Indarctos	, ,	_	-	_	_	+
Plesiogulo	crassa	_	+	-	-	_
Promeles	sp.	+	_	_	_	_
Plioviverrops	orbignyi	-	+	_	_	_
Plioviverrops	guerini	-	cf.	_	_	_
lctitherium [*]	viverrinum	_	+	+	_	_
Hyaenotherium	wongii	+	+	+	_	+
Lycyaena		_	_	_	_	sp.
Adcrocuta	eximia	-	+	+	_	+
Chasmaporthetes	bonisi	_	_	+	_	_
Machairodus	aphanistus	_	sp.	sp.	+	_
Orycteropus	gaudryi	+	_	_	_	+
Choerolophodon	pentelici	-	+	+	+	+
Zygolophodon	turicensis	sp.	_	+	-	-
Pliohyrax	graecus	-	-	-	sp.	+
Hipparion	proboscideum	cf.	-	+	-	-
Hipparion	dietrichi	-	+	+	-	-
Hipparion	macedonicum	-	+	+	_	_
Hipparion	mediterraneum	_	_	_	+	+
Hipparion	matthewi	-	_	-	?	+
Hipparion	sp. (small-sized)	+	_	-	+	?
Macrotherium	macedonicum	-	+	-	_	_
Ancylotherium	pentelicum	-	_	-	_	cf.
Aceratherium	500000000 4 00000	_	sp.	-	-	_
Chilotherium	persiae	-	_	_	aff.	? sp.
Dicerorhinus	pikermiensis	+	-	-	? +	_
Ceratotherium	neumayri	-	+	+	+	+
Microstonyx	major	+	+	+	_	_
Propotamochoerus	hysudricus	-	_	+	_	_
Dorcatherium	puyhauberti	-	+	_	_	
Palaeotragus	rouenii	-	-	+	+	+
Samotherium	boissieri	cf.	+	-	aff.	_
Samotherium	major	_	_	_	_	+
Helladotherium Bablinia	duvernoyi	_		+	_	_
Bohlinia Transportan	attica	-	+	_	_	_
Tragoportax	rugosifrons	cf.	+	+	_	_
Prostrepsiceros	zitteli	-	+	+	_	_
Prostrepsiceros	rotundicornis	-	_	+	100	_
Nisidorcas Gazella	planicornis	-	+	+		_
Gazella Gazella	pilgrimi	_	+	+		_
	sp.	+	, — ,	+	_	cf.
? Oiceros Palaeoreas	wegneri lindermayeri	_	+	_	_	CI.
Palaeoreas	zouavei	_	_	+	_	_
Palaeoreas Palaeoreas	elegans	_	_	_	cf.	_
Criotherium	argalioides	_	_	_		=
Protoryx	carolinae	_	en.	cn.	+	_
		+	sp.	sp.	_	+
Protoryx	laticeps					

The material from the other Samos localities. newly discovered, is still poor and the determinations preliminar. Nevertheless, they all contain typical Turolian taxa. In the future field work, we plan to pursue the excavations in different localities, along with detailed stratigraphy of the fossiliferous deposits. Our main aim is to provide reliable faunal associations correctly placed in the local stratigraphy in order to establish a biochronologic scale of the fossiliferous deposits in Samos island.

Acknowledgements

The new campaign of excavations in Samos would not have begun without the financial support of the Konstantinos and Maria Zimalis Foundation; for this reason we gratefully thank the Council of the Foundation and its president E. Zimalis. Many thanks to the Prefecture of Samos and to the prefect, Mr P. Vardikos, for the financial support given us in 1996 (Project No. 4623). Thanks also to the Community of Mytilinii, to the Major P. Konstantinidis and to the former Major K. Kaplantzis for their help. We wish to thank Prof. A. Psilovikos for his help during the excavations. There are many other persons and villagers who helped us during our work in the area, we thank all of them. Many thanks to Dr S. Sen for the usefull comments on the manuscript. The first author wish to express his warmest thanks to Mrs Stella Psilovikos and to Christos and Eutychia Seitanidis for their great hospitality during all his visits in Samos since the beginning of the 80's.

REFERENCES

Bernor R. L., Solounias N., Swisher III C. C. & van Couvering J. A. 1996. — The correlation of three classical "Pikermian" mammal faunas - Maragheh, Samos, Pikermi – with the european MN unit system: 137-156, in Bernor R. L., Fahlbusch V. & Mittmann H. W. (eds), The Evolution of Western Eurasian Neogene Mammal Faunas. Čolumbia University Press.

Black C., Krishtalka L. & Solounias N. 1980. — Mammalian fossils of Samos and Pikermi. Part 1. The Turolian rodents and insectivores of Samos. Annals of the Carnegie Museum 49: 359-378.

Bonis L. de, Bouvrain G. & Koufos G. D. 1988. – Late Miocene mammal localities of the lower Axios valley (Macedonia, Greece) and their stratigraphical significance. Modern Geology 13: 141-147.

Bonis L. de, Bouvrain G., Geraads D. & Koufos G. D. 1992. — Diversity and palaeoecology of Greek late Miocene mammalian faunas. Palaeogeography, Palaeoclimatology, Palaeoecology 91: 99-121.

Bonis L. de, Bouvrain G., Geraads D., Koufos G. D., Sen S. & Tassy P. 1994. — Les gisements de mammifères du Miocène supérieur de Kemiklitepe, Turquie: 11. Biochronologie, paléoécologie et relations paléobiogéographiques. Bulletin du Muséum national d'Histoire naturelle, Paris, série 4, C 16 (1): 225-240.

Brown B. 1927. — Samos - Romantic Island of the Aegean. Natural History, New York 27: 19-32.

Forsyth Major C.-J. 1894. — Le gisement fossilifère de Mytilini et catalogue d'ossements fossiles : 1-15.

Gentry A. W. 1971. — The earliest goats and other antelopes from the Samos Hipparion fauna. Bulletin of the British Museum of Natural History,

Geology 20: 231-296. Koufos G. D. 1990. — The hipparions of the lower Axios valley (Macedonia, Greece). Implications for the Neogene stratigraphy and the evolution of hipparions: 321-338, in Lindsay E., Fahlbusch V. & Mein P. (eds), European Neogene Mammal Chronology. Plenum Press.

Meissner B. 1976. — Das Neogen von Ost-Samos. Sedimentationsgeschichte und Korrelation. Neues Jahrbuch für Geologie und Paläontologie Abhandlung B 152: 161-176.

Melentis J. 1969. — Paläontologische ausgrabungen auf der insel Samos (eine vorläufige mitteilung). Proceedings of the Academy of Athens 43: 344-346.

Sen S. & Valet J. P. 1986. — Magnetostratigraphy of late Miocene continental deposits in Samos, Greece. Earth and Planetary Science Letters 80: 167-174.

Sen S., Bonis L. de, Dalfes N., Geraads D. & Koufos G. D. 1994. — Les gisements de mammifères du Miocène supérieur de Kemiklitepe, Turquie : 1. Stratigraphie et magnétostratigraphie. Bulletin du Muséum national d'Histoire naturelle, Paris, série 4, C 16 (1): 5-17.

Solounias N. 1981. — The Turolian fauna from the island of Samos, Greece, with special emphasis on the Hyaenids and the Bovids. Contributions to Vertebrate Evolution 6: 1-232.

Sondaar P. Y. 1971. — The Samos Hipparion. Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen B 74: 417-441.

Steininger F. F., Berggren W. A., Kent D. V., Bernor

R. L., Sen S. & Agusti J. 1996. — Circum Mediterranean Neogene (Miocene and Pliocene) marine continental chronologic correlations of European Mammal Units: 7-46, in Bernor R. L., Fahlbusch V. & Mittmann H. W. (eds), The Evolution of Western Eurasian Neogene Mammal Faunas. Columbia University Press.

Swisher III C. C. 1996. — 40År/39Ar dating of some key European and west Asian late Miocene age vertebrate localities and their contribution to mammal Neogene (MN) correlations: 64-77, in Bernor R. L., Fahlbusch V. & Mittmann H. W. (eds), The Evolution of Western Eurasian Neogene Mammal Faunas. Columbia University Press.

Theodoropoulos D. 1979. — Samos Island, Geological Map 1:50.000, with explanations. Institute of Geology and Mining Research, Athens.

Van Couvering J. A. & Miller J. A. 1971. — Late Miocene marine scale and non-marine time scale in Europe. *Nature* 230: 559-563.

Weidmann M., Solounias N., Drake R. & Curtis G. 1984. — Neogene stratigraphy of the eastern basin, Samos island, Greece. Geobios 17: 477-490.

Submitted for publication on 19 June 1997; accepted on 2 September 1997.