

The Late Miocene Mammal Faunas of the Mytilinii Basin, Samos Island, Greece: New Collection

4. Micromammals

by

Katerina Vasileiadou¹⁾ & Ioanna A. Sylvestrou²⁾

VASILEIADOU, K. & SYLVESTROU, I.A., 2009. The Late Miocene Mammal Faunas of the Mytilinii Basin, Samos Island, Greece: New Collection. 4. Micromammals. — Beitr. Paläont., 31:37–55, Wien.

Abstract

The small number of micromammalian fossils found in the Samos Middle Turolian localities MTLA and MTLB are identified as *Pseudomeriones pythagorasi*, ‘*Karnimata*’ *provocator*, *Spermophilinus* cf. *bredai* and *Pliospalax* cf. *sotirisi*. The presence of these species on Samos gives additional information on the size and morphological variation within the species, which are known only from a few localities (*Spermophilinus bredai* excepted). Additionally, three of them suggest a dry, open environment for Samos during the Middle Turolian.

Keywords: Late Miocene, Samos, Greece, Micromammals, Systematics.

Zusammenfassung

Unter den wenigen Kleinsäugerfunden aus mittelturolianischen Fundstellen (MTLA und MTLB) aus Samos konnten *Pseudomeriones pythagorasi*, ‘*Karnimata*’ *provocator*, *Spermophilinus* cf. *bredai* und *Pliospalax* cf. *sotirisi* identifiziert werden. Die Anwesenheit dieser Arten ergibt zusätzliche Informationen über die Größe und die morphologische Variation innerhalb dieser Arten, die nur aus einigen Lokalitäten bekannt sind (mit Ausnahme von *Spermophilinus bredai*). Drei Taxa sprechen für eine trockene offene Landschaft auf Samos während des mittleren Turoliums.

Schlüsselworte: Obermiozän, Samos, Griechenland, Kleinsäuger, Systematik.

1. Introduction

Samos Island has some of the richest known late Miocene mammal localities of Greece and Europe. Even though the Samos collection of macromammals is extremely large, the micromammalian fossils are certainly underrepresented. Most of them, coming from the micromammalian locality S3, were reported by BLACK et al. (1980). The recent sampling expeditions, organised since 1990 by Prof. G. Koufos [Geology Department, Aristotle University of Thessaloniki Greece (AUTH)], have yielded a small number of micromammalian fossils from the fossiliferous localities MTLA and MTLB. The locality S3 is located in the Potamies ravine, at the lower part of the Main Bone Beds member of the Mytilinii Formation (BLACK et al., 1980, SOLOUNIAS, 1981, SWISHER, 1996; BERNOR et al., 1996; KOSTOPOULOS et al., 2003), whereas the localities MTLA and MTLB are located in the Adrianos ravine, at the middle-upper part of the Main Bone Beds (KOUFOS et al., 1997; KOSTOPOULOS et al., 2003). The stratigraphic and sedimentologic characteristics of the region are given in KOSTOPOULOS et al. (this volume).

BLACK et al. (1980) reported the presence of one insectivore and six rodent species, one of which (*Pseudomeriones pythagorasi*) was new. The new collection includes only four of the previously reported rodents, including the gerbilline *Pseudomeriones pythagorasi*. The study of the new collection provides additional information about the presence of these four rodents in the late Miocene of Samos and the Eastern Mediterranean region.

2. Methodology

The matrix sampled has been screen-washed, through sieves of mesh size 0.5 mm. The residue was dried at room temperature. The micromammalian elements were picked

¹⁾ Dr. Katerina VASILEIADOU, Natural History Museum of the Lesvos Petrified Forest, Sigri 81103, Lesvos, Greece, e-mail: k.vasileiadou@geo.aegean.gr

²⁾ Dr. Ioanna A. SYLVESTROU, Aristotle University of Thessaloniki, Department of Geology, Laboratory of Geology & Paleontology, 54124 Thessaloniki, Greece, e-mail: sylvest@geo.auth.gr

out of the residue and studied under a light microscope at various magnifications. The measurements were taken using a Wild Photomakroskop M4000, at the Department of Geology, Aristotle University of Thessaloniki, Greece (AUTH) and are given in tenths of millimeters (0.1 mm). The teeth were photographed uncoated, using a LEO 1455VP Scanning Electron Microscope with a solid backscattered detector, at the Natural History Museum, London, United Kingdom (NHM). The drawings were made using a light microscope with a camera lucida attached, at the Department of Geology, Aristotle University of Thessaloniki (AUTH), Greece.

The terminology and the measuring method used for each taxon are according to the following authors: TONG (1989) and SEN (2001) for the Gerbillinae, VAN DE WEERD (1976) for the Murinae and Sciuridae and TOPACHEVSKI (1969) for the Spalacidae. All the material is stored at the Aegean Museum of Natural History (Samos; NHMA).

3. Taxonomy

Order: Rodentia BOWDICH, 1821

Family: Muridae GRAY, 1821

Subfamily: Gerbillinae GRAY, 1825

Genus: *Pseudomeriones* SCHAUB, 1934

Pseudomeriones pythagorasi BLACK, KRISHTALKA & SOLOUNIAS, 1980

Type species: *Pseudomeriones abbreviatus* (TEILHARD DE CHARDIN, 1926)

Holotype: m1 dex (CM 36305)

Type locality: S3 (Old collection)

Type material: M1 dex, CM 36303; M1 dex, CM 36304; M1 dex, CM 36307; M1 dex, CM 36284 - not available; m1, CM 36306 - not available; m1 dex, CM 36298.

Locality: Mytilinii-1A, B (MTLA, MTLB) Adrianos ravine, Mytilinii Basin, Samos, Greece.

Material:

MTLA: M1 sin, MTLA-1; M2 sin, MTLA-4; m1 sin, MTLA-2; m1 dex, MTLA-3; anterior part of right mandible with incisor, m1-m2, MTLA-5.

MTLB: M1 dex, MTLB-1; M2 sin, MTLB-3; M2 dex, MTLB-2; M2 dex, MTLB-4; m2 dex, MTLB-5.

Age: Middle Turolian, MN12 (late Miocene); 7.1-7.0 Ma

Measurements: The measurements are given in Table 1.

Description:

M1 (Plate 1a-b & Fig. 1.1-1.6): The anterocone is triangular in shape. The cusps are alternating from moderate to strong. The anteroloph and the neoloph are parallel to each other and oblique to the longitudinal axis of the tooth. There is a posteroloph in early stage of wear. Three main roots are present.

M2 (Plate 1c-f & Fig. 1.7-1.10): It is formed by two lobes, separated by a very deep and wide lingual sinus, which is

curved backwards at its tip, even in advanced stages of wear. The mesosinus is very shallow, wide and transverse to the longitudinal axis of the tooth. There is a posteroloph in the unworn teeth which also remains after some degree of wear. There is a strong anteroloph on the unworn specimens. There are two anterior and one posterior roots.

m1 (Plate 1g-h, j & Fig. 1.11-1.15): It is relatively wide with an advanced degree of wear. The alternation of the cuspids shows a "cricetid" pattern. The anteroconid is crescent-shaped even in advanced stages of wear. It has a strong labial arm that reaches the base of the protoconid (a character better noticeable in the new collection). The metaconid is narrower than the protoconid in early stages of wear. The lobe formed by the hypoconid and the entoconid (posterior lobe) is large. The posterolophid appears as an oblique short ridge and disappears only in advanced stages of wear.

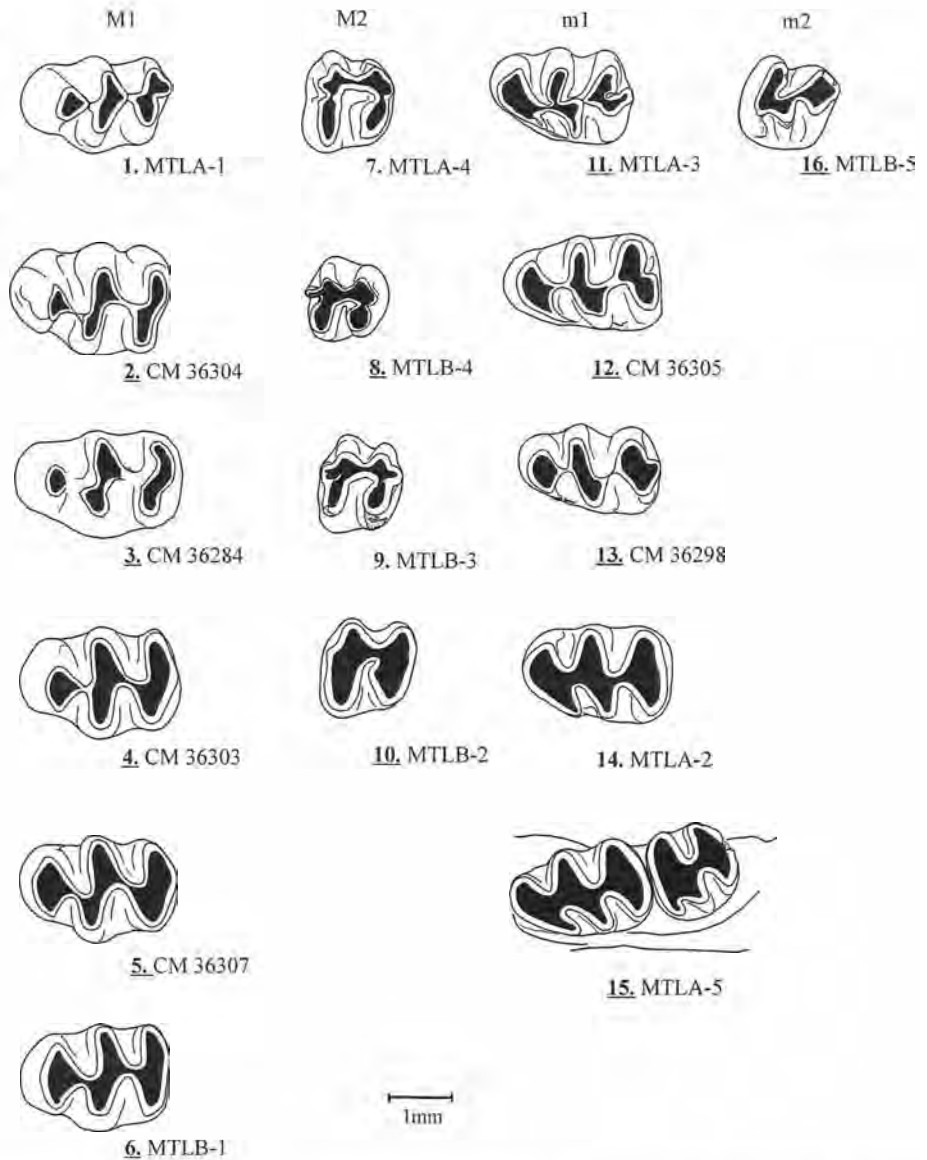
m2 (Plate 1i-j & Fig. 1.15-1.16): It is formed by two lobes. Lingually, there is a deep mesosinusid that curves strongly anteriorly in early stages of wear and becomes almost transverse in more advanced stages of wear. Labially, there are two sinusids; the protosinusid is shallower than the posterior sinusid. The protosinusid seems to become deeper with wear. In the worn teeth the antero-external cuspid, seems to be well separated and curves posteriorly.

Mandible (Fig. 2a): The anterior tip of the incisor is situated below the alveolar level of the molars. The mental foramen is situated directly under the deepest point of the diastema and is marked posteriorly by a rather strong tubercle, which

<i>Pseudomeriones pythagorasi</i>	Length	Width	Length/Width
M1			
sin MTLA-1	23.48	16.50	1.42
dex MTLB-1	24.50	17.01	1.44
dex CM36304	26.35	16.79	1.57
dex CM36307	25.92	17.16	1.51
dex CM36303	24.49	17.09	1.43
M2			
sin MTLA-4	13.44	15.53	0.87
dex MTLB-2	14.78	15.51	0.95
sin MTLB-3	13.97	15.76	0.89
dex MTLB-4	13.01	13.86	0.94
m1			
sin MTLA-2	23.40	15.12	1.55
dex MTLA-5	23.53	15.34	1.53
dex MTLA-3	22.94	15.85	1.45
dex CM 36305	24.10	14.89	1.62
dex CM36298	22.71	13.98	1.62
m2			
dex MTLA-5	15.41	15.92	0.97
dex MTLB-5	15.33	15.31	1.00

Table 1. Tooth measurements and length/width ratios of *Pseudomeriones pythagorasi* from Samos (in 10^{-1} mm).

Figure 1: Occlusal surface of *Pseudomeriones pythagorasi* molars from Samos new (MTLA, MTLB) and old (CM) collection, showing an increasing stage of wear from top to bottom. All teeth are drawn as left. The teeth which the underlined numbers are originally from the right side of the jaws. Scale bar equals 1 mm.



defines the anterior end of the strong lower masseteric crest associated with a weak upper masseteric crest.

Short Literature Review: *Pseudomeriones* appeared as early as Late Vallesian and became extinct at the end of Pliocene; it can be used in biochronology, since its evolution is relatively well-known (TONG, 1989; ZHANG, 1999). Its geographical range covers the area from Inner Mongolia to Greece via Afghanistan, Turkmenistan and Turkey (TONG, 1989; ZHANG, 1999). Reviews on the genus are given by SEN (1977, 1983, 2001), DE BRUIJN (1989), TONG (1989), AGUSTÍ (1991) and WESSELS (1998, 1999).

The most primitive species of *Pseudomeriones*, *P. latidens* SEN, 1998a (SYLVESTROU & KOSTOPOULOS, 2007) has been found in the localities Karaözü, Kaleköy, Dendil (Turkey, MN10-MN11) and Molayan (Afghanistan MN12) (SEN, 1998a, 2001; SÜMENGİN ET AL., 1990; WESSELS, 1998; SUATA-ALPAŞLAN, 2004). A slightly younger species, *P. abbreviatus* TEILHARD DE CHARDIN, 1926, shows a wide distribution and occurs frequently in the Upper Miocene and Pliocene of North China (localities: Qingyang, Yushe, Ertemte, Wenwanggou, Bilike, Ningxian) (QIU & LI, 2003), in the Latest Miocene of King-yan-fou

(type locality, Gansu, China) and the Lower Pliocene of Afghanistan (locality: Pul-e Charki) (BRANDY, 1981; SEN, 1983). One of the youngest representatives of *Pseudomeriones*, *P. tchaltaensis* SEN, 1977, has been described from the Late Ruscinian (MN15) of Çalta, Turkey (SEN, 1977, 1998b). Another species of *Pseudomeriones*, *P. hansii* SUATA-ALPAŞLAN, 2003 (in SUATA-ALPAŞLAN, in press), was described from the Early Ruscinian (MN14) of İğdeli (Turkey). Finally, *P. complicidens* ZHANG, 1999 is present in the Pliocene (early MN16) deposits of Ningxian (China) (ZHANG, 1999).

In Greece, *Pseudomeriones* shows a significant distribution, as it is quite common on both some islands and on the mainland. Four species have been described from Greece up to now. *P. rhodius* SEN, 1977 was initially described from the earliest Pliocene (MN14) of the island of Rhodes (Maritsa) (DE BRUIJN ET AL., 1970; SEN, 1977, 1983, 1990; WESSELS, 1998). It has also been reported from the Late Turolian (MN13) locality of Develi (Turkey) (SEN, 1977, 1990; SEN ET AL., 1989). *P. pythagorasi* BLACK, KRISHTALKA & SOLOUNIAS, 1980, has been described from the Late Miocene (MN12) of the island of Samos (BLACK ET AL., 1980;

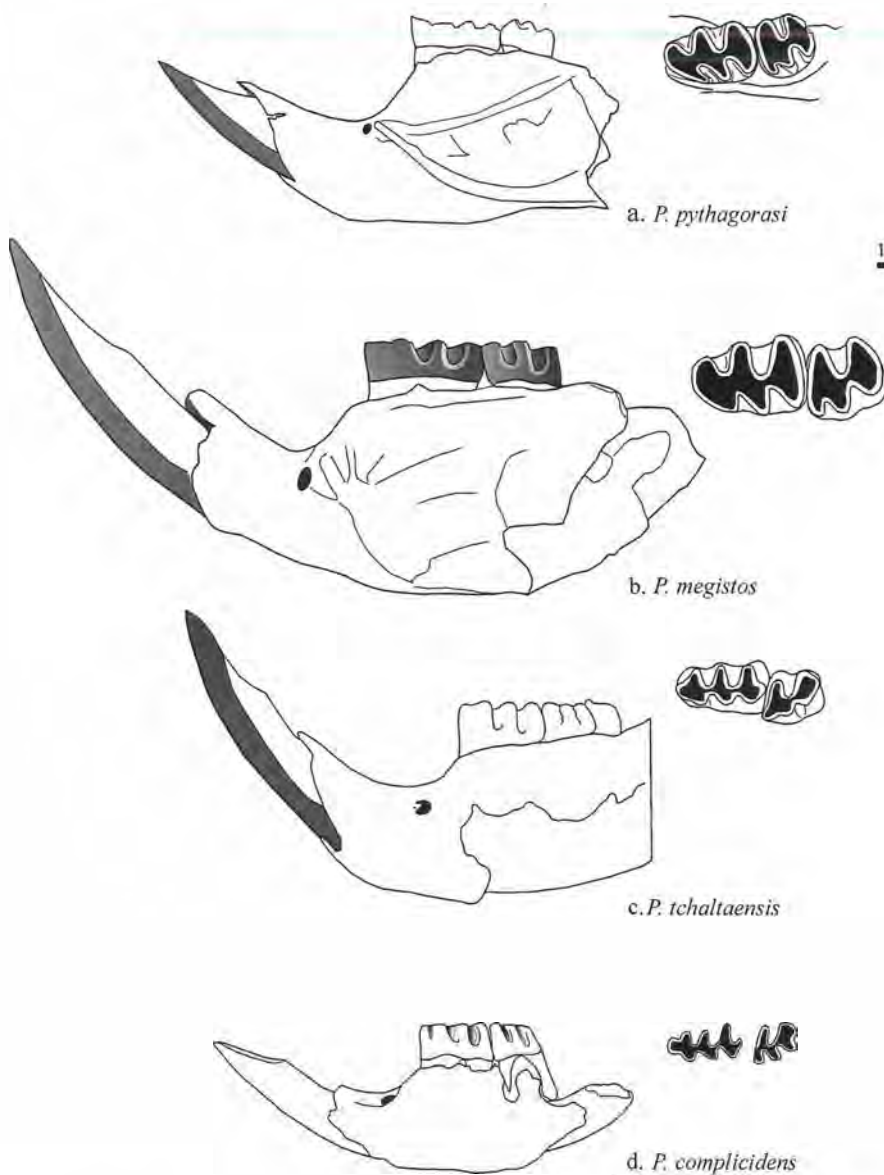


Figure 2: Side views of mandibles of some *Pseudomeriones* species. The scale bar equals 1 mm.

a) *P. pythagorasi* (Samos): (MTLA-5); b) *P. megistos*: (PLM-2, Katerini, holotype) from SYLVESTROU & KOSTOPOULOS, 2007; c) *P. tchaltaensis* (Çalta): (ACA-974) from SEN, 1977; d) *P. complicidens* (Ningxian): (V5954.2) from ZHANG, 1999.

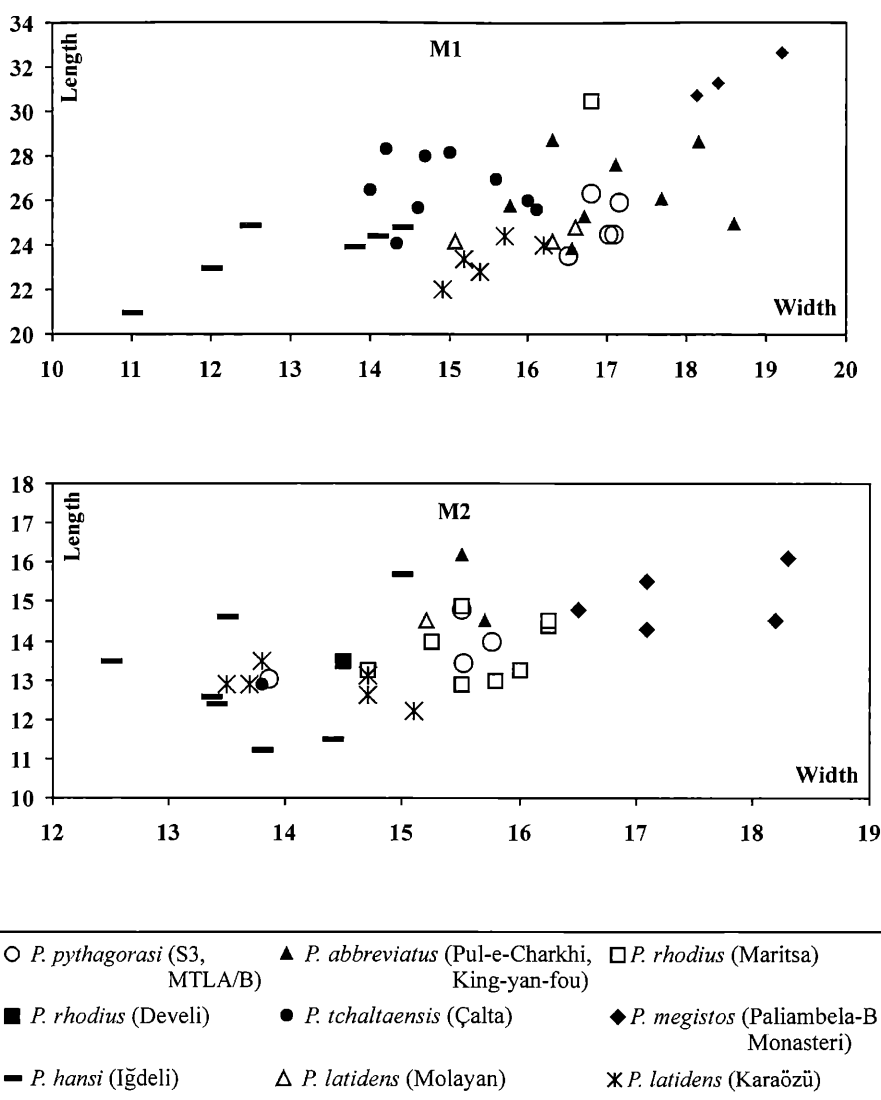
KOUFOS et al., 1997). BLACK et al. (1980) mentioned that one worn m1 from Kalithies (island of Rhodes, Greece) that was initially reported as *Gerbillus?* sp. (DE BRUIJN, 1976) could belong to *P. pythagorasi*, based on its size. *P. pythagorasi* has also been reported from the locality Düzyayla, (Turkey, MN12) (FAHLBUSCH, 1996; AKGÜN et al., 2000). The largest species of the genus, *P. megistos* SYLVESTROU & KOSTOPOULOS, 2007 is known from the Late Miocene (MN13) of two sites located in Northern Greece: Monasteri (Strimon Basin) and Paliambela-B (Katerini Basin) (SYLVESTROU & KOSTOPOULOS, 2007). *Pseudomeriones* from Ano Metochi 3 in the Strimon basin (Northern Greece) was initially described as *P. abbreviatus* (ARMOUR-BROWN et al., 1979; DE BRUIJN & VAN DER MEULEN, 1979; SEN, 1983) and later as *P. rhodius* (DE BRUIJN, 1989), whereas WESSELS (1998, 1999) referred to it as *Pseudomeriones* sp. *Pseudomeriones* from Tomea Eksi 1+2 (MN13/14, Ptolemais Basin) (WESSELS, 1999; HORDIJK & DE BRUIJN, 2009) is represented by a low number of specimens and, therefore, has been reported as *Pseudomeriones* sp. Recently SYLVESTROU & KOSTOPOULOS

(2007) discussed the morphological evolution inside the genus and provide a phylogenetic scenario involving all above mentioned species.

Comparison: The old Samos material of *Pseudomeriones* that is stored at the Carnegie Museum of Natural History of New York was collected from the locality S3 and includes seven fossil teeth (BLACK et al., 1980). Casts of five out of those seven specimens became available to us for comparison and new measurements have been taken on them (Table 1).

The old collection of *P. pythagorasi* included only M1 and m1 and for that reason the comparison with the known species of *Pseudomeriones* was not complete. As the new collection also includes second molars, the comparisons that are now possible show important resemblances of *P. pythagorasi* from Samos to *P. latidens* from the Molayan of Afghanistan. The locality Molayan is placed at similar biochronological level with the Samos locality S3 (MN12) or is a little older (SEN, 1998a, 2001). Even though the stratigraphic position of the fossiliferous sites MTLA and MTLB is different from that of the Loc. S3, morphological

Figure 3: Scatter diagrams of width against length in the upper molars of *Pseudomeriones* species. *P. pythagorasi* (S3, MTLA/B); *P. abbreviatus* (Pul-e Charkhi, King-yan-fou) from SEN, 1983; *P. rhodius* (Maritsa) from DE BRUIJN et. al., 1970, SEN, 1977, 1983; *P. rhodius* (Develi) from SEN, 1990; *P. tchaltaensis* (Çalta) from SEN, 1977, 1983; *P. megistos* (Paliambela-B, Monasteri) from SYLVESTROU & KOSTOPOULOS, 2007; *P. hansi* (Iğdeli) from SUATA-ALPAŞLAN, 2003 (in SUATA-ALPAŞLAN, in press); *P. latidens* (Molayan) from SEN, 1983, 2001; *P. latidens* (Karaözü) (personal data).



or metrical differences between the old and new material cannot be found. This suggests that all the fossils belong to the same species, *P. pythagorasi*.

Specimens of *P. abbreviatus* from King-Yan Fou (type locality, China, Latest Miocene) and Pul-e Charkhi (Afghanistan, MN14) have similar dimensions (Figs. 3, 4) to those of *P. pythagorasi*. Comparisons show that the M2 of both species is relatively long compared to the M1 (length ratio M1/M2 ~1.74-1.80). However, there are several morphological differences between the two assemblages. On the m1 of *P. abbreviatus* from Pul-e-Charkhi, the anterocone has a triangular shape, forming a labial angle, but lacks the labial arm which is present on the m1 of *P. pythagorasi* (Fig. 5.3, 5.4). On the M2 from Pul-e-Charkhi the mesosinus is as deep as the lingual sinus and only in 18 out of 29 specimens the lingual sinus curves backwards, whereas on the other specimens it is almost transverse (SEN, 1983; Fig. 5.2). The anteroloph is weak even in unworn specimens (Fig. 5.2). On the M2 of *P. pythagorasi* the lingual sinus is very deep and wide and curved backwards even in advanced stages of wear and the anteroloph is strong and becomes weak only in advanced stages of wear (Plate 1c-f). However, the number of M2s in the Samos assemblage is rather low (four) to

draw definite conclusions on this feature to be drawn. On the M2 of *P. abbreviatus* there are two roots, whereas the *P. pythagorasi* M2 has three roots (two anterior and one posterior). On the m2 of *P. abbreviatus*, in contrast with the m2 of *P. pythagorasi*, the antero-external cuspid is not curved backwards and the protosinusid is shallow even in worn teeth (Fig. 5.5).

Pseudomeriones from Ano Metochi 3 has similar morphological characteristics to *P. abbreviatus* from the type locality King-Yan Fou (SEN, 1983), but the size of the specimens is similar to that of *P. pythagorasi* of Samos (SYLVESTROU & KOSTOPOULOS, 2007; I. S. personal observations).

P. rhodius from Develi (Turkey; Fig. 5.8, 5.10) [which seems to reside morphologically between *P. abbreviatus* and *P. tchaltaensis* (SEN et al., 1989; SEN, 1990)] has more archaic characteristics than *P. rhodius* from Maritsa (Rhodes Island, Greece; Fig. 5.6-5.7, 5.9, 5.11), but it is large in size (a more derived characteristic) (Fig. 4). Specimens from Develi have morphological similarities to specimens of *P. pythagorasi* from Samos [i.e. a strong anteroloph and posteroloph and backwards-curved lingual sinus on the M2 (Fig. 5.8), the presence of a posterolophid on the m1 (Fig. 5.10)], but the m1 is much longer (Figs. 3, 4) and its anteroconid has a triangular shape (Fig. 5.10).

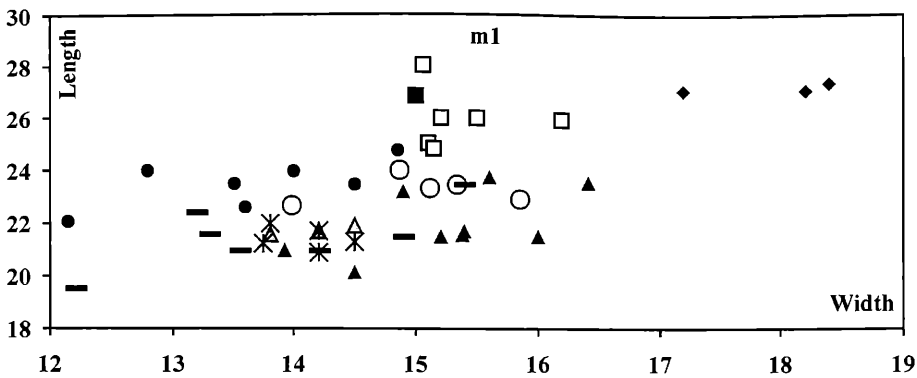
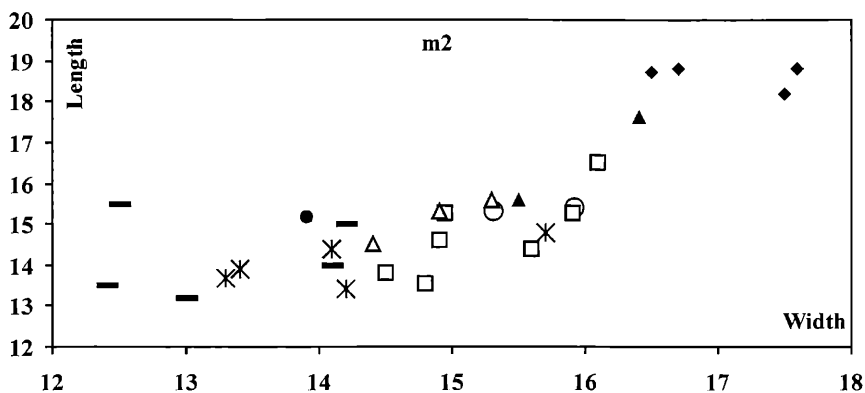


Figure 4: Scatter diagrams of width against length in the lower molars of *Pseudomeriones* species. Symbols and abbreviations as in Fig. 3.



The length/width ratio of m1 is 1.79 for *P. rhodius* from Develi and 1.43-1.62 for *P. pythagorasi*. *P. rhodius* from Maritsa has also longer M1 and m1 than *P. pythagorasi* (Figs. 3, 4) and the m1 length/width ratio is high (1.75 on average), showing that the m1 is narrow. The anteroconid on the m1 of *P. rhodius* has a triangular, almost symmetrical shape (Fig. 5.9), there is a straight-symmetrical lingual sinus on the M2, almost twice as deep as the mesosinus, the anteroloph is very weak, almost absent and the posteroloph is weak (Fig. 5.7). On the m2 of *P. rhodius* from Maritsa, the antero-external cuspid is curved anteriorly, the protosinusid is shallow and the anterior side of the tooth appears slightly concave (Fig. 5.11). The M1 of *P. rhodius* from Maritsa is twice as long as the M2 (length ratio >2), whereas in *P. pythagorasi* the M1/M2 length ratio is almost 1.75, showing that the M2 is long relative to the M1.

P. megistos is very large compared to *P. pythagorasi* (Figs. 3, 4). There is no evidence of a labial arm on the m1 and the anteroconid is semi-circular to crescent-shaped (Fig. 5.15). On the M2 the lingual sinus is as deep as the mesosinus and is transverse, whereas the anteroloph is weak even on unworn specimens (Fig. 5.13, 5.14). The mandible of *P. megistos* is significantly larger than that of *P. pythagorasi* and the anterior tip of the incisors is situated significantly higher than the occlusal level of the molars (Fig. 2d).

P. tchaltaensis from Çalta (Turkey), one of the youngest species of the genus, shows derived characteristics (narrow first upper and lower molars, straight mesosinus on

the M2, shallow protosinusid on the m2) (SEN, 1998b). *P. tchaltaensis* differs from *P. pythagorasi* by the narrow and elongated M1 (Fig. 5.17), the clear asymmetry between the labial (shorter with rounded edges) and lingual sinusids on the m1 and the symmetrical and triangular shape of the m1 anteroconid (Fig. 5.19). Moreover, the antero-external cuspid of the m2 is not curved backwards (Fig. 5.20) and there is no curvature on the lingual sinus of worn M2s (Fig. 5.18). Finally, the M1 is twice as long as the M2 (length ratio >2), whereas the *P. pythagorasi* M2 is quite elongate. In the mandible of *P. tchaltaensis* the anterior tip of the incisors is situated higher than the occlusal level of the molars (Fig. 2c).

P. hansii from İğdeli is smaller than *P. pythagorasi* (Figs. 3, 4). It differs from the latter by the more symmetrical and triangular-shaped anteroconid, without evidence of a labial arm on the m1 (Fig. 5.27), the shallow protosinusid and the anteriorly curved antero-external cuspid on the m2 (Fig. 5.28) and the weak or absent anteroloph on the M2 (Fig. 5.26).

P. complicidens from Ningxian is considered to be the most derived species of *Pseudomeriones* (ZHANG, 1999). It has a high length/width ratio of the m1 molar (>1.85), two persistent sinusids on the anteroconid of the m1 (Fig. 5.29), on the m2 the antero-external cuspid is curved anteriorly (Fig. 5.30) and is very small and narrow compared to *P. pythagorasi*. The mandible of *P. complicidens* is significantly smaller than that of *P. pythagorasi* (Fig. 2d). In lateral view the horizontal level defined by the anterior

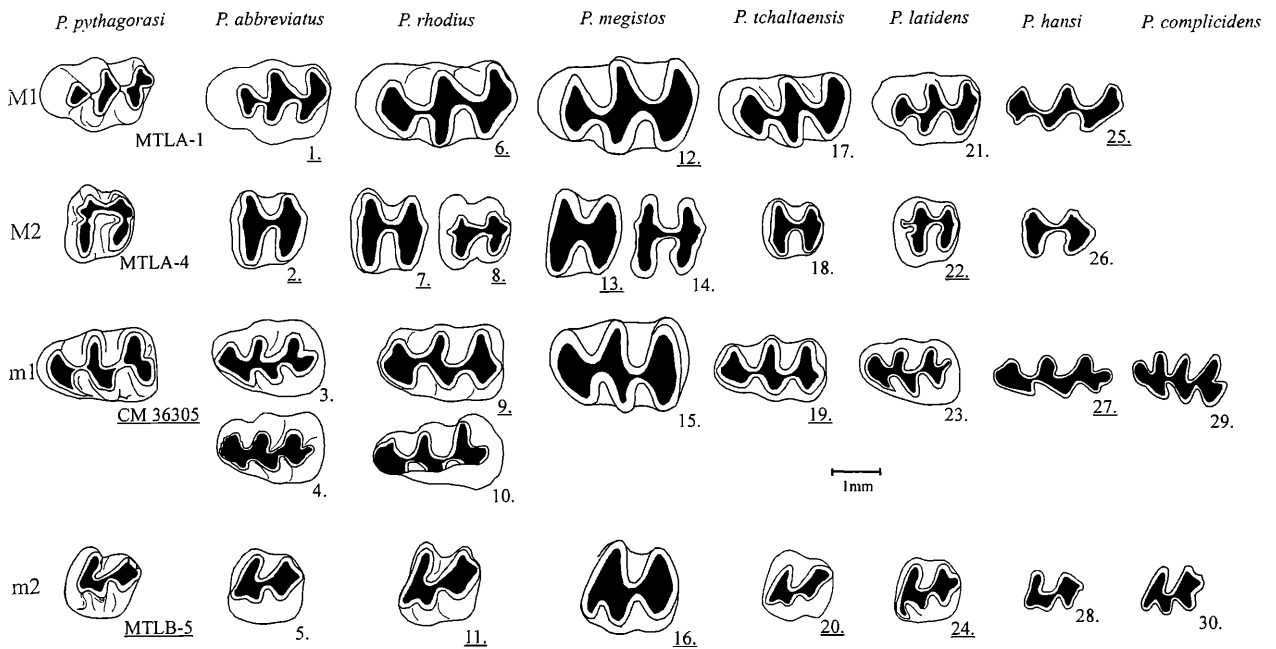


Figure 5: Occlusal surface of *Pseudomeriones* teeth. The scale bar is 1mm. All teeth are drawn as left. The teeth with the underlined numbers are originally from the right side of the jaws. *P. abbreviatus*: 1. M1 dex (AFG 281, Pul-e Charkhi), 2. M2 dex (AFG 302, Pul-e Charkhi), 3. m1 sin (AFG 320, Pul-e Charkhi), 4. m1 sin (King-yan-fou, holotype), 5. m2 sin (AFG 370, Pul-e Charkhi) from SEN, 1983; *P. rhodius*: 6. M1 dex (192, Maritsa), 7. M2 dex (171, Maritsa), 8. M2 dex (Develi), 9. m1 dex (164, Maritsa), 10. m1 sin (Develi), 11. m2 dex (207, Maritsa) from DE BRUIJN et. al., 1970; SEN, 1990; *P. megistos*: 12. M1 dex (PLM-3, Paliambela-B), 13. M2 dex (PLM-3, Paliambela-B), 14. M2 sin (MNS-3b, Monasteri), 15. m1 sin (PLM-1, Paliambela-B, Katerini), 16. m2 dex (PLM-2, Paliambela-B, holotype) from SYLVESTROU & KOSTOPOULOS, 2007; *P. tchaltaensis* (Çalta): 17. M1 sin (ACA-917), 18. M2 sin (ACA-946), 19. m1 dex (ACA-962), 20. m2 dex (ACA-1006), from SEN, 1977; *P. latidens* (Molayan): 21. M1 sin (MNHN MOL-55), 22. M2 dex (MNHN MOL-58), 23. m1 sin (MNHN MOL-65, holotype), 24. m2 dex (MNHN MOL-67) from SEN, 1998a, 2001; *P. hansii* (İğdeli): 25. M1 dex, 26. M2 sin, 27. m1 dex, 28. m2 sin, from SUATA-ALPAŞLAN, 2003 (in SUATA-ALPAŞLAN, in press); *P. complicidens* (Ningxian): 29. m1 sin (V5954.1), 30. m2 sin (V5954.1), from ZHANG, 1999.

tip of the incisors passes through the molars (Fig. 2d). SEN (2001) used the crown height of the teeth as a discreet characteristic for distinguishing *P. latidens* from all the other species of *Pseudomeriones*. Measurements taken on the Samos specimens show that the M1 and m1 are rather high-crowned, as the crown height is about half of their length even in worn teeth, instead of one-third in *P. latidens*. This is the only difference that can be observed between *P. latidens* of Molayan and *P. pythagorasi*, since the other morphological and metrical features between the two species are quite similar (Figs. 3, 4, 5.21-5.24). The presence of a strong labial arm that reaches the base of the protoconid on the m1 is a morphological characteristic present in both *P. latidens* and *P. pythagorasi* (Fig. 5.23). Only on worn m1s from Samos the labial arm is not visible, but the asymmetrical shape of the anteroconid suggests that it was probably present in previous stages of wear. The presence of three roots on the M2 of *P. latidens* (two anterior and one posterior) is also observed on the M2 of *P. pythagorasi* from Samos, increasing their similarity. Furthermore, in both species the mesosinus on the M2 is short and wide, almost one-third of the lingual sinus (Fig. 5.22). The protosinusid on the *P. latidens* m2 is deep and the anteroexternal cuspid curves slightly posteriorly (Fig. 5.24), similarly to the m2 of *P. pythagorasi*. Specimens of *P. latidens* from Karaözü show all of the above morpho-

logical features, but metrically are slightly smaller than *P. pythagorasi* (Figs. 3, 4). The above discussion suggests that *P. pythagorasi* shares a lot of common primitive characteristics with *P. latidens* (m1 anteroconid with a labial arm, wide molars, deep protosinusid), but it also has some derived characteristics (high-crowned molars, larger especially than *P. latidens* of Karaözü, MN10-11) indicating a more advanced evolutionary stage. *P. latidens* is considered to be the ancestor of *P. pythagorasi* which later gave rise to the Eastern European population of *Pseudomeriones* (SYLVESTROU & KOSTOPOULOS, 2007).

Subfamily: Murinae GRAY, 1821

'*Karnimata*' provocator (DE BRUIJN, 1976)

Locality: Mytilinii-1A (MTLA) Adrianos ravine, Mytilinii Basin, Samos, Greece.

Material: m1 dex, MTLA-7: 17.6 x 10.5; right mandible fragment with m2-m3, MTLA-8a, 8b: 12.8 x 11.1 & 10.9 x 9.2; m2 dex, MTLA-9: ~13 x 10.8; m3 sin, MTLA-10: 10.2 x 9.2; m3 sin, MTLA-11: 10.3 x 9.9. The wear stage of the m1 is similar to that of the m2 and m3 on the mandible fragment. Furthermore, the posterior interstitial facet of the m1 fits very well with the anterior facet of the m2. The m1 (MTLA-7) is therefore considered to be from the

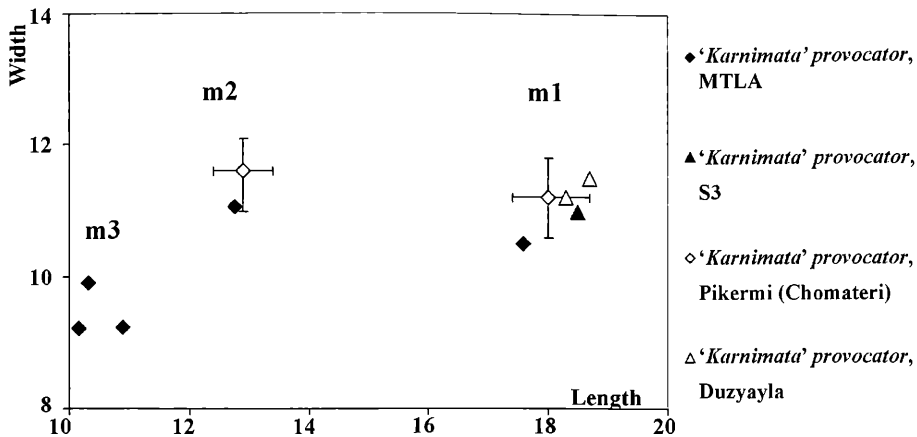


Figure 6: Scatter diagram of length against width in the lower molars of 'Karnimata' species. 'Karnimata' *provocator* from MTLA (Samos); 'Karnimata' *provocator* from S3 (Samos) from BLACK et al., 1980; 'Karnimata' *provocator* from Pikermi (Chomateri) (type locality of species) from DE BRUIJN, 1976; 'Karnimata' *provocator* from Düzyayla from DE BRUIJN et al., 1999.

same individual as the mandible fragment (MTLA-8).

Description:

m1 (Plate 2a): The molar is rather worn. There is a very small and rounded antero-central cuspid. The lingual cuspids are situated somewhat more anteriorly than the labial ones and, thus, the molar is slightly asymmetrical. The two anterior cuspids are connected to each other and also with the medial pair of cuspids. The posterior pair of cuspids does not bear a longitudinal spur facing anteriorly towards the medial pair. The c1 is large and connected to the hypoconid. There are no more cuspulids on the labial edge (besides the c1), but there is a wide and low enamel ridge situated next to the protoconid. The terminal heel is small and elongated.

m2 (Plate 2b): The posterior part of the molar is narrower than the anterior part. There is no longitudinal spur connecting the two pairs of cuspids. The antero-labial cuspid is large, isolated and rounded. There is no labial cingulum, but there is one rounded c1. The terminal heel is larger than in the m1 and elongated.

m3 (Plate 2c): It bears a very small antero-labial cuspid. The hypoconid and entoconid are fused into one rounded cuspid.

Discussion: The absence of the longitudinal spur connecting the cusp-pairs in the m1 and m2 and the presence of a very small antero-central cuspid in the m1 are morphological features that the MTLA material shares with *Occitanomys? provocator* DE BRUIJN, 1976 from Pikermi (Chomateri), the type locality of the species. Furthermore, the cingulum cuspids, except for the c1, are weak - absent in the m1 and m2 of both species. The m1 from MTLA is slightly narrower than the m1s from Pikermi (Fig. 6); however, the m2 is metrically within the size range of the m2s from Pikermi (Fig. 6). The m3 of *Occitanomys? provocator* is not known.

BLACK et al. (1980) described one right M1, one left m1 and a partial skull with dentition (all molars present except for the right M3) in an advanced stage of wear from the Samos locality S3. Based on the morphological and metric similarities of these findings to *Occitanomys? provocator* DE BRUIJN, 1976 from Pikermi (Chomateri), they identified the findings as *O.? provocator*. The material from the locality MTLA (slightly younger than the S3 locality) confirms

the presence of this species in the Middle Turolian of Samos. DE BRUIJN (1976) had already suggested that the species *provocator* might not belong to *Occitanomys*, based on differences between the new species and all the previously known *Occitanomys* species. The Pikermi species was recently referred to as 'Karnimata' *provocator* (DE BRUIJN et al., 1999), but it was clarified that the attribution to this genus is provisional (since the status of the genus is uncertain after MEIN et al., 1993 synonymised the type species of *Karnimata*, *K. darwini* JACOBS, 1978, with *Progonomys woelferi* (BACHMAYER & WILSON, 1970). Unfortunately, the material from Samos is not adequate enough to help with a more detailed comparison and discussion on the generic status of the species *provocator*. Except at its type locality and Samos, a few specimens of this species have also been found at the MN12 locality Düzyayla (Central Anatolia; DE BRUIJN et al., 1999).

Family: Sciuridae GRAY, 1821

Genus: *Spermophilinus* DE BRUIJN & MEIN, 1968

Spermophilinus cf. *Spermophilinus bredai* (VON MEYER, 1848)

Type species: *Spermophilinus bredai* (VON MEYER, 1848)

Locality: Mytilinii-1A, B (MTLA, MTLB) Adrianos ravine, Mytilinii Basin, Samos, Greece.

Material:

MTLA: M1/2 dex, MTLA-6: 16.85 x 19.23

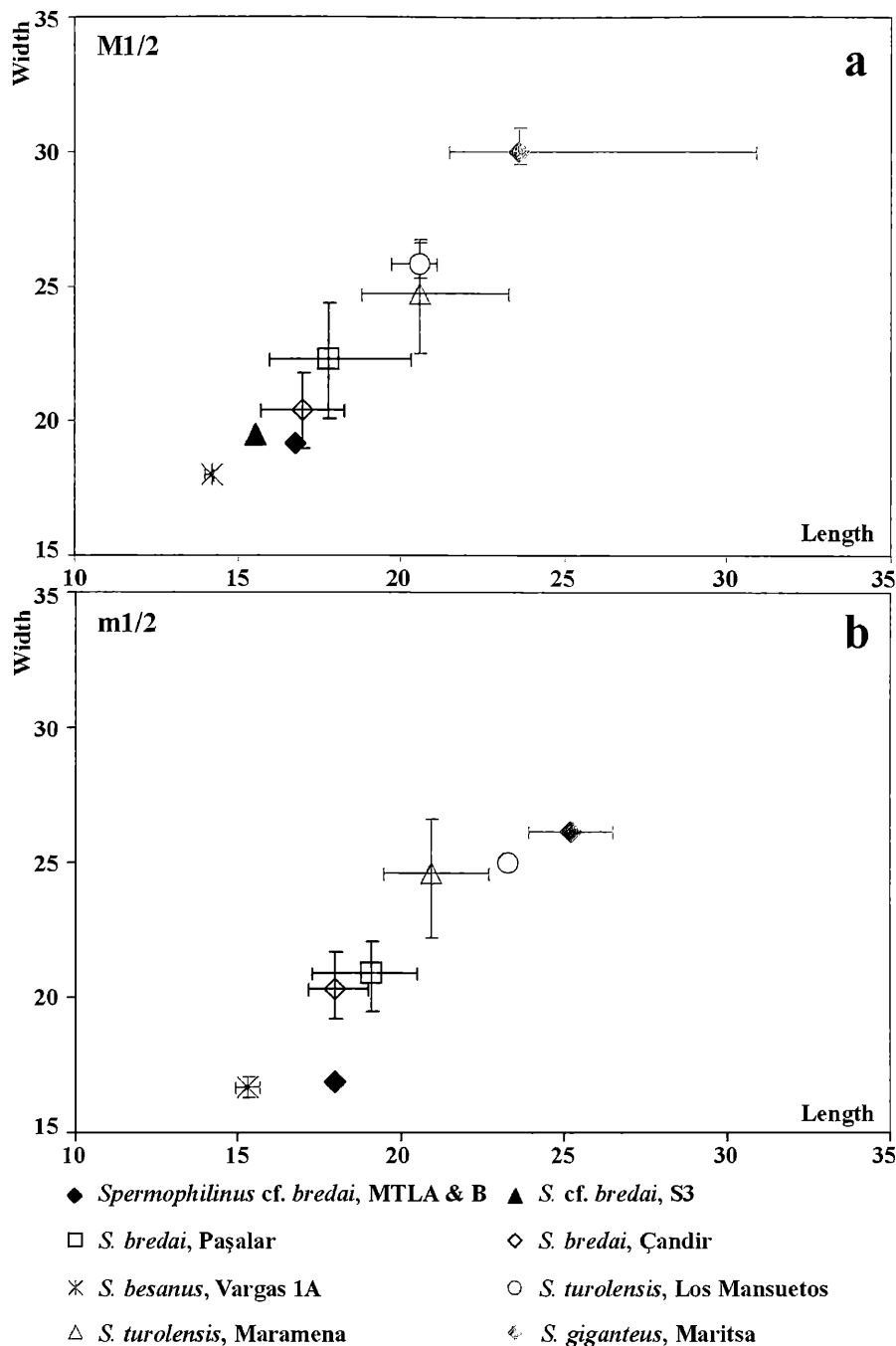
MTLB: m2 sin, MTLB-6: ~ 17.97 x 16.94

Description:

M1/2 (Plate 2d): The protocone is the largest cusp, whereas the hypocone is incorporated in the endoloph. The metacone is situated at the end of the posteroloph. The anteroloph ends at the anterior side of the protocone and is connected with it at its base. The protoloph and metaloph connect on the protocone, forming a "V" on the occlusal surface. There is a well-developed metaconule and a small mesostyle.

m2 (Plate 2e): The protoconid, hypoconid and metaconid are large, the protoconid being only slightly larger than

Figure 7: Scatter diagram of length against width in the molars of *Spermophilinus* species. *Spermophilinus* cf. *bredai* from MTLA/B (Samos); *S. cf. bredai* from S3 (Samos) from BLACK et al., 1980; *S. bredai* from Paşalar from PELÁEZ-CAMPOMANES & DAAMS, 2002; *S. bredai* from Çandır from DE BRUIJN et al., 2003; *S. besanus* from Vargas 1A (type locality of species) from CUENCA, 1988; *S. turolensis* from Los Mansuetos (type locality of species) from DE BRUIJN & MEIN, 1968; *S. turolensis* from Maramena from DE BRUIJN 1995; *S. giganteus* from Maritsa (type locality of species) from DE BRUIJN et al. 1970.



the other two cusps. The anterolophid connects with the anterior base of the protoconid. There is a short, low and slightly anteriorly-directed metalophid. The ectolophid is very low, showing no mesoconid. The enamel of the molar shows a high degree of etching, a feature that hinders more detailed observations on the surface morphology (e.g. entoconid).

Discussion: Even though the elements coming from the two localities (MTLA and MTLB) are not alike and direct comparisons are not possible, their size and their morphology is proportioned and equally simple, so there is no reason to believe that they belong to different species. BLACK et al. (1980) described one right M1/2 from the Samos locality S3. The morphology of that molar is identical to the morphology of the molar from MTLA and the two teeth are very similar in size, the tooth from MTLA

being slightly longer than the one from S3. Therefore, it is considered here that the *Spermophilinus* material from the two collections (S3 and MTLA/MTLB) belong to the same species.

The four species currently assigned to *Spermophilinus* are *S. besanus* CUENCA, 1988, *S. bredai* (VON MEYER, 1848), *S. turolensis* DE BRUIJN & MEIN, 1968 and *S. giganteus* DE BRUIJN et al., 1970. These species are mainly distinguished based on the size of their cheek teeth: *S. besanus* is the smallest species, whereas *S. giganteus* is the largest one (DE BRUIJN, 1995).

The two upper molars from Samos are much smaller than the molars of both *S. turolensis* and *S. giganteus*, whereas they are somewhat larger than the molars from the type locality of *S. besanus* (Fig. 7a). There also are morphological differences between the molars from Samos and those of

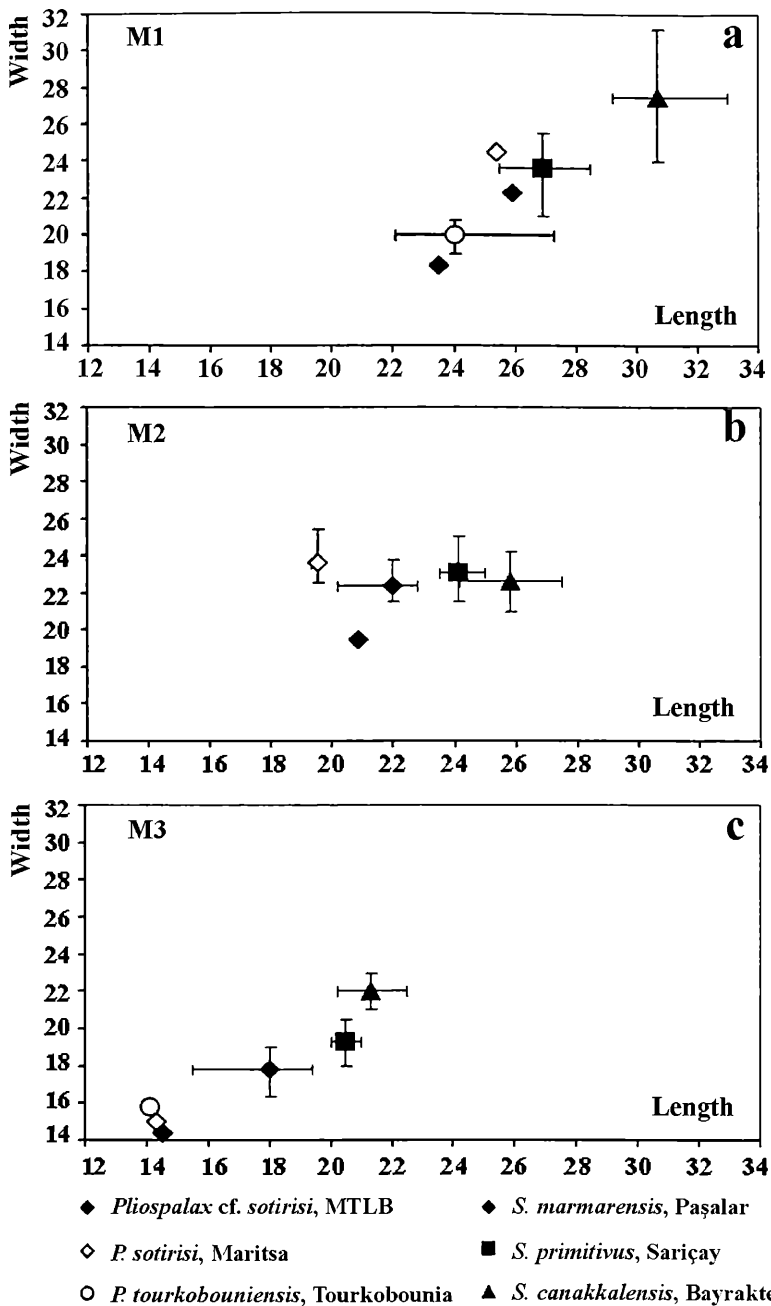


Figure 8: Scatter diagram of length against width in the upper molars of *Pliospalax* and *Sinapospalax* species. *Pliospalax cf. sotirisi* from MTLB (Samos); *P. sotirisi* from Maritsa (type locality of species) from DE BRUIJN et al. 1970; *P. tourkobouniensis* from Tourkobounia 1 (type locality of species) from DE BRUIJN & VAN DER MEULEN, 1975; *S. marmarensis* from Paşalar (type locality of species) from ÜNAY, 1990; *S. primitivus* from Sariçay (type locality of species) from ÜNAY, 1978; *S. canakkalensis* from Bayraktepe-1 (type locality of species) from ÜNAY, 1981.

S. besanus. According to CUENCA (1988), the anteroloph of the *S. besanus* M1/2 is isolated from the protocone and there is no metaconule. On the Samos molars, however, the anteroloph connects to the base of the protocone and the metaconule is well-developed.

Both of the Samos upper molars have a size very close to the size range of the upper molars of *S. bredai* from Çandır, described by DE BRUIJN et al. (2003), but are smaller than the molars from Paşalar, assigned to *S. bredai* by PELÁEZ-CAMPOMANES & DAAMS (2002) (Fig. 7a). The Samos upper molars show also morphological similarities with the molars from Çandır, the only difference being that the metaconule is stronger in the Samos molars than in the Çandır ones (DE BRUIJN et al., 2003: pl. 1, figs. 10, 11), whereas the mesostyle forms a small isolated cusp in some molars from Çandır (DE BRUIJN et al., 2003), just like in the Samos molars. The lower molar from MTLB,

on the other hand, is as long as *S. bredai* from Çandır and Paşalar, but the width is similar to that of *S. besanus* from the type locality of this species (Fig. 7b). However, as Plate 2e shows, a large amount of enamel is missing from the surface of the molar and, therefore, the measurements taken here are thought to be lower than they should be on the unetched tooth. Furthermore, the etching of the surface enamel does not allow an accurate observation of the morphology of the occlusal surface. According to CUENCA (1988), the anterolophid of the lower molars of *S. besanus* is separated from the protoconid, the entoconid is absent and the metalophid is absent or very small, whereas the anterolophid of the *S. bredai* lower molars is connected slightly to the protoconid, the entoconid is reduced but visible and the metalophid is small but complete. The presence of a short metalophid and the connection between the anterolophid and the protoconid on the MTLB m2 suggest

that the morphology of the tooth is closer to that of the *S. bredai* lower molars. However, the morphology of the tooth is difficult to describe with confidence and therefore, it cannot with certainty be assigned to a species.

Based on the similarity of the S3 upper molar with the molars from La Grive, BLACK et al. (1980) identified that molar as *S. cf. S. bredai* (VON MEYER, 1848). Here, we agree with their identification and assign the new material from MTLA and MTLB to the same species, *S. cf. bredai*.

According to DE BRUIJN et al. (2003), the stratigraphic range of *S. bredai* covers MN6 and MN7/8, whereas later the species gets replaced by the larger *S. turolensis*. DE BRUIJN (1995), however, mentioned that this seems to be the case only in Western Europe, whereas 'Anatolia served as a refuge for the species *bredai*' during the Late Miocene, as suggested by the presence of the species in the Anatolian locality Düzyayla, correlated to MN12. The possible presence of this species in the MN12 Samos localities strengthens the validity of DE BRUIJN's (1995) hypothesis. Furthermore, *S. cf. bredai* has been described from the MN11 Austrian locality Kohfidisch (BACHMAYER & WILSON, 1970) and *S. bredai* from the MN9 Hungarian locality Rudabánya (DAXNER-HÖCK & FEJFAR, 2003). Therefore, it seems that this species persisted not only in Anatolia, but also in Central Europe at least until MN11.

Family: Spalacidae GRAY, 1821

Subfamily: Spalacinae THOMAS, 1896

Genus: *Pliospalax* KORMOS, 1932

***Pliospalax cf. Pliospalax sotirisi* (DE BRUIJN et al., 1970)**

Type species: *Pliospalax macoveii* (SIMIONESCU, 1930)

Locality: Mytilinii-1B (MTLB) Adrianos ravine, Mytilinii Basin, Samos, Greece.

Material:

MTLB: Part of the skull with the left M1-3 (MTLB-7a-7c), M1: 23.5 x 18.31; M2: 20.9 x 19.5; M3: 14.5 x 14.4.

Description:

M1 (Plate 2f): The molar is rather worn. There are two labial and one lingual sinuses. The labial ones are equally very deep, wide and both strongly posteriorly facing, whereas the lingual one is anteriorly facing. This leaves a narrow entoloph just posteriorly to the protocone. Both labial sinuses have just closed due to wear, so they close simultaneously at the same crown height. The lingual one continues to the height of the crown that is visible from the mandible.

M2 (Plate 2g): The lingual sinus is very deep, anteriorly facing and continues till the height of the crown that is visible from the mandible. There is one labial and strongly posteriorly pointing deep sinus that ends at a small distance from the posterior wall of the crown, closer to the lingual than the labial side. This sinus has also just closed labially, simultaneously with the two labial sinuses of the M1. The anterior labial sinus that must have existed has already closed and there is an enamel island remaining in its place. From the shape of the island it appears

that the antero-labial sinus was pointing anteriorly. **M3 (Plate 2h):** The occlusal surface is almost rounded. The labial sinus is closed labially and there is a remaining enamel island in the centre of the occlusal surface. The shape of the island shows that the sinus was pointing posteriorly. There is no lingual sinus.

Discussion: *Pliospalax* is a common taxon in the Mio-Pliocene localities of Anatolia and Greece. The *Pliospalax* material from Samos is too scanty to allow detailed comparisons with the known species. The molars from MTLB have a very simple morphology and are high-crowned. Except for the three molars described above, two left lower *Pliospalax* molars have also been found in the Samos locality S3 described by BLACK et al. (1980). Based on the resemblance between the S3 m2 and the m2 from Maritsa of Rhodes described by DE BRUIJN et al. (1970), BLACK et al. (1980) identified the S3 spalacid as *Pliospalax cf. sotirisi*.

SARICA & SEN (2003) included in their genus *Sinapospalax* species of *Pliospalax* with a complex morphology, namely the species *P. marmarensis* ÜNAY, 1990 (type locality: Paşalar, Turkey, MN6), *P. canakkalensis* ÜNAY, 1981 (type locality: Bayraktepe-1, Turkey, MN7/8) and *P. primitivus* ÜNAY, 1978 (type locality: Sariçay, Turkey, MN7/8). All these species have a more complex morphology and larger size than the molars from MTLB (Fig. 8a-c).

The morphology of the molars of *Pliospalax* n.sp.1 from Çandir (Turkey, MN6), described by ÜNAY (1996), is more complicated than that of the MTLB, with a well-developed mesoloph, a posteroloph separated from the metaloph and a transverse lingual sinus on the M1. *Pliospalax* n. sp. from Düzyayla 1 (Turkey, MN12), described by ÜNAY (1996) is the largest known *Pliospalax* species, since its M1 measures 44.5 x 43, which is much bigger than the MTLB M1. ÜNAY & DE BRUIJN (1998) reported the presence of an M1 and an M3 of *Pliospalax* sp. at the locality Kadiözü (Turkey, MN16). They differ from the MTLB molars, as the Kadiözü M1 has a very well-developed posterior cingulum and a small mesoloph and the M3 shows two isolated islets on its occlusal surface.

SARICA & SEN (2003), after the creation of the genus *Sinapospalax*, included the species *P. macoveii* (SIMIONESCU, 1930), *P. compositodontus* TOPACHEVSKI, 1969, *P. sotirisi* (DE BRUIJN et al., 1970) and *P. tourkobouniensis* DE BRUIJN & VAN DER MEULEN, 1975 in the genus *Pliospalax*. *P. compositodontus* from Andreevka and Berezan (Ukraine, MN10) shows a more complicated morphology than the MTLB molars, with a well-developed mesoloph on the M1 (TOPACHEVSKI, 1969). *P. tourkobouniensis* (type locality: Tourkobounia-1, Greece, MN16) shows a mesoloph and a posterior cingulum on the M1 and a lingual sinus on the M3 (DE BRUIJN & VAN DER MEULEN, 1975), whereas its molars are wider than the MTLB ones (Fig. 8a, c).

The only *Pliospalax* species present in Central Europe is *P. macoveii*. The lack of a mesoloph in the M1 is a diagnostic feature of the species (type locality Malushteni, Romania, MN15). The M1 of this species from MN15 localities of the Ukraine (TOPACHEVSKII, 1969) does not show a mesoloph; the postero-labial sinus closes with slight wear, as

the metacone fuses with the posterior cingulum very early; the antero-labial sinus closes with an advanced stage of wear, as the paracone fuses with the anteroloph, and the centro-labial sinus closes even later. The morphological features of this species are similar to those of the MTLB molars, the exception being that the antero-labial sinus closes earlier than the centro-labial one in the M1 of this species, whereas these two sinuses close simultaneously in the MTLB M1.

The species *P. sotirisi* has been found only in the type locality, Maritsa (Rhodes, Greece, MN14). The paratypes of the species, a left M1 and M2 on a maxillary fragment (DE BRUIJN et al., 1970: Pl. 6, Fig. 1), are slightly more worn than the molars from MTLB, but show similar morphological features. The lingual sinus is very deep and the two labial ones close simultaneously with wear in the M1 of *P. sotirisi*, similar to the M1 from MTLB. Also, the postero-labial sinus in the M2 closes at approximately the same height as the sinuses in the M1, whereas the antero-labial sinus closes earlier and forms an enamel island on the anterior part of the occlusal surface. The M3 of *P. sotirisi* (DE BRUIJN et al., 1970: Pl. 6, Fig. 2) is somewhat different from the MTLB M3, since it has an almost triangular shape and an open labial sinus, which, however, closes in a slightly more advanced stage of wear. Since the M3 of this species is less worn than the MTLB M3, this difference is reasonable. Even though the morphology of the MTLB molars is very similar to the Rhodes ones, the MTLB M1 and M2 are quite narrower than the Rhodes M1 and M2 (Figs. 8a, b). However, both samples are too small and the size variability is not known for either. Thus it cannot be confirmed that the MTLB material falls within the size variation of *P. sotirisi*.

The spalacid material from MTLB is too scanty to allow a certain identification of the species. The morphology and the size of the spalacid molars are quite variable with wear, which makes identification of very small samples, such as the MTLB one, very difficult. The molars resemble those of the species *Pliospalax sotirisi* in morphology. However, as the material is scanty and there is also a considerable size difference between the first and second molars from Samos and their equivalent from Rhodes, the MTLB spalacid can only be determined as *Pliospalax* cf. *sotirisi*. This identification agrees with the attribution of the two spalacid lower molars found in the Samos locality S3 to *Pliospalax* cf. *sotirisi* by BLACK et al. (1980).

ÜNAY (1996) mentioned that the age range of *Pliospalax* in South-Eastern Europe, into which she included all the Greek localities, is late MN8–MN16, with gaps in MN9, MN11 and MN12, whereas the genus has a continuous record from MN6 to MN15 in Anatolia. However, the presence of *Pliospalax* in the MN12 localities of Samos (MTLB in the present study and S3 in BLACK et al., 1980) suggests that there is no gap in MN12. It is not common, though, to consider the Late Miocene localities of Eastern Greece as “European”, since the faunas of these localities and the ones of Anatolia are very similar. The presence of *Pliospalax* in MN12 of Samos, with its simple morphology, resembling *P. sotirisi* from the Late Pliocene

of Rhodes and slightly less *P. macoveii* from the MN13 in South-Eastern Europe and MN15 in Anatolia and Central Europe, indicates that the record of this genus is still very poorly known and understood, mainly due to the small *Pliospalax* samples usually recovered.

4. Conclusion

The Middle Turolian Samos localities have been known for a long time for their large numbers of large mammal fossils. The localities MTLA and MTLB have also yielded a limited number of rodent fossils, which are here identified as *Pseudomeriones pythagorasi*, ‘*Karnimata*’ *provocator*, *Spermophilinus* cf. *bredai* and *Pliospalax* cf. *sotirisi*. These are all rodents with Anatolian affinities, since they have been found at various Eastern Mediterranean localities (at species or genus level).

Even though the micromammalian collection from MTLA and MTLB is very small, some interesting remarks can be made. The genus *Pseudomeriones* is represented in both the old (by seven molars) and new collection (by eleven molars), with the species *P. pythagorasi* BLACK et al. (1980). Since the type locality of the species is the locality S3, which is in the same formation, but stratigraphically slightly lower than the MTLA and MTLB localities, the new findings are of great significance, because they provide additional information about the size and morphological variation within the species. The very poor murine sample from S3 (two molars and a partial skull with five molars in situ, but very worn) is enriched by six additional molars from MTLA, which confirm the initial identification by BLACK et al. (1980) as ‘*Karnimata*’ *provocator*. Since the species is known by a few molars only from its type locality, Pikermi, and the Anatolian locality Düzyayla, the sample from Samos establishes its presence in the MN12 of the Eastern Mediterranean area and gives additional information about the size and morphological variation of the species. The sample from S3 includes one single sciurid molar; two additional were found in the new localities, which verify the presence of a small *Spermophilinus* cf. *bredai* in the Late Miocene of the Eastern Mediterranean area, contemporaneously with a larger ground squirrel (*S. turoloensis*).

Finally, the finding of one complete upper left chewing dentition in the MN12 of Samos of a *Pliospalax* with simple morphology resembling *P. sotirisi* from the Late Pliocene of Rhodes, additionally to the two lower molars previously recovered from the Samos locality S3, suggests that the stratigraphic range of spalacids with simple dental morphology in the Eastern Mediterranean area is wider than estimated up to now. The micromammalian sample from MTLA and MTLB is very small and possibly too biased to be used for detailed palaeoenvironmental reconstructions but it is of importance that at least three of the four rodent species found can be associated with a specific type of habitat. The gerbilline *Pseudomeriones pythagorasi*, the ground squirrel *Spermophilinus* and the spalacid *Pliospalax* are all indicative of rather dry, open environments.

5. Acknowledgements

The excavations on Samos have been supported by the Prefecture of Samos and the “Konstantinos and Maria Zimalis” Foundation. The Municipality of Mytilinii provided generous help too. The Natural History Museum of the Aegean offered us the premises for the preparation and storage of the fossils. We are grateful to Dimitris Kostopoulos, Dora Vlachou, Elsa Tsombachidou and Dimitris Koufos for their help during sampling/picking. We would like to thank Dimitris Kostopoulos for helpful suggestions and comments, Nikos Solounias and the Carnegie Museum of Natural History of New York for providing us with casts of *Pseudomeriones pythagorasi* original material. Alex Ball’s and Ben Williamson’s assistance with the use of the scanning electron microscope is very much appreciated. Thanks are also due to our reviewer Dr. G. Daxner-Höck for valuable comments.

6. References

- AGUSTÍ, J., 1991. Gerbillidés fossiles d’ Europe occidentale. — [in:] BERRE, M. Le & GUELTE, L. Le (eds.). *Le Rongeur et l’ Espace*. — 177–182.
- ARGÜN, F., KAYA, T., FORSTEN, A. & ATALAY, Z., 2000. Biostratigraphic data (Mammalia and Palynology) from the Upper Miocene İncesu Formation at Düzyayla (Hafik-Sivas, Central Anatolia). — *Turkish Journal of Earth Sciences*, 9:57–67.
- ARMOUR-BROWN, A., BRUIJN, H. de, MANIATI, C., SIATOS, G. & NIESEN, P., 1979. The Geology of the Neogene Sediments North of Serrai and the Use of Rodent faunas for Biostratigraphic control. — [in:] KALLERGIS, G. (ed.). *Proceedings of the VI colloquium on the Geology of the Aegean region (Athens)*. — 2:615–622.
- BACHMAYER, F. & WILSON, R.W., 1970. Small Mammals (Insectivora, Chiroptera, Lagomorpha, Rodentia) from the Kohfidisch Fissures of Burgenland, Austria. — *Annalen des Naturhistorischen Museums Wien*, 74:533–587, Wien.
- BERNOR, L.R., SOLOUNIAS, N., SWISHER, C.C. & VAN COUVERING, A.J., 1996. The correlation of the classical “Pikermian” mammal faunas Maragheh, Samos and Pikermi, with the European MN unit system. — [in:] BERNOR, R., FAHLBUSCH, V., MITTMANN, H.-W. (eds.). *The evolution of Western Eurasian Neogene Mammal Faunas*. — 137–154, Columbia University Press.
- BLACK, C.C., KRISHTALKA, L. & SOLOUNIAS, N., 1980. Mammalian fossils of Samos and Pikermi, Part 1. The Turolian rodents and insectivores of Samos. — *Annals of Carnegie Museum*, 49:359–378.
- BOWDICH, T.E., 1821. An analysis of the natural classifications of Mammalia, for the use of students and travellers, Paris, 115 pp.
- BRANDY, L.D., 1981. Rongeurs müroïdes du Néogène supérieur d’Afghanistan. Evolution, biogéographie, corrélations. — *Palaeovertebrata*, 11:133–179.
- CUENCA-BESCOS, G., 1988. Revisión de los Sciuridae del Aragoniense y del Ramblense en la Fosa de Calatayud-Montalban. — *Scripta Geológica*, 87:1–116.
- DAXNER-HÖCK, G. & FEJFAR, O., 2003. Cricetidae, Sciuridae, Gliridae and Eomyidae. — [in:] BERNOR, R.L., KORDOS, L. & ROOK, L., (eds.). *Recent Advances on Multidisciplinary Research at Rudabánya, Late Miocene (MN9), Hungary: a compendium*. — *Palaeontographia Italica*, 89:1–34, Pisa.
- DE BRUIJN, H., 1976. Vallesian and Turolian rodents from Biotia, Attica and Rhodes (Greece). I. — *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen, Ser. B*, 79(5):361–384.
- DE BRUIJN, H., 1989. Smaller mammals from the Upper Miocene and Lower Pliocene of the Strimon Basin, Greece. Part 1. Rodentia and Lagomorpha. — *Bolletino della Società Paleontologica Italiana*, 28(2-3):189–195.
- DE BRUIJN, H., 1995. The Vertebrate Locality Maramea (Macedonia, Greece) at the Turolian-Ruscinian Boundary (Neogene). 8. Sciuridae, Petauristidae and Eomyidae (Rodentia, Mammalia). — *Münchener Geowissenschaftliche Abhandlungen, (A)*, 28:87–102.
- DE BRUIJN, H. & MEIN, P., 1968. On the mammalian fauna of the *Hipparion*-beds in the Calatayud-Teruel Basin (Prov. Zaragoza, Spain). Part V. The Sciurinae. — *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen, Ser. B*, 71(1):73–90.
- DE BRUIJN, H., DAWSON, M.R. & MEIN, P., 1970. Upper Pliocene Rodentia, Lagomorpha and Insectivora (Mammalia) from the Isle of Rhodes (Greece), I, II and III. — *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen, Ser. B*, 73(5):535–584.
- DE BRUIJN, H. & VAN DER MEULEN, A.J., 1975. The Early Pleistocene rodents from Tourkobounia-1 (Athens, Greece). I & II. — *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen, Ser. B*, 78(4):314–338.
- DE BRUIJN, H. & VAN DER MEULEN, A., 1979. A review of the Neogene rodent succession in Greece. — *Annales Géologiques de Pays Helléniques*, 1:207–217.
- DE BRUIJN, H., SARAÇ, G., VAN DEN HOEK OSTENDE, L.W. & ROUSIAKIS, S., 1999. The status of the genus name *Parapodemus* SCHAU, 1938; new data bearing on an old controversy. — [in:] REUMER, J.W.F. & DE VOS J., (eds.). *Elephants have a snorkel! Papers in honour of Paul Y. Sondaar*. — *Deinsea*, 7:95–112.
- DE BRUIJN, H., HOEK OSTENDE, L. van den, KRISTKOIZBOON, E., RUMMEL, M., THEOCHAROPOULOS, C. & ÜNAY, E., 2003. Rodents, lagomorphs and insectivores from the middle Miocene hominoid locality of Çandır (Turkey). — *Courier Forschungsinstitut Senckenberg*, 240:51–87.
- FAHLBUSCH, V., 1996. Middle and Late Miocene Common Cricetids and Cricetids with Prismatic teeth. — [in:] BERNOR, R., FAHLBUSCH, V., MITTMANN, H.-W., (eds.). *The evolution of Western Eurasian Neogene Mammal Faunas*. — 216–219, Columbia

- University Press.
- GRAY, J.E., 1821. On the natural arrangement of vertebrate animals. — *The London Medical Repository, Monthly Journal and Review*, 15:296–310.
- GRAY, J.E., 1825. An outline of an attempt at the disposition of the Mammalia into tribes and families with a list of the genera apparently appertaining to each tribe. — *The Annals of Philosophy, (new series)*, 10:337–344.
- HORDIJK, K. & DE BRUIJN, H., 2009. The succession of rodent faunas from the Mio/Pliocene lacustrine deposits of the Florina-Ptolemais-Servia Basin (Greece). — *Hellenic Journal of Geosciences*, 44:1–83.
- JACOBS, L.L., 1978. Fossil rodents (Rhizomyidae & Muridae) from Neogene Siwalik deposits, Pakistan. — *Museum of Northern Arizona Press, Bull.*, 52:1–103.
- KORMOS, T., 1932. Neue pliozäne Nagetiere aus der Moldau. — *Palaeont. Z.*, 14:193–200.
- KOSTOPOULOS, S.D., SEN, S. & KOUFOS, D.G., 2003. Magnetostratigraphy and revised chronology of the Late Miocene mammal localities of Samos, Greece. — *International Journal of Earth Science*, 92:779–794.
- KOSTOPOULOS, D.S., KOUFOS, G.D., SYLVESTROU, I.A., SYRIDES, G. & TSOBACHIDOU, E., this volume. The Late Miocene Mammal Faunas of the Mytilinii Basin, Samos Island, Greece: New Collection. 2. Lithostratigraphy and Fossiliferous Sites. — *Beiträge zur Paläontologie*, 31:13–26, Wien.
- KOUFOS, D.G., SYRIDES, G., KOSTOPOULOS, S.D., KOULADIMOU, K.K., SYLVESTROU, I., SEITANIDES, G. & VLACHOU, D., 1997. New excavations in the Neogene mammalian localities of Mytilinii, Samos island, Greece. — *Geodiversitas*, 19(4):877–884.
- MEIN, P., MARTIN SUAREZ, E. & AGUSTÍ, J., 1993. *Progonomys* SCHAU, 1938 and *Huerzelerimys* gen. nov. (Rodentia); their evolution in Western Europe. — *Scripta Geologica*, 103:41–64.
- MEYER, C.E.H. von, 1848. Letter on various fossils. — *Neues Jahrbuch fuer Mineralogie*, 1848:465–473.
- PELÁEZ-CAMPOMANES, P. & DAAMS, R., 2002. Middle Miocene rodents from Paşalar, Anatolia, Turkey. — *Acta Palaeontologica Polonica*, 47(1):125–132.
- QUI, Z. & LI, C., 2003. Rodents from the Chinese Neogene: Biogeographic Relationships with Europe and North America. — *Bulletin American Museum of Natural History*, 279:586–602.
- SARICA, N. & SEN, S., 2003. Spalacidae. — [in:] FORTELIUS, M., KAPPELMAN, J. & SEN, S. (eds.). *Geology and Paleontology of the Miocene Sinap Formation, Turkey*. — 141–162, Columbia University Press, New York.
- SCHAUB, S., 1934. Über einige Simplizidentaten aus China und der Mongolei. — *Abhandlungen der Schweizerischen Paläontologischen Gesellschaft*, 54:1–4.
- SEN, S., 1977. La faune de Rongeurs Pliocènes de Çalta (Ankara, Turquie). — *Bulletin du Muséum National d'Histoire Naturelle, Paris, Sciences de la Terre*, 61:89–171.
- SEN, S., 1983. Rongeurs et Lagomorphes du gisement Pliocène de Pul-e Charkhi, bassin de Kabul, Afghanistan. — *Bulletin du Muséum National d'Histoire Naturelle, Paris, Série C*, 1:33–74.
- SEN, S., 1990. Les mammifères du gisement de Develi (Manisa, Turquie). — *Mémoire de D.E.A. de Paléontologie Option Vertébrés Université de Sciences et Techniques du Languedoc-Montpellier II*, 44 pp. + appendices.
- SEN, S., 1998a. The age of the Molayan mammal locality, Afghanistan. — *Geobios*, 31(3):385–391.
- SEN, S., 1998b. Pliocene vertebrate locality of Çalta, Ankara, Turkey. 4. Rodentia and Lagomorpha. — [in:] SEN, S. (ed.). *Geodiversitas*, – 20(3):359–378.
- SEN, S., 2001. Rodents and insectivores from the Upper Miocene of Molayan, Afghanistan. — *Palaeontology*, 44(5):913–932.
- SEN, S., JAEGER, J.-J., DALFES, N., MAZIN J.-M. & BOCHERENS, H., 1989. Découverte d' une faune de petits mammifères pliocènes en Anatolie occidentale. — *Comptes Rendus de l'Académie des Sciences de Paris*, 309:1729–1734.
- SOLOUNIAS, N., 1981. The Turolian fauna from the island of Samos, Greece. — *Contributions to Vertebrate Evolution*, 6:1–232.
- SIMIONESCU, I., 1930. Vertebratele Pliocene de la Măluşteni (Covurlui). — *Academia Română*, 9(49):1–69.
- SUATA-ALPAŞLAN, F., 2003. The Rodentia and Lagomorpha (Mammalia) of the Early Pliocene from Anatolia: biochronological, paleogeographical, paleoecological and paleoclimatological implications. — PhD Thesis, Cumhuriyet University, Department of Geology, Sivas (in Turkish with English summary), “unpublished”
- SUATA-ALPAŞLAN, F., 2004. *Pseudomeriones latidens*, SEN, 2001 (Rodentia, Mammalia) from Karaözü, Kaleköy and Dendil (Sivas, Turkey). — *Antropoloji*, 16:17–29, University of Ankara (in Turkish with English abstract).
- SUATA-ALPAŞLAN, F., in press. *Pseudomeriones hansii* nov. sp. from the early Pliocene/Ruscian fauna of İğdeli (Turkey). — *The Open Geology Journal*.
- SÜMENGİN, M., ÜNAY, E., SARAÇ, G., DE BRUIJN, H., TERLEMEZ, I. & GURMUZ, M., 1990. New Neogene rodent assemblages from Anatolia (Turkey). — [in:] LINDSAY, E.H. et al. (eds.). *European Neogene Mammal Chronology*. — 61–72, Plenum Press, New York.
- SWISHER, C.C., 1996. New ⁴⁰Ar/³⁹Ar Dates and their contribution toward a revised chronology for the late Miocene non-marine of Europe and West Asia. — [in:] BERNOR, R., FAHLBUSCH, V., MITTMANN, H.-W. (eds.). *The evolution of Western Eurasian Neogene Mammal Faunas*. — 64–77, Columbia University Press.
- SYLVESTROU, I.A. & KOSTOPOULOS, D.S., 2007. *Pseu-*

- domeriones megistos* nov. sp. (Gerbillinae, Mammalia) from the Latest Miocene of Northern Greece and its phylogenetic relationships. — *Geobios*, 40:833–848.
- TEILHARD DE CHARDIN, P., 1926. Mammifères du Tertiaire de Chine et de Mongolie. — *Annales de Paléontologie*, 15:1–51.
- THOMAS, O., 1896. On the genera of rodents: an attempt to bring up to date the current arrangement of the order. — *Proceedings of the Zoological Society of London*, 1896:1012–1028.
- TONG, H., 1989. Origine et évolution des Gerbillidae (Mammalia, Rodentia) en Afrique du Nord. — *Mémoires de la Société Géologique de France*, 155:1–120.
- TOPACHEVSKI, V.A., 1969. Fauna of the USSR: Mammals, Mole Rats, Spalacidae. — *Academii Nauk U.S.S.R., New Ser.* 99, Mammiferes, 3(3):1–247. (in Russian, translated in English, Amerind Publ. Co Pvt. Ltd. New Delhi, 1976).
- ÜNAY, E., 1978. *Pliospalax primitivus* n.sp. (Rodentia, Mammalia) and *Anomalomys gaudryi* GAILLARD from the Anchitherium Fauna of Sariçay (Turkey). — *Bulletin of the Geological Society of Turkey*, 21:121–128.
- ÜNAY, E., 1981. Middle and Upper Miocene Rodents from the Bayraktepe Section (Çanakkale, Turkey). — *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen, Ser. B*, 84(2):217–238.
- ÜNAY, E., 1990. A new species of *Pliospalax* (Rodentia, Mammalia) from the Middle Miocene of Paşalar, Turkey. — *Journal of Human Evolution*, 19:445–453.
- ÜNAY, E., 1996. 19. On Fossil Spalacidae (Rodentia). — [in:] BERNOR, R.L., FAHLBUSCH, V. & MITTMANN, H.W. (eds.). *The Evolution of Western Eurasian Neogene Mammal Faunas*. — 246–252, Columbia University Press, New York.
- ÜNAY, E. & DE BRUIJN, H., 1998. Plio-Pleistocene rodents and lagomorphs from Anatolia. — *Mededelingen Nederlands Instituut voor Toegepaste Geowetenschappen TNO*, 60:431–466.
- VAN DE WEERD, A., 1976. Rodent faunas of the Mio-Pliocene continental sediments of the Teruel-Alfambra region, Spain. — *Utrecht Micropaleontological Bulletins, Special Publications*, 2:1–217.
- WESSELS, W., 1998. Gerbillinae from the Miocene and Pliocene of Europe. — *Mitteilungen der Bayerischen Staatssammlung für Paläontologie und historische Geologie*, 38:187–207.
- WESSELS, W., 1999. 38. Family Gerbillidae. — [in:] RÖSSNER, G. & HEISSIG, K. (eds.). *The Miocene Land Mammals of Europe*. — 395–400.
- ZHANG, Z., 1999. Pliocene micromammal fauna from Ningxian, Gansu province. — *Proceedings of the Seventh Annual Meeting of the Chinese Society of Vertebrate Paleontology*, 167–177. (in Chinese with English abstract).

PLATE 1

Pseudomeriones pythagorasi from MTLA and MTLB:

- Fig. a M1 sin, MTLA-1
- Fig. b M1 dex, MTLB-1
- Fig. c M2 sin, MTLA-4
- Fig. d M2 sin, MTLB-3
- Fig. e M2 dex, MTLB-4
- Fig. f M2 dex, MTLB-2
- Fig. g m1 sin, MTLA-2
- Fig. h m1 dex, MTLA-3
- Fig. i m2 dex, MTLB-5
- Fig. j m1-m2 dex, MTLA-5.

Figs. a-h, scale bar 1mm; fig. i, scale bar 300 μ m; fig. j, scale bar 200 μ m.

All teeth are illustrated as coming from the left side.

PLATE 1

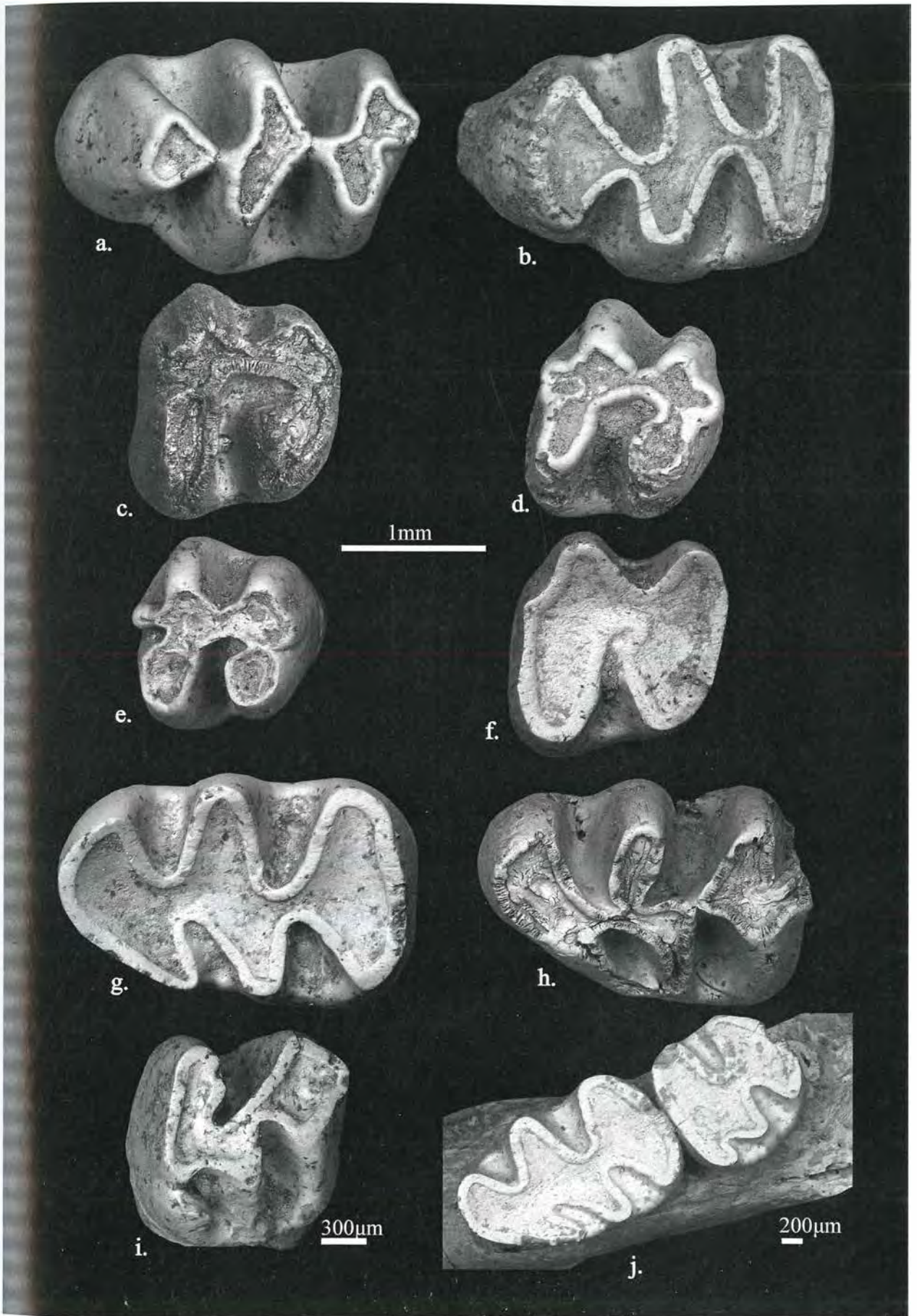


PLATE 2*'Karnimata' provocator* from MTLA:

- Fig. a m1 dex, MTLA-7
Fig. b m2 dex, MTLA-8a
Fig. c m3 dex, MTLA-8b

Spermophilinus cf. bredai from MTLA and MTLB:

- Fig. d M1/2 dex, MTLA-6
Fig. e m2 sin, MTLB-6

Pliospalax cf. sotirisi from MTLB:

- Fig. f M1 sin, MTLB-7a
Fig. g M2 sin, MTLB-7b
Fig. h M3 sin, MTLB-7c

The scale bar is 1 mm. All teeth are illustrated as coming from the left side.

PLATE 2

