Beitr. Paläont., **31**:283–297, Wien 2009

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

12. Suidae

by

Ioanna A. Sylvestrou*) & Dimitris S. Kostopoulos*)

Sylvestrou, I.A. & Kostopoulos, D.S., 2009. The Late Miocene Mammal Faunas of the Mytilinii Basin, Samos Island, Greece: New Collection. 12. Suidae. — Beitr. Paläont., **31**:283–297, Wien.

Abstract

New suid material from Samos is described and compared to that from old Samos collections. Apart from a partially preserved skull of *Propotamocherus* of unknown stratigraphic origin the rest of the Samos suid specimens belong to a population of large-sized *Microstonyx major*, and this study adds some more information on the sexual dimorphism of the species. *Microstonyx major* appears to be constantly present in the whole chronological succession of Samos mammal assemblages but it shows a size reduction towards late Turolian.

Keywords: Late Miocene, Samos, Greece, Mammalia, Suidae, Systematics.

Zusammenfassung

Neues Suidenmaterial von Samos (Griechenland) wird beschrieben und mit Material aus den alten Sammlungen verglichen. Abgesehen von einem teilweise erhaltenen Schädel von *Propotamochoerus* von unbekannter stratigraphischer Herkunft, stammen alle anderen Suidenfunde von Samos aus einer Population der großen Form *Microstonyx major*. Diese Studie bringt zusätzliche Informationen zum Geschlechtsdimorphismus der Art. *Microstonyx major* dürfte in der ganzen chronologischen Abfolge der Samos Säugetiervergesellschaftung anwesend gewesen sein, zeigt aber eine Größenreduktion gegen Ende des Turoliums.

Schlüsselworte: Obermiozän, Samos, Griechenland, Mammalia, Suidae, Systematik.

*) Dr. Ioanna A. Sylvestrou & Dr. Dimitris S. Kostopoulos, Aristotle University of Thessaloniki. Department of Geology. Laboratory of Geology and Palaeontology. GR-54124 Thessaloniki, Greece. e-mail: sylvest@geo.auth.gr, dkostop@ geo. auth.gr

1. Introduction

Suid material from Samos is rare. Thenius (1950) described a sub-adult skull (Fig. 1) of a small suine as a new subgenus *Postpropotamochoerus hyotheriodes* (Schlosser, 1903), a species that is currently placed into an unnamed species of *Propotamochoerus* Pilgrim, 1926 (de Bonis & Bouvrain, 1996; van der Made & Moya-Sola, 1989; van der Made et al., 1999). Although Bernor et al. (1996) place this form in the Main Bone Beds Member of Mytilinii Formation of Samos (Weidmann et al., 1984) in co-existence with *Microstonyx*, the stratigraphic provenance of the material studied by Thenius (1950) is unknown and thus chronological suggestions are highly speculative.

In contrast to the rare *Propotamochoerus*, Samos collections in several Museums and Institutions include important, though not abundant, large suine specimens assigned to the widespread genus *Microstonyx* (Pilgrim, 1926). Recent studies and reviews of this taxon recognize a single species *M. major* (Gervais, 1848) of Turolian age (Liu et al., 2004, 2005), whereas the Vallesian *Sus antiquus* Kaup, 1833 is transferred to *Hippopotamodon* Lydekker, 1887 (Fortelius et al., 1996; Bernor & Fessaha, 2000). *M. major* appears at the very beginning of Turolian (Kostopoulos, 1994) and is known from almost every Turolian site of the Greco-Iranian province, showing however a quite complicated history that is probably controlled by ecological factors (Liu et al., 2004). The 1994-2006 excavations in the Mytilinii Basin of Samos (Koufos et al., 1997) brought to light a new *Microstonyx* sample from Mytilinii-1A (MTLA) site to light, which is studied here in combination with the old material.

Abbreviations: NHMA(Aegean Museum of Natural History), AMNH (American Museum of Natural History), MGL (University of Lausanne), NHNW (Natural History Museum of Vienna), NHML (Natural History Museum London) and MNHNP (Museum national d' Histoire naturelle, Paris); upper case letters (I, C, P, M) for upper teeth; lower case letters (i, c, p, m) for lower teeth; D/d for milk teeth; L = length; W = width;

Figure 1: *Propotamochoerus* sp. from Samos, NHMW-exposition. Scale bar 2 cm.

W1, W2, W3 = width of the anterior lobe, posterior lobe and talon/talonid respectively; DAP = anteroposterior diameter

2. Systematics

Family Suidae Gray, 1821

Subfamily Suinae Gray, 1821

Genus *Microstonyx* Pilgrim, 1926

Microstonyx major **(Gervais, 1848)**

Localities - Ages:
Mytilinii-1A (MTLA), Adrianos ravine; middle Turolian (MN12), 7.1-7.0 My
Quarry 4 (Q4), Potamies ravine; early middle Turolian (MN11), <7.3 My
Quarry 1 (Q1), Adrianos ravine; middle Turolian (MN12), 7.1-7.0 My
Quarry 5 (Q5), Limitzis; early late Turolian (MN13), 6.9-6.7 My
MGLS Stefano (MGLSs), Stefana Hill, late early Turolian (MN11), 7.6-7.4 My
The material from NHMW has no locality indication.

Studied Material:
NHMA: skull, MTLA-537; mandible with p2-m3 dex and sin, MTLA-300; right mandible with p2-m3, MTLA-479; snout with incisors and canine, MTLA-10; distal part of radius, MTLA-428; astragalus, MTLA-375; left metacarpal IV, MTLA-383; distal part of left metacarpal III, MTLA-384.
AMNH:
Q4: left and right milk tooth row with DP1-M1, AMNH20797A; left juvenile mandible with dp2-m1 and right juvenile mandible with dp3-m1, AMNH22882;
Q1: right juvenile maxilla with DP3-M1, AMNH 20616.
Q5: part of opisthocranium, AMNH20769; palate with P2-M3 dex and sin, AMNH20653; palate with P2-M3 dex and sin, AMNH20795; left mandible with m1-m2, AMNH20795.
MGL: skull specimen with P1-M3, MGL S197, Stefano.
NHMW: skull specimen, NHMW A4789; mandible with i1-m3 dex and i1-c sin, NHMW 1911v211. The provenance of the material is unknown but judging from the type of fossilization it seems that it could originate from the lower fossil horizons.

Description: The skull specimen (MTLA-537) is well-preserved and belongs to an adult male individual (M2 in moderate stage of wear) (Pl. 1, Figs. 1-3). The skull is large and typically *Microstonyx*-like (Table 1). The posterior part of the skull is strongly elevated. The occiput is large, triangular shaped, concave in its middle, and ending upwards into a strong and straight nuchal crest. The temporo-parietal region is concave. The fronto-parietal region is flat and wide, marked laterally by the well-developed parallel-running parietal crests. The nasal bones are elongated, broad and slightly concave in their distal part; their posterior end is placed above M3, while the nasal notch is situated above the anterior level of the alveolar crests. The zygomatic arches are strong, significantly extended laterally and prolonged to the front with a short and rather weak facial crest, whose anterior end is placed above the middle of M1. The orbit is small and oval-shaped, with a large and moderately deep lacrymal notch. The anterior rim of the orbit is placed well behind M3. The alveolar crests are strongly developed with rough surfaces. In ventral view, the occipital condyles are small, the choanae opens more than 10 mm behind M3, the palate is elongated and narrow and the muzzle is oval-shaped. The P1 is missing and the canine is small compared to the skull size and oval shaped. A fragmentary part of an opisthocranium at the AMNH (AMNH20769)

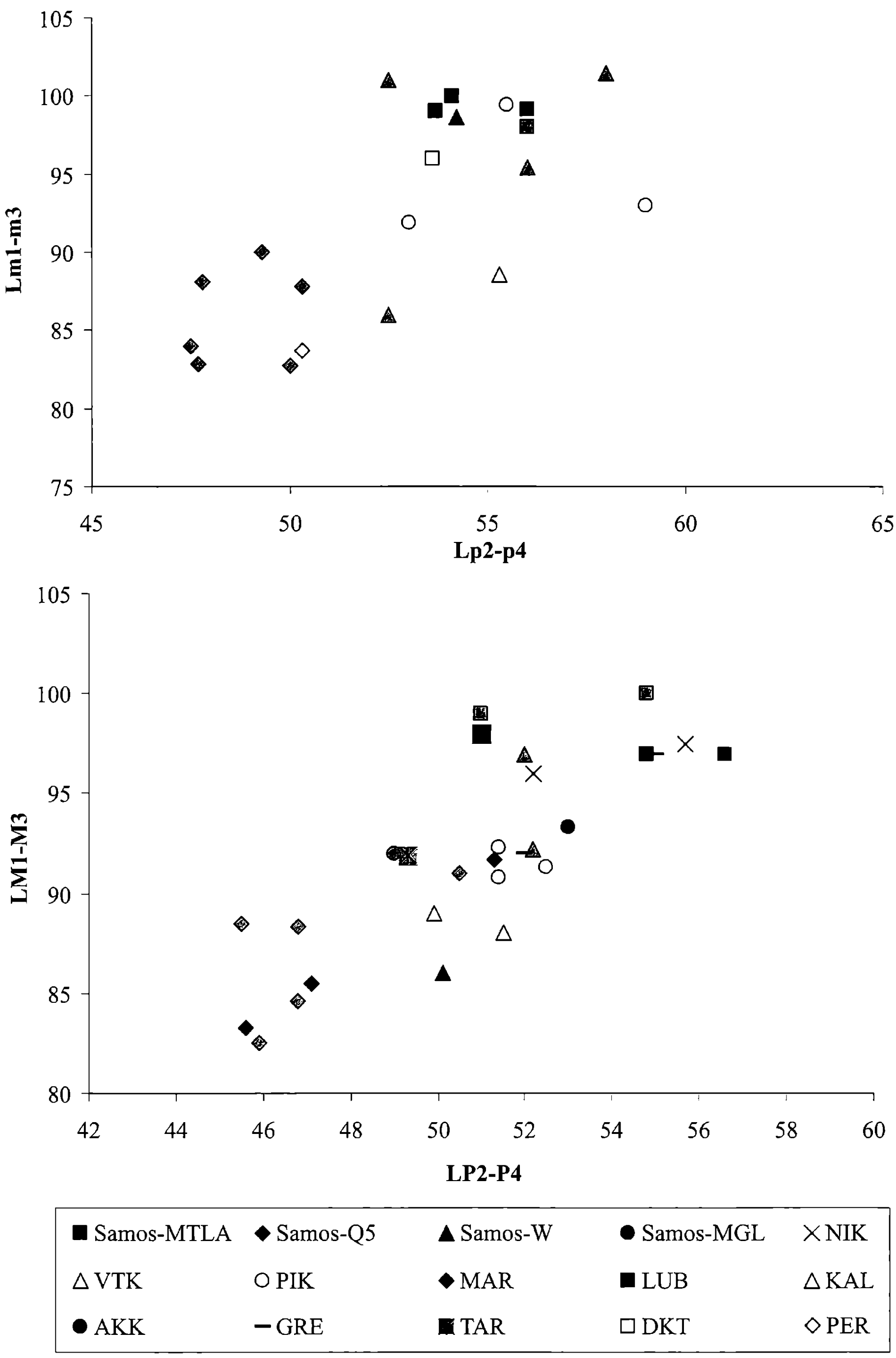

Figure 2: Lower and upper premolar-molar ratio in several populations of *Microstonyx major* from SE Europe. Data from GAUDRY (1873), TROFIMOV (1954), KOSTOPOULOS (1994), DE BONIS & BOUVRAIN (1996), KOSTOPOULOS et al. (2001), LIU et al. (2005), SYLVESTROU & KOSTOPOULOS (2006), and personal data.

Abbreviations: Samos-MTLA: Mytilinii-1A, Samos, Greece; Samos-Q5: Q5, AMNH, Samos, Greece; Samos-W: unknown locality, NHMW, Samos, Greece; Samos-MGL: Stefano, MGL, Samos, Greece; PER: Perivolaki, Greece; VTK: Vathylakkos, Greece; PIK: Pikermi, Greece; DTK: Dytiko, Greece; NIK: Nikiti-1, Greece; MAR: Maragheh, Iran; LUB: Mont Luberon, France; KAL: Kalimantsi, Bulgaria; AKK: Akkasdaği, Turkey; GRE: Grebeniki, Ukraine; TAR: Taraklija, Ukraine.

from Q5 is also similar to MTLA-537, and according to its strong parietal crests, it should also belong to a male individual.The skull NHMW A4789 is weakly compressed medio-laterally and lacks the opisthocranium (Pl. 2, Fig. 1). Judging by the moderately worn M3, the specimen should belong to an adult individual. The general skull structure is entirely comparable to that of MTLA-537, but the zygomatic arch is less protruding laterally and shifted more posteriorly (its anterior end is placed above the middle of M2), the choanae opens just behind M3, the supraorbital region is less flat and wide, the alveolar crests are barely visible, the canine is extremely small and placed closer to I3, whereas the muzzle is pointed more anteriorly. The left tooth row looks as if a P1 was present in life. The skull MGL S197 from Stefano is strongly damaged, lacking most of the occiput, the muzzle and the entire zygomatic arches, and therefore cranial morphometrical observations are limited. The freshly erupted teeth indicate a young adult individual, whereas the tooth row preserves a bi-rooted P1 in line with P2-P4. The alveolar crests are minute and the orbit is placed well behind M3. The morphology of the upper milk teeth of the specimens AMNH20616 from Q1 and AMNH20797A from Q4 is similar to each other, as well as to that of *M. major* from Pikermi (MNHNP PIK762). The DP1 is present in both milk tooth rows of AMNH20797A from Q4; the tooth is bi-rooted and strong with a main cusp placed anteriorly, associated with additional anterior and posterior cusplets. In

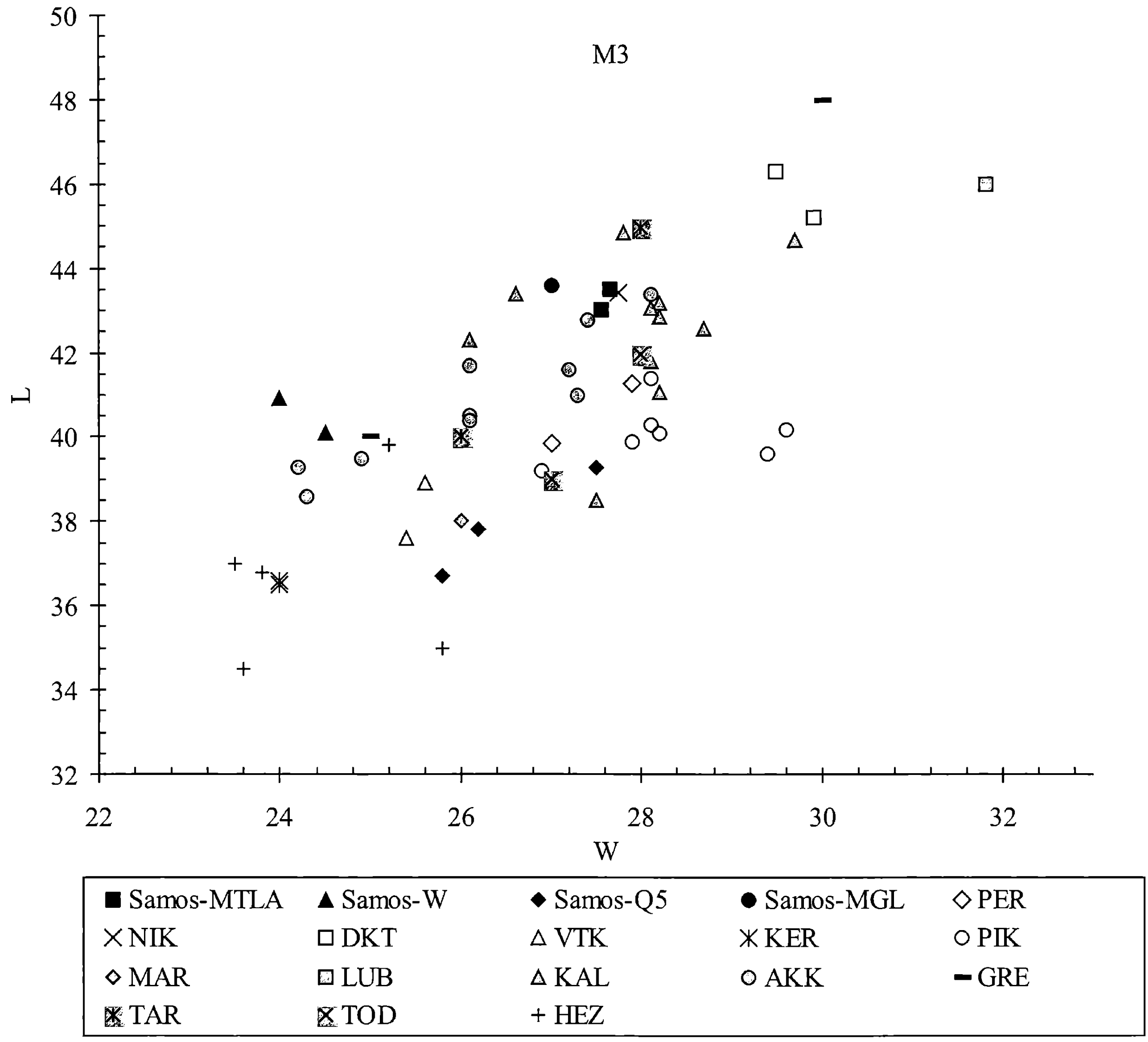

Figure 3: M3 proportions in several populations of *Microstonyx major* from SE Europe. Data from Kostopoulos (1994), Kostopoulos et al. (2001), Sylvestrou & Kostopoulos (2006), de Bonis & Bouvrain (1996), Liu et al. (2004, 2005) and personal data. **Abbreviations** as in Fig. 2 plus: KER: Kerassia, Greece; TOD: Todurovo, Ukraine; HEZ: Hezheng, China.

the DP2 the main cusp is placed centrally, there is a strong postero-lingual cusp and a strong antero-posterior labial cingulum. The DP3 is sub-triangularly shaped with three main cusps and strong postero-labial and lingual cingula. The DP4 is similar to the M1, but with a stronger anterior cingulum and weaker talon (Pl. 2, Fig. 6). The upper incisor's morphology of MTLA-537 is closely comparable to that described by Liu et al. (2004) for *Microstonyx major* from China but the canine morphology is not available in the Samos sample.

The length of the upper toothrow (P2-M3) is 155.1 mm in MTLA-537, 146.7 mm in MGL S197 and 137.2 mm in NHMW A4789, whereas it ranges between 130.4-144.8 mm in AMNH samples from Q5 (n = 3). The premolar/molar ratio ranges from 56.5-58.4 in MTLA, NHMW and MGL specimens (n = 3) but it appears somewhat lower in Q5 (54.7-55.9; n = 3), probably indicating a weak reduction of the premolar row. Tooth measurements are given in Tables 2, 3. The P2 is simple, with a main central and a secondary posterior cusp associated by strong postero-lingual and anterior cingula, both forming additional cusplets in some cases. The P3 is sub-triangularly shaped with a strong antero-posterior lingual cingulum that forms a well developed postero-lingual talon which might bear a cusp (protocone). The paracone and the metacone are equally developed, separated by a weak labial groove. The postero-labial cingulum is variably developed. The P4 is sub-squarish and wider than long. The posterior cingulum is strong. The metacone and the paracone are well developed and distinct. Lingually, the specimens MTLA-537, AMNH20653 and AMNH20795 have a main cusp (protocone), occasionally associated with a small posterior cusplet, whereas in the P4 of the specimen MGL S197, there are two equally developed lingual cusps (protocone and hypocone). The M3 bears a strong anterior cingulum. Its talon is placed lingually in series with the protocone and the hypocone and is formed by a main posterior cusp (pentacone of van der Made, 1996) and several second-

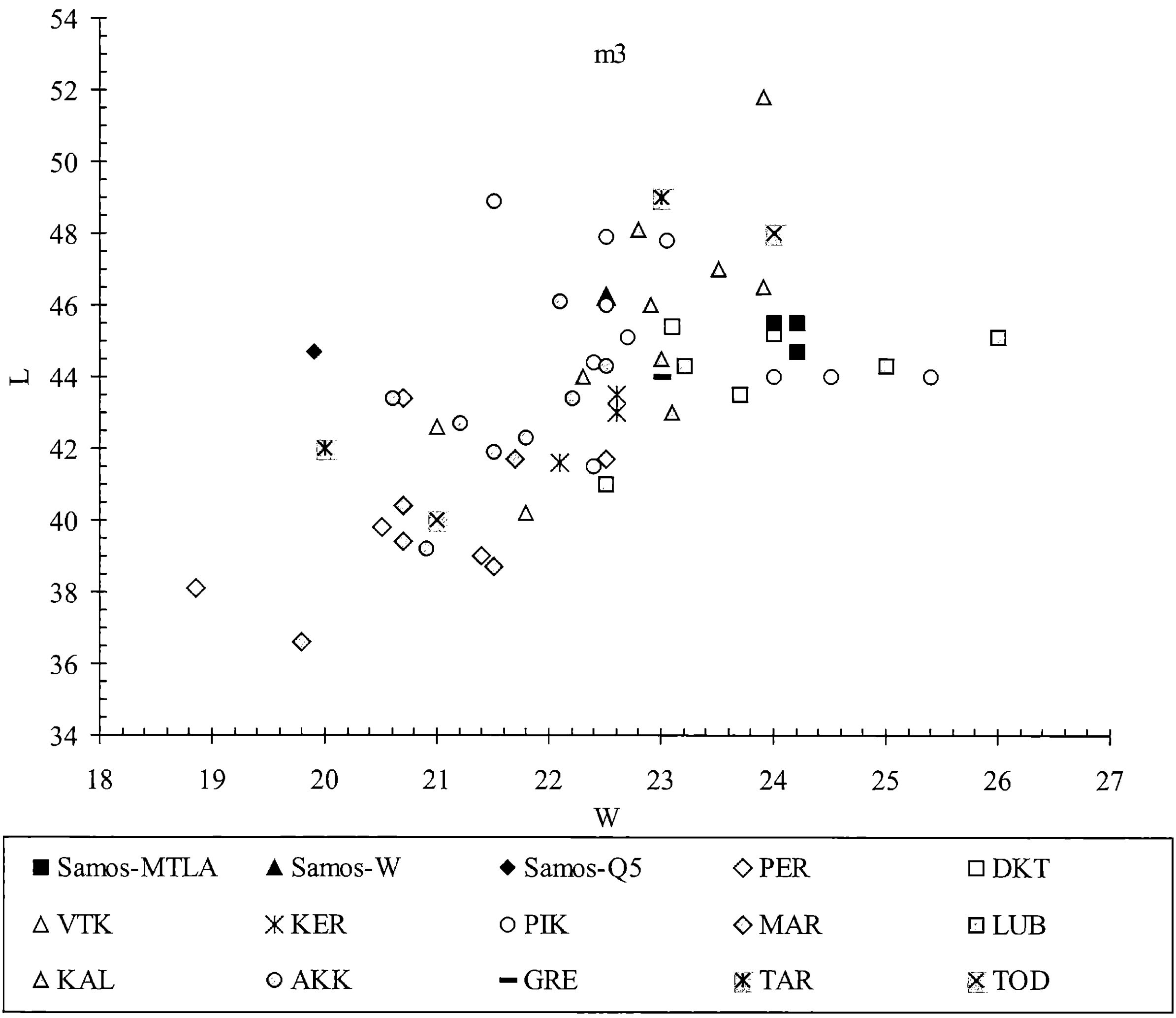

Figure 4: m3 proportions in several populations of *Microstonyx major* from SE Europe. Data sources and abbreviations as in Figs 2, 3.

ary peripheral cusplets (Pl. 1, Fig. 3; Pl. 2, Fig. 8). The mandibles MTLA-300 and NHMW1911v211 preserve the snout and the horizontal rami, whereas MTLA-10 represents another snout-specimen (Pl. 2, Figs 2, 3, 4). The Vienna mandible fits perfectly with the cranium NHMW1911v211 and it is quite possible that they represent a single individual. In all cases the snout is long and relatively narrow; the posterior edge of the symphysis is placed well in front of p2. The canines of MTLA-10 and MTLA-300 are larger than those of NHMW1911v211 and are curved antero-laterally, whereas the canines of the Vienna specimen are straight and pointed forwards. Although the length of the symphysis is similar in all specimens, its minimum width appears to be somewhat larger in both specimens from MTLA than in NHMW1911v211. The i1 is long with a sub-triangular cross-section and pointed forwards. The larger i2 is asymmetrical, gradually shortened towards the rear and with a clear labial notch caused by the attachment of the i3. The main part of the wear surfaces of both the i1 and i2 is rather horizontal. The i3 is a smaller version of i2 but the wear surface is convex in lateral view. The dp2 is very small and simple with a main central elongated cuspid. The dp3 is larger than dp2 but it has a similar morphology with an additional small postero-labial cusplet. The dp4 is long and narrow formed by three lobes that increase towards the rear (Pl. 2, Fig. 5).

The p2-m3 length varies between 151.0 and 156.5 mm with a premolar/molar ratio (Lp2-p4 x 100/Lm1-m3) of 54-56. Lower tooth measurements are given in Tables 4, 5. The p2 is simple, with a main central elongated cuspid. The p3 is quite similar to p2, but the main cuspid extends medio-laterally being separated from the posterior cuspid. In the p4 the metaconid, protoconid and hypoconid are well developed. The first two lower molars have a similar morphology. In the adult individuals, there is no evidence for an anterior cingulum whereas the posterior cingulum is weak. Nevertheless, on the m1 of a juvenile specimen (AMNH22882-Q4), there also is an anterior cingulum. The accessory cuspids (preconulid and pentaconid of van der Made, 1996) are present. The main cuspids of m3 are equally developed, whereas in NHMW1911v211 an anterior cingulum is evident. The talonid is large with two main and one accessory cuspid. The entoconulid and the preconulid are present (Pl. 2, Fig. 7). The few available postcranials (Table 6) are insufficient for detailed morphological observations but they look similar (Pl. 2, Fig. 9) to the *M. major* limbs from Akkaşdaği (Liu et al., 2005).

Comparison: The general morphological features of the Samos large suid, such as its large size, the elevated occiput, the wide and flat frontopariental region, the inflated and laterally extended zygomatic arches, the strong lacrymal notch, the narrow and elongated palate, the elongated snout and the strong alveolar crests associated by small canines and suine dental morphology are typical for *Microstonyx* (Gaudry, 1862-67, 1873; Trofimov, 1954; van der Made & Moya-Sola, 1989; Kostopoulos et al., 2001; Liu et al., 2004, 2005).

The skull MTLA-537 is metrically placed among the largest known specimens of *M. major* from Pikermi (MN 12/13, Greece), Grebeniki (MN 11/12, Ukraine), Taraklija (MN12, Ukraine) and Kalimantsi (MN12, Bulgaria), being slightly larger than the specimens from Nikiti-1 (latest MN10, Greece) and Akkaşdaği (MN12, Turkey) and significantly larger that the Hezheng suid (China) (Table 1). The NHMW A4789 skull is slightly smaller than that of MTLA (Table 1) and closer to the Nikiti-1 skull and NHML M9048 from Pikermi which represent females of the species *M. major*. Indeed, the strong alveolar crests (see Liu et al., 2005:fig. 9, where "Samos" represents MTLA-537) and the great width of the skull MTLA-537 at the zygomatic arches indicate a stout boar, whereas the tiny alveolar crests and the weaker zygomatic arches of the specimen NHMW A4789 rather suggest a female individual. A metrical comparison of the skull MGL S197 from Stefano is not possible because of its bad preservation; its basicranial length does not, however, exceed 400 mm indicating a quite smaller morphotype, which is comparable to a female individual.

If indeed the Vienna sample originates from the lowermost fossil level of Samos (Qx-Vryssoula level; 8.0-7.6 Ma), as its preservation status lets us assume, then *M. major* appears to be constantly present in the entire Samos faunal succession, being recorded from Stefano (7.65-7.45 Ma), Q4 (7.3-7.2 Ma), Q1 and MTLA (7.1-7.0) and Q5 (~6.8 Ma) with certainity.

Metrical analysis of *M. major* dentition carried out by Kostopoulos et al. (2001) and Liu et al. (2004) showed that most local populations of the species are placed either into a small or a large sized morphotype, without, however, a chronological or geographical distinction being possible between them. Both the upper and lower dentitions from Samos fall within the variation range of large-sized *M. major* (Fig. 2). Nevertheless, the upper toothrow indicates a gradual increase of the P2-M3 length from the lower fossil level to Q1-MTLA, with the premolar/molar ratio being stable between 56 and 58. On the contrary, from Q1-MTLA level to Q5 *M. major*'s upper dentition implies an overall decrease in absolute dimensions and an associated reduction of the premolar row compared to the molars (Fig. 2). From the Vienna sample to the Stefano and MTLA specimens, the M3 widens, retaining its length whereas from MTLA to Q5 the M3 shortens but remains as wide as previously (Fig. 3). Samos data concerning the lower dentition is fewer. Although the Vienna p2-m3 tooth rows appear slightly shorter than those of MTLA, the premolar/molar ratios of both samples are similar and close to those from Mont Luberon (France), Dytiko (Greece), Ezerovo (Bulgaria) and the largest specimens from Pikermi and Kalimantsi (Fig. 2). Similar to the upper dentition, the Vienna m3 has a greater width than the MTLA sample, whereas the Q5 m3 is narrower than the MTLA sample (Fig. 4).

Kostopoulos et al. (2001) and Liu et al. (2004, 2005) already discuss several aspects of sexual dimorphism in the skull and dentition of *Microstonyx major*. The Samos collection confirms most of their conclusions and permits us to add some new information. According to Liu et al. (2004, 2005) the P1 is more frequently retained in the female skulls of *M. major*. Both the presumed female skulls of Lausanne (MGL S197) and Vienna (NHMW A4789) bear P1. Nevertheless, and since the maintenance of this tooth is certainly a plesiomorphic feature, we cannot exclude the possibility that the tooth is also more frequently present in the earlier populations of the species than in the later ones. Hence, a bi-rooted P1 in series with P2 occurs in Nikiti-1, as well as in the early Samos populations, whereas in Pikermi, Kalimantsi, Grebeniki, Taraklija, Titov Veles and Hezheng the tooth if present is either single or bi-rooted but always separated from P2 by a diastema. Liu et al. (2004) note a weak canine bi-modality in *M. major* that is also evident between the MTLA and Vienna skulls of Samos, where the female muzzle appears to be more pointed additionally than the male one. Apart from being slightly larger, the lower canines of male individuals from Samos curve antero-laterally, whereas the female ones are straighter and pointed forwards. The female canine morphology is associated by a narrower symphysis than in males, whereas the body of the horizontal ramus is more bulbous in males than in females. This differentiation in the mandibular shape is also recorded of *M. major* from Maragheh (MNHNP MAR601-603-females, MNHNP MAR3302, 3307-males; pers. obs.) Bulgaria (Kostopoulos et al., 2001:fig. 6), Hezheng (Liu et al., 2004:fig. 4C) and Akkaşdaği (Liu et al., 2005:fig. 2B - female, 2C - male).

3. Conclusion

Two suoid lineages appear in the Samos record during Turolian time. The first one is represented by a small *Propotamochoerus* of unknown stratigraphic origin that most probably belongs to a rare distinct Balkan species (Geraads et al., 2008). The second one is represented by a large-sized morphotype of the common suine *Microstonyx major* that appears to be constantly present in the whole succession of the Samos mammal assemblages. Although statistically insufficient, the Samos samples from chronologically successive horizons indicate proportional fluctuations especially in teeth, that might be related to ecological adaptations. Liu et al. (2004) have already shown that cranial and dental polymorphy seen in *M. major* is due to ecological flexibility, allowing for local ecotypes.

4. 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. Thanks are also due to Dr. R. Bernor for insightful comments on the original manuscript.

5. References

Bernor, R.L. & Fessaha, N., 2000. Evolution of Late Miocene Hungarian Suinae (Artiodactyla, Suidae). — Carolinea, **58**:83–92.

Bernor, R.L., Solounias, N., Swisher, C.C. & Couvering, J.A. van, 1996. The correlation of the classical "Pikermian" mammal faunas Maragheh, Samos and Pikermi, with the European MN unit system. — [in:] Bernor, R.L., Fahlbusch, V., Mittmann, H.-W. (eds.). The Evolution of Western Eurasian Neogene Mammal Faunas. – 137–154, New York (Columbia University Press).

Bonis, L. de & Bouvrain, G., 1996. Suidae du Miocène supérieur de Grèce. — Bulletin du Musèum national d'Histoire Naturelle, Paris, 4eme ser., **18**:107–132.

Fortelius M., Made van der, J. & Bernor R., 1996. Middle and late Miocene Suoidea of central Europe and the eastern Mediterranean: evolution, biogeography and paleoecology. — [in:] Bernor, R.L., Fahlbusch, V., Mittmann, H.-W. (eds.). The Evolution of Western Eurasian Neogene Mammal Faunas. – 348–377, New York (Columbia University Press).

Gaudry, A., 1862-1867. Animaux fossiles et geologie de l'Attique. – Savy, F. (ed.). 1–472, Paris.

Gaudry, A., 1873. Animaux fossiles du Mont Lubéron (Vaucluse), Étude sur les Vertébrés. – Savy, F. (ed.). 1–180, Paris.

Geraads, D., Spassov, N. & Garevski, R. 2008. New specimens of *Propotamochoerus* (Suidae, Mammalia) from the late Miocene of the Balkans. — Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, **248**(1):103–113.

Gervais, P., 1848-1852. Zoologie et paléontologie française. – Bertrand A. (ed.). 1–271, Paris.

Kaup, J.J., 1833. Description d'ossements fossiles de mammifères. – Meyer, J. G. (ed.). 2:1–31, Darmstadt.

Kostopoulos, D.S., 1994. *Microstonyx major* (Suidae, Artiodactyla) from the late Miocene locality of "Nikiti-1", Macedonia, Greece; some remarks about the species. — Bulletin of the Geological Society of Greece, **30**(1):341–355.

Kostopoulos, D.S., Spassov, N. & Kovachev, D., 2001. Contribution to the study of *Microstonyx*: evidence from Bulgaria and the SE European populations. — Geodiversitas, **23**(3):411–437.

Koufos, G., Syrides, G., Kostopoulos, D., Koliadimou, K., Sylvestrou, I., Seitanidis, G. & Vlachou, Th., 1997. New excavations in the Neogene mammalian localities of Mytilinii, Samos island, Greece. — Geodiversitas, **19**(4):877–885.

Liu, L.P., Kostopoulos, D.S. & Fortelius, M., 2004. Late Miocene *Microstonyx* remains (Suidae, Artiodactyla) from Hezheng areas. — Geobios, **37**(1):49–64.

Liu, L.P., Kostopoulos, D.S. & Fortelius, M., 2005. Suidae (Mammalia, Artiodactyla) from the late Miocene of Akkaşdaği, Turkey. — Geodiversitas, **27**(4):715–733.

Pilgrim, G., 1926. The fossil Suidae of India. – Memoirs of the Geological Survey of India. — Palaeontologica Indica, **8**:1–65.

Schlosser, M., 1903. Die fossilen Säugethiere Chinas nebst einer Odontographie der recenten Antilopen. — Abhandlungen der Bayerischen Akademie der Wissenschaften, II, **22**(1):1–221, München.

Sylvestrou, I. & Kostopoulos, D.S., 2006. The late Miocene vertebrate locality of Perivolaki, Thessaly, Greece. 7. Suidae. — Palaeontographica, Abt. A, **276**:121–133, Stuttgart.

Thenius, E., 1950. *Postpropotamochoerus* nov. subgen., *hyotheriodes* aus dem Unterpliozän von Samos (Griechenland) und die Herkunft der Potamochoeren. — Sitzungsberichte der Akademie der Wissenschaften, mathemat.-naturwiss. Kl., **159**(1-5):25–36.

Trofimov, B.A., 1954. The fossil suids of the genus *Microstonyx*. — [in:] Tertiary Mammals, part 2: On the Mammalia of the Southern SSSR and Mongolia. — Doklady Akademii Nauk SSSR, 47:61–99.

van der Made, J., 1996. Listriodontinae (Suidae, Mammalia), their evolution, systematics and distribution in time and space. — Contributions to Tertiary and Quaternary Geology, **33**:3–254.

van der Made, J. & Moyà-Solà, S., 1989. European Suinae (Artiodactyla) from the late Miocene onwards. — Bolletino della Società Paleontologica Italiana, **28**(2-3):329–339.

van der Made, J., Krakhmalnaya, T. & Kubiak, H., 1999. The pig *Propotamochoerus palaeochoerus* from the Upper Miocene of Grutsiv, Ukraine. — Estudios Geologicos, **55**:283–292.

Weidmann, M., Solounias, N., Drake, R.E. & Curtis, G.H., 1984. Neogene stratigraphy of the eastern basin, Samos Island, Greece. — Geobios, **17**(4):477–490.

	SAMOS		Nikiti	Pikermi		Akkaşdaği	Hezheng	Grebeniki		Taraklija	Bulgaria		
skull measurements	MTLA 537	MNHWA 4789	NKT-68	NHML M9048	Gaudry's specimen	AK3-131 female	HMV0976 male	MGRI-1781	MOGU-2642	MOGU-2641	K-5258	K-5260	K-5259
Maximal basal length	475.0	427.0	430.0	420.0	470.0	468.0	<380	450.0	450.0	483.0	>450	>420	
Length prosthion-opisthion	600.0		510.0		(600)			550.0	587.0	610.0	435		
Length from the end of nasal bones to the middle of occipital crest	~530.0		>450					516.0	565.0	580.0			
Length of nasal bones	>216		260+					290.0	302.0	310.0			
Length from the basion to the posterior end of sphenoid	75.0		69.0					70.0	80.0				
Length from basion to the anterior end of choane	132.3	130.0	124.5	125.9		114.0	123.0	125.0	132.0	132.0			
Greatest breadth of the skull (at the zygomatic arches)	294.0		220.0	272.0	(310)	262.0	>220	255.0	295.0	257.0	235.0	260.0	
Breadth of the frontal (at the supraorbital processes)	159.7		137.0	156.5				146.0		136.0		153.0	
Minimal breadth of nasal bones	63.3		68.0					65.0	79.0	56.0			
Palatal breadth in the anterior end of M3	42.5		44.0	51.0		42.0	38.3	45.0	48.0	45.0			
Palatal breadth in the anterior end of P2	63.0		56.7					52.0	65.0	56.0			
Palatal breadth in the posterior end of I2	57.8		53.0					48.0	50.0	40.0			
Height of the skull from basion to the middle of occipital crest	212.2		150.0	184.0				197.0	215.0	233.0			
Minimal distance between the orbits	121.8		96.0					112.0	127.0	116.0			
Maximal length of the orbit	47.2		52.0				42.5	63.0	54.0				
Length of the diastema between canine and P2	51.7			44.0		40.8	51.7						
P2-P4/M1-M3	0.57-0.58			0.58		0.57	0.53				0.54-0.57		
alveolar tuberosities DAP x Height	90.4 x 38.5			58 x 24	87 x 41	64 x -		75 x 32	85 x 34			60 x 24	78x35.3
Length M3-I1	304.3	275.0											

Table 1: Cranial measurements of *Microstonyx major* from Samos and other late Miocene sites. Data from Trofimov (1954), Kostopoulos (1994), Kostopoulos et al. (2001), Liu et al. (2004, 2005), and personal data.

Maxilla	MTLA 537	MGL S197	AMNH 20797-Q4 dex	AMNH 20797-Q4 sin	AMNH 20653-Q5 sin	AMNH 20653-Q5 dex	AMNH 20795-Q5 dex	NHMW A4789
Length P2-P4	54.8-56.6	53.0	50.9	52.0	45.6	47.1	51.3	50.1
Length M1-M3	97.0	93.3			83.3	85.5	91.7	86.0
Length P2-M3	155.16	146.7			130.4	133.0	144.8	137.2

Table 2: Upper toothrow segments in *Microstonyx major* from Samos.

		I1	I2	I3	C	P1	P2	P3	P4	M1	M2	M3
MTLA-537 dex	L	26.6	28.2				18.6	19.8	17.1	24.0	29.5	43.6
	W1						9.9	14.3	19.0	20.5	25.7	27.7
	W2									19.1	25.0	25.5
	W3											15.3
MTLA-537 sin	L			15.5			18.5	19.7	16.5	22.9	30.7	43.1
	W1						10.5	15.4	19.6	20.3	25.5	27.6
	W2									19.8	25.1	25.6
	W3											14.1
AMNH 20653-Q5sin	L						15.2	17.8	14.8	18.3	28.7	37.8
	W						8.1	12.1	16.0		22.8	26.2
AMNH 20653-Q5dex	L						16.6	16.9	15.7	20.4	26.4	36.7
	W						9.2	13.9	18.1	17.9	23.6	25.8
AMNH 20795-Q5dex	L						16.4	18.6	15.3	22.9	31.0	39.3
	W						9.9	15.5	19.5	20.0	23.6	27.5
		DI1	**DI2**	**DI3**	**C**	**DP1**	**DP2**	**DP3**	**DP4**	**M1**	**M2**	**M3**
AMNH 20616-Q1dex	L							16.8	18.6	23.0		
	W							12.8	15.8	19.0		
AMNH 20797-Q4dex	L						12.8	17.9	20.4	24.0		
	W						8.3	13.3	16.5	20.2		
AMNH 20797-Q4sin	L						13.1	18.1	20.4	23.7		
	W						9.0	13.3	16.7	20.5		

Table 3: Upper teeth measurements of *Microstonyx major* from Samos.

Mandible	MTLA 300dex	MTLA 300sin	MTLA 479dex	MNHW 1911v211
Length p2-p4	53.7-56.0		54.1	54.2
Length m1-m3	99.1-99.2		100.0	98.7
Length p2-m3	156.5		155.2	151.0

Table 4: Lower toothrow segments in *Microstonyx major* from Samos.

		i1	i2	i3	c	p1	p2	p3	p4	m1	m2	m3
MTLA-479dex	L						14.0	18.0	21.5	21.2	29.9	45.5
	W1						6.4	8.3	(13.5)	15.8	18.5	24.2
	W2									15.9	20.4	22.1
	W3											19.2
MTLA-300dex	L							20.1	20.8	22.1	30.7	45.5
	W1							10.1	15.3	16.4	20.0	24.0
	W2									16.8	21.6	23.0
	W3											18.9
MTLA-300sin	L							20.2	20.8	23.1	30.3	44.7
	W1							9.8	15.1	16.8	21.0	24.2
	W2									17.2	20.9	22.7
	W3											18.5
MTLA-10sin	L	34.6	39.0	22.5	14.6							
	W	16.0	23.7	18.8								
AMNH 20795-Q5sin	L										27.0	44.7
	W1										18.0	19.9
	W2											19.5
	W3											16.6
NHMW 1911v211	L						15.4	18.5	19.9	20.9	30.1	46.3
	W1						7.2	10.2	15.3	15.2	20.9	22.5
	W2									16.2	21.6	22.2
	W3											17.1
		di1	di2	di3	c	dp1	dp2	dp3	dp4	m1	m2	m3
AMNH 22882-Q4dex	L							12.5	27.3	22.4		
	W							7.4	12.4	15.9		
AMNH 22882-Q4sin	L						12.7	14.0	27.3	23.0		
	W						5.6	8.1	12.5	15.7		

Table 5: Lower teeth measurements of *Microstonyx major* from Samos.

		1	2	3	4	5	6
MTLA-375	astragalus	57.5				38.3	
MTLA-383	metacarpal IV	103.7	30.1	25.0	23.5		27.5
MTLA-384	distal metacarpal III					26.2	
MTLA-428	distal radius					67.1	58.3

Table 6: Postcranial measurements of *Microstonyx major* from Samos. 1. maximal length; 2. proximal transverse diameter; 3. proximal anteroposterior diameter; 4. transverse diameter at the middle of diaphysis; 5. distal transverse diameter; 6. distal anteroposterior diameter.

PLATE 1

Microstonyx major from Samos

Fig. 1. Male skull MTLA-537 in lateral view.

Fig. 2. Male skull MTLA-537 in dorsal view.

Fig. 3. Male skull MTLA-537 in ventral view.

Scale bar equals 8 cm

PLATE 1

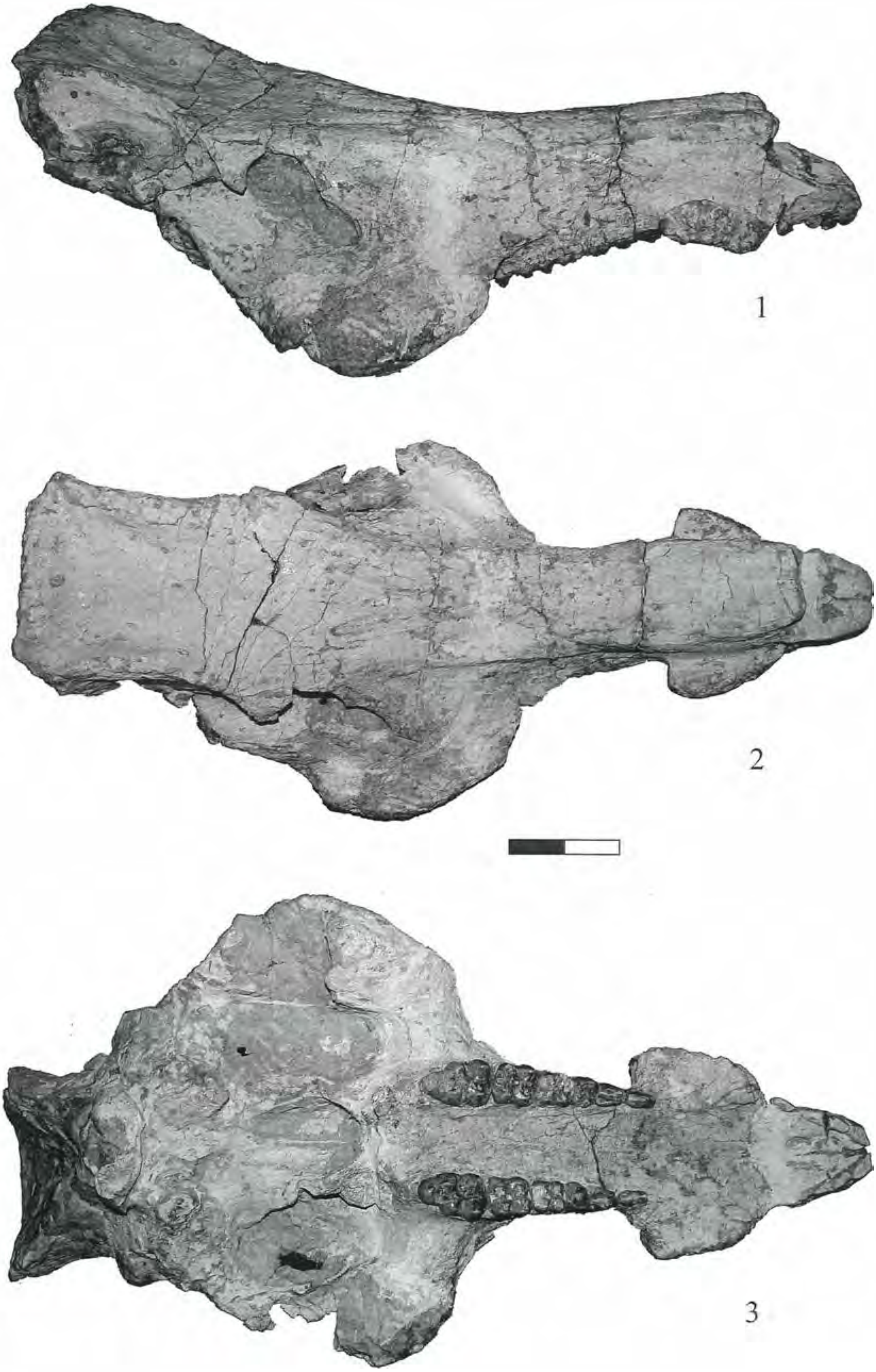

PLATE 2

Microstonyx major from Samos

Fig. 1. Female skull MNHNW A4789 in lateral view.

Fig. 2. Mandible MNHNW1911v211 in occlusal view.

Fig. 3. Mandible MTLA-300 in occlusal view.

Fig. 4. Snout MTLA-10 in occlusal view.

Fig. 5. dp2-m1sin, AMNH 22882 – Q4 in occlusal view.

Fig. 6. DP3-M1dex, AMNH 20616 – Q1 in occlusal view.

Fig. 7. m3dex, MTLA-479 in occlusal view.

Fig. 8. P2-M3 sin, NHMW A4789 in occlusal view.

Fig. 9. Metacarpal IV, MTLA-383 in anterior view.

Figs 1-4 with 8 cm scale (black & white); Figs 5-8 with 4 cm scale (black)

PLATE 2