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Suidae (Mammalia, Artiodactyla) from the late Miocene of Akkaşdağı, Turkey

Liping LIU
Institute of Vertebrate Paleontology and Paleoanthropology,
P.O. Box 643, Beijing, 100044 (China)
liuliping@ivpp.ac.cn

Dimitris S. KOSTOPOULOS
Department of Geology, Laboratory of Paleontology,
University of Thessaloniki, Thessaloniki, GR-54124 (Greece)
dkostop@geo.auth.gr

Mikael FORTELIUS
Department of Geology, University of Helsinki,
P.O. Box 64, Helsinki, FIN-00014 (Finland)
mikael.fortelius@helsinki.fi

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ABSTRACT
The suid remains from Akkaşdağı, late Miocene of Central Anatolia (Turkey), represent the widespread, long-ranging, and polymorphic species *Microstonyx major* (Gervais, 1848). The rich material represents at least 10 individuals, two of which are juveniles, and comprises both postcranial and craniodental material, including one nearly complete skull. The Akkaşdağı population is characterised by medium size, strong elongation of the skull, and moderate reduction of premolar size. These characteristics are shared with other populations of late middle Turolian age (MN 12). The elongation of the skull appears elsewhere to be associated with the arid end of the species' ecological range.

KEY WORDS
Mammalia,
Suidae,
Microstonyx,
Miocene,
Akkaşdağı,
Central Anatolia,
Turkey,
palaeoecology.

RÉSUMÉ
Suidae (Mammalia, Artiodactyla) du Miocène supérieur d'Akkaşdağı, Turquie.
Le matériel de suidés du Miocène supérieur d'Akkaşdağı (Anatolie Centrale, Turquie) est attribué à l'espèce polymorphe *Microstonyx major* (Gervais, 1848), d'une extension géographique très vaste. Un crâne presque complet

MOTS CLÉS
Mammalia,
Suidae,
Microstonyx,
Miocène,
Akkaşdağı,
Anatolie Centrale,
Turquie,
paléoécologie.

fait partie de cette collection ; les éléments crânio-dentaires et postcraniens représentent au moins 10 individus : deux jeunes et huit adultes. La population d'Akkaşdağı est caractérisée par sa taille moyenne, l'allongement du museau et la réduction de la série prémolaire, morphologie habituelle des populations du Turolien moyen terminal (MN 12). L'allongement du crâne, caractéristique du point extrême de la variation écologique de l'espèce, est probablement associé aux conditions arides.

INTRODUCTION

The late Miocene fossil land mammal locality Akkaşdağı is situated in Central Anatolia (Turkey), in the Çankırı-Çorum Basin, NNW of Kaman, in a thick volcanic tuff layer in the mesatype Akkaşdağı Hill (Kazancı *et al*. 1999). The sedimentological and taphonomical evidence suggests that the tuff and the fossil material preserved within represent a single depositional event, radiometrically dated to 7.1 ± 0.15 Ma (Karadenizli *et al*. 2005), an age close to the MN 12-13 boundary of recent calibrations of the European land mammal chronology (Steininger *et al*. 1996; Sen 1997; Daams *et al*. 1998; Steininger 1999; Agustí *et al*. 2001).

Since no taxa characteristic of MN 13 are known from the locality, and most of the studied families (e.g., hipparions, bovids and giraffids) rather agree with a middle-late Turolian age, the Akkaşdağı fauna can be referred to late MN 12 with certain confidence (Kazancı *et al*. 1999; Koufos & Vlachou 2005; Kostopoulos 2005; Kostopoulos & Saraç 2005).

Previous material collected by Heintz and coworkers during the 1970s (labelled GOK and stored in the Muséum national d'Histoire naturelle, Paris) does not include suid remains. The material is stored at the Natural History Museum in Ankara. The Akkaşdağı suid material studied here derives from 14 fossiliferous pockets, excavated during the 1999-2001 field seasons (labelled AKA,B,K, AK2-AK7 and AK10-AK14) and is thought to represent a single taxon: *Microstonyx major*.

The suines of the continental late Miocene of Europe and western Asia comprise two distinct clades, variably split between two to four genera. One is the *Hippopotamodon-Microstonyx* group, the other the *Korynochoerus-Propotamochoerus* group (Pickford 1988, 1993; Van der Made & Hussain 1989; Bonis & Bouvrain 1996; Fortelius *et al*. 1996). The rich and well preserved collection from the well dated Akkaşdağı locality allows us to explore previous hypothesis (Liu *et al*. 2004) about the morphological variability of *Microstonyx* further.

COMPARATIVE MATERIAL AND DATA

The comparative material of *Microstonyx* (casts and originals) used in the study is stored in the following institutions: IVPP (Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Science, Beijing), BMNH (The Natural History Museum, London), MNHN (Muséum national d'Histoire naturelle, Paris), LGPUT (Laboratory of Geology and Paleontology of the University of Thessaloniki), LMNHA (Local Museum of Natural History, Assenovgrad, Bulgaria). Other comparative material was studied mainly from figures in the published literature. Some of our localities data are gained from the ongoing database NOW (NOW database 2003).

SYSTEMATICS

Family SUIDAE Gray, 1821
Genus *Microstonyx* Pilgrim, 1926

Microstonyx major (Gervais, 1848)
(Figs 1-5; Appendix: Tables 1-6)

Sus major Gervais, 1848: pl. XII, fig. 2.

Microstonyx major – Kazancı *et al*. 1999: 507.

MATERIAL EXAMINED. — Skull: AK3-131, skull with all cheek teeth; AK5-501, broken skull with partial face and all cheek teeth.
Maxilla: AK7-153, maxilla with all cheek teeth; AK11-66, right maxilla with P2-M3; AK5-443, juvenile right maxilla with DP3-DP4 and M1; AK5-623, left maxilla with left P3-M3; AK7-100, right maxilla with DP4 and M1.
Mandible: AK2-112, left mandible with p2-m3; AK11-72, mandible with both rami and complete dentition; AK11-67, juvenile mandible with both rami, which bears i1 (right), i2 (left) and both side dp3, dp4, m1; AK3-126, left mandible with p3-m3; AK4-187, mandible with both rami, with both side p2-m3, incisor and canine are missing; AK4-251, left mandible with p3-m3; AK5-270, juvenile left mandible with dp2-dp4, m1-m2; AK5-442, left mandible with p2-m3; AKB-51, right mandible with p3-m2; AKK-120, female(?) mandible with both rami and all incisors (di2), canine, and p2-p4 (half left p4); AKK-121, left mandible with m1-m3.
Isolated teeth: AK12-5, right I1; AK2-488, left i3; AK4-186, right M3; AK5-624, left I1; AK6-85, a right broken m3; AK7-154, left m2; AK7-183, right m3; AKA-1, right M3; AKK-192, germ fragment of left M2; AKK-286, left m1; AKK-287, left m2; AKK-288, right m2; AKK-83, right I2.
Postcranial: AK3, AK5-236, AK5-258, AK5-346, AK6-91, AK5-628, AK5b-838, atlases; AK6-96, vertebra centrum; AK4-109, left humerus; AK7-184, left distal humerus; AK11-52, right radius; AK3-302, left radius and ulna; AK5-188, left distal radius; AK5-570, AK6-258, left proximal radii; AK5-625, right proximal metacarpal III; AKB-54, left metacarpal III; AKK-82, right metacarpal III; AK5-48, right metacarpal IV; AK2-489, left tibia; AK4-88, left astragalus; AK5-149, right metatarsal IV; AK5-199, metapodial.

AGE. — Late Miocene, radiometric age 7.1 ± 0.15 Ma (Karadenizli *et al*. 2005).

LOCALITY. — Akkaşdağı, Çankırı-Çorum Basin, Turkey.

DESCRIPTION

According to the mandibular data, seven adult, one young adult and two young individuals compose the local population, which includes one mature male, and at least two mature females.

Skull

There are two skulls in the Akkaşdağı suid collection, AK3-131 and AK5-501. The latter is only a middle part of a skull with the face partially preserved. Apart from showing clearly that the occiput is very high, it adds little to what is seen in the well preserved skull AK3-131 (Fig. 1). The latter skull is almost complete but dorso-ventrally compressed, especially in the occipital region (Fig. 1A). Judging from the completely erupted M3 it belongs to an adult individual. In dorsal view (Fig. 1B), the caudal part of the skull is broken at the posterior part of the parietal, and much of the braincase is not preserved. The left zygomatic arch is missing, while the right side is well preserved. The nasals are long, of nearly constant width almost to the tip. In ventral view (Fig. 1C), the specimen is almost complete from the apices of the premaxillae to the occipital condyles, but the pterygoid process is heavily deformed by compression and difficult to investigate. The right zygomatic arch is robust and extends strongly towards lateral. There are no facial crests, and the anterior rim of the zygomatic arch originates at the anterior end of M3. The orbit is small and far behind M3. The rim of the orbit is incomplete but there is a distinctive, deep lachrymal notch (infraorbital fossa). The occipital condyles and sphenoid surfaces are of typical suid form. Although broken, the jugular processes seem robust and the tympanic bullae are oriented downwards, both suggesting a modern suid form. The choanae open posteriorly, far behind M3. The cheek dentition (P1-M3) is well preserved, but all the canines and incisors are missing. The small and shallow canine alveolus suggests that the canine was small. The alveolar crest is elongated and relatively slender.

Mandible

The mandible is the most common element in the Akkaşdağı suid collection. The best preserved specimen is labelled as AK3-126 (Fig. 2A), and is certainly associated with the skull AK3-131. The mandible is almost complete except for minor damage, but the canine is unfortunately missing. Two mandibles preserve canines, AK11-72 (Fig. 2B) and AKK-120 (Fig. 2C). The description of the mandibular morphology of the Akkaşdağı suid is mainly based on specimens AK3-126, AK11-72, and AKK-120.

The horizontal ramus is shallow and slim, while the ascending ramus is high, about three times the

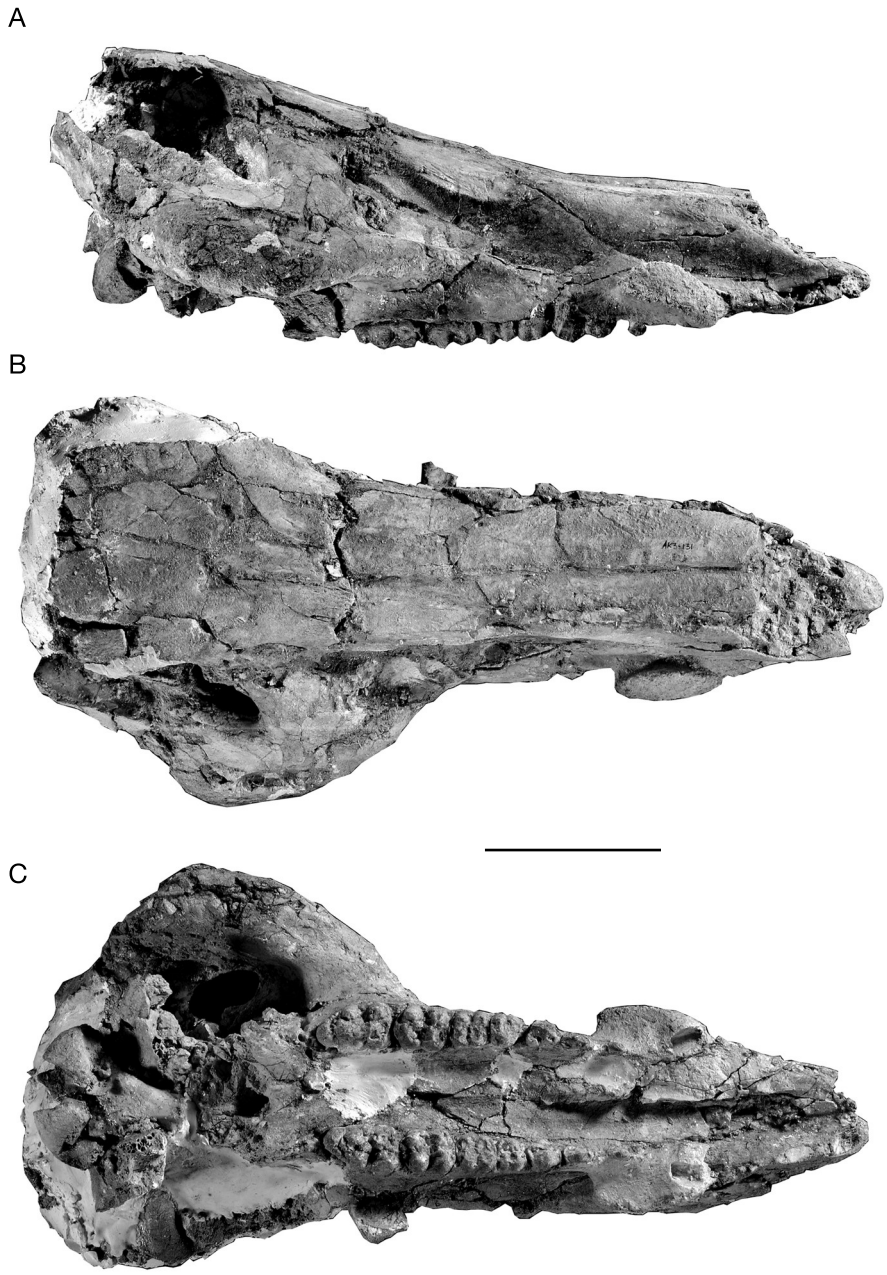

FIG. 1. — *Microstonyx major* (Gervais, 1848) from Akkaşdağı, skull AK3-131; **A**, lateral view; **B**, dorsal view; **C**, ventral view. Scale bar: 10 cm.

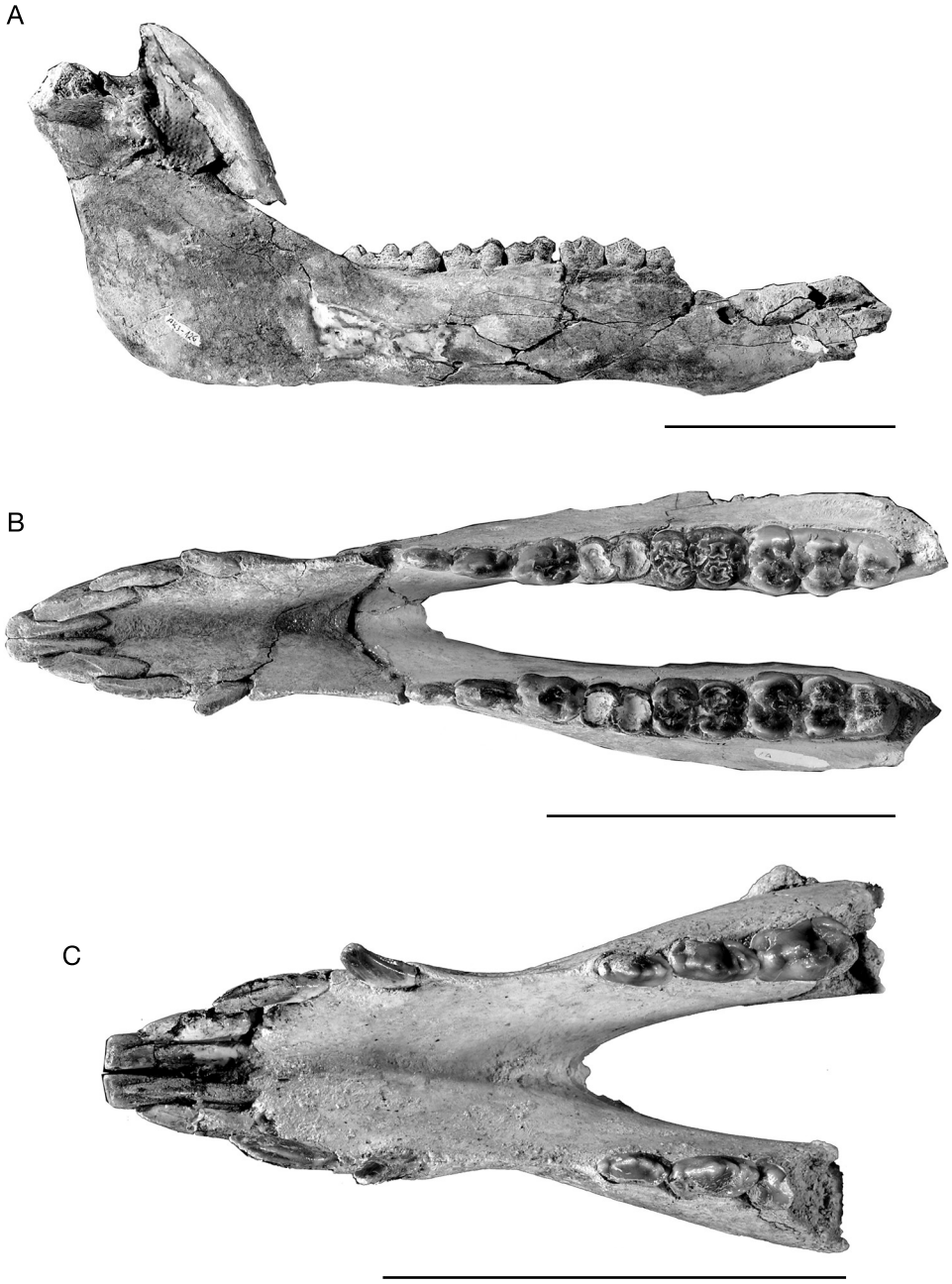

FIG. 2. — *Microstonyx major* (Gervais, 1848) from Akkaşdağı; **A**, lateral view of mandible AK3-126; **B**, occlusal view of mandible AK11-72; **C**, occlusal view of mandible AKK-120. Scale bars: 10 cm.

FIG. 3. — *Microstonyx major* (Gervais, 1848) from Akkaşdağı, dorsal view of atlas AK5-258. Scale bar: 5 cm.

height of the horizontal ramus. The ascending ramus rises gently upwards and backwards, with a mandibular angle of about 120°. The ascent begins well behind m3, so that this tooth is completely visible in lateral view. The glenoid condyle of the mandible is broken at the surface, but what remains clearly shows its robustness. The pointed coronoid process is a little higher than the glenoid condyle, and the mandibular notch is quite shallow. The symphysis is elongated, ending before p2. There seem to be two kinds of canine, but the distinction is not very sharp. The canine in mandible AKK-120 is short and narrow, almost symmetrical, with a very narrow posterior facet separated from the lateral facets by two crests. Since the tooth is narrow, the boundary of the lateral facets forms a sharp anterior crest. Enamel covers the whole tooth and ends above the alveolus. It is virtually identical with the canine that we described from Hezheng as a female individual (Liu *et al.* 2004). The canine in mandible AK11-72 is slightly more robust, with an oval transverse section and no obvious crests separating the posterior facet from the lateral ones.

Dentition

The dental morphology of *Microstonyx* is greatly variable, and has been shown extensively in previous publications (e.g., Van der Made *et al.* 1992; Kostopoulos *et al.* 2001; Liu *et al.* 2004, and literature listed herein), and the Akkaşdağı suid fits well within the known range. Notable characteristics of the Akkaşdağı population include a somewhat complicated M3/m3 occlusal pattern, and

FIG. 4. — *Microstonyx major* (Gervais, 1848) from Akkaşdağı, astragalus AK4-88. Scale bar: 2 cm.

the main lingual cusp of p4 being placed as far forward as the labial one.

Postcranials

Late Miocene suid limb bones are rarely described and figured, making it difficult to supply a comparative study of the abundant postcranial material of the Akkaşdağı suid. In order to facilitate future comparative work we here present figures and measurements of the material (Appendix: Tables 1; 2; Figs 3-5).

COMPARISON AND DISCUSSION

The general morphological characters of the Akkaşdağı suid, such as its large size, the elevated occiput, the wide and flat frontoparietal region, the elongated snout, the inflated and laterally extended zygomatic arches, the wide and deep lachrymal notch, and well developed alveolar

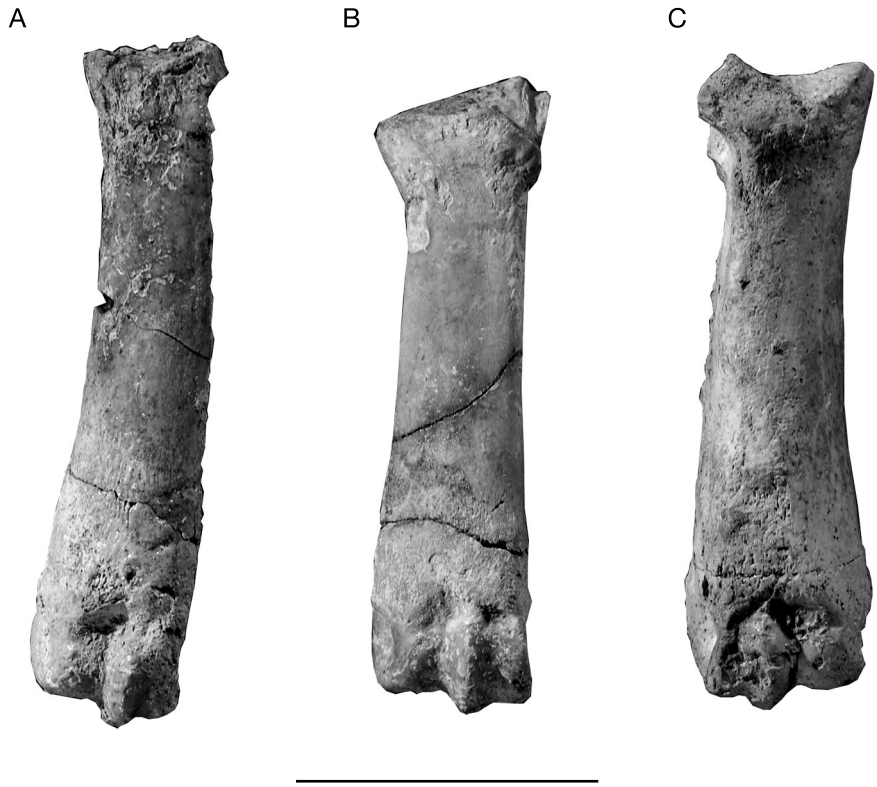

FIG. 5. — *Microstonyx major* (Gervais, 1848) from Akkaşdağı, metapodials; **A**, AK5-199; **B**, AKK-82; **C**, AK5-48. Scale bar: 5 cm.

crest show unambiguously that it belongs to the Eurasian *Hippopotamodon-Microstonyx* large suine group (Trofimov 1954; Pickford 1988; Van der Made & Moyà-Solà 1989; Kostopoulos *et al.* 2001; Liu *et al.* 2004). The suines of the late Miocene Eurasian *Hippopotamodon-Microstonyx* group are characterised by considerable morphological variability, with a confusing pattern of sexual, temporal, and regional differences. *Hippopotamodon* (Lydekker, 1877) and *Microstonyx* are very similar in cranial and dental morphology. The characteristics of *Hippopotamodon* emphasized by Pickford (1988), such as the gigantic size, the large and flaring canine, the short snout, the less developed alveolar crest, and the short diastema between C-P1-P2, do not qualitatively distinguish the two genera, especially not when the material is incomplete, as is usually the case. The Akkaşdağı suine does have a reduced canine, but since canine size in female individuals of *Hippopotamodon* is unknown, this is not in itself decisive.

In size and general proportions the Akkaşdağı suid skull is similar to the skull from Pikermi figured by Gaudry (1862-1867), as well as to the skull specimen BMNH M9048 that probably represents a female individual. The Akkaşdağı skull is also close to the Russian (Trofimov 1954) and Bulgarian skull samples (especially to the presumed female skull specimen K5260 from Kalimanci; Kostopoulos *et al.* 2001) and is obviously larger and more elongated than any specimen from the Chinese latest Miocene locality Hezheng (Liu *et al.* 2004) (Appendix: Tables 3; 4).

Microstonyx, as conventionally conceived, has two species, *M. antiquus* (Kaup, 1833) and *M. major*.

Microstonyx antiquus was larger and distributed earlier in time than *M. major*. Fortelius *et al.* (1996) tentatively assigned *M. antiquus* to *Hippopotamodon* and we follow this taxonomy here. Under this usage, *Hippopotamodon* differs from *Microstonyx* primarily in the premolar proportions, especially the relative stoutness of the fourth premolar in the former (Liu *et al.* 2004). As the dental logarithmic ratio diagrams show (Fig. 6), it is easy to assign the Akkaşdağı suid to *M. majo*r as opposed to *Hippopotamodon*.

Microstonyx major was a common element of the late Miocene mammal faunas of Europe and West Asia. It is also known from East Asia, but was a rare element there, with evidence of substantial size decrease (Liu 2003). Some workers (Van der Made & Moyà-Solà 1989; Van der Made *et al.* 1992; Pickford 1993; Kostopoulos 1994; Bonis & Bouvrain 1996; Van der Made 1997) have interpreted the spatiotemporal variability of *M. major* as possible evidence of multiple evolving lineages. In contrast, we have recently argued (Liu *et al.* 2004) that the morphological variability of *M. major* s.l. is best interpreted as polymorphism within a single evolving species. The substantial inter-population size variability in *M. major*, is owing to intra-specific polymorphism, representing local ecotypes (Liu *et al.* 2004). We have specifically proposed that elongation of the skull in *M. major* tends to be associated with arid conditions and a dietary shift towards herbivory (Liu *et al.* 2004). Following this view here, we recognise only one formal species-level taxon, *M. major*.

The tooth dimensions of *Microstonyx* from Akkaşdağı (Appendix: Tables 5; 6) are well within the range of the middle-late Turolian European *M. major*, and larger than those of other Asian samples (Maragha and China; Bonis & Bouvrain 1996; Liu *et al.* 2004) or from some early Turolian populations of SE Europe (Vathylakkos, Kerassia, Perivolaki; Kostopoulos *et al.* 2001) (Fig. 7). Logarithmic ratio diagrams illustrating the relative proportions of the Eurasian *Microstonyx major* toothrows are shown in Figure 8. The Akkaşdağı *M. major* is close to the Pikermian and Bulgarian samples but with somewhat reduced premolars. Under our ecotype hypothesis, the great elongation of the skull of the Akkaşdağı form would indicate the arid end of the habitat spectrum inhabited by the species. In the Balkans, similar ecotypes with long muzzles and medium sized molars occur mainly in the middle Turolian, MN 12 (Kostopoulos *et al.* 2001).

MICROSTONYX IN TURKEY

Microstonyx is poorly documented in the late Miocene of Turkey, even if references are numerous. Şenyürek (1952) described as *Sus erymanthius* (= *Microstonyx major*) a suid mandible with p3-m3 from the undated site Akkırma II near Gökdere. The specimen belongs to a large form with stout p4, correctly recognized by Bonis & Bouvrain (1996) as belonging to *Microstonyx* (*Limnostonyx*) *antiquus*. *Dicoryphochoerus meteai* Ozansoy, 1965 from the Vallesian locality of Yassıören (middle Sinap) is mainly based on a left mandibular ramus, which has been later considered by Pickford & Ertürk (1979) as belonging to *Hippopotamodon* and assigned by Bonis & Bouvrain (1996) to *Microstonyx* (*Limnostonyx*) *antiquus*. Both the Yassıören and Akkırma II suids, referred here to *Hippopotamodon antiquus*, differ from the Akkaşdağı one in the larger dimensions, stronger canine, persistence of p1 and more robust p4.

Microstonyx major (including *M. erymanthius*) has been reported from several Turkish localities ranging from MN 10 to MN 12 (Gülpınar, Çorak Yerler, Çevril, Muğla Garkın, Kayadibi, upper Kavakdere, Çoban Pınar, Mahmutgazi and Kınık; Ozansoy 1965; Sickenberg 1975; Pickford & Ertürk 1979; Fortelius *et al.* 1996; NOW database 2003) but we usually deal with faunal lists or fragmentary and isolated specimens which preclude a direct comparison with the Akkaşdağı form. As far we know the Akkaşdağı *M. major* provides the clearest evidence of the species in Turkey. The absence of the species in the isochronous and very similar fauna of Kemiklitepe A, B looks rather anomalous.

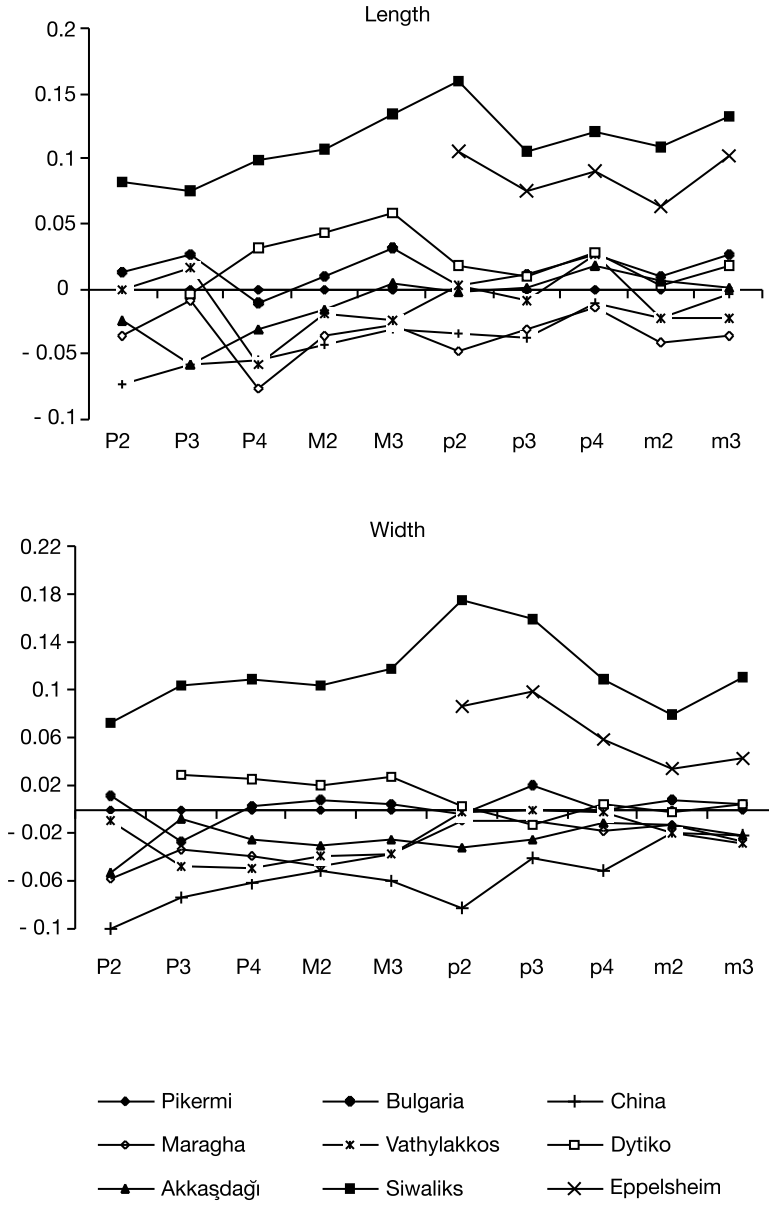

FIG. 6. — Logarithmic ratio diagram of dental proportions of *Microstonyx major* (Gervais, 1848), *M. antiquus* (Kaup, 1833) and *Hippopotamodon* (Lydekker, 1877); standard: Pikermi. Data sources: Siwaliks (Pickford 1988); Eppelsheim (Hünermann 1968); Pikermi (Pearson 1928; Hellmund 1995; Bonis & Bouvrain 1996); Bulgaria (Kostopoulos *et al*. 2001); China (Pearson 1928; Liu *et al*. 1978, 2004; Tang *et al*. 1985); Maragha (Bonis & Bouvrain 1996).

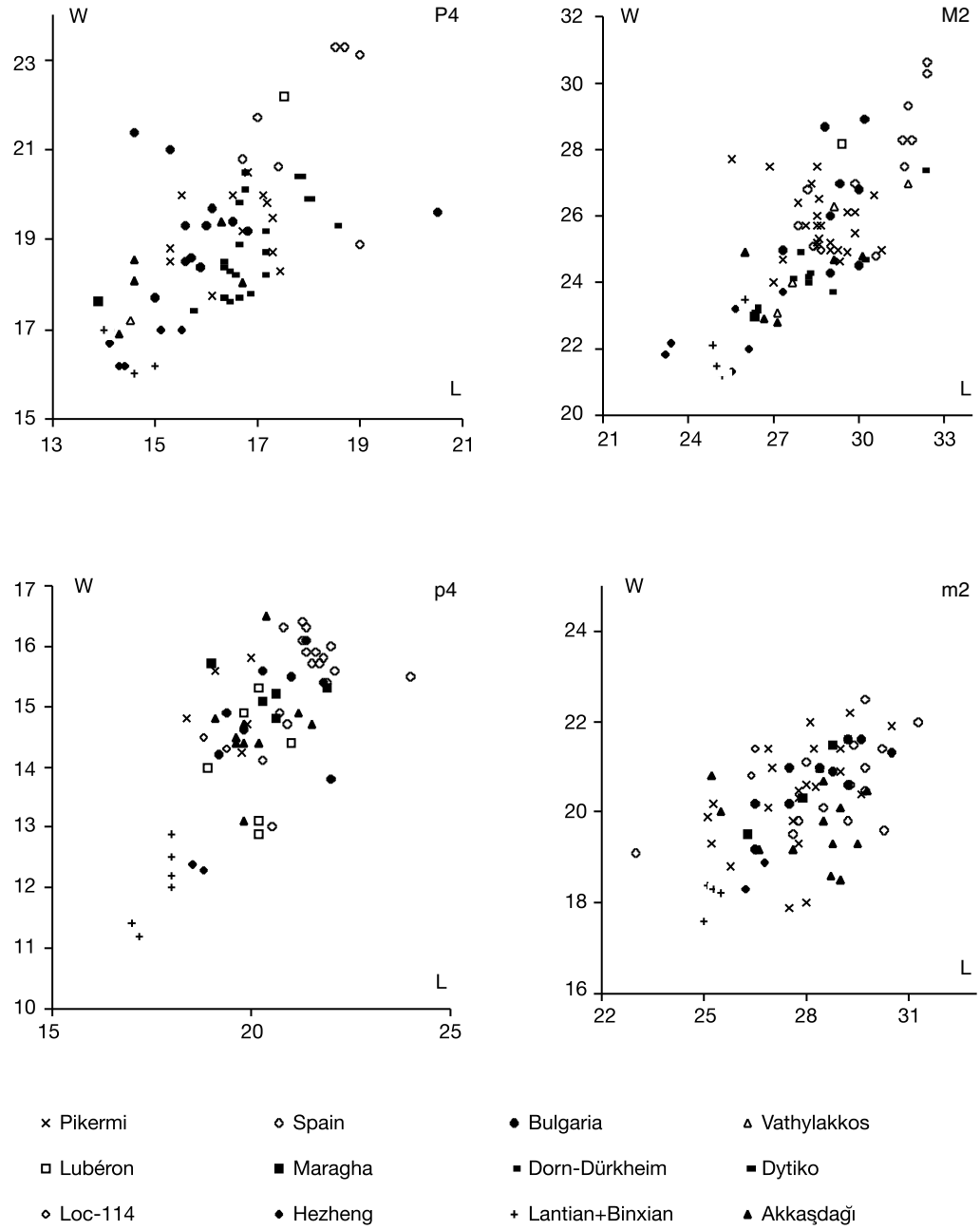

FIG. 7. — Bivariate scatter plots of *Microstonyx major* (Gervais, 1848) from different localities. Data sources: Lantian (Liu *et al*. 1978); Binxian (Tang *et al*. 1985); Pikermi (Pearson 1928; Hellmund 1995; Bonis & Bouvrain 1996); Spain (Van der Made *et al*. 1992); Bulgaria (Kostopoulos *et al*. 2001); Vathylakkos (Bonis & Bouvrain 1996); Lubéron (Bonis & Bouvrain 1996); Maragha (Bonis & Bouvrain 1996); Dorn-Dürkheim (Van der Made 1997); Dytiko (Bonis & Bouvrain 1996); Loc-114 (Pearson 1928); Hezheng (Liu *et al*. 2004).

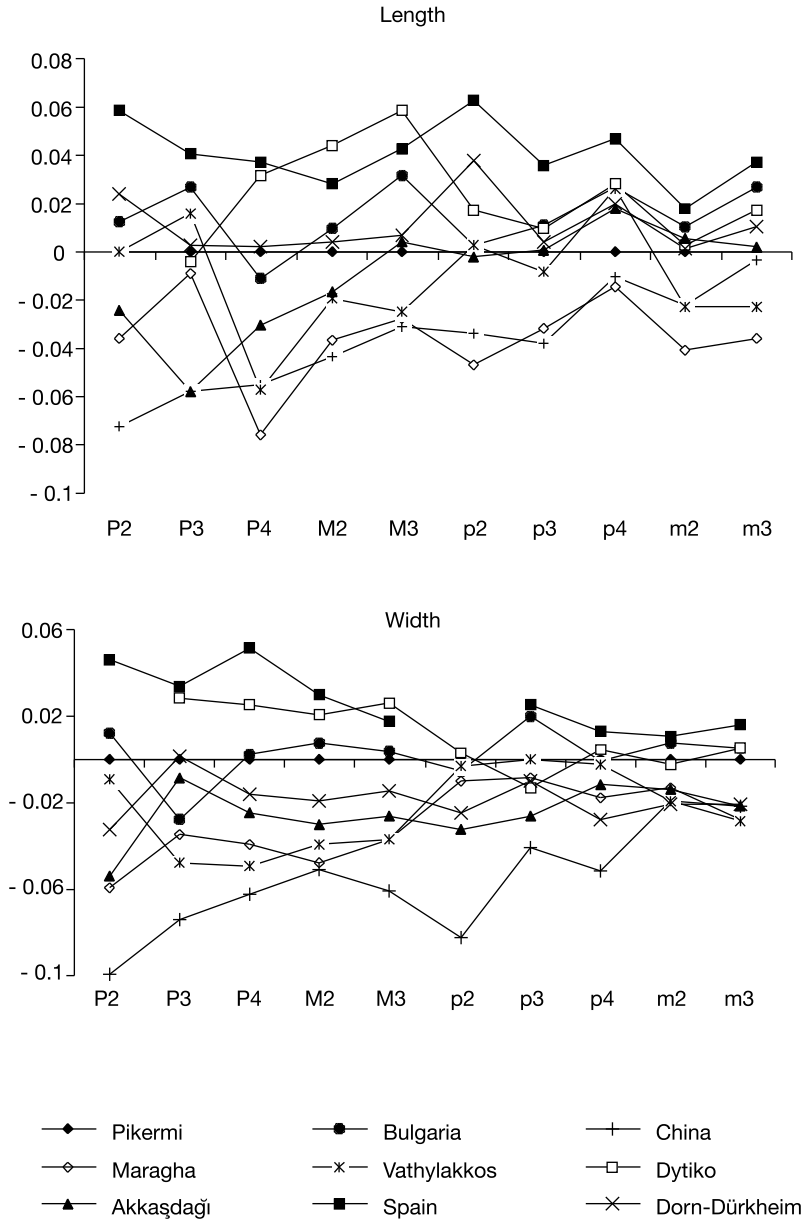

FIG. 8. — Logarithmic ratio diagram of dental proportions of *Microstonyx major* (Gervais, 1848); standard: Pikermi. Data sources: Siwaliks (Pickford 1988); Eppelsheim (Hünermann 1968); Pikermi (Pearson 1928; Hellmund 1995; Bonis & Bouvrain 1996); Bulgaria (Kostopoulos *et al*. 2001); China (Pearson 1928; Liu *et al*. 1978, 2004; Tang *et al*. 1985); Maragha (Bonis & Bouvrain 1996).

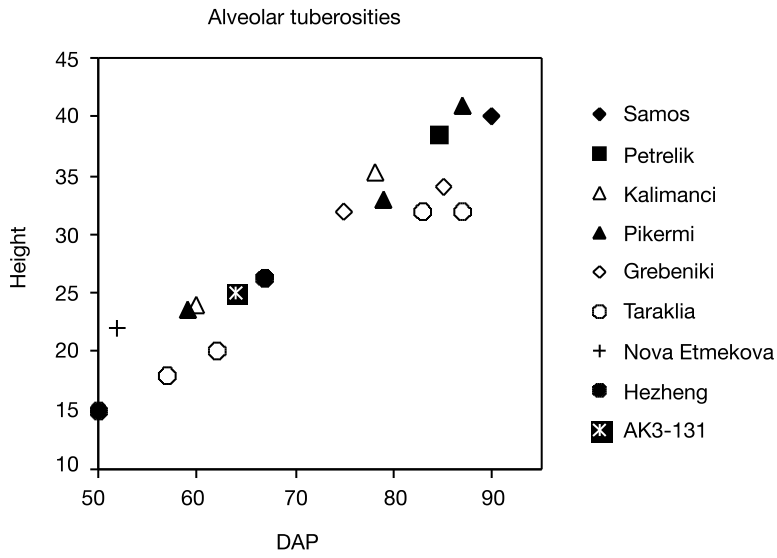

FIG. 9. — Bivariate scatter plots of the alveolar crest development in *Microstonyx major* (Gervais, 1848) (anteroposterior diameter [DAP] against height) from several localities (from Kostopoulos *et al*. 2001, modified; two specimens from Pikermi from the BMNH collection added).

SEXUAL DIMORPHISM

The Akkaşdağı suid collection does not at present add decisively to our understanding of sexual dimorphism in *M. major* (Kostopoulos *et al*. 2001; Liu *et al*. 2004). The weaker alveolar crest and the lesser width of the skull AK3-131 compared to those of other samples suggest that the Akkaşdağı skull belongs to a female individual (Kostopoulos *et al*. 2001; Liu *et al*. 2004). Figure 9 summarizes the available data on the distribution of the alveolar crest dimensions according to sex. Evidently, the Akkaşdağı suid is located among the female individuals of *M. major* from Pikermi (Greece) and Kalimanci (Bulgaria) while the Hezheng form represents a shift toward smaller overall size.

The fact that the presumed female skull retains P1 supports our previous suggestion that females retained P1 more frequently than males (Liu *et al*. 2004). In contrast to the presumed male skull from Hezheng (Liu *et al*. 2004), the presumed female skulls from Hezheng and Akkaşdağı have almost no development of facial crests. Similarly, the deep preorbital fossa found in the Hezheng presumed male individual is not as strongly developed in the presumed females.

It is not possible to establish beyond all doubt that the minor differences observed in the lower canines from Akkaşdağı reflect sexual dimorphism, but the pattern observed supports the suggestion of weak sexual bimodality (Liu *et al*. 2004).

CONCLUSIONS

The study of the suid material from Akkaşdağı allows its attribution to *Microstonyx major*, as this species is considered in the frame of our last works (Kostopoulos *et al*. 2001; Liu 2003; Liu *et al*. 2004). The Akkaşdağı form represents a typical middle Turolian (MN 12) eastern Mediterranean population with close similarities to the Greek and Bulgarian samples. Morphological cranial characters indicate relatively arid conditions, still within the range of a generalist species. Although the presence of the long-ranging *M. major* cannot as such provide certain biochronological conclusions, the population characteristics do appear to support a middle-late Turolian age for the Akkaşdağı assemblage.

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REFERENCES

AGUSTÍ J., CABRERA L., GARCÉS M., KRIJGSMAN W., OMS O. & PARÉS J. M. 2001. — A calibrated mammal scale for the Neogene of Western Europe. State of the art. *Earth-Science Review* 52: 247-260.

BONIS L. DE & BOUVRAIN G. 1996. — Suidae du Miocène supérieur de Grèce. *Bulletin du Muséum national d'Histoire naturelle*, Paris, 4e sér., section C, 18 (1): 107-132.

DAAMS R., ALCALA L., ALVAREZ SIERRA M. D. L. A., AZANZA B., DAM J. V., MEULEN A. J. V. D., MORALES J., NIETO M., PELÁEZ-CAMPOMANES P. & SORIA D. 1998. — A stratigraphical framework for Miocene (MN 4-MN 13) continental sediments of central Spain. *Comptes Rendus de l'Académie des Sciences*, Paris, Sciences de la Terre et des Planètes 327: 625-631.

FORTELIUS M., VAN DER MADE J. & BERNOR R. 1996. — Middle and late Miocene Suoidea of central Europe and the eastern Mediterranean: evolution, biogeography and paleoecology, *in* BERNOR R., FAHLBUSCH V. & MITTMANN H. (eds), *The Evolution of Western Eurasian Neogene Mammal Faunas*. Columbia University Press, New York: 348-377.

GAUDRY A. 1862-1867. — *Animaux fossiles et géologie de l'Attique*. F. Savy, Paris, 2 vols, 472 p.

GERVAIS P. 1848-1852. — *Zoologie et paléontologie francaises*. A. Bertrand, Paris, 2 vols, 3 vols.

HELLMUND M. 1995. — The vertebrate locality Maramena (Macedonia, Greece) at the Turolian-Ruscinian boundary (Neogene) 13. Suidae (Artiodactyla, Mammalia). *Münchener Geowissenschaftliche Abhandlungen*, series A (28): 143-156.

HÜNERMANN K. A. 1968. — Die Suidae (Mammalia, Artiodactyla) aus den Dinotheriensanden (Unterpliozän+pont) Rheinhessens (Südwestdeutschland). *Schweizerische Paläontologische Abhandlung* 86: 1-96.

KARADENIZLI L., SEYITOĞLU G., SEN S., ARNAUD N., KAZANCI N., SARAÇ G. & ALÇIÇEK C. 2005. — Mammal bearing late Miocene tuffs of the Akkaşdağı region; distribution, age, petrographical and geochemical characteristics, *in* SEN S. (ed.), Geology, mammals and environments at Akkaşdağı, late Miocene of Central Anatolia. *Geodiversitas* 27 (4): 553-566 (this volume).

KAZANCI N., SEN S., SEYITOĞLU G., BONIS L. DE, BOUVRAIN G., ARAZ H., VAROL B. & KARADENIZLI L. 1999. — Geology of a new late Miocene mammal locality in Central Anatolia, Turkey. *Comptes Rendus de l'Académie des Sciences*, Paris, Sciences de la Terre et des Planètes 329: 503-510.

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. 2005. — The Bovidae (Mammalia, Artiodactyla) from the late Miocene of Akkaşdağı, Turkey, *in* SEN S. (ed.), Geology, mammals and environments at Akkaşdağı, late Miocene of Central Anatolia. *Geodiversitas* 27 (4): 747-791 (this volume).

KOSTOPOULOS D. S. & SARAÇ G. 2005. — Giraffidae (Mammalia, Artiodactyla) from the late Miocene of Akkaşdağı, Turkey, *in* SEN S. (ed.), Geology, mammals and environments at Akkaşdağı, late Miocene of Central Anatolia. *Geodiversitas* 27 (4): 735-745 (this volume).

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. D. & VLACHOU T. D. 2005. — Equidae (Mammalia, Perissodactyla) from the late Miocene of Akkaşdağı, Turkey, *in* SEN S. (ed.), Geology, mammals and environments at Akkaşdağı, late Miocene of Central Anatolia. *Geodiversitas* 27 (4): 633-705 (this volume).

LIU D. S., LI C. K. & ZHAI R. J. 1978. — [Pliocene vertebrates of Lantian, Shensi]. *Professional Papers*

on Stratigraphy and Paleontology 7: 149-200 (in Chinese).

LIU L. P. 2003. — *Chinese Fossil Suidea: Systematics, Evolution and Paleoecology*. University Printing House, Helsinki, 41 p.

LIU L. P., KOSTOPOULOS D. S. & FORTELIUS M. 2004. — Late Miocene *Microstonyx* remains (Suidae, Artiodactyla) from Hezheng areas. *Geobios* 37 (1): 49-64.

NOW DATABASE 2003. — Neogene of the Old World. Database of fossil mammals: www.helsinki.fi/science/now

OZANSOY F. 1965. — Étude des gisements continentaux et de mammifères du Cénozoïque de Turquie. *Mémoires de la Societé géologique de France* N. S. 102: 5-92.

PEARSON H. 1928. — Chinese fossil Suidae. *Palaeontologia Sinica* C (5): 1-75.

PICKFORD M. 1988. — Revision of the Miocene Suidae of the Indian Subcontinent. *Münchener Geowissenschaftliche Abhandlungen*, series A, 12 (1): 1-95.

PICKFORD M. 1993. — Old world suoid systematics, phylogeny, biogeography and biostratigraphy. *Paleontologia i Evolucio* 26-27: 237-269.

PICKFORD M. & ERTÜRK C. 1979. — Suidae and Tayassuidae from Turkey. *Bulletin of the Geological Society of Turkey* 22: 141-154.

SEN S. 1997. — Magnetostratigraphic calibration of the European Neogene mammal chronology. *Palaeogeography Palaeoclimatology Palaeoecology* 133: 181-20.

ŞENYÜREK M. S. 1952. — A study of the Pontian fauna of Gökdere (Elmadagi), southeast of Ankara. *Türk Tarih Kurumu Belleten* 16: 449-492.

SICKENBERG O. 1975. — Die Gliederung des höheren Jungtertiärs und Altquartärs in der Türkei nach Vertebraten und ihre Bedeutung für die internationale Neogen-Stratigraphie. *Geologisches Jahrbuch* B, 15: 1-167.

STEININGER F. F. 1999. — Chronostratigraphy, geochronology and biochronology of the Miocene "European Land Mammal Mega-Zones" (ELMMZ) and the Miocene "Mammal-Zones (MN-Zones)", *in* RÖSSNER G. E. & HEISSIG K. (eds), *The Miocene Land Mammals of Europe*. Verlag Dr. Friedrich Pfeil, München: 9-24.

STEININGER F. F., BERGGREN W. A., KENT D. V., BERNOR R. L., SEN S. & AGUSTÍ J. 1996. — Circum-Mediterranean Neogene (Miocene-Pliocene) marine-continental chronologic correlations of European mammal units, *in* BERNOR R. L., FAHLBUSCH V. & MITTMANN H. W. (eds), *The Evolution of Western Eurasian Neogene Mammal Faunas*. Columbia University Press, New York: 7-46.

TANG Y. J., LIU Z. Q., CHEN D. & CHEN L. Q. 1985. — The fossil Suidae from late Miocene of Binxian, Shaanxi. *Vertebrata PalAsiatica* 23 (1): 60-68.

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. 1997. — The fossil pig from the late Miocene of Dorn-Dürkheim 1 in Germany. *Courier Forschungs-Institut Senckenberg* 197: 205-230.

VAN DER MADE J. & HUSSAIN S. T. 1989. — "*Microstonyx*" *major* (Suidae, Artiodactyla) from Nagri. *Estudios Geologicos* 45: 409-416.

VAN DER MADE J. & MOYÀ-SOLÀ S. 1989. — European Suinae (Artiodactyla) from the late Miocene onwards. *Bollettino della Società Paleontologica Italiana* 28 (2-3): 329-339.

VAN DER MADE J., MONTOYA P. & ALCALÁ L. 1992. — *Microstonyx* (Suidae, Mammalia) from the upper Miocene of Spain. *Geobios* 25 (3): 395-413.

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APPENDIX

TABLE 1. — Measurements of atlases and one indetermined vertebra of *Microstonyx major* (Gervais, 1848) from Akkaşdağı (in mm). **M1**, centrum length; **M2**, centrum width; **M3**, centrum height; **M4**, maximal length; **M5**, maximal width; **M6**, maximal height; **M7**, proximal articulation width; **M8**, proximal articulation height; **M9**, distal articulation width; **M10**, distal articulation height.

Specimen	Element	M1	M2	M3	M4	M5	M6	M7	M8	M9	M10
AK3	Atlas						66.0	77.0	42.0	76.0	36.0
AK5-236	Atlas						77.0	76.0	39.0		33.0
AK5-258	Atlas					148.0	63.0	83.0	38.5	76.4	32.0
AK5-346	Atlas						60.0	77.0	34.0		
AK5-628	Atlas	81.8				153.0	70.0	81.2	38.0	75.0	34.0
AK5b-838	Atlas						67.0	85.0	38.0	77.0	35.0
AK6-91	Atlas						67.0				
AK6-96	Vertebra		55.0	45.0	37.0						

TABLE 2. — Measurements of limb bones of *Microstonyx major* (Gervais, 1848) from Akkaşdağı (in mm). **M1**, maximal length; **M2**, functional length; **M3**, proximal width; **M4**, proximal antero-posterior depth; **M5**, shaft width; **M6**, antero-posterior depth of shaft; **M7**, distal width; **M8**, distal antero-posterior depth; **M9**, distal articulation width; **M10**, antero-posterior depth of distal articulation.

Specimen	Element	Side	M1	M2	M3	M4	M5	M6	M7	M8	M9	M10
AK4-109	Distal humerus	left							57.5	62.4	47.5	43.3
AK7-184	Distal humerus	left							66.8	69.0	51.2	47.8
AK11-52	Proximal radius	right			51.9	33.6	34.6	27.2				
AK3-302	Distal radius	left					33.0		60.0	40.0	52.2	29.4
AK5-188	Distal radius	left					28.0	24.0	54.0	37.0	44.4	29.5
AK5-570	Proximal radius	left			44.1	30.9						
AK6-258	Proximal radius	left			49.0	35.0						
AK3-302	Distal ulna	left									23.3	17.1
AKB-54	Metacarpal III	left	109.0	105.0	30.4	29.1	21.9	15.7	26.9	29.6	25.3	29.6
AKK-82	Metacarpal III	right	107.0	103.0	32.6	30.6	22.6	16.1	29.8	27.1	26.7	27.0
AK5-625	Proximal metacarpal III	right			30.0	24.4						
AK5-48	Metacarpal IV	right	105.0	99.0	30.0	24.4	21.3	13.3	25.8	27.2	26.1	27.2
AK2-489	Distal tibia	left							43.7	39.6	35.4	34.1
AK4-88	Astragalus	left	62.2	35.1	34.9	30.4	34.1	34.7	26.3			
AK5-149	Metatarsal IV	right	113.0	109.0	25.0	34.3	20.0	15.7	25.1	27.9	24.4	28.2

TABLE 3. — Skull measurements of *Microstonyx major* (Gervais, 1848) from Akkaşdağı compared with specimens from Pikermi (Greece) and Hezheng (China) (in mm). Data from Gaudry (1862-1867), Liu *et al.* (2004) and personal data.

Skull	Akkaşdağı	Pikermi		Hezheng	
	AK3-131 female	Gaudry's specimen	BMNH M9048	HMV 0976 male	HMV 0977 female
Basal length of the skull	468	470	420	< 380	–
Condyles to posterior border of palatine fissure	374	310		350	–
Condyles to posterior border of palate	114		125.9	123	–
Posterior border of palatine fissure to posterior border of palate	260			227	–
Posterior border of palatine fissure to the end of M3	234			202	195
Posterior border of palate to M3	26		33	25	–
Length of the diastema between canine and P2	40.8		44	51.7	44
Length of P2-M3	153	141	143	123.6	121.6
P2-P4/M1-M3	0.57		0.58	0.53	0.52
Length of alveolar crest	64	87	59	67	50
M3 to the anterior end of orbit	64			50	–
Maximal length of the orbit	–			42.5	–
Maximal width of the skull	262	310	272	< 225	–
Width of palate at alveolar crest	109	140	133	122	89.5
Width of palate at anterior end of M3	42			38.3	32
Breadth of frontal at the supraorbital process				150	128.6
Nasal width above preorbital foramen	83			75	–
Nasal width above P2	66.5			56	–
Nasal width at the end of incisor notch	69			59	–
Width of the palatine fissure	21			22	–

TABLE 4. — Mandible measurements of *Microstonyx major* (Gervais, 1848) from Akkaşdağı compared with specimens from Hezheng (China) and Kalimanci (Bulgaria) (in mm). Data from Kostopoulos *et al.* (2001), Liu *et al.* (2004).

Mandible (sex)	Akkaşdağı AK11-72/ AKK-120 (male/female)	Akkaşdağı AK3-126 (female)	Kalimanci K-5277/K-5276 (male/female)	Hezheng HMV 0576 (female)
Mandible length from tip to m2	212/–	–	233/239	192
Length of p2-m2	99/–	102	111/111	98
p2-p4/m1-m2	0.56/–	0.54		
Length of symphysis	100.5/85.5	100	102/87	80
Diastema between c-p2	47/38.5	56.8	52/50	40
Height of mandible at p2	52.6/43.6	53.8	56/47	
Height of mandible at muscular process	–	171	–	–
Height of mandible at articular process	–	152	–	_

TABLE 5. — Upper dentition measurements of *Microstonyx major* (Gervais, 1848) from Akkaşdağı (in mm). **L**, maximum length of incisor (basal measured), canine and cheek teeth; **W1**, maximum width of incisor, canine, premolar or first moist width of the molar; **W2**, second moist width of molar or the height of incisor and canine; **W3**, width of talon; **upper data-line**, left toothrow; **lower data-line**, right toothrow.

Specimen		I1	I2	I3	C	P1	P2	P3	P4	M1	M2	M3
AK11-66	L						16.0	16.6	14.3	19.7	27.1	39.5
	W1						10.0	15.5	16.9	18.0	22.2	24.9
	W2									18.4	22.8	22.2
	W3											14.8
AK12-5	L											
	W1	9.9										
	W2	16.1										
AK3-131	L					9.3	15.3	16.8	17.0	21.8	29.7	40.5
						9.6	15.3	16.6	16.4	21.5	28.5	40.4
	W1					4.5	9.5	14.9	18.2	19.5	24.5	26.1
						4.6	9.3	14.4	17.9	19.5	23.5	26.1
	W2									19.2	24.0	23.5
										19.6	24.9	23.7
	W3											13.4
												13.8
AK4-186	L											43.4
	W1											28.1
	W2											24.4
	W3											12.0
AK5-501	L						15.3	16.9	15.4	19.6	26.0	41.6
							15.9	15.3	14.7	18.9	26.0	41.0
	W1						9.5	15.5	18.7	20.1	24.2	27.2
							8.7	15.4	18.4	20.2	24.7	27.3
	W2									21.0	24.8	24.3
										21.9	24.9	24.8
	W3											15.0
												15.8
AK5-623	L							17.6	16.3	22.5	30.1	42.8
	W1							16.8	19.4	19.6	24.8	27.4
	W2									19.0	23.8	24.6
	W3											17.1
AK5-624	L	22.5										
	W1	10.6										
	W2	27.0										
AK7-100	L									21.6		
	W1									18.7		
	W2									18.3		
AK7-153	L						15.9	16.5	14.9	20.2	26.8	38.6
								16.1	14.5	21.0	26.5	39.3
	W1						10.1	14.9	18.1	18.7	23.0	24.3
								14.5	18.0	18.7	22.8	24.2
	W2										22.4	22.2
											22.8	22.0
	W3											11.3
												11.3
AKA-1	L											41.7
	W1											26.1
	W2											23.2
	W3											12.8
AKK-83	L	11.8										
	W1	8.2										
	W2	16.2										

TABLE 6. — Lower dentition measurements of *Microstonyx major* (Gervais, 1848) from Akkaşdağı (in mm). **L**, maximum length of incisor (basal measured), canine and cheek teeth; **W1**, maximum width of incisor, canine, premolar or first moist width of the molar; **W2**, second moist width of molar or the height of incisor and canine; **W3**, width of talonid; **upper data-line**, left toothrow; **lower data-line**, right toothrow.

Specimen		i1	i2	i3	c	p2	p3	p4	m1	m2	m3
AK11-67	L		6.5						22.9		
									22.8		
	W1		9.3						16.0		
									15.9		
	W2								15.0		
									15.8		
AK11-72	L	8.6	18.3	17.5	9.0	15.0	18.3	19.6	20.7	28.7	41.9
		9.1	17.8	16.2	11.0	14.6	18.4	20.2	20.6	27.6	42.7
	W1	14.0	14.1	6.3	6.0	6.6	9.3	14.5	14.9	18.4	21.5
		14.5	12.1	6.5	6.5	6.6	8.5	14.4	14.7	18.2	21.2
	W2	35.7	30.2	19.3	12.2				14.3	18.6	20.0
		34.0	32.0	19.0	11.0				14.3	19.2	20.3
	W3										15.9
											16.0
AK2-112	L					14.2	17.2	19.6	20.4	28.8	48.9
	W1					6.4	9.0	14.4	14.1	19.2	21.5
	W2								14.8	19.3	20.2
	W3										16.1
AK2-488	L			21.6							
	W1			7.3							
	W2			17.5							
AK3-126	L						18.3	19.8	21.8	29.0	46.1
	W1						8.4	13.1	14.0	18.3	22.1
	W2								14.8	18.5	20.6
	W3										17.0
AK4-187	L					14.0	17.5	19.8	18.5	25.5	43.4
							17.8	19.1	18.4	25.2	42.3
	W1					7.2	9.2	14.7	14.7	18.9	20.6
							9.0	14.8	14.2	19.1	21.8
	W2								15.2	20.8	20.9
									14.6	20.0	20.3
	W3										16.4
											17.0
AK4-251	L						19.4	20.4	21.6	28.5	46.0
	W1						10.5	16.5	16.3	20.7	22.5
	W2								15.9	20.4	21.0
	W3										17.3
AK5-270	L								21.5		
	W1								14.4		
	W2								14.3		
AK5-442	L					14.3	17.5	19.8	20.5	26.6	43.4
	W1					7.5	9.9	14.4	14.6	18.9	22.2
	W2								15.5	19.2	20.7
	W3										16.1
AK7-154	L									28.4	
	W1									20.4	
	W2									21.0	

Specimen		i1	i2	i3	c	p2	p3	p4	m1	m2	m3
AK7-183	L										44.3
	W1										22.5
	W2										20.8
	W3										16.9
AKB-51	L						18.4	21.1	23.0	29.8	
	W1						10.0	12.4	15.9	20.5	
	W2								15.6	20.2	
AKK-120	L	10.1	16.5	17.2		15.2	19.2	21.5			
		9.5	17.2	16.5		15.8	19.5				
	W1	8.0	7.5	6.9		7.4	9.7	14.7			
		8.0	6.9	7.5		7.4	10.1				
	W2	12.3	18.2	18.2							
		13.4	18.4	18.4							
AKK-121	L								22.2	29.5	39.2
	W1								15.1	18.9	20.9
	W2								15.3	19.3	20.8
	W3										16.3
AKK-286	L								22.3		
	W1								14.2		
	W2								15.0		
AKK-287	L								29.0		
	W1								19.8		
	W2								20.1		
AKK-288	L								28.5		
	W1								18.5		
	W2								19.8		