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Microstonyx (Suidae, Artiodactyla) from the Upper Miocene of Hayranlı-Haliminhanı, Turkey

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Abstract: The suid remains from localities 58-HAY-2 and 58-HAY-19 in the Late Miocene Derindere Member of the İncesu Formation in the Hayranlı-Haliminhanı area (Sivas, Turkey) are described and referred to as *Microstonyx* major (Gervais, 1848–1852). *Microstonyx* shows changes in incisor morphology, which are interpreted as a further adaptation to rooting. This occurred probably in a short period between 8.7 and 8.121 Ma ago and possibly is a reaction to environmental change. The incisor morphology in locality 58-HAY-2 suggests that it is temporally close to this change, which would imply that this locality and the lithostratigraphically lower 58-HAY-19 belong to the lower part of MN11 and not to MN12. The findings are discussed in the regional context and contribute to the knowledge of the Anatolian fossil mammals.

Key words: Suidae, *Microstonyx*, rooting, ecology, Late Miocene

1. Introduction

The first of the Hayranlı-Haliminhanı fossil localities was discovered in 1993 by members of the Vertebrate Fossils Research Project, a collaborative survey effort. The current survey area includes a number of localities within an area encompassing roughly 50 km^2, centered around 39°44′N, 36°49′E (Figure 1). The project group consists of the University of Ankara (E. Güleç), the General Directorate of Mineral Research Exploration in Turkey (MTA), and the Human Evolution Research Center, University of California at Berkeley (F.C. Howell and T. White).

By now, nearly 100 localities are known in the basin, which, after Demirci et al. (2007) and Bibi and Güleç (2008), yielded the following large mammals: *Choerolophodon* (Proboscidea), *Hipparion* (Equidae), *Ceratotherium* (Rhinocerotidae), *Microstonyx* (Suidae), cf. Cervidae/Moschidae indet. cf. *Micromeryx*, *Gazella* cf. *capricornis*, *Tragoportax* cf. *amalthea*, *Tethytragus* cf. *koehlerae*, *Prostrepsiceros houtumschindleri syricidi*, cf. *Protoryx* sp. (all Bovidae), and Mustelidae indet. (Carnivora).

Localities 2 and 19, coded 58-HAY-2 and 58-HAY-19 (Figure 2), yielded remains of Suidae. It is the aim of this paper to describe these remains and discuss their classification, evolution, ecology, and age.

1.1. Location and stratigraphy

Anatolia lies at the intersection of Asia, Europe, and Afro-Arabia, and its geology has been subject to the plate tectonic processes that resulted in the collision of these continents. The latest subduction–collision processes between the Arabian and Eurasian plates took place at the end of the Middle Miocene (Şengör and Yılmaz, 1981; Kaymakcı et al., 2006). These orogenic events resulted in the formation of extensive intramontane or foreland sedimentary basins, mostly of Late Cretaceous to Late Miocene age, in the area of the Neotethyan suture zones (Kaymakci, 2000). The sedimentation in the central Anatolian basins started with marine deposits (turbidites, carbonates, etc.), but after the Middle Eocene, thick Oligocene to Pliocene sequences of terrestrial sediments, rich in vertebrate fossils, accumulated (Kaymakci, 2000; Kaymakçi et al., 2001).

The Sivas Basin in eastern Anatolia is situated between the Taurides (of Gondwana affinity) in the south and the Pontides (of Laurasian affinity) in the north. Its sedimentary sequence consists of more than 3000 m of Late Paleocene to Middle Eocene marine deposits and more than 2000 m of Oligocene to Pliocene terrestrial deposits, which locally interfinger with Early Miocene shallow marine deposits (Kaymakci, 2000). The İncesu Formation

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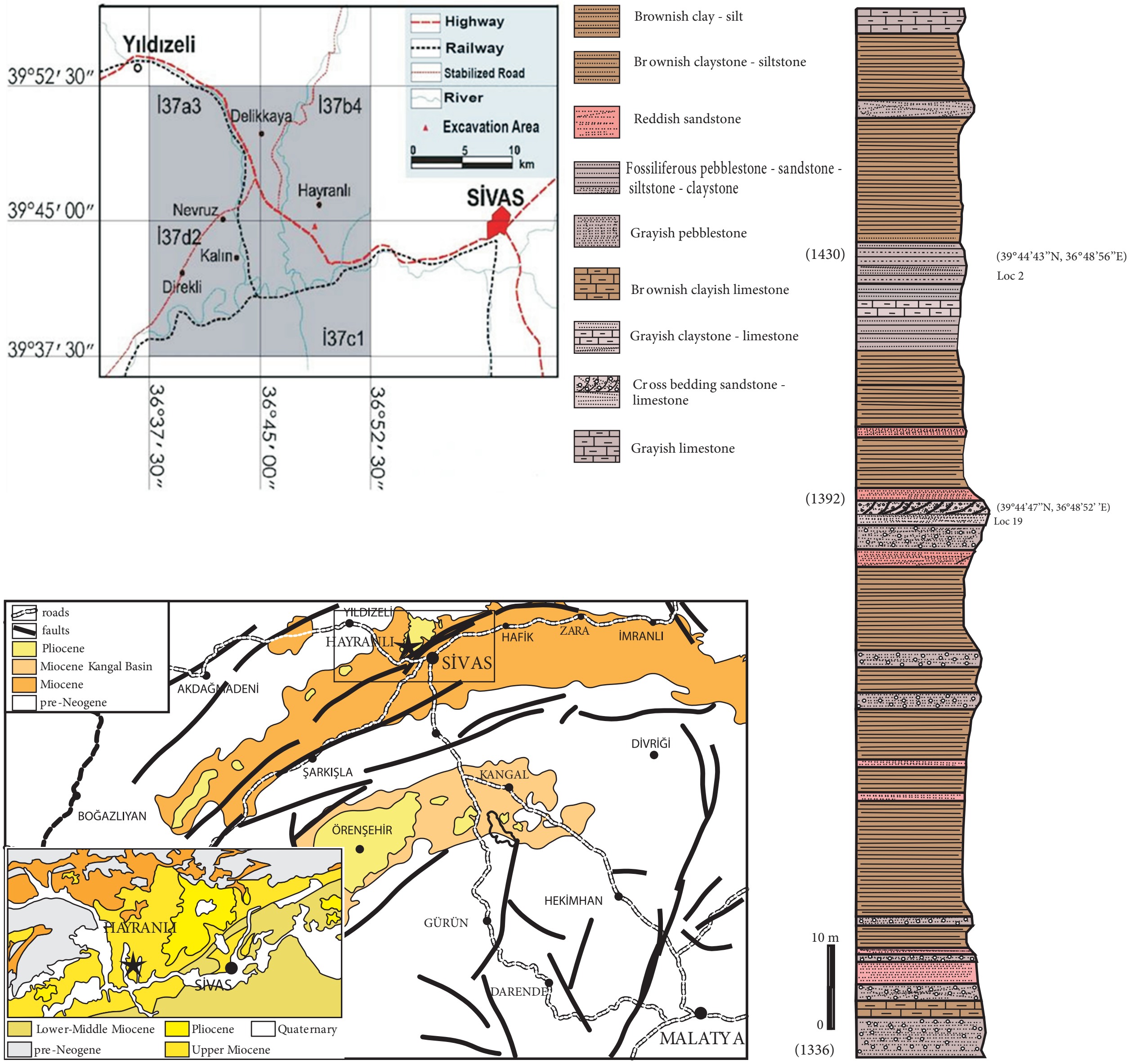

Figure 1. The position of the localities on a geographic and a geologic map and in a stratigraphic column of part of the İncesu Formation. Locality 2 is situated in the stratigraphic section, while locality 19 is correlated from a short distance into the column.

discordantly overlies Early Miocene marine sediments and Middle Miocene red beds and consists of more than 200 m of fluvial sediments, with fining-and-thinning up cycles of conglomerates to mudstones, and alternating playa lake deposits with limestone and occasional gypsum occurrences (Kaymakci, 2000). The sequence becomes gradually more lacustrine upward.

Most of the fossil localities are in the lower 50 m of the İncesu Formation. Locality 2 is situated about 1 km from locality 19 and about 38 m higher in the Derindere Member of the İncesu Formation. There are various papers dealing with the age of the İncesu Formation or even with one of these localities in particular.

The bovids from several localities in the Sivas basin were described in detail by Bibi and Güleç (2008): *Gazella* cf. *capricornis* from localities 58-HAY-9, 14, 19, 23, 70; *Tragoportax* cf. *amalthea* from localities 58-HAL-1 and 58-HAY-9, 14, 19; *Tethytragus* cf. *koehlerae* from localities 58-HAY-14, 19, 23; *Prostrepsiceros houtumschindleri syricidi* from localities 58-HAY-1 and 58-HAY-14, 19, 24, 70; and cf. *Protoryx* sp. from 58-HAY-14. The bovids from these different localities were interpreted to indicate MN11 or

Figure 2. Locality 2 (upper photograph) and locality 19 (lower photograph).

early MN12 (9–7 Ma). Four of the 5 species occur in 58-HAY-19, which is among the localities yielding the fossils of *Microstonyx* described here. As the authors noted, the occurrence of *Tethytragus* is much more recent than in most of the localities from which it is known. There are morphological differences of systematic value in that the horn cores from the older localities (such as Paşalar, Çandır, Arroyo del Val, and La Barranca) are more curved, more vertical at their bases, and more directed backwards at their tips.

The localities Düzyayla 1 and 2 are in the İncesu Formation. Rodents from these localities, usually classified up to the genus level, were discussed by De Bruijn and Mein (1996), De Bruijn et al. (1996a), Fahlbusch and Bolliger (1996), and Ünay (1996), who placed both localities in MN11, and by De Bruijn et al. (1996b), who placed the Düzyayla 1 in MN12. De Bruijn et al. (1999), in discussing the fauna from Düzyayla 1, indicated that there are 2 associations of small mammals from superposed clay and lignite beds and placed the locality in MN12. Akgün et al. (2000), discussing pollen and large mammals, did not specify locality 1 or 2 at Düzyayla, but indicated that the locality is in the upper part of the İncesu Formation and concluded on a Turolian age, conforming with MN11–12 as indicated by the small mammal fauna. The composite faunal list for the different levels at Düzyayla is: *Apodemus* sp., *Parapodemus* sp., *Schizogalerix* cf. *zapfei*, *Amblycoptus* sp., *Archaeodesmana* sp., *Petenyia hungarica*, *Permenella* sp., *Alilepus turolensis*, *Keramidomys* sp., *Spermophilinus bredai*, *Pliopetaurista* sp. nov., *Hylopetes macedoniensis*, *Glirulus lissiensis*, *Eozapus intermedius*, *Dipoides* sp., "*Blancomys*" sp., *Pliospalax* sp. nov. 1 and 2, *Pseudomeriones pythagorasi*, *Hansdebruijnia neutrum*, "*Karnimata*" cf. *provocator*, *Hipparion* sp., *Ceratotherium neumayri*, *Deinotherium giganteum*, *Choerolophodon pentelici*, *Adcrocuta* cf. *eximia*, *Oioceros wegneri*, *Helladotherium duvernoyi*, and *Microstonyx erymanthius*.

2. Materials and methods

The material from Sivas is kept in the laboratory of the Anthropology Department of Ankara University. The specimen numbers consist of a code for the geographic area (58 for Sivas in this case), an acronym indicating a more precise area (HAY for Hayranlı), a locality number (2 or 19 here), and a specimen number. This material is compared with material from other localities, which is kept in institutes indicated by the following acronyms:

FISF	Forschungsinstitut Senckenberg, Frankfurt
GSM	Georgian State Museum, Tbilisi
GSP	Geological Survey of Pakistan, Islamabad
HGSB	Hungarian Geological Survey, Budapest
HLD	Hessisches Landesmuseum, Darmstadt
HUJ	Hebrew University of Jerusalem
IM	Indian Museum, Calcutta
IPS	Institut Paleontòlogic Dr. M. Crusafont, Sabadell
IPUW	Institut für Paläontologie der Universität Wien
IVAU	Instituut voor Aardwetenschappen, Utrecht
KME	Krahuletz-Museum, Eggenburg
MGB	Museu de Geologia de Barcelona
MGL	Musée Guimet, Lyon
MGSCB	Museo Geológico del Seminario Conciliar, Barcelona
MGPUSB	Museo di Geologia e Paleontologia, Università degli Studi di Bologna
MNCN	Museo Nacional de Ciencias Naturales, Madrid
MNHN	Musée National d'Histoire Naturelle, Paris
MHMN	Museu Històric Municipal de Novelda
MPV	Museo Paleontológico de Valencia
MPZ	Museo de Paleontología, Universidad de Zaragoza
MRA	Musée Requien, Avignon
MSNO	Muséum des Sciences Naturelles, Orléans
MTA	Maden Tetkik ve Arama (Geological Survey), Ankara
NCUA	National and Capodistrian University, Athens
NHM	Natural History Museum, London
NMB	Naturhistorisches Museum, Basel
NMBe	Naturhistorisches Museum, Bern
NMW	Naturhistorisches Museum, Wien (Vienna)

NNML	Nationaal Natuurhistorisch Museum, Leiden
NHMI	Natural History Museum, Islamabad
PIMUZ	Paläontologisches Institut und Museum der Universität, Zürich
PIN	Paleontological Institute, Moscow
SP	Sinap Project
TMH	Teylers Museum, Haarlem
UA	University of Ankara
UCBL	Université Claude Bernard, Lyon
UL	University of Lahore
VMM	Vernadsky Museum, Moscow

Measurements were taken according to van der Made (1991, 1996, 1997). They are given in millimeters and are indicated by the following abbreviations:

D	Depth of mandible measured at the lingual side.
DAP	Antero-posterior diameter.
DTa	Transverse diameter of the anterior lobe.
DTp	Transverse diameter of the posterior or second lobe.
DTpp	Transverse diameter of the third lobe in M3.
DTpalate	Width of the palate between the cheek teeth measured between the 2 lobes.
DMD	Meso-distal diameter in incisors.
DLL	Labio-lingual diameter in incisors.
Ta	Enamel thickness measured at the lingual side of the metaconid.
W	Width of the mandible.

When biostratigraphy is discussed, MN units are used (Mein, 1975, 1977, 1990; De Bruijn et al., 1992; Agustí et al., 2001).

2.1. Systematics

Suids of the type of *Microstonyx* are abundant in the Late Miocene. Many names have been proposed for them, and recently different classifications have been proposed. Therefore, it is useful to summarize the nomenclatorial history.

Three species were named from the European Miocene and one from Anatolia: *Sus antiquus* Kaup, 1833; *Sus major* Gervais, 1848–1852; *Sus erymanthius* Roth and Wagner, 1854; and *Dicoryphochoerus meteai* Ozansoy, 1965. The type material of the first species is from Eppelsheim and is kept in the HLD. The holotype of the second species is an M^3 from Cucuron (France). Though Bonis and Bouvrain (1996) indicated that it is in the MRA, we were not able to find it, nor any other material that comes from the type locality, though there is a specimen in the MRA with the indication "Cucuron or Vaugines". There is additional material from Cucuron (Mont Lubéron) in the MNHN. The holotype of the third species is a mandible from Pikermi, of which we do not know its whereabouts, but a cast is kept in the NHM. Fossils from this locality are present in many collections and the NHM, MNHN, NMW, and NCUA each have skulls that may serve as a reference. The type of the last species is a mandible in the MNHN. With the passage of time, *Microstonyx erymanthius* became considered as a junior synonym of *Microstonyx major*, but was occasionally reused.

Lydekker (1877) named the genus and species *Hippopotamodon sivalense* for material from the Siwaliks (Pakistan), but these names were forgotten. Pilgrim (1926) named the genus *Dicoryphochoerus*, but Pickford (1988) pointed out that *Dicoryphochoerus* is a junior synonym of *Hippopotamodon*. Van der Made and Hussain (1989) raised the question of whether *Microstonyx* should be included in *Hippopotamodon*, but did not resolve the question. Fortelius et al. (1996) included *Dicoryphochoerus meteai* in *M. antiquus* and transferred that species to *Hippopotamodon*, but not the other 2 European species.

In addition to the Indian *H. sivalense*, presently there are 3 species names in use for suids of this type and 2 generic names. The delimitation of the material assigned to *Hippopotamodon antiquus* or *M. major* varied among the authors, as well as the recognition of a species or subspecies *erymanthius* as separate from *M. major*.

Thenius (1972) described a skull from Stratzing (Austria), which he assigned to *Microstonyx antiquus*, and another one from Pikermi (Greece) as *Microstonyx major*. He suggested that they lived in different habitats, but now these localities are thought to be of different ages (belonging to units MN10 and MN12, respectively). Ginsburg (1974) indicated these 2 species to be at least in part coeval, but Ginsburg (1980) indicated the first to occur in MN9 and possibly MN10, and the second species in MN11 to MN12. Golpe-Posse (1980a) described material from Das and Terrassa (both MN10; Spain) as *Microstonyx antiquus* and material from younger levels as *Microstonyx major-erymanthius*. After this time, *Microstonyx antiquus* was generally seen as an earlier and *M. major* (and/or the species *M. erymanthius*) as a later species.

Ginsburg (1988), based on the study of material from Montredon (MN10; France), which he assigned to *M. antiquus*, named the subgenus *Limnostonyx* for that species. Van der Made and Moyà-Solà (1989), van der Made et al. (1992), and van der Made (1990a and 1990b) included the MN10 to "early? MN12" material in *Microstonyx major major* and recognized *M. major erymanthius* as either a geographical or chronological subspecies possibly restricted to "late? MN12". This has an important implication: the skulls that were previously assigned to *M. antiquus* were now assigned to *M. m. major*, and those assigned to *M. major* were now assigned to *M. m. erymanthius*. Fortelius et al. (1996) recognized 2 separate species with overlapping temporal ranges. The resulting situation is that the good skulls are from MN10 (Stratzing, and Terrassa, Spain) or MN11 (Grebeniki, Ukraine) and are assigned to *M. major*, and the skulls assigned to *M. erymanthius* are from Pikermi (MN12). The morphological differences in the skulls that before served to separate *M. antiquus* and *M. major* now serve to separate a taxon indicated as *M. major* and *M. erymanthius*, while the skull of *M. antiquus* is unknown.

Van der Made (1997) named the subspecies *Microstonyx erymanthius brevidens* for material from Dorn Dürkheim (Germany) with shorter I^2 than *M. e. erymanthius* from Pikermi and Samos.

While Bonis and Bouvrain (1996) and Kostopoulos et al. (2001) recognized the 2 subspecies *M. m. major* and *M. m. erymanthius*, Liu et al. (2004) considered *M. major* merely a "polymorphic" species that includes *M. erymanthius*. In view of the morphological and metrical variation in dentition and skull material, this is not entirely satisfactory, but the problem is to find a temporal or geographic pattern in this variation. An additional problem is that Mont Lubéron, the type locality of *M. major*, is considered to be MN12, which is younger than the skulls assigned to this species and coeval with Pikermi, the type locality of *M. erymanthius*. A revision of the material from Mont Lubéron (Cucuron) is needed. Pending this revision, here the material from the different localities is assigned to *M. erymanthius* and *M. major* as done by Fortelius et al. (1996), or the assignment is done according to similar criteria.

Material from Turkey of the characteristics of *M. major* and *M. erymanthius* was assigned to *Sus* (*Microstonyx*) *erymanthius* (Thenius, 1949), *Sus erymanthius* (Şenyürek, 1952), *Sus erymanthius* (Ozansoy, 1965; Akgün et al., 2000), the "*Dicoryphochoerus* - *Microstonyx* - Formenkreis" (Hünermann, 1975), to *Microstonyx major* (Pickford and Ertürk, 1979, who considered *M. erymanthius* to be a synonym), and to either *M. major* or *M. erymanthius* (Fortelius et al., 1996; van der Made, 2003).

Suidae Gray, 1821
Suinae Gray, 1821
Dicoryphochoerini Schmidt-Kittler, 1971
Microstonyx Pilgrim, 1926
Microstonyx major (Gervais, 1848–1852)

2.2. Material

58-HAY-2/43 – palate with left P^4 and M^{1-2} and right M^{1-3} from locality 2.

58-HAY-2/45 – anterior part of a skull with left I^{1-2}, C^f, and P^2–M^3 and right I^{1-2}, C^f, and P^2–M^3 from locality 2.

58-HAY-2/134 – premaxillae with left I^{2-3} and right I^2–C^f from locality 2.

58-HAY-2/237 – palate with right and left P^4–M^3 from locality 2.

58-HAY-2/239 – skull with frontals and posterior part of the nasals, left zygomatic arch, and palate with right and left P^4–M^3 from locality 2.

58-HAY-19/05 – mandible with left P_3–M_3 and root of P_2 and right P_2–M_3 from locality 19.

58-HAY-19/250 – left M_1 from locality 19.

58-HAY-19/251 – right M^3 from locality 19.

58-HAY-19/252 – left M_2 from locality 19.

2.3. Description and comparison

Skull 58-HAY-2/45 (Figure 3) lacks the posterior part and is damaged dorsally. The snout is elongate with diastemata between the I^2, I^3, C^f, and P^2. On the right side the distances P^2–C^f and P^2–I^3 are 44.4 and 74.2 mm, respectively. In recent Suidae, these distances are sexually bimodal and in both sexes increase at least until complete adulthood (van der Made, 1991). The P^2–C^f distance is slightly more than in male and female skulls from Terrassa (IPS), Udabno (GSM; Georgia), Stratzing (KME), and Eldar (GSM; Azerbaijan), localities of MN10 to MN11, while it is less than in most males and females from Grebeniki (VMM), Concud (NHM; Spain), and Pikermi (NHM), all MN12, and an unknown locality at Maragah (NMW; Iran). There were no P^1. These teeth tend to disappear in the later samples, though this seems to be a very gradual process. On both sides there is a well-developed crista alveolaris above and

Figure 3. Skull 58-HAY-2/45 of *Microstonyx* from locality 2; dorsal view and inferior view.

Figure 4. Skull 58-HAY-2/239 of *Microstonyx* from locality 2; dorsal and inferior views.

Figure 5. Snout 58-HAY-2/134 of *Microstonyx* from locality 2; left, inferior, and right views.

behind the canine, which does not extend upwards (unlike in *Potamochoerus*, for instance). The palate extends >8 mm behind the M^3. The foramina palatina are between the anterior lobes of the M^3. The zygomatic arches depart at a blunt angle from the side of the skull and are massive.

Another skull fragment (58-HAY-2/239; Figure 4) preserves part of the dorsal surface. The frontals are wide. What is preserved of the left zygomatic arch is not very massive, but this is probably due to the fact that the lower part is lacking, which is usually more inflated. The orbits are relatively, but not very, far behind the M^3. The later specimens of *Microstonyx* tend to have the orbit placed further back with respect to the cheek teeth, but the character is difficult to observe objectively. The posterior edge of the foramina palatina is at the level of the second lobe of the third molar. The palate extends well behind the third molar. The glenoid for the left mandibular condyle is preserved; it is saddle-shaped.

Palate 58-HAY-2/237 confirms some of the morphology described above. It also has complete sets of right and left

Table 1. Measurements in mm of the upper incisors and canines of *Microstonyx* from Sivas.

			DMD	DLL
58-HAY-2/45	S	I^1	14.7	9.2
58-HAY-2/45	D	I^1	16.2	9.1
58-HAY-2/45	S	I^2	23.1	8.9
58-HAY-2/45	D	I^2	22.7	8.7
58-HAY-2/45	D	I^3	15.5	6.5
58-HAY-2/45	S	C^f	11.9	..
58-HAY-2/45	D	C^f	12.2	8

Table 2. Measurements in mm of the upper cheek teeth and palate width of *Microstonyx* from Sivas.

			DAP	DTa	DTp	DTpp	DTpalate
58-HAY-2/45	S	P^2	<17.7	<7.7	--		49.7
58-HAY-2/45	D	P^2	16.7	8.7	10.5		
58-HAY-2/45	S	P^3	17.9	11.9	15.2		50.8
58-HAY-2/45	D	P^3	17.4	11.4	16.6		
58-HAY-2/45	S	P^4	16.9		19.8		
58-HAY-2/45	D	P^4	16.5		19.9		
58-HAY-2/45	S	M^1	21.8	19.8	--		46.6
58-HAY-2/45	D	M^1	20.6	19.9	19.4		
58-HAY-2/45	S	M^2	31.2	25.6	25.7		46.5
58-HAY-2/45	D	M^2	31.2	25.3	24.9		
58-HAY-2/45	S	M^3	42.0	27.4	24.5	16.9	43.9
58-HAY-2/45	D	M^3	45.6	27.7	24.0	17.7	
58-HAY-2/43	S	P^4	15.9		18.0		
58-HAY-2/43	S	M^1	--	--	--		.46
58-HAY-2/43	D	M^1	20.9	--	--		
58-HAY-2/43	S	M^2	29.4	--	24.0		
58-HAY-2/43	D	M^2	29.9	23.8	23.9		
58-HAY-2/43	S	M^3	40.8	25.6	24.1	15.9	46.3
58-HAY-2/43	D	M^3	40.3	25.6	22.4	14.9	
58-HAY-2/25	D	M^3	41.3	26.7	24.0	15.6	

cheek teeth, but again the first premolar is lacking because of reduction. The diastema between P^2 and canine on the left side is slightly smaller than in 58-HAY-2/45.

The upper incisors, including the I^1, are flattened and elongate (Figures 3 and 5, Table 1). The I^2 is very elongate as in most Suinae and some Tetraconodontinae. The I^1 assigned to *Microstonyx major* are less flattened (van der Made et al., 1993), while those assigned to *M. e. brevidens* are similar in their degree of flattening (van der Made, 1997). The C^f are small and simple. The cheek teeth of *Microstonyx* have often been described and these teeth do not present particularities. The M^3 have simple talons with a large main cusp. The measurements of the cheek teeth are given in Table 2, while Figures 6 and 7 compare the sizes of the upper cheek teeth of the different species. Teeth from *Hippopotamodon sivalense* and *H. antiquus* are clearly larger than those from Sivas. The teeth assigned to *Microstonyx major* tend to be larger than those assigned to *M. erymanthius*, but also have a greater range of variation, including also small specimens. The specimens from Sivas are well within the metrical ranges of *M. major*, but occasionally outside those of *M. erymanthius* (in particular in the M^3).

The mandible (Figure 8) has an elongate and relatively slender aspect, which is principally caused by the symphysis being elongate and narrow. The length of the symphysis is 86, the thickness is 22.7, and the minimum transverse width in this area is 48.3 mm. The posterior end is situated just before the P_2. The length of the diastema P_2–C_f is 64.5 mm. Symphysis length and P_2–canine distance are sexually dimorphic and tend to increase at least until the individual is completely adult. It seems that these distances are longer in the geologically younger *Microstonyx*, but it is difficult to evaluate this because of variability. The specimen from locality 19, being female, has among the highest P_2–canine distances of the available *Microstonyx* samples.

The lower dentition has the common morphology of the Suidae. The following details are of particular interest. The incisors are high crowned to a degree that is common in the Suinae. None of the specimens had a P_1. This tooth tends to disappear in the later samples, and does so somewhat more rapidly than the P^1. The P_4 are of the dicoryphochoerine type and have a large metaconid that is separate from the protoconid. The M_3 have third lobes with 2 major cusps. The complexity of this lobe is very variable in *Microstonyx* (van der Made et al., 1993). The lower cheek teeth are relatively small (Table 3), but within the ranges of the material assigned to *Microstonyx major*, as well as that assigned to *Microstonyx erymanthius* (Figures 7 and 9).

2.4. Taxonomical assignment

The elongate I^2 occurs in Suinae and Tetraconodontinae, but the latter subfamily has P_4 with only one main cusp.

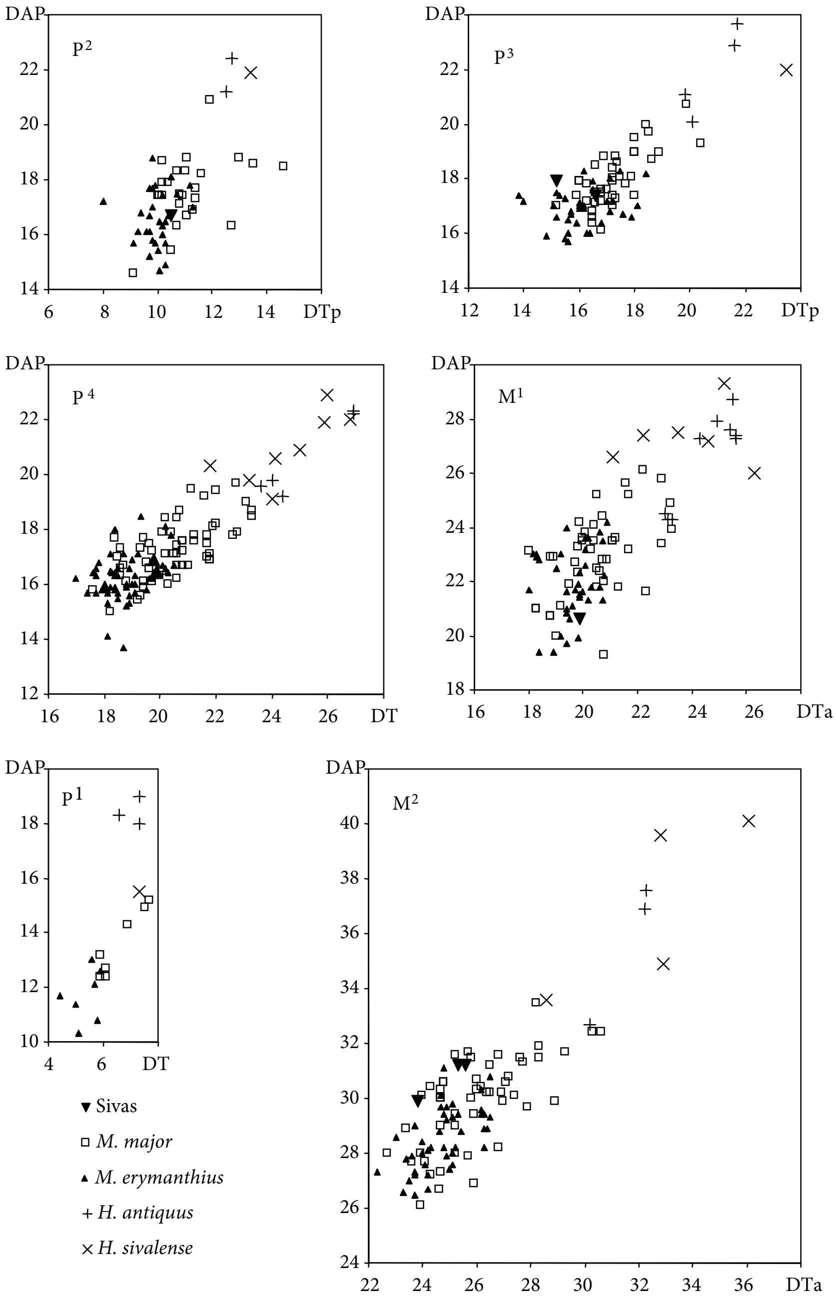

Figure 6. Bivariate plots of the upper cheek teeth: length (DAP) versus width of the anterior (DTa) or posterior lobes (DTp). Legend for the lower and upper cheek teeth (Figures 2–4): *Hippopotamodon sivalense* from the Siwaliks (IM, GSP, NHI, UL, NMB, BSP, FISF); *Hippopotamodon antiquus* from Bayraktepe (MTA), Eppelsheim (HLD), Esme Akçaköy (PIMUZ), Kayincak (UA), Montrigaud (MLG), Middle Sinap (MTA, MNHN), St. Jean-de-Bournai (NMB), Usak (MTA); *Microstonyx major* from Allisas (MGL), Baltavár (HGSB, NMW), Basaleti (GSM), Bayir (MTA), Bayramkalesi (UA), Çeltek Küyü (MTA), Chalon (UCBL), Çobanpınar (MTA, UA), Concud (NHM), Concud - Barranco de las Calaveras (IVAU), Concud - Cerro de la Garita (MNCN, IVAU, IPS, MPZ, Collection Pepe Orrios, Teruel), Çorak Yerler (UA, PIMUZ), Crevillente 2 (MHMN, MPV), Crevillente 15 (MHMN), Csákvár (HGSB), Cucuron or Vaugines (MRA), Das (MLGSB), Eldar (GSM), Evciköy (MTA), Garkin (MTA), Grebeniki (VMM), Gökdere (UA), Elmadağ (UA), Gülpınar (MTA), Igbek (= Sinap loc. 49; SP), Kayadibi (MTA, PIMUZ), Kohfiddisch (NMW), Küçük Yozgat (UA), Lapsehi-Subasi (MTA), Luzinay (MGL), Mahmutgazi (MTA), Montredon/Mont Léberon (UCBL, MGL), Paşabağı (UA), Piera (IPS, MLGSB, MGB), Polgárdi (HGSB, NMB), Puente Minero (CPO), Salihpaşalar (MTA), Salmendingen (NMB), Schernham (NMW), Sehlek (MTA), Sinap loc. 26 (SP), Sivas-Hayranlı (MTA), Sivas loc. 2 (UA), Sivas loc. 19 (UA), Siwaliks (IM, cast IGF), Stratzing (NMW, KME), Taraklia (PIN), Terrassa (IPS), Tersanne (UCBL), Titov Veles (IVAU), La Tour du Pin (MGL), Udabno (GSM), Várpalota (HGSB), Vaugines (MRA); *Microstonyx erymanthius* from Ano Metochi 4 (IVAU), Dorn Dürkheim (FISF), Kavakdere (= Sinap loc. 33; MTA, PIMUZ, SP), Kerasia (IVAU), Maragha (NMW, MTA, IVAU), Maragha - Kopran (NMW), Pikermi (NHM, IPUW MGL, MSNO, TMH, MGPUSB), Pikermi - Chomateri (NMW), Samos (NMW, HLD, NMB, NMBe), Soblay (UCBL, MGL).

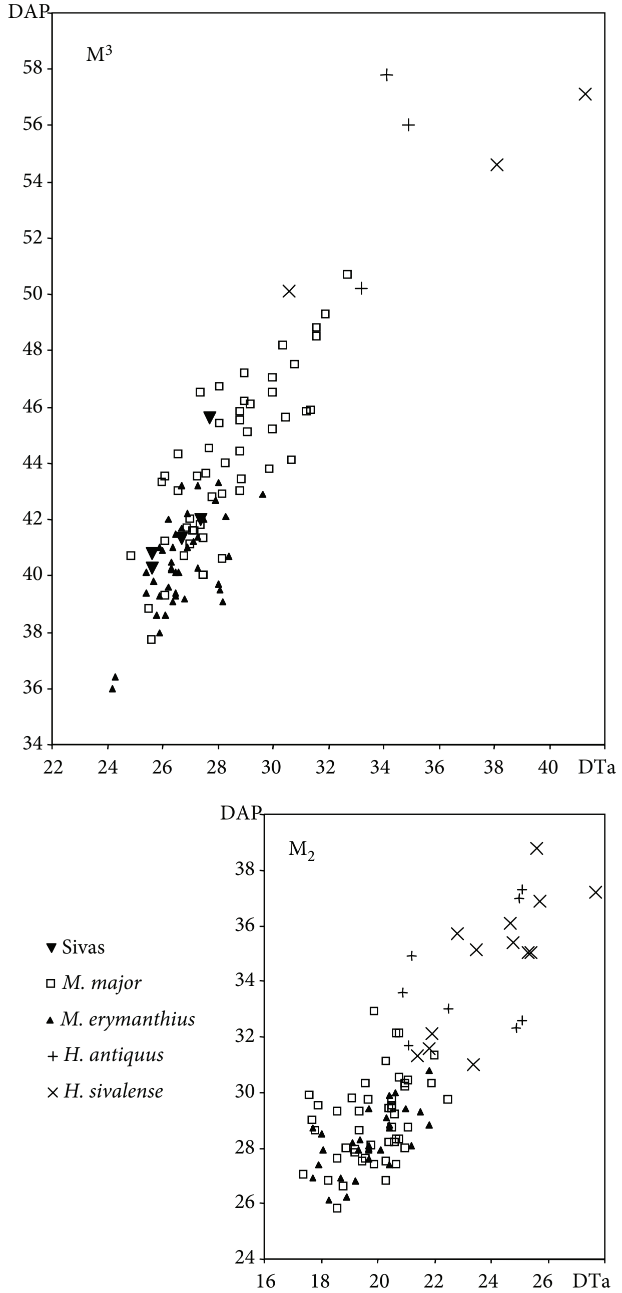

Figure 7. Bivariate plots of the M^3 and M_2: length (DAP) versus width of the anterior (DTa) or posterior lobes (DTp). Legend as in Figure 2.

The shape of the P_4 is of the dicoryphochoerine type, with a metaconid placed well lingually of the protoconid, whereas in the Suini, it is placed slightly behind and close to the protoconid. This points to the Dicoryphochoerini. The elongate and low I^3 differs from the shorter and higher tooth in *Propotamochoerus*, but is similar in *Microstonyx* and *Hippopotamodon*. The size of the cheek teeth is clearly smaller than in *Hippopotamodon sivalense* and *H. antiquus*. In most cases, the sizes of the cheek teeth are in the overlap of the material assigned to *M. major* and *M. erymanthius*, but in some cases they are just outside the range of the latter but still within the ranges of the former species. Therefore, we assign the material to *H. major*, but we note that a revision of the *M. major* - *M. erymanthius* material is necessary.

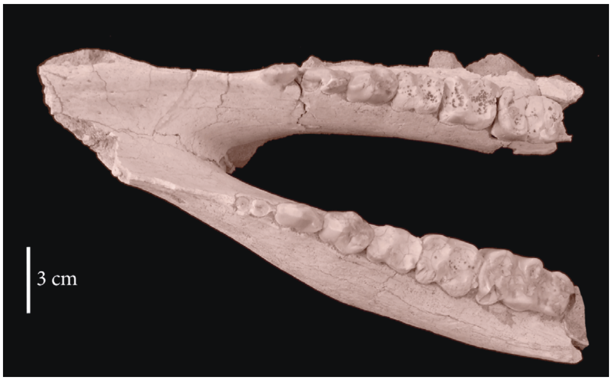

Figure 8. Mandible 58-HAY-05 of *Microstonyx* from locality 19; occlusal view.

4. Discussion

Suidae have a unique adaptation: they use their snout to root. This makes resources available to them, including roots, bulbs, and small animals, that are not used by other ungulates and that allow them to survive in a wider range of environments and during harsh seasons (Cumming, 1975). This affects the structure of the whole skull. It appears that rooting ability is related to the force rate of the complex muscle, which elevates the skull, and thus to occiput height and width (Sicuro and Oliveira, 2002). *Microstonyx* has a particularly wide and high occiput and must have been a powerful rooter. The nasal disc is used in rooting and is moved by muscles that originate on the face in the preorbital fossa and below the root of the zygomatic arch (Ewer, 1956). Again these structures suggest that *Microstonyx* was an able rooter. Once a food item is located in the soil, the incisors are used to extract it. Suidae evolved large and high crowned incisors, particularly the I_{1-2} and the I^1. In suid evolution, the I_3 increased less in crown height and size, or was even reduced, and as a result a gap grew between the tips of the I_2 and I_3, exposing an increasingly long part of the distal side of the I_2. The I^2 articulates with the distal side of the I_2 and became elongate as that gap grew. This evolution occurred in parallel in different suid lineages (van der Made, 2010), and this is also documented within *Microstonyx* (van der Made, 1997, 2003). The degree of elongation of the I^2 gives 2 types of information: biostratigraphic and ecological.

Figure 10 shows several localities with *Microstonyx* I^2, which were radiometrically dated or are dated with the

Table 3. Measurements in mm of the lower cheek teeth and mandible of *Microstonyx* from Sivas.

			DAP	**DTa**	**DTp**	**DTpp**	**Ta**	**D**	**W**
58-HAY-05	D	P_2	14.9	6.3	7.8				
58-HAY-05	S	P_3	17.3	8.8	8.8			59.1	27.6
58-HAY-05	D	P_3	17.3	--	9.1				
58-HAY-05	S	P_4	19.4	11.7	14.5			52.2	29.9
58-HAY-05	D	P_4	19.4	11.4	14.6				
58-HAY-05	S	M_1	>20.1	14.3	14.8				
58-HAY-05	D	M_1	>20.6	>14.2	>14.4				
58-HAY-05	S	M_2	24.6	>18.3	>19.1		1.3		
58-HAY-05	D	M_2	>22.6	18.9	19.7		1.4		
58-HAY-05	S	M_3	41.7	21.9	20.3	17.0	2.2		
58-HAY-05	D	M_3	--	--	--	--	1.9		
58-HAY-19/250	S	M_1	23.4	14.6	15.8				
58-HAY-19/252	S	M_2	--	--	20.4				

help of paleomagnetism, while the age of the others is inferred from their assignment to an MN unit. First, we will discuss the ages of the localities.

The locality Eldar is placed in MN10 (De Bruijn et al., 1992; Gabunia et al., 2001). The locality Udabno II is placed in MN11, while Udabno I, with *Microstonyx*, is slightly older, but is younger than Eldar and could be Upper Sarmatian or Lower Meotian (Gabunia et al., 2001). The boundary between these 2 stages is estimated to be around 9.88 Ma and close to the MN9–10 transition (Rögl and Daxner-Höck, 1996; Rögl, 1999).

Several localities near the city of Terrassa are generally grouped under the name Terrassa (e.g., De Bruijn et al., 1992) and have a more or less homogeneous fauna, placed in the upper part of MN10. The localities Trinchera Norte Autopista and Talud Sur Autopista are in sediments with reversed polarity, correlated with the earlier part of Chron C4Ar.1r, and the locality Torrent de Fibulines is in normally polarized sediments higher in the sequence, which are correlated to the earlier part of Chron C4An (Garcés et al., 1996). The incisor from Terrassa is of unknown exact provenance (Golpe-Posse, 1980b), but its age is probably around 9.0–9.3 Ma.

The locality of Crevillente 2 (Spain) is the reference locality of MN11 (De Bruijn et al., 1992).

The locality Dorn Dürkheim 1 is placed in MN11 (De Bruijn et al., 1992).

The locality of Csákvár (Hungary) is placed in MN10 (Mein, 1975, 1977; De Bruijn et al., 1992, p. 74) or MN11 (Rabeder, 1989; De Bruijn et al., 1992, p. 95). The faunal list includes *Brachypotherium* (Rabeder, 1989), a rhinoceros that was supposed to appear last in MN9 (De Bruijn et al., 1992, p. 78; Cerdeño, 1998), though no one has proposed this age for Csákvár. The locality was placed in MN11 in a recent paper that revised material from there (Scott et al., 2005).

The skull with I^2 from Kavakdere (Turkey) is from the old collections without exact indication of provenance, but it is probably from the same level as localities 26 and 33 of the Sinap project (van der Made, 2003). Kappelman et al. (2003) correlated Kavakdere localities 26 and 33 with Chron C4r.1r and estimated an age of 8.121 Ma.

Two of the three incisors from Maragha in Figure 10 were indicated to come from Kopran, while the third had no precise provenance indication in the collection. Bernor et al. (1996, fig. 10.1, pp. 140–141) estimated an age of 9 Ma for Kopran.

The incisors from Samos (Greece) are in the Basel collections. We do not know from which precise locality at Samos they come, but Solounias (1981) suggested that material in Swiss collections might come from the Potamies area, where Quarry 2 is situated. This locality is in the Main Bone Beds. Bernor et al. (1996, p. 143) indicated the localities of the Main Bone Beds to have ages between 7.1 and 7.660 Ma and the Old Mill Beds to have an age around 8.33 Ma, while the overlying Marker Tuff is dated to 6.17 Ma. Kostopoulos et al. (2003) studied the paleomagnetism. Their results suggest that the different sites are less widely spread in age and are concentrated in what is usually considered to be MN12.

Bernor et al. (1996, p. 143) indicated that Chomareri (Greece) is late MN12 and younger than the main locality

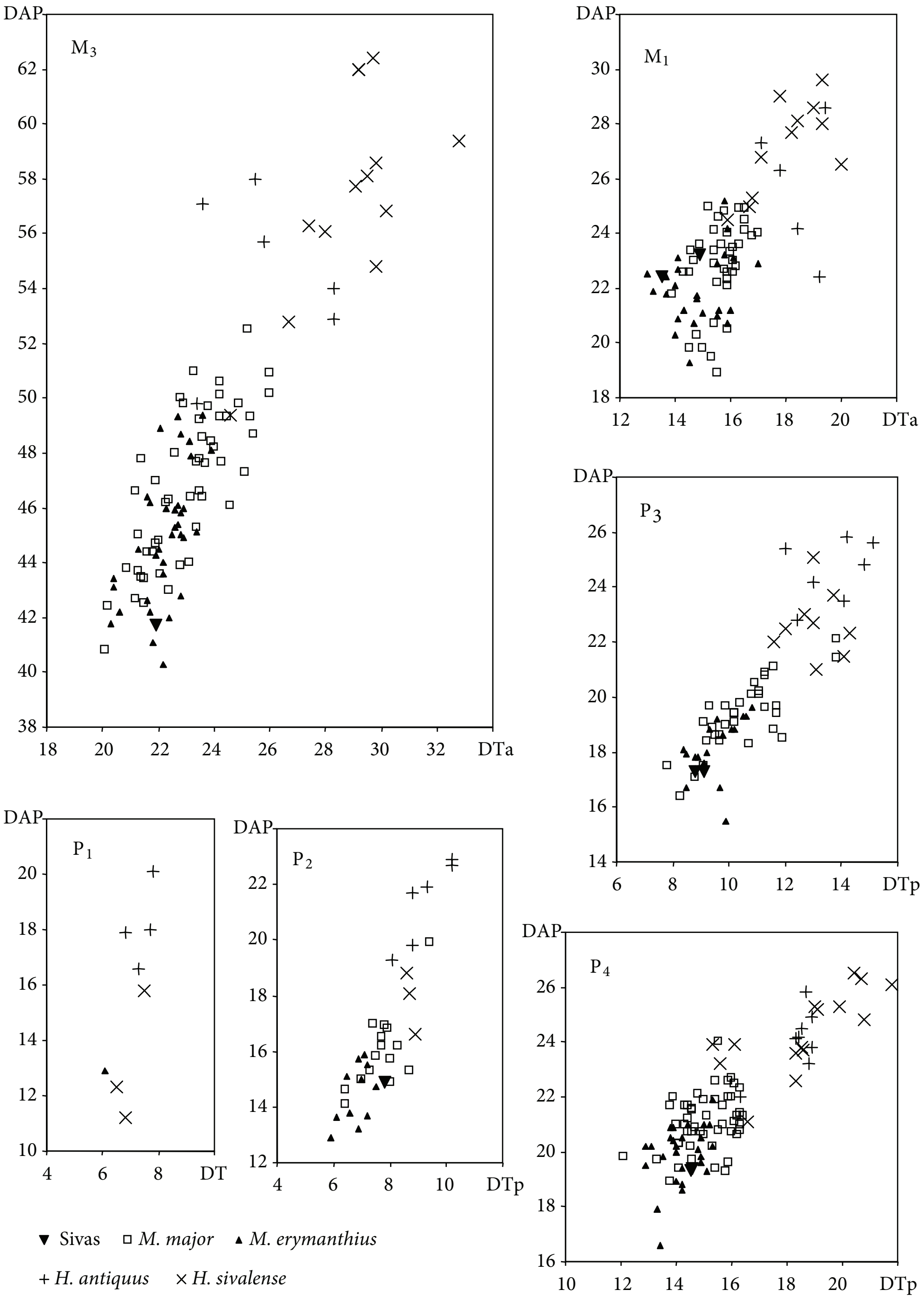

Figure 9. Bivariate plots of the lower cheek teeth: length (DAP) versus width of the anterior (DTa) or posterior lobes (DTp). Provenance of data as in Figure 2.

of Pikermi, which suggests that Pikermi might be early MN12 or at least not the latest part of MN12.

Van Dam et al. (2006) estimated an age of 7.1 Ma for Concud - Cerro de la Garita on the basis of correlation to the local paleomagnetic section.

There are several localities at Polgárdi, numbered 1 to 5 (Venczel, 2006): Polgárdi 1 is poor and yielded only some bones, Polgárdi 2 is rich and is the one that is usually cited as just "Polgárdi", Polgárdi 3 is a small locality with "strongly brecciated sediments", Polgárdi 4 is a microvertebrate locality, and the material of Polgárdi 4 and 5 is kept in the Hungarian Geological Institute. The latter 2 localities were indicated to be MN13. Polgárdi 2 was discovered in 1910 and Polgárdi 3–5 from the 1970s

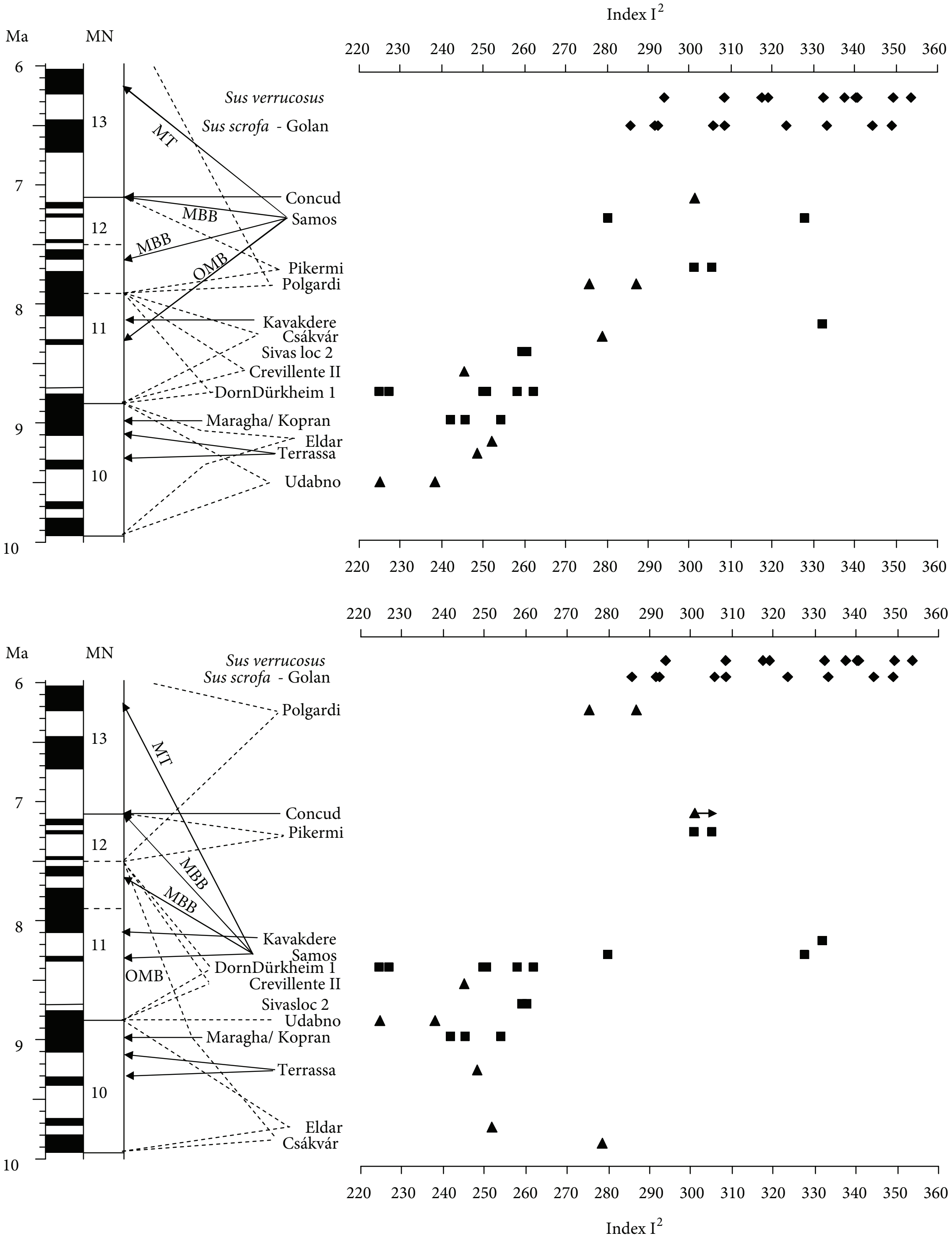

Figure 10. The increase in elongation of the I^2 of *Microstonyx* as indicated by the index 100 DMD/DLL. A value from Concud is a minimum value because of breakage; this is indicated with an arrow. Legend: triangles = material assigned to *M. major*; squares = material assigned to *M. erymanthius*; rhombs = *Sus*. As a comparison, indices of samples of recent *Sus verrucosus* from Java (Indonesia; NNML) and of recent *Sus scrofa* from the Golan Heights (Syrian territory occupied by Israel; HUJ). The provenance of the remaining data is as in Figure 4. Correlations or ages of the localities based on paleomagnetism or radiometric dating are indicated by arrows; assignments to MN units are indicated by dotted lines. For Samos: MT = Marker Tuff; MMB = Main Bone Beds; OMB = Old Mill Beds. All localities are placed within the ranges of their possible age as indicated by their MN units or "absolute" age; in addition, they have been arranged according to ascending (upper figure) or descending index values (lower figure), with the only constraint that a locality with very low values cannot be below Kavakdere. There are 2 options for the MN11-12 boundary: 7.5 and 7.9 Ma. The upper figure favors the idea of an evolution with increasing index values, while the lower figure blurs this pattern.

onward. If the remark that Polgárdi 1 yielded only a few bones is taken literally, this means that there were no teeth. One of us studied 3 teeth in the NMB, with the indication "Polgárdi 1927". These are probably from the classic Polgárdi 2. Casts of 2 of the specimens are also in the HLD. The rest of the material studied was studied in the HGSB, including the incisors, and also has to be from Polgárdi 2. Apparently, Polgárdi 2, 4, and 5 are MN13, and for the others no indication was given (Venczel, 2006). It is assumed here that the material studied is from the classic Polgárdi 2. Ever since the beginning of the MN units, the locality was placed low in MN13 (Mein, 1975, 1977, 1990; De Bruijn et al., 1992). A faunal list of Polgárdi given by Rabeder (1989) includes several species that suggest an age older than MN13, but a taxonomic revision might be necessary. Some material has been revised. Freudenthal and Martín Suárez (1999) indicated Polgárdi to be MN12, and Scott et al. (2005) listed it as MN12 to 13 (the latter authors also placed Baltávar in MN12, a locality which, along with Polgárdi, has figured low in MN13 in all the MN tables). We treat the locality as if MN13, but note that this may prove to be too young.

In the upper part of Figure 10, these localities are arranged in chronological order. Correlations or ages based on paleomagnetism or radiometric dating are indicated by arrows; assignments to MN units are indicated by dotted lines. In addition, but within the constraint of their MN units and numerical ages, the localities have been arranged according to ascending index values so as to favor an evolutionary trend of increasing index values. The right side of Figure 10 shows an index value for the I^2 describing their elongation: $I = 100 \times DMD/DLL$, which is the length expressed as a percentage of the width. As a reference, 2 samples of recent *Sus* are given. The MN10 localities have values below 270 and the MN12–13 localities have values above 270. The material assigned to *Microstonyx major* and *M. erymanthius* is given different symbols. The pattern shows up independently of taxonomy.

Within MN11 (8.7 to 7.5 or 7.9 Ma; Agustí et al., 2001), the variation is greater than in the recent samples, and it seems unlikely that the samples from Kavakdere and Dorn Dürkheim could have been drawn from similar populations. The greater variation in MN11 could be explained by an evolutionary increase in the values within this unit, with the transition from the shorter to the more elongate I^2 occurring between Kavakdere (dated 8.121 Ma) and Dorn Dürkheim (with a maximum age of about 8.7 Ma).

In the lower part of Figure 10, the localities are also placed within their MN units and "absolute" time ranges. However, they are secondarily ordered according to descending index values, but with the constraint that localities with low index values cannot be placed above Samos and Kavakdere. This is because such a placement would imply a period with a variability significantly higher than in the recent samples. This procedure tends to blur the pattern of elongation of the I^2. However, the pattern still shows up, but in this case there has to be an even faster change between Samos (now taken as 8.33 Ma) and Dorn Dürkheim (maximum 8.7 Ma).

Once the increase in elongation of the I^2 is established and dated, it can be used in biostratigraphy. Here it can be used as an indication of the stratigraphic position and age of locality 58-HAY-2. The incisors from 58-HAY-2 are close to the maximum of the older and the minimum value of the younger group of localities. It seems likely that the locality is older than Kavakdere (8.121 Ma) and Samos (oldest possible age 8.33 Ma, but more probably between 7.1 and 7.660 Ma). This means that 58-HAY-2 is probably below 8.121 Ma, possibly even below 8.33 and above 8.7 Ma, and in the lower half of MN11. Locality 19 is 38 m lower in the sequence and thus still older (on the basis of *Microstonyx* MN10 to lower MN11). This does not contradict the earlier results of Bibi and Güleç (2008) who, on the basis of the bovids, placed a group of localities in MN11 or MN12; 4 of the 5 species of bovid are present in 58-HAY-19. Nor does a placement of this locality in MN11 contradict the placement of the Düzyayla, in the top of the İncesu Formation, in MN11 or MN12 or the Turolian on the basis of microvertebrates, pollen, and large mammals (De Bruijn et al., 1996a, 1996b; De Bruijn and Mein, 1996; Fahlbusch and Bolliger, 1996; Ünay, 1996; Akgün et al., 2000). Looking at it the other way around, if Düzyayla were finally placed in MN12, this would not necessarily support a placement of localities 58-HAY-2 and -19 in MN11, but if Düzyayla were placed in MN11, this would support placing localities 2 and 19 in MN11.

The increase in I^2 elongation is not an isolated feature, but rather occurs along with many other changes that are related to rooting. Though not discussed in detail here, it is part of a modification of the anterior dentition as an adaptation to rooting, which also involves the other incisors (van der Made, 2010). Thenius (1972) noted that, in what he believed to be *M. major*, the snout is longer and the orbit placed more backwards than in what he believed to be *M. antiquus*. This conforms to the observation, made above, that there seems to be an increase in diastema length from earlier to later forms coincident with the changes in incisor morphology. The apparent evolutionary shift to a more posterior position of the orbit can also be understood as a forward shift of the dentition or snout. All these changes have the effect that the snout becomes more elongate, which allows for deeper rooting. The necessary force rate and size of the complex muscle to root such a long snout deep in the soil is indicated by the very high and wide occiput of this suid. Present *Sus scrofa* roots to a depth of about 25 cm (Sicuro and Oliveira, 2002), but *Microstonyx* may have been able to reach resources much deeper in the soil. This interpretation contrasts with an earlier interpretation comparing the concave dorsal skull profile of the suid with that of domestic pigs that have less opportunity to root (Trofimov, 1954; Thenius, 1972). By rooting, suids have access to resources that are not available to other ungulates.

Before the Middle Miocene there is no good fossil record of large mammals in Anatolia, but from that time onward, Anatolia and Europe have broadly the same species of suids. In both areas the so-called Vallesian Crisis is noted in a decrease in the suid diversity (Fortelius et al., 1996). Many species went extinct and *Hippopotamodon antiquus* was replaced by *Microstonyx major*, which after this date was the most abundant suid until the end of the Miocene, though there are some localities with a smaller suid indicated as *Propotamochoerus* sp. and at the very end of the Miocene *Propotamochoerus provincialis* appeared (Fortelius et al., 1996; van der Made, 2003). The Vallesian Crisis also marked the demise of the European Hominoidea and has been interpreted as caused by an increase in seasonality (Suc et al., 1999). The spread at this time and the abundance afterwards of *Microstonyx major* suggests that it was well adapted to the new environments, unlike the suids that went extinct. Its morphology suggests that it was a good rooter, which may have played a part in its success. The availability or nutritive value of plant parts above the ground tends to be reduced during winters in seasonal climates. Ungulates have different strategies to counter seasonal fluctuations in food supply (e.g., migration, seasonal shifting between browsing and grazing), and suids may fall back on subsurface resources such as earthworms, beetles, roots, tubercles, and bulbs. In this sense a better adaptation to rooting might be a decisive advantage in more seasonal climates.

The morphological changes suggest that *Microstonyx* became a more specialized rooter in a short period between 8.7 and 8.121 Ma or, alternatively, in a still shorter period between 8.7 and 8.33 Ma. The passage of MN11 to MN12 is characterized more by extinctions than by dispersals of new taxa (De Bruijn et al., 1992), suggesting that conditions became harsher (dryer, maybe more seasonal). These extinctions leading to a decreased diversity were also noted in a study on the Bovidae from Turkey (Köhler, 1987) that included many of the localities with *Microstonyx* treated here. Fortelius et al. (1996) found a decrease in species richness from MN9 to MN10 in the western part of their study area followed by relative stability (Portugal to Poland), while they found an increase in the eastern part (Hungary to Kazakhstan and Afghanistan) from MN10 to MN11, followed by relative stability, until at least MN13. This corresponds to Kızılhisar "Pollenbild" of the Turkish sequence (Benda et al., 1975; Becker-Platen, 1977). The Turkish vertebrate localities are interpreted to show steppe with a decreasing amount of dry bush across the MN11–12 transition (Becker-Platen et al., 1975), and attempts were made to subdivide the "Pollenbild", but this has been contested (Akgün et al., 2000). *Microstonyx* occurred in an area extending from Spain to China, and its increased rooting ability may have been an adaptation to environmental change on this scale, but a direct link to environmental change in Turkey is at present not straightforward.

5. Conclusions

The following conclusions are drawn:

- The suid material from localities 58-HAY-2 and 58-HAY-19 at Sivas is assigned to *Microstonyx major*.
- Changes in incisor morphology suggest that *Microstonyx* became a more specialized rooter during a short time interval between about 8.7 and 8.121 Ma ago. This increase in adaptation may have been a reaction to environmental change.
- The relatively primitive incisor morphology in locality 58-HAY-2 suggests an older age than 8.121 Ma, while an earlier study of the bovids of 58-HAY-19 suggested a correlation to MN11–12 (with a maximum age of about 8.7 Ma). 58-HAY-2 is above 58-Hay-19 such that both localities in the Derindere Member of the İncesu Formation have to be of between 8.7 and 8.121 Ma in the lower part of MN11, while the locality Düzyayla in the top of this formation is either MN11 or MN12.

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References

Agustí, J., Cabrera, L., Garcés, M., Krijgsman, W., Oms, O. and Parés, J.M. 2001. A calibrated mammal scale for the Neogene of Western Europe. State of the Art. Earth Science Reviews 52: 247–260.

Akgün, F., Kaya, T., Forstén, A. and 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.

Becker-Platen, J.D., Benda, L. and Steffens, P. 1977. Litho- und biostratigraphische Deutung radiometrische Altersbestimmungen aus dem Jungetriär der Türkei (Känozoikum und Braunkohlen der Türkei, 18). Geologisches Jahrbuch, Reihe B 25: 139–167.

Becker-Platen, J.D., Sickenberg, O. and Tobien, H. 1975. Die Gliederung der känozoischen Sedimente der Türkei nach Vertebraten-Faunengruppen. Geologisches Jahrbuch, Reihe B 15: 19–45.

Benda, L., Heissig, K. and Steffens, P. 1975. Die Stellung der Vertebraten-Faunengruppen der Türkei innerhalb der chronostratigraphischen Systeme von Tethys und Paratethys. Geologisches Jahrbuch, Reihe B 15: 109–116.

Bernor, R.L., Solounias, N., Swisher, C.C. and Van Couvering, J.A. 1996. The correlation of three classical "Pikermian" mammal faunas – Maragheh, Samos, and Pikermi – with the European MN unit system. In: The Evolution of Western Eurasian Neogene Mammal Faunas (Eds. R. Bernor, V. Fahlbusch and W. Mittmann). Columbia University Press, New York, pp. 137–154.

Bibi, F. and Güleç, E.S. 2008. Bovidae (Mammalia: Artiodactyla) from the Late Miocene of Sivas, Turkey. Journal of Vertebrate Paleontology 28(2): 501–519.

Bonis, L. de and Bouvrain, G. 1996. Suidae du Miocène supérieur de Grèce. Bulletin du Muséum national d'Histoire naturelle, 4e série, 18, section c, 1: 107–132.

Cerdeño, E. 1998. Diversity and evolutionary trends of the family Rhinocerotidae (Perissodactyla). Palaeogeography, Palaeoclimatology, Palaeoecology 141: 13–34.

Cumming, D.H.M. 1975. A field study of the ecology and behaviour of warthog. Museum Memory 7: 1–179.

De Bruijn, H., Daams, R., Daxner-Höck, G. Fahlbusch, V., Ginsburg, L., Mein, P., Morales, J., Heizmann, E., Mayhew, D.F., van der Meulen, A.J., Schmidt-Kittler N. and Telles Antunes, M. 1992. Report of the RCMNS working group on fossil mammals, Reisensburg 1990. Newsletters on Stratigraphy 26(2/3): 65–118.

De Bruijn, H. and Mein, P. 1996. The Middle and Late Miocene record of the Sciuridae and Petauristidae in France, central Europe, southeastern Europe, and Anatolia. In: The Evolution of Western Eurasian Neogene Mammal Faunas (Eds. R.L. Bernor, V. Fahlbusch and H.W. Mittmann). Columbia University Press, New York, pp. 213–215.

De Bruijn, H., Saraç, G., van den Hoek Ostende, L. and Roussiakis, S. 1999. The status of the genus name *Parapodemus* Schaub, 1938; new data bearing on an old controversy. In: Elephants Have a Snorkel: Papers in Honor of Paul Y. Sondaar (Eds. J.W.F. Reumer and J. de Vos). Rotterdam: Deinsea 7: 95–112.

De Bruijn, H., Ünay, E. and van den Hoek Ostende, L. 1996a. The composition and diversity of small mammal associations from Anatolia through the Miocene. In: The Evolution of Western Eurasian Neogene Mammal Faunas (Eds. R.L. Bernor, V. Fahlbusch and H.W. Mittmann). Columbia University Press, New York, pp. 266–270.

De Bruijn, H., van Dam, J.A., Daxner-Höck, G., Fahlbusch, V. and Storch, G. 1996b. The genera of the Murinae, endemic insular forms excluded, of Europe and Anatolia during the Late Miocene and Early Pliocene. In: The Evolution of Western Eurasian Neogene Mammal Faunas (Eds. R.L. Bernor, V. Fahlbusch and H.W. Mittmann). Columbia University Press, New York, pp. 253–260.

Demirci, S., Güleç, E., Özer, İ., Pehlevan, C., Yiğit, A., Kaya, F. and Erkman, C. 2007. 2005 Yılı Sivas/Hayranlı Haliminhanı Kazısı. TC. Kültür ve Turizm Bakanlığı 28. Kazı Sonuçları Toplantısı 2: 141–156.

Ewer, R.F. 1956. Adaptive features in the skulls of African Suidae. Proceedings of the Zoological Society London 131: 135–155.

Fahlbusch, V. and Bolliger, T. 1996. Eomyids and Zapodids (Rodentia, Mammalia) in the Middle and Upper Miocene of central and southeastern Europe and the eastern Mediterranean. In: The Evolution of Western Eurasian Neogene Mammal Faunas (Eds. R.L. Bernor, V. Fahlbusch and H.W. Mittmann). Columbia University Press, New York, pp. 208–252.

Fortelius, M., van der Made, J. and Bernor, R.L. 1996. Middle and Late Miocene Suoidea of Central Europe and the Eastern Mediterranean: evolution, biogeography and paleoecology. In: The Evolution of Western Eurasian Neogene Mammal Faunas (Eds. R.L. Bernor, V. Fahlbusch and H.W. Mittmann). Columbia University Press, New York, pp. 344–377.

Freudenthal, M. and Martín Suárez, E. 1999. Family Muridae. In: The Miocene Land Mammals of Europe (Eds. G. Rössner and K. Heissig). Verlag Dr. Friedrich Pfeil, Munich, pp. 401–409.

Gabunia, L., Gabashvili, E., Vekua, A. and Lordkipanidze, D. 2001. The Late Miocene hominoid from Georgia. In: Hominoid Evolution and Climate Change in Europe. Volume 2. Phylogeny of the Neogene Hominoid Primates of Eurasia (Eds. L. de Bonis, E.D. Koufos and P. Andrews). Cambridge University Press, Cambridge, pp. 316–325.

Garcés, M., Agustí, J., Cabrera, L. and Parés, J.M. 1996. Magnetostratigraphy of the Vallesian (late Miocene) in the Vallès-Penedès Basin (northeast Spain). Earth and Planetary Science Letters 142: 381–396.

Gervais, P. 1848–1852. Zoologie et paléontologie françaises. 3 Volumes. A. Bertand, Paris.

Ginsburg, L. 1974. Les Tayassuids des phosphorites du Quercy. Palaeovertebrata 6: 55–85.

Ginsburg, L. 1980. *Xenohyus venitor*, suid nouveau (Mammalia, artiodactyla) du Miocène Inferieur de France. Geobios 13: 861–877.

Ginsburg, L. 1988. Contributions a l'étude du gisement Miocène Supérieur de Montrédon (Herault). Les grands mammifères. 4 – Les artiodactyles Suidae. Palaeovertebrata, Mém. extr.: 57–64, 1 pl.

Golpe-Posse, J.M. 1980a. Le genre *Microstonyx* en Espagne et ses relations avec les autres espèces du même genre hors d'Espagne. Palaeovertebrata, Montpellier, Mém. Jubil. R. Lavocat: 213–231, 3 pl.

Golpe-Posse, J.M. 1980b. Notas sobre la dentición anterior de *Microstonyx antiquus* (Kaup, 1833). Acta Geologica Hispanica 15: 109–111.

Gray, J.E. 1821. On the natural arrangement of vertebrose animals. London Medical Repository 15(1): 296–310.

Hünermann, K.A. 1975. Die Suidae aus dem Türkischen Neogen. In: Die Gliederung des höheren Jungtertiärs und Altquartärs in der Türkei nach Vertebraten und ihre Bedeutung für die internationale Neogen-Stratigraphie (Ed. O. Sickenberg). Geologisches Jahrbuch, Reihe B 15: 153–156.

Kappelman, J., Duncan, A., Feseha, M., Lunkka, J.P., Ekart, D., McDowell, F., Ryan, T.M. and Swisher, C.C. 2003. Chronology. In: Geology and Paleontology of the Miocene Sinap Formation, Turkey (Eds. M. Fortelius, J. Kappelman, S. Sen and R.L. Bernor). Columbia University Press, New York, pp. 41–66.

Kaup, J.J. 1833. Description d'ossements fossiles de Mammifères 2. J. G. Heyer, Darmstadt.

Kaymakci, N. 2000. Tectono-stratigraphical evolution of the Çankiri Basin (Central Anatolia, Turkey), PhD thesis, Utrecht University Faculty of Earth Sciences, the Netherlands.

Kaymakçi, N., De Bruijn, H. White, S.H., Van Dijk, M., Saraç, G. and Ünay, E. 2001. Tectonic implications of the Neogene stratigraphy of the Çankiri basin with special reference to the Çandir locality (North–Central Anatolia, Turkey). In: Geology and Vertebrate Paleontology of the Miocene Hominoid Locality of Çandir (Eds. E. Güleç, D.R. Begun and D. Geraads). Courier Forschungsinstitut Senckenberg 240: 9–28.

Kaymakcı, N., İnceöz, M. and Ertepınar, P. 2006. 3D-architecture and Neogene evolution of the Malatya Basin: inferences for the kinematics of the Malatya and Ovacık Fault Zones. Turkish Journal of Earth Sciences 15: 123–154.

Köhler, M. 1987. Boviden des türkischen Miozäns (Känozoikum und Braunkohlen der Türkei. 28). Paleonologia i Evolució 21: 133–246.

Kostopoulos, D.S., Sen, S. and Koufos, G.D. 2003. Magnetostratigraphy and revised chronology of the late Miocene mammal localities of Samos, Greece. International Journal of Earth Sciences (Geologische Rundschau) 92: 779–794.

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

Krijgsman, W., Garcés, M., Langereis, C.G., Daams, R., Van Dam, J., Van der Meulen, A.J., Agustì, J. and Cabrera, L. 1996. A new chronology for the middle to late Miocene continental record in Spain. Earth and Planetary Science Letters 142: 367–380.

Liu, L., Kostopoulos, D.S. and Fortelius, M. 2004. Late Miocene *Microstonyx* remains (Suidae, Mammalia) from Northern China. Geobios 37: 49–64.

Lydekker, R. 1877. Notices of new and rare mammals from the Siwaliks. Records of the Geological Survey of India 10: 76–83.

Mein, P. 1975. Proposition de biozonation du Néogène méditerranéen à partir des mammifères. Trabajos sobre Neógeno-Cuaternario 4: 112.

Mein, P. 1977. Tables 1–3. In: Round Table on Mastostratigraphy of the W. Mediterranean Neogene (Eds. M.T. Alberdi and E. Aguirre). Trabajos Sobre Neogeno Cuaternario 7.

Mein, P. 1990. Updating of MN zones. In: European Neogene Mammal Chronology (Eds. E.H. Lindsay, V. Fahlbusch and P. Mein). Plenum Press, New York and London, pp. 73–90.

Ozansoy, F. 1965. Études des gisements continentaux et de Mammifères du Cénozoïque du Turquie. Mémoires de la Societé Géologique de France, Nouvelle Série 44: 1–92.

Pickford, M. 1988. Revision of the Miocene Suidae of the Indian Subcontinent. Münchener Geowissenschaftliche Abhandlungen, Reihe A, Geologie und Palontologie 12: 1–91.

Pickford, M. and Ertürk, Ç. 1979. Suidae and Tayassuidea from Turkey. Bulletin of the Geological Society of Turkey 22: 141–154.

Pilgrim, G.E. 1926. The Fossil Suidae of India. Memoirs of the Geological Survey of India New Series 8(4).

Rabeder, G. 1989. 4.5. Pontian Mammals. 4.5.1. Die Säugetiere des Pontien in Österreich und Ungarn. In: Chronostratigraphie und Neostratotypen. Neogen der Westlichen ("Zentrale") Paratethys. VIII Pontien. Jugoslawische Akademie der Wissenschaften und Künste and Serbische Akademie der Wissenschaften und Künste, Zagreb and Belgrade: 812–836.

Rögl, F. 1999. Circum-Mediterranean Miocene paleogeography. In: The Miocene Land Mammals of Europe (Eds. G. Rössner and K. Heissig). Verlag Dr. Friedrich Pfeil, Munich, pp. 39–48.

Rögl, F. and Daxner-Höck, G. 1996. Late Miocene Paratethys correlations. In: The Evolution of Western Eurasian Neogene Mammal Faunas (Eds. R.L. Bernor, V. Fahlbusch and H.W. Mittmann). Columbia University Press, New York, pp. 47–55.

Roth, J. and Wagner, A. 1854. Die Fossilen knochenberreste von Pikermi in Griechenland. Abhandlungen der bayerische Akademie der Wissenschaften, München 7: 371–464.

Schmidt-Kittler, N. 1971. Die obermiozäne Fossillagerstätte Sandelzhausen 3. Suidae, Artiodactyla, Mammalia. Mitteilungen der Bayerische Staatssamlung für Palontäontologie und Historische Geologie 11: 129–170.

Scott, R.S., Bernor, R.L. and Raba, W. 2005. Hipparionine horses of the Greater Pannonian Basin: morphometric evidence from the postcranial skeleton. Palaeontographia Italica 90: 189–209.

Şengör, A.M.C. and Yılmaz, Y. 1981. Tethyan evolution of Turkey: a plate tectonic approach. Tectonophysics 75: 181–241.

Şenyürek, M.S. 1952. A study of the Pontian fauna of Gökdere (Elmadağı), southeast of Ankara. Türk Tarih Kurumu Belleten 16: 449–492.

Sicuro, F.L. and Oliveira, L.F.B. 2002. Coexistence of peccaries and feral hogs in the Brazilian Pantanal wetland: an ecomorphological view. Journal of Mammalogy 83(1): 207–217.

Solounias, N. 1981. The Turolian fauna from the island of Samos, Greece. Contributions to Vertebrate Evolution 6: 1–232.

Suc, J.P., Fauquette, S., Bessedik, M., Bertini, A., Zheng, Z., Clauzon, G., Suballyova, D., Diniz, F., Quézel, P., Feddi, N., Clet, M., Bessais, E., Bachiri Taoufiq, N., Meon, H. and Combourieu-Nebout, N. 1999. Neogene vegetation changes in West European and West circum-Mediterranean areas. In: Hominoid Evolution and Climatic Change in Europe. Vol 1. The Evolution of Neogene Terrestrial Ecosystems in Europe (Eds. J. Agustí, L. Rook and P. Andrews). Cambridge University Press, Cambridge, pp. 378–388.

Thenius, E. 1949. Über die Säugetierfauna aus dem Unterpliozän von Ilhan bei Ankara (Türkei). Österreichische Akademie der Wissenschaften. Mathematisch-naturwissenschaftliche Klasse, Sitzungsberichte, Abt. I 158(9-10): 656–661.

Thenius, E. 1972. *Microstonyx antiquus* aus dem Alt-Pliozän Mittel-Europas. Zur Taxonomie und Evolution der Suidae (Mammalia). Annalen des Naturhistorishes Museums Wien 76: 539–586.

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 Akademia Nauk SSR 47: 61–99.

Ünay, E. 1996. On fossil Spalacidae (Rodentia). In: The Evolution of Western Eurasian Neogene Mammal Faunas (Eds. R.L. Bernor, V. Fahlbusch and H.W. Mittmann). Columbia University Press, New York, pp. 248–252.

van Dam, J.A., Aziz, H.A., Alvarez Sierra, M.A., Hilgen, F.J., van den Hoek Ostende, L.W., Lourens, L.J., Mein, P., van der Meulen, A.J. and Peláez-Campomanes, P. 2006. Long-period astronomical forcing of mammal turnover. Nature 443: 687–991.

van der Made, J. 1990a. Iberian Suoidea. Paleontologia i Evolució 23: 83–97.

van der Made, J. 1990b. A range chart for European Suidae and Tayassuidae. Paleontologia i Evolució 23: 99–104.

van der Made, J. 1991. Sexual bimodality in some recent pig populations and application of the findings to the study of fossils. Zeitschrift für Säugetierkunde 56: 81–87.

van der Made, J. 1996. Listriodontinae (Suidae, Mammalia), their evolution, systematics and distribution in time and space. Contributions to Tertiary and Quaternary Geology 33(1–4): 3–254.

van der Made, J. 1997. The fossil pig from the Upper Miocene of Dorn Dürkheim in Germany. Courier Forschungsinsitut Senckenberg 197: 205–230.

van der Made, J. 2003. Fossil Suoidea of the Miocene Sinap Formation, Turkey. In: Geology and Paleontology of the Miocene Sinap Formation, Turkey (Eds. M. Fortelius, J. Kappelman, S. Sen and R.L. Bernor). University of Columbia Press, New York, pp. 308–327.

van der Made, J. 2010. The pigs and "Old World peccaries" (Suidae and Palaeochoeridae, Suoidea, Artiodactyla) from the Miocene of Sandelzhausen (southern Germany): phylogeny and an updated classification of the Hyotheriinae and Palaeochoeridae. Paläontologische Zeitschrift 84: 43–121.

van der Made, J. and Hussain, S.T. 1989. *"Microstonyx" major* (Suidae, Artiodactyla) from Nagri. Estudios geológicos 45: 409–416.

van der Made, J., Montoya, P. and Alcalá, L. 1992. *Microstonyx* (Suidae, Mammalia) from the Upper Miocene of Spain. Geobios 25(3): 395–413.

van der Made, J. and Moyà-Solà, S. 1989. European Suinae (Artiodactyla) from the Late Miocene onwards. Bolletino de la Società Paleontologica Italiana 28(2/3): 329–339.

Venczel, M. 2006. Lizards from the late Miocene of Polgardi (W-Hungary). Nymphaea 33: 25–38.