

Contribution to the study of *Microstonyx*: evidence from Bulgaria and the SE European populations

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ABSTRACT

The suid material from four Turolian localities (MN11-13) in Bulgaria has been studied and compared. All specimens belong to *Microstonyx major* (Gervais, 1848), a common faunal element of the late Miocene South-East European faunas. The Greek and Bulgarian fossil record allows several suggestions to be made, concerning metrical and morphological features of *Microstonyx major*, as well as the species-level taxonomic diversity. The elaboration and evaluation of several characters allow us to distinguish three groups of *M. major*, in the Balkan territory. The first group (MN11-12) represents a small sized form, probably related with the Maragha suid (MN11). The second group (MN12-13) includes the typical *M. major erymanthius* and the third one *M. major major* (MN13). The last two groups indicate relation between them, as well as with the latest Vallesian *Microstonyx major* from Nikiti (end of MN10). The first group of *Microstonyx major* from Perivolaki, Kerassia and Vathylakkos probably consists in new subspecies, characterized by small to medium sized toothrow, small third molar and relatively elongated premolar row. The molar row reduces from the early to the middle Turolian representatives of the group.

KEY WORDS

Mammalia,
Suidae,
Microstonyx,
late Miocene,
Bulgaria,
Greece,
fossil species.

RÉSUMÉ

Contribution à l'étude de Microstonyx: les données de Bulgarie et des populations de l'Europe du Sud-Est.

Le matériel de Suidae, provenant de quatre localités bulgares du Turolien (MN11-13), a été étudié et comparé. Tous les spécimens sont attribués à l'espèce *Microstonyx major* (Gervais, 1848), un élément faunique assez commun dans les faunes du Miocène supérieur de l'Europe du Sud-Est. Les données des archives bulgare et grecque permettent de discuter quelques caractères métriques et morphologiques, ainsi que la diversité taxonomique de l'espèce dans le territoire des Balkans. Trois groupes sont considérés. Le premier groupe (MN11-12) représente une petite forme, qui montre une liaison avec *Microstonyx* de Maragha (MN11). Les deuxième (MN12-13) et troisième groupe (MN13) correspondent à *M. major erymanthius* et *M. major major* respectivement. Ces deux groupes indiquent une relation entre eux ainsi qu'avec *Microstonyx major* de la localité du Vallésien supérieur de Nikiti (tard MN10). *Microstonyx major* de Perivolaki, Kerassia et Vathylakkos (premier groupe) représente probablement de nouvelles sous-espèces, caractérisées par leur série dentaire réduite, leur petite troisième molaire et relativement longue série de prémolaires. La série de molaires montre une réduction entre les formes du Turolien inférieur et moyen.

MOTS CLÉS

Mammalia,
Suidae,
Microstonyx,
Miocène supérieur,
Bulgarie,
Grèce,
espèces fossiles.

INTRODUCTION

Bakalov (1934) first mentioned the existence of late Miocene suids in Bulgaria. Later on, Bakalov & Nikolov (1962) refer to a few fossil remains from two localities in the well-known late Miocene site of Kalimantsi as "*Sus*" *erymanthius*. A "Pontian" age, in the old sense of the term, is suggested. The check-list of Tertiary mammals from Bulgaria given by Nikolov (1985) included several western Bulgarian localities, where *Microstonyx major* was also mentioned:

- Gaber (the Mine of Bolshhevik, Sofia District, Gnilianska Fm). A "Pontian" age was proposed (Nikolov 1985), but a middle Turolian (late Maeotian) age is most probable for the basal fossiliferous level of the locality where the suid remains were found in association with *Choerolophodon* and *Tetralophodon longirostris* (N. S. pers. obs.);
- Kocherinovo (Blagoevgrad District), probably early Turolian age (middle Maeotian), zone MN11? (N. S. pers. obs.);
- Djurovo (Blagoevgrad District), Sandanski Formation, ?Maeotian age.

The suid remains studied here come from four distinct localities in three different basins of South

Bulgaria (Fig. 1). The material was collected and prepared by D. Kovachev during the 70s and 80s field missions. It is now stored in the Paleontological Museum of Assenovgrad (Bulgaria).

ABBREVIATIONS

DTK	Dytiko-1;
Ez	Ezerovo;
GRE	Grebeniki;
KAL	Kalimantsi;
KER	Kerassia;
LUB	Luberon;
MAR	Maragha;
NETM	Nova Etmekova;
NKT	Nikiti-1;
PER	Perivolaki;
PIK	Pikermi;
Pk	Petrelilik;
PXM	Proxoma;
RZO	Ravin de Zouaves-5;
SAM	Samos (new locality MTLA);
Soph	Sophades;
STR	Stratzing;
TAR	Taraklija;
TOD	Tudurovo;
TVETIT	Titov Veles;
VTK	Vathylakkos-2;
L	length;
B	breadth;
DAP	anteroposterior diameter.

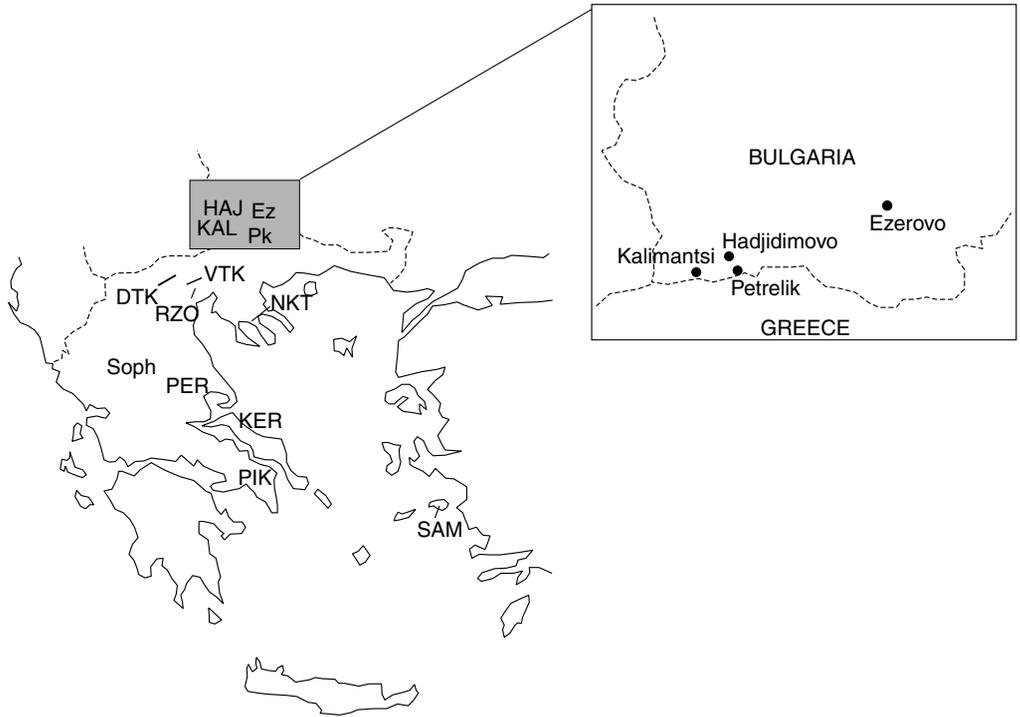


FIG. 1. — Sketch map of the Greco-Bulgarian territory, indicating the position of several localities where *Microstonyx major* (Gervais, 1848) is recorded. Abbreviations: **KAL**, Kalimantsi; **HAJ**, Hadjidimovo; **Ez**, Ezerovo; **Pk**, Petrelik; **VTK**, Vathylakkos-2; **RZO**, Ravin de Zouaves-5; **DTK**, Dytiko-1; **NKT**, Nikiti-1; **Soph**, Sophades; **PER**, Perivolaki; **KER**, Kerassia; **PIK**, Pikermi; **SAM**, Samos (locality MTLA).

LOCATION AND STRATIGRAPHY

HADJIDIMOVO LOCALITY, MESTA BASIN

It is the richest known Bulgarian locality with *Hipparion*-fauna (Spassov in press). The Hadjidimovo locality is situated in the Mesta river valley between the town of Hadjidimovo and the Bulgarian-Greek border (Fig. 1). It represents a late Miocene fossil assemblage with four vertebrate faunal localities. The sediments (light clay sands) belong to the Nevrokop Formation (Vatsev 1980). The preliminary faunal list of the locality Hadjidimovo-1 (Hadjidimovo-Girizite) includes 31 mammal species (determination by N. Spassov, D. Kovachev). The faunal complex shows similarities with some faunal associations from the Balkans, Asia Minor and Ukraine, indicating a middle/late Maeotian age (most probably first half of MN12; Spassov in press). Only two fragmentary *Microstonyx*-like molars and one

metapodial are known from the locality of Hadjidimovo. The material is not complete enough for certain comparison and conclusion, but it comprises clear evidence for the presence of *Microstonyx* in the locality.

LOCALITY KALIMANTSI, STRUMA BASIN

The fossiliferous locality of Kalimantsi (Fig. 1) is among the most important Bulgarian sites with *Hipparion*-fauna. It belongs to the Kalimantsi Formation of Sandanski Graben (Kojumdgieva *et al.* 1982). The locality covers a large area (*c.* 10 km²) where a number of fossiliferous lenses have been found. The locality is placed in the cycle II of the Kalimantsi Formation (“svita”), located in Blagoevgrad District. Nikolov (1985) mentioned four distinct fossiliferous sites with associated fauna: — Kalimantsi 1: boundary between the Kalimantsi Fm and the underlying strata (boundary I-II cycle):

Aceratherium (?) *zernowi*, “*Metaschizotherium fraasi*”, *Hipparion* cf. *theobaldi*, *Prodeinotherium bavaricum*;

– Kalimantsi 2: 50 to 150 m above the base of the Kalimantsi Fm: *Adcrocuta eximia*, *Paramachairodus* gr. *orientalis*, *Ancylotherium pentelicum*, *Hipparion mediterraneum*, *Microstonyx major*, *Tragoportax amalthea*, *Mesopithecus* cf. *pentelicus*;

– Kalimantsi 3: 250 to 300 m above the base: *Dicerorhinus* sp., *Hipparion matthewi*, *Helladotherium duvernoyi*, *Bohlinia attica*, *Gazella brevicornis*, *Palaeoreas lindermayeri*;

– Kalimantsi 4: 400 to 450 m above the base: *Ictitherium orbigny* (?), *Dicerorhinus* sp., *Hipparion* cf. *crassum*, *Hipparion mediterraneum*, *Palaeoryx pallasii*, *Palaeoryx majori*.

During the last decades, 10 new localities were found in the area by D. Kovachev. Of special importance is the locality Kalimantsi-Pehtsata (Kovachev 1988), from where six species of Turolian age (most probably MN11) were recently determined (Geraads *et al.* in press).

Preliminary analysis of the Kalimantsi fauna, including antelopes, giraffes, deinotheres, etc., shows that the richly fossiliferous sediments represent a series of faunas, that existed over a long period of time. The faunal remains at the base of the fossiliferous layers are probably of late Vallesian age, while most of the later faunal findings belong to mammal zones MN11 and MN12, probably till the very end of the latter zone. So, a late Sarmatian (i.e. Vallesian) age could be suggested for Kalimantsi 1 and a Maeotian age (= early-middle Turolian, MN11/12) for Kalimantsi 2-4, Kalimantsi-Pehtsata and the other known localities. The Kalimantsi suid material is abundant, including several parts of skulls, mandibles and toothrows; among them, there are some specimens of darker color, which are carefully studied, because of their possible different stratigraphic origin. Kalimantsi appears, today, to include more than 15 different sites of uncertain stratigraphic position and range.

LOCALITY PETRELIK, STRUMA BASIN

The locality is situated about 3 km South of Hadjidimovo and belongs to the same formation

(Fig. 1). Some undescribed and undetermined bovid, cervid and proboscidean remains were found by D. Kovachev, but the exact age of this Turolian locality is not clear. A single skull fragment represents a suid.

EZEROVO LOCALITY, MARITSA BASIN

It is located near the village of Ezerovo, Plovdiv District (Fig. 1) and belongs to the Akhmatovska Formation with two sedimentary cycles. The fauna and stratigraphy are based on Nikolov (1985), with some nomenclature/taxonomic changes and additions by N. S.:

– I cycle: *Deinotherium giganteum* (referred as *D. gigantissimum* or *D. thraciensis* in the local bibliography), *Choerolophodon* sp., *Aceratherium incisivum*, *Hipparion* sp. (referred as *H. “microtaton”* by Nikolov 1985);

– lower part of the II cycle: *Choerolophodon* sp., *Tetralophodon longirostris*, *Hipparion mediterraneum*, aff. *Dicerorhinus* sp. After Nikolov (1985), the II cycle belongs to the “Pontian” but judging from the noted check-list the age of the entire fauna is probably from middle Maeotian to Pontian *s. str.* Suids are represented by a part of mandibular ramus, founded in the fossiliferous levels of the first cycle, close to the *Deinotherium* skeleton. The *Choerolophodon* skull and the rest of the material is found at an horizontal distance of 100 m from and 10 m above the fossiliferous level of the first cycle.

SYSTEMATICS

Genus *Microstonyx* Pilgrim, 1926

Microstonyx major (Gervais, 1848)

MATERIAL EXAMINED. — Skull specimens (K-5253, K-5254, K-5256, K-5258, K-5260, K-5262, K-5263, Pk-5265); juvenile maxillae (K-5264); palate (K-5259, K-5269); upper toothrows (entirely or partly preserved) (K-5257, K-5261, K-5266, K-5267, K-5268, KA1, KA2, K-743); lower toothrows (entirely or partly preserved) (K-5276, K-5277, K-5278, K-5280, K-5282, K-5283, K-5284, K-5285, K-5286, K-5287, K-5289, K-5290, K-5292, K-5293, K-5298, E-5299); juvenile mandibular rami (K-5264, K-5294, K-5295, K-5296, K-5297).

LOCALITIES. — Kalimantsi (K), Petrelik (Pk), Ezerovo (Ez), Bulgaria.

AGE. — Late Miocene, Turolian (MN11-MN13).

PRESERVATION STATUS. — (K-5253): central part of the skull with zygomatic arches and frontals; (K-5254): part of the basioccipital and the right lateral side without teeth; (K-5256): only the palate, the zygomatic arches and a part of the frontals are preserved; (K-5258): laterally compressed, probably young female individual without teeth, except the canine roots; (K-5259): palate; (K-5260): broken right zygomatic arch and anterior part of the snout; (K-5261): palate; (K-5262): basioccipital, toothrows, left zygomatic arches and anterior part of the snout are missing; (K-5263): only the basioccipital and the left lateral side of the skull are preserved; (K-5264): part of juvenile skull (palate, maxillary bones, part of the nasal bones); (K-5269): palate; (Pk-5265): anterior part of the skull with toothrows.

DESCRIPTION

Skull

The description of the skull morphology of the Kalimantsi suid is mainly based on specimens K-5256, 5260 and 5262, while additional information are also taken from the specimens K-5253, 5254, 5258, 5259 and 5263 (Figs 2; 3). Most of the skulls are badly or partly preserved, belonging to adult individuals. The skull specimen from Petrelik (Pk-5265) (Fig. 4) is very similar to that from Kalimantsi and therefore morphological characters are presented together. Skull measurements are given in Table 1.

The occiput is triangular, moderately elevated and strongly concave, both in lateral and posterior view (Fig. 2). The anterior apophysis of the basioccipital is small, while the paroccipital process is strong. The choanae opens behind M3. The palate is elongated and relatively narrow. The frontoparietal is flat, limited laterally by the well-developed temporo-parietal crests. The temporals are slightly concave. The anterior rim of the orbit is placed well behind M3. The lachrymal notch (referred also in some French bibliography as “incisure infraorbitale”) is large and wide. The zygomatic arches are strongly inflated and laterally extended. Their anterior end is placed above the limit M1/M2. The snout is elongated and narrow (Fig. 5). The posterior end of the

elongated nasals is placed at the point of the greatest extension of the zygomatic arches. In lateral view the nasals appear to be slightly concave. The posterior end of the narial notch is placed just above the anterior border of the canine. The maxillary depression for the elevator and depressor rostrii muscles is elongated and deep. The maxillary foramen is located above the anterior lobe of M2 or between M1/M2. The alveolar tuberosities are strongly developed with rough surfaces (Figs 2; 4; 5).

Despite the general morphological homogeneity between the skull specimens, there is some developmental and size variability. Thus, the specimens K-5260 and K-5258 are relatively smaller and have less developed alveolar tuberosities than specimens K-5262, K-5269 and Pk-5265.

Mandible

Only four specimens from Kalimantsi (K-5276, 5277, 5278 and 5283) and a mandibular ramus from Ezerovo (E-5299) are available for morphological and metrical observations (Table 2; Figs 6; 7).

The two best preserved specimens K-5276 and K-5277 (Fig. 6) belong to adult individuals. They are characterized by elongated and relatively narrow snout with shallow horizontal rami. Nevertheless, the specimen K-5277 is slenderer with a more elongated symphysis (102 mm) than specimen K-5276 (87 mm) (Table 2) which appears to have a shallower horizontal ramus (Table 2). The dark colors of preservation in specimen K-5277 may be indicate a different fossiliferous horizon than K-5276. Taking into account the similar ontogenetic age of the two individuals, the observed differences could be also attributed to sexual dimorphism. The mandible from Ezerovo (Fig. 7) has a deeper horizontal ramus than that from Kalimantsi (height of the mandible behind m3: 74.7 mm in E-5299 *versus* 67.5 in K-5283) and similar to that of *M. major* from Dytko (Greece) (73.5 mm).

Upper toothrow

The morphology and dimensions of the upper incisors and canines is unknown; they are

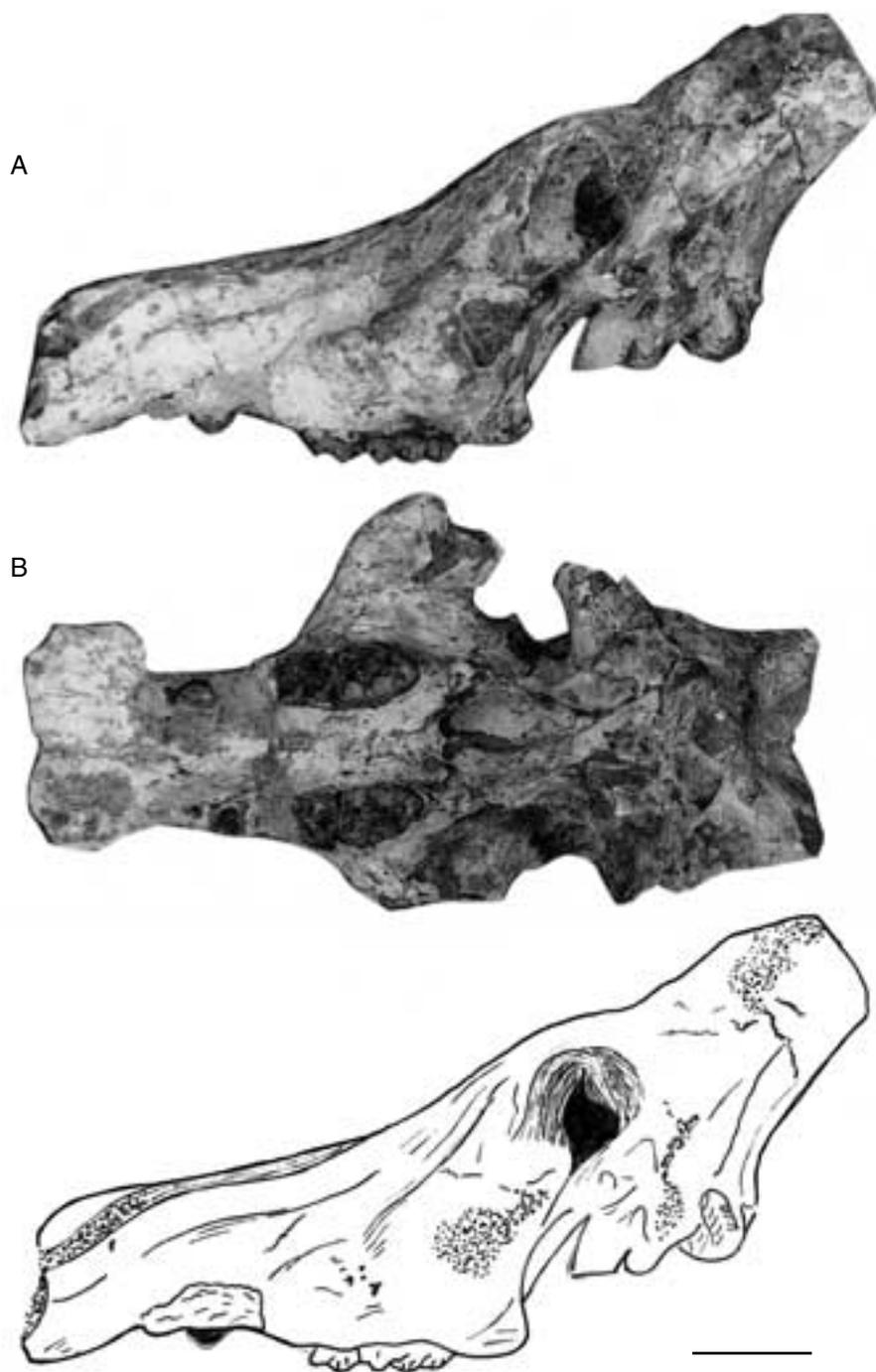


FIG. 2. — *Microstonyx major* (Gervais, 1848) from Kalimantsi, Bulgaria, skull (K-5260); A, lateral view; B, occlusal view. Scale bar: 6 cm.

TABLE 1. — Skull measurements of *Microstonyx major* (Gervais, 1848) from the late Miocene localities of Bulgaria.

Skull measurements	K-5258	K-5260	K-5262	K-5263	K-5259	K-5257	Pk-5265
Maximal length (prosthion-opisthion)	> 450	> 420	-	-	-	-	-
Basal length	435	-	-	-	-	-	-
Maximal breadth							
(in the zygomatic arches)	(235)	(260)	-	-	-	-	-
Breadth of the frontal	-	153	-	-	-	-	-
(in the zygomatic protuberances)							
Maximal breadth of the occiput	-	121	150	-	-	-	-
Height of occiput (basion-middle of occipital crest)	-	133.5	178	-	-	-	-
Breadth at the occipital condyles	59.2	82	-	75	-	-	-
DT of the occipital foramen	23	28.2	-	30	-	-	-
Height of occipital foramen	-	29.6	-	29.3	-	-	-
Breadth of the palate behind M3	-	53.5	-	53	-	-	-
Length I1-P2	62.7	-	-	-	-	-	-
Breadth of the palate at the level of P1	32	-	-	-	-	-	-
Alveolar tuberosities DAP × Height	-	60 × 24	-	-	78 × 35.3	-	84.7 × 38.5
Length Choanae-M3	120.1	122	-	(140)	-	-	-
Length M3-I1	-	-	-	-	-	-	310
Length M3-P2	-	-	-	-	-	148.3	151
Length M1-M3	-	-	-	-	-	92.2	97
Length P2-P4	-	-	-	-	53	52.2	52
Distance C-I3	-	-	-	-	7.2	-	43
Distance C-P1	-	-	-	-	35.2	-	39.4

usually broken or in an advanced stage of wear. A single I2 from the specimen Pk-5265 has DAP = 22.5 mm. According to their alveoli, the canines seem to be small relatively to the skull size (Fig. 5). The length of the upper toothrow (P2-M3) is 148.3 mm in K-5257 and 151 mm in Pk-5265. The length of the molar row ranges between 89.6-93.6 mm in Kalimantsi (n = 5; K-5261: 89.6 mm, K-5256: 91 mm, K-5257: 92.2 mm, K-5267: 93.6 mm), while it appears slightly larger in Petrelik (n = 1; Pk-5265: 97 mm). Tooth measurements are given in Tables 3 and 4.

P1. Looking at the Bulgarian material of *Microstonyx*, three different situations can be observed:

– P1 small, rudimentary, single cuspid and single rooted, separated from P2: case K-5259 (Fig. 5); the obviously vestigial P1 is present only in the left side of the palate, while it is missing from the right one. The specimen belongs to an adult individual (M2 in the first stage of wear). The distance

between P1-P2 is 11 mm, while the distance between P1-C is 35.2 mm;

– P1 well-developed, double rooted and separated from P2: case Pk-5265 (Fig. 4); P1 is present in both toothrows and has a simple elongated form. The distance P1-P2 is 14.5 mm and the distance P1-C is 39.4 mm;

– P1 well-developed, double rooted and close to P2: case K-5268; only the roots are preserved, indicating a normally developed P1. The specimen K-5268 is darker colored than the rest of the specimens, allowing for a possibly different stratigraphical origin.

P2. The three available specimens (K-5257, 5259 and 5266) show a simple P2 with weak anterior and strong postero-lingual cingulum.

P3. In the unworn specimen K-5268, the para- and metastyles and the antero-lingual cingulum are strong. In its upper part, the main cusp is divided into three tubercles. The internal talon is strong. In the worn specimens K-5259, 5260, 5266, 5269 and Pk-5265 the occlusal outline of

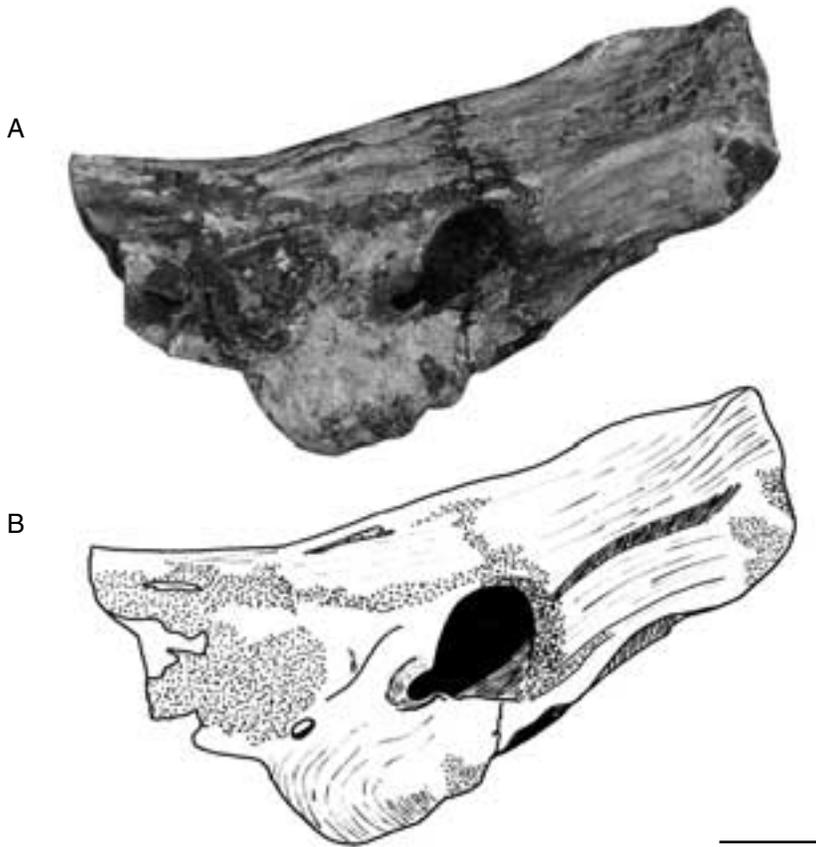


Fig. 3. — *Microstonyx major* (Gervais, 1848) from Kalimantsi, Bulgaria, skull (K-5262), dorso-lateral view. Scale bar: 6 cm.

the tooth is triangular with strong postero-labial style (metastyle) and internal talon.

P4. P4 is clearly molarized, subsquarish and wider than long (K-5256, 5259, 5267, 5260, 5266, 5261, 5268, 5269, Pk-5265). The protocone is well-developed, while the paracone and the metacone are divided in the labial wall by a shallow furrow. The anterior and postero-lingual cingula are strong.

M1/2. The anterior cingulum is moderately to strongly developed. The posterior cingulum is strong, forming a rudimentary talon, more developed in M2 than in M1. Based on the studied specimens, the lingual and labial accessory cusps are more or less well-developed but low.

M3. Similar to M2 with a strong anterior cingulum. There are two morphotypes of the talon:

- the first one has a main cusp in the postero-lingual position (K-5260, 5256, 5253, 5259, 5267, 5257, Pk-5265, KA1);
- the second one is less frequent (K-743, KA2) with two posterior cusps and double “hypocnule” (Fig. 8A).

Lower toothrow

The incisors present a crest on the lingual surface, due to the lateral compression of the teeth. The maximal measured length (DAP) is 33.3 mm for i2 (K-5284) and 23.3 mm for i3 (worn). The canines are small and slightly curved posteriorly (Fig. 6). The length of the Kalimantsi lower toothrow (p2-m3) ranges between 142.8-161 mm (Table 2) with a length of the molar row between 86 and 101.5 mm (n = 7; data as in Table 2 and

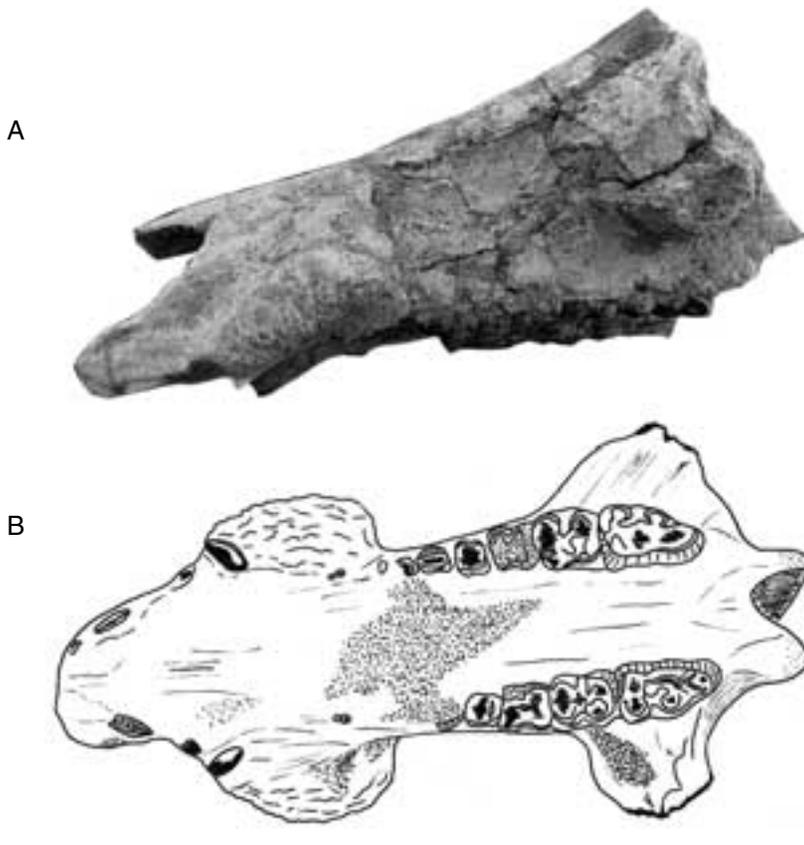


FIG. 4. — *Microstonyx major* (Gervais, 1848) from Petrelik, Bulgaria, skull (Pk-5265); **A**, lateral view; **B**, occlusal view. Scale bar: 5 cm.

K-5280: 87 mm, K-5292: 90.8 mm, K-5285: 92.4 mm). The respective values for the mandible from Ezerovo are Lp2-m3: 153.6 mm and Lm1-m3: 101.5 mm. Tooth measurements are given in Tables 4 and 5.

p1. It is absent from the two best preserved specimens K-5276 and K-5277.

p2/3. They are very similar morphologically, although the third premolar is larger. The anterior stylid (parastylid) is well developed, while the metastylid is larger and more complicated.

p4. It is even larger than p2/3 and more complicated. The cingulum is very weak and the anterior stylid moderately developed. The labial (protoconid) and the lingual (metaconid) cusps are strong, separated only in the first stage of wear. The talo-

nid is well-developed with a main cuspid, separated from the trigonid by a weak furrow.

m1/2. The first two molars have a weak anterior and a strong posterior cingulum, which forms a rudimentary talonid. The accessory cuspid are small, both lingually and labially.

m3. It is similar to m1/2. Two types of talonid can be distinguished:

- with rounded or quadrangular posterior border (K-5276, 5277, 5285, 5280). The endoconid is slightly stronger than the hypoconulid, limited posteriorly by a small cuspid. The posterior accessory cuspid can be single or double;

- with elongated, rhomboid posterior border (K-5298, 5286) (Fig. 8B). The posterior cuspid is strong. The endoconulid is formed of a number of smaller accessory cuspid.

TABLE 2. — Mandibular measurements of *Microstonyx major* (Gervais, 1848) from the late Miocene localities of Bulgaria.

Mandible	K-5277	K-5276	K-5278	K-5282	E-5299
Length i1-m3	255	255	-	-	-
Length p2-m3	161	150.4-153.4	142.8	-	153.6
Length m1-m3	101.5	95.4-96	86	-	101.1
Length p2-p4	(58)	56-56.9	52.5	56.8	52.5
Distance of horiz. rami behind C	34.6	42.6	33.7	-	-
Distance c-p2	49.5	55.4	45	-	-
Height of horiz. ramus in front of p2	56	47	-	63	54
Height of horiz. ramus behind m3	-	-	-	-	74.7
Length of symphysis	102	87	81.4	-	-

TABLE 3. — Upper tooth measurements of *Microstonyx major* (Gervais, 1848) from the late Miocene localities of Bulgaria. Abbreviations: **L**, length; **B**, breadth. Measurements without brackets: occlusal level. Measurements in brackets: alveolar level.

	LM3	BM3	LM2	BM2	LM1	BM1	LP4	BP4	LP3	BP3	LP2	BP2
K-5260 dex.	38.9 (42.9)	28.2		26.2			21	15.3	19	11.8		
K-5260 sin.	38.4 (42.6)	28.7					21.4	14.6				
K-5263	36.5 (43.4)	26.6										
K-5256 dex.	38.5	27.5	29	26	21		16.1	19.7				
K-5256 sin.	39 (43.2)	28.2										
K-5257 dex.	36.4 (41.1)	28.2	30.7		23.3	20					16.5	11
K-5259 dex.				24.7	22.5	20.2	15.9	18.4	20.1	14.6	17.4	11
K-5259 sin.			30	24.5			15.7	18.6			17.7	11.2
K-5267 dex.	39.1 (44.7)	29.7	30	26.8	21.3	21.3	16.5	19.4				
K-5261 dex.	41.8	28.1	28.7									
K-5261 sin.	43 (42.3)	(43) 26.1	28.8	28.7	27	21.1	20.5	19.6				
K-743												
K-5253	38 (43.1)	28.1										
K-A1	36.5 (44.9)	27.8										
K-5269					24.3	21.1	16.8	19.2	19	14.6		
K-5268			29	24.3	22.7	19.8	15	17.7	17.6	15.3		
K-A2	34	26.2	27.3	25								
K-5266							15.6	18.5	16.8	16.1	16.5	
Pk-5265 dex.	(44.5)	28.2	29.3	27	22.5		15.6	19.3	17.8	17.2		
Pk-5265 sin.	(43.6)	30.2	30.2	28.9			16	19.3				

COMPARISON AND DISCUSSION

The general morphological and dimensional characters of the Bulgarian suid, such as the large size, the elevated occiput, the wide and flat frontoparietal region, the elongated snout (nasals-maxillary bones), the inflated and laterally extended zygomatic arches, the narrow

and elongated palate, the wide and large lachrymal notch, the small canines, the elongated incisors, the absence of pm1, the morphology of p4 with two main cuspids and the large tooththrows, indicate its attribution to *M. major* (Trofimov 1954; Hünemann 1968; Thenius 1972; Ginsburg 1988; Van der Made & Moya-Sola 1989).



Fig. 5. — *Microstonyx major* (Gervais, 1848) from Kalimantsi, Bulgaria, palate (K-5259), occlusal view. Scale bar: 5 cm.

Among the local samples of SE Europe, the Greek one is quite representative, coming from 10 localities at least (Fig. 1). The presence of *Microstonyx* in Greece covers the entire Turolian, represented mainly by one species: *M. major* (including both, *M. major major* and *M. major erymanthius*). *M. antiquus* is also recorded from the locality of Sophades (Soph) in central Greece (Thenius 1955). The material, a right mandibular fragment with p2-m1, was later transferred to *M. major* (Fortelius *et al.* 1996), while several authors referred it to *M. antiquus* (Golpe-Posse 1980; Ginsburg 1988). The specimen came from the lignitic deposits of Karditsa (central Greece), the age of which is unclear. Original study of the specimen (stored in the Department of Geology, University of Athens, Greece) showed that the supposed presence of p1 is dubious; the mandibular fragment is broken 0.5 cm in front of p2. In comparison to *M. major* from several Greek localities, more elongated premolar row, slenderer premolars, larger p2 and clearly smaller m1 characterize the Sophades form. These differences allow us to separate the Sophades specimen from *M. major*. Moreover the tooth measurements (p2-p4: 56.5 mm; p2: 16.5 × 6.8 mm; p3: 18.7 × 11 mm; p4: 20.4 × 12.85 mm; m1: 19.3 × 14.15 mm) clearly indicate a smaller form than *M. antiquus* from Eppelsheim (Germany), Montredon (France) and Goedkere (Turkey)

(Senyuerek 1952; Thenius 1972; Ginsburg 1988). Despite the great dimensional and morphological variability observed in *M. major* (see below) and *M. antiquus*, the form in question seems quite distinct at specific level. Therefore we prefer to assign the Sophades suid to *Microstonyx* sp.

In Greece, *M. major* first appears in the latest Vallesian locality of Nikiti-1 (NKT; Kostopoulos 1994). The material includes a complete skull and some mandibular fragments. An elongated snout, relatively small zygomatic arches, large dentition and absence of alveolar tuberosities characterize it. *M. major* is also recorded from the late early/early middle Turolian localities Ravin de Zouaves (RZO), Vathylakkos 2 (VTK) and Proxoma (PXM) of the lower Axios valley (Bonis & Bouvrain 1996). Small dentition and absence of P1 characterize this form, which seems very similar to *Microstonyx* from Maragha, Iran (Bonis & Bouvrain 1996).

Four samples of *M. major* are known from the middle-middle/late Turolian of Greece: Pikermi (PIK), Samos (SAM), Kerassia (KER) and Perivolaki (PER). *Microstonyx* from Pikermi and Samos is characterized by large and wide skull, elongated snout, well-developed zygomatic arches and alveolar tuberosities and medium to large dentition (the Samos material referred here, is from the new excavations on the island; e.g.,

TABLE 4. — Milk-tooth measurements of *Microstonyx major* (Gervais, 1848) from the late Miocene localities of Bulgaria. Abbreviations: **L**, length; **B**, breadth.

Juvenile skull / mandibles	Skull K-5264	Mandible K-5294	Mandible K-5295	Mandible K-5296	Mandible K-5297	Mandible K-5264
dP4-dM1	68.3					
M1 (L × B)	22.5 × 20.6					
dp2-dp4			53.4			54.7
m1 (L × B)		23 × 15.4				23.2 × 15.2
Lp4			28	26.7	27.7	

TABLE 5. — Lower tooth measurements of *Microstonyx major* (Gervais, 1848) from the late Miocene localities of Bulgaria. Abbreviations: **L**, length; **B**, breadth. Measurements without brackets: occlusal level. Measurements in brackets: alveolar level.

	Lm3	Bm3	Lm2	Bm2	Lm1	Bm1	Lp4	Bp4	Lp3	Bp3	Lp2	Bp2
K-5292	41.8	21.5	27.5	20.2	22.8		19.2	14.2				
K-5277	41.4 (46.5)	23.9	30.5	21.3	25.5	16.7	22	13.8	18.8	9.3		
K-5276 dex.	42.6	23.3	28.4	21	21.9	17	21.4	16.1	20.4	11.5	15.4	8.2
K-5276 sin.	42 (47)	23.5	29.6	21.6	21.6	17	21.8	15.4	19.8	11.5	15.7	8
K-5278 sin.	38 (44)	22.3	26.5	20.2	22.5		20		18.5		13.2	6.9
K-5280	43 (43)	23.1	26.5	19.2			19.8	14.6	16.6			
K-5282							21	15.5	19.5	10.7	15.8	7.4
K-5285	42.7	24.2	29.2	20.6	21.5	16.3	20.3	15.6				
K-5298	(48.1)	22.8	29.2	21.6								
K-5290	41.4 (44.5)	23	27.5	21								
K-5286	(51.8)	23.9										
K-5287	43.2 (46)	22.9										
E-5299	(47.1)	22.4	28.8	20.9	23		19.4	14.9	17.7	9.4	14.2	6.8

Koufos *et al.* 1997). *Microstonyx* from Kerassia (Euboa, Greece) is briefly discussed by Van der Made & Moya-Sola (1989) and Van der Made *et al.* (1992). Original study of the material (collection of Prof. C. Doukas, University of Athens, Dept. of Geology) shows a smaller form than that of Pikermi and Samos. The single skull Ke-70, belonging to a young adult individual (M3 is just erupted), has smaller zygomatic arches than the specimens from Pikermi and Samos and less developed alveolar tuberosities. The suid material from Perivolaki (Thessaly, Koufos *et al.* 1999) is still unpublished. Nevertheless its size is comparable to that of *Microstonyx* from Vathylakkos and Kerassia and smaller than Pikermi and Samos forms. There is no evidence about the skull morphology.

Microstonyx major from Dytiko (DTK) represents the late Turolian form of the genus in Greece. It is characterized by relatively larger dentition and shorter snout than Pikermi and Samos forms (Bonis & Bouvrain 1996).

The basi-cranial length of the Kalimantsi suid exceeds 400 mm (435 mm in K-5258), with maximum breadth at the zygomatic arches about 250 mm (234 mm in K-5260 and 260 mm in K-5262). These measurements are similar to those referred to *M. major* from Samos, Pikermi, Nikiti (Greece), Titov Veles (former Yugoslavia-FYROM), and Grebeniki (Ukraine) and larger than those of *M. antiquus* from Terassa and Stratzing (Gaudry 1862; Trofimov 1954; Thenius 1972; Golpe-Posse 1978; Kostopoulos 1994 and pers. obs.). The Petrelik skull fragment

and the mandible from Ezerovo look very similar to that of *M. major* from Dytiko, Greece (Bonis & Bouvrain 1996).

The cheek tooth morphology of *Microstonyx major* is highly variable and, therefore, no major differences between the local samples can be distinguished. The most usually referred features concern the morphology of p4 and the complication and size of the third molars (Van der Made & Moya-Sola 1989; Van der Made *et al.* 1992; Bonis & Bouvrain 1996). The lingual cusp of p4 from Kalimantsi is placed as far forward as the labial cusp, similarly to the Greek samples of the species and unlike the Spanish ones (Van der Made *et al.* 1992). The complication of the third molars (referred to the development of cingulum and accessory cusplets; Van der Made *et al.* 1992; Bonis & Bouvrain 1996) is a subjective character, which can not be expressed quantitatively. The morphological variation observed on the third molars from Kalimantsi does not permit the distinction of clear characters in order to be usable. Although slightly shorter, the third molars from Kalimantsi are closely comparable to those of *M. major erymanthius* from Pikermi (Figs 9; 10). In contrast, the third molars from Petrelik and Ezerovo are placed together with the largest specimens from Kalimantsi and Pikermi and closer to the specimens from Dytiko (Figs 9; 10).

Some of the usually referred cranial and dental features (e.g., development of zygomatic arches and alveolar tuberosities, complication of the molars, size variation), with uncertain systematic value, seem to depend on several factors such as the ontogenetic age and the sex of the individual, while others (presence of P1, deepness of mandibular corpus) probably consist of evolutionary trends. Considering, mainly, the available material from Bulgaria and Greece, we will try to examine several of these characteristics, in order to interpret their significance and taxonomic value.

PRESENCE OF P1

The presence or absence of the first upper premolar was considered to be of (some) systematic value for *Microstonyx* (e.g., Trofimov 1954; Thenius 1972; Ginsburg 1988; Van der Made &



FIG. 6. — *Microstonyx major* (Gervais, 1848) from Kalimantsi, Bulgaria, mandibles, occlusal view; A, K-5276; B, K-5277. Scale bar: 5 cm.

Moya-Sola 1989). Thus, *M. antiquus* is always associated with a well-developed P1 (Stratzing, Terassa, ?Eppelsheim, Montrigaud, Goedkere, Sinap Moyen), while the presence of this tooth in *M. major* appears to be more or less sporadic (Senyuerek 1952; Ozansoy 1965; Thenius 1972; Golpe-Posse 1978; Ginsburg 1988). Early representatives of *M. major* (Grebenediki, Taraklija, Nikiti) are reported to retain their upper first premolar and lose their p1 early in life, while later representatives (Tudurovo, Pikermi, Samos, Kerassia) have no p1 and often lack their P1 (Van



FIG. 7. — *Microstonyx major* (Gervais, 1848) from Ezerovo, Bulgaria, mandible (E-5299); **A**, occlusal view; **B**, lateral view. Scale bar: 4 cm.

der Made & Moya-Sola 1989). Nevertheless, the taxonomic significance of this feature has been questioned many times because of the great variability both in the development of the tooth and its presence. Some times the presence of P1 in *Microstonyx* is compared with the presence of the first upper premolar of *Hipparion*, also known as “dent de loup” (Gromova 1952). However, the available specimens of *Microstonyx* from Europe show that the presence of P1 is independent of the ontogenetic age and the sex. Old and adult individuals could possess P1 (Pikermi, Petrelik, Kalimantsi), while in some young individuals it could be missing (Kalimantrsi, Kerassia). Moreover, male individuals (Samos, K-5259) have no P1, while the tooth appears in several females (Nikiti).

Evidently, the evolutionary trend in the *Microstonyx* lineage is the loss of P1 with time: the ancestor form *Korynochoerus palaeochoerus* (MN8), as well as the earlier *Microstonyx* forms (Stratzing skull, MN9/10), have a well-developed and double rooted P1 separated from P2 (Hünberman 1968; Thenius 1972). The index LP1/LP2 is 85 and 83 respectively. P1 is also

present in the late-latest Vallesian forms of *Microstonyx* from Terassa (*M. antiquus*, Spain; Golpe-Posse 1978) and Nikiti (*M. major*, Greece; Kostopoulos 1994): in both cases the tooth is placed very close to P2 (4 mm in Terassa *vs.* 0 mm in Nikiti) and it is still well-developed and double rooted with an index LP1/LP2 68 and 70 respectively. A similar situation of P1 also appears in the specimen K-5268 from Kalimantsi, which is probably from a different (earlier?) horizon than the rest of the material. The displacement of P1 in these pre- or early Turolian specimens is difficult to explain but recalls that of the recent European wild pigs. The available skull material of extant suids in the Departments of Geology and Forestry, University of Thessaloniki (seven specimens) shows that the presence and position of P1 is a stable character. The position of P1 in these *Microstonyx* specimens is provisionally correlated with a more functional use of the tooth than in other representatives of the genus.

The sparse material from the Greek early and early-middle Turolian (MN11, 11/12) localities of VTK, RZO and PXM, as well as from Maragha (Iran) do not provide any data about

the presence of P1. Similarly, P1 has not been recorded from the early Turolian Spanish sample (Crevillente, Puente Minero, Pierra), probably because of the fragmentary nature of the material. Van der Made (1997) reported a double rooted and well-developed P1 from the early Turolian (MN11) locality of Dorn-Duerkheim (Germany) but there are no indications about the disposition of the tooth. According to the data given by Trofimov (1954), P1 is present in two out of six individuals (min MNI = 6) from Grebeniki and in one out of three (min MNI = 3) individuals from Taraklija. Both localities are placed in MN11/12 (probably early middle Turolian). In some cases the tooth is present only on one side of the maxilla (Trofimov 1954), indicating evidence of degeneracy; in these specimens P1 is small, single rooted and separated from P2 by a long diastema.

The study of the middle Turolian (MN12) samples from Spain (Cero de la Carita, Crevillente 15/16, Baranco de las Calaveras) and Ukraine (Tudurovo) does not provide information about P1. The Petrelik skull (Bulgaria) has a double rooted and probably well-developed P1 separated from P2. Gaudry (1862) notes that P1 is present in two out of six skulls from Pikermi. The tooth is also present, double rooted but variously developed in three out of five skulls from Pikermi stored at the Department of Geology of the University of Athens (pers. obs.; Athanassiou & Roussiakis pers. comm.). In Pikermi, PM1 appears to be present in a percentage lower than 50%. In all cases where P1 is present there is a long diastema from P2. The single skull from the new excavations in the Samos island (locality MTLA; Koufos *et al.* 1997) and the skull Ke-70 from Kerassia have no P1. Garevski (1956) also reports a small P1, separated from P2, in two out of three specimens from Titov Veles. In 10 skull and maxillary specimens from Kalimantsi (excluding K-5268), P1 is present only in the right side of specimen K-5259. It is a simple, single rooted tooth, well-separated from P2. The index LP1/LP2 is 38.

Concerning the late Turolian (MN12/13) forms of the genus, the evidence about the presence of the tooth are less numerous. Gaudry (1873)

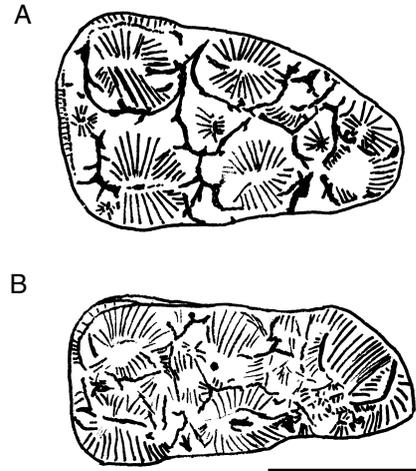


FIG. 8. — *Microstonyx major* (Gervais, 1848) from Kalimantsi, Bulgaria, occlusal view; **A**, upper third molar; **B**, lower third molar. Scale bar: 2 cm.

notes the absence of P1 in the skull from Luberon (MN12/13; Bonis & Bouvrain 1996), while its presence/absence in DTK is unknown.

The evolutionary loss of P1 in *M. major* is difficult to use as a chronological indicator. This is mainly due to the progressive character of the tooth's disappearance and the incomplete fossil record concerning this feature. In a broad sense, four successive groups could be distinguished:

- well-developed double rooted P1 close to P2: Kalimantsi (lower horizons?), Nikiti. Provisional age: latest Vallesian-early Turolian;
- more or less well-developed double rooted P1 separated from P2: Grebeniki, Taraklija, Pikermi, Petrelik. Provisional age: early Turolian-late middle Turolian;
- small, single rooted and separated from P2: Kalimantsi, Grebeniki (partly). Provisional age: middle Turolian;
- absence of P1: Samos, Luberon, Dytiko (?). Provisional age: middle-late Turolian.

SEXUAL DIMORPHISM IN CRANIAL AND DENTAL METRIC CHARACTERS

Trofimov (1954) gave the possible morpho-functional use of the alveolar tuberosities in *Microstonyx*. Starting from the principal idea of a

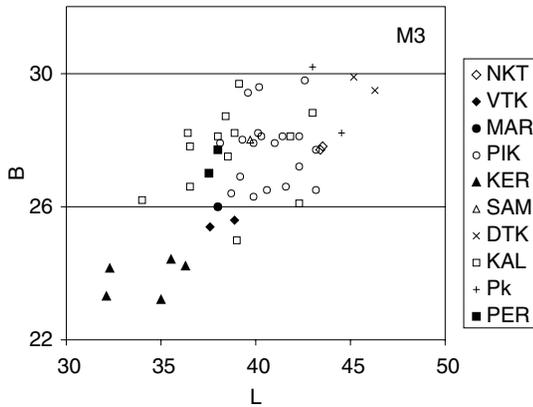


FIG. 9. — Scatter diagram of *Microstonyx major* (Gervais, 1848) M3 distribution (Length against Breadth). Data from Bonis & Bouvrain 1996; Kostopoulos 1994 and original measurements. **NKT**, Nikiti-1; **VTK**, Vathyakkos-2; **MAR**, Maragha; **PIK**, Pikermi; **KER**, Kerassia; **SAM**, Samos; **DTK**, Dytiko-1; **KAL**, Kalimantsi; **Pk**, Petrelik; **PER**, Perivolaki.

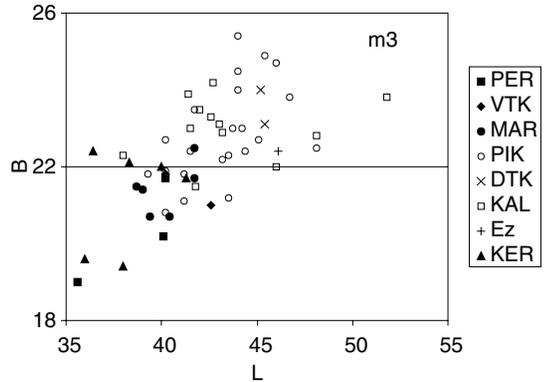


FIG. 10. — Scatter diagram of *Microstonyx major* (Gervais, 1848) m3 distribution (Length against Breadth). Data from Bonis & Bouvrain 1996; Kostopoulos 1994 and original measurements. **PER**, Perivolaki; **VTK**, Vathyakkos-2; **MAR**, Maragha; **PIK**, Pikermi; **DTK**, Dytiko-1; **KAL**, Kalimantsi; **Ez**, Ezerovo; **KER**, Kerassia.

cranial digging tool, he concluded that the alveolar tuberosities increased in order to balance the reduction of the canines and to support the muzzle muscles for the advanced rooting habit (see also Thenius 1972).

The sexual bimodality seen in the canines of living suids is traditionally considered to be expressed in the alveolar tuberosities of *Microstonyx*. Observations on 17 skulls and skull fragments of the genus from several localities (Table 6) allow interesting suggestions. Although available measurements of alveolar tuberosities are few, their projection in the scatter diagram of Fig. 11 shows clear separation into two groups. Taking into account that specimens from Kalimantsi (Bulgaria) and Taraklija (Ukraine) are present in both groups, the possibility of sexual dimorphism seems to be confirmed. Thus, the alveolar tuberosities of female individuals appear to be about 30-40% smaller than those of males:

- males: $L_{max} = 84.95 \pm 3.8$, $n = 7$ (the specimen MGRI 1781, Trofimov 1952, is excluded, see below); $H_{max} = 36.11 \pm 3.7$, $n = 7$;
- females: $L_{max} = 59.6 \pm 4.5$, $n = 6$; $H_{max} = 22.6 \pm 7.6$, $n = 6$.

Despite the low statistical credibility, this percentage seems sufficient enough to demonstrate a high sexual bimodality in the species *M. major*.

In two specimens, the Nikiti skull (Kostopoulos 1994) and the Luberon skull fragment (Gaudry 1873), the alveolar tuberosities are totally missing. Both belong to adult individuals of comparable ontogenetic age (M3 unworn), while there is no chronological correlation between the localities: the Nikiti skull is latest MN10 (Koufos 1993; Kostopoulos 1994), while the Luberon one is MN12 (Bonis & Bouvrain 1996). Ontogenetic age seems to be out of question, because males and females of similar age with the Nikiti and Luberon specimens possess strong tuberosities (Table 6). Since alveolar tuberosities are well-developed in female individuals from Kalimantsi and Taraklija, their absence in NKT and Luberon is difficult to explain. It would be, however, possible to suggest that in some populations the alveolar tuberosities have been not “expressed” in female individuals. If this is the case, the real use of these exostoses seems to be more complicated than Trovimov (1954) suggested. Taking into account that the maxillary depressions for the rooting muscles are also strong in the specimens from Nikiti and Luberon, the relation of alveolar tuberosities with a display function should be in consideration. Ecological factors, such as a more forested habitat, indicating a low display value, could be also related to their absence.

TABLE 6. — Development of alveolar tuberosities and zygomatic arches of *Microstonyx major* (Gervais, 1848) from several localities (in relation with the sex, size and ontogenetic age of the individual). Data from Gaudry 1862, 1873; Garevski 1956; Trofimov 1954 and original measurements. Abbreviation: L, length; *, mean values.

Specimens	Alveolar tuberosities	Zygomatic arches	Age	Size	Sex
Nikiti (NKT-68)	absent	relatively small (max breadth = 220 mm)	young adult (M3 unworn)	basal length : 430 LM3 = 43.5	female (?)
Samos MTLA	very large (90 × 40)	very large (max Breadth = 310 mm)	adult (M3 worn)	basal length : 480 LM3 = 39.7	male
Pikermi (Gaudry 1862)	very large (87 × 41)	very large (max breadth = 310 mm)	adult (M3 worn)	basal length : 470 LM3 = 40	male
Tito (Sp. No. 56)	very large	very large	adult (M3 worn)	— LM3 = 42	?
Grebeniki (MOGU-2642)	large (85 × 34)	very large (max breadth = 295 mm)	adult (M3 worn)	basal length : 480 LM3 = 46*	male (?)
Grebeniki (MOGU-1781)	medium (75 × 32)	large (max breadth = 255 mm)	adult (?)	basal length : 450 LM3 = 44*	(?)
Taraklija (MOGU-2641)	large (83 × 32)	large (max breadth = 257 mm)	—	basal length : 483 LM3 = 42.5*	male
Kerassia (Ke-70)	very small	medium	young (M3 non erupted)	basal length : 380 LM3 = 33 (Ke-73, 74)	?
Kalimantsi (K-5258)	relatively small	relatively small (max breadth = 234 mm)	adult	basal length : 435	female
Kalimantsi (K-5260)	relatively small	large (max breadth = 260 mm)	old (M3 very worn)	— LM3 = 40-42	female
Kalimantsi (K-5259)	very large (78 × 35)	—	old (M3 worn)	—	?
Kalimantsi (K-5262)	—	very large	adult	—	?
Petreliek (Pk-5265)	very large (87 × 41)	—	old (M3 very worn)	— LM3 = 44	male
Luberon (Gaudry 1873)	absent	—	young adult (M3 unworn)	comparable to Pikermi LM3 = 40	(?)

The development of alveolar tuberosities appears proportional to the size of the skull and the development of the zygomatic arches (and *vice versa*) (Table 6). Although the number of available specimens for such a comparison is

remarkably low, Fig. 12 indicates that there is a relative analogy between the developments of these three characters ($R^2 = 0.73$), which are strongly influenced by sex. Fig. 13 shows that, except the Kerassia skull (Ke-70), which seems

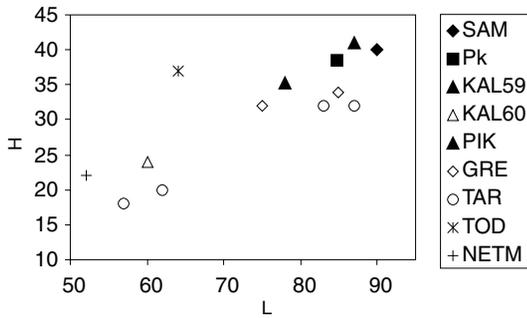


FIG. 11. — Scatter diagram of *Microstonyx major* (Gervais, 1848) alveolar tuberosities distribution (Length against Height). Data from Trofimov 1954 and original measurements. **SAM**, Samos; **Pk**, Petreljik; **KAL59**, K-5259; **KAL60**, K-5260; **PIK**, Pikermi; **GRE**, Grebeniki; **TAR**, Taraklija; **TOD**, Tudurovo; **NETM**, Nova Etmekova.

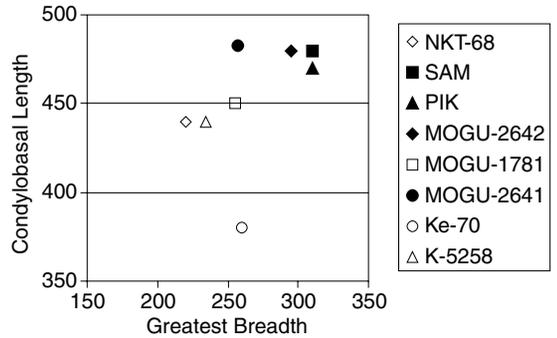


FIG. 13. — Scatter diagram of *Microstonyx major* (Gervais, 1848) zygomatic arches distribution (Condylobasal Length of the skull against Greatest Breadth at the zygomatic arches). Data from Gaudry 1862; Trofimov 1954; Kostopoulos 1994 and original measurements. The identity of the specimens is given in Table 6.

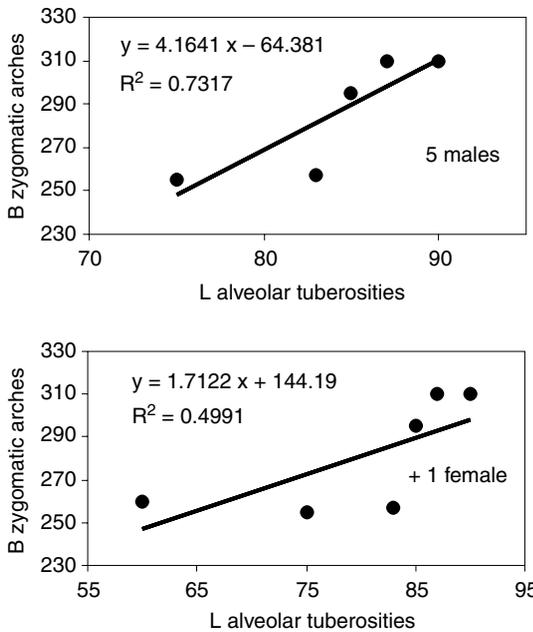


FIG. 12. — Correlation between alveolar tuberosities and zygomatic arches in *Microstonyx major* (Gervais, 1848). Data from Trofimov 1954 and original measurements.

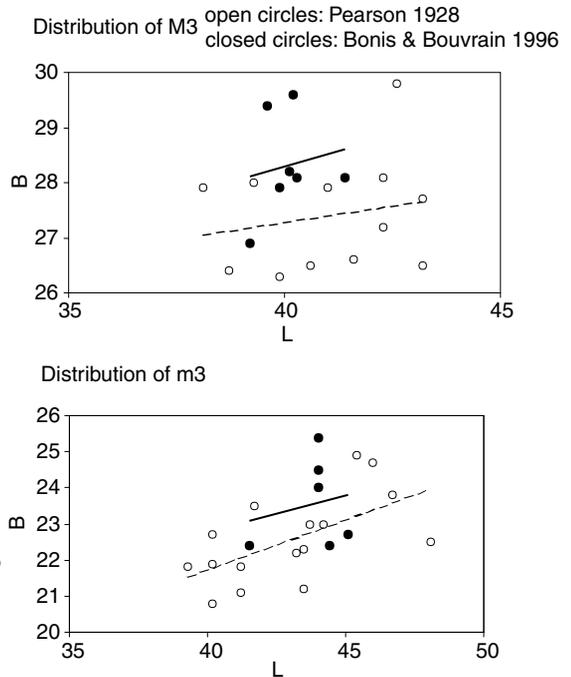


FIG. 14. — Scatter diagram, indicating the distribution of *Microstonyx major* (Gervais, 1848) M3/m3 from Pikermi (Length against Breadth). Data from Pearson 1928 and Bonis & Bouvain 1996.

quite independent, the rest of the material could be grouped in two subsamples, probably representing males and females. It should be noted that the Nikiti skull, as well as the specimen No. 1781 from Grebeniki (Trofimov 1954), are placed in the female subsample. The

zygomatic arches of female individuals appear 20% smaller than those of males. Several authors relate the great development of the zygomatic arches in *Microstonyx* with the strengthening of

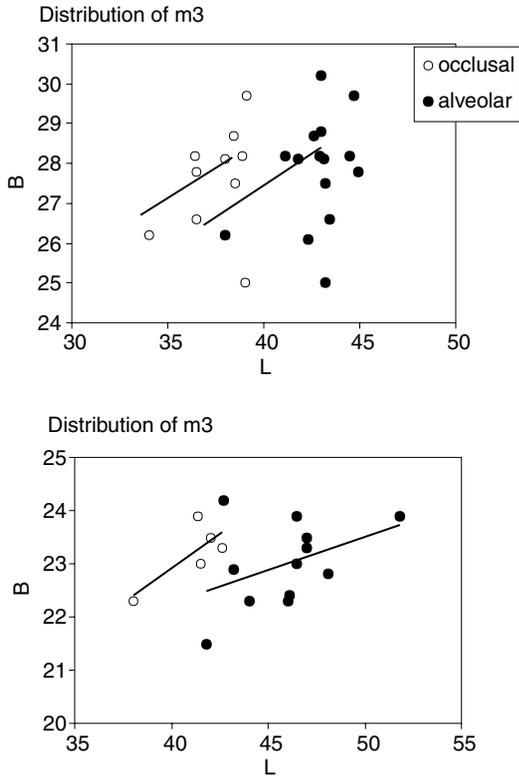


FIG. 15. — Scatter diagram, indicating the distribution of *Microstonyx major* (Gervais, 1848) M3/m3 from Kalimantan (Length against Breadth in the occlusal and alveolar surface). Original measurements.

the skull and the support of rooting and masseter muscles, as well as to a defense function against lateral attacks. Nevertheless, Thenius (1972) notes that the idea of musculature support is not very reliable. Although the available data seem quite insufficient for certain conclusions, the display function should be taken into consideration.

Van der Made (1991) notes that linear measurements of female cheekteeth of the extant wild suid (*Sus scrofa*) are 97% of males. This 3% difference is hardly observable by plotting and smaller than the difference observed on cranial characters, such as the condylobasal length of the skull, which is 5-10% larger in males (Groves & Grubb 2000). Data about *Microstonyx* are much less creditable, because of low number of specimens

from the same locality and subjectivity in the distinction of sexes.

The Kalimantan material shows that – regardless of the stage of wear – the length of female M3 is about 93% of that of males ($n = 4$, two females, two males), while this percentage for m3 is about 98% ($n = 2$, one female, one male).

Three m3 (one female, two males) from Perivolaki show that the mean length of m3 of “probably female” individuals is 89% of that of “probably males”, while in six m3 from Kerassia (four females, two males) this percentage is about 91%.

Two main sources of *Microstonyx* M3/m3 measurements from Pikermi can be found in the literature: the Pearson sample (Pearson 1928) and the Bonis & Bouvrain sample (Bonis & Bouvrain 1996). Plotting of those measurements does not reveal any significant difference, indicating a great dispersion (Fig. 14). The M3 average length of the Bonis & Bouvrain sample is 98% of that of Pearson, while the respective percentage for m3 is 102%. These small differences permit us to include both samples into the same Pikermian (PIK) sample. Having in mind that this sample – of 10 individuals at least – should include both female and male individuals, we try to separate them statistically. Excluding all intermediate specimens of M3/m3, we have formed two clear distinct subgroups, representing the largest (e.g., probably male) and the smallest (e.g., probably female) adult individuals. The mean values of each subgroup are:

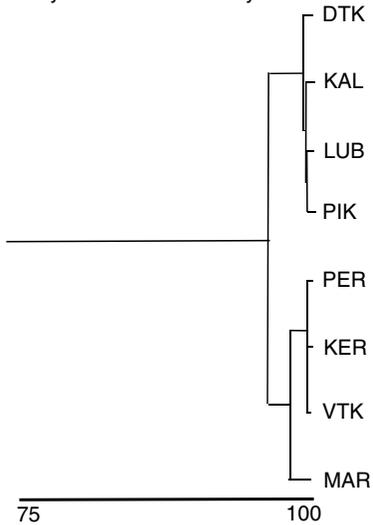
	n	L (mm)	B (mm)	Average length (mm)
M3 “largest”	3	> 41	> 28	42.13
M3 “smallest”	4	< 41	< 27	39.60
m3 “largest”	6	> 43	> 23	45.05
m3 “smallest”	5	< 42	< 22	40.44

Thus, for M3 the length of the “smallest” group is 94% of that of the “largest” one, while for m3 it is about 90%. The obtained percentages are comparable to those previously referred to females and males from other localities.

TABLE 7. — Comparative percentages of *Microstonyx major* (Gervais, 1848) M3/m3 mean lengths from several localities. **NKT**, Nikiti-1; **MAR**, Maragha; **VTK**, Vathylakkos 2; **PIK**, Pikermi; **PER**, Perivolaki; **KER**, Kerassia; **KAL**, Kalimantsi; **DTK**, Dytiko 1; **LUB**, Luberon.

M3	NKT	MAR	VTK	PIK	PER	KER	KAL	DTK	LUB
NKT	100	114	105	107	115	131	107	95	94
MAR		100	92	94	101	115	93	83	82
VTK			100	98	110	125	102	91	89
PIK				100	107	122	99	88	87
PER					100	114	93	83	81
KER						100	81	72	71
KAL							100	89	88
DTK								100	99
LUB									100
m3	MAR	VTK	PIK	PER	KER	KAL	DTK	LUB	
MAR	100	105	93	104	105	90	89	92	
VTK		100	88	99	100	86	84	87	
PIK			100	112	113	97	95	99	
PER				100	101	87	85	88	
KER					100	86	85	88	
KAL						100	98	101	
DTK							100	104	
LUB								100	

m3 Bray-Curtis Cluster Analysis



M3 Bray-Curtis Cluster Analysis

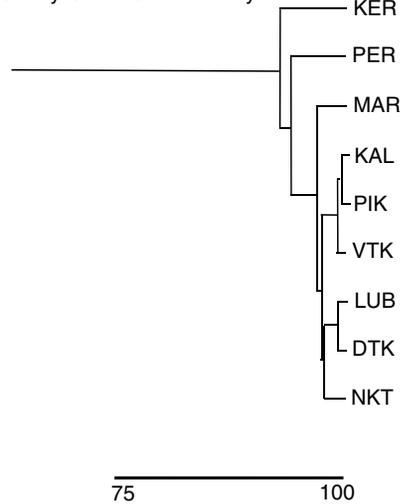


FIG. 16. — Bray Curtis Cluster Analysis based on the comparative percentages of *Microstonyx major* (Gervais, 1848) M3/m3 mean lengths (Table 7). **DTK**, Dytiko-1; **KAL**, Kalimantsi; **LUB**, Luberon; **PIK**, Pikermi; **PER**, Perivolaki; **KER**, Kerassia; **VTK**, Vathylakkos 2; **MAR**, Maragha; **NKT**, Nikiti-1.

All these values indicate that sexual dimorphism in cheekteeth is probably more developed in *Microstonyx* than it is in the extant wild pig. Female linear dental measurements appear to be about 10% smaller than those of males. Similarly to the wild pig, sexual dimorphism in *Microstonyx* cheekteeth appears to be less expressed (10%) than the other cranial characters, like the alveolar tuberosities (35%) or the zygomatic arches (20%).

Other factors, such as the stage of wear could influence the results of a dental size analysis. Fig. 15 shows that the occlusal length of M3 represents at mean the 88% of alveolar length in the Kalimantsi sample ($n = 25$). A similar value (89.5%) has been estimated for m3 ($n = 17$). These values indicate that the length of the *Microstonyx* third molar is probably stronger – or at least equally – related with the stage of wear than with the sex of the individual.

As in many extant suids, size variation is strongly developed in *M. major*. This is partly due to sexual dimorphism, which appears to be stronger in SE European *M. major* than in living European wild pig. This could also be evidence of a more advanced social life. The degree of sexual dimorphism is expressed more in cranial metric characters (20–40%) than in linear dental measurements (10%). Display should be of great importance for such a highly sexually diversified species. Two of the most characteristic cranial features of *M. major* (alveolar tuberosities and zygomatic arches) seem to be closely related with this kind of function.

SIZE VARIATION

Size differences have been frequently used for the distinction of the *Microstonyx* forms. As skull specimens are usually few or even absent in many samples and their size is related with the ontogenetic age and the sex of the individual, the tooth measurements are better for comparison, from the point of view of representation and statistical credibility. The third molar is one of the most commonly used teeth for such a comparison. The dimensional distribution of the third molars from SE European samples (in absolute values; Figs 9;

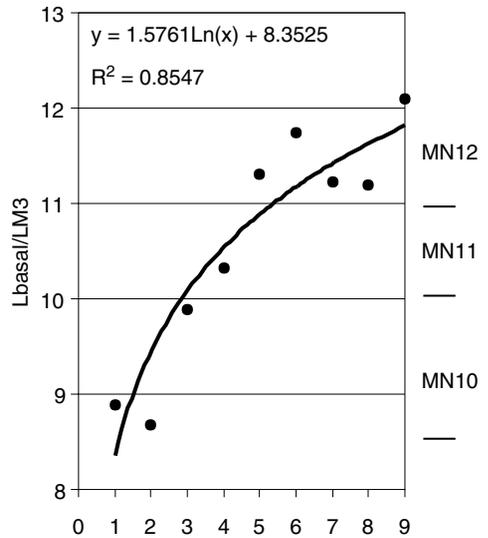


Fig. 17. — Development of M3 with evolution. Abbreviations: **Lbasal**, condylobasal length of the skull; **LM3**, length of M3; **MN**, MNzones; **1–9**, specimens from several European localities; **1**, Stratzing; **2**, Terrassa; **3**, Nikiti; **4**, Grebeniki; **5**, Taraklija; **6**, Pikermi; **7**, Kalimantsi; **8**, Kerassia; **9**, Samos. Data from Trofimov 1954; Thenius 1972; Van der Made *et al.* 1992; Kostopoulos 1994; Bonis & Bouvrain 1996 and original measurements.

10) indicates a main and a secondary group: the first one includes the Nikiti, Pikermi, Samos, Dytiko, Kalimantsi, Ezerovo and Petrelik material, while the second one the Maragha, Vathylakkos, Kerassia and Perivolaki specimens. The overlap between these two samples is about 40%.

In order to compare the mean values of M3/m3 length of *Microstonyx* from several local samples we have constructed Table 7 of percentages and the Bray-Curtis Clusters of Fig. 16. According to the sexual dimorphism analysis, a difference of less than 10% between the average values of M3/m3 length of two samples, seems insignificant, while a difference of more than 15% could be important from a systematic point of view, because it appears independent of sex variability and stage of wear. Table 7 and Figs 9, 10 and 16 show that *Microstonyx* from Kerassia, Perivolaki and Maragha could constitute a quite distinct group of a small *Microstonyx* form, different from the “classic” *Microstonyx* group of Pikermi (including Samos and Kalimantsi). The

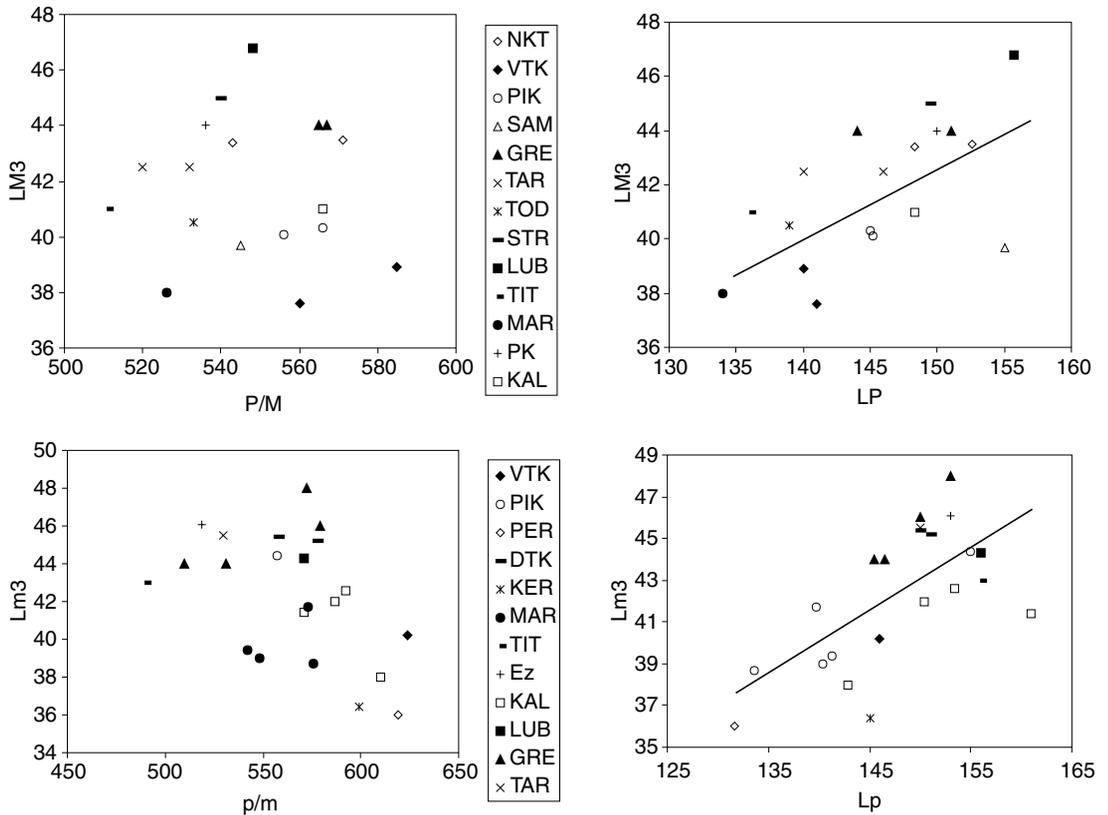


Fig. 18. — Correlation between several metrical characters of the upper and lower tooththrows of *Microstonyx major* (Gervais, 1848). Data from Trofimov 1954; Thenius 1972; Kostopoulos 1994; Bonis & Bouvrain 1996 and original measurements. **NKT**, Nikiti-1; **VTK**, Vathyakkos-2; **PIK**, Pikermi; **SAM**, Samos; **GRE**, Grebeniki; **TAR**, Taraklija; **TOD**, Tudurovo; **STR**, Stratzing; **LUB**, Luberon; **TIT**, Titov Veles; **MAR**, Maragha; **PK**, Petreluk; **KAL**, Kalimantsi; **PER**, Perivolaki; **DTK**, Dytiko-1; **KER**, Kerassia; **Ez**, Ezerovo. LP(p) = Length P2-M3 (p2-m3).

Vathyakkos sample is placed in the lower limit of the second group, but it seems more related with the first one, while the Nikiti, Dytiko and Ezerovo samples are closer to the second group.

Van der Made *et al.* (1992), having studied the Spanish material of the genus, noted that “the third molar may become longer by evolution and the index (L/B) may gradually increase [...]”. Similarly, Bonis & Bouvrain (1996) suggest that the complexity and size of M3/m3 increase from early to late Turolian. The evolutionary elongation of M3/m3 is evident in Fig. 17. The relative length of *Microstonyx* M3 (Index “Condylbasal length of the skull/LM3”) gradually increases from late Vallesian to middle Turolian forms (Fig. 17),

regardless of the absolute dimensions of the tooth. This could mean that regardless of the size, the forms from Pikermi and Kerassia are similar from an evolutionary point of view. Moreover the Nikiti *Microstonyx* is clearly distinguished by its primitive status and is placed between Terrassa /Statzing and Grebeniki (Fig. 17).

Taking into account all these data and introducing other metrical characters of the tooththrow, such as the relation P/M (p/m), the absolute length of the tooththrow and the index LP2-M3/LM3 (Lp2-m3/Lm3) (Fig. 18), we can recognize three or less well-separated groups:

– group A: it is characterized by small to medium sized tooththrow, small third molar,

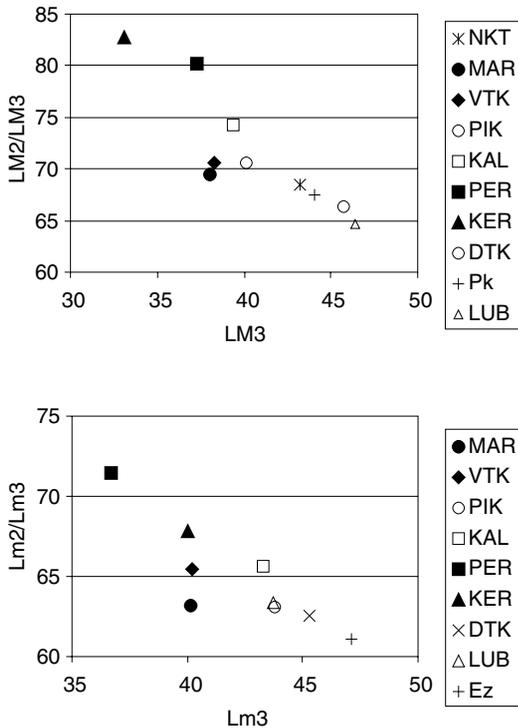


FIG. 19. — *Microstonyx major* (Gervais, 1848), distribution of the indices “LM2/LM3” and “Lm2/Lm3” from several Greco-Bulgarian samples. Data from Kostopoulos 1994; Bonis & Bouvrain 1996 and original measurements. **NKT**, Nikiti-1; **MAR**, Maragha; **VTK**, Vathylakkos-2; **PIK**, Pikermi; **KAL**, Kalimantsi-1; **PER**, Perivolaki; **KER**, Kerassia; **DTK**, Dytiko-1; **Pk**, Petrelik; **LUB**, Luberon; **Ez**, Ezerovo.

medium to high index premolar/molar row and medium (to high) index LP2-M3/LM3. *Microstonyx* from Perivolaki, Kerassia and Vathylakkos are placed here, while Maragha is very close to this group, with the exception of a shorter index P/M;

– group B: moderate to elongated toothrow, elongated M3/m3, medium values of the index P/M and medium to high index LP2-M3/LM3 characterize it. Pikermi, Kalimantsi and Samos should be included in this group;

– group C: it is characterized by (moderate to) long toothrow, very elongated M3/m3, small to medium values of the index P/M and small to medium index LP2-M3/LM3. *Microstonyx* from Dytiko, Petrelik, Ezerovo and Luberon are placed here.

The data for the Titov Veles form are controversial (A and B characters), while the more primitive Nikiti form is placed between the groups B and C (medium to high toothrows and M/m3, medium index P/M and small to medium index LP2-M3/LM3).

The above mentioned distinction corresponds, of course, to the cores of the groups, representing basic characters, while there is significant overlap, due to intermediate individuals.

The relation LM(m)2/ LM(m)3 has been selected as an index of the development of the third molar. Calculation of this index by specimen and plotting of the mean values, by locality, against the respective mean length of the third molar yield additional information (Fig. 19). Thus, forms with small third molar (MAR, VTK, KER, PER) show an increase of the index from early to middle Turolian, while the index diminishes from Kalimantsi (MN12) to Petrelik/Ezerovo (?MN12/13), as well as from Pikermi (MN12) to Dytiko (MN13). During the middle Turolian two distinct groups are present: one with high values of this index (KER, PER) and another with medium-small values (KAL, PIK). Although older (latest MN10), the Nikiti suid shows stronger similarities with the youngest group of Dytiko, Ezerovo and Petrelik.

The development of M3 is also related to the general dimensional changes of the toothrow. Plotting of the total length (LM3 + LM2 + LM1) of the upper molar row against its summed breadth (BM3 + BM2 + BM1) shows that (Fig. 20):

- group A (quite distinct from groups B and C) presents a reduction of the molar row from early to middle Turolian;
- from middle to late Turolian (or from group B to group C) the molar row increases.

CONCLUSION

Microstonyx appears to be a common faunal element in the late Miocene faunas of SE Europe (Greece, former Yugoslavia, Bulgaria, Turkey) known from several fossiliferous sites. The origin and systematics of the genus and its chronoge-

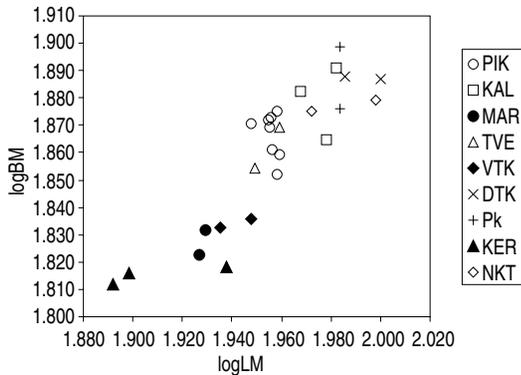


FIG. 20. — *Microstonyx major* (Gervais, 1848), distribution of the summed length (LM1 + LM2 + LM3) of the upper toothrow against its summed breadth (BM1 + BM2 + BM3), in logarithmic scale. Data from Kostopoulos 1994; Bonis & Bouvrain 1996 and original measurements. **PIK**, Pikermi; **KAL**, Kalimantsi; **MAR**, Maragha; **TVE**, Titov Veles; **VTK**, Vathyakkos-2; **DTK**, Dytiko-1; **Pk**, Petrelisk; **KER**, Kerassia; **NKT**, Nikiti-1.

graphic affiliations have been extensively discussed by many authors (e.g., Thenius 1972; Ginsburg 1988; Van der Made & Moya-Sola 1989; Van der Made *et al.* 1992; Pickford 1993; Fortelius *et al.* 1996; Van der Made 1997; Hünberman 1999). The genus, created in 1926 by Pilgrim, includes, today, three main late Miocene European taxa of Suinae, distinguishing from each other at specific or subspecific level. Relations with the Asian *Hippopotamodon* have been also indicated (Pickford 1993; Fortelius *et al.* 1996; Hünberman 1999). Nevertheless, the taxonomic status of Turolian *Microstonyx* is still open to discussion. Originally described as distinct species, *Microstonyx erymanthius* and *M. major* were later considered to have subspecific value (Van der Made *et al.* 1992; Pickford 1993), in order to be re-transferred by some authors to specific level (Fortelius *et al.* 1996; Van der Made 1997). The small differences in morphology and dimensions make their distinction extremely delicate. Therefore, the presence of two distinct subspecies has been widely based upon two principal thoughts: a chronological succession or a geographical separation. According to Van der Made & Moya-Sola (1989) and Van der Made *et al.* (1992) the smaller (sub)species, *M. major erymanthius*, was indicated to occur in Pikermi,

Kerassia (Greece) and Tudurovo (Ukraine), while the larger one, *M. m. major*, in older Ukrainian (Greibeniki, Taraklija) and western European (Spanish, French) localities. The authors gave two possible explanations:

- the presence of a geographical subspecies, restricted into the SE European region;
- a size decline within MN12.

The proposal of a geographical division today seems questionable. *M. major* from Nikiti, Ezerovo, Dytiko, Grebeniki, etc., looks closer to the western European forms (e.g., Luberon) than to the eastern ones, while the suids from Terral d'en Matias (Spain) and Dorn-Duerkheim (Germany) seem more similar to the eastern forms of the genus (e.g., Van der Made *et al.* 1992; Van der Made 1997).

On the other hand, the suggestion of a size decline may fit well with the Spanish sample, but it looks incompatible in the Greek case: starting from the large Nikiti form (latest MN10) we can observe a size decrease in MN11/12 (VTK, RZO), two samples – small and large sized – during MN12 (KER, PER *vs.* PIK, SAM) and a large form in MN12/13 (DTK, ?Ez, Pk).

Bonis & Bouvrain (1996) include the forms from VTK, RZO, PXM, Pikermi and Maragha into the same group, despite some metrical differences from the Pikermi sample. The younger and larger DTK form is considered to be more evolved and similar to the Luberon one. The authors imply a chronological distinction between *M. major major* and *M. major erymanthius*, with the first form younger than the second one. But, if this model seems quite reliable on the basis of the material referred by the authors, the NKT skull indicates the presence of an earlier (latest Vallesian) form, with larger dentition than the early/middle Turolian group of *Microstonyx*. Kostopoulos (1994) also suggest a chronological division, but in reverse sense (*M. major major* earlier than *M. major erymanthius*). In any case, the samples from Perivolaki and Kerassia, both dated to MN12, show the presence of a small *Microstonyx* form more or less simultaneously with the large form from Pikermi, Kalimantsi

and Samos. Therefore, the idea of chronological (sub)species also seems unjustified.

The elaboration and evaluation of several metric dental characters allow us to distinguish three groups of *Microstonyx major*, in the Balkan territory at least:

– group A: small size, including the Vathylakkos-2, Prochoma, Kerassia and Perivolaki samples;

– group B (corresponding to *M. m. erymanthius*): medium size, including the Pikermi, Kalimantsi, Samos and probably Titov Veles samples;

– group C (corresponding *M. m. major*): large size, including the Dytiko, Petrelik and Ezerovo samples.

The great dental similarities between these three forms (A, B and C) do not permit a separation at specific level. The first group (MN11-MN12), with quite distinct metrical features, is closely related to the Maragha *Microstonyx* (MN11) (see also Bonis & Bouvrain 1996). The molar row and especially M3/m3 become smaller with evolution.

The second (MN12) and the third (MN12-13) groups are closely related with each other, as well as with the earlier Nikiti form (end of MN10). The molar row and especially M3/m3 becomes larger from the first group to the second.

The size differences between the groups A and B could be attributed either to taxonomy or local ecology. During the middle Turolian representatives of both group A (KER, PER) and B (PIK, KAL, SAM) lived in parallel, suggesting a different ecological profile, while they have never been reported from the same locality. In contrast, evolutionary trends (development of the molar row and the third molar) seem to be opposite into these two groups. These elements allow us to suggest that group A probably constitutes a different taxon than those of group B and C.

Size differences between group B and C should more likely be attributed to ecological changes. Today, living suids of forested biomes (*Sus scrofa*, *Hylochoerus*, *Babyroussa*) appear to be larger than those of open habitats (*Phacochoerus*) (Grubb 2000; Groves & Grubb 2000). The presence of the earlier larger form *M. antiquus* in association with lignitic deposits (Thenius 1972; Ginsburg 1988) supports this idea. The Nikiti and Dytiko

palaeoecology indicate more closed/humid conditions than those of Pikermi, Samos and Kalimantsi (Bonis *et al.* 1992; Koufos 1993). We could, therefore, suggest that the transition from the one group (B = *M. m. erymanthius*) to the other (C = *M. m. major*) is most probably an ecological adaptation, which result in larger individuals.

The idea for the presence of a smaller distinct taxon already exists in Bonis & Bouvrain (1996), who note: “On pourrait peut-être envisager un découpage taxonomique différent dans lequel la sous-espèce *M. m. erymanthius* disparaît au profit de *M. m. major* alors que le matériel de Vathylakkos et Maragha serait rassemblé sous un nom subsppécifique différent.” Recent studies on Eurasian wild pigs (Groves & Grubb 2000) indicate that, in many cases, the southern races are smaller than the northern ones; the distinction between these races at subspecific level could be appropriate. If the idea of a smaller race is true, it leads to the following suggestions:

1. a local evolution of *M. major* in place. In this case the species appears to be very flexible on ecological changes, providing populations of smaller size in more arid conditions;

2. different geographic origin of the smaller form: – during the latest Vallesian (MN10), a large *M. major* form of probably northeastern origin (NKT suid), occur in the S Balkan region, where a savanna woodland-like environment predominates (Bonis *et al.* 1992);

– at the beginning of the Turolian (MN11), the increase of aridity and the predominance of more open landscapes allowed a smaller form of Asiatic origin (group A) towards West (N-C Greece), where it persisted until the middle Turolian (MN12). The large form seems to disappear temporarily from the study area (the genus is absent from the earliest Turolian locality of Nikiti-2);

– during the middle Turolian, larger northern forms (group B) invaded the southern Balkans, occupying the enlarged area from south Bulgaria/former Yugoslavia to Pikermi/Samos. The small form disappeared;

– during the late Turolian (MN13), the species appears to be geographically restricted to areas of

more humid conditions (Dytiko), where the increase of the forested environment allowed *Microstonyx major* a progressive (?) ecological adaptation associated with an increase in size (group C).

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