

The Large Mammals from the Miocene/Pliocene Locality of Silata, Macedonia, Greece with Implications about the Latest Miocene Palaeoecology

by

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Abstract

The Miocene/Pliocene locality of Silata is well known from its micromammalian fauna, described earlier. However, there are also some interesting remains of large mammals which are described in this article. The material is fragmentary and in most cases difficult to be identified, but it is interesting as from that time period the data are very few in Greece. The locality is situated in the Chalkidiki peninsula (Macedonia, Greece) about 45 km south-east of Thessaloniki. The identified fauna of large mammals includes: Hyaenidae indet., *Paramachaerodus orientalis*, *Hipparion* cf. *mediterraneum*, **Rhinocerotidae indet.**, *Microstonyx major*, *Helladotherium* sp. or *Samotherium* sp., and Bovidae indet. The entire fauna (macro- and micro-mammals) and its similarity to the Maramena (Serres basin, Greece) fauna allow an age determination to the Miocene/Pliocene boundary or at the end of MN 13 zone. The analysis of the Turolian faunas of Greece indicates a relatively open environment. The comparison of the late Turolian Dytiko, Maramena and Silata faunas with recent and other faunas of Turolian age and their faunal composition suggest that they represent water-points in a wider open landscape and the palaeoenvironment was patchy during latest Miocene.

Keywords: Mammalia, Miocene/Pliocene, Greece, description, biochronology, palaeoecology

Zusammenfassung

Die vom Miozän ins pliozän reichende Fundstelle Silata ist bekannt für ihre Kleinsäuger-Faunen. Es gibt aber auch einige interessante Reste von Großsäugern, die in diesem Artikel beschrieben werden. Das Material ist fragmentiert und daher meistens schwer bestimmbar, da aber in Griechen-

land nur wenige Fossilien aus dieser Zeitstufe bekannt sind, ist es die Mühe wert. Die Fundstelle liegt auf der Halbinsel Chalkidiki (Mazedonien, Griechenland), etwa 45 km südöstlich von Thessaloniki. Die Großsäuger-Faunenliste umfaßt: Hyaenidae indet., *Paramachaerodus orientalis*, *Hipparion* cf. *mediterraneum*, Rhinocerotidae indet., *Microstonyx major*, *Helladotherium* sp. or *Samotherium* sp., and Bovidae indet. Die Zusammensetzung der Gesamtfauuna und ihre Ähnlichkeit mit Maramena (Serres-Becken, Griechenland) erlaubt eine Alterseinstufung im Bereich der Miozän/Plioizän-Grenze oder gegen Ende von MN 13. Die Analyse der turolichen Faunen Griechenlands deutet auf verhältnismäßig offene Landschaften hin. Der Vergleich der spät-turolichen Dytiko-, Maramena- und Silata-Fauna mit rezenten oder anderen Faunen turolichen Alters zeigt, dass diese Fundstellen Wasserstellen in einer weitläufigen Offenlandschaft repräsentieren und dass das palaeoenvironment im obersten Miozän eher fleckenhaft angelegt war.

1. Introduction

Late Turolian and early Ruscinian large mammals are very rare in Greece as they are in the whole Eastern Mediterranean. In Greece the localities Dytiko-1, 2, 3 of Axios valley (Macedonia, Greece) are dated to late Turolian, MN 13 (KOUFOS, 2006). The locality of Maramena (Serres basin, Macedonia, Greece) includes several large mammals and a rich micromammalian fauna which allows its dating to Turolian / Ruscinian, MN 13/14 (SCHMIDT-KITTLER et al., 1995). The locality of Megalo Emvolon (Thessaloniki area) includes a small fauna of large mammals and it is dated to late Ruscinian, MN 15 (KOUFOS et al., 1991). Sporadic fossils of large mammals have been found in the Pliocene ligniferous deposits of Ptolemais basin (Western Macedonia, Greece) (KOUFOS, 1982; DOUKAS & DE BRUIJN, 2002), as well as in the basin of Xanthi-Komotini (Thrace, Greece) dated to early Ruscinian (SYRIDES et al., 1997). Some remains of large mammals have been also described from the locality of Apolakkia, Rhodes island and were dated to Early Ruscinian (VAN DER MEULEN & VAN KOLFSCHOTEN, 1978; KOUFOS, 2006). The record of Pliocene large mammals is also poor in the neighbouring

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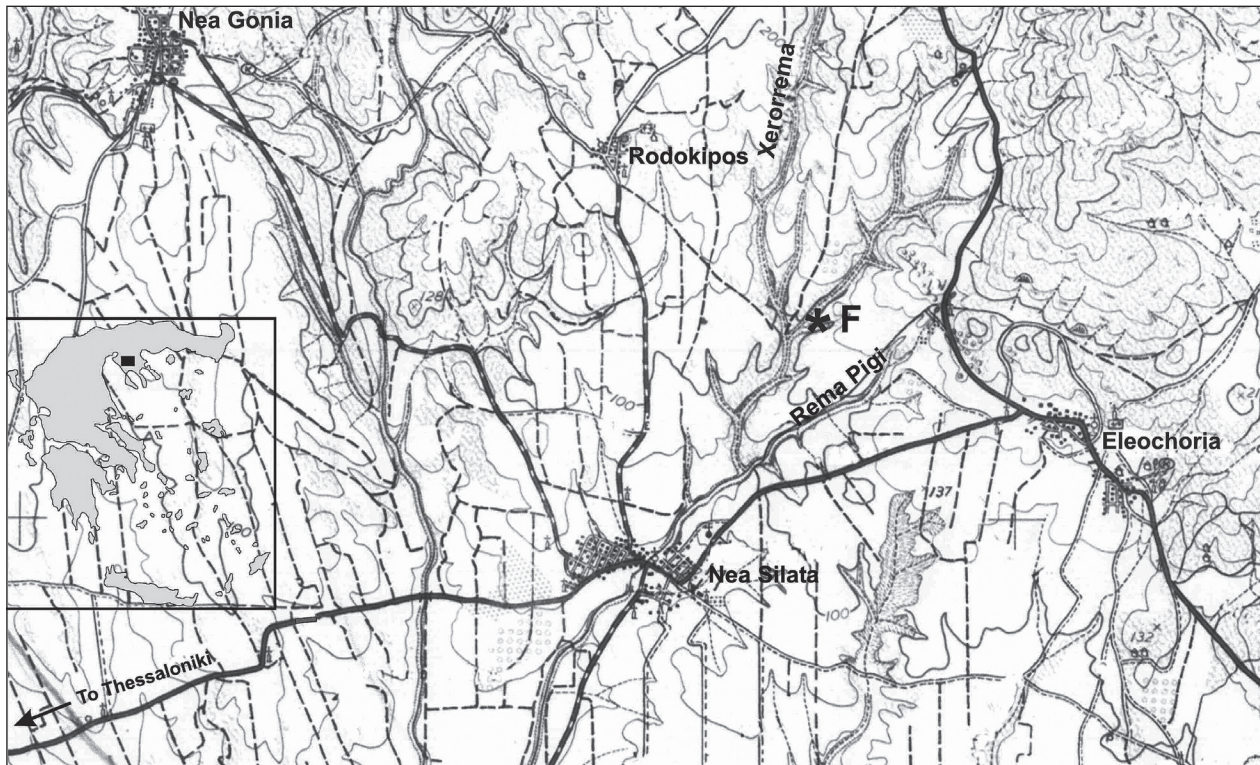


Figure 1: Topographic map indicating the position of the fossiliferous site Silata (SLT), Macedonia, Greece. F = fossiliferous site.

countries. In Bulgaria there is the Ruscinian locality of Dorkovo, which includes large mammals, mainly mastodonts (THOMAS et al., 1986). The locality of Çalta in Turkey includes a quite rich fauna of large mammals, dated to Ruscinian too (SEN, 1998). These are the main known Ruscinian localities with large mammals in Greece and the neighbouring area, but there are also several localities with small mammals, which include some fragments of large mammals.

The locality of Silata was found in Chalkidiki Peninsula (Macedonia, Greece) in the late 1980s. The main fauna includes small mammals, studied earlier (VASSILEIADOU et al., 2003). However, there are few remains of large mammals which will be described and compared in this article. The studied material is poor and fragmentary, but it is very interesting as our knowledge about the Turolian/Ruscinian faunas of Greece is very poor and any additional information is very important and enriches our knowledge.

Abbreviations:

LGPUA= Laboratory of Geology and Palaeontology, University of Athens

LGPUTh= Laboratory of Geology and Palaeontology, University of Thessaloniki

MGL= Musée de Géologie de Lausanne

MNHN= Muséum National d'Histoire Naturelle, Paris

NHMW=Naturhistorisches Museum Wien

2. Geological setting

The studied locality is placed in the western part of Chalkidiki peninsula and it is situated between the villages of Nea Silata, Rodokipos and Eleochoria (Fig. 1). The

pre-Neogene basement of the area belongs to the zone of Peonias and consists mainly of Mesozoic semi-metamorphic, alpine sediments. The rocks are mainly limestones, sandstones, conglomerates, phyllites, schists and volcano-sedimentary deposits. In the area surrounding the locality, the limestones outcrop and are covered by thick Neogene deposits. Their thickness can reach 700m and they consist of a variety of sediments. According to SYRIDES (1990) the Neogene deposits are divided in six different formations, which are briefly described below.

Antonios Fm. The sediments are unconsolidated conglomerates and sands alternated with lenses of pebbles and gravels, having a thickness of more than 100m and representing the first deposits that began to fill the basin. In the upper part, the Antonios Fm sediments are alternated with the red-beds of Triglia Fm, indicating a gradual transition to this formation. A mammalian fauna has been found in the base of the Antonios Fm which allows the dating of the formation. The fauna includes both micro- and macro-mammals and suggests an Early/Middle Miocene (MN 4/5) age (KOUFOS & SYRIDES, 1997; VASSILEIADOU & KOUFOS, 2005).

Triglia Fm. It consists of coarse-fine grained sands rich in clays-silts, having a reddish-brownish colour and a thickness that varies from 20-200m. The Triglia Fm includes a large mammal fauna which indicates a late Vallesian-early Turolian age (SYRIDES, 1990).

Trilophos Fm. It overlays the Triglia Fm unconformably and consists of well-stratified brackish sands, clays, sandstones and limestones with a *Paratethys* mollusc fauna. It represents the transgression of *Paratethys* in the wider northern Aegean region. The mollusc fauna suggests a "Pontian" age, or in other words a latest Miocene age (SYRIDES, 1990).

Figure 2: Stratigraphic column of the deposits in the fossiliferous site (VASSILEIADOU et al., 2003).

Gonia Fm. It consists of terrestrial deposits mainly lenses or len-shaped beds of sands, clays, marls, sandstones, gravels and massive marly limestones alternating each other. The formation includes three beds of a massive-tuffaceous limestone which separating three different members: Silata Mb, Rodokipos Mb, and Kallikratia Mb. The locality of Silata has been found in the base of this formation, into the Silata Mb, just above the brackish deposits of Trilophos Fm. The Gonia Fm is dated to Ruscinian.

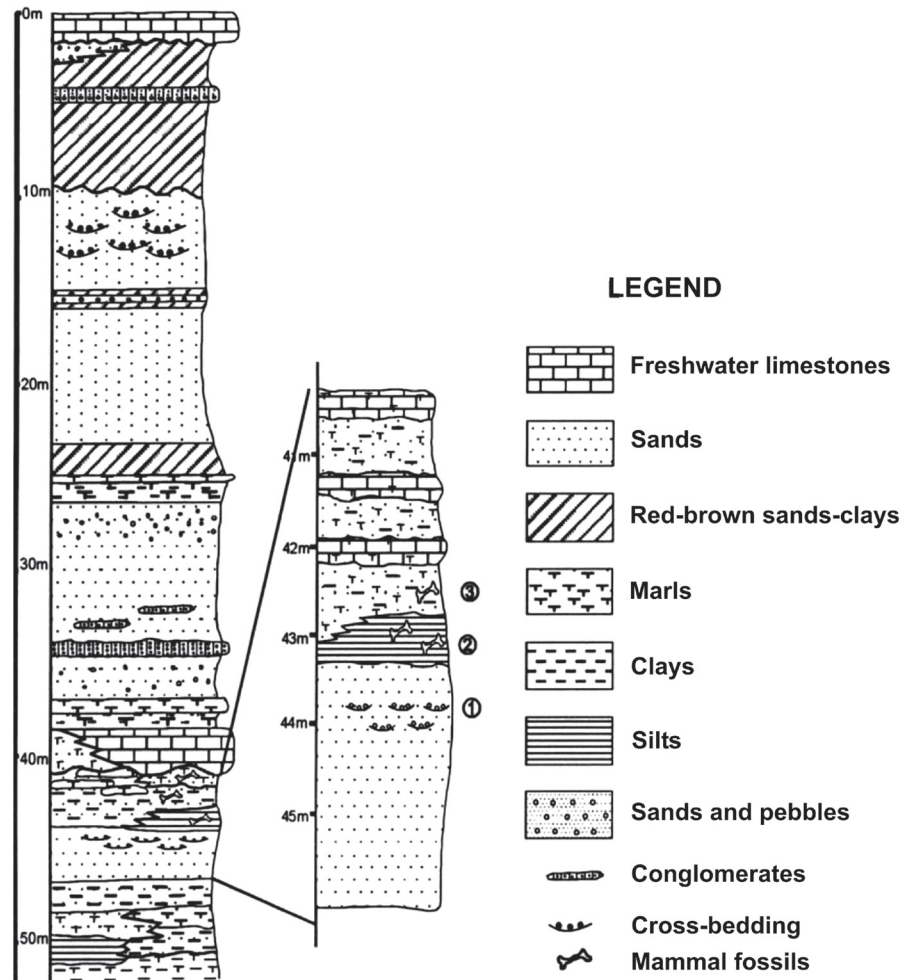
Moudania Fm. It consists of thick red-beds overlying unconformably Gonia Fm with variable thickness, which can sometimes reaches 200 m. As no fossils have been found in this formation its age is estimated from the stratigraphy as being Villafranchian (Late Pliocene-Early Pleistocene).

Eleochoria Fm. It includes the youngest deposits of the basin, consisting mainly of tuffaceous limestones and travertines deposited diachronically in the area. Its age is estimated as Middle/Late Pleistocene-Holocene.

3. The fossiliferous site

The fossiliferous site is situated near the village of Nea Silata in Chalkidiki peninsula, Macedonia, Greece (Fig. 1). The site lies about 1.5 km north-east of the village Nea Silata. The locality is situated in a small ravine which includes deposits belonging to the Silata Mb of the Gonia Fm. In the bottom of the ravine there are whitish-greyish sands and gravels overlaid by a len-shaped bed of a grey-green silt-clay with lignitic traces (Fig. 2). The deposits are continued by three alternations of yellowish-greyish sands-clays with massive white-grey limestones. The upper limestone of the section corresponds to the upper limestone of the Silata Fm. (SYRIDES, 1990).

The large mammal remains are dispersed in the whole section but the majority of them was found in the grey silts-clays and in the above layers of sands-clays and limestones. The suid and rhino dental remains were found in the lower bed of sands. The small mammals come mainly from the bed of grey silts-clays, as well as from the above clayey-marly sands. There is not a concentration of large mammals, but



their remains are scarcely dispersed throughout the deposits, making them to track down. This kind of concentration is common in the Ruscinian deposits of the area. Similar concentration was also recognized in the deposits of the Ruscinian locality of Megalo Emvolon (KOUFOS et al., 1991). In the upper two beds of the section (grey silts-clays and clayey-marly sands), several fragments of turtles have been found, together with some small reptiles and abundant fresh-water mollusks and gastropods opercula. The turtle remains are small pieces of the carapax which cannot be determined and they are referred to as *Testudo* sp. The large mammals were mainly collected during regular visits to the area from time to time when the erosion had brought them out. Some remains were also found while washing the sediments in search of micromammals and some bones of hipparions and the giraffid were found in situ.

4. Systematic Palaeontology

Order Carnivora BOWDICH, 1821

Family Hyaenidae GRAY, 1869

Hyaenidae indet.

(Plate 1, figs. 1a, b)

Material: Anterior part of the right upper carnassial, SLT-16.

Description: It is a piece of P⁴ preserving the anterior part with the parastyle and protocone. Both cusps are worn, indicating a quite old individual. The protocone is relatively large, well separated from the parastyle and situated slightly behind the anterior border of the parastyle. The parastyle is relatively large and worn. There is a well-distinguished labial cingulum.

Discussion: The identification of such a fragmentary tooth is difficult but a comparison with some late Miocene carnivores, can give more information. As *Paramachaerodus orientalis* has been recognized in the Silata locality a comparison with this taxon should be useful. The P⁴ of *P. orientalis* has a smaller protocone situated more posteriorly than in SLT-16 (KITTL, 1887: taf. XIV, fig. 3) and its breadth at the protocone's level is smaller (Tab. 1). In *Machairodus aphanistus* the protocone is large (BONIS, 1994) but it is situated more posteriorly than in SLT-16. On the contrary, in *Machairodus giganteus* the protocone is rudimentary restricted in the basis of the lingual root of the tooth (KOUFOS, 2000) and it is situated more posteriorly than in SLT-16. This feature reflects to the breadth of the carnassial at the protocone level (Tab. 1). Moreover, there is a clear ectoparastyle in *Machairodus* which is absent in

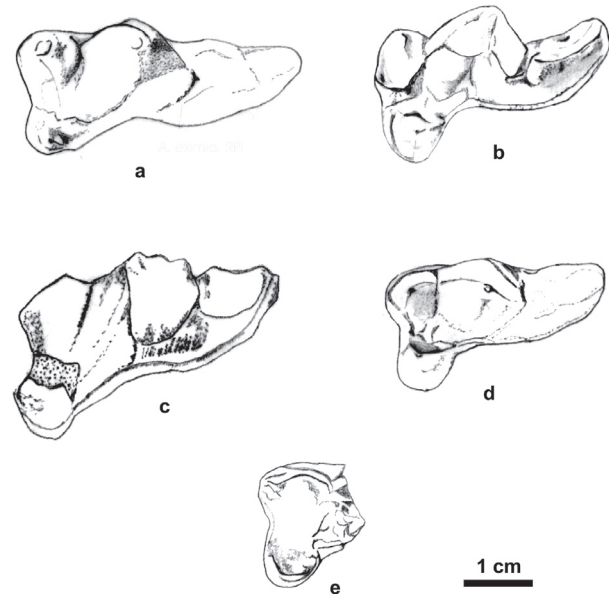


Figure 3: Morphology and position of the protocone in some Miocene hyaenids. a. *Adcrocuta eximia leptoryncha*, Ravin de la Pluie, Axios valley, Macedonia, Greece, RPI-14., b. *Hyaenictis graeca*, Pikermi, Greece, NHMW-A.4715, c. *Chasmaporthetes bonisi*, Ravin des Zouaves-5, Axios valley, Macedonia, Greece, RZO-125, d. *Lycyaena chaeretis*, Samos, Greece, NHMW-A.4744, e. Hyaenidae indet., Silata, Macedonia, Greece, SLT-16. All teeth were drawn as left.

Taxa/Sites	Carnassial breadth at the protocone's level
SLT-16	17.5
<i>Paramachaerodus orientalis</i> Maragha (PILGRIM, 1931)	14.0
<i>Paramachaerodus cf. orientalis</i> Spain, Las Casiones (ALCALA, 1994)	14.7
<i>Machairodus aphanistus</i> Kemiklitepe, Turkey (BONIS, 1994)	19.0
<i>Machairodus giganteus</i> Halmyropotamos, Greece (MELENTIS, 1967)	14.8
R-X, Axios valley (KOUFOS, 2000)	15.6
<i>Metailurus major</i> Halmyropotamos, Greece (MELENTIS, 1967)	13.5
China (MELENTIS, 1967)	14.0
<i>Metailurus parvulus</i> Halmyropotamos, Greece (MELENTIS, 1967)	10.1
Chomateres, Greece (SYMEONIDIS, 1978)	10.4
<i>Adcrocuta eximia</i> Pikermi, Greece (NHMW A.4716)	15.6
Pikermi, Greece (MNHN PIK-3000)	21.6-21.9
Samos, Greece (NHMW A.4727)	16.3-17.0
Axios Valley, RZO-52 (BONIS & KOUFOS, 1995)	16.8
<i>Hyaenictis graeca</i> Pikermi, Greece (MNHN PIK-3003)	17.8
Pikermi, Greece (NHMW A.4715)	18.7
<i>Chasmaporthetes bonisi</i> Axios valley, RZO-125 (BONIS & KOUFOS, 1994)	19.0-20.7
<i>Lycyaena chaeretis</i> Pikermi, Greece (PILGRIM, 1933)	17.0
Samos, Greece (NHMW A.4744); orig. measurements	17.1-17.5
Samos, Greece (MGL L.21788); meas. from cast	17.5

Table 1: Breadth of the upper carnassial at the protocone's level of various Miocene felids and hyaenids.

SLT-16. Both species of the genus *Metailurus* (*M. major* and *M. parvulus*) have smaller and more posteriorly situated protocone; the breadth at the protocone level is significantly smaller than in SLT-16 (Tab. 1). The comparison of SLT-16 with the Miocene machairodontids suggests that it is different and cannot belong to them.

The comparison of SLT-16 with the Hyaenidae is also necessary as this family is very common in the Neogene. The size of the studied specimen indicates that it belongs to a medium-sized taxon and thus the small-sized ictitheres and the large-sized hyaenas, like *Percrocuta* and *Dinocrocuta*, can be excluded from the comparison. The most common hyaena of the Miocene is *Adcrocuta eximia* which is present in all Turolian localities of Greece. It is clearly distinguished from SLT-16 in having a quite smaller (rudimentary) protocone and smaller breadth at the protocone's level (Fig. 3a; Tab. 1). Another hyaenid is *Hyaenictis graeca* known from Pikermi, Athens, Greece. Two maxillary fragments are known. The first is stored in MNHN (PIK-3003) and the second in NHMW (A.4715). The comparison of SLT-16 with the Vienna specimen indicates similar size of the protocone and slightly larger breadth at the protocone's level (Fig. 3b; Tab. 1). However, the protocone of *Hyaenictis graeca* is situated more anteriorly than in SLT-16 (Fig. 3b). The hyaenid *Chasmaporthetes bonisi* has been originally described from the late Turolian locality of Dytiko and later it was found in the early Turolian locality of "Ravin des Zouaves-5" (RZO) of the lower Axios valley, Macedonia, Greece (KOUFOS, 1987a; BONIS & KOUFOS, 1994). The protocone of *C. bonisi* has similar size to that of SLT-16, but it is more distinct and

on line with the parastyle while the breadth of the P⁴ at the protocone level is larger than in SLT-16 (Fig. 3c, Tab. 1). *Lycyaena chaeretus* is known in Greece from Pikermi and Samos (KOUFOS, 2006). It is characterized by a prominent protocone, situated slightly posterior (Fig. 3d). In this feature SLT-16 is close to *Lycyaena*. The breadth of the tooth at the protocone level is also very close to this taxon (Tab. 1). The direct comparison of SLT-16 with *Lycyaena* from Samos (NHMW-A.4744) and also with the cast of MGL-L.21788 from Samos, indicate close similarities. The above comparison suggests that SLT-16 cannot be a machairodont. On the other hand it is closed to the hyaenids. In spite of its similarities to *Lycyaena* it is better to refer it to as Hyaenidae indet., because the limited and fragmentary material does not allow a certain identification.

Family Felidae GRAY, 1821

Genus *Paramachaerodus* PILGRIM, 1913

Paramachaerodus orientalis (KITTL, 1887)
(Plate 1, fig. 2)

Material: Right upper canine, SLT-15.

Measurements: Length at the base of the crown = 17.0 mm, breadth idem = 9.5 mm, preserved height from the enamel base to the tip = 38.5 mm.

Description: It is an almost complete upper canine of a machairodont from which only a small part of its root is broken (Pl. 1, fig. 2a). The canine is relatively small, weakly curved distally and pointed. The labial surface is relatively more flat than the lingual one, which is more curved. The root is strong and wider than the crown. The mesial border is sharp and has a crest along it. The crest is quite worn at the base but in the stereoscope the crenulations of the enamel are clearly distinguishable. The distal border is sharper and less worn than the mesial one. The crenulation of the enamel of the distal border is clear in the stereoscope and stronger than in the mesial border.

Discussion: The size of the canine suggests a small machairodont and such machairodonts are known from the Late Miocene. The genus *Machairodus* has a large size and clearly distinguished from the studied species by its size (Fig. 4). Its upper canine is quite larger than the studied one and has clear crenulations across the anterior and posterior crest. The upper canine of *Metailurus* and *Paramachaerodus* have similar dimensions to SLT-15

(Fig. 4) and the comparison with these genera is necessary for the attribution.

The upper canine of *Paramachaerodus* has crenulated mesial and distal crests (PILGRIM, 1931) and in this feature SLT-15 resembles this genus. The upper canine of *P. orientalis* is weakly curved and the distal border is more strongly crenulated than the mesial one (KITTL, 1887; PILGRIM, 1931). In these characters SLT-15 also resembles *P. orientalis*. The morphology of SLT-15 is also similar to the material from Spain (ALCALA, 1994). Moreover, the size of SLT-15 is very close to *P. orientalis* from Maragha (Iran), and Spain (Fig. 4). The genus *Metailurus* is known from Greece by two species, *M. major* and *M. parvulus*. The upper canine of *Metailurus major* is larger than SLT-15 (Fig. 4) and has no crenulations in its mesial and distal border. A direct comparison of SLT-15 with the canine of the skull of *M. major* from Halmyropotamos, Evia, Greece (MELENTIS, 1967) confirms the above differences between the two specimens. The studied canine has been compared with the skulls of *Metailurus parvulus* from Pikermi and Chomateres stored in LGPUA. Their upper canines have no crenulations and they are smaller than those of SLT-15 and *P. orientalis* (Fig. 4). In conclusion the morphology and size of SLT-15 allow its attribution to *Paramachaerodus orientalis*.

Order Perissodactyla OWEN, 1848

Family Equidae GRAY, 1821

Genus *Hipparion* CHRISTOL, 1832

Hipparion cf. *H. mediterraneum* (ROTH & WAGNER, 1855)

(Plate 1, figs. 3-15; Plate 2, figs. 1-9)

Material: 2I³, SLT-18, 19; P²dex, SLT-5; P^{3,4}sin, SLT-26; M³dex, SLT-20; i₃ dex, SLT-30; dp_{3,4} dex, SLT-21; dp₄ dex, SLT-4; p₂ dex, SLT-31; 4 p_{3,4} SLT-1,2,13,25; m_{1,2} sin, SLT-3; distal part of humerus, SLT-12; os carpi ulnare

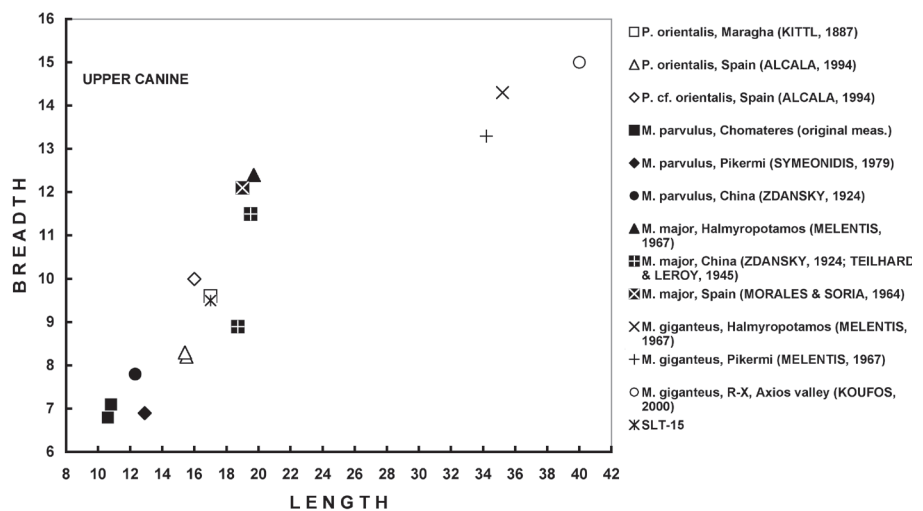


Figure 4: Scatter diagram (length/breadth at the base) comparing the upper canine of some Miocene machairodonts.

Teeth	Lo	Bo	Lp	Bp	Boant	Bopost	Lprfl	Lptfl	E.F.
P2 dex, SLT-5	30+	22	8.5	4.3	—	—	—	—	3,4,3,1/1
P3,4 sin, SLT-26	26.9	20.1	7.0	4.7	—	—	—	—	2,8,4,0/1
M3 dex, SLT-20	21.4	17.5	5.8	2.6	—	—	—	—	5,6,3,1/1
p2 dex, SLT-31	32.5	—	—	—	9.5	11.2	—	—	Unworn
p3,4 sin, SLT-1	24	—	—	—	12.0	11.5	6.5	11.3	1,1,2/1
p3,4 sin, SLT-2	25.1	—	—	—	11.5	12.0	9.0	12.5	1,1,3/1
p3,4 sin, SLT-13	22.7	—	—	—	12.4	12.0	7.3	6.8	0,1,1/0
p3,4 dex SLT-25	23.7	—	—	—	12.4	11.0	7.0	11.0	1,1,2/1
m1,2 sin, SLT-3	23.4	—	—	—	9.5	9.0	6.6	8.7	0,1,0/0
dp4 dex, SLT-21	30,1	—	—	—	11.0	11.4	9.4	12.7	Unworn
dp3,4 sin, SLT-21	30+	—	—	—	12.2	—	—	—	1,1,0/0

Table 2: Dental dimensions of *Hipparion* cf. *H. mediterraneum* from Silata. Lo=occlusal length; Bo = occlusal breadth; Lp = protocone length; Bp = protocone breadth; Boant. = anterior occlusal breadth; Bopost. = posterior occlusal breadth; Lprfl = preflexid length; Lptfl = postflexid length, E.F. = enamel formula.

(pyramidal), SLT-6; part of os lunatum, SLT-24; part of os magnum, SLT-9; distal part of tibia (young individual), SLT-10; astragalus, SLT-7; calcaneum, SLT-29; os tarsale naviculare, SLT-14; second phalanx, SLT-28; 2 lateral first phalanges, SLT-22,23.

Measurements: The measurements of the material are given in tabs 2, 3.

Description: The dental and postcranial dimensions of the Silata hipparion suggest a medium-sized form. In the P² (SLT-5) the anterostyle is broken but it seems to

be relatively small and not strongly projected (Pl. 1, Fig. 6). The fossettes are free with moderate enamel plication (12 plis) but the tooth is relatively little worn and probably their number will slightly increase with ongoing wear. The pli-caballin is single and long. The protocone is isolated, elongated and relatively narrow, having a small spur in its distal end. The hypocone is angular and the distal hypoconal groove is shallow. In the P^{3,4} (SLT-26), which belongs to a very old individual, the enamel plication in the fossette's border is moderate (15 plis) and the plis are

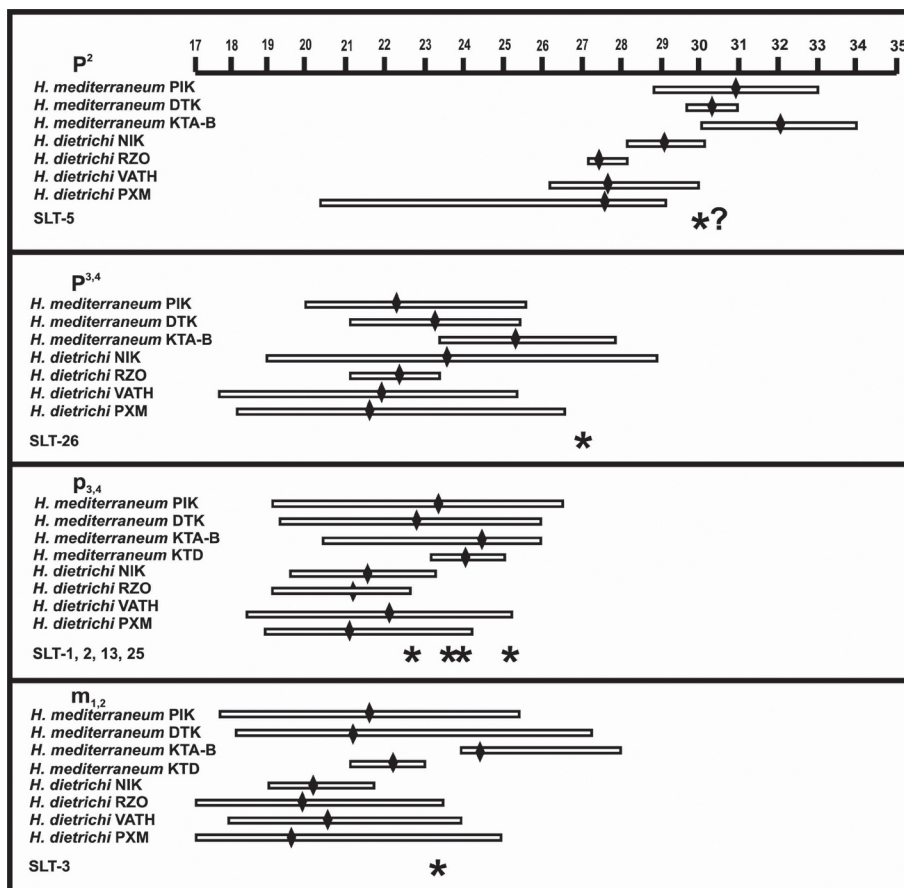


Figure 5: Comparison of the occlusal length of the dental *Hipparion* remains from Silata with *H. mediterraneum* and *H. dietrichi* from various localities. The horizontal line gives the range of length variation and the rhombs the mean value of the tooth length. The Silata specimens are indicated by stars.

PIK = *H. mediterraneum*, Pikerimi (KOUFOS, 1987b); DTK = *H. mediterraneum*, Dytiko, Axios valley, Macedonia, Greece (KOUFOS, 1988a); KTA-B = *H. mediterraneum*, Kemiklitepe A-B, Turkey (KOUFOS & KOSTOPOULOS, 1994); KTD = *H. mediterraneum*, Kemiklitepe D, Turkey (KOUFOS & KOSTOPOULOS, 1994); NIK = *H. dietrichi*, Nikiti 2, Macedonia, Greece (VLACHOU & KOUFOS, 2002); RZO = *H. dietrichi*, Ravin des Zouaves 5, Axios valley, Macedonia, Greece (KOUFOS, 1987c); VATH = *H.*

dietrichi, Vathylakkos 1, 2, 3, Axios valley, Macedonia, Greece (KOUFOS, 1988b); PXM = *H. dietrichi*, Prochoma, Axios valley, Macedonia, Greece (KOUFOS, 1987d).

Postcranials	1	2	3	4	5	6	7	8	9	10	11
Humerus, SLT-12	—	—	—	—	—	—	58.7	57.7	40	28.6	35
Os carpi ulnare, SLT-6	29.4	32.5	14	18.5	—	—	—	—	—	—	—
Os lunatum, SLT-24	—	22.4	22.9	—	—	—	—	—	—	—	—
Astragalus, SLT-7	51	49.1	23.1	47.4	37.6	27.6	39.4	—	—	—	—
Calcaneum, SLT-29	—	—	17.6	—	—	44.2	42.1	—	—	—	—
Os naviculare tarsale, SLT-14	30.7	37	—	—	—	—	—	—	—	—	—
Phalanx II, SLT-28	36.2	28.7	27.7	33.5	22.8	31.4	—	—	—	—	—
1 st lateral phalanx, SLT-22	27.2	9.7	18.6	10.5	7.5	—	—	—	—	—	—
1 st lateral phalanx, SLT-23	32.2	9.5	16.5	9.8	12.8	—	—	—	—	—	—

Table 3: Postcranial dimensions of *Hipparion* cf. *H. mediterraneum* from Silata. **Humerus:** 7. Maximal breadth of the trochlea; 8. Distal maximal DAP; 9. Maximal trochlear height (medial); 10. Maximal trochlear height (in the middle); 11. Trochlea height at the sagittal crest near the condyle. **Os carpi ulnare:** 1. Oblique height; 2. Anterior height; 3. Maximal breadth; 4. Maximal DAP (in projection). **Os lunatum:** 2. Maximal length; 3. Maximal height. **Astragalus:** 1. Maximal length (height): articular facet for navicular-top of the internal condyle; 2. Maximal diameter of the internal condyle; 3. Trochlear breadth: middle of the internal-middle of the external condyle; 4. Maximal breadth (in projection); 5. Distal articular breadth; 6. Distal articular DAP; 7. Maximal DAP of the internal condyle. **Calcaneum:** 3. Minimal breadth of the diaphysis; 6. Distal maximal breadth (in projection); 7. Distal maximal DAP (in projection). **Os naviculare tarsale:** 1. Maximal DAP; 2. Breadth. **Second phalanx:** 1. Maximal length; 2. Anterior length: middle of the proximal articular facet- middle of the distal facet; 3. Minimal breadth of the diaphysis; 4. Maximal proximal breadth; 5. Proximal DAP; 6. Maximal distal articular breadth. **First lateral phalanx:** 1. Maximal length; 2. Proximal maximal breadth; 3. Proximal maximal depth; 4. Distal maximal breadth; 5. Minimal breadth of the diaphysis.

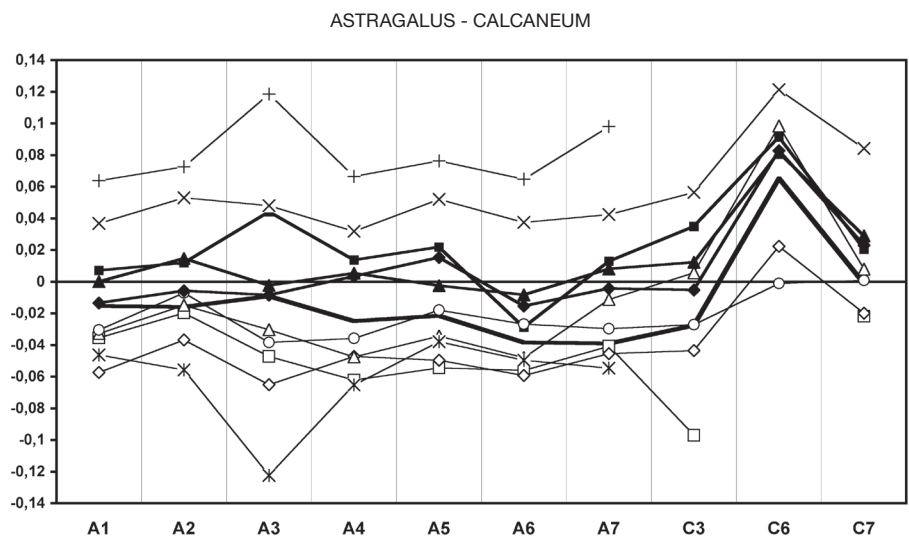
narrow and shallow (Pl. 1, fig. 7). The protocone is isolated and oval-shaped, while the pli-caballin is single and large. The M³ (SLT-20) is little worn having a moderate enamel plication (16 plis). The protocone is elliptical and very narrow, while the hypocone is restricted by a lingual and distal deep hypoconal groove (Pl. 1+, fig. 8).

The p₂ is unworn and as a result it is impossible to see its occlusal morphology. The p_{3,4} have moderately developed parastylid and the protostylid ends at about ¾ of the tooth's height. The metaconid and metastylid are asymmetric in

the little worn teeth, but as the wear increases they become more rounded. The entoconid is more quadrangular in the more worn teeth. The postflexid has a plicated external border, which becomes more regular with wear. The linguaflexid is open V-shaped and relatively deep. The ectoflexid is relatively narrow and not very deep, reaching the middle of the tooth's breadth. The pli-caballinid is present and large in the less worn SLT-2, while it is just distinguished in the more worn SLT-1, 25 and absent in the worn SLT-13. The m_{1,2} (SLT-3) has a similar morphology,

Figure 6: Logarithmic ratio diagram comparing the astragalus (A) and calcaneum (C) of the Silata *Hipparion* with those from other localities. Standard *H. mediterraneum*, Pikermi, Greece, n=7-25 (KOUFOS, 1987b).

■ - *Hipparion* cf. *H. mediterraneum*, Silata, Macedonia, Greece, n = 1, ▲ - *H. mediterraneum*, Dytiko-1, 2, 3, Axios valley, Macedonia, Greece, n = 12-21 (KOUFOS, 1988a), ■ - *H. mediterraneum*, Kemiklitepe-D, Turkey, n = 1-3 (KOUFOS & KOSTOPOULOS, 1994), ◆ - *H. cf. mediterraneum*, Perivolaki, Thessaly, Greece, n = 4-9 (original measurements), ◇ - *H. dietrichi*, Nikiti-2, Macedonia, Greece, n = 5-12 (VLACHOU & KOUFOS, 2002), △ - *H. dietrichi*, Ravin des Zouaves-5, Axios valley, Macedonia, Greece, n = 1 (KOUFOS, 1987c), ○ - *H. dietrichi*, Vathylakkos-1, 2, 3, Axios valley, Macedonia, Greece, n = 2-5 (KOUFOS, 1988b), □ - *H. dietrichi*, Prochoma, Axios valley, Macedonia, Greece, n = 4-5 (KOUFOS, 1987d), * - *Hipparion* sp. (small-sized), Maramena, Macedonia, Greece, n = 1 (SONDAAR & EISENMANN, 1995), + - *Hipparion* sp. (large-sized), Maramena, Macedonia, Greece, n=1 (SONDAAR & EISENMANN, 1995), × - *H. cf. longipes*, Akkasdagi, Turkey, n=6-11 (KOUFOS & VLACHOU, 2005).



◆ - *H. cf. mediterraneum*, Perivolaki, Thessaly, Greece, n = 4-9 (original measurements), ◇ - *H. dietrichi*, Nikiti-2, Macedonia, Greece, n = 5-12 (VLACHOU & KOUFOS, 2002), △ - *H. dietrichi*, Ravin des Zouaves-5, Axios valley, Macedonia, Greece, n = 1 (KOUFOS, 1987c), ○ - *H. dietrichi*, Vathylakkos-1, 2, 3, Axios valley, Macedonia, Greece, n = 2-5 (KOUFOS, 1988b), □ - *H. dietrichi*, Prochoma, Axios valley, Macedonia, Greece, n = 4-5 (KOUFOS, 1987d), * - *Hipparion* sp. (small-sized), Maramena, Macedonia, Greece, n = 1 (SONDAAR & EISENMANN, 1995), + - *Hipparion* sp. (large-sized), Maramena, Macedonia, Greece, n=1 (SONDAAR & EISENMANN, 1995), × - *H. cf. longipes*, Akkasdagi, Turkey, n=6-11 (KOUFOS & VLACHOU, 2005).

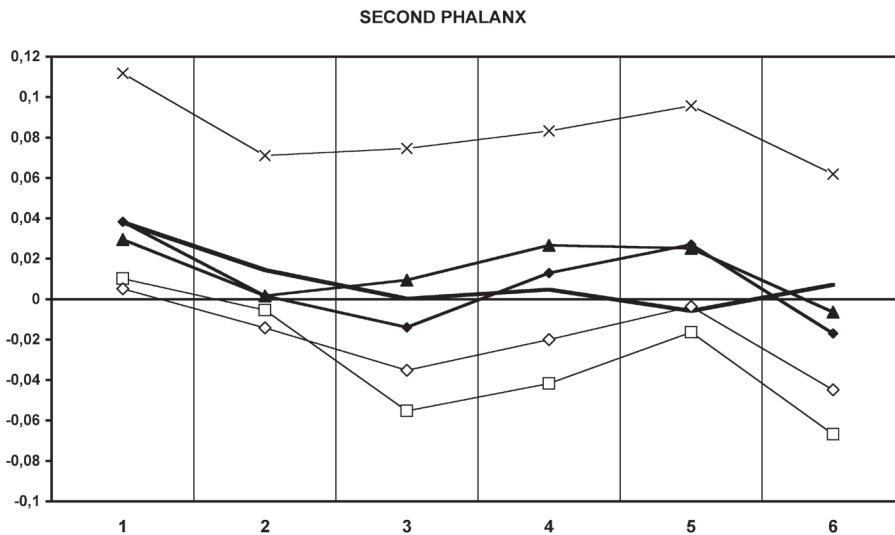


Figure 7: Logarithmic ratio diagram comparing the second phalanx of the Silata *Hipparion* with that from other localities. Standard *H. mediterraneum*, Pikermi, Greece, n = 5-6 (KOUFOS, 1987a).

■ – *H. cf. H. mediterraneum*, Silata, Macedonia, Greece, n = 1, ▲ – *H. mediterraneum*, Dytiko-1, 2, 3, Axios valley, Macedonia, Greece, n = 11-13 (KOUFOS, 1988b), ◆ – *H. cf. mediterraneum*, Perivolaki, Thessaly, Greece, n = 8-9 (original measurements), ◇ – *H. dietrichi*, Nikiti-2, Macedonia, Greece, n = 11-12 (VLACHOU & KOUFOS, 2002), □ – *H. dietrichi*, Prochoma, Axios valley, Macedonia, Greece, n = 6 (KOUFOS, 1987d), × – *H. cf. longipes*, Akkasdagi, Turkey, n = 5-6 (KOUFOS & VLACHOU, 2005).

but the ectoflexid is deeper and touches the linguaflexid (Pl. 1, fig. 13). The hypoconulid is more developed and there is no clear pli-caballinid.

Discussion: The material of hipparions from Silata is fragmentary and difficult to be determined accurately. However, a comparison with the known Greek hipparions can provide some information. As mentioned above the Silata material suggests a medium-sized hipparion. Taking in mind the age of the locality, it is useful to compare our material with the Turolian/Ruscinian hipparionine horses. The comparison of the isolated teeth of hipparions is difficult, as the different degree of wear affects their dimensions, which decrease with the attrition. In this case the use of scatter diagrams (length/breadth) cannot give useful results. Moreover, an identification based on size is hampered by the overlapping dimensions of the various species. However, a comparison of the tooth's length with the mean values and ranges of variation for the various species could give better results.

Two medium-sized hipparions are well known from the Turolian of Greece: *Hipparion mediterraneum* and *H. dietrichi*. The former species is known from: a. Pikermi, near Athens (Attica) and b. Dytiko-1, 2, 3 (Axios valley, Macedonia, Greece). A form similar to *H. mediterraneum* is known from the locality of Perivolaki, near Volos, Thessaly and from the localities Mytilinii 1, 4 of Samos (KOUFOS, 1987b, 1988a; VLACHOU & KOUFOS, 2004, 2006). *H. dietrichi* is quite common and it was recognized in various localities of Northern Greece, as well as in Samos (KOUFOS, 1987c, 1987d, 1988b; VLACHOU & KOUFOS, 2002, 2004, 2006). In

Fig. 5 the length of the teeth from Silata is compared to that of these two Turolian species from various localities. The studied M³ SLT-20 is not compared in the diagram because the way of attrition in M³ cannot allow certain measurements of its length. Although there is an overlapping between *H. dietrichi* and *H. mediterraneum*, the SLT material is closer to the mean values of *H. mediterraneum*. The studied P² seems to be also close to *H. dietrichi*, but as the anterostyle is broken its length is certainly larger than the measured one.

Among the available postcranials the comparison of astragalus and calcaneum, as well as of second phalanx is possible. They are also compared with *Hipparion mediterraneum* and *H. dietrichi*. The Silata astragalus and calcaneum are very close to those of *H. mediterraneum*

from various localities but they are smaller than all of them (Fig. 6). *H. dietrichi* is quite smaller than the Silata material. However, the Silata astragalus and calcaneum seems to be close to *H. dietrichi* from Ravin des Zouaves-5 (RZO) and Vathylakkos 2 (VTK). Apart from their size similarity, the SLT astragalus is higher (meas. A1, A4 in Fig. 6), the calcaneum is wider and longer distally (meas. C6, C7 in Fig. 6) and thus they differ from *H. dietrichi*. The comparison of the second phalanx indicates that the Silata hipparion is again very close to *H. mediterraneum* and larger than *H. dietrichi* from the various localities (Fig. 7).

Two different hipparions, a very large-sized and a small-sized one, have been described from the isochronous Greek locality of Maramena, Serres basin (SONDAAR & EISENMANN, 1995). The material is very limited and fragmentary but there are two astragali which can be compared to that from Silata. The one is larger and the other smaller than the studied one (Fig. 6), indicating that the Silata astragalus belongs to a different form. Unfortunately, no good dental remains from Maramena are known to allow a comparison with the Silata sample.

The Pliocene *Hipparion crassum* has been described from the ligniferous basin of Ptolemais, Macedonia, Greece (KOUFOS, 1982). The material is poor consisting of a single P²-P³ row and some postcranials. The size of the Silata teeth is similar but there are some differences in the size and shape of the protocone. The latter is smaller and more rounded in the Ptolemais sample (KOUFOS, 1982: fig.1, pl. I, fig.1) than the studied one. The material from Ptolemais is discussed by EISENMAN & SONDAAR (1989) and they argued

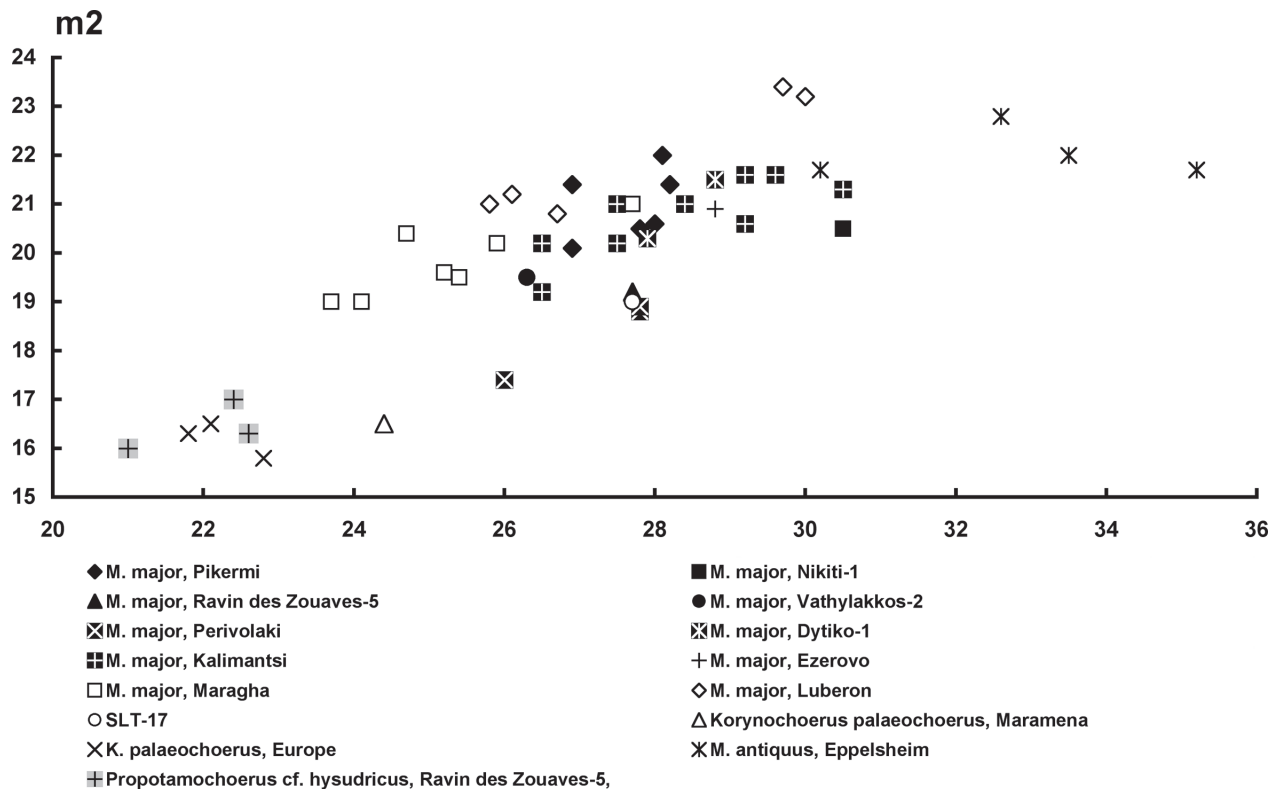


Figure 8: Scatter diagram (length/breadth) comparing the M_2 of *Microstonyx major* from various localities.

that it belongs to *H. crassum*. The argument is based to the comparison of the Ptolemais Mc_{III} (especially to its length) with other material. However, the length of Mc_{III} (228 mm) in their diagram was estimated from the illustrations of KOUFOS (1982: pl. 3) and not taken from the table 1 of KOUFOS (1982), which states the accurate dimensions. This gives a wrong idea about the length of the Mc_{III} and its comparison with the other samples. Using the real length of the Mc_{III} (195 mm) given in the article (KOUFOS, 1982: tab. 1), the comparison shows that the length of the Ptolemais Mc_{III} is similar to *H. crassum* from Perpignan, as it is clear in KOUFOS (1982: fig. 2). The other arguments referred by EISENMANN & SONDAAR (1989) also concern the size and are probably based on a single specimen from Ptolemais, which provides no insight in the ranges of variation of the different dimensions.

Another Ruscinian hipparion known from Greece is *Hipparion longipes*, referred from the locality of Megalo Emvolon, near Thessaloniki (ARAMBOURG & PIVETEAU, 1929; EISENMANN & SONDAAR, 1989). It is a very large hipparion whose size is clearly larger than the Silata material. A form similar to *H. longipes* was found in the Turolian (~ 7.1 Ma) locality of Akkashdagi in Turkey (KOUFOS & VLACHOU, 2005). The dimensions of astragalus and second phalanx (Figs 6, 7) indicate that it is larger and different than the Silata form.

In conclusion, the hipparion sample of Silata belongs to a medium-sized hipparion, which is closed to *H. mediterraneum*. The limited and fragmentary material does not allow certain comparisons and results and for this reason it is attributed as *Hipparion* cf. *H. mediterraneum*.

Family Rhinocerotidae OWEN, 1845

Rhinocerotidae indet.

Among the collected material from Silata there are several dental fragments of rhinocerotids which cannot be determined. They only indicate the presence of rhinos in this locality.

Order Artiodactyla OWEN, 1848

Family Suidae GRAY, 1926

Genus *Microstonyx* PILGRIM, 1926

Microstonyx major (GERVAIS, 1848-52)

(Plate 2, fig. 10)

Material: Isolated M_2 dex, SLT-17.

Measurements: 27.7 x 19.0 mm

Description: The M_2 is relatively elongated and narrow with the anterior lobe wider than the posterior one. It has four main cuspids. In the middle of the mesial edge it preserves a small secondary cuspid. The mesial cingulum is well developed. A large secondary cuspid is developed in the middle of the valley between the two lobes of the tooth. The talonid is large and preserves a large cuspid (hypoconulid) situated in its center.

Discussion: The morphological characters of the studied M_2 are similar to those of *Microstonyx major* from the various European localities (GINSBURG, 1988; VAN DER MADE & MOYA-SOLA, 1989; KOSTOPOULOS, 1994; BONIS &

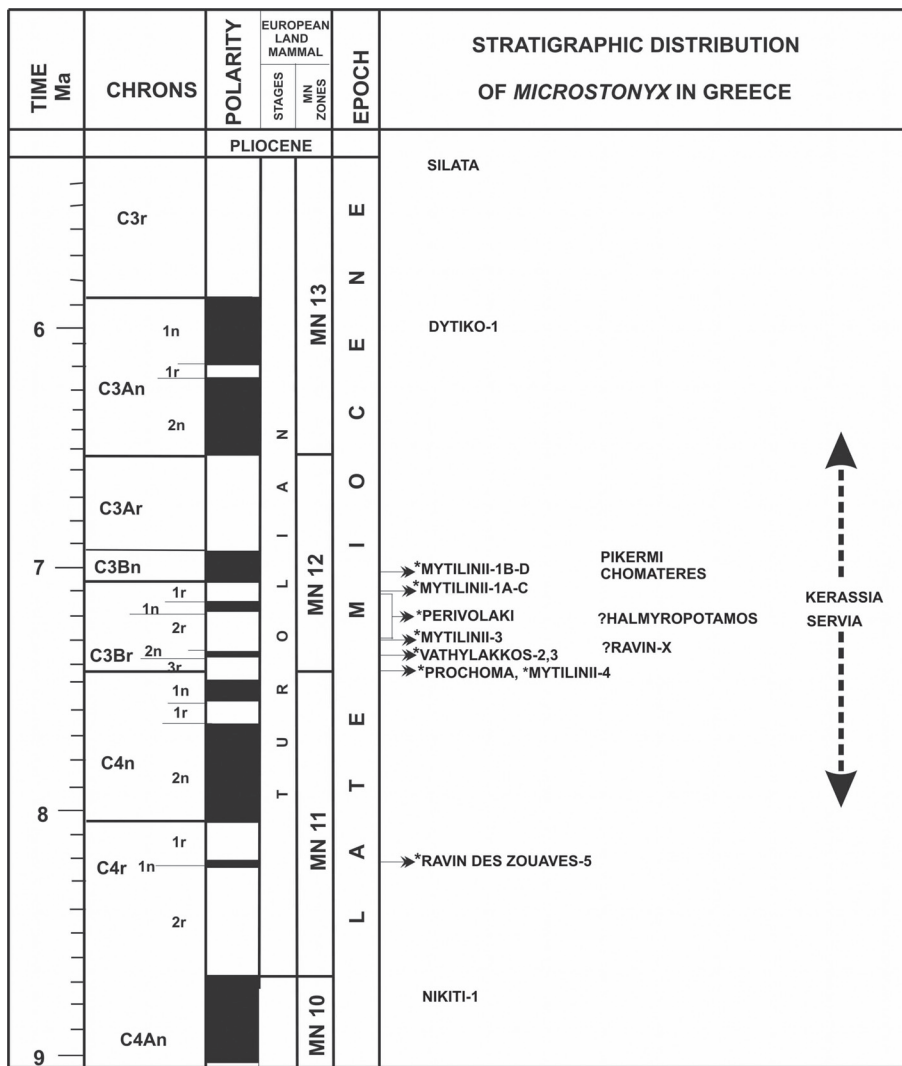


Figure 9: Chronology and biostratigraphy of the *Microstonyx* bearing mammal localities of Greece. Stars indicate the localities having GPTS age. The vertical dot line indicates the range for the age of the corresponding localities.

erymanthius and including the samples of Pikermi and Samos (Greece), Kalimantsi (Bulgaria), and probably Titov Veles (F.Y.R.O.M.);

- a large-sized group corresponding to *M. major major* and including the Dytiko (Greece), as well as the Petreluk and Ezerovo (Bulgaria) samples (KOSTOPOULOS et al., 2001).

The Silata M_2 belongs to the small-sized group, which could represent a separate taxon (KOSTOPOULOS et al., 2001). According to the latter authors the small-sized form of *M. major* disappeared during middle Turolian, while in the late Turolian the species was living under more humid conditions and adapted to them with an increase to its size. Recent results about

BOUVRAIN, 1996; KOSTOPOULOS et al., 2001; SYLVESTROU & KOSTOPOULOS, 2006). The dimensions of SLT-17 are in the ranges of variation for *M. major* (fig. 8). It is closer to the Perivolaki and Ravin des Zouaves-5 material, while it is smaller than the m_2 from Pikermi and Dytiko (Greece), Kalimantsi (Bulgaria) and Luberon (France) sample. The species *Korynochoerus palaeochoerus* has been described from the locality of Maramena (Serres basin, Macedonia, Greece), which is isochronous to Silata. The larger size of the studied M_2 distinguishes it clearly from *K. palaeochoerus* (Fig. 8). Another species of *Microstonyx* is *M. antiquus* which differs from the studied M_2 by its larger size. The morphological characters of m_2 in all these taxa are similar but the dimensions of SLT-17 suggest similarities to *M. major*. The genus *Propotamochoerus* is also referred from the Turolian localities of Greece. It is known from the locality Ravin des Zouaves-5 of Axios valley, Macedonia, Greece (BONIS & BOUVRAIN, 1996); its smaller size distinguishes it from the studied M_2 (Fig. 8). Three groups of *M. major* have been recognized recently, in the Balkans at least:

- a small-sized group including the material from the Greek localities of Vathylakkos-2, Prochoma, Kerassia and Perivolaki;
- a medium-sized group corresponding to *M. major*

the palaeoenvironmental conditions of the late Turolian suggest a patchy environment with more water spots in a wider open landscape (KOUFOS, in press). Taking in mind that Silata is dated to the end of late Turolian it is quite possible that the small-sized form of *M. major* survived during that period living in the open areas, while a large-sized form was developed and lived in the more closed and humid habitats around the water spots.

M. major is well-known in Greece during the entire Turolian. Its first occurrence is in the locality Nikiti-1 (Chalkidiki, N. Greece) dated to latest Vallesian with an age between 9.3- 8.7 Ma (KOUFOS, 2003; 2006). *Microstonyx* is the commonest suid of the Turolian, present in the majority of the known Greek localities (Fig. 9) and disappeared at the end of Miocene.

Family Giraffidae GRAY, 1821

***Helladotherium* sp. or *Samotherium* sp.**
(Plate 2, fig. 11)

Material: Distal part of Mc_{3+4} , SLT-11.

Measurements: The measurements are given in Tab. 4.

Description: The available material is the distal part of a metacarpal which preserves the internal distal condyle.

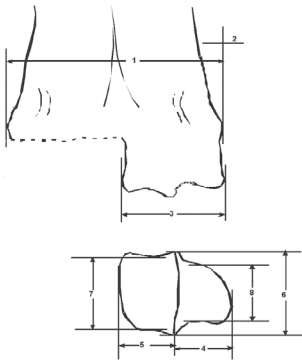
	Measurements	<i>Helladotherium duvernoyi</i>				
		SLT-11	PIK-1972/9	PIK-1972/11	PER-116	PER-1182
	1	91	100	105	92	91,2
	2	46,8	60	58	52,7	50,2
	3	43,7	50	49	45,5	46,1
	4	25,5	27	29	26,2	26,6
	5	21	24	21	21,1	20,3
	6	56	61	60	60,7	61,3
	7	48,4	58	56	52,8	51,9
	8	40,5	49	46	44,7	45

Table 4: Measurements of the Mc₃₊₄ of the Silata giraffid.

The preserved part of the diaphysis is relatively flat and has a shallow anterior channel across its length which is weak in the distal end, suggesting that it is metacarpal. In the metatarsals of the giraffids the channel is deep across the whole bone and in the distal part it is not weak as in the metacarpals. Based on a direct comparison with the Mc₃₊₄ of *Helladotherium* the preserved condyle seems to be the internal one, which would make SLT-11 part of a right metacarpal

Discussion: The late Miocene giraffids of Greece belong to the following taxa: *Palaeotragus*, *Samotherium*, *Helladotherium*, *Bohlinia* and *Palaeogiraffa*. The early Ruscinian faunas of large mammals in Eastern Mediterranean are almost unknown. The sole known locality of Çalta (Turkey), dated to MN 15, includes *Giraffa* cf. *jumae* (GERAADS, 1998). There is one metacarpal whose distal part is badly preserved but it seems to be slenderer than that from Silata. *Palaeogiraffa* is a Vallesian taxon known from dental remains only. As the age of Silata is latest Miocene seems to be impossible to have this taxon in its fauna. *Palaeotragus* is a relatively small-sized giraffid (GERAADS, 1978; KOSTOPOULOS et al., 1996; KOSTOPOULOS & KOUFOS, 2006) and it is clearly distinguished from the studied one by its size. *Bohlinia* is a giraffid with elongated and slender metapodials, known from various late Miocene localities (GERAADS, 1979; KOSTOPOULOS et al., 1996). It differs from SLT-11 because its distal part is narrower. The other two late Miocene giraffids *Samotherium* and *Helladotherium* are known from latest Vallesian and Turolian of Greece (KOUFOS, 2003). The main differences in their bones are related with their proportion. The metacarpals of *Helladotherium* are wider having more robust appearance. On the other hand, the metacarpals of *Samotherium* are narrower and slenderer than those of *Helladotherium*. The SLT-11 preserves a small part of its diaphysis near the distal end and it is difficult to see its proportions. Moreover, the distal articular facet is broken and thus it provides no information about its robustness. A direct comparison with some metapodials of *Helladotherium* from the middle Turolian (MN 12) locality of Perivolaki (KOSTOPOULOS & KOUFOS, 2006) suggests that the SLT-11 has somewhat smaller dimensions. In comparison to *Samotherium* metacarpals, SLT-11 seems to be slightly larger or very close to its maximum values. So, SLT-11 could belong to either *Helladotherium* or *Samotherium*.

Family Bovidae GRAY, 1821

Bovidae indet.
(Plate 2, figs. 12, 13)

Material: M³ sin, SLT-8; M₃ sin, SLT-31.

Measurements: M³ = 13.6 x 11.0, M₃ = (17) x 8.6

Description: The M³ is unworn and relatively hypsodont. The talonid of M₃ is broken distally and it seems hypsodont too. The available material is too limited for a certain determination even at the generic level and thus it is referred to as Bovidae indet.

5. Biochronology-Palaeoecology

The large mammal fauna of Silata is poor with fragmentary material, allowing limited attributions. The determined material of the large mammals includes the following taxa: Hyaenidae indet., *Paramachaerodus orientalis*, *Hipparion* cf. *mediterraneum*, Rhinocerotidae indet., *Microstonyx major*, *Helladotherium* sp. or *Samotherium* sp., and Bovidae indet. Such a fauna cannot provide strong evidences for the age of the locality. However, it is useful to check if it is possible to get some age information from this fauna.

In Greece *Paramachaerodus orientalis*, is only referred from Pikermi (NOW 2006). The Pikermi collection is old and the biochronological data are doubtful because of probable mixing of the material. Thus there are different opinions about its age. An age at the end of middle Turolian (MN 12) is suggested by several authors (DE BRUIJN et al., 1992; BONIS & KOUFOS, 1999; KOUFOS, 2003, 2006). However, BERNOR et al. (1996) refers Pikermi to the early Turolian MN 11 and based on this STEININGER et al. (1996) suggest that Pikermi belongs to MN 11/12. If Pikermi has an early Turolian age then almost all late Miocene localities of Greece must be older, Vallesian or earliest Turolian. But such a chronology is not supported by the faunal data. The Pikermi fauna is more evolved than the early Turolian fauna of Vathylakkos in Axios Valley which are dated biochronologically to the base of MN 12 and magnetostratigraphically to ~7.5 Ma (KOUFOS, 2003, 2006). Moreover, the fauna from the new locality of Perivolaki, dated to 7.1-7.3 Ma (KOUFOS et al., 2006), is

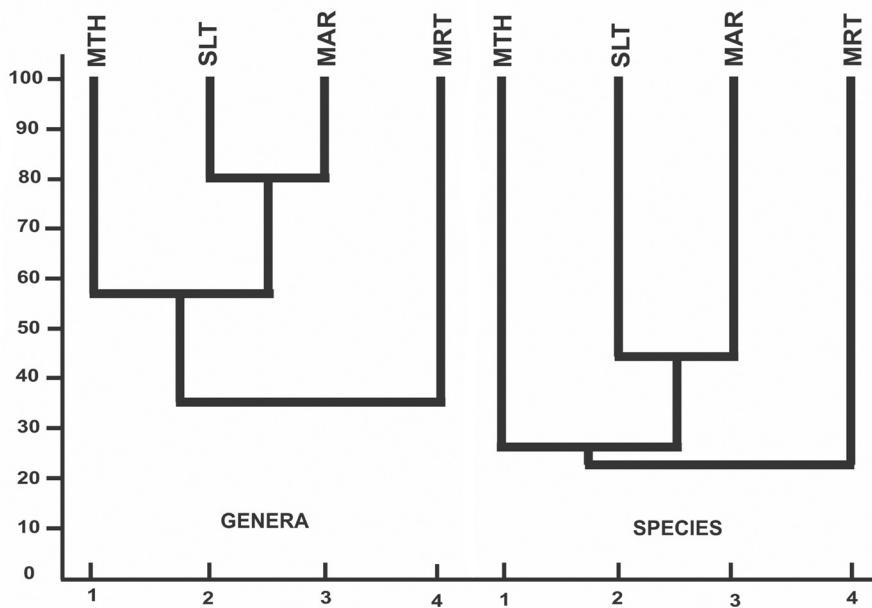


Figure 10: Cluster analysis at generic and specific level for the faunas of Silata (SLT), Maramena (MAR), Ano Metochi (MTH) and Maritses (MRT). The faunal data are taken from KOUFOS (2006). The program PAST is used for the analysis (HAMMER, 2006).

2004). Taking into account all the available data from the large mammals an age from middle Turolian (MN 12) to late Turolian (MN 13) can be supported for the Silata fauna.

In contrast to the poor large mammal fauna there is a quite rich micromammalian fauna

more primitive than that of Pikermi. Similarly the Samos MYT fauna is older than Pikermi and it is dated to ~7.3 Ma (KOSTOPOULOS et al., 2003). On the other hand the hipparions from the localities MTL and Q4 of Samos dated to ~7.1 Ma (KOSTOPOULOS et al., 2003) are very similar to Pikermi ones. The Pikermi fauna is more primitive than the Dytiko fauna of Axios Valley dated to MN 13 (KOUFOS, 2003, 2006). Thus, an age at the end of MN 12 is the most likely for Pikermi. The species *Paramachaerodus orientalis* is known from several Eurasian localities from Spain to Ukraine and Iran with a wide stratigraphic distribution from late Vallesian (MN 10) to late Turolian (MN 13), (NOW 2006). *Microstonyx major* is also a widespread taxon known from Iberian Peninsula to China with a great stratigraphic distribution from early Vallesian to late Turolian (MN 9-13), (NOW 2006). In Greece it is known from several localities dated from the end of late Vallesian (MN 10) to late Turolian (MN 13), (Fig. 9) and disappeared at the end of Miocene (KOUFOS, 2003). Thus, *Microstonyx* is mainly known from the Turolian of Greece and can suggest a similar age for the Silata fauna. The giraffids *Helladotherium* and *Samotherium* both appeared in Eastern Mediterranean at the beginning of Turolian and disappeared at the end of Miocene (KOUFOS, 2003). Their presence in the Silata fauna suggests a Turolian age too. The Silata hipparion has close similarities to *H. mediterraneum*. In Greece *H. mediterraneum* is known from Pikermi, dated to the end of middle Turolian (MN 12) and from Dytiko localities of Axios valley, dated to late Turolian (MN 13), (KOUFOS, 2003, 2006). A form similar to *H. mediterraneum*, referred as *H. cf. mediterraneum*, is known from the locality of Perivolaki (Thessaly), dated to middle Turolian (MN 12) or to 7.3-7.1 Ma by magnetostratigraphy (VLACHOU & KOUFOS, 2004, 2006; KOUFOS et al., 2006). A similar hipparion form is also found in the Samos localities of Mytilinii-1, 4, dated to middle Turolian (MN 12) or magnetostratigraphically to ~7.1 Ma and ~7.4 Ma respectively (KOSTOPOULOS et al., 2003; KOUFOS et al.,

from Silata, including the following taxa: *Vespertilionidae* sp.1, *Vespertilionidae* sp.2, *Erinaceus* sp., *Amblycoptus* cf. *jessiae*, *Asoriculus gibberodon*, *Deinsdorfia kerkhoffi*, *Occitanomys brailloni*, *Apodemus dominans*, *Apodemus gorafensis*, *Micromys* cf. *paricioi*, *Mesocricetus primitivus*, *Pliopetaurista dehneli*, *Spermophilinus* cf. *turolensis*, *Myomimus maritsensis*, *Pliospalax* cf. *macovei*, Leporidae indet., and *Prolagus michauxi* (VASSILEIADOU et al., 2003).

The micromammalian fauna of Silata provides more and more certain biochronological data for a better age determination. Several taxa of the Silata micromammals are also known from the locality of Maramena (Serres basin, Greece). The fauna of Maramena is quite rich, including large and small mammals and it is dated to the end of Miocene, MN 13/14 (SCHMIDT-KITTLER et al., 1995). Two new taxa, *Deinsdorfia kerkhoffi* and *Amblycoptus jessiae*, are originally described from Maramena (DOUKAS et al., 1995). The first taxon and a form similar to the second one are also present in the Silata fauna, suggesting age similarities. Furthermore, the Silata form of *Asoriculus gibberodon* and *Pliopetaurista dehneli* are very similar to those from Maramena (VASSILEIADOU et al., 2003), also indicating age similarities between the two faunas. Moreover, the majority of the taxa found in Silata is also present in the Maramena fauna (Tab. 5) indicating a high similarity. The similarity index of Simpson at generic and specific level for the faunas of Silata (SLT), Maramena (MAR) and two other Greek faunas, Ano Metochi (MTH) and Maritses (MRT) is given in the dendrograms of Fig. 10. The Ano Metochi locality is situated in Serres basin, near that of Maramena and it is dated to late Turolian MN 13 (DE BRUIJN et al., 1992; KOUFOS, 2006). The other locality, Maritses is situated in Rhodes island and it is dated to early Ruscinian, MN 14 (VAN DER MEULEN & VAN KOLFSCHOTEN, 1986; KOUFOS, 2006). The dendrograms of Fig. 10 demonstrates clearly that the Silata and Maramena faunas match together at specific and generic level, indicat-

GENUS	SPECIES	MAR	SLT	MRT	MTH	GENUS	SPECIES	MAR	SLT	MRT	MTH
<i>Alilepus</i>	<i>turolensis</i>	+	—	—	—	<i>Miopetaurista</i>	<i>thaleri</i>	+	—	—	—
<i>Allocricetus</i>	cf. <i>ehiki</i>	+	—	—	—	<i>Muscardinus</i>	cf. <i>plioacaenicus</i>	+	—	—	—
<i>Amblycoptus</i>	<i>jessiae</i>	+	cf.	—	—	<i>Myomimus</i>	<i>dehmi</i>	+	—	—	—
<i>Apodemus</i>	<i>gorafensis</i>	+	+	—	—	<i>Myomimus</i>	<i>maritsensis</i>	+	+	+	+
<i>Apodemus</i>	<i>dominans</i>	cf.	+	cf.	+	<i>Norbertia</i>	<i>hellenica</i>	+	—	—	—
<i>Apodemus</i>	<i>gudrunae</i>	—	—	—	+	<i>Occitanomys</i>	<i>neutrum</i>	+	—	—	—
<i>Asoriculus</i>	<i>gibberodon</i>	+	+	—	—	<i>Occitanomys</i>	<i>brailloni</i>	—	+	—	—
<i>Atlantoxerus</i>	<i>rhodius</i>	—	—	+	—	<i>Occitanomys</i>	<i>adroveri</i>	—	—	—	+
<i>Boselaphini</i>	indet.	+	—	—	—	<i>Ouzocerus</i>	aff. <i>gracilis</i>	+	—	—	—
<i>Bovidae</i>	indet.	—	+	—	—	<i>Paraethomys</i>	<i>anomalus</i>	—	—	+	—
<i>Calomyscus</i>	<i>minor</i>	—	—	+	—	<i>Paramachae-</i> <i>rodus</i>	<i>orientalis</i>	—	+	—	—
<i>Castillomys</i>	sp.	—	—	sp.	—	<i>Pelomys</i>	<i>europaeus</i>	—	—	+	—
<i>Castoridae</i>	indet.	+	—	—	—	<i>Petenya</i>	<i>hungarica</i>	+	—	—	—
<i>Chasmaporthetes</i>	sp.	+	—	—	—	<i>Pliocervus</i>	<i>graecus</i>	+	—	—	—
<i>Chiroptera</i>	indet.	+	—	—	—	<i>Pliopetaurista</i>	<i>dehneli</i>	+	+	—	—
<i>Choerolophodon</i>	<i>pentelici</i>	+	—	—	—	<i>Pliospalax</i>	<i>macovei</i>	—	cf.	—	+
<i>Cricetus</i>	<i>lophidens</i>	—	—	+	—	<i>Pliospalax</i>	<i>rhodius</i>	—	—	+	—
„ <i>Cricetus</i> “	sp.	—	—	—	+	<i>Pliospalax</i>	sp.	—	—	—	+
<i>Deinsdorfia</i>	<i>kerkhoffi</i>	+	+	—	—	<i>Prolagus</i>	cf. <i>sobrini</i>	+	—	—	—
<i>Desmanella</i>	<i>dubia</i>	+	—	—	—	<i>Prolagus</i>	<i>michauxi</i>	—	+	—	+
<i>Eliomys</i>	<i>intermedius</i>	—	—	cf.	—	<i>Promeles</i>	<i>macedonicus</i>	+	—	—	—
<i>Erinaceus</i>	<i>samsonowiczi</i>	+	sp.	—	—	<i>Promephitis</i>	sp.	+	—	—	—
<i>Gazella</i>	sp.	+	—	—	+	<i>Prostrepsiceros</i>	<i>woodwardi</i>	—	—	—	+
<i>Glis</i>	cf. <i>minor</i>	+	—	—	—	<i>Pseudomeriones</i>	<i>rhodius</i>	—	—	+	+
<i>Helladotherium</i>	cf. <i>duvernoyi</i>	—	—	—	+	<i>Rhagapodemus</i>	<i>primaevus</i>	+	—	—	—
<i>Hipparion</i>	sp. (large)	+	—	—	—	<i>Rhagapodemus</i>	<i>vanderweardi</i>	—	—	+	—
<i>Hipparion</i>	sp. (medium)	—	+	—	+	<i>Rhagapodemus</i>	<i>hautimagnensis</i>	—	—	—	+
<i>Hipparion</i>	sp. (small)	+	—	—	—	<i>Rhinocerotidae</i>	indet.	—	+	—	—
<i>Hyaenidae</i>	indet.	—	+	—	—	<i>Ruemkelia</i>	<i>dekkersi</i>	+	—	—	—
<i>Hypsochricetus</i>	<i>strimonis</i>	+	—	—	—	<i>Samotherium</i>	<i>boissieri</i>	cf.	?	—	—
<i>Keramidomys</i>	<i>carpathicus</i>	cf.	—	+	—	<i>Schizogalerix</i>	<i>macedonica</i>	+	—	—	—
<i>Korynochoerus</i>	<i>palaeochoerus</i>	+	—	—	—	<i>Sorex</i>	sp.	+	—	—	—
<i>Kowalskia</i>	<i>browni</i>	+	—	—	—	<i>Spemophilinus</i>	<i>giganteus</i>	—	—	+	—
<i>Kowalskia</i>	sp.	+	—	—	—	<i>Spermophilinus</i>	<i>turolensis</i>	+	cf.	—	—
<i>Leptodontomys</i>	<i>catalaunicus</i>	+	—	—	—	<i>Talpa</i>	<i>fossilis</i>	+	—	—	—
<i>Lutra</i>	<i>affinis</i>	+	—	—	—	<i>Tamias</i>	<i>atsali</i>	+	—	—	—
<i>Martes</i>	<i>lefkonensis</i>	+	—	—	—	<i>Tamias</i>	sp.	—	—	—	+
<i>Mesocricetus</i>	<i>primitivus</i>	—	+	+	—	<i>Tragoportax</i>	<i>gaudryi</i>	+	—	—	—
<i>Mesopithecus</i>	<i>pentelicus</i>	+	—	—	—	<i>Tragoportax</i>	cf. <i>amalthea</i>	+	—	—	—
<i>Micromys</i>	<i>paricioi</i>	—	cf.	—	—	<i>Urotrichus</i>	sp.	+	—	—	—
<i>Micromys</i>	<i>cingulatus</i>	+	—	—	—	<i>Vespertilionidae</i>	sp.1	—	+	—	—
<i>Micromys</i>	<i>bendai</i>	—	—	—	+	<i>Vespertilionidae</i>	sp.2	—	+	—	—
<i>Microstonyx</i>	<i>major</i>	+	+	—	—	<i>Viverridae</i>	indet.	+	—	—	—

Table 5: Faunal list of some late Turolian (MN13) and early Ruscinian (MN 14) mammal localities of Greece. SLT = Silata, MAR = Maramena, MTH = Ano Metochi, MRT = Maritses. The faunal data are taken from KOUFOS (2006).

ing their high faunal similarity. The Silata and Maramena faunas are clustered together with the Late Miocene Ano Metochi fauna at specific and generic level, indicating that their faunal character is closer to Miocene than Pliocene. The early Rucinian (early Pliocene) fauna of Maritses is separated from the other three ones in both diagrams, suggesting less faunal similarity with them (Fig. 10). The analysis of the biostratigraphical range of the micromammals found in the Silata fauna suggests an age at the end

of Miocene similar to that of Maramena (VASSILEIDADOU et al., 2003). The data from the study of the entire Silata fauna allow its dating to the end of Miocene. Both Silata and Maramena fauna have more Miocene faunal character but they also include some Pliocene elements, like *Amblycoptus jessiae*, *Asoriculus gibberodon*, *Micromys paricioi*, *Mesocricetus primitivus*. This is normal because at the end of Miocene some Pliocene taxa already made their appearance.

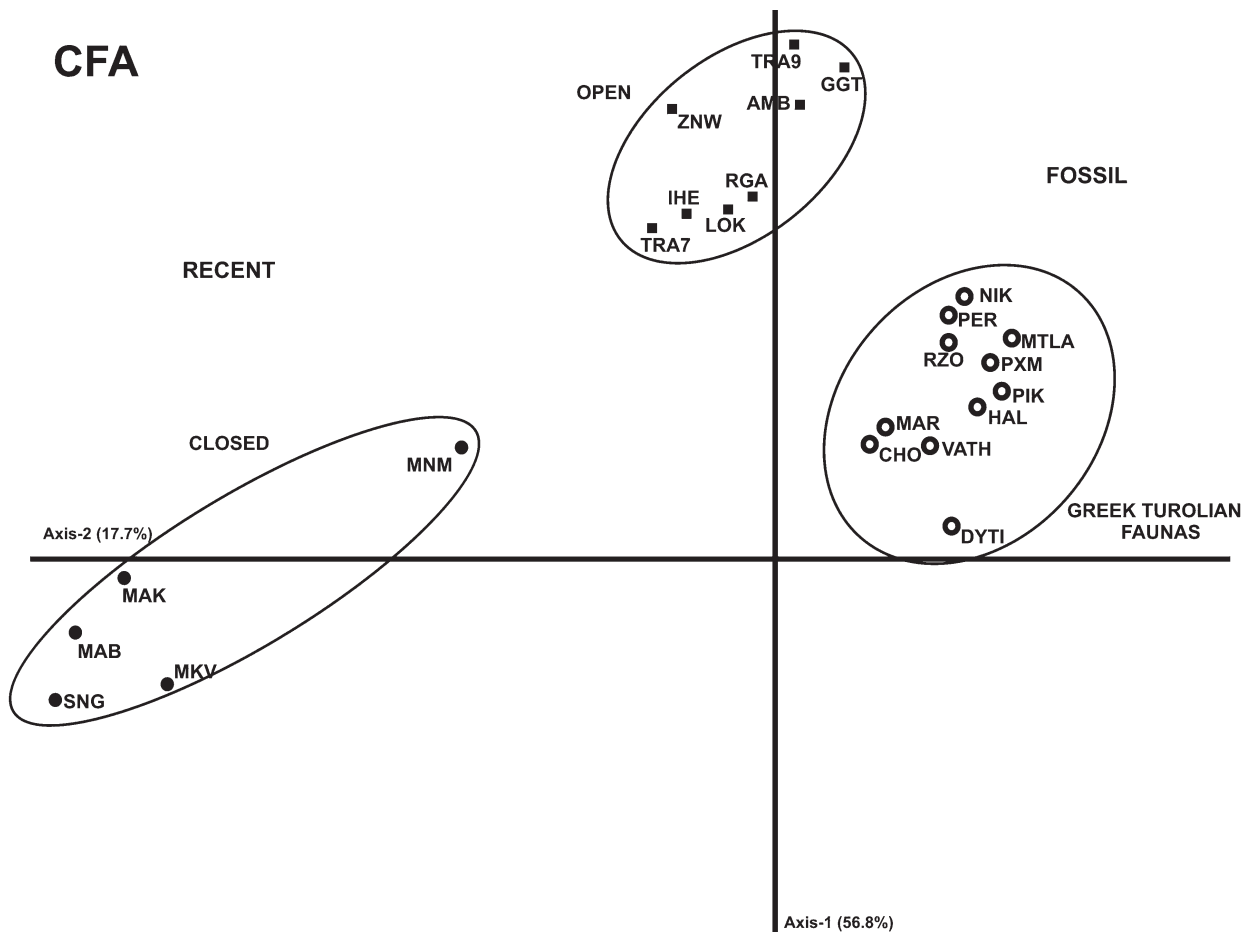


Figure 11: Correspondence Factor Analysis of the modern faunas from certain environments and the Greek Turolian faunas, based on the number of macromammalian species per family. The program PAST is used for the analysis (HAMMER, 2006). Recent Faunas (data from LEGENDRE, 1989). Closed: MAB = La Maboke; MAK = Makokou; MKV = Mont Kiwu; MNM = Mont Nimba; SNG = Sangmellina. Open: AMB = Amboseli; GGT = Golden Gate; IHE = Ihema; LOK = Lokori; RGA = Region Gabiro; TRA7 = Transvaal-7; TRA9 = Transvaal-9; ZNW = Zinawe. Greek fossil faunas (data from KOUFOS, 2006). NIK = Nikiti-2; RZO = Ravin des Zouaves-5; VATH = Vathylakkos-1, 2, 3; PXM = Prochoma-1; MLN = Mytilinii-4; MYT = Mytilinii-3; PER = Perivolaki; MTLA = Mytilinii-1A; HAL = Halmyropotamos; CHO = Chomateres; PIK = Pikermi; DYTI = Dytiko-1, 2, 3; MAR = Maramena.

Concerning the palaeoecology of the Silata locality, the few and fragmentary large mammals cannot provide certain data. In contrast, the rich micromammalian fauna can give more and better data about the palaeoenvironmental conditions. The analysis of the environmental preferences of the Silata micromammals suggests that 34% of the taxa can live in variable ecological conditions, 47% in open and dry landscape and 19% in forested environment (VASSILEIADOU et al., 2003). The great abundance of the taxa living in open and dry conditions suggests that this type of environment must have been dominant in the area. This hypothesis is also supported by the presence of the girafid *Samotherium* or *Helladotherium* in the Silata fauna. Both genera characterise the open and dry environments of Turolian in Eastern Mediterranean (BONIS et al., 1992; KOUFOS, 2006). Moreover, the characters of the hipparion's teeth from Silata (high hypsodonty, low enamel plication with shallow plis) indicate forms living in relatively open areas (KOUFOS, 1990). On the other hand, the presence of a relatively high abundance of taxa (including glirids, petauristids, eomyids and soricids), living in wet-forested conditions, suggests the presence of a more closed palaeoenvironment.

The desmanine moles and shrews *Amblycoptus*, *Asoriculus*, and *Deinsdorfia* usually characterise forest conditions or swamps or open water (DOUKAS et al., 1995). Especially *Amblycoptus*, which is eating molluscs, needs feeding points with water. The wet-conditions of Silata are also supported by the presence of gastropod operculi and lignitic traces in the sediments (VASSILEIADOU et al., 2003). As it was referred in the introduction, the majority of the micromammals was collected from a grey-green bed with lignitic remains. Thus, Silata must correspond to a water-point (swamp, open water, small lake) in a wider open landscape. Around the water-point the conditions were closed with dense vegetation and trees which allowed the presence of wet and forest taxa. The wider open and dry area was a fruitful environment for the majority of the fauna (open – dry micromammals, giraffids, hipparions, bovids). The remains of the large mammals either were carried in the water-point by the floods during the rain period or were killed on the spot by the carnivores when they were going for water. So, the locality includes representatives of both open-dry and wet-closed taxa. The palaeoecological conditions of the isochronous Maramena

locality are similar representing a water-point in a wider open area (SCHMIDT-KITTLER et al., 1995), which is in line with the observed faunal similarity.

The palaeocological analysis of the Greek Late Miocene faunas suggests that the environment was open and dry. During the Turolian the conditions were more open and dry than in the Vallesian but at the end of Turolian there are indications for more wet conditions, traced in the localities of Pikermi (Attica, Greece) and Dytiko in Axios valley, Macedonia, Greece (BONIS et al., 1992, 1999; KOUFOS, 2004, 2006, in press). Recently the Greek Turolian mammal faunas were analyzed in comparison with modern ones from certain environments KOUFOS (in press). The Correspondence Factor Analysis (CFA) of the Greek Turolian faunas (Fig. 11) indicates that all of them cluster together, forming a group that can be correlated to the modern open faunas. This suggests that during the Turolian the palaeoenvironment was open in the area. The Silata fauna is not included in this analysis because the few large mammals cannot allow a certain comparison. However, the isochronous fauna of Maramena is included in the group of the Greek Turolian faunas and corresponds to an open landscape. On the other hand, the Maramena fauna includes several faunal and sedimentological characters, indicating also a wet-closed environment (SCHMIDT-KITTLER et al., 1995), like that of Silata. The analysis of the Miocene ruminant's association in the various European regions suggests an open palaeoenvironment for Eastern Mediterranean region. But, during the Late Turolian there are evidences of more wet conditions because of the presence of cervids and tragulids, the decrease of the hypsodonty and the decrease of the body weight of ruminant (RÖSSNER & KOUFOS 2004, in press). We can, thus, conclude that during late Turolian the palaeoenvironment was patchy in Greece. In a wider open landscape there are several water spots (lakes, swamps, open waters), which allow the development of a more closed habitat around them and which harboured the wet-forest mammalian taxa, while in the wider open landscape there are several bovids, giraffids, rhinos (*Ceratotherium*) as well as, open-dry hipparions and micromammals (KOUFOS, in press). The localities of Silata and Maramena represent such water spots with their fauna including both open and closed elements. The palaeoenvironment was gradually changed to the more closed and wet conditions of early Pliocene.

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PLATE 1

Fig. 1 Hyaenidae indet., Silata, Macedonia, Greece, latest Turolian.

Anterior part of the upper carnassial, SLT-16; a. occlusal, and b. labial view.

Fig. 2 *Paramachaerodus orientalis.*, Silata, Macedonia, Greece, latest Turolian.

Right upper canine, SLT-15; a. labial, and b. lingual view.

Hipparion cf. *H. mediterraneum*, Silata, Macedonia, Greece, latest Turolian

Fig. 3 I³ dex, SLT-19.

Fig. 4 I³ dex, SLT-18.

Fig. 5 i₃ dex, SLT-30.

Fig. 6 P²dex, SLT-5.

Fig. 7 M³dex, SLT-20.

Fig. 8 P^{3,4}sin, SLT-26.

Fig. 9 p_{3,4}, SLT-2.

Fig. 10 p_{3,4}, SLT-13.

Fig. 11 p_{3,4}, SLT-13.

Fig. 12 m_{1,2}, SLT-3.

Fig. 13 p_{3,4}, SLT-25.

Fig. 14 dp₄ dex, SLT-4.

Fig. 15 dp_{3,4} dex, SLT-21.

PLATE 1

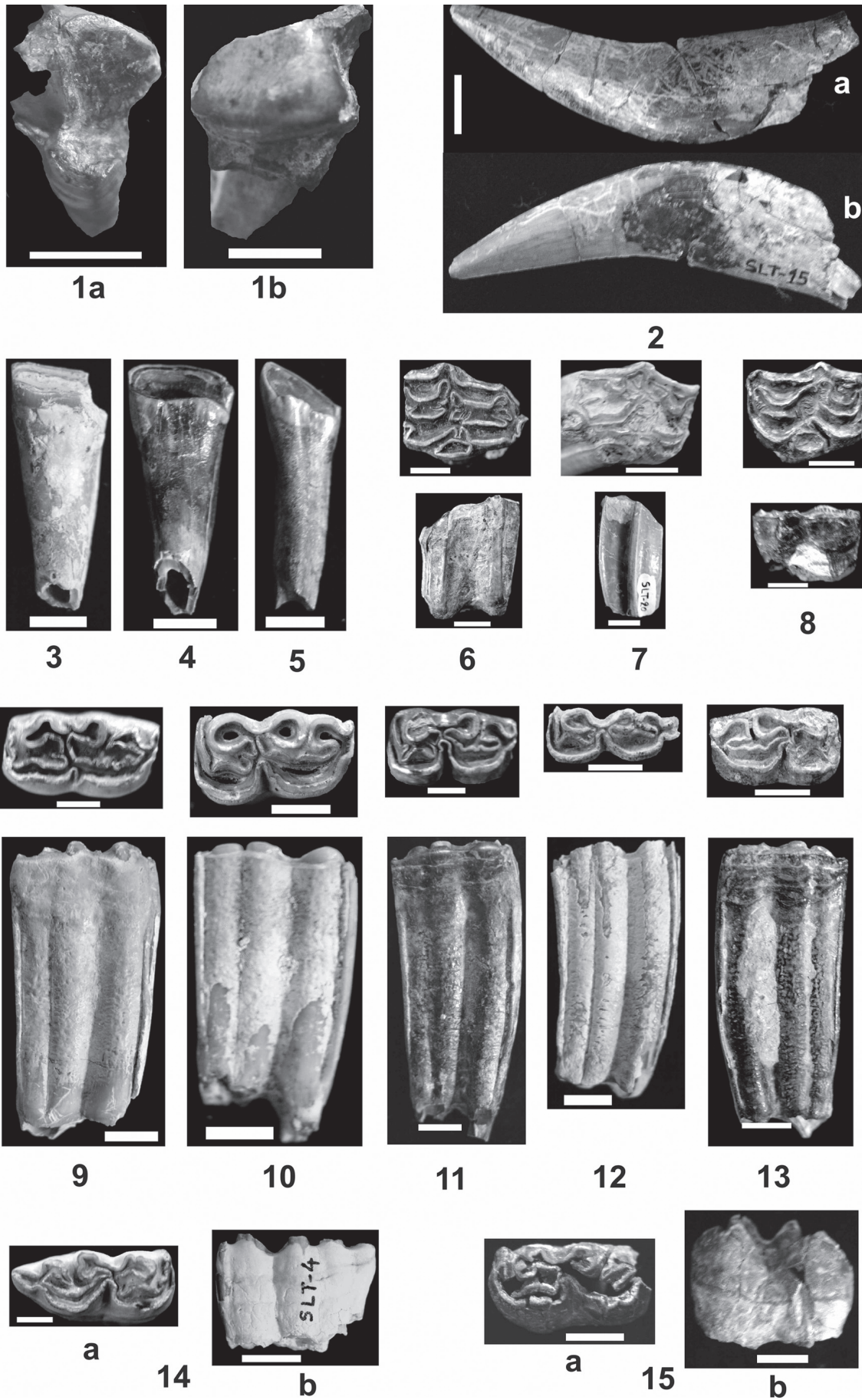


PLATE 2***Hipparion* cf. *H. mediterraneum*, Silata, Macedonia, Greece, latest Turolian**

- Fig. 1 Distal part of humerus, SLT-12; a. anterior, b. posterior view.
- Fig. 2 Calcaneum, SLT-29; a. posterior, b. anterior view.
- Fig. 3 Astragalus, SLT-7.
- Fig. 4 Lateral first phalanx, SLT-23, internal view.
- Fig. 5 Lateral first phalanx, SLT-22, internal view.
- Fig. 6 Part of os magnum, SLT-9.
- Fig. 7 Os carpi ulnare (pyramidal), SLT-6.
- Fig. 8 Os tarsale naviculare, SLT-14.
- Fig. 9 Second phalanx, SLT-28.
- Fig. 10 *Microstonyx major*, Silata, Macedonia, Greece, latest Turolian. m₂ dex, SLT-27; a. labial, b. lingual, and c. occlusal view.
- Fig. 11 *Helladotherium* sp. or *Samotherium* sp., Silata, Macedonia, Greece, latest Turolian. Distal part of Mc₃₊₄, SLT-11; a. anterior, and b. posterior view.
- Fig. 12 Bovidae indet., Silata, Macedonia, Greece, latest Turolian. M³ sin, SLT-8; a. occlusal, b. lingual, and c. labial view.
- Fig. 13 Bovidae indet., Silata, Macedonia, Greece, latest Turolian. m₃ sin, SLT-31; a. occlusal, b. labial, and c. lingual view.

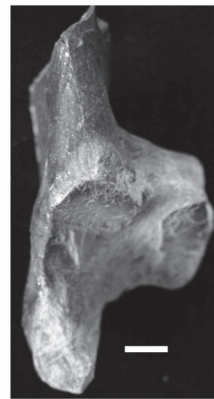
PLATE 2



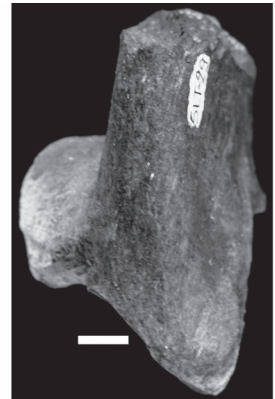
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1b



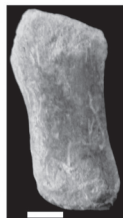
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2b



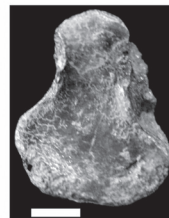
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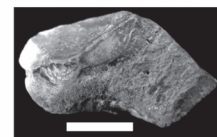
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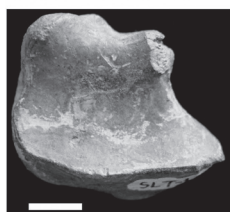
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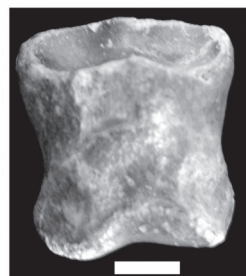
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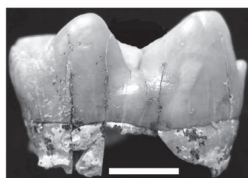
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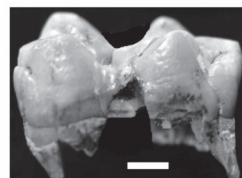
11a



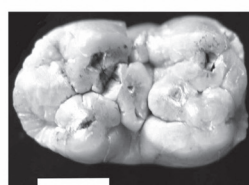
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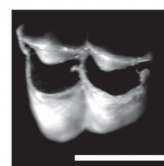
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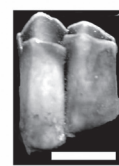
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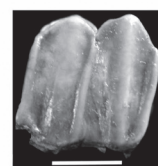
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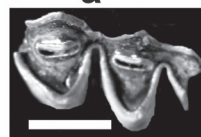


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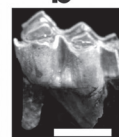


c

12



a



b



c

13

