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Suoids (Mammalia, Artiodactyla) from the Early/Middle Miocene locality of Antonios, Macedonia, Greece

With 11 Text-figures and 3 Tables

George D. Koufos

Abstract

The Antonios locality is situated in Chalkidiki Peninsula (Macedonia, Greece) about 30 km east of Thessaloniki city. Its fauna includes both micro- and macro-mammals. The suoids of the fauna include two taxa, *Sanitherium schlagintweiti* and *Bunolistriodon lockharti*. The sanithere is morphologically similar to that from Pakistan, Leoben (Austria) and Chios island (Greece) and smaller than all of them. *B. lockharti* is also similar to that from Western Europe and different from *B. meidamon* known from Turkey. The age of the Antonios fauna is estimated at the beginning of late Orleanian ELMA or at the beginning of the European mammal biozone MN 5. This age was also proposed from the earlier study of the micromammals.

Key words: Suoidea, *Sanitherium*, *Bunolistriodon*, early/middle Miocene, Greece, systematics, biochronology.

Introduction

The Early-Middle Miocene large mammal localities of Greece are few and the locality of Antonios (ANT) is one of them. It is situated in Chalkidiki Peninsula about 50 Km south-east of Thessaloniki city. The other known Greek locality is Thymiana-B (Chios Island, Aegean Sea) with a quite rich large mammal fauna; two other levels are also known from Chios, Thymiana-A, C with small mammals (Kondopoulou et al. 1993; Koufos 2006). Finally there is another locality named Gavathas situated in the island' of Lesvos whose fauna includes only *Prodeinotherium bavaricum* and it is dated to MN 3 (Koufos et al. 2003). Except these three localities there are some others, as the localities of Aliveri (Evia Island), Karydia I+II (Thrace), Plakia (Crete) and Chrysavgi (near Thessaloniki) which yielded mainly small mammals and rarely some large mammals (Koufos 2006). Generally, the early-middle Miocene localities are few and the known faunal data poor in the wider Eastern Mediterranean region (Balkans, Asia Minor). One well known locality is that of Prebreza (Serbia) which includes a large mammal fauna (Pavloviç 1969). In Turkey there are two well known localities, Çandir and Paşalar both including large mammals (NOW 2006), as well as the localities of Kultak and Sabuncubeli (Kaya et al. 2001; Mayda 2004). However there are several early-middle Miocene localities with small mammals (Ünay et al. 2003)

The Antonios locality was found in 1996 and the preliminary study of the locality and the fauna is given by Koufos & Syrides (1997). Initially the fauna is dated to the Orleanian/Astaracian ELMA (early/middle Miocene, MN4/5) as it was referred at that time (Steininger et al. 1996). The fauna of Antonios includes both large and small mammals. The study of the small mammals proposed a similar age for the fauna (Vassileiadou & Koufos 2004, 2005). The suoids found in

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Antonios include several sanitheres and few teeth of *Bunolistriodon*. The sanitheres are relatively rare in Europe, known from Leoben (Austria) and Thymiana (Greece) and their findings are always interesting. The other suid *Bunolistriodon* is more common as it is referred from the Balkans and Turkey. The description, comparison, determination and relationships of the Antonios suoids are given in the present article. The studied material is compared with the known material from the neighboring area, as well as with the material from the rest Europe and Africa, too. The sanitheres are mainly compared to the sample from Thymiana which is the best known and stored in LGPUT while the material of *Bunolistriodon* is compared to that stored in MNHN.

Abbreviations

ELMA=European Land Mammal Age
LGPUT= Laboratory of Geology and Palaeontology, University of Thessaloniki
MNHN= Muséum National d'Histoire Naturelle, Paris
NHMW= Naturhistorisches Museum Wien

Palaeontology

Order Artiodactyla OWEN, 1848
Superfamily Suoidea COPE, 1887
Family Sanitheriidae SIMPSON, 1945

Genus *Sanitherium* VON MEYER, 1866

Sanitherium schlagintweiti (VON MEYER, 1866)

Figs 1, 2

Synonyms: *Sanitherium schlagintweiti* KOUFOS & SYRIDES, 1997
Locality: Antonios (ANT), Chalkidiki, Macedonia, Greece.
Age: Middle/late Orleanian ELMA (early/middle Miocene, MN 4/5).
Material: Left maxillary fragment with P3-M1, ANT-74; Left I3, ANT-79; Left P4, ANT-72; Fragment of the right P4, ANT-76; Left M2, ANT-80; Right M3, ANT-75; Right dP4, ANT-77; Left mandibular fragment with m1-m2, ANT-112; Right mandibular fragment with m1, ANT-28; Left m1, ANT-1; Distal half of a left m2, ANT-78; Left mandibular fragment with m3, ANT-71; Left mandibular fragment with m3, ANT-111; Right m3; ANT-73; Left mandibular fragment with dp2-dp4, ANT-70. The measurements are given in Tab. 1.

Description: The nomenclature of the teeth is according to PICKFORD (1984). The upper dental remains of the sanitheres are few, but there is a maxillary fragment with P3-M1; the distobuccal part of the M1 is missing (Fig. 1a). The P3 is molarized having six cusps, but its occlusal outline is more rounded than squarish, as in the typical molars of *Sanitherium*. The paracone and metacone are almost equal-sized (the paracone seems to be slightly larger) and the higher cusps of the tooth, separated by a relatively deep and clear buccal groove. The metaconule is well developed, low and well separated from the hypocone. On the contrary, the protoconule is small and compressed on the protocone, making difficult its distinction. However, there is a clear deep groove in the mesial and distal surface separating the two cusps. The posterior cingulum is well developed projecting distally and forming a wide flat area

▶ Fig. 1. *Sanitherium schlagintweiti*, Antonios, Chalkidiki, Greece, early/middle Miocene, MN 4/5.
a. Left maxillary fragment with P3-M1, ANT-74; a_1.occlusal, and a_2. buccal view.
b. Fragment of the right P3, ANT-76; occlusal view.
c. Left P4, ANT-72; occlusal view.
d. Left M2, ANT-80; occlusal view.
e. Right M3, ANT-75; occlusal view.
f. Left I3, ANT-79; occlusal view.
g. Right dP4, ANT-77; buccal, lingual and occlusal view.

in the distal part of the tooth in which three secondary cusplets can be distinguished. The mesial cingulum is strong. The P4 is more squarish and completely molarized having six well separated cusps (Figs 1a, c). The paracone and metacone are the highest cusps of the tooth. The protoconule is connected with the protocone by a crest, while the metaconule is free from the metacone and hypocone. In the distal face of the paracone there is a clear groove which is reported as "palaeomeryx-fold" (PICKFORD 1984). The distal cingulum is strong consisted by a series of small secondary cusplets (multicuspid). The M1 (Fig. 1a) is partially broken lacking the metacone. The preserved cusps (paracone, protocone, and hypocone) are well developed with a small but clearly distinguished protoconule. The cusps tend to get a selenodont form, like in the ruminants. There is well developed mesial, distal and buccal cingulum. The M1 is enough worn, especially the protocone and protoconule cusps which form two dentine pits almost connected. The M2 (Fig. 1d) is squarish having the typical morphology of the molars (like M1). The metaconule is small and connected with the hypocone by a low crest making the cusp more seleniform. On the other hand, the protoconule extends mesially and distally around the base of the metacone making it more seleniform. Thus, the general aspect of the tooth is being more selenodont. This feature is clear in all cheek teeth of *Sanitherium*. The M3 has more triangular shape with well developed talon, consisting of small secondary cusplets (Fig. 1e). The protoconule and metaconule are connected by crests with the protocone and hypocone respectively, strengthening the selenodont character of the tooth. The cingulum is strong. Among the studied material there is an isolated I3 (Fig. 1f). It has a mesiodistally elongated crown with high buccal wall and lower lingual one, while between them there is an elongated groove.

The lower dentition is represented by molars only. The m1 is rectangular having four main cuspids (Figs 2b, c, e). The lingual cuspids are compressed buccolingually. The mesial cuspids are separated from the distal ones by a deep and large valley. There is a strong mesial, buccal and distal multicuspid cingulum. In the distal face of the metaconid there is a small metastylid, while in the distal face of the protoconid there is a groove known as "palaeomeryx fold" (PICKFORD 1984). The entoconid and hypoconid have equal height. There is a small and low hypoconulid situated in the distolingual corner of the tooth. The m2 (Fig. 2c, f) has similar morphology to m1 but it is larger. The m3 is triangular-shaped with large talonid (Figs 2d, g, h). The hypoconulid is strong representing the fifth cuspid, while a sixth one is developed in the lingual face of the hypoconulid. There is a multicuspid mesial and lingual cingulum.

The upper deciduous dentition is represented by a single dP4 which has triangular shape (Fig. 1g). It has six cusps with the metaconule and protoconule being smaller. The cusps are

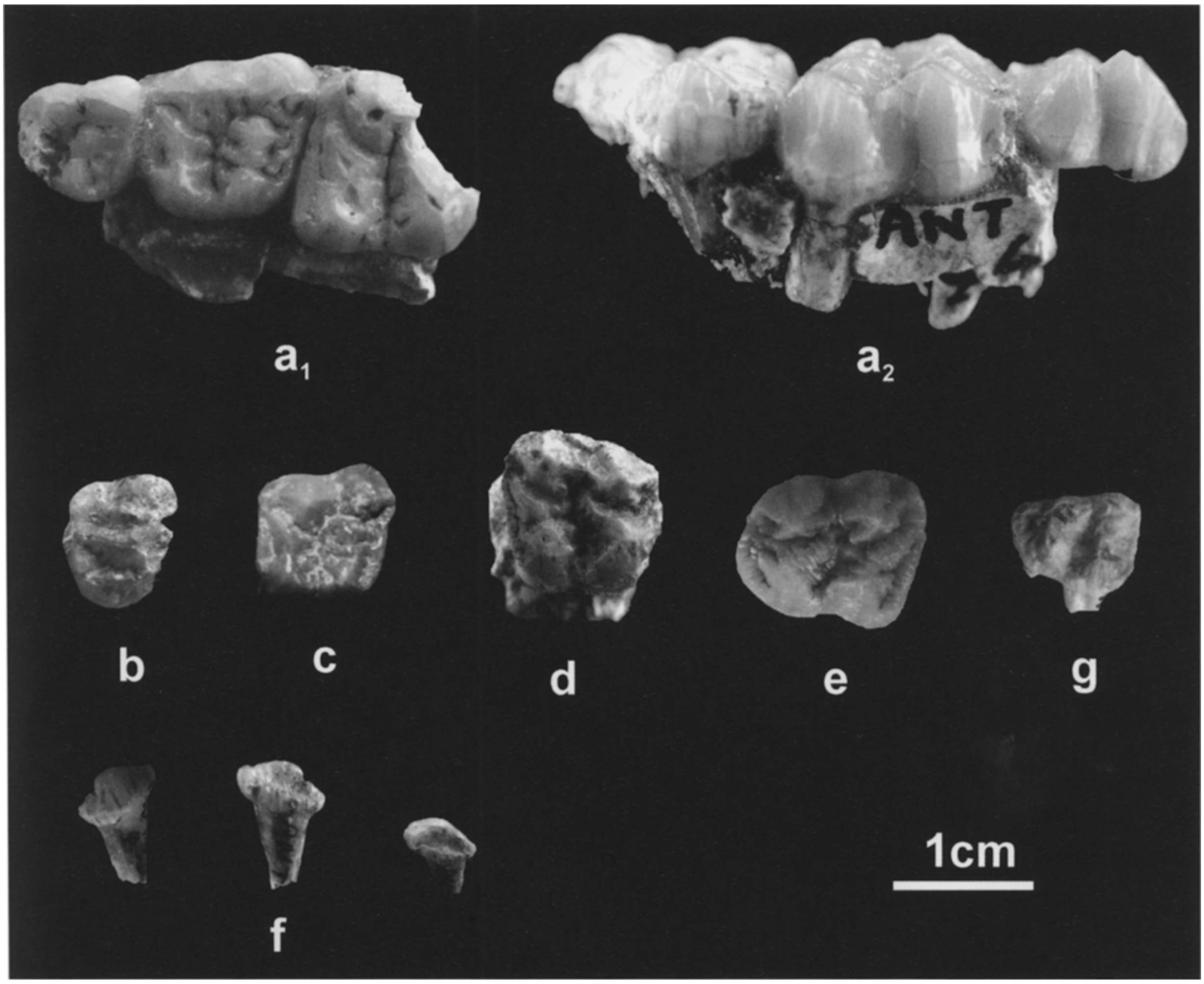
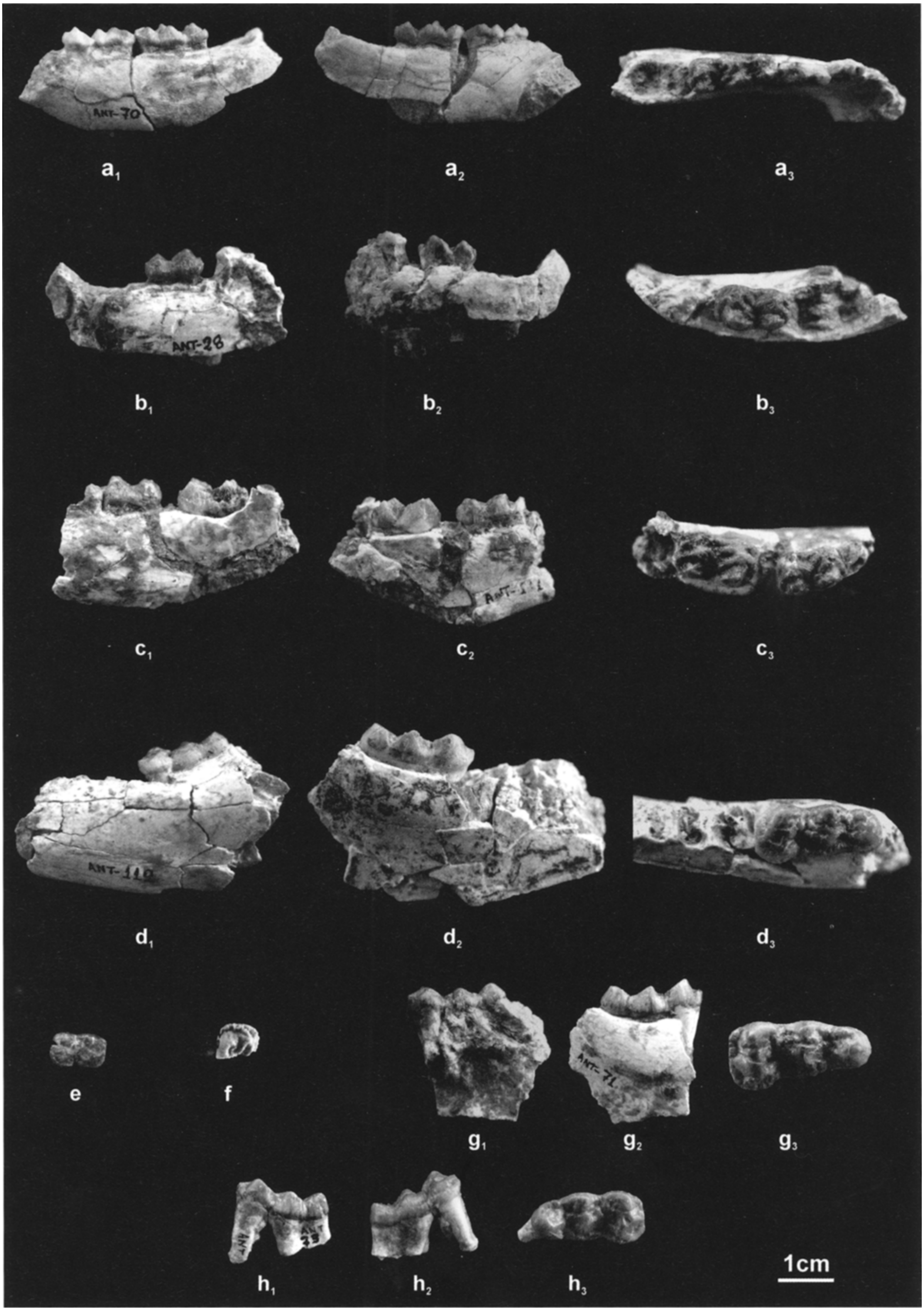


Table 1. Dental measurements of the Antonios sanitheres.

	I3		DP4		P3		P4		M1		M2		M3	
	L	B	L	B	L	B	L	B	L	B	L	B	L	B
ANT-79	6.1	3.6	-	-	-	-	-	-	-	-	-	-	-	-
ANT-77	-	-	8.9	7.6	-	-	-	-	-	-	-	-	-	-
ANT-74	-	-	-	-	7.4	6.8	9.2	9.1	-	9.6	-	-	-	-
ANT-76	-	-	-	-	-	-	-	8.2	-	-	-	-	-	-
ANT-72	-	-	-	-	-	-	8.8	9.0	-	-	-	-	-	-
ANT-80	-	-	-	-	-	-	-	-	-	-	11.5	11.6	-	-
ANT-75	-	-	-	-	-	-	-	-	-	-	-	-	12.4	10.7
	dp2		dp3		dp4		m1		m2		m3			
	L	B	L	B	L	B	L	B	L	B	L	B		
ANT-1	-	-	-	-	-	-	10.3	6.2	-	-	-	-	-	-
ANT-28	-	-	-	-	-	-	10.0	6.1	-	-	-	-	-	-
ANT-70	5.5	2.7	7.4	3.4	13.1	5.3			-	-	-	-	-	-
ANT-71	-	-	-	-	-	-	-	-	-	-	17.5	8.3	-	-
ANT-73	-	-	-	-	-	-	-	-	-	-	16.7	7.8	-	-
ANT-78	-	-	-	-	-	-	-	-	-	7.3	-	-	-	-
ANT-111	-	-	-	-	-	-	10.3	6.2	11.7	7.2	-	-	-	-
ANT-112	-	-	-	-	-	-	-	-	-	-	16.5	7.3	-	-


ANT-70
a1
a2
a3
ANT-28
b1
b2
b3
c1
c2
c3
d1
d2
d3
e
f
ANT-71
g1
g2
g3
h1
h2
h3
1cm

◀ Fig. 2. *Sanitherium schlagintweiti*, Antonios, Chalkidiki, Greece, early/middle Miocene, MN 4/5.

a. Left mandibular fragment with dp2-dp4, ANT-70; a_1. buccal, a_2. lingual, and a_3. occlusal view.
b. Right mandibular fragment with m1, ANT-28; b_1. buccal, b_2. lingual, and b_3. occlusal view.
c. Right mandibular fragment with m1-m2, ANT-111; c_1. buccal, c_2. lingual, and c_3. occlusal view.
d. Left mandibular fragment with m3, ANT-112; d_1. buccal, d_2. lingual, and d_3. occlusal view.
e. Left m1, ANT-1; occlusal view.
f. Distal half of a left m2, ANT-78; occlusal view.
g. Left mandibular fragment with m3, ANT-71; g_1. buccal, g_2. lingual, and g_3. occlusal view.
h. Right m3, ANT-73; h_1.buccal, h_2. lingual, and h_3. occlusal view.

worn enough and tend to connect each other. There is a clear "palaeomeryx fold" in the distal face of the paracone. The talon is large and well developed. The advanced attrition makes difficult the distinction of any cuspid in the talon. Between the mesial and distal lobe there is a large valley open lingually. There is multicuspid mesial, lingual and distal cingulum.

The lower deciduous dentition is represented by a mandibular fragment preserving the teeth dp2-dp4 (Fig. 2a). The dp2 is elongated and narrow consisting of three cuspids situated on line across mesiodistal axis of the tooth. The distal cuspid has a deep groove in its distal face indicating its separation in two different cuspids. The dp3 is longer than dp2 with more developed distal part, in which a fourth cuspid is developed buccally. The dp4 is molariform with six cuspids and three lobes.

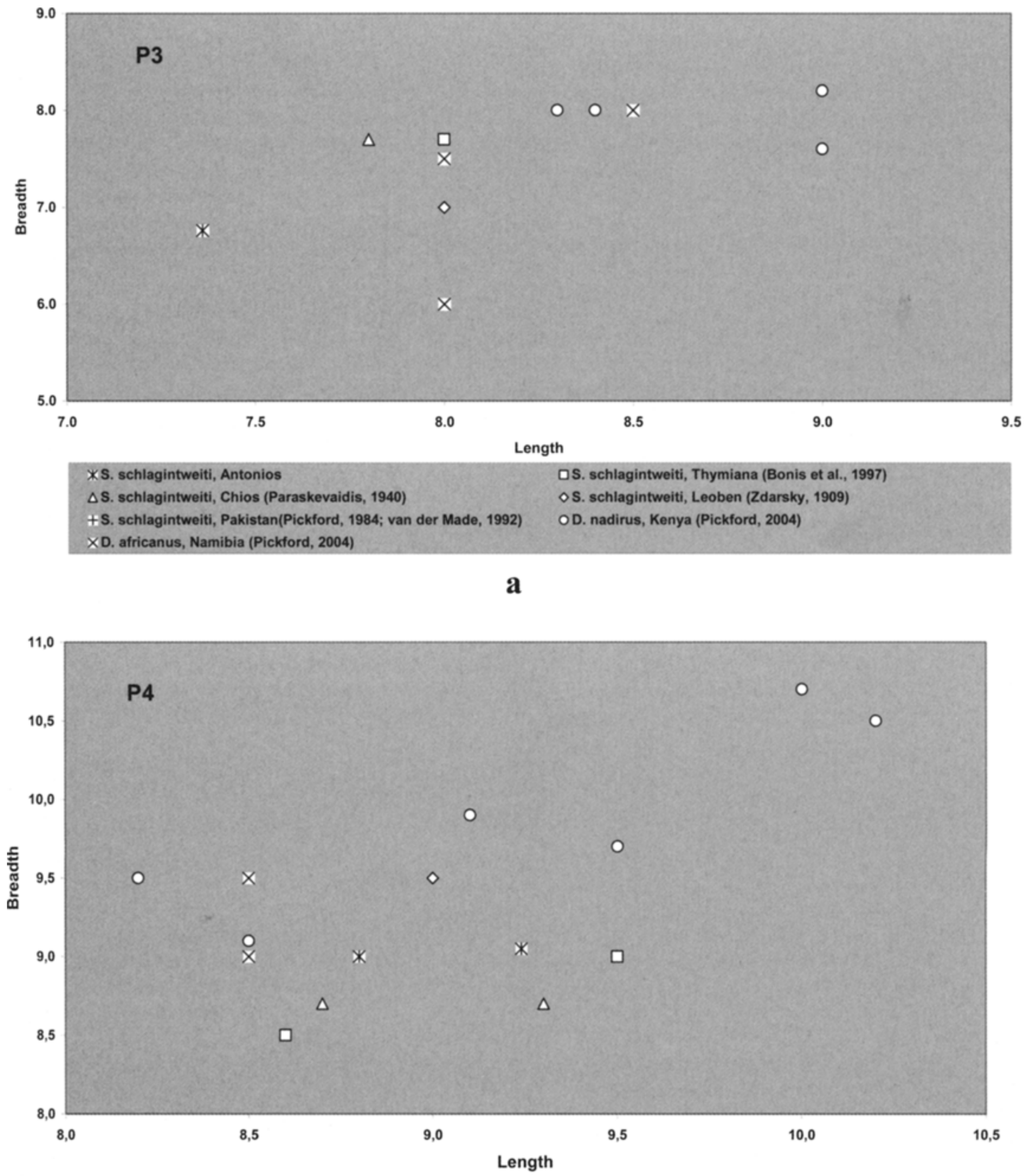


Fig. 3. Scatter diagram comparing the upper premolars of various Sanitheriidae.

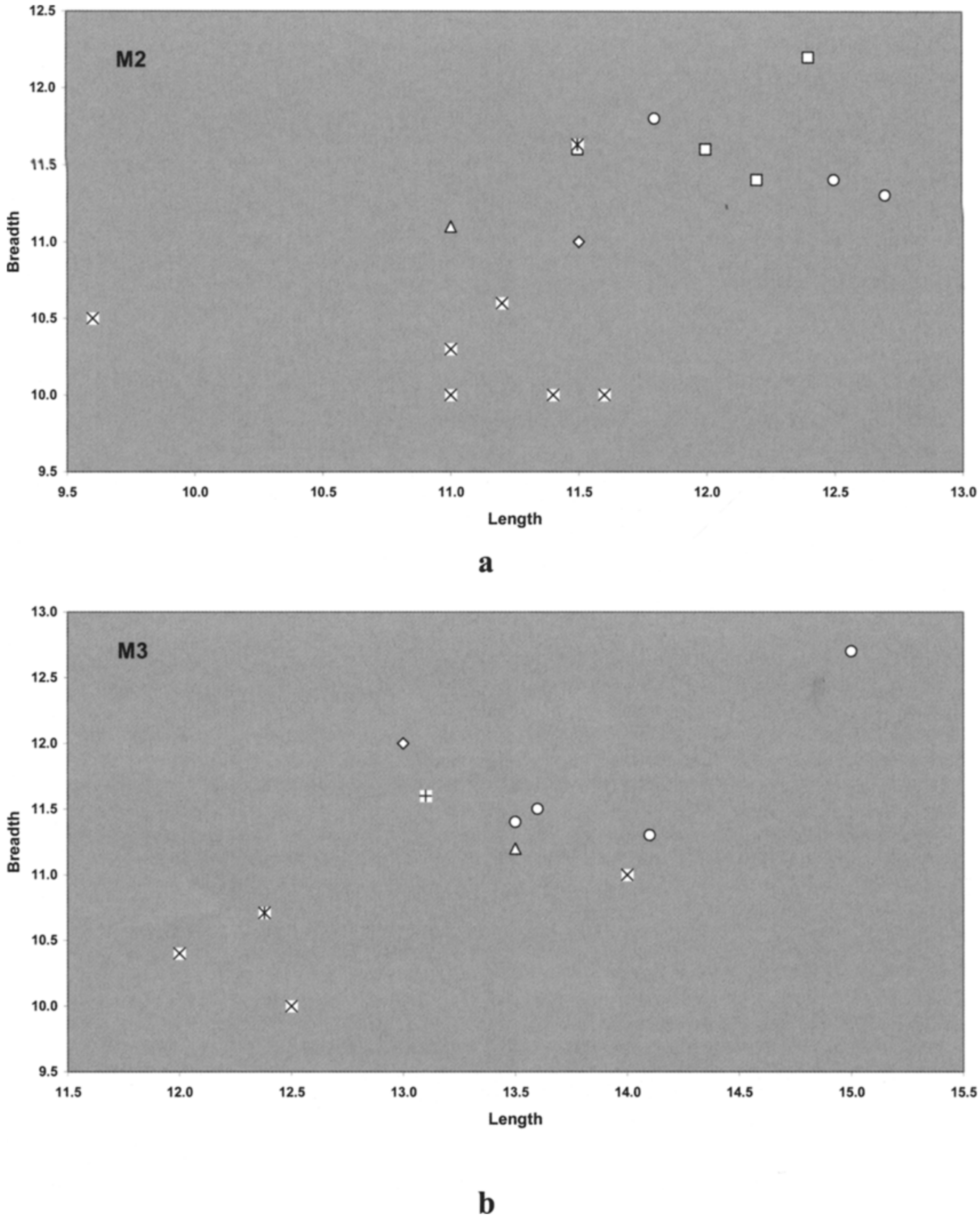


Fig. 4. Scatter diagram comparing the upper molars of various Sanitheriidae. Abbreviations as in Fig.3.

The mesial lobe is the narrower one. There is well developed multicuspid mesial, buccal and distal cingulum.

Discussion: The systematic position of the sanitheres detains the scientists for a long time. They reported either as a sub-family (Sanitheriinae) of Suidae or as a separated family (Sanitheriidae) of Suoidea, erected by SIMPSON (1945). However, THENIUS (1956, 1979) included the sanitheres to the family Suidae. The family Sanitheriidae acquired its validity again by PICKFORD (1984) and it was accepted later by VAN DER MADE & HUSSAIN (1992) and BONIS et al. (1997). Recently PICKFORD (2004) revised the African sanitheres and gave an extensive diagnosis for the family. Iniatially, only the genus *Sanitherium* was included in the family, while later the genera *Diamantohyus* and *Xenochoerus* were included to it either as separated taxa or synonyms. Today the genera *Sanitherium* and *Diamantohyus* are recognized as valid ones. A set of characters such as the presence of the "metastylid" and the narrower lower molars of *Sanitherium* distinguish it from *Diamantohyus* (PICKFORD 1984). The validity of these two

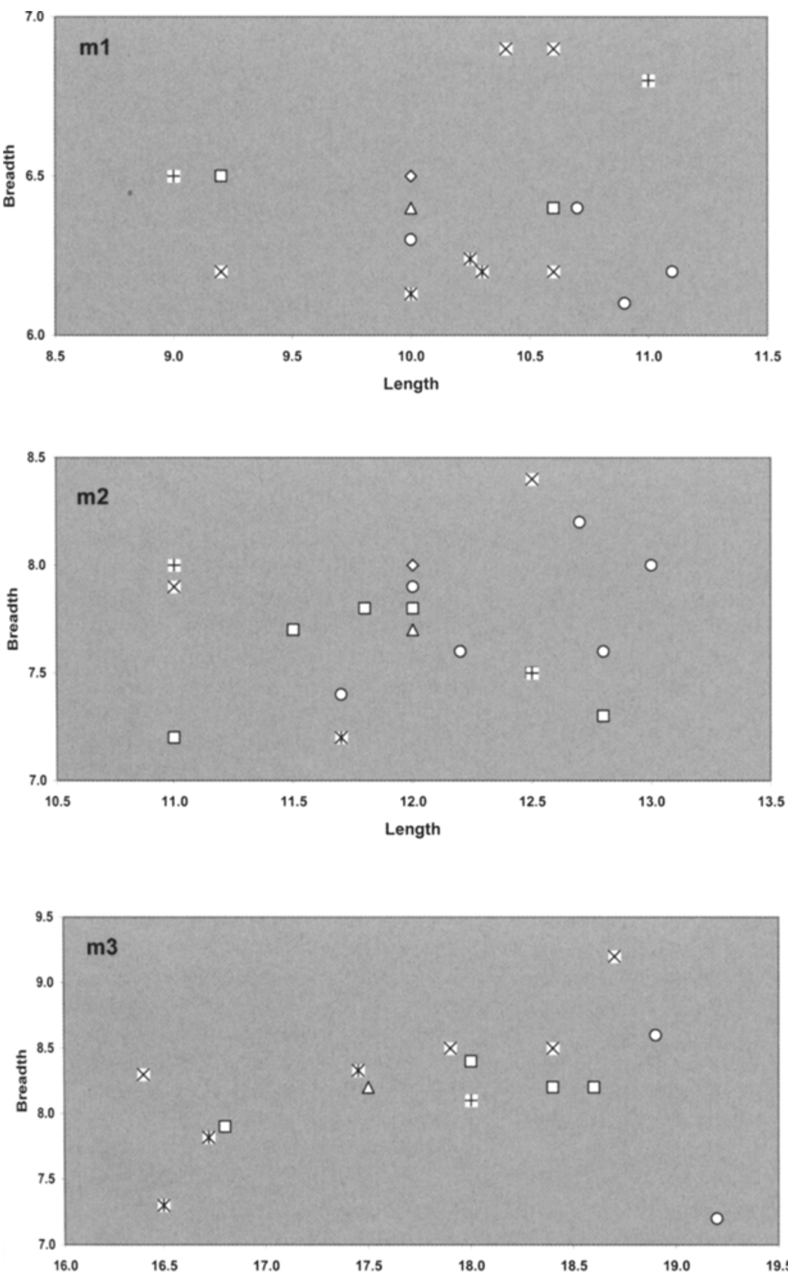


Fig. 5. Scatter diagram comparing the lower molars of various Sanitheriidae. Abbreviations as in Fig.3.

characters is doubtfull (see VAN DER MADE & HUSSAIN 1992; BONIS et al. 1997). The number of cusps(-ids) in the premolars is referred as the main diagnostic character, distinguishing the two genera *Diamantohyus* and *Sanitherium*. The upper and lower premolars of *Diamantohyus* possess less cusps (-ids); the p4 of *Diamantohyus* has three, while that of *Sanitherium* has six cuspids (PICKFORD 2004). The studied upper premolars from Antonios have six cusps suggesting that they to the genus *Sanitherium*.

The systematic of the sanitheres is complicated and there are several opinions. PICKFORD (1984) reported the following species:

- *S. schlagintweiti*, including the material from Pakistan only.
- *S. leobense*, including the Leoben sample and *S. masticum* of PARASKEVAIDIS (1940).
- *S. nadirum*, including the African sample. Recently PICKFORD (2004) tranferred *S. nadirum* to *Diamantohyus nadirus* and thus *Sanitherium* is restricted to Eurasia only.

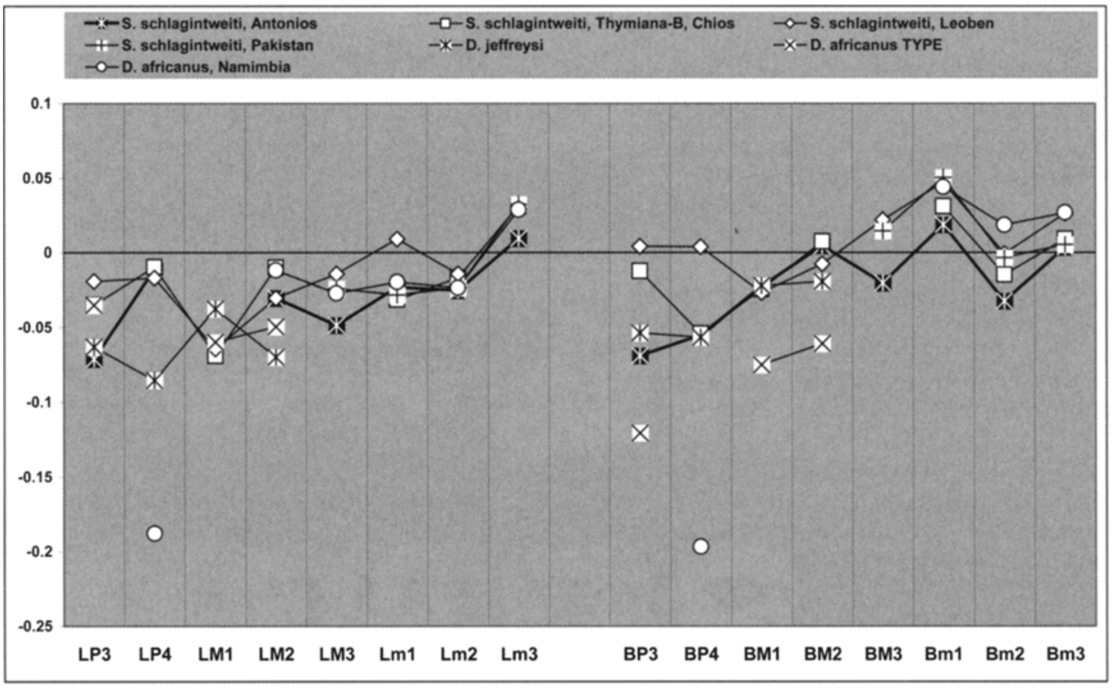
VAN DER MADE & HUSSAIN (1992) recognized the genus *Sanitherium* only, separating the following species:

- *S. schlagintweiti*, including the species *S. leobense* and *S. nadirum*.
- *S. africanus*, including *Diamantohyus africanus* of PICKFORD (1984)
- *S. jeffreysi*, including *Diamantohyus jeffreysi* of PICKFORD (1984)

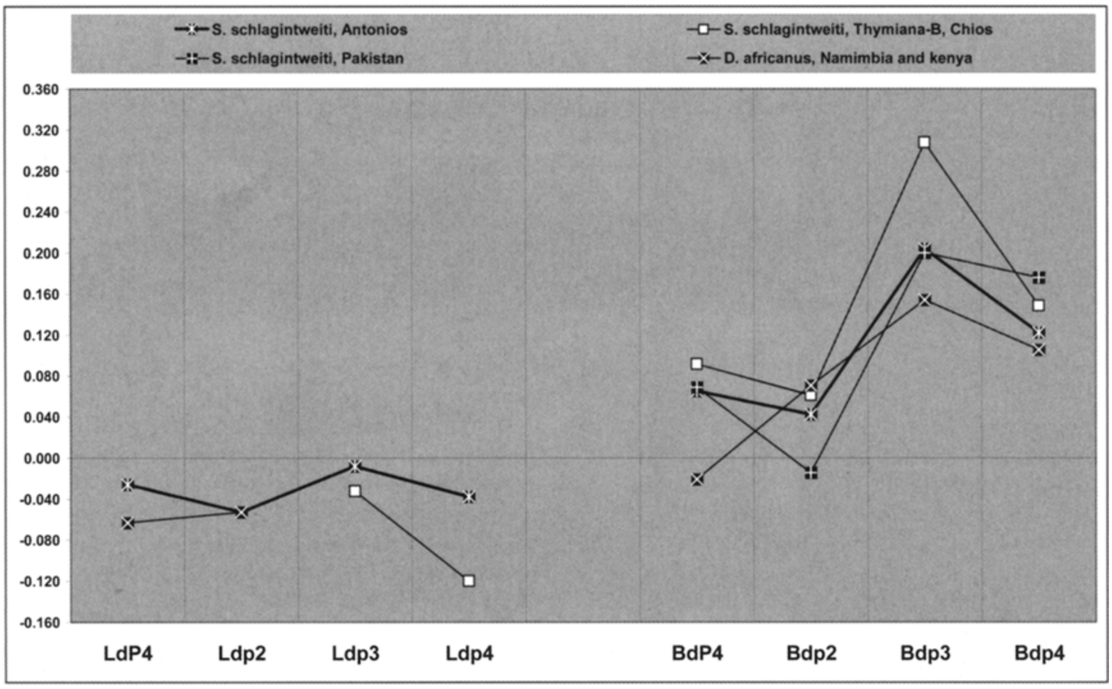
BONIS et al. (1997) accepted the synonymy of *S. schlagintweiti*, *S. leobense* and *S. masticum*, while they proposed to leave the African material as a separate species under the name *S. nadirum*. According to PICKFORD (2004) *S. nadirum* differs from *Sanitherium* and belongs to *Diamantohyus*. Summarizing all the above mentioned opinions the sanitheres today includes two genera, the older African *Diamantohyus* and the younger Eurasian *Sanitherium*.

The species *S. schlagintweiti* was originally described by few and fragmentary material from Pakistan (VON MEYER 1866). Later, several authors have described more material from the area (LYDEKKER 1879; PILGRIM 1926; COLBERT 1935). Later on, the known material from Pakistan (including an undescribed mandibular fragment with m1) revised and all is reffered to *S. schlagintweiti* (PICKFORD 1984). More recently, some new material has been described, while the old one has been revised, and all included to *S. schlagintweiti* (VAN DER MADE & HUSSAIN 1992). The morphological characters of *S. schlagintweiti* from Pakistan fit very well to those of Antonios, while their size is also very close (Figs 3-6). However, the Antonios lower teeth are slightly narrower (Figs 4, 6). This is probably due to the younger age of the Pakistan sample. The material of Pakistan was found in the lower Manchar Formation dated to late Orleanian ELMA (upper MN 5) and to Chinji Formation dated from Astaracian-early Vallesian ELMA (MN 6-9) (VAN DER MADE & HUSSAIN 1992) and it is younger than that of Antonios, dated to middle Orleanian ELMA (MN 4/5) (KOUFOS & SYRIDES 1997; VASSILEIADOU & KOUFOS 2005).

The best known sample of Sanitheres is known from Chios Island (Aegean Sea, Greece). The locality was found in 1940 and the first material of sanitheres described as a new species *S. masticum* (PARASKEVAIDIS 1940). A new collection from Chi-



a



b

Fig. 6. Logarithmic ratio diagram comparing the permanent (a) and deciduous (b) teeth of Sanitheriidae. Standard: *D. nadirus*, Kenya and Uganda (PICKFORD 2004).

os (locality Thymiana-B, THB) gave several mandibular and maxillary remains of sanitheres. The description and comparison of the new material allow its determination to *S. schlagintweiti* (BONIS et al. 1997). The studied upper cheek teeth have a morphology similar to that of the Thymiana-B material, while their proportions are very close (Figs 3-6). The size of the

P4 and M2 is very close to that of Chios material, while the P3 and M3 are slightly smaller (Figs 3, 4). Similarly, the m1 and m2 are slightly smaller than those of Chios (Fig. 5). The comparison of the dental dimensions by a logarithmic ratio diagram is given in Fig. 6. It is quite clear that the lines for Antonios, Chios and Leoben sample are very close to each other and they are going parallel. However, the P3, M3 and m1 of Antonios are shorter than those of Chios, while the lower teeth of Antonios are narrower than those of Chios (Fig. 6a). The milk dentition of Antonios resembles to that of Thymiana-B, Chios, but again the Antonios sample has narrower teeth (Fig. 6b). Like the Pakistan sample the smaller size of Antonios sanithere is possibly a primitive feature, indicating that the Chios form is slightly younger than Antonios one. The localities of Thymiana, Chios are dated to late Orleanian ELMA, MN 5 (Bonis et al. 1998), while Antonios is considered as belongimg to middle Orleanian, MN 4/5 (Fig. 11), (Koufos & Syrides 1997; Vassiliadou & Koufos 2005).

The sanitheres found in Leoben (Austria) have been described as *S. leobense* which is reported as a younger synonym of *S. schlagintweiti* (Bonis et al. 1997). In fact all the morphological characters of the Leoben material fit quite well to those of *S. schlagintweiti* from Pakistan and Chios (Bonis et al. 1997). Concerning its dimensions it is the largest form of *S. schlagintweiti* (Figs 3, 4, 6) and possibly the most derived one; Leoben is dated to early Astaracian ELMA, MN 6 (NOW 2006).

Taking in mind all the above mentioned comparisons the Antonios sanitheres belong to *S. schlagintweiti* and they have smaller size than Pakistan, Chios and Leoben material. This size increase in *S. schlagintweiti* is possibly related to the geological age.

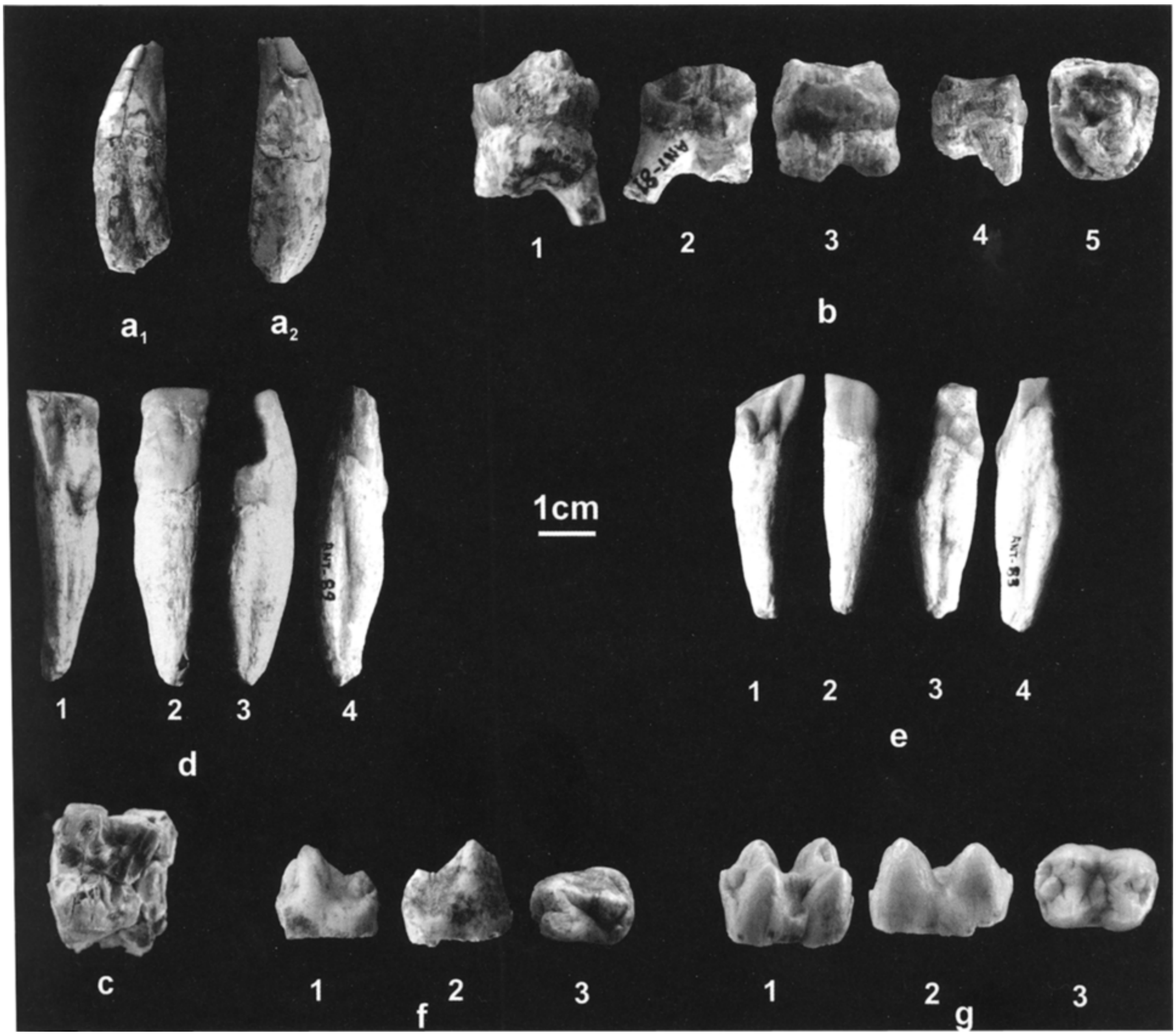


Fig. 7. *Bunolistriodon lockharti,* Antonios, Chalkidiki, Greece, early/middle Miocene, MN 4/5.
a. Left female upper canine, ANT-43; a_1=lingual, and a_2=buccal view.
b. Right P4, ANT-81; b_1=lingual, b_2=buccal, b_3=distal, b_4=mesial, and b_5=occlusal view.
c. Left M2, ANT-12; occlusal view.
d. Lower second incisor, ANT-82; d_1=lingual, d_2=buccal, d_3=distal, and d_4=mesial view.
e. Lower second incisor, ANT-83; e_1=lingual, e_2=buccal, e_3=distal, and e_4=mesial view.
f. Right p4, ANT-42; f_1=lingual, f_2=buccal, and f_3=occlusal view.
g. Right m2, ANT-41; g_1=buccal, g_2=lingual, and g_3=occlusal view.

Family Suidae GRAY 1821
Subfamily Listriodontinae GERVAIS 1859

Genus *Bunolistriodon* ARAMBOURG 1963

Bunolistriodon lockharti (POMEL 1848)

Fig. 7

Synonyms: *Sanitherium schlagintweiti* KOUFOS & SYRIDES, 1997
Locality: Antonios (ANT), Chalkidiki, Macedonia, Greece
Age: Middle/late Orleanian ELMA (early/middle Miocene, MN 4/5).
Material: Cf sin, ANT-43; P4 dex, ANT-81; M1 dex, ANT-12; i2 dex, ANT-82; i2 sin, ANT-83; p4 dex, ANT-42; m2 dex, ANT-41. The measurements are given in Tab. 2.

buccal cuspid there is a crest-like cuspid running from the tip to the base of the tooth. It is well distinguished by a relatively lingual groove tending to form a cuspid. A similar large crest runs in the distal face of the buccal cuspid and connects it with the distal cuspid, which is well developed and low. The distal cingulum is well developed.

The m2 has four main cuspids; the lingual cuspids are higher than the buccal ones (Fig. 7g). The mesial cuspids are separated from the distal ones by a deep valley having an accessory cuspid in the middle. A well developed and small hypoconulid is situated distally between the metaconid and hypoconid. The lingual and buccal cuspids are connected by a low crest, giving to them a lophodont form (sub-lophodont). The distal cingulum is strong; the buccal one is weak restricted in the valley between the protoconid and hypoconid. The mesial cingulum is also well developed but it is weaker than the distal one.

Table 2. Dental measurements of Antonios *Bunolistriodon*.

	P4		M1		i2		p4		m2		
	L	B	L	B	L	B	L	B	L	Bant	Bpost
ANT-81	14.1	16.3	-	-	-	-	-	-	-	-	-
ANT-12	-	-	18.8	18.7	-	-	-	-	-	-	-
ANT-82	-	-	-	-	13.4	11.2	-	-	-	-	-
ANT-83	-	-	-	-	11.9	10.7	-	-	-	-	-
ANT-42	-	-	-	-	-	-	-	12.3	-	-	-
ANT-41	-	-	-	-	-	-	-	-	22.5	16.4	16.3

Description: The available material from Antonios is few and includes only isolated teeth. The upper canine ANT-43 belongs to a female individual (Fig. 7a). It has a strong root, while the crown is relatively weaker. The lingual wall of the canine is flat but in the lingual wall of the root it has a slight groove running across it (Fig. 7a$_1$). The labial wall is rounded having a crest in the posterior border. The curvature of the canine is weak. The P4 is wider than long with rounded lingual border (Fig. 7b). All around the tooth there is well developed cingulum; the buccal one is weaker. The protocone is large dominating the lingual part of the tooth. In the buccal border there are two cusps the paracone and metacone; the previous one is larger. The cusps of the tooth are connected by the attrition. The M1 is badly preserved and very worn (Fig. 7c). The buccal cusps are well developed and almost equal-sized, separated by a deep valley. The lingual cusps are broken and their characters cannot be distinguished.

The i_2 is shovel-like (Figs 7d, e). Two strong pillars, a mesial and a median one are distinguished in the lingual wall of the i2. The median pillar seems to be slightly stronger. In the less worn ANT-82 the pillars are clearer (Figs 7d). In the disto-lingual corner of the tooth there is a strong cingular projection. In the worn i2, ANT-83, the occlusal surface is elliptical and inclines distally (Fig. 7e). The root is strong and elongated; its buccal length from the base of the enamel is 31.0-32.5 mm. The p4 is rectangular, unworn and its mesial part is broken (Fig. 7). It has two cuspids, of equal height and compressed each other; the buccal one is larger. The cuspids are well distinguished by a deep mesial groove. In the mesial face of the

Discussion: Among the first material collected from the locality of Antonios an isolated p4 (ANT-42) of *Bunolistriodon lockharti* was recognized (KOUFOS & SYRIDES 1997). The later collections provided the rest teeth of this listriodont suid. The genus *Bunolistriodon* was erected by ARAMBOURG (1963) and includes listriodont suids with bunodont or sub-lophodont teeth, in which the paraconule (protoconule) is sometimes fused to the cingulum. In many cases the *Bunolistriodon* material is referred to *Listriodon* and there is a synonymy problem (see synomymy lists in FORTELIUS et al. 1996; VAN DER MADE 1996, 2003). Recently the two genera *Bunolistriodon* and *Listriodon* are synonymized under the name *Listriodon* (PICKFORD & MORALES 2003). As the systematic of the suids is not the main goal of this article the name *Bunolistriodon* will be used to avoid confusion with the older publications for Antonios fauna.

The material of *Bunolistriodon* from Antonios is directly compared with the material stored in MNHN which comes from various localities. The type locality of *B. lockharti* is Chevilly (France), dated to middle Orleanian ELMA, MN 4 (NOW 2006) from which there are some isolated teeth. Their comparison with the Antonios material suggests that they resemble morphologically but the m2 is slightly larger than that of Antonios (Fig. 9b). The comparison of the Antonios material with the sample of *B. lockharti* from the locality of Pontlevoy (France), dated to late Orleanian ELMA, MN 5 (NOW 2006) indicates some similarities and differences. The studied i2 is morphologically similar to that of MNHN-FP 1029 from Pontlevoy. However, it differs in having smaller

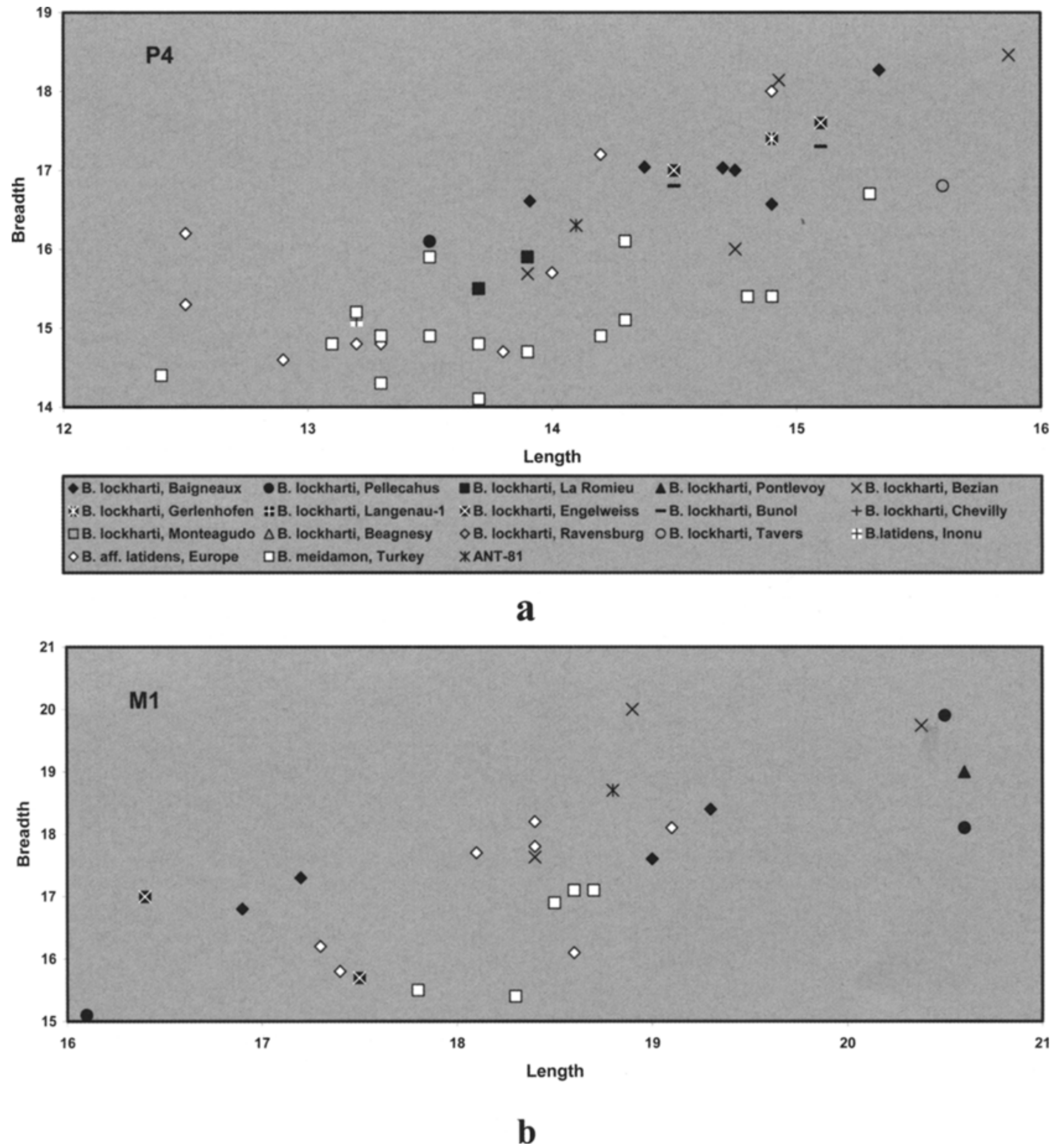
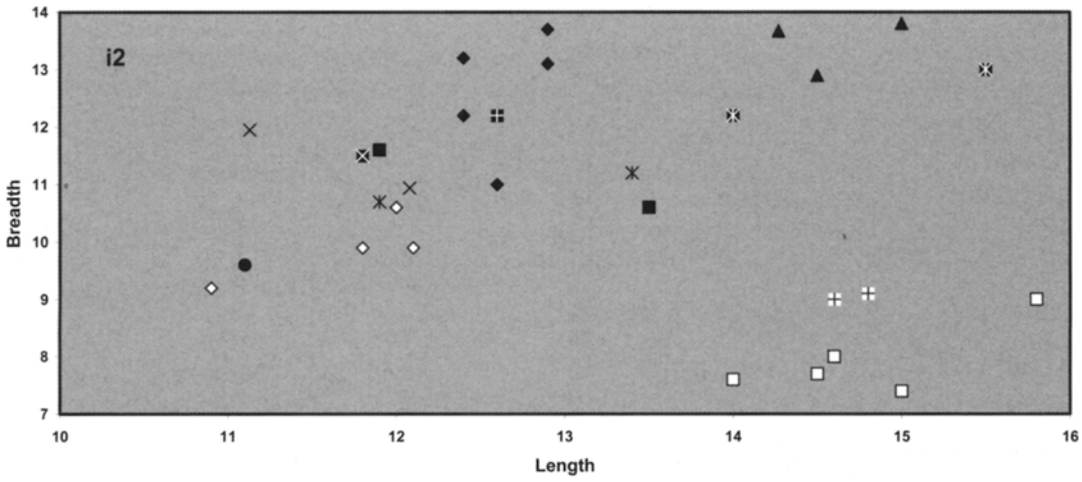


Fig. 8. Scatter diagram comparing the P4 and M1 of *Bunolistriodon* from Antonios with those from the various European localities. The data are partially original and partially taken from VAN DER MADE (1996).

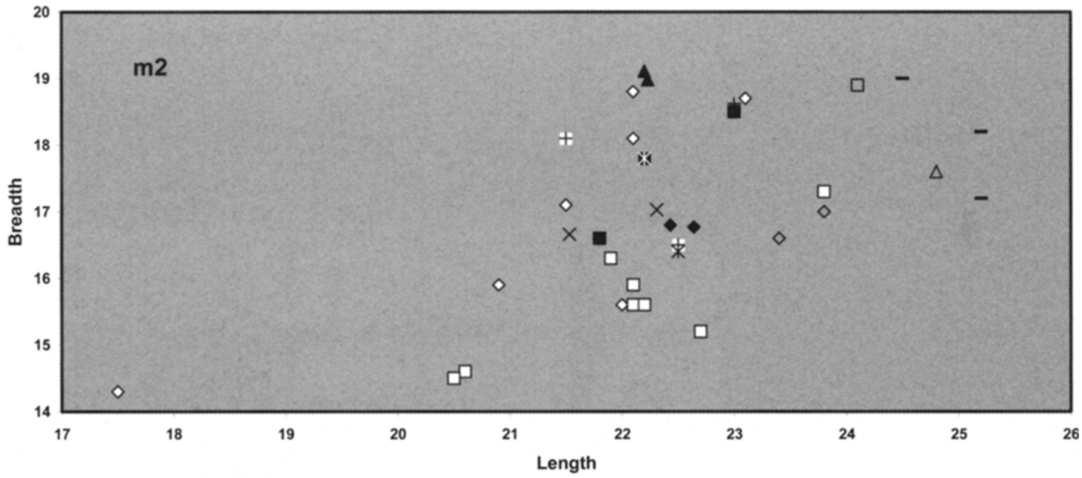
size (Fig. 9a), less inclined upper part of the distal border, stronger distolingual cingular projection and probably stronger pillars (Fig. 10). The later difference is not so clear as the pillars of the Pontlevoy i2 are worn. The p4, ANT-42 has similar morphology and size to the Pontlevoy material (MNHN-FP 226, 1035) but the Antonios p4 has stronger cingulum and less compressed lingual cuspid on the buccal one than that of the Pontlevoy sample. The m2 ANT-41 differs from that of Pontlevoy in being narrower (Fig. 9b), slenderer and with less developed cuspids.

A nice sample of *B. lockharti* is known from Bezian (France), dated to middle Orleanian ELMA, MN 4 (NOW 2006). The direct comparison indicates strong similarities but the m2 of Antonios is slenderer, the i2 has slightly stronger distolingual cingular projection and the p4 has stronger buccal cingulum which is almost absent in the Bezian specimens. The size of the Bezian material is similar or slightly larger than that of Antonios (Figs 8, 9). The locality of Baigneaux (France), dated to late Orleanian ELMA, MN-5 (NOW 2006), includes a rich collection of *B. lockharti*. The P4 ANT-81 has similar morphology and dimensions (Fig. 8a), but it has stronger lingual and buccal cingulum, which is absent in the Baigneaux material. The M1 ANT-12 seems to have similar morphology and size (Fig. 8b) to that of Baigneaux. The p4 has similar morphology to the majority of the Baigneaux sample. However, it differs from MNHN-Ba 421 in having higher and more distinguishable lingual cuspid, weaker cingulum, weaker cuspid in front of the buccal cuspid and lacks the crest connecting the posterior accessory cuspid with the main cuspid, a feature which is clear in MNHN-Ba 421. The m2 ANT-41 has similar morphology and size to the Baigneaux sample (Fig. 9b).

The material from Pellecahus (France), dated to middle Orleanian ELMA, MN 4 (NOW 2006) is also rich and includes several specimens. The P4 ANT-81 is morphologi-



a



b

Fig. 9. Scatter diagram comparing the i2 and m2 of *Bunolistriodon* from Antonios with those from the various European localities. The data are partially original and partially taken from VAN DER MADE (1996).

cally and metrically similar (Fig. 8a) to that of Pellecahus but it has strong buccal cingulum, which is absent in the Pellecahus material. The i2 ANT-82, 83 differs from the Pellecahus material in having slightly larger size (Fig. 9a), more expressed pillars in the lingual wall, stronger distoligual cingular projection, and less inclined upper part of the distal border of the crown. The p4 ANT-42 is similar but slenderer and with less high cuspids than those of Pellecahus. The m2 ANT-41 differs from the Pellecahus material because it is slenderer, lacks the accessory cuspid situated in the distal surface of the protoconid (the latter cuspid is also present in the material from Baigneaux and Bezian), and it has a small fovea in the mesial border instead of an accessory cuspid present in the Pellecahus sample (this accessory cuspid is also absent in the Baigneaux material). A maxilla and a mandibular fragment (MNHN-FSL 320098, 320095) from the locality La Romieu (France), dated to MN-4 (GINSBURG & BULOT 1987) are referred to *B. lockharti*. The morphology of the Antonios P^4 and m_2 is similar to La Romieu material, but with weaker cingulum. Their size is quite similar to the Antonios one being, however, somewhat larger (Figs 8, 9).

In Greece a sole M^3 from Chios is referred to as *Listriodon* (n. sp.?) *lockharti* var. *michali* by PARASKEVAIDIS (1940). However, its comparison is not possible to the Antonios sample because there are no corresponding teeth. A similar form is also referred from Prebreza (Serbia) by ĆIRIĆ & THENIUS (1959), which the same year raised its rank to species level and it is referred as *Listriodon michali* (PAVLOVIĆ & THENIUS 1959; PAVLOVIĆ 1969); later on, it is referred to *B. lockharti* (VAN DER MADE 1996). The Chios material is difficult to be determined accurately and the Prebreza one needs a revision for more certain determination.

In Eastern Mediterranean region a well known listriodont suid is *Bunolistriodon meidamon* represented by two different sub-species found in the Turkish localities of Paşalar (*B. m. meidamon*) and Çandir (*B. m. ultimus)* (FORTELIUS *et al.* 1996; VAN DER MADE 2003). The main distinctive character of *B. meidamon* is the shape of the incisors, which are longer mesiodistally and narrow labiolingually, being more flat than those of *B. lockharti.* Moreover, the lower incisors of *B. meidamon* preserve very weak lingual pillars (FORTELIUS *et al.* 1996)

Table 3. Index Buccolingual diameterx100/Mesiodistal diameter of i2 for various *Bunolistriodon*. BL=Buccolingual diameter; MD=Mesiodistal diameter; *=mean.

	Bunolistriodon lockharti				*B. latidens*	*B. meidamon*	*L. splendens*
	Antonios	Pontlevoy	Bézian	Europe	Europe	Pa_alar	Europe
	Original measurements			Fortelius et al. (1996)			
Index BLx100/MD of i2	83.6-90.0	95.6	91.5;108.5	101.8*	73.1*	63.8 (66.5) 70.6	84.7*

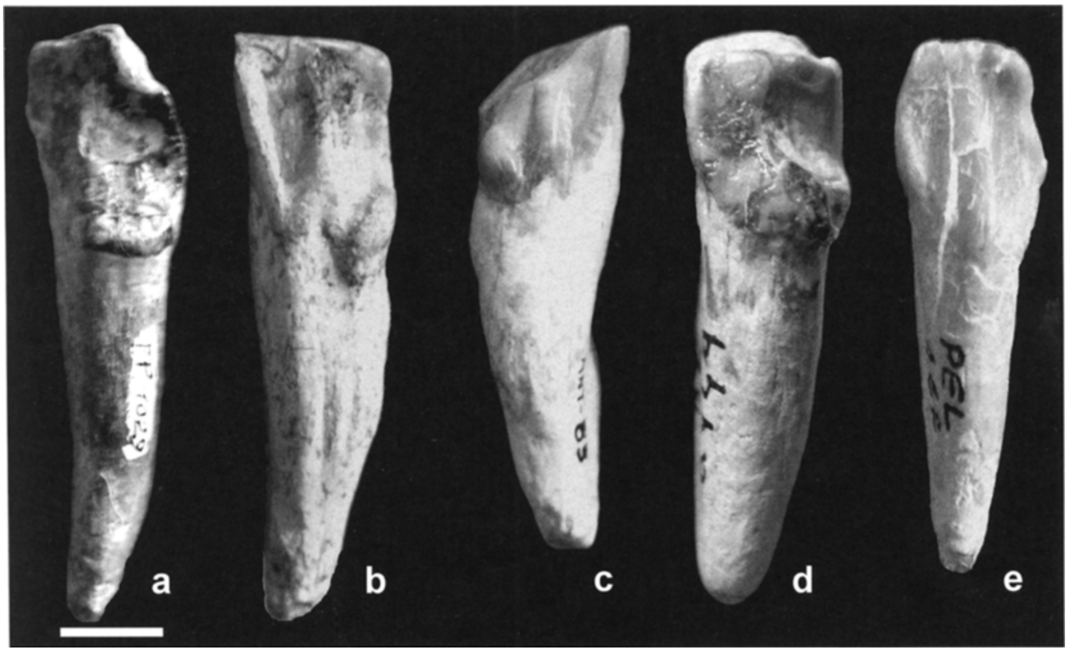


Fig. 10. Comparison of the i2 of *B. lockharti* from various localities.
a. MNHN-FP 1029, Pontlevoy
b. ANT-82
c. ANT-83
d. MNHN-Be 8449, Bezian
e. MNHN-PEL n.n., Pellecahus

contrary to the large ones of *B. lockharti.* Both lower incisors from Antonios have well developed lingual pillars and they are not so flat. The comparison of the studied incisors with those of *B. meidamon* suggests that the latter ones are quite narrow (Fig. 8a). The Index buccolingual diameter x 100/mesiodistal diameter of the i2 is closer to the mean of *B. lockharti* (Tab. 3). Those of *B. meidamon* and *B. latidens* are higher indicating narrower incisors. According to the diagnosis of *B. meidamon,* the premolars are narrow and non-molarized (FORTELIUS *et al.* 1996). The Antonios P4 is near the maximum values for *B. meidamon*, whose P4 is generally smaller and quite narrower than that of *B. lockharti* (Fig. 8a). The molars of *B. meidamon* are narrower, more brachyodont and with less pointed cusp tips than in *B. lockharti* (FORTELIUS *et al.* 1996). The available M1 is badly preserved and worn, but the cusps are well separated from one another. Its size is clearly larger than that of *B. meidamon* (Fig. 8b). The studied m_2 is again larger than *B. meidamon* and closer to *B. lockharti* from Europe (Fig. 9b). The P4 of *B. meidamon* is characterized by a strong development of the mesial and distal cingulum and lacks the simple crest running down the distal side of the main cusp (FORTELIUS *et al.* 1996). In the studied P4 the last feature is present, while the cingulum is less developed than that of *B. meidamon,* indicating relations to *B. lockharti.* As the mesial part of the studied tooth is broken a complete metrical comparison is not possible. However, its breadth (12.3 mm) is closer to the mean value of *B. lockharti* (12.5 mm) than to *B. meidamon* (11.1 mm); the last two values are taken from FORTELIUS *et al.* (1996). The above mentioned comparison indicates that the Antonios listriodont suid has morphology and size different from that of *B. meidamon.*

Another known European species is *B. latidens*; the type specimen is in Lausanne. The Antonios p4 differs from the type of *B. latidens* in having larger size and weaker cingulum. The distolingual cingulum of p4 is well developed and el-

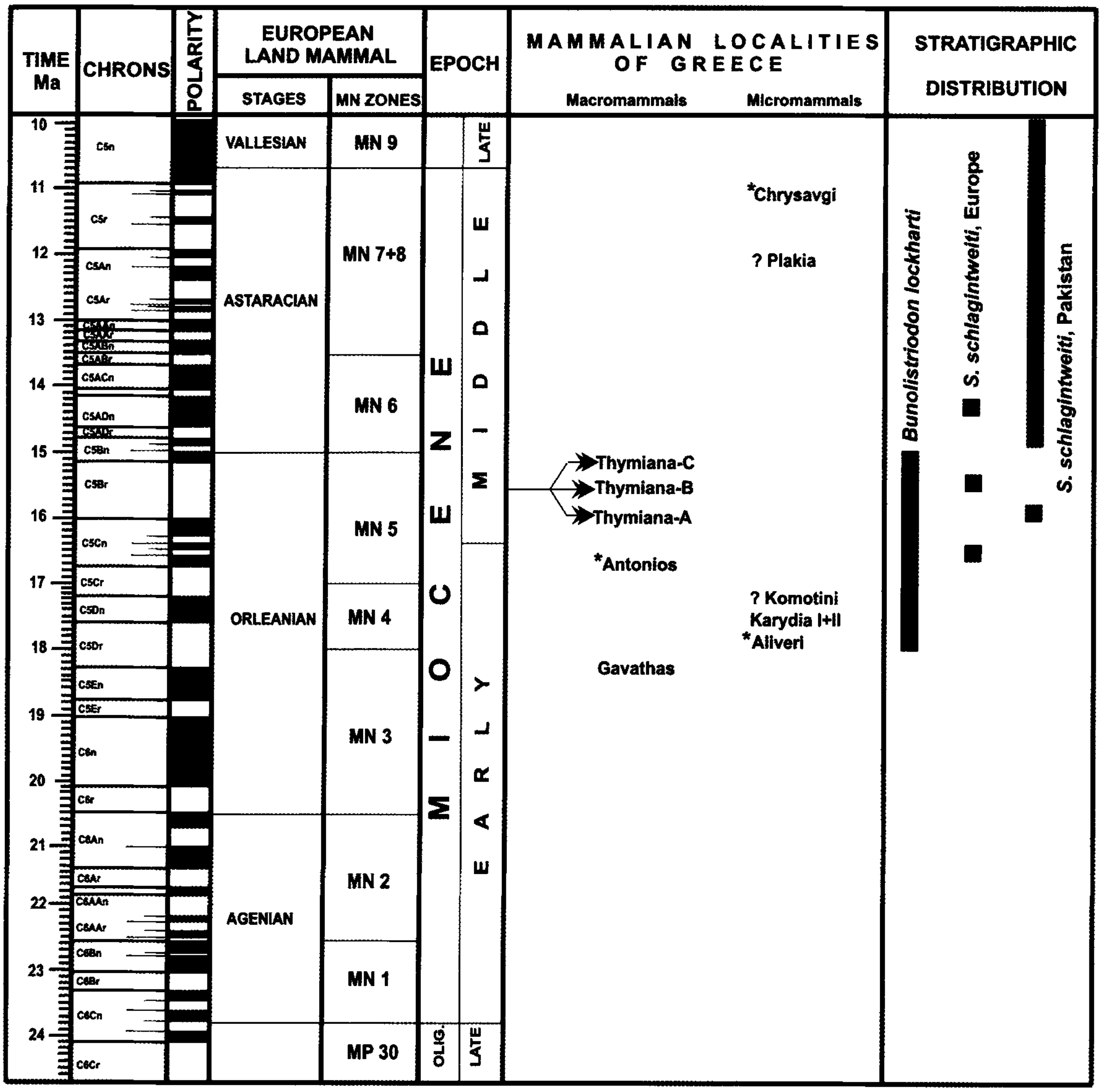


Fig. 11. The early-middle Miocene mammal localities of Greece and the stratigraphic distribution of the suoids found in Antonios. The division of the Miocene is based to STEININGER (1998).

evated in *B. latidens* forming a fovea in this part of the tooth. The Antonios m2 is also larger and with weaker cingulum and thus different from the type of *B. latidens*. The Antonios i2 has similar morphology to that of the type of *B. latidens* but it is larger with stronger pillars and remarkably stronger distolingual cingular projection. A form similar to *B. latidens* from Spain is referred to as *B.* aff. *latidens* (VAN DER MADE 1996). It is smaller than Antonios sample (Figs 8, 9) and has some morphological differences. The P4 ANT-81 has stronger buccal cingulum and the mesiobuccal cusp is more developed and clear than that of *B.* aff. *latidens* (VAN DER MADE 1996: pl.15, fig.15). The p4 ANT-4 has less rounded occlusal outline and weaker cingulum than *B.* aff. *latidens*, while the Antonios i2 has stronger pillars and distolingual cingular projection (VAN DER MADE 1996; pl. 16, figs 2, 3, 10, 11). Taking in mind all the above mentioned comparisons, the Antonios listriodont suid fits better with *Bunolistriodon lockharti*.

Biochronology-Conclusions

The Antonios fauna has been originally dated from the upper part of MN 4 to the lower part of MN 5 (KOUFOS & SYRIDES 1997). The MN 4/5 boundary was considered at that time as the early/middle Miocene one dated to ~17.0 Ma (STEININGER et al. 1996; SEN 1997). Later, the early/middle Miocene boundary changed and it is referred to the lower part of MN 5 at ~16.5 Ma (STEININGER 1999). The micromammals of Antonios suggested an age at the MN 4/5 boundary as they include both taxa of MN 4 and MN 5 (VASSILEIADOU & KOUFOS, 2005).

The detailed study of the Antonios suoids provides also some data about the age of the fauna. The species *B. lockharti* is known from several European localities with a great stratigraphic range from middle-early Orleanian ELMA, MN 4-5 (Fig. 11). Its presence in Antonios fauna and its similarity to the material of the most European localities cannot provide a more precise age. The other suoid of Antonios, *S. schlagintweiti*, is known from Pakistan where it was found in the Lower Manchar Formation dated to late Orleanian ELMA, MN 5, as well as to the Chinji Formation dated from Astaracian- early Vallesian ELMA, MN 6-9 (VAN DER MADE & HUSSAIN 1992). The same taxon was also recognized in Leoben (Austria), dated to early Astaracian ELMA, MN 6 (NOW, 2006). In Greece *S. schlagintweiti* is known from the locality Thymiana B (Chios, Aegean Sea). The Thymiana fauna suggests a late Orleanian ELMA, MN 5 age, while the magnetostratigraphic record provides an age of ~15.5 Ma for the fossiliferous sites of Thymiana (KONDOPOULOU et al. 1993; KOUFOS et al. 1995; BONIS et al. 1997, 1998). The Antonios sanithere is smaller than that of Thymiana, indicating a probable older age. Accepting that the MN 4/5 boundary is at ~16.5 Ma and the Antonios sanithere is older than Chios one, then an age at the beginning of the MN 5 is quite possible for Antonios. This age determination fits quite well with that provided by the micromammals (VASSILEIADOU & KOUFOS, 2005).

In conclusion the Antonios suoids are very interesting as they increase our knowledge about them in early/middle Miocene of Eastern Mediterranean. Especially the sanitheres' which are very rare in Eurasia, provided interesting data about their morphology and age.

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