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Musteloids and feloids (Mammalia, Carnivora) from the late Miocene locality of Pikermi (Attica, Greece)

Mustéloïdés et féloïdés (Mammifères, Carnivores) du Miocène supérieur de Pikermi (Attique, Grèce)

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Abstract

Some relatively rare carnivore remains from Pikermi are studied. The present specimens include *Simocyon primigenius* (ROTH and WAGNER, 1854), *Promeles palaeatticus* (WEITHOFER, 1888), *Martes woodwardi* PILGRIM, 1931, *Felis attica* WAGNER, 1857 and *Machairodus giganteus* (WAGNER, 1848), as well as some postcranial remains that resemble *Enhydriodon*? *latipes* PILGRIM, 1931 and are assigned to Mustelidae gen. et spec. indet. Some of these species were not known until now but from their holotypes as *M. woodwardi* and *E.*? *latipes*. Other species such as *F. attica* and *M. giganteus* are better known but from relatively scant material. Since the material of the earlier mentioned species comes from Pikermi, their type locality, it is of especial importance and improves our knowledge for the Pikermi carnivores and their relationships to other species. In some cases where the material comes from ossiferous blocks, the accompanying faunal context is discussed.

Résumé

Ce travail concerne quelques restes de carnivores de Pikermi rarement représentés. Les échantillons étudiés comprennent des restes de *Simocyon primigenius* (ROTH et WAGNER, 1854), *Promeles palaeatticus* (WEITHOFER, 1888), *Martes woodwardi* PILGRIM, 1931, *Felis attica* WAGNER, 1857 et *Machairodus giganteus* (WAGNER, 1848), ainsi que quelques fossiles qui ressemblent à *Enhydriodon* ? *latipes* PILGRIM, 1931 et qui sont attribués à Mustelidae gen. et spéc. indét. Jusqu'à présent, quelques unes des espèces mentionnées n'étaient connues que par leur holotype, comme *M. woodwardi* et *E.*? *latipes*, ou un matériel peu nombreux comme *F. attica* et *M. giganteus*. Puisque le matériel des espèces étudiées provient de Pikermi, leur localité-type, il est important de bien connaître la morphologie des carnivores de Pikermi et leurs relations avec les espèces et les formes voisines. Dans le cas où les échantillons proviennent de blocs ossifères, le contenu faunique est discuté.

Keywords: Mammalia; Carnivora; Late Miocene; Pikermi; Greece

Mots clés: Mammifères; Carnivores; Miocène supérieur; Pikermi; Grèce

1. Introduction

The Pikermi fauna is known world-wide for its wealth in late Miocene mammals. This fauna includes many type genera and species, found subsequently in many other localities of Europe and Asia. Thus, a good knowledge of their characters and variation is quite important. Despite, many important works on the carnivores of the Pikermi fauna, a lot of material still remains unstudied in various museum collections.

The present study is based essentially on the Pikermi collections stored in the Athens Museum of Palaeontology and Geology. A part of these collections comes from the

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excavations carried out in Pikermi by Woodward and Skouphos in 1901. It is well known that many of the specimens collected by Woodward and Skouphos are now in the British Museum (Woodward Collection) and have been studied by Pilgrim and Hopwood (1928) and Pilgrim (1931). A lot of material, however, was left in the Athens Museum of Palaeontology and Geology, and was found in wooden boxes where the specimens were wrapped with newspapers of 1901. Some of these newspapers, dated from 1 to 23 May 1901, also had articles dedicated to these excavations (Roussiakis, 1996). The mentioned dates are in accordance with the information provided by Woodward (1901) that he excavated in Pikermi from the early April until the middle of July.

Purpose and scope of this work is to compare some relatively rare carnivore remains from Pikermi to those stored in other museum collections, and increase our knowledge for their size and morphological variation. Some of the specimens come from ossiferous blocks prepared by the author. In these cases the accompanying faunal context is given. This is especially important since the fossils collected from Pikermi come from two or three different fossiliferous levels (Gaudry, 1862; Woodward, 1901; Abel, 1922, fig. 132) and the exact faunal composition of each level is unknown.

1.1. *Methodology*

The measurements used for the teeth are the maximum anteroposterior diameter of the tooth (L) and the maximum transverse diameter (W). The Ltrd signifies the length of the trigonid and the Ltld the length of the talonid. The height of the mandibular corpus, whenever used, has been measured lingually, under the middle of M_1. The measurements of the postcranial material are as following: Lmax, maximum length; Lf, maximum functional length; DTpr, transverse diameter of the proximal extremity; DAPpr, anteroposterior diameter of the proximal extremity; DTdia, transverse diameter of the diaphysis on its middle; DAPdia, anteroposterior diameter of the diaphysis on its middle; DTdistmax, maximum transverse diameter of the distal extremity; DTdistart, transverse diameter of the distal articular surface, DAPdistart, anteroposterior diameter of the distal articular surface; DAPdistmax, maximum anteroposterior diameter of the distal extremity; Hmax, maximum height of a carpal or tarsal bone; DTmax, maximum transverse diameter of a carpal or tarsal bone; DAPmax, maximum anteroposterior diameter of a carpal or tarsal bone; Htr, height of the astragalus trochlea measured laterally. DT(tub), transeverse diameter of the tuber calcaneum; DAP(tub), anteroposterior diameter of the tuber calcaneum. All measurements are given on millimetres.

1.2. *Abbreviations*

AMPG, Athens Museum of Palaeontology and Geology, National and Kapodistrian University of Athens; BM(NH), British Museum of Natural History; LGPUT, Laboratory of Geology and Palaeontology, Aristotelian University of Thessaloniki; MGL, Musée Géologique, Lausanne; MNHNP, Muséum national d'Histoire naturelle, Paris.

2. Systematic palaeontology

Order: CARNIVORA Bowdich, 1821

Superfamily: MUSTELOIDEA Fischer von Waldheim, 1817

Family: PROCYONIDAE Gray, 1825

Subfamily: SIMOCYONINAE Zittel, 1893

Genus: *Simocyon* WAGNER, 1858

Simocyon primigenius (ROTH and WAGNER, 1854)

Material: PG 01/104: left mandibular ramus with C_i, and P_4–M_2.

Description: The mandible (Fig. 1) is robust, with a symphysis that measures about 29 mm in length and extends posteriorly to the middle of the postcanine diastema. There is a large mental foramen below the anterior root of P_4 and two smaller foramina below the alveolus for the P_1. The anterior border of the masseteric fossa is below the posterior border of M_2. The number of the incisor alveoli cannot be evaluated precisely, but at least two alveoli are visible. A slightly ovoid alveolus for the P_1 is also present just behind the canine.

The lower canine is robust and relatively low, with a strong mesiolingual keel and a less robust posterior one. It also has a faint groove at the labial side and its upper half. There is no P_2 or P_3. The remaining teeth are arranged in a strongly curved line and the posterior part of P_4 slightly overlaps the anterior part of M_1. The P_4 has a high main cusp, a well developed posterior accessory cusp, and a slightly elevated posterior cingulum. There is no anterior accessory cusp. There is a faint anterior cingulum at the mesiolingual corner of the tooth. The greatest width of the tooth is at the region of the posterior accessory cusp. The M_1 is large and robust. Its protoconid is especially higher than the paraconid, and the metaconid is appressed to the protoconid for most of its height. The trigonid comprises about two-third of the total length of the tooth (Table 1). The hypoconid is large and forms an anteroposteriorly directed cutting crest. The entoconid is significantly lower than the hypoconid. There is a labial cingulum at the base of the talonid. The M_2 is large relatively to M_1 and elongated (Table 1). Its protoconid is clearly higher than the metaconid and is situated slightly more anteriorly. From the tip of the protoconid start two crests, an anterior and a posterior one. The posterior crest (hypoconid crest) continues posteriorly and meets the posterior cingulum, while the anterior one meets a transverse crest, which could correspond to the paraconid. Behind the metaconid there is an undulated area that most probably corresponds to the entoconid. The trigonid is practically half of the total length of the tooth (Table 1) and the talonid is surrounded by a crenulated

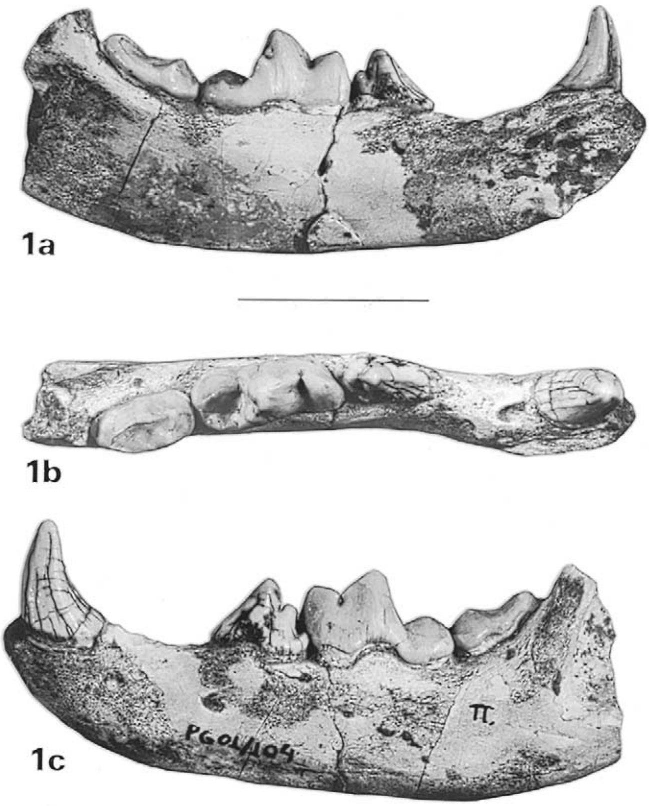

Fig. 1. *S primigenius* (ROTH and WAGNER, 1854), Pikermi. **1.** Left mandible (AMPG PG 01/104); **a)** lingual view, **b)** occlusal view, **c)** labial view. Scale bar 30 mm.

Fig. 1. **1.** Mandibule gauche (AMPG PG 01/104); **a)** vue linguale, **b)** vue occlusale, **c)** vue labiale. Échelle graphique 30 mm.

cingulum. There is also a cingulum at the base of the anterior part of the tooth and labially.

Discussion: The first remains of *S. primigenius* were found in Pikermi and described by Roth and Wagner (1854). These authors referred the mandibles under the name "*Gulo primigenius*" and the skulls as "*Canis lupus primigenius*" (Roth and Wagner, 1854: Pl. 8, figs. 1 and 2, fig. 7). Later, Wagner (1858, fide Pilgrim, 1931) considered the mandible figured by Roth and Wagner (1854: Pl. 8, figs. 1 and 2) as "*Gulo primigenius*" conspecific with the associated skull and mandible figured under the name "*Pseudocyon robustus*" (Wagner, 1857: Pl. 6, fig. 13), but transferred these remains to the new genus *Simocyon* WAGNER, 1858. Gaudry (1861, 1862) regarded *Gulo diaphorus* KAUP, 1832 from the Eppelsheim conspecific with *S. primigenius* from Pikermi, but referred these remains to a new genus introduced earlier, the genus *Metarctos* GAUDRY, 1860, and named both the Eppelsheim and Pikermi specimens *Metarctos diaphorus*. Later, however, Gaudry (1865, 1866) used the name *Simocyon diaphorus*. Pilgrim (1931) considered the Eppelsheim form different from the Pikermi one, both on the specific and the generic level. The Eppelsheim and Pikermi forms have been considered different species but attributed to the same genus, the genus *Simocyon* WAGNER, 1858, by most subsequent authors as Thenius (1949a), de Beaumont (1964), Wolsan (1993), Morlo (1997) and Ginsburg (1999).

As mentioned by Pilgrim (1931) *S. primigenius* shows important variation. Of three mandibles available to Pilgrim, only one (BM(NH) M. 9034) has an alveolus for P_1, and none more than one incisor alveolus. The mandible of *S. primigenius*, however, figured by Wagner (1857: Pl. 6,

Table 1
Measurements of the lower teeth of *S. primigenius* from Pikermi. MNHNP PIK. 3343 is a cast of "*P. robustus*", described by Wagner (1857: Pl. 6, fig. 13) and re-figured by de Beaumont (1964: Pl. 1, *fig. 5*)
Dimensions des dents inférieures de *S. primigenius* de Pikermi

	AMPG PG 01/104 Pikermi	MNHNP, Pikermi (after the author)						Pilgrim, 1931		
		PIK.3343		PIK.3020		PIK.3017	PIK.3018	Pikermi, BM(NH)		
		(sin.)	(dext.)	(sin.)	(dext.)			M.9032	M.9033	M.9034
LC_i	12.6	12.0	11.1	12.4	–	(12.3)	–	–	12.0	–
WC_i	9.9	10.0	8.5	10.2	–	–	–	–	–	–
C_i-P_4	17.0	14.6	15.0	21.5	–	19.4	–	–	–	–
LP_4	15.1	14.0	14.7	13.7	14.0	14.2	14.0	–	15.0	13.5
WP_4	(8.4)	9.0	9.5	9.2	8.8	–	9.2	–	9.0	9.0
LM_1	23.7	23.0	21.9	22.9	22.8	22.0	22.5	24.0	25.0	23.0
WM_1	10.5	10.1	10.5	10.3	9.9	10.0	10.2	10.0	11.0	10.0
$LtrdM_1$	17.7	16.2	16.5	17.3	17.1	16.8	16.8	–	–	–
LM_2	16.9	15.7	15.8	17.3	16.4	16.6	17.2	15.5	(16.0)	–
WM_2	9.1	8.3	8.7	8.8	8.6	8.6	8.8	9.0	12.0	–
$LtrdM_2$	8.5	7.7	8.1	9.0	8.6	8.2	9.0	–	–	–
$L(P_4–M_2)$	53.0	47.3	48.4	51.2	53.2	50.8	51.9	–	–	–
$(WC_i/LC_i) \times 100$	78.6	83.3	76.6	82.3	–	(65.0)	–	–	–	–
$(WP_4/LP_4) \times 100$	55.6	64.3	64.6	67.2	62.9	–	65.7	–	60.0	66.7
$(WM_1/LM_1) \times 100$	44.3	43.9	47.9	45.0	43.4	45.5	45.3	41.7	44.0	43.5
$(WM_2/LM_2) \times 100$	53.8	52.9	55.1	50.9	52.4	51.8	51.2	58.1	(75.0)	–
$(LtrdM_1/LM_1) \times 100$	74.7	70.4	75.3	75.5	75.0	76.4	74.7	–	–	–
$(LtrdM_2/LM_2) \times 100$	50.3	49.0	51.3	52.0	52.4	49.4	52.3	–	–	–
$(LM_2/LM_1) \times 100$	71.3	68.3	72.1	75.5	71.9	75.5	76.4	64.6	64.0	–

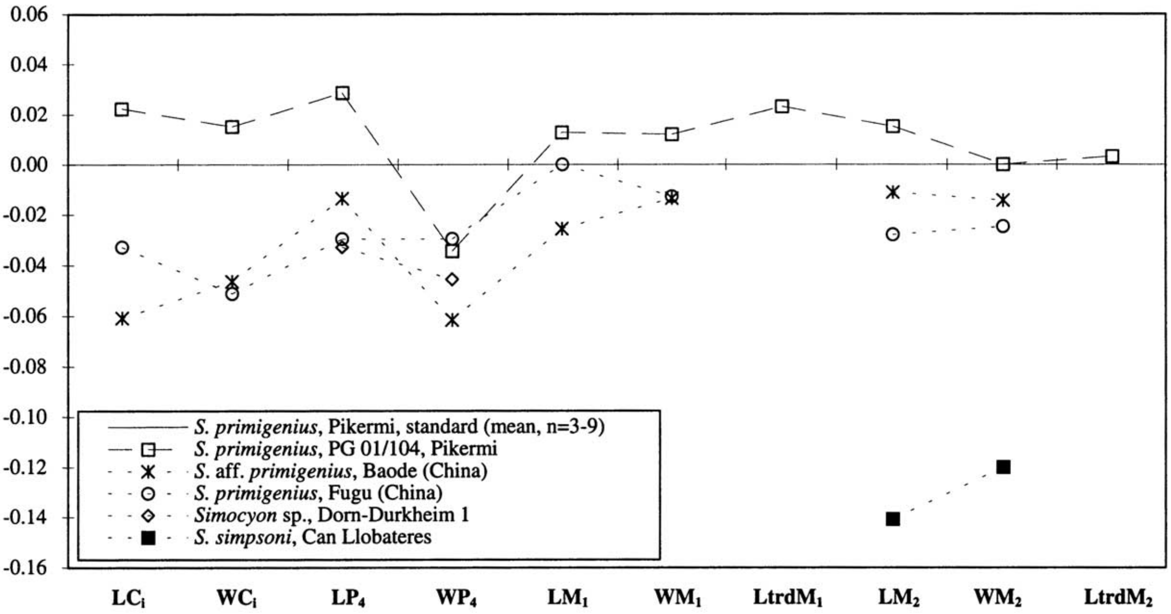

Fig. 2. Logarithmic ratio diagram comparing the lower teeth of AMPG PG 01/104 to *Simocyon* from various localities. Standard, *S. primigenius*, Pikermi, mean of the specimens of Table 1. *S. primigenius* from Fugu according to Wang (1997); *S.* aff. *primigenius* according to Zdansky (1924); *Simocyon* sp. according to Morlo (1997); *S. simpsoni* according to Crusafont-Pairó and Kurtén (1976).

Fig. 2. Diagramme logarithmique des rapports des dimensions des dents inférieures de AMPG PG 01/104 et *Simocyon* provenant des différentes localités.

fig. 13) and re-figured by de Beaumont (1964: Pl. 1, Fig. 5) has three incisors. The present specimen of the lower canine is not well preserved anteriorly, but shows at least two incisor alveoli. The variation that concerns the presence or not of an alveolus for P$_1$ is also mentioned by Gaudry (1862). The development of the anterior accessory cusp of P$_4$ also varies, since for example an anterior accessory cusp is present in BM(NH) M. 9033 but absent in M. 9034 (Pilgrim, 1931). Compared to other specimens of *S. primigenius* from Pikermi, the present specimen has a relatively narrower P$_4$ (possible due to its slightly damaged posterolingual corner) the observable difference, however, is not important (Table 1 and Fig. 2).

Except Pikermi, which is the type locality, *S. primigenius* is also referred from the late Miocene (possible MN 11–12) of Halmyropotamos (Melentis, 1968) in Greece, the middle Turolian (MN 12) of Cerro de la Garita (Alcalá, 1994) and Concud (Fraile et al., 1997) in Spain, and Kalimanci in Bulgaria (Ginsburg, 1999). This species has not been recorded until now from Samos or Maragha (Solounias, 1981; Bernor et al., 1996; Koufos et al., 1998).

There is no recent review of the various species from Europe, Asia and America that have been referred to *Simocyon*. *Simocyon diaphorus* (KAUP, 1832) from the Vallesian (MN 9) of Eppelsheim is a primitive species that retains the P$_2$ and P$_3$. *Protursus simpsoni* CRUSAFONT PAIRÓ and KURTÉN, 1976, from the Vallesian of Can Llobateres in Spain, has been based on a M$_2$, but referred to *Simocyon* WAGNER, 1858 by Thenius (1977). *S. simpsoni* is significantly smaller than the present specimen (Fig. 2). *Simocyon batalleri* (VIRET, 1929) from the Vallesian (MN 9) of Can Llobateres in Spain retains the P$_3$ (Wang, 1997), as well as *Simocyon hungaricus* KRETZOI, 1942, from the early Turolian (MN 11) of Csákvár in Hungary (Morlo, 1997). A specimen from Baode, in China, mentioned as *S.* aff. *primigenius* by Zdansky (1924: Pl. 2, figs. 1 and 2) is only slightly smaller than *S. primigenius* from Pikermi (Fig. 2) and presents a small anterior accessory cusp in P$_4$. This specimen has been attributed to the new species *Simocyon zdanskyi* KRETZOI, 1951 (fide Morlo, 1997), or *S. primigenius* by Wang (1997). I have not seen the specimens of the BM(NH) that according to Pilgrim (1931) have an anterior accessory cusp, but the MNHNP *S. primigenius* specimens do not have a true anterior accessory cusp, except sometimes a small bulge at their anterior part, especially smaller from Zdansky's specimen in all cases. An anterior accessory cusp in P$_4$ is also present in a specimen from the early Turolian locality of Dorn-Dürkheim 1 in Germany, described as *Simocyon* sp. by Morlo (1997: Pl. 1, fig. 2). As we see (Fig. 2) the dimensions of this specimen are close to those of the Pikermi and Baode *Simocyon*. Its anterior accessory cusp, however, is even larger than that of the Chinese *Simocyon*. Another *Simocyon* specimen from China is the associated skull and mandibles from Fugu referred to *S. primigenius* by Wang (1997). This specimen, however, posses reduced P$_2$ and P$_3$, and according to Wang (1997) occupies an intermediate stage of premolar reduction between *S. diaphorus* and *S. batalleri*. Its peculiar dental formula, similar to that of *S. diaphorus*, could be, according to Wang (1977), an individual variation in a species with long diastema, occupied sometimes by vestigial, not functional premolars. It is interesting, however, to notice that none of the available Pikermi specimens of *S. primigenius* presents similar dentition to the Fugu *Simocyon*. Outside

Europe and Asia, *S. marshi* (THORPE, 1921) from the Rattlesnake Formation in North America, has been considered as a geographic subspecies of *S. primigenius* by Wang (1997).

Family: MUSTELIDAE Fischer von Waldheim, 1817
Subfamily: MUSTELINAE Fischer von Waldheim, 1817
Genus: *Promeles* ZITTEL, 1890
Promeles palaeatticus (WEITHOFER, 1888)

Material: PG 01/105: skull with its associated mandibular rami, the right mandibular ramus has been removed in order to display the upper dentition; PA 3501/91: right mandibular ramus with P_2–M_1 and the alveolus for M_2; PA 161/91: left tibia, lacking its most proximal part; PA 3502/91: associated bones of the left hind limb, including the astragalus, calcaneum, navicular, cuboid, the three cuneiforms and the Mts I–IV, found connected in anatomical position, in the same small ossiferous block with the mandible PA 3501/91.

Description: The preorbital region is short and the anterior margin of the orbit is situated above the anterior part of P^4. The infraorbital foramen is large (greatest height about 4 mm) and opens above the middle of P^4. The lateral wall of the maxilla has a deep depression above the anterior half of the P^4. The palate is significantly prolonged (about 8 mm) behind M^1 (Fig. 3[1]). In dorsal view, the lateral walls of the braincase, behind the postorbital processes of the frontals, are almost parallel to each other and for a distance of about 10 mm. Then the skull widens abruptly. The smallest width of the braincase behind the postorbital processes measures about 19.5 mm, while the greatest width of the braincase is 37 mm. There is a sagittal crest that bifurcates about 16 mm behind the postorbital processes of the frontals. The length from the prosthion to the occipital condyles is about 93 mm, and the length from the prosthion to the posterior border of M^1 is about 42 mm.

The postglenoid process projects significantly at its medial part and looks forward. The paroccipital process is anteroposteriorly compressed, forming a crest that directs laterally. The posterior lacerate foramen is simple and clearly separated from the condyloid foramen.

The P^1 is missing. The P^2 is obliquely oriented in relation to P^3, with its long axis mesiolingually–posterolabially directed. The main cusp of P^2 is situated slightly anteriorly. The P^3 is more symmetrical than P^2. Both P^2 and P^3 have a small posterior cingulum, slightly more developed in P^3. The P^4 is Mustelinae on its shape. At its anterior part the cingulum is slightly inflated. The anterior contour of the tooth, between the protocone and the parastyle, is concave. Contrary to P^4, the M^1 is Melinae-like. The protocone is elongated and crescentic. The metaconulus is clearly separated from the protocone. The lingual cingulum is thick and elevated. The posterior outline is slightly concave, just lingually of the metaconulus.

The depth of the mandibular corpus (Fig. 3[2]) under M_1 is slightly smaller than the total length of the M_1 (Table 2). The masseteric fossa extends anteriorly to the middle of M_2. The mental foramina are variable in number and position. The right mandibular ramus of PG 01/105 has one mental foramen under the middle of P_2 and one more under the posterior part of the P_3. PA 3501/91 has one mental foramen under the P_2 and P_3 contact, and one more under the posterior half of the P_3. In PA 3501/91 and PG 01/105 (sin.) there is one more very small foramen under the P_2 and C_i contact. The distance from the anterior part of the canine to the mandibular condyle is about 62 mm. The mandibular condyle is slightly higher from the alveolar level. The symphysis is about 19 mm in length.

The lower canine is strongly curved and very robust at its base (Fig. 3[2]). The available mandibles do not show P_1 or an alveolus for it. The rest of the premolars have a slightly triangular outline with anterior part more narrow than the posterior. The P_2 is obliquely situated relatively to P_3 and its long axis has a mesiolabial–posterolingual direction. The P_2 and P_3 have no accessory cusps. Their main cusp is slightly anteriorly situated, so these teeth in lateral view are asymmetrical. The P_4 is more symmetrical and has a high posterior accessory cusp, strongly appressed to the posterior slope of the main cusp. In P_3 and P_4 the anterior cingulum is slightly elevated, especially in P_4. In both specimens, M_1 is worn. Its trigonid is low and slightly larger than the talonid (Table 2 and Fig. 3[2]). Due to the worn, the structure of the talonid is not clearly visible. The hypoconid, however, seems the most developed cusp of the talonid. The M_2 is surrounded from small cusps.

The skeleton of *P. palaeatticus* is relatively well known from Weithofer (1888) and Pilgrim (1931). The present material is in good state of preservation except for the third metatarsal that is broken distally and the tibia whose proximal-most part is lacking. All the hind-limb bones, except the tibia, were found connected in anatomical position (Fig. 3[4]), in the same small ossiferous block with the mandible PA 3501/91.

The tibia (Fig. 3[3]) is not completely preserved (maximum measurable length of the tibia = 76 mm), while the greatest transverse diameter of the distal epiphysis measures 12 mm and the greatest anteroposterior diameter 8.4 mm. The distal articular surface is relatively flat. Two well-marked crests at the posterior surface of the distal epiphysis define a groove for the attachments of ligaments. The surface for the *tibialis posticus* is wide and distally expanded, taking up a large part of the diaphysis. The calcaneum (Fig. 4) is wide relative to its height. Two low processes at the *tuber calcanei* define a wide groove for the *tendo calcaneus communis*. From these two processes the medial one is the higher. At the lateral surface of the bone there is a large and deep fossa for the *quadratus plantae*. The peronial process is slightly above the distal articular surface and has on its surface a narrow groove for the *peroneus longus*. The cuboid facet is ovoid, concave, and its larger diameter directs slightly laterally. The most characteristic of the astragalus (Fig. 3[6]) is the high neck, which

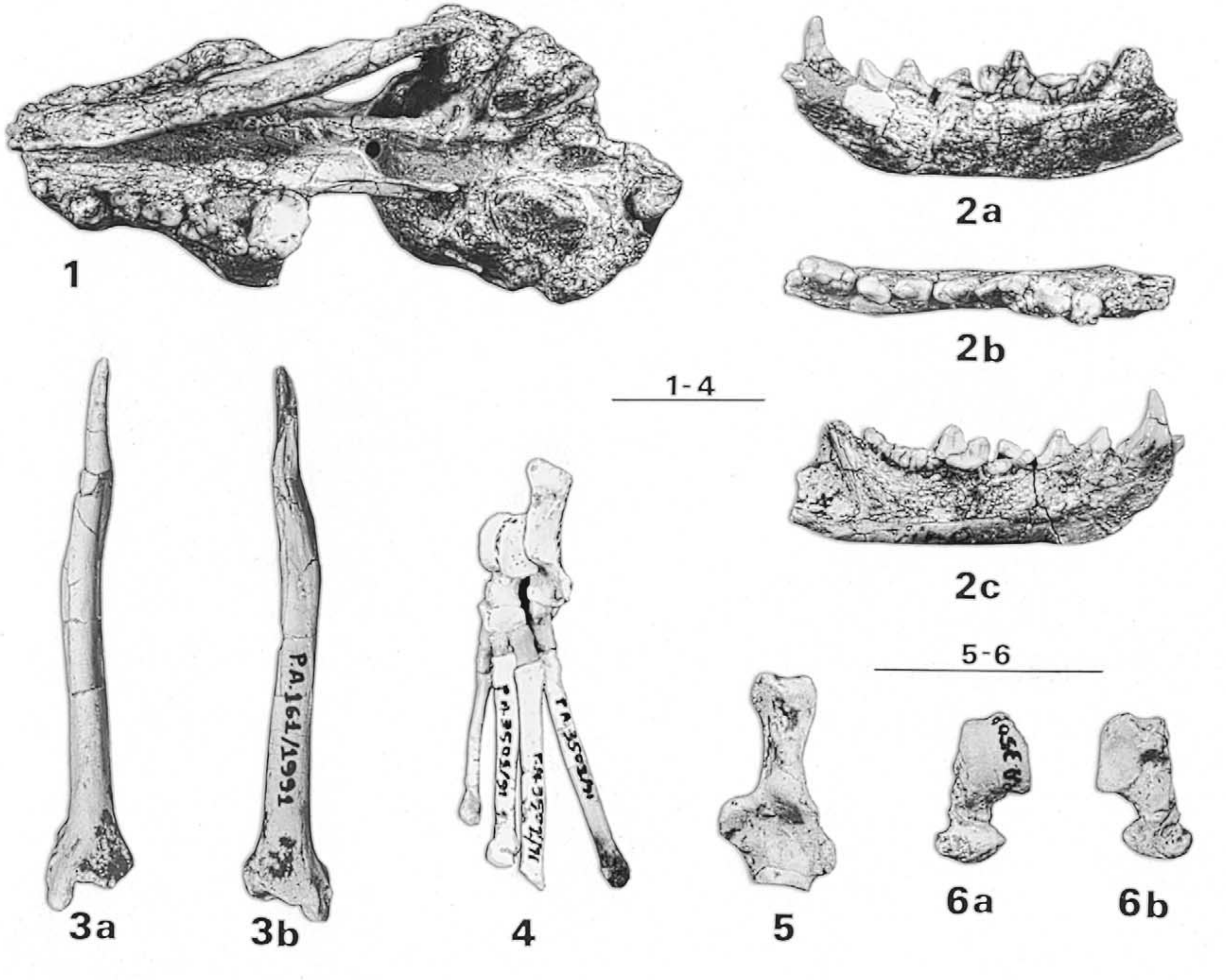

Fig. 3. *P. palaeatticus* (WEITHOFER, 1888), Pikermi. **1.** Skull with its associated left mandible (AMPG PG 01/105), ventral view. **2.** Right mandible (AMPG 01/105); **a)** lingual view, **b)** occlusal view, **c)** labial view. **3.** Left tibia (AMPG PA 161/91); **a)** anterior view, **b)** posterior view. **4.** Left pes (AMPG PA 3502/91), anterior view. **5.** Left calcaneus (AMPG PA 3502/91), anterior view. **6.** Left astragalus (AMPG PA 3502/91); **a)** anterior view, **b)** posterior view. Scale bar 20 mm.

Fig. 3. **1.** Crâne avec sa mandibule gauche (AMPG PG 01/105), vue ventrale. **2.** Mandibule droite (AMPG 01/105); **a)** vue linguale, **b)** vue occlusale, **c)** vue labiale. **3.** Tibia gauche (AMPG PA 161/91); **a)** vue antérieure, **b)** vue postérieure. **4.** Pes gauche (AMPG PA 3502/91); vue antérieure. **5.** Calcaneus gauche (AMPG PA 3502/91), vue antérieure. **6.** Astragalus gauche (AMPG PA 3502/91); **a)** vue antérieure, **b)** vue postérieure. Échelle graphique 20 mm.

Table 2
Measurements of the lower teeth of *P. palaeatticus* from Pikermi. BM(NH) M. 9029 and M. 9030 (described first by Pilgrim, 1931) were measured on casts of the MNHNP collections
Dimensions des dents inférieures de *P. palaeatticus* de Pikermi

	AMPG PA 3501/91	AMPG PG 01/105 (dext.)	Weithofer, 1888	Major, 1902	BM(NH) M. 9028 (Pilgrim, 1931)	BM(NH) (after the author)	
						M. 9029	M. 9030
(L × W)C_i	–	(5.5) × 4.7	–	5.7 × –	–	–	–
(L × W)P_2	4.9 × 2.6	4.7 × 2.7	4.3 × 2.4	4.5 × –	(5.5) × (3.5)	–	4.2 × 2.6
(L × W)P_3	5.9 × 3.1	5.4 × 3.1	4.8 × 2.6	5.0 × –	7.0 × 3.5	5.4 × 2.9	5.0 × 3.0
(L × W)P_4	6.9 × 3.5	6.6 × 3.3	6.3 × 3.0	6.5 × –	7.0 × 4.0	7.0 × 3.6	–
(L × W)M_1	13.2 × 6.0	12.9 × 6.2	11.8 × 5.0	12.4 × –	15.5 × 7.0	13.0 × 6.7	13.4 × 6.5
LtrdM_1	(7.6)	(7.7)	5.4	–	–	7.4	7.5
(L × W)M_2	–	5.6 × 5.0	4.5 × 4.2	–	–	5.9 × 5.8	–
(LM_2/LM_1) × 100	–	43.4	38.1	–	–	45.4	–
(LtrdM_1/LM_1) × 100	(57.6)	(59.7)	45.8	–	–	56.9	56.0
HmM_1	9.7	11.8	–	–	–	11.8	11.0

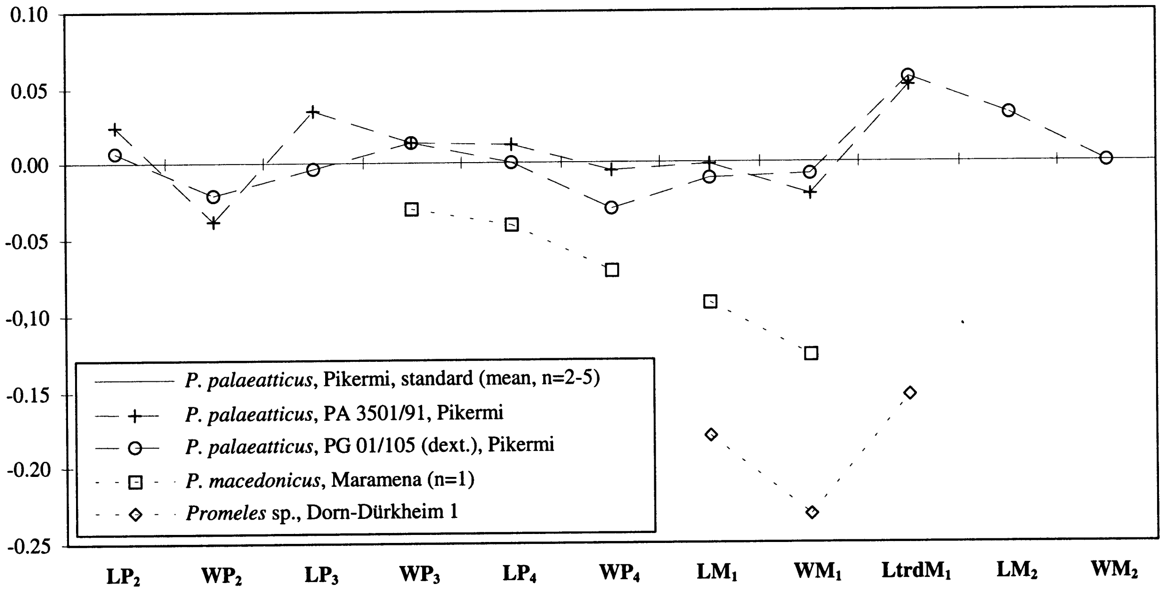

Fig. 4. Logarithmic ratio diagram comparing the lower teeth of AMPG PG 01/105 and AMPG PA 3501/91 to *Promeles* from various localities. Standard, *P. palaeatticus*, Pikermi, mean of the specimens of Table 2. *P. macedonicus* according to Schmidt-Kittler (1995); *Promeles* sp. according to Franzen and Storch (1975).

Fig. 4. Diagramme logarithmique des rapports des dimensions des dents inférieures de AMPG PG 01/105, AMPG PA 3501/91 et *Promeles* provenant des différentes localités.

directs medially and together with the head measures about half of the total height of the bone. The head of the astragalus is elongated (length/width almost 2/1) with its long axis almost transversely directed relatively to the trochlea. The trochlea is relatively shallow, in accordance with the form of the astragalus facet of the tibia. The navicular is anteroposteriorly elongated. It articulates with the cuboid through a narrow lateral surface but not with the calcaneum. The cuboid is wide relative to its height. Its proximal articular surface is transversely elongated with transverse diameter almost twice than the anteroposterior one. Its distal articular surface for the Mt IV is slightly concave. The first cuneiform is higher than the third. The metatarsals are slightly curved in lateral view. The Mt I has at its proximal part a lateral tuberosity that extends higher than its articular surface for the first cuneiform. All the available metatarsals have proximal articular surfaces more (Mt I) or less (Mt II) convex anteroposteriorly. The Mt III is not completely preserved but it could be similar in length to the Mt IV (Tables 3 and 4).

Discussion: The species *P. palaeatticus* has been variously included in the Mustelinae (Weithofer, 1888; Major, 1902; Thenius, 1949b; Schmidt-Kittler, 1995; Morlo, 1997) or the Melinae (Pilgrim, 1931; Petter, 1971; Ginsburg, 1999). Following Thenius (1949b), we include *P. palaeatticus* in the Mustelinae. This species is known from Pikermi and Samos (Weithofer, 1888; Major, 1888, 1894, 1902). Solounias (1981) mentions its occurrence in the quarries A and Q1 of Samos, while Bernor et al. (1996) mention it in the “Upper Maragha” also. Morlo (1997) also reports *P. palaeatticus* in the early Turolian of Dorn-Dürkheim 1 in Germany, based on a M_1 referred firstly to *Promeles* sp. by Franzen and Storch (1975). As we shall see later, however, this specimen is significantly smaller than the Pikermi *P. palaeatticus*. *Promeles* sp. is also referred from the probable early Turolian locality of MTL–A in Samos (Koufos et al., 1998).

The M^1 of *P. palaeatticus* shows some variation on its posterior outline. This is almost straight in the holotype (Weithofer, 1888: Pl. 10, fig. 1; Schmidt-Kittler, 1995: fig. 4), but more concave lingually of the metaconulus in the present specimen and in the specimen described by Major (1902: Pl. 7, figs. 3 and 4). The available upper teeth are not different in size from other specimens of *P. palaeatticus* (Table 5 and Fig. 5). Concerning the lower teeth, the specimen described by Weithofer (1888) seems to have M_1 with smaller trigonid than other specimens of *P. palaeatticus* (Table 2). According to the measurements given by Weithofer (1888) the trigonid (“Vorderpartie”) of the M_1 is larger than the posterior part (“Hinterpartie”) of the tooth. This, however, does not correspond to the figures given by Weithofer (1888: Pl. 10, figs. 3–5), or the re-drawing of Weithofer’s specimen by Schmidt-Kittler (1995: fig. 6) where the trigonid seems larger than the talonid. Otherwise, the present specimens have M_1 with trigonid almost equally elongated relatively to the total length of the tooth as other specimens of *P. palaeatticus* (Table 2). Compared to *Promeles macedonicus* SCHMIDT-KITTLER, 1995, the upper molar of *P. palaeatticus* is larger (Fig. 5) and differs on its metaconulus. This is well separated from the posterior part of the protocone in *P. palaeatticus* and does not extend labially. In *P. macedonicus*, on the other hand, the metaconulus is connected by a ridge to the protocone and extends to the posterolabial cingulum of the tooth (Schmidt-

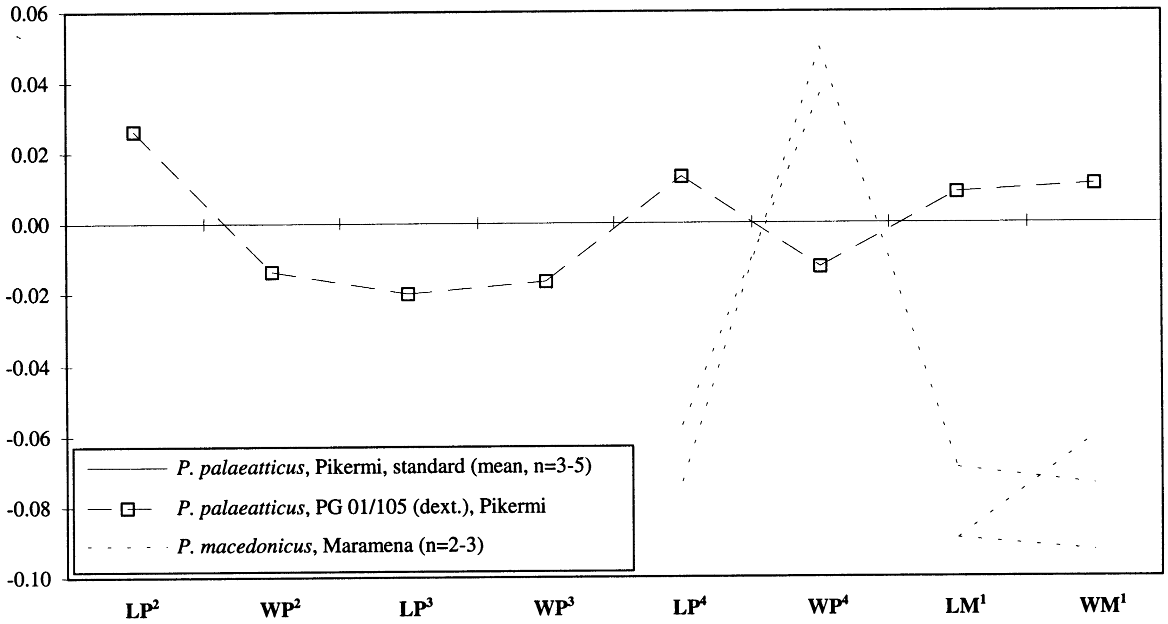

Fig. 5. Logarithmic ratio diagram comparing the upper teeth of AMPG PG 01/105 to *Promeles* from various localities. Standard, *P. palaeatticus*, Pikermi, mean of the specimens of Table 5. *P. macedonicus* according to Schmidt-Kittler (1995).

Fig. 5. Diagramme logarithmique des rapports des dimensions des dents supérieures de AMPG PG 01/105 et *Promeles* provenant des différentes localités.

Kittler, 1995: fig. 3). The P^4 of *P. macedonicus* is relatively more robust than in *P. palaeatticus* (Fig. 5) and has less developed anterior cingulum (Schmidt-Kittler, 1995: fig. 3a). The lower carnassial of *P. palaeatticus* differs from *P. macedonicus* on its larger size (Fig. 4), as well as on its lower trigonid (Schmidt-Kittler, 1995: fig. 3a). A M_1 from Dorn-Dürkheim 1 described as *Promeles* sp. by Franzen and Storch (1975) has been attributed by Morlo (1997) to *P. palaeatticus*. This specimen, however, is significantly smaller than the Pikermi *P. palaeatticus* (Fig. 4), and it would be preferable to retain the first determination, *Promeles* sp., for it. Similarities to *Promeles* shows a specimen from China referred as “*Martes pentelici palaeosinensis*” by Erdbrink (1968: Pl. 3, fig. A). This specimen, however, differs from both “*Martes*” *pentelici* GAUDRY, 1861 and “*Martes*” *palaeosinensis* ZDANSKY, 1924. These two species have M_1 with larger trigonid and not basin like talonid. On the contrary, the Chinese specimen has smaller trigonid, and oval, wide and basin-like talonid, surrounded by small cusplets.

From the postcranial specimens we attribute in *P. palaeatticus*, the calcaneum was previously known from a specimen described by Pilgrim (1931). The present specimen agrees both in dimensions and morphology with the specimen described by Pilgrim (1931). Some of the characters of the hind limb as the presence of a fossa for the *quadratus*

Table 3
Measurements of the tarsal bones of *P. palaeatticus* from Pikermi (AMPG PA 3502/91)
Dimensions des os du tarse de *P. palaeatticus* de Pikermi (AMPG PA 3502/91)

	Hmax	DTmax	DAPmax	Htr	DT(tub)	DAP(tub)
Astragalus	13.8	10.5	–	8.0	–	–
Calcaneus	20.0	11.1	9.7	–	5.9	7.2
Navicular	4.1	5.7	8.3	–	–	–
1st Cuneiform	7.4	2.6	4.3	–	–	–
2nd Cuneiform	3.3	2.7	4.0	–	–	–
3rd Cuneiform	5.4	3.6	7.0	–	–	–
Cuboid	7.8	6.5	5.2	–	–	–

Table 4
Measurements of the metatarsals of *P. palaeatticus* from Pikermi (AMPG PA 3502/91)
Dimensions des os métatarsiens de *P. palaeatticus* de Pikermi (AMPG PA 3502/91)

	Lmax	DTpr	DAPpr	DTdia	DAPdia	DTdistmax	DTdistart	DAPdistart
Mt I, Pikermi	22.3	4.2	4.6	2.1	1.8	3.2	–	–
Mt II, Pikermi	29.0	3.1	4.6	2.7	2.1	4.3	3.9	(3.6)
Mt III, Pikermi	> 30.6	4.3	6.0	3.0	2.4	–	–	–
Mt IV, Pikermi	34.3	2.8	5.7	3.0	2.5	4.5	–	3.9

Table 5
Measurements of the upper teeth of *P. palaeatticus* from Pikermi. BM(NH) M. 9029 (described first by Pilgrim, 1931) was measured on a cast from the MNHNP collections
Dimensions des dents supérieures de *P. palaeatticus* de Pikermi

	Major, 1902 PG 01/105 (dext.)	Weithofer, 1888	Major, 1902	BM(NH) M. 9028 (Pilgrim, 1931)	BM(NH) M. 9029 (after the author)	
					(sin.)	(dext.)
(L × W)C^s	(5.2 × 4.4)	4.6 × 3.7	–	6 × –	–	4.9 × 4.1
(L × W)P^1	–	–	2.5 × –	2.5 × 2.5	–	(1.9 × 2.0)
(L × W)P^2	4.7 × 2.4	4.0 × 2.5	4.3 × –	5.0 × 2.5	4.3 × 2.4	4.5 × 2.5
(L × W)P^3	5.6 × 3.3	6.0 × 3.3	6.0 × –	6.5 × 4.0	5.3 × 3.2	5.5 × 3.2
(L × W)P^4	10.0 × (5.9)	9.0 × –	9.2 × –	11.0 × (7.0)	9.5 × 5.6	9.8 × 5.6
(L × W)M^1	7.9 × 11.3	6.5 × 10.0	7.5 × 10.5	9.0 × 13.5	(7.9) × 10.5	(7.8) × 10.6
L(P^2–P^4)	20.9	–	–	–	20.3	19.8

plantae at the calcaneum, the shallow trochlea and the transversely elongated head of the astragalus, and the expanded surface for the *tibialis posticus* at the tibia are characters common in the plantigrade carnivores (Ginsburg, 1961, 1999). On the contrary, in the digitigrade carnivores the astragalus has deep trochlea and rounded head, the fossa for the *quadratus plantae* is small or absent, and the surface for the *tibialis posticus* is less expanded (Ginsburg, 1961, 1999).

Genus: *Martes* PINEL, 1792

Martes woodwardi PILGRIM, 1931

Material: PA 2032/91: part of a left mandibular ramus with the M_1 and the alveolus for M_2. This specimen comes from the excavations made in Pikermi by Woodward and Skouphos in 1901 (Woodward, 1901).

Description: The height of the mandibular corpus below the middle of M_1 is equal to the total length of this tooth (Table 6 and Fig. 6[1]). The anterior margin of the masseteric fossa lies below the alveolus for M_2. The condyle is slightly lower than the alveolar level and extends posteriorly, slightly more than the coronoid process. There is an angular process. The mandibular foramen opens almost on the same level with the condyle.

Only the M_1 is preserved (Fig. 6[1]). Its metaconid is lower than the protoconid and slightly behind it. There is a labial cingulum at the base of the trigonid. The talonid is basin shaped and rounded. The hypoconid is robust but lower than the metaconid. The hypoconulid is less robust than the hypoconid and lies slightly more labially in relation to the metaconid–protoconid junction. The hypoconid and the hypoconulid have almost the same height. The remaining part of the talonid is composed of small cuspids. The alveolus for M_2 is ovoid with length that is about 4 mm.

Discussion: The species *M. woodwardi* is not known but from its holotype, a right mandibular fragment from Pikermi preserving the P_4, the M_1 and the alveolus for the M_2 (BM(NH) M. 9031). This species has been referred recently to the Melinae and attributed to the new genus *Pilgrimeles* GINSBURG, 1999. In my opinion, however, the characters used by Ginsburg (1999) for the erection of the new genus *Pilgrimeles* are not sufficiently supported and the older name *M. woodwardi* has to been retained.

The specimen in consideration here is not different in dimensions from the holotype of *M. woodwardi* (Table 6). According to Pilgrim (1931), the talonid of *M. woodwardi* has an entoconid and a hypoconid, and the remaining part is surrounded by a ridge. At the figures of the holotype given by Pilgrim (1931: Pl. 2, fig. 2, 2a), however, the entoconid is missing, as well as in the present specimen. In these figures, there is a hypoconid and another cusp at the posterior part of the talonid that corresponds to the hypoconulid. Petter (1964) also reports the presence of a hypoconulid in *M. woodwardi*, character that according to that author distinguishes this species from the equally sized *Martes basilii* PETTER, 1964, from the Los Algezares in Spain. Furthermore, judging from an available photograph of the holotype of *M. woodwardi*, it is clear that the ridge mentioned by Pilgrim is composed of small cuspids, as in PA 2032/91. Such cuspids are common in Melinae, but we also observed their presence in a specimen of recent *Martes foina*. Recently Ginsburg (1999) referred *M. woodwardi* to Melinae, and erected the genus *Pilgrimeles* for it. Ginsburg

Table 6
Measurements of the M_1 of *M. woodwardi* from Pikermi (AMPG PA 2032/91) and other mustelids from various localities
Dimensions du M_1 de *M. woodwardi* de Pikermi (AMPG PA 2032) et de mustélides provenant des différentes localités

	LM_1	WM_1	$LtldM_1$	HmM_1
M. woodwardi (AMPG PA 2032/91), Pikermi	11.4	4.6	3.9	11.4
M. woodwardi, Pikermi (Pilgrim, 1931)	12.0	5.0	4.0	11.0
M. palaeosinensis, China (*n* = 4) (Zdansky, 1924)	11.0–13.0	3.9–5.2	–	–
M. anderssoni, China (*n* = 1–2) (Schlosser, 1924)	9.5	–	–	7.0–8.0
M. leporinum, Taraklia (Zdansky, 1924)	13.5	–	–	–
M. basilii, Los Algezares (Petter,1964)	11.0	4.0	3.5	10.0
M. lefkonensis, Maramena (Schmidt-Kittler, 1995)	7.6	3.2	–	6.1

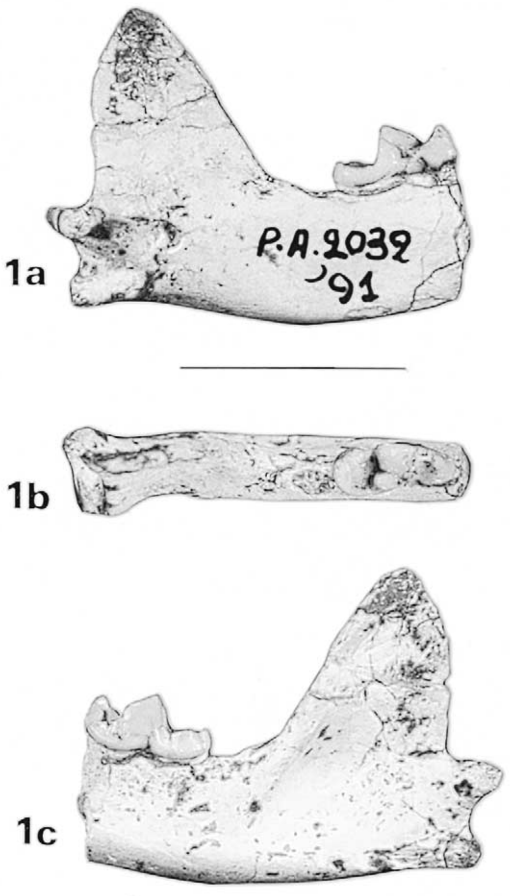

Fig. 6. *M. woodwardi* PILGRIM, 1931, Pikermi. **1.** Left mandibular fragment (AMPG PA 2032/91); **a)** lingual view, **b)** occlusal view, **c)** labial view. Scale bar 20 mm.
Fig. 6. **1.** Fragment de mandibule gauche (AMPG PA 2032/91); **a)** vue linguale, **b)** vue occlusale, **c)** vue labiale. Échelle graphique 20 mm.

(1999) comments that the talonid of *M. woodwardi* is longer than that of *Martes* and its lingual wall is divided in several small cuspids. As mentioned above, however, the last character cannot be taken as a definite character of Melinae. Concerning the talonid development, in the holotype of *M. woodwardi* the talonid is equal to 33% of the M_1, and in the present specimen equal to the 34%. In two specimens of recent *M. foina* the talonid comprises the 33 and 32% of the total length of the tooth, differences that can not be considered important. From the above it seems that the criteria used by Ginsburg (1999) for the systematic position of *M. woodwardi*, as well as for the erection of the genus *Pilgrimeles* are not sufficient. It would be preferable in my opinion to keep *M. woodwardi* in *Martes* and Mustelinae, until more material to be found, especially upper teeth and skull remains. It is true, however, that a revision of the late Miocene mustelids is needed since most of these are poorly known, mainly from isolated teeth, and sometimes only from upper or only from lower teeth.

Martes palaeosinensis (ZDANSKY, 1924) from the Pontian of China and *Martes leporinum* (KHOMENKO, 1914) from Taraklia in Moldavia, differ from the present specimen on their not hollow talonid (fide PILGRIM 1931). *Martes anderssoni* SCHLOSSER, 1924, is smaller. Also, significantly smaller is *Martes lefkonensis* SCHMIDT-KITTLER, 1995, from Maramena in Northern Greece (Table 6).

Fig. 7. Mustelidae gen. spec. indet., Pikermi. **1.** Left Mc II (AMPG PG 98/22), anterior view. **2.** Right Mc III (AMPG PG 98/20), anterior view. **3.** Left Mc IV (AMPG PG 98/23), anterior view. **4.** Left Mc V (AMPG PG 98/21), anterior view. Scale bar 30 mm.
Fig. 7. **1.** Mc II gauche (AMPG PG 98/22), vue antérieure. **2.** Mc III droit (AMPG PG 98/20), vue antérieure. **3.** Mc IV gauche (AMPG PG 98/23), vue antérieure. **4.** Mc V gauche (AMPG PG 98/21), vue antérieure. Échelle graphique 30 mm.

Family: MUSTELIDAE Fischer von Waldheim, 1817
gen. et sp. indet.

Material: PG 98/20: right, Mc III; PG 98/21: left Mc V; PG 98/22: left Mc II; PG 98/23: left Mc IV, subadult.

Description and discussion: From the available metacarpals Fig. 7[1–4]), PG 98/23 belongs to a subadult individual since its distal epiphysis remains in position but is still not completely fused with the shaft. The available specimens belong to a large sized mustelid. They are stoutly built, their distal epiphyses as well as their shafts have transverse diameter larger than the anteroposterior one, and their distal extremities are significantly wider than the shaft (Table 7 and Fig. 7[1–4]) The proximal articular surfaces for the carpal bones are anteroposteriorly convex, especially those of the fifth and the fourth metacarpal. The shaft of the second and fifth metacarpal is slightly curved, that of the third and fourth metacarpal is straighter.

The present specimens show important similarities to *Enhydriodon*? *latipes* PILGRIM, 1931 (Table 7). According to Pilgrim (1931), this species is clearly Lutrinae, with aquatic specialisation even more pronounced than modern otters. *E.*? *latipes*, however, is not known but from postcranial material, mainly of the manus and the pes. Dental remains that could be attributed in this species are not known from Pikermi, neither bones as the scapula, the humerus or the ulna that show clearer possible aquatic adaptations. As already mentioned by Willemsen (1992), if

Table 7
Measurements of the metacarpals of various mustelids from various localities
Dimensions des métacarpiens de mustelidés provenant des différentes localités

	Lmax	DTpr	DAPpr	DTdia	DAPdia	DTdistmax	DTdistart	DAPdistart
Mc II (AMPG PG 98/22), Pikermi	46.0	8.3	12.3	7.3	6.0	12.0	11.2	8.3
Mc II (AMPG PG 98/25), Pikermi	44.1	8.2	11.9	6.5	5.5	11.4	10.1	8.0
E. ? *latipes*, Mc II, Pikermi (Pilgrim, 1931)	42	–	–	7	5.5	–	–	–
Mc III (AMPG PG 98/20), Pikermi	53.9	8.7	12.9	6.9	6.2	11.8	10.9	9.0
E. ? *latipes*, Mc III, Pikermi (Pilgrim, 1931)	50.5	–	–	6.5	5.5	–	–	–
Mc IV (AMPG PG 98/23), Pikermi	54.0	9.3	12.5	6.6	5.9	12.3	11.9	–
E. ? *latipes*, Mc IV, Pikermi (Pilgrim, 1931)	54	–	–	7	5.5	–	–	–
Mc IV (LGUT VAT-93), VAT (after the author)	55.4	9.7	12.0	7.6	6.1	11.2	11.2	10.1
Mc V (AMPG PG 98/21), Pikermi	48.8	9.7	14.2	7.4	6.1	12.5	11.7	9.0
E. ? *latipes*, Mc V, Pikermi (Pilgrim, 1931)	45	–	–	7	6	–	–	–

this species really belongs in *Enhydriodon* it could be identical with some other *Enhydriodon* species.

The large sized mustelids are relatively rare in the late Miocene of Greece. A metacarpal from Vathylakkos 3 (VAT–93) originally described as Mc II of "*Ictitherium robustum*" by Koufos (1980: Pl. 5, Fig. 6) actually is a Mc IV of a mustelid. It shows many similarities in dimensions to the available Mc IV (PG 98/23), but it has slightly more robust shaft and relatively less wide distal extremity (Table 7). From the locality of Vathylakkos 3 the only known mustelid of this size is *Plesiogulo crassa* (Koufos, 1980, 2000). In Pikermi, *Plesiogulo* sp. is referred by Symeonidis (1974) from two humerus fragments.

Superfamily: FELOIDEA Fischer von Waldheim, 1817

Family: FELIDAE Fischer von Waldheim, 1817

Subfamily: FELINAE Fischer von Waldheim, 1817

Genus: *Felis* LINNAEUS, 1758

Felis attica WAGNER, 1857

Material: PG 01/106: skull fragment with the left P^3, the right P^3–P^4, the alveoli for the left and right P^2, the right M^1 and the root of the left canine; PG 01/107: left mandibular ramus with C_i, P_3–M_1; PG 01/108: right mandibular ramus with the M_1, and the posterior parts of P_3–P_4; PA 1021/91: right Mt V; PA 1022/91: right Mt IV; PA 1023/91: right Mt III; PA 1024a/91: right Mt II; PA 1024b/91: right Mt I; PA 1025/91: ph 1, dig. IV, right pes; PA 1026/91: ph 1, dig. III, right pes; PA 1027a/91: ph 1, dig. II, right pes; PA 1027b/91: ph 2, dig. II, right pes; PA 1028/91: right calcaneum; PA 1029a/91: right lateral (3rd) cuneiform; PA 1029b/91: right medial (1st) cuneiform; PA 1030/91: right cuboid; PA 1031/91: right navicular; PA 1035/91: left Mc II; PA 1036/91: distal part of a left Mc IV; PA 1037/91: distal part of a left Mc V; PA 1091/91: distal part of a right Mc II; PA 1092/91: ph 1, dig. II, right manus; PA 1093/91: ph 2, dig. II, right manus; PA 1094/91: ph 3, dig. II, right manus; PA 1095/91: distal part of a right Mc III; PA 1096/91: sesamoid, dig. III; PA 1097/91: sesamoid, dig. III; PA 1098/91: ph 1, dig. III, right manus; PA 1099/91: ph 2, dig. III, right manus; PA 1100/91: ph 3, dig. III, right manus; PA 1101/91: distal part of a right Mc IV; PA 1102/91: ph 1, dig. IV, right manus; PA 1103/91: ph 2, dig. IV, right manus; PA 1104/91: ph 3, right manus; PA 1105/91: distal part of a right Mc V; PA 1106/91: ph 2, dig. V, right manus; PA 1107/91: ph 3, dig. V, right manus; PA 2566/91: proximal part of a left humerus; PA 2803/91: distal part of a left humerus; PA 2804/91: proximal part (olecranon) of a left ulna; PA 3550/91: proximal half of a left radius; PA 3551/91: distal part of a right radius.

From the above specimens, PA 1021/91 to PA 1031/91, PA 1091/91 to PA 1107/91 and PA 2803/91 to PA 2804/91 were found in anatomical position, and PA 1021/91 to 1037/91 in the same ossiferous block. The specimens PA 1021/91 to 1037/91 and PA 1091/91 to PA 1107/91 come from the excavations made in Pikermi by Woodward and Skouphos in 1901.

Description: The available skull fragment is badly damaged and does not offer important morphological information (Fig. 8[1]). The distance from the prosthion to the middle of the line connecting the posterior borders of P^4 can be estimated to 40–41 mm, and the distance from the nasion to the bregma to 40 mm. The distance from the prosthion to the anterior border of the orbit is 32 mm. The sagittal crest is well indicated, and bifurcates about 17 mm behind the postorbital processes of the frontals. The bregma almost coincides with the point that the sagittal crest bifurcates. The width of the skull at the postorbital processes of the frontals is 37.5 mm. The paroccipital process extends ventrally more than the mastoid process and looks backwards. The infraorbital foramen opens above the middle of P^3. The depression of the palate lingually of the P^4 that receives the M_1 is deep.

The P^2 is not preserved. The P^3 has a strong posterior accessory cusp and a very small anterior accessory cusp in a slightly lingual position. The main cusp of P^3 is high and symmetrical in labial view. There is a high posterior cingulum. The greatest width of the tooth is at the region between the posterior accessory cusp and the main cusp. In P^4 a cutting crest connects the paracone with the protocone. There is not an ectoparastyle. There is a cingulum at the posterior part of the tooth and lingually. On the present specimen, the M^1 is represented only by its alveolus that measures about 6.1 mm in width.

At the mandible (Fig. 8[2]) there are two mental foramens. The anterior one is larger and opens under the

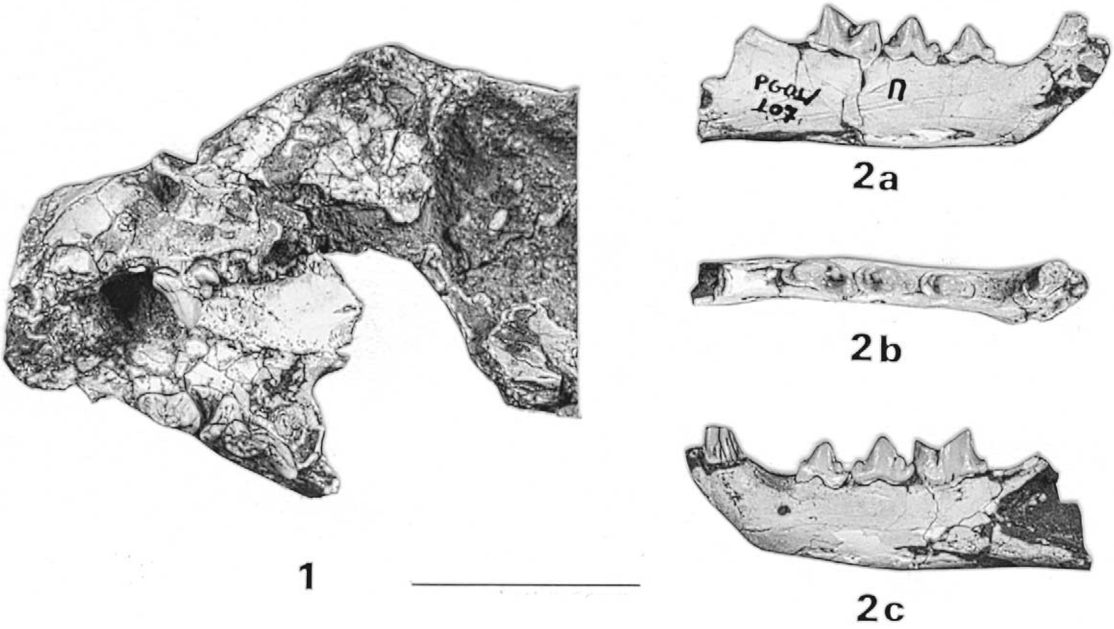

Fig. 8. *F. attica* WAGNER, 1857, Pikermi. **1.** Skull (AMPG PG 01/106), ventral view. **2.** Left mandible (AMPG PG 01/107); **a)** lingual view, **b)** occlusal view, **c)** labial view. Scale bar 30 mm.

Fig. 8. **1.** Crâne (AMPG PG 01/106), vue ventrale. **2.** Mandibule gauche (AMPG PG 01/107); **a)** vue linguale, **b)** vue occlusale, **c)** vue labiale. Échelle graphique 30 mm.

anterior border of P_3. The posterior mental foramen is very small and opens under the middle of P_3. The mandibular foramen opens about 11 mm behind M_1 and 8 mm below the alveolar level. The anterior margin of the masseteric fossa lies slightly behind M_1. The P_3 has a faint anterior accessory cusp and a larger posterior one. The main cusp of this tooth and its accessory cusps lie almost on the same line. Behind the posterior accessory cusp there is a weak cingulum. The P_4 is similar to P_3 but larger, while the accessory cusps and the cingulum are stronger. The M_1 has no metaconid but only a very small talonid. Its protoconid is larger and higher than the paraconid.

We attribute to *F. attica* an important number of postcranial specimens Fig. 9[1–5]), found mostly in anatomical position. The humerus is represented from a proximal part (PA 2566/91, not figured, DAPpr = 28.9 mm, DTpr = 21.8 mm) and a distal part (Fig. 9[1], Dtdist = 25.1 mm, Dtdistart = 19.2 mm). The greater trochanter is only slightly higher than the head of the humerus and the fossa for the infraspinatus is not especially deep. The tuberosity for the teres minor is only slightly developed. The biccipital groove is wide. The distal part of the humerus shows very well an entepicondylar foramen, 6 mm in height. The olecranon fossa is positioned at a small angle to the long axis of the humerus (Fig. 9[1]). The available ulna specimen (PA 2804/91, not figured, DAP of the olecranon process = 14.0 mm) was found in anatomical position with the distal humerus fragment. Its olecranon has two tuberosities. The medial tuberosity for the internal humeral part of the triceps is higher than the lateral one for the anconeus. The radius is represented by a proximal part (Fig. 9[3], DTpr = 10.3 mm, DAPpr = 7.0 mm) and a distal part (Fig. 9[4], Dtdist = 16.3 mm, DAPdist = 10.1 mm). The proximal articular surface of the radius is oval. At the distal extremity, the dorsal tubercle of the radius is high and situated slightly medially in relation to the long axis of the bone. The grooves for the extensors *carpi radialis longior* and *brevior*, and the *extensor communis digitorum* are almost equal in width. The groove for the *extensor indicis* is small but well marked. The distal articular surface for the scapholunar is transversely oval and strongly concave. Posteriorly and near to the styloid process this surface continues proximally. The articular surface for the ulna is transversely oval and slightly concave. Unfortunately, the metacarpals are not well preserved. Only one complete Mc II was found (Table 8 and Fig. 9[2]), and the distal portions of the Mcs II–V of another individual, associated with their phalanges (not figured). On the second metacarpal the articular surface for the trapezium is oval and proximodistally elongated. The proximal phalanges of the front limb are strongly curved in lateral view. The proximal phalanx of the third metacarpal is slightly longer (22.9 mm) than that of the fourth (21.1 mm). On the middle phalanges, the distal trochlea is offset laterally making space for the distal phalanx when this is retracted.

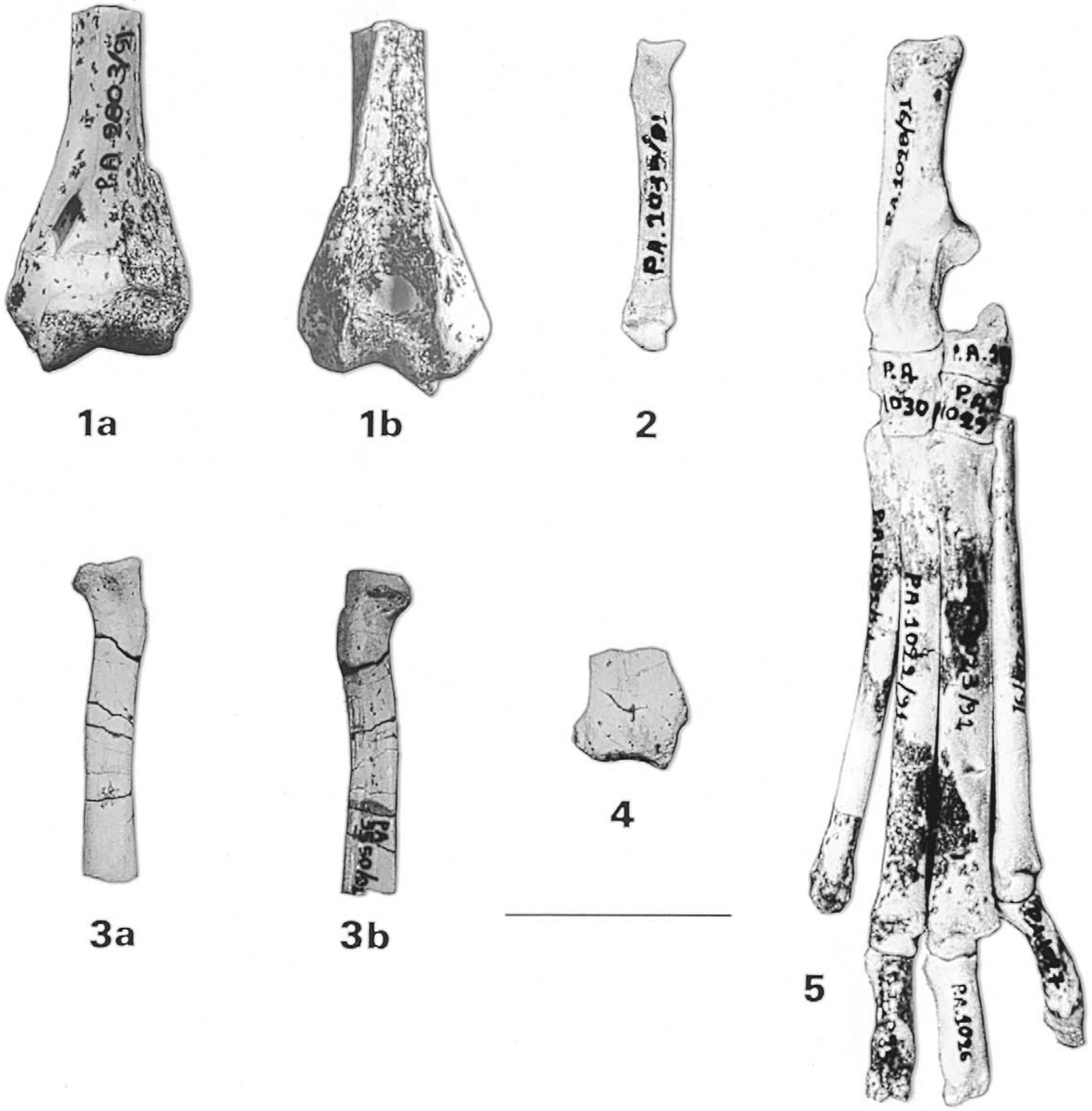

Fig. 9. *F. attica* WAGNER, 1857, Pikermi. **1.** Left humerus (AMPG PA 2803/91), distal part; **a)** anterior view, **b)** posterior view. **2.** Left Mc II (AMPG 1035/91), anterior view. **3.** Left radius (AMPG PA 3550/91), proximal part; **a)** anterior view, **b)** posterior view. **4.** Right radius (AMPG PA 3551/91), distal part, anterior view. **5.** Right pes (AMPG PA 1021–1031/91), anterior view. Scale bar 30 mm.

Fig. 9. **1.** Humérus gauche (AMPG PA 2803/91), partie distale; **a)** vue antérieure, **b)** vue postérieure. **2.** Mc II gauche (AMPG 1035/91), vue antérieure. **3.** Radius gauche (AMPG PA 3550/91), partie proximale; **a)** vue antérieure, **b)** vue postérieure. **4.** Radius droit (AMPG PA 3551/91), partie distale, vue antérieure. **5.** Pes droit (AMPG PA 1021–1031/91), vue antérieure. Échelle graphique 30 mm.

The middle phalanx of the third metacarpal is the longest one (17.3 mm) and that of the fifth metacarpal the shortest (12.5 mm).

The tuberosity of the calcaneum (Table 9 and Fig. 9[5]) has an almost circular outline in proximal view. It has two low processes, the medial one being the higher, which define a very shallow groove for the tendon calcaneus. The peroneal tuberosity is situated slightly higher than the cuboid facet. On the peroneal tuberosity, the groove for the *peroneus longus* is scarcely indicated. The sulcus for the flexor hallicus longus is deep and well defined. The cuboid facet is ovoid, with a transverse diameter slightly larger than the anteroposterior one. The depression for the *quadratus plantae* is relatively deep, proximodistally elongated and close to the *sustentaculum tali* level. The pit for the annular ligament of the *extensor longus digitorum* is well marked, but not so the groove for the interosseous ligament. The navicular is anteroposterior elongated (Table 9) and does not show any peculiarities. It articulates with the cuboid but there is not a distinct articular surface for the calcaneum. The proximal articular surface of the lateral cuneiform is ovoid and concave, while the distal one for the Mt III is flat. The cuboid has a proximal articular surface with transverse diameter significantly larger than the anteroposterior one and the concave distal articular surface for the Mt IV. The groove for the *peroneus longus* is very well marked. The

Table 8
Measurements of the metapodials of *F. attica* from Pikermi and Samos
Dimensions des métapodes de *F. attica* de Pikermi et Samos

	Lmax	DTpr	DAPpr	DTdia	DAPdia	DTdistmax	DTdistart	DAPdistart
Mc II (AMPG PA 1035/91), Pikermi	42.2	6.0	9.7	4.1	4.4	7.1	6.5	6.5
Mt I (AMPG PA 1024b/91), Pikermi	6.7	–	–	–	–	–	–	–
Mt II (AMPG PA 1024a/91), Pikermi	66.4	4.6	8.8	5.0	4.5	7.8	6.8	7.5
Mt II (MGL 805 S), Samos (de Beaumont, 1961, 1986)	70.5 ?	–	10.0	6.0	5.0	8.0	–	–
Mt III (AMPG PA 1023/91), Pikermi	71.6	9.1	12.5	7.1	5.2	9.7	7.7	7.7
Mt III (MGL 805 S), Samos (de Beaumont, 1961, 1986)	74.0 ?	–	13.5	7.5	6.0	9.0	–	–
Mt IV (AMPG PA 1022/91), Pikermi	72.5	6.5	10.4	5.5	5.2	7.7	6.6	7.5
Mt IV (MGL 805 S), Samos (de Beaumont, 1961, 1986)	74.0 ?	–	10.0	6.0	5.5	8.5	–	–
Mt V (AMPG PA 1021/91), Pikermi	(70.0)	(5.6)	7.1	4.3	3.8	6.6	5.5	7.0
Mt V (MGL 805 S), Samos (de Beaumont, 1961, 1986)	–	–	–	5.0	4.5	7.0	–	–

proximal articular surface of the medial cuneiform (entocuneiform), for the navicular, is larger than the distal one, relatively concave and slopes laterally. The distal articular surface is small and anteroposteriorly elongated. It articulates with the first metatarsal.

The Mt I is rudimentary (Table 8), and articulates only with the medial cuneiform. The Mt IV is the largest of the metatarsals but only slightly larger than the Mt III (Table 8). The Mt III, however, is the more robust of the metatarsals (Table 8 and Fig. 9[5]). The Mt V is not completely preserved (its proximal tuberosity is broken) but its length can be estimated to 70 mm. The phalanges of the hind limb are not different from those of the front limb, except their larger size. The proximal phalanx of the third metatarsal is not completely preserved, but it can be expected slightly longer than that of the fourth metatarsal (21.8 mm). It is, however, clearly more robust.

Discussion: The type material of *F. attica* comes from Pikermi and is a skull missing the braincase, but with its associated mandible (Wagner, 1857: Pl. 1, fig. 4). Another skull with its associated mandible and atlas comes from Samos and is referred by Major (1894: No. 482) under the name *Felis neas*, but it is not described or figured. Pilgrim (1931) described this skull under the name *F. neas*, but de Beaumont (1961) considered it as a synonym of *F. attica* and is followed by most authors as Koufos (2000).

The upper teeth of PG 01/106 are very close in dimensions to MGL 482 S from Samos except the slightly smaller P^3 relatively to the P^4 (Table 10 and Fig. 10). The type skull from Pikermi has less robust P^3 compared to both the Samos and the present skull, and larger P^3 relatively to the P^4. The present skull differs from both the type and the Samos skull on its large P^4 in relation to the distance between the upper canine and the carnassial (Table 10, ratio $LP^4/C^S–P^4$). Probably connected with that, is the relative short P^3 as mentioned above. de Beaumont (1961) gives special importance to the last ratio, and compares *F. attica* to various fossil and recent Felinae (de Beaumont, 1961:42) but he does not give any data for the range of this character in the recent Felinae. Moreover, even the slighter deformation at the preorbital region of a specimen could significantly affect the ratio in question. The last applies in our specimen, which is badly deformed and compressed at the preorbital region. In addition to the specimens from Pikermi and Samos, some specimens from Maragha and Vathylakkos 3 (Ravin du Vatiluk) have been related or attributed to *F. attica*. The Maragha specimen (MNHNP unnumbered) is a maxilla fragment referred to *F. attica* by de Mecquenem (1925: Pl. 9, fig. 5) and de Beaumont (1961). This specimen is slightly smaller in dimensions but very close in proportions to *F. attica* from Pikermi and Samos (Fig. 10) and has a small ectoparastyle in P^4, something mentioned by Arambourg and Piveteau (1929) also. The ectoparastyle, however, does not affect the size of the P^4 and its development relatively to the P^3 (ratio $LP^3/LP^4 = 65.3$). The Vathylakkos 3 specimen is a skull (MNHNP SLQ 935) referred by Arambourg and Piveteau (1929) and de Beaumont (1961) under the name *Felis* cf. *attica*, and as *Felis* sp. by Koufos (2000). This

Table 9
Measurements of the tarsal bones of *F. attica* from Pikermi and Samos
Dimensions des os du tarse de *F. attica* de Pikermi et Samos

	Hmax	DTmax	DAPmax	DT(tub)	DAP(tub)
Calcaneus (AMPG PA 1028/91), Pikermi	41.8	17.4	15.1	10.4	10.9
Calcaneus (BMNH M. 9010), Pikermi (Pilgrim 1931)	41.5	–	–	–	–
Navicular (AMPG PA 1031/91), Pikermi	9.9	10.2	13.7	–	–
1st Cuneiform (AMPG PA 1029b/91), Pikermi	9.6	3.8	5.6	–	–
3rd Cuneiform (AMPG PA 1029a/91, Pikermi	9.2	8.3	15.0	–	–
3rd Cuneiform (BMNH M. 9010), Pikermi (Pilgrim, 1931)	8.5	9.0	16.0	–	–
3rd Cuneiform (MGL 805 S), Samos (de Beaumont, 1961, 1986)	10.0	9.0	16.5	–	–
Cuboid (AMPG PA 1030/91), Pikermi	12.7	10.7	11.8	–	–
Cuboid (BMNH M. 9010), Pikermi (Pilgrim, 1931)	12.0	10.0	11.5	–	–

Table 10
Measurements of the upper teeth of *F. attica* from Pikermi and Samos
Dimensions des dents supérieures de *F. attica* de Pikermi et Samos

	AMPG PG 01/106, Pikermi		de Beaumont, 1961	
	(sin.)	(dext.)	Pikermi, (type)	MGL 482 S, Samos
$(L \times W)C^s$	(6.3) × (4.6)	–	6.2 × 4.6	7.2 × 5.2
C^s–P^4	(15.9)	(16.0)	17.4	18.5
$(L \times W)P^2$	–	–	3.1 × 2.7	(3.6) × (2.9)
$(L \times W)P^3$	8.6 × 4.9	8.7 × 5.0	9.1 × 4.2	9.0 × 4.8
$(L \times W)P^4$	–	13.7 × 6.9	12.7 × 6.1	13.4 × 6.8
$(L \times W)M^1$	–	(2.4 × 6.1) alv.	– × 6.0	– × 5.1
$(WC^s/LC^s) \times 100$	(73.8)	–	74.2	72.2
$(WP^3/LP^3) \times 100$	57.0	57.5	46.2	53.3
$(WP^4/LP^4) \times 100$	–	50.4	48.0	50.7
$(LP^3/LP^4) \times 100$	–	63.5	71.7	67.2
$(LP^4/C^s\text{-}P^4) \times 100$	–	(85.6)	73.0	72.4

specimen also has an ectoparastyle in P^4, still larger than that of the Maragha specimen. Moreover, the upper carnassial of the Vathylakkos 3 specimen has smaller protocone compared to the Pikermi, Samos and Maragha specimens. These characters have as result a less robust P^4 and especially large P^4 in relation to the P^3, the indices $(WP^4/LP^4) \times 100$ and $(LP^3/LP^4) \times 100$ are 39.4 and 56.3, respectively. The index P^4/C–P^4 is 93 (Koufos, 2000), large compared to other specimens.

The present mandibles have teeth close in robustness to the specimen MGL 482 S from Samos, but slightly smaller in dimensions, and M_1 slightly larger relative to the P_4 (Table 11 and Fig. 11). Compared to the type mandible from Pikermi, M_1 is almost equally developed in relation to the P_4 but P_3 is less robust (Table 11 and Fig. 11). A specimen from China, referred under the name *Felis* sp. by Zdansky (1924: Pl. 27, fig. 5), has a P_3 similar in dimensions and proportions to *F. attica* from Pikermi and Samos (Fig. 11) and only slightly larger C_i and could belong in *F. attica* as has been proposed by de Beaumont (1961). *F. attica* is also referred in the middle Turolian (MN 12) locality of Valdecebro 5 in Spain by Alcalá (1994) and Fraile et al. (1997). This occurrence has been based on a P^4, comparable in size to the Pikermi specimens but with broken protocone. Recently Morlo (1997) referred a M_1 from Dorn-Dürkheim 1, originally described as *Pseudaelurus turnauensis* (HOERNES, 1881) by Franzen and Storch (1975), as well as a fragmentary P^4 (a metastyle) from the same locality, to *F. attica*. The P^4 is very fragmentary to be discussed. Concerning the M_1, this is not different in dimensions from *F. attica*, but shows interesting morphological characters, as the presence of a small metaconid (also present in the

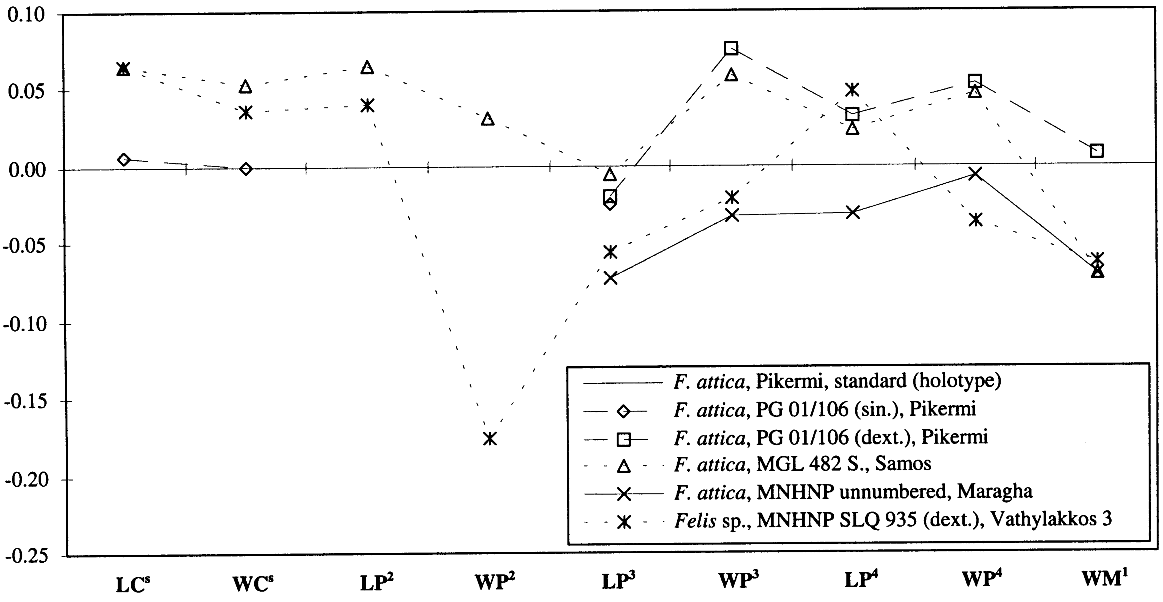

Fig. 10. Logarithmic ratio diagram comparing the upper teeth of AMPG PG 01/106 to *F. attica* and *Felis* sp. from various localities. Standard, *F. attica*, Pikermi, holotype, according to de Beaumont (1961). *F. attica* from Samos according to de Beaumont (1961); *F. attica* from Maragha and *Felis* sp. from Vathylakkos 3 according to the author.

Fig. 10. Diagramme logarithmique des rapports des dimensions des dents supérieures de AMPG PG 01/106, *F. attica* et *Felis* sp. provenant des différentes localités.

Table 11
Measurements of the lower teeth of *F. attica* from Pikermi and Samos
Dimensions des dents inférieures de *F. attica* de Pikermi et Samos

	Pikermi		de Beaumont, 1961	
	AMPG PG 01/107	AMPG PG 01/108	Pikermi, (type)	MGL 482 S, Samos
(L × W)C$_i$	5.4 × 4.2	–	5.6 × 4.7	6.2 × 5.0
C$_i$–P$_3$	7.4	–	–	–
(L × W)P$_3$	7.1 × 3.4	–	7.1 × 3.4	8.0 × 4.0
(L × W)P$_4$	8.3 × 3.8	– × (4.0)	9.2 × 4.2	9.8 × 4.2
(L × W)M$_1$	10.2 × 4.3	10.3 × 4.3	11.0 × 5.0	11.1 × 4.4
L(P$_3$–P$_4$)	15.6	(15.7)	–	–
ÇmM$_1$	12.4	12.8	–	–
(WC$_i$/LC$_i$) × 100	77.8	–	83.9	80.6
(LP$_4$/LM$_1$) × 100	81.4	–	83.6	88.3
LM$_1$/LP$_{3+4}$) × 100	66.2	(65.6)	67.5	62.4
(WP$_3$/LP$_3$) × 100	47.9	–	57.7	50.0
(WP$_4$/LP$_4$) × 100	45.8	–	45.7	42.9
(WM$_1$/LM$_1$) × 100	43.9	41.7	45.5	39.6

holotype according to de Beaumont, 1961) and an elevated talonid (Morlo, 1997; Franzen and Storch, 1975: Pl. 6, fig. 6, 7a–c). The above mentioned material from Dorn-Dürkheim 1 is very poor, but the M$_1$ has a talonid more primitive in structure than *F. attica*, and its attribution to this species is doubtful in my opinion.

The front limb of *F. attica* is not known, but the hind limb is almost completely known from the specimen MGL 805 S from Samos, and the specimens BM(NH) M. 9010 and M. 9011 from Pikermi. MGL 805 S was referred by Major (1894) under the name *Felis* sp., and includes the medial and lateral cuneiforms, the Mts II–V and part of a phalanx. de Beaumont (1961) considered MGL 805 S large, and attributed this to a small sized *Metailurus parvulus* (HENSEL, 1862). Later, however, correctly de Beaumont (1986) referred the above specimen to *F. attica*. It is important to notice here that Solounias (1981: Pl. 4) and Bernor et al. (1996) reported *M. parvulus* in Samos, but it is not known if they were based on the initial reference of de Beaumont (1961) or on some undescribed until now specimens stored in a museum collection. de Beaumont (1986) also referred to *F. attica* the specimens BM(NH) M. 9010 and M. 9011 from Pikermi, firstly attributed with reservations by Pilgrim (1931) to "*Ictitherium robustum*". BM(NH) M. 9011 is a right femur, and M. 9010 an almost complete left hind limb preserving the femur, the tibia, the patella, the calcaneum, the astragalus, the navicular, the lateral cuneiform, the cuboid, the Mts II–V and the corresponding

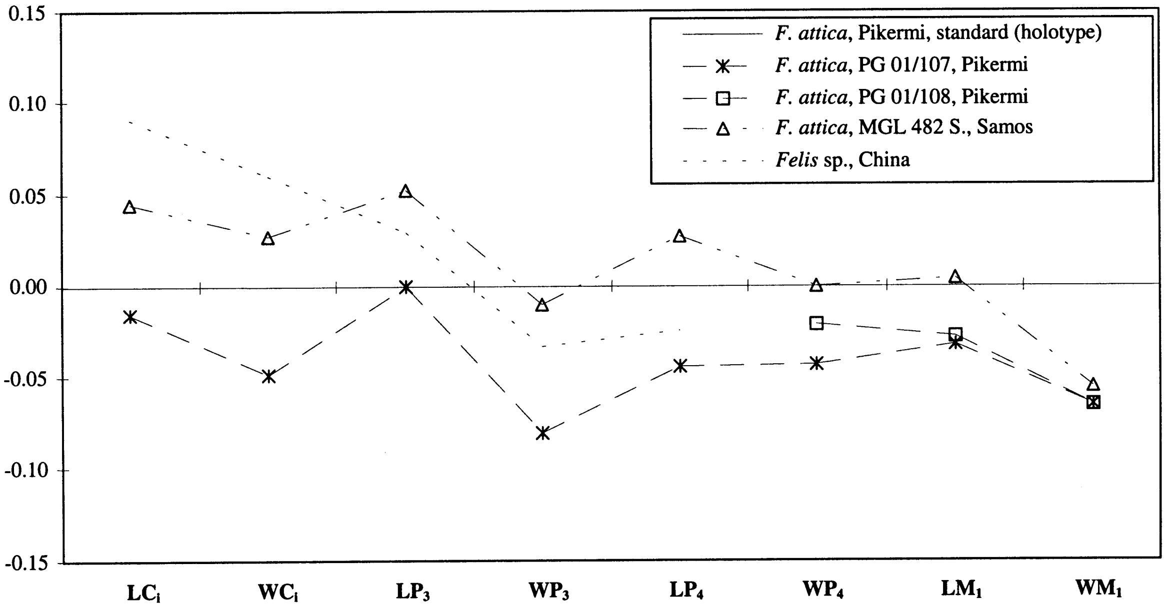

Fig. 11. Logarithmic ratio diagram comparing the lower teeth of AMPG PG 01/107 and AMPG PG 01/108 to *F. attica* and *Felis* sp. from various localities. Standard, *F. attica*, Pikermi, holotype, according to de Beaumont (1961). *F. attica* from Samos according to de Beaumont (1961); *Felis* sp. from China according to Zdansky (1924).

Fig. 11. Diagramme logarithmique des rapports des dimensions des dents inférieures de AMPG PG 01/107, AMPG PG 01/108, *F. attica* et *Felis* sp. provenant des différentes localités.

phalanges. Concerning the front limb a proximal radius fragment from Kinik in Turkey has been referred to *F. attica* by Schmidt-Kittler (1976). This specimen, however, as well as a lower canine from Karain referred to *F. attica* by Schmidt-Kittler (1976) are inadequate to demonstrate the presence of this species in Turkey.

The available postcranial specimens could belong in the small *F. attica* or the larger *M. parvulus*. The postcranial skeleton of *M. parvulus*, however, is badly known. As far as we know the only postcranial specimen that can be attributed to *M. parvulus* is a distal part of a radius from Pikermi (MNHNP PIK. 3128) referred to “Felis 3ème espèce” by Gaudry (1863: Pl. 27, fig. 8) and to *M. parvulus* by Thenius (1951) and de Beaumont (1961). This specimen has been referred to *F. attica* by Ginsburg (1999), but is large in my opinion (Dtdist = 27.4 mm, DAPdist = 15.7 mm) and must be attributed to *M. parvulus*.

The available specimens are small compared to the above mentioned radius of *M. parvulus* and must be attributed to *F. attica*. This could easily be shown (Roussiakis, 1996) comparing the maximum distal width of the radius (PA 3551/91) and the humerus (PA 2803/91), or the length of the Mc II and the Mt III to the distal width of the radius of *M. parvulus* (PIK. 3128). Compared to the proximal radius fragment from Kinik referred to *F. attica* by Schmidt-Kittler (1976), the available specimen (PA 3550/91) is not different in size but it has a slightly more elongated transversely head. The dimensions of the present tarsal and metatarsal bones are very close to those of the specimens MGL 805 S from Samos and BM(NH) M. 9010 from Pikermi (Tables 8 and 9). It is important to notice, however, that concerning the specimen MGL 805 S from Samos there are some differences in some of the dimensions given by de Beaumont (1961) and de Beaumont (1986). This is the reason some of the measurements of this specimen are given with a question mark (Table 8).

Unfortunately, the front limb of *F. attica* is not completely known and the brachial and intermembral indices cannot be estimated. Its crural index, however, is 101.2 (based on the specimen BM(NH) M 9010, measurements after Pilgrim, 1931), value not especially different from that of the domestic cat where the crural index ranges from 102.8 to 109.4 ($n = 10$, males and females included, estimated from Jayne, 1898). Based on the assumption that the Mc II PA 1035/91 comes from the same individual with the hind-limb bones PA 1021/91–1031/91 (since they were found in the same ossiferous block), the index Lmax Mt III/Lmax Mc II is 1.70, only slightly smaller than in the domestic cat (about 1.77). The above data shows that *F. attica* probably had limb proportions not especially different from the smaller sized domestic cat. The small inclination of the olecranon fossa relative to the long axis of the humerus, as well as the large medial tuberosity of the olecranon, characterise recent felids that inhabit open terrain (Gonyea, 1978). The above characters are also present in *F. attica* and indicate that this species was an inhabitant of open terrain, possibly not exclusively, however.

Subfamily: MACHAIRODONTINAE Gill, 1872

Genus: *Machairodus* Kaup, 1833

Machairodus giganteus (WAGNER, 1848)

Material: PA 1928/91: right tibia; PA 1962/91: left tibia, missing the proximal part; PA 3256/91: right Mt III; PA 2799/91: distal part of a right humerus; PG 98/26: right humerus; PG 98/30: right femur; PA 3552/91: distal part of a right humerus; PK1/379: right Mt IV, proximal part. The specimens PA 1928/91 and PA 1962/91 come from the excavations made in Pikermi by Woodward and Skouphos in 1901.

Description and discussion: Following de Beaumont (1975), *M. giganteus* is considered different from *Machairodus aphanistus* (KAUP, 1833), and includes the forms *leoninus*, *copei*, *palanderi*, and *taracliensis*. *M. giganteus* is known from the Turolian of Halmyropotamos (possible MN 11 or MN 12), the early-middle Turolian (MN11–12) of Ravin X in Greece, and from the middle Turolian (MN 12) of Mont Lubéron (France), Kalimanchi (Bulgaria), Samos, Pikermi (Greece) and Taraklia (Moldavia) (Ginsburg, 1999; Koufos, 2000). It is also known from the Turolian of Kerassia 4 in Euboea (Theodorou and Roussiakis, 2001; Roussiakis and Theodorou, in press).

From three available humerus specimens only one is complete (Fig. 12[1]) but anteroposteriorly compressed on its proximal half, so no measurements can be given for its proximal end. The upper edge of the greater tuberosity projects slightly above the head of the humerus. The fossa for the infraspinatus is deep and wide. Compared to *Homotherium crenatidens* FABRINI, 1890 the articular eminence of the humerus is more elongated transversely (in distal view).

The available femur (Fig. 12[2]) is complete but anteroposteriorly compressed on its distal part. The shaft of the bone has an ovoid section with transverse diameter slightly larger than the anteroposterior one (Table 12) and acute lateral border. The greater trochanter is situated slightly higher than the head of the femur and the neck passes almost horizontally from the head to the greater trochanter. The lesser trochanter is not situated very close to the medial border of the shaft. In the last character the Pikermi specimen differs from *H. crenatidens* from Senèze, where the lesser trochanter lies closer to the medial border (Ballesio, 1963). A femur fragment from Sesklo referred to cf. *H. crenatidens* by Athanassiou (1998) differs on its remarkably deeper neck and its third trochanter that is situated lower than the head.

The shaft of the tibia (Fig. 12[3]) has subtriangular section. The medial and lateral tuberosities of the spine project remarkably. The posterior intercondyloid fossa is deep. As in *H. crenatidens* (Ballesio, 1963) the posterior surface of the diaphysis is convex on its distal half. Moreover, the diaphysis shows some more interesting

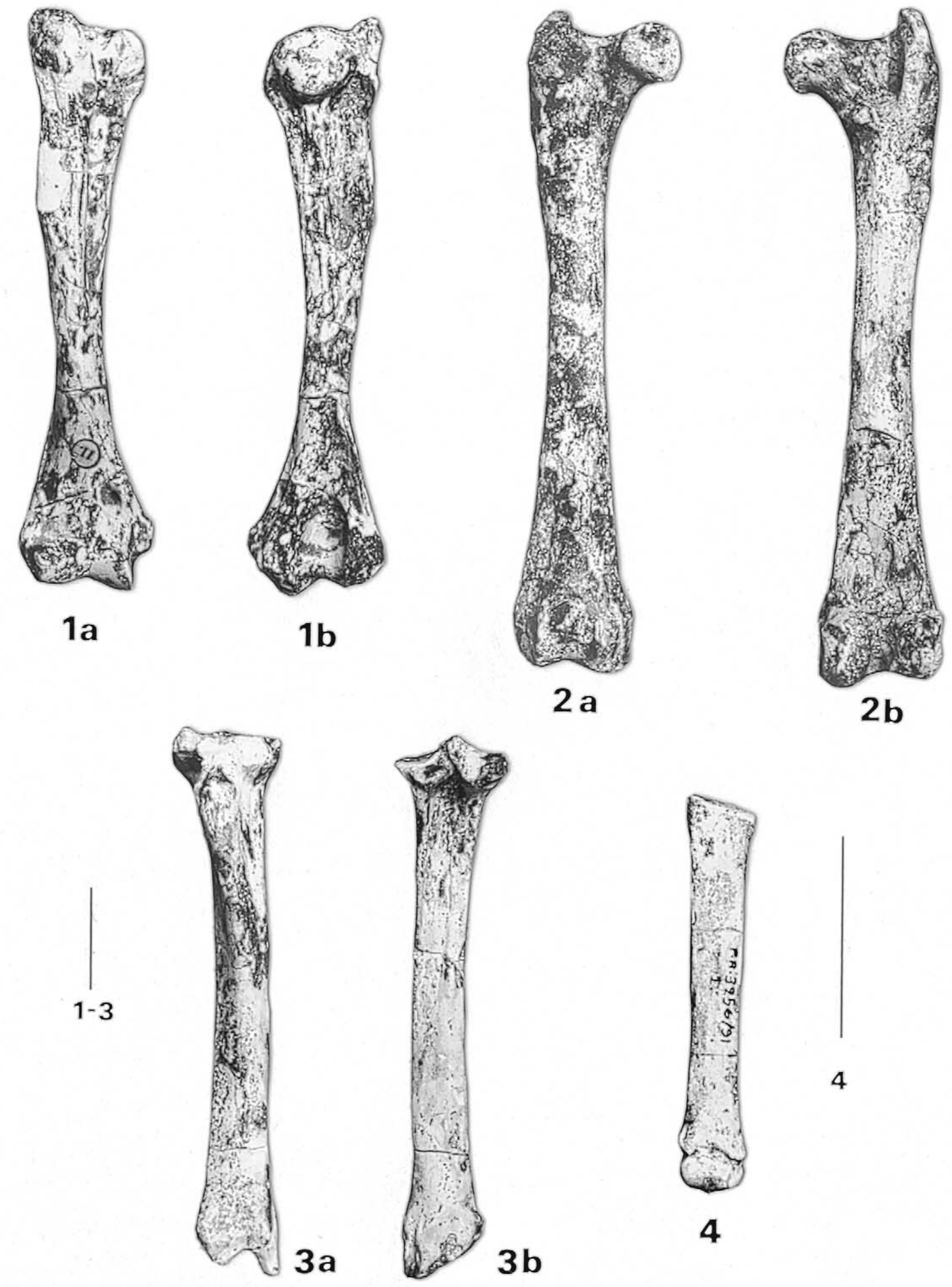

Fig. 12. *M. giganteus* WAGNER, 1848, Pikermi. **1.** Right humerus (AMPG PG 98/26); **a)** anterior view, **b)** posterior view. **2.** Right femur (AMPG PG 98/30); **a)** anterior view, **b)** posterior view. **3.** Right tibia (AMPG PA 1928/91); **a)** anterior view, **b)** posterior view. **4.** Right Mt III (AMPG PA 3256/91), anterior view. Scale bar 60 mm.

Fig. 12. **1.** Humérus droit (AMPG PG 98/26); **a)** vue antérieure, **b)** vue postérieure. **2.** Fémur droit (AMPG PG 98/30); **a)** vue antérieure, **b)** vue postérieure. **3.** Tibia droit (AMPG PA 1928/91); **a)** vue antérieure, **b)** vue postérieure. **4.** Mt III droit (AMPG PA 3256/91), vue antérieure. Échelle graphique 60 mm.

characters concerning the muscle scars of its posterior surface. The area for the popliteus muscle is small while the area for the *tibialis posticus* is expanded to the distal fourth of the bone. On the contrary the area for the *flexor longus hallicus* is reduced as in *H. crenatidens* (Ballesio, 1963). According to Ballesio (1963) in the cursorial felids the area for the flexor longus hallicus is larger. Distally, the groove for the tendon of *flexor longus digitorum* is scarcely

Table 12
Measurements of the limb bones of *M. giganteus* from Pikermi
Dimensions des diverses pièces squelettiques de *M. giganteus* de Pikermi

	Lmax	Lf	DTpr	DAPpr	DTdia	DAPdia	DTdistmax	DTdistart	DAPdistmax
Humerus (AMPG PG 98/26)	350.0	341.0	–	–	–	–	83.8	59.6	–
Humerus (AMPG PA 2799/91)	–	–	–	–	–	–	79.4	57.4	–
Humerus (AMPG PA 3552/91)	–	–	–	–	–	–	78.7	58.9	–
Humerus, MNHNP un., (after the author)	(350.0)	338.0	–	–	–	–	90.6	56.2	–
Femur (AMPG PG 98/30)	395.3	382.6	93.3	–	36.0	29.1	69.6	–	68.8
Tibia (AMPG PA 1928/91)	325.3	–	66.3	86.0	33.2	31.6	53.6	–	40.6
Tibia (AMPG PA 1962/91)	–	–	–	–	34.3	30.2	53.3	–	39.0
Tibia, MNHNP PIK. 3271 (after the author)	–	–	–	–	–	–	57.6	–	39.7
Mt III (AMPG PA 3256/91)	119.7	–	22.3	30.5	15.4	15.8	20.7	19.2	–
Mt IV (AMPG PK1/379)	–	–	14.0	24.1	–	–	–	–	–

indicated while the groove for the tendon of *tibialis posticus* is especially deep.

The third metatarsal (Fig. 12[4]) is almost similar in dimensions and robustness to that of *H. crenatidens*. It presents, however, important differences from *H. crenatidens*. In this species the third metatarsal articulates with the fourth metatarsal through one articular surface close to the plantar surface and another one close to the dorsal part of the bone. This last articular surface in *H. crenatidens* is almost flat and extends to the proximal articular surface (Ballesio, 1963). The same articular surfaces are also present on the available specimen but the dorsal one is strongly concave as in the large recent felins and does not reach the proximal border. The plantar one is convex and corresponds to a concave articular surface on the Mt IV.

Some associated hind limb bones from Pikermi referred by Pilgrim (1931) as "*Epimachairodus* ? *taracliensis*" do not differ significantly in size from the described specimens of *M. giganteus*.

3. Conclusions

The present specimen of *S. primigenius* is not different from other *S. primigenius* specimens from Pikermi. Various *Simocyon* remains have been described from Europe and Asia, and a revision of the genus is needed. *S.* aff. *primigenius* from the Baode in China is not but slightly only smaller than the Pikermi *Simocyon* and also preserves a small anterior accessory cusp in P_4. An anterior accessory cusp in P_4 is also present in *Simocyon* sp. from Dorn-Dürkheim 1 (Morlo, 1997), which does not differ especially from *S. primigenius* in size. Comparable in dimensions is the *Simocyon* specimen also, from Fugu (China), referred by Wang (1997) to *S. primigenius*. This specimen, however, preserves the P_2 and P_3, teeth never observed, as far we know, in the Pikermi specimens of *S. primigenius*.

P. palaeatticus from Pikermi is larger than *P. macedonicus* from Maramena. Following Thenius (1949b) and Schmidt-Kittler (1995) we refer *Promeles* to the Mustelinae. A lower carnassial from Dorn-Dürkheim 1, referred to *P. palaeatticus* by Morlo (1997), is especially smaller than the Pikermi species and is preferable to retain for this the determination *Promeles* sp., originally given by Franzen and Storch (1975).

A mandibular fragment preserving the M_1 is referred to *M. woodwardi*. This specimen is not different from the holotype of *M. woodwardi* described by Pilgrim (1931). In the context of this paper, this mustelid is referred to the genus *Martes*, but a revision of the late Miocene mustelids is clearly necessary.

Some metacarpals show great similarities both in morphology and dimensions to *E.*? *latipes*. Since this species is poorly known, only from postcranial material, the present remains are referred as mustelidae, gen. et sp. indet.

A skull fragment and two mandibular fragments of *F. attica* are not different from other *F. attica* remains from Pikermi or Samos. The same is true for the postcranial material referred to *F. attica*. The limb proportions cannot be evaluated precisely but possibly *F. attica* had limb proportions similar to the domestic cat. Some morphological characters of the humerus and the olecranon indicate that *F. attica* very probably was an inhabitant of relatively open terrain. The presence of *F. attica* in Dorn-Dürkheim 1 (Morlo, 1997) is not clearly demonstrated in my opinion.

The present postcranial specimens of *M. giganteus* are not different from those already known by Gaudry (1863) or Pilgrim (1931). Their morphological characters indicate that this machairodont probably had not especially developed cursorial capabilities.

From the above described carnivore remains, the ossiferous block that contained the third metatarsal (AMPG PA 3256/91) of *M. giganteus* also contained a lot of other specimens. That most of these specimens belong in *Mesopithecus pentelicus* (WAGNER, 1839), as an almost complete pes with its bones articulated, an almost complete tibia, a perone, a femur, an isolated metacarpal and various isolated phalanges (AMPG PA 3255/91, PA 3266–69/91, PA 3271–76/91 etc.). Most probably all these *Mesopithecus* remains belong to the same individual. A very rare specimen found in the same ossiferous block is the distal half humerus (AMPG PA 3287/91) of a bird, 3/4 in width than the *Grus pentelici* described and figured by Gaudry (1865: Pl. 59, fig. 4). The *Hipparion* remains of the same block are three distal tibial parts (AMPG PA 3252/91, PA 3261/91 and PA 3264/91), two complete Mt III (AMPG PA 3253/91 and PA 3262/91), one Mt III fragment (AMPG PA 3260/91) and a proximal Mc III fragment (AMPG PA 3263/91). Following Koufos (1987), all these specimens can be referred to *Hipparion mediterraneum* (ROTH and WAGNER, 1854), except the Mt III PA 3253/91, which must be referred to *Hipparion brachypus* HENSEL, 1862. It is not necessary to give more information for these specimens except for the two complete third metatarsals. From these two metatarsals, PA 3262/91 is longer (243.6 mm), its absolute dimensions are within the range of *H. mediterraneum* and its index 11/1 (following the methodology of Koufos, 1987) is equal to 13.1, value in accordance with that of *H. mediterraneum*. PA 3253/91 on the other hand is slightly shorter (237.1 mm) but more massive (index 11/1 = 16.4). Most of the absolute dimensions of this metatarsal are outside the range of *H. mediterraneum* but within the range of *H. brachypus* and we must refer it to this latter species. The same ossiferous block also contained one astragalus (AMPG PA 3254/91) of *Bohlinia attica* (GAUDRY and LARTET, 1856) and a bovid palate (unnumbered) that could belong in *Palaeoreas lindermayeri* (WAGNER, 1848). The teeth of this palate, however, are so damaged that any determination would be very doubtful at the present moment.

This information is especially important because the Pikermi specimens come from at least two different fossiliferous levels (Gaudry, 1862: 14; Woodward, 1901: 483; Abel, 1922: fig. 132), and there are no data for the exact provenance of the specimens and the faunal content of each level. These problems led to many discussions concerning the coexistence of the various species in Pikermi, especially the common and frequently used for stratigraphic correlation hipparions (Dermitzakis, 1976; Theodorou and Nikolaides, 1988). The above data, however, indicate that *M. giganteus*, *M. pentelicus*, *B. attica*, *H. mediterraneum* and *H. brachypus* coexisted in Pikermi for at least some period of time.

Moreover, it is clear, that careful recording and exploitation of any information during the preparation and preservation of old museum collections can help us to solve various problems, despite the fact that many data were lost during the old-fashioned excavations of the past.

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