Estudios Geológicos, 67(2)
julio-diciembre 2011, 291-320
ISSN: 0367-0449
doi:10.3989/egeol.40560.190

The Miocene carnivore assemblage of Greece

La asociación de carnívoros miocenos de Grecia

G.D. Koufos[1]

ABSTRACT

The Miocene carnivore assemblage of Greece includes a great number of taxa, described in numerous articles since the first decades of the 19th Century. The present article is a revision of all these taxa, providing information about their history, localities, age, as well as their stratigraphic distribution and palaeoenvironment. The Early/Middle Miocene carnivore record of Greece is poor as the available fossiliferous sites and material are rare. However, the Late Miocene one is quite rich, including numerous taxa. The Miocene localities with carnivores and their age are given in a stratigraphic table covering the European Mammal zones from MN 4 to MN 13. The type locality, holotype, and some historical and morphological remarks are given for each taxon. Several carnivore taxa were erected from Greek material and new photos of their holotypes are given. The stratigraphic distribution of the Greek carnivore taxa indicates that they are covering the time span from ~19.0-5.3Ma. The majority of the Miocene taxa (*Adcrocuta, Hyaenictitherium, Plioviverrops, Protictitherium, Ictitherium, Indarctos, Dinocrocuta, Promephitis*) disappeared at the end of Miocene. The composition of the Early/Middle Miocene carnivore assemblage of Greece includes mainly viverrids (*Lophocyon, Euboictis*), while the hyaenids, percrocutids, felids and mustelids are very few. On the contrary the Late Miocene assemblage is richer, including more subfamilies and species; the hyaenids and mustelids dominate, while the viverrids are absent. The Late Miocene carnivore guild structure is similar to that of the modern Serengeti, indicating a relatively open, savannah-like environment.

Keywords: Carnivora, Miocene, Greece, Systematic, Diversity, Chronology

RESUMEN

La asociación de carnívoros miocenos de Grecia incluye un gran número de taxones, descritos en numerosos artículos desde las primeras décadas del siglo XIX. El presente artículo supone un esfuerzo de síntesis de todos estos taxones, suministrando información sobre su historia, localidad, edad, así como su distribución estratigráfica e inferencias paleoambientales. El registro de los carnívoros del Mioceno inferior y medio es pobre, debido a que las localidades existentes y los fósiles son raros. Sin embargo, el Mioceno superior es considerablemente rico, incluyendo numerosos taxones. Las localidades miocenas con carnívoros y su edad se exponen en un cuadro estratigráfico que abarca las Zonas de Mamíferos Europeas desde la MN4 a la MN 13. La localidad tipo, holotipo y algunas notas históricas y morfológicas se suministran para cada taxón. Algunos taxones de carnívoros fueron definidos sobre material griego, nuevas fotografías de los holotipos sonfiguradas. La distribución estratigráfica de los taxones de carnívoros griegos cubren un lapso de tiempo comprendido entre los 19,0 a los 5,3 Ma. La mayoría de los taxones miocenos (*Adcrocuta, Hyaenictitherium, Plioviverrops, Protictitherium, Ictitherium, Indarctos, Dinocrocuta, Promephitis*) desaparecen al final del Mioceno. La composición de la asociación de carnívoros miocenos de Grecia incluye principalmente vivérridos (*Lophocyon, Euboictis*), mientras que los hiénidos, percrocútidos, félidos y mustélidos son más escasos. Por el contrario la asociación del Mioceno superior es más rica, incluyendo más subfamilias y más especies; dominando hienas y mustélidos, mientras que los vivérridos están ausentes. La estructura de la comunidad (gremio) de carnívoros del Mioceno superior es similar a la del actual Serengeti, indicativo de un ambiente relativamente abierto, similar a la sabana, de acuerdo con los resultados de otros trabajos realizados en el área.

Palabras clave: Carnivora, Mioceno, Grecia, Sistemática, Diversidad, Cronología

[1] Aristotle University of Thessaloniki. Department of Geology. Laboratory of Geology and Palaeontology. GR-54124, Thessaloniki. Greece. Email: koufos@geo.auth.gr

Introduction

The Miocene carnivore record of Greece is quite rich, including a significant number of taxa. Since 1980 the Greek carnivore assemblage compised mainly from the taxa found in Pikermi and Samos. During the last decades several new material has been unearthed, enriching it. The long-time field work in Axios Valley, near Thessaloniki, provided a great number of fossils from various fossiliferous levels, including many new carnivore taxa. The carnivore assemblage was also enriched from new excavations in Samos Island, Perivolaki, Aliveri, Chios Island, Maramena, Kerassia, Nikiti (Fig. 1) and several other localities. Although the Late Miocene carnivore assemblage of Greece is quite rich, the evidences from Early/Middle Miocene are limited, as the known localities are few and poor in fossils (Koufos, 2006a and ref. cited). The Miocene carnivores of Greece were described in numerous articles from the middle of 19th Century until now. Several holotypes are included in this material, while some specimens are unique. In the present article the known carnivore taxa of Greece are revised, giving information for their type locality and material, the Greek localities in which they were recognized, their age and some main morphological features, coming from the bibliography and our observations. Illustrations of the known Greek taxa will also included; the effort is to give new photos of the holotypes based on Greek material. Finally some information about their stratigraphic range and palaeoecology are given.

The article is written for this volume, dedicated to the memory of Prof. L. Ginsburg, a palaeontologist who devoted a large part of his life studying the Miocene carnivores. I had the opportunity to meet him several times in the Institute de Paléontologie, Muséum Nationale d'histoire Naturelle of Paris during my visits there since 1983. He always discussed with me and helped me to find what I wanted to see, providing useful information about the fossils, as well as casts and bibliography from his personal collection.

Greek localities

The Greek Miocene carnivore sample comes from several localities (Fig. 1), which will be given below with the main and most recent references about their carnivore fauna and age.

1. **Aliveri (ALI),** Evia Island; Middle Orleanian, MN 4 (Schmidt-Kittler, 1983; Doukas, 2003).

2. **Antonios (ANT),** Chalkidiki Peninsula; Middle/Late Orleanian, MN 4/5 (Vasileiadou & Koufos, 2005; Koufos, 2008).

3. **Chomateres (CHO),** Attica, Middle Turolian, MN 12 (Symeonidis, 1978; Koufos, 2006a)

4. **Diavata (DVT)**, Axios Valley, Vallesian-Early Turolian, MN 9-11 (Koufos, 1995, 2006a).

5. **Dytiko-1 (DTK)**, Axios Valley, Late Turolian, MN 13 (Bonis & Koufos, 1991; Koufos, 2000, 2006a).

6. **Dytiko-2 (DIT)**, Axios Valley, Late Turolian, MN 13 (Bonis & Koufos, 1991; Koufos, 2000, 2006a).

7. **Dytiko-3 (DKO)**, Axios Valley, Late Turolian, MN 13 (Bonis & Koufos, 1991; Koufos, 2000, 2006a).

8. **Halmyropotamos (HAL),** Evia Island; Middle Turolian, MN 12 (Melentis, 1967; Koufos, 2006a).

9. **Kerassia (KER)**, Evia Island; Early-Middle Turolian, MN 11-12 (Roussiakis &Theodorou, 2003; Koufos, 2006a).

10. **Maramena (MAR)**, Serres Basin, Latest Turolian, MN 13/14 (Schmidt-Kittler, 1995; Schmidt-Kittler *et al*., 1995).

11. **Mytilinii-1A (MTLA),** Samos Island; Middle Turolian, MN 12; GPTS ~7.1 Ma (Koufos, 2009; Koufos *et al*., 2009)**.**

12. **Mytilinii-1B (MTLB)**, Samos Island; Middle Turolian, MN 12; GPTS ~7.1 Ma (Koufos, 2009; Koufos *et al*., 2009).

13. **Mytilinii-1C (MTLC)**, Samos Island; Middle Turolian, MN 12; GPTS ~7.1 Ma (Koufos, 2009; Koufos *et al*., 2009).

14. **Mytilinii-4 (MLN)**, Samos Island, end of Early Turolian, MN 11; GPTS ~7.5 Ma (Koufos, 2009; Koufos *et al*., 2009).

15. **Pentalophos-1 (PNT)**, Axios Valley; ?Early Vallesian, ?MN 9 (Bonis & Koufos, 1991; Koufos, 2000, 2006a).

16. **Perivolaki (PER),** near Volos, Thessaly; Middle Turolian, MN 12; GPTS ~7.3-7.1 Ma (Koufos, 2006b, Koufos *et al*., 2006a).

17. **Pikermi (PIK)**, Attica, Middle Turolian, MN 12; the PIK carnivore record is the richest one (see Koufos, 2006a; Roussiakis, 1996; NOW, 2010).

18. **Prochoma-1 (PXM)**, Axios Valley; Middle Turolian, MN 12; GPTS ~7.4 Ma (Bonis & Koufos, 1991; Koufos, 2000; Koufos *et al.,* 2009; Sen *et al*., 2000).

19. **Ravin de la Pluie (RPl)**, Axios Valley, Late Vallesian, MN 10; GPTS ~9.3 Ma (Bonis & Koufos, 1991, Koufos, 2000, 2011a, b; Sen *et al*., 2000).

20. **Ravin des Zouaves-1 (RZ1)**, Axios Valley, Late Vallesian, MN 10 (Bonis & Koufos, 1991; Koufos, 2000, 2006a).

21. **Ravin des Zouaves-5 (RZO)**, Axios Valley; Early Turolian, MN 11; GPTS ~8.2 Ma (Bonis & Koufos, 1991; Koufos, 2000, 2006a).

22. **Ravin-X (R-X),** Axios Valley; ?Early Turolian, ?MN 11(Koufos, 2000, 2006a).

23. **Silata (SLT),** Chalkidiki Peninsula, Latest Turolian, MN 13/14 (Koufos, 2006a,c).

24. **Thermopigi (TMP)**, Serres Basin, Turolian, MN 11-13 (Geraads *et al*., 2007).

25. **Thymiana-B (THB),** Evia Island; Late Orleanian, MN 5 (Koufos *et al.,* 1995, Koufos, 2006a).

26. **Vathylakkos-2 (VTK)**, Axios Valley; Middle Turolian, MN 12; GPTS ~7.3 Ma (Bonis & Koufos, 1991; Koufos, 2000, 2006a; Koufos *et al*., 2009).

27. **Vathylakkos-3 (VAT)**, Axios Valley; Middle Turolian, MN 12 (Bonis & Koufos, 1991; Koufos, 2000).

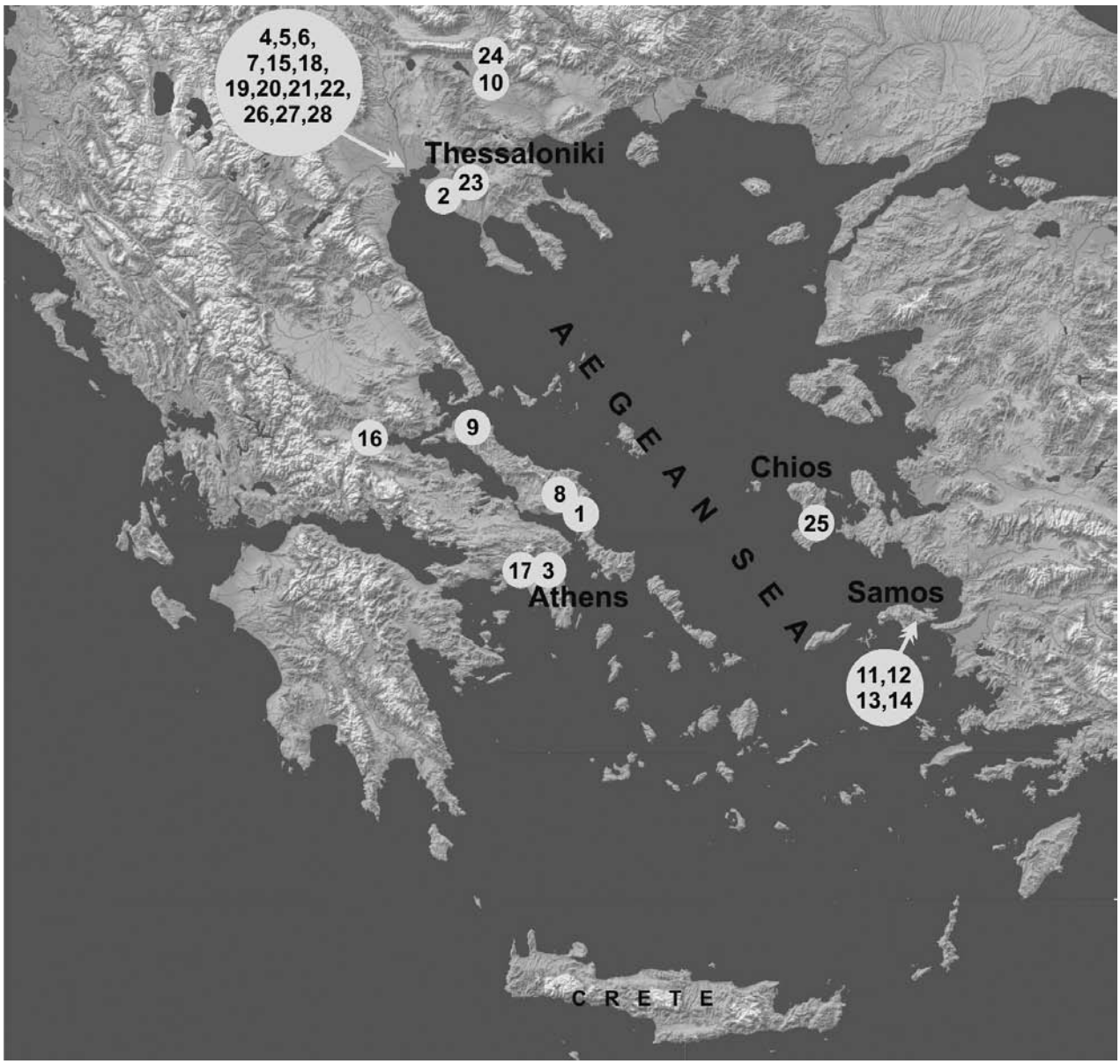

Fig. 1.—Geographic map of Greece, indicating the position of the Miocene mammal localities with carnivores; the numbers correspond to the localities (see text). The map is taken from http://www.shaded-relief.com

28. **Xirochori-1 (XIR)**, Axios Valley, Late Vallesian, MN 10; GPTS ~9.6 Ma (Bonis & Koufos, 1991; Koufos, 2000, 2006a).

Besides these localities there are some references for the presence of some carnivore taxa in the old Samos localities A, Q1-6, S3, Main Bone Beds, and Adrianos ravine; for the age of these localities and their correlation with the new Samos ones see Kostopoulos *et al*. (2009) and Koufos *et al*. (2009).

Abbreviations

AMNH= American Museum of Natural History, New York
AMPG= Athens Museum of Palaeontology and Geology
BSPM= Bayerische Staatssammlung für Paläontologie und Historische Geologie, München
LGPUT= Laboratory of Geology and Palaeontology, University of Thessaloniki
MNHN= Museum Nationale d'histoire Naturelle, Paris
NHMA= Natural History Museum of the Aegean, Samos
NHMB= Natural History Museum of Basel
NHML= Natural History Museum of London
NHMW= Naturhistorisches Museum of Wien
PIUW=Paläontologische Institut, University of Wien
SAM= Samos, old collections
SMNS= Staatliches Museum für Naturkunde, Stuttgart

Each specimen is referred by an abbreviation consisting of three parts. The first is the Museum or institute housing the specimen, the second is the locality and the third the catalogue number.

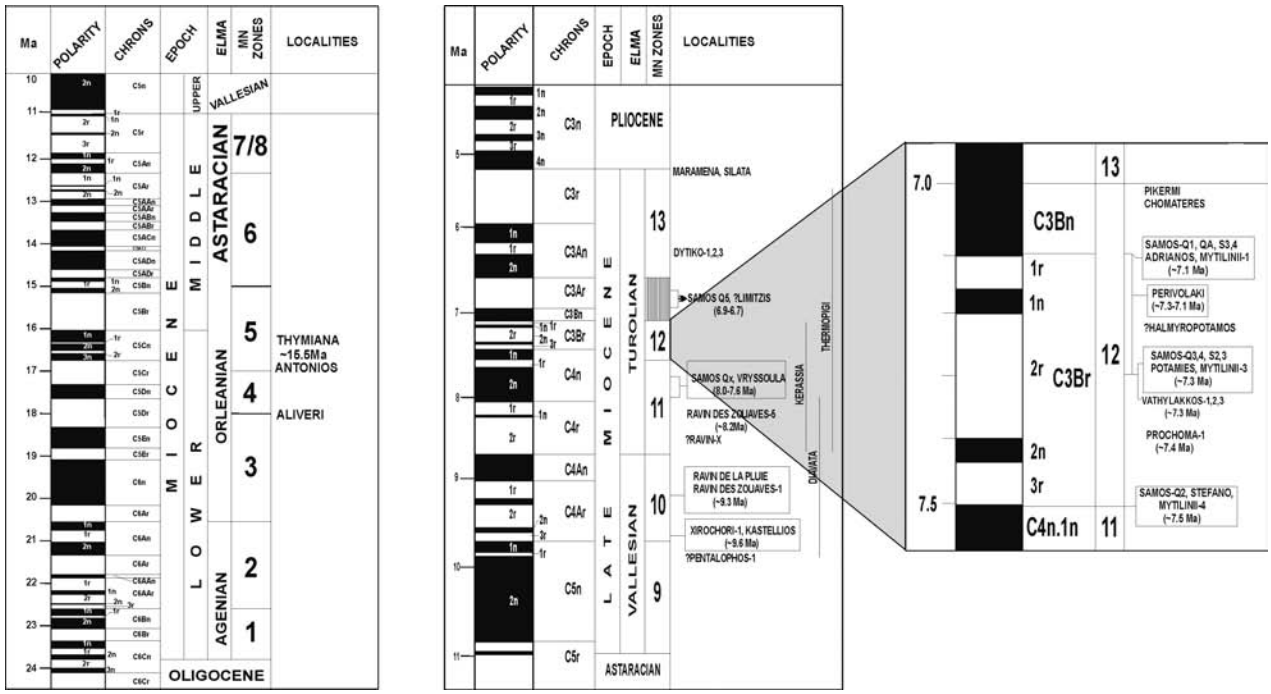

Fig. 2.—Biostratigraphic table, including the Miocene Greek localities with their age. Data taken from Koufos (in press).

Palaeontology

Order CARNIVORA Bowdich, 1821
Family URSIDAE Fischer von Waldheim, 1817
Sub-Family Ursinae (Fischer de Waldheim, 1817) Burmeister, 1866
Indarctos punjabiensis atticus (Weithofer, 1888)

Type locality. Pikermi, Attica; Middle Turrolian, MN 12 (Figs. 1, 2).

Holotype. Left mandibular fragment with m1-m2, described and figured (Weithofer, 1888: (p. 231; pl. 12, figs. 1-2).

Greek localities. Pikermi (PIK), Attica (Roussiakis, 2001a); it is referred from the locality A of Samos, as *Indarctos* cf. *atticus*, without description and reference of the material based on (Solounias, 1981).

Age. Middle Turolian, MN 12.

Remarks. A mandibular fragment of an ursid from Pikermi was described as *Hyaenarctos* sp. (Dames, 1883). This author told to Weithofer that this specimen was a new species and labeled it as *H. atticus* and this name was used for the description of the holotype (Weithofer, 1888). Quite later, Helbing (1932) described *Indarctos atticus* from Samos, while Erdbrink (1953) transferred the Pikermi material to this species. Recently, the Greek sample of *Indarctos* was included to *I. punjabiensis atticus* (Baryshnikov, 2002). Some postcranials of *Indarctos* from PIK were recently described by Roussiakis (2001a). It has relatively large size, more or less squarish upper teeth, M2 rather longer than the M1 with quite

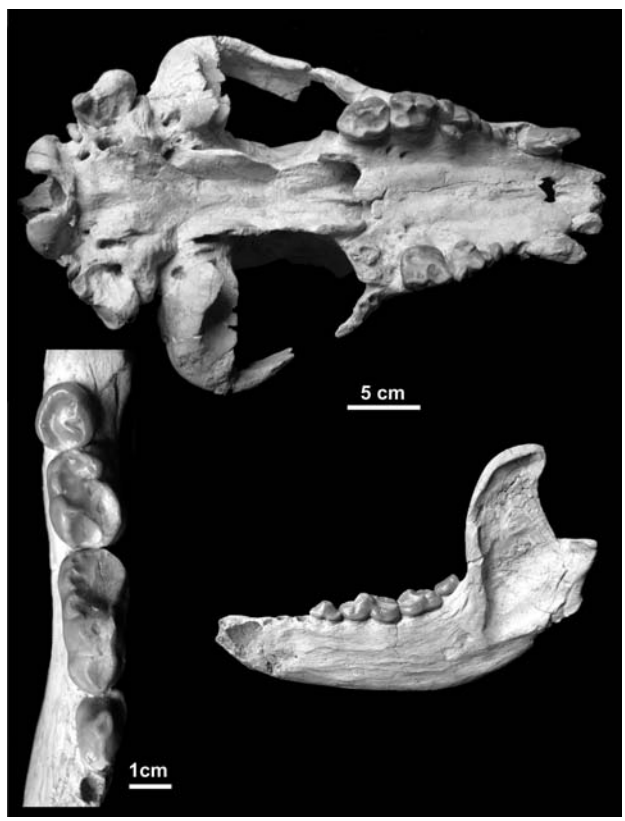

Fig. 3.—*Indarctos atticus*, skull and mandible, NHMW-SAM-no 25, Loc. unknown, Samos Island, Turolian, MN 11-13.

developed talon, moderate protocone and small parastyle in the P4, relatively long m1 with talonid slightly shorter than trigonid and high entoconid, m2 with talonid like m1 and rounded m3.

Ursavus depereti Schlosser, 1902

Type locality. Melchingen, Germany; Early Vallesian, MN 9 (NOW, 2010).

Holotype. Left m1 and m2 described and figured by Schlosser (1902: p. 149; pl. II, figs. 19, 20, 22, 23).

Greek localities. Perivolaki (PER), Thessaly (Koufos, 2006b). Solounias (1981) refers *U*. cf. *depereti* from the locality A of Samos but without description and the material based on.

Age. Middle Turolian, MN 12.

Remarks. *U. depereti* was certainly recognized in the locality PER from a mandible (Fig. 4), described by Koufos (2006b). The genus *Ursavus* includes a number of species and *U. depereti* is well distinguished from the others by its larger size. It is characterized by wide and roughly inclined backwards symphysis, strong canine with elliptical transverse section, elongated and narrow p4 with long talonid and small-rounded metaconid, elongated and more bunodont m2, as well as large-rounded m3 with low protoconid (Koufos, 2006b: text-figs. 1, 2).

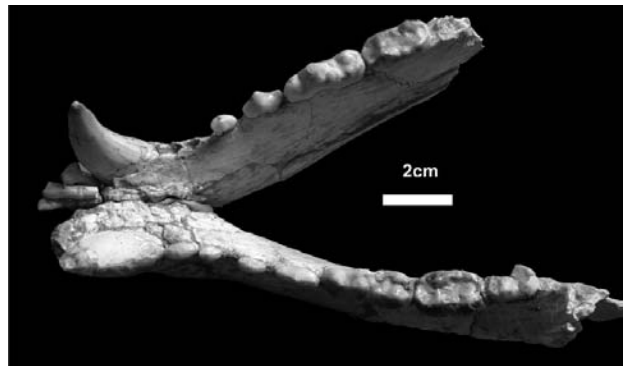

Fig. 4.—*Ursavus depereti*, mandible, LGPUT-PER-1270, Perivolaki, Thessaly, Middle Turolian, MN 12.

Ursavus ehrenbergi Thenius, 1947

Type locality. Halmyropotamos (HAL), Evia Island; Middle Turolian, MN 12 (Figs. 1, 2).

Holotype. Maxilla with P4-M2 dex and P1-M2 dex, AMPG-HAL-nn (Fig. 5), described and figured by Thenius (1947).

Greek localities. It is only known from Halmyropotamos.

Age. Middle Turolian, MN 12.

Remarks. The new species of *Ursavus* has the size of a small wolf, slightly concave palate, short muzzle, zygomatic arches situated above the M1, elliptical transverse section in the canine, P4 shorter than the M1 with three strong cusps and a small ptotocone situated before the middle of the tooth, more squarish M1 and M2 with relatively flattened cusps, and M2 with slightly longer talon and arc-like, in buccal view, lingual aspect of the top of the main cusp (Thenius, 1947).

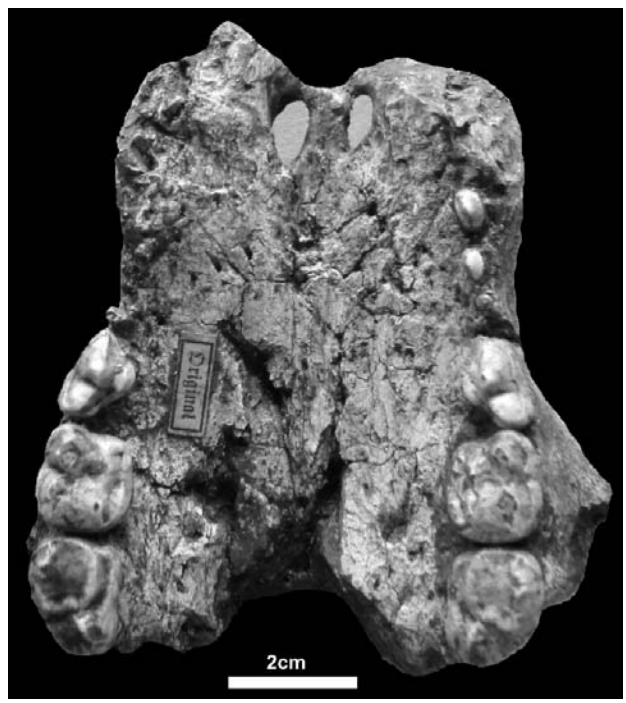

Fig. 5.—*Ursavus ehrenbergi*, maxilla, AMPG-HAL-nn, HOLOTYPE, Halmyropotamos, Evia Island, Middle Turolian, MN 12.

Family VIVERRIDAE Gray, 1821
Sub-Family Lophocyoninae Fefjar & Schmidt-Kittler, 1987
Euboictis aliverensis (Schmidt-Kittler, 1983)

Type locality. Aliveri, Evia Island; Middle Orleanian, MN 4 (Figs. 1, 2).

Holotype. Right P4, ALI-AL-23, described and figured by Schmidt-Kittler (1983: p. 303, fig.1; pl.1, fig. 6).

Greek localities. It is only known from Aliveri.

Age. Middle Orleanian, MN 4.

Remarks. Originally, it was described as *Sivanasua aliverensis*, but one year later it was transferred to the new genus *Euboictis* (Schmidt-Kittler, 1983; Fejfar & Schmidt-Kittler, 1984). It is characterized by a single-rooted P1 with three cusps, slightly molarized P2,3 with the paracone-metastyle blade similar to that of the P4, relatively short metastyle in the P4, W-like paracone and metacone in the M1,2 with continued lingual cingulum in the protocone and lacking conules (Fig. 6). The lower dentition has relatively molarized p1, p2-4 with trigonid and short-broad talonid, m1 shorter than the m2 with very low trigonid, m2 talonid longer than trigonid, and equal-sized hypoconid and hypoconulid in the m2 (Schmidt-Kittler, 1983; Fefjar & Schmidt-Kittler,1984).

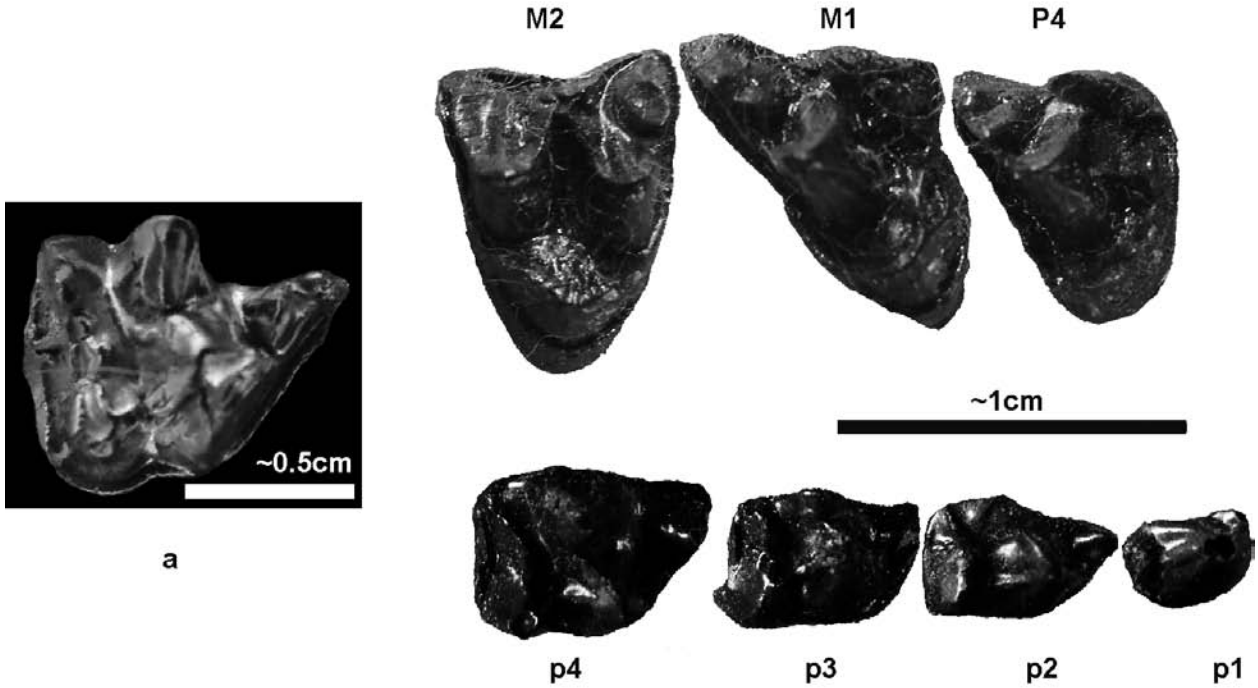

Fig. 6.—*Euboictis aliverensis*, **a**. p4 dex, ALI-AL23, HOLOTYPE; **b**. upper and lower composite dentition, Aliveri, Evia Island, Middle Orleanian, MN 4. The holotype has been gilded as all other original material; the latter was shot from the casts.

Lophocyon paraskevaidisi Koufos, Bonis & Sen, 1995

Type locality. Thymiana-B (THB), Chios Island; Late Orleanian, MN 5 (Figs. 1, 2).

Holotype. Mandible with both tooth rows, LGPUT-THB-1 (Fig. 7), described and figured by Koufos *et al*. (1995: p. 512, fig. 3; pl. 67, fig. 2).

Greek localities. It is only known from Thymiana-B.

Age. Late Orleanian, MN 5.

Remarks. Two species of *Lophocyon* are known, that from Chios and *L. carpathicus* from Kosice-Bankov, Slovakia (Fejfar & Schmidt-Kittler, 1987). According to Koufos *et al*. (1995) *L. paraskevaidisi* is characterized by molarized P3,4 with strongly projected metastyle and shallow groove between it and the parastyle, high-crowned lower teeth, molarized premolars with broad talonid and strongly developed hypoconulid in the m2. It is smaller than *L. carpathicus*, with higher degree of molarization and less developed basal cingulum.

Fig. 7.—*Lophocyon paraskevaidisi*, maxilla LGPUT-THB-12 and mandible LGPUT-THB-1, HOLOTYPE, Chios Island, Late Orleanian, MN 5.

Family MUSTELIDAE Swainson, 1835
Sub-Family Lutrinae (Bonaparte, 1837) Baird, 1857
Enhydriodon (?) latipes Pilgrim, 1931

Type locality. Pikermi (PIK), Attica; Middle Turolian, MN 12 (Figs. 1, 2).

Holotype. Left hind foot, NHML-PIK-M.9002, described and figured by Pilgrim (1931: p. 56, figs. 6-27).

Greek localities. Pikermi (PIK), Attica (Roussiakis, 2002).

Age. Middle Turolian, MN 12.

Remarks. Some postcranials from PIK in the Woodward's collection of NHML were described as a possible new species of *Enhydriodon* (Pilgrim, 1931). After that description nobody worked on this material. Recently, some new postcranials from PIK are referred to this species (Roussiakis, 2000).

Lutra affinis Gervais, 1859

Type locality. Sables de Montpellier; Early Ruscinian, MN 14 (NOW, 2010).

Holotype. A hemimandible with m1 is referred, but not figured, as the holotype of this species (Gervais, 1859). The specimen is probably lost and the material of MAR is referred as the neotype of the species (Ginsburg, 1999: p. 147).

Greek localities. Maramena (MAR), Serres Basin (Schmidt-Kittler, 1995).

Age. Latest Turolian, MN 13/14.

Remarks. The sole known material of this taxon are some dental remains from MAR (Fig. 8); (Schmidt Kittler, 1995: p. 83; pl. 2, fig. 2). The material includes the fragments of the two rami of a mandible and some isolated teeth housed in AMPG. The MAR *Lutra* resembles to the modern *Lutra lutra* but it is remarkably smaller. Based on the size it is closer to *L. affinis* from the Ruscinian Sables de Montpellier (Schmidt-Kittler, 1995).

Fig. 8.—*Lutra affinis*, mandibular fragment, AMPG-MAR-MA12, Maramena, Serres Basin, Latest Turolian, MN 13/14.

Sub-Family Mustelinae Gill, 1872
Palaeogale sp.

The genus is mentioned from the Middle Orleanian locality of Aliveri. Its presence is only referred without description or reference of the material based on (Schmidt-Kittler, 1983).

Proputorius sp. cf. *P. sansaniensis* (Fihlol, 1890)

Type locality. The type locality of *P. sansaniensis* is Sansan, France; Early Astaracian, MN 6 (NOW, 2010).

Holotype. The holotype of *Proputorius sansaniensis* is a left hemimandible with c-m1, Sa 776, described and figured by Filhol (1891: pl. 5, figs. 1-3).

Greek localities. Antonios (ANT), Chalkidiki (Koufos, 2008).

Age. Middle/Late Orleanian, MN 4/5.

Remarks. The p3,4 lack accessory cuspids and the main one is high and pointed; its top is slightly inclined lingually. The distal cingulum is strong and widened lingually, forming a small talonid-like projection. The horizontal ramus of the mandible is elongated, shallow with curved inferior border and deep triangular-shaped masseteric fossa with its anterior margin below the m2 (Koufos, 2008).

Martes woodwardi Pilgrim, 1931

Type locality. Pikermi (PIK), Attica; Middle Turolian, MN 12 (Figs. 1, 2).

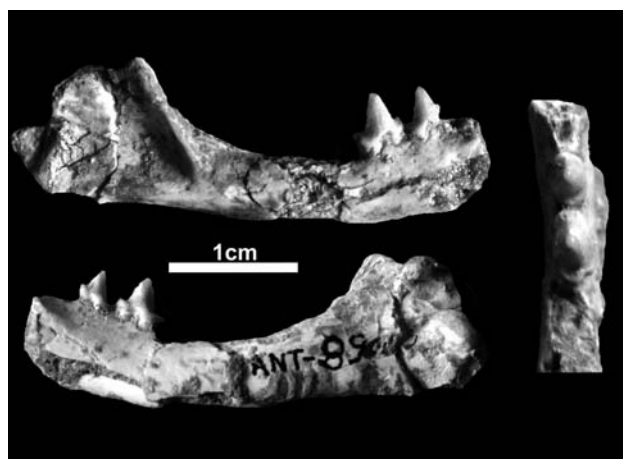

Fig. 9.—*Proputorius* sp. cf. *P. sansaniensis*, mandibular fragment, LGPUT-ANT-89, Antonios, Chalkidiki, Middle/Late Orleanian, MN 4/5.

Holotype. Right mandibular fragment with p4-m1, NHML-PIK-M.9031, described and figured by Pilgrim (1931: p. 40; pl. 2, figs. 2, 2a).

Greek localities Pikermi (PIK), Attica (Roussiakis, 2002).

Age. Middle Turolian, MN 12.

Remarks. Ginsburg (1999) considers the mandible referred to *M. woodwardi* as belonging to Melinae and he erected the

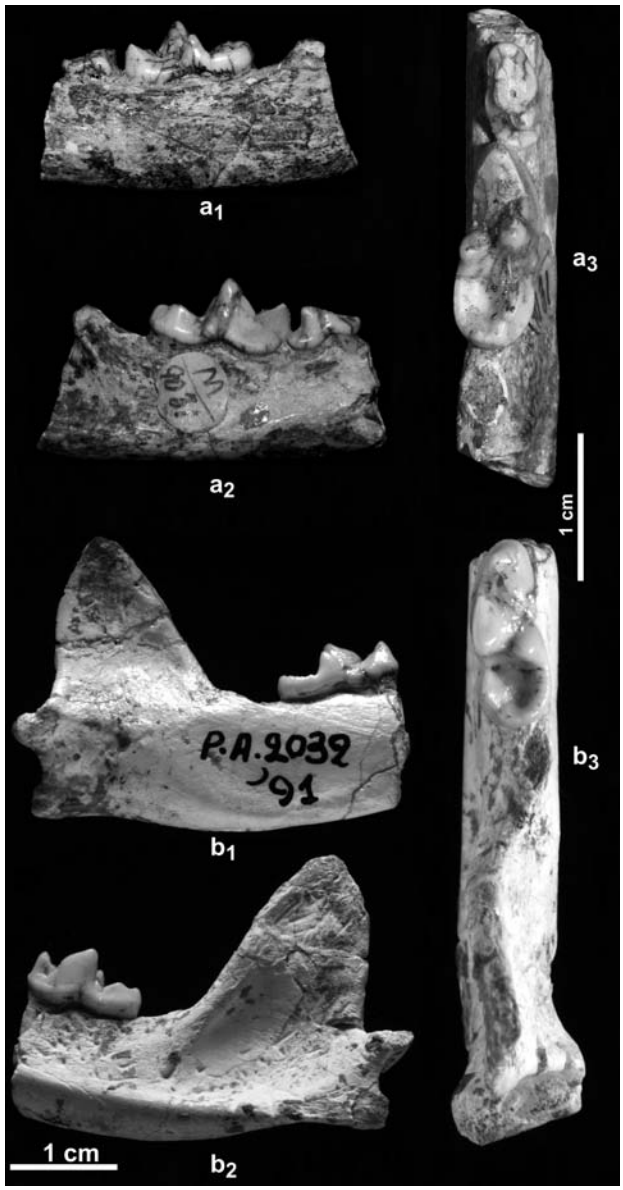

Fig. 10.—*Martes woodwardi*, **a.** mandibular fragment, NHML-PIK-M.9031, HOLOTYPE, Pikermi, photo kindly provided by G. Konidaris, LGPUT; **b.** mandibular fragment, AMPG-PIK-PA2032-91, Pikermi, Attica, Middle Turolian, MN 12; photo kindly provided by S. Roussiakis, AMPG.

new genus *Pilgrimeles* with the sole known species *P. woodwardi*. However, there are some arguments about the validity of the diagnostic characters of the new genus (Roussiakis, 2002). According to Pilgrim (1931) it is a large-sized *Martes*, having elongated m2 and an m1 with relatively large metaconid, as well as elongated and strongly concave talonid (Fig. 10). Roussiakis (1996) in his description of the lower carnasial mentions the presence of a small metaconid and a basin-like and rounded talonid, situated slightly more labially to the metaconid-protoconid junction. More material from the type locality is necessary to define the systematic position and validity of this taxon.

Fig. 11.—*Martes lefkonensis,* mandibular fragment, AMPG-MAR-MA401, HOLOTYPE, Maramena, Serres Basin, Latest Turolian, MN 13/14.

Martes lefkonensis Schmidt-Kittler, 1995

Type locality. Maramena (MAR), Serres Basin, Latest Turolian, MN 13/14 (Figs. 1, 2).

Holotype. Right mandibular fragment with p4-m1, AMPG-MAR-MA401 (Fig. 11), described and figured by Schmidt-Kittler (1995: p. 76; pl. 1, fig. 1).

Greek localities. It is only known from the type locality.

Age. Latest Turolian, MN 13/14.

Remarks. It is a small-sized *Martes* with relatively short m1, which bears a strong metaconid and steeply sloping anteriorly lingual border; there is well developed basal cingulum all around the protocone of the m1. The primitive dental characters distinguish it from the known Turolian and Ruscinian forms and put it closer to the Middle Miocene ones (Schmidt-Kittler, 1995).

Sinictis (?) pentelici (Gaudry, 1861a, b)

Type locality. Pikermi, Attica; Middle Turolian, MN 12 (Figs. 1, 2).

Holotype. Left mandibular fragment with p2-m1, MNHN-PIK-3260 (Fig. 12), described and figured by Gaudry (1861b: p. 527; pl.10, figs. 4, 5).

Greek localities. It is only known from the type locality.

Age. Middle Turolian, MN 12.

Remarks. The species was originally described as *Mustella pentelici* by Gaudry (1861a,b) and latter transferred question-

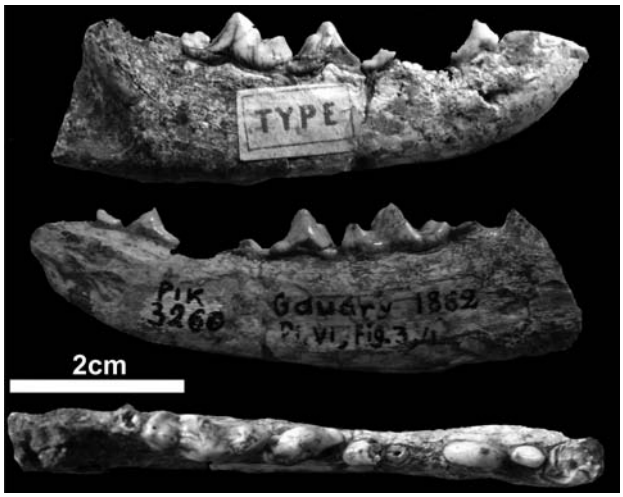

Fig. 12.—*Sinictis* (?) *pentelici*, mandibular fragment, MNHN-PIK-3260, HOLOTYPE, Pikermi, Attica, Middle Turolian, MN 12.

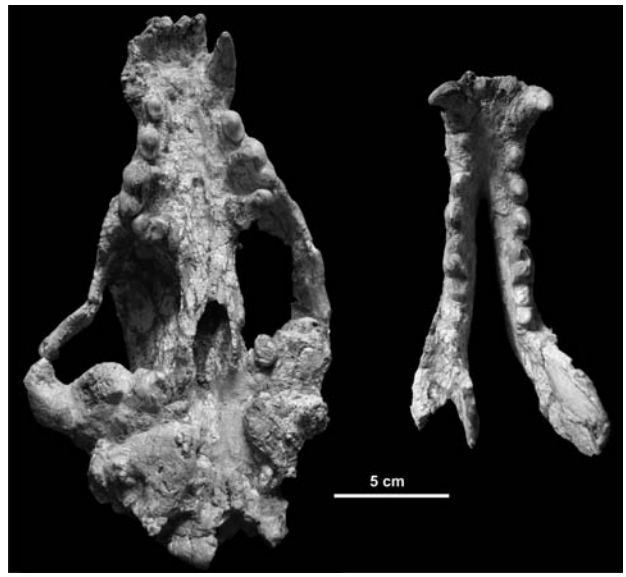

Fig. 13.—*Plesiogulo crassa*, skull and associated mandible, LGPUT-PER-1239, Perivolaki, Thessaly, Middle Turolian, MN 12.

ably to *Sinictis* by Pilgrim (1931). The p2 is small with strong distal cingulum; the p2,3 are elongated and narrow with strong proximal and distal cingulum. The p4 has a large posterior accessory cuspid on a distal projection of the distal cingulum. The carnasial is long with strong metaconid; the talonid is relatively short (1/3 of the tooth's length) and bears a large hypoconid, a small hypoconulid and lacks entoconid. The m2 has rounded occlusal surface (Pilgrim, 1931).

Sub-Family Mellivorinae Gray, 1865
Genus *Eomellivora* Zdansky, 1924
Eomellivora wimani, Zdansky, 1924

Type locality. Loc. 12 of Zdansky (1924.

Lectotype. Kretzoi (1965:p.132) defined the skull fragment associated with the left mandibular fragment, described and figured by Zdansky (1924: pl. XI, figs 5-6; pl.XII, figs 1-2) as the lectotype of the species.

Greek localities. Ravin de la Pluie (RPl), Axios Valley (Koufos, 2011a).

Age. Late Vallesian, MN 10.

Remarks. The sole known isolated M1 is morphologically and metrically similar to *E.wimani* (Koufos, 2011a).

Sub-Family Guloninae (Gray, 1825) Miller, 1912
Plesiogulo crassa Teilhard & Leroy, 1945

Type locality. Yushe, Shansi, China; Turolian, MN 11-13 (NOW, 2010).

Holotype. Frontal part of a skull and associated mandible, described and figured by Teilhard (1945: figs. 9, 10B).

Greek localities. Vathylakkos-3 (VAT), Axios Valley, (Koufos, 1982); Perivolaki (PER), Thessaly (Koufos, 2006b).

Age. Middle Turolian, MN 12.

Remarks. In Greece *Plesiogulo crassa* was recognized for the first time in the locality VAT by a mandibular fragment (Koufos, 1982). Quite later, it discovered in the locality PER by a skull and associated mandible (Fig. 13), (Koufos, 2006b). It is characterized by relatively long skull with short facial region, oval and wide narial opening, high sagittal crest, large triangular-shaped and flattened bullae, relatively short and narrow palate with narrow choanae, robust P4 with rounded protocone well separated by a deep constriction, elongated and abruptly inclined posteriorly symphysis, deep and oval-shaped masseteric fossa, long and narrow m1 with elongated basin-like talonid and small metaconid (Koufos 2006b). The genus *Plesiogulo* is mentioned from Pikermi by two fragments of humerus (Symeonidis, 1975), as well as from Maramena by some dental remains (Schmidt-Kittler, 1995).

Sub-Family Melinae Burmeister, 1850
Promeles palaeattica Weithofer, 1888

Type locality. Pikermi (PIK), Attica; Middle Turolian, MN 12 (Figs. 1, 2).

Holotype. Skull and associated mandible (Fig. 14) described and figured by Weithofer (1888: p. 226; taf. 1, figs. 1-11).

Greek localities. Pikermi (PIK), Attica (Roussiakis, 2002); Perivolaki (PER), Thessaly (Koufos, 2006b). It is also referred from Samos (Forsyth Major, 1888), while Solounias (1981) refers it from Q1 and A of Samos Island without description and reference of the material based on.

Age. Middle Turolian, MN12.

Remarks. It was originally described as *Mustella palaeattica* from Pikermi (Weithofer, 1888); however, Gaudry (1862-

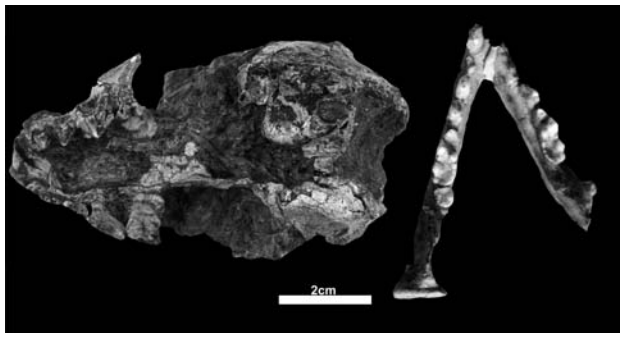

Fig. 14.—*Promeles palaeattica*, skull and mandible, PIUW-PIK-nn., HOLOTYPE, Pikermi, Middle Turolian, MN 12; Photo kindly provided by D. Nagel, PIUW.

67) refers the presence of a small *Martes* in Pikermi, different from *Promephitis*. Based to Pilgrim (1931) list of synonyms the Pikermi material transferred to *Promeles* by Zittel in 1893, when he erected this genus. The main characters of the species are the relatively short and wide snout, the oval shaped narial opening with almost vertical lateral margins, the flattened frontals, the absence of the parastyle and the well developed protocone in the P4, the strong metaconule and lingual cingulum in the M1, the long m1 with elongated basin-like talonid and strong metaconid connected to the crest-like entoconid, as well as the small, rounded and bicuspid m2 (Koufos, 2006b).

Promeles macedonicus Schmidt-Kittler, 1995

Type locality. Maramena (MAR), Serres basin; Latest Turolian, MN 13/14 (Figs. 1, 2).

Holotype. Right P4-M1, AMPG-MAR-MA406 (Fig. 15a), described and figured by Schmidt-Kittler (1995: p. 77, fig. 3; pl. 1, figs. 2-4).

Greek localities. It is only known from Maramena.

Age. Latest Turolian, MN 13/14.

Remarks. It resembles to *P. palaeattica* but it is distinguished from it by the longer trigonid and shorter talonid of the m1, as well as the slightly concave distal border and the more expressed parastyle angle of the M1 (Schmidt-Kittler, 1995).

Parataxidea maraghana (Kittl, 1887)

Type locality. Middle Maragheh, Iran; Middle Turolian, MN 12 (NOW, 2010).

Holotype. Right maxillary fragment with C-M1, NHMW-MRG-nn, described and figured by Kittl (1887: p. 337; taf. 15, fig. 4).

Greek localities. Mytilinii-1A (MTLA), Samos Island (Koufos, 2009); it is also referred from the localities A and Q1 of Samos without description and reference of the material based on (Solounias, 1981).

Age. Middle Turolian, MN 12.

Remarks. The species was erected by Kittl (1887) as *Meles maraghanus* and later it was transferred to *Parataxidea* by

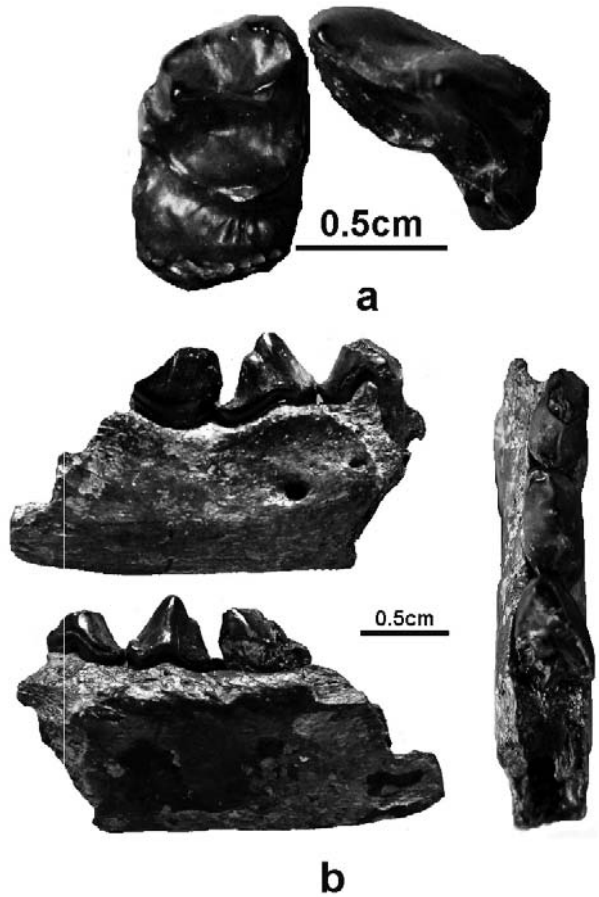

Fig. 15.—*Promeles macedonicus*, **a**. P4-M1, AMPG-MAR-MA406, HOLOTYPE; **b**. mandibular fragment, AMPG-MAR-MA411, Maramena, Serres Basin, Latest Turolian, MN 13/14.

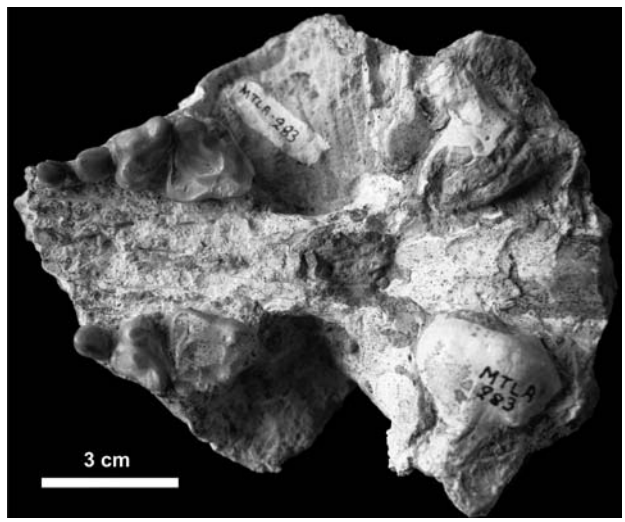

Fig. 16.—*Parataxidea maraghana*, skull, NHMA-MTLA-283, Mytilinii-1A, Samos Island, Middle Turolian, MN 12.

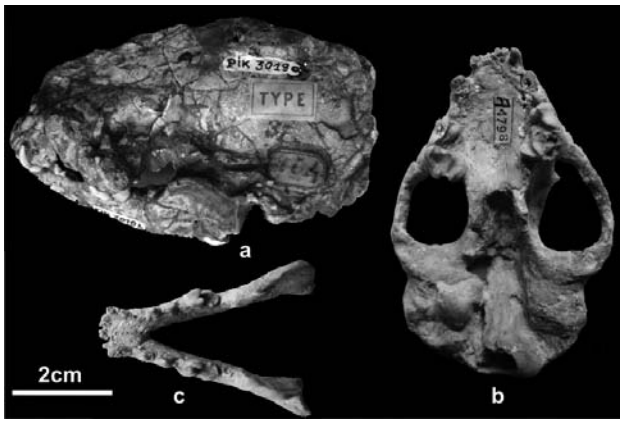

Fig. 17.—*Promephitis lartetii.* **a**. skull and associated mandible, MNHN-PIK-3019, HOLOTYPE, Pikermi, Attica, Middle Turolian, MN 12. **b, c**. skull and associated mandible, NHMW-SAM-A.4798, Loc. unknown, Samos Island, Turolian, MN 11-13.

Zdansky (1924). It is characterized by short and wide muzzle, oval narial opening, narrow frontals, rounded orbits, absence of sagittal crest, elongated and narrow palate with relatively wide choanae whose anterior border is well behind the M1 (Fig. 16), robust P2,3 with strong cingulum, short and wide P4 with strong protocone, small mesial cusp and a small lingual cuspule in the middle of the lingual cingulum, large M1 with large lingual mesiodistal diameter and straight mesial border, as well as large and robust m1 with narrow talonid (Koufos, 2009).

Sub-Family Mephitinae Gill, 1872

Promephitis lartetii Gaudry, 1861a, b

Type locality. Pikermi (PIK), Attica; Middle Turolian, MN 12 (Figs. 1, 2).

Holotype. Skull associated with the mandible, MNHN-PIK-3019 (Fig. 17a) described by Gaudry (1861b).

Greek localities. Perivolaki (PER), Thessaly (Koufos, 2006b); it is also referred without description from Q1, 2, 6 and A of Samos (Solounias, 1981).

Age. Middle Turolian, MN12.

Remarks. The holotype of the species is quite deformed, while its connection with the mandible (Fig. 17a) cannot allow to see precisely its dental morphology. According to Pilgrim (1931) the M1 of *P. lartetii* is characterized by convex inner side and straight outer one and by a metaconid situated somewhat in front of the protoconid. A very deformed skull with the mandible from PER has been described by Koufos, (2006b; pl. 2, figs. 4-6). Based on the description of this skull, *P. lartetii* is characterized by wide narial opening, strong post-orbital processes, strong sagittal crest, short and relatively wide palate, small and deep choanae with their anterior border well behind the distal margin of the M1. The upper carnasial is short and broad with large protocone and without parastyle. The M1 is large with the paracone larger than the metacone and a large crest-like protocone. The p4 is robust without accessory cuspids, the m1 is elongated with relatively wide talonid and the m2 is rounded (Koufos, 2006b).

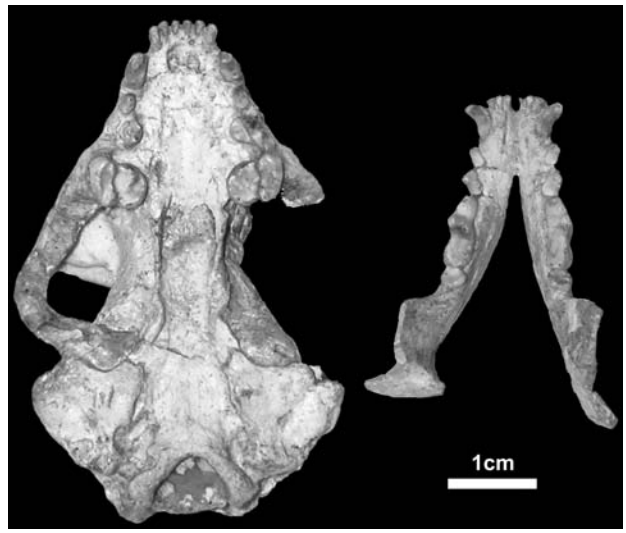

Fig. 18.—*Promephitis majori*, skull and associated mandible, AMNH-SAM-20585, HOLOTYPE, Adrianos ravine, Samos Island, Middle Turolian, MN 12. Photo kindly provided by D. Kostopoulos, LGPUT.

Promephitis majori Pilgrim, 1933

Type locality. Adrianos ravine, Samos Island; Middle Turolian, MN 12 (Figs. 1, 2).

Holotype. Skull and associated mandible, AMNH-SAM-20585 (Fig. 18), described and figured by Pilgrim (1933: p. 2, figs. 1-6).

Greek localities. It is only known from the type locality.

Age. Middle Turolian, MN 12.

Remarks. The main characters of *P. majori* are the smaller size, the stronger post-orbital processes, the less prominent occipital condyles and the smaller transverse diameter of the M1 than those of *P. lartetii* (Pilgrim, 1933). Some of these characters vary in the known material of both species and only the smaller size of *P. majori* seems to be a valuable difference (Koufos, 2006b).

Family FELIDAE (Fischer von Walheim, 1817)
Sub-Family Felinae (Fischer von Walheim, 1817), Trouessart, 1885

Pseudaelurus romieviensis (Roman & Viret, 1934)

Type locality. La Romieau, France; Middle Orleanian, MN 4 (NOW, 2010).

Holotype. Left mandibular fragment with p3-m1, FSL-1779, housed in the University of Lyon. It was originally described as *P. lorteti romieviensis* (Roman & Viret, 1934) and later upgraded as a separate species (Heizmann, 1973).

Greek localities. Antonios, Chalkidiki (Koufos, 2008).

Age. Middle/Late Orleanian, MN 4/5.

Remarks. The systematic of these early felids is quite unclear and there are different opinions. Salesa (pers. com.,

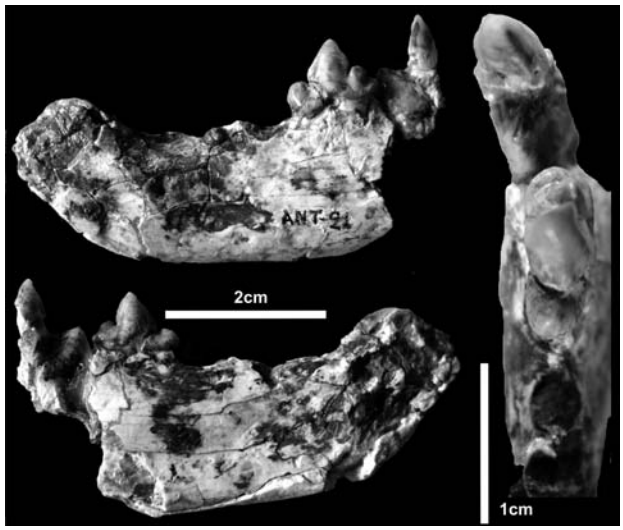

Fig. 19.—*Pseudaelurus romieviensis*, mandibular fragment, LGPUT-ANT-21, Antonios, Chalkidiki Peninsula, Middle/Late Orleanian, MN 4/5.

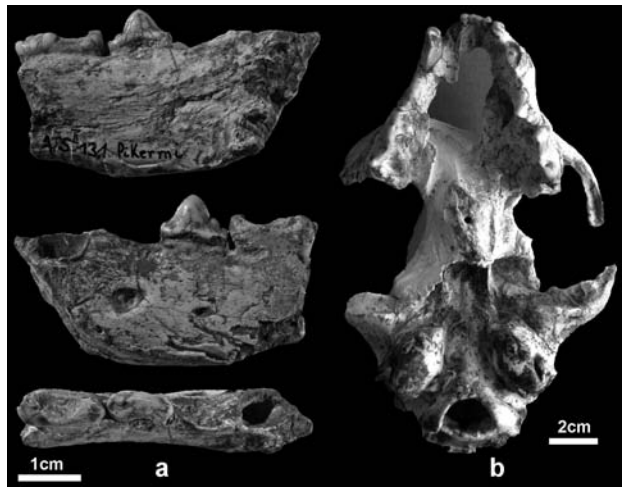

Fig. 21.—**a**. *Metailurus parvulus*, mandibular fragment, BSPM-PIK-AS II.131, HOLOTYPE, Pikermi, Attica, Middle Turolian, MN 12; Photo of M. Schellenberger kindly provided by G. Rössner BSPM. **b**. *Metailurus parvulus*, AMPG-CHO-nn, Chomateres, Attica, Middle Turolian, MN 12.

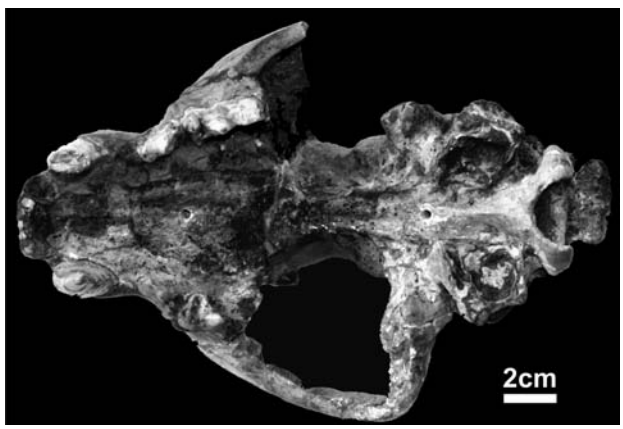

Fig. 20.—*Metailurus major*, skull, AMPG-HAL-1967/1, Halmyropotamos, Evia Island, Middle Turolian, MN 12. Photo kindly provided by S. Roussiakis, AMPG.

2011) considers that all species of *Pseudaelurus* must be included to *Styriofelis* (Kretzoi, 1929). The species is known from the locality ANT by a mandibular fragment with the p4 and the anterior part of the m1 (Fig. 19). The morphology and size of the p4 is similar to *P. romieviensis* (Koufos, 2008).

Metailurus major Zdansky, 1924

Type locality. Loc. 30, Shansi, China; Turolian, MN 11-13 (NOW, 2010).

Holotype. Skull described and figured by Zdansky (1924; taf. 29, figs. 1, 2).

Greek localities. Pikermi (PIK), Attica (Roussiakis, 2001b); Halmyropotamos (HAL), Evia Island (Melentis, 1967). The species is also referred from an unknown locality of Samos, without description and reference of the material based on (Solounias, 1981).

Age. Middle Turolian, MN 12.

Remarks. The first reference about its presence in Greece is that of Melentis (1967), describing some cranial and mandibular remains from HAL (Fig. 20). A complete skull of the species is recently described from Pikermi (Roussiakis, 2001b). The latter author mentions its large size, the relatively wide anteriorly P3 with strong posterior accessory cusp, the smaller and lingually situated anterior accessory cusp in the P3 and the relatively large M1.

Metailurus parvulus (Hensel, 1862)

Type locality. Pikermi, Attica; Middle Turolian, MN 12 (Figs. 1, 2).

Holotype. Left mandibular fragment with p3-p4 and the alveole of the canine, BSPM-PIK-AS II. 131 (Fig. 21a), described and figured by Hensel (1862: fig. 6).

Greek localities. Pikermi (PIK), Attica (Roussiakis & Theodorou, 2003); Halmyropotamos (HAL), Evia Island (Melentis, 1967); Chomateres (CHO), Attica (Symeonidis, 1978), (Fig. 21b); Kerassia (KER), Evia Island (Roussiakis *et al.,* 2006); Mytilinii-1A (MTLA), Samos Island (Koufos, 2009); Ravin de la Pluie (RPl), Axios Valley (Koufos, 2011a) it is also referred from the localities A and Q5 of Samos Island (Solounias, 1981) but without mentioning the material based on and description.

Age. Late Vallesian-Middle Turolian, MN 10-12.

Remarks. The species was originally described from Pikermi as *Machairodus parvulus* (Hensel, 1862). The skull is small with short muzzle, rounded orbit, voluminous braincase with flattened upper surface, ovoid bullae, wide choanae and short and wide palate. The P3 bears a posterior accessory cusp and

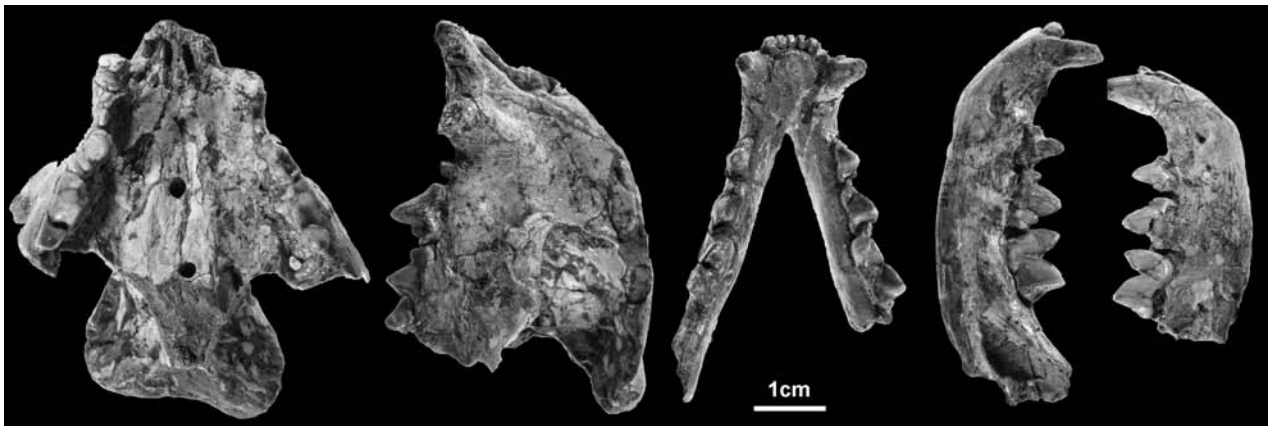

Fig. 22.—*Felis attica*, partial skull and mandible BSPM-PIK-AS II.116, HOLOTYPE, Pikermi, Attica, Turolian, MN 12; Photo of M. Schellenberger kindly provided by G. Rössner, BSPM.

the P4 has very small and low protocone, situated well posterior of the parastyle. The M1 is small, situated vertically to the P4. The mandibular corpus is shallow with short symphysis, almost vertical to the ramus and deep masseteric fossa with its anterior margin well behind the m1. The p3 is without anterior but with small posterior accessory cuspid, situated on a distal cingular projection. The p4 has both accessory cuspids and a slightly elevated distal cingulum, while the m1 has a small talonid and a tiny metaconid (Roussiakis et al., 2006; Koufos, 2009).

Felis attica Wagner, 1857

Type locality. Pikermi (PIK), Attica; Middle Turolian, MN 12 (Figs. 1, 2).

Holotype. Facial part of a skull associated with the mandible (Fig. 22), described and figured by Wagner (1857: p. 122; tab. 3, fig. 4)

Greek localities. Pikermi (PIK), Attica (Roussiakis, 2002); It is referred from an unknown locality of Samos (Forsyth Major, 1891) and from locality A (Solounias, 1981) without description; it is also referred without description and reference of the material based on from TMP (Geraads *et al*., 2007)

Age. Middle Turolian, MN 12.

Remarks. Except the holotype, a mandibular fragment is also known from Pikermi described as Felidae indet. (Gaudry, 1862-67); however, the author refers that it may belong to *F. attica*. Both Pilgrim (1931) and Beaumont (1961) agree with this determination. Some postcranials of *F. attica* from Pikermi were also described recently (Roussiakis, 2002). The skull with the mandible of a small felid is referred without description from Samos (unknown locality) as *Felis neas* (Forsyth Major, 1891, 1894). This specimen is considered either as a separate species (Pilgrim, 1931) or as a synonym of *F. attica* (Beaumont, 1961). A skull of *Felis attica* (NHMW-SAM-A.4751) is referred from an unknown locality of Samos; some characters of this skull are given by Koufos (2000). Some postcranials of Samos, referred to *Felis* sp. (Forsyth Major, 1894), were described as *Metailurus parvulus* (Beaumont, 1961) but later he transferred them to *Felis attica* (Beaumont, 1986). The skull is

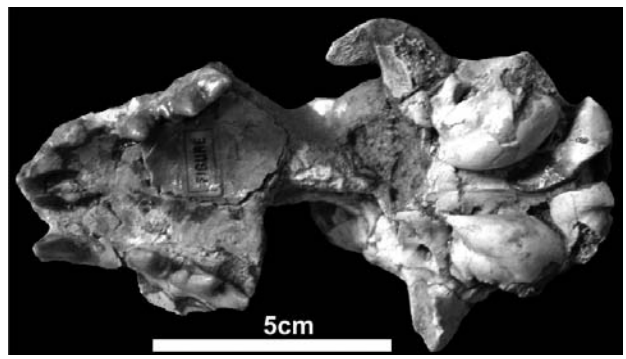

Fig. 23.—*Felis* sp., skull, MNHN-SLQ-935, Vathylakkos 3, Axios Valley, Middle Turolian, MN 12.

elongated with relatively long muzzle, oval-shaped orbits and oval nasal cavity. The P4 lacks the ectoparastyle and has relatively small protocone. The P2 is small and the P3 has a small posterior accessory cusp. The symphysis is wide and short, the mandibular corpus high, the masseteric fossa is elongated with its anterior margin below the posterior half of the m1. Both p3 and p4 bears anterior and posterior accessory cuspids and the m1 has a small metaconid.

Felis sp.

Type locality. Ravin du Vatilük (R.G.), Axios Valley; this locality is correlated to the new one Vathylakkos-3 (VAT); Middle Turolian, MN 12 (Figs. 1, 2).

Type material. Skull, MNHN-SLQ-935 (Fig. 23), described and figured by Arambourg & Piveteau (1929: p. 125; pl. 11, figs. 1, 1a).

Greek localities. It is only known from VAT.

Age. MiddleTurolian, MN 12.

Remarks. The VAT skull was originally described as *Felis* cf. *attica* because of its larger size, the presence of the ectoparastyle and the reduced protocone in the P4 (Arambourg

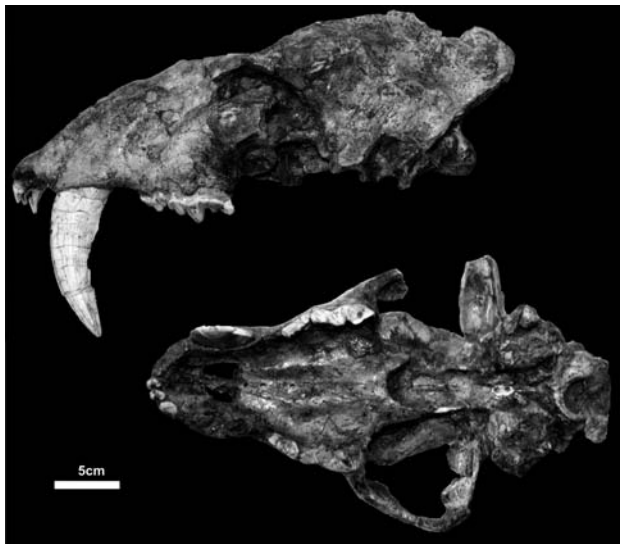

Fig. 24.—*Amphimachairodus giganteus*, skull, AMPG-HAL-1967/6, Halmyropotamos, Evia Island, Middle Turolian, MN 12. Photo kindly provided by S. Roussiakis, AMPG.

Fig. 25.—*Paramachaerodus orientalis*, mandibular fragment, NHML-PIK-M.8959, Pikermi, Attica, Middle Turolian, MN 12.

& Piveteau, 1929; Beaumont, 1961). Pilgrim (1931) added that MNHN-SLQ-935 has longer facial region than that of *F. attica* and kept the original determination. A more recent comparison of SLQ-935, except of the above mentioned differences, indicates that its teeth are generally longer and narrower than the typical *F. attica* (Koufos, 2000). However, the limited material of these small felids cannot allow certain comparisons and definition of the variability of their characters and thus it is referred as *Felis* sp. (Koufos, 2000). A similar *Felis* with an ectoparastyle and a reduced protocone is also known from Maragheh (Mequenem, 1924-25).

Sub-Family Machairodontinae (Gill, 1872) Hay, 1930

Amphimachairodus giganteus (Wagner, 1848)

Type locality. Pikermi, Attica; Middle Turolian, MN 12 (Figs. 1, 2).

Holotype. Olecranon described and figured by Wagner (1848: p. 375; tab. 2, fig. 6), as *Felis giganteus*.

Greek localities. Pikermi (PIK), Attica (Gaudry, 1862-67; Roussiakis, 2002); Ravin X (R-X), Axios Valley (Arambourg & Piveteau, 1929; Koufos, 2000); Halmyropotamos (HAL), Evia Island (Melentis, 1967); Kerassia (KER), Evia Island (Roussiakis & Theodorou, 2003); Ravin des Zouaves 5 (RZO), Axios Valley (Koufos, 2011a); Mytilinii-1 (MTL), Samos Island (Koufos, 2009); it is also referred without description from the locality A, Samos Island (Solounias, 1981). Some material without description, referred as *Machairodus* sp., is known from TMP (Koufos, 2006a; Geraads *et al*., 2007).

Age. Early-Middle Turolian MN 11-12.

Remarks. According to Beaumont (1975) *A. giganteus* is the Turolian machairodont, which differs from the Vallesian *M. aphanistus* by its narrower upper canine, the more pronounced ectoparastyle in the P4, the reduced and more backwardly situated protocone in the P4 and the longer and narrower upper teeth. In the lower teeth the accessory cuspids of the p4 are higher and more slender, the protoconid of the m1 is longer and the talonid of the m1 is strongly reduced.

Paramachaerodus orientalis (Kittl, 1887)

Type locality. Maragheh, Iran; Early-Middle Turolian, MN 11-12.

Holotype. Frontal part of the skull with both tooth rows, described and figured by Kittl (1887: p. 329; taf. 14, figs. 1-5).

Greek localities. Pikermi (PIK), Attica (Pilgrim, 1931); Silata, Chalkidiki Peninsula (Koufos, 2006c). Some remains from TMP are referred as *Paramachaerodus* sp. without description (Geraads et al., 2007).

Age. Middle-Latest Turolian, MN 12-13/14.

Remarks. It was originally described as *Machairodus orientalis* from Maragheh (Kittl, 1887). Pilgrim (1931) transferred it to *Paramachaerodus,* considering that *Machairodus schlosseri* of Weithofer (1888: taf. 11, figs. 1-7) and *Machairodus hungaricus* of Kormos (1911: fig. 17) are synonyms of it. According to Pilgrim (1931) its main characters are the size of the mental foramen, the stoutness of the ramus, the weakly curved upper canine with its posterior keel more serrated than the anterior one, the slightly serrated margins of the lower canine and relatively strong anterior accessory cuspid in the p4.

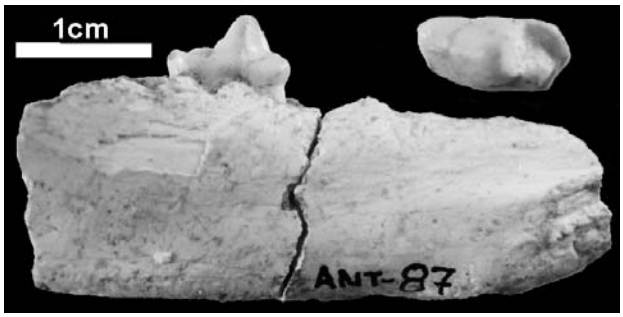

Fig. 26.—*Protictitherium gaillardi*, mandibular fragment LGPUT-ANT-87, Antonios, Chalkidiki Peninsula, Middle/Late Orleanian, MN 4/5.

Family HYAENIDAE Gray, 1821
Sub-Family Ictitheriinae (Trouessart, 1897) Dietrich, 1927
Protictitherium gaillardi (Forsyth Major, 1903)

Type locality. La Grive, France, Late Astaracian, MN 7+8 (NOW, 2010).

Holotype. Maxilla and the associated mandible, described and figured by Gaillard (1899: p. 60; pl. II, figs. 1,3).

Greek localities. Antonios (ANT), Chalkidiki Peninsula (Koufos, 2008).

Age. Middle/Late Orleanian, MN 4/5.

Remarks. Iniatially it was wrongly described as *Herpestes crassus* Gaillard (1899), but then it was referred to *Progenetta gaillardi* (Forsyth Major, 1903); finally it was transferred to *Protictitherium gaillardi* by Schmidt-Kittler (1976). The Greek material is poor, including a maxillary fragment with M1-M2 and a mandibular fragment with p4 (Fig. 26), described by Koufos (2008). According to the original description and figures of the type material (Gaillard, 1899), the upper premolars are slender with well developed cingulum. The P4 has strong protocone with its anterior margin situated in front of the parastyle. The M1 is triangular-shaped. The M1 of the Greek material is characterized by strongly projected buccally paracone, small metacone and well developed protocone higher than the other two cusps. The p3 is elongated with strongly projected distally distal cingulum; the p4 has well developed posterior accessory cuspid. The m1 has high main cuspids with well metaconid and bicuspid talonid (Koufos, 2008).

Protictitherium thessalonikensis Koufos, 2011

Greek localities. Ravin de la Pluie (RPl), Axios Valley (Bonis & Koufos, 1991).

Age. Late Vallesian, MN 10.

Remarks. Some maxillary and mandibular remains (Fig. 27) of a protictithere from RPl have been described as *P.* cf. *gaillardi* because their size is smaller than the other known material of *P. gaillardi* (Bonis & Koufos, 1991; Koufos, 2000). The revision of the RPl protictithere suggests that it belongs to a new species named *P. thessalonikensis* (Koufos, 2011b).

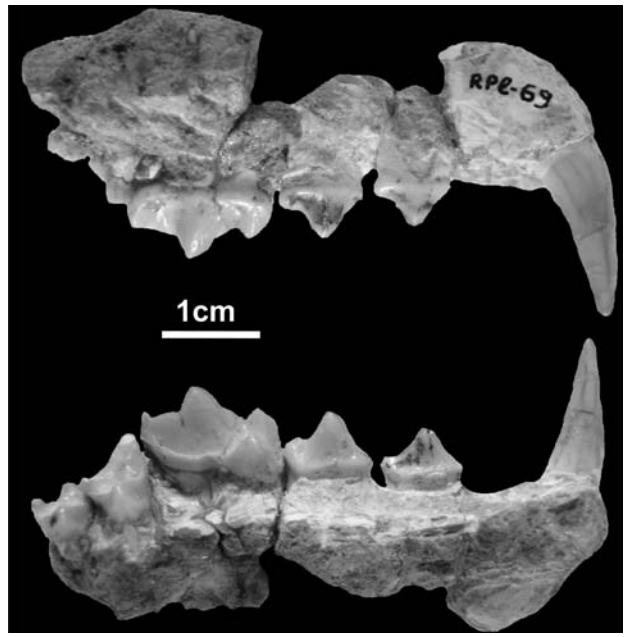

Fig. 27.—*Protictitherium* thessalonikensis, maxillary fragment, LGPUT-RPl-69, Ravin de la Pluie, Axios Valley, Late Vallesian, MN 10.

Fig. 28.—*Protictitherium* sp. aff. *P. intermedium*, m1 sin, LGPUT-RPl-66, Ravin de la Pluie, Axios Valley, Late Vallesian, MN 10.

Protictitherium sp. aff. *P. intermedium* Schmidt-Kittler, 1976

Type locality. Çandir, Turkey; Late Orleanian, MN 5 or early Astaracian MN 6 (Schmidt-Kittler, 1976; Begun *et al*., 2003; Van der Made, 2003, 2005).

Holotype. The holotype of *P. intermedium* is the left mandibular fragment, BSPM-1967V1736, described and figured by Schmidt-Kittler (1976: p. 66; taf. 3, fig. 1, abb. 61).

Greek localities. Ravin de la Pluie (RPl), Axios Valley (Koufos, 2000).

Age. Late Vallesian, MN 10.

Remarks. An isolated m1 (Fig. 28) from RPl is morphologically and metrically very similar to *P. intermedium* but the sole known specimen cannot allow precise determination and thus it is referred as *Protictitherium* sp. aff. *P. intermedium* (Koufos, 2000).

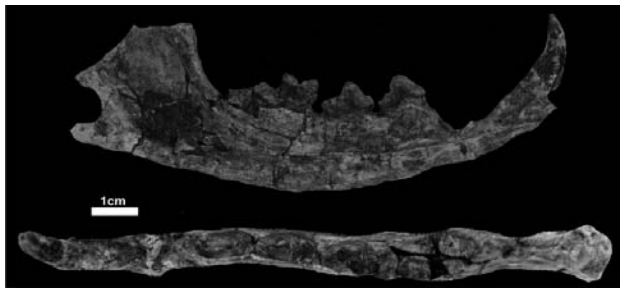

Fig. 29.—*Protictitherium crassum*, hemimandible, LGPUT-DKO-20, Dytiko, Axios Valley, Late Turolian, MN 13.

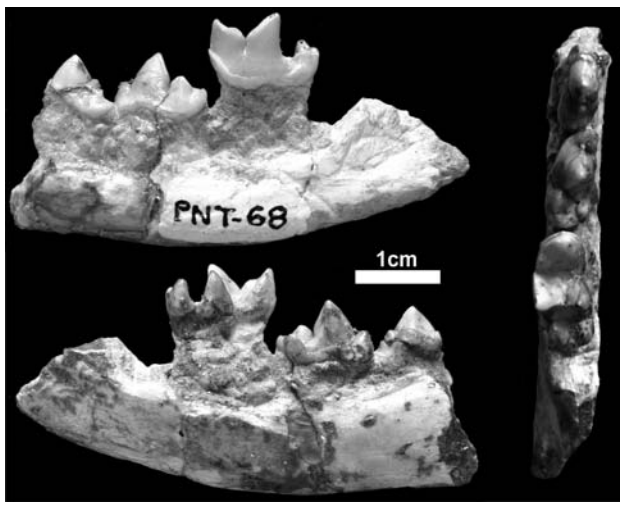

Fig. 30.—*Protictitherium* sp. cf. *P. crassum*, mandibular fragment, LGPUT-PNT-68, Pentalophos, Axios Valley, ?Early Vallesian, ?MN 9.

Protictitherium crassum (Depéret, 1892)

Type locality. La Grive, France, Late Astaracian, MN 7+8 (NOW, 2010).

Type material. Some mandibular remains and an isolated P4, described and figured by Depéret (1892: p. 31; pl. 1, figs. 14-17).

Greek localities. Xirochori-1 (XIR), Axios Valley (Koufos, 2000); Dytiko-3 (DKO) Axios Valley (Bonis & Koufos, 1991); Mytilinii-4 (MLN), Samos Island (Koufos, 2009).

Age. Late Vallesian- Late Turolian, MN 10-13.

Remarks. The species was described under the name *Herpestes crassus* from La Grive, France (Depéret, 1892). It is a large-sized protictithere, with molarized lower premolars especially p4, as well as short and wide m1 with high cuspids, well separated talonid and high entoconid (Koufos, 2000, 2009).

Protictitherium sp. cf. *P. crassum* (Depéret, 1892)

Greek localities. Antonios (ANT), Chalkidiki Peninsula (Koufos, 2008); Pentalophos (PNT), Axios Valley (Bonis & Koufos, 1991; Koufos, 2000).

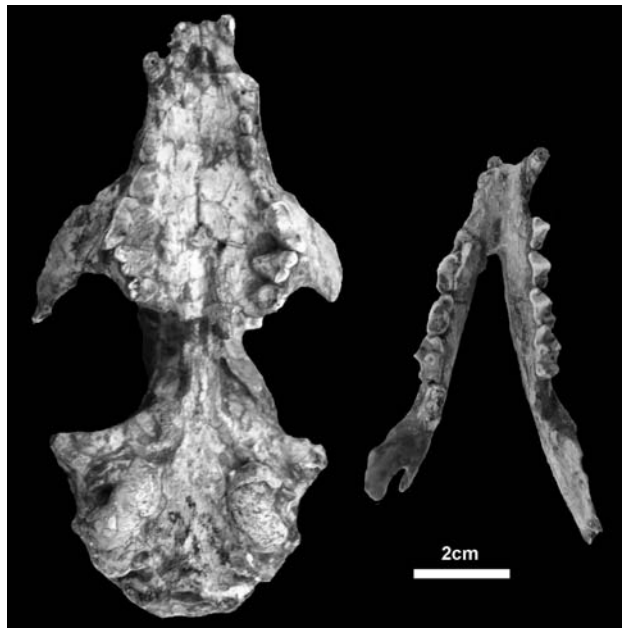

Fig. 31.—*Plioviverrops orbignyi*, skull and associated mandible, MNHN-PIK-3022, HOLOTYPE, Pikermi, Attica, Middle Turolian, MN 12.

Age. Middle/Late Orleanian -?Early Vallesian, MN 4/5-?9.

Remarks. Two Greek localities ANT and PNT include some protictitheres, which are similar to *P. crassum* (Koufos, 2000, 2008). The ANT material, although it has strong similarities with *P. crassum* it is not determined to it because it is poor and fragmentary (Koufos, 2008). The slightly smaller size, the more molarized premolars, the relatively longer talonid in the m1, the higher and stronger metaconid in the m1 and the more robust teeth of the PNT material distinguishes it from *P. crassum* and cannot allow its certain determination to this species (Bonis & Koufos, 1991).

Plioviverrops orbignyi (Gaudry & Lartet, 1856)

Type locality. Pikermi, Attica; Middle Turolian, MN 12 (Figs. 1, 2).

Holotype. Skull associated with the mandible, MNHN-PIK-3022 (Fig. 31) described and figured by Gaudry & Lartet (1856).

Greek localities. Ravin des Zouaves-5 (RZO), Prochoma-1 (PXM), and Vathylakkos-2,3 (VTK, VAT), Axios Valley (Koufos, 2000); Perivolaki (PER), Thessaly (Koufos, 2006b); Mytilinii-1B (MTLB), Samos Island (Koufos, 2009). It is also referred from Q1 and A of Samos (Solounias, 1981). Recently some postcranials from KER, resembling greatly to *P. orbignyi,* have been described as *Plioviverrops* sp., (Roussiakis & Theodorou, 2003).

Age. Early-Middle Turolian, MN 11-12.

Remarks. Originally it was described as *Viverra orbignyi* by Gaudry & Lartet (1856). It is a well known small hyaenid in Greece but it is rare in the contemporaneous countries. It is

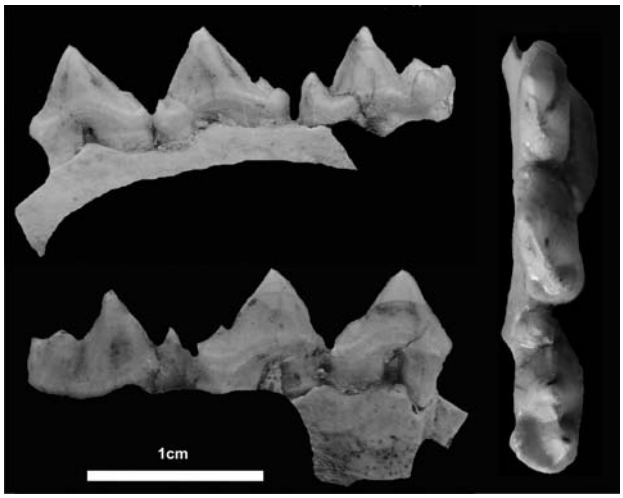

Fig. 32.—*Plioviverrops* sp. cf. *P. guerini*, mandibular fragment, LGPUT-VAT-74a, Vathylakkos, Axios Valley, Middle Turolian, MN 12.

characterized by oval narial opening, large elliptical orbits, large auditory bullae, short-wide palate, very long postorbital processes, long-narrow and roughly inclined backwards symphysis, pointed cusps in the teeth, without or with rudimentary accessory cusps in the P2,3, elongated P4 with relatively large protocone situated in front of the parastyle, long talonid with high entoconid in the m1 and high metaconid equal to protoconid in the m1 (Pilgrim, 1931; Koufos, 2006b, 2009).

Plioviverrops sp. cf. *P. guerini* Villalta & Crusafont, 1945

Type locality. The type locality of *Plioviverrops guerini* is Pierra, Spain; Early Turolian, MN 11 (NOW, 2010).

Holotype. The holotype of *Plioviverrops guerini* is a left mandibular fragment with p3-m1, described and figured by Villalta & Crusafont (1945: p. 95; pl. II, fig. 2).

Greek localities. Vathylakkos-3 (VAT), Axios Valley (Bonis & Koufos, 1991).

Age. Middle Turolian, MN 12

Remarks. A left tooth row with p1-4 and a right one with p3-m1 (LGPUT-VAT-74, 74a) is the only known material (Fig. 32). It has some differences from *P. orbignyi* as the slightly larger size, the higher and narrower p2,3 without accessory cuspids and the less molarized teeth. These morphological characters are closer to those of *P. guerini* and for this reason it was referred to it (Bonis & Koufos, 1991). However, the study of the new material from Greece indicates that the size of the teeth and the development of the accessory cuspids vary in the material of *P. orbignyi* and the taxonomic value of *P. guerini* must be re-examined (Koufos, 2006b, 2009).

Ictitherium viverrinum (Roth & Wagner, 1854)

Type locality. Pikermi (PIK), Attica; Middle Turolian, MN 12 (Figs. 1, 2).

Type material. Right mandibular fragment with p2-m1, BSPM-PIK-AS II.66 and the left mandibular fragment with c-p4, BSPM-PIK-AS II. 56, described and figured by Roth & Wagner (1854: p. 49; taf. 8, figs. 3, 5).

Greek localities. Pikermi (PIK), Attica (Roussiakis, 1996); Ravin des Zouaves-5 (RZO), Prochoma-1 (PXM) and Vathylakkos-3 (VAT), Axios Valley (Koufos, 2000). It is also referred from the localities Q1 and A of Samos (Solounias, 1981). An isolated p2 from PER is morphologically and metrically close to *I. viverrinum* but it is referred as *Ictitherium* sp. because of the poor material (Koufos, 2006b).

Age. Early-Middle Turolian, MN 11-12.

Remarks. The species has a long taxonomic history referred under different generic and specific names, but Kurtén (1982) obtained its validity. It is a medium-sized ictithere with weakly developed anterior accessory cuspid in the lower premolars; however, it is larger in the p3,4. The m1 cuspids are not pointed, the paraconid + protoconid blade is not very high and the metaconid relatively to protoconid is high. The P4 is short and robust with small and less distinguished protocone. The P2,3 lack anterior accessory cusp but they bear a strong posterior one, situated in a distal projection of the distal cingulum (Kurtén, 1982; Koufos, 2000).

cf. *Ictitherium pannonicum* Kretzoi, 1952

Type locality. The type locality of *I. pannonicum* is Polgardi, Hungary; Middle-Late Turolian, MN 12-13 (NOW, 2010).

Type material. The type material of *I. pannonicum* is a mandibular fragment with p1-p2, Ob/2653, described by Kretzoi (1952: p. 18). More details about the type material are given by Werdelin & Solounias (1991).

Greek localities. It is only known from Kerassia.

Age. Early-Middle Turolian, MN 11-12.

Remarks.The sole known specimen is the right mandibular ramus with c, p3-m1, AMPG-KER-K3/204, described and figured by Roussiakis & Theodorou (2003: p. 471; pl. 1, figs. 6-8). It has larger p3, m1 and m2 than *I. viverrinum*. The large m2 is characteristic for *I. pannonicum* and in this feature AMPG-KER-K3/204 is similar to it. Moreover, its m1 is also similar to *I. pannonicum* but the p3 is more robust. The poorly known material cannot allow certain attribution and thus it is referred to as cf. *I. pannonicum* (Roussiakis & Theodorou, 2003).

Hyaenictitherium wongii (Zdansky, 1924)

Type locality. Zdansky (1924) refers a series of localities with *H. wongii* from Yushe, Shansi, China; Turolian, MN 11-13 (NOW, 2010).

Type material. Several skulls and mandibles described and figured by Zdansky (1924, p.73; taf. 14, figs. 3-6, taf. 15, figs. 1-4, taf. 16, figs. 1, 2), but he did not define a holotype.

Greek localities. Pikermi (PIK), Attica Gaudry (1862-67); Ravin des Zouaves-1 (RZ1), Ravin des Zouaves-5 (RZO) and Vathylakos 2, 3 (VTK, VAT), Axios Valley (Koufos, 2000); Mytilinii-1A, B, C (MTLA, MTLB, MTLC), Samos Island (Koufos, 2009); it is also referred from Q1, 4, 5 and S3 of Samos (Solounias, 1981).

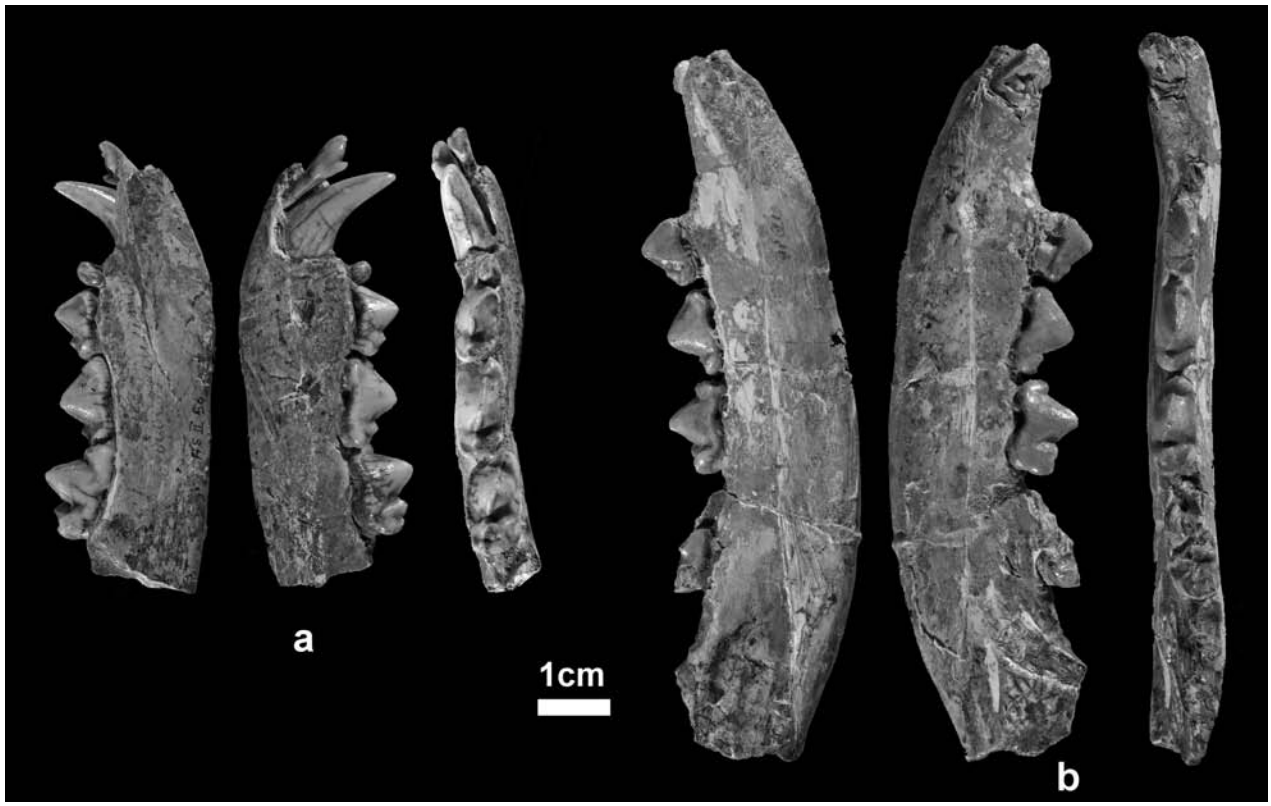

Fig. 33.—*Ictitherium viverrinum*, mandibular fragments, BSPM-PIK-AS II.56 (**a**) and BSPM-PIK-AS II.66 (**b**), TYPE MATERIAL, Pikermi, Attica, Middle Turolian, MN 12; Photo of M. Schellenberger kindly provided by G. Rössner, BSPM.

Fig. 34.—cf. *Ictitherium pannonicum*, mandibular fragment with c, p3-m1, AMPG-KER-K3/204, Kerassia, Evia Island, Turolian, MN 11-12. Foto shooted from Roussiakis & Theodorou (2003: pl. 1, figs. 6-8).

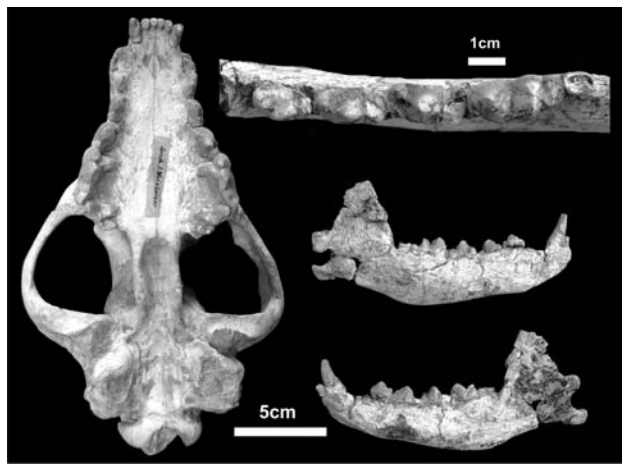

Fig. 35.—*Hyaenictitherium wongii*, skull, MNHN-SAM-A.4746, Loc. unknown, Samos Island, Turolian, MN 11-13; mandible, NHMA-MTLB-171, Mytilinii-1B, Samos Island, Middle Turolian, MN 12.

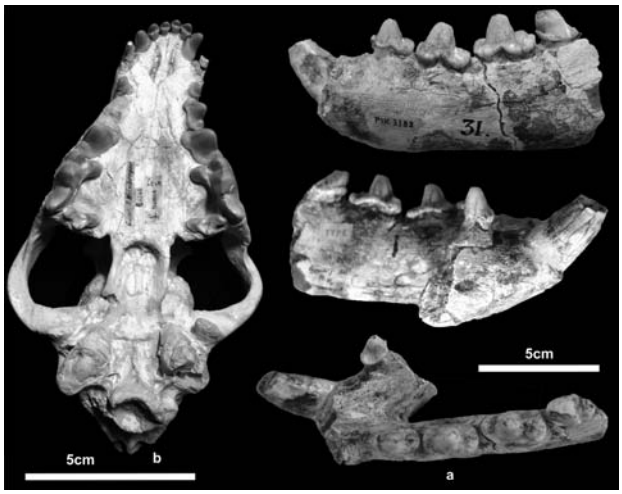

Fig. 36.—*Lycyaena chaeretis*, **a**. mandible, MNHN-PIK-3383, HOLOTYPE, Pikermi, Attica, Middle Turolian, MN 12, **b**. skull, NHMW-SAM-4744, Loc. unknown, Samos Island, Turolian, MN 11-13.

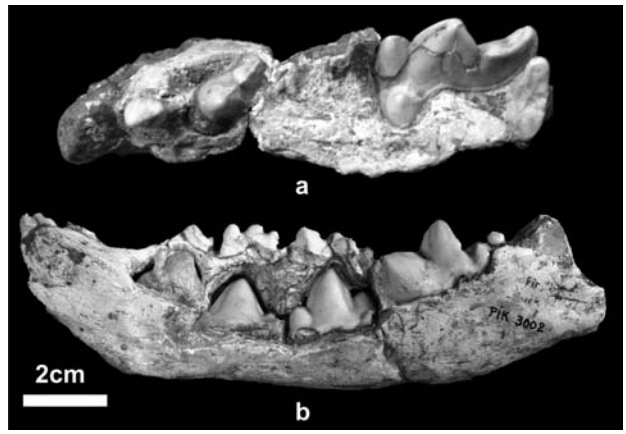

Fig. 37.—*Hyaenictis graeca*, **a**. maxillary fragment, NHMW-PIK-A.4715, **b.** mandibular fragment, MNHN-PIK-3002, HOLOTYPE, Pikermi, Attica, Middle Turolian, MN 12.

Age. Late Vallesian-Middle Turolian, MN 10-12.

Remarks. The name *Ictitherium wongii* was used for a set of cranial remains of an ictithere found in various Chinese localities (Zdansky, 1924); *Palhyaena* aff. *hipparionum* of Schlosser (1903) was also included to this species. Its taxonomic history is long and complicated (see Koufos, 2000, 2009 and ref. cited). It is a medium-sized ictithere very common in Eurasia known from China to Spain. It differs from *Ictitherium* in the elongated blade and the relatively larger protocone of the P4, the reduced molars and the relatively shorter talonid of the m1. It is also different from *Thalassictis* in the elongated blade of the P4, the less high protoconid of the m1, the weaker talonid with lower cuspids of the m1 and the smaller size. An isolated tooth from the locality Mytilinii-4 (MLN) resembles to *H. wongii* and it is referred to as *H.* cf. *wongii* (Koufos, 2009).

Lycyaena chaeretis (Gaudry, 1861b)

Type locality. Pikermi (PIK), Attica; Middle Turolian, MN 12 (Figs. 1, 2).

Holotype. Mandibular fragment with c-p2 dex and p2-m1 sin, MNHN-PIK-3383 (Fig. 36a) described and figured by Gaudry (1861b: p. 534; pl. 11, figs. 3-6).

Greek localities. Pikermi (PIK), Attica (Roussiakis, 1996); the taxon is also referred from the locality A, Samos Island (Solounias, 1981).

Age. Middle Turolian, MN 12.

Remarks. It was originally described as *Hyaena chaeretis* by Gaudry (1861b) and later transferred to the new genus *Lycyaena* by Hensel (1862). The P2,3 lack anterior accessory cusp but they bear a strong posterior one. The P4 is elongated and narrow with strong and well separated protocone. The M1 is large. The lower premolars have well developed posterior accessory cuspid, situated in a distal projection of the distal cingulum. The anterior accessory cuspid is strong in the p4 but it is rudimentary (like a cingular projection) in the p2,3 (Pilgrim, 1931).

Sub-family Hyaeninae (Gray, 1821) Mivart, 1882
Hyaenictis graeca (Gaudry, 1861b)

Type locality. Pikermi (PIK), Attica; Middle Turolian, MN 12 (Figs. 1, 2).

Holotype. Left mandibular ramus with dP2-dP4 and P4-M1, MNHN-PIK-3002 (Fig. 37b), described and figured by Gaudry (1861b: p. 527; pl. 11, figs. 1-2).

Greek localities. It is only known from Pikermi.

Age. Middle Turolian, MN 12.

Remarks. The known material of *Hyaenictis graeca* is few, including a maxillary and mandibular fragment of a young individual, housed in MNHN and a maxillary fragment of a young individual stored in NHMW; the two maxillary fragments belong possibly to the same individual. It is distinguished from *A. eximia*, having larger protocone in the P4, and more narrow and slender premolars. However, it was synonymized to *Adcrocuta eximia* (Solounias, 1981) but soon retrieved its taxonomic value as a separate taxon (Howell & Petter, 1985). An isolated P2 from the Late Vallesian locality RPl of Axios Valley has some similarities to this species and it is referred to as ?*Hyaenictis* (Koufos, 2011a).

Chasmaporthetes bonisi Koufos, 1987

Type locality. Dytiko-1 (DTK), Axios Valley; Late Turolian, MN 13 (Figs. 1, 2).

Holotype. Part of the left mandibular ramus with p2-m1, LGPUT-DTK-126 (Fig. 38b), described and figured by Koufos (1987: p. 918; pl. 1, figs. 1, 2, 3c).

Greek localities. Ravin des Zouaves-5 (RZO), Axios Valley (Bonis & Koufos, 1994a)

Age. Early-Late Turolian, MN 11-13.

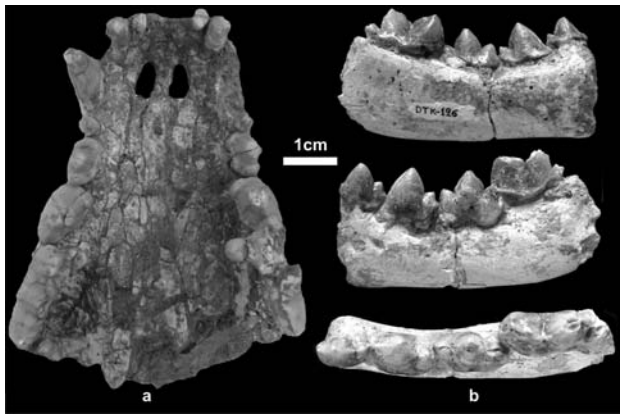

Fig. 38.—*Chasmaporthetes bonisi*, **a**. frontal skull, LGPUT-RZO-125, Ravin des Zouaves-5, Axios Valley, Early Turolian, MN 11; **b**. mandibular fragment, LGPUT-DTK-126, HOLOTYPE, Dytiko, Axios Valley, Late Turolian, MN 13.

Fig. 39.—*Adcrocuta eximia*, **a**. hemimandible, BSPM-PIK-AS II.105, HOLOTYPE, Pikermi, Attica, Turolian, MN 11-13, Photo of M. Schellenberger kindly provided by G. Rössner, BSPM; **b**. skull, NHMW-SAM-4727, Loc. unknown, Samos Island, Early-Late Turolian, MN 11-13.

Remarks. Primitive form of the genus with relatively narrow palate, moderately developed P1, large and not labially directed protocone in the P4, well developed M1, curved and imbricated lower tooth row, oval distal margin in the lower premolars, absence or rudimentary anterior accessory cuspid in the p2,3, absence of metaconid in the m1, and small-bicuspid talonid with reduced entoconid in the m1 (Koufos, 1987; Bonis & Koufos, 1994a).

Adcrocuta eximia (Roth & Wagner, 1854)

Type locality. Pikermi (PIK), Attica; Middle Turolian, MN 12 (Figs. 1, 2).

Holotype. Right mandibular ramus with i3-m1, BSPM-PIK-105 (Fig. 39a), described and figured by Roth & Wagner (1854: p. 396; tab. 8, fig. 6).

Greek localities. Halmyropotamos (HAL), Evia Island (Melentis, 1967); Xirochori-1 (XIR), Ravin de la Pluie (RPl), Ravin des Zouaves-1, 5 (RZ1, RZO), Prochoma-1 (PXM) and Vathylakkos-3 (VAT), Axios Valley (Koufos, 2000); Mytilinii-1A (MTLA), Samos Island (Koufos, 2009); Perivolaki (PER), Thessaly (Koufos, 2006b); Kerassia (KER), Evia Island (Roussiakis & Theodorou, 2003). It is also referred from the old Samos localities Q4, Q5, A, Q1 (Solounias, 1981).

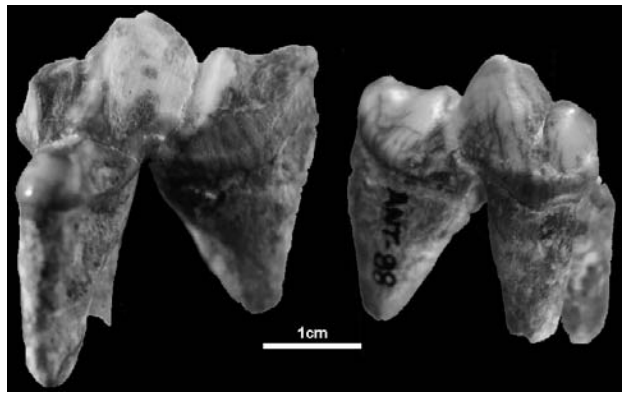

Fig. 40.—*Percrocuta* sp., upper carnasial, LGPUT-ANT-88, Antonios, Chalkidiki Peninsula, Middle/Late Orleanian, MN 4/5.

Age. Late Vallesian-Middle Turolian, MN 10-12

Remarks. It is very common and widespread in Turolian extended from Spain to China. It is characterized by robust teeth, absence of anterior accessory cusp(-ids) in the P2, and p2,3, rudimentary protocone in the P4, absence of metaconid and small talonid in the m1. In Greece two subspecies were recognized: the Vallesian *A. e. leptoryncha* Bonis & Koufos, 1981 and the Turolian *A. e. eximia*. The former one is characterized by longer snout and narrower palate, less compressed jugal tooth row and slenderer premolars (Bonis & Koufos 1981; Koufos, 2000, 2011a).

Family PERCROCUTIDAE Werdelin & Solounias, 1991

Percrocuta Kretzoi, 1938

Percrocuta sp.

Type species. The type species is *Percrocuta carnifex,* described and figured by Pilgrim (1932).

Type locality. The type locality of *P. carnifex* is Upper Chinji, Siwaliks, Pakistan; Astaracian (Pilgrim, 1932; Barry *et al.*, 2002)

Greek localities. Antonios, Chalkidiki (Koufos, 2008).

Age. Middle/Late Orleanian, MN 4/5.

Remarks. A sole P4 is known from ANT (Fig. 40), which has similarities with *P. carnifex* and *P. abessalomi* (Koufos, 2008).

Belbus beaumonti (Qiu, 1987)

Type locality. Samos Island, Loc. unknown; the possible horizon where it was found is the Main Bone Beds (Werdelin & Solounias, 1991).

Fig. 41.—*Belbus beaumonti,* hemimandible, SMNS-SAM-13118, Loc. unknown, Samos Island, Turolian, MN 12. Photo kindly provided by S. Roussiakis, AMPG.

Fig. 42.—*Dinocrocuta gigantea*, mandible, LGPUT-PNT-70, Pentalophos, Axios Valley, ?Early Vallesian, ?MN 9.

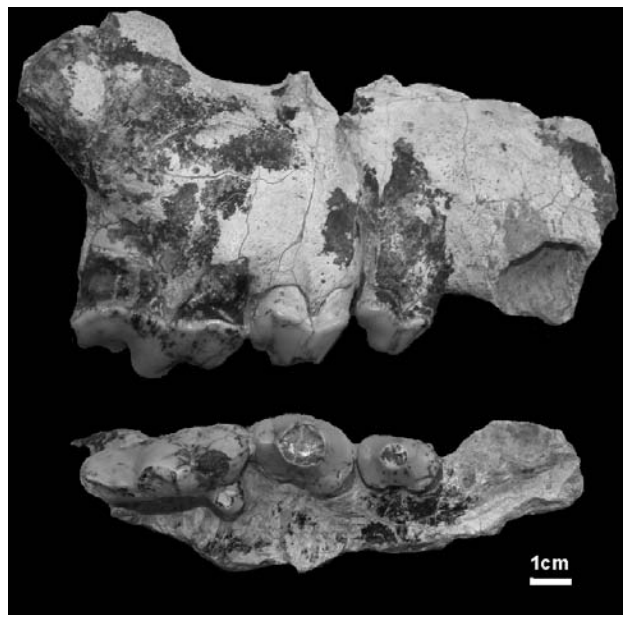

Fig. 43.—*Dinocrocuta salonicae*, maxillary fragment, BMNH-DVT-M.11413, HOLOTYPE, Diavata, Axios Valley, Vallesian-?Early Turolian, MN 9-?MN 11.

Holotype. Left mandibular ramus with c-p3, m1, NHMB-SAM-33, described and figured by Beaumont (1968: p. 21-26; pl. 1, figs. 1, 2). The type specimen belongs to the old collection of Basel without locality indication and it is difficult to certify its exact stratigraphic position.

Greek localities. It is only known from Samos.

Age. The Main Bone Beds are dated to Middle Turolian, MN 12 (Koufos *et al*., 2009a).

Remarks. The type specimen was originally described as *Hyaena* sp. due to its derived premolars and carnassial (Beaumont, 1968). Extensive history of the taxon is given by Werdelin & Solounias (1991) and Turner *et al*. (2008). Beaumont (1968) mentioned the large m1 with relatively long talonid and strong metaconid, the hypoconid's dominance in the talonid of the m1, the presence of the p1 and m2, and the large posterior accessory cuspid in the p2,3.

Dinocrocuta gigantea (Schlosser, 1903)

Type locality. The Chinese sites Tientsin, Shansi, Tibetfluss as referred by Schlosser (1903); Late Miocene.

Type material. A set of isolated teeth described and figured by Schlosser (1903: p. 35; taf. 2, figs. 1-8).

Greek localities. Pentalophos-1 (PNT), Axios Valley (Koufos, 1995).

Age. ?Early Vallesian, ?MN 9.

Remarks. The species was erected by Schlosser (1903) as *Hyaena gigantea*; Pilgrim (1932) included some material from Siwaliks to it under the name *Crocuta gigantea* var. *latro*. Part of the Pilgrim's material transferred to *Crocuta (Percrocuta) grandis* (Kurtén, 1957). The material of *D. gigantea* was referred to *Allohyaena (Dinocrocuta) gigantea* by Howell & Petter (1985) and finally Qiu *et al*. (1988), based on a skull from China, defined the genus *Dinocrocuta* and included Schlosser's material to this genus. It is characterized by large-very large size, thick and broad nasal bones, sharp bending of the cranial roof, long meatus acusticus, short and high cranial proportions, absence of internal root in the P3, long p4 relative to the p3, hyperthrophied p2 and short m1 relative to the p3. The sole known material from Greece is a mandible (Fig. 43) and two upper canines (Koufos, 1995). The genus was recently recognized in the Vallesian locality XIR of Axios Valley by a maxillary fragment with deciduous dentition (Koufos, 2011a).

Dinocrocuta salonicae Andrews, 1918

Type locality. Diavata (DVT), Axios Valley; this locality is possibly similar to Pentalophos-1 (PNT) but it cannot be proved because of lacking information (Andrews, 1918; Koufos, 1995).

Holotype. Right maxillary fragment with P2-P4, NHML-DVT-M.11413, (Fig. 44), described and figured by Andrews (1918: p. 541)

Fig. 44.—*Simocyon primigenius*, mandibular fragment, BSPM-PIK-AS II.53, HOLOTYPE, Pikermi, Attica, Middle Turolian, MN 12. Photo of M. Schellenberger kindly provided by G. Rössner, BSPM.

Greek localities. It is only known from Diavata locality.

Age. Vallesian-?Early Turolian, MN 9-?11.

Remarks. This specimen has a long taxonomic and chronologic history (see Koufos, 1995). The author discussed the problem of *D. salonicae* and compare it with *D. gigantea* from PNT and other taxa. Although the limited and not comparable (maxilla-mandible) material from both species makes difficult the comparison, it seems that *D. salonicae* is a separate species different than *D. gigantea*

Family AILURIDAE Gray, 1843
Simocyon primigenius (Roth & Wagner, 1854)

Type locality. Pikermi (PIK), Attica; Middle Turolian, MN 12 (Figs. 1, 2).

Holotype. Right mandibular ramus with c-m1, BSPM-PIK-AS II.53 (Fig. 44), described and figured by Roth & Wagner (1854: taf. 8, figs. 1,2).

Greek localities. Pikermi (PIK), Attica (Roussiakis, 2002); Halmyropotamos (HAL), Evia Island (Melentis, 1968).

Age. Middle Turolian, MN 12.

Remarks. The species has a complicated taxonomic history; even now it is included either to the family Procyonidae or Ailuridae or Canidae. It is characterized by long and robust mandibular ramus and a blunter muzzle. There is a variability in the number of the incisors and the presence of the p1 (Pilgrim, 1931).

Composition of the Carnivore Fauna

As it was referred in the introduction, the Early-Middle Miocene localities of Greece are few and their carnivore fauna poor. The available data give a limited idea about the composition of the carnivores, as in most cases they include only one species (Fig. 45a). The viverrids are more abundant (29%), including two lophocyonines, found in Aliveri and Thymiana-B. The Lophocyoninae are very rare in Europe and they are known by three genera *Sivanasua, Euboictis* and *Lophocyon*; the second taxon is known only from Greece, while *Lophocyon* is known from Greece and Slovakia (Koufos *et al.*, 1995). The hyaenids include only ictitheres and together with the mustelids, felids and percrocutids are represented by a single taxon. The genus *Palaeogale* is included in the group of the *incertae sedis* and it is referred without description from Aliveri (Schmidt-Kittler, 1983).

On the contrary, the late Miocene carnivore assemblage of Greece is rich and includes a great number of taxa (Fig. 45b). The hyaenids (38%) and the mustelids (30%) are the dominant families. The hyaenids include a great number of ictitheres (27% or 10 species), while the true hyaenas are less (8% or 3 species). The mustelids, however, are more diversified, including six sub-families with the dominance of Mustelinae and Melinae (8% or 3 species each sub-family); the presence of the large Guloninae *Plesiogulo* is characteristic. The Lutrinae (6% or 2 species) and Mephitinae (5% or 2 species) are equally represented in the fauna. The Mellivorinae are recently recognized in the RPl fauna (Koufos, 2011) but they are not included in this analysis. The Felidae are quite abundant (16% or 6 species) characterized by the dominance of Felinae (11% or 4 species); the machairodonts are less (5%), including two taxa only. The percrocutids although they are abundant as the true hyaenas (8%) and quite diversified (3 species) they are represented by few specimens; each species is known by a single specimen. The ursids, although they are relatively abundant (8% or 3 species), their known material is poor, including few specimens. The Simocyoninae are rare, represented by the sole taxon *Simocyon primigenius*, reported only from Southern Greece. The majority of the known Greek

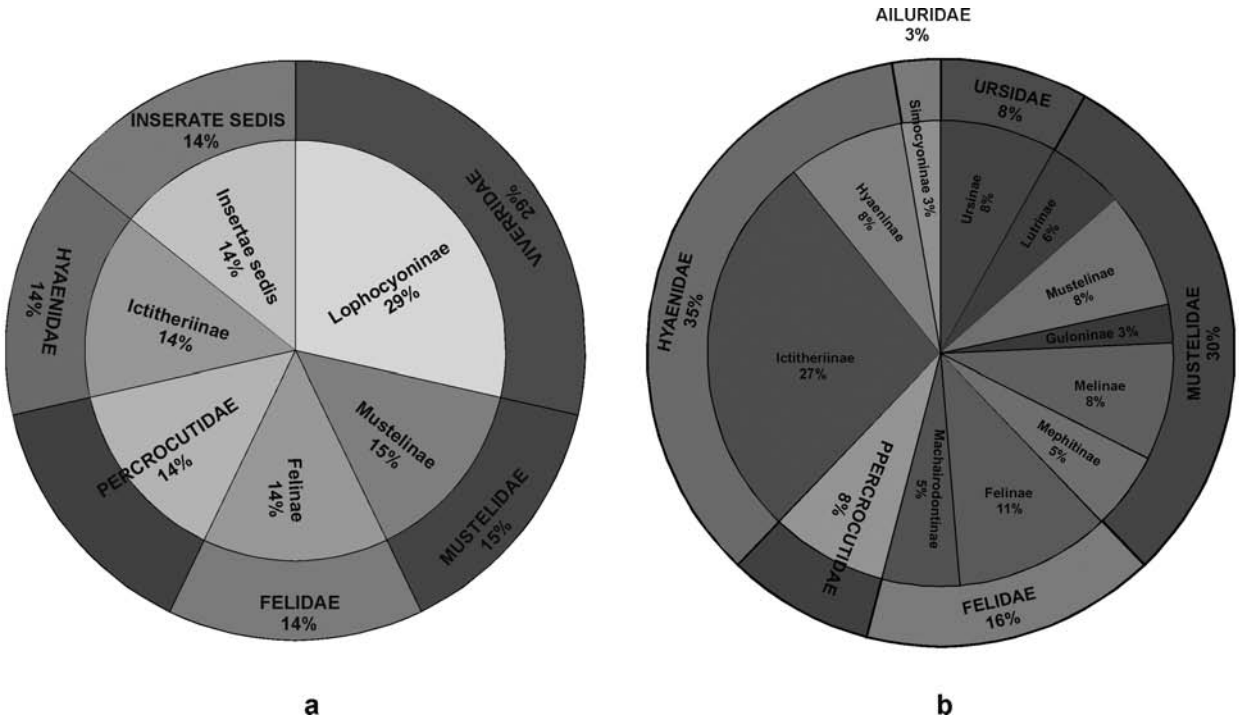

Fig. 45.—Composition of the Greek carnivore assemblage (% number of species per family or sub-family); **a.** Middle Miocene, **b.** Late Miocene.

carnivore taxa is accumulated in Middle Turolian, MN 12 (Fig. 46). The Ictitheriinae and Hyaeninae dominate in Late Vallesian and Early-Middle Turolian; they are present with several taxa. Both subfamilies are rare in Late Turolian; this is due to the few known localities and the poor material. The percrocutids are also rare and their presence is mainly referred from the Vallesian, except *Belbus,* known from the Middle Turolian. The ursids and mustelids are mainly known from Middle Turolian. The Lutrinae are present in Late Turolian by a single taxon, while they are possibly present in the Middle Turolian, too.

Guild structure

The guild structure of a carnivore palaeocommunity can provide information about their habitat in comparison with modern ones from known environments, using the guild structure diagrams (Morlo, 1999; Morlo *et al*., 2010). The guild structure graph of the Late Miocene carnivore assemblage of Greece is given in Fig. 47. The absence of the arboreal predators, the rarity of the semiaquatic ones, the abundance of the middle to large-sized taxa, the abundance of terrestrial and cursorial forms, the dominance of the carnivorous-bone/meat eaters and the presence of hyaenas indicate similarities to an open habitat. In these features the late Miocene carnivore guild graph resembles to the modern one of Serengeti (Morlo *et al*., 2010). This resemblance indicates a similar palaeoenvironment; as Serengeti is an open environment (open savannah grassland) similar environmental conditions can be supposed for the Late Miocene of Greece. The presence of some scansorial primitive hyaenids (mainly protictitheres) suggests the presence of some trees and bushes. These predators are relatively more abundant in the Vallesian, indicating more close conditions than in the Turolian. The sole known semi-aquatic *Lutra affinis,* known from the Latest Miocene locality of Maramena, as well as the possible presence of *Enhydriodon* in Pikermi indicates that during Late Turolian the environmental conditions started to change being more wet.

The late Miocene palaeoenvironment of Eastern Mediterranean has been determined, using various methods. The Vallesian palaeoenvironment of

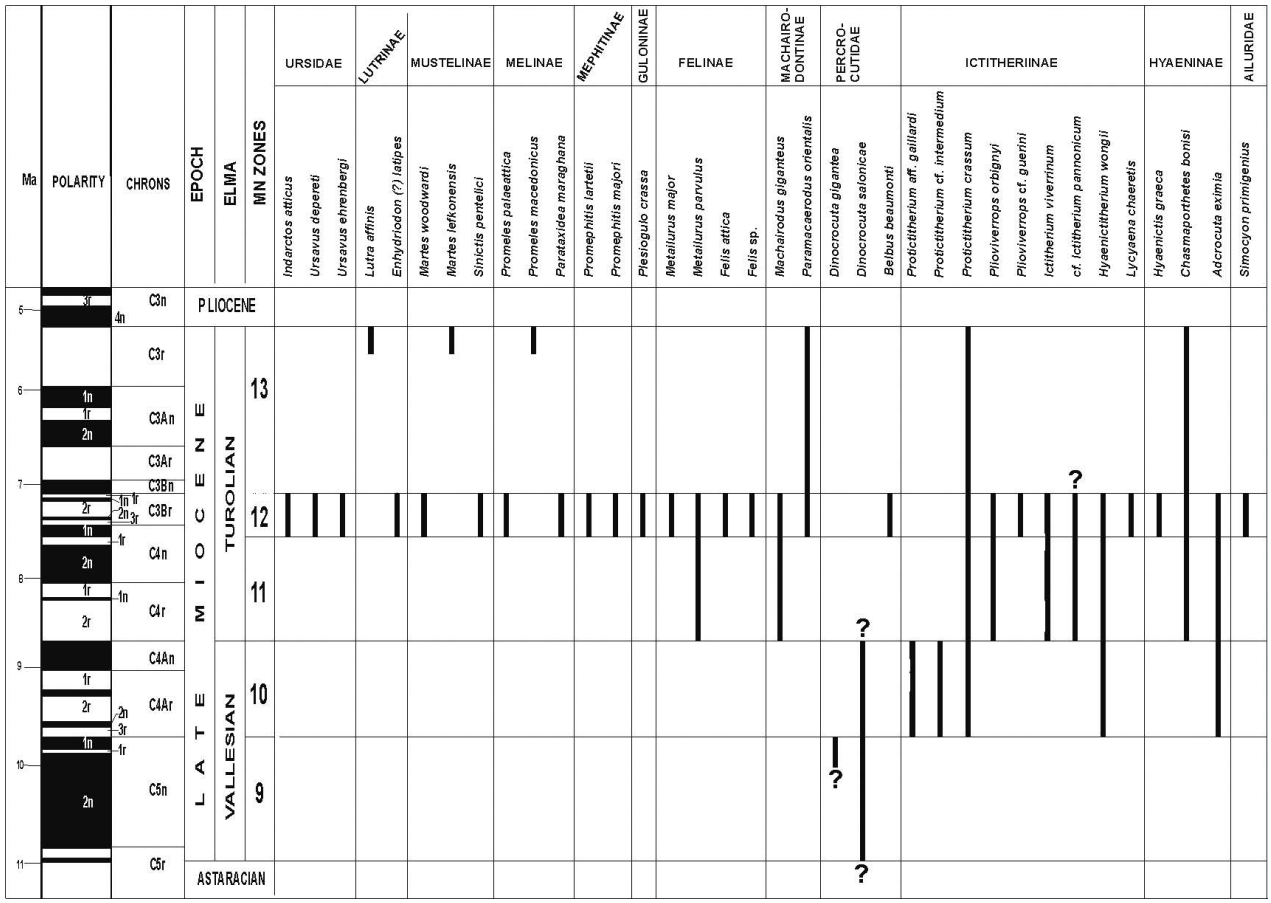

Fig. 46.—Stratigraphic distribution of the Late Miocene Carnivores of Greece.

Greece was an open habitat of savannah type with thick grass floor, some trees, bushes and schrubs (Bonis *et al*., 1992, 1999; Bonis & Koufos, 1994b; Koufos, 2006d). The dental microwear of the Vallesian herbivores of Greece, as well as of the hominoid *Ouranopithecus macedoniensis* indicates similar palaeoenvironmental conditions (Merceron *et al*., 2005, 2007). The study of the Turolian mammal assemblages and their comparison with modern ones from known environments suggest a habitat similar to that of the Vallesian, but more open and drier (Bonis *et al*., 1992; Bonis & Koufos, 1994b; Koufos *et al*., 2006b, 2009b; Kostopoulos, 2009). The dental microwear of the Turolian herbivores of Eastern Mediterranean suggests also a similar open/dry habitat (Merceron *et al*., 2004, 2006). During late Turolian there are evidences that the palaeoenvironment changed, being more wet, having more close areas, as indicated from the study of the mammal faunas (Koufos, 2006c; Vasileiadou & Koufos, 2005). The mammal hypsodonty palaeoprecipitation proxy, suggests that in Eastern Europe and Western Asia the Turolian habitat was dry, taking its maximum in the Middle Turolian. However, the humidity gradually increased in the late Turolian and the palaeoenvironment became more wet (Bonis *et al*., 1992; Eronen & Rook, 2004; Eronen *et al*., 2009). The palaeofloral data suggests open/arid conditions during Turolian in Eastern Mediterranean, confirming the above mentioned results for Greece (Suc *et al*., 1999; Ioakim *et al*., 2005; Kovar-Eder *et al*., 2006; Strönberg *et al*., 2007; Ioakim & Koufos, 2009).

The guild structure of the Samos Late Miocene carnivores indicates an open savannah-like habitat (Nagel & Koufos, 2009). Recently, the guild structure of the late Miocene carnivore assemblages of the Greco-Iranian Province (Balkans, Turkey, Iran, Afganistan) were studied. Their comparison with the modern carnivore assemblages indicates open and relatively dry conditions for the late Miocene

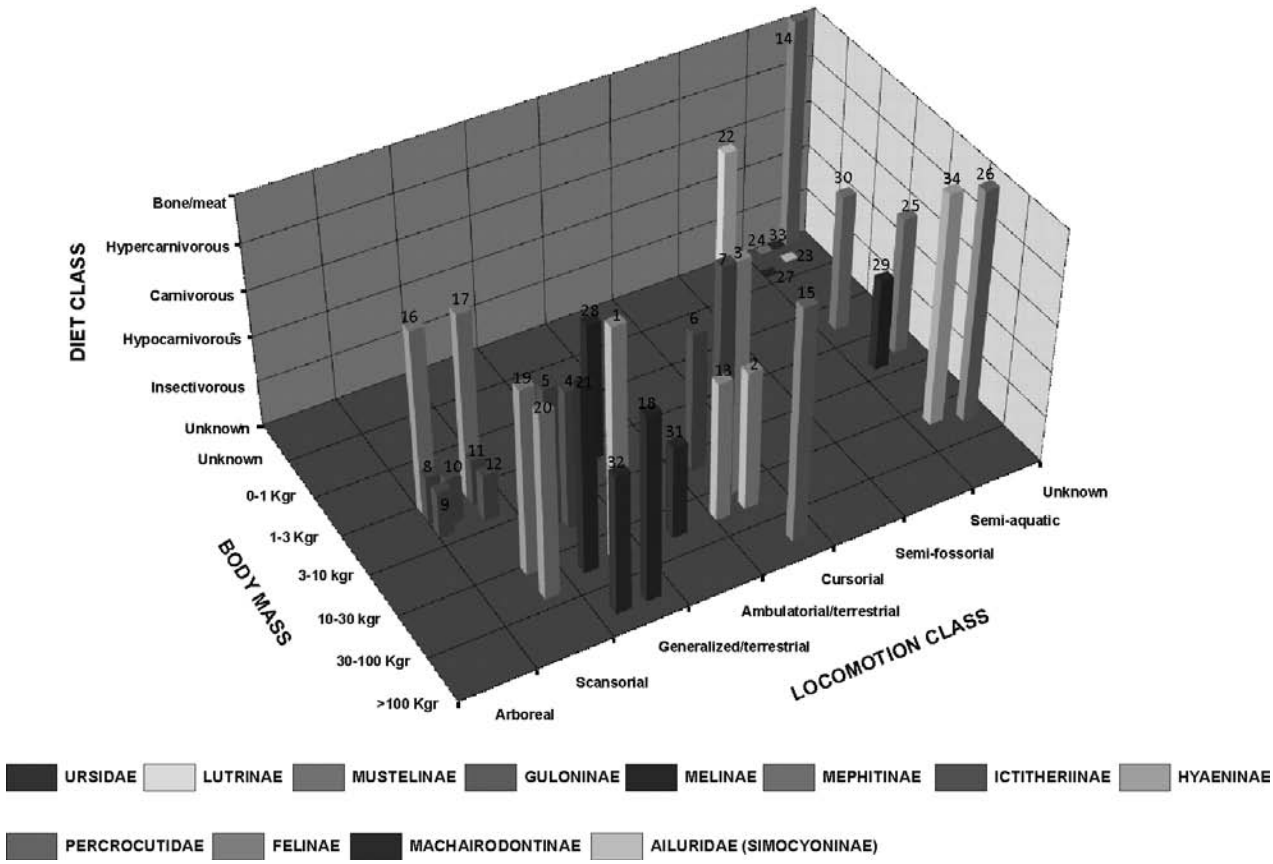

Fig. 47.—Guild structure of the Late Miocene carnivore assemblage of Greece. **1**. *Adcrocuta eximia,* **2**. *Chasmaporthetes bonisi,* **3**. *Hyaenictis graeca,* **4**. *Hyaenictitherium wongii,* **5**. cf. *Ictitherium pannonicum,* **6**. *Ictitherium viverrinum,* **7**. *Lycyaena chaeretis,* **8**. *Plioviverrops* cf. *guerini,* **9**. *Plioviverrops orbignyi,* **10**. *Protictitherium crassum,* **11**. *Protictitherium thessalonikensis,* **12**. *Protictitherium* aff. *intermedium,* **13**. *Belbus beaumonti,* **14**. *Dinocrocuta salonicae,* **15**. *Dinocrocuta gigantea,* **16**. *Felis attica,* **17**. *Felis* sp., **18**. *Machairodus giganteus,* **19**. *Metailurus parvulus,* **20**. *Metailurus major,* **21**. *Paramachaerodus orientalis,* **22**. *Lutra affinis,* **23**. *Enhydriodon (?) latipes,* **24**. *Martes lefkonensis,* **25**. *Martes woodwardi,* **26**. *Plesiogulo crassa,* **27**. *Promeles macedonicus,* **28**. *Promeles palaeattica,* **29**. *Promephitis lartetii,* **30**. *Sinictis (?) pentelici,* **31**. *Ursavus depereti,* **32**. *Indarctos atticus,* **33**. *Ursavus ehrenbergi,* **34**. *Simocyon primigenius.*

(Koufos & Konidaris, 2011). All the above mentioned results, provided by different methods, fit quite well with those taken from the study of the guild structure of the Late Miocene Greek carnivores. The few Early/Middle Miocene carnivores of Greece cannot provide a useful and indicable guild structure diagram in order to get some reliable results for the palaeoenvironment.

ACKNOWLEDGEMENTS

Many thanks to the editors for inviting me to participate in this volume to the memory of Prof. L. Ginsburg. Financial support to visit various museums and institutes to study the Greek carnivore material was provided to me by the European Commission's Research Infrastructure Action (EU-SYNTHESYS: AT-TAF-702, FR-TAF-3102, GB-TAF-1842). I am indebted to M. Dermitzakis, G. Theodorou, C. Doukas, S. Roussiakis, (AMPG), G. Daxner-Höck, M. Harzhauzer (NHMW), C. Soligo, A. Currant, J. Hooker (BMNH), and P. Tassy, S. Sen, C. Sagne, C. Argot (MNHN) for giving me access to the collections at their disposal and for their great hospitality and help during my visit to their institutes. Thanks are also due to G. Konidaris (LGPUT), D. Kostopoulos (LGPUT), D. Nagel (PIUW), G. Rössner (BSPM), S. Roussiakis (AMPG) and M. Schellenberger (BSPM) for providing me photos of some specimens. Finally, I wish to thank the reviewers Dr J. Morales and Dr M. Salesa for their useful comments on the manuscripts.

References

Andrews, C.W. (1918). Note on some fossil mammals from Salonica and Imbros, *Geological Magazine*, 6: 540-543. doi:10.1017/S0016756800201076

Arambourg, C. & J. Piveteau, J. (1929). Les Vertébrés du Pontien de Salonique. *Annales de Paléontologie,* 18: 59-138.

Baird, S.F. (1857). Mammals: general report upon the zoology of the several Pacific railroad route. *Repts, Explorations and Surveys for railroad route from Mississippi River to Pacific Ocean*, 8: 1-757.

Baryshnikov, G. (2002). Late Miocene *Indarctos punjabiensis atticus* (Carnivora, Ursidae) in Ukraine with survey of *Indarctos* records in the former USSR. *Russian Journal of Theriology*, 1(2): 83-89.

Barry, J.; Morgan, M.; Flynn, L., Pilbeam, D.; Khan, I.; Badgely, C.; Hicks, J. & Kelley, J. (2002). Faunal and environmental change in the Late Miocene Siwaliks of Northern Pakistan. *Palaeobiology*, 28: 1-72. doi:10.1666/0094-8373(2002)28[1:FAECIT]2.0.CO;2

Beaumont, G. de (1961). Recherches sur *Felis attica* Wagner eurasiatique avec quelques observations sur les genres *Pseudaelurus* Gervais et *Proailurus* Filhol. *Nouvelles Archives du Muséum d'Histoire Naturelle de Lyon* 6: 1-45.

Beaumont, G. de (1968). Une interessante mandibule de Hyaenidae (Carnivora) du Pontien de Samos. *Archives des Sciences Geneve*, 32: 247-250.

Beaumont, G. de (1975). Recherches sur les félidés (Mammifères, Carnivores) du Pliocène inférieur des sables a *Dinotherium* des environs d'Eppelsheim (Rheihessen). Archives *des Sciences*, 28: 369-405.

Beaumont G. de (1986). La patte postérieure de *Felis attica* Wagn. (Mammifère,Carnivore) du Turolien de Grèce. *Archives des Sciences Geneve*, 39(3): 377-386.

Begun, D.; Güleç, E. & Geraads, D. (2003). The Çandir hominoid locality: Implications for the timing and pattern of hominoid dispersal events. In: *Geology and Vertebrate Palaeontology of the middle Miocene hominoid locality Çandir (Central Anatolia, Turkey)*, (Güleç, E.; Begun, D. & Geraads, D., eds). *Courier Forschung-Institut Senckenberg*, 240, 240-265.

Bonaparte, C.L. J.L. (1837). New systematic arrangement of vertebrated animals. *Transanctions Linnean Society of London*, 18 :247-304. doi:10.1111/j.1095-8339.1838.tb00177.x

Bonis, L. de & Koufos, G.D. (1981). A new hyaenid (Carnivora, Mammalia) in the Vallesian (late Miocene) of Northern Greece. *Scientific Annals Faculty Physics Mathematics, Univ. Thessaloniki,* 21: 79-94.

Bonis, L. de & Koufos, G.D. (1991). The late Miocene small carnivores of the lower Axios Valley (Macedonia, Greece). *Geobios*, 24(2): 361-379. doi:10.1016/S0016-6995(09)90015-8

Bonis, L. de & Koufos, G.D. (1994a). Some hyaenids from the late Miocene of Macedonia (Greece) and the phylogeny of hunting hyaenas. *Münchener Geowissenschaftliche Abhandlungen,* 26: 81-96.

Bonis, L. de & Koufos, G.D. (1994b). Our ancestors' ancestor: *Ouranopithecus* is a Greek link in human ancestry. *Evolutionary Anthropology*, 4(3): 75-83.

Bonis, L. de; Bouvrain, G. & Koufos, G.D. (1999). The Miocene large mammal succession in Greece. In: *Hominoid Evolution and climatic change in Europe", vol. I "The evolution of the Neogene terrestrial ecosystems in Europe* (Agusti, J.; Rook, L. & Andrews, P., eds). Cambridge University Press, Cambridge, 205-237.

Bonis, L. de; Bouvrain, G.; Geraads, D. & Koufos, G.D. (1992). Diversity and palaeoecology of Greek late Miocene mammalian faunas. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 91: 99-121. doi:10.1016/0031-0182(92)90035-4

Bowdich, T.E. (1821). *An analysis of the natural classifications of Mammalia for the use of students and travelers*. J. Smith, Paris, 115 pp.

Burmeister, G. (1850). *Verzeichniss der im Zoologischen Museum de Universität Halle-Wittenberg aufgestellten Säugethiere, Vögel und Amphibien*. Halle, Friedrichs-Universität, 84pp.

Burmeister, G. (1866). Lista de los mamíferos fósiles del terreno diluviano. *Anales del Museo Público de Buenos Aires*, 1: 121-232.

Dames, W. (1883). Über das Vorkommen von *Hyaenarctos* in den Pliocän-Ablagerungen von Pikermi bei Athen. *Sitzungsber. Gesellsch. naturf. Freunde Berlin,* 8: 132-139.

Depéret, C. (1892). La faune des mammiferes miocènes de la Grive Saint-Alban. *Archives Museum Histoire naturelle Lyon*, 5: 31-96.

Dietrich, W.O. (1927). Ueber einen schädel von *Ictitherium* (fam. Viverridae). *Neues Jahrbuch fur Mineralogie, Geologie und Paläontologie,* 57: 364-371.

Doukas, C. (2003). The MN4 faunas of Aliveri and Karydia (Greece). *Coloquios de Paleontología,* Vol. Ext. 1: 127-132.

Erdbrink, D.P.B. (1953). *A review of fossil and recent bears of the Old World*. D.J. de Lange, Deventer, 597 pp.

Eronen, J.T. & Rook, L. (2004). The Mio-Pliocene European primate fossil record: dynamics and habitat tracking. *Journal of Human Evolution*, 47: 323-341. doi:10.1016/j.jhevol.2004.08.003

Eronen, J.T.; Mirzaie Ataabadi, M.; Micheels, A.; Karme, A.; Bernor, R.-L. & Fortelius, M. (2009). Distribution history and climatic controls of the Late Miocene Pikermian chronofauna. *Proceedings National Acadedy of Sciences USA*,106(29): 11867-11871. doi:10.1073/pnas.0902598106

Fejfar, O. & Schmidt-Kittler, N. (1984). *Sivanasua* und *Euboictis* nv. gen.- zwei pflanzenfressende Schleichkatzenvorläufer (Viverridae, Carnivora, Mammalia) im europäischen Untermiozän. *Mainzer Geowissenschaften Mitteilungen*, 13: 49-72.

Fejfar, O. & Schmidt-Kittler, N. (1987). *Lophocyon carpathicus* nov gen. nov. sp. aus dem Jungtertiär der Ostslowakei und eine neue unterfamilie der schleikatzen (Viverridae). *Palaeontographica*, 199: 1-22.

Filhol, H. (1890). Étude sur les mammifères de Sansan. *Bibliothèque de l'École des Hautes Études, section des Sciences Naturelles*, 37, 1-319.

Filhol, M. (1891). Étude sur les mammifères fossiles de Sansan. *Annales Societe géologique*, 21: 1-319.

Fischer von Waldheim, G. (1817). Adversaria Zoologica, fasciculus primus. *Mémoires de la Société des Naturalistes de Moscou*, 5: 357-446.

Forsyth Major, C.I. (1888). Sur un gisement d'ossements fossiles dans l'île de Samos contemporains de l'âge de Pikermi. *Compte Rendus Hebd. Séances Societe Geologique France*, 107: 1178-1181.

Forsyth Major, C.I. (1891). Considerations nouvelles sur la faune des Vertebres du Miocene superieur dans l'ile de Samos. *Compte Rendus Academie Sciences Paris,* CXIII:608-610.

Forsyth Major, C.J. (1894). *Le gisement ossifère de Mytilinii et catalogue d'ossements fossiles recueillis à Mytilini, île de Samos, et déposés au Collège Galliard, à Lausanne*. Georges Bridel & C[ie], Lausanne, 51 pp.

Forsyth-Mayor, C.I. (1903). New Carnivora from the Middle Miocene of La Grive St-Alban. *Geological Magazine*, n.s. 1: 534-538.

Gaillard, C. (1899). Mammifères miocènes nouveaux ou peu connus de La Grive St-Alban. *Archives Museum Lyon* 7: 1-79.

Gaudry, A. (1861a). Résultats des fouilles enteprises en Grèce sous les auspices de l'Académie des Sciences. *Compte Rendus Academie Sciences Paris*, 52: 722-724.

Gaudry, A. (1861b). Note sur les carnassiers fossils de Pikermi (Gréce). *Bulletin de la Sociéte géologique de France,* 18: 527-538.

Gaudry, A. (1862-67). *Animaux fossils et géologie de l'Attique*. Savy, Paris, 476 pp.

Geraads, D.; Tsoukala, E., & Spassov, N. (2007). A skull of *Ancylotherium* (Chalicotheriidae, Mammalia) from the Late Miocene of Thermopigi (Serres, N.Greece), and the relationships of the genus. *Journal of Vertebrate Palaeontology*, 27(2): 461-466. doi:10.1671/0272-4634(2007)27[461:ASOACM]2.0.CO;2

Gervais, P. (1859). *Zoologie et Paléontologie francaise*. Paris, 544 pp.

Gill, T. (1872). Arrangement of the families of mammals with analytical tables. *Smithsonian Miscellaneous collection*, 11: 1-98.

Ginsburg, L. (1999). Order Carnivora. In: *The Miocene land mammals of Europe* (Rössner, G. & Heissig, K., eds). Verlag Dr Friedrich Pfeil, Munchen, 109-148.

Gray, J.E. (1821). On the natural arrangement of vertebrate animals. *London Medical Repository* 15: 296-310.

Gray, J.E. (1843). *List of the specimens of Mammalia in the collection of the British Museum*. British Museum (Natural History), London, 216 pp.

Hay, O.P. (1930). *Second bibliography and catalogue of the fossil Vertebrata of North America*. Carnegie Intitute publications, Washington, no. 390, vol. 1, 916 pp; vol. 2, 1074 pp.

Heizmann, E.P.J., 1973. Die Tertiären Wirbeltiere des Steinheimer Beckens. *Palaeontographica*, 8 (Suppl.): 1-95.

Helbing, H. (1932). Über einen *Indarctos*-Schädel aus dem Pontien der Insel Samos. Nebst einen Anhang: *Hyaenarctos* spec. aus dem Pliocaen von Vialette (Haute-Loire). *Mémoires Societe Paléontologique Suisse*, 52: 1-18,

Hensel, R.F. (1862). Über die Reste einiger Säugetierarten von Pikermi in der Münchener Sammlung. *Monatsberichte der Akademie der Wissenschaften,* 27 :560-569.

Howell, F.C. & Petter, G. (1985). Comparative observations on some middle and upper Miocene hyaenids genera: *Percrocuta* KRETZOI, *Allohyaena* KRETZOI, *Adcrocuta* KRETZOI (Mammalia, Carnivora, Hyaenidae). *Geobios*, 18: 419-476. doi:10.1016/S0016-6995(85)80001-2

Ioakim, C. & Koufos, G.D. (2009). Palynology. In: *The Late Miocene Mammal Faunas of the Mytilinii Basin, Samos Island, Greece: new collection* (Koufos, G.D. & Nägel, D., eds), *Beiträge zur Paläontologie*, 31: 27-35.

Ioakim, C.; Rondoyianni, T. & Mettos, A. (2005). The Miocene basins of Greece (Eastern Mediterranean) from a palaeoclimatic perspective. *Revue Palaeobiologique*, 24(2): 735-748.

Kittl, E. (1887). Beiträge zur Kennthniss der fossilen Säugethiere von Maragha in Persia. I. Carnivora. *Annalen des Naturhistorischen Hofmuseums*, 2: 317-338.

Kormos, T. (1911). Der Pliozäne Knochenfund bei Polgárdi (vorläufiger Bericht). *Földtani Közlöny*, 41: 171-189.

Kostopoulos, D.S. (2009). The Pikermi Event: temporal and spatial resolution of the Turolian large mammal fauna in SE Europe. *Palaeogeography, Palaeoclimatology, Palaeoecology,* 274, 82-95. doi:10.1016/j.palaeo.2008.12.020

Kostopoulos, D.S.; Koufos, G.D.; Sylvestrou, I.A.; Syrides, G.E. & Tsompachidou, E. (2009). Lithostratigraphy and Fossiliferous Sites. In: *The Late Miocene Mammal Faunas of the Mytilinii Basin, Samos Island, Greece: New Collection* (Koufos, G.D. & Nagel, D., eds). *Beiträge zur Paläontologie*, 31: 13-26.

Koufos, G.D. (1982). *Plesiogulo crassa* from the Upper Miocene (lower Turolian) of Northern Greece. *Annales Zoologici Fennici*, 19: 193-197.

Koufos, G.D. (1987). *Chasmaporthetes bonisi*, a new hyaenid (Carnivora, Mammalia) from the late Miocene of Macedonia (Greece). *Bulletin Societe Géologique France*, (8), t. III, no 5: 913-920.

Koufos, G.D. (1995). The late Miocene percrocutas of Macedonia (Greece). *Palaeovertebrata*, 24: 67-84.

Koufos, G.D. (2000). Revision of the late Miocene carnivores from the lower Axios valley. *Münchner Geowissenschaften Abhandlungen*, (A) 39: 51-92.

Koufos, G.D. (2006a). The Neogene mammal localities of Greece: faunas, chronology and biostratigraphy. *Hellenic Journal of Geosciences*, 41: 183-214.

Koufos, G.D. (2006b). Carnivora. In: *The late Miocene Vertebrate locality of Perivolaki, Thessaly, Greece* (Koufos, G.D., ed.), *Palaeontographica,* Abt. A, 276: 39-74.

Koufos, G.D. (2006c). The large mammals from the Miocene/Pliocene locality of Silata, Macedonia, Greece with implications about the Latest Miocene palaeoecology. *Beitrage zur Paläontologie*, 30: 293-313.

Koufos, G.D. (2006d). Palaeoecology and chronology of the Vallesian (late Miocene) in the Eastern Mediterra-

nean region. *Palaeogeography, Palaeoclimatology, Palaeoecology,* 234: 127-145.

Koufos, G.D. (2008). Carnivores from the early/middle Miocene locality of Antonios (Chalkidiki, Macedonia, Greece). *Geobios*, 41: 365-380. doi:10.1016/j.geobios.2007.05.003

Koufos, G.D. (2009). Carnivora. In: *The Late Miocene Mammal Faunas of the Mytilinii Basin, Samos Island, Greece: New Collection* (Koufos, G.D. & Nagel, D., eds). *Beiträge zur Paläontologie*, 31: 57-105.

Koufos, G.D. (2011a). New material of Carnivora (Mammalia) from the Late Miocene of Axios Valley, Macedonia, Greece. *Comptes Rendus Palevol* (in press).

Koufos, G.D. (2011b). A new protictithere from the late Miocene hominoid locality Ravin de la Pluie of Axios Valley (Macedonia, Greece).

Koufos, G.D. (in press). Neogene Mammal Biostratigraphy and Chronology of Greece. In: *Asian Neogene Mammal Biostratigraphy and Chronology* (Xiaoming, W., Fortelius, M. & Flynn, L., eds). Columbia University Press.

Koufos, G.D. & Konidaris, G.E., (2011). Late Miocene carnivores of the Greco-Iranian Province: Composition, guild structure and palaeoecology. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 305: 215-226. doi:10.1016/j.palaeo.2011.03.003

Koufos, G.D.; Bonis de L. & Sen, S. (1995). *Lophocyon paraskevaidisi* a new viverrid (Carnivora, Mammalia from the middle Miocene of Chios Island (Greece). *Geobios*, 28(4): 511-523. doi:10.1016/S0016-6995(95)80028-X

Koufos, G.D.; Kostopoulos, D.S. & Merceron, G. (2009b). Palaeoecology-Palaeobiogeography. In: *The Late Miocene Mammal Faunas of the Mytilinii Basin, Samos Island, Greece: New Collection* (Koufos, G.D. & Nagel, D., eds). *Beiträge zur Paläontologie*, 31: 409-428.

Koufos, G.D.; Kostopoulos, D.S. & Vlachou, T.D. (2009a). Chronology. In: *The Late Miocene Mammal Faunas of the Mytilinii Basin, Samos Island, Greece: New Collection* (Koufos, G.D. & Nagel, D., eds). *Beiträge zur Paläontologie*, 31: 397-408.

Koufos, G.D.; Merceron, G.; Kostopoulos, D.S.; Vlachou, T.D. & Sylvestrou, I. (2006b). Palaeoecology and Palaeobiogeography. In: *The late Miocene Vertebrate locality of Perivolaki, Thessaly, Greece* (Koufos, G.D., ed.), *Palaeontographica,* Abt. A, 276: 201-221.

Koufos, G.D.; Sen, S.; Kostopoulos, D.S.; Sylvestrou, I.A. & Vlachou, T.D. (2006a). Chronology. In: *The late Miocene Vertebrate locality of Perivolaki, Thessaly, Greece* (Koufos, G.D., ed.), *Palaeontographica,* Abt. A, 276: 185-200.

Kovar-Eder, J.; Kvacek, Z.; Martinetto, E. & Roiron, P. (2006). Late Miocene to early Pliocene vegetation of Southern Europe (and-4 Ma) as reflected in the megafossil plant record. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 238: 321-339. doi:10.1016/j.palaeo.2006.03.031

Kretzoi, M. (1929): Materialen zur phylogenetischen Klassification der Ailuroïden. *10th Congress. International of Zoology, Budapest*, 1927, 2: 1293-1355.

Kretzoi, M. (1938). Die Raubtiere von Gombaszog nebst einer Übersicht der Gesamtfauna (ein beitrag zur stratigraphie des Altquataers). *Annals Museum Naturalis Hungarici*, 31: 89-157.

Kretzoi, M. (1952). Die Raubtiere der *Hipparion*fauna von Polgardi. *Annales Instituti Geologici Hungarici*, 40(3): 5-42.

Kretzoi, M. (1965). Die Hipparion-fauna von Győrszentmárton in NW-Ungarn. *Annales Historico-Naturales Musei Nationalis Hungarici,* 57:127-143.

Kurtén, B. (1957). *Percrocuta* Kretzoi (Mammalia, Carnivora), a group of Neogene hyaenas. *Acta Zoologica Cracoviensia*, 2: 375-404.

Kurtén, B. (1982). Status of the fossil hyaenids *Ictitherium viverrinum* and *Thalassictis robusta* (Mammalia). *Zeitschrift für geologische Wissenschaften*, 10: 1009-1018.

Melentis, J.K. (1967). Studien über fossile Vertebraten Griechenland. 19. Die Pikermifauna von Halmyropotamos (Euböa, Griechenlands). I Teil: Odontologie und Kraniologie. *Annales géologiques Pays helleniques*, 18: 283-411.

Mequenem, R. de (1924-1925). Contribution à l'étude des fossiles de Maragha. *Annales de Paléontologie* 13-14: 135-160, 1-36.

Merceron, G.; Blondel, C.; Bonis, L. de; Koufos, G.D. & Viriot, L. (2005). A new dental microwear analysis: Application to extant Primates and *Ouranopithecus macedoniensis* (Late Miocene of Greece). *Palaios*: 20, 551-561.

Merceron, G.; Blondel, C.; Viriot, L.; Koufos, G.D. & Bonis, L. de (2007). Dental microwear analysis of bovids from the Vallesian (late Miocene) of Axios Valley in Greece: reconstruction of the habitat of *Ouranopithecus macedoniensis* (Primates, Hominoidea). *Geodiversitas*, 29(3): 421-433.

Merceron, G.; Zazzo, A.; Spassov, N.; Geraads, D. & Kovachev, D. (2006). Bovid paleoecology and paleoenvironments from the Late Miocene of Bulgaria: Evidence from dental microwear and stable isotopes. *Palaeogeography, Palaeoclimatology., Palaeoecology.,* 241: 637-654. doi:10.1016/j.palaeo.2006.05.005

Merceron, G.; Blondel, C.; Brunet, M.; Sen, S.; Solounias, N.; Viriot, L. & Heintz, E. (2004). The late Miocene paleoenvironment of Afganistan as inferred from dental microwear in artiodactyls. *Palaeogeography, Palaeoclimatology, Palaeoecology,* 207, 143-163. doi:10.1016/j.palaeo.2004.02.008

Miller, G.S. (1912). *Catalogue of the mammals of western Europe (Europe exclusive of Russia) in the British Museum.* British Museum (Natural History), London, 1019 pp.

Mivart, S.G. (1882). On the classification and distribution of the Aeluroidea. *Proceedings of the Zoological Society of London*, 135-208.

Morlo, M. (1999). Niche structure and evolution in creodont (Mammalia) faunas of the European and North American Eocene. *Geobios*, 32(2): 297-305. doi:10.1016/S0016-6995(99)80043-6

Morlo, M.; Gunnell, G.F. & Nagel, D. (2010). Ecomorphological analysis of carnivore guilds in the Eocene through Miocene of Laurasia. In: *Carnivore Evolution: New views on phylogeny, form and function* (Goswami, A & Friscia, A., eds), Cambridge University Press, 269-310.

Nagel, D. & Koufos, G.D. (2009). Carnivore guild structure. In: *The Late Miocene Mammal Faunas of the Mytilinii Basin, Samos Island, Greece: New Collection* (Koufos, G.D. & Nagel, D., eds). *Beiträge zur Paläontologie*, 31: 391-396.

NOW (2010). Neogene Old World (database with the Neogene localities and their faunal lists). www.helsinki.fi/science/now/database.htm.

Pilgrim, G.E. (1931). *Pontian Carnivora of Europe*. British Museum Natural History, London, 174 pp.

Pilgrim, G.E. (1932). The fossil Carnivora of India. *Memoirs of the Geological Survey of India, Palaeontologia Indica,* 18: 1-232.

Pilgrim, G.E. (1933). A fossil skunk from Samos. *Annals Museum Novitates*, 663: 1-15.

Qiu, Z. (1987). Die Hyeniden aus dem Ruscinium and Villafranchium Chinas. *Münchner Geowissenschaften Abhandlungen*, (A) 9: 1-110.

Qiu, Z.; Xie, J. & Yan, D. (1988). Discovery of the skull of *Dinocrocuta gigantea*. *Vertebrata Palasiatica*, 26: 128-138.

Roman, F. & Viret, J. (1934). La faune de mammifères du Burdigalien de La Romieu (Gers). *Mémoires de la Société géologique de France*, n. s. 18: 1-67.

Roth, J. & Wagner, A. (1854). Die fossilen Knochenüberreste von Pikermi in Griechenland. *Abhandlungen Bayerische Akademie Wissenschaften, München Math.-Phys. Kl.*, 7: 371-464.

Roussiakis, S. (1996). Contribution to the study of the mammalian findings in the type locality of Pikermi. *PhD thesis, University of Athens*, 1-259. (in Greeks, unpublished).

Roussiakis, S. (2001a). Postcranial remains of *Indarctos atticus* (Ursidae, Mammalia) from the classical locality of Pikermi (Attica, Greece), with a description of the front limb. *Senckenbergiana lethaea*, 81(2):347-358.

Roussiakis, S. (2001b). *Metailurus major* Zdansky, 1924 (Carnivora, Mammalia) from the classical locality of Pikermi (Attica, Greece). *Annales de Paléontologie*, 87(2):119-132.doi:10.1016/S0753-3969(01)80006-9

Roussiakis, S. (2002). Musteloids and feloids (Mammalia, Carnivora) from the late Miocene locality of Pikermi (Attica, Greece). *Geobios*, 35: 699-719. doi:10.1016/S0016-6995(02)00083-9

Roussiakis, S. & Theodorou, G. (2003). Carnivora from the late Miocene of Kerassia (Northern Euboea, Greece). *Deinsea* 10: 469-497.

Roussiakis, S.; Theodorou, G. & Iliopoulos, G. (2006). An almost skeleton of *Metailurus parvulus* (Carnivora, Felidae) from the late Miocene of Kerassia (Northern Euboea, Greece). *Geobios,* 39: 563-584. doi:10.1016/j.geobios.2005.04.002

Schlosser, M. (1902). Beiträge zur Kenntniss der Saugerthierreste auf den Süddeutschen Bohnherzen. *Geologische Pälaontologische Abhandlungen Iena*, N.F., V(3): 115-258.

Schlosser, M. (1903). Die fossilen Säugetiere Chinas nebst einer Odontographie der recenten Antilopen. *Abhanlungen Bayerische Akademie Wissenschaften*, (IIC_1) 22: 1-221.

Schmidt-Kittler, N. (1976). Carnivores from the Neogene of Asia Minor. *Palaeontographica*, Abt. A, 155: 1-131.

Schmidt-Kittler, N. (1983). The mammals from the lower Miocene of Aliveri (island of Evia, Greece). On a new species of *Sivanasua* PILGRIM, 1931 (Felidae, Carnivora) and the phylogenetic position of the genus. *Proceedings Koniklijke Nederlandse Akademie Wetenschappen,* B.86: 301-318.

Schmidt-Kittler, N. (1995). Carnivora, Mammalia. In: *The Vertebrate locality Maramena (Macedonia, Greece) at the Turolian/Ruscinian boundary (Neogene*), (Schmidt-Kittler, N., ed.). *Münchner Geowissenschftische Abhandlungen,* Abt. A, 28: 75-86.

Schmidt-Kittler, N.; de Bruijn, H. & Doukas, C. (1995). General Introduction. In: *The Vertebrate locality Maramena (Macedonia, Greece) at the Turolian/Ruscinian boundary (Neogene*), (Schmidt-Kittler, N., ed.). *Münchner Geowissenschftische Abhandlungen,* Abt. A, 28: 1-18.

Sen, S.; Koufos, G.D.; Kondopoulou, D. & Bonis, L. de (2000). Magnetostratigraphy of the late Miocene continental deposits of the lower Axios valley, Macedonia, Greece. In: *Mediterranean Neogene cyclostratigraphy in marine-continental deposits* (Koufos, G.D. & Ioakim, Ch, eds). *Bulletin Geological Society of Greece*, sp. publ., 9: 1197-206.

Solounias, N. (1981). The Turolian fauna from the island of Samos, Greece. *Contribution in Vertebrate Evolution*, 6: 1-232.

Strömberg, C.E.; Werdelin, L.; Friis, E.M. & Saraç, G. (2007). The spread of grass-dominated habitats in Turkey and surrounding areas during the Cenozoic: Phytolith evidence. *Palaeogeography, Palaeoclimatology, Palaeoecology,* 250: 18-49. doi:10.1016/j.palaeo.2007.02.012

Suc, J-P.; Fauquette, S.; Bessedik, M.; Bertini, A.; Zheng, Z.; Clauzon, G.; Suballyova, D.; Diniz, F.; Quézel, P.; Feddi, N.; Clet, M.; Bassais, E. & Combourieu-Nebout, N.N. (1999). Neogene vegetation changes in West European and West circum Mediterranean areas. In: *Hominoid Evolution and Climatic Change in Europe: The Evolution of the Neogene Terrestrial Ecosystems in Europe* (Agusti, J.; Rook, L. & Andrews, P., eds). Cambridge University Press, Cambridge, 378-388.

Symeonidis N.K. (1975). Ein grosser Mustelidae aus Pikermi. *Annales Géologiques des Pays Helléniques*, 26: 314-319.

Symeonidis, N. (1978). Ein schädel von *Metailurus parvulus* (Hensel) aus Pikermi (Attica, Griechenland). *Annales géologiques des Pays helleniques,* 29: 698-703.

Swainson, W. (1835). On the natural history and classification of quadrupeds. In : *The cabinet cyclopaedia* (Lardner, D., ed.). Longman, London, 397.

Teilhard de Chardin, P. & Leroy, P. (1945). Les Mustelidés de Chine. *Institute of Geology*, 4181-4185.

Thenius, E. (1947). *Ursavus ehrenbergi* aus dem Pont von Euböa (Griechenland). *Sitzber. Akademie Wissenschaften Wien*, 156: 225-249.

Trouessart, E.L. (1885). Catalogue des mammifères vivants et fossiles. Carnivores. *Bulletin de la Sociète Études Sciences Angers*, 14: 1-108.

Trouessart, E.L. (1897). *Catalogue mammalium tam viventium quam fossilium*. R. Friedlander und Sohn, Berlin, 218 pp.

Turner, A.; Anton, M. & Werdelin, L. (2008). Taxonomy and evolutionary patterns in the fossil Hyaenidae of Europe. *Geobios*, 41(5): 677-687. doi:10.1016/j.geobios.2008.01.001

Van der Made, J. (2003). Suoidea (pigs) from the Miocene hominoid locality Çandir in Turkey. In: *Geology and Vertebrate Palaeontology of the middle Miocene hominoid locality Çandir (Central Anatolia, Turkey)*, (Güleç, E.; Begun, D. & Geraads, D., eds). *Courier Forschung-Institut Senckenberg*, 240: 149-179.

Van der Made, J. (2005). Errata and reply to Guests Editor's notes. *Courier Forschung-Institut Senckenberg*, 254, 473-477.

Vasileiadou, K. & Koufos, G.D. (2005). The micromammals from the Early/Middle Miocene locality of Antonios, Chalkidiki, Greece. *Annales de Paléontologie*, 91: 197-225. doi:10.1016/j.annpal.2005.06.002

Villalta, J.F. & Crusafont, M. (1945). Nuevas aportaciones al conocimiento de los carnivoros Pontienses del Valles-Penedes. *Dip. Prov. Barcelona. Publ. Inst. Geol. Miscelanea Almera,* 7: 11-121.

Wagner, A. (1848). Urweltliche Säugetier-Ueberreste aus Griechenland. *Abhandlungen der Bayerischen Akademie der Wissenschaften, 2kl.*, 5(2):155-170.

Wagner, A. (1857). Neue Beiträge zur Kenntniss der fossilen Saugthier-Ueberreste von Pikermi. *Abhandlungen der Bayerischen Akademie der Wissenschafte,* 8: 111-158.

Weithofer, A. (1888). Beiträge zur kenntniss der fauna von Pikermi bei Athen. *Beiträge zur Pälaontologie Östereich-Ungarns*, 6: 225-292.

Werdelin, L. & Solounias, N. (1991). The hyaenidae: taxonomy, systematics and evolution. *Fossil and Strata*, 30: 1-104.

Zdansky, O. (1924). Jungtertiäre Carnivoren chinas. *Paleontologica Sinica*, C.2: 38-45.

Recibido el 17 de enero de 2011
Aceptado el 24 de junio de 2011