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New material of Carnivora (Mammalia) from the Late Miocene of Axios Valley, Macedonia, Greece

Nouveau matériel de Carnivora (Mammalia) du Miocène supérieur de la vallée de l'Axios, Macédoine, Grèce

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ABSTRACT

A new collection of carnivores from the Late Miocene deposits of Axios Valley, Macedonia, Greece was collected in 2004–2009 at the localities named Xirochori 1 (XIR) and Ravin de la Pluie (RPl), dated to the Late Vallesian (MN 10), as well as at Ravin des Zouaves 5 (RZO), dated to the Early Turolian (MN 11). The studied material is described and compared morphologically and biometrically with other materials from Greece and its neighboring area. The following species are determined: **XIR**: *Dinocrocuta* sp.; **RPl**: *Eomellivora wimani, Adcrocuta eximia leptoryncha,* ?*Hyaenictis* sp., *Metailurus parvulus*; **RZO**: *Plioviverrops orbignyi, Machairodus giganteus*. This collection is interesting because it includes the upper deciduous dentition of *A. eximia* and *Dinocrocuta*, which are only known from limited material until now, especially the latter taxon. *E. wimani* is recognized for the first time in Greece and the Balkans, while *M. parvulus* is identified for the first time in the Vallesian of Greece. The possible presence of *Hyaenictis* in RPl is the first indication of its presence in the Vallesian. The guild structure diagrams of the carnivore fauna from the three studied localities provide some indications of their palaeoenvironment, which fits quite well with the results of previous studies on the palaeoenvironments of these localities and of the wider Eastern Mediterranean region.

RÉSUMÉ

Une nouvelle récolte de carnivores dans les dépôts Miocène récent de la vallée d'Axios, Macédoine, Grèce a été effectuée de 2004 à 2009 dans les localités dénommées Xirochori 1 (XIR) et Ravin de la Pluie (RPI), datées du Vallésien récent (MN10), et Ravin des Zouaves (RZO), datée du Turolien ancien (MN11). Le matériel étudié est décrit et comparé morphologiquement et biométriquement à d'autres matériels de Grèce et des

Abbreviations: a.a.c., anterior accessory cusp(-id); AMNH, American Museum of Natural History, New York; B, breadth; NHML, Natural History Museum, London; BSPM, Bayerische Staatssammlung für Palaeontologie und historische Geologie, Munich; DTK, Dytiko 1; EPP, Eppelsheim, Germany; GPTS, Geomagnetic Polarity Time Scale; HD, Hadjidimovo, Bulgaria; HAL, Halmyropotamos, Greece; KTA+B, Kemiklitepe A+B, Turkey; KTD, Kemiklitepe D, Turkey; L, length; LGPUT, Laboratory of Geology and Palaeontology, University of Thessaloniki; MNHN, Musée national d'Histoire naturelle, Paris; MRG, Maragheh; NHMA, Natural History Museum of Aegean, Samos; NHMW, Naturhistorisches Museum, Wien; p.a.c., posterior accessory cusp(-id); PER, Perivolaki; PIK, Pikermi; PIUW, Paläontologische Institut, Universität Wien; PMMS, Palaeontological Museum of Mytilinii, Samos (old collection of Prof. J. Melentis housed in NHMA); PNT, Pentalophos 1; R.I., robusticity index; RPl, Ravin de la Pluie; RZO, Ravin des Zouaves 5; SAM, Samos (unknown localities); SLQ, Salonique (Arambourg's collection at MNHN); TRQ, Turquie (Middle Sinap collection at MNHN); XIR, Xirochori 1.

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alentours. Les espèces suivantes ont été déterminées : **XIR** : *Dinocrocuta* sp. ; **RPI** : *Eomellivora wimani, Adcrocuta eximia leptoryncha, ?Hyaenictis sp., Metailurus parvulus* ; **RZO** : *Plioviverrops orbignyi, Machairodus giganteus*. La récolte est intéressante, car elle inclut la dentition de lait supérieure d'*A. eximia* et de *Dinocrocuta*, qui ne sont connues jusqu'à présent que par un matériel limité. En particulier, le dernier taxon *E. wimani* est reconnu pour la première fois en Grèce et dans les Balkans, tandis que *M. parvulus* est identifié pour la première fois dans le Vallésien de Grèce. La présence possible de *Hyaenictis* à RPl est la première indication de sa présence dans le Vallésien. Les diagrammes de structure de guilde de la faune de carnivores des trois localités étudiées fournissent quelques indications sur leur paléoenvironment, tout à fait conformes aux résultats de précédentes études sur ces localités et sur un secteur plus large de la Méditerranée orientale.

1. Introduction

The Late Miocene mammal localities of Axios Valley near Thessaloniki, have been known since the beginning of the last century. A new series of excavations in the Axios Valley, begun in 1972 and still active, led to the discovery of several localities and to a great amount of fossils. The mammal localities belong to three different stratigraphic horizons, covering all Late Miocene European mammal biozones. More details about the Axios Valley localities, their stratigraphy and fauna are given in Koufos (in press and refs. cited).

The Axios Valley mammal faunas are quite diversified, including several new taxa (Koufos, 2006a). The carnivores are represented by relatively little material, which includes several taxa (Koufos, 2000, and refs. cited). During the latest field seasons, 2004–2009, several carnivores were collected from the Axios Valley localities. Although the carnivore material is not rich, it is very interesting because it contains several taxa unknown in the Balkans or the Late Miocene stratigraphic biozones of Greece. The present article describes, compares, and classifies the new carnivore material of the Axios Valley and provides information about the carnivore faunal composition, structure, and palaeoenvironment.

The studied material comes from three localities of the Axios Valley: Xirochori 1 (XIR), Ravin de la Pluie (RPl) and Ravin des Zouaves 5 (RZO), (Fig. 1). The localities XIR and RPl are well known because of the presence of the hominoid primate *Ouranopithecus macedoniensis*. Both are situated in the Nea Messimvria Formation; their mammalian fauna suggests a Late Vallesian age (MN10). The locality RZO is situated at the base of the Vathylakkos Formation in a yellowish calcitic marl. The Vathylakkos Formation conformably overlies the N. Messimvria Formation. The RZO mammal fauna is quite rich and suggests an Early Turolian age (MN 11). The magnetostratigraphic record suggests an estimated age of ~9.6 Ma for XIR, ~9.3 Ma for RPl, and ~8.2 Ma for RZO (Koufos, 2006a and refs. cited).

The studied material is stored in the LGPUT. The name of the collection to which each fossil belongs to is noted as the first part of its number. The locality and the catalogue number of each specimen comprise the second and third parts of its number. All the measurements are given in mm; the parentheses indicate estimated values.

2. Palaeontology

Order Carnivora Bowdich, 1821
Family Mustelidae Fischer de Waldheim, 1817
Genus *Eomellivora* Zdansky, 1924
Eomellivora wimani Zdansky, 1924
Locality. Ravin de la Pluie (RPl), Axios Valley, Macedonia, Greece (Fig. 1).
Age. Late Vallesian, MN 10; GPTS = ~9.3 Ma
Material. Left upper first molar, LGPUT-RPl-252.
Measurements. **M1**: 9.1×19.7, $L_{lingual} = 12.2$

Description: The cusps of the tooth are worn and low, indicating a relatively old individual (Fig. 2). The tooth has a strong constriction in the middle of its width. The paracone is strong, but the metacone is weak and quite worn (barely distinguishable). The paracone is surrounded by a strong mesio-labial cingulum. The protocone is large, situated in the mesial part of the lingual lobe of the tooth. It is connected through the pre-protocrista (nomenclature according to Bryant et al., 1993) with the paracone. It is surrounded mesially, lingually and distally by a strong cingulum; although it shows advanced wear, it is clear that the cingulum consists of small cusps. The mesial extension of the lingual cingulum is smaller than the distal one. The posterocrista is slightly distinguished in its origin from the paracone but cannot be followed because the enamel is slightly broken.

Discussion: An extensive revision of the genus *Eomellivora,* as well as its synonymy and systematics, are given by Wolsan and Semenov (1996), whose conclusions are accepted in this article. *Eomellivora,* compared to the modern *Mellivora capensis*, is clearly larger (Fig. 3). Apart from its smaller size, the M1 of *M. capensis* has a longer lingual than buccal mesiodistal diameter, a relatively larger paracone, and no metacone. The protocone is surrounded by a stronger and more prominent cingulum than those of LGPUT-RPl-252 and *Eomellivora wimani*.

The comparison of LGPUT-RPl-252 with the M1 of *E. wimani* from China (Zdansky, 1924: p. 61; taf. XII, Fig. 1) indicates that they are morphologically and metrically (Fig. 3) similar. However, the metacone is better developed in the Chinese sample but this is possibly due to the more advanced attrition of the studied specimen. The metacone of *Eomellivora* is vestigial (Wolsan and Semenov, 1996) and attrition decreases it rapidly. A maxillary fragment with P4-M1 and an isolated M1 (MNHN-TRQ-1005, 1006)

Fig. 1. Geographic map, indicating the position of the Axios Valley mammal localities. **DTK**: Dytiko 1; **PNT**: Pentalophos 1; **RPl**: Ravin de la Pluie; **RZO**: Ravin des Zouaves-5; **R-X**: Ravin X; **XIR**: Xirochori 1.

Fig. 1. Localisation des sites fossilifères de la vallée de l'Axios.

from the Turkish locality of Middle Sinap are referred to *E. piveteaui* (Ozansoy, 1965: p. 23: pl. I, Figs. 1–5) and recently to the subspecies *E. w. piveteaui* (Wolsan and Semenov, 1996). A direct comparison of LGPUT-RPl-252 with the Sinap M1 indicates that they have similar morphology and size (Fig. 3). Because the Sinap teeth are less worn, their metacone and posterocrista seem to be stronger and more expressed. A skull and an incomplete mandible of a large mustelid from Grebeniki, Moldavia were described as *Perunium ursogulo* (Orlov, 1948) and later synonymized with *E. wimani* (Ozansoy, 1965; Wolsan and Semenov, 1996). LGPUT-RPl-252 is similar to the Grebeniki M1 (Orlov, 1948: Figs. 2 and 5) in occlusal morphology and size (Fig. 3). One M1 from the Early Vallesian Spanish locality of Los Valles de Fuentidueña was described as a new species under the name *E. liguritor* and later synonymized with *E. wimani* (Crusafont Pairo and Ginsburg, 1973; Wolsan and Semenov, 1996). The morphological characters of the Spanish *Eomellivora* are similar to those of *E. wimani.* The differences noted for the latter, such as the more developed lingual cingulum and the slightly less developed protocone (Crusafont Pairo and Ginsburg, 1973) are not as indicative. The M1 size of *E. liguritor* is quite similar to that of *E. wimani* from China, Grebeniki and LGPUT-RPl 252 (Fig. 3), confirming

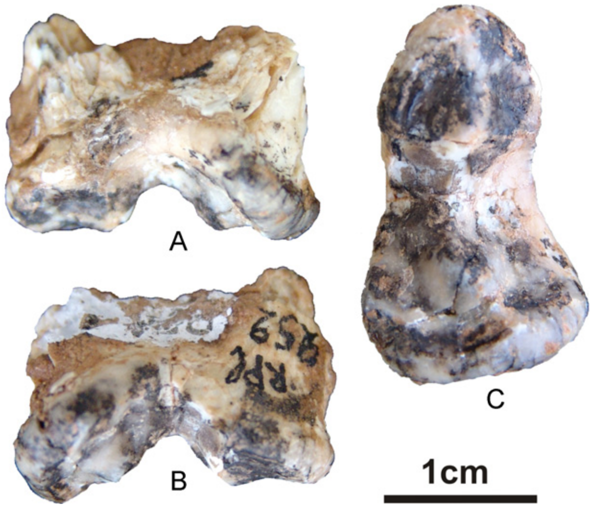

Fig. 2. *Eomellivora wimani*, Ravin de la Pluie, RPl, Axios Valley, Macedonia, Greece, left M1, RPl-252; **A**. distal, **B**. mesial and **C**. occlusal view.

Fig. 2. *Eomellivora wimani*, Ravin de la Pluie, RPl, vallée de l'Axios, Macédoine, Grèce, M1 gauche, RPl-252; **A**. vue distale, **B**. vue mésiale et **C**. vue occlusale.

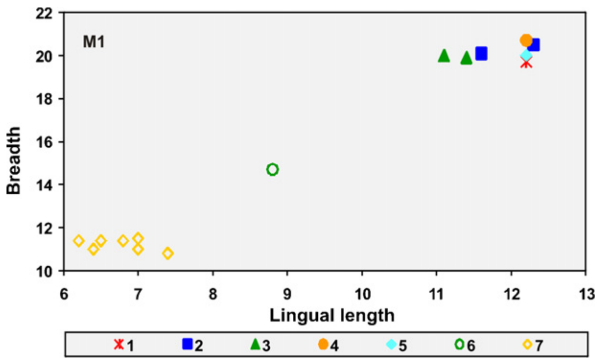

Fig. 3. Bivariate plot, comparing the dimensions of the M1 of the various species of *Eomellivora* and *Mellivora*. **1**. LGPUT-RPl-252; **2**. *Eomellivora wimani*, China (Zdansky, 1924); **3**. *E. wimani*, Sinap (orig. meas.); **4**. *E. liguritor*, Los Valles de Fuentidueña (Crusafont Pairo and Ginsburg, 1973); **5**. *E. wimani*, Grebeniki (Orlov, 1948); **6**. *E. tugenensis*, Ngorora (Morales and Pickford, 2005); **7**. *M. capensis*, recent (Morales and Pickford, 2005).

Fig. 3. Proportions de la M1 des espèces d'*Eomellivora* et de *Mellivora*.

the synonymy of *E. liguritor* with *E. wimani* (Wolsan and Semenov, 1996). A new species of *Eomellivora*, under the name *Eomellivora tugenensis* is referred from Ngorora, Kenya (Morales and Pickford, 2005). Its M1 resembles that of *E. wimani* but it is much smaller (Fig. 3). *Eomellivora* is rare in eastern Mediterranean, and known only from Middle Sinap (Turkey) until now. Its presence at RPl marks its first appearance in Greece and the Balkan Peninsula.

Family Hyaenidae Gray, 1821

Genus *Plioviverrops* Kretzoi, 1938

Plioviverrops orbignyi (Gaudry and Lartet, 1856)

Locality. Ravin des Zouaves-5, RZO, Macedonia, Greece (Fig. 1).

Age. Early Turolian, MN 11; GPTS = ~8.2 Ma.

Material. Right mandibular fragment with m1–m2, LGPUT-RZO-166.

Measurements. **m1** = 9.0 × 4.5; **m2** = (5.2) × –.

Height of the mandibular corpus below m1 (lingual) = 11.7

Height of the mandibular corpus below p4 (lingual) = 11.0

Thickness of the mandibular corpus below m1 = 6.1

Description: The studied specimen preserves the mandibular corpus from the p4 to the mandibular angle and the two molars; the m2 is broken disto-buccally (Fig. 4A). The mandibular corpus is shallow and quite thick. The masseteric fossa is deep and its anterior border ends below the distal border of the m2. The m1 is short and wide with very high cuspids; the trigonid cuspids (proto-, para- and meta-conid) are of almost similar height. The talonid is well distinguished from the trigonid by a deep valley and bears a high entoconid and a weak hypoconid (Fig. $4A_3$). The labial cingulum is well developed. The m2 preserves only the paraconid, which is high.

Discussion: Extensive comparisons of *P. orbignyi* with the other species of the genus and with those of *Protictitherium*, as well as its stratigraphic distribution, have been given recently (Koufos, 2006b, 2009, and ref. cited). The high trigonid cuspids, the bicuspid and well separated talonid, as well as the deep valleys of the carnassial in the studied specimen characterize *P. orbignyi* and allow its attribution to this species. The dimensions of the studied carnassials are also in the range of variation of *P. orbignyi*, confirming its attribution.

Genus *Adcrocuta* Kretzoi, 1938

Species *Adcrocuta eximia* (Roth and Wagner, 1854)

Adcrocuta eximia leptoryncha Bonis and Koufos, 1981

Locality. Ravin de la Pluie (RPl), Axios Valley, Macedonia, Greece (Fig. 1).

Age. Late Vallesian, MN 10; GPTS = ~9.3 Ma.

Material. Right upper canine, LGPUT-RPl-269; left mandibular fragment with i2, c-m1, LGPUT-RPl-272.

Measurements. **C**:16.2 × (11)

Mandible: Length anterior c-distal side of condyle = 194.5; Height ventral border of angular process-dorsal side of condyle = 43.4; Symphysis length = 60.0; Height in front of p2 (lingual) = 43.0; Idem in the middle of p3 (lingual) = 40.8; Idem in p4 (lingual) = 43.0; Idem in m1 (lingual) = 46.2; Diastema c-p2 = 10.0; Alveolar length c-m1 = 106.2; Alveolar length p2-m1 = 81.2; Alveolar length p2-p4 = 55.1.

i2: 7.0 × 5.5; **c** = 15.0 × 13.3; **p2** = 13.7 × 9.0; **p3** = 18.3 × 11.5; **p4** = 20.5 × 11.7, **m1** = 27.6 × 11.7, $\mathbf{L_{m1\ tal.}}$ = 5.0 (the talonid length is measured from the distal wall of the protoconid to the distal end of the talonid).

Description: The hemimandible LGPUT-RPl-272 lacks the ascending ramus and the teeth i1 and i3 (Fig. 4B). The mandibular corpus is elongated and shallow for its size, with two mental foramina that are connected and situated below the p2. The symphysis is strong and inclines abruptly backwards. The masseteric fossa is large and oval, and its anterior border is well behind the m1. The dentition is well preserved and the p1 is absent. The premolars are narrow and their main cuspid inclines backwards. The p2 is small without an a.a.c. and with a small p.a.c (Fig. $4B_{1,3}$). The p3 bears a small a.a.c. and p.a.c., as well as a strong distal cinglum. The p4 has a strong a.a.c. and a smaller p.a.c., situated on a large distal projection of the distal cingulum. The carnassial is narrow, without metaconid, and it has a small and bicuspid talonid. The isolated upper canine has the typical morphology and size of *A. eximia* (Fig. 4E).

Discussion: The general morphology of the studied mandible and teeth fits that of *A. eximia*; however, the RPl *A. eximia* differs from the Pikermi one, representing the new subspecies *A. e. leptoryncha*; it is known by a skull and a badly preserved mandibular fragment (Bonis and Koufos, 1981). The absence of the p1, the more slender teeth, the smaller premolars, and the narrower m1 of the studied mandible distinguish it from the typical *A. e. eximia* of Axios Valley, Pikermi and Samos. On the other hand, its dental dimensions are similar to those of *A. e. leptoryncha* (Fig. 5) and allow its attribution to this subspecies.

Adcrocuta eximia (Roth and Wagner, 1854)

Locality. Ravin de la Pluie (RPl), Axios Valley, Macedonia, Greece (Fig. 1).

Age. Late Vallesian, MN 10; GPTS = ~9.3 Ma.

Material. Left maxillary fragment with DP2-DP4, LGPUT-RPl-244; fragment of a left DP3, LGPUT-RPl-271.

Measurements. The measurements are given in Table 1.

Description: The DP2 is small and relatively short and wide. In its mesiolingual corner there is a small projection of the cingulum, like a vestigial a.a.c., whereas the p.a.c. is distinct and low (Fig. $4C_2$). The DP3 is elongated and narrow, with a very low protocone extended lingually from the middle of the tooth; the protocone is worn and its height does not exceed the root of the tooth (Fig. $4C_2$). The parastyle is moved mesially and it is distinguished like a cusp; in its mesiolingual corner there is a small cuspule (Fig. $4C_2$). The metastyle is blade-like, elongated and slightly curved buccally. The DP4 is triangular and low-crowned. Both paracone and metacone are very low and they are connected by a thin crest, running from the mesial border of the paracone to its apex and through the metacone's apex to its distal border (Fig. $4C_2$). The protocone is more developed than the other cusps but still low, and it is situated in the lingualmost angle of the tooth. The paracone

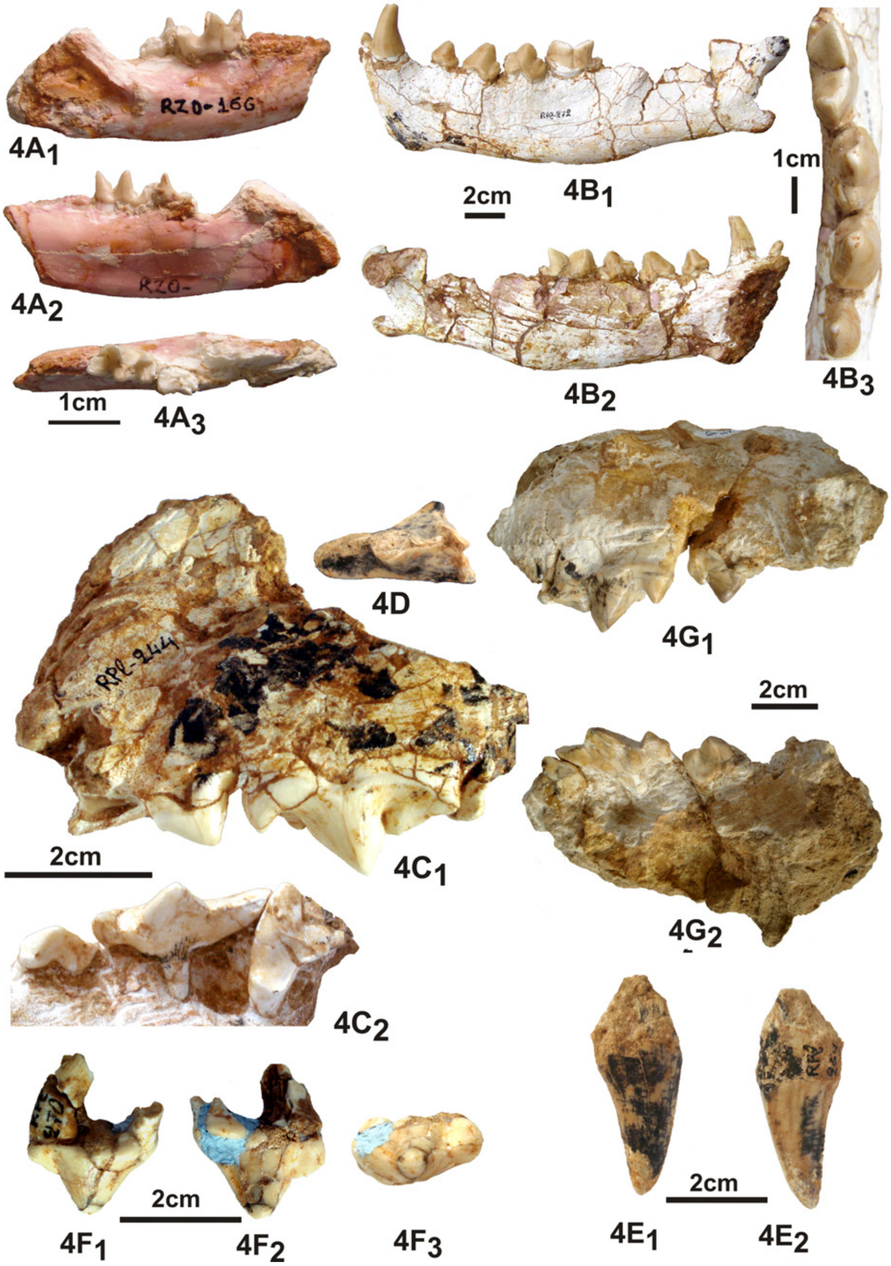

Fig. 4. *Plioviverrops orbignyi*, Ravin des Zouaves 5, RZO, Axios Valley, Macedonia, Greece. **A**. Right mandibular fragment with m1-m2, LGPUT-RZO-166; $\mathbf{A_1}$: buccal, $\mathbf{A_2}$: lingual, and $\mathbf{A_3}$: occlusal view. *Adcrocuta eximia leptoryncha*, Ravin de la Pluie, RPl, Axios Valley, Macedonia, Greece. **B**. Left mandibular fragment with i2, c-m1, LGPUT-RPl-272; $\mathbf{B_1}$: buccal, $\mathbf{B_2}$: lingual, and $\mathbf{B_3}$: occlusal view. **E**. Right upper canine, LGPUT-RPl-269; $\mathbf{E_1}$: buccal, and $\mathbf{E_2}$: lingual view. *A. eximia*, Ravin de la Pluie (RPl), Axios Valley, Macedonia, Greece. **C.** Left maxillary fragment with DP2-DP4, LGPUT-RPl-244; $\mathbf{C_1}$: buccal, and $\mathbf{C_2}$: occlusal view. **D.** Fragment of the left DP3, LGPUT-RPl-271. ?*Hyaenictis* sp., Ravin de la Pluie (RPl), Axios Valley, Macedonia, Greece. **F**. Right P2, LGPUT-RPl-270, $\mathbf{F_1}$: buccal, $\mathbf{F_2}$: lingual, and $\mathbf{F_3}$: occlusal view. *Dinocrocuta* sp., Xirochori 1, XIR, Axios Valley, Macedonia, Greece. **G.** Right maxillary fragment with DP2-DP4, LGPUT-XIR-5; $\mathbf{G_1}$: buccal, and $\mathbf{G_2}$: occlusal view.

Fig. 4. *Plioviverrops orbignyi*, Ravin des Zouaves-5, vallée de l'Axios, Macédoine, Grèce. **A**. Fragment de mandibule avec m1-m2, LGPUT-RZO-166 ; $\mathbf{A_1}$: vue buccale, $\mathbf{A_2}$: vue linguale, et $\mathbf{A_3}$: vue occlusale. *Adcrocuta eximia leptoryncha*, Ravin de la Pluie, RPl, vallée de l'Axios, Macédoine, Grèce. **B**. Fragment de mandibule gauche avec i2, c-m1, LGPUT-RZO-272 ; $\mathbf{B_1}$: vue buccale, $\mathbf{B_2}$: vue linguale, et $\mathbf{B_3}$: vue occlusale. **E**. Canine supérieure droite, LGPUT-RPl-269 ; $\mathbf{E_1}$: vue buccale, et $\mathbf{E_2}$: vue linguale. *A. eximia*, Ravin de la Pluie, RPl, vallée de l'Axios, Macédoine, Grèce. **C.** Fragment de maxillaire gauche avec DP2-DP4, LGPUT-RPl-244 ; $\mathbf{C_1}$: vue buccale, et $\mathbf{C_2}$: vue occlusale. **D**. Fragment de DP3 gauche, LGPUT-RPl-271. ?*Hyaenictis* sp., Ravin de la Pluie, RPl, vallée de l'Axios, Macédoine, Grèce. **F**. P2 droite, LGPUT-RPl-270 ; $\mathbf{F_1}$: vue buccale, $\mathbf{F_2}$: vue linguale, et $\mathbf{F_3}$: vue occlusale. *Dinocrocuta* sp., Xirochori 1, XIR, vallée de l'Axios, Macédoine, Grèce. **G**. Fragment de maxillaire droit avec DP2-DP4, LGPUT-XIR-5 ; $\mathbf{G_1}$: vue buccale, et $\mathbf{G_2}$: vue occlusale.

is projected buccally, and between it and the metacone there is a deep buccal sinus. The DP3 fragment lacks its mesial part with the parastyle, and it is similar to the one described but more worn (Fig. 4D).

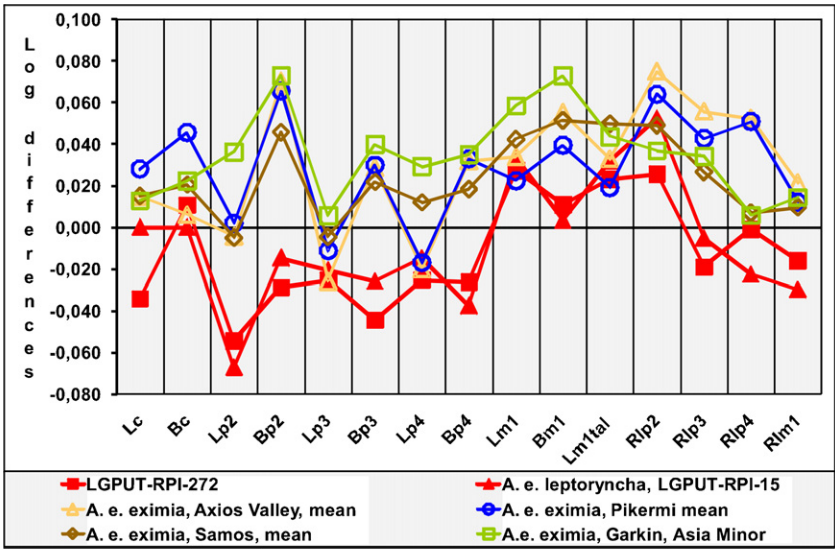

Fig. 5. Logarithmic ratio diagram, comparing the lower teeth dimensions and robusticity index (RI) of *Adcrocuta eximia* from various localities. Standard: *A. eximia*, Pikermi, BSPM-PIK-AS II 105, TYPE.

Fig. 5. Écarts logarithmiques des dimensions et indice de robustesse des dents inférieures d'*Adcrocuta eximia* de divers sites. Standard : *A. eximia*, Pikermi, BSPM-PIK-AS II 105, TYPE.

Discussion: The species *A. eximia* is well known and widespread in the Late Miocene, covering the whole of Eurasia from Spain to China. Although it is a common taxon, the remains of its deciduous dentition are few. The upper deciduous dentition is known by two fragments from Pikermi (Gaudry, 1862–67:pl. 12, Figs. 4 and 5) and another two from Perivolaki (Koufos, 2006b: pl. 4, Fig. 6). Another maxillary fragment is known from the Turkish locality of Akkaşdaği (de Bonis, 2005). Some undescribed material of *A. eximia* with deciduous teeth from Samos is included in Brown's collection at AMNH (Kostopoulos, pers. comm.). The Pikermi specimen MNHN-PIK-3025 preserves the DP3-DP4 and the just erupted M1. The M1 resembles that of *A. eximia* and its size falls within the range of variation for this species (Fig. 6), certifying its assignment to *A. eximia*. The milk teeth studied are similar in morphology and size to those from Pikermi and Perivolaki (Table 1) and can be attributed with certainty to *A. eximia*. A maxillary fragment of *Hyaenictis graeca* with the DP3-DP4 and P4-M1 is known from Pikermi (Gaudry, 1862–67). A direct comparison of the studied material with a cast of *H. graeca* suggests that the general morphology of its deciduous dentition is similar to LGPUT-RPl-244; however, the DP3 protocone is higher and more projected lingually, the metacone of the DP4 is higher and the teeth are slenderer than in *A. eximia* (Table 1). As mentioned above, the RPl *Adcrocuta* belongs to the subspecies *A. e. leptoryncha*. The deciduous teeth studied could belong to this subspecies but it is impossible to confirm this, becasue they have no differences from the Pikermi ones; hence they are referred to as *A. eximia* subsp. indet.

Genus *Hyaenictis* Gaudry, 1861

?*Hyaenictis* sp.

Locality. Ravin de la Pluie (RPl), Axios Valley, Macedonia, Greece (Fig. 1).

Age. Late Vallesian, MN 10; GPTS = ~9.3 Ma.

Material. Right P2, LGPUT-RPl-270.

Measurements. **P2**: 20.3 × (10.8) mm.

Description: The studied tooth is badly preserved, lacking parts of its mesial and lingual base (Fig. $4F_{2,3}$). The distolingual part is also broken postmortem and lacks the cingulum. The mesial cingulum seems to project mesiolingually but the presence of the a.a.c. cannot be checked. The main cusp is relatively low and without inclination. The p.a.c. is large and relatively high, although it is worn. The distal cingulum is not projected but it forms

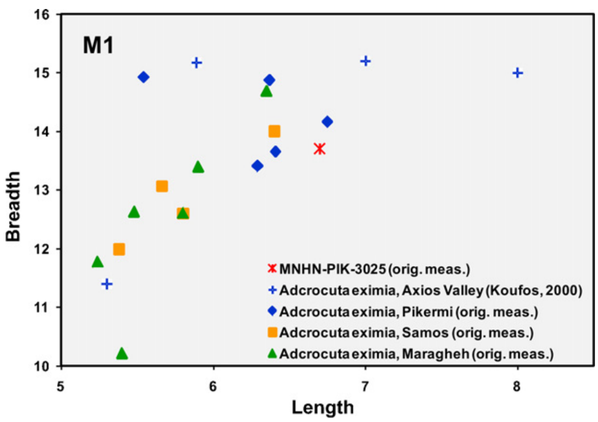

Fig. 6. Bivariate plot comparing the M1 of *Adcrocuta eximia* from various localities.

Fig. 6. Proportions de la M1 d'*Adcrocuta eximia* de divers sites.

Table 1
Measurements of the deciduous teeth of various hyaenids. R.I.: B × 100/length.
Tableau 1
Mesures des dents de lait de divers hyaenidés. R.I : largeur × 100/longeur.

	A. eximia	*Dinocrocuta sp.*	*A. eximia*			*H. graeca*	*D. seny ü reki*	*P. miocenica*	*P. aff. tungurensis*	
	Ravin de la Pluie	Xirochori-1	Pikermi	Perivolaki		Pikermi	Middle Sinap	*Paşalar*	*Çandir*	
	LGPUT-RPI-244	LGPUT-XIR-5	MNHN-PIK-3025	LGPUT-PER-1240		MNHN-PIK-3003	MNHN-TRQ-1053	No 673	No701	No702
			original meas. s	Koufos (2006a,b)		original meas.	original meas.	original meas.		
LDP2	11.0	18.5	–	11.8	11.8	–	15.6	–	–	–
BDP2	5.2	9.9	–	5.8	5.8	–	–	–	–	–
LDP3	25.0	29.4	22.0	22.5	–	24.6	28.9	20.4	–	–
BDP3	12.4	12.7	12.3	11.7	–	9.0	16.5	11.5	–	9.3
LDP4	9.8	[8.7]	8.5	–	–	10.6	–	–	7.8	–
BDP4	16.2	[20.3]	16.3	–	–	–	–	–	17.5	–
R.I.										
DP2	47	54	–	49	49	–	–	–	–	–
DP3	50	43	56	52	–	37	57	56	–	–
DP4	165	233	192	–	–	–	–	–	224	–

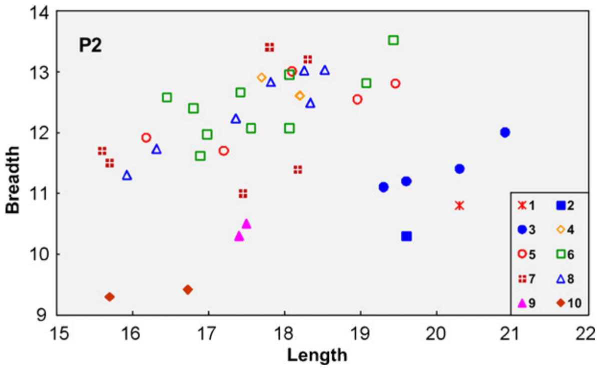

Fig. 7. Bivariate plot comparing the P2 of various Late Miocene large hyaenids. **1**. LGPUT-RPl-270; **2**. *Hyaenictis graeca*, Pikermi, NHMW-PIK-A.4715 (orig. meas.); **3**. *H. graeca*, Pikermi (Roussiakis, pers. comm.); **4**. *Adcrocuta eximia leptoryncha*, RPl-14, TYPE (orig. meas.); **5**. *A. eximia*, Axios Valley (orig. meas.); **6**. *A. eximia*, Pikermi (orig. meas.); **7**. *A. eximia*, Samos (orig. meas.); **8**. *A. eximia*, Maragheh (orig. meas.); **9**. *Chasmaporthetes bonisi*, RZO-125 (orig. meas.); **10**. *Lycyaena chaeretis*, Pikermi+Samos (orig. meas.).
Fig. 7. Proportions de P2 chez divers hyaenidés du Miocène supérieur.

a slight edging in the distolingual part of the tooth. The buccal cingulum is weak.

Discussion: The studied P2 has hyaenid features and must belong to a species of this family. Excluding the smaller ictitheres, several large hyaenids are known from the Late Miocene of Greece. The most common and well-known is *A. eximia*. The P2 of *A. eximia* differs from the one studied in its more robust features, the almost straight mesial and distal border, the higher main cusp, the presence of a large a.a.c., the larger and more mesio-distally compressed p.a.c., and its larger size (Fig. 7).

Chasmaporthetes bonisi is a large hyaenid known from Ravin des Zouaves-5, (RZO) and Dytiko-1 (DTK) of the Axios Valley (Koufos, 2000 and refs. cited). The P2 studied differs from that of *C. bonisi*, in having more slender features, a lower main cusp, a more angular distal border, absence of the distal projection of the distal cingulum, and smaller size (Fig. 7). A large hyaenid named *Lycyaena chaeretis* is known from Pikermi and Samos (Forsyth Major, 1894; Gaudry, 1862–67). The P2 studied is significantly larger than that of *L. chaeretis* (Fig. 7) and differs from it in having a lower main cusp, more slender features, and a less mesio-distally compressed p.a.c. The P3 of *L. chaeretis* is similar in size to LGPUT-RPl-270, but it differs from it in having a more elongated-elliptical occlusal aspect, a slenderer feature, and a stronger p.a.c.

Another large hyaenid known from Pikermi is *H. graeca* (Gaudry, 1862–67). A direct comparison of the studied tooth with a cast of *H. graeca* from the specimen NHMW-PIK-A.4715 indicates some similarities, such as the general aspect of the P2, the strong lingual cingular projection, the large and narrow p.a.c. and the similar size (Fig. 7). The above-mentioned comparisons suggest that LGPUT-RPl-270 is morphologically and metrically closer to *Hyaenictis*. However, the sole known and badly preserved specimen cannot allow certain determination; hence it is referred to ?*Hyaenictis* sp.

Family Percrocutidae Werdelin and Solounias, 1991

Genus *Dinocrocuta* Schmidt-Kittler, 1976

Dinocrocuta sp.

Locality. Xirochori-1 (XIR), Axios Valley, Macedonia, Greece (Fig. 1).

Age. Late Vallesian, MN 10; GPTS = ~9.6 Ma.

Material. Right maxillary fragment with DP2-DP4, LGPUT-XIR-5.

Measurements. See Table 1.

Description: The specimen preserves well the DP2-DP4; the DP4 lacks its lingual half, but its alveolus is distinct, allowing estimation of its breadth (Fig. 4G). The DP2 is relatively short and robust without an a.a.c. but with a strong mesial cingular projection, a large p.a.c. and a strong lingual cingulum in the distal half of the tooth (Fig. $4G_2$). The DP3 is elongated and relatively narrow with a weak protocone restricted to a basal lingual projection (Fig. $4G_2$). The parastyle is moved mesially, forming a large cusp, well separated from the paracone by a deep valley. In the mesio-buccal base of the parastyle there is a strong cingulum. The paracone is high and narrow with a well developed cuspule situated in its mesio-lingual border; the cuspule is connected with the paracone's apex by a slight crest. The metacone is straight, short and low. The preserved part of the DP4 includes its buccal half, which bears a low paracone that is strongly projected bucco-distally, and a very small metacone, situated distally and separated from the paracone's projection by a deep sinus (Fig. $4G_2$).

Discussion: The deciduous dentition studied differs remarkably from that of *A. eximia*. In addition to its larger size (Table 1), there are some morphological differences. The DP2 of LGPUT-XIR-5 has a clear and large mesial cingular projection, which is absent in *A. eximia* (Fig. 4C and G) and it is more robust than the DP2 of *A. eximia*; its robusticity index (R.I. = B × 100/Length is 54 versus 47–49 in *A. eximia* (Table 1). The protocone of the DP3 in LGPUT-XIR-5 is more developed and the metacone relatively shorter than that of *A. eximia*; the index $L_{metacone} \times 100/LDP3$ is 32 in the studied DP3 versus 36 in *A. eximia.* The DP3 of LGPUT-XIR-5 is more robust than that of *A. eximia;* its R.I. is 43 versus 50–56 in *A. eximia* (Table 1). The studied DP4 is remarkably different than that of *A. eximia.* It is shorter and less triangular than in *A. eximia*; the paracone's projection is stronger and the metacone is smaller than in *A. eximia.* A maxillary fragment with DP2-DP3 (MNHN-TRQ-1053) of a large hyaenid from Middle Sinap (Turkey) was described as *Hyaena senyüreki* and later transferred to *Percrocuta* (Howell and Petter, 1985; Ozansoy, 1965; Schmidt-Kittler, 1976). It differs from the specimen studied in having more slender teeth (Table 1), a stronger protocone in the DP3, and a slightly smaller DP2. A fragment of the DP3 and a DP4 of a large hyaenid from Çandir, Turkey are described as *Percrocuta* aff. *tungurensis* (Schmidt-Kittler, 1976: p. 55; Figs. 49 and 50). The stronger protocone of the DP3, the stronger metacone of the DP4 and its smaller size (Table 1) distinguish the Çandir teeth from the ones studied.

The studied deciduous dentition is clearly larger than that of *A. eximia* and different from *D. senyüreki.* Two hyaenas larger than *A. eximia* are known from the Vallesian of the Axios Valley: *D. salonicae,* discovered in an unknown locality near the village of Diavata and *D. gigantea,* found at Pentalophos-1 PNT (Fig. 1), (Koufos, 1995). A direct comparison with these two species is not possible, but the large size of LGPUT-XIR-5 is an indication that it possibly belongs to one of these species. Based on these observations the studied specimen must belong to *Dinocrocuta*, but its specific determination is pending; hence it is referred to *Dinocrocuta* sp.

Family Felidae Fischer de Waldheim, 1817

Genus *Metailurus* Zdansky, 1924

Metailurus parvulus (Hensel, 1862)

Locality. Ravin de la Pluie (RPl), Axios Valley, Macedonia, Greece (Fig. 1).

Age. Late Vallesian, MN 10; GPTS = ~9.3 Ma.

Material. Right maxillary fragment with C-M1, LGPUT-RPl-268; isolated right P4, LGPUT-RPl-267

Measurements. The measurements are given in Table 2.

Description: The dentition of LGPUT-RPl-268 is badly preserved, but the isolated carnassial LGPUT-RPl-267 is better preserved (Fig. 8A and B). The canine is broken in the crown, has lost the enamel layer, and cannot provide accurate measurements. Its root is elongated, flattened bucco-lingually, and relatively strong. Based on its size, the canine is quite strong for the size of the animal. The P3 is broken, lacks its lingual and mesial part, and bears a small and well distinguished p.a.c. The carnassial is elongated and relatively narrow with a strong parastyle in front of the paracone. Along its mesial border there is a small cingu-

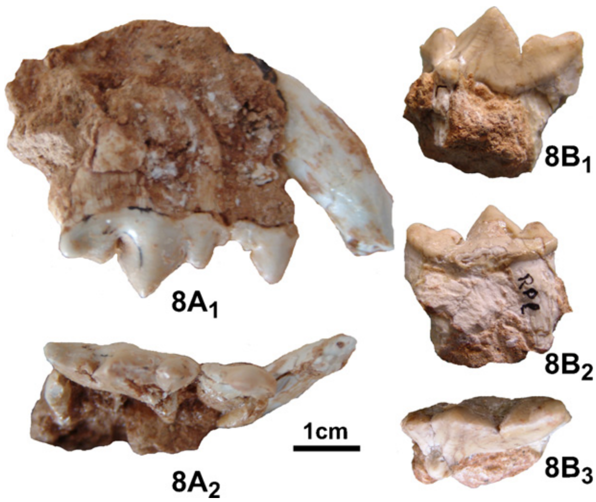

Fig. 8. *Metailurus parvulus*, Ravin de la Pluie (RPl), Axios Valley, Macedonia, Greece. **A**. Right maxillary fragment with C-M1, LGPUT-RPl-268; $\mathbf{A_1}$: buccal, and $\mathbf{A_2}$: occlusal view. **B**. Right M1, LGPUT-RPl-267; $\mathbf{B_1}$: lingual, $\mathbf{B_2}$: buccal, and $\mathbf{B_3}$: occlusal view.

Fig. 8. *Metailurus parvulus,* Ravin de la Pluie, RPl, vallée de l'Axios, Macédoine, Grèce. **A**. Fragment du maxillaire droit avec C-M1, LGPUT-RPl-268 ; $\mathbf{A_1}$: vue buccale, et $\mathbf{A_2}$: vue occlusale. **B**. M1 droite, LGPUT-RPl-267 ; $\mathbf{B_1}$: vue linguale, $\mathbf{B_2}$: vue buccale et $\mathbf{B_3}$: vue occlusale.

Table 2
Measurements of the upper teeth of *Metailurus* from various localities.
Tableau 2
Mesures des dents supérieures de *Metailurus* de divers sites.

	Metailurus parvulus													*Metailurus major*					
UPPER	LGPUT-RPl-268	LGPUT-RPl-267	NHMA-MTLA-234		AMPG-HAL-1967/5	PIUW-PIK-nn					AMPG-CHO-nn		AMPG-HAL-1967/1	AMPG-PIK-PA1257/91		AMPG-PIK-PG95/1532	China	China	
TEETH	Axios Valley		Samos		Halmyropotamos	Pikermi	China				Chomateres		Halmyropotamos			Pikermi		Teilhard and Leroy (1945)	
			Koufos (2009)		Melentis (1967)	Melentis (1967)	Zdansky (1924)				Symeonidis (1978)		Melentis (1967)	Roussiakis (2001)			Zdansky (1924)		
											dex	sin		dex	sin				
LI1					3		3.6				3.5	3.5	3.1				4.7		
BI1					2.5		2.8				2.6	2.5	2				3		
LI2							4.3				4.2	4.2	4.2				5.4		
BI2							3.5				3.2	3.5	3.1				4		
LI3							5.2					5.2	7.1				8.2		
BI3							4.8					4.7	5.5				6.7		
LC	10++					12.9	12.3	11.6		12.3	11	11	19.7	[16.7]		[18.1]	18.7		
BC	5.5++					6.9	7.8	7.7		7.5	7	7	12.4	[10.8]		[10.9]	11.5		
LP1																			
BP1																			
LP2																			
BP2																			
LP3	10.5+		14		13.6	13.5	13.7	13.6	13	12.5	13	13.5	18.2	18.8	19		20.2	17	20
BP3	5+		–		6.6	6.7	6.6	6.7	6.6	6.1	6.5	6.5	10	9.6	9.7		8.9	8.5	10
LP4	21.8	22.4	22.2	21.6	21.7	21.4	24	23	23.4	22.3	21	21.3	29	29.7		28.9	31.2		32
BP4 ant.	9.3	10.1	–	10	10.1	9.5	10.6	9.3	10	10.2	10	10.5	13.5	14.1		14.9	14		16
BP4 post.	7.3	7.3	–	7.1	–	–	–						–						
LM1	3.5				4.1	4.1	4.7	4.8	4.4	4.2	4	4	3.8	5.5	5.5	[4.9]	5.5		
BM1	7.5		7.2		9.1	9.3	10	9.8	10.5	8.3	9.1	9.1	9.1	12.5	12	[12.2]	11.9		

lar projection, like a vestigial ectoparastyle (Fig. 8A_2). The protocone is broken in LGPUT-RPl-268 but it is well preserved in LGPUT-RPl-267 (Fig. 8A_2, B_3). It is a small cusp at the base of the paracone and far behind the mesial border of the parastyle. The metacone is blade-like, relatively low, and curved buccally. It is distinguished from the paracone by a deep buccal valley (Fig. 8A_3). The M1 is reduced, situated vertically to the P4; it has an elliptical occlusal shape and bears a small cusp, situated buccally (Fig. 8A_2).

Discussion: *Metailurus parvulus* is known from several Eurasian localities (NOW, 2011); it was originally described from Pikermi as *Machairodus parvulus* by a mandibular fragment with p3–p4 (Hensel, 1862: p. 568, Fig. 6). Later, it was recognized in Halmyropotamos, Chomateres and Samos (Forsyth Major, 1894; Koufos, 2009; Melentis, 1967; Symeonidis, 1978). In Europe, it is known from the Late Vallesian locality of Montredon and in China from the Early Vallesian locality of Lantian-12 (NOW, 2011).

The two specimens from RPl have a dental morphology similar to that of *M. parvulus* from the various Greek localities. The elongated and narrow P3 with a clear p.a.c., the elongated upper carnassial with a small and low protocone situated well behind the mesial border of the parastyle, the large parastyle with a small mesial cingular projection like ectoparastyle and the very small M1 of the studied material are characteristic of *M. parvulus*. Although the canine of LGPUT-RPl-268 is badly preserved, its measured dimensions are closer to those of *M. parvulus*; the size of the other teeth from RPl is also similar to this species (Table 2). The comparison of the carnassial size indicates that *M. parvulus* is clearly distinguished from *M. major* and both studied specimens are situated in the ranges of variation of the previous species (Fig. 9). Hence, the studied specimens can be attributed with certainty to *Metailurus parvulus*. The studied material is the first evidence for its presence in the Vallesian of Greece and the wider eastern Mediterranean region.

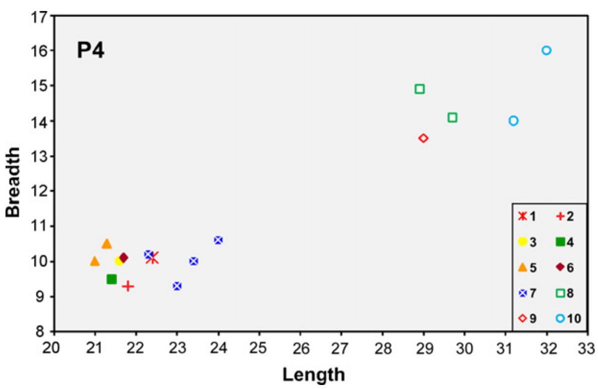

Fig. 9. Bivariate plot comparing the length versus breadth of the upper carnassial of *Metailurus* from various localities. *M. parvulus*: **1**. LGPUT-RPl-267; **2**. LGPUT-RPl-268; **3**. Samos (Koufos, 2009); **4**. Pikermi (Melentis, 1967); **5**. Chomateres, AMPG-CHO-nn (orig. meas.); **6**. Halmyropotamos (Melentis, 1967); **7**. China (Zdansky, 1924); *M. major*: **8**. Pikermi (Roussiakis, 2001); **9**. Halmyropotamos, AMPG-HAL-1967/1 (orig. meas.); **10**. China (Zdansky, 1924).

Fig. 9. Proportions de la carnassière supérieure de *Metailurus* de divers sites.

Genus *Machairodus* Kaup, 1833

Machairodus giganteus (Wagner, 1848)

Locality. Ravin des Zouaves-5 (RZO), Axios Valley, Macedonia, Greece (Fig. 1).

Age. Early Turolian, MN 11; GPTS = ~8.2 Ma.

Material. Right upper canine, LGPUT-RZO-205; left p4, LGPUT-RZO-240; left humerus, LGPUT-RZO-238; left calcaneum, LGPUT-RZO-239.

Measurements. **Cs**: 37.5 × 14.0, H_t = 178.7, H_m = 81.5, H_d = 99.0

p4: 30.2 × 12.7

The measurements of the postcranials are given in Table 3.

Description: The upper canine LGPUT-RZO-205 is almost complete, lacking only the end of its apex (Fig. 10A). It belongs to an adult individual, because its mesial border is quite worn. The canine is strongly curved backwards; its mesial curvature is larger than the distal one (Fig. 10B_5). The canine is also slightly curved buccally. Its lingual surface is flattened and the buccal one is convex. The distal border of the crown is serrated (Fig. 10A_3); the serrations of the mesial border have disappeared because of advanced wear. The root is very strong, wide and thick, corresponding almost to half of the total height. The studied p4 is badly preserved because it is crushed in the middle; its posterior root is also broken lingually (Fig. 10B). The tooth is elongated and narrow with three cuspids. The a.a.c. is strong and it is situated slightly lingually; it is surrounded by a strong buccal and mesial cingulum. The lingual part of the tooth is damaged and the cingulum is broken. The p.a.c. is weaker than the a.a.c. and it is situated on a strong distal cingular projection. The distal cingulum is worn but it seems to be strong and elevated. The roots are very strong and deep (Fig. 10$B_{1,2}$).

The humerus LGPUT-RZO-238 is almost complete, lacking the greater and lesser tubercles in its proximal part and the anterior part of the distal articular surface (Fig. 10C). The head of the humerus is well preserved (Fig. 10$C_{1,2}$), slightly curved and quite large; its mesiodistal diameter is 63.3 mm and the buccolingual 58.3 mm. The deltoid tuberosity is distinct and ends ~160 mm from the head of the humerus. The diaphysis is strongly curved distally; in lateral view, the diaphysis starts to curve at about the end of the deltoid tuberosity (Fig. 10$C_{1,2}$). The transverse diameter of the diaphysis is tear-shaped. The coronoid fossa is wide, shallow and not connected to the olecranon fossa; there is no supratrochlear foramen. The olecranon fossa is deep and oval (Fig. 10C_3); its maximum dimensions are 43.4 × 38.8 mm. The medial epicondyle is strong and strongly projected laterally; above it there is a large supracondylar foramen (Fig. 10C_3). The lateral epicondyle is relatively weak and quite smaller than the medial one.

The calcaneum LGPUT-RZO-239 is well preserved and almost complete; the calcaneal tuberosity is slightly damaged and some parts are broken (Fig. 10D). The articular facet for the cuboid is rounded and its dimensions are 27.9 × 24.5 mm. The anterior talar articular surface is elongated and narrow with a sinus along its anterior bor-

Table 3
Measurements of the humerus and calcaneum of *Machairodus giganteus*. For the measurements of calcaneum see also Fig. 10D.
Tableau 3
Mesures de l'humérus et du calcanéum de *Machairodus giganteus*. Voir aussi Fig. 10D pour les mesures du calcanéum.

HUMERUS	Hmax	DTprox.	DAPprox.	DT dist.	DAP dist.		
LGPUT-RZO-238	370	–	–	110	–	–	–
AMPG-PIK-PG98/6[a]	350	–	–	83.8	59.6	–	–
AMPG-PIK-PA2799/91[a]	–	–	–	79.4	57.4	–	–
AMPG-PIK-PA2799/91[a]	–	–	–	78.7	58.9	–	–
AMPG-PIK-nn[a]	[350]	–	–	90.6	56.2	–	–
MNHN-PIK-3361	375			93.2	58.1		
MNHN-PIK-3358	–			94.0	61.0		

CALCANEUM	Hmax	DT max	DAP max	DT tuber	DAP tuber	DT diaph.	DAP diaph.
RZO-239	110.7	48.2	49.3	(27.0)	–	19	40
NHML-PIK-M.8964	98.5	47.9	47.9	–	–	–	–

[a] Roussiakis (2002).

der; its dimensions are 31.8 × 14.2 mm. The posterior talar articular surface is quite large and elliptical. The calcaneal sulcus is deep and wide, distinguishing well the anterior and posterior talar articular surfaces. The talar shelf is pointed and less projected. The calcaneal tuberosity, although broken, seems to be large with a deep sulcus.

Discussion: Two main large machairodonts are known from the Late Miocene of Europe: *Machairodus aphanistus* from the Vallesian and *M. giganteus* from the Turolian, which are well separated by several characters (de Beaumont, 1975). A third smaller taxon, named *M. alberdiae,* is only reported from Spain (Ginsburg et al., 1981). The upper canine, although it has similar morphology in the two main taxa, is more flattened in *M. giganteus* (Anton et al., 2004). The index L (= bucco-lingual diameter) × 100/B (= mesio-distal diameter) expresses the flattening of the canine (Table 4). Apart from the Charmoile specimen, which has a high index, the rest of the material of *M. aphanistus* group has similar index values to *M. giganteus*. There is great variation in the size of the upper canine in the two species, due to sexual dimorphism (Anton et al., 2004 and refs. cited). The mean size of the canine of the *M. giganteus* group is larger than the canine of *M. aphanistus* group (Fig. 11). The overlap between the two species is great and indicates the above-mentioned sexual dimorphism. The two available upper canines of *M. alberdiae* are close to the minimum values of *M. aphanistus* group and could represent another smaller taxon. The canine of *M. giganteus* group has a stronger curvature than that of the *M. aphanistus* group; both curvature angles of the studied canine are closer to those of the previous group (Fig. 10E). The dimensions of LGPUT-RZO-205 are closer to those of the *M. giganteus* group. They exceed the mean dimensions of *M. aphanistus* group, being near its highest values, and they are closer to the mean values of the *M. giganteus* group (Fig. 11).

The available p4 is directly compared with a cast of a mandibular fragment from the Axios Valley (MNHN-SLQ-936) that was described as *M. aphanistus* and later transferred to *M. giganteus* (Arambourg and Piveteau, 1929; Koufos, 2000). The studied p4 is morphologically similar to that of MNHN-SLQ-936 with three cuspids and well developed distal cingulum; its size is also very close to that of MNHN-SLQ-936 (28.9 × 12.5 mm), confirming their similarity. The studied p4 is compared to a cast of *M. aphanistus* (NHML-EPP-M.49667a) from the type locality of Eppelsheim, (de Beaumont, 1975; Pilgrim, 1931). The main cuspid of the p4 in NHML-EPP-M.49667a is broken but it seems to be high and strong. The a.a.c. is situated slightly lingually, as in the studied one but weaker. Likely the distal morphology of the tooth resem-

Table 4
Flattening index of the upper canine in *Machairodus* (see text). B. Batallones 1.
Tableau 4
Indice d'aplatissement de la canine supérieure chez *Machairodus* (voir texte). B. Batallones 1.

UPPER CANINE	B × 100/L
M. aphanistus group	
B-1523	37
B-4711	41
B-4272	38
B-ss 1	38
B-ss 2	45
B-4151 (1)	45
B-3797	42
B-955	36
B-970	41
B-4963	42
B-1392	38
B-4256	46
B-2268	39
B-ss 3	49
Charmoile (Ginsburg et al., 1981)	53
MNHN-KTD-66 (de Bonis, 1994)	41
MNHN-MRG-3366 (pers. meas.)	41
M. giganteus group	
LGPUT-RZO-205	37
MNHN-SLQ-938 (pers. meas.)	42
MNHN-SLQ-938 (pers. meas.)	40
NHMA-PMMS-69 (Koufos, 2009)	41
NHMW-SAM-1913/23 (pers. meas.)	40
NHMW-SAM-A.4752 (pers. meas.)	41
AMPG-HAL-1967/6 (Melentis, 1967)	41
AMPG-PIK-1967/7 (Melentis, 1967)	39
KTA-B-UEK-124 (Geraads et al., 2004)	44
Hadjidimovo (Kovachev, 2002)	44
M. palanderi (Zdansky, 1924)	37
M. palanderi (Zdansky, 1924)	41
M. alberdiae	
LVF-1 (Ginsburg et al., 1981)	45
I.G.M.E. (Ginsburg et al., 1981)	54

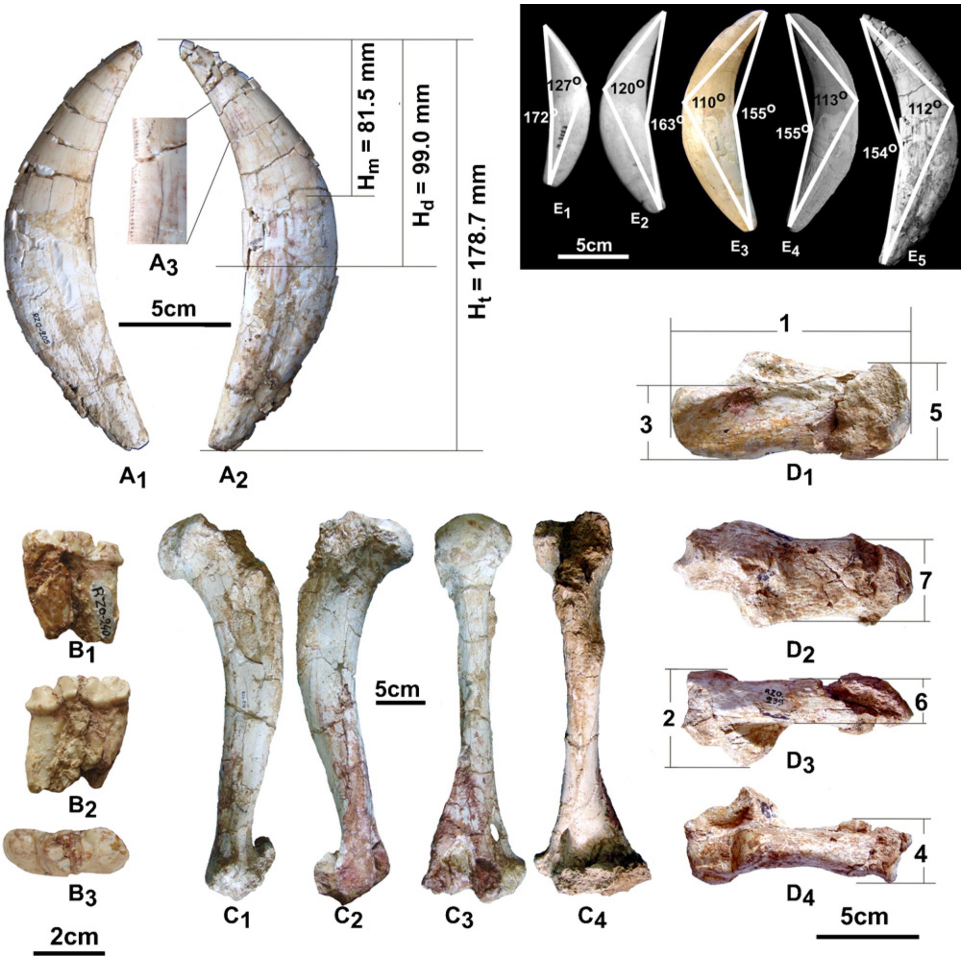

Fig. 10. *Machairodus giganteus*, Ravin des Zouaves-5 (RZO), Axios Valley, Macedonia, Greece. **A**. Right upper canine, LGPUT-RZO-205; $\mathbf{A_1}$: buccal, $\mathbf{A_2}$: lingual view, and $\mathbf{A_3}$: part of the distal border. **B**. Left p4, LGPUT-RZO-240; $\mathbf{B_1}$: buccal, $\mathbf{B_2}$: lingual, and $\mathbf{B_3}$: occlusal view; **C**. Left humerus, LGPUT-RZO-238; $\mathbf{C_1}$: medial, $\mathbf{C_2}$: lateral, $\mathbf{C_3}$: posterior, and $\mathbf{C_4}$: anterior view. **D**. Left calcaneum, LGPUT-RZO-239, $\mathbf{D_1}$: proximal, $\mathbf{D_2}$: distal, $\mathbf{D_3}$: medial, and $\mathbf{D_4}$: lateral view. 1. H_{max}, 2. DT_{max}, 3. DAP_{max}, 4. DT_{tuber}, 5. DAP_{tuber}, 6. DT_{diaph}., 7. $DAP_{diaph.}$ For the calcaneum measurements see also Fig. 10D. **E.** Curvature angle of the upper canine in *Machairodus aphanistus* and *M. giganteus*. $\mathbf{E_1}$-$\mathbf{E_2}$. *M. aphanistus*, Batallones 1, B-3553, 3797 (re-figured from Anton et al., 2004: Fig. 7); $\mathbf{E_3}$–$\mathbf{E_4}$: *M. giganteus*, Samos, loc. unknown, NHMW-SAM-1923/23, A.4752; $\mathbf{E_5}$. *M. giganteus*, LGPUT-RZO-205.

Fig. 10. *Machairodus giganteus*, Ravin des Zouaves-5 (RZO), vallée de l'Axios, Macédoine, Grèce. **A.** Canine supérieure droite, LGPUT-RZO-205 ; $\mathbf{A_1}$: vue buccale, $\mathbf{A_2}$: vue linguale, et $\mathbf{A_3}$: partie distale. **B.** p4 gauche, LGPUT-RZO-240 ; $\mathbf{B_1}$: vue buccale, $\mathbf{B_2}$: vue linguale, et $\mathbf{B_3}$: vue occlusale. **C.** Humérus gauche, LGPUT-RZO-238 ; $\mathbf{C_1}$: vue médiale, $\mathbf{C_2}$: vue latérale, $\mathbf{C_3}$: vue postérieure, et $\mathbf{C_4}$: vue antérieure. **D.** Calcanéum gauche, LGPUT-RZO-239 ; $\mathbf{D_1}$: vue proximale, $\mathbf{D_2}$: vue distale, $\mathbf{D_3}$: vue médiale, et $\mathbf{D_4}$: vue latérale. 1. H_{max}, 2. DT_{max}, 3. DAP_{max}, 4. DT_{tuber}, 5. DAP_{tuber}, 6. DT_{diaph}., 7. $DAP_{diaph.}$ Pour les mesures du calcanéum voir Fig. 10D. **E.** Angle de courbure de la canine supérieure de *M. aphanistus* et *M. giganteus*. $\mathbf{E_1}$–$\mathbf{E_2}$: *M. aphanistus*, Batallones 1, B-3553, 3797 (d'après Anton et al., 2004 : Fig. 7) ; $\mathbf{E_3}$–$\mathbf{E_4}$: *M. giganteus*, Samos, localité inconnue, NHMW-SAM-1923/23, A.4752 ; $\mathbf{E_5}$: *M. giganteus*, LGPUT-RZO-205.

bles that of LGPUT-RZO-240, but the p.a.c. is also weaker. The cingulum is strongly developed in both specimens. Pilgrim (1931) noted that the p4 has two p.a.c. He possibly considered the strong elevation of the distal cingulum as the second cuspid.

The known postcranial remains of *Machairodus* are rare and the comparisons limited. In the description of the Pikermi material (Gaudry, 1862–67) referred four humerus remains. He noted that they are large and the transverse diameter of the proximal articular facet is 87 mm, whereas the distal one is 90 mm. I found in the MNHN a complete humerus and a distal part of one from Pikermi. Their size and general shape are similar to those of LGPUT-RZO-238 (Table 3). Some remains of humeri from Pikermi are also described as belonging to *M. giganteus* (Roussiakis, 2002); the available dimensions of the distal part of humerus seem to be slightly smaller (Table 3). Some hind bones from Pikermi, described as "*Epimachairodus*"?*taracliensis*, possibly belong to *M. giganteus* (Pilgrim, 1931; Roussiakis, 2002). Among them there is a calcaneum, whose dimensions are similar to those of LGPUT-RZO-239 (Table 3). Based on these similarities the studied postcranials from RZO could belong to *M. giganteus*.

M. giganteus is rare in the Axios Valley localities. It is recorded by a fragmentary skull and a mandibular fragment from Ravin-X (R-X), (Arambourg and Piveteau, 1929; Koufos, 2000). A single metapodial in the MNHN collec-

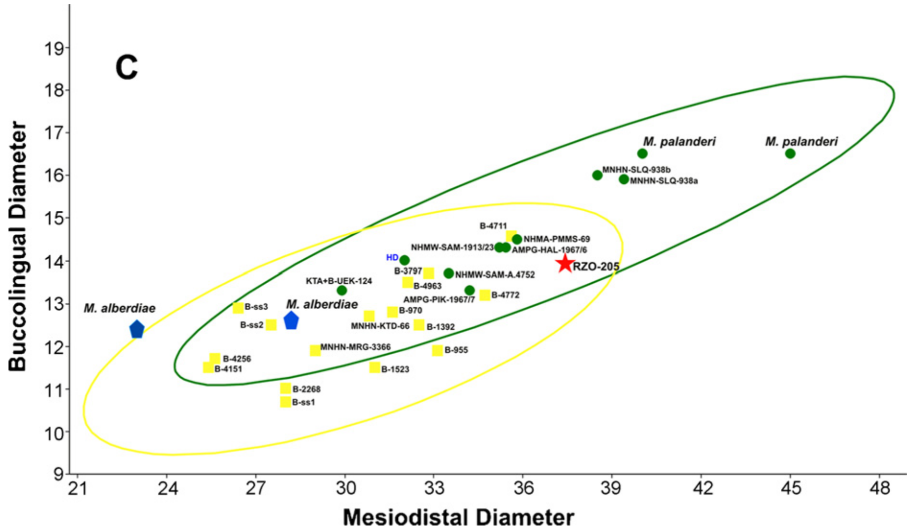

Fig. 11. Bivariate plot comparing the upper canine of *Machairodus* from various localities. ***M. aphanistus* group**: **B**: Batallones 1 (the measurements are provided by M. J. Salesa and J. Morales); **KTD**: Kemiklitepe- D (de Bonis, 1994), **MRG**: Maragheh (orig. meas.).***M. giganteus* group**: **PIK**: Pikermi (Melentis, 1967), **HAL**: Halmyropotamos (Melentis, 1967), **KTA+B**: KemiklitepeA+B (Geraads et al., 2004), **SLQ**: Thessaloniki, old Arambourg collection (Koufos, 2000), **SAM**: old collection from Samos in NHMW (orig. meas.), **HD**: Hadjidimovo (Kovachev, 2002), **PMMS**: Samos in NHMA (Koufos, 2009), *M. alberdiae* (Ginsburg et al., 1981), *M. palanderi* (Zdansky, 1924).

Fig. 11. Proportions de la canine supérieure de *Machairodus* de divers sites.

tion is similar in size to this species; it is without locality indication but the type of fossilization resembles that of the Vathylakkos localities. The specimen from RZO is the only one found during our excavations in the Axios Valley since 1973. The species is also known from Samos (Forsyth Major, 1894; Koufos, 2009). Personal observations in the old Samos collections, housed in NHML, NHMW and BSPM showed the presence of the species in the NHMW collection by a maxillary fragment and two upper canines. All are without locality indications and thus impossible to correlate them with the local stratigraphy. The species is also mentioned from the localities of Halmyropotamos and Kerassia, Evia Island (Melentis, 1967; Roussiakis et al., 2006). All these Greek localities are dated from early to middle Turolian, MN 11-MN 12, (Koufos, 2006a). The genus *Machairodus* has a wide distribution, covering the whole of Eurasia from Spain to China (NOW, 2011) and thus it is a useful biostratigraphic marker.

3. Discussion and conclusion

As mentioned above, several articles have been published on the Axios Valley carnivores, describing the material found in the area since 1972. Recently a revision of the old and new material of the Axios Valley carnivores was given by Koufos (2000). In spite of forty years of field work and the great quantity of the collected fossils, the carnivore remains are few compared to other mammal groups. In this respect the Late Miocene fauna of the Axios Valley differs from those of Pikermi and Samos, which are comparatively rich in carnivore taxa (Koufos, 2006a). Although relatively poor, the carnivore fauna of the Axios Valley contains several taxa unknown from Pikermi and Samos, enlarging our knowledge of the Late Miocene carnivores of Greece. The studied carnivores, as noted in the introduction, originate from three different localities of the Axios Valley.

The Late Vallesian (MN 10) locality of XIR includes a poor mammal fauna. Two carnivore taxa, *A. eximia* and *Protictitherium crassum*, have been described earlier (Koufos, 2000). The new material indicates the additional presence of a giant hyaena belonging to *Dinocrocuta* after those of Pentalophos 1 and Diavata (Koufos, 1995, 2000). Although the age of XIR is clear (Late Vallesian, MN 10; ~9.6 Ma), the age of the other two localities is questionable. The PNT fauna is quite peculiar, including some taxa different from those of XIR and RPl and indicating a possible older age than them; for this reason an Early Vallesian (MN 9) age is quite possible for PNT (Koufos, 2006a, in press). The exact site of Diavata is unknown; except *D. salonicae*, the Diavata fauna includes some hipparion remains belonging to a form similar to the Vallesian/Early Turolian ones of the Axios Valley (Koufos, 1985). All these indicate that the dinocrocutas are certainly present in the Vallesian of Greece. However, they are absent from the Turolian faunas of the Axios Valley, as well as from the other Turolian faunas of Greece.

The available carnivore faunas from the three referred localities are quite poor (Fig. 13). Despite this, I have tried to make their guild structure diagrams and check whether there are indications for the palaeoenvironment similar to those provided by previously published results. The XIR carnivore fauna is poor, but its guild structure diagram (Fig. 12A) provides some information on the palaeoenvironment. *Dinocrocuta* is included in this diagram as a genus; its body mass and diet are considered similar to those of *D. salonicae* and *D. gigantea*, the two possible species

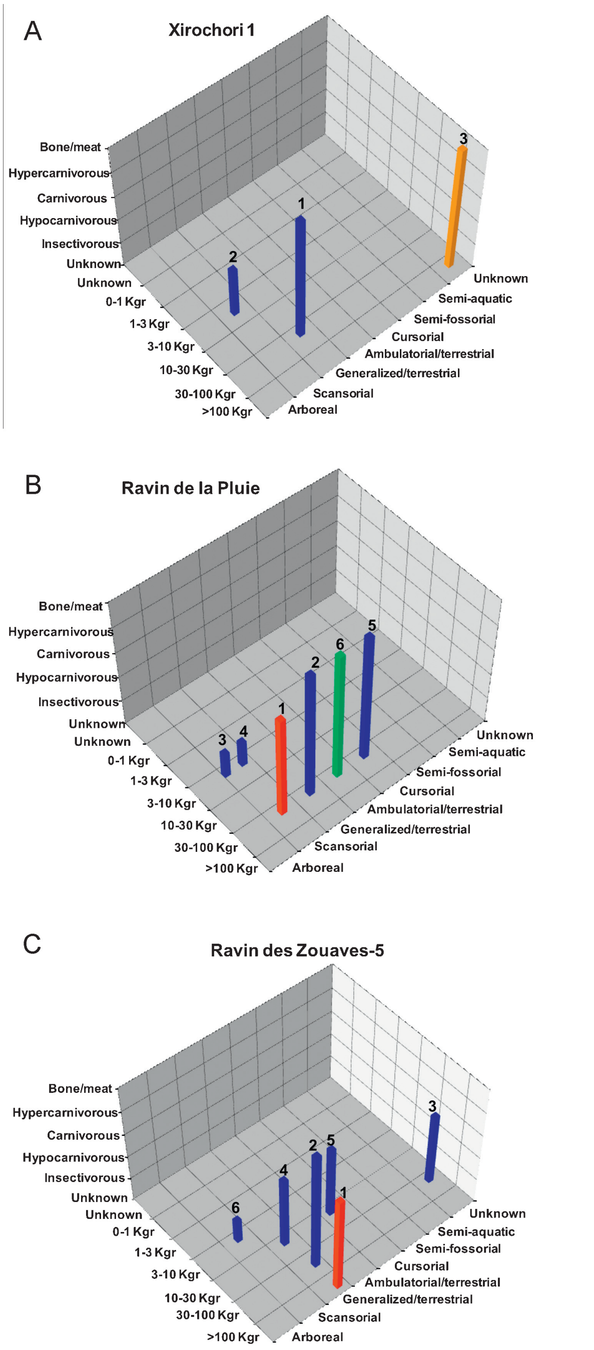

Fig. 12. Carnivore guild structure of the Axios Valley mammal localities of Xirochori 1 (XIR), Ravin de la Pluie (RPl) and Ravin des Zouaves 5 (RZO). The taxon numbers are given in Tab. 5. **green**: Mustelidae, **blue**: Hyaenidae, **orange**: Percrocutidae, **red**: Felidae.

Fig. 12. Structure des guildes des carnivores des sites de la vallée de l'Axios, Xirochori 1 (XIR), Ravin de la Pluie (RPl) et Ravin des Zouaves 5 (RZO). Abréviations numériques selon Fig. 13. **vert** : Mustelidae, **bleu** : Hyaenidae, **orange** : Percrocutidae, **rouge** : Felidae.

to which the XIR specimen may belong. The XIR hyaenas belong to the large ones (30 ≥ 100 kg) and they are bone/meat eaters with a terrestrial way of life. Such forms characterize open modern faunas, like Serengeti (Morlo et al., 2010), as well as open fossil ones, like Samos, Pikermi (Nagel and Koufos, 2009). On the other hand the presence of *Protictitherium crassum*, a scansorial, insectivorous and small (3–10 kg) carnivore, is an indication for the presence of some higher vegetation (bushes, shrubs, small trees).

The earlier known carnivores from RPl were few, including *A. e. leptoryncha*, *Protictitherium* aff. *gaillardi* and *Protictitherium* aff. *intermedium* (Koufos, 2000). The study of the new material added three new taxa: *E. wimani*, ?*Hyaenictis* sp. and *Metailurus parvulus*. The felid *M. parvulus* is well documented in RPl and it is new for the Axios Valley fauna. Although it is well known in the Turolian faunas of Greece (Pikermi, Samos, Kerassia, Halmyropotamos), its presence in RPl is the first one in the Vallesian of Greece and southeastern Europe. The large mustelid *E. wimani* is rare in Eurasia and the single tooth found in RPl is the first evidence of its presence in the Balkan Peninsula. The third taxon found in RPl is ?*Hyaenictis*, represented by an isolated tooth very similar to *H. graeca* from Pikermi. This is the first indication of the possible presence of the genus in the Axios Valley and in the Vallesian of Greece and Eastern Mediterranean. The RPl carnivore fauna is richer than XIR one and its guild structure diagram is more representative (Fig. 12B). The RPl ?*Hyaenictis* is given in the diagram, using the characters of *H. graeca* from Pikermi (Fig. 13). The presence of large, terrestrial-cursorial, meat/bone-hypercarnivorous elements and the abundance of hyaenids are indications of an open environment. On the other hand, the two scansorial, insectivorous and small ictitheres suggest the presence of small trees, shrubs and bushes (Morlo et al., 2010; Nagel and Koufos, 2009). A recent analysis of the Vallesian carnivores in the eastern Mediterranean suggests an open environment, similar to a modern open savannah with small trees and bushes, confirming the indications from the XIR and RPl guild structure diagrams. These indications also fit well with previous results for the Vallesian environment of the eastern Mediterranean and more precisely for the RPl suggested environment (Koufos and Konidaris, 2011 and refs. cited).

The new collection from RZO does not include any new carnivore taxon, but it offers several new pieces of evidence for the presence of *Machairodus*. The RZO carnivore fauna includes six species (Fig. 13) and its guild structure diagram is quite representative (Fig. 12C). The dominance of the hyaenids is clear in the diagram; five of the six taxa are hyaenids, and there is also a large-sized felid (Fig. 12C). The locomotor character of the carnivores, mainly terrestrial and cursorial, indicates an open environment, such as the modern Serengeti ones and the fossil ones of Pikermi and Samos. The carnivorous-meat/bone-hypercarnivorous diet is another indication of an open environment, whereas the small, insectivorous and scansorial *Plioviverrops orbignyi* is an indication of the presence of some small trees and bushes (Morlo et al., 2010). The RZO carnivore guild structure diagram is closer to that of Samos and Pikermi (Nagel and Koufos, 2009), as well as to the Turolian one of the

XIR	FAMILY	SPECIES	BODY MASS	LOCOMOTOR CLASS	DIET CLASS
	Hyaenidae	1. *Adcrocuta eximia*	30-100 kg	generalized terrestrial	meat/bone
	Hyaenidae	2. *Protictitherium crassum*	3-10 kg	scansorial	insectivorous
	Percrocutidae	3. *Dinocrocuta* sp.	> 100 kg	unknown	meat/bone

RPI	FAMILY	SPECIES	BODY MASS	LOCOMOTOR CLASS	DIET CLASS
	Felidae	1. *Metailurus parvulus*	30-100 kg	scansorial	hypercarnivorous
	Hyaenidae	2. *Adcrocuta eximia*	30-100 kg	generalized terrestrial	meat/bone
	Hyaenidae	3. *Protictitherium* aff. *gaillardi*	3-10 kg	scansorial	insectivorous
	Hyaenidae	4. *Protictitherium* aff. *intermedium*	3-10 kg	scansorial	insectivorous
	Hyaenidae	5. *Hyaenictis* sp.	30-100 kg	cursorial	meat/bone
	Mustelidae	6. *Eomellivora wimani*	30-100 kg	terrestrial	meat/bone

RZO	FAMILY	SPECIES	BODY MASS	LOCOMOTOR CLASS	DIET CLASS
	Felidae	1. *Machairodus giganteus*	> 100 kg	generalized terrestrial	hypercarnivorous
	Hyaenidae	2. *Adcrocuta eximia*	30-100 kg	generalized terrestrial	meat/bone
	Hyaenidae	3. *Chasmaporthetes bonisi*	30-100 kg	unknown	carnivorous
	Hyaenidae	4. *Hyaenictitherium wongii*	10-30 kg	generalized terrestrial	carnivorous
	Hyaenidae	5. *Ictitherium viverrinum*	10-30 kg	cursorial	carnivorous
	Hyaenidae	6. *Plioviverrops orbignyi*	3-10 kg	scansorial	insectivorous

Mustelidae
Hyaenidae
Percrocutidae
Felidae

Fig. 13. List of carnivore taxa found in each locality with their ecomorphological parameters. green: Mustelidae, blue: Hyaenidae, orange: Percrocutidae, red: Felidae.

Fig. 13. Liste des taxons de carnivores par localité avec leurs paramètres écomorphologiques ; vert : Mustelidae ; bleu : Hyaenidae ; orange : Percrocutidae ; rouge : Felidae.

Greco-Iranian Province (Koufos and Konidaris, 2011). All indications provided by the RZO carnivore guild structure diagram fit well with the previous results for the RZO and the Turolian eastern Mediterranean palaeoenvironment (Koufos and Konidaris, 2011 and ref. cited).

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