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Carnivora from the Late Miocene of Kerassiá (Northern Euboea, Greece)

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Excavations carried out in recent years in Kerassiá brought to light many fossiliferous sites. In this study, the carnivores from the three richest sites, Kerassiá 1 (K1), Kerassiá 3 (K3) and Kerassiá 4 (K4), are discussed. K1 includes *Metailurus* cf. *parvulus* and possibly *Adcrocuta eximia*; K3 includes *Plioviverrops* sp. and cf. *Ictitherium pannonicum*; and K4 includes *Adcrocuta eximia* and *Machairodus giganteus*. The carnivores as well as the other faunal remains from these localities indicate an early to middle Turolian age.

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INTRODUCTION

The existence of Miocene fossil vertebrates in Euboea has been known since 1878 (Cordella 1878). Further information is provided in Woodward (1901), Déprat (1904), Mitzopoulos (1947), Melentis (1968, 1969), Jacobi (1982), and others. These authors present information on the Limni, Hagia Anna, Rhovies, Achladi, Eria, Prokopi, Palaeovrissi and Halmyropotamos localities. The presence of fossils in Kerassiá has been known to local people since 1966, when fossil bones were found during the construction of a road close to the village. In 1981, Köhler tracked down the fossil bones of Kerassiá during geological fieldwork in the area. The first excavations in Kerassiá were carried out in 1982 by Hans de Bruijn and Albert van der Meulen (University of Utrecht) and Constantin Doukas (University of Athens). The excavations were not resumed until 1992, when the University of Athens (Department of Historical Geology and Palaeontology) started systematic excavations in the area. These excavations, financed by the University of Athens, the Municipality of Nileas and the General Secretary of Research and Technology (Project 95 ∑YN107) brought to light more than seven fossiliferous sites. The fauna of Kerassiá has been described until now by Köhler (1983), Van der Made & Moyà-Solà (1989), Theodorou *et al.* (1995, 1998, this volume) and Kostopoulos *et al.* (2001). Köhler (1983) mentions the presence of *Microstonyx* sp., Bovidae, Giraffidae, two Hipparion species, two species of Proboscidea and a large carnivore. Van der Made & Moyà-Solà (1989) briefly describe the suids and attribute these to *Microstonyx major erymanthius*. Moreover, they mention the presence of *Deinotherium* and *Dorcatherium* and give a middle Turolian age for Kerassiá. According to Kostopoulos *et al.* (2001), the Kerassiá *Microstonyx major* is smaller than the Pikermi *M. major erymanthius* and probably represents a new subspecies.

The carnivores of Kerassiá are represented from a small number of specimens, and the material is not always in a good state of preservation. In the present study, we discuss the carnivores of the three richest sites, the sites Kerassiá 1 (K1), Kerassiá 3 (K3) and Kerassiá 4 (K4). The material of this study comes from the excavations carried out from 1992 onwards and is temporarily stored in the Athens Museum of Palaeontology and Geology. In the future, this material will be exhibited in a new museum in Kerassiá that is planned by the local prefecture.

Methodology and abbreviations

The methodology used for the dental measurements follows Werdelin (1988a). A value inside parenthesis signifies an approximate measurement, "a" signifies a measurement taken at the alveolus and "r" signifies a measurement taken at the root. The methodology used for the postcranial material is given with each table of measurements. AMPG: Athens Museum of Palaeontology and Geology. MNHNP: Muséum National d'Histoire Naturelle, Paris. BMNH: The Natural History Museum, London.

SYSTEMATICS

Family: Hyaenidae GRAY, 1869
Subfamily: Ictitheriinae TROUESSART, 1897
Genus: Plioviverrops KRETZOI, 1938
Plioviverrops sp.
Locality: Kerassiá 3 (K3)

Material

K3/B1/4: left humerus, lacking the proximalmost end. K3/B1/15: distal epiphysis of a right femur, juvenile. K3/B1/18: distal epiphysis of a left femur, juvenile. K3.192: right calcaneum, damaged on its sustentaculum tali. K3.206: proximal epiphysis of a left humerus, juvenile. K3.161: left Mt IV. K3.195: right Mt IV. Of the specimens listed above, those with the indication B1 come from the same ossiferous block and most probably from the same individual.

Description and comparisons

From Tables 1-3 it is clear that the available postcranial material is similar in its dimensions to that of *Plioviverrops orbignyi* (GAUDRY & LARTET, 1856) from Pikermi, mentioned by Gaudry (1862, pl. 11, figs. 6, 10) and Pilgrim (1931). The available fourth metatarsals are only slightly larger than the specimen mentioned by Pilgrim (1931). In their morphological characters, the present specimens also show great resemblance to *P. orbignyi*. The distal articular surface of the calcaneum is flat and narrow as in *P. orbignyi* (Pilgrim 1931). The cuboid facet of the Mt IV is not extended posteriorly more than the tuberosity for the ligament of the peroneus longus, something also observed in *P. orbignyi* (Pilgrim 1931). The humerus is similar to that of *P. orbignyi* from Pikermi, except in its smaller supratrochlear foramen. Otherwise, the humerus has an entepicondylar foramen accompanied by a strong bar, as in *P. orbignyi*.

Except for *P. orbignyi*, the postcranial material of the Miocene small carnivores is poorly known. "*Progenetta crassa*" (=*Protictitherium crassum*) from the Can Llobateres II in Spain (Crusafont-Pairó & Petter 1969, fig. 5, pl. 3, fig. 7) is significantly larger from the Kerassiá 3 material. *Promeles palaeatticus* (WEITHOFER, 1888) has a smaller calcaneum and metatarsals (Pilgrim 1931; Roussiakis 1996), and its fourth metatarsal is shorter relative to the calcaneum. The ratio height calcaneum/length Mt IV is 58.3 in *P. palaeatticus* (data from Roussiakis 1996) but 51.7-52.7 in the Kerassiá *Plioviverrops*. Moreover, in *P. palaeatticus* the cuboid facet of the calcaneum is concave and oval, with its greater diameter obliquely oriented. In the *Plioviverrops* sp. of Kerassiá the cuboid facet is almost flat and anteroposteriorly elongated, as in *P. orbignyi*.

The available postcranial material thus shows dimensions similar to *P. orbignyi* from

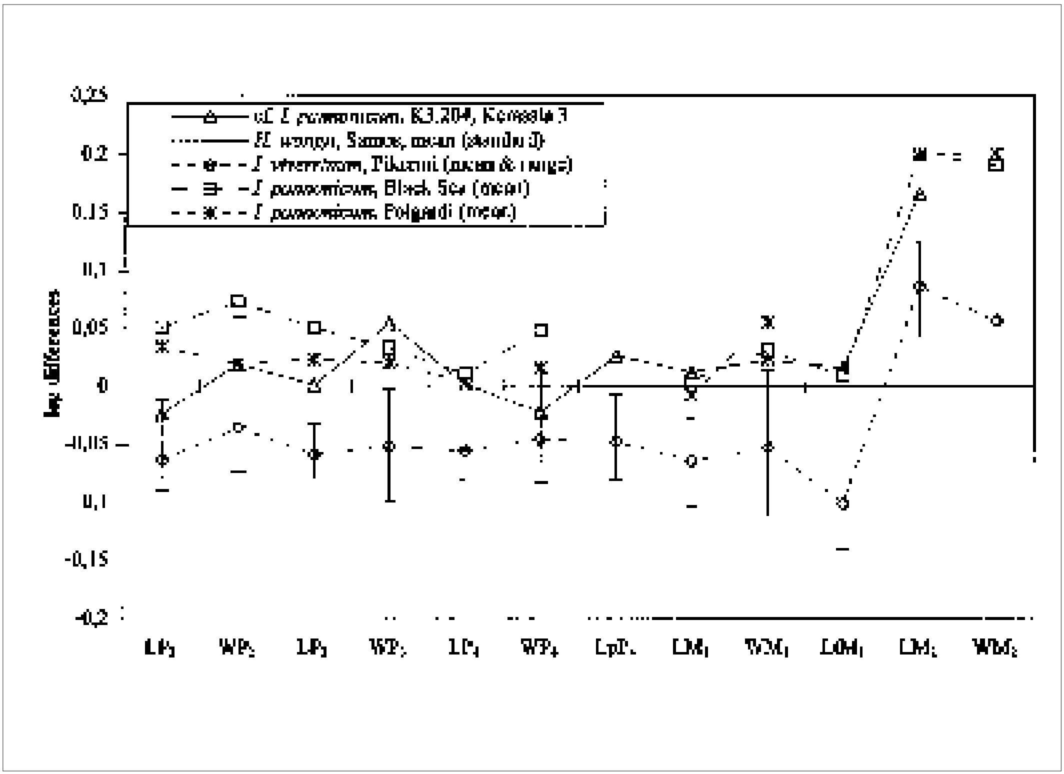

Figure 1 Logarithmic ratio diagram comparing the Kerassia 3 ictithere with various species of icitheres. *H. wongii* from Samos according to Werdelin (1988a), *I. viverrinum* from Pikermi according to Werdelin (1988b), *I. pannonicum* from Polgardi and the Black Sea from Table 4.

Pikermi. In most of their morphological characters, the Kerassiá specimens also agree with *P. orbignyi*. Nevertheless, at the present time we prefer to refer the specimens considered here to *Plioviverrops* sp., since the lack of more material, especially teeth, does not permit us a more precise determination.

The genus *Plioviverrops* is considered to be the oldest known hyaenid, appearing first in MN2a of Laugnac in France, with the species *Plioviverrops collectus* (De Bonis, 1973) (Ginsburg 1999). Various other species of *Plioviverrops* are known, such as *Plioviverrops gervaisi* De Beaumont & Mein, 1972, from MN7/8 of La Grive (France), *Plioviverrops guerini* (Villalta & Crusafont, 1948) from MN11 of Piera and Viverro de Pinos and MN12 of Cerro de la Garita and Los Mansuetos in Spain (Ginsburg 1999), and *Plioviverrops faventinus* Torre, 1989 from the late Turolian (MN13) of Brisighella in Italy and MN14 of La Gloria 4 in Spain (Alcalá 1994). *P. orbignyi*, which shows resemblance to our findings, is reported from the early-middle Turolian (MN11/12) of Ravin des Zouaves 5, Vathylakkos 2, 3, Prochoma 1 and Perivolaki (De Bonis & Koufos 1991, Koufos *et al.* 1999, Koufos 2000), and from the middle Turolian (MN12) of Pikermi and Samos (Major 1888, Major 1894, De Beaumont 1969, Bernor *et al.* 1996) in Greece. It is interesting to notice that in Vathylakkos 3, *P. orbignyi* seems to have coexisted with another form, listed as *P.* cf. *guerini* by De Bonis & Koufos (1991) and Koufos (2000).

Genus: *Ictitherium* Roth & Wagner, 1854
cf. *Ictitherium pannonicum* Kretzoi, 1952
Locality: Kerassiá 3 (K3)

Material

K3/204: right mandibular ramus with ci, p3, p4 and m1. The alveoli of p1, p2 and m2 are visible.

Description

The available mandible is badly damaged and some of its characters cannot be evaluated precisely. The mandibular corpus has a mental foramen below the middle of the alveolus for p2. The lower border of the mandibular corpus slopes down from the symphysis to a point under m1. The depth of the mandible thus increases from the anterior to the posterior part and the depth in front of p2 is smaller than that behind m1 (Table 4). The total length of the symphysis measures about 40 mm and its posterior border lies under the middle of the alveolus for p2. The alveolus for p1 is separated from the canine by a diastema of 9.9 mm. The p3 has a posterior accessory cusp and most probably a smaller anterior one. The p4 is more elongated than p3 (Table 4) and has a robust anterior accessory cusp. The posterior part of p4 is not very well preserved but almost certainly had an accessory cusp. The most important character of m1 is the presence of a strong metaconid. The protoconid and paraconid are almost equal in height. The talonid of m1 is large and wide, but very worn and its morphological details are not visible. The only preserved cusp is the entoconid, which is high. The m2 is not preserved, but judging from its elongated alveolus it was large.

Comparisons

The group of the ‘ictitheres’ contains many species and genera that share numerous characters and sometimes have slight differences that make their identification difficult. In this study, we follow the revision of Werdelin & Solounias (1991). The various species of the ‘ictitheres’ have been referred mainly to the genera *Ictitherium* Wagner, 1848, *Thalassictis* Gervais ex Nordmann, 1850, *Hyaenictitherium* Kretzoi, 1938, *Palinhyaena* Qiu, Huang & Guo, 1979, and *Hyaenotherium* Semenov, 1989.

Ictitherium viverrinum Roth & Wagner, 1854 is a well-known species with a wide geographical range. Compared to *I. viverrinum* from Pikermi, K3.204 has clearly larger p3, m1 and m2 (Fig. 1). *Thalassictis robusta* Gervais ex Nordmann, 1850, from Kishinev, is also smaller than the Kerassiá ictithere (Fig. 2). *Hyaenictitherium hyaenoides* (Zdansky, 1924) has larger teeth than the Kerassiá specimen and a small m2 (Fig. 3). Moreover, the mandible of that species has a more "hyaenoid" appearance. It is robust, straight, and with a lower border that is almost parallel to the alveolar border (Qiu 1985). The mandibular corpus of K3.204, on the other hand, is deeper in its posterior part (Table 4). *Palinhyaena reperta* Qiu, Huang & Guo, 1979, is known from Chinese localities only (Werdelin & Solounias 1991). This species is also larger than the Kerassiá 3 ictithere, but with a smaller m2 (Fig. 3). The mandible of *P. reperta* is similar to that of *H. hyaenoides*, i.e., ‘hyaenoid’ in appearance.

The lower premolars of K3.204 are slightly more robust than those of *Hyaenotherium wongii* (Zdansky, 1924) from Samos (Fig. 3). This is especially true for p3, while p4 is badly damaged and its width is only approximately given (Table 4). The most important difference concerns m2. This tooth is not preserved in the Kerassiá specimen, but judging from its elongated alveolus that measures about 8.9 mm, it was especially large (Table 4, Fig. 3). Such a character differentiates our specimen from *H. wongii* and makes it more similar to *Ictitherium pannonicum* Kretzoi, 1952, a species that was first described from Polgardi in Hungary, but it was actually ignored until Semenov (1985, 1989) restudied these specimens and attributed some more specimens from the Black Sea area to it. Werdelin & Solounias (1991), however, note that we cannot be certain if the Black Sea specimens belong to the same species as the Polgardi specimens. *I. pannonicum* is slightly larger overall than *H. wongii*, but in some of its dimensions is within the range of *H. won-*

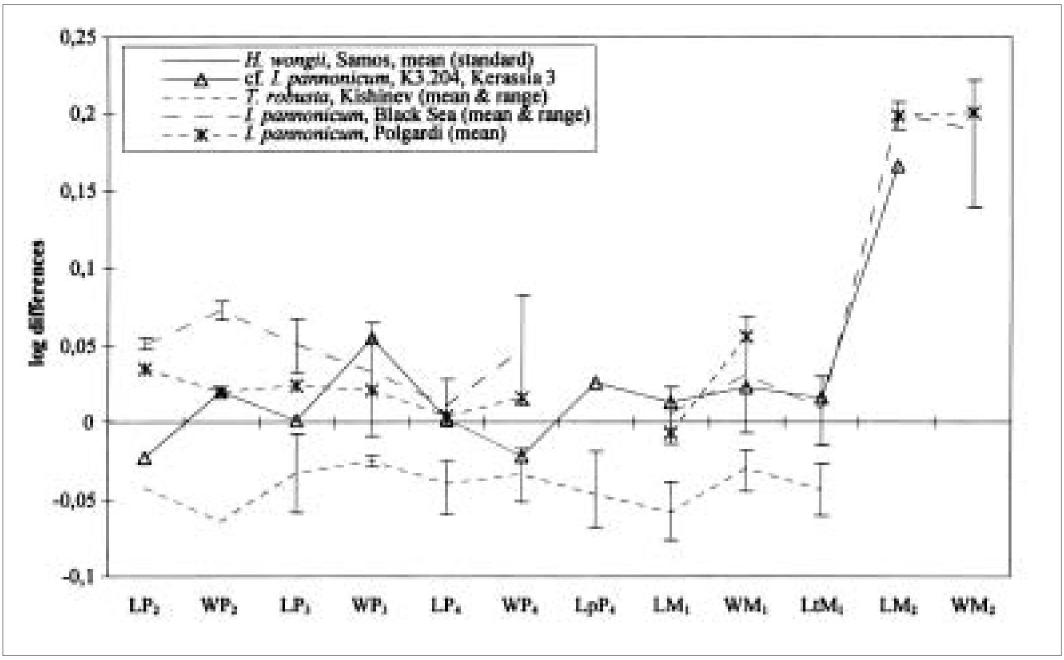

Figure 2 Logarithmic ratio diagram comparing the Kerassia 3 ictithere with various species of icitheres. *H. wongii* from Samos according to Werdelin (1988a), *T. robusta* from Kishinev according to Kurtén (1982), *I. pannonicum* from Polgardi and the Black Sea from Table 4.

gii (Fig. 3). The most important distinguishing character of *I. pannonicum* is the large m2 (Figs. 2, 3). As mentioned earlier, such a character is also present in our specimen. Aside from the large m2, the Kerassiá 3 specimen resembles *I. pannonicum* in its m1 but it has more robust p3 (Table 4, Fig. 2).

Unfortunately, the species *I. pannonicum* is poorly known. In addition to Polgardi (Kretzoi 1952), which is the type locality, specimens referred to that species are also known from Chobruchi in Moldova, and Novaja Emetovka 2 and Cherevichnoe in Ukraine (Semenov 1985, 1989). A specimen from Valdecebro 5 in Spain referred to *Thalassictis* aff. *hipparionum* by Adrover *et al.* (1986), may, according to Werdelin & Solounias (1991), also belong to *I. pannonicum*. Alcalá (1994) further mentioned a fragmentary mandible from the middle Turolian (MN12) of Cerro de la Garita in Spain under the name '*Ictitherium* aff. *I. pannonicum*'. The p2 and p3 of that specimen are comparable in size to those of *I. pannonicum*, but the p4 is larger. Moreover, that specimen lacks any teeth posterior to p4. Another species possibly related to *I. pannonicum*, is *Ictitherium intuberculatum* OZANSOY, 1965, from the Yassiören in Turkey. Werdelin & Solounias (1991) emphasize the possibility that this form might be conspecific with *I. pannonicum*, but Ozansoy (1965) does not give metric data for the lower dentition and comparison with the Kerassiá ictithere is not possible.

Of the localities mentioned, Chobruchi is considered to be early Turolian (MN11) (Semenov 1989), Valdecebro 5, Novaja Emetovka 2 and Cherevichnoe middle Turolian (MN12) (Adrover *et al.* 1986, Semenov 1989) and Polgardi late Turolian (MN13) (Ginsburg 1999).

Subfamily: Hyaeninae MIVART, 1882
Genus: *Adcrocuta* KRETZOI, 1938
Adcrocuta eximia (ROTH & WAGNER, 1854)
Locality: Kerassiá 4 (K4)

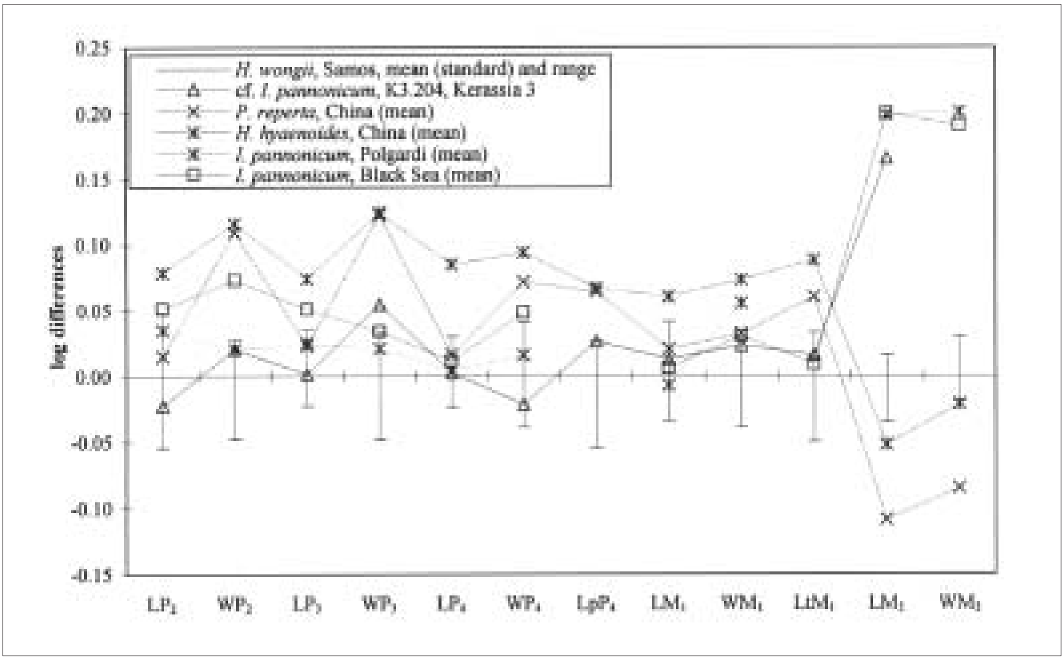

Figure 3 Logarithmic ratio diagram comparing the Kerassia 3 ictithere with various species of icitheres. *H. wongii* from Samos, *P. reperta* and *H. hyaenoides* from China according to Werdelin (1988a), *I. pannonicum* from Polgardi and the Black Sea from Table 4.4.

Material

K4.7: skull fragment with the right P3 and P4. The P3 is badly damaged and the alveolus of M1 is visible. K4/Δ388/1: skull fragment with the left I1-P3, Cs, P1-P4 and M1, and the right I1-I3, Cs, and P3-P4. K4/Δ388/2: left mandibular ramus with the complete dentition (i1-i3, ci, p1-p4 and m1). K4/Δ388/3: right mandibular ramus with the complete dentition except p1. The lower mandibles K4/Δ388/2-3 were found connected at their symphysis, and so come from the same individual. The specimen K4/Δ388/1 was found next to these mandibles, and it is almost certain that all these specimens belong to the same individual. This is also indicated from their ontogenetic stage, since the teeth are almost unworn and neither the upper nor the lower canines have fully erupted.

Description of the skull and the upper dentition

The infraorbital foramen opens above the posterior half of P3. The maxillopalatine suture is not clearly visible, but most probably its anterior limit lies opposite the posterior part of P3. The anterior palatine foramina are situated level with the middle of P2. The posterior palatine foramina are not visible. The I1 and I2 are arranged in an almost straight line, while I3 is situated slightly posteriorly. The I2 is only slightly larger than I1, but I3 is significant larger. The I1 and I2 have a distal cingulum composed from two cusps, with the lingual one slightly larger than the lateral one. The upper canine has a mesiolingual and a distal crest. The P2 is not well preserved, but shows a posterior accessory cusp. On its anterior part, we cannot clearly observe an accessory cusp, but only a small bulge at the lingual side of the base of the anterior crest. The P3 has a posterior accessory cusp and a small anterior one in a mesiolingual position. The greatest width is at the anterior part of the tooth. The P4 is characterized by a small protocone, a parastyle that is smaller and lower than the paracone, and a metastyle that is slightly longer than the paracone (Table 5). The distal part of the metastyle blade is directed labially. M1 is small and its metacone projects slightly posteriorly.

Description of the lower mandible and the lower dentition

The mandibular corpus has two mental foramina. The anterior foramen opens under the middle of p2 and the posterior one under the contact between p2 and p3. The symphysis measures about 52 mm in length and extends posteriorly to the anterior part of p2. The anterior border of the masseteric fossa is situated posterior to m1. The incisors increase in size from i1 to i3 and they have a lateral cusp, which shows an increase in size from i1 to i3. The lower canine has a mesiolingual and a distal crest and is slightly more curved than the upper canine. The cheek teeth are arranged in a curved line. The posterior part of p3 slightly overlaps the anterior part of p4, and the posterior part of p4 the anterior part of m1. The anterior and posterior borders of p3 and p4 are almost straight, giving them a rectangular outline. The p1 is small and situated lingually relative to p2. The p2 has a posterior accessory cusp but not an anterior one. The p3 has a posterior accessory cusp and a faint anterior one at the lingual side of the base of the anterior crest. The p4 has two accessory cusps, an anterior and a posterior one. The anterior one is more robust and situated slightly lingually. Behind the posterior accessory cusp, the cingulum is elevated. The premolars lack a lingual cingulum. The m1 lacks a metaconid, while the talonid is small and two-cusped, retaining the entoconid and the hypoconid, of which the hypoconid is the larger. There is a weakly developed cingulum at the anterior part of the paraconid, both lingually and buccally. There is no m2 or an alveolus for it.

Comparisons

Hyaena eximia was first described by Roth & Wagner (1854) from the classical locality of Pikermi. Later it has been found at many fossilliferous sites in Europe and Asia. The generic attribution of the species has changed several times, and it is now attributed in *Adcrocuta* KRETZOI, 1938, opinion followed also here.

The available specimens from Kerassiá have all the morphological characters of *A. eximia*. This species shows some variation in the position and the number of the mental foramina (Gaudry 1863, Werdelin & Solounias 1991, Koufos 2000). The specimen figured by Roth & Wagner (1854, pl. 8, fig. 6) has two mental foramina, almost in the same positions as the Kerassiá specimens. Gaudry (1863) mentioned that of three specimens available to him, two had two mental foramina, but another specimen had only one mental foramen. The same variation is also present in the Axios material. The specimen RZO-126 has two mental foramina, while the specimen RZ1-4 has one (Koufos 2000). Some variation is also observable on the accessory cusps of the upper and lower premolars. This variation concerns their presence or not, as well as their development. The P2 and P3 generally have small accessory cusps. The anterior accessory cusp of p2 is small or absent, while that of p3 is present but sometimes small. The m1 most commonly lacks a metaconid. It has been observed, however, in some cases, as on MNHNP MAR G.12 from Maragha figured by De Mecquenem (1925, pl. 9, fig. 7) and on RZ1- 4 from Ravin des Zouaves 1 (Koufos 2000). A small metaconid, appressed to the main body of the protoconid, has also been observed (Roussiakis 1996) on AMPG P.G. 95/1505 from Pikermi (specimen mentioned with the number 113 by Howell & Petter 1985, tab. 6a).

The dimensions of the specimens K4/Δ388/1 and K4/Δ388/2-3 are within the range of variation of *A. eximia* from Pikermi (Tables 5-6, figs. 4,5). The observable differences are not statistically significant. The M1 of K4/Δ388/3 is slightly large relative to the premolars, but is damaged at the area between the trigonid and the talonid. The P3 and P4 of K4.7 are comparable to the largest specimens from Pikermi (Fig. 4). The metastyle of the P4 of K4.7 is large (Table 5) but that tooth is badly damaged and broken at the limit of the paracone and metastyle.

The present specimens show significant differences from *Adcrocuta eximia leptoryncha* BONIS & KOUFOS, 1981, from the Vallesian of Ravin de la Pluie. According to Bonis & Koufos (1981) and Koufos (2000), this subspecies differs from the typical *A. eximia* in its longer snout, narrower palate and more slender premolars. With regard to the lower premolars, there are no significant differences from the Pikermi *A. eximia*, something mentioned also by Howell & Petter (1985). The p3 and p4 are slightly smaller in some of their dimensions (Fig. 5) and p4 has an index of compression (Wp4/Lp4) equal to 50.7 on RPL-15, which is slightly lower than the Pikermi range (Table 6). The indices of the upper premolars are within the range of *A. eximia* from Pikermi (Table 5, fig. 4). The skull characters of *A. eximia leptoryncha*, however, distinguish that subspecies from the Pikermi, Samos and Maragha *A. eximia*. The skull of *A. eximia leptoryncha* has a longer snout and relatively narrower palate, the length/width ratio of the palate being 154 (Bonis & Koufos 1981). The corresponding ratio (estimated following the methodology of Bonis & Koufos 1981) for K4/Δ388/1 is 123, a value very close to those given by Bonis & Koufos (1981) for the *A. eximia* from Pikermi (125) and Maragha (117). On P.A. 490/91 from Pikermi, this ratio is about 127.

The species *Chasmaporthetes bonisi* KOUFOS, 1987 is known from the early Turolian locality of Ravin des Zouaves 5 and the late Turolian locality of Dytiko 1. This species differs from *A. eximia* mainly in the upper dentition. The M1 is larger than that of *A. eximia* (Fig. 4) and the protocone of P4 is more developed and directed slightly anteriorly. The P2 is also slightly less robust than that of *A. eximia* from Pikermi, but not significantly so. In *C. bonisi* the robusticity of the lower premolars, lies close the minimum values of the A. *eximia* from Pikermi. The robusticity index for the p2 of DTK-126 (sin.) is also similar to that of the *A. eximia* specimen RZ1-4 (sin.) (Fig. 5). The morphology of the lower premolars of *C. bonisi*, however, differs from those of *A. eximia*. The lower premolars of *C. bonisi* have a more elliptical outline, especially anteriorly, while the accessory cusps lie almost on the axis of the teeth. In *A. eximia* the anterior cusps of the lower premolars are in a more lingual position, and the anterior and posterior borders are almost straight, giving an almost rectangular shape to the teeth.

Most probably *A. eximia* is also present at the Kerassiá 1 (K1) site. This is indicated by the specimen K1/Δ104 (a left P4). Unfortunately, this specimen is so fragmentary that no measurements can be taken.

The species *A. eximia* is known mainly from the Turolian (MN11-13) of Europe and Asia as well as from northern Africa, with its maximum in the middle Turolian (MN12; Howell & Petter 1985, Koufos 2000). Its existence in the Vallesian of Hostalets de Pierola in Spain and Soblay in France, has been shown to be unconfirmed (Howell & Petter 1985). Ravin de la Pluie, Ravin des Zouaves 1 and Xirochori 1 are the only known late Vallesian localities with *Adcrocuta eximia* remains (De Bonis *et al.* 1988; Koufos 2000). As shown earlier, the Ravin de la Pluie subspecies *A. e. leptoryncha*, is clearly different from the Kerassiá *A. eximia*. The Ravin des Zouaves 1 *A. eximia* is also different from the Kerassiá specimens. According to Koufos (2000), the late Vallesian *A. eximia* from Ravin des Zouaves 1 has strong lingual cingulum on the lower premolars, a character considered to be primitive by Koufos (2000). Such a cingulum is absent on the Kerassiá specimens, indicating that the Kerassiá *A. eximia* is more similar to the typical Turolian forms.

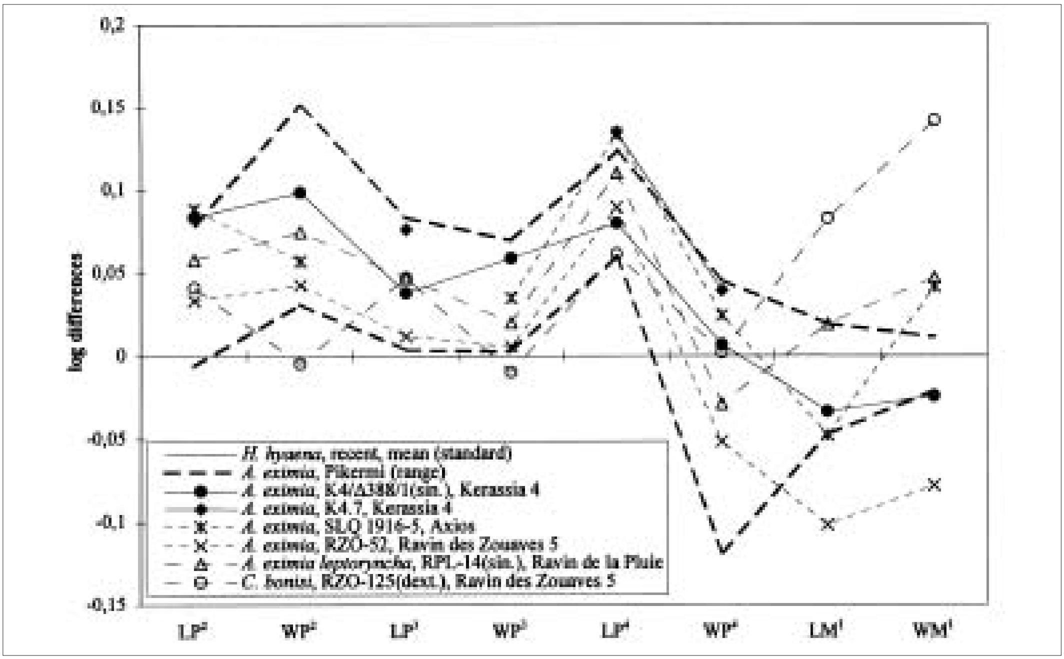

Figure 4 Logarithmic ratio diagram comparing the upper dentition of the Kerassia 4 *Adcrocuta* with *A. eximia* and *C. bonisi* from various localities. *H. hyaena* (standard) according to Howell & Petter (1980). Data for the Axios, Ravin des Zouaves 5 and Ravin de la Pluie hyaenids according to Koufos (2000). The rest from Table 5.

Family: Felidae GRAY, 1821
Subfamily: Machairodontinae GILL, 1872
Genus: *Machairodus* KAUP, 1833
Machairodus giganteus (WAGNER, 1848)
Locality: Kerassiá 4 (K4)

Material

K4.14: right upper canine. K4/Δ69/1: mandible, with both left and right mandibular rami. The condyles are only partly preserved, while the mandibular angles and the coronoid processes are broken. In the right ramus the i1-i3, p3-p4 and m1 are preserved, but the tips of i2 and i3 are broken and the posterior part of p4 is badly damaged. Only the root of the right ci is preserved. In the left ramus the complete dentition (i1-i3, ci, p3-p4 and m1) is preserved but the main cusp of p3, the anterior half of p4 and the posterior half of m1 are broken. K4/Δ110/16: Left radius, complete. K4/Δ82: Right Mt IV, badly damaged.

Description

The upper C (K4.14) is laterally compressed, has an anterior keel in a slightly lingual position, as well as a posterior one. Both keels are poorly preserved, but show crenulations at least near the tip of the canine. The length at the base of the canine is about 30.0 mm and the width about 11.6 mm. The resulting index (W × 100/L) Cs is 38.7, showing the degree of compression of the canine.

The mandible has a strong, downwardly expanded and angular mental crest. The height of the symphysis measured anteriorly is about 75 mm. The area of the symphysis just below the incisors and anteriorly is deeply grooved, while its lower part is smoother. The upper part of the symphyseal area is situated in front of the mental crests. There are two mental foramina. These foramina are on the same level and closer to the lower margin of the mandible than to the upper one. The anterior mental foramen opens under the middle of the postcanine diastema and the poste-

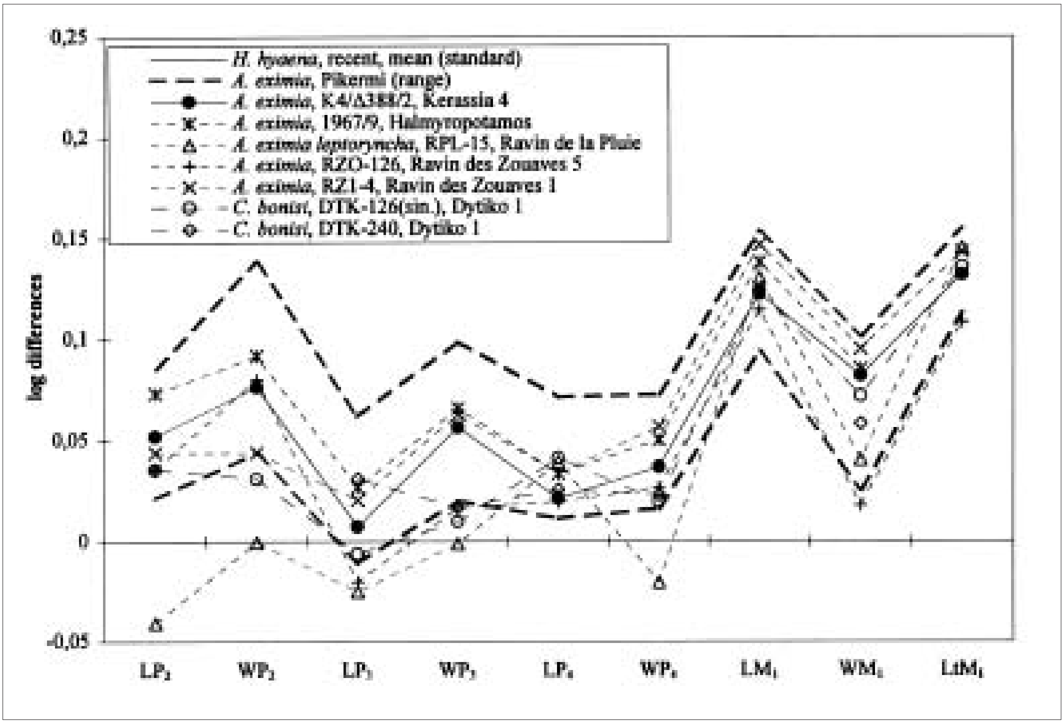

Figure 5 Logarithmic ratio diagram comparing the lower dentition of the Kerassia 4 *Adcrocuta* with *A. eximia* and *C. bonisi* from various localities. *H. hyaena* (standard) according to Howell & Petter (1980). Data for the Ravin des Zouaves 1 & 5, Dytiko 1 and Ravin de la Pluie hyaenids according to Koufos (2000). *A. eximia* from Halmyropotamos according to Melentis (1968). The rest

rior one just in front of p3. The masseteric fossa is deep and well defined by an acute crest on its upper part. It extends anteriorly to the posterior limit of m1 on the right ramus, slightly more anteriorly on the left. The condyle is situated 1.5 cm lower than the level of the cheek teeth, while the incisors and the canine are clearly at a higher level. The mandibular foramen opens close to the lower margin of the mandible and about 65 mm in front of the condyle.

The lower incisors are arranged in an almost straight line, are conical in shape, increasing in size from i1 to i3 and situated clearly in front of the lower canines. Their tips are directed upwards. The total width of the incisors (i3-i3) measures about 43 mm. The lower canine is not significantly laterally compressed (Table 7). A large diastema separates the lower canine from p3 (Table 7) and a small diastema of 2.5 mm separates p3 from p4. The mandibular corpus, at the region of the diastema and on its upper part, is laterally concave and an acute crest is formed dorsally. There is no trace of a p2. The p3 is elongated (Table 7). The right p3 has a faint anterior accessory cusp and the left one a larger one. There is also a posterior accessory cusp that is larger than the anterior one. The greatest width of the tooth is in its posterior part. In p4, both the anterior and the posterior accessory cusps are strong, but the anterior one is thicker. Behind the posterior accessory cusp there is also a small supplementary cuspid. Both the posterior accessory cusp and the supplementary cuspid are directed slightly backwards. The greatest width of the tooth lies posteriorly. In m1, the paraconid is robust while the protoconid is more slender and slightly longer. There is a small metaconid. The greatest width of the tooth lies in the posterior part of the paraconid.

Comparisons

Various species of *Machairodus* have been described from the Late Miocene of Europe and Asia, but De Beaumont (1975) retained only two species, the Vallesian *Machairodus aphanistus* (Kaup, 1833) and the Turolian *Machairodus* giganteus (Wagner, 1848). These two species are of comparable dimensions, but differ in many morphological characters. De Beaumont (1975) considered the species *Machairodus leoninus* (Roth & Wagner, 1854), *Machairodus tarakliensis* Riabinin, 1929, *Machairodus* palanderi Zdansky, 1924, and possibly *Machairodus* tingii Zdansky, 1924, to be synonyms of *M. giganteus*. The available Kerassiá 4 specimens are compared to bibliographic data as well as to three undescribed specimens of *M. giganteus* from Pikermi stored in the AMPG (Table 7).

As is indicated by De Beaumont (1975) and Koufos (2000) the upper canine of *M. aphanistus* is less compressed than that of *M. giganteus*. According to Koufos (2000), the index of compression (Wx100/L) of the upper canine in *M. aphanistus* ranges from 41.5-52 and in *M. giganteus* from 38-41. The canine from Kerassiá 4 has an index of compression equal to 38.7, well within the range of *M. giganteus*. An upper canine from Pikermi (AMPG no 1967/7) has an index of compression 38.8. This specimen is attributed by Melentis (1968) to *M. aphanistus*, but in our opinion must be attributed in *M. giganteus*. For the *Machairodus* skull from *Halmyropotamos* (Melentis 1968), the compression index of the upper canine is about 40.6. This specimen has been referred to *M. aphanistus* by Melentis (1968), but was considered to belong to *M. giganteus* by Petter & Howell (1987) and Koufos (2000).

In lateral view, the lower incisors of K4/Δ69/1 are clearly in front of the canines. They are arranged in an almost straight line, while in P.G. 01/100 from Pikermi the incisors are arranged in an arc. De Beaumont (1975) observed that in *M. giganteus* the lower incisors are arranged in an arc. It is not known, however, on how many specimens this has been observed and how much variability is involved. Judging from the drawings of some mandibles in lateral view, the arrangement of the lower incisors varies in *M. giganteus*. On the mandible from Pikermi figured by Roth & Wagner (1854, pl. 9, fig. 1), for example, i2 is only just in front of i3. On another mandible (Wagner 1857, pl. 5, fig. 11), i2 is significantly in front of i3. These observations show that the disposition of the lower incisors varies. The width of the lower incisor row (i3-i3) of K4/Δ69/1 is 43 mm, only slightly different from P.G. 01/100 (estimated at 47 mm). The height of the symphysis of P.G. 01/100 is about 67 mm, slightly smaller than that of the Kerassiá mandible. De Beaumont (1975) mentioned that the postcanine diastema is generally large in *M. giganteus* (as also on the *Machairodus* from Kerassiá 4) and shorter in *M. aphanistus*, but he also mentioned that there is considerable variation in this character. On the type specimen of *M. aphanistus* from Eppelsheim, this diastema is 30-35 mm and in another specimen from the same locality, it is 35 mm (De Beaumont 1975). The length of this diastema varies significantly in *M. giganteus* from Pikermi. It is 55 mm in a specimen from Pikermi described by Roth & Wagner (1854, pl. 9, fig. 1) and only 24 mm in another specimen from the same locality described by Wagner (1857, pl. 5, fig. 11). On P.G. 01/100 from Pikermi, this diastema is 48.8 mm, which is slightly less than that of K4/Δ69/1 (Table 7). In P.G. 01/100, there is a minute alveolus for p2 at the middle of the diastema. De Beaumont (1975) mentioned that in *M. giganteus* there is no trace of p2. In our opinion, however, such a character is not very important since, as we mention also later, it is sometimes present in *Machairodus alberdiae* Ginsburg, Morales & Soria, 1981, as well as in species such as *Metailurus parvulus* (Hensel, 1862). In the Kerassiá 4 *Machairodus*, the width of the lower canines is much less than the distance that separates them from the symphysis. Such a character is always found in *M. giganteus* while in *M. aphanistus* the opposite is observed (De Beaumont 1975). According to the same author, the lower canine of *M. giganteus* is less compressed than that of *M. aphanistus*. In a specimen of *M. giganteus* from Samos, the lower canine has dimensions (L × W) at the base of the crown of 18.0 × 14.0 (De Beaumont 1975), giving it an index of compression of 77.8. According to the measurements given by De Beaumont (1975), the lower canine of *M. aphanistus* from Eppelsheim described by Kaup (1833, pl. I, fig. 3) under the name "*Agnotherium antiquum*" has an index of 59.6, while in another specimen of *M. aphanistus* from Eppelsheim (BMNH 4996a) the corresponding index is 58.1. The index of compression of the lower canine of K4/Δ69/1 is 74.7, a value significantly greater than in *M. aphanistus* and closer to *M. giganteus*. In P.G. 01/100 from Pikermi, the lower incisor has an index of compression of 66.9. This value, however, is taken at the root of the tooth. Higher on the crown, we would expect a greater value, since the anteroposterior diameter (L) of the canine decreases more than the transverse diameter (W).

The lower premolars and the lower carnassial of *M. giganteus* show no significant differences from those of *M. aphanistus*. As shown in Figure 6, the cheek teeth vary significantly in size, something also mentioned by De Beaumont (1975). Aside from the size variation, De Beaumont (1975) also emphasized the morphological variation of *M. giganteus*, a variation that concerns the postcanine diastema that we mentioned above, the development of the anterior accessory cusp of p3, and the development of the metaconid/talonid complex of m1. As shown in Figure 6, the p3 and p4 of *M. giganteus* are generally more elongated than they are in *M. aphanistus*. There are, however, specimens referred to *M. aphanistus* with p3 and p4 equally or almost equally elongated as those of *M. giganteus*, as for example the *M. aphanistus* from Charmoille and the type specimen from Eppelsheim (Fig. 6). The p3 of P.G. 01/100 has a larger anterior accessory cusp than K4/Δ69/1, but De Beaumont (1975) mentioned that in *M. giganteus* the anterior cusp varies from faint to well developed. The accessory cusps of p4 in K4/Δ69/1 are not different from those of P.G. 01/100 and P.G. 01/101 from Pikermi, the anterior one being slightly more robust than the posterior one. In K4/Δ69/1, the metaconid of M1 is slightly more developed than in P.G. 01/100, P.G. 01/101 and P.G. 01/102, in which feature it is more like two specimens of *M. giganteus* figured by De Beaumont (1975, figs. 6e, 6f). In *M. giganteus*, however, the m1 is, in general, more slender than in *M. aphanistus* (Fig. 6).

The species *M. pseudailuroides* Schmidt-Kittler, 1976, from the localities of Akçakoy and Eskihisar in Turkey, differs from the *Machairodus* from Kerassiá in its shorter p4 and m1. The upper canine of this species is more slender than that of *M. giganteus*, with an index of compression of 35.9.

M. alberdiae Ginsburg, Morales & Soria, 1981, from the Vallesian locality of Los Valles de Fuentidueña has been considered as a possible ancestor of *M. giganteus* (Ginsburg 1999). This species has smaller dimensions than the specimens described here and sometimes preserves a p2. Its upper canine is significantly less compressed (W × 100/L=50.0-53.9, n=2) than that of the Kerassiá 4 machairodont, but its lower canine is slightly more compressed (W × 100/L=63.4-71.4, n=4). Most characteristic of *M. alberdiae* is the large p3 relative to p4 and m1 (Fig. 7).

Two machairodonts have been described from the Late Miocene of China, *M. tingii* and *M. palanderi* (Zdansky 1924). As we mentioned earlier, *M. palanderi* has been considered conspecific with *M. gignateus* by De Beaumont (1975), and the same may be true also of *M. tingii*. As we can see (Fig. 7) *M. tingii* is very similar in dimensions to K4/ × 69/1, but *M. palanderi* has shorter p3 relative to p4 and m1.

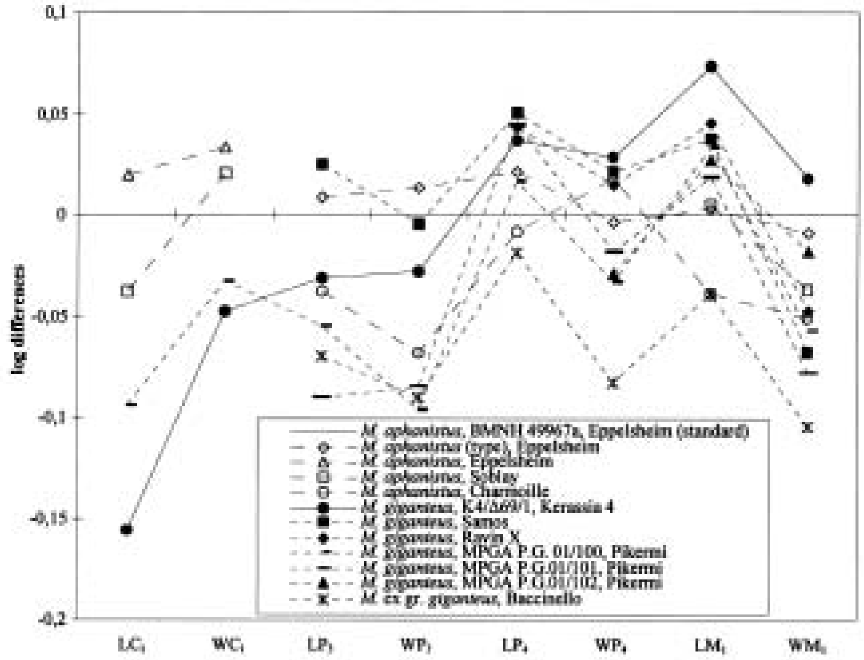

Figure 6 Logarithmic ratio diagram comparing the Kerassia 4 Machairodus with *M. giganteus* and *M. aphanistus* from various localities. *M. aphanistus* from Eppelsheim, Soblay and Charmoille according to Beaumont (1975), *M. giganteus* from Samos and *M.* ex *gr. giganteus* from Baccinello according to Rook *et al.* (1991), *M. giganteus* from Ravin X according to Koufos (2000), *M. giganteus* from Pikermi according to the authors.

Sotnikova (1992) described a new species, *M. kurteni*, from the Late Miocene locality of Kalmakpai in Kazakhstan. According to Sotnikova (1992), this species has a proportionally narrower P4 than other species of *Machairodus*, retains a small P2, the tips of the lower incisors are directed upwards, the length of the lower premolars is small compared with that of m1, and has completely lost the metaconid/talonid complex on M_1. Sotnikova (1992) did not support her statements with adequate comparisons, but actually compared her specimens to '*M. taracliensis*' from Taraklia, a form that has been considered a synonym of *M. giganteus* by De Beaumont (1975) and a subspecies of *M. giganteus* by Sotnikova (1992). Most of the above mentioned characters of *M. kurteni* are also found in *M. giganteus*. Concerning for example the upper teeth of the Kalmakpai form, a compression index of P4 of 38.7 signifies that P4 is not narrower than that of *M. giganteus*. The *M. giganteus* from Halmyropotamos, for example, has a compression index equal to 34.3, which indicates a narrower P4 compared to the Kalmakpai form. The same is true for the Ravin X skull portion of *M. giganteus*, which has a compression index of P4 equal to 36.4 (Koufos 2000). A similar comparison shows that the P3 of the Kalmakpai form is not shortened relative to P4, more than it is in *M. giganteus*. Concerning the lower teeth, the index Lm1 × 100/Lp3-4, which shows the relative development of the premolars, varies in the Kalmakpai form from 67.7 to 74.5 (n=3). These values are not different from the Pikermi specimens P.G. 01/100 (73.2) and P.G. 01/101 (70.4). According to Sotnikova (1992), the tips of the lower incisors of the Kalmakpai form are directed upwards, contrary to the Taraklia M. *giganteus*, where they are directed forwards. In P.G. 01/100, however, as well as on the mandible figured by Roth & Wagner (1854, pl. 9, fig. 1), the tips of the lower incisors are also directed upwards. Other characters, such as the presence of P2 and p2 are not reliable alone, but only in combination with other characters, since they seem variable. Sotnikova (1992) for example figured a mandible of *M. laskarevi* from Kalfa, where there is a p2 on the right ramus but not on the left. The same tooth varies in development in *M. alberdiae*, being absent or rudimentary. The P2 is in general absent in *M. giganteus*, but present in *M. palanderi* and *M. tingii*. *M. kurteni* has completely lost its metaconid/talonid complex on m1. This character varies significantly in *M. giganteus* and can be almost absent (De Beaumont 1975). From the above observations is seen that, except for the last character, *M. kurteni* is not clearly different from *M. giganteus* and further comparison has to be made.

The available radius is comparable in size to that described by Gaudry (1863, pl. 16, figs. 2, 3). The radial tuberosity is not very prominent. The radius has two wide grooves in its anterodistal part, a medial one for the extensors carpi radialis longior and brevior indicis and a lateral one for the extensor communis digitorum. These two grooves are separated by a blunt crest. More medially lies the groove for the extensor ossis metacarpi pollicis and more laterally the triangular articular surface for the ulna. A proximal part of a radius from Halmyropotamos is also mentioned by Melentis (1969) under the name *Machairodus aphanistus*. In our opinion it is not certain that this specimen represents a *Machairodus*, since it has smaller dimensions. The maximum diameter of the head of that specimen is 23 mm (Melentis 1969), significantly smaller than in the radius of Kerassiá 4. The present Mt IV has a badly damaged shaft and its distal epiphysis is slightly broken. Its total length is 128 mm, and must be expected to have been slightly greater. The anteroposterior diameter of the proximal part is 29 mm.

The species *M. giganteus* is known from the Turolian of Halmyropotamos (possibly MN11 or MN12), the early-middle Turolian (MN11-12) of Ravin X in Greece and from the middle Turolian (MN12) of Mont Leberon (France), Kalimanchi (Bulgaria), Samos, Pikermi (Greece) and Taraklia (Moldavia) (Ginsburg 1999, Koufos 2000). It is reported also under the name *Amphimachairodus giganteus* from various localities in Spain, ranging from MN11 to MN13 (Fraile *et al.* 1997). Rook *et al.* (1991) also mentioned some specimens under the name *Machairodus* ex gr. *giganteus* from the MN12 locality of Baccinello-V3 in Italy.

Subfamily: Felinae Trouessart, 1885
Genus: *Metailurus* Zdansky, 1924
Metailurus cf. *parvulus* (Hensel, 1862)
Locality: Kerassiá 1 (K1)

Material

K1/Δ18: left mandible with ci, p3 and p4. The m1 has fallen out and the tip of the canine is broken.

Description

The mandibular corpus has a large mental foramen situated under the middle of the postcanine diastema and a very small one under the front end of p4. The lower canine is in a poor state of preservation, but shows an antero-lingual keel and most possibly a posterior one. The p3 has only a posterior accessory cusp and its greatest width is in its posterior part. The p4 has an anterior and a posterior accessory cusp, the posterior one being slightly stronger. As in p3, the greatest width occurs in the posterior part of the tooth. The alveolus for m1 is especially large and its posterior limit lies well up on the ascending ramus of the mandible. Moreover, the mandibular corpus shows an abrupt thickening at the region of the m1. The above characters may indicate that our specimen is a pathological one.

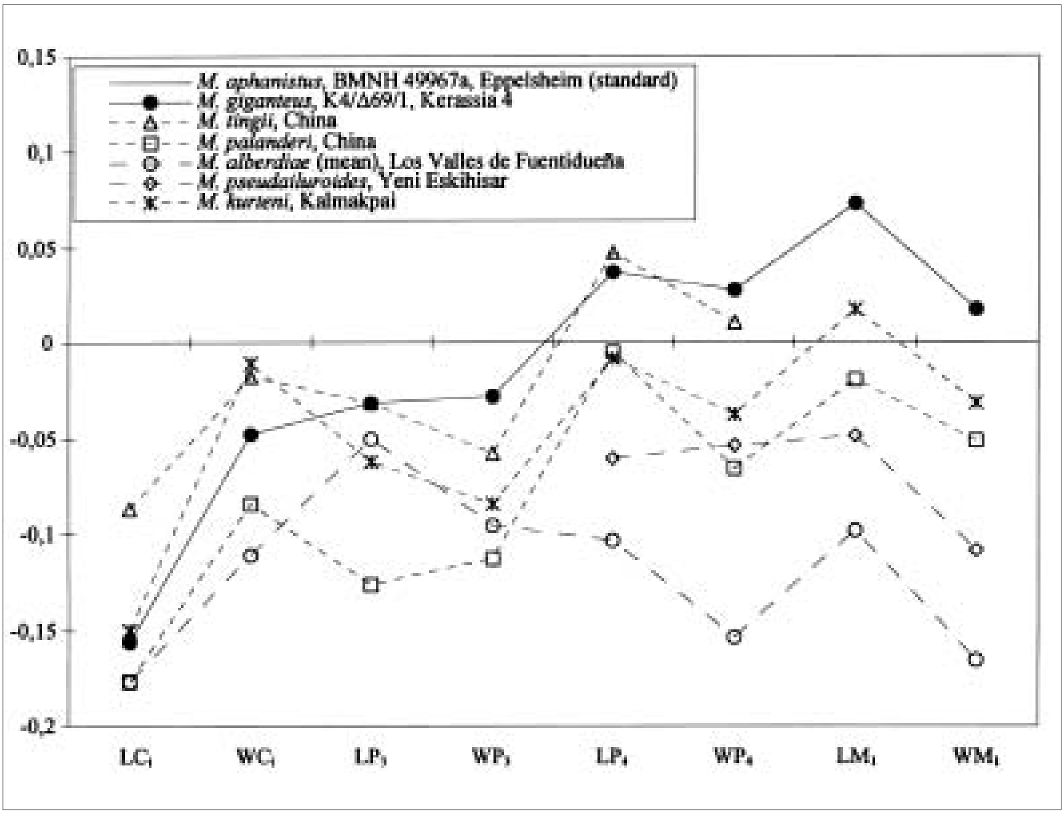

Figure 7 Logarithmic ratio diagram comparing the Kerassia 4 *Machairodus* with other species. *M. aphanistus* from Eppelsheim (standard) according to Beaumont (1975), *M. tingii* and *M. palanderi* according to Zdansky (1924), *M. alberdiae* according to Ginsburg *et al.* (1981), *M. pseudailuroides* according to Schmidt-Kittler (1976) and *M. kurteni* according to Sotnikova (1992).

Discussion and comparisons

The species *M. parvulus* (Hensel, 1862) has a wide range from Spain to China. Following Thenius (1951) and De Beaumont (1961), we include in this species the "Felidae indet., 3rd species" (Gaudry 1863), *Felis leiodon* Weithofer, 1888, *Metailurus minor* Zdansky, 1924, and other remains referred to under various specific or generic names.

The available specimen from Kerassiá 1 has been compared with specimens of *M. parvulus* from Pikermi, Chomateri and China. We have included also in our comparison an undescribed until now specimen from Pikermi, with the catalogue number AMPG P.G. 01/103 (Table 9). The mandible of K1/Δ18 has the typical form of the Felinae, without a mental crest. The height of the mandibular corpus in front of P3 is only slightly smaller than that of the Chomateri specimen (Symeonidis 1978) or P.G. 01/103 (Table 9). There is no alveolus for p2 between the lower canine and the p3. Such an alveolus, with a single, very small root, exists on the specimen from Chomateri, on the specimen P.G. 01/103 from Pikermi, as well as in one specimen from China (Zdansky 1924, ex. 3).

Unfortunately, the teeth are not very well preserved and some of their measurements could not be taken with the appropriate precision. The p3 is slightly smaller than other specimens of *M. parvulus*, but the indices of the teeth are within the range of *M. parvulus*

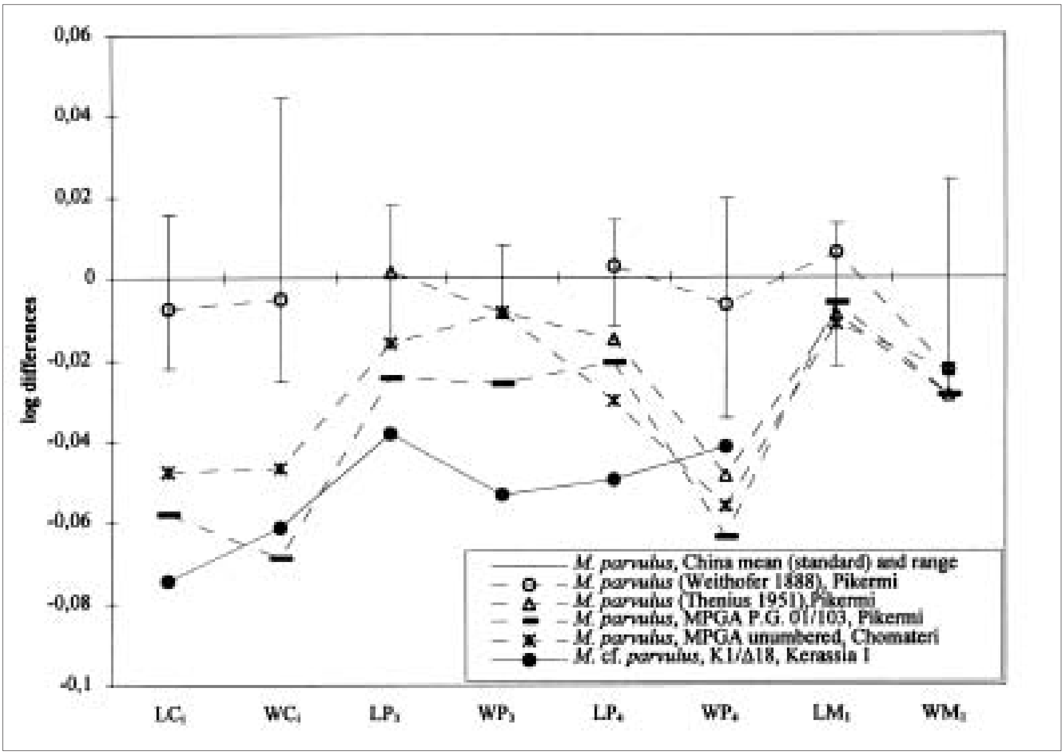

Figure 8 Logarithmic ratio diagram comparing the Kerassia 1 *Metailurus* with *M. parvulus* from Pikermi, Chomateri and China. Data from Table 9.

from China (Table 9). As we can see (Fig. 8), the Greek specimens show a tendency to smaller size than the Chinese specimens. Some of these specimens also show a narrower p4. The Kerassiá one specimen is slightly smaller in most of its dimensions than other specimens referred to *M. parvulus*, but the observed differences are of little value, as the statistical sample is not adequate. The present specimen, however, lacks the m1 and it is preferable to refer it as *Metailurus* cf. *parvulus*.

Paramachairodus ogygius (KAUP, 1832) has teeth comparable is size with the largest specimens of *M. parvulus* from China. The Kerassiá one specimen, however, differs from *P. ogygius*. The height of the mandibular corpus in front of p3 measures about 26 mm (measurement from the figure) on the specimen figured by Kaup (1833, pl. 2, fig. 3), as opposed to 17.5 mm on K1/Δ18. Moreover, in the type specimen of *P. ogygius* the postcanine diastema measures about 17 mm (De Beaumont 1975), as opposed to 8,5 mm in the Kerassiá one specimen.

M. parvulus is known from the Turolian of Halmyropotamos (possibly MN11 or MN12) (Melentis 1968), the middle Turolian (MN12) of Pikermi (Hensel 1862, Thenius 1951) and Chomateri (Symeonidis 1978) in Greece, Los Mansuetos in Spain (Morales & Soria 1979, Fraile *et al.* 1997) and the late Turolian of El Arquillo in Spain (Morales & Soria 1979, Fraile *et al.* 1997).

GENERAL DISCUSSION AND CONCLUSIONS

The carnivores of K1, K3 and K4 are consistent with a Turolian age for these sites. *A. eximia* is very common in the middle Turolian, but rarer in the early or late Turolian (Howell & Petter 1985). In Greece, *A. eximia* seems absent from the late Turolian localities, such as those of Dytiko (De Bonis *et al.* 1992, Koufos 2000). The same is true for the rare *M. giganteus*, which is absent from Dytiko. Both species are present in the Main Bone Beds of Samos (Bernor *et al.* 1996), dated to 7.1 Ma (Swisher 1996), while *A. eximia* is also present in the older White Beds of Samos (Bernor *et al.* 1996; Swisher 1996). According to the recent calibration of the MN zones (Steininger 1999), the Main Bone Beds of Samos can be placed in MN12. In addition to the carnivores discussed here, the K1 faunal list (Theodorou *et al.* this volume) also includes a *Tragoportax*, provisionally referred to *Tragoportax* cf. *amalthea*. *T. amalthea* (Roth & Wagner 1854) is a boselaphine that is well known from many Late Miocene localities, with a stratigraphic range from the early to the middle Turolian (Gentry *et al.* 1999).

The suids referred to *M. major erymanthius* by Van der Made & Moyà-Solà (1989) most probably come from K1 and according to these authors indicate a middle Turolian age. Kostopoulos *et al.* (2001), however, have shown that the Kerassiá *M. major* is smaller than the Pikermi *M. major erymanthius*, and probably represents a new subspecies. The geological prospecting of the Kerassiá sites has shown that K1 is situated at a higher level than K3 and K4, so K1 must be slightly younger. K3 and K4 possibly belong to the same stratigraphic level, but no suids have been found in these sites until now (Theodorou *et al.* this volume).

A biostratigraphic distinction between K1, K3 and K4 is not possible at the moment, but judging from the above data, an early to middle Turolian age is plausible for the fauna of Kerassiá. In the future, we plan to continue the fieldwork, while sedimentological and taphonomic study of the numerous fossiliferous sites at Kerassiá is already in progress.

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REFERENCES

Adrover, R., Alcalá, L., Mein, P., Moissenet, E. & Orrios, J., 1986 – Mamíferos del Turoliense Medio en la Rambla de Valdecebro (Teruel) – Estudios Geológicos 42: 495-509

Alcalá, L., 1994 – Macromamíferos neógenos de la fosa de Alfambra-Teruel – Museo Nacional de Ciencias Naturales, Teruel

Bernor, R.L., Solounias, N., Swisher III, C.C. & Van Couvering, J.A., 1996 – The correlation of three classical 'Pikermian' mammal faunas-Maragheh, Samos, and Pikermi-with the European MN unit system – in: Bernor, R.L., Fahlbush, V. & Mittmann, H.-W. (eds.) – The Evolution of Western Eurasian Neogene Mammal Faunas – pp. 137-154, Columbia University Press, New York

Cordella, A., 1878 – La Grèce sous le rapport géologique et minéralogique – Parent, Paris

Crusafont-Pairó, M. & Petter, G., 1969 – Contribution à l'étude des Hyaenidae. La sous-famille des Ictitheriinae – Annales de Paléontologie (Vertébrés) 55 (1): 89-127

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

De Beaumont, G., 1969 – Brèves remarques sur *Plioviverrops* Kretzoi (Carnivora) – Bulletin des Laboratoires de Géologie, Minéralogie, Géophysique et du Musée géologique de l'Université de Lausanne 180: 1-7

De Beaumont, G., 1975 – Recherches sur les Félidés (Mammifères, Carnivores) du Pliocène inférieur des Sables à Dinotherium des environs d'Eppelsheim (Rheinhessen) – Archives des Sciences 28 (3): 369-405

De Beaumont, G. & Mein, P., 1972 – Recherches sur le genre *Plioviverrops* Kretzoi (Carnivora, ?Hyaenidae)– Comptes Rendus des Séances 25 (3): 383-394

De Bonis, L., 1994 – Les gisements des mammifères du Miocène supérieur de Kemiklitepe, Turquie. 2. Carnivora – Bulletin du Muséum national d'Histoire naturelle, C 16 (1): 19-39

De Bonis, L., Bouvrain, G. & Koufos, G.D., 1988 – Late Miocene mammal localities of the Lower Axios Valley (Macedonia, Greece) and their stratigraphic significance – Modern Geology 13: 141-147

De Bonis, L., Bouvrain, G., Geraads, D. & Koufos, G.D., 1992 – Diversity and paleoecology of Greek late Miocene mammalian faunas – Palaeogeography Palaeoclimatology Palaeoecology 91: 99-121

De Bonis, L. & Koufos, G.D., 1981 – New Hyaenid (Carnivora, Mammalia) in the Vallesian (Late Miocene) of Northern Greece – Scientific Annals of the Faculty of Physics and Mathematics, University of Thessaloniki 21: 79-94

De Bonis, L. & Koufos, G.D. 1991 – The late Miocene small carnivores of the lower Axios valley (Macedonia - Greece) – Géobios 24 (2): 361-379

De Bonis, L. & Koufos, G.D., 1994 – Some Hyaenidae from the Late Miocene of Macedonia (Greece) and a contribution to the phylogeny of the hunting hyaenas – Münchner Geowissenschaftliche Abhandlungen 26: 81-96

De Mecquenem, R., 1924-25 – Contribution à l'étude des fossiles de Maragha – Annales de Paléontologie 13: 135-160; 14: 1-34

Déprat, J., 1904 – Étude géologique et pétrographique de l'île d'Eubée – Besançon, Paris

Fraile, S., Pérez, B., De Miguel, I. & Morales, J., 1997 – Revisión de los carnívoros presentes en los yacimientos del Neógeno español – in: Calvo, J.P. & Morales, J. (eds.) – Avances en el conocimiento del Terciario Ibérico – pp. 77-80

Gaudry, A. & Lartet, E.A.I.H., 1856 – Sur les résultats des recherches paléontologiques entreprises dans l'Attique sous les auspices de l'Académie – Comptes Rendus des Séances de l'Académie des Sciences 43: 271-274

Gaudry, A., 1862-67 – Animaux Fossiles et Géologie de l'Attique – F. Savy, Paris

Gentry, A.W., Rössner, G.E. & Heizmann, E.P.J., 1999 – Suborder Ruminantia – in: Rössner, G.E. & Heissig, K. (eds.) – The Miocene Land Mammals of Europe – pp. 225-258, Dr Friedrich Pfeil, München

Ginsburg, L., 1999 – Order Carnivora – in: Rössner, G.E. & Heissig, K. (eds.) – The Miocene Land Mammals of Europe – pp. 109-148, Dr Friedrich Pfeil, München

Ginsburg, L., Morales, J. & Soria, D., 1981 – Nuevos datos sobre los carnivoros de Los Valles de Fuentidueña (Segovia) – Estudios Geológicos 37: 383-415

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

Howell, F.C. & Petter, G., 1980 – The *Pachycrocuta* and *Hyaena* lineages (Plio-Pleistocene and extant species of the Hyaenidae). Their relationships with Miocene ictitheres: *Palhyaena* and *Hyaenictitherium* – Géobios 13 (4): 579-623

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) – Géobios 18 (4): 419-476

Jacobi, B., 1982 – Zur Stratigraphie und Sedimentpetrographie der Neogenen Süßwasserablagerungen im Bereich von Agia Anna im Nordosten der Insel Euböa (Ägäis) – Diplomarbeit, Christian-Albrechts-Universität, Kiel

Kaup, J.J., 1832-1839 – Description d'ossements fossiles de Mammifères inconnus jusqu'à présent qui se trouvent au Muséum grand-ducal de Darmstadt, Darmstadt

Köhler, R.W., 1983 – Zur Stratigraphie, Sedimentologie und Petrographie Neogener Ablagerungen im Gebiet Kerassiá – Papades - Ag. Anna im Nordosten der Insel Euböa (Ägäis) – Diplomarbeit, Christian-Albrechts-Universität, Kiel

Kostopoulos, D.S., Spassov, N. & Kovachev, D., 2001 – Contribution to the study of *Microstonyx*: evidence from Bulgaria and the SE European populations – Geodiversitas 23 (3): 411-437

Koufos, G.D., 1987 – *Chasmaporthetes bonisi*, a new hyaenid (Carnivora, Mammalia) from the late

Miocene of Macedonia (Greece) – Bulletin de la Société Géologique de France 3 (5): 913-920

Koufos, G.D., 2000 – Revision of the late Miocene car nivores from the Axios valley, Macedonia, Greece – Münchner Geowissenschaftliche Abhandlungen 39: 51-92

Koufos, G.D., Koutsouveli, A., Galanakis, D., Sylvestrou, I., Vlachou, T., 1999 – A new Late Miocene mammalian locality from Velestinon, Thessaly, Greece. Contribution to the biochronology of the Neogene deposits – Comptes Rendus de l'Académie des Sciences 328 (7): 479-483

Kretzoi, M., 1952 – Die Raubtiere der Hipparionfauna von Polgardi – Annales Instituti Geologici Publici Hungarici 40 (3): 1-41

Major, C.I.F., 1888 – Sur un gisement d'ossements fossiles dans l'île de Samos, contemporains de l'âge de Pikermi – Comptes Rendus des Séances de l'Académie des Sciences 107: 1178-1181

Major, C.I.F., 1894 – Le gisement ossifère de Mytilini et cataloque d'ossements fossiles recueillis à Mitylini, île de Samos, et déposés au Collège Galliard, à Lausanne – pp. 1-51, Lausanne

Melentis, J.K., 1968 – Studien über fossile Vertebraten Griechenlands. 19. Die Pikermifauna von Halmyropotamos (Euböa - Griechenland). 1. Teil: Odontologie und Kraniologie – Annales Géologiques des Pays Helléniques 19: 285-411

Melentis, J.K., 1969 – Studien über fossile Vertebraten Griechenlands. 28. Die Pikermifauna von Halmyropotamos (Euböa - Griechenland). 2. Teil: Osteologie – Annales Géologiques des Pays Helléniques 21: 217-306

Mitzopoulos, M.K., 1947 – Die Verbreitung der Pikermistufe auf der Insel Euböa – Annales Géologiques des Pays Helléniques 1: 209-216

Morales, J. & Soria, D., 1979 – Nuevos datos sobre los carnivoros del área de Teruel. Sintesis y biostrati grafía – Estudios Geológicos 35: 497-504

Ozansoy, F., 1965 – Étude des gisements continentaux et des mammifères du Cénozoique de Turquie – Mémoires de la Société Géologique de France 102: 1-92

Petter, G. & Howell, F.C., 1987 – *Machairodus africanus* Arambourg, 1970 (Carnivora, Mammalia) du Villafranchien d'Ain Brimba, Tunisie – Bulletin du Muséum national d'Histoire naturelle 16 (1): 97-119

Pilgrim, G.E., 1931 – Catalogue of the Pontian Carnivora of Europe in the Department of Geology – British Museum (Natural History) Geology, London

Qiu, Z., 1985 – Restudy of "*Ictitherium hyaenoides*" in the Lagrelius Collection – Bulletin of the Geological Institutions of the University of Uppsala 11: 91-112

Qiu, Z., Huang, W. & Guo, Z., 1979 – Hyaenidae of the Qingyang (K'Ingyang) hipparion fauna – Vertebrata Palasiatica 17 (3): 200-221

Rook, L., Ficcarelli, G. & Torre, D., 1991 – Messinian carnivores from Italy – Bollettino della Societá Paleontologica Italiana 30 (1): 7-22

Roth, J. & Wagner, A., 1854 – Die fossilen Knochen-Ueberreste von Pikermi in Griechenland – Abhandlungen der Bayerischen Akademie der Wissenschaften 7: 371-464

Roussiakis, S.J., 1996 – Contribution to the study of the mammals of the classical locality of Pikermi – Unpublished PhD Thesis, University of Athens

Schmidt-Kittler, N., 1976 – Raubtiere aus dem Jungtertiär Kleinasiens – Palaeontographica, A 155: 1-131

Semenov, Y.A., 1985 – *Ictitherium pannonicum* (Carnivora, Viverridae) from Maeotic deposits of the Northern Black Sea area – Vestnik Zoologii 6: 23-27

Semenov, Y.A., 1989 – Ictitheres and morphologically related *hyaena*s from the Neogene of the USSR – Naukova Dumka, Kiev

Solounias, N., 1981 – The Turolian fauna from the island of Samos, Greece, with special emphasis on the hyaenids and bovids – Contributions to Vertebrate Evolution 6: 1-232

Sotnikova, M.V., 1992 – A new species of *Machairodus* from the late Miocene Kalmakpai locality in eastern Kazakhstan (USSR) – Annales Zoologi Fennici 28: 361-369

Steininger, F.F., 1999 – Chronostratigraphy, Geochronology and Biochronology of the Miocene "European Land Mammal Mega-Zones" (ELMMZ) and the Miocene "Mammal-Zones (MN-Zones)" – in: Rössner, G.E. & Heissig, K. (eds.) – The Miocene Land Mammals of Europe – pp. 9-24, Dr Friedrich Pfeil, München

Swisher III, C.C., (1996): New 40Ar/39Ar dates and their contribution toward a revised chronology for the late Miocene of Europe and West Asia – in: Bernor, R.L., Fahlbush, V. & Mittmann, H.-W. (eds.) – The Evolution of Western Eurasian Neogene Mammal – pp. 64-77, Columbia University Press, New York

Symeonidis, N.K., 1978 – Ein Schädel von *Metailurus parvulus* (Hensel) aus Pikermi (Attica, Griechenland) – Annales Géologiques des Pays Helléniques 29 (2): 698-703

Thenius, E., 1951 – Zur odontologischen Charakteristik von "*Felis*" *leiodon* aus Pikermi (Griechenland) – Neuen Jahrbuch für Geologie und Paläontologie 3: 88-96

Theodorou, G., Athanassiou, A., Roussiakis, S. & Iliopoulos, G., 1998 – Preliminary results on the recent excavations of the Kerassiá locality (Euboea) – in: abstracts Interim-Colloquium/RCMNS ‘Mediterranean Neogene Cyclostratigraphy in marine-continental palaeoenvironments’, Patras-Greece, 27-29 May 1998

Theodorou, G., Athanassiou, A., Roussiakis, S. & Iliopoulos, G., this volume – Remarks on the Late Miocene Vertebrates of Kerassiá (Northern Euboea, Greece)

Theodorou, G.E., Roussiakis, S.J. & Athanassiou, A., 1995 – Contribution to the study of the terrestrial Neogene of Greece: Artiodactyla and Rhinocerotidae from the Kerassiá and Chalkoutsi localities – in: abstracts 10th RCMNS Congress, 4 - 9 September 1995, Bucharest - Romanian Journal of Stratigraphy

Torre, D., 1989 – *Plioviverrops faventinus* n. sp., a new carnivore of late Messinian age – Bollettino della Societá Paleontologica Italiana 28 (2-3): 323-327

Van der Made, J. & Moyà-Solà, S., 1989 – European Suinae (Artiodactyla) from the Late Miocene onwards – Bollettino della Societá Paleontologica Italiana 28 (2-3): 329-339

Wagner, A., 1848 – Urweltliche Säugthier-Ueberreste aus Griechenland -– Abhandlungen der Bayerischen Akademie der Wissenschaften 5: 335-378

Wagner, A., 1857 – Neue Beiträge zur Kenntniss der fossilen Säugthier-Ueberreste von Pikermi Abhandlungen der Bayerischen Akademie der Wissenschaften 8: 11-158

Weithofer, A., 1888 – Beiträge zur Kenntniss der Fauna von Pikermi bei Athen – Beiträge zur Paläontologie Oesterreich-Ungarns 6 (3): 225-292

Werdelin, L., 1988a – Studies of fossil hyaenids: the genera *Thalassictis* Gervais ex Nordmann, *Palhyaena* Gervais, *Hyaenictitherium* Kretzoi, Lycyaena Hensel and *Palinhyaena* Qiu, Huang & Guo – Zoological Journal of the Linnean Society 92: 211-265

Werdelin, L., 1988b – Studies of fossil hyaenids: the genera *Ictitherium* Roth & Wagner and *Sinictitherium* Kretzoi and a new species of *Ictitherium* – Zoological Journal of the Linnean Society 93: 93-105

Werdelin, L. & Solounias, N., 1991 – The Hyaenidae: taxonomy, systematics and evolution – Fossils and Strata 30: 1-105

Woodward, A.S., 1901 – On the bone beds of Pikermi, Attica and on similar deposits in Northern Euboea – Geological Magazine 8 (11): 481-486

Zdansky, O., 1924 – Jungtertiäre Carnivoren Chinas – Palaeontologia Sinica 2 (1): 1-149

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PLATE 1 *Plioviverrops* sp., Kerassia 3. Fig. 1: Left humerus (K3/B1/4), anterior view. Fig. 2: Head of a left humerus (K3.206), juvenile, proximal view. Fig. 3: Distal epiphysis of a right femur (K3/B1/15), juvenile, distal view. Fig. 4: Left Mt IV (K3.191), lateral view. Fig. 5: Right calcaneum (K3.192) medial view. × 1. cf. *Ictitherium pannonicum*, Kerassia 3. Fig. 6: Right mandibular ramus (K3/204), labial view. Fig. 7: idem, occlusal view. Fig. 8: idem, lingual view. × 3/4.

PLATE 2 *Adcrocuta eximia*, Kerassia 4. Fig. 1: Skull fragment (K4/Δ388/1), occlusal view. Fig. 2: idem, labial view. x 3/4.

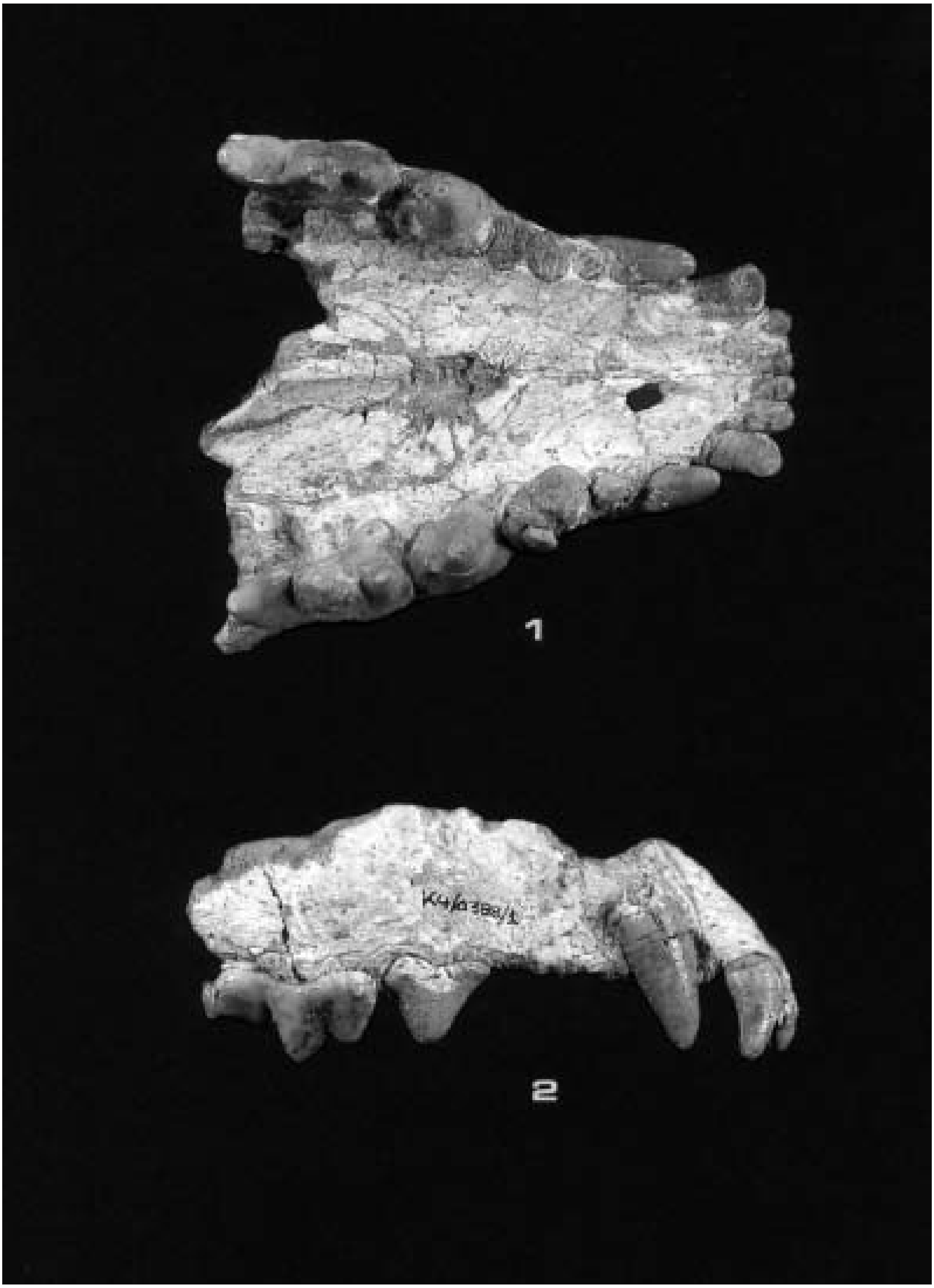

PLATE 3 *Adcrocuta eximia*, Kerassia 4. Fig. 1: Left mandibular ramus (K4/Δ388/2), labial view. Fig. 2: idem, occlusal view. Fig. 3: idem, lingual view. x 3/4.

PLATE 4 *Machairodus giganteus*, Kerassia 4. Fig. 1: Mandible (K4/Δ69/1), labial view. Fig. 2: idem, occlusal view. × 1/2.

PLATE 5 *Machairodus giganteus*, Kerassia 4. Fig. 1: Right upper canine (K4.14), labial view (× 1/2). Fig. 3: Left radius (K4/Δ110/16) anterior view (× 1/3). *Machairodus giganteus*, Pikermi. Fig. 2: Left upper canine (No 1967/7), lingual view (× 1/2). Fig. 4: Left mandibular ramus (P.G. 01/100), labial view. Fig. 5: idem, occlusal view. × 1/2.

PLATE 6 *Metailurus* cf. *parvulus*, Kerassia 1. Fig. 1: Left mandibular ramus (K1/Δ18), labial view. Fig. 2: idem, occlusal view. Fig. 3: idem, lingual view. × 1. *Metailurus parvulus*, Pikermi. Fig. 4: Left mandibular ramus (P.G. 01/103), labial view. Fig. 5: idem, occlusal view. × 1.

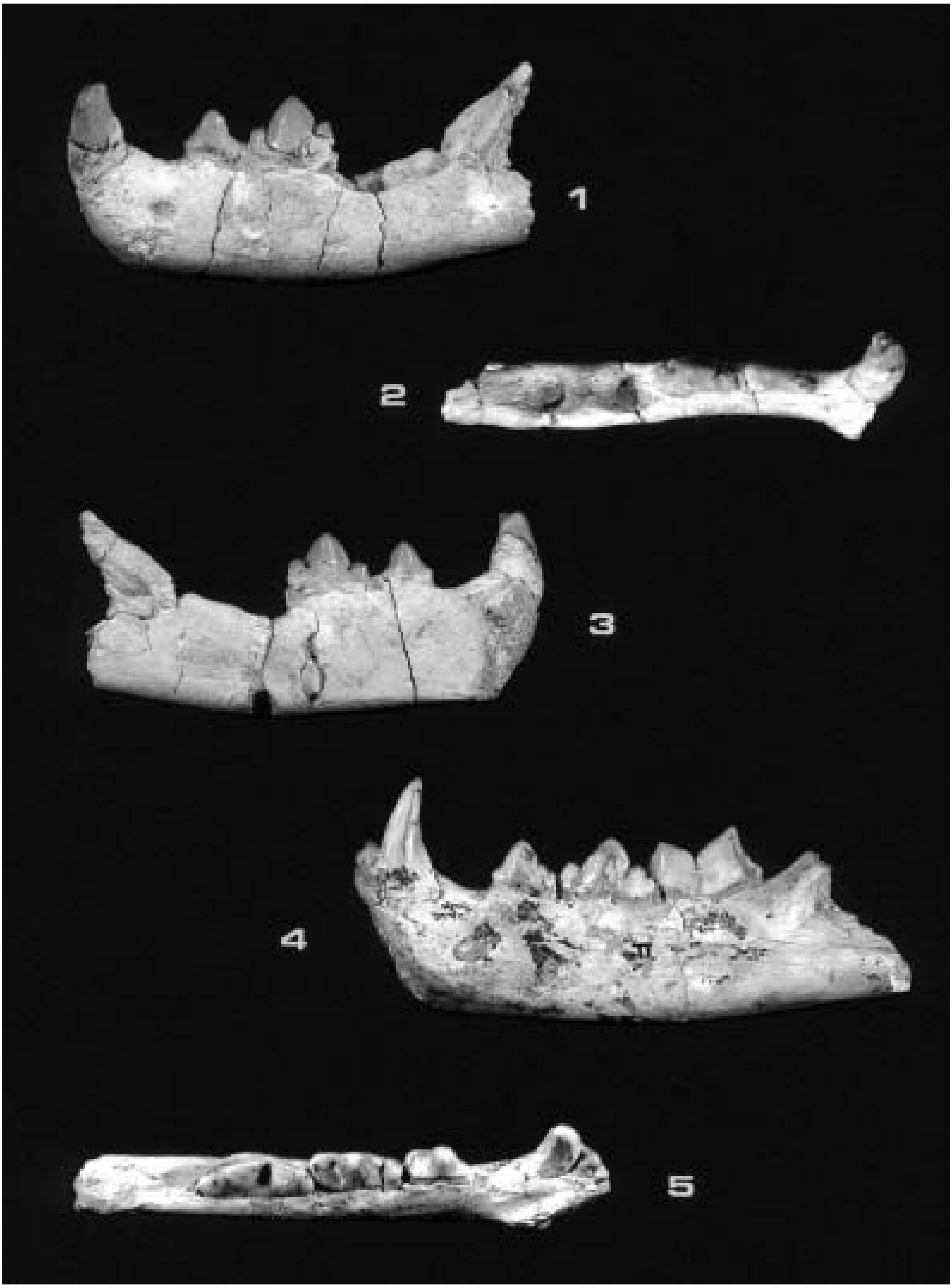

Table 1 Measurements of the humerus. Lmax: maximum length; Lf: maximum functional length; DTpr: maximum transverse diameter of the proximal epiphysis; DAPpr: maximum anteroposterior diameter of the proximal epiphysis; DTdist: maximum transverse diameter of the distal epiphysis; DAPdist: maximum anteroposterior diameter of the distal epiphysis.

	Lmax	**Lf**	**DTpr**	**DAPpr**	**DTdist**	**DAPdist**
Plioviverrops sp., K3.206, Kerassia 3	—	—	15.5	19.9	—	—
Plioviverrops sp., K3/B1/4, Kerassia 3	—	—	—	—	15.3	9.7
P. orbignyi, MNHNP PIK.3107, Pikermi	93.8	90.5	(13.8)	19.5	15.2	(10.5)
P. orbignyi, (Pilgrim 1931), Pikermi	(81)	—	—	—	14	—

Table 2 Measurements of the calcaneum. Hmax: maximum height; DTpr: maximum transverse diameter of the head; DTcol: transverse diameter at the middle of the neck; DTmax: maximum transverse diameter: DAPpr: maximum anteroposterior diameter of the head; DAPcol: anteroposterior diameter at the middle of the neck; DAPmax: maximum anteroposterior diameter.

	Hmax	**DTpr**	**DTcol**	**DTmax**	**DAPpr**	**DAPcol**	**DAPmax**
Plioviverrops sp., K3.192, Kerassia 3	25.6	6.9	4.5	+8.3	8.9	8.7	11.3
P. orbignyi, MNHNP PIK. 3111, Pikermi	24.2	6.5	4.5	10.1	8.8	9.0	10.0

Table 3 Measurements of the fourth metatarsal. Lmax: maximum length; DAPpr: maximum anteroposterior diameter of the proximal end; DAPdistart: anteroposterior diameter of the distal articular surface; DTpr: maximum transverse diameter of the proximal end; DTdistart: transverse diameter of the distal articular surface; DTdistmax: maximum transverse diameter of the distal end.

	Lmax	**DAPpr**	**DAPdistart**	**DTpr**	**DTdistart**	**DTdistmax**
Plioviverrops sp., K3.161, Kerassia 3	48.5	(6.8)	(4.5)	(3.2)	3.9	4.4
Plioviverrops sp., K3.195, Kerassia 3	49.3	7.6	4.8	(3.5)	3.8	4.3
P. orbignyi, (Pilgrim 1931), Pikermi	44	—	—	—	—	—

Table 4 Measurements of cf. *I. pannonicum* from Kerassia 3 and *I. pannonicum* from Polgardi and the Black Sea.

	cf. I. pannonicum K3.204, Kerassia 3	*I. pannonicum*, Polgardi (Semenov 1985)			*I. pannonicum*, Black Sea (Semenov 1985, 1989)		
		n	mean	min-max	n	mean	min-max
LC$_1$	(10.6)	—	—	—	2	12.05	11.5-12.6
WC$_1$	(8.1)	—	—	—	3	7.83	7.5-8.3
LP$_2$	11.3 a	3	12.90	12.7-13.0	2	13.40	13.3-13.5
WP$_2$	6.2 a	1	6.2	—	2	7.00	6.9-7.1
LP$_3$	14.8	5	15.60	15.3-16.0	4	16.58	15.9-17.2
WP$_3$	8.1	1	7.5	—	4	7.72	7.0-8.3
LP$_4$	16.6	3	16.67	16.0-17.8	4	16.95	16.4-17.6
WP$_4$	(7.7)	2	8.40	8.2-8.6	4	9.05	8.3-9.8
LpP$_4$	8.2	—	—	—	—	—	—
LM$_1$	20.5	2	19.58	19.3-20.4	5	20.18	19.3-21.0
WM$_1$	9.0	1	9.7	—	5	9.16	8.4-10.0
LtM$_1$	(14.9)	—	—	—	5	14.66	13.9-15.4
LM$_2$	8.9 a	1	9.6	—	3	9.63	9.4-9.8
WM$_2$	—	1	8.3	—	3	8.10	7.2-8.7
(WP$_3$/LP$_3$) × 100	54.7	—	—	—	4	46.55	44.1-48.2
(WM$_1$/LM$_1$) × 100	43.9	—	—	—	5	45.56	43.9-47.8
(LM$_2$/LM$_1$) × 100	(43.4)	—	—	—	3	46.8	46.2-47.3
LP$_2$-M$_1$	(64.0)	—	—	—	3	—	64-68
LP$_2$-M$_2$	(79.0)	—	—	—	1	77	—
Hdia	24.3	—	—	—	—	—	—
HbehM$_1$	28.7	—	—	—	—	—	—

Table 5 Measurements of *A. eximia* upper teeth from Kerassia and Pikermi. The data concerning the *A. eximia* from Pikermi are from Roussiakis (1996). These are based on the specimens mentioned by Howell & Petter (1985, tab. 6a) as well as on AMPG P.A. 490/91 described by Roussiakis (1996) and original measurements of MNHNP PIK. 3000 and AMPG P.G. 95/1507. The last specimen is mentioned as unnumbered by Howell & Petter (1985, tab. 6a). The statistical data have been recalculated, since there are some statistical inaccuracies in Howell & Petter (1985, tab. 7).

	A. eximia, Kerassia 4				*A. eximia*, Pikermi	
	K4/Δ388/1		K4.7	n	mean	min-max
	sin.	dext.				
LP^1	6.7	—	—	3	7.7	7.6-8.0
WP^1	6.4	—	—	3	7.4	7.0-8.0
LP^2	(19.3)	—	—	11	11.9	15.7-19.1
WP^2	(13.3)	—	—	11	12.7	11.4-15.0
LP^3	22.5	22.1	(24.6)	12	22.8	20.8-25.0
WP^3	16.4	15.9	—	12	15.4	14.4-16.8
LP^4	36.2	36.1	(41.1)	11	37.4	34.6-40.0
WP^4	19.2	19.3	(20.7)	12	18.0	14.4-21.0
LpP^4	13.2	12.9	(13.3)	3	13.2	13.0-13.5
LmP^4	15.5	15.5	(17.8)	4	15.5	14.5-16.4
LM^1	6.2	—	—	4	6.6	6.0-7.0
WM^1	12.9	—	—	4	13.4	13.0-14.0
(WP^2/LP^2) × 100	(68.9)	—	—	11	70.8	63.5-88.2
(WP^3/LP^3) × 100	72.9	71.9	—	12	67.8	60.0-72.7
(WP^4/LP^4) × 100	53.0	53.5	50.4	11	48.3	41.6-52.5
(WP^3/WP^4) × 100	85.4	82.4	—	11	85.6	76.2-108.3
(LmP^4/LP^4) × 100	42.8	42.9	(43.3)	4	41.4	40.0-43.0
(LP^4/LP^{2+3}) × 100	86.2	—	—	9	92.6	84.1-102.6
C-C	62.8		—	—	—	—
P-P	99.4		—	—	—	—

Table 6 Measurements of *A. eximia* lower teeth from Kerassia and Pikermi. The data concerning the *A. eximia* from Pikermi are from Roussiakis (1996). These are based on the specimens mentioned by Howell & Petter (1985, tab. 6a) as well as on AMPG P.A. 57/91, P.A. 445/91 and P.A. 1296/91 described by Roussiakis (1996) and original measurements of MNHNP PIK. 3001, AMPG P.G. 95/1505 and P.G. 95/1506. The last two specimens are mentioned as No 113 and unnumbered respectively, by Howell & Petter (1985, tab. 6a). The statistical data have been recalculated since there are some statistical inaccuracies in Howell & Petter (1985, tab. 7).

	A. eximia, Kerassia 4			*A. eximia*, Pikermi	
	K4/Δ388/2	K4/Δ388/3	n	mean	min-max
LP$_1$	5.0	—	6	5.7	5.5-9.1
WP$_1$	5.4	—	6	5.8	5.0-7.0
LP$_2$	16.1	16.0	13	16.6	15.0-17.4
WP$_2$	11.1	11.2	12	11.5	10.3-12.8
LP$_3$	19.4	19.5	12	19.8	18.6-22.0
WP$_3$	13.7	13.1	12	13.7	12.6-15.1
LP$_4$	21.4	21.5	11	22.3	20.9-24.0
WP$_4$	12.9	12.9	10	13.3	12.3-14.0
LM$_1$	27.7	(29.0)	10	27.4	25.9-29.7
WM$_1$	13.1	13.0	10	12.7	11.5-13.7
LtM$_1$	22.8	24.0	7	22.8	21.8-24.0
(WP$_2$/LP$_2$) × 100	68.9	70.0	12	69.7	64.7-75.7
(WP$_3$/LP$_3$) × 100	70.6	67.2	12	69.4	63.6-76.3
(WP$_4$/LP$_4$) × 100	60.3	60.0	10	60.2	53.7-65.4
(WP$_3$/WP$_4$) × 100	106.2	101.6	10	104.4	100.0-110.6
(LtM$_1$/LM$_1$) × 100	82.3	82.7	7	82.6	80.8-84.2
(LM$_1$/LP$_4$) × 100	129.4	(134.9)	8	126.9	117.7-133.3
(LM$_1$/LP$_{2+3+4}$) × 100	48.7	50.9	8	47.96	44.7-50.9
LP$_2$-M$_1$	81.2	(84.0)	—	—	—
HbehM$_1$	43.3	44.1	—	—	—
Hdia	41.2	41.2	—	—	—

Table 7 Measurements of *M. giganteus* from Kerassia 4 and Pikermi

	M. giganteus, K4/Δ69/1, Kerassia 4		*M. giganteus*, Pikermi		
	sin.	dext.	AMPG P.G.01/100	AMPG P.G.01/101	AMPG P.G.01/102
(L × W)C_1	15.0 × 11.2	— × 10.9	(17.3 × 11.6) r	—	—
(W × 100/L)C_1	74.6	—	(66.9) r	—	—
(L × W)P_3	(18.7 × 9.2)	18.8 × 9.0	17.8 × 7.7	(16.4) × 7.9	—
(L × W)P_4	— × 12.8	28.3 × 12.9	(27.0) × 11.2	28.8 × 11.6	— × 11.3
(L × W)M_1	— × (14.2)	35.6 × 15.1	32.5 × 12.7	31.4 × 12.1	32.0 × 13.9
LP_3-M_1	(77.2)	81.4	75.7	(73.2)	—
L$P_{3\text{-}4}$	47.0	48.4	44.4	44.6	—
diastema C_1-P_3	60.2	58.0	48.8	—	—
C_1-cond	240.6	244.0	—	—	—
Hdia	42.3	43.3	39.9	40.1	—
HbehM_1	42.2	43.8	45.6	45.0	42.0

Table 8 Measurements of the radius. Lmax: maximum length; DTpr: maximum transverse diameter of the proximal epiphysis; DTcol: transverse diameter of the neck; DAPpr: maximum anteroposterior diameter of the proximal epiphysis; DTdia: transverse diameter at the middle of the diaphysis; DAPdia: anteroposterior diameter at the middle of the diaphysis; DTdist: maximum transverse diameter of the distal epiphysis; DAPdist: maximum anteroposterior diameter of the distal epiphysis.

	Lmax	**DTpr**	**DTcol**	**DAPpr**	**DTdia**	**DAPdia**	**DTdist**	**DAPdist**
K4/Δ110/16, Kerassia 4	306.1	38.1	26.2	31.5	35.8	20.8	59.9	40.6
MNHNP PIK.3236, Pikermi	—	37.6	24.6	29.0	—	—	—	—

Table 9 Measurements of *M.* cf. *parvulus* from Kerassia 1 and *M. parvulus* from Pikermi, Chomateri and China.

	M. cf. *parvulus*	*M. parvulus*				
	K1/Δ18 Kerassia 1	Pikermi (Weithofer 1888)	Pikermi (Thenius 1951)	P.G. 01/103 Pikermi	Chomateri	China (Zdansky 1924)
LC_1	(7.8)	9.1	—	8.1	8.3	8.8-9.6 (n=5)
WC_1	(5.8)	6.6	—	5.7	6.0	6.3-(7.4) (n=5)
diastema C_1-P_3	8.5	7.5	9.2	8.9	8.6	6.8-(11.0) (n=5)
LP_3	(9.4)	—	10.3	9.7	9.9	9.9-10.7 (n=3)
WP_3	(4.6)	—	5.1	4.9	5.1	5.1-5.3 (n=3)
LP_4	(13.3)	15.0	14.4	14.2	13.9	14.5-15.4 (n=4)
WP_4	6.0	6.5	5.9	5.7	5.8	6.1-6.9 (n=4)
LM_1	—	17.8	17.2	17.3	17.1	16.7-18.1 (n=4)
WM_1	—	7.0	6.9	6.9	7.0	6.9-7.8 (n=4)
C_1-cond	—	—	—	—	101.2	—
Hdia	(17.5)	—	—	18.8	18.9	—
HbehM_1	—	—	—	20.1	19.4	—
(WC_1/LC_1) × 100	(74.4)	72.5	—	70.4	72.3	69.2-(77.1) (n=5)
(WP_3/LP_3) × 100	(48.9)	—	49.5	50.5	51.5	48.6-53. 5 (n=3)
(WP_4/LP_4) × 100	45.1	43.3	41.0	40.1	41.7	42.1-45.4 (n=4)
(WM_1/LM_1) × 100	—	39.3	40.1	39.9	40.9	39.8-45.1 (n=4)
(LP_3/LP_4) × 100	(70.7)	—	71.5	68.3	71.2	68.3-70.3 (n=3)
(LP_4/LM_1) × 100	—	84.3	83.7	82.1	81.3	80.1-86.8 (n=3)
(LM_1/L$P_{3\text{-}4}$) × 100	—	—	69.6	72.4	71.8	67.6-74.2 (n=3)

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