Carnivora (Mammalia) from the late Miocene of Akkaşdağı, Turkey

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ABSTRACT

Volcanic ashes in Akkaşdağı (Turkey) have yielded well preserved remains of late Miocene Carnivora belonging to three families. The Hyaenidae are the most abundant. *Adcrocuta eximia*, a very common large animal, and *Ictitherium viverrinum* were first described from the Greek locality Pikermi. The type specimen of *Hyaenictitherium wongii* has been found in China but the species is also present in European or Western Eurasian localities. *Thalassictis spelaea* and cf. *Thalassictis* sp. are less common but they were recovered from several European localities. The felid *Felis* cf. *attica* is a cat which is similar in size to *Leptailurus serval*; its type locality is Pikermi but it has also been found at some other sites in Europe and Asia. Another, larger felid is known from some limb bones. Skunks are not very common in Asian or European fossil localities. Nevertheless several species have been described. The Akkaşdağı skunk belongs to *Promephitis hootoni*.

KEY WORDS
Mammalia,
Carnivora,
Hyaenidae,
Felidae,
Mustelidae,
late Miocene,
Turolian,
Akkaşdağı,
Central Anatolia,
Turkey.

RÉSUMÉ

Carnivora (Mammalia) du Miocène supérieur d'Akkaşdağı, Turquie.

Un niveau de cendres volcaniques à Akkaşdağı (Turquie) a livré des restes fossiles appartenant à trois familles de carnivores. La famille des Hyaenidae est de loin la mieux représentée essentiellement par la grande espèce *Adcrocuta eximia* ; décrite tout d'abord dans le gisement du Miocène supérieur de Pikermi, elle a été retrouvée dans d'innombrables sites d'Eurasie. Son mode de vie devait ressembler à celui de la hyène tachetée actuelle, *Crocuta crocuta*, avec peut-être une prédilection plus grande pour les proies vivantes. *Hyaenictitherium wongii* et *Ictitherium viverrinum* avaient sans doute un régime alimentaire plus varié avec une denture plus broyeuse que celle d'*Adcrocuta*. En revanche *Thalassictis spelaea* et cf. *Thalassictis* sp. présentaient une denture plus proche de celle des hyènes « chasseresses » du Miocène

MOTS CLÉS
Mammalia,
Carnivora,
Hyaenidae,
Felidae,
Mustelidae,
Miocène supérieur,
Turolien,
Akkaşdağı,
Anatolie Centrale,
Turquie.

supérieur, *Chasmaporhetes* ou *Lycyaena*. Le petit félin de la taille du serval, *Felis* cf. *attica*, présente peu de variation dans les quelques gisements où il a été signalé ; la signification exacte de ces variations est difficile à interpréter dans la mesure où les restes sont toujours assez fragmentaires et où les espèces modernes diffèrent souvent par des détails anatomiques qui échappent à la fossilisation. Quelques éléments du squelette appendiculaire appartiennent à un autre félin, plus grand qu'une panthère. La petite moufette *Promephitis hootoni* est aussi assez proche des autres espèces décrites et même de certaines espèces actuelles ; signalons que ces dernières sont toutes américaines.

INTRODUCTION

There are many late Miocene fossil mammal bearing localities in Anatolia. Most of them have yielded carnivore remains mentioned or studied by Turkish or foreign researchers (Nafiz & Malik 1933; Yalçınlar 1946, 1950; Şenyürek 1952, 1953, 1954, 1957, 1958, 1960; Ozansoy 1957, 1961a, b, 1965; Tekkaya 1973; Becker-Platen *et al.* 1974; Schmidt-Kittler 1976; Sen 1990; Bonis 1994; Bonis *et al.* 1994; Kazancı *et al.* 1999; Lunkka *et al.* 1999; Viranta & Werdelin 2003). The Carnivora from Akkaşdağı add to the knowledge of this order in Anatolia. As is usual in a "catastrophic" fossil mammal locality (Kazancı *et al.* 1999), the carnivorans are relatively scarce in the volcanic ash sites of Akkaşdağı. They are represented by about 20 specimens among the 5000 teeth and bones recovered during the field campaigns. The family Hyaenidae is especially represented with four different genera which express each other different evolutionary trends. The remains are principally jaws and teeth but there are also some limb bones. There are no new species and so for the lists of synonymy I principally refer to Werdelin & Solounias (1991). Two other families, Felidae and Mustelidae, are also present with a few specimens representing two and one species respectively.

The material comes from the excavations at Akkaşdağı between 1997 and 2001. The bone pockets, all at the same stratigraphic horizon, are numbered as AK2, AK3... (2000-2001 excavations) or AKA and AKB (1997 excavations). Material is presented at the Natural History Museum in Ankara (MTA).

SYSTEMATICS

Family HYAENIDAE Gray, 1869
Genus *Adcrocuta* Kretzoi, 1938

Adcrocuta eximia (Roth & Wagner, 1854)

Hyaena eximia Roth & Wagner, 1854: 396. — Wagner 1857: 120. — Kittl 1887: 332.

Hyaena hipparionum Gervais, 1859: 242.

Hyaena sp. – Schlosser 1903: 33.

Hyaena variabilis Zdansky, 1924: 93.

Hyaena honanensis Zdansky, 1924: 103.

Crocuta eximia – Pilgrim 1931: 116. — Şenyürek 1958: 1.

Crocuta gigantea latro Pilgrim, 1932: 146.

Crocuta mordax Pilgrim, 1932: 150.

Adcrocuta eximia – Kretzoi 1938: 118. — Ficcarelli & Torre 1970: 25. — Schmidt-Kittler 1976: 59. — Koufos 1980: 83. — Solounias 1981: 91. — Bonis & Koufos 1981: 79. — Howell & Petter 1985: 460. — Werdelin & Solounias 1991: 24. — Bonis 1994: 20.

Adcrocuta praecursor Kretzoi, 1938: 118.

Adcrocuta variabilis – Kretzoi 1938: 118.

Crocuta (*Percrocuta*) *eximia* – Kurtén 1957: 397.

Crocuta miriani Meladze, 1967: 31.

MATERIAL. — Upper carnassial of an old individual (AK7-131), two right lower carnassials of two cubs (AK6-x and AK6-y), two right mandibles of probably the same young individuals as the cubs (AK3-128 and AK3-203), piece of maxilla with D3 and broken D4 (AK6-z), right mandible of a young adult (AK7-68), both rami of an adult mandible (AK3-82 and AK3-129), lower canine (AK3-83), left lower canine (AK5-251), lower p3 (AK5-317), lower i2 (AK5-571), right M1 (unnumbered), broken left M1(unnumbered), piece of distal humerus, phalanges.

DESCRIPTION (FIGS 1-4)

The large sized *Adcrocuta eximia* (size of the extant *Crocuta crocuta* (Erleben, 1877) the spotted hyena) is certainly the most common late Miocene hyaenid, having been found from China to Spain. The powerful jaws and crushing premolars are allied to an elongated carnassial and the presence of a well developed anterior accessory cusp on p4 which indicate a quite high shearing power. This animal was probably a carrion eater and bone crusher as well as a skill hunter. The species was first attributed to the genus *Hyaena* Linnaeus, 1758 (Roth & Wagner 1854), then to the genus *Crocuta* Kaup, 1828 by Pilgrim (1931) and finally to the new genus *Adcrocuta* Kretzoi, 1938. It is the most common hyaenid of Akkaşdağı with a minimum number of individuals of five with a piece of upper carnassial of an old individual (AK7-131), two right lower carnassials of two cubs (AK6-x and AK6-y) and the two right mandibles of probably the same young individuals (AK3-128 and AK3-203), a right mandible of a young adult (AK7-68), both rami of an adult mandible (AK3-82 and AK3-129) and some isolated teeth or bones.

The adult mandible AK3-129 and AK3-82 (Fig. 1) is quite complete on the left side except for the incisors, the canine and the p1 which are all represented by their alveoli. The ascending ramus is tall with very well marked muscular insertions which indicate a very powerful masseter muscle. The corpus is deep and there are two mental foramina, one below p2 and another one below the anterior root of p3. The premolars are slightly worn on their tips, especially p3. The shape does not differ from the numerous specimens described in the literature. The carnassial,

FIG. 1. — *Adcrocuta eximia* (Roth & Wagner, 1854), mandible AK3-83, AK3-129, Akkaşdağı, late Miocene (Turolian), Turkey, occlusal view. Scale bar: 5 cm.

FIG. 2. — *Adcrocuta eximia* (Roth & Wagner, 1854), right hemimandible AK7-68, p2-m2, Akkaşdağı, late Miocene (Turolian), Turkey, buccal view. Scale bar: 5 cm.

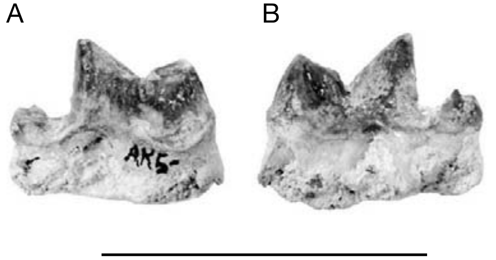

FIG. 3. — *Adcrocuta eximia* (Roth & Wagner, 1854), lower right d4 AK6-x, Akkaşdağı, late Miocene (Turolian), Turkey; **A**, buccal view; **B**, lingual view. Scale bar: 3 cm.

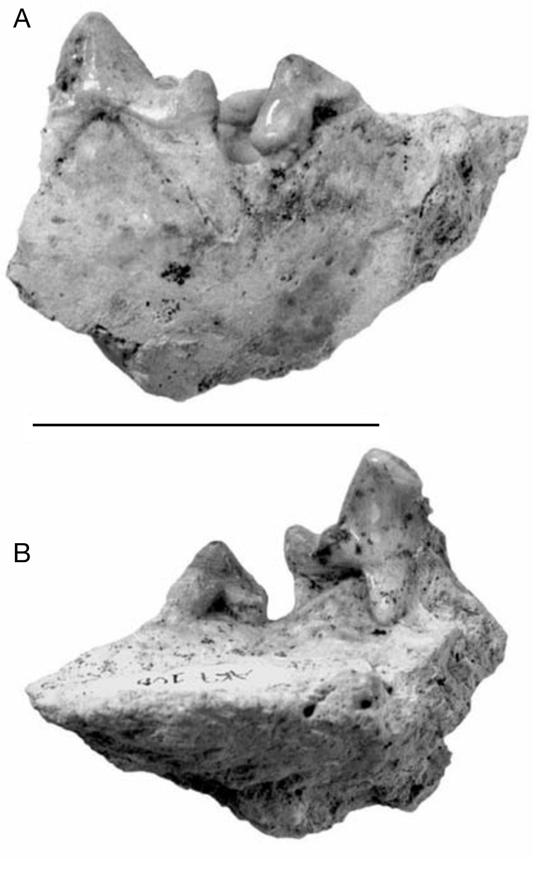

FIG. 4. — *Adcrocuta eximia* (Roth & Wagner, 1854), upper left D2-D3, Akkaşdağı, late Miocene (Turolian), Turkey; **A**, buccal view; **B**, lingual view. Scale bar: 3 cm.

m1, is elongated. There is a tiny cingulum at the base of the anterobuccal part of the paraconid. The protoconid is a little taller than the paraconid. The metaconid is very small and there is only one visible small cuspid on the talonid (hypoconid) with a low lingual crest in the place of the entoconid. There is no trace of a m2. An isolated right lower canine probably belongs to the same individual.

The right mandible AK7-68 has the alveolus of p1 and a very fresh dentition from p2 to m1 without any trace of m2 (Fig. 2). The corpus is a little less deep than that of the previous specimen but also has two mental foramina. The premolars are quite similar but the m1 differs in that its buccal cingulum is more developed, in the absence of a metaconid and in the presence of a very small but distinct entoconid on the talonid. The other mandibles, with very fresh premolars, are similar to AK7-68. They have the same degree of development as a very fresh left lower canine (AK5-251). Two right milk lower carnassials (AK6-x and y) have quite low and elongated paraconids and protoconids, the latter being a little higher, but no metaconids (Fig. 3). This is a derived state which differs from the more plesiomorphic deciduous carnassial of *Percrocuta* Kretzoi, 1938 (see Chen & Schmidt-Kittler 1983). On AK6-x the talonid is less worn and there are three cuspids, a high entoconid, a hypoconulid and a very worn hypoconid.

A piece of maxilla with D3 and broken D4 could belong to one of these individuals (Fig. 4). The D2 is low, simple and elongated. The piece of milk carnassial has a well developed parastyle and a lingually elongated protocone.

The piece of upper carnassial is very worn on the lingual face of the metastyle and it belongs to an individual older than those described above. An upper worn left M1 (5.7/29.2 mm) and a broken right M1 may belong to this individual.

A piece of distal humerus and a very uncomplete femur are quite similar to, although a little larger than the bones of *A. eximia* from Pikermi (Gaudry 1862-1867: pl. XIV, fig. 3). The distal humerus reaches a total distal breadth of 62.9 mm against 54.7 mm for the specimen figured by

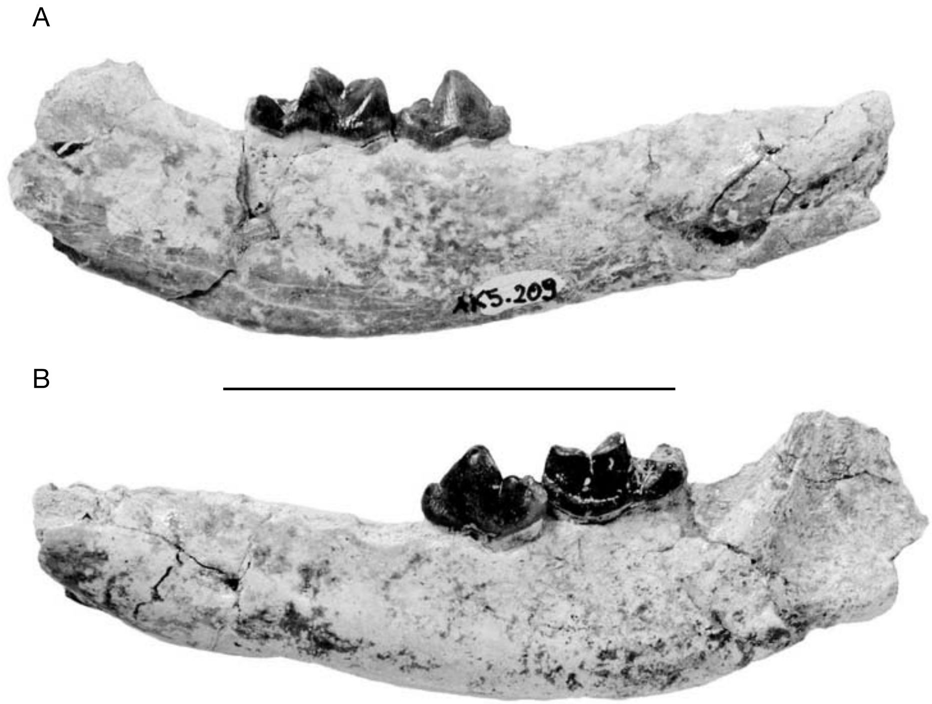

FIG. 5. — *Ictitherium viverrinum* Roth & Wagner, 1854, left hemi-mandible AK5-209, p4-m1, Akkaşdağı, late Miocene (Turolian), Turkey; **A**, buccal view; **B**, lingual view. Scale bar: 5 cm.

Gaudry (1862-1867: pl. XIV, fig. 3); on both bones, the epitrochlear foramen is absent, replaced by a small bony process. Some phalanges, especially phalanges of immature individuals, probably belong to *Adcrocuta eximia*.

Genus *Ictitherium* Wagner, 1848

Ictitherium viverrinum Roth & Wagner, 1854

Ictitherium viverrinum Roth & Wagner, 1854: 392. — Kretzoi 1938: 113. — Solounias 1981: 61. — Kurtén 1982: 1009. — Werdelin 1988: 101. — Beaumont 1988: 28. — Semenov 1989: 45. — Werdelin & Solounias 1991: 24.

Ictitherium robustum – Gaudry 1862-1867: 52. — Arambourg & Piveteau 1929: 65.

Thalassictis gracilis Hensel, 1862: 566.

Thalassictis viverrina – Hensel 1862: 566.

Ictitherium gaudryi Zdansky, 1924: 67.

Ictitherium sinense Zdansky, 1924: 72.

Palhyaena? *gaudryi* – Kretzoi 1938: 113.

Sinictitherium sinense – Kretzoi 1938: 114.

MATERIAL. — Left half mandible (AK5-209) with p4-m1, right p3, distal part of hind limb.

BACKGROUND

This is one of the smallest hyaenid recovered in Akkaşdağı. A mandible with p4-m1 (Fig. 5) is the sole specimen belonging to this species. Although the species was perfectly defined by Roth & Wagner (1854) for specimens coming from the late Miocene locality of Pikermi (Greece) which is the type locality of the species, *Ictitherium viverrinum* has a complicated history. Some years before the work of the two Austrian palaeontologists, Gervais (1850) named a species *Thalassictis robusta* for specimens recovered in the locality Kishinev (Ukraine) from figures in a manuscript written by von Nordmann. Some years later (1862-1867), Gaudry went back to the genus *Ictitherium* Wagner, 1848 and he called *Ictitherium robustum* the sample from Pikermi (Greece) nowadays housed in the Muséum national d'Histoire naturelle, Paris (MNHN). So the two species *viverrinum* and *robustum* were confused. The latter species was even considered as the type species of *Ictitherium* in so far as *viverrinum* and *robustum* (or *robusta*) were synonyms (Pilgrim 1931: 83) or attributed to other genera (see Werdelin & Solounias 1991). The question was revisited by Kurtén (1954) when redescribing and refiguring the type collection from Kishinev housed in the Museum of the Geological Institute of Helsinki University (Finland). Leaving these specimens in the genus *Ictitherium* Wagner, 1848, he compared the collection with other species and he also considered in the genus *Ictitherium* the following species: *I. wongii* Zdansky, 1924, *I. hipparionum* (Gervais, 1846) whose type specimen is lost, *I. sivalense* (Lyddeker, 1877), *I. hyaenoides* Zdansky, 1924, *I. gaudryi* Zdansky, 1924, *I. indicum* (Pilgrim, 1910) and *I. tauricum* Borissiak, 1915 but strangely he did not take into account *I. viverrinum* because he probably believed that it was really a synonym of *I. robustum*. Solounias (1981), in revising the hyaenids and bovids from the late Miocene of Samos (Greece), stressed clearly the differences between the species *viverrinum* and *robusta*, the first belonging to the genus *Ictitherium* and the second to the genus *Thalassictis* Gervais ex. Nordmann, 1850, with both being the type species of their genera. He gave a detailed description of *I. viverrinum* principally from the specimens of Samos. Shortly afterwards, in a parallel work, Kurtén (1982) reached the same conclusion that these species are not congeneric and that the two genera have different evolutionary trends and adaptations. He figured both lower and upper carnassials of these species to show the differences (Kurtén 1982: fig. 1) and nowadays this conclusion is generally accepted. One mandible from Akkaşdağı has the characters of *Ictitherium viverrinum*.

DESCRIPTION (FIG. 5)

The corpus is shallow with two mental foramina, the anterior under p2 and the second one under the anterior root of p3. The masseteric fossa is not very deep. The corpus bears the alveolus of c, p1 (single rooted), p2 and p3 (both double-rooted). The p4 is elongated with traces of buccal and lingual cingula. The anterior accessory cuspid is quite small and bulging. The main cuspid ("protoconid") has a faint vertical anterior crest and is as high as the paraconid of m1. The talonid is long and broad with a large buccal accessory cuspid ("hypoconid") and a smaller but well distinct lingual accessory cuspid ("entoconid") and a distal crest which ends the talonid basin. This talonid looks a little like that of a molar. This premolar is very close to that of *I. viverrinum* from Pikermi. The m1 is long especially because of the long talonid (Fig. 5). The trigonid is low but the metaconid is well developed. The hypoconid is linked by a low crest to the distal base of the protoconid. The entoconid is well developed and clearly separated from the metaconid. The hypoconulid exists as a distal crest which terminates the trigonid basin, separated by two notches from the other cuspids of the talonid. There is a single quite large alveolus for m2. There is a well developed cingulum along the base of the buccal face. There is a single quite large alveolus for m2. All these characters are present in the m1 of *Ictitherium viverrinum* from Pikermi. The size of the teeth lies among that of the smallest specimens of this species measured in the MNHN (Appendix: Table 1). An isolated third lower premolar matches this species.

A distal portion of a hind limb with astragalus, naviculum (tarsal scaphoid), ectocuneiform, mesocuneiform, metatarsals II to V and some phalanges are quite similar to the foot figured by Gaudry (1862-1867: pl. 9, figs 5, 6) under the name *Ictitherium* "*robustum*".

Genus *Hyaenictitherium* Kretzoi, 1938

Hyaenictitherium wongii (Zdansky, 1924)

Ictitherium hipparionum – Gaudry 1862-1867: 68. — Major 1894: 27. — Mecquenem 1925: 50. — Krokos 1939: 160. — Beaumont 1964: 339. — Koufos 1980: 56.

FIG. 6. — *Hyaenictitherium wongii* (Zdansky, 1924), left hemi-mandible AKK-115, Akkaşdağı, late Miocene (Turolian), Turkey; **A**, buccal view; **B**, lingual view. Scale bar: 5 cm.

Palhyaena hipparionum – Kittl 1887: 333. — Kretzoi 1938: 113.

Ictitherium wongii Zdansky, 1924: 73.

Ictitherium ?wongii – Kretzoi 1938: 113.

Hyaenalopex atticus Kretzoi, 1952: 21.

Ictitherium (*Palhyaena*) *hipparionum* – Schmidt-Kittler 1976: 81.

Palhyaena wongii – Howell & Petter 1980: 584.

Thalassictis wongii – Solounias 1981: 71. — Werdelin 1988: 223.

Thalassictis mesotes Kurtén, 1985: 81.

Hyaenotherium magnum Semenov, 1989: 94.

Hyaenotherium wongii – Semenov 1989: 105. — Werdelin & Solounias 1991: 33. — Bonis 1994: 21.

MATERIAL. — Mandible (AKK-115) with left c, p2-m2 and right c-p3.

BACKGROUND

Among the huge amount of material unearthed from late Miocene Chinese localities, a hyaenid smaller than *Adcrocuta eximia* but larger than *Ictitherium viverrinum* was described under the name *Ictitherium wongii* by Zdansky (1924). *H. wongii* is also intermediate between the two other species in its evolutionary trends, having a more cutting dentition than *I. viverrinum* but less than *Adcrocuta*. This species had been described outside China before Zdansky's publication under different names especially as *Ictitherium* (or *Palhyaena*) *hipparionum* (see above for this name) and later as *Thalassictis wongii* (see Werdelin & Solounias 1991 for synonymy) and finally as belonging to the new genus *Hyaenotherium* Semenov, 1989 with *H. wongii* as the type species.

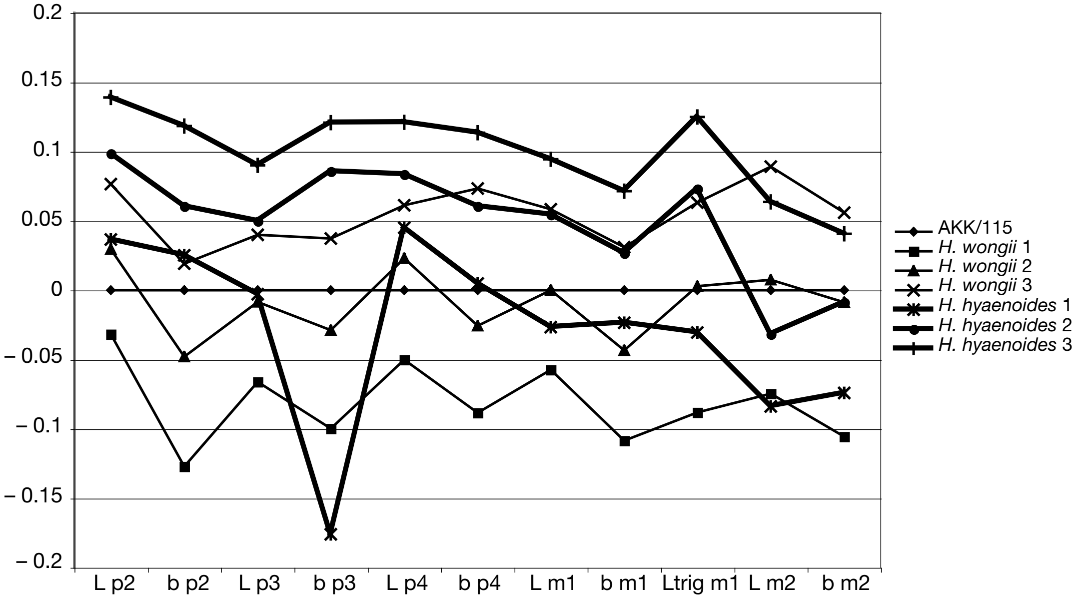

FIG. 7. — Logarithmic comparison of AKK-115 with specimens of *Hyaenictitherium wongii* (Zdansky, 1924) and *H. hyaenoides* Zdansky, 1924 from China (data from Werdelin). Abbreviations: **b**, breadth; **L**, length; **Ltrig**, length of the trigonid.

But in the Chinese late Miocene localities where *H. wongii* is most common, there is also another medium sized hyaenid *Ictitherium hyaenoides* Zdansky, 1924, later included in the new genus *Hyaenictitherium* by Kretzoi (1938). The differences between *wongii* and *hyaenoides* have been clearly stressed by Werdelin (1988). At that time the former was attributed to the genus *Thalassictis* (Werdelin, 1988) and then to *Hyaenotherium* Semenov, 1989. But if the specific differences are quite clear, we doubt the generic separation between the two species. *Hyaenictitherium hyaenoides* is generally larger than *H. wongii*, the premolars are broader but the main cuspid of p4 is relatively smaller, the talonid of m1 is slightly smaller and m2 is a little shorter, the upper carnassial is quite similar to that of *H. wongii* but the upper molars are more reduced, especially M2. These features allow us to differentiate the species but are not so strong as to separate two genera. Werdelin put both in the same genus *Hyaenictitherium* (in Zhang *et al.* 2002 and pers. comm.) and this is also my own opinion (Bonis 2004). A mandible from Akkaşdağı with the left ramus, part of the right one and isolated teeth of the same individual belongs to this species.

DESCRIPTION (FIGS 6; 7)

The mandible is broken in front of the p2 but the ramus is quite complete except for a part of the condyle that is missing (Fig. 6). The corpus is relatively deeper than that of *I. viverrinum* but less than that of *Adcrocuta*. The depth increases from the level of p2 to m1 and then decreases to the ramus, so the lower profile shows a bump under m1. A mental foramen is situated anteriorly under the mesial root of p2. The coronoid process is moderately elevated and the masseteric fossa is deep. The condyle is situated 2 cm above the short gonial process.

The corpus bears the alveolus of the canine and of the single rooted p1. The premolars are elongated and have a horizontal wear facet on the tip of the main cuspid. The p2 is asymmetric without any accessory cuspid. There are a very small mesial and a small distal accessory cuspids on p3. The accessory cuspids are more developed on p4 which has also a small linguo-distal accessory cusp like that of *Ictiherium viverrinum* but less developed. There is no clearly distinct distal crest. The proportions of the lower carnassial differ from that of *I. viverrinum* in having a shorter talonid relative to the trigonid. The metaconid is also more reduced. The single rooted m2 has an oval occlusal outline. It is completely worn and it is impossible to see the morphology of the crown.

The characters of this dentition and the measurements (Appendix: Table 1) fit quite well with *H. wongii* from China (Zdansky 1924; Werdelin 1988). This species has been recovered from China to Greece and has previously been described from Turkey (Bonis 1994; Viranta & Werdelin 2003). A logarithmic comparison (Fig. 7) shows that the dimensions of the Turkish fossil are closer to those of *H. wongii* but the differences between the two Chinese species are slight and some specimens could be difficult to identify.

Genus *Thalassictis* Gervais ex. Nordmann, 1850

The genus *Thalassictis* has been created by Gervais from drawings coming from a manuscript of Nordmann which was published later (Nordmann 1858). So the two names, Gervais and Nordmann, must be associated. *Thalassictis* was often mixed with *Ictitherium* (see above the discussion for *Ictitherium*).

Thalassictis spelaea (Semenov, 1988)

Ictitherium spelaeum Semenov, 1988: 46; 1989: 66.

Thalassictis spelaea – Werdelin & Solounias 1991: 47.

MATERIAL. — Right half mandible (AKK-114) with p1-m1.

A right hemi-mandible (AKK-114) with p1-m1 differs from all the other carnivores from Akkaşdağı. The size is similar to that of *Ictitherium viverrinum* but the morphology is clearly different.

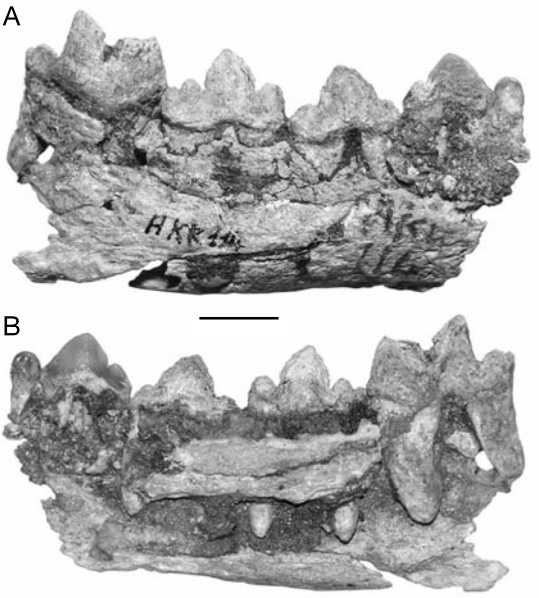

FIG. 8. — *Thalassictis spelaea* (Semenov, 1988), fragment of right mandible p1-m1, Akkaşdağı, late Miocene (Turolian), Turkey; **A**, buccal view; **B**, lingual view. Scale bar: 1 cm.

DESCRIPTION (FIG. 8)

The corpus mandibulae is destroyed in the lingual face and the roots of the teeth are visible. It was quite shallow. The teeth are unworn but the enamel of p3 to m1 is marked by weathering. The premolars are larger and larger from p1 to p4. The p1, one-rooted, is small and the crown is slightly buccolingually flattened and slightly asymmetrical, the mesial part being a little smaller and more steeply inclined than the distal one. The p2 has a tiny lingually situated mesial accessory cuspid and a distal one followed by a tiny cingulum. The p3, almost symmetrical, has two developed accessory cuspids, the distal one with a cingulum lingually enlarged. The p4 is also symmetrical with two, mesial and distal, very well developed accessory cuspids, trefoil or felid-like profile, and a more developed distal cingulum (Fig. 8). The m1 has a high trigonid with the protoconid clearly taller than the paraconid and a reduced metaconid. A cingulum runs buccaly along the trigonid and the metaconid. The talonid is moderately reduced. The hypoconid is on a thin crest running from the distal face of the protoconid and joining distally the end of the cingulum together with a hypoconid small crest which is separated by a small notch from the tiny entoconid. The latter is separated from the metaconid by a deep notch.

COMPARISONS

Some late Miocene hyaenid genera, *Chasmaporthetes* Hay, 1921, *Lycyaena* Hensel, 1861, *Miohyaenotherium* Semenov, 1989, *Metahyaena* Viranta & Werdelin, 2003, *Palinhyaena* Qiu, Huang & Guo, 1979 and *Thalassictis*, can be compared to the carnivores from Akkaşdağı.

All the species of *Chasmaporthetes* are larger, more robust with robust dentition.

The type species of *Lycyaena*, *L. chaeretis* (Gaudry, 1861), comes from the Greek locality Pikermi and is larger than AKK-114 (m1 = 26.6 mm). In the mandible (Gaudry 1861: pl. 15, figs 1, 2) the premolars, p3 and p4, are a little relatively taller but have the same accessory cuspids. We note that the mesial cuspid of the p4 is more developed in the specimen itself than in the Gaudry's drawing. The morphological characters of m1 match very well with AKK-114, particularly the pattern of the talonid. Nevertheless the metaconid of *L. chaeretis* is more reduced and the talonid is shorter (21.6% of the total length versus 26.3%). These two features are derived characters. Other species of *Lycyaena* are far larger than AKK-114.

Miohyaenotherium bessarabicum (Simionescu, 1937), sole species of the genus, has a p3 without mesial accessory cuspid and the same cuspid in p4 is relatively smaller. The talonid of m1 is shorter (21.4 to 23.4% versus 26.3%) and the p4 is shorter relative to m1.

Metahyaena confector Viranta & Werdelin, 2003 differs by the lack of accessory cuspids in p2 and p3, by the conical shape of the main cuspid of p4 and the greater width of the m1 talonid.

The premolars of *Palinhyaena* are taller, there is no accessory cuspid in p3 and the mesial accessory cuspid of p4 is relatively smaller. The metaconid of m1 is more reduced and the talonid is shorter (21% versus 26.3%).

Two species of *Thalassictis*, *T. robusta* and *T. spelaea*, match AKK-114 by the size and the depth of the mandible under p3-p4 is quite the same. The two species have developed accessory cuspids on the premolars, more developed in *T. spelaea*. The proportions of the m1 are similar to those of AKK-114. I identify this mandible as *Thalassictis spelaea* despite the difference in the geological age, Vallesian for *T. spelaea* and Turolian for AKK-114.

cf. ***Thalassictis*** sp.

MATERIAL. — Piece of right half mandible with m1 (AK7-107).

A m1 in a piece of mandible (AK7-107) does not match the Carnivora described above. Smaller than that of *Adcrocuta eximia*, it is a little larger than *Hyaenictitherium wongii* (Fig. 9).

DESCRIPTION (FIG. 9)

The tooth is in a fragment of mandible with a bit of the ramus but without the inferior part of the corpus. It belongs to a young adult and its morphology is very clear without any trace of wear. The paraconid is short relative to the protoconid. The latter is slightly taller than the former. The occlusal blades of both cuspids are almost in a straight line. The metaconid is reduced and it is sligthly visible in buccal view. There is a moderate buccal cingulum. The talonid is slightly reduced in length and is narrow, tapering toward the distal end. The hypoconid is centrally situated and linked by a small crest to the middle of the distal face of the protoconid. The entoconid is small and the talonid basin is closed by a clear hypoconulid which bears very tiny cusplets. There is no m2.

COMPARISONS

AK7-107 differs clearly from the species of *Ictitherium* by the higher trigonid, the reduced metaconid, the reduced talonid and the absence of m2. It differs from *Palinhyaena* Qiu, Huang & Guo, 1979 (see Werdelin 1988) by the slightly lower trigonid, the less reduced metaconid, the less reduced talonid and the absence of m2. It differs by the same characters from *Lycyaena* Hensel, 1861 of which the proportions between paraconid and protoconid are different: the paraconid is longer and the protoconid is higher in the type specimen of *L. chaeretis* (Gaudry, 1861) from Pikermi, type species of the genus. The buccal cingulum at the base of the paraconid is stronger in the Greek species. The metaconid is more reduced and more distally situated. The talonid is also a little different with a more trenchant hypoconid, a smaller entoconid and a very weak hypoconulid. The absence of m2 is sometimes considered as a character of *Lycyaena* but it is impossible to know if this tooth is present or not on the two mandibles from Pikermi that I have studied.

The talonid of *Hyaenictitherium wongii* or *H. hyaenoides* has quite the same length reduction relative to the trigonid length as that of AK7-107, and the metaconid is similar but the talonid is broader.

The morphology of the *Thalassictis robusta* lower carnassial is quite similar to that of AK7-107 (Kurtén 1982: fig. 1) and the proportions of the talonid length relative to the trigonid are similar but the talonid of *T. robusta* is less narrow. The *T. robusta* m1 is smaller than AK7-107 and the m2 is present. The type specimens of *T. certa* (Forsyth-Major, 1903) was recovered in the late middle Miocene (MN 7-8) of La Grive Saint-Alban (Isère, France). This species was considered the type of the genus *Miohyaena* Kretzoi, 1938. The m1 is a little smaller than AK7-107 and the trigonid is higher relative to the talonid which is more reduced. In fact this species does not differ substantially from the proportions of the genus *Miohyaenotherium* Semenov, 1989. *T. spelaea* (Semenov, 1988) from the late Miocene of Gritsev (Ukraine) is smaller than AK7-107. *T. proava* from the late middle Miocene or late Miocene of Pakistan is smaller and the metaconid of m1 is more reduced. The largest species of *Thalassictis* is *T. montadai* (Villalta Comella & Crusafont Pairo, 1943) described from Hostalets de Pierola in the late middle Miocene of Spain (Villalta Comella & Crusafont Pairo 1943) under the name *Ictitherium montadai*. It is a little smaller than AK7-107 but the morphological characters of the m1 seems to be quite similar except that the metaconid of m1 is a little less reduced in the Spanish species and the talonid is more reduced (J. Morales *in litt.*). Nevertheless, the absence of m2 on the Akkaşdağı carnivore seems to be a great difference but we know that this tooth is quite reduced and regressive in the species of *Thalassictis*. The same species has been identified as *Progenetta montadai vallesiensis* in the early Vallesian of Can Barra (San Quirza), Spain (Crusafont Pairo & Petter 1969). The m1 (20/10 mm) is smaller than that of AKK-107. The late middle Miocene Turkish locality Yeni Eskihisar has also yielded remains of *T. montadai* although attributed to the genus *Miohyaena* Kretzoi, 1938. The size of m1 is quite similar to that of Akkaşdağı but m2 is present. The Turolian locality Akkaşdağı is younger than the Spanish ones

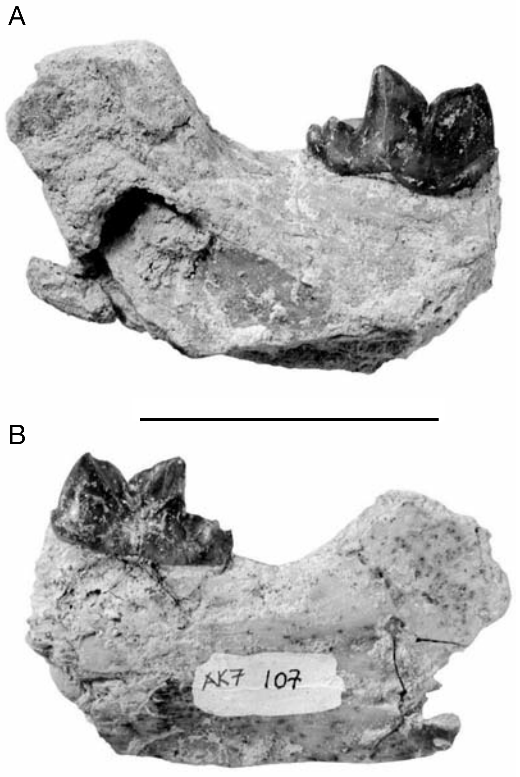

FIG. 9. — Cf. *Thalassictis* sp., fragment of right mandible with m1 AK7-107, Akkaşdağı, late Miocene (Turolian), Turkey; **A**, buccal view; **B**, lingual view. Scale bar: 3 cm.

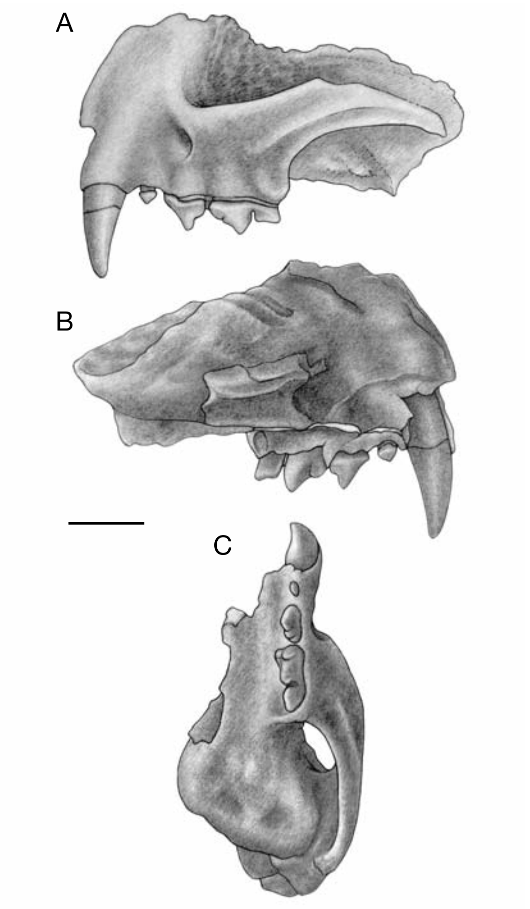

FIG. 10. — *Felis* cf. *attica*, piece of left maxilla with C-P4 AKK-212 (drawings), Akkaşdağı, late Miocene (Turolian), Turkey; **A**, lateral view; **B**, medial view; **C**, occlusal view. Scale bar: 1 cm.

with *T. montadai* as well as the locality Yeni Eskihisar, so if the loss of m2 is not an individual character, it could be a derived feature of a new younger species of *Thalassictis*. But, however, another specimen identified as *Hyaena namaquensis* Stromer, 1931 and later referred to *Hyaenictitherium* (Werdelin & Solounias 1991) seems to be close to AKK-107 in the morphology of m1. The metaconid seems to be reduced in the same way and the talonid is narrow but it bears three distinct and well developed cuspids. Nevertheless, the m2 is present in the mandible of *H. namaquensis* although the type specimen is younger geologically than AK7-107 (early Pliocene). Another mandible recovered from the locality of Sahabi (latest Miocene or early Pliocene) first described as *Ictitherium* (*Palhyaena*) *arkesilai* Esu & Kotsakis, 1980 and later referred to *Hyaenictitherium namaquensis* (Werdelin & Solounias 1991) can be compared to AK7-107. The lower m1 is quite similar in the morphology but it is larger and m2 is present. So with this poor material it is difficult to reach a firm conclusion. Another species, *Miohyaenotherium bessarabicum* (Simionescu, 1938), with a relatively high trigonid and short talonid has also been described from localities of Ukraine and Georgia. The m1 can reach 20 mm in length but the morphological characters do not differ substantially from those of some species of *Thalassictis*. So the relationships between some *Hyaenictitherium*, *Thalassictis*, *Miohyaena* or *Miohyaenotherium* species are yet unclear. Until the recovering of new documents, it is better to consider the fragmentary mandible AK7-107 as cf. *Thalassictis* sp. despite the lack of m2.

Family FELIDAE Fischer de Waldheim, 1817
Genus *Felis* Linnaeus, 1758

Felis cf. ***attica*** Wagner, 1857

MATERIAL. — Piece of left maxilla (AKK-212) with C-P4.

DESCRIPTION (FIG. 10; APPENDIX: TABLE 2)
A small feline (Fig. 10) a little larger than a wild cat and reaching the size of the serval is represented in Akkaşdağı by an undistorted fragment of a left maxilla with the zygomatic arch and bearing C-P4 (AKK-212). On the maxilla, the quite large pear-shaped infra-orbital foramen is above the anterior root of P3. The muzzle seems to have been very high, relatively short and steeply forwardly inclined. The zygomatic arch is robust, high and it bears a strong lateral antero-posterior ridge like in most felines. In ventral view, the temporal fossa appears to be narrower than in other cats of similar size, like *Leptailurus* Severtzov, 1858 or *Leopardus* Gray, 1852. The canine is robust and laterally flattened, especially on the lingual face; there is only a posterior crest,

a little worn near the tip of the crown. P2 is very small with a somewhat laterally flattened asymmetric crown; there is a diastema between canine and premolar, and another between P2 and P3. The P3 is high, without an anterior accessory cusp but with a small posterior cingular cusp. On P4, the parastyle is small, smaller for instance than in *Leptailurus*, and there is no ectoparastyle (preparastyle); the paracone and metastyle are lengthened; the protocone is more reduced than in the modern felines and it passes by a little the level of the parastyle. The first molar is absent on the specimen.

COMPARISONS

The small felines are rare in sites of the late Miocene. The first specimens were described by Kaup (1833) under the names *Felis prisca* and *F. antediluviana*. Both came from the *Dinotherium* sands of the late Miocene (Vallesian) of Eppelsheim. Wagner (1857) described, under the name *Felis attica*, the anterior part of a calvarium accompanied by its mandible, currently housed in the Palaeontological Museum of Munich. The lower jaw was not separated from the calvarium until recently, so the observation of the dentition was difficult. A fragment of maxilla from Maragha (Iran) has been published by de Mecquenem (1924-1925) and a skull from "Vatilük" (nowadays Vathylakkos 3) near Thessaloniki (Greece) by Arambourg & Piveteau (1929) as *Felis attica* or *F.* cf. *attica*, both from the late Miocene. Another skull from the late Miocene of Samos (Greece) and housed in the Museum of Lausanne, had been published by Major (1891) as *F. neas* Major, 1891 but renamed with the same name by Pilgrim (1931) who did not consider the designation of Major valid. The same skull has been also considered as close to *F. attica* (Beaumont 1961). Some fragmentary late Miocene remains of small felines have also been assigned to one of the previous species sometimes without figuration or description. This is the case, for example, of *F. attica* (Schmidt-Kittler 1976; Azanza *et al.* 1993; Morales *et al.* 1999), *F. antediluviana* Kaup, 1833 (Morales & Soria 1979), *F.* aff. *prisca* Kaup, 1833 (Nicolas 1978), *Felis* sp. (Kretzoi 1952; Qi 1983; Qiu & Qiu 1995).

Both type specimens of *Felis antediluviana* and *F. prisca* are larger than the Akkaşdağı maxilla (Kaup 1832) and they probably do not belong to the genus *Felis*. So we shall compare only our specimens with *F. attica* and *F. neas*. Pilgrim (1931) attempted to specify differences between the two species. *F. attica* is a little bigger than the present European wild cat with an elongated skull and a muzzle that is relatively longer than the occiput. The teeth are rather strong, P2 is small, P3 is provided with a small posterior accessory cusp and P4 with an ectoparastyle (preparastyle) and a more reduced protocone than in extant felids except *Leopardus*. M1 is relatively larger than that of the cat. For Pilgrim (1931) *F. neas* is of medium size, a little larger with a relatively more slender skull than in any other species, but with a short muzzle and a stretched out occipital region. The orbits are elongated antero-posteriorly, the post-orbital process is not prominent, the zygomatic arch slightly projecting to the outside, so the temporal cavity is longer than broad, the jugal process of the zygomatic overhangs the infra-orbital foramen, which is pear-shaped, the lachrymal is bounded above by a sharp ridge above which are the flat, rather broad nasals, while below the face falls very steeply to the alveolar margin. The upper canine is oval in cross-section. P2 is rather long, and separated from the canine. P3 has a small posterior accessory cusp but no anterior cusp or cingulum. The carnassial does not have an ectoparastyle. But from the study of the skull in the Lausanne Museum, Beaumont (1961) reached a different conclusion. A careful comparison with the specimens from Pikermi shows that there are only slight differences between them and they must belong to the same species *Felis attica*.

A survey of the small feline of "Salonika" has recently been undertaken (Koufos 2000) and the author took this opportunity to review the description of the type specimen of *F. attica*. It seems not to possess an ectoparastyle, contrary to the affirmation of Pilgrim (1931) which was a result of the figures of the specimen of

FIG. 11. — Felidae indet., right distal humerus AK5-670, Akkaşdağı, late Miocene (Turolian), Turkey; **A**, cranial face; **B**, caudal face. Scale bar: 5 cm.

Vathylakkos which was better described at this time than that of Pikermi. *F. attica* did not possess an ectoparastyle, as it is the case in the specimens of Samos, Maragha and Akkaşdağı. Therefore Vathylakkos constitutes an exception in this respect and one may wonder about the importance of this character in the diagnosis of the species. The size is rather variable between all these specimens. The length of the upper carnassial can vary between 12.3 and 13.0 mm (Appendix: Table 2) with a mean of 12.85 and a standard deviation of 0.46 for only four specimens. In the extant European wild cat, *Felis sylvestris* Schreber, 1777, the mean is 10.89 and the standard deviation is 0.69 for 17 specimens (original data from S. Peigné). It seems that the size of the different specimens could correspond to a single species, *Felis attica*. Nevertheless AKK-212 differs a little from the other specimens in the height of the maxilla and its steepler inclination. It is probably better to consider it as *Felis* cf. *attica* until the cranial variation of this species is better known.

Felidae indet.

MATERIAL. — Right distal humerus and proximal ulna (AK5-670), ulna (AK5-unnumbered), proximal (AK5-668) and distal (AK5-669) of a right radius, left astragalus (AK5-377).

DESCRIPTION (FIGS 11; 12)
Some limb bones belong to a species of a large felid. A distal humerus and associated ulna (AK5-670) are larger than those of *Panthera pardus* (Linnaeus, 1758) and smaller than a lion or a tiger (Figs 11; 12). On the humerus, the capitulum is partially broken; the deltoid crest may have been shorter and less pronounced than in extant large felids; the distal maximal breadth is about 60.5 mm; the trochlea is well developed and relatively larger than in a lion; the epitrochlea (medial epicondyle) is relatively as large as that of a lion but the epitrochlear arcade is more robust; the epicondyle (lateral epicondyle) and the epicondyliar crest are relatively weaker than in a lion; on the caudal face, the olecranon fossa is as large as in a lion but it is expanded more proximodistally than laterally and the lateral epicondylar crest is weaker. On the ulna, part of the anconeal process and part of the lateral margin of the radius articular surface are missing. The articular surface for the humeral trochlea is less medially oriented than in a lion ulna. The preserved part of the shaft is straight, narrowing from proximal to distal; well marked grooves on the lateral and medial surface indicate strong *abductor pollicii* and *pronator quadratus* muscles respectively. Another piece of ulna (AK5-unnumbered) reaches the same size but the olecranon is smaller. It could indicate a variation between two individuals of the same species or perhaps another species. I favour the first hypothesis. Two pieces, proximal (AK5-668) and distal (AK5-669) of a

FIG. 12. — Felidae indet., right proximal ulna AK5-670, Akkaşdağı, late Miocene (Turolian), Turkey; **A**, lateral face; **B**, medial face. Scale bar: 5 cm.

right radius, certainly belong to the same individual that the humerus and ulna (AK5-670).

A left astragalus (AK5-377) with a deep trochlea, especially in the lateral part (Fig. 13), has a head whose great axis is almost dorso-plantally oriented. The lateral part of the facet for the coracoid process of the calcaneum is laterally extended as a process. This specimen may also belong to the same individual.

In the late Miocene localities of Asia and Europe, there are few carnivores whose size is intermediate between a panther and a small lion. *Machairodus* Kaup, 1833 is too big and *Paramachairodus* Pilgrim, 1913 seems too small. These bones could belong to *Metailurus major* Zdansky, 1924 or to a species of *Dinofelis* Zdansky, 1924, but it is difficult to be certain.

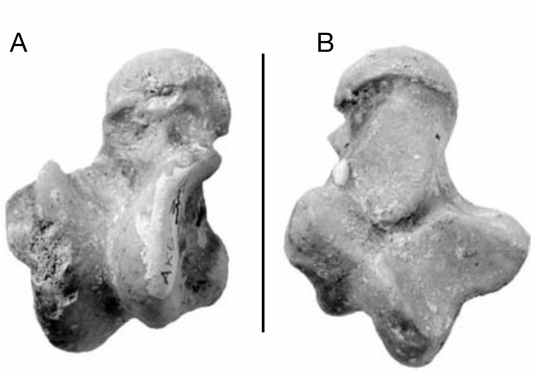

FIG. 13. — Felidae(?) indet., left astragalus AK5-377, Akkaşdağı, late Miocene (Turolian), Turkey; **A**, dorsal view; **B**, plantar view. Scale bar: 3 cm.

Family MUSTELIDAE Fischer de Waldheim, 1817
Subfamily MEPHITINAE Bonaparte, 1845
Genus *Promephitis* Gaudry, 1861

Promephitis hootoni Şenyürek, 1954

Promephitis hootoni Şenyürek, 1954: 276.

MATERIAL. — Right half mandible (AK5-674) with i1-m1.

Remains of small carnivorans are quite rare in the late Miocene Turkish localities (Şenyürek 1952, 1953, 1954; Ozansoy 1965; Schmidt-Kittler 1976; Bonis 1994) so the discovery of a small carnivore half mandible in AK5 yields new insights into this group of mammals in the Near East. This is a well preserved right mandible with the right incisors, the canine, the p2 alveolus and p3-m1 followed by the m2 alveolus. The corpus and the ascending ramus are complete.

DESCRIPTION (FIG. 14; APPENDIX: TABLE 3)

The body of the mandible (corpus) is short, deep (Appendix: Table 3) and robust. The symphysis is steeply inclined and the maximum deep is beneath p3. The inferior border is quite straight under p3 to m2 and ascends steeply under the coronoid process; it ends in a short angular process. The coronoid process (ramus) is tall and triangular, the top not being distally curved. The masseteric fossa is quite shallow but limited mesially along the coronoid process by a strong crest; on the corpus, the

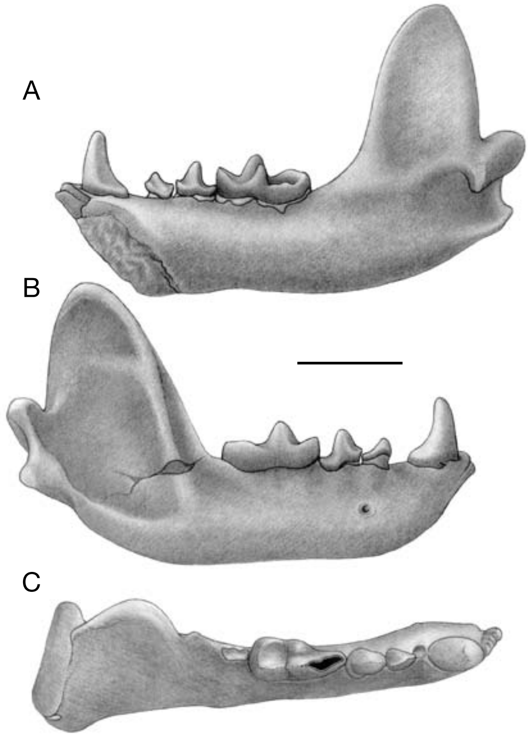

FIG. 14. — *Promephitis hootoni* Şenyürek, 1954, right half mandible with c, p3-m1 AK5-674 (drawings), Akkaşdağı, late Miocene (Turolian), Turkey; **A**, lingual view; **B**, buccal view; **C**, occlusal view. Scale bar: 1 cm.

fossa ends anteriorly under the posterior part of m2. The lingual surface of the coronoid process is a little hollow which could indicate a strong temporal muscle. The articular condyle is situated a little above the level of the top of the m1 protoconid; it is very extended bucco-lingually. A mental foramen is situated at mid-height beneath the distal root of p3 (Fig. 14).

The incisors are small and much worn. It is impossible to observe any detail on the crowns. Their size increases slightly from i1 to i3. The basal sections of the i1 and i2 crowns are oval, while that of i3 is more rounded. The canine is tall and robust especially at the base of the crown. There is a very smooth distal crest. The crown is oval in cross section but the mesio-distal axis increases greatly from the tip to the base. There is a lingual cingulum. We can see a small, horizontal wear facet on the tip of the canine. There is no diastema between the canine and the premolars, nor between the cheek teeth themselves. The p2 is represented only by a small rounded alveolus which is placed slightly lingual to the rest of the toothrow. The other premolars are reduced and simple without any accessory cuspids and their size increases from p3 to p4. The basal sections of the crowns are egg-shaped with the maximum breadth at the distal part. In lateral view, both p3 and p4 are asymmetric, the distal part being longer than the mesial one. A distal cingulum demarcates a small hollow talonid. The top of p4 is slightly higher than the protoconid of m1. The first molar is low; the protoconid is higher than the paraconid but the latter is partially worn. The metaconid is as tall as the paraconid, robust and situated in front of the distal part of the protoconid but not visible in buccal view. The hollow talonid is as long as the trigonid and surrounded by a crest. The hypoconid is taller and larger than the entoconid and another cuspid situated between the latter and the metaconid. The alveolus of m2 is oval and is not horizontal, but slightly inclined along the ramus. The dentition on the whole shows a crushing adaptation.

COMPARISONS

If we except otters, with whom the Akkaşdağı mandible shares no characters, three subfamilies of mustelids have crushing dentitions: Leptarctinae Gazin, 1936, Melinae Bonaparte, 1838 and Mephitinae. Among these we can find some species of a size similar to AK5-674. The differences between species are sometimes tiny and the genera can be put in one subfamily or another depending on the authors' opinions.

The Miocene Leptarctinae are represented by three genera (Ginsburg 1999). *Trochotherium* Fraas, 1870 (*T. cyamoides* Fraas, 1870) is a very derived carnivore whose mandible is robust like that of AK5-674 but the coronoid process is lower. The base of the canine is large and the premolars, p2 and p3, are reduced. But p4 is larger and more asymmetric, and the lower carnassial has no metaconid and is so inflated that it is difficult to see the demarcation between the other cuspids of the trigonid. This species was certainly a shell crusher. *Gaillardina* Ginsburg, 1999 is known from "*Mustela*" *transitoria* Gaillard, 1899 with only a skull from La Grive Saint-Alban (middle Miocene, MN 7-8). The third genus, *Trocharion* Major, 1903 (*T. albanense* Major, 1903), is less derived and well known through material from La Grive Saint-Alban in France, Valles Pénédes in Spain (Petter 1963, 1967, 1976) and especially Steinheim in Germany (Helbing 1936). The mandible is deep but less so than AK5-674. There is a full premolar dentition and the premolars are larger, p2 is double-rooted and p4 is considerably more than half the length of m1. The carnassial is lower-crowned with a larger metaconid. The talonid is as long as the trigonid with small cusps on the hypoconid ridge. The m2 is double-rooted. Most of the characters are different from those of AK5-674. We must note that *Trocharion* is a Melinae for Helbing (1927) or Petter (1967), a Leptarctinae for Ginsburg (1999), while for Pilgrim (1932) it is allied to *Mephitis* E. Geoffroy Saint-Hilaire & G. Cuvier, 1795.

The Melinae are well represented in the Miocene by several genera. Some have only large species or are known through upper dentitions and cannot be compared to AK5-674. *Taxodon* Lartet, 1851 is known through two species; one, *T. sansaniensis* Lartet, 1851, from Sansan, dated to the middle Miocene (MN 6) and another, *T. hessicum* Ginsburg, 1999, from the late Miocene of Spain and Germany (MN 9 to MN 12). The premolars are longer and p4 has a posterior accessory cuspid and a bulging anterior cingulum. There is a deep notch between protoconid and talonid of m1 whose metaconid is more reduced and the talonid a little shorter. Several species belong to the genus *Trochictis* Meyer, 1842. They differ from AK5-674 by a slender mandible, the presence of p1, the double-rooted p2, and the longer p3 and p4 (Meyer 1842; Schlosser 1888; Helbing 1927; Pilgrim 1932; Viret 1933; Petter 1976). *Plesiomeles cajali* Viret & Crusafont, 1955 is founded on a mandible with m1 from the Vallesian of Spain. The mandible is badger-like, slender with a double-rooted p2 and the m1 has a long talonid with several cusplets on the entoconid edge. *Grivamephitis* Beaumont, 1973 was first established as a subgenus of *Plesiomeles* Viret & Crusafont, 1955. The best known species *G. pusilla* (Major, 1903) is a minute one and has a slender mandible, a p4 with a small posterior accessory cuspid and a notch on the distal crest of the crown and a m1 with a metaconid placed rather posteriorly, a longer talonid and cusplets on the entoconid crest. *Palaeomeles* Villalta & Crusafont, 1943 (*P. pachecoi* Villalta & Crusafont, 1943 from the latest middle Miocene) differs from AK5-674 in a m1 with a more reduced and distally situated metaconid and a huge multicuspid talonid. *Promeles* Zittel, 1890 species (*P. palaeattica* (Weithofer, 1888) and *P. macedonica* Schmidt-Kittler, 1995), both in the late Miocene, are far larger than AK5-674. The mandible is robust but less than in AK5-674. The top of the coronoid process is rounded and not sharp. The lower p1 is absent, but p2 is double-rooted and the premolars are relatively longer, while p4 has a small posterior accessory cuspid. The metaconid of m1 is posteriorly placed and the talonid longer, with several cusplets on the entoconid edge.

Nowadays, the Mephitinae live in northern and southern America but during the Miocene they were present in Eurasia. They have been described from the late early Miocene of Wintershof-West in Germany with *Miomephitis pilgrimi* Dehm, 1950. This primitive species shows some of the main characters of the group. The mandible is robust, the canine is stout and the premolars are reduced. The m1 has a large metaconid and is adapted to a crushing diet. AK5-674 differs from *Miomephitis* Dehm, 1950 in its deeper mandible, more reduced premolars and the shape of the coronoid process. *Proputorius* Filhol, 1891 from the late middle Miocene and the upper Miocene is founded on *P. sansaniensis* Filhol, 1891. It differs from AK5-674 in its less robust mandible, double-rooted p2, less reduced premolars with a large cingulum and less crushing m1 with a shorter talonid. There are two other species, *P. pusillus* (Viret, 1951) and *P. medius* Petter, 1963, of which the latter is sometimes considered as belonging to a different genus, *Mesomephitis* Petter, 1967. Both have similar characters.

The genus *Promephitis* Gaudry, 1861 was created for *P. larteti* Gaudry, 1861, recovered from the Turolian (MN 12) locality Pikermi. The size is similar to AK5-674, as is the robustness of the mandible and the shape of the coronoid process. But the inferior border of the mandible is not upwardly directed under the ascending ramus. The lower carnassial is also similar to that of AK5-674. We note the same difference for *P. alexejevi* Schlosser, 1924 from Mongolia which is also larger than AK5-674. The p3 is also shorter relative to m1. *P. majori* Pilgrim, 1933 from Samos has a less robust canine and smaller premolars relative to m1; the metaconid of m1 is more distally situated. Another species, *P. hootoni* Şenyürek, 1954, was recovered from Asia Minor in the Turolian locality of Küçükyozgat. The shape of the mandible is very similar to that of AK5-674 but the corpus is a little less robust (robustness index under m1 = 79.5 against 99); the size of the dentition is also similar. For Şenyürek, this species differs from *P. larteti*, whose lower p2 is missing and whose m2 alveolus is horizontal. In *P. hootoni* this alveolus "is seen to be slanting upward, in side view". It differs also from *P. majori* in its less reduced lower premolars. Two other species, *P. maeotica* Alexejew, 1916 and *P. malustenensis* Simionescu, 1930, are larger. The latter one has a large distance between p4 and m1; the m1, which has a cingulum, is larger absolutely and relatively, the metaconid of the carnassial is also smaller than that of AK5-674 and this specimen could belong to another genus. In summary, I refer the specimen from Akkaşdağı to *Promephitis hootoni*. The skunks seem to have been quite diversified in Eurasia through the late Miocene, but the differences between the species are slight. It seems that they invaded the New World before becoming extinct in the Old one after the Pliocene if the Asian genus *Mydaus* F. Cuvier in Geoffroy Saint-Hilaire & F. Cuvier, 1821 is closer to the badger than to the skunks.

We can remark that *Promephitis gaudryi* Schlosser, 1902, described from an isolated m1 from the Vallesian of Melchingen, seems very similar to the m1 of *Trocharion albanense* and does not belong to the Mephitinae.

CONCLUSION

The carnivore fauna of Akkaşdağı is quite poor in species as well as in minimum number of individuals except for the large hyaenid *Adcrocuta eximia*. The main reason may be the type of fossiliferous deposits. Most of the fossils from Akkaşdağı come from a cinerite and they were certainly killed suddenly by a volcanic eruption. Their remains are generally very well preserved. Nevertheless in some places bones have been broken by reworking in small streams because of heavy rain some time after the volcanic eruption. This type of fossilisation causes sorting and selection in the complete fauna of the area and a bias in the sampling of the populations, wherein only animals present in this restricted place have been selected. Most of the species which are present belong to the Hyaenidae. Some isolated incomplete bones (ulna, radius, astragalus) cannot be identified to the genus level but they correspond to middle-sized ictitheres. *Adcrocuta eximia* was a typical carnivore of the Eurasian late Miocene (Turolian). It is found in all the rich Eurasian fossil deposits from China to Spain and it was probably very abundant. It can be compared to the recent spotted hyena *Crocuta crocuta*. The robust premolars indicate a powerful jaw for bone crushing and *A. eximia* probably fed on carrion but the large and cutting lower carnassial without metaconid or with a very tiny one and a very short talonid indicates that, like the extant species, it also fed on living prey. The three other species belong to the group which is called ictitheres but they are quite different each other. The smallest species is *Ictitherium viverrinum* which is also the more omnivorous. It is characterised by a lower carnassial with a low trigonid with a well developped metaconid and a long talonid. The lower m2 is also elongated and so the crushing part of the dentition is well developed. *Hyaenictherium wongii* is also a very common species in the late Miocene Eurasian fossil bearing localities from China to Greece and possibly Germany. It probably had a more fleshy diet than *I. viverrinum* but the relatively broad talonid of m1 and the size of m2 indicate a diet which could have been similar to that of some extant canids. The last species, *Thalassictis spelaea* and cf. *Thalassictis* sp., have a more cutting lower carnassial with a very reduced metaconid and the m2 is lacking. The premolars of *Thalassictis* are not adapted to bone crushing and in some way this species shows an evolutionary trend which is parallel to that of some late Miocene hunting hyenas like *Lycyaena* or *Hyaenictis*. Each of the four genera of the Akkaşdağı hyaenids occupied its own place in the guild of late Miocene carnivores and the whole shows the Miocene diversity of a family which is now reduced to a few species. The felid *Felis* cf. *attica* looks quite similar to other specimens from late Miocene Eastern Mediterranean realm. It is nevertheless impossible to definitely ascribe the material to the species without a complete skull. We must note also that the extant genera and species of small felids are often distinguished by characters which cannot be observed on fossils.

Promephitis hootoni is a small skunk first described in Küçükyozgat. It is slightly different from other species coming from Samos or Pikermi.

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APPENDIX

TABLE 1. — Lower permanent tooth measurements of Akkaşdağı Hyaenidae. Abbreviations: **b**, breadth; **L**, total length; **Ltr**, length of the trigonid.

	No.	**i2**		**ci**		**p1**		**p2**		**p3**		**p4**		**m1**			**m2**	
		L	**b**	**L**	**b**	**L**	**b**	**L**	**b**	**L**	**b**	**L**	**b**	**L**	**b**	**Ltr**	**L**	**b**
Hyaenictitherium wongii	AKK-115 sin			10.9	7.9			11.4	6.7	15.6	7.8	16.5	8.7	20.2	9.5	14.7	5.7	5.1
Hyaenictitherium wongii	AKK-115 dex			10.6	7.6	3.1	3.4	11.2	6.4	15.3	7.8							
Ictitherium viverrinum	AK5-209											13.8	7.3	16.4	7.5	11.4		
cf. *Thalassictis* sp.	AK7-107													21.1	9.5	14.4		
Thalassictis spelaea	AKK-11					4.7	3.4	11.8	5.7	13.5	7.1	15.5	8.0	18.6	8.8	13.7		
Adcrocuta eximia	AK5-317									16.0	8.7							
Adcrocuta eximia	AK3-82							16.7	13.0	21.5	14.7	23.4	14.2	28.9	13.6	23.8		
Adcrocuta eximia	AK3-129							16.5	13.4	20.6	14.4	22.7	14.2	28.2	14.0	24		
Adcrocuta eximia	AK3-83				19.8	15.0												
Adcrocuta eximia	AK5-251				20.0	15.4												
Adcrocuta eximia	AK5-571	8.6	8.0															
Adcrocuta eximia	AK7-68							16.5	11.8	19.6	13.5	23.2	13.8	29.3	13.4	24.0		
Adcrocuta eximia	AK3-203							16.2	12.2		13.0	22.3	14.2					
Adcrocuta eximia	AK3-128									20.4								

TABLE 2. — Measurements of upper teeth of *Felis* cf. *attica*. Abbreviations: **b**, breadth; **ba**, anterior breadth; **bms**, breadth of the metastyle; **L**, total length; **Lms**, length of the metastyle; **Lpa**, length of the paracone.

No.	**C**		**P2**		**P3**		**P4**				
	L	**b**	**L**	**b**	**L**	**b**	**L**	**Lpa**	**Lms**	**ba**	**bms**
AKK-212	6.6	4.9	3.0	1.9	8.0	4.3	13.5	8.3	5	6.3	4.0

TABLE 3. — Measurements of the mandible and lower teeth of *Promephitis hootoni* Şenyürek, 1954. Abbreviations: **Br-tal**, breadth of the talonid; **Br-trig**, breadth of the trigonid; **H-md**, height of the mandible; **L-trig**, length of the trigonid; **Ro-ind**, robustness index (height of corpus × 100/length of m1).

	c	**p2**	**p3**	**p4**	**m1**
Length	4.2		2.6	3.9	8.5
Breadth	2.9		2	2.9	
L-trig					4.9
Br-trig					3.2
Br-tal					3.9
H-md below		9	9.2	8.8	8.4
Ro-ind below		106	108	104	99