

A new Late Miocene mammalian fauna in the Karaburun Peninsula (W Turkey)

Tanju Kaya, Izmir, Denis Geraads, Paris, and Vahdet Tuna, Izmir

With 7 figures and 4 tables

KAYA, T., GERAADS, D. & TUNA, V. (2005): A new Late Miocene mammalian fauna in the Karaburun Peninsula (W Turkey). – N. Jb. Geol. Paläont. Abh., **236**: 321–349; Stuttgart.

Abstract: The locality of Esendere, in the Karaburun peninsula, west of Izmir, Turkey, yielded a small mammalian fauna of early Turolian (Late Miocene) age that is especially interesting because it includes two new species of Carnivores. *Protictitherium aegaeum* n. sp. is one of the latest representatives of this group, which survived later in Turkey than elsewhere. *Promeles smyrnensis* n. sp. differs by its skull and upper tooth morphology from the two previously known species from continental Greece, but looks closer to the Samos form, and perhaps also to “*Mustela*” *palaeosinensis* from China.

Zusammenfassung: Die Lokalität Esendere auf der Karaburun-Halbinsel, westlich von Izmir (Türkei) gelegen, enthielt eine kleine Säugerfauna von frühem Turolium-Alter (Ober-Miozän), die aufgrund zweier neuer Carnivoren-Arten von besonderem Interesse ist. *Protictitherium aegaeum* n. sp. stellt einen der letzten Vertreter dieser Gruppe dar, die in der Türkei länger als andernorts existierte. *Promeles smyrnensis* n. sp. unterscheidet sich im Schädel und in der Morphologie der Oberkiefer-Bezahnung von den beiden schon bekannten Arten der Gattung aus Kontinental-Griechenland und steht hingegen der Form aus Samos und möglicherweise ebenso “*Mustela*” *palaeosinensis* aus China näher.

Key-words: Mammalian fauna, Carnivora, Late Miocene, Turkey.

1. Introduction

Late Miocene localities are known from many countries of the eastern Mediterranean. In Turkey, early Late Miocene localities (Vallesian-equivalent) are relatively few (SICKENBERG et al. 1975), being mostly represented in the Sinap Formation near Ankara (FORTELIUS et al. 2003). Most of the known localities are of Turolian-equivalent age, but only a few have been studied in detail (e.g. SEN 1994), and the fossil record for this period is very incomplete.

We describe here a new Turolian fauna from the upper part of the Karaburun formation, at the locality Esendere, south of Karaburun (N 38° 35' 37", E 26° 33' 46"), in the Karaburun Peninsula, west of Izmir (Fig. 1).

Two mammalian faunas are already known in the Karaburun Peninsula. The Çiftlikköy-Çesme fauna consists of *Gomphotherium* sp., *Sanitherium leobense* and Ruminantia indet., which indicate a Middle Miocene age (BESENECKER 1973). The Mordoğan fauna comprises *Ischyricitis* cf. *anatolicus* SCHMIDT-KITTLER, 1976; Carnivora indet., *Percrocuta miocenica* PAVLOVIC & THENIUS, 1965; *Protictitherium intermedium paraliium* KAYA et al., 2003; cf. *Protanancus* sp.; *Beliajevina* sp.; *Listriodon splendens* VON MEYER, 1846; *Giraffokeryx* sp.; *Micromeryx* sp.; ? *Turcocerus* sp.; ? *Tethytragus* sp., and *Hypsodontus pronaticornis* KÖHLER, 1987, and therefore belongs to the Middle Miocene (KAYA et al. 2003).

The Esendere fauna was discovered by Neset ÖZTEKİN in 1998, and excavated since then by two of us (T.K. and V.T.). The studied material is housed in the Natural History Museum, Ege University, Izmir, Turkey, and numbered IKE (for Izmir-Karaburun-Esendere).

The pre-Neogene basement in the Karaburun Peninsula consists of a Lower Triassic (ERDOĞAN et al. 1990) or Palaeozoic (ROBERTSON & PICKETT 2000) clastic assemblage, a Middle Triassic to Jurassic carbonate assemblage, and an upper unconformably overlying Late Cretaceous to Paleocene "Bornova Mélange" (ERDOĞAN et al. 1990; ROBERTSON & PICKETT 2000).

The Neogene sedimentary strata (Fig. 1) are primarily confined to the eastern shoreline, and overlie a volcanic succession terminating with a felsic tuff unit (KAYA 1981). They begin with the fluvialite Ardiç Formation, the uppermost part of which contains the Mordoğan mammalian fauna. The Aliğa limestone rests gradationally on the Ardiç formation, and unconformably on the older late Cenozoic rocks and the Mesozoic basement. It consists of white, thickly bedded limestone, and minor limy mudstone and felsic tuff. The limestone is microcrystalline, and contains sparse freshwater algae and mudstone detritus. The Karaburun formation lies unconformably on the older late Cenozoic rocks and the basement. It consists primarily of massive mudstone and lithic sandstone. However, thin interlayers of oolitic

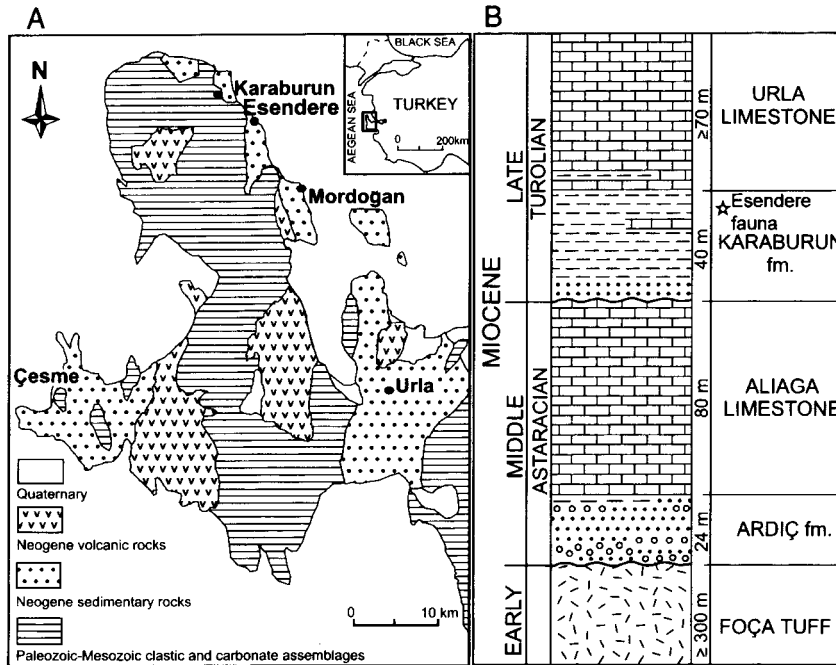


Fig. 1. **A** – Simplified geological map of the Karaburun peninsula. From ERDOĞAN et al. (1990) and BESENECKER (1973). **B** – Simplified stratigraphic column of the Miocene succession in the Karaburun peninsula. From KAYA (1981).

limestone, claystone and conglomerate occur subordinately. The Karaburun formation represents a muddy fluvial assemblage grading upwards into lacustrine facies (KAYA 1981). Its upper part contains the mammalian fossils described below, that indicate a Late Miocene age.

Abbreviations: MGL: Musée géologique, Lausanne; MNHN: Muséum National d'Histoire Naturelle, Paris; MTA: Maden Tetkik ve Arama, Ankara; TTMEU: Tabiat Tarihi Muzesi, Ege University, Izmir. Measurements are given in millimetres. Upper teeth are in uppercase, lower teeth in lowercase.

2. Systematic palaeontology

Order	Carnivora BOWDICH, 1821
Family	Hyaenidae GRAY, 1869
Genus	<i>Protictitherium</i> KRETZOI, 1938

Protictitherium aegaeum n. sp. Figs. 2C-G, 4A

Holotype: Crushed skull with mandible, IKE-46 (Figs. 2C-G, 4A).

Diagnosis: A species of *Protictitherium* of large size. P3 narrow, mesial cusp only slightly shifted lingually. P4 with large protocone; upper molars large, with crescent-shape protocone, mesio-buccal angle much expanded; p4 with strong mesial cuspid, main cuspid very high; m1 with high trigonid, paraconid almost as high as the protoconid, metaconid high, talonid long, with entoconid the highest cuspid; m2 large, with high metaconid. Differs mainly from the closely related *P. crassum* by its high p4, very high trigonid of m1 with paraconid almost as high as protoconid.

Description: Both halves of the skull are somewhat displaced relative to each other, and distorted. The skull is narrow, low and long (Fig. 2F-G). The frontal region is slightly swollen between the orbits. The anterior orbital margin is at the level of the front of P4. The large infraorbital foramen is above the distal part of P3. The temporal crests are Y-shaped; they meet to form a single sagittal crest, which extends posteriorly over the cranial vault as far as the supraoccipital bone. The occipital area is crushed.

The teeth are almost unworn (Figs. 2C-E, 4A). The incisors are set in a shallow arch; they increase in size from I1 to I3. The upper canine is large, compressed transversally and curved; it is separated from I3 by a diastema (7 mm). P1 and P2 are missing.

The P3 is small, being both short and not thickened, in contrast to typical hyaenids. The main cusp is high and keeled obliquely relative to the axis of the tooth. Two crests descend from its top towards the mesial and distal accessory cusps but the mesial cusp is only incipient, and almost in line with

Fig. 2. A – *Promeles smyrnensis* n. sp., IKE-33, occlusal view of P4-M1 (stereo). **B** – same specimen, occlusal view of left tooth-row. Scale = 10 mm for Fig. 2A, 15 mm for Fig. 2B. **C-G** – *Protictitherium aegaeum* n. sp., IKE-46. **C** – occlusal view of P3-M2; **D** – labial view of P3-P4; **E** – labial view of p2-m1. Scale = 1 cm for Figs. 2C-E. **F-G** – right and left lateral views of skull; scale = 10 cm.

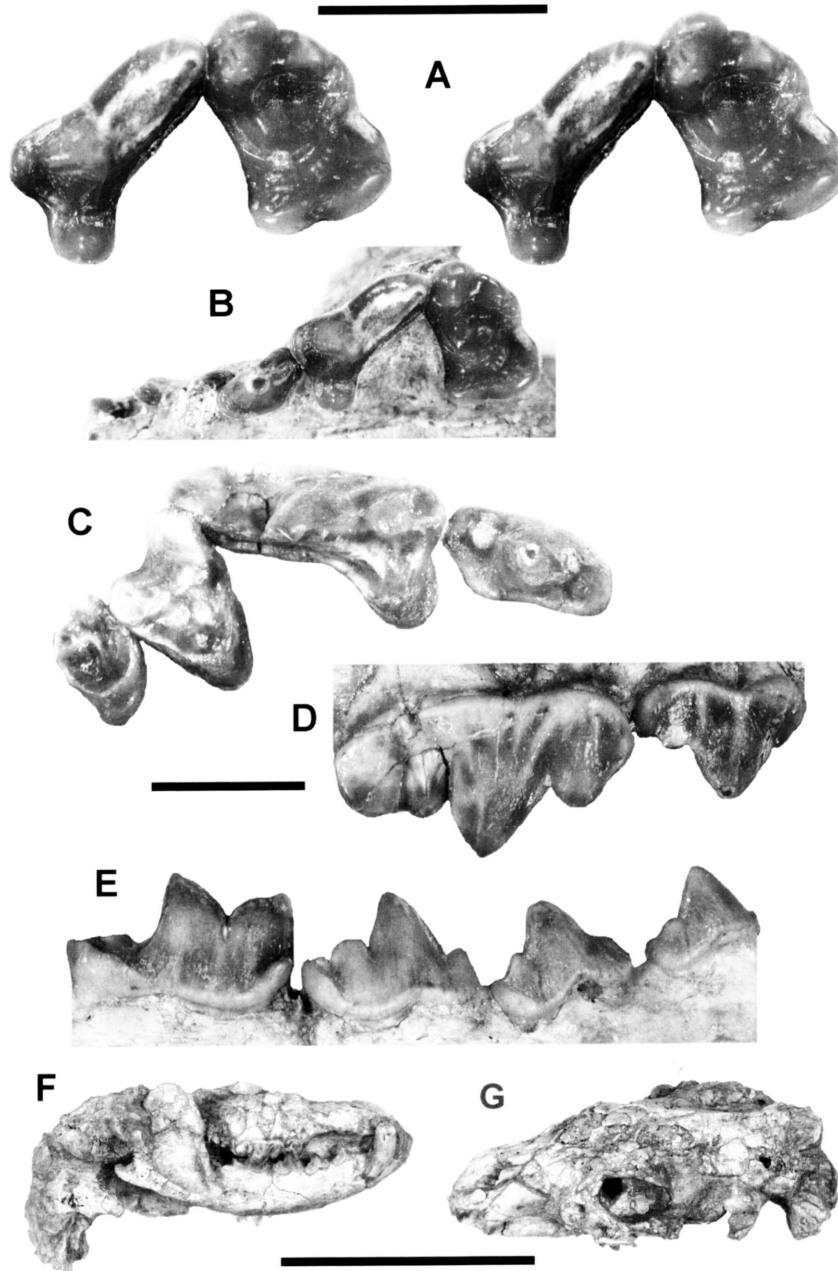


Fig. 2 (Legend see p. 324)

the major axis of the tooth. The distal cusp is strong. There is a weak lingual cingulum.

On P4, the protocone is large, conical, and at the same level as the parastyle mesially. Its connection to the blade is broad. Two weak crests run from its top: the mesial one to the base of the parastyle, the distal one to the lingual cingulum, whereas a third crest extends from the base of the protocone to the lingual side of the paracone. The parastyle is long; the paracone is the highest cusp; the metacone and metastyle are separated by a deep notch from the paracone on the buccal side. The buccal cingulum is well developed, and is elevated at the mesial and distal corners. The lingual cingulum is present, except around the protocone.

The buccal sides of M1 and M2 form an obtuse angle with P4. M1 is a large tooth, being almost as long as P4 is broad. The protocone is large, conical and extends far towards the middle of the tooth. Two crests run from the protocone to the buccal cusps, and there is also a crest running down from the paracone into the central valley. The paracone and metacone are hardly worn, while the protocone shows slight wear. The parastyle is large and much more projecting buccally than the metastyle, but the disto-buccal angle of the tooth is not reduced. There are mesial and distal cingula.

The M2 is large and more quadrangular than M1, but somewhat reduced relative to it. The protocone is large, with a more rounded outline than M1. The paracone and metacone are close to each other. There is a small crest from the paracone to the central basin of the tooth. The anterior cingulum is faint.

The horizontal ramus of the mandible is long and shallow. There are two mental foramina, a large one below the anterior half of p2 and a smaller one between p2 and p3. The masseteric fossa is deep and triangular; its anterior margin reaches the distal border of m2.

The lower incisors are badly damaged. The canine is transversely compressed, and separated from p1 by a diastema about 7 mm long. The p1 is small, low-crowned, and single-rooted. The p2 consists of a main cuspid plus an incipient mesial cuspid and a well-developed distal cuspid. The basal cingulum is strong buccally and lingually, and is thick around the distal cuspid. Both p3 and p4 are narrow, unlike typical hyaenids. The p3 has a high main cuspid with a faint mesial cuspid and a strong distal one. The latter is circled by an elevated cingular ridge. The p4 has a strong mesial cuspid. The main cuspid is very high and trenchant, quite unlike that of typical hyaenids. The buccal cingulum is strong, and elevated along the distal part.

The carnassial is long and narrow. The trigonid is short (10.5 mm) and very high, with the protoconid only slightly higher than the paraconid. The metaconid is lower than the protoconid, but much higher than the talonid

The few following measurements can be taken on the skull and mandible:
 Prosthion to top of occipital = 147; prosthion to anterior border of orbit = 58
 Prosthion to posterior border of P4 = 74
 Length of lower jaw, from i1 to angular process = 114; height of ramus = 43
 Depth of the corpus between p1-p2 = 15; between m1-m2 = 19
 Tooth measurements are given in Table 1.

Comparisons and discussion: The systematics of *Ictitherium* and related forms is still confused and difficult to resolve (WERDELIN & SOLOUNIAS 1981). According to these authors, *Ictitherium* s.str. is defined by a reduced protoconid on m1, and on this basis, the Esendere fossil is clearly not a member of this genus. On the other hand, they considered *Protictitherium* to be paraphyletic, being mostly characterized by primitive features, so that a short comparison with several species from this area is useful before assigning the Esendere fossil to this genus.

The common icthere of the eastern Mediterranean Turolian is *Hyaenotherium wongi*, which includes *Palhyaena hipparionum*, according to WERDELIN & SOLOUNIAS (1991). This is the most common form in Turkey, where it has been reported from many localities: Küçükyozgat (SENYÜREK 1960); Çobanpınar (OZANSOY 1965, but this occurrence is not confirmed by VIRANTA & WERDELIN 2003); Kemiklitepe (BONIS 1994); Gülpınar (SICKENBERG et al. 1975), Kinik, Akin, Garkin, Mahmutgazi (TEKKAYA et al. 1972; SCHMIDT-KITTLER 1976). However, *H. wongi* is quite different from the Esendere specimen in its long P4 and reduced upper molars (e.g. SCHMIDT-KITTLER 1976, figs. 85-86), and there is no doubt that the Esendere form does not belong to this species.

Several other Turkish finds, from Kuyutarla (Ankara), Çakillibağ (Nevşehir-Ürgüp), and Küçükçekmece have been left as *Ictitherium* sp., but they are all much larger than that of Esendere.

Ictitherium viverrinum ROTH & WAGNER, 1854, type-species of the genus, was originally described from Pikermi but has never been reported from Turkey. It was shown by KURTÉN (1976, 1982) and SOLOUNIAS (1981) to be different from *Thalassictis robusta* (NORDMANN, 1858).

Fig. 4. A – *Protictitherium aegaeum* n. sp., IKE-46, occlusal view of p4- m2 (stereo). **B** – *Cremohipparion* cf. *mediterraneum*, IKE-11, occlusal view of P2-M3. **C** – *Tragoportax* sp., IKE-25, occlusal view of P2-M3. Scale = 1 cm for Fig. 4A, 4 cm for Fig. 4B, 3 cm for Fig. 4C

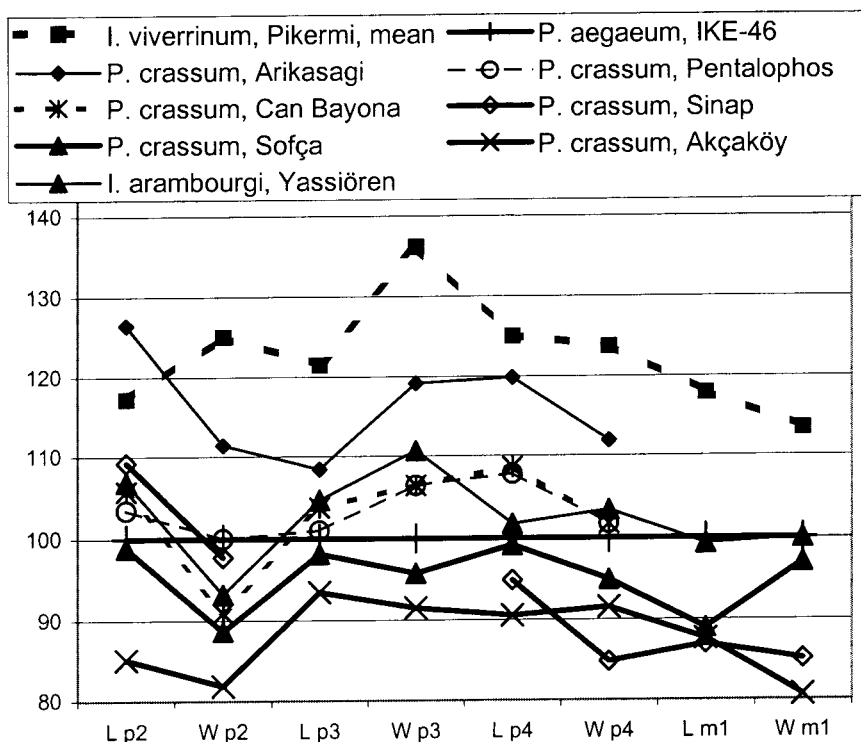


Fig. 3. Ratio diagram of *Protictitherium* from various localities (Turkish ones are in continuous lines) compared to IKE-46 as a standard.

cuspid. The entoconid is by far the highest talonid cuspid; it is separated from the metaconid by a deep valley, and is set very lingually, as it overhangs the cervix of the tooth. The hypoconid is low and conical, and is connected by a faint crest to the base of the protoconid. It is also lingually displaced, being completely surrounded by the buccal cingulum, which is well developed, and elevated along the distal part of the tooth.

The m2 is large. It is quadrangular, and has four main cuspid, of which the metaconid is the highest. There is a small cuspid in the valley between entoconid and metaconid.

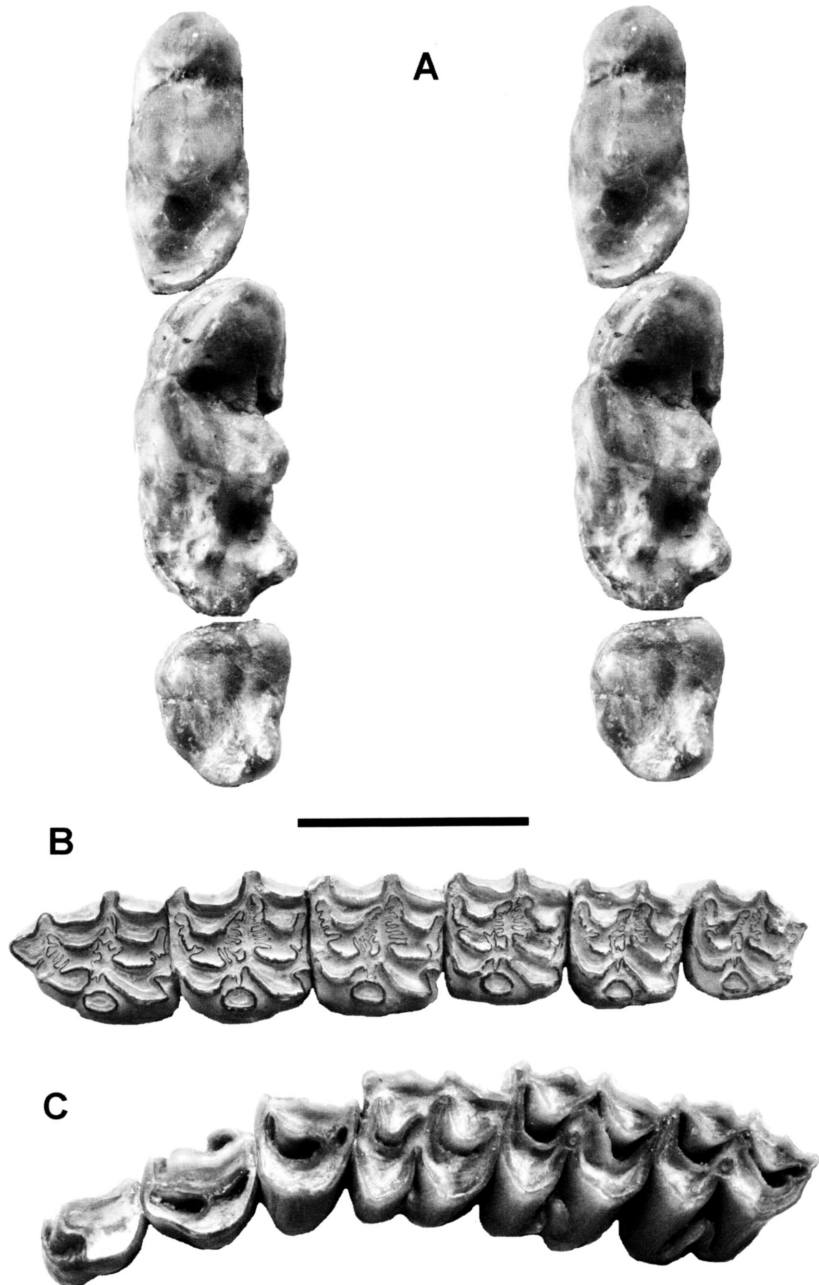


Fig. 4 (Legend see p. 328)

Table 1. Comparative tooth measurements of *Protictitherium aegaeum* and related species.

Upper teeth		P3	P4	M1	M2
<i>P. aegaeum</i>	IKE-46	11.8 x 5.9	17.8 x 9.4	8.3 x 12.7	6 x 7.5
<i>P. crassum</i>	Montredon ¹	10.2 x 4.9	16 x 8.0	6.1 x 12.6	
	Mahmutgazi ²	12.8 x 6.6	18.8 x 11.3	7.8 x 13.6	6.4 x 9.1
	Can Llobateres ³	11.7 x 5.5	18.7 x 10		
<i>P. intuberculatum</i>	Yassiören, type	16.9 x 9.1	24.7 x 14.1	17.6 x 10	
<i>I. viverrinum</i>	PIK-3023	14 x 7.5	19.8 x 11.4	8.4 x 14.1	6.3 x 8.3
	PIK-SAM, mean ⁴	14.8 x 7.9	20.9 x 12.8	8.1 x 14.4	6.9 x 9.8
Lower teeth		p2	p3	p4	m1
<i>P. aegaeum</i>	IKE-46	8.7 x 4.4	10.7 x 4.7	11.6 x 5.9	14.5 x 6.7
<i>P. crassum</i>	Arikasāği	11 x 4.9	11.6 x 5.6	13.9 x 6.6	
	Sofça ²	8.6 x 3.9	10.5 x 4.5	11.5 x 5.6	12.9 x 6.5
	Akçaköy ²	7.4 x 3.6	10.0 x 4.3	10.5 x 5.4	12.7 x 5.4
	Sinap ⁵	9.5 x 4.3		11 x 5	12.6 x 5.7
	Pentalophos ⁶	9 x 4.4	10.8 x 5	12.5 x 6.0	
	Montredon ¹		10.9 x 5.1	11.8 x 6.2	
	Can Llobateres ³		11.3 x 5	13 x 6	
	Can Bayona ³	9.2 x 4	11.1 x 5	12.6 x 6	
<i>P. intuberculatum</i>	Yassiören, type	13.5 x 6.2	16.8 x 7.5	17.7 x 9.1	19.9 x 9.5
<i>I. arambourgi</i>	Yassiören, type	9.3 x 4.1	11.2 x 5.2	11.8 x 6.1	14.4 x 6.7
<i>I. viverrinum</i>	Pikermi, mean ⁸	10.2 x 5.5	13 x 6.4	14.5 x 7.3	17.1 x 7.6

Lengths of tooth series of IKE-46: p1-m1 = 50.5; p2-p4 = 32.5; talonid length of m1 = 4.0; talonid length x 100 / m1 length = 27.5; protoconid height x 100 / m1 length = 7.8 x 100 / 14.5 = 54; P4 length x 100 / m1 length = 123; length x width of m2: 7.2 x 6.2.

¹) BEAUMONT (1988, isolated teeth); ²) SCHMIDT-KITTLER (1976); ³) CRUSAFONT & PETTER (1969); ⁴) SOLOUNIAS (1981, N = 2-8); ⁵) VIRANTA & WERDELIN (2003, isolated teeth); ⁶) BONIS & KOUFOS (1991); ⁷) MORLO (1997); ⁸) KURTÉN (1982, N = 10-15).

The material from Esendere is slightly smaller than *I. viverrinum* (Fig. 3) but is otherwise rather similar. However, several important differences can be observed on the teeth, and *I. viverrinum* is clearly more hyaenoid (ZDANSKY 1924; SCHMIDT-KITTLER 1976, fig. 87; WERDELIN 1988, fig. 7). In *I. viverrinum*:

- P3 is larger and thicker, with an anterior cusp shifted lingually;
- the blade of P4 is thicker, so that the carnassial is stouter;
- M1 is shorter, more U-shaped, and the parastyle is not much longer than the metastyle, so that the buccal border of this tooth is much less buccal than that of P4; its distobuccal corner is less rounded and protruding;
- p4 and m1 are much lower, the talonid of m1 is smaller.

The material from Esendere also differs from *Thalassictis robusta* from Kishinev described by KURTÉN (1954, 1982) by its much shorter carnassial blade. The upper M2 is quadrangular and large, but triangular and small in *T. robusta* (KURTÉN 1954, SOLOUNIAS 1981).

OZANSOY (1965) described three new species from Turkey. *Ictitherium prius* from İnönü II (upper Miocene) is based upon a single mandible that we could not find in the MNHN, TTMEU or MTA.

Ictitherium intuberculatum OZANSOY, 1965, from Yassiören, is a larger species, of which we have seen several specimens in the MNHN and MTA. The specimen from Esendere shares with this species the presence of mesial and distal cuspids on p3, the presence of large M1, M2 and m2, and a m1 with a high trigonid and long talonid. Differences are that the M1 from Esendere is slightly less elongated transversally, has a more expanded distobuccal angle, that P3 is relatively smaller, and mainly that overall size is smaller. Still, the available material suggests that both forms are closely related. WERDELIN & SOLOUNIAS (1991: 40) insisted that *I. intuberculatum* does belong to *Ictitherium* but, if we follow their definition of the genus, the high m1 protoconid (not illustrated by Ozansoy) rules out this generic assignment. Despite the large size, it is more likely to belong to *Protictitherium*.

Ictitherium arambourgi OZANSOY, 1965 is based upon a single mandible with very worn teeth, from Yassiören, but VIRANTA & WERDELIN (2003) referred a few other fragmentary specimens from Sinap to this species which was considered by SCHMIDT-KITTLER (1976) as synonymous with *Protictitherium crassum* (DÉPÉRET, 1892), typespecies of the genus *Protictitherium*.

Protictitherium crassum is mostly of Vallesian age, but is also known from some middle Miocene sites: La Grive (type-locality) and Vieux-Collonges in France (DÉPÉRET 1892; MEIN 1958), Paracuellos and Arroyo del Val in Spain (GINSBURG et al. 1981), and Sofça in Turkey (SCHMIDT-KITTLER 1976). The Esendere skull agrees in many features with this species, although there are a few differences. The maxilla from Mahmutgazi, referred to *P. crassum* by SCHMIDT-KITTLER (1976), differs only from the Esendere fossil in the slightly more anterior position of the P4 protocone, but the mandible from

Sofça has a p4 which is lower and a m1 with a lower paraconid and shorter talonid. The m1 of *P. cf. crassum* from Pentalophos (BONIS & KOUFOS 1991) has a lower trigonid with more splayed out protoconid and paraconid, a more labial hypoconid, and a very high entoconid. Early forms, from Vieux-Collonges (MEIN 1958, fig. 73), have lower lingual cuspids on m1, especially relative to the high protoconid, as in the smaller *P. intermedium* SCHMIDT-KITTLER, 1976, from the middle Miocene of Çandır, Paşalar (SCHMIDT-KITTLER 1976; NAGEL 2003) and Mordoğan (KAYA et al. 2003).

P. cingulatum from Yeni-Eskihisar has a m1 which is similar to that of Esendere, but p4 and m1 are lower-crowned, the cingulum is stronger, M1 is shorter, and the size is much smaller. *P. gaillardi* is a species of medium size, mostly known from the middle Miocene of France, but a similar form is known from Çandır and Paşalar (SCHMIDT-KITTLER 1976; NAGEL 2003). All these forms differ mostly by size (*P. gaillardi* was considered as probably synonymous with *P. crassum* by GINSBURG et al. 1981, although GINSBURG & BULOT 1982, retain the species), and their overall dental features agree well with those of the Esendere fossil which, however, looks more primitive in its high, viverrid-like, p4 and m1 trigonid.

Family Mustelidae FISCHER VON WALDHEIM, 1817
Genus *Promeles* ZITTEL, 1890

Promeles smyrnensis n. sp.

Fig. 2A, B

Holotype: Anterior part of skull with right P4-M1; left P1, P3-M1 (IKE-33; Fig. 2A, B).

Diagnosis: A mustelid of medium size, differing from *P. palaeatticus* and *P. macedonicus* by its long slender P4, and its M1 with a strongly expanded mesio-buccal angle and small metacone. Differs from "*Mustela*" *palaeosinensis* ZDANSKY, 1924 by its shorter muzzle and crowded premolars.

Description: The holotype skull is dorsoventrally crushed, and its posterior part is missing. A weak sagittal crest is visible posteriorly. The nasal bones are long, with parallel lateral borders. They extend posteriorly to the level of the lacrimal fossa. The infraorbital foramen is large, above the anterior root of P4. Beneath the infraorbital foramen, there is a deep depression between the buccal roots of P4. The anterior margin of the orbit is at the level of the front of P4. The palate extends far behind M1.

Neither the canines nor the incisors are preserved. There is no diastema between the canine alveolus and P1, which is small, single-rooted, with a low basal cingulum. P2 is missing, but two alveoli are visible. P3 has a high,

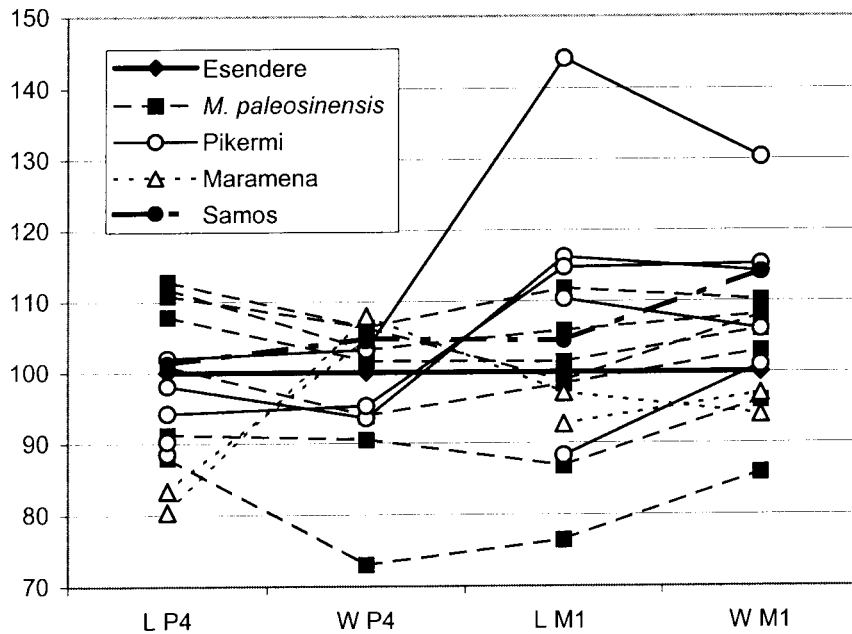


Fig. 5. Ratio diagram of *Promeles* and “*Mustela*” *paleosinensis* upper teeth, using *P. smyrnensis* from Esendere as a standard.

trenchant, and slightly asymmetrical main cusp. A mesio-lingual and a distal crest descend from its top towards the cingulum, which is continuous along the lingual side. P4 is a rather long and slender tooth, as it is slightly longer than M1 is broad. The parastyle is little more than a raised cingulum at the base of the paracone, its mesial border is at the same level as that of the protocone. Between them, the mesial border of the tooth is slightly concave. The protocone is small, low, and conical; a weak crest descend distally from its tip, to merge into the lingual cingulum, which is weak. The paracone is very high, with its tip at the center of the tooth. Two crests descend from it: one leads to the parastyle, the other to the base of the protocone. The carnassial blade, which shows a large abrasion facet, is rather thin, and is not notched.

M1 is constricted in its middle, both the mesial and distal borders being slightly concave, and the tooth is strongly concave transversally. The protocone is crescent-shaped. The posterior wing is worn, but comes into contact with a distinct metaconule. The latter, at the disto-buccal corner of the tooth, is separated from the metacone by a narrow but well-marked valley. The mesial wing of the protocone reaches the base of the paracone. The paracone is conical and situated more buccally than the metacone; it is expanded buccally into a thick cingular shelf, but the cingulum is completely absent at the base of the metacone, which is small, and the buccal border of the tooth is strongly oblique in occlusal view. The lingual cingulum is thick and expanded both mesially and distally, so that the lingual outline of the tooth is squared.

The few following measurements can be taken:

Prosthion to anterior border of the orbit = 23

Width of palate over P4s = 30

Length of palate from prosthion to back of M1 = 33

P1 = 1.8 x 1.6; P3 = 5.5 x 3.3; P4 = 10.2 x 6.3

M1 = 6.8 (maximum length) x 9.9.

Comparisons: The teeth from Esendere remind those of *Promeles pala-eatticus*, described by WEITHOFER (1888), MAJOR (1902), SCHMIDT-KITTLER (1995) and ROUSSIAKIS (2002) from Pikermi, and reported from several other localities: Samos, Greece (WEITHOFER 1888; MAJOR 1902; SOLOUNIAS 1981; ROUSSIAKIS 2002); Maragha, Iran (BERNOR et al. 1996), Dorn-Dürkheim-1, Germany (MORLO 1997). However, they differ from those of this species, as well as from those of *Promeles macedonicus* from Maramena, Greece (SCHMIDT-KITTLER 1995) in several features.

First, and most importantly, the Esendere species differs from both Greek species (SCHMIDT-KITTLER 1995, figs. 3-4 and pl. 1, figs. 2, 4) by the long slender P4 (slightly longer than the width of M1), and by its small P4 protocone, which does not reach farther mesially than the level of the parastyle. In both Greek species, the P4 is always significantly shorter than M1 is broad, and the protocone of P4 is more anterior than the parastyle. This position is clear in the figures of SCHMIDT-KITTLER (1995, figs. 3-4, and pl. 1, figs. 2, 4), as well as in specimens M9028 and M9029 from Pikermi in the BMNH. The M1 is more concave and more transversely widened, especially because the mesio-buccal cingulum is more expanded, and because the paracone is much more lateral than the small metacone, whereas they are almost at the same level in Greece, giving the tooth a less trapezoidal outline. The only

exception is M9028, but this specimen has a M1 which is so much enlarged (Fig. 5) that specific distinction with the Esendere mustelid is not in doubt.

The P4 of *P. macedonicus* is still stouter than that of *P. palaeatticus*. Fig. 5 depicts the relations between the measurements of P4 and M1. It shows the stoutness of P4 at Maramena, and the large size of M1 in both Greek species.

However, it should be noticed that the Samos specimen (MGL S-272), while generally similar to those from Pikermi, differs from them by its P4 protocone which is small and not more anterior than the parastyle, and by its short M1; both features make it closer to the Esendere form.

The Esendere mustelid differs from the previously known species of *Promeles* by some important features, but it matches this genus better than other "meline" forms, which have short stout P4s and/or much more expanded M1s, like the middle Miocene *Trochictis* VON MEYER, 1842, *Iberictis* GINSBURG & MORALES, 1992, *Lartetictis* GINSBURG & MORALES, 1996, and *Adroverictis* GINSBURG & MORALES, 1996.

Rhodanictis GINSBURG, 2000 was inserted by his author, in his cladogram of the Melinae, at a lower node than *Promeles*, but the short thick P4 of *R. depereti* stands against this position, and it is hard to believe that this species is close to the ancestry of *Promeles*.

The poorly known *Sabadellictis* PETTER, 1963, from the Vallesian of Can Llobateres, has been synonymised with *Promeles* by SCHMIDT-KITTLER (1995) and MORLO (1997), but the M1 (PETTER 1963, pl. 3, fig. 6) has a very strong metaconule, making the distal border of the tooth very concave, and the protocone is very incompletely crescent-shaped.

Ischyriictis HELBING, 1930, is mostly a Middle Miocene genus, present in Turkey at Çandır (SCHMIDT-KITTLER 1976; NAGEL 2003), but is also known from the early Upper Miocene of Spain (CRUSAFONT 1972). The P4 is long, but the shape of the protocone, connected to the blade by a narrow isthmus, is different from that of the Esendere fossil; the labial part of M1 is much shorter, and the protocone is not moonshaped.

From Loc. 111, of unknown age in the Sinap Formation, a M1 illustrated but left unidentified by VIRANTA & WERDELIN (2003, fig. 8.8) has a crescent-shape protocone, but is quite distinct from the Esendere M1 by the lack of metaconule, and its unique feature of a lingual shelf which is extremely expanded transversally.

The species closest to the Esendere mustelid is perhaps "*Mustela*" *palaeosinensis* ZDANSKY, 1924, from Baode (Shansi, China). Fig. 4 shows that the proportions of its P4 and M1 are identical to those of the Esendere specimen. ZDANSKY (1924) laid stress on the variability of P4 and still more of M1, and some of his specimens are indeed more similar to the Esendere form than others, but as a rule they display the same features. The P4 is long relative to M1, and it has a relatively small protocone. The M1 is moderately

elongated, it has a crescent-shape protocone and may also have a small metaconule (at least on Ex. 4, ZDANSKY 1924, pl. 6, fig. 15), and the labial wall is oblique. “*Mustela*” *palaeosinensis* differs from *Promeles smyrnensis* n.sp. in its longer snout, with premolars separated by short diastemata, and long P2, while the Esendere form has crowded premolars and a short P2 (inferred from its alveolus).

Table 2. Comparative measurements of *Cremohipparion mediterraneum*

Teeth	P2-M3	P2-P4	MI-M3	index	
IKE-11	141	76.5	65	117.6	
PIK ¹	129-154	70.7-87.5	57.4-68.1	123-128	
KTA ²	139	76	63	120	
Length dp2-dp4 IKE-7 = 87.3; IKE-9 = 81.4					
Tibia	IKE-2	IKE-37	PIK ¹	KTA ²	
Width of shaft	41	-		39	
Distal width	64	63	52.3-60.7	65.7	
Distal AP	43	42	35.7-41.7	41.5	
Talus	IKE-16	PIK ¹	KTD ²		
Max. height	54	48.3-53.1	53.7		
Max. width	51	-	51.8		
Distal width	38	35-40.9	41.5		
Distal AP	29	-	28.2		
Calcaneum	IKE-13	KTD ²	KTD ³		
Min. width of tuber	19.8	20.3	20		
Distal width	47.2	46.9	48		
Distal AP	44.0	44.2	47		
Mt-III	IKE-39	PIK ¹	KTA ²	KTA ³	KTA ³
Prox. width	41	34-41	40.4	38	41
Prox. AP	33	29.3-36.1	33.7	34	36

¹) FORSTÉN (1968); ²) ΚΟΥΦΟΣ & ΚΟΣΤΟΠΟΥΛΟΣ (1994); ³) TTMEU

"*Mustela palaeosinensis* has also been reported from the Turolian site of Puente Minero (ALCALÁ et al. 1991). The description of M1, unfortunately not illustrated, could match the Chinese form, but the lack of P4 prevents any definite identification.

We refrain from carrying the comparisons too far, and from including "*Mustela palaeosinensis* in *Promeles*, because the Chinese material, which we have not seen, has not been recently revised. It is clearly not a *Mustela*, but has often been referred to *Martes*. However, this latter genus, which has been reported from as early as the lower Miocene (GINSBURG 1999) is probably a waste-basket, and referring "*M.*" *palaeosinensis* to it still increases its range of variation. Alternatively, the Chinese form could be referred to *Pilgrimeles* GINSBURG, 1999, a genus erected (on a rather weak basis, as ROUSIAKIS 2002 remarked) for *Martes woodwardi* PILGRIM, 1931, from Pikermi. PILGRIM, while admitting that his new species was of the same size as ZDANSKY's, distinguished it on the basis that the latter has "a longer p3, a much less hollowed talonid to m1, and a circular m2" (PILGRIM 1931: 41). As p3 is missing in *M. woodwardi*, it must be a misprint for p4, but the difference in length is not supported by the measurements (those of *M. woodwardi*, 6.5 x 3.3 mm, are within the range of "*M.*" *palaeosinensis*). Since the m2 of *M. woodwardi* is known only by its alveolus, the only remaining difference is the shape of the talonid of m1, which is perhaps not great, since the talonid looks hollowed in some of ZDANSKY's specimens. This "*Pilgrimeles*" group (*palaeosinensis* + *woodwardi*) differs from *Promeles palaeatticus* in its m1 trisoonid which is not so reduced relative to the talonid, but this tooth might well be more similar to the (unknown) m1 of *P. smyrnensis*. However, pending recovery of more complete specimens of both latter species, we prefer not to assign "*M.*" *palaeosinensis* and *Promeles smyrnensis* to *Pilgrimeles*.

Order	Perissodactyla OWEN, 1848
Family	Equidae GRAY, 1821
Genus	<i>Cremohipparion</i> QIU, WEILONG & ZHIUI, 1988

Cremohipparion cf. *mediterraneum* (ROTH & WAGNER, 1855)
Fig. 4B

Material: Left upper tooth row with P2-M3 (IKE-11; Fig. 3B), left upper tooth row with P3-M2 (IKE-8, IKE-12), mandible with dp2-dp4 right and dp2-dp3 left (IKE-7), left mandibular ramus with dp2-m1 (IKE-9), right mandibular ramus with dp3-m1 (IKE-10), distal part of Mc-III (IKE-38), distal part of tibia (IKE-2, IKE-37), proximal part of Mt-III (IKE-39), left calcaneus (IKE-13), right astragalus (IKE-16).

Table 3. Measurements of the proximal phalanx IKE-19, and means of those of *A. (A.) pentelicum* from Turolian sites (sample size and range in brackets)

	IKE-19	digit III or IV (9)	digit III (4)	digit IV (2)
L	78.5	96 (80-125)	108 (91-125)	96 (88-105)
Proximal width (max.)	49	63 (49-77)	63 (46-79)	62 (61-63)
Distal width (max.)	37	53 (45-58)	47 (37-56)	45 (45-45)

Description and comparison: The upper tooth series are of moderate length (P2-M3 = 141; P2-P4 = 76.5; M1-M3 = 65). The protocone is elongated-oval and isolated from the protoloph. There is no protoconal spur. The protocone index (PI = Protocone length \times 100 / tooth length) is 23.8 for P2, 31.2 for P3, 30.9 for P4, 35.2 for M1 and 33.1 for M2, and 29.3 for M3. The hypocone is antero-posteriorly aligned with the protocone. The hypoglyph is shallowly incised, but it is deeply incised in M3. The fossettes of the upper teeth are closed, except those of P2, which are open distally. The number of plications varies between 13-23 in the premolars and 13-16 in the molars. They are narrow and simple, and their depths decrease with tooth wear. The pli caballin is single in the molars and double in the premolars. Measurements are given in Table 2.

In the lower deciduous teeth, the protostylid is present. The ectostylid is pillar-shaped in IKE-9 and IKE-10, but does not reach the occlusal surface in IKE-7. The metaconid and metastylid are rounded, but elliptical-triangular in IKE-7. The parastylid is weak. The enamel of the flexid border is simple. The linguaflexid is V-shaped. The ectoflexid is narrow and does not reach the linguaflexid. The pli hypoconid is strong in dp2.

The Mc-III is long and slender. The metatarsal has a facet for the cuneiform II. The morphological and metrical comparison of the Esendere hipparion (Table 2) shows that the studied material is similar to *C. mediterraneum* from Pikermi and Kemiklitepe (FORSTÉN 1968; KOUFOS & KOSTOPOULOS 1994) and it can be tentatively referred to this species.

Family Chalicotheriidae GILL, 1872
 Subfamily Schizotheriinae HOLLAND & PETERSON, 1914
 Genus *Ancylotherium* GAUDRY, 1862

Ancylotherium (*Ancylotherium*) cf. *pentelicum* (GAUDRY & LARTET, 1856)

Material: Proximal phalanx (IKE-19; measurements: Table 3).

Description and comparison: The proximal part of the phalanx-I is much broader than the distal part. The proximal facet is heart-shaped, occupies less than half the dorsal surface of the phalanx, and faces proximo-dorsally. The two lobes are separated by a deep notch on the palmar side. This morphology is similar to that *A. (Ancylotherium) pentelicum* from Pikermi, Halmyropotamos and Pinaryaka (SCHAUB 1943; ROUSSIAKIS & THEODOROU 2001; MELENTIS 1970; SARAÇ et al. 2002). They share a heart-shaped proximal facet which faces proximo-cranially, and a large proximal part compared to the distal part. The proximal phalanx differs from *A. (Metaschizotherium) fraasi* from Kultak (KAYA et al. 2001) in that the distal part is larger. However, it is smaller than all published Turolian phalanges of *A. pentelicum*, even if it belongs to digit IV.

Family	Rhinocerotidae GRAY, 1821
Subfamily	Rhinocerotinae GRAY, 1821
Genus	? <i>Ceratotherium</i> GRAY, 1867

? *Ceratotherium neumayri* (OSBORN, 1900)

Material: Proximal part of right radius (IKE-17).

Description and comparison: The radial tuberosity is smooth, and the medial one is strong. The lateral ulnar facet is large and triangular, whereas the medial one is rectangular. Distal to these facets, on the caudal side, is a long and roughened attachment surface for the proximal *ligamentum interosseum*. The diaphysis has an oval cross section. Measurements of proximal articular surface are:

Transverse = 109; antero-posterior = 62.

In size and morphology, the material of Esendere is similar to the specimens described as *C. neumayri* from Garkin, Mahmutgazi (HEISSIG 1975), and Pikermi, but is larger than that of *C. neumayri* from Kayadibi. However, in no case can we be sure that the specific identification is correct, as there is at least one other species of similar size in this area, *Dicerorhinus piker-miensis*.

Order Artiodactyla OWEN
 Family Giraffidae GRAY, 1821
 Genus *Bohlinia* MATTHEW, 1929

Bohlinia attica (GAUDRY & LARTET, 1856)

Material: Upper molar (IKE-1).

Descriptions and comparison: The tooth has a first lobe not much longer than the second one, the lingual keels of the lingual lobes are parallel and not divergent, and the parastyle is not expanded; these features show that it is not a DP4. Still, the tooth is very brachyodont. The parastyle and mesostyle are very prominent and stronger than the metastyle, and the paracone rib is strong. The enamel of the tooth is rugose. The entostyle is well developed and high. The mesial cingulum is stronger than the distal cingulum, and there is no lingual cingulum. An hypoconal spur is present in the valley of the second lobe; this spur is constant in *Bohlinia attica*, a close relative of the Recent giraffe, best known from Pikermi. The size (length x width = 29 x 26) and brachyodonty (H = 19) of this tooth also match those of the Greek species (BOHLIN 1926; ARAMBOURG & PIVETEAU 1929; GERAADS 1979), and although definite identification is difficult on a single tooth, we refer it to this species rather than to a similar-sized *Palaeotragus*.

Genus ? *Samotherium* FORSYTH MAJOR, 1888

? *Samotherium* sp.

Material: Right (? posterior) phalanx-1 (IKE-26).

Description and comparisons: The phalanx-I is long, slender, with a rectangular proximal surface, suggesting that it is from the posterior limb (anterior phalanges are broader). The plantar tuberosities are short. The proportions of the bone suggest that it belongs to *Samotherium*. In size (Table 4) the phalanx-I from Esendere is similar to the phalanges of *S. neumayri* from Maragha, smaller than those of *Helladotherium*, and shorter than those of *Bohlinia* from Pikermi (GERAADS 1974, table 8).

Thus, two giraffid species were probably present at Esendere, although these identifications rest upon very few specimens. A few other bones might belong to either of these species. These are:

IKE-30, a talus (medial height 83.5; distal width 63.5); IKE-35, a semilunar (max. dorsal height 39.5), IKE-32, a scaphoid, and IKE-31, an unciform (max. height 34), all of similar size.

Table 4. Measurements of phalanx-I of Giraffid species.

	<i>Samotherium</i> sp.	<i>S. sinense</i>	<i>S. neumayri</i>	<i>S. major</i>	<i>Bohlinia</i> ²
	IKE	China ¹	MAR ²	SLQ ²	PIK, VAT
L	93	94	97-106	96	108, 110
Prox. width	39	43	37-40	44	39, 35
Prox. AP	47	49	39-41	41	43, 41

¹) BOHLIN (1926); ²) GERAADS (1974)

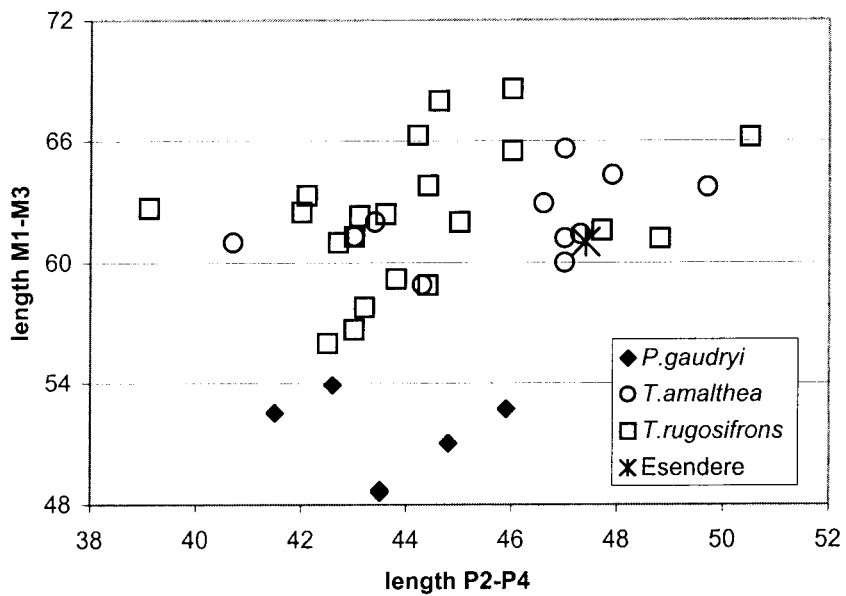


Fig. 6. Plot of P2-P4 vs. M1-M3 length in Late Miocene boselaphines. *Tragoportax amalthea* is from Pikermi, *T. rugosifrons* from Samos, Hadjidimovo, Greek Macedonia, and Maragha, *Miotragocerus (Pikermicerus) gaudryi* is from Pikermi and Samos.

Family	Bovidae GRAY, 1821
Tribe	Boselaphini KNOTTNERUS-MEYER, 1907
Genus	<i>Miotragocerus</i> STROMER, 1928
Subgenus	<i>Miotragocerus (Pikermicerus)</i> KRETZOI, 1941

Miotragocerus (Pikermicerus) gaudryi (KRETZOI, 1941)

Material: Right horn-core with skull fragment (IKE-29).

Description and comparisons: The horn-core is massive, very probably short, and strongly compressed transversally (55.5 x 30.7), with a flattened medial side, but there is no postero-lateral keel; a deep conspicuous longitudinal sulcus runs along the posterior face. The anterior edge is sharp, folded medially. The pedicel is short. The size and morphology of the Esendere horn-core are within the range of *M. (Pikermicerus) gaudryi* from Pikermi (SPASSOV & GERAADS 2004).

Genus *Tragoportax* PILGRIM, 1937

Tragoportax sp.

Fig. 4C

Material: Left maxilla with P2-M3 (IKE-25; Fig. 4c).

Description and comparisons: The upper teeth are mesodont, and their enamel is rugose. The lengths of the cheek-tooth series are:

P2-M3 = 102.9; P2-P4 = 47.4; M1-M3 = 61, hence a Pm / M index of 78.

P2 is longer than the posterior premolars. The buccal wall is strongly asymmetrical on P2 and P3, less so on P4. The same is true of the lingual crescent. There is an anterior cingulum on P2. P3 is trapezoidal, with a strong hypocone and a protruding, hooked metastyle, which is much weaker on P4. The basal pillar is weak in M1, but strongly developed and bifurcated in M2 and M3. On the upper molars, the central cavities are connected, and the parastyle and metastyle are well developed.

All these features clearly point to a boselaphine, but the large size, and relatively short premolars (especially P2) are more like *Tragoportax* than *Miotragocerus (Pikermicerus)*. Thus, although the premolar/molar ratio does not allow to distinguish between the two most common species of *Tragoportax* in this area (Fig. 6), there is no doubt that, as in a few other localities (SPASSOV & GERAADS 2004), these two genera co-existed at Esendere.

Genus *Gazella* BLAINVILLE, 1816

Gazella cf. *pilgrimi* BOHLIN, 1935

Material: 4 horn-cores, and a left maxilla with P3-M3 (IKE-47).

Description and comparisons: The horn-cores are rather long, markedly curved backwards, but are not twisted. They have a moderately compressed crosssection (IKE-21: 30.2 x 23.5 ; IKE-28: 30.7 x 23.4), with almost no flattening of the lateral surface near the base but the compression and flattening increase towards the tip.

These horn-cores are much larger than those of *G. deperdita* from Mont Lubéron and Gülpinar, but are only slightly larger than *G. pilgrimi* from Novaya Emetovka and Chimichlia (KRAKHMALNAYA 1996). They differ from *G. pilgrimi* from Northern Greece (BOUVRAIN 1996) by their larger size, stronger curvature, but their degree of compression is similar. However, the type-specimen of *G. pilgrimi* from Samos (SCHLOSSER 1904, pl. 13, fig. 1) and a second specimen from the same locality (ANDREE 1926) are very similar in size and compression to our specimens, although the type-specimen is less curved than the Esendere horn-cores. Thus, we will only tentatively refer them to this species.

Conclusions

The fauna from the Esendere formation includes *Promeles smyrnensis*, *Proictitherium aegaeum*, *Cremohipparion* cf. *mediterraneum*, ? *Ceratotherium neumayri*, *Ancylotherium* (*Ancylotherium*) cf. *pentelicum*, *Samotherium* sp., *Bohlinia attica*, *Miotragocerus* (*Pikermicerus*) *gaudryi*, *Tragoportax* sp., and *Gazella* cf. *pilgrimi*.

All the ungulates of this list are also found in Samos, but *Gazella pilgrimi* and *Samotherium* are absent from Pikermi, making the Esendere fauna slightly more distinct from that of the Attic site, which is not unexpected given the geographic position of the Karaburun Peninsula. Unfortunately, all these taxa have a rather long temporal range, covering the whole Turolian, and it is, at present, difficult to assign the Esendere fauna to one particular MN zone (an exercise that is often a matter of feeling). On the whole, the Esendere fauna is perhaps more like that of Samos A-1 (BONIS & KOUFOS 1999). However, it should be noticed that the *Samotherium* from Esendere is rather small, whereas the *Samotherium* major from the late Turolian of Samos is large. Similarly, the *Ancylotherium* phalanx is smaller than all

			<i>P. intermedium</i>	<i>P. i. parvum</i>	<i>P. cingulatum</i>	<i>P. aff. gaillardii</i>	<i>P. crassum</i>	<i>P. aegaeum</i>
TUROLIAN	12	Mahmutgazi					+	
	11	Esendere ?						+
VALLESIAN	10	Arikasağı					+	
	9	Sinap Eşme-Akçaköy					+	
ARAGONIAN	7+8	Yeni Eskihisar		+				
		Sofça					+	
	6	Mordoğan		+				
		Çandır	+			+		
	5	Paşalar	+			+		

Fig. 7. Stratigraphic distribution of *Protictitherium* species in Turkey.

reported Turolian ones. Thus, although the evidence is slight, we believe the Esendere ungulate fauna fits better the early Turolian.

Indeed, the carnivores are definitely distinct from those of the classic Turolian sites. It is unexpected to find *Protictitherium* in a Turolian fauna,

although there are some indications of the survival of this genus until the latest Miocene (Fig. 7). The age of Mahmutgazi is not known with precision. It was referred to MN 11 by KÖHLER (1987), but its bovid fauna consists mostly of fragmentary material, hardly usable for biochronological correlations. However, its *Machairodus* is similar to Turolian forms (GERAADS et al. 2004), and we believe that a middle Turolian age is probably the best estimate. Thus, it is likely that *Protictitherium crassum* extends well into the Turolian in Turkey. There are some other reports from the Turolian, such as those from Dytiko in Greece (KOUFOS 2000), which was questioned by WERDELIN & SOLOUNIAS (1991), or from Dorn-Dürkheim in Germany (MORLO 1997), based upon two lower premolars and a carnassial fragment, but these European finds are less convincing than the Turkish ones.

Concerning this family, the most remarkable difference is the late survival in Turkey of several primitive forins, *Protictitherium crassum*, *P. aegaeum* and *P. intuberculatum*, with similar dental adaptations, mainly a large P4 protocone and large molars. Indeed, WERDELIN & SOLOUNIAS (1996) noticed that “Greece and Turkey although closely adjacent to one another, have different hyaenid faunas”. However, the Turolian carnivore fauna of Turkey is still too poorly known for this difference to be explained. WERDELIN & SOLOUNIAS (1991) linked the decrease of primitive hyaenids near the Miocene – Pliocene boundary to the arrival of canids, but this eco-ethological explanation cannot be used for earlier periods, since the Canidae are almost unknown in Europe in the late Miocene. Another interesting point is the similarity of *Promeles smyrnensis* from Esendere with “*Mustela*” *palaeosinensis* from China, which confirms the Asiatic affinities of Turkey in the Turolian (GERAADS & al. 2002), and the major biogeographic role played by this country, at the crossroads between three continents.

Acknowledgments

Thanks to those who gave us access to the collections in their care: A. CURRANT (Natural History Museum, London), R. MARCHANT (Musée Géologique, Lausanne), C. SAGNE and P. TASSY (Muséum National d’Histoire Naturelle, Paris), B. KARABAĞLI (Maden Tetkik ve Arama Museum, Ankara). We also thank E. P. J. HEIZMANN (Stuttgart) for helpful comments on the manuscript, and N. ÖZTEKİN (Izmir). This study has been supported by an Aegean University grant to T.K. (TTM/001/2001).

References

- ALCALÁ, L., SESÉ, C., HERRÁEZ, E. & ADROVER, R. (1982): Mamíferos del Turoliense inferior de Puente Minero (Teruel, España). – Bol. Real Soc. Españ. Hist. Nat. (Secc. Geol.), **86** (1-4): 205-251.
- ANDRÉE, J. (1926): Neue Cavicornier aus dem Pliocän von Samos. – Palaeontographica, **67** (6): 135-175.
- ARAMBOURG, C. & PIVETEAU, J. (1929): Les vertébrés du Pontien de Salonique. – Ann. Paléont., **28**: 57-140.
- BEAUMONT, G. DE (1988): Contributions à l'étude du gisement Miocène supérieur de Montredon (Hérault). Les grands Mammifères. 2: les carnivores. – Palaeovertebrata, Mém. extraordinaire, p. 15-42.
- BERNOR, R. L., SOLOUNIAS, N., SWISHER, C. C. III & 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., FAHLBUSCH, V. & MITTMANN, H. W. (Eds.): The Evolution of western Eurasian Neogene Mammal faunas, p. 137-157; New York (Columbia Univ. Press).
- BESENECKER, H. (1973): Neogen und Quartär der Insel Chios (Agiäs). – Ph. D, Freie Universität Berlin, **184**: 59.
- BOHLIN, B. (1926): Die Familie Giraffidae mit besonderer Berücksichtigung der fossilen Formen aus China. – Palaeont. Sinica, (C), **4** (1): 1-178.
- BONIS, L. DE (1994): Les gisements de Mammifères du Miocène supérieur de Kemiklitepe, Turquie: 2. Carnivores. – Bull. Mus. Nat. Hist. Nat., C, 4e sér., **16** (1): 19-39.
- BONIS, L. DE & KOUFOS, G. (1999): The Miocene large mammal succession of Greece. – In: AGUSTI, J., ROOK, L. & ANDREWS, P. (Eds.): Hominoid evolution and climate change in Europe, p. 205-237; Cambridge (Univ. Press).
- BOUVRAIN, G. (1996): Les gazelles du Miocène supérieur de Macédoine, Grèce. – N. Jb. Geol. Paläont., Mh., **1996**: 111-132.
- CRUSAFONT-PAIRÓ, M., 1972. Les *Ischyriactis* de la transition Vindobonien-Vallésien. – Palaeovertebrata, **5**: 253-260.
- CRUSAFONT-PAIRÓ, M. & PETTER, G. (1969): Contribution à l'étude des Hyaenidae: la sous-famille des Ictitheriinae. – Ann. Paléont., **55** (1): 89-127.
- DEPÉRET, C. (1892): La faune de mammifères miocènes de La Grive-Saint-Alban (Isère) et quelques autres localités du bassin du Rhône. – Arch. Mus. Hist. Nat. Lyon, **5** (2): 1-93.
- ERDOĞAN, B., ALTINER, D., GÜNGÖR, T. & ÖZER, S. (1990): Stratigraphy of Karaburun Peninsula. – Bull. Min. Res. Expl. Inst., **111**: 1-20.
- FORSTÉN, A. (1968): Revision of the Palearctic *Hipparion*. – Acta Zool. Fenn., **119**: 1-134.
- FORTELIUS, M., KAPPELMAN, J., SEN, S. & BERNOR, R. L. (2003): Geology and Paleontology of the Miocene Sinap Formation, Turkey. – 409 pp.; New York (Columbia Univ. Press).
- GERAADS, D. (1974): Les Giraffidés du Miocène Supérieur de la région de Thessalonique (Grèce). – These Univ. Paris VI, p. 1-103 (unpublished).

- GERAADS, D. (1979): Les Giraffinae (Giraffidae, Mammalia) du Miocène supérieur de la région de Thessalonique (Grèce). – Bull. Mus. Nat. Hist. Nat., C, 4^{ème} sér., **1** (4): 377-389.
- GERAADS, D., GÜLEC, E. & KAYA, T. (2002): *Sinotragus* (Bovidae, Mammalia) from Turkey and the Late Miocene Middle Asiatic Province. N. Jb. Geol. Paläont., Mh., **2002**: 477-489.
- GERAADS, D., KAYA, T. & TUNA, V. (2004): A skull of *Machairodus giganteus* (Felidae, Mammalia) from the Late Miocene of Turkey. – N. Jb. Geol. Paläont., Mh., **2004**: 109-115.
- GINSBURG, L. (1999): Order Carnivora. – In: RÖSSNER, G. H. & HEISSIG, K. (Eds.): The Miocene Land Mammals of Europe, p. 109-148; München (Pfeil).
- (2000): Origine et evolution des Melinae (Mustelidae, Carnivora, Mammalia). – C. R. Acad. Sci., Sci. Terre Planètes, **330**: 221-225.
- GINSBURG, L. & BULOT, C. (1982): Les carnivores du Miocène de Bézian près de la Romieu (Gers, France). – Proc. Konink. Akad. Wetensch., (B), **85** (1): 53-76.
- GINSBURG, L., MORALES, J. & SORIA, D. (1981): Nuevos datos sobre los Carnívoros de Los Valles de Fuentidueña (Segovia). – Estudios geol., **37**: 383-415.
- HEISSIG, K. (1975): Rhinocerotidae aus dem Jungtertiär Anatoliens. – Geol. Jb., (B), **15**: 145-151.
- KAYA, O. (1981): Miocene reference section for the coastal parts of West Anatolia. – Newsl. Stratigr., **10**: 164-191.
- KAYA, T., TUNA, V. & GERAADS, D. (2001): A new Orleanian/early Astaracian mammalian fauna from Kultak (Milas-Muğla), southwestern Turkey. – Géobios, **34**: 673-680.
- KAYA, T., GERAADS, D. & TUNA, V. (2003): A new Middle Miocene mammalian fauna from Mordoğan (Western Turkey). – Paläont. Z., **77**: 293-302.
- KÖHLER, M. (1987): Boviden des türkischen Miozäns (Känozoikum und Braunkohlen der Türkei. 28). – Paleont. i Evol., **21**: 133-246.
- KOUFOS, G. D. (2000): Revision of the late Miocene carnivores from the Axios valley, Macedonia, Greece. – Münchner geowiss. Abh., (A), **39**: 51-92.
- KOUFOS, G. D. & KOSTOPOULOS, D. S. (1994): The late Miocene mammal localities of Kemiklitepe, Turkey: 3. Equidae. – Bull. Mus. Nat. Hist. Nat., C, 4e sér., **16**: 41-80.
- KRAKHMALNAYA, T. (1996): [Hipparion fauna from the North of the Black Sea]. – p. 1-225; Kiev (Naukova Dumka). [in Russian].
- KURTÉN, B. (1954): The type collection of *Ictitherium robustum* (Gervais ex von Nordmann) and the radiation of the ictitheres. – Acta Zool. Fenn., **86**: 1-26.
- (1976): Fossil Carnivora from the Late Tertiary of Bled Douarah and Cherichira, Tunisia. – Notes Serv. géol. Tunisie, **42**: 177-214.
- (1982): Status of the fossil hyaenids *Ictitherium viverrinum* and *Thalassictis robusta* (Mammalia). – Z. geol. Wiss., **10**: 1009-1018.
- MAJOR FORSYTH, C. I. (1902): On *Mustela palaeattica* from the Upper Miocene of Pikermi and Samos. – Proc. Zool. Soc. London, **1**: 109-114.
- MEIN, P. (1958): Les mammifères de la faune sidérolithique de Vieux-Collonges. – Nouv. Arch. Mus. Hist. Nat. Lyon, **5**: 1-122.

- MELENTIS, J. K. (1970): Studien über fossile Vertebraten Griechenlands. 28. Die Pikermitafauna von Halmyropotamos (Euböa-Griechenlands). – *Ann. Géol. Pays Hellén.*, **5**: 217-229.
- MORLO, M. (1997): Die Raubtiere (Mammalia, Carnivora) aus dem Turolium von Dorn-Dürkheim 1 (Rheinhessen). Teil 1: Mustelida, Hyaenidae, Percrocutidae, Felidae. – *Cour. Forsch.-Inst. Senckenberg*, **197**: 11-47.
- NAGEL, D. (2003): Carnivora from the middle Miocene Hominoid locality of Çandır (Turkey). – *Cour. Forsch.-Inst. Senckenberg*, **240**: 113-131.
- OZANSOY, F. (1965): Etude des gisements continentaux et des mammifères du Cénozoïque de Turquie. – *Mém. Soc. Géol. France*, **102**: 1-92.
- PETTER, G. (1963): Contribution à l'étude des Mustélidés des bassins néogènes du Vallès-Penedés et de Calatayud-Teruel (Espagne Orientale). – *Mém. Soc. Géol. France*, **42** (2): 1-44.
- PILGRIM, G. E. (1931): Catalogue of the Pontian Carnivora of Europe in the Department of Geology. – 174 pp.; London (British Museum Natural History, Geology).
- ROBERTSON, A. H. F. & PICKETT, E. A. (2000): Palaeozoic-Early Tertiary Tethyan evolution of mélanges, rift and passive margin units in the Karaburun Peninsula (Western Turkey) and Chios Island (Greece). – In: BOZKURT, E., WINCHESTER, J. A. & PIPPER, J. D. A. (Eds.): *Tectonics and Magmatism in Turkey and the surrounding areas*. – *Geol. Soc., Spec. Publ.*, **173**: 43-82.
- ROUSSIAKIS, S. J. (2002): Mustelids and feloids (Mammalia, Carnivora) from the Late Miocene locality of Pikermi. – *Géobios*, **35**: 699-719.
- ROUSSIAKIS, S. J. & THEODOROU, G. E. (2001): *Ancylotherium pentelicum* (Gaudry et Lartet, 1856) (Perissodactyla, Mammalia) from the classic locality of Pikermi (Attica, Greece), stored in the palaeontological and geological museum of Athens. – *Géobios*, **34**: 563-584.
- SARAÇ, G., KAYA, T. & GERAADS, D. (2002): *Ancylotherium pentelicum* (Perissodactyla, Mammalia) from the Upper Miocene of Central and Western Turkey. – *Géobios*, **35**: 241-251.
- SCHAUB, S. (1943): Die Vorderextremität von *Ancylotherium pentelicum* GAUDRY & LARTET. – *Schweiz. Paläont. Abh.*, **64**: 1-36.
- SCHLOSSER, M. (1904): Die fossilen Cavicornia von Samos. – *Beitr. Paläont. Geol. Österr. – Ungarn Orient*, **17**: 21-118.
- SCHMIDT-KITTLER, N. (1976): Raubtiere aus dem Jungtertiär Kleinasiens. – *Palaeontographica*, (A), **155**: 1-131.
- (1995): The vertebrate locality Maramena (Macedonia, Greece) at the Turolian-Ruscinian boundary (Neogene). 7. Carnivora (Mammalia). – *Münchner geowiss. Abh.*, **28**: 75-86.
- SEN, S. (1994): Les gisements de Mammifères du Miocène supérieur de Kemiklitepe, Turquie. – *Bull. Mus. Nat. Hist. Nat., C, 4e sér.*, **16** (1): 1-240.
- SENYÜREK, M. (1960): The Pontian Ictitheres from the Elmadağ district. – *Publ. Fac. Lang., Hist. Geog., Univ. Ankara*. 223 pp.
- SICKENBERG, O., BECKER-PLATEN, J. D., BENDA, L., BERG, D., ENGESSER, B., GAZIRY, W., HEISSIG, K., HÜNERMANN, K. A., SONDAAR, P. Y., SCHMIDT-KITTLER, N., STAESCHE, U., STEFFENS, P. & TOBIEN, H. (1975): Die Gliederung des höheren Jungtertiärs und Altquartärs in der Türkei nach Vertebraten und Bedeutung für die internationale Neogen-Stratigraphie. – *Geol. Jb., (B)*, **15**: 1-167.

- SOLOUNIAS, N. (1981): The Turolian fauna from the island of Samos, Greece with special emphasis on the hyaenids and bovids. – *Contr. Vert. Evol.*, **6**: 1-232.
- SPASSOV, N. & GERAADS, D. (2004): *Tragoportax* Pilgrim and *Miotragocerus* Stromer (Mammalia, Bovidae) from the Turolian of Hadjidimovo, Bulgaria, and a revision of the Late Miocene Mediterranean Boselaphini. – *Géodiversitas*, **26** (2): 0-0.
- TEKKAYA, I., SEN, S. & ATALAY, Z. (1972): Kinik memeli faunasi hakkında bir not. – *Bull. Min. Res. Expl. Inst.*, **78**: 58-68.
- VIRANTA, S. & WERDELIN, L. (2003): Carnivora. – In: FORTELIUS, M., KAPPELMAN, J., SEN, S. & BERNOR, R. L. (Eds): *Geology and Paleontology of the Miocene Sinap Formation, Turkey*, p. 178-193; New York (Columbia Univ. Press).
- WEITHOFER, A. (1888): Beiträge zur Kenntniss der Fauna von Pikermi bei Athen. – *Beitr. Paläont. Österr. – Ungarn Orient*, **6** (3): 225-292.
- WERDELIN, L. (1988): Studies of fossil hyaenas: the genera *Thalassictis* GERVAIS, ex NORDMANN, *Palhyaena* GERVAIS, *Hyaenictitherium* KRETZOI, *Lycyaena* HENSEL and *Palinhyaena* QIU, HUANG & GUO. – *Zool. J. Linn. Soc.*, **92**: 211-265.
- WERDELIN, L. & SOLOUNIAS, N. (1991): The Hyaenidae: taxonomy, systematics and evolution. – *Fossils and Strata*, **30**: 1-104.
- WERDELIN, L. & SOLOUNIAS, N. (1996): The evolutionary history of Hyenas in Europe and Western Asia during the Miocene. – In: BERNOR, R. L., FAHLBUSCH, V. & MITTMANN, H.-W. (Eds.): *The Evolution of western Eurasian Neogene Mammal faunas*, p. 290-307; New York (Columbia Univ. Press).
- ZDANSKY, O. (1924): Jungtertiäre Carnivoren Chinas. – *Palaeont. Sinica*, **2** (1): 1-149.

Manuscript received: June 24th, 2004.

Revised version accepted by the Stuttgart editor: September 25th, 2004.

Addresses of the authors:

TANJU KAYA, Ege Universitesi, Tabiat Tarihi Muzesi, 35100 Bornova-Izmir, Turkey.
DENIS GERAADS, CNRS UPR 2147, 44 rue de l'Amiral Mouchez, 75014 Paris, France;
e-mail: dgeraads@ivry.cnrs.fr
VAHDET TUNA, Ege Universitesi, Tabiat Tarihi Muzesi, 35100 Bornova-Izmir, Turkey.