

# The Late Miocene Mammal Faunas of the Mytilinii Basin, Samos Island, Greece: New Collection

## 5. Carnivora

by

George D. Koufos<sup>\*)</sup>

KOUFOS, G.D., 2009. The Late Miocene Mammal Faunas of the Mytilinii Basin, Samos Island, Greece: New Collection. 5. Carnivora. — Beitr. Paläont., 31:57–105, Wien.

### Abstract

The new collection from the late Miocene localities of the Mytilinii Basin, Samos, Greece include several carnivores which are studied in the present article. The study and comparison of the material allow the determination of seven different taxa which are distributed in the various fossiliferous sites.

MLN: *Protictitherium crassum*, *Hyaenictitherium* cf. *wongii*.

MTLA: *Parataxidea maraghana*, *Hyaenictitherium wongii*, *Adcrocuta eximia*, *Metailurus parvulus*.

MTLB: *Plioviverrops orbigny*, *Hyaenictitherium wongii*.

MTLC: *Hyaenictitherium wongii*.

PMMS (?MTLA): *Adcrocuta eximia*, *Machairodus giganteus*.

All the determined taxa, except *Protictitherium crassum*, are known from the old collections of Samos but in the new collection there are some specimens, adding new data to them. The species *Protictitherium crassum* was found for the first time in the late Miocene of Samos; it is known from the neighboring area, as well as being reported from Continental Greece and Asia Minor. All the studied material was described and compared with the known material from Greece and Eurasia. Bearing the stratigraphic distribution of each taxon and their presence in the Samos fauna in mind, a middle Turolian age is possible for the localities Mytilinii-1A, B (MTLA, MTLB). The carnivoran fauna of the other localities is poor and does not allow a precise age determination, except that of late Miocene. However, the various localities have been dated using the whole fauna and magnetostratigraphy (see chapter 16 of this volume).

**Keywords:** Late Miocene, Samos, Greece, Mammalia, Carnivora, Systematics.

### Zusammenfassung

Die neuen Aufsammlungen aus den obermiozänen Fundstellen des Mytilinii Beckes (Samos, Griechenland) beinhalten einige Carnivoren, die in der vorliegenden Arbeit untersucht werden. Die Untersuchungen erlauben eine Zuordnung der Funde, die aus unterschiedlichen Lokalitäten stammen, zu sieben Arten.

MLN: *Protictitherium crassum*, *Hyaenictitherium* cf. *wongii*.

MTLA: *Parataxidea maraghana*, *Hyaenictitherium wongii*, *Adcrocuta eximia*, *Metailurus parvulus*.

MTLB: *Plioviverrops orbigny*, *Hyaenictitherium wongii*.

MTLC: *Hyaenictitherium wongii*.

PMMS (?MTLA): *Adcrocuta eximia*, *Machairodus giganteus*.

Mit Ausnahme von *Protictitherium crassum*, sind alle anderen Taxa von früheren Aufsammlungen bekannt, aber unter den neuen Funden ergaben sich neue Erkenntnisse zu den Arten. *Protictitherium crassum* ist zum ersten Mal aus dem Obermiozän von Samos beschrieben. Diese Art ist aus angrenzenden Gebieten bekannt, zum Beispiel vom griechischen Festland und aus Kleinasien und wurde auch mit dem bisher bekannten Material aus Griechenland und Eurasien verglichen. Berücksichtigt man die stratigraphische Verbreitung dieses Taxons und seine Anwesenheit in der Samos Fauna, so ist Mittel-Turolium als Alter für die Lokalitäten Mytilinii-1A, B (MTLA, MTLB) möglich. Die Carnivorenreste aus den anderen Lokalitäten sind gering und lassen eine genauere Alterseinstufung, die über das Obermiozän hinausgeht, nicht zu. Die Datierung der verschiedenen Fundstellen erfolgte über die gesamte Fauna und mit Hilfe der Magnetostratigraphie (siehe Kapitel 16, dieser Band).

**Schlüsselworte:** Obermiozän, Samos, Griechenland, Mammalia, Carnivora, Systematik.

<sup>\*)</sup> Prof. George D. Koufos, Aristotle University of Thessaloniki. Department of Geology. Laboratory of Geology and Palaeontology. GR-54124 Thessaloniki, Greece. e-mail:koufos@geo.auth.gr

FORSYTH MAJOR (1894)	PILGRIM (1931)	SOLOUNIAS (1981)	BERNOR et al. (1996)	NOW, 2007	Present Article
<i>Mustela palaeattica</i>	? <i>Indarctos atticus</i>	<i>Ursavus</i> cf. <i>depereti</i>	<i>Ursavus</i> cf. <i>depereti</i>	<i>Ursavus</i> cf. <i>depereti</i>	<i>Parataxidea maraghana</i>
<i>Promephitis larteti</i>	<i>Promeles palaeattica</i>	<i>Indarctos atticus</i>	<i>Indarctos atticus</i>	<i>Indarctos atticus</i>	<i>Plioviverrops orbigny</i>
<i>Meles maraghana</i>	<i>Promephitis larteti</i>	<i>Promeles palaeattica</i>	<i>Promeles palaeattica</i>	<i>Promeles palaeattica</i>	<i>Protictitherium crassum</i>
<i>Ictitherium orbigny</i>	<i>Parataxidea</i> (?) <i>maraghana</i>	<i>Promephitis larteti</i>	<i>Promephitis larteti</i>	<i>Promephitis larteti</i>	<i>Hyaenictitherium wongii</i>
<i>Ictitherium robustum</i>	<i>Ictitherium orbigny</i>	<i>Parataxidea maraghana</i>	<i>Parataxidea polaki / maraghana</i>	<i>Parataxidea maraghana</i>	<i>Adcrocuta eximia</i>
<i>Ictitherium hipparionum</i>	<i>Ictitherium hipparionum</i>	<i>Plioviverrops orbigny</i>	<i>Plioviverrops orbigny</i>	<i>Plioviverrops orbigny</i>	<i>Metailurus parvulus</i>
<i>Lycyaena chaeretis</i>	<i>Lycyaena chaeretis</i>	<i>Ictitherium viverinum</i>	<i>Ictitherium viverinum</i>	<i>Ictitherium viverinum</i>	<i>Machairodus giganteus</i>
<i>Hyaena eximia</i>	<i>Crocota eximia</i>	<i>Thalassictis wongii</i>	<i>Hyaenotherium wongii</i>	<i>Hyaenotherium wongii</i>	
<i>Machairodus</i> sp.	<i>Felis neas</i>	<i>Thalassictis hyaenoides</i>	<i>Lycyaena chaeretis</i>	<i>Lycyaena chaeretis</i>	
<i>Felis neas</i>		<i>Thalassictis</i> ( <i>Lycyaena</i> ) n. sp.	<i>Belbus beaumonti</i>	<i>Belbus beaumonti</i>	
		<i>Thalassictis</i> ( <i>Lycyaena</i> ) <i>chaeretis</i>	<i>Adcrocuta eximia</i>	<i>Adcrocuta eximia</i>	
		<i>Hyaenictis eximia</i>	<i>Felis attica</i>	<i>Felis attica</i>	
		<i>Felis attica</i>	<i>Metailurus major</i>	<i>Metailurus major</i>	
		<i>Metailurus major</i>	<i>Metailurus parvulus</i>	<i>Metailurus parvulus</i>	
		<i>Metailurus parvulus</i>	<i>Machairodus giganteus</i>	<i>Amphimachairodus giganteus</i>	
		<i>Machairodus giganteus</i>			

**Table 1:** Various faunal lists of the carnivoran taxa found on Samos.

## 1. Introduction

The late Miocene mammal fauna of Samos has been known since the last decades of the 19<sup>th</sup> century, when C.J. Forsyth Major found and described several fossils. However, the presence of the mammal fossils on Samos was known earlier but without description (KOUFOS, this volume). Since 1994, a team from the Laboratory of Geology and Palaeontology of the Aristotle University of Thessaloniki, led by the author, excavated on Samos and collected a large amount of fossils. As all the old material of Samos is mixed and without or of limited stratigraphic indication, there are difficulties in the determination of the material and the age of the fauna. Although the new collection is not as rich as the old ones, its composition, as well as the certain and precise stratigraphic control can give good taxonomic and biochronologic results. The old collections of Samos include several carnivores, which have been described by various authors. Few carnivores are mentioned in the original list of FORSYTH MAJOR (1894) who was the first systematic excavator and collector of Samos mammal fossils. The late Miocene carnivoran fauna of Samos slowly increased at first (PILGRIM, 1931), while later, it increased remarkably (SOLOUNIAS, 1981; BERNOR et al., 1996; NOW, 2007), (Tab. 1).

The new collection of Samos includes several carnivores, mainly hyaenids, and less mustelids and felids. The major-

ity of the carnivores belong to *Hyaenictitherium wongii*, a well-known and widespread late Miocene hyaenid. In the present article, the new collection of carnivores is described and compared with the old Samos material, as well as with the late Miocene Eurasian material. The material has been originally compared with the material of Axios Valley, (Macedonia, Greece), housed at LGPUT (the best dated Late Miocene collection of the Eastern Mediterranean under certain stratigraphic control) for the first time, as well as with the old collections of Samos and Pikermi stored at AMPG, MNHN, NHML and NHMW. The carnivores of Prof. J. Melentis collection from Samos were also included in this article. The collection was described earlier (KOUFOS & MELENTIS, 1982) but it is included in the present paper with more details and comparisons. All the studied material is housed at NHMA, which is located in the village of Mytilinii, Samos.

The studied material has been unearthed from the following localities of the Mytilinii Basin:

**Locality Mytilinii-4 (MLN).** The locality "Mytilinii-4", MLN is situated in the southern outcrops of Potamies ravine and seems to be identical to B. Brown's Q4 (KOUFOS et al., 1997); KOSTOPOULOS et al., 2003). This locality yielded few carnivores. It is dated to middle Turolian (MN 12), but it is older than MTL, having an age of ~7.5 Ma (KOSTOPOULOS et al., 2003; KOUFOS et al., this volume). **Locality Mytilinii-1 (MTL).** It is located in the Adrianos

ravine and can be correlated to B. Brown's Q1 or QA. Four different fossiliferous sites have been recognized: MTLA, MTLB, MTLC, and MTLD.

MTLA corresponds to the site where Prof. Melentis excavated; MTLB and MTLC are new sites. MTLD corresponds to the site where B. Brown excavated, as we found several remains of his excavations (KOUFOS et al., 1997; KOSTOPOULOS et al., this volume). The studied material was found in MTLA, MTLB, and MTLC. All sites are dated to middle Turolian (MN 12), more precisely from 7.1-7.0 Ma, according to the palaeomagnetic record (KOSTOPOULOS et al., 2003; KOUFOS et al., this volume). **PMMS Collection.** The collection made by Prof. J. Melentis, who excavated on Samos in 1963, originated from Adrianos ravine. Prof. J. Melentis showed me the exact site from where he collected the fossils which corresponds to MTLA. Although this information is certain, the material is described separately. Over all this time it is quite possible, that fossils found by the villagers in various sites on Samos were mixed with Prof. J. Melentis' collection, falsifying the origin of the material. More details about the localities and their stratigraphic position are given in KOSTOPOULOS et al. (this volume).

**Abbreviations:**

- AMNH = American Museum of Natural History, New York
- AMPG = Athens Museum of Geology and Palaeontology, University of Athens
- BSPM = Bayerische Staatssammlung für Paläontologie und Historische Geologie, München.
- HAL = Halmyropotamos, Evia Island, Greece
- KER = Kerassia, Evia Island, Greece
- LGPOT = Laboratory of Geology and Palaeontology, University of Thessaloniki
- MGL = Musée de Géologie de Lausanne
- MLN = Mytilinii-4, Samos, Greece
- MNHN = Museum Nationale d'Histoire Naturelle, Paris
- MRG = Maragheh, Iran
- MTL = Mytilinii-1, Samos, Greece
- MTLA = Mytilinii-1A, Samos, Greece
- MTLB = Mytilinii-1B, Samos, Greece
- MTLC = Mytilinii-1C, Samos, Greece
- MTLD = Mytilinii-1D, Samos, Greece
- NHMA = Natural History Museum of Aegean, Mytilinii, Samos
- NHML = Natural History Museum of London
- NHMW = Naturhistorisches Museum, Wien
- NOW = Neogene Old World database
- PER = Perivolaki, Thessaly, Greece
- PIK = Pikerimi, Attica, Greece
- PMMS = Palaeontological Museum of Mytilinii, Samos
- PXM = Prochoma, Axios Valley, Macedonia, Greece
- QA = Quarry-A, Samos, Greece
- Q1 = Quarry-1, Samos, Greece
- Q2 = Quarry-2, Samos, Greece
- Q4 = Quarry-4, Samos, Greece
- Q5 = Quarry-5, Samos, Greece
- RP1 = Ravin de la Pluie, Axios Valley, Macedonia, Greece
- RZ1 = Ravin des Zouaves-1, Axios Valley, Macedonia, Greece
- RZO = Ravin des Zouaves-5, Axios Valley, Macedonia, Greece

SAM = Samos old collections

VAT = Vathylakkos-3, Axios Valley, Macedonia, Greece

VTK = Vathylakkos-2, Axios Valley, Macedonia, Greece

The specimens of the various museums or institutes, except NHMA, are given in the text by the abbreviation of the museum or institute, the locality and the serial number of the specimen.

**2. Palaeontology**

Order Carnivora BOWDICH, 1821

Family Mustelidae SWAINSON, 1835

Subfamily Melinae BURMEISTER, 1850

Genus *Parataxidea* ZDANSKY, 1924

*Parataxidea maraghana* (KITTL, 1887)  
(Pl. 1, figs. 1-5)

**Locality:** Mytilinii-1A (MTLA), Adrianos ravine, Mytilinii Basin, Samos, Greece.

**Age:** Middle Turolian, MN 12 (late Miocene); 7.1-7.0 Ma.

**Material:** Skull, MTLA-283; partial skull, MTLA-465; m1 sin, MTLA-7.

**Measurements:** The cranial measurements are given in Table 2.

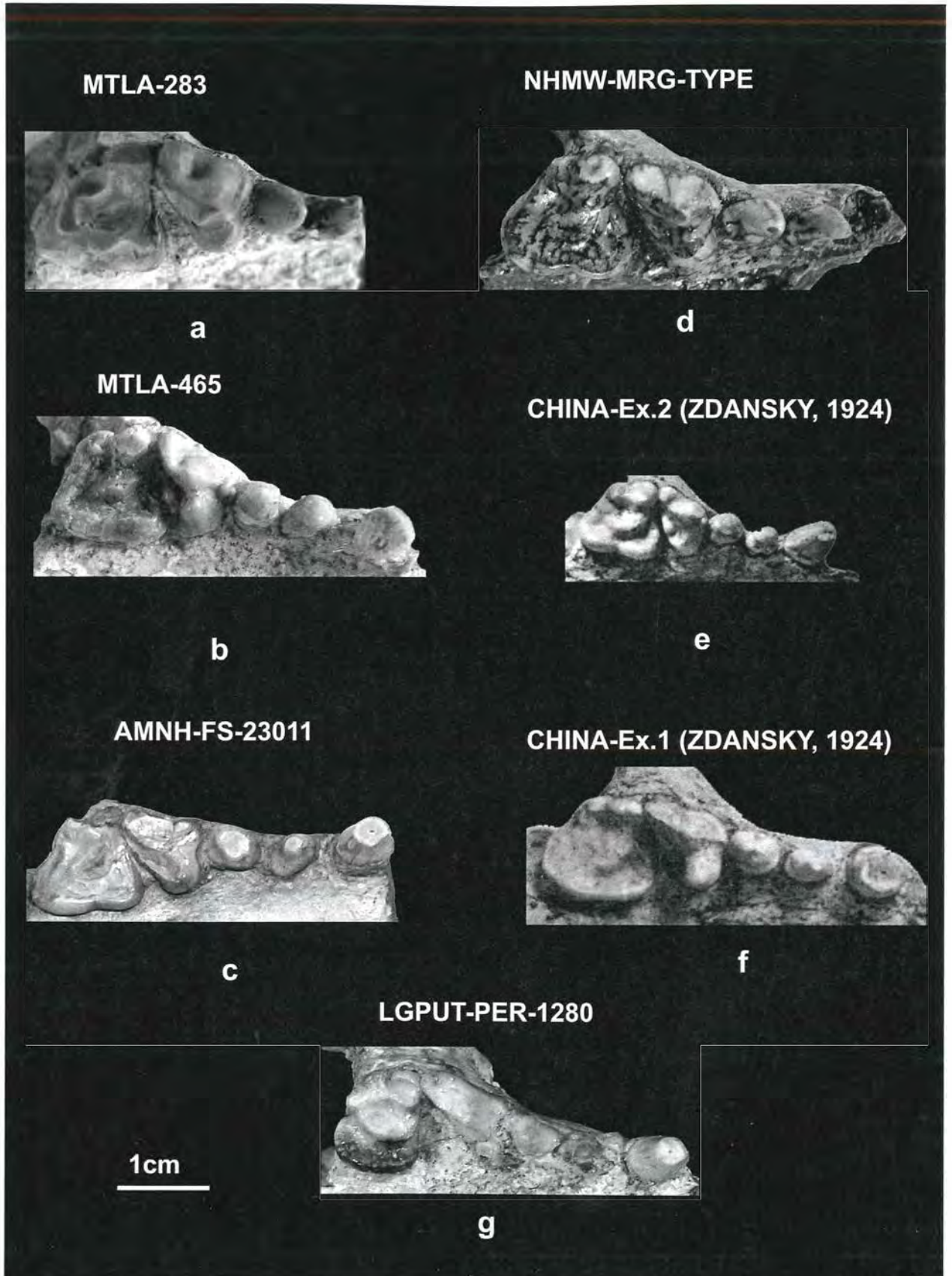
**Description:**

**Skull.** The skull MTLA-283 (Pl. 1, fig. 1) lacks the muzzle and the occipital region with the condyles; the right zygomatic arch and the bone in the posterior part of the braincase are broken. The specimen MTLA-465 is a

	MTLA-283		MTLA-465	
	dex	sin	dex	sin
LC	—	—	5.0	4.8
BC	—	—	4.0	4.2
LP1	—	—	—	—
BP1	—	—	—	—
LP2	4.5	—	5.1	5.0
BP2	3.6	—	3.5	3.7
LP3	5.7	5.6	5.7	5.6
BP3	4.4	4.3	4.8	4.5
LP4	8.1	7.8	8.5	7.8
BP4 ant.	8.0	8.0	7.7	7.5
LM1 buccal	7.8	7.7	7.6	7.4
LM1 lingual	11.0	11.6	11.3	11.2
BM1	11.4	11.2	11.2	11.2

MTLA-466 m1 = 11.3 x 7; L tal = 5.4

**Table 2:** Cranial dimensions of *Parataxidea maraghana* and *Promeles palaeattica*.



**Figure 1:** Comparison of the upper dentition of *Parataxidea* and *Promeles*.

a. Tooth row of the skull, MTLA-283, b. Tooth row of the skull MTLA-465, c. *P. maraghana*, tooth row of the skull, AMNH-FS 23011, Samos; d. *P. maraghana*, tooth row of the TYPE, Maragheh; e. *P. sinensis*, tooth row of the skull Ex. 2, China (taken from ZDANSKY, 1924); f. *P. crassa*, tooth row of the skull Ex. 1, China (taken from ZDANSKY, 1924); g. *Promeles palaeattica*, tooth row of the skull LGPUT-PER-1280. All tooth rows shown as if from right-hand side.

*Parataxidea maraghana*, Upper Teeth

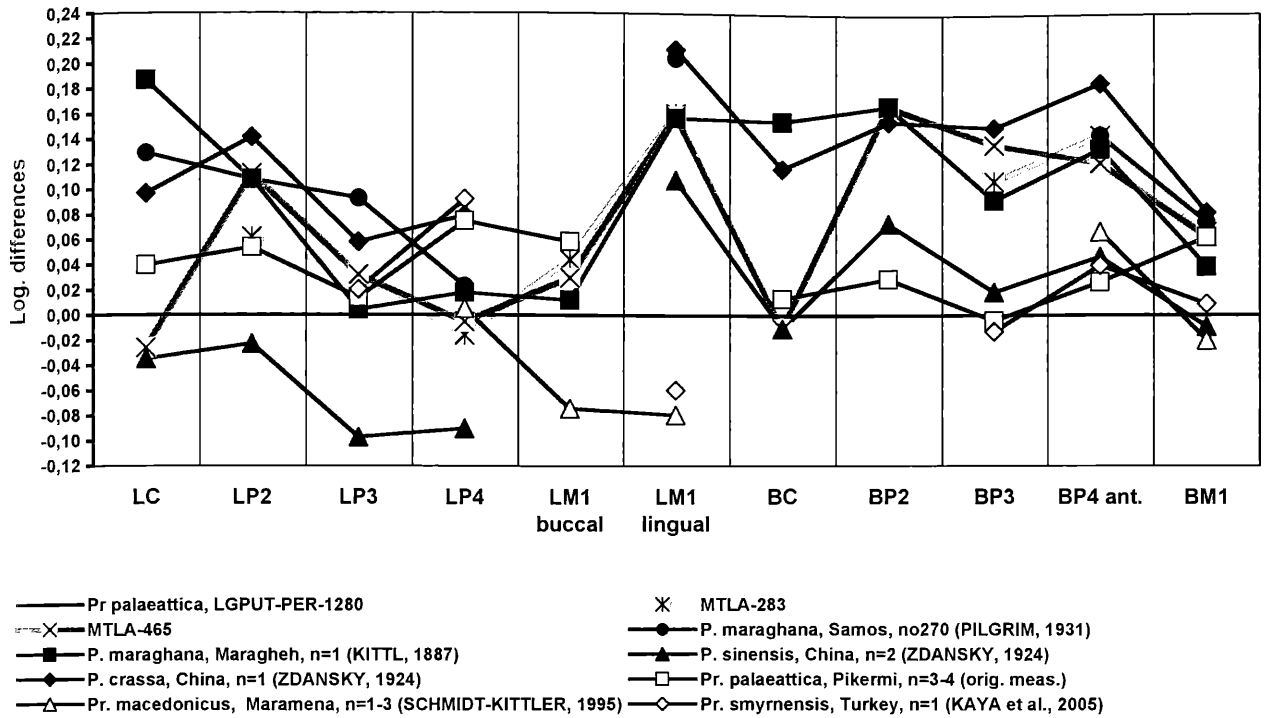


Figure 2: Logarithmic ratio diagram comparing the upper teeth of *Parataxidea* and *Promeles* from various localities.

partial skull lacking the posterior part and the zygomatic arches. The muzzle is short and relatively wide (Pl. 1, fig. 3c). The nasal cavity is oval and its lateral borders are almost vertical to the palate. Its posterior border is situated above the canine. The frontals are narrow. The infraorbital foramen is large. The orbit is rounded and its anterior border is above the middle of the P4. The zygomatic arches are relatively strong and project buccally; they begin above the contact between the P4 and M1. The postorbital projection is strong. A projection from the zygomatic arch to the postorbital projection almost closes the orbit; only a small part of the orbit's periphery remains open (Pl. 1, fig. 1b). There is no sagittal crest. The bullae are elliptical and their buccal surface inclines roughly buccally, while the lingual surface is more vertical. The anterior border of the bullae is level with the posterior surface of the post-glenoid processes. The choanae are relatively wide and their anterior border is well behind the M1, situated in the middle of the zygomatic arch, at about 8 - 9.5 mm behind the posterior border of the M1. The palate is elongated and narrow with almost parallel borders giving it a more or less rectangular shape.

**Upper Dentition.** The skull MTLA-283 preserves the tooth rows P3-M1 dex and P2-M1 sin (Pl. 1, figs 1, 2). The teeth are well preserved but worn, while the right M1 is slightly broken at its buccal border. The skull MTLA-465 preserves the tooth rows P4-M1 dex and C-M1 sin; the teeth are little worn (Pl. 1, figs 3, 4).

**C:** It is elongated and slender, slightly curved distally and with a round transverse section. It seems to have a mesial crest.

**P2:** It is monocuspid, single-rooted with rounded crown. There is a slight cingulum all around the tooth.

**P3:** It is similar to P2 but larger. The lingual cingulum is stronger and has a strong projection in its distal part.

**P4:** It is short and wide, having a triangular shape and strong protocone, while the paracone and metacone are relatively short. There is no parastyle, but there is a small cingular projection in the mesial base of the paracone, giving the idea of a rudimentary parastyle (Pl. 1, fig. 4). The protocone is robust, well separated from the paracone by a deep mesial valley and situated in front of the mesial border of the tooth. The metacone is blade-like, very short and faces buccally. There is a strong lingual cingulum connecting the protocone and the metacone. There is an elevation in the middle of the lingual cingulum, forming a small cusplule (Pl. 1, fig. 4) which gives a more squarish shape to the tooth. In the worn teeth the lingual cingulum forms a crest connecting the protocone and metacone (Pl. 1, fig. 2).

**M1:** The shape of the tooth is trapezoid with the mesial border perpendicular to the mesiodistal axis of the tooth. The posterior border has a deep groove with the lingual part projecting strongly distally. The paracone is larger and more buccally projected than the metacone. The protocone is strong and situated in the center of the occlusal surface. The hypocone is strong and is extended to the distolingual part of the tooth. There is a strong and elevated mesial, lingual and distal cingulum.

**Lower Dentition.** The lower dentition is represented by only one isolated m1, MTLA-7 (Pl. 1, fig. 5).

**m1:** It is short and wide with an elongated talonid. The paraconid is a large cuspid, situated mesially. The protoconid is equal in size to the paraconid. The metaconid is also large and situated level with the protoconid; both are

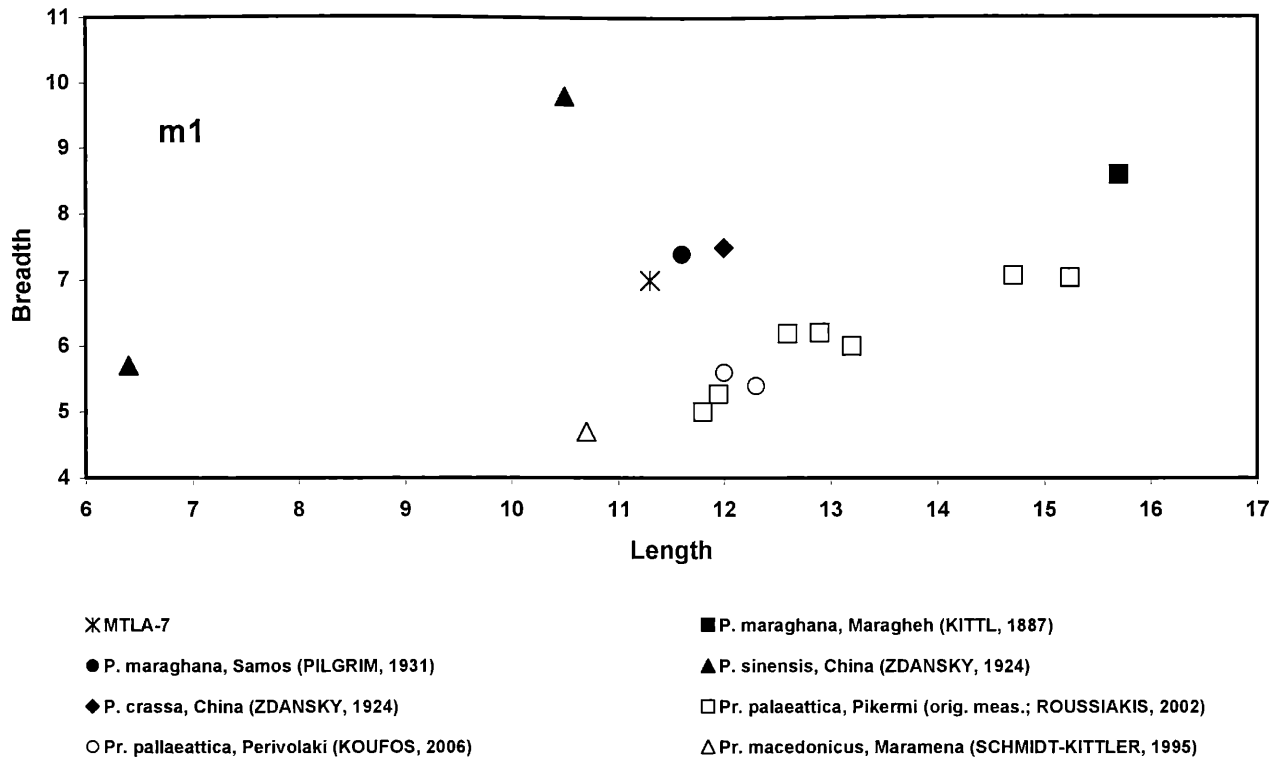


Figure 3: Scatter diagram length/breadth for the m1 of *Parataxidea* and *Promeles* from various localities.

separated by a small valley. The paraconid is distinguished from the metaconid and protoconid complex by a deep valley, which is open lingually. The talonid is large and wide, being about half of the tooth's length. The entoconid is large, situated behind the metaconid, from which it is separated by a very narrow valley. The hypoconid is stronger than the entoconid and is separated from the protoconid by a wide valley. The hypoconulid is large and crest-like, covering the whole distal border of the tooth. There is another small cusplet behind the entoconid, connecting it with the hypoconulid. Thus, the talonid is closed all around and has a basin-like form (Pl. 1, fig. 5c). There is a strong buccal cingulum.

**Discussion:** The taxon was originally described as *Meles maraghanus* from Maragheh, Iran. The type specimen is a right maxillary fragment with C-M1; the canine is broken (Fig. 1d), (KITTL, 1887; Taf. 15, fig. 4). Later, when ZDANSKY (1924) described some Chinese material and erected the new genus *Parataxidea*, the species was transferred to it and reported as *Parataxidea maraghana*. A complete skull associated with the mandible is reported as *Meles maraghana* in the list of Samos material given by FORSYTH MAJOR (1894) and is stored at MGL. This skull was described by PILGRIM (1931). The taxon is also reported from Q1 and QA of Samos as *Parataxidea maraghana* (SOLOUNIAS, 1981), while later it is referred to as *P. polaki/maraghana* (BERNOR et al., 1996). Some material of *P. maraghana* from Samos, coming from Q1 is stored at AMNH (<http://paleo.amnh.org/fossil/list.html>).

The genus *Parataxidea* resembles *Promeles* and can be easily confused with it, but a more careful comparison clearly distinguishes the two genera. The Samos skulls are

directly compared with the material of *Promeles palaeattica* from Pikermi, stored at NHML, and from Perivolaki (Thessaly, Greece), stored at LGPUT and described by KOUFOS (2006a). The comparison allows recognizing the differences between the genera *Promeles* and *Parataxidea*. The general shape and size of the skull is similar in the two genera, but the comparison of the dentition gives the following differences:

- the P2,3 of *Parataxidea* are more robust and have a strong cingulum which is absent in *Promeles* (Fig. 1).
- the P4 of *Parataxidea* is robust (short and wide), triangular-shaped and with a strong protocone, while in *P. palaeattica* it is slender (elongated and narrow), with a weaker and more mesiolingually projected protocone. In *Promeles*, the P4 lacks the small mesial cusp which corresponds to a rudimentary parastyle, as well as the small lingual cusplet developed in the middle of the lingual cingulum (Fig. 1g).
- the M1 is also completely different. In *Parataxidea* it is larger, with an elongated lingual mesiodistal diameter. On the contrary, the buccal mesiodistal diameter is shorter and parallel to the alveolar line, while it is oblique in *Promeles* (Fig. 3g). The lingual cingulum is stronger in *Parataxidea*. On the mesial border of the M1, there is a strong groove in *Promeles* which is absent in *Parataxidea* (Fig. 1).
- the m1 of *Parataxidea* is larger, more robust with shorter and narrower talonid, which is deeper than that of *Promeles*. The paraconid of the *Parataxidea* m1 is shorter than that of *Promeles*. There is strong buccal cingulum in *Parataxidea*, which is absent in *Promeles*.
- The dental size of *Promeles* is generally smaller than that of *Parataxidea*; the *Promeles* teeth are especially narrower

than those of *Parataxidea* (Figs 2, 3). These morphological and metrical differences clearly distinguish the genera *Parataxidea* and *Promeles*. The morphology and dimensions of the studied material from Samos fit quite well with those of *Parataxidea* and can be certainly ascribed to this genus.

The type specimen of *Parataxidea maraghana* has worn teeth (Fig. 1d). The species is characterized by a large infraorbital foramen situated above the P4. The premolars are monocuspid, single-rooted with strong cingulum and a lingual cingular projection in the P3. The P4 is short and wide with a large protocone well-separated from the paracone; there is no parastyle, but a mesial cingular projection while the lingual cingulum is strong. The M1 is trapezoid with a large paracone and a smaller metacone; its lingual anteroposterior diameter is remarkably longer than the buccal one (Fig. 1d). This morphology fits in quite well with the studied skulls from MTLA, which can be ascribed to *P. maraghana* with certainty. Moreover, the size of the upper teeth of MTLA-283, 465 is very close to *P. maraghana* (Fig. 2). The studied lower carnassial is also similar to that of *P. maraghana* but slightly smaller (Fig. 3). The upper canine of MTLA-465 is smaller than that of *P. maraghana* (Fig. 2); this difference could be due to sexual dimorphism. The canine of the type skull is even larger than that of *P. crassa*, which has the largest teeth (Fig. 2).

The Samos skull and mandible (MGL-SAM-no 270), reported by FORSYTH MAJOR (1894) and described by PILGRIM (1931), is an aged individual with almost completely worn P4, M1, p4 and m1, 2. The characteristics of this skull, as well as its dental morphology given by PILGRIM (1931), fit in quite well with those of the studied skulls. The upper teeth and m1 dimensions are also close to those of the studied material, although they are slightly larger (Figs 2, 3). The upper canine of the MGL skull is remarkably larger than that of MTLA-465, but this is probably due to sexual dimorphism. The studied material is also compared with some photos of the material stored at AMNH. The AMNH material includes a skull from Samos connected with the mandible (AMNH-FS-20700), a maxillary fragment with C-M1dex (AMNH-FS-23011), (Fig. 1c), and a mandibular fragment with i1-p3 sin (AMNH-FS-23006). The skull AMNH-FS-20700 lacks the braincase, but its frontal part is very similar to that of the studied skulls. The upper teeth of the specimen AMNH-FS-23011 (Fig. 1c) are well-preserved and their morphology is quite clear and fits in well with that of MTLA-283, 465 (Figs. 1a-c).

Two skulls associated with the mandible from Lok. 305 of China are described as *Parataxidea sinensis* (ZDANSKY, 1924; Taf. X, figs 5-10). The cranial and dental morphological characteristics of *P. sinensis* (Fig. 1e) are similar to those of MTLA-283, 465. The dental similarity of *P. sinensis* to the type of *P. maraghana* is reported by ZDANSKY (1924) too. Although they are morphologically similar, *P. sinensis* has smaller dimensions (Figs. 2, 3). The upper teeth of the studied skulls MTLA-283, 465 and the type of *P. maraghana* are significantly larger than those of *P. sinensis* (Fig. 2), and clearly distinguished from them.

Another partial skull with a mandible from the Lok. 30 of China are described as *Parataxidea crassa* (ZDANSKY, 1924; taf. XI, figs. 1-4). The dentition of the skull is quite worn (Fig. 1f), but its morphology is similar to that of MTLA-283, 465. Especially the teeth of MTLA-283, which are worn, closely resemble those of *P. crassa*. The dental dimensions of *P. crassa* are slightly larger than those of the studied skulls. The most significant difference is the size of the P4, whose length is smaller than that of *P. crassa*; the other teeth have similar dimensions (Figs. 2, 3). Bearing in mind that the available material from both localities (MTLA and Lok. 30) is rare, the dental size variability is not well-known and with their morphological similarity, *P. crassa* and *P. maraghana* could be synonyms. Unfortunately, I have not seen the skull of *P. crassa* from China and thus it is difficult to ascertain such a conclusion.

The genus *Parataxidea* is mainly an Asian taxon known from Middle Maragheh and Samos. The species is also known from the locality Karaçahasan (Turkey), dated to early Turolian, MN 11 (NOW, 2007). Bearing in mind, that Middle Maragheh and MTLA are dated to middle Turolian (MN 12) then the stratigraphic distribution of *P. maraghana* covers early - middle Turolian.

Family Hyaenidae GRAY, 1821

Genus *Plioviverrops* KRETZOI, 1938

*Plioviverrops orbignyi* (GAUDRY & LARTET, 1854)  
(Pl. 2, figs. 1, 2)

**Locality:** Mytilinii-1B (MTLB), Adrianos ravine, Mytilinii Basin, Samos, Greece.

**Age:** Middle Turolian, MN 12 (late Miocene); 7.1-7.0 Ma.

**Material:** Skull, MTLB-170.

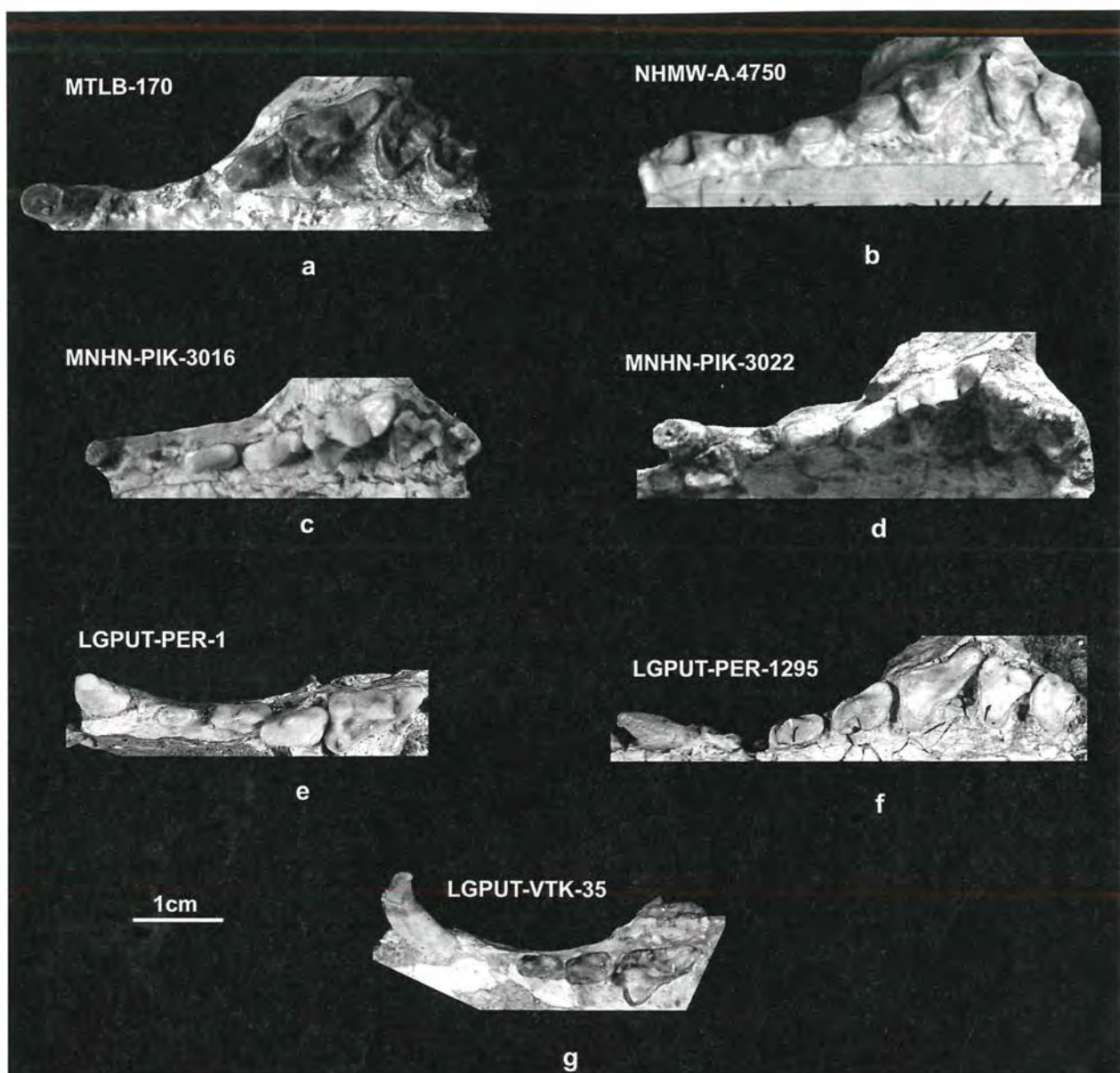
**Measurements:** The measurements of the skull are given in Table 3.

**Description:**

**Skull.** The skull is almost complete, lacking the incisor's border and the right zygomatic arch. The narial opening is slightly distorted on the distal border; it is oval, relatively wide, with its borders running parallel to the canine's root. The nasal bones are absent (Pl. 2, fig. 1a). The frontal bones are extended to the front, like spines, at about the distal border of the narial opening. A groove is running across the contact of the frontals. The orbit is elliptical and large, with its anterior border above the middle of the P3. The

	dex	sin		dex	sin
C	5.0 x 4.0	6.6 x 4.3	M1	— x 8.4	6.2 x 8.3
P3	7.7 x 4.7	7.6 x 4.6	M2	4.6 x 6.3	4.4 x 6.4
P4	— x 7.1	10.8 x 7.0	C-M2	46.5	46.8
LP4 <sub>blade</sub>	— x 3.8		C-P4	38.0	38.1
			C-M1	43.0	43.4

**Table 3:** Cranial dimensions of *Plioviverrops orbignyi* from various Greek localities.



**Figure 4:** Comparison of the upper dentition of *Plioviverrops orbigny* from various Greek localities.

a. Tooth row of the skull MTLB-170; b. Tooth row of the skull NHMW-A.4750, Samos; c. Tooth row of the skull MNHN-PIK-3016, Pikermi; d. Tooth row of the skull MNHN-PIK-3022, Pikermi, TYPE; e. Tooth row of the maxilla LGPUT-PER-1, Perivolaki, Thessaly; f. Tooth row of the skull LGPUT-PER-1295, Perivolaki, Thessaly; g. Tooth row of the skull LGPUT-VTK-35, Axios Valley. All specimens shown as if from left-hand side.

infraorbital foramen is large situated in front of the orbit and above the P3. The postorbital constriction is strong while the postorbital projections are partially broken, but seems to be large. A quite strong sagittal line starts from each postorbital projection and faces posteriorly. The two sagittal lines are connected at about the beginning of the parietals, forming a sagittal crest which ends at the external occipital protuberance (Pl. 2, fig. 1a). The occipital bone is triangular-shaped with a strong crista nuchae which projects distally, exceeding the level of the occipital condyles (Pl. 1, fig. 1e). The occipital condyles are strong and the foramen magnum is elliptical. The glenoid fossa is well-developed with strong post-glenoid processes (Pl. 2, figs. 1b, c, e). The auditory bullae are ovoid with a backwardly

inclined distal part, a large buccal fossa and a slight groove in their mesiolingual surface. The zygomatic arches are strong, projecting buccally. The palate is relatively short and wide. It is narrow between the canines and the first premolars, but it widens from the mesial border of the P3, reaching its maximal breadth at the distal border of the carnassial (Pl. 2, fig. 2). The anterior border of the choanae is behind the posterior border of the M2.

**Upper Dentition.** The skull preserves the tooth rows C, P3-M2 on both sides. The right P4 and M1 are partially broken, while the left P3 is somewhat inside the bone and thus not clearly shown (Pl. 2, fig. 2).

**C:** The tip of both canines is broken. They are relatively strong, flattened buccolingually and having an elliptical



*Plioviverops orbigny*, Upper Teeth

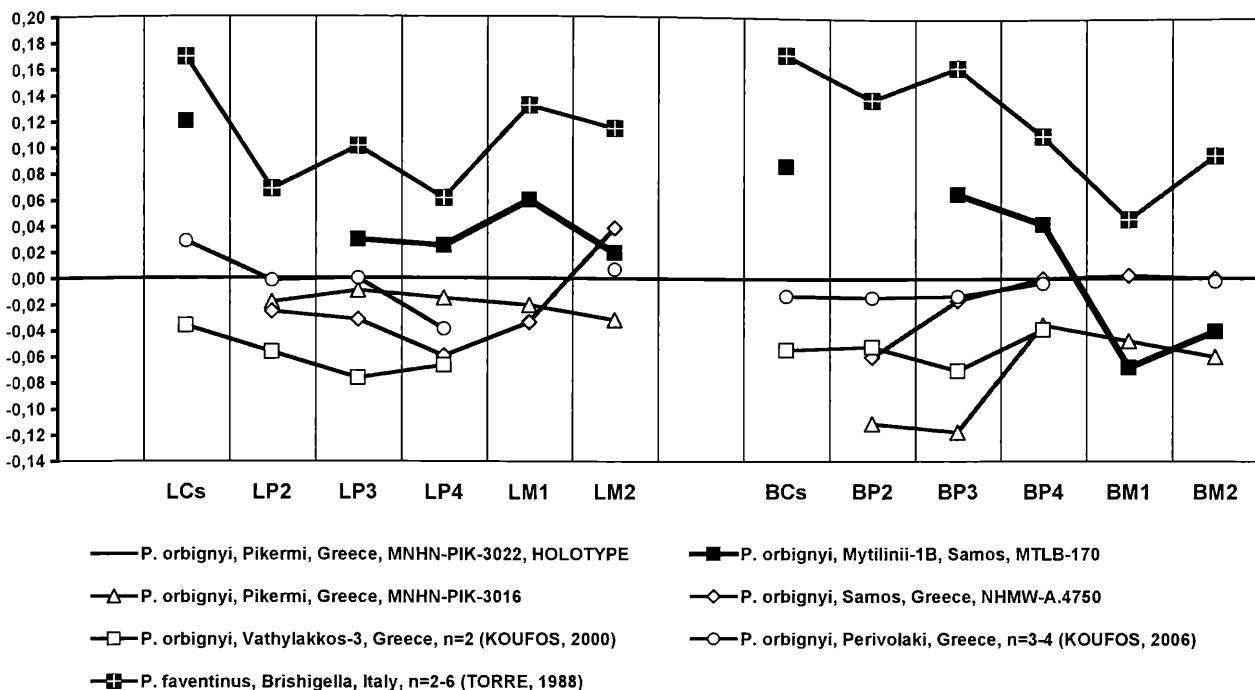


Figure 5: Logarithmic ratio diagram comparing the upper teeth of *Plioviverops* from various localities.

cross-section. They are curved distally and they are pointing buccally.

**P3:** It is short and wide, lacking the anterior accessory cusp. A strong crest begins from the top of the main cusp, running across its mesial border and ending at the mesiolingual corner of the tooth. There is a small posterior accessory cusp on a distal projection of the distal cingulum. The cingulum is strong all around the tooth. In the middle of the lingual cingulum there is a strong projection giving the idea of a rudimentary protocone; this feature indicates a relatively molarized premolar.

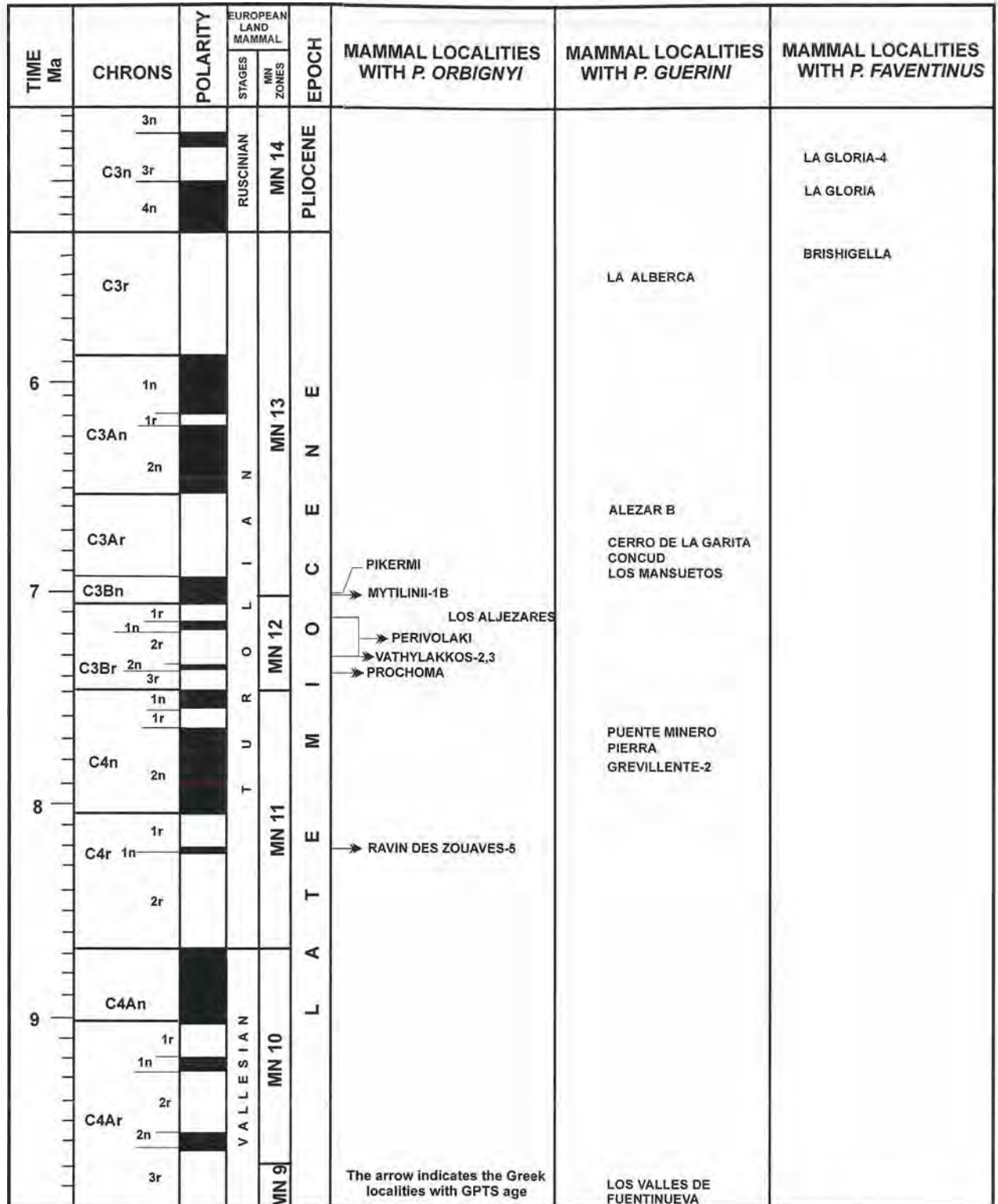
**P4:** The protocone is relatively large, well separated from the paracone and projects lingually. Its mesial border is projected in front of the parastyle. The parastyle is smaller than the protocone and paracone and it has a small cingular projection at the mesiobuccal corner. The metacone is blade-like and strongly curved buccally. The lingual cingulum is well-developed and continues with a crest to the top of the protocone. One weak crest starts from the tip of the paracone, and running through the valley between the paracone and protocone, ends at the tip of the protocone. The buccal cingulum is weak.

**M1:** It is triangular with three cusps. The paracone is stronger than the metacone, from which it is distinguished by a deep valley. The paracone and protocone are similar in height, and they are connected by a crest running across the mesial border of the tooth. Another weak crest begins at the tip of the protocone connecting it with the base of the metacone. There is a well-developed buccal cingulum.

**M2:** More rounded than M1 with the paracone stronger than the metacone. The protocone is similar to that of M1. The central basin is large and open distally near the base of the distobuccal cingulum. There is a strong buccal cingulum.

**Discussion:** The species *P. orbigny* is well-known from Greece, found in several late Miocene localities. Originally it was described from Pikermi as *Viverra orbigny* by GAUDRY & LARTET (1856). Later, it was transferred to *Thalassictis* by GAUDRY (1861), to *Ictitherium* by GAUDRY (1862-67) and finally to *Plioviverops* by KRETZOI (1938). Then afterwards, it was transferred to this taxon (BEAUMONT, 1969; BEAUMONT & MEIN, 1972; KOUFOS, 1979, 1980, 2000, 2006a; SOLOUNIAS, 1981; BONIS & KOUFOS, 1991; WERDELIN & SOLOUNIAS, 1991; ROUSSIAKIS, 1996). The type material is housed at MNHN and includes two skulls (MNHN-PIK-3022, 3016) associated with the mandible. I have seen this material and it is characterized by a relatively robust carnassial with a strong lingual cingulum; the P3 has a strong projection of the lingual cingulum, being quite molarized. In these features the studied skull MTLB-170 resembles the type material from Pikermi (Fig. 4). There are several skulls ascribed to *P. orbigny* from various localities (Tab. 3), but their metrical comparison is questionable as most of them are deformed and distorted, making the accurate measurement of their dimensions difficult. Nevertheless, the size of MTLB-170 is similar to that of the two skulls from Pikermi; its verified dimensions coincide with those of the type material (Tab. 3). The comparison of the teeth shows better results and indicates a general metrical similarity between them. However, the teeth of MTLB-170 are slightly larger than those of the type material from Pikermi (Fig. 5).

The species is reported by a skull, some isolated teeth and postcranials from Adrianos ravine in the list of FORSYTH MAJOR (1894) as *Ictitherium orbigny*, but without description. The skull was described by BEAUMONT (1969) and later by SOLOUNIAS (1981). Another skull from Samos



**Figure 6:** Stratigraphic distribution of the genus *Plioviverrops* during late Miocene of Europe. The data was taken from the bibliography and NOW (2007).

(NHMW-SAM-A.4750) is housed in Vienna; its direct comparison to the studied one indicates that it is morphologically and metrically similar to MTLB-170 (Tab. 3). The absence of an anterior accessory cusp, the small posterior cusp and the strong lingual cingular projection of the P3, as well as the robust P4 with well-separated protocone, strong lingual cingulum and buccally strongly

curved metastyle-blade are characters fitting in well with those of MTLB-170 (Fig. 4). The dental dimensions of NHMW-SAM-A.4750 seem to be slightly smaller than the type material from Pikermi and smaller than those of MTLB-170 (Fig. 5).

Several specimens of *Plioviverrops orbignyi* are known from the localities of Axios Valley (Macedonia, Greece). It was

found in the Turolian localities of Ravine des Zouaves-5 (RZO), Vathylakkos-3 (VAT) and Prochoma-1 (PXM) with cranial and mandibular remains (KOUFOS, 1979, 1980, 2000; BONIS & KOUFOS, 1991). The RZO material contains only mandibular remains and the comparison with the studied skull is impossible. A partially preserved skull with maxilla is known from Vathylakkos-3 (LGPU-VAT-135) described by BONIS & KOUFOS (1991). A direct comparison with MTLB-170 suggests that both skulls have similar cranial and dental morphological features and dimensions (Tab. 3, Fig. 4). Although the dimensions of the skulls are similar, the teeth of LGPUT-VAT-135 are smaller than those of the studied skull (Tab. 3, Fig. 5). The skull from Prochoma (LGPU-PXM-251) preserves the opisthocranium without the maxilla (BONIS & KOUFOS, 1991) and its available dimensions are close to those of MTLB-170 (Tab. 3).

Recently *P. orbigny* was found in the middle Turolian locality of Perivolaki, PER (Thessaly, Central Greece), a complete skull associated with the mandible (LGPU-PER-1295), and one frontal part of the skull associated with the mandible, (LGPU-PER-1), (KOUFOS, 2006a). The direct comparison of this material to MTLB-170 suggests that the cranial and dental morphology of both samples fit together quite well (Fig. 4). The metrical comparison also indicates that the cranial size is similar (Tab. 3), while the teeth of the Perivolaki material are slightly smaller than those of MTLB-170 (Fig. 5).

The small size differences in the cranial dimensions of *P. orbigny* from the various localities can be explained by deformation or distortion of the material. The differences in the teeth could either be due to sexual dimorphism or to the different geological age of the material (KOUFOS, 2006a). As is mentioned above, the dental dimensions of MTLB-170 are smaller than those of LGPUT-VAT-135 and LGPUT-PER-1, 1295. The age of these localities is very similar as all are middle Turolian. The magnetostratigraphic record indicates an age of 7.1-7.0 Ma for Mytilinii-1A, ~7.5 Ma for Vathylakkos and 7.3-7.1 Ma for Perivolaki (SEN et al., 2000; KOSTOPOULOS et al., 2003; KOUFOS et al., 2006). This age similarity strengthens the first hypothesis of sexual dimorphism. The prevalence of this hypothesis is supported by the presence of some mandibles from RZO and PER, which have larger teeth than the type material from Pikermi; however, these mandibles are also associated with larger canines than those of the Pikermi material and probably indicate male individuals (KOUFOS, 2006a).

Besides *P. orbigny*, the genus includes other species known mainly from Spain, France and Italy. The Early-Middle Miocene *P. gervaisi*, known from France, differs from *P. orbigny* by being smaller, having a very narrow P3 and a protocone higher than the parastyle in P4 (BEAUMONT & MEIN, 1972; PETTER, 1976). The Middle Miocene *P. gaudryi* has a significantly smaller size than *P. orbigny* (BEAUMONT & MEIN, 1972). Some mandibular remains of the Turolian *P. guerini* were found in Spain. It differs from the studied one in having a larger m1 with a longer trigonid and a posterior accessory cuspid in the p2,3 (CRUSAFONT

& PETTER, 1969). A mandibular fragment from the locality VAT of Axios Valley (Macedonia, Greece) is referred to as *P. cf. guerini* because it has a rudimentary posterior accessory cuspid in p2,3 and a slightly larger size (BONIS & KOUFOS, 1991). However, the size of the teeth and the development of the cuspids varies in the material of *P. orbigny*, and in the re-examination of the taxonomic value of *P. guerini*, it is necessary to bear all the new material and data in mind (KOUFOS, 2006a). The Late Turolian *P. faventinus* is known from Italy (TORRE, 1988) and differs from *P. orbigny* in having highly molarized premolars, a marked posterior accessory cusp in P3 and a remarkably larger size (Fig. 5).

The oldest appearance of the genus *Plioviverrops* is known from the locality of Laugnac (France) with the species *P. collectus*, dated to late Agenian, MN 2 (NOW, 2007). *P. gervaisi* is known from the locality of Vieux Collonges (France), dated to late Orleanian, MN 4-5, and the species *P. gaudryi* is known from the locality of La Grive/St. Alban, France, dated to late Astaracian, MN7/8 (NOW, 2007). *Plioviverrops* sp. is mentioned from the early Vallesian (MN 9) locality of Los Valles de Fuentidueva, Spain (NOW, 2007). However, the maximum spread of the genus is observed in the Late Miocene, where it is very common, especially in the Turolian (Fig. 6). Two species are mentioned: *P. orbigny*, known from the Eastern Mediterranean (mainly Greece, but it is also known from the Spanish locality of Los Aljezares), and *P. guerini*, known from Spain. A form similar to *P. guerini* is known from the Middle Turolian (MN 12) locality of Vathylakkos-3 (KOUFOS, 2000). The large-sized *P. faventinus* appeared in Italy at the end of Miocene, but is also recognized in the Pliocene of Spain (Fig. 6).

#### Genus *Protictitherium* KRETZOI, 1924

##### *Protictitherium crassum* (DÉPÉRET, 1892)

(Pl. 3, figs. 1, 2)

**Locality:** Mytilinii-4 (MLN), Mytilinii Basin, Samos, Greece.

**Age:** Middle Turolian, MN 12 (late Miocene); ~7.5 Ma.

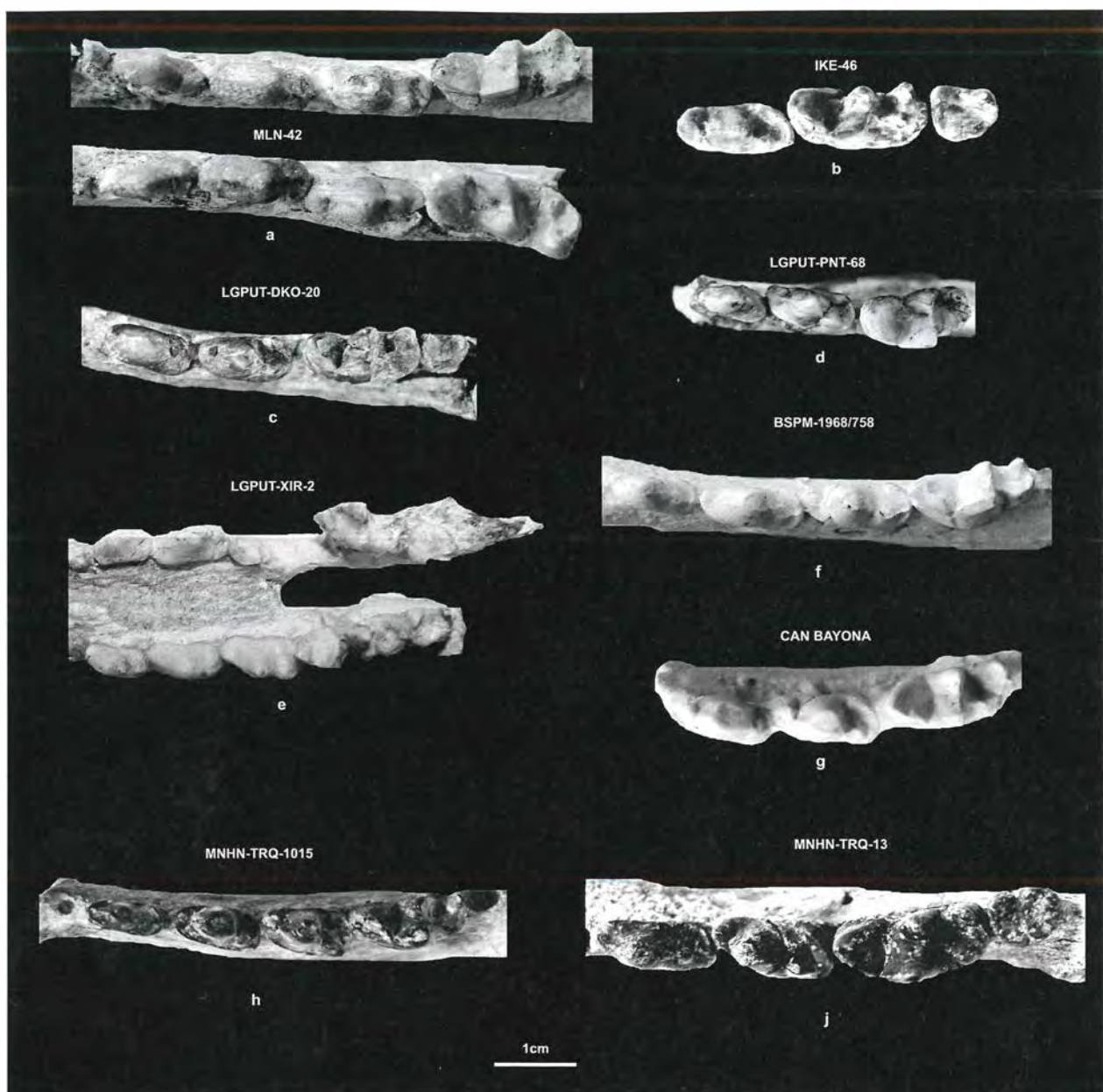
**Material:** Mandible, MLN-42; isolated lower canine, MLN-26.

**Measurements:** The measurements of the mandible are given in Tab. 4.

MLN-42	dex	sin		dex	sin
Lc	7.0	7.2	Lp3	11.5	11.0
Bc	5.5	5.4	Bp3	4.6	4.5
Lp1	—	2.7	Lp4	12.0	—
Bp1	—	2.0	Bp4	5.3	5.0
Lp2	9.5	9.4	Lm1	15.5	15.6
Bp2	4.0	3.9	Bm1	6.9	6.7
			L <sub>trig</sub>	10.4	10.6

MLN-26 c = 7.2 x 5.3

**Table 4:** Mandibular dimensions of various *Protictitherium* species, in mm.



**Figure 7:** Comparison of MLN-42 with various ictitheres.

a. Right and left tooth row of the mandible MLN-42; b. *Protictitherium aegaeum*, tooth row of the mandible IKE-46, Turkey (taken from KAYA et al., 2005); c. *Protictitherium crassum*, tooth row of the mandible LGPUT-DKO-20, Axios Valley, Macedonia, Greece; d. *Protictitherium cf. crassum*, tooth row of the mandible LGPUT-PNT-68, Pentalophos-1, Axios Valley, Macedonia, Greece; e. *Protictitherium crassum*, tooth row of the mandible LGPUT-XIR-2, Xirochori-1, Axios Valley, Macedonia, Greece; f. *Protictitherium crassum*, Sofça, Turkey; g. *Protictitherium llopsi*, tooth row of the Can Bayona mandible, Spain (cast); h. *Protictitherium arambourgi*, tooth row of the mandible MNHN-TRQ-1015, Sinap, Turkey; j. *Hyaenictitherium intuberculatum*, tooth row of the mandible MNHN-TRQ-1013, Sinap, Turkey. All specimens shown as if from left-hand side.

#### Description:

**Mandible.** The studied mandible consists of the two mandibular rami of the same individual; the right mandibular ramus preserves the tooth row c, p2-m1 and the left one the tooth row i3-m1 (Pl. 3, figs. 1, 2). Both mandibular fragments lack the ascending ramus. The mandibular corpus is relatively deep and thin, with a large mental foramen below the anterior root of the p2. The symphysis is elongated and narrow, and inclines gradually backwards. The

inferior border of the mandibular ramus is slightly curved. i3: It is small, not canine-like, with a strong buccal projection, giving it a triangular shape.

c: It is relatively strong, high, strongly curved backwards, with a pointed tip. Its lingual surface is flattened and has two crests running across its mesiolingual and distolingual border.

p1: It is very small, monocuspid and single-rooted.

p2: It is elongated and narrow. It lacks an anterior accessory

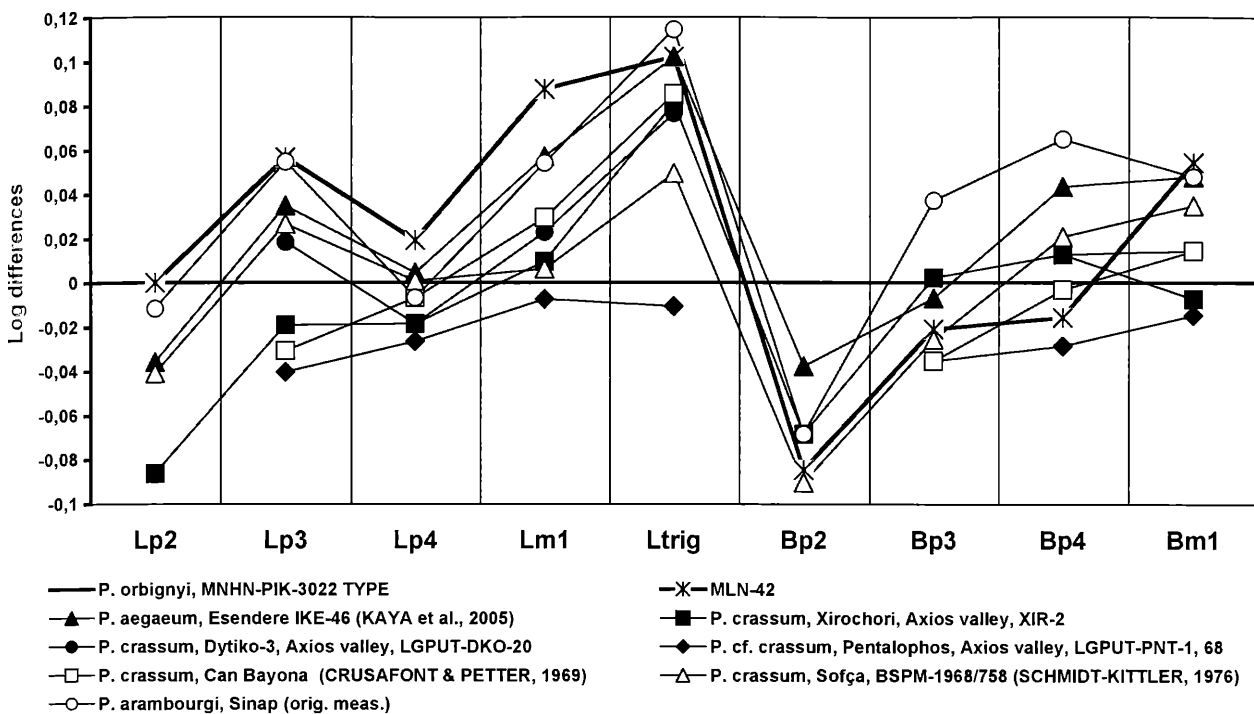
*Protictitherium crassum*, Lower Teeth

Figure 8: Logarithmic ratio diagram comparing the lower teeth of the various species of *Protictitherium*.

cuspid but there is a mesial cingular projection which is connected with the top of the main cuspid by a crest. The posterior accessory cuspid is well distinguished, situated slightly buccally on a small distal projection of the distal cingulum.

p3: Similar morphology to p2, but the distal part of the tooth is larger and more talonid-like.

p4: The anterior part of the left p4 is slightly broken (Pl. 3, fig. 1c). It is relatively short and narrow with a small anterior accessory cuspid and a large distal one, like a talonid (Pl. 3, fig. 2c). The posterior accessory cuspid is situated buccally, while a smaller one is developed lingually and a cingular elevation closes the distal border of the talonid. This morphology closely resembles that of the carnassial's talonid, indicating high molarization.

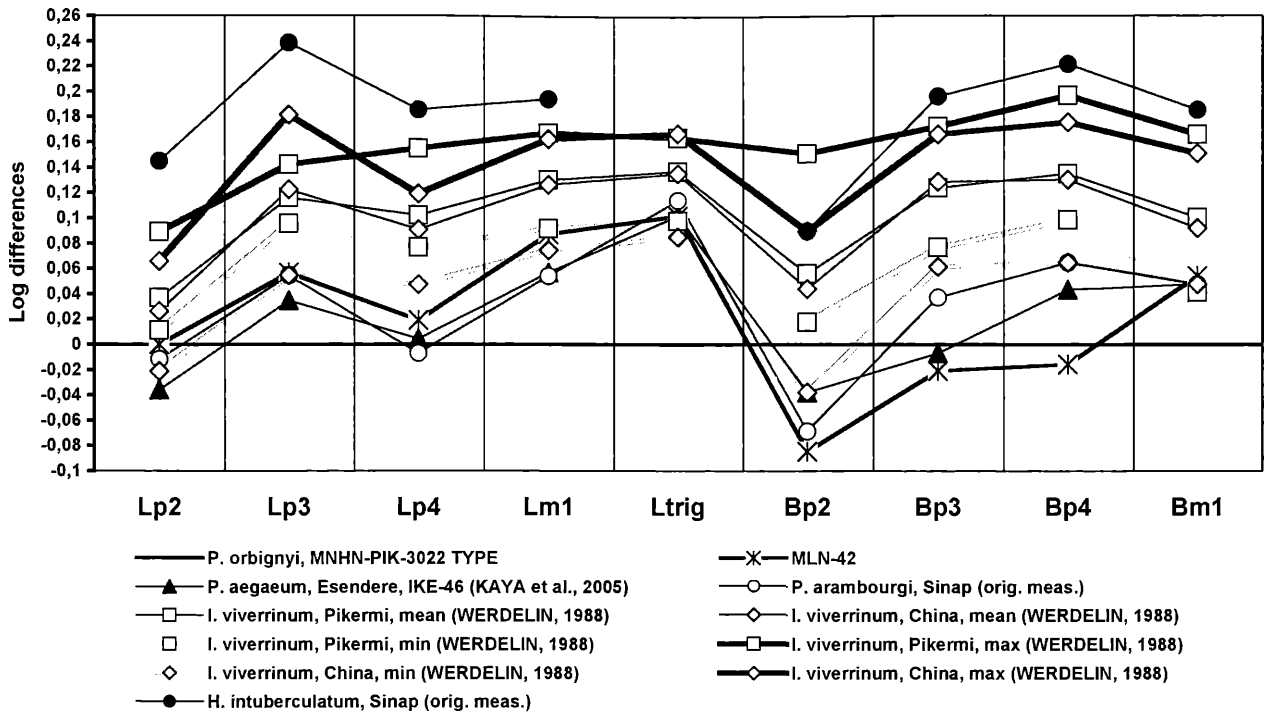
m1: It is relatively short and wide, with a strong and wide tricuspid talonid (Pl. 3, figs. 1, 2). The cuspids are high. The paraconid and protoconid are blade-like; the protoconid is higher than the paraconid. The metaconid is well-developed and high, reaching the two-thirds of the protoconid. The talonid is distinguished from the trigonid by a wide valley. The entoconid is the highest cuspid of the talonid. The hypoconulid is smaller and connected to the base of the hypoconid by a crest, closing the posterior end of the talonid. There is a strong buccal cingulum.

**Discussion:** The studied mandible is large and has relatively long and narrow premolars, as well as high cuspids in the carnassial, characteristics which suggest a large-sized *Protictitherium*. Such a large-sized *Protictitherium* is *P. crassum* and the recently described *P. aegaeum*.

*P. crassum* is known from various Eurasian localities. It was originally described as *Herpestes crassus* from La Grive,

France (DEPÉRET, 1892). The holotype is characterized by a highly molarized p4 and a carnassial with a high metaconid. Both characteristics exist in the studied mandible MLN-42. In Greece *P. crassum* is known from several late Miocene localities of Axios Valley (Macedonia, Greece). A right hemimandible with c-p3-m2 (DKO-20) is known from the late Turolian locality of Dytiko-3 (KOUFOS, 1980, 2000; BONIS & KOUFOS, 1991). The dental comparison of this specimen with MLN-42 indicates similar morphology (Fig. 7) but the premolars of DKO-20 are relatively shorter and wider than those of MLN-42 (Fig. 8); the robusticity index differs remarkably from those of DKO-20 (Tab. 4). The carnassial has a similar morphology in both specimens (Fig. 7). Although the carnassial of DKO-20 is worn, the metaconid and entoconid are high and this feature resembles MLN-42, but those of MLN-42 seem to be higher and more slender. The talonid in both specimens is large, wide and well separated from the trigonid by a deep valley. However, the m1 of MLN-42 is larger than that of DKO-20 (Fig. 8). A mandible with c-p3-m1-m3 dex and c-p2-m2 sin (XIR-2) of *P. crassum* has been described from the late Vallesian locality Xirochori-1 (XIR) of Axios Valley, Macedonia, Greece (Fig. 7e), (KOUFOS, 2000). The dental morphology of XIR-2 resembles that of MLN-42 but there are some differences. The premolars of XIR-2 are relatively shorter and wider; their robusticity index is smaller than that of MLN-42. The p2, 3 of XIR-2 lacks an anterior accessory cuspid like MLN-42, but they have a smaller posterior accessory cuspid than that of MLN-42 (Figs. 7, 8). The p4 of XIR-2 has a smaller anterior and posterior accessory cuspid and wider distal cingular projection than those of MLN-42. The carnassial of XIR-2 is

*Protictitherium crassum*, Lower Teeth



**Figure 9:** Logarithmic ratio diagram comparing the lower teeth of some *Protictitherium* species with *Ictitherium viverrinum* and *Hyaenictitherium intuberculatum*.

smaller and with relatively lower cusps than MLN-42 (Figs 7, 8). A mandibular fragment with p3-m1 sin (PNT-68) of *P. cf. crassum* is known from the Vallesian locality of Pentalophos-1 (PNT) of Axios Valley, Macedonia, Greece (BONIS & KOUFOS, 1991; KOUFOS, 2000). The premolars of both specimens, PNT-68 and MLN-42, have a similar morphology with high molarization, especially in the p4 (Fig. 7). However, they are more robust and the anterior accessory cuspid in the p4 of PNT-68 is stronger than that of MLN-42. The carnassial morphology is also similar in both specimens, with a high metaconid and entoconid. Although they are morphologically similar, the size of PNT-68 is significantly smaller than that of MLN-42, as well as smaller than all the other specimens of *P. crassum* (Fig. 8).

Some material of *P. crassum* is also known from Asia Minor (SCHMIDT-KITTLER, 1976). The MLN-42 is compared with a cast of *P. crassum* from the locality of Sofça, which is a mandibular fragment with p2-m1 sin (BSPM-1968/758). The teeth of BSPM-1968/758 are smaller than those of MLN-42, but the morphology of the premolars is similar (Figs. 7, 8). The premolars of the Sofça specimen are relatively elongated and narrow, like those of MLN-42. The carnassial is different in having a smaller and lower metaconid, a relatively smaller talonid with a smaller and less high entoconid and hypoconid.

*P. crassum* is also known from Spain, and MLN-42 is compared with a cast from the Vallesian locality of Can Bayona housed at LGPUT; the material was originally described as *P. crassum llopsi* (CRUSAFONT & PETTER, 1969) and was later considered as a separate species, *P.*

*llopsi* (WERDELIN & SOLOUNIAS, 1991). The premolars of MLN-42 are longer and narrower, having more slender features than those of *P. crassum* from Can Bayona. Their morphology is more or less similar, but the cingulum is more developed in the premolars and there is a small anterior accessory cuspid in the p3 of the Can Bayona teeth. The carnassial has a similar morphology, but the metaconid of MLN-42 is slightly higher. The talonid of the Can Bayona m1 is broken buccally, but it has a high entoconid. The size of MLN-42 is visibly larger than that of Can Bayona.

A mandible (IKE-46) of a large-sized *Protictitherium* was recently described from the locality of Esender, Turkey, as a new species, *P. aegaeum* (KAYA et al., 2005). The studied mandible MLN-42 is compared with a cast of this species. The premolars of IKE-46 are generally shorter and wider than those of MLN-42, having a more robust aspect (Tab. 5, Fig. 8). In this characteristic they are closer to those of *P. crassum*. The p2, 3 of MLN-42 differ from *P. aegaeum* in lacking the anterior accessory cuspid. The posterior accessory cuspid of p2 is stronger in MLN-42 and not circled by an elevated cingulum, as in *P. aegaeum*. The posterior accessory cuspid of the p3 has a similar size in both specimens, but there is a more elevated distal cingular projection in *P. aegaeum*. The p4 of *P. aegaeum* is shorter and broader than that of MLN-42 (Fig. 8) with a stronger anterior accessory cuspid and a lingually less elevated distal cingular projection (Fig. 7). In this feature, MLN-42 is closer to *P. crassum*. The lower carnassial of both specimens has similar a size, which is very close to the minimum values for *Ictitherium viverrinum* (Fig. 9).

Species	Reference	Lp2/Bp2	Lp3/Bp3	Lp4/Bp4	Lm1/Bm1
<i>P. crassum</i>	MLN-42	239	247	233	229
<i>P. crassum</i>	LGPU-T-XIR-2	189	197	200	220
<i>P. crassum</i>	LGPU-T-DKO-20	—	215	200	216
<i>P. crassum</i>	Can Bayona	209	213	219	—
<i>P. crassum</i>	BSPM-1968/758	221	233	205	198
<i>P. cf. crassum</i>	LGPU-T-PNT-1, 68	—	205	216	216
<i>P. aegaeum</i>	IKE-46	198	228	197	216
<i>P. arambourgi</i>	MNHN-TRQ-1015	226	214	181	215
<i>I. viverrinum</i>	mean, Pikerimi (WERDELIN, 1988)	188	203	199	227
<i>I. viverrinum</i>	mean, China (WERDELIN, 1988)	189	204	196	229
<i>H. intuberculatum</i>	MNHN-TRQ-1013,1014	218	224	195	209

**Table 5:** Robusticity Indices of the lower teeth of various *Protictitherium* species.

In spite of their metrical similarities, the carnassial of *P. aegaeum* differs morphologically in the talonid. The talonid of MLN-42 is stronger, with a similarly high, but more robust entoconid. Similar differences are also observed in the size of the metaconid. The hypoconid and hypoconulid of MLN-42 are stronger than those of *P. aegaeum*. But the most significant difference between the two specimens is the strong entoconid of MLN-42. Moreover, the buccal cingulum of the talonid of *P. aegaeum* is very strong; in MLN-42, the cingulum at this point is faint. Although there are similarities between MLN-42 and *P. aegaeum*, there are also some differences which distinguish them. The problem with these small hyaenids is how these differences can be explained: are they intraspecific differences or are they related to palaeoecology or geography?

Considering the presence of *P. crassum* in Eurasia, the rarity of the material and its stratigraphic and geographic dispersion are given as the main reasons for providing difficulties in the comparisons and the explanation of their relationships (KOUFOS, 2000). This is also clear from the comparison of MLN-42 and *P. aegaeum*. Both are of similar age (Turolian), geographically close, but have some differences. The question is if these differences are quite strong enough for a specific or subspecific distinction. As was mentioned above, the size of the m1 of MLN-42 is near the minimum values for *Ictitherium viverrinum* from Pikerimi and China (Fig. 9). However, the comparison of MLN-42 with *I. viverrinum* from Pikerimi and Axios indicates that the premolars of MLN-42 are remarkably smaller and more slender than those of *I. viverrinum*, and the cuspids of the m1 in *I. viverrinum* are relatively lower. These features and especially the size clearly distinguish MLN-42 from *I. viverrinum*.

OZANSOY (1965) described a hemimandible of a small ictithere from Sinap (Turkey) as *Ictitherium arambourgi*; he states that it is larger than *Plioviverris orbigny* and smaller than *Ictitherium intuberculatum* and *Hyaenictitherium* “*hipparionum*” (= *wongii*). Later, SCHMIDT-KITTLER (1976) synonymized this taxon with *Protictitherium crassum*, while even later on, WERDELIN & SOLOUNIAS (1991) transferred it to *Protictitherium* and kept the specific name of OZANSOY (1965). The latter opinion was also accepted by BONIS, (2004). The type specimen of *P. arambourgi* is

a right hemimandible with p2-m1, stored at MNHN. The direct comparison of *P. arambourgi* with MLN-42 suggests that it differs in having a smaller m1 with a relatively shorter talonid, more robust premolars, a stronger anterior accessory cuspid in the lower premolars and a wider distal cingular projection. Thus, the studied material is clearly different from *P. arambourgi*.

Another ictithere from Sinap (Turkey) was described by OZANSOY (1965) as *Ictitherium intuberculatum* and later transferred to *Hyaenictitherium* (BONIS, 2004). A maxillary fragment with P2-M1 and a mandible are known from this species which are stored at MNHN. It is quite larger than MLN-42, with a relatively lower metaconid and entoconid in the m1. The premolars have a similar morphology to those of MLN-42, an absent or weak anterior accessory cuspid in p2, 3 but the p2 of MLN-42 is relatively more elongated, having a stronger mesial cingular projection. However, the greater size of *H. intuberculatum* clearly distinguishes the studied material from it.

Bearing in mind all the above-mentioned comparisons, MLN-42 is morphologically closer to *P. crassum*, to which it has some differences which could be considered as intraspecific. Thus, the specimen MLN-42 is assigned to *P. crassum* at the moment, waiting for more material which will allow: a) a better comparison with the known material, and b) a better knowledge of its morphology. Although the known material from the late Miocene deposits of Samos is very rich, this taxon was unknown and this is the first evidence of its presence in the Samos fauna.

#### Genus *Hyaenictitherium* KRETZOI, 1938

##### *Hyaenictitherium wongii* (ZDANSKY, 1924)

(Pl. 3, fig. 3; Pls. 4-5; Pl. 6, figs. 1, 2)

**Localities:** Mytilinii-1A, B, C (MTLA, MTLB, MTLC), Adrianos ravine, Mytilinii Basin, Samos, Greece; Mytilinii-4 (MLN), Potamies ravine, Mytilinii Basin, Samos, Greece.

**Age:** Middle Turolian, MN 12 (late Miocene).

Mytilinii-1A (MTLA, B, C): 7.1-7.0 Ma.

Mytilinii-4 (MLN): ~7.5 Ma.

**Material:**

CRANIAL MEASUREMENTS	<i>Hyaeictitherium wongii</i>						
	Mytilini-1A		Samos				
	MTLA-200	MTLA-1	NHML-SAM-M. 4161	NHMW-SAM-A.4746	NHMW-SAM-A.4749	NHMW-SAM-A.4745	NHMW-SAM-A.4743
	Original measurements						
1. Prosthion-Acrocranium	196.4	—	—	204.0	—	—	—
2. Prosthion-Basion	164.5	—	—	181.0	—	—	—
3. Prosthion-Choanae	93.5	—	—	100.0	—	—	—
4. Prosthion-middle of the line connected the posterior borders of P4	78.0	90.0	—	91.0	—	—	—
5. Prosthion-Mandibular fossa	124.5	—	—	140.0	—	—	—
6. Prosthion-middle of the line connected the anterior borders of bullae	130.6	—	—	147.0	—	—	—
7. Prosthion-anterior border of the orbit	75.5	73.5	—	78.0	—	—	—
8. Basion-anterior border of choanae	71.0	—	—	81.5	70.0	—	—
9. Basion-anterior border of the orbit	100.0	—	—	119.0	98.5	—	—
10. Basion-middle of the line connected the posterior borders of P4	86.5	—	—	90.0	76.5	—	—
11. Breadth at the base of the zygomatic arcs	54.5	—	59.8	60.0	—	—	45.0
12. Maximal breadth at the zygomatic arcs	102.0	—	—	122.5	80.0	—	83.0
13. Breadth at the posterior borders of the orbits (in projection)	46.8	—	49.2	53.7	38.0	44.0	—
14. Breadth of the occipital condyles (external)	32.2	—	—	37.4	33.5	—	—
15. Breadth of foramen magnum	17.4	—	—	15.8	—	—	—
16. Height of foramen magnum	18.8	—	—	14.3	—	—	—
17. Height:occipital condyles-occipital protuberance	60+	—	—	53.7	—	—	53.0
18. Maximal height:posterior end of choanae-frontal	67.2	—	53.9	62.0	55.0	—	—
19. Length of bulla	31.0	—	—	32.5	—	—	30.0
20. Breadth of bulla	17.0	—	—	18.0	—	—	17.0
21. Breadth of maxilla between C (in the middle)	22.2	21.2	26.1	23.7	—	[22]	—
22. Idem in P2	24.1	25.7	29.3	28.5	20.5	22.2	—
23. Idem in P3	28.1	31.5	38.7	36.8	28.5	30.5	—
24. Idem in the posterior ends of P4	56.4	61.0	68.4	65.0	49.0	56.5	—
25. Idem in M2	31.5	32.5	38.9	35.2	26.3	30.0	—
26. Incisor's breadth	24.7	22.3	—	24.5	—	—	—
27. Diastema C-I3	5.1	6.0	—	5.1	—	—	—
28. Idem C-P2	10.1	10.0	14.0	9.6	—	9.6	—
29. Idem P2-I3	25.1	26.0	—	27.5	—	—	—

Table 6: Cranial dimensions of *Hyaeictitherium wongii* from various Greek localities.



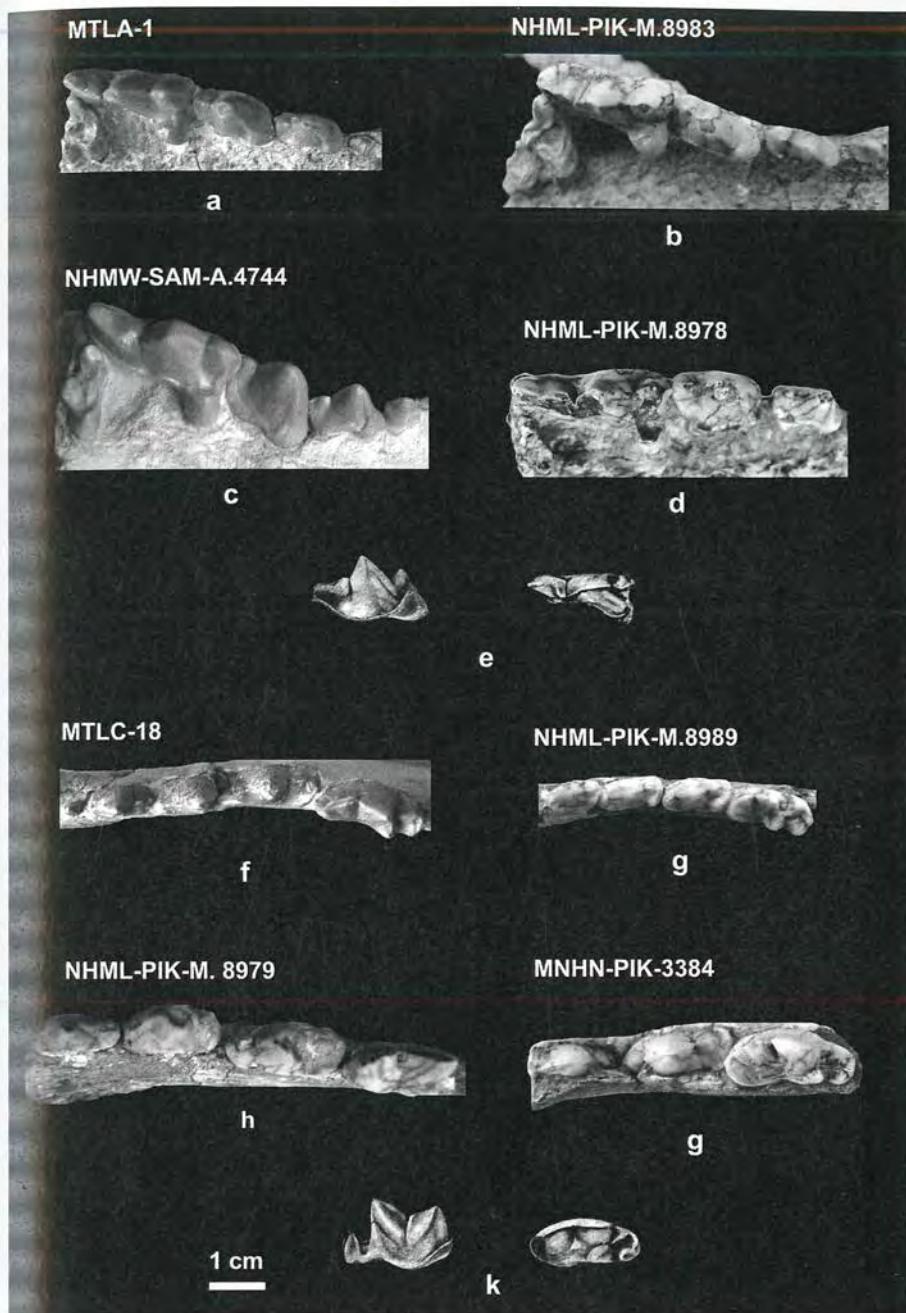
*Hyaenictitherium wongii*

MANDIBULAR MEASUREMENTS	Mytilinii-1A			Mytilinii-1B			Mytilinii-1C	Samos				Axios valley					
	MTLA-237	MTLA-266	MTLA-468	MTLB-1	MTLB-100	MTLB-171		NHMW-SAM-A.4745	MHNW-SAM-A.4743	NHMW-SAM-nn-1	NHMW-SAM-nn-2	LGPUR-ZO-10	LGPUR-VAT-100	LGPUR-SLQ-929	MNH-SLQ-930		
	Koufos (2000)																
	Original measurements																
1. Length anterior c-coronoid process	—	—	—	—	—	—	—	—	—	—	—	—	—	—	136.5	143.0	—
2. Length anterior c- condyle	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	154.0	—
3. Height inferior border at angle-coronoid	—	—	—	—	—	—	—	—	—	—	—	—	—	—	61.3	67.0	—
4. Height inferior border at angle-condyle	—	—	—	—	—	—	—	—	—	—	—	—	—	[26]	27.0	31.0	—
5. Height condyle-coronoid	—	—	—	—	—	—	—	—	—	—	—	—	—	—	35.2	36.0	—
6. Symphysis length	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	[37]	[36]
7. Height in front of p2	24.5	21.0	—	—	—	20.6	—	21.5	20.6	20.0	18.5	23.0	23.0	23.0	23.0	22.7	29.0
8. Idem in the middle of p3 (lingual)	24.7	22.0	19.6	—	—	22.4	—	26.0	19.0	18.5	23.0	24.0	24.0	23.0	23.0	22.7	29.5
9. Idem in p4 (lingual)	26.8	22.5	—	—	—	24.0	—	26.9	20.0	20.5	25.0	25.0	25.0	25.5	26.5	24.0	29.0
10. Idem in m1(lingual)	31.5	—	—	—	—	28.6	—	30.6	24.3	25.0	27.0	26.5	26.5	28.8	29.8	28.4	34.0
11. Idem behind m2	—	—	—	—	—	25.3	—	31.7	24.5	—	—	—	—	24.0	28.5	26.0	32.0
12. Diastema p2-c	11.5	6.4	—	—	—	13.1	—	17.0	7.8	—	11.0	12.5	12.5	13.6	—	13.3	11.0
12. Diastema p2-i3	64.0	[54]	—	—	—	58.8	—	67.0	—	—	—	—	—	22.6	—	—	—
13. Diastema i3-c	87.5	[80.5]	—	—	—	82.6	—	95.7	0.0	—	—	—	—	—	—	—	—
14. Length p2-m1	44.3	48.0	—	—	—	40.7	—	47.5	61.2	61.8	63.0	62.0	62.0	—	—	—	—
15. Length c-m1	—	—	—	—	—	25.5	—	—	80.8	—	86.2	84.1	84.1	—	—	—	—
16. Length p2-p4	—	—	—	—	—	47.0	—	53.8	42.7	44.0	45.3	42.2	42.2	—	—	—	—
17. Length p3-m1	—	—	—	—	—	64.7	—	[73.5]	49.0	49.5	50.3	49.8	49.8	—	—	—	—
18. Length p2-m2	—	—	—	—	—	88.2	—	[101.5]	—	—	—	—	—	—	—	—	—
19. Length c-m2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
20. Length p1-m3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

Table 7: Mandibular dimensions of *Hyaenictitherium wongii* from various Greek localities.

Upper Teeth	<i>Hyaenictitherium wongii</i>										<i>H. cf. wongii</i>				
	Mytilinii-1A					Lower Teeth	Mytilinii-1A					Mytilinii-1B		Mytilinii-1C	Mytilinii-4
	MTLA-200		MTLA-1				MTLA-2	MTLA-237	MTLA-266	MTLA-468	MTLB-1	MTLB-100	MTLB-171	MTLC-18	MLN-27
	dex	sin	dex	sin		sin	sin	sin	dex	sin	dex	sin	dex	sin	
LJ1	—	5.1	3.7	3.8	Li1	—	—	—	3.5	—	—	—	—	—	
BI1	—	3.8	2.5	3.1	Bi1	—	—	—	2.1	—	—	—	—	—	
LJ2	—	4.1	4.5	4.4	Li2	—	—	—	4.3	—	—	—	4.1	—	
BI2	—	3.0	3.7	3.8	Bi2	—	—	—	2.8	—	—	v	3.2	—	
LJ3	5.5	—	7.3	6.7	Li3	—	—	—	4.9	—	—	4.6	4.8	—	
BI3	5.2	—	5.6	5.5	Bi3	—	—	—	4.0	—	—	4.0	4.4	—	
LC	9.3	9.4	—	10.4	Lc	12.5	9.0	—	9.6	—	—	8.6	10.7	—	
BC	6.8	6.7	—	6.4	Bc	8.7	7.4	—	6.7	—	—	7.0	8.0	—	
LP1	5.2	—	—	5.6	Lp1	—	—	—	—	—	—	—	3.0	—	
BP1	4.5	—	—	[5]	Bp1	—	—	—	—	—	—	—	3.0	—	
LP2	12.0	11.2	13.3	13.3	Lp2	12.5	13.4	—	11.0	—	—	11.2	13.0	13.0	
BP2	6.4	6.4	6.6	6.7	Bp2	6.1	6.2	—	5.5	—	—	6.5	6.1	6.5	
LP3	15.0	[15]	17.0	[17]	Lp3	15.2	15.6	15.7	14.3	14.2	—	13.9	—	—	
BP3	9.1	[9.5]	9.0	9.8	Bp3	7.7	7.4	7.3	7.3	7.2	—	7.2	8.0	—	
LP4	24.4	[23.3]	26.2	25.7	Lp4	17.0	—	17.2	—	15.5	16.3	15.3	17.9	—	
BP4 ant.	13.3	[12.6]	14.0	[13.5]	Bp4	8.6	—	8.2	—	8.3	8.1	8.0	8.8	—	
BP4 post.	7.5	7.7	9.0	8.6	Lm1	20.7	—	—	—	20.2	20.5	18.2	21.8	—	
Lblade	18.3	—	19.4	19.4	Bm1	9.8	—	9.0	—	9.3	9.3	9.0	9.5	—	
LM1	7.3	7.5	8.0	7.7	Lm1tal	5.1	—	—	—	4.6	4.6	4.2	5.7	—	
BM1	16.3	15.5	14.8	15.3	Lm2	—	—	—	—	—	—	—	—	—	
LM2	4.2	4.0	4.0	—	Bm2	—	—	—	—	—	—	—	—	—	
BM2	8.3	7.4	6.4	6.6											

Table 8: Dental measurements of *Hyaenictitherium wongii* from Samos.



**Figure 10:** Upper and lower dentition of *H. wongii*, *Ictitherium viverrinum*, *Thalassictis robusta* and *Lycyaena chaeretis*.

a. *H. wongii*, upper tooth row of the maxilla MTLA-1, Samos, Greece; b. *Ictitherium viverrinum*, upper tooth row of the skull NHML-PIK-M. 8983, Pikermi, Greece; c. *L. chaeretis*, upper tooth row of the skull NHMW-PIK-A.4744, Samos, Greece; d. *L. chaeretis*, upper tooth row of the skull NHML-PIK-M. 8978, Pikermi, Greece; e. *T. robusta*, upper carnassial, Kishinev, Moldavia (taken from KURTÉN, 1982); f. *H. wongii*, lower tooth row of the mandible MTLC-18, Samos, Greece; g. *I. viverrinum*, lower tooth row of the mandible NHML-PIK-M.8989, Pikermi, Greece; h. *L. chaeretis*, lower tooth row of the mandible NHML-PIK-M.8979, Pikermi, Greece; i. *Lycyaena chaeretis*, lower tooth row of the mandible MNHN-PIK-3384, Pikermi, Greece; j. *T. robusta*, lower carnassial, Kishinev, Moldavia (taken from KURTÉN, 1982).

All specimens shown as if from right-hand side.

**MTLA:** Skull, MTLA-200; maxillary fragment with C-M2 dex and sin, MTLA-1; left mandibular fragment with c-p2-p4, MTLA-237; left mandibular fragment with p3-m1, MTLA-266; left mandibular fragment with c-m1, MTLA-2; right mandibular fragment with i1-p3, MTLA-468.

**MTLB:** Left hemimandible with i3-m2, MTLB-171; left mandibular fragment with p4 and m1, MTLB-1; right mandibular fragment with p4 and m1, MTLB-100.

**MTLC:** Right mandibular fragment with i2-m1, MTLC-18.

**MLN:** Isolated P2 sin, MLN-27.

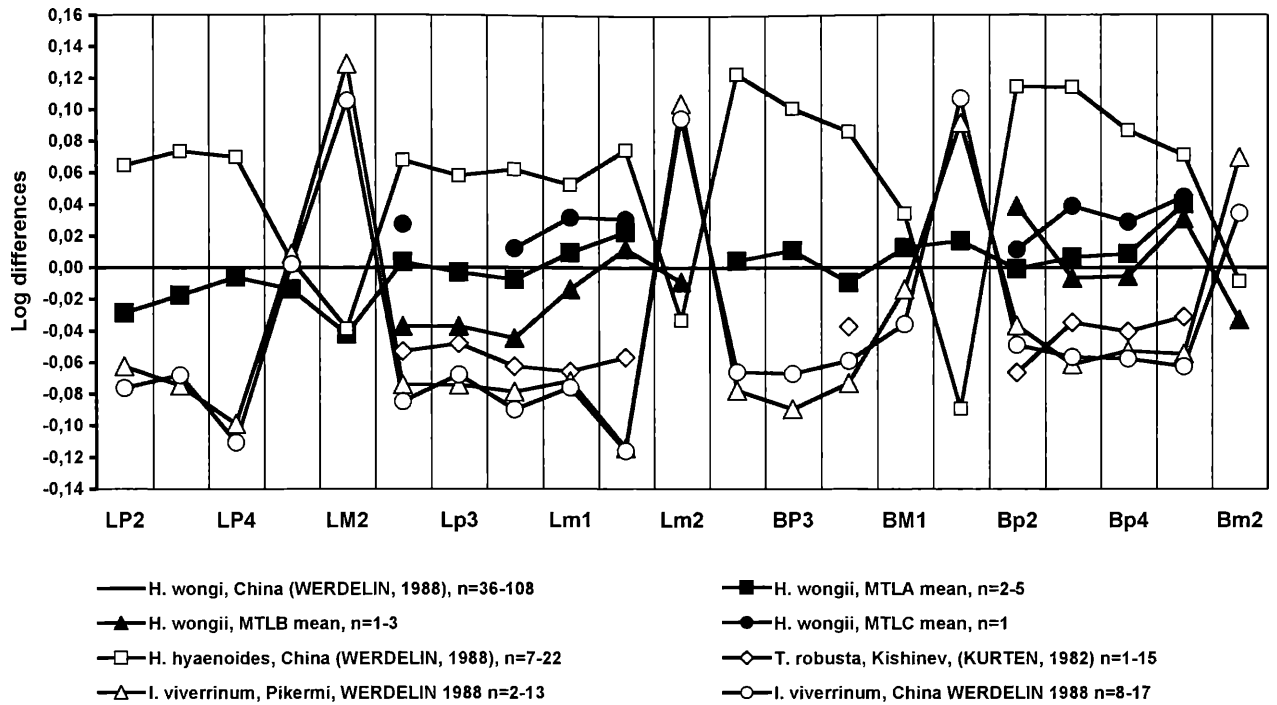
**Measurements:** The cranial mandibular and dental measurements are given in Tabs 6-8.

**Description:**

**Skull.** The skull MTLA-200 is complete, but slightly distorted in its left posterior part; the prosthion is slightly

broken, while the nasal cavity is broken in its anterior part (Pl. 4, figs 1, 2). The specimen MTLA-1 is the frontal part of the skull with the maxilla (Pl. 3, fig. 3). The nasal cavity is elliptical, elongated and almost vertical to the palate with its posterior border above the middle of the diastema P2-C, or rather above P1. In MTLA-1 the posterior border of the nasal cavity is above the middle of the canine. The nasals are narrow, pointed like spines and end at the anterior border of the orbits. The posterior border of the maxillary bones is situated at the middle of the orbits. The frontals are triangular-shaped and separated by a shallow groove running across them. The infraorbital foramen is large situated above the contact between the P3 and P4. The orbits are oval-shaped and their anterior border is above the middle of the P4. There is a strong postorbital constriction. The zygomatic arches are strong and strongly projected buccally. The braincase is relatively

### *Hyaenictitherium wongii*, Upper and Lower Teeth



**Figure 11:** Logarithmic ratio diagram comparing the teeth of *Hyaenictitherium wongii* from various localities.

small and rounded. A weak sagittal line starts from the tip of the postorbital projection, and is facing backwards. The two sagittal lines are connected near the bregma, forming a sagittal crest, which is connected with the occipital protuberance at the acrocranium. The occipital is strong, with a strong crista nuchae and external occipital crista. The occipital linea nuchae is strongly projected posteriorly, well behind the posterior surface of the condyles (Pl. 4, fig. 1e). The condyles are relatively weak and do not laterally exceed the occipital bone. The foramen magnum is large and rounded. The postglenoid processes are large. The bullae are relatively small, elliptical-shaped, and their anterior border is slightly behind the anterior surface of the postglenoid process (Pl. 4, fig. 1d). The palate is short and relatively narrow. The palatal borders are parallel till P2, but then they curve buccally, reaching their maximal breadth at the posterior end of the P4. The cheek teeth rows are straight without imbrication of the teeth, which are strongly in touch with each other. There is a small diastema between the canine and the third incisor, and a smaller one between the canine and P1.

**Upper Dentition.** The dentition of both specimens is well-preserved, except for some minor damages in that of MTLA-200 (Pl. 3, fig. 3d; Pl. 4; fig. 2).

**I1, 2:** The incisors are situated in a curved line. They have an elliptical crown and a strong buccal lingual projection.

**I3:** It is canine-like with a strong lingual projection distolingually.

**C:** The canine is strong with a flattened root and an elliptical transverse section. It has a strong mesiolingual and distal crest. The canine of MTLA-1 is relatively stronger and less flattened than that of MTLA-200.

**P1:** It is single-rooted with a rounded crown and a strong cingulum, especially lingually. The P1 of MTLA-1 is stronger relative to that of MTLA-200.

**P2:** It is short and wide without an anterior accessory cusp. In its mesiolingual corner there is a small lingual projection, from which a crest starts to the tip of the main cusp. The posterior accessory cusp is well developed and situated on a distal lingual projection. There is a well-developed cingulum around the tooth.

**P3:** It is relatively short and wide. The great width is due to a strong lingual projection situated in the distal lingual half of the tooth. There is a small anterior accessory cusp, situated in the mesiolingual corner of the tooth. The posterior accessory cusp is large. There is a well-developed buccal and lingual cingulum.

**P4:** The carnassial is elongated and narrow. The protocone is large and well separated from the parastyle. In MTLA-1, the anterior border of the protocone is slightly behind the anterior border of the parastyle, while in MTLA-200 it is on the same level. The parastyle is large and slightly smaller than the protocone. The metacone blade is relatively long and curves buccally. There is a strong lingual cingulum.

**M1:** It is large, triangular, with well-developed and labially strongly projected paracone. The metacone is smaller, while the protocone is large and high.

**M2:** It is very small with an elliptical crown.

**Mandible.** There are several mandibular fragments from the various fossiliferous sites of the locality MTL (Pl. 4, figs. 3, 4; Pl. 5; Pl. 6; figs. 1, 2). The symphysis is relatively elongated and narrow, strongly inclining backwards. Part of the ascending ramus is preserved in MTLB-171 (Pl. 5, fig. 6) and seems to be long and vertical to the mandibular

*Hyaenicttherium wongii*, Upper and Lower Teeth

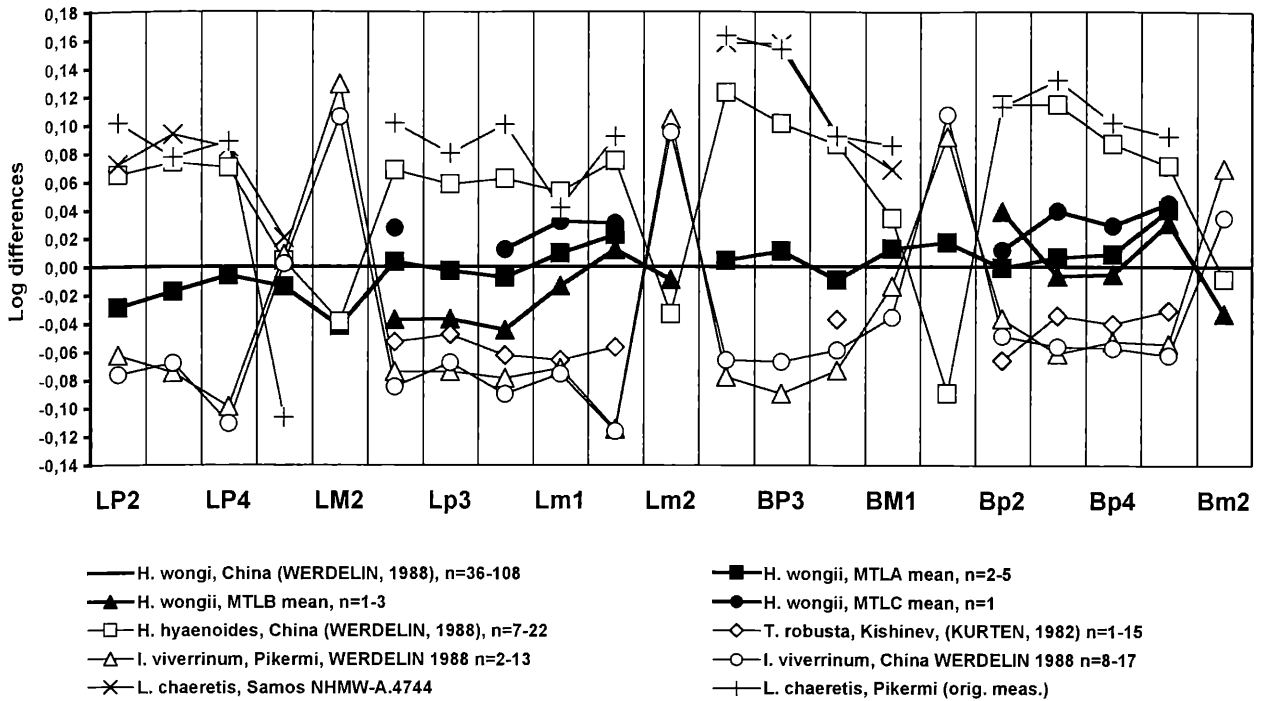


Figure 12: Logarithmic ratio diagram comparing the teeth of *Hyaenicttherium*, *Ictitherium*, *Lycyaena* and *Thalassictis*.

corpus. The masseteric fossa is oval-shaped, deep and its anterior border is situated below the m2. The mandibular corpus is elongated and relatively shallow. The inferior border of the corpus is curved and after the m1 it points upwards. There is a single mental foramen situated below the p2.

**Lower Dentition.** The studied mandibular remains preserve well the various teeth (Pl. 4, figs. 3, 4; Pl. 5; Pl. 6, figs. 1, 2).

i1, 2: They are slightly compressed laterally with an elliptical occlusal aspect.

i3: Larger than the other incisors and canine-like. It has a small cingular projection situated buccally (on the side of the canine).

c: The canine is strong, situated obliquely to the tooth row axis, curved backwards, compressed laterally, with a strong root and a rounded transverse section. It has a mesiolingual and distal crest running from the top to the base of the canine.

p1: It is very small, single-rooted and with a rounded crown.

p2: It is elongated relative to the p3, without an anterior accessory cuspid. The posterior accessory cuspid is strong, situated on a distal projection of the distal cingulum. It has a strong lingual and weaker buccal cingulum.

p3: Relatively short and wide, with a vestigial-rudimentary anterior accessory cuspid. The posterior accessory cuspid is small, situated on a wide distal cingular projection, giving the idea of a talonid. There is a well-developed buccal cingulum.

p4: It is short and wide, with a strong anterior accessory cuspid and a very strong posterior accessory cuspid, situ-

ated on a distal cingular projection. The lingual border of the distal cingular projection is elevated and forms a crest, like an entoconid. There is a well-developed buccal cingulum.

**m1:** It is relatively short with a small and narrow talonid. The metaconid is relatively small, about the 1/2 of the protoconid. The trigonid is about the 2/3 of the tooth's length. The protoconid and paraconid are blade-like and they are separated by a deep valley. The hypoconid is strong and situated somewhat to the center of the talonid basin. The entoconid is smaller and is connected with the hypoconulid, forming a crest covering the distal border of the talonid. A crest from the tip of the hypoconid is facing obliquely to the junction of the metaconid and protoconid. A well-developed cingulum runs all around the tooth.

**Discussion.** The taxonomy of the small-medium sized late Miocene hyaenids is complicated. These hyaenids known as "ictitheres" have a long taxonomic history (KURTÉN, 1982; SEMENOV, 1989; WERDELIN & SOLOUNIAS, 1991; KOUFOS, 2000; BONIS, 2005). The "ictitheres" are common in the Greek late Miocene faunas and were found in several localities: Pikermi, Samos, Axios Valley, Perivolaki (Thessaly), Kerassia (Evia Island), (KOUFOS, 2006d). Among the hyaenids of Pikermi there is one smaller than *Adcrocuta eximia* and larger than *Ictitherium viverrinum*, referred to as *Ictitherium hipparionum* for a long time. Its generic name changed several times between *Palhyaena*, *Thalassictis*, *Ictitherium* and *Hyaenotherium*. The name *Palhyaena hipparionum* was given to a hyaenid from Mt. Luberon, France (GERVAIS, 1859); the type of this taxon was stored at the museum of Avignon, but it was lost (KURTÉN, 1982). This hyaenid is a nomen nudum and it can only include only

the type from Mt. Luberon until it is found (WERDELIN, 1988; WERDELIN & SOLOUNIAS, 1991), an opinion with which I agree. A similar hyaenid, intermediate between *Adcrocuta eximia* and *Ictitherium viverrinum*, was also described from the late Miocene of China under the name *Ictitherium wongii* (ZDANSKY, 1924). After that, the similar European material was included in this species. Finally, this hyaenid was included in the genus *Hyaenotherium* with *H. wongii* as the type species of the genus (SEMENOV, 1989). However, there is another medium-sized one among the Chinese hyaenids, named *Ictitherium hyaenoides* ZDANSKY, 1924 which was later transferred to *Hyaenictitherium* (KRETZOI, 1938). Although the two hyaenids are different at specific level, they must belong to the same genus and as *Hyaenictitherium* has the priority, both are included in this genus (ZHANG et al., 2002; BONIS, 2004, 2005). Today the late Miocene hyaenid between *Adcrocuta eximia* and *Ictitherium viverrinum* is known as *Hyaenictitherium wongii* (ZDANSKY, 1924).

Such a medium-sized hyaenid, known as *Ictitherium hipparionum*, is reported in the old collections from Samos (FORSYTH MAJOR, 1894; PILGRIM, 1931). In the description of the Samos hyaenids it is referred to as *Thalassictis wongii* (SOLOUNIAS, 1981; WERDELIN, 1988), while later it was transferred to *Hyaenotherium* (WERDELIN & SOLOUNIAS, 1991). In our new collection from Samos localities a medium-sized hyaenid without description is reported as *Hyaenotherium wongii* (KOUFOS et al., 1997, 2004).

The most common hyaenids in the late Miocene faunas are *Adcrocuta eximia*, *Ictitherium viverrinum* and *Hyaenictitherium wongii*. The studied material is easily separated from *Adcrocuta* by its smaller size, the larger protocone in the P4 and the relatively larger and tricuspid talonid of the m1. The distinction from *Ictitherium* is also quite clear. The type species of the genus is *I. viverrinum*, known from Pikermi, Greece. The studied material from Samos was directly compared with the Pikermi *Ictitherium* housed at NHML, NHMW, and some casts of the BSPM collection housed at LGPUT, as well as with the material of *I. viverrinum* from Axios Valley (KOUFOS, 2000). The studied material differs from *Ictitherium viverrinum* in being a larger size, less wide canines, having an elongated blade in the P4, a relatively larger protocone in the P4, reduced molars and a relatively shorter talonid in the m1 (Figs. 10-12).

*Hyaenictitherium wongii* was considered as belonging to *Thalassictis* for a long time, but the distinction of the studied material from the genus *Thalassictis* is quite clear. *Thalassictis* is known by the single species *T. robusta* found in Kishinev, Moldavia, with fragmentary type material (KURTÉN, 1982). *Thalassictis* differs from *H. wongii* in having a shorter blade in the P4, a higher protoconid in the m1, a stronger talonid with higher cuspids of the m1 and a smaller size (Fig. 12).

Another medium-sized hyaenid from Samos is *Lycyaena chaeretis*. There is a complete skull (NHMW-SAM-A.4744) from Samos housed at NHMW, which is compared to the studied material of *H. wongii* from Samos. The skull MTLA-200 has a similar length to that of NHMW-SAM-A.4744, but this is due to the

fact that the latter is relatively young. However, the skull MTLA-200 is narrower and has smaller teeth (Fig. 12). Morphologically, the teeth of NHMW-SAM-A.4744 differ from those of *H. wongii* from Samos in having more robust (more hyaenid-like) premolars, and a relatively shorter upper carnassial, as well as in lacking a lingual cingular projection in the P3, and in the absence of the M2. A skull of *L. chaeretis* is also known from Pikermi and housed at NHML. This skull (NHML-PIK-M.8978) differs in the same characteristics as that from Samos, but there is a lingual cingular projection near the root like a protocone in the P3 (Fig. 10). Moreso, the cranial dimensions of NHML-PIK-M.8978 are clearly larger than those of the studied *H. wongii* from Samos. A hemimandible (NHML-PIK-M.8979) of *L. chaeretis* is also known from Pikermi and stored at NHML. This mandible differs from the studied ones of *H. wongii* from Samos in having a larger size and teeth (Fig. 12), a stronger anterior accessory cuspid in the p4, a weaker talonid significantly smaller than that of *H. wongii*, and in the absence of the m2. Another mandibular fragment (MNHN-PIK-3383) of *L. chaeretis* from Pikermi also differs from the studied material in the same characteristics as mentioned above, and its teeth are larger (Fig. 12).

The morphological characteristics and the size of the studied skulls and mandibles fit in well with those of *H. wongii* from Eurasia (SOLOUNIAS, 1981; WERDELIN, 1988; WERDELIN & SOLOUNIAS, 1991; KOUFOS, 2000; BONIS, 2005). The studied material has been compared for the first time to the material of *H. wongii* from Samos, stored at NHML and NHMW, as well as to that from Axios Valley, housed at LGPUT, and it has a similar morphology. The cranial and mandibular dimensions of the studied material are very close to those of the old material from Samos, as well as to that from Axios Valley (Tabs. 6, 7). The metrical comparison of both upper and lower teeth indicates that all the studied specimens are very close to the mean values for *H. wongii* from Axios Valley, and they are always within the ranges of variation for the Samos and China samples of *H. wongii* (Fig. 10, 11). Thus, the studied material can be ascribed to *H. wongii* with certainty. Some minor differences in the dental dimensions between the various specimens could be considered as sexual or ecological differences. There is a clear sexual dimorphism in carnivores, which could provide some minor metrical differences. *H. wongii* is a widespread taxon, known from China to Spain, and some minor differences could also be due to the different palaeoecological niches.

As was mentioned above, there is a medium-sized late Miocene hyaenid named *Hyaenictitherium hyaenoides* among the Chinese material. The latter differs from *H. wongii* by its reduced molars (especially M2 and m2), the smaller P2 and p2, the smaller main cuspid of the p4, the relatively smaller talonid of the m1 and the generally larger size (Fig. 12). Bearing in mind all the above mentioned comparisons, the studied material can be ascribed to *Hyaenictitherium wongii*. The sole P2 MLN-27 has a similar morphology and dimensions to *H. wongii*, but the limited material cannot allow a certain determination and thus it is referred to

as *Hyaenictitherium* cf. *H. wongii*. Besides its far-reaching expansion, the taxon also has a wide stratigraphic range from Vallesian to the end of middle Turolian.

### Genus *Adcrocuta* KRETZOI, 1938

#### *Adcrocuta eximia* (ROTH & WAGNER, 1854)

(Pl. 6, figs. 3-6; Pl. 7, figs. 1, 2)

**Locality:** Mytilinii-1A (MTLA), Adrianos ravine, Mytilinii Basin, Samos, Greece.

The material labelled as PMMS belongs to the collection of Prof. J. Melentis and is stored at NHMA. According to him it was collected from Adrianos ravine, more precisely from MTLA.

**Age:** Middle Turolian, MN 12 (late Miocene); 7.1-7.0 Ma.

#### **Material:**

MTLA. Isolated p2 sin, MTLA-6; right dp4, MTLA, 290; left dp4, MTLA-466.

PMMS. Frontal part of the skull with P2-M1 dex and P2-P3 sin, PMMS-70; left mandibular fragment with p1-p4, PMMS-70a; left upper canine, PMMS-71.

**Measurements:** The cranial and mandibular measurements are given in Tabs. 9, 10.

#### **Description:**

**Skull.** The specimen PMMS-70 is the frontal part of the skull with the maxilla (Pl. 6, fig. 3). The frontals are broken and only a part of the right orbit is preserved. The nasal cavity is oval-shaped and relatively wide. The lateral borders of the nasal cavity are almost vertical to the palate and its posterior border is above the anterior edge of the canine. There is a large infraorbital foramen situated above the P3. The orbit seems to be rounded and its anterior border is above the posterior border of the P3. The palate is relatively short and wide. The maxilla preserves the tooth rows P2-M1 dex and P2-P3 sin, as well as the roots of the P4 and M1. The metacone of the right P4 is broken. There are all the alveoles of the incisors, canines and P1. The alveole of the I3 suggests a large tooth like a canine. The canine's alveole also indicates a large tooth.

PMMS-70	dex	sin	PMMS-70a	
LP2	17.2	17.1	Lp1	4.8
BP2	11.7	11.7	Bp1	4.7
LP3	21.7	22.0	Lp2	16.2
BP3	16.0	16.0	Bp2	10.8
LP4	[37]	—	Lp3	18.2
BP4 ant.	16.3	—	Bp3	12.8
BP4 post.	11.8	—	Lp4	21.5
Lblade	—	—	Bp4	13.2
LM1	5.8	—		
BM1	12.6	—		

MTLA-6 p2 = 15.7 x 11.5

MTLA-290 dp4 = 19.2 x 7.1

MTLA-466 dp4 = 17.3 x 6.5

PMMS-71 C = 19.5 x 14.6

**P2:** The tooth is more or less squarish, with a vestigial anterior accessory cusp situated mesiolingually. A strong crest connects it with the tip of the main cusp. The posterior accessory cusp is larger and low, compressed on the distal part of the tooth.

**P3:** It is short and robust; the mesial breadth is longer than the distal one. Morphologically it is similar to P2 but larger.

**P4:** It is elongated and relatively slender; the protocone is partially broken but it seems to be very weak restricted to the base of the tooth, typical for *Adcrocuta*. The parastyle is strong and the paracone is high. The metacone is broken.

**M1:** It is very small, short and wide, with three cuspids and an almost elliptical crown. It is slightly worn and the preserved cuspids are low.

**Mandible.** The mandibular fragment (PMMS-70a) lacks the ascending ramus and preserves the alveoles of the incisors and canine as well as the tooth row p1-p4 (Pl. 6, fig. 4). The symphysis is strong and elliptical, pointing upwards after the p2. The mandibular corpus is high and its inferior border is straight till m1; then it curves roughly upwards. There is a large mental foramen below the middle of the p2 and a smaller one below the posterior border of the p2. The masseteric fossa seems to be deep and its anterior border is behind the posterior border of the m1. The tooth row is almost straight and there is no imbrication of the teeth. There is no diastema between them but all are in contact with each other. The canine is situated somewhat labially and the p1 lingually to the axis of the toothrow.

**c:** The canine seems to be large; the dimensions of the alveole are: 21.2 x 16 mm.

**p1:** It is small, single-rooted, monocuspid with a rounded crown.

**p2:** It is short and robust, without an anterior accessory cuspid, but with a basal mesiolingual cingular projection. The posterior accessory cuspid is larger, situated on a distal projection of the distal cingulum. There is a faint lingual and buccal cingulum.

**p3:** It is similar to the p2, but larger and with a large anterior accessory cuspid situated mesiolingually.

**p4:** It is relatively robust with a very strong anterior accessory cuspid. The posterior accessory cuspid is smaller than the anterior one and situated on a large distal projection of the distal cingulum, which is elevated all around the distal part of the tooth. The distal cingulum is strongly elevated lingually, giving the idea of an entoconid.

**Milk teeth:** Two isolated dp4 are included in the new collection. In MTLA-290 (Pl. 7, fig. 1) the talonid is partially broken, very small and seems to be monocuspid. The protoconid has twice the height of the paraconid, which is blade-like. The two cuspids are separated by a very deep valley open lingually. There is a faint buccal cingulum. The MTLA-466 (Pl. 7, fig. 2) is small and narrow. The tips of the paraconid and protoconid are broken, but they are blade-like. The talonid is small, monocuspid and situated lingually. There is a mesial, mesiolingual and mesiobuccal cingulum.

**Discussion:** *Adcrocuta eximia* is reported in all old collections from Samos (FORSYTH MAJOR, 1894; PILGRIM,

CRANIAL MEASUREMENTS	<i>Adcrocuta eximia</i>						<i>A. e. leptoryncha</i>	
	? Mytilinii-1	Samos			Pikermi		Axios valley	
	PMMS-70	NHML-SAM-M. 4162	NHML-SAM-A. 4727	NHML-SAM-A. 4726	MNHN-PIK-3000	NHML-PIK-M. 8967	LGPU-TP1-14	
	Original measurements			Original measurements			(Koufos, 2000)	
1. Prosthion-Acrocranium	—	—	276.0	281.0	295.0	—	287.0	297.0
2. Prosthion-Basion	—	236.0	237.0	242.0	232.0	—	242.2	268.0
3. Prosthion-Choanae	—	130.4	129.0	129.0	129.0	133.8	—	147.0
4. Prosthion-middle of the line connected the posterior borders of P4	117.0	124.0	125.0	125.0	125.0	126.4	126.9	141.0
5. Prosthion-Mandibular fossa	—	187.0	202.0	202.0	190.0	203.5	200.0	218.0
6. Prosthion-middle of the line connected the anterior borders of bullae	—	200.0	205.0	205.0	195.0	213.0	209.0	220.0
7. Prosthion-anterior border of the orbit	107.0	104.3	114.0	114.0	106.0	111.0	105.8	119.0
8. Basion-anterior border of choanae	—	104.1	129.0	113.0	103.5	—	—	109.0
9. Basion-anterior border of the orbit	—	153.7	170.0	170.0	106.0	—	179.5	167.0
10. Basion-middle of the line connected the posterior borders of P4	—	107.8	111.5	111.5	106.5	—	116.0	120.0
11. Breadth at the base of the zygomatic arcs	—	68.7	77.0	77.0	81.0	77.6	—	[76]
12. Maximal breadth at the zygomatic arcs	—	—	175.0	175.0	200.0	—	—	—
13. Breadth at the posterior borders of the orbits (in projection)	—	—	90.5	90.5	88.0	—	[88]	—
14. Breadth of the occipital condyles (external)	—	49.5	61.0	61.0	56.7	—	57.5	50.0
15. Breadth of foramen magnum	—	20.2	29.3	29.3	27.3	—	24.5	21.0
16. Height of foramen magnum	—	22.2	24.0	24.0	23.3	—	20.6	—
17. Height:occipital condyles-occipital protuberance	—	—	94.0	94.0	87.0	—	81.7	101.0
18. Maximal height: posterior end of choanae-frontal	—	—	106.0	106.0	90.0	73.4	78.3	121.0
19. Length of bulla	—	29.5	38.7	38.7	—	—	36.0	—
20. Breadth of bulla	—	17.4	21.0	21.0	—	—	23.7	—
21. Breadth of maxilla between C (in the middle)	37.5	35.0	39.5	39.5	44.0	40.2	38.7	43.0
22. Idem in P2	52.0	46.9	49.0	49.0	50.5	50.5	52.6	49.0
23. Idem in P3	64.0	56.0	62.0	62.0	60.7	61.3	62.9	53.5
24. Idem in the posterior ends of P4	90.0	86.7	90.0	90.0	97.5	94.5	97.6	80.5
25. Idem in M2	60.0	—	—	—	—	—	—	—
26. Incisor's breadth	42.0	40.7	47.0	47.0	44.0	—	—	47.5
27. Diastema C-I3	6.3	6.5	7.6	7.6	6.0	7.4	7.3	7.8
28. Idem C-P2	10.2	10.0	9.0	9.0	7.0	9.7	10.1	13.1
29. Idem P2-I3	33.5	33.2	35.0	35.0	32.0	34.9	35.0	40.5

Table 9: Cranial dimensions of *Adcrocuta eximia* from various Greek localities.



		<i>Adcrocuta eximia</i>									
MANDIBULAR MEASUREMENTS	?Mytilinii-1 PMMS-70a	Samos				Pikermi			Axios valley		
		NHMW- SAM-1912/ no 29	NHMW- SAM- 1911/V. 48	NHMW- SAM-A. 4728	NHML- SAM-M. 4162	NHML- SAM-M. 4164	NHML- PIK- M.8970	NHML- PIK- M.8971	NHML- PIK- M.8972	LGPUT- RZO-126	LGPUT- RZ1-4
		Original measurements									
1. Length anterior c-coronoid process	—	—	—	182.0	180.0	168.0	[190]	[195]	—	193.2	191.0
2. Length anterior c-condyle	—	—	—	183.0	183.0	174.0	180.0	196.0	151.3	192.5	195.5
3. Height inferior border at angle-coronoid	—	—	—	95.0	92.4	83.6	[96]	97.3	—	111.0	93.0
4. Height inferior border at angle-condyle	—	—	—	46.0	40.0	36.9	42.6	47.6	—	50.0	41.5
5. Height condyle-coronoid	—	—	—	55.0	48.3	45.0	[54]	50.8	—	61.5	52.7
6. Symphysis length	—	65.0	48.6	62.0	56.8	47.1	54.3	61.9	50.4	56.0	60.5
7. Height in front of p2	44.8	49.2	39.0	48.0	42.7	39.6	45.3	49.3	36.1	51.6	45.5
8. Idem in the middle of p3 (lingual)	45.0	45.5	—	46.5	38.4	34.4	41.4	43.0	28.8	46.5	41.0
9. Idem in p4 (lingual)	46.6	44.5	—	45.0	41.0	38.1	42.8	47.0	34.2	47.0	45.0
10. Idem in m1(lingual)	54.0	48.8	—	50.0	44.2	—	48.2	50.3	36.6	52.1	52.0
11. Idem behind m2	—	—	—	—	46.0	—	—	—	—	—	—
12. Diastema p2-c	8.5	10.0	6.8	14.0	11.5	10.1	13.5	11.7	—	10.8	10.5
12. Diastema p2-i3	—	29.0	21.7	—	26.5	—	28.5	—	—	—	30.7
13. Diastema i3-c	—	0.0	0.0	0.0	—	—	0.0	—	—	—	2.2
14. Length p2-m1	55.3	89.5	75.5	71.7	82.6	—	77.9	[87]	—	82.0	86.3
15. Length c-m1	—	118.0	102.0	108.3	113.1	—	107.2	[119]	—	109.6	118.0
16. Length p2-p4	—	62.0	53.5	53.3	55.2	54.3	52.6	60.1	54.8	56.0	57.0
17. Length p3-m1	—	73.0	63.3	62.5	68.3	—	63.9	[72]	—	66.0	73.2
18. Length p2-m2	—	—	—	—	—	—	—	—	—	—	—
19. Length c-m2	—	—	—	—	—	—	—	—	—	—	—
20. Length p1-m3	—	—	—	—	—	—	—	—	—	—	—

Table 10: Mandibular dimensions of *Adcrocuta eximia* from various Greek localities.

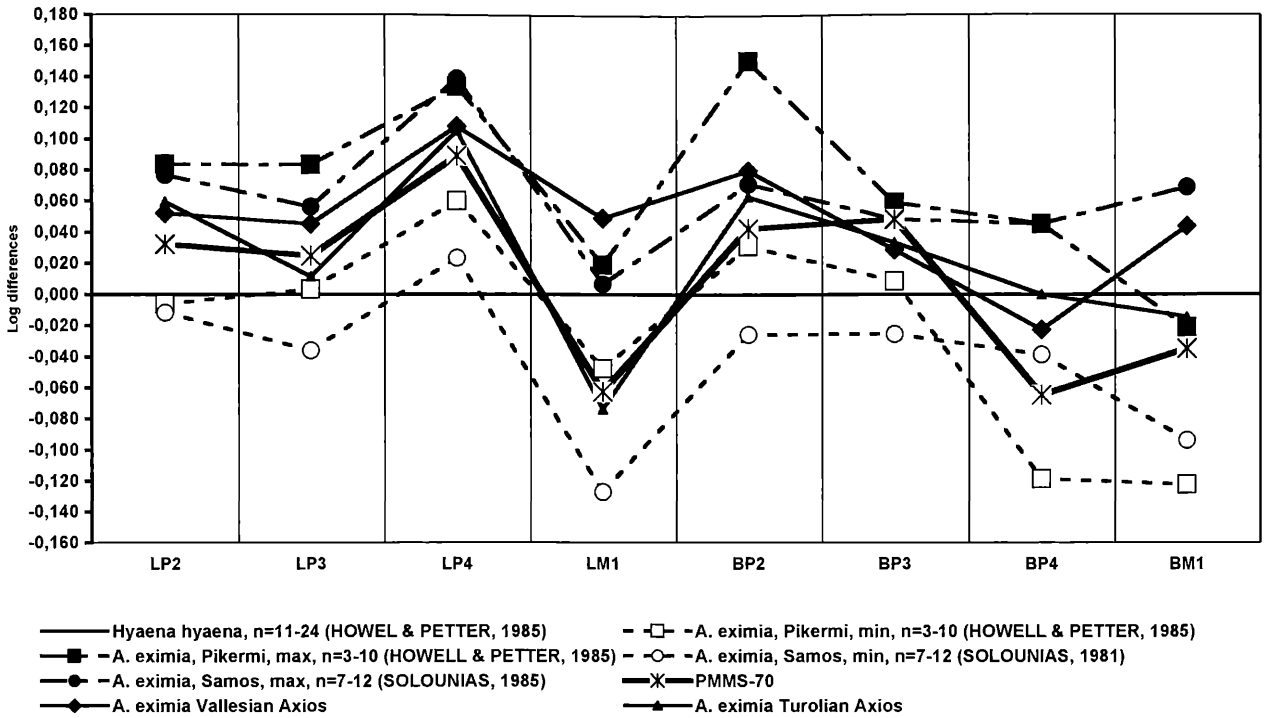
*Adcrocuta eximia*, Upper Teeth

Figure 13: Logarithmic ratio diagram comparing the upper teeth of *Adcrocuta eximia* from various localities.

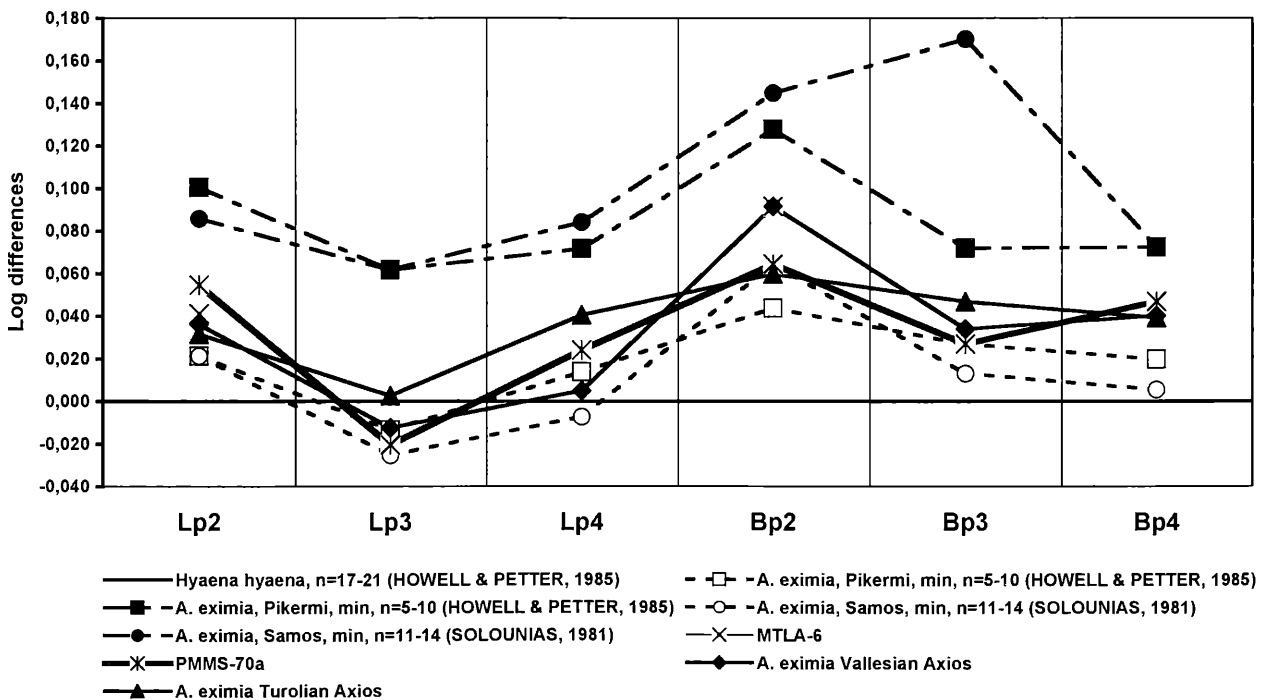
*Adcrocuta eximia*, Lower Teeth

Figure 14: Logarithmic ratio diagram comparing the lower teeth of *Adcrocuta eximia* from various localities.

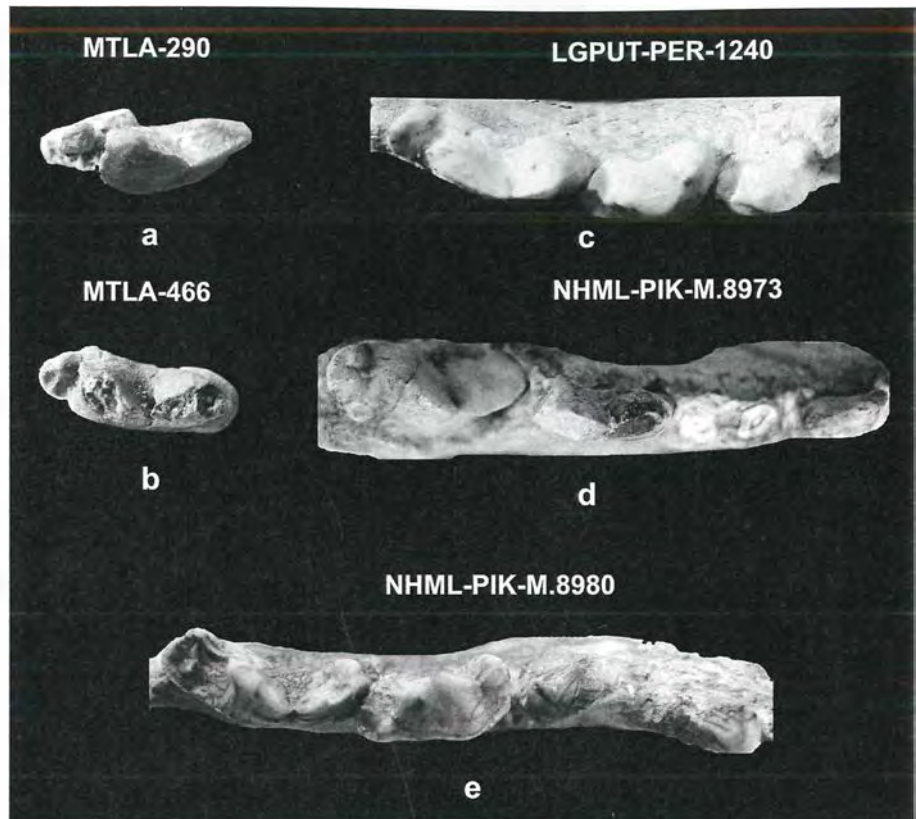
1931; SOLOUNIAS, 1981; KOUFOS & MELENTIS, 1982). The old material, or part of it, was described earlier under the name *Hyaenictis eximia* (SOLOUNIAS, 1981). However, *Hyaenictis* is a different taxon (HOWEL & PETER, 1985) and thus the Samos material was soon re-classified as *Adcrocuta*. The species was originally described as *Hyaena*

*eximia* from Pikermi (ROTH & WAGNER, 1854). Later, its name changed several times until being classified as *Adcrocuta* (SCHMIDT-KITTLER, 1976). The studied specimens PMMS-70, 70a, 71 have been described earlier (KOUFOS & MELENTIS, 1982) but I decided to include them in the present article together with the new collection of Samos,

**Figure 15:** Lower deciduous dentition of *Adcrocuta eximia* from various localities.

a. dp4, MTLA-290, Mytilinii-1A, Samos; b. dp4, MTLA-466, Mytilinii-1A, Samos; c. Lower deciduous dentition of the mandible LGPUT-PER-1240, Perivolaki, Greece; d. Lower deciduous dentition of the mandible NHML-PIK-M.8973, Pikermi, Greece; e. Lower deciduous dentition of the mandible NHML-PIK-M.8980, Pikermi, Greece.

All specimens are rotated to be right.



giving more data and comparisons for them. Although *A. eximia* is very common in the old Samos material, it is almost absent in our new collection, as it is represented by an isolated p2 and two milk molars only.

The morphological features of the studied material, such as the robust premolars, their squarish occlusal outline with a more or less straight mesial and distal outline, the relatively slender upper carnassial with a weak protocone, the very small M1, and the presence of a strong anterior accessory cuspid in the p4 are characteristics of *A. eximia*. The metrical comparison of the studied material suggests close similarities to *A. eximia*, too (Tabs. 9, 10; figs. 13-14). Both upper and lower dental dimensions are within the ranges of variation for *A. eximia* from Pikermi and Samos, as well as close to the Vallesian and Turolian form of *A. eximia* from Axios Valley, Macedonia, Greece (Figs. 13, 14). Bearing in mind all these comparisons and similarities, the studied material can be ascribed to *A. eximia* with certainty. Two subspecies are known, the typical Turolian *A. e. eximia* and the Vallesian *A. e. leptoryncha*, known from Axios Valley. The second subspecies is characterized by an elongated and narrow palate, a higher skull, a longer diastema C-P2 and narrower lower premolars (BONIS & KOUFOS, 1981; KOUFOS, 2000). The index "distance prosthion-middle of the line connecting the posterior end of the P4 / distance between the posterior ends of the P4" is 154 for *A. e. leptoryncha* versus 130 for PMMS-70. The corresponding index varies from 139-143 for the Samos *A. eximia* and from 130-141 for the Pikermi *A. eximia*. The diastema C-P2 is 13.1 mm in *A. e. leptoryncha* versus 10.2 mm in PMMS-70. In the Samos *A. eximia*, the diastema is 9-10 mm and in the Pikermi one 9.7-10 mm (the meas-

urements for the Pikermi and Samos skulls are original, coming from the material stored at NHML, MNHN and NHMW). The above indices and comparisons suggest that the studied material belongs to the typical subspecies *A. e. eximia*.

Three mandibular fragments with milk molars of *A. eximia* are known from Pikermi (PILGRIM, 1931). The specimen NHML-PIK-M.8973 also contains the m1, whose morphology and dimensions are very similar to the typical *A. eximia*. The length of the dp4 varies between 17-18.3 mm and the breadth between 6.8-7.2 mm being very close to those of MTLA-290, 466. A mandibular fragment with milk dentition is known from Perivolaki, Greece (KOUFOS, 2006a). Its morphology and dimensions (18.3 x 7.0 mm) are very close to the studied dp4 (Fig. 15).

*Adcrocuta eximia* is a large-sized form similar to the recent spotted hyaena *Crocuta crocuta* and for a long time it was referred to the same genus. The strong jaws, the crushing premolars, the elongated upper carnassial and the strong anterior accessory cuspid in the p4 suggest shearing and breaking action. This hyaena was mainly a carrion eater and it lived in groups like the recent ones. Its first appearance in the Eastern Mediterranean and Europe dates to late Vallesian (MN 10) at ~9.6 Ma and it disappeared at the end of Miocene at ~5.3 Ma (KOUFOS, 2003). The greatest abundance of the taxon is known from the Turolian, where it is very common in all Eurasian localities. The taxon is widespread, known from China to Spain. Considering its palaeoenvironment, it mainly lived under relatively open and dry conditions. In the Eastern Mediterranean, the palaeoenvironment changed at the beginning of Vallesian from a relatively

CRANIAL MEASUREMENTS	<i>Metailurus parvulus</i>			<i>Metailurus major</i>	
	Mytilini-1A	Halmypotamos	Chomateres	Pikermi	Halmypotamos
	MTLA-234	AMPG- HAL-1967/5	AMPG- CHO-nn	AMPG- PIK-1257/91	AMPG- HAL-1967/1
		Original measurements			
1. Prosthion-Acrocranium	—	[150]	157.5	[210]	217.0
2. Prosthion-Basion	—	—	127.5	[180]	180.5
3. Prosthion-Choanae	—	60.0	84.5	[84]	—
4. Prosthion-middle of the line connected the posterior borders of P4	—	58.5	57.5	[79]	82.0
5. Prosthion-Mandibular fossa	—	100.0	102.0	[136]	85.8
6. Prosthion-middle of the line connected the anterior borders of bullae	—	—	103.5	[141]	145.0
7. Prosthion-anterior border of the orbit	—	58.0	—	[66]	84.0
8. Basion-anterior border of choanae	53.5	—	44.0	[85]	—
9. Basion-anterior border of the orbit	83.4	—	—	131.5	133.5
10. Basion-middle of the line connected the posterior borders of P4	48.0	—	72.0	101.0	101.3
11. Breadth at the base of the zygomatic arcs	58.0	—	65.0	69.0	71.5
12. Maximal breadth at the zygomatic arcs	—	—	—	—	—
13. Breadth at the posterior borders of the orbits (in projection)	—	—	—	—	[67]
14. Breadth of the occipital condyles (external)	34.7	—	34.5	45.8	46.0
15. Breadth of foramen magnum	18.0	—	19.0	23.0	23.5
16. Height of foramen magnum	15.0	—	15.0	—	22.3
17. Height: occipital condyles-occipital protuberance	37.3	—	37.7	50++	62.0
18. Maximal height: posterior end of choanae-frontal	49.0	—	[42]	[64]	[64]
19. Length of bulla	25.6	—	27.0	32.6	33.0
20. Breadth of bulla	17.8	—	18.0	23.3	21.5
21. Breadth of maxilla between C (in the middle)	25.4	—	22.5	—	30.5
22. Idem in P2	—	—	—	—	—
23. Idem in P3	—	33.0	32.5	38.0	47.7
24. Idem in the posterior ends of P4	66.8	59.0	63.0	77.0	[80]
25. Idem in M2	—	—	—	—	—
26. Incisor's breadth	—	—	19.5	—	[32]
27. Diastema C-I3	—	—	3.8	5.5	5.7
28. Idem C-P2	—	—	5.5	8.2	10.5
29. Idem P2-I3	—	—	19.5	33.0	32.5

Table 11: Cranial dimensions of *Metailurus parvulus* and *M. major* from various Greek localities.

MANDIBULAR MEASUREMENTS	<i>Metailurus parvulus</i>					
	Mytilinii-1A	Pikermi	Pikermi	Chomateres	Kerassia	Maragheh
	MTLA-235	AMPG-PIK-PG 01/103	NHMW-PIK-A.4712	AMPG-CHO-nn	AMPG-KER-K1/210	NHML-MRG-M.3825
		Original measurements				
1. Length anterior c-coronoid process	—	—	—	—	110	—
2. Length anterior c-condyle	—	—	—	101	10.5	—
3. Height inferior border at angle-coronoid	—	—	—	—	61	—
4. Height inferior border at angle-condyle	—	—	—	21.5	22.5	—
5. Height condyle-coronoid	—	—	—	—	16.5	—
6. Symphysis length	—	—	26	24.5	22.8	20.5
7. Height in front of p2	20.3	—	—	—	—	—
8. Idem in the middle of p3 (lingual)	13.4	18.7	—	17.5	17.5	20.6
9. Idem in p4 (lingual)	16.3	18.5	20.2	18	17.5	20.3
10. Idem in m1(lingual)	16.4	18	—	18	—	19.9
11. Idem behind m2	—	—	—	—	8.5	—
12. Diastema p2-c	—	8.2	—	8.3	—	—
12. Diastema p2-i3	—	16.3	—	—	—	—
13. Diastema i3-c	—	0	59.3	0	—	—
14. Length p2-m1	—	—	—	—	—	—
15. Length c-m1	60	57	—	60	57	57
16. Length p2-p4	—	—	43.8	—	—	—
17. Length p3-m1	—	40.5	—	39.5	40.5	39.1
18. Length p2-m2	—	—	—	—	—	—
19. Length c-m2	—	—	—	—	—	—

**Table 12:** Mandibular dimensions of *Metailurus parvulus* from various Greek localities.

close and humid one to being more open and dry (Koufos, 2006b). During that time *A. eximia* appeared in the Eastern Mediterranean. The environment gradually changed to more and more open and dry during Turolian, providing more favourable conditions for *A. eximia*, which increased remarkably in numbers. During the end of Miocene another faunal change led to the more closed and wet palaeoenvironmental conditions of early Pliocene and to the disappearance of *A. eximia* (Koufos, 2003, 2006c).

Family Felidae GRAY, 1821

Genus *Metailurus* ZDANSKY, 1924

*Metailurus parvulus* ZDANSKY, 1924  
(Pl. 7, figs. 3-6)

**Locality:** Mytilinii-1A (MTLA), Adrianos ravine, Mytilinii Basin, Samos, Greece.

**Age:** Middle Turolian, MN 12 (late Miocene); 7.1-7.0 Ma.

**Material:** Skull, MTLA-234; right mandibular fragment with p3, MTLA-235.

**Measurements:** The cranial and mandibular measurements are given in Tabs. 9, 10.

	dex	sin
MTLA-234	P3 = 14.0 x —	—
	P4 = 22.2 x —	21.6 x 10.0
MTLA-235	p3 = 10.2 x 4.8	

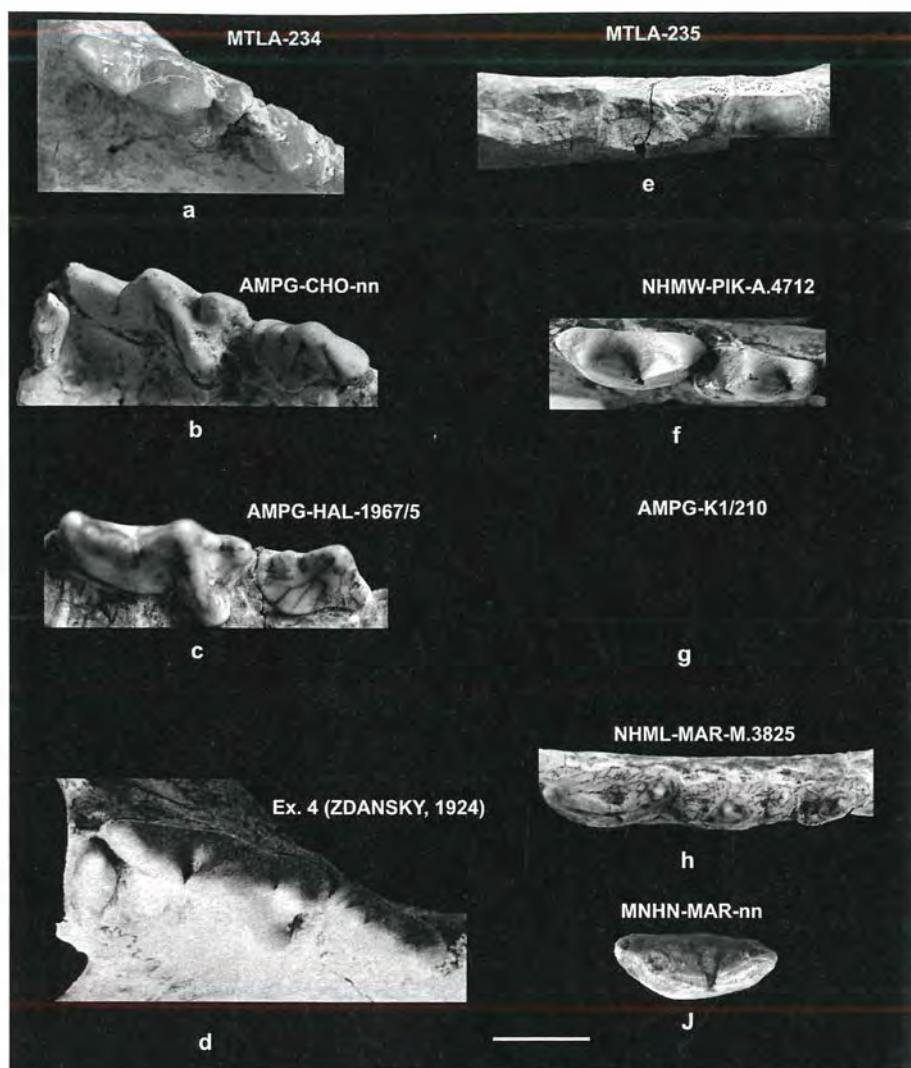
**Description:**

**Skull.** The skull lacks the muzzle, the left zygomatic arch, (the right one is partially preserved), and both orbits are badly preserved (Pl. 7, fig. 3). The skull seems to be short with a short muzzle. The infraorbital foramen is large, situated above the parastyle of the P4. The orbit seems to be rounded, with its anterior border above the P3. The braincase is voluminous, but its upper surface is flattened. There are no sagittal lines or crests. The zygomatic arches seem to be strong and strongly project buccally. The occipital is small, with a well-developed external occipital crest, starting from the posterior border of the postglenoid process. The nuchal crest is very small and restricted to the breadth of the external occipital crest. The occipital condyles are relatively small, while the foramen magnum is

**Figure 16:** Upper and lower dentition of *Metailurus parvulus* from various localities.

a. Upper tooth row of the skull MTLA-234, Mytilinii-1A, Samos; b. Upper tooth row of the skull AMPG-CHO-nn, Chomateres, Greece; c. Upper tooth row of the skull AMPG-HAL-1967/5, Halmyropotamos, Greece; d. Upper tooth row of the skull Ex.4, Maragheh, Iran (taken from ZDANSKY, 1924); e. Lower tooth row of the mandible MTLA-235, Mytilinii-1A, Samos; f. Lower tooth row of the mandible NHMW-PIK-A.4712, Pikermi, Greece; g. Lower tooth row of the mandible AMPG-KER-K1/210, Kerassia, Greece; h. Lower tooth row of the mandible NHML-MAR-M-3825, Maragheh, Iran; j. m1, MNHN-MAR-nn, Maragheh, Iran.

All specimens shown as if from right-hand side.



large and elliptical-shaped. The bullae are ovoid and relatively large. They are well-separated from the condyles by a wide and deep channel. Their anterior border is on line with the posterior surface of the postglenoid process. The bullae are separated in two parts by a shallow groove across their long axis. The choanae are wide and their anterior border is almost level with the posterior border of the P4. The palate is short and wide having a more triangular shape.

**Upper Dentition.** The dentition of the skull MTLA-234 includes the right P3-P4 and the left P4; there also are the alveoles of the canines, as well as the alveoles of both M1 (Pl. 7, figs. 3c, 4, 5). The tooth row is straight.

**C:** The alveoles of the canines indicate a relatively large canine. They are elliptical and their dimensions are 11.5 x 8 mm.

**P3:** It is mesially and labially broken. It is elongated and narrow with a clearly distinguished posterior accessory cusp.

**P4:** The left carnassial is very well-preserved, elongated, narrow and felid-like (Pl. 7, figs. 4, 5). The protocone is very small, situated well posterior to the parastyle. It is a small cusp situated at the base of the paracone, well distinguished (Pl. 7, figs 4, 5), but it disappears by attrition. The parastyle is small compared to the paracone and lower. It is well-distinguished from it and from the protocone

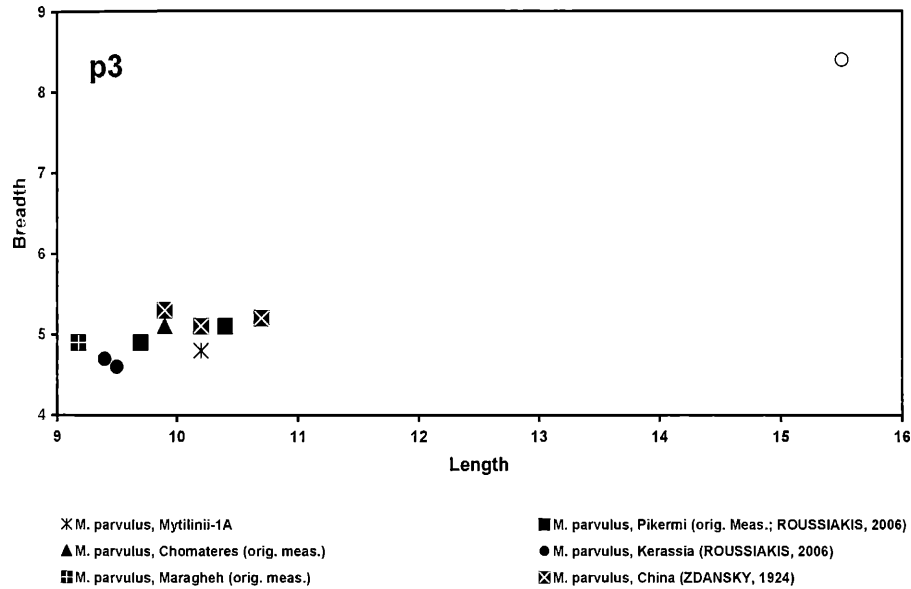
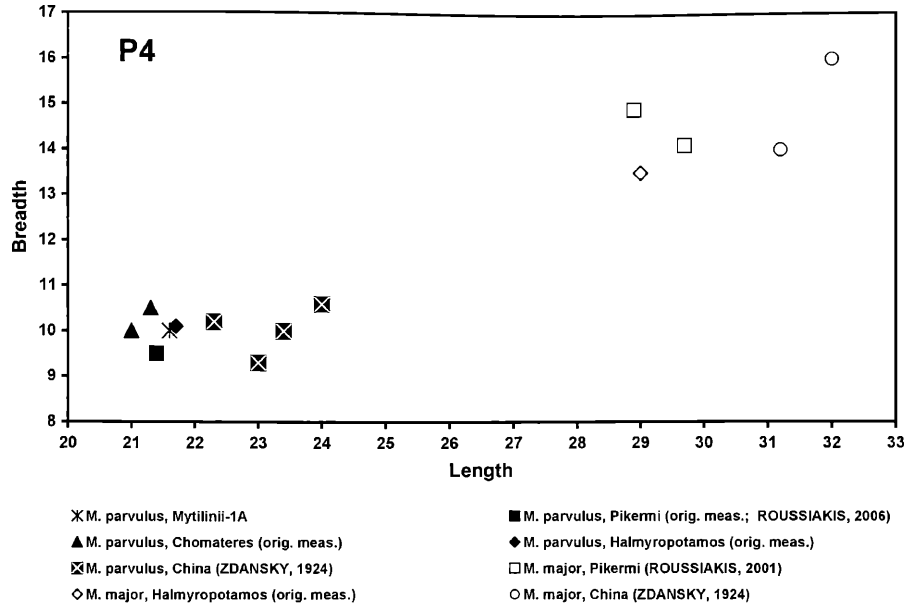
by a deep valley. There is a small cingular projection in its mesiobuccal corner. The metacone is blade-like, low and curved buccally. It is distinguished from the paracone by a deep valley, very well visible on the buccal surface of the tooth.

**M1:** It is situated vertically to the carnassial, and, from the alveole, seems to be small.

**Mandible.** The studied mandibular fragment lacks the ascending ramus and preserves the p3 and the alveoles of the p4 and m1 (Pl. 7, fig. 6). The mandibular corpus is shallow and its inferior border is straight from below the p3 to the anterior border of the masseteric fossa. The symphysis is short and almost vertical to the mandibular corpus, a characteristic feature in felids. The lower part of the symphysis projects and forms an angle, giving a strong construction to the anterior part of the jaw. There are two mental foramens, one large, below the middle of the diastema c-p3, and a smaller, below the contact between the p3 and p4. The masseteric fossa is deep and its anterior border is well behind the m1.

**p3:** It is short and narrow with its distobuccal corner slightly broken. There is no anterior accessory cuspid, but a small cingular projection, situated in the lingual part of the tooth. The posterior accessory cuspid is larger and

**Figure 17:** Scatter diagram length/breadth comparing the upper carnassial of *Metailurus* from various localities.



**Figure 18:** Scatter diagram length/breadth comparing the p3 of *Metailurus* from various localities.

situated on a cingular projection. In the labial corner of this projection, there is a very small cuspid level with the posterior accessory cuspid, like a hypoconid. There is a weak labial cingulum.

**Discussion:**

The species *Metailurus parvulus* was set up by HENSEL (1862), based on material found in Pikermi and described under the name *Machairodus parvulus*. Later, it was recognized in several late Miocene Eurasian localities. A mandible from Maragheh described as *Felis cf. brevirostris* by KITTL (1887) was later transferred to *Metailurus parvulus* (BEAUMONT, 1961). Some machairodont material from China was described as *Metailurus minor* by ZDANSKY (1924), but later it was ascribed to *Metailurus parvulus* (THENIUS, 1951; BEAUMONT, 1961). In Samos, the species is known from QA and Q5 (SOLOUNIAS, 1981; tab. 7), but without mentioning the material it is based on, and with no description. The new material from Samos described in this article is compared to the material from Pikermi,

Halmyropotamos and Chomateres, stored at AMPG, NHMW and PIUW, as well as to the material from Maragheh housed at NHML and MNHN.

A skull of *Metailurus parvulus* from Pikermi, stored in PIUW, is described by MELENTIS (1967); a mandibular fragment with P3-P4 (NHMW-PIK-4712), also from Pikermi, is stored at NHMW. A skull and a mandible of *Metailurus parvulus* without any number from Chomateres (a locality situated about 1 km from Pikermi) are stored at AMPG (SYMEONIDIS, 1978). The morphological characteristics of the studied skull and mandible resemble those of the Pikermi and Chomateres material (Fig. 16), while their dimensions are very similar (Tabs. 11, 12). The dimensions of the teeth are also very close to those of the Pikermi and Chomateres material (Fig. 17). A skull with P3-M1 (AMPG-HAL-1967/5) of *Metailurus parvulus* was described from the locality of Halmyropotamos, Evia Island (MELENTIS, 1967). The morphology and size of the upper carnassial of MTLA-234 fit in well with

	<i>Machairodus giganteus</i>					<i>M. aphanistus</i>
UPPER CANINE	Mytilinii-1	Halmyropotamos	Pikermi	Thessaloniki	Maragheh	Kemiklitepe-D
	PMMS-69	AMPG-HAL-1967/6	AMPG-PIK-1967/7	MNHN-SLQ-938	MNHN-MRG-3366	MNHN-KTD-66
		MELENTIS (1967)		Original measurements		
Dimensions at the base:	35.8 x 14.5	35.2 x 14.3	34.2 x 13.8	36.8 x 14.9	29.0 x 11.9	30.8 x 12.7
Idem 3 cm from the base:	32.5 x 11.5	32.2 x 11.8	27.9 x 11.0	31.0 x 11.0	—	—
Idem 6 cm from the base:	19.9 x 8.3	24.6 x 9.7	18.2 x 8.9	19.1 x 8.2	—	—

**Table 13:** Dimensions of the upper canine of *Machairodus* from various localities.

those of Halmyropotamos (Figs 16, 17). The species is also known from another locality of Evia Island, named Kerassia, from where an almost complete skeleton was described (ROUSSIAKIS et al., 2006). Although the skull is absent, the preserved mandibular ramus has similar morphological characteristics as those of MTLA-235, like the elongated and shallow mandibular corpus with a straight inferior border, the deep masseteric fossa ending behind the m1 and the two mental foramina (one below the postcanine diastema, and another below the posterior border of the p3). The Kerassia p3 lacks an anterior accessory cuspid and has a small posterior one, like that of MTLA-235 (Fig. 16).

The comparison of the Samos *Metailurus parvulus* with the Chinese sample described by ZDANSKY (1924) indicates close similarities. The general morphological features of the skull and mandible resemble each other, while their size seems to be similar too. Unfortunately, ZDANSKY (1924) does not give cranial measurements for a direct comparison, but some measurements taken from his illustrations fit in with those of the Samos material. Their dental measurements, however, are slightly larger than those of the studied material (Fig. 17).

The genus *Metailurus* is known from Greece by another species, named *M. major* and found in Pikermi and Halmyropotamos (MELENTIS, 1967; ROUSSIAKIS, 2001). This species is also mentioned in the lists of the old collection of Samos (SOLOUNIAS, 1981; tab. 7). *Metailurus major* clearly differs from *Metailurus parvulus* by its remarkably larger size (Fig. 17). Among the known late Miocene machairodonts, the species *Paramachaerodus orientalis*, *Machairodus aphanistus* and *Machairodus giganteus* are known from Greece. All of them are larger than *Metailurus parvulus*. Moreover, their upper carnassial has a clear ectoparastyle and reduced protocone, while the lower carnassial lacks or has a rudimentary talonid only.

Although it is rare, *Metailurus parvulus* spread widely and inhabited the whole of Eurasia, from China to Spain. Besides the Greek localities, it is also known from the Spanish localities of Los Mansuetos and El Arquillo, the Italian locality of Gravitelli and the Moldavian locality of Cimislia. In Asia, except from China and Iran, it is known from the Turkish locality of Sandikli Kinik. A form similar to *Metailurus parvulus* is traced in the French locality of

Montredon. All the *Metailurus parvulus*-bearing mammal localities are dated from middle to late Turolian (MN 12-13); the locality of Montredon is dated to late Vallesian (NOW, 2007). Thus, the species seems to appear earlier, during Vallesian, in Europe. This idea is supported by its recent discovery in the late Vallesian locality Ravine de la Pluie of Axios Valley (Macedonia, Greece), (pers. observ.).

#### Genus *Machairodus* KAUP, 1833

#### *Machairodus giganteus* (WAGNER, 1848) (Pl. 7, fig. 7)

**Locality:** ?Mytilinii-1A (MTLA), Adrianos ravine, Mytilinii Basin, Samos, Greece.

**Material:** Fragment of the upper canine, PMMS-69. The material labelled as PMMS belongs to the collection of Prof. J. Melentis and is stored at NHMA. According to him, it was collected from Adrianos ravine, more precisely from MTLA.

**Measurements:** The measurements are given in Tab. 13.

**Description:** The material was described by KOUFOS & MELENTIS (1982). The preserved canine has a height of about 77 mm from the base. It is flattened and curved backwards. Both mesial and distal borders are indented; the mesial indented border is double, from the base to the middle of the preserved tooth; then it becomes single. A strong crest goes over the middle of the buccal and lingual surfaces.

**Discussion:** The morphological characteristics of the studied canine fragment are similar to those ascribed to *M. giganteus* from Pikermi, Halmyropotamos and Axios Valley (WAGNER, 1848; MELENTIS, 1967; KOUFOS, 2000). Moreover, its dimensions are also similar to *M. giganteus* (Tab. 13).

### 3. Conclusions

Although the late Miocene Samos carnivores are numerous in the old collections, they are relatively fewer in the new material. In the lists given by SOLOUNIAS (1981), BERNOR



et al., (1996) and NOW (2007), 15 different carnivoran taxa are mentioned (Tab. 1). Six of them are present in the new collection, while *Protictitherium* was recognized for the first time on Samos (Tab. 1). Bearing in mind that the old material was collected a long time ago by various people excavating for many years on Samos, the new collection is comparatively rich in carnivores. The majority of the found carnivores are typical for the Turolian. The mustelid *Parataxidea maraghana*, apart from Samos, is known from Middle Maragheh, which is dated to middle Turolian, MN 12 (NOW, 2007). The species is also known from the early Turolian locality of Karaçahasan (Turkey), dated to early Turolian, MN 11 (NOW, 2007). The strong similarity of the MTLA material of *P. maraghana* to that of Middle Maragheh (type locality), indicates a similar middle Turolian age (MN 12). The hyaenid *Plioviverrops orbigny* is well known from Greece and mainly reported from the middle Turolian localities of Pikermi (type), Vathylakkos, Prochoma and Perivolaki; however, it is also found in the early Turolian locality of Ravine des Zouaves-5. Its presence in MTLB and its similarity to the known Greek material suggests an early - middle Turolian age, MN 11-12; bearing in mind that its main appearance is observed in middle Turolian (MN 12), a similar age is quite possible for MTLB. The hyaenid *Protictitherium crassum* has a wide stratigraphic distribution from MN 4 to MN 13 (NOW, 2008). However, the similarity of the MLN mandible to that from the Turolian of Axios Valley (Macedonia, Greece) indicates a possible Turolian age for the locality. The other two hyaenid taxa, *Hyaenictitherium wongii* and *Adcrocuta eximia*, are known from the Vallesian and Turolian, too. Thus, they cannot be very relevant to biochronology, suggesting only a late Miocene age. Likewise, *Metailurus parvulus* is reported from late Vallesian to late Turolian (MN 10-13), and *Machairodus giganteus* from late Vallesian to early Pliocene (MN 10-15), (NOW, 2007); their wide stratigraphic distribution cannot help with biochronology.

The available data from the study of the carnivores suggests that the age of the localities must be Turolian; more precisely, the MTLA and MTLB faunas could be dated to middle Turolian. These results fit in quite well with those from the study of the whole fauna and magnetostratigraphy (KOUFOS et al., this volume).

#### 4. Acknowledgements

The excavations on Samos have been supported by the Prefecture of Samos and the “Konstantinos and Maria Zimalis” Foundation. The Municipality of Mytilinii provided generous help too. The Natural History Museum of the Aegean offered us the premises for the preparation and storage of the fossils. The Synthesys Program supported my visits to Vienna (AT-TAF-702), London (GB-TAF-1842) and Paris (FR-TAF-3102). I thank Prof. M. Dermitzakis (AMPG), Prof. G. Theodorou (AMPG), Dr. S. Roussiakis (AMPG), Prof. P. Tassy (MNHN), Dr. S. Sen (MNHN), Prof. G. Rabeder (PIUW), Prof. D. Nagel (PIUW), Dr. A. Curren (NHML)

for granting me access to the fossils at their disposal. Many thanks to Dr. C. Sagne (MNHN), Dr. C. Argot (MNHN) and Dr. C. Soligo (NHML) for their help in searching the collections, and their great hospitality. I also thank Dr. D. Geraads for providing me with casts of *Protictitherium aegaeum*. Finally, I wish to thank my collaborators and several students who excavated with me and helped me with the collection and preparation of the fossils. I also thank Dr. M. Morlo for his useful comments on the manuscripts.

#### 5. References

- BEAUMONT, G. de., 1961. Recherches sur *Felis attica* WAGNER (Mammalia, Carnivora) du Turolien de Grèce. — Archives des Sciences, 39:377–386, Lausanne.
- BEAUMONT, G. de., 1969. Brèves remarques sur le genre *Plioviverrops* KRETZOI (Carnivora). — Bulletin Laboratoire Géologie Minéralogie Géophysique, Museum Géologique, Univ. Lausanne, 180:1–7, Lausanne.
- BEAUMONT, G. de. & MEIN, P., 1972. Recherches sur le genre *Plioviverrops* KRETZOI (Carnivora, ?Hyaenidae). — Comptes Rendus des Séances, SPHN, 25:383–394.
- BERNOR, R.L., SOLOUNIAS, N., SWISHER III, C. C. & VAN COUVERING, J.A., 1996. The correlation of three classical “Pikermian” mammal faunas - Maragheh, Samos and Pikermi - with the European MN unit system. — [in:] BERNOR R-L., FAHLBUSCH, V. & MITTMANN, H-W. (eds). The evolution of western Eurasian Neogene mammal faunas. — 1:137–156, New York (Columbia University Press).
- BONIS L. de., 2004. Carnivores hyaenidés du Miocène supérieur de Turquie. — Zona Arqueologica Miscelanea en homenaje a Emiliano Aguirre, 2. Paleontologia. Museo Arqueologico Regional, Madrid, pp. 108–117.
- BONIS L. de., 2005., Carnivora (Mammalia) from the late Miocene of Akkaşdağı, Turkey. — Geodiversitas, 27(4):567–589, Paris.
- BONIS, L. de & KOUFOS, G.D., 1981. A new hyaenid (Carnivora, Mammalia) in the Vallesian (late Miocene) of Northern Greece. — Scientific Annals, Faculty of Physics and Mathematics, University of Thessaloniki, 21:79–94, Thessaloniki.
- BONIS, L. de & KOUFOS, G.D., 1991. The late Miocene small carnivores of the lower Axios Valley (Macedonia, Greece). — Geobios, 24(2):361–379, Lyon.
- CRUSAFONT-PAIRÓ, M. & PETTER, G., 1969. Contribution à l'étude des Hyaenidae. La sous-famille des Ictitheriinae. — Annales de Paléontologie, 55(1):89–127, Paris.
- DEPÉRET, C., 1892. La faune des mammifères miocènes de la Grive Saint-Alban. — Archives Museum Histoire naturelle Lyon, 5:31–96, Lyon.
- FORSYTH MAJOR, C.J., 1894. Le gisement ossifère de Mitylini et catalogue d'ossements fossiles recueillis à Mitylini, île de Samos, et déposés au Collège Galliard, à Lausanne. Georges Bridel & Cie Editeurs,

- pp. 1-51, Lausanne.
- GAUDRY, A., 1861. Résultats des fouilles entreprises en Grèce sous les auspices de l'Académie des Sciences. — *Comptes Rendus Academie Sciences Paris*, 52:722–724, Paris.
- GAUDRY, A. & LARTET, E.A.I.H., 1856. Sur les résultats des recherches paléontologiques entreprises dans l'Attique sous l'auspice de l'Académie. — *Comptes Rendus Académie Sciences Paris*, 43:271–274, Paris.
- GAUDRY, A., 1862-67. Animaux fossiles et géologie de l'Attique. Editions Savy, Paris, pp.215-218.
- GERVAIS, P., 1859. Zoologie et Paléontologie française, 2<sup>nd</sup> édition, Paris.
- HENSEL, R.F., 1862. Über die Reste einiger Säugetierarten von Pikermi in der Münchener Sammlung. — *Monatsberichte der Akademie der Wissenschaften*, 27:560–569, München.
- HOWELL, F.C. & PETTER, G., 1985. Comparative observations on some middle and upper Miocene hyaenids genera: *Percrocuta* KRETZOI, *Allohyaena* KRETZOI, *Adcrocuta* KRETZOI (Mammalia, Carnivora, Hyaenidae). — *Geobios*, 18:419–476, Lyon.
- KAYA, T., GERAADS, D. & TUNA, V. 2005. A new late Miocene mammalian fauna in the Karaburun Peninsula (W Turkey). — *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, 236(3):321–349, Stuttgart.
- KITTL, E., 1887. Beiträge zur Kenntniss der fossilen Säugethiere von Maragha in Persia. I. Carnivora. — *Annalen des Naturhistorischen Hofmuseums*, 2:317–338, Wien.
- KOSTOPOULOS, D., SEN, S. & KOUFOS, G.D., 2003. Magnetostratigraphy and revised chronology of the late Miocene mammal localities of Samos, Greece. — *International Journal of Earth Sciences*, 92:779–794, Wien.
- KOSTOPOULOS, D.S., KOUFOS, G.D., SYLVESTROU, I.A., SYRIDES, G.E. & TSOMPACHIDOU, E., this volume. The Late Miocene Mammal Faunas of the Mytilinii Basin, Samos Island, Greece: New Collection. 2. Lithostratigraphy and Fossiliferous Sites. — *Beiträge zur Paläontologie*, 31:13–26, Wien.
- KOUFOS, G.D., 1979. Preliminary report of the study of mammalian fauna (Carnivora, Proboscidea, Perisodactyla) of Axios Valley (Macedonia - Greece). — *Proc. VII<sup>th</sup> Int. Cong. Medit. Neogene*, Athens, 1979. — *Annales géologiques de Pays Helleniques*, Hors series, 2:631–635, Athens.
- KOUFOS, G.D., 1980. Palaeontological and stratigraphical study of the Neogene continental deposits of the basin of Axios river. — *Scientific Annals, Faculty of Physics and Mathematics, University of Thessaloniki*, 19(11):1–322.
- KOUFOS, G.D., 2000. Revision of the late Miocene carnivores from the lower Axios Valley. — *Münchner Geowissenschaftliche Abhandlungen, (A)*, 39:51–92, München.
- KOUFOS, G.D., 2003. Late mammal events and biostratigraphy in the Eastern Mediterranean. — *Deinsea*, 10:343–371, Rotterdam.
- KOUFOS, G.D., 2006a. The late Miocene Vertebrate locality of Perivolaki, Thessaly, Greece. 4. Carnivora. — *Palaeontographica, Abt. A*, 276:39–74, Stuttgart.
- KOUFOS, G.D., 2006b. Palaeoecology and chronology of the Vallesian (late Miocene) in the Eastern Mediterranean region. — *Palaeogeography, Palaeoclimatology, Palaeoecology*, 234:127–145, Amsterdam.
- KOUFOS, G.D., 2006c. The large mammals from the Miocene/Pliocene locality of Silata, Macedonia, Greece with implications about the Latest Miocene palaeoecology. — *Beiträge zur Paläontologie*, 30:293–313, Wien.
- KOUFOS, G.D., 2006d. The Neogene mammal localities of Greece: faunas, chronology and biostratigraphy. — *Hellenic Journal of Geosciences*, 41(1):183–214, Athens.
- KOUFOS, G.D., this volume. The Late Miocene Mammal Faunas of the Mytilinii Basin, Samos Island, Greece: New Collection. 1. History of the Samos Fossil Mammals. — *Beiträge zur Paläontologie*, 31:1–12, Wien.
- KOUFOS, G.D. & MELENTIS, J., 1982. The Late Miocene (Turolian) mammalian fauna of Samos Island (Greece). Study of the collection of Palaeontological Museum of Mytilinii, Samos. 1. Carnivora. — *Scientific Annals, Faculty of Physics and Mathematics, University of Thessaloniki*, 22:175–193, Thessaloniki.
- KOUFOS, G.D., KOSTOPOULOS, D.S., & VLACHOU, T.D., this volume. The Late Miocene Mammal Faunas of the Mytilinii Basin, Samos Island, Greece: New Collection. 16. Chronology. — *Beiträge zur Paläontologie*, 31:397–408: Wien.
- KOUFOS, G.D., KOSTOPOULOS, D.S., VLACHOU, T.D. & SYLVESTROU, I.A., 2004. Reconsideration of the Mytilinii fossiliferous basin, Samos, Greece. — 5<sup>th</sup> International Symposium on Eastern Mediterranean Geology, Thessaloniki, April 2004, Abstracts, 1:326–329, Thessaloniki.
- KOUFOS, G.D., SEN, S., KOSTOPOULOS, D.S., SYLVESTROU, I.A. & VLACHOU, T.D., 2006. The late Miocene Vertebrate locality of Perivolaki, Thessaly, Greece. 10. Chronology. — *Palaeontographica, Abt. A*, 276:185–200, Stuttgart.
- KOUFOS, G.D., SYRIDES, G.E., KOSTOPOULOS, D.S., KOLIADIMOU, K.K., SYLVESTROU, J.A., SEITANIDIS, G.C. & VLACHOU, T., 1997. New excavations in the Neogene mammalian localities of Mytilinii, Samos Island, Greece. — *Geodiversitas*, 19(4):877–885, Paris.
- KRETZOI, M., 1938. Die Raubtiere von Gombaszög nebst einer Übersicht der Gesamtfaua. (Ein Beitrag zur Stratigraphie des Altquartärs). — *Annales Musei Nationalis Hungarici*, 31:88–157, Budapest.
- KURTÉN, B., 1982. Status of the fossil hyaenids *Ictitherium viverrinum* and *Thalassictis robusta* (Mammalia). — *Zeitschrift für geologische Wissenschaften*, 10:1009–1018, Berlin.

- MELENTIS, J.K., 1967. Studien über fossile Vertebraten Griechenlands. 19. Die Pikermifauna von Halmyropotamos (Euböa, Griechenlands). I. Teil: Odontologie und Kraniologie. — *Annales Géologiques des Pays Helleniques*, sér. 1, 18:283–411, Athens.
- NOW, 2007–08. Neogene of the Old World, database with the Neogene localities and their faunal lists. — [www.helsinki.fi/science/now/database.htm](http://www.helsinki.fi/science/now/database.htm)
- OZANSOY, F., 1965. Étude des gisements continentaux et des Mammifères du Cénozoïque de Turquie. — *Mémoires de la Société Géologique de France*, 102:1–92, Paris.
- PETTER, G., 1976. Étude d'un nouvel ensemble de petits carnivores du Miocène d'Espagne. — *Géologie Méditerranéenne*, 3(2):135–154, Paris.
- PILGRIM, G.E., 1931. Pontian Carnivora of Europe. — *British Museum Natural History*, pp. 1–174, London.
- ROTH, J. & WAGNER, A., 1854. Die fossilen Knochenüberreste von Pikermi in Griechenland. — *Abhandlungen der Bayerischen Akademie der Wissenschaften, Math.-Phys. Kl.*, 7:371–464, München.
- ROUSSIAKIS, S., 1996. Contribution to the study of the mammalian findings in the type locality of Pikermi. — PhD thesis, University of Athens, pp. 1–259. (in Greek, unpublished).
- ROUSSIAKIS, S., 2001. *Metailurus major* ZDANSKY, 1924 (Carnivora, Mammalia) from the classical locality of Pikermi (Attica, Greece). — *Annales de Paléontologie*, 87(2):119–132, Paris.
- ROUSSIAKIS, S., THEODOROU, G.E. & ILIOPOULOS, G., 2006. An almost complete skeleton of *Metailurus parvulus* (Carnivora, Felidae) from the late Miocene of Kerassia (Northern Euboea, Greece). — *Geobios*, 39:563–584, Lyon.
- SCHMIDT-KITTLER, N., 1976. Carnivores from the Neogene of Asia Minor. — *Palaeontographica*, Abt. A, 155:1–131, Stuttgart.
- SEMENOV, Y.A., 1989. Iktiteri i morfologicheski skhodnye hieni neogena USSR. (Ictitheres and morphologically related hyaenas from the Neogene of USSR). — *Naukova Dumka*, Kiev, pp. 178 (in Russian, with English summary).
- SEN, S., KOUFOS, G.D., KONDOPOULOU, D. & BONIS, L. de, 2000. Magnetostratigraphy of the late Miocene continental deposits of the lower Axios Valley, Macedonia, Greece. — [in:] KOUFOS, G.D. & IOAKIM, Ch. (eds). *Mediterranean Neogene cyclostratigraphy in marine-continental deposits*. — *Bulletin of the Geological Society of Greece*, Athens, sp. publ., 9:197–206, Athens.
- SOLOUNIAS, N., 1981. The Turolian fauna from the island of Samos, Greece. — *Contributions Vertebrate Evolution*, 6:1–232.
- SYMEONIDIS, N., 1978. Ein Schädel von *Metailurus parvulus* (HENSEL) aus Pikermi (Attica, Griechenland). — *Annales Géologiques des Pays Helleniques*, 29:698–703, Athens.
- THENIUS, E., 1951. Zur odontologischen Charakteristik von "*Felis leiodon*" aus Pikermi (Griechenland). — *Neues Jahrbuch für Geologie und Paläontologie*, 3: 88–96, Stuttgart.
- TORRE, D., 1988. *Plioviverrops faventinus* n.sp. a new carnivore of the late Messinian age. — *Bolletino della Società Paleontologia Italiana*, 28:323–327, Modena.
- WAGNER, A., 1848. Urweltliche Säugetier-Ueberreste aus Griechenland. — *Abhandlungen der Bayerischen Akademie der Wissenschaften*, 2. Kl., 5(2):155–170, München.
- WERDELIN, L., 1988. Studies of fossil hyaenas: the genera *Ibalassictis* Gervais ex Nordmann, *Palhyaena* Gervais, *Hyaenictitherium* Kretzoi, *Lycyaena* Hensel and *Palinhyena* Qiu, Huang & Guo. — *Zoological Journal of Linnean Society*, 92:211–265, London.
- WERDELIN, L. & SOLOUNIAS, N., 1991. The hyaenidae: taxonomy, systematics and evolution. — *Fossil and Strata*, 30:1–104, Oslo.
- ZDANSKY, O., 1924. Jungtertiäre Carnivoren Chinas. — *Paleontologica Sinica*, C, 2:38–45, Beijing.
- ZHANG, Z.P., GENTRY, A.W., KAAKINEN, A., LIU, L., LUNKKA, J.P., QIU, Z.D., SEN, S., SCOTT, R.S., WERDELIN, L., ZHENG, S. & FORTELIUS, M., 2002. Land mammal sequence of the late Miocene of China: new evidence from Lantian, Shanxi Province. — *Vertebrata Palasiatica*, 40(3):165–176, Beijing.

**PLATE 1**

*Parataxidea maraghana*, Mytilinii-1A (MTLA), Samos, Greece, middle Turolian (MN 12).

Fig. 1. Skull, MTLA-283; a. right lateral, b. left lateral, c. dorsal, and d. occlusal view.

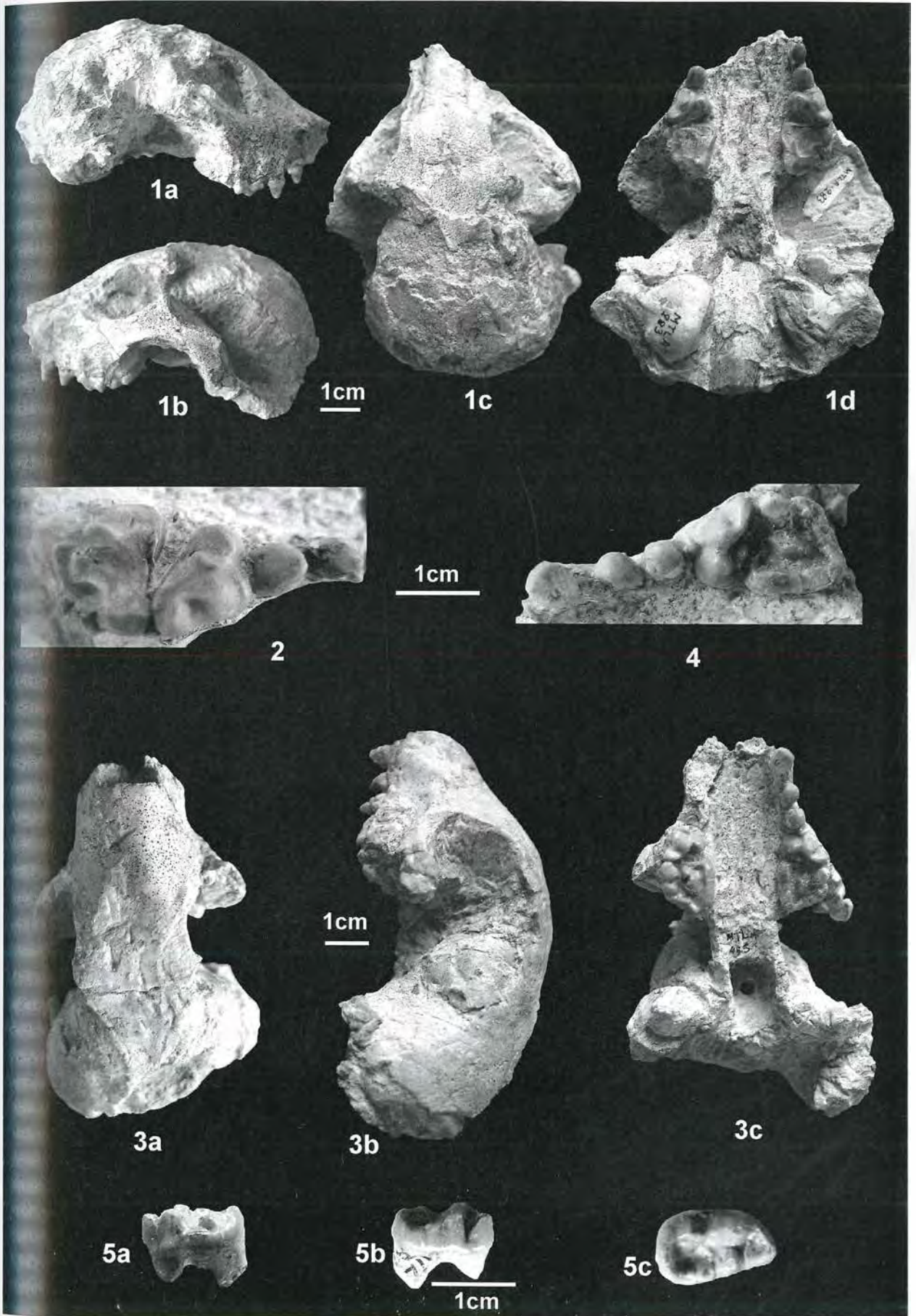
Fig. 2. Skull, MTLA-283; left tooth row, occlusal view.

Fig. 3. Skull, MTLA-465; a. dorsal, b. left lateral, and c. occlusal view.

Fig. 4. Skull, MTLA-465; left tooth row, occlusal view.

Fig. 5. Left m1, MTLA-7; a. buccal, b. lingual, and c. occlusal view.

PLATE 1



## PLATE 2

*Plioviverrops orbignyi*, Mytilinii-1B (MTLB), Samos, Greece, middle Turolian (MN 12).

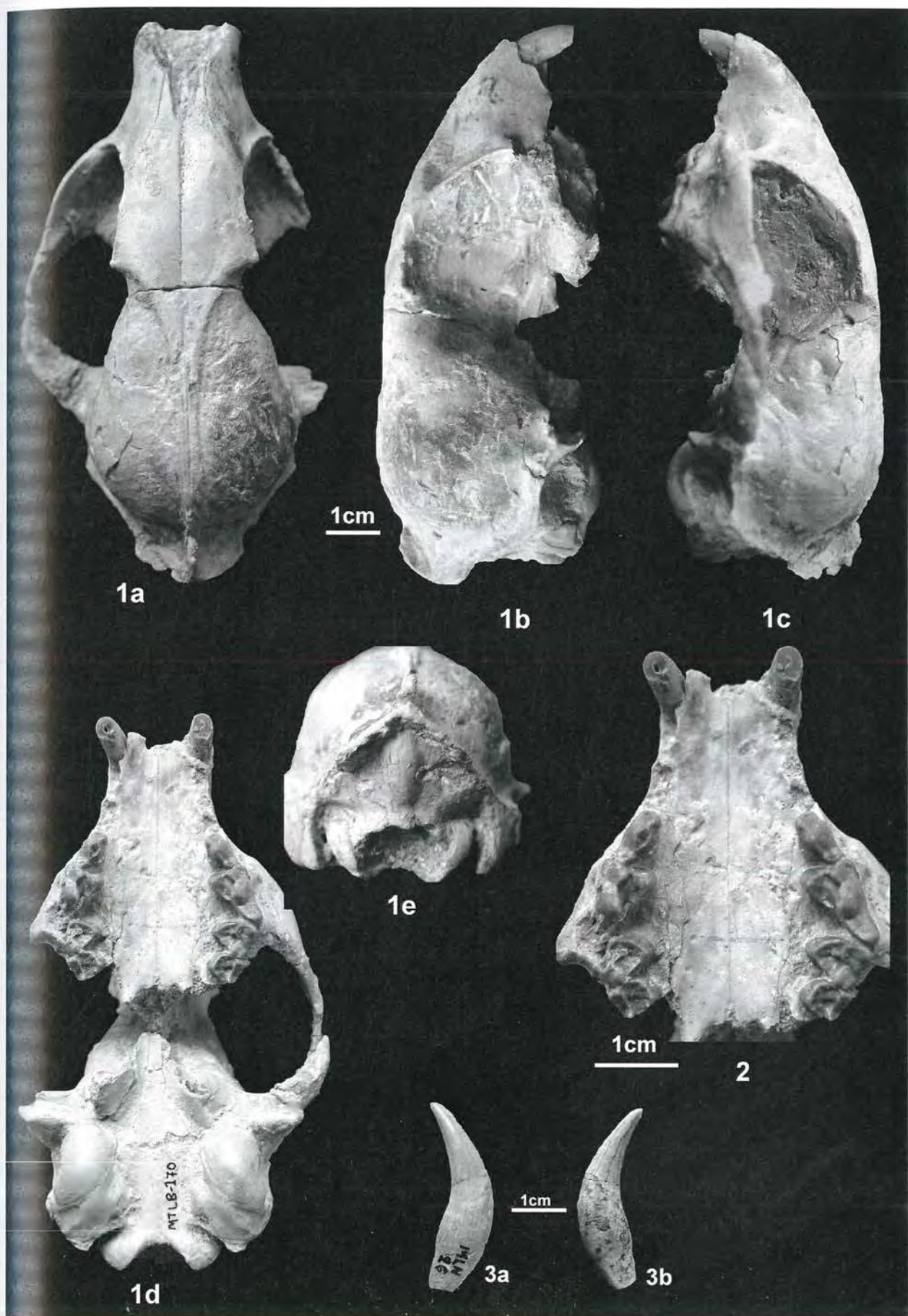
Fig. 1. Skull, MTLB-170; a. dorsal, b. right lateral, c. left lateral, d. occlusal, and e. occipital view.

Fig. 2. Skull, MTLB-170; both tooth rows, occlusal view.

*Protictitherium crassum*, Mytilinii-4 (MLN), Samos, Greece, middle Turolian (MN 12).

Fig. 3. Left lower canine, MLN-26; a. buccal, and b. lingual view.

PLATE 2



### PLATE 3

*Protictitherium crassum*, Mytilinii-4 (MLN), Samos, Greece, middle Turolian (MN 12).

Fig. 1. Left mandibular corpus of the mandible, MLN-42; a. buccal, b. lingual; and c. lateral view.

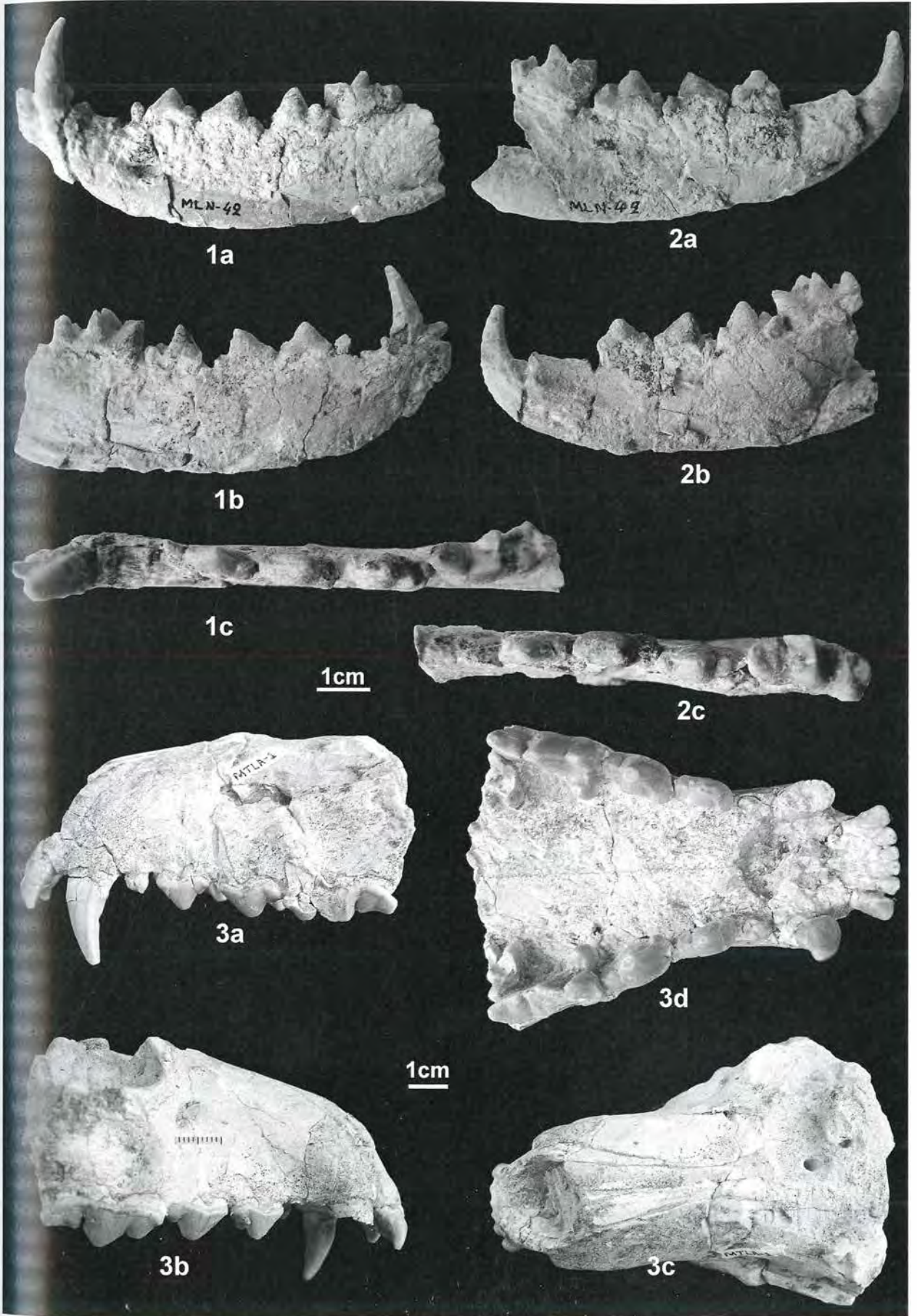
Fig. 2. Right mandibular corpus of the mandible, MLN-42; a. buccal, b. lingual; and c. lateral view.

*Hyaenictitherium wongii*, Mytilinii-1A (MTLA), Samos, Greece, middle Turolian (MN 12).

Fig. 3. Frontal part of the skull, MTLA-1; a. left lateral, b. right lateral, c. frontal, and d. occlusal view.



PLATE 3

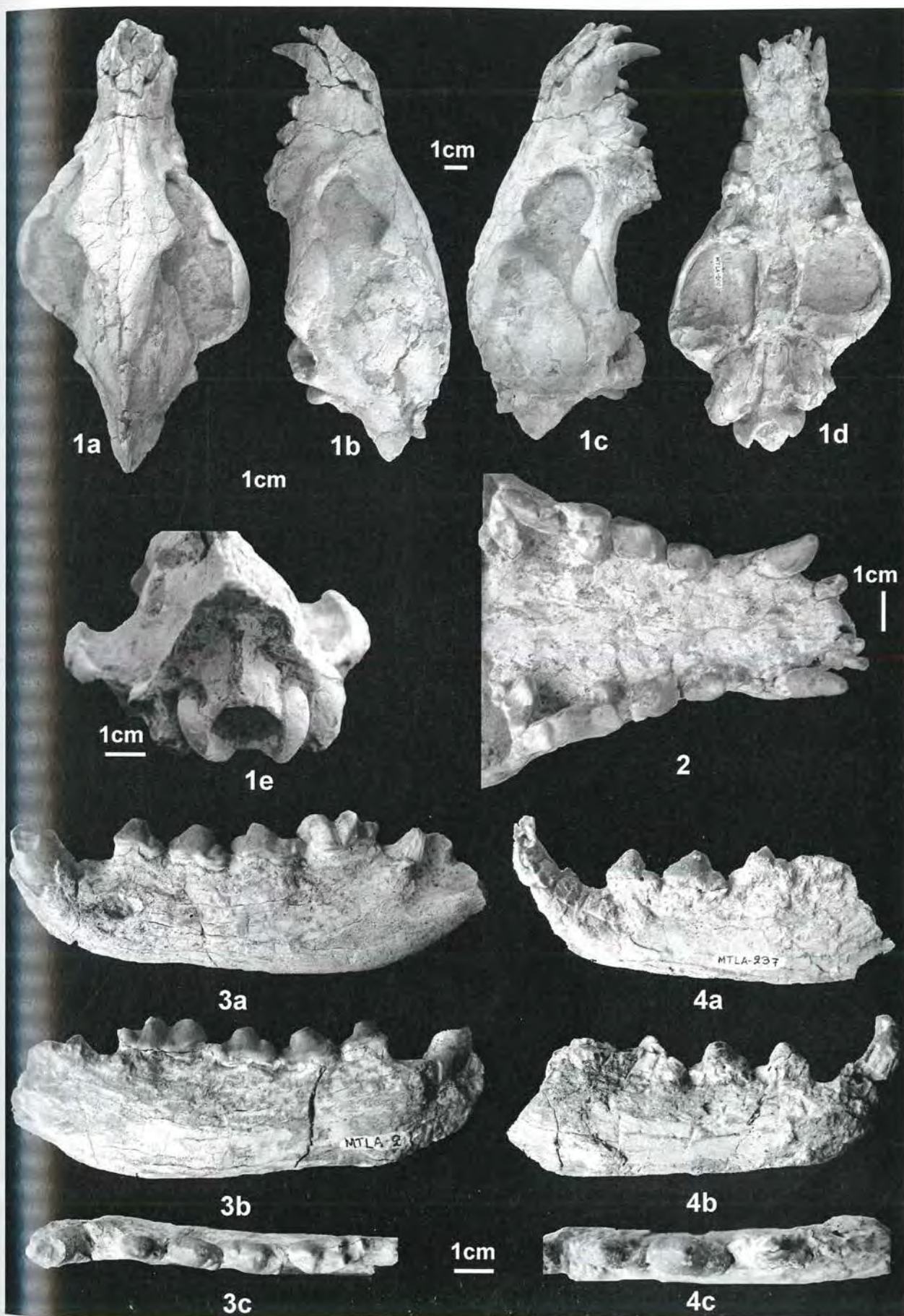


**PLATE 4**

*Hyaenictitherium wongii*, Mytilinii-1A (MTLA), Samos, Greece, middle Turolian (MN 12).

- Fig. 1. Skull, MTLA-200; a. dorsal, b. left lateral, c. right lateral, d. occlusal, and e. occipital view.
- Fig. 2. Skull, MTLA-200; both tooth rows; occlusal view.
- Fig. 3. Left mandibular fragment with c-m1, MTLA-2; a. buccal, b. lingual, and c. occlusal view.
- Fig. 4. Right mandibular fragment with c-m1, MTLA-237; a. buccal, b. lingual, and c. occlusal view.

PLATE 4

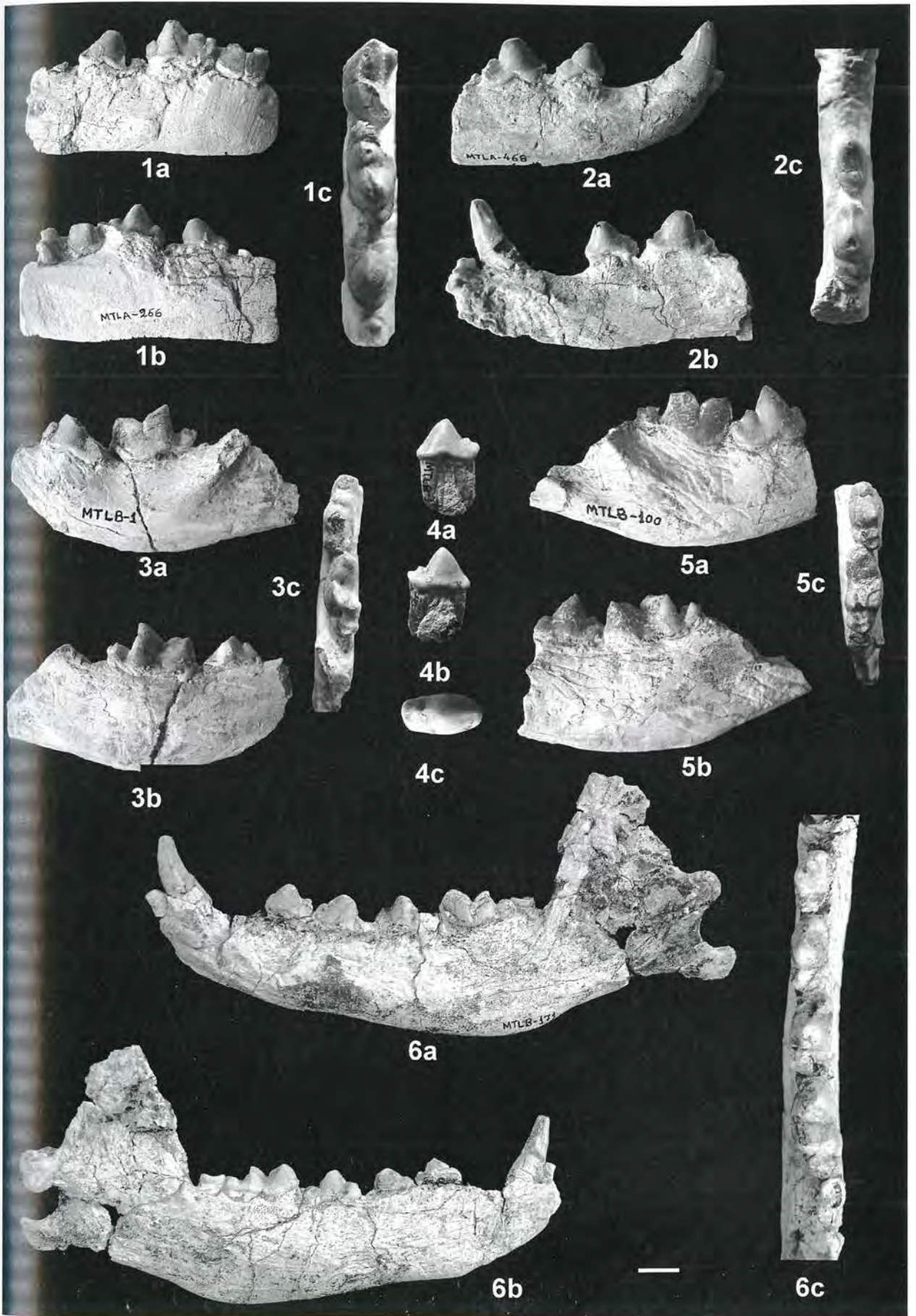


**PLATE 5**

*Hyaenictitherium wongii*, Mytilinii-1A, B, (MTLA, MTLB), Samos, Greece, middle Turolian (MN 12).

- Fig. 1. Left mandibular fragment with p3-m1, MTLA-266; a. buccal, b. lingual, and c. occlusal view.
- Fig. 2. Right mandibular fragment with i1-p3, MTLA-468; a. buccal, b. lingual, and c. occlusal view.
- Fig. 3. Left mandibular fragment with p4-m1, MTLB-1; a. buccal, b. lingual, and c. occlusal view.
- Fig. 4. Left p3 of the mandibular fragment MTLB-1; a. buccal, b. lingual, and c. occlusal view.
- Fig. 5. Right mandibular fragment with p4-m1, MTLB-100; a. buccal, b. lingual, and c. occlusal view.
- Fig. 6. Left hemimandible with i3-m2, MTLB-171; a. buccal, b. lingual, and c. occlusal view.

PLATE 5



## PLATE 6

*Hyaenictitherium wongii*, Mytilinii-1C, 4 (MTLC, MLN), Samos, Greece, middle Turolian (MN 12).

Fig. 1. Right mandibular fragment with i2-m1, MTLC-18; a. buccal, b. lingual, and c. occlusal view.

*Hyaenictitherium* cf. *wongii*, Mytilinii-1C, 4 (MTLC, MLN), Samos, Greece, middle Turolian (MN 12).

Fig. 2. Isolated left P2, MLN-27; a. buccal, b. lingual, and c. occlusal view.

*Adcrocuta eximia*, possibly Mytilinii-1 (?MTL), Samos, Greece, middle Turolian (MN 12).

Fig. 3. Frontal part of the skull with P2-M1 dex and P2-P3 sin, PMMS-70; a. right lateral, and b. occlusal view.

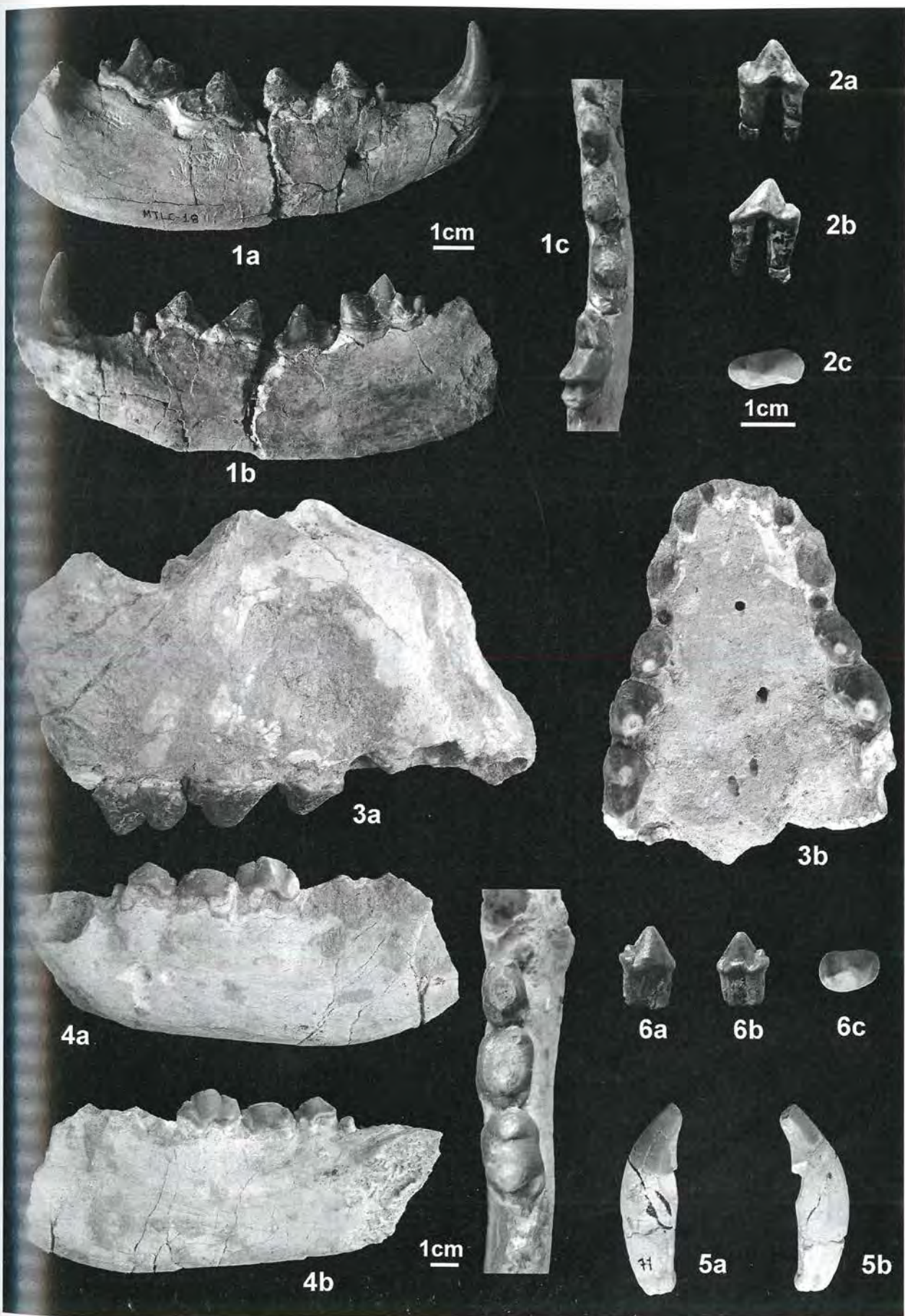
Fig. 4. Left mandibular fragment with p1-p4, PMMS-70a; a. buccal, b. lingual, and c. occlusal view.

Fig. 5. Left upper canine, PMMS-71; a. buccal, and b. lingual view.

*Adcrocuta eximia*, Mytilinii-1A (MTLA), Samos, Greece, middle Turolian (MN 12).

Fig. 6. Isolated p2 sin, MTLA-6; a. buccal, b. lingual, and c. occlusal view.

PLATE 6



**PLATE 7**

*Metailurus parvulus*, Mytilinii-1A (MTLA), Samos, Greece, middle Turolian (MN 12).

- Fig. 1. Right m1, MTLA, 290; a. buccal, b. lingual, and c. occlusal view.
- Fig. 2. Left m1, MTLA, 466; a. buccal, b. lingual, and c. occlusal view.
- Fig. 3. Skull, MTLA-234; a. dorsal, b. right lateral, and c. occlusal view.
- Fig. 4. Skull, MTLA-234; right tooth row, occlusal view.
- Fig. 5. Skull, MTLA-234; left P4; occlusal view.
- Fig. 6. Right mandibular fragment with p3, MTLA-2325; a. buccal, b. lingual, and c. occlusal view.

*Machairodus giganteus*, possibly Mytilinii-1 (?MTL), Samos, Greece, middle Turolian (MN 12).

- Fig. 7. Fragment of the upper canine, PMMS-69; a. buccal, and b. lingual view.



PLATE 7

