

## Hyaenidae (Carnivora, Mammalia) from late Miocene and Pliocene of Çalta (Ankara, Turkey)

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### Abstract

The two vertebrate localities of Çalta are located about 50 km northwest of Ankara in Central Anatolia. Çalta-1 has yielded a rich early Pliocene fauna that was the subject of an exhaustive study in 1998, to which Claude Guérin contributed two articles. From this locality, Ginsburg described *Chasmaporthetes kani anatolicus* as a new subspecies. Re-examination of the initial material and new dental specimens makes it possible to review the systematic status of this hyena. In addition, a recently found fragment of maxillary, bearing the dental series C-M2, could be attributed to the smallest Hyaenidae, *Plioviverrops* cf. *orbignyi*, whose presence in Turkey is reported for the first time. Another locality, named Çalta-2, stratigraphically about 60 m below Çalta-1, has yielded some scarce mammalian fossils, including a mandible of *Adcrocuta eximia*, which is the common hyena of the Turolian Stage all over Eurasia. Mammals from these two fossiliferous horizons indicate that the sedimentary series around Çalta village encompass the late Miocene-Pliocene transition.

### Keywords

Hyaenidae, Carnivora, late Miocene, Pliocene, systematics, Turkey.

### Résumé

**Hyaenidae (Carnivora, Mammalia) du Miocène supérieur et du Pliocène de Çalta (Ankara, Turquie).**- Deux gisements de vertébrés de Çalta sont situés à environ 50 km au NW d'Ankara en Anatolie centrale. Çalta-1 a livré une riche faune datée du Pliocène inférieur. Sa faune de vertébrés a fait l'objet d'une étude exhaustive en 1998, à laquelle Claude Guérin a contribué avec deux articles. De ce gisement, Ginsburg a décrit *Chasmaporthetes kani anatolicus* comme une nouvelle sous-espèce. L'étude du matériel initial et des nouveaux spécimens dentaires permet de reconsidérer la systématique de cette sous-espèce. En outre, un fragment maxillaire récemment découvert dans ce gisement, portant la série dentaire C-M2, est attribué à un petit Hyaenidae, *Plioviverrops* cf. *orbignyi*, dont la présence est signalée pour la première fois en Turquie. Un niveau inférieur à celui de Çalta-1 a livré entre autres restes de mammifères une mandibule de *Adcrocuta eximia* qui est une hyène commune du Turolien dans toute l'Eurasie. Les mammifères de ces deux horizons fossilifères indiquent que la série sédimentaire autour du village de Çalta inclut la transition Miocène supérieur - Pliocène.

### Mots-clés

Hyaenidae, Carnivora, Miocène supérieur, Pliocène, systématique, Turquie.

## 1. INTRODUCTION

Hyaenids are the main predators of Neogene mammalian faunas in southeastern Europe and western Asia. Their remains are generally more abundant in Neogene mammal localities than those of other carnivores. Their relative abundance, their dispersal over large areas and their role in the regulation of mammalian communities make this group an important component of Neogene mamma-

lian faunas. In addition, they are considered as having great stratigraphic interest for dating mammal localities. In Turkey, a large number of Neogene localities have yielded hyaenid fossils. They were studied in particular by Senyürek (1954, 1958, 1960), Ozansoy (1961, 1965), Schütt (1971), Schmidt-Kittler (1976), De Bonis (1994a, 2004, 2005), Ginsburg (1998), Viranta & Werdelin (2003) and Mayda *et al.* (2015).

Two localities in the vicinity of Çalta village (department

of Ankara, Central Anatolia, Turkey) have yielded some jaws and teeth belonging to three genera of Hyaenidae. From the Pliocene locality of Çalta-1, Ginsburg (1998) referred the remains of a large hyaenid to *Chasmaporthetes kani anatolicus* n. subsp. As shown below, the systematic status of this hyena needs to be reconsidered. The specimens referred below to the genera *Plioviverrops* and *Adcrocuta* are new and unpublished. To the southwest of Çalta village (department of Ankara), there are two different horizons with vertebrate fossils: Çalta-1 and Çalta-2. These localities belong to the Sinap Formation, which covers large areas between the towns of Ayas, Kizilcahamam and Kazan to the

northwest of Ankara department (Fig. 1). The Sinap Formation is mainly formed of fluvio-lacustrine deposits. It unconformably overlies the volcanic rocks of the Galatean Volcanic Complex and/or the mainly lacustrine and volcanoclastic deposits of the Pazar Formation, which is dated as early-middle Miocene thanks to some mammal localities (Inönü Loc 24 and 24A), lava flow intercalations and magnetostratigraphy (Lunkka *et al.*, 2003; Kappelman *et al.*, 2003). All these sedimentary units are deposited in the Kazan Basin (Toori, 2005; Sen *et al.*, 2017), which was previously interpreted as the northeastern part of the large Bey pazari Basin (Inci *et al.*, 1986).

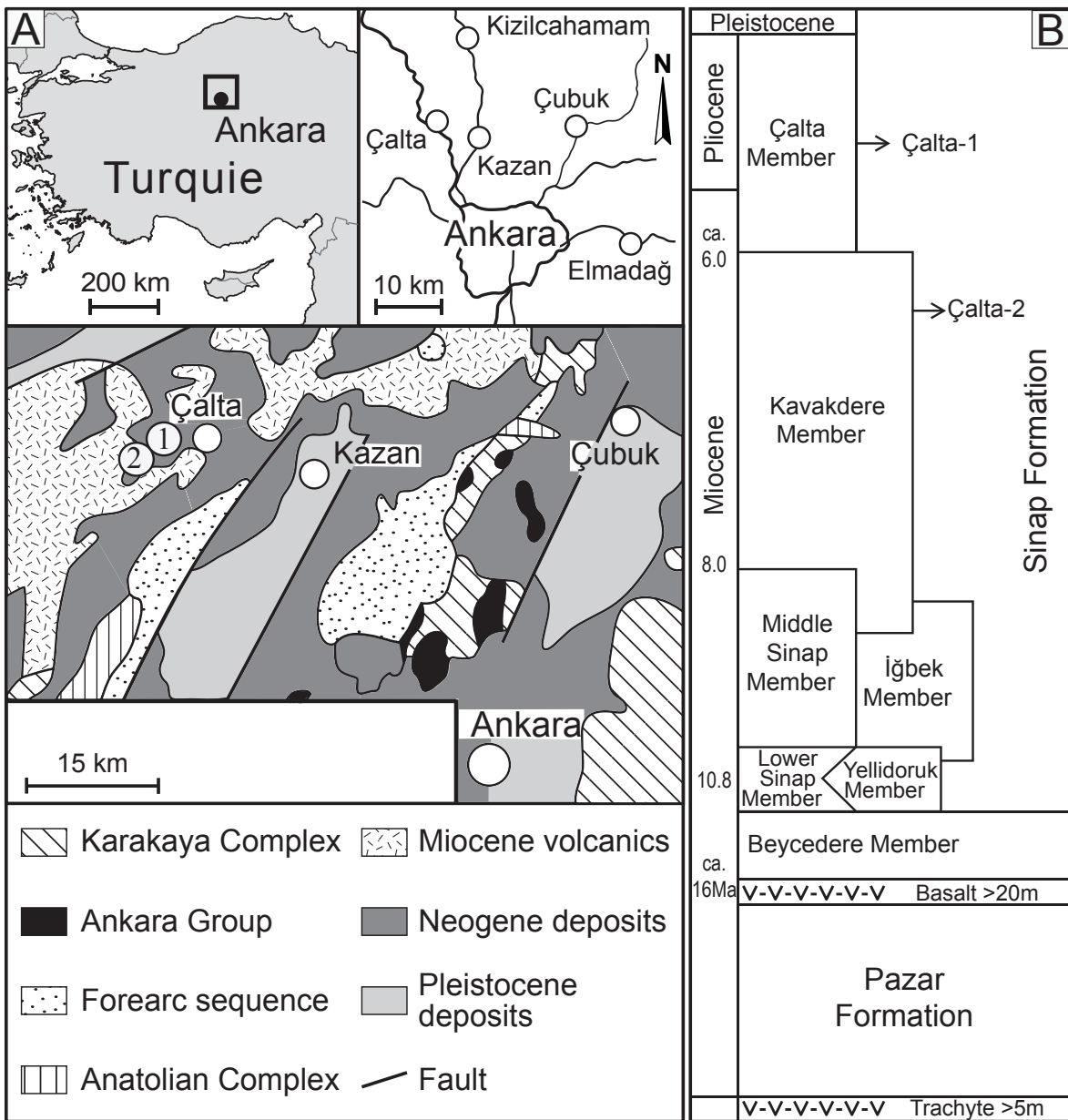


Fig. 1: A, Simplified geologic map of the Kazan-Çalta area (modified from Lunkka *et al.*, 1998); B, stratigraphy of the Sinap Formation as established by Lunkka *et al.* (2003), on which the stratigraphic positions of the localities Çalta-1 and Çalta-2 are indicated.

The Sinap Formation covers large areas in the Kazan Basin (Fig. 1). Lunkka *et al.* (1998, 2003) distinguished five members: from the oldest to the youngest, the Beycedere, Lower Sinap, Middle Sinap, Kavakdere and Çalta members. In the surroundings of Çalta village, the Kavakdere and Çalta members are superposed with a tectonic contact in between, making the Kavakdere Member faulted and folded, while the overlying Çalta Member displays a rather horizontal stratification.

The locality of Çalta-1 is in the Çalta Member while the locality Çalta-2 is in the upper part of the Kavakdere Member, the two members being separated in the Çalta area by an angular unconformity.

The more famous of these localities is Çalta-1, which has yielded a rich and diverse small and large mammalian assemblage (Sen, 1998a). It is situated at some 780 m SW of the mosque of Çalta village, upstream of the ravine of Koca Dere. Its geographic coordinates are 40° 14' 28.5" N and 32° 32' 04.6" E. Its vertebrate fauna clearly indicates an early Pliocene age.

The locality of Çalta-2 is on the other side of the valley of Fındık Dere stream, some 1.4 km west of the mosque of Çalta village, on the slopes of Beşpınar Sırtı (Lunkka *et al.*, 1998). Its geographic coordinates are 40° 14' 10.0" N and 32° 32' 44.4" E. At this locality, a hard sandstone horizon contains scarce bone fragments that are identified as belonging to *Adcrocuta eximia* (see below) and *Chilotherium habereri*. Its age is estimated as Turolian (Saraç, 2003).

Sen (1998a, b, 2003) presented a detailed history of excavations at Çalta and a synthesis of its fauna and environment. The whole fauna from Çalta-1 was the subject to a monograph (Sen, 1998a). Its mammalian assemblage is rather diversified with four species of insectivores (*Asoriculus gibberodon* [Petenyi, 1864], *Maftia csarnotense* Reumer, 1984, Soricidae indet., *Erinaceus* sp.), one ochotonid (*Ochotonoma anatolica* Sen, 1998), nine rodents (*Centralomys magnus* [Sen, 1977], *Occitanomys* sp., *Orientalomys galaticus* [Sen, 1975], *Apodemus dominans* Kretzoi, 1959, *Mesocricetus* cf. *primitivus* de Bruijn, Dawson & Mein, 1970, *Pseudomeriones tchaltaensis* Sen, 1977, *Mimomys davakosi* van de Weerd, 1979, *Pliospalax macoveii* [Simionescu, 1930], *Dryomimus eliomyoides* Kretzoi, 1959), six carnivores (*Vulpes galaticus* Ginsburg, 1998, *Nyctereutes donnezani* [Depéret, 1890], *Plioviverrops* cf. *orbigny* [Gaudry & Lartet, 1854], *Chasmaporthetes kani anatolicus* Ginsburg, 1998, *Lynx issiodorensis* [Croizet & Jobert, 1828], *Machairodus giganteus* [Wagner, 1848]), one rhinocerotid (*Dicerorhinus megarhinus* [de Christol, 1834]), two hipparionines (*Plesiohipparion* cf. *longipes* [Gromova, 1952], *Proboscidipparion heintzi* [Eisenmann & Sondaar, 1998]), one suid (*Sus arvernensis minor* Depéret, 1890), one cervid (*Cervus* cf. *perrieri* Croizet & Jobert, 1828), one giraffid (*G.* cf. *jumae* Leakey, 1965) and five species of bovids (*Gazella emilii* Bouvrain, 1998, *Tchaltacerus longicornis* Bouvrain, 1998, Bovidae

indet. cf. *Koufotragus bailloudi* [Arambourg & Piveteau, 1929], *Gazellospira* sp., Hippotragini indet.) (Bouvrain, 1998; Eisenmann & Sondaar, 1998; Geraads, 1998; Ginsburg, 1998; Guérin & Sen, 1998; Guérin *et al.*, 1998; Bernor & Sen, 2017). It is mainly composed of elements with European and Asiatic affinities. The age of the fauna is deduced from the stage of evolution of key taxa, and correlated to the mammalian biozone MN15 early Pliocene), with an absolute age of *ca.* 4 Ma. The fauna is dominated by animals adapted to relatively dry and open environments with loose soil and mainly seasonal water spots. The presence of short-limbed herbivores and abundance of ochotonids might indicate a landscape with some relief (Sen *et al.*, 1998).

Ginsburg (1998) identified five species of carnivores: *Vulpes galaticus*, *Nyctereutes donnezani*, *Lynx issiodorensis*, *Machairodus giganteus* and *Chasmaporthetes kani anatolicus*. The present study adds another hyaenid, *Plioviverrops* cf. *orbigny*. Concerning the locality Çalta-2, nothing exists in the literature except its mention in Saraç (2003). The aim of the present contribution is to provide up to date knowledge of the hyaenids from both localities.

## 2. MATERIAL AND METHODS

The specimens described by Ginsburg (1998) as *Chasmaporthetes kani anatolicus* are stored in the collections of the Natural History Museum in Paris, the remaining fossils at the MTA Natural History Museum in Ankara. Lower case letters are used for the abbreviation of lower teeth (p, m), upper case letters for upper teeth (P, M). The dental terminology follows Werdelin and Solounias (1991). In the descriptions and comparisons, we used the terms anterior/mesial, posterior/distal, interior/lingual and exterior/labial without particular difference. Measurements were taken with digital calipers and are given in the text and in the tables in millimeters to the nearest 0.1 mm. For teeth they indicate the maximum length and width. Institutional abbreviations are MNHN (Muséum National d'Histoire Naturelle, Paris) and MTA (General Directorate of Mineral Research and Exploration, Natural History Museum, Ankara).

## 3. SYSTEMATIC STUDY

Order Carnivora Bowdich, 1821  
Family Hyaenidae Gray, 1821  
Subfamily Ictitheriinae Trouessart, 1897  
Genus *Plioviverrops* Kretzoi, 1938

### *Plioviverrops* cf. *orbigny* (Gaudry & Lartet, 1854)

Fig. 2

**Material from Çalta-1:** Left maxilla bearing the canine, P1, P3-M2 (MTA-ÇA-111).

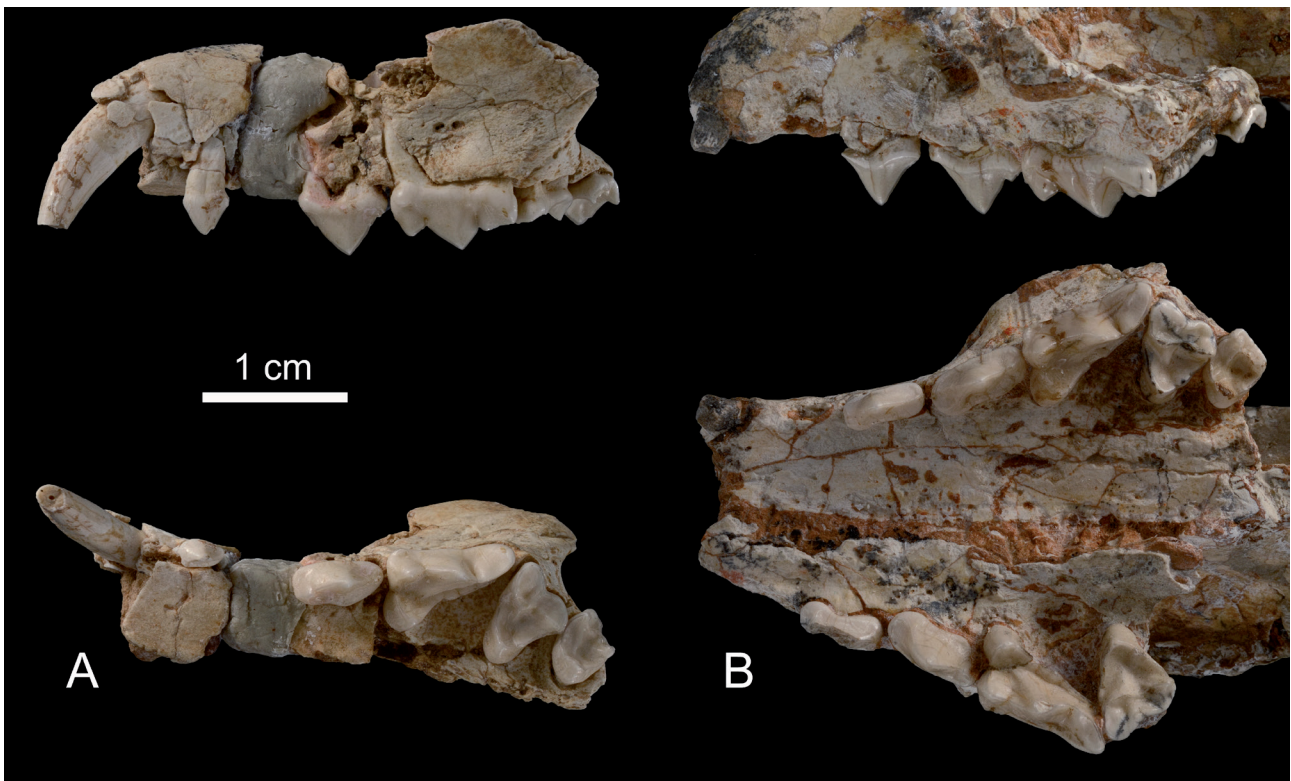


Fig. 2: A, Left maxillary fragment (MTA-ÇA-111) with canine, P1, P3-M2 of *Plioviverrops* cf. *orbigny* from Çalta-1. B, the anterior part of a skull (MNHN-PIK-3032) of *P. orbigny* from Pikermi, Greece, in labial (upper) and occlusal (lower) views.

**Measurements:** See Table 1.

**Description:** The maxillary bone is quite fractured and damaged. On the labial side it has a deep depression above the P4. The depression houses two small foramina. The notch between the anterior root of the zygomatic arc and the alveoli-bearing bone is over the distal part of M1. The suture between the maxillary and malar bones is almost horizontal but undulating. The infraorbital foramen is situated above the anterior root of P3.

The upper dentition is well preserved, except for the broken tip of the canine, and the missing P2. In lateral view, the canine has an oblique orientation (an angle of about  $120^\circ$  with the alveolar line, as opposed to about  $90^\circ$  in extant *Viverra*). It is slightly flattened lingually and bears mesiolingual and distal ridges. The P1 is separated from the canine by a 3 mm long diastema. This tooth is single rooted, but the root is flattened laterally and has a tiny vertical groove on its labial side. The occlusal outline is rather ellipsoid, being wider mesially than distally. The strong main cusp has an anterior ridge running from the apex to the anterolingual edge and a sharp distal ridge that twists distolabially. The P2 is missing. The P3 has an ellipsoid occlusal outline that tapers distally. The main cusp is sharp; the accessory cusps are present but barely distinguishable as a mesiolingual and a distal salience. The lingual cingulum is projected lingually in the posterior half of the tooth. At the base of the crown, the

enamel thickening forms a belt that is prominent along the mesial and distal margins. On the P4, the four cusps are well developed and distinct: the protocone protrudes mesially beyond the parastyle and its ridge is crescent shaped; the parastyle is large, in line with the paracone, and connected lingually to the protocone; its labial face bears an accessory cuspsule; the paracone blade is longer than the metacone blade; a thick lingual cingulum runs from the protocone to the base of the metacone, and bears several cuspsules. The lingual margin is not rectilinear but forms an open angle.

The angle between the labial line of P3-P4 and that of the molars (M1-M2) is  $125^\circ$ . The M1 has a triangular occlusal outline. The protocone is strong; its anterior ridge (preprotocrista) reaches the base of the paracone mesially; its posterior ridge (postprotocrista) is interrupted by a furrow close to the tip of the protocone, and beyond this furrow the posterior ridge is thickened to form a kind of hypocone. This ridge reaches the base of the metacone distally. The paracone and metacone are displaced lingually so that a large shelf exists between these cusps and the labial margin of the tooth. The preparacrista is directed mesially and then labially. Together with the labial cingulum it forms an enamel thickening that surrounds the shelf area. The postmetacrista joins this belt distally. An extra free ridge issues from the paracone and is directed toward the protocone without reaching it.

Table 1: Measurements in millimeters of upper and lower dentitions in three species of Hyaenidae from the localities of Çalta-1 and Çalta-2. L = length, W = width, Lbl = length of the blade in m1.

		<i>Plioviverrops cf. orbigny</i>	<i>Chasmaporthetes lunensis anatolicus</i>		<i>Adcrocuta eximia</i>
		Çalta-1	Çalta-1		Çalta-2
		Left	Left	Right	Left
C	L	4,3			
	W	2,8			
P1	L	3,2			
	W	2,3			
P2	L				
	W				
P3	L	6,4	23.6		
	W	3.3	14.7		
P4	L	9.1		32.4	
	W	5.8	19.0	18.2	
M1	L	5.6	5.2		
	W	7.4	17.0		
M2	L	4.2			
	W	5.5			
i3	L		5.7		
	W		5.9		
p1	L				5.2
	W				5.0
p2	L		16.7		15.6
	W		9.6		10.2
p3	L		20.1	20.2	18.0
	W		10.3	10.4	13.7
p4	L		23.8	23.7	21.5
	W		11.1	11.0	12.6
m1	L		24.7	24.2	27.1
	W		10.5	10.6	12.9
	Lbl		20.4	20.3	22.0

The central fossette between the cusps is deep and partly divided by this paracone spur. There is a tiny cingulum at the mesolingual margin of the protocone.

The M2 has a rather rounded occlusal outline, however its labial margin is rectilinear. The protocone, paracone and metacone are well defined, although the latter reduced. The ridges are as on the M1, but shorter. The same break on the postprotocrista, the same enamel thickening in the place of a hypocone and the same paracone spur are observed. A tiny basal cingulum is seen on the mesiolingual face of the protocone. The P3, P4, M1 and M2 have each three roots.

**Comparison:** As nothing is known of the Pliocene viverroid carnivores in Turkey, and taking into account the small size and primitive dentition (four premolars P1-P4 and two molars M1-M2) of this maxillary fragment from Çalta-1, we compared it first with the Herpestidae and Viverridae. Members of both families have similar numbers of premolars and molars, although in Herpestidae the first premolars are often lost and the second molars very reduced. These groups have P4 with a protocone that is more or less projected anteriorly, and with a small parastyle, which is generally a cusplike if it is not lacking. The Çalta specimen has a strong parastyle on the P4.

The presence and the size of the parastyle are used, at least since Depéret (1890), as distinctive features of the viverroid Hyaenidae to separate them from the Viverridae (inclusive of the Herpestidae at that time), which lack a parastyle on the P4 or have a small parastyle, while the Hyaenidae always have a large parastyle in front of the paracone. In addition, the Herpestidae commonly have a lingual root on P3 (lacking on the P3 from Çalta-1) and both families have M1 and M2 shorter and wider, and the paracone spur lacks while this spur is prominent in *Plioviverrops*.

In detailed comparison, *Viverra zibetha* (Linnæus, 1758) (India, Recent), *V. leakeyi* Petter, 1963 (East and North Africa, Pliocene) and *V. pepraxi* Depéret, 1890 (Pliocene, France) have P4 that are different from the Çalta specimen in having a small parastyle, a paracone that is strongly inclined backward, and a less protruding protocone.

In *Viverricula indica* (Horsfield, 1823) (India, Recent) the same differences are observed, except that in this species the protocone of P4 is strongly projected anteriorly, and the paracone is very inclined backward. Other Viverridae such as *Civettictis civetta* (Schreber, 1776) (East Africa, Recent) and *C. howelli* Morales, Pickford & Soria, 2005 (Kenya, Pliocene) have a squat P4, with a minute parastyle on the mesiolabial corner, and the paracone is a thick cusp. *Genetta genetta* (Linnæus, 1758) is a species similar in size to the small carnivore of Çalta. It differs in having almost vertical upper canines, a kind of lingual hump on the P3, a small parastyle, an elongated but low metacone on the P4; its M1 and M2 are short and wide, and very asymmetric in occlusal outline, and on the M1 the labial cusps are displaced much more lingually than on the Çalta specimen, and consequently the labial shelf is large. For all these reasons, the specimen MTA-ÇA-111 cannot be included in any genus of the families Herpestidae and Viverridae.

The dental formula, as well as the pattern of cheek teeth on the Çalta specimen fit with that of the small hyaenids, and among them the closest being the genus *Plioviverrops*. Kretzoi (1938) erected this genus to distinguish *Viverra orbigny* Gaudry & Lartet, 1856, later included by Gaudry (1862) in the genus *Ictitherium*, from the other small hyaenids.

Turner *et al.* (2008) recognized five species of the genus *Plioviverrops*: *orbigny*, *guerini*, *gervaisi*, *gaudryi* and *faventinus*. De Bonis (1994b) included a sixth and the oldest species *P. collectus* (De Bonis, 1973) from Laugnac (France, MN2) in *Plioviverrops*, but Turner *et al.* (2008) considered this attribution doubtful. *P. collectus* is only known from its type locality Laugnac. *Plioviverrops gervaisi* De Beaumont & Mein, 1972 from Vieux-Collonges (France, MN4) and *P. gaudryi* De Beaumont & Mein, 1972 from La Grive-Saint-Alban L5 (France, MN7/8) are poorly defined and based on a few specimens from their type localities. De Beaumont & Mein (1972) defined these species because of their similarities with

*P. orbigny*, and their age difference compared to the latter species, without however evidencing their morphological similarities and evolutionary relationships. *P. guerini* (Villalta & Crusafont, 1948) was initially described from Piera and Conclud (Spain, MN11-12) based on

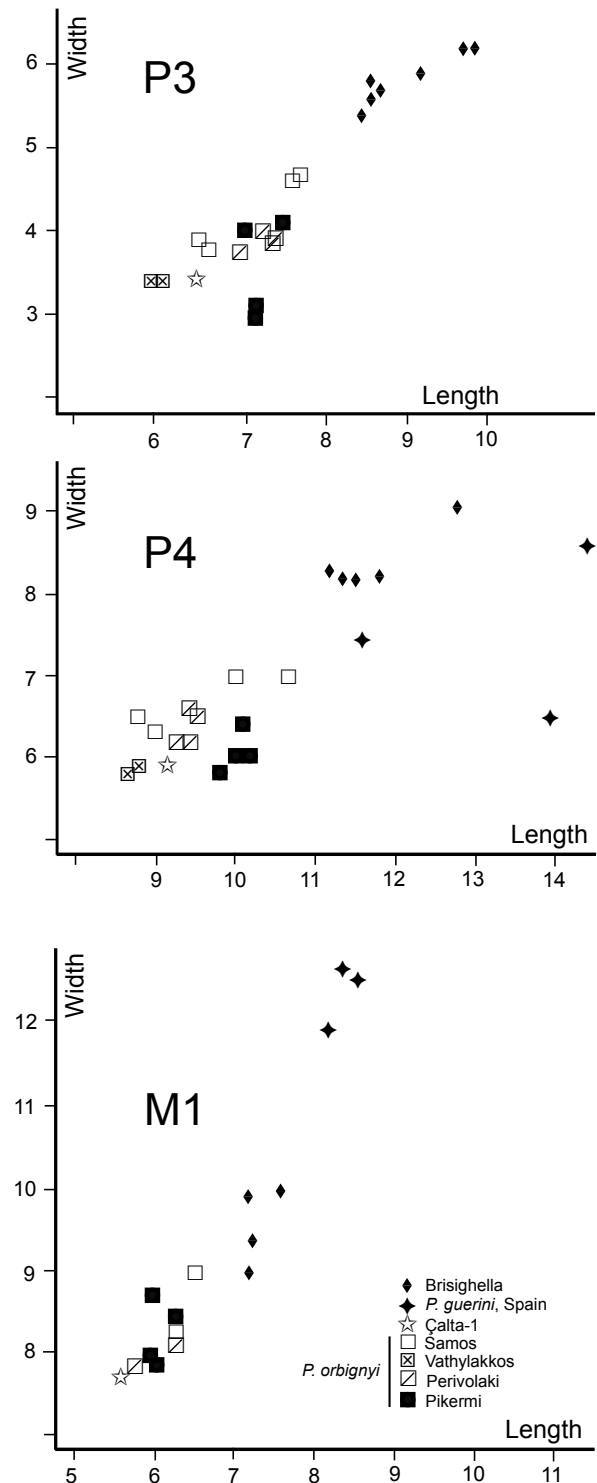


Fig. 3: Length-width dispersal diagrams of P3, P4 and M1 for diverse species of *Plioviverrops* from Europe and Çalta-1.

lower jaw fragments. Crusafont & Petter (1969) added two mandible fragments from Los Mansuetos (MN12). Outside Spain, Koufos (2000) referred to *P. cf. guerini* two mandible fragments from Vathylakkos 3 (Northern Greece, MN11). Montoya (1997) presented a complete account of the occurrence of this species in Spain and its characteristics. This is a large sized species (Fig. 3). On its m1 the trigonid has a similar pattern to that of *P. gaudryi* in having paraconid and metaconid of the same height, protoconid often higher than the metaconid, and talonid shorter but with three cusps. On the other hand, the talonid of this tooth is similar to that of *P. orbigny*, with entoconid larger than the other cusps. P4 notably wider than in *P. orbigny* and *P. faventinus*, with a slightly projecting protocone, as in *P. gervaisi*, but as strong as in *P. gaudryi*. M1 with a strong parastyle, similar in size to that of *P. gaudryi*. The specimen from Çalta-1 cannot be referred to this species, at least because of its elongated P4, in addition to its smaller size.

Torre (1989) added *P. faventinus* from the late Messinian Brisighella quarry in northern Italy. This is also a large sized species having some derived features in its dentition, such as “m1 with a developed entoconid, which tends to be as large as the metaconid, with a relatively low protoconid, which does not surpass the other conids in height; p4 with a strong anterior accessory cusp: p3 with a clear but small talonid and a feeble but distinct anterior accessory cusp; P3 and P2 with a marked accessory cusp in the strong, more or less notched, lingual cingulum; the mandible is strong and the masseteric fossa deep; a posterior mental foramen is sometimes present, but whenever present its size is highly variable” (Torre, 1989, p. 324).

As seen in Table 1 and Figure 3, the size of teeth on the Çalta specimen are in the range of *Plioviverrops orbigny* from Pikermi, Samos and Macedonian localities, or a little smaller. All these localities are in Greece and correlated to the Turolian. However, direct comparison with the type material of this species from Pikermi (Fig. 2B) in the MNHN collections shows that the Çalta specimen is somewhat different in morphology: its P3 has a tiny anterior accessory cusp (absent at Pikermi), P4 with angular lingual margin (rectilinear at Pikermi), M1 constricted at its middle by a distal depression (no distal depression at Pikermi) and M2 with reduced metacone (less reduced at Pikermi). These differences and also the lack of additional specimen to complete the knowledge on the dental and cranial features of the Çalta small hyaenid, we preferred to identify it as *P. cf. orbigny*. This species is only known in Turolian localities of Greece. The occurrence of a small icitheriine in the early Pliocene (MN15) locality of Çalta, similar in size and the characters of upper dentition to *Plioviverrops orbigny* from late Miocene (MN11-13) of Greece is difficult to explain. We have also considered that the above-mentioned morphological differences between *P. orbigny* and the Çalta specimen could express a

species difference and that the Çalta specimen will in fact belong to a new species. However, this can only be demonstrated with more and better preserved specimens, hence its provisional identification as *P. cf. orbigny*.

Subfamily Hyaeninae Gray, 1821  
Genus *Chasmaporthetes* Hay, 1921

***Chasmaporthetes lunensis anatolicus* Ginsburg, 1998**  
Figs 4, 5

**Material from Çalta:** Left P3 (ACA-913); fragment of left P4 (ACA-354); right P4 (MTA-CAL-1); left M1 (ACA-355); left i3 (ACA-914); left mandible (ACA-303) with canine in the bone, p2, p3 and p4; fragment of a right juvenile lower canine (MTA-CAL-2); right p3 (MTA-CAL-3); right p4 (MTA-CAL-4); left m1 (ACA-304); right m1 (MTA-CAL-5). All this material seems to belong to the same individual.

**Measurements:** See Table 1.

**Emended diagnosis:** P3 and lower premolars have crowns slightly lower than those of the specimens referred to *C. kani* from China and to *C. lunensis* from late Pliocene and early Pleistocene localities in Europe. P4 with a well individualized protocone that is aligned anteriorly with the parastyle. p2 without anterior accessory cusp. m1 slightly longer than p4.

**Remark:** Ginsburg (1998) studied the fossils housed in the collections of the Paris Museum (specimens numbered ACA), but not those of the MTA Museum in Ankara, unavailable at that time. He referred these remains to *Chasmaporthetes kani anatolicus* n. subsp. In his study, Ginsburg compared this hyena with *C. kani kani* Galiano & Frailey, 1977 and *C. kani progressus* Qiu, 1987, both from the Plio-Pleistocene of China, and with *Euryboas bielawskiyi* Schaub, 1941, from the late Pliocene of Perrier, France. He did not compare this Çalta hyaenid with other *Chasmaporthetes* species known at that time. He found that the Çalta hyena differs from *Euryboas bielawskiyi* in having P3 lower crowned and with a more elongated distal part, and P4 with a notch between the protocone and parastyle (this notch is lacking in *E. bielawskiyi*). In comparison with *C. kani kani* and *C. kani progressus*, he observed the following differences: on the Çalta hyaenid, the P3 has lower protocone and more enlarged lingual edge, the lower premolars are lower crowned, with smaller mesial accessory cusps and more developed distal cingulum, and the m1's talonid has entoconid and hypoconulid stronger.

Kurtén & Werdelin (1988) suggested synonymy of *C. kani* with *C. lunensis*. According to Sotnikova (1994), *C. kani* should be maintained as a subspecies of *C. lunensis* (Del Campana, 1914). More recently, in their systematic review of the European Hyaenidae, Turner *et al.* (2008) listed Çalta-1 among the localities where *C. lunensis* occurs, and they thus implicitly referred the Çalta hyena to *C. lunensis*. It appears therefore that the

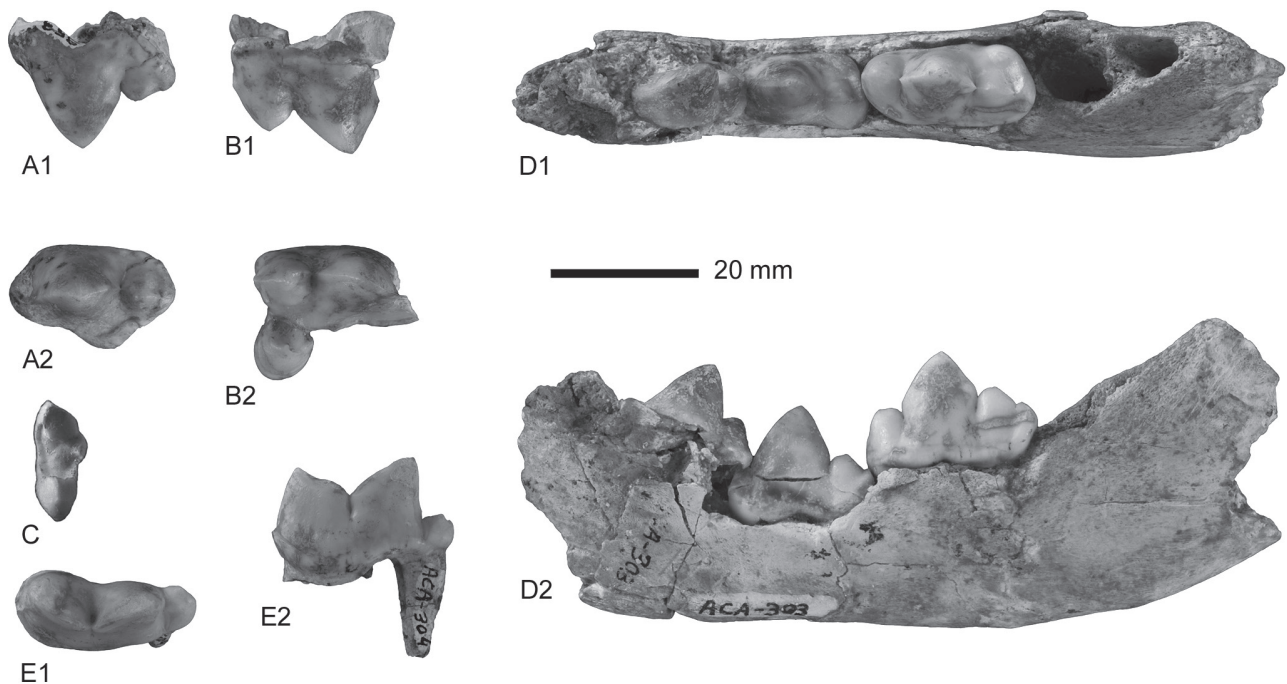


Fig. 4: *Chasmaporthetes lunensis anatolicus* from Çalta-1, Turkey. A, left P3 (ACA-913) in labial and occlusal views; B, fragment of left P4 (ACA-354) in labial and occlusal views; C, left M1 (ACA-355) in occlusal view; D, fragment of left mandible bearing p2-p4 in occlusal and lateral views; E, left m1 (ACA-304) in occlusal and lateral views. Scale bar 20 mm.

systematic assignment of the Çalta hunting hyena should be reconsidered.

**Description:** Ginsburg (1998) described this Çalta hyaenid in some detail. Here, the main characters of the mandible and dentition are emphasized. As noted above, all this material apparently belongs to one individual. The teeth are unworn, except the m1 which is slightly worn on its blade. The P3 lacks the mesial accessory cusp, but the mesial ridge of the main cusp thickens downward to form a cuspule at the mesiolingual margin. The distal accessory cusp is strong and surrounded by a thick cingulum, which continues inward. This tooth is broadened mesiolingually (mesiolingual bulging); the roots are broken, so it cannot be observed if a lingual root existed. The P4 has a gracile outline. The protocone is strong, and it does not protrude compared to the parastyle. A marked mesial notch separates the protocone from the parastyle. The metacone is twisted labially to form an angle with the parastyle-paracone line; it forms a long blade that represents 36% of the total length. The cingulum issued from the distal ridge of the protocone runs along the lingual margin.

The mandible has rather flat ventral margin below the p2-p4, whereas it swells distally below m1. The position of the foramen mentale cannot be observed. The lingual face of the lower canine is flat while the labial face is well rounded; both face are separated by an anterolingual ridge. The i3 is caniniform with an asymmetric crown that bears a sharp main cusp and a distinct secondary

distal cusp. The crown widens lingually. The state of preservation of the mandible does not make it possible to confirm the presence of a p1. The p2 lacks the mesial accessory cusp, but has a slight thickening of the anterior ridge. The p3 has a small mesial accessory cusp, while on the p4 the mesial accessory cusp is as strong as the distal accessory cusp. The size of the distal accessory cusp and distal cingular margin increases from p2 to p4. The m1 is a little longer but narrower than the p4. There is no metaconid, but in its place the enamel is wrinkled and thickened. The talonid, although reduced, bears a prominent hypoconid, a small entoconid on the lingual side, and a tiny hypoconulid near the distal margin.

**Comparison:** Galiano & Frailey (1977), Qiu (1987), Kurtén & Werdelin (1988), Sotnikova (1994), De Bonis & Koufos (1994), Koufos (2000), Antón *et al.* (2006), De Bonis *et al.* (2007) and Turner *et al.* (2008) presented detailed historical reviews and morphological and biometric comparisons to enlighten the systematics of hunting hyenas. The general agreement is that the large sized hunting hyenas, previously referred to the genera *Chasmaporthetes*, *Euryboas*, *Lycyaena* and *Ailuraena* are grouped in the genus *Chasmaporthetes*. This genus is characterized by a broad rostrum, a more trenchant and less crushing post-canine dentition than in the more typical scavenging hyenas, with slender limbs adapted for high speed running (Kurtén & Werdelin, 1988; Antón *et al.*, 2006). Its type species is *C. ossifragus* Hay, 1921 from the Val Verde Mine in Arizona, U.S.A. Kurtén

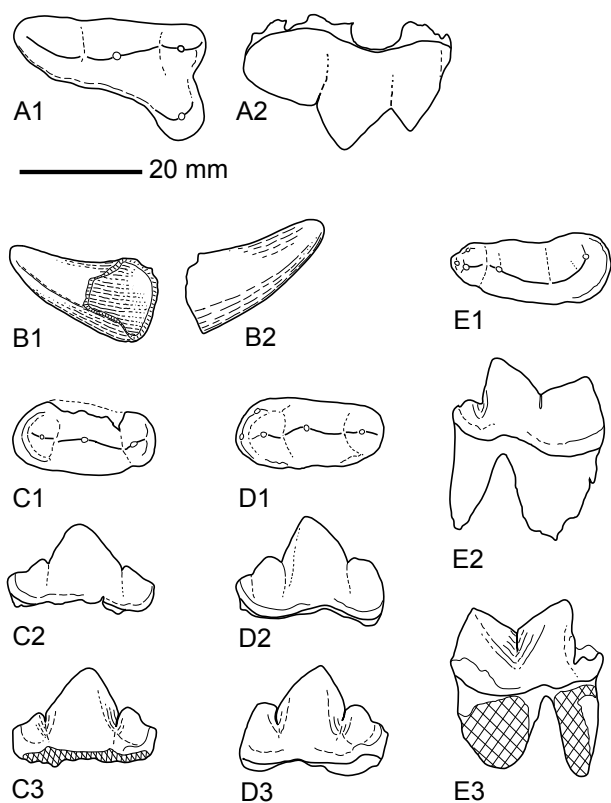


Fig. 5: *Chasmaporthetes lunensis anatolicus* from Çalta-1, Turkey. Isolated teeth in the collections of Natural History Museum of Ankara. A, right P4 (MTA-CAL-4) in occlusal and lateral views; B, fragment of right lower canine (MTA-CAL-2) in lingual and labial views; C, right p3 (MTA-CAL-3) in occlusal, lateral and lingual views; D, right p4 (MTA-CAL-4) in occlusal, lateral and lingual views; E, right m1 (MTA-CAL-5) in occlusal, lateral and lingual views. Scale bar 20 mm.

& Werdelin (1988) and later students considered the other North American species, *C. johnstoni* Stirton & Christian, 1940, a junior synonym of the type species. *Chasmaporthetes* is known in North America during the Blancan and early Irvingtonian Land Mammal Ages (=late Pliocene-early Pleistocene), in Eurasia from late Miocene to early Pleistocene and in Africa between latest Miocene and Early Pleistocene.

The systematic status of Pliocene and early Pleistocene occurrences of *Chasmaporthetes* in Eurasia has varied in time depending on the species concept of the students. For instance Kurtén & Werdelin (1988) and Werdelin & Solounias (1991) recognized two species in Europe (*C. lunensis* [Del Campana, 1914] and *C. borissiakii* [Khomenko, 1932]) and two species in Asia (*C. exitelus* Kurtén & Werdelin, 1988 and *C. lunensis*). They questioned the systematic status of *C. bonisi* Koufos, 1987 from Northern Greece (see below), and synonymized with *C. lunensis* not only some European occurrences of *Chasmaporthetes* known under various names

(*Euryboas bielawskii* Schaub, 1941; *Hyaena marini* Villalta Comella, 1952; *Euryboas lunensis*...) but also *C. kani* Galiano & Frailey, 1977 from China. Turner *et al.* (2008) followed these systematic assignments. On the contrary, Qiu (1987) strongly insisted on the distinction of *C. kani* from other species of *Chasmaporthetes*, and he recognized two subspecies in the Plio-Pleistocene of China: *C. kani kani* and *C. kani honanensis*. Rook *et al.* (2004) defined a new species, *C. malei*, endemic to the late Pliocene or early Pleistocene of Sardinia. Lastly, Tseng *et al.* (2013) reported a new species from the early Pliocene of Tibet, *C. gangsriensis*. Concerning the African continent, Werdelin & Peigné (2010) gave a revised account of the Hyaenidae and recognized three species of *Chasmaporthetes*, viz. *C. nitidula* (Ewer, 1954), *C. australis* (Hendey, 1974) and *C. darelbeidae* Geraads, 1997 for the interval of the latest Miocene-early Pleistocene.

As this short account shows, the genus *Chasmaporthetes* has a large palaeogeographic distribution, similar to that of some other late Miocene and Pliocene hyenas (*Adcrocuta*, *Pliocrocuta*...), but with a fossil record that is much less well documented, often restricted to a few specimens of fragmentary skulls or jaws and rare postcranial bones.

As noted above, Ginsburg (1998) referred the Çalta hyena to a new subspecies of *C. kani*. Galiano & Frailey (1977) defined *C. kani* on the basis of fossils from the Nihowanian (late Pliocene-early Pleistocene) localities in China. Galiano & Frailey (1977) and Qiu (1987) distinguished *C. kani* from *C. lunensis* based on some characters of the lower dentition: in *C. kani* the m1 is slightly longer than the p4, and the anterior accessory cusps of p2 and p3 are relatively weak as compared to other species of the genus. For Kurtén & Werdelin (1988), Werdelin & Solounias (1991) and Turner *et al.* (2008), these characters are shared with *C. lunensis*, and there is no room for a new species. They considered *C. kani* a junior synonym of *C. lunensis*, or at most a subspecies of it (Kurtén & Werdelin, 1988). This is reason enough to question the allocation of the Çalta hyena to a species, *C. kani*, that is not currently recognized and it forces us to reconsider its systematic status. Turner *et al.* (2008) included Çalta in the list of localities with *C. lunensis*, thus implicitly referring the Çalta hyena to this species. Among the species included in *Chasmaporthetes*, *C. malei* from Sardinia and *C. gangsriensis* from Tibet are smaller than all other species of the genus. In addition, *C. malei* has P3 and lower premolars with both anterior and posterior accessory cusps, which is a derived feature in this group. In addition to its smaller size, the dentition of *C. gangsriensis* is different from that of Çalta-1 in having lower crowned premolars, p4 notably shorter than m1, and upper carnassial with a shorter metastyle (39% of total length of P4).

The oldest representative of this genus is *C. bonisi* Koufos, 1987 from the Turolian of northern Greece.

The type mandible is from Dytiko 1 (Koufos, 1987), De Bonis & Koufos (1994) and Koufos (2000) referred to this species more material from the type locality (MN13) and Ravin des Zouaves 5 (late MN11). Werdelin & Solounias (1991) questioned the assignment of the type mandible from Dytiko 1 to the genus *Chasmaporthetes*, and suggested its synonymy with *Adcrocuta eximia* (see also Vinuesa *et al.*, 2017). On the contrary, De Bonis & Koufos (1994) and Koufos (2000) insisted on the characters shared with other species of *Chasmaporthetes*. In this species, the P3 is shorter while the P4 is longer than that of Çalta. The same difference is also observed for the lower cheek teeth: in *C. bonisi* the lower premolars p2-p4 are shorter and wider, while the m1 is larger and wider than that of Çalta. The P3 and lower premolars of *C. bonisi* have mesial and distal accessory cusps smaller, and their talonids (distal cingular part) are weak. These differences imply that *C. bonisi* probably had a mixed diet, having both flesh-eater and scavenger abilities, while the dentition of the Çalta hyena is clearly more felinoid and points out to a flesh-eater hyena.

Kurtén & Werdelin (1988) described a new species, *C. exitelus*, based on an anterior skull bearing left P3-M1 and right P4-M1, from the late Turolian of China. Its P3 is narrower and bears a strong mesial accessory cusp. Its P4 has protocone anteriorly protruding while in all other specimens referred to various species of *Chasmaporthetes*, the protocone remains mesially at the level of the parastyle or it is situated backward. In size, *C. exitelus* is closer to *C. bonisi* from northern Greece and *C. borissiaki* from Moldova, and smaller than *C. lunensis*. De Bonis & Koufos (1994: 93) noticed that “The morphology of this specimen as well as its dimensions fit very well with those of RZO 125 and DTK 238 and it must be considered as synonym of *C. bonisi*”. Khomenko (1932) reported an almost complete skeleton of a juvenile hyena from the early Pliocene locality of Dermedzhi in Moldova. Kurtén & Werdelin (1988) referred the Moldavian species to as *C. borissiaki*. The ontogenetic age of this individual is apparently similar to that of the Çalta hyena. However, this species is different in having cheek teeth smaller than that of Çalta, as well as smaller than the specimens referred to *C. lunensis* and “*C. kani*”. Its P2 and P3 lack the mesial accessory cusp, and their crown is notably higher. Another strong difference between *C. borissiaki* and the Çalta hyaenid is that the former has P4 with a protocone smaller, not detached from the body of the tooth, and it lacks the anterior notch to separate the protocone and parastyle.

Kurtén & Werdelin referred to *C. borissiaki* a fragment of left maxillary with P2-P4 from the Briqueterie Cavaillé near Perpignan (France). This specimen is preserved in the collections of MNHN (Fig. 6). Bonifay (1971, p. 175, fig. 35-1) provided a drawing of the specimen in lateral view and referred it to *Hyaena donnezani* Viret, 1954, which was initially defined on a series of upper and lower jaws from Serrat-d'en-Vacquer, another site

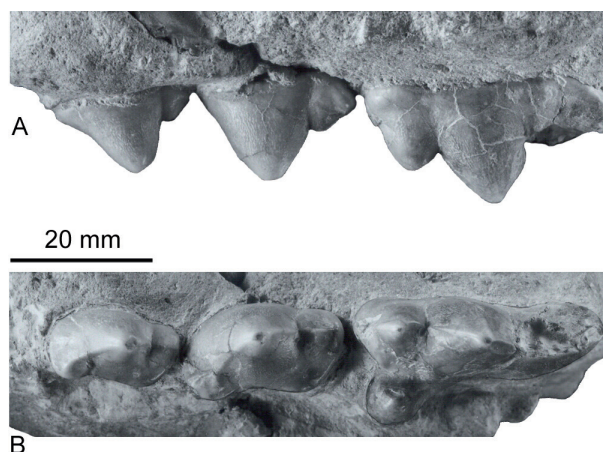


Fig. 6: *Pliocrocuta perrieri* from Tuilerie Cavaillé, near Perpignan. Fragment of left maxillary with P2-P4 (MNHN-Per 189). Scale bar 20 mm.

in the Roussillon Basin. Kurtén & Werdelin (1988: 48) argued that “the narrow proportions of P<sup>2-4</sup> indicate that it represents *C. borissiaki*. The teeth are only slightly larger than those of the holotype”. This attribution seems doubtful. As these authors noted, the upper teeth from Perpignan are larger and proportionally narrower than that of *C. borissiaki*. The P2 and P3 are narrower and are less lingually wide than in any species of *Chasmaporthetes*, and further this widening is situated distally, not at the level of the protocone as in *Chasmaporthetes*. In addition, the P4 from Perpignan has a larger protocone, well detached from the parastyle-paracone complex, and it lacks the anterior notch that separates the protocone and parastyle. The size and morphology of this specimen fit better with the holotype of *Hyaena donnezani* from Serrat-d'en-Vacquer (Depéret, 1890, pl. 10, fig. 1) rather than with that of *C. borissiaki*. Werdelin & Solounias (1991) synonymized *H. donnezani* with *Pliocrocuta perrieri* (Croizet & Jobert, 1828).

*C. lunensis* (Del Campana, 1914) was initially recorded at Olivola, early Pleistocene (MN17) of Italy. Later on, several occurrences from Spain, France, Germany, Italy, Greece, Ukraine and Turkey have been referred to this species (Kurtén & Werdelin, 1988; Turner *et al.*, 2008). As we noted above, the specimens from China and Eastern Russia (Beregovaya and Shamar) were also included in this species (Kurtén & Werdelin, 1988; Werdelin & Solounias, 1991; Sotnikova, 1994). *C. lunensis* is characterized by its large size compare to the other Eurasian species of *Chasmaporthetes*. Its lower premolars are narrow and have tiny anterior accessory cusps, except p2 in early forms, that become prominent in time, the p4 is slightly smaller than or as large as m1, P2 and P3 have an internal widening at the level of the paracone, without an anterior accessory cusp in early Pliocene occurrences, but with a small cusp in the later representatives of the species. P4 has a large protocone and an elongated metastyle. In all these characters, the

specimens from Çalta-1 fit with *C. lunensis*. However, the cheek teeth from Çalta-1 are gracile compared the specimens from late Pliocene and early Pleistocene localities of Europe, such as from Olivola, Saint-Vallier, Perrier and Puebla de Valverde (Del Campana, 1914; Viret, 1954; Argant, 2004; Antón *et al.*, 2006). These are the localities with the best record of this species. In these localities, the p4 is as large as the m1, the upper carnassial has a stout occlusal outline with protocone strongly connected to the parastyle-paracone complex, without or with a tenuous anterior notch and a large metastyle. In these respects, the specimens from Çalta-1 have rather primitive features of this species. The same reasons led Ginsburg (1998) to identify a new subspecies. Since there is a general consensus to include the species “*C. kani*” in *C. lunensis*, we suggest retaining the subspecies distinction of the Çalta hyena as *C. lunensis anatolicus* Ginsburg, 1998.

In Turkey, Schütt (1971) recorded the first remains of hunting hyena, a right upper jaw fragment with P3-P4, identified as *C. lunensis*, from the locality of Gülyazi (dept. of Afyon, MN 16). The P3 and P4 from Gülyazi and Çalta are morphologically identical. In size, the P3 from Gülyazi is about 10% smaller than that of Çalta, but the P4 has almost identical dimensions. We believe that the size difference of P3 rather indicates intraspecific variation.

In the surrounding countries, *Chasmaporthetes* is a little better known. In Greece, in addition to *C. bonisi* Koufos, 1987 from Dytiko and Ravin des Zouaves 5 (see above), Koufos (1993) described some remains of *C. lunensis* from the late Pliocene locality of Dafnero 1 (MN 16). In the lower jaws of Dafnero 1, the p2 and p3 have stronger anterior cusps. Otherwise, the P4 from this locality has a transverse protocone as at Çalta, and in size and other morphological features the Çalta specimens are similar to that of Dafnero 1. From Bulgaria, Sirakov *et al.* (2010)

reported a p4 as *C. lunensis*. It comes from Kozarnika Cave, which yielded a rich mammalian fauna correlated to early Pleistocene (MNQ 17-18). This p4 is robust, not elongated as in *Chasmaporthetes*, bears a small anterior accessory cusp, and the posterior cingulum is weak, not shelf-like as it is in *Chasmaporthetes*. All characters and the general pattern of this p4 suggest its identification as *Pliocrocota* sp.

Genus *Adrocuta* Kretzoi, 1938

***Adrocuta eximia* (Roth & Wagner, 1854)**

Fig. 7

**Material from Çalta-2:** A right lower jaw belonging to a young adult individual, bearing the root of the deciduous canine, the permanent canine still in the bone, dp1 (5.2 x 5.0), p2 (15.6 x 10.2), p3 (18.0 x 13.7), p4 (21.5 x 12.6) and m1 (27.1 x 12.9). Specimen number ÇAL2-1.

**Description:** This mandible belongs to a young adult individual. The body is still low, its depth under m1 is 27.7 mm. In an adult specimen, for instance in the type mandible from Pikermi, this depth is 52.5 mm. The ventral margin is curved instead of being rather rectilinear in adult individuals (Koufos, 2000). The mental foramen is placed below the posterior root of the p2. Of the ascending ramus, only the anterior part is preserved. The masseteric fossa extends anteriorly to the level of the m1's talonid. Initially this mandible still preserved the dp2 on the top of the p2. The dp2 was removed, as well as part of the bone, to reveal the p2 and p3, which were partly embedded in the bone.

On this mandible, the permanent canine is still in the bone. Its lingual face is rather flat, while its labial face is well rounded. There is an anterior ridge separating both faces. The dp1 is a single rooted button-like tooth. Its crown bears a main anterior cusp and a tiny posterior tubercle.



Fig. 7: *Adrocuta eximia* from the localities of Çalta-2 and Pikermi. A, left mandible (ÇAL2-1) with dp1 and p2-m1 from Çalta-2 in occlusal (upper) and labial views; B, cast of a right mandible (reversed) from Pikermi (cast MNHN-PIK 3014) in occlusal (upper) and labial views. Scale bar is 20 mm.

The dp2 (removed to reveal the p2) has an elongated crown that is narrow and low. The anterior ridge of the main cusp is lingually curved, forming a prominence on the antero-lingual edge. The posterior ridge is rectilinear. The posterior cingulum is rather strong.

The premolars and molars are completely unworn and consequently the ridges are sharp. The premolars are slightly imbricated, while the imbrication is strong between the p4 and m1 (about 3.5 mm). Their occlusal outline is rather short and wide. The anterior ridge of the main cusp is directed slightly lingually, while the posterior ridge is rectilinear. The p2 has no anterior cusp; instead, there is thickening of the anterior ridge on its antero-lingual edge. Otherwise, the size of the anterior and posterior cusps, as well the thickness of the posterior cingulum increase from p2 to p4. The m1 is notably longer than the p4. Its protoconid bears both anterior and lingual ridges, which are sharp. There is no metaconid. The talonid is short and single cusped. The cingulum runs all along the labial face of the m1, but it is stronger on its anterior part.

**Comparison and discussion:** The mandible from Çalta-2 is different from that of the hunting hyenas of the Late Miocene and Pliocene referred to the genera *Lycyaena* and *Chasmaporthetes*. In these genera, the lower premolars are narrower and the m1 is shorter. The species referred to *Lycyaena* and *Chasmaporthetes* have premolars with stronger posterior cingula and larger posterior cusps, and their ridges are sharper. On the m1 of *Chasmaporthetes*, the paraconid is lingually grooved, while it is flat on the lower jaw of Çalta-2. By its larger size, and by the shape and morphology of the cheek teeth, the Çalta 2 mandible is clearly different from all mandibles referred to the species of *Lycyaena* and *Chasmaporthetes* (Koufos, 2000, 2009; De Bonis *et al.*, 2007).

In size and morphology, the mandible from Çalta-2 fits with that of *Adcrocuta eximia*, the type locality of which is Pikermi in Greece (MN12 zone). From this locality, there are several mandibles preserved in the collections of the Paris Museum. A direct comparison with the Pikermi specimens shows that some individuals from Pikermi have premolars that are more rounded and more robust, and the posterior cingulum of the premolars is somewhat stronger than on the mandible of Çalta-2. However, in the same collection there are several other lower jaws, and in particular a cast of a left mandible (cast PIK 3014, original at Bayerische Staatssammlung für Paläontologie und historische Geologie in Munich), that are very similar to that of Çalta-2, which preserves, just as the specimen ÇAL2-1, the permanent canine still in the bone, dp1, permanent premolars still erupting and not yet worn, and a fresh m1. Comparison of these two mandibles does not reveal any reliable differences. The morphological characters and the dimensions of the ramus and cheek teeth are very similar. On this Pikermi mandible, the length and the width of cheek teeth are as follow: dp1:

5.7 x 5.8; p2: 16.9 x 11.1; p3: 20.5 x 13.7; p4: 23.0 x 13.5 and m1: 28.5 x 12.6. The Pikermi mandible is illustrated in Fig. 7B for ease of comparison. *Adcrocuta eximia* is the common hyaenid of Turolian faunas from Spain to China (Howell & Petter, 1985). In Turkey, 11 localities have yielded remains of *A. eximia* according the faunal lists presented by Saraç (2003), spanning all MN zones of the Turolian. It is not known in the Vallesian localities of Turkey.

#### 4. CONCLUSIONS

Three species of Hyaenidae are described in this study. Two of them (*Plioviverrops* cf. *orbigny* and *Chasmaporthetes lunensis anatolicus*) are from the early Pliocene locality of Çalta-1 and the third one (*Adcrocuta eximia*) is from the Late Miocene locality of Çalta-2. These localities are situated a few kilometers west of the village of Çalta, some 50 km northwest of Ankara.

*Plioviverrops* is the smallest hyaenid and is mainly known from Turolian localities of Greece (*P. orbigny*, type species) and Spain (*P. guerini*). Its early representatives are poorly documented from the early and middle Miocene of France. The youngest species *P. faventinus* is known from the late Messinian locality of Brisighella in Northern Italy, with some additional fossils from the early Pliocene of Spain. The maxillary from Çalta-1 is tentatively identified as *P. cf. orbigny* because of similarities in size and many characters of the upper dentition with the type material from Pikermi. However, several characters of the Çalta-1 specimen (lingual angle between the protocone and paracone-metacone blade, and labial cingulum reduced to a short cuspule next to the parastyle on the P4, m1 narrower, and metacone reduced on M2) indicate a derived form that may represent a new species. *Plioviverrops* displays a crushing-puncturing dentition (Ferretti, 2007) and had a mongoose-like insectivore/omnivore diet (Turner *et al.*, 2008).

The hunting hyena remains from Çalta-1 are referred to *Chasmaporthetes lunensis anatolicus* Ginsburg, 1998 instead of *C. kani* which is accepted as a junior synonym of *C. lunensis* following the synthetic studies of Kurtén & Werdelin (1988) and Werdelin & Solounias (1991). Çalta-1 is the second occurrence of this hyena in Turkey, after that of Gülyazi (Schütt, 1971). This subspecies is distinguished from the others by its cheek teeth slightly smaller than those of the late Pliocene-early Pleistocene *C. lunensis* from Europe, lack of anterior accessory cusps on P3 and p2, P4 with a protocone situated lingually and not fused to the parastyle-paracone complex as in *C. lunensis* from Olivola (type locality of *C. lunensis*) or Saint-Vallier and La Puebla de Valverde (Del Campana, 1914; Viret, 1954; Argant, 2004; Antón *et al.*, 2006).

The third species described in this paper, *Adcrocuta eximia*, comes from the locality Çalta-2, which is situated well below Çalta-1 in the local stratigraphy. It consists of

a lower jaw with dp1-m1. Comparison with specimens from Pikermi (Greece), which is the type locality of this species, does not reveal any size or morphological differences. *A. eximia* is the most common carnivore of Turolian localities from Spain to China.

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We dedicate this article to the memory of our late colleague Claude Guérin.

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