THE LATE MIOCENE PERCROCUTAS (CARNIVORA, MAMMALIA) OF MACEDONIA, GREECE

by

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Key-words: Mammalia, Carnivora, *Dinocrocuta*, late Miocene, Greece, Description, Comparisons, Biochronology.

Mots-clés: Mammifères, Carnivores, *Dinocrocuta*, Miocène supérieur, Grèce, Description, Comparaisons, Biochronologie.

Palaeovertebrata, Montpellier, **24** (1-2): 67–84, 6 fig., 2 pl.
(Reçu le 2 Avril 1993, accepté le 29 Avril 1993, publié le 14 Juin 1995)

ABSTRACT

Some new material of percrocutas from the late Miocene of Axios valley (Macedonia, Greece) is studied. They have been found in the locality of "Pentalophos 1" (PNT). The material has been described and compared with the known late Miocene percrocutas of Eurasia. This comparison indicates that it can be identified as *Dinocrocuta gigantea* (SCHLOSSER, 1903). A maxilla of a percrocuta, named *"Hyaena" salonicae*, was found in the same area (Andrews, 1918). *"Hyaena" salonicae* is smaller than the PNT material. It is also compared with other material from Eurasia while its taxonomic and age problems are discussed. It belongs to *Dinocrocuta* and shows close relationships with *D. robusta* and *D. senyureki;* its age can be considered as late Vallesian-early Turolian. The age of the locality PNT is also discussed and a possible Vallesian age is proposed for it.

RESUME

Des nouvaux spécimens d'une percrocuta du Miocène supérieur de la Vallée d'Axios (Macédoine, Grèce), provenants de la localité "Pentalophos-1" (PNT), font l'objet du présent travail. La description du matériel disponible et sa comparaison avec les percrocutas du Miocène supérieur d'Eurasie permettent de l'attribuer à *Dinocrocuta gigantea* (SCHLOSSER, 1903). Au début du siècle et dans la même région a été trouvé un maxillaire d'une percrocuta, déterminée comme *"Hyaena" salonicae* ANDREWS, 1918. La comparaison entre les deux espèces montre que *"H." salonicae* est plus petite que la hyène de PNT, constituant donc une espèce distincte. Le problème taxonomique ainsi que l'âge de la hyène de PNT sont discutés en detail. Il s'agit d'une *Dinocrocuta* qui présente des liens étroits avec *D. robusta* et *D. senyureki. "Hyaena" salonicae* suggère un âge Vallesien supérieur-Turolien inférieur. L'âge de la localité de PNT est également discuté et determiné probablement comme Vallesien.

INTRODUCTION

The percrocutas have been known from the Axios valley since 1918, when a piece of maxilla was described by Andrews (1918), under the name *"Hyaena" salonicae*. The exact locality of this specimen is unknown. It was found by an army officer and given to the British Museum (Natural History), BM(NH). Some *Hipparion* remains, found near the village of Diavata, are also described by Andrews (1918). According to the latter author both hyaena and hipparion may have been found in the same locality. During my visit in BM(NH) I found the letter of the army officer who collected the *Hipparion* remains. In this letter he mentions that the fossils were found in a ravine between the river of Gallikos and the hill Tris Toumbes (fig. 1). Our efforts to find this locality were unsuccessful because new buildings in the area have changed the terrain. In the same area, near the village of Pentalophos, a new mammalian locality was found in 1983; it was named "Pentalophos 1", PNT (fig. 1). Among the fossils collected there are some remains of a percrocuta. There are not other evidences for the presence of percrocutas in the late Miocene of Axios valley. The most common hyaena is *Adcrocuta eximia*, while the hunting hyaena *Chasmaporthetes bonisi* and other smaller hyaenids, mainly ictitheres, are also present (Arambourg & Piveteau, 1929; Koufos, 1980, 1986; Bonis &

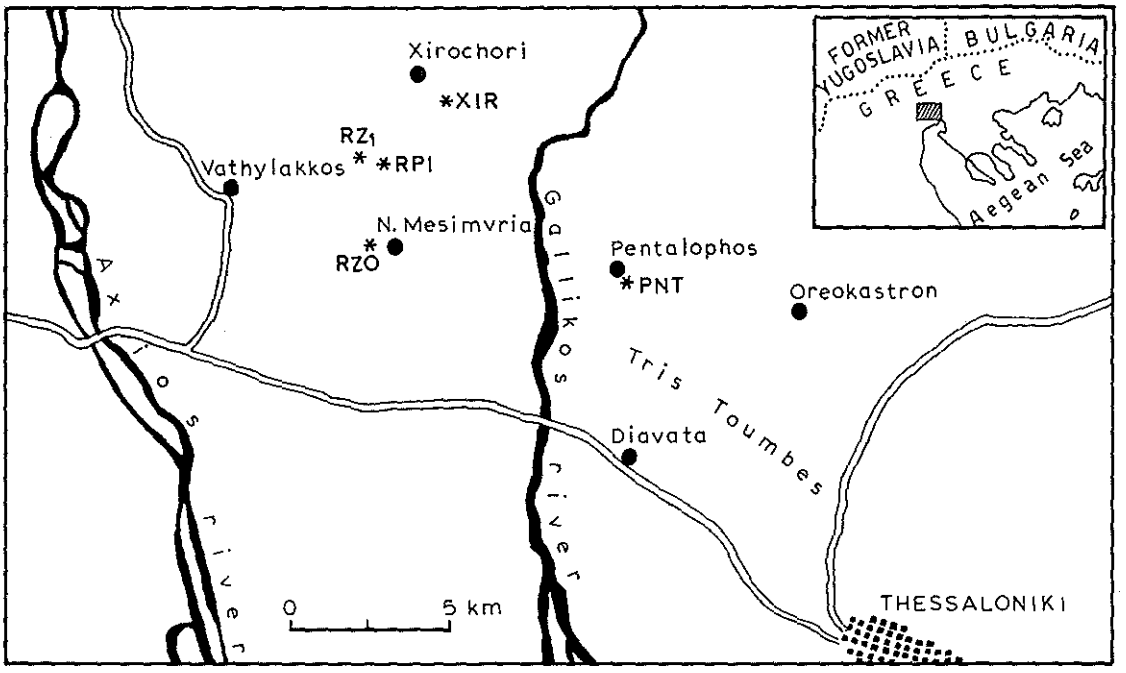


Figure 1.— Sketch map indicating the Vallesian fossiliferous sites of Axios valley.

Koufos, 1981, 1991). Besides the maxilla of *"Hyaena" salonicae*, no other percrocutas were known from Greece.

The locality of "Pentalophos 1" (PNT) is situated in a ravine near the village of Pentalophos (Thessaloniki, Macedonia, Greece), about 15 Km NW of Thessaloniki (fig. 1). It is situated in a series of red-beds which in the bottom of the ravine consist of hard conglomerates overlaid by consolidated sands, gravels and reddish clays. The lithological characterstics of the deposits indicate that they belong to Nea Mesimvria Fm, including the localities "Ravin de la Pluie" (RPl), "Ravin des Zouaves 1" (RZ1) and "Xirochori 1" (XIR) (fig. 1). The fauna of these localities has been dated to Vallesian (Bonis *et al.*, 1988, 1991).

The fauna collected from PNT contains the species *Choerolophodon pentelicus*, *Protictitherium* cf. *crassum*, *Hipparion* sp. (large size), *Hipparion* sp. (small size), *Aceratherium kiliasi*, *Ceratotherium neumayeri*, ?*Decennatherium macedoniae*, *Ouzoceros* sp., *Protoryx* sp., *Gazella* sp., Boselaphini ind., *Orycteropus pottieri*. In this article the new material of the percrocuta will be described and compared with the known eurasiatic forms. It will be also compared with *"Hyaena" salonicae* in order to see if it represents the same or another taxa. Finally, the age problem of *"H". salonicae* and the PNT percrocuta will be discussed, using all the presently available data.

PALAEONTOLOGY

Dinocrocuta gigantea (SCHLOSSER, 1903)

Locality: "Pentalophos 1", PNT, Macedonia, Greece.

Age: ? Vallesian (late Miocene).

Material: Right and left upper canine, PNT 71, 71a; mandible, PNT 70.

Description

The upper canine is very strong and large, curving backwards and slightly outwards. It has an elliptical transverse section and a strong crest is developed distolingually from the apex to the base. Another weaker crest is developed in the middle of its lingual surface. The root is very strong and long (77 mm). The maximal mesiodistal diameter of the root is 30 mm and the maximal buccolingual diameter is 23 mm.

The studied mandible preserves both rami with the teeth I_1–M_1 dex and C–P_4 sin; the right ramus is better preserved including a small part of the ascending ramus. The mandible belongs to a young adult individual and some of the teeth (C, P_2) are not fully erupted. The horizontal mandibular ramus is low (because of the young age of the individual) and not very thick. The thickness of the ramus below P_4-M_1 is 23.3 mm. Its inferior border is straight from the beginning of the symphysis but below M_1 it is upwardly inflected. The symphysis is strongly inclined backwards and projects inferior to the lower margin below P_2; its mesial border is curve. There is a large mental foramen below the middle of P_2. The masseteric fossa is shallow and its anterior border is situated below the talonid of M_1. The length P_2–M_1 is 120 mm. There is no trace of an alveolus for P_1. The incisors are comparatively small with a main cuspid and a smaller one situated in their buccal wall. The canine is still inside the bone and only its tip is observable; it seems to be strong.

The P_2 is situated laterally to the toothrow's axis, with its anterior part directed inwards. It has a high main cuspid with a strong crest across its mesial and distal border. A small posterior accessory cuspid is situated in a distal projection of the distal cingulum. In a mesial projection of the mesial cingulum there is a very small anterior accessory cuspid. There is a strong distolingual projection of the cingulum, enlarging the posterior part of the tooth.

The P_3 has a rectangular outline with a very strong and high main cuspid. A strong crest is developed across the mesial and distal surface of the main cuspid. A small anterior accessory cuspid is situated mesiolingually. The small posterior accessory cuspid is situated in a distal projection of the distal cingulum, which is elevated.

The P_4 is elongated and slender relative to P_3. There is a high main cuspid with mesial and distal crests. A very strong anterior accessory cuspid is present, while a smaller posterior one is situated in a distal projection of the distal cingulum. The distal cingulum is elevated forming a crest across the distal end of the tooth.

The carnassial is short relative to P_4, with a very small talonid. There is no

metaconid. The protoconid is higher and slender than the paraconid. A small crest is developed from the anterior top of the paraconid-blade across its lingual surface. The talonid has a well developed hypoconid and a very small entoconid. There is a well developed lingual cingulum and a strong mesiolabial one.

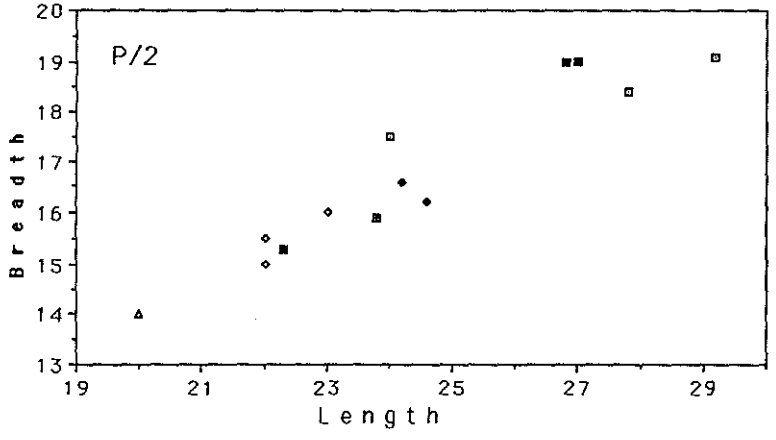
Discussion

Since a long time the percrocutas were considered as belonging to the family Hyaenidae. Recently the percrocutas were referred as a dinstinct group phylogenetically different than the Hyaenidae s.s. (Schmidt-Kittler, 1976; Chen & Schmidt-Kittler, 1983; Werdelin & Solounias, 1991). The last two authors consider that the percrocutas consist a new family Percrocutidae.

The species *Hyaena gigantea* was erected by some isolated teeth from China (Schlosser, 1903) and the type material is stored in München (Institüt für Historische Geologie und Paläontologie). Some material from the Siwaliks was described under the name *Crocuta gigantea* var. *latro* by Pilgrim (1932); part of Pilgrim's material (G.S.I. n^0 D 162 and G.S.I. n^0 D 231) were later referred by Kurtén (1957) to *Crocuta (Percrocuta) grandis*. Later, the known material of *D. gigantea* was transferred to the genus *Allohyaena* and it is referred to as *Allohyaena (Dinocrocuta) gigantea* by Howell & Petter (1985). Recently Qiu *et al.* (1988) described a complete skull of *Dinocrocuta gigantea* and also discussed the generic name of the species. They considered that the morphological features of this skull distinguish it from the known genera and allow the separation of *Dinocrocuta* as an independent genus. Thus they proposed for Schlosser's species the name *Dinocrocuta gigantea* (Schlosser, 1903). Because there are many proposed names for this hyaena and its systematic position is not the subject of this article the last proposed name *Dinocrocuta gigantea* will be used in the following.

The main characters of *Dinocrocuta* are the large to very large size, the absence of the internal root of P^3, the long P_4 relative to P_3, and the hypertrophied P_2 with high robusticity index (Howell & Petter, 1985). The short M_1 relative to P_4 is characteristic for *Dinocrocuta* (Schmidt-Kittler, 1976). Qiu *et al.* (1988) mentioned some additional cranial characters, such as the sharp bending of the skull roof, the thick and much broadened nasal bones, the exceptionally long meatus acusticus, the reduced processus paroccipitalis and the generally short and high proportions. The PNT mandible with its very large size, hypertrophied P_2, long P_4 relative to P_3 and short M_1 relative to P_4 clearly belongs to *Dinocrocuta*.

The studied teeth have been compared with the type material of *D. gigantea*, which is very fragmentary and stored in München. Some pieces of the upper canine from China are similar in morphology and size with those from PNT. The dimensions of the upper canines from PNT are 24.7 x 20.8 and 24.6 x 20.4 versus 28 x 21, 24.8 x — and — x 21.2 in the three upper canines of *D. gigantea* from Schlosser's collection. The lower third incisor and the canine are also similar to those of the type collection. The P_3 in Schlosser's collection is similar to those from PNT, except of the development of the anterior accessory cuspid. The later is very small in PNT 70. In the Chinese material there is a small mesiolingual projection of the cingulum. The morphology of P_4 and M_1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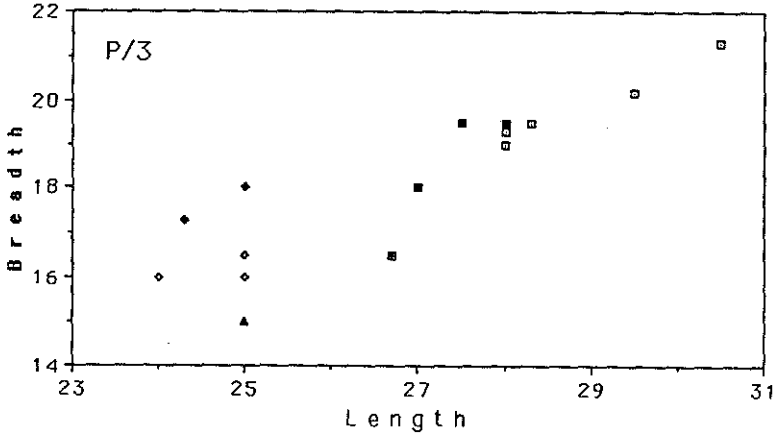
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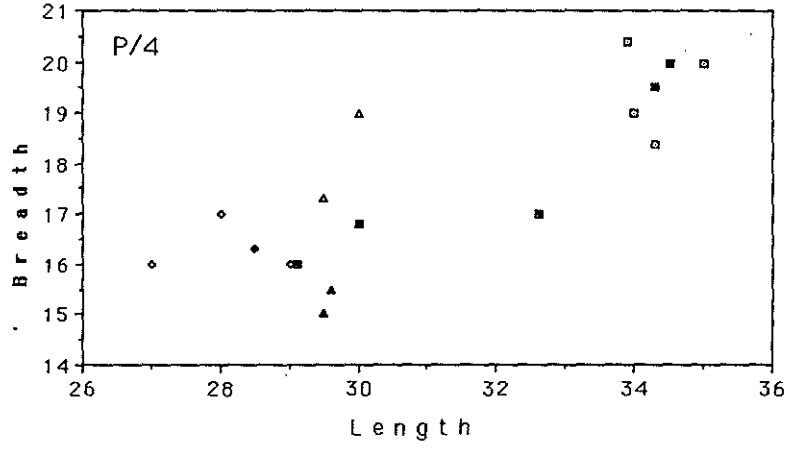
P/4
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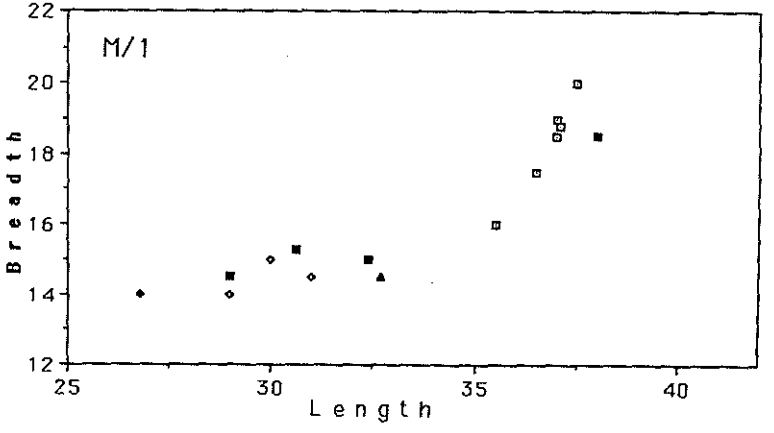
M/1
Breadth
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		PNT 70 dex	PNT 70 sin	Schlosser's coll. [1]	Koenigswald's coll. [2]	Songshan [2] V.6410	A. Teli [2] (Mongolia)	Algejares [3]	Ademuz [3]	
P_2	L	27.0	27.0	24	–	29.2	27.8	20.4	21.5	–
	B	19.0	19.0	17.5	–	19.1	18.4	14.3	–	–
P_3	L	28.1	27.5	28.2	28.3 28.0	30.5	29.5	–	25	–
	B		19.5	19.2	19.5 19.3	21	20.2	–	15	–
P_4	L	34.3	34.5	34.5	–	34.3	33.9	29.5	29.5	29.5
	B	19.5	19.7	19.4	–	–	20.4	17.3	15	15.5
M_1	L	38.0		36.3	37	–	37.1	–	–	32.7
	B	18.5		17.6	18.5	–	18.8	–	–	14.5
	L trig.	31.6		31	31.5	–	32.2	–	–	–

Table 1.— Lower teeth dimensions of *D. gigantea* from various localities. 1. original measurements; 2. data from Howell & Petter (1985); 3. data from Soria (1980).

from China and PNT is similar. The only difference is in the size of the entoconid of M_1, which is weaker in PNT 70. In Schlosser's collection there are three M_1: one (1900 XII 537) with well developed entoconid, another (1900 XII, 527) with weak entoconid and a third one (1900 XII 524) which seems to be without or with a very weak entoconid. Thus the entoconid size varies enough in *D. gigantea* and cannot be used as a distinctive character.

A piece of mandible with P_2–P_4 sin (V. 6410) from Songshan (Gansu, China), has been described as *D. gigantea* by Zeng (1982). A cast of this specimen was compared with PNT 70. The dental morphology is exactly the same except of the absence of a small anterior accessory cuspid in P_2 of V.6410. The occlusal view of P_2 and the large anterior accessory cuspid of P_4 are exactly the same in both specimens. The dental dimensions are also the same (fig. 3). A lower carnassial (M. 49998) from an unknown locality, stored in BM(NH), is referred to *D. gigantea* by Howell & Petter (1985). Except of its smaller size (tab. 1) and the slightly stronger entoconid it is identical with PNT 70.

The metrical comparison of the lower teeth of PNT 70 with those of the known percrocutoid hyaenas indicates that their dimensions are very close to those of *D. gigantea*. In the scatter diagrams of figure 2, the premolars and the carnassial of PNT 70 are very near to the sample of *D. gigantea* from Asia and far from all the other known percrocutas of late Miocene. The dimensions of the lower teeth are also compared in a logarithmic ratio diagram (fig. 3) and again the line for PNT 70 is parallel and very close to the material of *D. gigantea* from various localities. There is only an

Figure 2.— Scatter diagram for the lower cheek teeth of the late Miocene percrocutas.

■ *D. gigantea*, PNT 70; ⊡ *D. gigantea*, China, Mongolia, Moldavia (orig. meas.; Lungu, 1978; Howell & Petter, 1985); □ *D. algeriensis* (Howell & Petter, 1985); ● *D. senyureki*, Yassiören (Ozansoy, 1965); ⊙ *D. robusta*, Moldavia (Lungu, 1978); △ *Dinocrocuta* sp., Algezares (Soria, 1980); ▲ *Dinocrocuta* sp., Ademuz (Soria, 1980).

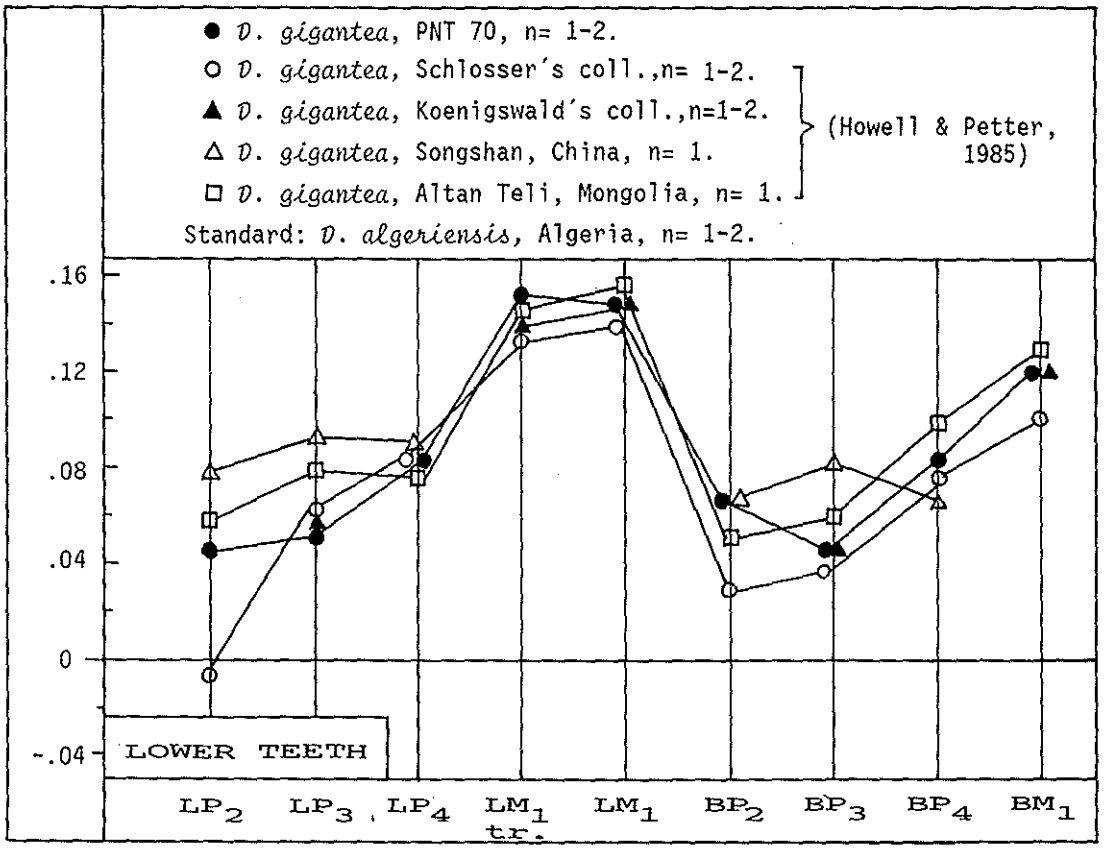

Figure 3.— Logarithmic ratio diagram comparing the dimensions of the lower cheek teeth of *D. gigantea* from various localities.

exception in the length of P_2 which is smaller in Schlosser's material. The morphological and metrical comparison of PNT 70 suggests that it is similar to the known material of *D. gigantea*. There are some minor morphological differences such as the presence of a small anterior accessory cuspid in P_2 and the reduced entoconid of M_1. The development of the entoconid varies as it was mentioned above, while the presence of a small anterior accessory cuspid is not enough for a specific distinction; it may be also varies within the species.

A percrocuta named *Hyaena algeriensis* is known from the Vallesian locality of Bou-Hanifia, Algeria (Arambourg, 1959). Later it was transferred to *Percrocuta (Dinocrocuta)* by Schmidt-Kittler (1976), to *Allohyaena (Dinocrocuta)* by Howell & Petter (1985) and recently to *Dinocrocuta* by Qiu *et al.* (1988). The material of *D. algeriensis* has been studied and compared with PNT 70 in the Muséum National d'Histoire Naturelle of Paris. The mandibular and dental morphology of PNT 70 is similar to that of *D. algeriensis*. The premolars of both specimens are morphologically very similar; those of *D. algeriensis* are small versions of PNT 70. The lower carnassial is smaller relative to P_4 in *D. algeriensis*. The index $LM_1 \times 100 / LP_4$ is 110.8 in PNT 70 versus 94 in *D. algeriensis*. The dental dimensions of *D. algeriensis* are clearly

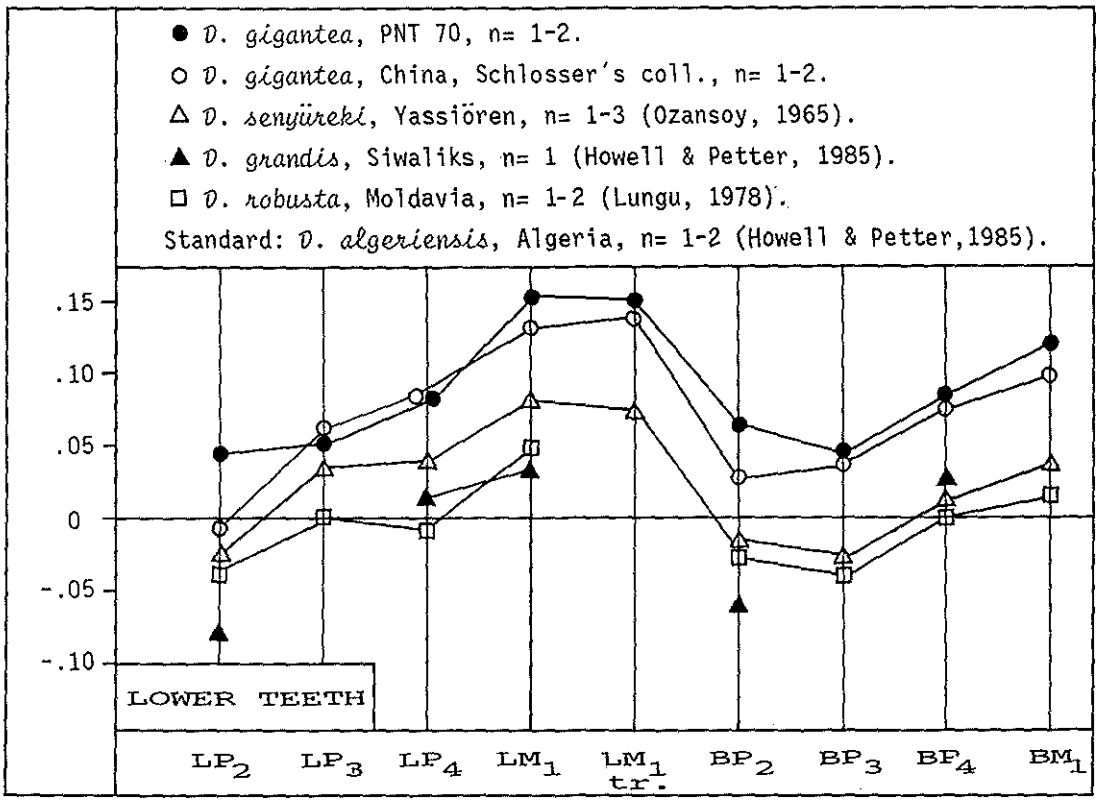

Figure 4.— Logarithmic ratio diagram comparing the dimensions of the lower cheek teeth of the various late Miocene percrocutas.

smaller than those of PNT 70 (fig. 2). In figure 4 the larger size of the teeth of PNT 70 is clear and distinguishes PNT 70 from *D. algeriensis*.

Dinocrocuta senyureki is a percrocuta known from Yassiören, Turkey (Ozansoy, 1965; Schmidt-Kittler, 1976) and from Sahabi, Libya (Howell, 1984). The type material is stored in the Muséum National d'Histoire Naturelle of Paris. *D. senyureki* has clearly smaller dental dimensions than those of PNT 70 and *D. gigantea* (fig. 2, 4). According to the description of Howell & Petter (1985) it is very similar morphologically to PNT 70. The $P_{2,3}$ have a small anterior accessory cuspid similar to those of PNT 70 but there is no trace of an entoconid in the talonid of M_1.

Some material of percrocutas known from Spain (localities of Algezares and Ademuz) has been described as *D. gigantea* (Soria, 1980). The dental dimensions of the Spanish material are significantly smaller than those of *D. gigantea* and closer to those of the smaller group (*D. senyureki, D. algeriensis, D. robusta*) (fig. 2). Their attribution is due to the proposed synonymy *D. gigantea* (= *D. salonicae* = *D. senyureki* = *D. gigantea latro* = *D. grandis*) (Soria, 1980). The Spanish material differs from *D. gigantea* by the smaller size and from *D. senyureki* because the latter has a strong anterior accessory cusp in P^3. The morphological features of the Spanish material are similar to those of *D. algeriensis*. In the latter the size of the lower

carnassial is sligthly smaller (fig. 2) and the talonid is larger and bicuspid. Nevertheless, the variation in size and development of these dental features is not well known and makes difficult the attribution of the Spanish material. The PNT teeth are clearly distinguished from the Spanish material by their larger size (fig. 2) and by the bicuspid talonid which is not appressed on the trigonid.

A percrocutoid hyaenid named *Percrocuta grandis* is known from the Siwaliks. It was described as *P. gigantea latro* by Pilgrim (1932) and later transferred to *Percrocuta grandis* (Kurtén, 1957). The distinction from *D. gigantea* was based to its smaller size. Some morphological differences such as the shorter M_1 relative to P_4, and the shorter metacone of P^4 relative to the tooth's length than in *D. gigantea* are added by Howell & Petter (1985). The dental dimensions of *D. grandis* are clearly smaller than those of PNT 70 and *D. gigantea* (fig. 4).

Some remains of a percrocuta named *Dinocrocuta robusta* are known from the locality of Kalfa, Moldavia (Lungu, 1978). Besides the smaller size (fig. 2, 4) there are not significant morphological differences from PNT 70. In the description of Lungu (1978) a tricuspid talonid (with a weak hypoconulid) is mentioned. He probably means the weak elevation of the distal cingulum, which looks like a hypoconulid.

THE PROBLEM OF *"HYAENA" SALONICAE* ANDREWS, 1918

As was mentioned in the introduction a part of maxilla with P^2–P^4 of a percrocuta, named *"Hyaena" salonicae*, is known from the area of Axios valley, Macedonia, Greece (Andrews, 1918). No certain data about the exact locality of this specimen are known. It was described together with some *Hipparion* remains, whose location is more certain (Koufos, 1985). It is possible that hyaena and hipparion come from the same locality (Andrews, 1918; Koufos, 1985). *"Hyaena" salonicae* differs from *D. gigantea* in the larger protocone which is situated far behind the mesial border of the parastyle (Andrews, 1918; Kurtén, 1957). Several opinions concerning the systematic and phylogenetic position of this hyaena have been proposed. It is referred to as *Crocuta* (Pilgrim, 1931), as *?Crocuta (Percrocuta)* (Kurtén, 1957), as *"Hyaena"* (Beaumont, 1979), as *Allohyaena (Dinocrocuta)* (Howell & Petter, 1985) and as *Dinocrocuta* (Qiu *et al.*, 1988; Werdelin & Solounias, 1991). Kurtén (1957) refers that *"H". salonicae* belongs to the *gigantea-carnifex-grandis* evolutionary lineage but it is still different enough in the position of the protocone to represent a new species.

Beaumont (1979) in his reconsideration of *"H". salonicae* suggests three possibilities.

1. *"H". salonicae* represents the particular extremes of the normal variability of a "Pontian" species. But in the common pontian hyaena *Adcrocuta eximia* there is no evidence for such a variability in the dental dimensions. Moreover, the protocone of *Adcrocuta* is reduced and both $P^{2,3}$ have a marked anterior accessory cusp, which is absent in *"H". salonicae.*
2. *"H". salonicae* is an early Pliocene species of *Pachycrocuta.* This possibility must

be excluded because of the age. All of the area around the village of Diavata is covered by red-beds of late Miocene age.

3. *"H". salonicae* represents a form of *Pliohyaena brevirostris* and has Villafranchian age. This hypothesis is also not possible because of the age and the different morphology of *"H". salonicae* and *P. brevirostris*. The latter is smaller than *"H". salonicae*, while the protocone is situated in line with or in front of the mesial border of the parastyle of P^4.

If it is accepted that *"H". salonicae* originated from another area (maybe from the younger fossiliferous levels of Axios valley, exposed in the area of Vathylakkos, few kilometers westwards, fig. 1) then the last two possibilities of Beaumont (1979) are verisimilar. However the type of fossilization (white colour with black dots) and the remains of matrix on the specimen of *"H". salonicae* are similar to those of *Hipparion* remains from Diavata (Koufos, 1985) and to those from PNT. All these data indicate the same origin of the various specimens and that *"H". salonicae* has a late Miocene age.

Howell & Petter (1985) considered *"H". salonicae* an independent species which differs from *D. senyureki* in the relatively shorter metacone of P^4, and in the absence of the anterior accessory cusp of P^3. The P^3 of *"H". salonicae* is similar to that of *D. grandis* and *D. gigantea* from which it is distinguished only by the larger protocone.

The new material from PNT cannot resolve the problem of *"H". salonicae*, because the available material (maxilla, mandible) cannot be compared. However a size comparison between the PNT large hyaena and *"H". salonicae* is possible. In the functional relationship between the skull and mandible of hyaenids, the talonid of M_1 is situated on the internal half of M^1, while the trigonid is extended across the lingual wall of P^4 to the posterior border of the protocone. If we put the maxilla of *"H". salonicae* and the mandible of PNT 70 (which belongs to *D. gigantea*) in such a functional position, the mesial end of M_1 of PNT 70 is situated well in front of the protocone of P^4. This means that *"H". salonicae* has smaller size than *D. gigantea*. I did the same with a maxilla of *D. gigantea* from China. In this case M_1 of PNT 70 fits very well with the P^4–M^1 complex of *D. gigantea*. Moreover, the upper carnassial in Schlosser's material has a length of 54 mm [the reference of Schlosser, 1903 that the length of P^4 is 44 mm is erroneous] which is considerably larger than that of *"H". salonicae* (44 mm). Qiu *et al.* (1988) described a complete skull of *D. gigantea* from China (Gansu, Hezheng County). The length of P^4 measured from the illustration is 58 mm, close to that of Schlosser's material and larger than that of *"H". salonicae*. Thus from the size of the upper carnassial, *"H". salonicae* is smaller than *D. gigantea* The original opinion of Andrews (1918) that *"H". salonicae* was similar in size to *D. gigantea* was probably due to the erroneous measurement of Schlosser (1903). On the other hand, there are two upper canines from PNT which have larger dimensions than those for the alveolus of the canine in *"H". salonicae*. All the above mentioned comparative data indicate that PNT percrocuta (=*D. gigantea*) is larger than *"H". salonicae*.

An extensive description of *"H". salonicae* is given by Andrews (1918) and Beaumont (1979). The morphological features of the teeth and their size allow an attribution to the genus *Dinocrocuta*. The specific determination is more difficult. Brief comparisons will be given in the following. The morphological differences between *"H". salonicae* and the various Miocene percrocutoid hyaenids of Eurasia are given in

table 2. The metrical comparison of *"H". salonicae* with the other known large-sized hyaenas is given in figure 5. The larger size of *D. senyureki* is clear, but it has similar proportions with*"H". salonicae* (parallell lines in the diagram of fig. 5). The size differences from *D. algeriensis* are not significant. *D. robusta* and *D. grandis* have similar tooth lengths to *"H". salonicae* but their breadth is significantly smaller. *D. gigantea* has a clearly longer upper carnassial than *"H". salonicae*, but the breadth of both P^3 and P^4 is exactly the same.

A big problem in the comparison is the limited material of percrocutas. In most cases only one specimen or some isolated teeth are known. Thus the variation in the dimensions and morphology is unknown. For this reason there has been an oversplitting of species.*"H". salonicae* is distinguished from *D. gigantea* by the smaller size, the larger protocone and the more robust P^4. Andrews (1918) and Kurtén (1957) refer that both species have similar dimensions of P^4 but this is due to the erroneous measurements of Schlosser (1903); the length of P^4 of *D. gigantea* is 54 mm and not 44 mm. Moreover the comparison of PNT *D. gigantea* with *"H". salonicae* indicates that it is larger. The only species without reduced protocone is *D. senyureki* which differs from *"H". salonicae* in the larger anterior accessory cusp of P^3. The differences of *D. robusta* from *"H". salonicae* are not significant in either the morphology or in the size of the teeth (tab. 2, fig. 5). Unfortunately the protocone of the sole described P^4 is broken (Lungu, 1978) and thus a comparison with that of *"H". salonicae* is not possible. Nevertheless a determination of the Moldavian material as *D.* cf. *salonicae* is more possible.

Summarizing the above, *"H". salonicae* belongs to *Dinocruta.* It differs from *D. gigantea*, while being closely related with *D. robusta* and *D. senyureki.* However, the latter two species are known from single specimens (sometimes badly preserved) and the variation in protocone size and position, as well as in the development of the anterior accessory cusp of P^3 are uncertain. Thus, the possibility that these three species

	D. salonicae	*D.gigantea*	*D. senyureki*	*D. algeriensis*	*D. robusta*	*D. grandis*
SIZE	Large	Very large	Large (larger than *D. salonicae*)	Large	Large	Large
P^2 AAC	Without	Without	Without	Without	Without	—
R.I.	67.6	—	59.2	70.8	60.5	
P^3 AAC	Rudimentary	Residual	Strong	Rudimenrary	Rudimentary	Rudimentary
R.I.	71.4	71.4	66.4	80.7	66.7	69.2
P^4 Protocone	Large	Reduced	Large	Reduced	—	Reduced
R.I.	55.5	46.0	54.5	61.0	—	51.2

AAC = anterior accessory cuspid; R.I. = robusticity index

Table 2.— Characteristics of the upper cheek teeth of *D. salonicae* and other species of *Dinocrocuta* from late Miocene. AAC = anterior accessory cusp, R.I. = robusticity Index (= L x 100 / B of the tooth).

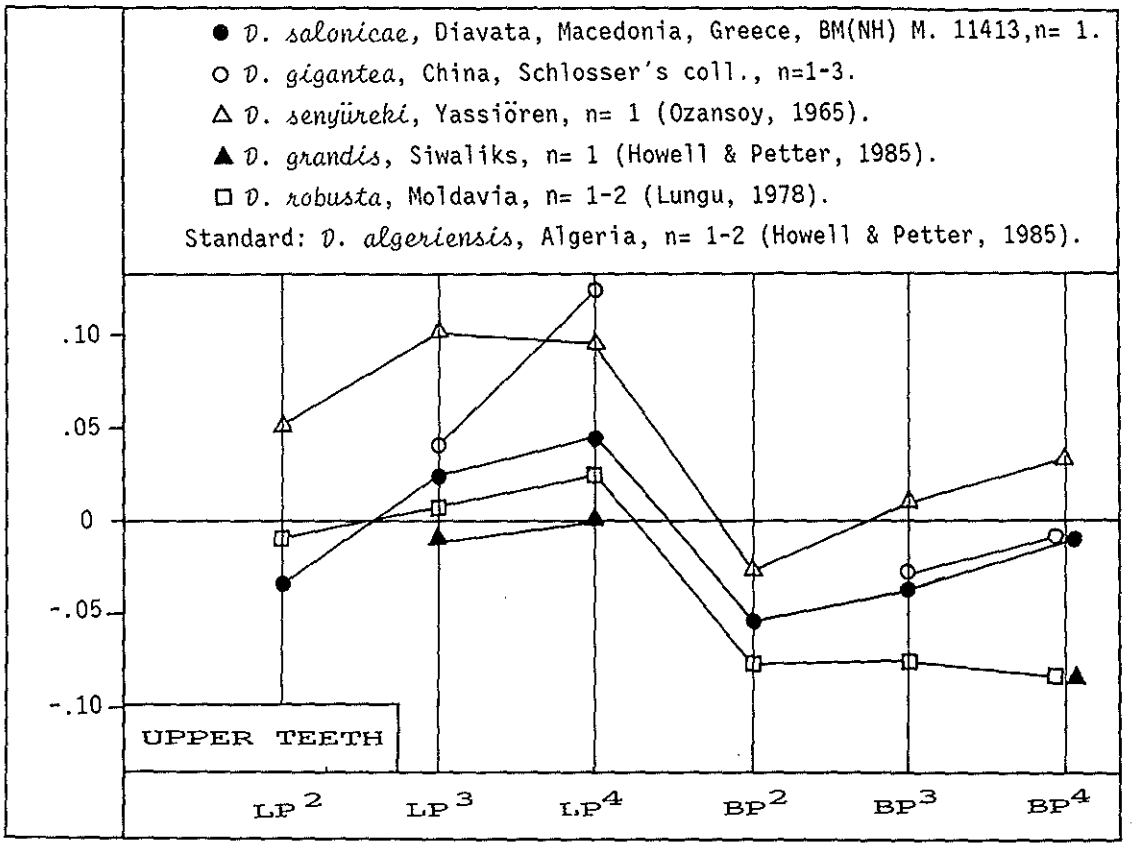

Figure 5.— Logarithmic ratio diagram comparing the dimensions of the upper cheek teeth of *D. salonicae* with other species of *Dinocrocuta*.

(*D. salonicae*, *D. senyureki* and *D. robusta*) are synonyms must be entertained. Thus two different percrocutoid hyaenas are known from the late Miocene of Greece: *D. salonicae* and the larger *D. gigantea*.

BIOCHRONOLOGY OF THE PERCROCUTAS

The age of *D. salonicae* has been much discussed without any definite results. When Andrews (1918) described the specimen he supposed a "Pontian" age, meaning late Miocene-early Pliocene. Later, Kurtén (1957) suggested an early Pliocene age, while Beaumont (1979) proposed three taxonomic schemes with three chronologic possibilities (late Miocene, early Pliocene, Villafranchian). Additional data about the age of *D. salonicae* have been obtained from the study of the *Hipparion* remains, which as it noted above, could come from the same locality as the hyaena. The morphological characters of *Hipparion* indicate a primitive form of late Vallesian/ early Turolian age (Koufos, 1985). Howell & Petter (1985) agree with a Vallesian/Turolian

age for *D. salonicae.*

As was mentioned in the introduction, the faunal data from PNT provide limited informations on the dating of the locality. The deposits of PNT suggest lithological similarities with Nea Mesimvria Formation, dated to Vallesian. In the upper levels of the formation the localities "Ravin de la Pluie" (RPl), "Ravin des Zouaves 1" (RZ1) and "Xirochori 1" (XIR) have been found. The fauna of these localities indicate a late Vallesian age, MN 10 (Bonis *et al.*, 1988). The PNT fauna and those of the Vallesian localities of Axios valley is given in table 3. The rhinoceroses of PNT are abundant and their study indicates an age between middle Vallesian and middle Turolian, inclusive (Geraads & Koufos, 1990). A new giraffid, ?*Decennatherium macedoniae*, similar to the large-sized giraffid from RPl, has been described from PNT and a possible Vallesian age has been proposed for it (Geraads, 1989). The bovid *Ouzoceros* from PNT is similar to that from RZ1, but belongs to another species (Bouvrain, pers. comm.). The

	RPl	RZ1	XIR	PNT
Choerolophodom pentelicus	+	+	+	+
Tetralophodon sp.	+		+	+
Hipparion primigenium	+	cf.		cf.
Hipparion macedonicum	+	cf.		cf.
Aceratherium kiliasi				+
Ceratotherium neumayri				+
Rhinocerotidae indet.	+			
Palaeotragus cf. *coelophrys*	+			
Bohlinia attica	+			
Decennatherium ? macedoniae				+
Decennatherium ? sp.	+			
Prostrepsiceros vallesiensis	+			
Samotragus praecursor	+	+		
Mesembriacerus melentisi	+	+		
Ouzoceros gracilis		+		
Ouzoceros sp.				+
Protoryx sp.				+
Bovidae indet.			+	
Adcrocuta eximia	+	+		
Adcrocuta sp.			+	
Protictitherium cf. *gaillardi*	+			
Protictitherium cf. *crassum*				+
Ictitherium sp.		+		
Ouranopithecus macedoniensis	+		+	
Progonomys cathalai	+			
Spermophilinus sp.	+			
Orycteropus pottieri				+

Table 3.— Fauna of the Vallesian mammalian localities of Axios valley (Macedonia, Greece). Data from Bonis *et al.* (1992, 1994), Bonis & Koufos (1991), Geraads (1989), Geraads & Koufos (1990), Bouvrain (pers. comm.) and personal observations.

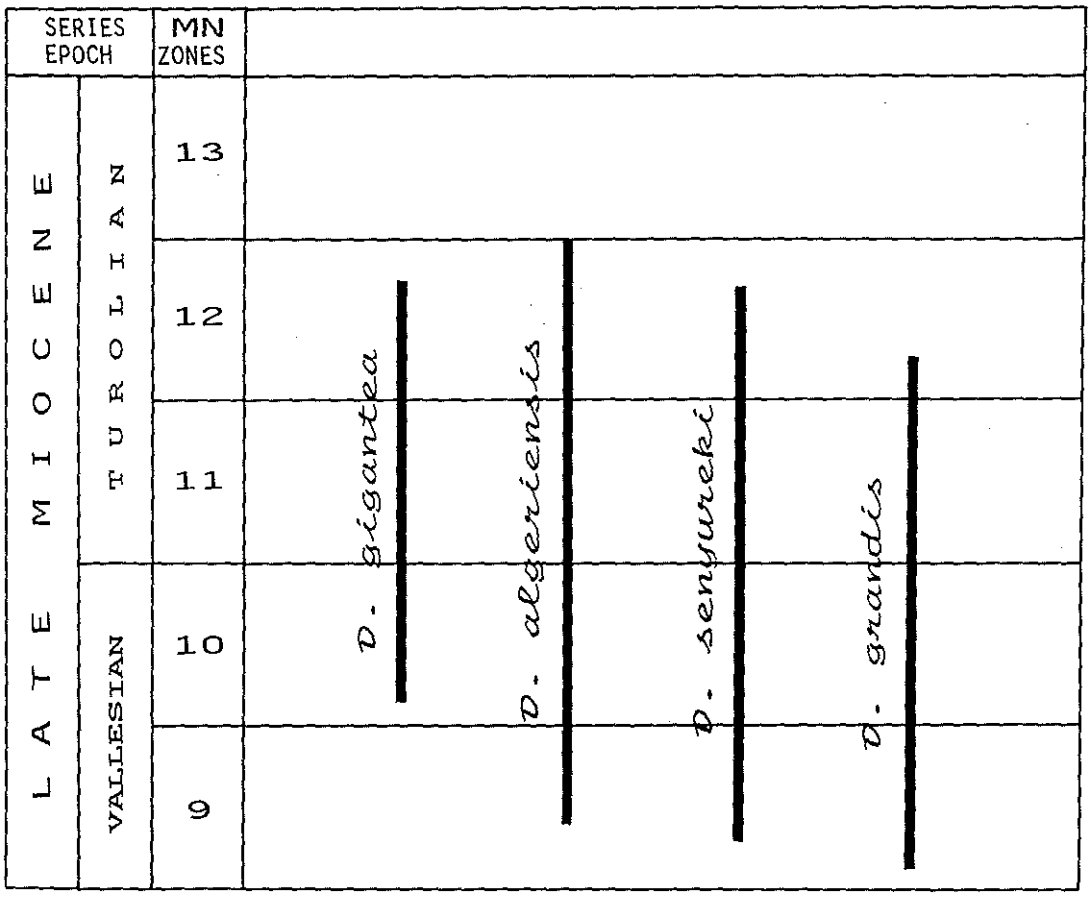

Figure 6.— Stratigraphic distribution of the late Miocene *Dinocrocuta* in Eurasia and Africa.

presence of the genus *Ouzoceros* in PNT might suggest a Vallesian age. The carnivores from PNT are different from those of RPl (tab. 3). The PNT hipparions belong to two forms: a large-sized and a small-sized one; both seem to be similar with those from RPl. The hipparions are still under study and no definite results regarding their morphology and relationships are in hand. The presence of *Orycteropus pottieri* in the PNT fauna and its great similarity with that from the Vallesian of Sinap area, Turkey (Bonis *et al.*, 1994) suggests a similar age for PNT. All these faunal data indicate a possible Vallesian age for PNT.

The age of *D. gigantea* is not quite clear because most of the localities found, are unknown. The type material and Koenigswald's collection come from China but the locality (ies) is (are) unknown. The isolated M_1 stored in BM(NH) has an unknown origin. The specimen V.6410 of *D. gigantea* has been found in Songshan 2-3 (?Baode Fm); the later formation has been dated to middle Turolian (Qiu, 1990). Another maxilla of *D. gigantea* (V. 3093) from the middle fossiliferous zone of Bahe Fm (Sanxi, China) is referred to late Vallesian, MN 10 (Qiu, 1990). Recently Qiu *et al.* (1988) found *D. gigantea* in Hezheng (Gansu, China) dated to late Vallesian, MN 10

(Qiu, 1990). The sample of *D. gigantea* stored in Moscow comes from an early Turolian level of Mongolia (Howell & Petter, 1985). Thus a Vallesian to middle Turolian age for *D. gigantea* is possible. On the other hand the known *Dinocrocuta* material from Eurasia and Africa has a stratigraphic extension from early Vallesian to middle Turolian (fig. 6) except of *D. senyureki* which is also reported from the early Ruscinian of Sahabi, Libya (Howell, 1987). A similar age can be proposed for the Axios valley percrocutoid hyaenas. This age for *D. salonicae* is supported by the age (late Vallesian- early Turolian) proposed on the basis of *Hipparion* (Koufos, 1985). The presence of the bovid *Ouzoceros* in PNT, the similarity of the large giraffid from PNT and RPl, the similarity of the hipparions from both localities and the similar lithology of the two sites also support the idea of a possible Vallesian age for the PNT *D. gigantea*.

ACKNOWLEDGEMENTS

I thank the L.S.B. Leakey Foundation, the French CNRS and the "Fondation Singer-Polignac" for the financial support of the excavations in Macedonia, Greece. Many thanks to Dr A. Gentry (British Museum Natural History, London), Dr L. Ginsburg (Muséum National d'Histoire Naturelle, Paris), Dr V. Fahlbusch and K. Heissig (Institüt für Historische Geologie und Paläontologie, München) for providing access to fossills in their care. I also thank the British Museum (Natural History), the Muséum National d'Histoire Naturelle of Paris and the Institute of Vertebrate Palaeontology and Palaeoanthropology, Beijing (China) for providing me casts of the material in their care.

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LEGENDS OF PLATES

PLATE 1

Dinocrocuta gigantea, "Pentalophos 1", PNT, Axios valley, Macedonia, Greece.

Fig. 1.— Right mandibular ramus with I_2–M_1, PNT 70; labial (a) and lingual (b) view.

Fig. 2.— Left mandibular ramus with C–P_4, PNT 70; labial (a) and lingual (b) view.

PLATE 2

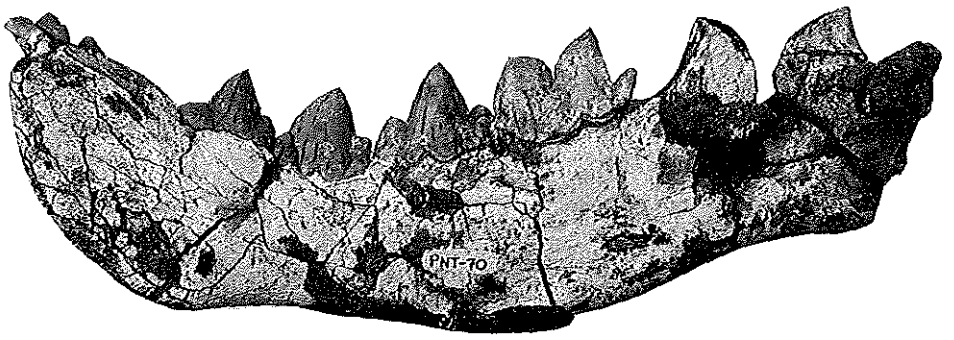
Dinocrocuta gigantea, "Pentalophos 1", PNT, Axios valley, Macedonia, Greece.

Fig. 1.— Right mandibular ramus with P_2–M_1, PNT 70; occlusal view.

Fig. 3.— Left mandibular ramus with C–P_4, PNT 70; occlusal view.

Fig. 3.— Left (a) and right (b) upper canine, PNT 71, 71a; lingual and labial view.

1a



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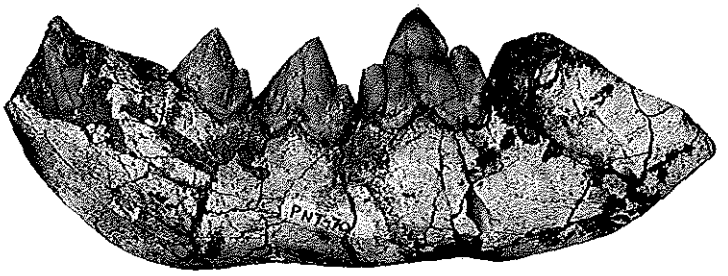

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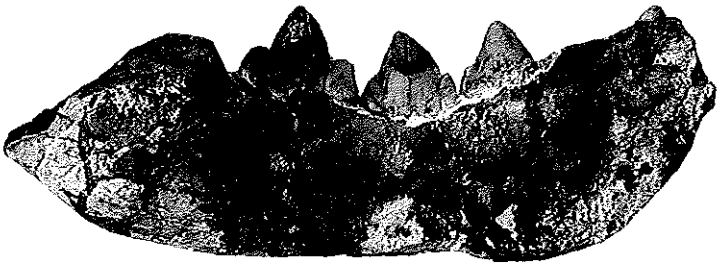

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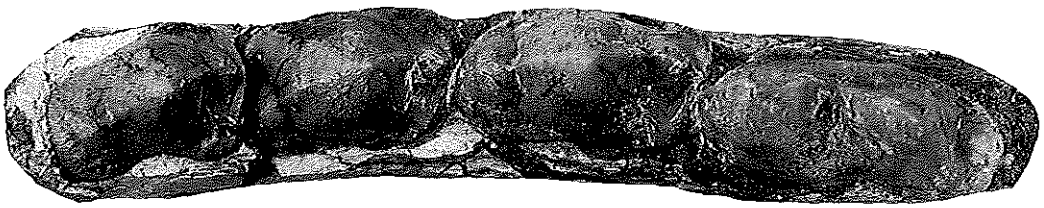

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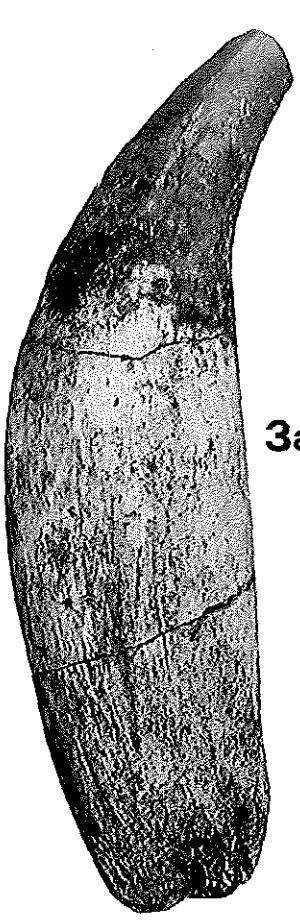

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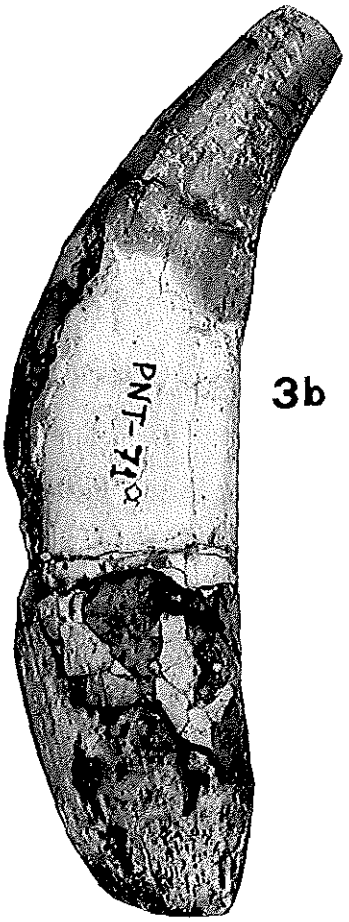

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