

The first appearance of *Dinocrocuta gigantea* and *Machairodus aphanistus* (Mammalia, Carnivora) in the Miocene of Bulgaria

NIKOLAI SPASSOV & GEORGE D. KOUFOS *)

With 9 figures

Abstract

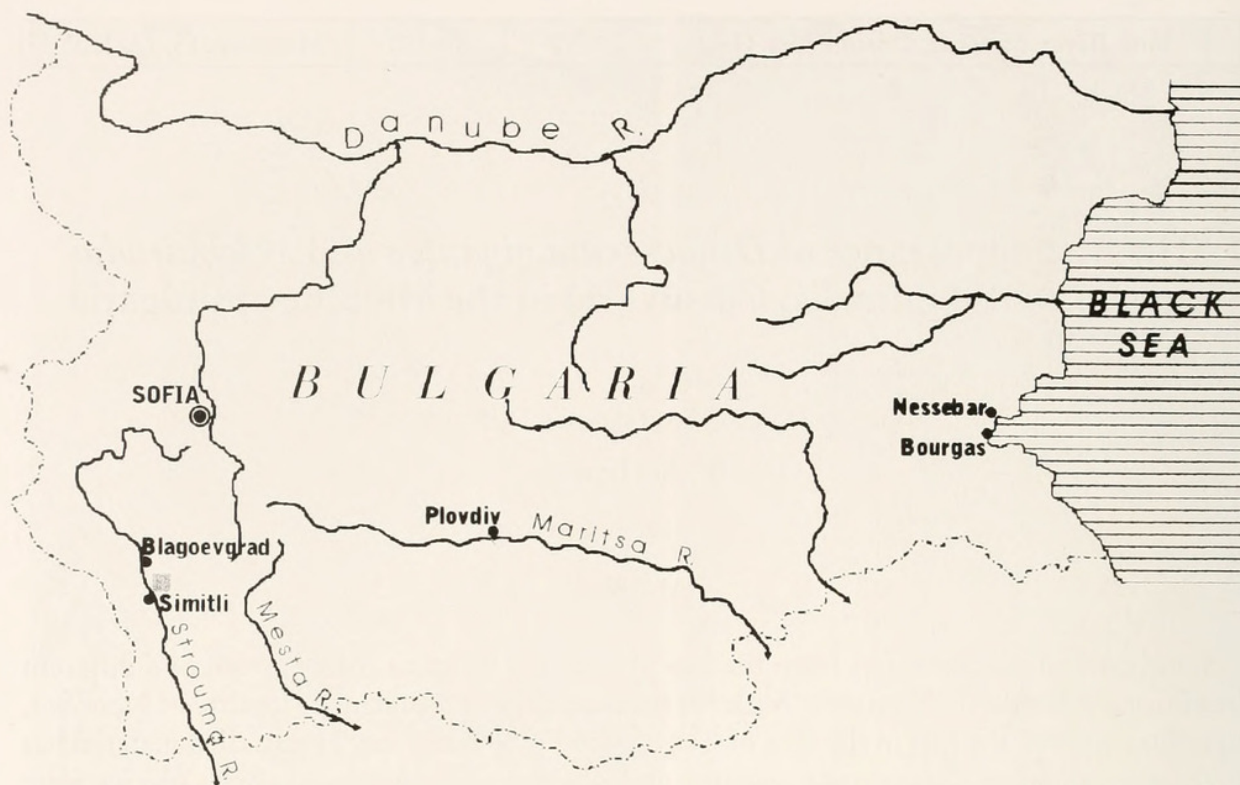
Some interesting carnivores from the late Miocene of Bulgaria coming from two different localities are studied in this article. A part of the material was found in the locality of Nessebar, near Bourgas and the rest in the area of Blagoevgrad (SW Bulgaria). The studied material has been determined to *Dinocrocuta gigantea* and *Machairodus aphanistus*. Both species were unknown in the Bulgarian late Miocene until now and their presence enlarges our knowledge about their distribution. The age of both localities is also discussed on the basis not only of the carnivores but of the rest fauna too. The localities have been dated to Vallesian without possibility for a more precise age (MN biozones) because of the scarce material and the lack of sufficient data.

Kurzfassung

Es werden einige interessante Carnivoren aus den Obermiozän von Bulgarien beschrieben, die aus zwei verschiedenen Gebieten kommen. Ein Teil des Materials wurde an der Lokalität Nessebar bei Burgas gefunden, das übrige im Gebiet von Blagoevgrad (SW-Bulgarien). Das untersuchte Material wurde als *Dinocrocuta gigantea* und *Machairodus aphanistus* bestimmt. Beide Arten waren im bulgarischen Obermiozän bisher unbekannt und ihre Gegenwart erweitert unsere Kenntnis über ihre Verbreitung. Das Alter beider Fundstellen wird nicht nur auf der Basis der Carnivoren, sondern auch der Gesamtfaua diskutiert. Beide wurden ins Vallesium eingestuft, da das spärliche Material und das Fehlen weiterer Daten eine genauere Einstufung (MN Biozonen) nicht erlauben.

*) Addresses of the authors. N. SPASSOV, National Museum of Natural History, Blvd. Tzar Osvoboditel 1, 1000 Sofia, Bulgaria.

G. D. KOUFOS, Aristotle University of Thessaloniki, Laboratory of Geology and Palaeontology, 54006 Thessaloniki, Greece. e-mail: koufos@geo.auth.gr



■ Area of the most probable place of the Blagoevgrad locality

Fig. 1. Map of Bulgaria indicating the geographic position of the localities.

1. Introduction

The late Miocene localities of Bulgaria are quite numerous, while a great amount of fossils have been collected (BAKALOV & NIKOLOV 1962; NIKOLOV 1985; SPASSOV 2000). The material is stored in the National Museum of Natural History (NMNH) of Sofia, its branch in Assenovgrad and in the University of Sofia. Among the collections of the NMNH one of the authors (N. S.) found some remains of carnivores from two different localities. One tooth of a large percrocute and another of a machairodont come from the locality of Nessebar (Fig. 1). The specimens are labeled by I. Nikolov as *Machairodus* sp. Some fragments of teeth and one lower carnassial of a large percrocute are also found with a label referring "*Percrocute senyürekli*" and Blagoevgrad area as their locality. The sediment's remains on the teeth indicate that they come from coal-bearing layers. Probably the teeth were brought to I. Nikolov by some industrial research geologists or the miners.

Since now, the large percrocutes were unknown in the Miocene of Bulgaria and very rare in Europe. In the Balkan Peninsula they are known from three localities. *Percrocute miocenica* is known from the middle Miocene locality of Prebreza, in Yugoslavia (PAVLOVIC & THENIUS 1965). Two large forms are also referred from the late Miocene of Axios valley (Macedonia, Greece), *Dinocrocute gigantea* from the Vallesian locality of "Pentalophos 1" and *Dinocrocute salonicae* from the ?Vallesian locality of Diavata (KOUFOS 1995). The genus *Dinocrocute* is also referred from the ?Turolian localities of Los Aljezares and Ademuz, Spain by few remains (SORIA 1980). Very fragmentary remains, probably belonging to a relatively small *Dinocrocute*, are recently found in the early Turolian locality of Dorn-Dürkheim 1, Germany (MORLO 1997).

The Miocene *Machairodus* finds are also very rare in Bulgaria. A lower carnassial of "*Machairodus schlosseri*" (= *Paramachairodus orientalis*) and a *Machairodus* humerus are referred from Kalimanci district (BAKALOV & NIKOLOV 1962). An undescribed skull associated with the mandible of *Machairodus giganteus* is also known from the Turolian locality of Hadjidimovo and stored in the Palaeontological Museum of Assenovgrad (KOVACHEV pers. comm.; SPASSOV in press). The studied specimen was found in the locality of Nessebar (Fig. 1) and the attribution to *Machairodus aphanistus* certifies the presence of this species in Bulgaria.

2. Localities

The locality of Nessebar (old Turkish cemetery) is situated northeastern to the city of Bourgas across the Bulgarian seashores of the Black Sea (Fig. 1). The initial collection from this locality was described by BAKALOV & NIKOLOV (1962), while later revised by NIKOLOV (1985). According to the later author the deposits consist of sandstones and limestones. The few traces of the sediments on the studied specimens suggest that they possibly come from the sandstone level. The determined mammalian fauna from Nessebar suggests Sarmatian (= Vallesian) age, while the mollusks indicate a middle Sarmatian age (NIKOLOV 1985).

The exact site of the Blagoevgrad material is unknown. Taking in mind, the traces of lignite on the fossils and their taxonomic status, the studied remains originate from the Neogene lignitic deposits of the area. The lignitic deposits outcrop near the villages of Oranovo and Arnautska Mahala, about 10 km south of Blagoevgrad (Fig. 1). The age of the deposits is questionable yet, most probably Sarmatian-Maeotian, i.e. roughly corresponding to Vallesian (MARINOVA 1993).

3. Systematic Palaeontology

Family Percrocutidae WERDELIN & SOLOUNIAS 1991

Genus *Dinocrocuta* SCHMIDT-KITTLER 1976

Dinocrocuta gigantea (SCHLOSSER 1903)
(Figs 2,3)

Localities: Nessebar (old Turkish cemetery), Bourgas area, SE Bulgaria;
Blagoevgrad vicinity (Oranovo - Arnautska Mahala region?), SW Bulgaria.

Age: Vallesian, late Miocene.

Material: Nessebar: Left upper carnassial, FM 1504.

Blagoevgrad: Left P³, FM 1500; fragment of the right upper canine, FM 1502;
fragment of the left lower canine, FM 1501; right lower carnassial, FM 1503.
All specimens from Blagoevgrad probably belong to one individual.

Measurements (in mm):

P⁴ FM 1504: Length=50.8; Length paracone+metacone = 33.9; Breadth at the protocone = (25); Breadth at the parastyle = 16.5

P³ FM 1500: Mesiodistal diameter = 18.0 Buccolingual diameter = 13.5

C^s FM 1502: Mesiodistal diameter = 29.0 Buccolingual diameter = -

M₁ FM 1503: Length = 37.8; Breadth = 18.2; Length of trigonid = 34.3

Description.

P³. It is robust, canine-like (Fig. 3a), flattened laterally and it has a very large contact surface with P². The tip of the cusp is curved distally and preserves a labial and lingual crest. The latter contacts a triangular, well pronounced lingual cingulum.

C³. The available specimen preserves the upper part of the canine having a weak wearing facet for the lower canine on its frontal surface (Fig. 3b).

P⁴. This unique tooth from Nessebar is totally unworn and belongs to a juvenile-subadult individual (Fig. 2). Before the preparation of the tooth part of the maxillary the bone was in connection with the basal half part of the tooth, showing that it was still not completely erupted. The tooth is long and narrow labio-lingually. The lingual surface of the cusp is more rounded than the labial one. The parastyle is relatively reduced, strongly pointed and assymetrical with strongly inclined and much longer mesial surface (Fig. 2c). A well pronounced vertical crest is present in its lingual and mesial surface and a weaker third one between them (Fig. 2c). The enamel crust of the protocone was damaged but we can judge about its form by the calciferous stuffing which forms a "cast" of the protocone. The protocone is reduced and directed obliquely in front and upwards. Its transverse diameter is at least $\frac{1}{3}$ shorter than the transverse diameter of the parastyle. The protocone seems to lack a real tip and it is like a mesiolingual projection of the base of parastyle and paracone (Fig. 2 a,c). The mesial border of the protocone does not exceed the mesial surface of the parastyle, while its distal border reaches the contact between the parastyle and the paracone. A well expressed transversal groove separates the parastyle from the paracone. The paracone is longer, broader and much higher than the parastyle. It preserves a well pronounced crest on its mesial surface, a trace of such a crest from the top on the labio-distal surface, and a sharp edge on its distal surface. The metastyle is slightly higher than the parastyle. It is long, evidently longer than the paracone and it is separated from this cusp by a deep and narrow groove. A slight, groove-like, depression is marked from the top of the labial surface of the metastyle separating this in two (anterior and posterior) parts. In occlusal and lateral view the paracone and metastyle edges form a wide angle, indicating high cutting specialization. A weakly pronounced cingulum is present in the lingual surface of the paracone-metastyle complex. No cingulum exists on the labial surface of the tooth.

C₁. The specimen lacks the root (Fig. 3c). A clear wearing facet is distinguished in its distolabial surface.

M₁. It belongs to an adult individual with strong wearing facet in the para- and protoconid (Figs 3d-f). The lower carnassial has a very strong mesial root and a strong derived trigonid; its vestibular surface is slightly convex and the lingual one slightly concave. The paraconid is longer and broader than the protoconid but the latter is evidently higher than the former. A crest runs across its lingual surface from the tip to the mid-height (Fig. 3d). The paraconid mesial surface is oblique and has a cutting edge, partially worn. Traces of a strong cingulum exist on its vestibular surface. The para- and protoconid are separated by a shallow groove. In occlusal and lateral view the cutting edges form a wide angle, indicating a derived carnivorous structure. The metaconid is absent. The talonid is relatively small and well separated from the trigonid. The entoconid exists and seems to be higher than the hypoconid but this is probably due to the stronger attrition of the vestibular side of the tooth. A small distal cingulum is present behind the two mentioned cuspids of the talonid.

Comparison and discussion:

The studied upper carnassial differs from the large Felidae (*Machairodus*) because it is more robust, lacks a preparastyle and has a relatively shorter metastyle. The lower carnassial differs

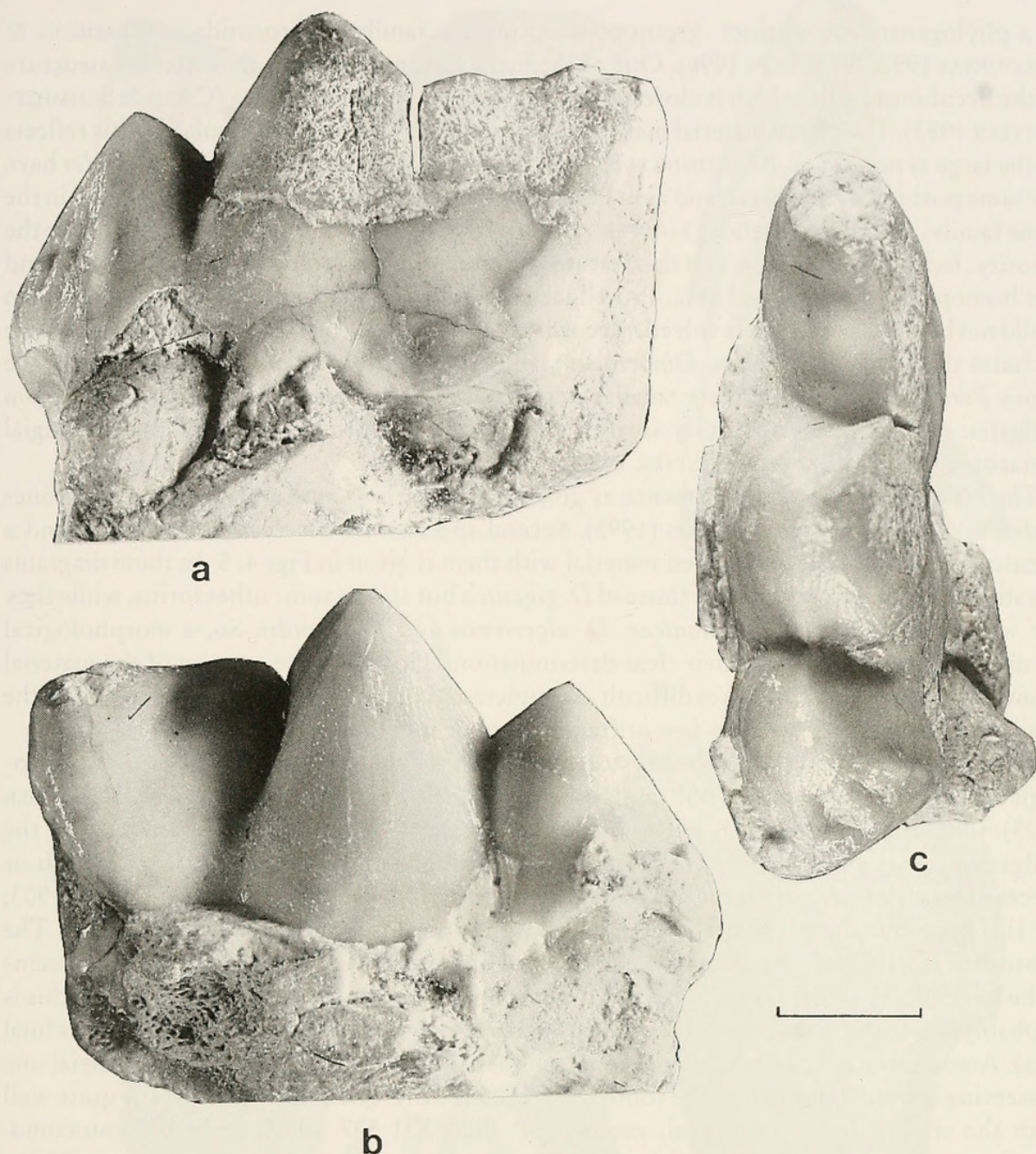


Fig. 2. *Dinocrocuta gigantea*, Nessebar, Bulgaria, Vallesian. Left upper carnassial, FM 1504; a. lingual, b. labial, and c. occlusal view.

in having a longer and broader paraconid, a more developed and wider (not cutting) talonid and an expressed cingulum. The studied P^4 differs from the late Miocene *Barbourofelis piveteaui* from Turkey (GERAADS & GÜLEC 1997) by the absence of the preparastyle, the presence of a protocone, the larger parastyle and the larger dimensions. The lower carnassial is significantly reduced in *B. piveteaui*. It differs from *Adcrocuta* by: a) the larger size, b) the strongly backwardly inclined mesial surface of the parastyle, c) the relatively longer parastyle with stronger lingual crests, d) the more distally situated protocone, e) the less curved laterally distal part of the metastyle, and f) the relatively reduced talonid with the absolute lack of the metaconid. On the contrary their large size and morphology indicate that they belong to the large percrocotids.

The percrocotids were referred to the family Hyaenidae for a long time (KURTÉN 1957; SCHMIDT-KITTLER 1976; HOWELL & PETTER 1985). Recently, they were separated from Hyaenidae

as a phylogenetically distinct group constituting the family Percrocutidae, (WERDELIN & SOLOUNIAS 1991; WERDELIN 1996). One of the main reasons for that is the different structure of the deciduous teeth, which is close to that of *Stenoplesictis* and Felidae (CHEN & SCHMIDT-KITTLER 1983). The scarce material makes the taxonomy of the family difficult and this reflects to the large synonymies. BARISHNIKOV & AVERIANOV (1995) note that the dp_4 of *Proteles* have the same position of the metaconid as in Percrocutidae and those taxa should be included in the same family. As far as Protelidae GEOFFROY 1851 is a senior synonym this name must have the priority. Indeed, if we assume that this feature is homologous in Percrocutidae and *Proteles* and not homoplastic for the noted taxa, Protelidae should be the valid name. The raised problem could not be considered finally solved. According to WERDELIN (1996) the family Percrocutidae includes the genera *Percrocuta*, *Dinocrocuta*, and possibly *Allohyaena*. The members of the genus *Percrocuta* have definitely smaller dental dimensions than the studied remains from Bulgaria. *Allohyaena* is obviously smaller, having a robust protocone on P^4 and a vestigial metaconid on M_1 (HOWELL & PETTER 1985).

The main characters of *Dinocrocuta* as given by the various authors with some new ones added are summarized in KOUFOS (1995). Several species of *Dinocrocuta* are known and a metrical comparison of the studied material with them is given in Figs 4, 5. In these diagrams the studied teeth are very close to those of *D. gigantea* but also to some other forms, while they are well separated from *D. salonicae*, *D. algeriensis* and *D. grandis*. So, a morphological comparison is necessary for their clear determination. However, the scarcity of the material from the various localities makes difficult a complete and certain comparison. In most cases the available material is either very few or fragmentary or it belongs to different jaws.

The type material of *D. gigantea* is stored in the Bayerische Staatssammlung für Paläontologie und Geologie, München (BSP) and comes from an unknown locality of China (SCHLOSSER 1903). One of the authors (G. K.) studied this chinese material and a comparison with the Bulgarian one is given below. The material is very fragmentary, including isolated teeth or pieces of teeth, while a part of the material is missing, i.e. one upper carnassial (SCHLOSSER 1903; pl. II, fig.2). But the illustrations of the last author are nice and allow a comparison. The protocone is strongly reduced like in the studied upper carnassial, while the parastyle seems to be larger in the studied one. The cusps of the chinese specimen seem to be higher but this is probably due to the young age of the studied tooth (it is not fully erupted in order to get its final size). Among the type material there is one complete M_1 (BSP 1900 XII 537) and a partial one preserving the posterior half of the tooth (BSP 1900 II 524). Their morphology fits quite well with the studied lower carnassial, except BSP 1900 XII 537 which lacks the entoconid. Concerning the size of the studied material it is very close to that of *D. gigantea* from China (Figs 4, 5).

A mandible of *D. gigantea* has been described from the Vallesian locality of „Pentalophos 1“ (PNT) of Axios valley, Macedonia, Greece (KOUFOS 1995). The studied M_1 has a similar size and morphology with the Pentalophos one. The latter has a slightly larger talonid and in the basis of the distal edge of the protoconid there is a small incision. According to one of us (N. S.) this incision indicates the position of the metaconid. A maxilla with P^2 - P^4 of a percrotutid is also known from the locality of Diavata in Axios valley (ANDREWS 1918). The specimen was initially referred to „*Hyaena*“ *salonicae* and later it followed all the taxonomic changes of the percrocutids. However, its characters indicate that it belongs to *Dinocrocuta* and it is referred as *D. salonicae* with strong similarities to *D. senyürekli* and *D. grandis* (KOUFOS 1995). The studied P^4 is larger than that of *D. salonicae* and evidently slender; the robusticity index of the former tooth is 49 versus 55.5 in *D. salonicae*. The most significant difference is the larger protocone of *D. salonicae* which is well separated from the parastyle and has well marked tip. A detailed comparison for the distinction of *D. salonicae* from *D. gigantea* is given in KOUFOS (1995).

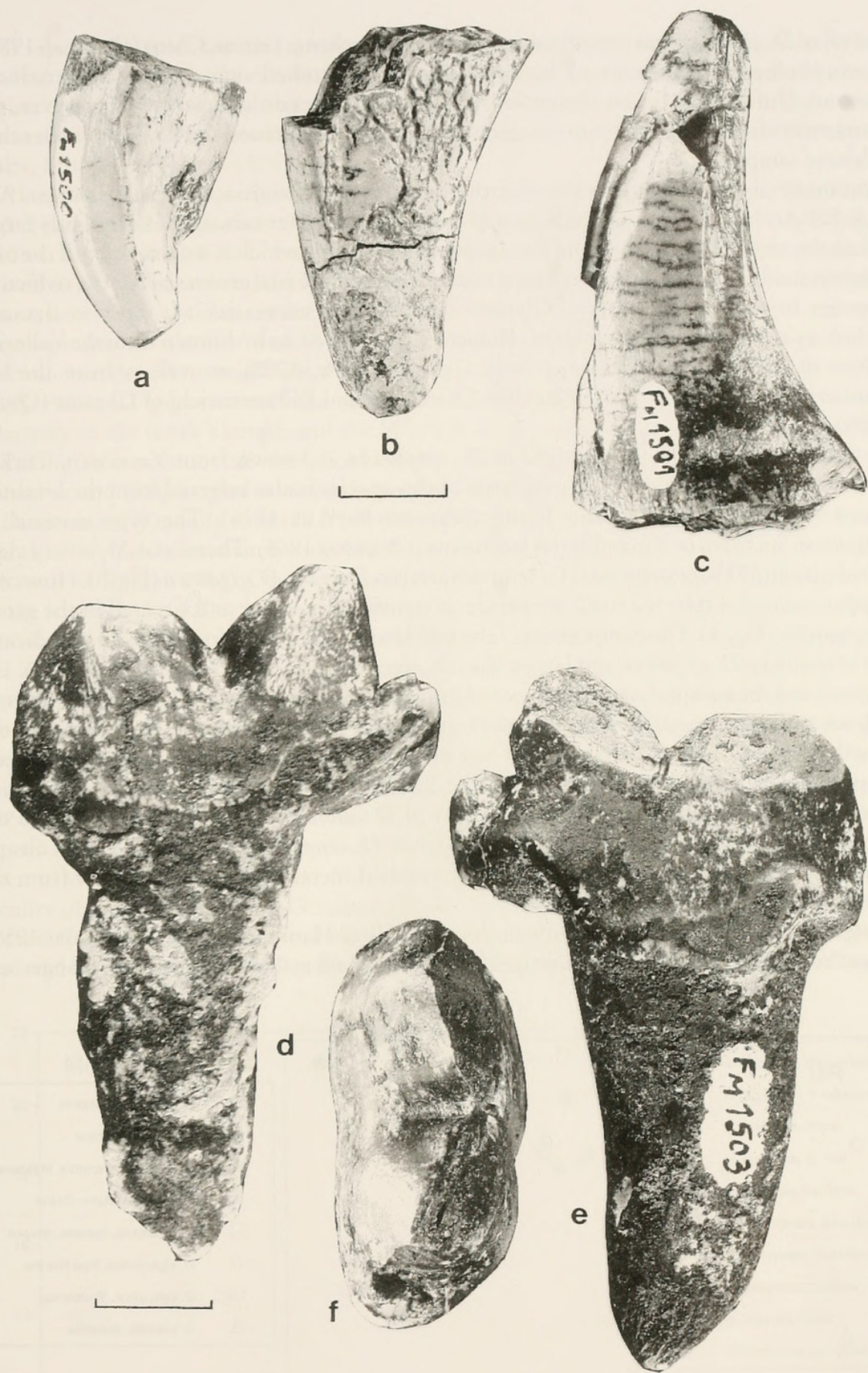


Fig. 3. *Dinocrocuta gigantea*, Blagoevgrad district, Bulgaria, ?Vallesian. a. Left I3, FM 1500, labial view. b. Fragment of the right upper canine, FM 1502, lingual view. c. Fragment of the left lower canine, FM 1501, labial view. d-f. Right lower carnassial, FM 1503; d. lingual, e. labial and, f. occlusal view.

A skull of *D. gigantea* was recently described from Hezheng, Gansu, China (QIU et al. 1988). The morphology of P⁴ seems to be similar with the studied one, preserving a reduced protocone. Unfortunately, no dimensions are given for certain comparison. However, the measurements from the illustrations suggest that the studied carnassial is slightly smaller than the chinese sample.

Some material of *D. gigantea* is known from the locality of Varnitsa, Moldavia (LUNGU 1978; figs 18, 20). According to his description and drawings the upper carnassial is of slightly larger size than the studied one (Fig. 4) and has a reduced protocone which is a continuity of the base of paracone and parastyle. In this feature it resembles to the studied carnassial but the reduction is stronger in the Moldavian one. Concerning the lower carnassial it is close in size and morphology to the Moldavian material. *Dinocrocutea gigantea* is also known from the Vallesian localities of Eldari 1 and Natlismtsemeli, Georgia (NOW, 2002), as well as from the late Sarmatian (=Vallesian) localities of Buzhor 2, Gritchev and Klimentovichi of Ukraine (QIU et al. 1999).

An interesting percrocutid, referred as *D. senyürekli*, is known from Yassiören, Turkey (OZANSOY 1965). Some fragmentary material of this species is also referred from the localities of Esme-Akcakoy, Kayadibi and İnönü (SCHMIDT-KITTLER 1976). The type material of *D. senyürekli* includes two mandibular fragments (OZANSOY 1965). The size of M₁ is very close to *D. robusta* and *D. algeriensis* and far from what it is referred as *D. gigantea* (Fig. 5). However, the upper carnassial referred to *D. senyürekli* is significantly larger and situated in the group of *D. gigantea* (Fig. 4). The comparison of the whole upper dentition from Yassiören indicates that it is closer to *D. gigantea* and larger than *D. algeriensis*, *D. salonicae* and *D. robusta*. On the other hand the comparison of the lower dentition shows that it is smaller than *D. gigantea* and closer to *D. algeriensis*, *D. robusta* and *D. grandis* (KOUFOS 1995; figs 4, 5). This difference means that either the two specimens do not belong to the same species or there is a great intraspecific size variability. Nevertheless, the Yassiören upper carnassial has a strong, well separated and high pointed protocone like that of *D. salonicae* and differs clearly from the studied Bulgarian material. The lower carnassial of *D. senyürekli* from Yassiören is clearly smaller than that of the studied M₁, while the residual metaconid differentiates it from the studied one.

D. algeriensis is referred from the Vallesian locality of Bou-Hanifia, Algeria (ARAMBOURG 1959). Besides the smaller size (Fig. 4, 5) it differs from the studied material in having a stronger and

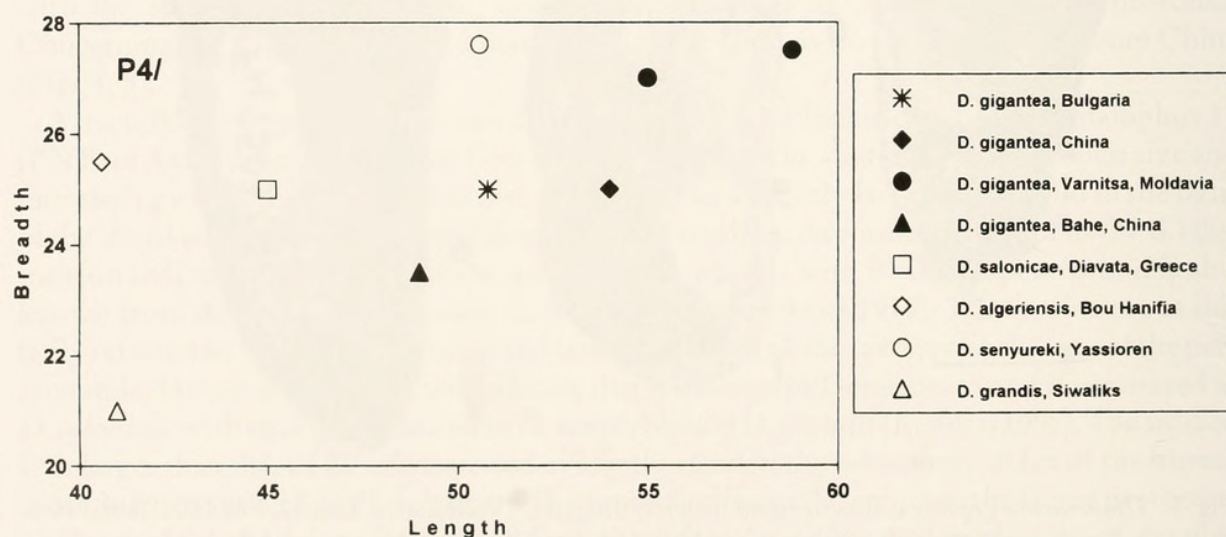


Fig. 4. Scatter diagram comparing length / breadth of the upper carnassial in various species of *Dinocrocutea*.

well separated protocone and a more robust P^4 (the robusticity index is 63 versus 49 in the studied carnassial). *D. algeriensis* differs from the studied lower carnassial by the shorter and higher trigonid, the relatively more robust and tricuspid talonid and the presence of a vestigial metaconid. The studied teeth differ approximately in the same features from *D. robusta* of Kalfa, Moldavia (LUNGU 1978).

A maxillary fragment with P^2 - P^4 (V. 3093) is known from the Bahe Formation, Shanxi, China and it is referred as *Crocuta* (*Percrocuta*) *macrodonta* and later transferred to *D. gigantea* (HOWELL & PETTER 1985). The shape of the protocone of P^4 is closer to that of the studied one, as well to *D. gigantea* from the Vallesian of Varnitsa, Moldavia. The Chinese and Moldavian forms, however, have more reduced protocones than the studied upper carnassial and may be they represent another form of *D. gigantea* which can belong to a different subspecies, *D. g. macrodonta*. A percrocutid from the Siwaliks, India is known as *D. grandis*. It is remarkably smaller than *D. gigantea* and the studied teeth. Moreover, the metacone of P^4 is shorter relatively to the tooth's length and the M^1 is relatively to P_4 shorter than in *D. gigantea*.

Taking into account all the above mentioned comparisons the studied material from Nessebar and Blagoevgrad must be determined to *Dinocrocuta gigantea*.

Dinocrocuta is mainly referred from the Vallesian of Europe but it is also known from the Turolian. It is rarely associated with *Adcrocuta* and this co-existence is probably not coincidence (HOWELL & PETTER 1985). On the other hand, this rarity is not accepted by WERDELIN (1996). In the lower Axios valley, Greece *Dinocrocuta* was found alone in the Vallesian localities of Pentalophos 1 and Diavata. But, in the slightly younger localities of Ravin de la Pluie, Ravin des Zouaves 1 and Xirochori 1 only *Adcrocuta* is present. Although the two genera have not been found together in any of these localities, they co-exist during Vallesian. Besides this, *Dinocrocuta* is associated with other small hyaenids; in Pentalophos 1 it was found together with *Protictitherium* cf. *crassum* (KOUFOS 2000a). The genus *Adcrocuta* is certainly known from late Vallesian of Greece (KOUFOS 2000a), while its presence is possible in Spain (ALBERDI, 1974) and France (HOWELL & PETTER 1985). *Adcrocuta* gets its great expansion in Turolian and especially in MN 12. During that time the remains of *Adcrocuta* are numerous in the various circum-Mediterranean localities. Moreover the two genera co-exist in the early Turolian locality of Dorn-Dürkheim 1, Germany (MORLO 1997) and Los Aljezares, Spain (SORIA 1980). So, it is clear that *Dinocrocuta* and other percrocutids lived in the Vallesian and they have been replaced by *Adcrocuta* in the Turolian; however both genera co-exist in the Vallesian/Turolian

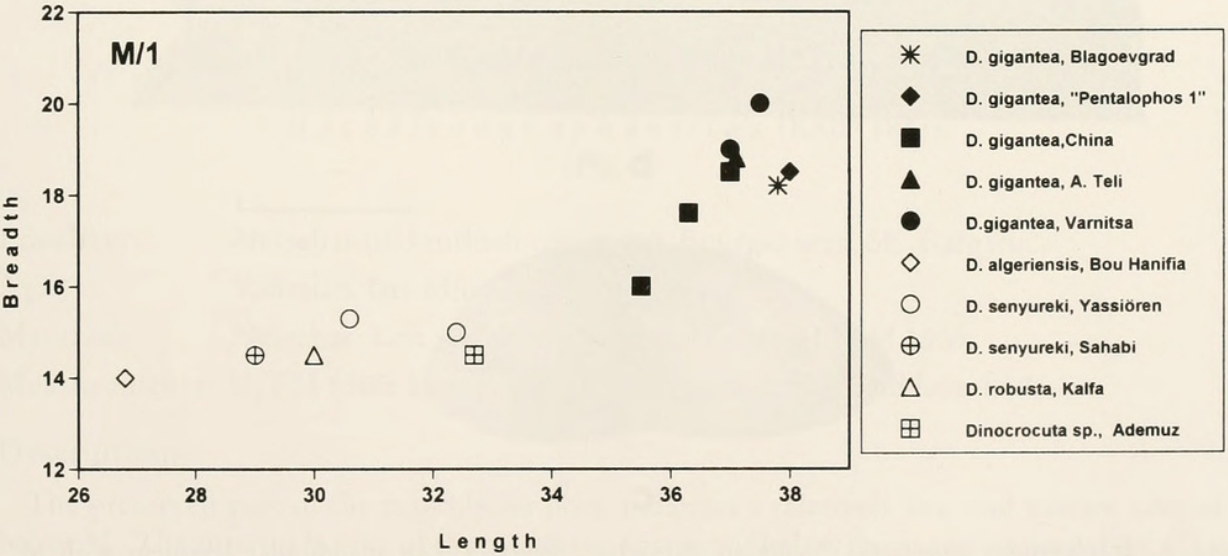


Fig. 5. Scatter diagram comparing length / breadth of the lower carnassial in various species of *Dinocrocuta*.

transition. It is necessary to refer here that *Dinocrocuta* re-appears again in the Pliocene of Sahabi with the species *D. senyürekli* (HOWELL 1984), if the age of Sahabi fauna is true. The question is why *Dinocrocuta* and the other percrocutids disappeared and they were replaced by the derived hyaenas like *Adcrocuta*?

The dispersion of the derived hyaenas could be the reason and it is probably due to unknown ecological differences shaping the evolution of the bone-cracking hyaenas and the late percrocutids (WERDELIN 1996). *Adcrocuta* resembles to the recent *Crocuta* in cranial and

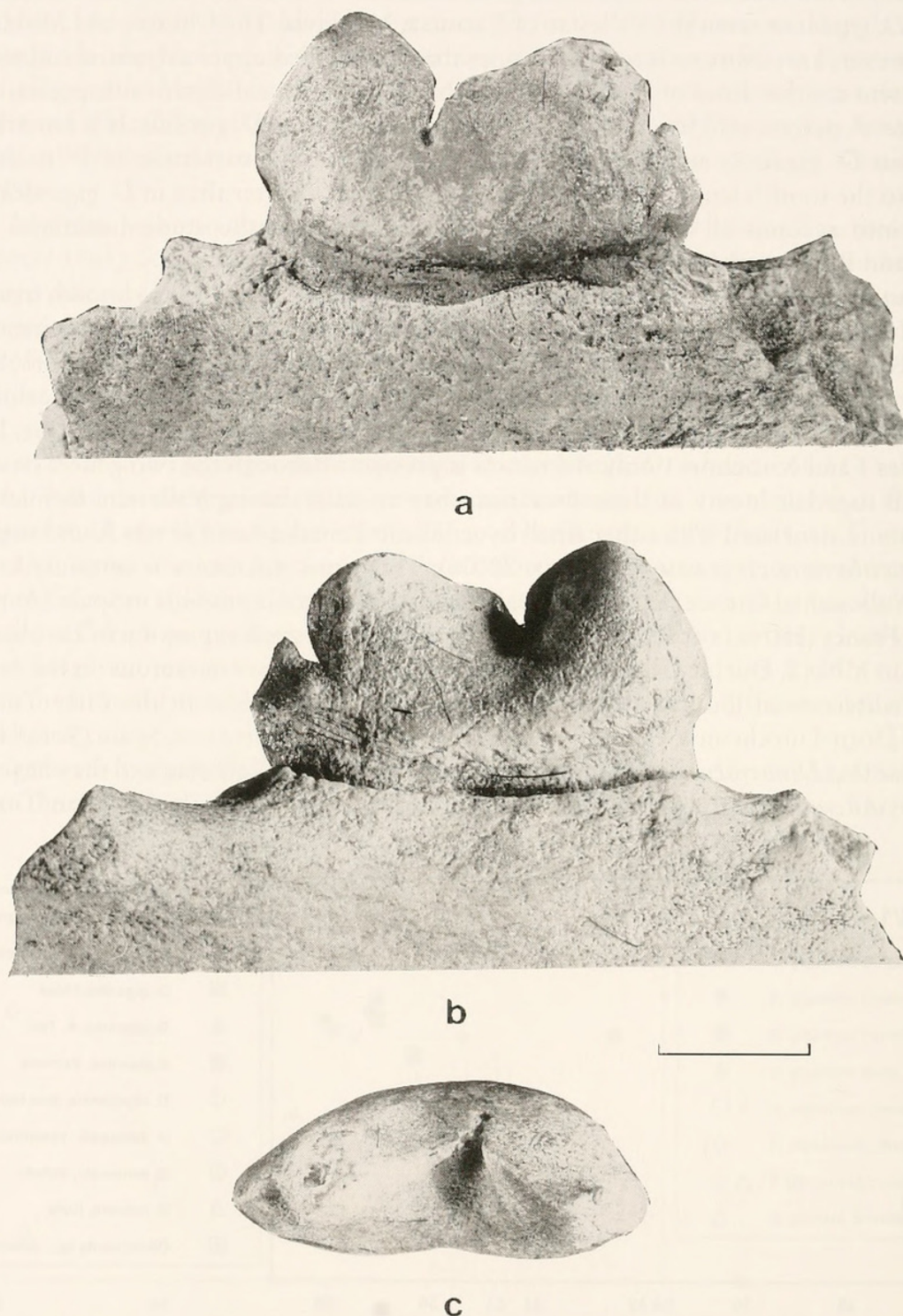


Fig. 6. *Machairodus aphanistus*, Vallesian, Nessebar, Bulgaria. Left mandibular fragment with M_1 , FM 1505; a. labial, b. lingual, and c. occlusal view.

skeletal morphology, while the analysis of the palaeoenvironment in *Adcrocuta* bearing localities suggests a mode of life close to the recent. That means a social, active and rapid carnivore, hunting by pursuit and at the same time a bone-cracking scavenger; it inhabited relatively open environments (savanna-like open forests and “forest-steppe” habitats). *Dinocrocuta*, on the other hand, has robust and long canines, evolved carnassials and its premolars are bulbous enough to break bones. Thus, this percrocutid attains to one or other extent the trophic specialization of the derived hyaenas and, as it seems, earlier than them. Although it was found in the Turolian of Europe, Asia and Africa too, *Dinocrocuta* is known mostly from the Vallesian or Vallesian/Turolian localities. Moreover, *Dinocrocuta* has been found in much less localities than *Adcrocuta* and the remains are rather scarce everywhere. Having in mind the more wet climate of Vallesian relatively to Turolian in Southeastern Europe and the scarcity of the *Dinocrocuta* remains one could suppose that the habitats typical for this predator were sylvatic. Two arguments support this statement: the discovery of *D. gigantea* remains in the coal layers near Blagoevgrad (Bulgaria) and the more close and wet palaeoenvironment in late Vallesian than in Turolian of Northern Greece (BONIS et al. 1999). The noted morpho-functional characteristics of *Dinocrocuta*, to which we could add the rather large size, together with the taphonomic and chronological distinctions of the localities permit the assumption that *Dinocrocuta* is a large, solitary supercarnivore with low population size and density compared to *Adcrocuta* (this is yet another reason for the scarcity of the percrocutid remains). *Dinocrocuta* should be adapted to kill by ambushing large prey and also to scavenge mostly on carcasses of large animals. The aridity taking place during Turolian gives an advantage to *Adcrocuta*. In the new palaeoecological conditions *Dinocrocuta* is “pressed” between the ecological niches of *A. eximia* and the large Turolian *Machairodus giganteus* (it pursues and kills large animals, feeding on their carcasses for long period, and inhabits relatively open landscapes). This is a strong reason for the disappearance of *Dinocrocuta* first from Southeastern and Eastern Europe, where the climatic conditions were more arid, even in the Vallesian. The genus survives longer in isolated regions (Spain) or in the northern more forestial territories which preserved habitats that were more suitable for its ecology (Germany). There it could co-exist with *Adcrocuta* in conditions of more diverse environment, occupying different ecological niches. This co-existence is also justified at the end of Vallesian beginning of Turolian representing the transitional time period for the replacement of one genus by the other.

Family Felidae GRAY 1821

Genus *Machairodus* KAUP 1833

Machairodus aphanistus (KAUP 1833) (Fig. 6)

Locality: Nessebar (old turkish cemetery), Bourgas area, SE Bulgaria.

Age: Vallesian, late Miocene.

Material: Nessebar: Left mandibular fragment with M_1 , FM 1505.

Measurements: M_1 FM 1505: Length=30.0; Breadth=12.8; Trigonid length=26.1.

Description:

The preserved part of the mandibular bone indicates a relatively low and narrow corpus below M_1 . The anterior border of the masseteric fossa ends below the posterior part of M_1 . The carnassial has typical felid features with very strong trigonid, wide angle between the cutting

blades and very reduced and labio-lingually compressed (“cutting”) talonid (Fig. 6). The labial surface is slightly convex and the lingual one straight to concave. The para- and protoconid are worn, having wearing facets on their labial surface and almost equal height. The protoconid is slightly longer and wider than the paraconid. Its cutting mesial edge is slightly longer than the cutting distal edge of the paraconid and both form a wide angle with a deep vertical groove in the lateral surface. A visible metaconid-talonid complex (where the metaconid is distinct as a small point just behind the distal ridge of the protoconid) is present at the distal end of the tooth. It is separated from the protoconid by a well expressed groove and has a cutting distal edge.

Comparison and discussion:

According to the revision of BEAUMONT (1975) two machairodonts are known in late Miocene of Europe, *Machairodus aphanistus* in the Vallesian and *Machairodus giganteus* in the Turolian (the latter includes also the Chinese forms *M. palanderi* and *M. tingii*, which could be probably regarded as geographic subspecies). The recently described (SOTNIKOVA 1999)

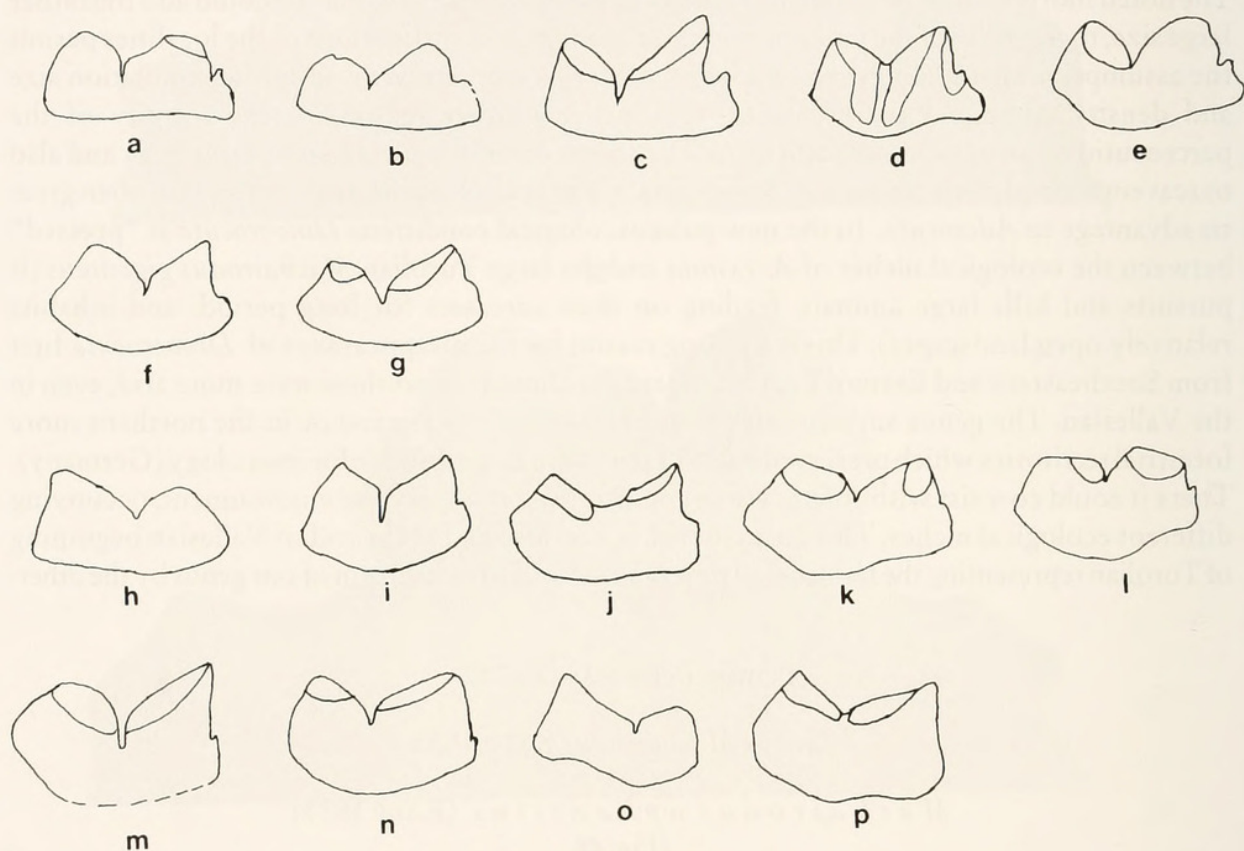


Fig. 7. Morphology of the lower carnassial in *Machairodus* from various Eurasian localities. a. *M. aphanistus*, FM 1505, Nessebar, Bulgaria. b. *M. aphanistus*, KTD-163, Kemiklitepe, Turkey (BONIS 1994). c. *M. cf. aphanistus* MTN-3173, Montredon, France (BEAUMONT 1988). d. *M. aphanistus*, Cm 244, Charmoille (BEAUMONT 1975). e. *M. aphanistus*, TD 1177, Eppelsheim, Germany (BEAUMONT 1975). f. “*M. laskarevi*” (= *M. aphanistus*), TGPI-1/2257, Kalfa, Moldavia (SOTNIKOVA 1992). g. “*M. aphanistus*” (= *M. giganteus*), Mahmutgazi, Turkey (SCHMIDT-KITTLER 1976). h. *M. giganteus*, Slq-936, Axios valley, Greece (ARAMBOURG & PIVETEAU 1929). i. *M. giganteus*, Pikermi, Greece. (WAGNER, 1857). j. *M. giganteus*, Inst. Palaeont. Vienna, Pikermi, Greece (BEAUMONT 1975). k. *M. giganteus*, AMNH 20606, Samos, Greece (BEAUMONT 1975). l. *M. giganteus*, Museum Berne, Samos, Greece (BEAUMONT 1975). m. *M. cf. giganteus*, Pavlodar (BEAUMONT 1975). n. *M. giganteus*, Taraklia, (BEAUMONT 1975). o. *M. ex gr giganteus*. Baccinello, Italy (ROOK et al. 1991). p. “*M. kurteni*”, Kalmakpai, Kazakstan (SOTNIKOVA 1992).

M. kurteni is very close to *M. giganteus*, while *M. laskarevi* resembles to *M. aphanistus*. *M. alberdiae* from Spain is synonymized with *M. aphanistus* (BEAUMONT 1988). *M. romeri* from Turkey with a plesiomorphic lower carnassial and double mesial blade on the upper canine could be a separate species or a subspecies of *M. aphanistus* (SCHMIDT-KITTLER 1976; MORLO 1997).

The two species *M. aphanistus* and *M. giganteus* are well distinguished by a series of characters. Concerning the lower carnassial two morphotypes have been recognized:

- a. The first and more primitive has a relatively broad (cutting and crushing) trigonid and a well expressed metaconid-talonid complex (plesiomorphic). It is present in *M. aphanistus* of Eurasia (incl. *M. "laskarevi"* and *M. "romeri"* as well as *M. alberdiae* from Spain).
- b. The other has a relatively narrow and cutting trigonid with a very reduced talonid, expressed as a basal prolongation of the cutting distal edge of the protoconid. The metaconid is not distinct from the talonid, nor from the distal surface of the protoconid (apomorphic). This morphotype is known in the later forms: *M. giganteus* of Eurasia (incl. *M. g. copei* from Grebeniki) and *M. kurteni* from Kalmakpai – Kazakhstan.

The first morphotype is quite clear in the type specimen from Eppelsheim, as well as in the material from Montredon and Charmoille (Fig. 7 c–e). In the Turolian *M. giganteus* the metaconid-talonid complex is quite reduced with variable development from rudimentary to absent. Even when it is present it seems like a distal cingulum (Fig. 7k–n). The size of the lower carnassial is also different in the two species. Although there is an overlapping (e.g. the studied material has the size of the Pikermi *M. giganteus*) the mean size of *M. aphanistus* is smaller than that of *M. giganteus* (Fig. 8). In this case the morphological characters of the tooth can easily distinguish the two species.

The studied tooth from Nessebar has a large metaconid-talonid complex which is clear and well distinguished (Fig. 7a). In this feature it is very similar to the type material from Eppelsheim, as well as to that from Montredon (Fig. 7c,e). *M. aphanistus* was recently described from the locality of Kemiklitepe-D, in Turkey (BONIS 1994). Even taking into account the bad preservation, the metaconid-talonid complex is important and large, like in the studied specimen. This locality is dated to early Turolian, MN 11 (BONIS et al. 1994) and represents an evidence for the presence of the species in Turolian.

The comparison with the lower carnassial of the typical Turolian material distinguishes the studied tooth clearly. A piece of mandible with P₄-M₁ is known from the Turolian of Axios valley and referred as *M. aphanistus* (ARAMBOURG & PIVETEAU 1929). Recently it was transferred

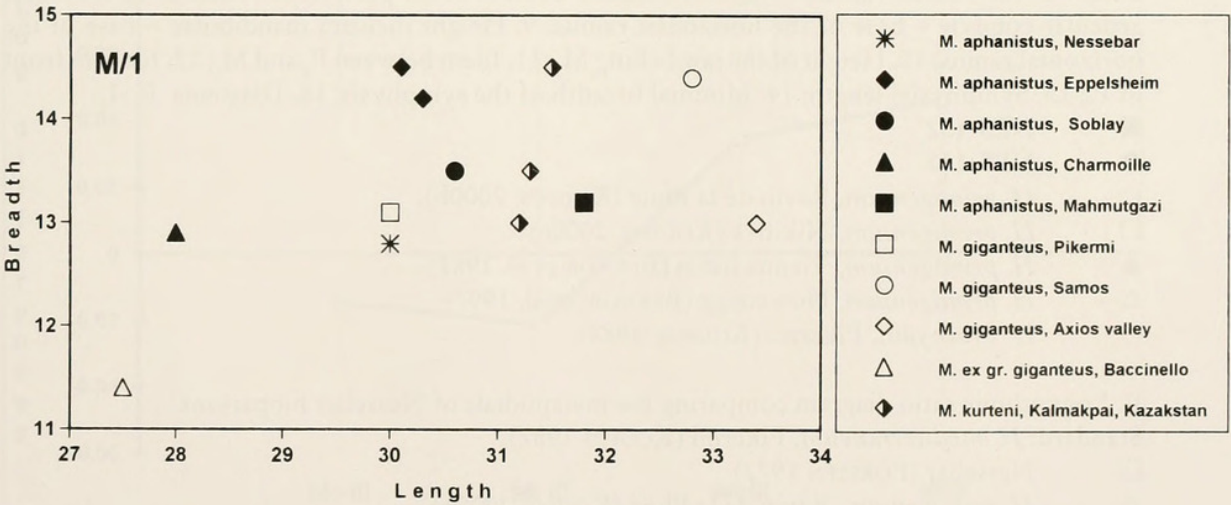


Fig. 8. Scatter digramm comparing length / breadth of the lower carnassial in *Machairodus* from various localities.

to *M. giganteus* (KOUFOS 2000a). The absence of the metaconid-talonid complex in this specimen separates it clearly from the studied M_1 (Fig. 7h). Several specimens of *M. giganteus* are known from Pikermi and Samos (Fig. 7i-l). They preserve a metaconid-talonid complex which is more strongly reduced than that of the studied specimen.

A mandibular fragment from Mahmutgazi (Turkey) has been described as *M. aphanistus* (SCHMIDT-KITTLER 1976). The size of the lower carnassial is somewhat larger than the typical *M. aphanistus* from Eppelsheim, taking a position between this species and *M. giganteus* (Fig. 8). The morphology of the tooth as it is shown in the illustration (SCHMIDT-KITTLER 1976, pl. 4; fig. 5) is closer to *M. giganteus*. The metaconid-talonid complex is not large but it is like a vestigial distal projection of the cingulum (Fig. 7g). Based on this character the Mahmutgazi specimen seems to be closer to *M. giganteus* and distinct from the studied one.

Some remains of a machairodont from Baccinello (Italy) are referred as *M. ex gr. giganteus* (ROOK et al. 1991). The size of M_1 is very small comparatively to the other material of both *M. aphanistus* and *M. giganteus* (Fig. 8), while the metaconid-talonid complex is practically absent (Fig. 7o). In this feature it is closer to *M. giganteus* from Axios valley but the size is significantly smaller. As the late Miocene faunas of Italy are isolated this size reduction probably represents an adaptation of *M. giganteus* to the local palaeoecological conditions.

A small-sized machairodont, named *M. alberdiae* is known from the Vallesian of Spain (GINSBURG et al. 1981). Besides the smaller size it also differs from the studied specimen in having a relatively stronger metaconid. *M. kurteni* from the latest Turolian locality of Kalmakpai, Kazakhstan (C. Asia) has similar size of M_1 (Fig. 8) but it differs strongly by the total lack of metaconid-talonid complex (Fig. 7p). It is very close to *M. giganteus* representing the most evolved stage of the upper and lower carnassial of this species (SOTNIKOVA 1992).

A mandible of a machairodont from Kalfa, Moldavia (upper MN 9) has been described under the name *M. laskarevi* (LUNGU 1978). It is very close to *M. aphanistus* both in size (Fig. 8) and morphology (SOTNIKOVA 1992). It preserves a small P_2 in the right branch which may be is an individual variability at the very early stage of *M. aphanistus*. The M_1 is similar to the studied one (Fig. 7f).

Fig. 9. A. Logarithmic ratio diagram comparing the mandible of Nessebar hipparions. Standard: *H. mediterraneum*, Pikermi (KOUFOS 1987). 2. Muzzle length: middle of the line connecting the anterior borders of P_2 to a point situated between the two I_1 ; 3. Premolar length (alveolar); 4. Molar length (alveolar); 5. Toothseries length (alveolar); 6. Distance from posterior end of M_3 – posterior border of the vertical ramus; 7. Muzzle breadth: breadth at the posterior borders of I_3 ; 8. Height articular condyle – base of the horizontal ramus; 9. Height incisura mandibulae – base of the horizontal ramus; 10. Height of the jaw behind M_3 ; 11. Idem between P_4 and M_1 ; 12. Idem in front of P_2 ; 13. Symphyseal length; 14. Minimal breadth of the symphysis; 16. Diastema P_2 – I_3 .

- NES-132
- NES-133
- ◇ *H. primigenium*, Ravin de la Pluie (KOUFOS 2000b).
- *H. primigenium*, Nikiti-1 (KOUFOS 2000c)
- ▲ *H. primigenium*, Vienna basin (BERNOR et al. 1988)
- △ *H. primigenium*, Höwenegg (BERNOR et al. 1997)
- *H. brachypus*, Pikermi (KOUFOS 1987).

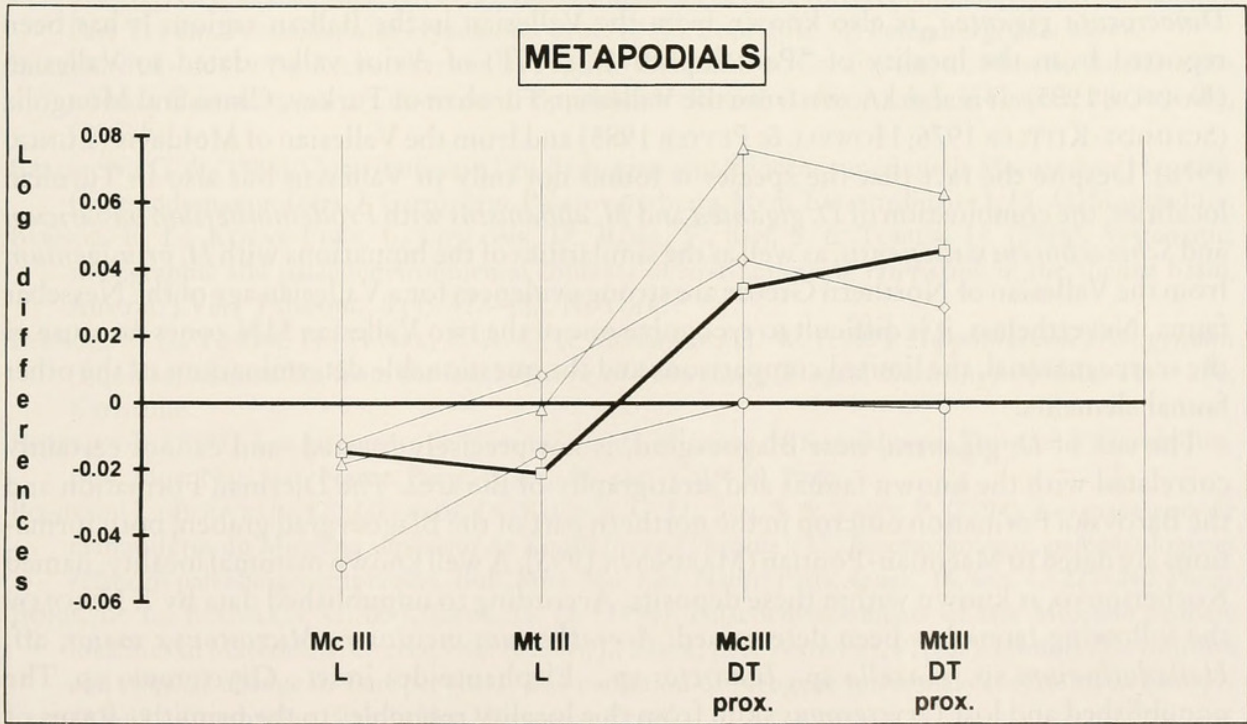
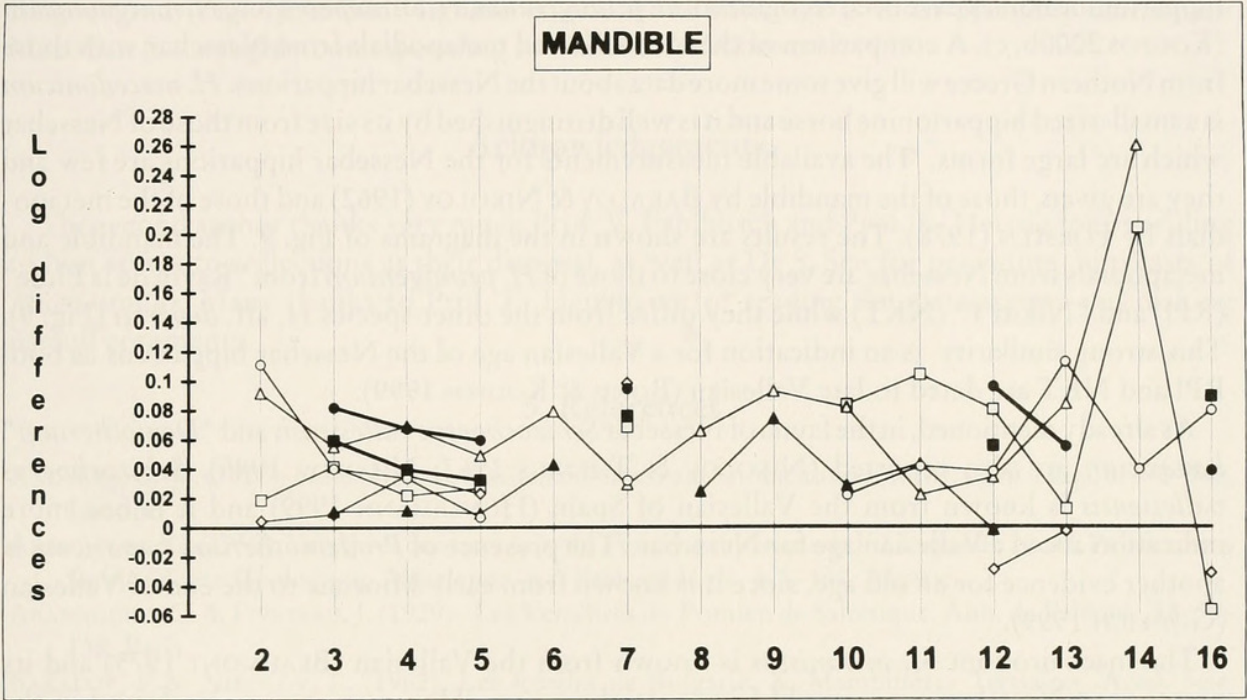
B. Logarithmic ratio diagram comparing the metapodials of Nessebar hipparions. Standard: *H. mediterraneum*, Pikermi (KOUFOS 1987).

- Nessebar (FORSTÉN 1972)
- △ *H. primigenium*, Ravin de la Pluie (KOUFOS 2000b).
- ◇ *H. primigenium*, Nikiti-1 (KOUFOS 2000c)
- *H. cf. depereti*, Pentalophos 1 (KOUFOS 2000b).

The above-mentioned morphological and metrical comparisons of the studied tooth from Nessebar allow the determination to *Machairodus aphanistus*.

4. Biochronology

According to the Eastern Paratethys marine biostratigraphy the locality of Nessebar is considered as Sarmatian (= Vallesian). The fauna includes the following species: *Hipparion mediterraneum*, *Hipparion nessebicum* and *Deinotherium giganteum* (BAKALOV & NIKOLOV



1962). Later on, another faunal list is given for Nessebar including the species: *Hipparion nessebricum*, *Hipparion praesulcatum*, *Deinotherium bavaricum* and *Schizochocerus vallesiensis*. The proposed age is again Sarmatian (= Vallesian), (NIKOLOV 1985).

According to the description of BAKALOV & NIKOLOV (1962) and NIKOLOV (1985) both hipparions from Nessebar are large-sized forms with rich enamel plication, the plis are narrow and deep and resemble to those of Vallesian forms. The characters of the Nessebar hipparions are: relatively massive metapodials, oval to pearshaped preorbital fossa situated far from the orbit, long and narrow protocone and rich enamel plication (FORSTÉN 1978). These characters suggest a primitive hipparionine horse. In the wider Balkan peninsula the Vallesian is well known from Northern Greece, where five different localities are known. Three different hipparionine horses have been recognized, *H. primigenium*, *H. aff. depereti* and *H. macedonicum* (KOUFOS 2000b, c). A comparison of the mandible and metapodials from Nessebar with those from Northern Greece will give some more data about the Nessebar hipparions. *H. macedonicum* is a small-sized hipparionine horse and it is well distinguished by its size from those of Nessebar which are large forms. The available measurements for the Nessebar hipparions are few and they are given, those of the mandible by BAKALOV & NIKOLOV (1962) and those of the metapodials by FORSTÉN (1978). The results are shown in the diagrams of Fig. 9. The mandible and metapodials from Nessebar are very close to those of *H. primigenium* from "Ravin de la Pluie" (RPL) and "Nikiti 1" (NKT) while they differ from the other species *H. aff. depereti* (Fig. 9). This strong similarity is an indication for a Vallesian age of the Nessebar hipparions as both RPL and NKT are dated to late Vallesian (BONIS & KOUFOS 1999).

As already mentioned, in the fauna of Nessebar *Schizochocerus vallesiensis* and "*Deinotherium*" *bavaricum* are also reported (NIKOLOV & THENIUS 1967; NIKOLOV 1985). *Schizochocerus vallesiensis* is known from the Vallesian of Spain (HÜNERMANN 1999) and it is one more indication about a Vallesian age for Nessebar. The presence of *Prodeinotherium bavaricum* is another evidence for an old age, since it is known from early Miocene to the end of Vallesian (GÖHLICH 1999).

The machairodont *M. aphanistus* is known from the Vallesian (BEAUMONT 1975) and its presence in Nessebar gives an old feature to the fauna. However, it was also found in the locality "Kemiklitepe D" (KTD) of Turkey which is dated to MN 11 (BONIS et al. 1994). *Dinocrocuta gigantea* is also known from the Vallesian in the Balkan region. It has been reported from the locality of "Pentalophos 1" (PNT) of Axios valley dated to Vallesian (KOUFOS, 1995). It is also known from the Vallesian-Turolian of Turkey, China and Mongolia (SCHMIDT-KITTLER 1976; HOWELL & PETTER 1985) and from the Vallesian of Moldavia (LUNGU 1978). Despite the fact that the species is found not only in Vallesian but also in Turolian localities, the combination of *D. gigantea* and *M. aphanistus* with *Prodeinotherium bavaricum* and *Schizochocerus vallesiensis*, as well as the similarities of the hipparions with *H. primigenium* from the Vallesian of Northern Greece are strong evidences for a Vallesian age of the Nessebar fauna. Nevertheless, it is difficult to recognize one of the two Vallesian MN zones because of the scarce material, the limited comparisons and the questionable determinations of the other faunal elements.

The site of *D. gigantea*, near Blagoevgrad, is not precisely located and cannot certainly be correlated with the known faunas and stratigraphy of the area. The Djerman Formation and the Barovska Formation outcrop in the northern part of the Blagoevgrad graben; both formations are dated to Maeotian-Pontian (MARINOVA 1993). A well known mammal locality, named Kocherinovo, is known within these deposits. According to unpublished data by I. NIKOLOV the following fauna has been determined: *Aceratherium incisivum*, *Microstonyx major*, aff. *Helladotherium* sp., *Gazella* sp., *Indarctos* sp., *Elephantoidea* indet., *Orycteropus* sp. The unpublished and lost *Orycteropus* skull from this locality resembles to the primitive forms of

the genus such as *O. browni*, *O. pottieri*, *O. mauritanicus* (determination of N. SPASSOV after existing photos). Such a fauna indicates that the locality could be at the Vallesian/Turolian boundary. It is worth noting here that the studied tooth keeps clear lignitic traces but no lignitic layers were found in the above mentioned formations. Some undivided Neogene deposits are also referred near the village of Dragodan, which possibly belong to the base of Neogene (MARINOVA 1993) and thus cannot include the studied tooth. Two areas near Blagoevgrad include lignites. The first is the area of Padaloto, west of Blagoevgrad but the deposits are considered as Oligocene (ZAGORCHEV, pers. comm.). The other is the coal formation around Razlog which is the most probable for the studied tooth. The Neogene deposits near the villages of Oranovo and Arnautska mahala, north of Simitli, about 10 km southeast of Blagoevgrad (Fig. 1), include lignitic layers, while their age is most probably Sarmatian-Maeotian (i.e. roughly corresponding to Vallesian) (MARINOVA 1993).

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