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BRIEF REMARKS ON CERTAIN LARGE-SIZED TUROLIAN HYAENIDS (MAMMALS, CARNIVORES) FROM PIKERMI AND SAMOS, GREECE

BY

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ABSTRACT

Apart from the group constituted by *Adcrocuta*, *Percrocuta* and *Hyaenictis*, the larger hyaenids from the Greek upper Miocene (Turolian) fall into two assemblages or trends, separated by their dentition, tending towards the crushing or the sectorial adaptation and both of them chiefly classified into the genus *Thalassictis*.

Without total exclusion of some other possibilities that are discussed, the first of the two trends, represented mainly by the subgenus *Hyaenictitherium*, has, according to the most likely hypothesis, three species distributed into four levels, starting with *T. wongi*, passing through *T. (H.) hyaenoides* and ending with a primitive *Pachycrocuta*-like form.

The second trend includes probably two species, grouped in the subgenus *Lycyanea*, of which the most primitive is *T. (L.) chaeretis* and the other one, left unnamed as *T(L.) sp.*, has a more sectorial dentition. *Lycyaena* is considered as ancestral to late Cenozoic "genera" *(Chasmaporthetes* and/or *Euryboas)* whose adaptations are even more caracteristic.

RÉSUMÉ

A part le groupe formé par *Hyaenictis*, *Adcrocuta* et *Percrocuta*, les Hyaenidés de forte taille du Miocène supérieur (Turolien) de Grèce se répartissent en deux ensembles ou tendances séparés par leur dentition, qui évolue vers un aspect broyeur ou sectorial et qui se classent tous deux surtout dans le genre *Thalassictis*.

Sans exclure tout à fait d'autres possibilités qui sont discutées, le premier de ces ensembles, représenté surtout par le sous-genre *Hyaenictitherium*, a, selon l'hypothèse la plus vraisemblable, trois espèces réparties en quatre niveaux, partant de *T. wongi*, passant par *T. (H.) hyaenoides* et se terminant avec une forme rappelant une *Pachycrocuta* primitive.

L'autre tendance compte probablement deux espèces groupées dans le sous-genre *Lycyaena* dont la plus primitive est *T. (L.) chaeretis* et l'autre, laissée sans nom comme *T(L.)* sp., a une dentition plus sectoriale. *Lycyaena* est considéré comme ancestral de genres du Cénozoïque tardif *(Chasmaporthetes* et/ou *Euryboas)* dont les adaptations sont encore plus caractéristiques.

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MATERIAL

The specimens involved in this paper are large-sized hyaenids except for *Hyaenictis* and the *Percrocuta-Adcrocuta* group. Table 1 includes the relevant material from Pikermi and Samos, Greece. Since Gaudry's (1862-1867) specimens have no numbers they are given the numbers 1, 2, 3 and 4 (Table 1). Number 3 is two specimens, one figured; measurements for both are given in Gaudry (1862-67, p. 72). The age of the Samos material is Turolian (approximately 8,5-9 *Ma*). Pikermi could be slightly older, synchronous or younger than Samos. We presently believe that Pikermi is also Turolian (see Solounias, 1981a for a review).

Table 2 includes material from other localities that is closely related to the Pikermi and Samos taxa. As a preliminary step, we have only compared the Greek sample with these localities. Even though a more comprehensive study is in demand, it has been impossible to examine all original material and therefore we cannot draw definitive and taxonomic statements; thus the Greek material must presently stand alone.

SYSTEMATICS

A preliminary nomenclature of the hyaenids sampled in Greece is given in Solounias (1981b). While detailed work awaits publication, we present here some general introductory statements about the status of these Turolian hyaenids. Although there are perhaps new species in the sample, we refrained for the moment to give them formal names.

We believe that the following taxa are distinct: *Ictitherium viverrinum* Roth and Wagner, 1854, p. 392, pl. II, figs. 3, 4 and 5 (type species for *Ictitherium*) and *Thalassictis robusta*, Nordmann 1858, p. 149, pl. 5, figs. 1 and 2 (Solounias 1981b). The upper P4/ of *T. robusta* is more sectorial than in *I. viverrinum*. *Thalassictis* is congeneric with *Palhyaena* and has priority.

We also believe that *Thalassictis* should be the proper genus for *Ictitherium wongi* (most specimens generally called "*hipparionum*" for example in Pilgrim, 1931, and for *Hyaenictitherium hyaenoides* and *Lycyaena chaeretis*. We propose to use *Hyaenictitherium* and *Lycyaena* as subgenera for the larger *Thalassictis* species. These are distinguished by the more cutting dentition of the latter one which also presents more robust canines with weak crests, more denticulated premolars (especially the paraconid of P/4), a different configuration of the M/1 talonid and nearly always no M2.

Because there is a number of undescribed species from Shan Si in the Uppsala and New York collections (PIU and AMNH), Solounias (1981b) has proposed that the type of *Thalassictis hyaenoides* is the skull figured by Zdansky (1924), p. 84,

plate 17, figs. 1 and 2. The jaw of the same individual is reported on p. 90, ex. 1, locality 44, Shan Si, China in PIU, Uppsala. Similarly, the type of *Thalassictis wongi* is the skull and jaw figured in ZDANSKY (1924), p. 73, pl. 15, from locality 109, Shansi, China, in PIU, Uppsala.

DISCUSSION

Introduction

As table 1 shows, the entire thirteen specimen sample having been described and figured, we can proceed to the discussion of this material.

The Pikermi and Samos sample is small and not complete enough to provide definite assessments, A major problem has been relating skulls to mandibles. An examination of recent viverrid and hyaenid material as well as more complete late Miocene material from Shan Si, China at the AMNH indicates that certain elements of lower dentition relate specifically with other elements of the upper as expected (fig. 1). Although measurements are not presented here, slender protoconids of the lowers relate with slender paracones of the uppers; the same is true for robust cusps. This observation makes sense since robust paracones and protoconids are an adaptation to bone crushing; they both should be similarly robust or slim. Similarly slim and long P4/ metastyles correlate with slim and long M/1

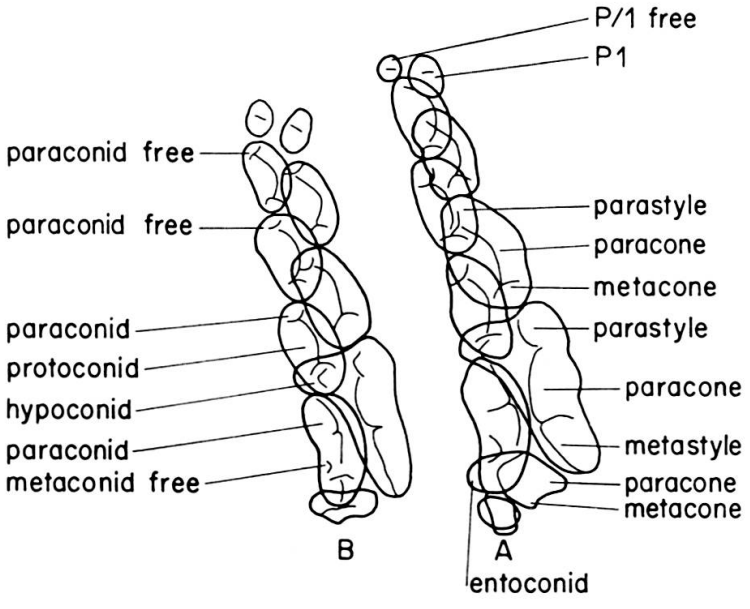

FIG. 1.

Schematic occlusal relationships in A, AMNH 14 L 35, *Thalassictis (Hyaenictitherium) hyaenoides* and B, AMNH 56 L 560, *Thalassictis (Lycyaena) sp. nov.* Undescribed specimens from Shan Si, China. Not to exact scale. Glass see-through technique (upper and lower right dentitions). Cusps free in vertical occlusion are marked (free).

trigonids. The M/1 metaconid does not occlude with any of the upper cusps and is presumably free. Its reduction could be associated with talonid reductions if they are genetically and/or mechanically related. The size of M1/ relates to the size of the M/1 talonid basin (fig. 1). M1/ fits in the talonid basin of M/1 and usually leaves the entoconid and/or hypoconid free (fig. 1). Most primitive hyaenids that have M2/ also have M/2. In more recent taxa usually the absence of M2/ is accompanied by the absence of M/2. An examination of hyaenid and other carnivore taxa suggests that the M2/ tends to become lost before M/2. For example this pattern (M1/2) occurs in *Nimravus*, *Dinictis* and certain *Proailurus*. In hyaenids it occurs in "*Hyaena*" *namaquensis*, *Hyaena abronia*, *Leecyaena lycyaenoides* and others. When the M1/2 pattern occurs either the talonid of M/1 is reduced or the M1/ is wide enough to have complete occlusion with the lower M/2. In some cases the presence of the M1/2 pattern is variable. For example *Hyaenictis graeca*, *Hyaenictis eximia* have a variably present M/2 (Solounias 1981b). Recent *Crocuta* and *Hyaena* specimens occasionally may have aberrant second molars which do not occlude with any upper teeth. More research is being done on hyaenid mastication and in plotting key upper measurements to predict the size of lower dentition (Solounias, work in progress). For the purpose of this paper, it suffices to say that we have used these observations for deciding how many taxa are represented at Samos and Pikermi.

The task of assigning isolated and fragmentary upper dentitions to lower is particularly difficult when five or six similar-sized hyaenids are present in one locality. As a result we present instead of one, a number of alternative hypotheses (figs. 2 and 3). They range from views accepting high diversity within a species to others accepting low diversity within species. Until more material is discovered and described, our views remain as alternative hypotheses.

The Pikermi and Samos sample considered here is divided into two broadly defined taxa: specimens that are *hyaenoides*-like and specimens that are *chaeretis*-like. Individual specimen problems and alternative hypotheses within each broad species group are probably independent from the other group and hence are treated here separately.

The *hyaenoides*-like group (fig. 2; table 3)

Hypothesis one. Figure 2A includes four specimens into one species: *Thalassictis (Hyaenictitherium) hyaenoides*. This hypothesis is likely but accepts high variability within this species. Perhaps the variability is partly due to geographic distance (from Greece to China) and to small time differences between the various localities (table 2).

The conspecificity of the upper dentitions (3) and NHMW A 4752 is difficult to accept, although possible, because (3) has an M2/ but NHMW A 4752 does not. The entire described and undescribed sample of *T. (H.) hyaenoides* has an M2 although it is always small as in (3).

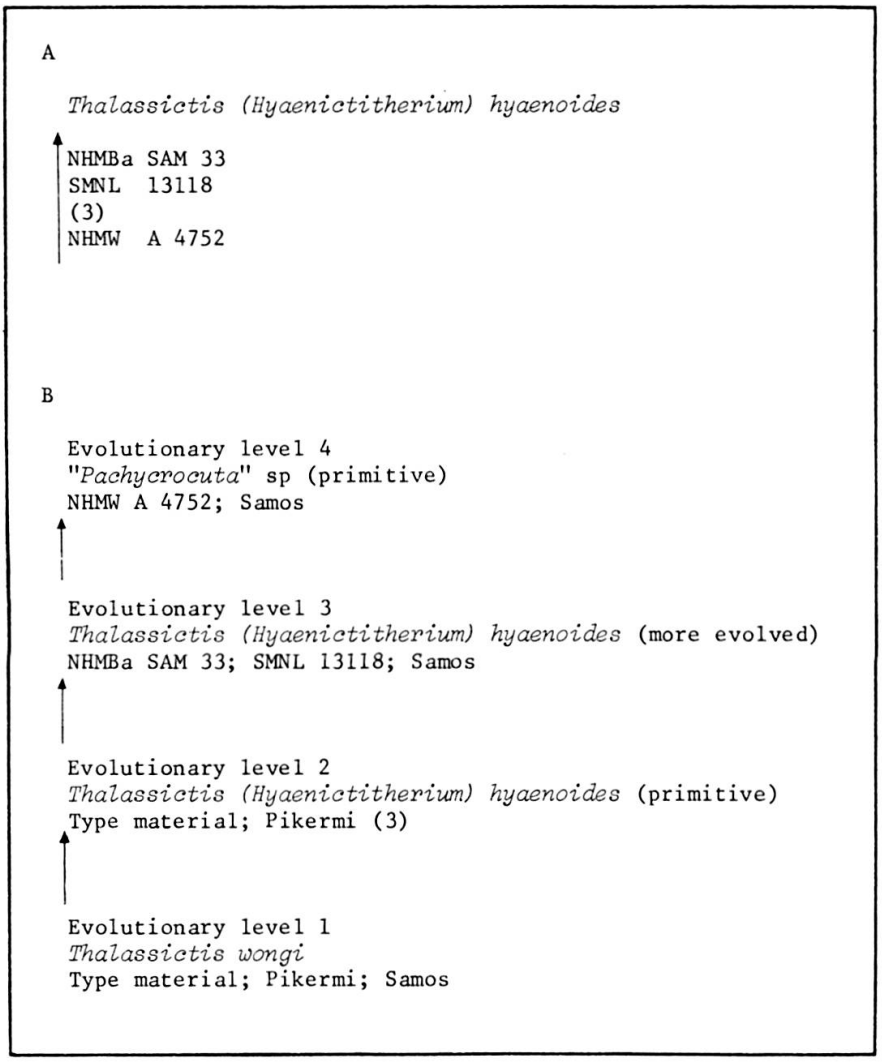

FIG. 2.

Possible relationships of Pikermi and Samos specimens belonging in the *Thalassictis (Hyaenictitherium) hyaenoides* group.
A) One species hypothesis.
B) 3 species, distributed in four "levels", hypothesis.

The P3/ paracone is robust in NHMW A 4752 but not in (3). Again (3) is most similar to the type *T. (H.) hyaenoides* from Shan Si.

In conclusion, although the sample is assignable to *T. (H.) hyaenoides*, the existence of more than one species is possible.

Hypothesis two. Figure 2B subdivides the sample (including *wongi*) into three species and four "levels". This hypothesis takes a view opposite from figure 2A and assumes that the variation observed reflects the existence of closely related species reflecting a trend perhaps towards the origin of "*Hyaena*" *brunnea*.

The dentitions NHMBa SAM33 and SMNL 13118, although most similar to the Shan Si type of *T. (H.) hyaenoides*, differ in the protoconids of P/4. Unlike the type of *hyaenoides* these protoconids are more robust resembling slightly those of "*Hyaena*" *brunnea*. Here we propose that the specimens are classified as *hyaenoides* but more evolved in the direction of "*H.*" *brunnea*. "*H.*" *brunnea* differs in a number of morphological features, i.e. the talonid and metaconid of M/1 are reduced, M2 is lost and the dentition is heavier. Also the premolars are more robust than in the Samos specimens. *Hyaena brunnea* is thought to be closer to the *Pachycrocuta* species than to *Hyaena hyaena* (*). Hence it will appear here under the generic designation of "*Hyaena*" or even *Pachycrocuta*.

The upper dentition (3) from Pikermi is placed again with *T. (H.) hyaenoides* as in hypothesis one. The P3/ paracone of (3) is not robust as in NHMW A 4752 and identical to the type of *T. (H.) hyaenoides*.

Skull NHMW A 4752 from Samos agrees rather well with NHMBa SAM33 and SMNL 13118. Nevertheless we propose to place it into distinct species close to NHMBa SAM33 and SMNL 13118 but slightly more towards the "*H.*" *brunnea* direction partly because of the absence of M2/. The determination of NHMW A 4752 as one of the oldest specimens belonging to the genus "*Hyaena*" is not new (de Beaumont, 1969; Howell and Petter, 1980, p. 583; Solounias, 1981a, table 8). We agree with Galiano and Frailey (1977) that "*H.*" *brunnea* is closer to *Pachycrocuta* spp than to *Hyaena hyaena*. Hence NHMW A 4752 may be a step in the *brunnea* lineage and is named *Pachycrocuta* sp.

In summary, the second hypothesis presents the possibility of the origin of "*H*". *brunnea* and the rest of *Pachycrocuta* species ultimately from a *Thalassictis* such as *T. wongi* through small but well defined evolutionary levels. These levels (fig. 2B) represent adaptations towards enhanced premolar crushing and the beginnings of molar reduction posterior to the carnassials.

The *chaeretis*-like group (fig. 3; table 3)

Hypothesis one. Figure 3A suggests the possibility that specimens (1), (2), SMNL 41654, (4), MGL (S) 273, SMF M 2460 and BM(NH) M 8979, 8978 belong to one species. This hypothesis is likely but it accepts again (as in fig. 2A) high variability within the sample. If this hypothesis is true, then the differences between *T. (H.) hyaenoides* (as in fig. 2A) and *Thalassictis (Lycyaena) chaeretis* are hardly more important in subdividing the presumed two species than other differences present among the specimens of each taxon. These other differences could result in numerous other ways of subdividing the material. The type of *T. (L.) chaeretis* (1)

* *Hyaena hyaena* is not considered in this discussion because it has a primitive P4/ blade as in *Ictitherium* and they are both believed to be part of another phylogeny. Close relationships are possible with *Palinhyaena* (Qiu Zhan-Xiang and Coll., 1979).

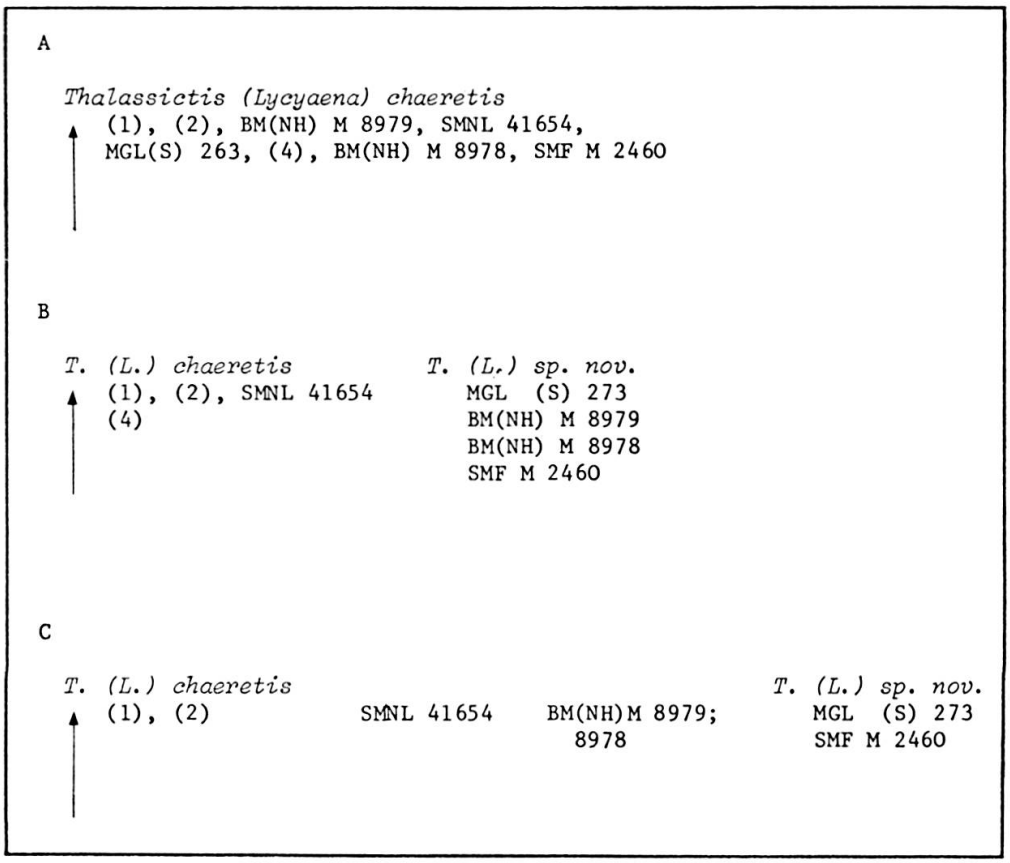

FIG. 3.

The *Thalassictis (Lycyaena) chaeretis*-like group.
A) One species hypothesis.
B) Two species hypothesis with the BM(NH) specimens as *T. (L.) chaeretis*.
C) A four species hypothesis.

is broken behind the M/1 and hence gives no information about the presence of an M/2.

Placing the material into one species as figure 3A shows is not a favorable hypothesis. MGL (S) 273 differs from the type of *T. (L.) chaeretis* (1) in having a reduced M/1 talonid basin (nearly unicuspid) and a small metaconid. SMNL 41654 is almost identical to (1) but the M/1 metaconid and talonid are still larger and hence to unite the Lausanne and Ludwigsburg specimens becomes specially difficult.

In conclusion we presently do not favour, according to the available material, the one species hypothesis for the *chaeretis*-like sample, although possible.

Hypothesis two. Figure 3B suggests the existence of two closely related species. We propose that specimens MGL (S) 273, SMF M 2460 and BM (NH) M 8979, 8978 are distinct from the type of *T. (L.) chaeretis* and belong to a new species. The differences between these species are: reduced M/1 talonid basin and metaconid

in *T. (L.) sp.* whose dentition is also more sectorial than in *chaeretis*. This last is therefore considered as more primitive.

Specimen AMNH 56 L 560 (skull and jaws) from China is very close to *T. (L.) sp.* and so seems to be *L. spathulata* Qui Zhan-xiang and Coll. (1979) and it could be the same species.

Hypothesis three. All the differences between specimens are attributable to species differences (fig. 3C). Only specimens (1), (2) and (4) are assigned to *T. (L.) chaeretis*. SMNL 41654 differs in the slightly larger M/1 metaconid and a slightly higher-crowned trigonid. BM(NH) M 8979 and 8978 resemble *T. (L.) chaeretis* but the M/1 talonid is slightly smaller and the premolars slimmer and in MGL (S) 273 these features are more accentuated than in all other specimens. If specimens SMNL 41654 and BM(NH) M 8978, 8979 represent two distinct species, they are most likely closely related to *T. (L.) chaeretis* and *T. (L.) sp.* as defined in figure 3B (see also definitions-descriptions by de Beaumont, 1967; Howell and Petter, 1980).

Remarks

Having considered the more probable alternative hypotheses (figs. 2 and 3), we conclude that with more or less probabilities any of these could be true. The problem is that the sample is still small and does not produce a clear pattern. As a result a number of equally likely hypotheses fit the data. It would be nice to have many specimens so that statistical analyses could be performed.

We favour hypotheses figure 2B and figure 3B the most. The *T. (H.) hyaenoides*-like sample appears to form a simple phylogenetic lineage leading probably towards *Pachycrocuta* (= "*Hyaena*") *brunnea*. If this lineage is actually true, an Eurasian origin for *Pachycrocuta* is suggested unlike African hypotheses (Petter and Howell, 1980).

The four evolutionary levels of the *hyaenoides*-like group are: (1) *Thalassictis wongi* (from Shan Si, Samos and Pikermi [Zdansky, 1924; Solounias, 1981b]). The Pikermi specimen is not figured but mentioned by Gaudry (1862-1867) p. 72, where he gives measurements of one lower dentition. *T. wongi* is a middle-sized animal with a slim P/4 protoconid, M2 present, M/1 talonid large and M/1 metaconid medium sized. (2) *Thalassictis (Hyaenictitherium) hyaenoides* (the type material from Shan Si and Gaudry [1862-1867] p. 72, columns one and two; one of the upper dentitions is figured [present table 1, number 3]). A larger species than *T. wongi* with a small M2/ that is always present. Note here that the P/4 protoconid is not enlarged. Hence the taxa of levels 1 and 2 are closely related. (3) *Thalassictis (Hyaenictitherium) hyaenoides* NHMBa SAM 33 and SMNL 13118 represent a third evolutionary level differing from 2 in the enlarged P/4 protoconid. (4) *Pachycrocuta* NHMW A 4752 represents a distinct level since there is no M2/, a longer P4/ meta-

style and a heavier dentition which make difficult to link it with Gaudry's material. Nevertheless, to unite the last two steps could be possible; what especially matters here, is the general trend.

Pachycrocuta brunnea differs in having a reduced M/1 talonid and metaconid, general loss of M2, premolar paracones and protoconids greatly expanded. Note that here the tibia is short. Other most evolved Pleistocene *Pachycrocuta* species are distinguished by large size and even more robust paracones and protoconids. Whether our suggested levels 3 and 4 are ancestral to the true *Pachycrocuta* species, although possible, is still an open question.

Whether *T. (L.) chaeretis* and *T. (L.) sp.* gave rise to any other taxa must be finally considered. It has been proposed by Thenius (1966) and Schmidt-Kittler (1976) that *Lycyaena* gave rise to *Crocuta*, presumably because of the slim and long carnassials (P4/, M/1). Actually the carnassials are not very different from those of *Thalassictis wongi*. *Thalassictis* species do have slim and long carnassials when compared with more primitive genera such as *Ictitherium* and *Plioviverrops* but this is a common adaptation to many Miocene taxa and not necessarily special to the *Crocuta* lineage. For example *Tungurictis*, several viverrids (extinct and extant), *Euryboas* and *Chasmaporthetes* have well developed long and slim carnassials. On balance, it seems that these last two "genera" are descending from the subgenus *Lycyaena*, probably through the post-Turolian species *borissiaki* as proposed by de Beaumont (1967).

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TABLE 1

Material studied

Mandibles and Lower Dentitions

From Pikermi

1. MHNP no number, Paris. Left mandible of a young adult figured by Gaudry 1862-1867, pl. 15, figs. 3 and 4.

2. MHNP no number, Paris. Left adult mandible with anterior symphysis figured by Gaudry 1862-1867, pl. 15, figs. 1 and 2.

BM (NH) M 8979, London. Two rami from Pikermi.

From Samos

NHMBa SAM 33, Basel. Left jaw figured by de Beaumont 1968, pl. 1; Solounias, 1981*b*, fig. 16*A-C*.

SMNL 13118, Ludwigsburg. Right jaw of a young adult figured by Solounias, 1981*b*, fig. 16*D*, *E* and *F*.

SMNL 41654, Ludwigsburg. Right jaw. Solounias 1981*b*, fig. 18*D-F*.

MGL (S) 273, Lausanne. Left mandible figured by de Beaumont 1967, text fig. 13*c*, pl. 3, fig. 4*a* and 4*b*; Solounias 1981*b*, fig. 19*C-E*.

Crania and Upper Dentitions

From Pikermi

3. MHNP no number, Paris. Upper right maxilla figured by Gaudry 1862-1867, pl. 12, figs. 1 and 2. Measurements for this and another similar-sized specimen given in Gaudry 1862-1867, p. 72, columns one and two.

4. MHNP no number, Paris. Right P4/ figured by Gaudry 1862-1867, pl. 15, fig. 5.

BM (NH) M 8978, London. Crushed skull figured by Pilgrim 1931, text figs. 28, 29, 30.

From Samos

NHMW A 4752 (1912) No. 29, Vienna. Skull of a young adult described and figured by de Beaumont, 1969, 1*a*, 1*b*, 1*c*. Described by Howell and Petter 1980, p. 583; Solounias 1981*b*, fig. 18*A-C*.

SMF M 2460, Frankfurt. Skull figured by Solounias 1981*b*, fig. 19*A* and *B*.

TABLE 2

Material from other localities

Country	Locality	Province	Author	Original published name	Age
Tunisia	Lower Beglia Fm loc. 17 20	Bled Douarah	Kurtén, 1976	*Lycyaena crusafonti*	Miocene pre-*Hipparion*
S. Africa	E Quarry	Langebaanweg	Hendey, 1978	"*Hyaenictis*" *preforfex* *Hyaena abronia* "*Hyaena*" *namaquensis*	latest Miocene earliest Pliocene
China	loc. 28, 30, 30/2, 30/5, 43, 44, 49, 108, 109, 110/2, 116 West.	Shan si	Zdansky, 1924	*Ictitherium hyaenoides*	either pre-*Hipparion* and or *Hipparion*
China	loc. 49	Shan Si	Zdansky, 1924	? *Lycyaena dubia*	late Miocene
China	loc. 12a, ? 109	Shan Si	Zdansky, 1924	*Hyaena honanensis*	late Miocene
China	Loc. ?	Shan Si	Zdansky, 1924	*Hyaena* sp.	
China	many localities	Shan Si	Undescribed material at the AMNH presently studied by Solounias		
China	?	Qingyang	Qiu Zhan-xiang and Coll, 1979	*Lycyaena spathulata*	late Miocene or early Pliocene
China	?	Qingyang	Qiu Zhan-xiang and Coll, 1979	*Ictitherium hipparionum hyaenoides*	late Miocene or early Pliocene
Pakistan	several localities	Chinji (Dhok Pathan) Hasnot	Pilgrim, 1932 Pilgrim, 1932	*Lycyaena* (?) *proava* *Lycyaena macrostoma*	Astaracian Turolian
		Chinji	Pilgrim, 1932	*Lycyaena* (?) *chinjiensis*	Astaracian

TABLE 3

Morphological comparison

			C	P2	P3	P4	M1	M2
as in fig. 2*A* (one species hypothesis) levels 3 and 4	*Thalassictis (Hyaenictitherium) hyaenoides*	UPPER		oval round as in *Hyaena*	robust paracone	less slim metastyle	paracone-metacone region less reduced	present but always small, rarely absent
		LOWER	small and conical (thin at the tip, broad at the base)	robust protoconid	robust protoconid, small paraconid	robust protoconid, small paraconid	large metaconid robust trigonid blade, less simple talonid basin	present but always small, rarely absent
as in fig. 3*B*	*Thalassictis (Lycyaena) chaeretis*	UPPER				slim metastyle		
		LOWER	large and tubular (broader at the tip and not so broad at the base)	less robust protoconid	less robust protoconid large paraconid	less robust protoconid large paraconid	large metaconid robust trigonid blade, less simple talonid basin	absent
as in fig. 3*B*	*Thalassictis (Lycyaena)* sp. nov.	UPPER			slim paracone	slim metastyle	paracone-metacone region more reduced	absent
		LOWER	large and tubular (broader at the tip, not so broad at the base)	least robust protoconid	least robust protoconid large paraconid	least robust protoconid large paraconid	small metaconid slim trigonid blade, simple talonic basin	absent