

## Systematic palaeontology (vertebrate palaeontology)

Taxonomical reappraisal of “ictitheres” (Mammalia, Carnivora)  
from the Late Miocene of Kenya

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Abstract

In 2003, Werdelin has identified three hyaenid species from the Late Miocene of Kenya (Lothagam Formation), including two “ictitheres” – a newly erected *Ictitherium ebu* Werdelin, 2003, and *Hyaenictitherium* cf. *parvum*. The present article discusses the published evidence on the Kenyan hyaenids and explores additional cranial and postcranial characters useful for differentiation between the true ictitheres (i.e., the genera of the subfamily Ictitheriinae Trouessart, 1897) and some small members of the subfamily Hyaeninae Gray, 1869. **To cite this article:** Y. Semenov, C. R. Palevol 7 (2008).

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## Résumé

**Réapparition taxonomique d’« ictithères » (mammifères, carnivores) dans le Miocène supérieur du Kenya.** En 2003, Werdelin a identifié trois espèces de Hyaenidae dans le Miocène supérieur du Kenya (formation de Lothagam) dont deux « ictithères », une nouvelle espèce, *Ictitherium ebu* et *Hyaenictitherium* cf. *parvum*. Le présent article discute les données publiées sur les Hyaenidae du Kenya et présente des caractères supplémentaires, crâniens ou postcrâniens, utiles pour distinguer les véritables ictithères (c’est-à-dire les genres de la sous-famille des Ictitheriinae Trouessart, 1897), de représentants de petite taille de la sous-famille des Hyaeninae. **Pour citer cet article :** Y. Semenov, C. R. Palevol 7 (2008).

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**Keywords:** Eurasia; Africa; Late Miocene; Carnivora; Hyaenidae; Taxonomy

**Mots clés :** Eurasie ; Afrique ; Miocène supérieur ; Carnivora ; Hyaenidae ; Taxonomie

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## 1. Introduction

The present article was inspired by the description [14] of a new hyaenid species, *Ictitherium ebu*, from the Lothagam Formation in Kenya. Its nearly complete skeleton allowed Lars Werdelin to characterize this

animal comprehensively and to present excellent reconstructions of its skeleton, made by Antón [14] (Fig. 1A). However, an illustration of the skeleton of *I. viverrinum* Roth and Wagner, 1854, from Pikermi – the type species of the genus *Ictitherium*, published by Gaudry [2] – as well as available reconstructions of this species including that by Werdelin and Solounias [15], depict an animal of very different external appearance (Fig. 1B). Contrary to the gracile, long-limbed Kenyan hyaenid,

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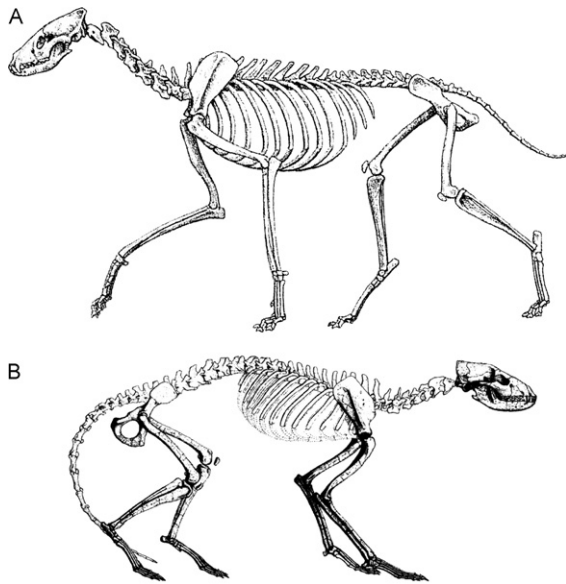


Fig. 1. Reconstructions of the skeletons. A. «*Ictitherium*» *ebu* from Lothagam (by Antón [14]). B. *Ictitherium viverrinum* from Pikermi [2].

Fig. 1. Reconstructions du squelette. A. «*Ictitherium*» *ebu* de Lothagam (par Antón [14]). B. *Ictitherium viverrinum* de Pikermi [2].

*I. viverrinum* was more robust and had relatively short limbs. Furthermore, there are many important cranio-dental distinctions between the two species. All this casts doubt upon the attribution of the Kenyan hyaenid to the genus *Ictitherium*. Another small primitive hyaenid from Lothagam, which was originally referred to *Hyaenictitherium* cf. *H. parvum*, also needs re-identification.

“Ictitheres” were among the most common and numerous carnivorans in the Vallesian and Turolian of the Old World. Their remains are known from most localities of the Eurasian *Hipparion* fauna ranging from Spain to China. It is quite possible that in the Late Miocene and Early Pliocene these animals might have inhabited the entire African continent as judged by the finds from Morocco and Libya through Chad and Kenya to South Africa. A constant interest in the “ictitheres” is not surprising because these carnivores demonstrate a diverse mosaic of morphological characters transitional between the herpestids to the extant true hyaenas.

However, this well-defined group of carnivores is still insufficiently studied. Most species have previously been included into the genus *Ictitherium*. Later, the majority of species possessing second molars in both upper and lower jaws and a reduced talonid in m1 have been assigned to different genera (e.g. *Palhyaena* Gervais, 1859, *Thalassictis* Nordmann, 1858, *Hyaenictitherium* Kretzoi, 1938). The subfamily Ictitheriinae Trouessart,

1897, lacks a definite taxonomic content and diagnosis. According to some authors, the genera *Lycyaena* Hensel, 1863, *Chasmaporthetes* Hay, 1921, *Hyaenictis* Gaudry, 1861, and even some species of *Hyaena* Brisson, 1762, are considered as ictitheriines [5,6]. The morphometric and phylogenetic analyses undertaken failed to yield significant results because of the use of inappropriate characters complicated by strong intraspecific variability. As concerns ecological inferences about the “ictitheres”, they depend mainly on the opinions about the extent to which these animals were adapted for scavenging. In general, the current state of “ictithere” taxonomy is not better than it was in the 1920s and 1930s when most species were classified into two groups: “smaller” or “related to *I. robustum*”, and “larger”, “hyaena-like” or “related to *I. hipparionum*”. Most recently, Tseng and Wang [12] grouped nearly all “ictitheres” possessing advanced dentition into the single genus *Hyaenictitherium*. This decision adds even more confusion, particularly when the inclusion of *Ictitherium intuberculatum* Osansoy, 1965 is taken into account; this taxon has a large m2 and the talonid of m1 is not reduced [9,13]. The latter species is nearly indistinguishable from the large individuals of *I. viverrinum* [11].

Indeed, most “ictitheres” species are, in many respects, very similar to each other and –despite considerable variability comparable to that observed in the extant spotted and brown hyaenas – look like a morphologically uniform group. Most species are small when compared with extant hyaenas, (condylobasal length rarely exceeds 220 mm), low skull with relatively narrow muzzle and more or less long pentadactyl limbs. In contrast to the viverrids and herpestids, the two-chambered auditory bulla lacks any constriction or external groove opposite the base of the septum bullae; the anterior chamber is larger than the posterior one and they are both strictly aligned anteroposteriorly; the auditory meatus is very short, and laterally surrounded by one or two osseous lips. The hard palate is relatively narrow and the masticatory system is not as powerful as in true hyaenas, but the zygomatic arches are broad, and the sagittal and temporal ridges are well developed. The lower jaw has a deep mandibular body, a broad mandibular ramus and a large masseteric fossa. However, it is the dentition that is most similar in “ictitheres”:

- the enamel is slightly rugose;
- m2 and M2 are present;
- premolars are low, narrow, crowded and placed slightly aslant;
- the protocon of P4 is not reduced;

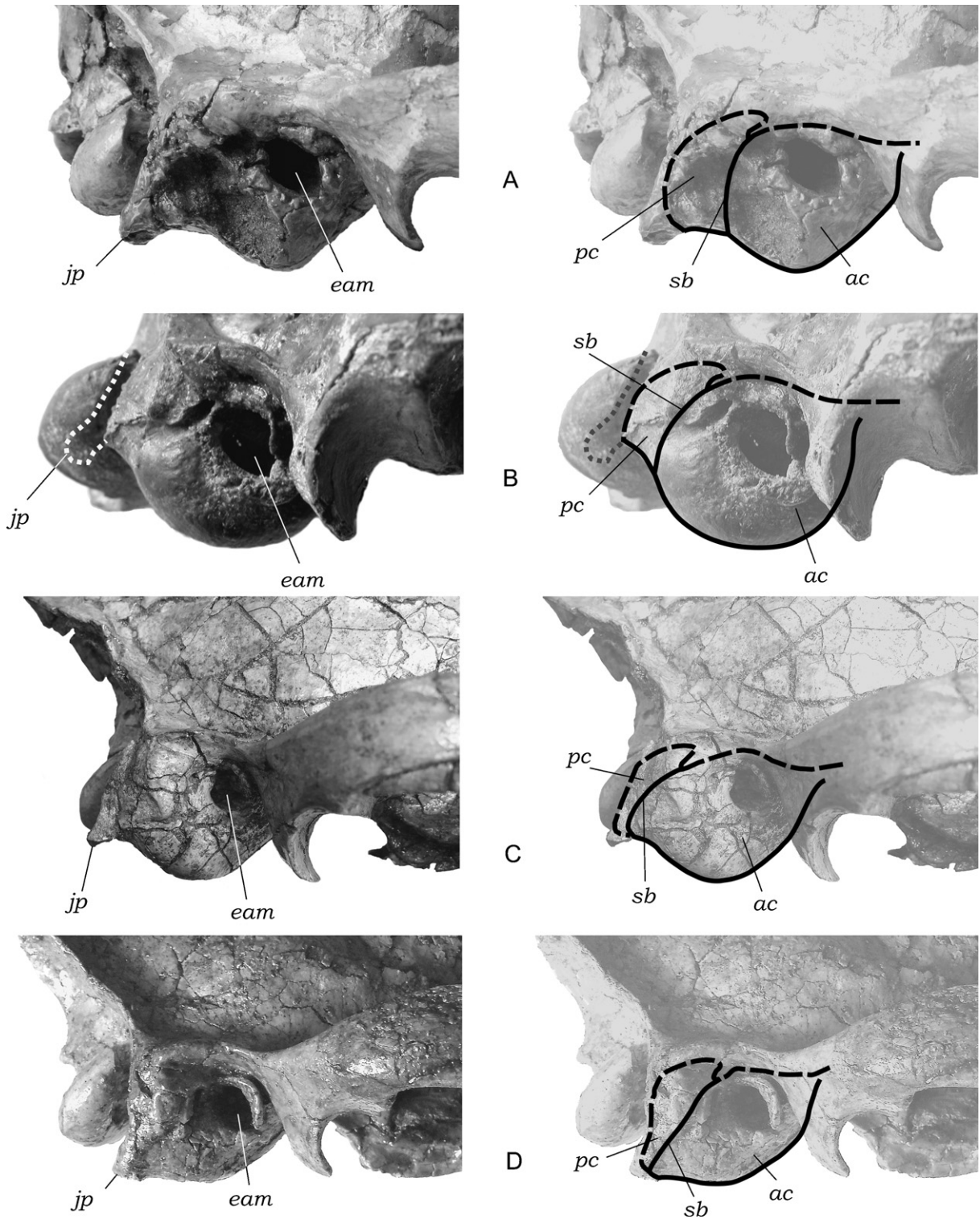


Fig. 2. Differences between Ictitheriinae and Hyaenotheriini in the shape of auditory bulla (lateral views) and the schematic representation of the relative position of bullar chambers. A. *Ictitherium viverrinum* from Novoelizavetovka (NNPM 43-2274). B. *Thalassictis robusta* from Kishinev (PMNUO 2971). C. *Hyaenictitherium venator* from Novoelizavetovka (NNPM 43-2275). D. *Hyaenotherium magnum* from Cherevichnoe (NNPM 45-4252, holotype). Not to scale. *ac* – anterior chamber, *eam* – external auditory meatus, *jp* – jugular process, *pc* – posterior chamber, *sb* – septum bullae.

Table 1

Discriminating characters of the tribe Hyaenotheriini and subfamily Ictitheriinae.

Tableau 1

Caractères discriminants de la tribu des Hyaenotheriini et de la sous-famille des Ictitheriinae.

Ictitheriinae	Hyaenotheriini
<i>Auditory bulla</i>	
Auditory bulla is not inflated posteriorly. It is of generalized feliformian type: its visible part is formed by the external walls of both anterior and posterior chambers (Fig. 2A and B).	Auditory bulla is evenly inflated. It is typical for Hyaeninae: in adult individuals all the visible part is formed by the external wall of the anterior chamber only, whereas the posterior chamber concealed inside the jugular process (Fig. 2A and B).
<i>Cranial vault and occipital part of skull</i>	
Temporal lines are short, their joint is not far than the level of glenoid fossa, sagittal crest is long. Cross-section of the cranial vault is rounded throughout its length posteriorly to the convergence of temporal lines. There is no sinus within the dorsal part of parietals. Occipital crest is large or very large (Fig. 3A and C).	Temporal lines are usually long, their joint is behind the level of glenoid fossa, sagittal crest is short (with the exception of some specimens of the spotted hyaena having a secondarily elongated sagittal crest), the cross-section of the cranial vault is triangular throughout its length posteriorly to the convergence of temporal lines. There is a sinus within the dorsal part of parietals, which extends from the frontal sinus to the occipital bone. Occipital crest is relatively small (Fig. 3B and D).
<i>Alisphenoid canal</i>	
Alisphenoid canal is always present.	Alisphenoid canal is generally absent.
<i>Mandible</i>	
Mental edge of the mandible is smoothly rounded. Lower contour of the mandibular body is convex: its depth under p2 is less than behind p3. Always two mental foramina are present (Fig. 4A and B).	Mental edge of the mandible is skewed (except in <i>Miohyaenotherium</i> ). Lower contour of the mandibular body is straight or slightly concave: its depth under p2 is slightly greater or equal to that behind p3. Two or, rarely, one mental foramen (Fig. 4C–E).
<i>Teeth</i>	
Protocone of P4 generally (except <i>Thalassictis</i> ) protrudes anteriorly to the parastyle (Fig. 5A and B).	Protocone of P4 generally (except <i>Miohyaenotherium</i> ) does not protrude anteriorly to the parastyle (Fig. 5C–E).
Talonid of m1 is generally long and always broad: respectively 24–39% and 37–46% of the crown length (Fig. 6A and B).	Talonid of m1 is short and narrow: respectively 20–29% and 30–38% of the crown length (Fig. 6C and D).
M2 and m2 are usually slightly reduced: their length is about 18–34% and 27–42% of the length of M1 and m1 respectively (Fig. 5A and B, Fig. 6A and B).	M2 and m2 are always appreciably reduced: their length is about 11–22% and 19–32% of the length of M1 and m1 respectively (Fig. 5C, Fig. 6C and D).
<i>Limbs</i>	
Limb bones are moderately long (Fig. 7A).	Limb bones are very long and slender (Fig. 7B).

- m1 invariably possesses a large metaconid and a relatively long three-cusped talonid (such dental traits might presumably have been in the ancestors of extant hyaenas).

At first glance, the “ictitheres” seem to represent a sufficiently homogeneous group deserving separate subfamily status. However, there is a set of characters which clearly distinguishes the true ictitheres (ictitheriines, i.e., the subfamily Ictitheriinae Trouessart, 1897) from the hyaenotheriins (the tribe Hyaenotheriini Semenov, 1989), as well as between their genera. These characters

were introduced and applied in a revision of “ictitheres” by Semenov [11]. Leaving aside some debatable questions, the proposed division of “ictitheres” into two family-group taxa remains reliable, as does the genus-level classification. The tribe Hyaenotheriini includes small primitive hyaenines that do not possess morphological adaptations to bone crushing and preserve the second molars in both upper and lower jaws. This taxon was erected to separate the well-defined “hyaena-like ictitheres” from the non-hyaenine ones.

The present article is not a detailed review of “ictithere” taxonomy and does not enter into details

Fig. 2. Différences entre les Ictitheriinae et les Hyaenotheriini concernant la forme de la bulle auditive (vues latérales) et représentations schématiques de la position relative des chambres auditives. A. *Ictitherium viverrinum* de Novoelizavetovka (NNPM 43-2274). B. *Thalassictis robusta* de Kishinev (PMNUO 2971). C. *Hyaenictitherium venator* de Novoelizavetovka (NNPM 43-2275). D. *Hyaenotherium magnum* de Cherevichnoe (NNPM 45-4252, holotype). Non à l'échelle. *ac* – chambre antérieure, *eam* – méat auditif externe, *jp* – processus jugulaire, *pc* – chambre postérieure, *sb* – septum bullae.

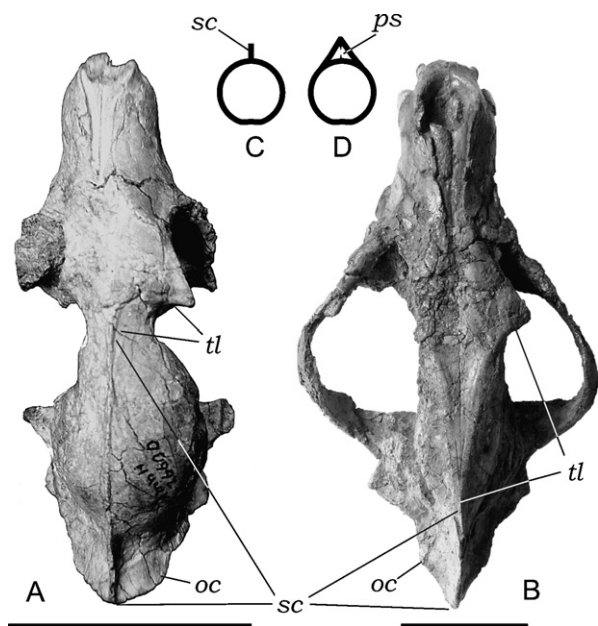


Fig. 3. Cranial vault (dorsal views) and schematic representation of its internal anatomy (cross-sectional views). A. *Tungurictis spocki* Colbert, 1939 from Tun-Gur, Mongolia (AMNH 26600, holotype). B. *Hyaenotherium magnum* from Cherevichnoe (NNPM 45-3373). C. Schematic cross-section of the ictitheriine braincase. D. Schematic cross-section of the hyaenine braincase. *tl* – temporal line, *oc* – occipital crest, *ps* – parietal sinus, *sc* – sagittal crest. Scale bars = 50 mm.

Fig. 3. Voûte crânienne (vues dorsales) et représentation schématique de son anatomie interne (vues en section transversale). A. *Tungurictis spocki* Colbert, 1939 de Tun-Gur, Mongolie (AMNH 26600, holotype). B. *Hyaenotherium magnum* de Cherevichnoe (NNPM 45-3373). C. Section transversale schématique de la boîte crânienne des ictithériinés. D. – Section transversale schématique de la boîte crânienne des hyéninés. *tl* – ligne temporale, *oc* – crête occipitale, *ps* – sinus pariétal, *sc* – crête sagittale. Échelles = 50 mm.

about many confused issues of nomenclature and higher-level classification of the group, particularly, the subfamily Ictitheriinae. Rather, it is a brief summary of the proposed characters in “ictithere” systematics [11] by using the hyaenids from Lothagam as a case study to illustrate some of the key characters.

## 2. Method

Usefulness of the morphological characters used for the generic taxonomy of “ictitheres” [11] was confirmed by examination of new finds and formerly inaccessible material. The latter includes the type specimens from China in the Lagrelus Collection, described by Zdan-sky [16], and the numerous cranial remains in the Frick Collection. In general, fossil and recent cranial material of hyaenids, viverrids and herpestids in the following institutions were examined:

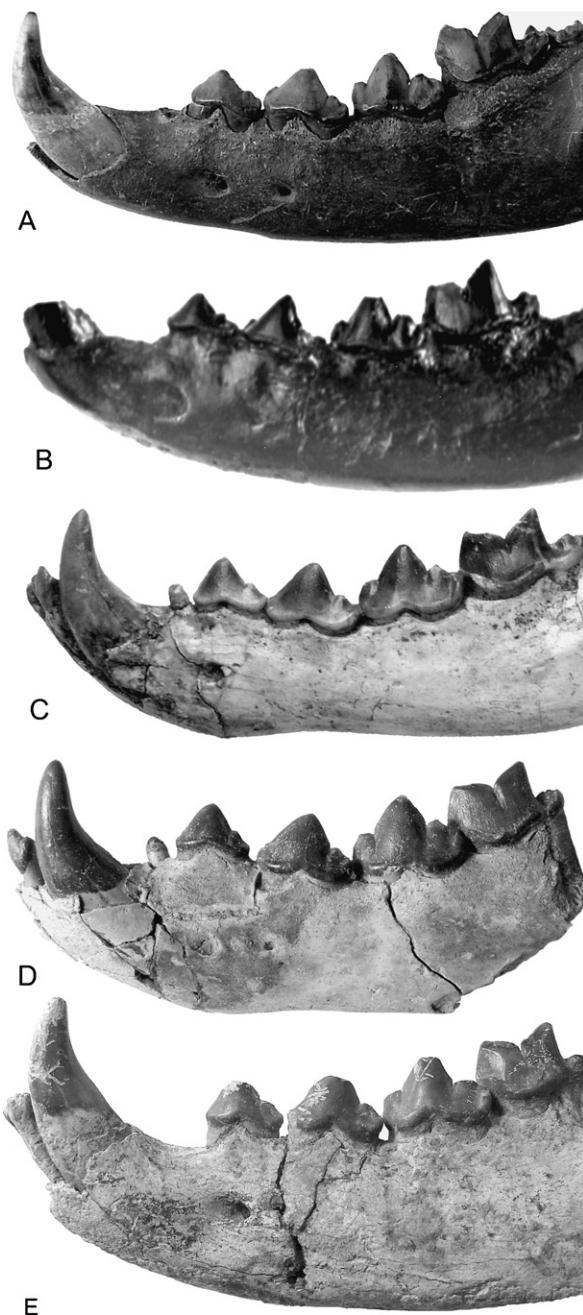


Fig. 4. Mandibular body (in lateral view). A. *Ictitherium spelaeum* from Gritsev (NNPM 22-1088). B. *Thalassictis robusta* from Kishinev (PMNUO, cast of lectotype). C. *Hyaenotherium magnum* from Cherevichnoe (NNPM 45-4253). D. *Hyaenictitherium venator* from Belka (NNPM 48-3452). E. *Miohyaenotherium bessarabicum* from Belka (NNPM 48-3698, holotype). Not to scale.

Fig. 4. Corps mandibulaire (en vue latérale). A. *Ictitherium spelaeum* de Gritsev (NNPM 22-1088). B. *Thalassictis robusta* de Kishinev (PMNUO, moulage du lectotype). C. *Hyaenotherium magnum* de Cherevichnoe (NNPM 45-4253). D. *Hyaenictitherium venator* de Belka (NNPM 48-3452). E. *Miohyaenotherium bessarabicum* de Belka (NNPM 48-3698, holotype). Non à l'échelle.

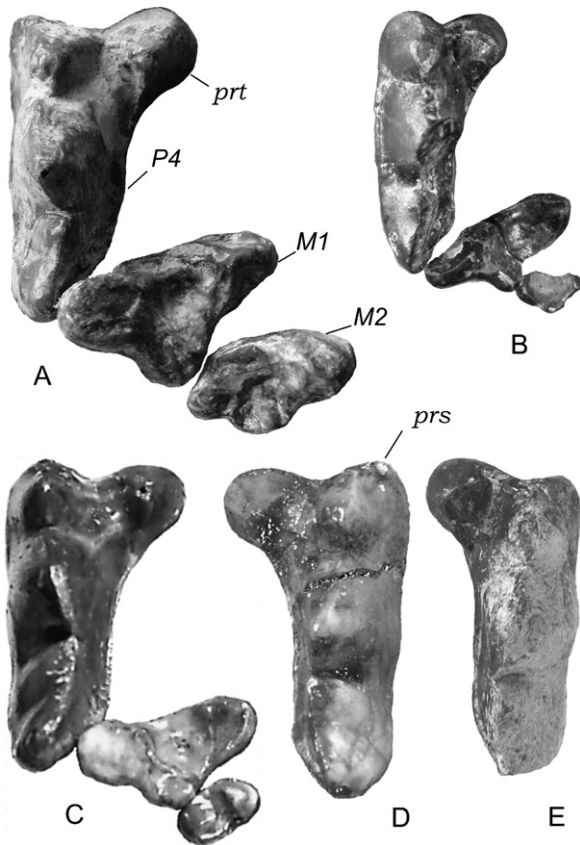


Fig. 5. Upper carnassials and molars (occlusal views). A. Right P4-M2 of *Ictitherium pannonicum* from Novaja Emetovka-2 (NNPM 25-2946). B. Right P4-M2 of *Thalassictis robusta* from Kishinev (PMNUO 2971). C. Right P4-M2 of *Hyaenotherium magnum* from Cherevichnoe (NNPM 45-4255). D. Left P4 of *Hyaenictitherium venator* from Novoelizavetovka (NNPM 43-2274, holotype). E. Left P4 of *Miohyaenotherium bessarabicum* from Belka (NNPM 48-3700). prt – protocone, prs – parastyle. Not to scale.

Fig. 5. Carnassières et molaires supérieures (vues occlusales). A. P4-M2 droites de *Ictitherium pannonicum* de Novaja Emetovka-2 (NNPM 25-2946). B. P4-M2 droites de *Thalassictis robusta* de Kishinev (PMNUO 2971). C. P4-M2 droites de *Hyaenotherium magnum* de Cherevichnoe (NNPM 45-4255). D. P4 gauche de *Hyaenictitherium venator* de Novoelizavetovka (NNPM 43-2274, holotype). E. P4 gauche *Miohyaenotherium bessarabicum* de Belka (NNPM 48-3700). prt – protocone, prs – parastyle. Non à l'échelle.

- American Museum of Natural History, New York (AMNH);
- Institute of Palaeobiology, Georgian Academy of Sciences, Tbilisi (IPG);
- Institute of Palaeontology, Russian Academy of Sciences, Moscow (PIN);
- Institute of Zoology, Kazakh Academy of Sciences, Almaty (IZK);
- Institute of Zoology, Russian Academy of Sciences, St. Petersburg (ZIN);

- National Museum of Natural History, National Academy of Sciences of Ukraine, Kiev (NNPM);
- National Museum of Natural History, Washington, D.C. (NMNH);
- Palaeontological Museum, National University of Odessa (PMNUO);
- Palaeontological Museum of the University of Uppsala (PMUU).

In this contribution, the “ictitheres” are considered as belonging to two different groups. The first one is the Ictitheriinae sensu stricto or true ictitheres [11]. It includes the following genera:

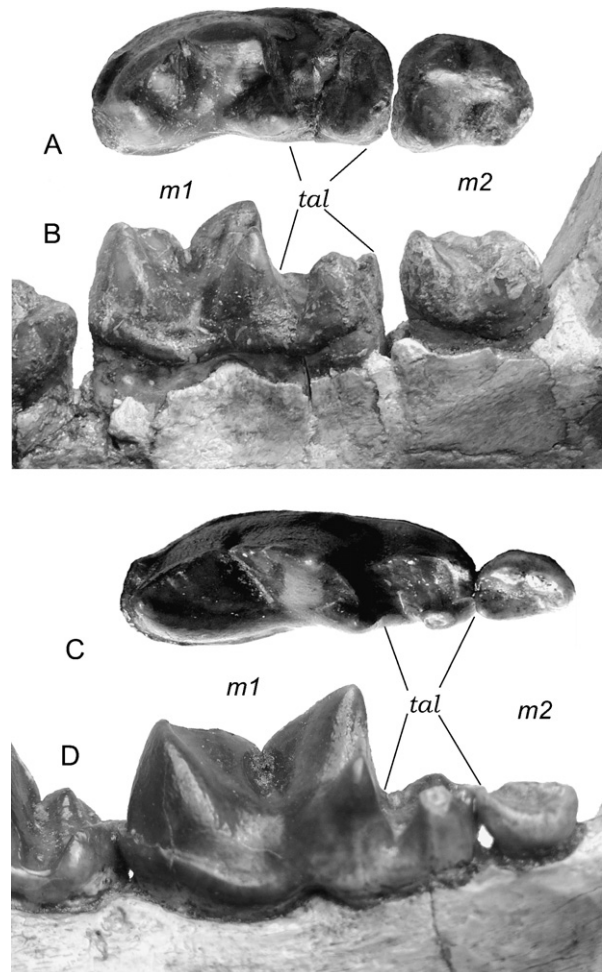


Fig. 6. Lower carnassials and molars (occlusal and lingual views). A., B. Right m1-2 of *Ictitherium pannonicum* from Novaja Emetovka-2 (NNPM 25-2946). C., D. Right m1-2 of *Hyaenotherium magnum* from Cherevichnoe (NNPM 45-4253). tal – talonid of m1. Not to scale.

Fig. 6. Carnassières et molaires inférieures (vues occlusale et linguale). A., B. m1-2 droites de *Ictitherium pannonicum* de Novaja Emetovka-2 (NNPM 25-2946). C., D. m1-2 droites de *Hyaenotherium magnum* de Cherevichnoe (NNPM 45-4253). tal – talonide de m1. Non à l'échelle.

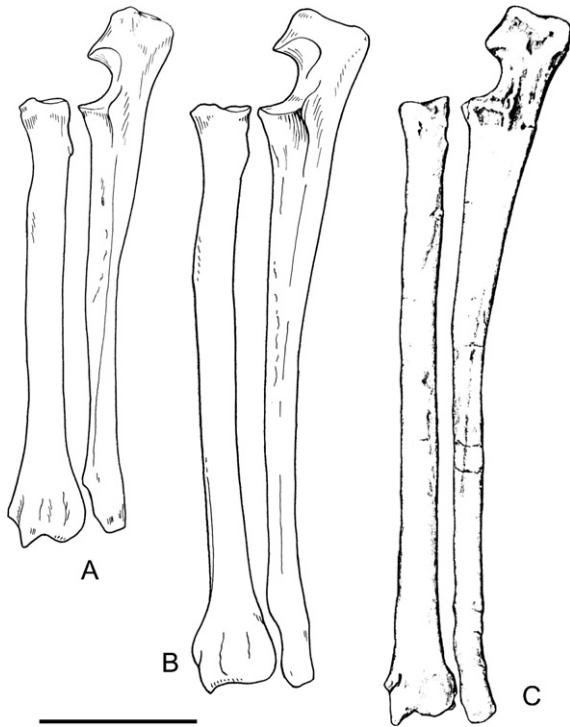


Fig. 7. Left ulna (posterior view) and radius (anterior view). A. *Ictitherium viverrinum* from Novoelizavetovka (NNPM 43-268, NNPM 43-267). B. *Hyainotherium magnum* from Cherevichnoe (NNPM 45-3771, NNPM 45-3772). C. «*Ictitherium*» *ebu* from Lothagam [14]. Scale bar = 50 mm.

Fig. 7. Ulna (vue postérieure) et radius (vue antérieure) gauches. A. *Ictitherium viverrinum* de Novoelizavetovka (NNPM 43-268, NNPM 43-267). B. *Hyainotherium magnum* de Cherevichnoe (NNPM 45-3771, NNPM 45-3772). C. «*Ictitherium*» *ebu* de Lothagam [14]. Échelle = 50 mm.

- the nominative genus *Ictitherium* Roth and Wagner, 1854—including *I. viverrinum* (= *I. ibericum* Meladze, 1967; *I. gaudryi* Zdansky, 1924; *I. sinense* Zdansky, 1924; *I. intuberculatum*), *I. pannonicum* Kretzoi, 1952 and *I. spelaeum* Semenov, 1988;
- the genus *Thalassictis* Nordmann, 1858—only the type species *T. robusta* Nordmann, 1858 (= *I. sarmaticum* Pavlow, 1908).

The second group is the tribe Hyainotheriini, namely:

- the nominative genus *Hyainotherium* Semenov, 1989—including *H. magnum* Semenov, 1989, *H. wongi* (Zdansky, 1924) and *Hyainictitherium hyaenoides orlovi* Semenov, 1989;
- the genus *Hyainictitherium* Kretzoi, 1938—including *H. hyaenoides* (Zdansky, 1924) and *H. venator* Semenov, 1989;

- the genus *Miohyainotherium* Semenov, 1989—only the type species *M. bessarabicum* Semenov, 1989.

In the present article, the focus is placed on the most common large species that are comparable in size to the Lothagam hyaenids. Smaller members of both groups (such as the genera *Plioviverrops* Kretzoi, 1938, *Protictitherium* Kretzoi, 1938 and *Tungurictis* Colbert, 1939, as well as *Hyainictitherium minimum* de Bonis et al., 2005) are almost excluded from the consideration.

### 3. Morphological differentiation of the tribe Hyainotheriini and subfamily Ictitheriinae

The main characters that differentiate the tribes Hyainotheriini and subfamily Ictitheriinae are presented in Table 1 (Figs. 2–7). It should be noted that body size is almost of no value for taxonomical identification above the species level. For example, *I. pannonicum*, being closely related to *I. viverrinum* and other relatively small species, is much larger than typical “hyaena-like” *Hyainictitherium minimum* (the m1 length is 19.3–21.0 mm in the former [11] and 15.0–16.5 mm in the latter [1]). In addition, the relative sizes of the second molars and the length of the m1 talonid vary greatly both within the genus and even species in ictitheriines.

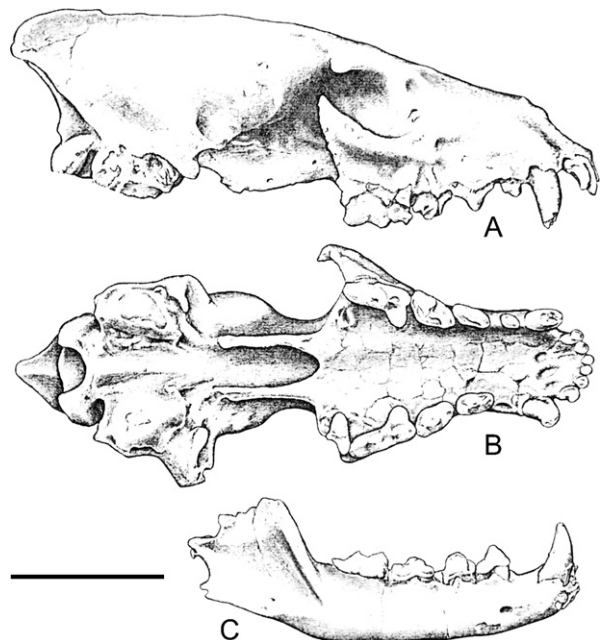


Fig. 8. Cranial remains of «*Ictitherium*» *ebu* from Lothagam (lateral views). A., B. Skull. C. Mandible [14]. Scale bar = 50 mm.

Fig. 8. Restes crâniens de «*Ictitherium*» *ebu* de Lothagam (vues latérales). A., B. Crâne. C. Mandibule [14]. Échelle = 50 mm.

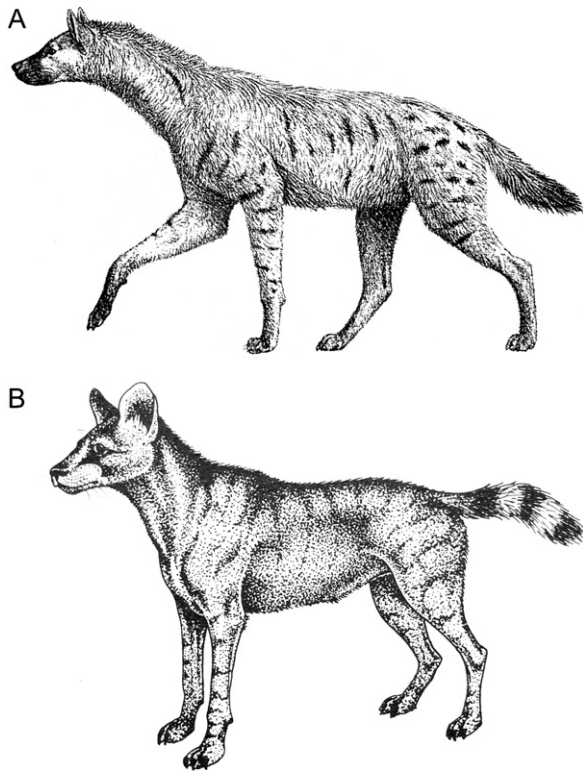


Fig. 9. Restorations of the external appearance. A. “*Ictitherium*” *ebu* from Lothagam (by Antón [14]). B. *Hyaenotherium magnum* from Cherevichnoe [11].

Fig. 9. Restaurations de l'apparence externe. A. «*Ictitherium*» *ebu* de Lothagam (par Antón [14]). B. *Hyaenotherium magnum* de Cherevichnoe [11].

#### 4. Reidentification of the Lothagam hyaenids

Judging from its description, measurements and drawings [14], “*Ictitherium*” *ebu* is clearly a member of the tribe Hyaenotheriini and hence cannot belong to *Ictitherium*. The specimen has evenly inflated auditory bullae; lacks an alisphenoid canal; as evidenced by the short and backwardly extended sagittal crest, the temporal lines are presumably long and converge behind the level of the glenoid fossa; occipital crest is relatively small (Fig. 8). Mandible has a single mental foramen, and the lower contour of the mandibular body is nearly straight. The P4 protocone does not protrude anteriorly to the parastyle; the m1 talonid is narrow (35.8% of the crown length) and moderately short (25.1% of the crown length); M2 is not “somewhat reduced” [14] because its length averages only 17.8% of the P4 length. Finally, the limbs of “*Ictitherium*” *ebu* are essentially longer and much more slender than even those of *H. wongi* (Fig. 7). These features reliably disprove the ictitheriine affinity of this hyaenid. The unusual length of its limbs would,

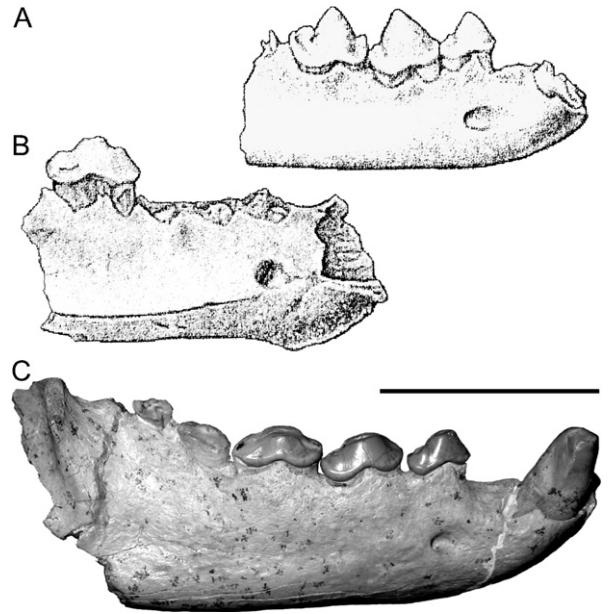


Fig. 10. Fragments of mandibles (lateral views). A. *Hyaenictitherium* cf. *H. parvum* from Lothagam [14]. B. *Hyaenictis* sp. from Lothagam [14]. C. *Lycyaena parva* from Taraklia (PMNUO 3005, holotype). Scale bar = 50 mm.

Fig. 10. Fragments de mandibules (vues latérales). A. *Hyaenictitherium* cf. *H. parvum* de Lothagam [14]. B. *Hyaenictis* sp. de Lothagam [14]. C. *Lycyaena parva* de Taraklia (PMNUO 3005, holotype). Échelle = 50 mm.

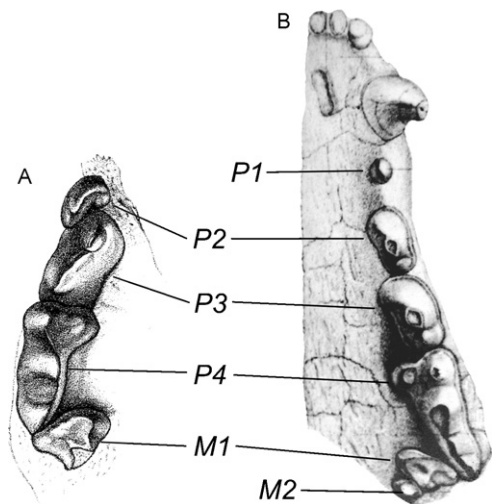


Fig. 11. Upper cheek teeth (occlusal views). A. *Palhyaena hipparionum* sensu Gervais from Mont Léberon [4]. B. *Ictitherium hipparionum* sensu Gaudry from Pikermi [3]. Not to scale.

Fig. 11. Dents jugales supérieures (vues occlusales). A. *Palhyaena hipparionum* sensu Gervais de Mont Léberon [4]. B. *Ictitherium hipparionum* sensu Gaudry de Pikermi [3]. Non à l'échelle.



Fig. 12. *Thalassictis robusta* from Kishinev. A. Skull in ventral view (PMNUO 2971). B. Skull in dorsal view (PMNUO 2971). C. Skull in lateral view (PMNUO 2971) [10]. D. Mandible in lateral view (PMNUO, cast of lectotype). Scale bar = 50 mm.

Fig. 12. *Thalassictis robusta* de Kishinev. A. Crâne en vue ventrale (PMNUO 2971). B. Crâne en vue dorsale (PMNUO 2971). C. Crâne en vue latérale (PMNUO 2971) [10]. D. Mandibule en vue latérale (PMNUO, moulage du lectotype). Échelle = 50 mm.

on its own, be sufficient to regard this carnivore as a member of the tribe Hyaenotheriini. Considering the slightly inflated auditory bullae and short postorbital and jugular processes of the species, it belongs most proba-

bly to the genus *Hyaenotherium*. Such a conclusion can explain why, in its main features the reconstruction of the Kenyan “*Ictitherium*” *ebu* is so similar to that of Ukrainian *Hyaenotherium magnum* (Fig. 9).

A mandibular fragment of another hyaenid from Lothagam was originally referred [14] to *Hyaenictitherium* cf. *H. parvum* (Fig. 10A). Although this specimen is incomplete, its degree of preservation allows reliable generic identification. First of all, it seems questionable that a hyaenid with very narrow and extremely high-crowned premolars (especially p3) could belong to the genus *Hyaenictitherium*. Dentally, the specimen more closely resembles *Hyaenictis*. This is also suggested by a single mental foramen and rounded mental part of the mandible in lateral view. Moreover, another fragment of the lower jaw was found in Lothagam, that of a senile individual. It was originally referred [14] to *Hyaenictis* sp. (Fig. 10B). This specimen differs from the “*parvum*” specimen in the age-related characters only, namely in the deepening of the mandibular body, particularly in its symphyseal region. This suggests a conspecific status of the two hyaenids, rather than their belonging to the different genera. The original assignment of the specimen to *Lycyaena parva* Khomenko, 1929 (described from Taraklia, Moldova [7]) seems unjustified. The only feature shared by these two hyaenines is their small size (Fig. 10).

## 5. Remarks

Importantly, the application of the generic name *Palhyaena* to any “ictitheres” and the name *Thalassictis* to any hyaenotheriins is a mistake [11]. The misuse of *Palhyaena* stems from the publications by Gaudry [2,3] who erroneously used this name for two non-congeneric specimens. Fig. 11 shows that *Palhyaena hipparionum* sensu Gervais from Mont Léberon [4] lacks M2 and its postcanine teeth differ appreciably from those of *I. hipparionum* sensu Gaudry from Pikermi [3]. This indicates that the former specimen having such a powerful P3, belongs neither to Ictitheriinae nor to Hyaenotheriini.

The generic name *Thalassictis* is often applied to the members of Hyaenotheriini, mainly with additions such as “Gervais, ex Nordmann”, “Gervais, non Nordmann” or “Nordmann, in Gervais”. Passing over the history and details of this evident nomenclatural problem, it could be said that in such a case this name can be applied only to *Mustela incerta* Gervais ex Lartet or become a synonym of *Ictitherium*. Originally the name *Thalassictis* was proposed by Nordmann [8] for the material from the Sarmatian deposits of Kishinev (Moldova). But this name is also quite suitable to the nearly complete skull from the same locality, later described by Pavlow [10] as *I. sarmaticum*, since many craniodental traits suggest the conspecific status of these finds [11]. Judging

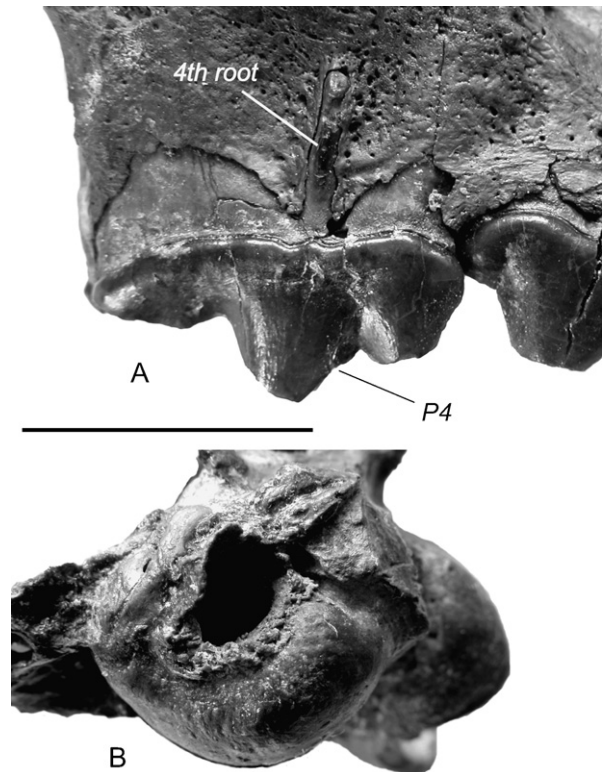


Fig. 13. *Thalassictis robusta* from Kishinev (PMNUO 2971). A. 4-rooted right P4 (buccal view). B. Isolated left auditory bulla (lateral view). Scale bar = 30 mm.

Fig. 13. *Thalassictis robusta* de Kishinev (PMNUO 2971). A. P4 droite tétraradiculée (vue buccale). B. Bulle auditive gauche isolée (vue latérale). Échelle = 30 mm.

by the morphology of the auditory region, cranial vault and occipital bone and in spite of considerable reduction of the second molars, P4 protocone and m1 talonid (Fig. 12), the species from Kishinev is undoubtedly related to the true Ictitheriinae, but not to any Hyaeninae. At the same time, the unique shape of its auditory bulla, very short postorbital process, slight reduction of the fourth root of the P4 (Figs. 2 and 13), protocone of the P4 not protruding (Figs. 6B, 12) and very tall m1 protoconid (Fig. 12D) make *T. robusta* easily distinguishable from all species of the genus *Ictitherium* and other ictitheriines.

## 6. Conclusions

The genera *Hyaenotherium*, *Miohyaenotherium* and *Thalassictis* are valid and morphologically well defined taxa, of which the former two belong to the tribe Hyaenotheriini and the latter one belongs to the subfamily Ictitheriinae.

The genus *Hyaenotherium*, represented by *H. ebu* Werdelin, 2005, from Lothagam, can be reliably added to the list of fossil African Carnivora. More cautiously, this species may belong to a new genus of Hyaeninae, but in any case, it cannot be a member of the Ictitheriinae and, even less so, of the genus *Ictitherium*.

The other small hyaenid remains from Lothagam, originally referred to *Hyaenictitherium* cf. *H. parvum* and *Hyaenictis* sp. [14], most probably belong to the same unidentified species of the genus *Hyaenictis*.

*Palhyaena hipparionum* from Mont Léberon belongs to the subfamily Hyaeninae, though not to the tribe Hyaenotheriini. Its generic name cannot be used for any “ictithere”.

The subfamily Ictitheriinae in its common usage is a collective group which needs a comprehensive revision.

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