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*Hyaenictitherium minimum*, a new ictithere  
(Mammalia, Carnivora, Hyaenidae)  
from the Late Miocene of Toros-Menalla, Chad

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**Abstract**

A new species of Hyaenidae, *Hyaenictitherium minimum*, is described in the carnivore fauna of the Late Miocene layers of Toros-Menalla (Chad). Its size is similar to that of a jackal and it had probably a similar ecological niche. It is found in several fossil-bearing localities of this area. The genus *Hyaenictitherium* is known from the early Late Miocene in Eurasia from China to Spain; the Chadian material is, perhaps with some specimens from Sahabi and Lothagam, the earliest occurrence of the genus in Africa. It results certainly from Eurasian migration, which will have to be taken into account for the analysis of the bulk of the fauna. **To cite this article:** L. de Bonis et al., C. R. Palevol 4 (2005).

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**Résumé**

***Hyaenictitherium minimum*, un nouvel ictithère (Mammalia, Carnivora, Hyaenidae) du Miocène supérieur de Toros-Menalla, Tchad.** La faune de carnivores du Miocène supérieur de Toros-Menalla (Tchad) contient une espèce nouvelle de Hyaenidae appartenant au genre *Hyaenictitherium*, *H. minimum*. De la taille d'un chacal, dont elle occupait peut-être une partie de la niche écologique, cette forme est répandue dans plusieurs gisements de cette région. Le genre est connu en Eurasie au Miocène supérieur. Le matériel tchadien, avec peut-être certains spécimens de Sahabi et Lothagam, marque son apparition en Afrique. Sa présence dans ce continent résulte certainement d'une migration d'origine eurasiatique. Ce phénomène devra être pris en considération lors de l'analyse des autres composantes de la faune. **Pour citer cet article :** L. de Bonis et al., C. R. Palevol 4 (2005).

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**Keywords:** Chad; Toros-Menalla; Late Miocene; Hyaenidae; *Hyaenictitherium*

**Mots clés :** Tchad ; Toros-Menalla ; Miocène supérieur ; Hyaenidae ; *Hyaenictitherium*

## Version française abrégée

### Introduction

Les localités fossilifères de Toros-Menalla sont situées à l'ouest de l'erg du Djourab, dans le Tchad central. Leur faune fossile a permis de les dater de la fin du Miocène supérieur, soit de 6 à 7 millions d'années (Ma), mais plus près de 7. Parmi les vestiges osseux recueillis, les restes de carnivores sont assez nombreux et répartis entre plusieurs familles (Canidae, Mustelidae, Felidae, Herpestidae, Viverridae, Hyaenidae). C'est un nouveau représentant de cette dernière famille qui sera décrit dans cet article. Il se rattache à un groupe de Hyaenidae, de taille petite à moyenne, auquel on donne le nom vernaculaire d'ictithères, d'après le genre *Ictitherium*, qui fait partie de cet ensemble.

### Systématique

Ordre Carnivora Bowdich, 1821

Sous-ordre Feliformia Kretzoi, 1945

Famille Hyaenidae Gray, 1829

Sous-famille Hyaeninae Gray, 1829

Genre *Hyaenictitherium* Kretzoi, 1938

*Hyaenictitherium minimum* n. sp.

Holotype : TM 204-01-029, fragment de mandibule gauche avec canine cassée, alvéoles de p1-p2, moitié mésiale de p3, p4-m1, alvéole de m2 et fragment de mandibule droite avec alvéoles de p2-4 et fragment du trigonide de m1, p4 droite isolée.

*Derivatio nominis* : allusion à la petite taille de l'espèce.

Localité type : localité TM 204, Toros-Menalla, Tchad.

Autres localités : TM 159, TM 200, TM 219, TM 266, TM 267, TM 278, TM 292. Toutes ces localités appartiennent à la zone fossilifère de Toros-Menalla, Tchad.

Âge géologique : Miocène supérieur, environ 7 Ma, à partir du grade évolutif de la faune de mammifères

par rapport à celui des autres faunes africaines datées du Miocène supérieur (par exemple celles de la formation de Lukeino ou de la formation de Nawata, Lothagam).

Autres spécimens rapportés à cette espèce : TM 159-01-12, fragment de mandibule gauche portant p3-m1 très abîmées et fragment de mandibule droite avec p2-p4 très abîmées ; TM 200-01-008, fragment de mandibule droite avec racines de p2 et p3-p4 ; TM 219-01-060, fragment de mandibule gauche avec alvéole de m2 ; TM 219-01-093, fragment de mandibule gauche avec racines de p3 et p4-m1 mal préservées ; TM 266-01-403, fragment de mandibule gauche avec alvéole de p1, racines de p2, p3-p4 très usées, fragment de m1, alvéole de m2 ; TM 266-01-192, fragment de mandibule droite avec i3, fragment de c, alvéole de p1, base de la couronne de p2-m1 ; TM 266-01-204, fragment de mandibule gauche avec racines de p2, partie distale de p3 et p4-m1 mal préservée ; TM 266-02-001, fragment de mandibule droite avec partie distale de p3 et p4 mal préservée ; TM 266-01-279, fragment de mandibule gauche avec m1 et m2 très usées ; TM 266-03-035, fragment de mandibule gauche avec base de p4-m1 mal préservée, alvéole de m2 ; TM 266-03-369, couronne de m1 gauche incomplète ; TM 266-03-341, fragment de maxillaire droit avec P4 mal préservée ; TM 267-02-014, fragment de mandibule gauche avec p3 cassée, p4-m1 et la racine de m2 ; TM 278-03-011, fragment de mandibule gauche avec p2-3 et m1 *in statu nascendi* mais complètement visibles ; TM 292-03-002, fragment de mandibule droite avec i3-c cassées, racine de p1, racine distale de p2, p3-m1, alvéole de m2. Ce matériel, en cours d'étude à l'université de Poitiers, sera conservé dans le département de conservation des collections du Centre national d'appui à la recherche (Cnar), N'Djamena, Tchad.

Diagnose différentielle : espèce de *Hyaenictitherium* différant des autres espèces par une taille corporelle nettement inférieure et par un tubercule accessoire mésial très faible ou absent sur p4 et, évidemment, sur les autres prémolaires inférieures.

### Description

Corpus mandibulae : malgré une variation assez grande, la branche horizontale est toujours très basse. Le bord inférieur, d'abord légèrement convexe, se redresse brusquement sous la branche montante.

Denture inférieure : la canine est relativement courte et forte. La p1, dont la couronne est inconnue, était uniradiculée. La p2 possédait deux racines. La p3, dissymétrique avec une face mésiale plus abrupte, est dépourvue de tubercule accessoire mésial, mais possède une minuscule cuspide accessoire distale. La p4 est un peu plus haute et longue que p3 ; la cuspide accessoire mésiale est faible ou absente ; une fine crête distale se termine à la base par une cuspide jouant le rôle d'un hypoconide qui borde un talonide creux, fermé lingualement par une crête entoconidienne. La carnassière, relativement courte par rapport à la longueur p2–p4, porte un trigonide bas pour un hyénidé, avec une très faible différence de hauteur entre paraconide et protoconide ; le métaconide est réduit, mais pas visible en vue buccale. Le talonide est modérément développé ; hypoconide, hypoconulide et entoconide entourent un bassin profond. La m2, non conservée sur tous les spécimens, était uniradiculée.

Denture supérieure : elle est réduite à une carnassière usée et brisée à son extrémité distale, portée par un fragment de maxillaire. Le protocône se projette en avant du parastyle comme chez *Hyaenictitherium* ou *Miohyaenotherium*.

### Comparaisons

Par rapport au matériel décrit ici, *Thalassictis* diffère surtout par la présence de cuspides accessoires plus développées sur les prémolaires et par la différence de hauteur entre paraconide et protoconide sur m1. *Palinhyana* a des prémolaires plus courtes, plus hautes et parfois imbriquées, ainsi qu'un talonide de m1 plus court. *Miohyaenotherium* est plus grand, avec un corpus mandibulaire proportionnellement plus haut, des prémolaires plus robustes, avec des cuspides accessoires plus développées, une m1 à trigonide plus élevé et une forte différence de hauteur entre paraconide et protoconide, ainsi qu'un talonide court. Plusieurs espèces ont été attribuées au genre *Ictitherium*. L'espèce type, *I. viverrinum*, s'écarte nettement de la forme tchadienne par une rangée pré-molaire relativement plus

courte, une m1 dont le métaconide est très développé et le talonide plus long. *Metahyaena* diffère de l'espèce du Tchad par un corpus mandibulaire proportionnellement plus haut et une p4 symétrique, avec une grande cuspide accessoire mésiale. Les espèces de *Hyaenictitherium* montrent certaines similitudes avec l'espèce tchadienne. L'espèce nominale, *H. hyaenoides*, a une morphologie semblable en vue latérale, mais elle est plus grande, avec des prémolaires plus épaisses et un talonide de m1 plus court. *H. wongii*, et surtout *H. namaquense*, *H. parvum*, *H. venator* et *H. barbarum* sont des espèces nettement plus grandes que celle du Tchad. Cette dernière peut donc être rattachée à ce genre, mais comme une espèce nouvelle, *H. minimum*. Il s'agit de la plus ancienne présence du genre en Afrique.

### Conclusions

La nouvelle espèce de carnivore *Hyaenictitherium minimum* était d'une taille voisine de celle d'un chacal dont elle occupait peut-être une partie de la niche écologique. Sa présence complète non seulement la liste de fossiles de Toros-Menalla, mais elle apporte également une indication sur l'origine d'une partie de la faune. Le genre *Hyaenictitherium* était surtout connu au Miocène supérieur en Asie et en Europe, depuis la Chine jusqu'à l'Espagne en passant par l'Afghanistan, l'Iran et la Turquie. Il a été signalé, avec quelques doutes, en Afrique, à Sahabi et Lothagam. Les nouveaux résultats confirment pleinement sa présence en Afrique vers la fin du Miocène et pourraient être la marque d'une immigration eurasiatique à cette époque, comme l'a suggéré Werdelin [18] pour les carnivores du Miocène supérieur de Lothagam. Cette donnée devra être prise en considération dans l'analyse du reste de la faune.

### 1. Introduction

Situated on the western central Chad, ca. 700 km northeast of N'Djamena, the fossil-bearing localities of Toros Menalla (Chad) have been dated to the end of the Late Miocene from 7 to 6 Ma [15], but probably closer to 7 Ma [3]. They have yielded many remains of fossil vertebrates, especially mammals. Numerous jaws and bones of Carnivora [12] have been recovered from

these localities and referred to several families (Canidae, Mustelidae, Felidae, Herpestidae, Viverridae, Hyaenidae). The family Hyaenidae is well represented, with several genera.

In this article, we describe a new middle-sized hyaenid that is present in several sites of Toro-Menalla, including TM 266, which has yielded remains of the hominid *Sahelanthropus tchadensis* [2,3]. The Late Miocene middle-sized hyaenids are known under the vernacular name ictitheres, from the genus *Ictitherium* whose type species, *I. viverrinum*, has been recorded in the well-known Greek locality Pikermi in Attica, not far from Athens. This group of Carnivora includes several genera (e.g., *Thalassictis*, *Palinhyena*, *Hyaenictitherium*) of different size and with different evolutionary trends. Phylogenetic relationships between these genera are yet unclear [19]. The most useful and the most used characters to distinguish genera and species are the overall size, the skull morphology (but the skulls are rare in the fossil record), the shape of the mandible, the relative size and the shape of the canine, the number and the morphology of the cheek teeth, particularly the presence of accessory cusps and the relative width of the premolars, the size and relative proportions of the upper carnassial cusps, the position and development of upper molars, the height of the cuspids of the trigonid of m1, the development of the m1 metaconid, the shape and size of the m1 talonid and of m2. These features will be used for comparisons when possible.

## 2. Systematics

Order Carnivora Bowdich, 1821  
 Suborder Feliformia Kretzoi, 1945  
 Family Hyaenidae Gray, 1829  
 Subfamily Hyaeninae Gray, 1829  
 Genus *Hyaenictitherium* Kretzoi, 1938  
*Hyaenictitherium minimum* n. sp.

*Holotype*. TM 204-01-029, fragment of left mandible with broken c, alveoli of p1–p3, isolated mesial half of p3, p4-m1, alveoli of m2 and fragment of right mandible with alveoli of p2–4 and fragment of m1 trigonid, isolated right p4.

*Derivatio nominis*. From the small size of this species.

*Type locality*. Locality TM 204, Toros Menalla, Chad.

*Other localities*. TM 159, TM 200, TM 219, TM 266, TM 267, TM 278, TM 292. All the localities are located in the fossiliferous area of Toros-Menalla, Chad.

*Geological age*. Late Miocene, ca. 7 Ma, based on the evolutionary grade of the faunas compared to that of other Late Miocene African faunas (e.g., Lukeino Formation; lower Nawata Formation, Lothagam) [3,10,15]. TM 200, TM 204 and TM 219 are ca. 60 km west–northwest of TM 266, TM 267, TM 278 and TM 292. All these sites are considered as similar in age, on the basis of their fauna. The presence of the species described here and of *Machairodus kabir* [12] in TM 266 and TM 112 (two localities separated from each other by ca. 30 km) supports the biochronological homogeneity of the TM area.

*Additional referred specimens*. TM 159-01-12, fragment of left mandible with damaged p3-m1 and fragment of right mandible with damaged p2-p4; TM 200-01-008, fragment of right mandible with p2 roots, p3-p4; TM 219-01-060, fragment of left mandible with alveolus of m2; TM 219-01-093, fragment of left mandible with p3 roots and very poorly preserved fragment of p4-m1; TM 266-01-403, fragment of left mandible with p1 alveolus, p2 roots, very worn p3-p4, poorly preserved m1 fragment, alveolus of m2; TM 266-01-192, fragment of right mandible with i3, fragmentary c, alveolus of p1, basis of the crown of p2-m1; TM 266-01-204, fragment of left mandible with p2 roots, distal part of p3 and very damaged p4-m1; TM 266-02-001, fragment of right mandible with distal part of p3 and poorly preserved p4; TM 266-01-279, fragment of left mandible with highly worn m1 talonid and worn m2; TM 266-03-035, fragment of left mandible with very damaged basis of p4-m1, alveolus of m2; TM 266-03-369, uncompleted isolated left m1; TM 266-03-341, fragment of right maxilla with broken P4; TM 267-02-014, fragment of left mandible with distal half of p3, p4-m1, m2 root; TM 278-03-011, fragment of left mandible with p2-3 and m1 erupting but completely visible; TM 292-03-002, fragment of right mandible with broken i3-c, p1 root, p2 distal root, p3-m1, alveolus of m2.

The material is currently studied at the University of Poitiers, France, and will be stored in the 'Département de conservation des collections', 'Centre national d'appui à la recherche' (CNAR), N'Djamena, Chad.

*Differential diagnosis*. Species of *Hyaenictitherium* differing from other species in being distinctly smaller

in size and in having a very small or absent mesial accessory cuspid on p4, and of course on the other lower premolars.

### 3. Description

#### 3.1. Corpus mandibulae (Figs. 1–3)

There is a great size variation of the corpus albeit the dental variation is far lesser. A large part of this variation is due to the age of the specimens: younger

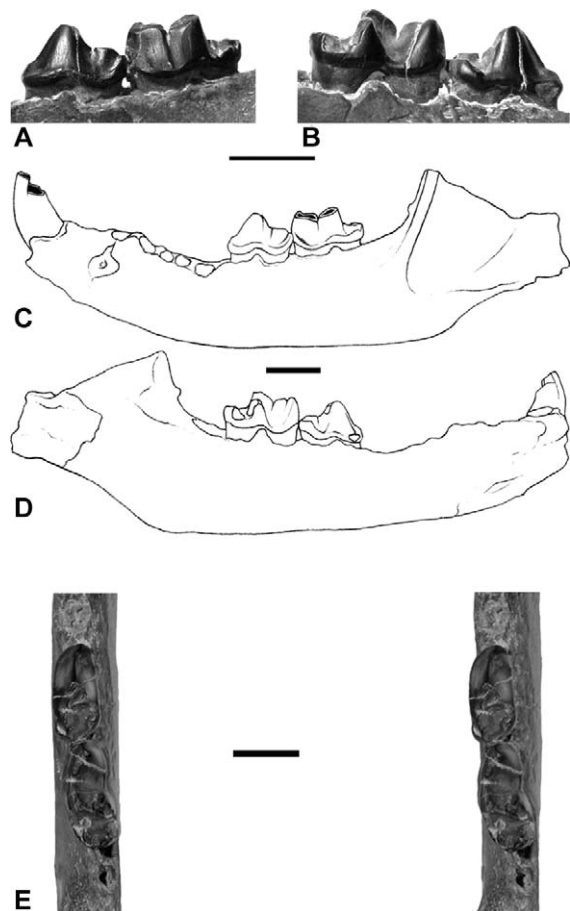


Fig. 1. *Hyaenictitherium minimum* n. sp. TM 204-01-29 (Toros-Menalla Late Miocene, Chad), holotype; left mandible; a, c: buccal view; b, d: lingual view; e: stereophotographs of an occlusal view. Scale bar = 1 cm.

Fig. 1. *Hyaenictitherium minimum* n. sp. TM 204-01-29 (Toros-Menalla, Miocène supérieur, Tchad), holotype ; mandibule gauche ; a, c : vue buccale ; b, d : vue linguale ; e : stéréophotographies d'une vue occlusale. Échelle = 1 cm.

individual being smaller than the older ones. The corpus is shallow, especially under p2, becoming gently deeper under m2 then the basal line turns up under the ramus. The only mental foramen is situated under the mesial root of p2.

#### 3.2. Lower dentition (Figs. 1–3; measurements: see Table 1)

The i3 (one worn specimen) is weak. The canine (two broken specimens) seems to have been relatively stout and short. No p1s are preserved on the holotype and referred specimens. It is represented only by a single small, rounded alveolus. The p2 is two-rooted, but the crown is not completely preserved or absent on the specimens. On TM 266-01-192, there is no accessory cusp on the preserved fragment. The crown of p3 is documented on TM 292-03-002, TM 200-01-08 and, for the distal part, on TM 261-02-014. It is asymmetrical, the mesial part being shorter than the distal one; its mesial face is more strongly sloped than the distal one

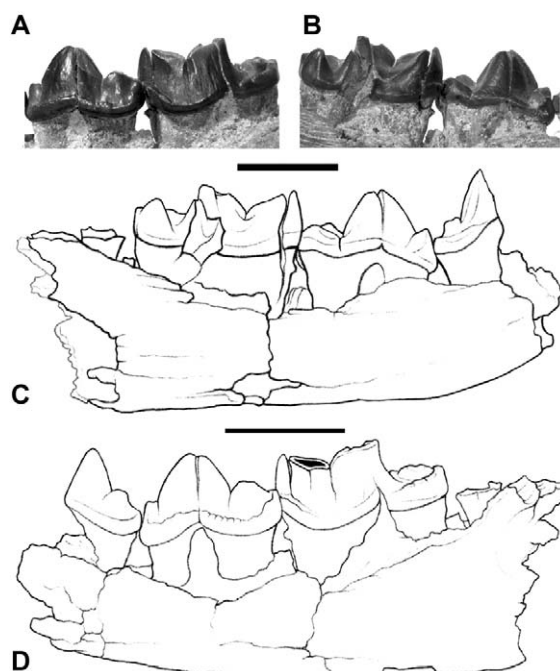


Fig. 2. *Hyaenictitherium minimum* n. sp. TM 267-02-014 (Toros-Menalla Late Miocene, Chad), left mandible; a, d: buccal view; b, c: lingual view. Scale bar = 1 cm.

Fig. 2. *Hyaenictitherium minimum* n. sp. TM 267-02-014 (Toros-Menalla, Miocène supérieur, Tchad), mandibule gauche ; a, d : vue buccale ; b, c : vue linguale. Échelle = 1 cm.

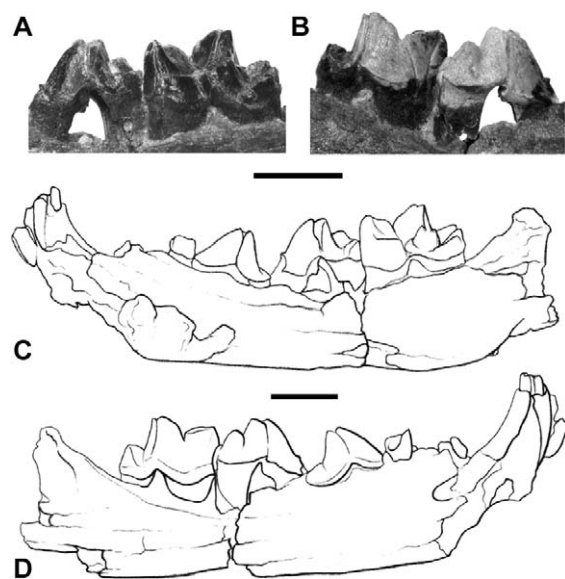


Fig. 3. *Hyaenictitherium minimum* n. sp. TM 292-03-002 (Toros-Menalla Late Miocene, Chad), right mandible; a, c: lingual view; b, d: buccal view. Scale bar = 1 cm.

Fig. 3. *Hyaenictitherium minimum* n. sp. TM 292-03-002 (Toros-Menalla, Miocène supérieur, Tchad), mandibule droite ; a, c : vue linguale ; b, d : vue buccale. Échelle = 1 cm.

and there is a delicate crest running from the top to the base. There is a small cingulum but no mesial accessory cuspid. The distal part of the crown is elongated and a little basally enlarged. There is a small distal crest interrupted by a tiny distal accessory cuspid. The crown is more bumped buccally than lingually. The p4 is higher and a little longer than p3. It is quite long relative to m1. Like that of p3, the crown is more inflated buccally than lingually. The mesial accessory cuspid is small, very small or absent depending on the speci-

mens; it is followed by a thin crest. The distal crest runs down to the well-developed distal accessory cuspid that looks like a hypoconid. Lingually there is a hollow talonid basin, which is closed by a lingual crest (entoconid) nearly reaching the distolingual basis of the main cuspid. The lower carnassial is quite short relative to the premolar length (p1–p4). The trigonid is relatively low for a hyaenid with a slight height difference between the paraconid and the protoconid. There is a slight buccal cingulum. The metaconid is reduced and not visible in buccal view. The talonid is moderately developed in length, less than that of *Ictitherium* but more than that of *Miohyaenotherium* for examples. The hypoconid is a high cuspid separated from the protoconid by a deep notch and from the hypoconulid by a lesser one. The latter and the entoconid are on a same crest but can be identified as independent cuspids on the fresh teeth. The entoconid is separated from the metaconid by a deep notch. The talonid basin is deep. No specimen preserves m2, which was single-rooted.

### 3.3. Upper dentition (Fig. 4)

The only known material from the upper jaw allocated to this species is an upper carnassial P4 on a small piece of maxilla. The crown is quite worn. The meta-style is broken in its distal part and the protocone is projected mesiolingually, like in *Hyaenictitherium* or *Miohyaenotherium*, and unlike *Ictitherium*. Other details are hardly observable due to the weathering. On this specimen, the total length of P4 is 19 mm and the buccal length is 16.9 mm, but these measurements would be a little greater on a complete tooth. The

Table 1

*Hyaenictitherium minimum* n. sp., Toros-Menalla, Chad. Measurements (mm) of lower teeth. L = total length; w = maximum width; L trig = length of the trigonid; w trig = width of the trigonid; w tal = width of the talonid; () = uncertain measurement

Tableau 1. *Hyaenictitherium minimum* n. sp., Toros-Menalla Tchad. Mensurations (mm) des dents inférieures. L = longueur totale ; W = largeur totale ; L trig = longueur du trigonide ; W trig = largeur du trogonide ; w tal = largeur du talonide ; () = mesure incertaine.

TM	c		p1		p2		p3		p4		m1			m2		
	L	w	L	w	L	w	L	w	L	w	L	L trig	w trig	w tal	L	w
204-01-029	9.6	8.3							13.9	7.3	15.7	11.1	7.1	6.8	(5.8)	—
266-01-192					(11.5)	—	13.9	(6.3)	14.0	(6.8)	15.1	11.2	(5.5)	(5.1)		
266-01-403							13.7	5.9	14.0	6.8	(15.2)	—	—	—		
266-03-035											15.2	—	—	—		
200-01-008							13.0	6.5	13.7	7.7						
267-02-014									14.7	6.0	16.5	11.4	7.0	6.3		
278-03-011											15.0	10.5	6.3	4.9		
292-03-002							12.5	6.4	15.2	6.5	15.8	11.5	7.5	5.6		

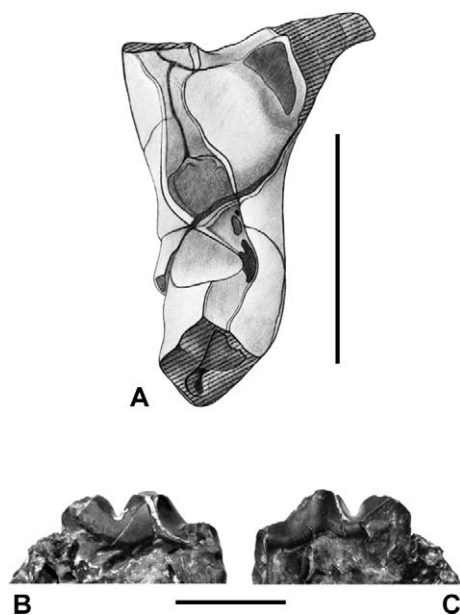


Fig. 4. *Hyaenictitherium minimum* n. sp. TM 266-03-341 (Toros-Menalla Late Miocene, Chad), right P4; a: occlusal view; b: lingual view; c: buccal view. Scale bar = 1 cm.

Fig. 4. *Hyaenictitherium minimum* n. sp. TM 266-03-341 (Toros-Menalla, Miocène supérieur, Tchad), P4 droite; a : vue occlusale ; b : vue linguale ; c : vue buccale. Échelle = 1 cm.

breadth is 11 mm at the level of the protocone and 5.7 mm at the level of the metastyle.

#### 4. Comparisons

The specimens of Toros-Menallas will be compared to the known ictitheres (*Thalassictis*, *Palinhyena*, *Miohyaenotherium*, *Ictitherium*, *Metahyaena* and *Hyaenictitherium*), except the smaller *Plioviverrops* and *Protictitherium*, whose lower carnassials have more grouped cuspids on the trigonid. Otherwise noticed, age and geographic distribution of the species mentioned below are from Werdelin and Solounias [19].

*Thalassictis* spp. differs from the Chadian ictithere in having premolars with a more developed mesial accessory cuspid, especially on p4, a m1 protoconid that is higher relative to the paraconid and sometimes a double-rooted m2 [9].

*Palinhyena reperta* Qiu, Huang & Guo, 1979 (= *P. imbricata*; see [17]) from the Turolian of China, is distinguished from our material by its relatively shorter, higher and sometimes overlapping premolars, a higher m1 trigonid and a shorter m1 talonid [13].

*Miohyaenotherium bessarabicum* Semenov, 1989 from the Turolian of Moldova (Cimislia, Udabno) and Ukraine (Belka), differs by a larger size, a deeper mandibular corpus, a more robust canine and more robust premolars with a larger mesial accessory cuspid, a higher m1 trigonid with a greater difference of height between the paraconid and protoconid, a shorter m1 relative to p1–4 length, which mainly results from a smaller talonid [14].

Several species have been allocated to the genus *Ictitherium* Wagner, 1848. *Ictitherium viverrinum* Roth and Wagner, 1854, the nominal species of the genus, is known from numerous Turolian localities of Europe (e.g., Pikermi, Samos) and Asia (especially Ukraine) and Asia (especially China). It has a low m1 trigonid with a slight height difference between paraconid and protoconid but it differs from the Chadian species in having relatively shortened premolar row (the length p2–p4 is the same though m1 is larger), a more developed buccal cingulum on p4 and m1, a far more developed m1 metaconid, a wider and longer m1 talonid, and a longer m2. *Ictitherium adroveri* Crusafont & Pether, 1969 (Turolian of Calatayud–Teruel Basin, Spain) is based on a P4 and a m1. The m1 metaconid is reduced, but a little more distally situated than in the Chadian species. This position suggests closer affinities with the genus *Thalassictis* than with *Ictitherium*; there is a thick buccal cingulum on m1. *Ictitherium ebu*, which was recently described by Werdelin [18] from the Late Miocene (Lothagam Formation) and Early Pliocene (Nachukui Formation) of Kenya, is larger than *H. minimum* and it has longer and slender premolars. *Ictitherium ibericum* Meladze, 1967 from the Late Turolian of Bazaleti (Georgia), has quite the same size as *H. minimum* but it has a shorter m1 talonid, a more asymmetrical p4 with a more developed talonid. The height of the corpus is quite the same from p1 to m1. '*Ictitherium*' *intuberculatum* Ozansoy, 1965 (Vallesian of Yassiören, Turkey) is in fact a large species of *Hyaenictitherium* with a deep corpus mandibulae different from *H. minimum* [1]. *Ictitherium pannonicum* Kretzoi, 1952 from the Turolian of Hungary, Spain and Ukraine, has a reduced metaconid on m1 (more *Hyaenictitherium*-like), but this species is larger than the Chadian material and it has a larger mesial accessory cuspid and a more developed talonid on p4. Like the Chadian species, *Ictitherium tauricum* Borissiak, 1915 from the Vallesian of Sebastopol (Ukraine) and

the Turolian of Küçükoyzgat (Turkey) [1], is small in size (m1 length = 15 mm), but it differs by its slender canines. *Ictitherium sarmaticum* Pavlow, 1908 (?Vallesian of Kishinev, Moldova) is known only from a skull that corresponds to a larger size than that of *H. minimum*.

*Metahyaena confector* Viranta and Werdelin, 2003, from the Early Vallesian of the Sinap Formation (Turkey), differs by a deeper corpus and a more symmetrical p4, with a larger mesial accessory cuspid [16].

The species of *Hyaenictitherium* Kretzoi, 1938 shows some similarities with the Chadian specimens with the same low m1 trigonid and reduced m1 metaconid. The mandible of the type species *H. hyaenoides* (Zdansky, 1924) (Turolian of China, Iran, Ukraine, Kazakhstan) is quite similar in buccal view to that of the Toros-Menalla species, but it is far larger; this species has relatively wider premolars and a relatively shorter m1 talonid [19]. *Hyaenictitherium namaquense* (Stromer, 1931) from Langebaanweg (Late Miocene to Early Pliocene, South Africa) and Lukeino (Late Miocene, Kenya [11]) is a larger species, with a much more developed mesial accessory cuspid on p4. The mandible (L 12848) has also a deeper corpus and more robust dentition [6]. Another specimen, recovered from the locality Sahabi (Late Miocene–Early Pliocene, Libya) and described as *Ictitherium arkesilai* Esu and Kotsakis, 1980, could be a species of *Hyaenictitherium* [20]; this species is, however, larger and more robust than *H. minimum* and the shape of the premolars is different [4,7]. *Hyaenictitherium parvum* is based on a single individual from Taraklia (Turolian, Moldova) described and illustrated by Khomenko [8]. This specimen is larger than our material and its highly worn dentition and the poor available illustration prevent us from having a good idea of the morphology of this species. *Hyaenictitherium venator* Semenov, 1989 (Turolian of Ukraine and Moldova) and *H. wongii* (Zdansky, 1924) (Late Miocene of China, Ukraine, Germany, Greece, Iran, etc.) are larger than *H. minimum*. *Hyaenictitherium wongii* is close to *H. hyaenoides*, but differs by its narrower premolars. *Hyaenictitherium barbarum* Geraads, 1997 (Late Pliocene, Ahl al Oughlam, Morocco) is much larger than *H. minimum* and also differs by the absence of p1, more robust premolars and a shorter m1 talonid; this species is more *Hyaena*-like [5]. The morphologic characters of the TM dentitions seem to be close to those of the species of

*Hyaenictitherium* although the TM sample does not fit exactly any of them. The TM localities are correlated with the lower Nawata Formation of Lothagam, Kenya and so the age of *H. minimum* is estimated to 6 to 7 Ma. It is, perhaps with those of Sahabi and Lothagam, the earliest known occurrence of the genus *Hyaenictitherium* in Africa.

## 5. Conclusions

The remains of the new hyaenid species *Hyaenictitherium minimum* are found in many fossil-bearing localities of the Toros-Menalla area. This species reached approximately the size of a jackal and, insofar there is no similar sized canid in the same localities, it occupied probably a similar ecological niche. The occurrence of *H. minimum* in the Toros-Menalla sites adds more than a new name in the faunal list, but it gives also new data on the origin of part of the fauna. Until recently, the genus *Hyaenictitherium* was known during the Upper Miocene in Asia and in Europe from China to Spain through Afghanistan, Iran or Turkey. Its occurrence in Chad and possibly in contemporaneous strata of Libya (Sahabi) and Kenya (Lothagam), i.e. during the late Upper Miocene, is the trade mark of Eurasian migration into Africa. These new data will have to be taken into account for the future analysis of the bulk of the fauna.

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