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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).***

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 Ictitherinae Trouessart, 1897), de représentants de petite taille de la sous-famille des Hyaeninae. ***Pour citer cet article : Y. Semenov, C. R. Palevol 7 (2008).***

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

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

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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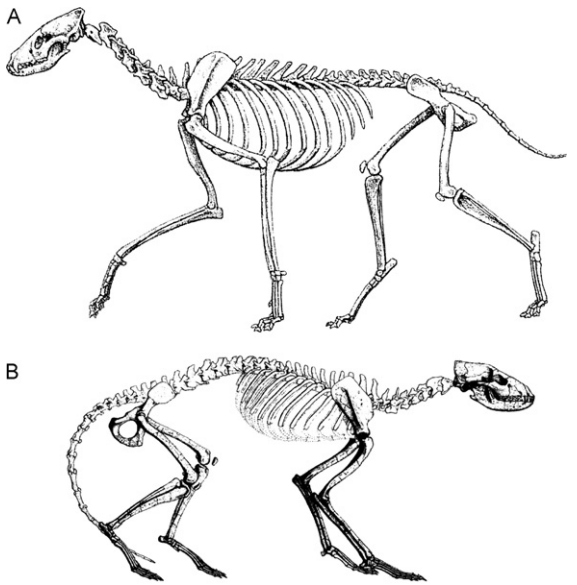

Fig. 1. Reconstructions of the skeletons. A. *"Ictitherium" ebu* from Lothagam (by Antón [14]). B. *Ictitherium viverrinum* from Pikermi [2].
Fig. 1. Reconstructions du squelette. A. « *Ictitherium* » *ebu* de Lothagam (par Antón [14]). B. *Ictitherium viverrinum* de Pikermi [2].

I. viverrinum was more robust and had relatively short limbs. Furthermore, there are many important craniodental 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;