

Systematic Palaeontology (Vertebrate Palaeontology)

# The fossil vertebrate locality Kossom Bougoudi, Djurab desert, Chad: A window in the distribution of the carnivoran faunas at the Mio–Pliocene boundary in Africa

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## Abstract

The fossil vertebrate bearing locality Kossom Bougoudi (KB) is situated in the Djurab desert (Chad, Africa), 600 km north-east of N'djamena. It has yielded about 1250 specimens with many mammalian remains, principally artiodactyls. Its geologic age has been estimated to be about 5 Ma by biochronologic estimation and about 5.3 Ma by radiometric studies on cosmogenic nuclides of beryllium (authigenic <sup>10</sup>B/<sup>9</sup>B). The carnivoran fauna contains few specimens which belong to five different families. All the taxa were unknown in central Africa. A large lutrine is close to *Sivaonyx* but different from known species of the genus. Another large lutrine is similar by its size to a species described from the Middle Pliocene of Uganda. An edentulous mandible of a small machairodont cat resembles a small species of *Dinofelis*, while a distal humerus indicates the presence of a larger member of the same genus. A hunting hyaenid is also much like the European species. An unidentified canid reaches the size of the recent *Canis aureus* and an isolated calcaneum matches that of the large extant viverrid. This small fauna allows a first look at the guild of the carnivorans at the Latest Miocene–Pliocene boundary in Central Africa and is a milestone between North African, East African and South African carnivore faunas. **To cite this article:** L. de Bonis et al., C. R. Palevol 7 (2008).

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## Résumé

**Le gisement de vertébrés fossiles de Kossom Bougoudi, désert du Djourab, Tchad : une fenêtre dans la distribution des faunes de carnivores à la limite Mio–Pliocène en Afrique.** Le gisement de vertébrés fossiles de Kossom Bougoudi (KB) se situe dans le désert du Djourab (Tchad, Afrique) à 600 km au nord-est de N'djamena. Il a livré environ 1250 spécimens, parmi lesquels une majorité de restes de mammifères, principalement des artiodactyles. Son âge géologique a été estimé aux alentours de 5 millions d'années par la biochronologie et à 5,3 Ma par des études radiochronologiques à partir de nucléides cosmogéniques du beryllium (<sup>10</sup>B/<sup>9</sup>B). La faune de carnivores contient peu de spécimens qui représentent cependant cinq familles. Tous les taxons sont nouveaux pour l'Afrique centrale. Un grand lutriné, proche de *Sivaonyx*, diffère cependant de toutes les espèces du genre, tandis qu'une autre loutre paraît se rapprocher d'une espèce décrite en Ouganda. Une portion de mandibule édentée appartient à une espèce de petite taille de *Dinofelis*, tandis qu'une extrémité distale d'humérus indique la présence d'une autre espèce, de très grande

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taille, du même genre. Une hyène « chasseresse » est proche d'une forme européenne, tandis qu'un Canidae atteint la taille du chacal *Canis aureus*. Enfin, un calcanéum isolé paraît correspondre à un viverridé de grande taille. Cette faunule permet d'avoir pour la première fois un regard sur la guildes des carnivores à la limite Miocène terminal–Pliocène, en Afrique centrale. Elle constitue un jalon entre les faunes de carnivores du Nord, de l'Est et du Sud de l'Afrique. **Pour citer cet article : L. de Bonis et al., C. R. Palevol 7 (2008).**

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**Keywords:** Carnivora; Miocene; Pliocene; Central Africa; Mustelidae; Felidae; Hyaenidae; Canidae

**Mots clés :** Carnivora ; Miocène ; Pliocène ; Afrique centrale ; Mustelidae ; Felidae ; Hyaenidae ; Canidae

## 1. Introduction

The fossil bearing localities Koro Toro (KT), Kollé (KL), Kossom Bougoudi (KB), and Toros Menalla (TM) are situated in the Djurab desert (Chad), north of N'djamena. Their geological ages span from the Middle Pliocene to the Late Miocene between 3.5 and 7 Ma [4,15]. The present article focuses on the carnivoran fauna from KB. This locality has yielded 1250 specimens of vertebrates of which few belong to the order Carnivora, the bulk of the mammalian remains belonging to Artiodactyla. After several field campaigns of the "Mission paléontologique Franco-Tchadienne" (MPFT), the age of this locality was first estimated by biochronology to be close to 5 Myr on the basis of the presence of *Anancus*, *Paracamelus*, and *Nyanzachoerus kanamensis* alone and on the primitive state of the bovids [4]. Later, radiochronology studies based on cosmogenic beryllium ( $B^{10}/B^9$ ) obtained, from four samples of a green pelite interbedded in the fossiliferous levels, an age of  $5.26 \pm 0.29$  Ma [15], so close to the Mio–Pliocene boundary. There is a fairly good fit between the results of the two independently conducted methods, thus the results are quite trustworthy. In the first list of mammals, Carnivora were cited as *Lycyaena* sp., *Dinofelis* sp. and Canidae indet. [4].

## 2. Material

Upper P4 (KB 07-98-039), mandible (KB4-97-183), mandible (KB4-97-94), distal humerus (KB3-96-22), mandible (KB2-98-08), mandible (KB3-96-72), maxilla (KB3-97-279), upper canine (KB3-98-2), mandible (KB24-97-16), calcaneum (KB3-00-02), fragment of mandible (KB15-97-20), isolated incisor and canine (KB3-99-14), fragment of mandible (KB4-97-105).

## 3. Systematics

Order Carnivora Bowdich, 1821  
Family Mustelidae Fischer, 1817

*Sivaonyx* aff. *S. ekecaman* (Werdelin, 2003)

2000 - *Sivaonyx africana*; Mazurier unpublished.

A well preserved unworn upper P4 (KB 07-98-039) probably belongs to a shellfish eating lutrine. We add to this specimen an edentulous mandible (KB4-97-183). Today there are some shellfish-eating lutrines. *Aonyx* lives in rivers and lakes of Africa. *Enhydra*, the marine otter, lives from the easternmost of Russia to California. This peculiar diet corresponds to some characteristics: large molars, shortened and widened P4, M2 very large, m1 with low and less trenchant cuspids, and large m2. Several fossil genera show a trend towards bunodonty, especially the genera *Paludolutra*, *Vishnuonyx*, *Sivaonyx* and *Enhydriodon*.

### Description

An isolated P4 may appear to be poor material to identify a specimen but the carnassial teeth are very significant into the order Carnivora. The occlusal outline of the crown (Fig. 1) is quadrangular and wider than long (length: 15,5/width: 16,3). There is a conical high paracone with a buccomesial ridge to the base of the well separated protocone, and a distal ridge to the low, short and no cutting metastyle. There is an incision between the latter and the paracone. The parastyle, slightly projected ahead, is very well distinct, pyramidal, and with a small mesial crest between the parastyle and protocone. The powerful conical protocone is slightly shorter and smaller than the paracone. There are two accessory cusplets situated on a distally and lingually oriented line, a tiny cingulum is along the lingual face of the protocone and of the cusplets. The central valley is lingually closed by a minute cusplet. There is a well developed conical hypocone, nevertheless smaller than the protocone. A low distal crest closes the central basin and is prolonged by a cingulum around the metastyle and along the buccal surface.

### Comparisons

Some studies [16,17,19,20,36] have recently increased the knowledge of fossil lutrines and particularly those with a quadrangular P4 due to development

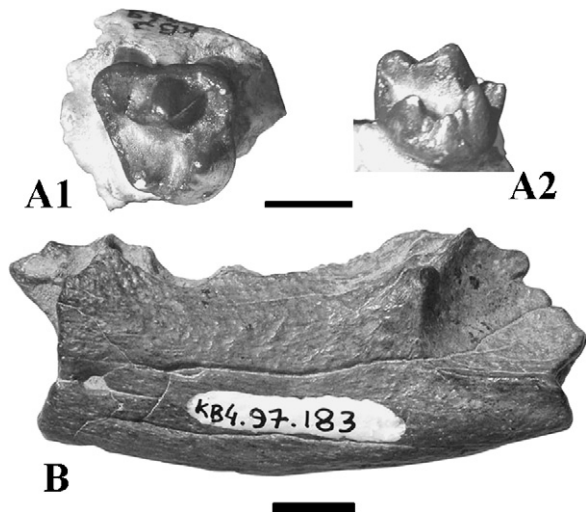


Fig. 1. *Sivaonyx* cf. *S. ekecaman*. A. P4 (KB 07-98-39). A1. Occlusal surface. A2. Lingual face. B. Mandible in lateral view (scale bar = 1 cm).

Fig. 1. *Sivaonyx* cf. *S. ekecaman*. A. P4 (KB 07-98-39). A1. Face occlusale. A2. Face linguale. B. Mandibule en vue latérale (échelle = 1 cm).

of the hypocone known as the bunodont lutrines. The piscivorous lutrines, whose P4 is very different, will not be included in the comparisons. These bunodont lutrines are placed into the tribe Enhyriodontini [17] with a conical protocone in P4 and few characters on m1 but a diagnosis is given later as “Lutrines in which the protocone of P4/ is well separated from the paracone by a wide valley; hypocone more or less enlarged and inflated and positioned on the lingual border of the talon. Mandibular ramus deeper than length of m/1. Lower p/4 bicuspid with the posterior cusplet inflated and shifted buccally”. It contains the genera *Enhyriodon* Falconer, 1868, *Sivaonyx* Pilgrim, 1931, *Vishnuonyx* Pilgrim, 1932, and *Paludolutra* Hürzeler and Engesser, 1976. *Paludolutra* is known by three European species. *P. lluecai* (Villalta and Crusafont, 1945) and *P. maremmana* Hürzeler, 1987 do not have a developed hypocone but only a more or less developed lingual shelf. *P. campanii* has a true hypocone that is less lingually situated than that of KB07-98-039; there is no incision between the paracone and metastyle, the parastyle is smaller, the paracone is closer to the protocone, the central valley is distally open and there is a large lingual cingulum [10,11].

*Vishnuonyx chinjiensis* Pilgrim, 1932 is smaller than the KB lutrine; there is a well marked buccal concavity and another one mesially situated, no notch between the paracone and metastyle, a relatively smaller parastyle, a large lingual cingulum, and less distally situ-

ated hypocone. *V. angolensis* Werdelin, 2003 is a little larger than the type species but differs from the KB lutrine by the same characters [36].

*Enhyriodon* seems to be an Asiatic form which is known from the Indian subcontinent and in China [20]. It is characterized by an “extremely bunodont dentition. Hypocone of P4/ larger than protocone and conical with low centrally directed ridge; postprotocone cusp conical and usually separated apically from the protocone; metastyle almost as voluminous as the paracone. Deeply concave outer wall to the buccal cusp pair” [20]. The P4 of *E. sivalensis* Falconer, 1868, type species of the genus, differs from that of KB07-98-039 by the concave buccal surface, the extreme bunodonty, the bulbous parastyle, the huge and inflated hypocone, the distally open central valley and the large cusplets between protocone and hypocone. The other species, *E. falconeri* Pilgrim, 1932 is a little smaller than the type species and the main characters of the genus are less marked. But nevertheless the main cusps are more bunodont than those of KB07-98-039. There is no incision between the paracone and metastyle, the parastyle is smaller, the cusplet between the protocone and hypocone is larger and bulges in the lingual face, and the hypocone is less lingually situated. Thus the KB lutrine cannot belong to the genus *Enhyriodon*.

The diagnosis of *Sivaonyx* has changed through the time. For Pilgrim [22] it is a “Lutrinae of large size; having a P4 of an approximately quadrate with a moderately trenchant paracone-metacone blade; paracone somewhat stoutly built; metacone very slightly elongate; parastyle well developed but low; with two internal cusps, protocone and hypocone, lower than the outer cusps, somewhat stoutened and expanded so that the basin-shaped area is contracted, with a strong internal cingulum”. Morales and Pickford ([16], fig. 6) include it in their tribe Enhyriodontini which is mostly defined by lower dentition characters and one feature on the upper P4: a “conical protocone”. *Sivaonyx* can be distinguished by other features: “P4 with protocone well separated from paracone and development of an anterior valley”. For Pickford [20], it is a “large lutrine with approximately quadrate P4/ having a trenchant outer blade (lacking the incision between the paracone and metacone). Lingual cusps of P4/ lower crowned than buccal cusps; strong to weak lingual cingulum”. The type species, *S. bathygnathus* (Lydekker, 1884) comes from the Hasnot upper limit (Dok Pathan stage) in the Siwalik hills. The P4 differs from that of KB 07-98-039 in the smaller size, the absence of notch between the paracone and metastyle, the less posteriorly situated hypocone and a large lingual cingulum. Several *Sivaonyx* species

have been named in Africa. *S. africana* (Stromer, 1931) has a smaller and less posteriorly situated hypocone. *S. senutae*, which could be a junior synonym of *S. soriae* [19], differs from the KB otter by a smaller parastyle and a distally tapering occlusal outline, but it has a notch between the paracone and metastyle as does KB 07-98-039. The type specimen of the species *S. ekecaman* (Werdelin, 2003) comes from Kanapoi, Kenya, a locality younger than KB, but the species has also been noted at Sagatia, Mabaget Formation, Kenya, which is dated to around 5 Ma like KB [16]. The P4 possesses similar proportions between length and width, a notch between paracone and metastyle, a very large parastyle and a vertical groove on the mesial surface just after the parastyle. All these characters fit the KB lutrine. But the distolingual corner is more rounded on the Kenyan species. Thus we identify this Lutrinae as *Sivaonyx* aff. *S. ekecaman*.

Other African species, like *S. soriae*, *S. kamuhangirei* or *S. beyi*, are not known from upper P4 and cannot be compared to the KB otter. In conclusion, KB 07-98-039 has some characters of *Sivaonyx* (quadrangular occlusal outline, paracone far from the protocone, well developed hypocone) but does not fit exactly the known species of this genus. Moreover, the presence of a notch between the paracone and metastyle does not fit the diagnosis of *Sivaonyx* in which the shearing blade of P4 is continuous [16,20]. The Chadian lutrine and the specimens allocated to the species *S. ekecaman* may belong to a different genus, probably a new one, but more material would be needed to christen a new taxon.

An edentulous robust mandible (KB4-97-183) belongs to a lutrine whose size would correspond to the P4 described above. This specimen includes the distal alveolus of p4, and the alveoli of m1 and m2. The estimated measurements of m1 are 20 mm × 10.4 mm. The height of the mandible below m1 is 25 mm, so larger than the estimated length of the carnassial. There is a large mental foramen at the first basal third of the mandible just below p4 but the ramus is broken ahead. There is also a deep masseteric fossa.

**Lutrinae indet.** (? *Sivaonyx kamuhangirei* Morales and Pickford, 2005)

A mandible (KB4-97-94) whose dentition is very worn probably corresponds to another species larger than the first one (Fig. 2). The alveolus of the canine is incomplete. It could have been oval-shaped, the transversal axis being the wider. The p1 and p2 are absent. The p3 is known by the alveolus of the anterior root and a part of the posterior crown. It is small and oblique relative to the dental row; p4 is larger, the anterior part is narrow but the posterior portion is widened. There are two roots present on the m1, the posterior being mesiodistally



Fig. 2. Lutrinae indet., (? *Sivaonyx kamuhangirei*) mandible (KB4-97-14) in lateral view (scale bar = 3 cm).

Fig. 2. Lutrinae indet., (? *Sivaonyx kamuhangirei*) mandibule (KB4-97-14) en vue latérale (échelle = 3 cm).

elongated. The measurements from the teeth or estimated from the alveoli are: p3: 10.4 × 7.4; p4: 11 × 8.5; m1: 25.1 × ?. We cannot take any measurements on the alveolus of m2. The m1 reaches a size close to that of *S. kamuhangirei* Morales and Pickford, 2005 from the slightly younger localities of Kazinga and Warwire from the Middle Pliocene of Uganda. This Ugandan species is the largest otter described in Africa until now and the KB lutrine could belong to the same species.

#### **Felidae** Fischer, 1813

##### ***Dinofelis* sp. 1**

A partially eroded distal humerus (KB3-96-22) belongs to a large felid (size of *Panthera leo*).

#### Description

This humerus (Fig. 3) is smaller than that of *Machairodus kabir* from the Chadian locality TM [18] and is the size of an average lion. The trochlea is relatively narrow mediolaterally compared to that of *Panthera* or *Machairodus*. There is a quite small epitrochlear (medial epicondylar) foramen that is distally prolonged by a wide groove. Thus there is a great distance between the foramen itself and the trochlea. The olecranon fossa is large with a very deep cavity in the mediolateral corner of the fossa. The morphology is similar to that of a distal humerus from Okote, Koobi Fora, Kenya attributed to *Dinofelis* sp. [37]. We reach the same conclusion for KB3-96-22. It is also close to the distal humerus of the Siwaliks attributed to *Dinofelis* probably *crinata*. KB3-96-22 is larger than all the humeri of African *Dinofelis* described by Werdelin and Lewis [37].

Thus KB3-96-22 is determined as *Dinofelis* sp. size of *D. cristata*.

##### ***Dinofelis* sp. 2**

This specimen is a front part of a right mandible (KB2-98-08) without any crown but with the roots of i3 and c and the alveoli of p3 (Fig. 4).

The mandibular corpus is relatively shallow, but the upper border angles upwards steeply toward the canine. The symphysis is very steeply inclined with a flat lower border. The angle between the front part and the lower border of the mandible is 111°. There are two mandibular



Fig. 3. *Dinofelis* sp. 1, distal humerus (KB3-96-22) in cranial view (scale bar = 3 cm).

Fig. 3. *Dinofelis* sp. 1, distal humerus (KB3-96-22) en vue crâniale (échelle = 3 cm).

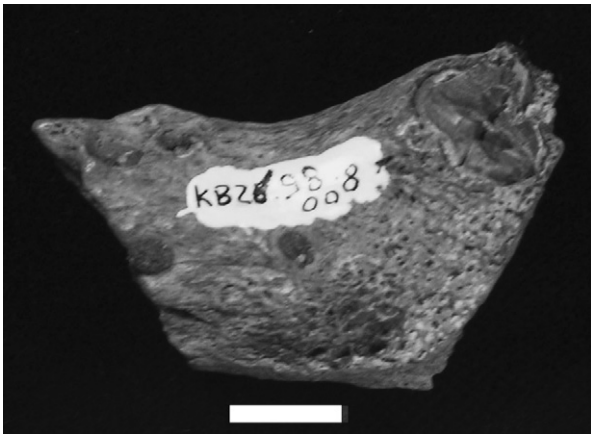


Fig. 4. *Dinofelis* sp. 2, anterior part of the mandible (KB2-98-08) in lateral view (scale bar = 1 cm).

Fig. 4. *Dinofelis* sp. 2, portion antérieure de mandibule (KB2-98-08) en vue latérale (échelle = 1 cm).

Table 1

Measurements of teeth in the genus *Metailurus*.

Tableau 1

Mensurations des dents dans le genre *Metailurus*.

<i>Metailurus parvulus</i>						
c		Dias.	p3		Dias./c	Dias./p3
L	W		L	W		
79.4	6.6	6.8	10.7	5.2	0.7	0.63
9.4	6.6	?11			1.17	
8.8	6.5	8.4	9.9	5.8	0.95	0.65
9.6	?7.4	?7.9			0.82	
9.1	6.3	7.4	10.2	5.1	0.81	0.61
"Metailurus pamiri"						
c		Dias.	p3		Dias./c	Dias./p3
L	W		L	W		
9.9	6.2	11.7	9.1	5.0	1.18	1.3

Dias.: diastema; L: length; w: width.

Dias. : diastème ; L : longueur ; w : largeur.

foramina at midheight: the anterior one in the middle of the diastema, the second one beneath the posterior root of p3. All these characters fit a small machairodont cat.

Length of the diastema c-p3: 29 mm

Height of the mandible beneath p3: 24.9

Length of the canine (from the root): 13.6

Length of p3 (alveolus): 13

Index diastema/canine: 2.13

Index diastema/p3: 2.23

The small machairodont cats comprise several genera: *Metailurus*, *Sivasmilus*, *Pontosmilus*, *Paramachairodus* and *Dinofelis*.

There are two species in the genus *Metailurus*. *M. major* Zdansky, 1924 differs from the KB small machairodont in having a slightly smaller canine (c = 12.7/9) and a smaller diastema (18.5) but its p3 is larger (15.5/8.4) and the indices are different (dias./c = 1.45; dias./p3 = 1.19) [38]. *M. parvulus* (Hensel, 1862) is smaller (Table 1) [9]. The indices relative to the relationships between canine, diastema and p3 are different (Table 1). The diastema is shorter, the dorsal face more upwardly directed in front of the p3 but the front face is less steeply inclined; the chin more rounded and the ventral surface less flat [12].

*Sivasmilus* Kretzoi, 1929 is based on a fragment of mandible with p3 and broken p4 described and figured by Pilgrim [21] as "*Sivaelurus chinjiensis*?". It comes from the lower Siwaliks of Chinji, Punjab (GSI D151), and thus is far older than KB. Kretzoi [14] remarked that the type of *Sivailurus* is feline while the mandible belongs to a small machairodont for which he created *S. copei*. This mandible differs from the KB carnivore

in its smaller size and the very small p3. The mental foramina are situated lower on the mandible corpus and they differ in size, the mesial one being bigger than the distal one. The angle between the lower border and the symphysis is more obtuse.

*Pontosmilus indicus* Kretzoi, 1929 was based on a fragmentary mandible from the Middle Siwaliks of Bahitta, Punjab, figured by Pilgrim ([21], pl. 5, fig. 2) as *Paramachairodus* cf. *schlosseri*. It is smaller than the KB mandible, with a smaller diastema between the canine and a relatively strong p3 (alveolus), and it has lower situated mental foramina. The angle between the lower border and the front surface of the symphysis is more open.

The type species of *Paramachairodus*, “*Machairodus*” *orientalis* Kittl, 1862, is based on a fragment of skull from the Late Miocene (Turolian) of Maraghe (Iran) [13]. Nevertheless, several remains from the Late Miocene (Turolian) locality Pikermi described as “*Machairodus*” *schlosseri* Weithofer, 1888 belong with a high probability to the same species and allow us to know the characters of the mandible [35]. Several species have been described in this genus but recent revisions reach the conclusion that probably two species are available [25–27].

*Pogygia* (Kaup, 1833) is the older one (Vallesian). It is smaller than the KB mandible with a shorter diastema between canine and p3; the angle between the front surface and the lower border of the symphysis is 105° on a figure ([12], pl. 2, fig. 3) and 110° on another figure ([35], pl. 11, fig. 9) of the same specimen from the Vallesian of Eppelsheim; there is no mental crest and the mental area is rounded. The indices are: diast./L canine = 1.4, diast./L p3 = 1.36. Thus the diastema is relatively shorter than in KB2-98-08.

The size of *P. orientalis* is similar to that of KB2-98-08 but the indices are different: diast./canine = 1.7; diast./p3 = 1.5. Thus the diastema is also relatively shorter in *P. orientalis*. The root of the canine is more vertical, the mental area is more rounded and the mental foramina are lower situated in the mandibular corpus. Thus the KB mandible does not correspond to any species of *Paramachairodus*.

There are several species of *Dinofelis* that are large in size [37]. The shape of the anterior part of the mandible from KB fits quite well those of some *Dinofelis* specimens as *D. diastemata* [1,23,24] or *D. aronoki* [37] with a similar angle between the anterior and the ventral faces. The mental foramina of *Dinofelis* are situated lower than those of the KB mandible like ER 30397 from Kanapoi ([37], fig. 6), or situated at the same level like ER 3880 from Koobi Fora or (BPI) M 607 from Makapansgat ([37], figs. 10 and 28). The dimensions of a

Table 2

Measurements of the teeth of ?*Lycyaena* sp.

Tableau 2

Mesures des dents de ?*Lycyaena* sp.

Canine		P3		P4		Lmet	Wpr	Wmet
Length	Width	Length	Width	Length	Width			
15.7	10.8	23	13.7	35		12.9	17.8	10.6
M1		Wm	Wd	P3				
Length	Width			Length	Width			
8.5	17.2	17.4	19.8	10.2				

L: length; Lme: length of the metastyle; W: width; Wd: width along the distal face; Wmet: width at the junction paracone–metastyle; Wpr: width at the level of the protocone.

L: longueur; Lme: longueur du métastyle; W: largeur; Wd: largeur le long de la face distale; Wm: largeur au niveau de la jonction paracone–métastyle; Wpr: largeur au niveau du protocone.

specimen from Kanapoi (Middle Pliocene, Kenya) identified as *D. petteri* are similar to those of the KB mandible (length of c = 13.9 mm; length of p3 = 13.1 mm); the length of the diastema and the shape of the anterior part of the mandible are also similar to those of the KB machairodont [24,37]. Thus, the Chadian carnivore is called *Dinofelis* sp. and is a rather small species.

### Hyaenidae Gray, 1821

#### ? *Lycyaena* sp.

The specimens KB3-96-72, a mandible with p3, KB3-97-279, a maxilla with P3-M1, and KB3-98-2, an upper canine, have been found during three different field campaigns. Nevertheless, because of their morphology, their state of wear, and the localisations in which they were found, we think that they belong to the same individual (Table 2). They represent a hyaenid with a quite trenchant dentition (Figs. 5–7).

During the Miocene, some hyaenids adopted a way of life different from that of the bulk of this family with a more cutting dentition reflecting a diet that included less carrions and more living preys. These “hunting hyaenas” include three genera: *Chasmaporthetes*, *Hyaenictis* and *Lycyaena*. The KB hyaenid certainly belongs to the same group.

#### Description

The lower third of the upper canine is broken, as is the tip of the root. The root is channelled and the crown is smooth except for a faint crest running from the base up the mesial quarter of the crown.

On the maxilla, the infraorbital foramen opens in intermediate position above the tip of the posterior root of P3 and that of the anterior root of P4. P3 is large and tall despite the tip of the crown being missing. There is no anterior accessory cusp (AAC) even though a small



Fig. 5. ? *Lycyaena* sp., upper canine (KB3-98-2) from a cast. A. Buccal face. B. Lingual face (scale bar = 1 cm).

Fig. 5. ? *Lycyaena* sp., canine supérieure (KB3-98-2) d'après un moulage. A. Face buccale. B. Face linguale (échelle = 1 cm).

piece of enamel is missing but there is a moderate posterior accessory cusp that is laterally, distally and lingually surrounded by a moderate bulge. Lingually, there is also a small bump at the base of the crown. P4 is large and cutting. The parastyle is well developed as is the shearing blade. The paracone is tall and the lingual face is flattened. The protocone is large, subconical and not forwardly projected beyond the parastyle, thus it is not visible in buccal view. Two very small ridges run from the tip to the base of the parastyle and the base of the



Fig. 6. ? *Lycyaena* sp., mandible (KB3=96-72) from a cast, lateral face (scale bar = 3 cm).

Fig. 6. ? *Lycyaena* sp., mandibule (KB3 = 96-72) d'après un moulage, face latérale (échelle = 3 cm).

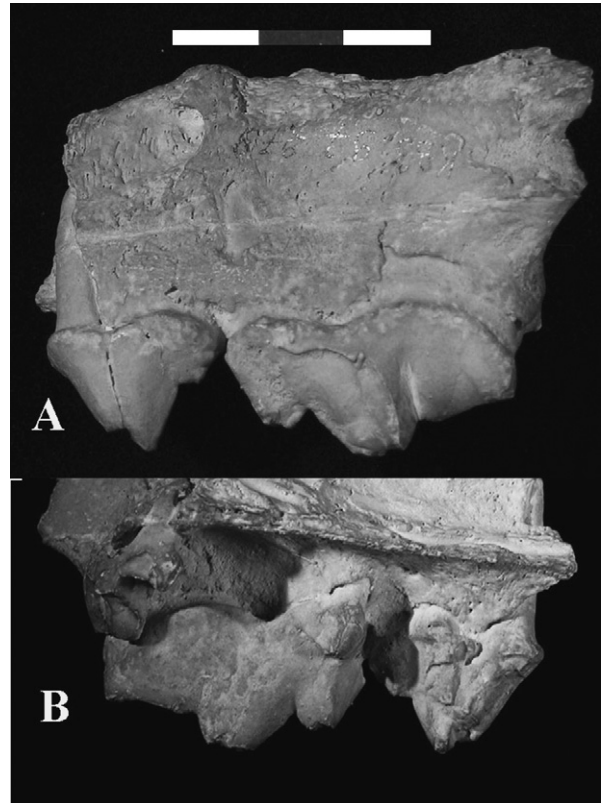


Fig. 7. ? *Lycyaena* sp., P3-M1 (KB3-97-279) from a cast. A. Buccal face. B. Lingual face (scale bar = 3 cm).

Fig. 7. ? *Lycyaena* sp., P3-M1 (KB3-97-279) d'après un moulage. A. Face buccale. B. Face linguale (échelle = 3 cm).

paracone respectively; the latter is prolonged by a cingulum along the base of the paracone and metastyle. There is a faint cingulum along the buccal surface of the crown. M1 has a triangular occlusal outline. The paracone and metacone are two tiny but distinct cusps on a small crest; the former extends to the moderately developed parastyle. The buccal surface tapers distally. Two small crests, mesial and distal, run from the crescent-shaped protocone to the parastyle and distal metacone, respectively. There is a small cingulum on the base of the lingual part of the distal surface of the crown.

The mandible is shallow, slender and bears only one tooth. The p3 is tall without an AACd. There is a medium-sized PACd and a weak buccal cingulum.

#### Comparisons

The comparisons will include only the hunting hyaenids, *Chasmaporthetes*, *Hyaenictis* and *Lycyaena*.

Compared to the KB specimen, all of the species of *Chasmaporthetes* have a deeper mandibular ramus; the p3 s have an AACd or a well indicated bulge and the PACd s are more developed. The P3 s have a larger PAC

and the lingual bulging is more developed. The comparison is more difficult with P4 insofar as there is a great variation in the P4 material referred to *Chasmaporthetes*. Thus the P4 of *Chasmaporthetes* “kani” is relatively shorter and more robust [5] while the P4 of *C. cf. australis* from Toros Menala is larger but morphologically quite similar [3]. The M1 of *Chasmaporthetes* is different with a more developed parastyle.

The type of *Hyaenictis graeca* Gaudry, 1861, type species of the genus, is a mandible of a young individual from Pikermi, Greece ([6,7], pl. 15, figs. 7 and 8). The milk molars are worn but present, the m1 is erupting and p3 and p4 have not erupted but are visible into the ramus. The p3 has a larger talonid and a well developed AACd and thus is more symmetrical than the p3 from KB. A maxilla from the same locality was referred to the same species and, on the basis of the individual age of the specimen with P4 visible below a worn D4, it belongs to the same individual with a very high probability ([7], pl. 15, fig. 6). The carnassial differs from that of KB by its large metastyle bent toward the buccal side. The same character does exist in the P4 of a maxilla from Pikermi housed in the Museum of Vienna (Austria) which could also belong to the same individual (personal observation). The M1 of *Hyaenictis* has a relatively more developed parastyle.

The type specimen of *Lycyaena chaereticis* (Gaudry, 1861) also comes from the Greek locality Pikermi and is a mandible with p2-p4 and the anterior part of the m1 ([7], pl. 15, figs. 1 and 2). The p3 looks fairly well similar to the KB p3 as it lacks an AACd and has a low PACd. An upper carnassial ([7], pl. 15, fig. 5) from Pikermi and attributed to the same species does not significantly differ from the P4 of KB. Another mandible of a younger individual from Pikermi ([7], pl. 15, figs. 3 and 4) bears the same p3 and p4 as the type but also has an m1. The lower carnassial has a small but well defined metaconid. We cannot see this character on the KB material. Another significant character, the absence of m2, is present in a mandible from Samos that is definitely *Lycyaena chaereticis* ([28], fig. 19). Unfortunately, this character cannot be observed in the KB material insofar as the posterior portion of the mandible is lacking. On the basis of our material, the KB hunting hyaena will be identified as ? *Lycyaena* species.

#### Canidae Fischer, 1817

#### Canidae indet.

KB24-97-16 is an edentulous mandible with the posterior part of the alveolus of p1, alveoli of p2, roots of p3 and p4, anterior root of m1 and alveolus of the posterior one, alveolus of m2 and part of that of m3 (Fig. 8). The corpus is slender and there are two mental



Fig. 8. Canidae indet., mandible (KB24-97-16). A. Medial face. B. Occlusal face (scale bar = 1 cm).

Fig. 8. Canidae indet., mandibule (KB24-97-16). A. Face médiale. B. Face occlusale (échelle = 1 cm).

Table 3

Measurements of the calcaneum (KB3-00-02).

Tableau 3

Mensurations du calcanéum (KB3-00-02).

TL	W	LPAS	ST	D-VH	LWB
34.8	16.3	11.7	4	15	6.9
W/TL	D-VH/TL	LWB/D-VH			
47	43	46			

TL: total length; W: width; LPAS: length of the posterior articular surface; ST: sustentacular thickness; D-VH: dorsoventral height; LWB: least width of the body (see [29], fig. 1).

TL: longueur totale; W: largeur; LPAS: longueur de la surface articulaire postérieure; ST: épaisseur du sustentaculum; D-VH: hauteur dorsoventrale; LWB: moindre largeur du manubrium (voir [29], fig. 1).

foramina, one beneath the anterior root of p2 and another one beneath the anterior root of p3. The size of the teeth in millimeters from the alveolus are approximately: p2: 10 × 6; p3: 12.2 × 5.6; p4: 13.4 × 6.5; m1: 18 × 9.9; m2: 10 × 8. The dental formula, the morphology of the ramus and the size of the dentition fit fairly well with a midsized canid such as the jackal *Canis aureus*. Canids occur in Africa during the Late Miocene with *Eucyon* [17] and *Vulpes* [2], while the genus *Canis* appears later in the Pliocene. If *Canis* could be a little older than previously thought, then this specimen may belong to this genus. However, it is very difficult to choose between *Canis* and *Eucyon* on the basis of some isolated teeth and, of course, an edentulous mandible.

#### Viverridae Gray, 1821

#### Viverridae indet. (large size)

The calcaneum (KB3-00-02) is the size of a midsized carnivore (Table 3) and could be referred to a canid or a viverrid. It is complete, except for the medial part of the distal articular surface which is a little eroded. The proportions between the anterior part and the manubrium are close to those of the canids [30] or the viverrids [33] and far from the felids or hyaenids whose manubrium



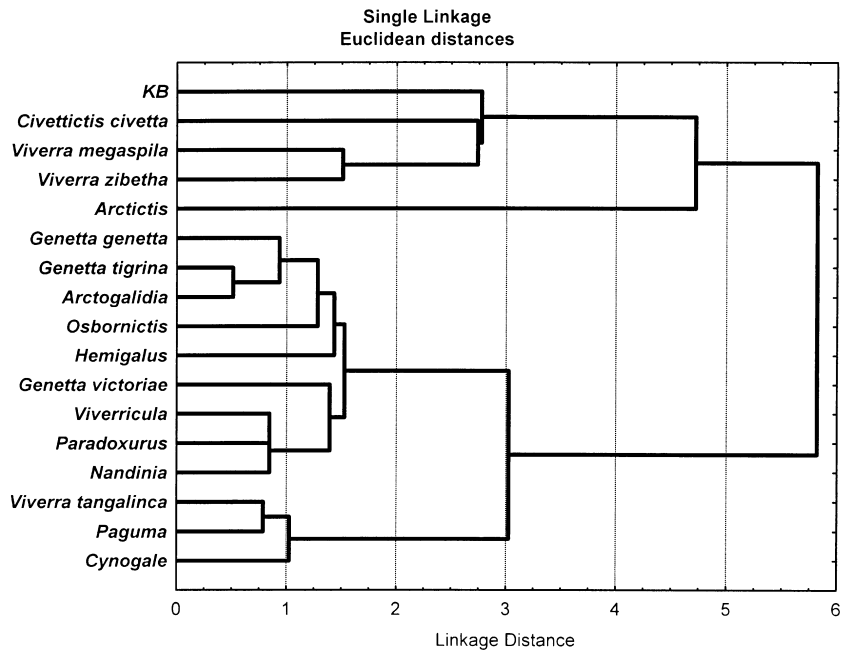


Fig. 9. Place of the calcaneum (KB3-00-02) within a cluster analysis of extant viverrid calcanea (data from Stains [33]).

Fig. 9. Place du calcanéum (KB3-00-02) dans une analyse de *cluster* du calcanéum de viverridés actuels (données de Stains [33]).

is longer. The size fits the range of *Canis aureus* (total length = 30.2 to 34.5 mm), *C. adustus* (total length = 30.1 to 36.2 mm) or *C. mesomelas* (total length = 31.2 to 35.5 mm) or *Viverra* and *Civettictis* (total length = 27.7 to 37.7 mm). There is no well defined trochlear process as in canids like in *C. aureus* or in viverrids like *Genetta genetta*. There are pits anterior and posterior to the posterior articular surface, a pit in front the sustentacular surface, and a ridge across the dorsal table between the inner distal corner of the posterior articular surface and the cuboid articular surface. The latter is a little eroded and a little oblique relative to the long axis of the bone, but less than in herpestids. There is no groove between the posterior articular surface and sustentaculum. The sustentacular surface is flat and not S-shaped like in *Canis*. A metric comparison with other families based on data taken from the literature [29–33] shows that the KB specimen does not fit any of the extant Carnivora families except the Viverridae (Fig. 9). It is close to the large viverrid of the genus *Viverra*, *Civettictis* and *Arctictis*. However, it differs from all the species by a larger least width of the body and a little higher dorsoventral height. Nevertheless, in these dimensions, it is not very far from *Civettictis civetta*. Thus, its identification will be Viverridae indet. (large size).

#### Carnivora indet.

Some remains certainly belong to the order Carnivora but are too fragmentary to be assigned to a family. A

fragment of a mandible with roots of two teeth (KB15-97-20) reaches the size of a midsized hyaenid. An incisor and a canine (KB3-99-14) correspond to a very small species of Carnivora. Another piece of mandible with the roots of p3 and p4, the crown of m1 completely eroded by the wind and the sand, and an eroded fragment of m2 (KB4-97-105) is clearly a small carnivoran. While it may belong to the Viverridae or Mustelidae, the only definite statement that can be made is that there is a small carnivoran in the locality (length of m1 = 12 mm).

#### 4. Conclusion

Despite the small number of specimens referred to the order Carnivora, several taxa (two species of Lutrinae, two species of Felidae, one species of Hyaenidae, one species of Canidae and, one species of Viverridae, are present in the KB site. These deposits, therefore, constitute a significant locality in the history of that order of mammals in Africa and allow us reach some conclusions.

While carnivorans are less useful than some other orders of mammals for indicating paleoenvironmental conditions, we show that three specimens are referred to the Lutrinae. The (relative) abundance of this subfamily probably indicates the omnipresence of water as is the case in other Chadian localities (for instance four species are referred to the Lutrinae in the Late Miocene locality TM) and, generally, in Late Miocene or Pliocene African

localities. Many fish remains, crocodiles with some fish-eating forms, other water-linked reptiles, aquatic birds, Anthracotheriidae, and Hippopotamidae confirm the presence of aquatic conditions. Many of these lutrines have crushing dentition and seem to have been adapted to a diet dealing with shellfish and/or crustaceans. Today, there are two genera and three lutrines species in Africa but during the Late Miocene and Pliocene periods there were four genera or more and a dozen of species, most of them being bunodont lutrines. The paleoenvironmental conditions of Africa probably were more favourable to these aquatic carnivorans than they are today.

As far as it is possible to conclude anything with this quite poor fauna, the presence of two species of *Dinofelis* is not surprising in the way the Earliest Pliocene is the time of the beginning of the split of this genus in Africa [37]. We must also note that, until now, this is one of the most northern African occurrences of the genus. *Dinofelis* is quite common in eastern and southern Africa. But this genus has only been documented in Pliocene or Early Pleistocene of northern Africa in Ahl al Oughlam (Morocco) [8] but not in quite species-rich localities such as Ain Brimba, Hamada Damous, Wadi Natrun, Ain Hanech, Ain Marouf, and Tighenif. We do not know the reason for the scarcity of *Dinofelis* in northern Africa.

The taxa documented in KB did not originate from the Middle Miocene of Africa with the probable exception of the viverrid. Most of them are unknown before the Late Miocene in Africa and they probably came from Eurasia and America just before the time when the guild of terrestrial carnivorans reached the “numerical peak of abundance” [34] of the Lower Pliocene.

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