



Systematic palaeontology (Vertebrate palaeontology)

New sabre-toothed cats in the Late Miocene of Toros Menalla (Chad)

Nouveaux félins à canines en lame de sabre dans le Miocène supérieur de Toros Menalla (Tchad)

Louis de Bonis^{a,*}, Stéphane Peigné^b, Hassane Taisso Mackaye^c,
Andossa Likius^c, Patrick Vignaud^a, Michel Brunet^{a,d}

^a Université de Poitiers, UFR SFA, UMR 6046 du CNRS, IPHEP, 40, avenue du Recteur-Pineau, 86022 Poitiers cedex, France

^b Muséum national d'histoire naturelle, UMR 7207 du CNRS, CR2P, 8, rue Buffon, CP 38, 75231 Paris cedex 05, France

^c Département de paléontologie, Université de N'Djamena, Tchad

^d Collège de France, chaire de paléontologie humaine, 3, rue d'Ulm 75231 Paris cedex 05, France

ARTICLE INFO

Article history:

Received 25 March 2010

Accepted after revision 22 July 2010

Presented by Philippe Taquet

Keywords:

Africa
Chad
Late Miocene
Mammalia
Carnivora
Felidae
Machairodontinae

Mots clés :

Afrique
Tchad
Miocène supérieur
Mammalia
Carnivora
Felidae
Machairodontinae

ABSTRACT

The Toros Menalla Late Miocene Formation (7 Ma), Djurab desert, Chad, has yielded a large number of vertebrate remains, and among them around twenty taxa of carnivores. Recent collections allow us to describe two sabre-toothed felids assigned to the genera *Lokotunjailurus* and cf. *Megantereon*. The former does exist in the Nawata Formation, Lothagam, northern Kenya with a slightly derived species and the TM specimens are considered as belonging to a new species. The latter cannot be identified to the species level, but it could be one of the earliest specimens of *Megantereon* known in the world and it would reinforce the hypothesis of an Old World origin for this taxon. Both allow us to put forward some biogeographical conclusions.

© 2010 Published by Elsevier Masson SAS on behalf of l'Académie des sciences.

RÉSUMÉ

Le Miocène supérieur de Toros Menalla (7 Ma), désert du Djurab, Chad, a livré un grand nombre de restes de vertébrés, parmi lesquels une vingtaine de taxons de carnivores. Des découvertes récentes permettent de décrire deux félins à canines en lames de sabre, attribués aux genres *Lokotunjailurus* et cf. *Megantereon*. Le premier a été décrit pour la première fois sur des éléments provenant de la Formation à Nawata à Lothagam dans le Nord du Kenya. L'espèce type est un peu plus dérivée que la forme de Toros Menalla, ce qui nous conduit à considérer cette dernière comme une espèce nouvelle un peu plus primitive. Le second montre que le genre *Megantereon*, connu jusqu'ici dans des niveaux pliocènes ou pléistocènes, pourrait être beaucoup plus ancien et que son origine devrait être recherchée dans l'Ancien Monde et non en Amérique du Nord, comme certains auteurs l'avaient pensé.

© 2010 Publié par Elsevier Masson SAS pour l'Académie des sciences.

* Corresponding author.

E-mail address: louis.debonis@univ-poitiers.fr (L. de Bonis).

1. Introduction

The fossiliferous localities of Toros Menalla (hereafter TM) are situated 800 km north of N'Djamena (Chad). They are well known from the discovery of *Sahelanthropus tchadensis* (Brunet et al., 2002, 2005). A very rich vertebrate fauna has been recorded in which there are more than 50 taxa of mammals (Le Fur et al., 2009; Vignaud et al., 2002) and unpublished data. Among these mammals several carnivores have been described until now belonging to different families as Felidae, Hyaenidae, Viverridae, Herpestidae, Canidae and Mustelidae (de Bonis et al., 2005, 2007a, 2007b; Peigné et al., 2005a, 2005b, 2008a, 2008b). Until now the sabre-toothed felids were represented by a very large form, *Machairodus kabir* Peigné et al., 2005a. New specimens recorded during the last field campaigns allow us to add two different machairodont felids to the list of the TM carnivores.

The fossils from Toros Menalla (Anthracotheriid Unit) are found in layers which are dated to the Late Miocene (ca 7 Ma) by a biochronological approach (Vignaud et al., 2002) and radiometrical data as well (Lebatard et al., 2008). The first new machairodont taxon, represented by a maxilla and two mandibles, has been referred to the genus *Lokotunjailurus* Werdelin (2003) from the Lothagam Nawata Formation (Kenya). The second one is represented by an edentulous mandible which shows characters of the genus *Megantereon* Croizet & Jobert, 1828 (Croizet and Jobert, 1828) and which would be one of the earliest occurrence of this taxon.

2. *Lokotunjailurus* Werdelin, 2003

Emended diagnosis: Machairodontinae of large size. Very large infra-orbital foramen. Robust upper incisors situated on a semi-circular line on the procumbent premaxilla. Mandibular horizontal ramus slender, ascending ramus relatively tall for a machairodont cat. Upper canine strongly laterally compressed, but not extremely tall. Serrations present on both anterior and posterior edges. The P2 present but small and peg-like. Upper carnassial long and slender with completely reduced protocone. The P3 small and single-rooted, though not peglike in appearance. Lower carnassial long, slender, and low. Metaconid-talonid complex absent.

Appendicular skeleton relatively slender, lacking extreme machairodont features. First digit of manus very robust, with extremely large claw, more than twice the size of the claws on the other digits.

Type species; *L. emageritus* Werdelin, 2003.

Emended diagnosis: *Lokotunjailurus* with reduced anterior premolars P2 and p3.

3. *Lokotunjailurus fanonei* n.sp.

Holotype: TM 265-09-01, left premaxilla and maxilla with alveoli of I1 and I2, I3, canine, alveolus of P2 and P3, P4 and alveolus of M1 (Fig. 1).



Fig. 1. *Lokotunjailurus fanonei* n.sp. Skull TM 265-09-01, a: in lateral view; b: in medial view. Scale bar = 1 cm.

Fig. 1. *Lokotunjailurus fanonei* n.sp. Crâne TM 265-09-01, a: en vue latérale; b: en vue médiale. Barre d'échelle = 1 cm.

Referred material: right mandible TM 269-08-39 with broken canine, alveolus of p2 and p3, p4-m1 (Fig. 2); left mandible TM 04-97-09 with m1 and the back part of the jaw (Fig. 3).

Localities: Toros Menalla, Chad (TM 265, 04 and 266).
Age: Late Miocene.

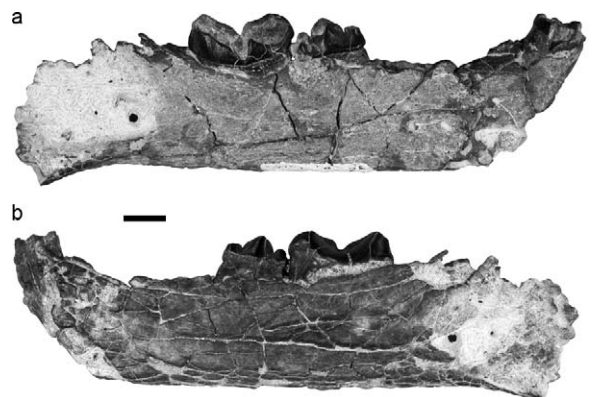


Fig. 2. *Lokotunjailurus fanonei* n.sp. Mandible TM 266-08-39, a: in lateral view; b: in medial view. Scale bar = 1 cm.

Fig. 2. *Lokotunjailurus fanonei* n.sp. Mandibule TM 266-08-39, a: en vue latérale; b: en vue médiale. Barre d'échelle = 1 cm.

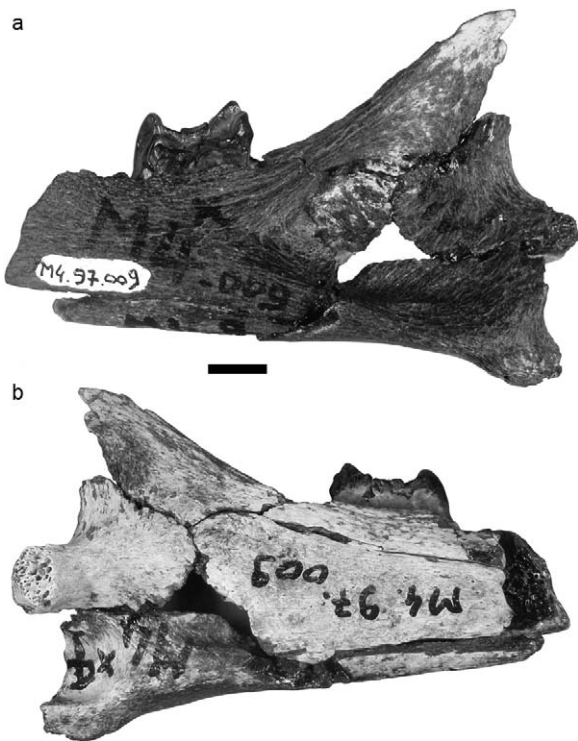


Fig. 3. *Lokotunjailurus fanonei* n.sp. Mandible TM 04-97-39, **a**: in lateral view; **b**: in medial view. Scale bar = 1 cm.

Fig. 3. *Lokotunjailurus fanonei* n.sp. Mandibule TM 04-97-39, **a**: en vue latérale; **b**: en vue médiale. Barre d'échelle = 1 cm.

Etymology: the species is dedicated to the late Gongdibe Fanone who worked several years with our team on the Chadian fossils.

Diagnosis: *Lokotunjailurus* more primitive than the type species of the genus by less reduced anterior premolars P2 and p3.

3.1. Description

3.1.1. Skull and upper dentition, Fig. 1

The premaxilla is clearly procumbent, a derived machairodont feature, and bears the I1 and I2 alveoli and I3; rather large in front with a long diastema till the canine, it begins to taper backward and then expands a little before to end. The maxilla is wedge-shaped with a long swelling which corresponds to the root of the canine; the huge infra-orbital foramen, another derived machairodont feature, is prolonged forward and downward by a shallow depression. The lachrymal foramen is quite large. The skull is broken at the level of the mid-orbit and only the anterior part of a quite robust zygomatic arch is preserved. A part of the left lateral side of the palate is preserved; there are three-rounded depression on a line along the fourth premolar, the anterior one shallow, the posterior one deeper and the central one in between.

The alveoli of I1 and I2 are large, the latter more than the former, and antero-posteriorly elongated. I3 is robust and canine-shaped, the lateral face is convex and smooth, there are vertically elongated wear facets in the mesial and

distal edges, the buccal face is gently convex with a bulge at the base of the mesial corner; there no any evidence of crenulations or serrations; it is separated from the canine by a large diastema. The canine is moderately high but elongated and transversally compressed; both mesial and distal edges are clearly serrated. P2 was smaller than P3 but each of them has two alveoli. P4 is long and bucco-lingually compressed; there is a small but clear preparastyle and a long metastyle shearing blade; a small bulge at the lingual base of the anterior part of the paracone indicates the proto-cone; a wear facet runs lingually along the distal portion of the paracone from the tip to midheight and on the lower part of the metastyle. M1 is represented by a small rounded alveolus.

3.1.2. Mandible and lower dentition, Figs. 2 and 3

The two mandibles TM 266-08-39 and TM 04-97-09 correspond to a machairodont cat whose size fits that of the fragment of skull TM 265-09-01 and they belong to the same species with a very high degree of plausibility. The mental angle is missing; two small mental foramina are situated below p2, the horizontal ramus is shallow, its ventral border is straight till the level of the ascending ramus and it turns down to the angular process which is oriented backward, downward and medially; the masseteric fossa is rather deep but relatively smaller when compared to an extant large felid; the coronoid process, partially broken, is less developed than that of a panther and is proportionally close to that of *Machairodus*.

The lower canine, whose crown is broken at midheight, is reduced. It is separated from p3 by a long diastema. The anterior premolars, p1 and p2 are absent; p3 was two-rooted and quite long; p4 is bucco-lingually compressed, lily-flower shaped with well developed anterior and posterior accessory cuspids (respectively aacd and pacd hereafter) and a distal very small trenchant talonid; there is a very small horizontal wear facet in the tip of the aacd, a larger oblique one in the main cuspid and a very small horizontal one in the pacd. There is no complex metaconid talonid in m1 but only large paraconid and protoconid, both with large sub-vertical wear facets from the tip to midheight. There is no m2.

3.2. Comparisons

The TM specimens differ from other Late Miocene machairodonts. *Metailurus* Zdansky, 1924 (Zdansky, 1924) is more primitive concerning the sabre tooth characters as is *Paramachairodus* Pilgrim, 1913 although in a lesser extent. *Stenailurus* Crusafont & Aguirre, 1972 is smaller with a less bucco-lingually compressed upper canine without any crenulations, a single-rooted P2 and a larger P3 relative to the canine. *Adelphailurus* Hibbard, 1934 was recorded in Late Miocene-Early Pliocene layers of North America; it is smaller with a less procumbent premaxilla, relatively smaller incisors, a single-rooted P2, a relatively larger P3 and a less elongated P4 with a shorter metastyle shearing blade. A morphological closer Late Miocene genus is *Machairodus* Kaup, 1933; but all the species of *Machairodus* are larger, the upper canines are more compressed, the index (Width/Length) × 100 of the canine varies from 35.5

Table 1

Measurements on TM 265 09 01.

Tableau 1

Mesures sur TM 265 09 01.

Upper teeth											
TM 265 09 01	C-P4	P2-P4	I1-I3	I3L	I3b	dias	CL	Cb	Ch	d CP2	d CP3
	103.9	65.7	23.1	10	10.1	9	26.9	12	61	10.6	18.8
	P2L	P2b	P3L	P3b	P4L	P4ab	P4paL	P4mtL	P4mtb	M1L	M1b
	8.4		16.7		37.3	12.8	9.6	16.3	10.5		

L=length; b=breadth; d=diastema or distance; h=height; a=anterior; pa=parastyle+preparastyle; mt=metastyle blade. Bold italics correspond to measurement on alveoli.

Table 2

Measurements on TM 266-08-39, TM 04-97-09, TM 160-06-02.

Tableau 2

Mesures sur TM 266-08-39, TM 04-97-09, TM 160-06-02.

Lower teeth										
	cl	cb	c-p3	p3L	p3b	p4L	p4b	m1L	m1b	
TM 266-08-39	14.5	10.5		15		19	8.5	28.7	10.1	
TM 04-97-09								26.6		
TM 160-06-02				5.3		16.8		22.6		

L=length; b=breadth; d=diastema or distance; h=height; a=anterior; pa=parastyle+preparastyle; mt=metastyle blade. Bold italics correspond to measurement on alveoli.

to 42.8 (Crusafont Pairó and Aguirre, 1972) in *Machairodus* while it is 44.6 for the TM machairodont described here. But the latter is more similar to *Lokotunjailurus* from the Late Miocene of the Nawata Formation in Lothagam, Kenya (Werdelin, 2003) and recovered in the Uppermost Miocene of Lemudong'o, Kenya (Howell and Garcia, 2007). Both samples have about the same size (Tables 1 and 2), the procumbent premaxilla, large I3, elongated and buccolingually compressed P4 with a very long metastyle blade and same m1 without metaconid-talonid complex. Thus we assign the TM felid to *Lokotunjailurus*. However, there are some minor differences concerning the premolars, which are more reduced in the Kenyan species. P2 is one rooted in *L. emageritus* but it has two clearly separated roots in the TM maxilla; in the mandible p3 is also small and one rooted in *L. emageritus* and larger and two rooted in Toros Menalla. These differences may be considered as the result of an intraspecific variation. Nonetheless, the reducing of the anterior premolars is a classical evolutionary trend into the machairodont lineages and we think that they may justify a specific distinction between the two samples. Thus we consider the Chadian carnivore as *Lokotunjailurus fanonei* n.sp. The differences may be due to the geographical separation, Toros Menalla being separated from Lothagam by 2500 km, or to difference in the geological time, Toros Menalla (Anthracotheriid Unit) being perhaps a little older than the Nawata Formation in Lothagam.

4. cf. *Megantereon* sp.

4.1. Material: TM 160-05-02. right edentulous mandible

The anterior part of the mandible is broken off and thus we cannot know exactly the shape of the mental area but there was not a large downwards directed mandibular flange. The horizontal ramus is shallow. There are two mental foramina; one is large and situated in the anterior



Fig. 4. cf. *Megantereon* sp. Mandible TM 160-05-02, **a**: in lateral view; **b**: in medial view. Scale bar = 1 cm.

Fig. 4. cf. *Megantereon* sp. Mandibule TM 160-05-02, **a**: en vue latérale; **b**: en vue médiale. Barre d'échelle = 1 cm.

part of the mandible, another one is smaller and situated 5.4 mm behind the former and 9 mm in front of p3. The ventral border is straight till p4 and then slightly convex till the angular process which is moderately developed, quite thin and slightly downwards oriented. The masseteric fossa is moderately deep and not very extended toward the coronoid process; it anteriorly stops a little behind the posterior end of m1. The coronoid process, whose tip is just a little eroded, is very low like those of much derived machairodont (*Homotherium* or *Megantereon*) but it is apparently not hook-shaped like in *Megantereon ekidoit* Werdelin and Lewis (2000, 2002). The condyle is partially broken and clearly situated below the level of the cheek teeth cervix. In the medial face, there is a large foramen mandibulare (Fig. 4).

The first premolar p3 was reduced and is represented by a unique oval shaped alveolus. The crown of p4 is broken off, only the two roots are apparent. Both premolars are small relative to m1. There is only the anterior root of the latter and the base of the posterior part of the crown but we can see that there is not any talonid.

4.2. Comparisons

The mandible TM 160-05-02 is clearly separated from the Miocene African representatives of the machairodont felid-like Barbourfelidae (Morales et al., 2001) by the larger size, the absence of p2 and the relatively smaller p3. It differs from that of *Lokotunjailurus* from TM by the smaller size, the more reduced premolars particularly p3, and the weak coronoid process. The two latter are derived characters for a sabre toothed cat. Other late Miocene machairodonts are very large (*Machairodus*, *Lokotunjailurus*) and less derived for the shape and size of the coronoid process and the position of the mandibular condyle. Other ones are far more primitive than *Metailurus*, which sometimes is classified into the Felinae, *Paramachairodus*, *Promegantereon*, *Adelphailurus* and *Dinofelis*, which have larger p3 and bigger mandibular coronoid process [see: Salesa et al., 2003, 2005a, 2005b, 2010; Werdelin and Lewis, 2001]. The mandible TM 160-05-02 belongs to a genus, which is unknown until now into the Late Miocene of Chad.

Two Plio-Pleistocene genera may be compared to TM 160-05-02. All the species of *Homotherium* Fabrini (1890) have reduced anterior premolars and reduced mandibular coronoid process but they are larger with a relatively deeper mandible (Ballésio, 1963; de Bonis, 1976). The genus *Megantereon* Croizet & Jobert, 1828 is more conve-

nient for the size, the shallow mandible, the reduction of p3, even absent in *M. ekidoit*, and of the reduced mandibular coronoid process. Most of the *Megantereon* species have a quite large mandibular flange which is clearly absent in TM 160-05-02, but in some species this large flange may be weak or even may be lacking (see specimen from Perrier in [Palmqvist et al., 2007, Fig. 1B]). Until recently, the oldest occurrence of *Megantereon* would be the Latest Hemphillian (4.5 Ma) in Florida (Berta and Galiano, 1983) although this occurrence is discussed. In Asia, some Late Miocene occurrences having been reported to *Paramachairodus* or *Promegantereon*, the genus *Megantereon* is recorded from a locality dated to 2.4–2 Ma (Qiu, 2003). It was considered as present in Europe in the Middle Pliocene (3.5 Ma) of Les Etouaires, France but the locality is certainly not older than 2.5 (Thouveny and Bonifay, 1984) and in Africa from the Lukeino Fm (5.7 Ma) with a question mark (Morales et al., 2005) and from younger levels (3.58–3.2 Ma) in South Turkwel, Kenya (Werdelin and Lewis, 2000). Thus the mandible of Toros Menalla, dated to about 7 Ma, would be the earliest occurrence of *Megantereon* in the world.

Some species have been allocated to *Megantereon*. Some researchers distinguish only one valid species (Turner, 1987) or two, *M. cultridens* and *M. whitei* (Palmqvist, 2002; Palmqvist et al., 2007), others add other ones, especially *M. ekidoit* (Werdelin and Lewis, 2000, 2002). It is difficult to compare carefully the TM specimen insofar it lacks the dentition. Nevertheless we may compare the dimensions taken from the alveoli of the mandible TM 160-05-02 with the measurements given in the literature (Martínez-Navarro and Palmqvist, 1995; Palmqvist et al., 2007; Turner, 1987; Werdelin and Lewis, 2000, 2002). We used the specific

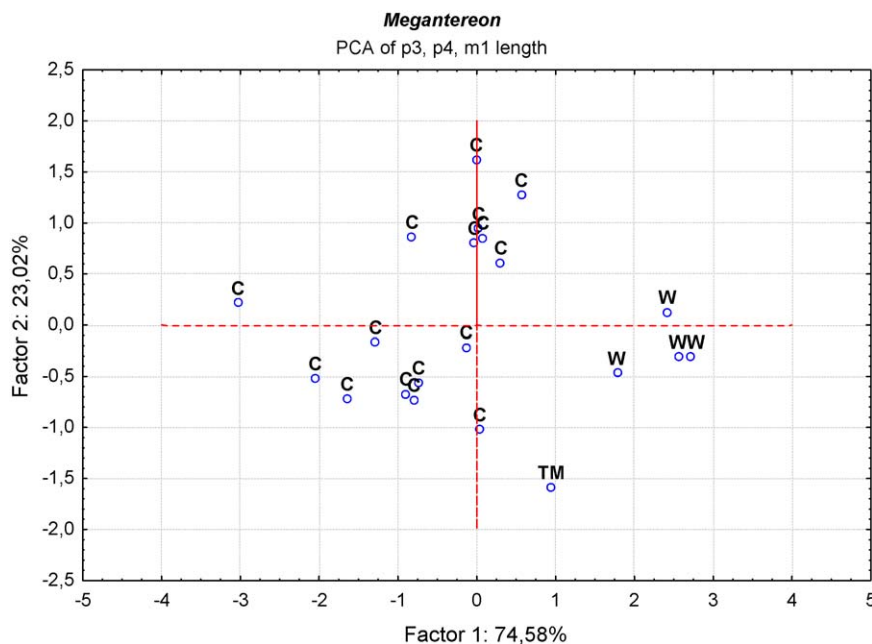


Fig. 5. Principal component analysis (PCA) on 3 dimensions (Length of p3, p4 and m1) of different *Megantereon* species. (data from (Palmqvist et al., 2007) and personal). C = *M. cultridens*; W = *M. whitei*; TM = Toros Menalla.

Fig. 5. Analyse en composantes principales (ACP) sur 3 dimensions (Longueur de p3, p4 et m1) de différentes espèces de *Megantereon*. (Données de (Palmqvist et al., 2007) et personnelles). C = *M. cultridens*; W = *M. whitei*; TM = Toros Menalla.

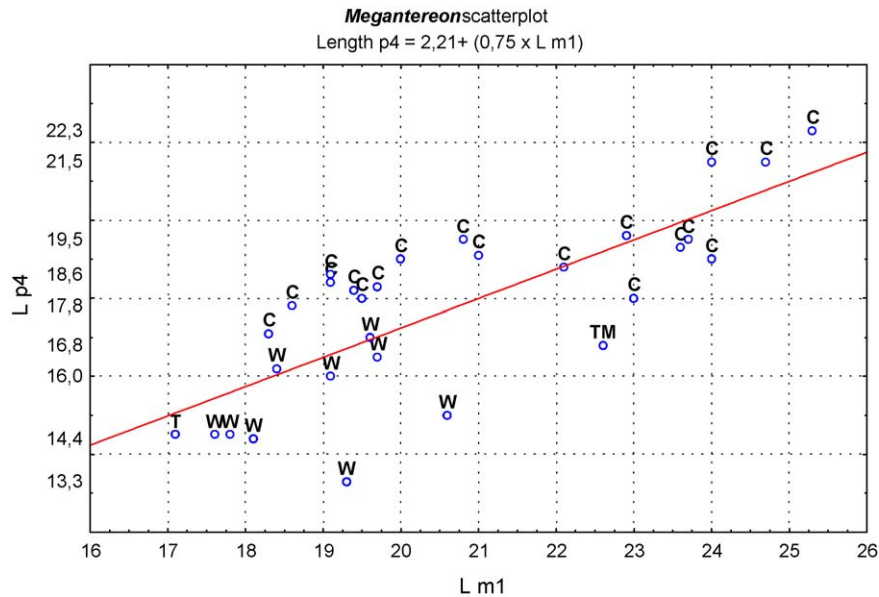


Fig. 6. Scatterplot (Length of m1/Length of p4) of different *Megantereon* species; C=*M. cultridens*; W=*M. whitei*; T=*M. ekidoit* from South Turkwell; TM= Toros Menalla (data from (Palmqvist et al., 2007; Werdelin and Lewis, 2000) and personal).

Fig. 6. Diagramme de répartition (Longueur de m1/Longueur de p4) de différentes espèces de *Megantereon*. C=*M. cultridens*; W=*M. whitei*; T=*M. ekidoit* de Turkwell Sud; TM= Toros Menalla (Données de (Palmqvist et al., 2007; Werdelin and Lewis, 2000) et personnelles).

names like in (Palmqvist et al., 2007). In a PCA (Fig. 5) based on the length of p3, p4 and m1, the specimens allocated to *M. cultridens* are clearly separated from those allocated to *M. whitei* in the first axis while the TM mandible plots in between. A scatterplot based on the length of p4 and m1 (Fig. 6) shows that *M. ekidoit* is the smallest specimen of the whole sample and that it plots close to *M. whitei* specimens but the distinction between the latter and *M. cultridens* is unclear and TM 160-05-02 is closer by the size to the latter species. The deepness of the mandible is also used to differentiate the species (Werdelin and Lewis, 2002). The ratio length of m1/depth of the mandible behind m1 is about 0.68 for *M. ekidoit* and *M. cultridens*, about 0.56 for *M. whitei* but it reaches 0.8 for the TM mandible. Morphologically, TM 160-05-02 differs also from a Kenyan specimen allocated to *M. whitei* (KNM ER793) by a deeper masseteric fossa and the absence of mental flange which could be a primitive character. Thus, in the state of the art, the Chadian specimen seems to belong to the genus *Megantereon* but it cannot be identified at the species level. Thus the best identification could actually be cf. *Megantereon* sp.

5. Conclusions

The carnivore fauna from Toros Menalla includes about 20 species of Canidae, Mustelidae, Herpestidae, Viverridae, Hyainidae and Felidae. The significant number of large size predators indicates the presence of numerous big games in the banks of the paleo-lake Chad. Several studies in the past conclude that the large machairodonts, here *Machairodus*, *Lokotunjailurus* (Scimitar toothed cats) and cf. *Megantereon* (dirk toothed cat), were particularly hunters of large mammals. The remains of the killed big herbivores left a large amount of food for some scavengers or occasionally

scavengers like the abundant jackal sized *Hyaenictitherium minimum* or even like the primitive hominids. Until now, the genus *Lokotunjailurus* was only known in East Africa. Its presence in Toros Menalla area indicates a link between two areas separated by 2500 km during the Late Miocene. On the other hand, the origin of the genus *Megantereon* has been discussed. Some authors proposed North America if the fossil of the Latest Hemphillian called *M. hesperus* (Berta and Galiano, 1983) really belongs to this genus (Turner, 1987) or even for authors considering that these fossils must be reported to *M. cultridens* (Martínez-Navarro and Palmqvist, 1995; Palmqvist et al., 2007; Qiu, 2003) and thus the genus dispersed later in the Old World. The new discovery shows that it was probably present in the Old World in the Late Miocene and later migrated to North America. These new results support the prominence of the Chadian faunas in understanding of the Neogene vertebrate evolution in Africa.

Acknowledgements

We thank the University of Poitiers (UMR 6046), the University of N'Djamena, the French Ministère des Affaires Étrangères (Commission des Fouilles Paris & SCAC Ambassade de France à N'Djaména), the programs ECLIPSE of the French CNRS and ANR, the program Revealing Hominid Origins Initiative of the National Science Foundation (USA) for granting field researches and the laboratory works. In Chad we were helped by the Centre National d'Appui à la Recherche. We thank also P. Tassy and C. Sagne Muséum National d'Histoire Naturelle, Paris for generous access to the collections in their care and R. Tedford, Carl Mehling, Judith Gaskin and Lorraine Meeker for great help to one of us in the Amer. Mus. Nat. Hist., New York, USA. We

are grateful to all the members of the Mission Paléontologique Franco-Tchadienne, who collected the fossils in the field in, sometimes, very difficult conditions. We wish also to thank X. Valentin for preparing and casting the fossil specimens, S. Riffaut for the arrangement of figures, G. Florent and C. Noel for administrative guidance. We are grateful to L. Werdelin, Stockholm, for remarks on the Kenyan material (Pers. com.). We thank also two anonymous reviewers whose comments helped the final version of the manuscript.

References

- Ballésio, R., 1963. Monographie d'un *Machairodus* du gisement vil-lafranchien de Senèze: *Homotherium crenatidens* Fabrini. Trav. Lab. Géol. Fac. Sciences Lyon 9, 1–129.
- Berta, A., Galiano, H., 1983. *Megantereon hesperus* from the Late Hemphillian of Florida with remarks on the phylogenetic relationships of Machairodonts (Mammalia, Felidae, Machairodontinae). J. Paleont. 57, 892–899.
- Brunet, M., Guy, F., Pilbeam, D., Mackaye, H.T., Likius, A., Djimdoumal-baye, A., Beauvilain, A., Blondel, C., Bocherens, H., Boisserie, J.R., de Bonis, L., Coppens, Y., Dejax, J., Denys, C., Düringer, P., Eisenmann, V., Fanone, G., Fronty, P., Geraads, D., Lehmann, T., Lihoreau, F., Louchart, A., Mahamat, A., Merceron, G., Mouchelin, G., Otero, O., Pelaez-Campomanes, P., Ponce de Leon, M., Rage, J.C., Sapanet, M., Schuster, M., Sudre, J., Tassy, P., Valentin, X., Vignaud, P., Viriot, L., Zazzo, A., Zollikofer, C., 2002. A new hominid from the Upper Miocene of Chad, Central Africa. Nature 418, 145–151.
- Brunet, M., Guy, F., Pilbeam, D., Lieberman, D.E., Likius, A., Mackaye, H.T., Ponce de León, M., Zollikofer, C.P.E., Vignaud, P., 2005. New material of the Earliest Hominid from the Upper Miocene of Chad. Nature 434, 753–755.
- Croizet, J.B., Jobert, A.C., 1828. Recherches sur les ossements fossiles du département du Puy-de-Dôme. Clermont-Ferrand, 1–224.
- Crusafont Pairó, M., Aguirre, E., 1972. *Stenailurus*, Félidé nouveau, du Tur-olien d'Espagne. Ann. Paleont. 58 (2), 211–223.
- de Bonis, L., 1976. Un Félidé à longues canines de la Colline de Perrier (Puy-de-Dôme): ses rapports avec les Félinés machairodontes. Ann. Paleont. 62 (2), 159–198.
- de Bonis, L., Peigné, S., Likius, A., Mackaye, H.T., Vignaud, P., Brunet, M., 2005. *Hyaenictitherium minimum*, a new icthithere (Mammalia, Carnivora Hyaenidae) from the Late Miocene of Toros-Menalla, Chad. C.R. Palevol 4 (8), 671–679.
- de Bonis, L., Peigné, S., Likius, A., Mackaye, H.T., Vignaud, P., Brunet, M., 2007a. The oldest African fox (*Vulpes riffautae* n. sp., Canidae, Carnivora) recovered in Late Miocene deposits of the Djurab desert. Chad. Naturwissenschaften 94 (7), 575–580.
- de Bonis, L., Peigné, S., Likius, A., Mackaye, H.T., Vignaud, P., Brunet, M., 2007b. First occurrence of the 'hunting hyena' *Chasmaporthetes* in the Late Miocene fossil bearing localities of Toros Menalla Chad (Africa). Bull. Soc. geol. France 178 (4), 317–326.
- Fabrini, E.I., 1890. *Machairodus (Megantereon)* del Valdarno superiore. Boll. R. Comitato geol. Italia 21 (121–144), 161–177.
- Howell, F.C., Garcia, N., 2007. Carnivora (Mammalia) from Lemudong'o (Late Miocene), Narok district, Kenya. Kirtlandia 56, 121–139.
- Lebatard, A.E., Bourlès, D., Düringer, P., Jolivet, M., Braucher, R., Carcaillet, J., Schuster, M., Arnaud, N., Monié, P., Lihoreau, F., Likius, A., Mackaye, H.T., Vignaud, P., Brunet, M., 2008. Cosmogenic nuclide dating of *Sahelanthropus tchadensis* and *Australopithecus bahrelghazali*: Mio-Pliocene hominids from Chad. Proc. Natl. Acad. Sci. U S A 105, 3226–3231.
- Le Fur, S., Fara, E., Mackaye, H.T., Vignaud, P., Brunet, M., 2009. The mam-mal assemblage of the hominid site TM266 (Late Miocene Chad Basin): ecological structure and paleoenvironmental implications. Naturwis-senschaften 96, 565–574.
- Martínez-Navarro, B., Palmqvist, P., 1995. Presence of the African Machairodont *Megantereon whitei* (Broom, 1937) (Felidae, Carnivora, Mammalia) in the Lower Pleistocene site of Venta Micena (Orce, Granada Spain), with some considerations on the origin, evolution and dispersal of the genus. J. Archaeol. Science 22, 569–582.
- Morales, J., Salesa, M.J., Pickford, M., Soria, D., 2001. A new tribe, new genus and two new species of Barbourfelinae (Felidae, Carnivora Mammalia) from the Early Miocene of East Africa and Spain. Trans. Royal Soc. Edinburgh Earth Sc. 92, 97–102.
- Morales, J., Pickford, M., Soria, D., 2005. Carnivores from the Late Miocene and basal Pliocene of the Tugen Hills, Kenya. Rev. Soc. Geol. España 18 (1–2), 39–61.
- Palmqvist, P., 2002. On the presence of *Megantereon whitei* at the South Turwel hominid site, northern Kenya. J. Paleont. 76 (5), 928–930.
- Palmqvist, P., Torregrasa, V., Pérez-Claros, J., Martínez-Navarro, B., Turner, A., 2007. A re-evaluation of the diversity of *Megantereon* (Mammalia, Carnivora, Machairodontinae) and the problem of species identification in extinct carnivores. J. Vert. Paleont. 27 (1), 160–175.
- Peigné, S., de Bonis, L., Likius, A., Mackaye, H.T., Vignaud, P., Brunet, M., 2005a. New machairodontine (Carnivora, Felidae) from the Late Miocene hominid locality of Toros-Menalla. Chad. C. R. Palevol 4, 243–253.
- Peigné, S., de Bonis, L., Likius, A., Mackaye, H.T., Vignaud, P., Brunet, M., 2005b. The oldest modern mongoose (Carnivora, Herpestidae) from Africa: *Galerella sanguinea* from the late Miocene hominid-bearing locality TM 266, Toros-Menalla, Chad. Naturwissenschaften 92, 287–292.
- Peigné, S., de Bonis, L., Likius, A., Mackaye, H.T., Vignaud, P., Brunet, M., 2008a. Late Miocene Carnivora from Chad: Lutrininae, Mustelidae. Zool. J. Linn. Soc., London 152, 793–846.
- Peigné, S., de Bonis, L., Likius, A., Mackaye, H.T., Vignaud, P., Brunet, M., 2008b. Late Miocene Carnivora from Chad: Herpestidae, Viverridae and small-sized Felidae. C.R. Palevol 7 (8), 499–528.
- Qiu, Z., 2003. Dispersals of Neogene Carnivorans between Asia and North America. In: Flynn, L.J. (Ed.), Vertebrate fossils and their context. Contributions in honor of Richard H. Tedford, Bull. Amer. Mus. Nat. Hist. 279 (2), 18–31.
- Salesa, M.J., Antón, M., Turner, A., Morales, J., 2005a. Aspects of the functional morphology in the cranial and cervical skeleton of the sabre-toothed cat *Paramachairodus ogygia* (Kaup, 1832) (Felidae, Machairodontinae) from the Late Miocene of Spain: implications for the origins of the machairodont killing bite. Zool. J. Linn. Soc. London 144, 363–377.
- Salesa, M.J., Antón, M., Turner, A., Morales, J., 2005b. El origen de los Félicos machairodontinos: aspectos funcionales de la anatomía cráneo-cervical de *Paramachairodus ogygia* (Kaup, 1832) (Felidae, Machairodontinae) de Batallones-1 (Vallesiense MN 10). Rev. Esp. Paleontol. 20, 133–141.
- Salesa, M.J., Montoya, P., Alcalá, L., Morales, J., 2003. El género *Paramachairodus* Pilgrim, 1913 (Felidae Machairodontinae) en el Mioceno superior español, Coloq. Paleontol. Vol Ext. 1, 603–615.
- Salesa, M.J., Anton, M., Turner, A., Morales, J., 2010. Functional anatomy of the forelimb in *Promegantereon ogygia* (Felidae, Machairodontinae, Smilodontini) from the Late Miocene of Spain and the origins of the sabre-toothed felid model. J. Anat. 216, 381–396.
- Thouveny, N., Bonifay, E., 1984. New chronological data on European Plio-Pleistocene faunas and hominid occupation sites. Nature 308, 355–358.
- Turner, A., 1987. *Megantereon cultridens* (Cuvier) (Mammalia, Felidae, Machairodontinae) from Plio-Pleistocene deposits in Africa and Eurasia, with comments on dispersal and the possibility of a new world origin. J. Paleont. 61 (6), 1256–1268.
- Vignaud, P., Düringer, P., Mackaye, H.T., Likius, A., Blondel, C., Boisserie, J.-R., de Bonis, L., Eisenmann, V., Etienne, M.-E., Geraads, D., Guy, F., Lehmann, T., Lihoreau, F., Lopez-Martinez, N., Mourer-Chauviré, C., Otero, O., Rage, J.-C., Schuster, M., Viriot, L., Zazzo, A., Brunet, M., 2002. Geology and palaeontology of the Upper Miocene Toros-Menalla hominid locality, Chad. Nature 418, 152–155.
- Werdelin, L., 2003. Mio-Pliocene Carnivora from Lothagam, Kenya. In: Leakey, M.G., Harris, J.D. (Eds.), Lothagam: The dawn of humanity in eastern Africa. Columbia University Press, New York, pp. 261–328.
- Werdelin, L., Lewis, M., 2000. Carnivora from the South Turkwel hominid site, northern Kenya. J. Paleont. 74, 1173–1180.
- Werdelin, L., Lewis, M.E., 2001. A revision of the genus *Dinofelis* (Mammalia, Felidae). Zool. J. Linn. Soc. London 132, 147–258.
- Werdelin, L., Lewis, M.E., 2002. Species identification in *Megantereon*: a reply to Palmqvist. J. Paleont. 76 (5), 931–933.
- Zdansky, O., 1924. Jungtertiäre Carnivoren Chinas. Palaeont. Sinica 2, 1–149.