Available online at www.sciencedirect.com
SCIENCE DIRECT®
C. R. Palevol 4 (2005) 243–253
COMPTES RENDUS PALEVOL
http://france.elsevier.com/direct/PALEVO/

Systematic palaeontology (Vertebrate Palaeontology)

A new machairodontine (Carnivora, Felidae) from the Late Miocene hominid locality of TM 266, Toros-Menalla, Chad

Stéphane Peigné [a,*], Louis de Bonis [a], Andossa Likius [b], Hassane Taïsso Mackaye [b], Patrick Vignaud [a], Michel Brunet [a]

[a] *Laboratoire de géobiologie, biochronologie et paléontologie humaine, UMR 6046 CNRS–université de Poitiers, 40, av. du Recteur-Pineau, 86022 Poitiers cedex, France*
[b] *Université de N'Djamena, BP 1117, N'Djamena, Chad*

Received 29 March 2004; accepted after revision 25 October 2004

Presented by Yves Coppens

Abstract

Machairodus kabir n. sp., described here, comes from the Late Miocene hominid locality of TM 266, Toros-Menalla, Chad. This species is more derived than the previously described *Machairodus* in having a more developed mental apophysis and more reduced premolars relatively to m1. *Machairodus kabir* n. sp. is the largest mammalian predator from the Toros-Menalla fossiliferous area, with an estimated body mass reaching 350–490 kg, which certainly allowed this felid to prey on large herbivores present at Toros-Menalla. ***To cite this article: S. Peigné et al., C. R. Palevol 4 (2005)***.

Résumé

Un nouveau machairodonte (Carnivora, Felidae) de la localité Miocène supérieur à Hominidae de TM 266, Toros-Menalla, Tchad. La n. sp. *Machairodus kabir* décrite dans ce travail provient du Miocène supérieur de TM 266, gisement à Hominidae de Toros-Menalla, Tchad. Cette espèce est plus dérivée que les *Machairodus* décrits jusqu'à présent, comme le montrent son apophyse mentonnière plus développée et ses prémolaires plus réduites par rapport à m1. *Machairodus kabir* n. sp. est le plus grand mammifère prédateur de Toros-Menalla, avec un poids corporel estimé à 350–490 kg, taille qui permettait certainement à ce félin de s'attaquer aux grands herbivores présents à Toros-Menalla. ***Pour citer cet article : S. Peigné et al., C. R. Palevol 4 (2005)***.

Keywords: Chad; Toros-Menalla; Late Miocene; Felidae; Machairodontinae; *Machairodus*

Mots clés : Tchad ; Toros-Menalla ; Miocène supérieur ; Felidae ; Machairodontinae ; *Machairodus*

* Corresponding author.
E-mail address: stephane.peigne@univ-poitiers.fr (S. Peigné).

1631-0683/$ - see front matter © 2005 Académie des sciences. Published by Elsevier SAS. All rights reserved.
doi:10.1016/j.crpv.2004.10.002

Version française abrégée

Introduction

La localité TM 266 (Toros-Menalla, Tchad) a livré le plus ancien Homininae connu à ce jour, *Sahelanthropus tchadensis* [5], associé à une faune de vertébrés de plus de 40 taxons, dont 25 sont des mammifères [30]. Les Carnivores comptent cinq espèces, dont un félin machairodonte de très grande taille, *Machairodus kabir* n. sp., décrit dans ce travail.

Paléontologie systématique

Ordre CARNIVORA Bowdich, 1821
Famille FELIDAE Fischer, 1817
Sous-famille MACHAIRODONTINAE Gill, 1872
Genre *Machairodus* Kaup, 1833
Machairodus kabir n. sp.

Matériel : TM-266-02-102 (holotype, Fig. 1), TM-266-03-208 (paratype, Fig. 2), TM-266-03-159 (paratype), TM-112-00-095, TM-112-00-96.

Âge et distribution : Miocène supérieur, environ 7 Ma ; présent à Toros-Menalla (localités 266 et 112).

Diagnose : espèce de *Machairodus* de très grande taille (350–490 kg) ; p3-4 nettement plus réduites (au moins en longueur) par rapport à m1 que chez les autres *Machairodus*, sauf ceux de Langebaanweg (Tableau 1). De plus, apophyse mentonnière nettement plus développée que chez les autres *Machairodus*, excepté *M. kurteni* (non préservée chez *M. irtyschensis*) ; m1 plus étirée que chez *M. robinsoni*, *M. aphanistus* et *M. giganteus* ; par rapport à *M. irtyschensis*, *M. kurteni* : complexe métaconide/talonide présent sur m1.

Description de l'holotype : le corpus mandibulaire est uniformément bas sur toute la longueur de p3–m1 ; son bord ventral est rectiligne. En vue occlusale, la rangée dentaire dessine une courbure prononcée. L'apophyse mentonnière était très développée ; elle s'étend vers l'arrière jusqu'au niveau de la racine mésiale de p3. Deux foramens mentonniers de grande taille sont présents. La fosse massétérique est profonde et s'insinue jusque sous le bord distal de m1. La face antérieure de l'apophyse coronoïdienne est fortement inclinée vers l'arrière. Un espace long de 36 mm sépare p3 du bord antérieur du fragment mandibulaire préservé ; l'alvéole de la canine n'est pas visible. La p3 est biradiculée. Les deux cuspides accessoires de p4 sont de grande taille, la distale étant un peu plus haute ; l'axe de la cuspide principale est nettement incliné vers l'arrière. Le cingulum distal est souligné d'une crête basse longitudinale. La carnassière, très usée, est très allongée par rapport aux prémolaires. Le paraconide est plus court que le protoconide. Le complexe métaconide/talonide, très réduit, est séparé du protoconide par un sillon peu profond.

Parmi les spécimens post-crâniens attribués à *M. kabir* n. sp., le plus significatif est une portion distale d'humérus droit (TM-266-03-208) ayant appartenu à un individu d'une taille nettement supérieure à celle des spécimens de *M. giganteus* du Turolien de Pikermi (Tableau 2). La tubérosité deltoïdienne ne s'étend pas très distalement. La crête latérale épicondylaire et l'épicondyle latéral sont peu développés. L'épicondyle médial est peu projeté latéralement et peu étendu proximodistalement. En vue postérieure, la fosse olécranienne est profonde, de largeur et hauteur subégales. En vue distale, la surface articulaire est étroite et, antéropostérieurement, épaisse ; la trochlée n'est pas très profonde et le capitulum peu arrondi. Deux phalanges sont provisoirement attribuées à *Machairodus kabir* n. sp.

Comparaisons et discussion

Le développement de l'apophyse mentonnière, la longueur du diastème post-canine, la faible hauteur du corpus mandibulaire et le degré de réduction des prémolaires par rapport à m1 sont les principaux caractères qui distinguent le machairodonte de TM, de tous les genres décrits auparavant, excepté *Machairodus*. *M. kabir* n. sp. se distingue de *M. robinsoni* [14] par une taille nettement plus grande et par une apophyse mentonnière très développée, des prémolaires plus réduites par rapport à m1, celle-ci étant également plus allongée. Du Miocène supérieur de Sahabi (Libye) ont été décrits quelques spécimens attribués à *Machairodus* sp. [12]. L'absence d'illustrations ne permet malheureusement pas une comparaison détaillée. Les *Machairodus* du Bed 2 de « E » Quarry à Langebaanweg sont de plus petite taille [11]. L'un diffère de *M. kabir* n. sp. par une apophyse coronoïdienne plus inclinée et par l'absence du complexe métaconide/talonide sur m1. L'autre, attribué à cf. *Machairodus* [11], se distingue du spécimen tchadien par une apophyse mentonnière plus réduite et la présence d'une p2 vestigiale ; la proportion des prémolaires par rap-

port à m1 est cependant semblable chez les spécimens tchadien et sud-africains. *Machairodus aphanistus* est l'espèce type du genre ; le matériel de comparaison utilisé dans ce travail inclut une grande partie des spécimens attribués à cette espèce et aux espèces très voisines (*M. laskarevi*, *M. alberdiae*). Nous considérons, comme d'autres auteurs [3,29], les espèces turoliennes *M. leoninus*, *M. taracliensis*, *M. palanderi* et *M. tingii* comme des synonymes ou des sous-espèces de *M. giganteus*. À quelques exceptions près, toutes ces espèces sont de plus petite taille que *M. kabir* n. sp., avec un développement moindre de l'adaptation machairodonte (notamment une apophyse mentonnière plus réduite). Deux autres espèces eurasiatiques, *Machairodus irtyschensis* de Pavlodar (Russie) et *M. kurteni* du Turolien de Kalmakpai (Kazakhstan) sont traitées comme valides par Sotnikova [29]. Toutes deux se distinguent de *M. kabir* n. sp. par des prémolaires moins réduites par rapport à m1 et par l'absence du complexe métaconide/talonide sur m1. Les deux espèces d'Amérique du Nord, *Machairodus coloradensis* et *M. tanneri* diffèrent également de *M. kabir* n. sp. par la moindre réduction de leurs prémolaires. L'humérus de *M. kabir* n. sp. est aussi robuste que celui des autres *Machairodus*. Sa morphologie générale devait être légèrement plus grêle que celle des humérus de lions et tigres actuels, avec des surfaces d'insertions pour les extenseurs et fléchisseurs de l'avant-bras moins développées. Le rapport entre la largeur maximum distale de l'humérus TM-266-03-208 et la longueur fonctionnelle de cette os, calculé chez plusieurs espèces de grands félins actuels et fossiles (Tableau 2), permet d'estimer la longueur fonctionnelle de l'humérus de *M. kabir* à 380–423 mm. Une droite de régression corrélant cette dimension au poids corporel chez les Felidae [1] indique que le poids corporel de *M. kabir* devait être compris entre 350 et 490 kg.

Conclusions

Machairodus kabir n. sp. se distingue donc aisément des autres espèces de *Machairodus*. C'était sans aucun doute le plus grand prédateur de Toros-Menalla. Sa taille considérable lui permettait certainement de s'attaquer aux grands herbivores vivant à Toros-Menalla, notamment l'anthracothère *Libycosaurus petrocchi* (600–800 kg ; voir [15]). La présence de ce dernier et d'une espèce proche ou identique de *Machairodus* à Sahabi indique, par ailleurs, des relations biogéographiques proches entre ces deux zones fossilifères au cours du Miocène supérieur. Au contraire, la faune de TM-266 et celle d'autres gisements contemporains (par exemple, Lower Nawata Formation à Lothagam) ont peu de taxons en commun.

1. Introduction

Since 1997, field campaigns conducted by the 'Mission paléoanthropologique franco-tchadienne' (MPFT) in the Toros-Menalla fossiliferous area of the Djurab desert, Chad, have resulted in the discovery of abundant and diversified Late Miocene faunas aged between 7 and 6 Ma [30]. The locality TM 266 is the most significant one, having yielded cranial and dental remains of the earliest known hominid, *Sahelanthropus tchadensis* [5], and an associated vertebrate fauna including more than 40 taxa, of which 25 are mammalian [30]. Carnivores are well represented, with five species, among which a giant sabretooth cat represented by two or three individuals. This material described here represents a new species of the genus *Machairodus*, *M. kabir* n. sp.

2. Systematic palaeontology

Order CARNIVORA Bowdich, 1821
Family FELIDAE Fischer, 1817
Subfamily MACHAIRODONTINAE Gill, 1872
Genus *Machairodus* Kaup, 1833
Machairodus kabir n. sp.

Etymology. From 'kabir', meaning large in Chadian Arabic.

Holotype. TM-266-02-102, fragment of right mandible with p4–m1 (Fig. 1).

Paratypes. From locality TM 266: TM-266-03–208, distal fragment of right humerus (Fig. 2); TM-266-03-159, middle phalanx, possibly from digit II of left pes or manus.

Additional referred material. From locality TM 112: TM-112-00-095, proximal phalanx; TM-112-00–96, isolated right p4.

All specimens are currently studied at the UMR 6046 (University of Poitiers, France) and they will be stored in the 'Département de conservation des collections', 'Centre national d'appui à la recherche' (CNAR), N'Djamena, Chad.

Fig. 1. *Machairodus kabir* n. sp., holotype, TM-266-02-102: fragment of right mandible with p4-m1 in A, labial view and B, lingual view. Scale bar = 2 cm.
Fig. 1. *Machairodus kabir* n. sp., holotype, TM-266-02-102 : fragment de mandibule droite avec p4-m1 en vue labiale (A) et linguale (B). Échelle = 2 cm.

Type locality. Toros-Menalla site 266 (TM 266), quarry of ca. 5000 m^2, western Djourab desert, Chad. See [30] for details.

Distribution. Toros-Menalla (TM 266, TM 112), Djourab desert, Chad.

Age. Late Miocene; a comparison with the faunas from the Lukeino Formation, Kenya (ca. 6 Ma) and from the Lower Nawata Formation, Lothagam, Kenya (7.4–6.5 Ma), indicates an age for the TM 266 fauna older than 6 Ma and estimated to ca. 7 Ma [30].

Diagnosis. A species of *Machairodus* of very large size; body weight range: 350–490 kg. p3-4 markedly more reduced, at least in length, relatively to m1 than in other species of *Machairodus* except those from Langebaanweg (Table 1). In addition, markedly greater development of the mental apophysis or flange (unpreserved in *M. irtyschensis*) than in other *Machairodus*, except *M. kurteni*; more elongated m1 than in *M. robinsoni*, *M. aphanistus* and *M. giganteus*; compared with *M. irtyschensis*, *M. kurteni*: metaconid/talonid complex on m1.

2.1. Description

All bones are distinctly, though not strongly, weathered, indicating that they have not been rapidly buried after death.

Mandible. The mandible lacks its posteriormost part (condyle, tip of coronoid and angular processes). Anteriorly, a significant portion of the mandible is also missing. The breakage is posterior to the symphysis and the canine alveolus, which are not visible lingually at this level. The corpus is of uniform depth below p3–m1, and becomes deeper posteriorly to m1. It is moderately thick, being slightly thicker across p3 than across m1. The ventral margin of the mandible is nearly straight. In occlusal view, the mandible does not display a marked labial curvature, though the toothrow curves labially, p4 being the most labial tooth. The dorsal edge of the postcanine diastema slightly curves lingually as well. The mental apophysis or flange is well developed. It consists of a tranversely thin lamina that is labially placed and extends from beneath the mesial root of p3 forwards. On the labial face of the mandible below p4–m1, a slightly prominent ridge delimitates a very elongated, triangular-shaped and smooth area, which is likely the insertion surface for the digastric muscle. Two mental foramina are present. The first one is

Fig. 2. *Machairodus kabir* n. sp., paratype, TM266-03-208: distal fragment of right humerus in A, posterior and B, anterior view. Scale bar = 4 cm.
Fig. 2. *Machairodus kabir* n. sp., paratype, TM266-03–208 : fragment distal d'humérus droit en vue postérieure (A) et antérieure (B). Échelle = 4 cm.

Table 1
Comparison of dental measurements (in mm) and proportions in *Machairodus* spp. Parentheses indicate measurements based on alveoli or roots; *: estimates. [1] from [14], [2] from [12], [3] from [11], [4] from [3], [5] from [28], [6] from [4], [7] from [21], [8] from [16], [9] from [13], [10] from [9], [11] from [26], [12] from [33], [13] from [22], [14] from [29], [15] from [25], [16] from [19]
Tableau 1. Comparaison des mesures (en mm) et proportions dentaires chez les espèces de *Machairodus*. Les parenthèses désignent les mesures au niveau alvéolaire ou radiculaire ; * : estimations. [1] de [14], [2] de [12], [3] de [11], [4] de [3], [5] de [28], [6] de [4], [7] de [21], [8] de [16], [9] de [13], [10] de [9], [11] de [26], [12] de [33], [13] de [22], [14] de [29], [15] de [25], [16] de [19]

	Lp3	Wp3	Lp4	Wp4	Lm1	Wm1	Lp3-m1	Lp3/Lm1	Lp4/Lm1
M. kabir n. sp. type TM-266-02-102	(16.50)	—	25.80	11.80*	34.70	13.70	81.50	0.48	0.74
TM-112-00-96	—	—	24.00	10.40	—	—	—	—	—
M. robinsoni type T-491[1]	16.00*	—	20.00*	—	25.00	11.50	—	0.64	0.80
Machairodus sp., Sahabi[2] (coll. Petrocchi)	14.60	—	(21.80)	—	31.50	—			
Machairodus sp., Langebaanweg[3]	—	—	—	—	(29.00)	11.20			
cf. *Machairodus*, Langebaanbweg[3]	12.30	5.50	20.50	9.50	(28.00)	11.00		0.44	0.73
M. aphanistus type HLMD-Din 1132[4]	20.60	9.90	27.30	12.00	30.30	14.20	—	0.68	0.90
Eppelsheim[4]: BMNH 49967a	20.20	9.60	26.00	12.10	30.10	14.50	—	0.67	0.86
Kemiklitepe: KTD 63	17.70	7.10	(21.50)	—	30.80	11.00	71.50	0.57	0.70
Mahmutgazi[5]: Ma 1/49	17.20	8.30	25.00	11.90	31.80	13.20	—	0.54	0.79
Charmoille[4]: NHMB Cm 244	18—19*	9.20	25.50	12.60	27—28*	12.90	—	0.67	0.92
Soblay[1]: NHMB TF 164	—	—	—	—	30.60	13.50	—	—	—
Zillingdorf[4]: Mus. Vienne	—	—	—	—	30.60	13.90	—	—	—
Polgardi[1]: HGI OB/2650	—	—	—	—	33.10	15.30	—	—	—
Montredon[6]: FSL 210390 (cf.)	19.00*	9.70*	24.50*	12.50*	—	—	—	—	—
Montredon[6]: MTN 3173 (cf.)	—	—	—	—	31.70	17.60	—	—	—
Dorn-Dürkheim[7]: DD 4796 (cf.)	—	—	29.00	12.30	—	—	—	—	—
M. laskarevi syntype TGPI-1/2257[8]	19.00	8.00	25.00	10.00	29.00	10.00	—	0.66	0.86
M. alberdiae type MNCN 3605	(16.00)	—	21.10	—	(24.00)	—	62.50	0.67	0.88
MNCN 32000	—	—	22.70	9.30	24.70	10.90	—	—	0.92
MNCN 45860	17.00	7.70	—	—	—	—	—	—	—
M. leoninus, cast of type	(15.60)	—	26.70	10.20	30.20	11.60	71.00	0.51	0.88
MNHN-PIK 418	16.70	7.80	—	—	(31.50)	—	—	0.53	—
Venta del Moro: MNCN 955	(21.00)	—	32.00	13.00	35.80	14.20	87.00	0.59	0.89
Samos[1]: AMNH 20606	21.40	9.50	29.20	12.70	32.80	14.40	—	0.65	0.89
Hadji Dimovo[9]	22.00	9.80	27.00	12.30	31.20	13.00	77.80	0.71	0.87
Kemiklitepe A-B: UEK-124[10]	18.50	7.50	27.20	11.20*	—	—	—	—	—
M. giganteus taracliensis syntype 3389[11]	18.50	8.50	29.00	11.50	30.50	14.50	75.50	0.61	0.95
M. palanderi syntype (locality 113)	15.55	6.95	26.65	10.20	28.10	12.30	67.75	0.55	0.95
M. tingii syntype (locality 30)[12]	18.80	8.40	29.00	12.40*	—	—	—	—	—
M. irtyschensis type PIN 2413/115[13]	21.50	10.50	32.00	14.00	35.50	15.50	91.00	0.61	0.90
M. kurteni type: PIN 2433/287[14]	(17.50)	—	26.80	11.50	31.20	13.00	76.40	0.56	0.86
PIN 2433/524[14]	17.25	7.90	25.25	11.10	31.40	14.00	73.10	0.55	0.80
M. palaeindicus type BMNH 48436[15]	—	—	23.50	11.00	—	—	—	—	—
M. coloradensis UNSM 25510 (cf.)[16]	(20.00)	(7.80)	(26.40)	(10.20)	31.90	14.00	77.60	0.63	0.83
M. tanneri type: UNSM 26036	19.60*	7.90*	26.30*	10.50*	32.00	12.60*	78.80	0.61	0.82

incompletely preserved on the holotype and located approximately above the posterior third of the flange, like in most machairodontines; it is at least 10 mm high. It is uncommon in *Machairodus*, but frequent in, e.g., *Homotherium*; it is rarely as large as in the Chadian mandible, however. A second, very large foramen, is located 16.5 mm posteriorly to the first one; it is 13 mm long and 7 mm high and is set very low beneath the mesial root of p3. The masseteric fossa is deep, about 50 mm long and 40 mm of maximum height. The anterior rim extends forwards beneath the distal part of m1. The coronoid apophysis lacks its superior half. It extends from just behind m1; its anterior edge is oriented posteriorly and the posterior one is subvertical and concave. The mandibular foramen is set very low, near the ventral edge of the mandible.

Dentition. The teeth are much worn, indicating an old individual age of the type specimen. A 36-mm-long diastema separates p3 from the anteriormost edge of the preserved fragment. The latter does not correspond to the distal edge of the canine alveolus, however (see description of mandible). The p3 is not preserved, but was double-rooted. The p4 and m1 are set well above the alveolar margin and their roots are distinct. The p4 of the holotype is much worn on its distolabial face, with nearly vertical wearing facets; the isolated left p4 from TM 112 is better preserved. The mesial accessory cusp of p4 is large and consists of a short and trenchant blade; its mesial face is slightly concave due to the basal cingulum. The main cusp is slender and it is oriented posteriorly; it is well separated from the accessory cusps by deep notches. The distal accessory cusp, although incompletely preserved on both specimens, is certainly taller, although not longer, than the mesial cusp; it has a trenchant mesial edge. A shallow notch separates this cusp from the short, longitudinal cingular crest. The distal cingulum extends forwards on each face of the tooth. It is particularly developed labially, having a slightly prominent margin; lingually, it extends slightly forwards to the distal cusp but remains poorly developed. The m1 is a large elongated tooth. It is heavily worn on the labial surface of both the paraconid and the carnassial notch; the wearing facets are nearly vertical and reach the cervix. From the probable location of the carnassial notch, the paraconid blade is shorter than the protoconid blade. Due to the wearing pattern, it is not possible to locate precisely the widest part of the tooth. The metaconid/talonid complex is reduced. It is separated from the protoconid by a shallow groove. The poor preservation of this part does not permit to say whether the metaconid and talonid were well distinct from each other.

Postcranials. A distal right humerus of a large individual (TM-266-03-208) is assigned to *Machairodus kabir* n. sp. The specimen is broken away across the distal extremity of the deltoid tuberosity. The olecranon fossa is also damaged and does not preserve its wall. The preserved part of the humerus is relatively slender and, considering the maximum distal width, is notably larger than studied specimens of *M. giganteus* from Pikermi (MNHN–PIK 3358, MNHN-PIK 3361); see also [27]. The deltoid tuberosity does not extend much distally but is well marked. The lateral epicondylar crest and lateral epicondyle are little developed in contrast to those of Smilodontini *Megantereon* and *Smilodon*. The medial epicondyle is poorly developed compared with that of humeri of these two genera. It is much similar, however, to that in *Homotherium* and *Machairodus* species in being little laterally projected and distoproximally extended. Therefore, the attachment surfaces for the pronator teres muscle and carpal and digital flexors are reduced in *M. kabir* n. sp. The entepicondylar foramen opens slightly proximoposteriorly. In posterior view, the olecranon fossa is deep and roughly of equal width and height; it has a well-curved proximal edge that is approximately at the level of the distal part of the entepicondylar foramen. The lateral and medial edges of the fossa are not convergent, in contrast to *Dinofelis* [32]. In distal view, the articular surface is transversely narrow and anteroposteriorly thick, and it has a moderately deep trochlea and a little rounded capitulum.

Two phalanges from Toros-Menalla are here provisionally assigned to *Machairodus kabir* n. sp. TM-112-00-095 is a proximal phalanx, 45 mm long and 13.5 mm wide across midshaft. It is more slender than, e.g., those of *Homotherium* from Senèze [2]. The shaft is distinctly bowed and, just proximal to midshaft, has two small markings for the proximal digital annular ligament holding in place the digital flexor tendons. TM-266-03-159 is a robust middle phalanx 32.4 mm long and its distal maximum width is 19 mm. The lateral displacement of the low head, the orientation of the distal articular surface, and the laterally curved shaft indicate that this phalanx may belong to the left digit II of manus or pes.

3. Comparisons and discussion

Dental and mandibular features (dental wearing pattern, long carnassial associated with short premolars, morphology of p4, long postcanine diastema, greatly developed flange) support the assignment of the Chadian material to the Felidae Machairodontinae. It differs from most of the machairodontine genera known from the Mio-Pliocene of Africa and Eurasia. Compared with *Dinofelis* spp., the felid from TM is much larger and has a much more developed flange, a more reduced coronoid apophysis, a longer postcanine diastema, a more reduced p4 relatively to m1, a slightly less reduced metaconid/talonid complex on m1, a humerus with a

less rounded capitulum and a shallower trochlea. Compared to *Megantereon* species, our material displays a much larger size, a less developed sabretooth adaptation (less developed flange, metaconid/talonid complex present on m1), a shallower mandibular ramus with front dentition not elevated above the cheek teeth level, and a more slender humerus. The Chadian species differs from *Homotherium* spp. by a less reduced coronoid process, a dorsally less concave, longer postcanine diastema, a shallower, more slender mandible, less reduced and double-rooted p3–4, and the presence of a reduced metaconid/talonid complex on m1. The distinction with the recently described *Lokotunjailurus emageritus* from the Nawata Formation of Lothagam (Late Miocene, Kenya) [31] is also marked. The Toros-Menalla material is distinguished by an anteriorly deeper mandible with a much more developed flange, less reduced and double-rooted premolars, a metaconid-talonid complex present on m1, and a more reduced medial epicondyle on the humerus. We do not find any significant differences between the material here described and that assigned to the primitive machairodontine genus *Machairodus*. The mandible TM-266-02-102 displays a combination of features (shallow ramus, reduced coronoid process, flange present, long postcanine diastema, double-rooted p3, m1 with a reduced but distinct metaconid-entoconid complex) that distinguishes *Machairodus* from other machairodontines. *Machairodus copei* from the Turolian of Grebeniki, southern Russia [23] and *M. africanus* from the Middle Pliocene of Ain Brimba, Tunisia [24] are only represented by cranial and/or upper dental remains not comparable with our material. Morphometric data are compiled from the literature and from personal studies, and are summarized in Table 1.

3.1. African Machairodus

So far, the earliest *Machairodus* from Africa is *M. robinsoni* [14], recorded from the early Late Miocene of Bled Douarah, Beglia Formation (ca 11 Ma, Tunisia) [7]. A significant difference in size separates the Chadian record from *M. robinsoni*. In addition, the latter differs in having a less developed or, most probably, no flange on the mandible, premolars (and especially p3) less reduced relatively to m1, and a less elongated m1. A symphysis fragment from the Chorora Formation (11–10 Ma, Ethiopia) and preserving the canine basis and the incisor alveoli has recently been assigned to *Machairodus aphanistus* [8]. This specimen displays a more reduced flange than in *M. kabir* n. sp. The fauna from Sahabi (Libya), generally believed to be Late Miocene in age, has yielded a few remains of *Machairodus* sp. (including cranial and dental specimens), described but not illustrated [12]. The description and measurements suggest some similarities (Table 1) but it is not possible to confirm the identity of the Chadian and Libyan *Machairodus*. A large *Machairodus* species is mentioned from the Adu-Asa and lower Sagantole Formations, Middle Awash (5.8–5.2 Ma, Ethiopia) [10]. The only feature mentioned by the authors is a m1 wider and shorter than in *Lokotunjailurus emageritus*. In contrast, this tooth is rather elongated in *M. kabir* n. sp. A more precise comparison is, however, necessary with our material to confirm the distinction between the Chadian and the Middle Awash species. *Machairodus* is also known from Bed 2 of the 'E' Quarry, Langebaanweg (Earliest Pliocene, South Africa) by individuals much smaller than those from Chad. A fragment of mandible with m1 on both sides is assigned to *Machairodus* sp. [11]; it differs from our material in having a less steeply inclined coronoid process and no metaconid/talonid complex on m1. A more complete fragment of mandible is assigned to cf. *Machairodus* [11] and can be distinguished from the Chadian mandible by a more reduced flange and a vestigial p2 present; both Chadian and South African specimens have similarly reduced premolars relatively to m1, however.

3.2. Eurasian Machairodus

An early revision of the Eurasian species [3] only retains two valid species, *Machairodus aphanistus* (Vallesian) and *M. giganteus* (Turolian). More recently, however, the synonymy of some Turolian species has been disputed [29].

3.2.1. M. aphanistus group

Machairodus aphanistus is the type species of the genus *Machairodus*. It is based on a specimen from Eppelsheim, Germany (MN 9, Late Miocene). Comparative specimens used in this study are from Charmoille (MN 9, Switzerland), Soblay (MN 10, France), Zillingdorf (Austria), Los Valles de Fuentidueña (MN 9, Spain), Kemiklitepe (MN 9, Turkey) and Mahmutgazi

(MN 11, Turkey). *Machairodus* cf. *aphanistus* specimens from Montredon (MN 10, France) and Dorn-Dürkheim (MN 11, Germany), *M. laskarevi* from Kalfa (Moldavia) and *M. alberdiae* from Los Valles de Fuentidueña (Spain) are also included. The two latter species display a very similar morphology to that of specimens assigned to *M. aphanistus*, although the former one retains a minute p2 and the latter species is much smaller in size. Dental proportion and mandibular morphology indicate that, besides a larger size, *M. kabir* n. sp. is distinguished from *M. aphanistus* group in displaying more advanced sabretooth features on the mandible (more reduced coronoid process and much more developed mental apophysis), two large mental foramina, a longer postcanine diastema, a p3 and, except in Kemiklitepe mandible, a p4 much more reduced relatively to m1 and a more elongated m1.

3.2.2. Machairodus (= Amphimachairodus) giganteus group

Following [3], most workers regard Turolian specimens of *Machairodus* as a single species, *M. giganteus*. This species displays slightly more derived sabertooth features than *M. aphanistus* such as a greater development of the flange, greater reduction of premolars relatively to m1 (especially p3), longer postcanine diastema, etc. Beaumont [3] indicates, however, a high degree of variability of these features. The comparative material studied here comes from Venta del Moro (MN 13, Spain), Pikermi (MN 12, Greece), Samos (MN 12–13, Greece), and Kemiklitepe A–B (MN 12, Greece). Following [3,29], we also consider *M. leoninus*, *M. taracliensis*, *M. palanderi* and *M. tingii* as synonyms or subspecies of *M. giganteus*. The mandibular flange of *M. kabir* n. sp. is much more developed than in most species, although it nearly reaches the same development in some mandibles from Samos and Pikermi; see fig. 6 in [3]. The dentition of *M. kabir* n. sp. is mainly distinguished by the premolar reduction (especially p4) relatively to m1 and by the elongation of m1, though the latter feature is somewhat variable.

3.2.3. Other species

Two other valid species were recognized by previous authors. *Machairodus irtyschensis*, described from Irtysch near Pavlodar (Siberia, Russia), is based on a fragment of left mandible and postcranial elements [22]. This species is slightly larger than *M. kabir* n. sp.; it has much less reduced premolars relatively to m1 (proportions as in *M. giganteus*) and lacks a metaconid/talonid complex on m1. *Machairodus kurteni* has been recently described from the Turolian (MN 13) of Kalmakpai, Kazakhstan [29]. It is slightly smaller than *M. kabir* n. sp. and displays a similarly developed flange. It differs by a lesser reduction of the premolars relatively to m1 and the absence of a metaconid-talonid complex on m1. *Machairodus palaeindicus* from the Pliocene of India has been previously described and illustrated on the basis of an associated fragment of maxillae and mandible [17,23]. Pilgrim [25] assigned the species to *Megantereon* on the basis of the reduction of p3 (single-rooted) and the great development of the flange. The latter is not more developed than in TM-266-02–102, but the single-rooted p3, the single mental foramen and the shorter postcanine diastema distinguish the Indian species from *M. kabir* n. sp.

3.3. North American taxa

Two species are known from North America, *Machairodus coloradensis* and *M. tanneri*; the genus, regarded as an immigrant from Eurasia, ranges between 7 and 4.5 Ma [18]. Dental proportions (more reduced premolars relatively to m1) distinguish these species from *M. kabir* n. sp.

3.4. Postcranial remains and body size estimate

Although fragmentary, the humerus of *M. kabir* n. sp. appears as robust as that of other *Machairodus*, for which this bone is documented (e.g., *M. giganteus* from Pikermi). In comparison with *Panthera leo* and *P. tigris* humeri, the specimen from Chad has a slightly more reduced medial epicondylar apophysis, a markedly less prominent lateral edge of the deltoid tuberosity, and a more reduced lateral epicondylar crest. Overall, the complete humerus of *Machairodus kabir* n. sp. should have a relatively slender morphology, with a lesser development of attachments for extensor and flexor muscles, than in *Panthera tigris* and *P. leo*. The maximum width of the distal humerus (MWDH) from Toros-Menalla is 107 mm, which corresponds to a very large individual. The relationship between this dimension and the functional length (FctL, distance between articular surfaces) of the humerus in some extant and extinct spe-

Table 2
Comparison of humeral proportions in some extant and extinct large felids. Mean values are associated with min–max range (in parentheses). Measurements (in mm) for extant species are from personal data; TL: total length of the humerus; FctL: functional length (distance between articular surfaces); MWDH: maximum width of the distal humerus; [1]from personal data and [27], [2]from [3], [3]from [6]; *: estimate
Tableau 2. Comparaison des proportions humérales chez quelques grands félins actuels et fossiles. Les valeurs moyennes sont accompagnées de l'étendue (entre parenthèses). Les mesures (en mm) pour les espèces actuelles sont dues aux auteurs ; TL : longueur totale de l'humérus ; FctL : longueur fonctionnelle (distance entre les surfaces articulaires) ; MWDH : largeur maximum distale de l'humérus ; [1] tirées de données personnelles et [27], [2] de [3], [3] de [6] ; * : estimation

	TL	FctL	MWDH	TL/MWDH	FctL/MWDH
Panthera leo (*N* = 17)	322 (280–373)	302 (261–353)	80 (74–92.5)	4.01 (3.52–4.44)	3.75 (3.25–4.12)
P. tigris (*N* = 9)	308 (276–330)	288 (263–307)	80 (72.5–86.3)	3.77 (3.61–4.00)	3.54 (3.32–3.82)
Machairodus giganteus[1] (*N* = 2)	365 (350–380)	347 (341–353)	88.4 (83.8–93)	4.14 (4.09–4.18)	3.90 (3.73–4.07)
Homotherium crenatidens[2] (*N* = 1)	354	328	85	4.16	3.86
H. latidens[3] (*N* = 2)	319 (318–320)	—	75.05 (72.8–77.3)	4.26 (4.11–4.40)	3.96*

cies is assessed. Table 2 summarizes data for *Panthera leo*, *P. tigris*, *Machairodus giganteus*, *Homotherium crenatidens*, and *H. latidens*. Ratios obtained from *P. leo*, *P. tigris*, *M. giganteus*, and *H. crenatidens* produce an estimated FctL of 400 mm, 380 mm, 417 mm, and 413 mm respectively for *M. kabir* n. sp. Available data for *H. latidens* [6] do not include FctL but in living and extinct species referred to above, FctL is consistently around 0.93 of the total length of the humerus (TL); MWDH / FctL in *H. latidens* is therefore 3.96, that produces an estimated FctL for *M. kabir* n. sp. of 423 mm. Reasonably, one can estimate that the FctL of *Machairodus kabir* n. sp. is 380–423 mm. Felid regressions [1], which correlate humeral length to body mass in Carnivora, provide an estimated body mass of 350–490 kg for *Machairodus kabir* n. sp. It is worth noting, however, that Anyonge [1] indicates that the humeral length is not a good predictor of body mass and it produces indeed the lowest estimates for all extant species included in his study. With a MWDH of 107 mm, the humerus of *M. kabir* n. sp. is within the known range of variation (85.7–111.3 mm) of the extinct American lion *P. atrox* from the Late Pleistocene of North America [20]. The body mass estimate of *M. kabir* n. sp. is consistent with that (344–523 kg) produced by Anyonge [1] for this extinct feline, based on predictors other than the humeral length (e.g., femoral or humeral circumference and cortical area).

4. Conclusions

The Carnivores from Toros-Menalla localities are known by numerous remains. *Machairodus kabir* n. sp. is, however, represented by a few specimens only. Despite that, this new species markedly differs from previously described *Machairodus* by the great development of the mandibular flange and the reduction of premolars relatively to m1. *M. kabir* n. sp. represents to date the largest predator of Toros-Menalla, with an estimate body mass of 350–490 kg. Given the sexual dimorphism known in Machairodontinae, with males larger than females, this range is expected to be even greater with a better fossil record. A predator of such a size was probably capable of preying on some of the largest herbivores found in Toros-Menalla, including anthracotheriids like *Libycosaurus petrocchi*, with a body weight of 600–800 kg [15] or sub-adult individuals of hippopotamids and proboscideans.

Although they are of similar age, the faunas from TM 266 and from Lower Nawata Formation of Lothagam do not have many taxa in common. In particular, *Machairodus kabir* n. sp. represents a lineage different from that of *Lokotunjailurus emageritus* from Lothagam; in addition, on the contrary to the Chadian locality, anthracotheriids are unknown from this time in East Africa. There are more affinities between the faunas from TM 266 and from Sahabi (e.g., *Libycosaurus petrocchii*, identical or closely related *Machairodus*) that indicates some biogeographical relationships between the two area during the Late Miocene, before and/or ca 7 Ma.

Acknowledgements

We thank authorities from Chad ('Ministère de l'Éducation nationale, de l'Enseignement supérieur et

de la Recherche, université de N'Djamena, CNAR, DRGM) and France ('Ministère de l'Enseignement supérieur, de la Recherche et de la Technologie', 'Ministère des Affaires étrangères') for supporting the field expeditions in the Djourab and all the MPFT participants for the field, technical and/or administrative work. Many thanks are also due to people who gave us access to comparative materials, to E. Fara (UMR 6046) for reviewing the English of the manuscript and to the two anonymous reviewers for their corrections and suggestions. Some of us benefit of a grant RHOI-NSF.

References

[1] W. Anyonge, Body mass in large extant and extinct carnivores, J. Zool. 231 (1993) 339–350.

[2] R. Ballesio, Monographie d'un *Machairodus* du gisement villafranchien de Senèze: *Homotherium crenatidens* Fabrini, Trav. Lab. Géol. Lyon (n.s.) 9 (1963) 1–129.

[3] G. de Beaumont, Recherches sur les Félidés (Mammifères, Carnivores) du Pliocène inférieur des Sables à *Dinotherium* des environs d'Eppelsheim (Rheinhessen), Arch. Sci. Genève 28 (1975) 369–405.

[4] G. de Beaumont, Contributions à l'étude du gisement Miocène supérieur de Montredon (Hérault). Les grands mammifères. 2 – Les Carnivores, Palaeovertebrata, mém. extraord. (1988) 15–42.

[5] M. Brunet, F. Guy, D. Pilbeam, H.T. Mackaye, A. Likius, D. Ahunta, A. Beauvilain, C. Blondel, H. Bocherens, J.-R. Boisserie, L. de Bonis, Y. Coppens, J. Dejax, C. Denys, P. Duringer, V. Eisenmann, G. Fanone, P. Fronty, D. Geraads, T. Lehmann, F. Lihoreau, A. Louchart, A. Mahamat, G. Merceron, G. Mouchelin, O. Otero, P. Pelaez Camponanes, M. Ponce de Leon, J.-C. Rage, M. Sapanet, M. Schuster, J. Sudre, P. Tassy, X. Valentin, P. Vignaud, L. Viriot, A. Zazzo, C. Zollikofer, A new hominid from the Upper Miocene of Chad, Central Africa, Nature 418 (2002) 145–151.

[6] À. Galobart, J. Pons-Moyà, M. Antón, J. Maroto, Descripción del material de *Homotherium latidens* (Owen) de los yacimientos del Pleistoceno inferior de Incarcal (Girona, NE de la Península Ibérica), Paleontol. Evol. 34 (2003) 99–141.

[7] D. Geraads, Vertébrés fossiles du Miocène supérieur du Djebel Krechem El Artsouma (Tunisie centrale). Comparaisons biostratigraphiques, Geobios 22 (1989) 777–801.

[8] D. Geraads, Z. Alemseged, H. Bellon, The Late Miocene mammalian fauna of Chorora, Awash basin, Ethiopia: systematics, biochronology and the ^{40}K–^{40}Ar ages of the associated volcanics, Tertiary Res. 21 (2002) 113–122.

[9] D. Geraads, T. Kaya, V. Tuna, A skull of *Machairodus giganteus* (Felidae, Mammalia) from the Late Miocene of Turkey, N. Jahrb. Geol. Paläontol. Mh. (2004) 95–110.

[10] Y. Hailé-Selassié, G. Woldegabriel, T.W. White, R.L. Bernor, D. Degusta, P.R. Renne, et al., Mio-Pliocene mammals from the Middle Awash, Ethiopia, Geobios 37 (2004) 536–552.

[11] Q.B. Hendey, The Late Cenozoic Carnivora of the South-Western Cape Province, Ann., S. Afr. Mus. 63 (1974) 1–369.

[12] F.C. Howell, Preliminary observations on Carnivora from the Sahabi Formation (Libya), in: N.T. Boaz, A. El-Arnauti, A.W. Gaziry, J. de Heinzelin, D.D. Boaz (Eds.), Neogene paleontology and geology of Sahabi, Alan R. Liss, New York, 1987, pp. 153–181.

[13] D. Kovachev, First finds of *Machairodus giganteus* Wagner in the Upper Meotian around the village Hadji Dimovo, Gotze Delchev District (Southwest Bulgaria), Rev. Bulg. Geol. Soc. 63 (2002) 77–88.

[14] B. Kurtén, Fossil Carnivora from the Late Tertiary of Bled Douarah and Cherichira, Tunisia, Notes Serv. géol. Tunisie 42 (1976) 177–214.

[15] F. Lihoreau, Systématique et paléoécologie des Anthracotheriidae (Artiodactyla; Suiformes) du Mio-Pliocène de l'Ancien Monde : implications paléobiogéographiques, PhD thesis, University of Poitiers, France, 2003, 398 p.

[16] A.N. Lungu, The Hipparion fauna of the Middle Sarmatian of Moldavia, Shtiintsa, Kichinev, 1978, 132 p. (in Russian).

[17] R. Lydekker, Indian Tertiary and Post-Tertiary Vertebrata – Siwalik and Narbada Carnivora, Mem. Geol. Surv. India – Palaeontol, Ind. Ser. 10 (2) (1884) 178–355.

[18] L.D. Martin, Felidae, in: C.J. Janis, K.M. Scott, L.L. Jacobs (Eds.), Evolution of Tertiary Mammals of North America, Vol. 1: Terrestrial Carnivores, Ungulates and Ungulatelike Mammals, Cambridge University Press, Cambridge, 1998, pp. 144–151.

[19] L.D. Martin, C.B. Schultz, Scimitar-toothed cats, *Machairodus* and *Nimravides*, from the Pliocene of Kansas and Nebraska, Bull. Univ. Neb. State Mus. 10 (1975) 55–63.

[20] J.C. Merriam, C. Stock, The Felidae of Rancho La Brea, Carnegie Inst., Washington Publ. 422 (1932) 1–231.

[21] M. Morlo, Die Raubtiere (Mammalia, Carnivora) aus dem Turolium von Dorn-Dürkheim 1 (Rheinhessen). Teil 1: Mustelida, Hyaenidae, Percrocutidae, Felidae, Cour. Forsch.-, Inst. Senckenb. 197 (1997) 11–47.

[22] J.A. Orlov, Tertiäre Raubtiere des westlichen Siberiens. I. Machairodontinae, Trav. Inst. Paléozool, Acad. Sci. URSS 5 (1936) 111–152.

[23] M. Pavlow, Mammifères tertiaires de la Nouvelle Russie, N. Mém. Soc. Nat. Moscou 17 (1914) 6–52.

[24] G. Petter, F.C. Howell, *Machairodus africanus* Arambourg, 1970 (Carnivora, Mammalia) du Villafranchien d'Ain Brimba, Tunisie, Bull. Mus. natn. Hist. nat., Paris, 4^{e} sér., section C 1 (1987) 97–119.

[25] G.E. Pilgrim, The fossil Carnivora of India, Mem. Geol. Surv. India – Palaeontol. Ind. (n.s.) 18 (1932) 1–232.

[26] A. Riabinin, Faune de mammifères de Taraklia. I. Carnivora vera, Rodentia, Subungulata, Trav. Mus. géol. Acad. Sci. URSS 5 (1929) 127–134.

[27] S.J. Roussiakis, Musteloids and feloids (Mammalia, Carnivora) from the Late Miocene locality of Pikermi (Attica, Greece), Geobios 35 (2002) 699–719.

[28] N. Schmidt-Kittler, Raubtiere aus dem Jungtertiär Kleinasiens, Palaeontographica Abt. A 155 (1976) 1–131.

[29] M.V. Sotnikova, A new species of *Machairodus* from the Late Miocene Kalmakpai locality in eastern Kazakhstan (USSR), Ann. Zool. Fennici 28 (1992) 361–369.

[30] P. Vignaud, P. Duringer, H.T. Mackaye, A. Likius, C. Blondel, J.-R. Boisserie, L. de Bonis, V. Eisenmann, M.-E. Etienne, D. Geraads, F. Guy, T. Lehmann, F. Lihoreau, N. Lopez-Martinez, C. Mourer-Chauviré, O. Otero, J.-C. Rage, M. Schuster, L. Viriot, A. Zazzo, M. Brunet, Geology and palaeontology of the Upper Miocene Toros-Menalla hominid locality, Chad, Nature 418 (2002) 152–155.

[31] L. Werdelin, Mio-Pliocene Carnivora from Lothagam, Kenya, in: M.G. Leakey, J.M. Harris (Eds.), Lothagam: the Dawn of Humanity in Eastern Africa, Columbia University Press, New York, 2003, pp. 261–328.

[32] L. Werdelin, M.E. Lewis, A revision of the genus *Dinofelis* (Mammalia, Felidae), Zool. J. Linn. Soc. 132 (2001) 147–258.

[33] O. Zdansky, Jungtertiäre Carnivoren Chinas, Palaeontol. Sin. ser. C 2 (1924) 1–149.