



General Palaeontology, Systematics and Evolution (Verebrate Palaeontology)

Civettictis braini nov. sp. (Mammalia: Carnivora), a new viverrid from the hominin-bearing site of Kromdraai (Gauteng, South Africa)



Civettictis braini nov. sp. (Mammalia : Carnivora), un nouveau viverridé du site à Homininés de Kromdraai (Gauteng, South Africa)

Jean-Baptiste Fourvel

UMR5608 TRACES – GDR3591 TaphEnA – Université de Toulouse-Jean Jaurès, 5, Allée Antonio-Machado, 31058 Toulouse cedex 9, France

ARTICLE INFO

Article history:

Received 17 September 2017

Accepted after revision 20 November 2017

Available online 1 February 2018

Handled by Lorenzo Rook

Keywords:

Kromdraai

Plio-Pleistocene

South Africa

Palaeontology

Carnivora

Viverridae

Civettictis braini nov. sp.

Mots clés :

Kromdraai

Plio-Pléistocène

Afrique du Sud

Paléontologie

Carnivora

Viverridae

Civettictis braini nov. sp.

ABSTRACT

A new Plio-Pleistocene viverrid species is described based on two newly discovered maxillae (KW 10141 and KW 10383) from the recent excavations at the hominin-bearing site of Kromdraai (Gauteng, South Africa). This major site allows us to address the conundrum of *Paranthropus* and *Homo* origins in South Africa and presents a highly diverse carnivore spectrum (at least 22 species) including herpestids and viverrids. *Civettictis braini* nov. sp. is a viverrid species comparable in size to the extant African civet *Civettictis civetta* (Schreber, 1776). However *C. braini* nov. sp. differs significantly from the extant species in its dental proportions. Its canine and three premolars (P1–P3) are relatively robust, while its carnassials (P4) and two molars (M1, M2) are extremely reduced. This new species supplements our knowledge on carnivore taxonomic diversity and paleoecology in Southern Africa about 2 millions of years ago.

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RÉSUMÉ

Une nouvelle espèce de viverridé plio-pléistocène est décrite à partir de deux maxillaires (KW 10141 et KW 10383) récemment découverts sur le site à Homininés de Kromdraai (Gauteng, Afrique du Sud). Ce site d'importance nous permet d'aborder la problématique de l'origine des genres *Paranthropus* et *Homo* en Afrique du Sud et présente un spectre de Carnivores très diversifié (au moins 22 espèces), parmi lesquels des Herpestidés et des Viverridés. *Civettictis braini* nov. sp. est un viverridé de taille comparable à la civette africaine *Civettictis civetta* (Schreber, 1776). Cependant, *C. braini* nov. sp. diffère significativement de l'espèce actuelle par ses proportions dentaires. La canine et les trois prémolaires (P1–P3) sont de forte taille et robustes, tandis que la carnassière (P4) et les deux molaires (M1, M2) sont extrêmement réduites. Cette nouvelle espèce complète notre connaissance de la diversité taxinomique des carnivores et de leur paléoécologie en Afrique australe vers 2 millions d'années.

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E-mail address: jbfourvel@yahoo.com

<https://doi.org/10.1016/j.crpv.2017.11.005>

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1. Introduction

The “Cradle of Humankind” (Gauteng, South Africa) is an important UNESCO area where numerous palaeontological sites preserve Pliocene, Plio-Pleistocene and Pleistocene deposits (e.g., Sterkfontein, Swartkrans, Kromdraai, Gondolin, Malapa, Rising Star). The hominin-bearing and Oldowan-tool bearing assemblages from this area are fundamental for our understanding of the origin of the genus *Homo* and its relationships with two of its closely affiliated lineages represented in South Africa, *Australopithecus* sp. and *Paranthropus robustus*.

Hominin remains and bone tools are abundant in the “Cradle of Humankind” sites but other faunal remains (e.g., carnivores, bovids or non-human primates) usually represent more than 90% of the Plio-Pleistocene assemblages. Therefore, these faunal remains provide important clues to reconstruct palaeoenvironmental conditions and to assess the age of these deposits (biochronology).

The carnivores from the “Cradle of Humankind” have been largely studied from the 1950s up to the 1980s (e.g. Ewer, 1954, 1955; Ficarelli et al., 1984; Hendeby, 1973, 1974a; Turner, 1984a, 1984b, 1986), but more recent studies are less abundant and focused mainly on either a few sites or on particular groups of large carnivores (e.g., Cooper’s D in Hartstone-Rose et al., 2010; Drimolen in O’Regan and Menter, 2009; Gladysvale in Mutter et al., 2001; Kuhn et al., 2017; Malapa in Kuhn et al., 2011, 2016; O’Regan et al., 2013; Reynolds, 2012).

Among the “Cradle of Humankind” assemblages, Kromdraai (26°00’41”S, 27°44’60”E) appears as a key site for our knowledge of the palaeoenvironmental conditions prevailing during the Plio-Pleistocene transition. It is an unroofed

dolomite cave partially shaped by the erosional surface and filled with fossil-bearing deposits, situated approximately 2 km east of Sterkfontein Caves, on the southern side of the Blaauwbank stream. It yielded the type specimen of *Paranthropus robustus*, TM 1517, the only partial skeleton of this species known thus far (Broom, 1938a,b, 1942, 1943), and more than 50 other individuals attributed to either *Homo* or *Paranthropus* (Braga and Thackeray, 2003, 2016; Braga et al., 2017), some representatives of this latter genus appearing more primitive than their congeners from Swartkrans (Braga et al., 2013).

The Kromdraai carnivores have been largely studied (e.g., Brain, 1981; Ewer, 1954, 1955, 1956a,b,c; Hendeby, 1973; Turner, 1984a,b; Turner, 1986; Vrba, 1981) and data highlight the high richness and specific diversity of the bone accumulations from this site. Five different families (Felidae, Canidae, Hyaenidae, Herpestidae, Viverridae), 18 genera and a minimum of 22 species have been recognized (for details see Fourvel et al., 2016). The first record of carnivores from the previously called “Kromdraai B” locality (see details in Braga et al., 2017) comes in Hendeby (1973) and was excavated by Brain from decalcified deposits in 1955–1956 (Brain, 1958). This list is subsequently used in Brain (1975) and Brain (1981) with some minor amendments. The second stage of publications comes from Vrba’s excavations and the carnivore material briefly presented and discussed in Vrba (1981). Subsequently, single specimens in one time studies, but no review on the Kromdraai carnivore fauna has been published. There is now a necessity to take into account the very rich and interesting carnivore material uncovered at Kromdraai since 2014 (mainly from the oldest Member 2 – or Member P – breccias) (see Braga and Thackeray, 2016; Braga et al., 2017 for

Table 1
Kromdraai carnivore list from the recent excavations (since 2014).

Tableau 1
Liste des Carnivores de Kromdraai Membre 2 mis au jour lors des fouilles récentes (depuis 2014).

Family	Sub-family	Genus	Species
Felidae	Machairodontinae	<i>Dinofelis</i>	<i>Dinofelis</i> cf. <i>barlowi</i>
	Machairodontinae	<i>Megantereon</i>	<i>Megantereon whitei</i>
	Pantherinae	<i>Panthera</i>	cf. <i>Panthera leo</i>
	Pantherinae	<i>Panthera</i>	<i>Panthera pardus</i>
	Felinae	<i>Caracal</i>	<i>Caracal caracal</i>
Canidae	Felinae	<i>Leptailurus</i>	<i>Leptailurus serval</i>
	Caninae	<i>Lycaon</i>	cf. <i>Lycaon</i> sp.
	Caninae	<i>Canis</i>	<i>Canis</i> sp.
	Caninae	<i>Canis</i>	<i>Canis mesomelas</i>
	Caninae	<i>Vulpes</i>	<i>Vulpes chama</i>
Hyaenidae	Otocyoninae	<i>Prototocyon</i>	<i>Prototocyon</i> cf. <i>recki</i>
	Hyaeninae	<i>Crocuta</i>	cf. <i>Crocuta</i>
	Hyaeninae	<i>Parahyaena</i>	<i>Parahyaena brunnea</i>
Mustelidae	Hyaeninae	<i>Hyaena</i>	<i>Hyaena hyaena</i>
	Protelinae	<i>Proteles</i>	<i>Proteles</i> cf. <i>amplidentus</i>
	Mustelinae	<i>Mellivora</i>	cf. <i>Mellivora capensis</i>
Herpestidae	Mustelinae	<i>Prepoecilogale</i>	<i>Prepoecilogale bolti</i>
	Lutrinae	<i>Aonyx</i>	<i>Aonyx capensis</i>
	Herpestinae	<i>Suricata</i>	<i>Suricata suricatta</i>
Viverridae	Herpestinae	<i>Cynictis/Galerella</i>	<i>Cynictis</i> sp./ <i>Galerella</i> sp.
	Herpestinae	<i>Herpestes</i>	<i>Herpestes</i> sp.
	Viverrinae	<i>Civettictis</i>	<i>Civettictis</i> cf. <i>civetta</i>
	Viverrinae	<i>Civettictis</i>	<i>Civettictis braini</i> nov. sp.
	Viverrinae	<i>Genetta</i>	cf. <i>Genetta</i>

Table 2

Herpestid and viverrid comparative datasets, labels, curation and references.

Tableau 2

Liste des échantillons de comparaison d'herpestidés et de viverridés. Numéro d'inventaire, Institution et Référence.

Species	Label	Site	Curation	Reference
<i>Civettictis civetta</i>	AZ 731, AZ 333, AZ 2441, AZ 1164, AZ 1729, AZ 2442, AZ 599, AZ 1190, AZ 730	(Extant)	Ditsong Museum	Fourvel, unpublished
<i>Atilax paludinosus</i>	AZ 1025, AZ 1938	(Extant)	Ditsong Museum	Fourvel, unpublished
<i>Suricata suricatta</i>	AZ 2214, AZ 614, AZ 2285	(Extant)	Ditsong Museum	Fourvel, unpublished
<i>Suricata major</i>	8669, 6873, 6893, 16558	Elandsfontein		Hendey, 1974b
<i>Cynictis penicillata</i>	BPI/C 312, BPI/C 310, BPI/C 314, AZ 1961, AZ 2342, AZ 527,	(Extant)	Ditsong Museum / ESI Wits	Fourvel, unpublished
<i>Galerella sanguinea</i>	AZ 743, AZ 1960, AZ 742, AZ 744, AZ 408, AZ 3323, AZ 2286, AZ 745	(Extant)	Ditsong Museum	Fourvel, unpublished
<i>Atilax mesotes</i>	KA 86	Kromdraai A	Ditsong Museum	Ewer, 1956c; Fourvel, unpublished
<i>Herpestes ichneumon</i>		(Extant)		Petter, 1963, 1987
<i>Mungos mungos</i>		(Extant)		Petter, 1963, 1987
<i>Mungos dietrichi</i>	L.3741, no number	Laetoli / Olduvai		Petter, 1963, 1987
<i>Pseudocivetta ingens</i>	no number	Olduvai		Petter, 1967
<i>Viverra leakeyi</i>	L. 12836, L. 13907, L.20253, L.16240A, L.16224, L.62240 C, L.15174 LIT 59/466	Langebaanweg Laetoli		Hendey, 1974b Petter, 1987

more details) because it is absent from the most recent review of the African Carnivora (Werdelin and Peigné, 2010).

New excavations initiated in 2014 indicate that the Kromdraai site extends more than 30 m towards the north. During the 2014/2017 period, the Kromdraai Research Project successive field seasons (Braga and Thackeray, 2016; Braga et al., 2017) led by JB and more occasionally in 2016 and 2017 by the author, have produced over 4600 faunal remains (including hominins) derived mainly from Member 2 (or Member P), an assemblage highlighting a high species diversity covering a wide faunal spectrum including birds, mammals and reptiles (Braga and Thackeray, 2016; Fourvel et al., 2016). Within that new sample, 459 specimens are related to carnivores (including coprolites) including 6 families, 22 genera and possibly up to 24 species (Fourvel et al., 2016; Table 1). These newly discovered specimens are curated at the Evolutionary Studies Institute of the University of Witwatersrand in Johannesburg.

Part of this important carnivore sample is related to the small herpestids and viverrids, two groups that are rarely studied in details with the exception of Petter (1963, 1987) for eastern Africa and Hendey (1974b) for southern Africa. Four genera of relatively rare viverrids and herpestids were previously identified (*Crossarchus*, *Atilax* at “Kromdraai A”, *Herpestes*, *Viverra* at “Kromdraai B”, the latter now related to *Mellivora*; Gommery et al., 2008) including two species (*Crossarchus transvaalensis* and *Atilax mesotes*). The newly discovered (since 2014) Kromdraai herpestids and viverrids sample comprises nearly 40 specimens that represent at least 6 genera, including recently two portions of maxilla (KW 10141 and KW 10383) likely related to the genus *Civettictis* Pocock, 1915 but significantly different from

the extant African civet *Civettictis civetta* (Schreber, 1776). Consequently, here I describe a new species according to the fossil specimens KW 10141 and KW 10383.

2. Sample and methods

I describe two portions of maxilla (KW 10141 and KW 10383) from the recent excavations (dir. J. Braga and F. Thackeray; discovered respectively in May and September 2017) and then compare it to extant and extinct species in order to discuss their affinities with some particular species, and to distinguish their specific features. The KW 10141 and KW 10383 specimens are compared to small canids: the black-backed jackal *Canis mesomelas* Schreber, 1775 and the bat-eared fox *Otocyon megalotis* (Desmaret, 1822). For comparative purposes, I also use morphological and metrical data from a large sample of skulls representing the African civet *C. civetta* and various herpestids including the marsh mongoose *Atilax paludinosus* Cuvier, 1829, the slender mongoose *Galerella sanguinea* Rüppell, 1836, the yellow mongoose *Cynictis penicillata* Cuvier, 1829 and the meerkat *Suricata suricatta* (Schreber, 1776) (all specimens curated at the Ditsong National Museum in Pretoria and the Evolutionary Studies Institute of the University of Witwatersrand in Johannesburg; Table 2). The comparative fossil sample is composed of some South African extinct species including *Atilax mesotes* (Ewer, 1956c) from “Kromdraai A”, and *Civettictis* cf. *civetta* from Cooper’s D (O’Regan et al., 2013) as well as published data on *Viverra leakeyi* Petter, 1963 from Langebaanweg (Hendey, 1974b) and eastern African species, including *Mungos dietrichi* Petter, 1963, *V. leakeyi* and *Pseudocivetta ingens* Petter, 1967 from Olduvai and Laetoli (described by Petter, 1963, 1967, 1969, 1987).

The measurement protocol follows [Von Den Driesch \(1976\)](#). The measurements that I considered as relevant for this study and the results are expressed in millimetres.

3. Abbreviations list:

C	Canine
for. infra orb.	Infra-orbital foramen
I	Incisor
L	Length
M	Molar
P	Premolar
R. tth	Raw teeth
W	Width
1 to 4	Tooth rank

4. Results

Order Carnivora Bowdich, 1821
 Sub-order Feliformia Kretzoi, 1945
 Family Viverridae Gray, 1821
 Sub-family Viverrinae Gray, 1821
 Genus *Civettictis* Pocock, 1915
Civettictis braini nov. sp.

4.1. Etymology

In honor of C. K. “Bob” Brain who contributed significantly for our understanding of ancient hominins’ behaviour in the “Cradle of Humankind” (including Kromdraai, Swartkrans and Sterkfontein) and hominin-carnivore interactions according to his invaluable work in the field of taphonomy.

4.2. Type specimen

Almost complete maxilla (KW 10141), including the complete left one and posterior part of the right one, as well as the left zygoma. Presence of C, P2, M1 and M2 as well as alveoli of I1 to I3, P1, P3, P4.

4.3. Paratype

Fragment of right edentate maxilla (KW 10383). Presence of alveoli of C, P1, P2, P3, P4 and M1.

4.4. Type locality

Kromdraai Member 2 (or Member P), Gauteng, South Africa (estimated age, Plio-Pleistocene Transition, early Pleistocene).

4.5. Diagnosis

Civettictis braini is a large-sized viverrid comparable in size to the extant African civet *C. civetta*, but differing from the latter in the extreme reduction of the P4 and the upper molars. *Civettictis braini* has a square-shaped rostrum and an elongated palate. The dental formula includes 3I, 1C, 4P,

2M with large diastema between the canine, the P1 and the P2. The canine and the P2 are well-developed and robust. The same comment applies to the P1 even though if only its alveolus is preserved. The P3 is double rooted (according to its alveoli). Its posterior root is located between the protocone and the parastyle of the P4.

4.6. Description

The specimen KW 10141 was found fragmented (post-depositional fragmentation) and was restored. KW 10141 is a partial rostrum composed of two distinct fragments belonging to the same individual. The first and smaller fragment of KW 10141 is a right maxilla preserving the alveoli of P4. The alveoli of the M1 and the M2 are preserved even though they are partially altered in the M2. The second and larger fragment is the almost complete left maxilla with the zygomatic arch (including a large portion of the zygomatic process of the temporal bone), the right premaxilla with the alveoli of the incisors as well as the anterior part of the right maxilla (up to the canine alveolus) ([Fig. 1](#)). The left canine, the left P2, the left protocone of the P4 as well as the M1 and M2 are still present.

KW 10141 belongs to an old individual. In viverrids, the M1 and the P4 erupt before the other raw teeth ([Slaughter et al., 1974](#)). This suggests that the DP3 and the DP4 (which are replaced by the M1 and the P4) are expelled before the eruption of the P2, P3 and M2. KW 10141 has alveoli for four premolars and two molars. This is consistent only with an adult individual. Moreover the permanent canine of KW 10141 is heavily worn.

The edentate paratype KW 10383 shows the same features (the alveoli are preserved for C, P1, P2, P3, P4 and M1) and represents at least a young adult ([Fig. 2](#)).

KW 10141 belongs to a viverrid with a long and wide rostrum, with metrics clearly comparable to the extant African civet *C. civetta* or even more robust ([Table 3](#)). KW 10383 is slightly smaller than KW 10141 but reflects the size variation in *C. braini*. In spite of an approximate measure of the palate length of KW 10141, the rostrum appears long and ends clearly behind the M2. The infra-orbital foramen (preserved on the left maxilla of KW 10141 and on KW 10383) is large and oval-shaped, located below the orbit at the basis of the zygomatic arch. This feature is typical of a viverrid and clearly different from a canid one (see below). The zygomatic arch is high and robust. It is well-developed suggesting an opened orbit and a marked zygomatic muscle attachment.

According to the preserved teeth and the alveoli on both specimens, the upper dentition could be described as follow: 3I, 1C, 4P, 2M. The canine and the P1 are separated by an important diastema (4.3 mm length). A similar diastema is observed between the P1 and the P2 (6.8 mm length) as well as between the P2 and the P3 (3.5 mm length). The location of the alveolus of the posterior root of the P3 between the alveoli of the parastyle and the protocone of the P4 suggests that the P3 flanked the P4. This comment applies on both KW 10141 and KW 10383. No diastema has been observed between the P4 and the molars M1 and M2.

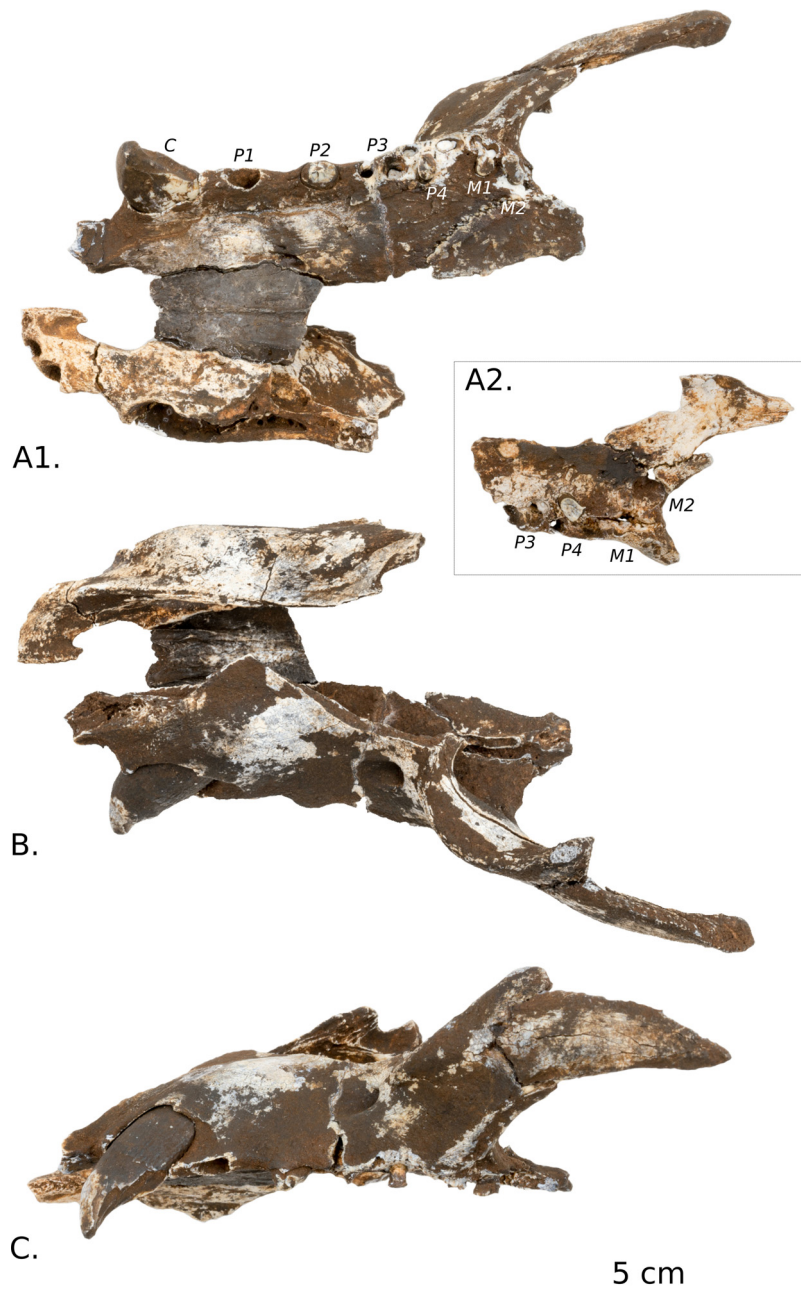


Fig. 1. *Civettictis braini* nov. sp. (KW 10141) maxilla. A1, Palate view; A2, palate view of right maxilla (note that the M1 and M2 alveoli are partially altered); B, upper view; C, lateral view. Scale: 50 mm.

Fig. 1. Maxillaire (KW 10141) de *Civettictis braini* nov. sp. A1, Vue palatine ; A2, vue palatine du fragment de maxillaire droit (notons que les alvéoles des M1 et M2 sont partiellement altérés) ; B, vue supérieure ; C, vue latérale. Échelle : 50 mm.

Photo. R. Hautefort.

The upper canine has an elongated and transversally compressed crown (its length is almost twice its width). In spite of the heavy wear of this tooth, the crown was relatively high. On the lingual surface of the canine and at its crown basis, there is a light groove forming a gutter that extends all along the root. The imprint of this gutter is observed on the canine alveoli (both left and right).

The P1 is missing. However the morphology of the alveoli allows some measurements on both KW 10141 and KW 10383 (W and L; Table 3). The P1 alveolus is oval-shaped and indicates a tooth with a single robust and large root, like in the P2 (see below).

The P2 is preserved on KW 10141. This tooth is an oval-shaped premolar with a partially fused double root. The tooth wear stage is too heavy to allow any detailed

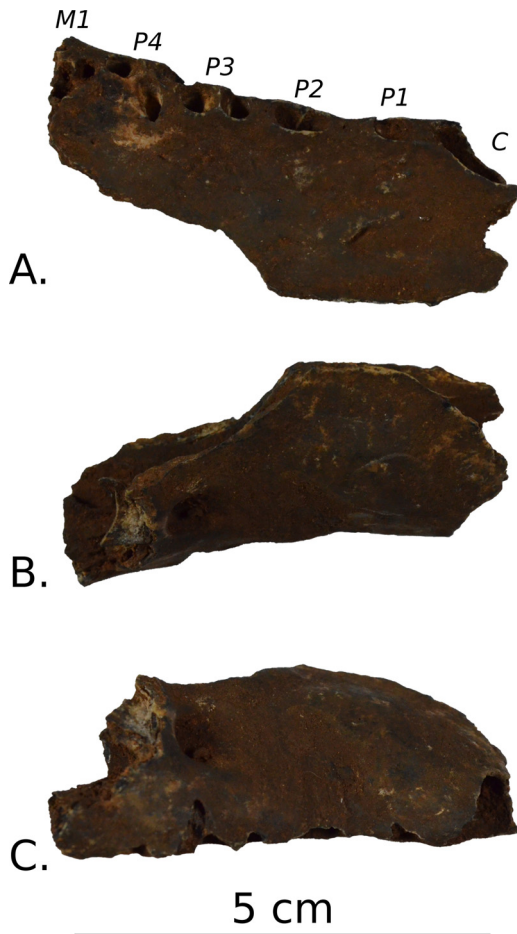


Fig. 2. *Civettictis braini* nov. sp. (KW 10383) maxilla. A, Palate view; B, upper view; C, lateral view. Scale: 50 mm.

Fig. 2. Maxillaire (KW 10383) de *Civettictis braini* nov. sp. A, Vue palatine ; B, vue supérieure ; C, vue latérale. Échelle : 50 mm.

Photo. B. Lans.

description of the crown. The alveolus of the P2 on KW 10383 attests that this tooth is characterized by a partially fused double root.

The P3 is missing on both KW 10141 and KW 10383. However the alveoli are preserved. The morphology of the alveoli indicates a long tooth (longer than wider) with a double root, one supporting the anterior lobe and another below the posterior lobe. As previously described, the P3 is located against the P4. The posterior lobe of the P3 is placed between the parastyle and the protocone of the P4.

A part of the protocone of the left and right P4 of KW 10141 is preserved. On KW 10383 only the alveoli of the P4 are preserved. According to the P4 alveoli, this tooth seems highly reduced, slightly longer than its width. However, the preserved portion of the P4 highlights the protocone position. This cusp is clearly dissociated from the rest of the tooth. The protocone is developed from the paracone and distally-oriented up to the same level than the parastyle.

The molars M1 and M2 are preserved. However the heavy wear stage does not allow any description of their occlusal surface. The M1 and M2 are globally triangular-

shaped teeth. Their widths are almost twice their length. However the molars are extremely reduced compared to the general size of the maxilla.

5. Comparison

KW 10141 is clearly different from the small canids. The maxilla in the black-backed jackal and the bat-eared fox is very wide at the level of the carnassial teeth and reduces progressively up to the canines and the third incisors. In KW 10141, the palate width between the canines (43.9 mm) is almost similar to the palate width between the P1 (43.7 mm) and the palate width between the P2 (46.1 mm).

In canids (*C. mesomelas*, *V. chama* and *O. megalotis*) the infra-orbital foramen is located above the P3 about 1 cm away from the inferior part of the orbit. In KW 10141 and KW 10383, the infra-orbital foramen is located above the P4 below the orbit.

The P2 of KW 10141 is less sharp and more conical than in the extant small canids.

In canids, the diastema between each raw tooth are shorter, the P2 has two separate roots and the molars are well-developed (two in *Canis* and *Vulpes* and three in *Otocyon*) compared to the Kromdraai specimens.

The palate in KW 10141 ends clearly behind the M2; this feature is typical of viverrids and herpestids. While in canids, the palate ends at the level of the M2.

KW 10141 differs from the herpestids. The water mongoose *A. paludinosus* has a short rostrum, the P2 is double-rooted, the P3 is wide and robust and the P4 is well-developed. In *A. paludinosus* the M1 and the M2 are triangular-shaped and are proportionally well-developed compared to the other raw teeth. The relative proportions of the P4 and the molars in *C. penicillata*, *S. suricatta* and *G. sanguinea* attest of their high crushing capacities even if these species are smaller than the Kromdraai specimens.

In the fossil context, the species that could be compared to KW 10141 and KW 10383 are rare: *A. mesotes* from “Kromdraai A”, *V. leakeyi* from Langebaanweg and *P. ingens* Laetoli, and *Civettictis* cf. *civetta* from Coopers’ D.

Ewer (1956c) described a new herpestid, *Herpestes mesotes*, from “Kromdraai A” based on an almost complete skull associated with mandibles as well as some post-cranial remains (specimen labelled KA 86). Firstly related to the genus *Herpestes*, this species has been recently referred to the genus *Atilax* (Werdelin and Peigné, 2010). *A. mesotes* from “Kromdraai A” is almost similar to the water mongoose *A. paludinosus* (for details see Ewer, 1956c). The morphological features recognized on KA 86 differ significantly from KW 10141 and KW 10383 excluding any affinities between these newly discovered specimens and *A. mesotes* (Fig. 3).

Petter (1963) described the first African fossil related to the Asian genus *Viverra*. *V. leakeyi* has been firstly identified in Laetoli (Tanzania). It is a large-sized viverrid sharing clear affinities with the Asian species (Petter, 1963). This extinct species is uncommon, even if its geographical range is wide. *V. leakeyi* has been recognized in southern Africa (Langebaanweg in Hendey, 1974b) as well as in eastern Africa (Petter, 1963, 1969, 1987), up to Morocco (Geraads, 2008). Few fossil specimens have been attributed to this

Table 3

Measurements of KW 10141 and KW 10383, maxilla fragments from Kromdraai Member 2 as well as comparative datasets (minimum–maximum, mean) of extant species *C. civetta* ($n = 9$), *A. paludinosus* ($n = 2$), *S. suricatta* ($n = 3$), *C. penicillata* ($n = 6$) and *G. sanguinea* ($n = 8$).

Tableau 3

Mesures des portions de maxillaire KW 10141 et KW 10383 de Kromdraai membre 2 et données de comparaison (minimum–maximum, moyenne) d'espèces actuelles : *Civettictis civetta* ($n = 9$), *Atilax paludinosus* ($n = 2$), *Suricata suricatta* ($n = 3$), *Cynictis penicillata* ($n = 6$) et *Gallerella sanguinea* ($n = 8$).

	<i>Civettictis braini</i>		<i>Civettictis civetta</i>		<i>Atilax paludinosus</i>		<i>Suricata suricatta</i>		<i>Cynictis penicillata</i>		<i>Gallerella sanguinea</i>	
	KW 10141	KW 10383	Min–max	Mean	Min–max	Mean	Min–max	Mean	Min–max	Mean	Min–max	Mean
W I3–I3	26.6		18.9–21.7	20.1	13.1–13.6	13.4	8.2–9.4	8.6	6.6–8.8	7.8	6.7–8.0	7.1
W. C–C	43.9		27.9–32.8	30.1	25.6–26.4	26.0	13.3–16.3	14.9	13.5–16.2	14.4	10.4–14.8	12.0
W for infra orb	40.2		33.0–36.7	34.9	26.1–26.5	26.3	13.2–16.8	15.4	15.6–18.2	16.8	12.7–17.7	13.9
L Cant–M2	63.7		55.1–61.9	59.0	38.1–38.8	38.5	22.2–24.4	23.0	23.3–26.7	25.4	20.8–25.4	22.8
L raw tth	48.1		47.5–52.0	49.7	29.2–31.1	29.9	16.5–19.1	17.4	19.9–22.1	21.1	17.0–21.0	18.7
L P	38.2	34.3	34.8–38.5	37.0	22.8–25.4	23.9	11.0–12.3	11.8	15.8–17.9	17.1	13.7–17.0	15.6
L M	8.0		13.8–18.3	15.8	9.3–11.5	10.2	6.0–6.8	6.3	4.9–6.5	5.7	3.6–5.5	4.6
L Palate	98.0 ^a		75.7–87.1	81.5	54.4–59.1	56.9	34.7–37.4	36.3	33.1–39.3	35.9	28.2–34.9	32.1
C W	6.9		5.0–5.5	5.2	4.7–5.2	4.9	2.1–2.8	2.6	2.3–2.8	2.5	1.6–2.6	2.0
C L	11.9		6.2–7.5	6.6	6.3–6.9	6.6	3.5–4.0	3.7	3.1–4.3	3.6	2.5–3.7	3.0
P1W	4.4 ^b	3.2 ^b	2.8–3.5	3.1	N/A	N/A	N/A	N/A	1.3–1.6	1.5	1.1–1.6	1.3
P1 L	6.0 ^b	4.8 ^b	3.8–4.8	4.2	N/A	N/A	N/A	N/A	1.3–1.6	1.4	1.3–2.1	1.6
P2W	4.5	3.6 ^b	4.1–4.8	4.4	3.7–4.4	4.0	1.7–2.3	2.0	1.9–2.5	2.1	1.6–2.3	1.8
P2 L	5.9	6.1 ^b	6.8–8.2	7.5	3.7–5.8	5.1	2.8–3.5	3.2	3.8–5.0	4.1	3.2–4.2	3.7
P3W	4.6 ^b	3.5 ^b	4.7–6.2	5.8	5.8–6.1	6.0	3.2–3.4	3.3	2.9–4.0	3.4	2.2–3.2	2.7
P3 L	8.2 ^b	7.9 ^b	7.4–9.7	8.5	7.2–7.3	7.3	2.3–4.1	3.5	3.9–5.0	4.3	3.5–4.4	3.9
P4W	7.2 ^b	6.3 ^b	9.1–11.5	10.2	8.0–8.3	8.2	4.9–6.5	5.7	5.1–5.5	5.3	3.7–5.3	4.4
P4 L	10.4 ^b	8.9 ^b	11.6–14.0	12.9	9.4–10.3	9.9	3.9–4.7	4.3	5.4–6.3	6.0	5.7–7.0	6.4
M1W	7.2	5.3 ^b	11.3–14.4	13.3	9.2–11.4	10.0	5.7–6.5	6.0	5.8–7.3	6.7	6.2–7.3	6.4
M1 L	4.6	4.5 ^b	8.9–10.8	9.7	6.4–8.0	7.3	3.4–3.6	3.5	3.0–3.8	3.4	2.6–3.6	3.1
M2W	5.3		8.7–10.2	8.9	N/A	N/A	4.1–4.9	4.5	4.2–5.3	4.8	2.7–4.5	3.5
M2 L	2.9		6.2–6.8	6.4	N/A	N/A	2.0–2.4	2.2	1.8–3.1	2.4	1.3–1.8	1.5

Measurements in mm.

^a Estimated measurement.

^b Alveolar measurement.

species and most of them are fragmentary. According to the dental morphology and the partially complete skull from Langebaanweg labelled LQ–L.51590 figured by [Werdelin and Peigné \(2010\)](#), KW 10141 is clearly different from *V. leakeyi*. In spite of the important diastema between C, P1, P2 and P3, the rostrum in *V. leakeyi* is transversally compressed and the carnassials and the molars are clearly larger than in KW 10141 and KW 10383. The canine L 12863 described by [Hendey \(1984\)](#) differs from KW 10141 by the presence of light grooves on both lingual and buccal surfaces. The P2 and the P3 are similar in *V. leakeyi* from Langebaanweg ([Hendey, 1974](#)). These premolars are elongated and double-rooted. In KW 10141 and KW 10383, the P2 and the P3 appear different according to their alveoli (partially fused double root in the P2, double root in the P3). The P4 from Langebaanweg (L 12863, L 20253 and L 16224) are significantly larger than KW 10141 and KW 10383 ([Hendey, 1974](#): Table 11, p.77; [Fig. 4](#)). The same comment applies for the M1 and the M2. The Langebaanweg specimens are larger than the Kromdraai specimens.

P. ingens has been defined by [Petter \(1967\)](#) in Olduvai Bed I (Tanzania). This species is significantly larger than the extant *C. civetta* and is characterized by square-shaped molars and bunodont teeth ([Petter, 1969](#)). KW10141 and KW 10383 have reduced molars (smaller than in the extant *C. civetta*) and the M1s are triangular-shaped. Thanks to these features, the Kromdraai specimens could not be referred to *P. ingens*.

Fossil relatives of *C. civetta* in palaeontological sites of southern Africa are extremely rare. Actually, *C. civetta* has

been identified in only two early Quaternary bone assemblages from the Cradle of Humankind: Cooper's D ([O'Regan et al., 2013](#)) and Kromdraai ([Fourvel et al., 2016](#)). The upper carnassial belonging to *C. cf. civetta* from Cooper's D is too large to be considered as similar to KW 10141 and KW 10383.

Even if there are evidence of morphological and metric differences between the Kromdraai specimens (KW 10141 and KW 10383) and the African civet *C. civetta*, the Kromdraai specimens share affinities with the viverrids and particularly the genus *Civettictis* ([Fig. 3](#)). The rostrum in *C. civetta* is relatively elongated and has sub-parallel margins from the canines up to the anterior part of the P3. The infra-orbital foramen in *C. civetta* is located below the orbit at the basis of the zygomatic arch just above the P3. The zygomatic arch is less high in *C. civetta* than in KW 10141. The frontal process of the arch is also less developed in the extant species. In *C. civetta* the palate ends about a centimetre behind the M2 like in the Kromdraai specimens. In *C. civetta*, there are diastema between the C and the P1, the P1 and the P2 as well as between the P2 and the P3 like in KW 10141 and KW 10383. However each diastema is clearly shorter in the extant species than in the Kromdraai specimens. The P3 location according to the P4 is similar in *C. civetta* than in KW 10141 and KW 10383. However the P2 in the extant species is a double-rooted tooth while the P3 could have up to three roots. The P4 and the molars are well developed in *C. civetta* while those teeth are very small in KW 10141 and KW 10383.

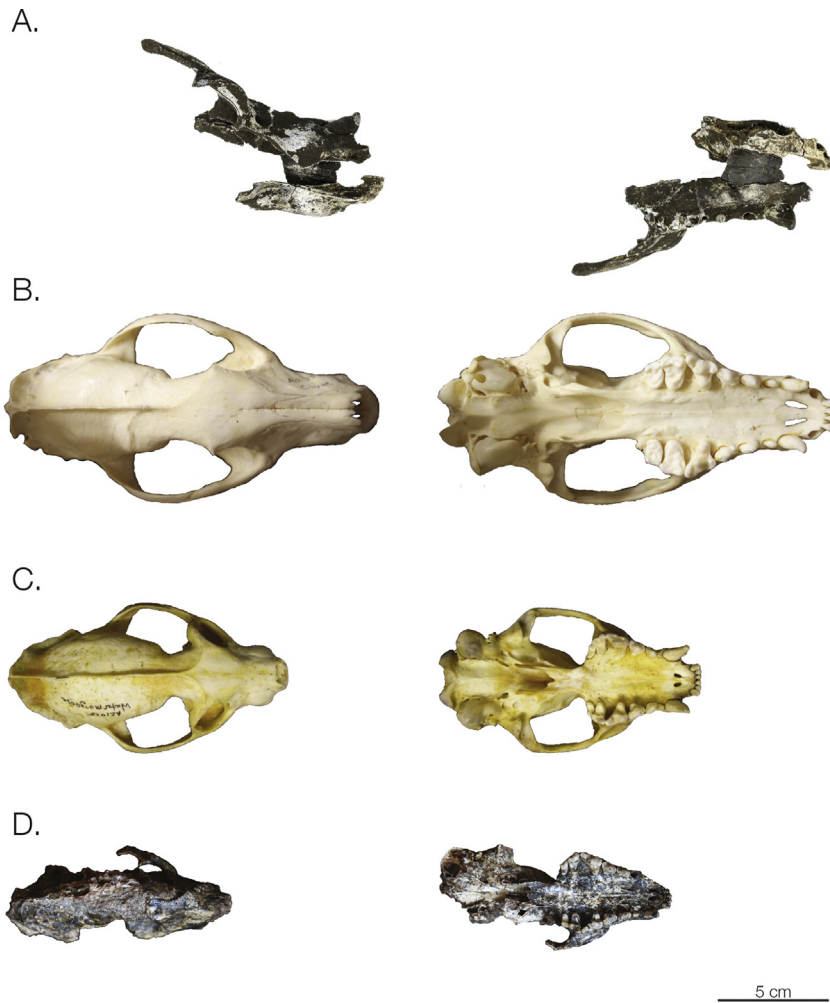


Fig. 3. Comparative plate of viverrid and herpestid skulls, upper and lower view. A, *Civettictis braini* nov. sp. (KW 10141); B, *Civettictis civetta* (AZ 333); C, *Atilax paludinosus* (AZ 1025); D, *Atilax mesotes* (KA 86). Scale: 50 mm.

Fig. 3. Comparaison de quelques crânes de viverridés et d'herpestidés. Vues supérieures et inférieures. A, *Civettictis braini* nov. sp. (KW 10141); B, *Civettictis civetta* (AZ 333); C, *Atilax paludinosus* (AZ 1025); D, *Atilax mesotes* (KA 86). Échelle : 50 mm.

Photo. J.-B. Fourvel et R. Hautefort.

According to the metrics, KW 10141 and KW 10383 seem to share more affinities with the genus *Civettictis* than any other viverrids (Table 3, Figs. 4 and 5). The width between the I3 as well as between the canines are slightly more important than in *C. civetta*. The same comment applies to the width between the infra-orbital foramen. The palatal length, the length from the anterior margin of the canine up to the posterior margin of the M2, the raw teeth length as well as the length of the premolars (P1 to P4), are nearly similar to the large-sized *C. civetta*. However the length of the molars (M1 and M2) is extremely reduced and almost similar to the genus *Atilax* (*A. paludinosus* and *A. mesotes*).

According to the metrical analysis, the teeth are the most distinctive element. The canine is a well-developed tooth, which is significantly larger (longer and wider) than the largest *C. civetta* as well as the extinct large-sized species *V. leakeyi* (Fig. 4). The P1 in KW 10141 is a very large

tooth which is significantly larger than the African civet *C. civetta* and the large-sized *V. leakeyi*. In KW 10383, the P1 is similar the largest *C. civetta*. The P2 is more reduced than the P1 in KW 10141 and KW 10383. The P2 of both specimens are included in the size variation range of the extant African civet *C. civetta* even if they are less elongated. The P2 are slightly larger than the P2 belonging to *Atilax* (both *A. mesotes* and *A. paludinosus*). In spite of alveolar measurements, the P3 in KW 10141 and KW 10383 are metrically similar to a small-sized civet (even smaller in the case of KW 10383). The P4 in KW 10141 and KW 10383 are of a very small size. The P4 are significantly smaller than the size variation range observed in the extant African civet *C. civetta* and nearly similar in size than the carnassials in *Atilax*. The raw teeth reduction in the Kromdraai specimens becomes intensified with the M1 in which the measurements are similar to the large-sized meerkat *S. major* as described by Hendey (1974b). Like in the M1, the M2 is also

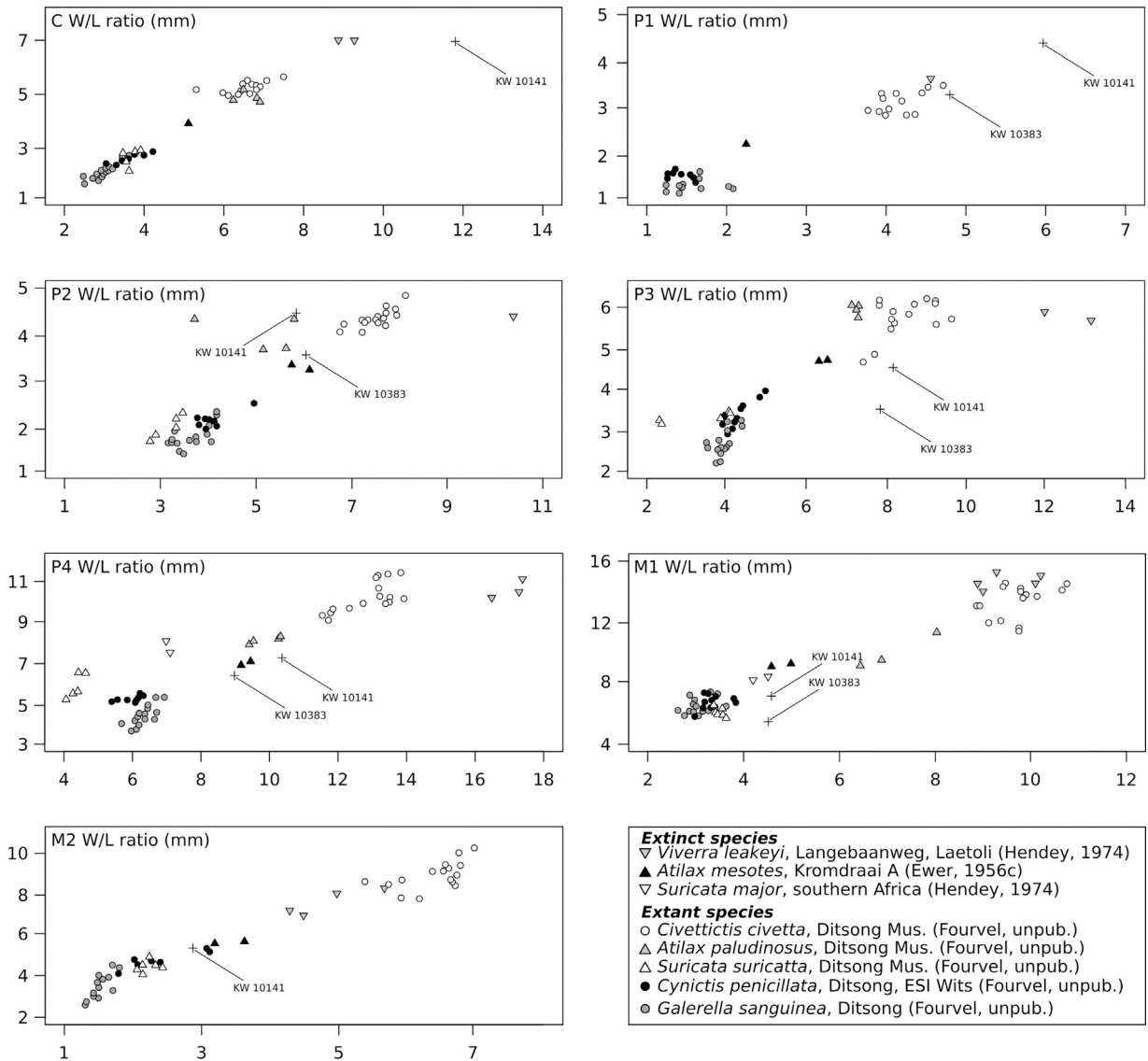


Fig. 4. Bivariate plot (width/length ratio) of the raw teeth (C, P1, P2, P3, P4, M1 and M2).

Fig. 4. Diagramme bvarié (rapport longueur/largeur) des dents supérieures (C, P1, P2, P3, P4, M1 et M2).

very small. The metrics of the M2 are included in *A. mesotes* variation range as well as in the meerkat *S. suricatta*.

Consequently, the identification of KW 10141 and KW 10383 to the new species *Civettictis braini* can be summarized as follows:

- the Kromdraai specimens share affinities with the large-sized viverrids according to the dental formula composed of 3I, 1C, 4P, 2M as well as the rostrum morphology and the palate elongation;
- the morphological features and the metrics of KW 10141 and KW 10383 are more similar to the genus *Civettictis* than any other viverrids;
- the identification of the Kromdraai specimens as a new civet species *Civettictis braini* is based on the metric dif-

ferences in the teeth proportions (highly reduced P4 and molars) with the African civet *C. civetta*.

6. Biochronology

We should report here the unusual wealth of the Plio-Pleistocene site of Kromdraai. Since 2014, more than 400 carnivore bone and dental remains have been collected, including about 8% of small specimens (NISP=38) attributed to herpestids and viverrids. The new species *Civettictis braini* presented in this paper has been found within the Member 2 (or Member P) at Kromdraai, in association with other carnivore species that support a Plio-Pleistocene transition/early Pleistocene age, including the false dirk-toothed cat *Dinofelis barlowi*, the extinct

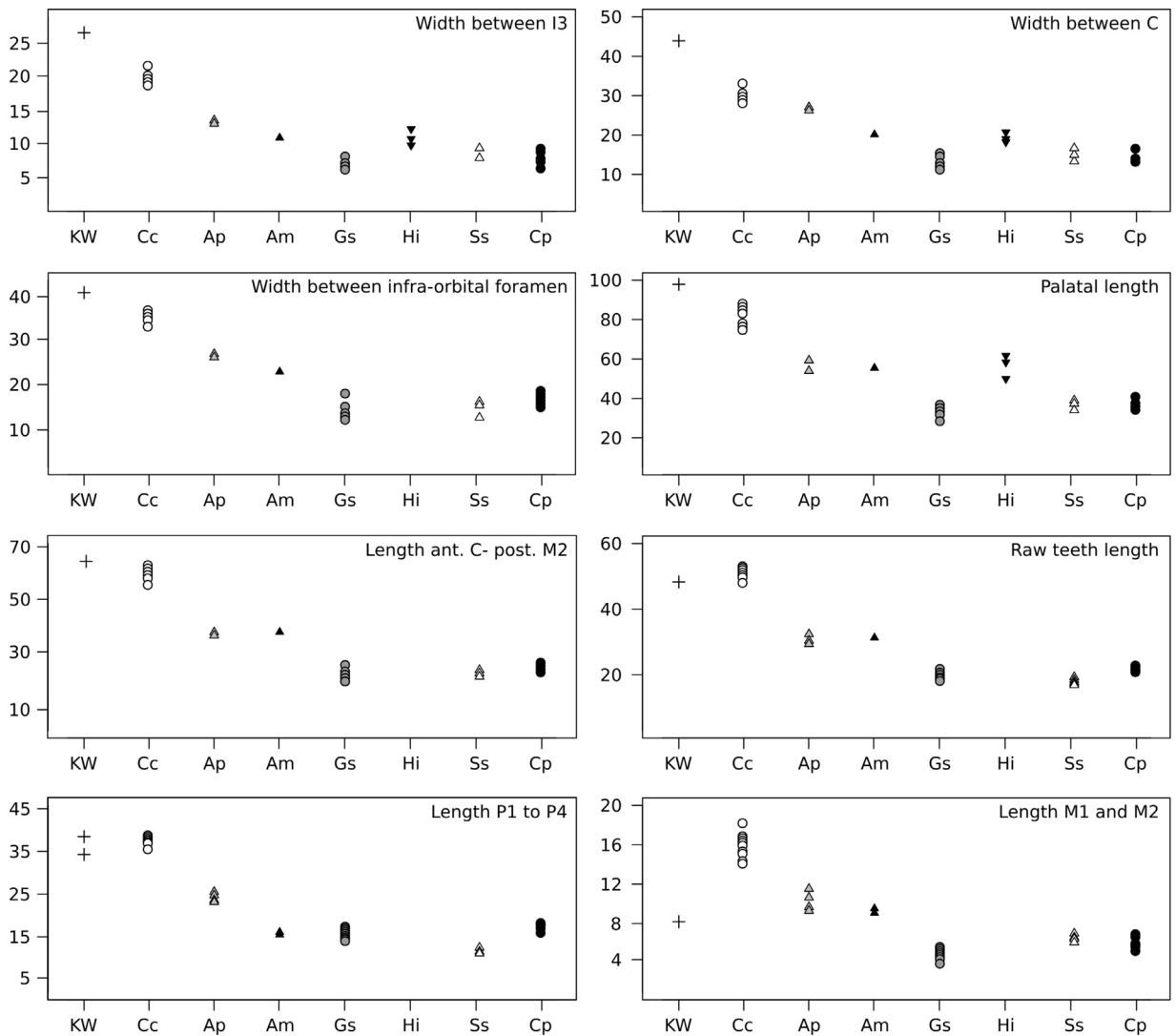


Fig. 5. Univariate plot of some skull measurements. Cross, KW: *Civettictis braini* nov. sp.; Open circle, Cc: *Civettictis civetta*; grey triangle, Ap: *Atilax paludinosus*; solid triangle, Am: *Atilax mesotes*; grey circle, Gs: *Gallerela sanguinea*; solid reverse triangle, Hi: *Herpestes ichneumon*; open triangle, Ss: *Suricata suricatta*; solid circle, Cp: *Cynictis penicillata*.

Fig. 5. Diagramme univarié de mesures crâniennes. Croix, KW : *Civettictis braini* nov. sp., Cercle blanc, Cc : *Civettictis civetta* ; Triangle gris, Ap : *Atilax paludinosus* ; Triangle noir, Am : *Atilax mesotes* ; Cercle gris, Gs : *Gallerela sanguinea*, Triangle noir inversé, Hi : *Herpestes ichneumon* ; Triangle blanc, Ss : *Suricata suricatta*, Cercle noir, Cp : *Cynictis penicillata*.

weasel *Prepoecilogale bolti* as well as the extinct bat-eared fox *Prototocyon cf. recki*. A detailed palaeontological analysis of the Kromdraai Member 2 carnivore community will be published soon. It will be an important contribution because this Member was previously considered as sterile (see Braga et al., 2017 for more details). The study of the bovid remains collected since 2014 will also be of interest. The co-occurrence of *Connochaetes taurinus prognus* and cf. *Connochaetes gentryi* is noteworthy because it is reminiscent of the late Pliocene and early Pleistocene of Kenya, as well as the older levels of Olduvai (Harris et al., 1988, Fourvel et al., 2016; Gentry, 2010; Harris, 1991). Moreover, the presence of a Makapania-like caprine could relate Kromdraai Member 2 (or Member P) to a Plio-Pleistocene transition/early Pleistocene age, since it is abundant at

Makapan Limeworks Members 3 and 4 as well as in the basal levels of Olduvai (Fourvel et al., 2016; Gentry, 2010; Gentry and Gentry, 1978).

7. Conclusion

Morphologically close to the genus *Civettictis*, it is reasonable to assign KW 10141 and KW 10383 to this genus. However, other features and metric data (particularly tooth size) differ significantly from the extant civet supporting that the Kromdraai specimens represent a new species, *Civettictis braini*. According to the relative scarcity of the fossil remains from Plio-Pleistocene viverrids (as well as the scarcity of the palaeontological analysis focused on the Plio-Pleistocene herpestids and viverrids) and the

edentate specimens from Kromdraai, it is difficult, or even impossible, to assess the phylogenetic relations between *C. braini*, *C. civetta* as well as the larger form *V. leakeyi* and *P. ingens*. Most detailed researches focused on those small carnivores from the African Quaternary have been mainly published by Petter (1963, 1969, 1987) in eastern Africa and Hendey (1974b) and Ewer (1956c) in southern Africa. Even if there are some recent studies on carnivore remains from the “Cradle of Humankind”, including herpestids and viverrids (Fourvel et al., 2016; Kuhn et al., 2011; O'Regan et al., 2013), these publications are not useful to assess the phylogenetic relations and discuss the evolution of these small carnivores.

It is also important to emphasize the scarcity of the palaeontological samples related to those small species. The small quantity of bone sample is not necessarily a reflection of the scarcity of the species during their living time. This could be the result of a bias due to taphonomical processes (e.g., biological or non-biological processes) or related to the excavation and the bone collecting methods. It seems more reasonable to suggest that the lack of specimen may be related to the excavations methods (e.g., wet and dry sieving of the excavated sediment allowing us to collect more small remains) as well as the difficulties to identify these small bone remains or teeth. The field works currently conducted in the Plio-Pleistocene sites in South Africa (like at Kromdraai) using modern excavations methods (specimen collecting methods, systematic sieving of all sediments, detailed examination of each bone remains) should fill partly this lack of small species.

The identification of a new species such as *Civettictis braini* is important to emphasize and will help to further describe the palaeoenvironmental conditions that prevailed when *Homo* and *Paranthropus* evolved and coexisted in South Africa.

Acknowledgments

This research is supported by the French Ministry of Foreign Affairs, the Institut des Déserts et des Steppes (Paris) and the Institut Picot de Lapeyrouse (Toulouse). The author was supported by the Erasmus Mundus AESOP+ program (Application ES15PD0043). I thank the Cradle Management Authority, the South African Heritage Resources Agency and M Ryan Lotz for their continuous support. I also thank Stephany Potze, Lazarus Kgasi, Shaw Badenhorst, Wynand Van Zyl (Ditsong Museum, Pretoria) and Bernhard Zipfel (Evolutionary Studies Institute, University of the Witwatersrand, Johannesburg) who gave me access to the modern and fossil samples under their care. I also thank Raphaël Hautefort and Benjamin Lans for their help with the photographs presented in this study. I am grateful to Jean-Philip Brugal (CNRS-UMR7269 LAMPEA) for his help providing data of the extant African civet. I would like to thank A. Hartstone-Rose and an anonymous reviewer for their helpful comments, which improved this paper.

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