

Systematic palaeontology (vertebrate palaeontology)

Late Miocene Carnivora from Chad: Herpestidae, Viverridae and small-sized Felidae

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Abstract

The small-sized feliforms (Viverridae, Herpestidae, Felidae) from the Late Miocene fossiliferous area of Toros-Menalla, Chad, are described. The Viverridae are represented by dental and postcranial remains of two species: a new, large-sized viverrid, *Sahelictis korei* n. gen. n. sp., which is characterized by a more trenchant dentition than in *Viverra* spp., and an indeterminate species similar in size to *Viverra howelli*. The Herpestidae are represented by a subcomplete mandible with partial dentition assigned to *Herpestes* sp., similar in size to the smallest individuals of the extant *Herpestes naso* and *H. ichneumon*. Felids are known from two, possibly three small-sized species. Fragmentary dental and postcranial remains indicate the presence of one or two species of the size of the golden cat (*Profelis aurata*). A partial skeleton of a wildcat-sized species assigned to *Felis* sp. is also described; this record is by far the earliest record for the genus in Africa. **To cite this article: S. Peigné et al., C. R. Palevol 7 (2008).**

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Résumé

Carnivores du Miocène supérieur du Tchad : Herpestidae, Viverridae et Felidae de petite taille. Les féliniformes (Viverridae, Herpestidae, Felidae) de petite taille du secteur fossilifère Miocène supérieur de Toros-Menalla, Tchad, sont décrits. Les Viverridae sont représentés par les restes dentaires et postcrâniens de deux espèces : un nouveau viverridé de grande taille, *Sahelictis korei* n. gen. n. sp., caractérisé par une denture plus coupante que celle des espèces de *Viverra* et une espèce indéterminée de la taille de *Viverra howelli*. Les Herpestidae sont représentés par une mandibule incomplète comprenant une partie de la denture attribuée à *Herpestes* sp., voisine par la taille des plus petits individus des actuelles *Herpestes naso* et *H. ichneumon*. Les petits Felidae sont connus par deux ou trois espèces. Des restes dentaires et postcrâniens fragmentaires révèlent la présence d'une ou deux espèces de la taille du chat doré (*Profelis aurata*). Un squelette partiel d'une espèce de la taille du chat sauvage et attribué à *Felis* sp. est également

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décrit ; il s'agit, de loin, de la plus ancienne trace du genre en Afrique. **Pour citer cet article** : S. Peigné et al., C. R. Palevol 7 (2008).

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Keywords: Late Miocene; Chad; Central Africa; Carnivora; Feliformia

Mots clés : Miocène supérieur ; Tchad ; Afrique centrale ; Carnivora ; Feliformia

1. Abbreviations

Abbreviations used in the text.

Aao	fossils from Ahl al Oughlam
BAR	fossils from Baringo District, Community Museums of Kenya
KNM-LT	fossils from Lothagam, Kenya National Museums, Nairobi
MNCN	Museo Nacional de Ciencias Naturales, Madrid
MNHN	CG catalogue général, Muséum national d'histoire naturelle, Paris
NMA-AKK	fossils from Akkasdagı, Natural History Museum (MTA), Ankara
SAM-PQ L	fossils from Langebaanweg, Iziko South African Museum, Cape Town
TM	fossils from Toros-Menalla

2. Introduction

Knowledge of the Neogene carnivoran faunas of Africa has greatly improved in the past few years with important discoveries in southern, eastern, and central Africa. These include the faunas from Arrisdrift (early Miocene of Namibia, eight species) [51], Ngorora (middle Miocene of Kenya, seven species) [49], Nawata Formation at Lothagam (late Miocene of Kenya, 18 species) [41,45,87], Lukeino Formation in the Tugen Hills (late Miocene of Kenya, 14 species) [50,53], Lemudong'o (late Miocene of Kenya, 12 species) [30], and Adu-Asa and lower Sagantole formations [67], Middle Awash (late Miocene–Early Pliocene of Ethiopia, 14 species) [25]. These six localities or formations have together yielded more than 60 species, including approximately 20 new species and genera. The carnivoran faunas from Sahabi (nine species) [90] and Langebaanweg (approximately 20 species) [90] also deserve to be mentioned, because they are still important references in African carnivoran studies; the latter is regarded as early Pliocene in age, however. Since 1994, the MPFT has conducted field research in Mio–Pliocene strata of central Chad. One of the richest fossiliferous areas, Toros-Menalla (TM), has yielded the earliest hominid *Sahelanthropus tchadensis* [13,14,86], associated with

a late Miocene faunal assemblage that has become a new, important reference for the late Miocene of Africa. Recently, a radiochronological age of 7 Ma was proposed for the biostratigraphical unit called “Anthracotheriid Unit” (AU) of this area (TM 254 and TM 266), based on cosmogenic nuclide dating [42]. Preliminary observations on the material indicate that the carnivoran fauna from Toros-Menalla is particularly rich and diverse. So far, only a part of the carnivoran material has been studied, including nine species belonging to the Felidae, Canidae, Herpestidae, Hyaenidae, and Mustelidae [9–12,57–59]. All the extant African families of Carnivora are represented at Toros-Menalla. It is noteworthy that TM has yielded the earliest Old World vulpine [11] and the earliest African modern mongoose [58]. The extinct family Amphicyonidae is also represented at Toros-Menalla, as far determinable based on the available remains. The present contribution deals with the material assigned to the small feliform carnivorans from Toros-Menalla. Five or six species are described, belonging to the families Viverridae (two species), Felidae (two or three species), and Herpestidae (one species). With the previously described small-sized herpestid [58] and hyaenid [9], TM includes seven to eight species of small feliforms (i.e. species of less than 20 kg body weight).

3. Material and method

The material from Toros-Menalla is currently stored in the collections of UMR 6046 IPHEP, University of Poitiers, France, for study. The material will be conserved in the collections of the Centre national d'appui à la recherche (CNAR), N'djamena, Chad. Definitions and illustrations of the measurements, which were taken with vernier callipers to the nearest 0.1 mm, can be found in Peigné and Heizmann [56].

4. Systematic paleontology

Carnivora Bowdich, 1821
 Feliformia Kretzoi, 1945
 Viverridae Gray, 1821
Sahelictis korei n. gen. n. sp.

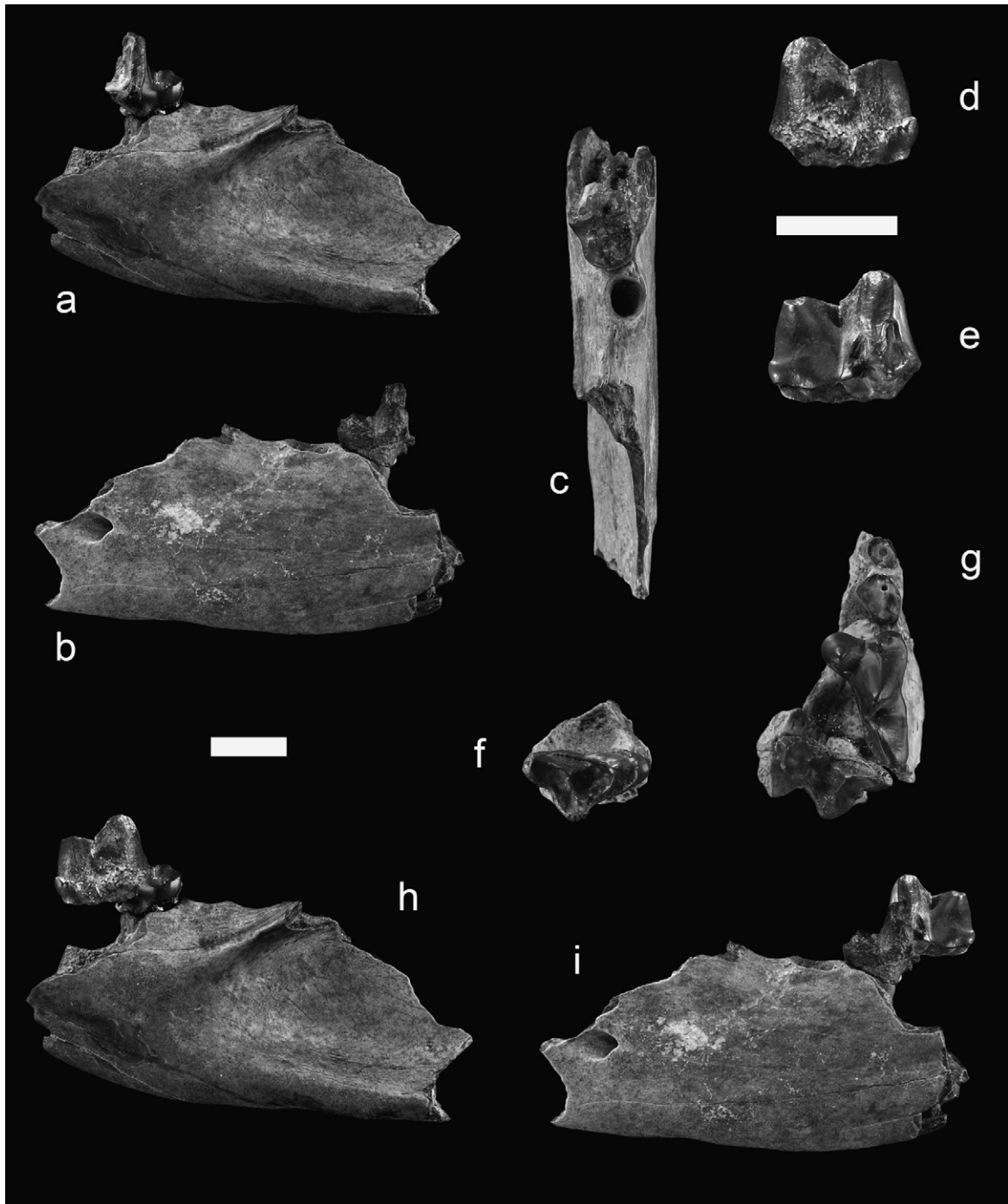


Fig. 1. *Sahelictis korei* n. gen. n. sp. from Toros-Menalla, late Miocene of Chad, dentition. TM 259-04-003, holotype: fragment of left hemimandible with part of m1 in labial (a), lingual (b), and occlusal view (c); right m1 trigonid in labial (d) and lingual (e) view; fragment of right maxilla with M1 in occlusal view (f); fragment of left maxilla with P4-M1 in occlusal view (g); reconstruction of the m1 based on the left and right fragmentary teeth in labial (h) and lingual (i) view. Scale = 10 mm.

Fig. 1. *Sahelictis korei* n. gen. n. sp. de Toros-Menalla, Miocène supérieur du Tchad, denture. TM 259-04-003, holotype : fragment d'hémimandible gauche avec m1 incomplète en vue labiale (a), linguale (b) et dorsale (c); trigonide de m1 droite en vue labiale (d) et linguale (e); fragment de maxillaire droit avec M1 en vue occlusale (f); fragment de maxillaire gauche avec P4-M1 en vue occlusale (g); reconstruction de la m1 fondée sur les m1 gauche et droite fragmentaires en vue labiale (h) et linguale (i). Échelle = 10 mm.

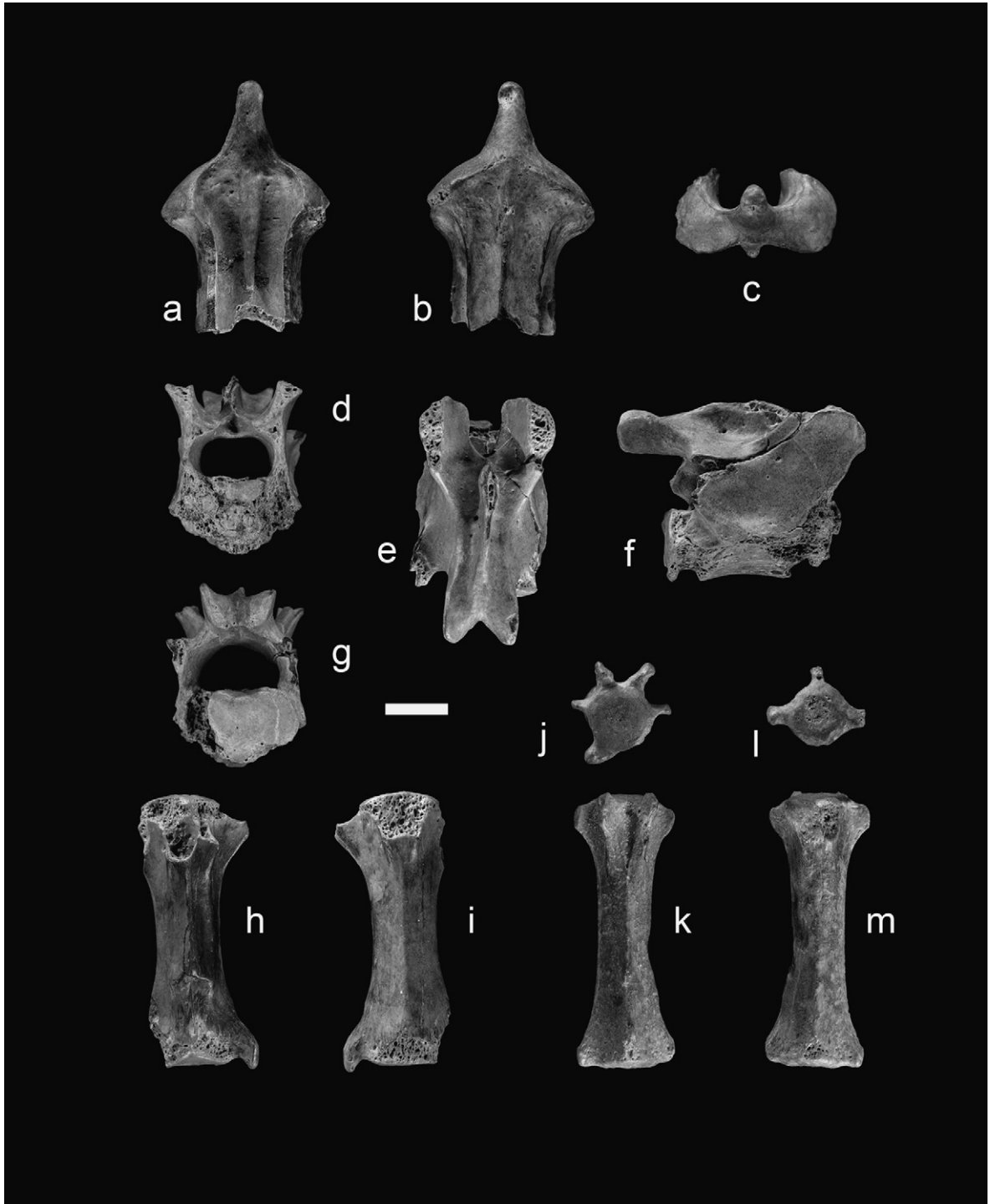


Fig. 2. *Sahelictis korei* n. gen. n. sp. from Toros-Menalla, late Miocene of Chad, vertebrae. TM 259-04-003, holotype: cranial part of the axis in dorsal (a), ventral (b), and cranial (c) view; subcomplete lumbar in cranial (d), dorsal (e), right lateral (f), and caudal (g) view; subcomplete eighth or ninth caudal in dorsal (h) and ventral (i) view; 11th or 12th caudal in cranial (j), dorsal (k), caudal (l), and ventral (m) view. Scale = 10 mm.

Fig. 2. *Sahelictis korei* n. gen. n. sp. de Toros-Menalla, Miocène supérieur du Tchad, vertèbres. TM 259-04-003, holotype : fragment crânial de l'axis en vue dorsale (a), ventrale (b) et crâniale (c) ; lombaire subcomplète en vue crâniale (d), dorsale (e), latérale droite (f) et caudale (g) ; huitième ou neuvième caudale subcomplète en vue dorsale (h) et ventrale (i) ; 11^e ou 12^e caudale en vue crâniale (j), dorsale (k), caudale (l) et ventrale (m). Échelle = 10 mm.

Holotype (Figs. 1–4, Table 1). TM 259-04-003: Fragment of left maxilla with broken P3, P4-M1, fragment of right maxilla with M1; fragment of left mandible with distal part of the trigonid and talonid of m1 and isolated left m1 with paraconid and protoconid; indeterminate fragments of skull; many fragmentary or complete postcranial bones: anterior part of the body of the axis, subcomplete lumbar vertebra, fragment of an indeterminate thoracic vertebra, four subcomplete caudal vertebrae, and numerous vertebra fragments, distal epiphysis of right humerus, diaphysis fragment of right ulna, distal part of right radius, proximal part of left radius, left scapholunar and subcomplete right scapholunar, right pyramidal, subcomplete left Mc II, proximal fragment of left and right Mc III, fragments of undetermined metapodials, fragment of diaphysis of right femur, distal two thirds of right tibia, right astragalus, fragment of right navicular, subcomplete left ectocuneiform, subcomplete left Mt IV, one complete proximal phalanx, distal fragment of a proximal phalanx.

Differential diagnosis. Compared to *Viverra leakeyi*, *V. howelli*, *V. pepratxi*, *V. peii*, m1 with reduced metaconid; compared to these species and to *Megaviverra carpathorum*, m1 talonid narrower, with a reduced hypoconid, no entoconid, no or greatly reduced hypoconulid, and a very low mesiolingual rim; compared to *Viverra leakeyi*, *V. howelli*, *V. pepratxi*, *V. peii*, *V. (?) chinjiensis*, and *Vishnuictis salmontanus*, m1 talonid shorter; compared to *V. leakeyi* and *V. bakerii*, M1 more reduced relative to P4 (or less shortened P4 relative to M1); compared to *V. leakeyi*, M1 transversely less elongated; compared to *Vishnuictis durandi*, long rostrum, skull lacking expanded frontal regions and marked postorbital constriction; compared to *Viverra howelli*, *V. pepratxi*, *V. (?) chinjiensis*, and *Vishnuictis salmontanus*, much larger size.

Etymology. Genus name refers to the geographic origin of the species and “-ictis”, meaning “marten” in Greek; species name derived from “korei”, meaning short in the Goran language, in reference to the reduction of the talonid and the metaconid on the lower carnassial.

Material. Holotype only.

Remarks. The material from Langebaanweg thus far assigned to *V. leakeyi* might represent the same species, but it remains to be confirmed whether it is conspecific with our material, because we have only studied a part of the viverrid material from that locality. The material from Langebaanweg is being revised by Rufus Churcher (pers. com.).

Distribution and age. TM 259, Anthracotheriid Unit, Toros-Menalla, Chad, Late Miocene, ca. 7 Ma [42]; ?Langebaanweg, ‘E’ Quarry, Langeberg Quartzose Sand

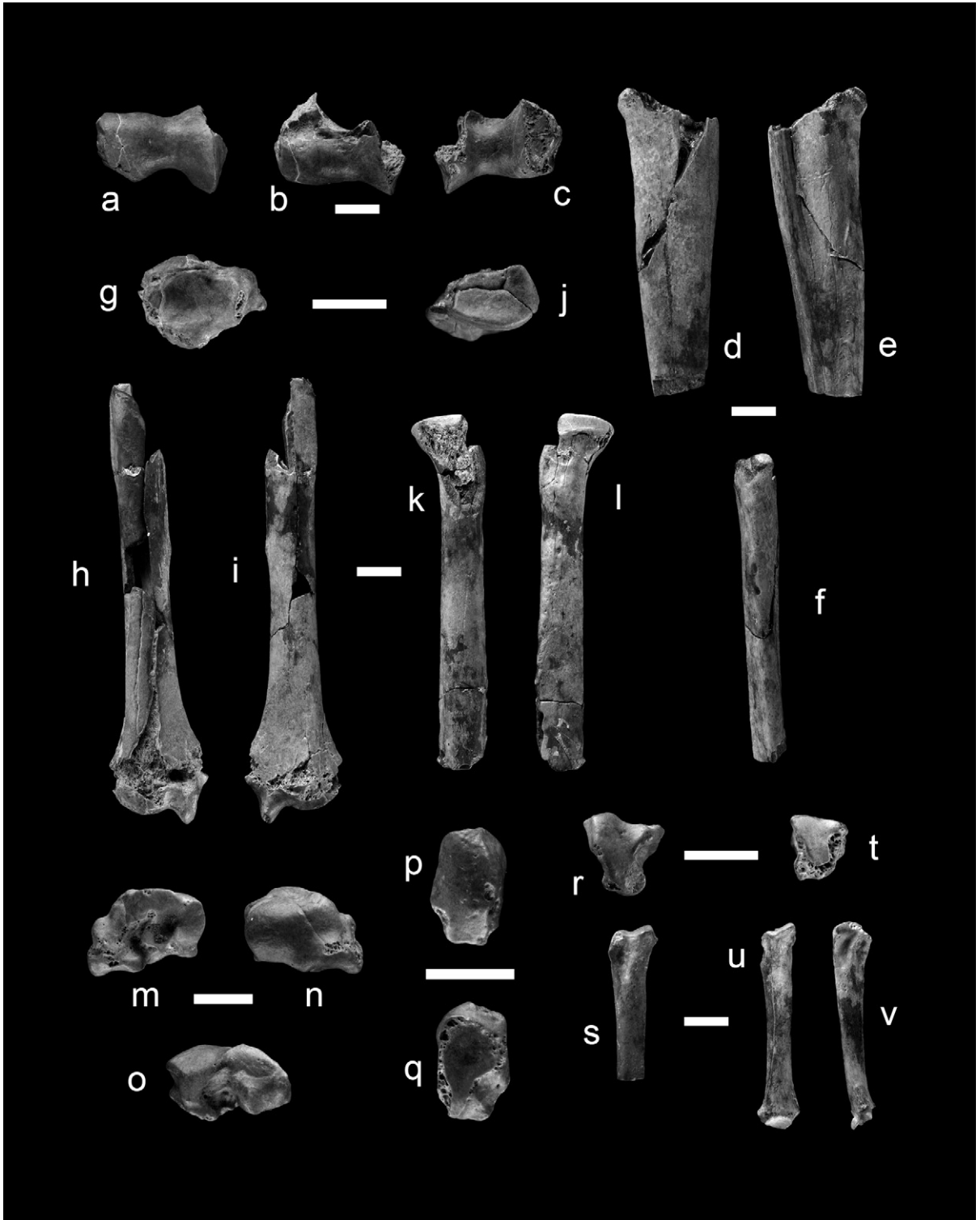
and Muishondfontein Pelletal Phosphorite members of the Varswater Formation [27], South Africa, Earliest Pliocene (i.e., ca. 5 Ma) [26,43].

Description

Mandible (Fig. 1a–c, Table 1). Only the posterior part of the body of the right hemimandible is preserved. The body is narrow and tall; the masseteric fossa is deep and extends forward below the m2 alveolus.

Dentition (Fig. 1, Table 1). The morphology of the lower carnassial is fully known thanks to the complementary left metaconid + talonid and right trigonid. The protoconid is much taller than the paraconid and has a vertical distal face. In labial view, the angle between the paracristid and the protocristid is slightly more than 90°; the protocristid is slightly longer than the paracristid. The metaconid is very reduced and low; it is only slightly distal to the protoconid so that it is not visible in labial view. The talonid is short, slightly narrower than the trigonid, not basined, and weakly trenchant. The lingual rim of the talonid is low and not ridge-like. The entoconid is poorly distinct and located distally. Labially, the hypoconid crest is prominent and short, located at the level of the middle of the distal face of the protoconid. The gap between the hypoconid and the protoconid is filled by a minute supplementary cuspid. The precingulid is well developed, while the hypocingulid is less so. The m2 is single-rooted.

Only the roots of P3 are preserved. Based on its length at root level, P3 is approximately two thirds of the total length of P4. P4 is a large tooth. The paracone is tall and has a convex, vertical distal crest. The parastyle is small and there is a prominent crest on the mesial face of the paracone, close to the parastyle. The protocone is a very strong cusp separated from the paracone by a deep V-shaped valley; it extends forward so that its mesial border is mesial to the mesial border of the parastyle. The metastyle is low and shorter than the paracone. The left and right M1 are represented, but only the right M1 is completely preserved. The tooth is transversely elongated and displays a labially extended parastyle. A labially concave crest links the parastyle, paracone and metacone, the two latter being poorly developed. The metacone is particularly reduced. The labial cingulum is developed; the labial face of M1 is distinctly concave at the level between the paracone and metacone. The part that is lingual to the paracone–metacone consists of a transversely elongated triangle. The protocone is much larger than the labial cusps; the antero- and postero-crista are equally developed, the former extending to the mesial base of the parastyle; a tiny crest-like paraconule is located lingually on the postero-crista. The post- and



precingulum are moderately developed and do not extend beyond the mid-width of the tooth. The infraorbital foramen is large (ca. 7 mm in height), slightly mediolaterally compressed, and located above the distal border of P3.

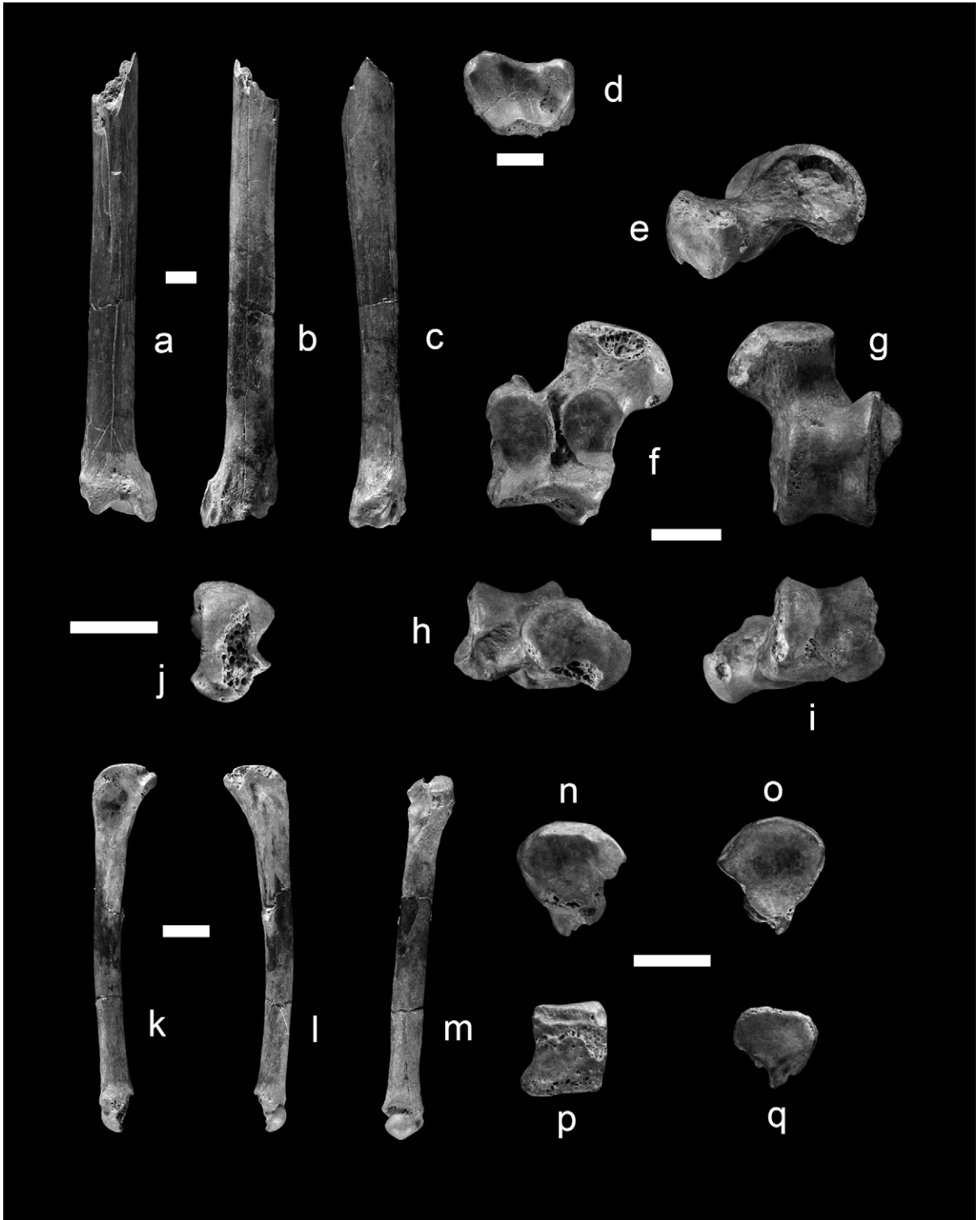
Postcranium (Figs. 2–4). The postcranial material is mostly fragmentary: only several vertebrae, the scapholunars, right pyramidal, left Mc II, right astragalus, left ectocuneiform, left Mt IV, and a proximal phalanx are complete or almost complete. As far as can be determined from this material, the postcranial anatomy of the TM species mostly resembles that of extant terrestrial viverrids such as *Civettictis civetta* and *Viverra zibetha*. The description will thus be restricted to the most prominent features. The dens (or odontoid process) of the axis (Fig. 2a–c) is very long, distinctly longer than in *Viverra zibetha*. The lateral parts of the articular surface for the atlas are approximately as high as they are wide; the mediolateral width of this face is 28 mm. The ventral surface of the body exhibits two elongated fossae for the attachment of the M. longus capitis, separated by a prominent, median longitudinal crest for the attachment of the ventral longitudinal ligament; laterally to each fossa, there is a very deep longitudinal groove bounded by a prominent ridge, corresponding to the broken anterior part of the transverse foramen. On the dorsal face of the body, another prominent ridge is present for the attachment of the dorsal longitudinal ligament. The body of the only preserved lumbar (Fig. 2d–g) is 29 mm long dorsally and the width across the postzygapophyses is 12.2 mm. Given the orientation between the pre- and postzygapophyses, the articular surfaces of which are almost parallel, this is probably one of the first lumbar vertebrae. The spinous process is broken off, but its base extended to almost the entire arch length; its posterior border is anteriorly oriented. The postzygapophyses are posteriorly projected well beyond the posterior articular surface of the body. The accessory processes are broken off, but based on their preserved base they were certainly well developed. The vertebral foramen is large, oval-shaped, and slightly more dorsoventrally flattened

anteriorly than posteriorly. Among the caudal vertebrae preserved in the material, three may be identified. Two of these probably belong to a segment ranging from the eighth to 10th caudal, based on a comparison with *V. zibetha* and *C. civetta*. One caudal may represent the eighth or ninth (Fig. 2h–j); it is 43 mm long and preserves a vestigial vertebral arch, with a posterior opening for the vertebral canal distinctly anterior to the posterior surface of the body. The latter is long and displays anterior and posterior transverse processes, the latter being dorsoventrally thicker than the former. The other caudal is a more posterior vertebra and could be the 10th or 11th caudal (Fig. 2k–m): it has a slightly longer (44.2 mm), but less robust body (the body length increases until the ninth to 11th caudal in *V. zibetha*), more reduced anterior and posterior transverse processes, and no vestigial vertebral arch or foramen. This caudal also preserves a vestigial hemal process anteriorly and vestigial nonfunctional prezygapophyses, but there are no postzygapophyses (replaced by a central, spinous-like process). An additional, incomplete caudal is represented by the main part of its body. It is smaller and certainly slightly shorter than the two caudals described above, and simpler in having more reduced processes; it certainly belongs to a rank posterior to the 11th.

The distal epiphysis of the humerus (Fig. 3a–c) is fragmentary and does not show significant differences from that of *C. civetta*. A fragment of the diaphysis exhibits a slightly prominent lateral epicondylar crest. The ulna is known from a short fragment of the diaphysis distal to the radial notch (Fig. 3d–f). The diaphysis is mediolaterally flattened and extended anteroposteriorly. The fragmentary right (Fig. 3g–i) and left (Fig. 3j–l) radii make it possible to describe almost the entire anatomy of this bone, but the total length of the bone cannot be estimated. The shaft is rather straight. The proximal epiphysis is far from complete and only the medial half is preserved, but it was certainly oval in shape and transversely extended; the capitular eminence is somewhat prominent and anteromedial, as in *V. zibetha*. The neck is

Fig. 3. *Sahelictis korei* n. gen. n. sp. from Toros-Menalla, Late Miocene of Chad, forelimb. TM 259-04-003, holotype: distal epiphysis of the right humerus in distal (a), anterior (b), and posterior (c) view; fragmentary right ulna in medial (d), lateral (e), and anterior (f) view; distal part of the right radius in distal (g), anterior (h), and posterior (i) view and proximal part of the left radius in proximal (j), anterior (k), and posterior (l) view; right scapholunar in distal (m), proximal (n), and posterior (o) view; right pyramidal in lateral (p) and medial (q) view; proximal part of left Mc III in proximal (r) and anterior (s) view; subcomplete left Mc II in proximal (t), anterior (u), and posterior (v) view. Scale = 10 mm.

Fig. 3. *Sahelictis korei* n. gen. n. sp. de Toros-Menalla, Miocène supérieur du Tchad, membre antérieur. TM 259-04-003, holotype : épiphysse distale d'humérus droit, en vue distale (a), antérieure (b) et postérieure (c) ; fragment d'ulna droite en vue médiale (d), latérale (e) et antérieure (f) ; fragment distal du radius droit en vue distale (g), antérieure (h) et postérieure (i) et fragment proximal de radius gauche en vue proximale (j), antérieure (k) et postérieure (l) ; scapholunaire droit en vue distale (m), proximale (n) et postérieure (o) ; pyramidal droit en vue latérale (p) et médiale (q) ; fragment proximal du Mc III gauche en vue proximale (r) et antérieure (s) ; Mc II gauche subcomplet en vue proximale (t), antérieure (u) et postérieure (v). Échelle = 10 mm.



pronounced. The bicipital tuberosity is distinct, located about 18 mm from the head on the posterior face, but it is not very prominent. The distal part of the diaphysis is semicircular in cross-section. The posteromedial face forms a wide, flat surface that is the attachment area for the *M. pronator quadratus*. This surface is much larger than in *C. civetta*. The distal articulation is very concave and the styloid process very prominent. Overall, the distal epiphysis is very similar to that of *V. zibetha* and slightly less transversely elongated than in *C. civetta*. The ulnar articulation is not preserved. The scapholunar (Fig. 3m–o) presents a general morphology similar to that of *V. zibetha* and *C. civetta*. The bone is proximodistally thick, very transversely elongated, and presents a concavoconvex proximal articulation: the convex part occupies the dorsal and main portion of the articulation, while the posteromedial concave surface is small and limited posteriorly by a ridge. This latter surface limits the degree of flexion of the manus relative to the forearm. The distal face of the scapholunar presents a trapezoid articulation that is less extended and less concave than in *V. zibetha*. The groove for the tendon of the *M. flexor carpi radialis* present on the ventral tubercle is also less pronounced than in this species. The morphology of the pyramidal (Fig. 3p–q) does not differ from that of the pyramidal of *C. civetta*. It is a small ovoid bone of 13.5 mm in proximodistal length and 8.4 mm in anteroposterior length; as in most extant species of the Felidae and Viverridae (e.g., *C. civetta* and *V. zibetha*), the pyramidal of *Sahelictis korei* has no articulation for metacarpals and scapholunar, and the articulation for the ulna is much more reduced than that for the pisiform; the articular surface for the hamate is relatively flat, proximally rounded, and tapers off distally. The Mc II (Fig. 3t–v) resembles that of *V. zibetha* and *C. civetta*. The main difference from that of *V. zibetha* is that the proximal articulation is oriented slightly more medially in the fossil species. The proximal articulation on the Mc III (Fig. 3r–s) is less concave medially and the articulation for the Mc II is less vertical and oriented less strictly medially than in *C. civetta*; such a subvertical orientation of the articulation for the Mc II is also observed in *V. zibetha*. The single proximal phalanx preserved in

the material is short (total length = 20 mm) and gently curved.

The hind limb is poorly represented and most of the bones are too fragmentary to be described in detail (Fig. 4). Two bones deserve a more detailed description, however: the astragalus (Fig. 4e–i) and the Mt IV (Fig. 4j–m), which are almost completely preserved. The astragalus is 30 mm long. Compared to that of *C. civetta*, the astragalus of *Sahelictis korei* has a wider head (17.4 of maximum diameter), a wider medial calcaneal articulation, and a slightly more developed lateral condyle (20 mm in proximodistal length). The Mt IV is 79.5 mm long; it has a long, slender, and slightly curved shaft that overall resembles that of the Mt IV of the extant terrestrial viverrids studied here. Compared to *V. zibetha* and *C. civetta*, the fossil species has a plantar tubercle that is well separated from the cuboid articulation. The proximal articulation is not completely preserved, but the facet for the cuboid is anterodorsally convex and extended further dorsally than ventrally. Medially, the distal articulation for the Mt III is prominent and convex and distinctly separated from the cuboid surface. Laterally, the distalmost part of the articulation with the Mt V is very deep.

Comparisons (Fig. 5, Table 1) and discussion

Late Miocene African viverrids have been assigned to three genera: *Herpestides* Beaumont, 1967 and the viverrines *Genetta* Cuvier, 1817 and *Viverra* Linnaeus, 1758. Of the former, we only know *Herpestides? afarensis* Geraads, Alemseged, Beillon, 2002 from Chorora [21]. The material is fragmentary and the generic assignment remains to be confirmed; the species may belong to *Kanuites* Dehghani and Werdelin, 2008 [90]. The genus *Genetta* is known from remains that are not diagnostic at species level from Beni Mellal, Morocco [23], the Upper and Lower members of the Nawata Formation at Lothagam [87], Lemudong'o [30], the Lukeino Formation, Tugen Hills, Kenya [53], and the Adu Asa and lower Sagantole formations, Middle Awash, Ethiopia [25]. *Viverra* is known from two extinct species, *V. howelli* Rook and Martinez-Navarro, 2004 (from Sahabi and as cf. from Lower Nawata Formation at Lothagam)

Fig. 4. *Sahelictis korei* n. gen. n. sp. from Toros-Menalla, late Miocene of Chad, hindlimb. TM 259-04-003, holotype: distal fragment of the right tibia in anterior (a), posterior (b), medial (c), and distal (d) view; right astragalus in medial (e), ventral (f), dorsal (g), distal (h), and proximal (i) view; subcomplete left Mt IV in proximal (j), lateral (k), medial (l), and anterior (m) view; fragment of the right navicular in distal (n) and proximal (o) view; fragment of left ectocuneiform in anterior (p) and distal (q) view. Scale = 10 mm.

Fig. 4. *Sahelictis korei* n. gen. n. sp. de Toros-Menalla, Miocène supérieur du Tchad, membre postérieur. TM 259-04-003, holotype : fragment distal de tibia droit en vue antérieure (a), postérieure (b), médiale (c) et distale (d) ; astragale droit en vue médiale (e), ventrale (f), dorsale (g), distale (h) et proximale (i) ; Mt IV gauche subcomplet en vue proximale (j), latérale (k), médiale (l) et antérieure (m) ; fragment de naviculaire droit en vue distale (n) et proximale (o) ; fragment d'ectocunéiforme gauche en vue antérieure (p) et distale (q). Échelle = 10 mm.

Table 1

Comparisons of dental and mandibular measurements (mm) of TM viverrids with some fossil and extant Viverridae.

Tableau 1

Comparaisons des mesures dentaires et mandibulaires (mm) des viverridés de TM avec certains Viverridae fossiles et actuels.

	Lp4	wp4	Lm1	wm1	Ltm1	Tm1	Dm1-2	LP4	wP4	LM1	wM1
<i>Sahelictis korei</i>											
TM 259-04-003 type			17.3	7.5	12.5	11	25.2	19.3	12	9.4	16.8
cf. <i>S. korei</i>											
SAM mean ^c (N=4–16)	14.41	6.26	16.95	8.21	11.84	11.18	24.38	17.83	10.98	8.82	15.32
range	13.4–15.3	5.5–6.8	15.5–19.6	7.5–9.0	10.6–12.9	10.3–11.7	22.5–25.5	16.5–19.2	9.8–12.85	8–10.15	13.8–17.15
<i>Viverra leakeyi</i>											
Lit 59/466 type ^a								17.2		10.1	14.5
OMO 151-1973-745			17	8.5	11						
OMO 18-1970-1839 ^b			16	8.8	9.5						
P-923-41								17.8	12.2		
AaO-35			18	9.5	11.1						
<i>Viverra cf. leakeyi</i>											
BAR 735'02											
KNM-LT 25413								19.1	12.6		
<i>Megaviverra carpat.</i>											
OF 65261 type			18.65	9.4	13.1						
OF 6512108								17.3	10.8		
<i>Viverra bakerii</i>											
BMNH 40183 type								15.5	9.5	8.9	15
BMNH 40180										8.7	13.8
<i>Viverra (?) chinjiensis</i>											
BMNH M13182 type			9.8	5	6.7						
<i>Vishnuictis durandi</i>											
BMNH M1338 type										10.85	18.5
N. gen. <i>hasnoti</i>											
BMNH M16928 type	10.9	5.6	14.4	7.6	9.1	9.2					
<i>Viverra peii</i>											
V 6092 holotype ^d								18.9	11.8		
V 6093 ^d	15.5	7	19	10			23				
<i>Viverra howelli</i>											
IGF 2890v type ^e			10.4	5.8	6.4						
302P28A ^b			11.2	5.8	6.5						
<i>Viverra cf. howelli</i>											
KNM-LT 23032			13.7	6.8	9.2	7.5	16.7				

Viverrinae indet.

TM 92-06-072	10.5	5.2				9.2	19.50				
TM 92-06-073						8.9	18.8				

Civettictis civetta

m (N=3)	10.6	5.6	14.07	7.67	8.13	9.30	16.57	12.60	9.27	8.6	13.43
range	10.1–11.2	4.9–6.5	13.7–14.4	7.2–8	7.6–8.4	8.5–9.8	16–17.2	11.9–13.1	9–9.5	8.2–9	13.4–13.5

Viverra zibetha

m (N=4)	9.75	4.68	12.73	6.38	8.50	7.28	12.57	12.98	7.45	6.60	10.85
range	8.7–10.3	4.4–5	11–13.4	6–6.5	7.3–9.3	6.9–7.5	11.5–13.9	10.9–14.1	7–8	5.9–7	9.1–11.6

L: length; w: width; Lt: trigonid length; Tm1: mandible thickness across m1; Dm1-2: mandible depth between m1 and m2; carpat.: carpathorum; m: mean.

^a From [60].

^b From [28].

^c Personal and Werdelin data (pers. comm.).

^d From [66].

^e From [69].

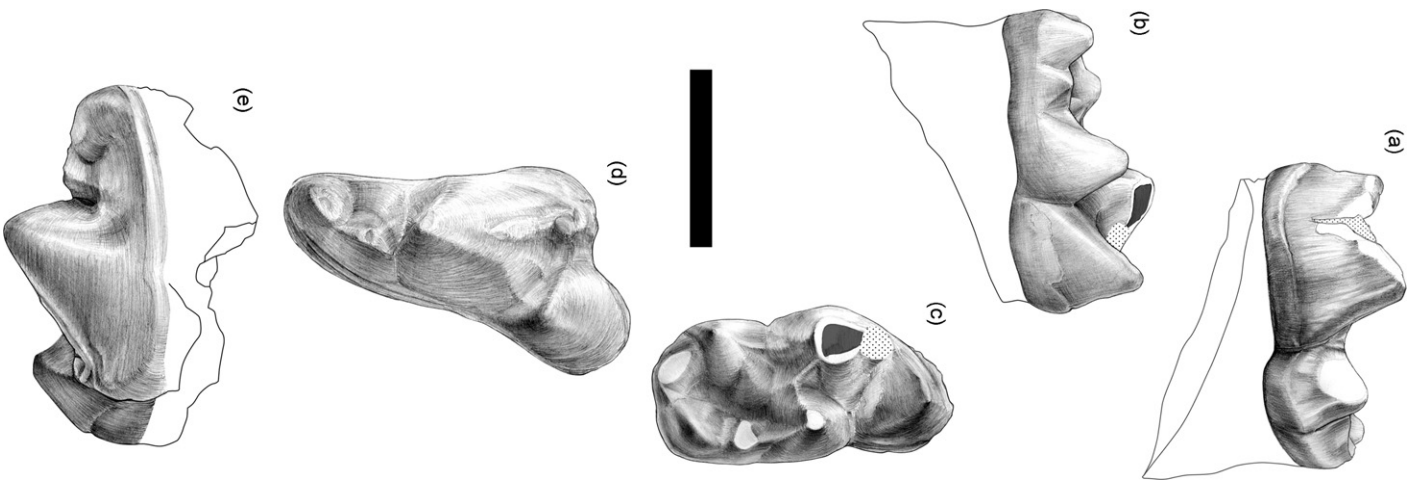


Fig. 5. *Viverra ledkeyi* from Omo, Late Pliocene of Ethiopia, dentition. OMO 151-1973-745: left m1 in labial (a), lingual (b), and occlusal (c) view. P 923-41: right P4 in occlusal (d) and labial (e) view. Scale = 10 mm.

Fig. 5. *Viverra ledkeyi* de l'Omo, Pliocène supérieur d'Éthiopie, denture. OMO 151-1973-745: m1 gauche en vue labiale (a), linguale (b) et occlusale (c). P 923-41: P4 droite en vue occlusale (d) et labiale (e). Échelle = 10 mm.

[28,69], and *Viverra* sp. cf. *V. leakeyi* Petter, 1963 (Lower Nawata Formation at Lothagam and lower Sagantole Formation in the Middle Awash) [25,87]. Although the fauna from Langebaanweg is probably Early Pliocene in age (approximately 5 Ma) [27,43], *Viverra* sp. cf. *V. leakeyi* from this locality [26] should also be included in the discussion. Indeterminate viverrids are also known from Beni Mellal (= *Felis* n. sp.) [23] and Lothagam (Viverridae gen. et sp. indet.) [87]. The systematics of fossil viverrids are still poorly constrained. Thus far, any viverrid specimen found from a Late Miocene or Early Pliocene site has generally been assigned to either *Genetta* or *Viverra*, and to *Viverra leakeyi* when the material represented a large species. The material from Toros-Menalla represents a large species, and we therefore compare the Chadian material to *V. leakeyi*. This comparison is based on casts and original specimens assigned to, or closely related to, *V. leakeyi* from Laetoli (casts), the Shungura Formation (casts), Langebaanweg (originals), the Lukeino Formation (originals), Lothagam (casts), and on the literature for the material from the lower Sagantole Formation and Sahabi. It is important to note that we have studied only a part of the viverrid sample from Langebaanweg, which includes approximately a dozen of specimens; additional comparative data have been kindly provided by L. Werdelin, Natural History Museum, Stockholm (Table 1).

Viverra leakeyi was described on the basis of a fragmentary maxilla with P3 to M2 from the Laetolil Beds, Upper Unit, Tanzania [60], late Pliocene (3.8–3.5 Ma) [89] (Table 1). The species was later mentioned from the members C, E, and G (i.e., from 2.85 to 1.88 Ma) ([46], fig. 5) of the Shungura Formation, Omo Group, Ethiopia [29]. This material was briefly described and illustrated further later [63]. It includes a right P4 (P 923-41, Shungura Fm, Mb G inf, i.e., less than G14; Fig. 5d–e), a fragment of right M1 (P 923-42, Shungura Fm., Mb G inf), a left m1 (OMO 18-1970-1839, Shungura Fm., Mb C9), and a left p4 (OMO 151-1973-213, Shungura Fm., Mb E3) (see McDougall and Brown [46] for the geochronology of the Shungura Formation). Petter [62] also described a p1 from Laetoli. *Viverra leakeyi* is also known from northern Africa in the form of a single m1 from Ahl al Oughlam (Morocco, 2.5 Ma) [20], that exactly matches the unpublished carnassial OMO 151-1973-745 (Shungura Fm., Mb E3, cast at the MNHN, illustrated here for the first time; Fig. 5a–c). Much older localities have also produced viverrid material assigned, or closely related, to this species. A large sample is known from the earliest Pliocene site of Langebaanweg [26], a right P4 from the Late Miocene lower Nawata Formation (7.4–6.5 Ma) [45] at Lothagam [87], a frag-

mentary mandible with m2 in crypt from Amba East, Sagantole Formation (5.55–5.18 Ma) [67] in the Middle Awash [25], and an m2 from the Kapsomin Member of the Lukeino Formation (5.9–5.8 Ma) [53,75]. Most of these authors based their comparison on the material from Langebaanweg, or on the available illustration of the holotype [60]; in this work, however, the illustrations are small in size and the protocone of P4 is not preserved.

As previously pointed out [20], there are some differences in the trigonid/talonid proportions among the material assigned to *V. leakeyi*. According to Geraads [20], the talonid of the m1s from the younger localities, OMO 151-1973-745 (Shungura Fm., Mb E3) and AaO-35 (Ahl al Oughlam) is distinctly longer than that of the carnassials from older sites such as OMO 18-1970-1839 (Shungura Fm., Mb C9, not C8 as mentioned in [20]) and the three Langebaanweg specimens with m1 mentioned by Hendey [26]. It is correct that the m1 from Shungura E3 has a slightly shorter talonid than the m1 from Shungura C8, but there is a much greater difference between the m1s known from all the Late Pliocene sites (i.e., Shungura Mb E to C, Ahl al Oughlam), which have a talonid length/trigonid length ratio of 0.59–0.65 ($N=3$), and the teeth from Late Miocene–Earliest Pliocene sites (Langebaanweg and Toros-Menalla) that show a ratio range of 0.72–0.76 ($N=5$). And there are additional differences that support this distinction. Compared to the holotype from Laetoli ([60] pl. 12, figs. 6–9), specimens from Toros-Menalla and the studied sample from Langebaanweg have a transversely less elongated M1 and a more reduced M1 relative to P4. This character was previously used [60] to distinguish *Viverra leakeyi* from Laetolil from *Civettictis civetta* and is confirmed by our measurements. Among the species included here, the ratio LP4/LM1 is the lowest in the extant *C. civetta* (1.32–1.56); it has an intermediate value in species like *V. leakeyi* from Laetolil and *V. bakerii* from the Siwaliks (1.70–1.75), and has the highest value (1.85–2.09) in specimens from Chad, Langebaanweg, and in the extant *V. zibetha*. Among the material from Shungura assigned by Petter and Howell [63] to *Viverra leakeyi*, only the fragmentary M1 and the P4 were comparable to the holotype material from Laetoli, but these authors [63] did not provide such a comparison and nobody has really questioned the assignment of the Shungura material to *V. leakeyi* since then. The M1 from Shungura is too fragmentary to allow a valuable comparison, while the P4 (P 923-41) is perfectly preserved and mostly unworn (Fig. 5d–e). Unfortunately, the holotype P4 is incomplete and has not been studied here; a comparison with the P4 from Shungura is therefore of unclear significance. The holotype has a parastyle,

which is absent from the Shungura tooth, but this character displays some variation in, e.g., the material from Langebaanweg; it may therefore be not diagnostic and must be used with caution. Differences are much prominent between P 923-41 (P4 from Shungura) and the P4 from Langebaanweg and Toros-Menalla. The tooth from Shungura is much thicker at the level of the paracone, this cusp is strongly backwardly oriented, and the protocone is located more mesially relative to the paracone. The other referred specimens from Shungura [63] represent lower teeth, which have not been found at the type locality Laetoli. However, large viverrids are rare in Africa during the Pliocene (only two recognized species, *Pseudocivetta ingens* and *Viverra leakeyi*, and an undescribed species from Koobi Fora not closely related to either of those species [L. Werdelin, pers. comm.]). Since these teeth are very distinct from *P. ingens* it is very likely that they belong to *Viverra leakeyi*. In comparison with the Shungura m1, the Late Miocene (Toros-Menalla) and Earliest Pliocene (Langebaanweg) material presents an m1 with a reduced metaconid, a shorter and narrower talonid on which the hypoconid crest is more reduced, the entoconid and hypoconulid absent or greatly reduced, and the lingual rim very low, especially mesially.

Based on the differences mentioned here, we distinguish the specimens of *Viverra leakeyi* known from the late Pliocene of Shungura Formation (members C to Ginf), Ahl al Oughlam, and Laetoli, from the material described here from the late Miocene of Toros-Menalla for which we propose to erect a new genus and species, *Sahelictis korei*. Based on our comparisons, the large viverrid from Langebaanweg hitherto known as *V. leakeyi* is closely related to the Chadian species, both dentally and postcranially. However, we have only studied a small part of the large viverrid sample recovered from this South African locality. In addition, given the wide stratigraphical and geographical gap that exists between the Chadian and South African species, a specific distinction cannot be ruled out. In our opinion, however, the species from Langebaanweg is certainly not a species of *Viverra*. A thorough analysis of the whole sample from Langebaanweg (under review by C.S. Churcher, pers. com.) will be necessary to determine the systematic position of the large viverrid from Langebaanweg.

Possible records of a viverrid similar, or closely related, to *Sahelictis korei* are known from Lothagam, Lukeino, and Sagantole, but this material is too fragmentary for a precise assignment.

Additional viverrids are known from Late Miocene and Early Pliocene sites in Africa. *Viverra howelli* is

based on material from Baccinello V3 (Italy, Latest Miocene, MN 13), but it is also known from Lothagam and Sahabi [69]. Beside a clearly smaller size, this species differs from *Sahelictis korei* n. gen. n. sp. in having an m1 with a less reduced metaconid and a longer and wider talonid with three distinct cuspids (hypoconid, hypoconulid, and entoconid). *Civettictis howelli* Morales, Pickford, Soria, 2005, recently described from the Magabet Formation, Tugen Hills (Kenya, Early Pliocene), and especially *Pseudocivetta ingens* Petter, 1967 (the name was not previously given as *Civettictis ingens* n. sp. in Leakey [40] (p. 22–23) contra Petter [61]), clearly differ from our material in their more bunodont dentition.

Outside Africa, except for a few indeterminate taxa and those assigned to *Semigenetta* or *Genetta* that are morphologically distinct from our material, species comparable to *Sahelictis korei* n. gen. n. sp. are assigned to *Viverra*, *Megaviverra*, and *Vishnuictis*. A number of viverrids have been found in Middle Miocene to Pleistocene sediments in the Siwaliks of India and Pakistan: *Viverra bakerii* Bose, 1880, *V. (?) chinjiensis* Pilgrim, 1932, *Vishnuictis durandi* (Lydekker, 1884), *V. salmontanus* Pilgrim, 1932, and Lutrinae genus indet. *hasnoti* (= “Viverridae n. gen. *hasnoti*” [28] = “large, probably new viverrid genus” [64]). The stratigraphical range of these species remains imprecise, but recent investigations in northern Pakistan indicate that *Viverra (?) chinjiensis* is known from the Chinji and Nagri Formations (i.e. 14.2 to 9.0 Ma) [4,64,72], “new genus *hasnoti*” is known from the Nagri Formation [64], and a small and a large species of *Viverra* are known at 8.5 Ma, i.e. in the early Dhok Pathan Formation [3]. All these records are earlier to much earlier than Toros-Menalla and Langebaanweg. The stratigraphical origin and age of the species of *Vishnuictis* and *Viverra bakerii* is also imprecise, but *Vishnuictis salmontanus* may come from Dhok Pathan stage of the Middle Siwaliks and *Viverra bakerii* and *Vishnuictis durandi* from the Upper Siwaliks, probably from the Pinjor stage [65]. The earliest species (“new genus *hasnoti*”, *Viverra (?) chinjiensis*, and *Vishnuictis salmontanus*) are smaller or much smaller than *Sahelictis korei* and have an m1 with a longer talonid than in the material from Chad (Table 1). If really from Pinjor stage or series, *Viverra bakerii* and *Vishnuictis durandi* would be Pleistocene in age, and therefore much younger than the TM material. In addition, in comparison with the latter, *V. bakerii* is of smaller size and has an M1 that is larger relative to P4. The dentition of *Vishnuictis durandi* is only partially known, and is less well preserved than suggested by Matthew’s illustration ([44], fig. 25), e.g., it now lacks the mesiolabial part of P4

and the lingual rim of molars. Beside a slightly larger size and the lower dentition being unknown, the distinction between *V. durandi* and *Sahelictis korei* n. gen. n. sp. is difficult to make. However, a comparison between the cranium of the species of *Vishnuictis* and that of the species from Langebaanweg, which is certainly closely related to *Sahelictis korei*, indicates that these African and Asian species belong to different hypercarnivorous viverrid lineages [31].

Viverra peii Qiu, 1980 from the “Cap” Travertine at Zhoukoudian [66], Late Pliocene in age, and *Megaviverra carpathorum* Kretzoi and Fejfar, 1982 from the late Early Pliocene of Ivanovce (Slovakia, MN 15) are also large taxa that deserve to be compared to our material. In contrast with the species from Toros-Menalla, the Chinese species resembles *V. leakeyi* (i.e., specimens from late Pliocene sites) in its long, wide, and three-cusped m1 talonid. Hunt [32] considers *V. peii* to be a synonym of *Vishnuictis durandi*. The talonid of *Megaviverra carpathorum* is about the same length as that of the Chadian species, but it displays three distinct cuspids, while the hypoconulid and the entoconid are absent or strongly reduced in *Sahelictis korei* n. gen. n. sp. The P4 of *Megaviverra carpathorum* is similar to that of *Sahelictis korei*. It is worth noting that, recently, Fejfar and Sabol [17] have redescribed the holotype material of *M. carpathorum* under the name *Hesperoviverra carpathorum*; without any further evidence, these authors have also proposed to assign to *Hesperoviverra* the species *Megaviverra* (?) *apennina* Kretzoi and Fejfar, 1982, *Viverra leakeyi*, and, more surprisingly, *Hyaenictitherium intuberculatum* (Ozansoy, 1965). As a result, there is some confusion in the literature regarding the names *Megaviverra* and *Hesperoviverra*, which needs to be clarified. The first mention of the generic name *Hesperoviverra* appears in a faunal list from the site Ivanovce [16] associated with the species *carpathorum*, previously assigned to *Megaviverra* [39]. This mention is not a valid nomenclatural act and the name *Hesperoviverra* Fejfar and Heinrich, 1985 is a nomen nudum (no definition, name not proposed expressly as a new replacement name, no fixation of a type species; see Art. 13 in the International Code of Zoological Nomenclature [33]). This first mention predates the valid nomenclatural act by which Kretzoi [38] proposed *Hesperoviverra* n. gen. as a replacement name for *Megaviverra* Kretzoi and Fejfar, 1982, which he believed to be a homonym of *Megaviverra* Qiu, 1980 (not 1981 as in Kretzoi [38]). However, as previously pointed out [20], *Megaviverra* Qiu, 1980 is a nomen nudum (for the same reasons as stated above for *Hesperoviverra*, see Art. 13 in International Code of

Zoological Nomenclature [33]). Therefore *Megaviverra* Kretzoi and Fejfar, 1982 is a valid name, of which *Hesperoviverra* Kretzoi, 1986 is a junior synonym. That being clarified, we do not agree with the assignment of *Hyaenictitherium intuberculatum* to *Megaviverra*, and hence to the Viverridae. Study of the holotype material of this species from Yassiören (Late Miocene, Turkey) clearly shows that the assignment of *H. intuberculatum* to the Hyaenidae is indisputable [7]. We also question the validity of the genus *Megaviverra* itself. According to the diagnosis of the genus [39], *Megaviverra* differs from the extant species of *Viverra* in being much larger in size and stouter, in having a poorly formed hypoconulid on m1, and a well-developed parastyle on P4. Though size may be used to make specific distinctions, it is certainly poor evidence for generic separation. In addition, in the extant *Viverra zibetha*, the m1 may present a distinct, small hypoconulid and the P4 may have a small parastyle; as previously mentioned here, the development of this cusp is variable in, e.g., the large viverrid from Langebaanweg (absent in, e.g., SAM-PQ L 40222, present but small in, e.g., SAM-PQ L 51590, TM 259-04-003). The difference in parastyle size seems a very subtle distinction between *Megaviverra carpathorum* and the large African *Viverra* and *Sahelictis*. For these reasons, and also for those previously stated [87], we do not agree with assigning the African large *Viverra* to the genus *Megaviverra*.

Viverra pepraxi Depéret, 1885 is known from a few dental and postcranial remains from the Early Pliocene of Corneilla-del-Vercol (approximately 10 km south-southwest from Perpignan) and Briquetrie Fajet (Perpignan), southern France, and was previously compared to the Siwaliks and African Mio–Pliocene viverrids [15,26,28,62]. Compared to *Sahelictis korei* n. sp., this species is much smaller and has a longer m1 talonid with three distinct cuspids as in typical *Viverra* spp.

Viverridae gen. et sp. indet.

Material. TM 92-06-073: fragments of left hemimandible with damaged p1, roots of p2, alveoli of p3-m2, distal epiphysis of left humerus, left calcaneum. TM 92-06-072: fragment of right hemimandible with p4 and p3 roots, fragment of edentulous left hemimandible.

Distribution and age. TM 92, Anthracotheriid Unit, Toros-Menalla, Chad, Late Miocene, ca. 7 Ma.

Description

Mandible (Fig. 6f–g, Table 1). The corpus is thick, more so anteriorly than posteriorly, but it is low throughout its length. There is one mental foramen below the mesial border of p2 and one below the mesial root of

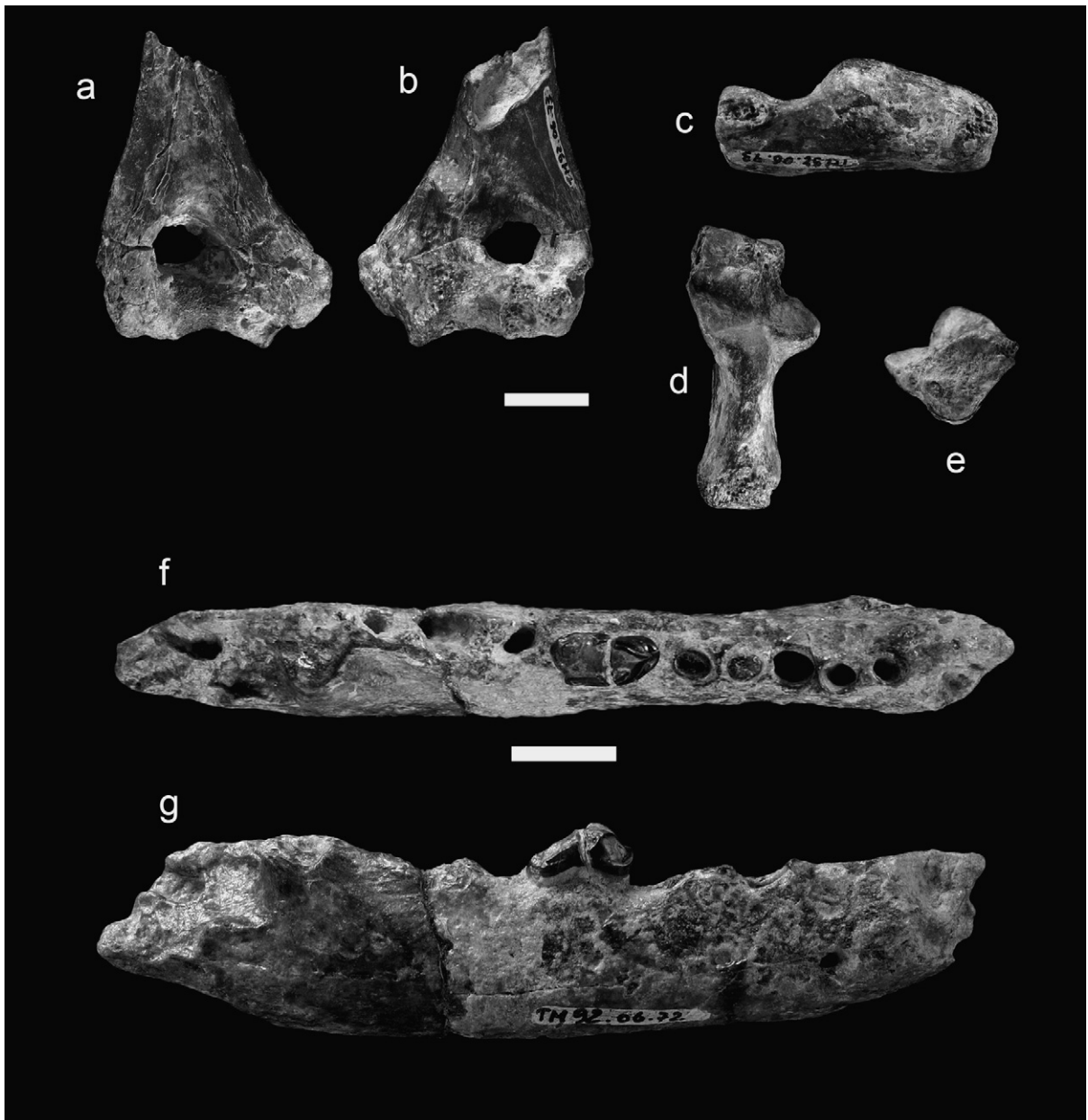


Fig. 6. Viverridae gen. et sp. indet. from Toros-Menalla, late Miocene of Chad, dentition and postcranium. TM 92-06-073: distal fragment of the left humerus in posterior (a) and anterior (b) view; left calcaneum in lateral (c), anterior (d), and posterior (e) view. TM 92-06-072: fragmentary right hemimandible with p4 in occlusal (f) and labial (g) view. Scale = 10 mm.

Fig. 6. Viverridae gen. et sp. indet. de Toros-Menalla, Miocène supérieur du Tchad, denture et post-cranium. TM 92-06-073 : fragment distal de l'humérus gauche en vue postérieure (a) et antérieure (b) ; calcanéum gauche en vue latérale (c), antérieure (d) et postérieure (e). TM 92-06-072 : fragment d'hémimandibule droite avec p4 en vue occlusale (f) et labiale (g). Échelle = 10 mm.

p3. The symphysis is long, reaching the interalveolar region of p2, and shows a posteroventral bulge. The ventral margin of the corpus is horizontal and almost parallel to the alveolar margin. Posterior to m2, however, the corpus curves upwards and the ventral margin then becomes convex. Only the anterior portion of the

masseteric fossa is preserved; it is very deep and located markedly posterior to the level of m2.

Dentition (Fig. 6f–g, Table 1). TM 92-06-073 includes a poorly preserved p1 and roots of p2. The former is single-rooted and separated from the canine by a 3 mm long diastema. Judging by their alveoli, p2

and p3 were approximately the same length. Only the p4 is preserved in TM 92-06-72, but the main cuspid and the distal half of the crown are heavily worn. The tooth is somewhat asymmetrical, with the main cuspid placed mesially; the widest part of the tooth is distal. Based on alveolar lengths, p4 is distinctly longer than p3 and shorter than m1. There is a small mesial accessory cuspid. Premolars are separated by short diastema. The m2 is single-rooted, and alveolus somewhat elongated (5.5 mm long and ca. 3 mm wide).

Postcranium (Fig. 6a–e). The distal fragment of the left humerus (Fig. 6a–b) is poorly preserved and shows evidence of gnawing. There is an entepicondylar foramen, but its medial margin is broken off. The olecranon fossa is also perforated, as in some extant viverrids [84], but an artifact of preservation cannot be ruled out; if so, the bone wall separating the olecranon fossa from the coronoid fossa was very thin. The supracondylar crest is distinct, but poorly developed. The articular surface is damaged, with many small cracks and probable weathering and/or gnawing. The capitulum and trochlea are moderately angular, being more like those of *Genetta* spp. than those of *Civettictis civetta* or *Nandinia binotata* ([84], fig. 7). The medial epicondyle is developed and protrudes posteriorly; the only distinct muscular attachment area is that of the M. flexor carpi ulnaris, which is rounded, slightly depressed and located distally on the epicondyle. The maximum distal width of the humerus is 28.5 mm, but it is certainly slightly underestimated because the lateral epicondyle is partly broken off.

A left calcaneum (Fig. 6c–e) was also associated with the dental remains of TM 92-06-073 in the field, and thus probably belongs to the same individual. The bone is almost complete, showing small cracks at its extremities and has a total length of 34 mm. The tuber calcanei is long and thick, especially its extremity. The posterior articular surface is strongly curved in dorsal view, and its distal part is almost at a right angle to the long axis of the bone. The sustentaculum tali is small and well separated from the cuboid surface; the medial articular surface is small and rounded. The trochlear process is not preserved, but the trochlear shelf is long and broad. The cuboid surface makes an angle of slightly less than 90° with the long axis of the bone; it is very different from the extreme mediolateral slope that characterizes this surface in herpestids ([82], fig. 1). This surface is oval-shaped, its long diameter making an angle of approximately 45° with the dorsoventral axis of the bone.

Comparisons and discussion

The size, dental formula (four premolars, two molars, with a reduced, single-rooted m2), the morphology of p4

and the calcaneum all suggest that the material belongs to a viverrid rather to another family with the same dental formula (Herpestidae, Mustelidae). The known dental remains are too fragmentary to allow for a more precise assignment, however. This species is intermediate in size between the fossil species *Viverra howelli* and *Viverra leakeyi*. It is the size of the extant *Civettictis civetta* and *Viverra zibetha* in the teeth, but the mandible is more comparable to that of the former, being much more robust and thicker than the mandible of *V. zibetha*. One of the distinctive characters of the single preserved tooth is the presence of a small mesial accessory cuspid. Late Miocene and Pliocene viverrids of Africa such as *Viverra leakeyi* and *S. korei* n. gen. n. sp. also display this feature; the p4 of TM 92-06-072 is otherwise much less elongated than that of *S. korei* and belongs to a much smaller species. The p4 of the other late Miocene–Early Pliocene *Viverra*, *V. howelli*, is not known; the size of the holotype from the Italian site of Baccinello V3 and the referred specimen from Sahabi are distinctly smaller than that of Viverridae gen. et sp. indet from TM. The specimen from Lothagam related to *V. howelli* [69] is about the size of TM 92-06-072 (alveolar length of p4 is 10.8 mm in KNM-LT 23032 from Lothagam); however, except for size, the known material is too fragmentary to support a close relationship between the Chadian specimen and *V. howelli*, if not to the genus *Viverra*. The presence of a small mesial cuspid in TM 92-06-072 is not significant at the generic level, since this may also be present in the extant species *V. zibetha* or *C. civetta*. TM 92-06-072 certainly represents a species distinct from *S. korei* n. gen. n. sp., which demonstrates the presence of two viverrids at Toros-Menalla, but its affinities remain to be determined.

The total length and dorsoventral height (14 mm) of the calcaneum of TM 92-06-073 are within the range of that of *Civettictis civetta* and *Viverra zibetha* ([82], table 1). The body of the Chadian calcaneum (least width of the body is 7.8 mm) is, however, much thicker than in these extant species. In *Sahelictis korei* the groove for the common calcaneal tendon is less marked than in *C. civetta*. The morphology of the fragmentary humerus and of the calcaneum, as far as it can be seen does not suggest a strict arboreal life, like *Arctictis binturong* or *Nandinia binotata* (though the latter is no longer regarded as a viverrid), but rather a terrestrial or semiarboreal habit. Thus, the capitulum and trochlear angulation and the moderate size of the medial epicondyle closely resemble those of terrestrial and semiarboreal (good climbers, but forage on the ground) species such as *C. civetta* and *Genetta* spp.

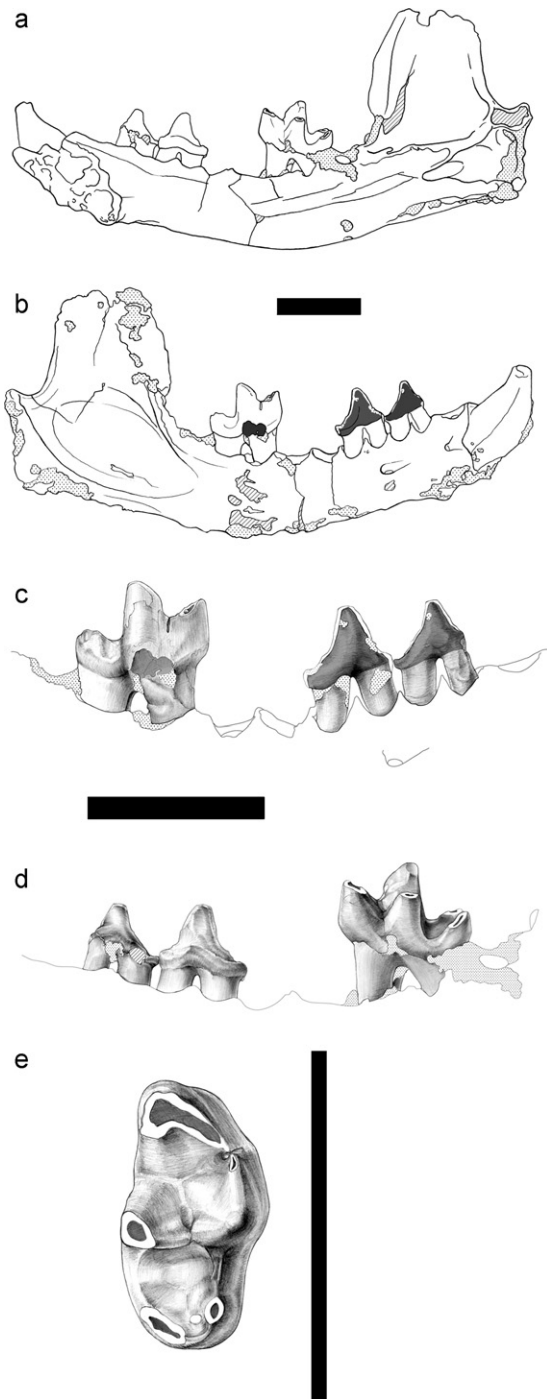


Fig. 7. *Herpestes* sp. from Toros-Menalla, late Miocene of Chad, dentition. TM 90-01-113: subcomplete right hemimandible with c, p2-3, m1 in lingual a and labial b view; detailed drawings of the dentition in labial c and lingual d view; enlarged occlusal view of m1 e. Scale = 10 mm. In the dentition, dentine is shown in dark grey, enamel in white; hatched areas represent broken bones and dotted areas represent sediment.

Fig. 7. *Herpestes* sp. de Toros-Menalla, Miocène supérieur du Tchad, denture. TM 90-01-113 : hémimandibule droite subcomplète avec c,

Herpestidae Bonaparte, 1845

Herpestes sp. indet.

Material. TM 90-01-113: right hemimandible with canine, p2-3, m1.

Distribution and age. TM 90, Anthracotheriid Unit, Toros-Menalla, Chad, late Miocene, ca. 7 Ma.

Description

Mandible (Fig. 7a–b). The mandible is almost complete. The corpus is low and slender, while the coronoid process is tall and has a rounded tip. The symphysis is strong, long, and extends backwards to the mid-length of p2. The two mental foramina are below p1 and the mesial root of p3, respectively. The masseteric fossa is deep and long, but dorsoventrally low.

Dentition (Fig. 7). The canine tip is broken off; the tooth is slender. The p1 is not preserved; it is a single-rooted tooth separated from the canine and p2 by very short diastema. The p2 and p3 are tall and narrow, although the nonpreservation of the enamel on the labial face certainly exaggerates their narrowness. Both teeth lack a mesial accessory cuspid, but have a very reduced distal cuspid and a short talonid; p2 is much smaller and more asymmetrical than p3, and has its main cuspid placed mesially. The m1 is typical of *Herpestes* spp.; the trigonid is tall, with a long but low trenchant paraconid, a taller protoconid and a developed, peaked metaconid; the latter is slightly lower than the paraconid and located across the protoconid from which it is separated by a deep notch. The talonid is narrow and somewhat basined; the labial crest is tall and trenchant, with a distinct, distally located hypoconid; the lingual margin is very low and crest-like only distally. The m2 is not preserved; the alveolus shows it to be single-rooted and placed slightly lingually relative to m1.

Comparisons and discussion

The assignment of this specimen to *Herpestes* Illiger, 1811 is relatively clear. This genus, together with *Galerella* Gray, 1865 is one of the most carnivorous genera of the family Herpestidae. The dental morphology of the species of these two genera is very distinctive. The teeth are slender, sharp, and trenchant, especially the carnassials. The lower carnassial has a low and long paraconid, widely separated from the metaconid, and a short, narrow, and lingually open

p2-3, m1 en vue linguale a et labiale b; dessins de détails de la denture en vue labiale c et linguale d; vue occlusale agrandie de m1 e. Échelle = 10 mm. Sur la denture, la dentine est indiquée en gris foncé, l'émail en blanc; les parties hachurées représentent des cassures et les parties pointillées du sédiment.

Table 2
Comparisons of dental and mandibular measurements (mm) of *Herpestes* sp. from TM with some fossil and extant Herpestidae.

Tableau 2
Comparaisons des mesures dentaires et mandibulaires (mm) de *Herpestes* sp. de TM avec certaines Herpestidae fossiles et actuels.

	Lc	wc	Lp2	wp2	Lp3	wp3	Lp4	wp4	Lm1	wm1	Ltm1	Hpr	Lmd	Lp1-m2	Lp2-m2	Tm1	Dm1-2
<i>Herpestes</i> sp.																	
TM 90-01-113	5.4	3.3	4.2	1.7	5.1	2			7.6	4.2	5	5.1	55.5	30	26.5	4.3	9.5
<i>Herpestes</i> sp. A																	
SAM-PQ L 11847				2	4.8	2.4	5.6	2.4	6.7		4.7			26.5	24.2	4.7	
SAM-PQ L 22234A	4.4	2.8	4.2	2.4	4.6	2.7	5.8	3.1	6.6	3.8				26	24	5.1	
<i>Herpestes</i> sp. cf. A																	
SAM-PQ L22322	4.1		4	1.9	4.8	2.1	6.2	2.8	6.9	3.6	5	4.9		26.4	24	4.5	
<i>Herpestes</i> sp. B																	
SAM-PQ L16177	2.6	1.5	2.8	1.4	3.3	1.6	3.8	1.8	4.3	2.4	2.9	3.3					
SAM-PQ L20666			3.1	1.5	3.3	1.8	4	2	4.4	2.6	3	3.2	32.5		16.3	2.9	
SAM-PQ L20668	2.3	1.8	2.8	1.3	3.5	1.5	3.8	1.7	4.4	2.4	3	3			15.5		
SAM-PQ L22333A					3.5	1.7	3.9	1.8	4.7	2.6	3.1						
<i>Herpestes</i> sp.																	
SAM-PQ L21002			4	2	5.1	2.5	6.5	2.8	7.4	4	5.3	5.1		26.8	24.8	5.3	
SAM-PQ L20674	5		4.5	2.3	5.2	2.8	6.3	3.5	7.5	4.2	5			27	25.9	5.1	
SAM-PQ L21392	4.6	3.1	4.2	2.4	5.2	2.5	6.2	2.8	7.5	4	5.3	5.4			24.9	4.9	
SAM-PQ L21013			4.3	2.3	6.2	2.8	6.2	2.8	7.5	4	5.3			27	25.1	4.5	
<i>Atilax mesotes</i>																	
KA 86	6	4.5	5.3	3.2	6.3	3.4	7.4	4	8.8	5.4	6.1		63.3		31.4	6.1	12.5
<i>H. abdelalii</i>																	
mean (N=3-9) ^a			4.77	2.5	5.38	2.93	6.41	3.22	7.08	3.95							
range			4.6–5	2.4–2.6	5.3–5.5	2.8–3.3	5.8–6.7	3–3.6	6.7–7.5	3.8–4.05							
<i>Herpestes</i> sp.																	
Old/62 DKIC			4.5	2.4	5.4	2.6	6.4	3.1									
L/4=L/3																	
<i>H. naso</i>																	
CG 1970-20	7.05	4.9	5.5	3.25	5.85	3.65	7.75	4.3	8.95	5.15	5.9	6.8		33		6	14.2
<i>H. ichneumon</i>																	
CG 1960-3684	5.8		5.55	2.95	6.4	3.5	8.1	4.1	8.6	4.95	5.95	6.3	61	32.5		5.2	10.8
CG 1860-467	5	3.5	5	2.8	5.8	3	7.4	3.6	7.6	4.5	5.7	5.6	59	31.5		4.5	10.5
CG 1962-1740	5.5	3.5	5.1	2.6	6	3	7.5	3.8	8.6	4.7	6	6	62	32		5.2	12.2
CG 1991-348	5.8	4	5.4	2.7	6.7	3.3	8.1	3.7	8.9	5	6.3		65.5	33.8		4.8	13.1
<i>H. urva</i>																	
CG 1929-386	5	3.7	4.7	2.8	5.6	3	6.9	3.6	8.5	4.9	6	5.9	65	32		5.4	11.5
CG 1929-381	5.7	4	5	2.9	6	3	7.5	3.8	9.1	5	6	5.7	64	32		5.1	10.5
<i>H. javanicus</i>																	
CG 1929-379	3.6		3.5	1.9	4	2.2	4.9	2.8	6	3.5	4	4.5	44.8	23		3.4	6.5
CG 2004-621	3.3		3	1.6	3.7	2	4	2.4	5.6	3.1	3.7	4.7	43	22.2		3	6.7
<i>Atil. paludinosus</i>																	
CG 1950-266	7.15	4.85	4.65	3.3	6.4	4.15	8.15	5.35	9.55	6	5.65	6.15	73		32.7	7.5	13.6

Hpr: height of the protoconid; Lmd: length of mandible; Lp1-m2: distance between mesial rim of p1 alveolus and distal rim of m2 alveolus; for other measurements abbreviations, see Table 1
Atil., *Atilax*.

^a From [20], systematics of Herpestidae from Langebaanweg follow Heney [26].

talonid with a prominent trenchant hypoconid. In these characters *Herpestes/Galerella* spp. differ from other herpestids, with the exception of *Atilax paludinosus* (Cuvier, 1829) which resembles these genera. Due to its fragmentary nature, the Chadian material is not diagnostic at the species level. Compared to extant species such as *Herpestes ichneumon* (Linnaeus, 1758), *H. urva* (Hodgson, 1836), *H. naso* (de Winton, 1901), *H. javanicus* (Geoffroy Saint-Hilaire, 1818), and the species of *Galerella* —e.g., *G. sanguinea* (Rüppell, 1836) and *G. pulverulentus* (Wagner, 1839)—, there are no differences in the dental morphology, in particular regarding the lower carnassial, which is well preserved in TM 90-01-113. Even considering the probable individual variation in size, the Chadian species was probably larger than the smallest solitary mongooses such as *H. javanicus* and *Galerella* spp., whereas it was approximately the size of the smallest individuals of the other *Herpestes* species used here for comparisons. The premolars of the TM specimen look somewhat narrower than those of the extant species, but this is exaggerated by the nonpreservation of the enamel on the labial side. The sole marked difference is that the mandible is very low in the fossil specimen, but this difference may turn out to be insignificant when a larger sample than ours is measured. A comparison with the fossil *Herpestes* did not help to identify the Chadian material. The mandible from TM belongs to a species similar in size and morphology to specimens assigned to *Herpestes* sp. from Langebaanweg (Table 2) and to *Herpestes abdelalii* Geraads, 1997 from Ahl al Oughlam, though p2 and p3 are proportionally longer relative to m1 in the latter species. A number of additional, similar-sized taxa have been described from South African caves (Table 2), but no evidence allows us to closely relate them to the Chadian species. Toros-Menalla has also produced remains of another herpestid, *Galerella sanguinea* [58], but TM 90-01-113 represents a much larger species of solitary mongoose.

Felidae Fischer, 1817

Felidae gen. et sp. indet. A

Material. TM 363-02-002: fragment of left hemimandible with damaged p4-m1 and fragment of right hemimandible with damaged p3-m1.

Distribution and age. TM 363, Anthracotheriid Unit, Toros-Menalla, Chad, late Miocene, ca. 7 Ma.

Description

Mandible (Fig. 8a–d, Table 3). The material is very fragmentary. The mandible lacks its anterior and posterior ends. The corpus is relatively tall and slender, with its

height increasing backwards. The postcanine diastema (between c and p3) is 6 mm long and has a strongly concave dorsal margin. Two mental foramina are present, one below the distal part of the postcanine diastema and one below the main cuspid of p3. The anterior margin of the masseteric fossa reaches approximately the level of the distal margin of m1. Dentition (Fig. 8, Table 3). Only the distal part of the canine alveolus is preserved. There is no p2. The p3 is a small slender tooth; its mesial border is broken off; there is a small distal accessory cuspid and a short talonid. The p4 is much larger and has strong mesial and distal accessory cuspids; there is no talonid, but a distolingual shelf is present; the main cuspid is incomplete and has convex, trenchant mesial and distal margins. The lower carnassial is poorly preserved on both sides; compared to p4, it is distinctly longer and more elongated.

Comparisons and discussion

The material from TM represents a species of approximately 15 kg in body weight, thus similar in size to the species of the extant African genera *Caracal* Gray, 1843, *Profelis* Severtzov, 1858, and *Leptailurus* Severtzov, 1858. The systematic relationships of the specimen are very difficult to establish due both to the fragmentary nature of the material and to the uniformity of the dentition of feline felids. Late Miocene and Pliocene small- and medium-sized felids are not as common as large-sized felids in the fossil record, as illustrated in eastern Africa [89]. On this continent, felines similar in size to the species from Toros-Menalla are represented in the late Miocene Lukeino Formation, Lemudong'o, and Sahabi, in the early Pliocene at Langebaanweg, and at a few later sites [90]. Most of the fossil medium-sized felines from Africa are assigned to the genera *Caracal* or *Leptailurus*, probably because *Caracal caracal* (Schreber, 1776) and *Leptailurus serval* (Schreber, 1776) are two living medium-sized African felines (respective range weight is 7–14 and 6–20 kg) [83]. In Africa, *Caracal* is not known earlier than Sterkfontein Member 2 and Usno Formation (i.e., not earlier than ca. 4.3 Ma) and *Leptailurus* not earlier than Laetoli Upper Beds, but a record of cf. *Leptailurus serval* is reported from Lemudong'o [30]; the third medium-sized cat of Africa, *Profelis aurata* (Temminck, 1827) [18], has no fossil record. Many records of indeterminate felids represent medium-sized species. Since dental features are uniform among these felids and, in addition, the teeth of TM 363-02-002 being imperfectly preserved, only metric comparisons with the Late Miocene and Earliest Pliocene material have been made here (Table 3). A great number of specimens from Langebaanweg are labeled

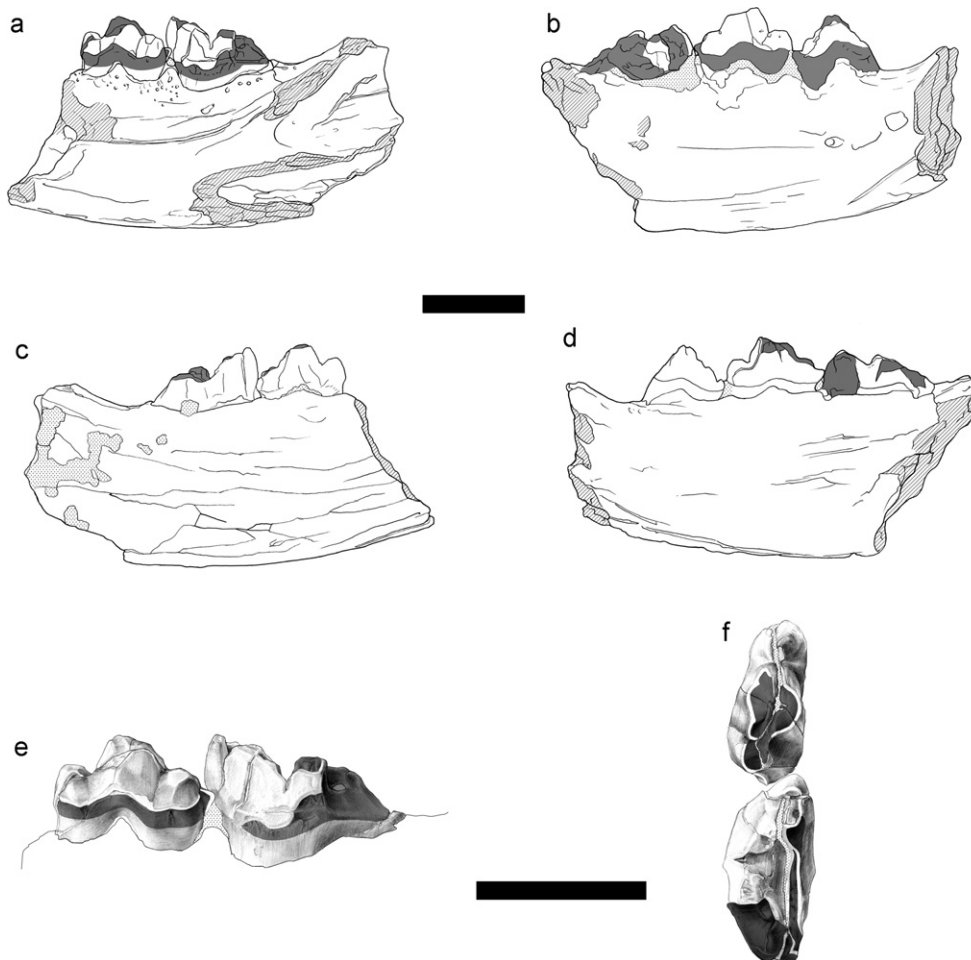


Fig. 8. Felidae gen. et sp. indet. A from Toros-Menalla, late Miocene of Chad, dentition. TM 363-02-002: fragment of left hemimandible with p4-m1 in labial a and lingual c view, fragment of right hemimandible with p3-m1 in labial b and lingual d view, detailed drawings of the left dentition in labial e and occlusal f view. Scale = 10 mm. For explanations of colors, see Fig. 7.

Fig. 8. Felidae gen. et sp. indet. A de Toros-Menalla, Miocène supérieur du Tchad, denture. TM 363-02-002 : fragment d'hémimandibule gauche avec p4-m1 en vue labiale a et linguale c, fragment d'hémimandibule droite avec p3-m1 en vue labiale b et linguale d, dessins de détails de la denture gauche en vue labiale e et occlusale f. Échelle = 10 mm. Pour la signification des couleurs, voir Fig. 7.

“Felidae indet” in the collection of the SAM, Cape Town. Hendey [26] assigned some of these specimens to a form close to *Lynx issiodorensis* (Croizet and Jobert, 1828), the latter being now assigned to *Caracal* [52]; no diagnostic features allow us to confirm these assignments. TM 363-02-002 is slightly to distinctly smaller than any of the studied specimens from Langebaanweg, but it is slightly larger than “*Felis*” sp. (BAR 2342'03) from the Lukeino Formation.

Felidae gen. et sp. indet. B

Material. TM-266-03-209: subcomplete right calcaneum.

Distribution and age. TM 266, Anthracotheriid Unit, Toros-Menalla, Chad, Late Miocene, ca. 7 Ma.

Description

Most of the distal part of the bone (articulation with the cuboid, distalmost part of the astragalar articular surface) and the proximal end of the tuber are not preserved. The proximal articular surface does not extend much proximally. The groove for *M. flexor hallucis longus* tendon is deep. The tuber is mediolaterally narrow. Its ventral and dorsal rims taper off proximally. The proximal extremity of the tuber bears a prominent medial tubercle. A wide, mesiodistally elongated groove is present in the anterior half of the lateral surface of the tuber; this is likely to be the insertion area of the *M. pronator quadratus*. This insertion is usually absent or greatly reduced in extant felids

Table 3

Comparisons of dental and mandibular measurements (mm) of Felidae gen. et sp. indet. from TM with some fossil and extant Felidae.

Tableau 3

Comparaisons des mesures dentaires et mandibulaires (mm) de Felidae gen. et sp. indet. de TM avec certains Felidae actuels et fossiles.

	Dia c-p3	Lp3	wp3	Lp4	wp4	Lm1	wm1	Tm1	Ddm1	Lp3-m1
Felidae gen. et sp. indet.										
TM 363-02-002	6	7.3	3.6	9.3	4.2	11.2	4.8	6.4	16.2	28.8
<i>Felis</i> sp. cf. <i>Caracal caracal</i>										
BAR 2342'03							4.1			
Felidae indet. cf. <i>L. issiodorensis</i>										
L 16055		8.6	4.5	11.2	5	15.2	>6			36.6
L 3199						12.9	6	8.4	17.7	
Felidae indet.										
L 41753		8.8	4.7	11.1	5.4	13.3	6.1	9.6	19	32.3
L 69615B				11						
L 25893A	7.7	7.3	4	9.4	4.7	11.4	5.3			29.3
L 41020		8.7	4.5	11.4	5.1	12.4	5.7			32.5
L 40321H	10.5	9	4.7	11.7	5.6	13.5	6.2	9.60	19.70	33.7
<i>Leptailurus</i> or <i>Caracal</i> sp.										
KNM-LT 23116				9.1	4.3	11.1	5			
<i>Caracal caracal</i>										
mean ($N=19$) ^a						12.2	5.4			31.1
range ^a						11-14	4.9-6.1			

Dia c-p3: length of postcanine diastema; Ddm1: mandibular depth distally of m1; Lp3-m1: distance between mesial alveolar margin of p3 and distal alveolar margin of m1.

^a From [26].

[73,85]. The maximum width across the sustentaculum and trochlear processes is 15 mm and the dorsoventral height at the level of the proximal articular surface is 13.5 mm.

Comparison and discussion

The referral of this specimen to the Felidae is based on a comparison with the calcaneum of extant Carnivora [78–82] (pers. obs.). The length and transverse compression of the tuber calcanei, the ventral and dorsal rims of the tuber that taper off proximally, the presence of a strong medial tubercle on the tuber, and the marked groove for the tendon of *M. flexor hallucis longus* (or *M. flexor digitorum pedis lateralis*) on the ventral face of the sustentaculum tali all suggest that this bone belongs to a felid. TM-266-03-209 belongs to a species similar in size to Felidae gen. et sp. indet. A from TM. Though these taxa might be conspecific, the presence of two medium-sized felids in the TM area cannot be ruled out and, therefore, we prefer to distinguish the two taxa.

Felis sp. size of a small *Felis silvestris* Schreber, 1775 (ca. 3.5 kg)

Material. TM 68-06-002: fragment of mandible with left p3-m1 and right c, p3-m1; fragment of right maxilla

with P3-4 and fragment of left maxilla with C, P3-4; indeterminate fragments of skulls; postcranial bones more or less encrusted by manganese comprising: subcomplete left humerus in anatomical connection with subcomplete ulna and radius; subcomplete left Mc III and IV, associated with the capitatum and the hamatum, right Mc I and proximal phalanx of digit I; isolated medial and distal phalanges of the manus; proximal part of right ulna and radius in anatomical connection; most of the hip bone associated with the sacrum and several lumbar vertebrae; distal half of left femur with patella and proximal two thirds of left tibia in connection with a short fragment of fibula; left foot including all the tarsals, and the proximal portion of the metatarsals.

Distribution and age. TM 68, Anthracotheriid Unit, Toros-Menalla, Chad, late Miocene, ca. 7 Ma.

Description

Although the specimen represents a virtually subcomplete individual, every bone or every associated bone is strongly encrusted by sediment. The preparation was difficult also due to the small size and hence the fragility of the material; some details of the anatomy of the postcranium therefore remain inaccessible.

Table 4

Comparisons of dental and mandibular measurements (mm) of *Felis* sp. from TM with some extinct and extant Felidae.

Tableau 4

Comparaisons des mesures dentaires et mandibulaires (mm) de *Felis* sp. de TM avec quelques Felidae éteints et actuels.

	Lc	wc	Dia c-p3	Lp3	wp3	Lp4	wp4	Lm1	wm1	Tm1	Ddm1	LC	wC	LP3	wP3	LP4	wP4	Hpa	Lme
<i>Felis</i> sp.																			
TM 68-06-002	3.1	2.5	4.5	4.2	2.2	5.7	2.4	7.5	2.9	4.50	7.8	3.7	2.7	5.2	2.6	9		4.8	4
<i>F. attica</i>																			
Type ^a	5.6	4.7	11.7	7.1	4.1	9.2	4.2	11				6.2	4.6	9.1	4.2	12.7	6.1		
MNHN PIK 3232						8.6	3.5	10.5											
AMPG PG 01/106 ^b												6.3 ^g	4.6 ^g	8.65	4.95	13.7	6.9		
AMPG PG 01/107 ^b	5.4	4.2	7.4	7.1	3.4	8.3	3.8	10.2											
AMPG PG 01/108 ^b								10.3											
<i>Felis</i> sp. cf. <i>F. attica</i>																			
MHL 482S ^a	6.2	5	13	8	4	9.8	4.2	11.1	4.4			7.2	5.2	9	4.8	13.4	6.8		
MNHN MAR 3370														8.2	3.8	13	6.2	6.4	
AKK-212												6.6	4.9	8	4.3	13.5	6.3		5
Baode ^c	6.9	5.4	8.3	7.6	3.8	8.7		10.8											
MNHN SLQ 935												8.7 ^g	5.5 ^g	8	4.2	14	5.7	5.7	5.8
1256-3079 ^d						9	4.5	11.6	5.2										
<i>F. christolii</i>																			
Type ^e						10.4 ^g		13.7 ^g											
NM-C 19 ^f								12.4	5.2										
MP 338 ^e								12.9	5.7										
MP 884 ^e			8	4.4	11	5.3	14.2 ^g												
BRS25/3 ^e						10.6 ^g	5.1 ^g	13	5.3										
<i>F. silvestris</i>																			
m (N=2–11)	4.92	3.42	6.31	5.85	2.67	7.24	3.17	8.08	3.44	5.63	10.5	5.23	3.78	6.90	3.36	10.92	5.31	5.84	4.64
range	4.1–6.05	2.85–3.9	5–8.3	5.2–6.5	2.3–3	6.4–7.95	2.8–3.5	6.5–8.95	3–3.8	4.65–6.75	9.5–11.5	4.5–6	3.4–4.2	6.3–7.4	3.1–3.7	9.5–11.75	4.6–5.75	5.1–6.5	3.9–5

Hpa: P4 paracone height; Lme: P4 metastyle length.

^a From [5].^b From [71].^c From Zdansky [91].^d From Riabinin [68].^e From [70].^f From [48].^g Estimated measurement.

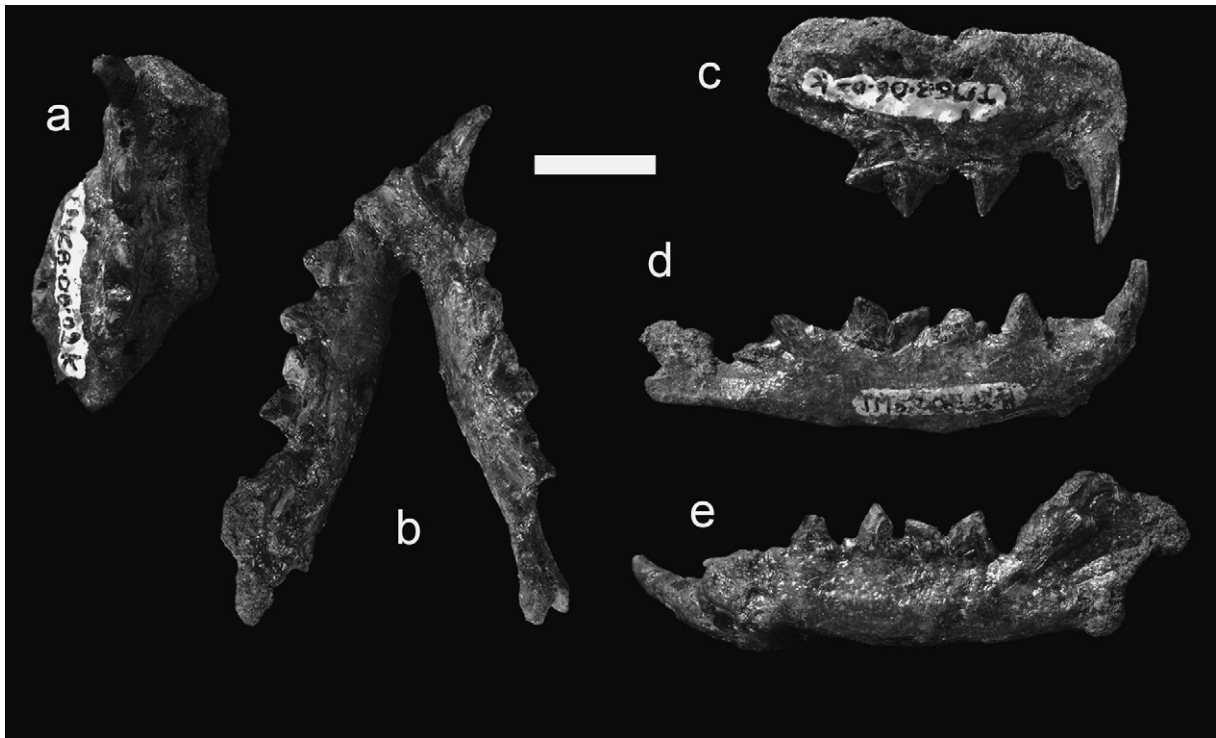


Fig. 9. *Felis* sp. from Toros-Menalla, late Miocene of Chad, dentition. TM 68-06-002: fragment of mandible with left p3-m1 and right c-m1 in occlusal (b), right lateral (d), and left lateral (e) view; fragment of right maxilla with C, P3-4 in occlusal (a) and lateral (c) view. Scale = 10 mm.

Fig. 9. *Felis* sp. de Toros-Menalla, Miocène supérieur du Tchad, denture. TM 68-06-002 : fragment de mandibule avec p3-m1 gauches et c-m1 droite en vue occlusale (b), latérale droite (d) et latérale gauche (e) ; fragment de maxillaire droit avec C, P3-4 en vue occlusale (a) et latérale (c). Échelle = 10 mm.

Mandible (Fig. 9, Table 4). The two mandibular bodies are still connected; both lack the posterior part. The masseteric fossa is deep and located considerably posterior to the m1.

Dentition (Fig. 9, Table 4). The teeth are well preserved and only slightly worn. The lower canine is small and slender; its apex is broken off. There is a longitudinal groove on the labial face. There is a 4.5 mm diastema between the canine and the p3. The latter is small, much smaller than p4, and does not have any accessory cuspid; the crown is slightly asymmetrical, with the main cuspid mesially located; the latter has trenchant rims. The p4 has a main cuspid displaying a well-convexed distal rim; the mesial accessory cuspid is small; the distal accessory cuspid is located slightly laterally; it is not fully preserved, but its base suggests that it was approximately the size of the mesial cuspid; the talonid is poorly preserved on both sides. The lower carnassial is typical of felids and presents no distinctive features, except that a small notch on the distal face of the protocone indicates the presence of a vestigial metaconid.

The upper canine is much longer than the lower one, straighter and slightly more transversely compressed; it

also displays a marked groove on the labial face. The postcanine diastema is short, less than 2 mm in length. The P2 is not preserved but was single-rooted; a small depression is visible in front of the alveolus, but it is likely an artifact of preservation rather than an alveolus for P1. The P3 is tall and slender; it has no mesial accessory cuspid and a tiny distal one, basally located and prolonged by a short narrow talon. The upper carnassial is incompletely preserved on both sides. The parastyle is small; the protocone is not preserved. The paracone is very trenchant and much taller than the metacone. The carnassial notch is very deep. The metastyle is slightly longer than the paracone. M1 is not preserved.

Postcranium (Fig. 10, Table 5). Only a couple of bones are complete enough to provide length measurements. We have compared our material to the skeleton of *Felis silvestris* (MNCN 21456, MNCN 21536) and *Felis attica* (for measurements only see Table 5). As far as can be seen, every bone is extremely similar to those of *Felis silvestris*. For this reason and because of the limited space here, we do not describe but provide at least illustrations of most of the bones (Fig. 10). The difference in size between our material and the wildcat skeletons stud-

Table 5

Comparisons of postcranial measurements (mm) of *Felis* sp. from TM with *Felis silvestris* and *Felis attica*.

Tableau 5

Comparaisons des mesures postcrâniennes (mm) de *Felis* sp. de TM avec *Felis silvestris* et *Felis attica*.

	<i>Felis</i> sp.	<i>Felis silvestris</i>		<i>Felis attica</i>	
	TM 68-06-002	MNCN 21536	MNCN 21456	BM 9010 ^a	AMPG PA 1028/91 ^b
L Fct radius	70 ^c	(103)	(91.8)		
L Mc I	8.9	14.3	12.5		
L ph I dig. I	6.3	10	8.7		
L ph II indet. dig.	7.3				
L ph III indet. dig.	6.5				
MWDE femur	13.8	21.4	19	28	
ML astragalus	11.6	17.8	15.8	24	
ML calca.	20.9	33.6	30.2	42	41.8

L: length; Fct: functional; dig.: digit; MWDE: maximum width of distal epiphysis; ML: maximum length; calca.: calcaneum.

^a From [6].^b From [71].^c Estimated measurement; parentheses indicate measurement based on non-epiphysed bone.

ied here is great and indicates that the former belongs to a very small individual.

Comparisons and discussion

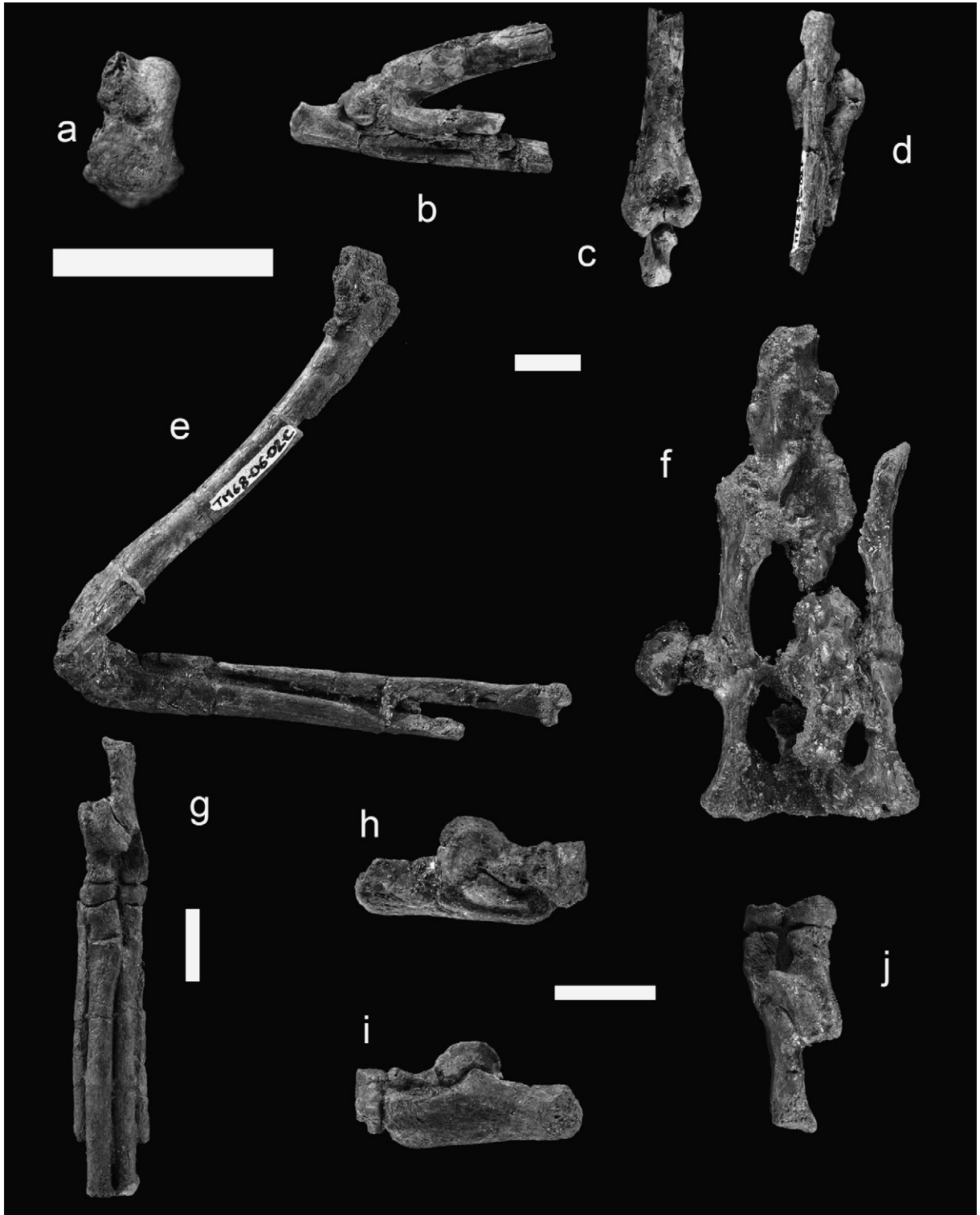
All the known records of species of *Felis* Linnaeus, 1758 in Africa are much younger than Toros-Menalla (*Felis* n. sp. from Beni Mellal is probably a viverrid) [90]. Thus far, African records of *Felis* are extremely rare in the early Pliocene and absent in the Miocene. Fragments of a P4 of a species approximately the size of *Felis silvestris libyca* Forster, 1780 have been described from Kanapoi (4.17–4.07 Ma) [88]. Howell [28] assigned two third metacarpals from Sahabi that are the size of those of a wildcat to Felidae indet. species C. Among the records that remain to be confirmed, there is a wildcat-sized species from the Langeberg Quartzose Sand Member, Varswater Formation at Langebaanweg, not described by Hendey [26], but mentioned in a faunal list published later [27]. The Chadian record is some 2 million years older than the next-earliest specimens previously assigned to *Felis* from Sahabi and Langebaanweg (i.e.,

species similar in size and morphology to extant African small-sized species of the genus *Felis*). This first appearance of *Felis* in Africa slightly precedes the divergence time (6.2 Ma) of the domestic cat lineage based on the recent molecular phylogeny [34], but the confidence interval of this divergence estimate (8.55–4.8 Ma) encompasses the Chadian record [34]. The divergence time estimation of the domestic cat lineage (4.23 Ma) is based on fossil constraints, which is the earliest Old World *Felis*, said to be *Felis lunensis* Kartelli, 1906 [34].

Late Miocene–Early Pliocene *Felis* are known from Europe mainly in the form of *Felis christolii* Gervais 1848–1852 and *Felis attica* Wagner, 1857; the former has been regarded as a descendant of the latter [24] or part of the same chronospecies [70]. *Felis attica*, which is based on material from Pikermi (MN 12), Greece, is represented by specimens from Europe and Asia. Other records are based on more or less fragmentary material from Greece (Ravin de Vatilik or Vathylakkos 3, MN 11/12, Samos, MN 12) [5,35,71], France (Aubignas, MN 12) [2], Germany (Dorn–Dürkheim 1, MN 11) ([54], but see Roussiakis [71], p. 713), Hungary (Csákvár,

Fig. 10. *Felis* sp. from Toros-Menalla, Late Miocene of Chad, postcranium. TM 68-06-002: proximal view of the right ulna (a); distal fragment of the right humerus in anatomical connection with proximal fragment of the ulna and radius in lateral view (b), posterior view relative to the humerus (c), and posterior view relative to the ulna (d); subcomplete left humerus, radius and ulna in anatomical connection in medial view (e); fragmentary lumbar, sacrum, caudals, hip bones, and proximal epiphysis of the left femur in anatomical connection in dorsal view; left tarsal and subcomplete metatarsals in anatomical connection in dorsal view (g); left calcaneum, astragalus, navicular and fragment of cuboid in anatomical connection in medial (h), lateral (i), and dorsal (j) view. Scale = 10 mm.

Fig. 10. *Felis* sp. de Toros-Menalla, Miocène supérieur du Tchad, postcranium. TM 68-06-002: vue proximale de l'ulna droite (a); fragment distal d'humérus droit en connexion anatomique avec un fragment proximal de l'ulna et du radius en vue latérale (b), postérieure par rapport à l'humérus (c) et postérieure par rapport à l'ulna (d); humérus, radius and ulna gauches subcomplets en connexion anatomique en vue médiale (e); lombaires, sacrum, et caudales fragmentaires, bassin et extrémité proximale du fémur gauche en connexion anatomique en vue dorsale; tarse et métatarses sunbcomplets gauches en connexion anatomique en vue dorsale (g); calcaneum, astragale, naviculaire et portion de cuboïde gauches en connexion anatomique en vue médiale (h), latérale (i) et dorsale (j). Échelle = 10 mm.



MN 11 and Polgárdi, MN 13) [36,37], Spain (Valdecebro 5, MN 12) [1], Moldova (Taraklia, MN 12) [68], Ukraine (Gritsev and Klimentovichi, MN 9) [55], Turkey (Karain, MN 10, Kınık and Gülpınar, MN 11, Akkasdagi, MN 12) [8,19,77], Iran (Maragha) [47], China (Baode) ([91] pl. 27, fig. 6), and Mongolia (Olan Chorea and Ertemte) [76]. However, no descriptions and/or illustrations have been yet published for the material from Gritsev, Klimentovichi, and Gülpınar; in addition, we consider that the material from Aubignas (two canines), Dorn–Dürkheim (an isolated m1 and a fragment of P4), Csákvár (an isolated lower canine), Polgárdi (fragmentary mandible with m1), Valdecebro 5 (an isolated P4), Karain (an isolated lower canine), Kınık (a proximal fragment of radius), Olan Chorea and Ertemte (a few postcranial bones) is too fragmentary and probably not diagnostic at the species level. Therefore, we here compare our material to the most complete material assigned, or related to *Felis attica*, i.e., that coming from Pikermi, Samos, Vathyakkos 3, Akkasdagi, Maragha, Taraklia and Baode. Our comparison is based on direct study of MNHN PIK 3232 from Pikermi (fragmentary right hemimandible with p4-m1), MNHN MAR 3370 from Maragha (fragmentary skull with P3-M1), NMA-AKK 212 from Akkasdagi (fragmentary left maxilla with C-P4), and MNHN-SLQ 935 from Ravin de Vatiluk or Vathyakkos 3 (subcomplete skull with left P3-P4, right C, P3-M1). We have also obtained measurements and/or illustrations of additional specimens from Greece, Moldova, and China from the literature (Table 4). Compared to this material, the species from Chad is a much smaller species and differs in having a more reduced P3 relative to P4, with a more reduced distal accessory cusp, shorter lower premolars relative to the m1, and a p3 with no mesial cuspid. Additional differences from the material from Maragha and Vathyakkos 3 include the absence of a preparastyle in the Chadian material. Finally, the marked groove present on the labial face of the canine of TM 68-06-002 is not mentioned in the material from Pikermi, is shallow in the skull from Vathyakkos 3, and absent in the maxilla from Akkasdagi. Similar differences are expected with *Felis christolii* (no direct comparison here), a species known from France (Montpellier, MN 14) [22,70], Spain (Venta del Moro, MN 13) [48], and Italy (Brisighella, MN 13) [70] that differs from *Felis attica* mainly in its slightly larger size.

The generic assignment of our material needs to be confirmed, however. Although the monophyly of the genus *Felis* is supported by numerous genetic synapomorphies, the species of the genus share only two morphological synapomorphies (deep external pterygoid fossa and enlargement of frontal breadth) [74]

that are not visible on our material. A comparison of our material with the extant species, *Felis silvestris* ($N=11$ from France and Spain) shows great dental and skeletal similarity overall. However, besides smaller size, the Chadian material differs from the European *F. silvestris* in the absence of a mesial accessory cuspid on p3, a taller P3 with a straight mesial rim (it is most often concave in *Felis silvestris*) and a more reduced distal accessory cusp, and an m1 that is proportionally much longer relative to p4. These differences could support specific distinction, which is also supported by a much younger molecular age for *Felis silvestris* (0.89–2.16 Ma) [34]. As mentioned earlier, the comparison of the postcranium does not indicate any visible anatomical and metric differences, although, given the fragmentary nature of our material, differences in bone proportions may appear when a more complete one is available (Table 5).

5. General discussion

Seven or eight small-sized feliform carnivorans are known from different sites of the Anthracotheriid Unit at Toros-Menalla, Chad. Most of the species are represented by a single individual (and hence at a single locality); *G. sanguinea* is known from three individuals from TM 266 and Viverridae gen. et sp. indet. from two individuals from TM 92. This indicates that these taxa were not frequent in the TM area, or, at least, that they were much less frequent than other taxa present at TM such as *Hyaenictitherium minimum* Bonis et al., 2005, the most common species in this area. This may be due to taphonomic and/or ecological conditions.

The small-sized feliforms from TM are new or poorly known taxa which do not allow us to make adequate comparisons with contemporaneous African sites. TM has yielded the earliest record for the modern genera *Galerella* and *Felis* (in Africa).

The current faunal list from Toros-Menalla includes 15 or 16 carnivoran species: the felids *Amphimachairodus kabir*, *Felis* sp. size of a *Felis silvestris* female, Felidae gen. et sp. indet. A size of *P. aurata*, and Felidae gen. et sp. indet. B size of *P. aurata*; the herpestids *Galerella sanguinea* and *Herpestes* sp.; the viverrids *Sahelictis korei* n. gen. n. sp. and Viverridae gen. et sp. indet.; the hyaenids *Hyaenictitherium minimum* and *Chasmaporthetes* sp. aff. *C. australis*; the canid *Vulpes riffautae*; the mustelids *Sivaonyx beyi*, *Djourabus dabba*, Lutrinae gen. et sp. indet. aff. *Torolutra* sp., Lutrinae gen. et sp. indet. aff. *Aonyx* sp., and a mellivorine n. gen. n. sp. [17].

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