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Creodonts and carnivores from the Middle Miocene Muruyur Formation at Kipsaraman and Cheparawa, Baringo District, Kenya

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Abstract

The Middle Miocene Muruyur Formation (ca 14.5 Ma), Tugen Hills, Kenya, has yielded a huge creodont and a variety of carnivores ranging in size from mongoose-sized viverrids and herpestids to lion-sized amphicyonids. The fauna partly fills what used to be a major gap in our knowledge of Neogene African carnivores, spanning the period between the better known Early Miocene assemblages of western Kenya and eastern Uganda, and the Late Miocene and Plio–Pleistocene faunas of East Africa. Present in the deposits are *Megistotherium*, two species of *Hecubides*, one species of *Agnotherium*, *Herpestes*, *Vishnuictis*, and one or two undetermined felids. ***To cite this article: J. Morales, M. Pickford, C. R. Palevol 7 (2008).***

Résumé

Créodontes et carnivores du Miocène moyen de la Formation de Muruyur à Kipsaraman et Cheparawa, district de Baringo, Kenya. La formation Muruyur du Miocène moyen (environ 14,5 Ma) des Tugens Hills, Kenya, a livré un énorme créodonte et des carnivores comprenant des viverridés et des herpestidés de la taille d'une mangouste et des amphicyonidés atteignant celle d'un lion. La faune remplit partiellement une lacune majeure de nos connaissances des carnivores du Néogène africain, remplissant la période entre, d'une part, les assemblages du Miocène inférieur les mieux connus de l'Ouest du Kenya et de l'Est de l'Ouganda et, d'autre part, les faunes du Miocène supérieur et du Plio–Pléistocène d'Afrique de l'Est. On retrouve dans ces dépôts *Megistotherium*, deux espèces d'*Hecubides* dont une nouvelle, une espèce nouvelle de *Vishnuictis*, une espèce respectivement d'*Agnotherium* et *Hespestes*, ainsi qu'un ou deux félins indéterminés. ***Pour citer cet article : J. Morales, M. Pickford, C. R. Palevol 7 (2008).***

Keywords: Africa; Middle Miocene; Creodonta; Carnivora

Mots clés : Afrique ; Miocène moyen ; Creodonta ; Carnivora

1. Introduction

The Middle Miocene Muruyur Formation crops out extensively along the crest of the Tugen Hills, Baringo District, Kenya. The sediments consist of lacustrine and

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pedogenic deposits sandwiched between phonolite lavas of Middle Miocene age. Behrensmeyer et al. [5] published radioisotopic dates from lavas underlying the fossiliferous deposits and ignimbrites within the sedimentary succession that suggested an age of about 15.5 Ma for the main fossil levels at Kipsaraman, but new analyses of the phonolite that underlies the fossil beds at Kipsaraman indicate that the sediments are younger than 14.7 Ma. In the type area at Muruyur [18], some 10 km north of Kipsaraman, the deposits are considerably thicker and span a greater period of time 15–14.5 Ma. Some of the fossils described here came from Chaparawa in the type area at Muruyur, whilst others were collected at Kipsaraman.

2. Systematic descriptions

Order Creodonta Cope, 1875
Family Hyaenodontidae Leidy, 1869
Genus *Megistotherium* Savage, 1973
Species *Megistotherium osteothlastes* Savage, 1973
Material. BAR 217'99, left upper canine from Cheparawa.

Description

The specimen is a huge canine with a massive root (Fig. 1). The apex of the crown is worn oblique to the long axis of the tooth indicating that it was oriented procumbently in the jaw. The wear facet is curved in section, suggesting that the lower canine was oval in outline. The upper canine crown is oval in section with a posterior crest but none anteriorly and the enamel is smooth. Lingually the cervix rises apically into an open u-shape. The crown is canted slightly outwards on its root. The root is huge, being about twice the size of the crown. It has a lingual groove in its rootward half, that fades out towards cervix. At cervix the crown measures $L = 46.0$ mm, $B = 36.5$ mm, but the greatest dimensions are in the middle of the root where it measures $L = 52.6$, $B = 39.0$ mm. The root is 104 mm deep, the crown, which is missing its tip due to wear is 64 mm high.

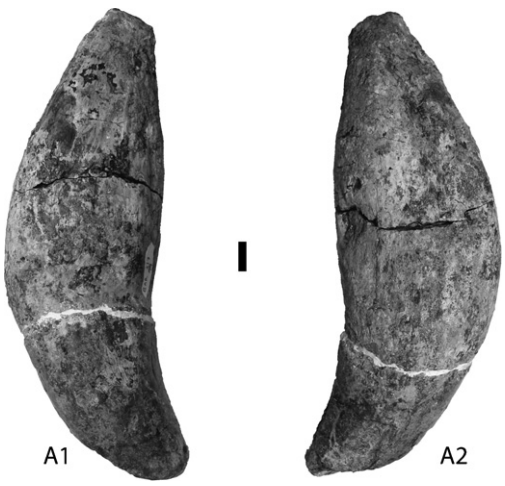

Fig. 1. BAR 217'99, *Megistotherium osteothlastes* left upper canine from Cheparawa (ca 14.5 Ma), Tugen Hills, Kenya, buccal (A1) and lingual (A2) views (scale: 10 mm).
Fig. 1. BAR 217'99, *Megistotherium osteothlastes*: canine supérieure gauche de Cheparawa (ca 14.5 Ma), Tugen Hills, Kenya, vue buccale (A1) et linguale (A2) (échelle : 10 mm).

Discussion

The Cheparawa canine is from a huge animal. Comparison with *M. osteothlastes* from Gebel Zelten, Libya indicates that it is about the same size, the canine alveoli of the Libyan skull being $L = 60$, $B = 37$ and the root depth 87 mm. Three Kenyan specimens figured by Savage ([21], Fig. 20) are similar in cervix dimensions, the specimen from Rusinga being $L = 51$, $B = 32$, and the two specimens from Fort Ternan each being $L = 51$, $B = 37$ mm. The only creodont that attains such a large size is *Megistotherium*, although *Hyainailouros* is almost as large. *Megistotherium* is known from Libya, Egypt, Kenya and Uganda whereas *Hyainailouros* has been reported from Namibia [13] and Egypt, as well as Europe and Asia. It has been suggested that *Megistotherium* and *Hyainailouros* could be synonyms [12], but until a revision of all the material from Europe, India and Africa is made, there will remain doubt about the status of these taxa. Rasmussen et al. [19] argued that *Hyainailouros* and *Megistotherium* differ at the generic level on the basis that the p4 of the latter genus bears a small, trenchant hypoconid and the tooth itself is obliquely oriented in the mandible, unlike the condition in *Hyainailouros*. However, some specimens of the European species *H. sulzeri* possess a posterior accessory cuspid in p4 [9] so this may be a variable character, and thus not significant for determining generic status. If Rasmussen et al. [19] is right, then Wadi Moghara would possess two genera of gigantic hyaenodonts, *Hyainailouros fourtaui* and *M. osteothlastes* [16].

Problems frequently encountered when interpreting the European species *H. sulzeri* are due to its rather poor representation in the fossil record and the large range of metric variation that it has, possibly due to a combination of significant sexual bimodality and individual variation. Partly because of this, the taxonomy of the various species of *Hyainailouros* is not settled. European material is usually classed as *H. sulzeri* [9] as has the collection from Arrisdrift, Namibia [13]. A specimen from Wadi Moghara, Egypt is the

holotype of *H. fourtaui*, the Gebel Zelten specimens are attributed to *M. osteothlastes* and material from East Africa has been classified in *Hyainailouros nyanzae* and *M. osteothlastes* [12]. The genus is also reported under the name *Hyainailouros bugtiensis* in Pakistan [20]. On account of its size, we attribute the Cheparawa specimen to *M. osteothlastes* pending a revision of the genera *Megistotherium* and *Hyainailouros*.

M. osteothlastes was recently recorded from the Ngorora Formation, Tugen Hills, Kenya [12] and it is also known from Grillental in the Sperrgebiet, Namibia and Moroto I, Uganda. It was thus widespread geographically and geochronologically, having been found in northern, central and southern Africa in deposits ranging in time from ca 22.5 to 12.5 Ma.

Order Carnivora Bowdich, 1821
Family Amphicyonidae Trouessart, 1885
Genus *Hecubides* Savage, 1965
Species *Hecubides macrodon* Savage, 1965

Material. BAR 635'99, right M2 and BAR 918'99, left lower canine from Kipsaraman.

Description

The molar ($L = 15.8$ mm, $B = 21.5$ mm) is lingually enlarged, and as a consequence has a pseudorectangular occlusal outline (Fig. 2B). The paracone is broken externally, but we can observe its large size relative to the metacone, and the presence of a well developed parastyle, whereas the metastyle is weak. The protocone is low and is located centrally, being united to the relatively strong paraconule and a weak metaconule, the three cusps being disposed in a semicircle, delimiting the central valley from the flat trigon and displaced posteriorly. The external cingulum is strong and joins the lingual cingulum which is strongly developed. Between the lingual cingulum and the protocone there is a semicircular valley.

The canine (Fig. 2C) is close in morphology to a lower canine of *Amphicyon major* from Sansan, France [8], but it is smaller. The crown is small relative to the root. The tooth is slightly compressed transversely with well marked vertical crests, one anteriorly, the other posterolingual. The external surface between these crests is convex, whereas the internal surface is almost flat. There is no trace of a basal cingulum.

Discussion

The M2 is larger than those of *Hecubides euryodon*, and could correspond in size to *H. macrodon*. Morphologically it is close to *H. euryodon*, in particular by its rectangular occlusal outline and the central position of the protocone. In other features it is close to the Lothagam amphicyonid sp. A described by Werdelin [27] which is appreciably larger, and could correspond to a large species such as *A. major* or *Amphicyon giganteus*. The molar attributed to *Cynelos* sp. nov. from Wadi Moghara [16] is somewhat larger than the molar from Kipsaraman, but the two teeth are morphologically similar.

Relationships of the Kipsaraman species to the Late Miocene amphicyonid from Samburu Hills, Kenya [24] are difficult to explore on account of the lack of common elements, the material from Samburu being two fragments of mandible.

Species *Hecubides minor* sp. nov.

Holotype. BAR 301'99, left m2 from Kipsaraman.

Type locality. Kipsaraman, Baringo District, Kenya.

Other material. BAR 2196'01, left m3 from Kipsaraman.

Diagnosis. Species of *Hecubides* appreciably smaller (ca 16%) than the type species of the genus *Hecubides euryodon* Savage, 1965.

Derivatio nominis. The species name refers to the small size of this amphicyonid.

Description

The m2 is rectangular in occlusal outline (Figs. 2D, 3B), with the trigonid only slightly larger than the talonid ($L = 11.5$ mm, $B = 7.3$ mm). The trigonid is dominated by the protoconid, which is much higher and bigger than the metaconid, the two cusps being located one in front of the other. The protoconid is pyramidal, and possesses a well developed anterior cristid, another internal one, almost transverse, which contacts the internal cristid of the metaconid, and a third one posteriorly, the last being slightly bifurcate, with one arm more developed that leads towards the buccal wall of the tooth, and another much smaller one that joins the anterior cristid of the hypoconulid. The metaconid, which is more extensive than the protoconid, also has three cristids; the internal one already mentioned, that contacts the protoconid is quite short. A well developed anterior cristid borders the entire anterior part of the tooth until it contacts the anterior cristid of the protoconid, but there is no sign of the presence of the paraconid. The junction of the two anterior cristids delimits a high and completely closed anterior valley. Finally, the posterior cristid of the metaconid, which is also well developed and peripheral, contacts the entoconid.

The talonid is dominated by the high and strongly developed hypoconid, its anterior cristid is very long and well developed, the posterior cristid is smaller and continues as a small high crest that closes the tooth pos-

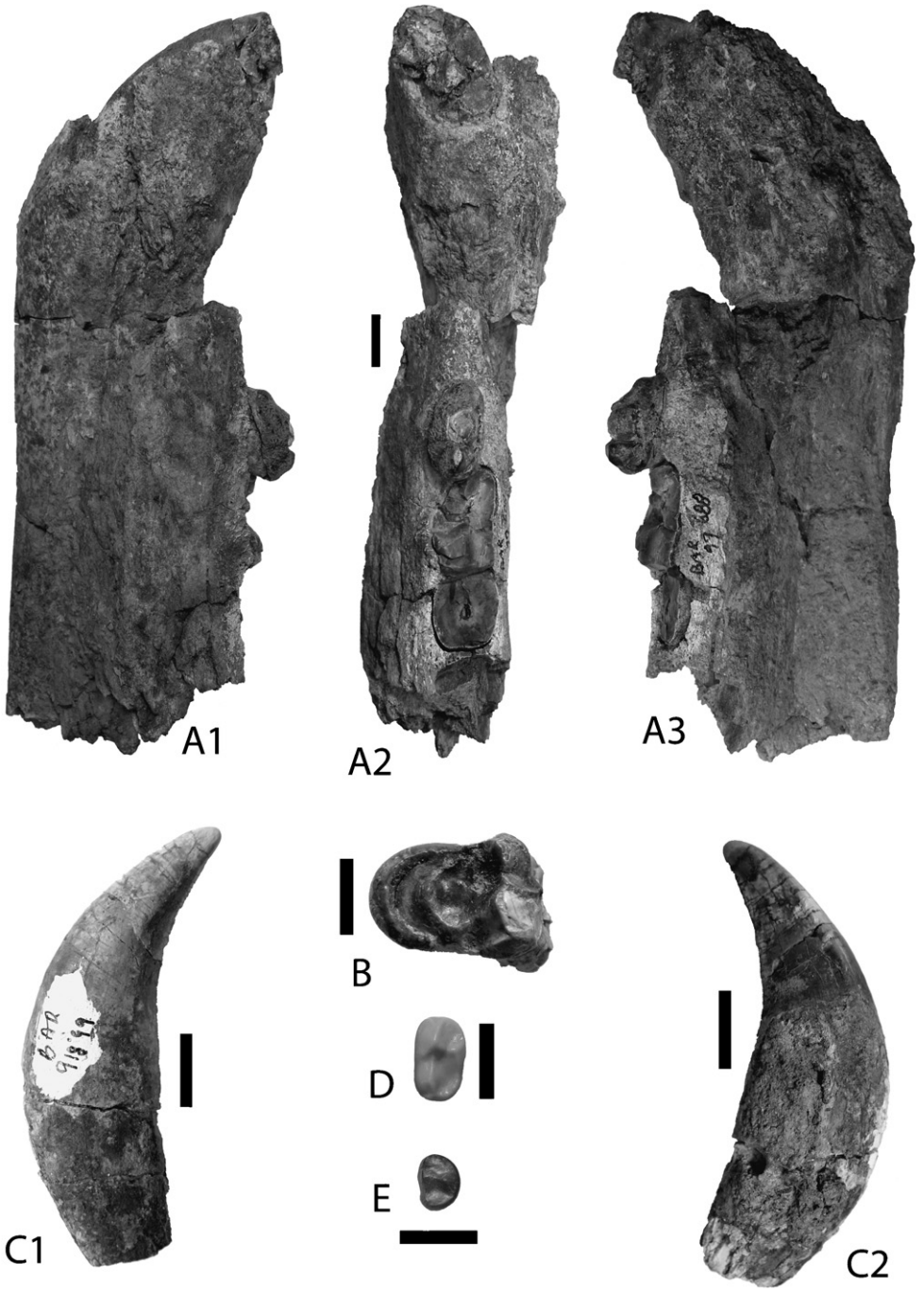

Fig. 2. Amphicyonidae from Kipsaraman (ca 14.5 Ma), Tugen Hills, Kenya. A: BAR 688'99, *Agnotherium* cf *kiptalami*, left mandible, buccal (A1), occlusal (A2) and lingual (A3) views; B: BAR 635'99, *Hecubides macrodon*, right M2, occlusal view; C: BAR 918'99 *Hecubides macrodon*, left lower canine, buccal (C1) and lingual (C2) views; D: BAR 301'99, *Hecubides minor* nov. sp., cast of holotype left m2, occlusal view; E: BAR 2196'01, *Hecubides minor* nov. sp., paratype left m3, occlusal view (scale: 10 mm).

Fig. 2. Amphicyonidae de Kipsaraman (ca 14.5 Ma), Tugen Hills, Kenya. A : BAR 688'99, *Agnotherium* cf *kiptalami*, mandibule gauche, vues buccale (A1), occlusale (A2) et linguale (A3) ; B : BAR 635'99, *Hecubides macrodon*, M2 droite, vue occlusale ; C : BAR 918'99 *Hecubides macrodon*, canine inférieure gauche, vues buccale (C1) et linguale (C2) ; D : BAR 301'99, *Hecubides minor* nov. sp., moulage de la m2 gauche holotype, vue occlusale ; E : BAR 2196'01, *Hecubides minor* nov. sp., m3 gauche paratype, vue occlusale (échelle : 10 mm).

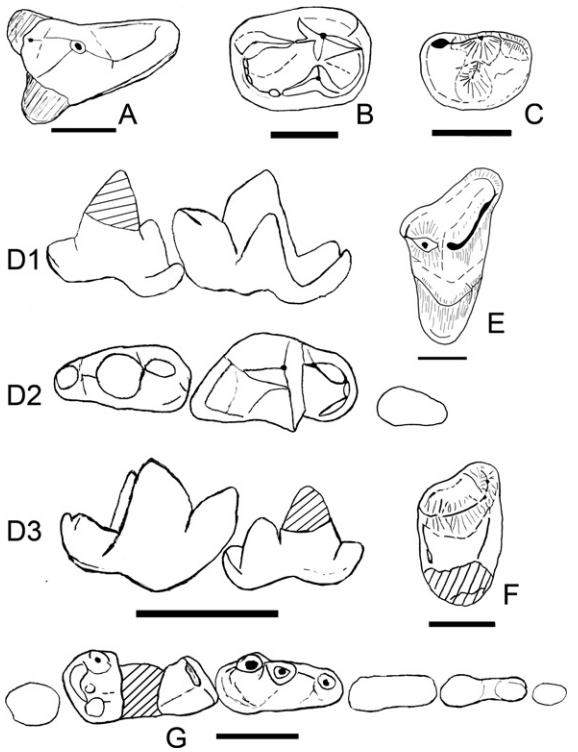

Fig. 3. Interpretive drawings of carnivore teeth from the Muruyur Formation (ca 14.5 Ma), Tugen Hills, Kenya. A: Felidae left P4, occlusal view; B: *Hecubides minor* nov. sp., holotype left m2, occlusal view; C: *Hecubides minor* nov. sp., paratype left m3, occlusal view; D: *Herpestes* sp., right mandible containing p4, m1, lingual (D1), occlusal (D2) and buccal (D3) views; E: *Herpestes* sp., right M1, occlusal view; F: *Herpestes* sp., right M2, occlusal view; G: *Vishnuictis africana* nov. sp., holotype left mandible occlusal view (scales: 5 mm except for Figs. E, F which are 2 mm).

Fig. 3. Dessins interprétatifs des dents de carnivores de la formation Muruyur (ca 14.5 Ma), Tugen Hills, Kenya. A : P4 gauche de Felidae, vue occlusale ; B : *Hecubides minor* nov. sp., m2 gauche holotype, vue occlusale ; C : *Hecubides minor* nov. sp., m3 gauche paratype, vue occlusale ; D : *Herpestes* sp., mandibule droite avec p4, m1, vues linguale (D1), occlusale (D2) et buccale (D3) ; E : *Herpestes* sp., M1 droite, vue occlusale; F : *Herpestes* sp., M2 droite, vue occlusale; G : *Vishnuictis africana* nov. sp., mandibule gauche holotype, vue occlusale (échelles: 5 mm, sauf pour Fig. E, F : 2 mm).

teriorly and could correspond to a hypoconulid and to the posterior continuation of the entoconid. The entoconid is weakly developed and is located at the periphery of the tooth. Because of this the talonid is completely closed, delimiting a wide medial valley, which is low and displaced lingually. The external cingulum is smooth, almost imperceptible, but anteriorly and posteriorly it forms a clear vertical cristid, the posterior one contacting the posterior cristid of the hypoconid.

The m3 ($L = 7.0$ mm, $B = 4.9$ mm) is small relative to the m2, as is usual in amphicyonids (Figs. 2E et 3C). The trigonid is large compared to the talonid, and comprises a well developed protoconid separated by a smooth incision from an anterior crest which can be interpreted as the paraconid, and a low metaconid which is displaced posteriorly. The trigonid valley is flat and opens lingually. The talonid is formed of a large hypoconid, the talonid valley is similar in morphology to the trigonid one and also opens posterolingually.

Discussion

The attribution of these specimens to *Hecubides* is based on the similarity of the morphology of m2 to the type species *H. euryodon*. Despite the scarcity of material, it is clear that the Kipsaraman species is substantially smaller than *H. euryodon* (Table 1), providing sufficient evidence that it represents a different species.

Despite the 16% difference in size, the species *Hecubides euryodon* and *H. minor* have m2 s that are similar morphologically, in particular in the obvious absence of the paraconid, which is present in *Cynelos*, *Pseudarctos* and *Ictiocyon* [6,10,25]. The presence of a paraconid in these genera indicates that the anterior valley of the trigonid is not as closed as it is in *Hecubides*. In the rest of its morphology, the m2 of *Hecubides minor* is quite close to that of *Ictiocyon dehmi*, in particular in its size and the morphology of the cristids of the protoconid and the morphology of the talonid.

Genus *Agnotherium* Kaup, 1833

Species *Agnotherium* cf. *kiptalami* Morales and Pickford, 2005

Material. BAR 688'99 left mandible from Cheparawa, with symphysis, canine root, p4, root of m1 and part of the alveolus of m2. The ramus is fractured into two large fragments which are displaced relative to one another.

Description

The strongly developed mandibular symphysis is an obvious feature of the specimen (Fig. 2A). It is broad and robust, and is separated from the ramus by a strong keel. The ramus is also robust and has what appears to be two small mental foramina in the upper third of the jaw, one beneath the anterior part of the p4 and the other 2.5 cm in front of it. The canine is represented only by its root, which is large ($L = 22$ mm, $B = 16$ mm). Between the canine and the p4 the upper part of the jaw is displaced and in the well preserved parts there are no obvious signs of alveoli for anterior premolars, but the bone is damaged, especially near the p4. The p4 ($L = 18.2$ mm, $B = 9.5$ mm) is robust, and its occlusal outline is oval, it has no anterior cuspid although there is a slight swelling of the basal part of the lingual cingulum from which departs a crest that reaches the main cusp.

Table 1
Comparison of dimensions (in mm) of *Hecubides euryodon* and *Hecubides minor*.
Tableau 1
Comparaison des dimensions (mm) d'*Hecubides euryodon* et *Hecubides minor*.

Species	Catalogue N°	Locality	Tooth	Length	Breadth
Hecubides euryodon	CMF 4027	Rusinga	m2	13.7	10.3
Hecubides minor	BAR 301'99	Kipsaraman	m2	11.5	7.3

The main cusp has lost its apex. The posterior cuspid is high and robust, dominating the posterior part of the premolar. The posterior cingulum is weak and the lingual one of moderate size. Only the roots of the carnassial are preserved (L = ca 34 mm, B = ca 15 mm) but they show the characteristic outline of amphicyonids and the large dimensions relative to the p4, as well as the great development of the part corresponding to the trigonid in relation to the talonid part.

Discussion

The dimensions of the amphicyonid mandible from Cheparawa correspond to an animal somewhat smaller than *Amphicyon major* from Sansan, France [8], but similar in dimensions to *Afrocyon burolleti* from Gebel Zelten, Libya [1]. However, morphologically it is clearly distinct from these two forms in the strong development of the mandibular symphysis, the broader ramus between the p4 and the canine, and in the morphology of the p4, which is more robust and with a better developed, more vertical posterior cuspid. A robust mandible with strongly developed symphysis occurs in *Thaumastocyon bourgeoisi* from Pont Levoy, France [23], which is similar in size to the African fossil, but its p4 is missing and the root obliterated, which makes comparison impossible. In contrast, in *Agnotherium antiquum* from Frohnstetten, Germany [11], the p4 is preserved but not the mandible. The Frohnstetten tooth is close to the one from Chepawara both in dimensions (L = 17.3 mm, B = 9 mm) and morphology, notably in the strong development of the posterior cuspid and its position and orientation. Finally, the jaw from Cheparawa corresponds in size and proportions to the snout of *Agnotherium kiptalami* from Ngorora (12.5 Ma) described by Morales and Pickford [12], and in consequence the Cheparawa fossil is reasonably attributed to this species.

The p4 in the mandible from Samburu Hills, Kenya, attributed to Amphicyonidae or Ursidae indet. by Tsujikawa ([24], Fig. 1) is incompletely erupted, so it is difficult to make morphological comparisons with the Cheparawa mandible. According to Tsujikawa the p4 has no anterior or posterior cusplets, in which case it is not the same as the Cheparawa specimen, but its dimensions (L = 15.3 mm × B = 9.5 mm) are the same order of magnitude.

Family Viverridae Gray, 1821
Genus *Vishnuictis* Pilgrim, 1932
Species *Vishnuictis africana* nov. sp.

Holotype. BAR 280'02 left mandible with p4-m1 and alveolus of m2, broken anterior premolars and canine alveolus, from Kipsaraman (Fig. 4E).

Type locality. Kipsaraman, Baringo District, Kenya.

Diagnosis. *Vishnuictis* of small size, gracile premolars and p4 with well developed posterior cuspid.

Derivatio nominis. The species name is to record the extension of the range of the genus to the African continent.

Description

The alveolus of the m2 is rounded, probably uniradiculate and of moderate size. The m1 (L = 9.2 mm, B = 4.4 mm) is broken at the level of the protoconid–metaconid, but we can observe many details of great interest (Fig. 3G, 4E). The paraconid is located in an anterobuccal position, which suggests that the carnassial blade (paraconid–protoconid) was quite extensive. The talonid is relatively short, with a hypoconid that is only slightly bigger than the entoconid, and the two cusps are united by way of a crestiform hypoconulid, such that the talonid is closed posteriorly. The talonid valley is relatively narrow and is partly occupied by an isolated cuspid located close to the hypoconulid. The p4 (L = 8.8 mm, B = 3.3 mm) is an elongated gracile tooth, with three aligned cusps, the posterior one is somewhat better developed than the anterior one. There is a well developed posterolingual cingulum that delimits a high and narrow valley between it, the posterior cusplet and the main cusp. The rest of the premolars are represented by the roots, p3 and p2 are elongated, and were probably similar in morphology to the p4, the p1 is reduced, with a single root. The diastema is very short, and the alveolus of the canine is oval.

Discussion

The morphology of the talonid of m1 and the p4 indicate that we are in the presence of a genus close to

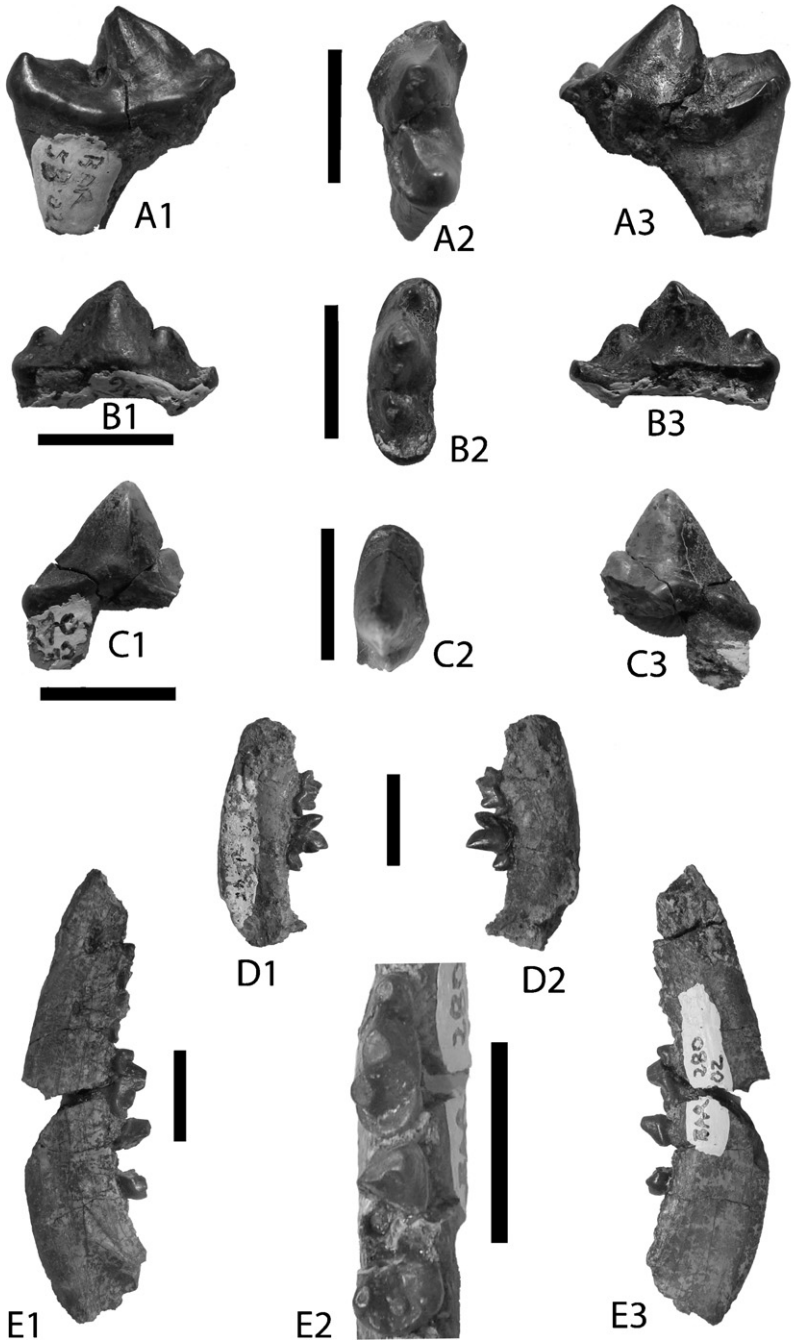

Fig. 4. Viverridae, Herpestidae and Felidae from Kipsaraman (ca 14.5 Ma), Tugen Hills, Kenya. A: BAR 58'02, Felidae left P4, buccal (A1), occlusal (A2) and lingual (A3) views; B: BAR 983'02, Felidae left p4, buccal (B1), occlusal (B2) and lingual (B3) views; C: BAR 270'02, Felidae incomplete left P3, buccal (C1), occlusal (C2) and lingual (C3) views; D: BAR 1045'99, *Herpestes* sp., right mandible fragment with p4, m1 and alveolus of m2, lingual (D1) and buccal (D2) views; E: BAR 280'02, *Vishnuictis africana* nov. sp. holotype left mandible with p4-m1 and alveoli of p1-p3 and m2, buccal (E1), occlusal (E2) and lingual (E3) views (scale: 10 mm).

Fig. 4. Viverridae, Herpestidae et Felidae de Kipsaraman (ca 14.5 Ma), Tugen Hills, Kenya. A : BAR 58'02, P4 gauche de Felidae, vues buccale (A1), occlusale (A2) et linguale (A3) ; B : BAR 983'02, p4 gauche de Felidae, vues buccale (B1), occlusale (B2) et linguale (B3) ; C : BAR 270'02, P3 gauche incomplète de Felidae, vues buccale (C1), occlusale (C2) et linguale (C3) ; D : BAR 1045'99, *Herpestes* sp., fragment de mandibule droite avec p4, m1 et alvéole de m2, vues linguale (D1) et buccale (D2) ; E : BAR 280'02, *Vishnuictis africana* nov. sp. mandibule gauche holotype avec p4-m1 et alvéoles de p1-p3 et m2, vues buccale (E1), occlusale (E2) et linguale (E3) (échelle : 10 mm).

Viverra. It differs from the primitive European hyaenids of the *Protictitherium* or *Plioviverrops* kind, in the lesser height of the cuspids of the talonid of m1 and its more bunodont morphology. *Viverrictis modica* from La Grive, France [4,26], differs in the distinct morphology of the talonid of the p4 and of the m1. It differs from *Viverra* in the lower talonid of m1, with lower cusps and by the presence of a well developed anterior cuspid on p4, and for similar reasons it differs from *Viverricula*, which besides possesses sharp cusps that distance it from the African form. It differs from *Orangictis*, from the basal Middle Miocene of Arrisdrift, Namibia, in the less robust structure of the dentition and the better development of the anterior cuspid of the p4.

Without doubt, the most similar form is *Viverra chinjiensis* Pilgrim, 1932 from Pakistan, from which the Kipsaraman species differs in its slightly smaller size, the more gracile aspect of the preserved teeth and a better developed posterior cuspid in p4. *Viverra chinjiensis* is close to *Vishnuictis salmontanus* Pilgrim, 1932, and these two species, together with the new African one, can be provisionally attributed to the genus *Vishnuictis*.

Family Herpestidae Bonaparte, 1845

Genus *Herpestes* Illiger, 1811

Species *Herpestes* sp. indet.

Referred material. BAR 1045'99, mandible fragment with p4, m1 and alveolus of m2, BAR 690'03, right M1 and BAR 2697'03, right M2.

Locality. Kipsaraman, Baringo District, Kenya.

Age. Middle Miocene, ca 14.5 Ma.

Description

BAR 1045'99 is a mandible with p4 and m1 in good condition (Figs. 3D, 4D, 5A) (p4: $L = 4.8$ mm, $B = 2.5$ mm; m1: $L = 6.5$ mm, $B = 3.4$ mm). The p4 is relatively narrow with a small anterior, vertically oriented cusplet projecting anteriorly. The central cusp is of moderate size, the posterior cuspid is bigger than the anterior one, is higher and leans backwards. There is a posterolingual basal expansion delimited by a high but weakly developed cingulum.

The trigonid of the m1 is V-shaped in occlusal view, with the paraconid located in an anterior position, lower than the protoconid and only a little bit higher than the metaconid. The talonid is short, formed of an individualized hypoconid, a tiny hypoconulid and a peripheral entoconid. In the lingual wall, the separation between the metaconid and entoconid is deep and wide.

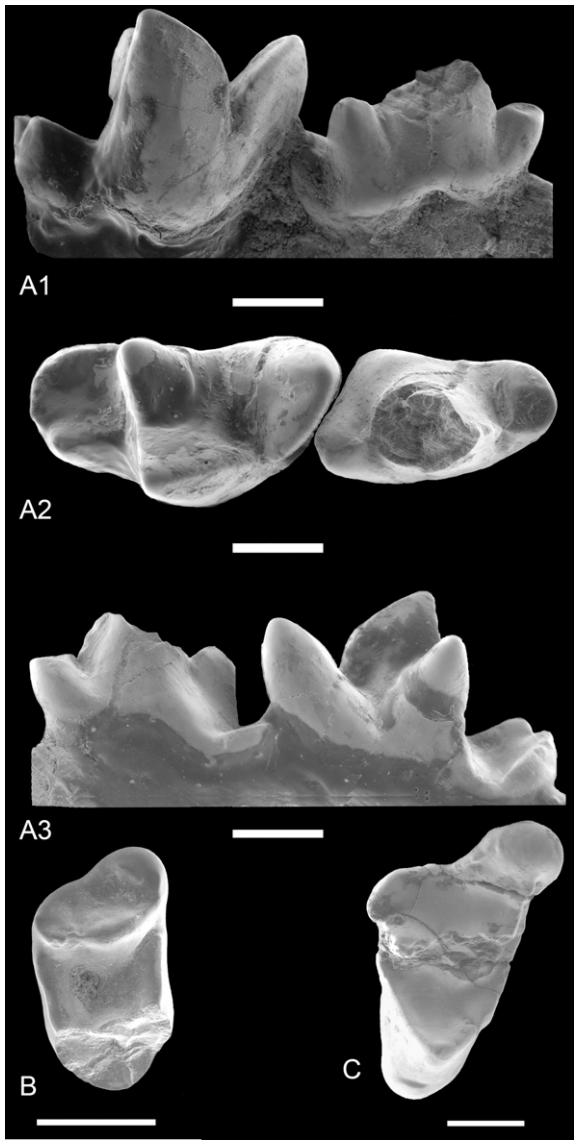

Fig. 5. Scanning electron microscope images of *Herpestes* sp. from Kipsaraman (ca 14.5 Ma) Tugen Hills, Kenya. A: BAR 1045'99, right mandible fragment containing p4-m1, buccal (A1), occlusal (A2) and lingual (A3) views; B: BAR 2697'03, right M2, occlusal view. C: BAR 690'03, right M1, occlusal view (scale: 2 mm).

Fig. 5. Images au microscope électronique à balayage de *Herpestes* sp. de Kipsaraman (ca 14.5 Ma) Tugen Hills, Kenya. A : BAR 1045'99, fragment de mandibule droite avec p4-m1, vues buccale (A1), occlusale (A2) et linguale (A3) ; B : BAR 2697'03, M2 droite, vue occlusale ; C : BAR 690'03, M1 droite, vue occlusale (échelle : 2 mm).

The mandible has an alveolus for the m2 which was probably quite a large tooth.

BAR 690'03, a right M1 (Figs. 3E, 5C) ($L = 3.8$ mm, $B = 7.3$ mm) has a crest-like protocone in the shape of a dune, which has a small lingual cingulum. The paracone is strong and continuous with the parastyle which is

elongated lingually. The metacone is small and conical. The labial cingulum is weak.

BAR 2697'03 is a right M2 (Figs. 3F, 5B) ($L = 2$ mm, $B = 4$ mm). It has a reduced paracone and metacone joined together by a crest. The paracone is noticeably more developed than the metacone and extends into a parastyle in the shape of a crest. The area of the protocone is slightly eroded.

Discussion

Herpestes sp. from Kipsaraman is comparable in size to, or smaller than, the smallest extant species of the genus *Herpestes*, such as *Herpestes javanicus* or *Herpestes pulverulentus*, and is smaller than the Pliocene fossil species *H. abdelalii* from Ahl Al Oughlam, Morocco [7] and *H. palaeoserengetensis* from Laetoli, Tanzania [17]. The Kipsaraman specimen shares the following features with the genus *Herpestes*: m1 with v-shaped trigonid, talonid formed of an individualized hypoconid, a minuscule hypoconulid and a peripheral entoconid. In the lingual wall the separation between metaconid and entoconid is deep and wide. The p4 is tricuspid with a large anterolingual platform. The M1 is relatively narrow, and the M2 is reduced. Several carnivore species from the Early Miocene of East Africa described by Schmidt-Kittler [22] show affinities to the Kipsaraman species, including *Herpestides aequatorialis*, *Leptoplesictis rangwai* (mandible KNM RU 15990) and *Leptoplesictis mbitiensis. Herpestides aequatorialis* differs markedly from European species of *Herpestides* in the greater development of the basal expansion in the P3, the relatively short P4 with a strong protocone and the structure of the m1. In all these features in which European *Herpestides* differs from *Herpestides aequatorialis*, it approaches *Protictitherium*, another genus on the line leading towards the modern hyaenas [3]. Despite the scarcity of material, *Herpestides aequatorialis* is very close to the species classified by Schmidt-Kittler [22] in the genus *Leptoplesictis*. For Beaumont [4] *Leptoplesictis* presented affinities with *Herpestides*, but in some features such as the reduction of the protocone of P4, the enlargement of the two carnassials and the gracility of the premolars, it recalls viverrids of the *Genetta* kind. In our opinion, it is possible that these three species from the Early Miocene of East Africa could be related to the Kipsaraman *Herpestes* sp., and if so then they would represent primitive members of the family Herpestidae, but additional evidence, in particular the morphology of the auditory region, would be necessary to confirm the presence of the family in the Early Miocene of East Africa. In conclusion *Herpestes* sp. from Kipsaraman possesses characteristics typical of extant *Herpestes*, and for the time being represents the oldest known evidence of the family Herpestidae in Africa. The earliest record of the genus in the Siwaliks of Pakistan is ca 10 Ma [2].

Family Felidae Gray, 1821

Genus and species indeterminate

Material. BAR 58'02, slightly damaged left P4; BAR 270'02, incomplete left P3; BAR 983'02, left p4; BAR 1051'99, lower premolar.

Description

BAR 58'02, a left P4, is missing the anterior basal part of the parastyle, which is low and moderate in size (Figs. 3A, 4A). The protocone is broken, but we can observe that the union with the paracone occurs at the anterior basal part of this cusp. The paracone ($L = 7.5$ mm) is longer than the metastyle ($L = 6.7$ mm) and is robust and high with two sharp crests, one anterior the other posterior, and a third, smoother crest which leads towards the base of the protocone. The metastyle is a low, relatively robust blade. There is a strong lingual cingulum and a more moderate buccal one.

BAR 270'02, a left P3, is broken posteriorly (Fig. 4C). The main cusp is high, there is no anterior cusplet, only a slight bump where the anterior crest of the main cusp meets the anterior cingulum, which is high and strong. There is a low posterior cusplet, and even though the rest of the tooth is missing, it is possible to make out that the base of the main cusp expands lingually, which means that there was a basal lingual expansion. The lingual cingulum is relatively strong and the buccal one more moderate.

BAR 983'02, a left p4 (Fig. 4B) ($L = 15.4$ mm, $B = 5.8$ mm), has no roots and the base of the tooth is eroded somewhat at the level of the cingulum. Where it is preserved the lingual cingulum appears stronger than the buccal one. The crown is elongated and narrow with a gently curved occlusal outline, concave lingually. The main cusp is relatively low, the anterior and posterior cusplets are the same height, but the posterior one is bigger than the anterior one. The tooth terminates distally in a long, narrow talonid.

Discussion

The p4 is quite peculiar, being elongated and narrow with a relatively low main cusp. It recalls *Pseudaelurus quadridentatus* from Sansan, France, but is more robust, especially in its posterior half. The incomplete P3 also shows a lengthening of the anterior part of the tooth, similar to that observed in the P3 of *Metailurus major*

Table 2
Carnivorans from the Muruyur Formation, Tugen Hills, Kenya.
Tableau 2
Carnivores de la formation Muruyur, Tugen Hills, Kenya.

Order	Family	Species
Creodonta	Hyaenodontidae	*Megistotherium osteothlastes* Savage, 1973
Carnivora	Amphicyonidae	*Hecubides macrodon* Savage, 1965
		Hecubides minor sp. nov.
		Agnotherium cf *kiptalami* Morales and Pickford, 2005
	Viverridae	*Vishnuictis africana* nov. sp.
	Herspestidae	*Herpestes* sp. indet.
	Felidae	2 spp. indet.

Zdansky, 1924, but not as much. In *P. quadridentatus* the anterior part of P3 is shorter and more vertical, as is the P3 of *Ginsburgsmilus napakensis* Morales, Salesa, Pickford and Soria, 2001 [13,15]. However, it is close to the latter in the retention of a sharp anterior crest on the main cusp, which is absent in *P. quadridentatus*.

The P4 is close to that of *G. napakensis* in the greater length of the paracone with respect to the metastyle. In this feature it differs from *P. quadridentatus*, in which the metastyle is equal in size to or longer than the paracone. It shares with both these species the scantily developed parastyle.

In summary, no Early or Middle Miocene felid from Africa possesses this combination of features, some of which are contradictory. The P4 is close to *Ginsburgsmilus napakensis*, but the P3 is more derived towards a morphology that occurs in Late Miocene felids. Whereas the p4 is elongated and narrow, as in *Diamantofelis ferox* Morales, Pickford, Fraile, Salesa, and Soria, 2003 the three cusps are noticeably higher. The classification of these four teeth into a single species is to say the least doubtful, if not improbable. The morphology of the P4 is more primitive than that of *G. napakensis*, whereas the premolars are clearly more derived. In its morphology, the p4 from Kipsaraman approaches *D. ferox*, which probably possessed an upper dentition of the *Ginsburgsmilus* type. But the elongation of the premolars and the lesser height of the cusps in p4 prevent us from classing these teeth in the Namibian genus.

3. General discussion

The carnivore fauna from basal Middle Miocene deposits at Kipsaraman (Table 2) helps to fill an important gap in the African fossil record that used to exist between the Early Miocene forms, on the one hand, and the Late Miocene ones, on the other.

It is notable that the presence of three species of Amphicyonidae of diverse sizes at Kipsaraman, indicates that the history of this group in Africa is more complex than hitherto considered possible. The Amphicyonidae were habitual elements of the African carnivore guild, at least from the Early Miocene until the Late Miocene, although their representation at fossil sites is generally restricted to one or two species [13,14,16,27]. The presence of *Herpestes* sp. at Kipsaraman is important, providing as it does, the earliest solid record of the family Herpestidae in Africa. The family is known at Ngorora, Kenya [12] and in later faunas from Lothagam and the Lukeino Formation [12,27]. Its presence at levels older than Kipsaraman is possible, but requires a revision of the Early Miocene mongoose-like species, and better documentation of the basicranium, in particular the ear region. The presence of the Viverridae *Vishnuictis africana* with Asian affinities is interesting as it suggests a closer relationship between the carnivores of Asia and Africa, than between those of Europe and Africa, as was already pointed out by Schmidt-Kittler [22]. The remaining carnivoran species at Kipsaraman (the large creodont *Megistotherium* and one or two species of Felidae) may be considered usual elements of African carnivore faunas of the epoch.

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