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CARNIVORES FROM THE MIDDLE MIOCENE NGORORA FORMATION (13-12 MA), KENYA

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ABSTRACT

The late Middle Miocene Ngorora Formation has yielded several interesting carnivore fossils. Among these are a huge creodont, *Megistotherium osteothlastes*, at 12 Ma, possibly the youngest record of the species, an amphicyonid, two species of mustelids (an otter and a honey badger), two kinds of viverrids (one about the size of a civet, one the size of a genet) and an extremely small herpestid the size of a dwarf mongoose. It has also yielded remains of a moderate sized percrocutid.

Perhaps the most interesting carnivore is a new genus and species of bundont viverrid that is intermediate in size and morphology between Early Miocene *Orangictis* on the one hand and Plio-Pleistocene *Pseudocivetta* on the other. This lineage of bundont viverrids appears to have been restricted to Africa.

RESUMEN

La Formación Mioceno medio final de Ngorora (Kenia) ha suministrado carnívoros muy interesantes. Entre los que se encuentran un enorme creodonto, *Megistotherium osteothlastes*, de 12 Ma, que posiblemente es el registro más moderno de la especie, un amphicyonido, dos especies de mustélidos (una nutria y un melivorino), dos diferentes tipos de vivérridos (uno de la talla de una civeta y el otro de la de una jineta) y un herpéstido diminuto de la talla de una mangosta enana. También hay fósiles de un percrocútido de talla moderada.

Tal vez el carnívoro más interesante es un nuevo género y especie de vivérrido bunodonto que presenta una talla y morfología intermedia entre Oragictis del Mioceno inferior y Pseudocivetta del Plio-Pleistoceno. Esta línea de vivérridos bunodontos parece estar restringida a Africa.

Introduction

The Ngorora Formation crops out widely in the Tugen Hills, Baringo District, Kenya (Fig. 1). It has been subdivided into five units (Bishop & Pickford, 1975) of which Members A-D are Middle Miocene (no signs of the equid *Hipparion*: strata equivalent to MN 7/8 in Europe) and Member E is basal Late Miocene (with *Hipparion*: strata equivalent to MN 9 in Europe) (Pickford, 2001). Radio-isotopic age determinations for the formation indicate that Member A is about 13 to 12.5 Ma, Member D about 12 to 11.5 Ma, and Member E about 11-10 Ma.

The formation is richly fossiliferous, and has yielded a rich diversity of plant and animal fossils (Bishop & Pickford, 1975) among which carnivores are well represented. Published faunal lists mention a large canid (in fact the amphicyonid *Agnotherium*) a mustelid related to *Mellivora* and a percrocutid, *Percrocuta tobieni* (Crusafont & Aguirre, 1971). A faunal list published by Hill *et al*., 1985, mentions the presence of three creodonts at Ngorora. In addition the same paper listed several fissipeds - *Pseudocyon* (?) *macrodon*, an unidentified arctoid, an otter *Vishnuonyx*, a mellivorine, cf *Thalassictis robusta*, *Protictitherium* sp., and *Percrocuta tobieni* but, apart from the last species, nothing has been published to substantiate these records. This paper describes a portion of the carnivore collection from Ngorora comprising a huge

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Fig. 1.—Location of Ngorora and Fort Ternan, late Middle Miocene, Kenya.

creodont, an amphicyonid, two mustelids, three viverrids and a percrocutid.

Systematic descriptions

Order Creodonta Cope, 1875
Family Hyaenodontidae Leidy, 1869
Genus *Megistotherium* Savage, 1973
Species *Megistotherium osteothlastes* Savage, 1973

Material: Bar 109'03 damaged right m/2 from Bartule, KNM BN 1328, distal left humerus from Kabarsero.

Locality and age: Bartule, Ngorora Formation, Member A, ca 13-12.5 Ma; Kabarsero, locality 2/10, Ngorora Formation, Member D, ca 12 Ma.

Description

Dentition: BAR 109'03, a right m/2 is an extremely large, but damaged tooth (Fig. 2a). Its morphology is typical of a lower carnassial with robust paraconid and protoconid, moderately compressed contour and of approximately equal size. The summit of the paraconid is broken. The buccal wall of the two cuspids is evenly convex but quite vertical, in contrast with the lingual wall which is inflated. The paraconid and protoconid are separated buccally by a deep notch and lingually by a high, wide valley. The two cusps are worn on the buccal side in typical carnassial fashion. The talonid is short, formed of a single cusplet, the hypoconid, which is quite compressed transversely. A smooth cingulum seems to surround the entire tooth, although parts of the base of the crown are not preserved. This cingulum is high in the talonid where it joins the crest of the talonid cusp. On the postero-buccal part of the hypoconid there is a possible contact facet caused by the m/2.

Measurements of the tooth are (L = ca. 53 mm; W = 26 mm).

Humerus: An isolated distal left humerus was found at locality 2/10, Kabarsero, Ngorora Formation (Fig. 2b). It has been slightly eroded and polished, but is otherwise well preserved. There is an elongated entepicondylar foramen. The trochlea is about 55 mm measured across the entepi- and ectepicondyles. The latter is appreciably larger than the former. The articular facet is shallowly conical for most of its breadth until it approaches the entepicondyle which flares steeply towards it. The trochlea is about 27 mm in diameter. The specimen is morphologically similar to a specimen from Gebel Zelten referred to *Megistotherium osteothlastes* by Savage (1973, fig. 14) but it is smaller. This record extends the range of the species upwards to Member D of the Ngorora Formation, ca 12 Ma.

Discussion: The size and morphology of the Bartule molar correspond closely with material attributed to *Megistotherium osteothlastes* by Rasmussen *et al*., (1989) from Wadi Moghara, Egypt.

Savage erected the genus *Megistotherium* for the species from Gebel Zelten, but it has never been clearly demonstrated that it differs morphologically from *Hyainailourus*. Doubts about the separation between the giant hyaenodont *Hyainailourus* from Europe, Asia and Africa (Helbing, 1925; Ginsburg, 1980; Pilgrim, 1912) and *Megistotherium* are reasonable (Rasmussen *et al*., 1989). However, pending resolution of the systematic status of these huge creodonts, we refer the Ngorora specimen to *Megistotherium osteothlastes*.

Gigantic creodonts are widespread in Early Miocene and Middle Miocene sites of Africa, although they are never very abundant (Savage, 1965, 1973). Giant hyaenodontids have been reported from various Middle Miocene localities in North Africa including Gebel Zelten, Libya (Savage, 1973) and Wadi Moghara, Egypt (Rasmussen *et al*., 1989; Von Koenigswald, 1947). In East Africa it is known from sites ranging in age from Meswa Bridge (ca 22.5 Ma) to Fort Ternan (ca 13.7 Ma) (Savage, 1973). Other East African sites that have yielded similar remains include Rusinga, Maboko, Ombo and Kipsaraman, Kenya, and Moroto

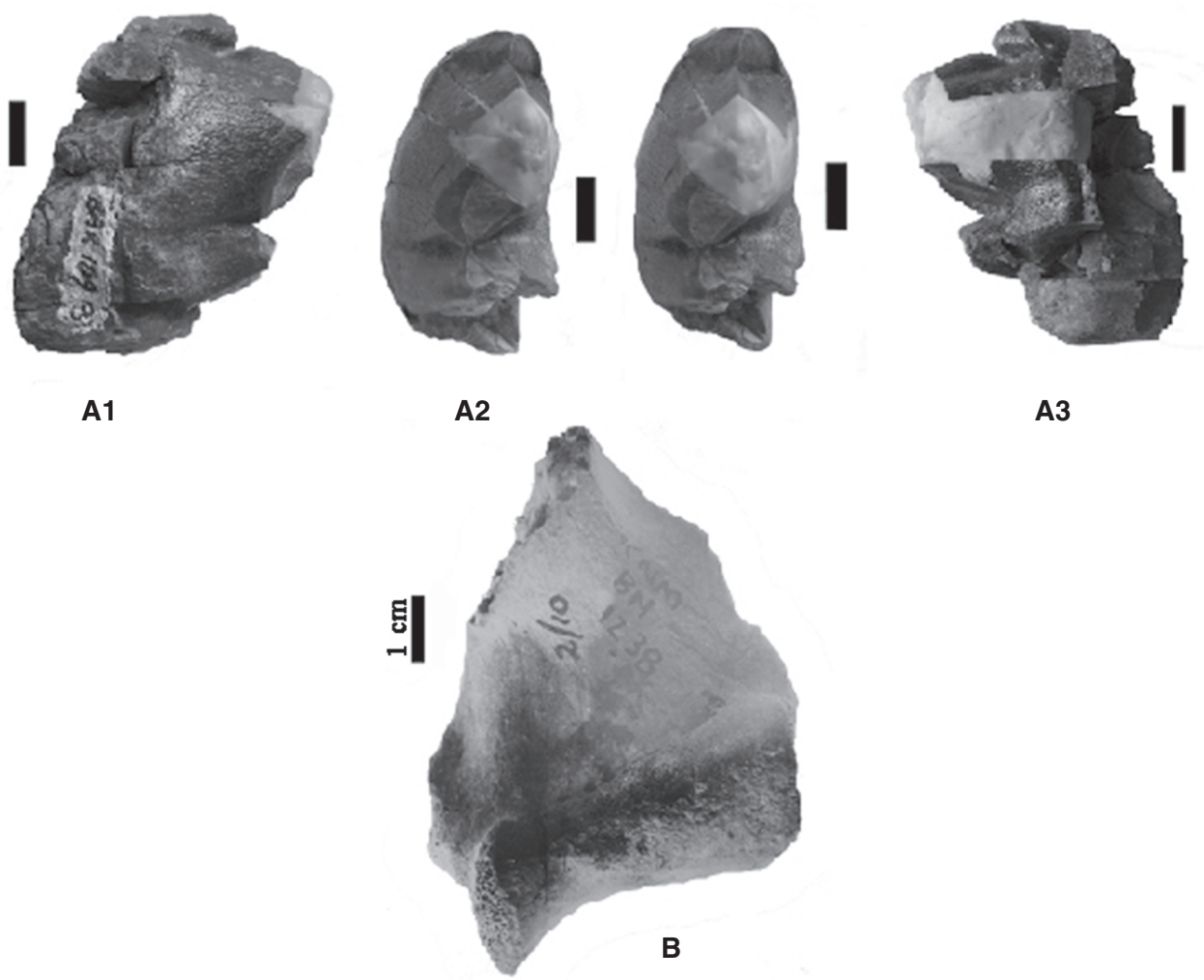

Fig. 2.—Hyaenodontidae from the Ngorora Formation, late Middle Miocene, Kenya. *Megistotherium osteothlastes*, A) Bar 109'03, right m/2 (Bartule) A1, buccal, A2, stereo occlusal, and A3, lingual views; B) KNM BN 1328, distal end of left humerus (Kabarsero) (Scale: 10 mm).

I, Uganda. The Ngorora records at 13-12 Ma are thus the youngest in Africa. Another large creodont, *Hyainailourus sulzeri* was described from the basal Middle Miocene site at Arrisdrift, Namibia (Morales *et al*., 2003) and it also occurs at Grillental, Namibia.

Order Carnivora Bowdich, 1821
Family Amphicyonidae Trouessart, 1885
Genus *Agnotherium* Kaup, 1833

Type species: *Agnotherium antiquum* Kaup, 1833.

Diagnosis: A genus of large amphicyonid in which felinoid characters are developed; snout shortened; canines elongated; anterior premolars reduced in dimensions; P3/ two rooted, small; P4/ large with small parastyle and reduced protocone; M1/-M2/ large canoid teeth; p/4 large, high crowned and pointed with marked backwards pitch; m/1 large, with high vertical paraconid and protoconid, no metaconid, talonid with a single lip, trenchant cusp; m/2 reduced; no m/3; jaw deep.

Species *Agnotherium kiptalami* nov.

Holotype: KNM BN 488, snout broken off behind the second molars (Fig. 3).

Diagnosis: A species of *Agnotherium* as large or slightly larger than a lion (*Felis leo*) in which the P3/ is rotated in the maxilla and tucked in close to the antero-lingual edge of P4/. Canines elongated, with sharp unserrated posterior edge and rounded anterior surface.

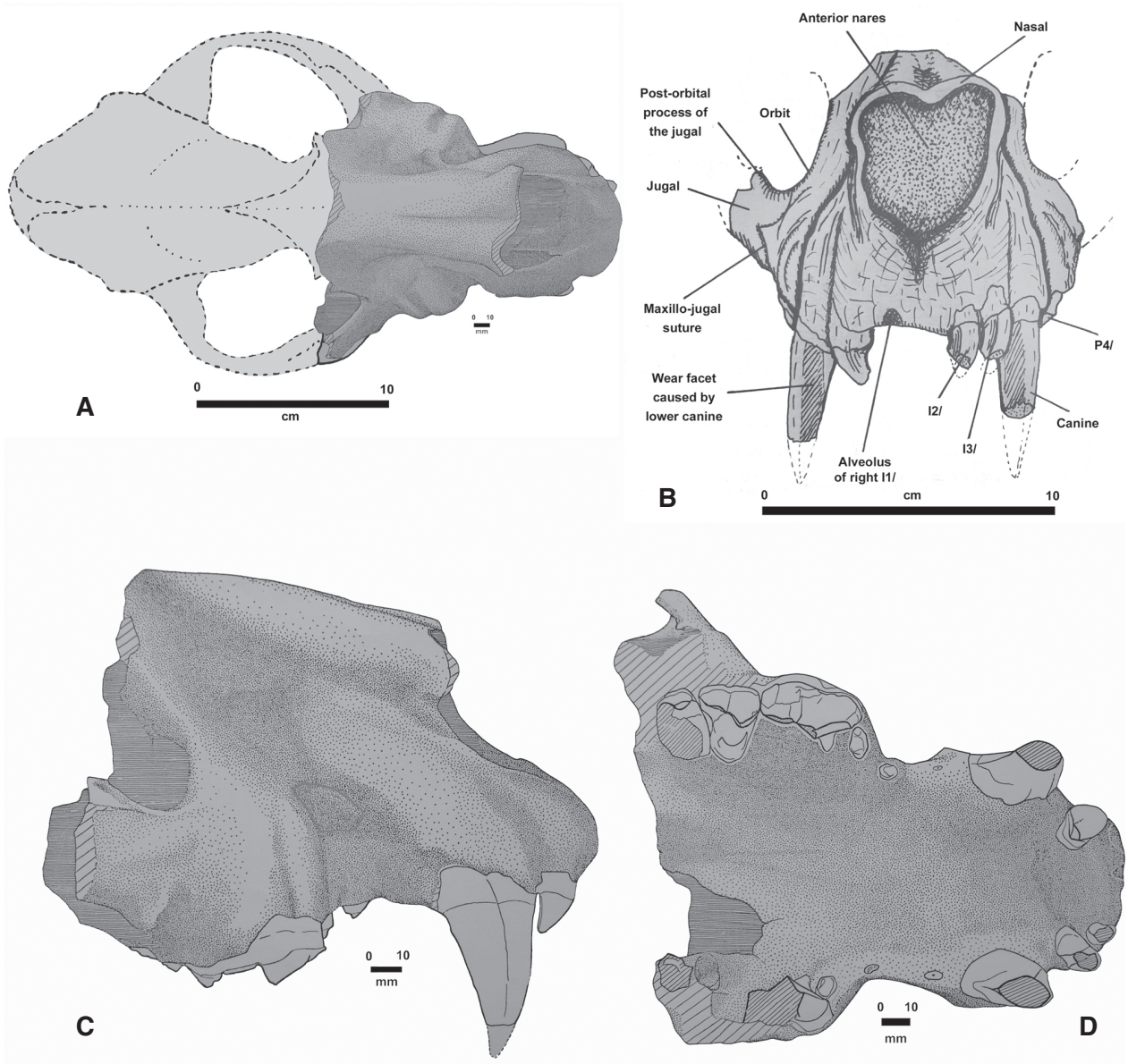

Fig. 3.—Amphicyonidae from the Ngorora Formation, late Middle Miocene, Kenya. *Agnotherium kiptalami* nov. sp. KNM BN 488, holotype snout, A.- Reconstruction of skull in dorsal view. B.- Anterior view. C.- Right lateral view. D.- Palatal view. (Scale: 10 cm).

Derivatio nominis: The species name honours Mr Kiptalam Cheboi who found the type specimen.

Locality: 2/10, Kabarsero, Ngorora Formation, Kenya.

Age: Late Middle Miocene, ca 12 Ma.

Stratigraphy: Member D, Ngorora Formation, Tugen Hills, Kenya.

Description:

Skull: The holotype snout (Fig. 3) is broken behind the second molars so that only the snout is preserved as far back as the orbits. A small portion of each orbit is present and the base of the right zygomatic arch is broken off about 35 mm from its point of departure from the main body of the maxilla. The left zygomatic arch is broken at its anterior root. The rest of the snout is complete and is only slightly distorted by crushing.

The most striking feature of the skull is its superficial resemblance to those of large felids. The short snout, enlarged canines and long diastemata recall machairodonts and nimravines rather than amphicyonids, but the presence of two typically amphicyonid molars indicates the true affinities of the specimen.

All the sutures are closed and difficult to discern, indicating that the individual was adult at the time of death, but the lightly worn carnassial and molars indicate that it was far from being senile. The maxillo-premaxillary suture does not appear to contact the nasals until it has reached the orbital line, much further back than in recent dogs. The anterior extremities of the nasals flare outwards and slightly downwards, resulting in a widening of the nares and the lateral shifting of the nasal notches, reminiscent of the situation in the lion. The upper border of the premaxilla is lower than it is in canids. It is a stout bone which projects anteriorly as in recent dogs, but is less pointed so that the incisors lie almost in a straight line, unlike the curved incisor battery of canids. The long axes of the incisors and roots is steep, the occlusal apices of the teeth point towards the rear quite sharply, unlie the more procumbent teeth of canids.

The maxilla is antero-posteriorly shortened, due to the outbowing of the maxilla in the region of the carnassial and molars. The P3/ is rotated to such an extent that it is oriented at 90° to the long axis of the tooth row, and it is tucked in behind the parastyle of the carnassial. Indeed, this tooth occupies the position where a protocone would normally occur in amphicyonids endowed with such a cusp.

The infraorbital foramen is large and lies above the third premolar. A large facial fossa occupies the region anterior to the orbit, extending anteriorly and ventrally as a curved furrow immediately behind the canine jugum. The zygomatic process is preserved only on the right side. The suture between it and the maxilla is faint, but rugose with a shallow fossa at the contact. The arch departs from the surface of the maxilla on a level with M1/-M2/ and sweeps laterally as in recent dogs. The root of the post-orbital process of the zygomatic is preserved.

Measurements of the specimen are given in Table 1.

Table 1.—**Measurements (in mm) of KNM BN 488, the holotype snout of *Agnotherium kiptalami* nov. sp.**

External breadth of snout at canines	89e
External breadth of snout at P2/	75.7
External breadth of snout at P4/	126.3
External breadth of snout at M1/	154.8
Height of snout above M2/	109
Width of nasals above M2/	36
Width of nasals above P1/	56
Width of external nares	44.5e
Distance between M2/ and lower edge of orbit	49.5
Depth of zygomatic arch at level of M2/	34.3
Thickness of zygomatic arch at level of M2/	8.2
Distance from front of orbit to tip of premaxilla	157
Distance from front of orbit to infraorbital foramen	45
Horizontal diameter of orbit at postorbital process of malar	36e
Estimated projection of canines beyond incisor apices	40e
Distance from apices of incisors to rear of M2/	161
Width of palate at P4/-M1/	106
Width of palate at canines	47.5
Width of palate at M2/	68e
Distance between mesial edge of P4/ and distal edge of canine	41.5
Length P4/-M2/	67

Upper dentition: I1/ is missing on both sides, but judging from the alveoli it must have been a fairly large tooth, the gap between the I2/s being 24 mm. I2/ is preserved on the left side. The tip is eroded but the remaining part of the tooth is similar to that of canids. I2/ is 9.0 mm long mesio-distally and 13.1 mm labio-lingually. I3/ is preserved on both sides, but the left one is lacking its apex. They are morphologically similar to their counterparts in *Canis*, except for the reduced cingulum. There are wear furrows across the distal surfaces of the I3/s near the cervix. These furrows are not produced by occlusion against the lower teeth, but are caused by abrasion of fibrous foodstuff.

There is a short gap between the I3/ and the upper canine. Both canines are preserved but have broken apices. The crowns are oval in section with a sharp knife-like posterior crest. This ridge is not serrated. The mesial surface of the crown is rounded and possesses a large wear facet caused by abrasion against the lower canine. Each upper canine has a long root housed in a prominent jugum extending dorsally and posteriorly to within 25 mm of the dorsal surface of the nasals. The cervix is positioned a few mm outside the alveolar margin of the maxilla.

P1/ is separated from the canine by a diastema of 7 mm on the left and 9 mm on the right. The tooth is tiny, the left one being about 4 mm x 4 mm. P2/ is separated from P1/ by a diastema of 13 mm on the left and 10 mm on the right. These premolars are small, the left one being 7.4 mm mesio-distal and 4.9 mm bucco-lingual. The corresponding measurements on the right are 7.3 x 5.5 mm. The main cusp is low and the accessory cusplets small. The tooth is surrounded by a low but wide cingulum, making it almost bunodont. It has two roots and its cervix is elevated about 2 mm above the alveolar margin.

P3/ is separated from the P2/ by a diastema of 6 mm on both sides. It resembles the P3/ of *Canis* but is relatively broader. The cingulum that surrounds the tooth makes the tooth almost bunodont. It is tucked in close to the P4/ and has been rotated at about 90° to the long axis of the tooth row. Because the maxilla swells laterally to a great extent just anterior to the P3/, the tooth lies outside the line that joins the canine to the P2/.

Table 2.—**Measurements (in mm) of the dentition of KNM BN 488, *Agnotherium kiptalami* nov. sp.**

Tooth	Length	Breadth
I2/, left	9.0	13.1
Canine, left	28.6	17.4
Canine, right	27.4	17.2
P1/, left	4	4
P2/, left	7.4	4.9
P2/ right	7.3	5.5
P3/, left	11.5	7.9
P3/, right	11.4	7.5
P4/, left	31.8	19.7
P4/, right	30.9	20.6
M1/, right	20.8	26.5
M2/, right	25.9e	24.2e

Table 3.—**Measurements (in mm) of the teeth of *Agnotherium* sp. from Fort Ternan, Kenya**

Specimen	Length	Breadth
KNM FT 3611, left P4/	23.3	14.9
KNM FT 3399 M1/	16.7	21.3
KNM FT 3379, left m/1	22.1	10.3

P4/ is close to but lateral to the P3/. The carnassial blade is comprised of well developed paracone and metastyle which lie in line with the posterior teeth. In front of the paracone is a small, low parastyle almost worn away by abrasion against the lower carnassial. The ectoparastyle is no more than a slight fold in the enamel at the anterior end of the tooth, and stands out only slightly from the cingulum. The protocone is almost entirely reduced and is located far back opposite the parastyle. The protocone is supported by a root that is large compared to the cusp. There is a cingulum running the along the lingual surface of the tooth, and the external cingulum is a low swelling. There are three wear facets on the teeth, one running from the apex of the paracone forwards to the parastyle and protocone, caused by abrasion against the posterior part of the p/4 which must have been a fairly large tooth. The other wear facets are on the lingual surfaces of the paracone and metastyle.

M1/ is preserved on the right side only, and has suffered some damage to the apex of the metastyle. It is a large tooth comprised of large para- and metastyles, well developed paracone and protocone, and small metacone. The parastyle is conical and about 13 mm high. There is a wear facet on its mesial surface. The metastyle is also conical but is lower, measuring only 7.9 mm high. There is a large but shallow fossette between the buccal cusps and the paracone, and the metacone is reduced to a small fold near the distal margin of the tooth. The protocone is large and separated from the paracone by a shallow crescentic fossette, presenting more the appearance of a cingulum rather than a distinct cusp. There is a buccal cingulum which extends onto the buccal portions of the mesial and distal margins of the tooth.

The second upper molar is morphologically close to the M1/, but is smaller and lower crowned than it. On the right side it is damaged distally and on the left only a portion of the protocone is preserved. M2/ is comprised of two low conical cusps, the para- and metastyles separated from the paracone by a shallow fossette. There is a buccal cingulum which curves apically mesially. The tip of the parastyle is worn deeply enough to expose dentine.

Agnotherium from Fort Ternan

There are three specimens from Fort Ternan that are confidently attributed to *Agnotherium*. The upper carnassial, KNM FT 3611 is morphologically similar to that of *Agnotherium kiptalami* but is substantially smaller (length of P4/s in the Ngorora specimen 30.9 mm and 31.8 mm; length of Fort Ternan specimen is 23.3 mm). The protocone is retired and very small, the anterior accessory cusplet is small, and the two carnassial cusps are high and slender. The crown is surrounded by a low swollen basal cingulum, and the enamel is slightly rugose where unabdraded. It has three roots.

An isolated upper molar KNM FT 3399 from Fort Ternan, is morphologically extremely similar to the M1/ in the specimen from Ngorora. The parastyle is higher than the metastyle as in the M1/ from Ngorora but the tooth is slightly smaller than the Ngorora specimen.

Also from Fort Ternan is a lower left carnassial, KNM FT 3379. It lacks the roots and is unworn. It has a large centrally positioned protoconid which is preceded by the paraconid in front and succeded by the talonid behind. The carnassial cusps are comprised of the paraconid and protoconid which are separated by an incision. The metaconid is weak and closely applied to the disto-lingual corner of the protoconid. The talonid is large but is damaged along its distal and buccal edges, making it difficult to discern the detailed morphology of the talonid basin. The surface of the tooth is marked by fine closely-spaced longitudinal striae, the perikymata.

Discussion: The gape of *Agnotherium kiptalami* must have been considerable. The upper canine tips would have projected about 40 mm beneath the occlusal surface of the carnassial and incisors. The

Table 4.—**Measurements (in mm) of the teeth of *Agnotherium* from Bled Douarah, Tunisia, and Hondeklip Baai, South Africa**

Specimen	Length	Breadth
T 370, P4/	33.4	15.8
T 370, M1/ (estimated from alveoli)	24e	23e
SAM PQ HB 504, P4/	27	14.3

Table 5.—**Measurements (in mm) of KNM BN 1730, the upper carnassial of *Vishnuonyx chinjiensis* from Kenya and Pakistan (Pilgrim, 1932)**

Specimen	Length	Breadth
KNM BN 1730, right P4/	11.6	9.4
GSI D 223, left P4/	11.6	9.8

snout is extremely short within an amphicyonid context. Shortening has been achieved by rotating the P3/ by about 90° along with the part of the maxilla in which it is housed, and by outbowing the carnassial-molar series.

A. kiptalami differs from *A. antiquum* from Europe and North Africa by the increased rotation of the P3/ and its position close to the antero-lingual edge of the P4/. In addition the blades of the carnassial are not as well developed as in *A. antiquum*. The length/breadth indices of the upper carnassial in the two species are 1.53 (31.8/19.7) in *A. kiptalami*, and 2.07 (33.4/15.8) in T 370, *A. antiquum* from Bled Douarah, Tunisia (Kurten, 1976).

The Middle Miocene locality at Hondeklip Baai, South Africa, yielded an isolated upper carnassial which is similar to the Ngorora specimen (Pickford & Senut, 1997). The genus thus had a pan-African distribution during the latter part of the Middle Miocene.

Given that the only known specimen of the large amphicyonid *Afrocyon burroleti* from Gebel Zelten, Libya, is a damaged mandible, it is difficult to make direct comparisons with *Agnotherium* from Ngorora. However, the lower carnassial from Fort Ternan attributed to *Agnotherium* differs from that of *Afrocyon* by being considerably smaller (m/1 is 32 mm long in *Afrocyon burolleti* and only 22.1 mm in KNM FT 3360) and having a retired metaconid and voluminous hypoconid (Arambourg, 1961).

The Ngorora *Agnotherium* snout is by far the most complete specimen known of this genus. The canines are elongated with a sharp posterior crest, in contradiction with the conclusion of Kurten (1976) who wrote that, because of the supposed lack of a downward projecting symphysis in the mandible, the canines would have been low crowned.

Agnotherium kiptalami differs markedly from the only other described amphicyonid from East Africa, *Hecubides euryodon* from the Early Miocene. Not only is it larger but the carnassial is considerably more hypercarnivorous. Furthermore, the P3/ in *Hecubides* is not rotated, its P3/ is in a more anterior position relative to the P4/, it has smaller canines, a smaller parastyle on M1/ and a relatively smaller carnassial than *Agnotherium*.

Family Mustelidae Swainson, 1835
Subfamily Lutrinae Baird, 1857
Genus *Vishnuonyx* Pilgrim, 1932
Species *Vishnuonyx chinjiensis* Pilgrim, 1932

Material: KNM BN 1730, right P4/.

Locality and age: Locality 2/11, Kabarsero, Member D, Bed 3, Ngorora Formation, ca 12 Ma.

Description: KNM BN 1730 is an isolated right P4/ (Fig. 8A). The paracone is situated in the centre of the buccal side of the tooth and there is a low, small parastyle growing out of the mesio-buccal cingulum. The protocone is far from the paracone, being close to the lingual border of the tooth. To the rear of the paracone, there is the metastyle, the tip of which forms the most distal part of the tooth. Centrally, there is an antero-posterior valley bordered lingually by two cusps, the protocone and hypocone which are both somewhat expanded, thereby reducing the extent of the basin between the buccal and lingual pairs of cusps. There is a cingulum on the lingual portion of the metacone but the lingual cusp pair has only a trace of such a structure. The protocone is made up of two closely joined cusplets which with wear would coalesce into a single cusp. The angle between the buccal and mesial edges of the crown is 90°. The height of the paracone is 7.4 mm.

Discussion: The incipient subdividion of the protocone in the P4/ of the Ngorora lutrine is important, as in the genus *Enhydriodon* the protocone develops an accessory cusplet which becomes larger and more inflated. The buccal edge of the crown is straight, in contrast to the inflected margin that occurs in *Potamotherium*. This tooth is similar in morphology and dimensions to the type specimen of *Vishnuonyx chinjiensis* from similar aged deposits in Pakistan (Pilgrim, 1932).

Subfamily Mellivorinae Gill, 1872
Genus *Eomellivora* Zdansky, 1924
Species *Eomellivora tugenensis* nov.

Diagnosis: A species of *Eomellivora* similar in size to present day *Mellivora capensis* (Schreber), in which the upper carnassial and first molar are

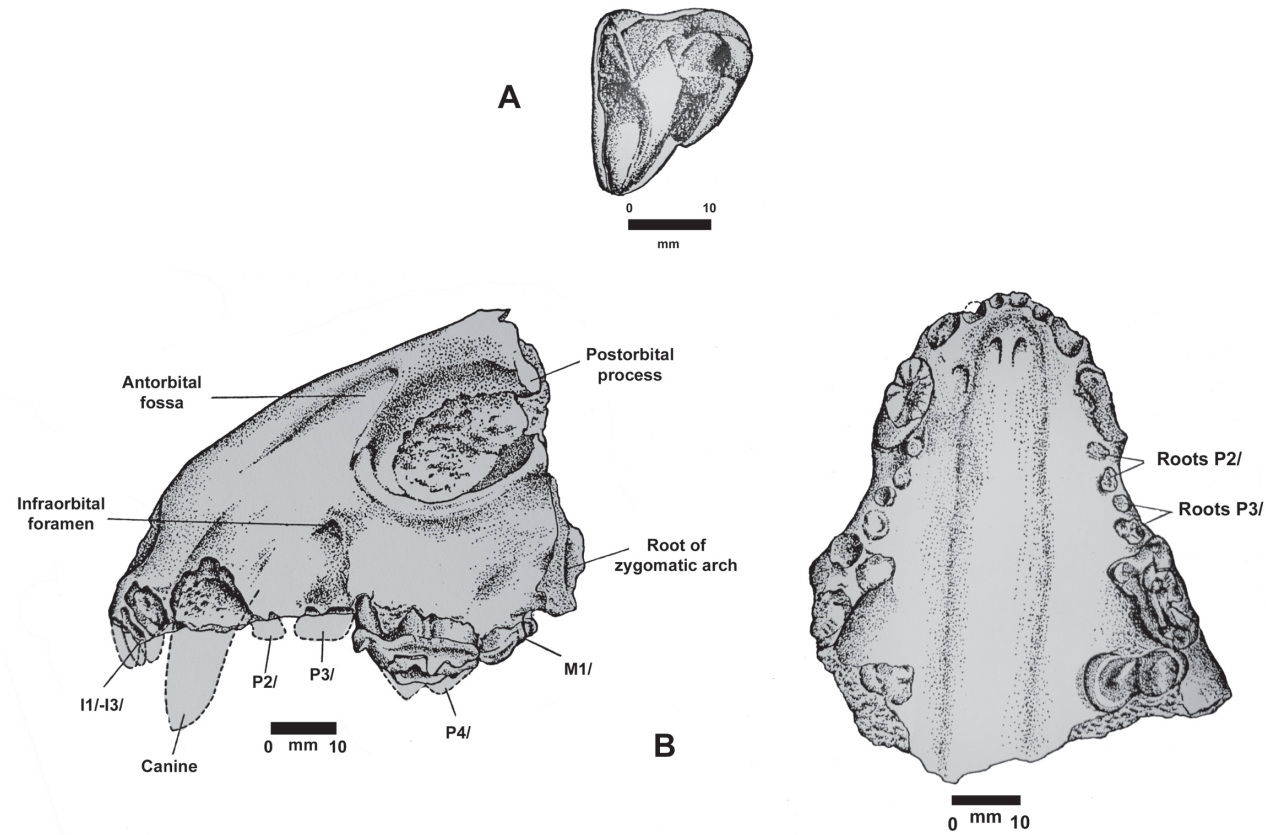

Fig. 4.—Mustelidae from the Ngorora Formation, late Middle Miocene, Kenya. A) *Vishnuonyx chinjiensis*, KNM BN 1730, right P4/, occlusal view (Scale: 10 mm). B) *Eomellivora tugenensis* sp. nov. KNM BN 328, snout, left lateral and palatal views (Scale: 10 mm).

similar to their homologues in *Eomellivora wimani* Zdansky, but in which the P1/ has been lost. Canines more procumbent than in *M. capensis*.

Holotype: KNM BN 328, snout with left P4/-M1/ and roots of right canine (Fig. 4B).

Locality and age: Locality 2/11, Kabarsero, Member D, Bed 3, Ngorora Formation, ca 12 Ma.

Derivatio nominis: The species name is for the Tugen Hills, where the specimen was found.

Description:

Skull: The fossil consists of most of the snout in front of the post-orbital processes of the frontals. It has been slightly crushed and warped. The only teeth present are the left P4/ and M1/. The snout is similar in size to that of extant *Mellivora capensis*, but there are several clear morphological differences between the two species.

In the fossil the lacrymal process is more strongly developed than it is in the extant honey badger, and its zygomatic arch is more robust. The latter is 17 mm deep measured from the orbital margin to the alveolar level at M1/ whereas in *M. capensis* it averages 13.5 mm in seven specimens measured. The fossil has a doubled infra-orbital foramen, while in the recent sample two out of seven specimens had doubled foramina, the remainder having only one. There are several nutritive foramina scattered over the snout, as in recent forms, but there is a foramen in the fossil just in front of the canine that has not been observed in any of the extant specimens examined. The position of the infraorbital foramen is similar in the Ngorora fossil and extant honey badgers. The antorbital fossa is extensive and evenly curved in the fossil with an uninterrupted border, whereas in most recent specimens there is a re-entrant in the dorsal outline of the fossa (Fig. 9). A single recent specimen (female) had no re-entrant, but the outline of the fossa in this individual is more angular than in the fossil.

The palate of *E. tugenensis* is more pointed anteriorly than it is in *M. capensis*. This is reflected in the measurements of the distance between the orbit and the labial border of the I1/ and the length of the palate measured from the rear of M1/. The widths of the palate at P4/-M1/ is similar in the Ngorora fossil and recent material.

Table 6.—**Measurements (in mm) of KNM BN 328, the snout of *Eomellivora tugenensis* nov. sp. (KNM BN 328) and *Mellivora capensis***

Measurement	Ches 0	No N°	OM 3594	OM 180	Chep	OM 3597	OM 5166	KNM BN 328
Postorbital process to infraorbital foramen	29.5	31.4	30.0	27.0	26.7	27.2	26.9	30.3
Front of orbit to roots of M1/	14.4	13.7	13.5	13.5	12.9	13.4	12.0	17.0
Palatal width at P4/-M1/	42.5	42.0	38.4	38.3	38.4	38.2	—	41.3
Palatal width at canines	20.4	22.4	20.8	19.0	18.5	21.0	—	21.0
Palatal length from I1/ to M1/	45.9	49.6	49.0	45.4	42.9	45.0	—	53.0
Front of orbit to tip of snout	40.1	44.0	43.5	40.0	40.0	39.6	—	45.1
Vertical diameter of orbit	20.0	22.0	18.5	18.0	19.5	17.0	18.6	20.8
Horizontal diameter of orbit	20.0	21.2	20.7	19.0	18.6	18.5	19.5	21.2
Width of skull at P4/-M1/	69	66	60	62	64	67	65	74
Width of skull at canines	37.5	40	36.5	33.2	35.7	33.4	—	37e

Dentition: As far as can be judged from the snout the dental formula would have been 3-1-3-1 for the upper tooth row. The arrangement of the teeth in the fossil palate differs from that of *Mellivora* mainly in its more curved incisor row and more procumbent canine roots. In addition, there is no diastema between the incisors and canine in the fossil, whereas all the recent skulls examined had a gap between these teeth (an average of 4.5 mm in seven specimens measured).

The upper canine roots in *E. tugenensis* are more procumbent than they are in *M. capensis*. The root lies at an angle of 40° to the alveolar margin in the fossil whereas in *M. capensis* it makes an angle of 70°. The extant honey badger shows marked sexual dimorphism in canine dimensions (small in females, large in males) and temporal crest morphology (doubled in females, single in males). On the basis of canine dimensions, the fossil is thought to have been a male, but because the neurocranium is lacking this cannot be confirmed by other evidence.

There is no trace of a P1/ alveolus in *E. tugenensis*, which differentiates the Ngorora specimen from *Eomellivora wimani* and other species of the genus. P2/ is a two rooted tooth, but no crown is preserved. The position of the P2/ roots is similar to that of *M. capensis* specimens which have two roots (some individuals have a single rooted P2/). In contrast, the two roots of the fossil P3/ are oriented in the maxilla, such that the mesial root is buccal to the rear of P2/, whereas in *M. capensis* the root is lingual to the rear of P2/.

The left P4/ is damaged, but what is preserved reveals that it is a more massive tooth than in *M. capensis*. It has three roots, the distal one being larger than that of the extant species. The protocone is smaller in the fossil and is more distally located with respect to the parastyle, forming an angle of 76° between the mesial and buccal edges of the tooth, compared with 108° in extant honey badgers (Fig. 5).

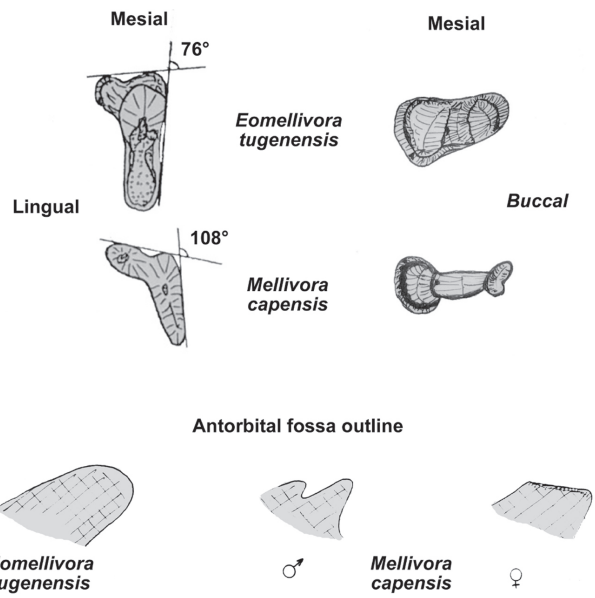

Fig. 5.—Comparison of the morphology of the teeth and antorbital fossa outline of *Eomellivora tugenensis* and *Mellivora capensis*.

This arrangement of cusps is similar to that of other species of *Eomellivora*.

The left M1/ is much wider bucco-lingually than the corresponding tooth of *M. capensis*. It is almost as wide as the P4/ is long (95%) whereas in *M. capensis* the M1/ is 20% narrower than the length of the P4/. In addition the morphology of the tooth differs greatly in the fossil and extant species. In recent forms the ridge on the lingual cusp is better developed than it is in the fossil, in which it reaches only half way across the tooth from its mesial border. In the fossil the edge of the cingulum is sharp and evenly curved in outline, but in recent specimens it is beaded. The buccal cusp is more evenly curved in *E. tugenensis* than it is in *M. capensis*, in which the same cusp has two relatively strong indentations in

Table 7.—**Measurements (in mm) of the teeth of KNM BN 328, *Eomellivora tugenensis* sp. nov. and extant *Mellivora capensis* (NB measurements of the incisors in the fossil are based on the alveoli)**

Measurement	Ches 0	No N°	OM 3594	OM 180	Chep	OM 3597	OM 5166	KNM BN 328
Length P2/-M1/	31.2	32.3	32.3	28.3	30.1	29.5	29.8	36.0
Length I1/	4.8	6.0	7.0	5.0	2.4	5.0	—	6.8
Width I1/	2.2	7.3	6.6	5.9	5.0	4.5	—	7.4
Length I2/	5.9	3.0	3.0	2.7	2.2	2.5	—	2.7
Width I2/	2.3	5.0	5.6	4.7	4.7	4.0	—	5.5
Length I3/	4.9	2.5	2.5	2.2	4.3	2.0	—	2.2
Width I3/	6.0	4.7	4.6	4.5	5.9	4.0	—	4.9
Length P4/	14.5	14.5	14.0	13.2	14.1	13.0	13.6	16.4
Width P4/	11.7	11.5	11.6	10.0	10.7	10.0	11.0	9.4
Length M1/	7.4	6.2	6.4	6.8	6.5	7.0	7.0	8.8
Width M1/	10.8	11.4	11.0	11.4	11.4	11.5	11.0	14.7

its border (Fig. 5). In its morphology the fossil M1/ resembles that of *Eomellivora wimani*.

Discussion: Dentally, *Eomellivora tugenensis* is morphologically close to *E. wimani* but it differs from it by its loss of P1/. The Ngorora fossil snout has resemblances to that of recent honey badgers, not only in size but also in several morphological features. However, the more procumbent canine roots, the different outline of the antorbital fossa and the more pointed incisor battery and the morphology of P4/ and M1/ differentiates the fossil from extant *Mellivora*.

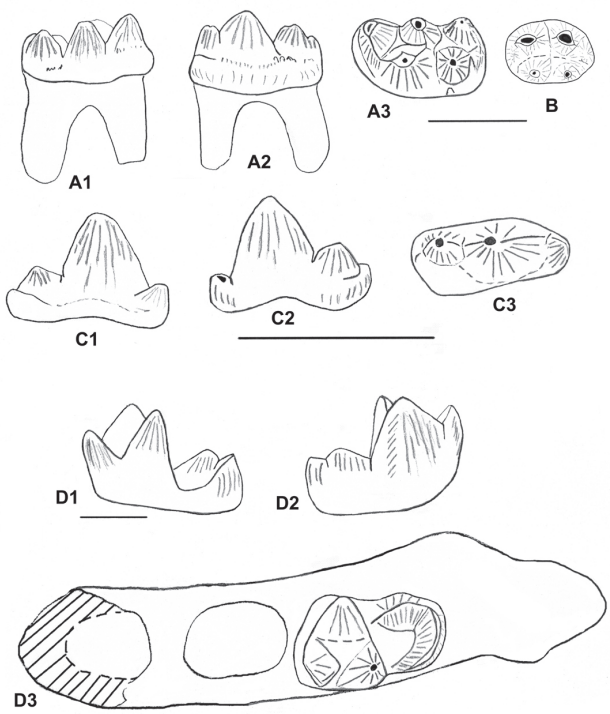

Fig. 6.—Viverridae and Herpestidae from the Ngorora Formation, late Middle Miocene, Kenya. A-B) *Tugenictis ngororaensis* nov. gen. nov. sp. A, Bar 2065'05, left m/1, A1, lingual; A2) buccal; and A3, occlusal views; B) Bar 35'98, m/2, occlusal view (Scale: 10 mm); C) Viverridae genus and species indet. Bar 898'03, left p/4, C1, lingual, C2, buccal and C3, occlusal views (Scale: 10 mm); D) Herpestidae genus and species indet. Bar 1645'05, right mandible with m/2, D1, lingual, D2, buccal and D3, occlusal views (Scale: 1 mm).

Family Viverridae Gray, 1821
Subfamily Viverrinae Gill, 1872
Genus *Tugenictis* nov.

Type species: *Tugenictis ngororaensis* sp. nov.

Species *Tugenictis ngororaensis* nov.

Holotype: BAR 2065'05 right m/1 (Fig. 7A, 8A, B & C).

Type Locality: Koibo Chepserech, near Bartabwa, Ngorora Formation, Member A.

Age: Middle Miocene, ca 12.5 Ma.

Etymology: The genus name is for the Tugen Hills with the suffix "ictis", Greek for weasel; the species name is for the Ngorora Formation.

Diagnosis: Viverridae the size of *Civettictis civetta*, with robust m/1, with high, bunodont cusps. Paraconid located anteriorly. The metaconid is the smallest cusp in the trigonid. Talonid relatively short, with cuspids (hypoconid and entoconid) the same height as the trigonid. Hypoconid pyramidal, possessing an antero-lingual crest which runs obliquely to the axis of the tooth as far as the contact between the protoconid and metaconid. Entoconid high and crescentiform. The m/2 has a reduced trigonid, formed of a voluminous protoconid, a small residual paraconid, and a metaconid that is somewhat narrower than the protoconid and apparently a bit higher than it. The talonid is dominated by a strong,

Fig. 7.—Viverridae and Percrocutidae from the Ngorora Formation, late Middle Miocene, Kenya. A-C) *Tugenictis ngororaensis*, nov. gen. nov. sp. Bar 2065'05, left m/1, lingual, buccal and stereo occlusal views (Scale: 10 mm); D-E) *Percrocuta tobieni*, Bar 1550'03, left mandible with canine root and anterior premolars, buccal, occlusal and lingual views (Scale: 10 mm).

rounded hypoconid well separated from the protoconid, and a hypoconid joined to the entoconid which is relatively small and well separated from the metaconid.

Differential diagnosis: Differs from *Orangictis gariepensis* Morales *et al*., (2001) by its greater dimensions, more bunodont dentition and m/1 with the trigonid cusps the same height as the talonid. It differs from *Pseudocivetta ingens* (Petter, 1967) by the more primitive morphology of the trigonid —in which the metaconid is well separated from the paraconid and facing the protoconid— and the talonid, in which the entoconid is deeply separated from the metaconid.

Description:

Locality: Koibo Chepserech, Ngorora Formation, Member A. BAR 2065'05, a right m/1 is a robust molar with high, bunodont cuspids (Fig. 7A; 11A-8A,B&C). The trigonid is V-shaped, in which the paraconid and protoconid are almost equal in size, the protoconid being the higher. The two cusps are pyramidal. The paraconid occupies all the anterior part of the trigonid such that it almost touches the metaconid basally, but leaving open the lingual valley of the trigonid. The metaconid is the smallest cusp of the trigonid, and is slightly lower than the paraconid. It possesses a lingual crest (internal) which touches the buccal crest (external) of the protoconid, making the separation of the trigonid from the talonid clean and vertical. The internal valley of the trigonid is high. The talonid is relatively short, with a high pyramidal hypoconid with an antero-lingual crest which runs obliquely to the axis of the tooth reaching the junction of the protoconid and metaconid. The hypoconid is located on the buccal wall deeply separated from the protoconid, and by an incision from the entoconid which is high and crescentiform, with its antero-lingual crest well separated from the metaconid. The talonid valley is open lingually, is narrow and, like the trigonid valley, is high. There is a clear buccal and anterior cingulum .

Measurements of the tooth are (L = 12.9 mm; W = 7.6 mm).

Locality: Kabarsero, 2/1, Ngorora Formation, Member B. BAR 35'98, a left m/2 has a reduced trigonid formed of a voluminous, rounded protoconid which has a small cusplet anteriorly, perhaps representing a residual paraconid (Fig. 7B). The metaconid is somewhat narrower than the protoconid and apparently higher than it, the two cusps being separated by a flat valley, which extends as far as the talonid. The talonid is dominated by the strong, rounded hypoconid which is well separated from the protoconid. The posterior part of the talonid is closed by the hypoconid joined to the entoconid, the latter cusp being relatively small and well separated from the metaconid.

Measurements of the tooth are (L = 9.0 mm; W = 6.3 mm).

Discussion: The morphology of the lower carnassial of *Tugenictis ngororaensis* is very unusual and rare among viverrids. In general it recalls the dentition of bunodont carnivores such as *Procyon lotor* (Procyonidae), *Arctictis binturong* (Viverridae) or the herpestid *Bdeogale crassicaudata*. But its dentition is slightly more hypsodont and the m/1 retains quite a primitive disposition of the structural elements. It differs from *Bdeogale* and other Herpestidae by the strong development of the entoconid and the development of a cristid obliqua which joins the hypoconid to the junction of the protoconid and metaconid. These two features are also present in *Viverra* and *Civettictis*, although these two genera retain a trigonid which is higher than the talonid. The species *Pseudocivetta ingens* (Petter, 1967; Petter & Howell, 1977) appears to be much closer to it morphologically, which like the form described here, is bunodont and possesses talonid cusps the same height as the trigonid. However, *Pseudocivetta ingens*, judging from the figure in Petter & Howell (1977), has a paraconid that is displaced towards the lingual side, thereby closing the lingual valley of the trigonid. The same applies to the lingual valley separating the entoconid and protoconid which is deep in *Tugenictis ngororaensis* and is practically inexistent in *P. ingens*. These differences are consistent with a generic separation between the species described here. *Tugenictis ngororaensis* is also related to *Orangictis gariepensis* from the Early Miocene of Arrisdrift, Namibia (Morales *et al*., 2001, 2003), despite the great difference in size between the two species. *Orangictis* shares with *Tugenictis* the basic structure of the m/1, although it is more primitive by possessing a trigonid with slightly higher cusps than those of the talonid and less bunodont cuspids in the trigonid and talonid. A few forms classified in the family Hyaenidae also show comparable basic morphology to the two genera cited above, for example, *Pliovierrops faventinus* (Torre, 1989; Alcalá, 1994), but although the talonid cuspids are the same height as the trigonid ones, the cuspids retain a sharp, pointed morphology quite different from the more bunodont condition of the new Kenyan form.

Genus and species of Viverridae indet.

Material: BAR 898'03, left mandible with fragment of p/2 and p/4.

Locality: Kabarsero, Ngorora Formation, Member B.

Description: BAR 898'03, is a left mandible with p/4 and a fragment of p/2. The p/4 is a gracile, sectorial tooth, with a high, transversely compressed main cusp, a well developed anterior cusplet, and a larger posterior cusplet surrounded by a basal cingulum which widens lingually (Fig. 7C). The only part of the p/2 preserved is the posterior half, which reveals a small cuspid located at the junction of the posterior cristid and the posterior cingulum.

Measurements of the p/4 are (L = 8.0; W = 3.6 mm).

Discussion: The p/4 is slightly larger than the corresponding tooth in extant *Genetta genetta*, its morphology is close to that of this species and different from that of *Viverra* and related forms.

Family Herpestidae Bonaparte, 1845
Genus and species indet.

Material: BAR 1645'05, right mandible fragment with m/2.

Locality: Chepkogel, Ngorora Formation, Member A.

Description: BAR 1645'05 is a right mandible with m/2 and part the alveoli of m/1 (Fig. 7D). The m/2 has a complete trigonid with the three cusps arranged in a v-shape. The protoconid is the highest and most voluminous of the trigonid cusps, whereas the paraconid is the lowest. The trigonid is higher than the talonid, the latter being formed of a large hypoconid, slightly doubled and strongly sloping. The alveoli for the m/1 reveal that it was appreciably larger than the m/2.

Measurements of the m/2 are (length ca 2.5 mm)

Discussion: Morphologically similar m/2s are found in several small extant African Herpestidae. Given the restricted nature of the specimen, together with the paucity of data concerning the great diversity of extant small herpestids, allied to the scarcity of data about pre-Pliocene members of the

family, it is not possible to propose a precise identification of this fossil. All we can say is that the specimen represents a dwarf herpestid, rivalling in size the smallest extant mongooses such as *Galerella sanguinea cana*, the m/2 of which is 2.4 mm long (Rosevear, 1974).

Family Percrocutidae Werdelin & Solounias, 1991
Genus Percrocuta Kretzoi, 1938
Species *Percrocuta tobieni* Crusafont-Pairo & Aguirre, 1971

Material: BAR 1550'03, left mandible fragment with p/2 and p/3.

Locality: Kelonechun, Ngorora Formation, Member E.

Description: BAR 1550'03, is a fragment of left mandible with the p/2 and p/3 and the roots of the canine and i/2-i/3 (Fig. 8D-8F). The body of the mandible is robust with prominent mental foramina. The incisor alveoli are small and compressed, except that for i/3 which is triangular. The canine root is almost circular at the alveolar level with weak transverse compression. There is no alveolus for a p/1 and the diastema is short (5.1 mm). The p/2 is a simple robust tooth, practically unicuspid with a weak buccal cingulum slightly swollen anteriorly, but without forming a cusplet. The posterior cristid is longer and more gently inclined than the anterior one with a posterior swelling but no distinct cusp. The p/3 is high and robust, with a small antero-lingual basal cuspid and a modestly sized posterior cuspid.

Measurements of the teeth are p/2 (L = 12.9 mm; W = 7.7 mm), p/3 (L = 16.2 mm; W = 9.4 mm).

Discussion: The percrocutid jaw fragment from Kelonechun is typical of the species *P. tobieni* a species originally created for two mandibles from Kabarsero, Member B and Member D of the Ngorora Formation (Crusafont-Pairo & Aguirre, 1971). It is from a slightly younger level than the previously known sample, being about 11 Ma.

General discussion: The huge creodont from Bartule represents the youngest record of the genus *Megistotherium* which is now known to span the period from Meswa Bridge (ca 22 Ma) to Ngorora (ca 12 Ma). In Europe, the closely related genus *Hyainailourus* is known from MN 4 (Artenay) to MN 7/8 (La Grive-St-Alban) and in the Indian Suubcontinent a similar huge creodont has been reported from Bugti and the Siwaliks (Pilgrim, 1932).

The herpestid from Ngorora belongs to a minute species possibly as small as the smallest extant African carnivore. Known only from a mandible with m/2, it is left unidentified. A genet-sized viverrid is described but left un-named on account of its fragmentary nature. The large viverrid *Tugenictis ngororaensis* nov. gen. nov. sp. is represented by two teeth, m/1 and m/2, which are unusual among viverrids, but which show underlying morphology similar to that of two other extinct African genera, *Orangictis* from the basal Middle Miocene of Namibia (Morales *et al*., 2001), and *Pseudocivetta* from the Plio-Pleistocene of East Africa (Petter, 1967). As such, *Tugenictis* possibly represents part of an evolutionary lineage linking *Orangictis* and *Pseudocivetta*. This lineage has not been reported outside Africa.

The detailed affinities and origin of *Pseudocivetta* have long been enigmatic, to such an extent that some specimens have been included in the lutrine genus *Enhydriodon* (Petter, in: Geraads *et al*., 2004), mainly because of the bunodont nature of the carnassials. It is not impossible that other Plio-Pleistocene fossils from Kenya, Tanzania, and Ethiopia hitherto attributed to *Enhydriodon* belong instead to *Pseudocivetta*. The convergence in dental morphology between *Enhydriodon* and *Pseudocivetta* indicate that they probably had similar diets, possibly comprising crabs and/or molluscs.

The carnivore fauna from the Ngorora Formation comprises one creodont and seven fissipeds (Table 8).

Table 8.—**Carnivore fauna from the Ngorora Formation (12.5 - 11 Ma), Baringo District, Kenya**

Creodonta	
Hyaenodontidae	*Megistotherium osteothlastes*
Fissipeda	
Amphicyonidae	*Agnotherium kiptalami* nov. sp.
Mustelidae	*Vishnuonyx chinjiensis*
	Eomellivora tugenensis nov. sp.
Viverridae	*Tugenictis ngororaensis* nov. gen. nov. sp.
	Small indeterminate viverrid
Herpestidae	Tiny unidentified herpestid
Percrocutidae	*Percrocuta tobieni*

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