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# New carnivoran material (Creodonta, Carnivora and Incertae sedis) from the Early Miocene of Napak, Uganda

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**Abstract.** Eight species of creodonts and carnivores have previously been reported from the Early Miocene deposits at Napak, Uganda. This paper takes into account unpublished material from old collections made by W.W. Bishop during the 1950s and 1960s, as well as new samples made by the Uganda Palaeontology Expedition between 1985 and 2005. Four carnivoran species are reported from the site for the first time, of which one is a new genus and species, and one species is removed from previous lists, making for a grand total of 12 species for Napak comprising 6 creodonts, 4 fissipeds and two incertae sedis.

**Key words:** Carnivora, Creodonta, Early Miocene, Napak, Uganda

## Introduction

The Napak fossil deposits consist of intercalated volcanic ashes and palaeosols that accumulated on the flanks of Napak volcano, northeast Uganda. The strata are of Early Miocene age, about 20–18.5 Ma (Pickford, 2002). A highly diverse fauna and abundant floral remains have been collected from the sediments, many taxa of which are similar to those from Songhor, Koru, Rusinga and other Early Miocene sites in Kenya.

Creodonts and carnivores from Napak have been described on four previous occasions (Morales *et al.*, 2001; Savage, 1965; Schmidt-Kittler, 1987; Schmidt-Kittler and Heizmann, 1991). This paper takes into account described and undescribed fossils from the collections amassed by W.W. Bishop during the 1950s and 1960s, as well as newer material found by the Uganda Palaeontology Expedition between 1985 and 2005.

The carnivores thus far described from Napak consist of the following taxa.

### Creodonta

*Metasinopa napaki*\*

*Pterodon africanus*

### Carnivora

*Hecubides euryodon*\*

*Kichechia zamanae*

*Leptoplesictis rangwai*°

*Ginsburgsmilus napakensis*\*

Incertae sedis

*Kelba quadeemae*

*Prionogale breviceps*

\* = type locality is Napak

° = Here considered to belong to *Ugandictis napakensis* gen. et sp. nov.

The collections described herein include five new records for the site, of which one is a new genus and species of viverrid, and one species (*Leptoplesictis rangwai*) is removed from the list, making a total of 12 taxa of carnivorans for the site.

## Materials

Carnivore specimens from Napak are stored in the Uganda Museum, Kampala (UM) (specimens with various prefixes, usually Nap) and the Natural History Museum (NHM), London (specimens with the prefix M). New or undescribed specimens are discussed in the following section, but for completeness, the previously described material is listed in Table 1.

**Table 1.** Previously described carnivoran specimens from Napak.

Specimen	Storage	Publication	Original attribution	Locality	Specimen	Revision	Revised attribution
M 19095	NHM	Savage, 1965	<i>Kelba quadeemae</i>	Napak IV	Left M3/		
M 19097	NHM	Savage, 1965	<i>Metasinopa napaki</i>	Napak I	Left mandible		
M 19090	NHM	Savage, 1965	<i>Pterodon africanus</i>	Napak I	Left maxilla		
UMP 64.33	UM	Savage, 1965	<i>Pterodon nyanzae</i>	Napak IIA	Right M2/		
M 19084	NHM	Savage, 1965	<i>Hecubides euryodon</i>	Napak I	Snout		
M 19099	NHM	Savage, 1965	<i>Hecubides euryodon</i>	Napak I	Left m/1		
HMV 5830	UM	Savage, 1965	<i>Hecubides euryodon</i>	Napak I	Left m/1		
UMP 64.32	UM	Savage, 1965	<i>Hecubides euryodon</i>	Napak I	Right m/2	Schmidt-Kittler, 1987	<i>Cynelos euryodon</i>
UMP 64.35	UM	Savage, 1965	<i>Kichechia zamanae</i>	Napak V	Left mandible	Schmidt-Kittler, 1987	<i>Leptoplesictis rangwai</i>
UMP 64.34	UM	Savage, 1965	<i>Kichechia zamanae</i>	Napak IV	Right m/1		
Nap IV-65	UM	Schmidt-Kittler, 1987	<i>Prionogale breviceps</i>	Napak IV	Right mandible		
Nap IV-65 Trench II	UM	Schmidt-Kittler, 1987	<i>Prionogale breviceps</i>	Napak IV	Right mandible		
Nap IV IC	UM	Schmidt-Kittler, 1987	<i>Prionogale breviceps</i>	Napak IV	Left mandible		
P67-13	UM	Morales <i>et al.</i> , 2001	<i>Ginsburgsmilus napakensis</i>	Napak IX	Left maxilla		

### Systematic paleontology

Order Creodonta Cope, 1875  
 Family Hyaenodontidae Leidy, 1869  
 Subfamily Hyaenodontinae Leidy, 1869  
 Genus *Isohyaenodon* Savage, 1965  
*Isohyaenodon pilgrimi* Savage, 1965

Figures 1-3, 3-1

*Locality*.—Napak IV.

*Material*.—NAP IV-64, fragment of left maxilla with M1/-M2/ (Figures 1-3, 3-1).

*Description*.—M2/ somewhat larger than the M1/, the two molars showing similar morphology, comprising a large metastyle elongated into a sharp blade, a high and pointed paracone, quite compressed and almost pyramidal, with a posterior crest, that connects to the metastyle blade, separated from it by a vertical slit. An antero-buccal crest reaches the basal cingulum, forming a swelling similar to a parastyle, a bit better developed in M2/ than in M1/. The third paracone crest is smooth and is located antero-lingually,

and joins a reduced protocone, which is basically a swelling similar to a cingulum. As in the case of the parastyle, this protocone is stronger in M2/ than in M1/. The two molars possess a complete basal cingulum, moderately strong at the base of the paracone, and weaker at the base of the metastyle.

Measurements of the specimens are M1/ (L = 4.7 mm; W = 3.0), M2/ (L = 4.7 mm; W = 3.8 mm).

*Discussion*.—The morphology and size of the Napak maxilla is similar to the specimen from Songhor, Kenya, figured by Savage (1965) as *Isohyaenodon pilgrimi*.

### *Isohyaenodon zadoki* (Savage, 1965)

*Locality*.—Napak I.

*Material*.—NAP-I-63, fragment of right mandible with m/3-m/2 (Figure 1-1).

*Description*.—The two molars in NAP-I-63 are heavily worn and the enamel has broken off in places. The morphology of the two molars is similar, the m/3 being a bit larger than the m/2. They are relatively ro-

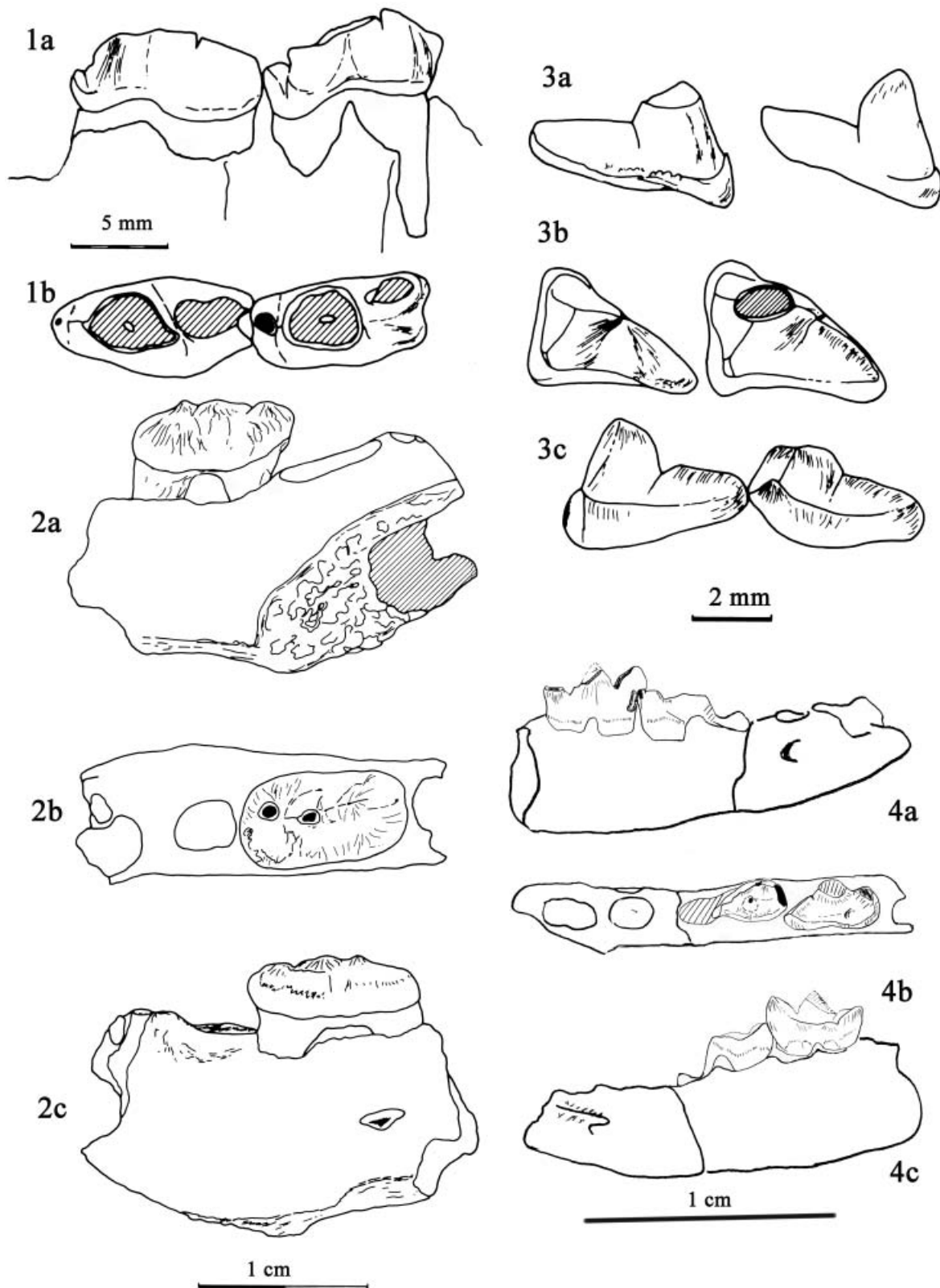


Figure 1.

bust molars formed of a paraconid that is smaller than the protoconid. The anterior margin of the paraconid is vertical and is enlarged buccally, such that the anterior wall has a median valley into which the talonid of the preceding molar fits. This valley is stronger in m/2 than in m/3. The protoconid occupies almost 2/3 of the tooth. The m/3 has a minuscule talonid backing onto its posterior crest, whereas in m/2, the talonid is better developed. The basal cingulum is weak, being clear only at the lingual base of the protoconid.

Measurements of the specimens are m/2 (L = 10.3 mm; W = 4.6 mm), m/3 (L = 10.9 mm, W = 5.4 mm).

**Discussion.**—*Isohyaenodon zadoki* is a combination proposed by Morales *et al.* (1998) for *Metapterodon zadoki* and *Isohyaenodon matthewi*, two species defined by Savage (1965), the former on the basis of an upper dentition and the latter on a lower dentition. The attribution of the Napak mandible is based partly on size, but mainly on the morphology of the two lower molars, both teeth possessing carnivorous morphology with a weakly developed talonid. This morphology occurs in the m/3 of *Isohyaenodon zadoki* from Songhor (Savage, 1965, figures 41 to 43) and in other species of *Isohyaenodon*, such as *I. pilgrimi* (Savage, 1965, figures 44 to 46).

Genus ***Leakitherium*** Savage, 1965  
***Leakitherium*** sp.

**Locality.**—Napak I.

**Material.**—NAP I 44'99, fragment of left lower molar (m/2?), with paraconid and part of the protoconid.

**Description.**—In NAP I 44'99 the paraconid is robust with its anterior wall swollen and a median valley similar to that described in the m/2 of *Isohyaenodon zadoki*. It differs from this species by its greater dimensions.

Measurements of the specimen are m/2? (L = ?; W = 8.0 mm).

**Discussion.**—This specimen has features such as the mesial valley on its anterior margin which recalls the morphology observed in *I. zadoki* and *I. pilgrimi* but it is about 50% larger than the former species. The surface of the enamel has vertical, rounded parallel ridges or swellings quite different from the usual cre-

dont enamel which is finely wrinkled. Similar ridges occur in the teeth of *I. zadoki* and *Leakitherium hiwegi* (see plate 4, figures 1 and 4 in Savage, 1965). The latter species is 50% larger than *I. zadoki* and thus is similar in size to *Isohyaenodon andrewsi*. *Leakitherium* is known only by upper dentitions while *Isohyaenodon andrewsi* is represented only by lower dentitions, and we consider it possible that the two may go together into a single species, or at least into sister taxa. Whether this lineage should be called *Leakitherium* or *Isohyaenodon* requires further study but if they are synonymous, then *Leakitherium* will be the valid name, because of page priority.

Family Teratodontidae Savage, 1965  
Genus ***Teratodon*** Savage, 1965  
***Teratodon spekei*** Savage, 1965

Figure 1-2

**Locality.**—Napak I.

**Material.**—Nap I 48'00, left mandible fragment with p/3 (Figure 1-2).

**Description.**—In Napak I 48'00, the mandible is low and its inferior border quite sharp, the symphysis is extremely rugose. The p/1 is very reduced, the p/2, which is represented by its alveoli was probably a robust tooth. The fragment of mandible preserves part of the symphysis from its posterior termination as far forwards as the anterior root of p/3. The symphysis extends back below the p/3 as a lingual swelling with a rugose texture. The p/3 is the only tooth preserved, but it is in good condition and unworn. It is oval in occlusal outline, it is bunodont with low weakly developed cusps. In front of it there are two alveoli for the p/2, the anterior one being broken off anteriorly, the distal part being deep and vertical. Judging from the size, the p/2 would have been about the same size as the p/3. A small alveolus is located slightly antero-lingually to the anterior alveolus of p/2, and we take this to be one of the alveoli of p/1.

Measurements (in mm) of the specimen are p/3 (L = 9.5; W = 5.2 mm).

**Discussion.**—The dimensions and morphology of the p/3 correspond well with the description and figures of *Teratodon spekei* (Savage, 1965). The presence

← **Figure 1.** 1. *Isohyaenodon zadoki* (Savage, 1965). Napak I, NAP-I-61, fragment of right mandible with m/3-m/2; a) buccal view, b) occlusal view. 2. *Teratodon spekei* Savage, 1965. Napak I, NAP 48'00 fragment of left mandible with p/3; a) lingual view, b) occlusal view, c) buccal view. 3. *Isohyaenodon pilgrimi* Savage, 1965. Napak IV, NAP IV-64, fragment of left maxilla with M1-M2; a) lingual view, b) occlusal view, c) buccal view. 4. *Prionogale breviceps* Schmidt-Kittler & Heizmann, 1991. Napak IV, NAP IV 53'04, fragment of right mandible with p/4 and m/1; a) buccal view, b) occlusal view, c) lingual view.

of two large alveoli in front of the p/3 and an offset distal root of p/1 are characteristic of this strange species, otherwise represented at Koru and Songhor, Kenya. This is the first record of the lineage from Napak.

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

Figures 2-1–6

*Locality*.—Napak I.

*Material*.—NAP I 45'02, fragment of right mandible with p4/ and roots of p/3 and anterior ones of the m/1. NAP I 44'02, right m/1. NAP IV V 5830, left m/1 (Savage, 1965, p. 290). NAP I 128'99, right mandible with deciduous dentition. NAP I 129'99, fragment of right maxilla with D3/-D4/. NAP I 26'00, fragment of left maxilla with D3/-D4/ (Figures 2-1 to 2-6).

*Description*.—The two lower molars (m/1) have the same morphology but are slightly different in size (a bit more than 10%). They have a paraconid that is lower than the protoconid, with the anterior crest slightly inclined backwards. The protoconid is high and voluminous, and has a moderately sized metaconid backing onto it at mid-height. The talonid is large, being dominated by a strong and high hypoconid, separated by a longitudinal valley from the moderately sized entoconid. In NAP IV V 5830 the unworn entoconid is slightly subdivided. The cingulum is very weak, only lightly marked at the base of the buccal wall. The p/4 is a relatively short tooth, with a moderately sized main cusp, a much smaller anterior cuspid and a stronger and higher posterior cuspid, and with a voluminous and rounded talonid. The cingula are weak, being imperceptible over most of the base of the tooth.

Measurements of the specimens are p/4 (L = 13.6 mm; W = 7.0 mm), left m/1 (L = 23.7 mm; W = 9.4 mm), right m/1 (L = 20.8 mm; W = 9.6 mm), left D3/ (L = 13.1 mm; W = 5.8 mm), left D4/ (L = 10.4 mm; W = 9.8 mm), right D3/ (L = 12.4 mm; W = 5.9 mm), right d/c (L = 7.8 mm; W = 3.8 mm), right d/4 (L = 11.8 mm; W = 6.1 mm), left d/3 (L = 9.6 mm, W = 4.3 mm), left d/4 (L = 11.8 mm; W = 5.8 mm) (e = estimated measurements).

*Deciduous dentition*.—Of the two maxillae fragments with milk teeth, the better preserved is NAP I 26'00. DM4/ is a triangular tooth, having a broken paracone which was probably quite low but somewhat larger than the metacone, which is a small, conical cusp. It has a strongly outwardly projecting parastyle

(observable in NAP I 129'99) and a strong, rounded metastyle. The protocone is dune-shaped and is united by a high cingulum to the parastyle and metastyle. In the centre of the tooth there is a wide valley. The buccal cingulum is strong. The D3/ is an elongated trenchant tooth, with a sharp bladelike metastyle, a strongly transversely compressed paracone that basally extends greatly anteriorly but without forming a true parastyle. The protocone is weak, almost without any relief.

The lower deciduous dentition is not as well preserved, the d/4 having the cusps displaced, but the basic morphology can be deduced to be comparable to that of the m/1, with a conical hypoconid less well developed than in the m/1, and projecting further exteriorly. In addition the entoconid appears to be weaker and is located in a more anterior position. The talonid seems to be relatively shorter than in the m/1.

*Discussion*.—The genus *Hecubides* was created by Savage (1965) for the amphicyonid species from Napak. This author included in *Hecubides* the species *Amphicyon lemanensis* (Lower Miocene of Saint-Gérard-Le-Puy, France), that Kuss (1965) used as the type species of the genus *Cynelos*. This provided a very good argument for Schmidt-Kittler (1987) to include *H. euryodon*, the type species of the genus, in *Cynelos*. It is clear that *Hecubides euryodon* and *Cynelos lemanensis* are quite close, not only in morphology but also in size. But taking into account the marked constancy of the “*Amphicyon*” morphotype, it is likely that it is primitive for the family Amphicyonidae.

This leads us to reconsider the value of the differences observed between *H. euryodon* and *C. lemanensis*, and to conclude that the genus *Hecubides* is valid. The P4/ of *H. euryodon* shows a clearly individualised protocone, joined by a crest to the apex of the paracone, this combination of features, pointed out by Savage (1965), differentiate this tooth from that of *Cynelos*, in which the protocone is less individualised, is wider and the crest of the paracone weak or inexistent (Viret, 1929; Ginsburg, 1980). The M1/ and M2/ of *H. euryodon* also have some differences from their homologues in *C. lemanensis*, in particular the greater strength of the protocone and the lingual cingulum. There are also clear differences in the occlusal outline of these upper molars, which in *H. euryodon* are wider lingually than those of *C. lemanensis*, and its anterior and posterior margins straighter and more parallel than those of the European amphicyonid, in which the outline is more triangular.

In the lower dentition, the teeth are somewhat more robust in *H. euryodon* than in *C. lemanensis*, this-

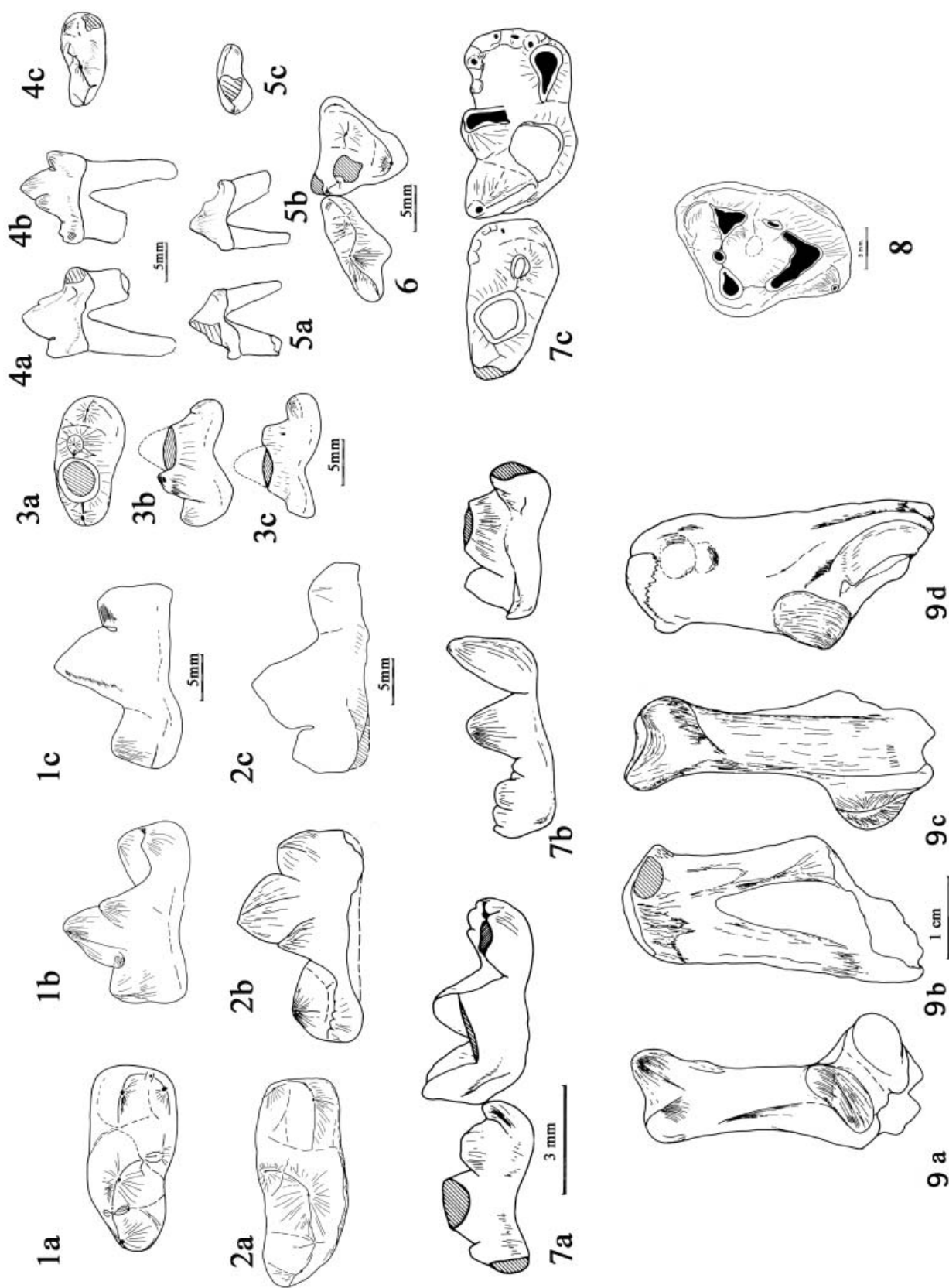


Figure 2.

being particularly evident in the p/4 from Napak described above that is not only more robust but also possesses a higher and better developed talonid than in *C. lemanensis*. The morphology of the p/4 clearly separates *Hecubides* from *Pseudarctos* and *Ictiocyon*, two genera in which the p/4 is more or less as robust as in *Hecubides*, but in which the posterior cuspid and talonid are greatly reduced (Ginsburg, 1992), as well as the P4/ of these two genera, which is closer to *Cynelos* than to *Hecubides*. The morphology of the m/2 is quite different from that of *Cynelos*, *Pseudarctos* and *Ictiocyon* by the presence of a paraconid, which indicate that in these genera the anterior valley of the trigonid is as closed as it is in *Hecubides* (Viret, 1929; Belinchón & Morales, 1989; Ginsburg, 1992).

Family Viverridae Gray, 1821

Genus *Ugandictis* gen. nov.

*Type species*.—*Ugandictis napakensis* sp. nov.

*Type locality*.—Napak.

*Diagnosis*.—As for the species.

*Ugandictis napakensis* sp. nov.

Figures 2-7, 3-3–6

*Type locality*.—Napak.

*Holotype*.—UMP 62-13, fragment of left mandible with m/1-p/4 (Figure 2-7, Figure 3-5).

*Paratypes*.—NAP I 44'02, left P4/ (Figure 3-3), NAP-no number, mandible with alveolus of m/2, m/1, alveolus of p/4, p/3, p/2, alveolus of p/1 and canine (Figure 3-4).

*Other material*.—NAP I 32'03, left m/1, lacking most of the enamel (Figure 3-6); NAP I 111'99, left mandible with dm/4, dm/3 and dm/2.

*Other localities*.—Songhor, Kenya.

*Age*.—Early Miocene.

*Diagnosis*.—Primitive viverrid of small size, m/2 medium sized, m/1 with v-shaped trigonid, with large metaconid that is lower than the paraconid, which is located in an antero-lingual position. The talonid is smaller than the trigonid (approximately 1/3 of the length of the tooth), with a strong hypoconid, sub-

divided hypoconulid and entoconid, these cuspids closing the talonid posteriorly. The p/4 is smaller than the m/1, narrow, with anterior, central and posterior cuspids and a basal platform in a postero-lingual position, p/3 and p/2 relatively short and with posterior cuspid. P4/ with short metastyle, forming a sharp blade, paracone similar in size to the metastyle, conical in form, prominent parastyle. The protocone is strong, dune-shaped, located anteriorly in front of the parastyle, joined by a crest to the parastyle, and posteriorly to the basal cingulum of the metastyle, which is well developed. Upper premolars (P3/ and P4/) elongated, with basal cingula weakly developed. Upper molar crowns unknown, but both possess three roots and are not greatly reduced.

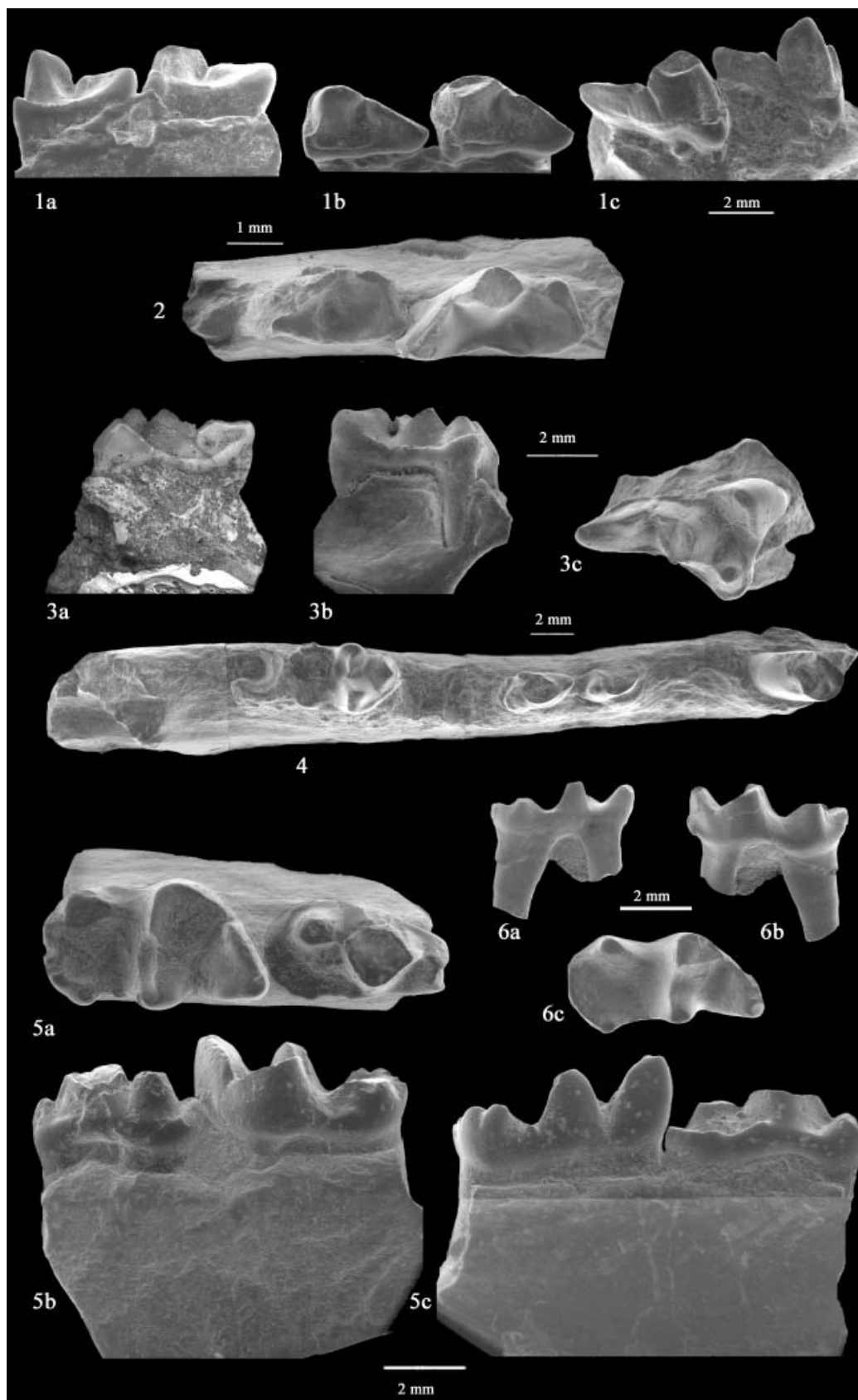
*Differential diagnosis*.—*Ugandictis* differs from *Legetetia nandii* by the smaller dimensions of m/2 and p/4 with respect to m/1, and by the simpler morphology of the trigonid of m/2, the talonid of m/1 closed posteriorly, by shorter lower premolars, and the simpler morphology of the talonid of p/4. It differs from *Kichechia zamanae* by the more complex morphology of the premolars, which are more elongated and trenchant. In addition, because of the smaller relative size of the paracone of P4/ and its more elongated shape, it is very different from the subtriangular outline of the tooth in *Kichechia*. It differs from *Leptoplesictis rangwai* by the closed v-shaped form of the trigonid of m/1, the better development of its talonid, the less reduced m/2 and the simpler morphology of the p/4.

*Description*.—The P4/ has a short metastyle in the shape of a sharp blade, a paracone similar in size to the metastyle which is voluminous and conical, and a strong parastyle. The dune-shaped protocone is very strong and is located in front of the parastyle. It is joined by a crest to the parastyle, and posteriorly to the basal cingulum of the metastyle, which is well developed.

NAP no number. The alveolus of the m/2 is elongated, m/1 is poorly preserved, possesses a trigonid that is almost equal in development to the talonid. The cuspids of the trigonid are disposed in a triangle with the paraconid in an antero-lingual position, the metaconid lingual, and the protoconid buccal. The

◆ **Figure 2.** *Hecubides euryodon* Savage, 1965. Napak I and Napak IV. **1.** NAP I 44'02, right m/1; a) occlusal view, b) lingual view, c) buccal view. **2.** NAP IV V 5830, left m/1; a) occlusal view, b) lingual view, c) buccal view. **3.** NAP I 45'02, right p/4; a) occlusal view, b) buccal view, c) lingual view. **4.** NAP I 128'99 left d/4; a) buccal view, b) lingual view, c) occlusal view. **5.** NAP I 128'99 left d/3; a) lingual view, b) buccal view, c) occlusal view. **6.** NAP I 26'00, fragment of left maxilla with D3/-D4/, occlusal view. **7.** *Ugandictis napakensis* nov. gen. nov. sp., Napak I, holotype: UMP 62-13, fragment of left mandible with m/1-p/4; a) buccal view, b) lingual view, c) occlusal view. **8.** *Kelba quadeemae* Savage, 1965. Napak IV, Nap IV 24'02, left M2/; occlusal view. **9.** *Ginsburgsmilus napakensis* Morales *et al.*, 2001. Napak I, Nap I 5'00, right calcaneum; a) dorsal, b) lateral, c) plantar, d) medial views.



**Figure 3.**

strength of the metaconid is an obvious feature. The big talonid has a broken hypoconid, but the hypoconulid is present and the entoconid is subdivided. The p/3 has a main cuspid, and anteriorly there is a small cusplet and posteriorly a moderate-sized cusplet positioned buccally with respect to the main cusp. The talonid is moderate. The p/2 is partly broken, but apparently its morphology would have been like that of the p/3, but smaller. In the mandible there is an alveolus for the p/1, which was uniradicate. The canine has a broken crown, the section is oval, with a sharp anterior crest.

UMP 62-13. The m/1 is better preserved than in the specimen described above. The metaconid is not as high as the paraconid, but is high and voluminous. The paraconid is positioned antero-lingually. In the talonid the hypoconid stands out, being clearly separated from the protoconid and joined posteriorly to the hypoconulid and this to a high and subdivided entoconid such that the posterior part of the talonid is closed off. The p/4 is elongated, with a large anterior cuspid (although it is broken on the anterior margin), the central cusp is moderate in size, and the posterior one strong and well individualised. The antero-lingual cingulum is strongly developed, forming a wide platform in an antero-lingual position with respect to the posterior cuspid.

Measurements of the specimens are left p/4 (L = 4.7 mm; W = 2.7 mm), left m/1 (L = 6.0 mm; W = 3.4 mm), left m/1 lacking enamel (L = 6e mm, 3e mm), right c/1 (L = 3.3 mm, W = 2.1 mm), right p/2 (L = 3.5 mm; W = 1.9 mm), right p/3 (L = 3.8 mm; W = 2.0 mm), right m/1 (L = 6.4e mm; W = 3.2 mm), left P4/ (L = 6.2 mm; W = 4.3 mm), left dm/2 (L = 3.4 mm; W = 1.5 mm), left dm/3 (L = 4.5 mm; W = 2.0 mm), left dm/4 (L = 5.7 mm; W = 2.6 mm) (e = estimated measurements).

**Discussion.**—There are three species of viverrids described from the Early Miocene of East Africa, the sizes of which are close to that of the new material from Napak (Figures 4, 5), namely, *Kichechia zamanae*, *Legetetia nandii* and *Leptoplesictis rangwai*. Out of these three species, two (*K. zamanae* and *L. rangwai*) have previously been recorded at Napak.

The morphology of the m/1 of *Ugandictis napakensis* with a closed v-shaped trigonid and well developed talonid is markedly different from that of *Leptoplesictis rangwai*, the trigonid of which is a more open v-shape, is more trenchant and in addition shows greater reduction of the talonid. The p/4s are also different, being simpler in *U. napakensis* than in *L. rangwai*.

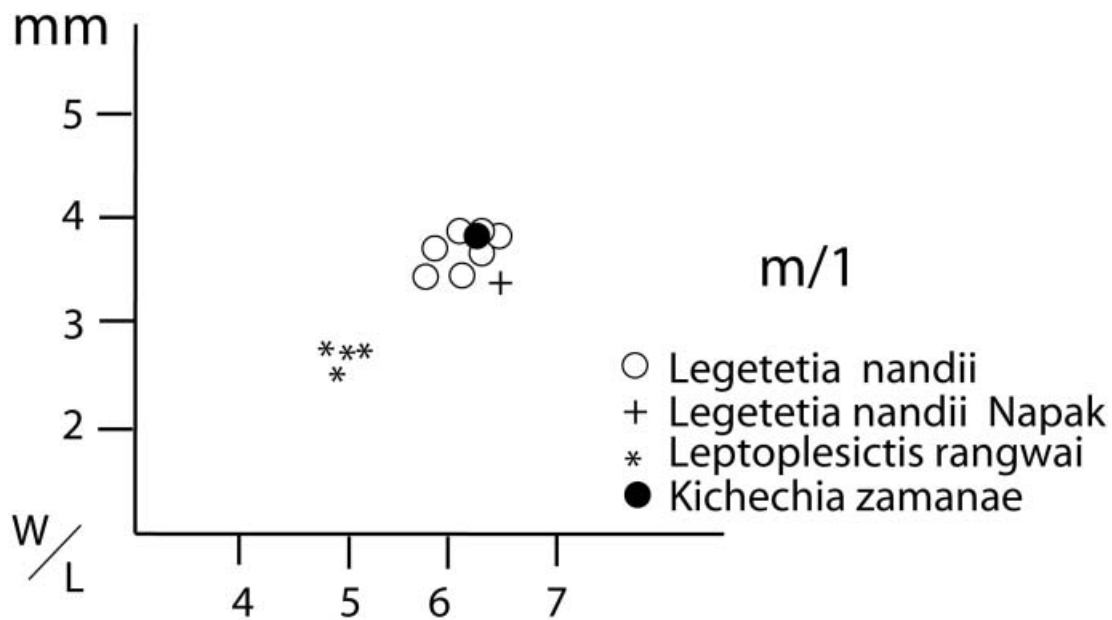
The lower dentitions of *U. napakensis* differ from those of *Kichechia zamanae* by the morphology of the premolars, which are more elongated with better developed anterior cusplets, and the presence of posterior cusplets in p/3 and p/2. They are far from the robust, more bunodont-looking premolars of *K. zamanae*.

These mandibles from Napak also differ from those of *Legetetia nandii* by the smaller m/2, deduced from the alveolus of NAP-un-numbered specimen, and by the morphology and size of the p/4 of UMP 62-13, notably smaller than the p/4 in *L. nandii* which is almost as long as the m/1.

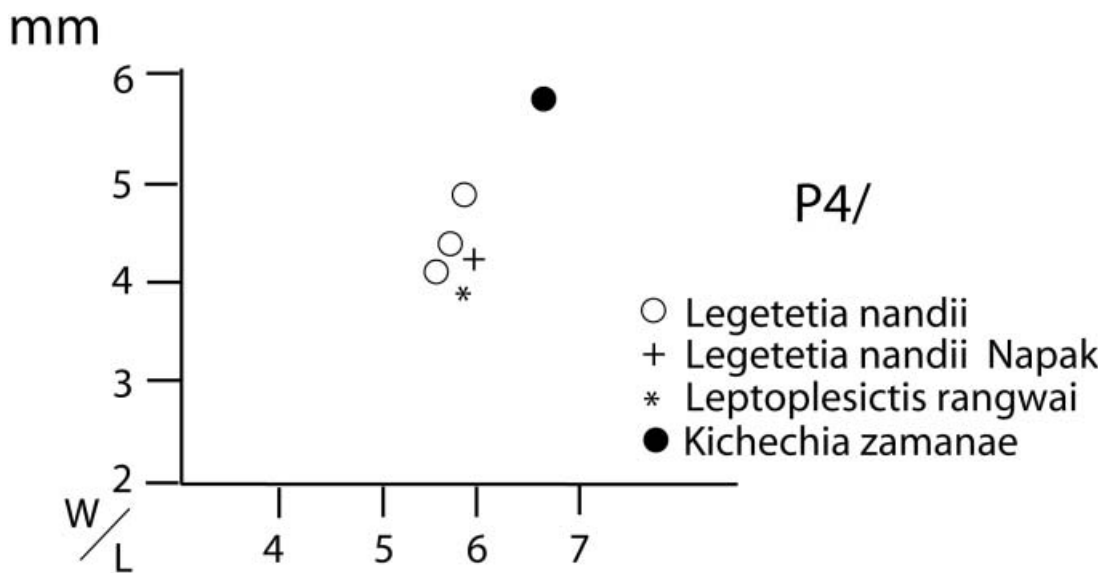
Other specimens from Napak and Songhor published by Savage (1965) and Schmidt-Kittler (1987) can be referred to *Ugandictis napakensis*. This is the case with the mandible from Songhor (CMF-M 19080) with p/4, m/1 and m/2 identified by Savage (1965) as *Kichechia zamanae* and which Schmidt-Kittler (1987) figured, manifesting quite reasonable doubts about its attribution to *Kichechia*. This mandible, despite its poor state of preservation, corresponds well in size and morphology to the new jaws from Napak, and yields additional information about the morphology of m/2.

The maxilla from Napak V (NAP-64) with P2/, P3/ and P4/, the latter two premolars being somewhat damaged, and the tri-radicate alveoli of M1/ and M2/ that Schmidt-Kittler (1987) included in *Leptoplesictis rangwai* should also be attributed to this new species, meaning that *L. rangwai* is no longer present in the Napak sample. The P4/ has the same size as the one described above (NAP I 44'02), and, as can be seen, its size corresponds closely to the P4/ of *Legetetia nandii* (Figure 5) even though the m/1s of *L. rangwai* are slightly smaller than those of *U. napakensis* and *L. nandii*.

◆ **Figure 3.** 1. *Isohyaenodon pilgrimi* Savage, 1965. Napak IV, NAP IV-64, fragment of left maxilla with M1/-M2/; a) lingual view, b) occlusal view, c) buccal view. 2. *Prionogale breviceps* Schmidt-Kittler & Heizmann 1991. Napak IV, NAP IV 53'04, fragment of right mandible with p/4 and m/1; occlusal view. 3. *Ugandictis napakensis* nov. gen. nov. sp. Napak I, NAP I 44'02, left P4/; a) lingual view, b) buccal view, c) occlusal view. 4. *Ugandictis napakensis* nov. gen. nov. sp. Napak I, NAP-no number, mandible with alveolus of m/2, m/1, alveolus of p/4, p/3, p/2, alveolus of p/1 and canine; occlusal view. 5. *Ugandictis napakensis* nov. gen. nov. sp. Napak I, holotype: UMP 62-13, fragment of left mandible with m/1-p/4; a) occlusal view, b) buccal view, c) lingual view. 6. *Ugandictis napakensis* nov. gen. nov. sp. Napak I, NAP I 32'03, left m/1, lacking most of the enamel; a) lingual view, b) buccal view, c) occlusal view.



**Figure 4.** Bivariate (length-breadth) plot of lower first molars of Early Miocene viverrids from East Africa.



**Figure 5.** Bivariate (length-breadth) plot of upper fourth premolars of Early Miocene viverrids from East Africa.

The affinities of *Ugandictis napakensis* to the species with which we have compared it are difficult to discern, given the limitations of our knowledge of the Early Miocene viverrids. The new form is in many ways primitive with respect to *Kichechia zamanae* and *Leptoplesictis rangwai*, species specialised in opposite ways, the former being hypocarnivorous and the latter being more hypercarnivorous. With respect

to *Legetetia* it is more difficult to decide, the new genus shares the morphology of the carassials (m/1 and P4/) but diverges drastically in the size of m/2 and p/4, and it is probable that *Legetetia* has a mixture of derived and primitive characters associated. The trigonid of m/2 is clearly primitive, but the elongation of its talonid could be interpreted as being derived.

Family Felidae Gray, 1821  
 Subfamily Barbourfelinae Schultz *et al.*, 1970  
 Tribe Afrosmilini Morales *et al.*, 2001  
 Genus *Ginsburgsmilus* Morales *et al.*, 2001  
*Ginsburgsmilus napakensis* Morales *et al.*, 2001

Figure 2-9

**Material.**—Napak I 5'00, right calcaneum (Figure 2-9).

**Description.**—The specimen is broken below the sustentaculum. In comparison with a felid (?feline) the talar facets are equal in size (as in *Lynx rufus*) and it is short and robust. The body has a quite constant subrectangular section, being slightly compressed transversely, the lateral and medial surfaces are parallel, the dorsal margin is wide and the antero-posterior diameter barely changes from the coracoid process to the tuber. The plantar border is proximo-distally straight and regular in width.

In the lateral surface, near the dorsal border, there is a small rugose depression for the short collateral ligament. The rest of this surface is practically occupied by a large area limited by two crests where the accessory flexor muscles of the digits (quadratus plantae = flexor digitorum accessorius) insert.

The sustentaculum is in a very dorsal position and, above all, is more distal than in *Felis* or *Lynx*. It is not greatly developed dorso-plantarly or medially. The talar facet of the sustentaculum is rounded. The groove for the tendon of the lateral flexor of the digits is well developed.

In the tuber calcanei the plantar surface for the insertion of the superficial flexor of the digits is large and is limited distally by a strong crest (somewhat similar to *Paramachairodus ogygia*). The medial border of the tuber is high, the lateral one is partly damaged, but the dorso-plantar diameter appears to be greater than the transverse one.

In comparison with *P. ogygia* it shares the shape of the body, the large development of the areas for the superficial and accessory flexors. It differs in the position of the sustentaculum, which is more proximal and dorsal in *P. ogygia* from Batallones, Spain.

The accessory flexor of the digits actuates flexion of the phalanges in relation with the tarsus and is reduced in cursorial carnivores. For Turner and Antón (1997) the presence of well developed accessory flexors of the digits is a primitive character within the family Felidae. Salesa (2002) relates it to the climbing capacity of certain small felids such as *Leopardus wiedii*, but in the case of *Paramachairodus ogygia* we think that it could be related to the mode of hunting of the species.

The calcaneal body is short and robust, the sustentaculum forward and distal, and there is a large surface for insertion of the accessory flexor of the digits, all features which, according to Ginsburg (1961a) correspond to plantigrade carnivores. Within this wide category, the Napak calcaneum is closely similar to the morphology of *Sansanosmilus palmidens* (Ginsburg, 1961a, b) differing from it by its considerably smaller size, lesser proximal enlargement of the body and lesser medial expansion of the sustentaculum.

Order Incertae sedis

Family Incertae sedis

Genus *Prionogale* Schmidt-Kittler & Heizmann, 1991

*Prionogale breviceps* Schmidt-Kittler & Heizmann, 1991

Figures 1-4, 3-2

**Material.**—Nap IV 53'04, right mandible with canine alveolus, uniradicate alveolus of p/3, p/4 lacking the anterior half and m/1 (Figures 1-4, 3-2).

**Description.**—The p/4 is an elongated tooth, longer than the m/1. Only the anterior part of the tooth is preserved, formed of a well developed and quite deep basin, in the centre of which there is a circular depression, probably caused by occlusion with the posterior cusp of P4/. The m/1 is a carnassial, with the paraconid and protoconid comprising a blade, the two cusps being separated from each other by a notch as is typical of carnassials. The talonid is short, formed of a crestlike hypoconid which continues round the posterior part of the talonid and the lingual margin of the tooth, closing an obliquely oriented talonid valley that reaches the base of the paraconid, an unusual morphology.

Measurements of the specimens are p/4 (L = 4.6e mm; W = 1.7 mm), m/1 (L = 3.6 mm; W = 1.6 mm) (e = estimated measurement).

**Discussion.**—The size and morphology of the teeth preserved in the Napak mandible are similar to those described as *Prionogale breviceps* by Schmidt-Kittler & Heizmann (1991) a species which is also represented at various Early Miocene localities in East Africa, including Napak.

Genus *Kelba* Savage, 1965

*Kelba quadeemae* Savage, 1965

Figure 2-8

**Material.**—Nap IV, 24'02, left M2/ (Figure 2-8).

**Description.**—The occlusal outline of the M2/ is subquadrangular due to the well developed cingulum of the anterior wall which almost forms a separate

cusplet. The paracone and metacone are similar in size, relatively low and pyramidal. Between them there is a low, small cusplet. There is a prominent metastyle, separated by a small incision from the metacone. The protocone is well developed and is located centrally and joined to the paraconule and metaconule, such that the central valley is completely surrounded by cusplets. With the exception of the central part of the base of the protocone, the tooth is surrounded by strong cingula.

Measurements of the specimen are left M2/ (L = 9.5 mm, W = 11.3 mm).

**Discussion.**—The Napak *Kelba* tooth is similar to the holotype from Rusinga, Kenya, but is slightly smaller, and has a slightly squarer occlusal outline. Savage (1965) considered the type specimen to be a right upper molar, but it is in fact a left one. What he took to be the hypocone is a slight swelling on the lingual end of the anterior cingulum, and what he took to be the parastyle is the metastyle.

Previous researchers have classified *Kelba* in Creodonta (Savage, 1965), Pantolestidae (Van Valen, 1967) or Carnivora (McKenna and Bell, 2000). Morales *et al.* (2000) considered that *Kenyalutra* and *Ndamathaia* were synonyms of *Kelba*, and they classified the genus in Viverridae. An undescribed snout of this genus from Songhor, Kenya, shows that it is probably not a carnivore. The fourth upper premolar is completely molarised and there are three molars. Furthermore, previous interpretations of the holotype, an isolated M2/ are incorrect in the sense that what was taken to be a right tooth (Savage, 1965) is in fact a left one, and therefore what was considered to be the hypocone at the distolingual corner of the tooth is in fact a swelling at the lingual extremity of the mesial cingulum.

Pending further analysis of the Songhor specimen, we refer *Kelba* to an unknown order of mammals.

### General discussion and conclusions

An up-to-date list of the Napak carnivorans contains 12 species, up from 8 in the previous literature.

#### Creodonta

*Metasinopa napaki*  
*Pterodon africanus*  
*Isohyaenodon pilgrimi*  
*Isohyaenodon zadoki*  
*Leakitherium* sp.  
*Teratodon spekei*

#### Carnivora

*Hecubides euryodon*

?*Kichechia zamanae*

*Ugandictis napakensis* gen. nov. sp. nov.

*Ginsburgsmilus napakensis*

Incertae sedis

*Kelba quadeemae*

*Prionogale breviceps*

#### Creodonta

There is no new material of the larger creodonts from Napak. Savage (1965) described *Metasinopa napaki* and *Pterodon africanus*, the former based on a mandible and maxilla, and the latter on the basis of a maxilla with three cheek teeth. None of the smaller creodonts was previously reported from Napak but there are at least three taxa present there. In addition the small carnivore of uncertain affinities *Prionogale breviceps* is present.

The species *I. zadoki* was originally ranged within the genus *Metapterodon* by Savage (1965) but was transferred to the genus *Isohyaenodon* by Morales *et al.* (1998). The species *I. pilgrimi* was initially attributed to the subgenus *Isohyaenodon*, genus *Hyaenodon* by Savage (1965), whereas Morales *et al.* (1998) raised its rank to a full genus. Thus there are two small species of *Isohyaenodon* at Napak. In addition, there is part of a lower carnassial with similar morphology to those of *I. zadoki* but somewhat larger indicating the presence of a third species at the site which we attribute to the closely related genus *Leakitherium*.

For the first time, the genus *Teratodon* has been recognised at Napak, on the basis of a symphyseal portion of mandible with alveoli of p/1 and p/2 and a complete, unworn p/3. *Teratodon* was a peculiar creodont with robust, bunodont premolars and sectorial carnassials. Pickford (1995) considered that its main prey consisted of gastropods, in particular *Achatina leakeyi*, a large achatinid which is common at sites where *Teratodon* has been found. The robust premolars, large symphysis and anteriorly positioned zygomatic arches of the snout suggest that the anterior dentition was used to crack open the gastropod shells in order to gain access to the soft body inside, which was then processed by the sharp carnassials at the back of the dental series.

There are thus at least 6 species of creodonts at Napak.

#### Carnivora

The amphicyonid genus *Hecubides* is resurrected because fossils from Napak, Uganda, which is the type locality of the type species (*H. euryodon*), show significant differences from *Cynelos*, in which Schmidt-Kittler (1987) classed it. New fossils from Napak in-

clude associated upper and lower deciduous dentition as well as additional permanent teeth which broaden our knowledge about variation within the species *H. euryodon*.

The small fissiped carnivores from the Early Miocene of East Africa have had a somewhat complicated history, as was shown by Schmidt-Kittler (1987) who subdivided the material initially attributed to *Kichechia zamanae* by Savage (1965) into at least three taxa (*Kichechia*, *Herpestides*, and *Leptoplesictis*). They are all rather small carnivores but show a wide variety of adaptations ranging from hypocarnivory to hypercarnivory. One of the paratypes of *K. zamanae* listed by Savage (1965) and used in the composite figure of the lower dentition of the species (Savage, 1965, figs. 58–60) is in fact a mandible fragment of *Ugandictis napakensis*. Some of the material doubtfully attributed to *Kichechia zamanae* by Schmidt-Kittler (1987, text-fig. 13) is here identified as *Ugandictis napakensis*, bringing to two the total of small viverrids at Napak (*Kichechia zamanae* and *Ugandictis napakensis*). The Napak specimen attributed to *Leptoplesictis rangwai* by Schmidt-Kittler (1987) is here attributed to *Ugandictis napakensis*.

A calcaneum is the first postcranial bone to be attributed to the medium sized barbourufeline *Ginsburgmilus napakensis* and it suggests that this species may have had plantigrade adaptations.

The present study brings to 4 the list of fissiped species known at Napak. There was thus a lower diversity of carnivores than creodonts at the site.

### Incertae sedis

Two enigmatic “carnivore” taxa present at Napak occur in other Lower Miocene deposits of East Africa. The tiny one which Schmidt-Kittler & Heizmann (1991) classified in *Prionogale breviceps* is considered by them to be a member of an unknown clade independent of the Carnivora and Hyaenodontida. A dog-sized carnivoran *Kelba quadeemae* was originally classified as an oxycenine creodont by Savage (1965) but Morales *et al.* (2000) considered that it was more likely to be a hemigaline viverrid. The new fossil of this species from Napak IV is typical of the genus, but an undescribed snout from Songhor, Kenya, shows that it is unlikely to be either a creodont or a fissiped. Pending further analysis, we prefer to treat it as incertae sedis.

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