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# Middle Miocene Carnivora and Hyaenodonta from Fort Ternan, western Kenya

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# Middle Miocene Carnivora and Hyaenodonta from Fort Ternan, western Kenya

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## ABSTRACT

Fort Ternan is a middle Miocene (*c.* 13.7-13.8 Ma) site famous for its fossils of *Kenyapithecus wickeri* Leakey, 1962, considered the earliest African hominoid. Herein, the Carnivora and Hyaenodonta from this site are described and placed in their temporal context, showing the middle Miocene to be a time of transition from archaic carnivores of the early Miocene and carnivores of more modern aspect from the late Miocene. Fort Ternan includes: Amphicyonidae represented by ?*Myacyon peignei* n. sp., a new form distinguished by its hypercarnivorous m1, P4 with large protocone shelf, and M1 with reduced lingual shelf; Barbourofelidae, represented by a derived form; Percrocutidae, represented by abundant material of *Percrocuta tobieni* Crusafont & Aguirre, 1971; Viverridae, represented by the paradoxurines *Kanuites lewisae* Dehghani & Werdelin, 2008, and cf. *Orangictis* Morales & Pickford, 2005, and a putative viverrine; and Hyaenodonta represented by the teratodontine *Dissopsalis pyroclasticus* Savage, 1965 and a very large hyainailourine. This assemblage is a melange of forms harkening back to the early Miocene (the Hyaenodonta and Amphicyonidae), an evolving, still extant lineage (Viverridae), and more typical late Miocene forms (derived Barbourofelidae and Percrocutidae).

KEY WORDS
Middle Miocene,
Carnivora,
Hyaenodonta,
Africa,
Kenya,
new species.

## RÉSUMÉ

*Les Carnivora et les Hyaenodonta du Miocène moyen de Fort Ternan, Kenya occidental.*
Le site Miocène moyen (*c.* 13.7-13.8 Ma) de Fort Ternan est célèbre en raison de la présence de *Kenyapithecus wickeri* Leakey, 1962, premier hominoïde africain. Cet article décrit les Carnivora et les Hyaenodonta de Fort Ternan dans leur contexte temporel. Il montre que le Miocène moyen est une période de transition entre les carnivores archaïques du Miocène inférieur et les carnivores beaucoup plus modernes du Miocène supérieur. Les carnivores de Fort Ternan comportent : un Amphicyonidae, représenté par ?*Myacyon peignei* n. sp., une espèce nouvelle caractérisée par une m1 hypercarnivore, une P4 avec un protocône allongé et une M1 avec une part linguale réduite ; un Barbourofelidae, représenté par une forme avancée ; un Percrocutidae, représenté par un matériel abondant de *Percrocuta tobieni* Crusafont & Aguirre, 1971 ; trois Viverridae, représentés par les paradoxurines *Kanuites lewisae* Dehghani & Werdelin, 2008 et par cf. *Tugenictis* Morales & Pickford, 2005, et un viverriné ; deux Hyaenodonta, représentés par la teratodontine *Dissopsalis pyroclasticus* Savage, 1965 et un hyainailouriné géant. Cet assemblage est un mélange de formes qui ont des affinités avec celles du Miocène inférieur (Hyaenodonta et Amphicyonidae), d'une lignée qui existe encore (Viverridae), et des formes qui caractérisent le Miocène supérieur (Barbourofelidae avancés et Percrocutidae).

MOTS CLÉS
Miocène moyen,
Carnivora,
Hyaenodonta,
Afrique,
Kenya,
espèce nouvelle.

## INTRODUCTION

Fort Ternan is a middle Miocene site in western Kenya, lying 40 miles east of Kisumu at 0°13'S, 35°21'E. Its dating has been much discussed but the most recent evidence, from whole-rock K/Ar and single-crystal $^{40}$Ar/$^{39}$Ar, gives a date of 13.7-13.8 Ma (Pickford *et al.* 2006). Fort Ternan has received considerable attention in the past because of the presence at the site of a range of primates including *Kenyapithecus wickeri*, considered the earliest African hominoid (Leakey 1962; Harrison 2010). This has stimulated interest in the paleoenvironment of Fort Ternan, producing a range of analyses and opinions (Shipman *et al.* 1981; Shipman 1986; Kappelman 1991; Cerling *et al.* 1992, 1997; Retallack 1992a, b).

Parts of the fauna have also been studied, including the bovids (Gentry 1970), rhinos (Hooijer 1968), and rodents (Lavocat 1964). Despite the interest in the site, and despite their appearance in faunal lists, the carnivores have received limited attention. Evidence from collection records indicate that the late Professor R. J. G. Savage intended to publish on the Fort Ternan carnivores, but no such publication exists, and inquiries have failed to produce any trace of an unpublished manuscript. The only published paper dedicated to the Fort Ternan carnivores is Dehghani & Werdelin (2008) on the beautifully preserved cranium of *Kanuites lewisae* (see below). In addition, the *Percrocuta* from the site was briefly mentioned in Howell & Petter (1985), the amphicyonid in several publications (Morales & Pickford 2005; Werdelin & Simpson 2009; Morales *et al.* 2016), and *Dissopsalis* in Barry (1988). The present paper represents the first study bringing all the Fort Ternan carnivores together.

## MATERIAL AND METHODS

The material studied is housed in the paleontology collections of the National Museums of Kenya, Nairobi under the prefix KNM-FT.

The phylogenetic analysis was carried out in TNT version 1.5 (Goloboff *et al.* 2008; Goloboff & Catalano 2016) using the implicit enumeration option (exhaustive search). All characters were unordered. Bremer support was obtained in TNT by a round of TBR (Tree Bisection-Reconnection) on the shortest trees, saving all trees up to five steps away from the shortest trees.

### Abbreviations

| | |
|---|---|
| KNM | National Museums of Kenya; |
| FT | Fort Ternan collection; |
| P | upper premolar; |
| p | lower premolar; |
| M | upper molar; |
| m | lower molar; |
| d | deciduous tooth; |
| L | length; |
| W | width; |
| Lt | trigonid length; |
| Wa | anterior width of upper carnassial; |
| Wbl | blade width of upper carnassial; |
| Lp | paracone length of upper carnassial; |
| Lm | metastyle length of upper carnassial. |

### Measurements

All measurements are in millimeters (mm).

## SYSTEMATIC PALAEONTOLOGY

Order CARNIVORA Bowdich, 1821
Family Amphicyonidae Haeckel, 1866

Genus *Myacyon* Sudre & Hartenberger, 1992

Type species. — *Myacyon dojambir* Sudre & Hartenberger, 1992 (by monotypy).

### ?*Myacyon peignei* n. sp.
(Fig. 1)

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Small amphicyonid – Shipman *et al.* 1981: 64.

*Agnotherium* sp. – Morales & Pickford 2005: 276. — Werdelin & Simpson 2009: 782. — Werdelin & Peigné 2010: 605.

*Myacyon* sp. I – Morales *et al.* 2016: 145.

Holotype. — KNM-FT 3611, left P4 (Fig. 1A-C).

Etymology. — Honoring the memory of Stéphane Peigné and his achievements in the field of carnivore paleontology.

Locality. — Fort Ternan (type locality) only.

Stratigraphic range. — Middle Miocene; upper Serravallian; 13.7-13.8 Ma (Pickford *et al.* 2006).

Material examined. — KNM-FT 3379, left m1; KNM-FT 3399, right M1; KNM-FT 3611, left P4.

Judging by size and morphology, all three specimens represent the same taxon, but not the same individual, given their differing states of wear. The identity of this taxon has been discussed several times in the past 15 years. In 2005 Morales & Pickford described the species *Agnotherium kiptalami* Morales & Pickford, 2005 based on a cranium from the Middle Miocene of Kabarsero, Ngorora Formation, Tugen Hills, Kenya. At the same time, they also discussed the Fort Ternan specimens, attributing them to *Agnotherium*, but without assigning them to species. The attribution to *Agnotherium* was followed by Werdelin & Simpson (2009) and Werdelin & Peigné (2010). More recently, Morales *et al.* (2016) revised the Amphicyonidae of Africa. In so doing they transferred *A. kiptalami* to *Myacyon* Sudre & Hartenberger, 1992, tentatively suggesting that the Fort Ternan specimens might also belong in that genus.

Diagnosis. — Amphicyonidae of moderate size. P4 short and broad with protocone shelf well developed and extended distally to the metastyle. M1 protocone shelf short mesiodistally. m1 hypercarnivorous with low paraconid and tall protoconid. Small metaconid present, appressed to distolingual part of protoconid and jutting out distally from it. Talonid short.

### Description

*KNM-FT 3379 (Fig. 1D-F).*

This m1 is relatively tall for its length. The paraconid is low and short with robust and slightly worn pre- and postparacristids. The paraconid is much smaller than the protoconid in all dimensions. The protoconid, which is nearly unworn, is tall and trenchant with salient pre- and postprotocristids and a sharp apex. The metaconid is small and located at the distal end of the protoconid, appressed to it and jutting out distally. The talonid is broken distally but has a substantial hypoconid and cristid obliqua and a very low but nevertheless distinct entoconid. In occlusal view the lingual side has a wavy outline, bulging out at the center of the trigonid and between the protoconid and talonid, whereas the lingual side is convex throughout. There is a weak lingual cingulum that runs from the protoconid to the mesial end of the metaconid.

**Measurements.** Lm1 *c.* 21; Wm1 10.2; Ltm1 14.0.

*KNM-FT 3399 (Fig. 1G-H)*
This M1 has large paracone and metacone and a mesiodistally shortened lingual shelf that is worn nearly flat. In occlusal view the paracone is slightly larger than the metacone and in distal view it can be seen to be considerably taller. Both cusps are broad and pyramidal. There is a very small cusp located at the base of the lingual side of the paracone. The lingual shelf shows a crest-like, low hypocone, but the protocone cannot be discerned at all. The tooth is too worn for the development of the cingula to be determined with certainty.

**Measurements.** LM1 16.8; WM1 *c.* 20.5.

*KNM-FT 3611 (holotype, Fig. 1A-C)*
Like the m1 this P4 is relatively short and tall and nearly unworn. There is a low parastyle cusp that is closely appressed to the paracone. The paracone is tall and trenchant. The metastyle is of about the same length as the paracone, but considerably lower and lacks a distinct cusp. The protocone is very low and set in a large shelf that extends from the parastyle cusp to the mesial end of the metastyle, reminiscent of the morphology of some Lutrinae. This shelf continues as a lingual cingulum to the distal end of the metastyle.

**Measurements.** LP4 22.9; WaP4 15.1; WblP4 9.3; LpP4 9.2; LmP4 9.0.

### DISCUSSION

The specimens described above cannot be attributed to any named species of Amphicyonidae. Therefore, a new species is indicated, a conclusion also reached by Morales *et al.* (2016). Generic attribution is, on the other hand, a very complicated and unresolved issue. The material was attributed to *Agnotherium* by Morales & Pickford (2005), Werdelin & Simpson (2009), and Werdelin & Peigné (2010). *Agnotherium* is, however, a poorly characterized genus, despite work by, e.g., Kuss (1962). Morales *et al.* (2016) present sound arguments why the Fort Ternan material cannot be attributed to that genus and they tentatively assign the material to *Myacyon* Sudre & Hartenberger, 1992. This is not an implausible attribution, but the holotype (and only specimen) of the type species, *Myacyon dojambir*, is a severely damaged distal half of a mandible corpus with m1 and damaged m2. The illustrations of this material in Sudre & Hartenberger (1992) are, in addition, entirely inadequate and their published measurements confusing. The verbal description by Sudre & Hartenberger (1992: 554) fits the Fort Ternan m1 quite well but is fairly general and the only truly distinctive character is the distally positioned metaconid. A distinctive feature of the Fort Ternan P4 is the development of the protoconid shelf, but this feature is not known in *Myacyon*, including '*Agnotherium*' *kiptalami* (also reassigned to *Myacyon* by Morales *et al.* [2016]). This protocone shape bears some resemblance to a specimen from Frohnstetten, Germany attributed by Kuss (1962: fig. 5c) to *Agnotherium antiquum*; however, that specimen is broken and its actual shape cannot be definitively determined. In summary, I here attribute the material to ?*Myacyon peignei* n. sp. in anticipation of more material that can definitively clarify the generic attribution.

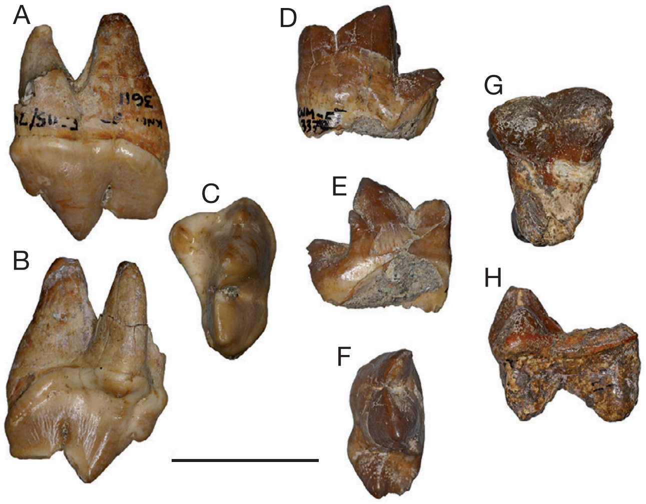

FIG. 1. — ?*Myacyon peignei* n. sp. from Fort Ternan: **A**-**C**, KNM-FT 3611 (holotype), left P4 in buccal (**A**), lingual (**B**) and occlusal (**C**) views; **D**-**F**, KNM-FT 3379, left m1 in buccal (**D**), lingual (**E**), and occlusal (**F**) views; **G**, **H**, KNM-FT 3399, right M1 in occlusal (**G**), and distal (**H**) views. Scale bar: 20 mm.

## Family BARBOUROFELIDAE
## Schultz, Schultz & Martin, 1970
## Subfamily BARBOUROFELINAE
## Schultz, Schultz & Martin, 1970

### BARBOUROFELINAE gen. et sp. indet.

MATERIAL EXAMINED. — KNM-FT 3366, right P4 broken mesial to the paracone.

### DESCRIPTION

*KNM-FT 3366 (Fig. 2A-C)*
A nearly unworn P4. The preserved part of the tooth is long and slender. The protocone is tall and has a sharply pointed apex. It is buccolingually narrow, with trenchant pre- and postparacone crests. The outline of the cusp is sinuous on the lingual side, with a narrow bulge at the apex that continues

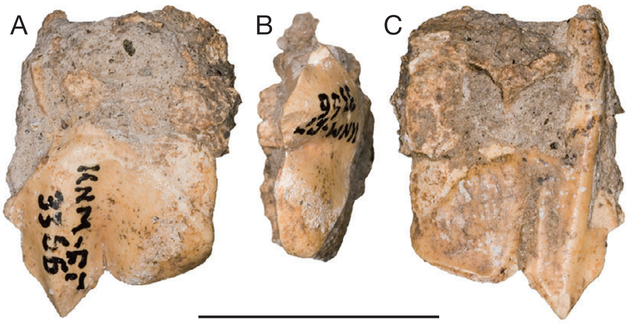

Fig. 2. — Barbourofelinae gen. et. sp. indet. from Fort Ternan, KNM-FT 3366, right P4, in buccal (**A**), occlusal (**B**), and lingual (**C**) views.

The marked hypsodonty of the nearly unworn carnassial is a characteristic of derived Barbourofelidae, seen in *Barbourofelis morrisi* (Schultz *et al.* 1970: fig. 1A), *B. lovei* (Baskin 1981: fig. 1), and *B. piveteaui* (Geraads & Güleç 1997: fig. 1). The Fort Ternan tooth is very similar in appearance to these but is considerably smaller.

To estimate the length of KNM-FT 3366, I used measurements of the three specimens of *Barbourofelis* listed above. The preparacone length and total length are provided for *B. morrisi* in Schultz *et al.* (1970). In the case of the other two specimens only the total length is given, and I have estimated the preparacone proportion of that length from the illustrations. Despite the crudity of this approach the three specimens give quite similar estimates, indicating that the preparastyle length of the P4 in these species was 26-28% of total length. This gives a length estimate for KNM-FT 3366 of *c.* 23.5 mm. This can be compared with 42.1 (*B. morrisi*), 48.4 (*B. lovei* – mean of four specimens), and 40.3 (*B. piveteaui*). The localities where these three species were found are all estimated to be early late Miocene, about 3 million years younger than Fort Ternan.

Older Barbourofelidae from Africa (*Ginsburgsmilus, Afrosmilus, Syrtosmilus*) have, where known, a more 'normal' felid P4 that does not display the extreme hypsodonty seen in KNM-FT 3366 and other derived species (see, e.g., Savage [1965: fig. 62] and Morales *et al.* [2001a: fig. 1B]). There are, however, two occurrences of Barbourofelidae in Africa that are of similar or younger age.

One of these is *Vampyrictis vipera* from the Beglia Formation of Tunisia (Kurtén 1978), which straddles the middle-upper Miocene boundary, making *Vampyrictis* slightly younger than KNM-FT 3366. *Vampyrictis* is represented by an m1 that is distinctive by its great slenderness and minute metaconid, and an upper deciduous canine fragment that is mediolaterally very narrow. Judging by the m1, *Vampyrictis* was clearly highly derived, perhaps more so than KNM-FT 3366. In the absence of overlapping material, no direct comparisons can be made, but with a reported length of 27.3 mm (Kurtén 1978: table 1) this tooth is close in length to that of *Barbourofelis piveteaui* reported by Geraads & Güleç (1997) to be 26.6 mm. The latter specimen has a P4 that measures 40.3 mm in total length, which is far greater than the estimated 23.5 mm for KNM-FT 3366.

The other younger barbourofelid from Africa is the damaged skull KNM-SH 17991 described by Tsujikawa (2005) from earliest Miocene of the Namurungule Formation, Samburu Hulls, Kenya. This specimen, originally described as Machairodontinae gen. et sp. indet. (Tsujikawa 2005) but transferred to Barbourofelidae by Werdelin & Peigné (2010) is, like *Vampyrictis*, considerably larger than the individual to which KNM-FT 3366 belonged. A rough estimate based on the photographs in Tsujikawa (2005: fig. 2) indicates a P4 length in this specimen well in excess of 40 mm.

A new genus and species of Barbourofelidae is indicated by KNM-FT 3366, but the present material is not adequate for formal recognition of such a taxon. It should be noted that the specimen might represent a dP3, in which case the taxon would be similar in size, or identical to, that described by Tsujikawa (2005). Nevertheless, the primary identification is a P4.

## Family PERCROCUTIDAE Werdelin & Solounias, 1991

### Genus *Percrocuta* Kretzoi, 1938

TYPE SPECIES. — *Hyaena carnifex* Pilgrim, 1913 (subsequent designation by Kretzoi [1938]).

### ***Percrocuta tobieni*** Crusafont & Aguirre, 1971

*Percrocuta tobieni* Crusafont & Aguirre, 1971: 55.

TYPE SPECIMEN. — KNM-BN 1469, right mandible corpus with c, p2-m1.

TYPE LOCALITY. — Kabarsero, Ngorora Formation, Kenya.

MATERIAL EXAMINED. — KNM-FT 3362, right dp4; KNM-FT 3364, right dP3; KNM-FT 3375a, right m1; KNM-FT 3375e, left P2; KNM-FT 3408, right dP2; KNM-FT 3610, left P3; KNM-FT 3614a, right maxilla with P1 (emerging) and dP2-dP4; KNM-FT 3614b, right maxilla fragment with P3-P4 in crypt; KNM-FT 3614c, right M1; KNM-FT 12693, left p3; KNM-FT 12694, broken left p4; KNM-FT 12695, left mandible corpus with alveolus for dp2, complete dp3-dp4, emerging m1; KNM-FT 14140, right p3.

#### DESCRIPTION

*KNM-FT 3362 (Fig. 3E, F)*

A long, slender deciduous carnassial in which the paraconid is longer and lower than the protoconid. The metaconid is well developed and set distal to, and well separate from, the protoconid. The talonid bears small, crestiform entoconid and hypoconid. The position of the metaconid and development of the talonid identify the specimen as Percrocutidae.

**Measurements.** Ldp4 16.6; Wdp4 6.2.

*KNM-FT 3364 (Fig. 3G-H)*

A dP4 that is broken anteriorly. The extent of the preparastyle is not clear, but it appears to have formed a distinct

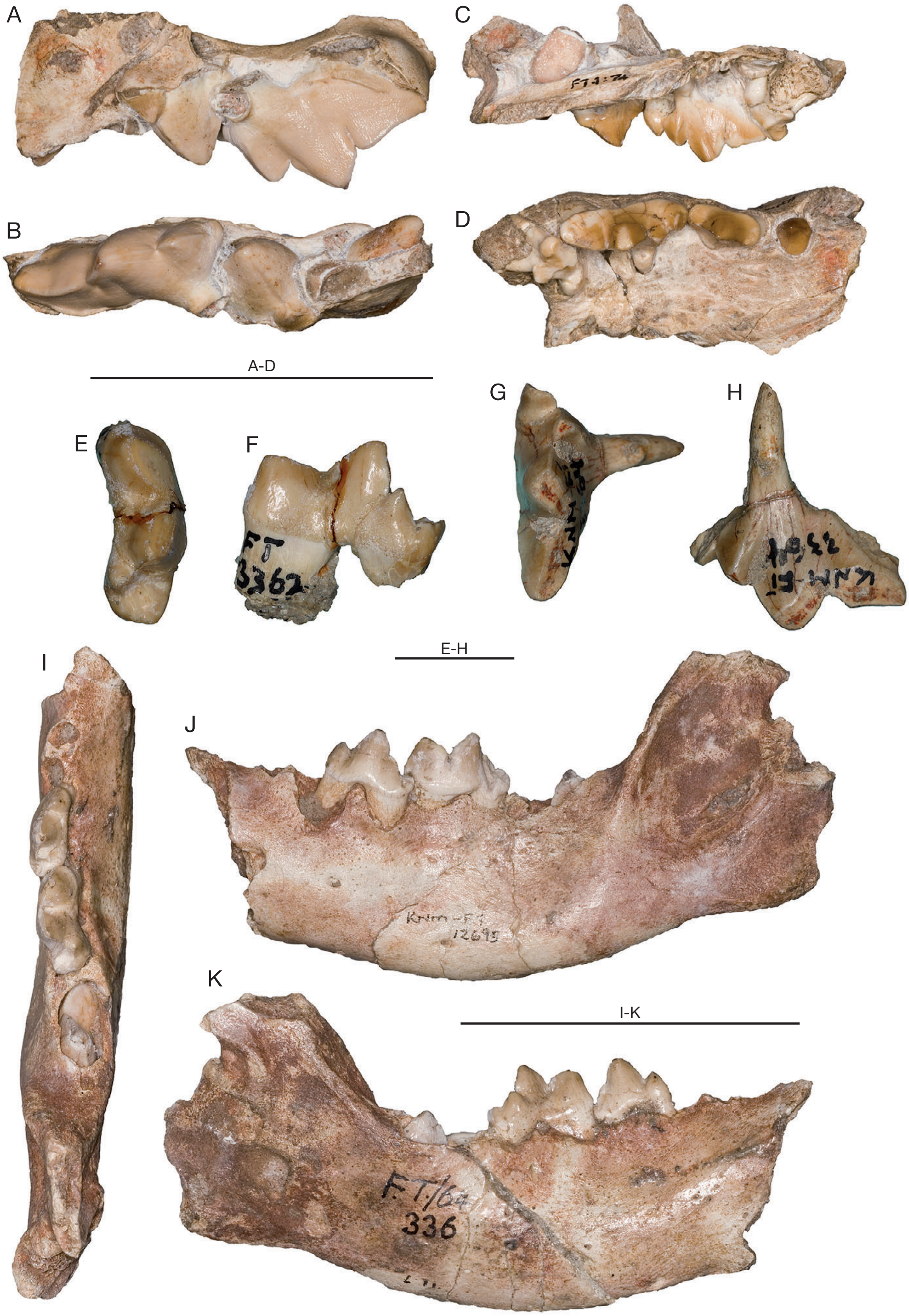

FIG. 3. — *Percrocuta tobieni* from Fort Ternan: **A**, **B**, KNM-FT 3614A, right maxilla with P4 in lingual (**A**) and occlusal (**B**) views; **C**, **D**, KNM-FT 3614B, right maxilla with dP2-dP4 in lingual (**C**) and occlusal (**D**) views; **E**, **F**, KNM-FT 3362, right dp4 in occlusal (**E**) and lingual (**F**) views; **G**, **H**, KNM-FT 3364, right dP3 in occlusal (**G**) and lingual (**H**) views; **I**, **J**, left mandibular corpus with dp3-dp4 in occlusal (**I**), buccal (**J**), and lingual (**K**) views. Scale bar: A-D, I-K, 50 mm; E-H, 10 mm.

cusp. The parastyle cusp is large and triangular. It is located mesiolingual to the paracone. The protocone is reduced to a low lingual bump. The paracone is the tallest cusp and is rhomboid in occlusal view. The preparacrista is strong. The metastyle is long, straight and low. There are no distinct cingula.

**Measurements.** LdP4 18.3+; WadP4 7.3; WbldP4 5.7; LpdP4 5.6; LmdP4 6.4.

*KNM-FT 3375a*
A trenchant carnassial with paraconid and protoconid that are subequal in length, with the latter being the taller of the two. The metaconid is absent. The talonid is very reduced and shows evidence of only a very small and weak hypoconid. The mesial root is large and the distal root is small.

**Measurements.** Lm1 22.4; Wm1 11.3; Ltm1 18.9.

*KNM-FT 3375e*
A small, robust P2 with prominently wrinkled enamel. The mesial accessory cusp is small and low, set mesiolingually and appressed to the main cusp. The latter is pyramidal, with strong mesiolingual and distal crests. The distal accessory cusp is low but sharp and is less appressed to the main cusp than is the mesial accessory cusp.

**Measurements.** LP2 12.0; WP2 7.8.

*KNM-FT 3408*
A long, relatively slender dP2. The mesial accessory cusp is very low and set mesiolingual to the main cusp. In occlusal view the mesial shelf of the tooth is longer than the distal shelf. The main cusp is tall and ovoid in occlusal outline. The distal accessory cusp is more distinct than the mesial accessory cusp but set in a truncated shelf. There is a lingual root that in occlusal view forms a bulge near the base of the enamel on the lingual side.

**Measurements.** LdP2 11.6; WdP2 6.4.

*KNM-FT 3610*
A tall, pyramidal P3. The mesial accessory cusp is low but distinct, set mesiolingual to the main cusp and only somewhat appressed to it. The main cusp is tall and nearly round in occlusal outline. It has strongly wrinkled enamel. The distal accessory cusp is strong, somewhat trenchant and set away from the main cusp in a short shelf.

**Measurements.** LP3 17.8; WP3 12.0.

*KNM-FT 3614a (Fig. 3C, D)*
This maxilla includes three deciduous teeth in position. The DP2 is in every respect similar to KNM-FT 3408 described above, except for being nearly unworn. An occlusal view clearly shows the slight lingual bulge of the lingual root. The DP3 is complete and shows the anteriormost cusp to be large, with transverse shear. The preparastyle is identical to that of KNM-FT 3375a. The protocone shelf is more distinct than in that tooth, but is still very low, with an almost obliterated cusp. The paracone is relatively shorter than in KNM-FT 3375a and the metastyle appears slightly less straight than in that tooth. The DP4 is large and subtriangular, with a distinct, though worn paracone bordered buccally by a cingulum. There is also a low, very worn metacone, and a large, crescentic protocone. The remarkable length of the root under the paracone can be seen in buccal view.

**Measurements.** LdP2 10.9; WdP2 6.6; LdP3 19.1; WadP311.2; WbldP3 5.3; LpdP3 6.9M LmdP3 7.2; LdP4 7.2; WdP3 13.0.

*KNM-FT 3614b (Fig. 3A, B)*
This is not the same individual as KNM-FT 3614a. The P3 was clearly a large, robust tooth suitable for bone-cracking and had a low mesiolingually set accessory cusp. The P4 is long and comparatively slender. It has a small cingulum mesial to the parastyle. There is a distinct, sharp parastyle and a large, sharp paracone. The metastyle is low and lingually convex. It gradually becomes lower distally. The protocone is set lingual to the parastyle with an embayment of the mesial part of the tooth between them. There are weak cingula mesiobuccally and lingually along the mesial half of the metastyle.

The P4 of this specimen is practically indistinguishable from that of late Miocene hyaenids of the genus *Hyaenictitherium* and related forms. The only middle Miocene hyaenid that approaches this morphology is *Thalassictis montadai* (Villalta Comella & Crusafont Pairó 1943). The P4 of this species (Crusafont Pairó & Petter, 1969) appears more robust, lacks the anterior cingulum and has a straighter mesial face. These differences are small and I cannot exclude the possibility that this specimen represents a hyaenid. However, this would make it the oldest hyaenid specimen in Africa and in view of the demonstrated presence of *Percrocuta* at Fort Ternan I tentatively refer it to *P. tobieni*.

**Measurements.** LP4 31.0; WblP4 10.3; LpP4 10.1; LmP4 12.1.

*KNM-FT 3614c*
A small, dumbbell-shaped M1 with a large, blunt paracone and somewhat smaller protocone. The metastyle shelf is almost entirely reduced and can be seen only as a very small widening of the distal border of the tooth just distolingual to the protocone.

**Measurements.** LM1 7.4; WM1 20.9

*KNM-FT 12693*
This p3 forms a rounded rectangle in occlusal view. There is no distinct mesial accessory cusp, just a small swelling at the center of the mesial cingulum. The main cusp is worn. It is ovoid in occlusal outline and would have been pyramidal if unworn. The distal shelf is worn down and broken, so the presence and size of the distal accessory cusp cannot be determined. The distolingual shelf is large.

**Measurements.** Lp3 14.0+; Wp3 9.3.

*KNM-FT 12694*
A severely damaged tooth that can be identified as a p4 by the development of the distal shelf of the crown, which is clearly longer and better developed than the distal shelf of the p3

described above. Very little else can be said concerning the morphology of the tooth.

**Measurements.** Lp4 16.2+; Wp4 9.8+.

*KNM-FT 12695 (Fig. 3I-K).*
A mandibular corpus with dp3 and dp4 and an emerging m1. It also has alveoli for dp2, showing it to be two-rooted. No dp1 appears to have been present. The dp3 is a slender tooth with well developed mesial and distal accessory cusps and a sharply upturned distal cingulum cusp. The main cusp is short and has a sharp tip. The dp4 is morphologically very similar to KNM-FT 3362, described above, but the metaconid is relatively slightly smaller.

**Measurements.** Ldp3 13.5; Wdp3 5.7; Ldp4 15.8; Wdp4 6.3.

*KNM-FT 14140*
This p3 is broken mesially and distally, so the development of the accessory cusps is not clear, although the mesial one must have been quite small and the distal one situated in a short shelf. The main cusp is pyramidal.

**Measurements.** Lp3 14.7+; Wp3 9.5.

### Discussion

This material can be assigned to Percrocutidae on the basis of several features, most important of which is the morphology of the deciduous fourth premolar (dp4). This tooth was shown by Chen & Schmidt-Kittler (1983) to differ from the homologous tooth of Hyaenidae in the following: The metaconid is set distal to and well separate from the protoconid; the talonid is very short; and the talonid cusps are restricted to small buds at the distal end of the tooth. In Hyaenidae, on the other hand, the metaconid is set only slightly distal to the protoconid and appressed to it (in derived Hyaenidae such as *Crocuta* the dp4 metaconid is lost); the talonid is long; in primitive Hyaenidae (e.g., *Hyaenictitherium*), there are distinct entoconid and hypoconid and commonly a third cusp that may be an entoconulid; and in derived Hyaenidae only the entoconid is distinct. The Fort Ternan material includes two dp4 that both match the morphology of dp4 in Percrocutidae. In addition to these features, all of the Fort Ternan percrocutid specimens are considerably more derived than contemporaneous Eurasian Hyaenidae, which at that time (ca MN 6 or early MN 7/8 depending on opinion in the European mammal zonation) were confined to small, omnivorous forms such as *Protictitherium* and *Plioviverrops* (Turner *et al.* 2008): type 2 hyenas in the classification of Werdelin & Solounias (1996).

*Percrocuta tobieni* was described from the middle Miocene of the Ngorora Formation (Crusafont Pairó & Aguirre 1971). Finds from this formation are dated to approximately 12.5-11 Ma (Morales & Pickford 2005), i.e., somewhat younger than Fort Ternan. To the extent that they overlap, the Fort Ternan material does not differ in any substantial way from the Ngorora Formation material. Therefore, despite some minor differences, e.g., in the relative length of the m1 talonid, assigning the Fort Ternan material to *P. tobieni* appears justified. This is in agreement with, e.g., Morales & Pickford (2006), in which the faunal list for Fort Ternan includes *P. tobieni* as one of a number of taxa shared with the Ngorora Formation. This makes the Fort Ternan record the oldest of this species.

Thus, the taxonomic home of the Fort Ternan percrocutid is clear. However, the material is of considerable interest because it includes both lower and upper dentitions, including lower and upper deciduous teeth. This not only is the first instance of associated upper and lower deciduous teeth in Percrocutidae, but these upper deciduous teeth are the first known for Percrocutidae and allow for a consideration of the full percrocutid dentition.

The following is a comparison of the deciduous upper dentition with that of *Hyaena hyaena*, discussed and illustrated in Baryshnikov & Averianov (1995). *Percrocuta tobieni* and *H. hyaena* share a similar overall structure of the deciduous dentition, so the differences are all in the details, none of which are as revealing as the dp4. All the observations made are confirmed by the deciduous upper dentition of *C. crocuta* although the latter is more reduced and hypercarnivorous than that of either *P. tobieni* or *H. hyaena*.

*dP2*
This tooth is relatively larger and more robust in *P. tobieni*. In particular, the mesial end is broader and has a more distinct mesial accessory cusp in *P. tobieni*. In both taxa the tooth has a marked lingual bulge, however, this bulge is set further mesially in *P. tobieni*, in which the maximum width is attained directly lingual to the apex of the main cusp, whereas in *H. hyaena* it is set lingual to the notch between the main cusp and the distal accessory cusp. In contrast to the mesial accessory cusp, the distal one is more developed in *H. hyaena* than in *P. tobieni*.

*dP3*
The preparastyle is of similar size relative to the whole tooth in the two taxa but the cusp of the preparastyle in *P. tobieni* is distinctly transversely extended. In *P. tobieni* the parastyle is more prominent, triangular, and set distinctly lingual to the long axis of the paracone. In *H. hyaena* this cusp is less developed, round and set closer to the paracone. The paracone and metastyle are similar in the two taxa, but they differ in the position of the protocone. In *P. tobieni* the protocone is centered lingual to the notch between parastyle and paracone, whereas in *H. hyaena* the protocone is set lingual to the apex of the paracone. This obviously reflects a difference in the position of the lingual root of the dP3.

*dP4*
The dP4 of *P. tobieni* is more buccolingually extended than the dP4 of *H. hyaena* This means that the dP4 of the extant species is more triangular in occlusal outline that it is in *P. tobieni*. The dP4 of *P. tobieni* has a larger protocone and a more bowed distal edge than dP4 of *H. hyaena*.

*Upper dentition*
The permanent upper dentition of *P. tobieni*, previously unknown, presents no remarkable features, except one: that it is practically indistinguishable from that of late Miocene Hyaenidae such as *Hyaenictitherium* or *Lycyaena*. In particular, it does not share with other, more derived Percrocutidae the reduced and distally shifted protocone of P4, an observation that has consequences for our understanding of the evolution of the family.

## Family VIVERRIDAE Gray, 1821
## Subfamily PARADOXURINAE Gray, 1864

REMARK
The Fort Ternan collection includes two or three taxa that can be assigned to Paradoxurinae. Exactly how the material is to be assigned between these putative taxa is a complicated issue. There is great morphological variability despite the small sample, and most specimens are isolated teeth. Comparisons with other taxa are also difficult, because these are either separated by a large temporal gap, or by considerable geographic distance, or both. Hence, some of the identifications below may be subject to revision in the future, as more material of small middle Miocene carnivorans becomes available.

### Genus *Kanuites* Dehghani & Werdelin, 2008

TYPE SPECIES. — *Kanuites lewisae* Dehghani & Werdelin, 2008 (by monotypy).

### ***Kanuites lewisae*** Dehghani & Werdelin, 2008

*Kanuites lewisae* Dehghani & Werdelin, 2008: 234.

MATERIAL EXAMINED. — KNM-FT 3367, left maxilla fragment with M1-M2; KNM-FT 3372, left P4; KNM-FT 3390, right P2; KNM-FT 8747, cranium with right C-P4, left P2-P4 (Fig. 4P; holotype).

DESCRIPTION
This material was fully described by Dehghani & Werdelin (2008) and the descriptions need not be repeated here.

### cf. ***Kanuites lewisae***

MATERIAL EXAMINED. — KNM-FT 3369, left m1; KNM-FT 3370, right hemimandible with m1; KNM-FT 3371, left dp4; KNM-FT 3876, right m1; KNM-FT 8744A-B, juvenile mandible with p1 and dp2-dp4, left dp3; KNM-FT 8745, partial juvenile cranium with right P1 and dP2-dP4, left dP3-dP4; KNM-FT 8750, partial juvenile cranium with right P1 and dP2-dP4, left P1 and dP3-dP4; KNM-FT 15093, left m1.

DESCRIPTION
*KNM-FT 3876 (Fig. 4A-C)*
This is the best preserved of the lower carnassials and its description will also serve for KNM-FT 3369 and KNM-FT 15093, as well for as the m1 of KNM-FT 3370. The tooth is short and broad with a trigonid that accounts for about 60% of the total length of the tooth. The protoconid is the tallest cusp by far, whereas the paraconid and metaconid are of similar height. The angle metaconid-paraconid-carnassial notch is about 63°. In occlusal view the paraconid is slightly larger than the protoconid and both are considerably larger than the metaconid. The central valley is wide but not flat in the middle. The angle between pre- and postprotocristids is about 92°. The talonid is about equal in width to the trigonid. The talonid has three distinct cusps: a large hypoconid that is connected to the trigonid by a weakly developed cristid obliqua, an entoconid that is nearly the same size as the hypoconid, and a hypoconulid that is low situated at the distalmost point of the tooth.

**Measurements.** KNM-LT 3876.: Lm1 8.1; Wm1 4.1; Ltm1 4.9. KNM-FT 3369 Lm1 8.3; Wm1 3.9; Ltm1 5.2. KNM-FT 15093: Lm1 7.5; Wm1 3.7; Ltm1 4.5.

*KNM-FT 3370*
Apart from the slightly damaged m1 (which is accounted for under the m1 description above) this specimen also includes the hemimandible and a very damaged p4. The corpus is long and low with its deepest part beneath m1. There is one discernible mental foramen, located near the anterior alveolus for p2. The alveoli for p2 and p3 are separated by short diastemas, but no alveolus for p1, if present, can be seen. The alveolus or alveoli for m2 also cannot be seen. The masseteric fossa ends near the inflection point between corpus and ascending ramus. The latter is low and has a squared-off rim. The condyle is substantial and set somewhat obliquely to the anteroposterior axis of the corpus. The angular process is large and extends nearly as far posteriorly as the condyle.

**Measurements.** Lm1 6.7; Wm1 3.8; Ltm1 4.1.

*KNM-FT 8744A, B (Fig. 4M-O)*
These hemimandibles have long and slender corpuses. There is a large mental foramen beneath dp2, near the ventral edge of the corpus. Smaller foramina are present anteroventral to the large one. The symphysis is long, slender, and low, reaching the middle of dp2. The ascending ramus is slender, with a rounded rim (unlike the squared-off rim described for the adult hemimandible above). The p1 is more or less triangular in occlusal view, with the apex facing mesially, and is about equal in length and width. The dp2 is a small, slender tooth with its apex above the mesial root. There are no mesial or distal cusps. The greatest width is distal to the main cusp. The dp3 is also slender, with its widest part distally, where the tooth widens into a short shelf. The mesial accessory cusp has a marked mesial lean. The distal accessory cusp is large and appressed to the main cusp. The dp4 has a trigonid that forms about 60% of the length of the tooth. The paraconid is the largest trigonid cusp and is situated mesially, where it cups the mesial margin of the tooth. The protoconid is the tallest trigonid cusp. It is crest-like and located at the buc-

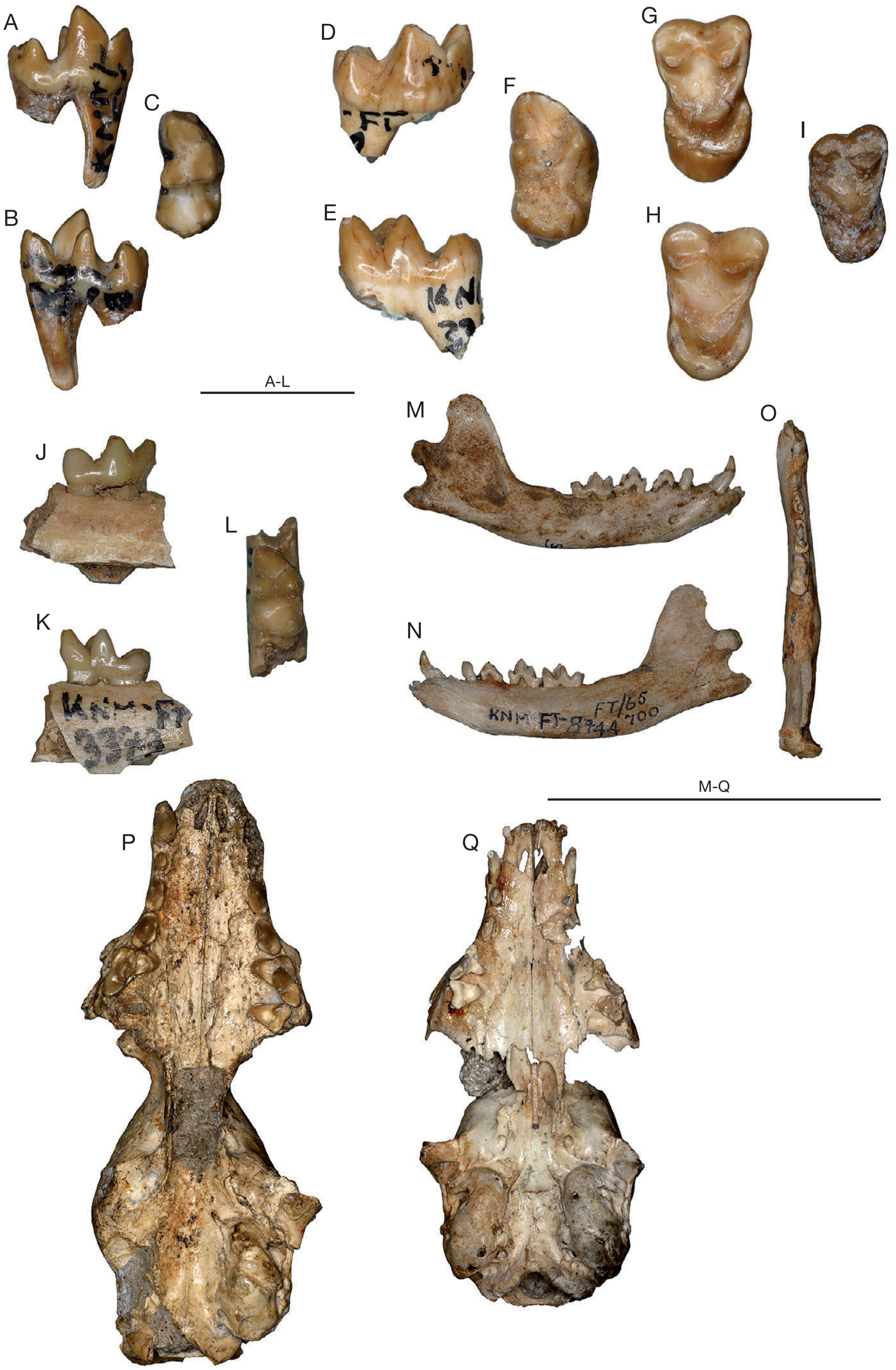

Fig. 4. — Viverridae from Fort Ternan: **A**-**C**, *Kanuites lewisae* KNM-FT 3876, right m1 in buccal (**A**), lingual (**B**), and occlusal (**C**) views; **D**, **E**, cf. *Tugenictis* sp., KNM-FT 15093, right m1 in buccal (**D**), lingual (**E**), and occlusal (**F**) views; **G**, cf. *Tugenictis* sp., KNM-FT 3361, left M1 in occlusal view; **H**, cf. *Tugenictis* sp., KNM-FT 3398, left M1 in occlusal view; **I**, cf. *Tugenictis* sp., KNM-FT 3363, right M2 in occlusal view; **J**-**L**, Viverrinae gen. et sp. indet., KNM-FT 3373, right m1 in buccal (**J**), lingual (**K**), and occlusal (**L**) views; **M**-**O**, *Kanuites* cf. *lewisae*, KNM-FT 8744A, right hemimandible with dc, p1, dp2-dp4 in buccal (**M**), lingual (**N**), and occlusal (**O**) views; **P**, *Kanuites lewisae* (holotype), KNM-FT 8747, cranium with right C-P4, left P2-P4 in ventral view; **Q**, *Kanuites* cf. *lewisae*, KNM-FT 8750, cranium with right P1 and DP2-DP4, left P1 and DP3-DP4. Scale bars: A-L, 10 mm; M-Q, 50 mm.

cal edge of the tooth. The metaconid is of about the same height as the protoconid, but is the smallest of the three cusps. It is located at the distolingual corner of the trigonid, well separated from the protoconid. The talonid is slightly broader than the trigonid. The cristid obliqua is prominent and leads to a moderately tall hypoconid. The entoconid is of about equal height to the hypoconid, and there is a small distal hypoconulid.

**Measurements.** Ldp2 3.6; Wdp2 1.4; Ldp3 5.2; Wdp3 2.1; Ldp4 6.5; Wdp4 2.7; Ltdp4 3.9.

*KNM-FT 3371*
A dp4 that is closely similar to, but larger than, the one described above from KNM-FT 8744A.

**Measurements.** Ldp4 8.0; Wdp4 3.9; Ltdp4 5.3.

*KNM-FT 8745, KNM-FT 8750 (Fig. 4Q)*
Two juvenile crania that are closely similar, especially dentally, and therefore will be described together. Some incisors are preserved in KNM-FT 8745, but their crowns are damaged and provide little or no useful information beyond being typical small carnivore incisors. The same can be said of the upper canine, which is long, slender, and relatively straight. The P1 is pear-shaped, with its widest point close to the distal end of the tooth. It is separated from the canine by a short diastema that is half the length of the diastema between P1 and DP2. The dP2 is long and slender. Its apex lies anterior to the middle of the tooth. There are no accessory cusps either mesially or distally. The dP3 has a crescent-shaped preparastyle situated at the mesialmost point of the tooth. The parastyle is small and located mesiolingual to the paracone. The paracone is tall and sharp and connects to the metastyle by a shallow notch. There is a distinct metacone close to this notch. The protocone is low but broad and set lingual to the apex of the paracone. The dP4 is triangular with a concave lingual border. There is a stylar cusp at the mesiobuccal corner of the tooth. The stylar shelf is wide. The paracone is low and crescentic and the metacone set near the distobuccal corner of the tooth. The protocone is large and set lingually, separated from the paracone and metacone by a wide shelf.

The cranium will not be described here. In the absence of suitable comparative material, it is difficult to evaluate any characteristics of the sutures and other structures. The auditory bullae are intact, so their internal structure cannot be evaluated at present.

**Measurements.** KNM-FT 8745: LP1 2.3; WP1 1.6; LdP2 3.6; WdP2 1.5; LdP3 6.6; WadP3 3.8; WbldP3 2.1; LpdP3 2.3; LmdP3 2.7; LdP4 4.6; WdP4 4.7. KNM-FT 8750: LdP2 3.5; WdP2 1.6; LdP3 6.4; WadP3 3.8; WbldP3 1.8; LpdP3 2.4; LmdP3 2.6; LdP4 4.5; WdP4 4.5.

### Discussion

*Kanuites lewisae* was described on the basis of the well-preserved cranium KNM-FT 8747 (Dehghani & Werdelin 2008). The material definitively assigned to *K. lewisae* above is identical with the original hypodigm of the species, identified due to overlap with the dentition of the holotype cranium. This material did not include any of the lower dentition, making any identification of such elements tentative, as is the case with the juvenile specimens. The main argument for the identifications is size. Leaving the very small m1 KNM-FT 3373 (see below) aside, there are two sizes of lower m1 that might fit with the *K. lewisae* upper dentition. Of these the m1s KNM-FT 3360 and KNM-FT 3368 are, barring very odd dental proportions, too large to match the P4 of *K. lewisae.* A similar argument, if more tenuous, applies to the deciduous dentition. In addition to these arguments by size it is also possible to make an argument by commonality, i.e., that the most common elements in each dental region are likely to belong to the same taxon. In this case the two arguments coincide. If correct, this makes *K. lewisae* the best characterized Miocene viverrid in Africa.

*Kanuites* bears similarities to both Viverridae and Hyaenidae. Among the latter it is broadly similar to species of *Protictitherium* in size. This genus is known from the early and middle Miocene in Eurasia and the middle Miocene of Africa (Werdelin & Solounias 1991; Werdelin & Peigné 2010). African finds come from two North African sites (Beni Mellal, Morocco; Beglia Formation, Tunisia) and a single find in eastern Africa (Namurungule Formation, Kenya). The two North African sites are similar in age to Fort Ternan, whereas the Kenyan find is early late Miocene in age. None of the finds were originally described as *Protictitherium*.

I will here focus on the find from the Beglia Formation, originally described by Kurtén (1978) as *Tungurictis punica*, but reassigned to *Protictitherium punicum* by Werdelin & Solounias (1991). The specimen consists of a maxilla fragment with P3-M2 and thus overlaps with the type specimen of *Kanuites lewisae* in both age and representation. It should be noted that where overlap in representation occurs the *P. punicum* specimen is closely similar to the Beni Mellal material assigned by Ginsburg (1977) to *Ictitherium* cf. *arambourgi* as far as can be determined from photographs in the latter publication. Comparison between *P. punicum* (Kurtén 1978: figs 1, 2) and the type specimen of *K. lewisae* (Fig. 4P; Dehghani & Werdelin 2008: fig. 1) shows some general similarities in size and structure but considerable differences in detail. The P3 is similar in size and proportions, but the *P. punicum* specimen has a hyaenid-like cingulum surrounding the crown, whereas in *K. lewisae* the cingulum is absent buccal and the lingual cingulum bulges further lingually than in *P. punicum*. The morphology of the P4 in *P. punicum* is typically hyaenid, with paracone and metastyle longer and more slender than in *K. lewisae*, whereas the P4 protocone of *P. punicum* is short and has its distal connection to the paracone near the anterior end of the latter cusp. In *K. lewisae* the protocone reaches distally to about the middle of the paracone. The M1 of *P. punicum* is mesiodistally foreshortened and its mesial and distal margins are curved. In *K. lewisae* the mesial and distal margins are straight and the tooth overall longer mesiodistally compared to buccolingual breadth. Thus, *K. lewisae* differs from the penecontemporaneous *P. punicum* in a number of characters that precludes referral to Hyaenidae. Referral to Herpestidae is unlikely for reasons discussed in Dehghani & Werdelin (2008) and therefore Viverridae remains as the likely family assignment for *Kanuites lewisae*.

Subfamily designation for *Kanuites* is difficult but it is here referred to Paradoxurinae for the following reasons. It shows some overall similarities to *Kichechia zamanae*, assigned to Paradoxurinae by Morales & Pickford (2011) in molar shape. It is less hypercarnivorous, with short, relatively broad carnassials and molars, than known African Viverrinae. Most importantly, the M1 of *K. lewisae* shows the presence lingually of a cingulum surrounding the protocone, as well as overall occlusal surface symmetry. I interpret this as a less derived version of the condition seen in the M1 of cf. *Tugenictis*, described below. The cingulum is also seen in *Kichechia*, but not in Viverrinae that I have observed.

### Genus *Tugenictis* Morales & Pickford, 2005

Type species. — *Tugenictis ngororaensis* Morales & Pickford, 2005 (by monotypy).

### cf. *Tugenictis* sp.

Material examined. — KNM-FT 3360, right m1; KNM-FT 3361, left M1; KNM-FT 3363, right M2; KNM-FT 3368, left m1; KNM-FT 3398, left M1.

#### Description

*KNM-FT 3360, KNM-FT 3368 (Fig. 4D-F).*
These lower carnassials are short, broad teeth. The trigonid makes up about 60% of the total length of the tooth. The three trigonid cusps are nearly equally tall. The protoconid is set far buccally. The paraconid is set anteriorly with the angle metaconid-paraconid-carnassial notch close to 75°, showing the central valley to be broader than in the m1s described above, and almost flat centrally. The protoconid is set near the buccal border. The angle between pre- and postprotocristids is about 125°. The metaconid is set on the lingual margin directly distal to the paraconid. There is a notable cristid extending from the mesiobuccal margin of the metaconid and halfway across the tooth, where a notch separates it from the postprotocristid. The cristid obliqua is prominent and ends distally at a large and tall hypoconid. The entoconid is nearly as tall as the hypoconid but more crescentic in shape. There is no distinct hypoconulid.

**Measurements.** KNM-FT 3360: Lm1 9.6; Wm1 5.8; Ltm1 6.0. KNM-FT 3368: Lm1 9.9; Wm1 5.9; Ltm1 6.2.

*KNM-FT 3361, KNM-FT 3398 (Fig. 4G, H)*
These upper first molars are distinctive and very similar morphologically, though they differ in details. They are superficially similar to amphicyonid upper molars, but their lingual shelf and buccal cingulum are broader and their trigon structure different. They are also smaller than known African amphicyonid upper molars (M1 or M2 – M3 is morphologically very different and reduced) and no known amphicyonid has an upper molar in which the buccal shelf is the broadest part of the tooth. The teeth are mesiodistally very symmetric and it is difficult to determine which end is mesial and which is distal. The identification mesial-distal made here is tentative, with the larger and more rounded part of the buccal margin considered the paracone and therefore mesial. In this interpretation the paracone is longer and more crescent-shaped than the metacone. The stylar shelf is about equally wide buccal to both cusps. Neither specimen shows any sign of stylar cusps, but in KNM-FT 3361 the paracone shelf has a distinct marginal crest. The metacone is slightly smaller and rounder than the paracone. In both teeth there are strong pre- and postprotocristae that run from mesial to the paracone and distal to the metacone lingually towards the protocone, which is large and crescent-shaped. In KNM-FT 3398 these cristae show considerable wear. Both teeth have a small protoconule mesial to the protocone. The lingual cingulum is developed enough to be considered a shelf, especially in KNM-FT 3361. In both teeth the highest point of the cingulum is slightly mesial to the midline.

**Measurements.** KNM-FT 3361: LM1 6.5; WM1 10.7. KNM-FT 3398: LM1 7.0; WM1 10.2.

*KNM-FT 3363 (Fig. 4I)*
This M2 is closely similar in many respects to the preceding two molars, but is smaller, with curved mesial and distal margins and a reduced metastyle wing and metacone. Apart from this, the stylar shelf, paracone, metacone, and buccal shelf are very similar to the M1s. All these features combined make it clear that this is the M2 of the same species. In fact, it is possible that KNM-FT 3361 and KNM-FT 3363 belong to the same individual because they are cataloged under the same field number, but this cannot be demonstrated definitively.

**Measurements.** LM2 5.2; WM2 8.7.

#### Discussion

The association between the upper and lower teeth here is tentative and motivated by the similarity of the m1s to those of *Kanuites* as described above, and *Orangictis gariepensis* as described by Morales *et al.* (2001b) and Morales & Pickford (2011). The approximately coeval *Tugenictis ngororaensis* Morales & Pickford (2005) is only known from lower dentition material, but also shares similarities with the Fort Ternan specimens where comparisons are possible. Given that all these species have been identified as paradoxurines, the Fort Ternan m1s are also likely to belong to a paradoxurine. The upper teeth assigned here can be identified as paradoxurine by their broad stylar and buccal shelves and, in the case of M1, by the occlusal surface symmetry. In size they fit with the m1s listed here and therefore all these teeth are tentatively assigned to the same taxon, which likely has affinities to the paradoxurine taxa mentioned above.

### Subfamily VIVERRINAE Gray 1821

### VIVERRINAE gen. et sp. indet

MATERIAL EXAMINED. — KNM-FT 3373, right m1.

DESCRIPTION

*KNM-FT 3373 (Fig. 4J-L)*

This m1 is smaller than the m1s of the preceding taxa. It has paraconid, protoconid, and metaconid that are subequal in height, with the paraconid being the largest in occlusal view and protoconid and metaconid nearly equal to each other. The three trigonid cusps are located close together and there is no central valley, only narrow notches between the cusps. The talonid is initially broad but tapers distally obliquely, such that the buccal side is straight and longer than the lingual side, resulting in the hypoconid being located somewhat distal to the entoconid. These two cusps are nearly equal in height, but the hypoconid is larger. There is no hypoconulid in evidence.

**Measurements.** Lm1 6.1; Wm1 3.5; Ltm1 3.6.

DISCUSSION

There is little to go on in the taxonomic identification of this tooth. Structurally it differs considerably from the two taxa discussed above. The closest similarity appears to be with *Legetetia nandii* (cf. Schmidt-Kittler [1987: figs 17d-f, 18e-g]). Without suggesting specific phylogenetic affinity, the overall structure of the trigonid, as well as the asymmetric form of the talonid, are reminiscent of *Genetta* and the tooth is therefore tentatively placed in Viverrinae.

## GENERAL DISCUSSION OF VIVERRIDAE

Morales & Pickford (2011) assigned a group of more or less bunodont viverrids from Africa to the otherwise Asian subfamily Paradoxurinae. They acknowledged that this was a bit of a leap and that convergence is also possible. Nevertheless, there are other Carnivora (fossil and recent) that are vicariously distributed across the two continents and the identification is certainly plausible on these grounds as well as on morphology. Thus, I here follow the lead of Morales & Pickford (2011) in assigning two of the three viverrids from Fort Ternan to Paradoxurinae.

Morales & Pickford (2011) further subdivided the Paradoxurinae into three tribes: 1) Paradoxurinae Gray, 1864, including extant Paradoxurinae as well as the extinct *Mioparadoxurus* Morales & Pickford, 2011; 2) Pseudocivettini Morales & Pickford, 2011, including the genera *Pseudocivetta* Petter, 1967 and *Tugenictis* Morales & Pickford, 2005; 3) Kichechiini Morales & Pickford, 2011, including the genera *Kichechia* Savage, 1965, *Orangictis* Morales, Pickford, Soria & Fraile, 2001, and *Ketketictis* Morlo, Miller & El-Barkooky, 2007. Unfortunately, of these only the Paradoxurini is monophyletic by evidence from the phylogenetic analysis of Morales & Pickford (2011). Therefore, this subdivision has little meaning.

I carried out a phylogenetic analysis based on the characters and matrix used by Morales & Pickford (2011) incorporating codings for *Kanuites* (matrix shown as Supplementary Online Data, see Appendix 1). A TNT 1.5 (Goloboff *et al.* 2008; Goloboff & Catalano 2016) analysis with implicit enumeration generated three trees of 32 steps (consistency index 0.75, retention index 0.72). The topology is identical to that found by Morales & Pickford (2011) and the trees differ only in the position of *Kanuites*: either as sister taxon to all ingroup taxa except *Ketketictis*; as sister taxon to *Kichechia* + *Orangictis*; or as sister taxon to 'Pseudocivettini' + Paradoxurini. Support for all nodes is limited – no Bremer support is greater than 1 and in addition several branch lengths are 0, including that between outgroup and ingroup. I conclude that although the assignment of these African forms to Paradoxurinae is plausible, their interrelationships are still uncertain and, given that dental data have been shown to perform relatively poorly in mammalian phylogenetics (Sansom *et al.* 2016), are unlikely to be fully resolved until much better material of all parts of the skeleton are recovered.

### Order HYAENODONTA Van Valen, 1967
### Superfamily HYAINAILOUROIDEA Pilgrim, 1932
### Subfamily TERATODONTINAE Savage, 1965

### Genus *Dissopsalis* Pilgrim, 1910

TYPE SPECIES. — *Dissopsalis carnifex* Pilgrim, 1910 (by monotypy).

### ***Dissopsalis pyroclasticus*** Savage, 1965

*Dissopsalis pyroclasticus* – Savage 1965: 265.

TYPE SPECIMEN. — NHMUK M19082, Mandible corpus with p4-m3.

TYPE LOCALITY. — Kaboor (= Maboko, cf. Morales & Pickford 2017), Kenya.

MATERIAL EXAMINED. — KNM-FT 3357, left maxilla fragment with alveoli for dP1-dP2, complete dP3-dP4, alveolus for M1; KNM-FT 3375c, right P2; KNM-FT 3375f, right dP4; KNM-FT 3562b, left p3-p4; KNM-FT 3562e, left m2-m3; KNM-FT 13770, right m3; KNM-FT 13771, right m2; KNM-FT 13772, left m2; KNM-FT 14125, left m3; KNM-FT 15092, left M1. Tentatively referred specimen: KNM-FT 14217, left ?dP2.

DESCRIPTION

*KNM-FT 3357*

This specimen was fully described by Borths & Stevens (2017) and need not be redescribed here.

**Measurements.** LdP3 15.6; WdP3 9.5; LdP4 15.8; WadP4 13.0.

*KNM-FT 3375c*

A small, slender P2. There is no mesial accessory cusp, but a small bump on the mesial end of the cingulum. The main cusp is low but robust. The distal accessory cusp is prominent and separated from the main cusp by a wide notch. It is a little less than half the height of the main cusp. Most characteristic of the tooth is the prominent cingulum that encircles the entire crown.

**Measurements.** LP2 12.0; WP2 7.6.

*KNM-FT 3375f*
To all intents and purposes this tooth is identical in morphology to the dP4 of KNM-FT 3357 and I therefore refer to the description of the latter by Borths & Stevens (2017).

**Measurements.** LdP4 16.1; WadP4 14.1

*KNM-FT 3562b*
A corpus fragment with damaged p3-p4. The p3 has broken off and is glued in a position that is dorsal to its position in life. The p2 is short and broad. There is no mesial accessory cusp in evidence although a very small one may have been present in the unworn tooth. The main cusp is nearly round in occlusal view. It has a short distal shelf and would have had a low distal accessory cusp that is now almost completely worn down. The p4 is more elongated than p3 but is still broad and robust. The mesial end rises straight to the main cusp without a mesial accessory cusp. The main cusp is oval in occlusal view. There is no distal accessory cusp preserved although there may have been a low one in the unworn tooth.

**Measurements.** Lp3 14.0; Wp3 9.5; Lp4 17.4; Wp4 10.6.

*KNM-FT 3562e*
This corpus fragment includes heavily worn m2-m3. The m2 is short and robust. The paraconid is heavily worn, with a wear facet that includes the apex of the cusp and continues mesially to the mesial end of the tooth. The apex of the protoconid is also worn and broken, making it impossible to adequately compare the proportions of paraconid and protoconid. No metaconid is in evidence. The talonid is long and includes a ridge-like hypoconid, as well as entoconid and entoconulid. The m3 is tall and short. The paraconid and protoconid are about equal in length but the protoconid is the taller cusp. There is a distinct cingulum cusp on the mesiobuccal side of the paraconid. There is no metaconid and the talonid is reduced and 'V'-shaped.

**Measurements.** Lm2 15.6; Wm2 9.3; Ltm2 11.9; Lm3 19.3; Wm3 10.1; Ltm3 16.8.

*KNM-FT 13770 (Fig. 5G-I)*
This tooth is identical in morphology to the m3 of KNM-FT 3562e except that the paraconid of KNM-FT 13770 is distinctly longer than the protoconid.

**Measurements.** Lm3 20.2; Wm3 9.5; Ltm3 15.5.

*KNM-FT 13771 (Fig. 5D-F)*
This tooth is identical in morphology to the m2 of KNM-FT 3562e but has a very interesting wear pattern on the buccal side of the protoconid and talonid that may be due to a specific hard foot item in the diet or to chipping and subsequent wear, possibly caused by some pathology to the occluding upper tooth.

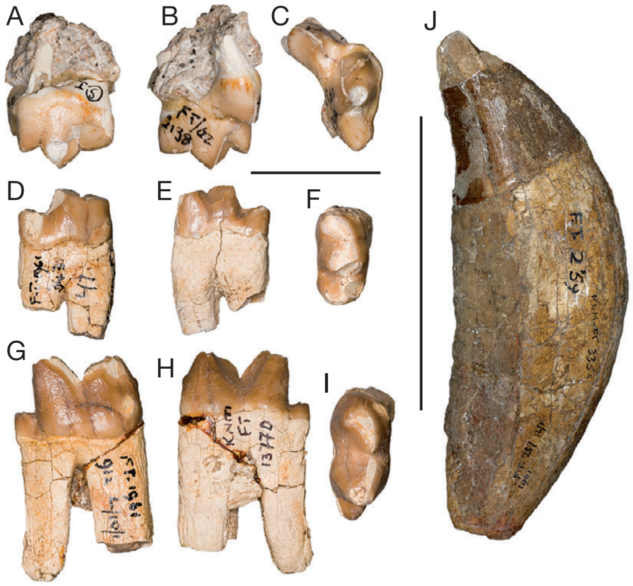

Fig. 5. — Hyaenodonta from Fort Ternan: **A**-**I**, *Dissopsalis* cf. *pyroclasticus*; **A**-**C**, KNM-FT 15092, left M1 in buccal (**A**), lingual (**B**), occlusal (**C**) views; **D**, **E**, KNM-FT 13771, right m2 in buccal (**D**), lingual (**E**), and occlusal (**F**) views; **G**-**I**, KNM-FT 13770, right m3 in buccal (**G**), lingual (**H**), and occlusal (**I**) views; **J**, Hyainailourinae gen. et sp. indet., KNM-FT 3359, left upper canine in medial view. Scale bars: **A**-**I**, 20 mm; J, 100 mm.

**Measurements.** Lm2 14.8; Wm2 8.1; Ltm2 10.5.

*KNM-FT 13772*
Another specimen that is identical in morphology to the m2s KNM-FT 3562e and KNM-FT 13771. Interestingly, it has a distobuccal wear pattern that is identical to that of KNM-FT 13771, which may suggest that the wear is due to some specific food item and that these two teeth belonged to the same individual.

**Measurements.** Lm2 14.6; Wm2 7.8; Ltm2 10.4.

*KNM-FT 14135*
Another m3 that is practically identical in morphology to the m3s KNM-FT 3562e and KNM-FT 13770. Like the latter it has a longer paraconid than protoconid.

**Measurements.** Lm3 19.4; Wm3 9.0; Ltm3 16.4.

*KNM-FT 15092 (Fig. 5A-C)*
This M1 has a protocone shelf that is set at about a 45° angle to the buccal edge of the tooth. The protocone is large but not tall, being significantly lower than the other cusps of the tooth, including the metastyle. The protocone is bordered lingually by a stout basal bulge. The paracone is smaller and lower than the metacone and is round in occlusal view. The

Table 1. — List of identified carnivore taxa from Fort Ternan.

| Order | Superfamily/ Family | Subfamily | Genus and species |
|---|---|---|---|
| Carnivora | Amphicyonidae | – | ?*Myacyon peignei* n. sp. |
| | Barbourofelidae | Barbourofelinae | gen. et sp. indet. |
| | Percrocutidae | – | Percrocuta tobieni |
| | Viverridae | Paradoxurinae | *Kanuites lewisae* |
| | – | – | cf. *Tugenictis* sp. |
| | – | Viverrinae | gen. et sp. indet. |
| Hyaenodonta | Hyainailouroidea | Teratodontinae | *Dissopsalis* cf. *pyroclasticus* |
| | – | Hyainailourinae | gen. et sp. indet. |

metacone is the largest cusp and set closely distal to the paracone. The metacrista is notched and curved. The distal end of the tooth is broken.

**Measurements.** LM1 (buccal) 16.9; WM1 (at paracone) 8.9.

*KNM-FT 14217*

The dP2 of *Dissopsalis* is not previously known, so the identification of this specimen as that tooth position is tentative, as is its referral to *Dissopsalis*. The tooth is morphologically very similar to the P2 KNM-FT 3375c described above but is slenderer and has an overall less developed cingulum. It is the right size to match the alveoli for dP2 in KNM-FT 3357.

**Measurements.** LdP2 11.6; WdP2 5.4.

Discussion

The type species of *Dissopsalis*, *D. carnifex*, is a fairly well known hyaenodont from the Siwaliks of Pakistan and India (Pilgrim 1910, 1913, 1914; Colbert 1933; Barry 1988). African material of *Dissopsalis* has been referred to the species *D. pyroclasticus*, first described on the basis of a mandibular ramus from Maboko, Kenya (Savage 1965; Morales & Pickford 2017) and later listed in faunal lists from a number of sites in Kenya and Uganda (see references in Barry [1988]), but these materials have never been studied in detail (but see Borths & Stevens [2017]) and doubts have been raised concerning their taxonomic attribution (Barry 1988). The most complete, as well as the youngest, material assigned to the species is that from Fort Ternan (e.g., Shipman *et al.* [1981]).

Referral of the Fort Ternan material described above to *Dissopsalis* seems unproblematic in view of the many similarities between the type specimen and KNM-FT 3562, as well as similarities of the upper dentition material to that of *D. carnifex* (Colbert 1933). However, there are also some differences. The type specimen shows m3 to be shorter than m2, which the reverse of the condition in KNM-FT 3562. In KNM-FT 3562 (as well as KNM-FT 13370 and KNM-FT 14135), the m3 talonid is, judging from figures in Savage (1965) somewhat longer than that of the type specimen. Finally, the type specimen of *D. pyroclasticus* is smaller overall than the Fort Ternan specimens. These differences suggest, but do not clearly demonstrate, a difference at the species level between *D. pyroclasticus* from Maboko and the Fort Ternan material. Therefore, I here leave this material in open nomenclature.

### Subfamily Hyainailourinae Pilgrim, 1932

### Hyainailourinae gen. et sp. indet.

Material examined. — KNM-FT 3359, left upper canine.

Description

This specimen is of gigantic size (lingual root to apex length *c.* 171 mm). It is nearly complete, except for some loss of enamel of the crown. The buccal margin is strongly curved, whereas the lingual margin is nearly straight.

Discussion

The size of this specimen excludes identification to all but the very largest hyaenodonts, such as the hyainailourines *Hyainailouros* or *Megistotherium*.

## CONCLUSIONS

It should be noted that there remain unstudied carnivore material from Fort Ternan housed in the paleontology collections of the National Museums of Kenya, Nairobi. This material includes 128 teeth or tooth fragments (mostly incisors and canines, but also a few premolars that are difficult to assign in the absence of suitable comparative material), as well as 62 postcranial elements, most of which belong to juvenile individuals associated with the juvenile crania and mandibles here assigned to *Kanuites lewisae*. Thus, further study may add to the faunal list summarized in Table 1.

The faunal list is an interesting mixture of old and new. Taxa that harken directly back to the early Miocene and beyond include the Hyaenodonta, the Fort Ternan occurrence of which represents one of the very last of the order prior to its extinction.

The amphicyonid at Fort Ternan also represents a member of a carnivore family on the path to extinction and in this sense is another throwback to the carnivore guild of the Oligocene and early Miocene. Unlike the hyaenodonts, however, Amphicyonidae at this time were still evolving new forms in Africa and did not become extinct until the late Miocene (Werdelin & Simpson 2009; Morales *et al.* 2016).

In contrast, the Fort Ternan viverrids, although clearly linked to the small carnivore faunas of the early Miocene (Savage 1965; Schmidt-Kittler 1987) represent evolving lineages. If correctly interpreted by Morales & Pickford (2011) paradoxurine viverrids continued to evolve in Africa until the early Pleistocene (*Pseudocivetta ingens*), although they are extinct on the continent today.

The presence of Barbourofelidae and Percrocutidae, on the other hand shows little or no connection to the early Miocene of Africa. Although Barbourofelidae likely evolved in Africa and had a modest presence in the early Miocene in the form of the genera *Afrosmilus*, *Ginsburgsmilus*, and *Syrtosmilus* (Werdelin & Peigné 2010), the Fort Ternan specimen is more derived than any of these and is more akin to the genus *Barbourofelis.* Rather than having evolved from earlier African forms the Fort Ternan barbourofelid is likely to represent an immigrant from Eurasia, where a number of Barbourofelidae were present in the middle and late Miocene (e.g., Ginsburg [1961]; Geraads & Güleç [1997]). These derived barbourofelids persisted in Africa in the middle and earliest late Miocene (Werdelin & Peigné 2010) before becoming extinct.

*Percrocuta tobieni*, on the other hand, represents, together with *P. abessalomi* and *P. miocaenica*, the earliest Percrocutidae (Howell & Petter 1985), opening the possibility (although unlikely) that this family is of African origin. Subsequent to this time the family was successful throughout Eurasia until near the end of the Miocene, when it became extinct.

Thus, the Fort Ternan carnivore fauna mixes some of the last occurrences of archaic groups, representatives of the middle parts of some carnivore lineages, and some of the earliest occurrences of successful late Miocene lineages. Missing are three families in particular: Mustelidae, Felidae and Herpestidae. Mustelids and felids are rare in Africa until the late Miocene and may be absent from Fort Ternan due to sampling vagaries or habitat requirements. Although none of the small carnivores described above are likely to represent Herpestidae, the family may be present in the unidentified material. Only additional investigation using better comparative material than that available to me will demonstrate if this is the case.

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Appendix 1. — Phylogenetic analysis based on the characters and matrix used by Morales & Pickford (2011) incorporating codings for Kanuites. The matrix file is available as Supplementary Online Data, at the following address: http://sciencepress.mnhn.fr/sites/default/files/documents/fr/geo2019v41a6_1.nex or via its DOI: https://doi.org/10.5252/geodiversitas2019v41a6_1.

| **Matrix for phylogenetic analysis** | | | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Paradoxurus hermaphroditus* | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 1 |
| *Pseudocivetta ingens* | ? | ? | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 |
| *Kichechia zamanae* | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | ? | 0 |
| *Orangictis gariepensis* | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 |
| *Orangictis ngororaensis* | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | 0 | 1 | 1 | 0 | 1 | 0 | ? | 0 |
| *Pseudocivetta howelli* | ? | ? | 0 | 0 | 1 | 1 | 0 | 0 | ? | ? | 1 | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| *Mioparadoxurus meini* | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | 0 | 1 | 0 | ? | 1 | 0 | 1 | 1 | 1 | 1 | 0 | ? | 1 |
| *Crossarchus obscurus* | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Ketketictis solida* | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 |
| *Kanuites lewisae* | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | ? | ? | ? | ? | ? | 0 | 0 | 0 | 0 | 1 | 0 | ? | ? |
| *Tugenictis* sp. FT | ? | ? | ? | ? | ? | ? | ? | 1 | 1 | 1 | 0 | 1 | ? | ? | ? | ? | ? | 0 | 0 | 0 | 1 | 1 | 0 | ? | ? |