

CARNIVORES FROM THE LATE MIOCENE AND BASAL PLIOCENE OF THE TUGEN HILLS, KENYA

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Resumen: Se han encontrado 19 especies de carnívoros en los sedimentos del Mioceno final y Plioceno inicial de las laderas de las colinas Tugen (Formaciones Lukeino y Magabet), Distrito de Baringo, Kenia. La muestra contiene tres especies de félidos, tres vivérridos, tres herpéstidos, tres hiénidos, un cánido, un úrsido y cuatro mustélidos. De estas formas, tres son nuevas especies (*Civettictis howelli* nov.sp., *Agriotherium aecuatorialis* nov. sp. y *Eucyon intrepidus* nov. sp.). La nutria de Langebaanweg (Sudáfrica) es clasificada como *Enhydriodon hendeyi* nov. sp. Algunas de las especies de carnívoros de las colinas Tugen estuvieron ampliamente distribuidas no sólo en África, sino en Eurasia, y en algunos casos en Norteamérica. Existió un importante cambio faunístico entre Lothagam (7,4-6,5 Ma) y Lukeino (6,1-5,7 Ma) que afectó de forma muy considerable a los carnívoros. Un cambio faunístico de magnitud comparable modificó las faunas de carnívoros del Mioceno final (MN 13) en la región mediterránea; algunos de los taxones involucrados en el cambio son los mismos que los determinados en Kenia.

Palabras clave: Carnívora, Mio-Plioceno, formaciones Lukeino y Magabet, Colinas Tugen, Kenia.

Abstract: 19 species of carnivores have been collected from the Late Miocene and early Pliocene sediments of the eastern foothills of the Tugen Hills (Lukeino and Mabaget Fms), Baringo District, Kenya. The sample comprises three species of felids, three viverrids, three herpestids, three hyaenids, a canid, an ursid and four mustelids. Of these three (*Civettictis howelli* nov.sp., *Agriotherium aecuatorialis* nov. sp. and *Eucyon intrepidus* nov. sp) are new species. The Langebaanweg (South Africa) otter is classed as *Enhydriodon hendeyi* nov. sp. Some of the Tugen Hills carnivore species were extremely widespread, not only within Africa, but also in Eurasia, and in some cases, North America. There was a major faunal change between Lothagam (7.4-6.5 Ma) and Lukeino (6.1-5.7 Ma) which greatly affected the carnivores. A faunal change of comparable magnitude modified the Late Miocene (MN 13) carnivore faunas of the Mediterranean region, some of the taxa involved in the turnover being the same as those occurring in Kenya.

Key words: Carnívora, Mio-Pliocene, Lukeino and Magabet Fms, Tugen Hills, Kenya.

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The carnivores described in this publication were collected from the Late Miocene and early Pliocene sediments of the eastern foothills of the Tugen Hills (Lukeino and Mabaget Fms), Baringo District, Kenya by MP in the 1970s and by the Kenya Palaeontology Expedition from 1998 to 2004.

Although many of the specimens are broken jaws or isolated teeth, much of the material is complete enough for accurate identification to specific or generic levels (Table I).

Some of the taxa represented in the Baringo region belong to extremely widespread lineages, the genera *Agriotherium*, *Megantereon* and *Plesiogulo* for example, being known from as far afield as North America (Janis *et al.*, 1998). The canid *Eucyon* is the earliest

known from Africa, and is close to material from Europe and Asia (China).

Geology

The Lukeino and Mabaget Fms crop out widely between the eastern escarpment of the Tugen Hills and Lake Baringo (Figs. 1 and 2). Geological mapping and radioisotopic dating, complemented by palaeomagnetic stratigraphy and faunal studies, indicate that the Lukeino Fm spans the period 6.1 to 5.7 Ma and the base of the Mabaget Fm from which some of the fossils described herein came, is between 5.1 and 4.5 Ma. (Pickford and Senut, 2001; Sawada *et al.*, 2001). In previous literature the Mabaget Fm was considered to be part of the

Taxon	Lukeino 6.1-5.7 Ma	Mabaget 5.1-4.5 Ma
<i>Felis</i> sp.	X	-
<i>Metailurus</i> sp.	X	-
<i>Dinofelis diastemata</i>	X	-
? <i>Megantereon obscura</i>	X	-
<i>Genetta</i> sp.	X	-
<i>Civettictis howelli</i> sp. nov.	-	X
<i>Megaviverra</i> aff. <i>leakeyi</i>	X	-
<i>Nandinia</i> sp.	X	-
cf <i>Ichneumia</i> sp.	X	-
Herpestidae indet.	-	X
<i>Ikelohyaena abronia</i>	-	X
<i>Hyaenictitherium namaquensis</i>	-	X
<i>Hyaenictis hendeyi</i>	sp	X
<i>Eucyon intrepidus</i> sp. nov.	X	-
<i>Agriotherium aecuatorialis</i> sp. nov.	-	X
<i>Plesiogulo praecocidens</i>	X	-
<i>Torolutra ougandensis</i>	X	-
<i>Sivaonyx africana</i>	X	-
<i>Enhydriodon</i> sp.	-	X

Table I.- Carnivore faunas from the Lukeino and Mabaget Fms, Tugen Hills, Kenya (x present; - not recorded).

Chemeron Fm but was distinguished from the type sequence of the Chemeron Fm by adding the suffix (Northern Extension). The deposits are 2-2.5 million years older than those in the type area of the Chemeron Fm, and occur in a separate basin, so to avoid continued confusion between the two units, the older deposits have been attributed to a separate formation.

Systematic Descriptions

Order Carnivora Bowdich, 1821

Family Felidae Gray, 1821

Genus *Felis* Linnaeus, 1758

Felis sp.

Material. KNM LU 665, calcaneum (Locality 2/260, Kukwassas, Lukeino Fm). BAR 2342'03, left m/1 (Kapsomin, Lukeino Fm).

Age. Late Miocene, 6.1 - 5.8 Ma.

Description. BAR 2342'03 (Fig. 3 A1), a left m/1 is broken towards the front of the paraconid and the posterior part of the protoconid. It corresponds in morphology and size to that of a felid similar to caracal and serval cat, but it is not possible to be more precise.

KNM LU 665 (Fig. 3 B2), is a medium sized calcaneum, similar in size and morphology to that of the caracal, *Caracal caracal* (Schreber, 1776) and the serval, *Leptailurus serval* (Schreber, 1776). It is morphologically closer to the former, even down to details of the articular facets.

Discussion. It is probable that BAR 2342'02 and KNM LU 665 belong to the genus *Felis*, more likely a caracal than a serval, but the sample is insufficient for determination to species.

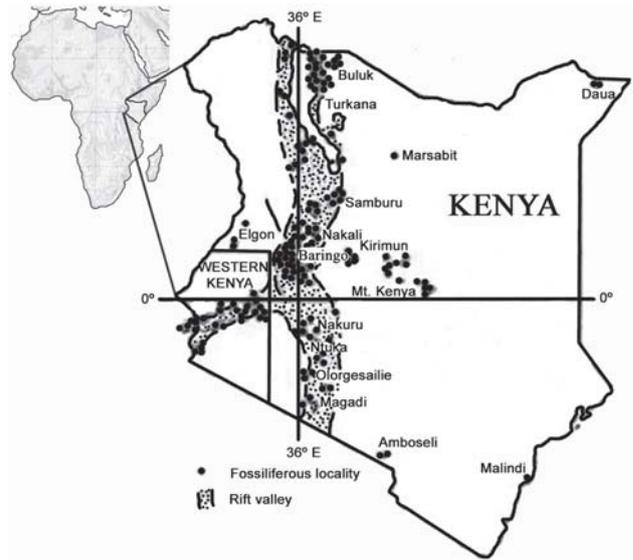


Figure 1.- Location of fossiliferous localities in the Kenya Rift Valley. Baringo area is located in the middle part of the Central Rift.

Genus *Metailurus* Zdansky, 1924

Metailurus sp.

Material: BAR 55'04 (Fig. 3C) fragment of left maxilla with P3/ (Kapsomin, Lukeino Fm).

Description: The P3/ (11.2-5.1 mm) is a long and transversely compressed tooth. The anterior part is well developed with the crest displaced labially but with no well defined cuspid. The main cusp is relatively low, the posterior accessory cusp is of moderate size and is followed by a very high posterior cingulum. The basal cingulum is quite strong on the labial wall, but is weaker lingually, but this part of the tooth is not well preserved. There is no basal posterolingual expansion. The maxilla possesses a small alveolus for a very reduced P2/. The anterior part of the canine alveolus appears to have been quite large.

Discussion: The morphology of the premolar is typical of primitive machairodont felids such as *Metailurus* Zdansky or *Paramachairodus* Kretzoi. In these genera the P3/ is long, with the main cusp relatively low and with prolongation of the anterior part of the tooth. The Kenyan specimen is slightly smaller than *Metailurus minor* of the Late Miocene of China (Zdansky, 1924). As in this species, the posterolingual basal expansion is reduced, and as a consequence, the tooth is narrower and more sectorial than is the case in species of *Paramachairodus*.

Genus *Dinofelis* Zdansky, 1924

Dinofelis diastemata (Astre) 1923

Material. BAR 157'01, left m/1 (Kapsomin, Lukeino Fm); BAR 387'02, right I3/ (Kapsomin, Lukeino Fm); BAR 288'03, right P4/ (Kapcheberek, Lukeino Fm). KNM LU 336, calcaneum (2/225, Kapcheberek,

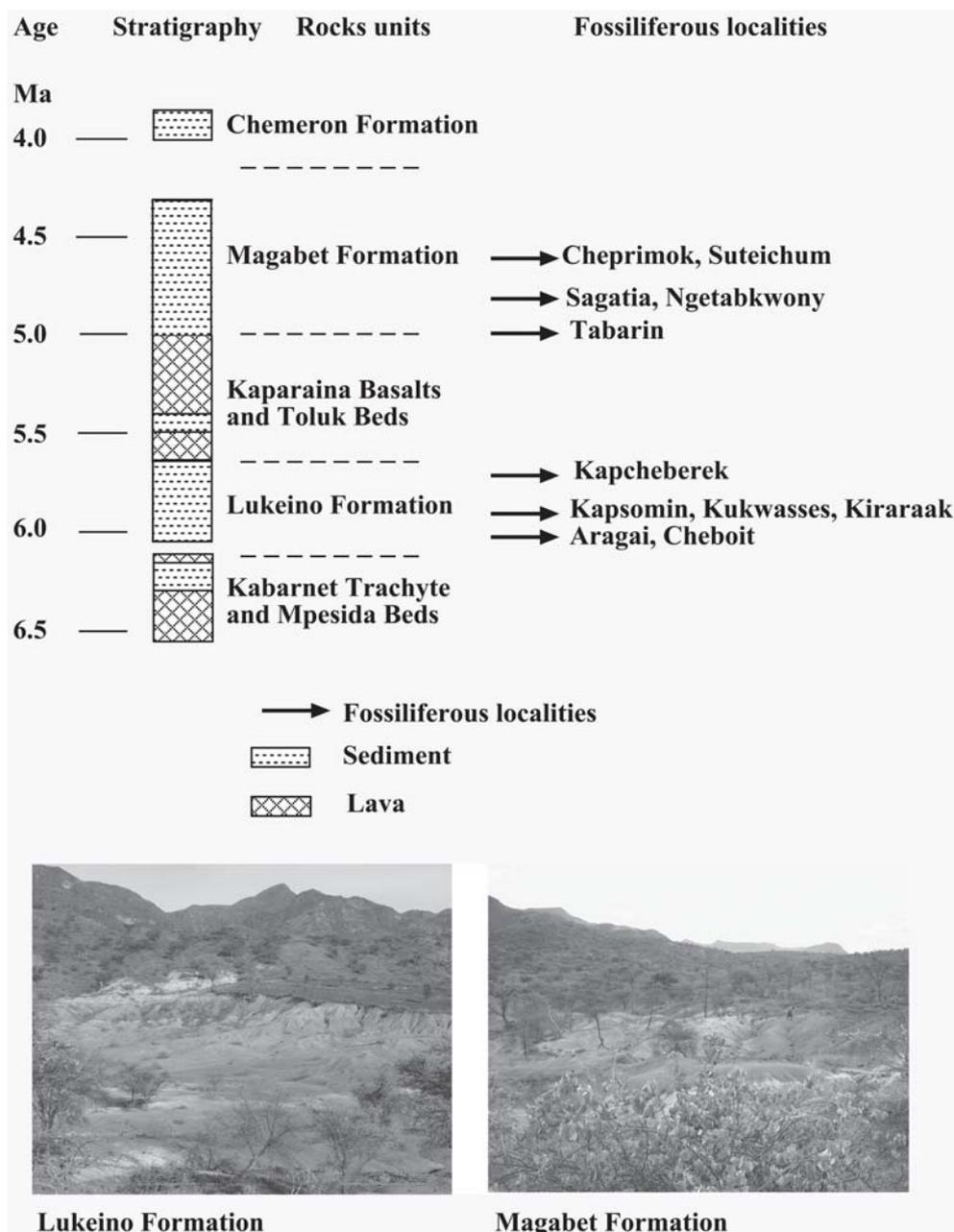


Figure 2.- Late Miocene and early Pliocene stratigraphy of the eastern foothills of the Tugen Hills. Baringo District, Kenya.

Lukeino Fm). KNM LU 667, phalanx (2/260, Kukwassess, Lukeino Fm).

Age. Late Miocene, 6.1 - 5.8 Ma.

Description. BAR 387'02, is a right I3/ (L = 8.9 mm, B = 8.1 mm). It has a high crown (ca 14 mm), the outer wall is smoothly convex, the inner one concave, separated from each other by sharp crests that converge towards cervix. There is a prominent basal cuspid in a lingual position. The root is well developed.

BAR 157'01 (Figs. 3E and 4A) is a left m/1 (L = 24.9 mm, B = 10 mm). The paraconid and metaconid are almost the same size but slightly longer than the protoconid.

The talonid is tiny, only a slight inflexion shows its position. The basal cingulum is smooth and is more marked in the posterior part of the tooth than the anterior part.

BAR 288'03, right P4/ (Figs. 3D and 4B) (L = ?, B = 13 mm). The specimen is an upper carnassial which has lost the metastyle. It has a large, voluminous paracone, and a well developed parastyle, both cusps being moderately compressed transversely. It has no ectostyle but does have a smooth postero-labial cingulum. The protocone is reduced, and is located in a posterior position reaching as high as the separation between the parastyle and the paracone, and unites with the latter cusp forming a vertical crest. There is a small hollow in the surface of the

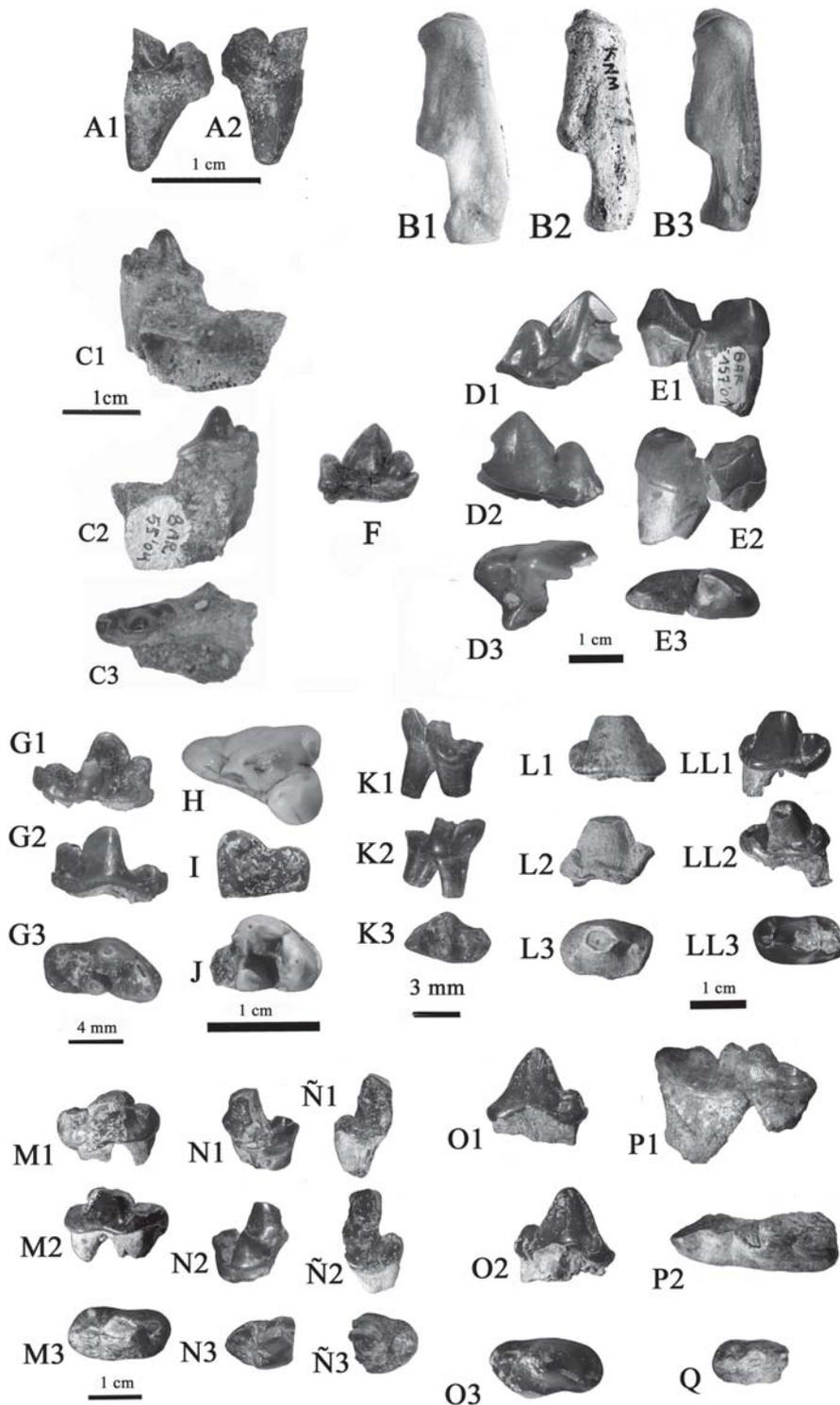


Figure 3.- A) *Felis* sp. from Kapsomin, Lukeino Fm BAR 2342'03 left m/1: lingual view (A1), labial view (A2), B) *Felis* sp., left calcaneum, 2/260, Kukwasses, Lukeino Fm. KNM LU 665 (B2) compared with *Felis caracal* (B1) and *Felis serval* (B3), C) *Metailurus* sp from Kapsomin, Lukeino Fm. BAR 55'04 fragment of left maxilla with P3/: lingual view (C1), labial view (C2), occlusal view (C3), D) *Dinofelis diastemata* from Kapsomin, Lukeino Fm. BAR 157'01, left m/1: lingual view (D1), labial view (D2), occlusal view (D3), E) *Dinofelis diastemata* from Kapcheberek, Lukeino Fm. BAR 288'03, broken right P4/: lingual view (E1), labial view (E2), lingual view (E3), F) *?Megantereon obscura* from Kapcheberek, Lukeino Fm. KNM LU 617, right p/4 in lingual view, G) *Genetta* sp. from Kapsomin, Lukeino Fm. BAR 155'01, left m/1: lingual view (G1), labial view (G2), occlusal view (G3), H) *Civettictis howelli* nov. sp. from Suteichun, Magabet Fm. BAR 1812'01 (holotype) right P4/: occlusal view (E1), labial view (E2), I) *Civettictis howelli* nov. sp. from Tabarin North, Magabet Fm. BAR 1448'03 left M1/ in occlusal view, J) *Civettictis howelli* nov. sp. from Tabarin North, Magabet Fm. BAR 1075'99 left broken m/1 in occlusal view, K) Herpestidae indet. from Tabarin, Magabet Fm. BAR 2638'03 right m/1: lingual view (K1), labial view (K2), occlusal view (K3), L) *Ikelohyaena* cf. *abronia* from Ngetabkwony, Magabet Fm. BAR 1200'03, right P3/: labial view (L1), lingual view (L2), occlusal view (L3), LL) *Ikelohyaena* cf. *abronia* from Tabarin, Magabet Fm. BAR 1480'03 left p/4: labial view (LL1), occlusal view (LL2), lingual view (LL3), M) *Ikelohyaena* cf. *abronia* from Tabarin, Magabet Fm. BAR 1627'01, right p/4: labial view (M1), lingual view (M2), occlusal view (M3), N) *Ikelohyaena* cf. *abronia* from Tabarin, Magabet Fm. BAR 1479'03 left m/1 fragment: labial view (N1), lingual view (N2), occlusal view (N3), Ñ) *Hyaenictis hendeyi* from Tabarin, Magabet Fm. BAR 487'02 left m/1: lingual view (Ñ1), labial view (Ñ2), occlusal view (Ñ3), O) *Hyaenictis hendeyi* from Tabarin, Magabet Fm. BAR 1000'03, right P2/: labial view (O1), lingual view (O2), occlusal view (O3), P) *Hyaenictitherium namaquensis* from Tabarin, Magabet Fm. BAR 1003'03 left P4/: labial view P1), occlusal view P2), Q) *Hyaenictitherium namaquensis* from Tabarin, Magabet Fm. BAR 1001'03 right p/2. in occlusal view.

enamel between the protocone and the parastyle.

KNM LU 336 is a large and robust left calcaneum lacking part of the tuber calcis and somewhat affected by arthritis. It is slightly larger than its homologue in *Pantheras pardus* (Linnaeus, 1758), the leopard. The main astragalar facet is wider and not as evenly curved as in the leopard calcaneum, and the fossil is more robust. This specimen accords in size with the m/1 described above, which is itself slightly larger than that of a leopard. This specimen is tentatively attributed to *Dinofelis diastemata* but it could belong to *Megantereon* which

is possibly also present in the Lukeino Fm.

KNM LU 667 is a felid toe bone larger than those of the leopard and the lion *Panthera leo* (Linnaeus, 1758). It is decidedly more robust than a leopard phalanx, even though it is about the same length. The shaft is thicker than in the leopard and lion and it is possible that this specimen also belongs to *Dinofelis*. The specimen is 32.5 mm long.

Discussion. The size and morphology of the m/1 and the fragment of P4/ correspond closely with the material

from Langebaanweg described by Hendeby (1974) as *Dinofelis diastemata*. The P4/ fragment is the same breadth as the corresponding tooth of *?Megantereon obscura* from Langebaanweg but clearly differs from this species by the greater development of the parastyle, instead conforming more closely to *Dinofelis diastemata*.

Genus *? Megantereon* Croizet and Jobert, 1828
? Megantereon obscura (Hendeby) 1974

Material. KNM LU 617, right p/4 (Locality 2/225, Kapcheberek, Lukeino Fm)

Age. Late Miocene, 5.7 Ma.

Description. KNM LU 617, is an unworn, well preserved right p/4 (Figs. 3F and 4C) (L = 18.3 mm, B = 8.6 mm). The crown was unerupted and has no roots. The cusps are vertical and very sharp with crenulated edges. The anterior cuspid is quite well developed with a vertical anterior border clearly separated from the main cusp. The posterior cusp is large and possesses a strong posterior cingulum.

Discussion. *Felis obscura* was defined by Hendeby (1974) on the basis of a maxilla from Langebaanweg close in size to *Panthera pardus*, but with clear mor-

phological differences. This author considered that it was related to the genus *Sivapanthera* Kretzoi (1929) (= *Sivafelis* Pilgrim, 1932) the species of which are related to the extant *Acinonyx* (Lydekker, 1884; Zdansky, 1925). The relation of *F. obscura* to *Sivapanthera* is based on two lines of evidence; the short mandible of *Sivapanthera* which could correspond to the equally short maxilla from Langebaanweg, and the morphology of the P4/ of *Sivapanthera potens* described and figured by Pilgrim (1932). However, the latter P4/ is quite different from that of *F. obscura*, in particular by its quite robust aspect.

An alternative to be considered is its identity to or at least a close relationship with *Megantereon*, a hypothesis that we support with a certain amount of caution since we do not know the mandible of this species. The genus *Megantereon* is relatively common in the Pliocene of Africa (Ewer, 1955c; Turner, 1987b; Werdelin and Lewis, 2000), the various species possessing a short maxilla, as is the case in *F. obscura*. Loss of the P2/ is another character in common, together with elongation of the upper carnassials which characterises these machairodonts. The upper canine in the Langebaanweg maxilla has a broken crown, but it would have been high (Hendeby, 1974), and was certainly quite compressed transversely, measurements of the base being L = 14.5 mm, B = 9.2 mm.

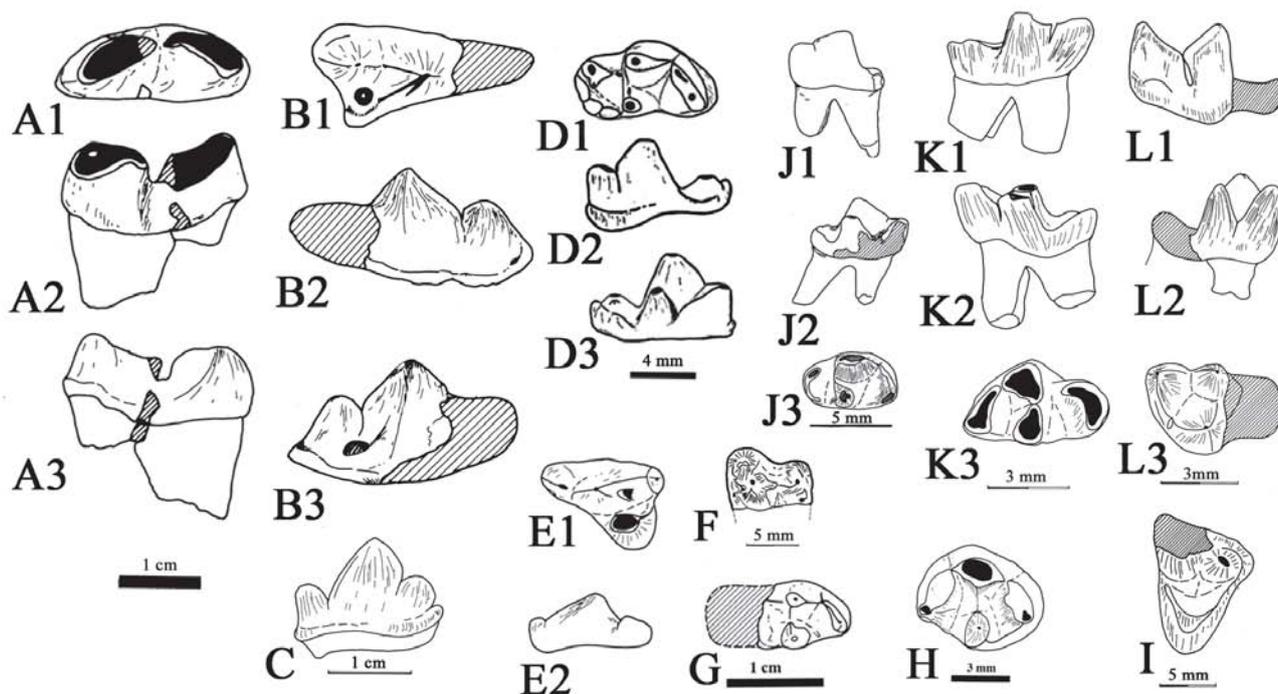


Figure 4.- A) *Dinofelis diastemata* from Kapsomin, Lukeino Fm. BAR 157'01, left m/1: occlusal view (A1), labial view (A2), lingual view (A3), **B)** *Dinofelis diastemata* from Kapcheberek, Lukeino Fm. BAR 288'03, broken right P4/: occlusal view (B1), labial view (B2), lingual view (B3), **C)** *?Megantereon obscura* from Kapcheberek, Lukeino Fm. KNM LU 617, right p/4 in lingual view, **D)** *Genetta* sp. from Kapsomin, Lukeino Fm. BAR 155'01, left m/1: occlusal view (D1), labial view (D2), lingual view (D3), **E)** *Civettictis howelli* nov. sp. from Suteichum, Magabet Fm. BAR 1812'01 (holotype) right P4/: occlusal view (E1), labial view (E2), **F)** *Civettictis howelli* nov. sp. from Tabarin North, Magabet Fm. BAR 1448'03 left M1/ in occlusal view, **G)** *Civettictis howelli* nov. sp. from Tabarin North, Magabet Fm. BAR 1075'99 left broken m/1 in occlusal view, **H)** *Megaviverra* aff. *leakeyi* from Kapsomin, Lukeino Fm. BAR 735'02, right m/2 in occlusal view, **I)** *Ichneumia* sp. 2/252, Kiraraak, Lukeino Fm. KNM LU 613, upper molar, occlusal view, **J)** *Nandinia* sp. from Kapsomin, Lukeino Fm. BAR 475'03, left m/1: labial view (J1), lingual view (J2), occlusal view (J3), **K)** Herpestidae indet. from Tabarin, Magabet Fm. BAR 2638'03 right m/1: labial view (K1), lingual view (K2), occlusal view (K3), **L)** Herpestidae indet. from Tabarin, Magabet Fm. BAR 1484'03 left m/1: labial view (L1), lingual view (L2), occlusal view (L3).

The p/4 from Lukeino could correspond to a species the size of ?*M. obscura*, but it also shows a morphology that corresponds closely with what is known of the various species of the genus, in particular the height and verticality of the anterior accessory cuspid. This tooth is close to the material figured by Viret (1954) from Saint Vallier (France) as *Megantereon megantereon*.

If our identification of the tooth as ?*Megantereon obscura* is correct, it would join *Megantereon hesperus* from North America (Berta and Galiano, 1983) as the oldest known species in the world. This could explain the retention of primitive characters in the African form such as the moderate size of the upper canine - we note that several lineages, such as the species figured by Viret (1954) possess upper canines of moderate size - and the shorter P4/.

Family Viverridae Gray, 1821
Subfamily Viverrinae Gray, 1821
Genus *Genetta* Linnaeus, 1758
Genetta sp.

Material. BAR 155'01, left m/1 (Kapsomin, Lukeino Fm).

Age. Late Miocene (5.8 Ma).

Description. A left m/1, BAR 155'01 (Figs. 3G and 4D) has a relatively tall trigonid with the paraconid and protoconid in line with it, a reduced metaconid and a talonid formed by a hypoconid and a relatively strong postero-lingual crest. The basal cingulum is well marked only on the external wall of the paraconid-protoconid.

Discussion. The morphology of this tooth is close to that of European *Genetta genetta* (Linnaeus, 1758), but the fossil m/1 is a bit bigger and the talonid is very strong. It is however, larger than the form identified as *Genetta* sp. by Stromer (1931) from Kleinzee (South Africa). Hendeby (1974) also identified a mandible from Langebaanweg as *Genetta* sp., but this form is also smaller, being even smaller than the specimen from Kleinzee (South Africa).

Genus *Civettictis* Pocock, 1915
Civettictis howelli nov. sp.

Type locality. Suteichun, Mabaget Fm.

Age. Lower Pliocene, ca 4.5 - 5 Ma.

Holotype. BAR 1812'01, right P4/.

Other material. BAR 1075'99, fragment of m/1 (Tabarin North, Mabaget Fm), Bar 1448'03, M1/ (Tabarin, Mabaget Fm).

Derivatio nominis. Named for Dr Francis Clark Howell, for his contribution to the study of African fossil carnivores.

Diagnosis. *Civettictis* similar in size to the extant *Civettictis civetta*. P4/ with voluminous paracone, but with reduced height, small parastyle, and short, blunt metastyle. The protocone is conical, well separated from the rest of the tooth and located in an anterior position.

Differential diagnosis. *Civettictis howelli* differs from species of *Megaviverra* by its more bunodont dentition, with lower cusps, and by the more retired position of the protocone and the shortening of the metastyle in the P4/. Apart from its smaller size, it differs from *Pseudocivetta ingens* by the possession of a massive rounded protocone, which is well separated from the rest of the crown. In *P. ingens* it is more trenchant and is united by a crest to the base of the metastyle. It also differs from *P. ingens* Petter, 1963 by the retention of m/1 trigonid morphology which is more primitive and by the lesser development of the external wall of M1/. It differs from *Civettictis civetta* (Schreber, 1776) by the morphology of the protocone of P4/ which in the new species is more massive and bunodont and by the greater development of the parastyle on the external wall of the M1/.

Description. Holotype. Right P4/, BAR 1812'01 (Figs. 3H and 4E) (L = 12.8 mm, B = 9.5 mm). Outstanding is the large size and the almost spherical shape of the protocone, which is located in an anterior position without passing beyond the projection of the parastyle. There is a smooth lingual cingulum which touches the base of the protocone. The paracone comprises the major part of the tooth and from its apex there depart three crests, the anterior one uniting with a moderately sized parastyle, the antero-lingual one is quite damaged and joins the base of the protocone, and the posterior one, which is separated by an incision, contacts the metastyle. The latter cusp is low, short and not sharp. The labial cingulum is very smooth.

The M1/, BAR 1448'03 (Figs. 3I and 4F) preserves the lingual part of the tooth. It has an undulating external wall with rounded, clearly bunodont external cusps. The paracone is somewhat larger than the metacone, and backs onto a strong parastyle which is also bunodont. This parastyle produces an irregular outline on the external wall. In the anterior wall of the paracone and the parastyle, there is a discontinuous basal cingulum. Lingually of the metacone there is a hint of small cusplet, but it is difficult to determine whether it represents a metaconule, or a small accessory cusplet.

An m/1, BAR 1075'99 (Figs. 3J and 4G) from Tabarin North preserves only the trigonid, but it is compatible in size to the upper P4/ described above. The disposition of the cuspid is similar to those of the m/1 of *Viverra zibetha*, with the metaconid much smaller than the paraconid, and well separated from it. The protoconid and metaconid are united internally by two sharp crests. The cuspid is more robust and rounded than their homologues in *V. zibetha*.

Discussion. At least two lineages of large Viverrinae are known (Petter and Howell, 1977); into the first, which comprise species close morphologically to *Viverra*, can be assigned the genus *Megaviverra* proposed by Qiu (1980) (= *Megaviverra* Kretzoi and Fejfar, 1982 and *Hesperoviverra* Kretzoi, 1986). The second lineage, apart from its large size, is characterised by the possession of quite bunodont dentitions, adapted to more omnivorous diets; this group includes *Pseudocivetta* and the extant *Civetta*, genera which Hendey (1974) considered to be close to each other. The new species described here clearly belongs to the latter group, and at least in reference to its marked bunodonty in P4/, it also presents affinities with some Hemigalinae, in particular with *Paradoxurus*. Probably the latter is due to parallelism between these two lineages of viverrids which are certainly closely related to each other.

Genus *Megaviverra* Qiu, 1980

Megaviverra aff. *leakeyi* (Petter) 1963

Material. BAR 735'02, right m/2 (Kapsomin, Lukeino Fm).

Age. Late Miocene (5.8 Ma).

Description. BAR 735'02 (Fig. 4H) (L = 6.5 mm; B = 5.5 mm), a lower second molar, has a subrounded occlusal outline and is superficially corroded, but the morphology can be made out clearly. It has a complete trigonid with the paraconid and protoconid forming a continuous labial peripheral wall. The metaconid is located in front of the protoconid and is separated from the paraconid by a wide valley. The talonid is formed of a cuspid that occupies almost its entire extent.

Discussion. This tooth is somewhat smaller than the m/2 of *Megaviverra leakeyi* (Petter, 1963) from Langebanweg (dimensions of the m/2, L = 7.5 mm, B = 6.2 mm). The morphology of the two teeth is the same, but the South African one has a very reduced metaconid, while in the Kapsomin specimen it is quite well developed.

Family Nandiniidae Pocock, 1929

Genus *Nandinia* Gray, 1843

Nandinia sp.

Material. BAR 475'03, left m/1, Kapsomin, Lukeino Fm.

Description. BAR 475'03 (Fig. 4J) (L = 6.4 mm, B = 3.7 mm) is a complete but somewhat corroded first lower molar. The occlusal outline is oval with a short trigonid, formed of a low paraconid located in an antero-lingual position, a relatively reduced metaconid positioned posteriorly, which is the same height as the paraconid and the protoconid which is strong. The talonid is short, with a conical quite weakly developed hypoconid, while the entoconid is weak and in the form of a crest.

Discussion. The oval occlusal outline of the tooth is markedly different from that of Viverridae which is notably more elongated. Neither does it resemble the m/1s of Herpestidae, even though they are shorter than those of viverrids. This ovoid occlusal morphology in m/1 occurs in the extant Palm Civet, *Nandinia binotata* (Gray, 1830). Other features of the Lukeino tooth which approach this species are: the antero-lingual position of the paraconid, different from the much more lingual position that characterises Herpestidae, the reduction of the talonid, and the relatively low trigonid cusps, the protoconid being higher than the paraconid and metaconid. Furthermore, the fossil is similar in size to the extant *Nandinia binotata*.

Family Herpestidae Bonaparte, 1845

Genus *Ichneumia* Geoffroy, 1837

Ichneumia sp.

Material. KNM LU 613 (locality 2/252, Kiraraak, Lukeino Fm).

Age. Late Miocene 6 Ma.

Description. An isolated left upper molar, KNM LU 613 (Fig. 4I) from Kiraraak, Lukeino Fm, is slightly larger than its homologue in *Ichneumia albicauda* (Cuvier, 1829). The parastyle, which is partly broken, and metastyle are lower than in the extant species. The central fossa between the labial cusps and the protocone is shallower than in *Ichneumia*, but otherwise the teeth of the two are similar. There is a weak labial cingulum and a weak but distinct lingual cingulum. The metacone and paracone are almost completely reduced as in *Ichneumia*. The specimen measures L = 9.9e mm, B = 11.3 mm compared with L = 6.4 mm, B = 8.3 mm in *I. albicauda*.

Discussion. The upper molar from Kiraraak reveals the presence of a third viverrid of modern aspect in the Lukeino Fm. Its closest affinities appear to be with the extant white-tipped mongoose (*Ichneumia albicauda*), but differences in cusp heights and the depth of the central fossa indicate that it does not belong to the same species. Until more informative specimens are found we refer to this specimen as *Ichneumia* sp..

Herpestidae indet.

Material. BAR 1085'99 left p/4 (Tabarin, Mabaget Fm), BAR 1484'03, trigonid of left m/1 (Tabarin), BAR 2638'03, right m/1 (Tabarin).

Description. BAR 2638'03 (Figs. 3K and 4K), a right m/1 is in medium wear, but the morphology can still be made out. The trigonid is similar to that of BAR 1484'03 (Fig. 4L) which is unworn. Both teeth have a trigonid in which the paraconid is in an anterior position while the metaconid and protoconid facing each

other. The paraconid and metaconid are almost the same height and are only slightly lower than the protoconid. The talonid is short and is comprised of a chisel-shaped cuspid in the position of the hypoconid, there is no sign of an entoconid, so that the talonid valley opens lingually.

BAR 1085'99 left p/4 (L = 4.5 mm, B = 2.5 mm). The specimen is a short, robust tooth, with a relatively low main cusp, an individualised anterior cuspid of moderate size and height, a posterior cuspid which is much larger than the anterior one, and quite a bit taller, a strong posterior cingulum, and a wide antero-lingual cingular platform.

Discussion. The size of these teeth is notably less than that of other viverrids described in this paper, the p/4 differs from that of *Genetta* by its robustness and by the better development of the antero-posterior cingular platform. The m/1 is also different from *Genetta* by the closed V-shape of the trigonid cusps, in which the metaconid is as well developed as the paraconid. Both teeth are morphologically close to those of the small African mongooses.

Family Hyaenidae Gray, 1821

Genus *Ikelohyaena* Werdelin and Solounias, 1991

Ikelohyaena abronia (Hendey) 1974

Material. BAR 1479'03, left m/1 fragment (Tabarin, Mabaget Fm); BAR 1480'03, left p/4 (Tabarin, Mabaget Fm); BAR 1627'01, right p/4 (Tabarin, Mabaget Fm); BAR 1200'03, left P3/ (Ngetabkwony, Mabaget Fm); BAR 1478'03, fragment of left P3/ (Tabarin, Mabaget Fm).

Age. Early Pliocene, 5.0 - 4.5 Ma.

Description. BAR 1479'03 (Figs. 3N and 5A), a broken left m/1 preserves the protoconid and talonid. It is a typical hyaenid carnassial. There is a strong metaconid about half the height of the posterior cristid of the protoconid. The talonid is short, clearly reduced and is deeply worn. It is formed of a hypoconid located labially which is surrounded by a small posterior cingulum. On the labial side, backing onto the cingulum and the hypoconid there are two small cusplets

BAR 1480'03 (Figs. 3LL and 5B), a left p/4 (L = 18.7 mm, B = 10 mm) is an elongated tooth with the main central cusp of moderate size, a poorly developed anterior cusplet, which is clearly smaller than the posterior one. The posterior cingulum is strong, particularly on the postero-lingual border, where it forms an additional cusplet.

A lower right p/4, BAR 1627'01 (Figs. 3M and 5C) (L = 19.6 mm, B = 10.5 mm) is an elongated tooth with the main central cusp of moderate size, and anterior and posterior cusps strong and of similar

size. The posterior cingulum is strong, particularly on the postero-lingual border, where it forms an additional cusplet.

BAR 1200'03, a right P3/ (L = 18.6 mm, B = 12 mm) (Figs. 3L and 5D) is a short, robust upper premolar with a small anterior cusplet in the antero-lingual corner, a moderately sized posterior cusplet and a postero-lingual expansion which is relatively weakly pronounced. The main cusp has strong anterior and posterior crests. The tooth is surrounded by a cingulum, weak externally and stronger internally.

Genus *Hyaenictitherium* Kretzoi, 1938

Hyaenictitherium namaquensis (Stromer) 1927

Material. BAR 1003'03, left P4/ (Tabarin, Mabaget Fm); BAR 1001'03, right p/2 (Tabarin, Mabaget Fm).

Age. Early Pliocene, 5.0 - 4.5 Ma.

Description. BAR 1003'03 (Figs. 3P and 5G), a left P4/ is badly eroded on its lingual side so it is difficult to make out the morphology. However, the root of the protocone is preserved from which it is possible to say that the protocone was located in front of the parastyle. The parastyle is long, only slightly less than the length of the protocone and the metastyle, which are subequal. The metastyle curves lightly towards the exterior. There is quite a well developed basal cingulum externally.

BAR 1001'03 (Figs. 3Q and 5H) is a right p/2. The specimen is damaged at the base of the external wall and anteriorly, and for this reason the dimensions are approximate (L = ca 15 mm, B = ca 9 mm). It is an elongated tooth, probably with a reduced anterior cusplet, a low central cusp and a very large posterior cuspid. There is quite a strong basal cingulum on the internal wall.

Genus *Hyaenictis* Gaudry, 1861

Hyaenictis hendeyi Werdelin, Turner and Solounias, 1994

Material. BAR 487'02, left m/1 fragment (Tabarin, Mabaget Fm); BAR 1000'03, right P2/ (Tabarin).

Age. Early Pliocene, ca 5 - 4.5 Ma.

Description. BAR 487'02 (Figs. 3Ñ and 5F), a fragment of left m/1 preserves part of the protoconid and talonid. It is a typical hyaenid carnassial. Notable is the almost complete suppression of the metaconid which is limited to a small incision which is almost imperceptible at mid-height of the posterior cristid of the protoconid. The talonid is short and narrow, clearly reduced and is formed of a central cuspid (hypoconid) which occupies almost the entire expanse of the talonid, and a small cusplet attached to the lingual side of the hypoconid.

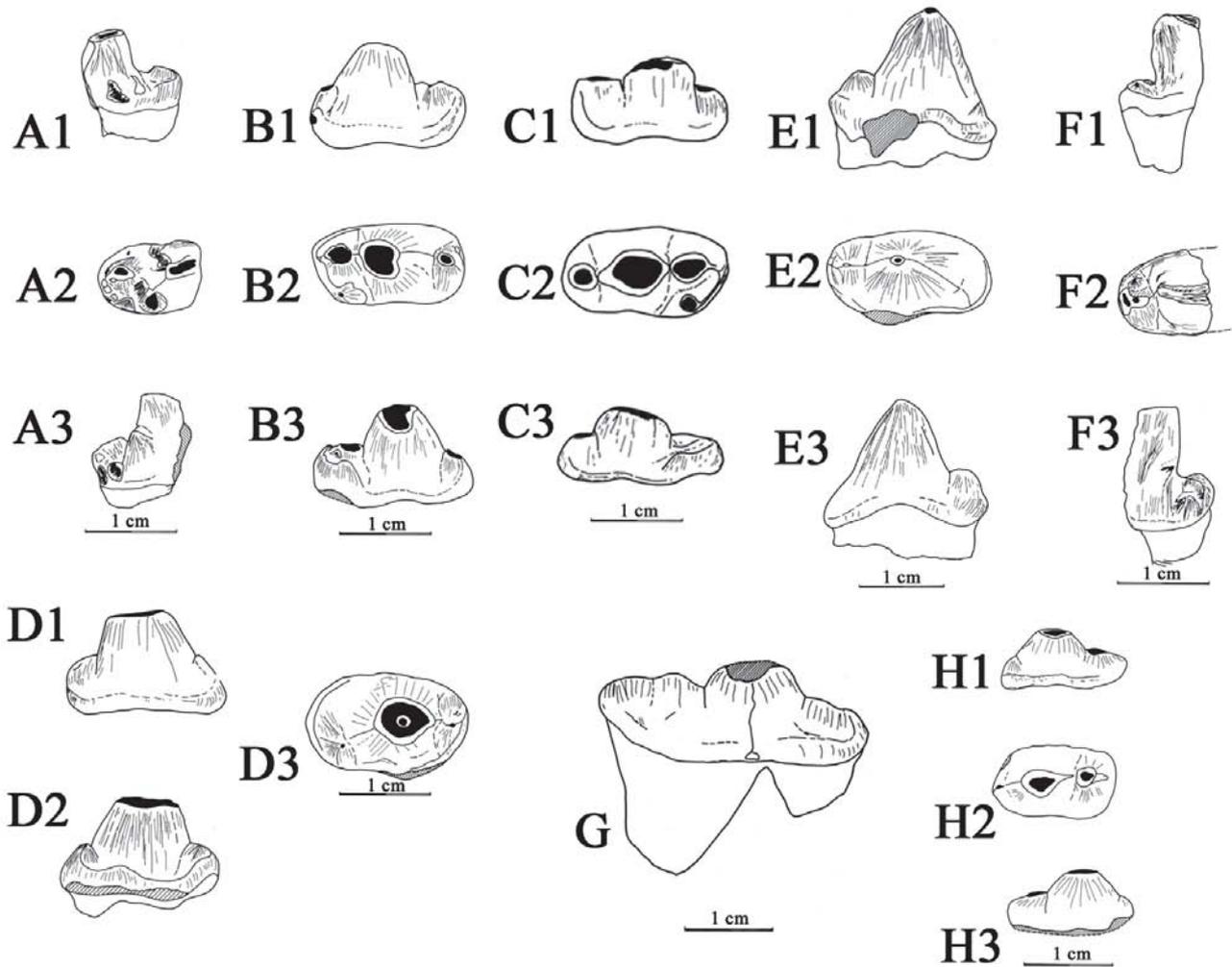


Figure 5.- A) *Ikelohyaena cf. abronia* from Tabarin, Magabet Fm. BAR 1471'03 left m/1 fragment: labial view (A1), occlusal view (A2), lingual view (A3). **B)** *Ikelohyaena cf. abronia* from Tabarin, Magabet Fm. BAR 1480'03 left p/4: labial view (B1), occlusal view (B2), lingual view (B3). **C)** *Ikelohyaena cf. abronia* from Tabarin, Magabet Fm. BAR 1627'01, right p/4: labial view (C1), lingual view (C2), occlusal view (C3). **D)** *Ikelohyaena cf. abronia* from Ngetbkwony, Magabet Fm. BAR 1200'03, right P3/: labial view (D1), lingual view (D2), occlusal view (D3). **E)** *Hyaenictis hendeyi* from Tabarin, Magabet Fm. BAR 1000'03, right P2/: lingual view (E1), occlusal view (E2), labial view (E3). **F)** *Hyaenictis hendeyi* from Tabarin, Magabet Fm. BAR 487'02 left m/1: labial view (F1), occlusal view (F2), lingual view (F3). **G)** *Hyaenictitherium namaquensis* from Tabarin, Magabet Fm. BAR 1003'03 left P4/ in labial view. **H)** *Hyaenictitherium namaquensis* from Tabarin, Magabet Fm. BAR 1001'03 right p/2: lingual view (H1), occlusal view (H2), labial view (H3).

BAR 1000'03 (Figs. 3O and 5E), an unworn right P2/ is elongated and narrow with a high main cusp. There is no anterior cusplet, only a slight swelling at the contact between the anterior crest of the main cusp and the basal cingulum. The main cusp is narrow. The posterior cuspid is moderately well developed. The tooth is a bit damaged at the antero-posterior basal expansion, but the impression is that it was relatively weak. There is a basal cingulum surrounding the tooth, weak labially but quite well formed lingually.

Genus *Hyaenictis* Gaudry, 1861
Hyaenictis sp.

Material. KNM LU 751, right P4/ fragment (locality 2/225, Kapcheberek, Lukeino Fm); KNM LU 752 fragment of left p/4 (locality 2/224, Kapsomin, Lukeino Fm).

Age. Late Miocene, ca 5.7 - 5.8 Ma.

Description. Two damaged premolars from the Lukeino Fm consist of a distal half of a right P4/ from locality 2/225, Kapcheberek, and KNM LU 752, the distal third of a left p/4 from locality 2/224, 11.8 mm wide. The former specimen differs slightly in size and morphology from *Hyaena*, while the latter is closer to this genus in both size and shape. Both specimens could belong to *Hyaenictis*.

Discussion. The co-existence of at least two hyaenids of almost the same size in the Mabaget Fm is based on the morphology of the talonids of the m/1s (BAR 1479'03 and BAR 487'02, both from Tabarin). The former has a strong metaconid, and the latter lacks this cusp, and the talonids of the two forms are different. The talonid in the former which is attributed to *Ikelohyaena abronia* (Hendey, 1974, 1978a), is formed of a hypoconid in a labial position surrounded by a small posterior cingulum and with small cuspules lingually. This morpho-

gy is close to that seen in *Pliohyaena pyrenaica* of the Early Pliocene of Eurasia (Qiu, 1987), and close to that of the extant *Hyaena hyaena*; more or less corresponding to the talonid morphology of primitive hyaenas (*Protictitherium*, *Thalassictis*, etc.). Unfortunately it is not possible to measure the tooth precisely, but it could well correspond in size to the m/1 of *Ikelohyaena abronia* (Hendey, 1974, 1978a), as do BAR 1002'03 (right P3/), BAR 1480'03 (left p/4), and BAR 1478'03 (fragment of left P3/). BAR 1627'01 is a right p/4 which is also the size of *I. abronia*, even though it has some differences from the p/4 BAR 1480'03, in particular a better development of the anterior cuspid which is almost the same size as the posterior one.

In contrast, BAR 1003'03, left P4/ and BAR 1001'03, left p/2, are larger, the P4/ falling within the range of variation of the P4/ of *Hyaenictitherium namaquensis*, whereas the p/2 is at the upper limit of this species. The differences between *Ikelohyaena abronia* and *Hyaenictitherium namaquensis* are small, Werdelin *et al.*, (1994) point out that the proportions of the dentition in the two species are similar, and that the main differences occur in the shape of the teeth and the height of the premolar crown. As far as the size is concerned there is no discontinuity in the metric data of the two taxa. The state of conservation of the P4/ is quite poor, but the proportions of the labial cusps are close to the P4/ (L 12848) figured by Hendey (1974) as *Hyaena* sp B, which has since been included in *Hyaenictitherium namaquensis* (Stromer, 1931; Hendey, 1978a). The identification of these two teeth as *Hyaenictitherium namaquensis* is in any case a compromise solution until better material is recovered.

Finally, a third hyaenid is represented in the Mabaget Fm by a fragment of m/1 (BAR 487'01) the morphology of which corresponds perfectly with that of the genus *Chasmaporthetes*, characterised, as it is, by the reduction of the metaconid which is practically absent, and by the very short talonid, with a central hypoconid and a small lingual cusplet. The morphology of this fragment of tooth is close to *Chasmaporthetes lunensis* (Del Campana, 1914) from the Pliocene of Layna (Spain) and to *C. kani* (Qiu, 1987). To this third hyaenid we attribute a P2/ (BAR 1000'03) which is quite different from the upper premolars of *I. abronia*, in particular by the height of the crown and its more elongated and sectorial aspect. This tooth is larger than the P2/ measured by Hendey (1978), but in any case the difference in size is minor. Alternatively this tooth could correspond to a P3/, since the differences in morphology of the P2/ and P3/ in *Chasmaporthetes* are small, and in cases the anterior cuspid of P3/ can be very reduced, as in material from Layna, for example. If the specimen is a P3/ then it could represent *Hyaenictis hendeyi*. It should be noted however, that the differences between this species and those attributed to *Chasmaporthetes* are really quite minor.

The hyaenid teeth from the Lukeino Fm (KNM LU 751, right P4/ fragment and KNM LU 752 fragment of

left p/4) are insufficiently preserved for much to be said, save for the possibility that they could belong to *Ikelohyaena abronia*.

Family Canidae Gray, 1821

Genus *Eucyon* Tedford and Qiu, 1996

Eucyon intrepidus nov. sp.

Type specimen. BAR 2127'01, right M1/ (Kapsomin, Lukeino Fm).

Other material. KNM LU 753, left m/3 (Lukeino Fm); KNM LU 754, right p/3 or p/4 (Lukeino Fm); BAR 719'02 left M1/ (Kapsomin, Lukeino Fm).

Age. Late Miocene, 5.8 - 6.1 Ma.

Derivatio nominis. Named for the intrepid journey of the lineage from America to Africa via China during the Late Miocene.

Diagnosis: *Eucyon* the size of extant European *Vulpes vulpes*, M1/ with a triangular occlusal outline, relatively narrow with the main cusps high and sharp.

Differential diagnosis: *E. intrepidus* differs from *E. monticinensis* (Rook, 1992) and *E. davisii* (Harrison, 1983) by its smaller size and the greater relative heights of the trigon cusps.

Description. BAR 2127'01 (Figs. 6A and 7A) a right M1/ (L = 9.3 mm, B = 11 mm), has a subtriangular outline with pyramidal paracone and metacone which are quite sharp. The parastyle and metastyle are strong. The protocone is dune-shaped, joined to the well developed metaconule and to two internal crests, one which joins the parastyle, the other the base of the paracone. The central valley is deep. The labial cingulum is smooth, the anterior cingulum stronger and the postero-lingual one stronger and more elevated, almost forming an independent cusplet (hypocone) separated by a narrow but deep valley from the protocone.

BAR 719'02 (Fig. 6B) is a left M1/ (L = 9.6 mm; B = 12.7 mm). It is deeply worn but the basic layout of the cusps is similar to that of the holotype.

KNM LU 754 is a right p/3 or p/4 of a canid (L = 14.6 mm, B = 11.9 mm). It consists of a prominent main cusp, a reduced anterior accessory cusplet and three tubercles forming the posterior accessory cusps as in recent *Canis*. It has two closely applied roots fore and aft.

KNM LU 753 is a left m/3 (L = 10.4 mm, B = 8.6 mm). It is squarer than its homologue in extant *Canis* and the cusp arrangement is similar although the proportions of the teeth and constituent cusps are different.

Discussion. Even though the material assigned to the new species is scarce, we consider that it is sufficient

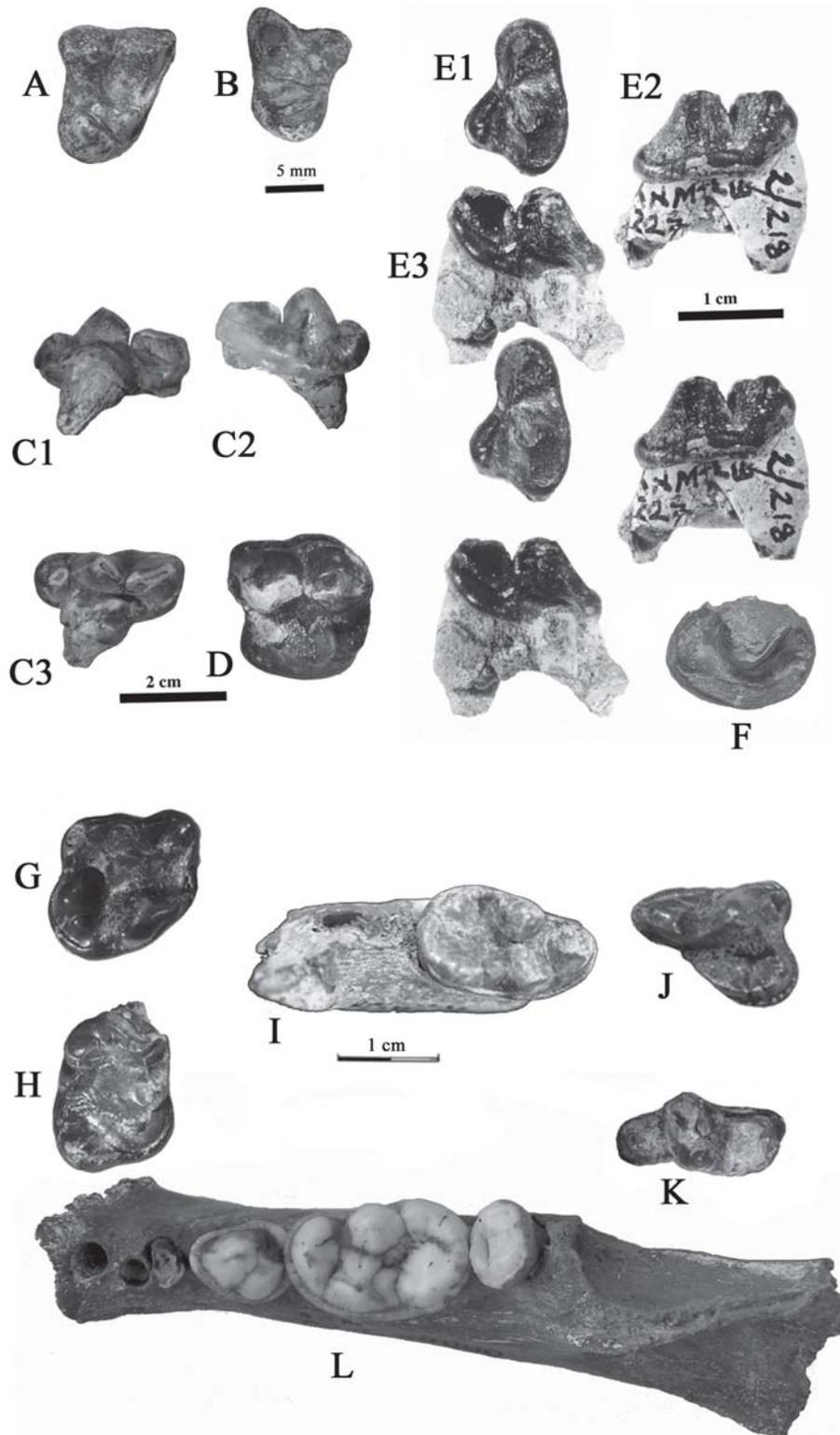


Figure 6.- A) *Eucyon intrepidus* nov. sp. from Kapsomin, Lukeino Fm. BAR 2127'02 (holotype) right M1/ in occlusal view, B) *Eucyon intrepidus* nov. sp. from Kapsomin, Lukeino Fm. BAR 719'02 left M1/ in occlusal view, C) *Agriotherium aecuatorialis* nov. sp. from Ngetabkwony, Magabet Fm. BAR 465'02, left P4/: lingual view (C1), labial view (C2), occlusal view (C3), D) *Agriotherium aecuatorialis* nov. sp. from Cheprimok, Magabet Fm. BAR 66'00, left M1/ in occlusal view, E) *Plesiogulo praecocidens* from Cheboit, Lukeino Fm. KNM LU 227, right P4/ (stereo pair): occlusal view (E1), lingual view (E2), labial view (E3), F) *Plesiogulo praecocidens* from Kapcheberek, Lukeino Fm. BAR 1893'00, broken left M1/ in lingual view, G) *Sivaonyx africana* from Kapcheberek, Lukeino Fm. BAR 1720'00, left P4/ in occlusal view, H) *Sivaonyx africana* from Kapcheberek, Lukeino Fm. BAR 1082'01, right M1/ in occlusal view, I) *Sivaonyx africana* from Kapcheberek, Lukeino Fm. KNM LU 337 right mandible in occlusal view, J) *Torulutra ougandensis* from Kapcheberek, Lukeino Fm. BAR 270'03, left P4/ in occlusal view, K) *Torulutra ougandensis* from Kapcheberek, Lukeino Fm. BAR 348'00, right m/1 in occlusal view. L) *Enlydriordon hendeyi* nov. sp. Langebaanweg, S. Africa (holotype), left Mandible in occlusal view.

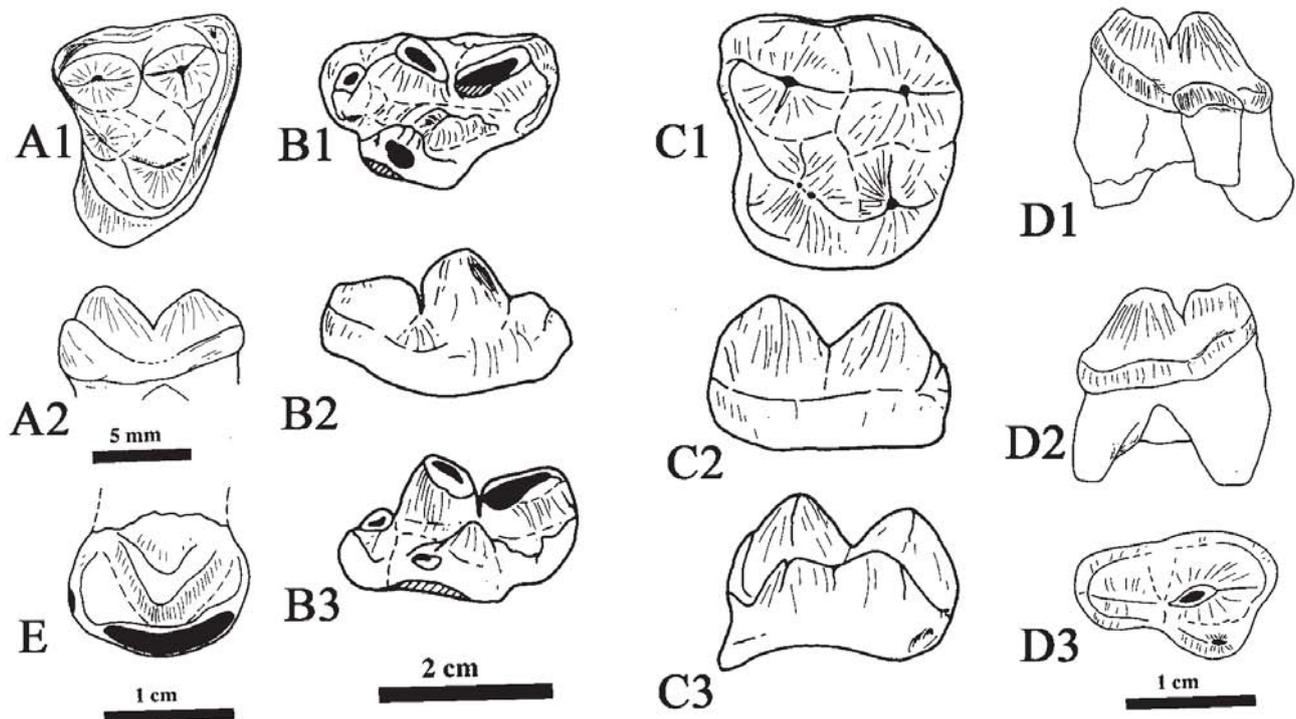


Figure 7.- **A)** *Eucyon intrepidus* nov. sp. from Kapsomin, Lukeino Fm. BAR 2127'02 (holotype) right M1/: occlusal view (A1), labial view (A2), **B)** *Agriotherium aecuatorialis* nov. sp. from Ngetabkwony, Magabet Fm. BAR 465'02, left P4/: occlusal view (B1), labial view (B2), lingual view (B3), **C)** *Agriotherium aecuatorialis* nov. sp. from Cheprimok, Magabet Fm. BAR 66'00, left M1/: occlusal view (C1), labial view (C2), lingual view (C3), **D)** *Plesiogulo praecoidens* from Cheboit, Lukeino Fm. KNM LU 227, right P4/: lingual view (D1), labial view (D2), occlusal view (D3), **E)** *Plesiogulo praecoidens* from Kapcheberek, Lukeino Fm. BAR 1893'00, broken left M1/ in lingual view.

to be able to define a new species. The difference in size from the known forms from the late Miocene of Eurasia and North America (Harrison, 1983; Morales, 1984; Rook, 1992; Tedford and Qiu, 1996) is clear (Fig. 8), but there also exist morphological differences such as the higher trigon cusps, and the deeper and narrower central valley, that indicate that the m/1 had a low sharp hypoconid. This new species is the earliest known canid in Africa. The family is also known from Langebaanweg (Hendey, 1974) at which locality there is an unidentified species which is close in size to *C. monticinensis* from Venta del Moro (Spain) and Brisighella (Italy). However, it differs from this species by the subquadrangular outline of the M1/ and M2/ due to the absence of an inflexion in the posterior wall.

Family Ursidae Gray, 1821
Subfamily Hemicyoninae Frick, 1926
Genus *Agriotherium* Wagner, 1837
Agriotherium aecuatorialis nov. sp.

Synonymy: 1970 *Agriotherium africanus*, Hendey; Petter *et al.*, 1994.

Holotype: Right m/2, NK 497'91.

Type locality. NK 115, Nkondo, Uganda.

Age of type specimen. Late Miocene (Petter *et al.*, 1994).

Age of additional material. Basal and Middle Pliocene (5.1-4.5 Ma)

Diagnosis. *Agriotherium* of moderate size, m/2 with reduced metaconid, located in front of the protoconid, talonid strongly dominated by the hypoconid. P4/ with moderately sized protocone.

Differential diagnosis: *Agriotherium aecuatorialis* differs from Eurasian species of the genus by the reduction of the metaconid of m/2, which is thus more sectorial, as is the p/4. It differs from *A. africanum* Hendey, 1972 by the weaker and simpler protocone of P4/.

Additional material from Kenya and Uganda. BAR 465'02, left P4/ (Ngetabkwony, Magabet Fm); BAR 66'00, left M1/ (Cheprimok, Mabaget Fm); NK 99'89, right P4/ (NK 73, Nkondo).

Age. Lower Pliocene, 4.5 - 5 Ma.

Description: In BAR 465'02, (Figs. 6C and 7B) a left P4/, the parastyle is strong, voluminous and with a smooth cingulum on its anterior wall. The paracone and metastyle are almost the same size, being quite compressed transversely. The protocone is comprised of a wide platform on which is differentiated a relatively small cusplet located opposite the base of the incision between the paracone and metastyle. The lingual cingulum is smooth at the base of the protocone and strong at the base of the metastyle.

BAR 66'00, left M1/ (Figs. 6D and 7C) (L = 28.4 mm, B = 30 mm), has a voluminous paracone only slightly higher than the metacone and both are pyramidal cusplets. At the base of the paracone there is a well developed cingulum. The protocone is comprised of two cusps almost completely fused together, and is quite high, slightly extended and in a central position. The metaconule (= hypocone of several authors) is high and pyramidal. The central valley is small and deep and is completely surrounded by cusps and crests. An antero-lingual expansion is clearly present at the base of the protocone, such that the anterior wall of the cusp is concave. The entire surface of the crown is finely wrinkled. The external cingulum is weak and is almost absent round the rest of the tooth.

Discussion. The morphology of the M1/ presents noticeable differences from those of other species of the genus *Agriotherium*, in particular the shape of the protocone and the central valley of the molar. In *Agriotherium insigne* (Viret, 1939), *Agriotherium roblesi* (Morales and Aguirre, 1976), and *Agriotherium intermedium* from China (Qiu and Schmidt-Kittler, 1983) or the various species of the genus from the Siwaliks (Lydekker, 1884; Matthew, 1929) and North America (Frick, 1926), the protocone is doubled, forming a crest that is parallel to the paracone such that the central valley is somewhat elongated and relatively shallow. This morphology is not only common in *Agriotherium*, but is also generally the case in primitive and extant ursids. In *Agriotherium africanum* this tooth has the basic quadricuspidate pattern, but Hendey (1980) did not mention the differences. Nevertheless, in every specimen figured by this author, as in the case of the fragmentary maxilla L55012 (Hendey, 1980, Fig. 6A) the protocone is disposed in an oblique position with respect to the anterior-posterior axis of the tooth, just as in the Kenyan material, with the exception that the cuspid is doubled and has the typical crest-shaped morphology. Other M1/s from Langebaanweg, such as the one figured by Hendey (1972) or the maxilla fragment L45137 (Hendey, 1980, Fig. 7) show the typical disposition of the protocone almost parallel to the antero-posterior axis.

At Mabaget, we thus have an M1/ which does not fall within the range of variation of the known species of *Agriotherium*. It could be that the M1/ of this genus was polymorphic as in many ursids, or it could be that the protocone is corroded and lacks part of the anterior crest. The latter is not impossible, considering the slight corrosion that has affected this part of the tooth. Furthermore, it is also notable in this tooth that all the cusps are high including the protocone and metaconule.

The P4/ from Baringo stands out by its small size, only *A. intermedium* is somewhat smaller. This difference in size is most obvious with respect to the known P4/s of *A. africanum*, which are among the largest known in the various species of the genus. The holotype of the species *A. africanum* (PQ L2045) is morphologically different, in particular by the greater development of the pro-

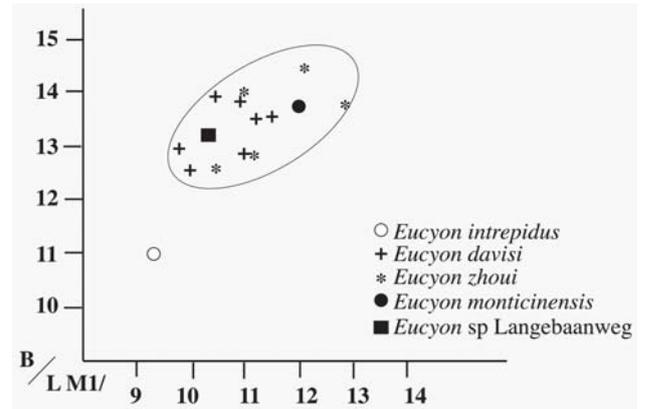


Figure 8.- Plot of length/width relationship of M1/ of *Eucyon* species.

tocone cusplets, which are subdivided. Much closer is the P4/ in PQ L46074 which possesses a simple protocone, although it is higher and more extended.

Petter *et al.* (1994) described a P4/ and an m/2 from the late Miocene of Nkondo (Uganda) as *Agriotherium africanum*. According to these authors the regression of the metaconid of the m/2 differentiated it from the known species of *Agriotherium*, except for *A. africanum*, which showed two very different morphologies (Hendey, 1980, Fig. 11 A and B). One morphotype is common in other species of *Agriotherium*, such as *A. insigne* from Montpellier (Viret, 1939) and consists of a quadricuspidate pattern with the protoconid and metaconid of similar width, with the internal cristids contacting each other to enclose an elevated valley anteriorly, the talonid formed of a strong hypoconid, an entoconid and an entoconulid. The second morphotype was interpreted by Hendey (1980) and Petter *et al.* (1994) as being characterised by regression of the metaconid. In this form the trigonid is formed of a protoconid and a residual antero-lingual cuspid, whereas the talonid does not differ from the more general morphology. In our opinion this interpretation poses a serious problem, which is the position of the internal cristid of the protoconid, which in the second morphotype is oblique and contacts the postero-lingual cuspid, which could be better interpreted as a displacement of the metaconid into the position of the entoconid, which is either inexistant or would be represented by the small cuspid which is located postero-lingually.

Whatever the case, it is not the morphology seen in the m/2 from Nkondo, which in this tooth is clearly visible, as the internal cristid of the protoconid is perpendicular to the antero-posterior axis of the tooth and contacts the metaconid, which remains in its habitual position, even though it is smaller. The talonid of this m/2 is dominated by a strong hypoconid, whereas the entoconid is very reduced and peripheral.

In sum, the m/2 from Nkondo cannot be attributed to either of the two morphotypes of *A. africanum* described from Langebaanweg, being in certain features intermediate between the two, that is to say that it conserves the primitive disposition of the cuspid, but the width of the internal cuspid is clearly reduced. Howe-

ver, it also differs from these two morphotypes by the predominance of the hypoconid in the talonid and its more central position, in consequence of which the talonid valley is reduced. This is to say that there is a tendency for a more sectorial dentition, which agrees with the morphology of the M1/ from Kenya, which corresponds to an m/1 in which the talonid is dominated by a strong hypoconid.

The same can be said of the P4/ (BAR 465'02) which corresponds to none of the P4/s described from Langebaanweg (Wolf *et al.*, 1973), in particular the holotype of the species, which represents a more hypocarnivorous tendency, contrary to what can be interpreted in the Kenyan teeth.

To call these forms from Kenya and Uganda *Agriotherium africanum* does not seem reasonable, given that they do not correspond to the holotype of the species, nor with the other morphotypes observed at Langebaanweg (Hendey, 1977). In addition, the two morphotypes from Langebaanweg could well belong to separate species. For these reasons were erect a new species, *Agriotherium aecuatorialis* for the dental remains from Kenya and Uganda.

Finally, we note that the m/2 from Sahabi described by Howell (1982, 1987) corresponds to the general morphology of the genus. Thus there was a diversity of morphologies in the latest Miocene / early Pliocene of Sub-Saharan Africa, which is not encountered in the rest of the range of the genus.

Family Mustelidae Gray, 1821

Subfamily Guloninae Gray, 1825

Genus *Plesiogulo* Zdansky, 1924

Plesiogulo praecocidens Kurten, 1970

Material. KNM LU 227, right P4/ (2/218, Cheboit, Lukeino Fm); BAR 1893'00, left M1/ (Kapcheberek, Lukeino Fm).

Age. Late Miocene, 6.1 - 5.7 Ma.

Description. BAR 1893'00 (Figs. 6F and 7E) is a left M1/ (L = 14.6 mm, which probably corresponds to the maximum length of the tooth). Only the lingual half of the crown is preserved which is well preserved, in which can be seen a strong protocone in the shape of a dune which occupies almost the entire lingual area, slightly displaced towards the anterior border of the tooth. A well developed cingulum encircles the preserved margin of the tooth.

KNM LU 227 (Figs. 6E and 7D) a right P4/ (L = 16.9 mm, B = 10.9 mm) is a robust tooth comprised of a voluminous conical paracone, and a short, robust metastyle. The protocone is located in front of the paracone and is moderately developed.

Discussion. In size, these two teeth correspond to the smallest species of the genus *Plesiogulo* (Zdansky, 1924). In particular it is close to *P. praecocidens* Kur-

ten (1970) with which it shares the rounded morphology of the lingual wall of the protocone of P4/ and the moderate size of the protocone of the P4/. The morphology of the M1/ is unknown in *P. monspessulanus* Viret (1939) from Langebaanweg (Hendey, 1978), but this was a larger species. The M1/ of *P. monspessulanus* however, is known from the type locality Montpellier, France (Viret, 1939). Alcalá *et al.*, (1994) attributed an M1/ from the late Miocene of Las Casiones, Teruel to this species. This tooth is clearly different from that assigned to *P. praecocidens* from Africa, by the doubling of the protocone, its very anterior position, with development of a wide posterior platform, and the less rounded lingual wall. Nevertheless, we note that there is a certain variability in the morphology of this tooth (Zdansky, 1924; Harrison, 1981).

Subfamily Lutrinae Bonaparte, 1838

Tribe Lutrini Bonaparte, 1838

Genus *Torolutra* Petter, Pickford and Howell, 1991

Torolutra ougandensis Petter. Pickford and Howell, 1991

Material. BAR 534'99, right p/4 (Kapcheberek, Lukeino Fm); BAR 348'00, right m/1 (Kapcheberek, Lukeino Fm); BAR 270'03, left P4/ (Kapcheberek, Lukeino Fm).

Age. Late Miocene, 5.7 Ma.

Description: BAR 270'03 (Figs. 6J and 9C) left P4/ (L = 13.8 mm, B = 11.2 mm) has a paracone of moderate size, forming a continuous blade with the metastyle, and the parastyle is small. The protocone and hypocone are crestiform, the protocone being taller than the hypocone. Between the two cusps there is a small protoconule. These three cusps form a talon continuous from the anterior border to the middle of the base of the metastyle. This talon is clearly separated by a parallel valley from the rest of the tooth. There is a basal cingulum which almost entirely surrounds the tooth, which is stronger at the base of the protocone and protoconule, with a sharp aspect.

BAR 348'00 (Figs. 6K and 9B) is a right m/1 (L = 15.8 mm, B = 7 mm). The trigonid is relatively long compared to the talonid. The low pyramidal paraconid is well separated from the protoconid and metaconid. The metaconid is strong and is displaced lingually, sensibly increasing the width of the trigonid valley. The talonid is eroded on its labial border which may have been occupied by a strong, wide and elongated hypoconid. There is no sign of an entoconid and the valley is inclined towards the lingual side. There are indications of an almost continuous basal cingulum completely surrounding the tooth.

BAR 534'99 (Fig. 9A) is a right p/4 (L = 9.6 mm, B = 6.5 mm). It is a short premolar, which is quite enlarged in its posterior half. The principal cusp is high and sectorial, and has a postero-lingual crest which descends

to the cingulum, and a postero-labial one which joins the high and sharp postero-labial cusp, with a sharp posterior crest which also joins the cingulum, forming a kind of posterior wall. The cingulum is strong and encircles the tooth.

Discussion. The dimensions and morphology of these specimens reveal with little doubt that they are closely related to the otter from the Pliocene of Lake Albert described by Petter *et al.*, 1991, as *Torolutra ougandensis*. There are differences in the talonid of the m/1, which is less robust in the Kenyan form, but they are close enough to be classified in the same species. The new P4/ from Lukeino appears to be extremely close in size and morphology to *Vishnuonyx angolensis* Werdelin (2003) from Lothagam.

Tribe Enhydrini Gray, 1825

Diagnosis. Lutrinae with a tendency to mastoidization of the dentition. P4/ with hypocone and a tendency to be molarized.

Genus *Sivaonyx* Pilgrim, 1931

Type species: *Lutra bathygnatha* Lydekker, 1884.

Other species: *S. iluecai* (Crusafont and Golpe, 1962), *S. africana* Stromer, 1931, *S. campanii* (Meneghini, 1863)

Diagnosis. Enhydrini with P4/ with a continuous cutting blade, with no incision separating the paracone and metastyle. Protocone moderate, hypocone moderate, well separated from the protocone and the paracone-metastyle. M1/ somewhat wider than long, with peripheral cusplets and a wide, flat central valley. The m/1 has a relatively long trigonid, and an unmolarised talonid with a wide valley.

Sivaonyx africana (Stromer, 1931)

Emended diagnosis. *Sivaonyx* the size of *S. campanii*. P4/ with relatively strong parastyle. The lingual cuspid between the protocone and hypocone is weak, not blocking off the valley between the two, the cusps equal in

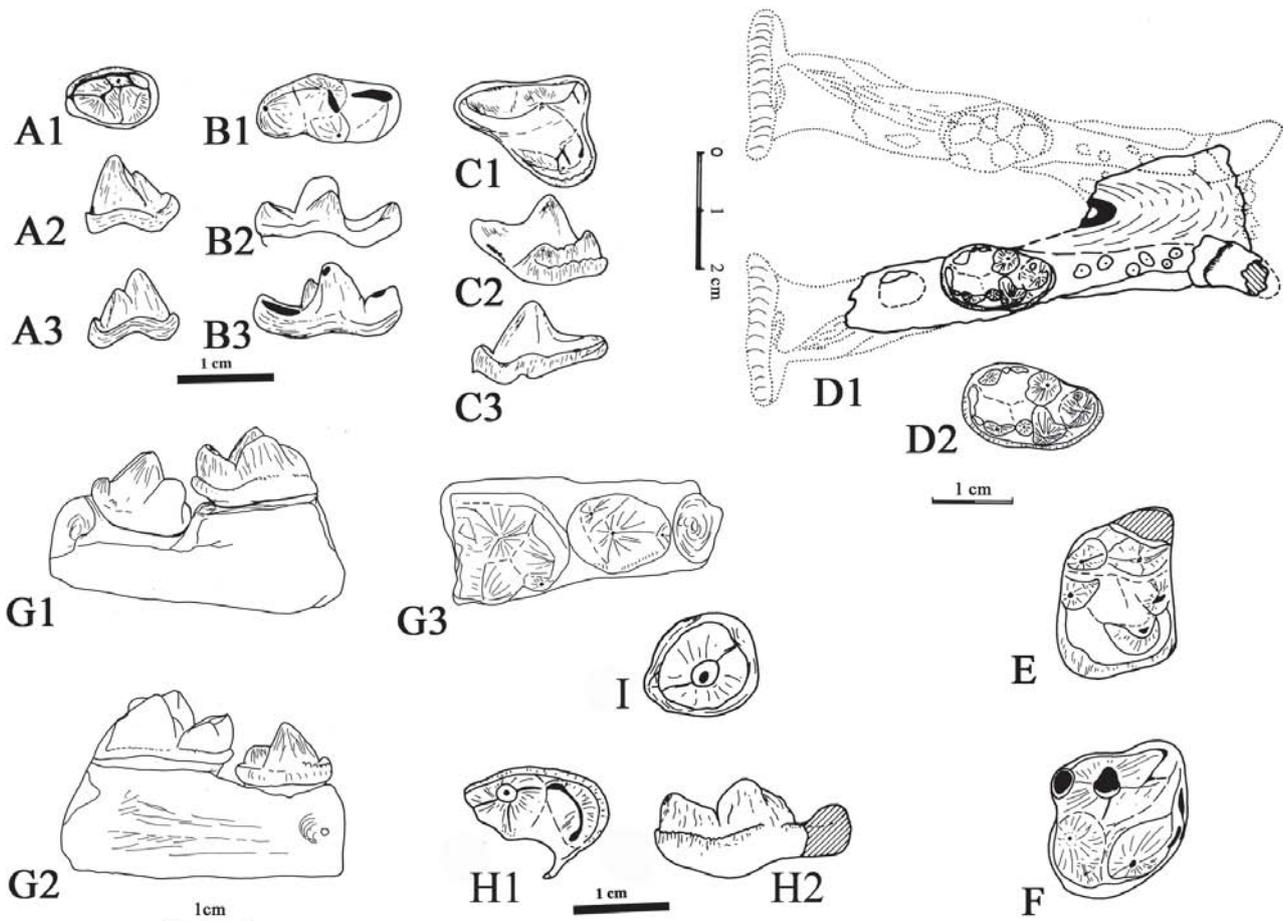


Figure 9.- A) *Torolutra ougandensis* from Kapcheberek, Lukeino Fm. BAR 534'99 right p/4: occlusal view (A1), lingual view (A2), labial view (A3), **B)** *Torolutra ougandensis* from Kapcheberek, Lukeino Fm. BAR 348'00, right m/1: occlusal view (B1), lingual view (B2), labial view (B3), **C)** *Torolutra ougandensis* from Kapcheberek, Lukeino Fm. BAR 270'03, left P4/: occlusal view (C1), lingual view (C2), labial view (C3), **D)** *Sivaonyx africana* from Kapcheberek, Lukeino Fm. KNM LU 337 right mandible occlusal view (D1), m/1 in occlusal view (D2), **E)** *Sivaonyx africana* from Kapcheberek, Lukeino Fm. BAR 1082'01, right M1/ in occlusal view, **F)** *Sivaonyx africana* from Kapcheberek, Lukeino Fm. BAR 1720'00, left P4/ in occlusal view, **G)** *Enhydrionodon* sp. indet. from Sagatia, Magabet Fm. BAR 720'03, left mandible with p/4 and broken m/1: lingual view (G1), labial view (G2), occlusal view (G3), **H)** *Enhydrionodon* sp. indet. from Mosionin, Magabet Fm. BAR 416'00, broken left m/1: occlusal view (H1), labial view (H2), **I)** *Enhydrionodon* sp. indet. from Sagatia, Magabet Fm. BAR 1231'01, P3/ in occlusal view.

size to those of the trigonid of the m/1, tending to be massive and rounded. M1/ with metacone small with respect to the paracone, and internally displaced. The protocone is strong and in an anterior position, and the cingulum is very strong and elevated. The m/1 has a relatively long trigonid and the talonid is not molarized.

Differential diagnosis. *S. africana* differs from *S. Iluecai* and *S. bathygnathus* by its greater size and by the cusps of P4/ and m/1 being more massive and rounded. In addition, the P4/ has a noticeably stronger parastyle. It differs from *S. campanii* by the better development of the parastyle of the P4/ and by the weaker development of the lingual cusp located between the hypocone and the protocone. Thus the M1/s are very different, in particular from those of *S. campanii*, by the smaller metacone and protocone.

Material. BAR 1720'00, left P4/; BAR 1082'01, right M1/; BAR 1894'00, lower canine (Kapcheberek, Lukeino Fm); KNM LU 337, right mandible with m/1; KNM LU 338, symphysis of mandible; KNM LU 614, canine (2/225, Kapcheberek, Lukeino Fm).

Age. Late Miocene to Early Pliocene, 5.7 to 4.5 Ma.

Description. BAR 1720'00 is a left P4/ (Figs. 6G and 9F) (L = 14.8 mm, B = 15 mm). The occlusal outline is almost square. The parastyle is moderately strong. The paracone is very voluminous, without any incision separating it from the metastyle, which is small. The protocone is strong, rounded and has a small cusplet backing onto its base. The hypoconid is somewhat smaller than the protocone, well separated from both the protocone and the paracone-metastyle. The cingulum is strong and completely surrounds the tooth.

BAR 1082'01, a right M1/ (Figs. 6H and 9E) (L = 12.3 mm, B = ca 18 mm) has a small break in the area of the parastyle, which could have been quite well developed. The paracone is better developed than the metacone, which is displaced postero-lingually. There is a strong paraconule, almost fused to the protocone, the two cusps being close to the anterior border of the tooth. Almost fused to the metacone is a metaconule which is rounded and positioned very posteriorly. Between all these cusps there is a wide, almost flat valley. The tooth is surrounded by a cingulum which is strong lingually, in particular postero-lingually where it rises to form a hypocone.

BAR 1894'00 is a lower canine without roots (L = 12.2 mm, B = 9.6 mm). The basal cingulum is smooth, with a weak lateral crest. It has a slightly swollen base standing out near the cervix.

KNM LU 337 (Figs. 6I and 9D) a right mandibular ramus containing the m/1 and alveolus for m/2 is from

locality 2/225, Kapcheberek. KNM LU 338, a symphysis with damaged right canine and roots of the left canine, incisors and right p/2-p/4 was found close to the preceding specimen and is likely from the same individual. Nearby was found KNM LU 614, an isolated canine tip.

The lower first molar (L = 17.6 mm, B = 10.5 mm) is in excellent condition and differs from that of *Aonyx capensis* in several respects. It is a larger tooth and possesses a larger talonid basin which is more expanded lingually. The paraconid is situated closer to the labial edge of the jaw so that the carnassial cusps lie at about 25° to the axis of the jaw (from m/1 to canine). This compares with an angle of about 35° in *A. capensis*. The talonid basin of the Lukeino specimen is characterised by a beaded edge and the labial cingulum is well developed, running from the mesial edge of the tooth backwards to the talonid where it merges with the raised lip of the talonid basin. There is an accessory cusplet behind the protoconid as in some specimens of *A. capensis*, in which it is usually poorly developed.

The second lower molar is missing from its alveolus but it was obviously a single rooted tooth and occupied a similar position on the lingual side of the jaw behind m/1 as in *A. capensis*. The occlusal surface of the tooth would have dipped towards the m/1 as in the clawless otter. The p/4 was a two-rooted tooth, but was somewhat transversely oriented in the jaw. This arrangement is similar to that seen in the extant forms of *Aonyx*, but the rotation of the tooth is more marked in the Lukeino specimen and indicates a greater shortening of the mandible than occurs in *Aonyx*. The canine is a large, robust, single-rooted tooth, similar to its counterpart in *Aonyx capensis*. The symphysis from Lukeino is much more massive than that of *Aonyx*, and it reaches backwards to the anterior end of p/3. The fossa for the insertion of the geniohyoid muscle is deep and more strongly developed than it is in *A. capensis*. The incisors, only the roots of which are preserved, were arranged in a pattern like that seen in *Aonyx*, in which the incisors have the appearance of being crowded together into a space which is too small for them. Thus the second incisor lies slightly behind the line between the first and third incisors and its crown overlaps both of them, forming an M-shaped battery of teeth. The canines are 12 mm apart compared with 7.2 mm measured on an extant specimen of *A. capensis*. The i/1 was tiny, but i/2 and i/3 were larger, as in the extant clawless otter.

KNM LU 614 is an isolated canine referred to this species. It is probably an upper canine and possesses a lingual cingulum. It is a robust and stout peg. Measurements of C1/ are L = 9.6 mm, B = 7.7 mm.

Discussion. The distinction between *Enhyriodon* and *Sivaonyx* has probably been the main difficulty experienced in the understanding of the systematics of this tribe. In effect, *Enhyriodon sivalensis* Falconer 1868, was

described on the basis of skull material from the Siwalik Hills, with no precise locality data or age (Pilgrim, 1932). Pilgrim (1931), in his revision of the Pontian carnivores (Late Miocene) of Europe, defined the second genus, *Sivaonyx*, nominating *Lutra bathygnatha*, Lydekker (1884), as the type species, with characteristics that are close to those of *Enhydriodon*, but which was apparently more primitive. The same author specifically mentioned that the definition of the new genus was based fundamentally on the P4/ from Hasnot, and which he attributed to this genus. The differences between the P4/s of *S. bathygnathus* and *Enhydriodon falconeri*, a species defined in the same publication are clear (in particular for the distinct development of the hypocone and the morphology of the metastyle), and also justify in our opinion the generic separation of the two.

The differences between *E. falconeri* and *E. sivalensis* are quite marked, in particular the different development of the lingual region of the P4/. Thus *E. sivalensis* shows hyper-development of the protocone and hypocone, exaggerating the width of the tooth compared to its length (Fig. 10). It is possible that *E. falconeri* represents a species that is more primitive than the type of the genus.

The difficulties experienced in distinguishing these two genera are well reflected in the fossils attributed to this group in Spain (lower dentition to *Enhydriodon*, upper to *Sivaonyx*); thus Villalta and Crusafont (1945) assigned a mandible from Los Aljezares (Late Miocene, Teruel) to a new species of the genus *Enhydriodon*, named *E. lluecai*. Crusafont and Golpe (1962) attributed to this species an m/1 from Los Mansuetos (MN 12, Teruel), despite the fact that a P4/ from Rambla de Valdecebro II (Late Miocene of Teruel) was attributed to a new species of *Sivaonyx*, *S. lehmani*. Later Alcalá (1994) described another P4/ from Conclud (MN12, Teruel), and synonymised the two species, *Sivaonyx lluecai* having priority. The conclusion is that there are no clear criteria by which to distinguish the lower dentitions of the two genera, but this problem was already resolved by Pilgrim (1931, 1932) who based the generic diagnosis on the upper dentition.

This species, as was noted by Willemsen (1992), is closely related to the Italian otters from Baccinello, classed in the genus *Paludolutra* (Hürzeler, 1987; Hürzeler and Engesser, 1976). The type species is *Lutra campanii* Meneghini (1863), which was included in the genus *Enhydriodon* by Forsyth-Major (1873), a decision that was followed by most subsequent authors. Willemsen (1992) used *Paludolutra* as a subgenus of *Enhydriodon*, in an evolutionary lineage which included the Spanish form known as *Enhydriodon lluecai*, to *Enhydriodon (Paludolutra) maremmana* and to *Enhydriodon (Paludolutra) campanii*, whereas *Sivaonyx bathygnathus*, which he considered to be close to *E. lluecai*, is located in an uncertain position.

However, on the basis of the diagnosis of Pilgrim (1931, 1932) we consider that *Paludolutra* should be treated as a synonym of *Sivaonyx*.

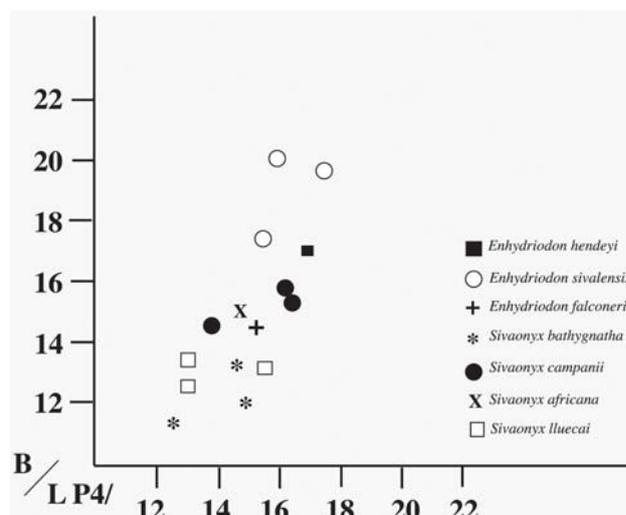


Figure 10.- Plot of length/width relationship of P4/ of *Enhydriodon* and *Sivaonyx* species.

To this genus we attribute the Kenyan form described above which we classify as *S. africana* Stromer (1931). Unfortunately we do not know the morphology of the P4/ of the Kleinzee otter, the type locality of the species *E. africana*, but the morphology of the M1/ and m/1 are sufficiently compatible to justify this proposition, even though they are different in size.

Genus *Enhydriodon* Falconer, 1868
Enhydriodon sp.

Material. BAR 1231'01, left P3/ (Sagatia, Magabet Fm); BAR 416'00, left m/1 (Mosionin, Mabaget Fm), BAR 720'03 fragment of left mandible (Sagatia, Mabaget Fm).

Description. BAR 1231'01 (Fig. 9I) is a left P3/ (L = 10 mm; B = 8.5 mm). It is almost circular in occlusal outline, with an incisiform aspect. It has a conical main cusp, somewhat bunodont, with a smooth, low posterior crest, a wide anterior platform, and the tooth is completely surrounded by a basal cingulum.

BAR 720'03 (Fig. 9G) is a fragment of left mandible with the incompletely erupted p/4 and the trigonid of the m/1. The trigonid of m/1 is wide with low pyramidal cusps. The paraconid is in an anterior position and has a small paraconulid close to it. The protoconid is the largest of the three cusps, and has a small but distinct protoconulid attached to it posteriorly. The metaconid is higher than the paraconid and is pyramidal. The trigonid valley is wide and completely surrounded by the main cusps. The p/4 is robust and in occlusal view is subtriangular with rounded corners. The main cusp is pyramidal and there is a small anterior cusplet, which emerges from the cingulum, and a posterior one which is high and displaced labially. There is a wide basal platform disto-lingually. The tooth possesses a strong basal cingulum.

BAR 416'00, is a left m/1 (Fig. 9H). Only the trigonid is preserved. Outstanding is the strength of the protoconid, which is low, with swollen posterior and interior crests. The paraconid is located in a very anterior position, and is separated from the protoconid by a wide valley. The labial cingulum is strongly developed. The trigonid measures ca 14 mm long and ca 12 mm wide.

Discussion. The three specimens from the Mabaget Fm are from an otter species that is appreciably larger (11%) than the Lukeino *Sivaonyx africana*.

From Uganda, there are two otter specimens from the Western Rift deposits which are slightly larger than the material from Mabaget being 13% larger than the Lukeino *Sivaonyx africana*. NK 1988'89, the talonid of a left m/1 of a large otter from Nkondo is 14.5 mm wide and was attributed to *Enhydriodon* sp. by Petter *et al.* (1991). From Kazinga, there is a complete, un-numbered left m/1, now housed in the Uganda Museum, Kampala, which measures L = 25.9 mm, B = 15.5 mm, the trigonid of which measures ca 15.9 mm long by ca 13.5 mm wide. This compares with *Sivaonyx africana* from Lukeino, KNM LU 337 (L = 17.6, B = 10.5) and from Klein Zee (L = 22, B = 12+) (Stromer, 1931). The specimens from Mabaget and Uganda are closer to *Enhydriodon* species, not only in size but also in morphology.

Hendey (1978b) referred several specimens from Langebaanweg to *Enhydriodon*. In our opinion this material cannot be ascribed to the species *S. africana* nor to the same species as the Mabaget and Uganda otters. We observe in the figures and descriptions published by the South African author (Hendey, 1978b), that the m/1 is constructed in a completely different way from the Kleinzee specimen which is the holotype of the *S. africana*, in particular by the huge and bunodont cuspids as well as the better development of the cingulum. Overall the Langebaanweg m/1 approaches in several features the morphology seen in *Enhydra lutris*. Certainly, the morphology of the p/4s is similar in the two South African localities, except for the size of the posterior accessory cusplet. No other comparison can be made between the species from Kleinzee and Langebaanweg. In its shape the P4/ attributed by Hendey (1978b) to *Enhydriodon africanus* is very different from that described from Kenya and of those attributed to other species of the genus *Sivaonyx*. In effect the P4/ from Langebaanweg possesses a clear notch between the paracone and metastyle, as in *Enhydriodon sivalensis* but not in *Sivaonyx* whereas the voluminous hypocone and the size of the protocone are also characteristic of *E. sivalensis*. This P4/ accords with the ones described by Repenning (1976) as *Enhydriodon* cf. *lluecai* and *Enhydriodon* sp., in particular the latter - today classified in the genus *Enhydritherium* (Berta and Morgan, 1985; Lambert, 1997) as *Enhydritherium terranova* and *Enhydritherium* sp., but differ from them by the absence of a parastyle in these North American forms, and related to this, the shortening of the tooth with respect to its width.

In conclusion, the material described by Hendey (1978b) cannot be classed either as *Sivaonyx africana* Stromer (1931), or *Enhydritherium* (which thus also excludes it from the Spanish species *S. lluecai*). The P4/ from Langebaanweg is closer in morphology to *Enhydriodon sivalensis* (Matthew, 1929; Verma and Gupta, 1992), but not the m/1 which is certainly distinct from those known in *Enhydriodon*, and for this reason we propose the name *Enhydriodon hendeyi* nov. sp. for the specimens from Langebaanweg, the holotype of which is PQ-L 50000 (Hendey, 1978b, Fig. 9A).

Enhydriodon hendeyi nov. sp.

Holotype. PQ-L 50000 (Fig. 9L) left mandible with p/4-m/2 (Hendey, 1978b, Fig. 9A).

Referred material. PQ-L 50000, isolated left P4/ (possibly associated with the holotype (Hendey, 1978b, Fig. 10)); PQ-L 9138, right mandible fragment with broken p/4; PQ-L 41523, left femur (Hendey, 1978b, figs. 9B and 11A).

Type locality. Langebaanweg, South Africa.

Age. Lower Pliocene.

Derivatio nominis. Named for Dr Q.B. Hendey who described the first known specimens of this species.

Diagnosis: *Enhydriodon* of large size, dentition bunodont, m/1 with talonid occupied by an enormous hypoconid surrounded by a hyper-developed entoconid. P4/ with well developed cingulum, strong parastyle and relatively poorly developed hypocone.

Enhydriodon hendeyi has dental morphology (Fig. 6L), such as mastoidization of the cusps, similar to those of *Enhydra lutris* (Linnaeus, 1758) but it is unlikely that the two are closely related phylogenetically in view of the quite primitive morphology of the dentition of *Enhydritherium*, a genus which, by the shortening of the P4/ and m/1, may be considered a close relative of extant *Enhydra*.

General Discussion

With the recent publication on the carnivores of Lothagam (Werdelin, 2003) our knowledge of this group of mammals has increased substantially. The earlier part of the Lothagam succession covers a temporal span immediately prior to that represented at Lukeino, the richest fossil levels of the Lower Nawata Fm being dated between 7.4 to 6.5 Ma, whereas the Upper Nawata Fm is not well dated but is probably Late Miocene (McDougall and Feibel, 2003).

Important changes between the carnivore assemblages of Lothagam and Lukeino are evident. The most obvious absences from Lukeino are the Amphicyonidae (certainly a relict group of carnivores in Africa, which

disappeared in Europe about 9 Ma) and the primitive hyaenids of the *Ictitherium* type. In contrast, at Lukeino there appear relatively modern forms that have not been reported from Lothagam, such as the first canids, or ?*Megantereon obscura* and *Plesiogulo praecoci-dens*, and even later in the Mabaget fauna of *Agriotherium* and *Civettictis* (Table II).

In the two localities there are certainly some shared taxa, such as *Torolutra*, *Ikelohyaena*, *Dinofelis*, and *Megaviverra* and probably other felids and viverrids will be found common to the two localities. However, the shared elements of the carnivore fauna do not negate the major change that occurred between these two Kenyan localities. It is important to highlight the temporal coincidence between this change and that which occurred in the Late Miocene faunas of the Mediterranean area (Made *et al.*, 2005), in which several of the same taxa were implicated, including *Plesiogulo*, *Agriotherium*, *Eucyon* and *Dinofelis*.

Late Miocene and early Pliocene East African carnivores are in general poorly known. Patterson *et al.* (1970) recorded an indeterminate hyaenid from Lothagam I dated about 7 Ma and *Hyaena* sp. from Kanapoi dated about 4.2 Ma. *Percrocuta*, *Hyaena*, and *Crocota* are recorded from Omo Group formations in Southern Ethiopia and the Hadar area, northeastern Ethiopia (Howell and Petter, 1973, 1976a, b, 1979, 1985) and both *Hyaena* and *Crocota* are known from faunal zones 1, 2 and 3 at East Turkana and other sites in northern Kenya (Werdelin, 1999a, b; Werdelin and Lewis, 1997, 2000; Werdelin and Solounias, 1991; Werdelin and Tur-

ner, 1996; Werdelin *et al.*, 1994). From Uganda, (Petter, 1994; Petter *et al.*, 1991, 1994) a restricted but interesting carnivore fauna from Nkondo and similar aged deposits of the Western Rift Valley was described, which included the ursid *Agriotherium* and two otters *Torolutra* and *Enhydriodon*. But most of the East African records are appreciably younger than those from the Mabaget and Lukeino Fms described here. Carnivores from earlier in the upper Miocene are known at Chorora (Ethiopia) (Geraads *et al.* 2002), Samburu Hills (Narurungule Fm) and Nakali (both sites in Kenya), but they are generally poorly known save for *Hyperhyaena leakeyi* from Nakali (Aguirre and Leakey, 1974).

In North Africa there is also a somewhat limited understanding of the carnivores of this time period, the main localities that have yielded material being Menacer (Algeria) (Petter and Thomas, 1986), Sahabi (Libya) (Howell, 1982, 1987) and Wadi Natrun (Egypt) (Stromer, 1921). The Late Miocene carnivores from the Beglia Fm (Vallesian equivalent of Tunisia) have been the subject of debate (Kurten, 1978; Chen and Schmidt-Kittler, 1983) but the fauna as a whole appears to have no 'modern' lineages, the viverrids, hyaenids, felids and amphicyonids all belonging to extinct genera. Younger material has been described from the Late Pliocene of Ain Brimba (Tunisia) (Arambourg, 1979; Van den Brink, 1981) and Ahl-al-Oughlam (Morocco) (Geraads, 1997).

In contrast, the carnivores from the Early Pliocene of South Africa (Kleinsee and Langebaanweg) are much better known (Stromer, 1931; Hendey, 1970,

Taxon	Localities
<i>Felis</i> small sp.	Langebaanweg, Beni Mellal, Laetoli, Hadar, Lukeino, Ahl-al-Oughlam, Eurasia, North America
<i>Metailurus</i> sp.	Lothagam, Eurasia
<i>Dinofelis</i>	Hadar, Lothagam, Langebaanweg, Bolt's Farm, Makapansgat, Ahl -al-Oughlam, Lukeino, Matabaietu, Kossom Bougouda, Eurasia, North America
<i>Megantereon</i>	South Turkwell, Matabaietu, Hadar, Langebaanweg, Lukeino, Eurasia, North America
<i>Genetta</i>	Beni Mellal, Ahl -al-Oughlam, Lothagam, Lukeino, Langebaanweg, Kleinsee, Eurasia
<i>Civettictis</i>	Lothagam, South Turkwell, Mabaget, Hadar
<i>Ichneumia</i>	Ahl-al-Oughlam, Lukeino
<i>Megaviverra</i>	Laetoli, Lukeino, Omo, Langebaanweg, Ahl-al-Oughlam, Eurasia
<i>Nandinia</i>	Lukeino
<i>Ikelohyaena</i>	Lothagam, Langebaanweg, Lukeino
<i>Hyanictitherium</i>	Lothagam, Langebaanweg, Kleinsee, Eurasia
<i>Hyanictis</i>	Lothagam, Langebaanweg, Eurasia
<i>Eucyon</i>	Lukeino, Eurasia, North America
<i>Agriotherium</i>	Sahabi, Mabaget, Sinda -Mohari, Langebaanweg, Eurasia, North America
<i>Plesiogulo</i>	Langebaanweg, Lukeino, Eurasia, North America
<i>Torolutra</i>	Nyaburogo, Nkondo, Omo Brown Sands, Lukeino, Eurasia
<i>Sivaonyx</i>	Nkondo, Kazinga, Lukeino, Kleinsee, Eurasia
<i>Enhydriodon</i>	Nkondo, Kazinga, Mabaget, Omo, Langebaanweg, Eurasia

Table II.- Distribution in Africa, Eurasia and North America of the carnivore genera from Lukeino (Late Miocene) and Mabaget (Basal Pliocene), Kenya.

1972, 1974, 1978a, b) than those of equivalent age in East Africa as are the younger species from the karst deposits of Gauteng Province (South Africa) (Ewer, 1954, 1955a-c, 1956a-d, 1962, 1967; Toerien, 1952, 1955; Turner, 1985, 1986a-c, 1987a-b, 1988, 1990a-b, 1997; Turner and Anton, 1998).

Conclusions

The present publication, even though it deals with a limited sample of carnivore fossils, helps to fill a great gap in our knowledge of late Miocene and early Pliocene carnivores of tropical Africa, and it throws light on the evolution of carnivores from the predominantly archaic faunas of the late Middle Miocene and basal Late Miocene on the one hand, and the more modern ones that occurred from late Pliocene times onwards, on the other. Not unexpectedly, the Lukeino and Mabaget carnivore faunas possess some taxa with a 'modern' aspect (felids, canids, viverrids) but retain some relatively 'archaic' forms (ursids, some of the felids, hyaenids, mustelids).

Interestingly, some of the Lukeino and Mabaget carnivores belonged to extremely widespread lineages, including *Agriotherium*, *Plesiogulo*, *Eucyon*, *Dinofelis*, *Megantereon*, and *Sivaonyx*. This feature of the assemblages permits intercontinental correlations to be made between Africa (Faunal Set P VII), Europe (MN 13), Asia (NMU 11 of China, Qiu *et al.*, 1999) and even North America (Hemphillian, Berta and Morgan, 1985). Strangely, all these lineages except the canids became extinct soon after evolving and dispersing so widely over the surface of the Earth.

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References

- Aguirre, E. and Leakey, P. (1974): Nakali: nueva fauna de *Hipparion* del Rift Valley de Kenya. *Estudios Geológicos*, 30: 219-227.
- Alcalá, L. (1994): *Macromamíferos neógenos de la fosa de Alfambra-Teruel*. Instituto de Estudios Turolenses-CSIC, 1-554.
- Alcalá, L., Montoya, P. and Morales, J. (1994): New large mustelid from the Late Miocene of the Teruel Basin (Spain). *Comptes Rendus de l'Académie des Sciences de Paris*, 319: 1093-1100.
- Arambourg, C. (1979): Vertébrés villafranchiens d'Afrique du Nord (Artiodactyles, Carnivores, Primates, Reptiles, Oiseaux). *Fondation Singer-Polignac*, Paris, 1-141.
- Berta, A. and Galiano, H. (1983): *Megantereon hesperus* from the Late Hemphillian of Florida with remarks on the phylogenetic relationships of machairodonts (Mammalia, Felidae, Machairodontinae). *Journal of Paleontology*, 57: 892-899.
- Berta, A. and Morgan, G.S. (1985): A new sea otter (Carnivora: Mustelidae) from the Late Miocene and early Pliocene (Hemphillian) of North America. *Journal of Paleontology*, 59: 809-819.
- Chen Guanfang and Schmidt-Kittler, N. (1983): The deciduous dentition of *Percrocuta Kretzoi* and a diphyletic origin of the hyaenas (Carnivora, Mammalia). *Paläontologische Zeitschrift*, 57: 159-169.
- Crusafont, M. and Golpe, J.M. (1962): Nuevos hallazgos de lútridos aonicooides (*Sivaonyx*, *Enhydriodon*) en el Pikermiense español (Cuenca de Teruel). *Notas y Comunicaciones del Instituto Geológico y Minero de España*, 67: 5-16.
- Ewer, R.F. (1954): The fossil carnivores of the Transvaal caves: The Hyaenidae of Kromdraai. *Proceeding of the Zoological Society of London*, 124: 565-585.
- Ewer, R.F. (1955a): The fossil carnivores of the Transvaal caves: The Hyaenidae other than *Lycyaena*, of Swartkrans and Sterkfontein. *Proceeding of the Zoological Society of London*, 124: 815-837.
- Ewer, R.F. (1955b): The fossil carnivores of the Transvaal caves: The Lycyaenas of Sterkfontein and Swartkrans, together with some general considerations of the Transvaal fossil hyaenids. *Proceeding of the Zoological Society of London*, 124: 839-857.
- Ewer, R.F. (1955c): The fossil carnivores of the Transvaal caves: Machairodontinae. *Proceeding of the Zoological Society of London*, 125: 587-615.
- Ewer, R.F. (1956a): The fossil carnivores of the Transvaal caves: Felinae. *Proceeding of the Zoological Society of London*, 126: 83-95.
- Ewer, R.F. (1956b): The fossil carnivores of the Transvaal caves: Canidae. *Proceeding of the Zoological Society of London*, 126: 97-119.
- Ewer, R.F. (1956c): The fossil carnivores of the Transvaal caves: two new viverrids, together with some general considerations. *Proceeding of the Zoological Society of London*, 126: 259-274.
- Ewer, R.F. (1956d): Some fossil carnivores from the Makapansgat Valley. *Palaeontologia Africana*, 4: 57-67.
- Ewer, R.F. (1962): A note on some South African fossil otters. *Research of the National Museum*, 1: 275-279.
- Ewer, R.F. (1967): The fossil hyaenids of Africa. In: *Background to Evolution in Africa* (W.W. Bishop and J. D. Clark, Eds). Chicago University Press, Chicago, 109-123.
- Forsyth-Major, C. (1873): La faune des vertébrés de Monti Bamboli (Maremmes de la Toscana), *Atti Società Italiana de Scienza Naturali*, 15: 290-303.
- Frick, C. (1926): The Hemicyoninae and an American Tertiary bear. *Bulletin of the American Museum of Natural History*, 56: 1-119.
- Geraads, D. (1997): Carnivores du Pliocène terminal de Ahl al Oughlam (Casablanca, Maroc). *Geobios*, 30: 127-164.

- Geraads, D., Alemseged, Z. and Bellon, H. (2002): The Late Miocene mammalian fauna of Chorora, Awash Basin, Ethiopia: systematics, biochronology and the ^{40}K - ^{40}Ar ages of the associated volcanics. *Tertiary Research*, 21: 113-122.
- Harrison, J.A. (1981): A Review of the Extinct Wolverine, *Plesiogulo* (Carnivora: Mustelidae), from North America. *Smithsonian Contribution to Paleobiology*, 46: 1-27.
- Harrison, J.A. (1983): The Carnivora of the Edson Local Fauna (Late Hemphillian), Kansas. *Smithsonian Contributions to Paleobiology*, 54: 1-42.
- Hendey, Q.B. (1970): A review of the geology and palaeontology of the Plio-Pleistocene deposits of Langebaanweg, Cape Province. *Annals of the South African Museum*, 56: 75-117.
- Hendey, Q.B. (1972): A Pliocene ursid from South Africa. *Annals of the South African Museum*, 59: 115-132.
- Hendey, Q.B. (1974): The late Cenozoic Carnivora of the Southwestern Cape Province. *Annals of the South African Museum*, 63: 1-369.
- Hendey, Q.B. (1977): Fossil bear from South Africa. *South African Journal of Science*, 73: 112-116.
- Hendey, Q.B. (1978a): Late Tertiary Hyaenidae from Langebaanweg, South Africa, and their relevance to the phylogeny of the family. *Annals of the South African Museum*, 76: 265-297.
- Hendey, Q.B. (1978b): Late Tertiary Mustelidae (Mammalia, Carnivora) from Langebaanweg, South Africa. *Annals of the South African Museum*, 76: 329-357.
- Hendey, Q.B. (1980): *Agriotherium* (Mammalia, Ursidae) from Langebaanweg, South Africa, and relationships of the genus. *Annals of the South African Museum*, 81: 1-109.
- Howell, F.C. (1982): Preliminary observations on Carnivora from the Sahabi Formation (Libya). *Garyounis Science Bulletin Special Issue*, 4: 49-61.
- Howell, F.C. (1987): Observations on Carnivora from the upper Neogene Sahabi Formation (Libya). In: *Neogene Paleontology and Geology of Sahabi* (N. Boaz, A.W. Gaziry, J. de Heinzelin and A. El-Arnauti, Eds). Alan Liss, New York, 153-181.
- Howell, F.C. and Petter, G. (1973): Carnivora from Omo formations, Southern Ethiopia. In: *Stratigraphy, paleoecology and evolution in the Lake Rudolf Basin*. Sept. 8-20, 1973, Wenner-Gren Foundation for Anthropological Research, Papers in Advance, 1-26.
- Howell, F.C. and Petter, G. (1976a): Carnivora from Omo Group Formations, Southern Ethiopia. In: *Earliest man and environments in the Lake Rudolf basin* (Y. Coppens, F.C. Howell, G. Isaac and R. Leakey, Eds). Chicago University Press, Chicago, 314-332.
- Howell, F.C. and Petter, G. (1976b): Indications of age from the carnivores of the Hadar Formation (Eastern Ethiopia). *Comptes Rendus de l'Académie des Sciences de Paris*, 282: 2063-2066.
- Howell, F.C. and Petter, G. (1979): Diversification et affinités des carnivores pliocènes de la groupe de l'Omo et de la Formation d'Hadar (Ethiopie). *Bulletin de la Société Géologique de France*, 21: 289-293.
- Howell, F.C. and Petter, G. (1985): Comparative observations on some middle and upper Miocene hyaenids. *Geobios*, 18: 419-476.
- Hürzeler, J. (1987): Die Lutrinen (Carnivora, Mammalia) aus dem «Grosseto-Lignit» der Toscana. *Schweizerische Paläontologische Abhandlungen*, 110: 26-48.
- Hürzeler, J. and Engesser, B. (1976): Les faunes des mammifères néogènes du bassin du Baccinello (Grosseto, Italie). *Comptes Rendus de l'Académie des Sciences de Paris*, 283: 333-336.
- Janis, C.M., Baskin, J.A., Berta, A., Flynn, J.J., Gunnell, G.F., Hunt, R.M., Martin, L.D. and Munthe, K. (1998): Carnivorous mammals. In: *Evolution of Tertiary Mammals of North America*. (C.M. Janis, K.M. Scott and L.L. Jacobs, Eds.). Cambridge University Press, 73-90.
- Kretzoi, M. (1929): Materialien zur phylogenetischen Klassifikation der Ailuroiden. *10th Congress. International of Zoology, Budapest, 1927*, 2: 1293-1355.
- Kretzoi, M. (1986): Nochmals über *Thalassictis* und *Ichthitherium*. *Zeitschrift für Geologische Wissenschaften Berlin*, 14: 367-372.
- Kretzoi, M. and Fejfar, O. (1982): Viverriden (Carnivora, Mammalia) im europäischen Altpleistozän. *Zeitschrift für Geologische Wissenschaften Berlin*, 10: 979-995.
- Kurten, B. (1970): The Neogene Wolverine *Plesiogulo* and the Origin of *Gulo* (Carnivora, Mammalia). *Acta Zoologica Fennica*, 131: 1-22.
- Kurten, B. (1978): Fossil Carnivora from the late Tertiary of Bled Douarah and Cherichera, Tunisia. *Notes Service Géologique de Tunis*, 42: 177-214.
- Lambert, W.D. (1997): The osteology and paleoecology of the giant otter *Enhydritherium terranova*. *Journal of Vertebrate Paleontology*, 17: 738-749.
- Lydekker, R. (1884): Indian Tertiary & Post-Tertiary Vertebrata. Siwaliks and Narbada Carnivora. *Memoirs of the Geological Survey of India, Palaeontologia Indica*, 2: 178-355.
- Matthew, W.E. (1929): Critical notes on Siwaliks Carnivora in the British Museum. *Bulletin of the American Museum of Natural History* 56: 466-507.
- McDougall, I. and Feibel, C.S. (2003): Numerical Age Control for the Miocene-Pliocene Succession at Lothagam, a Hominoid-bearing Sequence in the Northern Kenya Rift. In: *Lothagam: The Dawn of Humanity in Eastern Africa* (M. G. Leakey and J. M. Harris, Eds.). Columbia University Press, 43-64.
- Meneghini, G. (1863): Descrizione dei resti di due fiere trovati nelle ligniti mioceniche di Montebamboli. *Atti della Società italiana di Scienza Naturali*, 4: 17-33.
- Morales, J. (1984): Venta del Moro: su macrofauna de mamíferos, y biostratigrafía continental del Mioceno terminal mediterráneo. *Editorial de la Universidad Complutense de Madrid, Tesis Doctoral*, 15/84: 1-313
- Morales, J. and Aguirre, E. (1976): Carnívoros de Venta del Moro (Valencia). *Trabajos sobre Neógeno-Cuaternario*, 5: 31-74
- Patterson, B., Behrensmeyer, A.K. and Sill, W.D. (1970): Geology and fauna of a new Pliocene locality in northwestern Kenya. *Nature*, 226: 918-921.
- Petter, G. (1963): Etude de quelques viverridés (Mammifères, Carnivores) du Pléistocène inférieur du Tanganyika (Afrique orientale). *Bulletin de la Société Géologique de France*, 5: 265-274.
- Petter, G. (1994): Carnivores des régions de Nkondo et de Kisegi-Nyabusosi (Rift Occidental, Ouganda). In: *Geology and Palaeobiology of the Albertine Rift Valley* (B. Senut and M. Pickford, Eds). *CIFEG Orléans, Publication 1994/29*, Vol. II, Palaeobiology: 207-215.
- Petter, G. and Howell, F.C. (1977): Diversification des civettes (Carnivora, Viverridae) dans les gisements pléistocènes de l'Omo. *Comptes Rendus de l'Académie des Sciences de*

- Paris, 284: 283-286.
- Petter, G., Pickford, M. and Howell, F.C. (1991): La loutre piscivore du Pliocène de Nyaburogo et de Nkondo (Mammalia, Carnivora). *Comptes Rendus de l'Académie des Sciences de Paris*, 312: 949-955.
- Petter, G., Pickford, M. and Senut, B. (1994): Présence du genre *Agriotherium* (Mammalia, Carnivora, Ursidae) dans le Miocène terminal de la Formation de Nkondo (Ouganda, Afrique orientale). *Comptes Rendus de l'Académie des Sciences de Paris*, 319: 713-717.
- Petter, G. and Thomas, H. (1986): Les Agriotheriinae (Mammalia, Carnivora) néogènes de l'Ancien Monde. Présence du genre *Indarctos* dans la faune de Menacer (ex-Marceau), Algérie. *Geobios*, 19: 573-586.
- Pickford, M. and Senut, B. (2001): The geological and faunal context of Late Miocene hominid remains from Lukeino, Kenya. *Comptes Rendus de l'Académie des Sciences de Paris*, 332: 145-152.
- Pilgrim, G. E. (1931): *Catalogue of the Pontian Carnivora of Europe*. British Museum (Natural History), 1-174.
- Pilgrim, G. E. (1932): The Fossil Carnivora of India. *Memoirs of the Geological Survey of India, Palaeontologia Indica*, 18: 1-232.
- Qiu, Z. (1980): *Viverra peii*, a New Species from the «Cap» Travertine of Zhoukoudien. *Vertebrata Palasiatica*, 18: 304-313.
- Qiu Z. (1987): Die Hyaeniden aus dem Ruscinium und Villafranchium Chinas. *Münchner Geowissenschaftliche Abhandlungen A9*: 1-108.
- Qiu, Z. and Schmidt-Kittler, N. (1983): *Agriotherium intermedium* (Stach, 1957) from a Pliocene Fissure Filling of Xiaoxiaan County (Anhui Province, China) and the Phylogenetic Position of the Genus. *Palaeovertebrata*, 13: 65-81.
- Qiu, Z., Wu, W., and Qiu, Z. (1999): Miocene Mammal Faunal Sequence of China: Palaeozoogeography and Eurasian Relationships. In: *The Miocene Land Mammals of Europe* (G.E. Rössner and K. Heissig, Eds). Friedrich Pfeil, München, 443-455.
- Repenning, C.A. (1976): *Enhydra* and *Enhydriodon* from the Pacific Coast of North America. *Journal Research of the U. S. Geological Survey*, 4: 305-315.
- Rook, L. (1992): «*Canis*» *monticinensis* sp. nov., a new Canidae (Carnivora, Mammalia) from the late Messinian of Italy. *Bolletino della Società Paleontologica Italiana*, 31: 151-156.
- Sawada, Y., Miura, T., Pickford, M., Senut, B., Itaya, T., Kashine, C., Hyodo, M., Chujo, T. and Fujii, H. (2001): The age of *Orrorin tugenensis*, a late Miocene hominid from the Tugen Hills, Kenya. *Abstract Annual Meeting of the Geological Society of Japan*. Nagoya, 26-27 May, 2001
- Stromer, E. (1921): Mitteilungen über Wirbeltierreste aus dem Mittelpliocän des Natrontales (Ägypten) 5. Nachtrag zu 1. Affen. 6. Nachtrag zu 2. Raubtiere. *Sitzungsberichte der bayerischen Akademie der Wissenschaften zu München*, 1920: 345-370.
- Stromer, E. (1931): Reste Süßwasser und Land bewohnender Wirbeltiere aus den Diamantfeldern Klein-Namaqualandes (Südwest Afrika). *Sitzungsberichte der bayerischen Akademie der Wissenschaften zu München*, 1931: 17-47.
- Tedford, R.H. and Qiu, Z. (1996): A New Canid Genus from the Pliocene of Yushe, Shansi Province. *Vertebrata palasiatica*, 34: 27-40.
- Toerien, M. (1952): The fossil hyaenas of the Makapansgat Valley. *South African Journal of Science*, 48: 293-300.
- Toerien, M. (1955): A sabre-tooth cat from the Makapansgat Valley. *Palaeontologia Africana*, 3: 43-46.
- Turner, A. (1985): Extinction, speciation and dispersal in African larger carnivores, from the Late Miocene to Recent. *South African Journal of Science*, 81: 256-257.
- Turner, A. (1986a): Miscellaneous carnivore remains from Plio-Pleistocene deposits in the Sterkfontein Valley (Mammalia: Carnivora). *Annals of the Transvaal Museum*, 34: 203-226.
- Turner, A. (1986b): Some features of African larger carnivore historical biogeography. *Palaeoecology of Africa*, 17: 237-244.
- Turner, A. (1986c): Correlation and causation in some carnivore and hominid evolutionary events. *South African Journal of Science*, 82: 75-76.
- Turner, A. (1987a): New fossil carnivore remains from the Sterkfontein hominid site (Mammalia: Carnivora). *Annals of the Transvaal Museum*, 34: 319-347.
- Turner, A. (1987b): *Megantereon cultridens* (Cuvier) (Mammalia, Felidae, Machairodontinae) from Plio-Pleistocene deposits in Africa and Eurasia, with comments on the possibility of a New World origin. *Journal of Paleontology*, 61: 1256-1268.
- Turner, A. (1988): On the claimed occurrence of the hyaenid genus *Hyaenictis* Gaudry at Swartkrans (Mammalia: Carnivora). *Annals of the Transvaal Museum*, 34: 523-533.
- Turner, A. (1990a): Late Neogene-Lower Pleistocene Felidae of Africa: evolution and dispersal. *Quartärpaläontologie*, 8: 247-256.
- Turner, A. (1990b): The evolution of the guild of large terrestrial carnivores during the Plio-Pleistocene in Africa. *Geobios*, 23: 349-368.
- Turner, A. (1997): Further remains of Carnivora (Mammalia) from the Sterkfontein hominid site. *Palaeontologia Africana*, 34: 115-126.
- Turner, A. and Anton, M. (1998): Climate and evolution: Implications of some extinction patterns in African and European machairodontine cats of the Plio-Pleistocene. *Estudios Geológicos*, 54: 209-230.
- Van den Brink, S. (1981): A propos du Cercopithecidae (Mammalia, Primates) Villafranchien de l'Aïn Brimba, Tunisia. *Geobios*, 14: 421-425.
- Verma, B.C. and Gupta, S.S. (1992): *Enhydriodon sivalensis*, a Giant Fossil Otter from the Saketi Formation (Upper Pliocene), Siwaliks Groups, Sirmur District, Himachal Pradesh. *Journal of the Palaeontological Society of India*, 37: 31-36.
- Villalta, J.F. and Crusafont, M. (1945): *Enhydriodon lluecai* nova sp. El primer lútrido del Pontiense español. *Boletín de la Real Sociedad Española de Historia Natural* 43: 383-396.
- Viret, J. (1939): Monographie Paléontologique de la Faune de Vertébrés des Sables de Montpellier. III Carnivora Fissipedia. *Travaux du Laboratoire de Géologie de la Faculté des Sciences de Lyon*, 37: 1-26.
- Viret, J. (1954): Le Loess a bancs durcis de Saint-Vallier (Drome) et sa faune de mammifères villafranchiens. *Nouvelles Archives du Muséum d'Histoire Naturelle de Lyon*, 4: 3-200.
- Werdelin, L. (1999a): *Pachycrocuta* (hyaenids) from the

- Pliocene of East Africa. *Paläontologische Zeitschrift*, 73: 157-165.
- Werdelin, L. (1999b): Late Tertiary Carnivora from Lothagam, Northern Kenya. *Journal of Vertebrate Paleontology*, 19 Suppl. 3: 84A.
- Werdelin, L. (2003): Mio-Pliocene Carnivora from Lothagam, Kenya. In: *Lothagam: The Dawn of Humanity in Eastern Africa* (M. Leakey and J.M. Harris, Eds.). Columbia University Press, Columbia, 261-328
- Werdelin, L. and Lewis, M. (1997): The genus *Dinofelis* in Africa. *Journal of Vertebrate Paleontology*, 17: 84a.
- Werdelin, L. and Lewis, M. (2000): Carnivora from the South Turkwell hominid site, Northern Kenya. *Journal of Paleontology*, 74(6): 1173-1180.
- Werdelin, L. and Solounias, N. (1991): The Hyaenidae: taxonomy, systematics and evolution. *Fossils and Strata*, 30: 1-104.
- Werdelin, L. and Turner, A. (1996): The fossil and living Hyaenidae of Africa: present status. In: *Palaeoecology and palaeoenvironments of Late Cenozoic Mammals: Tributes to the career of C.S. (Rufus) Churcher* (K.M. Stewart and K.L. Seymour, Eds.). Toronto, University of Toronto Press, Toronto, 635-659.
- Werdelin, L., Turner, A. and Solounias, N. (1994): Studies of fossil hyaenids: the genera *Hyaenictis* Gaudry and *Chasmaporthetes* Hay, with a reconsideration of the Hyaenidae of Langebaanweg, South Africa. *Zoological Journal of the Linnean Society*, 111: 197-217.
- Willemsen, G.F. (1992): A revision of the Pliocene and Quaternary Lutrinae from Europe. *Scripta Geologica*, 101: 1-115.
- Wolf, R.G., Singer, R. and Bishop, W.W. (1973): Fossil Bear (*Agriotherium* Wagner, 1837) from Langebaanweg, Cape Province, South Africa. *Quaternaria*, 17: 209-236.
- Zdansky, O. (1924): Jungtertiäre Carnivoren Chinas. *Palaeontologia Sinica*, 2 (1): 1-149.
- Zdansky, O. (1925): Quartäre Carnivoren aus Nord-China. *Palaeontologia Sinica*, 2 (2): 1-26.

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